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GLOBAL DIVERSITY IN THE THALASSINIDEA (DECAPODA)

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ABSTRACT

Among the 516 taxa of thalassinideans so far described, there is a strong latitudinal increase in species numbers from high latitudes towards the equator in both hemispheres. Numbers of species in the northern hemisphere are similar to those in the southern one. Thirty-two percent of the species are found in the Indo-West Pacific and 22% in the Southwest Atlantic. All species are benthic and live either in marine or brackish water. Ninety-five percent of all thalassinideans inhabit shallow water (0–200 m); only three species have been found below 2,000 m. Especially the families Callianassidae, Upogebiidae, Thalassinidae, and Strahlaxiidae occur in the intertidal to very shallow waters (0–20 m), while most members of the Axiidae and Calocarididae are bathyal (200–2,000 m).

The Thalassinidea are a group of mainly burrowing decapod shrimps. They have attracted increased attention in recent ecological studies on marine soft-bottom benthos, especially in terms of their influence on the whole sedimentology and geochemistry of the seabed (Ziebis *et al.,* 1996a, b), their bioturbating activities (Rowden and Jones, 1993; Rowden *et al.,* 1998a, b) and consequent effects on benthic community structure (Posey, 1986; Posey *et al.,* 1991; Wynberg and Branch, 1994; Tamaki, 1994).

Biodiversity as a field of scientific and common interest has rapidly become a catchword in the literature, particularly since the conclusion of the Convention on Biological Diversity at the UNCED Conference in Rio de Janeiro in 1992. One question raised in many papers on this topic is "How many species are there?" (Diamond, 1985; May, 1988, 1990; Stork, 1983). Stork (1993) summarized five methods of obtaining an answer to this general question. These are based either on counting all species, extrapolations from known faunas and regions, extrapolations from samples, methods using ecological criteria, and censusing taxonomists' views. Another approach outlined by Hammond (1992) is the exploration of how far global biodiversity may have been accounted for by taxonomic descriptions referring to the total number of species currently recognized and the degree to which we can estimate the completeness of taxonomic knowledge.

The aim of this paper is to give a census of the known species within the Thalassinidea, together with a survey on their latitudinal, regional and depth distribution.

MATERIALS AND METHODS

Data in Figs. 1–3 and Table 1 were derived from a database. This database was begun by the author in 1983 on cards, later entered into the computer using dBase (Ashton Tate, U.S.A.). In 1996, the database was transferred to MS-Access (Microsoft Corp., U.S.A.) and holds, as of 31 December 1998, 3,110 records on Recent and fossil Thalassinidea. A preliminary list of known species up to 1995 based on this database can be found in van der Land (1996). Known data on species numbers from the past (Fig. 1) were considered retrospectively, i.e., under current views of validity. The systematic arrangement of superfamilies and families follows that of Poore (1994). For practical reasons, the following families were pooled for figures on cumulative species numbers and latitudinal distribution: Ctenochelidae with the Callianassidae as Callianassidae s.l.; and Calocarididae, Micheleidae and Strahlaxiidae with the Axiidae as Axioidea. Due to low species numbers, the families Thomassiniidae, Laomediidae, Callianideidae and Thalassinidae are not shown separately in the graph on cumulative species numbers, but are included in the total Thalassinidea.

A particular species was considered valid when it was mentioned as such in several papers or—in case of single records—was never synonymized with any other taxon. In case of conflicting views of taxonomists in subsequent publications, the most recent opinion was adopted.

Discovery curves and description rates were calculated using the methods outlined in May (1990) and Hammond (1992).

Latitudinal distribution of species was evaluated using 5° bands assuming a continuous distribution between endpoints in cases of widely scattered records. For regional distribution, the geographic index of the Aquatic Science

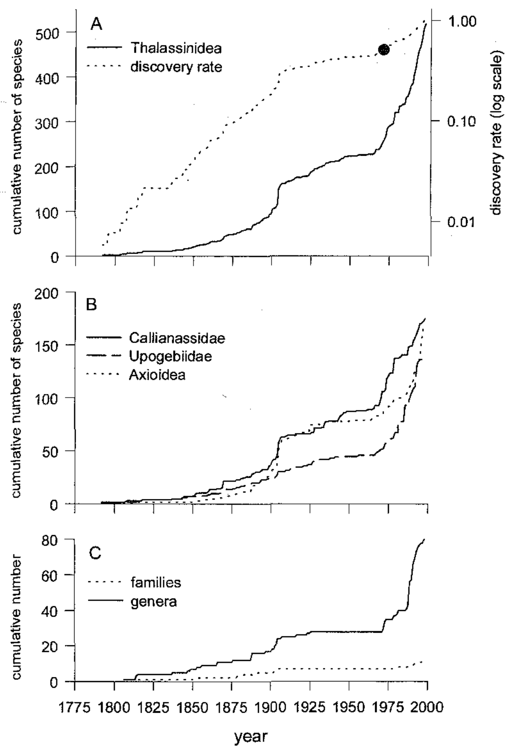

Fig. 1. Time series for A: cumulative number all thalassinidean species described up to 1998 (solid line), cumulative number of known species expressed as a fraction of those known in 1998 on a logarithmic scale (dotted line), the black circle indicates the point at which half of the 1998 total had been reached; B: cumulative numbers of species in major (super)families; and C: cumulative numbers of genera and families within the Thalassinidea.

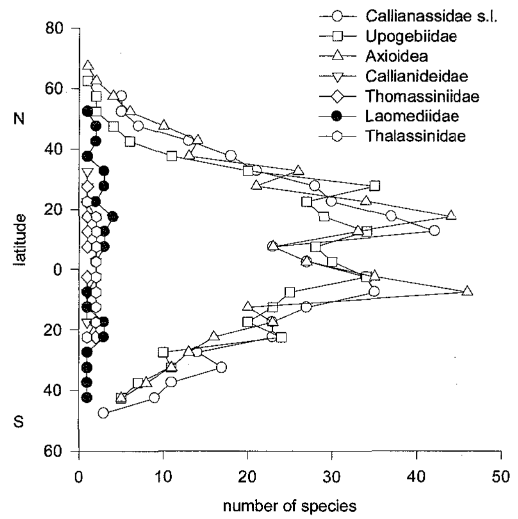

Fig. 2. Latitudinal distribution of species numbers in the thalassinidean (super)families. Data for bands of 5° latitude.

and Fisheries Abstracts (ASFA, Cambridge, U.K.) was used.

RESULTS

Historical Data on Thalassinidean Biodiversity

The first three species were described from the Mediterranean in 1792: *Astacus pusillus* Petagna, 1792; *Astacus tyrrhenus* Petagna, 1792; and *Cancer candidus* Olivi, 1792, currently known as *Upogebia pusilla*, *Callianassa tyrrhena,* and *Callianassa candida*, respectively. From then on, the number of known species increased rapidly with doubling times between 23 and 24 years (Fig. 1). A very rapid increase in species numbers occurred between 1901 and 1906 with the major contributions of M. J. Rathbun, G. Nobili, and especially J. G. de Man, who described numerous species collected during the Siboga Expedition 1899–1900. Between 1907 and 1950, species numbers increased slowly, and a plateau of around 220 species seemed to be reached in 1960. From that time on, species numbers increased rapidly, doubling within 30 years. This pattern in the time series—with some deviations—is visible in the curves for the three species-rich (super)families. In the Callianassidae, the steep increase after 1900 is prominent compared to the weak one in the Upogebiidae. The time series of the number of families and genera also mirrors this pattern. Currently, 11 families and 80 genera are recognized. In addition to the 73 genera listed by Poore (1994), the following genera were included in the counts: *Paracalocaris* Sakai, 1991; *Aethogebia* Williams, 1993; *Paraglypturus* Türkay and Sakai, 1995; *Marianaxius* Kensley, 1996; *Paraxiopsis* de Man, 1905 (as reinstated by Kensley, 1996b); *Necallianassa* Heard and Manning, 1998; and *Nihonotrypaea* Manning and Tamaki, 1998. Besides 516 valid taxa, 80 taxa are currently considered as junior synonyms. This represents a synonymisation rate of approximately 13%. Some 180+ names have been attributed to exclusively fossil Thalassinidea.

Latitudinal and Regional Distribution

The distribution of the Thalassinidea shows a clear latitudinal gradient with low species

Table 1. Regional distribution of the Thalassinidea. Number of species recorded for each region. ANE: Atlantic Northeast; MED: Mediterranean; ASE: Atlantic Southeast; ANW: Atlantic Northwest; ASW: Atlantic Southwest; ISW: Indian Ocean; ISEW: Pacific Southwest; INW: Pacific Northwest; INE: Pacific Northeast; ISE: Pacific Southeast; PSE: Polar-Antarctic-Eastward; PSW: Polar-Antarctic-Westward. Ca: Callianassidae; Ct: Ctenochelidae; Up: Upogebiidae; Ax: Axiidae; Cc: Calocarididae; St: Strahlaxiidae; Cd: Callianideidae; To: Thomassiniidae; La: Laomediidae; Mi: Micheleidae; Ta: Thalassinidae. Sum of numbers may exceed that of total number of species because those species occurring in more than one region are added to each region separately.

Region	Ca	Ct	Up	Ax	Cc	St	Cd	To	La	Mi	Ta	All
ANE	4	1	4	2	2				1			14
MED	7	1	6	2	1				1			18
ASE	14	4	7	2	2				1			30
ANW	4		1	2	1				1			9
ASW	35	6	27	22	6	1	1	1	5	11		115
ISW	25	1	28	16	3	1	1	1	2	3	2	81
ISEW	46	4	43	43	2	5	1	5	3	11	2	163
INW	5	1	13	13	2		1			1		36
INE	5	1	4	3	2				1			16
ISE	16		14	19	1	2		1	2			55
PSE	5	1	9	5	2	2			2	1		27
PSW	11	1	3	2	1					1		19
Total	155	20	139	113	23	9	2	7	19	27	2	516

numbers in high latitudes and high species numbers in low latitudes (Fig. 2). For all three species-rich groups (Callianassidae s.l., Upogebiidae, and Axioidea) two peaks can be recognized, one between 25° and 10°N and one between 0° and 15°S. The latter peak is more pronounced in the Axioidea than in the other two families. All three groups show a drop in species number between 10°N and 5°S. The smaller families exhibit—due to low species numbers—no clear pattern; the Thalassinidae occur in low latitudes whereas members of the Laomediidae are found only north and south of the equator. The northernmost record (about 69°N) is for the axiid *Calocarides coronatus* (Trybom, 1904) on the coast of Norway. The southernmost record is, according to Ferrari (1981), that of the callianassids *Anacalliax argentinensis* (Biffar, 1971) and *Notiax brachyophthalmus* (A. Milne-Edwards, 1870) in the Atlantic (about 48°S) and that of *Callianassa filholi* A. Milne-Edwards, 1878, from Stewart Island (about 47°S) in the Pacific (de Man, 1906). The widest north-south distribution is given by Sakai and de Saint Laurent (1989) for *Calocaris macandreae* Bell, 1853, from 65°N to 26°S; that the southern record is indeed this species, however, is doubtful. Another species with a wide north-south range is *Callichirus major* (Say, 1818), which occurs from North Carolina (about 35°N) to southern Brazil (about 27°S). A wide circumtropical distribution has been attributed to *Axiopsis serratifrons* (A. Milne-Edwards, 1873) (Kensley, 1980).

The highest species numbers (32%) are found in the Indo-West Pacific (ISEW in Table 1) followed by the Atlantic Southwest with 22%, where two-thirds of those occur in the Caribbean and Gulf of Mexico. In the Indian Ocean species numbers (15.7%) are similar to those in the Caribbean. Only a few species (1.7%) occur in the Atlantic Northwest compared to the Atlantic Northeast (2.7%) and the Mediterranean (3.5%). The Pacific Southeast is relatively species rich (10.7%) compared to the Pacific Northwest and Pacific Northeast with 7% and 3.1%, respectively.

Depth Distribution

Generally, the sea bottom is arbitrarily divided into shallow water (0–200 m), bathyal (200–2,000 m), abyssal (2,000–6,000 m) and hadal (> 6,000 m). Figure 3 shows that most (95% of the species) Thalassinidea occur in shallow water; 20% of the species occur in the bathyal, and only very few species (3) are found below 2,000 m (Fig. 3).

Among the Callianassidae, 54% inhabit very shallow waters (0–2 m); only 8.4% occur between 200 and 2,000 m, and the deepest record is 724 m for *Cheramus profundus* Biffar, 1973. The Ctenochelidae live only sublittorally, with 80% of the species between 20 and 2,000 m. Among the Upogebiidae, the percentage of species living in very shallow

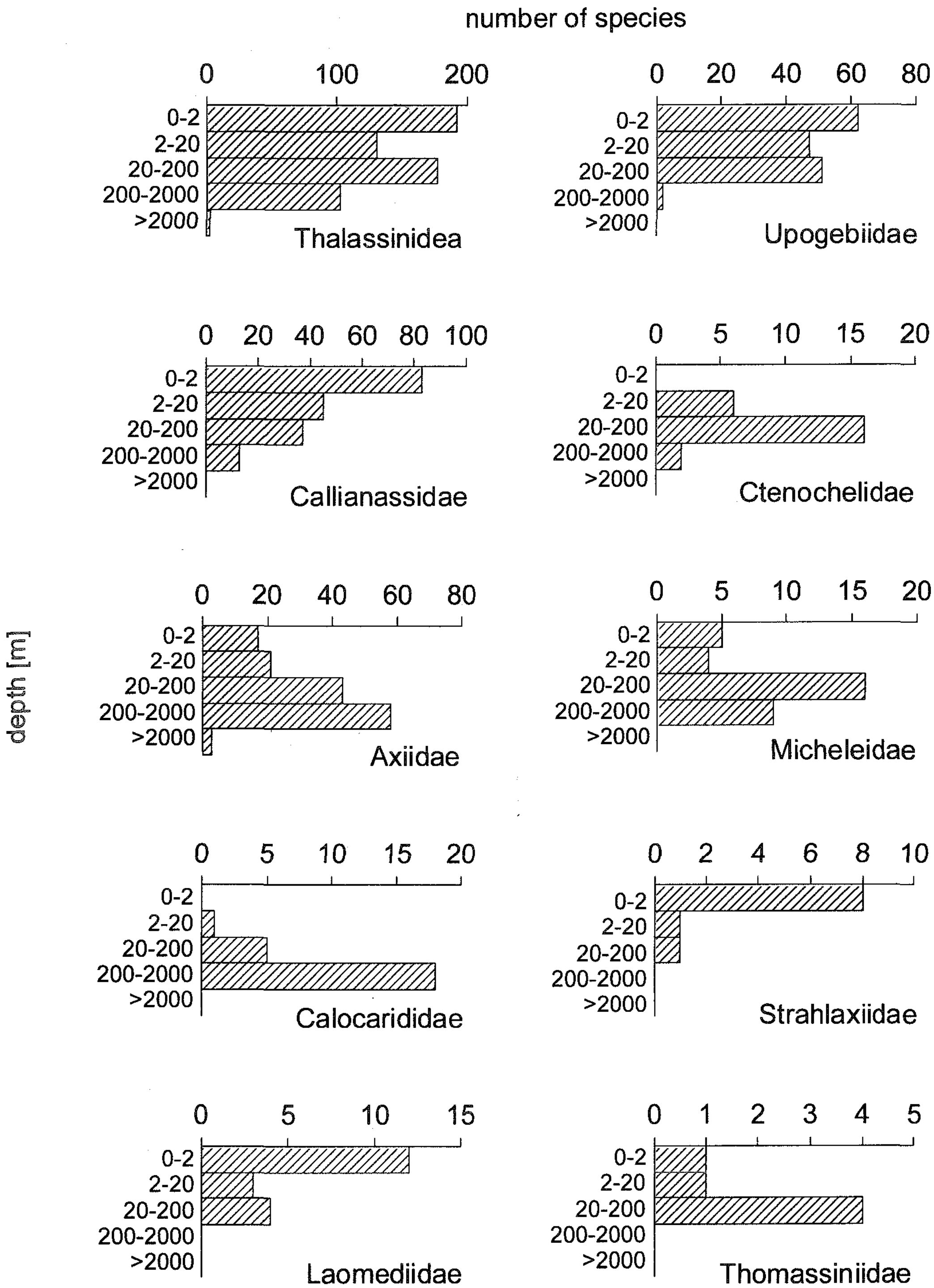

Fig. 3. Depth distribution of species numbers in thalassinidean families.

water is highest (44.6%) and only 1.4% occur between 200 and 2,000 m. Here, the greatest depth recorded is 485 m for *Gebicula exigua* Alcock, 1901. The depth distribution is quite heterogeneous within the Axiidae, even within particular genera; the majority are sublittoral, with the most species in the bathyal. The greatest depths reported are: 2,130 m for *Eiconaxius acutifrons* Bate, 1888 (Wicksten, 1982); 2,036 m for *Calocarides lev* (Zarenkov, 1989); and 2,013 m for *Calocarides quinqueseriatus* (Rathbun, 1902) (Kensley, 1996a). The Calocarididae have no exclusively shallow-water species, but *Calocaris macandreae* Bell, 1853, has a bathymetric range from 13 to 1,432 m. The members of Strahlaxiidae live predominantly (89%) in shallow waters. Within the Micheleidae most species occur between 20 and 200 m, and only a few occur intertidally. Among the Laomediidae, the genus *Laomedia* and *Naushonia* are mainly reported from the intertidal, whereas members of *Jaxea* occur sublittorally up to 147 m. Both the Callianideidae (100%) and Thalassinidae (100%) live predominantly intertidally and in very shallow water.

The majority of the Thalassinidea burrow in various types of sediments from coarse coral rubble to sand and mud, and even in firmground, e.g., *Upogebia mediterranea* Noël, 1992 (Asgaard *et al.,* 1998). Some axiids are found in crevices on corals reefs, e.g., members of the genus *Coralaxius* (Kensley, 1994), or are sponge commensals, e.g., members of the genus *Eiconaxius* (Kensley, 1996c); *Eutrichocheles pumilus* Sakai, 1994; and *Spongaxius brucei* Sakai, 1986. Some members of the Upogebiidae also live in sponges, including *U. savignyi* (Strahl, 1861); *U. acanthura* Coelho, 1973; *U. balmeorum* Ngoc-Ho, 1990; *U. brucei* Sakai, 1975; *U. cargadensis* Borradaile, 1910; *U. casis* Williams, 1993; *U. darwini* Nobili, 1906; *U. laemanu* Ngoc-Ho, 1990; *U. australiensis* de Man, 1927; *U. ovalis* Ngoc-Ho, 1991; *U. stenorhynchus* Ngoc-Ho, 1991; and *U. tractabilis* Hale, 1941. Other species have been found between corals, among them *U. corallifora* Williams and Scott, 1989. Coral borers are *U. trypeta* Sakai, 1970, and especially species of the genus *Pomatogebia* such as *P. operculata* (Schmitt, 1924); *P. rugosa* (Lockington, 1878); and *P. cocosia* Williams, 1986 (Kleemann, 1984; Scott *et al.,* 1988; Williams and Ngoc-Ho, 1990).

All species of the Thalassinidea live in marine habitats or in habitats under seawater influence. Many Upogebiidae and Callianassidae are found in estuaries with reduced salinity. Especially members of the genus *Lepidophthalmus* are known for low-salinity habitats (Manning and Felder, 1991). Mass migrations into rivers have been reported in Cameroon for *Callianassa turnerana* White, 1861 (Vanhöffen, 1911; Monod, 1927).

Discussion

A latitudinal gradient in species numbers of marine animals, with high numbers of species in low latitudes and lower numbers of species in high latitudes, has been observed in several groups, e.g., in bivalves (Stehli *et al.,* 1967), pelagic fish, ostracods, decapods and euphausiaceans (Angel, 1993), prosobranch gastropods (Roy *et al.,* 1998), and also for decapods in general (Abele, 1982). However, other groups such as isopods and amphipods are more numerous in temperate to cold waters (Abele, 1982). A latitudinal cline as a general rule for marine organisms was therefore questioned by Clarke (1992).

Noteworthy in the latitudinal distribution of the Thalassinidea is the relatively low species numbers between 10°N and 5°S compared to the neighbouring northern and southern latitudes. To some unknown degree, this plot (Fig. 2) is a record of actual occurrence as well as of collectors' activities. The Caribbean is a very well-studied region, and the thalassinidean fauna of Brazil is also fairly well known. However, a gap in the distribution is visible, i.e., for the Upogebiidae along the Atlantic shore of South America between the mouths of the Orinoco and Amazon Rivers (Williams, 1993: Fig. 2), with only two species reported along the shores of the Guyanas. On the Pacific side of Central America, only 13 species of thalassinids are listed for Colombia (about 5°N) (Lemaitre and Alvarez León, 1992), whereas 47 species have been listed for the eastern Pacific by Lemaitre and Ramos (1992). The thalassinidean fauna of the Gulf of Guinea has been covered in detail by LeLoeuff and Intes (1974) and de Saint Laurent and LeLoeuff (1979), but few records exist for Somalia. In the Indian Ocean, only four species have been reported from the Maldives; more recent studies are lacking. In the Indo-West Pacific, the best-studied regions are the Indonesian Archipelago, northeast Australia, New Caledonia, and French Polynesia, whereas the Philippines and the South China Sea are less well covered. In the Pacific Ocean east of the Marshall Islands, only a few islands that would provide adequate habitats for thalassinideans are located between 10°N and 5°S.

Not surprisingly, thalassinideans do not occur in the cold Arctic and Antarctic. Only a few lithodids, hermit crabs, galatheid and true crabs have been found in the Arctic, and only three species of Reptantia were found south of the Antarctic Convergence (Tiefenbacher, 1994; Klages *et al.,* 1995). Here, only members of the Caridea appear to have been successful in colonising the cold waters (Arntz and Gorny, 1991). Frederich *et al.* (1998) hypothesised that the absence of Reptantia in cold waters may be explained with their higher hemolymph Mg_{2+} concentrations compared to those of the Caridea.

The current census of taxa described in the infraorder Thalassinidea was concluded in 1998 and yielded 516 species considered valid. Chace (1951) gave a number of 257 species described up to 1945. His number seemed to be an overestimate compared to the 202 species at that time according to the present study and is probably due to more recent synonymisations. The discovery curve—the numbers of known species expressed as a fraction of those known in 1998 on a logarithmic scale plotted against time—shows that up to 1998 new species were described at an ever-increasing pace, with the 1972 total doubled by 1998 (Fig. 1A). The overall description rate between 1758 and 1998 is 2.5 species a^{-1}; it is currently proceeding at a rate of 10 species a^{-1}. Discovery curves and description rates of the Thalassinidea obtained in the present census are in the same range as those listed for Crustacea and some insect groups by Hammond (1992). From the time series of descriptions in Fig. 1A, no extrapolation for the total number of thalassinideans seems possible, except that the actual number will be much larger than the present one. Wittmann (1999) made extrapolations of actual numbers of mysidaceans by comparing species numbers of "best studied" areas with randomly selected areas in the northern and southern hemisphere. He came to the conclusion that the actual number of Mysidacea is 4 (3–5) times that of the currently known number. This estimate may be even higher in the thalassinideans due to their cryptic and burrowing lifestyle. Snelgrove (1999) stressed that in marine benthic habitats, only a small proportion of overall species is known; he lists an estimated total species number which is eight times the currently described macrofauna. Much of this expected diversity in marine sediments is based on recent findings of remarkably high species numbers in the deep sea (Grassle and Maciolek, 1992; Poore and Wilson, 1993). It is, however, very unlikely that any thalassinidean will be found well below 2,000 m. Low temperatures between 3.6° and –0.6°C (Menzies, 1965)—similar to those in the high Arctic and Antarctic—may have precluded the colonisation of deep-sea sediments by the Thalassinidea.

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