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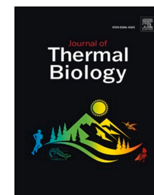

Thermal stress has greater impact on the zebrafish skin microbiota than host genotype

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ABSTRACT

Climate change is increasing the frequency of temperature changes in aquatic environments potentially affecting host microbiota. Microbiota composition can also be affected by host genotype and therefore it is important to understand effects of a stressor across genetically different populations. Size-selective harvesting is an example of an anthropogenic stressor, that drives genetic change in exploited populations. To examine the effects of water temperature and host genotype on skin microbiota, we used three zebrafish selection lines and exposed them to three temperatures: elevated (34 °C), ambient (28 °C), and low (22 °C) for 250 days. Thermal stress had no significant impact on skin microbiota alpha-diversity but did elicit a small, but significant change in microbiota composition (beta-diversity) that included an increase in relative abundance of pathogenic bacteria (e.g., *Vibrio*) and altered microbiota network structure. By contrast, selection lines (genotypes) did not significantly differ in skin microbiota alpha- or beta-diversity. Our results suggest that skin microbiota is not profoundly impacted by either thermal stress or genotype but may become more prone to an increase in pathogenic taxa under thermal stress. Our results contribute to the understanding of how the interactions of anthropogenic stressors (thermal stress and size-selective harvesting) may potentially affect fish health and fitness.

1. Introduction

Aquatic systems are experiencing marked changes in their thermal environments due to climate change (IPCC, 2022), with a notable increase in the frequency of severe weather events (Smith et al., 2025) during which temperature increases of up to 5 °C may occur over a period of several months (Oliver et al., 2018; Sen Gupta et al., 2020). Moreover, climate change will drive greater unpredictability of future temperatures (Canale and Henry, 2010; Day and Hall, 2016) potentially increasing the frequencies of cold weather events and heatwaves (Schlegel et al., 2021). Such extreme changes in temperature can be stressful for marine organisms (Smith et al., 2025). Of particular importance are teleost fish, which are a key taxon in most aquatic ecosystems where they are essential for ecosystem function (Holmlund and Hammer, 1999) and also supply millions of humans with livelihoods and a source of food (Tacon and Metian, 2013; Sharma et al., 2025). Climate change negatively impacts fish physiology and thus fitness-related traits, such as body size (Atkinson, 1994), growth rate (Pörtner and Farrell, 2008; Neuheimer et al., 2011), and reproductive output (Pankhurst and Munday, 2011). These changes in turn can negatively affect population growth (Brander et al., 2010) and thus have ecosystem-level consequences (Smith et al., 2025).

Water temperature is an important environmental stressor affecting fish physiology, behaviour, and life-history (Killen et al., 2010; Pankhurst and Munday, 2011; Neubauer and Andersen, 2019; Alix et al., 2020; Alfonso et al., 2021). Another important fitness proxy is the microbiota, which can be associated with host immunity and metabolic processes (Kau et al., 2011; Sepulveda and Moeller, 2020). Temperature change can alter the gut microbiota potentially leading to reductions in fish health in species including largemouth bass (*Micropterus salmoides*, Ma et al., 2025), rainbow trout (*Oncorhynchus mykiss*, Huyben et al., 2018) and yellowtail kingfish (*Seriola lalandi*, Soriano et al., 2018). However, the effect of water temperature on host skin microbiota is less studied. In a meta-analysis of 43 species on the effect of temperature on host microbiota, only four were fish, and only one was on skin microbiota. This is an important knowledge gap, given that fish skin acts as a physical barrier between the host's body and its environment (Rakers et al., 2010; Xu et al., 2013). Additionally, the mucosal layer of the skin

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is colonised by diverse taxa of microbial species (Llewellyn et al., 2014; Zhang et al., 2018; Gomez and Primm, 2021; Wang et al., 2023), which interacts with the host's immune system (Guardiola et al., 2014; Yu et al., 2021; Wang et al., 2023) helping to protect the host against pathogens (Balcázar et al., 2007). Hence, it is important to understand how internal and external factors, including temperature affect fish skin microbiota (Llewellyn et al., 2014; Chiarello et al., 2018; Gomez and Primm, 2021).

Fish skin is in direct contact with water, making the diversity and/or composition of their skin microbiota sensitive to changes in environmental factors (Gomez and Primm, 2021; Wang et al., 2023), such as in salinity (Schmidt et al., 2015; Hieu et al., 2022), pH (Sylvain et al., 2016), oxygen concentration (Wang et al., 2021), and temperature (Ghosh et al., 2022; Yang et al., 2022; Liu et al., 2025). Studies that focus on the effects of water temperature on fish skin microbiota show that deviations from temperature optima can disrupt diversity and composition of the microbiota. Elevated temperatures have led to a disruption in microbiota composition and an increase in the relative abundance of pathogenic taxa in yellowtail kingfish (*Seriola lalandi*, Horlick et al., 2020), sturgeons (*Acipenser spp.*, Yang et al., 2022; Liu et al., 2025), and chum salmon (*Oncorhynchus keta*, Ghosh et al., 2022). Some studies have additionally indicated that a decrease in temperature can cause similar disruptions (Yang et al., 2022; Liu et al., 2025). However, studies examining an increase and decrease in temperature within the same species are rare (but see Yang et al., 2022; Liu et al., 2025), highlighting a gap in our understanding of how temperature affects skin microbiota in different fish species.

It is also relevant that abiotic processes, such as variation in water temperature, do not act on the host microbiota independently, but rather concurrently with other changes in the environment and host genetics (Moitinho-Silva et al., 2022; Skowron et al., 2021). While human studies have shown association between skin microbiota and genetic loci linked to immunity and cell proliferation (Moitinho-Silva et al., 2022), less is known about such genotype effects in ectotherms such as fish (but see Boutin et al., 2014). Overharvesting has caused marked phenotypic and genetic changes in fish populations (van Wijk et al., 2013; Uusi-Heikkilä et al., 2015, 2017; Therkildsen et al., 2019; Sadler et al., 2024a), including, a reduction in size and growth rate (van Wijk et al., 2013; Uusi-Heikkilä et al., 2015; Sadler et al., 2024b) analogous to cell differentiation and proliferation in human studies. Additionally, overharvesting can increase parasite load and affect immunocompetence (Bartuseviciute et al., 2022), factors that may influence skin microbiota composition, though this remains unstudied. Experimental research often overlooks genetic variation, leaving the interaction between host genotype and temperature stress on fish skin microbiota largely unknown. (e.g., Ghosh et al., 2022; Yang et al., 2022; but see Boutin et al., 2014). Given the skin's constant exposure to water and microbes (Woodhams et al., 2020), temperature likely plays a significant role, but its interplay with host genotype is still unclear.

Temperature change can alter skin microbiota, the relative abundance of both beneficial and potentially pathogenic taxa. Deviations from optimal water temperature may decrease the relative abundance probiotic bacteria (Sepulveda and Moeller, 2020), and disrupt mucus production (Quiniou et al., 1998; Xavier et al., 2024) weakening the skins protective barrier. Changes in water temperature may increase susceptibility to disease-associated microbes in aquatic organisms (Karvonen et al., 2010; Maynard et al., 2015; Neuman et al., 2016; Ghosh et al., 2022; Li et al., 2023) such as some *Vibrio* and *Flavobacteria* species (Starliper, 2011; Neuman et al., 2016; Ghosh et al., 2022). Although skin microbiota is important for fish health, the impact of thermal stress on pathogen dynamics remains relatively understudied.

To quantify the relative contributions of water temperature, host genotype, and their possible interaction, on the composition of the fish skin microbiota, we exposed three zebrafish (*Danio rerio*) selection lines representing distinctly different genotypes (Sadler et al., 2024a, 2024b) to three temperatures (ambient: 28 °C, low: 22 °C, and elevated: 34 °C) representing upper and lower temperature stress. We predicted that (i) exposure to low (22 °C) and elevated (34 °C) temperatures would reduce host skin microbiota diversity compared with the ambient temperature (28 °C), (ii) thermal stress would cause differences in skin microbiota composition and lead to an increased prevalence of pathogenic bacteria, and (iii) different selection lines (genotypes) would exhibit differences in skin microbiota, and each selection line would have a different response to thermal stress. Our study can help to better comprehend the complex interactions human-induced changes in populations and environment can have on fish fitness through alterations in skin microbiota composition.

2. Materials and methods

2.1. Experimental design

To examine whether host genotype and water temperature affect the composition of the skin microbiota we used three selection lines of zebrafish (*Danio rerio*), established from wild fish that had been caught in West Bengal, India (Uusi-Heikkilä et al., 2010). These selection lines have diverged phenotypically, for example in growth rate and body size (Sadler et al., 2024b), and genetically (Sadler et al., 2024a, 2024c) as a consequence of three regimes of size-selective harvesting over five generations: (1) small-selected (where 75 % of the largest fish were removed each generation), (2) large-selected (75 % of smallest fish removed), and (3) random-selected (where 75 % of fish were removed; see Uusi-Heikkilä et al., 2015 for full details). Two replicate lines were created for each selection line. The random-selected lines exhibited higher growth rate, metabolic rate, and adult body size (Sadler et al., 2024b) and exhibited a greater copy number variation in response to variation in water temperature (Sadler et al., 2024c) but the response of the skin microbiota is not known.

To quantify the effect of water temperature on skin microbiota in different selection lines, fish (50 days post fertilization) were exposed for 250 days to three temperatures: (1) low temperature (22 °C), (2) ambient (28 °C), and (3) an elevated temperature (34 °C). Ambient temperature represents a control as this was the standard laboratory rearing temperature for these lines. A 6 °C increase (above ambient) in temperature reflects a thermal stress to zebrafish (Åsheim et al., 2020; Morgan et al., 2022) and this increase in temperature is similar in magnitude to that attained during aquatic heatwaves (Oliver et al., 2018; Sen Gupta et al., 2020). A 6 °C reduction in temperature below ambient examines the impact of a comparable level of cooling on fish skin microbiota.

A total of 254 zebrafish were selected at random across each of the selection line replicates (see Table S1 for sample sizes). Groups of five fish were placed in cylindrical wire mesh cages within nine 30L glass aquaria. This amounted to eight cages per thermal treatment aquarium, with each temperature treatment having three independent tanks, but the same starting water supply. Each cage contained fish from one selection line. Individuals from the same selection line were partitioned among aquaria to prevent any confounding effects of a single aquarium. Prior to the start of the thermal stress experiment, juvenile fish were acclimated to the new aquaria for 2 weeks at ambient temperature (28 °C). To achieve the low and elevated temperature treatments, the temperature was either decreased or increased by 1 °C day^{-1}. Full details of the thermal stress experiment can be found in Sadler et al. (2024b). After 250 days at the experimental temperature, fish were euthanised individually (using 2-phenoloxyethanol, 1.5 % concentration, Sigma-Aldrich, Darmstadt, Germany).

Skin microbiota were collected by swabbing the skin five times from operculum to caudal peduncle (Breacker et al., 2017) with sterile rayon-tipped swabs (Fisher Scientific, Dublin, Ireland). Samples were stored at −20 °C until DNA extraction. Three water samples (150 ml filtered through 0.22 μm membranes) were collected from each aquarium to quantify the environmental microbiota, with DNA extracted from

the filters. Negative controls (blank swabs and filters) were taken at the end of the experiment (day 250) to identify potential contamination during DNA extraction and library construction.

2.2. DNA extraction, amplicon sequencing, and read processing

We used a PowerSoil Pro DNA kit (Qiagen, Germany) to extract DNA from skin swabs and filters. We used an extended bead beating period of 20 min to increase DNA yield. Library preparation and amplicon sequencing was performed by Novogene (Cambridge, UK). Samples were sequenced on an Illumina NovaSeq 6000 (250 bp paired-end reads) using primers 341F and 806R (Yu et al., 2005) to amplify the V3-V4 region of the 16S rRNA. Demultiplexing and removal of adapter sequences from the read data was completed by Novogene.

Read data were imported into *qiime2* v.2023.5 (Bolyen et al., 2019), and primer sequences were removed using the *cutadapt* plugin (Martin, 2011). There were 37,371,395 reads in total (between 560-198,228 pairs of reads per sample, with an average of 137,394 reads per sample), negative controls had an average of 304 reads per sample, which were later excluded from the analysis. Read pairs were merged (*vsearch merge-pairs* parameters: -p-minlen 190 –p-minovlen 15 –p-maxdiffs 5 –p-minmergelen 350 –p-maxmergelen 450) and the sequences dereplicated (*vsearch dereplicate-sequences* parameters: default) and clustered at 97 % identity (*vsearch cluster-features-de-novo* parameters: -p-perc-identity 0.97) using the *vsearch* (Rognes et al., 2016) plugin for *qiime2*. We also used the *vsearch* plugin (*vsearch uchime-denovo* parameters: default) to identify and remove chimeras. After removing low (<10 reads) abundance features (*qiime feature-table filter-features* parameters: -p-min-frequency 10), taxonomy was assigned to the features using a naive Bayes classifier (Bokulich et al., 2018) and a database trained on SILVA v.138_99 bacterial V3-V4 rRNA sequences (Yilmaz et al., 2014). We removed the features whose taxonomy was unassigned, as well as those that were classified as either mitochondria, chloroplasts, Archaea, or eukaryotes (*qiime taxa filter-table* parameters: -p-include p__ –p-exclude Archaea, Mitochondria, Chloroplast, Eukaryota) and then constructed a mid-point rooted phylogenetic tree using *fasttree* (Price et al., 2010). The feature table, phylogenetic tree, taxonomic classification were exported as a *phyloseq* object (McMurdie and Holmes, 2013) and contaminant features from negative controls removed using the prevalence method (threshold = 0.5) implemented by *decontam* v.1.16.0 (Davis et al., 2018).

2.3. Statistical analyses

All statistics were performed using *R* v.4.3.1 (R Core Team, 2024). For analyses of alpha and beta diversity, the feature table was rarefied to 10,000 reads per sample (resulting in the loss of 23 samples). Alpha diversity was calculated as observed richness and evenness (Shannon's index) in *phyloseq* v.1.40.0 (McMurdie and Holmes, 2013). Potential significant differences in alpha diversity among temperature treatments and selection lines were determined using a Wilcoxon's test. Beta diversity was estimated using Jaccard's, Bray-Curtis, and Unifrac (weighted and unweighted) indices generated with *phyloseq* (McMurdie and Holmes, 2013), with variation among individuals and treatments visualised using principal coordinate analysis (PCoA). Significance of any differences in beta diversity indices among temperature treatments and selection lines were calculated using a permutation multivariate analysis of variance (PERMANOVA) implemented by the *adonis2* function (999 permutations) within the *R* package *vegan* v.2.6.2 (Oksanen et al., 2013) and using the model distance ~ temperature + selection line, strata = tank. We further analysed variation in beta diversity using constrained ordination within *phyloseq* (method = CAP) to assess only the variation attributed to temperature treatment. Homogeneity of dispersion in beta diversity was calculated using the *betadisper* function in *vegan*, with the *permutest* function (999 permutations) used to determine the significance of any differences in dispersion among temperature treatments and selection lines.

As we found no significant effect of selection line on alpha and beta diversity, we only examined the effect of temperature for the network analyses, and the analyses of differential abundance. Microbiota networks were created for each temperature treatment using *ggClusterNet* v.2.0 (corMicro parameters: N = 1000, method.scale = TMM, r.threshold = 0.6, p.threshold = 0.05, method = pearson) (Wen et al., 2022).

We used *ancom-bc2* v.1.6.4 (*ancom-bc2* parameters: tax_level = “Genus”, alpha = 0.05, p_adj_method = “holm”, prv_cut 0 0.10, lib_cut = 200, neg_lb = F, pseudo_sens = T) (Lin and Peddada, 2024) on the unrarefied feature table to calculate the differential abundance of features among all three pairwise comparisons of temperature treatments. Finally, to determine whether temperature affected the connectedness of bacteria present in the water and on the fish skin we used source tracking within *FEAST* v.0.1.0 (Shenhav et al., 2019) to quantify percentage of bacteria shared between the skin microbiota and the aquarium water (*i.e.* the environment).

3. Results

3.1. Bacterial taxonomic composition in zebrafish skin microbiota

The community composition was representative of zebrafish skin microbiota previously reported by Coetzer et al. (2021). We identified 12,124 and 12,119 features from 56 bacterial phyla in the zebrafish skin microbiota and the water column, respectively. Zebrafish skin microbiota was dominated by Proteobacteria (>80 % relative abundance at 22 °C and 34 °C, and >76 % relative abundance at 28 °C; Fig. 1a; Table S2). Other dominant bacterial phyla in the zebrafish skin microbiota included the Firmicutes and Actinobacteria (both phyla about 5 % relative abundance; Fig. 1a–Table S2). The dominant bacterial orders were the Burkholderiales (>30 % relative abundance) and Xanthomonadales (>20 % relative abundance; Fig. 1b).

3.2. Neither temperature nor selection line influence alpha diversity of the skin microbiota

The skin microbiota comprised of approximately 200 (median = 207, range = 37-1738) bacterial taxa per individual (Fig. 2a). While the levels of alpha diversity (measured as observed taxa and Shannon's index) varied among individuals, contrary to expectation that temperature and selection line would influence alpha diversity, there was no significant effect of either selection line or temperature (Fig. 2; Tables S3 and S4).

3.3. Beta diversity is affected by temperature but not selection line

Variation in water temperature had a significant effect on skin microbiota beta diversity, as estimated by Bray-Curtis (PERMANOVA, $p < 0.001$, $r^2 = 0.033$; Fig. S1, Table S5), Jaccard's (PERMANOVA, $p < 0.001$, $r^2 = 0.019$; Fig. S1, Table S5), Unifrac (PERMANOVA, $p < 0.001$, $r^2 = 0.021$; Fig. S1, Table S5), and weighted Unifrac (PERMANOVA, $p = 0.046$, $r^2 = 0.019$; Fig. S1, Table S5). Constrained ordination visualised this divergence distinctively supporting the PERMANOVA results (Fig. 3). By contrast, selection line did not explain a significant amount of variation among fish skin microbiota for any metric of beta diversity (Table S5). Thus, while the significant effect of temperature on beta diversity is manifested by a comparatively weak effect size of around 2–3 % of the variation in the data explained ($r^2 = 0.019$–0.033; Table S5), this effect was nonetheless considerably more influential than the effect of selection line ($r^2 = 0.008$–0.009; Table S5). There was no significant effect of either temperature or selection line on the level of dispersion among samples (Tables S6–S8).

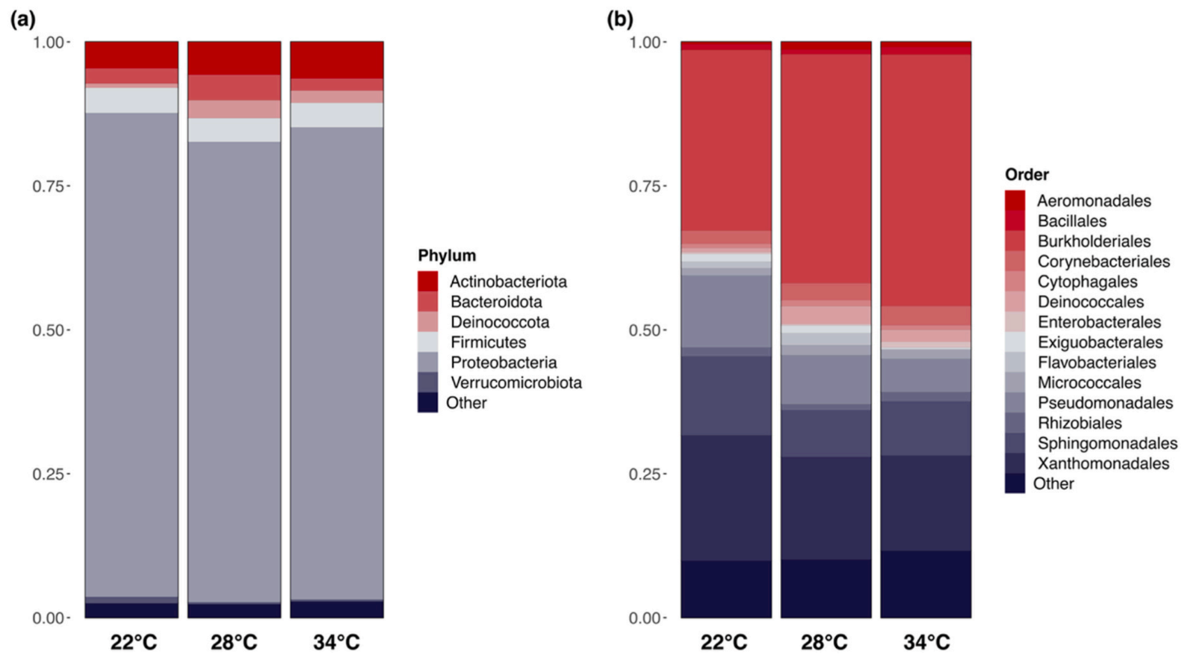

Fig. 1. Relative abundance of (a) phyla and (b) orders of skin microbiota (bacteria) of zebrafish housed for 250 days in three temperatures 22 °C, 28 °C, and 34 °C. Taxa with <1 % abundance are grouped within the category 'Other'.

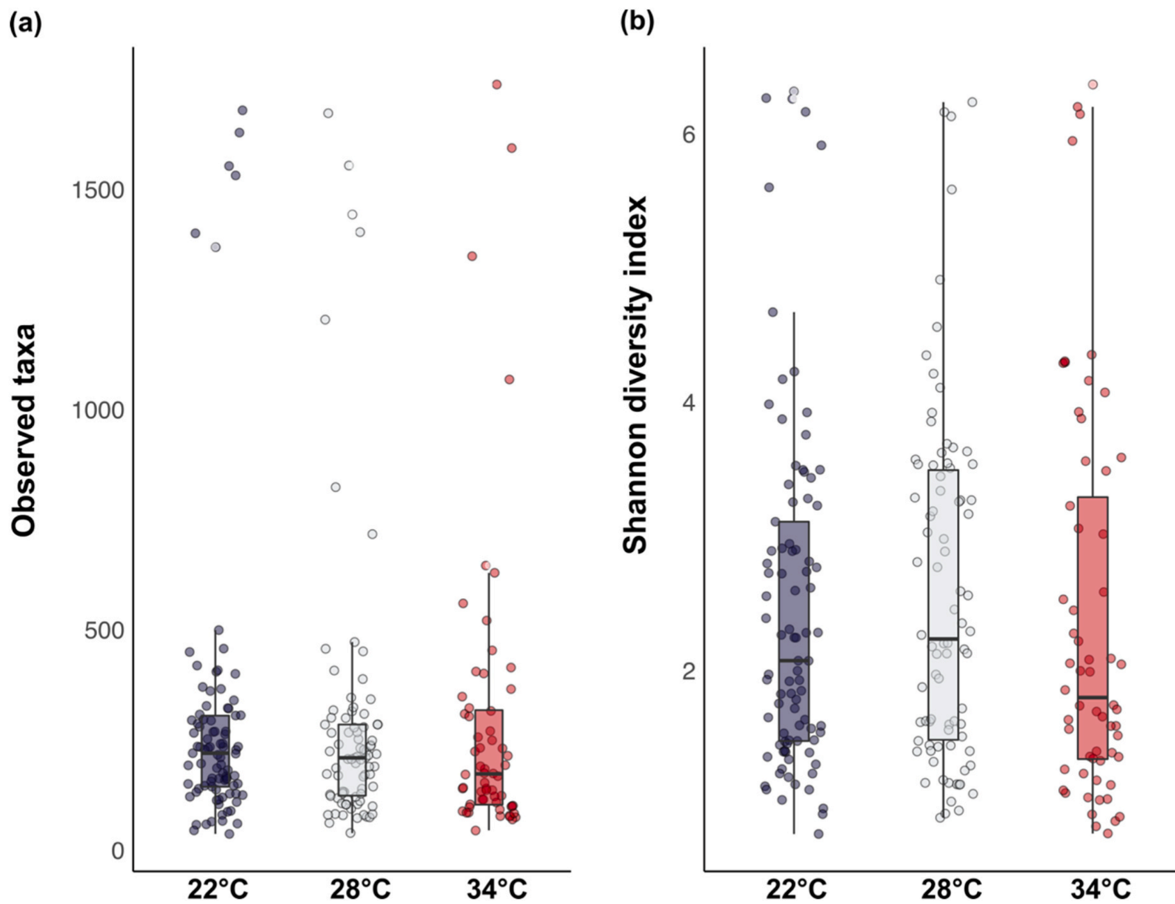

Fig. 2. Alpha diversity of skin microbiota (bacteria), measured as (a) number of observed taxa and (b) Shannon's diversity of zebrafish maintained at three temperatures 22 °C, 28 °C, and 34 °C. Different selection lines (genotypes) had no significant effect on alpha diversity and are not displayed. Data are individual observations per fish, and the median with quartiles across temperatures.

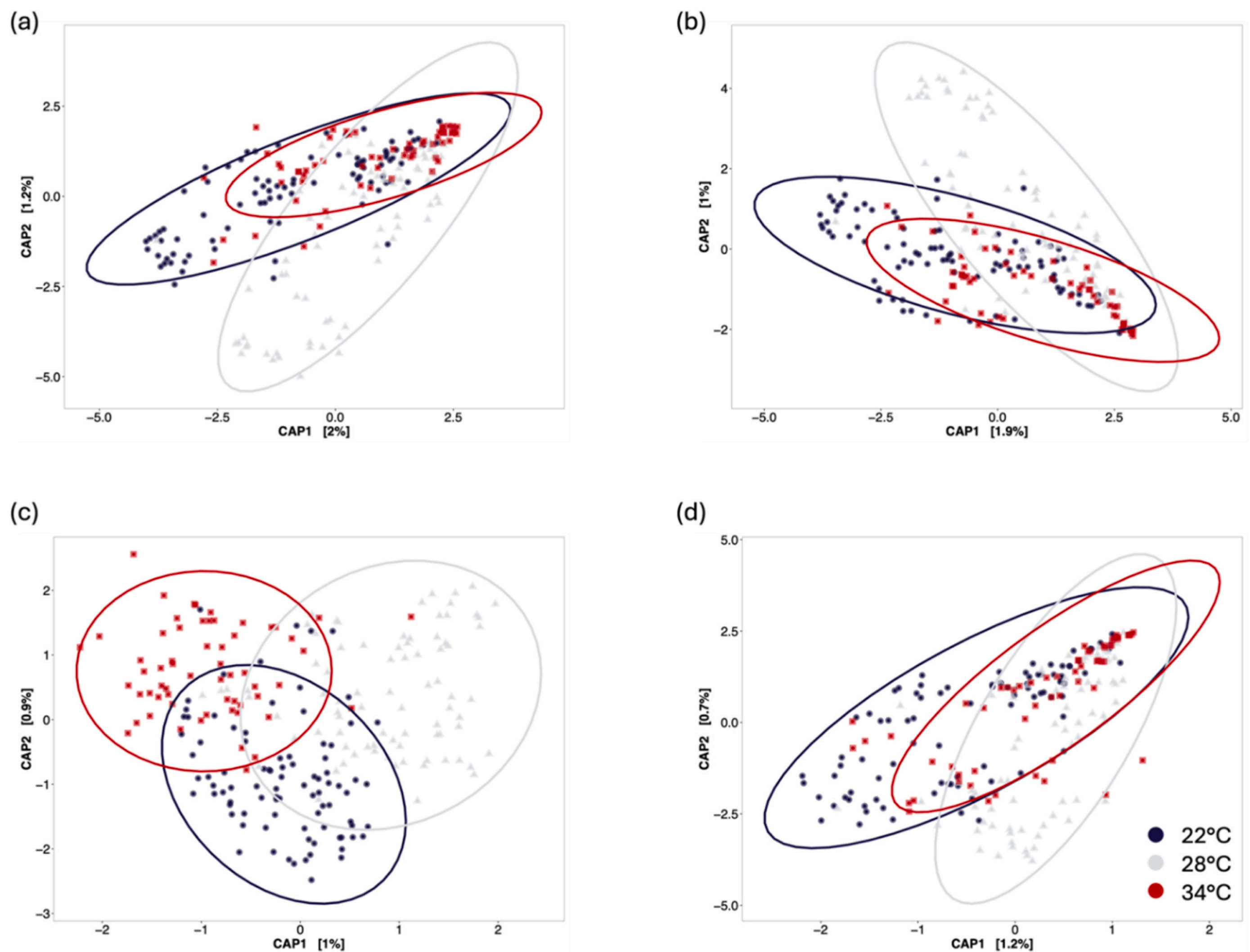

Fig. 3. Variation in beta diversity of zebrafish skin microbiota among temperature treatments (22 °C, 28 °C, and 34 °C) using constrained ordination with (a) Bray-Curtis, (b) Jaccard's, (c) unweighted UniFrac, and (d) weighted UniFrac indices. Points represent individuals within each treatment, and ellipses represent 95 % confidence intervals. Separate analyses for the three selection lines are not displayed because selection line had no significant effect on beta diversity (*p>0.05*).

3.4. *Temperature affects the relative abundance of specific taxa, including pathogens*

Compared to the ambient temperature (28 °C), we identified 15 positively differentially abundant bacterial genera (i.e., their abundance was increased) at 22 °C and nine positively differentially abundant genera at 34 °C, whilst there were seven positively differentially abundant genera in the comparison between 22 °C and 34 °C (Fig. 4).

Potentially opportunistic pathogenic bacteria *Carnobacterium* (Leisner et al., 2007) and *Plesiomonas* (Duman et al., 2023) were positively differentially abundant at an elevated temperature. The bacterial genus *Vibrio*, another common fish pathogen (Frans et al., 2011; Castillo et al., 2017) was positively differentially abundant in both elevated and low temperatures, and *Flavobacterium* (Wood and Yasutake, 1956) was positively differentially abundant at the low temperature (Fig. 4).

3.5. *Thermal stress disrupts microbial network structure*

Temperature altered the network structure of the zebrafish skin microbiota (Fig. 5), with networks becoming sparser (a reduction in connectance) in warmer water temperatures (both in 28 °C and 34 °C compared to 22 °C) and, accordingly, having a reduction in mean number of connections per node (average degree) at 34 °C. This indicates that taxa tend to be less connected in the elevated temperature (34 °C; Table 1). Consistent with these differences in connectance and degree, there is a lower clustering coefficient and more clusters at the elevated temperature, which indicates that the bacterial skin microbiota of zebrafish in warm temperatures are fragmented into weaker clusters and subgroups (Table 1). Indeed, average path length and diameter increase with temperature indicating that the skin microbiota networks become less compact and more fragmented when there is a rise in water temperature (Table 1).

3.6. *Similarity between the skin and water microbial communities*

Microbial communities of the environment (rearing water) and fish skin were similar (>75 % overlap; Fig. S2). Moreover, no significant differences in the overlap of microbiota from the skin and environment were demonstrated among selection lines (Tables S9 and S10) or temperature treatments (Table S9; S10). Additionally, we showed that water microbiota composition was clustered by temperature treatment (Fig. S3) similarly to the skin microbiota (Fig. 3).

4. Discussion

Climate change will cause an increase in temperature stress in

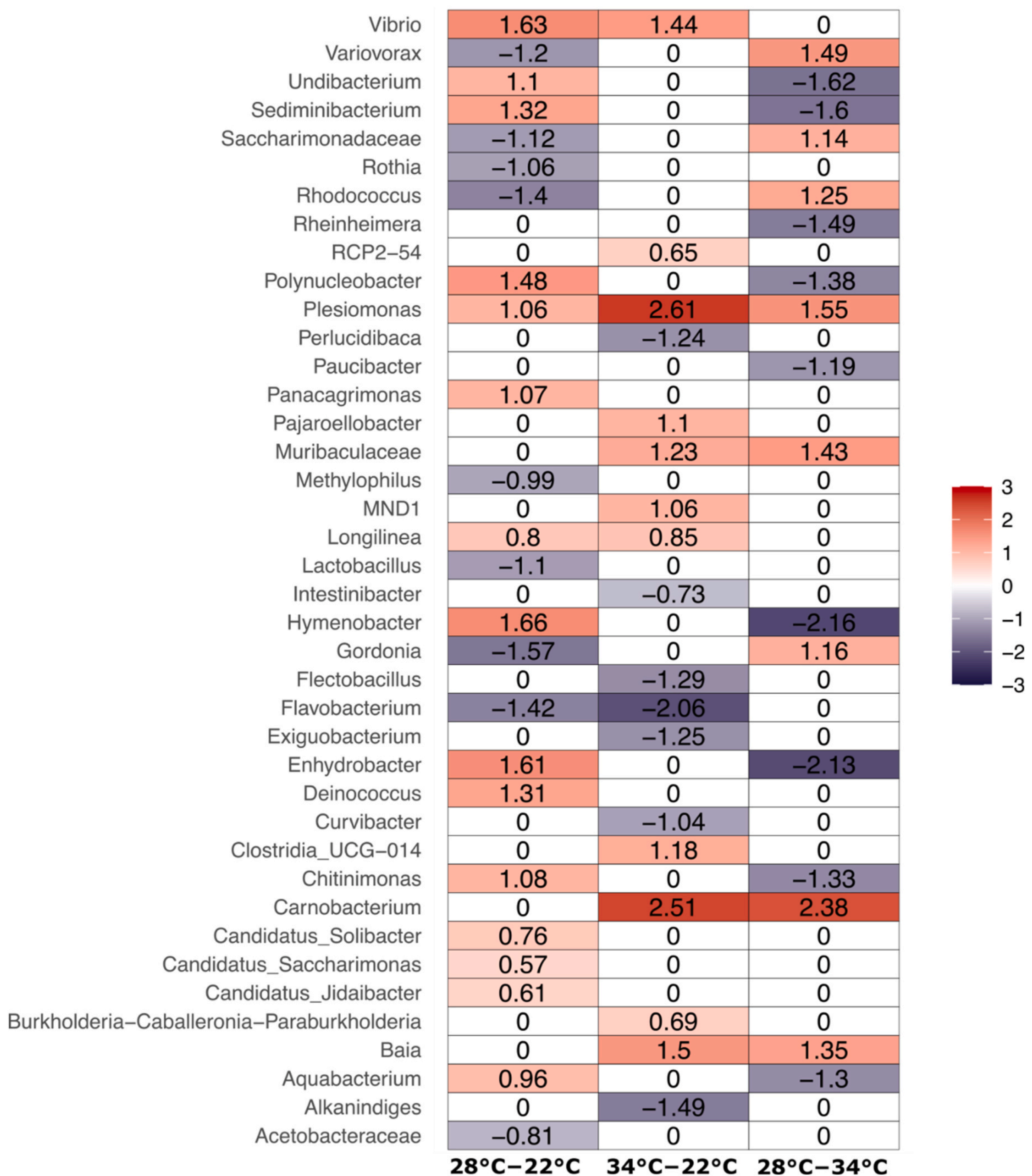

Fig. 4. Differential abundance of bacterial genera in the zebrafish skin microbiota between pairwise combinations of temperature treatments. Colours indicate level and direction of log fold-change (red positive and blue negative) of differentially abundant bacterial genera.

aquatic environments, which in turn may impact the host-associated microbiota of many aquatic species (Ghosh et al., 2022; Li et al., 2023), decreasing microbial diversity (Ghosh et al., 2022; Yang et al., 2022; Liu et al., 2025), altering community composition, and increasing the abundance of certain pathogenic taxa (Ghosh et al., 2022; Yang et al., 2022; Liu et al., 2025; Maynard et al., 2015), but the influence, of the host genotype is less well studied. Here, we show that exposure to either elevated or lowered temperatures (from an optimal temperature) did not alter the alpha diversity, but it did change the composition (beta diversity) of fish skin microbiota. While the relevance to the host of this shift in bacterial community composition remains unclear, exposure to high and low temperature stress were associated with an increase in the prevalence of certain genera of pathogenic bacteria. Contrary to our hypotheses, we did not find any effect of the selection line (host genotype) on the skin microbiota composition, suggesting environmental conditions have a more important role than host genetic background in structuring the fish skin microbiota.

Fish skin microbiota shows high taxonomic diversity (Lowrey et al., 2015; Hamilton et al., 2019; Sylvain et al., 2020; Gomez and Primm, 2021) due to the nutrient rich mucosal membrane (Brinchmann, 2016), and constant exposure to a microbial rich aquatic environment. Compared to gut microbiota, which is mainly shaped by diet (Xiao et al., 2021), skin microbiota can be more diverse. Studies have shown a high level of skin microbiota diversity of 600–800 taxa per individual (Hu et al., 2021), we detected approximately 200 features per individual in the zebrafish skin microbiota, twice that found, in the zebrafish gut

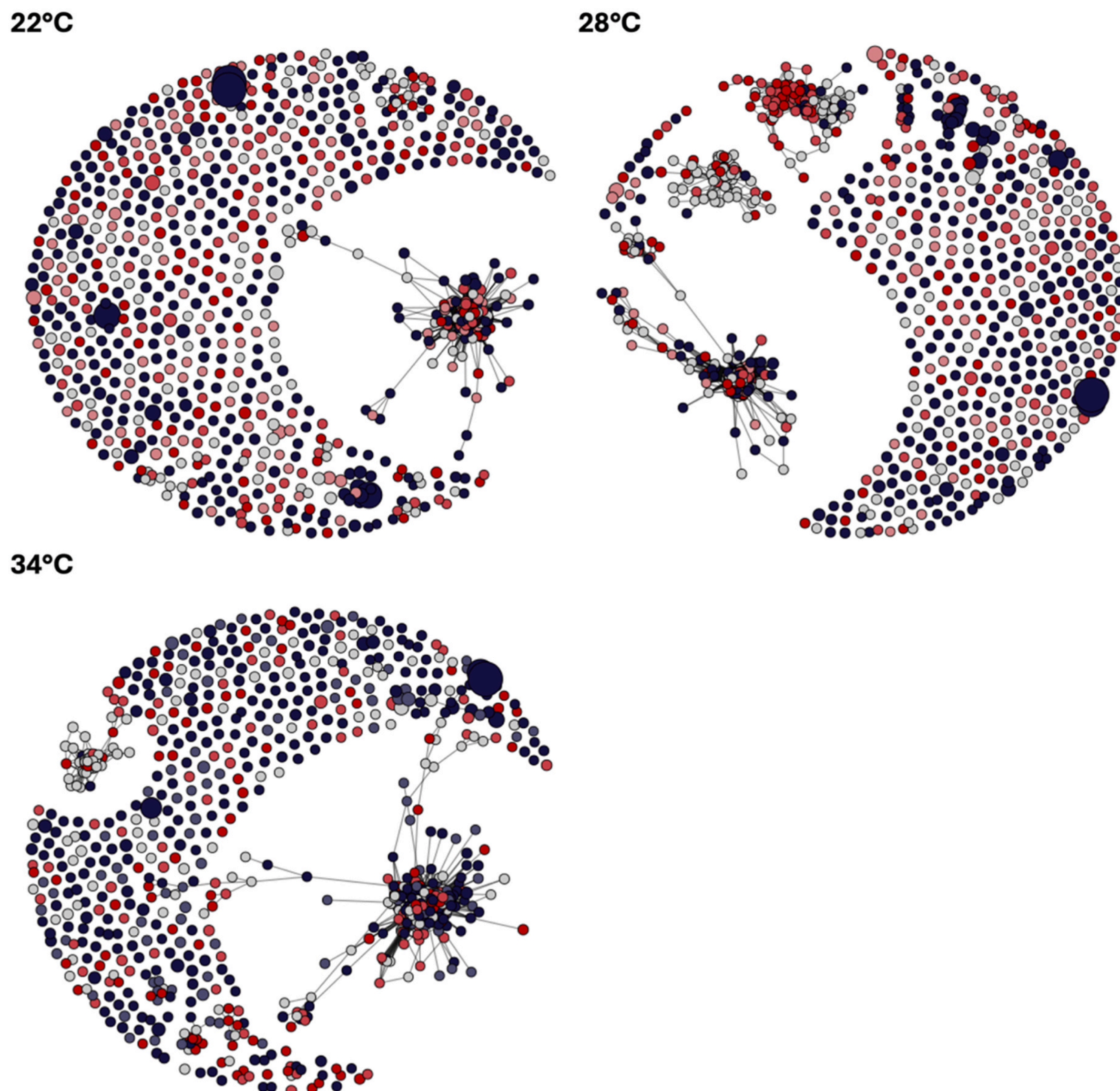

Fig. 5. Variation in network structure of the skin microbiota of zebrafish housed at three different water temperatures. Blue (Proteobacteria, 81 % average relative abundance) and red (Actinobacteriota, 5 % relative abundance; Firmicutes, 5 % relative abundance and Bacteroidota, 3 % relative abundance) colours highlight whether taxa belong to one of the four dominant bacterial phyla (Fig. 1a), while taxa belonging to less abundant phyla are coloured grey. Properties of these networks are given in Table 1.

Table 1
Summary properties of networks for skin microbiota of zebrafish housed at three different water temperatures.

Network properties	22 °C	28 °C	34 °C
number of edges	26,858	31,499	25,037
number of vertices	491	606	658
connectance	0.22	0.17	0.12
average degree	109.40	103.96	76.10
average path length	1.40	1.59	2.01
diameter	7.56	8.14	11.91
clustering coefficient	0.78	0.88	0.66
number of clusters	33	25	39
centralization degree	0.32	0.27	0.27
centralization betweenness	0.019	0.035	0.033
centralization closeness	0.79	0.94	1.03

microbiota (Stephens et al., 2016). However, results vary by species and sample site, for example flag cichlids (*Mesonauta festivus*), black piranha (*Serrasalmus rhombeus*) and pacu (*Mylossoma duriventre*) skin microbiota had higher phylogenetic diversity than gut microbiota (Sylvain et al., 2020), whilst chum salmon (*Oncorhynchus keta*) showed the opposite pattern (Ghosh et al., 2022). These inconsistencies suggest that environmental factors have a strong effect on skin microbiota composition, making it difficult to generalise broad patterns.

Exposure to thermal stress has been shown to alter skin microbiota in fish including, salmonids (Ghosh et al., 2022), yellowtail (Horlick et al., 2020), and sturgeon (Yang et al., 2022; Liu et al., 2025), However, one study observed no change in diversity and richness across temperatures (20 °C and 24 °C) in European sea bass (*Dicentrarchus labrax*) (Cardoso et al., 2023). Only a few studies included lower water temperature stress (Ghosh et al., 2022; Yang et al., 2022; Liu et al., 2025) and showed that it can also alter microbiota composition and diversity. Although we exposed our experimental fish to relatively large changes in temperature, these elicited a weak change in beta diversity. Reasons for the differences among these assessments of temperature, compared to other studies on microbiota are not known, but likely reflect the diverse experimental designs. For example, most studies are based on 7–14 day period of temperature intervention (e.g., Ghosh et al., 2022; Yang et al.,

2022; Liu et al., 2025) while our experiment lasted for 250 days. Thus, while there may be a consistent impact of short-term, rapid heat stress on skin microbiota (Ghosh et al., 2022; Yang et al., 2022; Liu et al., 2025; Li et al., 2023), the relatively weak effect size of our data could imply that skin microbiota can acclimate to a long-term exposure to elevated and lowered temperatures. Additionally, studies have shown general patterns of extensive inter-individual variation (i.e., in alpha diversity) in fish skin microbiota (e.g., Berggren et al., 2022) and this may make it difficult to disentangle any temperature effects from other interacting effects on microbiota composition without integrating longitudinal data and combining other methods of taxa identification such as shotgun metagenomics and metabolomics. Despite the apparently small shift in beta diversity, such shifts can lead to structural alterations of the skin, increase the abundance of pathogens (Xavier et al., 2024) and lead to a reduction in host health.

Ambient temperature (28 °C) is presumably optimal for the zebrafish skin microbiota and accordingly is characterised by a cohesive network, for example with the highest clustering coefficient and most edges (see Kajihara and Hynson, 2024). At cooler (22 °C) temperatures, zebrafish can maintain dense and cohesive network in their skin microbiota (e.g. short path length and high average degree, but with fewer edges and more clusters despite slightly higher connectance than at 28 °C) implying that interactions among skin microbiota are majorly impacted by cooling. By contrast, at 34 °C the zebrafish skin microbiota is defined by a fragmented (e.g. low connectance, low average degree, low clustering coefficient, and many clusters) network, indicating that a rise in temperatures can induce a breakdown in microbial interactions. Such changes in network properties are largely consistent with the apparently reduced success in assigning microbiota at higher temperature. This apparent sensitivity to rising temperatures is consistent with the impact of warming-induced disruption of gut microbiota networks in largemouth bass (Wei et al., 2025). Thus, our experiment shows that change, especially a rise, in temperature impacts the network topology of the teleost skin microbiota, comparable to effects of simulated warming in free-living aquatic microbial communities (Liu et al., 2024).

Fish skin microbiota is shaped by constant exposure to water leading to frequent colonisation by transient microbes. While evidence suggests the presence of a core microbiota (Moran, 2015), its similarity to surrounding water communities may explain why temperature stress had limited impact on composition. However, species differences exist, for example, in sturgeon they found large overlap of OTUs with water, however in yellowtails the amount shared was low (92 OTUs) (Horlick et al., 2020). Such differences in water and skin bacterial community may be due to bacterial shedding from the skin to the water column or bacterial uptake from water column to the skin, highlighting the complex interactions between skin and water microbes. Future studies should explore long term temperature effects, and consider approaches such as genetic manipulation to understand microbiota colonisation on a 'sterile' skin. Understanding whether temperature effects are muted or microbiota is simply highly transient is crucial as disrupted skin microbiota composition is associated with impaired health, including reduced growth rate (Gomez and Primm, 2021) and increased mortality (Mohammed and Arias, 2015; Gomez and Primm, 2021).

Climate change driven warming increases the prevalence of potentially pathogenic bacteria in the environment (Harvell et al., 2002; Lafferty, 2009; Byers, 2021). Fish skin microbiota may change in response to internal (e.g. enteritis) and external (e.g. skin lesions) diseases (Legrand et al., 2018), as well as the concomitant effect of warmer temperatures (Karvonen et al., 2010; Maynard et al., 2015; Neuman et al., 2016; Ghosh et al., 2022; Li et al., 2023). Here, we show change in temperature may lead to higher relative abundance in potentially harmful bacteria genera associated with fish disease including *Vibrio* (Ghosh et al., 2022), *Tenacibaculum*, (Ghosh et al., 2022), *Carnobacterium* (Leisner et al., 2007) and *Flavobacterium* (Wood and Yasutake, 1956; Starliper, 2011), which may lead to aquaculture losses (Frans et al., 2011; Castillo et al., 2017). The exact mechanisms that drive an increase in abundance of potentially opportunistic pathogens in fish skin bacteria are unclear, but may involve stress-induced immune suppression (Uren Webster et al., 2020). Future work should assess absolute pathogen levels and link microbiota change with immune responses (e.g., immunity assays and immune gene expression) and fitness outcomes, as elevated temperatures (34 °C) has been shown to increase mortality and decrease reproductive success (Sadler et al., 2024b).

Genotype can affect skin microbiota composition in animals including cows (Bay et al., 2023), humans (Moitinho-Silva et al., 2022), frogs (Belasen et al., 2021), and fish (Boutin et al., 2014). Although overharvesting leads to phenotypic and genetic changes in fish it is not clear whether these changes impact the skin microbiota, but the altered growth is interesting in the light of a recent study on humans where loci that included cell differentiation associated with skin microbiota (Moitinho-Silva et al., 2022). Despite clear phenotypic (Uusi-Heikkilä et al., 2015; Sadler et al., 2024b) and genetic differences (Sadler et al., 2024a, 2024c) in experimental fish lines no consistent impact on skin microbiota was observed. Lack of genotype effect may be because environmental factors (e.g., water temperature) play a stronger role than genotype in shaping fish skin microbiota, potentially muting any genetic effects (Li et al., 2023).

Exposure to high and low temperature, but not host genotype influenced the composition of zebrafish skin microbiota, indicating that environmental factors may have a greater impact than genetic factors on the skin microbiota. While a comparatively large (6 °C) difference in temperature explained a relatively small amount of variation in microbiota composition, temperature change nonetheless altered microbiota network structure and increased the prevalence of potentially opportunistic pathogenic bacteria. Our findings demonstrate the importance of thermal stress in shaping skin microbiota and underscore the importance of understanding its effects on fish health in the face of climate change.

CRediT authorship contribution statement

Daniel E. Sadler: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Phillip C. Watts:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Stephan N. van Dijk:** Writing – review & editing, Investigation, Data curation. **Silva Uusi-Heikkilä:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Ethical statement

All experimental protocols were approved by the Finnish Project Authorisation Board (Licence no. ESAVI/24,875/2018) and all experiments followed the ARRIVE guidelines.

Data availability statement

All data is included in the electronic supplementary and the raw 16S rRNA fastq files are available in the SRA repository (BioProject: PRJNA1114059). All additional relevant data and resource can be found within the article and its supplementary information.

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Declaration of competing interest

No competing interests declared.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2026.104397.

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