Small-scale species richness of the Great Barrier Reef tanaidaceans—results of the CReefs compared with worldwide diversity of coral reef tanaidaceans

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Abstract

The Great Barrier Reef (GBR) is considered to be one of the most important marine biodiversity hotspots on Earth. At the same time, knowledge on the smallest inhabitants of this habitat is extremely scarce, which is particularly apparent with respect to small peracarid crustaceans of the order Tanaidacea. Prior to this study, as few as 20 tanaidacean species had been reported from Australian coral reefs, this study yielding 56 species new to science. Our analysis of a high number of qualitative samples collected at two GBR sites (Heron and Lizard Islands) from a depth range of 0 to about 30 m in the framework of the Census of Coral Reef Ecosystem program (one of the Census of Marine Life-related projects) almost doubled the total number of coral reef-associated tanaidacean species known worldwide. Altogether, 60 species (distributed among 7622 individuals) were identified, 46 and 41 species being recorded on Heron and Lizard Islands, respectively. The tanaidaceans were dominated by members of the families Leptocheliidae (8 species and more than half of all specimens at both sites) and Metapseudidae (11 species, 6 and 3% of individuals, respectively). The most speciose genera were *Pseudoapseudomorpha* (4 species), *Paradoxapseudes*, *Parapseudes*, *Pugiodactylus*, and *Zeuxo* (3 species each). Most species were rare, their frequency of occurrence in samples not exceeding 15%. The species accumulation curves did not reach the asymptote.

Keywords Australia · CoML · Coral reefs · CReefs · Great Barrier Reef · Peracarida · Tanaidacea

Introduction

Coral reefs belong to the most diverse marine ecosystems on oceanic shelves (Bouchet 2006; Roberts et al. 2002) and support a high number of rare species (Selig et al. 2014). Despite increasing scientific effort, reefs represent the most endangered and least-sampled marine ecosystems (Poloczanska et al. 2007; Plaisance et al. 2011; De'ath et al. 2012). As estimated by Reaka-Kudla (1997), the number of species associated with coral reefs is close to one million. Similar results have been recently reported by Fisher et al. (2015), but the most realistic diversity assessments exist for a few taxonomic groups only, e.g., corals, sponges, bryozoans, fish, parasitic flatworms, or molluscs (Kohln 1997; Kensley 1998; Fisher

et al. 2015). Therefore, a different picture may emerge when smaller and poorly studied organisms, like peracarid crustaceans, are included in the assessment (Appeltans et al. 2012).

The CReefs Program—The Australian Node was linked to the Census of Marine Life project and aimed at completing a broad-scale taxonomic survey, collecting information about faunal distributions, and estimating invertebrate diversity of Australian coral reefs. The program provided an opportunity to collect less-known organisms, often small and difficult to sample. The CReefs expeditions yielded a large collection of peracarids of the order Tanaidacea. These crustaceans are considered to represent the smallest members of the macrobenthos and are an important element of marine benthic communities at all latitudes (Larsen 2005; Błażewicz-Paszkowycz et al. 2014; Poore et al. 2014; Pabis et al. 2014). Tanaidaceans are sediment-burrowing or tube-building organisms occasionally occurring at high population densities (Bamber 2005). Most are detritivores (Błażewicz-Paszkowycz and Ligowski 2002), although other trophic modes are known as well (Alvaro et al. 2011; Heard 2011; Błażewicz-Paszkowycz et al. 2014). The order is currently represented by over 1300 species (Anderson

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2017), yet its species richness is considered to be greatly underestimated, with as little as 2–3% of the true species richness being currently known to science (Appeltans et al. 2012; Błażewicz-Paszkowycz et al. 2012).

The Tanaidacea associated with coral reefs worldwide remain almost completely unknown and the list of 96 species reported so far is undoubtedly incomplete (see Fig. 1, Table 1 and citation therein). As few as 20 species were described from Australian coral reefs (Whitelegge 1901; Băcescu 1981; Edgar 1997; Błażewicz-Paszkowycz and Bamber 2009; Błażewicz-Paszkowycz and Zemko 2009; Stępień and Błażewicz-Paszkowycz 2009, 2013; Stępień 2013; Heard et al. 2018).

The aim of this paper is to analyze the small-scale tanaidacean species richness and composition at two sites (Lizard Island and Heron Island) at the Great Barrier Reef. We are also comparing our data with current global-scale knowledge on the coral reef tanaidacean fauna.

Material and methods

Study area

The materials were collected in 2008–2010 within the framework of the CReefs Program—The Australian Node. The field-work was coordinated by the Australian Institute for Marine Research (AIMS). We analyzed

materials collected during four expeditions: two each to Lizard and Heron Islands, both located at the Great Barrier Reef (GBR) (Fig. 2).

Heron Island is located in the southernmost part of the GBR (23° 25' S; 151° 59' E). It is a typical coral island in the Capricorn-Bunker group situated over 50 km offshore (Hutchings et al. 2009). The island is surrounded by a reef lagoon, built mainly by *Acropora* corals. Low tides isolate corals from the open ocean (Ahmad and Neil 1994).

Lizard Island (14° 41' S; 145° 28' E) is located in the northern part of the GBR and, together with two smaller islands (Bird and Palfrey), forms a small archipelago of continental origin surrounded by fringing reefs. This group of islands lies within the mid-continental shelf region, 30 km away from the Australian shore and 19 km away from other barrier reefs (Littman et al. 2008).

The GBR is affected by various oceanographic regimes. The part of the South Equatorial Current that reaches the continental slope (Ganachaud et al. 2007) splits into two branches between 15 and 19° S which flow south and north as the East Australian Current (EAC) and the Coral Coastal Current, respectively. The first forms the Tasman Front and warm eddies in the distinctively cooler Tasman Sea (Suthers et al. 2011), while the other forms the Hiri Current (Choukroun et al. 2010). The Queensland Plateau and the GBR apparently reduce the westward flow from the Pacific, and the currents entering the GBR, although weak, are highly variable. The

Fig. 1 State of knowledge on coral reef tanaidaceans (cf. Table 1). Described species known from the CReefs collection marked blue

Table 1 State of knowledge on world's coral reef tanaidaceans

Species	Area	Region	Habitat	Number of specimens	Number of stations/samples	Source
Apseuidae						
<i>Apsuoides buccinosus</i> Guțu 2006	East Australia	Heron Island, Wistari reef	Bottom covered with sand	1	1	Guțu 2006
<i>Apsuoides curtiramus</i> (Guțu, 2007)	East Africa	Reunion Island, lagoon near “La-salines-les Bais”	Dead coral	4	1	Guțu 2007
<i>Apsuoides galapagensis</i> Richardson, 1912	Northwest of Southern America	Galapagos Island	Coral and mud	nd	nd	Menzies 1953
<i>Apsuoides fecunda</i> (Guțu, 2006)	North Australia	Darwin	Reef flat pools	1	1	Guțu 2006
<i>Paradoxapsuoides botosaneamui</i> (Guțu, 2001)	Gulf of Mexico	Curacao Island	Coralloid sediment	1	1	Guțu 2001
<i>Paradoxapsuoides garthi</i> (Menzies, 1953)	West of Northern America	Mexico, Gulf of California, Isabel Island	Coral head	3	nd	Menzies 1953
<i>Paradoxapsuoides floppae</i> Bird, 2015	North of New Zealand	Kermadec Islands, Herald Islands, Milne Islets, Nugent Island, South Meyer Island (all Raoul group), Macauley Island, Cheeseman & Curtis Islands, L'Esperance	From rocks, cobbles, coarse sand, coral, shell debris, and antipatharian and yellow sponge	13	several	Bird 2015
<i>Paradoxapsuoides larakia</i> (Edgar, 1997)	North Australia	Darwin, Nightcliff, Charles Point, South Shell Island, East Point, Dudley Point, Weed Reef Malaysia, Timon Island	Coral rubble biotop	240	10	Edgar 1997
<i>Pugiodactylus coralensis</i> Guțu, 1998	Indonesia		Coral reef	1	1	Guțu 1998
Kalliapseudidae						
<i>Mesokalliapseudes bahamensis</i> (Sieg, 1982)	Gulf of Mexico	Bahama, Dumb Reef	nd	194	nd	Sieg 1982
<i>Tanapseudes ormuzana</i> (Băcescu, 1978)	Indonesia	Thailand, Adaman Sea, Tarang Island	Fine sand near coral reefs	8	1	Guțu and Angsupanich 2005
Leptocheliidae						
<i>Alloleptochelia insolita</i> Guțu, 2016	East Africa	Réunion Island	From dead corals covered with algae	9	3	Guțu 2016
<i>Kallileptochelia maiorina</i> Guțu, 2016	East Africa	Réunion Island	From dead corals	3	2	Guțu 2016
<i>Kallileptochelia paucilla</i> Guțu, 2016	Indonesia	Malaysia, Strait of Malacca, Langkawi Island, Pantai Kok	Collected at outer reef margin from <i>Pocillopora</i> corals	2	nd	Guțu 2016
<i>Leptochelia acrolophus</i> Bird, 2015	North of New Zealand	Kermadec Islands, Herald Islands, North and South Meyer Islands (all Raoul group), Raoul Island, Macauley Island, and L'Esperance Rock;	From various hard substrata in rockpools, sublittorally on rock surfaces, under boulders, among coarse sand, coral, clumping red algae, and gravel	70	19	Bird 2015
<i>Leptochelia dubia</i> (Krøyer, 1842)	East Australia	Great Barrier Reef	nd	nd	nd	Hale 1933

Table 1 (continued)

Species	Area	Region	Habitat	Number of specimens	Number of stations/samples	Source
<i>Leptochelia dubia</i> (Krøyer, 1842)	Gulf of Mexico	Bermudas, Castle Harbor	Dead coral	nd	nd	Richardson 1905
<i>Leptochelia elongata</i> Larsen and Rayment, 2002	Indonesia	Thailand, Adaman Sea, Racha Yai Island	Coral rubble	12	nd	Larsen and Rayment 2002
<i>Leptochelia longimana</i> Shiino, 1963	Gulf of Mexico	Caribbean, Florida to Gulf of Mexico	Back reef	nd	nd	Heard, Hansknecht and Larsen 2004
<i>Leptochelia savignyi</i> (Krøyer, 1842)	Indonesia	Bismarck Archipelago	Outlet of lagoon	nd	nd	Shiino 1965
<i>Pseudonototanaia</i> sp. A Heard, Hansknecht and Larsen, 1998	Gulf of Mexico	Florida	In association with coral (<i>Oculina</i>)	nd	nd	Heard, Hansknecht and Larsen 2004
Metapseudidae						
<i>Apsedomorpha hirsuta</i> (Stebbing, 1910)	Indian Ocean	Egmont Island	Reef edge	nd	nd	Stebbing 1910
<i>Apsedomorpha negoescuae</i> Guṭu, 2007	East Africa	Reunion Island, lagoon near 'La-salines-les Bais'	Dead coral	34	2	Guṭu 2007
<i>Apsedomorpha ortizi</i> Guṭu, 2006	Gulf of Mexico	Cuba	Dead coral	5	1	Guṭu 2006
<i>Apsedomorpha veleronis</i> (Menzies, 1953)	Northwest of Southern America	Colombia, Ocetavia Bay	Coral	2	nd	Menzies 1953
<i>Bamberus jinigudinus</i> Stepień and Błażewicz-Paszkowycz, 2013	West Australia	Ningaloo	Edge of large coral heads (small bommies), dead <i>Acropora</i>	16	7	Stepień and Błażewicz-Paszkowycz, 2013
<i>Calozodion suluk</i> Bamber and Shearer, 2005	Indonesia	Malaysia, Pantai Kok	Dead coral, outer reef margin	6	1	Guṭu 2007
<i>Creffs heronum</i> Stepień and Błażewicz-Paszkowycz, 2013	East Australia	Heron Island	Coral rubble on sand	52	4	Stepień and Błażewicz-Paszkowycz, 2013
<i>Cryptopsesdes acutifrons</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island	Coral reefs biotop	2	nd	Băcescu 1976c
<i>Cryptopsesdes leroyi</i> David and Heard, 2015	Hawaii	Hawaii Island, Ni'ihau Island, Hawaii'i	Coral reef	6	nd	David and Heard 2015
<i>Cryptopsesdes sankarakuttyi</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island	Coral reefs	3	nd	Băcescu 1976c
<i>Curtipelon carinatoides</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island, Dar es Salaam area	Scrapped dead corals	> 100	nd	Băcescu 1976c
<i>Curtipelon chadi</i> Stepień and Błażewicz-Paszkowycz, 2013	East Australia	Heron Island	small coral rubble and sand	14	5	Stepień and Błażewicz-Paszkowycz, 2013
<i>Curtipelon heterochelatum</i> Larsen, 2002	Indonesia	Thailand, Adaman Sea, Racha Yai Island	Coral reef	4	nd	Larsen 2002
<i>Cyclopsesdes estaficana</i> Băcescu, 1975	East Africa	Tanzania, Mbudya Island	Dead coral	2	nd	Băcescu 1975

Table 1 (continued)

Species	Area	Region	Habitat	Number of specimens	Number of stations/samples	Source
<i>Cycloapseudes</i> sp. A Heard, Hansknecht and Larsen 1998	Gulf of Mexico	Florida	Coral reef	nd	nd	Heard, Hansknecht and Larsen 2004
<i>Hoplomachus propinquus</i> (Richardson, 1902)	Gulf of Mexico	Bermudas, Florida	Back reef rubble	nd	nd	Heard, Hansknecht and Larsen 2004
<i>Msangia larvoides</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island	Coral reefs	> 100	nd	Băcescu 1976c
<i>Msangia mussida</i> Stepień and Błażewicz-Paszkowycz 2013	East Australia	Heron Island	Reef slope, coral rubble on sand	23	3	Stepień and Błażewicz-Paszkowycz 2013
<i>Msangia tarangensis</i> Gutu & Angsupanich, 2006	Indonesia	Thailand, Adaman Sea, Tarang Island	Bottom covered with fragments of dead coral	1	1	Gutu and Angsupanich 2006
<i>Pseudoapseudomorpha ornata</i> Gutu, 2006	Indonesia	Malaysia, Babi Besar Palau	Dead coral, algae, sponges, hydroids, ascidians	134	1	Gutu 2006
<i>Pseudoapseudomorpha wagait</i> (Edgar, 1997)	North Australia	Lee Point, East Point, West Point	Coral rubble	37	6	Edgar 1997
<i>Pseudoapseudomorpha</i> sp. A Heard, Hansknecht and Larsen, 1998	Gulf of Mexico	Florida, Bahama, North Caribbean Sea	Reef habitats	nd	nd	Heard, Hansknecht and Larsen 2004
<i>Synapseudes acroporae</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island, Kunduchi	Colonies of <i>Acropora</i> , sponge, sand	50	4	Băcescu 1976b
<i>Synapseudes australianus</i> Băcescu, 1981	East Australia	Heron Island, Wistari Reef Channel	nd	3	nd	Băcescu 1981
<i>Synapseudes hancocki</i> Menzies, 1953	Northwest of Southern America	Galapagos Island, Lobos de Afura Island, Ningaloo	From coral	2	nd	Menzies 1953
<i>Synapseudes caleyi</i> Stepień and Błażewicz, 2018	West Australia		Reef slope, coral heads	183	30	Heard al. 2018
<i>Synapseudes hansmuelleri</i> Gutu, 2006	Indonesia	Malaysia, Babi Besar Palau	Dead coral, algae, sponges, hydroids, ascidians	1032	4	Gutu 2006
<i>Synapseudes intumescens</i> Menzies, 1949	West of Northern America	California, Tomales Bluff	Reef on holdfasts of the alga <i>Laminaria</i> sp	3	nd	Menzies 1949
<i>Synapseudes menziesi</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island, Logg Cabine	Coral reefs, sponge	26	7	Băcescu 1976b
<i>Synapseudes minimus</i> Gutu, 2006	Indonesia	Malaysia, Babi Besar Palau	Dead coral, algae, sponges, hydroids, ascidians	1	1	Gutu 2006
<i>Synapseudes rudis</i> Menzies, 1953	West of Northern America	Guadalupe Island, Santa Catalina Island	Rocks encrusted with corals and bryozoa	11	nd	Menzies 1953
<i>Synapseudes singularis</i> Stepień and Błażewicz, 2018	East Australia	Lizard Island	Fore reef (mid shelf), coarse coral rubble, dead coral heads	15	8	Heard al. 2018
<i>Synapseudes violaceus</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island, Kunduchi	Coral reefs, sponge	11	3	Băcescu 1976b
<i>Synapseudes</i> sp. A Heard, Hansknecht and Larsen, 1998	Gulf of Mexico	South Carolina	Hard bottom or coral reef's habitat	nd	nd	Heard, Hansknecht and Larsen 2004

Table 1 (continued)

Species	Area	Region	Habitat	Number of specimens	Number of stations/samples	Source
<i>Vicininydes mirabilis</i> Guṭu, 2007	East Africa	Reunion Island, lagoon near “La-salines-les Bais”	Dead coral	1	1	Guṭu 2007
<i>Zaraza linda</i> Guṭu, 2006	Gulf of Mexico	Hispaniola Island	Dead coral with algae	6	1	Guṭu 2006
Mirandotanaidae						
<i>Pooreotanales ningaloo</i> Błażewicz-Paszkowycz and Bamber, 2009	West Australia	Ningaloo	Dead coral	2	2	Błażewicz-Paszkowycz and Bamber 2009
Numbakullidae						
<i>Numbakulla srilankensis</i> Guṭu, 2006	Central Indian Ocean	Sri Lanka	Fringing reef, dead coral	10	nd	Guṭu 2006
<i>Numbaculla pii</i> Stepień, 2013	East Australia	Heron Island	Reef flat, coral rubble on sand	31	5	Stepień, 2013
Pagurapseudidae						
<i>Indoapseudes brycesoni</i> Băcescu, 1976	East Africa	N of Dar es Salaam area: Mbudya Island, Changani, Oyster Bay	Coral reefs	69	60	Băcescu 1976c
<i>Indoapseudes secundus</i> Guṭu, 1997	Indonesia	Malaysia, Babi Besar Palau	Dead coral rocks	26	1	Guṭu 2006
<i>Macrolabrum aenigmaticus</i> Guṭu, 1997	Indonesia	Sanur Beach	Dead coral, dredging on bottom coarse sand	2	1	Guṭu 1997
<i>Macrolabrum boeri</i> Băcescu, 1981	East Australia	Heron Island, Westari Reef Channel	nd	2	nd	Băcescu 1981
<i>Macrolabrum trichopteroides</i> Băcescu, 1976	East Africa	Tanzania, Makatumbé	Coral reef biotop, from from sponge <i>Cynachya australiensis</i>	4	nd	Băcescu 1976a
<i>Macrolabrum trifidus</i> Guṭu, 1997	Indonesia	Sanur Beach	Dead coral, dredging on bottom coarse sand	1	1	Guṭu 1997
<i>Pagurapseudes abrauei</i> (Băcescu, 1981)	East Australia	Heron Island, Westari Reef Channel	nd	2	nd	Băcescu 1981
<i>Pagurapseudes dactylifrons</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island	Coral reefs, from shells	> 100	nd	Băcescu 1976c
<i>Pagurapseudes longicarpus</i> Guṭu, 1997	Indonesia	Bunaken Island	Dead coral, dredging on bottom coarse sand	1	1	Guṭu 1997
<i>Pagurapseudes pangitruhuli</i> Guṭu, 1992	Indonesia	Sanur Beach	Dead coral, dredging on bottom coarse sand	several	nd	Guṭu 1992
<i>Pagurapseudes razvani</i> Guṭu, 1997	Indonesia	Bali Island, Bunaken Island, Makassar Strait	Dead coral, dredging on bottom coarse sand	18	2	Guṭu 1997
<i>Pagurapseudes varians</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island, Makatumbé, Kunduchi, Logg Kabine	Coral reef biotop, sand, coarse sand	23–34	18	Băcescu 1976a
<i>Pagurapseudes tricola</i> Băcescu, 1976	East Africa	Tanzania, Mbudya Island	Coral reef biotop, <i>Tricola</i> shells	1	1	Băcescu 1976a
Parapseudidae						
<i>Ascumella caymanensis</i> Guṭu and Heard, 2002	Gulf of Mexico	Cayman Islands, Grand Cayman	Back reef	40	1	Guṭu and Heard 2002

Table 1 (continued)

Species	Area	Region	Habitat	Number of specimens	Number of stations/samples	Source
<i>Bunakenia indonesiana</i> Guṭu, 1995	Indonesia	Bunaken Island	Rest of dead coral head	24	1	Guṭu 1995
<i>Brachyolicoa estasiatica</i> Guṭu, 2007	Indonesia	Malaysia, Palau Babi Besar	Dead coral	3	1	Guṭu 2007
<i>Gutapseudes manda</i> Edgar, 1997	North Australia	Darwin, Nightcliff, South Shell Island, Weed Reef	Algal and coral rubble washings	14	6	Edgar 1997
<i>Parapseudes latifrons</i> (Grube, 1864)	Northwest of Southern America	Colombia, Octavia Bay	Coral	nd	nd	Menzies 1953
<i>Podictenius espinosus</i> (Moore, 1901)	Gulf of Mexico	Porto Rico	Coral bottom	nd	nd	Richardson 1905
Paratanaididae						
<i>Aparatanais hawaiiensis</i> Morales-Núñez, Pelleteri and Heard, 2016	Hawaii	Kaizers Channel, Kapua Channel, KYC Patch Reef, Haki'ui Reef, Channel Marker 12 Reef, Moku Manu Island, Kaizer's Wreck, Outside Pops, Toggs Wreck, Aquarium outside reef, Atlantis Wreck, Kapua Channel, Kaizers Channel, Ft. DeRussy Reef	nd	78	14	Morales-Núñez et al., 2016
<i>Metatanais spinipropodus</i> Morales-Núñez, Pelleteri and Heard, 2016	Hawaii	North Channel, Haki'ui Reef, Channel Marker 12, Kawaihae Reef	nd	8	4	Morales-Núñez et al., 2016
Sphaeromapseudidae						
<i>Sphaeromapseudes plumosetosa</i> Larsen, 2011	Gulf of Mexico	Caribbean Sea	Intertidal coral rubble	2	1	Larsen 2011
Sphyrapodidae						
<i>Sphyrapoides tuberculifrons</i> Guṭu and Heard, 2002	Gulf of Mexico	Cayman Islands, Grand Cayman	Shallow back reef rubble	9	1	Guṭu and Heard 2002
Tanaidae						
<i>Sineleobus stanfordi</i> (Richardson, 1901)	Indonesia	Bismarck Archipelago	Outlet of lagoon	nd	nd	Shiino 1965
<i>Tanais vanis</i> Miller, 1940	Hawaii	Kauai, Haeana Reef	nd	1	1	Sieg 1980
<i>Zuexo coralensis</i> Sieg, 1980	Indian Ocean	Maldiven, Attu-atol	In <i>Acropora</i>	10	nd	Sieg 1980
<i>Zuexo kermadecensis</i> Bird, 2015	North of New Zealand	Milne Islets, North Chanter Island, North and South Meyer Islands (all Raoul group), Raoul Island, Macauley Island, Cheeseman & Curtis Islands, and L'Esperance Rock	from various substrata including antipatharian sponge, boulders, cobbles, coral, pebbly-sand, rock walls, shelly debris, and tufting red algae	45	15	Bird 2015
Tanzanapseudidae						
<i>Acanthapseudes elegans</i> Roman, 1976	East Africa	Madagaskar	Coral reef	9	nd	Roman 1976

Table 1 (continued)

Species	Area	Region	Habitat	Number of specimens	Number of stations/samples	Source
<i>Tanzanapseudes langi</i> Băcescu, 1975	East Africa	Tanzania, Mbudya Island	On a sponge, in coral reef biotop	1	1	Băcescu 1975
<i>Tanzanapseudes levis</i> Stepień and Błażewicz-Paszkowycz, 2009	West Australia	Ningaloo	Coral rubble on sand	2	2	Stepień and Błażewicz-Paszkowycz 2009
<i>Tanzanapseudes longiseta</i> Băcescu, 1975	East Africa	Tanzania, Mbudya Island, Kunduchi	Coral reef	7	nd	Băcescu 1975
<i>Tanzanapseudes nieli</i> Stepień and Błażewicz-Paszkowycz, 2009	West Australia	Ningaloo	Coral rubble on sand	1	1	Stepień and Błażewicz-Paszkowycz 2009
<i>Tanzanapseudes polynensis</i> Müller, 1992	French Polnesia	Bora-Bora, Moorea	Dead coral in channel	295	nd	Müller 1992
<i>Tanzanapseudes mirificus</i> Guṭu, 2010	East Africa	Mauritius Island	Reef flat, dead corals	25	1	Guṭu 2010
<i>Tanzanapseudes bacescui</i> Guṭu, 2010	Central Indian Ocean	Sri Lanka Island	Wave-exposed coral reef flat	1	1	Guṭu 2010
incerte sedis						
<i>Metatanais bipunctata</i> Błażewicz-Paszkowycz and Zemko, 2009	East and West Australia	Lizard Island, Ningaloo	Dead coral	3	3	Błażewicz-Paszkowycz and Zemko 2009

water mass that flows into the GBR can reside there for a few days to weeks, to become later transformed into a strong and consistent northward jet and a substantially weaker, but more variable, southward jet (Choukroun et al. 2010). A westward jet from the Coral Sea enters the Arafura Sea (Gordon 2005; Saint-Cast and Condie 2006) through the shallow Torres Strait with depths > 20 m, which extends between the Cape of York and Papua New Guinea (Wolanski et al. 1988).

Sampling

Qualitative samples were collected from depths of 0–30 m by SCUBA divers. The bottom deposit from different, arbitrarily selected, microhabitats (e.g., coral rubble, soft sediments, algae, sand, gravel) was gathered by hand, placed in a 0.3-mm mesh size bag, and transported in 20 L buckets to the laboratory where, following addition of 5 ml formaldehyde or fresh water the buckets were left for an hour. Subsequently, the samples were rinsed with seawater, tanaidaceans were sorted live under a dissecting microscope and preserved in 80% ethanol. The tanaidaceans identified were found in 99 samples collected from 47 localities (out of a total of 231 samples and 152 localities) on the reef surrounding Heron Island (e.g., the Heron Reef) as well as from a few neighboring reefs: the Broomfield, Must Head, Lamont, Sykes, and Wistari (Fig. 2). The Tanaidacea were also recorded in 131 samples collected at 63 localities (out of a total of 191 samples and 118 localities) in the closest vicinity of Lizard Island as well as from barrier reefs such as the Carter, Yonge, Day, Hick, Martin, North Direction, Yewell, and Waining (Fig. 2).

Data analysis

As our data are not quantitative, we used relative abundance to describe the tanaidacean communities from Heron and Lizard Islands. Frequency of occurrence (F) and dominance (D) were calculated for each species in each area. Frequency of occurrence is defined as the percentage of samples containing a species relative to the total number of samples; dominance is the percentage of individuals of a given species relative to the total number of individuals of all species. Species-area curves were developed for each island. The curve is constructed by adding the cumulative number of different species observed as samples are added randomly. The species-area curves were constructed using Primer v.5 with 999 permutations (Clarke and Warwick 2001). In addition, based on the literature data, we analyzed global diversity of the Tanaidacea associated with coral reef habitats.

Results

Tanaidacean fauna of heron and Lizard Islands

The materials collected during the CReefs—The Australian Node program yielded a total of 7922 tanaidacean individuals. More than half of the collection (56%; 4243 individuals) came from Lizard Island, the rest (44%; 3379 individuals) being obtained from Heron Island. The specimens collected were found to represent 60 species from 17 families and 47 genera. More than half of the species identified (56, i.e., 87% of the entire collection) were new to science (Table 2). The species-accumulation curves for the two sites did not reach the asymptote (Fig. 3).

The two sites were very similar in their tanaidacean species richness: the Heron Island collection comprised 46 species representing 34 genera and 14 families, 41 species (38 genera from 14 families) being identified on Lizard Island. The two sites shared 26 species; 20 and 15 species were recorded only on Heron Island and on Lizard Island, respectively (Table 2). The most speciose families were the Metapseudidae Lang, 1970 (12 species) and the Leptocheliidae Lang, 1973 (8 species). The most speciose genera were *Pseudoapseudomorpha* (4 species), followed by *Paradoxapseudes*, *Parapseudes*, *Pugiodactylus*, and *Zeuxo* (3 species each).

Generally, the number of individuals and frequency of occurrence of most species were very low at both sites. On Heron Island, 34 species were found to occur in less than 15% of all samples, Lizard Island collection yielding 33 species present in less than 15% of samples. Twenty species were represented by fewer than 10 individuals each. Only 3 species (*Araleptocheliinae* subfam. gen.1 sp., *Paratanais* sp. 3, and *Leptochelia* sp.) were common and abundant at both sites (Table 2). Among the already known species, common and abundant was *Paradoxapseudes* aff. *larakia* (Edgar, 1997), but on Lizard Island only (Table 2).

The tanaidaceans found were numerically dominated by the Leptocheliidae (59 and 67% of individuals found on Heron and Lizard Islands, respectively). Three other families, the Metapseudidae (6 and 3%), the Aapseudidae (8 and 12%), and the Paratanaididae (10 and 7%), contributed substantially to the material as well.

Global diversity of coral reef tanaidaceans (previous studies)

Current knowledge on diversity of the tanaidacean fauna associated with coral reefs is incomplete. So far, there have been as few as 96 species from 13 families reported from this habitat worldwide (Table 1, Fig. 1). The most speciose families include the Metapseudidae, the Pagurapseudidae, and the Leptocheliidae with 36, 13 and 10 known species, respectively. Thus, the three families account for more than half of coral

Table 2 Species composition of tanaidacean fauna on Heron and Lizard Islands. Number of individuals (N), dominance (D), and frequency of occurrence (F). Italicized characters indicate names of the most frequent and abundant species

Family/ species	Heron Island			Lizard Island		
	N	D [%]	F [%]	N	D [%]	F [%]
Apseudidae						
<i>Apseudes</i> sp.	12	0.35	10.10	20	0.47	8.40
<i>Bilobatus</i> sp.	7	0.2	2.02	1	0.02	0.76
<i>Paradoxapseudes</i> aff. <i>larakia</i> (Edgar, 1997)	80	2.36	20.20	474	11.17	42.75
<i>Paradoxapseudes</i> sp. 2	53	1.56	18.18			
<i>Pugiodactylus</i> sp. 1	1	0.02	1.01	7	0.16	1.35
<i>Pugiodactylus</i> sp. 2	136	4.02	30.30	12	0.28	4.58
<i>Pugiodactylus</i> sp. 3				7	0.16	2.29
Kalliapseudidae						
<i>Kalliapseudes</i> sp. 1	19	0.56	3.03			
<i>Kalliapseudes</i> sp. 2	1	0.02	1.01			
Metapseudidae						
<i>Apseudomorpha</i> sp.	40	1.18	13.13			
<i>Creeps heronum</i> Stepień & Błażewicz-Paszkowycz, 2013	52	1.53	4.04			
<i>Cryptoapseudes</i> sp.	2	0.05	2.02	3	0.07	1.35
<i>Curtipleon chadi</i> Stepień & Błażewicz-Paszkowycz, 2013	14	0.41	5.05			
<i>Julmarichardia</i> sp.	3	0.08	2.02	96	2.26	14.50
<i>Msangia</i> sp.				6	0.14	3.82
<i>Msangia mussida</i> Stepień & Błażewicz-Paszkowycz, 2013	23	0.68	3.03			
<i>Pseudoapseudomorpha</i> sp. 1	21	0.62	6.06	26	0.61	4.58
<i>Pseudoapseudomorpha</i> sp. 2	29	0.85	10.10	19	0.44	3.05
<i>Pseudoapseudomorpha</i> sp. 3	24	0.71	10.10			
<i>Pseudoapseudomorpha</i> sp. 4	4	0.11	4.04			
<i>Synapseudes singularis</i> Stepień and Błażewicz, 2018				15	0.35	6.10
Numbakullidae						
<i>Numbakulla pii</i> Stepień, 2013	31	0.91	5.05			
Pagurapseudidae						
<i>Indoapseudes</i> sp.				11	0.25	4.58
<i>Macrolabrum boeri</i> Bacescu, 1981	24	0.71	7.07			
<i>Macrolabrum</i> sp.				8	0.18	5.34
<i>Pagurapseudes</i> sp.	14	0.41	7.07	4	0.09	3.05
Pagurapseudopsidae						
<i>Paguroapseudopsis</i> sp.	20	0.59	3.03			
Parapseudidae						
<i>Brachylycoa</i> sp.	5	0.14	4.04	18	0.42	5.34
<i>Pakistanapseudes</i> sp.	3	0.08	1.01	3	0.07	2.29
<i>Parapseudes</i> sp. 1	142	4.2	26.26			
<i>Parapseudes</i> sp. 2	3	0.08	3.03			
<i>Parapseudes</i> sp. 3	36	1.06	8.08	3	0.07	1.53
Sphaeromapseudidae						
<i>Sphaeromapseudes</i> sp.				8	0.18	1.53
Whiteleggiidae						
<i>Whiteleggia multicarinata</i> (Whitelegge, 1901)	5	0.14	4.04	1	0.02	0.76
Cryptocopidae						

Table 2 (continued)

Family/ species	Heron Island			Lizard Island		
	N	D [%]	F [%]	N	D [%]	F [%]
<i>Iugentotana</i> sp.	2	0.05	2.02	20	0.47	11.45
Heterotanoididae						
<i>Heterotanoides</i> sp.				134	3.15	16.79
Leptocheliidae						
<i>Leptocheliidae</i> subfam. gen.1 sp.	277	8.19	42.42	1103	25.99	48.85
<i>Leptocheliidae</i> subfam. gen. 2 sp.	65	1.92	20.20	904	21.3	17.76
<i>Grallatotana</i> sp.				151	3.55	3.82
<i>Konarus</i> sp.	55	1.62	20.20	8	0.18	23.66
<i>Leptochelia</i> sp.	1616	47.82	80.81	156	3.67	74.05
<i>Leptocheliinae</i> gen. 1 sp.				6	0.14	10.69
<i>Neoleptochelia</i> sp.				337	7.94	3.05
<i>Poorea</i> sp.				188	4.43	0.76
Nototanoidae						
<i>Nesotana</i> sp.	15	0.44	7.07	81	1.9	16.79
Paratanoidae						
<i>Bathytana</i> sp. 2	2	0.05	2.02			
<i>Pseudobathytana</i> sp. 1	1	0.02	1.01	1	0.02	0.76
<i>Paratana</i> sp. 2	107	3.16	29.29			
<i>Paratana</i> sp. 3	259	7.66	51.52	310	7.3	45.80
Pseudotanoidae						
<i>Pseudotana</i> sp. 1	79	2.33	26.26	25	0.58	6.11
<i>Pseudotana</i> sp. 2	3	0.08	1.01			
Typhlotanoidae						
<i>Antiplotana</i> sp.				25	0.58	4.58
Tanaidae						
<i>Tana</i> sp.				26	0.61	1.53
<i>Zeuxo</i> sp. 1	42	1.24	17.17	13	0.3	4.58
<i>Zeuxo</i> sp. 2	20	0.59	1.01			
<i>Zeuxo</i> sp. 3	5	0.14	5.05			
Incerte sedis						
<i>Metatana bipunctata</i> Błażewicz-Paszkowycz & Zemko, 2009	6	0.17	5.05	1	0.02	0.76
<i>Tangalooma</i> sp.	12	0.35	8.08		0	
<i>Incerte sedis</i> gen. 1 sp.				1	0.02	0.76
<i>Incerte sedis</i> gen. 2 sp.				2	0.04	1.53
<i>Incerte sedis</i> gen. 3 sp.	9	0.26	6.06	9	0.21	0.76

reef tanaidacean diversity. Coral reef habitats have been reported as supporting a total of 43 tanaidacean genera, *Synapseudes* (in the family Synapseudidae) being the most speciose one (12 species).

Most of earlier studies have been based on very limited datasets. The majority of sites sampled yielded a single specimen each, found in single randomly collected samples. Species lists from even larger areas seem far from complete (Table 1). For example, African coral reefs are known to support as few as 22 species (Băcescu 1975, 1976a, b, c; Roman

1976; Guțu 2007, 2010, 2016), 21 species were recorded in Indonesia (Stebbing 1910; Shiino 1965; Guțu 1992, 1995, 1997, 1998, 2006, 2007, 2016; Larsen 2002; Larsen and Rayment 2002; Guțu and Aguspanich 2005, 2006), and 20 species from off Australia (Hale 1933; Edgar 1997; Băcescu 1981; Guțu 2006; Błażewicz-Paszkowycz and Zemko 2009; Błażewicz-Paszkowycz and Bamber 2009; Stępień and Błażewicz-Paszkowycz 2009, 2013; Stępień 2013; Heard et al. 2018), and yet those three areas belong to the most comprehensively studied regions of the world in terms of coral

Fig. 3 Species-area curves constructed for Heron Island (HER) and Lizard Island (LIZ) tanaidacean faunas

reef tanaidacean fauna diversity. Coral reefs in some regions or even in entire basins, e.g., the Red Sea, have not been surveyed for tanaidacean diversity at all. There is only a few tanaidacean species known from the Great Florida Reef, the world's third largest barrier reef (Heard et al. 2004); few species only have been reported from the Caribbean Sea reef systems (Richardson 1905; Sieg 1982; Guțu 2001, 2006; Guțu and Heard 2002; Larsen 2011). The scale of tanaidacean diversity underestimation is therefore huge, and there is hardly any recent information available as most of current knowledge is based on data published more than 30 years ago.

The spatial scale of research is also very restricted, as most surveys have been focused on a single small island each. Most often data are scattered in different publications. For example, the 21 tanaidacean species known from Indonesia were described in 12 papers published between 1965 and 2016 (Shiino 1965; Guțu 1992, 1995, 1997, 1998, 2006, 2007, 2016; Larsen 2002; Larsen and Rayment 2002; Guțu and Agusanich 2005, 2006). Moreover, no ecological research on the coral reef tanaidaceans has been carried out, so knowledge on habitat characteristics is very limited and unreliable, and information on factors controlling distribution and diversity of the fauna is absent.

Discussion

Fifty six (out of a total of 60) tanaidacean species identified from the coral reefs surveyed in this study (CReefs samples) proved new to science. Moreover, 10 out of the 20 species reported previously from Australian coral reefs were also described from the CReefs collections (Błażewicz-Paszkowycz and Bamber 2009; Błażewicz-Paszkowycz and Zemko 2009; Stępień and Błażewicz-Paszkowycz 2009, 2013; Stępień, 2013; Heard et al. 2018). Our results significantly extend the list of Australian tanaidaceans. Recent studies, carried out mainly off the southern part of the continent and based on collections from different habitats and depths, including the deep sea, yielded more than 170 described species (Bamber

2005; Edgar 2008; Błażewicz-Paszkowycz and Bamber 2007a, b, 2012). In view of considerable underestimation of tanaidacean diversity in coral reef habitats worldwide, it is not surprising to find a high number of new species in an area not sampled before, as highlighted by our analysis and previous studies on other peracarids (Plaisance et al. 2011). The materials obtained for this study from a very restricted area resulted in the number of tanaidacean species known from world's coral reefs being almost doubled (Fig. 1). On both islands, samples were collected along a distance as short as several kilometers, the area surveyed accounting for much less than 0.01% of the entire GBR. Moreover, as indicated by the shape of the species-accumulation curves, more species should still be present in each of the two localities investigated. In addition, further studies based on quantitative materials amenable to comprehensive and reliable statistical analyses are needed. Therefore, the species list presented in this paper is undeniably not complete; more species will be recorded when more habitats, including deeper areas, are sampled on wider spatial scales. Logistic and environmental restrictions limited the number of samples which could have been collected in this study from deeper (> 20 m) areas, from outer reefs and from living corals. On the other hand, had deeper parts of the reefs (> 30 m) be explored, the species list would have been presumably supplemented with members of families such as the Typhlotanidae or Tanaellidae, reported from deeper waters of the Bass Strait (Błażewicz-Paszkowycz and Bamber 2012), Esperance (Bamber 2005) or the deeper shelf off West Australia (McCallum et al. 2014; Poore et al. 2014).

Nevertheless, our results and records in the World Register of Marine Species (Appeltans et al. 2012; Błażewicz-Paszkowycz et al. 2012) allow to assume that the GBR tanaidacean fauna is diverse but the diversity is highly underestimated. The number of species reported tends to be low when compared against that of large taxa studied far more extensively and on much larger spatial scales, e.g., shelled gastropods (represented in the GBR by 2500 species), bivalves, brachyurans and stomatopods, each represented on the GBR by some 500 species (Ahyong 2009; Willan 2009). It would be more reasonable to compare the GBR tanaidacean

diversity with that of some other peracarids (Preston and Doherty 1994). Lowry and Myers (2009) showed amphipods, with 235 species, to be the most diverse peracarids on the GBR, but their study, although based on collections from only three distant locations (Lizard, Orpheus and Heron Islands), involved a long-term and intensive field work. Our results should rather be compared with data on isopods, the crustaceans which often share habitats with tanaidaceans and are behaviourally similar to them (low mobility, burrowers). The CReefs collection contains about 100 isopod species (Bruce, personal communication), although the total number of isopods known from Australian coral reefs is twice as high (Ahyong, 2009). In any case, diversity of the three peracarid orders mentioned above is most probably still underestimated due to the paucity of studies, low sampling effort and a restricted spatial scale of biodiversity inventories.

In terms of species richness, the Australian tanaidacean fauna associated with coral reefs is far more diverse (Fig. 1) than the fauna from similar habitats in other parts of the world, although this conclusion is most probably an artifact resulting from sampling bias. For example, as few as 15 and 22 species were reported from coral reefs in the Gulf of Mexico and off the east coast of Africa, respectively (see Table 1 and citation therein). It is also worth noting that tanaidacean faunas associated with coral reefs in other regions are dominated, like in this study, by members of the Leptochelliidae and Metapseudidae (Fig. 1). Families such as the Whiteleggiidae and Numbakullidae, recorded in our materials, are restricted in their distribution to the Indo-Pacific and Australia, and presumably radiated in those regions (Bamber and Błażewicz-Paszkowycz 2013). Our data from Heron and Lizard Islands (Table 2) as well as results of previous studies (Table 1) demonstrate high dominance of three tanaidacean families in coral reef habitats. The Leptochelidae are common and abundant in various shallow water sites all over the world (e.g., Edgar 2012; Bamber 2013), and their being an important component of coral reef communities it is not surprising. Similarly, members of the family Pagurapseudidae are found in shallow waters (including coral reefs habitats) of temperate and tropical regions (e.g., Băcescu 1981; Bamber 2009; Błażewicz-Paszkowycz and Bamber 2012). Current knowledge on the Metapseudidae might suggest that the group is associated mostly with coral reefs (Băcescu 1976b; Guțu 2006; David and Heard 2015). Metapseudids are most probably typical inhabitants of hard bottom habitats, especially crevices and coral rubble, as observed for some species of the genus *Msangia*. Nevertheless, the absence of more comprehensive data concerning the family's biology and phylogenetic relationships precludes any reliable conclusion at the moment. Moreover, it cannot be ruled out that such high dominance of the families mentioned is an artifact resulting from low sampling effort and a very restricted spatial coverage in all the studies conducted so far.

Bearing in mind that tanaidaceans are non-motile benthic brooders, to find 26 species apparently shared by the two sites more than 2000 km apart is perhaps the most unexpected outcome of the present study. Passive dispersal by marine currents or rafting can be invoked as the potential responsible mechanisms (Bamber 2012; Bamber and Błażewicz-Paszkowycz 2013). Tanaidaceans usually live in self-constructed tubes (Johnson and Attramadal 1982; Hassack and Holdich 1987); alternatively, they burrow in the sediment, although some are associated with algal mats (Edgar 2012), mangroves or sunken wood (Larsen et al. 2013; Błażewicz-Paszkowycz et al. 2014). The tanaidacean specimens found in this study were far too small to be directly observed in their microhabitats, but since some of them were numerous in coral rubble samples, they may be inferred—similarly to many other invertebrates (Plaisance et al. 2011)—to inhabit crevices, fissures, and cracks in scleractinian skeletons. Intuitively, it is feasible to imagine that association with certain objects increases the chance for passive dispersal (but see Reidenauer and Thistle 1985). Jackson (1986 and citations therein) emphasized the role of benthic storms in passive transport of sessile organisms and showed fragments of branching corals to have been transported, during a single storm, for a distance of up to 50 m. It might therefore be possible that dispersal along with a fragment of their habitat is possible at least for some tanaidaceans, for example members of the Leptocheliidae. Experiments (Choukroun et al. 2010) have documented water flow convection between the northern and the southern parts of the GBR, although such potential connectedness that might minimize the genetic divergence between remote populations in the GBR was questioned (e.g., Planes et al. 2001; Campbell et al. 2005). A possibility that at least some tanaidaceans recorded at both GBR sites sampled in this study represent cryptic species, alternatively “pseudo-sibling” species, cannot be ruled out and requires further examination by molecular techniques. However, the CReefs material examined here cannot be used for such studies due to methodological problems, associated mainly with the sample preservation method used.

Our study is the first attempt to assess the tanaidacean species richness on the Great Barrier Reef. In addition to the high, previously unexplored, diversity of those crustacean taxon, urgent need to develop a more comprehensive approach to studies of those invertebrates associated with coral reef habitats worldwide is demonstrated. If the diversity and distribution patterns of tanaidaceans (and all other small peracarids) are to be analyzed, the research should involve quantitative samples supplemented with comprehensive data concerning environmental conditions in various microhabitats, collected on larger spatial scales. Despite obvious restrictions associated with sampling in protected areas such as the GBR and other coral reefs, it is also important to plan molecular analyses, including phylogeographic studies that will help to explain

distribution patterns and origin of the fauna, particularly with respect to taxa such as the Metapseudidae that seem to be most closely associated with coral reefs.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Sampling and field studies Permits and approval of field or observational studies are not applicable for authors.

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