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Diversity and ecology of Pilargidae (Annelida: Polychaeta) from the Gulf of Carpentaria and Arafura Sea, northern Australia

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Abstract

This study identifies to species or species units 572 lots (>1000 specimens) of pilargids from six localities in the Arafura Sea and Gulf of Carpentaria (including the ports at Gove and McArthur River). We analyze the taxonomic data against geomorphic unit, depth, and sediment type. Preliminary results show that pilargid fauna of northern Australia comprises 13 species in seven genera (*Ancistrosyllis, Cabira, Litocorsa, Loandalia, Pilargis, Sigambra,* and *Synelmis*). Although all four localities have a similar diversity of species (six or seven species each), the species composition differs between each region: *Litocorsa annamita* and *Synelmis rigida* were found in all sediment types in the Arafura Sea and Gulf of Carpentaria; *Ancistrosyllis* cf. *hartmanae* (mud and sand dominated sediments only) and *Sigambra pettiboneae* (all sediment types) were restricted to the inshore localities of Gove and McArthur River; *Loandalia gladstonensis* and *Sigambra* sp. 2 were found on the shelf and in the inshore habitats of the Gulf of Carpentaria only; *Litocorsa* sp. 'arafura', *Sigambra* sp. 'arafura' and *Synelmis gibbsi* were found only in the Arafura Sea, with sediments dominated by sand and gravel; and *Cabira* sp. 1 and *Sigambra* cf. *tentaculata* were found at all locations, in all sediment types. Based on these distribution patterns and the Recent Quaternary geological history of the area, hypotheses of post-glacial colonization of the Gulf of Carpentaria are presented. The pilargid species composition in northern Australia is also compared to neighboring Indo-west Pacific regions.

Key words: Indo-west Pacific, Arafura Sea, Gove, McArthur River, systematics, ecology, habitat, biogeography, diversity

Introduction

Pilargids are free-living sediment dwellers, found throughout the oceans from abyssal plains to inshore shelf waters, estuaries, and lagoons (Glasby 2000). Members of the group are normally thought of as being rare (e.g., Salazar-Vallejo 1987; Salazar-Vallejo & Orensanz 1991; Fiege & Böggemann 1999), but other studies (e.g., Flint & Rabalais 1980; Nishi et al. 2007) and the present data suggest that members of some genera, particularly *Litocorsa* or *Sigambra*, may be well represented in shelf sediments. In the Australasian region there is a lack of published records on the group, even though pilargids are regularly collected in benthic samples. Consequently little is known about habitat preferences and biogeography of Australian pilargids. Moreover, studies on polychaetes of the northeastern Australian shelf are limited to a few reports and ecology papers including Long & Poiner (1994), Wilson (2006) and Russell & Smit (2007). Other studies of benthic invertebrates in the Gulf of Carpentaria have only considered the larger epibenthic forms.

In northern Australia, the Gulf of Carpentaria (GoC) and Arafura Sea are adjacent water bodies separated by the shallow (55 m) Arafura Sill (Fig. 1). The region experiences a pronounced seasonal climate with a wet monsoon from November to March and dry southeasterly trade winds from May to September. The shelf is occasionally affected by tropical cyclones that mobilize sediment and may affect the associated benthos. The region has been greatly influenced by Late Quaternary sea level changes and sedimentary discharges from rivers in northern Australia and Papua New Guinea such that modern-day sediments in both areas comprise mainly poorly-sorted terrigenous and carbonate muddy sands (Heap et al. 2004). Present-day, fully-open marine conditions were established in the GoC only about 9–10,000 years ago following inundation of the Arafura Sill approximately 12,000 years ago; prior to that, at least to about 70,000 years ago, the GoC was above sea level and was represented by a large fresh to brackish water lake (Lake Carpentaria) of varying extent (Torgersen et al. 1988; Yokoyama et al. 2001; Heap et al. 2004). During this glacial period of low sea level the Arafura Sill would have corresponded to a delta for Lake Carpentaria and its drainage system, with terrigenous sediments passing through it and ultimately into the Arafura Sea. Seaward of the Sill are a series of now submerged ridges and valleys (Fig. 1). Thus the GoC and adjacent Arafura Sea share a similar sedimentary environment as a result of a common paleo-drainage system; however, the history of the biota inhabiting the sediments in the two regions is likely to be very different – GoC marine species have been there for less than 10,000 years but species inhabiting the northern Arafura Sea could be much older as marine conditions persisted there during periods of low sea level.

The pilargid fauna analyzed in this study were collected from several different studies over a 40year period from six different sites, including offshore sites in the Arafura Sea, GoC and inshore sites at Gove and MacArthur River (Fig. 2). These sites represent four distinct geomorphic units: outer shelf ridge and valleys (site 1), shelf (sites 5, 6), bank/shoals (site 3), and inshore sites that may have seagrass beds and seasonally lowered salinity (sites 2, 4). [The first three geomorphic units are based on Heap et al. (2004)].

This study aims to document the pilargid fauna of the GoC–Arafura Sea region and characterize each species in terms of its geomorphic, sediment, and depth preferences. Also we review the present-day distribution of each species, and based on distributional, ecological, and geological data, suggest possible historical scenarios for the post-glacial colonization of the GoC by Pilargidae.

Materials and methods

Specimen and sediment collections. Pilargid specimens were reviewed from survey collections over the last 40 years (mostly the last 18 years), including samples from the Arafura Sea, Gove, McArthur River and the Gulf of Carpentaria. The Arafura Sea samples were collected in May 2005 on the R.V. Southern Surveyor cruise 05–2005 (Wilson 2006). The GoC benthic invertebrates were collected in February–March 2005 on the Southern Surveyor cruise 03–2005; this cruise sampled in the vicinity of Groote Eylandt and the Vanderlins and Mornington Island groups. The specimens from Gove and McArthur River were collected as part of NTM benthic baseline surveys conducted at the ports of Melville Bay (July 1991, March 1992, March 1993) and Bing Bong (March 1993), respectively. Identifications were verified and standardized across all surveys based on recent generic revisions. Specimens examined are housed at the Museum and Art Gallery of the Northern Territory, Darwin (NTM) and Queensland Museum, Brisbane (QM). Type material of Sigambra pettiboneae Hartmann-Schröder, 1979 from the Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Germany (HZM) was also examined.

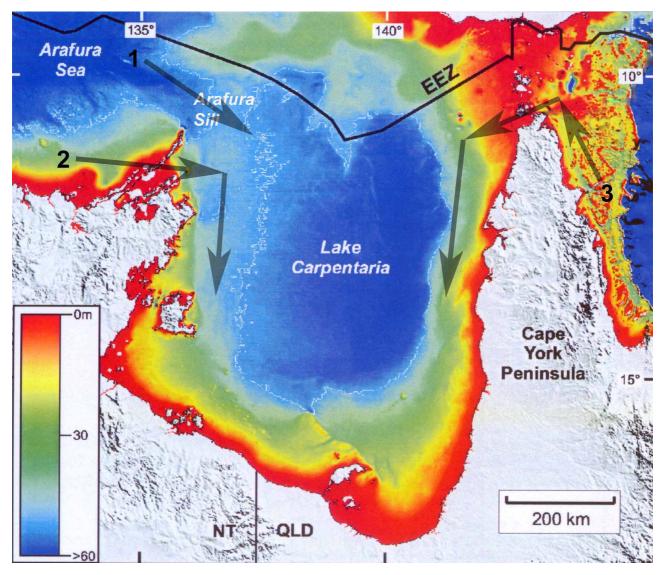


FIGURE 1. False-color image showing a period about 23, 000 to 26, 000 years ago when the sea level was about 65 m below its current level and Lake Carpentaria had reached its maximum extent within the area known at present day as GoC. The arrows indict possible tracks for colonization of pilargid species into the GoC as sea level rose to its present position. See text for explanation. Modified from Heap et al. (2004).

Sediment grain size data for the Arafura Sea were supplied by the Marine Sediment Database (Geosciences Australia 2006). The GoC sediment data were collected and analyzed by Geosciences Australia at the time of benthic invertebrate collection in 2005.

Data Analysis. Sediment preferences for 10 of the 13 pilargid species were determined statistically (*Pilargis* sp. 1, *Sigambra* cf. *robusta* and *Sigambra* sp. 'arafura' were not analyzed because they were represented by only one or a few specimens). Sediment grain size data (% mud, sand, and gravel) was analyzed using a covariance-based PCA utilizing PAST software (Hammer 2001). A total of 146 stations were represented in the plots from Arafura Sea, Gove, McArthur River, and the GoC (Groote Eylandt, Vanderlins and Mornington). Species occurrence data were reduced to presence/absence (i.e., abundances removed) because of the differing sampling techniques used across the surveys.

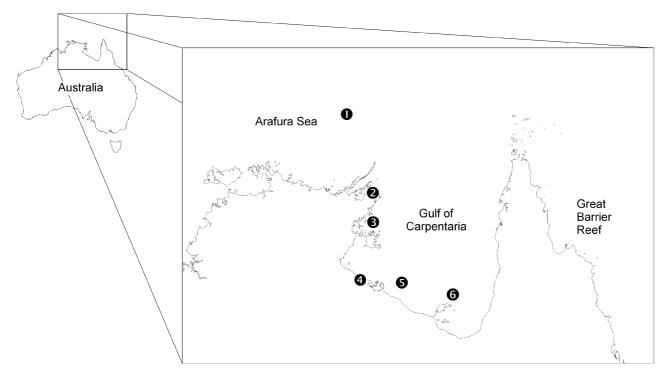


FIGURE 2. Location of pilargid material identified in this study, including Arafura Sea (1); inshore sites at Gove (2) and McArthur River (4); and three locations in the Gulf of Carpentaria: Groote Eylandt (3), Vanderlins (5), Mornington Islands (6).

Results

Taxonomy

Pilargidae de Saint-Joseph, 1899 Pilarginae de Saint-Joseph, 1899

Ancistrosyllis McIntosh, 1879

Ancistrosyllis cf. hartmanae Pettibone, 1966

Material examined. NTM (W7799, W16798, W16799, W16800, W16801, W16802, W16803, W16804, W16806, W16807, W16808, W16809, W16810, W016811, W16812, W16813, W16814, W16815, W16816, W16817).

Location. Gove, McArthur River (Table 1).

Remarks. Ancistrosyllis, as currently defined, is one of a few genera of Pilargidae (indeed Phyllodocida) that have a variable number of prostomial antennae: the 14 currently valid species may have either one, two, or three antennae (Fiege & Böggemann 1999). The Ancistrosyllis specimens collected in this study belong to the group having three antennae. In particular they are similar to A. hartmanae, originally described from Chesapeake Bay, USA, in having both ventral cirri and notopodial hooks from the third chaetiger. They differ from A. hartmanae however in having dorsal body papillae, or verrucae (new term suggested by Salazar-Vallejo & Harris 2006), arranged in distinct transverse rows (especially anteriorly—papillae are less dense posteriorly), and the lateral antennae being about three times longer than the median one. This genus is currently poorly represented in the Indo-West Pacific, but this record and two different forms from the Solomon Islands (G. Read pers. com.) suggest that several undescribed species, including this one, occur here.

		Gulf of		McArthur	
Species	Arafura Sea	Carpentaria	Gove	River	Extralimital
Ancistrosyllis cf. hartmanae	x	x	\checkmark	\checkmark	N/A
Cabira sp.1	\checkmark	\checkmark	\checkmark	\checkmark	N/A
Litocorsa annamita	\checkmark	\checkmark	x	x	Vietnam, South China Sea
Litocorsa sp. 'arafura'	\checkmark	x	x	x	N/A
Loandalia gladstonensis	x	\checkmark	\checkmark	\checkmark	Gladstone, Qld
Pilargis sp. 1	x	\checkmark	x	x	N/A
Sigambra cf. robusta	x	x	\checkmark	x	N/A
Sigambra sp. 2	x	\checkmark	\checkmark	\checkmark	Cairns, Brisbane, Qld
<i>Sigambra</i> sp. 'arafura'	\checkmark	x	x	x	N/A
Sigambra cf. tentaculata	\checkmark	\checkmark	\checkmark	\checkmark	N/A
Sigambra pettiboneae	x	x	\checkmark	\checkmark	Broome, NW Australia
Synelmis gibbsi	\checkmark	x	x	x	Indo-west Pacific, ?Red Sea
Synelmis cf. rigida	\checkmark	\checkmark	x	x	Central and West Pacific

TABLE 1. Occurrence of pilargid species in the four main study areas in northern Australia and extralimitally. (×) Absent, (\checkmark) Present, N/A = Not Available.

Cabira Webster, 1879

Cabira sp. 1

Material examined. QM (GOCI01000008, GOCI01000012, GOCI01000020, GOCI01000029, GOCI01000046, GOCI01000047, GOCI01000061, GOCI01000065). NTM (W534, W584, W585, W586, W587, W589, W590, W591, W593, W594, W653, W1977, W2002, W7801, W8230, W16818, W16819, W16820, W16821, W16822, W21889, W21890, W21891, W21892, W21893, W21894, W21895).

Location. Arafura Sea; Gove, McArthur River and GoC (Table 1).

Remarks. *Cabira* currently contains six species/subspecies (Mandal et al. 2007). Unlike other pilargid genera, the parapodia on which the first notopodial hooks occur is quite conservative among species (range, typically chaetigers 6–8); in our specimens the range was also chaetigers 6–8. The present specimens appear to differ from other species in the genus in having smooth tapered neurochaetae of two different lengths, a body divided by a constriction into a short 'thorax' and longer 'abdomen', which often displayed marked beading of segments, and the parapodia and dorsal cirri which lacked verrucae unlike the rest of the dorsum. Also, some specimens had distinctive subcutaneous brown pigments spots on the abdomen like some species of *Pilargis* (Salazar-Vallejo & Harris 2006).

Pilargis Saint-Joseph, 1899

Pilargis sp. 1

Material examined. NTM W21896.

Location. Mornington Island, GoC (Table 1).

Remarks. The single specimen found in this study confirms the observation of Salazar-Vallejo & Harris (2006) that *Pilargis* are not common. We are unable to assign it to species at this time. This species appears to be rare in space/time and is therefore not included in the discussion of ecology.

Sigambra Müller, 1858

Sigambra pettiboneae Hartmann-Schröder, 1979

Type material examined. Holotype (HZM P-16826), paratypes 4(HZM P-15498)

Other material examined. NTM (W7798, W16582, W16584, W16586, W16587, W16589, W16590, W16592, W16593, W16594, W16595, W16596, W16597, W16599, W16600, W16601, W16603, W16604, W16605, W16607, W16610, W16611, W16614, W16615, W16616, W16620, W16621, W16624, W16629, W16630, W16639, W16643, W16653, W16668, W16671, W16672, W16673, W16676, W16680, W16683, W16687, W16690, W16692, W16693, W16696, W16697, W16699, W16716, W16717, W16718, W16720, W16727, W16740, W16763, W16764).

Location. Gove and McArthur River (Table 1).

Remarks. As this is one of only a few pilargid species originally described from the region (type locality: Broome, NW Australia), the types were reexamined and compared to the study specimens. The type material had a moderately long median antenna $(1.5-2.0 \times \text{length of laterals})$, chaetiger 2 lacked ventral cirri, dorsal cirri were approximately $2 \times \text{longer than the ventral cirri, and the pharynx}$ had approximately 14 distal papillae encircling its rim. Interestingly, the start of the notopodial hooks showed significant variation ranging from chaetiger 8 (holotype, large specimen) to chaetiger 14 (paratypes, smaller specimens). Specimens from Gove and MacArthur River compared well with the type material in all characters; the notopodial hooks started from chaetigers 7–16.

Sigambra cf. robusta (Ehlers, 1908)

Material examined. NTM W16755

Location. Gove (Table 1).

Remarks. The single specimen found in this study is tentatively identified as *S*. cf. *robusta*. It differed from other *Sigambra* found in this study in having a ventral cirrus on chaetiger 2 (but only on one side), a median antenna about $1.5 \times$ the length of the lateral antenna, dorsal cirri about $2 \times$ longer than ventral cirri, about 8 distal pharyngeal papillae, and notopodial hooks from about chaetiger 23. This species appears to be rare in space/time and is therefore not included in the discussion of ecology.

Sigambra cf. tentaculata (Treadwell, 1941)

Material examined. QM (GOCI01000010, GOCI01000023, GOCI01000028, GOCI01000032, GOCI01000034, GOCI01000038, GOCI01000041, GOCI01000043, GOCI01000051, GOCI01000054, GOCI01000057, GOCI01000059, GOCI01000060, GOCI01000062, GOCI01000064, GOCI01000088, GOCI01000074, GOCI01000075, GOCI01000077, GOCI01000080, GOCI01000082, GOCI01000083, GOCI01000084, GOCI01000085, GOCI01000086, GOCI01000087). NTM (W16591, W16642, W16659, W16669, W16675, W16679, W16681, W16682, W16689, W16695, W16698, W16700, W1671, W16704, W16705, W16706, W16707, W16708, W16709, W16711, W16713, W16714, W16715, W16721, W16725, W16732, W16733, W16736, W16742, W16744, W16745, W16748, W16749, W16752, W16753, W16758, W16759, W16767, W16768, W16772, W16783, W16785, W16793, W16794, W21897, W21898, W21899, W21900, W21901, W21902, W21903, W21904, W21905, W21906, W21907, W21908, W21909, W21910, W21912, W21913, W21914, W21915, W21916, W21917, W21918, W21919, W21920, W21931, W21932, W21933, W21934, W21935, W21936, W21937, W21938, W21939, W21940).

Location. Arafura Sea; Gove, McArthur River and GoC (Table 1).

Remarks. Moreira & Parapar (2002) redescribed the holotype of *Sigambra tentaculata*, which is from Long Island, New York. The specimens from this study generally fit the description of these

authors, although the characteristic pharyngeal papillation (tooth-like papillae and distal papillae) could not be properly assessed as most specimens had their pharynx retracted. A recent publication by Nishi et al. (2007) reestablished *S. hanaokai* (Kitamori, 1960), which was previously considered to be a junior synonym of *S. tentaculata* (Treadwell, 1941). Unfortunately due to time restrictions it was not possible to compare material of *S. hanaokai* with our specimens. Future studies comparing the present material with *S. tentaculata* and other similar species (*S. parva* Day, 1963 and *S. hanaokai*) are planned.

Sigambra sp. 2

Material examined. QM (GOCI01000022, GOCI01000039, GOCI01000058). NTM (W8226, W16608, W16628, W16635, W16637, W16650, W16654, W16684, W16688, W16691, W16702, W16710, W16724, W16737, W21941).

Location. Gove, McArthur River, and GoC (Table 1).

Remarks. Sigambra sp. 2 is closest to Sigambra cf. tentaculata but differs from this species in having only 8–12 distal pharyngeal papillae (S. cf. tentaculata has 14), and in having the first dorsal cirrus equal in length to the peristomial cirri (S. cf. tentaculata has the first dorsal cirrus about $1.2-1.5 \times$ longer than the peristomial cirri). This species has also been recorded from Brisbane and Cairns, Queensland (SAM, pers. obs.).

Sigambra sp. 'arafura'

Material examined. NTM W21942

Location. Arafura Sea (Table 1).

Remarks. This is an unusual, probably new, species of *Sigambra* characterized by having a median antenna that is several times (4–5) longer then the laterals, lacking a ventral cirrus on chaetiger 2, dorsal cirri only slightly larger than ventral cirri, and notopodial hooks occurring only on posterior chaetigers (after chaetiger 40). In this last feature it resembles *S. rugosa* Fauchald, 1972 and *S. robusta* (Ehlers, 1908), but the former has a much shorter median antenna and the latter has ventral cirri on chaetiger 2. It bears slightly less similarity to *Sigambra* sp. 3 reported from the South China Sea by Al-Hakim & Glasby (2004).

Synelminae Salazar-Vallejo, 1987

Litocorsa Pearson, 1970

Litocorsa annamita (Gallardo, 1968)

Material examined. QM (GOCI01000002, GOCI01000004, GOCI01000005, GOCI01000011, GOCI01000015, GOCI01000024, GOCI01000027, GOCI01000030, GOCI01000033, GOCI01000044, GOCI01000048, GOCI01000050, GOCI01000052, GOCI01000053, GOCI01000055, GOCI01000056, GOCI01000063, GOCI01000066, GOCI01000067, GOCI01000069, GOCI01000070, GOCI01000072, GOCI01000078, GOCI01000088, GOCI01000306. NTM (W21943, W21944, W21945, W21946, W21947, W21948, W21949, W21950, W21951, W21952, W21953, W21954, W21955, W21956, W21957, W21958, W21959, W21960, W21961, W21962, W21963, W21964, W21965, W21966, W21967, W21968, W21969).

Location. Arafura Sea and GoC (Table 1).

Remarks. The genus *Litocorsa* has not been reviewed recently, and therefore species allocation is difficult. The above specimens have been tentatively identified as *L. annamita* based on the presence of three antennae, smooth neurospines (without arista or subterminal teeth) first present in median chaetigers, and notospines first emerging from chaetiger 12–14. This species was originally described from Vietnam, but is now known to occur throughout the South China Sea (Al-Hakim & Glasby 2004).

Litocorsa sp. 'arafura'

Material examined. NTM (W21970, W21971, W21972, W21973, W21974, W21975, W21976, W21977, W21978.

Location. Arafura Sea (Table 1).

Remarks. This species is most probably undescribed. It seems to be closest to *L. acuminata* (Wolf, 1986) in having an anterior cleft between the palps, notospines from about chaetiger 5–6, and aristate neurospines; however, the present material differs from this species in that the neurospines are tridentate and they start from chaetiger 20–26 rather than from chaetiger 15–18 (see Darbyshire & Mackie 2003).

Loandalia Monro, 1936

Loandalia gladstonensis Marks & Hocknull, 2006

Material examined. QM (GOCI01000001, GOCI01000003, GOCI01000006, GOCI01000007, GOCI01000009, GOCI01000013, GOCI01000014, GOCI01000016, GOCI01000017, GOCI01000018, GOCI01000019, GOCI01000021, GOCI01000025, GOCI01000026, GOCI01000031, GOCI01000035, GOCI01000036, GOCI01000037, GOCI01000040, GOCI01000042, GOCI01000045, GOCI01000049). NTM (W592, W7800, W8229, W16823, W16824, W16825, W16826, W16827, W16828, W16829, W16830, W16831, W16832, W16834, W16835, W16836, W16837, W16838, W16839, W16840, W16841, W16842, W16843, W16844, W16845, W16846, W16847, W16848, W16849, W16850, W16851, W16852, W16853, W16854, W16856, W21979, W21980, W21981).

Location. Gove, McArthur River, and GoC (Table 1).

Remarks. The material examined in this study extends the distribution of this species, which was previously known only from Gladstone, Queensland. In general the specimens fit within the variation range described for this species. The only differences appear to be the presence in some specimens of additional minute subdermal eyespots (which appear to correspond to paired pigment spots on the hind, mid and anterior brain) and a pair of large eyespots (or pigment patches) on the anal plate.

Synelmis Chamberlin, 1919

Synelmis gibbsi Salazar-Vallejo, 2003

Material examined. NTM (W21982, W21983, W21984, W21985, W21986).

Location. Arafura Sea (Table 1).

Remarks. The present material fits within the variation range described for this species by Salazar-Vallejo (2003). It can be easily distinguished from the other species of *Synelmis* found in the study, *S. rigida*, by the earlier start of the notospines (chaetiger 5 vs. chaetigers 11–19) and the presence of a pair of eyes, which sometimes appear as two pairs of closely set eyes (absent in *S. rigida*) This species is widespread in the Indo-West Pacific and questionably also occurs in the Red Sea (Salazar-Vallejo 2003).

Synelmis cf. rigida (Fauvel, 1919)

Material examined. QM (GOCI01000073, GOCI01000076, GOCI01000081). NTM (W21987, W21988, W21989, W21990, W21991, W21992, W21993, W21994).

Location. Arafura Sea and GoC (Table 1).

Remarks. The present material fits within the variation range described for this species by Salazar-Vallejo (2003), except for the presence of eyespots which are lacking in the present material but said to be present in *S. rigida*. For this reason, and the fact that our material also fits the description of the poorly known species *S. sinica* Sun and Chen, 1990 (type locality, South China

Sea), we tentatively identify it as *S. cf. rigida*. The present material should, however, be compared with the types of *S. sinica*. *Synelmis rigida* has previously been reported in the tropical Central and West Pacific (Salazar-Vallejo 2003). The present record extends its distribution westward to northern Australia.

Ecology

In total, 572 specimen lots (comprising one to several specimens per lot) of pilargids, comprising 90 lots from the Arafura Sea, 293 lots from the GoC, 143 from Gove, and 46 from McArthur River, were examined and identified to species or species units. Individuals were assigned to 13 species (or species units) and seven genera. Although all four localities have a similar diversity of species (6–7 species each), the species composition differs between each region. Table 1 lists all 13 species and their presence or absence from each of the four locations, and whether or not the species has been reported outside the study areas.

Several species currently appear to be endemic at the regional level: *Litocorsa* sp. 'arafura' and *Sigambra* sp. 'arafura' were collected only from the Arafura Sea, *Pilargis* sp. 1 was collected only within the GoC, and *Sigambra* cf. *robusta* was only collected from Gove. Although *Synelmis gibbsi* was only reported from the Arafura Sea stations in this study, the species is known to be widely distributed in the Central and West Pacific. Two species were present in all sampled locations: *Cabira* sp. 1 and *Sigambra* cf. *tentaculata*.

The habitat of pilargid fauna can be partitioned into three components: (1) a deep continental shelf component with a depth of 69–233 m characteristic of the Arafura Sea—includes ridges and valleys; (2) a shallow continental shelf component with a depth of 26–52 m characteristic of the GoC regions—includes banks and shoals, and (3) an inshore component with seagrasses and seasonally lowered salinity and a depth of 0.5–15 m characteristic of the Gove and McArthur River regions. Three species, *Ancistrosyllis* cf. *hartmanae, Sigambra* cf. *robusta* and *Sigambra pettiboneae* appear to be found solely in the inshore habitat; *Synelmis* cf. *rigida* and *Litocorsa annamita* appear to be offshore generalists occurring in both the Arafura Sea and GoC in a range of depths between 26 and 233 m; and *Litocorsa* sp. 'arafura', *Sigambra* sp. 'arafura' and *Synelmis* gibbsi are offshore species occurring only in the Arafura Sea, at depths between 69 and 233m.

Figs. 3–4 show the sediment-based PCA plots with the presence/absence of each pilargid species represented by the filled squares and cross symbols respectively. The majority of the species are found in all sediment types from high percentage of gravel to high percentage of mud. However, three species appear to have more selective grain size preferences: *Litocorsa* sp. 'arafura' and *Synelmis gibbsi* are found in sand and gravel dominated sediments, and *Ancistrosyllis* cf. *hartmanae* is the only species found in mud and sand dominated sediments. All PCAs shown in Figs. 3–4 are represented by a variance of 83.26% for PC1 and a variance of 16.72% for PC2.

Discussion

The results of this study need to be viewed within the context of the following limitations. Despite our efforts to standardize data across all surveys by removing abundance data (as different sampling techniques were used), there still remains the possibility that the data could be affected by differences in collection time, viz. annual and seasonal variation was not accounted for. This is probably more problematical for the inshore sites (Gove and McArthur River), as shallow water benthic fauna could be more affected by storms and cyclones than deep shelf fauna. A seasonal cycle

of polychaete occurrence and abundance has been reported for intertidal sites in Darwin Harbour (Metcalfe & Glasby 2008). However, despite these limitations, we believe that the large number of samples analyzed provides us with reasonable confidence that at each site the pilargid fauna was reasonably comprehensively sampled.

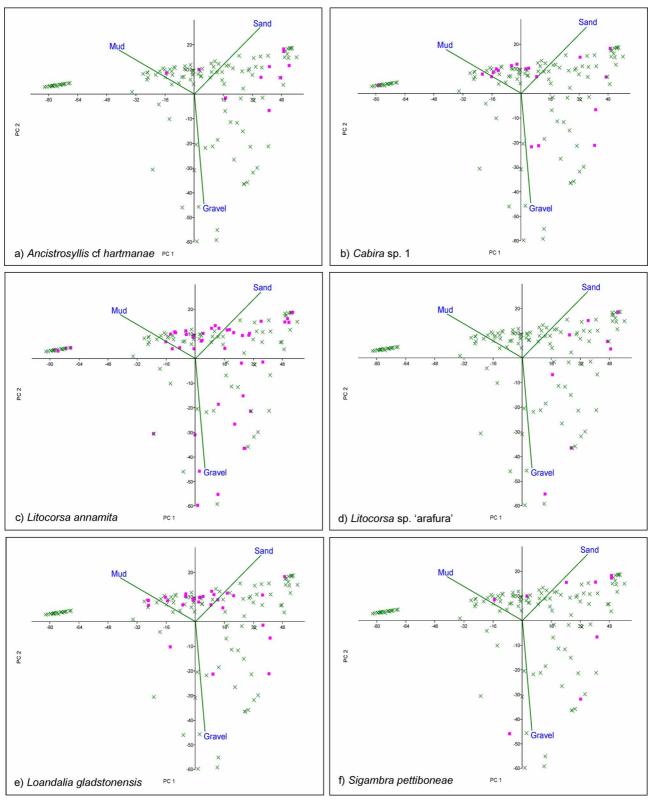


FIGURE 3. Principal Component Analysis (PCA) of sediment grain size for Arafura Sea and the GoC locations. PCAs are represented by a combined variance of 99.98% for PC1 and PC2. For the six species shown, green cross = absence of species from site and pink filled square = presence of species at site.

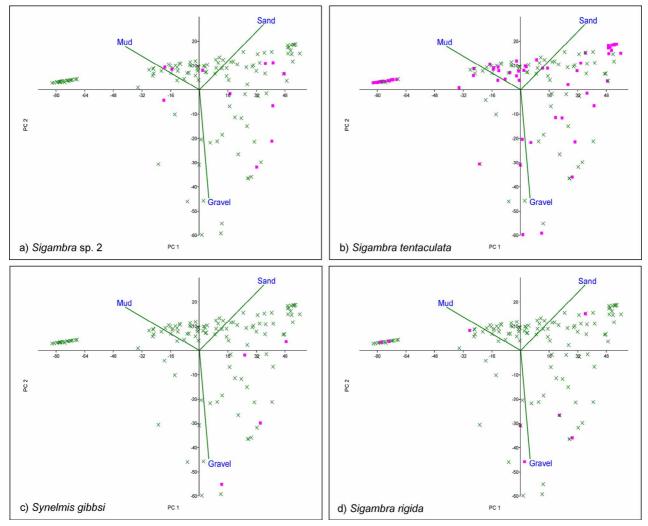


FIGURE 4. Principal Component Analysis (PCA) of sediment grain size for Arafura Sea and the GoC locations. PCAs are represented by a combined variance of 99.98% for PC1 and PC2. For the four species shown, green cross = absence of species from site and pink filled square = presence of species at site.

Diversity and Endemism. Niche preference of pilargids can be described through a number of environmental characteristics, including depth, sediment type, and geomorphic unit (Table 2). Together with the information on the occurrence of each species at each of the four locations (Table 1), we can draw some preliminary conclusions on the degree of endemism of each species and routes (tracks) of post-glacial colonization of the GoC, as follows:

- 1) Widespread generalists—found at all locations, in all sediment types (*Cabira* sp. 1 and *Sigambra* cf. *tentaculata*); widespread post-glacial colonization of GoC
- 2) Offshore-only widespread generalists—found in the Arafura Sea and Gulf of Carpentaria, in all sediment types (*Litocorsa annamita* and *Synelmis* cf. *rigida*); both species also occur in the South China Sea; limited post-glacial colonization of GoC (track 1, Fig. 1)
- 3) Endemic to inshore habitats of northern Australia—found in Gove and McArthur River, with Ancistrosyllis cf. hartmanae being unique to mud and sand dominated sediments, and Sigambra pettiboneae collected from all sediment types; S. pettiboneae also occurs in northwest Australia; possible eastward shoreline colonization of GoC (track 2, Fig. 1)
- 4) Endemic to northeastern Australia—found on the shelf and in the inshore habitats of the GoC and Queensland, includes *Loandalia gladstonensis* and *Sigambra* sp. 2; possible westward shoreline colonization of GoC (track 3, Fig. 1)

5) Endemic to the Arafura Sea—found only in the Arafura Sea, with sediment dominated by sand and gravel includes *Litocorsa* sp. 'arafura', *Sigambra* sp. 'arafura' (although *Synelmis gibbsi* also occurs in the Arafura Sea it has been reported more widely in the Indo-West Pacific). *Litocorsa* sp. 'arafura' appears to occupy a similar ecological niche as the Gulf of Mexico species, *Litocorsa stremma* Pearson, 1970, which is known to prefer near shore sandy sediments with a relatively low mud content (Flint & Rabalais 1980) and is thought to be a scavenger (Pearson 1970).

The high diversity and endemism of Pilargidae in the epicontinental seas of northern Australia is most likely attributable to a favorable prograding sedimentary environment that existed during the Quaternary and beyond, its position between the Pacific Ocean and Indian Ocean (via Arafura Sea), and the shallowness of the region (esp. the Gulf of Carpentaria), which combined with fluctuations in sea level would have promoted speciation. A comparable level of diversity has been found in Mexico, which has 14 species and seven genera (Salazar-Vallejo 1987), but this count includes both the east and west coasts of Mexico, and therefore does not represent a single epicontinental sea as does the region considered here. Further studies are required in order to corroborate the patterns found here. In particular, more environmental data and taxonomic clarity is required for species occurring not only in northern Australian waters, but also those surrounding areas.

Species	Geomorphic unit	Depth range (m)	Sediment type
Ancistrosyllis cf. hartmanae	Inshore	0.5–15	Mud / Sand
Cabira sp.1	Inshore, Sill and canyon, Shelf, Bank and shoals?	0.5–233	Mud / sand / gravel
Litocorsa annamita	Sill and canyon, Bank and shoals?	26-52	Mud / sand / gravel
Litocorsa sp. 'arafura'	Sill and canyon	69–233	Sand & gravel
Loandalia gladstonensis	Inshore, Shelf, Bank, and shoals?	0.5–52	Mud / sand / gravel
Pilargis sp. 1	Bank and shoals?	26–52	N/A*
Sigambra cf. robusta	Inshore	5–15	N/A*
Sigambra sp. 2	Inshore, Shelf, Bank, and shoals?	0.5–52	Mud / sand / gravel
<i>Sigambra</i> sp. 'arafura'	Sill and canyon	69–233	N/A*
Sigambra cf. tentaculata	Inshore, Shelf, Bank, and shoals?	0.5–233	Mud / sand / gravel
Sigambra pettiboneae	Inshore	0.5–15	Mud / sand / gravel
Synelmis gibbsi	Sill and canyon	69–233	Sand & gravel
Synelmis cf. rigida	Shelf, Bank, and shoals?	26–52	Mud / sand / gravel

TABLE 2. Habitat preference of pilargids from northern Australia locations. *Data not quantifiable as only one individual specimen of this species has been collected.

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