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Geographical distribution of pelagic decapod shrimp in the Atlantic Ocean

DAVID C. JUDKINS
3132 NE 51st Ave, Portland, OR 97213, USA. E-mail: dcjudkins@gmail.com

Abstract

Ninety-one species of pelagic decapod shrimp were identified in 938 midwater-trawl collections taken between 1963 and 1974 from the North and South Atlantic. Distributional maps are provided for the most frequently occurring species. Nighttime abundance of most species was greatest within the upper 200 m. Degree of geographical overlap was estimated using the geometric mean of the proportion of joint occurrences with a value ≥ 0.5 deemed significant. Geographical distributions tended to be unique, and only 31 species had values ≥ 0.5 with one or more other species. Species within genera and within phylogenetic subgroups of *Sergia* were generally parapatric or partially overlapping in distribution. Five geographical groupings of co-occurring species across genera were identified: Subpolar-Temperate, Southern Hemisphere, Central, Tropical, Eastern Tropical and Western Tropical. The two species of the Southern Hemisphere group are circumpolar at temperate latitudes. The 12 species of the Central group occurred throughout the subtropical and tropical North and South Atlantic. The eight species of the Tropical group occurred broadly across the equatorial Atlantic and Caribbean with ranges usually extending into the Gulf of Mexico and northward in the Gulf Stream. The two species of the Western Tropical group occurred most often in the western tropics, but there were scattered occurrences at subtropical latitudes. The four species of the Eastern Tropical group were endemic to the Mauritanian Upwelling and the Angola-Benguela Frontal zones off western Africa. Two of the three species in the Subpolar-Temperate group had bipolar distributions, and all three occurred in the Mediterranean and in the Mauritanian Upwelling zone. Most Central, Tropical and Western Tropical species were present in the in the Gulf of Mexico. The 10 species from the Mediterranean were a mixture of Subpolar-Temperate, Central and benthopelagic species. Patterns of distribution in Atlantic pelagic decapods closely parallel those of other pelagic taxa, but myctophid fishes from the same collections appear to partition subtropical regions more finely.

Key words: decapod shrimp, pelagic, geographical distribution, Atlantic Ocean, ocean circulation and water masses

Introduction

Decapod shrimp are a major component of the micronekton (2–10 cm) in subpolar to tropical regions of the world ocean, exceeded in number and biomass among the crustaceans only by the generally much smaller euphausiids (Brodeur *et al.* 2004). Although the shrimp fauna is phylogenetically diverse, with representatives of many genera and families within both decapod suborders, species are similar in general morphology, behavior and diet. Decapod shrimp collectively play an important role in the transfer of biomass within the marine food web. They scavenge organic debris but also actively prey on a wide spectrum of zooplankton, especially copepods, and appear to be the main competitors of midwater fish, the other major predatory group in the micronekton (Hopkins & Sutton 1998). In turn, they are eaten by a range of predators including other shrimp, siphonophores, cephalopods, dimersal and pelagic fish, and in the case of at least one species, *Eusergestes similis*, baleen whales (Pereyra *et al*. 1969, Pinkas *et al.* 1971, Omori *et al.* 1972, Biggs 1977, Brock 1985, Bulman & Koslow 1992, Cartes 1993, Bjelland & Monstad 1997, Yamamura & Inada 2001, Bergstadt *et al*. 2003).

Decapod shrimp have been the subject of several vertical distribution and regional faunal studies in the Atlantic and confluent seas (Foxton 1970a, 1970b, 1972a, Kensley 1971a, 1971b, Crosnier & Forest 1973, Foxton & Roe 1974, Donaldson 1975, Heffernan & Hopkins 1981, Roe 1984, Pohle 1988, Hopkins *et al*. 1989, Andersen & Sardou 1992, Cartes *et al*. 1994, Flock & Hopkins 1992, Hopkins *et al*. 1994, Hargreaves 1999, Koukouros *et al*. 2000, Politou *et al*. 2005, Pequegnat & Wicksten 2006, MacIsaac 2013, Cardoso *et al*. 2014), but there has not been an accounting to date of the entire shrimp fauna over the entire ocean. This study is based on examination of 938

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midwater-trawl collections taken in the North and South Atlantic, the Mediterranean, the Caribbean and the Gulf of Mexico by ships of the Woods Hole Oceanographic Institution (WHOI) between 1963 and 1974. The primary objective of this program, directed by WHOI oceanographer Richard H. Backus, was to identify the relationship between midwater fish distribution and sound scattering levels. To accomplish this, most net hauls were at or close to the sound scattering layer. Decapod shrimp are among the assemblage of crustaceans, fish, squid and other micronekton found in sound scattering layers (Smith 1954, Balino & Aksnes 1993, Torgersen et al 1997), suggesting that acoustic echoes, although not useful for calculating abundance within the entire water column, can be effective for revealing the presence of shrimp along a tow track. The lack of systematic sampling of the water column by the WHOI program precludes comparisons of total abundance between locations, and the geographical ranges of decapod shrimp species are presented as presence or absence within net hauls.

The objectives of this study are to map the distribution of individual species, to describe geographical patterns within genera and phylogenetically related species groups, to identify frequently co-occurring groups of species across taxa, to investigate the relationship of distributional patterns to currents and other oceanographic processes and to compare the distributional patterns of Atlantic decapod shrimp with those of other taxa.

Materials and methods

Collections were made with a 10-ft. Isaacs-Kidd Midwater Trawl (IKMT) equipped with outer netting of 2.5 inch stretch mesh and an inner liner of 0. 5 inch mesh in the posterior fourth (Isaacs & Kidd 1953, Clarke 1963). An opening-closing device was not used. A rigid plan of sampling preselected depths was not followed, and the chosen depth typically was that of the sound scattering layer (Backus & Craddock 1977). In 779 cases, the net was lowered to the chosen depth where it was towed at approximately 3 knots for two to three hours before being rapidly raised to the surface. An additional 159 tows were brought immediately from depth (usually 500 m) to the surface either continuously or in steps. Often more than one tow was made during a single night period. A smaller number of daytime tows at usually deeper depth and longer duration were interspersed along cruise tracks. Table 1 shows numbers of night, day and twilight horizontal tows within 50 m strata. Of the horizontal tows, 567 were made at night, 182 were done during the day, and 30 were made during hours of twilight. Over 80% of all nighttime tows took place in the upper 225 m, and three-quarters of those were within the upper 125 m. Small numbers of nighttime tows were made within deeper strata down to depths exceeding 1000 m. The majority of daytime tows (76%) took place between 276 and 725 m, with the largest number taking place within the 476–525 m stratum. Small numbers of daytime tows were made in strata above 276 m and below 725 m.

Collections from the South Atlantic were relatively few, especially from the central parts of that ocean, and thus species distributions there cannot be described fully.

The invertebrate portion of each collection was examined in its entirety and all decapod shrimp were removed. Specimens were examined under a microscope and separated to species. Classification of families and higher taxa follows De Grave & Fransen (2011). The material resides at the Museum Support Center of the National Museum of Natural History (NMNH) of the Smithsonian Institution.

Species collection information and partial station data is available online at the NMNH web site (http://www.mnh.si.edu/). WHOI collections are identified by the prefix RHB in the station code field. Complete station data is available in a WHOI technical report (Backus & Craddock 1974) and also reside in electronic format at the Museum of Comparative Zoology of Harvard University.

Distribution maps were prepared with Tilemill, an open source application from MapBox (http://www.mapbox.com). A freeware graphics program, Paint.NET (http://www.getpaint.net/), was used to assemble and label maps within the illustrations (Figs. 1–12). The lack of consistent depth sampling makes comparison of abundance problematic, and for this reason the maps show only presence or absence.

The geometric mean of the proportion of joint occurrences (GMPJO), corrected for sample size, was used to calculate distributional similarity between species: $[J/(N_A N_B)]^{1/2} - 1/2\ (N_B)^{1/2}$ where J is the number of joint occurrences; N_A is the total number of occurrences of species A; N_B is the total number of occurrences of species B; and species are assigned to the letters so that $N_A \leq N_B$ (Fager & McGowan 1963). This index can exhibit a range of 0 to 1.0.

TABLE 1. Number and hours of WHOI IKMT tows within depth strata. Not included are 159 oblique tows from ~500 m.

Mean tow	Night			Day			Twilight		
Depth (m)	Number	%	Hours	Number	%	Hours	Number	%	Hours
25–75	198	34.9	421	3	1.6	6	1	3.3	2
76–125	155	27.3	316	2	1.1	6	3	10.0	4
126–175	81	14.3	159	3	1.6	6	1	3.3	1
176–225	43	7.6	94	3	1.6	7	5	16.7	10
226–275	22	3.9	54	9	4.9	30	5	16.7	16
276–325	14	2.5	35	11	6.0	31	9	30.0	25
326–375	8	1.4	24	14	7.7	41	3	10.0	9
376–425	10	1.8	26	19	10.4	65	1	3.3	2
426–475	5	0.9	15	17	9.3	57	0	0	0
476–525	7	1.2	14	24	13.2	77	1	3.3	3
526–575	2	0.4	5	14	7.7	47	0	0	0
576–625	5	0.9	16	10	5.5	31	0	0	0
626–675	3	0.5	7	15	8.2	44	0	0	0
676–725	2	0.4	7	10	5.5	32	1	3.3	4
726–775	2	0.4	5	7	3.8	19	0	0	0
776–825	3	0.5	6	9	4.9	23	0	0	0
826–875	0	0	0	2	1.1	10	0	0	0
876–925	0	0	0	1	0.5	2	0	0	0
926–975	0	0	0	2	1.1	9	0	0	0
976–1025	2	0.4	10	4	2.2	15	0	0	0
1026–1075	1	0.2	3	2	1.1	8	0	0	0
1076–1125	2	0.4	11	0	0	0	0	0	0
> 1125	2	0.4	11	1	0.5	8	0	0	0
Total	567		1239	182		574	30		76

The use of the term “Tropical” in this work refers loosely to the latitudes between 23°N and 23°S, “Subtropical” to latitudes in the north and south between 23° and 38°, “Temperate” to latitudes between 38° and 50° and “Subpolar” to latitudes between 50° and 70°. No tows were made south of about 35°S, but the ocean climate at that latitude in the South Atlantic can be considered temperate. It is recognized that these definitions are to an extent arbitrary and that species respond to a wide range of factors.

Results

The WHOI midwater-trawl material yielded 91 species of decapod shrimp, representing two suborders, seven families and 24 genera (Table 2). Among families Sergestidae provided the most species (32), followed by the Acanthephyridae (24). Of the 20 most frequently occurring species, 11 were of the family Sergestidae (overall rank is in parentheses following the name): *Allosergestes sargassi* (1), *A. pectinatus* (2), *Parasergestes vigilax* (3), *Sergia splendens* (5), *Sergestes atlanticus* (6), *Parasergestes armatus* (8), *Eusergestes arcticus* (9), *Deosergestes henseni* (10), *Neosergestes edwardsi* (12), *Sergia robusta* (17) and *Deosergestes corniculum* (18). Other frequently occurring species within the suborder Dendrobranchiata were *Funchalia villosa* (11) in the family Penaeidae and *Gennadas valens* (14), *G. scutatus* (15), *G. tinayrei* (16) and *G. elegans* (20) in the Benthesicmyidae. Frequently occurring species within the infraorder Caridea of the suborder Pleocyemata were *Acanthephyra purpurea* (13) in the Acanthephyridae, *Oplophorus spinosus* (5), *Systellaspis debilis* (4) and *Janicella spinicauda* (19) in the Oplophoridae and *Stylopandalus richardi* (7) in the Pandalidae.

TABLE 2. Numbers of occurrences of decapod shrimp species identified in WHOI IKMT tow collections. Twilight occurrences are not shown separately but are included in All Tows column.

Species	Number of Occurrences					
	All Tows	Rank	Night Tows	Rank	Day Tows	Rank
Suborder Pleocyemata/Infraorder Caridea						
Family Acanthephyridae						
Acanthephyra acanthitelsonis Spence Bate, 1888	44	36	38	33	6	31
Acanthephyra acutifrons Spence Bate, 1888	11	52	10	47	1	36
Acanthephyra brevirostris Smith, 1885	2	61	1	56	1	36
Acanthephyra curtirostris Wood-Mason & Alcock, 1891	24	45	22	41	2	35
Acanthephyra eximia Smith, 1884	3	60	0	57	3	34
Acanthephyra kingleyi Spence Bate, 1888	73	30	66	26	7	30
Acanthephyra pelagica (Risso, 1816)	97	22	56	29	40	10
Acanthephyra prionota Foxton, 1971	3	60	2	55	1	36
Acanthephyra purpurea A. Milne Edwards, 1881	199	13	156	14	41	9
Acanthephyra quadrispinosa Kemp, 1939	26	44	22	41	4	33
Acanthephyra stylorostratis (Spence Bate, 1888)	15	49	11	46	4	33
Ephyrina benedicti Smith, 1885	3	60	2	55	1	36
Ephyrina bifida Stephensen, 1923	2	61	0	57	2	35
Ephyrina figueirai Crosnier & Forest, 1973	4	59	1	56	3	34
Ephyrina ombango Crosnier & Forest, 1973	8	55	3	54	5	32
Hymenodora glacialis (Buchholz, 1874)	4	59	2	55	2	35
Hymenodora gracilis Smith, 1886	12	51	2	55	10	27
Meningodora miccyla (Chace, 1940)	15	49	8	49	7	30
Meningodora mollis Smith, 1882	24	45	20	42	4	33
Meningodora vesca (Smith, 1886)	50	35	26	38	24	15
Notostomus auriculatus Barnard, 1950	10	53	4	53	6	31
Notostomus distirus Chace, 1940	1	62	1	56	0	37
Notostomus elegans A. Milne Edwards, 1881	17	48	13	44	4	33
Notostomus gibbosus A. Milne Edwards, 1881	6	57	5	52	1	36
Family Oplophoridae						
Janicella spinicauda (A. Milne Edwards, 1883)	120	19	82	21	32	14
Oplophorus gracilirostris A. Milne Edwards, 1883	66	31	46	30	15	22
Oplophorus novaezeelandiae (De Man, 1931)	41	38	40	31	1	36
Oplophorus spinosus (Brullé, 1839)	392	5	321	6	63	4
Systellaspis cristata (Faxon, 1893)	1	62	1	56	0	37
Systellaspis debilis (A. Milne Edwards, 1881)	443	4	369	4	63	4
Systellaspis pellucida (Filhol, 1884)	5	58	3	54	2	35
Family Pandalidae						
Stylopandalus richardi (Coutière, 1905)	349	7	304	7	39	11
Family Pasiphaeidae						
Eupasiphae gilesii (Wood-Mason, 1892)	3	60	3	54	0	37
Parapasiphae cristata Smith, 1884	3	60	2	55	1	36

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TABLE 2. (Continued)

Species	Number of Occurrences					
	All Tows	Rank	Night Tows	Rank	Day Tows	Rank
Parapasiphae sulcatifrons Smith, 1884	29	42	8	49	21	18
Pasiphaea hoplocerca Chace, 1940	22	47	15	43	6	31
Pasiphaea merriami Schmitt, 1931	23	46	7	50	13	24
Pasiphaea multidentata Esmark, 1866	59	33	31	35	21	18
Pasiphaea sivado (Risso, 1816)	28	43	24	39	3	34
Pasiphaea tarda Krøyer, 1845	11	52	3	54	2	35
Suborder Dendrobranchiata						
Family Benthesicymidae						
Bentheogennema intermedia (Spence Bate, 1888)	13	50	8	49	5	32
Gennadas bouvieri Kemp, 1909	84	27	76	22	7	30
Gennadas brevirostris Bouvier, 1905	55	34	39	32	16	21
Gennadas capensis Calman, 1925	87	26	75	23	11	26
Gennadas elegans (Smith, 1882)	119	20	67	25	44	8
Gennadas gilchristi Calman, 1925	26	44	23	40	3	34
Gennadas incertus (Balss, 1927)	5	58	5	52	0	37
Gennadas kempi Stebbing, 1914	4	59	3	54	1	36
Gennadas parvus Spence Bate, 1881	3	60	3	54	0	37
Gennadas propinquus Rathbun, 1906	6	57	5	52	1	36
Gennadas scutatus Bouvier, 1906	171	15	150	15	19	19
Gennadas talismani Bouvier, 1906	102	21	89	20	12	25
Gennadas tinayrei Bouvier, 1906	149	16	131	17	17	20
Gennadas valens (Smith, 1884)	182	14	139	16	40	10
Family Penaeidae						
Funchalia danae Burkenroad, 1940	4	59	3	54	1	36
Funchalia villosa (Bouvier, 1905)	249	11	204	11	38	12
Funchalia woodwardi Johnson, 1868	34	41	31	35	3	34
Pelagopenaeus balboae (Faxon, 1893)	8	55	8	49	0	37
Family Sergestidae						
Allosergestes pectinatus (Sund, 1920)	486	2	397	1	76	2
Allosergestes sargassi (Ortmann, 1893)	488	1	371	3	99	1
Deosergestes corniculum (Krøyer, 1855)	128	18	105	18	21	18
Deosergestes disjunctus (Burkenroad, 1940)	7	56	6	51	1	36
Deosergestes henseni (Ortmann, 1893)	257	10	208	10	41	9
Deosergestes paraseminudus (Crosnier & Forest, 1973)	89	25	72	24	13	24
Deosergestes pediformis (Crosnier & Forest, 1973)	42	37	34	34	8	29
Eusergestes arcticus (Krøyer, 1855)	262	9	179	13	70	3
Neosergestes edwardsi (Krøyer, 1855)	234	12	185	12	40	10
Neosergestes orientalis (Hansen, 1919)	13	50	9	48	4	33
Parasergestes armatus (Krøyer, 1855)	317	8	244	9	62	5
Parasergestes diapontius (Spence Bate, 1881)	84	27	67	25	16	21

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TABLE 2. (Continued)

Species	Number of Occurrences					
	All Tows	Rank	Night Tows	Rank	Day Tows	Rank
Petalidium foliaceum Spence Bate, 1881	4	59	2	55	2	35
Sergestes atlanticus H. Milne Edwards, 1830	360	6	297	8	58	7
Sergestes cornutus Krøyer, 1855	93	23	64	28	23	16
Sergia burukovskii Vereshchaka, 2000	8	55	8	49	0	37
Sergia extenuata (Burkenroad, 1940)	37	39	28	36	8	29
Sergia gardineri (Kemp, 1913)	1	62	0	57	1	36
Sergia grandis (Sund, 1920)	80	28	64	28	12	25
Sergia japonica (Spence Bate, 1881)	34	41	12	45	22	17
Sergia laminata (Burkenroad, 1940)	65	32	56	29	9	28
Sergia manningorum Froglia & Gramitto, 2000	36	40	27	37	9	28
Sergia plumea (Illig, 1927)	2	61	2	55	0	37
Sergia potens (Burkenroad, 1940)	7	56	5	52	2	35
Sergia prehensilis (Spence Bate, 1881)	23	46	20	42	3	34
Sergia regalis (Gordon, 1939)	80	28	75	23	3	34
Sergia robusta (Smith, 1882)	132	17	92	19	36	13
Sergia scintillans (Burkenroad, 1940)	7	56	4	53	3	34
Sergia splendens (Sund, 1920)	392	5	346	5	39	11
Sergia talismani (Barnard, 1947)	92	24	72	24	14	23
Sergia tenuiremis (Krøyer, 1855)	9	54	5	52	4	33
Sergia wolffi Vereshchaka, 1994	77	29	65	27	10	27

Vertical distribution studies in the Atlantic of several pelagic shrimp taxa (Foxton 1970a, 1970b, 1972a, Donaldson 1975, Heffernan & Hopkins 1981, Hopkins *et al*. 1989, Flock & Hopkins 1992, Hopkins *et al*. 1994, Hargreaves 1999, Vestheim & Kaartvedt 2009) found that species aggregated within narrow and often distinct strata during both day and night. However, these studies also revealed that nearly all species had extensive total vertical ranges that often extended into the upper 200 m at night (Table 3) where at least small numbers were likely to be captured in WHOI tows. Species found to aggregate at night in the epipelagic zone, and therefore most likely to be taken by WHOI tows, were all species of the sergestid genera *Allosergestes*, *Deosergestes*, *Eusergestes*, *Neosergestes*. *Parasergestes* and *Sergestes*, the sergestids *Sergia splendens* and *S. talismani* (Foxton 1970b, Donaldson 1974, Flock & Hopkins 1992, Hargreaves 1999, Vestheim & Kaartvedt 2009), the benthesicymids *Gennadas elegans* (Andersen & Sardou 1992), *Gennadas scutatus* and *G. valens* (Heffernan & Hopkins 1981), the penaeid *Funchalia villosa* (Foxton 1970b), the oplophorids *Janicella spinicauda*, *Oplophorus gracilirostris* and *Systellaspis debilis* and the pandalid *Stylopandalus richardi* (Foxton 1970a, Hopkins *et al*. 1989). Each of those species occurred in 50 or more WHOI collections (Table 4). Several species with night maxima reported below 200 m also occurred with regularity in both night and day WHOI collections (Table 4). These deeper living species include *Acanthephyra purpurea*, *A. pelagica* (Foxton 1970a, 1972a, Hopkins et al. 1989), *Gennadas bouvieri*, *G. capensis*, *G. talismani* (Heffernan & Hopkins 1981), *Sergia regalis*, *S. grandis* and *S. laminata* (Donaldson 1974).

Capture locations of species occurring in fewer than 20 tows are listed in Table 5. Several species of *Acanthephyra, Ephyrina*, *Hymenodora*, *Meningodora*, *Notostomus*, *Bentheogennema*, *Petalidium* and *Sergia* in the list inhabit deep mesopelagic or bathypelagic waters (Foxton 1970a, 1972a, Hopkins *et al*. 1989, Hargreaves 1999) that were not well sampled by the WHOI program. Certain pasiphaeids appeared to be benthopelagic in habit, and not many tows were taken over the outer shelf and slope bottoms where they might have occurred. For instance, *Pasiphaea tarda* was taken only in the Gulf of St. Lawrence and off the Faroe Islands. Species restricted to the southern hemisphere comprise another poorly sampled group. These included *Gennadas incertus*, *G. kempi*, *G. parvus*, *G. propinquus*, *Deosergestes disjunctus*, *Neosergestes orientalis*, *Sergia burukovskii*, *S. gardineri*, *S. plumea*, *S. potens* and *S. scintillans* (Kensley 1971a, 1971b, Judkins 1978, Vereshchaka 2000).

TABLE 3. Shallowest occurrences (in meters) of pelagic decapod shrimp in WHOI IKMT tows and in published studies: Fa = Foxton 1970a; Fb = Foxton 1970b; Fc = Foxton 1972; D = Donaldson 1975; HH = Heffernan & Hopkins 1981; HGF = Hargreaves, Gartner & Flock 1989; FH = Flock & Hopkins 1992; H = Hargreaves 1999; VK = Vestheim & Kaartvedt 2009.

	Night .		Day .	
Species	WHOI	Literature	WHOI	Literature
Acanthephyra acanthitelsonis	50	250(Fc), 700(HGF)	400	700(Fc), (HGF)
Acanthephyra acutifrons	490	700(HGF	950	700(HGF)
Acanthephyra brevirostris	2030	–	2150	–
Acanthephyra curtirostris	370	700(HGF)	1000	700(HGF)
Acanthephyra eximia	–	–	2000	–
Acanthephyra kingsleyi	50	–	430	–
Acanthephyra pelagica	45	100(Fc), 500(H)	300	600(Fc)
Acanthephyra prionota	1100	–	1000	–
Acanthephyra purpurea	35	200(Fa), 100(Fc),150(HGF), 200(H)	170	700(Fa), 600(Fc), 150(HGF)
Acanthephyra quadrispinosa	135	–	540	–
Acanthephyra stylorostratis	100	700(HGF)	950	700(HGF)
Ephyrina benedicti	1100	700(HGF)	1000	700(HGF)
Ephyrina bifida	–	–	860	–
Ephyrina figueirai	800	800(H)	700	–
Ephyrina ombango	500	–	250	–
Hymenodora glacialis	1500	–	770	–
Hymenodora gracilis	1100	–	650	–
Meningodora miccyla	100	–	400	–
Meningodora mollis	460	925(Fa), 700(HGF)	250	700(HGF)
Meningodora vesca	250	625(Fa), 700(HGF)	400	875(Fa), 700(HGF)
Notostomus auriculatus	65	–	480	–
Notostomus elegans	140	–	400	–
Notostomus gibbosus	515	–	1000	–
Janicella spinicauda	18	50 (HGF)	50	150(HGF)
Oplophorus gracilirostris	47	50(HGF)	55	150(HGF)
Oplophorus novaezeelandiae	60	–	80	–
Oplophorus spinosus	30	75(Fa)	55	100(Fa)
Systellaspis cristata	1100	–	–	875(Fa)
Systellaspis debilis	30	125(Fa), 50(HGF), 100(H)	50	650(Fa), 600(HGF)
Systellaspis pellucida	500	–	660	–
Stylopandalus richardi	15	125(Fa), 50(HGF)	80	575(Fa), 150(HGF)
Eupasiphae gilesii	50	975(Fa)	–	800(Fa)
Parapasiphae cristata	1100	–	–	–
Parapasiphae sulcatifrons	40	900(H)	480	–
Pasiphaea hoplocerca	90	225(Fa)	170	725(Fa)
Pasiphaea merriami	140	–	350	–
Pasiphaea multidentata	30	300(H)	350	–
Pasiphaea sivado	32	–	170	–

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TABLE 3. (Continued)

Species	Night .		Day .	
	WHOI	Literature	WHOI	Literature
Pasiphaea tarda	–	–	490	–
Bentheogennema intermedia	500	–	400	950(Fa)
Gennadas bouvieri	130	275(HH)	250	775(HH)
Gennadas brevirostris	50	–	290	–
Gennadas capensis	100	275(HH)	350	300(HH)
Gennadas elegans	25	575(Fb), 200(H)	290	775(Fb)
Gennadas gilchristi	80	–	540	–
Gennadas incertus	135	–	–	–
Gennadas kempi	600	–	–	–
Gennadas parvus	370	–	–	–
Gennadas propinquus	135	–	80	–
Gennadas scutatus	35	100(HH)	80	275(HH)
Gennadas talismani	50	325(HH)	350	400(HH)
Gennadas tinayrei	30	–	80	–
Gennadas valens	35	175(Fb), 100(HH)	170	700(Fb), 250(HH)
Funchalia danae	–	–	580	–
Funchalia villosa	15	75(Fa)	50	450(Fa)
Funchalia woodwardi	35	–	540	–
Pelagopenaeus balboae	60	–	–	–
Allosergestes pectinatus	18	75(Fa), 25(D), 25(FH)	57	575(Fa), 500(D), 100(FH)
Allosergestes sargassi	22	125(Fa), 25(D), 25(FH)	80	450(Fa), 350(D), 100(FH)
Deosergestes corniculum	35	75(Fa), 75(D)	170	575(Fa), 500(D)
Deosergestes disjunctus	80	–	–	–
Deosergestes henseni	35	25(FH)	102	100(FH)
Deosergestes paraseminudus	35	25(FH)	57	100(FH)
Deosergestes pediformis	36	–	480	–
Eusergestes arcticus	22	25(VK), 100(H)	80	25(VK)
Neosergestes edwardsi	20	25(FH)	57	150(FH)
Neosergestes orientalis	65	–	80	–
Parasergestes armatus	20	125(Fa), 25(D), 25(FH)	50	450(Fa), 500(D), 150(FH)
Parasergestes diapontius	36	–	290	–
Parasergestes vigilax	15	125(Fa), 25(FH),	50	125(Fa), 25(FH)
Petalidium foliaceum	70	–	800	–
Sergestes atlanticus	15	25(D), 25(FH)	30	425(D), 25(FH)
Sergestes cornutus	18	50(D), 25(FH)	30	450(D), 200(FH)
Sergia burukovskii	95	–	480	–
Sergia extenuata	45	–	80	–
Sergia gardineri	–	–	120	–
Sergia grandis	35	200(D)	460	600(D)
Sergia japonica	70	575(Fa), 775(D)	290	800(Fa), 775(D)
Sergia laminata	50	–	430	–

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TABLE 3. (Continued)

	Night .		Day .	
Species	WHOI	Literature	WHOI	Literature
Sergia manningorum	55	–	290	–
Sergia potens	95	–	540	
Sergia prehensilis	65	–	80	–
Sergia regalis	50	–	350	–
Sergia robusta	34	225(Fa), 200(D), 150(FH)	170	775(Fa), 700(D), 200(FH)
Sergia scintillans	75	–	80	–
Sergia splendens	15	125(Fa), 25(D), 50(FH)	30	775(Fa), 700(D), 150(FH)
Sergia talismani	22	100(FH)	170	100(FH), 150(FH)
Sergia tenuiremis	135	550(Fa), 550(D), 25(FH)	950	775(Fa), 800(D)
Sergia wolffi	50	–	170	–

TABLE 4. Pelagic decapod species ranked by number of occurrences in night and day WHOI IKMT tow collections. Only species occurring in 50 or more of total tows are shown.

	Night Tows		Day Tows	Day Rank
Rank		Rank		Difference
1	*Allosergestes pectinatus*	1	*Allosergestes sargassi*	+2
2	*Parasergestes vigilax*	2	*Allosergestes pectinatus*	-1
3	*Allosergestes sargassi*	3	*Eusergestes arcticus*	+10
4	*Systellaspis debilis*	4	*Oplophorus spinosus*	+2
5	*Sergia splendens*	4	*Systellaspis debilis*	0
6	*Oplophorus spinosus*	5	*Parasergestes armatus*	+4
7	*Stylopandalus richardi*	6	*Parasergestes vigilax*	-4
8	*Sergestes atlanticus*	7	*Sergestes atlanticus*	+1
9	*Parasergestes armatus*	8	*Gennadas elegans*	+17
10	*Deosergestes henseni*	9	*Acanthephyra purpurea*	+5
11	*Funchalia villosa*	9	*Deosergestes henseni*	+1
12	*Neosergestes edwardsi*	10	*Neosergestes edwardsi*	+2
13	*Eusergestes arcticus*	10	*Acanthephyra pelagica*	+19
14	*Acanthephyra purpurea*	10	*Gennadas valens*	+6
15	*Gennadas scutatus*	11	*Sergia splendens*	-6
16	*Gennadas valens*	11	*Stylopandalus richardi*	-4
17	*Gennadas tinayrei*	12	*Funchalia villosa*	+1
18	*Deosergestes corniculum*	13	*Sergia robusta*	+5
19	*Sergia robusta*	14	*Janicella spinicauda*	+7
20	*Gennadas talismani*	16	*Sergestes cornutus*	+12
21	*Janicella spinicauda*	18	*Pasiphaea multidentata*	+14
22	*Gennadas bouvieri*	18	*Deosergestes corniculum*	0
23	*Gennadas capensis*	19	*Gennadas scutatus*	-4
23	*Sergia regalis*	20	*Gennadas tinayrei*	-3
24	*Sergia talismani*	21	*Gennadas brevirostris*	+11
24	*Deosergestes paraseminudus*	21	*Parasergestes diapontius*	-4

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TABLE 4. (Continued)

	Night Tows		Day Tows	Day Rank
Rank		Rank		Difference
25	*Gennadas elegans*	22	*Oplophorus gracilirostris*	+8
25	*Parasergestes diapontius*	23	*Sergia talismani*	-3
26	*Acanthephyra kingsleyi*	24	*Deosergestes paraseminudus*	0
27	*Sergia wolffi*	25	*Gennadas talismani*	-5
28	*Sergestes cornutus*	25	*Sergia grandis*	+1
28	*Sergia grandis*	26	*Gennadas capensis*	-3
29	*Sergia laminata*	27	*Sergia wolffi*	0
29	*Acanthephyra pelagica*	28	*Sergia laminata*	+1
30	*Oplophorus gracilirostris*	30	*Gennadas bouvieri*	-8
32	*Gennadas brevirostris*	30	*Acanthephyra kingsleyi*	-4
35	*Pasiphaea multidentata*	34	*Sergia regalis*	-11

TABLE 5. Catch locations of pelagic decapod shrimp species occurring in fewer than 20 WHOI IKMT tows.

Species	Locations
Acanthephyra acutifrons	Western Tropical Atlantic, Eastern Subtropical N. Atlantic (10°20´S, 30°32´W; 1°20´S, 27°37´W; 8°58´N, 57°40´ W; 9°05´N, 55°17´W; 9°03´N, 49°16´W; 11°24´N, 59°34´W; 11°30´N, 65°19´W;11°37´N, 65°32´W; 14°27´N, 50°17´W; 14°38´N, 50°12´W;26°33´N, 21°27´W)
Acanthephyra brevirostris	Gulf of Mexico, Western Tropical Atlantic (10°20´S, 30°32´W; 26°12´N, 87°54´W)
Acanthephyra eximia	Mediterranean (33°22´N, 19°10´E; 34°02´N, 25°49´E; 36°36´N, 0°51´W)
Acanthephyra prionota	Western Tropical Atlantic (2°38´S, 28°47´W; 1°44´S, 27°44´W; 1°20´S, 27°37´W)
Acanthephyra stylorostratis	Gulf of Mexico, Tropical Atlantic, Subtropical N. Atlantic (10°20´S, 30°32´W; 2°38´S, 28°47´W; 1°44´S, 27°44´W; 11°30´N, 65°19´W; 11°37´ N, 65°32´W; 11°45´N, 65°33´W; 17°04´N, 38°38´W;23°04´N, 45°10´W; 23°13´N, 44°56´W; 26°12´N, 87°54´W; 26°33´N, 21°27´W; 26°57´N, 42°53´W; 32°17´N, 59°45´W; 32°30´N, 60°30´W; 37°56´ N, 72°25´W)
Ephyrina benedicti	Western Tropical Atlantic (2°38´S, 28°47´W; 1°44´S, 27°44´W; 11°30´N, 65°19´W)
Ephyrina bifida	Western Temperate N. Atlantic (39°33´N, 70°56´W; 48°54´N, 43°25´W)
Ephyrina figueirai	Eastern Temperate and Subarctic N. Atlantic (33°42´N, 16°08´W; 34°47´N, 14°57´W; 51°18´N, 20°23´W; 56°24´N, 12°41´W)
Ephyrina ombango	Tropical Atlantic (15°28´S, 3°04´E; 8°27´S, 30°04´W; 9°03´N, 51°05´W; 11°37´N, 65°32´W; 13°12´N, 72°47´W; 14°43´N, 25°27´W; 16°14´N, 20°44´W;16°27´N, 22°17´W)
Hymenodora glacialis	Western Tropical Atlantic, Temperate N. Atlantic (10°20´S, 30°32´W; 11°30´N, 65°19´W; 48°54´N, 43°25´W; 52°22´N, 34°51´W)

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TABLE 5. (Continued)

Species	Locations
Hymenodora gracilis	Gulf of Mexico, Western Temperate N. Atlantic, Subarctic N. Atlantic, Western Tropical–Subtropical S. Atlantic (26°30´S, 36°33´W; 1°44´S, 27°44´W; 1°20´S, 27°37´W; 26°12´N, 87°54´W; 37°28´N, 68°32´W; 37°56´N, 72°25´W; 39°22´N, 70°49´W; 39°33´N, 70°56´W; 39°38´N, 70°03´W; 52°05´N, 36°46´W; 53°15´N, 19°55´W; 63°25´N, 2°40´W)
Meningodora miccyla	Temperate–to–Tropical N. Atlantic (8°58´N, 53°10´W; 9°05´N, 55°17´W; 11°00´N, 41°31´W; 11°20´N, 64°40´W; 11°45´N, 65°33´W; 13°12´N, 72°47´W; 13°23´N, 40°00´W; 23°13´N, 44°56´W; 23°19´N, 49°50´W; 28°17´N, 45°21´W; 31°38´N, 15°46´W; 37°56´N, 72°25´W; 39°38´N, 70°03´W; 40°22´N, 58°51´W; 52°05´N, 36°46´W)
Notostomus auriculatus	Eastern Tropical Atlantic, EasternTemperate S. Atlantic (35°42´S, 4°06´E; 14°08´S, 5°49´E; 12°51´S, 8°15´E; 0°09´S, 34°38´W; 14°43´N, 25°27´W; 16°14´N, 20°44´W; 16°27´N, 22°17´W; 16°42´N, 19°11´W; 19°13´N, 18°17´W; 21°08´N, 18°13´W)
Notostomus distirus	Eastern Temperate N. Atlantic (37°56´N, 72°25´W)
Notostomus elegans	Subtropical–to–Tropical N. and S. Atlantic (15°59´S, 2°02´E; 1°12´N, 44°39´W; 6°18´N, 20°40´W; 9°02´N, 43°48´W; 9°00´N, 40°53´W; 9°03´N, 49°16´W; 9°36´N, 40°37´W; 9°37´N, 40°37´W; 9°45´N, 40°41´W; 10°59´N, 41°38´W; 11°20´N, 64°40´W; 13°12´N, 56°34´W; 13°28´N, 52°55´W; 13°30´N, 50°58´W; 19°30´N, 30°00´W; 21°35´N, 18°09´W; 26°33´N, 21°27´W)
Notostomus gibbosus	Western Tropical Atlantic (10°20´S, 30°32´W; 2°38´S, 28°47´W; 1°44´S, 27°44´W; 1°20´S, 27°37´W; 11°45´N, 65°33´W; 14°38´N, 50°12´W)
Systellaspis cristata	Central Tropical Atlantic (1°20´S, 27°37´W)
Systellaspis pellucida	Central Tropical Atlantic (15°28´S, 3°04´E ; 11°30´N, 65°19´ W; 11°45´N, 65°33´W; 14°43´N,25°27´W; 16°27´N, 22°17´W)
Eupasiphae gilesii	Subtropical–to–Tropical N. Atlantic 35°33´N, 13°16´W; 35°18´N, 13°32´ W; 11°37´N, 65°32´W)
Parapasiphae cristata	Gulf of Mexico, Western Tropical Atlantic, Western Temperate N. Atlantic (1°20´S, 27°37´W; 26°12´N, 87°54´W; 37°56´N, 72°25´W)
Pasiphaea tarda	Gulf of St. Lawrence, Faroe Islands (48°20´N, 61°28´W; 48°32´N, 69°01´W; 48°36´N, 68°57´ W; 48°38´N, 68°49´W; 48°41´N, 62°16´W; 49°00´N, 63°25´W; 49°43´N, 66°33´W; 49°40´N, 66°23´W; 49°44´N, 66°18´W; 60°58´N, 4°14´W;61°04´N, 4°12´W)
Bentheogennema intermedia	Subtropical–to–Tropical N. and S. Atlantic (26°30´S, 36°3´W; 2°38´S, 28°47´W; 1°20´S, 27°37´W; 9°03´N, 51°05´W; 11°20´N, 64°40´W; 11°30´N, 65°19´W; 11°37´N, 65°32´W; 11°45´N, 65°33´W; 23°03´N, 45°01´W; 26°12´N, 87°54´W; 26°33´N, 21°27´W; 32°17´N, 59°45´W; 37°56´N, 72°25´W)
Gennadas incertus	Eastern Subtropical–Temperate S. Atlantic (36°03´S, 17°07´E; 36°03´S, 17°10´E; 34°58´S, 14°36´E; 34°26´S, 16°11´E; 31°54´S, 9°50´E)
Gennadas kempi	Subtropical–Temperate S. Atlantic (35°50´S, 2°16´W; 35°50´S, 2°09´W; 35°19´S, 7°30´E; 34°43´S, 49°28´W)

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TABLE 5. (Continued)

Species	Locations
Gennadas parvus	Eastern Subtropical–Temperate S. Atlantic (36°03´S, 17°07´E; 34°59´S, 14°28´E; 34°26´S, 16°11´E)
Gennadas propinquus	Eastern Subtropical–Temperate S. Atlantic (36°03´S, 17°07´E; 36°03´S, 17°10´E; 35°56´S, 17°20´E; 34°59´S, 14°28´E; 34°58´S, 14°36´E; 31°54´S, 9°50´E)
Funchalia danae	Tropical N. Atlantic (6°18´N, 20°40´W; 8°56´N, 46°36´W; 8°57´N, 46°29´W; 9°00´N, 40°53´W)
Pelagopenaeus balboae	Tropical S. Atltantic (23°53´S, 8°19´W; 16°01´S, 2°00´E; 15°59´S, 2°02´E; 0°26´N, 32°06´W; 9°02´N, 40°47´W; 9°45´N, 40°41´W; 15°27´N, 26°12´W; 15°30´N, 26°12°W)
Deosergestes disjunctus	Subtropical–Temperate S. Atlantic (36°45´S, 53°06´W; 36°11´S, 7°27´W; 35°43´S, 0°52´E; 35°43´S, 0°55´E; 35°31´S, 4°47´E; 34°43´S, 49°28´W; 32°59´S, 35°08´W)
Neosergestes orientalis	Eastern Subtropical–Temperate S. Atlantic (36°03´S, 17°07´E; 36°03´S, 17°10´E; 35°59´S, 17°15´E; 35°56´S, 17°20´E; 34°59´S, 14°28´E; 34°59´S, 14°32´E; 34°58´S, 14°36´E; 34°36´S, 16°21´E; 34°31´S, 16°16´E; 33°38´S, 16°58´E; 32°50´S, 13°15´E; 32°51´S, 13°20´E; 30°51´S, 6°44´E)
Petalidium foliaceum	Subtropical–Temperate S. Atlantic (35°59´S, 17°15´E; 35°19´S, 7°30´E; 34°43´S, 49°28´W; 33°38´S, 16°58´E)
Sergia burukovskii	Tropical and Eastern Subtropical S. Atlantic (27°31´S, 0°23´W; 26°00´S, 3°27´W; 23°56´S, 8°43´W; 14°08´S, 5°49´ E; 11°23´S, 10°55´E; 9°04´S, 10°55´E; 5°30´S, 8°37´E; 0°58´S, 27°34´W)
Sergia gardineri	Eastern Temperate S. Atlantic (35°56´S, 17°20´E)
Sergia plumea	Eastern Tropical N. Atlantic (9°02´N, 43°48´W; 11°18´N, 59°33´W)
Sergia potens	Temperate S. Atlantic (34°59´S, 14°28´E; 34°59´S, 14°32´E; 34°58´S, 14°36´E; 34°43´S, 49°28´W; 34°31´S, 16°16´E; 34°26´S, 16°11´E; 34°06´S, 42°44´W)
Sergia scintillans	Eastern Subtropical and Temperate S. Atlantic 36°03´S, 17°07´E; 35°59´S, 17°15´E; 36°03´S, 17°10´E; 35°56´S, 17°20´E; 34°36´S, 16°21´E; 34°26´S, 16°11´E; 20°04´S, 7°05´W
Sergia tenuiremis	Subtropical N. and S. Atlantic (26°30´S, 36°33´W; 23°13´N, 44°56´W; 26°33´N, 21°27´W; 32°17´N, 59°45´W; 32°30´N, 60°30´W; 33°42´N, 16°08´W; 35°11´N, 14°44´W; 37°28´N, 68°32´W; 37°56´N, 72°25´W)

When species occurring 20 or more times were considered, co-occurrence and GMPJO values within-genus and within-*Sergia* phylogenetic group revealed that most species pairs overlapped in distribution to some degree, with relatively few clear cases of either sympatry or allopatry (Table 6).

Acanthephyra exhibited a spectrum of geographical patterns (Fig. 1): subpolar-temperate-Mediterranean with separate bipolar populations (*A. pelagica*), temperate to tropical (*A. purpurea*), broadly tropical (*A. acanthitelsonis, A. kingsleyi*), western tropical (*A. curtirostris*) and southern hemisphere temperate (*A. quadrispinosa*). Nine WHOI tows from the Caribbean Sea and Gulf of Mexico yielded specimens tentatively identified as *Acanthephyra purpurea*. Those occurrences are not shown because of the possibility that some specimens actually may belong to the similar *A. pelagica*, a species also reported from the region (Pequenant & Wicksten 2006). *Acanthephyra acanthitelsonis* and *A. kingsleyi* co-occurred extensively, with a GMPJO approaching the 0. 5 threshold (Table 6).

The acanthephyrid *Meningodora vesca* occurred throughout the temperate to tropical North Atlantic, its range overlapping that of its tropical congener, *M. mollis* (Fig. 2).

TABLE 6. Co-occurrences of pelagic decapod shrimp species within genera or species groups in WHOI IKMT tows. N = total occurrences of a species. The geometric mean of the proportion of joint occurrences (GMPJO) is enclosed in parentheses following the number of co-occurrences. GMPJO values > 0.5 are set in boldface. Only species occuring in more than 20 IKMT tows are compared.

Acanthephyra

	N	*quadrispinosa*	*purpurea*	*pelagica*	*kingsleyi*	*curtirostris*
acanthitelsonis	44	1(<0.01)	5(0.02)	4(0.01)	30(0.48)	15(<0.39)
curtirostris	24	0(0)	2(<0.01)	0(0)	8(0.13)	
kingsleyi	73	1(<0.01)	17(0.10)	8(0.04)		
pelagica	97	13(0.21)	27(0.16)			
purpurea	208	0(0)				
quadrispinosa	26					

Meningodora

	N	*vesca*
mollis	24	7(0.13)
vesca	50	

Oplophorus

	N	*novaezeelandiae*
spinosus	474	11(0.06)
novaezeelandiae	41	

Pasiphaea

	N	*merriami*	*sivado*	*multidentata*
hoplocerca	22	0(0)	2(<0.01)	4(0.05)
multidentata	59	0(0)	3(0.01)	
sivado	28	0(0)		
merriami	23			

Gennadas

	N	*valens*	*tinayrei*	*talismani*	*scutatus*	*gilchristi*	*elegans*	*capensis*	*brevirostris*
bouvieri	84	21(0.13)	4(<0.01)	42(0.40)	62(0.48)	2(<0.01)	3(<0.01)	66(**0.72**)	1(<0.01)
brevirostris	55	18(0.14)	7(0.04)	30(0.35)	27(0.24)	1(<0.01)	7(0.04)	2(<0.01)	
capensis	87	24(0.15)	10(0.05)	44(0.42)	62(0.47)	1(<0.01)	4(<0.01)		
elegans	119	20(0.10)	11(0.04)	7(0.02)	7(0.01)	0(0)			
gilchristi	26	12(0.14)	10(0.12)	0(0)	4(0.02)				
scutatus	171	19(0.07)	19(0.08)	87(**0.62**)					
talismani	102	11(0.04)	4(<0.1)						
tinayrei	149	57(0.31)							
valens	182								

Funchalia

	N	*woodwardi*
villosa	249	21(0.20)
woodwardi	34	

Allosergestes

	N	*sargassi*
pectinatus	486	321(0.64)
sargassi	483	

Deosergestes

	N	*pediformis*	*paraseminudus*	*henseni*
corniculum	128	0(0)	8(0.03)	46(0.22)
henseni	257	19(0.15)	44(0.26)	
paraseminudus	89	2(<0.01)		
pediformis	42			

Parasergestes

	N	*vigilax*	*diapontius*
armatus	313	217(**0.55**)	20(0.10)
diapontius	84	18(0.07)	
vigilax	452		

Sergestes

	N	*cornutus*
atlanticus	358	47(0.23)
cornutus	93	

Sergia 'phorca' species group

	N	*wolffi*
grandis	87	31(0.32)
wolffi	78	

Sergia 'robusta' species group

	N	*robusta*	*regalis*	*manningorum*
extenuata	36	16(0.17)	3(<0.01)	16(0.36)
manningorum	36	2(<0.01)	1(<0.01)	
regalis	78	0(0)		
robusta	132			

Sergia 'japonica' species group

	N	*laminata*
japonica	34	6(0.07)
laminata	65	

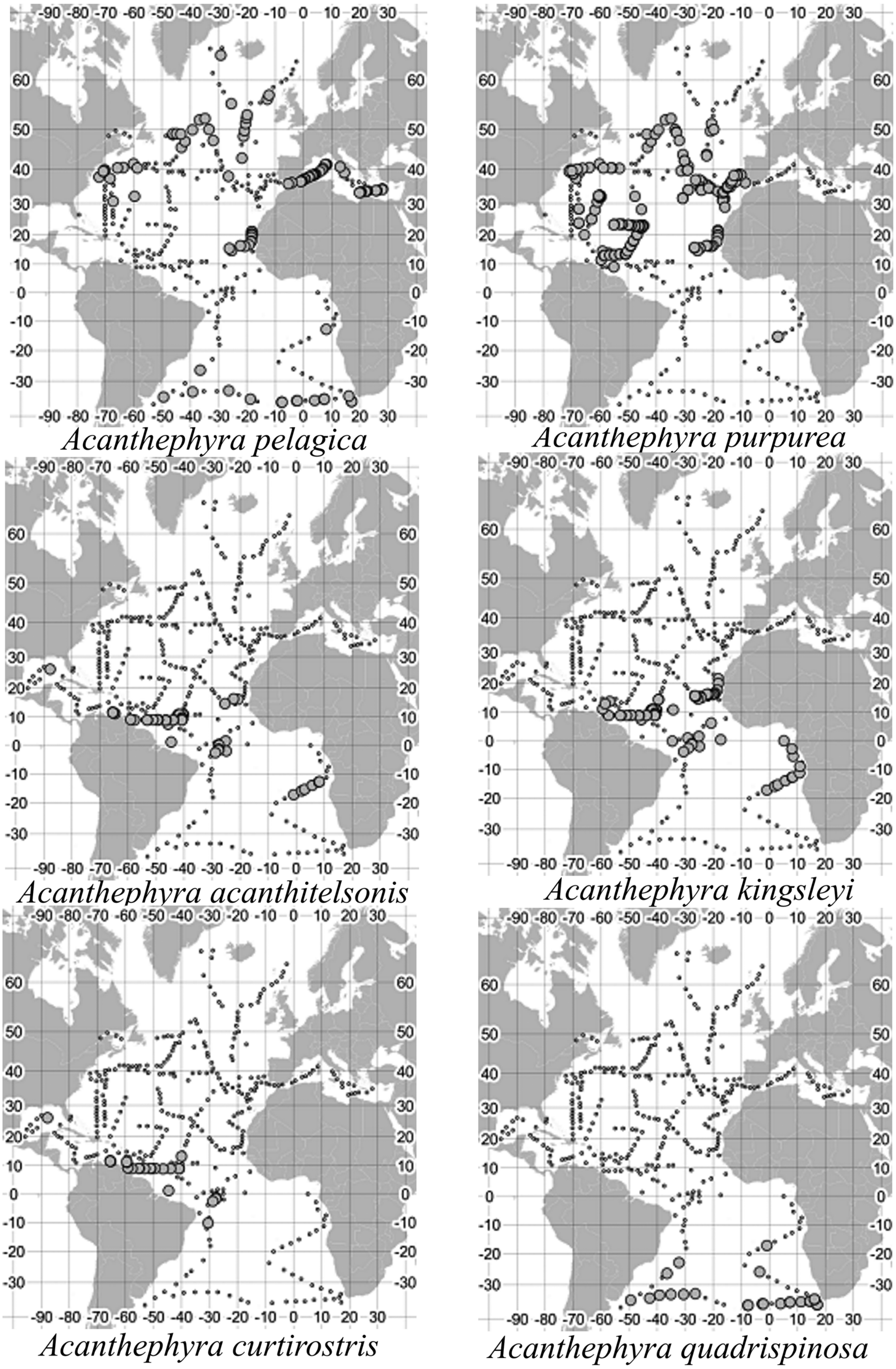

FIGURE 1. Atlantic ranges of the acanthephyrids *Acanthephyra pelagica, A. purpurea, A.acanthitelsonis*, *A. kingsleyi*, *A. curtirostris* and *A. quadrispinosa* . See Pequegnat & Wicksten (2006) for *A. pelagica* and *A. purpurea* in Caribbean and Gulf of Mexico. In Figures 1–14, the small dots indicate absence of the species from tows at that location. A circle may represent more than one midwater trawl tow at a location.

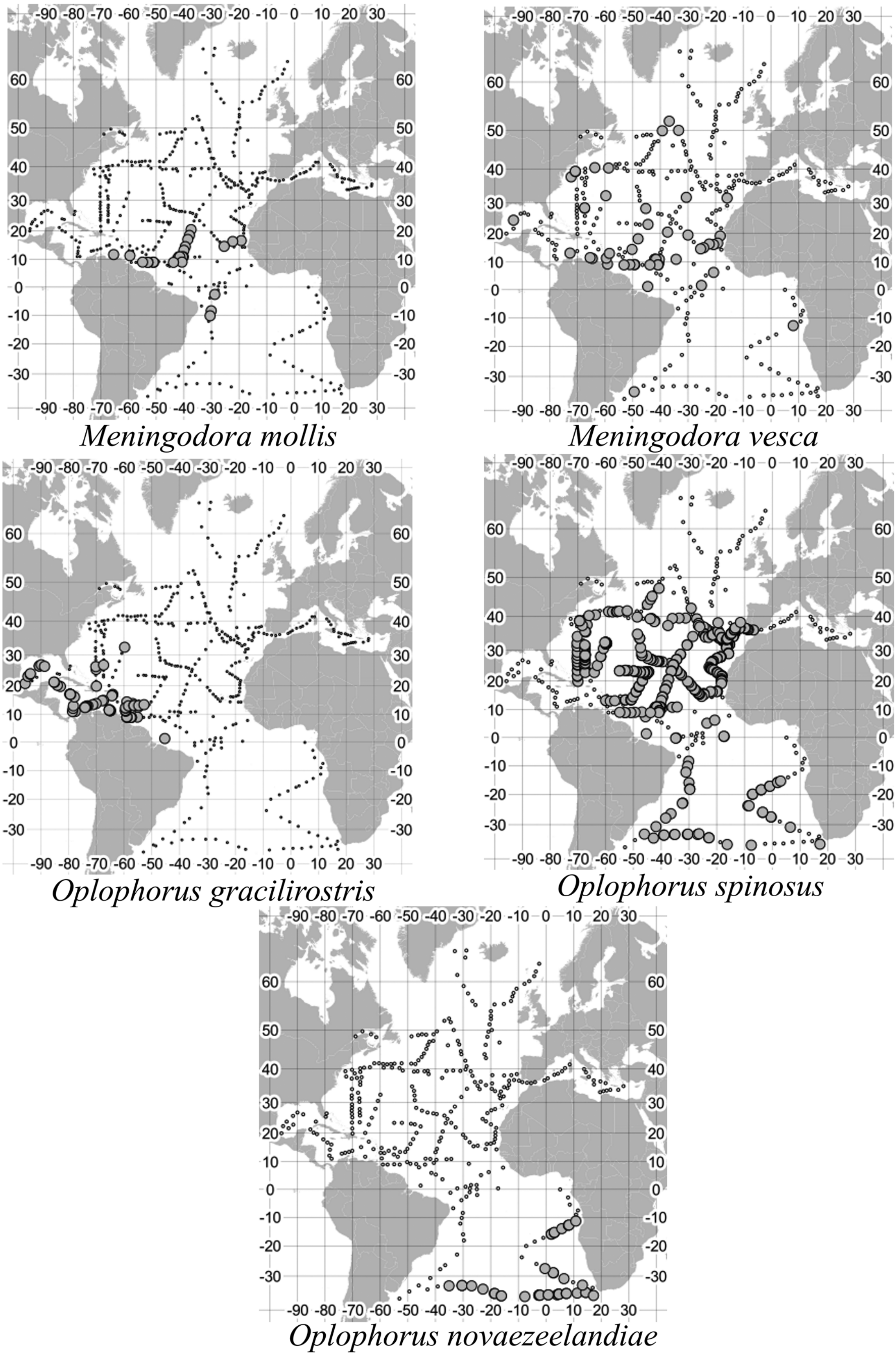

FIGURE 2. Atlantic ranges of the acanthephyrids *Meningodora mollis* and *M. vesca* and the oplophorids *Oplophorus gracilirostris*, *O. spinosus* and *O. novaezeelandiae*. See Figure 1 for an explanation of the symbols.

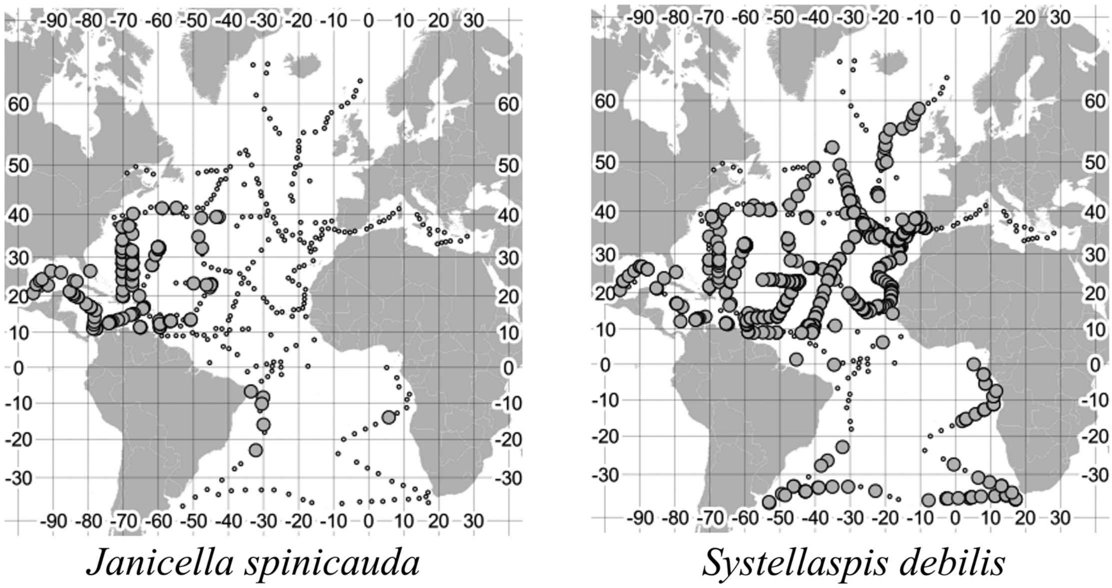

FIGURE 3. Atlantic ranges of the oplophorids *Janicella spinicauda* and *Systellaspis debilis*. See Figure 1 for an explanation of the symbols.

Within *Oplophorus* (Fig. 2), *O. spinosus* was broadly distributed from northern temperate waters through the tropics into the South Atlantic where it encountered *O. novaezeelandiae*. *Oplophorus spinosus* was replaced in the Caribbean and Gulf of Mexico by *O. gracilirostris*, but the two species overlapped in the western Atlantic. Of other oplophorids, *Janicella spinicauda* and *Systellaspis debilis* were the most frequently found in these collections; the former was captured often in the Caribbean, Gulf of Mexico and western subtropical North Atlantic and the later occurred throughout the temperate, subtropical and tropical Atlantic (Fig. 3).

Of *Pasiphaea* species (Fig. 4), *P. sivado* was captured only in the Mediterranean and adjacent Atlantic where it co-occurred with *P. multidentata*. Both species are considered to be benthopelagic (Company *et al.* 2006), but the latter also was taken in oceanic waters of the temperate-subpolar North Atlantic. *Pasiphaea hoplocerca* occurred most frequently in the Atlantic adjacent to the entrance of the Mediterranean, and *P. merriami* occurred most often in the Caribbean and Gulf of Mexico, but there were scattered captures of both species elsewhere in the tropical and subtropical North Atlantic. These last two *Pasiphaea* may be benthopelagic species of the continental slope with open ocean occurrences the result of expatriation by currents. *Parapasiphae sulcatifrons* was most frequently taken in the temperate North Atlantic, but there were scattered occurrences elsewhere in both hemispheres (Fig. 4).

The pandalid *Stylopandalus richardi* occurred throughout the temperate, subtropical and tropical Atlantic (Fig. 4).

A wide range of distributional patterns was found among species of *Gennadas* (Figs. 5, 6): subarctic-temperate-Mediterranean (*G. elegans*), anti-tropical subtropical (*G. tinayrei*, *G. valens*), broadly tropical (*G. scutatus*, *G. talismani*), eastern tropical (*G. brevirostris*), western tropical (*G. bouvieri, G. capensis*) and southern temperate (*G. gilchristi*). There was considerable distributional overlap between species, and *G. bouvieri* and *G. capensis* had nearly sympatric ranges, as did *G. scutatus* and *G. talismani.* GMPJO values between the species of those pairs were well above 0.5, and there were several instances among other *Gennadas* pairs approaching that threshold (Table 6). The range of *Gennadas gilchristi* extends into the Indian Ocean and *G. bouvieri*, *G. scutatus* and *G. tinayrei* occur throughout the Indo-Pacific (Kensley 1971b). The infrequently occurring *G. clavicarpus*, *G. incertus*, *G. kempi*, *G. parvus* and *G. propinquus* (Table 5) also have extensive Indo-Pacific ranges (Pérez Farfante & Kensley 1997).

Of the two frequently encountered species of *Funchalia* (Fig. 6), *F. villosa* occurred throughout the temperate, subtropical and tropical Atlantic whereas *F. woodwardsi* was captured most frequently in the eastern Atlantic with only scattered occurrences elsewhere.

Among sergestids, *Allosergestes sargassi* and *A. pectinatus* were nearly sympatric in distribution, the major difference being the presence of only the former species in the Mediterranean (Fig. 7). The GMPJO for this pair, the only two Atlantic species within the genus, was 0.64 (Table 6).

Species of *Deosergestes* showed greater separation in their distributions (Fig. 7): *D. henseni* occurred throughout temperate and subtropical waters of both hemispheres and also the Mediterranean; *D. corniculum* also was captured in the temperate-subtropical North and South Atlantic but not in the Mediterranean and only infrequently in the tropics; *D. pediformis* occurred only in the eastern tropics in contrast to the western tropical *D. paraseminudus*.

Neosergestes edwardsi was taken across the tropical Atlantic, through the Caribbean and Gulf of Mexico and north in the Gulf Stream (Fig. 8). A second species, *N. orientalis* was taken infrequently in the South Atlantic (Table 5).

Within *Parasergestes* (Fig. 8), *P. armatus* and *P. vigilax* co-occurred widely throughout temperate through tropical waters of the Atlantic, but only *P. vigilax* was present in the Mediterranean. The GMPJO for this pair was 0.55 (Table 6). A third species, *P. diapontius* was taken primarily in the eastern tropics.

Sergestes atlanticus and *S. cornutus*, the only species in the genus, were captured throughout the temperate, subtropical and tropical Atlantic (Fig. 8). *Sergestes cornutus* occurred relatively infrequently, and this contributed to the low GMPJO between it and *S. atlanticus*. However, *S. cornutus* was probably inadequately sampled due to escapement by this small shrimp through the course nets and the paucity of tows within the upper 25 m, the stratum apparently favored by this species (Donaldson 1975).

Eusergestes arcticus is subpolar-temperate species with a bipolar distribution that extends into the Mediterranean (Fig. 9), a distribution similar to that of the myctophid fish *Benthosema glaciale* (Backus *et al*. 1977). Vereshchaka (2009) recognized the Southern Ocean population as a separate species that he named *Eusergestes antarcticus*, but the species is not accepted in the World Register of Marine Species (http://www.marinespecies.org/, accepted 5 December 2014).

Vereshchaka (2000) divided the large sergestid genus *Sergia* into seven species groups and two taxonomically isolated species. Species within the "gardeneri", "japonica", "phorca", "prehensilis" and "robusta" groups were found in the WHOI material. The material also contained a single species of the "challengeri" group and a few occurrences of the isolated species *S. tenuiremis* (Table 5).

Within the "prehensilis" group, *Sergia prehensilis* occurred off Africa and South America in the southernmost WHOI tows (Fig. 9), and the infrequently occurring *S. scintillans* was captured along the eastern margin of the South Atlantic (Table 5).

Sergia grandis and *S. wolffi* of the "phorca" group had very similar tropical and subtropical North Atlantic ranges (Fig. 9). They differed in frequency in the Gulf of Mexico and western Atlantic, perhaps accounting for the relatively low GMPJO value between the pair (Table 6). Cardoso *et al*. (2014) reported that *Sergia grandis* was collected in the central South Atlantic above the Mid-Atlantic Ridge, a region not sampled in the WHOI program. Two other species within the group, *S. plumea* and *S. potens*, were taken infrequently in the North Atlantic (Table 5).

Sergia talismani, the only species of the "challengeri" group found in the WHOI material, appears to have separate eastern and western tropical populations (Fig. 9).

Sergia splendens, the only species of the "gardineri" group in the collections, ranged from temperate latitudes in the North Atlantic through the tropics into the South Atlantic (Fig. 9).

The five species of the "robusta" group in the material displayed little overlap (Fig 10): *Sergia robusta* occurred throughout the temperate North Atlantic and the Mediterranean; its close relative *S. manningorum* was restricted to the eastern tropics; *S. extenuata* had a broader tropical range; *S. regalis* also had a broad tropical distribution but also occurred in the southernmost tows in the South Atlantic; *S. burukovskii* occurred in a few tows off southern Africa (Table 5). Cardoso *et al*. (2014) reported that *Sergia robusta* occurred in the South Atlantic above the Mid-Atlantic Ridge. *Sergia manningorum* and *S. extenuata* had the most overlap and had the highest GMPJO within the "robusta" group (Table 6).

Sergia japonica and *S. laminata*, sole species in the "japonica" group, overlapped in range but differed in distribution: *S. laminata* occurred widely throughout the tropics and also at many locations in the subtropical South Atlantic; *S. japonica* occurred often in the eastern tropical North Atlantic but also ranged north into temperate waters (Fig. 10). *Sergia laminata* occurred frequently in nighttime epipelagic tows, unlike the deeper dwelling *S. japonica* (Table 3).

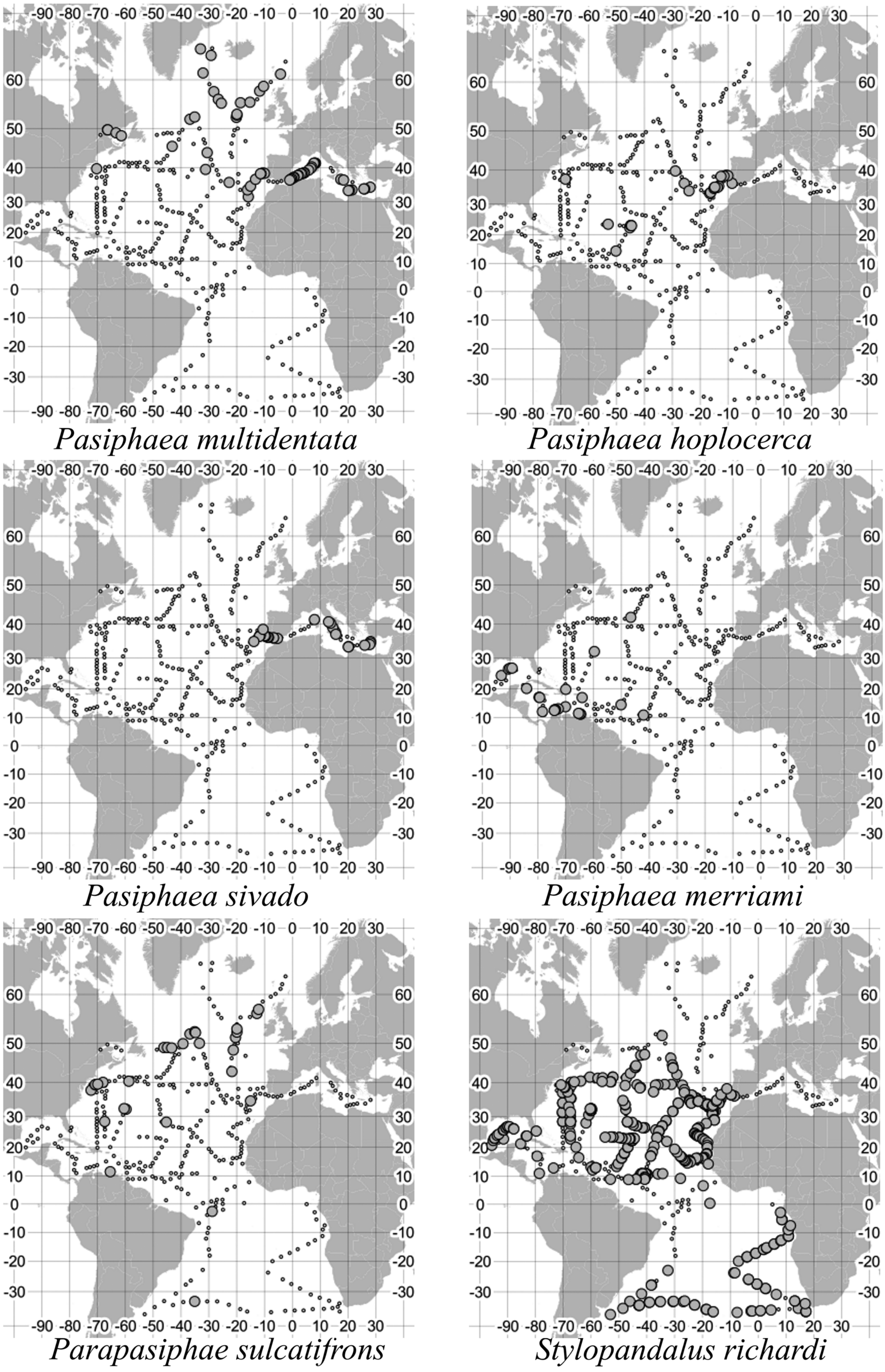

FIGURE 4. Atlantic ranges of the pasiphaeids *Pasiphaea multidentata*, *P. hoplocerca*, *P. sivado, P. merriami* and *Parapasiphae sulcatifrons* and the pandalid *Stylopandalus richardi*. See Figure 1 for an explanation of the symbols.

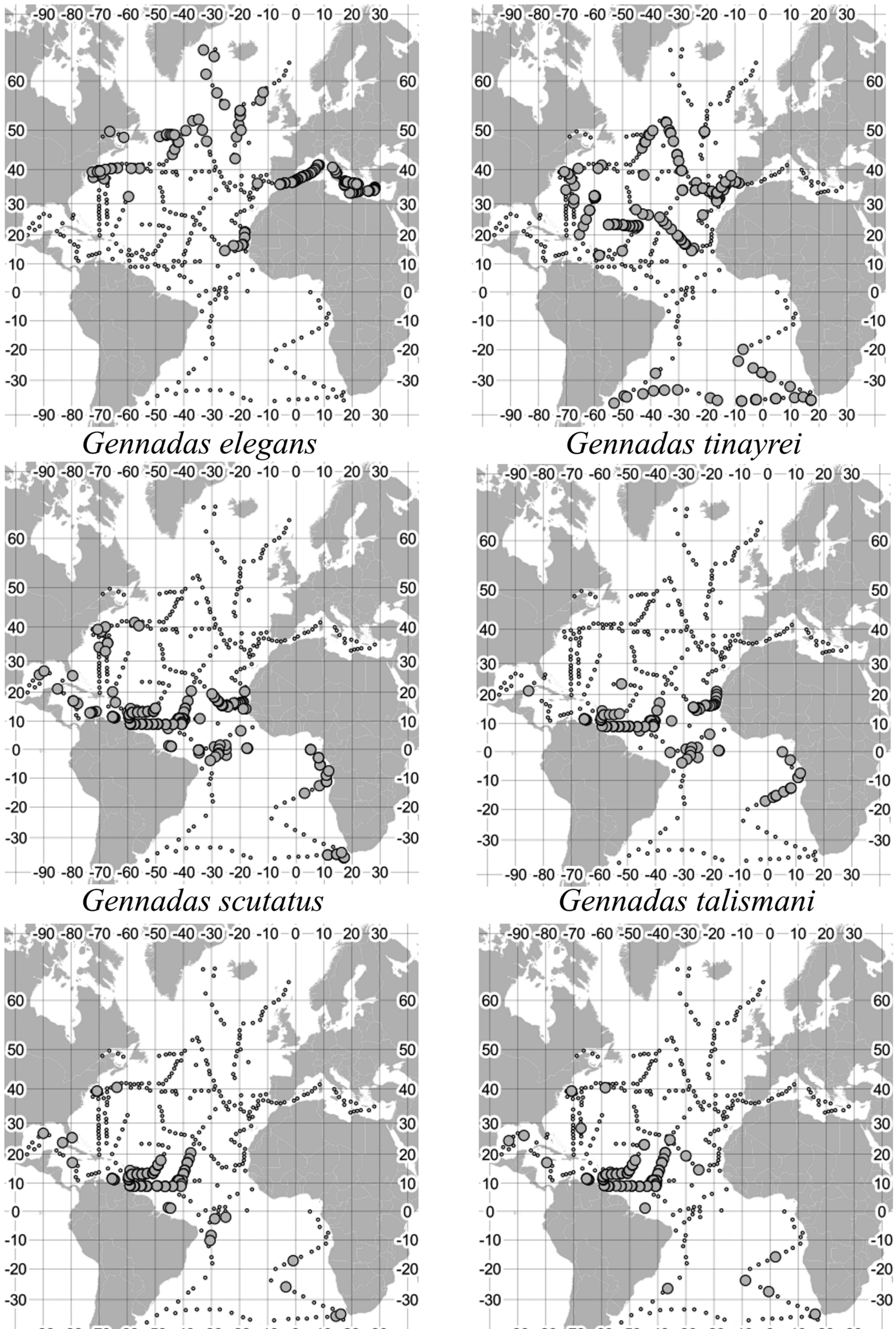

FIGURE 5. Atlantic ranges of the benthesicymids *Gennadas elegans*, *G. tinayrei*, *G. scutatus, G. talismani, G. bouvieri* and *G. capensis*. See Figure 1 for an explanation of the symbols.

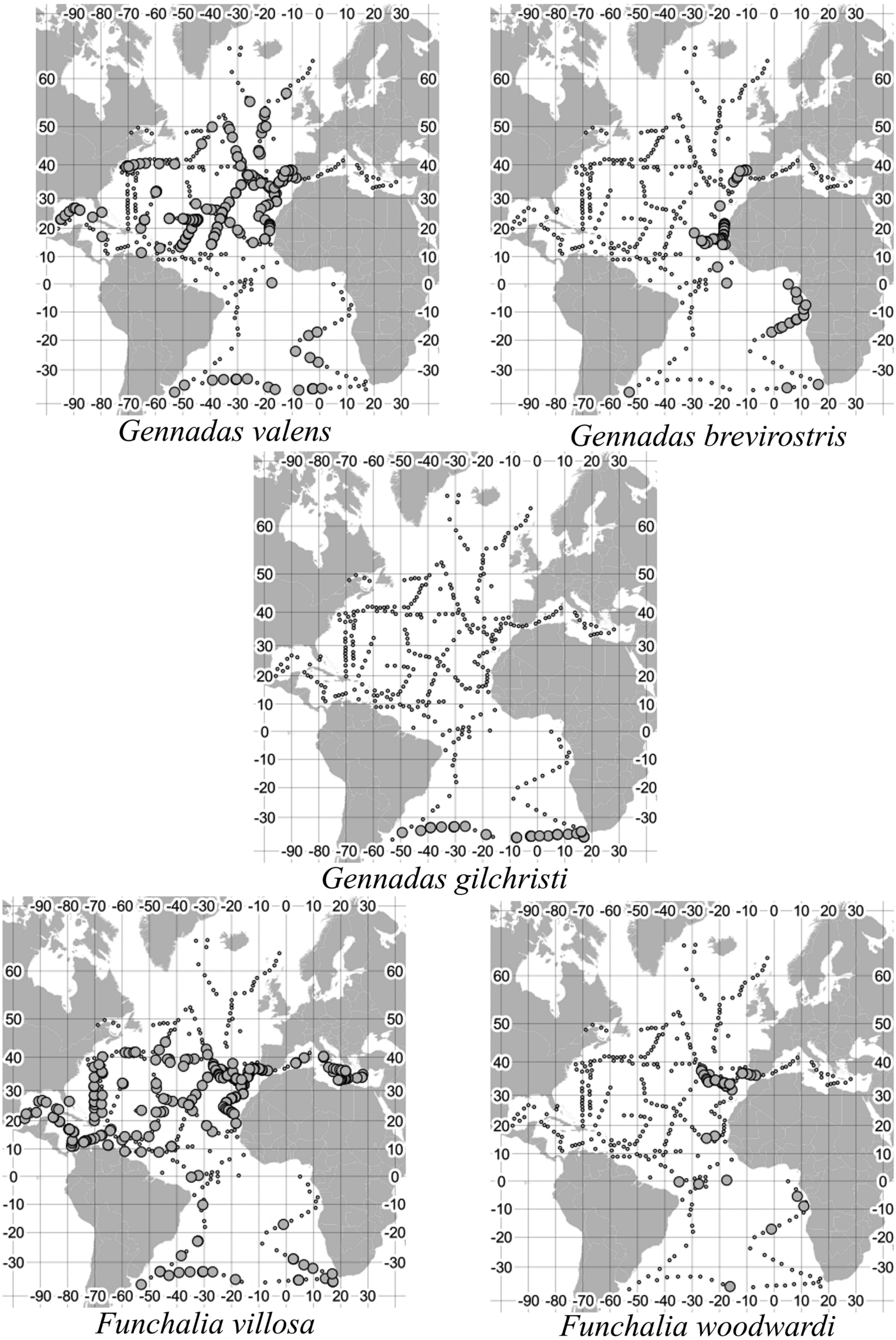

FIGURE 6. Atlantic ranges of the benthesicymids *Gennadas valens*, *G. brevirostris* and *G. gilchristi* and the penaeids *Funchalia villosa* and *F. woodwardi*. See Figure 1 for an explanation of the symbols.

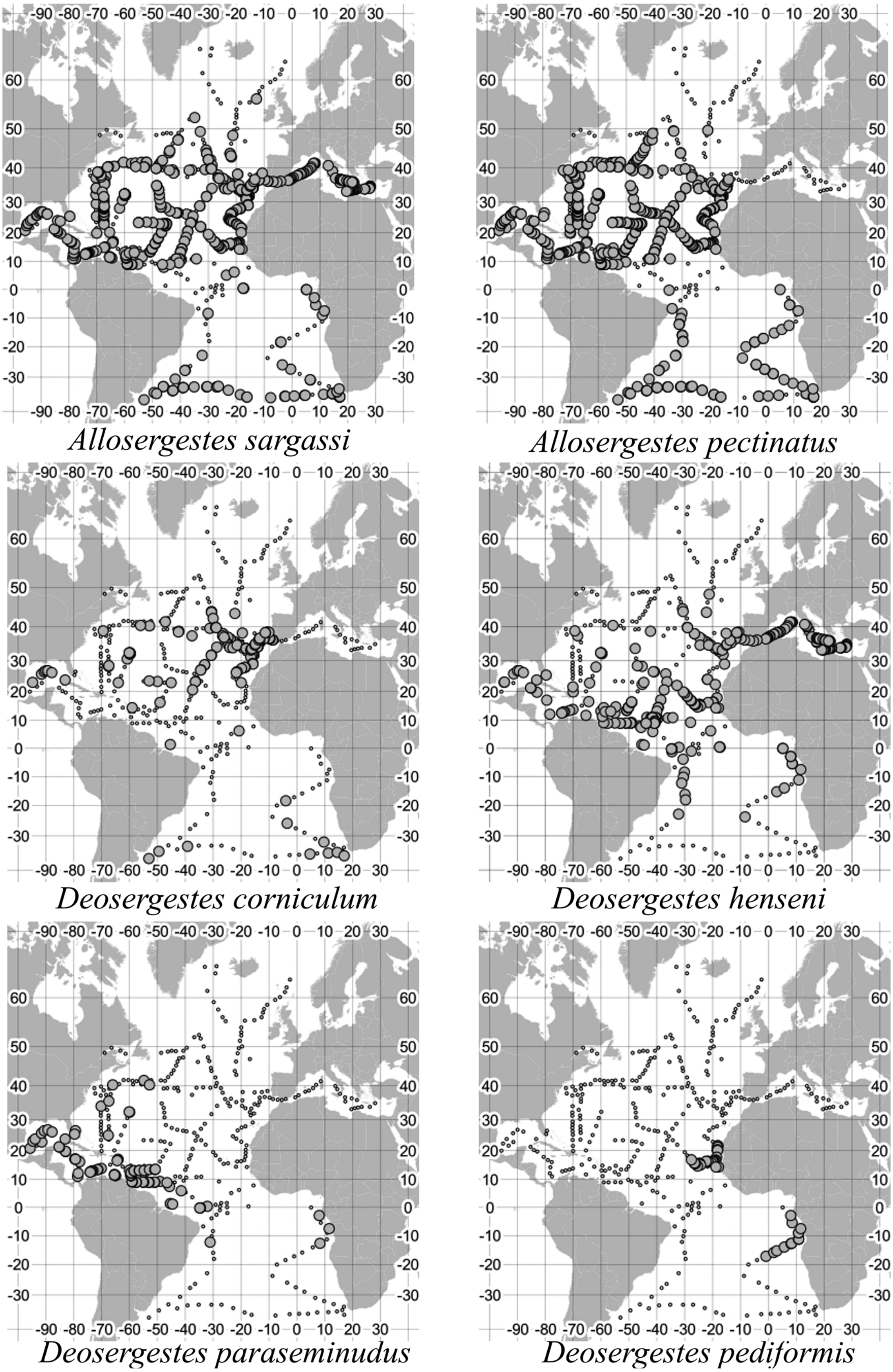

FIGURE 7. Atlantic ranges of the sergestids *Allosergestes sargassi*, *A. pectinatus*, *Deosergestes corniculum, D. henseni*, *D. paraseminudus* and *D. pediformis* See Figure 1 for an explanation of the symbols.

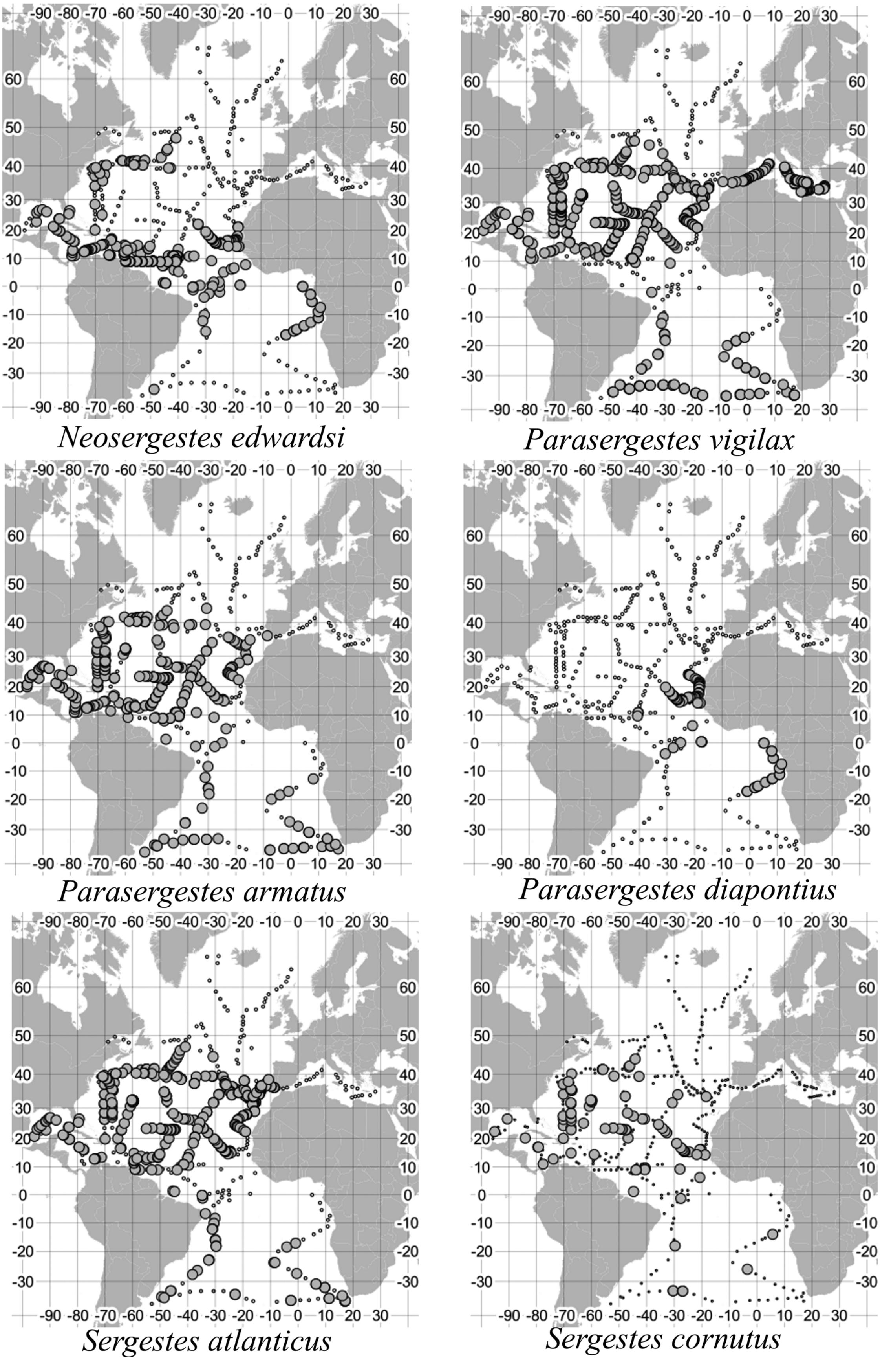

FIGURE 8. Atlantic ranges of the sergestids *Neosergestes edwardsi, Parasergestes vigilax, P. armatus, P. diapontius*, *Sergestes atlanticus* and *S. cornutus.* See Figure 1 for an explanation of the symbols.

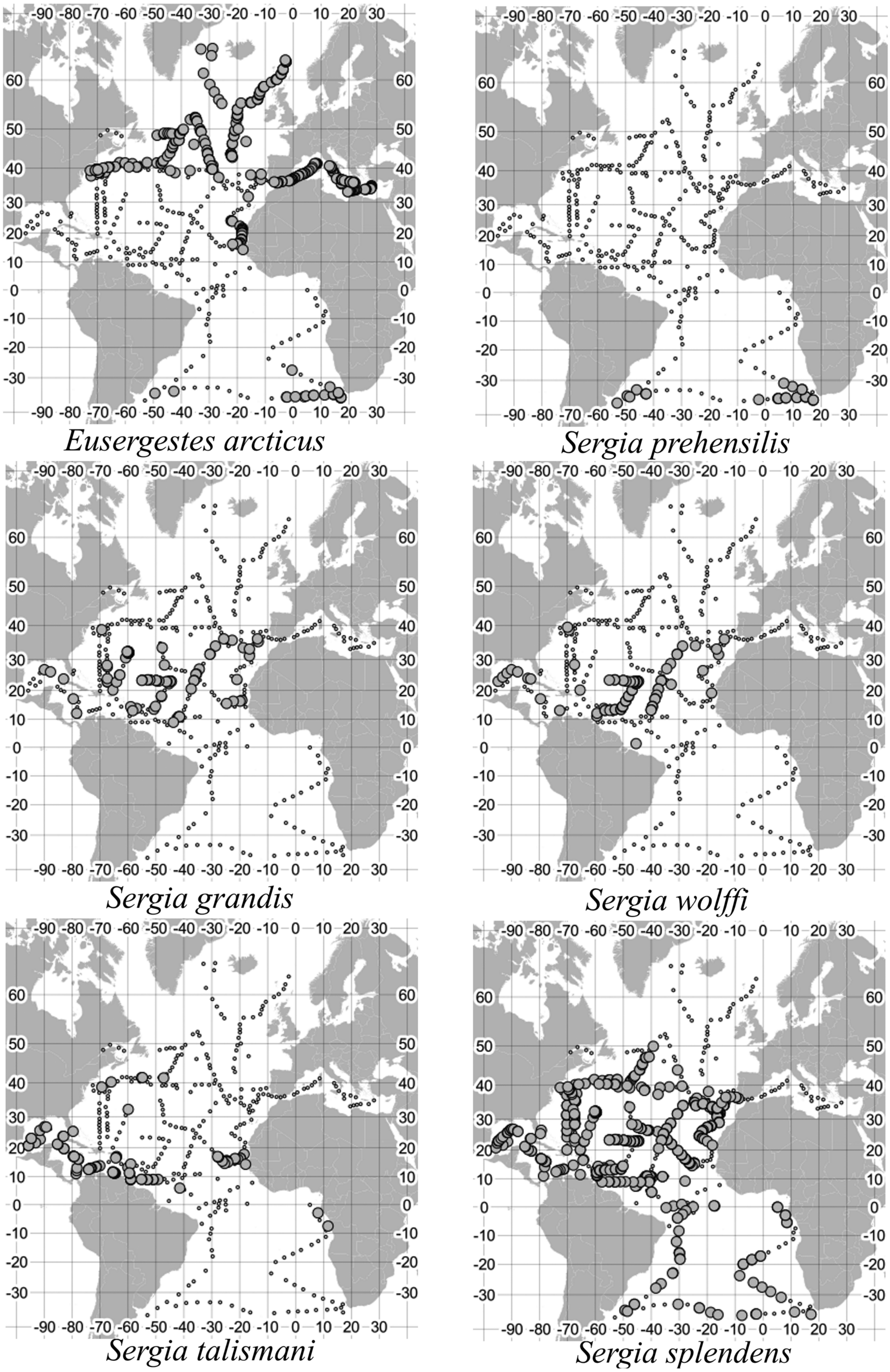

FIGURE 9. Atlantic ranges of the sergestids *Eusergestes arcticus, Sergia prehensilis* of the “prehensilis” species group, *S. grandis* and *S. wolffi* of the “phorca” species group, *S. talismani* of the “challengeri” group and *S. splendens* of the “gardineri” group. See Figure 1 for an explanation of the symbols.

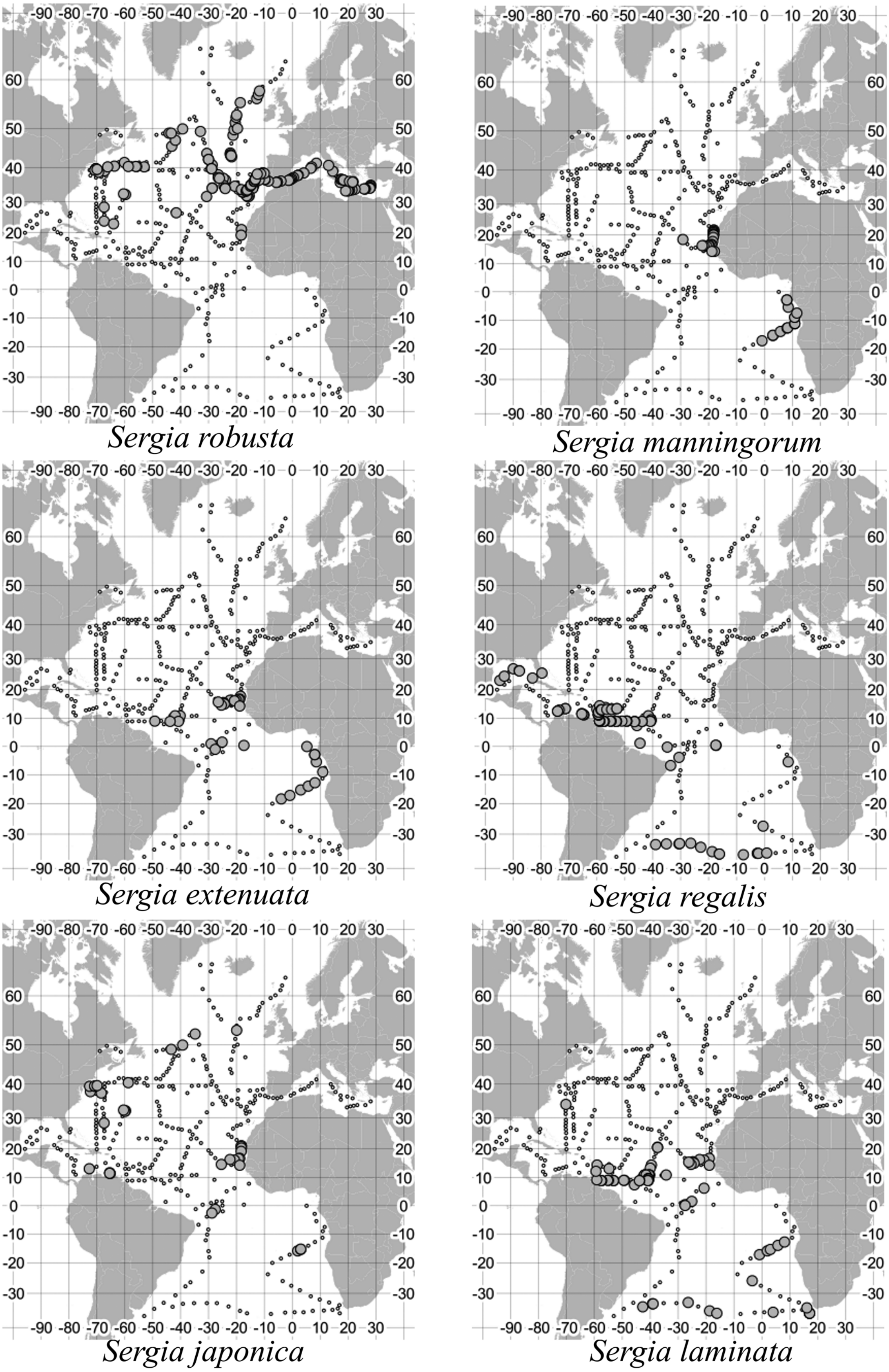

FIGURE 10. Atlantic ranges of the sergestids *Sergia robusta*, *S. manningorum*, *S. extenuata* and *S. regalis* of the "robusta" species group and *S. japonica* and *S. laminata* of the "japonica" group. See Figure 1 for an explanation of the symbols.

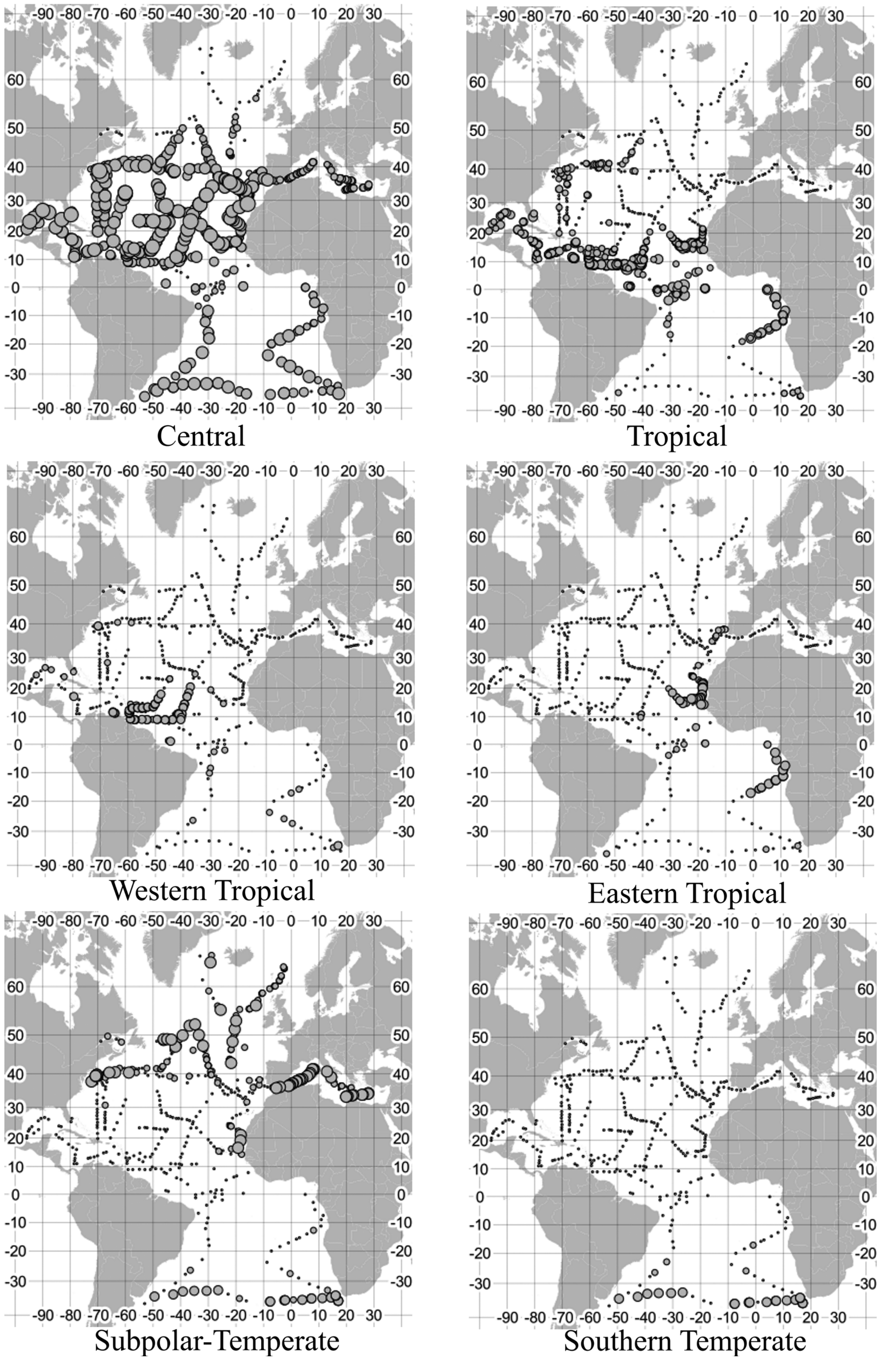

FIGURE 11. Distribution patterns of the Central, Tropical, Western Tropical, Eastern Tropical, Subpolar-Temperate and Southern Temperate recurrent groups of pelagic decapod shrimp. The size of circle is proportional to the number of species occurring in a WHOI IKMT tow. The small dots indicate absence from tows at that location.

TABLE 7. Recurrent groups of pelagic decapod shrimp in WHOI IKMT tows based on the geometric mean of the proportion of joint occurrences (GMPJO) between species pairs. GMPJO values within recurrent groups are ≥ 0.5, unless otherwise noted. Only species occurring in more than 20 IKMT tows are included. Distributional maps of the recurrent groups are shown in Figures 15 and 16.

Subpolar–Temperate Recurrent Group
- *Acanthephyra pelagica* (Fig. 1)
- *Gennadas elegans* (Fig. 5)
- *Eusergestes arcticus* (Fig. 9)

Southern Hemisphere Recurrent Group
- *Acanthephyra quadrispinosa* (Fig. 1)
- *Gennadas gilchristi* (Fig. 6)

Central Recurrent Group
- *Acanthephyra purpurea* (Fig. 1, GMPJO ≥ 0.5 with *Systellaspis debilis* only)
- *Oplophorus spinosus* (Fig. 2)
- *Systellaspis debilis* (Fig. 3)
- *Stylopandalus richardi* (Fig. 4)
- *Gennadas valens* (Fig. 6, GMPJO ≥ 0.5 with *Acanthephyra purpurea* only)
- *Allosergestes pectinatus* (Fig. 7)
- *Allosergestes sargassi* (Fig. 7)
- *Deosergestes henseni* (Fig. 7, GMPJO ≥ 0.5 with *Allosergestes sargassi* only)
- *Parasergestes armatus* (Fig. 8)
- *Parasergestes vigilax* (Fig. 8)
- *Sergestes atlanticus* (Fig. 8)
- *Sergia splendens* (Fig. 9)

Tropical Recurrent Group
- *Acanthephyra acanthitelsonis* (Fig. 1, GMPJO ≥ 0.5 with *Gennadas talismani* only)
- *Acanthephyra kingsleyi* (Fig. 1)
- *Gennadas scutatus* (Fig. 5)
- *Gennadas talismani* (Fig. 5)
- *Deosergestes paraseminudus* (Fig. 7, GMPJO ≥ 0.5 with *Sergia talismani* only)
- *Neosergestes edwardsi* (Fig. 8)
- *Sergia extenuata* (Fig. 10, GMPJO ≥ 0.5 with *Acanthephyra kingsleyi* only)
- *Sergia talismani* (Fig. 9, GMPJO ≥ 0.5 with *Neosergestes edwardsi* only)

Western Tropical Recurrent Group
- *Gennadas bouvieri* (Fig. 5)
- *Gennadas capensis* (Fig. 5)

Eastern Tropical Recurrent Group
- *Gennadas brevirostris* (Fig. 6)
- *Deosergestes pediformis* (Fig. 7)
- *Parasergestes diapontius* (Fig. 8)
- *Sergia manningorum* (Fig. 10, GMPJO ≥ 0.5 with *Gennadas brevirostris* and *Parasergestes diapontius* only)

Species not in a recurrent group (no GMPJO ≥ 0.5)
- *Acanthephyra curtirostris* (Fig. 1, western tropical N. Atlantic)
- *Meningodora mollis* (Fig. 2, tropical Atlantic)
- *Meningodora vesca* (Fig. 2, temperate to tropical N. Atlantic, scattered S. Atlantic)
- *Oplophorus gracilirostris* (Fig 2, tropical W. Atlantic, Caribbean, Gulf of Mexico)
- *Oplophorus novaezeelandiae* (Fig. 2, subtropical S. Atlantic)
- *Janicella spinicauda* (Fig. 3, western temperate to tropical N. Atlantic, scattered S. Atlantic)
- *Parapasiphae sulcatifrons* (Fig. 4, subarctic to temperate N. Atlantic, scattered tropical to subtropical N. and S. Atlantic)
- *Pasiphaea hoplocerca* (Fig. 4, subtropical N. Atlantic, most frequently taken in east)
- *Pasiphaea merriami* (Fig. 4, western tropical N. Atlantic, Caribbean, Gulf of Mexico)

Pasiphaea multidentata (Fig.4, subarctic to temperate N. Atlantic, Gulf of St. Lawrence, Mediterranean)
Pasiphaea sivado (Fig. 4, Mediterranean, adjacent N. Atlantic)
Gennadas tinayrei (Fig. 5, temperate to subtropical N. Atlantic and subropical S. Atlantic)
Funchalia villosa (Fig. 6, temperate to tropical N. Atlantic, subtropical S. Atlantic)
Funchalia woodwardi (Fig. 6, eastern subtropical N. Atlantic, scattered S. Atlantic)
Deosergestes corniculum (Fig. 7, temperate to subtropical N. Atlantic, scattered S. Atlantic)
Sergestes cornutus (Fig. 8, temperate to tropical N. Atlantic, scattered S. Atlantic, Caribbean, Gulf of Mexico)
Sergia grandis (Fig. 9, subtropical to tropical N. Atlantic, Gulf of Mexico)
Sergia japonica (Fig. 10, scattered temperate to tropical N. Atlantic, scattered S. Atlantic)
Sergia laminata (Fig. 10, tropical N. Atlantic, subtropical S. Atlantic)
Sergia prehensilis (Fig. 9, subtropical S. Atlantic)
Sergia regalis (Fig. 10, western tropical Atlantic, Caribbean, Gulf of Mexico, S. Atlantic)
Sergia robusta (Fig. 10, subarctic to subtropical N. Atlantic, Mediterranean)
Sergia wolffi (Fig. 9, subtropical to tropical N. Atlantic, Gulf of Mexico)

GMPJO values were calculated across genera for every species pair in which both occurred in more than 20 of the total 939 tows (Table 7). Species pairs with a GMPJO value ≥ 0.5 were assumed to be spatially closely associated and to belong to the same recurrent group (*sensu* Fager & McGowan 1963). Subpolar-Temperate, Southern Hemisphere, Central, Tropical, Western Tropical and Eastern Tropical recurrent groups containing a total of 31 species were identified by this criterion. Species within those six groups, along with 23 species showing no strong geographical overlap with other species, are listed in Table 7 with cross references to individual distribution maps. Composite occurrences of species within groups are depicted in Figure 11. Infrequency of occurrence can result in a low GMPJO value. However, several of the unaffiliated species listed in Table 7 occurred in more than 50 tows and 5 occurred in more than 100 tows (Table 2), suggesting that their distributions differed from that of any recurrent group.

Of the three species comprising the Subpolar-Temperate recurrent group, *Eusergestes arcticus* and *Acanthephyra pelagica* are bipolar in distribution. These species, like *Acanthephyra quadrispinosa* and *Gennadas gilchristi* of the Southern Hemisphere recurrent group, occur throughout southern temperate and subpolar waters in a circumpolar pattern. The third species of the group, *Gennadas elegans*, is restricted to the North Atlantic.

The Central recurrent group contained the largest number of species (12) and encompassed the largest area, spanning the Atlantic from temperate latitudes in the north to the most southern extent of sampling in the south. All but *Oplophorus spinosus* occurred in tows from the Gulf of Mexico. *Acanthephyra purpurea* was taken in only two tows in the South Atlantic, but all other species occurred frequently in southern waters. The frequency of species in this group was lowest near the equator, suggesting restricted exchange between northern and southern populations.

The Tropical recurrent group spanned the Atlantic between about 20° N and 10° S and extended through the Caribbean and the Gulf of Mexico into the temperate western North Atlantic. Of the eight species in this group, only *Gennadas scutatus* was taken south of 20° S.

The Western Tropical recurrent group was centered between 10° and 20° N in the western half of the North Atlantic. The group consists of *Gennadas bouvieri* and *G. capensis*. There also were scattered occurrences of these species in the Gulf of Mexico, the temperate western North Atlantic and the South Atlantic.

The four species of the Eastern Tropical recurrent group favored the Mauritian upwelling region off North Africa and an area centered on the equator to the south. Strong seasonal upwelling in the northern Gulf of Guinea (Verstraete 1992) may provide a pathway between Mauritian and equatorial populations, but there was a gap in sampling in the area. *Gennadas brevirostris* also was frequently taken in the Atlantic adjacent to the Mediterranean.

Although 23 species failed to meet the criterion for inclusion in a recurrent group, most of these exhibited a geographical pattern similar to that of a recognized group (Table 7). *Parapasiphae sulcatifrons*, *Pasiphaea multidentata* and *Sergia robusta* ranged across the temperate North Atlantic and into the subarctic. *Pasiphaea hoplocerca*, *Sergia wolffi* and *S. grandis* occurred throughout subtropical waters of the North Atlantic. *Meningodora vesca*, *Gennadas tinayrei*, *Funchalia villosa* and *Deosergestes corniculum* ranged from the northern subtropics into the subtropical South Atlantic. The ranges of *Janicella spinicauda* and *Sergia regalis* were centered in the western tropical Atlantic, whereas *Meningodora mollis* and *Sergia laminata* occurred throughout the tropics. *Funchalia woodwardsi* occurred in scattered tows in the tropical waters but was taken most frequently in the Atlantic adjacent to the Mediterranean. *Oplophorus novaezeelandiae* and *Sergia prehensilis* occurred only in tows from the South Atlantic and are circumglobal in the southern hemisphere. The circumglobal species *Sergia japonica* occurred in deep tows throughout the temperate and subtropical Atlantic.

The pelagic decapod shrimp fauna of the Mediterranean is uniquely restricted with only 10 species occurring in the WHOI material (Table 8). These included all three species of the Subpolar-Temperate recurrent group (*Acanthephyra pelagica, Gennadas elegans, Eusergestes arcticus*) but only three species of the Central group (*Allosergestes sargassi, Deosergestes henseni, Parasergestes vigilax)*. The widely distributed subpolar-temperate species, *Pasiphaea multidentata* and *Sergia robusta*, also were prominent in Mediterranean collections. *Pasiphaea sivado*, a benthopelagic species (Company *et al.* 2006), was restricted to the Mediterranean and adjacent Atlantic. A morphometric study found that Mediterranean populations of *Acanthephyra pelagica*, *Pasiphaea multidentata*, *Gennadas elegans* and *Sergia robusta* have diverged from populations in the Atlantic (Casanova 1977, Casanova & Judkins 1977). Further research may justify the elevation of the Mediterranean populations as separate species and recognition of an endemic Mediterranean fauna.

TABLE 8. Pelagic decapod shrimp species in 79 WHOI IKMT tows from the Mediterranean Sea.

	Number of Tows		Percentages	
Species	All Tows	Mediterranean	All Tows % Med	% Within Med
Acanthephyra eximia	3	3	100	100
Acanthephyra pelagica	97	32	34.0	40.5
Pasiphaea sivado	28	13	46.4	16.4
Pasiphaea multidentata	59	26	44.1	32.9
Gennadas elegans	119	61	51,2	64.6
Allosergestes sargassi	483	61	12.7	77.2
Deosergestes henseni	257	62	24.1	78.5
Eusergestes arcticus	262	69	26.3	87.3
Parasergestes vigilax	452	64	14.2	81.0
Sergia robusta	132	38	28.8	48.1

Two upwelling regions off the African coast harbored rich decapod shrimp assemblages that included members of the Subpolar-Temperate, Central, Tropical and the Eastern Tropical recurrent groups (Fig. 12). The Mauritanian Upwelling zone is located between about 15° and 25° N and inshore of about 20° W where the Canary Current swings west to form the North Equatorial Current (Wooster *et al.* 1976). The other upwelling region, known as the Angola-Benguela Frontal Zone (ABFZ), is the area shoreward of 20° W between the equator and 20° S where the northward flowing Benguela Current converges with the southward flowing Angola Current (Shannon *et al*. 1987). That region was less well sampled with 24 tows as opposed to 47 in the Mauritanian region. Thirty-four species were captured in the Mauritanian Upwelling zone and 46 in the Angola- Benguela Frontal zone (Table 9).

The four members of the Eastern Tropical recurrent group (*Sergia manningorum, Deosergestes pediformis, Parasergestes diapontius, Gennadas brevirostris*) appear to be endemic to the West African upwelling regions, with the majority of occurrences from the combined upwelling areas. The majority of occurrences of *Sergia extenuata* were from these regions, but it was also loosely associated with the broadly distributed Tropical recurrent group (Table 7). Most members of the Central and Tropical recurrent groups occurred in both the Mauritanian and ABFZ upwelling zones, and many of them were present in the majority of tows from the two regions. An exception was *Deosergestes pariseminudus* that was taken only in the ABFZ. The Subpolar-Temperate species *Acanthephyra pelagica, Eusergestes arcticus* and *Gennadas elegans* were captured in the Mauritanian region, but only *A. pelagica* was taken in the ABFZ.

The pelagic decapod shrimp faunas of the Caribbean Sea and Gulf of Mexico consisted of a mixture of species from the Central, Tropical and Western Tropical recurrent groups. The Caribbean-Gulf fauna was a subset of that found at the same latitudes in the central and western Atlantic (Table 10), a conclusion also of Hopkins *et al*. (1984) and Pequegnat & Wicksten (2006). The major distinction was the near absence of the dominant Atlantic species *Oplophorus spinosus* in the Caribbean and Gulf, and its replacement there by the similar *O. gracilirostris* (Fig. 2).

TABLE 9. Pelagic decapod shrimp species in WHOI IKMT tows from the Mauritanean Upwelling and the Angola-Benguala Frontal Zones.

	Mauritanean Upwelling		Angola-Benguala Frontal	
Species	Number of Tows	Percent of Tows	Number of Tows	Percent of Tows
Acanthephyra acanthitelsonis	2	4.3	6	25.0
Acanthephyra kingsleyi	15	32	11	45.8
Acanthephyra pelagica	12	25.5	1	4.2
Acanthephyra purpurea	15	31.9	2	8.3
Acanthephyra quadrispinosa	0	0	1	4.2
Ephyrina ombango	2	4.3	1	4.2
Meningodora mollis	0	0	2	8.3
Meningodora vesca	5	10.6	1	4.2
Notostomus auriculatus	5	10.6	2	8.3
Notostomus elegans	1	2.1	1	4.2
Janicella spinicauda	0	0	1	4.2
Oplophorus novaezeelandiae	0	0	8	33.3
Oplophorus spinosus	31	66.0	8	33.3
Systellaspis debilis	31	66.0	16	66.7
Systellaspis pellucida	1	2.1	1	4.2
Stylopandalus richardi	31	66.0	21	87.5
Gennadas bouvieri	0	0	1	4.2
Gennadas brevirostris	21	44.7	14	58
Gennadas capensis	0	0	1	4.2
Gennadas scutatus	16	34.0	13	54.2
Gennadas talismani	16	34.0	12	50.0
Gennadas tinayrei	0	0	1	4.2
Gennadas valens	12	25.5	2	8.3
Funchalia villosa	9	19	1	4.2
Funchalia woodwardi	2	4.3	3	12.5
Pelagopenaeus balboae	0	0	2	8.3
Allosergestes pectinatus	30	63.8	11	45.8
Allosergestes sargassi	32	68.1	8	33.3
Deosergestes corniculum	0	0	1	4.2
Deosergestes henseni	12	25.5	10	41.7
Deosergestes paraseminudus	0	0	3	12.5
Deosergestes pediformis	22	47.8	13	54.2
Eusergesytes arcticus	24	51.1	0	0
Neosergestes edwardsi	21	44.7	20	83.3
Parasergestes armatus	12	25.5	4	16.7
Parasergestes diapontius	39	82.9	20	83.3
Parasergestes vigilax	14	29.8	4	16.7
Sergestes atlanticus	14	29.8	2	8.3
Sergestes cornutus	3	6.4	1	4.2
Sergia burukovskii	0	0	4	16.7

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TABLE 9. (Continued)

Species	Mauritanean Upwelling		Angola-Benguala Frontal	
	Number of Tows	Percent of Tows	Number of Tows	Percent of Tows
Sergia extenuata	14	29.8	10	41.7
Sergia japonica	8	17.0	3	12.5
Sergia laminata	6	12.8	5	20.8
Sergia manningorum	19	40.4	14	58.3
Sergia regalis	0	0	1	4.2
Sergia splendens	0	0	11	45.8
Sergia talismani	12	25.5	2	8.3
Number of Species	34		46	
Number of Tows	47		24	

TABLE 10. Pelagic decapod shrimp species in WHOI IKMT tows from the Caribbean, the Gulf of Mexico and the Atlantic between 10° and 30° N west of 30° W.

Species	Atlantic		Caribbean		Gulf of Mexico	
	Number of Tows	Percent Tows	Number of Tows	Percent Tows	Number of Tows	Percent Tows
Acanthephyra acanthitelsonis	4	2.1	0	0	1	3.4
Acanthephyra brevirostris	3	1.6	0	0	1	3.4
Acanthephyra curtirostris	3	1.6	0	0	1	3.4
Acanthephyra kingsleyi	15	8.1	0	0	0	0
*Acanthephyra purpurea**	76	41.1	3	7.1	6	20.1
Acanthephyra stylorostratis	4	2.1	0	0	1	3.4
Meningodora miccyla	5	2.7	1	2.3	0	0
Meningodora mollis	10	5.4	0	0	0	0
Meningodora vesca	15	8.1	1	2.3	1	3.4
Notostomus elegans	5	2.7	0	0	0	0
Notostomus gibbosus	1	0.5	0	0	0	0
Janicella spinicauda	44	23.7	31	73.8	16	55.2
Oplophorus gracilirostris	17	9.2	25	59.5	12	41.4
Oplophorus spinosus	125	67.6	1	2.3	0	0
Systellaspis debilis	122	73.1	17	40.4	13	44.8
Stylopandalus richardi	83	44.9	5	11.9	19	65.5
Parapasiphae cristata	0	0	0	0	1	3.4
Pasiphaea hoplocerca	6	3.2	0	0	0	0
Pasiphaea merriami	3	1.6	1	2.3	5	17.2
Bentheogennema intermedia	1	0.5	0	0	1	3.4
Gennadas bouvieri	46	24.9	1	2.3	2	6.9
Gennadas capensis	48	25.9	1	2.3	2	6.9
Gennadas scutatus	41	22.9	10	23.8	3	10.3
Gennadas talismani	23	12.4	1	2.3	1	3.4
Gennadas tinayrei	39	21.1	1	2.3	0	0

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TABLE 10. (Continued)

Species	Atlantic		Caribbean		Gulf of Mexico	
	Number of Tows	Percent Tows	Number of Tows	Percent Tows	Number of Tows	Percent Tows
Gennadas valens	56	30.3	2	4.7	9	31.0
Funchalia villosa	34	18.4	26	61.9	12	41.4
Allosergestes pectinatus	143	77.3	34	81.0	26	89.7
Allosergestes sargassi	96	51.9	34	81.0	23	79.3
Deosergestes corniculum	16	8.6	0	0	7	24.1
Deosergestes henseni	47	25.4	13	30.9	10	34.4
Deosergestes paraseminudus	19	10.3	20	47.6	13	44.8
Neosergestes edwardsi	43	23.2	34	81.0	13	44.8
Parasergestes armatus	111	60.0	31	73.8	24	82.8
Parasergestes vigilax	127	68.6	20	47.6	16	38.1
Sergestes atlanticus	83	44.9	16	38.1	17	40.5
Sergestes cornutus	29	15.7	6	14.2	3	10.3
Sergia extenuata	2	1.0	0	0	0	0
Sergia grandis	45	24.3	3	7.1	3	10.3
Sergia japonica	1	0.5	1	2.3	0	0
Sergia laminata	15	8.1	0	0	0	0
Sergia regalis	18	9.7	5	11.9	6	20.1
Sergia splendens	109	58.9	23	54.8	25	86.2
Sergia talismani	6	3.2	25	59.5	15	51.7
Sergia wolffi	58	31.3	3	7.1	7	24.1
Number of Species	44		31		35	
Number of Tows	185		42		29	

* May include some *Acanthephyra pelagica* (see Pequegnat & Wicksten (2006))

Discussion

Geographical distributions illustrated in this study are only approximate. Material was collected in different months over several years thus obscuring seasonal and inter-annual variation, and the water column was not sampled in a systematic manner. Despite these limitations, patterns can be discerned both for individual taxa and in the pelagic decapod assemblage as a whole.

Pelagic decapod shrimp species within the same genus and within the *Sergia* species groups tended to be parapatric or partially sympatric in their Atlantic ranges. However, these genera and species groups are circumglobal in distribution, and a study restricted to a single ocean cannot resolve issues of geographic patterns among closely related species when nearest relatives may inhabit different oceans. Among the sergestids, the taxonomy and distribution of only *Sergia* (Vereshchaka 2000) and *Neosergestes*, termed the *Sergestes* "edwardsi" species group by Judkins (1978) and elevated to genus by Judkins & Kensley (2008), have been studied on a global scale, and the distributions of other genera have not been described previously even within a single ocean. Closely related species within *Sergia* and *Neosergestes* and within well studied genera of planktonic calanoid copepods (Frost and Fleminger 1968, Fleminger 1973, Fleminger & Hulsemann 1974) and meso- and bathypelagic fishes (Ebeling 1962, Ebeling & Weed 1963, Gibbs 1969, Baird 1971, Johnson 1974, Pietsch 2009) tend to be allopatric. These studies support the idea that the prevailing mode of speciation in sexually reproducing animals begins with genetic divergence of spatially separated stocks (Mayr 1970). A possible counterpoint to this view is the co-occurrence, both in the Atlantic and Pacific, of *Sergestes atlanticus* and *S. cornutus, Allosergestes sargassi* and *A.*

pectinatus and *Parasergestes armatus* and *P. vigilax* (Walters 1976, Griffiths & Brandt 1983a, 1983b). *Allosergestes* and *Parasergestes* each contain several described species, and in neither case do the co-occurring species in the Atlantic appear to be closely related. *Sergestes atlanticus* and *S. cornutus*, the only described species in the genus, differ significantly in the structure of their internal bioluminescent organs (Foxton 1972b). None of these genera have been subjected to adequate taxonomic analysis, and examination of collections throughout their ranges is likely to separate additional species, including geographically distinct siblings of the currently recognized species. In recent years genetic analysis increasingly has been used in population studies, and this powerful tool has been employed to distinguish morphologically similar species and geographic sub-populations of zooplankton species (Goetze 2005, 2011, Goetze & Bradford-Grieve 2005). Molecular genetics also have provided insight into the evolution of the deep-sea fish genus *Cyclothone* (Miya & Nishida 1996).

It is well established that the geographic ranges of epipelagic zooplankton species in the world's oceans are influenced by surface current systems and water masses (McGowan 1974, Reid *et al.* 1978, Haedrich & Judkins 1979). The subtropical central water masses of the North and South Atlantic are enclosed within gyres consisting of a poleward flowing warm current along the western margin, an eastward ocean drift at temperate latitudes, an equatorward flowing cool current on the eastern margin and a westward flowing equatorial current (Fig. 12). Circulation to the north is more complicated with the cold water of the Labrador and East Greenland currents flowing south to meet the Gulf Stream and its northward extensions, the West Greenland and Norwegian currents.

The distribution of pelagic species is strongly influenced by the northeastward flow of the Gulf Stream, and the zone of transition between warm- and cold-water faunas to its north. All species of the Central recurrent group occurred in tows across the Atlantic between 40º and 50º N, with some declining but others increasing in frequency from west to east. Species of the Subpolar-Temperate recurrent group also were frequently encountered, and *Eusergestes arcticus* was the overall dominant species at those latitudes (Table 11). The presence of cold water species, such as *Eusergestes arcticus*, in slope water at mid-latitudes off North America can be attributed to the influence of the Labrador Current (Townsend *et al*. 2006). A feature of the western Sargasso Sea is the occurrence of rings of Gulf Stream water surrounding cores of cold slope water (The Ring Group 1981). Subarctic species trapped in the cold cores are likely lost to their parent populations as the core decays.

Patterns in oceanic species diversity parallel those found in the terrestrial environment. Relatively few species inhabit the seasonally very productive subpolar regions as opposed to the large number found in subtropical and tropical waters. Species diversity is highest within the oligotrophic subtropical central gyres. The relatively productive waters of the westward flowing equatorial currents contain somewhat fewer species, and these often are restricted to either the eastern or western portions of those systems. The distribution of mesopelagic decapod shrimp in the Atlantic corresponds to these patterns, as would be expected from organisms whose early life stages are mostly epiplanktonic (Omori 1974, Omori & Gluck 1979, Criales & McGowan 1993, Fernandes *et al*. 2007) and thus responsive to oceanic circulation and water mass properties.

In laboratory rearing studies, Omori (1971, 1979) determined that growth and survival of larvae in the sergestids *Sergia lucens* and *Eusergestes similis* are highly sensitive to temperature. This suggests that temperature is a major factor in limiting the geographic ranges of pelagic decapod shrimp having epiplanktonic larvae. The influence of temperature on adults is less clear. Adult shrimp encounter wide temperature ranges during their extensive diel vertical migrations, and Donaldson (1975) found that neither the seasonal nor permanent thermoclines affected the migratory range of decapod shrimp species near Bermuda. WHOI bathythermograph data showed that most species experienced a wide temperature range, even at tow depths within the upper 200 m (Table 12). Some temperature sensitivity is expected, and Foxton (1972a) found that the vertical range of *Acanthephyra* species varied with geographical gradients in temperature.

The Subpolar-Temperate species *Acanthephyra pelagica, Eusergestes arcticus* and *Gennadas elegans* were prominent in the northern Gulf Stream and its poleward extensions, but they also frequently were captured in the Mediterranean and in the Mauritanian Upwelling Zone. The upper north Atlantic and Mauritanian Upwelling Zone are areas of seasonally high primary production, but production levels in the Mediterranean are only moderate in comparison (Estrada 1996). *Gennadas elegans* is restricted to the North Atlantic, but *E. arcticus* and *A. pelagica* have disjunct circumpolar populations in the southern hemisphere. The only other species in the genus *Eusergestes, E. similis*, is restricted to the subpolar-temperate North Pacific. This pattern is very similar to that of the euphausiid pair *Nematocelis difficilis*, which is restricted to the North pacific, and *N. megalops* that has disjunct North Atlantic and circumglobal southern hemisphere populations (Gopalakrishnan 1974).

TABLE 11. Pelagic decapod shrimp species in WHOI IKMT tows from the northwest and northeast Atlantic between 40º and 50º N.

	West of 45° W		East of 45° W	
Species	Number of Tows	Percent of Tows	Number of Tows	Percent of Tows
Acanthephyra pelagica	6	14.0	15	24.6
Acanthephyra purpurea	8	18.6	17	27.9
Ephyrina bifida	0	0	1	1.6
Hymenodora glacialis	0	0	1	1.6
Meningodora miccyla	1	2.3	0	0
Meningodora vesca	2	4.7	2	3.3
Janicella spinicauda	3	7.0	0	0
Oplophorus spinosus	8	18.6	4	6.6
Systellaspis debilis	7	16.3	22	36.1
Stylopandalus richardi	12	27.9	10	16.4
Parapasiphae sulcatifrons	3	7.0	6	0
Pasiphaea merriami	1	2.3	0	0
Pasiphaea multidentata	4	9.3	7	11.5
Pasiphaea sivado	0	0	3	3.3
Pasiphaea tarda	9	20.9	0	0
Gennadas bouvieri	1	2.3	0	0
Gennadas capensis	1	2.3	0	0
Gennadas elegans	11	25.6	19	31.4
Gennadas scutatus	3	7.0	0	0
Gennadas tinayrei	3	7.0	15	24.6
Gennadas valens	5	11.6	15	24.6
Funchalia villosa	6	14.0	5	8.3
Allosergestes pectinatus	23	53.4	12	19.7
Allosergestes sargassi	15	34.9	24	39.3
Deosergestes corniculum	3	7.0	5	8.2
Deosergestes henseni	1	2.3	0	0
Deosergestes paraseminudus	3	7.0	0	0
Eusergestes arcticus	22	51.2	58	95.1
Neosergestes edwardsi	15	34.9	3	3.3
Parasergestes armatus	19	44.2	1	1.6
Parasergestes vigilax	18	41.9	16	26.2
Sergestes atlanticus	18	41.9	6	9.8
Sergestes cornutus	5	11.6	1	1.6
Sergia japonica	1	2.3	2	3.3
Sergia robusta	7	16.3	21	34.4
Sergia splendens	18	41.9	9	14.8
Sergia talismani	4	9.3	0	0
Number of species	34		27	
Number of tows	43		61	

TABLE 12. Temperatures (°C) encountered by pelagic decapod shrimp in the horizontal portion of nighttime WHOI IKMT tows in the upper 200 m.

Species	Minimum	Maximum	Average
Acanthephyra acanthitelsonis	10.0	13.1	12.0
Acanthephyra kingsleyi	10.0	22.0	14.5
Acanthephyra pelagica	9.7	22.5	14.8
Acanthephyra purpurea	8.6	25.4	14.9
Acanthephyra quadrispinosa	13.4	20.0	16.3
Notostomus auriculatus	23.5	25.2	24.4
Notostomus elegans	15.5	16.7	16.1
Janicella spinicauda	18.0	27.8	22.9
Oplophorus gracilirostris	14.5	27.0	22.3
Oplophorus novaezeelandiae	12.5	19.2	15.9
Oplophorus spinosus	10.0	27.0	18.5
Systellaspis debilis	5.8	22.2	16.8
Stylopandalus richardi	7.0	15.6	18.1
Eupasiphae gilesi	16.5	16.6	16.6
Parapasiphae sulcatifrons	10.7	10.8	10.8
Pasiphaea hoplocerca	12.9	16.1	14.4
Pasiphaea merriami	20.5	24.3	22.4
Pasiphaea multidentata	9.3	16.5	13.5
Pasiphaea sivado	13.6	19.2	15.9
Gennadas bouvieri	16.1	17.3	16.7
Gennadas brevirostris	12.0	19.2	15.1
Gennadas capensis	15.2	15.4	15.3
Gennadas elegans	4.1	15.6	14.7
Gennadas gilchristi	16.0	18.9	17.6
Gennadas incertus	13.4	16.1	14.8
Gennadas propinquus	13.4	16.1	14.8
Gennadas scutatus	10.0	26.0	17.7
Gennadas talismani	10.0	23.9	16.0
Gennadas tinayrei	6.3	15.6	16.5
Gennadas valens	9.7	25.5	15.4
Funchalia villosa	13.8	27.8	19.3
Funchalia woodwardi	13.4	19.6	16.8
Pelagopenaeus balboae	16.5	22.2	19.2
Allosergestes pectinatus	6.1	15.6	19.3
Allosergestes sargassi	12.0	22.2	17.7
Deosergestes corniculum	13.3	22.2	15.9
Deosergestes disjunctus	13.3	17.5	15.7
Deosergestes henseni	10.0	28.0	17.0
Deosergestes paraseminudus	10.0	27.8	20.9
Deosergestes pediformis	12.0	22.4	15.6
Eusergestes arcticus	2.8	15.6	14.1

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TABLE 12. (Continued)

Species	Minimum	Maximum	Average
Neosergestes edwardsi	10.0	27.8	20.1
Neosergestes orientalis	13.4	18.1	15.5
Parasergestes armatus	5.8	23.9	20.1
Parasergestes diapontius	12.0	24.0	17.0
Parasergestes vigilax	6.1	23.9	19.3
Petalidium foliaceum	14.1	14.9	14.5
Sergestes atlanticus	5.8	23.9	19.4
Sergestes cornutus	13.8	26.0	21.4
Sergia burukovskii	12.5	16.7	14.8
Sergia extenuata	13.4	20.7	16.0
Sergia grandis	12.0	23.2	17.9
Sergia japonica	16.4	16.5	16.5
Sergia laminata	10.0	22.0	15.7
Sergia manningorum	12.0	18.5	15.2
Sergia potens	13.4	14.8	14.1
Sergia prehensilis	13.4	20.0	16.7
Sergia regalis	10.0	20.6	16.0
Sergia robusta	9.7	19.6	15.0
Sergia scintillans	18.2	19.0	18.6
Sergia splendens	6.1	12.0	19.7
Sergia talismani	12.2	27.8	20.2
Sergia tenuiremis	14.3	14.5	14.4
Sergia wolffi	13.5	27.4	19.6

Near bottom concentrations of *E. arcticus* and *G. elegans* have been reported in the Mediterranean (Cartes *et al.* 1994). This simply may be the result of Mediterranean bottom depths being shallower than the normal vertical range of these presumably holopelagic species. However, Hargreaves (1999) reported daytime near-bottom populations of *E. arcticus* in the Porcupine Seabight of the northeastern-Atlantic Ocean, suggesting that near-bottom occurrences may not be accidental.

The group of decapod shrimp species endemic to the eastern tropical Atlantic has a parallel in the eastern tropical Pacific, where there also are several endemic species, including sergestids (Judkins 1978, Vereshchaka 2000) and euphausiids (Brinton 1962). Eastern tropical regions in both oceans are characterized by closed circuits of circulation and by strong upwelling of cool, nutrient rich deep water to the surface with resulting high production at all trophic levels (Brinton 1979, Le Borgne 1982, Fernández-Álamo & Färber-Lorda 2006, Pennington *et a*l. 2006, Piontkovski *et al*. 2006). Sinking of decaying material produces intense oxygen-minimum zones located relatively near the surface and extending into the vertical range of euphausiids and shrimp (Karstensen *et al*. 2008).

In addition to an east equatorial euphausiid assemblage, Brinton (1962) identified trans-equatorial and west equatorial groups, similar to the broadly tropical and western tropical Atlantic decapod shrimp groups found in this study. Although most subtropical decapod shrimp species also occurred in equatorial waters, the distributions of *Gennadas tinayrei*, *G. valens* and *Janicella spinicauda* were anti-tropical. This pattern is also seen in Atlantic and Pacific populations of the euphausiid *Euphausia brevis* (Brinton 1975).

Most species inhabiting the central waters of the north and south Atlantic also occur throughout subtropical regions of the Indo-Pacific, a pattern seen in other taxa, including euphausiids (Brinton 1962, 1975) and calanoid copepods (Frost & Fleminger 1968, Fleminger 1973, Fleminger & Hulsemann 1973, 1974). The possibility that some circumglobal forms may consist of multiple sibling species has been noted. In fact, genetic analysis accompanied by detailed morphological inspection revealed that the previously accepted circumglobal calanoid species *Eucalanus hyalinus* consists of two sister species*, E. hyalinus* and *E. spinifer.* The sister species are sympatric throughout much of their circumglobal ranges, but with *E. spinifer* dominating oligotrophic waters of the subtropical gyres and *E. hyalinus* more abundant along central water mass boundaries and in frontal zones and upwelling systems (Goetze 2005, Goetze & Bradford-Grieve 2005). In a subsequent study of the calanoid *Pleuromamma xiphias,* Goetze (2011) observed strong genetic breaks across known oceanographic fronts or current systems in all three ocean basins. However, Goetze did not elevate any of these populations to species.

Studies have found that pelagic decapod shrimp species feed on a wide variety of living prey and to varying degrees on detritus (Judkins & Fleminger 1968, Foxton & Roe 1974, Donaldson 1975, Walters 1976, Heffernan & Hopkins 1981, Flock & Hopkins 1992, Karuppasamy & Menon 2004). They are a major predatory group among the micronekton and likely play an important role in the dynamics of prey zooplankton populations. The diet of larger species included chaetognaths, fish, euphausiids, and decapod shrimp, but the dominant prey of most species in the aforementioned studies was small crustaceans, especially calanoid copepods (Foxton & Roe 1974, Donaldson 1975, Karuppasamy & Menon 2004). Flock & Hopkins (1992) reported that *Parasergestes armatus*, *P. vigilax* and *Neosergestes edwardsi* also fed to a lesser degree on ostracods, and the enlarged third maxillipeds in those genera (Judkins & Kensley 2008) may be a specialization for that prey.

Comparisons of vertical distributions and diets suggest resource partitioning among sergestids (Donaldson 1974, Flock & Hopkins 1992). However, several species may be in close proximity within the epipelagic zone at night, and overlap in diet found in the aforementioned studies suggests the existence of interspecific competition. The nature and degree of competition is speculative, with imagined scenarios ranging from multi-species aggregations similar to avian feeding guilds to spatially segregated single-species swarms. In an analysis of midwater shrimp and fishes, the two dominant groups in low-latitude micronekton communities, Hopkins & Sutton (1998) concluded that competition for limited resources exists and provided evidence of resource partitioning between multi-species groups. They considered this competition to be "diffuse", a term coined by MacArthur (1972) to describe a situation where each species is impacted by many other species sharing the environment. However, midwater tows are usually one or more kilometers in length and thus are not useful in investigating distribution at a scale where interactions between individuals might occur. Videography from tethered or free devices may be useful in investigating behavior within closely spaced micronektonic aggregations. Omori & Ohta (1981) used a film camera to study the vertical distribution and swimming behavior of the commercially harvested benthopelagic species *Sergia lucens* in Suruga Bay, Japan. The maximum concentration observed was 6 individuals/m^3, but much lower concentrations would be expected in oceanic waters.

Backus *et al.* (1977) recognized nine distributional patterns among 82 species of the teleost fish family Myctophidae collected in the same midwater-trawl tows as the decapod shrimp of this study: Subpolar-temperate, Temperate, Temperate-semisubtropical, Subtropical, Tropical-subtropical, Tropical-semisubtropical, Tropical, Mauritanian Upwelling and Eastern. This a larger number than the five shrimp recurrent groups identified in this study. The Central shrimp group encompasses the boundaries of the Temperate-semisubtropical, Subtropical, Tropical-subtropical, and Tropical-semisubtropical myctophid patterns. The bipolar, anti-tropical distributions of *Gennadas tinayrei* (Fig. 5), *G. valens* (Fig. 6) and *Funchalia villosa* (Fig. 6) correspond to the Subtropical pattern, but the range of no other shrimp species shows close similarity to any myctophid group. Among the shrimp, there is no Temperate group distinct from the Subpolar-Temperate group. The Mauritanian Upwelling myctophid pattern falls within the more broadly distributed Eastern Tropical shrimp group. No pattern among the myctophids corresponds to the Western Tropical shrimp group. Myctophid patterns were identified by visual comparison of distributional maps as opposed to the GMPJO algorithm used in this study, and that may partially account for the apparent dissimilarity between patterns in the two taxa. However, shrimp species within the Central recurrent group do appear to be more broadly distributed than myctophid species in the warm temperate, subtropical and tropical waters of the Atlantic. The number of North Atlantic myctophids, all within a single family (Nafpaktitis *et al*. 1977), is comparable to that of the entire Atlantic shrimp assemblage, with its 91 species from seven families and the two major suborders of decapod crustaceans. The myctophids have responded to environmental variables in a manner that resulted in a higher degree of speciation. In a study of species richness of the deep-benthic fauna of the northern Gulf of Mexico Haedrich *et al*. (2008) concluded that different mixes of environmental factors have applied to different phylogenetic groups and that each taxonomic group's diversity needs to be examined individually.

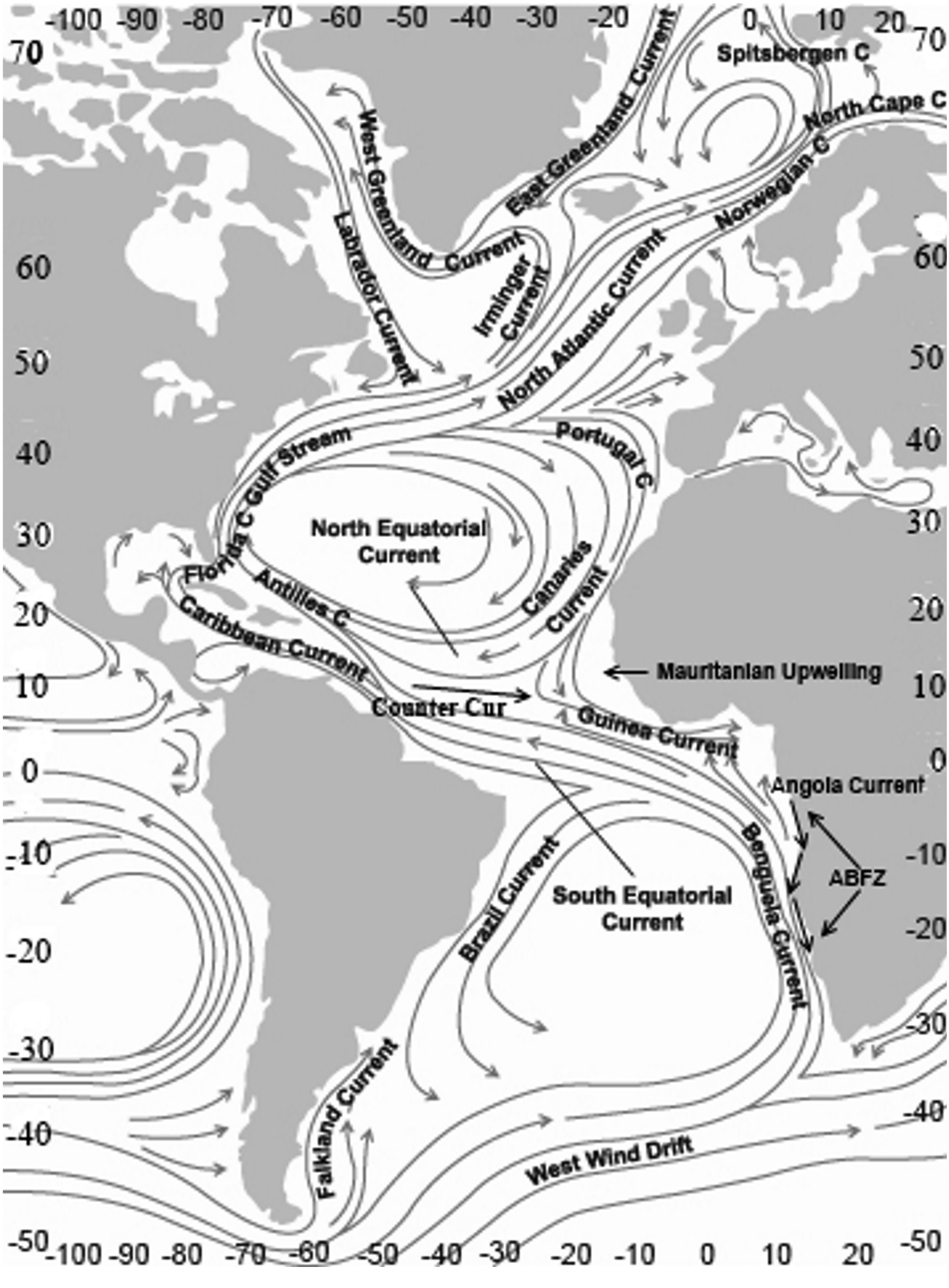

FIGURE 12. Atlantic Ocean surface currrents (adapted from Bartholomew 1957). ABFZ = Angola-Benguela Frontal Zone.

Patterns in geographical distribution associated with circulation, temperature, nutrient levels and primary production are repeated across many pelagic taxa. However, a high degree of variability within faunal groups also is apparent, and the uniqueness of each species range must be recognized. Only 31 of 91 pelagic shrimp species in the Atlantic could be assigned to geographic groups using the criteria of this study. In no case was there more than partial congruity between species. This suggests that co-occurring species have evolved independently to similar combinations of physical climate and general food availability and not to each other. Species that share core ranges, which can be very extensive, differ strongly in the degree to which they extend across the gradients that eventually restrict all of them. In a study of mesopelagic fish assemblages in the northwest Atlantic McKelvie (1985) concluded that individual species may respond to environmental gradients but faunal groups do not. In McKelvie's opinion it is probably fruitless to continue searching for recurrent groups. This indicates the need for study at the species level, and the limitations of generalization across taxa. The major reason to continue studies of geographical distribution is their importance to ecological and evolutionary research. Geographical distributional studies identify habitats, and this information is necessary for research into the physiological, reproductive and behavioral adaptations of species to their environment. Distributional information is the core of biogeographical research and is necessary for interpretation of speciation within phylogenetic groups. Studies combining genetic analysis with precise morphological examination may reveal that pelagic species described with broad ranges may consist actually of multiple sibling species that inhabit distinct hydrographic regions of the global ocean.

More than forty years have passed since the last trawl tow in this study was made, and during that interval there has been an increase in average global sea surface temperature (Environmental Protection Agency 2012) with expectation that it will continue to increase. Have the Atlantic ranges of pelagic decapod shrimp and other micronekton changed in response to warming? Unfortunately, a study on the scale of the WHOI program is unlikely to be repeated, and that question likely will not be satisfactorily answered.

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