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Pelagic Amphipods in the Eastern Fram Strait With Continuing Presence of *Themisto compressa* Based on Sediment Trap Time Series

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Pelagic amphipods represent a large fraction of organisms entering sediment traps as so-called "swimmers." These swimmers were sampled with sediment traps (∼200–300 m water depth) with two mooring arrays deployed at two different positions in the Long-Term Ecological Research observatory HAUSGARTEN in the northeastern Fram Strait. This sampling allowed us to investigate amphipod year-round abundances and inter-annual trends from 2000 onward. In this study, newly analyzed data from a 3-years period (August 2011–June 2014) are presented, extending this long-term investigation. In our results, the species *Themisto abyssorum*, *T. libellula*, and *T. compressa* dominated the swimmer biomass, corroborating previous studies. The observed increase of amphipod abundances persisted in all three species, additionally implying that *Themisto compressa* maintained its population off Svalbard, which appeared for the first time here after a warm anomaly in 2004–2007. This study provides evidence for changes in amphipod community patterns that can mainly be attributed to growing abundances of *T. compressa*. Similarly, another hyperiid, *Lanceola clausii*, also increased in abundance over the investigated period. For *T. libellula*, almost no juvenile individuals were recorded in the sampling period 2013/14, even though juveniles of this species were common in earlier records. The three more years of observations clearly suggest that recently documented environmental shifts persist in the eastern Fram Strait. They also highlight the merit of using sediment trap time series to obtain year-round data sets needed to reveal processes and range shift dynamics in the pelagic system on a long-term basis.

Keywords: sediment traps, hyperiids – pelagic amphipods, Arctic marine ecology, biodiversity, range shifts

INTRODUCTION

The Arctic environment is in rapid transition and is severely impacted by climate change (Schiermeier, 2007; Beaugrand, 2009). The sea ice is thinning (Hansen et al., 2013; Renner et al., 2014; Krumpen et al., 2015), and its extent is shrinking, with predictions of nearly ice-free summers in the Arctic within the next 25 years (Nghiem et al., 2007; Wang and Overland, 2012;

Liu et al., 2013). Decreasing sea ice in the high Arctic impacts the prevailing ice situation in the Fram Strait where sea ice, transported via the Transpolar Drift, leaves the Arctic Ocean. In addition, oceanographic surveys reveal an increase in warm water anomalies throughout the Arctic (Polyakov et al., 2005) that are largely transported via the Fram Strait. The Fram Strait is considered the main gateway to the Arctic Ocean: in its western part, the East Greenland Current transports polar water southward; in its eastern part, relatively warm water flows northward with the West Spitsbergen Current (WSC). Mixing, eddies, and recirculating water of the warm WSC add to the hydrographic complexity observed in the strait (e.g., Gascard et al., 1988; Walczowski, 2013*;* Von Appen et al., 2015). In the eastern part, both increasing water temperature and heat flux have been observed over the last two decades (Schauer et al., 2004, 2008; Piechura and Walczowski, 2009; Walczowski, 2013; Walczowski et al., 2017). Hence, the increasing influence of Atlantic waters in the Arctic domain, termed "Atlantification," is extending its area of impact to a great extent through the eastern Fram Strait northward into the Arctic (Piechura and Walczowski, 2009; Beszczynska-Möller et al., 2012; Polyakov et al., 2017).

In general, alterations of environmental parameters have been shown to change plankton communities by impacting species distributions (e.g., Beaugrand, 2009) and life cycles/development (Weydmann et al., 2018). This is particularly true for the Arctic. The observed occasional warm water peaks in the eastern Fram Strait (Beszczynska-Möller et al., 2012) were accompanied by changes in phytoplankton biomass and particle flux (Bauerfeind et al., 2009; Nöthig et al., 2015; Soltwedel et al., 2016). Biogeographical shifts are also occurring in higher trophic levels, e.g., copepods in the WSC (Weydmann et al., 2014; Gluchowska et al., 2017), krill around Svalbard (Buchholz et al., 2010; Dalpadado et al., 2016), Atlantic cod in the western Greenland Sea (Christiansen et al., 2016), pteropods (Busch et al., 2015), and amphipods (Kraft et al., 2013; Dalpadado et al., 2016) in the Fram Strait. These changes consequently propagate through the Arctic food web, affecting predators such as seabirds and fish (Stempniewicz et al., 2007; Kwasniewski et al., 2012; Kortsch et al., 2015; Dalpadado et al., 2016).

Due to their abundance and their being a major prey for higher trophic levels, the three dominating pelagic amphipod species play a key role in the Arctic pelagic food web (Koszteyn et al., 1995; Dalpadado et al., 2001, 2008a,b; Auel and Werner, 2003; Melle et al., 2004). The three dominant amphipod species found in Arctic waters belong to the genus *Themisto*, namely the Arctic *T. libellula*, the Arctic-boreal *T. abyssorum* (both natives to the eastern Fram Strait), and the North Atlantic species *T. compressa* (Klekowski and Węsławski, 1991; Weigmann-Haass, 1997; Dalpadado et al., 2001; Dalpadado, 2002). *Themisto abyssorum* co-exists with *T. libellula* throughout the Arctic (Klekowski and Węsławski, 1991; Weigmann-Haass, 1997; Dalpadado et al., 2001; Dalpadado, 2002); however, *T. abyssorum* is thought to be more abundant in waters of Atlantic origin and therefore displays a greater tolerance of fluctuations in water temperature (Dalpadado, 2002). The distribution center of *T. compressa* is temperate, North Atlantic waters. It is seldom found, and only in low abundances, in the Arctic marginal seas such as the Barents Sea off Svalbard (Dalpadado, 2002) and the Greenland Sea (Weigmann-Haass, 1997) and was recorded for the first time in the eastern Fram Strait in 2004 (Kraft et al., 2013). After its establishment in the Fram Strait, abundances of *T. compressa* have been increasing between 2005 and 2008 (Kraft et al., 2011, 2013); this was attributed to a warm surface water anomaly in the area (Soltwedel et al., 2016).

As warmer waters of Atlantic origin have been entering the Arctic Ocean via the WSC during the last 20 years, the amphipod community composition was expected to change accordingly. Set up in 1999, the Long-Term Ecological Research (LTER) observatory HAUSGARTEN (79°N, 4°, **Figure 1**) has provided data to detect environmental and biological changes in the Fram Strait. Since pelagic amphipods are good indicators of the presence of distinct water masses and therefore suitable for monitoring the effect of environmental change, this study aimed to assess the temporal and spatial differences in amphipod composition in the gateway to the Arctic. We investigated swimmer time series from the LTER sediment traps during the years 2011–2014, including and building on time series previously analyzed by Kraft et al. (2011, 2013) to assess trends in the prevailing pelagic amphipod population.

MATERIALS AND METHODS

All samples were collected using automatic Kiel sediment traps (*K/MT 234; K.U.M. Umwelt- und Meerestechnik Kiel GmbH*) with an opening of 0.5 m^2 and 20 collection cups. Two different localities were sampled over the period from September 2000 to July 2014 (**Figure 1**); sampling intervals lasted from summer to the following summer. The moorings were located at approximately 79°00′ N, 04°19′ E and 79°44′ N 04°30′ E. The sampling depth of the upper traps that were used for the present analysis were located between 190 and 280 m water depth. Traps were retrieved during 16 expeditions to the Arctic LTER observatory HAUSGARTEN located the eastern Fram Strait. Details of positions and traps for each year are found in **Table 1**. Collector cups of the sediment traps were filled with filtered, sterile North Sea water at an adjusted salinity of 40 psu and poisoned with $HgCl_2$ (0.14% final solution). Automatic sampling was set to rotate to new collectors every 7–26 days during times of high primary and secondary production (May-September), with longer sampling intervals (up to 32 days) during other months (see **Supplementary Table S1** for more details of sampling intervals).

Collected amphipods were removed and rinsed under a dissecting microscope (Olympus SZX10, magnification 20–50×). They were identified to species level and life stage and counted. For *T. abyssorum* and *T. compressa*, specimens <8 mm were considered as juveniles, whereas for *T. libellula*, the range <11 mm was chosen (lower size-limit: 2 mm, respectively), based on Kraft et al. (2011). In addition, numbers of *Lanceola clausii* were evaluated, because it was the most abundant amphipod after the three *Themisto* species.

We observed erratic peaks in amphipod abundances, especially in *T. abyssorum* (see also results **Figure 3**), suggesting

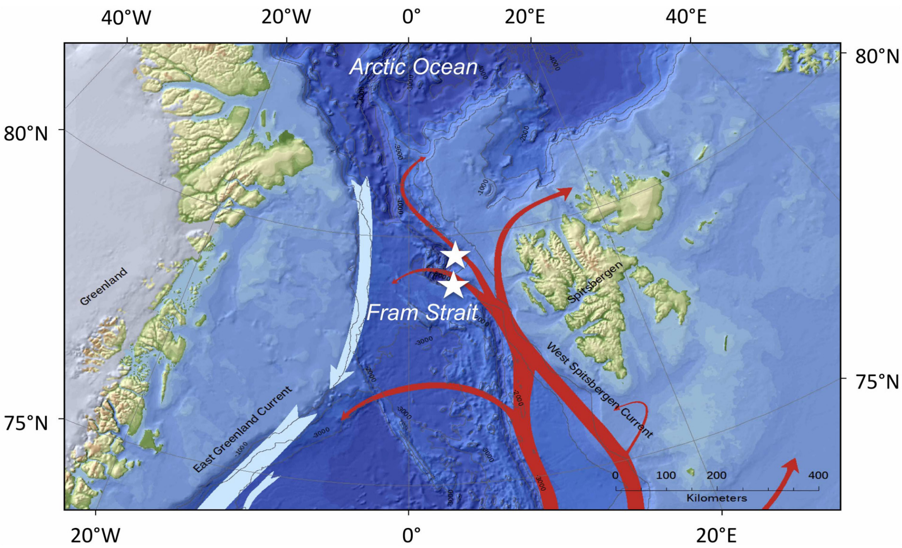

FIGURE 1 | Schematic map of the marine circulation patterns in the Fram Strait. The West Spitsbergen Current is delineated by red arrows; the East Greenland Current is depicted by light blue arrows. The stars in the center indicate the two mooring positions, North (upper asterisk) and Central (lower asterisk), in the LTER observatory HAUSGARTEN. The map was created using ArcGIS 10.3 and based on the General Bathymetric Chart of the Oceans (GEBCO)-08 grid, version 20100927, http://www.gebco.net, with permission from the British Oceanographic Data Centre (BODC).

TABLE 1 | Location, sampling time, water depth, and trap depth of moored sediment traps in the HAUSGARTEN and Greenland Sea analyzed for their amphipod composition with multivariate analyses.

Mooring period *in years*	Lat. N	Long. E	Water depth	Trap depth (*m*)	Number of samples	Remarks
2000–2001						
31.08.2000–14.08.2001	79°01.70′	04°20.86′	2456	280	18	Last two cups did not run
2004–2005						
15.07.2004–19.08.2005	**79°35.98′**	**05°09.86′**	**2784**	**280**	**20**	
15.07.2004–21.08.2005	79°00.99′	04°20.62′	2584	280	18	Last two cups did not run
2006–2007						
07.09.2006–20.06.2007	**79°36.07′**	**05°09.87′**	**2739**	**190**	**20**	
25.08.2006–20.06.2007	79°00.82′	04°20.50′	2540	230	20	
2007–2008						
21.07.2007–15.07.2008	79°00.82′	04°20.62′	2589	190	20	
2008–2009						
17.07.2008–18.07.2009	79°00.40′	04°20.00′	2557	201	20	
2011–2012						
01.08.2011–15.07.2012	**79°44.38′**	**04°30.37′**	**2690**	**200**	**20**	
01.08.2011–15.07.2012	79°00.42′	04°19.90′	2605	200	19	One cup degraded
2012–2013						
27.07.2012–30.06.2013	**79°44.38′**	**04°30.37′**	**2666**	**205**	**20**	
29.07.2013–30.06.2013	79°00.42′	04°19.90′	2554	205	19	One cup degraded
2013–2014						
05.07.2013–15.06.2014	**79°44.34′**	**04°30.24′**	**2675**	**205**	**16**	Four cups degraded
10.07.2013–15.06.2014	79°03.76′	04°1.81′	2567	205	17	Three cups degraded

If deviations from the routine occurred, the respective information is given in the last column. A complete sample set consisted of 20 cups (Bold shows moored traps at the northern position, normal font represents the central HAUSGARTEN site, see also ***Figure 1****). Degraded: Most of the sedimented material had disintegrated and was impossible to identify.*

an underestimation of individuals in some of the samples. Reasons for this are discussed below.

Incorporating data obtained in the study period 2000–2009, multivariate analysis was carried out using PRIMER 6 (Plymouth Marine Laboratory, United Kingdom) (Clarke and Gorley, 2005) to visualize the similarity between the abundances of the different *Themisto* species obtained in every sample for the different sampling periods and sites.

The averaged amphipod flux data (including rare species) were standardized and square root transformed to avoid large values (abundant species) overwhelming the analysis. Nevertheless, the rare species only marginally contributed to the clustering. Thereafter, similarities between the groups of sample sets were checked. Comparing these sample sets, a resemblance matrix was generated applying the Bray-Curtis measure, because this measure was shown to apply best to marine data (Field et al., 1982). Based on the resemblance matrix, a multidimensional scaling (MDS) plot was generated for the established spatial and temporal criteria (Field et al., 1982; Clarke and Gorley, 2005). Similarity Percentage (SIMPER) routines were applied to highlight the species mainly responsible for the differences between the sample clusters (Clarke and Gorley, 2005).

RESULTS

Amphipod Swimmer Composition in Traps 2011–2014

Analyzing six sediment traps of three consecutive years, a total of 10,906 specimens comprising seven different amphipod species were found in the traps – in order of decreasing abundance: *T. abyssorum*, *T. libellula*, *T. compressa* (**Figure 2**), *L. clausii*, *Eusirus holmii*, *Hyperia medusarum*, and *Gammarus wilkitzkii*, representing four different families (Hyperiidae, Lanceolidae, Eusiridae, and Gammaridae) (see **Supplementary Table S1** for all and **Supplementary Table S2** for rare species abundances).

The hyperiid genus *Themisto* dominated the epipelagic amphipod counts by >97%. The three dominating pelagic *Themisto* spp. showed significant seasonal, inter-annual and spatial variability over the studied period 2011–2014 (**Figure 3**), with high abundances in summer and lower numbers in winter. The highest peaks of *T. libellula* were observed at the end of summer (August–September), at both sites, in most cases with maximal abundances in periods of maximum ice cover. Monthly abundances of *T. abyssorum* were more variable regionally; for the northern HAUSGARTEN site they were highest in August, whereas in the central site they were highest in June for 2012 and in September for 2013, coinciding with ice-free periods. Overall, *T. abyssorum* dominated the amphipod community by >50%. However, in 2012/13, *T. abyssorum* and *T. libellula* were present in nearly equal proportions (∼40%, respectively), over the entire year at both HAUSGARTEN sites. Whereas the two native *Themisto* species were present and dominating throughout the year, *T. compressa* was absent in the trap samples over long periods in winter (November–February), reappearing in spring. Abundances of this North Atlantic species remained elevated compared to the mid-2000s, with noteworthy counts in late summer 2011. *L. clausii* was the most abundant amphipod species after the three *Themisto* spp. with 19 specimens collected between 2011 and 2014. Previously, this species was absent, but, similarly to *T. compressa* – it became more abundant although to a much lower degree.

Population Structures (2011–2014), Sex Ratio and Life Stages of *Themisto* spp.

Examination of the occurrences of the different life stages (**Figure 4**) showed noteworthy proportions of juveniles of *T. abyssorum* (up to 8% of the total specimens). These were found at each site both in winter and summer, with higher proportions in winter. Focusing on the sample sites, higher proportions of juvenile *T. abyssorum* were observed at the northern HAUSGARTEN site compared to the central location. For *T. libellula*, juveniles did not reach more than 1% of the total individuals. Not a single juvenile specimen of *T. compressa* was recorded in this study during winter, and only very few occurred in summer (max. 1% of the total individuals). Females were always dominant for all three species, with a maximum value of 96% in *T. libellula*. For both *T. abyssorum* and *T. libellula*, the sex ratio was even more skewed toward female dominance in summer than in winter at both sites. The opposite was true for *T. compressa*, where the largest proportions of females occurred in winter at both sites.

Trends in *Themisto* spp. Abundances Over the Entire Sampling Period (2000–2014)

We combined our abundance data from the different years of observations (2011–2014) with the data (2000–2011) of Kraft's (2010) Ph.D. thesis and detected a compositional dissimilarity of the amphipod community between different sampling periods. A separation of earlier samples from those collected for this study is apparent (**Figure 5**). Altogether, the ordination plot suggests three different clusters: the 2000/01 sample, both 2012/13 samples, and the remaining samples. SIMPER analysis (**Supplementary Table S3**) showed a clear trend of increased contributions of high *Themisto compressa* abundances toward the right domain of the ordination chart (**Figure 5**). Furthermore, a tendency of increasing *T. libellula* abundances toward the upper domain of the chart could be identified, and vice versa for *T. abyssorum*. The exclusive position of the sample on the very left in the MDS-plot (2000/01 in **Figure 5**) was mainly due to the absence of *T. compressa* in that sampling period. The joint isolated positions of the 2012/13 samples were caused by increased abundances of *T. compressa* and *T. libellula*, as well as by relatively low abundances of *T. abyssorum*, compared to other years.

DISCUSSION

General Long-Term Trends of *Themisto* spp. at LTER HAUSGARTEN in the Eastern Fram Strait

The focus of this study was to verify the trends in dominating pelagic amphipod swimmer abundances recorded by Kraft et al. (2011, 2013) by investigating three more consecutive years (2011–2014) of amphipod sampling at two locations within the LTER observatory HAUSGARTEN. As amphipod species are more abundant in particular water masses

FIGURE 2 | Proportion of amphipod abundances (%) at HAUSGARTEN Central Station per sampling period. Details for the years 2009/10 and 2010/11 can be found in the **Supplementary Material**.

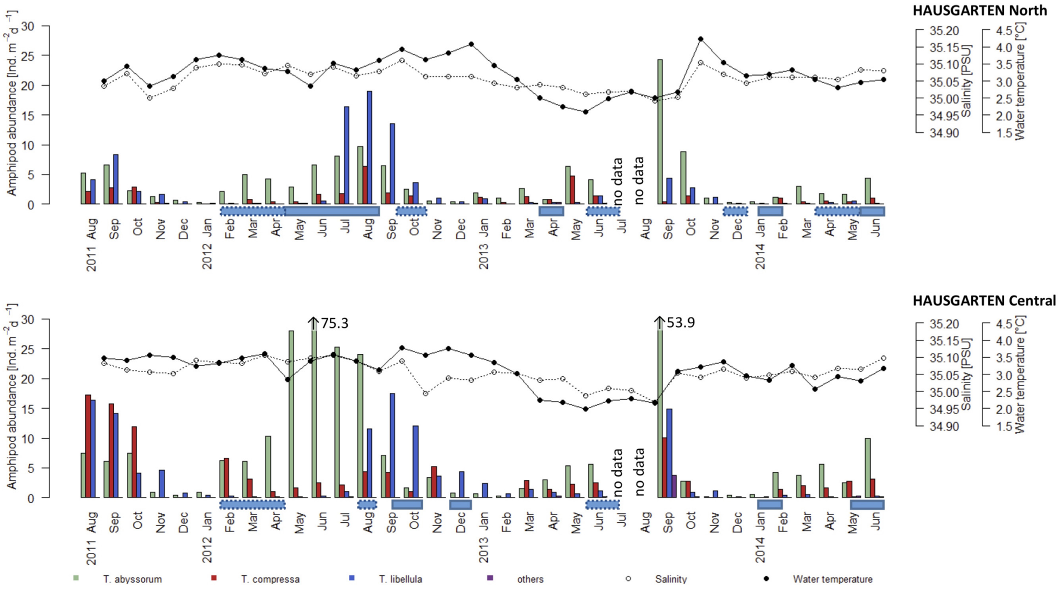

FIGURE 3 | Progression of mean monthly amphipod abundance (Ind.m^{-2}d^{-1}) in HAUSGARTEN sediment traps along a latitudinal gradient: northern (upper panel) and central position (lower panel). Note the off-scale values of *Themisto abyssorum* in the lower panel (dashed boxes = periods of occasional ice cover, solid boxes = permanent ice cover). Connected dots represent the salinity (open circles) and temperature (filled circles) values across the years (for amphipod species color codes, see **Figure 2**).

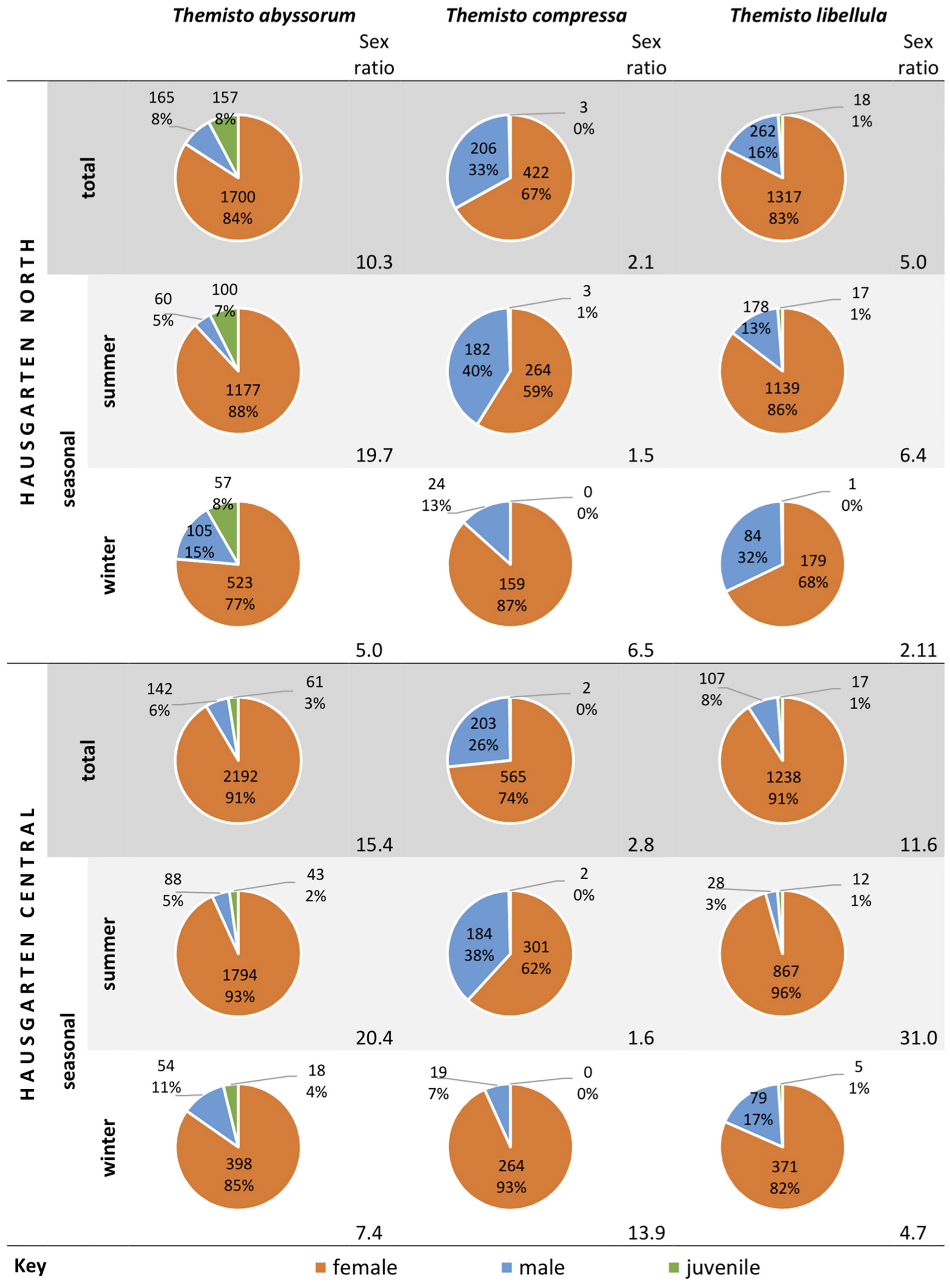

FIGURE 4 | Total and seasonal percentages of gender and maturity of the *Themisto* species between 2011 and 2014; absolute numbers are counts, relative numbers are proportions of total counts. Sex ratios = female counts/male counts. Missing data were replaced with comparative means of the respective month.

(Dalpadado et al., 2001), they may serve as sentinel species to detect changes in the pelagic environment. With this new dataset, we also analyzed the population structure of the three dominating amphipod species.

The trends of respective abundances of the two native *Themisto* species – the boreal *T. abyssorum* and the Arctic *T. libellula* – as well of that of the intruding *T. compressa*, corroborated the observations from the period 2000–2012 described by Kraft et al. (2013). In the period 2000–2012, total amphipod counts increased by a factor of 14 during and after a warm anomaly (**Supplementary Figure S1**) observed in the HAUSGARTEN area, and counts remained equally high until 2014 (**Figures 2, 3**) despite the more stable water temperatures (**Supplementary Figure S1**).

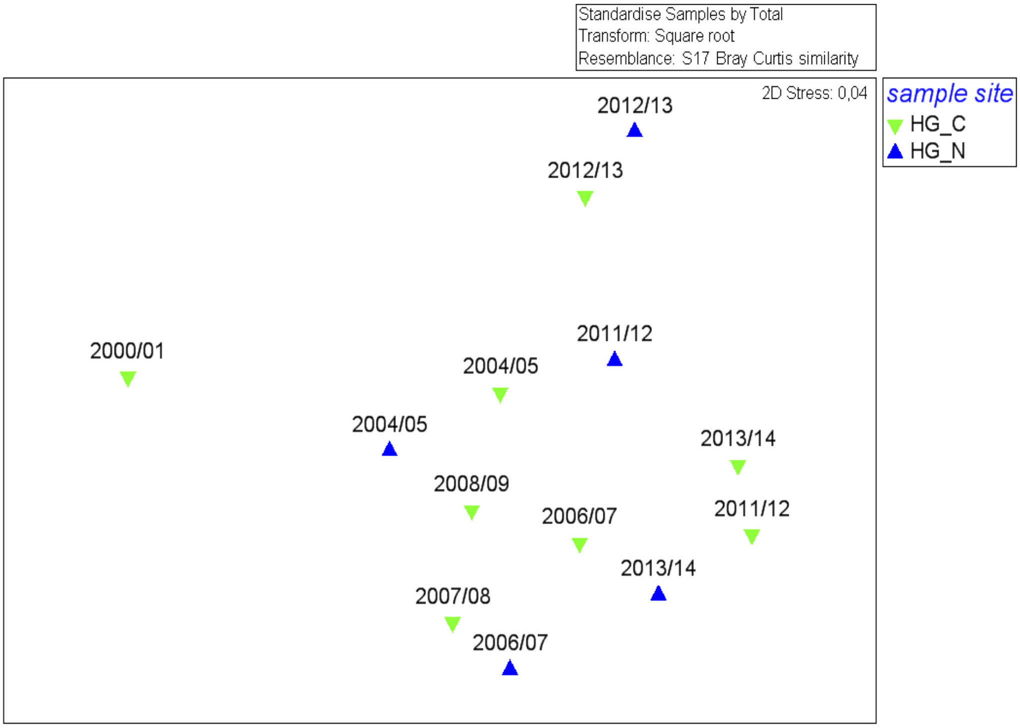

FIGURE 5 | Multi-Dimensional Scaling plot of mean amphipod abundances (Ind.m^{-2}d^{-1}) in HAUSGARTEN sediment traps (2000–2014) based on the Bray Curtis similarity measure. Blue upright triangles indicate the northern sampling locations, green inverted triangles represent the central moorings. Data ranging from 2000 to 2009 were obtained and analyzed by Kraft (2010).

Bottom-up and top-down processes similarly could have caused this tremendous increase in amphipod counts. Soltwedel et al. (2016) reported a slight increase of chlorophyll *a* biomass in the Fram Strait's surface waters as well as in the water column. Hence, they suggested an increase of phytoplankton biomass in the region from 2008 onward (Soltwedel et al., 2016). These findings are complemented by Nöthig et al. (2015) documenting increasing chlorophyll *a* concentrations in the WSC since the 1990s during summer months. This development provided more food for pelagic herbivorous copepods, which in the Fram Strait mainly comprises the genus *Calanus* (Hirche et al., 1994; Mumm et al., 1998; Hop et al., 2006; Hildebrandt et al., 2014). It has been shown that egg production in *Calanus glacialis* was positively correlated to chlorophyll *a* concentration (Hirche et al., 1994). Supporting this, an increase of ∼50% in copepod abundances in central HAUSGARTEN sediment taps was evident between 2000 and 2014 (Nöthig et al., unpublished data). It is thus possible that raptorial carnivores, such as amphipods of the genus *Themisto* (Dalpadado et al., 2008b; Kraft et al., 2015), found sufficient prey, which might have caused the continuously increasing amphipod abundances. However, we do not know whether the 50% increase in food availability would have been enough to sustain the very high numbers of amphipods we report. One could speculate that, in addition, amphipods were not so heavily preyed upon by higher trophic levels.

Similarly, a top-down mechanism could have caused increased amphipod abundances. Amphipods are important prey for fish (e.g., capelin, cod), birds (e.g., little auk), and marine mammals (e.g., ringed seal) (Klekowski and Węsławski, 1991; Dalpadado et al., 2001, 2008b; Auel and Werner, 2003; Melle et al., 2004). For the Barents Sea, Dalpadado et al. (2001) suggested a strong predator-prey interaction between amphipods and fish such as cod and capelin. They further demonstrated that low abundances in predatory fish were accompanied by increased amphipod stocks, and vice versa (Dalpadado et al., 2001). Hence, it is very likely that in this trophic interaction, the release of predation pressure results in the recovery of amphipods preyed upon. Dalpadado et al. (2001) also suggested that this mechanism mainly controls amphipod populations in the Barents Sea. According to the Norwegian Directorate of Fisheries (2015), catches of capelin, haddock, and herring declined between 2010 and 2014, whereas Atlantic cod (*Gadus morhua*) catches increased by ∼30% for the same time frame. Given the high commercial value of Atlantic cod and haddock (Norwegian Directorate of Fisheries, 2015), a recently observed northward shift of Atlantic cod (Christiansen et al., 2016) and an enormous increase of fishing vessel sightings near Svalbard (Bergmann and Klages, 2012), the potential fishing pressure may remain high, relieving the amphipods from predation impact.

The three dominant pelagic *Themisto* species showed significant seasonal, inter-annual and spatial variability (**Figure 3**), with high abundances in summer and lower numbers in winter. Overall, *T. abyssorum* dominated the amphipod community by >50% during the period 2011–2014, corresponding to Kraft et al. (2011) results. However, in 2012/13, *T. abyssorum* and *T. libellula* were present in nearly equal proportions (∼40%, respectively) at both HAUSGARTEN sites. This sampling period was characterized by extraordinary ocean temperatures starting with a warm winter followed by a pronounced temperature drop, with cold water prevailing the entire summer of 2013 (Walczowski et al., 2017). It has been demonstrated that *T. abyssorum* was more abundant than *T. libellula* when warm WSC water predominated (Koszteyn et al., 1995; Dalpadado, 2002; Dalpadado et al., 2008a,b, 2016). Hence, the broad impact of the WSC may explain the observed predominance of *T. abyssorum* at the HAUSGARTEN, potentially coupled with increased reproductive rates and/or less predation mortality as discussed above. High reproductive rates were observed at both sites over the study period as indicated by the high proportions of juveniles compared with the two other species and their ubiquity over both seasons.

Whereas the two common species in the study area were present and dominating throughout the year, *T. compressa* was absent in the trap samples over long periods in winter (November–February). The reappearance of this species in spring may thus indicate an "allochthonous origin" as speculated by Kraft et al. (2013). Abundances of this North Atlantic species remained elevated compared to the mid-2000s, with noteworthy counts in late summer 2011, which may be attributed to inflow of warmer Atlantic water causing higher ocean temperatures in the eastern Fram Strait between 2011 and 2012 (Beszczynska-Möller et al., 2012; Walczowski, 2013; Gluchowska et al., 2017). This warm event has also been shown to be related to a substantial increase in abundances of the Atlantic-associated copepod *Calanus finmarchicus* in the WSC (Gluchowska et al., 2017). Irrespective of its winter absences, *T. compressa* appears to have become a common species in the eastern Fram Strait. To date, however, the species has not yet been recorded in the central Arctic (Kosobokova et al., 2011; Kosobokova, personal communication). *L. clausii* was the most abundant amphipod species after the three *Themisto* spp. with 19 specimens collected between 2011 and 2014. Previously, it was absent, but, – similarly to *T. compressa* in July 2004 – it became more abundant, although on a lower scale.

In this study we observed erratic peaks in amphipod abundances, especially in *T. abyssorum* (see **Figure 3**). Swarms or high density aggregations of *T. abyssorum*, *T. compressa* and *T. libellula* have previously been recorded both on the seafloor and in the water column (Lampitt et al., 1993; Vinogradov, 1999; Angel and Pugh, 2000). We assume that swarms of *Themisto* spp. were present at the sediment traps no later than the end of July 2013 (**Figure 3**), accumulating in the instruments' funnels, filling the sample cups to the top, and thus exceeding the poison's capacity to preserve the samples and resulting in degraded samples (Lee et al., 1992). A funnel full of swimmers would also explain the prolonged event lasting until early September 2013, with swimmer material filling up the next sample cup entirely when it was exposed for sampling. Strikingly, degraded samples occurred concurrently at both the central and the northern locations between July and early September 2013, for which similar mechanisms causing the degradation can be assumed. Furthermore, we suggest that due to degradation, significant numbers of amphipods are not included in the data, possibly leading to an underestimation of the maximum abundances recorded. In this context, the occasional *T. abyssorum* abundance peaks as in June 2012 and September 2013 (75.3 and 53.9 Ind. $m^{-2}d^{-1}$, respectively; **Figure 3**) were unexpected and can similarly be considered records of swarming events.

Population Structure of *Themisto* spp. in the Eastern Fram Strait During 2011–2014

Noteworthy proportions of juveniles of *T. abyssorum* (up to 8% of the total individuals) were recorded, which is consistent with Kraft et al. (2012). These were higher at the northern HAUSGARTEN site compared to the central location (**Figure 4**). This difference between sites coincides with a difference of ca. + 0.1°C in mean water temperature between August 2011 and June 2014 at the northern station compared to the central station and differences in sea ice cover. Juveniles were present in both seasons at both sites (contradicting Kraft, 2010), indicating more than one spawning period per year, as discussed by Koszteyn et al. (1995). This outcome contrasts with Kraft (2010), who obtained a seasonal pattern for juvenile *T. abyssorum* abundances, hence suggesting a seasonal migration of juveniles or lower reproductive rates. Not a single juvenile specimen of *T. compressa* was recorded in this study during winter, and only very few occurred in summer (max. 1% of the total specimen count), indicating no or only limited reproduction in the area; this is supported by Kraft et al. (2012). However, the record of Kraft et al. (2013) of brooding females in the traps may indicate that reproduction of *T. compressa* in the area is possible, but still rare. Very low numbers of juvenile *T. libellula* were recorded, irrespective of location and season (max. 1% of the total specimen count), whereas other investigations reported elevated numbers of juveniles between May and June (Percy, 1993; Koszteyn et al., 1995; Dale et al., 2006; Kraft et al., 2012). This may imply unfavorable reproductive conditions for the true Arctic *T. libellula* in a warming environment, as suggested by Dalpadado et al. (2016).

Maturity studies based on net hauls (e.g., Williams and Robins, 1981; Koszteyn et al., 1995; Dalpadado, 2002; Dale et al., 2006; Dalpadado et al., 2016) do not provide year-round data sets as do sediment trap catches (e.g., Kraft et al., 2012). Whereas net catches conducted in the Barents Sea by Dalpadado (2002) between August-September 1993 yielded juvenile proportions of up to 88% for *T. abyssorum* and 80% for *T. libellula*, a maximum percentage of 8% was recorded for *T. abyssorum* herein. Large relative numbers of juveniles have also been found in similar studies in the Greenland and Barents seas (e.g., Koszteyn et al., 1995; Dale et al., 2006). On the other hand, size distributions found herein agree with other sediment trap-approaches, such as Kraft et al. (2012), who generally observed very few juveniles. The different approaches target different depths, and it is known that *Themisto* spp. are often segregated by depth in the water column according to sex and life stage (Williams and Robins, 1981; Węsławski et al., 2006). Varying criteria for classifying life stages (juveniles, immature adults, mature adults) (Williams and Robins, 1981; Percy, 1993; Węsławski et al., 2006) and seasonal migratory behavior (Percy, 1993; Kraft, 2010) may also account for the large discrepancies in the outcomes.

Community Changes of *Themisto* spp. at LTER HAUSGARTEN in the Eastern Fram Strait

By combining data on pelagic amphipods species from this study (2011–2014) with Kraft (2010) *Themisto* spp. and other pelagic amphipod data sets from her Ph.D. thesis (2000–2011), we obtained a broader view of the amphipod community development between 2000 and 2014. Within this time frame, a separation of older and more recent samples is apparent (**Figure 5**), indicating a development of the system.

According to the similarity analyses of species composition between the different years and sites, the trend of increased *T. compressa* proportions most probably caused the dissimilarity over years. In general, the system has changed to a state of higher *T. compressa* abundances reflected by an increasing contribution of this species to the observed cluster patterns. Thus, the lack of *T. compressa* in the 2000/01 sample resulted in its strong dissimilarity with other samples. Furthermore, increased *T. libellula* abundances mainly contributed to the vertical separation of the samples with increasing numbers in the upper domain. Similarly, high *T. abyssorum* abundances contributed to the vertical clustering with highest values in the lower domain of the chart. However, these trends do not seem to indicate a continuous temporal development as discussed for *T. compressa*. These trends are reflected in the 2012/13 samples because their dissimilarity was mainly due to high cluster contributions of increased abundances of *T. compressa* and *T. libellula* as well as to low abundances of *T. abyssorum*. Interestingly, the 2012/13 winter was characterized by notably high ocean temperatures followed by a subsequent cold summer (**Supplementary Figure S1**, as mentioned in Gluchowska et al., 2017). We speculate that the abundances of *T. libellula* did not appear to be affected by increased abundances of the intruding *T. compressa*, at least under cold water conditions; however, abundances of *T. abyssorum* appeared to be adversely influenced (see also Stempniewicz et al., 2007). We further speculate that even though *T. abyssorum* is assumed to tolerate a high temperature gradient and show high abundances in Atlantic water masses (Dalpadado, 2002), competition between *T. compressa* and *T. abyssorum* may play a role, given their similar sizes and ecological roles (e.g., carnivorous feeding type – see Kraft et al., 2015).

Variations and possible shifts in amphipod proportions of the three dominant pelagic hyperiids are evident based on our long-term data series. The occurrence of the North Atlantic species *T. compressa* (Kraft et al., 2013) continued until 2014, which may be attributed to higher water temperatures (**Supplementary Figure S1**; Walczowski et al., 2017). The latter was confirmed by the observation that the abundances observed at the central HAUSGARTEN site were considerably higher than at the northern location. The system is evidently shifting toward a warm, more North Atlantic-influenced state (Gluchowska et al., 2017), potentially causing Arctic species to decline (Dalpadado et al., 2016). This is corroborated by the low numbers of juveniles of the true Arctic *T. libellula* in the sampling period 2013/14, even though previously, these were commonly detected. The replacement of the larger, lipid-rich *T. libellula* by the sub-Arctic and temperate species *T. abyssorum* and *T. compressa* in the Arctic could change the food chain pattern with possible consequences for fish, whale and bird populations that depend on this species as major prey. For example, little Auks (*Alle alle*) feed predominantly on the largest size class of *T. libellula* (Lønne and Gabrielsen, 1992), and hence, the other *Themisto* species cannot eventually act as substitutes because of their smaller size.

Warming water temperatures are a likely cause of the increasing amphipod abundances between 2000 and 2014 that are potentially affecting trophic interactions and increasing competition between *Themisto* spp. Thus, more temperate species evidently extended their range into the Arctic, as we demonstrated by the seasonal establishment of the North Atlantic species *T. compressa*. Other, previously unsampled species are newly appearing in the Fram Strait sediment traps, with the most abundant being the hyperiid *L. clausii*. These outcomes suggest ongoing environmental shifts taking place in the seasonally ice-covered eastern Fram Strait. For a better understanding of species interactions and for firm predictions regarding future pelagic communities, more regionally and temporally extensive studies on the topic are urgently needed.

DATA AVAILABILITY

The datasets for the 2011–2014 data can be found in the supplementary information. The existing data (2000–2011) can be found in the PANGAEA repository: Oceanographic data sets see Bauerfeind et al. (2015), amphipod numbers see Kraft et al. (2012).

AUTHOR CONTRIBUTIONS

FS wrote the manuscript together with E-MN and CH. AK, AB-M, NK, and EB provided the data of amphipods, hydrography as well as trap, and mooring logistics and analyzed the respective data sets. All authors involved in discussions about the amphipod development in the Fram Strait in the long-term perspective of environmental change in the Arctic Ocean and revised and approved the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00311/full#supplementary-material

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