



# As little as we know: current understanding and future outlook of benthic tanaid diversity and distribution in the Clarion–Clipperton Zone (CCZ)

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## Abstract

In the present Paper, we provide an overview of the diversity and distribution of benthic tanaid crustaceans, a dominant macrofaunal taxon, found in 4000 to 6000 m water depth in the Clarion–Clipperton Zone (CCZ) (north-eastern Pacific). There is increasing recognition that the CCZ is a potentially promising area for minerals supply through polymetallic nodules, with abundance estimates in the magnitude of billions of tons, representing significant economic potential involving metals such as nickel, cobalt, manganese, and copper. In the CCZ, Tanaidacea (called tanaids) are represented by 33 formally described species. With the current sampling effort, many of the taxa found in the CCZ are represented by one or two individuals (58%), with up to 70% found in one surveyed contract area. Their spatial distribution and abundances are influenced by a combination of environmental factors, including water depth, sediment type, and food availability. Our study, including datasets from various sources, highlights several challenges, including scarce and uneven sampling efforts, the use of non-standardised sampling protocols, and limited collaboration between scientists, contractors, and other stakeholders. Additionally, a significant number of species that are new to science further complicate biodiversity assessment. To improve our understanding of the diversity of tanaids in the CCZ, we suggest increasing sampling efforts in a standardised manner, increasing taxonomic studies, as well as facilitating the exchange of samples and data among scientists and contractors. This increased knowledge can contribute to appropriate environmental management measures to conserve deep-sea biodiversity of the CCZ.

**Keywords** Tanaidacea · Peracarida · Polymetallic nodules · Biodiversity · Deep-sea mining · Macrobenthos · Central Pacific

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## Introduction

### Tanaidacea in the Clarion–Clipperton Zone (CCZ) and other Pacific regions—state-of-the-art

Tanaidacea (tanaids) are peracarid crustaceans that represent an abundant and diverse element of benthic assemblages in the Clarion–Clipperton Zone (CCZ), which, together with Polychaeta and Isopoda, make up the core of macrofaunal communities (Washburn et al. 2021; Pasotti et al. 2021). They are found worldwide in marine benthic ecosystems at practically all depths. Most of them are small-sized, measuring 2–3 mm in body length. In terms of morphology, ecology, and lifestyle, they exhibit significant levels of diversity (Błażewicz-Paszkowycz et al. 2012), covering a wide spectrum of lifestyles, from free-living (e.g., Neotanaisidae Gardiner, 1975; (Fig. 1) to burrowing forms (e.g., Apseudomorpha [Kakui and Fujiwara 2020]), or tube-dwelling organisms (e.g., Tanaidomorpha [Hassack and Holdich 1987; Kakui 2021]). Despite their high diversity and relative abundance (Brandt et al. 2015a; McCallum et al. 2015), the understanding of their biogeography remains limited, with only a small proportion (~2–3%) of their estimated total diversity documented to date. So far, approximately only 1300 species in total have been formally described (WoRMS Editorial Board 2023), and only 410 of these (31%) occur below the continental slope and are classified as deep-sea taxa (Glover et al. 2024). The hemisessile lifestyle of most tanaids renders this taxon suitable for investigating biodiversity patterns since they exhibit restricted mobility, especially during certain life stages (Johnson and Attramadal 1982). As they are associated with the sediment substrate, they are directly influenced by local environmental conditions. This dependency makes them valuable indicators of small-scale



**Fig. 1** Male of *Neotanais* sp. on a polymetallic nodule captured during an ROV operation in the Interoceanmetal Joint Organization contract area (IOM) claim area during the SO239 cruise to the Clarion–Clipperton Zone (CCZ) for the complementing JPIOceans project "Ecological Aspects of Deep-Sea Mining" (2015) © GEOMAR, Germany

habitat variations, offering insights into microhabitat biodiversity patterns, but also on anthropogenic impacts, such as those resulting from habitat alteration or climate change (Larsen 2005; Błażewicz-Paszkowycz et al. 2012).

The understanding of the diversity and community structure of deep-sea tanaids in the Pacific is limited (Table 1). Despite research efforts, extending as far back as to the HMS *Challenger* voyage (1872–1876), notable knowledge gaps persist (Smith et al. 2020; Rabone et al. 2023). The significance of that first expedition exploring the Pacific seafloor lies in the discovery of the first deep-water tanaid species, *Typhlotanais brachyurus* Beddard 1886, not far from the CCZ, at a depth of 3750 m (Beddard 1886; Błażewicz-Paszkowycz 2005). Further contributions to the understanding of tanaids in the Pacific were not made until a century later, with research focused predominantly on peripheral regions of the Pacific, such as the Kuril–Kamchatka and Aleutian Trenches in addition to relevant adjacent areas (e.g., Kudinova-Pasternak 1970, 1973, 1976). Those studies were later supplemented by a series of Japanese and joint German–Russian expeditions, which revisited these regions and explored also the Sea of Japan and the Sea of Okhotsk, as well as the Japan, Kuril–Kamchatka and Aleutian Trenches (Table 1).

### Exploration of the CCZ with a focus on tanaids

The CCZ is a vast expanse of abyssal plain located in the north-eastern Pacific spanning approximately six million km<sup>2</sup>, at depths ranging from 4000 to 6000 m. This region is renowned for its abundant deposits of polymetallic nodules, which contain valuable metals, including manganese, nickel, copper, cobalt, and rare earth elements (Thiel 2001; Belkin et al. 2021), all of which are currently in high demand for the energy transition away from fossil fuels (Tisserant and Pauliuk 2016; Campbell 2020). As a result, the CCZ is considered as a highly promising area for mineral extraction, with estimates suggesting the presence of billions of tons of these nodules and therefore significant economic potential (Glasby 2000).

The CCZ is located in the Area Beyond National Jurisdiction, also known as “the Area,” i.e., the seafloor beyond the (extended) continental shelf, where activities related to mineral exploration and extraction are regulated by the International Seabed Authority (ISA). In accordance with the legal framework established under the United Nations Convention on the Law of the Sea (UNCLOS), the ISA manages and regulates current exploration and future exploitation of mineral resources in the CCZ and other regions, aiming at ensuring a responsible and sustainable use of its mineral resources whilst also protecting the marine environment. To reconcile resource extraction with environmental conservation, the ISA has designated Areas of Particular

**Table 1** Overview of advances in knowledge on Tanaidacea research in the CCZ and North Pacific. CCZ—Clarion–Clipperton Zone; DOMES A—Deep-sea mining Environmental Studies); ECHO1—referred to as DOMES site C; JPIO—Joint Programming Initiative Healthy and Productive Seas and Oceans “Ecological Aspects of Deep-Sea Mining” completed during RV *Sonne* expedition SO239; GSRNOD15A and GSRNOD17—expeditions to GSR contract area in 2015 and 2017; KODOS—Korea Deep Ocean Study; KuramBIO I and II—Kuril–Kamchatka Biodiversity—German-Russian Expedition exploring the Kuril–Kamchatka Trench and adjacent area completed during RV *Sonne* expeditions (SO223, SO250); SoJaBio—The Russian-German deep-sea expedition to the Sea of Japan onboard of the R/V *Akademik Lavrentyev* (AK51); SokhoBio—The Russian-German deep-sea expedition exploring Sea of Okhotsk onboard of the R/V *Akademik Lavrentyev* (AK71); BC—box corer; EBS—epibenthic sledge

Region	Region/expedition	Year	Depth [m]	Gear	n samples	n ind	n species	New species	Singletons	%	Doubletons	%	Density	References
Central Pacific	DOMES Site A	1977–1978	4900–5200	BC (USNEL)	26	371	77	77	21	27	8	10	29.27	Wilson (1987)
	DOMES Site C and ECHO 1	1983	4480–4567	BC	15	181	77	77	21	27	6	8	48.8	Wilson (1987)
	DOMES sites A, C, PRA	1977–1978, 1983, 1989	4480–5200	BC	21 (3 new)	439							29.3–48.8	Wilson (2017)
	GSRNOD15A; GSRNOD17	2015, 2017	4420–4591	BC	10	62	28		16	57	5	18		De Smet et al. (2017); Passotti et al. (2021); this study
	KODOS	2012–2014	4628–5278	BC	36		29							Yu et al. (2018)
NW Pacific	JPIO	2010	3405–4393	BC	74	858	98	84	45	3	3			Blazewicz et al. (2019a, b); Washburn et al. (2021) This study
	Mangan + JPIO; GSR	2015	4093–5030	BC, EBS	20	1220								
	Sea of Japan (RV <i>Vijaz</i> )	1966, 1976	100–3350	Trawl	31	600	10	5	0	0	0			Kudinova-Pasternak (1984)
	Kuril-Kamchatka Tr. (KuramBIO I+II)	2012 and 2016	5120–9584	EBS	38	2467	9	9	0	1	1			Jakiel et al. (2020); Gellert et al. (2022); unpublished
	Kuril-Kamchatka Tr. (Japan Expedition)	1954, 1955, 1958, 1966	180–6580	Trawl	23	242	37	23	19	3	3			Blazewicz et al. (2015) Kudinova-Pasternak (1966, 1970, 1976)
	Kuril-Kamchatka Tr. (Japan Expedition)	2001	537–5664	Trawl	23	138	27	21	4	4	4			Larsen and Shimomura (2007)
	Sea of Japan (SoJaBio)	2010	455–3666	EBS	12	3288	14	9	2	0	0			Blazewicz-Paszkowycz et al. (2013); Golovan et al. (2013)
	Sea of Okhotsk (SokhoBio)	2015	1696–4579	EBS	19	2072	46							Stepień et al. (2019)
	Aleuts Is + Aleutian Tr. (RV <i>Vijaz</i> )	1950	180–6520	Various	26	658	34	9	11	7	7			Kudinova-Pasternak, (1973)

Environmental Interest (APEIs) Within the CCZ. These are regions set aside from mining contracts and are designated to protect representative habitats and ensure the functionality of deep-sea ecosystems. By the end of 2024, the ISA has awarded a total of 31 contracts for the exploration of polymetallic nodules, all of them in the CCZ, with the exception of one in the Indian Ocean ([www.isa.org.jm](http://www.isa.org.jm), consulted on 19/11/2024). To date, no contracts for exploitation exist. Exploration contractors have various obligations, including the carrying out and reporting of environmental baseline studies and Environmental Impact Assessments (EIAs) for certain exploration activities such as test mining or testing mining components (ISBA/25/LTC/6/Rev.3). Through comprehensive collections of robust biological, geological, and environmental baseline data, these assessments evaluate the risk and the effect of potential environmental and ecological impacts of their operations, including any effects on deep-sea ecosystem functioning and biodiversity.

Several studies have revealed the low biomass, yet high biodiversity found in CCZ sediments (De Smet et al. 2017; Yu et al. 2018; Macheriotou et al. 2020; Pape et al. 2021; Pasotti et al. 2021; Rabone et al. 2023; Uhlenkott et al. 2023). The studied benthic ecosystems in the region support a high number of abyssal potentially endemic taxa, many of which are represented by single or just a few individuals in the samples taken and are unknown to science. The reportedly high degree of endemism and/or potential/localised rarity for many benthic CCZ taxa may make these benthic ecosystems particularly sensitive to natural and anthropogenic disturbances (Gollner et al. 2015, 2017; Vanreusel et al. 2016; Amon et al. 2016; Simon-Lledó et al. 2019). This highlights the importance of establishing appropriate environmental management measures, such as a network of representative set-aside areas. On the other hand, high biodiversity may provide some overall resistance/resilience for biological communities, and with respect to rarity, it is possible that the low-numbered species are in fact widespread, but have infrequent distributions, and/or they may be locally rare. Like any extractive activity, long-lasting effects on the structure and diversity of ecosystems, where mining occurs, can be expected (Wilson 2017; Gollner et al. 2017; Macheriotou et al. 2020; Lins et al. 2021). In the deepsea, a slow recovery process is also anticipated (Gollner et al. 2017).

The first data on peracarid deep-sea communities originated from research initiatives financed by the United States' National Oceanic and Atmospheric Administration (NOAA) that took place between 1970 and 1992, where tanaids and isopods were reported as the two most diverse peracarid groups. In total, 83 tanaid morphospecies were recorded from two locations known as DOMES A (Deep-sea Mining Environmental Studies) and ECHO 1 (Wilson 2017). Similar to isopods, the tanaid community was found to be a rich and diverse community ( $37.2 \pm 26.7$  ind./0.25m<sup>2</sup>) with an exceptionally

large percentage of new-to-science species and a number of taxa identified from specimens that appeared as singletons or doubletons (Table 1). Furthermore, in DOMES A, resampled with a 1-year gap, 77 morphospecies were recorded, with 66 morphospecies (85%) recorded during both campaigns.

The most recent biological studies within the CCZ have led to a considerable advance in our understanding of tanaids in the Area (Washburn et al. 2021). The “Ecological Aspects of Deep-Sea Mining” program under the umbrella of The Joint Programming Initiative Healthy and Productive Seas and Oceans (JPIO), which started in 2015 (Martínez Arbizu and Haeckel 2015), procured a substantial biological collection, contributing 40% of tanaid specimens to the overall count (Table 2; Fig. 2). Moreover, a meta-analysis of data coming from this and other contractor-funded and independent research programs, encompassing data from ten designated contract areas and three APEIs, has resulted in the compilation of 5368 individual tanaid records for the CCZ, assembled into a comprehensive database (Rabone et al. 2023). A significant portion of these collections (78%) has been successfully identified to family level, demonstrating substantial progress in taxonomic characterisation, but only a small fraction (2.8%) has been identified to (morpho) species level (Fig. 3). Nevertheless, the JPIO SO239 “Ecological Aspects of Deep-Sea Mining” campaign procured a substantial biological collection and enabled the acquisition of initial barcoding data for abyssal tanaids as well as the first genetic data for the families Agathotanaidae, Caudaloniae, Paranarthurellidae, and Pseudotanaidae (Błażewicz et al. 2019b, 2024; Jakiel et al. 2019; Stępień et al. 2022b, a).

## Study objective

The aim of this study is to provide a comprehensive synthesis of the available data on Tanaidacea within the CCZ. Additionally, we used data from a better-known region in the Northwest Pacific (Sea of Japan, Sea of Okhotsk, and Kuril-Kamchatka adjacent area) as a point of comparison to evaluate their diversity and spatial distribution, particularly focusing on endemism and rarity.

Furthermore, we assessed the efficacy and discrepancies in collecting tanaid fauna in the CCZ using two standardised sampling devices: the box core (BC) and epibenthic sledge (EBS). Both types of sampling equipment are commonly used in deep-sea research (Frutos et al. 2022). Given the recent application of these recommended methodologies for investigating tanaids and collecting data on their community assemblages in the CCZ and NW Pacific, we aim to develop a model that explains the patterns of tanaid abundance and diversity across longitudinal gradients. Furthermore, material suitable for genetic analysis was gathered during the JPIO expedition SO239 in 2015 to uncover genetic diversity and phylogeographic patterns of tanaids in the CCZ. Finally, our

objective is to identify remaining gaps in our understanding of CCZ tanaid communities, encompassing areas such as taxonomy and biogeography, with an aim to offer recommendations for addressing these gaps in future research initiatives.

## Material and methods

### Data collection

Our analyses build on previous studies, integrating all data collected from the scientific literature concerning diversity and population connectivity of Tanaids in the CCZ (Larsen 2011a, b; Wi et al. 2015b, a; Błażewicz et al. 2019a, b; Jakiel et al. 2019; 2022; Chim and Tong 2020; Gellert et al. 2022) in addition to outlying regions located in the NW Pacific Ocean, e.g., Sea of Okhotsk (SoO), Sea of Japan (SoJ), Kuril-Kamchatka Trench (KKT), and Aleutian trench (AT) (Kudinova-Pasternak 1970, 1973, 1976; Józwiak and Błażewicz-Paszkowycz 2007; Larsen 2011a; Błażewicz-Paszkowycz et al. 2015b; Błażewicz et al. 2019a; Stępień et al. 2019; Chim and Tong 2020; Jakiel et al. 2020; Washburn et al. 2021; Pasotti et al. 2021). In the CCZ, the tanaid collection was obtained from macrobenthic samples taken by box corer (BC) and epibenthic sledge (EBS) during four expeditions conducted between 2010 and 2017: (1) the MANGAN expedition (RV *Sonne*: SO205; 670 tanaid specimens) in 2010, in the eastern Bundesanstalt für Geowissenschaften und Rohstoffe (BGR, Germany) (Rühlemann et al. 2010); (2) the pilot action Environmental impacts and risks of deep-sea mining program (“MiningImpact”) (RV *Sonne*: SO239; 1098 tanaid specimens) in 2015, as part of the Joint Programming Initiative Healthy and Productive Seas and Oceans (JPI Oceans) sampling in the four exploration contract areas of BGR, the Interoceanmetal (IOM: jointly Bulgaria, Cuba, Czech Republic, Poland, Russian Federation, and Slovakia), GSR (Global Sea Mineral Resources, Belgium), and Institut Français de Recherche pour l’Exploitation de la Mer (Ifremer, France), as well as in one APEI (APEI3) (Martínez Arbizu and Haeckel 2015); (3) the GSRNOD15A (Pape et al. 2016; De Smet et al. 2017); and (4) and the GSRNOD17 expeditions (396 tanaid specimens) (Pape et al. 2018; Pasotti et al. 2021) to the GSR contract area in 2015 and in 2017, respectively. In total, 2164 tanaid specimens were identified from 19 EBS and 73 BC samples (metadata provided in Table 2). The distribution of stations and gear deployments are presented in Fig. 4.

### Sampling devices and sample processing onboard

In this study, box corer (BC) deployments sampled areas With a surface of 0.25 m<sup>2</sup>. Unless otherwise specified,

sample processing followed this protocol: upon arrival on deck, the seawater above the sediment was removed using a hose and sieved through a 300-µm mesh. Next, a photo of the BC sample surface was taken. Visible biota on the surface, whether attached to the nodules or present on the sediment, were removed and fixed separately in DESS (Yoder et al. 2006) or 96% ethanol. Nodules were carefully removed, washed to eliminate surface sediment, measured, and weighed. The sediment Within the BC was then divided into three depth layers: 0–3 cm, 3–5 cm, and 5–10 cm. Each layer was transferred into cold filtered seawater (2–4 °C), carefully elutriated, sieved through a 300-µm mesh, and fixed separately. During the JPIO expedition (SO239), the top layer (0–3 cm) was promptly sorted and specimens were fixed individually in 96% undenatured ethanol. The remaining layers were fixed in 4% formalin and later transferred to 80% denatured ethanol. During the GSRNOD15A expedition, the top 0–3-cm layer was bulk-fixed in 96% undenatured ethanol and stored at –20 °C, while the deeper layers were initially stored in 10% formaldehyde for 48 h before being transferred to 80% undenatured ethanol. In GSRNOD17, all sediment layers were stored in 96% undenatured ethanol at –20 °C. Some sorting of the BC material was carried out onboard (Ifremer in Plouzané, France; Senckenberg am Meer—DZMB in Wilhelmshaven, Germany during the JPIO expedition), although for the most part, it was conducted later in the laboratories at the home institutions (Marine Biology Research Group Laboratory facilities in Ghent, Belgium for the GRSNOD15A and GSRNOD17 expeditions).

The construction and function of the epibenthic sledge (EBS) are described in detail by Brenke (2005). In summary, the EBS consists of two nets, a lower epinet, and an upper supranet, With a mesh size of 500 µm and cod ends of 300 µm. A door with an opening/closing mechanism is located in front of the nets, so that when the sledge touches the seafloor, the door opens, and then closes again in the water column to minimise contamination with planktonic organisms. To prevent nodules from entering the nets and damaging the samples, a metal grid is placed in front of the mesh openings. In warm, tropical waters, a box surrounding the cod ends holds cold deep-sea water to maintain a “continuous cooling chain”, recommended for ensuring the samples remain viable for successful genetic analyses (Riehl et al. 2014).

To standardise sampling for faunal density assessment (ind. per 1000 m<sup>2</sup>) during the trawled transects of 1000 m, during the JPIO MiningImpact (SO239) deployments, the trawling distance ( $d$ ) was calculated. The EBS sampling unit is 1-m wide, and the formula used for the calculation is as follows:  $d = \frac{V1 \times t1 + V2 \times t2 + V3 \times t3}{1}$ , where  $V1$  is ship velocity during trawling (knots),  $t1$  is trawling time (knots),  $V2$  is ship velocity during haul,  $t2$  is hauling time (sledge off bottom),  $V3$  is winch velocity, and  $t3$  is hauling time (sledge off bottom).

**Table 2** Station list of sampling sites in the Clarion–Clipperton Zone (CCZ) and DISCOL area (Peru basin, SE Pacific) where tanaid specimens were obtained including contractor area (CA), gear type, date, position [degrees] and depth [m]). APEI: area of particular environmental interest, BGR: eastern German CA; GSR: Global Sea Mineral Resources NV C, \_E: east, \_W: west; EBS —epibenthic sledge; BC —box corer

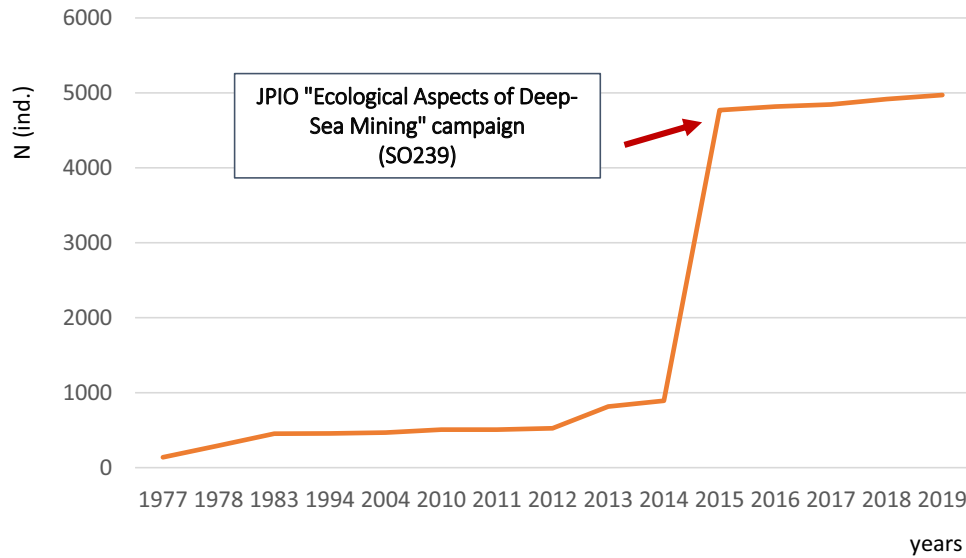
Expedition	Area	Gear	Station	Dare	Latitude (N)	Longitude (N)	
GSRNOD15A	GSR_E	BC	BC011-BIO	21.09.2015	13°53'38.54	123°17'49.34	
	GSR_E	BC	BC012-GEO	21.09.2015	13°53'52.80	123°16'55.20	
	GSR_E	BC	BC013-BIO	21.09.2015	13°53'17.45	123°17'19.39	
	GSR_E	BC	BC014-GEO	22.09.2015	13°48'25.20	123°17'24.00	
	GSR_E	BC	BC015-BIO	22.09.2015	13°52'59.66	123°16'55.96	
	GSR_E	BC	BC016-GEO	22.09.2015	13°56'38.40	123°18'57.60	
	GSR_W	BC	BC017-GEO	27.09.2015	14°4'55.20	125°53'31.20	
	GSR_W	BC	BC018-BIO	27.09.2015	14°6'44.93	125°52'17.29	
	GSR_W	BC	BC019-BIO	27.09.2015	14°7'3.65	125°52'46.38	
	GSR_W	BC	BC020-GEO	28.09.2015	14°9'43.20	125°53'31.20	
	GSR_W	BC	BC021-BIO	28.09.2015	14°6'15.66	125°52'39.76	
	GSR_W	BC	BC022-GEO	28.09.2015	14°1'40.80	125°51'39.60	
	GSR_W	BC	BC023-GEO	30.09.2015	14°8'9.60	125°52'4.80	
	GSR_W	BC	BC024-BIO	1.10.2015	14°3'20.07	125°55'35.27	
	GSR_W	BC	BC025-GEO	2.10.2015	14°2'9.60	125°55'30.00	
	GSR_W	BC	BC026-BIO	4.10.2015	14°42'23.08	125°27'40.25	
	GSR_W	BC	BC027-BIO	4.10.2015	14°42'22.86	125°26'32.75	
	GSR_W	BC	BC028-GEO	5.10.2015	14°42'21.60	125°25'15.60	
	GSR_W	BC	BC029-BIO	5.10.2015	14°42'22.90	125°27'5.90	
	GSR_W	BC	BC030-GEO	6.10.2015	14°38'52.80	125°27'14.40	
	GSR_W	BC	BC031-GEO	6.10.2015	14°45'50.40	125°25'4.80	
	GSR_W	BC	BC032-GEO	9.10.2015	14°44'34.80	125°26'42.00	
	GSR_W	BC	BC034-GEO	8.10.2015	14°44'20.40	125°25'15.60	
	GSR_W	BC	BC035-BIO	9.10.2015	14°38'50.82	125°24'31.82	
	GSR_W	BC	BC036-BIO	9.10.2015	14°40'17.40	125°27'21.82	
	GSRNOD17	GSR_W	BC	BC035-BIO	9.10.2015	14°38'50.82	125°24'31.82
		GSR_W	BC	BC037-BIO	26.05.2017	14°04'02.81	125°55'44.40
		GSR_W	BC	BC039-BIO	27.05.2017	14°03'32.45	125°55'15.66
GSR_W		BC	BC042-BIO	28.05.2017	14°02'09.48	125°55'29.03	
GSR_W		BC	BC043-BIO	28.05.2017	14°02'01.97	125°55'44.47	
GSR_W		BC	BC045-BIO	29.05.2017	14°01'44.58	125°55'31.03	
GSR_W		BC	BC050-BIO	29.05.2017	14°06'16.68	125°52'41.482	
GSR_W		BC	BC052-BIO	30.05.2017	14°06'16.68	125°52'41.42	
GSR_W		BC	BC054-BIO	31.05.2017	14°07'04.34	125°52'45.42	
GSR_W		BC	BC056-BIO	2.06.2017	14°02'58.50	125°55'19.39	
GSR_W		BC	BC057-BIO	3.06.2017	14°02'08.90	125°54'35.58	
GSR_E		BC	BC060-BIO	21.06.2017	13°53'15.74	123°17'18.87	
GSR_E		BC	BC063-BIO	22.06.2017	13°52'55.24	123°18'20.37	
GSR_E		BC	BC065-BIO	26.06.2017	13°52'55.24	123°18'20.37	
JPIO	APEI3	BC	JPIO_195	21.04.2015	18°47.75	128°21.73	
	APEI3	BC	JPIO_196	21.04.2015	18°47.83	128°20.77	
	APEI3	BC	JPIO_203	23.04.2015	18°46.44	128°21.19	
	APEI3	BC	JPIO_204	23.04.2015	18°46.40	128°20.17	
	APEI3	BC	JPIO_209	24.04.2015	18°47.07	128°22.35	
	APEI3	EBS	JPIO_188	21.04.2015	18°44.81	128°21.87	
	APEI3	EBS	JPIO_192	21.04.2015	18°44.81	128°21.87	
	APEI3	EBS	JPIO_197	22.04.2015	18°48.66	128°22.75	
	APEI3	EBS	JPIO_210	24.04.2015	18°49.27	128°25.80	
	BGR	BC	JPIO_12	20.03.2015	11°50.83	117°3.56	
	BGR	BC	JPIO_15	21.03.2015	11°50.66	117°3.13	
	BGR	BC	JPIO_16	21.03.2015	11°51.44	117°3.12	

**Table 2** (continued)

Expedition	Area	Gear	Station	Dare	Latitude (N)	Longitude (N)
	BGR	BC	JPIO_21	22.03.2015	11°51.21	117°3.57
	BGR	BC	JPIO_23	22.03.2015	11°51.00	117°3.16
	BGR	BC	JPIO_51	27.03.2015	11°49.42	117°31.42
	BGR	BC	JPIO_57	28.03.2015	11°48.45	117°31.46
	BGR	BC	JPIO_58	28.03.2015	11°49.23	117°32.50
	BGR	BC	JPIO_60	29.03.2015	11°48.46	117°33.02
	BGR	EBS	JPIO_20	22.03.2015	11°49.81	117°00.28
	BGR	EBS	JPIO_24	22.03.2015	11°51.52	117°01.19
	BGR	EBS	JPIO_50	27.03.2015	11°49.92	117°29.31
	BGR	EBS	JPIO_59	28.03.2015	11°48.55	117°29.03
	IOM	BC	JPIO_105	5.04.2015	11°4.27	119°39.32
	IOM	BC	JPIO_106	5.04.2015	11°4.30	119°39.29
	IOM	BC	JPIO_107	5.04.2015	11°4.33	119°39.27
	IOM	BC	JPIO_88	2.04.2015	11°4.74	119°39.53
	IOM	BC	JPIO_89	2.04.2015	11°4.55	119°39.65
	IOM	BC	JPIO_90	3.04.2015	11°4.44	119°39.85
	IOM	BC	JPIO_94	3.04.2015	11°4.42	119°39.33
	IOM	BC	JPIO_95	3.04.2015	11°4.24	119°39.20
	IOM	BC	JPIO_97	4.04.2015	11°4.37	119°39.37
	IOM	EBS	JPIO_81	01.04.2015	11°03.97	119°37.67
	IOM	EBS	JPIO_99	04.04.2015	11°02.61	119°39.52
	GSR_E	BC	JPIO_119	08.04.2015	13°51.55	123°15.16
	GSR_E	BC	JPIO_127	9.04.2015	13°50.66	123°14.76
	GSR_E	BC	JPIO_128	9.04.2015	13°51.10	123°15.12
	GSR_E	BC	JPIO_137	11.04.2015	13°51.36	123°14.28
	GSR_E	BC	JPIO_138	11.04.2015	13°50.89	123°14.08
	GSR_E	EBS	JPIO_117	07.04.2015	13°52.39	123°15.30
	GSR_E	EBS	JPIO_118	08.04.2015	13°52.38	123°15.09
	GSR_E	EBS	JPIO_133	10.04.2015	13°50.98	123°15.07
	Ifremer	BC	JPIO_159	15.04.2015	14°2.94	130°8.06
	Ifremer	BC	JPIO_162	16.04.2015	14°2.56	130°7.33
	Ifremer	BC	JPIO_169	17.04.2015	14°2.53	130°7.64
	Ifremer	BC	JPIO_180	18.04.2015	14°2.50	130°8.18
	Ifremer	BC	JPIO_181	18.04.2015	14°2.79	130°8.49
	Ifremer	BC	JPIO_182	18.04.2015	14°2.54	130°7.65
	Ifremer	EBS	JPIO_158	15.04.2015	14°03.41	130°07.99
	Ifremer	EBS	JPIO_171	17.04.2015	14°02.68	130°05.97
	Ifremer	EBS	JPIO_181	18.04.2015	14°2.79	130°08.49
MANGAN	BGR	EBS	MAN_12	28.04.2010	11°18.55	119°15.08
	BGR	EBS	MAN_26	2.05.2010	11°34.65	116°12.39
	BGR	EBS	MAN_40	5.05.2010	11°48.26	116°49.42
	BGR	EBS	MAN_47	7.05.2010	11°57.27	116°58.69
	BGR	EBS	MAN_61	16.05.2010	13°10.44	118°06.36

The same standard sample processing procedure was followed for all expeditions: after retrieving the EBS on board, the nets were rinsed with seawater up to the cod. The cod ends were removed and immediately transferred to a cold room (~2–4 °C). Epinet and supranet samples were processed separately. Elutriation With filtered precooled sea

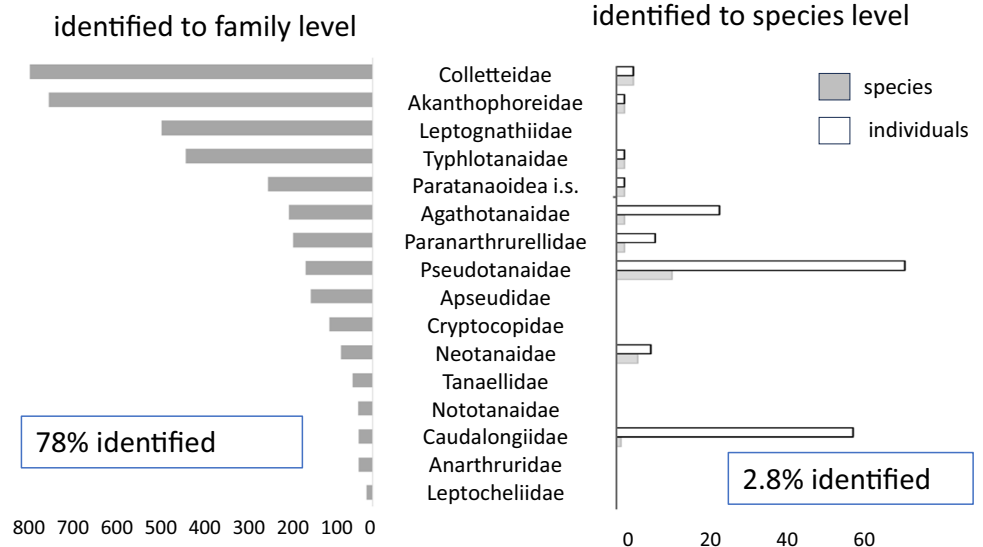
water was performed, and the macrofauna was placed on a 300- $\mu$ m mesh. Each sample was preserved in 96% precooled undenatured ethanol and stored at –20 °C for at least 48 h (Riehl et al. 2014). Macrofauna samples were sorted on board and at DZMB using stereomicroscopes to higher taxonomic level (phylum, class, order) and stored



**Fig. 2** Cumulative number of tanaidacean individuals collected over the course of studies across ten designated contract areas in the Clarion–Clipperton Zone (CCZ): BGR, eastern German contract area; GSR, Global Sea Mineral Resources NV; Ifremer, L’Institut Français de Recherche pour l’Exploitation de la Mer (French contract area); IOM, Interoceanmetal Joint Organization contract area; OMS, Ocean

Mineral Singapore Pte. Ltd. (Singapore contract area); UK Seabed Resources Ltd. (UK contract areas); KR, contract area of the Korean Republic; DORD, Deep Ocean Resources Development Co. Ltd. (Japanese contract area); YUZM, JSC Yuzhmoregeologiya (contract area of the Russian federation) and three Areas of Particular Environmental Interest (APEIs) from (Rabone et al. 2023)

**Fig. 3** State of knowledge in tanaids collected in the CCZ with number of the specimens identified to family and species level. Data is derived from ten contractor regions and three Areas of Particular Environmental Interest (APEI)

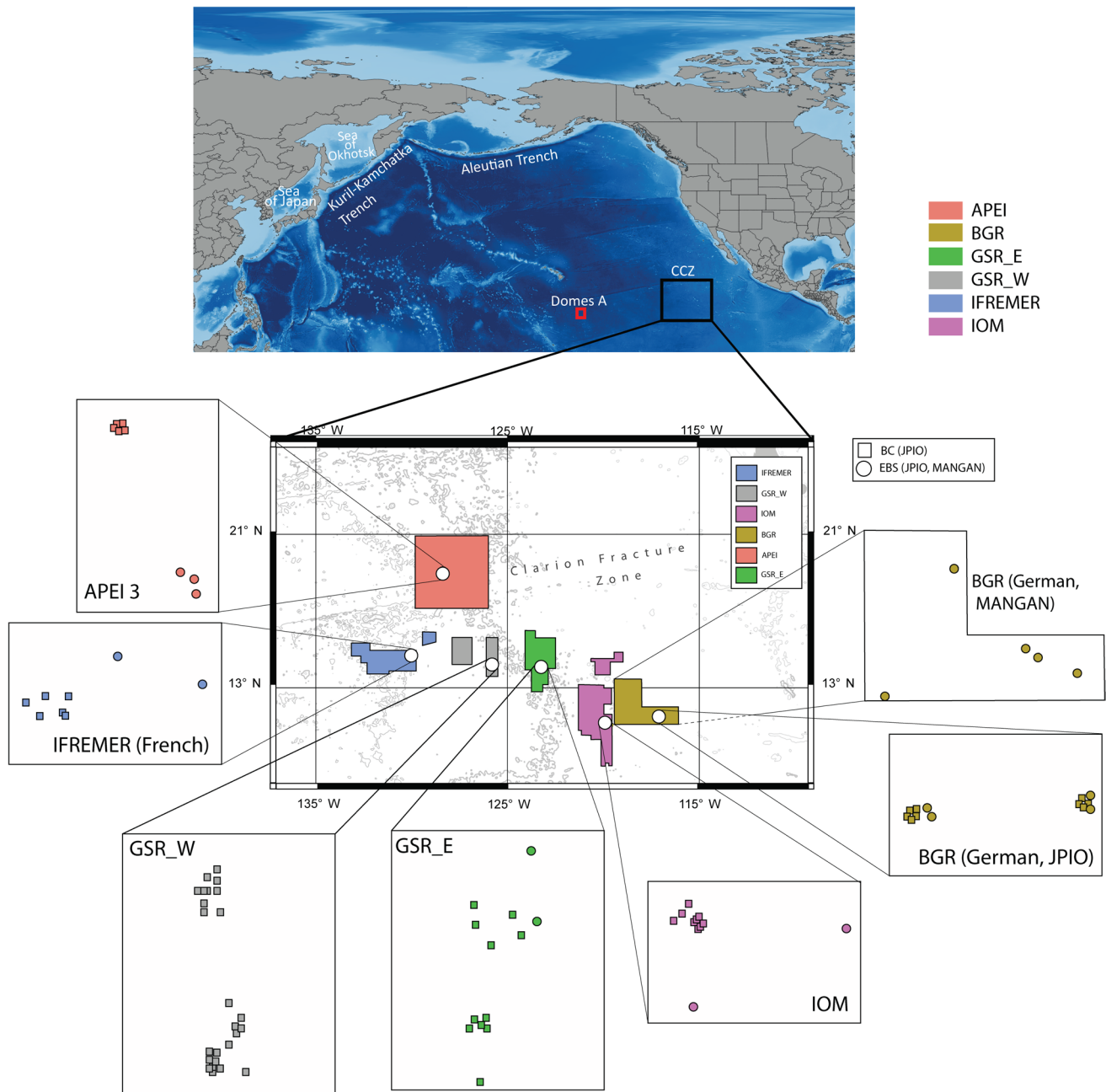


in 96% undenatured ethanol until further species analyses and annotation.

**Abundance and alpha diversity patterns in the CCZ and other Pacific regions**

To search for the potential shift in tanaid diversity between the CCZ, in the Central Pacific, and other

deep-sea regions in the Pacific, the total abundance of tanaids (including unidentified specimens and juvenile stages—mancas) and family richness (i.e., number of tanaid families, excluding unidentified specimens) were modelled with Gamma generalised additive models (GAMs) with the function *gam* of the package “mgcv” v.1.9 (Wood 2011). The different deep-sea regions (i.e., Sea of Japan, Sea of Okhotsk, Kuril-Kamchatka Trench,



**Fig. 4** Map indicating the sampling stations during the MANGAN (2010) and EcoResponse/SO239 (2015) projects. BC, box corer; EBS, epibenthic sledge; APEI, Area of Particular Environmental Interest; BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, eastern BGR; GSR, Global Sea Mineral Resources NV; Ifremer, L’Institut Français de Recherche pour l’Exploitation de la Mer (French contract area); IOM, Interoceanmetal Joint Organization contract area

and the CCZ), in addition to the gear used (i.e., only BC and EBS), were included as factors, and sampling depth as the smooth term. The basis dimensions of the smooth (i.e., 3) were checked, and adjusted accordingly, with the function *gam.check* from the “mgcv” package.

When necessary, post hoc comparisons were performed with the *emmeans* function and Bonferroni adjustments from the “emmeans” package v.1.10.0 (Lenth 2022). All fitted models were validated by simulating their residuals using the package “DHARMA” v.0.4.6 (Hartig 2022).

**Beta diversity patterns in the CCZ and other Pacific regions**

First, total tanaid abundance, species richness, and the Shannon–Wiener index were calculated for each sample with

the *specnumber* and *diversity* functions of the R package “vegan” v.4.3.0 (Oksanen et al. 2022). After visually checking for extreme outliers for each index, which were removed to ensure that the analysis reflects general patterns rather than anomalies, a generalised linear model (GLM) was run with *glmmTMB* from the “homonymous” package v.1.1.8 (Brooks et al. 2017). For all models, the different (sub)areas of the CCZ (i.e., BGR, IOM, GSR\_E, GSR\_W, Ifremer, APEI3) were included together with the gear (i.e., BC or EBS) as factors. Given the integer nature of the dataset, a Poisson family distribution was used for species richness and total abundance, while a Gaussian distribution was used for the Shannon–Wiener diversity index. The *Anova* function of the package “car” v.3.2 was used to run the Wald Chi-square test for each factor through analysis of deviance (Fox and Weisberg 2019). Family richness was also compared between areas and gear by means of a permutational multivariate analysis of covariance (PERMANCOVA) using area and gear (and their interaction) as factors and the longitude of the sampling station as a covariate with the function *adonis2* With 999 permutations (vegan package). To account for the number of species (but not their abundance), the Hellinger distance was used in the analysis to allow us to consider the possibility of more abundant samples (*vegdist* function of “vegan”). When necessary, a posthoc analysis was performed through *pairwise.adonis* of the “pairwiseAdonis” package With the Bonferroni correction and 999 permutations (Martinez 2017). To visualise differences, a non-metric multidimensional scaling plot (nMDS) was drawn with *metaMDS*, of the package “vegan”, using the same distance matrix. In addition, *k*-means and cluster analyses were performed to test for the possible grouping of the samples, with *fviz\_nbclust* (with *gap\_stat*) and *hcut*, respectively, of the “factoextra” package v.1.0.7 (Kassambara and Mundt 2020). Then, rarefaction curves of the species richness for each area were plotted using the R package “iNEXT” v.3.0.0 (Chao et al. 2014) to examine the effect of sampling effort and extrapolating to 40 samples, i.e., 10 more than the GSR\_W—the region with the highest sampling effort per gear).

## DNA barcoding

Representatives of tanaid morphotypes collected during the JPIO expedition in the CCZ were identified using an integrated approach with morphology and molecular barcoding. A whole specimen was taken using sterile needles as starting material for DNA extraction using Chelex (InstaGene Matrix, Bio-Rad). The cytochrome oxidase subunit I (COI)<sub>2</sub>PCR amplification was performed in a 26 µL reaction volume containing 200 nM of each primer (5 µM stock), 13 µL of 2x AccuStart II GelTrack PCR SuperMix (Quantabio), and DNA template With concentrations ranging from 9 to 23 ng/µL (based on 2 µL of sample). The final reaction volume was

adjusted With sterile water to 26 µL. COI PCR reactions were performed using two pairs of primers polyLCO and polyHCO (Carr et al. 2011), and LCO–1490 and HCO–2198 (Folmer et al. 1994) were used. PCR protocol for pair polyLCO/polyHCO were run as follows: 94 °C for 3 min, 40 cycles of 94 °C for 40 s, 42 °C for 30 s, 72 °C for 1 min, and a final elongation step of 72 °C for 10 min, while the PCR reaction with pair of primers LCO–1490 and HCO–2198 was 94 °C for 5 min, 35 cycles of 94 °C for 30 s, 50 °C for 1 min, 72 °C for 1 min, and final elongation 72 °C for 5 min. PCR purification and sequencing using forward and reverse primers were conducted by MACROGEN (Amsterdam, Netherlands). The chromatograms and sequences were then edited in Geneious Prime 2023.2.1 (<https://www.geneious.com>) and compared with the GenBank database (<https://www.ncbi.nlm.nih.gov/genbank/>) using BLAST to discard contamination from non-arthropod sources. The newly obtained sequences have been deposited in GenBank under accession numbers PX258219–PX259302; PX262632–PX262633 (Appendix 1). To complement this dataset, a total of 185 sequences, newly obtained (147) and accessible from GenBank, representing nine families (Akanthophoreidae, Apseudidae, Caudalongidae, Colletteidae, Leptognathiidae, Neotanaidae, Paranarthrurellidae, Pseudotanaidae, and Typhlotanaidae), have been aligned and used for phylogenetic analyses. *Homarus americanus* (Decapoda) was designated as the outgroup (Appendix 2). DNA analysis was performed as in Jakiel et al. (2019). Sequences were aligned using alignment option L-INSi of MAFFT62 as implemented in Geneious. Selection of the best nucleotide substitution model was performed according to the lowest Akaike information criterion (AIC) as implemented in raxmlGUI (Silvestro and Michalak 2012) and used to run a maximum likelihood phylogenetic analysis With 1000 bootstraps (Darriba et al. 2020; Edler et al. 2021).

## Species delimitation

To estimate the number of putative species, a total of 185 DNA sequences were used for the analyses. Species delimitation was settled by two different approaches: a genetic distance-based barcode-gap approach that assembles species by automatic partitioning ASAP (Puillandre et al. 2012), and a tree-based method, the general mixed Yule coalescent model-based method GMYC (Pons et al. 2006). ASAP was run With a genetic distance range of 0.005 to 0.03 with the Kimura substitution model.

The GMYC method requires an ultrametric tree, and thus, we first calculated a Bayesian phylogenetic tree for all tanaid sequences. The tree was generated in BEAST 2.6.7 (Drummond et al. 2012). Four independent runs under the lognormal relaxed molecular clock model were performed. The analysis was run for 100 million of the Markov chain Monte Carlo (MCMC) generations, sampled every 10,000

generations. The general time-reversible (GTR) evolution models with invariable sites (I) and gamma-distributed (G) rate heterogeneity for each of the partitions were set as priors based on the AIC value (Akaike 1974). Convergence of the parameters and effective sample size for the individual parameters were inspected using Tracer 1.7.2 (Rambaut et al. 2018). The tree files were combined using LogCombiner 2.6.7 (Drummond et al. 2012) after removal of the 10% burn-in phase. The consensus tree was annotated using TreeAnnotator v1. (Drummond et al. 2012) With a 15% burn-in. The consensus tree was visualised in FigTree 1.4.4 and run on a webpage (<https://species.h-its.org/gmyc/>) using the single threshold model. Results of ASAP and GMYC were visualised in Adobe Illustrator. The overall mean genetic distance and pairwise genetic distances were calculated in MEGAX (Kumar et al. 2018) using the Kimura 2-parameter (K2P) substitution model (Kimura 1980) and the standard error estimates were obtained from 1000 bootstraps.

### Microscopic imaging

All images were obtained With a confocal laser scanning microscope LSM 780 (Zeiss), as described in detail by Gellert et al. (2022). The microscope was equipped With an EC Plan-Neofluar 10x/0.30 M27 objective and an InTune tuneable excitation laser system. Ethanol-fixed specimens were stained overnight With Congo Red and acid fuchsin, and imaged in 100% glycerol. Fluorescence was excited With a 555-nm-wavelength laser line and registered in the 561–695-nm emission channel. The number of tile images collected and the optimal number of Z-frames were adjusted depending on the size of the specimen. The acquired images were then combined and presented as a maximum intensity projection, pseudo-coloured in gold, and stitched into a single image using ZEN 2012 software (Zeiss).

## Results

### Alpha and beta diversity patterns for tanaids in the CCZ and other Pacific regions

Our analyses revealed that the tanaids so far collected in the CCZ are represented by 15 families (Table 3; Figs. 3 and 5). To date, only 37 tanaid species have been described, all belonging to the suborder of the Tanaidomorpha and encompassing 20 different genera across seven families (Table 4), With clear dominance of the Colletteidae, Akanthophoreidae, Leptoganthiidae, and Typhlotanaiidae. The 37 nominal tanaid species were identified based on 185 individuals, which account for only 2.8% of all tanaids collected in the studies covered by this meta-analysis (Fig. 3). A high proportion of these taxa from the CCZ were represented by low

abundances, With 15 out of the 37 species (44.5%) and being described solely on holotypes—single specimens designated as the representative example of the species when species are formally described (The International Code of Zoological Nomenclature Art. 73.1.1.).

Approximately 58% of the tanaid specimens collected in the CCZ and identified to morphospecies level (yet to be described) were based on 1–2 individuals, With 44% of these taxa known from only one area (Fig. 6). An analysis of 143 tanaid morphospecies revealed that the GSR area within the CCZ exhibited the least degree of species overlap—i.e., in the GSR\_W area, where 34 taxa (23.8%) were identified that have not been found elsewhere With the current sampling effort, and had 18 additional taxa (12.6%) shared with GSR\_E. In contrast, APEI3 was the least diverse, hosting only 12 morphospecies (3.5%), of which three (2.1%) were not found elsewhere based on currently available data, and two were shared with GSR\_W, GSR\_E, and IOM. The highest faunal similarity was observed among the geographically proximate areas—BGR, IOM, GSR\_E, and GSR\_W—which collectively shared 46 morphospecies (32.2%). Overall, BGR, where 18 samples were collected in total, emerges as the most diverse area, characterised by both high morphospecies richness (68 morphospecies), and high variability across stations, as reflected in the highest mean number of morphospecies per station ( $12.4 \pm 4.7$ ) (Table 5). Moderate levels of species richness were observed in the IOM and APEI3 areas, With mean morphospecies values of  $9.8 \pm 3.1$  and  $9.6 \pm 3.1$ , respectively, derived from 11 and 9 samples. Similarly, GSR\_E and GSR\_W displayed comparable mean morphospecies counts ( $8.7 \pm 2.7$  and  $8.7 \pm 3.8$ , respectively). Total species richness and sampling effort differed substantially with 30 and 17 samples collected in GSR\_W and GSR\_E, respectively. In contrast, the Ifremer area exhibited the lowest mean number of morphospecies per station ( $7.5 \pm 1.6$ ) across nine samples, making it the region with the lowest diversity among those analysed. Across all areas, EBS samples consistently detected higher morphospecies richness than box corer samples although the differences were not significant, i.e., the standard deviations overlapped. (Table 5). For example, in BGR, the EBS captured  $13.0 \pm 5.3$  morphospecies per station compared to the BC ( $11.0 \pm 2.4$ ), and in IOM, EBS recorded  $11.0 \pm 3.5$  versus BC  $8.4 \pm 1.9$ . This pattern was consistent in other areas, including GSR\_E ( $10.3 \pm 2.4$  vs.  $7.9 \pm 2.4$ ). For APEI-3, the difference was significant ( $10.4 \pm 2.0$  for EBS vs.  $2.6 \pm 0.6$  for BC).

The tanaid communities recovered in the samples collected using the recommended sampling devices (BC and EBS) revealed discernible and significant differences in total individual abundance between sampling gears, With the EBS collecting more tanaid specimens than the BC i.e.,  $2.91 \pm 34.6$  versus  $1.2 \pm 2.0$ , respectively (mean  $\pm$  SD,  $p$ -value  $< 0.001$ ; Fig. 7A). The highest tanaid abundance

**Table 3** List of described tanaid species known from the (CCZ) (modified after Chim and Tong, 2020)

pecies	region/depth	reference
Agathotanaidae Lang, 1971		
<i>Agathotanais ahyongi</i> Larsen, 1999	DOMES A, 5034–5107 m	Larsen 1999
<i>Agathotanais manganicus</i> Larsen, 1999	DOMES A, 4934–5260 m	Larsen 1999
<i>Agathotanais beatae</i> Józwiak & Pełczyńska, 2022	Ifremer, BGR, IOM 4100–4977 m	Stępień 2022b
<i>Agathotanais jani</i> Józwiak & Pełczyńska, 2022	BGR, IOM, GSR; 4093–4511 m	Stępień 2022a
<i>Akanthophoreidae</i> Sieg, 1986		
<i>Stenotanais arenasi</i> Larsen, 2011	Ifremer 4835–5166 m	Larsen, 2011
<i>Tumidochelia tuberculata</i> Larsen 2011	Ifremer, 5044 m	Larsen, 2011
Caudalongiidae		
<i>Universitatotanais gandavensis</i>	BGR, IOM, GSR, 4007–5023	Błażewicz et al., 2024
<i>Facultatotanais bios</i>	BGR, IOM, GSR, 4007–5023	Błażewicz et al., 2024
Colletteidae Larsen & Wilson, 2002		
<i>Collettea aspera</i> Wi, Suh & Kim, 2015	KODOS, 4988 m	Wi, Suh & Kim, 2015
<i>Collettea eminula</i> Wi, Suh & Kim, 2015	KODOS, 5036 m	Wi, Suh & Kim, 2015
<i>Collettea longisetosa</i> Larsen 2011	Ifremer >4000 m	Larsen 2011
<i>Collettea prominentia</i> Wi, Suh & Kim, 2015	KODOS, 5155 m	Wi, Suh & Kim, 2015
Neotanaidae Lang, 1956		
<i>Neotanais brevis</i> Wi, Suh & Yu, 2015	KODOS, 5180 m	Wi, Suh & Kim, 2015
<i>Neotanais capillus</i> Wi, Suh & Yu, 2014	KODOS, 5026 m	Wi, Suh & Kim, 2014
<i>Neotanais pacificus</i> Wi, Suh & Yu, 2014	KODOS, 4934 m	Wi, Suh & Kim, 2014
<i>Neotanais triqueturus</i> Wi, Suh & Yu, 2015	KODOS, 5180 m	Wi, Suh & Kim, 2015
<i>Venusticrus thor</i> Araujo-Silva & Larsen, 2015	BGR, 4274–4986 m	
Paranarthrurellidae Błażewicz, Józwiak & Frutos, 2019		
<i>Paranarthrurella polonez</i> Błażewicz, Józwiak, 2019	IOM, 4365–4823 m	Błażewicz et al., 2019
<i>Paranarthrurella spinimaxillipeda</i> Larsen, 2011	BGR, 4259–4261 m	Larsen, 2011
Pseudotaniadae Sieg, 1976		
<i>Beksitanais apocalyptica</i> Jakiel, Palero & Błażewicz, 2019	IOM, GSR 4365–4510 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais chaplini</i> Jakiel, Palero & Błażewicz, 2019	GSR, Ifremer 4093–4946 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais chopini</i> Jakiel, Palero & Błażewicz, 2019	BGR, IOM, 3093–4401 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais gaiiae</i> Jakiel, Palero & Błażewicz, 2019	APEI3, 4877 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais georgesandae</i> Jakiel, Palero & Błażewicz, 2019	APEI3, 4877 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais geraldii</i> Jakiel, Palero & Błażewicz, 2019	IOM, GSR, 4365–4496 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais julietae</i> Jakiel, Palero & Błażewicz, 2019	GSR, 4507 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais kobro</i> Jakiel, Palero & Błażewicz, 2019	GSR, 4342–4496 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais mariae</i> Jakiel, Palero & Błażewicz, 2019	BGR, IOM, 4093–4401 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais oloughlini</i> Jakiel, Palero & Błażewicz, 2019	APEI3, 4805–4877 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais romeo</i> Jakiel, Palero & Błażewicz, 2019	BGR, 4093–4100 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais uranos</i> Jakiel, Palero & Błażewicz, 2019	APEI3, 4805 m	Jakiel, Palero & Błażewicz, 2019
<i>Pseudotanais yenneferae</i> Jakiel, Palero & Błażewicz, 2019	APEI3, 4805–4877 m	Jakiel, Palero & Błażewicz, 2019
Typhlotanaidae Sieg, 1984		
<i>Typhlotanais froufesa</i> Larsen, 2011	Ifremer, 4909 m	Larsen, 2011
<i>Typhlotanais pereosetulosa</i> Larsen, 2011	Ifremer, 5051 m	Larsen, 2011
Family: Incertae sedis		
<i>Portarathrum birdi</i> Chim & Tong, 2020	Singapore 4148–4172 m	Chim & Tong, 2020
<i>Robustochelia pacifica</i> Larsen 2011	Ifremer, 5045 m	Larsen, 2011
<i>Unispinosus eopacificus</i> Chim & Tong, 2020	OMS, 4127–4172 m	Chim & Tong, 2020

was observed in samples from the Kuril-Kamchatka Trench, while the lowest values were recorded for SoJ and SoO ( $p$ -value  $< 0.002$ ; Fig. 7C). Furthermore, The GAMs highlighted a significant decline in tanaid abundance and richness with increasing water depth, (Table 6; Fig. 7B, E). However, no pronounced discrepancies in tanaid family richness were noted between samples collected using the EBS and BC (Fig. 7D). Nevertheless, some differences were apparent across the four regions (SOJ, SoO, KKT, and CCZ) with SoO hosting the richest tanaid fauna (Fig. 7F).

### Barcoding and species delimitation

A total of 160 COI barcodes were successfully obtained from 320 individuals sampled in the CCZ (Table 7). The sequence alignment spanned 846 basepairs, and the GTR+I+G model (Yang 1994) was selected as the best model to describe the substitution pattern. The maximum likelihood tree constructed with representatives from 10 tanaid families recorded in the CCZ, grouped into 12 clades (Fig. 8). Notably, two families, Apseudidae and Typhlotanaidae, formed multiple distinct clades. For instance, Apseudidae 1 included a single haplotype identified as *Eliomosa* sp., while Apseudidae 2 comprised haplotypes from the genus *Leviapseudes*, and Apseudidae 3 included two other genera, *Caprapseudes* and *Fageapseudes*. In the case of Typhlotanaidae, taxa such as *Torquella* (with 5 haplotypes), *Meromonakantha* sp., and a subclade of five species morphologically related to *Typhlotanais spinicauda*, formed clade Typhlotanaidae 1, that was well separated from other typhlotanuids that grouped in the clade Typhlotanaidae 2.

Different species delimitation methods identified varying numbers of putative species within the dataset. By analysing the entire dataset, which included 45 barcodes obtained from GeneBank and the 160 newly sequenced barcodes from the CCZ, we identified a total of 57 to 82 entities (Appendix 2). The number of species delimited using molecular methods generally exceeded those identified solely based on morphological characteristics. Morphological identification revealed 78 morphospecies, while the genetic-distance-based ASAP method detected between 57 and 80 putative species (with 43–65 from the CCZ), with genetic intraspecific thresholds ranging from 0.0204 to 0.2117. The tree-based GMYC method suggested a maximum 82 putative species (between 78 and 82) of which 67 occurred in the CCZ. The number of molecular taxonomic units (MOTUs) identified using both ASAP and GMYC methods was consistent with those identified through morphological analysis. Pairwise genetic distances for all 160 barcodes ranged from 0 to 50.4%, with an overall mean distance of  $36 \pm 1\%$ . Based on the COI sequences, 73 distinct haplotypes were identified within the CCZ. Intraspecific variation was low, with more than one haplotype observed in only nine out of the 57–82 species in total.

### Species diversity of tanaids within the CCZ

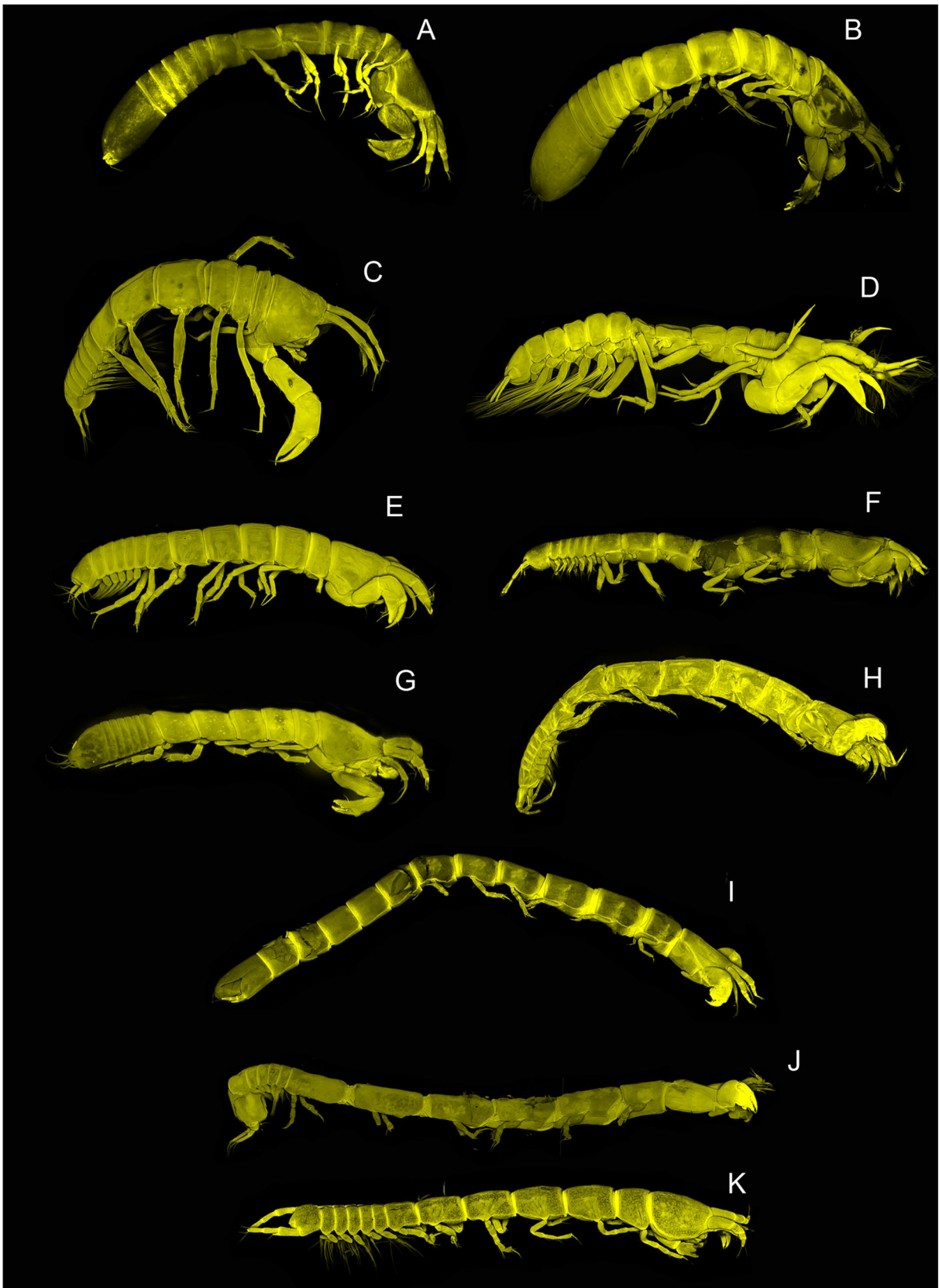
The sample-based rarefaction curves for tanaids collected in specific studied areas in the CCZ displayed different shapes (Fig. 9). The curves exhibited a plateau for the IOM and Ifremer area, and saturated quite rapidly for APEI3. In contrast, the curves for the GSR and BGR contract areas indicated that total species richness has not been fully captured. Particularly, the GSR\_E area showed the highest species richness, with  $> 100$  species identified in 40 samples. The curves for BGR and GSR\_W largely overlap, although the former appeared to approach saturation towards the end, with approximately 70 species detected in 40 samples, rather than 60, as observed in the latter. In the case of IOM and Ifremer, species richness saturation occurred at approximately 30 samples, with estimates of about 40 species for both. In contrast, APEI3 showed the lowest species richness, with approximately ten species when reaching the asymptote at about ten samples.

The results of the GLMMs revealed statistically insignificant effects of the area on total family richness and the Shannon–Wiener diversity index, although significant variability in total abundance was observed across areas especially between BGR and GSR\_W, as well as between BGR and Ifremer ( $p$ -value  $< 0.001$ ; Fig. 9). Additionally, the analyses of tanaids collected with the different sampling devices resulted in non-significant effects of sampling equipment for all univariate diversity indices. Comparative analyses mainly showed a higher contribution of the Colletteidae and of non-identified taxa (indet.) in samples collected with the BC, and higher contributions of Pseudotanaidae and Apseudidae in EBS samples (Fig. 10). On the other hand, the cluster analysis (Fig. 11A) and nMDS (Fig. 11B) for tanaid family species composition collected across four contract areas suggest notable disparities between communities when sampled using the BC versus the EBS. This result is supported by the PERMANCOVA, where longitude, contract area, and sampling gear used were significant (all  $p$  values  $< 0.001$ ; Table 8).

## Discussion

### Patterns in individual abundance and diversity for tanaids in the CCZ and other Pacific regions

Understanding large-scale biodiversity patterns in deep-sea ecosystems is often hindered by the lack of reliable baseline data on ecosystem characteristics including faunal composition (Carney 2007; McClain and Hardy 2010; McCallum and Riehl 2020; O'Hara et al. 2020). The limited number of samples, primarily due to the logistical challenges of retrieving abyssal samples from remote



**Fig. 5** Diversity of tanaids in the Clarion–Clipperton Zone (CCZ) illustrated with confocal laser scanning microscope images of selected species: **A, B**, *Colletta* sp. (Colletteidae); **C, D**, *Pseudotanaia* sp. (Pseudotanaidae): female and male, respectively; **E**, *Forcipatia* sp.; **F**, Akanthophoreidae sp.; **G**, *Leptognathia* sp. (Leptognathiidae); **H**, *Stenotanaia* sp. (Akanthophoreidae); **I, J**, unknown taxa from the suborder Paratanaoidea

offshore locations, restricts the collection of comprehensive data, necessary for robust statistical analyses (e.g. sufficient level of replication). Furthermore, the limited use of standardised sampling protocols has hampered the analysis of data originating from multiple sources (Washburn et al. 2021; Frutos et al. 2022). However, recent advancements in the standardisation of sampling methodology have addressed the issue.

By applying a standardised methodology for collecting abyssal fauna, specimens were gathered from several remote locations in the North Pacific, facilitating comparative analysis across the region. This approach not only improved comparability through complementary data but also involved the use of advanced equipment capable of capturing even small-sized organisms, thus providing a more comprehensive representation of deep-sea biodiversity (Brandt et al. 2015a, 2016; Golovan et al. 2018; Rühlemann et al. 2010; Martínez Arbizu and Haeckel 2015). These improvements have enabled the first assessment of tanaid diversity across several remote locations in the North Pacific, including the SoJ, SoO, KKT, and the CCZ. Despite the limited number of the samples available for our analyses, we were able to compare the total individual abundance of tanaids among four Pacific regions. The results show that the KKT exhibits the highest abundance of tanaids, followed by the CCZ region, whereas lower abundances were recorded in the SoJ and SoO. Similar patterns were observed for both types of sampling equipment used (BC and EBS) yielding consistent results. Water depth emerged as a significant factor, with a nonlinear relationship observed between depth and tanaid abundance.

The distribution and abundance patterns of tanaids across the surveyed deep-sea regions of the Pacific (KKT, SoJ, SoO, and CCZ) reflect the interplay of biotic and abiotic factors, including spatial variability, geological history, hydrodynamic conditions, and the flux of organic matter to the seafloor (Bober et al. 2019). In the KKT, continuous deposition of terrigenous material from Siberian and Kamchatkan rivers enriches the seafloor with particulate organic matter (POM), promoting benthic productivity (Jamieson 2011; Schwabe et al. 2015; Oguri et al. 2022). This consistent influx supports a dynamic and dense benthic community, which is evident in the high biomass and abundance observed in this region (Błażewicz-Paszkowycz et al. 2015; Brandt et al. 2015a, 2019; Elsner et al. 2015; Golovan et al. 2018;). In contrast, despite substantial inputs of organic matter to the SoJ and the SoO, these regions exhibit lower

benthic densities compared to the KKT. The comparatively lower oxygen levels in the SoO, intensified by restricted water circulation and upwelling (Chen et al. 2004; Seki et al. 2004), reduce the number of individuals in benthic communities (Tyler 2002; Frutos and Jażdżewska 2019). Additionally, the geologically younger age of the SoJ suggests that its benthic communities are still in the process of colonisation and ecological establishment, which could explain the observed lower faunal abundance (Zenkevich 1963; Tyler 2002). These combined physical and biological factors highlight the variability in colonisation rates and ecosystem stability within these marginal seas (Brandt et al. 2010, 2018; Malyutina et al. 2015). In sharp contrast, the oligotrophic waters of the CCZ are characterised by low particulate organic carbon (POC) fluxes, resulting in energy-limited conditions for benthic organisms. This region exhibits low overall biomass and low population densities across most faunal groups due to the scarce availability of food sources, which are primarily reliant on sporadic phytodetritus deposition from the surface waters (Washburn et al. 2021). Despite this, the CCZ hosts specialised species adapted to survive under these low-nutrient conditions, highlighting the role of environmental filtering and resource allocation in shaping deep-sea biodiversity (Glover et al. 2018).

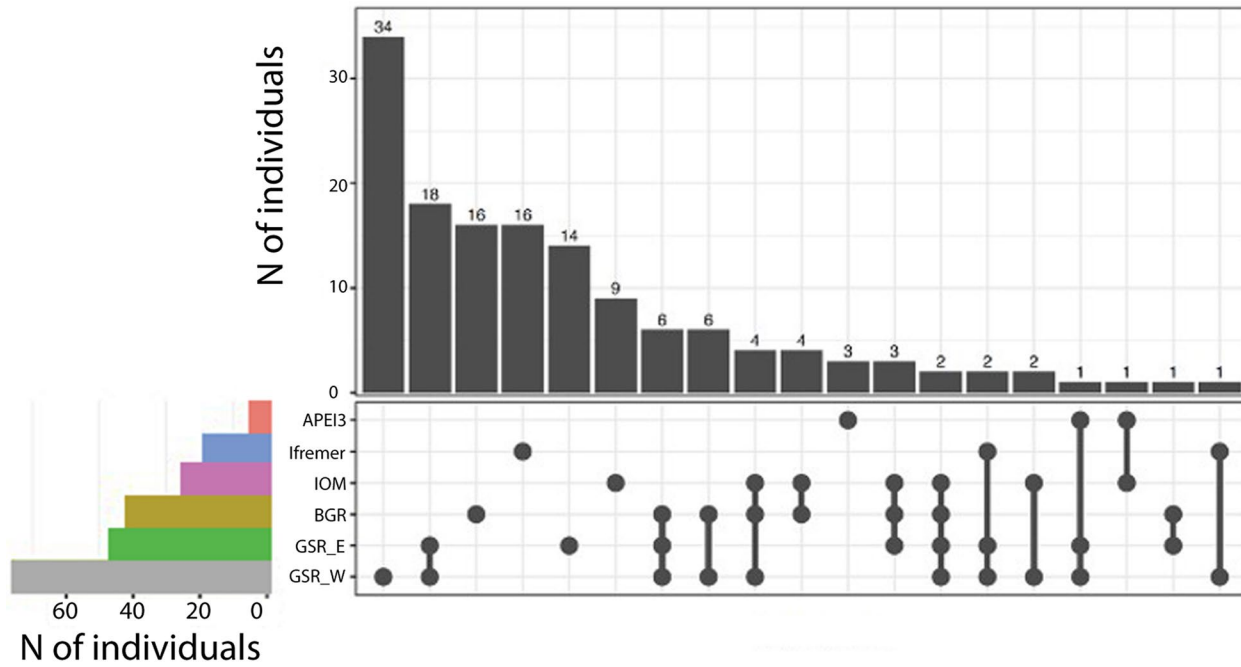
### Challenges associated with exploring tanaid diversity in the deep sea

Recent research has uncovered highly diverse assemblages of tanaids in benthic deep-sea communities (e.g. Głuchowska et al. 2025; Błażewicz et al. 2019b; Washburn et al. 2021; Pasotti et al. 2021; Chim and Tan 2025). However, many tanaids collected in the CCZ could only be identified to family level, evidencing the difficulty of lower taxonomical level (genus or species) identification. Notably, less than 1% of over 3000 tanaid specimens collected since the first published study on macrobenthos (Wilson 1989, 2017) from the CCZ have been identified to species level. Such information adds to the knowledge base for assessing and mitigating the potential effects of mining activities, as accurate species delimitation and ecological characterisation are important for informing environmental conservation and management strategies (Kaiser et al. 2017; Jażdżewska et al. 2018; Frutos et al. 2022; Kürzel et al. 2022).

The difficulty for species delimitation of small, rare, and previously undescribed taxa collected from a taxonomically relatively understudied area such as the deep Pacific is well known (Lamshead et al. 2003; Kennedy et al. 2019; Bonifácio et al. 2020; Pasotti et al. 2021). In case of the tanaids, the problem of species delimitation is exacerbated by the poor condition of collected specimens (caused by physical disturbance during sampling and sample processing [Frutos et al. 2022; Kaiser et al. 2023]), alongside their immaturity,

**Table 4** Family composition of tanaids collected in multiple Clarion–Clipperton Zone (CCZ) exploration contract areas and three Areas of Particular Environmental Interest (APEIs) using data compiled by Rabone et al. (2023). Numbers shown are abundances (*n*) and relative abundances (%). The names of the areas are according to Rabone et al., 2023

family	APEI-3		APEI-6		APEI-9		BGR		COMRA		DORI		GSR		IFRI		IOM		KOREAI		OMS	
	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	<i>n</i>	%
Agathotanaidae	12	3	2	6	1	25	33	4	11	100			17	3	42	5	32	4	10	10	3	1
Akanthophoreidae	76	19	4	11			171	20				95	18	117	13	171	19	22	22	6	2	
Anarthruridae	4	1					9	1				5	1	6	1	9	1					
Apseudidae	12	3			1	25	27	3				17	3	21	2	27	3	5	5	5	5	
Caudalongidae																						
Colletteidae	92	23	2	6			207	24				121	23	173	20	207	23	17	17	12		
Cryptocopidae	12	3					27	3				17	3	18	2	27	3					
Leptocheiliidae							0	0						0	0	0						
Leptognathiidae	24	6	2	6	1	25	54	6				135	26	205	23	54	6	3	3			
Neotanaidae		0					4	0				1		3	0			2	2			
Nototanaidae	4	1					9	1				5	1	6	1	9	1	1	1			
Paranarthrurellidae	20	5					45	5				38	7	33	4	50	6					
Pseudotanaidae	22	6					28	3				30	6	30	3	47	5					
Tanaellidae		0	8	22			0	0						0	2	0	0	6	6			
Typhlotanaidae	40	10	1	3			90	10				71	14	83	9	90	10	16	16	1		
Paratanaoidea <i>incertae sedis</i>	28	7					63	7				36	7	44	5	63	7			7	3	
indet	48	12	17	47	1	25	327	12			28	100	141	27	103	12	108	12	16	16	228	87
<b>Total</b>	<b>394</b>		<b>36</b>		<b>4</b>		<b>1094</b>		<b>11</b>		<b>28</b>		<b>729</b>		<b>886</b>		<b>894</b>		<b>98</b>		<b>262</b>	<b>100</b>



**Fig. 6** Upset matrix design bi-plots representing tanaid species in four contract area and APEI3 of the Clarion-Clipperton Zone (CCZ). Points integrated by a line indicate the shared species between the dif-

ferent contract areas, for which the total number of species is reported on top of the bar. Single dots represent unique species per station

**Table 5** Number of samples, number of morphospecies (morpho-sp) and mean value of morphospecies per station collected in six areas of the Clarion-Clipperton Zone (CCZ) using the epibenthic sledge (EBS) and the box corer (BC) collectively and separately. APEI: Area of Particular Environmental Interest, BGR: eastern German CA; GSR: Global Sea Mineral Resources NV C, \_E: east, \_W: west

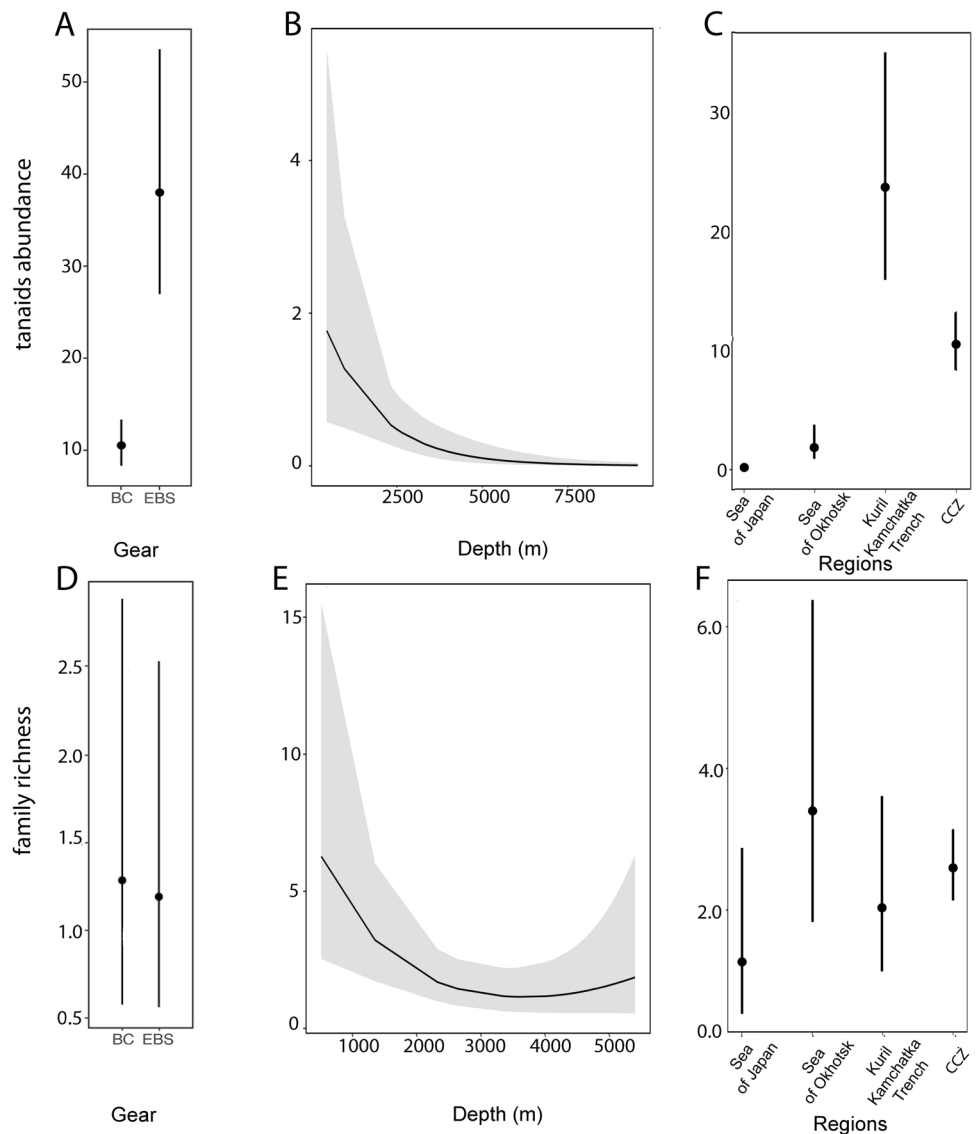
Area	Gear	EBS + BC			EBS and BC separately		
		N samples	N morpho-sp	Mean morpho-sp/station	N samples	N morpho-sp	Mean morpho-sp/station
BGR	BC	18	68	12.4 ± 4.7	9	46	11.0 ± 2.4
BGR	EBS				9	32	13.0 ± 5.3
IOM	BC	11	39	9.8 ± 3.1	9	30	8.4 ± 1.9
IOM	EBS				2	14	11.0 ± 3.5
GSR_E	BC	17	60	8.7 ± 2.7	14	49	7.9 ± 2.4
GSR_E	EBS				3	19	10.3 ± 2.4
GSR_W	BC	30	86	8.7 ± 3.8	30	86	8.7 ± 3.8
Ifremer	BC	9	34	7.5 ± 1.6	6	22	6.4 ± 2.2
Ifremer	EBS				3	14	8.2 ± 0.4
APEI3	BC	9	21	9.6 ± 3.1	5	8	2.6 ± 0.6
APEI3	EBS				4	17	10.4 ± 2.0

and uncertainties regarding life histories and sexual dimorphism (Frutos et al. 2022). Particular challenges stem from the lack of diagnostic morphological traits in juvenile tanaids (manca stage) and pronounced sexual dimorphism, with deep-sea Paratanoidea “swimming males” often lacking clear features for species identification (Błażewicz-Paskowycz et al. 2014; Gellert et al. 2022).

Our study showed that the proportion of undeterminable (indet.) individuals in EBS samples were lower than for

the BC. Although the use of EBS nets With a mesh size of 0.3-0.5 mm may lead to the inadvertent loss of some juveniles, the sediment volume in an EBS sample is smaller, which subsequently lowers the risk of damage during sample processing. Species identification of tanaids recovered from BC samples pose a particular challenge, caused by the high number of singletons, the prevalence of juvenile stages and presence of the small-sized, often undescribed taxa. While data from BC are most suitable for local biodiversity

**Fig. 7** Generalized Additive Model (GAM) predictions for mean (solid black line) and 95% confidence intervals (grey) of the tanaid abundances and richness observed in the four regions of the North Pacific: the Clarion–Clipperton Zone (CCZ); the Kuril–Kamchatka Trench, the Sea of Japan, and the Sea of Okhotsk



**Table 6** Analysis of deviance tables for each GLM performed investigating the effect of subregions and sampling gear on tanaid family richness, abundance, and the Shannon diversity index. Wald chi-square statistics (Chisq), degrees of freedom (Df), and *p* values (Pr(> Chisq)) for each term (i.e., explanatory variable) of the relative model (richness, abundance, and Shannon index)

Tanaid	Terms	Chisq	Df	Pr(> Chisq)
Richness	Subregion	5.751	5	0.331
	Gear	1.767	1	0.184
Abundance	Subregion	20.687	5	0.001***
	Gear	0.040	1	0.842
Shannon diversity index	Subregion	7.452	5	0.189
	Gear	3.970	1	0.046*

Asterisks indicate levels of statistical significance: \* *p* < 0.05; \*\*\* *p* < 0.001

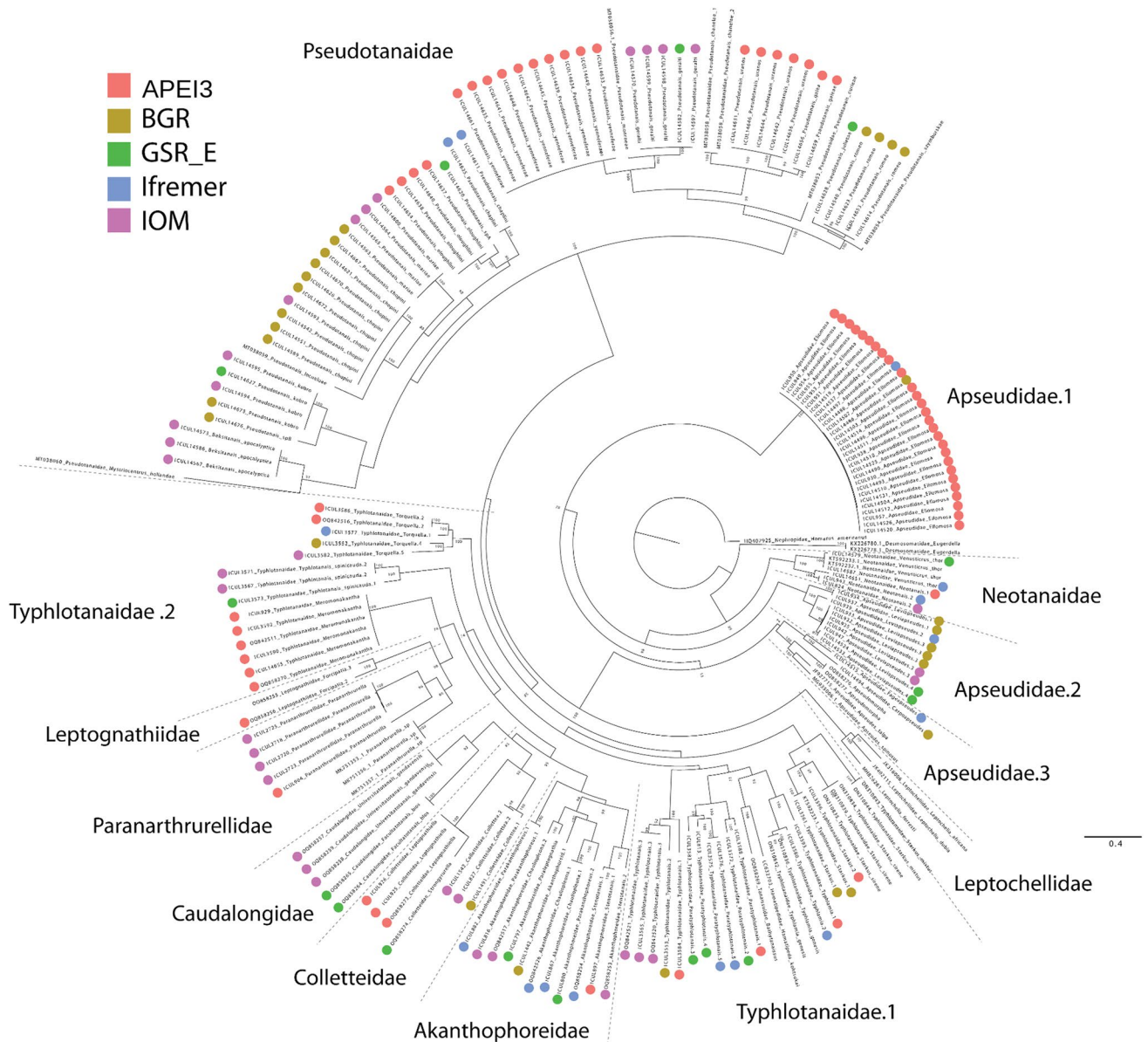
assessments due to their quantitative nature, this challenge complicates taxonomic integration of datasets (e.g. the same species might be annotated differently by different researchers), and thus can hinder large-scale meta-analyses (Glover et al. 2015; Janssen et al. 2015).

### DNA Barcoding and species delimitation

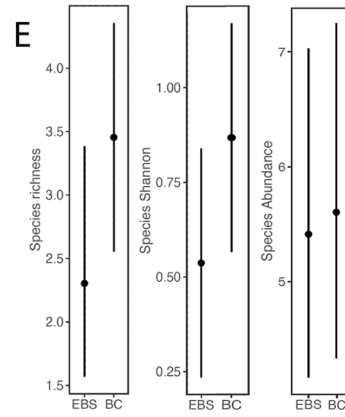
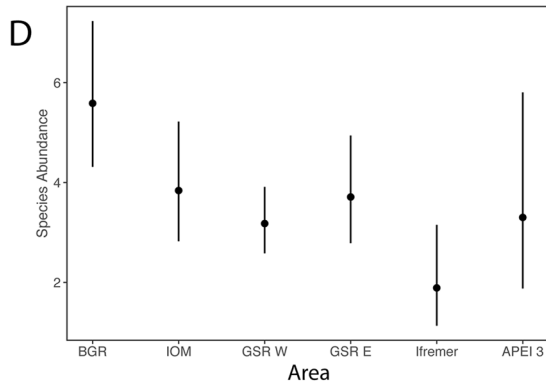
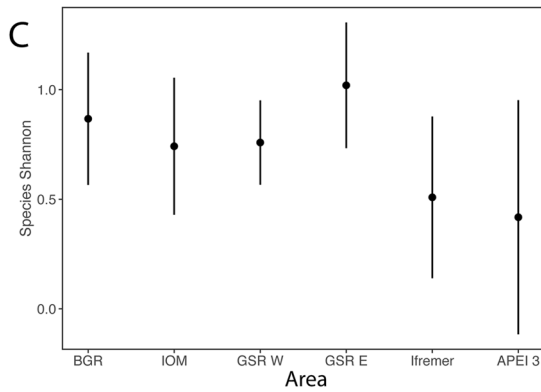
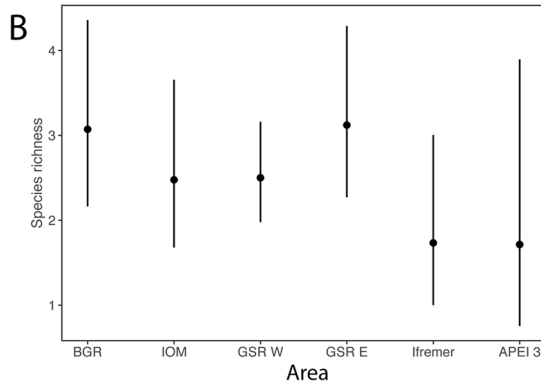
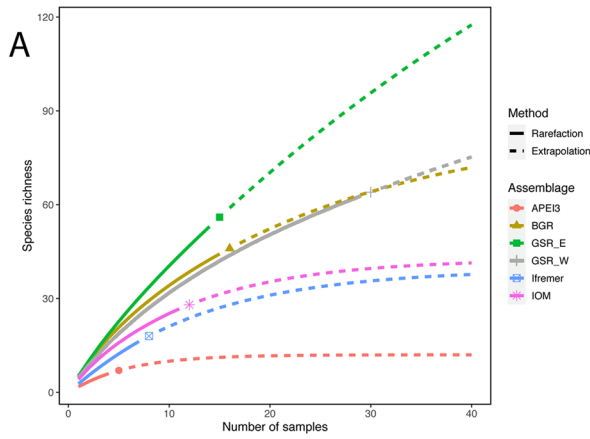
Overall, our results of molecular species delimitation methods, i.e., ASAP and GMYC, were generally consistent with our morphological identifications. However, in our analyses, the GMYC approach appeared to overestimate the actual number of species, as previously observed for scavenging amphipods (Bribiesca-Contreras et al. 2021). Nevertheless, a part of the discrepancies between the molecular and morphological results may be attributed to uncertain

**Table 7** Number of tanaid DNA sequences, species, and haplotypes identified from the CCZ in the present study.

Family	BGR	IOM	JPIO_GSR	Ifremer	APEI3	n sequences	n species	n haplotypes
Akanthophoreidae	1	3	2	3	1	12	7	7
Apseudidae	5	1	1	3	1	40	6	13
Caudalongidae		1	1			5	2	2
Colletteidae	1	1	2		1	7	4	5
Leptognathiidae					1	1	1	1
Neotanaiidae		1	1	1	1	5	3	4
Paranarthrurellidae		1			1	5	2	5
Pseudotanaiidae	6	6	4	1	4	56	16	18
Typhlotanaiidae	3	3	4	3	7	29	18	18
<b>total</b>	<b>16</b>	<b>17</b>	<b>15</b>	<b>11</b>	<b>17</b>	<b>160</b>	<b>59</b>	<b>73</b>



**Fig. 8** Genetic diversity of tanaid species from the Clarion–Clipperton Zone (CCZ) inferred by using the COI molecular marker sequences and the Maximum Likelihood method. Details on specimen voucher and sequence registration number are shown in Appendix 1



Poisson Glmm (total Richness)			
Coefficient	Log-Mean	Conf. Int (95%)	P-value
(Intercept)	1.11	0.75 – 1.46	<0.001
IOM	-0.20	-0.71 – 0.30	0.425
GSR_E	-0.15	-0.72 – 0.41	0.597
GSR_W	-0.11	-0.52 – 0.30	0.596
Ifremer	-0.56	-1.19 – 0.06	0.079
APEI3	-0.58	-1.44 – 0.27	0.181
Gear EBS	-0.25	-0.68 – 0.18	0.257
Observations	80		
R <sup>2</sup> conditional / R <sup>2</sup> marginal	NA / 0.113		

Gaussian Glmm (total Shannon)			
Coefficient	Estimates	Conf. Int (95%)	P-value
(Intercept)	0.84	0.54 – 1.15	<0.001
IOM	-0.11	-0.53 – 0.31	0.602
GSR_E	-0.05	-0.53 – 0.42	0.829
GSR_W	0.00	-0.35 – 0.36	0.982
Ifremer	-0.35	-0.80 – 0.11	0.135
APEI3	-0.45	-1.03 – 0.13	0.127
Gear EBS	-0.29	-0.62 – 0.05	0.094
Observations	80		
R <sup>2</sup> conditional / R <sup>2</sup> marginal	NA / 0.036		

Poisson Glmm (total Abundance)			
Coefficient	Log-Mean	Conf. Int (95%)	P-value
(Intercept)	1.72	1.46 – 1.98	<0.001
IOM	-0.37	-0.75 – 0.01	0.055
GSR_E	-0.44	-0.89 – 0.01	0.056
GSR_W	-0.53	-0.84 – -0.21	0.001
Ifremer	-1.08	-1.64 – -0.53	<0.001
APEI3	-0.53	-1.11 – 0.06	0.077
Gear EBS	-0.03	-0.34 – 0.29	0.870
Observations	80		
R <sup>2</sup> conditional / R <sup>2</sup> marginal	NA / 0.259		

**Fig. 9** Rarefaction curves; (A) and best Generalized Linear Mixed Models (GLMM) describing species richness; (B), Shannon index; (C) and species abundance; (D) for four contract areas and APEI3 in the Clarion–Clipperton Zone (CCZ) and collected with BGR, Bundesanstalt für Geowissenschaften und Rohstoffe; GSR, Global Sea Mineral Resources NV; Ifremer, L’Institut Français de Recherche pour l’Exploitation de la Mer (French contract area); IOM, Interoceanic metal Joint Organization contract area, using a box corer (BC) and epibenthic sledges (EBS) as sampling devices, respectively

morphological identifications. For morphospecies such as *Leviapseudes* sp. 4 and *Collettea* sp. 1, only two and one individuals, respectively, were available, which limited our ability to confirm morphological identification and complicated species delimitation analyses.

The effectiveness of species delimitation methods is best tested using closely related species (Jakiel et al. 2019). In our study, two delineated pseudotanaid species, *P. romeo* and *P. julietae*, which were present in two CCZ contract areas (BGR and GSR-E, respectively) and exhibited a genetic distance of  $0.0602 \pm 0.0117$ , were merged into a single species by the ASAP delimitation method despite being morphologically distinct and collected from separate CCZ areas. Similarly, *Leviapseudes* sp. 3 and *Leviapseudes* sp. 4 were considered as one species with the ASAP approach, but were separated by the GMYC method, despite a relatively low genetic distance of  $0.0261 \pm 0.0044$ . These results suggest that closely related tanaid species in the CCZ may have undergone recent speciation or exhibit polymorphic traits, making them difficult to distinguish genetically and therefore are leading to their merger into a single species by one of the applied methods. This result highlights the challenge of relying solely on genetic data for species delimitation, particularly in regions like the CCZ, where cryptic speciation may be prevalent (Janssen et al. 2015; Jakiel et al. 2019).

### Community composition of tanaids in the CCZ

The here reported family composition of tanaids in the CCZ differs from what Wilson (1987) documented, who emphasised considerable frequency and dominance of the family Leptognathiidae in the tanaid community at the DOMES A site (centred 9°24’N, 151°27’W; Fig. 4). Over the last three decades, the taxonomic classification of the family Leptognathiidae has undergone substantial revision, leading to the redefinition of several tanaid families, such as Typhlotanaiidae, Akanthophoreidae, Colletteidae, or Tanaellidae, in addition to the establishment of two new ones, Paranarthrurellidae, and Mirandotanaiidae (Larsen 2005; Błażewicz-Paszkowycz and Bamber 2009; Błażewicz et al. 2019a, 2024). Some members previously classified under Leptognathiidae in Wilson’s (1987) research might belong to these newly established families. For instance, the species

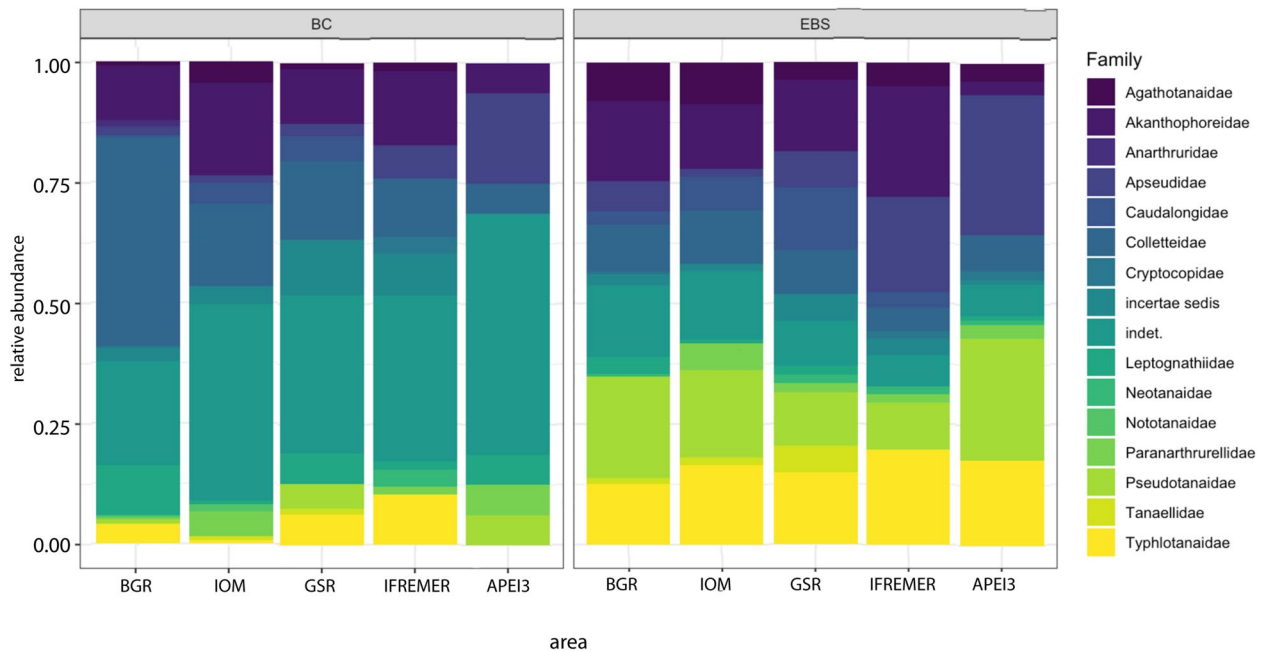
previously identified as *Leptognathia* sp. 23,019 unequivocally falls now into the family Akanthophoreidae, underscoring the necessity for a comprehensive reassessment of tanaid specimens collected previously in the CCZ considering these updated taxonomic insights.

### Spatial variability in species richness of tanaids within the CCZ

Tanaids are generally reported to be an important component of abyssal macrobenthic communities in terms of abundance, following polychaets and isopods (Brandt et al. 2015b, 2019; Washburn et al. 2021; Pasotti et al. 2021; Kaiser et al. 2023). In the analyses by Washburn et al. (2021) tanaids slightly surpassed the species richness and biodiversity of isopods, which usually dominate peracarid communities in the CCZ (Wilson 1987; Pasotti et al. 2021). Interestingly, species diversity was higher in the eastern CCZ contract areas (BGR, IOM, and GSR) when compared to the more westward located Ifremer contract area (Błażewicz et al. 2019b). However, APEI3, located to the north of all other studied areas, exhibited the lowest species richness underscoring the disparity of this area, as shown also for other taxa in other studies (e.g., Macheriotou et al. 2020, Hauquier et al. 2019).

Despite our limited dataset, our results align with previous studies on other macrofauna taxa such as polychaetes or isopods (Janssen et al. 2015; Bonifácio et al. 2020; Kaiser et al. 2023). These studies have linked POC flux (Wilson 2017; De Smet et al. 2017; Chuar et al. 2020; Washburn et al. 2021) and the abundance of polymetallic nodules (Pape et al. 2021; Washburn et al. 2021; Pasotti et al. 2021) to benthic diversity, supporting the well-established model that explains the positive relationship between biodiversity and organic matter (food) availability in the abyssal zone (Woolley et al. 2016). For instance, Washburn et al. (2021) found that POC flux in the CCZ accounts for 47% of the variability in tanaid abundances.

The southern boundaries of the CCZ extend into the “eutrophic abyss” within the equatorial upwelling zone, which benefits from favorable nutrient conditions and relatively high seafloor POC fluxes (about 1–2 gC/m<sup>2</sup>/year) (Hannides and Smith 2003). In contrast, the northern boundaries encompass the extremely oligotrophic zone beneath the North Pacific subtropical gyre (<0.5 gC/m<sup>2</sup>/year), while the central part of the CCZ can be classified as mesotrophic (0.62–0.73/m<sup>2</sup>/year). This zonation is reflected in the gradients of species diversity and abundance spanning from the southeast to the northwest for benthic taxa (Janssen et al. 2015; Bonifácio et al. 2020; Macheriotou et al. 2020). Additionally, the unique location of APEI3 within an extremely oligotrophic zone may explain its remarkably low diversity, although the undersampling of



**Fig. 10** Composition of tanaid families gathered from four contract areas (BGR, IOM, GSR, Ifremer) within the Clarion–Clipper-ton Zone (CCZ) and one Area of Particular Environmental Interest (APEI3) contrasting samples collected using a box corer (BC) vs. epibenthic sledge (EBS). BGR, Bundesanstalt für Geowissenschaft-

ten und Rohstoffe; GSR, Global Sea Mineral Resources NV (W = West; E = East); Ifremer, L’Institut Francais de Recherche pour l’Exploitation de la Mer (French contract area); IOM, Interocean-metal Joint Organization contract area

this APEI must be acknowledged impeding comparisons with better studied areas in the region (Christodoulou et al. 2020; Washburn et al. 2021; Kaiser et al. 2023).

Besides POC flux, other environmental factors, such as water depth and nodule densities, have been suggested to influence the abundance and diversity of macrobenthos (Pasotti et al. 2021; Washburn et al. 2021) and meiobenthos (Pape et al. 2017, 2021) in the CCZ. The gradual longitudinal eastward decrease in water depth (> 1000 m) could indeed have a significant impact on macrofauna diversity and may (partly) explain the differences observed between the locations in the eastern BGR, IOM, and GSR; the more centrally located contract areas IFREMER; and the most western KODOS (Błażewicz et al. 2019a; Washburn et al. 2021). However, distinguishing between the individual contributions of these factors poses a challenge, given that in the CCZ both water depth and surface productivity vary with longitude (Kaiser et al. 2023).

Finally, nodule densities have been demonstrated to affect the abundance and diversity of various benthic groups (Vanreusel et al. 2016), though the importance varies between taxa and size classes (Vanreusel et al. 2016; Bonifácio et al. 2020; Pape et al. 2021; Washburn et al. 2021; Pasotti et al. 2021; Kaiser et al. 2023). Nodule densities within the CCZ exhibit significant spatial heterogeneity, varying considerably over distances of tens to hundreds of meters (Peukert et al.

2018). However, the presence of nodules was assumed to provide habitats unsuitable for capturing small-scale biological variation (Washburn et al. 2021). Nevertheless, Washburn et al (2021), albeit using modelled nodule densities, have shown that regions with intermediate nodule densities (~ 12 kg/m<sup>2</sup>) harbour more macrofaunal species and families than regions with high nodule density (≥ 19 kg/m<sup>2</sup>).

### Rarity of tanaids in the CCZ and other abyssal regions

A considerable proportion of tanaid species within the CCZ are represented by a low number of specimens (Błażewicz et al. 2019b). According to Washburn et al. 2021, out of the 98 species known for the region, 78 were limited to only one contract area, With the highest percentage of species not found elsewhere being 95% in the Ifremer area, and the lowest being 48% in the IOM contract area. Many species were encountered only once or twice (i.e., as singletons or doubletons), possibly indicating a high proportion of rare taxa within the benthic assemblages (Wilson 1987), or taxa that are widespread but with infrequent distribution.

Low individual abundances of tanaids are not restricted to the CCZ (McClain 2021; Frutos et al. 2022). While environmental conditions certainly (partly) explain low specimen numbers, the discussion often turns to the appropriateness of

the sampling methodology. The small numbers of deep-sea tanaids pose challenges for sampling devices traditionally designed for collecting larger benthic organisms (Hessler and Sanders 1967). Recent investigations employing standard sampling devices, such as the EBS or BC, along with rigorous sampling protocols (Riehl et al. 2014; Frutos et al. 2022), have revealed that many deep-sea taxa can be remarkably abundant, occupying relatively large biogeographical ranges, sometimes extending beyond well-defined marine basins (Brandt et al. 2015b, 2019; Golovan et al. 2018; Jakiel et al. 2020).

Differences in tanaid community composition collected using two standardised sampling devices can be attributed to the performance of the BC and EBS. The BC collects a relatively small fragment of the sea bottom (0.25 m<sup>2</sup>) in contrast with the EBS, which samples fauna along numerous (micro-) habitats distributed along its trawling path (Jóźwiak et al. 2020; Frutos et al. 2022). The probability of capturing a substantial number of individuals using an EBS is quite high; however, this method may not necessarily provide an accurate representation of the actual community structure and is considered qualitative (Jóźwiak et al. 2020). Interpretation of these results is complicated by a limited understanding of the behaviour and lifestyles of tanaids. In particular, the higher abundance of the family Pseudotanaidae in EBS samples may be related to their behaviour. Pseudotanaids, which have long, slender legs, short bodies, and one pair of oostegites (a unique feature for Tanaidomorpha), are assumed to have a mobile lifestyle (Jakiel et al. 2019, 2020). Although they construct tubes at least during certain life stages (A. Jakiel, personal observation), they are assumed to be more mobile compared to other tanaidomorphs, and to constitute the “lighter” fraction of the macrobenthos. This higher mobility likely makes them easier to be captured by the EBS (Jakiel et al. 2018, 2020; Błażewicz et al. 2021). In contrast, Typhlotanaidae, exhibit different behaviour, with short and compact pereopods adapted for clinging inside their tubes (Błażewicz-Paszkowycz 2007). These tubes are often short, stout, and usually encrusted with Foraminifera, sediment grains and sponge spicules, making them heavier than those of other families (Bird and Holdich 1985; Hassack and Holdich 1987; Larsen and Heard 2004; Kakui 2021). The tubes constructed by pseudotanaids are assumed to be more easily lifted from the sediment and thus more frequently captured by the EBS net, unlike the long and incrustated tubes of other families, which might be more likely washed away before entering the EBS net opening. In light of this knowledge, to obtain a more comprehensive view of tanaid diversity, it is recommended to use both BC and EBS, as each device captures different aspects of the benthic community. The BC provides quantitative data from a small, localised area, while the EBS,

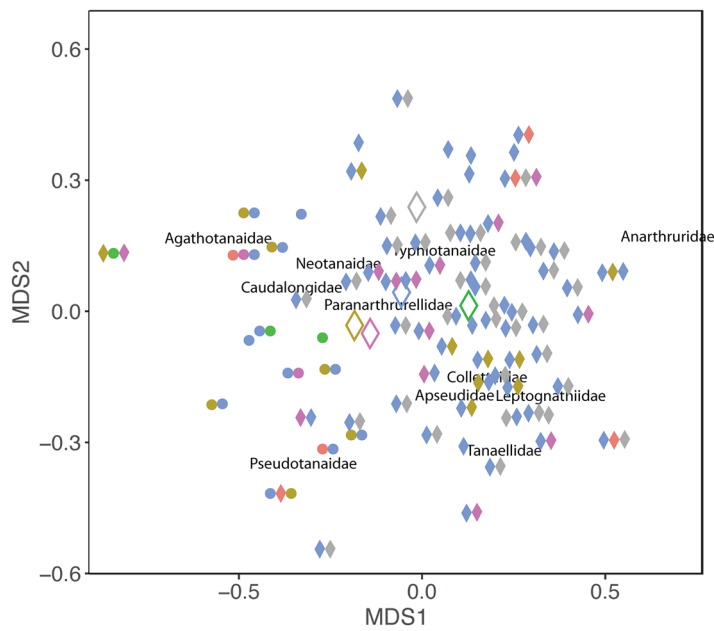
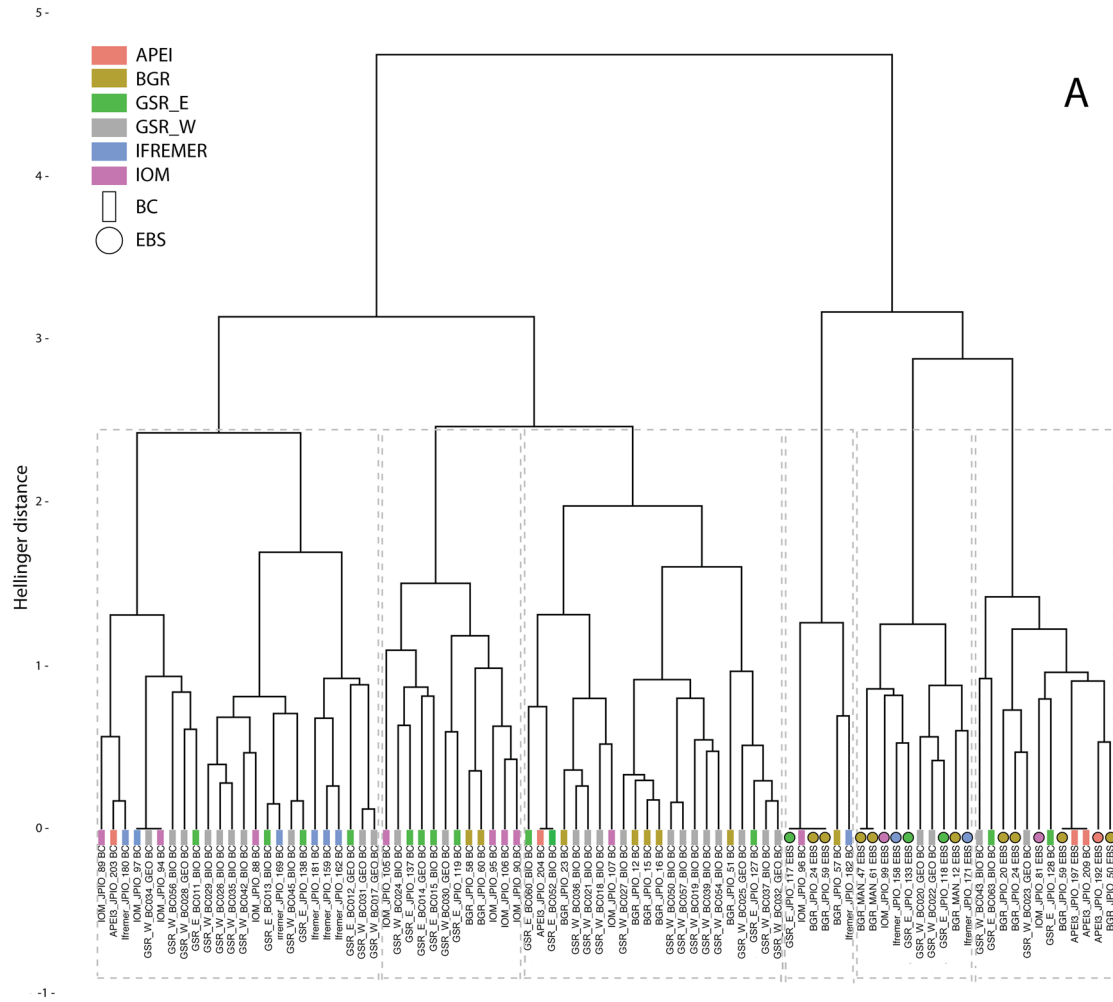
by sampling across diverse habitats, captures more mobile fauna but offers a qualitative assessment (Jóźwiak et al. 2020; Frutos et al. 2022).

An understanding of the species diversity and the relationship with fundamental ecosystem functioning is important knowledge that can contribute to developing informed conservation strategies, along with evaluating the regenerative capacity of these ecosystems (Gollner et al. 2017; Niner et al. 2018; Brix et al. 2020; Kaiser et al. 2023). Further, it is recommended that additional investigations into those species that display rarity and small population sizes should be undertaken to enable an understanding of the importance of these species in terms of ecosystem function. Current knowledge of benthic ecosystem diversity and structure in the CCZ remains limited and incomplete, hindering the identification of genuinely rare species. This gap is further complicated by the lack of comprehensive understanding of key life history traits, such as fecundity, age at maturity, and mobility—factors critical for assessing species’ resilience and recovery potential in the face of disturbances (Niner et al. 2018; Rabone et al. 2023).

Many populations in the deep sea are fragmented, and perceptions of rarity may be biased due to our currently limited knowledge. This bias could result from skewed sampling efforts, with most samples located primarily at the boundaries of species distributional ranges, where genetic variability and population densities are generally lower (McClain et al. 2009; McClain 2021). It is indeed possible that the species currently found as singletons and doubletons are widespread geographically but have infrequent distributions. Additionally, the unevenness observed in species ranges could be influenced by a variety of physical and environmental variables such as depth, chemical composition, and currents. While not many studies have addressed this topic, Gellert et al. (2022) noted that in the NW Pacific, *Typhlamia genesis* was more prevalent at depths over 5000 m in regions abundant in manganese and potassium. In contrast, *Baratheonus roberti* was found in areas with strong bottom currents, whereas *Starkus sirene* was observed in environments with lower oxygen levels and slower bottom currents (Gellert et al. 2022). In addition, demographic and genetic traits could limit species ranges, as modified by both contemporary and historical factors (Pironon et al. 2017).

## Conclusions, future directions and research priorities

Tanaids, primarily due to their abundance, are viewed as integral members of deep-sea benthic communities, and may play important roles in ecosystem dynamics, nutrient cycling, and trophic interactions (Larsen 2005; Błażewicz-Paszkowycz et al. 2012). Their distribution and abundances are influenced



**Fig. 11** (A) Dendrogram of similarity; (B) and Nonmetric Multidimensional Scaling (nMDS) ordination applied to the Hellinger distance matrix, based on tanaid community species composition of the of the Clarion–Clipperton Zone (CCZ) collected in four contract areas (BGR, IOM, GSR, Ifremer), and APEI3 with box corer (BC) and epibenthic sledge (EBS) in 2015 (JPIO and GSR) and 2017 (GSR). The two main clades pointed to differences in tanaid communities collected with the BC and EBS. BGR, Bundesanstalt für Geowissenschaften und Rohstoffe; GSR, Global Sea Mineral Resources NV; Ifremer, L’Institut Français de Recherche pour l’Exploitation de la Mer (French contract area); IOM, Interoceanmetal Joint Organization contract area

by a combination of environmental factors, including water depth, sediment type, and food availability as shown in this and studies. The CCZ, with its vast expanse on the abyssal seafloor, provides an opportunity to study tanaid communities and their responses to natural gradients in environmental parameters (e.g., depth, oxygen, trace metals, organic matter), habitat heterogeneity, and potential (anthropogenic) disturbances.

As the prospects for deep-sea mining in CCZ continue to grow, it is important to evaluate the potential impacts on tanaid populations and the broader deep-sea ecosystem. The limited dispersal abilities of most tanaids make them particularly vulnerable to disturbances, underscoring the need for precautionary management strategies to ensure the long-term sustainability of these communities. Mitigation efforts should incorporate protective measures, thorough environmental impact assessments, and ongoing research to monitor the health of tanaid populations and the associated ecosystems.

Deep-sea tanaid research in the Pacific and particularly in the CCZ, represents a promising opportunity for advances in several areas. To gain a deeper understanding of tanaid biodiversity and its ecological and evolutionary drivers, we propose the following directions and

**Table 8** PERMANCOVA results for species richness of the different tanaid families collected in the Clarion–Clipperton Zone (CCZ) during different sampling campaigns in different areas and using different sampling devices. Significance given for 999 permutations under restricted model and sequential addition of the terms (i.e., explanatory variable). Df: degrees of freedom, SumOfSqs: sum of squares,  $R^2$ :  $R^2$ ,  $F$ : pseudo- $F$  values after permutations,  $\text{Pr}( > F)$ :  $p$  values after permutations.

Terms	Df	SumOfSqs	$R^2$	$F$	$\text{Pr}( > F)$
Longitude	1	2.012	0.037	3.861	0.001***
Area	5	5.990	0.109	2.299	0.001***
Gear	1	7.040	0.128	13.510	0.001***
Area:Gear	4	1.587	0.029	0.761	0.824
Residual	74	38.563	0.699		
Total	85	55.193	1.000		

Asterisks indicate levels of statistical significance: \*\*\*  $p < 0.001$

recommendations for future research. These will not only pave the way for deeper insights but also provide effective means to address potential anthropogenic impacts.

- **Taxonomic refinement:** Continued taxonomic efforts, including integrative taxonomic approaches, DNA barcoding, and advanced imaging techniques, will aid in accurate species identification and description, minimising taxonomic uncertainties, and thus more accurate biodiversity assessments.
- **Increased and standardised sampling:** There is a need for standardised sampling protocols and systematic sample processing. While sampling and reporting has mainly occurred in the central and eastern areas of the CCZ, it would be beneficial to extend sampling and reporting efforts to the more western contract areas to allow comparisons within and among contract areas, and the APEIs (Kaiser et al. 2023).
- **Assessing population dynamics:** Further sampling will enable increased knowledge on tanaid life-history, reproductive strategies, population size, and its structure. A larger dataset, enabling robust statistical analyses, are essential for assessing the tanaid communities’ resilience to disturbances and developing effective conservation strategies.
- **Impact of anthropogenic activities:** Rigorous assessments of tanaid communities including their potential responses to future shifts and their recovery dynamics will help to gauge the ecological consequences of anthropogenic disturbances.
- **Insights into population connectivity:** Investigating the genetic connectivity and dispersal patterns of tanaid populations can elucidate their potential for recolonisation after disturbances and help guide the design of protected areas.
- **Environmental drivers of tanaid communities and habitat preferences:** Unravelling the influences of environmental factors, such as temperature, water depth, or sediment composition, on tanaid distribution and abundance will help decipher their habitat preferences and responses to changing conditions.
- **Long-term monitoring and temporal trends:** Establishing long-term monitoring programs to track tanaid populations over time will facilitate the identification of temporal trends, enabling us to discern natural variability from impacts by anthropogenic disturbances.

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