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Mgr. Martin Kopecký

Evolution of fishes at deep-sea hydrothermal vents

Evoluce ryb z oblastí hlubokomořských hydrotermálních vývěrů

Bachelor´s thesis

Supervisor:

Mgr. Zuzana Musilová, Ph.D.

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Prohlášení

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Při tvorbě práce jsem využil také nástroj umělé inteligence pro jazykovou korekturu. Tato práce, ani její podstatná část, nebyla předložena k získání jiného nebo stejného akademického titulu.

Declaration

I declare that I have completed this thesis independently and that I have cited all sources of information and literature used. I have also utilised an artificial intelligence tool for partial language proofreading during the preparation of this work. This thesis, or any substantial part of it, has not been submitted for the award of any other or the same academic degree.

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Poděkování

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Abstrakt

Tato bakalářská práce shrnuje dosavadní poznatky o geografickém rozšíření a evolučních adaptací hlubokomořských ryb v prostředí hydrotermálních vývěrů. Hydrotermální vývěry jsou jedním z nejextrémnějších hlubokomořských prostředí, které je převážně osídleno bezobratlými živočichy a chemosyntetickými prokaryotickými organismy. Zároveň však je ze všech hlavních hlubokomořských hydrotermálních oblastí zaznamenáno několik desítek druhů ryb, paryb a sliznatek. Jen několik málo čeledí zahrnuje druhy skutečně endemické pro ekosystémy hydrotermálních vývěrů. Jejich přítomnost napříč biogeografickými oblastmi se navíc velmi liší. Je však patrné, že částečně si tyto druhy vyvinuly obdobné fyziologické a evoluční adaptace, které jim umožňují přežít za vysokého hydrostatického tlaku, vysokých teplot, nedostatku kyslíku, v kyselém a toxickém prostředí. Některé z těchto adaptací sdílejí se sladkovodními druhy popsanými z hydrotermálních pramenů s vysokým obsahem sulfidů. Zároveň odlišnosti v adaptacích poukazují na rozdílnou evoluční historii druhů, přičemž jim umožnily osídlit různé niky v rámci hydrotermálních ekosystémů. Toto prostředí slouží i ostatním hlubokomořským druhům, které jej využívají jako zdroj potravy, ale v některých případech i jako líhniště a přechodná útočiště.

Klíčová slova

hlubokomořské ryby, hydrotermální vývěry, biogeografie, evoluční adaptace

Abstract

This bachelor's thesis is a review of the geographical distribution and evolutionary adaptation of deep-sea fishes from the deep-sea hydrothermal vents. Hydrothermal vents are one of the most extreme deep-sea environments which has been successfully colonised mostly by invertebrates and chemolithotrophic bacteria. Yet, various fish, elasmobranch and hagfish species are described from all of the main biogeographical provinces. Only a few fish families are represented with true vent-endemic species that vary across the biogeographical provinces. However, they seem to have evolved similar physiological and life-history adaptations enabling them to withstand the high pressure, low oxygen, acidic and toxic environment and elevated temperatures. Some of these adaptations are shared with freshwater fish species from sulphide-rich hot springs. At the same time, some of the adaptations vary across the species, indicating different evolutionary histories and the ecological diversification within the vent habitat. Moreover, hydrothermal vents are visited by other deep-sea fishes using them as an energy source, but potentially as nurseries and safe refugia.

Key words

deep-sea fish, hydrothermal vents, biogeography, evolutionary adaptation

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1. Introduction

Deep-sea hydrothermal vents[1] present an extreme environment par excellence. They are located along mid-ocean ridges across the globe. According to the InterRidge Global Database, there are currently more than 600 active vent fields worldwide, with an average depth of 2,100 metres (Beaulieu and Szafrański 2020). In these divergent zones, ocean water enters the seabed and reacts with the ocean crusts and subsoil minerals before emerging back through the ocean floor (Edmond and Von Damm 1983). Based on the dissolved compounds and temperature, the vents are divided into two types – so-called "black smokers" and "white smokers". Black smokers are characterised by higher temperatures reaching 380 to 400 °C and low pH – around 3 (Jannasch and Mottl 1985; Von Damm and Bischoff 1987). The water temperature of white smokers is lower, usually between 40 and 70 °C, and pH is higher, around 9 (Kelley et al. 2001). As the pH value suggests, both types differ in the main dissolved compounds. Water plumes from black smokers are rich in hydrogen sulphide (H_2S), pyrite (FeS_2), ferrous (FeS) and manganese sulphide (MnS) (Jannasch and Mottl 1985), whereas for white smokers, they are typical calcium-rich fluids and carbonate and sulphate deposits (Kelley et al. 2001).

At the base of the vent ecosystems are chemolithotrophic bacteria which oxidise sulphur, sulphides, and other vent fluids, producing organic compounds (Jannasch and Mottl 1985). These primary producers are at the basis of the trophic structure of vents, providing an energy source for macrofauna inhabiting the vent ecosystem. The most numerous phyla present are *Annelida, Mollusca,* and *Crustacea* (Tunnicliffe 1992; Wolff 2005; Lelièvre et al. 2018). To survive such extreme temperatures, these animals have evolved different physiological and ecological responses, as will be described in Chapter 2.

Nevertheless, since the first discovery of vent fauna (Ballard and Corliss 1977), new fish species have been described. However, they have been poorly studied in comparison to invertebrates (Boschen-Rose and Colaço 2021). This thesis examines the evolution of fishes located within the vent sites, focusing on their biogeography and evolutionary adaptations to such an extreme environment.

[1] The "deep-sea hydrothermal vents" will be further referred to as just „vents" in the text.

2. Physiological and evolutionary adaptation of vent fauna

Animals that live in the vent environment must adapt to several extreme conditions, such as elevated pressure, temperature and toxicity of vent fluids. Different strategies to cope with elevated temperatures and toxicity of vent fluids may be observed in the general distribution of vent fauna around the active venting sites. The faunal composition changes on the gradient from the vent opening towards the periphery of the vent field (Hessler and Smithey jr. 1983). At the vent opening, thermophilic species, usually dependent on symbiosis with chemolithotrophic bacteria, may be found, such as tubeworms *Riftia pachyptila* Jones 1981 or *Alvinella pompejana* Desbruyères & Laubier, 1980 (Grassle 1985), snails such as the genus *Alviniconcha* (Castel et al. 2022), followed by non-chemosynthetic obligate filtrators, microbial mat grazers, scavengers, detritivores and predators (Dykman et al. 2021).

One of the evolutionary adaptations of vent fauna is the symbiosis with chemolithotrophic bacteria (Zhang et al. 2024). It may be divided into two main types: either the bacteria live inside the body of the host as an endosymbiont, or they are on the host's body surface as an ectosymbiont. The well-studied case regarding the former is the tubeworm *R. pachyptila,* which lacks digestive organs and relies completely on the nutrients provided by bacteria that are hosted in its trophosome (Cavanaugh et al. 1981). Through a highly vascularised trophosome where the gills are located, oxygen and nitrates, which are used by the endosymbiotic gamma bacteria to oxidise the H_2S, producing adenosine triphosphate (ATP) to be used in the fixation of inorganic carbon from CO_2 into organic compounds (Cavanaugh et al. 1981; De Oliveira et al. 2022). To facilitate the transport of the H_2S to the trophosome, they have evolved haemoglobin, which has elevated reversible sulphide-binding capacity (Arp et al. 1987; De Oliveira et al. 2022). Moreover, some species have evolved molecular adaptations in their extracellular and intracellular haemoglobin enabling them to bind oxygen more efficiently from such a low-oxygen habitat despite the low pH and elevated temperature (Hourdez et al. 2000).

Furthermore, the bacterial symbiont contributes to the amino acid synthesis of the host by reducing dissolved nitrates provided from the surrounding environment (Lee et al. 1999; Jiang et al. 2020). Similar symbiotic relationships were also identified in other tubeworms from vents (Campbell et al. 2003; Gardebrecht et al. 2012), from their relatives from cold seep habitats (Kimura et al. 2003; Yang et al. 2020), but also in many vent molluscs (Stein et al. 1988; Lan et al. 2021; Castel et al. 2022).

However, as mentioned above, the relationship may also be ectosymbiotic, as is the case between the vent-endemic shrimps from the genus *Rimicaris* and different bacterial symbionts (Jiang et al. 2020). These bacteria are located on the setae of exopodites near the gills (Van Dover et al. 1988) that produce organic compounds which are absorbed through the gill chamber integument (Jiang et al. 2020; Ponsard et al. 2013; Streit et al. 2015).

Symbiosis with sulphide-oxidising bacteria is not limited to providing nutrients to their hosts but also helps them detoxify the H_2S (Compère et al. 2002; Lan et al. 2021). Some species have further evolved various molecular mechanisms that facilitate the detoxification of sulphides from their bodies. Such adaptations include the previously mentioned higher affinity of haemoglobin to H_2S, the presence of sulphide-oxidising bodies in gill cells (Powell and Somero 1985), as well as the whole enzymatic pathway of sulphide oxidation present in mitochondria (Powell and Somero 1986; Lin et al. 2021). Similarly, metal tolerance proteins or metal detoxifying enzymes were identified in vent invertebrates (Hardivillier et al. 2004; Liu et al. 2019).

Elevated temperatures are another extreme condition that the vent fauna must face. One of the adaptations is the distribution of different niches within the vent ecosystem. Thermophiles such as tubeworms, mussels, clams, or even certain crustaceans such as the crab *Bythograea thermydron* Williams, 1980 inhabit the proximity of the active venting site (Grassle 1985; Zhou et al. 2018; Perez et al. 2021). Mesophiles of all kinds, crabs, shrimps, mussels, gastropods, anemones, siphonophores or acorn worms inhabit the periphery (Hessler and Smithey jr. 1983; Grassle 1985; Zhou et al. 2018). The second type of adaptation to high temperatures is observed primarily in thermophile species. It includes different molecular adaptations such as increased stability of cuticular collagen in *A. pompejana* (Sicot et al. 2000), increased expression of heat shock protein genes in *R. exoculata* (Cottin et al. 2010), or increased metabolic rate and extracellular haemoglobin production in *Paralvinella pandorae* Desbruyères & Laubier, 1986 (Boutet et al. 2009).

3. Fishes of the deep-sea and their adaptation to the hydrothermal vent habitats

Fishes colonised the deep-sea probably in the mid-Palaeozoic (Priede and Froese 2013). Whether the colonisation occurred once or was periodically recolonised after the main extinction events is still disputed (Xu et al. 2025). The fish have evolved various life-history and genetic and physiological adaptations that enabled them to cope with the high hydrostatic pressure, lack of energy resources, light, and low temperatures (Andresen et al. 2025; Xu et al. 2025). The physiological adaptations include enhanced vision in mesopelagic fish, reduced or enhanced olfactory genes, or changes in protein properties to withstand high-hydrostatic pressure (Xu et al. 2025). They also often reduced their metabolic rate and select for the K-strategy, producing fewer offspring with a slower sexual maturation rate (Andresen et al. 2025).

Since the first discovery of the vents in 1977, more than 60 confirmed fish species have been observed in the vent habitats (Table 1). However, as will be described in subchapter 3.1, only a few of them can be considered as endemic to vent ecosystems. Such low level of endemism may be due to the fact that while colonising the vent habitat, fish have to overcome two main obstacles: the extreme temperature and high level of toxic sulphide compounds, and the ephemeral nature of these ecosystems, as, due to the plate tectonics, some of the active sites may have a life span of only tens of years (Vrijenhoek 2010). Concerning the latter, the recolonisation of different vent sites is less of a problem for fish species than for many sessile invertebrates. Thus, they may not disperse in their larval stadium but may do so as adults. The adaptation to the extreme conditions of vent sites has not yet been adequately researched, except for a few species, as will be described in subchapter 3.2.

3.1. Biogeography and ecology of "vent fishes"

The vent site around the world may be divided into the following main biogeographical provinces: The Mid-Atlantic Ridge (MAR), the Indian Ocean, composed of the Central Indian Ridge and its southwest and southeast branches, the West Pacific Ocean, the Northeast Pacific Ocean, and the East Pacific Rise (EPR) (Moalic et al. 2012) (Figure 1). The West Pacific Ocean and the EPR may be divided into northern and southern parts (Bachraty et al. 2009). Since vent fields have been located in the Arctic Ocean (Ramirez-Llodra et al. 2023) and the Southern Ocean (Rogers et al. 2012) as well, these two provinces should be added due to endemic species, until a thorough study is made that would prove their connectivity with already known provinces.

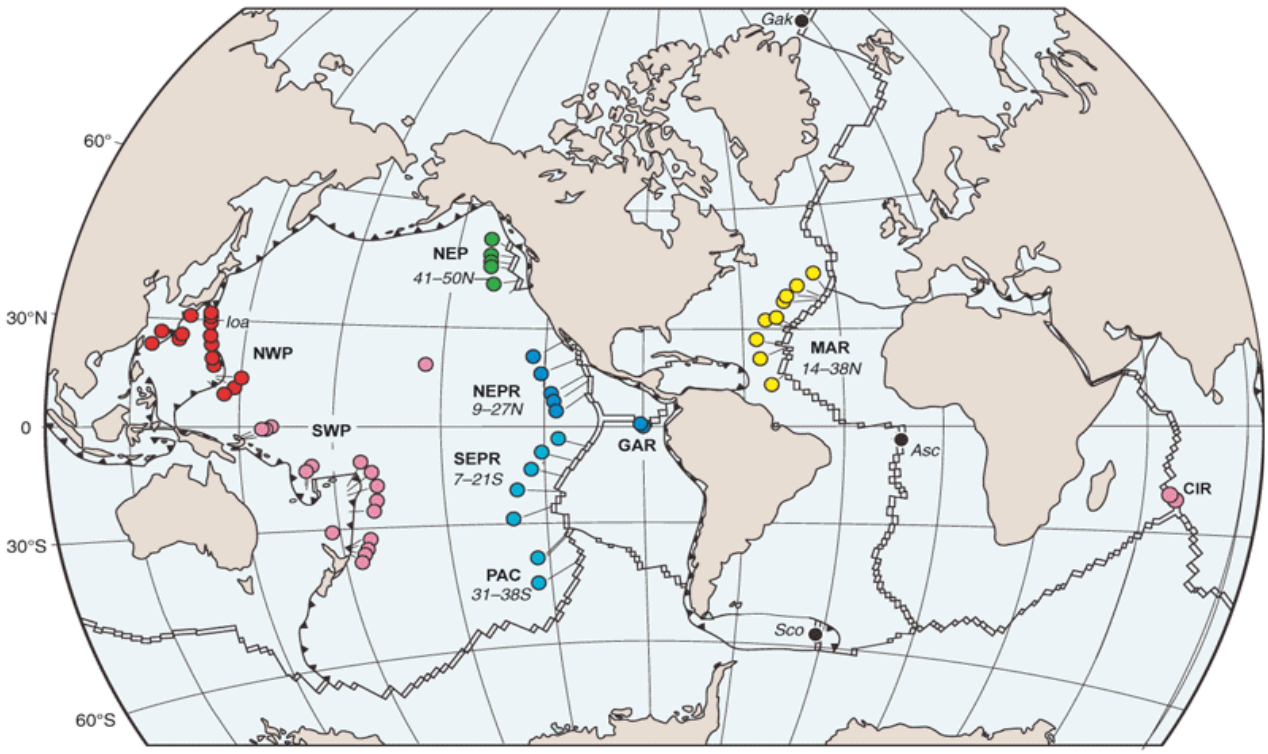

Figure 1: Map of main hydrothermal vent regions. CIR – Central Indian Ridge, GAR – Galapagos Rift, MAR – Mid-Atlantic Ridge, NEP – Northeast Pacific, NEPR – Northern East Pacific Rise, NWP – Northwest Pacific, PAC – Pacific-Antarctic Ridge, SEPR – Southern East Pacific Ridge, SWP – Southwest Pacific. Edited from (Vrijenhoek 2010).

The distribution of fish at vents is summarised in Table 1 – Overview of identified fishes from the hydrothermal vent regions. The division into vent regions follows the structure proposed by Vrijenhoek (2010) and Beaulieu and Szafrański (2020), with the following modifications and additional information. The Mid-Atlantic Ridge (MAR) is not divided into northern and southern parts, as all the documented distribution has been reported northward from the equator, from vent sites lying approximately between 37°N and 12°N. Vent regions in the West Pacific are further divided into the northwestern (NWP) and southwestern (SWP) areas. Fishes that are present both in the northern and southern area of the EPR are indicated with the abbreviation "EPR" only; otherwise, the abbreviations "N EPR" or "S EPR" are used. Galapagos Rift, although considered here as an individual region, forms part of the larger EPR; therefore, this information is included in the brackets.

The orders are arranged based on recent comprehensive phylogenetic studies both for Teleost fishes (Betancur-R et al. 2017) and Chondrichthyes (Vélez-Zuazo and Agnarsson 2011). The question mark is indicated in the column "Vent-endemic" for uncertain species

(indicated cf. for those specimens that resembled such species, or sp. for those specimens for which the identification of particular species has not been provided).

Table 1*:* Overview of identified fishes from the hydrothermal vent regions

No.	Species	Order (Family)	Vent region	Vent-endemic	References
		TELEOST FISHES			
1.	*Halosauropsis macrochir* (Günther, 1878)	*Notacanthiformes (Halosauridae)*	Mariana Arc (NWP)	No	Koeda et al. 2021
2.	*Polyacanthonotus* cf.*rissoanus* (De Filippi & Verany, 1857)	*Notacanthiformes (Notacanthidae)*	MAR	No	Saldanha and Biscoito 1997
3.	*Conger erebennus* (Jordan & Snyder, 1901)	*Anguilliformes (Congridae)*	Mariana Arc (NWP)	No	Koeda et al. 2021
4.	*Dysommina rugosa* Ginsburg, 1951	*Anguilliformes (Synaphobranchidae)*	Lau Basin (SWP)	No	Staudigel et al. 2006
5.	*Ilyophis blachei* Saldanha & Merrett, 1982	*Anguilliformes (Synaphobranchidae)*	MAR	No	Saldanha and Biscoito 1997
6.	*Ilyophis saldanhai* Karmovskaya & Parin, 1999	*Anguilliformes (Synaphobranchidae)*	MAR, S EPR	No	Biscoito et al. 2002 ; Segonzac et al. 2006
7.	*Simenchelys parasitica* Gill, 1879	*Anguilliformes (Synaphobranchidae)*	MAR	No	Saldanha and Biscoito 1997; Marques and Almeida 2000;
8.	*Synaphobranchus kaupii* Johnson, 1862	*Anguilliformes (Synaphobranchidae)*	MAR	No	Saldanha and Biscoito 1997; Marques and Almeida 2000 Martins et al. 2006

9.	*Thermobiotes mytilogeiton* Geistdoerfer, 1991	*Anguilliformes (Synaphobranchidae)*	Lau Basin (SWP)	Yes	Geistdoerfer 1991; Geistdoerfer 1995; Biscoito et al. 2002
10.	*Chlorophthalmus* sp.	*Aulopiformes (Chlorophthalmidae)*	Mariana Arc (NWP)	No	Koeda et al. 2021
11.	*Bathypterois grallator* (Goode & Bean, 1886)	*Aulopiformes (Ipnopidae)*	Mariana Arc (NWP)	No	Koeda et al. 2021
12.	*Neocyttus helgae* (Holt & Byrne, 1908)	*Zeiformes (Oreosomatidae)*	MAR	No	Saldanha and Biscoito 1997
13.	*Gaidropsarus mauli* Biscoito & Saldanha, 2018	*Gadiformes (Gaidropsaridae)*	MAR	No	Biscoito and Saldanha 2018
14.	*Coelorinchus* cf. *labiatus* (Köhler, 1896)	*Gadiformes (Macrouridae)*	MAR	No	Saldanha and Biscoito 1997; Marques and Almeida 2000
15.	*Coryphaenoides anguliceps* (Garman, 1899)	*Gadiformes (Macrouridae)*	Galapagos Rift (EPR)	No	Cohen and Haedrich 1983; Geistdoerfer 1985
16.	*Coryphaenoides armatus* (Hector, 1875)	*Gadiformes (Macrouridae)*	MAR, EPR	No	Cohen and Haedrich 1983; Geistdoerfer 1985 ; Dahlhoff 1990; Segonzac 1992; Marques and Almeida 2000
17.	*Coryphaenoides bulbiceps* (Garman, 1899)	*Gadiformes (Macrouridae)*	Galapagos Rift (EPR)	No	Cohen and Haedrich 1983

18.	*Coryphaenoides macrocephalus* Günther, 1878	*Gadiformes (Macrouridae)*	MAR	No	Marques and Almeida 2000; Guerreiro et al. 2004
19.	*Antimora rostrata* (Günther, 1878)	*Gadiformes (Macrouridae)*	MAR	No	Martins et al. 2006
20.	*Guttigadus latifrons* (Holt & Byrne, 1908)	*Gadiformes (Moridae)*	MAR	No	Saldanha and Biscoito 1997
21.	*Laemonema robustum* Johnson, 1862	*Gadiformes (Moridae)*	Mariana Arc (NWP)	No	Koeda et al. 2021
22.	*Lepidion guntheri* (Giglioli, 1880)	*Gadiformes (Moridae)*	MAR	No	Guerreiro et al. 2004
23.	*Lepidion schmidti* Svetovidov, 1936	*Gadiformes (Moridae)*	MAR	No	Saldanha and Biscoito 1997; Guerreiro et al. 2004
24.	*Mora moro* (Risso, 1810)	*Gadiformes (Moridae)*	MAR	No	Saldanha and Biscoito 1997; Guerreiro et al. 2004; Martins et al. 2006
25.	*Physiculus rhodopinnis* Okamura, 1982	*Gadiformes (Moridae)*	Mariana Arc (NWP)	No	Koeda et al. 2021
26.	*Physiculus yoshidae* Okamura, 1982	*Gadiformes (Moridae)*	Izu-Bonin Arc (NWP)	No	Koeda et al. 2021
27.	*Beryx splendens* Lowe, 1834	*Beryciformes (Berycidae)*	MAR	No	Saldanha and Biscoito 1997; Marques and Almeida 2000;

28.	*Cataetyx laticeps* Koefoed, 1927	*Ophidiiformes (Bythitidae)*	MAR	No	Saldanha and Biscoito 1997
29.	*Thermichthys hollisi* (Cohen, Rosenblatt & Moser, 1990)	*Ophidiiformes (Bythitidae)*	EPR	Yes	Cohen et al. 1990; Dahlhoff 1990; Geistdoerfer 1995; Biscoito et al. 2002;
30.	*Ventichthys biospeedoi* Nielsen, Møller & Segonzac, 2006	*Ophidiiformes (Ophidiidae)*	S EPR	Yes	Nielsen et al. 2006
31.	*Acanthonus armatus*	*Ophidiiformes (Ophidiidae)*	Galapagos Rift (EPR)	No	Cohen and Haedrich 1983; Geistdoerfer 1985
32.	*Chiasmodon niger* Johnson, 1864	*Scombriformes (Chiasmodontidae)*	MAR	No	Marques and Porteiro 2000
33.	*Ruvettus pretiousus* Cocco, 1833	*Scombriformes (Gempylidae)*	Mariana Arc	No	Koeda et al. 2021
34.	*Symphurus maculopinnis* Munroe, Tyler, Tunnicliffe, 2013	*Pleuronectiformes (Cynoglossidae)*	Tonga Arc (SWP)	Yes	Munroe et al. 2011
35.	*Symphurus orientalis* (Bleeker, 1879)	*Pleuronectiformes (Cynoglossidae)*	Okinawa Trough, Mariana Arc (NWP)	No	Hashimoto et al. 1995
36.	*Symphurus thermophilus* Munroe & Hashimoto, 2008	*Pleuronectiformes (Cynoglossidae)*	Okinawa Trough, Mariana Arc (NWP)	Yes	Munroe and Hashimoto 2008, Tunnicliffe et al. 2010; Tunnicliffe et al. 2013; Stevens et

					al. 2016; Koeda et al. 2021; Chen et al. 2024);
37.	*Chaunax sp.*	*Lophiiformes (Lophiidae)*	MAR	?	Saldanha and Biscoito 1997
38.	*Lophiodes sp.*	*Lophiiformes (Lophiidae)*	Mariana Arc (NWP)	?	Koeda et al. 2021
39.	*Epigonus telescopus* (Risso, 1810)	*Acropomatiformes (Epigonidae)*	MAR	No	Saldanha and Biscoito 1997; Martins et al. 2006
40.	*Careproctus hyaleius* Geistdoerfer, 1994	*Perciformes (Liparidae)*	N EPR	Yes	Geistdoerfer 1994a°; Geistdoerfer 1995; Biscoito et al. 2002
41.	*Careproctus rhodomelas* Gilbert & Burke, 1912	*Perciformes (Liparidae)*	Okinawa Trough (NWP)	No	Takemura et al. 2010
42.	*Psychrolutes inermis* (Vaillant, 1888)	*Perciformes (Psychrolutidae)*	Okinawa Trough (NWP)	No	Hashimoto et al., 1995
43.	*Trachyscorpia echinata* (Köhler, 1896)	*Perciformes (Sebastidae)*	MAR	No	Saldanha and Biscoito 1997
44.	*Pachycara angeloi* Thiel, Knebelsberger, Kihara & Gerdes, 2021	*Perciformes (Zoarcidae)*	CIR	Yes	Thiel et al. 2021
45.	*Pachycara carribaeum* Anderson, Somerville & Copley, 2016	*Perciformes (Zoarcidae)*	Mid-Cayman Rise	Yes	Anderson et al. 2016

46.	*Pachycara gymninium* Anderson & Peden, 1988	*Perciformes (Zoarcidae)*	Juan de Fuca Ridge (NEP)	No	Anderson 1989; Biscoito et al. 2002; Almeida and Biscoito 2006 in Desbruères et al. 2006
47.	*Pachycara rimae* Anderson, 1989	*Perciformes (Zoarcidae)*	Galapagos Rift (EPR)	Yes?	Anderson 1989; Biscoito et al. 2002; Almeida and Biscoito 2006 in Desbruères et al. 2006
48.	*Pachycara saldanhai* Biscoito & Almeida, 2004	*Perciformes (Zoarcidae)*	MAR	Yes	Geistdoerfer 1994b; Biscoito and Almeida 2004; Stefanni et al. 2007
49.	*Pachycara thermophilum* Geistdoerfer, 1994	*Perciformes (Zoarcidae)*	MAR	Yes	Geistdoerfer 1994b; Geistdoerfer 1995; Biscoito et al. 2002; Biscoito and Almeida 2004; Stefanni et al. 2007;
50.	*Pyrolycus manusanus* Machida & Hashimoto, 2002	*Perciformes (Zoarcidae)*	Manus Basin (SWP)	Yes	Machida and Hashimoto 2002
51.	*Pyrolycus moelleri* Anderson, 2006	*Perciformes (Zoarcidae)*	Kermadec Arc (SWP)	Yes	Anderson, 2006

52.	*Thermarces cerberus* Rosenblatt & Cohen, 1986	*Perciformes (Zoarcidae)*	Galapagos Rift, N EPR	Yes	Geistdoerfer 1985 ; Cohen and Rosenblatt 1986; Grassle 1987; Geistdoerfer 1995; de Buron et al. 2000; Biscoito et al. 2002; Micheli et al. 2002; Geistdoerfer and Seuront 2005; Sancho et al. 2005; Pond et al. 2008
53.	*Thermarces andersoni* Rosenblatt & Cohen, 1986	*Perciformes (Zoarcidae)*	N EPR	Yes	Rosenblatt and Cohen 1986; Grassle 1987; Dahlhoff 1990; Biscoito et al. 2002;
CHONDRICHTHYES - SHARKS, SKATES AND RAYS					
54.	*Deania calceus* (Lowe, 1839)	*Squaliformes (Centrophoridae)*	MAR	No	Martins et al. 2006 ; Drazen et al. 2009;
55.	*Deania hystricosa* (Garman, 1906)	*Squaliformes (Centrophoridae)*	MAR	No	Guerreiro et al. 2004
56.	*Etmopterus princeps* Collett, 1904	*Squaliformes (Etmopteridae)*	MAR	No	Saldanha and Biscoito 1997; Marques and Almeida 2000; Guerreiro et al.

					2004; Martins et al. 2006
57.	*Etmopterus pusillus* (Lowe, 1839)	*Squaliformes (Etmopteridae)*	MAR	No	Saldanha and Biscoito 1997
58.	*Centroscymnus coelolepis* Barbosa du Bocage & de Brito Capello, 1864	*Squaliformes (Somniosidae)*	MAR	No	Saldanha and Biscoito 1997; Marques and Almeida 2000;
59.	*Centroscymnus crepidater* (Bocage Capelo, 1864)	*Squaliformes (Somniosidae)*	MAR	No	Guerreiro et al. 2004
60.	*Apristurus laurusonii* (Saemundsson, 1922)	*Carcharhiniformes (Pentanchidae)*	MAR	No	Saldanha and Biscoito 1997
61.	*Bathyraja abyssicola* (Gilbert, 1896)	*Rajiformes (Arhynchobatidae)*	Juan de Fuca Ridge	No	Kuhnz et al. 2019
62.	*Amblyraja hyperborea* (Collett, 1879)	*Rajiformes (Rajidae)*	Juan de Fuca Ridge	No	Kuhnz et al. 2019
63.	*Bathyraja microtrachys* (Osburn & Nichols, 1916)	*Rajiformes (Arhynchobatidae)*	Juan de Fuca Ridge	No	Kuhnz et al. 2019
64.	*Bathyraja spinosissima* (Beebe & Tee-Van, 1941)	*Rajiformes (Arhynchobatidae)*	Galapagos Rift (EPR), Juan de Fuca Ridge	No	Salinas-de-León et al. 2018 ; Kuhnz et al. 2019 ;
65.	*Bathyraja trachura* (Gilbert, 1892)	*Rajiformes (Arhynchobatidae)*	Juan de Fuca Ridge	No	Kuhnz et al. 2019
CHONDRICHTHYES - CHIMAERAS					
66.	*Hydrolagus affinis* (de Brito Capello, 1868)	*Chimaeriformes (Chimaeridae)*	MAR	No	Saldanha and Biscoito 1997; Martins et al. 2006

67.	*Hydrolagus pallidus* Hardy & Stehmann, 1990	*Chimaeriformes (Chimaeridae)*	MAR	No	Saldanha and Biscoito 1997; Guerreiro et al. 2004; Martins et al. 2006
HAGFISH					
68.	*Eptatretus okinoseanus* (Dean, 1904)	*Myxiniformes (Myxini)*	Okinawa Trough (NWP)	No	Hashimoto et al. 1995;
69.	*Eptatretus strickrotti* Møller & Jones, 2007	*Myxiniformes (Myxini)*	S EPR	Yes	Møller and Jones 2007
70.	*Myxine garmani* Jordan & Snyder, 1901	*Myxiniformes (Myxini)*	Okinawa Trough (NWP)	No	Hashimoto et al. 1995

Most of the species reported from vent sites are not endemic to the vent habitat. These non-vent endemic species were usually observed at the periphery of the active fields, either swimming in the water column or lying on the seabed away from the vent chimneys (Saldanha and Biscoito 1997; Biscoito et al. 2002; Koeda et al. 2021). The study conducted by Guerreiro et al. (2004) on fish caught at vent sites in the MAR proved that bathypelagic fish use vent fauna as the nutrient source. The analysis of tissues' fatty acids showed that certain polyunsaturated fatty acids may have a bacterial origin through feeding on vent invertebrates. Another study analysing the fatty acid composition in non-vent endemic species such as *C. armatus* showed that it feeds on chemosynthetic organisms from vent ecosystems (Mayor et al. 2013), which would also explain the presence of these non-vent species at vent sites, and consequently, it could also provide an explanation why bathypelagic sharks occur there, as they may prey on the smaller fish feeding on vent invertebrates.

Moreover, vent sites may be used as a safe haven for the larvae of fish, and they may also serve as egg incubators even for bathypelagic species. Such a case has been observed at the vent site at the Galapagos, where eggs of *Bathyraja spinosissima* were observed in aggregations around the active chimneys, suggesting that the warm water plumes may induce the development of embryos in surrounding cold waters (Salinas-de-León et al. 2018).

Similarly, the eggs of deep-sea sharks and skates have been reported from cold seeps in the Mediterranean and the Southeast Pacific Ocean, suggesting that cold seeps, as another chemosynthetic-based ecosystem, may act as nurseries as well (Treude et al. 2011).

Furthermore, a hypothesis proposed, however, for freshwater shortfin molly (*Poecilia mexicana*, *Poeciliidae, Cyprinodontiformes*) (Steindachner, 1863), suggests that extreme habitats such as hydrothermal vent springs may protect the species from certain parasites (Tobler et al. 2007).On the other hand, new trematode species have been identified in vent-endemic species *Thermichthys hollisi* and *Ventichthys biospeedoi* (Bray et al. 2014).

With regard to the distribution of non-vent species, it is noteworthy that *Chondrichthyes,* specifically sharks and chimaeras, are reported only from the MAR (Saldanha and Biscoito 1997; Drazen et al. 2009; Guerreiro et al. 2004), despite some of the identified species, such as *E. pusillus*, *C. coelolepis,* or *D. calceus,* being deep-sea species distributed also across the Indian and the Pacific Ocean. Skates have been reported so far only from two vent regions in the East Pacific Ocean – the Galapagos Rift and the EPR (Salinas-de-León et al. 2018; Kuhnz et al. 2019).

Similarly, only a few species of hagfish have been reported from vent sites only in the Pacific Ocean. Unlike the *Chondrichthyes*, there may be vent-endemic species present at vent sites, as *Eptatretus strickrotti* has been described so far only from the vent field near Easter Island in the EPR (Møller and Jones 2007). Molecular analysis has shown that it is probably a basal species for the whole genus *Eptatretus* (Møller and Jones 2007). Yet, more observations are necessary to describe its ecology and role in the vent ecosystem. However, it may be premature to consider it as a vent-endemic species, as the aforementioned study is the only observation of this species. Neither can it be excluded that there are hagfish present at vent sites in other regions.

Non-vent-endemic Teleost fishes are reported from all main vent regions; however, most of the species have been observed or caught in the MAR (Geistdoerfer 1995; Saldanha and Biscoito 1997; Martins et al. 2006) or the EPR (Cohen and Haedrich 1983; Geistdoerfer 1985; 1995) vent sites. Such a discrepancy between relatively more data from these regions in comparison to, for example, the Central Indian Ridge must not be interpreted as the fish biodiversity is higher in the MAR and the EPR; rather, it may be due to the research focus on these two areas.

The most common families that are present in vent regions both in the Atlantic and the Pacific Oceans are cutthroat eels (*Anguilliformes: Synaphobranchidae*), rattails (*Gadiformes: Macrouridae*), morid cods (*Gadiformes: Moridae*), livebearing brotulas (*Ophidiiformes: Bythitidae*), goosefishes (*Lophiiformes: Lophiidae*), and eelpouts (*Perciformes: Zoarcidae*) (Table 1). These families are in general cosmopolitan bathypelagic or pelagic (Priede 2017), and therefore the observation of their species also at deep-sea vents is not surprising. The non-vent-endemic species have usually been observed either on the seabed or swimming in the water column on the periphery or outside the vent field (Marques and Almeida 2000; Guerreiro et al. 2004; Koeda et al. 2021; Takemura et al. 2010). It is also noteworthy that deep-sea orders of fish such as *Alepocephaliformes, Myctophiformes, Saccopharyngiformes, Stomiiformes,* and *Stylephoriformes* seem not to be significantly present at the vent sites.

Only six families – *Bythitidae*, *Ophidiidae* (*Ophidiiformes*), *Synaphobranchidae*, *Zoarcidae, Liparidae* (*Perciformes*), and *Cynoglossidae* (*Pleuronectiformes*) – include vent-endemic species (Table 1). All these families are entirely marine and have widespread distribution across the Atlantic, Indian and Pacific Oceans (Nelson 2016). Concerning their phylogeny, both relatively old, tens of millions of years old, and relatively young, only a few million years old, clades are represented. The aforementioned families and orders are divided into two main clades – *Elopomorpha* with the order *Anguilliformes*, and all others included in clade *Osteoglossocephalai* (Betancur-R et al. 2017). *Elopomorpha* formed around 250 million years ago (Ma) (Parey et al. 2023). From the second clade, all vent-endemic species are from the clade *Percomorpha,* which diversified in the mid to late Jurassic around 150 Ma (Betancur-R et al. 2017). From these, the oldest are the orders *Ophidiiformes,* which occurred around 100 million years ago (Wong and Chen 2024) and *Perciformes,* diversifying around 90 – 100 million years ago (Wei et al. 2014; Betancur-R et al. 2017), whereas *Pleuronectiformes* are a relatively young order, from around 75 million years ago (Campbell et al. 2013).

The highest number of identified vent species belongs, however, only to *Zoarcidae* (Table 1). It is also the family that has the biggest share of vent-endemic species. Even though *Perciformes* diversified in the late Mesozoic around 100 million years ago, *Zoarcidae* diversified in the early Miocene around 20 million years ago (Hotaling et al. 2021). They are considered one of the fastest speciating clades of marine fish, which enables them to pioneer into new ecological niches and extremophile habitats. Whether they possessed the best preadaptation for colonising the chemosynthetic ecosystems remains to be seen, as more studies about the physiological adaptations of other vent species from other families need to be done.

Looking at the distribution of vent-endemic species (Figure 2), *Zoarcidae* are present in all main vent regions, except for the Northwest and the Northeast Pacific Ocean.

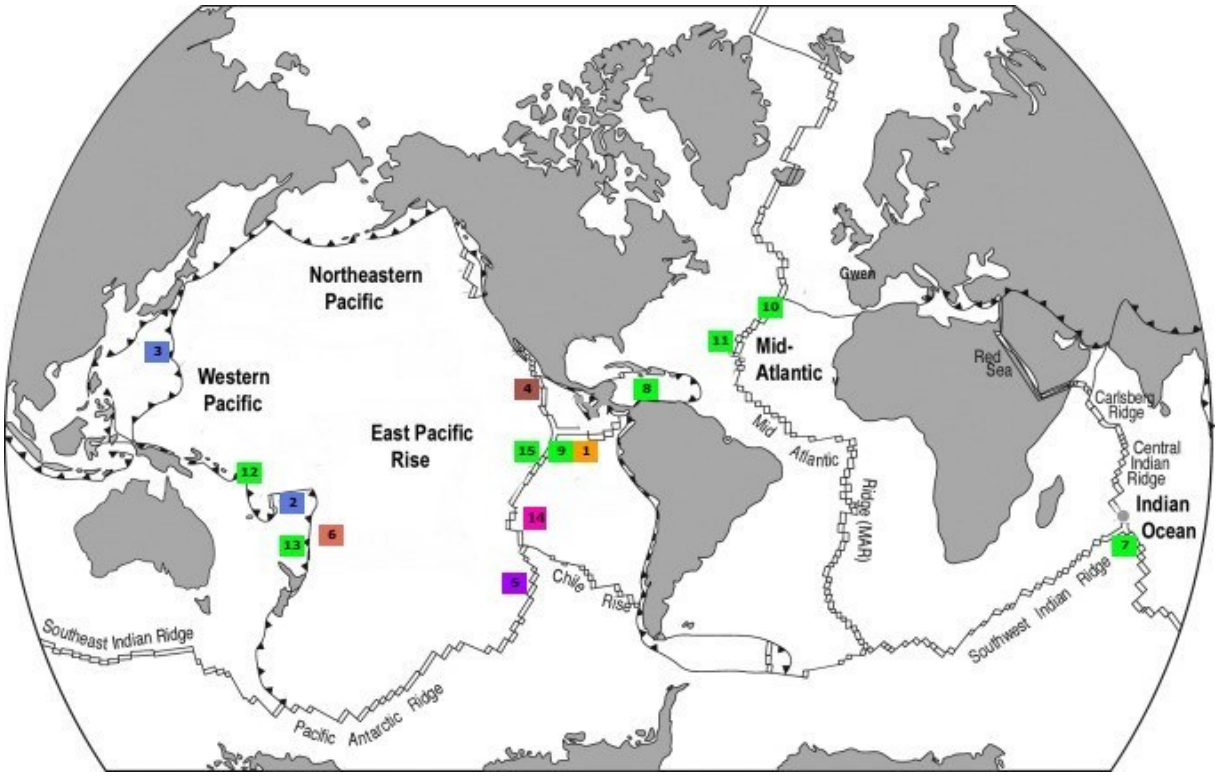

Figure 2: Global distribution of vent-endemic species. Numbers and colours are indicated below. Map edited from (Neubert et al. 2006), original map (Van Dover et al. 2002)**.**

1	*Thermichthys hollisi*
2	*Symphurus maculopinnis*
3	*Symphurus thermophilus*
4	*Careproctus hyaleius*
5	*Eptatretus strickrotti*
6	*Thermobiotes mytilogeiton*
7	*Pachycara angeloi*
8	*Pachycara carribeum*
9	*Pachycara rimae*
10	*Pachycara saldanhai*
11	*Pachycara thermophilum*
12	*Pyrolycus manusanus*
13	*Pyrolycus moelleri*
14	*Ventichthys biospeedoi*
15	*Thermarces cerberus/ andersoni*
	Bythitidae (Ophidiiformes)
	Cynoglossidae (Pleuronectiformes)
	Liparidae (Perciformes)
	Myxinidae (Myxiniformes)
	Synaphobranchidae (Anguilliformes
	Zoarcidae (Perciformes)
	Ophidiidae (Ophidiiformes)

The vent-endemic eelpouts were observed close to the active vent chimneys, usually lying on sulphide deposits (Hashimoto et al. 1995; Biscoito and Almeida 2004; Anderson 2006; Thiel et al. 2021). The genera *Thermichthys* and *Ventichthys* seem to include species only bound to vent ecosystems. *Thermarces* and *Pyrolycus* have the majority of species bound to vents, but also include species adapted to cold seeps at the Lesser Antilles (Geistdoerfer 1999; Anderson et al. 2016; Frable et al. 2023). The presence of these genera in the eastern Central Pacific Ocean and in the Caribbean Sea supports the theory of connectivity between the Central Pacific and the Central Atlantic Ocean fauna and also the theory of preadaptation and colonisation of similar lineages of both hydrothermal vents and cold seeps (Sibuet and Olu 1998; Bachraty et al. 2009). A similar conclusion can be drawn from the presence of *Pyrolycus jaco* (Frable, Seid, Bronson & Møller, 2023) found in hydrothermal seeps in the Central East Pacific (Frable et al. 2023) and its vent relatives *P. manusanus* and *P. moelleri* from the SWP, the former from the Manus Basin vents near Papua-New Guinea (Machida and Hashimoto 2002), and the latter from the Kermadec Ridge near New Zealand (Anderson 2006). Furthermore, another eelpout species, *Pachycara carribeum,* has been identified both from vent sites and cold seeps in the Caribbean Sea (Anderson et al. 2016), further supporting the hypothesis about the connectivity of vent and cold-seep fauna.

The theory of connectivity between different vent sites has also been studied on the species of tonguefishes (*Pleuronectiformes: Cynoglossidae*) – *Symphurus thermophilus* and *S. maculopinnis*. *S. thermophilus* is known from the NWP, where it usually inhabits soft bottom around active vent fields, where the water temperature reaches around 20 °C (Munroe and Hashimoto 2008). However, it has been observed in a wide range of vent habitats, spanning from molten and early-formed sulphide banks to the periphery of the vent field (Tunnicliffe et al. 2013). *S. maculopinnis* is known from the SWP (Tunnicliffe et al. 2010), occurring in the same habitats as the former. This species was originally described as *S. thermophilus* and distinguished only based on phylogenomic analysis, which may indicate that the biodiversity of not only vent tonguefish but also other identified species may be higher.

Similarly, there are doubts about the *P. saldanhai* and *P. thermophilum* being two distinct species. Both are known from vent fields south of the Azores (Geistdoerfer 1994b; Biscoito and Almeida 2004). In fact, the molecular analysis of the mtDNA of specimens of both species has shown that they are probably the same species that either colonised distant vent sites, dispersing, making use of a series of vent fields, or they are more common throughout the whole MAR and vent fields are only part of their overall habitat (Stefanni et al. 2007). However,

no other analysis has been made, and both species are still recognised as distinct species by Eschmayer's catalogue of fishes (Eschmayer's catalogue) and World Register of Marine Species (WoRMS) (WoRMS Editorial Board 2025; Fricke et al. 2025). Both for vent-endemic *Symphurus* and *Pachycara*, and potentially for other species, the identification as two different species, respectively the same species, may be caused partially by the lack of information about their morphological diversity or dimorphism in different maturity stages.

From the aforementioned remaining families, *Bythitidae, Ophidiidae, Synaphobranchidae,* and *Liparidae*, only one vent-endemic species per family has been described, all from the Pacific Ocean. The cutthroat eel *Thermobiotes mytilogeiton* has been observed near the active chimneys in the vent fields in the SWP, in the water flows of temperature around 20 °C (Geistdoerfer 1991); however, except for this observation, no more studies related to its ecology have been conducted. The other three vent-endemic species – the snailfish *Careproctus hyaleius*, the brotula *Thermicthys hollisi*, and the cusk-eel *Ventichthys biospeedoi* – are all known from the vent sites in the N EPR, living in the same habitat as *T. mytilogeiton* within the reach of warm water plumes from the active chimney (Cohen et al. 1990; Geistdoerfer 1994a; Nielsen et al. 2006).

3.2. Physiological and genetic adaptation of "vent fishes"

Vent sites are rich in H_2S, and any species that lives in the vent fluids had to evolve a strategy to overcome its toxicity. For the invertebrates, as described in Chapter 2, these evolutionary adaptations include symbiosis with chemolithotrophic bacteria and specific enzymes and organelles that help them metabolise H_2S or excrete it from their body. Studies on freshwater mollies and mosquitofishes/gambusia (genus *Gambusia*) have provided evidence for behavioural, genetic, morphological, and life-history adaptations (Riesch et al. 2015), some of which may also explain the resilience of marine vent fish species.

Several comparative studies, which were conducted on populations of shortfin mollies from sulphide-rich and clear water habitats, have shown that males from sulphide-rich environments tend to reduce the costly sexual activities, such as mating and harassment behaviour towards females (Plath et al. 2006). Furthermore, due to the chemistry of these environments and the lower level of dissolved oxygen, facultative surface air breathing was observed, which accounted for more than 70 % of their activity time (Plath et al. 2007).

Since deep-sea fishes generally reduce their metabolic activity (Priede 2017), it may be deduced for the vent-endemic species. From the few observations in their habitats, most of the

specimens were seen lying or slowly swimming above the seabed and, except for the genus *Thermarces,* they tend to avoid high-temperature water plumes and prefer the warm-water plumes with temperatures on average between 7 and 20 °C (Geistdoerfer 1985; Dahlhoff et al. 1990; Saldanha and Biscoito 1997; Nielsen et al. 2006).

Adaptation to a hypoxic environment is reflected in the morphological adaptations as well. One of the significant traits is a larger head of sulphide-spring populations of mollies, which enables them to increase their gill surface and thus get more oxygen from water (Tobler et al. 2011). Larger heads also mean bigger jaws, which may enable them to increase the surface air breathing (Winemiller 1989) or the ventilation efficiency (Riesch et al. 2015). Contrary to a large head, their brain volume, as well as optic tecum, is smaller, which may be due to the limited energy resources and oxygen, but it may also be an adaptation to reduced light amount in the murky sulphide springs (Eifert et al. 2015).

Concerning vent-endemic species, a bigger head/body ratio has not been adequately studied, but looking at the photographs of holotypes, it seems to be verified only partially. *T. hollisi, V. biospedoi,* and *C. hyaleius* confirm this theory (Cohen et al. 1990; Geistdoerfer 1994a; Nielsen et al. 2006), but it is just an estimate that should be verified with proper morphometric methods.

Fishes from freshwater sulphide-rich environments are predominantly viviparous and produce fewer but bigger offspring than their relatives from non-sulphide habitats (Riesch et al. 2010; 2016). A larger body of offspring decreases the volume/surface ratio, thus exposing less skin to the toxic H_2S and reducing the relative metabolic rate and energy consumption (Riesch et al. 2010). On the other hand, the reduction of metabolism is also influenced by other environmental factors, such as lower oxygen concentrations and limited resource availability.

The reproductive strategy of vent-endemic species has not been properly researched; however, the selection for viviparous species has not been confirmed for vent-endemic species yet. On the other hand, it may be presumed that some species belonging to the families *Bythitidae* (Nelson 2016) and *Zoarcidae* are viviparous (Anderson 1994; Møller et al. 2016; Dallarés et al. 2021). However, it can be inferred that vent-endemic species will also be K-selected, like other deep-sea fishes, producing fewer offspring (Frable et al. 2023). Moreover, it would be interesting to investigate this strategy in relation to the ephemeral nature of vent ecosystems. One of the morphological adaptations seems to be thicker skin in vent-endemic

species, which may protect them from the high temperature of vent fluids (Nielsen et al. 2006). Still, it may also increase their protection from the toxic compounds.

Although the genetic and physiological adaptations differ across freshwater sulphide-resistant species, and some species have probably evolved independently for each population of those species (Pfenninger et al. 2014), they mainly target the tolerance to higher levels of H_2S. A study conducted by Tobler et al. (2014) has shown that exposure to elevated concentrations of H_2S led to increased expression of sulphide: quinone oxidoreductase (SQR) genes in liver and gill cells. Another study proved that the mutations in subunits of cytochrome-c oxidase complex (COX) decreased its susceptibility to H_2S (Pfenninger et al. 2014). Different gene expression of COX and SQR may be correlated with H_2S-induced changes in miRNA gene expression that lead to further genetic adaptations (Kelley et al. 2021).

A comparative study conducted by Weber et al. (2003) on vent-endemic *T. cerberus,* non-vent-endemic *S. parasitica*, and shallow-water *Zoarces viviparus* (Linnaeus, 1758) (*Zoarcidae, Perciformes*) provides insights into the physiological adaptation of haemoglobin in the presence of H_2S and under high temperature. It found that the oxygen affinity to haemoglobin in *T. cerberus* decreased less with lower pH than for *Z. viviparus* for all its haemoglobin types, indicating the physiological adaptation of the former to the vent habitat. Similarly, the oxygen-haemoglobin affinity decreased slightly with higher temperatures in *T. cerberus,* whereas in *Z. viviparus* the decrease was more rapid (Weber et al. 2003). For *S. parasitica* that makes incursions to vent-sites but otherwise is generally deep-sea dwelling, with decreasing pH and increased temperature, the type I haemoglobin's affinity did not significantly change, and type II's affinity dropped in line with the Bohr effect (Weber et al. 2003).

High temperature also has a possible deteriorating effect on enzymatic activities. Dahlhoff et al. (1990) made a comparative study on the impact of elevated temperature and pressure on muscular lactate dehydrogenase (M_4-LDH) activity in vent-endemic *T. hollisi* and *T. andersoni*, and non-vent-endemic *C. armatus.* In *T. hollisi*, the enzymatic activity of M_4-LDH almost did not change for the pressure increase from 1 to 350 atmospheres and temperature increase from 5 to 10 °C, and for the rise to 15, respectively 20 °C, the activity decreased only slightly (Dahlhoff et al. 1990). On the other hand, the enzymatic activity in the second vent-endemic species – *T. andersoni*, was similar to that of non-vent endemic *C. armatus*, as in both species there was a sharp decrease already for the temperature of 10 °C (Dahlhoff et al. 1990). The authors hypothesise that such a difference in vent-endemic species

may be due to their different ecology, as the genus *Thermarces* is more benthic and has been observed closer to the active vent chimneys than *Thermichthys hollisi,* which, although being observed at the active chimneys, may spend more time swimming further from them (Dahlhoff et al. 1990). Since both vent-endemic species are from different families, follow-up studies could provide insights into this hypothesis concerning other species from the same family and their observed behaviour.

Only a few studies on the trophic position of vent-endemic species have been made so far. Analysis of different tissues from vent-endemic *Symphurus thermophilus* and another so-far-unidentified species of the same genus collected at the vent site in the Southwest Pacific Ocean has found that the composition of polyunsaturated fatty acids (PUFA) did not show significant differences from non-vent endemic bathydemersal species, indicating that the vent-endemic species make excursions to the surrounding environment for scavenging or catching prey (Stevens et al. 2016). However, the vent-endemic species feed on chemosynthetic-obligate fauna as well, as proved from the fatty acid composition of *T. cerberus* (Pond et al. 2008) but also from the stomach content analysis of *T. cerberus* or the genus *Pachycara,* where the remnants of vestimentiferans, shrimps, and mussels were found (Biscoito et al. 2001; Geistdoerfer and Seuront 2005). Furthermore, fish may feed directly on mats of chemosynthetic bacteria. However, this hypothesis has been inferred mainly from observations (Tunnicliffe et al. 2013) and a few fatty acid analyses. On the other hand, their composition may also indicate the origin from photosynthetic bacteria (Guerreiro et al. 2004) as the chemosynthetic vent bacteria do not produce some of the PUFA found in the tissue of vent fishes (Pond et al. 2008).

4. Conclusion

Fishes are the most successful vertebrates, and they have demonstrated great resilience and marvellous adaptations in colonising the deep ocean. Deep-sea hydrothermal vents may seem like a habitat too hostile for them to colonise. Yet, studies on the composition of fauna at various vent sites throughout the world have shown that not only are they able to occasionally exploit these habitats for food or use them as temporary refugia, but they are also able to live constantly there.

The vent-endemic species come from different clades, indicating that the evolutionary adaptations to the vent environment evolved independently more than once in evolutionary history. From the few comparative studies conducted on some vent species, it is clear that the responses to high temperatures, low oxygen and toxicity of vent fluids may vary across species. One of the key adaptations seems to be the ability of haemoglobin to bind effectively to oxygen and simultaneously purify from the hydrogen sulphide. Yet, more studies are needed, especially concerning genera with both vent-endemic and non-vent-endemic species, to provide more insights into the evolution of these adaptations in the singular lineages and related species.

The adaptations are also reflected in ecological preferences and life-strategies, as different species colonised different niches and can probably use the series of vent sites for successful dispersal and thus cope with the transient nature of vent fields. However, thorough genetic analysis may bring more insights into the kinship between the vent-endemic species, possibly uncovering cryptic species and convergent evolutionary adaptations, and answer the distribution pathways.

Lastly, more thorough studies on vent ichthyofauna would contribute to understanding the overall ecology and interdependence between these ecosystems and the surrounding deep-sea environment. This is important, especially nowadays, when plans on deep-sea mining of sulphide nodules present the risk of losing part of the biodiversity before fully understanding the consequences of such loss.

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