

Research Article

Harpacticoid copepods associated with Japanese tsunami debris along the Pacific coast of North America

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Abstract

Six families and at least 15 species of harpacticoid copepods were found on debris, generated from the earthquake and tsunami that struck Japan on 11 March 2011, that landed in North America. Harpacticoids occurred on a wide variety of objects, ranging from small plastic items to a massive floating dock. At the genus level, the harpacticoid copepod assemblage was similar to that found with floating algae by previous authors. Two of the species identified—*Harpacticus nicaeensis* Claus, 1866 and *Dactylopodamphiascopsis latifolius* (G.O. Sars, 1909)—are not previously known from the eastern Pacific Ocean. Six of the species are cosmopolitan or amphi-Pacific in distribution. None of the species were originally described from Japan, and some may have been acquired after the debris had left the Japanese coast, either from floating algae at sea or near the North American coast. Interpretation of the original source of the harpacticoids is difficult because regional taxonomic knowledge is lacking, especially for outer coast habitats where most of the tsunami debris was deposited. Identifying the harpacticoid sources is also complicated by many unresolved species complexes in the group—five of the taxa found were either very similar to or identified as species that taxonomists have regarded to be part of species complexes. Despite these difficulties, decreases over time in copepod diversity, in the frequency of unique species, and in the number of species per object, all suggest that many species were acquired in Japanese coastal waters.

Key words: Tohoku earthquake, anthropogenic debris, Harpacticoida, northeast Pacific, introduced species

Introduction

Harpacticoid copepods are abundant and diverse in algae and among sessile invertebrates attached to natural rock substrates as well as among fouling organisms on floating structures such as docks (Hicks and Coull 1983; Cordell et al. 2013). They can also be abundant in both unattached and detached intertidal algae floating in nearshore and offshore waters (Ingólfsson 1998; Ólafsson et al. 2001; Abé

et al. 2013). At least one species, *Parathalestris croni* (Krøyer, 1842) is closely associated with floating macroalgae clumps, using them as nests for their non-swimming nauplii (Ingólfsson and Ólafsson 1997). The two papers that focus on drift algal rafting of harpacticoids at the species level (Yeatman 1962; Ólafsson et al. 2001) found it likely that the largely benthic copepod communities on the seaweed could be dispersed across oceans because the algae remained healthy for months.

Harpacticoids are also common components of hull fouling communities on commercial ships entering port after cross-ocean journeys (Chan et al. 2015). Another potential source of harpacticoid transport across long distances is plastic debris, which can contain a diverse assemblage of photoautotrophic and heterotrophic protists and bacteria as well as Maxillopoda (the class, recently divided into Oligostraca and Multicrustacea, previously containing Harpacticoida) and other metazoan taxa (Bryant et al. 2016). Larger anthropogenic debris (such as vessels and docks) from natural events, such as the Tohoku earthquake and tsunami that struck Japan on 11 March 2011, may also provide rafting substrates for harpacticoid copepods, but this has not been previously documented. Here I describe the harpacticoid copepods collected from tsunami debris retrieved between Alaska and California, USA, 2012 to 2016.

Materials and methods

JTMD objects

Copepods were recovered from a wide variety of Japanese Tsunami Marine Debris (JTMD) objects, ranging from large docks to medium-sized vessels and small buoys, landing in North America from Alaska to California between 2012 and 2016 (Supplementary material Table S1). Objects were identified as directly related to the March 2011 tsunami through multiple lines of evidence as detailed in Carlton et al. (2017). Each object was assigned a unique identification number preceded by JTMD-BF- (Japanese Tsunami Marine Debris-Biofouling) (Carlton et al. 2017). Copepods were picked from fouling samples that had been either initially placed in ethanol, or frozen and then later transferred to alcohol.

Copepod samples

Harpacticoid copepods were collected from 24 JTMD objects. Copepods from each sampling location were sorted into putative species under a dissecting microscope. Representative specimens of each species were dissected and parts placed in a streak of 50:50 glycerin:water on a microscope slide, and a cover slip with a drop of the glycerin solution was added. I narrowed down the possible species to which each specimen belonged using the comprehensive keys in Wells (2007) and several other sources published thereafter (cited within systematic section, below). I compared the dissected specimens with original descriptions and/or re-descriptions to arrive at a species designation. In cases where published descriptions are poor or difficult to find I took digital photographs

of diagnostic parts with a Nikon Coolpix 8700 digital camera (Nikon Corporation, Tokyo, Japan) mounted on a compound microscope, at 400× magnification. The photographs are intended to illustrate characters useful in distinguishing each species, but are not intended to be definitive taxonomic characterizations.

Results

Copepod diversity and frequency

At least 15 species of copepods in six families were identified from JTMD samples. These include: 10 species to which I assigned, at times with some reservation, species names; two species assigned to additional species complexes (as “groups”); two species that were resolved to genus only; and one or more species of tsiandid copepods that were also assigned to genus only.

Five species (*Harpacticus nicaeensis* Claus, 1866, *Harpacticus* sp. *flexus* Brady and D. Robertson, 1873 group, *Harpacticus* sp., *Dactylopodamphiascopsis latifolius* (Sars G.O., 1909), and *Sarsamphiascus* sp. *varians* (Norman and Scott T., 1905) group) were encountered only once, each on five different objects. Five species or species-groups each occurred on 5 or more objects: *Harpacticus septentrionalis* Klie, 1941, *H. compsonyx* Monard, 1926, *Parastenhelia spinosa* (Fischer, 1860), *Sarsamphiascus minutus* (Claus, 1863), and *Tisbe* spp.

The most species (at least 6) were found on JTMD-BF-1, a massive floating dock from the Port of Misawa, Aomori Prefecture, which landed, after being at sea for slightly over 14 months, in central Oregon on June 5, 2012. Of the 12 objects which arrived between June 2012 and April 2013, half supported 4 to 6 species of copepods (average 2.92 species per object—Table S1). Twelve more objects sampled from the summer of 2013 to the summer of 2016 supported 1 or 2 species, except for BF-131 and BF-176, which had 3 species (average 1.58 species per object).

Systematic Account

Order Harpacticoida G.O Sars, 1903

Family Harpacticidae Dana, 1846

Genus *Harpacticus* Milne-Edwards, 1840

Harpacticus nicaeensis Claus, 1866

Locality—BF-36; 6 ♀, 3 ♂.

This record of *Harpacticus nicaeensis* represents the first report of this species in the Pacific Ocean. This species appears to be common in the Mediterranean, and reliable records of *H. nicaeensis* are from the Ponto-Caspian basin (Huys and Song 2004).

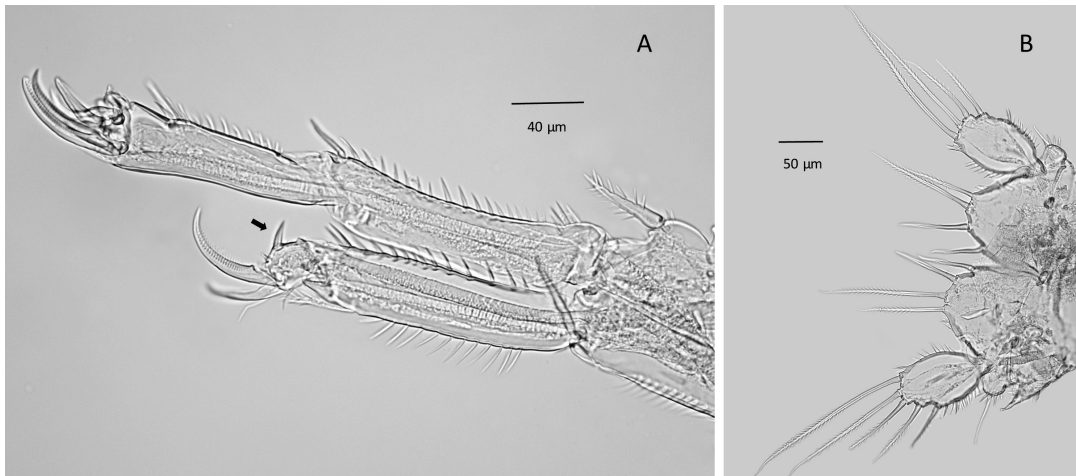


Figure 1. *Harpacticus nicaeensis*, adult female. A, first pereopod, arrow indicates upward-directed spikes on second segment of endopod; B, fifth pereopods.

Harpacticus nicaeensis is readily distinguished by the first pereopod endopod, which is about as long as the proximal exopod segment and has a characteristic, slightly upwardly recurved outer spike on the distal segment (Figure 1A). Most species of the genus have a small row of spinules at this location; Huys and Song (2004) found the latter character so distinctive that they used it to confirm other figured records of the species. In this respect, and in the shape of the female pereopod 5 exopod (oval, with convex edges—Figure 1B) these specimens agree with the descriptions of *H. nicaeensis*. However, I note that these specimens were found a very long distance from any previous records, and the one fairly well described record from outside the Ponto-Caspian region (Angola—Candeis 1959) was treated by Huys and Song (2004) as a *species inquirenda*, regarding it as circumstantial evidence for the existence of a *nicaeensis*-complex. Thus, while I designated these specimens as *H. nicaeensis*, I acknowledge that they may be a closely related undescribed species that differs from *H. nicaeensis* based on heretofore unrecognized characters.

***Harpacticus septentrionalis* Klie, 1941**

Objects—BF-1, BF-43, BF-50, BF-97, BF-176; multiple ♀ and ♂.

Harpacticus septentrionalis was described from Iceland, and has also been recorded from algal habitats in several locations in the British Isles (Hicks 1980, 1982; Huys et al. 1996). It has been found to be associated with drift algae off the west coast of Iceland (Ólafsson et al. 2001). This species occurs in the boreal Pacific (Sibert 1981; Huys et al. 1996;

Cordell 2007); Itô (1976) described a subspecies, *H. septentrionalis yamadai* from Hokkaido.

Harpacticus septentrionalis is characterized in having the exopod of the maxillule with nearly parallel margins and four terminal setae (Figure 2A); P1 exopod-2 marginal spinules are close together at right-angles to the segment margin (Figure 2B); and the female P5 baseopodopod has few pores and no proximal rows of spinules on the face of the article (Figure 2C). The specimens from this study would fit into the subspecies *yamadai*, but the characters that Itô used to designate the subspecies—distance between the outer two setae on baseopodopodite of the female fifth pereopod and comparative size of adult males and females are subtle and the former is poorly figured in the original description of *H. septentrionalis*. In addition, the extent to which these characters are variable in other *Harpacticus* species is largely unknown. Specimens commonly collected elsewhere along the US Pacific coast are also like *H. septentrionalis yamadai* in these respects as well as to *Harpacticus arcticus* (Poppe, 1888) (J. Cordell, personal observations). The latter may in fact be a senior synonym for *H. septentrionalis*, because there are apparent intermediates between the two species (the late Richard Hamond, personal communication).

***Harpacticus compsonyx* Monard, 1926**

Objects —BF-50, BF-97, BF-134, BF-176, BF-352, BF-363; multiple ♀ and ♂.

Huys et al. (1996) characterized *H. compsonyx* as a warm water species, occurring in most of the Mediterranean Sea north to the Isles of Scilly and Roscoff, France. It was found at Murrell's Inlet, South Carolina,

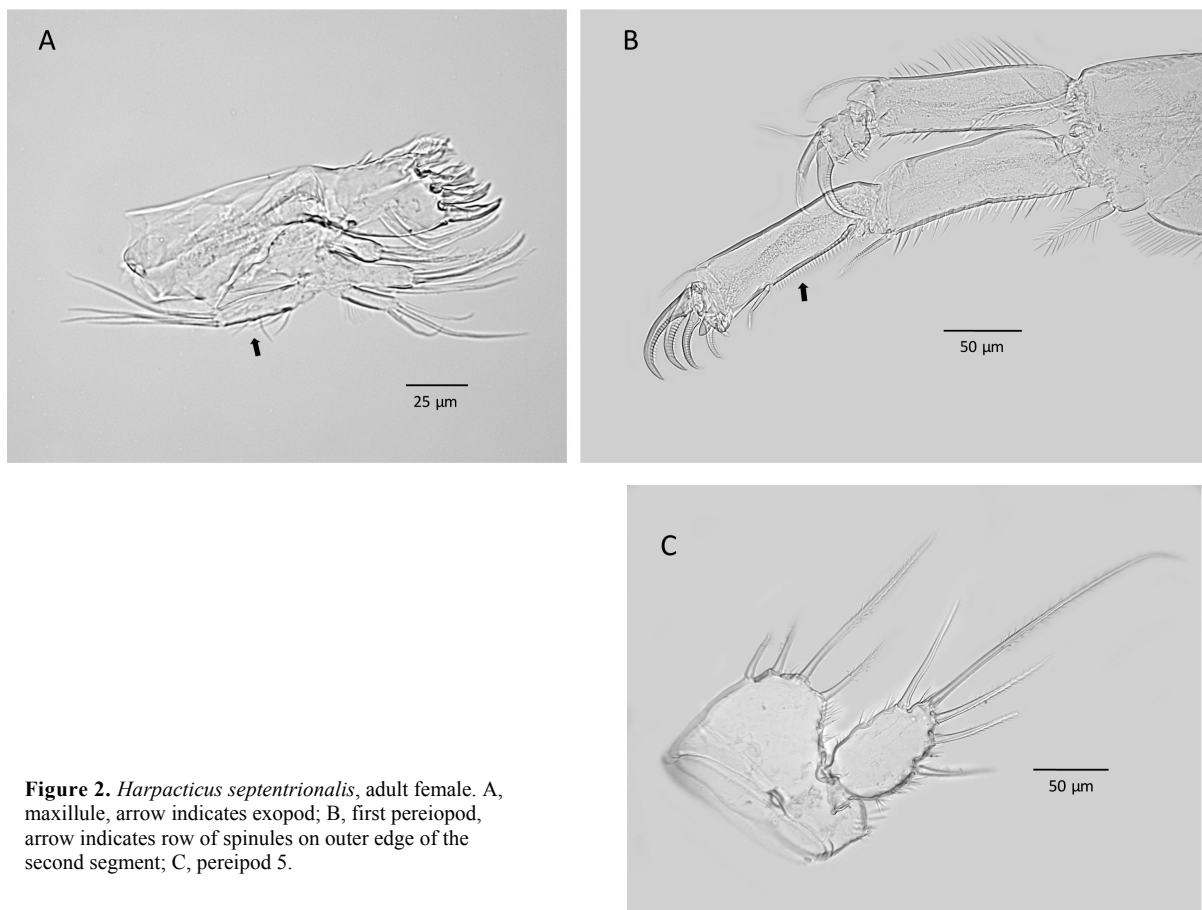


Figure 2. *Harpacticus septentrionalis*, adult female. A, maxillule, arrow indicates exopod; B, first pereopod, arrow indicates row of spinules on outer edge of the second segment; C, pereopod 5.

where it comprised 89% of the harpacticoid numbers inhabiting algae collected along a recently constructed jetty (Coull et al. 1983). It has been recorded from Korea (Song and Young 1993), the tropical Pacific (Vervoort 1964; Boxshall and Huys 2007), and in Mozambique in the southern Indian Ocean (Wells 1967). There is one previous record in the northeast Pacific, where it was recorded from subtidal eelgrass in southern British Columbia (Kask et al. 1982).

Harpacticus compsonyx is part of a species group (including *H. nicaeensis* and the endemic *H. pacificus* Lang, 1965) in which the endopod of the first pereopod is two segmented (vs. three segmented) (Figure 3A) and has one inner seta (vs. two) on the second endopodal segment of pereopod 2 (Figure 3B). Like *H. nicaeensis*, it also has small upwardly curving spikes on the distal segment of the second segment of the first pereopod endopod (Figure 1A). However, it differs from this species and other congeners in the group in having only three setae on the distal segment of the endopod of pereopod 2 (Figure 3B). It differs from *H. pacificus* in these respects and in lacking a row of setae on the face of

the fifth pereopod exopod, having setae only along the borders of that article (Figure 3C). *H. compsonyx* is also apparently unique among *Harpacticus* species in having six, seven, and eight setae and spines on the distal segment of the exopods of pereopods two, three, and four, respectively (Wells 2007).

Harpacticus sp. *flexus*

Brady and D. Robertson, 1873 group

Object —BF-8; 1 ♂.

A single male specimen from this group was found. There is one species from this group recorded from the Pacific coast of North America, *H. spinulosus* Lang, 1965. However, differentiation of this species from others in the group has thus far been based on females (Lang 1965).

Harpacticus sp.

Object —BF-526; one ♀ and four ♂.

On this object were five specimens of *Harpacticus* that I could not assign to a species. It is in the species

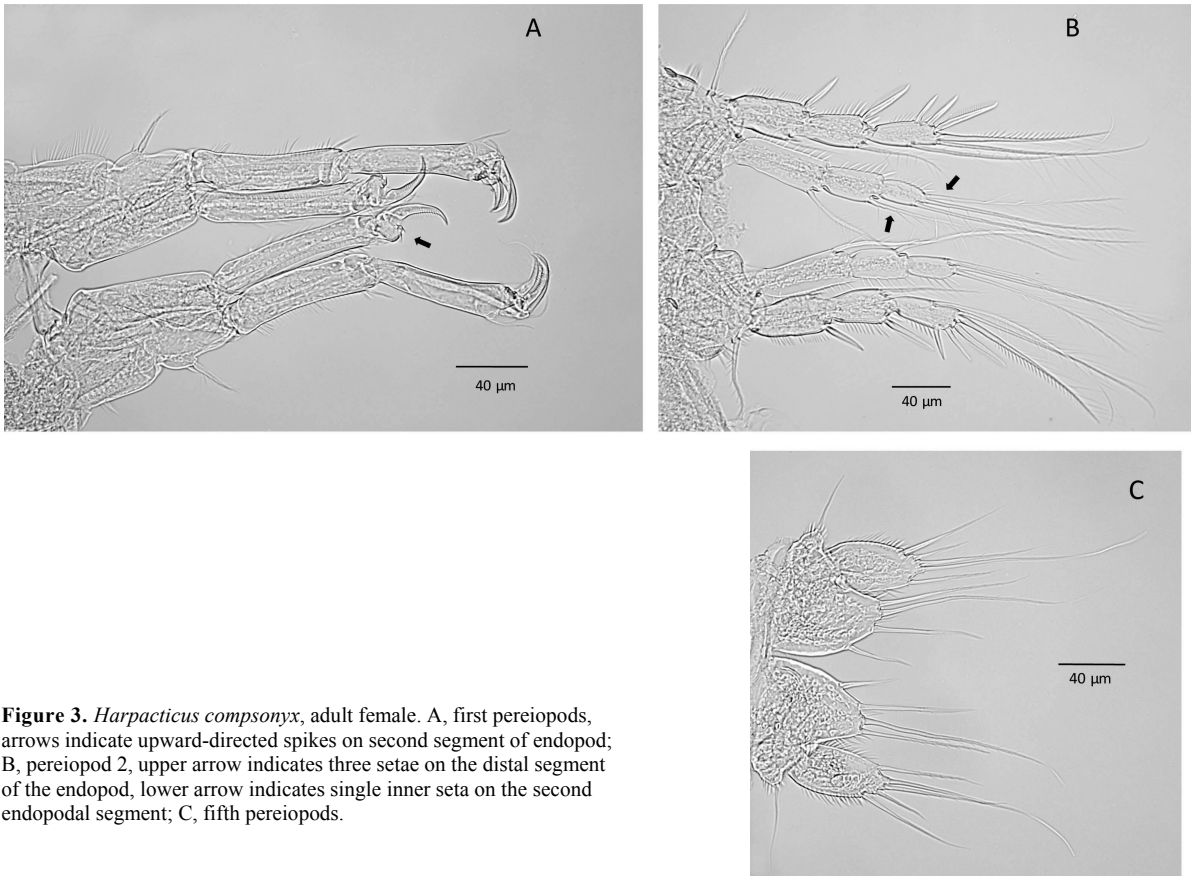


Figure 3. *Harpacticus compsonyx*, adult female. A, first pereiopods, arrows indicate upward-directed spikes on second segment of endopod; B, pereiopod 2, upper arrow indicates three setae on the distal segment of the endopod, lower arrow indicates single inner seta on the second endopodal segment; C, fifth pereiopods.

group with *H. compsonyx*, *H. nicaeensis* and *H. pacificus* in which the endopod of the first pereiopod is two segmented. However, it has a peculiar exopod of the first pereiopod in which the second (terminal) segment is shortened and distally broadened (Figure 4). This segment is about two-thirds length of the first segment of the exopod, while in other *Harpacticus* species it is nearly as long as the exopod first segment (e.g., Figures 1A, 2B, 3A). This species is also notable among the *Harpacticus* collected in this study in having one of the three claws on the terminal segment of the exopod of P1 deflexed (Figure 4).

Family Parastenheliidae Lang, 1936
Genus *Parastenhelia*
Thompson I.C. and Scott A., 1903

***Parastenhelia spinosa* (Fischer, 1860)**

Objects —BF-1, BF-2, BF-8, BF-13, BF-23, BF-40, BF-43; multiple ♀ and ♂.

In his *Monographie der Harpacticiden*, Lang (1948) summarized the worldwide occurrences of *P. spinosa* and argued that it is a single variable species with

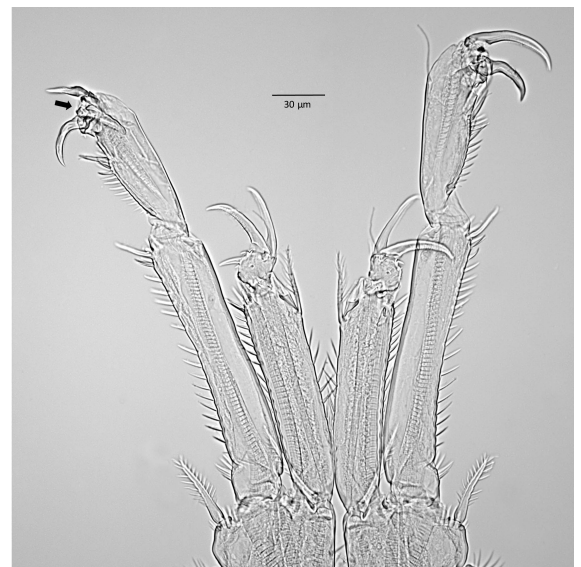


Figure 4. *Harpacticus* sp., adult male. First pereiopods, arrow indicates deflexed terminal claw on terminal segment of the exopod.

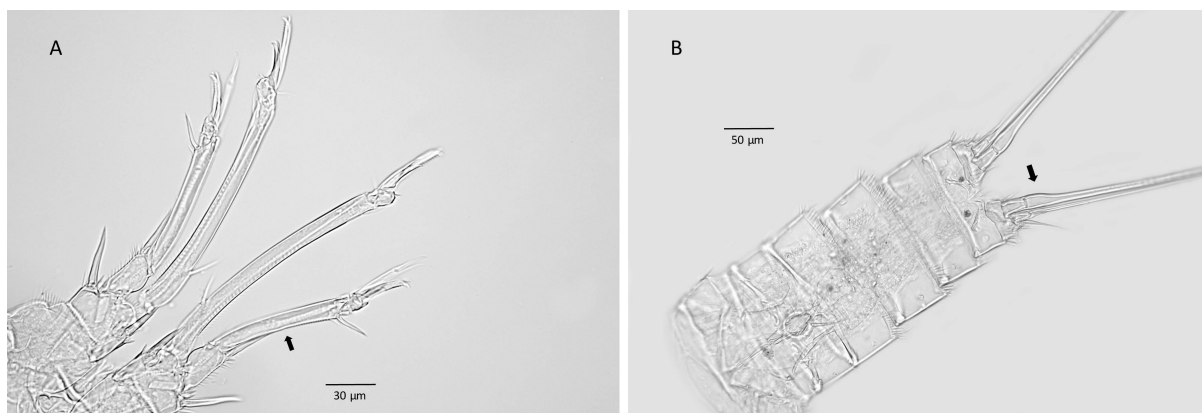


Figure 5. *Parastenhelia spinosa*, adult female. A, first pereiopod, arrow indicates second segment of the exopod; B, urosome, arrow indicates swelling at the base of the principal terminal furcal seta.

cosmopolitan distribution. However, in a paper that re-described and placed one form of *P. spinosa* in a new species (*P. bulbosa*), Gee (2006) asserted that a more thorough and much more critical review of *P. spinosa*-like material from around the world was needed. Gee (2006) pointed out that the five or six forms of *P. spinosa* that have been recorded may represent additional species, citing several cases in which harpacticoid species previously thought to be cosmopolitan and variable are separate species differing in small and subtle morphological characters such as mouthpart structure and body ornamentation, to which earlier descriptions paid little attention. Thus, while I designated the specimens found in this study as *P. spinosa*, I acknowledge that they may be a different species within a species complex. Although there are relatively few reports of *P. spinosa* from the Pacific Ocean, those that exist are geographically widespread, with records from the South Pacific (Vervoort 1964), British Columbia (Kask et al. 1982), Alaska (J. Cordell, personal observation), and central California (Watkins 1983).

Parastenhelia. spinosa sensu lato is in a group of species having the second exopod segment of pereiopod 1 more than 3 times length of the third exopod segment (Figure 5A). Also, in all the female specimens that I examined the inner principal terminal seta was somewhat swollen near the base (Figure 5B). This character is variable (Gee 2006), and specimens that I have previously examined from the northeast Pacific have had almost no swelling at the base of this seta.

Family Miraciidae Dana, 1846

Genus *Dactylopodamphiascopsis* Lang, 1944

Dactylopodamphiascopsis latifolius (G.O. Sars, 1909)

Object —BF-131; 10 ♀, 4 ♂, 1 copepodid.

D. latifolius, described from Norway, is the monotypic species in the genus *Dactylopodamphiascopsis*. Though not often reported, it is another species that occurs across a wide geographic area, with records from New Zealand (Keable and Reid 2015), Korea (Song et al. 1999, who also re-described the species), southeastern Brazil (Sarmiento et al. 2012), Iceland (Steinarsdóttir et al. 2003), and the Canadian Arctic near Greenland (Sars 1909). It has also been found in hull-fouling on ships sampled at the Canadian port of Halifax, Nova Scotia (J. Cordell, personal observation). This species is not known from the northeast Pacific Ocean.

Genus *Sarsamphiascus* Huys, 2009

Sarsamphiascus minutus (Claus, 1863)

Objects —BF-1, BF-8, BF-12, BF-23, BF-43, BF-50, BF-129, BF-176; multiple ♀ and ♂.

A cosmopolitan species, *S. minutus* is a common inhabitant of floating algae (Ólafsson et al. 2001) and submerged phytal detritus (Mascart et al. 2015), and is found in a variety of habitats on the North American Pacific coast (Cordell 2007). It was also found in hull fouling samples from ships visiting the port of Churchill, Manitoba, Canada (Chan et al. 2015). Lang (1965) described a species from California that he referred to as “*Amphiascus* (= *Sarsamphiascus*) *minutus* sp. 1” and regarded *A. minutus* as a species complex. Both this form and a form resembling *A. minutus* from Europe (as figured by Sars 1906) occur in several locations in the northeast Pacific (J. Cordell,

personal observations) but those from the tsunami debris were all the latter type. One of the main characters that separates these two forms is the shape of the third segment of the exopod of the first pereopod, which is relatively long and rectangular in *A. minutus* sp. 1 and short and rounded in *A. minutus* sensu Sars 1906.

Sarsamphiascus* sp. *varians
(Norman and Scott T., 1905) group

Object —BF-40; 2 ♀, 1 ♂.

There are 12 described species in the *Sarsamphiascus* *varians* group, none of which has been formally reported from the northeast Pacific. However, at least one species in this group is common in eelgrass and algae habitats in the US Pacific northwest (J. Cordell, personal observations). One species, *S. elongatus* (Itô, 1972) has been described from Japan.

Hicks (1989) reviewed this group but species differentiation still suffers from the problems caused by inadequate descriptions and from uncertainties about the limits of intraspecific variation (Wells 2007). It is apparent from Hicks's discussion that the ornamentation of the urosome is important for species differentiation, but this character is not well described for most species. I dissected one female of the three specimens found in this study. It is similar but not identical to *S. propinquus* (Sars, 1906) in shape of the fifth pereopod and in the ornamentation of the urosome as described by Hicks (1989) but because of the uncertainties in taxonomy of this group I did not assign a species to these specimens.

Genus *Paramphiascella* Lang, 1944

Paramphiascella* *fulvofasciata
Rosenfield and Coull, 1974

Objects —BF-40, BF-4; 8 ♀, 4 ♂, 3 copepodids.

P. fulvofasciata was described from Massachusetts Bay, USA, where it was common in wood infested with the boring isopod *Limnoria tripunctata* Menzies, 1951 (Sleeter and Coull 1973). It has been recorded from other biogenic substrates including laminarian algae in Europe (Dahms 1987), seagrass (*Zostera* sp.) in South Korea (Kim et al. 2015), and non-indigenous tunicates in Puget Sound (Cordell et al. 2013). Kim et al. (2015) provide a complete re-description of both male and female adults.

Family Laophontidae Scott, 1905
Genus *Heterolaophonte* Lang, 1948

***Heterolaophonte* *discophora* (Wiley, 1929)**

Objects —BF-8, BF-43, multiple ♀ and ♂.

H. discophora was described from Nova Scotia, where it is associated with macroalgae (Johnson and Scheibling 1987). It occurs on the west coast of the U.S. from Alaska to Monterey Bay, where it is associated with macroalgae and detritus-rich habitats (Cordell 2007), and has also been recorded from Japan (Itô 1974). Lang (1965) provided a re-description of the species. *H. discophora* can be distinguished by the exopod of pereopod 4 which in females is reduced to varying degrees and is also extremely variable in shape and setation (see Lang 1965).

***Heterolaophonte* sp.**

Objects —BF-131, BF-363, BF-590, 5 ♀.

Five individuals of a *Heterolaophonte* species were found that correspond to the pereopod setal formula given in keys by Wells (2007) and Lang (1965) for the species *H. stroemi* var. *stroemi* (Baird, 1837) and *H. uncinata* (Czerniavski, 1868). However, it differs from *H. stroemi* var. *stroemi* in the caudal rami which are barely longer than wide (Figure 6A) (they are about twice as long as wide in *H. stroemi* var. *stroemi*) and from *H. uncinata*, which has been recently re-described (Kaymak and Karaytuğ 2014), in having more elongated second segments of the endopods of the pereopods (Figure 6B) and in having the exopod of the fifth pereopod almost as wide as long vs. more elongated in *H. uncinata* (Figure 6C). Wells (2007) indicates that the two species may be distinguished by the antenna exopod, which bears 4 small setae in *H. stroemi*, but at most has only 1 seta in *H. uncinata*. However, Kaymak and Karaytuğ (2014) show 4 setae on this article in their redescription of the species, but do not comment further on this character. The dissected specimen from the tsunami debris has 4 setae on the antennal exopod (Figure 6D). An important diagnostic feature for *H. uncinata* is the structure of the modified inner spine on the second segment of the endopod of pereopod 2 of the male, and I could not verify this because only female specimens were present. Because of these factors, and the fact that neither *H. stroemi* var. *stroemi* or *H. uncinata* are known to occur in the Pacific Ocean, I did not assign these specimens to a species. Because of variations among previous descriptions of *H. uncinata*, Kaymak and Karaytuğ (2014) speculated that the name may represent a species complex and it is possible that the specimens in this report are part of that complex.

Genus *Paralaophonte* Lang, 1948

Paralaophonte* *congenera congenera
(G. O. Sars, 1908)

Objects —BF-1, BF-23, 5 ♀, 5 ♂, 2 copepodids.

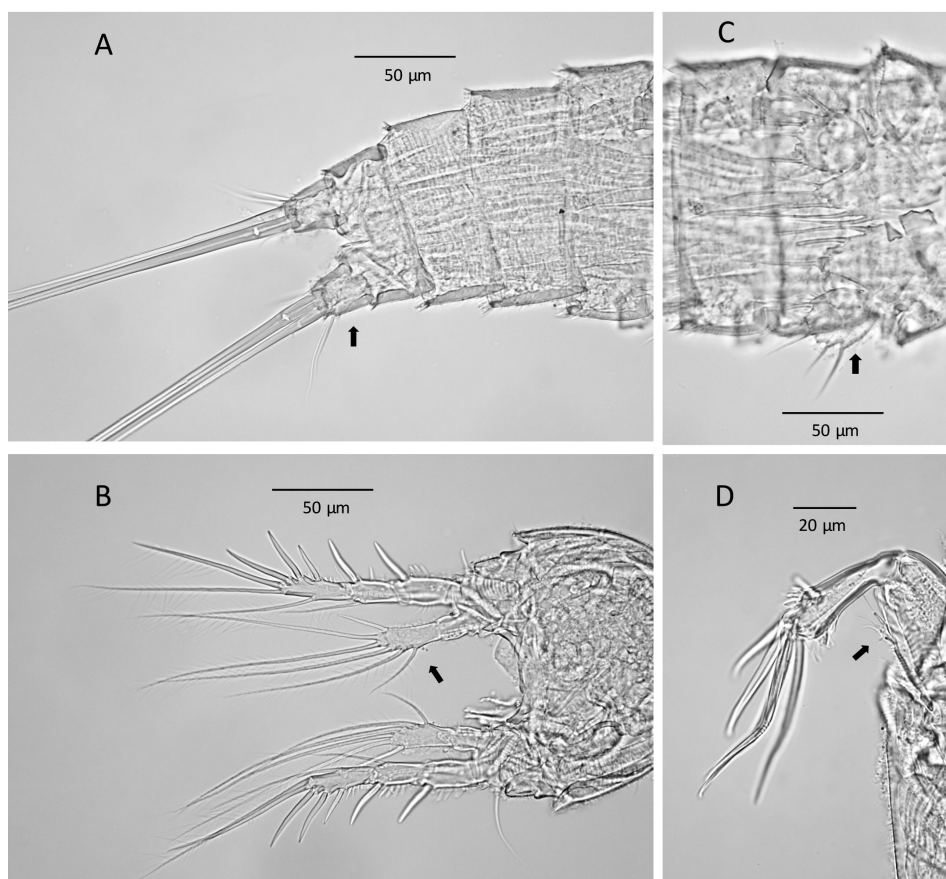


Figure 6. *Heterolaophonte* sp., adult female. A, last four abdominal somites and caudal rami, arrow indicates caudal ramus; B, third pereopods, arrow indicates terminal segment of endopod; C, genital double somite and fifth pereopods, arrow indicates exopod of fifth pereopod; D, antenna, arrow indicates exopod bearing 4 setae.

P. congenera is one of the most widely distributed members of the genus, and is usually associated with phytal and other biogenic substrates (e.g., sponges in Chesapeake Bay—Yeatman 1970, seagrasses in southwest India—Arunachalam and Nair 1988; algal turfs in southeastern Brazil—Sarmiento et al. 2012; non-indigenous tunicates in Puget Sound—Cordell et al. 2013). It has been subdivided into subspecies but *P. congenera mediterranea* Lang, 1948 appears to be more closely related to *P. lacerdai* Jakobi, 1953 than to its nominotypical subspecies *P. congenera congenera* (Huys and Lee 2009). However, I retain the subspecies designation here as was done in the recent key to *Paralaophonte* in Huys and Lee (2009).

Family Ambungiipedidae Huys, 1990

Genus *Ambungiipes* Huys, 1990

***Ambungiipes* aff. *rufocincta*
(Norman in Brady, 1880)**

Objects —BF-1, BF-23, BF-402, 4 ♀.

Ambungiipes rufocincta is a widespread species with a probable distribution from the Caribbean and Bermuda around to the northeastern Atlantic seaboard between Norway and the Canary Islands and throughout the Mediterranean and Black Sea basins (Huys 1990). It also occurs in phytal habitats in the Pacific including Korea (Song et al. 2012), Japan (Shimode and Shirayama 2006), and the west coast of the United States (Cordell 2007). Huys (1990) identified only one other species of *Ambungiipes* that could be reliably recognized using extant descriptions, *A. similis* (A. Scott, 1909). *Ambungiipes similis* has been reported from several locations in the Indo-Pacific (Huys 1990).

The most reliable character to separate the two species appears to be the relative length of the male pereopod 5 endopodal lobe, which reaches the end of the exopod in *A. rufocincta* and is much shorter in *A. similis* (Huys 1990). However, only females were found in this study, and female characters that have been used to differentiate the two species are

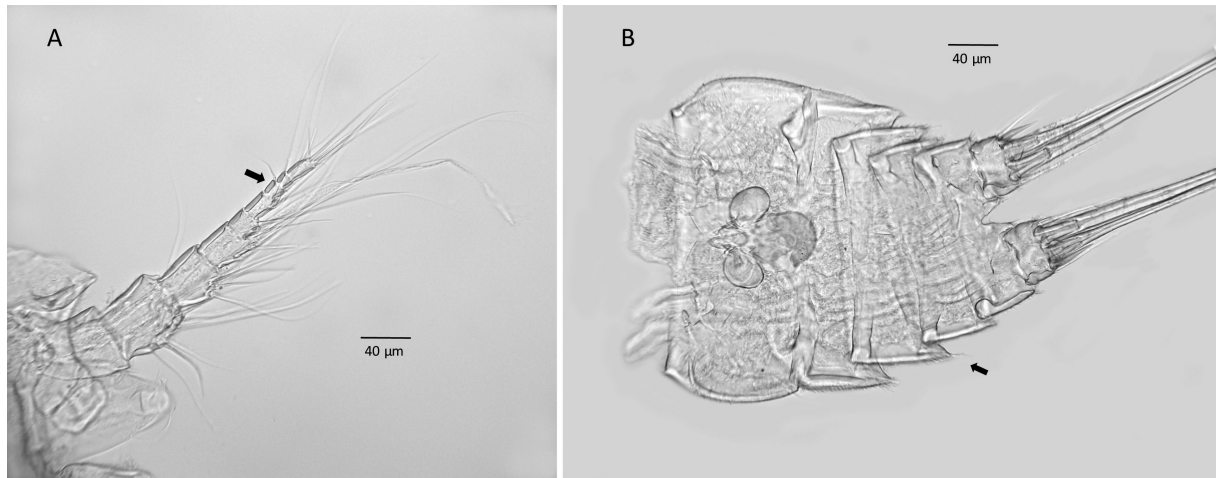


Figure 7. *Ambunguipes* aff. *rufocincta* adult female. A, antennule, arrow indicates seventh segment; B, urosome, arrow indicates produced posterior angle of the first free somite.

ambiguous or variable. For example, in his original description of *A. similis*, Scott (1909) indicated that the lengths of the seventh and eighth segments of the antennule were diagnostic, being of nearly equal length in *A. similis* while in *A. rufocincta* the eighth segment is distinctly smaller than the seventh segment. But later descriptions of *A. rufocincta*, including that of Huys (1990) show these segments being equal in length, as they are in the specimens from the tsunami debris (Figure 7A). Also, in his re-description of *A. rufocincta*, Huys (1990) indicated that *A. similis* differs from that species in the absence of well developed, backwardly produced angles of the first free abdominal somite in the female. In the present specimens, these angles are somewhat produced, but not to the degree figured in Huys (1990) (Figure 7B). Therefore, I refer to these specimens as *A. aff. rufocincta*.

Family Tisbidae Stebbing, 1910
Genus *Tisbe* Lilljeborg, 1853

Tisbe spp.

Objects —BF-1, BF-2, BF-40, BF-43, BF-50, BF-129, BF-131, BF-134, BF-239, BF-255, BF-382; multiple ♀ and ♂.

The genus *Tisbe* is characterized by many groups of sibling species, rendering species level identification problematic (Boxshall and Halsey 2004). An example of the extent of the problem cited by Wells (2007) in his comprehensive key to harpacticoids is that two independent redescriptions of the type species, *T. furcata*, from locations only 500 km apart (Bergmans 1979, Belgium; Dahms et al. 1991, Helgoland, southern

North Sea) show several differences indicating that they are two different species. In addition, *Tisbe* species remain largely undescribed from the Pacific coast of North America. Thus, I elected to leave *Tisbe* at the genus level.

Discussion

Harpacticoid copepods are common rafting organisms in the Atlantic Ocean, especially on floating macroalgae (Yeatman 1962; Ingólfsson and Ólafsson 1997; Ólafsson et al. 2001). The degree to which harpacticoids are associated with rafting materials in the Pacific Ocean is largely unknown due to the paucity of studies on the subject. Goldstein et al. (2014) recorded harpacticoids as part of the fauna associated with floating plastic in the North Pacific Ocean, but did not identify any species. The harpacticoid copepod assemblage associated with the Tohoku earthquake and tsunami debris has some similarities to that found with floating algae in the Atlantic. For example, the most speciose genus found here and with the seaweeds *Ascophyllum nodosum* (Linnaeus, 1753) Le Jolis, 1863 and *Fucus vesiculosus* Linnaeus, 1753 offshore of western Iceland was *Harpacticus* (Ólafsson et al. 2001). Five of the other species that I found also occurred in the studies by Yeatman (1962) and Ólafsson et al. (2001)—*Ambunguipes* aff. *rufocincta*, *Paralaophonte congenera*, *Harpacticus septentrionalis*, *Parastenhelia spinosa*, and *Sarsamphiascus minutus*.

All the genera found in this study were also found in the previously cited studies. The six families and 14 species (plus *Tisbe* spp.) found in the tsunami

debris are fewer than those found associated with algae off Iceland (10 families, 38 species plus *Tisbe*—Ólafsson et al. 2001) but exceeded those found among the floating brown alga *Sargassum* in the Gulf Stream between Europe and North America (five families, six species—Yeatman 1962). Notably missing from the tsunami debris were any species in the family Thalestridae, which were prominent and comprised 10 species in these studies. This may have resulted from sampling the debris on shore after it had been exposed to high wave energy, which could have washed off the thalestrids, some of which do not have highly developed prehensile appendages for securing themselves to the substrates (e.g., *Dactylopusia* and *Diarthrodes* spp.).

Some of the species encountered could have colonized the tsunami debris upon arrival near north American shores, especially those that have been previously found in the region. Colonization experiments have shown that harpacticoids colonize floating algal clumps close to the shore within 8 to 9 days and the colonizing assemblage is different than that on free floating algal clumps occurring in the ocean nearby (Ólafsson et al. 2001).

Interpretation of the original source of the harpacticoids collected is rendered difficult by the lack of regional knowledge about taxonomy and community structure of this group. Harpacticoid assemblages have been poorly studied in the region sampled, especially outer coast habitats where the tsunami debris was deposited. While harpacticoids of more inland regional waters have been sampled or catalogued by a few studies (e.g., Salish Sea (Strait of Georgia, Strait of Juan de Fuca, and Puget Sound)—Cordell et al. 2013; Webb and Parsons 1992; Kask et al. 1982), the geographically closest compendium of open coast species was that of Lang (1965), who collected and described many species from tide pools and algae on the central California coast. Otherwise, information about open coast harpacticoids is virtually non-existent in the vast area spanning the Aleutian Islands to central California.

Likewise, floating algal or other debris has not been sampled in the northeast Pacific Ocean, so harpacticoids “normally” associated with rafts are also unknown. Thus, even species that have rarely or never been reported from the northeast Pacific—such as *Harpacticus nicaeensis*, *H. compsonyx*, and *Dactylopodamphiascopsis latifolius*—may be more common (*H. nicaeensis*) or be present (*H. compsonyx* and *D. latifolius*) along northeast Pacific coastal shores and algal rafts. The harpacticoids from Japan are comparatively well known due to the series of papers on harpacticoids from Hokkaido by T. Itô (e.g., Itô 1972, 1974, 1976). While some of the

species found in the tsunami debris were also recorded from Japan (as noted in the systematic section), none were originally described from Japan, and it is possible that some of them were acquired after the debris had left the Japanese coast, either from floating algal rafts or from the northeast Pacific coast.

Identifying the sources of the harpacticoids found in this study is also complicated by the difficult nature of harpacticoid taxonomy. Species complexes abound in this group and five of the taxa found in this study are either similar to or were identified as species that have been regarded as members of species complexes by previous authors—*Harpacticus nicaeensis*, *Parastenhelia spinosa*, *Sarsamphiascus minutus*, *Heterolaophonte* sp., and *Tisbe* spp. Many harpacticoid species were only rudimentarily figured in original descriptions, and while for some modern redescrptions have been done (e.g., *Ambunguipes rufocincta*—Huys 1990), others have not been re-described (e.g., *Harpacticus nicaeensis*). Thus, virtually all species identified in this paper could be regarded as provisional identifications until taxonomy of the regional harpacticoids is studied in depth.

Despite the difficulties in precisely identifying the source of the copepods on the tsunami debris, three temporal patterns in the copepod assemblage suggest that many of the species were acquired in Japanese coastal waters. First, there was a decrease in diversity over time: during the 10-month period between June 2012 and April 2013, 15 species were encountered (with *Tisbe* spp. assigned as one “species”), seven of which were not subsequently seen. Between summer 2013 and summer 2016 only eight species were seen. Second, there was a change in frequency of unique species occurrences: of the five species encountered only once (on five different objects: (*Harpacticus nicaeensis*, *Harpacticus* sp. *flexus*-group, *Harpacticus* sp., *Dactylopodamphiascopsis latifolius*, and *Sarsamphiascus* sp. *varians*-group), four arrived in 2012–2013 window and only one arrived after that. Third, there was a decline in number of species per object over time (Table S1): Of the 12 objects which arrived between June 2012 and April 2013, half had 4 to 6 species of copepods (average 2.92 species per object). The 12 additional objects sampled from the summer of 2013 to the summer of 2016 only supported one or two species, apart from BF-131 and BF-176, which had three species each (average 1.58 species per object).

All three of these indicators suggest that longer times at sea resulted in fewer species on the tsunami debris. If the bulk of the copepods had been acquired in the Eastern Pacific, it would be difficult to explain why these changes in diversity—all in the same direction—occurred. Knowledge about naturally

occurring copepods in rafting debris in the Pacific Ocean would be helpful in understanding potential sources of the tsunami debris copepods, but this information is, as yet, unfortunately lacking.

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Supplementary material

The following supplementary material is available for this article:

Table S1. JTMD Objects: BF numbers, copepod species found, landing site locations in Alaska (AK), Oregon (OR) and Washington (WA) states and British Columbia province (BC), dates and object types, and prefecture and city origins if known.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_JTMD_Cordell_Table_S1.xlsx