

Richness and large-scale distribution of marine benthic caridean shrimps (Decapoda: Caridea) from the Eastern Tropical Pacific

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ABSTRACT

Based on an updated checklist of the benthic caridean shrimp fauna of the Eastern Tropical Pacific (ETP), we analyzed their large-scale species richness distribution patterns using a grid approximation. Caridean fauna is composed of 183 species belonging to 67 genera and 18 families. Alpheidae, Palaemonidae and Thoridae contributed largely to species richness. *Alpheus* and *Synalpheus* were the most diverse genera. Most species (24%) have a narrow distribution inhabiting a single grid, and as many as 135 are restricted to < 5 grids. Mexico has the largest richness (130) besides Ecuador (98) and Panama (75). Richness among grids varies largely; overall, it is larger around Galapagos and Panama, Colombia, Costa Rica and the Gulf of California. There was a meaningful correlation between a proxy of sampling intensity and richness, suggesting that along with habitat heterogeneity or large-scale evolutionary processes currently invoked as richness drivers, the pattern can also be related to differences in research efforts. Exponential fitting and Chao2 index suggest that the caridean faunal inventory from the ETP is still far from being complete. Overall, the results call for a more thoughtful and systematic sampling scheme in order to get information from poorly sampled environments and areas in the ETP.

KEY WORDS

Checklist, faunal gap, species rarity, latitudinal patterns.

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INTRODUCTION

Shrimps included in the infraorder Caridea are the most diverse group of decapod shrimps (Gorny, 1999; De Grave and Fransen, 2011). Caridean shrimps are mostly benthic organisms inhabiting muddy to rocky bottoms from a wide diversity of habitats (e.g., tidal pools, seaweeds), either free or associated to other marine organisms (Wicksten, 1983; Bauer, 2004; Guzmán, 2008). They can be found from intertidal to hydrothermal vents, and in freshwater, estuarine and marine habitats worldwide, from the equator to the poles but mainly inhabiting tropical waters (Carvacho and Ríos, 1982; Martin, 2003; Anker *et al.*, 2006a).

Caridean shrimp studies in the Eastern Tropical Pacific (ETP) started as early as 1869 in Panama (Smith, 1869) and studies in the Pacific coast of Mexico and Ecuador contributed steadily via the discrete addition of new species to the regional fauna (Faxon, 1893; 1896). This early trend was occasionally disrupted by large-scale works where the caridean taxonomy of large areas (Coutière, 1909) or entire supraspecific groups (Holthuis, 1951; 1952; Kim and Abele, 1988) were addressed. Recently, as a result of studies conducted by local taxonomists (Abele and Kim, 1989; Wicksten, 1991; Li and Poupin, 2009) and ecologists (Hernández *et al.*, 2013), there has been an increase in the knowledge of the caridean shrimp fauna from the ETP.

The most recent checklist of the benthic caridean shrimp fauna from the ETP was published by Wicksten and Hendrickx (2003). Since then, species descriptions (Wicksten and Martin, 2004; Hermoso-Salazar and Álvarez, 2005; Anker *et al.*, 2006a; 2007; 2009; Hermoso-Salazar and Hendrickx, 2006; Li, 2006; Marin and Anker, 2008; Li and Poupin, 2009; Hendrickx, 2010), geographic range extension (Hermoso-Salazar and Hendrickx, 2005), and changes in taxonomy and systematics (Marin, 2009; Bracken *et al.*, 2010) have substantially modified the previously known information concerning caridean shrimp faunal inventory and its distribution patterns in the area. Current distribution patterns of ETP caridean shrimps were known after studies focused on more inclusive groups such as macroinvertebrates, crustaceans or decapods (Arntz *et al.*, 1999; Blanchette *et al.*, 2008) and at large-scale levels (*i.e.*, Province) (Boschi, 2000; Wicksten and Hendrickx, 2003). For

example, Boschi (2000) indicates that the so called Panamic province hosts the largest number of both planktonic and benthic caridean species (161), followed by the Galapagos (67 species) and Cortes (50 species) provinces. Additionally, the same general pattern emerges when only benthic caridean species are considered (Wicksten and Hendrickx, 2003). While there is an overall agreement among studies regarding richness patterns, the previously used spatial scale precludes direct comparisons among areas which obscure intraregional species richness patterns. Beside taxonomic bias, databases resulting from field exploration projects and/or previously published information allow for large-scale analyses that evaluate current species richness and distribution scenarios (Costello *et al.*, 2010). In this regard, there is a need to integrate previously published findings such as spatially explicit checklist, to gain perspective on what is known and what are the major scientific gaps regarding benthic caridean shrimp species richness and distribution in the ETP.

In this paper, species composition and distribution of the benthic caridean shrimp fauna of the Eastern Tropical Pacific are analyzed. An updated (up to 2017) checklist of the benthic caridean shrimp fauna from the ETP, at a 1° of latitude by 1° longitude, was assembled and further analyzed to address a set of interrelated questions. What is the richness and composition of the ETP benthic caridean shrimp fauna? Has the accumulative historic species record been homogeneous over the entire region or do discrepancies exist among areas? Does species richness show any distribution pattern in the area? Are ETP benthic caridean shrimp species widely or narrowly distributed in the area? Finally, how complete is the benthic caridean shrimp fauna inventory?

MATERIAL AND METHODS

We compiled a checklist of the marine benthic caridean shrimps that have been collected and/or recorded in the coastal and shelf area of the Eastern Tropical Pacific. A database was generated from primary references that have been formally published as papers, monographs and books (mainly, but not restricted to Kingsley, 1878; Faxon, 1893; Rathbun, 1904; Coutière, 1909; Chace, 1937; 1962; Holthuis, 1951; 1952; Abele,

1975; Abele and Patton, 1976; Wicksten, 1983; 1991; 2000; Kim and Abele, 1988; Abele and Kim, 1989; Lemaitre and Álvarez-León, 1992; Wicksten and Hendrickx, 1992; 2003; Burukovsky, 2001; complete reference list is included in Tab. 1). In order to minimize taxonomic bias, only valid species were included,

hence all taxa names were crosschecked in the World Register of Marine Species (WoRMS) and Integrated Taxonomic Information System (ITIS). Systematic arrangement of benthic caridean shrimps follows De Grave and Fransen (2011). The taxa (genera and species) were arranged alphabetically (Tab. 1).

Table 1. Checklist of marine benthic caridean shrimps from the Tropical Eastern Pacific. Systematic arrangement follows De Grave and Fransen (2011). Mexico-Revillagigedo: MEX, Clipperton: CLP, El Salvador: SAL, Nicaragua: NIC, Costa Rica: CR, Panama: PAN, Colombia-Malpelo: COL, Ecuador-Galapagos: ECU, Peru: PER, Central Pacific: PC, Indopacific: IP, Indian: IND, Atlantic: ATL, s: shallow.

Taxon	Distribution	Depth (m)	Reference
Pasiphaeidea Dana, 1852			
Pasiphaeidae Dana, 1852			
<i>Glyphus marsupialis</i> Filhol, 1884	PAN, IP, ATL	500 – 4,000	Hendrickx and Wicksten, 2004
Bresilioidea Calman, 1896			
Alvinocarididae Christoffersen, 1986			
<i>Alvinocaris lusca</i> Williams and Chace, 1982	ECU	2,450	Williams and Chace, 1982
Bresiliidae Calman, 1896			
<i>Encantada spiniculata</i> Wicksten, 1989	ECU	55 – 92	Wicksten, 1991
Disciadidae Rathbun, 1902			
<i>Discias serrifer</i> Rathbun, 1902	ECU	0 – 55	Wicksten, 1991
Nematocarcinoidea Smith, 1884			
Nematocarcinidae Smith, 1884			
<i>Nematocarcinus agassizii</i> Faxon, 1893	MEX, CR, PAN, COL, ECU, PER	224 – 1,883	Burukovsky, 2001
<i>Nematocarcinus faxoni</i> Burukovsky, 2001	MEX, ECU, ATL	660 – 1,680	Burukovsky, 2001
Rhynchocinetidae Ortmann, 1890			
<i>Cinetorhynchus hendersoni</i> (Kemp, 1925)	COL	2.5	Wicksten and Hendrickx, 2003
<i>Cinetorhynchus hiatti</i> (Holthuis and Hayashi, 1967)	ECU, IP	s	Wicksten and Hendrickx, 2003
<i>Rhynchocinetes typus</i> H. Milne Edwards, 1837	ECU	s	Wicksten, 1991
Stylodactyloidea Spence Bate, 1888			
Stylodactylidae Spence Bate, 1888			
<i>Bathystylodactylus echinus</i> Wicksten and Martin, 2004	MEX	3,427 – 3,630	Wicksten and Martin, 2004
Palaemonoidea Rafinesque, 1815			
Palaemonidae Rafinesque, 1815			
<i>Allopontonia brockii</i> (de Man, 1888)	MEX, IP, IND		Wicksten and Hernandez, 2000
<i>Ancylomenes lucasi</i> (Chace, 1937)	MEX, CR, PAN, COL	0 – 90	Hendrickx, 2005
<i>Ascidonia pusilla</i> (Holthuis, 1951)	CR, PAN, ECU	5 – 23	Fransen, 2002
<i>Brachycarpus biunguiculatus</i> (Lucas, 1849)	MEX, CLP, CR, PAN, COL, ECU, PC, IP, IND, ATL	1 – 30	Hendrickx, 2005
<i>Chacella kerstitchi</i> (Wicksten, 1983)	MEX, PER	30	Hendrickx, 2005
<i>Fennera chacei</i> Holthuis, 1951	MEX, CLP, CR, PAN, COL, ECU, PC, IP, IND	10	Li and Poupin, 2009
<i>Gnathophylloides mineri</i> Schmitt, 1933	MEX, COL, ECU, PC, IP, IND, ATL		Hermoso-Salazar and Solis-Weiss, 2001a
<i>Gnathophyllum panamense</i> Faxon, 1893	MEX, PAN, COL, ECU, IP	0 – 20	Wicksten, 1991
<i>Harpiliopsis depressa</i> (Stimpson, 1860)	MEX, CLP, CR, PAN, COL, ECU, PC, IND	4.6 – 15	Hendrickx, 2005
<i>Harpiliopsis spinigera</i> (Ortmann, 1890)	MEX, CLP, PAN, COL, ECU, IP, IND	10 – 48.8	Li and Poupin, 2009
<i>Hymenocera picta</i> Dana, 1852	CR, PAN, COL, ECU, PC, IP, IND	5 – 12	Wicksten and Hernandez, 2000
<i>Nematopalaemon colombiensis</i> (Squires and Mora L., 1971)	COL	9.1 – 200	Wicksten and Hendrickx, 2003
<i>Neopontonides dentiger</i> Holthuis, 1951	MEX, COL, ECU	3.3	Hendrickx, 2005
<i>Neopontonides henryvonprahli</i> Ramos, 1995	CR, COL	1 – 6	Werthmann and Vargas, 2003
<i>Palaemon gladiator</i> Holthuis, 1952	CLP, ECU	s	Wicksten and Hendrickx, 2003
<i>Palaemon gracilis</i> (Smith, 1871)	MEX, NIC, PAN		Hendrickx, 2005
<i>Palaemon hancocki</i> Holthuis, 1950	PAN, COL, ECU, PER		Wicksten and Hendrickx, 2003
<i>Palaemon hiltoni</i> (Schmitt, 1921)	MEX, COL	0.4 – 1	Hendrickx, 2008
<i>Palaemon peruanus</i> Holthuis, 1950	PER		Wicksten and Hendrickx, 2003
<i>Palaemon ritteri</i> Holmes, 1895	MEX, CR, PAN, ECU, PER	0 – 40	Hendrickx, 2005

Table 1. Cont.

Taxon	Distribution	Depth (m)	Reference
<i>Palaemon schmitti</i> (Holthuis, 1950)	PAN, COL		Wicksten and Hendrickx, 2003
<i>Palaemonella asymmetrica</i> Holthuis, 1951	CLP, ECU	4 – 67	Li and Poupin, 2009
<i>Palaemonella holmesi</i> (Nobili, 1907)	MEX, CR, PAN, COL, ECU	2 – 117	Hendrickx, 2005
<i>Periclimenaeus hancocki</i> Holthuis, 1951	MEX, PAN, COL	53.5	Hendrickx, 2005
<i>Periclimenaeus pacificus</i> Holthuis, 1951	PAN, COL, ECU	3.3 – 53.5	Wicksten and Hendrickx, 2003
<i>Periclimenaeus spinosus</i> Holthuis, 1951	MEX, CR		Hendrickx, 2005
<i>Periclimenes infraspinis</i> (Rathbun, 1902)	MEX, CR, ECU	5 – 110	Hendrickx, 2005
<i>Periclimenes murcielagensis</i> Vargas, 2000	CR	25	Wicksten and Hendrickx, 2003
<i>Periclimenes veleronis</i> Holthuis, 1951	ECU	6.7	Wicksten and Hendrickx, 2003
<i>Pontonia chimaera</i> Holthuis, 1951	MEX, PAN		Hendrickx, 2005
<i>Pontonia longispina</i> Holthuis, 1951	MEX		Hendrickx, 2005
<i>Pontonia margarita</i> Verrill, 1869	MEX, CR, PAN, COL, ECU, ATL	0 – 10	Martinez-Guerrero and Hendrickx, 2011
<i>Pontonia panamica</i> Marin and Anker, 2008	PAN	s	Marin and Anker, 2008
<i>Pontonia pinnae</i> Lockington, 1878	MEX, PAN, COL, ATL	30.5	Hendrickx, 2005
<i>Pontonia simplex</i> Holthuis, 1951	MEX	20	Martinez-Guerrero and Hendrickx, 2011
<i>Pseudocutierea elegans</i> Holthuis, 1951	MEX, COL, ECU, PER	75.2 – 83.5	Hendrickx, 2005
<i>Pseudoveronina laevifrons</i> (Holthuis, 1951)	MEX, COL, ECU	2 – 20	Marin, 2008
<i>Sandyella bicornuta</i> (Li and Poupin, 2009)	CLP	55	Li and Poupin, 2009
<i>Sandyella mclaughlinae</i> (Li, 2006)	CLP	54 – 55	Marin, 2009
<i>Sandyella quadricornuta</i> (Li and Poupin, 2009)	CLP	54 – 55	Li and Poupin, 2009
<i>Sandyella sexicornuta</i> (Li and Poupin, 2009)	CLP	54	Li and Poupin, 2009
<i>Sandyella tricornuta</i> (Hendrickx, 1990)	MEX	30 – 40	Marin, 2009
<i>Tuleariocaris holthuisi</i> Hipeau-Jacquotte, 1965	MEX, PC, IND	5 – 10	Wicksten and Hendrickx, 2003
<i>Typton crosslandi</i> Bruce, 1978	ECU		Wicksten and Hendrickx, 2003
<i>Typton hephaestus</i> Holthuis, 1951	MEX	15.8	Hendrickx, 2005
<i>Typton serratus</i> Holthuis, 1951	MEX, ECU, COL	13.3 – 25	Hendrickx, 2005
<i>Typton tortugae</i> McClendon, 1911	MEX, ATL	0 – 20	Hendrickx, 2005
<i>Veleronia serratifrons</i> Holthuis, 1951	CR, ECU, PER	7 – 25	Marin, 2008
<i>Veleronia sympathes</i> (De Ridder and Holthuis, 1979)	CLP, GAL	8 – 55	Li and Poupin, 2009
<i>Waldola schmitti</i> Holthuis, 1951	MEX, COL	16.7 – 41.7	Hendrickx, 2005
<i>Zenopontonia soror</i> (Nobili, 1904)	MEX, PAN, COL, ECU, PC, IP, IND	3 – 30.5	Hendrickx, 2005
Alpheoidea Rafinesque, 1815			
Alpheidae Rafinesque, 1815			
<i>Alpheopsis allanhancocki</i> Wicksten, 1992	MEX, ECU	10	Hickman Jr. and Zimmerman, 2000
<i>Alpheopsis cortesiana</i> Wicksten and Hendrickx, 1986	MEX	20 – 90	Wicksten and Hendrickx, 2003
<i>Alpheus aequus</i> Kim and Abele, 1988	CR, PAN, ECU	0 – 5	Anker <i>et al.</i> , 2007b
<i>Alpheus agrogon</i> Ramos, 1997	COL	s	Ramos, 1997
<i>Alpheus antepaenultimus</i> Kim and Abele, 1988	CR, PAN		Wicksten and Hendrickx, 2003
<i>Alpheus arenensis</i> (Chace, 1937)	MEX, CR, PAN, COL, ECU	0 – 10	Anker <i>et al.</i> , 2008b
<i>Alpheus bellimanus</i> Lockington, 1877	MEX, CR, PAN, COL, ECU	0 – 300	Vargas and Wehrmann, 2008
<i>Alpheus californiensis</i> Holmes, 1900	MEX		Kerstitch and Bertsch, 2007
<i>Alpheus clamator</i> Lockington, 1877	MEX, ATL	0 – 0.5	Wicksten, 1994
<i>Alpheus colombiensis</i> Wicksten, 1988	CR, PAN, COL		Wicksten and Hendrickx, 2003
<i>Alpheus confusus</i> Carvacho, 1989	MEX		Wicksten and Hendrickx, 2003
<i>Alpheus cylindricus</i> Kingsley, 1878	MEX, CR, PAN, COL, ATL	0 – 37	Wicksten and Hendrickx, 2003
<i>Alpheus distinctus</i> Kim and Abele, 1988	PAN		Wicksten and Hendrickx, 2003
<i>Alpheus exilis</i> Kim and Abele, 1988	MEX, ECU	64 – 146	Wicksten, 1994
<i>Alpheus fasciatus</i> Lockington, 1878	MEX, IND		Wicksten, 1994
<i>Alpheus felgenhaueri</i> Kim and Abele, 1988	MEX		Wicksten and Hendrickx 2003
<i>Alpheus firmus</i> Kim and Abele, 1988	PAN	0 – 1	Wicksten and Hendrickx 2003
<i>Alpheus galapagensis</i> Sivertsen, 1933	MEX, SAL, CR, PAN, COL, ECU, ATL	s	Anker <i>et al.</i> 2007a
<i>Alpheus grahami</i> Abele, 1975	MEX, COL, ECU	0 – 46	Kerstitch and Bertsch 2007
<i>Alpheus hebes</i> Kim and Abele, 1988	MEX, CR, PAN, COL, ECU		Wicksten and Hendrickx 2003
<i>Alpheus hoonsooi</i> Kim and Abele, 1988	COL, ECU	9 – 128	Wicksten and Hendrickx 2003
<i>Alpheus hyeoungae</i> Kim and Abele, 1988	MEX, CR, PAN	0 – 10	Hendrickx 2008
<i>Alpheus inca</i> Wicksten and Mendez G., 1981	ECU	4 – 8	Wicksten and Hendrickx, 2003
<i>Alpheus latus</i> Kim and Abele, 1988	PAN		Wicksten and Hendrickx, 2003

Table 1. Cont.

Taxon	Distribution	Depth (m)	Reference
<i>Alpheus longinquus</i> Kim and Abele, 1988	MEX, CR, PAN, COL, ECU	0 – 36	Wicksten and Hendrickx, 2003
<i>Alpheus lottini</i> Guérin-Meneville, 1838	MEX, CLP, PAN, COL, ECU, PC, IP, IND	0 – 30	Kerstitch and Bertsch, 2007
<i>Alpheus martini</i> Kim and Abele, 1988	PAN	0 – 1	Martinez-Guerrero and Hendrickx, 2011
<i>Alpheus mazatlanicus</i> Wicksten, 1983	MEX, COL	0 – 1	Wicksten and Hendrickx, 2003
<i>Alpheus millsae</i> Anker, Hurt and Knowlton, 2007	PAN	s	Anker <i>et al.</i> , 2007a
<i>Alpheus naos</i> Anker, Hurt and Knowlton, 2007	PAN	s	Anker <i>et al.</i> , 2007b
<i>Alpheus normanni</i> Kingsley, 1878	MEX, PAN, ECU, ATL	0 – 73	Wicksten and Hendrickx, 2003
<i>Alpheus pacificus</i> Dana, 1852	MEX, CLP, CR, ECU, PC, IP, IND	0 – 20	Poore, 2004
<i>Alpheus panamensis</i> Kingsley, 1878	MEX, SAL, CR, PAN, COL, ECU, PER	30 – 55	Wicksten and Hendrickx, 2003
<i>Alpheus rectus</i> Kim and Abele, 1988	MEX, PAN	55 – 73	Wicksten and Hendrickx, 2003
<i>Alpheus rostratus</i> Kim and Abele, 1988	MEX, CR, ECU	0 – 5.5	Wicksten and Hendrickx, 2003
<i>Alpheus saxidomus</i> Holthuis, 1980	CR, COL, ECU		Wicksten and Hendrickx, 2003
<i>Alpheus scopulus</i> Kim and Abele, 1988	PAN, ECU	0 – 2	Wicksten and Hendrickx, 2003
<i>Alpheus sulcatus</i> Kingsley, 1878	MEX, PAN, COL, ECU, PER, IP, IND, ATL	0 – 24	Kerstitch and Bertsch, 2007
<i>Alpheus tenuis</i> Kim and Abele, 1988	MEX, PAN	0 – 1	Martinez-Guerrero and Hendrickx 2011
<i>Alpheus umbo</i> Kim and Abele, 1988	MEX, CR, COL		Wicksten and Hendrickx, 2003
<i>Alpheus utriensis</i> Ramos and Von Prahl, 1989	MEX, CR, PAN, COL, ATL	0 – 35	Hendrickx and Hermoso-Salazar, 2005
<i>Alpheus villus</i> Kim and Abele, 1988	MEX, CR, PAN		Wicksten and Hendrickx, 2003
<i>Alpheus wickstenae</i> Christoffersen and Ramos, 1987	COL		Wicksten and Hendrickx, 2003
<i>Automate rugosa</i> Coutière, 1902	MEX, PAN	30 – 70	Wicksten and Hendrickx, 2003
<i>Betaeus harfordi</i> (Kingsley, 1878)	MEX		Wicksten, 1994
<i>Betaeus longidactylus</i> Lockington, 1877	MEX		Wicksten, 1994
<i>Coronalpheus natator</i> Wicksten, 1999	ECU	9 – 17	Wicksten and Hendrickx, 2003
<i>Leptalpheus mexicanus</i> Rios and Carvacho, 1983	MEX, COL		Wicksten and Hendrickx, 2003
<i>Leslibetaeus coibita</i> Anker, Poddoubtchenko and Wehrmann, 2006	PAN		Anker <i>et al.</i> , 2006a
<i>Pomagnathus corallinus</i> Chace, 1937	MEX, CLP, CR, PAN, COL, ECU	5 – 30	Wicksten and Hendrickx, 2003
<i>Synalpheus bannerorum</i> Abele, 1975	MEX, COL	2 – 10	Wicksten and Hendrickx, 2003
<i>Synalpheus charon</i> (Heller, 1861)	MEX, CLP, PAN, COL, ECU, PC, IP, IND	0 – 50.1	Wicksten and Hernandez, 2000
<i>Synalpheus lani</i> Hermoso and Alvarez, 2005	MEX	0 – 3	Hermoso-Salazar and Alvarez, 2005
<i>Synalpheus lockingtoni</i> Coutière, 1909	MEX, CLP	12 – 498.2	Hermoso-Salazar and Solis-Weiss, 2001b
<i>Synalpheus mexicanus</i> Coutière, 1909	MEX, COL	0 – 35	Hermoso-Salazar <i>et al.</i> , 2005
<i>Synalpheus mulegensis</i> Rios, 1992	MEX		Wicksten and Hendrickx, 2003
<i>Synalpheus nobilii</i> Coutière, 1909	MEX, CLP, COL, ECU, IP	0 – 25.7	Hickman Jr. and Zimmerman, 2000
<i>Synalpheus occidentalis</i> Coutière, 1909	MEX	18 – 73	Hermoso-Salazar, 2001
<i>Synalpheus paulsonoides</i> Coutière, 1909	MEX	15 – 55	Hermoso-Salazar and Hernandez-Alcantara, 2001
<i>Synalpheus peruvianus</i> Rathbun, 1910	MEX, COL, PER	0 – 20	Hermoso-Salazar <i>et al.</i> , 2005
<i>Synalpheus recessus</i> Abele and Kim, 1989	CR, PAN	20	Vargas and Cortes, 1999
<i>Synalpheus sanjosei</i> Coutière, 1909	MEX, CR, COL	0 – 20	Wicksten and Hendrickx, 2003
<i>Synalpheus sanlucasi</i> Coutière, 1909	MEX, PAN	4 – 7	Wicksten and Hendrickx, 2003
<i>Synalpheus stylopleuron</i> Hermoso-Salazar and Hendrickx, 2006	MEX	3 – 4	Hermoso-Salazar and Hendrickx, 2006
<i>Synalpheus superus</i> Abele and Kim, 1989	PAN		Wicksten and Hendrickx, 2003
<i>Synalpheus wickstenae</i> Hermoso-Salazar and Hendrickx 2006	MEX	0 – 10	Hermoso-Salazar and Hendrickx, 2006
Barbouriidae Christoffersen, 1987			
<i>Parahippolyte cavernicola</i> Wicksten, 1996	MEX	6	Wicksten, 1996a
Hippolytidae Spence Bate, 1888			
<i>Hippolyte californiensis</i> Holmes, 1895	MEX, CR	7.5	Wicksten and Hendrickx, 2003
<i>Hippolyte williamsi</i> Schmitt, 1924	MEX, ECU	5	Wicksten and Hendrickx, 2003
<i>Hippolyte zostericola</i> (Smith, 1873)	COL, ATL		Roman-Contreras and Romero-Rodriguez, 2005
<i>Latreutes antiborealis</i> Holthuis, 1952	MEX, ECU, PER	4 – 46	Hermoso-Salazar and Hernandez-Alcantara, 2001
<i>Trachycaris restricta</i> (A. Milne-Edwards, 1878)	MEX, PAN, ECU, ATL	0 – 100	Wicksten and Hendrickx, 2003
Lysmatidae Dana, 1852			
<i>Lysmata argentopunctata</i> Wicksten, 2000	MEX, CR, ECU	0 – 35	Wicksten and Hendrickx, 2003
<i>Lysmata californica</i> (Stimpson, 1866)	MEX, PAN, ECU	0 – 24	Rhyne and Lin, 2006

Table 1. Cont.

Taxon	Distribution	Depth (m)	Reference
<i>Lysmata chica</i> Wicksten, 2000	ECU		Hickman Jr. and Zimmerman, 2000
<i>Lysmata galapagensis</i> Schmitt, 1924	MEX, CR, PAN, COL, ECU	10 – 18.3	Kerstitch and Bertsch, 2007
<i>Lysmata gracilirostris</i> Wicksten, 2000	MEX, CR, PAN, ECU	0 – 183	Wicksten and Hendrickx, 2003
<i>Lysmata holthuisi</i> Anker, Baeza and De Grave 2009	PAN	0 – 138	Anker <i>et al.</i> , 2009
<i>Lysmata nayaritensis</i> Wicksten, 2000	MEX, PAN	0 – 10	Wicksten and Hendrickx, 2003
<i>Lysmata trisetacea</i> (Heller, 1861)	MEX, CLP, COL, PC, IND	0 – 150	Wicksten and Hendrickx, 2003
Thoridae Kingsley, 1879			
<i>Eualus dozei</i> (A. Milne-Edwards, 1891)	ECU	8 – 300	Wicksten and Hendrickx, 2003
<i>Eualus lineatus</i> Wicksten and Butler, 1983	MEX	17 – 232	Jensen and Jonson, 1999
<i>Eualus subtilis</i> Carvacho and Olson, 1984	MEX	30	Wicksten and Hendrickx, 2003
<i>Heptacarpus palpator</i> (Owen, 1839)	MEX	8 – 37	Wicksten, 2006
<i>Heptacarpus yaldwyni</i> Wicksten, 1984	MEX	1,052 – 1,145	Wicksten and Hendrickx, 1992
<i>Lebbeus scrippsi</i> Wicksten and Mendez G., 1982	MEX	768 – 1,208	Wicksten and Hendrickx, 2003
<i>Lebbeus washingtonianus</i> (Rathbun, 1902)	MEX		Wicksten and Hendrickx, 2003
<i>Thor algicola</i> Wicksten, 1987	MEX, PAN, IP, ATL	2 – 25	Wicksten and Hendrickx, 1992
<i>Thor amboinensis</i> (de Man, 1888)	CR, PAN, COL, ECU, IP, IND, ATL	6 – 11	Wicksten and Hernandez, 2000
<i>Thor cocoensis</i> Wicksten and Vargas, 2001	CR, ECU	4 – 35	Wicksten and Hendrickx, 2003
<i>Thor cordelli</i> Wicksten, 1996	MEX, COL	3 – 15	Wicksten, 1996b
<i>Thor spinosus</i> Boone, 1935	MEX, PC, IP, IND	6 – 9	Wicksten and Hendrickx, 2003
Ogyrididae Holthuis, 1955			
<i>Ogyrides alphaerostris</i> (Kingsley, 1880)	MEX, ATL	5 – 50	Wicksten and Hendrickx, 2003
<i>Ogyrides tarazonai</i> Wicksten and Mendez G., 1988	NIC, COL, ECU		Wicksten and Hendrickx, 2003
Processoidea Ortmann, 1896			
Processidae Ortmann, 1896			
<i>Ambidexter panamensis</i> Abele, 1972	MEX, PAN, ECU		Wicksten and Hendrickx, 2003
<i>Ambidexter swifti</i> Abele, 1972	MEX, PAN, COL, ECU	0.5	Wicksten and Hendrickx, 2003
<i>Ambidexter symmetricus</i> Manning and Chace, 1971	MEX, ATL	1 – 2	Wicksten and Hendrickx, 2003
<i>Processa aequimana</i> (Paulson, 1875)	MEX, IP, IND	0 – 74	Wicksten and Hendrickx, 2003
<i>Processa hawaiiensis</i> Dana, 1852	MEX, CLP, PC		Wicksten and Hendrickx, 1992
<i>Processa peruwiana</i> Wicksten 1983	MEX, CR, PAN, ECU, PER	31 – 185	Wicksten and Hendrickx, 2003
Pandaloidae Haworth, 1825			
Pandalidae Haworth, 1825			
<i>Heterocarpus affinis</i> Faxon, 1893	MEX, CR, PER	760 – 1,244	Wicksten and Hendrickx, 2003
<i>Heterocarpus hostilis</i> Faxon, 1893	CR, PAN, COL	1,161 – 1,705	Wicksten and Hendrickx, 2003
<i>Heterocarpus vicarius</i> Faxon, 1893	MEX, PAN, PER	62 – 1,454	Wicksten and Hendrickx, 2003
<i>Pandalopsis ampla</i> Spence Bate, 1888	MEX, ATL	132 – 2,000	Wicksten and Hendrickx, 2003
<i>Pantomus affinis</i> Chace, 1937	MEX, CR, ECU	3 – 744	Wicksten and Hendrickx, 2003
<i>Plesionika carinirostris</i> Hendrickx, 1990	MEX	360 – 380	Wicksten and Hendrickx, 2003
<i>Plesionika mexicana</i> Chace, 1937	MEX, PAN, COL, ECU, PER	28 – 258	Wicksten and Hendrickx, 2003
<i>Plesionika trispinus</i> Squires and Barragan, 1976	MEX, COL, PER	96 – 500	Wicksten and Hendrickx, 2003
Crangonoidea Haworth, 1825			
Crangonidae Haworth, 1825			
<i>Crangon nigromaculata</i> Lockington, 1877	MEX	14 – 31	Wicksten, 2006
<i>Mesocrangon munitella</i> (Walker, 1898)	MEX	6.5 – 74	Wicksten and Hendrickx, 2003
<i>Metacrangon procax</i> (Faxon, 1893)	MEX, COL	1,103 – 1,513	Wicksten and Hendrickx, 2003
<i>Neocrangon resima</i> (Rathbun, 1902)	MEX, COL	9.2 – 444	Wicksten and Hendrickx, 2003
<i>Paracrangon areolata</i> Faxon, 1893	MEX, ECU, PER	1,016 – 1,136	Wicksten and Hendrickx, 2003
<i>Pilocheras lapillus</i> Wicksten, 1989	ECU	37 – 65	Wicksten and Hendrickx, 2003
<i>Parapontophilus occidentalis</i> (Faxon, 1893)	MEX, CR, PAN, COL, ECU	1,635 – 4,082	Wicksten and Hendrickx, 2003
<i>Sclerocrangon atrox</i> Faxon, 1893	MEX	1,103 – 1,130	Wicksten and Hendrickx, 2003
Glyphocrangonidae Smith, 1884			
<i>Glyphocrangon alata</i> Faxon, 1893	MEX, PAN, ECU, PER	219 – 1,350	Wicksten and Hendrickx, 2003
<i>Glyphocrangon loricata</i> Faxon, 1895	ECU, PER	553 – 769	Wicksten and Hendrickx, 2003
<i>Glyphocrangon sicaria</i> Faxon, 1893	MEX, CR, PAN	1,454 – 2,997	Wicksten and Hendrickx, 2003
<i>Glyphocrangon spinulosa</i> Faxon, 1893	MEX, PAN	1,027 – 1,586	Wicksten and Hendrickx, 2003
<i>Glyphocrangon taludensis</i> Hendrickx, 2010	MEX	780 – 1,879	Hendrickx, 2010
<i>Glyphocrangon vicaria</i> Faxon, 1896	MEX, CR, PAN, COL, ECU	938 – 3,880	Wicksten and Hendrickx, 2003

After checking for species validity, historic species accumulation curves (species added by year of publication) were constructed for each country and for the entire ETP. Further, the data was fitted with an exponential function (larger r^2).

The occurrence of each taxon was mapped on the ETP. When there was a lack of geographic information of the species record or the accuracy of the data was larger than 1° of latitude by 1° longitude, the information was discarded. Once the distribution of each species was mapped on the ETP, we traced a grid of 1° of latitude by 1° longitude and obtained the species richness per grid. Since not all records have accurate geographic data, the amount of information included in the following analysis is slightly reduced (~0.03%) than the published information. Nonetheless, mapping of species distribution was a methodological prerequisite to generate an accurate picture of the knowledge and gaps of the marine biodiversity of the benthic caridean shrimp species in the ETP. In addition, occurrence of spatially rare (inhabiting 1 to 2 grids) species in the area was also mapped. After mapping, we fitted species richness and species richness of rare species (inhabiting 1 to 2 grids) against latitude through a linear model. Additionally, we related the number of caridean species against the number of caridean references (proxy for sampling intensity) per grid with a Spearman Rank correlation.

We used the species occurrence per grid to generate sample-based rarefaction curves of observed species and calculated the species richness estimator Chao2 for the ETP (Colwell, 2009). While the former analysis indicates the observed species accumulation curve, the latter is a sample-based nonparametric estimator for addressing expected species richness of the benthic caridean shrimp in the Eastern Tropical Pacific. EstimateS (Colwell, 2009) were used to compute observed and expected rarefaction curves and their confidence intervals (95%) after 10,000 randomizations with replacement.

RESULTS

The present checklist of the marine benthic caridean shrimp of the Eastern Tropical Pacific includes 183 species considered as currently valid, belonging to 67 genera, 18 families and 9 superfamilies (Tab. 1).

According to the data, families Alpheidae (66 spp.), Palaemonidae (51 spp.) and Thoridae (12 spp.) contribute to most of the species (>70%) (Fig. 1A), while *Alpheus* (41 species) and *Synalpheus* (16 species) were the most diverse genera of benthic caridean shrimps in the ETP (Fig. 1B).

México (including Revillagigedo Archipelago) is the country with the greatest number of benthic caridean species (130 species) (Fig. 2A), followed by Ecuador (including Galapagos Archipelago) (98 species) (Fig. 2B), Panama (75 species) (Fig. 2C), Colombia (including Malpelo Island) (65 species) (Fig. 2D), Costa Rica (including Cocos Island) (48 species) (Fig. 2E), Peru (20 species) (Fig. 2F) and France (Clipperton Atoll) (19 species) (Fig. 2G). Meanwhile, there are only two records in El Salvador (*Alpheus galapagensis* Sivertsen, 1933 addressed in La Unión [Kim and Abele, 1988], and *A. panamensis* Kingsley, 1878 founded in Acajutla [Wicksten, 1994]), and two more in Nicaragua (*Palaemon gracilis* (Smith, 1871) recorded in Realejo [Wicksten, 1983] and *Ogyrides tarazonai* Wicksten and Mendez, 1988 in San Juan del Sur [Wicksten and Mendez, 1988]). To date, no marine benthic caridean species have ever been recorded in Guatemala or Honduras.

Historic accumulation curves varied along the ETP, nevertheless, some results were similar among countries (Fig. 2). For example, for countries such as Mexico (Fig. 2A), Ecuador (Fig. 2B) and Panama (Fig. 2C), small but steady early increases were followed by sudden increments in species richness. Likewise, the same trend is recorded when data are pooled across the ETP (Fig. 2H). The observed trend was meaningfully fitted with an exponential function, indicating that during the last three decades many more species records were added to the benthic caridean fauna than those recorded in the ETP during the previous 110 years. Function fitting also indicates that the current increment of species records still not leveling off for any particular country neither for the entire ETP (Fig. 2).

According to species mapping, richness varies largely among grids in the ETP (Fig. 3). Except for a few empty spots in the northern Gulf of California, the Tropical Mexican Pacific, Guatemala and Honduras, marine benthic caridean shrimp have been recorded in the coastal margin of the entire ETP and its oceanic islands (*i.e.*, Revillagigedo, Clipperton, Malpelo, Cocos,

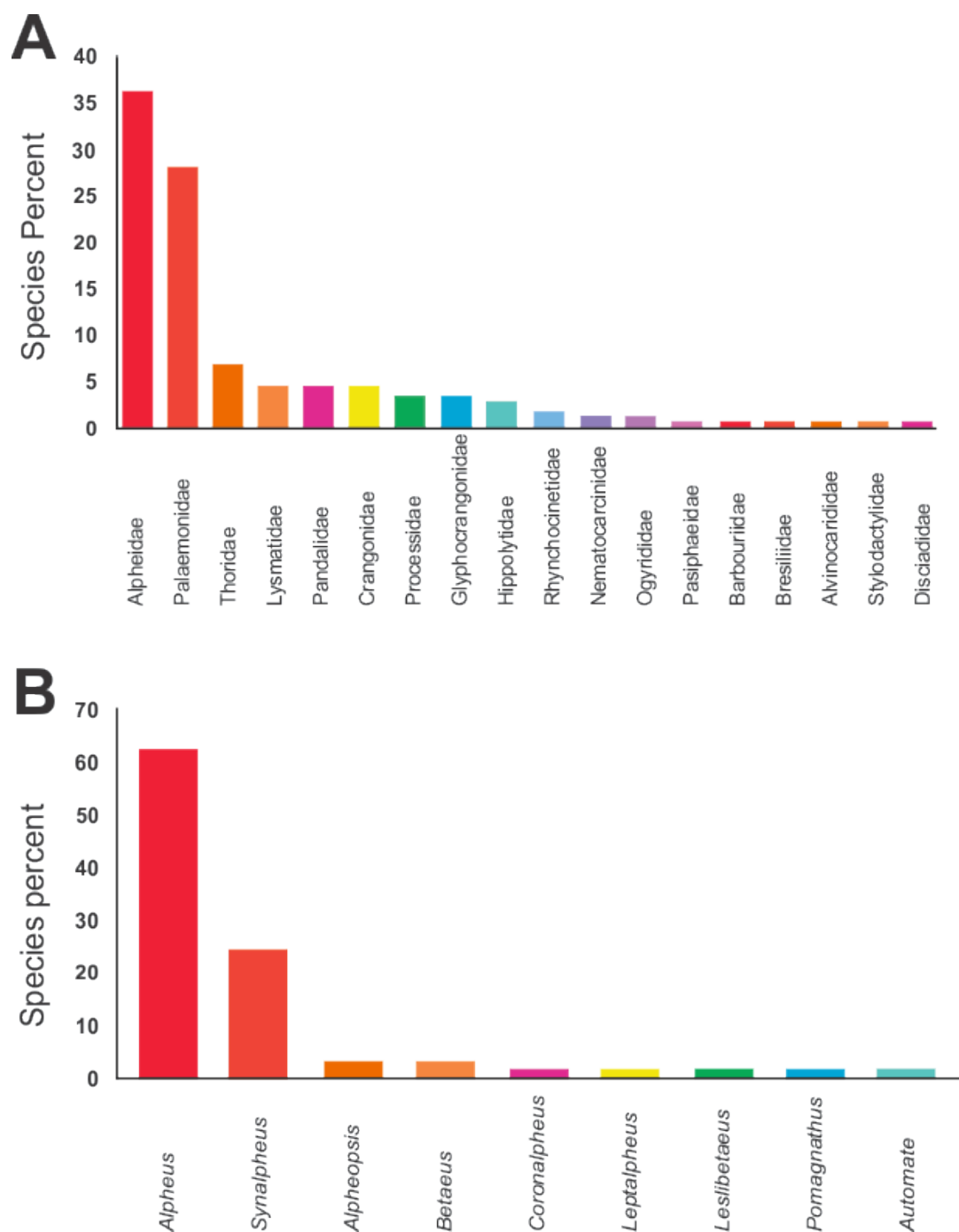


Figure 1. Richness of marine benthic caridean shrimps in the Eastern Tropical Pacific. A, Species per family (n = 183). B, Species per genera of Alpheidae (n = 160).

Galapagos). Species richness is concentrated in grids located around Galapagos and Panama (*i.e.*, Central America), but relatively rich spots can also be observed in Colombia, Costa Rica and the Gulf of California, hence disrupting any meaningful trend between richness and latitude ($r^2 = 0.002$, $n = 37$, $p > 0.05$).

Data indicates that up to 44 species (24%) inhabit a single grid and hence may be considered spatially

rare, but as many as 135 species (~74%) are restricted to less than five grids each. In contrast, just 22 species (12%) inhabit more than 10 grids and hence may be considered as spatially common. The species *Processa peruviana* Wicksten, 1983 (15 grids), *Harpiliopsis depressa* (Stimpson, 1860) (17 grids), *Alpheus hebes* Kim and Abele, 1988 and *Palaemonella holmesi* (Nobili, 1907) (18 grids), *Brachycarpus biunguiculatus* (Lucas,

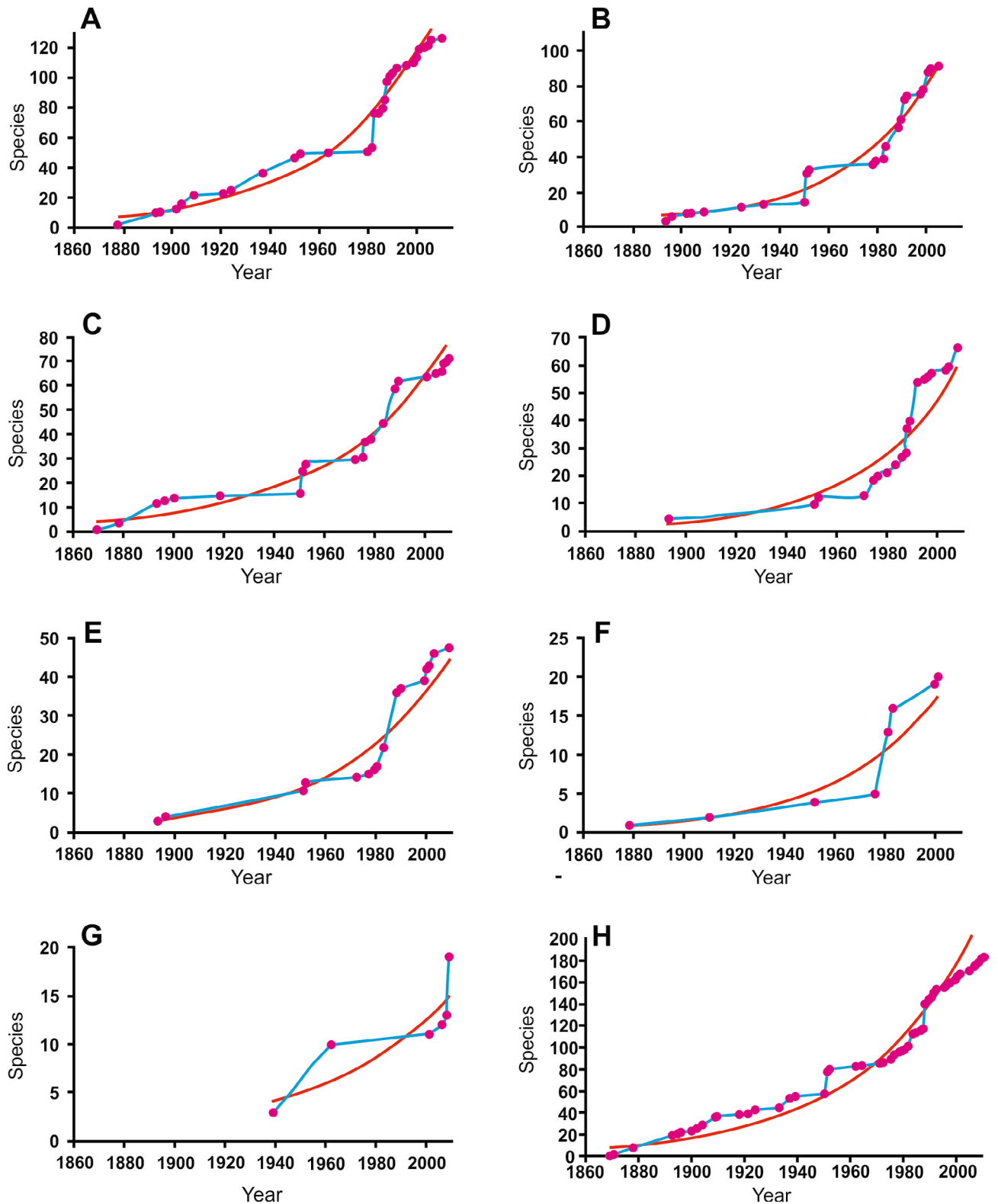


Figure 2. Temporal accumulation species curves of marine benthic caridean shrimps in the Eastern Tropical Pacific. A, Mexico (Mexico-Revillagigedo Archipelago). B, Clipperton Atoll. C, Ecuador (Ecuador-Galapagos Archipelago). D, Costa Rica (Costa Rica-Cocos Island). E, Panama. F, Colombia (Colombia-Malpelo Island). G, Peru. H, Tropical Eastern Pacific. Dotted line= observed values, continuous line= exponential fit.

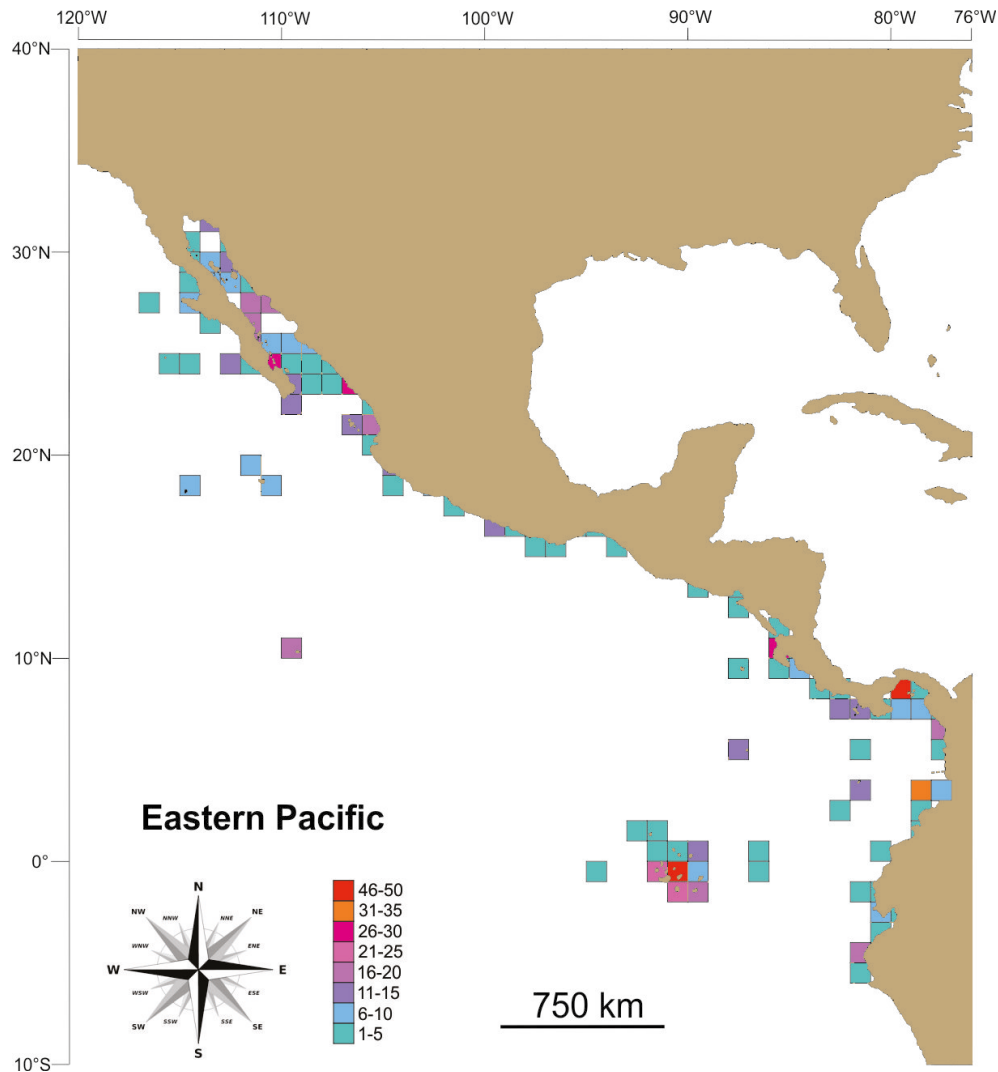


Figure 3. Species richness of marine benthic caridean shrimps per grid (1° latitude by 1° longitude) in the Eastern Tropical Pacific. Notice color scale.

1849) (19 grids), and *Alpheus bellimanus* Lockington, 1877 (21 grids) are the most widespread distributed species in the ETP.

Rare species, inhabiting one to two grids, concentrated around Central America (Costa Rica, Panama, Colombia and Galapagos Islands) and the entrance of the Gulf of California, Mexico; however, from northern Costa Rica (~11°N) up to the Central Mexican Pacific (~19°N) spatially rare species are lacking (Fig. 4). Overall, linear regression models indicates no latitudinal trend ($r^2 = 0.001-0.004$) in the number of rare species (*i.e.*, inhabiting 1 to 2 grids).

Nevertheless, grids around Clipperton Atoll (10°N 109°W) (5 species), Galapagos Islands (0° 90°W), entrance of the Gulf of California (24°N 110°W) (7 species) and Panama (8°N 79°W) (10 species) have relatively large number of rare species.

Finally, the non-parametric Chao2 species estimator indicates that the observed species richness is lower than expected (Fig. 5), in fact with a 95% confidence the model suggests that the expected species richness of marine benthic caridean shrimp in the ETP may lay somewhere between 202–269 species, a number 11%–47% larger than the observed.

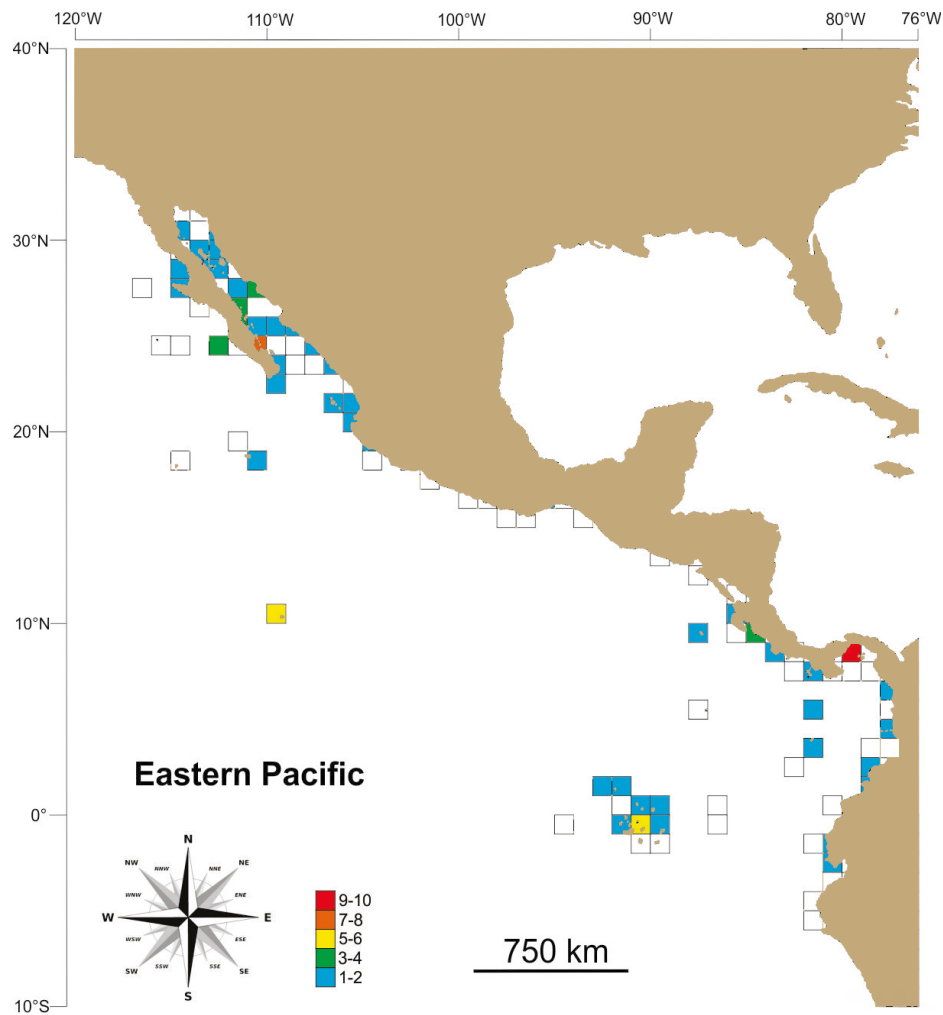


Figure 4. Species richness of narrow-distributed (1-2 grids) marine benthic caridean shrimps per grid (1° latitude by 1° longitude) in the Eastern Tropical Pacific. Notice color scale.

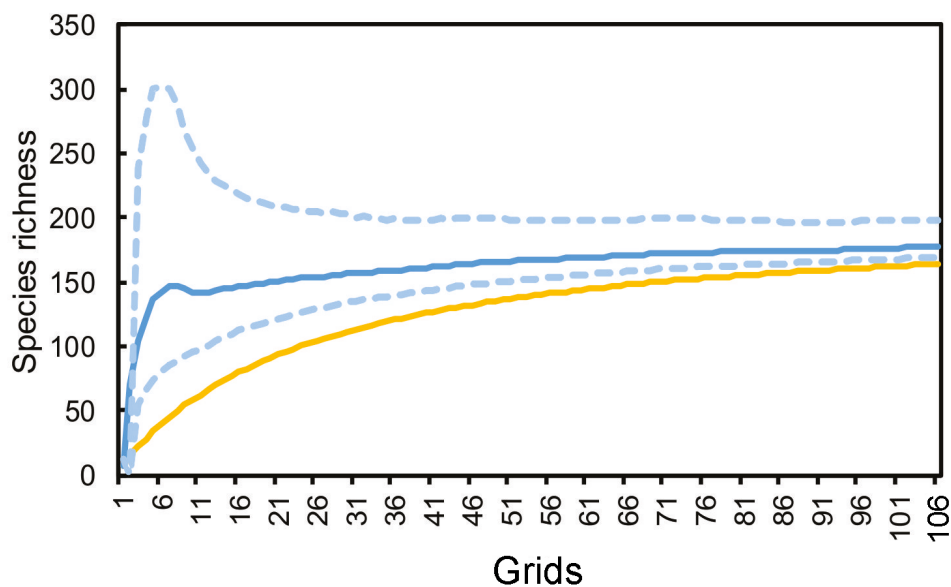


Figure 5. Species richness of marine benthic caridean shrimps in Eastern Tropical Pacific. Orange continuous line = observed richness, blue continuous line = expected richness, blue long-cut lines = confidence interval (95%). Expected species number and confidence intervals (95%) were generated after 10,000 randomizations with replacement using non-parametric Chao2 estimator.

DISCUSSION

As a result of recent species descriptions (Wicksten and Martin, 2004; Hermoso-Salazar and Álvarez, 2005; Anker *et al.*, 2006a; 2007; 2009; Hermoso-Salazar and Hendrickx, 2006; Li, 2006; Marin and Anker, 2008; Li and Poupin, 2009; Hendrickx, 2010), geographic range extensions (Martínez-Guerrero and Hendrickx, 2011) and new records of previously recorded species (Ríos *et al.*, 2003; Wicksten and Hendrickx, 1992; 2003; Poupin, 2008), we assembled a list of 183 species of caridean regarded as currently valid in the Eastern Tropical Pacific. The number of species is slightly smaller compared with similar but previous studies (188 species, Wicksten and Hendrickx, 1992; 204 species, Wicksten and Hendrickx, 2003). The observed differences in species numbers among studies are mainly due to the exclusion of 30 species, either because they have a freshwater affinity (Hendrickx and Estrada-Navarrete, 1989; Guzmán, 2008), distribute outside of the ETP (Cardoso and Serejo, 2007; Anker *et al.*, 2008), or have an invalid taxonomic status (*nomen dubium*).

Data revealed that families Alpheidae and Palaemonidae, and genus *Alpheus* contributed to most of the species. Dominance of the former two families was previously recognized by Wicksten and Hendrickx (1992) and Anker *et al.* (2006b). The trend, however, is not exclusive to the ETP but it is also observed in the Caribbean and the Indo West Pacific (Boschi, 2000). Bauer (2004) and Poupin (2008) have suggested that Alpheidae and Palaemonidae dominance is related to its ability to inhabit a large number of substrates, its reduced size and the capacity of its individuals to establish symbiotic relations with vertebrates or other invertebrates. In other invertebrate and vertebrate taxa such as ophiuroids (Granja-Fernández *et al.*, 2014) and gobies (Zepeta-Vilchis *et al.*, 2013), such attributes have also been signaled as responsible for increasing species richness and dominance of the groups in marine habitats. On the contrary, taxa included on Pasiphaeidae or Pandalidae members of which often constitute an important component of the mesopelagic and bathypelagic planktonic communities (Komai *et al.*, 2012) are relatively larger than Alpheidae and Palaemonidae, and does not establish symbiotic relations with other taxa and hence not as species rich as Alpheidae.

Grid data indicates that species richness concentrates in Galapagos and Panama, but relatively rich spots can also be observed in Colombia, Costa Rica, and the Gulf of California. Boschi (2000) and Wicksten and Hendrickx (2003) recognized the Panamic Province as the most diverse caridean shrimp area in the entire Eastern Tropical Pacific. However, if we further analyze the number of caridean species against the number of caridean references per grid, we will notice that rich spots correspond with the most heavily studied areas in the ETP; in fact there is a meaningful positive relationship (Spearman rank correlation $r = 0.88$, $p = 0.00$) between species richness and the number of caridean references per grid. While the number of references is not an adequate proxy for sampling intensity and a correlation is not a cause-consequence proof, the observed relation suggests to some extent that the observed benthic caridean species richness in the ETP may have not exclusively resulted from habitat heterogeneity or large-scale evolutionary processes currently invoked as one of the several speciation or richness drivers in the marine realm (Tittensor *et al.*, 2010), instead they may have also arisen from differences in research effort and hence from sampling bias. In the same way, spatial analyses of rare species are not meaningfully related to latitude in the studied area (*i.e.*, no meaningful increase toward Central America). The observed results, rather than plea against the currently recognized caridean spatial richness pattern (Boschi, 2000; Wicksten and Hendrickx, 2003), call for a more thoughtful and systematic sampling protocol in order to get information from poorly sampled areas in the Eastern Tropical Pacific.

The function that explains the historic patterns per country and for the entire region suggest that the inventory of the marine benthic caridean shrimp fauna from the ETP is still incomplete. The extent of the gap between the observed and the expected caridean diversity in the ETP is unknown, but several evidence lines may suggest its size. First, if we considered that the benthic caridean records are restricted to an area that occupies 8.8% of the entire ETP, it becomes obvious that most of the region (~91%) is still not inventoried. In this regard if the species-area relationship is invoked, then marine benthic caridean shrimp fauna of the ETP must be nine times larger than the observed and hence is still far from being complete. According to

the species-area relationship and the Chao2 species estimator, the marine benthic caridean shrimp fauna of the ETP must be 11% to 900% larger than the current observed. Species-area relationships have been invoked to explain species richness for several biological groups (Connor and McCoy, 2001) including marine invertebrates (Alvarado *et al.*, 2010; Costello *et al.*, 2010; Granja-Fernández and López-Pérez, 2012). Nonetheless, this number must be considered with caution since habitat diversity, area per se, passive sampling and edge effects are not mutually exclusive mechanisms and may operate individually and/or in synergy to cause and or modify species-area relationships (Connor and McCoy, 2001). On the other hand, the non-parametric Chao2 species index indicates that caridean richness is 11% to 47% larger than recorded; this number, however, is sensibly minor compared to the suggested by species-area relationship, though it is in agreement with estimations regarding the entire crustacean fauna from the Mexican Tropical Pacific using different approaches (González-Oreja *et al.*, 2010; García-Madrigal *et al.*, 2012; López-Pérez *et al.*, 2012). In the absence of complete inventories, nonparametric estimators (for example, Chao2) have been shown to perform better than most other methods, such as observed species richness, species-area curves or asymptotic estimators (Colwell, 2009), but the Chao2 estimator still gives a lower bound to expected species richness, thus producing conservative estimates (Hortal *et al.*, 2006).

It is revealing that 44 species (24%) inhabit a single grid (as much as ~11,200 km²) but as many as 135 species (~74%) are restricted to less than five grids each. This either indicates that most of the caridean shrimp species in the ETP have a narrow distribution (*i.e.*, provincialism) or that current distribution of narrowly distributed species (74%) resulted from sampling deviations. Previous statements about endemism or narrowness in species distribution in taxonomic groups such as corals, crustaceans, echinoderms or fishes in the ETP indicating that species are spatially restricted to Central America or the Gulf of California, have been contradicted by recent genomic analyses, detailed taxonomic studies or intensive sampling protocols across the area (Combosch *et al.*, 2008; Zepeta-Vilchis *et al.*, 2012; Granja-Fernández *et al.*, 2013; Paz-García *et al.*, 2015; Reyes-Bonilla *et al.*, 2017; Valencia-Méndez

et al., 2017). While work on this regard is pending on ETP caridean fauna, the relatively large sampling gaps (~ 91%, see above) regarding the group is the most likely scenario for explaining the narrow distribution of a large number of species in the area, not only for caridean shrimps (this contribution) but across several taxonomic marine groups and areas worldwide (Costello *et al.*, 2010).

Finally, integrative databases (such as the current one) resulting from previously published information to make generalizations in ecology, without any doubt is subjected to errors that distort our view. In particular, bias in sample size, but also in space, time and taxonomy may have altered the stated generalizations about the species richness distribution pattern on ETP caridean fauna; nevertheless the current meta-analysis has an advantage over simple verbal reviews because unbiased estimates of the overall strength of a hypothetical relationship can be obtained, heterogeneity in research findings identified and new research questions developed (Møller and Jennions, 2001). In this regard, detailed taxonomy of the Caridea and intensive sampling across environments in the ETP still is the most urgent need in the studied area.

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