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IDENTIFICATION OF GENERALIZED TRACKS FOR THE SPECIES OF ISOPODA (PERACARIDA) FROM THE EASTERN PACIFIC

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ABSTRACT

A panbiogeographic analysis of the distributional patterns of 196 species of eastern Pacific Isopoda led to the recognition of three generalized tracks, which correspond to major biotic components. The northern cold-temperate track extends from 62° to 35°N, in the northern cold-temperate sub-region (Aleutian Islands, Gulf of Alaska and coast of British Columbia, Washington, Oregon and northern California). The 57 endemic species assigned to it belong mainly to suborders Flabellifera, Valvifera and Asellota, although species of Oniscidea, Epicarida, Anthuridea, and Gnathiidea are also present. The northern warm-temperate/ tropical track extends from 33°N to 1°S, covering the Warm-Temperate and Tropical sub-regions, i.e., southern California to about halfway south into Ecuador. The 27 endemic species assigned to it belong mainly to the Flabellifera, most of them Cirolanidae and Cymothoidae, and Sphaeromatidae, Valvifera, Anthuridea, Asellota, Epicaridea, Oniscidea, and Gnathiidea are also present. The southern warm/cold-temperate track extends from 19° to 52°S, covering the Southern Warm and Cold-Temperate sub-regions, i.e., coast of Chile south to the Magellan Strait. The 27 endemic species assigned to it belong mostly to the Flabellifera, Asellota, and Valvifera.

KEY WORDS: biogeography, generalized tracks, Isopoda, panbiogeography, parsimony analysis of endemicity.

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INTRODUCTION

Isopods are common inhabitants of nearly all marine natural environments. Their high diversity (approximately 9500 aquatic species; Brusca and Brusca, 2002) and evolutionary success are reflected by their presence in virtually every marine and brackish water habitat, from intertidal zones to deep sea. Species of Isopoda inhabit basically the benthic realm, where densities of up to 53,000 organisms per square meter have been found (Nelson and Demetriades, 1992). Isopods undergo direct development with brooding, hence true larval forms do not occur in this group, which may be potentially correlated, from a biogeographic view point, with a high degree of endemism.

The western coast of America extends over about 127 degrees of latitude, from Point Barrow (ca. 70°N) to the Magellan Strait (ca. 55°S). It corresponds to the Eastern Pacific marine region, which encompasses six subregions, roughly defined by the prevailing average water temperature. Constant environmental conditions in these subregions, basically related to the climatic patterns and to the ocean and coastal currents, have led to the establishment of typical biotas with a well documented, high degree of endemism (Briggs, 1974; Brusca and Wallerstein, 1979; Brattström and Johanssen, 1983; Hendrickx, 1992).

Some papers dealing with the distribution of isopods of the eastern Pacific have been already published. Menzies (1962) and Jaramillo (1982) reviewed the biogeography of Chilean marine Isopoda. Brusca and Wallerstein (1979) analyzed the distribution of North Pacific Idoteidae. Kussakin (1990) reviewed the biogeography of isopods in the boreal Pacific, whereas Carlton and Iverson (1981) studied species of *Sphaeroma* in Californian waters. Espinosa-Pérez (1999) and Espinosa-Pérez and Hendrickx (2002, 2006) addressed the distribution and biogeographic affinities of the isopods of the Mexican Pacific. Other studies dealing with isopods, crustaceans or several animal taxa (including isopods) provided information regarding the distribution of eastern Pacific isopods (Brandt, 1992: Antarctic Isopoda; Carvacho and Saavedra, 1994: crustaceans from Chiloé island; Mariani et al., 1996: Polychaeta and Isopoda from the Magellan Strait; Brandt et al., 1999: Mollusca and Crustacea from the Magellan Strait). Although no particular biogeographic issues were addressed in their papers, Brusca et al. (1995) and Espinosa-Pérez and Hendrickx (2001) presented what is to date the only

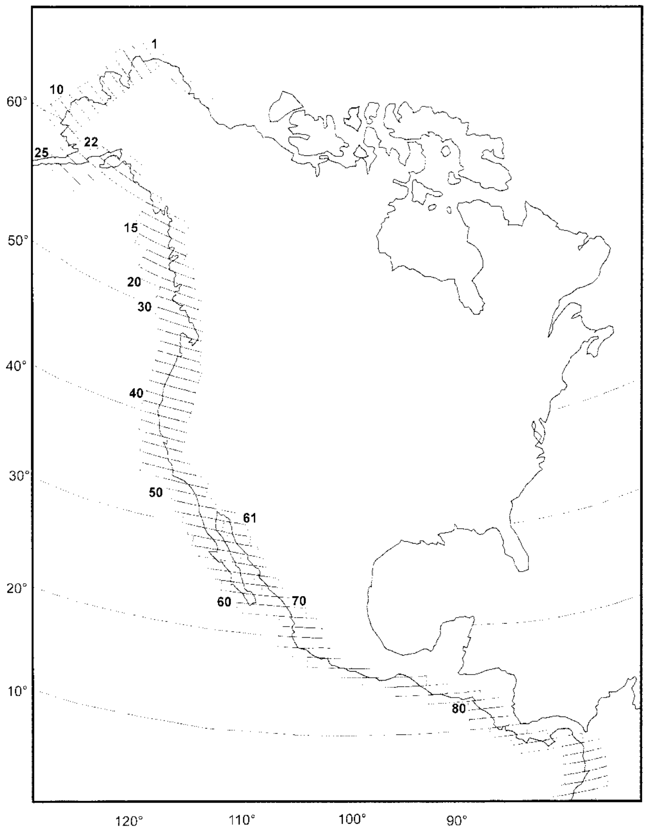

Fig. 1. Map with the North and Central American grid-cells analyzed.

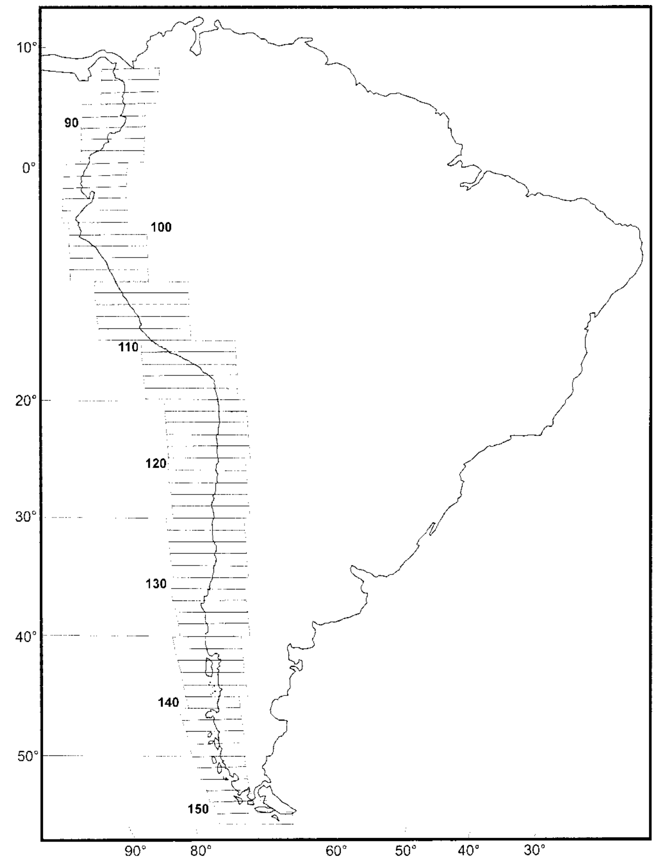

Fig. 2. Map with the South American grid-cells analyzed.

checklist of isopods for the Eastern Tropical Pacific sub-region. Brusca et al. (2001) produced a comprehensive list of species from California. Notwithstanding the relative importance of each of these works, none has addressed distributional patterns at a regional level. Espinosa-Pérez and Hendrickx (2006) presented a comprehensive review of the biogeography of the isopod fauna of the eastern Pacific based on the traditionally recognized biogeographic provinces, including a checklist of all species of isopods known to that moment in the northern and southern cold-temperate sub-regions of the East Pacific. Combining results obtained in their previous checklist for the eastern tropical Pacific (Espinosa-Pérez and Hendrickx, 2001), they compiled distribution information related to 420 shallow (< 200 m depth) species.

Panbiogeography, originally proposed by Croizat (1958, 1964) and subsequently developed by several authors (see Craw, 1989; Morrone and Crisci, 1995; Craw et al., 1999; Grehan, 2001), is an approach that emphasizes the importance of the spatial or geographical dimension of biodiversity for an appropriate understanding of evolutionary patterns and processes. Panbiogeographic or track analyses are intended to identify biogeographically homologous distributions, by searching for repetitive distributional patterns, allowing the correlation of distributional patterns of unrelated taxa and leading to the recognition of ancestral biotic components (Morrone and Márquez, 2001). Published analyses by Aguilar-Aguilar and Contreras-Medina (2001) and Moreno et al. (2006) have shown that this approach may be also useful for marine biogeographic studies.

We analyze herein the geographical distribution of the order Isopoda of the eastern Pacific applying a track analysis, to determine generalized tracks for these species, in order to contribute to the knowledge of their biotic evolution and the natural regionalization of the area.

Material and Methods

Distributional data were taken from available literature dealing mostly with the eastern Pacific (see Espinosa-Pérez and Hendrickx, 2001) and obtained from material loaned from several Mexican collections (Laboratorio de Invertebrados Bentónicos, Instituto de Ciencias del Mar y Limnología, UNAM, Mazatlán; Instituto de Biología, UNAM, Mexico City; and Departamento de Oceanografía Naval, Secretaría de Marina, Mexico City). Coordinates of localities corresponding to each isopod lot cited in reviewed literature or examined during this study were obtained either from the literature, collection logs or cruise reports, or calculated directly on maps on the basis of original data provided in the literature or labels.

The oceanographic sub-regions considered in the present analysis (Brusca and Wallerstein, 1979; Brattström and Johanssen, 1983; Hendrickx, 1992) are the following: 1) polar sub-region: north of the Bering Strait; 2) northern cold-temperate sub-region: from the Bering Strait to Point Conception, California; 3) northern warm-temperate sub-region: from Point Conception to Magdalena Bay, western coast of Baja California, Mexico; 4) tropical sub-region: from Magdalena Bay to Paita, Peru; it is subdivided in two zones: one with subtropical conditions, from Magdalena Bay to Point Mita, Jalisco, Mexico; and another with tropical conditions, from Point

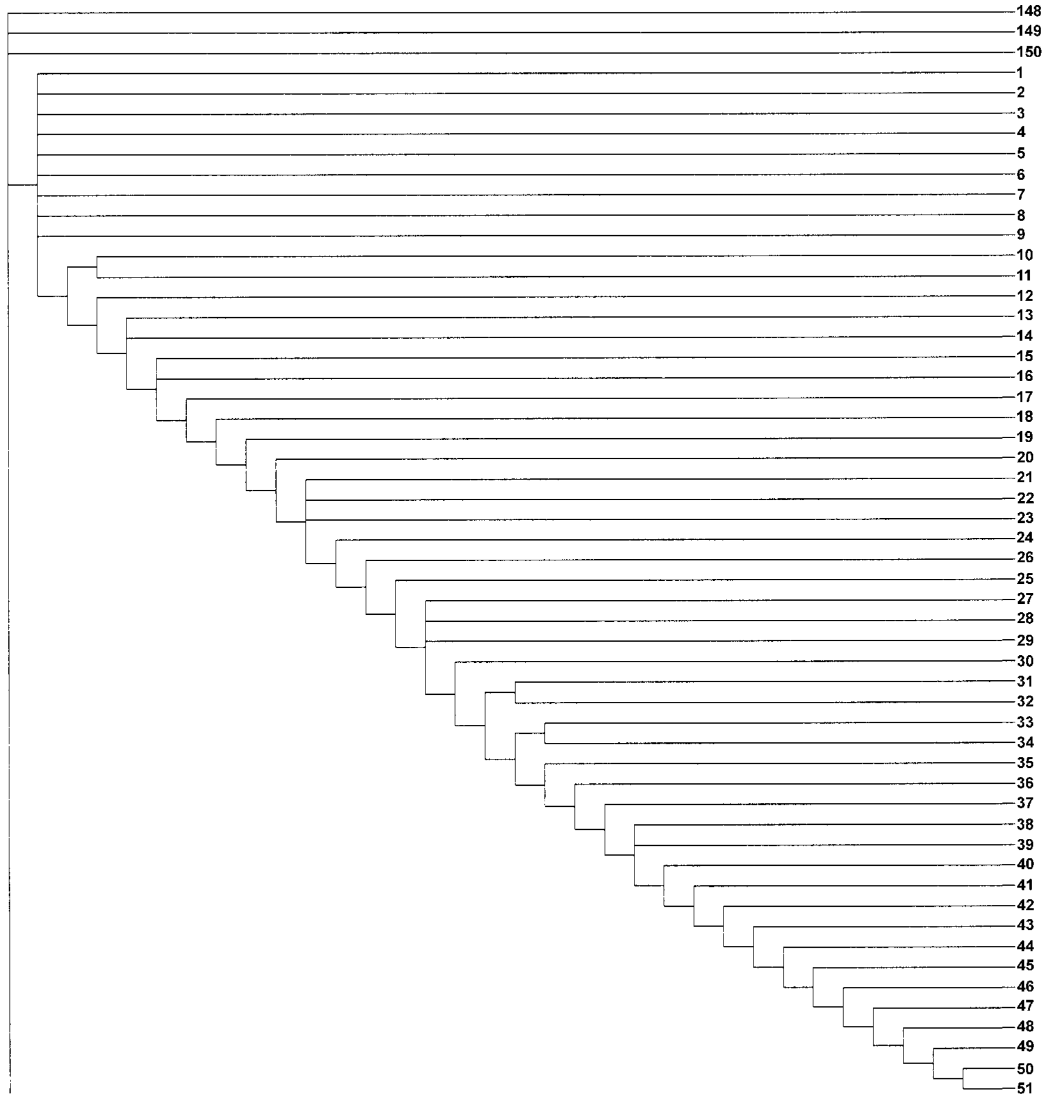

Fig. 3. Strict consensus cladogram obtained in the parsimony analysis of endemicity.

Mita to Paita, Peru; 5) southern warm-temperate sub-region: from Paita, Peru to Chiloé island, Chile; and 6) southern cold-temperate sub-region: from Chiloé Island to Malvinas Islands, Argentina.

The panbiogeographic approach basically consists of plotting distribution of different taxa on maps, and connecting their separate localities together with lines called individual tracks, according to a nearest neighbor joining criterion. When individual tracks for different taxa coincide, the resulting summary lines are considered generalized tracks, which indicate the existence of sets of species that share biogeographic affinities, and were isolated by geological or climatic changes (Craw et al., 1999; Morrone and Márquez, 2001; Morrone, 2004). Parsimony Analysis of Endemicity (PAE) (Rosen, 1988; Morrone, 1994) discovers area relationships based on shared taxa according to the most parsimonious cladogram. Data for PAE consist of area x taxa matrices and the resulting cladograms represent nested sets of areas. PAE is considered as a panbiogeographic method (see Smith, 1992; Craw et al., 1999; Luna et al., 2000; Morrone and Márquez, 2001; Morrone, 2004).

In order to undertake the PAE, 196 individual tracks of isopod species were drawn and then coded in a data matrix (available upon request from the senior author) for their absence (0) or presence (1) in 150 one degree latitudinal grid-cells, drawn up from 70°N south to 55°S (Figs. 1, 2; modified from Hayden and Dolan, 1976). Each gird-cell covers the area extending from the intertidal zone to 200 m depth. Grid-cells were numbered consecutively beginning along the northern coast of Alaska south to Patagonia. The 150 grid-cells located at the gulfs of Alaska and California were divided in order to separate the internal (eastern) and external (western) coasts of each area; cells located in the inner zone followed the consecutive numeration southwards. This analysis was carried out with NONA (Goloboff, 1996) and Winclada (Nixon, 1999). The cladogram was rooted with a hypothetical area coded all zeros.

Results

Analysis of the data matrix yielded three most parsimonious cladograms, with 364 steps, a consistency index of 0.53, and a retention index of 0.94. These indices are relatively high for a matrix of these dimensions, indicating a robust hypothesis. A strict consensus cladogram (Figs. 3, 4) was obtained. The three main clades identified in the

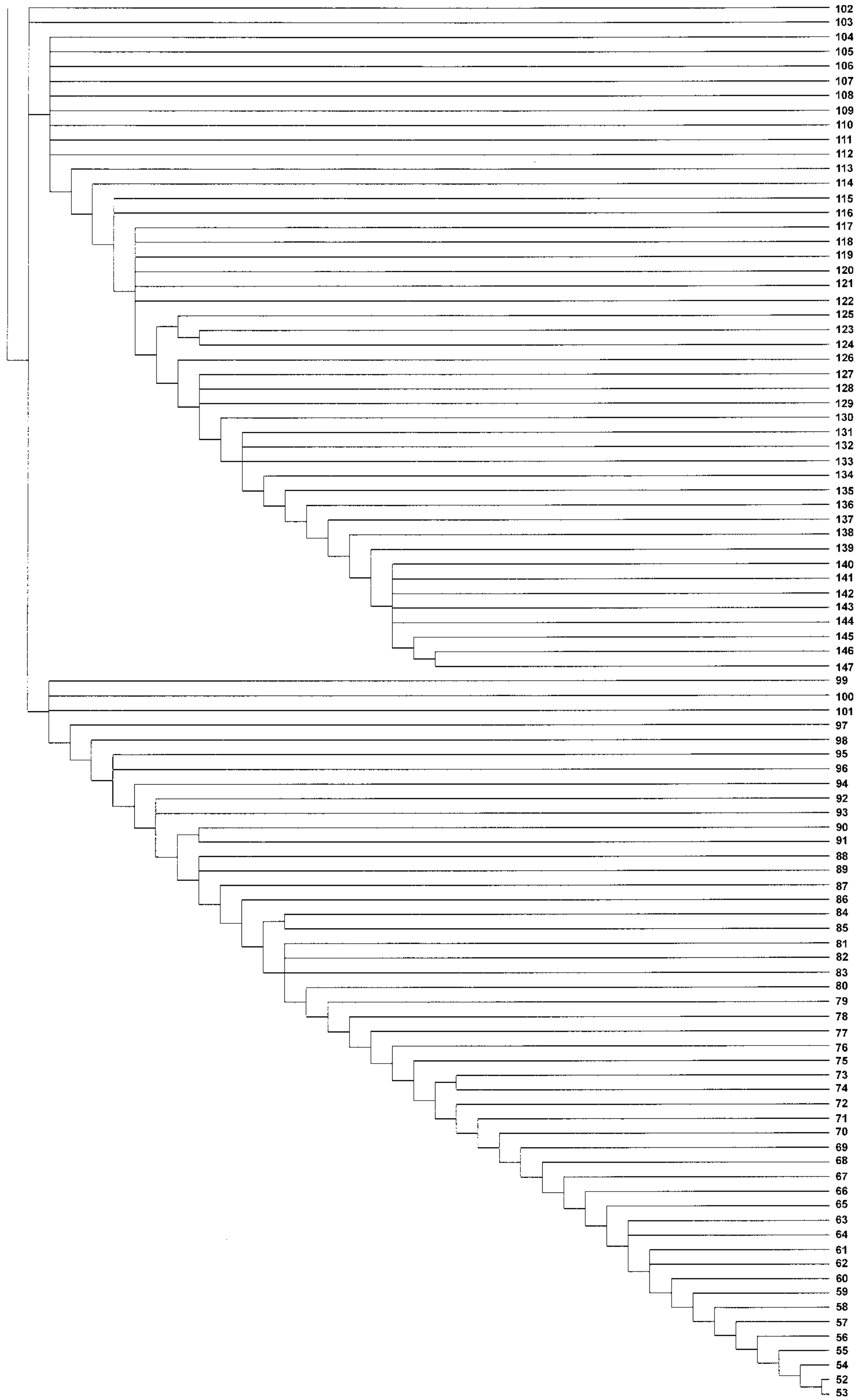

Fig. 4. Strict consensus cladogram obtained in the parsimony analysis of endemicity (continues from fig. 3).

consensus cladogram were translated into generalized tracks (Fig. 5).

Northern Cold-temperate Track

It extends from 62°N to 33°N, corresponding to the whole northern cold-temperate sub-region, i.e., the Aleutian Islands, the Gulf of Alaska and the coast of British Columbia, Washington, Oregon, and northern California (south to San Luis Obispo Bay). The 57 species endemic to this track (Table 1) belong mainly to the suborders Flabellifera, Valvifera, and Asellota. Species of Oniscidea, Epicarida, Anthuridea, and Gnathiidea are also present. Three species extend their distribution northwards to the Polar region and 57 species are also distributed southwards (55 of them reach the tropical sub-region and two to the southern warm/cold-temperate region).

Northern Warm-temperate/Tropical Track

It extends from 32°N to 1°S, corresponding to the Warm-Temperate and Tropical sub-regions, i.e., southern California to about halfway south into Ecuador. The 27 species endemic to this track (Table 1) belong mainly to the suborder Flabellifera, most of them Cymothoidae, Cirolanidae, and Sphaeromatidae. Species of Valvifera, Anthuridea, Asellota, Epicaridea, Oniscidea, and Gnathiidea are also present. About 44% of the species assigned to this track have geographic distributions restricted to the sub-regions included, 56% extend their distribution northwards to the northern cold temperate sub-region and only three species extended their distribution southwards to the southern cold-temperate sub-region. Species restricted to tropical and subtropical waters represent 30% of total (most of them are Flabellifera) and species restricted to the warm-temperate sub-region, 26% (mostly Asellota and Valvifera).

Southern Warm/Cold-temperate Track

It extends from 19°S to 52°S, covering the southern warm and cold-temperate sub-regions, i.e., coast of Chile south to the Magellan Strait. The 27 species endemic to this track (Table 1) belong mostly to the suborder Flabellifera, most of them Sphaeromatidae and Cirolanidae. Suborders Asellota and Valvifera are also represented in this track. 34% of the species is registered only for the Warm-Temperate sub-region and 8% for the cold-temperate sub-region. Three non-endemic species extended their distribution northwards to the northern cold-temperate sub-region.

Discussion

The three generalized tracks obtained represent biotic components, which we interpret as representing three different ancestral biotas. Analyses based on other taxa should allow us to test them or to discover smaller components nested within them. For example, Poupin and Bouchard (2006) analyzed the eastern Pacific species of hermit crabs of the genus *Calcinus*, finding a species group distributed from the Gulf of California to Peru, which basically coincides with the northern warm-temperate/tropical generalized track.

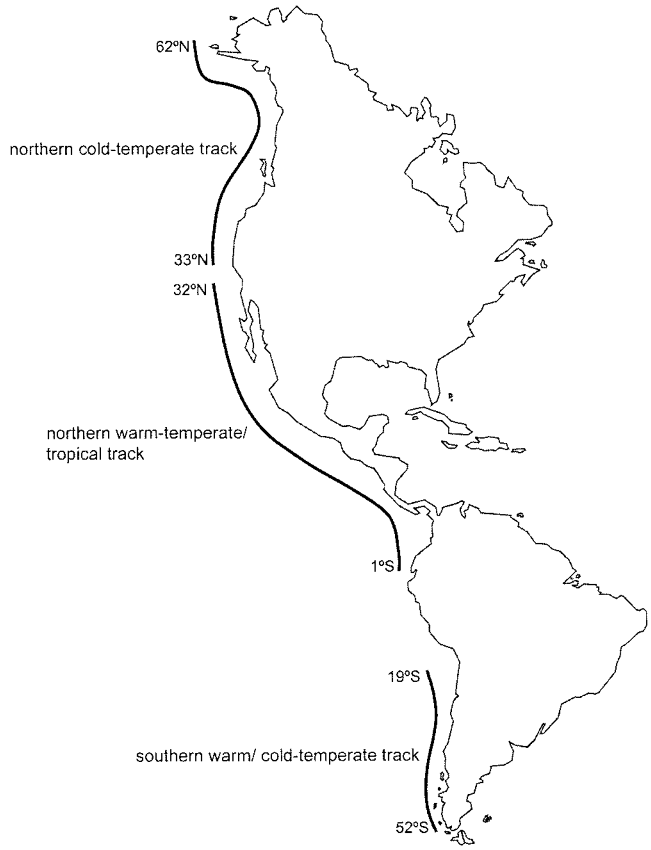

Fig. 5. Three generalized tracks or biotic components hypothesized herein for the species of Isopoda from the eastern Pacific.

The boundary between the northern cold-temperate and northern warm-temperate/tropical generalized tracks at 33-32°N seems to represent a well-established biotic frontier between the temperate and subtropical-tropical biota. It coincides with the boundary between the Nearctic and Neotropical regions, as delimited for terrestrial taxa (Morrone, 2006).

Hayden and Dolan (1976) analyzed the geographical distribution of 968 marine species of ascidians, crustaceans, and mollusks along coastal areas of the Americas, in order to determine co-ranges (along-the-coast distributional extent of two or more species that begin and end their distributional ranges at the same two coastal locations). Their results for the Pacific coast partially agree with our analysis, because generalized tracks obtained herein mostly coincide with their co-range termini, except for the northern end of the southern warm/cold temperate generalized track. This latter, however, was considered in a biogeographic regionalization based on fish taxa (Pequeño, 2000) to be the northern limit of the Atacaman district.

Acknowledgements

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Table 1. Endemic species of the three generalized tracks identified in this paper.

Northern cold-temperate track	Northern warm-temperate/tropical track	Southern warm/cold-temperate track
Antheluridae: *Ananthura luna* (Schultz, 1966)	**Anthuridae:** *Cortezura penascoensis* Schultz, 1977; *Cyathura guaroensis* Brusca and Iverson, 1985; *Paranthura longitelson* Wägele, 1984	**Cirolanidae:** *Cirolana robusta* Menzies, 1962; *C. urostylis* Menzies, 1962; *Excirolana hirsuticauda* Menzies, 1962; *E. monodi* Carvacho, 1977; *Natatolana californiensis* (Schultz, 1966)
Aegidae: *Aega symmetrica* Richardson, 1905	**Aegidae:** *Rocinela tuberculosa* Richardson, 1898	**Sphaeromatidae:** *Amphoroidea typa* H. Milne-Edwards, 1840; *Cymodocella foveolata* Menzies, 1962; *Dynamenella acuticauda* Menzies, 1962; *Ischyromene eatoni* (Miers, 1875); *I. tuberculata* (Menzies, 1962); *Isocladus bahamondei* Carvacho, 1997; *Paradella bakeri* (Menzies, 1962); *Pseudosphaeroma lundae* (Menzies, 1962)
Limnoriidae: *Limnoria algarum* Menzies, 1957; *L. lignorum* (Rathke, 1799); *L. quadripunctata* Hothuis, 1949	**Ancinidae:** *Ancinus panamensis* Glynn and Glynn, 1974	**Acanthaspidiidae:** *Ianthopsis laevis* Menzies, 1962
Sphaeromatidae: *Dynamene tuberculosa* Richardson, 1899; *Dynamenella conica* Boone, 1923; *D. dilatata* (Richardson, 1899); *D. glabra* (Richardson, 1899); *D. sheareri* (Hatch, 1947), *Exosphaeroma amplicauda* (Stimpson, 1857); *E. inornata* Dow, 1958; *Gnorimosphaeroma noblei* Menzies, 1954; *G. oregonensis* (Dana, 1853); *Paracerceis cordata* (Richardson, 1899); *P. gilliana* (Richardson, 1899)	**Cirolanidae:** *Anopsilana oaxaca* Carvacho and Hassmann, 1984; *Cirolana nielbrucei* Brusca, Wetzer and France, 1995; *Conilera bullisi* Brusca, Wetzer and France, 1995; *Natatolana carlanae* Brusca, Wetzer and France, 1995	**Janiridae:** *Ianiropsis chilensis* Menzies, 1962; *I. perplexus* Menzies, 1962; *I. tridens* Menzies, 1952; *Neojaera elongatus* Menzies, 1962
Tecticipitidae: *Tecticeps alascensis* Richardson, 1897; *T. convexus* Richardson, 1899	**Corallanidae:** *Excorallana bruscai* Delaney, 1984; *E. conabioae* Hendrickx and Espinosa-Pérez, 1998; *E. houstoni* Delaney, 1984	**Munnidae:** *Joeropsis bidens* Menzies, 1962
Tridentellidae: *Tridentella glutacantha* Delaney and Brusca, 1985	**Cymothoidae:** *Elthusa californica* (Schiödte and Meinert, 1884); *Mothocya rosea* Bruce, 1986; *M. gilli* Bruce, 1986, *M. panamica* Bruce, 1986; *M. rosea* Bruce, 1986	**Joeropsididae:** *Uromunna nana* (Nordenstam, 1933)
Gnathiidae: *Caecognathia crenulatifrons* (Monod, 1926); *Gnathia tridens* Menzies and Barnard, 1959	**Sphaeromatidae:** *Exosphaeroma bruscai* Espinosa-Pérez and Hendrickx, 2001; *Paracerceis spinulosa* Espinosa-Pérez and Hendrickx, 2002; *Dynoides crenulatus* Carvacho and Haasmann, 1984; *D. saldanai* Carvacho and Haasmann, 1984; *Paracerceis richardsoni* Lombardo, 1988; *Sphaeroma peruvianum* Richardson, 1910; *Striella balani* Glynn, 1968	**Paramunnidae:** *Munnogonium trillerae* (Menzies and Barnard, 1959)
Asellidae: *Caecidotea tomalensis* (Harford, 1877)	**Arcturidae:** *Cleantioides vonprahli* Ramos and Rios, 1988	**Santiidae:** *Santia laevifrons* (Menzies, 1962); *S. mawsoni* (Hale, 1937)
Janiridae: *Caecianiropsis psammophila* Menzies and Pettit, 1956; *Iais californica* (Richardson, 1904); *Ianiropsis epilittoralis* Menzies, 1952; *I. kincaidi* (Richardson, 1904); *I. magnocula* Menzies, 1952; *I. montereyensis* Menzies, 1952; *Janira maculosa* Leach, 1814; *Janiralata holmesi* (Richardson, 1905); *J. solasteri* (Hatch, 1947)	**Idoteidae:** *Eusymmerus antennatus* Richardson, 1899	**Chaetiliidae:** *Chaetilia paucidens* Menzies, 1962; *Macrochiridothea setifer* Menzies, 1962
Joeropsididae: *Joeropsis concava* (Schultz, 1966); *J. dubia paucispinis* (Menzies, 1951); *J. lobata* (Richardson, 1899)	**Bopyridae:** *Probopyrus markhami* Roman-Contreras, 1996	**Idoteidae:** *Edotia dahli* Menzies, 1962; *E. magallanica* Cunningham, 1871
Munnidae: *Munna chromatocephala* Menzies, 1952; *M. kroyeri* Goodsir, 1842; *M. spinifrons* Menzies and Barnard, 1959		
Munnopsididae: *Ilyarachna acarina* Menzies and Barnard, 1959		
Arcturidae: *Arcturus glaber* Benedict, 1898j *Idaturus allelomorphus* Menzies and Barnard, 1959		
Chaetiliidae: *Mesidotea entomon* (Linnaeus, 1767); *Eusymmerus pseudoculata* (Boone, 1923); *Idotea fewkesi* Richardson, 1905; *I. ochotensis* Brandt, 1851; *Synidotea angulata* Benedict, 1897; *S. berolzheimeri* Menzies and Miller, 1972; *S. nebulosa* Benedict, 1897; *S. ritteri* Richardson, 1904		
Bopyridae: *Argeia pugettensis* Dana, 1853; *Bopyroides hippolytes* (Kroyer, 1838); *Hemiarthrus abdominalis* (Kroyer, 1840); *Ione cornuta* Bate, 1864; *Munidion parvum* Richardson, 1904		
Armadillidae: *Cubaris californica* (Budde-Lund, 1885)		
Ligiidae: *Ligia pallasii* Brandt, 1833; *Ligidium gracile* (Dana, 1856); *L. latum* Jackson, 1923		

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