

NOTE

First evidence of reproductive success in a southern invader indicates possible community shifts among Arctic zooplankton

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ABSTRACT: Pelagic zooplankton were monitored from 2000 to 2012 at a permanent location near the Svalbard archipelago, at the boundary between the central Arctic Ocean and the Greenland Sea in the eastern Fram Strait. The temporal results reveal the first evidence of successful reproduction in Arctic waters by an Atlantic pelagic crustacean from temperate waters. The Atlantic hyperiid amphipod *Themisto compressa* is shown to have expanded its range from more southerly and warmer waters from 2004 onwards. Successful reproductive activity by *T. compressa* in Arctic waters was confirmed in 2011, indicated by the presence of a complete temporal series of developmental stages including ovigerous females and recently hatched juveniles. The Arctic amphipod community is currently in transition and a continuing northward spread of southern invaders could cause a biodiversity shift from large Arctic to smaller Atlantic species.

KEY WORDS: Hyperiid amphipod · Arctic marine ecology · Biodiversity · Biogeographic boundaries

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INTRODUCTION

Shifts in Arctic ecosystems are expected to be coupled with changing environmental conditions, such as increasing temperature and disappearing sea-ice cover (Wassmann et al. 2011). With a new record low sea-ice minimum of 3.41×10^6 km² (NSIDC 2012) recorded on September 16, 2012, indications are that the Arctic is in transition towards a new, warmer state (Polyakov et al. 2007, Lenton 2012). Current climate

models predict the contraction and thinning of Arctic sea ice, with ice-free summers in the Arctic Ocean by 2050 or earlier (Stroeve et al. 2007, Wang & Overland 2009). With climate warming come new impacts on established Arctic ecosystems, including shifts among the marine communities. Published examples include the re-appearance of the blue mussel *Mytilus edulis* in the Arctic for the first time since the Viking Age, 1000 to 1300 BP (Berge et al. 2005) and the occurrence of 3 temperate euphausiids (*Thysanoessa longi-*

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caudata, *Meganyctiphanes norvegica* and *Nematoscelis megalops*) in Kongsfjorden, West Spitsbergen, Svalbard (Buchholz et al. 2010). However, none of those southern invaders are considered to be breeding in the Arctic, presumably because of the low temperature constraint (Berge et al. 2005, Dalpadado et al. 2008a,b, Buchholz et al. 2010). Reproductive success for a given species could be indicated by observing a temporal sequence of egg maturation and recording the presence of live juveniles in the new environment. Such reproductive activity of newly introduced species in Arctic waters would indicate warming events in their habitats, or a successful adaptation to lower temperatures, and possibly a shift in food web composition of high Arctic ecosystems. Here we report the first appearance of breeding females and juvenile individuals of a North Atlantic (Sheader 1981, Williams & Robins 1981, Lampitt et al. 1993), free-swimming, open-water invader, the hyperiid amphipod *Themisto compressa*, in the high Arctic waters of the northern Fram Strait.

MATERIALS AND METHODS

All samples were collected using modified automatic Kiel sediment traps (0.5 m² opening and 20 collection cups) from September 2000 to July 2012. Traps were retrieved during 12 expeditions to the Arctic long-term HAUSGARTEN observatory in the northeastern Fram Strait. The mooring was located at 79° 03' N, 04° 11' E, with a sampling depth of 190 to 280 m. Water depth at this location was 2567 m. Recorded water temperatures for 2000 to 2004 originated from an oceanographic mooring located 20 km south of the sediment trap moorings, and for 2005 to 2012, from current meter measurements at a nominal depth of ~250 m at the sediment trap moorings. Collector cups of the sediment traps were filled with filtered, sterile North Sea water at an adjusted salinity of 40 psu and poisoned with HgCl₂ (0.14 % final solution). Automatic sampling was set to rotate to new collectors every 10 to 16 d during times of high primary and secondary production (May to September), with longer sampling intervals (up to 32 d) during other months. Collected individuals (known as 'swimmers') were removed and rinsed under a dissecting microscope (Olympus SZX10, magnification ×20–50). Amphipods were identified to species and stage, counted and measured. Maturity was determined by examination of secondary sexual characters. As live bearers, females contain brood lamellae (oostegites) which develop into a brood chamber

(marsupium); in fully mature females, the oostegites carry setae. Males were recognized by long, segmented antennae and considered mature when 13 or more segments were counted (Kane 1963).

RESULTS AND DISCUSSION

Since 2000, a long-term observatory has been maintained by the Alfred Wegener Institute Helmholtz Center for Polar and Marine Research (the 'HAUSGARTEN') at the boundary between the central Arctic Ocean and the Greenland Sea, providing a serendipitous opportunity to collect year-round zooplankton samples known as 'swimmers' from moored sediment traps. From the beginning of observations in September 2000, pelagic amphipods of the genus *Themisto* (Hyperiididae) have dominated the amphipod community in the traps in terms of biomass (Kraft et al. 2011, 2012). In July 2004, we first observed the appearance of the North Atlantic hyperiid amphipod *Themisto compressa* at 79° N in the European Arctic (Kraft et al. 2011). The number of collected individuals over time increased until June 2012 (Fig. 1). The sampling site was located in the Fram Strait, an important transition zone, characterized by a large exchange of Arctic waters with those of Atlantic origin (Quadfasel et al. 1987, Schauer et al. 2008). With the northward-flowing West Spitsbergen Current located over the upper continental slope, relatively warm Atlantic waters are transported from the North Atlantic into the Arctic Ocean Boundary Current (Quadfasel et al. 1987, Manley 1995). At the HAUSGARTEN site, the core of the West Spitsbergen Current is present throughout the year. A characteristic feature of this current system is a high seasonal to inter-annual variability of temperature of Atlantic water flowing into the Arctic Ocean (Saloranta & Haugan 2001, Beszczynska-Möller et al. 2012). A progressive warming of the core of the West Spitsbergen Current has been recorded since the continuous measurements made by oceanographic moored array at 78° 5' N started in 1997 (Beszczynska-Möller et al. 2012). The highest recorded values of temperature and salinity in the core of Atlantic Water were observed in 2006 (Walczowski & Piechura 2007, Walczowski et al. 2012). Concomitantly, a progressive reduction of sea ice coverage and increased sea ice export through the Fram Strait has been observed since 2003 (Spren et al. 2009).

Among Arctic macrozooplankton, pelagic amphipods act as predators on herbivorous zooplankters, forming a link to higher trophic levels as a food

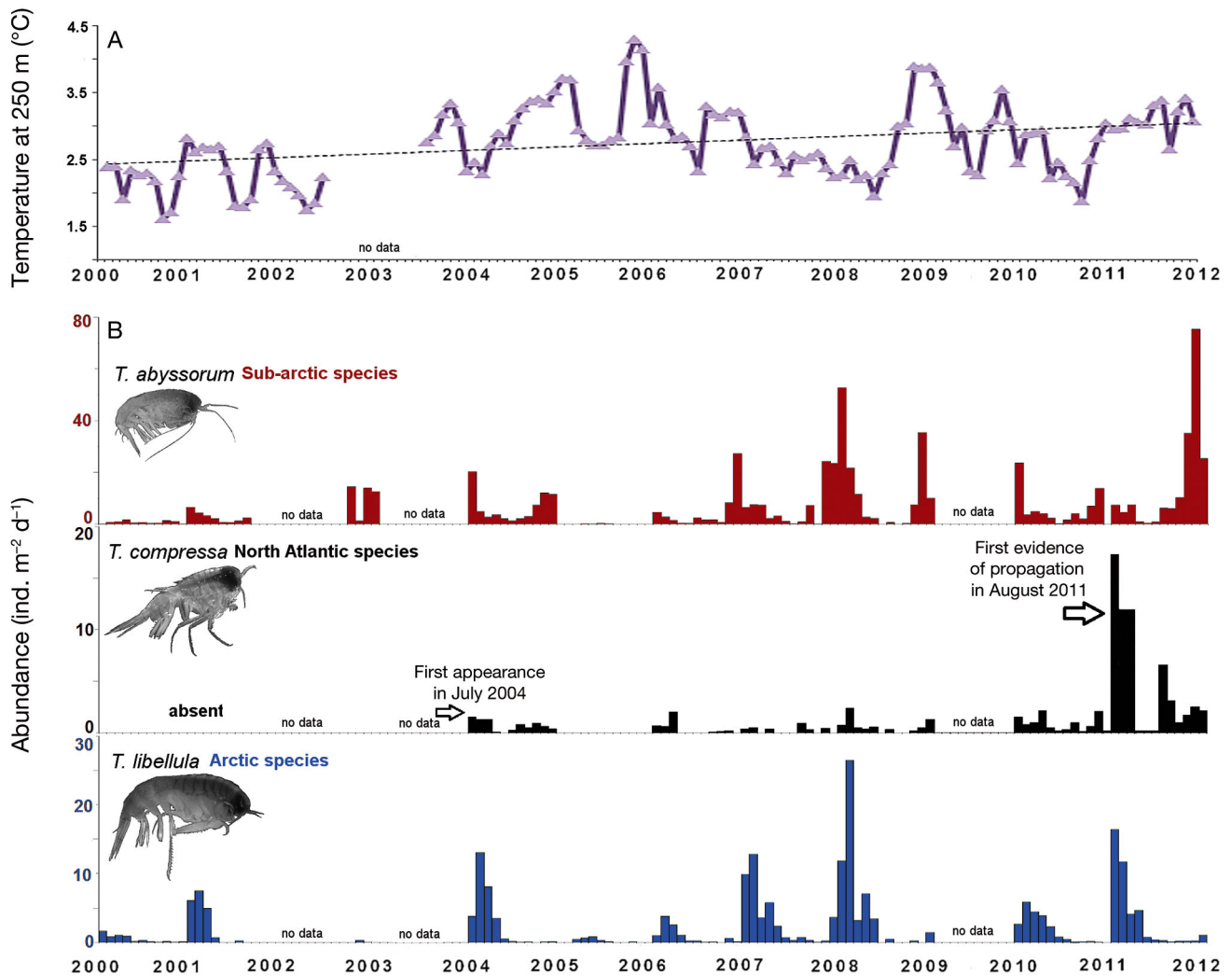


Fig. 1. *Themisto abyssorum*, *Themisto compressa*, and *Themisto libellula*. (A) Long-term progression of Atlantic water temperature at 250 m depth, showing an increasing trend of 0.06°C yr⁻¹ from 2000 to 2012, and (B) occurrences of 3 different temperature-adapted amphipod species (genus *Themisto*, family Hyperiididae) in the northeastern Fram Strait, Arctic Ocean

source for sea birds and marine mammals (Bradstreet & Cross 1982, Lønne & Gulliksen 1989, Hobson et al. 2002, Dalpadado & Bogstad 2004, Dalpadado et al. 2008b, Noyon et al. 2009). Our observations show that numbers of collected individuals of the North Atlantic invader *Themisto compressa*, which ranks third in abundance (ind. m⁻² d⁻¹) in sediment trap samples, have significantly increased compared to its sub-Arctic and Arctic relatives (*Themisto abyssorum* and *Themisto libellula*, respectively) (Fig. 1). Furthermore, *T. compressa* has established an annually re-appearing population at higher latitudes. A trend towards more frequent appearances of North Atlantic species such as *T. compressa*, as a result of Atlantification processes and its potential competi-

tion with *T. abyssorum* and *T. libellula*, was also suggested by Stempniewicz et al. (2007). Here, we recorded an increasing contribution of both the sub-arctic *T. abyssorum* and the temperate *T. compressa* to the zooplankton community over a period of 8 yr (Fig. 1).

Our most recent trap samples provided an even greater surprise: based on late summer samples from August to early September 2011, we found, for the first time, evidence of reproductive success within *Themisto compressa*. Since the first appearance of this southern, temperate invader in 2004 in the northern Fram Strait, neither evidence of reproducing individuals nor presence of juveniles of *T. compressa* had been recorded in our trap samples or elsewhere.

Our observations in 2011 included a total of 21 ovigerous individuals with fertilized eggs, as well as recently hatched juveniles (Fig. 2). Developmental stages of juveniles appeared in September and October 2011. The species has a presumed life span of up to 2 yr in sub-arctic waters, and we recorded up to 3 size cohorts (juveniles, sub-adults and adults) from October 2011 onwards in the traps. The cohort structure of *T. compressa* indicated a time span of 10 to 12 wk for the development from newly hatched juveniles to sub-adult individuals. Our samples also indicated that after 9 to 12 mo of maturation, a new generation of fertile *T. compressa* individuals might have been present in the investigation area (Fig. 2). The mean current speed of $\sim 13 \text{ cm s}^{-1}$ in the core Atlantic water of the West Spitsbergen Current (Beszczynska-Möller et al. 2012) suggests that passive transport of ovigerous females from southern breeding grounds, such as from the North Atlantic (60°N), would take at least 150 d for organisms to reach the northeastern Fram Strait. Given an estimated egg incubation time of 1 to 2 mo for females and a development time of 3 mo from hatched juveniles to sub-adults, the alternate hypothesis that the juveniles originated from more southern breeding grounds seems unlikely, though possible. In support of active Arctic reproduction, different stages of egg maturation were represented in samples from August to October 2011. Each female carried 23 to 56 fertilized eggs (mean diameter $125 \mu\text{m}$) or newly hatched juveniles in their brood pouch (Fig. 2). Furthermore, the

seasonally oriented sediment trap sampling revealed the temporal sequence of egg maturation within *T. compressa* females. Although we are not certain about the retention mechanisms involved that allow the establishment of a stable population of this species in high Arctic waters, our findings may indicate the first evidence that this species has successfully reproduced in high Arctic waters. This supersedes recently published results of its non-reproducing state up to 2010 (Kraft et al. 2012).

The fertility of sub-arctic and temperate species in Arctic waters has been the subject of debate, with different opinions within the zooplankton research community. For example, among euphausiids, the North Atlantic species *Thysanoessa longicaudata* is not considered to be reproductively competent in Arctic habitats, such as the fjords of Svalbard, due to low temperature constraint (Dalpadado et al. 2008a,b). It has also been suggested that the Arctic marginal ice zone, characterized by mean water temperatures below 5°C , may be the reproductive barrier for *T. longicaudata* (Dalpadado et al. 2008b). However, if temperate amphipods successfully reproduce and establish a stable population in high Arctic waters, the effects of shifting sea ice conditions and Atlantification (Reigstad et al. 2002, Gabric et al. 2005) should be studied in the context of integrated food web analysis (Hirche & Kosobokova 2007). Observations of full reproductive competence may thus serve to indicate a regime shift from Arctic to boreal conditions.

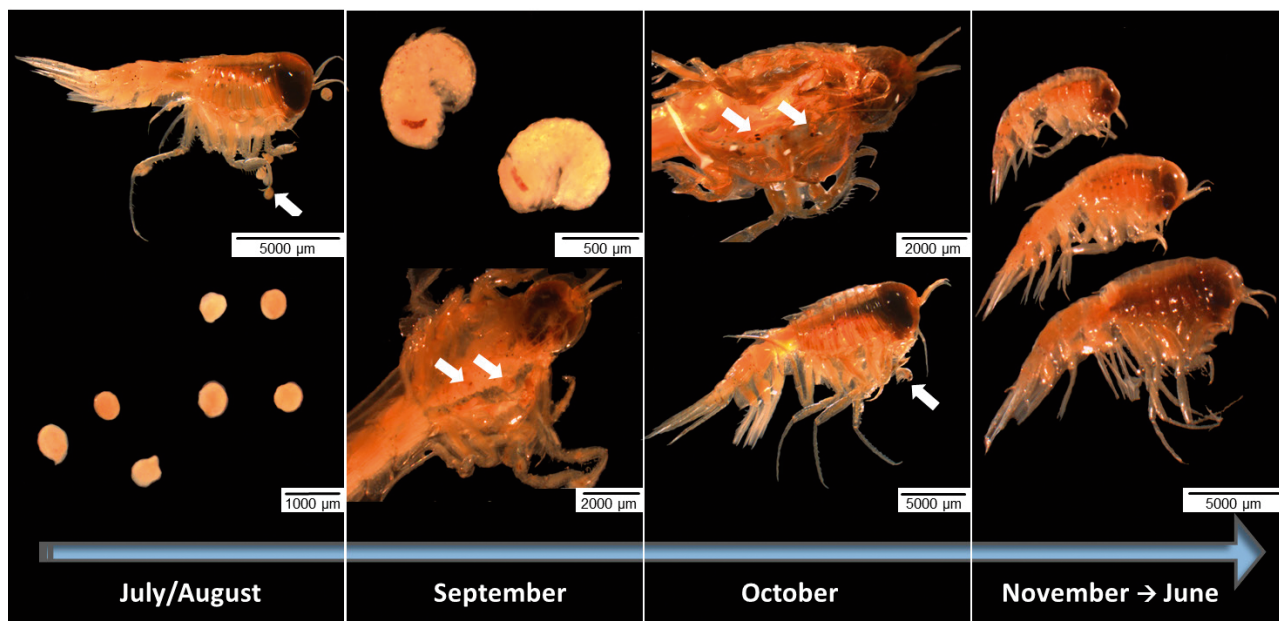


Fig. 2. *Themisto compressa*. Ovigerous individuals with fertilized eggs and recently hatched juveniles from July 2011 to June 2012. Arrows indicate eggs and juveniles observed in or next to the brood pouch

We conclude that a continuing northward spread of southern temperate species might cause an ecosystem and biodiversity shift from large Arctic to smaller Atlantic species. With such a modification of the short Arctic food web, there will certainly be winners and losers, as suggested by recent reviews across numerous Arctic environments (Weslawski et al. 2010, 2011). One consequence could be a dissipation of the energy flow by a higher diversity and abundance of small carnivorous zooplankton, and a resulting increased competition for habitat and food sources among cold-adapted taxa. Arctic top predators such as fishes, sea birds and marine mammals will have to adjust to a new diet, consisting not only of large Arctic zooplankters such as *Themisto libellula* but also smaller temperate congeners such as *T. compressa*. Finally, if our conclusions are correct, our results provide biological evidence that the Arctic zooplankton community is already transitioning towards a new, warmer ecosystem state.

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