Unexpected low genetic differentiation between Japan and Bering Sea populations of a deep-sea benthic crustacean lacking a planktonic larval stage (Peracarida: Tanaidacea)

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Short running title: low genetic differentiation of a deep-sea tanaidacean

Information on the extent, diversity, and connectivity of populations is lacking for most deep-sea invertebrates. Species in the order Tanaidacea, one of the most diverse and abundant macrofaunal groups in the deep sea, are benthic, lack a planktonic larval stage, and thus would be expected to have narrow distributional ranges. But here we show that, with molecular evidence from the COI gene, the deep-sea tanaidacean *Carpoapseudes spinigena* has a distributional range spanning at least 3700 km, from off northern Japan to the southeastern Bering Sea. Living individuals found in a sediment core indicated that the species is a sedentary burrower. COI analyses revealed a low level of genetic diversity overall for *C. spinigena*, and low differentiation (*p*-distance, 0.2–0.8%) between the Japan and Bering Sea populations. One hypothesis to explain the low genetic diversity over a broad region is the Japan population was founded by individuals transported by ocean currents from the Bering Sea; however, due limited data, other explanations cannot be ruled out. Our results underscore that continued sampling is of fundamental importance to understanding how genetic and taxonomic diversity originate and are maintained in the deep sea.

ADDITIONAL KEYWORDS: COX1 - Crustacea - direct development - Malacostraca - Pacific - phylogeography - population genetics.

INTRODUCTION

Sea bottoms deeper than 200 m occupy about 70% of the Earth's surface, yet the population genetic data necessary to understand the extent, diversity, and connectivity of deep-sea invertebrate populations have been very limited (Taylor & Roterman, 2017). Population genetic studies are now appearing for various groups (e.g. Boavida *et al.*, 2019; Janssen *et al.*, 2019; Cheng *et al.*, 2020; Guggolz *et al.*, in press). As with shallow-water species, dispersal of planktonic larvae by ocean currents is probably the main factor maintaining connectivity between populations of most deep-sea invertebrates (e.g. Yahagi *et al.*, 2017; Kobayashi *et al.*, 2018). However, the migration of adults in species with high swimming capability (e.g. Winkelmann *et al.*, 2013) and the transport of epibenthic adults by bottom currents (e.g. Braby *et al.*, 2009; Hamel *et al.*, 2019) could also enable gene flow between populations. Dispersal barriers proposed for deep-sea animals include strong currents crossing between populations, low-oxygen zones, topographical factors (e.g. shallow straits, mid-ocean ridges, depth differences), and long distances between patches of suitable habitat (McClain & Hardy, 2010).

The superorder Peracarida is the most speciose crustacean group with ca. 17000 described species (Appeltans *et al.*, 2012) and is well represented in the deep sea (e.g. Grassle & Maciolek, 1992). Although peracarids show diverse modes of living, such as benthic, planktonic (including symbionts on gelatinous plankton), and parasitic (Ohtsuka *et al.*, 2009; Kakui, 2016; Castellani *et al.*, 2017; Smit *et al.*, 2019), peracarids generally lack a primary planktonic larval stage but instead undergo direct development, although parasitic species tend to have highly mobile stages (Smit *et al.*, 2019). The innate dispersal capability of peracarids thus depends largely on their mode of living, and sedentary, benthic species are expected to have low dispersal capability.

Some deep-sea benthic peracarids show restricted distributions (Riehl & De Smet, 2020), but others have much broader distributions (Brandt *et al.*, 2012) than expected from their mode of living; in some cases, conspecificity has been confirmed by molecular phylogeographic studies based on mitochondrial gene markers, i.e., cytochrome *c* oxidase subunit I (COI), 12S rRNA, and/or 16S rRNA genes (e.g. Brix *et al.*, 2011; Riehl & Kaiser, 2012; Riehl *et al.*, 2018). Riehl & Kaiser (2012) discussed the importance of bottom currents and other erosion-deposition events on continental shelves as factors allowing deep-sea infaunal peracarids to achieve broad distributions.

The peracarid order Tanaidacea contains about 1500 described species worldwide (Anderson, 2020), most of which are small (up to a few millimeters long) and are free living in benthic habitats (Kakui, 2016). Tanaidaceans comprise one of the most diverse and abundant macrofaunal groups in the deep sea (Larsen *et al.*, 2015), but little is known of their biology there, and no previous study has examined their population structure in that

environment.

Carpoapseudes spinigena Bamber, 2007, a member of the relatively rare, deep-sea tanaidacean genus *Carpoapseudes* Lang, 1968 (Apseudoidea: Apseudidae), has not been reported since its original description which was based on fixed specimens collected from a single site in the Pacific Ocean off northern Japan (Fig. 1; 974–965 m depth; Bamber, 2007). During research cruises in 2007 and 2017, we collected *C. spingena* from two localities several thousand kilometers apart, one being the type locality around northern Japan (1028–1075 m depth) and the other located in the southeastern Bering Sea (1536–1569 m depth). In addition, we observed the behavior of living *C. spinigena* trapped in a core sampler, and examined the morphology of juvenile individuals at stage of release from the maternal brood pouch. Here we show the genetic relationship between these two *C. spinigena* populations based on partial COI gene sequences, describe the mode of living of this species, and discuss the wide distribution of *C. spinigena*.

MATERIAL AND METHODS

Tanaidaceans were collected with a beam trawl having a 3 m opening, a dredge installed on a Deep Tow Camera System, and a multiple corer during research cruises of the research vessel (R/V) *Tansei-maru* and R/V *Mirai* (Japan Agency for Marine-Earth Science and Technology, JAMSTEC) (Table 1), near the type locality in northern Japan and in the eastern Aleutian Islands, USA, respectively (Fig. 1). Specimens from the two Bering Sea sites were regarded as samples from a single population, because the two sites were only ca. 1.2 km apart, shorter than the distance between net-in and net-out (ca. 2.7 km) of the beam trawl at station KT-07-29-K1 in northern Japan. Living individuals collected with the multiple corer, and some fresh specimens collected during the R/V *Mirai* cruise, were photographed before fixation. Whole bodies or dissected parts of specimens were fixed in 80% ethanol, and later transferred to 99% ethanol for preservation. See Supporting Information S1 for additional details.

Morphological terminology follows Larsen (2003). The identification of specimens was based on Bamber (2007) and Hansknecht & Santos (2008). Female tanaidaceans have a marsupium (brood pouch) for brooding eggs (cf. Kakui *et al.*, 2017) and release juveniles at the “manca II” stage directly from the marsupium (Larsen, 2003); manca II individuals resemble adults, but are unisex and lack pereopod 6 (6th walking leg) and pleopods (abdominal legs used for ventilating the burrow or for swimming). Male apseudoid tanaidaceans have a genital cone whereas females lack it. Specimens were identified to stage (manca II, female, or male) under a Nikon SMZ1500 stereomicroscope, and deposited with JAMSTEC (JAMSTEC nos. 1170055975, 1170055978, 1170055979, 1170055985,

1170055986) and in the Invertebrate Collection of the Hokkaido University Museum (ICHUM), Sapporo (ICHUM-6092–6112).

Total DNA was extracted from the cheliped or whole body of adults, and from an embryo collected from a marsupium, by using a NucleoSpin Tissue XS Kit (TaKaRa Bio, Japan); after extraction, each exoskeleton was recovered and preserved in 80% ethanol. Part of the COI gene was amplified by PCR using primers LCO-1490 and HCO-2198 (Folmer *et al.*, 1994). PCR amplification conditions with TaKaRa Ex Taq DNA polymerase (TaKaRa Bio) were 94°C for 1 min; 35 cycles of 98°C for 10 sec, 42 or 50°C for 30 sec, and 72°C for 50 sec; and 72°C for 2 min. Nucleotide sequences were determined by direct sequencing with a BigDye Terminator Kit ver. 3.1 and a 3730 Genetic Analyzer (Life Technologies, USA). Sequences (658 nt, encoding 219 amino acids) were aligned by using MEGA7 (Kumar *et al.*, 2016) (the dataset contained no indels), and *p*-distances among sequences were calculated with MEGA7. All sequences we determined were deposited in the International Nucleotide Sequence Database (INSD) through the DNA Data Bank of Japan (DDBJ), under accession numbers LC545527–545558.

An integer neighbor-joining (IntNJ) network (Leigh & Bryant, 2015) for the COI sequences was constructed with PopART v. 1.7 (Leigh & Bryant, 2015) at 0.50 reticulation tolerance. Haplotype diversity (h) and nucleotide diversity (π) were calculated with DnaSP v. 6.12.03 (Rozas *et al.*, 2017). Tajima's D (Tajima, 1989), Fu's F_S (Fu, 1997), and Φ_{ST} were calculated with Arlequin v. 3.5.2.2 (Excoffier & Lischer, 2010).

RESULTS

Male and female *C. spinigena* were similar in general body shape and had narrow, rod-shaped pleopods; manca II specimens were generally similar to males and females but lacked pleopods (Fig. 2A–F, f1). In one core from the multiple corer, we found three living individuals on the sediment surface, each of which was positioned at the entrance to a burrow, with the posterior part of the body in the burrow (Fig. 2G; also see Kakui, 2020a).

We identified 10 COI haplotypes (H1–10) among 32 *C. spinigena* individuals (21 from Japan and 11 from the Bering Sea). The aligned sequences (658 nt) contained 10 polymorphic sites (Table 2) involving only synonymous substitutions. In the IntNJ network (Fig. 3), haplotypes H1–4 from the Japan population and H5–10 from the Bering Sea population formed separate groups; the two populations shared no haplotypes. Eighteen of the 21 sequences from Japan were H4. The most common haplotypes in the Bering Sea population were H5 (three individuals) and H7 (four individuals). The most nucleotide substitutions observed in pairwise comparisons among haplotypes was five (H1, H2, H3 vs. H10), corresponding to a *p*-distance of 0.8%. The fewest nucleotide substitutions between

haplotypes from the two populations was one (H4 vs. H5).

Overall *h* for *C. spinigena* was moderately high (0.673) but π was low (0.0020) (Table 2). In the Japan population, both *h* and π values were low (0.271 and 0.0004, respectively); in the Bering Sea population, *h* was high (0.836) but π was low (0.0022). Tajima's *D* value for the Japan population was a significant, negative value (–1.727; $p = 0.024$), whereas other values were not significant. Fu's F_S values for *C. spinigena* overall and for both populations were significant ($p < 0.02$; Holsinger, 2017), negative values (Table 2). Φ_{ST} between Japan and Bering Sea populations was significant and high (0.6797; $p < 0.001$).

DISCUSSION

Low dispersal capability of *Carpoapseudes spinigena*

The life cycle, morphology, and mode of living of *Carpoapseudes spinigena* indicate that its native dispersal capability is quite low. As a tanaidacean (cf. Kakui *et al*., 2017), the species lacks planktonic larval stages, and females directly release manca II individuals from their marsupium. In both males and females, as described by Bamber (2007), the pleopods are narrow and rod-shaped, rather than wide and leaf-shaped (cf. Shiino, 1966: fig. 7G), indicating that both sexes have poor swimming ability. Manca II individuals are similar in body shape to males and females but lack pleopods. None of the developmental stages we observed show apparent swimming adaptations such as the enormously long or paddle-shaped pereopods known in deep-sea swimming isopods (Marshall & Diebel, 1995). Our multiple corer sample showed that *C. spinigena* lives as a burrower (Fig. 2G). All of these observations indicate that *C. spinigena* individuals are likely sedentary throughout their life.

Genetic diversity in *C. spinigena* overall and in two populations

Our phylogeographic analysis of the COI sequences revealed low genetic diversity in *C. spinigena*. The maximum *p*-distance of 0.8% that we detected among 32 *C. spinigena* sequences from two populations ca. 3700 km apart is much lower than that observed within a single population in a shallow-water apseudoid species, *Mesokalliapseudes macsweenyi* (Drumm, 2003) (ca. 3% *p*-distance; Drumm & Kreiser, 2012). The moderately high *h* (0.673) and low π (0.0020) and significantly negative Fu's F_S values suggest that the overall population we sampled underwent a population reduction followed by rapid population growth and accumulation of mutations (Grant & Bowen, 1998). The Japan and Bering Sea populations shared no haplotypes, and the Φ_{ST} value between the two populations was significant and high, indicating low connectivity between the two populations.

The Japan and Bering Sea populations appear to have different histories. The two

clusters in our haplotype network are separated by one nucleotide substitution. The Japan cluster shows a star-like pattern, with haplotype H4 comprising 18 of 21 sequences (86%) and three haplotypes each connected to H4 by one mutational step (Fig. 3). Both the *h* and π values were low (0.271 and 0.0004, respectively), and Tajima's *D* and Fu's F_S values were significant and negative, indicating that the Japan population underwent a recent population bottleneck or was established by a founder event (Grant & Bowen, 1998). The Bering Sea cluster was more branched and more diverse, with high *h* (0.836), low π (0.0022), and a significant, negative Fu's F_S value. These indices indicate that the Bering Sea population underwent a past reduction in size followed by expansion, but may have been affected by small sample size (n = 11).

How did *C. spinigena* become widely distributed?

The low genetic distance between the two widely separate populations we examined is difficult to reconcile with the low innate dispersal capability expected for a small, deep-sea fossorial crustacean lacking planktonic larval stages. One possible explanation is that the Japan population originated through a founder from the Bering Sea population via transport by deep ocean currents, a mechanism that Riehl & Kaiser (2012) suggested for dispersal by deep-sea macrostylid isopods. In our study area, bottom currents at the depths where we found *C. spinigena* (1000–1500 m) are complex and have been minimally investigated, but do occur along the Aleutian Ridge (flowing eastward) and Bering Sea Slope (flowing northwestward) (Kinder *et al.*, 1975; Roden, 1995); additionally, a southward flow dominated by the East Kamchatka Current occurs at depths of 1500 m or shallower on the western side of the Kamchatka Strait (Stabeno *et al.*, 1999; the maximum depth of the strait is 4420 m), and a southwestward flow of the Oyashio Current has been observed at the depths of 1000 m or shallower off the eastern coast of northern Japan (Uehara & Miyake, 1999) (Fig. 1).

A pattern similar to our COI haplotype network, where the Bering Sea cluster is more branched and more diverse than the Japan cluster, was observed in the crangonid shrimp *Argis lar* (Owen, 1839) (Fujita *et al*., 2017). In that species, however, more nucleotide substitutions (six or 14 substitutions in 571 nt) were detected between a Bering cluster (Lineage C) and Japan clusters (Lineages A and B), indicating older divergences in *A. lar* than in *C. spinigena* and that the two species have different evolutionary histories. *Argis lar* differs from *C. spinigena* in having a relatively short (15–20 days at 5°C; Nakano, 1993) pelagic larval phase in its life cycle and in inhabiting shallower depths (10–350 m; Komai & Komatsu, 2009), both of which would increase the feasibility of dispersal by surface currents.

Other hypotheses than a single long-distance dispersal event are possible to account for the low genetic diversity of *C. spinigena* between the southeastern Bering Sea and northern Japan. The haplotype pattern and diversity values apparently indicating a founder event for the population in northern Japan could also have resulted from a local bottleneck.

Furthermore, it is unknown whether *C. spinigena* is continuously distributed in the relevant depth interval between northern Japan and the southeastern Bering Sea. A continuous distribution along the Kurile Islands, eastern Kamchatka, Aleutian Basin, and Aleutian archipelago could have been achieved by relatively rapid but stepwise dispersal mediated by deep-sea currents, or by slower, stepwise range expansion. Even poorly dispersing bottom dwellers can expand their range gradually by local currents (e.g. Martel & Chia, 1991; Norkko *et al*., 2001). Finally, even if a founder population of *C. spinigena* was established in northern Japan by long-distance dispersal, the source population could have been closer than the Bering Sea, i.e., the Kuriles or Kamchatka. Data from across the putatively broad range of *C. spinigena* are necessary to determine the most likely among these various possibilities.

It is unknown whether other deep-sea tanaidaceans show similarly wide distributions. Species in *Protanais*, one of the main indicators of successional stages in deep-sea wood-fall communities (McClain & Barry, 2014), may show narrower distributions restricted to areas where sunken wood is abundant. Species in some groups producing males adapted for swimming (natatory males; Błażewicz-Paszkowycz *et al*., 2014) possibly show wider distributions and more connectivity among populations.

The main results of our study are 1) that the deep-sea tanaidacean species *Carpoapseudes spinigena* is a burrower, which together with the lack of swimming appendages and a larval phase, indicate poor dispersal capability, and 2) that two populations thousands of kilometers apart show remarkably low genetic divergence. Explaining these incongruent results is of fundamental importance to understanding how genetic and taxonomic diversity originate and are maintained in the deep sea, and our results underscore the need for continued sampling in this environment.

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SUPPORTING INFORMATION

Supporting information S1. Details on sampling, sorting, and sample fixation.

446 **Figure legends**

447

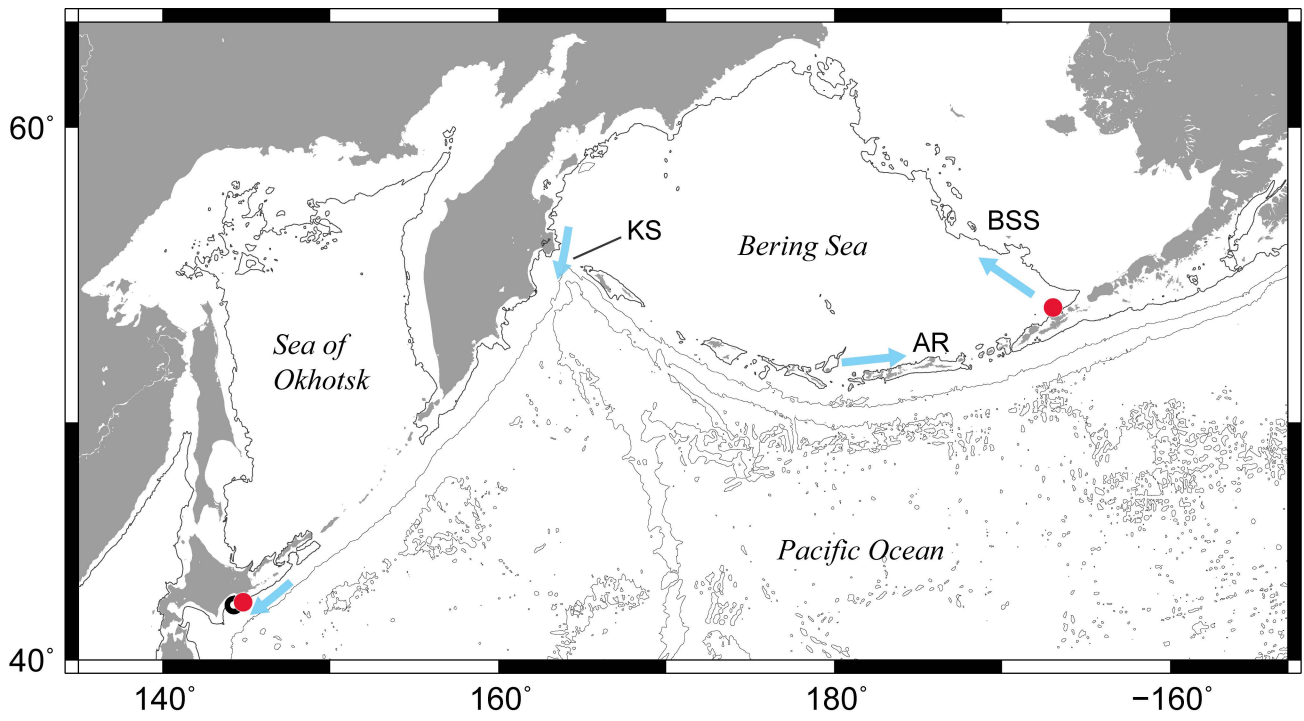
448 **Figure 1.** Map showing our sampling sites for *Carpoapseudes spinigena* (red circles) and the
449 type locality (black open circle; Bamber, 2007). Bathymetric contours are 200 m (thicker
450 lines) and 5000 m (thinner lines). Map and plots were generated using GMT5 (Wessel *et al.*,
451 2013) based on data publicly available from ETOPO1 (Amante & Eakins, 2009). Bottom
452 currents around 1000–1500 m depth (thick blue arrows) were drawn with reference to Kinder
453 *et al*. (1975), Roden (1995), Stabeno *et al*. (1999), and Uehara & Miyake (1999).
454 Abbreviations: AR, Aleutian Ridge; BSS, Bering Sea Slope; KS, Kamchatka Strait.

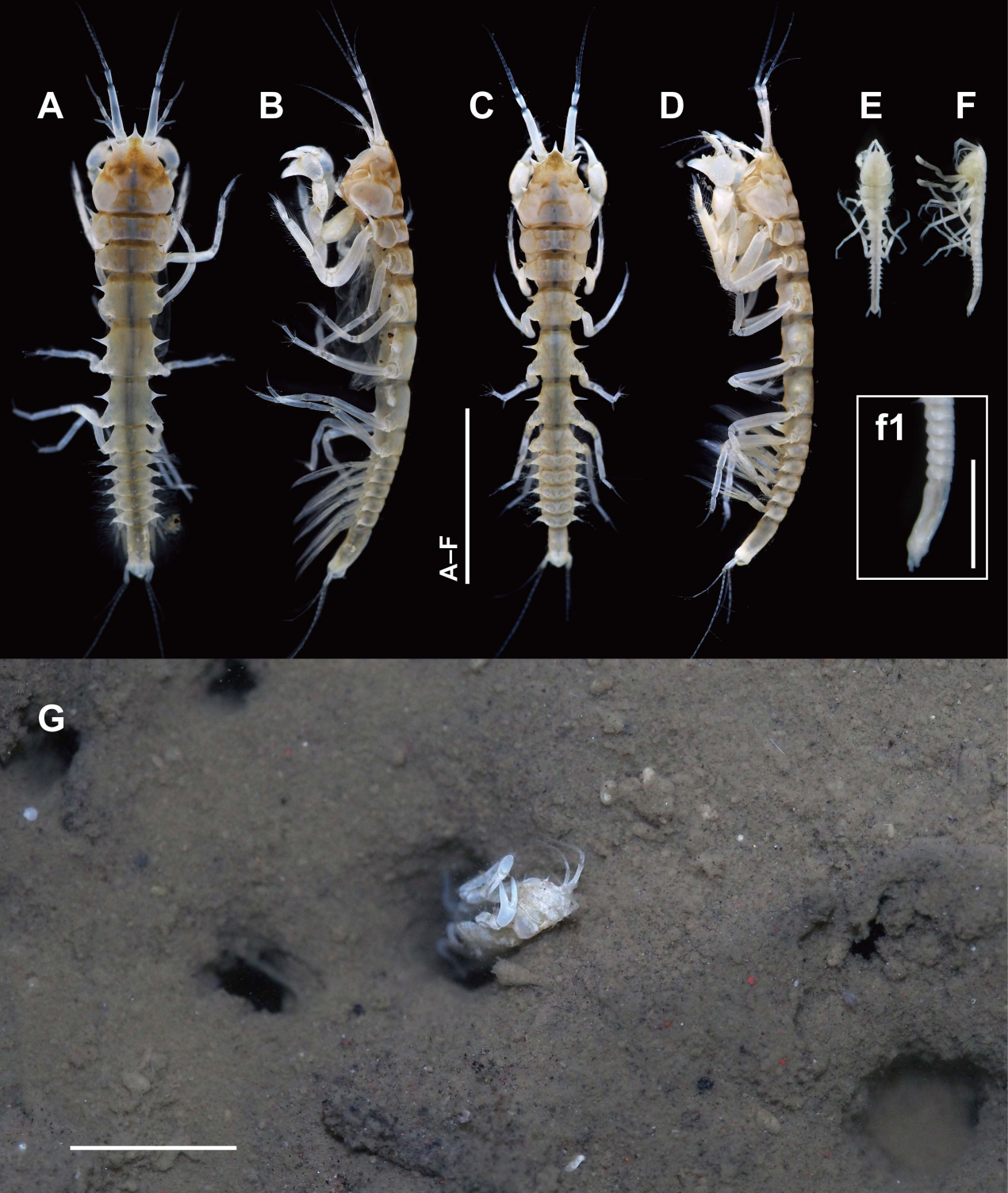
455

456 **Figure 2.** *Carpoapseudes spinigena* collected from the Bering Sea. **A, B,** Fresh female,
457 dorsal (**A**) and left (**B**) views; **C, D,** fresh male, dorsal (**C**) and left (**D**) views; **E, F, f1,**
458 ethanol fixed manca II, dorsal (**E**) and left (**F**, **f1**) views (**f1**, pleon and pleotelson), most of
459 uropod lost; **G,** living individual without major disturbance in collection, with its posterior
460 half in a burrow, found in a sediment core sample. Scale: f1, 1 mm; others, 5 mm.

461

462 **Figure 3.** IntNJ network for COI haplotypes (658 nt) from 21 and 11 *Carpoapseudes*
463 *spinigena* individuals from the Japan and Bering Sea populations, respectively. Labeled
464 circles indicate haplotypes, with size of the circle proportional to frequency of the haplotype;
465 number of individuals > 1 also labeled inside circles. Smaller, black circle indicates an
466 intermediate haplotype not observed; each line between circles indicates a single mutational
467 substitution. H1–10, haplotypes 1–10.


60˚
40˚
140˚
160˚
180˚
−160˚
KS
Bering Sea
BSS
AR
Sea of
Okhotsk
Pacific Ocean


A
B
C
D
E
F
A–F
f1
G

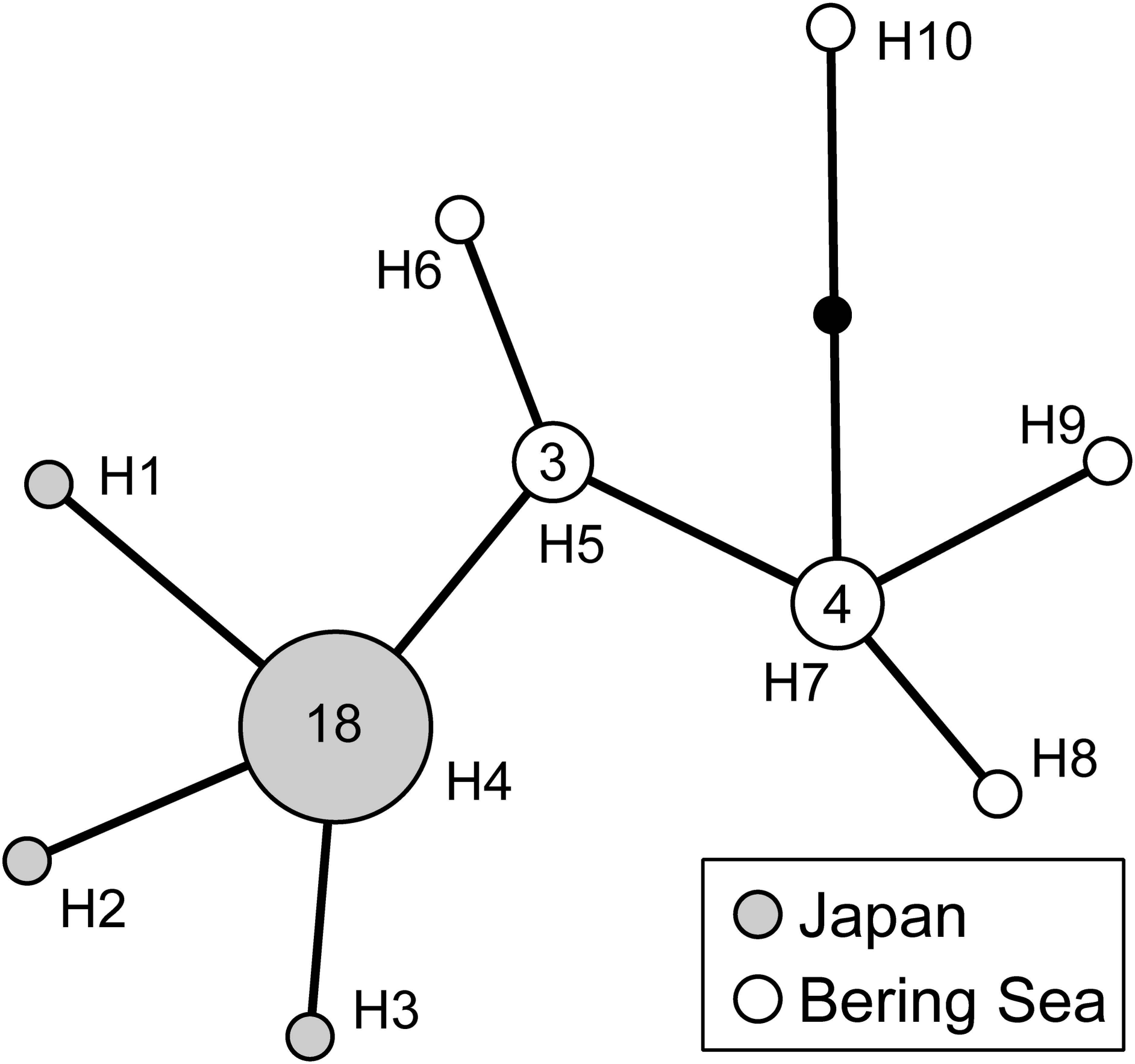

H10
H6
H9
H1
3
H5
4
H7
18
H4
H8
H2
H3
Japan
Bering Sea

Table 1. List of stations by R/V *Tansei-maru* (KT) and R/V *Mirai* (MR). BT, beam trawl with 3 m opening; D, dredge installed on a Deep Tow Camera System; MC, multiple corer. [a], net in; [b], net out.

Station no.	Gear	Date	Start position	End position	Depth (m)
Japan population KT-07-29-K1	BT	7 Nov 2007	42°35.0´N 144°48.0´E[a]	42°34.7´N 144°49.9´E[b]	1028–1075
Bering Sea population MR17-04_Leg2 St. G	D	15 Aug 2017	54°11.6378´N 166°59.3735´W	54°11.6336´N 166°59.4198´W	1566–1569
MR17-04_Leg2 St. G	MC	15 Aug 2017	54°11.7635´N 166°58.3413´W		1536

Table 2. Genetic diversity indices for two *Carpoapseudes spinigena* populations. *N*, number of individuals; N_h, number of haplotypes; N_p, number of polymorphic sites; *h*, haplotype diversity; π, nucleotide diversity.

Population	N	N_h	N_p	H	π	**Tajima's *D***	**Fu's F_S**
Japan	21	4	3	0.271	0.0004	–1.727 (p = 0.024)	–2.820 (p < 0.001)
Bering Sea	11	6	6	0.836	0.0022	–1.218 (p = 0.115)	–2.508 (p = 0.013)
Overall	32	10	10	0.673	0.0020	–1.465 (p = 0.064)	–5.076 (p = 0.001)