Arctic pelagic amphipods - community patterns and life-cycle history in a warming Arctic Ocean

von

Angelina Kraft

Dissertation zur Erlangung des akademischen Grades

eines Doktors der Naturwissenschaften - Dr. rer. nat. -

vorgelegt dem Fachbereich 2 Biologie / Chemie
der Universität Bremen

Bremerhaven, Januar 2013

1. Gutachter: PD Dr. Holger Auel, Universität Bremen
2. Gutachter: Prof. Dr. Ulrich V. Bathmann, Leibniz-Institut für Ostseeforschung,
Warnemünde

Tag des Promotionskolloquiums: 18. Februar 2013

Anlage zur Dissertation

Eidesstattliche Erklärung

(Gem. § 6(5) Nr. 1-3 PromO)

Hiermit versichere ich, dass ich

1.) die vorliegende Arbeit ohne unerlaubte, fremde Hilfe angefertigt habe
2.) keine anderen, als die von mir im Text angegebenen Quellen und Hilfsmittel benutzt habe
3.) die den benutzen Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Bremerhaven, 16. Januar 2013

Angelina Kraft

When we try to pick out anything by itself, we find
it hitched to everything else in the universe.
John Muir (1911)

-

A true statement for many aspects of life, especially
when it comes to being an ‘Amphipodologist’

CONTENTS

Summary

Indications accumulate that the Arctic Ocean is in transition towards a new, warmer state. Physical evidence is provided by changing environmental conditions, such as increasing temperature of inflowing water currents (e.g., the West Spitsbergen Current) and disappearing sea-ice cover. With this development, we expect shifts in the composition of Arctic zooplankton communities, as well as adaptations in the life-cycle history of established species. In the Arctic marine food web, carnivorous pelagic amphipods are an important link between herbivorous mesozooplankton and higher trophic levels such as planktivorous fish and seabirds.

The present study closely investigates the community patterns of this group of open-water crustaceans with special attention on the three important epipelagic species *Themisto abyssorum*, *T. libellula* and *T. compressa*, and the deep-water amphipod *Cyclocaris guilelmi*. The objectives of this work focus on the year-round life-cycle characteristics of pelagic amphipods and on their function in the food web structure at study sites between Greenland and the Svalbard archipelago. In the investigation area, the concurrent presence of Atlantic and Arctic water masses characterizes the Arctic ecosystem. This causes the appearance of amphipod species of Arctic and North Atlantic origin at the same sampling sites. A comparison of long-term, station-based data of amphipods obtained by sediment traps (2000-2012) with short-term, ship-based data obtained by net samples during summer and winter, provides a coherent overview of pelagic amphipod distribution and ecology, and increases our understanding of the effects of a physically changing environment on this key plankton group.

In this thesis, three publications address the year-round life-cycle characteristics of *Themisto* spp. (**publications I and V**) and *C. guilelmi* (**publication III**) sampled by moored sediment traps in the northeastern Fram Strait. The sediment traps are deployed in a long-term observatory, the HAUSGARTEN, which is maintained by the Alfred Wegener Institute for Polar and Marine Research at the boundary between the central Arctic Ocean and the Greenland Sea since 2000. This facility provides a serendipitous opportunity to collect year-round zooplankton samples, which now cover a time span of twelve years. Such long plankton records are rare from high polar waters. In the epipelagic trap samples (deployed at 190-280 m water depth) hyperiids of the genus *Themisto* represent the dominant taxa among the collected amphipod community. Length-frequency analyses of year-round samples from 2000 to 2009 indicate a life span of two years for the sub-arctic species *T. abyssorum* and at least three years for the typical Arctic amphipod *T. libellula*.

Furthermore, *T. libellula* seems to release their brood earlier (February-March) compared to *T. abyssorum* (April-June) (**publication I**). From 2004 to 2008, the meso- and bathypelagic amphipod communities in the sediment traps from 800 to 2700 m depth show the prevalent appearance of the deep-water amphipod *C. guilelmi*. Throughout the year, *C. guilelmi* has a population structure consisting of four cohorts. In addition, the presence of egg-bearing females and young juvenile individuals suggests a year-round reproduction of this species (**publication III**). An important finding in the context of biological adaptations to a changing environment is the first record of successful reproduction by the southern invader *T. compressa* in the most recent year-round sediment trap samples (2011-2012). This North Atlantic species was first observed in July 2004 at 79° N in year-round open water traps in the European Arctic (**publication V**).

Two other studies focus on the winter feeding strategies of *Themisto* spp. (**publication II**) and investigate for the first time summer and winter lipid composition of *Themisto* spp. and *C. guilelmi* (**publication IV**). In **publications II and IV**, net samples of pelagic amphipods are obtained during a R/V *Polarstern* expedition in the summer of 2011 and two research cruises in fall 2011 and winter 2012 on R/V *Helmer Hanssen* to the northern Fram Strait and Svalbard. The results from the gut content analyses indicate for the first time that *T. abyssorum* and *T. libellula* are active predators during the Arctic winter, with calanoid copepods as their major prey (**publication II**). Furthermore, a gregarine endoparasite of the genus *Ganymedes* infected both species. This finding is the first record of a parasitic infection with *Ganymedes* sp. in the gut of the hyperiid amphipod *T. abyssorum* (**publication II**).

In **publication IV**, the analysis of the seasonal variations of lipid classes indicates that wax esters are the major year-round energy reserve in *T. libellula*, *T. compressa* and *C. guilelmi*. Consequently, the importance of this lipid class as an important source in times of a high metabolic energy demand (for example during reproduction) is discussed. In addition, a comparison of summer and winter fatty acid profiles shows a dominance of copepod biomarkers of the genus *Calanus* in the four investigated amphipod species, indicating that *T. abyssorum*, *T. libellula*, *T. compressa* and *C. guilelmi* are all part of *Calanus*-based food web and perform a 'business-as-usual' feeding-mode during the polar night.

To conclude, I show that long-term observations and a detailed knowledge of species specific ecology are of high importance for the identification of possible shifts within zooplankton community patterns and to predict their consequences in the food web structure of Arctic ecosystems. Evidence of such a shift provided data from a continuing northward spread of the invasive North Atlantic species, *T. compressa*, among the pelagic amphipod community, and recent findings of its reproductive competence in the northern Fram Strait. Thus, a possible ongoing transition from large Arctic to smaller Atlantic species in the Arctic marine food web is very likely to occur.

Zusammmenfassung

Immer mehr Anzeichen weisen darauf hin, dass sich im Arktischen Ozean ein wärmerer Klimazustand einstellt, der durch physikalische Veränderungen in der Umwelt und in der Atmosphäre hervorgerufen wird. Solche Veränderungen zeigen sich zum Beispiel in der Erwärmung des in die zentrale Arktis fließenden Westspitzbergenstroms sowie im Abschmelzen des arktischen Meereseises. Gleichzeitig ist davon auszugehen, dass diese Entwicklung das Potential besitzt, die Zusammensetzung arktischer Planktonorganismen zu verändern und umweltbedingte Anpassungen ihrer Lebensweise und ihrer Biologie nach sich zieht.

Vor diesem Hintergrund untersucht die vorliegende Arbeit die Planktongruppe der pelagischen Amphipoden, welche im arktischen Nahrungsgefüge ein wichtiges Bindeglied zwischen herbivorem Mesozooplankton und höheren trophischen Ebenen (zum Beispiel sich von Plankton ernährenden Fischarten und Seevögeln) bilden. Schwerpunkt hierbei ist die Untersuchung der Gemeinschaftsstrukturen dieser freischwimmenden Crustaceen, mit dem Hauptaugenmerk auf den drei epipelagischen Schlüsselarten *Themisto abyssorum*, *T. libellula*, *T. compressa* und dem Tiefseeamphipoden *Cyclocaris guilelmi*. Die weiterführenden Zielsetzungen dieser Arbeit sind das Erkennen charakteristischer Lebenszyklen der dominierenden pelagischen Amphipodenarten, sowie die Erfassung ihrer Rolle im Nahrungsgefüge in den Gewässern zwischen Grönland und dem Svalbard Archipel. Das Ökosystem dieser Region wird durch ein simultanes Auftreten atlantischer und arktischer Wassermassen beeinflusst. Diese Tatsache ermöglicht das gleichzeitige Vorkommen von Amphipodenarten arktischen und nordatlantischen Ursprungs im selben Untersuchungsgebiet.

Ein wichtiger Teil dieser Studie basiert auf dem Vergleich stationsbasierter Langzeitdatensätze pelagischer Amphipoden aus Sinkstofffallen (2000-2012) mit Kurzzeitdatenreihen aus Planktonnetzen, welche im Rahmen von Sommer- und Winterexpeditionen in das Nordpolarmeer erfasst wurden. Ziel dieses Vergleiches ist es, einen umfassenden Einblick in die Verbreitung und Ökologie pelagischer Amphipoden zu erlangen und gleichzeitig unser Verständnis für diese Schlüsselgruppe des arktischen Zooplanktons vor dem Hintergrund sich verändernder Umweltbedingungen zu stärken.

Im Rahmen dieser Dissertation befassen sich drei Publikationen mit dem ganzjährigen Vorkommen und den saisonalen Lebenszyklen der Amphipodenarten *T. abyssorum*, *T. libellula*, *T. compressa* (**Publikationen I und V**) und *C. guilelmi* (**Publikation III**), die in fest verankerten Sinkstofffallen der nordöstlichen Framstraße auftreten. Diese Sinkstofffallen werden im Tiefsee-Langzeitobservatorium HAUSGARTEN, das sich in der Übergangsregion

zwischen dem Nordatlantik und dem Arktischen Ozean befindet, eingesetzt. Das Observatorium wird seit dem Jahr 2000 vom Alfred-Wegener-Institut für Polar- und Meeresforschung betreut und bietet die einmalige Möglichkeit, ganzjährige Datensätze zu den Zooplanktonvorkommen dieser Region zu erhalten. Heute umfassen diese Datensätze einen Zeitraum von zwölf Jahren, was für Planktondaten aus den Gebieten des Nordpolarmeeres selten ist.

In den epipelagischen Sinkstofffallenproben, die aus einer Wassertiefe von 190-280 m stammen, dominieren hyperiide Flohkrebse der Gattung *Themisto* die Artengemeinschaft der Amphipoden. Aus der Analyse von ganzjährigen Längenhäufigkeitsverteilungen der Jahre 2000 bis 2009 (**Publikation I**) zeigt sich, dass diese Tiere eine unterschiedliche Lebenserwartung besitzen: die subarktische Art *T. abyssorum* weist eine Lebenserwartung von zwei Jahren auf, während die rein arktische Art *T. libellula* mit mindestens drei Jahren deutlich älter werden kann. Zudem konnte dargestellt werden, dass sich die weiblichen Tiere beider Arten im Zeitpunkt der Freisetzung ihrer Nachkommen unterscheiden. *T. libellula* Weibchen entlassen ihren Nachwuchs deutlich früher aus der Bruttasche (Zeitraum Februar bis März) als die Weibchen der subarktischen Art *T. abyssorum* (Zeitraum April bis Juni).

Die Untersuchungen der Zusammensetzung der meso- und bathypelagischen Amphipodengemeinschaft zeigen das häufige Auftreten des Tiefseeamphipoden *C. guilelmi* in den Sinkstofffallenproben der Jahre 2004-2008 auf einer Wassertiefe von 800-2700 m. Eine erste detailliertere Studie dieser Art zeigt, dass die Populationsstruktur von *C. guilelmi* aus vier Kohorten besteht, welche ganzjährig auftreten. Zudem sind das ganze Jahr hindurch eiertragende Weibchen und kleine juvenile Tiere anwesend, was auf eine ganzjährig stattfindende Fortpflanzung von *C. guilelmi* schließen lässt (**Publikation III**). Eine weitere wichtige Feststellung in dieser Dissertation ist der erste Nachweis von *T. compressa*, einer invasiven Art nordatlantischen Ursprungs, auf 79° nördlicher Breite im Juli 2004, sowie das erstmalige Auftreten eiertragenden Weibchen in den aktuellsten Proben des Untersuchungszeitraums 2011-2012 (**Publikation V**). Damit konnte die erfolgreiche Fortpflanzung von *T. compressa* in der nördlichen Framstraße belegt werden.

Zwei weitere Studien dieser Arbeit befassen sich mit dem Fressverhalten von *Themisto* spp. während des arktischen Winters (**Publikation II**) und vergleichen die Lipidzusammensetzung der pelagischen Amphipoden *Themisto* spp. und *C. guilelmi* zu unterschiedlichen Jahreszeiten (Sommer und Winter, **Publikation IV**). Für beide Studien wurden die Amphipodenbestände in den Gewässern der nördlichen Framstraße und Svalbards im Sommer und Winter beprobt. Dies umfasste die Teilnahme an einer Sommerexpedition mit dem Forschungseisbrecher F/S *Polarstern* im Juni und Juli 2011, sowie die Teilnahme an einer Herbst- und einer Winterexpedition auf dem Forschungsschiff *Helmer Hanssen* im August 2011 und Januar 2012. Mit der Auswertung dieser Proben konnte erstmalig gezeigt werden, dass *T. abyssorum* und *T. libellula* während der arktischen Polarnacht aktiv fressen, indem sie bevorzugt calanoide Copepoden (eine Gruppe der Ruderfußkrebse) bejagen (**Publikation II**). Bei Mageninhaltsanalysen beider Amphipodenarten wurde zudem der Befall mit Endoparasiten der Gattung *Ganymedes* festgestellt. Damit konnte erstmalig das Auftreten von *Ganymedes* sp. im Verdauungstrakt von *T. abyssorum* nachgewiesen werden (**Publikation II**).

Die **vierte Publikation** dieser Arbeit befasst sich mit der Analyse saisonaler Muster in der Zusammensetzung der Lipidklassen der vier untersuchten Amphipodenarten. Die Auswertung verdeutlicht die herausragende Rolle einer Gruppe von Langzeitspeicher-molekülen, der Waxester, welche ganzjährig die Hauptspeicherform für Stoffwechselenergie in den Arten *T. libellula*, *T. compressa* und *C. guilelmi* bilden. Zudem wird die Verwendung der in Waxestern gespeicherten Energie zu Zeiten eines erhöhten Energiebedarfs, zum Beispiel während der Fortpflanzungsphase, diskutiert. Des Weiteren zeigt ein Vergleich der Fettsäurezusammensetzung in Sommer- und Winterproben aller vier Zielarten ein vermehrtes Auftreten von Copepoden-Biomarkern, wie sie in der Gattung *Calanus* zu finden sind. Dieses Ergebnis bestätigt die Funde der Mageninhaltsuntersuchungen und macht deutlich, dass neben *T. abyssorum* und *T. libellula* auch die Arten *T. compressa* und *C. guilelmi* ganzjährig aktive Prädatoren im arktischen Nahrungsnetz sind und herbivore Copepoden eine Hauptnahrungsquelle darstellen.

Zusammenfassend kann ich feststellen, dass Langzeitstudien und ein gutes Verständnis der Ökologie der Arten von zentraler Bedeutung sind: das gilt zum Einen für die Identifizierung möglicher Verschiebungen der Zooplanktonstrukturen in der Arktis, als auch für die Voraussage möglicher Konsequenzen eines solchen Strukturwandels auf das Nahrungsgefüge des arktischen Ökosystems. Anhaltspunkte hierfür bildet das vermehrte Auftreten der nordatlantischen Art *T. compressa* in der Gemeinschaft pelagischer Amphipoden, und der kürzlich erfolgte Nachweis einer aktiven Fortpflanzung von *T. compressa* in den Gewässern der nördlichen Framstraße. Diese Befunde lassen auf die wachsende Bedeutung kleinerer, subarktischer und atlantischer Arten im arktischen Nahrungsnetz schließen.

List of abbreviations

ARK	Abbreviation of the respective R/V *Polarstern* cruises to the Arctic
AWI	Alfred Wegener Institute for Polar and Marine Research
ARCTOS	Arctic Marine Ecosystem Research Network
BMBF	Bundesministerium für Bildung und Forschung (English: German Federal Ministry of Education and Research)
BP	Before Present; time scale
C	Carbon
CO_2	Carbon dioxide
DHA	Docosahexaenoic Acid
DM	Dry Mass
EGC	East Greenland Current
ELSD	Evaporative Light Scattering Detector
EPA	Eicosapentaenoic Acid
ERMS	European Register of Marine Species
GC	Gas Liquid Chromatography
GS	Greenland Sea
HG	HAUSGARTEN
$HgCl_2$	Mercuric chloride
HPLC	High Performance Liquid Chromatography
IMR	Institute for Marine Research, Bergen, Norway
MIK	Methot Isaac Kidd (plankton net)
MOCNESS	Multiple Opening / Closing Net and Environmental Sensing System
MUFAs	Monounsaturated Fatty Acids
na	not applicable
nd	no data
nMDS	non-metric Multidimensional Scaling Analysis
NP	Norwegian Polar Institute
NSIDC	National Snow and Ice Data Center, Boulder, Colorado, USA
NwAC	Norwegian Atlantic Current
PAR	Photosynthetically Active Radiation
PC	Phosphatidylcholine
PCA	Principal Component Analysis
PE	Phosphatidylethanolamine
POC	Particulate Organic Carbon
PSU	Practical Salinity Units
PUFAs	Polyunsaturated Fatty Acids
RAC	Return Atlantic Current
RMT	Rectangular Midwater Trawl
R/V	Research Vessel
SFAs	Saturated Fatty Acids
SI	Separation Index / Indices
TBL	Total Body Length
TL	Total Lipid content
WSC	West Spitsbergen Current

1. General introduction

1.1 Arctic marine environments

At high latitudes, marine ecosystems are unique and characterized by an extreme seasonality. Within the last decade these environments have received increased attention: Arctic systems experience changes in seasonal sea-ice extent and retreat, increased ocean temperatures, and are considered to be most sensitive to climate change (Polyakov et al. 2005, 2010; Stroeve et al. 2007, 2008; Steele et al. 2010; Carmack and McLaughlin 2011; Grebmeier 2012). The question of how Arctic marine ecosystems will respond to the phenomenon of rapid sea-ice loss and rising water temperatures is foundation for many research studies (e.g., Weslawski et al. 2010, 2011), and a reorganization and regime shift among the Arctic marine communities is expected. In the European Arctic, research areas cover a wide geographical range; this includes semi-enclosed systems, such as the fjords on Svalbard (Willis et al. 2008; Walkusz et al. 2009), sub-arctic open water areas like the Barents Sea and the Greenland Sea (Dalpadado et al. 2008a), as well as deep-sea passages, such as the Fram Strait (Hop et al. 2006) and the central Arctic Ocean (Fig. 1.1).

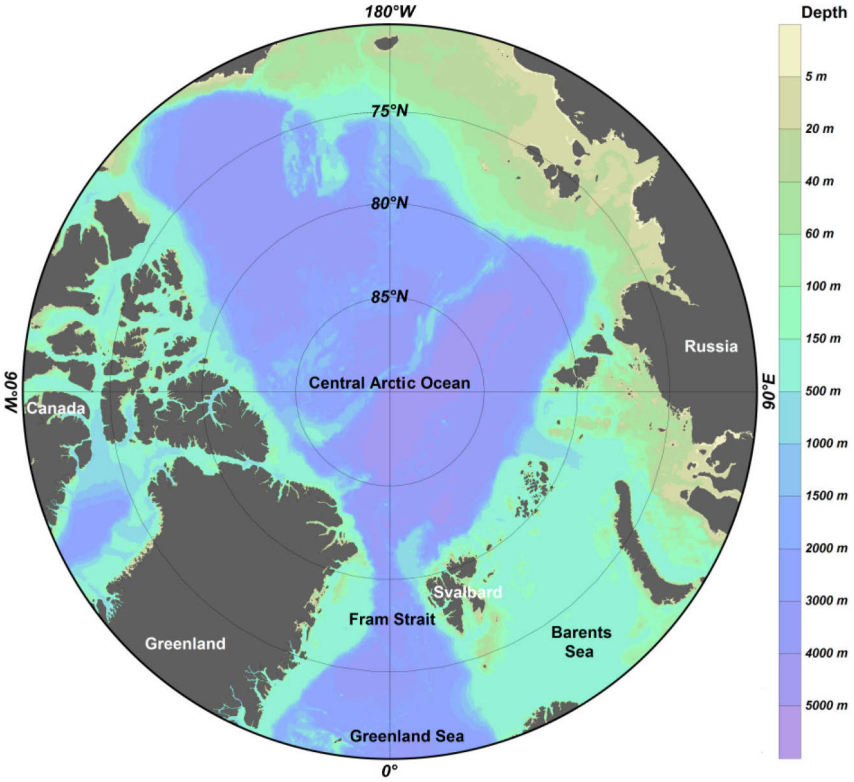

Fig. 1.1 Bathymetry of the European and central Arctic. In this high-latitude environment, the Fram Strait is the only deep-water connection between the central Arctic Ocean and the North Atlantic Ocean

Hydrography and warming events in the Fram Strait and adjacent Arctic waters

The central Arctic Ocean is composed of deep marine basins surrounded by continents. The basins experience an exchange of water masses via several passages, one being the Fram Strait. This sea-passage is the only deep-water connection with the North Atlantic Ocean, with a mean water depth of ~2,500 m. At the boundary between the Fram Strait and the central Arctic Ocean, an inflow of warm Atlantic waters from the south and the outflow of cold Arctic waters and drift-ice from the northeast shape the hydrographic structure (Rudels et al. 2004; Walczowski and Piechura 2011). With the West Spitsbergen Current (WSC) located over the continental slope, Atlantic waters are transported into the Arctic Ocean Boundary Current along the west coast of Svalbard (Quadfasel et al. 1987; Manley 1995). The WSC determines local conditions in terms of heat transport, freshwater and salt fluxes. In the northeastern Fram Strait, a complex bathymetry leads to a split of the WSC into three branches: one enters the Arctic Ocean north of Svalbard, the second continues north- and further eastward around the rim of the Yermak Plateau, and the third recirculates to the west as the Return Atlantic Current directly in the strait or shortly north of it (Gascard et al. 1995; Schauer et al. 2008) (Fig. 1.2).

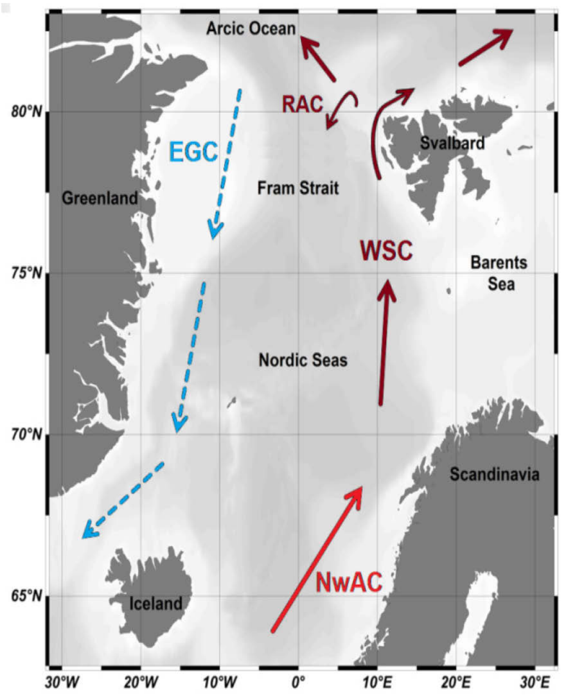

Fig. 1.2 Schematic current system in the European Arctic. EGC - East Greenland Current; WSC - West Spitsbergen Current; NwAC - Norwegian Atlantic Current; RAC - Return Atlantic Current

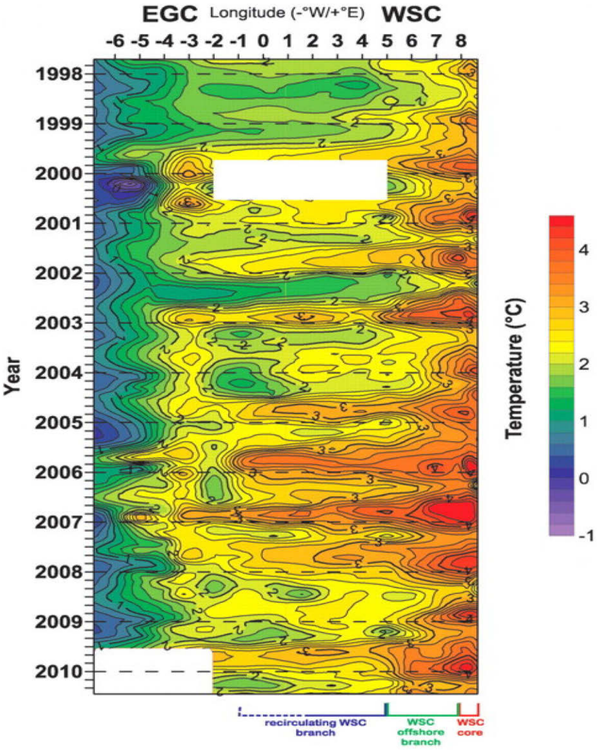

Fig. 1.3 Spatio-temporal diagram of monthly mean temperature measurements of the EGC, the WSC and transition zones of mixed water at 250 m water depth along a 78°50' N transect across the Fram Strait; diagram modified after Beszczynska-Möller et al. (2012)

Along the east coast of Greenland, cold, low salinity water masses are transported southwards by the East Greenland Current system (EGC), which originates in the central Arctic Ocean (Bourke et al. 1987). With the WSC and the EGC as the major current systems, the Fram Strait is an important transition zone between the North Atlantic and the Arctic Ocean, were a voluminous exchange of oceanic water masses occurs (Quadfasel et al. 1987; Schauer et al. 2008) (Fig. 1.2). Between the WSC and the EGC, mixed water masses are formed (Piechura 2004). In addition, local oceanographic processes such as freshwater run-off, variable patterns of surface currents, wind driven circulation and cooling modify the hydrography and sea-ice distribution in Svalbard waters (e.g., Soltwedel et al. 2005). With regard to climate change, the core of the WSC displayed a progressive warming of 0.06 °C year^{-1} since the start of continuous measurements by an oceanographic moored array at 78°50’ N in 1997 (Schauer et al. 2008; Beszczynska-Möller et al. 2012). The highest observed values of temperature and salinity in the core of Atlantic Water were observed in 2006 (Walczowski and Piechura 2007; Walczowski et al. 2012) (Fig. 1.3).

Sea-ice cover

In the Arctic, sea-ice coverage is characterized by a seasonally driven distribution and affects plankton communities twofold: for one by limiting the penetration of photosynthetically active radiation (PAR), and secondly by stratifying the water column due to the release of fresh water with the sea-ice melt and river run-off during the summer season. During the year, the sea-ice cover in the Arctic extends from a summer minimum of ~4 x 10^6 km² to a winter maximum of 16 x 10^6 km² (Comiso 2003; Comiso et al. 2008). In the past, the Arctic Ocean has frequently been ice-free during the summers of the Quaternary Period (Polyakov et al. 2010), with the most recent ice-free summer only 8000 years ago (Funder et al. 2011). Over the last decade, an accelerating decrease of the Arctic sea-ice extent and thickness was found (Stroeve et al. 2007; Comiso et al. 2008) and more recent assessments of climate change predict similar conditions with ice-free summers within the next 30 years (Wang and Overland 2009). These predictions are supported by recent satellite observations on September 16, 2012, with a new record low sea-ice minimum of 3.41 x 10^6 km² (NSIDC 2012) (Fig. 1.4). Between the seasonal maximum sea-ice extent that occurred on March 20, 2012, and the September 16 minimum, the Arctic Ocean lost a total of 11.83 x 10^6 km² of sea-ice cover. This is by far the largest seasonal loss of sea-ice ever recorded since the start of observations (NSIDC 2012) (Fig. 1.5). Simultaneously, an increased sea-ice export through the Fram Strait has been found since 2003 (Spreen et al. 2008), and recent investigations show a change in the dominant fresh water content in the central Arctic Ocean; thereby, a freshening in the Canada basin is balanced by a respective decrease of fresh water content in the Eurasian basin (Morison et al. 2012). Given these observations, indications are that Arctic marine environments are transitioning towards a new, warmer state.

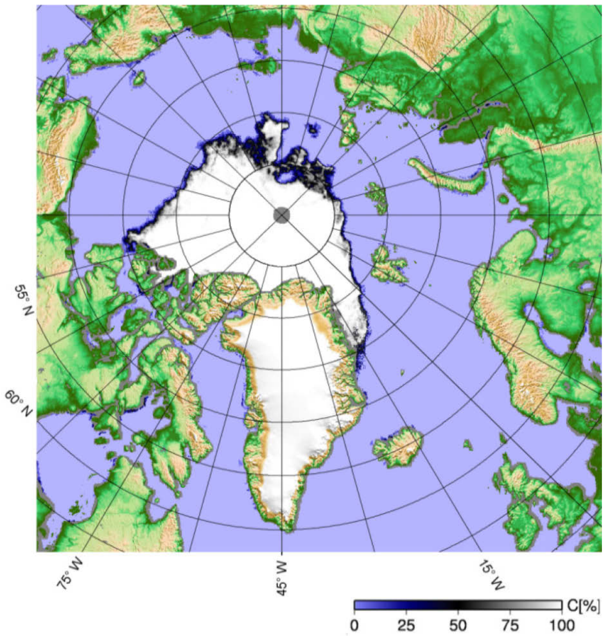

Fig. 1.4 Arctic sea-ice minimum recorded on September 16, 2012, covering an area limited to 3.41 x 10^6 km². C [%] = Color code of ocean area with sea-ice cover in percent. Modified from NSIDC (2012)

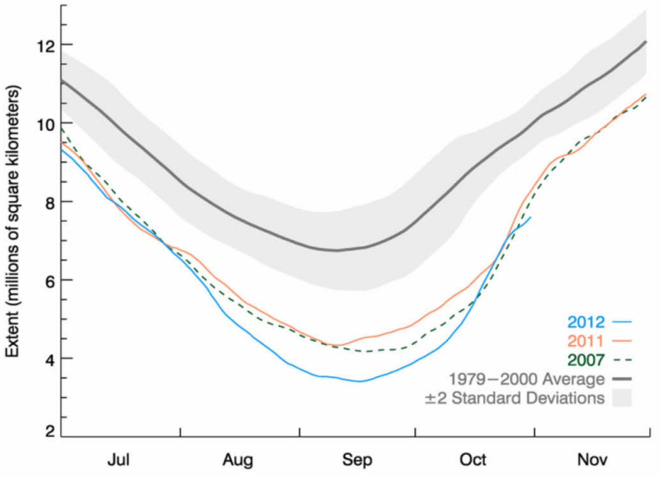

Fig. 1.5 Arctic sea-ice extent from summers 1979 to 2012 with minima in 2007, 2011 and 2012. The data are based on an ocean area with at least 15 % sea-ice. Provided by NSIDC (2012)

1.2 Pelagic amphipods – an introduction

The Arctic Ocean and its marginal seas sustain, despite severe climatic conditions, a diverse fauna, including about 5000 species of free-living invertebrates (Vassilenko and Petryashov 2009). Of these, pelagic organisms including marine crustaceans of the order Amphipoda are a major element of the macrozooplankton composition and contribute significantly to marine pelagic food webs. Amphipods have long been recognized as sensitive indicators of environmental conditions such as water and sediment quality, and some species are even used as biomonitors for pollutants and toxicants such as heavy metals and pesticides in limnic and coastal marine habitats (e.g., Thomas 1993; Simpson et al. 2005). In addition, a high degree of niche specificity is a characteristic feature of many amphipod species, which makes them well suited to document both spatial and temporal shifts of abiotic parameters such as water temperature and ice conditions in their habitats (Marques and Bellan-Santini 1993).

In the pelagic waters of high-latitude ecosystems, the most abundant suborder is the Hyperiidea (Vinogradov 1999) (Fig. 1.6). Hyperiid amphipods are exclusively found in marine pelagic habitats, including carnivorous, omnivorous and suppositional parasitic life forms. While this suborder has a diverse distribution over the world oceans with about 250 described species so far, only ten species have been reported from the Arctic region (Bowman and Gruner 1973; Vinogradov et al. 1996; Vassilenko and Petryashov 2009; Kraft et al. 2011). As with other regions, hyperiids are distributed over large depth ranges from the surface down to 7000-8000 m (Vassilenko and Petryashov 2009) and possess long life-cycles, usually taking one ore more years to complete. Among ice-associated (termed sympagic) and free-swimming deep-water amphipod taxa, the suborder Gammaridea is the most important suborder. At high latitudes, gammarid amphipods show significant morphological and ecological differences when compared to warm-water species from lower latitudes: they are larger in terms of body size, have a delayed maturity, a great longevity and only few broods during their lifespan (Sainte-Marie 1991).

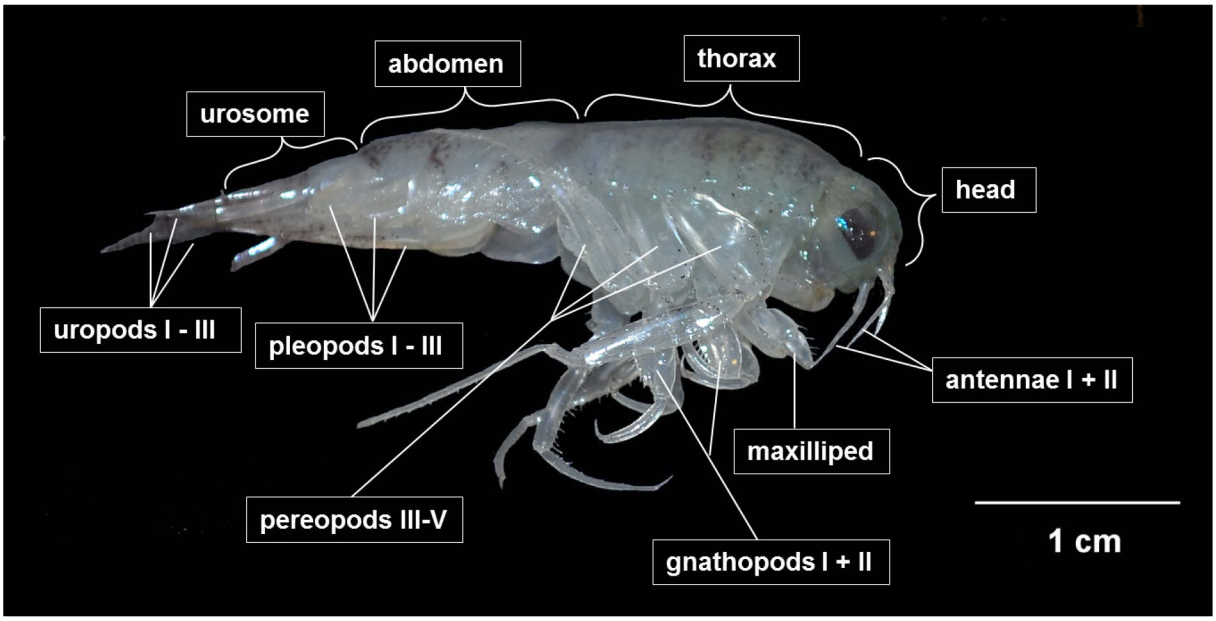

Fig. 1.6 The structure of a hyperiid amphipod on the example of a female *Themisto libellula*

A common feature of both suborders, Hyperiidea and Gammaridea, is a general, laterally flattened body structure. As with other amphipods, the body of hyperiids and gammarids comprises three sections: the head (cephalon), thorax (peraeon) and abdomen (pleon) (Fig. 1.6). The head consists of the acron and five body segments, bearing six paired (antenna I, antenna II, mandibles, maxillae I, maxillae II, maxillipeds) and two unpaired (labrium and labrum) appendages. The thorax is segmented into seven thoracic articles (also termed somites) which each contain a pair of walking legs or pereopods. In the pereopods I and II, the fifth and sixth segment often form pincers. In this case they are also called gnathopods. The abdomen consists of six somites with the first three carrying paired, biramous swimming legs (pleopods) and the last three containing biramous appendages called uropods. The distinction between the suborders is based on key morphological features such as the structure of the first two pairs of walking legs (gnathopods), the size and shape of the eyes (e.g., small in gammarids, while large in hyperiids), the presence (Hyperiidea) or absence (Gammaridea) of a maxilliped palp and coxal plates (Tencati 1970).

Hyperiid amphipods are frequently encountered in epi- and mesopelagic amphipod communities in Arctic and Antarctic regions; among them, the members of the genus *Themisto*, family Hyperiidae, overwhelmingly dominate the epipelagic amphipod fauna in the European Arctic (Dunbar 1957, 1964; Auel et al. 2002; Dalpadado et al. 2001, 2008a, b; Dalpadado 2002). In the Greenland Sea, the Barents Sea and the northern Fram Strait, two species are the most abundant epipelagic hyperiids: *Themisto libellula* and *T. abyssorum*. The large species *T. libellula* (20-60 mm total body length) is considered an indicator of Arctic water masses (Dalpadado 2002) and has been recorded from all Arctic and sub-arctic regions, including the Barents Sea (Lønne and Gulliksen 1989), around the Svalbard archipelago (Dalpadado et al. 2008a, b), northern Greenland waters (Tencati and Geiger 1968; Auel and Werner 2003; Kraft et al. 2011) and the Norwegian Sea (Bowman 1960; Brandt 1997; Wencki 2000). In regions influenced by predominantly Atlantic water masses, the boreal sub-arctic species *T. abyssorum* has been recorded in higher abundances then the typically Arctic species *T. libellula* (Koszteyn et al. 1995; Dalpadado 2002; Dalpadado et al. 2008a). A third *Themisto* species, *T. compressa*, is a typical North Atlantic amphipod which has been newly introduced into sub-arctic regions (Dalpadado et al. 2001, 2008).

The inhabited water depths of the genus *Themisto* range from 0 to 1000 m for *T. libellula* and 0 to 2000 m for *T. abyssorum*, at temperatures usually below 4 °C (Dunbar 1946; Klekowski and Weslawski 1991). Both species have been recognized for a marked vertical migration capacity, with juveniles restricted to shallower depths (<100 m) than adult individuals (Dunbar 1957, 1964; Koszteyn et al. 1995; Auel et al. 2002). Unlike sympagic (ice-associated) amphipods such as *Gammarus wilkitzkii*, most pelagic amphipod species are stenohaline osmoconformers which cannot regulate their haemolymph concentrations of sodium and chloride (Aarset and Aunaas 1987). Therefore, hyperiids cannot withstand salinities <30 PSU for long, making them more vulnerable to shifts of thermohaline circulation patterns, as it was shown by a mass mortality event of *T. libellula* in Adventfjorden, Svalbard, in September 2001 (Eiane and Daase 2002).

1.3 The performance of pelagic amphipods in a warming Arctic

In high-latitude ecosystems, sea-ice cover and strong seasonality of the light regime limit primary production and food supply for pelagic organisms, especially during winter. Following the short and intensive period of primary production in spring, ice-algae and phytoplankton blooms provide valuable sources of food and energy. This energy is predominantly stored in the form of lipids within herbivore zooplankton (Bradstreet and Cross 1982; Conover 1988; Falk-Petersen et al. 1990, 2009; Carmack and Wassmann 2006; Lee et al. 2006). The total primary production in the Fram Strait region has been suggested to be about 100-140 g C $m^{-2}y^{-1}$ in areas influenced by northward-flowing Atlantic waters, with a sharp decrease towards the out-flow region on the North-East Greenland Shelf with 40-60 g C m^{-2} y^{-1} (Wassmann 2011). In this context, five major zooplankton-mediated processes are known to transfer organic carbon down to the seafloor: ingestion, demineralization, destruction of fecal pellets and other aggregates, production of large debris and vertical migration (Angel 1989; Noji 1991). Grazers, such as herbivorous copepods, are required to synchronize their feeding and reproductive patterns to the seasonal fluctuations in food availability provided by blooms. Being visual predators, pelagic amphipods form an important link in the energy flux from herbivore zooplankton to higher trophic levels within the Arctic ecosystem. Most pelagic amphipod species, such as *T. abyssorum* and *T. libellula*, actively feed on herbivores, and at the same time become prey for fishes, seabirds and marine mammals (e.g., Lønne and Gulliksen 1989; Dalpadado and Bogstad 2004). However, the functional role of pelagic amphipods in high-latitude ecosystems with regard to geographical range shifts, seasonal life-cycle strategies, energetic value as a food source for higher trophic levels, and consequently their possible adaptations to global climate change scenarios, are still largely unknown. And in the times of a warming Arctic Ocean, an understanding of the mechanisms which govern Arctic food web regimes are of crucial importance, as these processes sustain large amounts of animal life (e.g., Hop et al. 2006).

With the inflow of warmer Atlantic (Holliday et al. 2008; Schauer et al. 2008) and Pacific (Woodgate et al. 2010) waters since the early 1990s, a large-scale shift to warmer conditions has been observed in the Arctic (Beszczynska-Möller et al. 2011). Based on the fact that the boreal regions of the North Atlantic inhabit about ~25,000 taxa of pelagic and benthic species, which is five times more than the Arctic (~5,000 taxa) (ERMS 2012), this so called 'Atlantification' may lead to an increased biodiversity in the Arctic (Weslawski et al. 2009). Within pelagic amphipods, a regime shift will most likely show by increased appearances of smaller taxa, including sub-arctic species (e.g., *T. abyssorum*), and North Atlantic species. Small taxa may serve to replace large amphipods, such as the typical Arctic hyperiid *T. libellula*. As a consequence, the process of warming could result in a higher diversity and increased numbers of small carnivores, which dissipate the energy flow (Weslawski et al. 2009; Fig. 1.7). Examples of new appearances of typical Atlantic species in the high North are the re-appearance of the blue mussel (*Mytilus edulis*) on Svalbard (Berge et al. 2005) and the northward shift of zooplankton communities in the Norwegian Sea (Beaugrand et al. 2002). In this context, my thesis focuses on the poorly studied group of pelagic amphipods in the Arctic food web, including studies of their ecology and life-cycle characteristics during summer and winter in the Fram Strait and adjacent Svalbard waters.

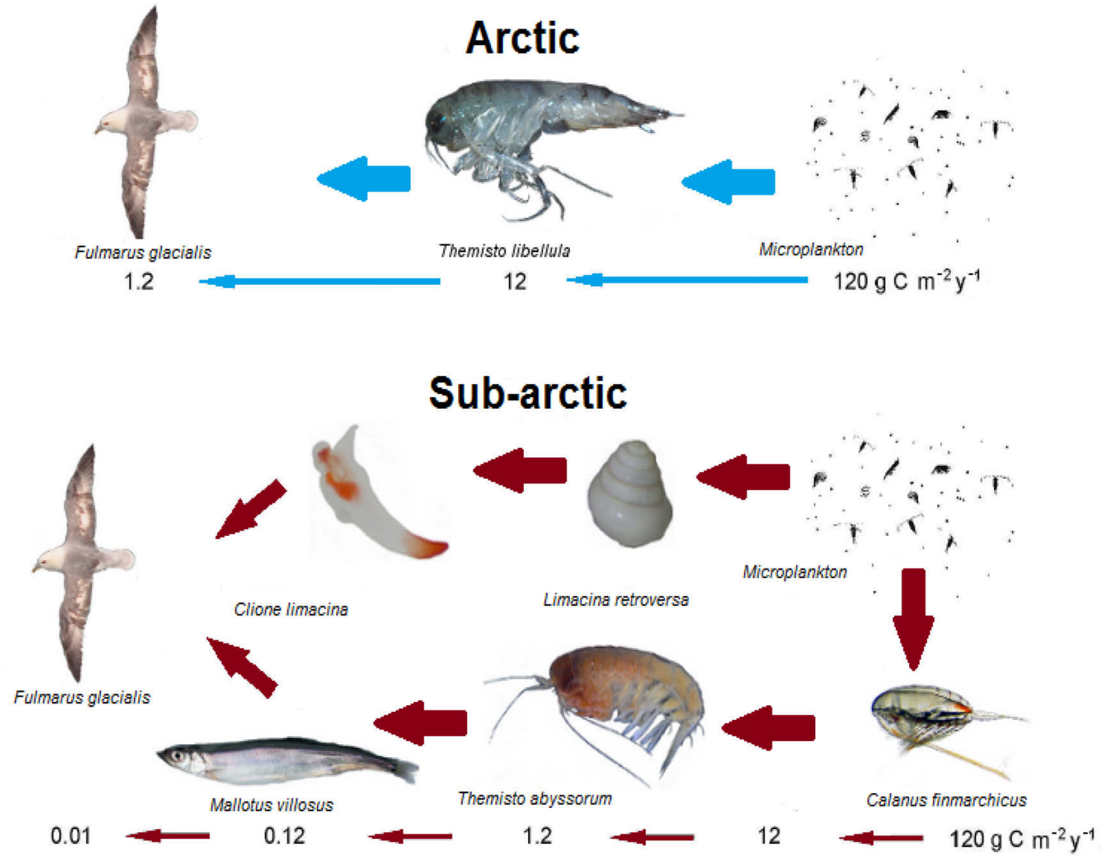

Fig. 1.7 A schematic display of the energy flow at high-latitude waters contrasting an Arctic, efficient short food web versus a warmed-up, sub-arctic situation. Organisms are not displayed to scale. The numbers indicate the share of the initial primary production which is transferred to the next trophic level; modified from Weslawski et al. (2009) and Wold et al. (2011)

2. Aims and outline of the thesis

2.1 Aims

Within polar field research, there is often a trade-off between spatial and temporal coverage. While ship-based studies, carried out mostly during the summer, offer a good spatial but a restricted temporal coverage, station-based research provides often good temporal data with a lack of broad spatial coverage. Within the present thesis, an attempt was made to combine long-term station-based data with ship-based studies from summer and winter in high Arctic waters. This combination is expected to provide a broad picture of pelagic amphipod distribution and ecology and will add understanding how changes to the physical environment of the Arctic affect this key group. The ecological understanding of pelagic amphipod communities, their status in the Arctic food web and their long-term development will contribute to the assessment of biodiversity and sustainability of polar processes for the global climate system.

The specific objectives of this thesis are:

1) to investigate the year-round life-cycle biology and population structure of dominant epi-, meso-, and bathy-pelagic amphipod taxa in the northern Fram Strait.

2) to examine the seasonal performance of true pelagic amphipods by the investigation of differences in their nutritional ecology (lipid biomarkers and gut content), especially during the polar night.

3) to address long-term shifts in amphipod species composition under the aspect of changing temperature and sea-ice properties.

2.2 Outline

The main part of this thesis contains five publications which were written during my studies according to the aims of the research themes as stated above. The general concept of the present thesis was developed in discussions with Dr. Eva-Maria Nöthig and Prof. Dr. Ulrich V. Bathmann and funded by the German Federal Ministry of Education and Research (Bundesministerium für Bildung und Forschung (BMBF), project grant 03F0629A). Project-related laboratory analyses and field methods were undertaken by Angelina Kraft using laboratories and equipment supplied by the Alfred Wegener Institute for Polar and

Marine Research in Bremerhaven, the Norwegian Polar Institute Tromsø and the University Centre in Svalbard.

Publications I-V

Publication I: Kraft A, Bauerfeind E, Nöthig E-M, Bathmann UV (2012) Size structure and life-cycle patterns of dominant pelagic amphipods collected as swimmers in sediment traps in the eastern Fram Strait. Journal of Marine Systems 95:1-15.

The initial idea for this paper was elaborated by the first author and further refined by the input of the other authors. The sampling was conducted by E. Bauerfeind and A. Kraft. Analyses of sediment trap samples, including species identification, determination of cohort development and size structure, and statistical testing were done by A. Kraft. The manuscript was written by A. Kraft with assistance of E.-M. Nöthig, E. Bauerfeind and U.V. Bathmann.

Publication II: Kraft A, Berge J, Varpe Ø, Falk-Petersen S (2013) Feeding in Arctic darkness: mid-winter diet of the pelagic amphipods *Themisto abyssorum* and *T. libellula*. Marine Biology 160:241-248.

The initial idea for this paper was developed by the first author, S. Falk-Petersen, J. Berge and Ø. Varpe during the research expedition ARCTOS BIO-8510 around the Svalbard archipelago in January 2012. The sampling was carried out by the first author, J. Berge, Ø. Varpe and participating students. Sorting of the samples, including species identification, measuring and stomach and gut content analyses were performed by A. Kraft. The manuscript was written by A. Kraft with input by J. Berge, Ø. Varpe and S. Falk-Petersen.

Publication III: Kraft A, Bauerfeind E, Nöthig E-M, Klages M, Beszczynska-Möller A, Bathmann UV (2013) Amphipods in sediment traps of the eastern Fram Strait with focus on the life-history of the lysianassoid *Cyclocaris guilelmi*. Deep-Sea Research Part I: Oceanographic Research Papers 73:62-72.

The concept of the third paper was initiated by the first author upon discovering frequent occurrences of *Cyclocaris guilelmi* in pelagic deep-sea sediment traps. The trap sampling was carried out by E. Bauerfeind and A. Kraft. Species identification, length measurements, cohort and statistical analysis were performed and results evaluated by A. Kraft. The manuscript was written by A. Kraft with input by E. Bauerfeind, E.-M. Nöthig, A. Beszczynska-Möller, U.V. Bathmann and M. Klages.

Publication IV: Kraft A, Graeve M, Janssen D, Falk-Petersen S (submitted to Canadian Journal of Fisheries and Aquatic Sciences) Lipids in Arctic pelagic amphipods – A comparison between summer and winter: do seasons matter?

The concept of the fourth publication was initiated by the first author upon the successful sampling of four key species of pelagic amphipods during different seasons (summer and winter) in high Arctic waters. Sampling during all cruises was conducted by the first author, with the help of other group and ship members. Sorting and further processing of the samples on board was performed by A. Kraft. Lipid analyses were carried out by A. Kraft, M. Graeve and D. Janssen. The manuscript was written by A. Kraft with contributions from M. Graeve, S. Falk-Petersen and D. Janssen.

Publication V: Kraft A, Nöthig E-M, Bauerfeind E, Pohle GW, Wildish DJ, Bathmann UV, Beszczynska-Möller A, Klages M (submitted to Nature Climate Change) Reproduction in a southern invader indicates community shifts among Arctic zooplankton.

The idea of this manuscript is based on the surprising finding of breeding *Themisto compressa* females during the analyses of sediment trap samples from the sampling year 2011/2012 by the first author. The discovery was confirmed by Canadian taxonomists during a research period at the Atlantic Reference Centre in St Andrews, New Brunswick, Canada. Consequently, a report was written by the first author, with input from all of the co-authors.

Implications of the studies

Five publications benefited from the long-term sediment trap sampling in the northern Fram Strait since the year 2000 undertaken by the Alfred Wegener Institute for Polar and Marine Research, one R/V *Polarstern* expedition in the summer of 2011 and two research cruises in fall 2011 and winter 2012 on R/V *Helmer Hanssen*. An overview of the study sites, applied sampling methods and applied analytical techniques is presented in Appendix A1, Tables 12.1-12.3. As a first step, the community composition, population structure, length-frequency distributions, reproductive patterns and seasonal vertical migration capacity of the dominant epipelagic (**publication I**) and deep-water (**publication III**) amphipods from sediment trap samples were studied. Furthermore, species specific growth rates, reproduction times and population dynamics were investigated and compared. **Publication I** included a detailed literature review of published life history data of the genus *Themisto* from both hemispheres. With an understanding of life history strategies, a closer investigation was given to their survival strategies during the time of the Arctic polar night (**publication II**). A major question when it comes to high-latitude ecosystems is how zooplankters, including assumed visual predators such as pelagic hyperiid amphipods, survive during the Arctic winter, a season without visible light (to human perception). To contribute new insights to winter survival strategies, amphipod samples of the hyperiids *T. abyssorum* and *T. libellula* obtained during the 'Polar night cruise' north of the Svalbard archipelago in January 2012 were analyzed and compared for their stomach and gut content (**publication II**). These new winter data contribute to our limited knowledge of winter behavior and distribution of Arctic zooplankton. In a more extensive step, **publication IV** investigated seasonal variations of lipid classes and fatty acid compositions of the *Themisto* species and the deep-water amphipod *Cyclocaris guilelmi*. Here, we analyzed and compared summer and winter samples across the Fram Strait and in the Svalbard area with respect to possible differences in their allometric relationships, the contribution of dominant lipid classes and the contribution, origin and possible function of fatty acid biomarkers. From the results we gained a better understanding of seasonality in Arctic food web structure. **Publication V** presents the first evidence of successful reproduction by a southern invader, the Atlantic hyperiid amphipod *Themisto compressa*, at 79° N in year-round open water traps in the European Arctic. In combination, the five publications addressed the overall role and performance of four pelagic key amphipods in the European Arctic, with their main results summarized and put into a global climate change context in the final synoptic discussion.

Study areas

The study areas covered in this thesis included a long-term observatory maintained by the Alfred Wegener Institute for Polar and Marine Research in the northeastern Fram Strait (the HAUSGARTEN), a transect at 78°50’ N between Svalbard and Greenland, and different sampling locations around the Svalbard archipelago, including the fjords Isfjorden and Rijpfjorden (Fig. 2.1). All sampling locations are characterized by a strong seasonality in incident solar radiation, with four months of midnight sun and polar night during summer and winter, respectively. Besides a variable hydrography (see section 1.1), the waters around Svalbard are characterized by strong variations in sea-ice cover, which are mainly caused by variable patterns of surface currents in the area and the overall annual variation in Arctic sea-ice distribution. A detailed description of the hydrographic conditions of the individual study areas is included in the respective **publication (I-V)**.

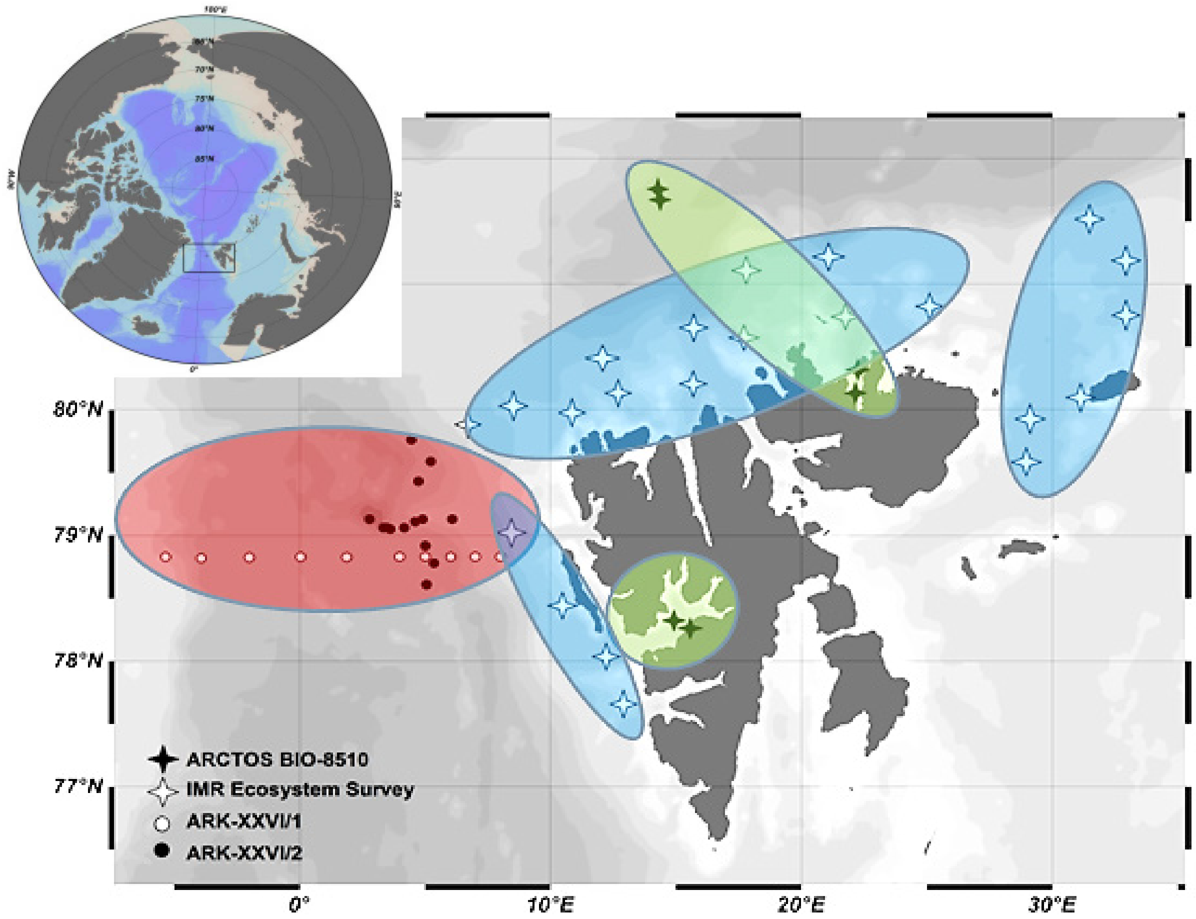

Fig 2.1 Sampling areas investigated during three expeditions to the northern Fram Strait and Svalbard waters. Sampling stations during the summer 2011 cruise with R/V *Polarstern*, ARK-XXVI/1 and ARK-XXVI/2 (red area), are indicated by dots. White dots indicate sampling sites along a 78°50’ N transect and black dots sites at the long-term observatory HAUSGARTEN. White stars refer to sites sampled onboard R/V *Helmer Hanssen* during the IMR Ecosystem survey in fall 2011 (blue areas), and black stars during the ARCTOS polar night cruise in winter 2012 (green areas)

PUBLICATION I

Size structure and life-cycle patterns of dominant pelagic amphipods collected as swimmers in sediment traps in the eastern Fram Strait

Angelina Kraft[a]*, Eduard Bauerfeind[a], Eva-Maria Nöthig[a], Ulrich V. Bathmann[a]

[a]Alfred Wegener Institute for Polar and Marine Research
Am Handelshafen 12,
27570 Bremerhaven, Germany
* Contact information:
E-mail: Angelina.Kraft@awi.de
Phone: + 49-471-48311085
Fax: + 49-471-48311149

Published in Journal of Marine Systems 95:1-15 (2012),

doi:10.1016/j.jmarsys.2011.12.006

Abstract

Time series length-frequency data are presented for *Themisto* amphipods collected as swimmers by moored sediment traps since 2000 at the AWI deep-sea observatory HAUSGARTEN (79° N/4° E) in the eastern Fram Strait. Amphipod occurrences increased significantly from 2000 to 2009 at 200-300 m depth, and the North Atlantic species *Themisto compressa* was continuously present in the samples starting in 2004. We present year-round records of large adult *Themisto* amphipods, including the appearance of *T. libellula* with a total body length of up to 56.7 mm and juveniles starting from 4.0 mm. The length of *T. abyssorum* ranged from 4.2-25.6 mm, whereas it varied for *T. compressa* from 8.8-24.4 mm. Length-frequency analysis indicated a life span of two years for *T. abyssorum* and at least three years for *T. libellula*. The absence of juveniles for *T. compressa* suggested its reproduction in southern subarctic areas and its occasional northward migration with warmer Atlantic water into the eastern Fram Strait. The seasonal and long-term size structure of the three pelagic species were consistent over the course of the study, indicating no changes occurred in cohort development due to increasing abundances or warming water temperatures.

Keywords: Hyperiid amphipod • *Themisto* • Life-cycle • Sediment traps • Population dynamics • Size distribution • Fram Strait • HAUSGARTEN

Introduction

Within the marine zooplankton community, pelagic amphipods are recognized as an important component of the Arctic food web. They represent a key link between herbivorous mesozooplankton (mainly copepods) and higher trophic levels including planktivorous fishes like polar cod (*Boreogadus saida*), capelin (*Mallotus villosus*) and herring (*Clupea harengus*), seabirds such as the little auk (*Alle alle*) as well as marine mammals including ringed- and harp seal (*Phoca hispida* and *Phoca groenlandica*) (Lampert 1960; LeBrasseur 1966; Lydersen et al. 1989; Lønne and Gulliksen 1989; Dalpadado et al. 2000, 2001; Dalpadado and Bogstad 2004). The ecological importance of this group was described recently by Skjoldal et al. (2004) for the North Atlantic, and Bowman (1960) described pelagic amphipods in Arctic waters as an important component of the marine zooplankton community with a 'respective status' next to copepods and krill. Many studies followed Bowman's (1960) paper (Weigmann-Haas 1997; Dalpadado et al. 1998; Wencki 2000; Dalpadado 2002; Weslawski and Legezynska 2002), which describe the biology, distribution and appearances of pelagic

Amphipoda in high Arctic ecosystems, especially in the Norwegian, Greenland and Barents Sea.

The most frequently encountered pelagic amphipods in the Arctic belong to the genus *Themisto*, with the species *Themisto libellula* and *Themisto abyssorum* (Hyperiidea) being dominant (Dunbar 1957; Bowman 1960; Schneppenheim and Weigmann-Haas 1986; Koszteyn et al. 1995; Dalpadado et al. 2001; Dalpadado 2002). Occasionally, a third *Themisto* species, *T. compressa*, is collected in the Arctic Ocean and its surrounding seas (Dunbar 1964; Williams and Robins 1981; Weigmann-Haas 1997; Weslawski et al. 2006). Studies over the past decade included investigations on geographic and vertical distribution patterns, reproduction strategies, food sources, and abundance of *Themisto* (Koszteyn et al. 1995; Wencki 2000; Dalpadado et al. 2001, 2008; Auel et al. 2002; Dalpadado 2002; Dale et al. 2006; Weslawski et al. 2006; Kraft et al. 2011). It was found that in the Barents Sea, the Greenland Sea and the eastern Fram Strait, *T. libellula* and *T. abyssorum* are the most abundant pelagic amphipod species in the epipelagic zone. At sampling sites influenced by Atlantic water, the subarctic species *T. abyssorum* was found to appear in higher abundances than its Arctic congener *T. libellula* (Dunbar 1957; Koszteyn et al. 1995; Dalpadado 2002; Dalpadado et al. 2008). Furthermore, the occurrence of the typical North Atlantic species *T. compressa* was restricted to warmer Atlantic water masses in the Barents Sea, Norwegian Sea and eastern Fram Strait (Weigmann-Haass 1997; Dalpadado 2002; Kraft et al. 2011) and has been shown to occur in large swarms in the northeast Atlantic (Lampitt et al. 1993; Angel and Pugh 2000).

The ecological role and life-cycles of *Themisto* species at high latitudes have not been fully investigated: during few studies has the pelagic amphipod community been sampled year-round in seasonally ice-covered Arctic regions (Dalpadado et al. 2008; Makabe et al. 2010). Regular sampling with plankton nets in the Barents Sea suggested interspecific differences between the live cycles of *T. abyssorum* and *T. libellula*; for example a 1-year life span was hypothesized for the boreal-Atlantic species *T. abyssorum*, while its Arctic congener *T. libellula* seemed to show a 2-year life-cycle (Dalpadado 2002). Other studies addressing the size structure for the genus *Themisto* from the Barents, Greenland and Norwegian Seas as well as the central Arctic Ocean indicated that the life-spans of the species seemed to increase with increasing latitude, reaching up to two years for *T. abyssorum* (Bogorov 1940; Bowman 1960; Hoffer 1972; Koszteyn et al. 1995; Vinogradov et al. 1996) and three or more years for *T. libellua* (Koszteyn et al. 1995; Auel and Werner 2003; Dale et al. 2006; Weslawski et al. 2006). However, sampling for those studies mostly took place during a short period in summer. In addition, data on the life-cycle patterns of *T. compressa* are scarce and restricted to sampling regions in the North Atlantic and North Sea, but these data indicate that the species breeds multiple times per year (Sheader 1977, 1981). For Arctic waters, a few studies did mention the presence of *T. compressa* in the present day, but the respective authors did not give information on life-cycle features of this species (Brandt 1997; Weigmann-Haass 1997; Dalpadado et al. 2001; Dalpadado 2002).

One useful tool to extend our knowledge of the seasonal appearances and size structures of the pelagic amphipod community now seems to be the use of long-term datasets, which are obtained by time-series sediment traps deployed at different positions and depths in the open water column. This sampling method has been shown to successfully collect samples throughout the year in various Arctic regions including the open waters of the eastern Fram Strait, the Beaufort Sea and Kongsfjorden, West Spitsbergen (Willis et al. 2006, 2008; Bauerfeind et al. 2009; Makabe et al. 2010; Kraft et al. 2011). While predominantly used for assessing sinking organic matter in the water column, sediment traps are expected to provide an improved understanding of pelagic processes in times of climate change (Bauerfeind et al. 2009). Zooplankton collected in sediment traps, termed ‘swimmers’, have been analyzed in previous studies in order to improve our knowledge of zooplankton patterns, e.g. in the Greenland Sea (Seiler and Brandt 1997), in the eastern Fram Strait (Kraft et al. 2011) and in the southeastern Beaufort Sea (Makabe et al. 2010). Zooplankton which are collected in moored sediment traps first enter the trap actively; the organisms then die instantly when they come into contact with the poison or preservative in the collector cups (Knauer et al. 1979). As swimmers do not belong to the sinking particles (e.g., zooplankton fecal pellets and dead planktonic organisms), most protocols require the separation of these swimmers from the samples prior to the analysis of the sediment matter (e.g., Michaels et al. 1990; Buesseler et al. 2007). Removing and sorting these swimmer zooplankton groups may provide the opportunity of new insight into zooplankton composition and the important ability to study year-round datasets.

To our knowledge, none of the past studies on the genus *Themisto* in the Eurasian Arctic addressed a continuous multi-year analysis of length-frequency data, as all the data were collected during short time frames of less than one year or during repeated summer sampling covering several years. Therefore, the present study was conducted to investigate the year-round and long-term size structure development of the dominant *Themisto* species in the eastern Fram Strait. Based on the results, we follow the growth of cohorts throughout the year and highlight similarities and differences between *T. abyssorum*, *T. compressa* and

T. libellula, respectively, using time series samples of sediment traps during the years 2000 to 2009.

Material and methods

Investigation site

Sampling was conducted at HAUSGARTEN, a deep sea long-term observatory in the eastern Fram Strait, established by the Alfred Wegener Institute for Polar and Marine Research (AWI) in 1999. In this area, the inflow of the warm and saline Atlantic waters into the Nordic seas and the Arctic Ocean serves as structuring feature for marine processes in the Arctic ecosystems. Prevailing current systems in the Fram Strait are the north-flowing West Spitsbergen Current (WSC) and the south-flowing East Greenland Current (EGC). While the WSC transports relatively warm Atlantic waters into the Arctic Ocean Boundary Current (Quadfasel et al. 1987), the EGC in the west brings colder and less-saline Arctic waters away from the Arctic Ocean. Furthermore, the Atlantic water is the major source of the heat transport into the Arctic (Hansen et al. 2003; Schauer et al. 2004; Furevik et al. 2007). In the northern Fram Strait, a complex topography causes the splitting of the warmer WSC in three branches: one enters the Arctic Ocean north of Svalbard, the second continues north- and farther eastward around the rim of the Yermak Plateau, and the third one recirculates to the west as the Return Atlantic Current directly in the strait or shortly north of it (Schauer et al. 2008). Furthermore, transition zones with mixing water masses are formed along the WSC and EGC current systems (Piechura 2004). Within the HAUSGARTEN, the upper ~700 m are mostly affected by inflowing Atlantic water masses (Bauerfeind et al. 2009).

Sediment trap sampling

The HAUSGARTEN area contains the first deep-sea mooring arrays equipped with sediment traps which provide samples on a regular basis at high northern latitudes. During this study, samples of the sediment trap moorings deployed at the central (79°00.9' N, 04°20.6' E) HAUSGARTEN position were analyzed (Table 3.1, Fig. 3.1). Sediment particles and zooplankton swimmers were collected from September 2000 to June 2009 by modified automatic Kiel sediment traps, with an aperture of 0.5 m^2 and 20 collection cups (Zeitzschel et al. 1978; Kremling et al. 1996; Bauerfeind and von Bodungen 2006). The sampling cups were set to automatically rotate every 4 to 17 days during the productive period (May to September) and in longer intervals (up to 49 days) during the other months. The samples were obtained at a depth of 190-280 m. The collector cups were filled with filtered sterile North

Sea water and salinity was adjusted to 40 psu and poisoned with $HgCl_2$ in a final solution of 0.14 %. Following collection, samples were sorted in the laboratory of the Alfred Wegener Institute (Bremerhaven, Germany).

Table 3.1 Location, sampling time, water depth and trap depth of moored sediment traps analyzed for amphipod composition and size structure at the deep-sea long-term observatory HAUSGARTEN in the eastern Fram Strait

Mooring period	Lat. N	Long. E	Water depth (m)	Trap depth (m)	No of samples
31.08.2000-14.08.2001	79°01.70’	04°20.86	2456	280	18
12.07.2004-19.08.2005	79°00.99’	04°20.62’	2584	280	20
05.08.2006-20.06.2007	79°00.82’	04°20.50’	2540	230	20
21.07.2007-15.07.2008	79°00.82’	04°20.62’	2589	190	20
17.07.2008-18.07.2009	79°00.40’	04°20.00’	2557	201	20

Swimmers were removed under a dissecting microscope (Olympus SZX10, magnification 20-50), sorted into common systematic groups (i.e., Amphipoda, Chaetognatha, Copepoda, Ostracoda and Pteropoda) and refrigerated until further treatment. All collected amphipods, including *Themisto abyssorum*, *T. compressa* and *T. libellula* were identified, counted and classified according to sex and life history stage. The total body length (TBL; accuracy 0.1 mm) of all encountered *Themisto* specimens was measured by image analysis using the software cell^P (Olympus Europa Holding GmbH) from the anterior side of the head to the tip of the third pair of uropods (Dunbar 1957; Hoffer 1972). According to Percy (1993), Yamada and Ikeda (2006) and Weitkamp and Sturdevant (2008), possible body shrinkage due to preservation was not calculated or adjusted for. To determine maturity, an examination of secondary sexual characters was carried out. As amphipods are livebearers, female individuals were identified by the presence of oostegites, which develop into a brood chamber (Marsupium) among the inner coax margin of the anterior walking legs (Periopoda). In the case of fully mature females the oostegites carried setae. A segmented and longer second antenna was used as a criterion to recognize males. Males were considered fully mature when ≥ 13 segments were counted (after Kane 1963; Dalpadado et al. 2008). Small individuals without recognizable sexual features were recorded as juveniles.

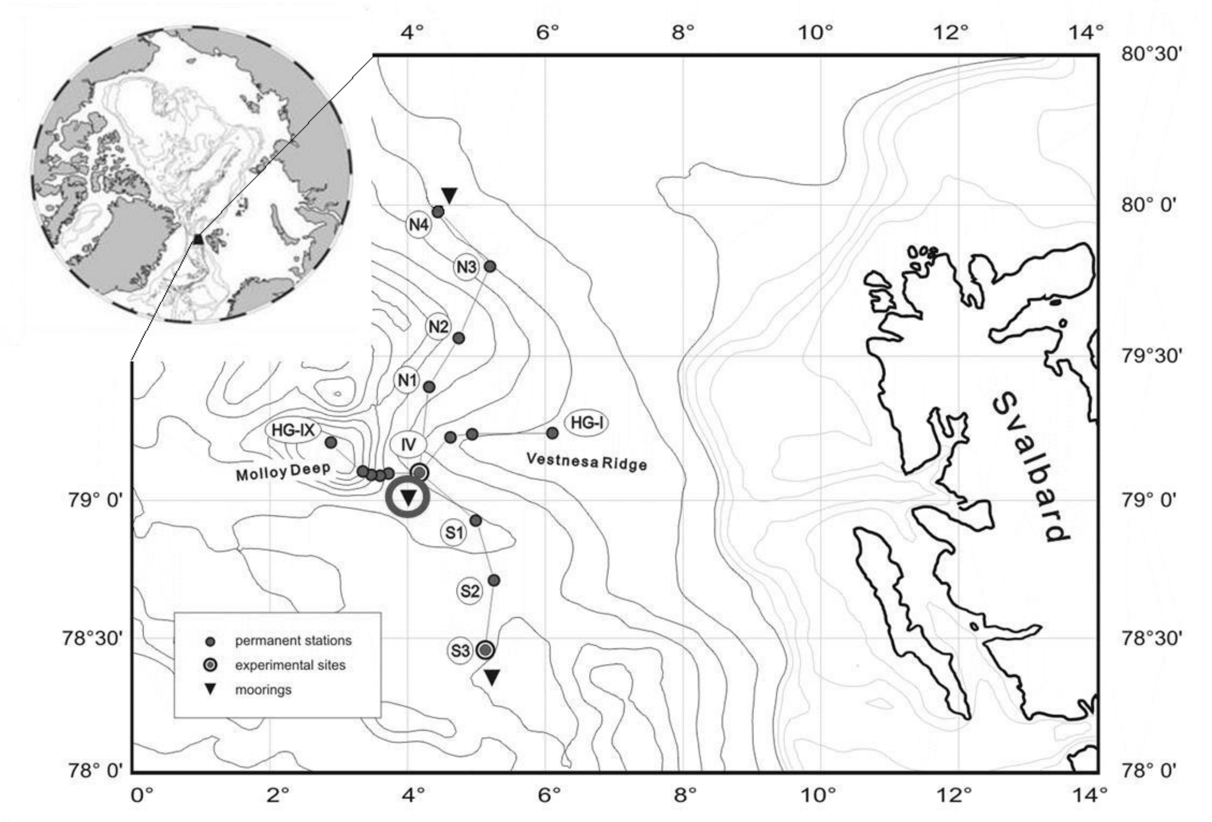

Fig. 3.1 The analyzed sampling site (indicated by a circled inverted triangle) at the deep-sea long-term observatory HAUSGARTEN in the Fram Strait (Arctic Ocean)

Data analysis

During the sampling times from September 2000 to June 2009, an abundance index and length-frequency histograms were calculated for pairs of two months (July-August, September-October, November-December, January-February, March-April and May-June) due to different sampling intervals between summer (7-17 days) and winter (up to 49 days).

Thus, the abundance index was determined as follows for each pair:

Abundance index [ind. m^{-2} d^{-1}] = (Total number of amphipods * 2) / Collection time [days]

[2 = conversion factor to 1 m^2]

Furthermore, mean abundance indices of the sampling years (2000/01, 2004/05, 2006/07 and 2008/09) were calculated from September to June for the respective time periods to facilitate analysis despite missing datasets from July to August 2000 and 2006. The length measurements were plotted in histograms for pairs of two months, indicating male, female and juvenile individuals. Length-frequency distributions for each pair were analyzed for normally-distributed components equaling cohorts according to Sparre (1988) and Dalpadado (2002) using Bahttacharya's analysis. For this study, we assumed in accordance with Dalpadado (2002) that each size group (also referred to as cohort) corresponded to the respective appearance of a year-class. Within the Bahttacharya's analysis, a reliable separation between the appearing cohorts was given with a separation index (SI) >2.0. During months with few recorded individuals (<15 counted specimens), the statistical test could not be applied. For these cases, no separation index was given and the recorded length-frequencies were classified in cohorts on the basis of previous statistical results derived from the respective seasonal timeframes of other sampling years. In order to establish a fitting growth function, the mean lengths of the cohorts were used. The data was tested on several growth models in a pre-established Excel spreadsheet provided by Brey (2001). Tested models included the

Gompertz growth model

$$L_t = L_{t\,\infty} * e^{-e\wedge[-k * (t - t^*)]}$$

where L_t = total body length, $L_{t\,\infty}$ = asymptotic final length, k = growth constant, t^* = age of growth inflexion and t = age.

The growth parameters were estimated by a

Ford-Walford-Plot (Ricker 1975):

$$\ln(L_t{+}1) = a + b * \ln(L_t) \rightarrow k = -\ln(b)\ ;\ L_{t\,\infty} = e^{a\,/\,(1-b)}$$

where a and b are constants.

Results

Abundance index

All three species of the genus *Themisto* (*Themisto abyssorum*, *T. compressa* and *T. libellula*) were collected at the long-term observatory HAUSGARTEN in the eastern Fram Strait (Table 3.2), with 4034, 269 and 1568 individuals of each species respectively being collected in the analyzed sediment traps samples from 2000 to 2009. Among the three species, the two-month abundance indices for *T. abyssorum* were highest (range 0.1-31.5 ind. m^{-2} day^{-1}), followed by *T. libellula* (0.0-20.4 ind. m^{-2} day^{-1}) and *T. compressa* (range 0.0-1.8 ind. m^{-2} day^{-1}) (Table 3.2). It was noted that the Atlantic species *T. compressa* was absent during the first sampling period 2000/2001.

Table 3.2 Grouped abundance indices for pairs of two months (ind. m^{-2} day^{-1}) of three *Themisto* species and relative composition in sediment trap samples, presented for the collection period from 2000 to 2009 at the long-term observatory HAUSGARTEN in the eastern Fram Strait

Time period		***Themisto* total**	***T. abyssorum***		***T. compressa***		***T. libellula***	
		ind. m^{-2} day^{-1}	ind. m^{-2} day^{-1}	% of total *Themisto*	ind. m^{-2} day^{-1}	% of total *Themisto*	ind. m^{-2} day^{-1}	% of total *Themisto*
Sep./Oct.	2000	1.6	0.6	37.5	0.0	0.0	1.0	62.5
Nov./Dec.	2000	1.6	1.0	62.5	0.0	0.0	0.6	37.5
Jan./Feb.	2001	0.8	0.5	62.5	0.0	0.0	0.3	37.5
Mar./Apr.	2001	0.7	0.6	85.7	0.0	0.0	0.1	14.3
May/Jun.	2001	1.5	1.2	80.0	0.0	0.0	0.3	20.0
Jul./Aug.	2004	13.3	8.7	65.4	1.3	9.8	3.3	24.8
Sep./Oct.	2004	8.7	3.0	34.5	0.7	8.0	5.0	57.5
Nov./Dec.	2004	2.1	1.7	80.9	0.1	4.8	0.3	14.3
Jan./Feb.	2005	2.5	1.7	68.0	0.7	28.0	0.1	4.0
Mar./Apr.	2005	5.5	4.8	87.3	0.7	12.7	0.0	0.0
May/Jun.	2005	12.2	11.5	94.3	0.6	4.9	0.1	0.8
Jul./Aug.	2006	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Sep./Oct.	2006	6.8	2.2	32.4	1.4	20.6	3.2	47.0
Nov./Dec.	2006	1.1	0.4	36.4	0.0	0.0	0.7	63.6
Jan./Feb.	2007	2.0	1.8	90.0	0.0	0.0	0.2	10.0
Mar./Apr.	2007	1.4	1.2	85.8	0.1	7.1	0.1	7.1
May/Jun.	2007	12.7	12.2	96.1	0.1	0.8	0.4	3.1
Jul./Aug.	2007	16.9	6.5	38.4	0.4	2.4	10.0	59.2
Sep./Oct.	2007	9.3	4.9	52.7	0.2	2.1	4.1	45.2
Nov./Dec.	2007	3.8	2.2	57.9	0.0	0.0	1.6	0.0
Jan./Feb.	2008	1.5	0.6	40.0	0.4	26.7	0.5	33.3
Mar./Apr.	2008	4.1	3.7	90.2	0.2	4.9	0.2	4.9
May/Jun.	2008	19.7	17.7	89.9	0.2	1.0	1.8	9.1
Jul./Aug.	2008	53.7	31.5	58.7	1.8	3.3	20.4	38.0
Sep./Oct.	2008	11.9	7.1	59.7	0.3	2.5	4.5	37.8
Nov./Dec.	2008	2.5	0.9	36.0	0.2	8.0	1.4	56.0
Jan./Feb.	2009	1.7	0.8	47.1	0.4	23.5	0.5	29.4
Mar./Apr.	2009	0.1	0.1	100.0	0.0	0.0	0.0	0.0
May/Jun.	2009	21.1	20.7	98.1	0.3	1.4	0.1	0.5

n.d. = no data

Over the course of this study, the average yearly contribution (ind. m^{-2} day^{-1}) of *Themisto* amphipods (all species) in swimmer samples collected in the eastern Fram Strait increased significantly from 1.2 ind. m^{-2} day^{-1} during 2000/01 to 7.7 ind. m^{-2} day^{-1} in 2007/08 ($p < 0.05$, Student's t test) (Fig. 3.2). During the other time periods (2004/05, 2006/07 and 2008/09), the average yearly appearances were recorded at 6.2, 4.8 and 7.5 ind. m^{-2} day^{-1}, respectively. In addition to this general trend, a strong seasonal pattern including abundance peaks from May to October could be observed (Table 3.2, Fig. 3.2). A detailed description and discussion of this seasonality is given in Kraft et al. (2011).

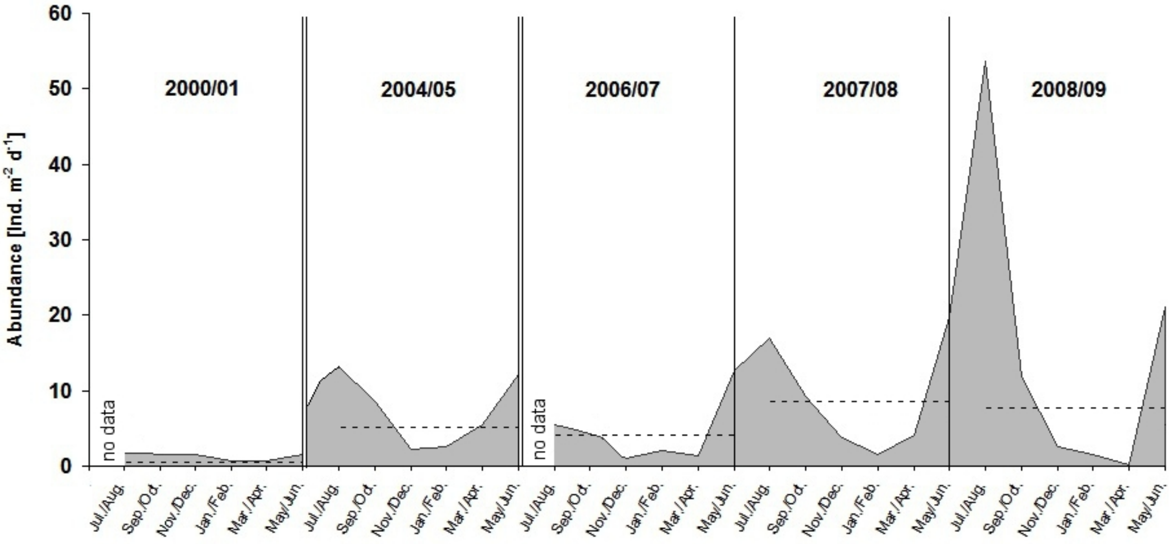

Fig. 3.2 Grouped abundance indices for pairs of two months (ind. m^{-2} day^{-1}) for *Themisto* amphipods at the central sediment trap mooring station during 2000 to 2009. The dashed line indicates average yearly contributions from September to June, ranging from 1.2 ind. m^{-2} day^{-1} during 2000/01 to 7.7 ind. m^{-2} day^{-1} in 2007/08. At other time periods 2004/05, 2006/07 and 2008/09 the average yearly appearances were calculated at 6.2, 4.8 and 7.5 ind. m^{-2} day^{-1}, respectively. No data exist for the sampling months from July/August in 2000 and 2006

Population structure

Length-frequency analysis showed a dominance of female individuals of *T. abyssorum*, *T. compressa* and *T. libellula* for all sampling periods, along with an absence of small juveniles (<4 mm TBL) for all species (Fig. 3.3, 3.4, 3.5). While no seasonal patterns in the appearance of male versus female individuals could be observed for *T. compressa* (Fig. 3.4) or *T. libellula* (Fig. 3.5), it became apparent that the proportion of male individuals of *T. abyssorum* was higher during the winter months (January-April) (Fig. 3.3).

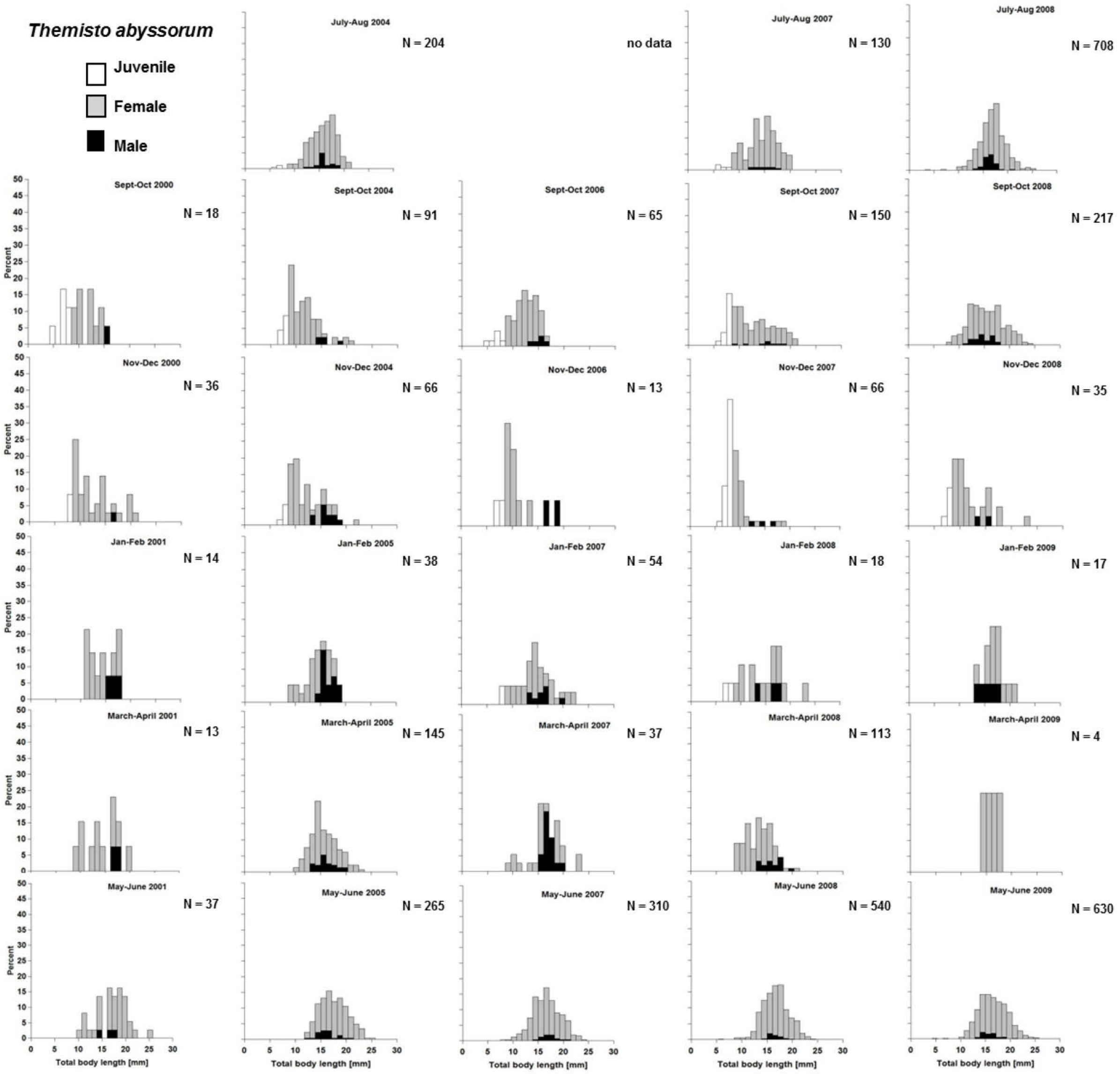

Fig. 3.3 Length-frequency distribution for pairs of two months for *Themisto abyssorum* collected from September 2000 to June 2009. No data exist for the sampling months July/August 2000 and 2006

During the observed time frames in 2000/01, 2004/05, 2006/07, 2007/08 and 2008/09, the total body length of *T. abyssorum* ranged from 5.1-24.7 mm, 6.3-25.6 mm, 5.2-23.9 mm, 5.6-24.1 mm and 4.2-25.5 mm, whereas it varied for *T. libellula* from 7.5-56.7 mm, 11.0-49.7 mm, 4.0-50.0 mm, 8.7-49.5 mm and 7.7-49.8 mm, respectively. In the case of *T. compressa*, no individuals were observed in the traps during 2000/2001. For the other time periods, the TBL was recorded as 8.8-24.4 mm, 9.1-21.5 mm, 11.7-23.2 mm and 10.8-21.7 mm, respectively.

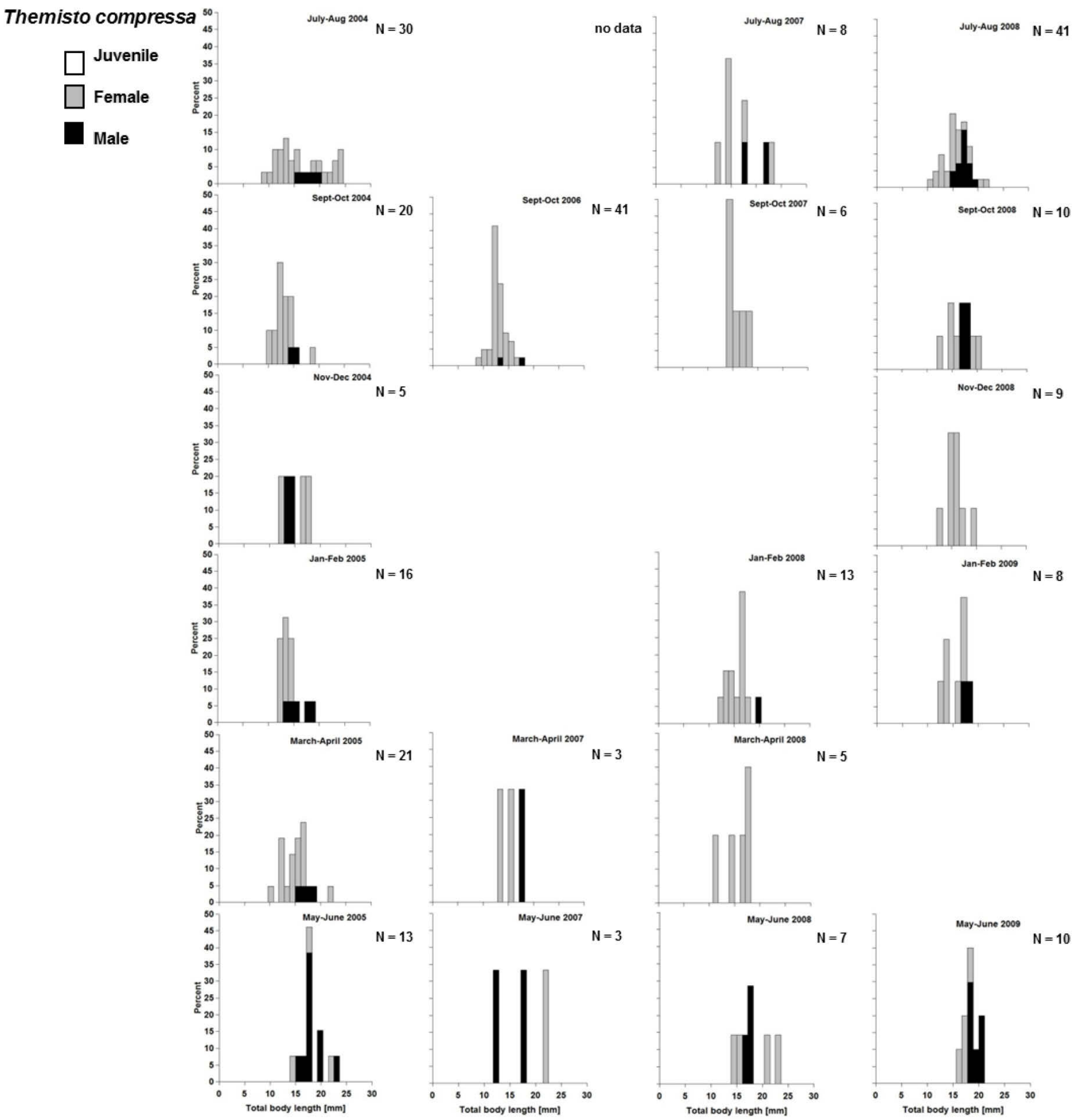

Fig. 3.4 Length-frequency distribution for pairs of two months for *Themisto compressa* collected from September 2004 to June 2009. This species was absent from the samples during the sampling period 2000/2001. No data exist for the sampling months July/August in 2000 and 2006. Note that no individuals were present in the trap in November/December 2006 as well as during January/February 2007, November/December 2007 and March/April 2009

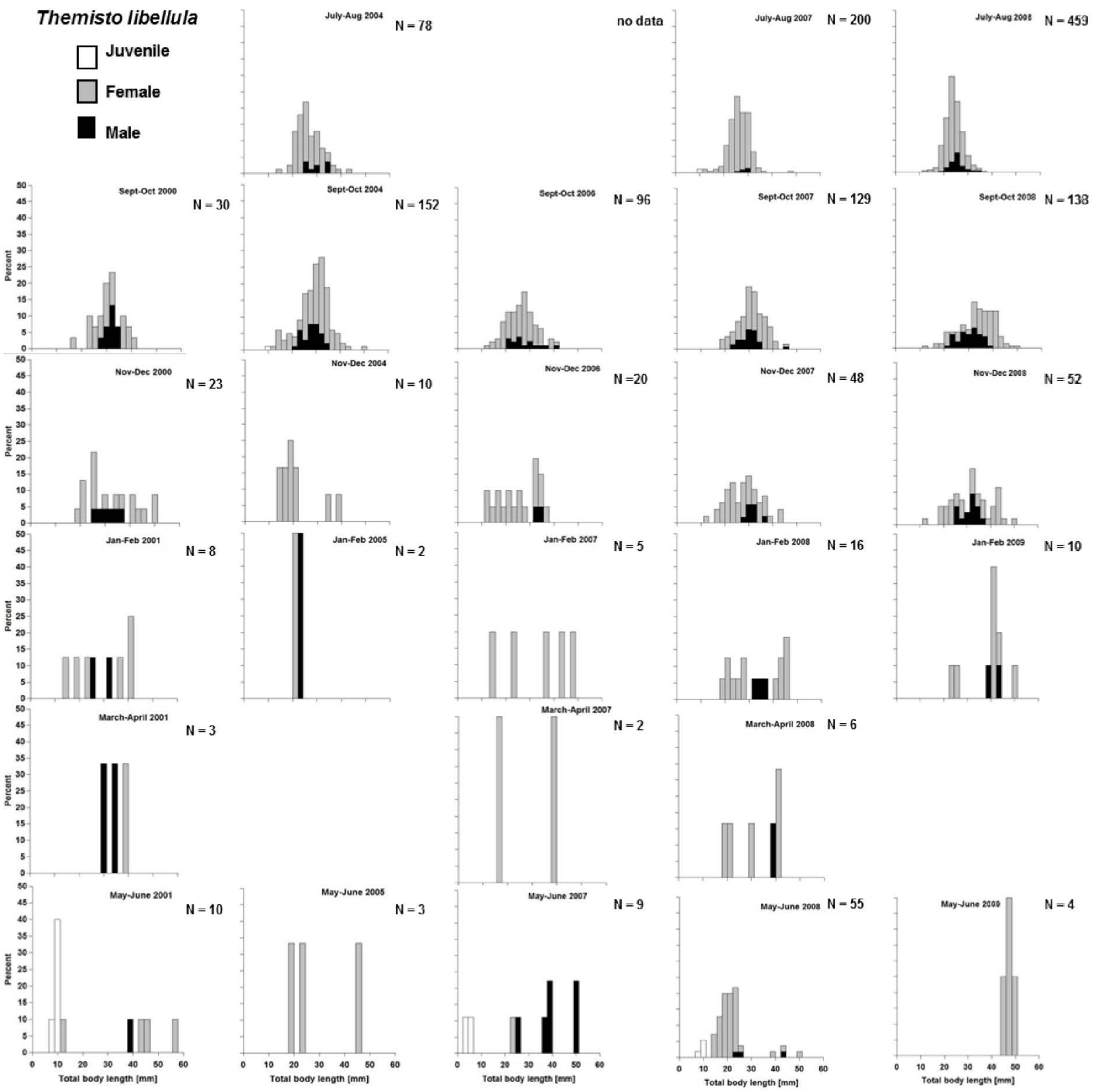

Fig. 3.5 Length-frequency distribution for pairs of two months for *Themisto libellula* collected from September 2000 to June 2009. No data exist for the sampling months July/August 2000 and 2006. In March/April 2005 and March/April 2009 no individuals were present in the trap

Themisto abyssorum

The statistical analysis of size groups within the length-frequency distributions of *T. abyssorum* showed 1 to 3 cohorts for the respective two-month time periods from 2000 to 2009 (Fig. 3.6 and Table S1 in the Supplement). Thus, the mean length (including ranges in brackets) for each detected size group was: Cohort no. 0+ = 9.3 (7.0-11.5) mm, cohort no. 1+ = 14.8 (11.8-17.8) mm, cohort no. 2+ = 20.2 (17.0-24.7) mm. Throughout the observed sampling years, both immature (0+ cohort) and mature female individuals

(1+ and 2+ cohort) were present at almost all studied time periods in the samples. However, no females with full brood pouches were recorded.

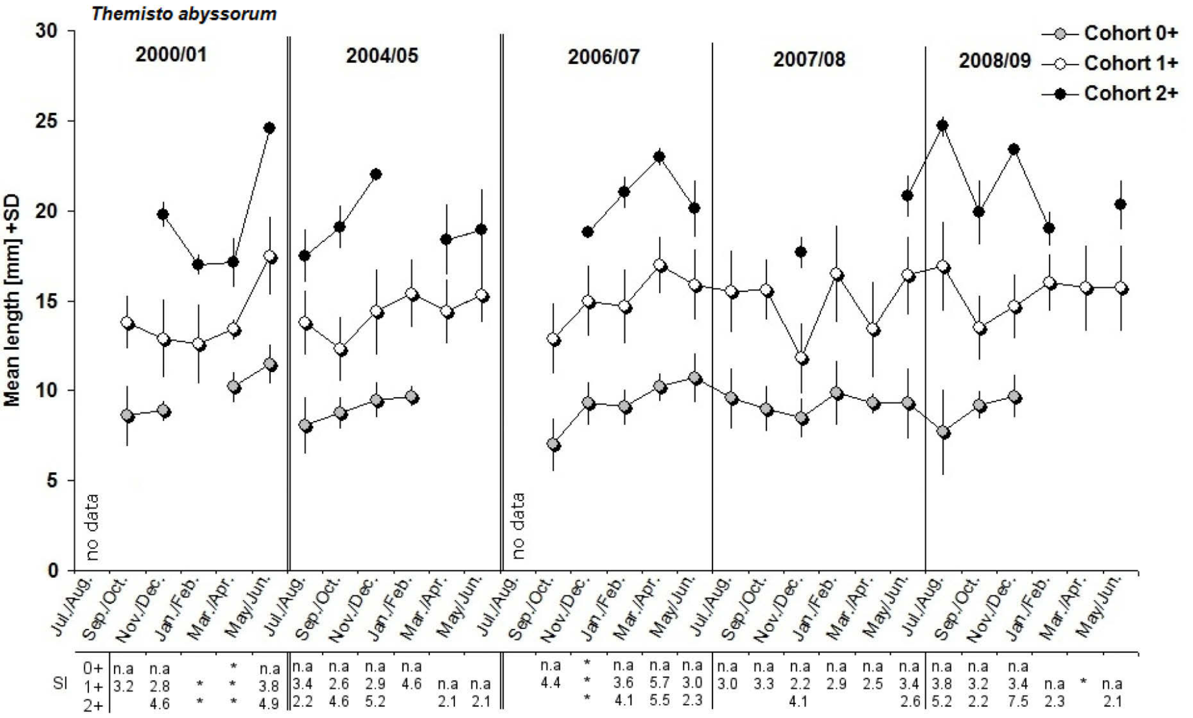

Fig. 3.6 Seasonal and interannual development of recognized cohorts for *Themisto abyssorum* in sediment trap samples during 2000-2009. Missing dots indicate absence of respective cohort. Separation indices (SI) of the cohorts are given; n.a = not applicable; * Too few individuals - not included in statistical analysis. No data present for July/August 2000 and 2006

Most males were already fully matured when collected in the traps. The appearance of smaller male individuals was restricted to the summer season (May-October) (Fig. 3.3). Within analyzed time frames, male and female individuals of *T. abyssorum* attained a different maximum size, with the males being generally smaller (up to 20.9 mm) compared to the females (up to 25.6 mm). Furthermore, the prominent and regular appearance of juvenile and immature individuals could be observed during autumn, being particularly distinct during the months September-December (Fig. 3.3). This pattern of juvenile return was also displayed by statistical analysis, with mean lengths of 7.0-9.7 mm for the 0+ cohort (Table S1 in the Supplement).

Themisto compressa

Among the collected specimens of *T. compressa*, a species considered to be of North Atlantic origin, no juveniles were recorded in the eastern Fram Strait. The statistical analysis for size groups indicated the presence of up to 3 cohorts for the observed time periods during 2000-2009, with the following mean length (including ranges): Cohort no. 1+ = 12.6 (11.9-13.4) mm, cohort no. 2+ = 16.4 (14.8-19.8) mm and cohort no. 3+ = 22.1 (21.2-23.5) mm (Fig. 3.7 and Table S2 in the Supplement). Compared to *T. abyssorum*, most of the collected specimens of *T. compressa* were slightly larger (~2-3 mm). However, the presence of the 3+ cohort was restricted to summer and early spring during 2004-2009 (Fig. 3.7). With a TBL of 22.6 mm and 23.3 mm for male and female individuals of *T. compressa* respectively, the females showed a slightly larger body size than males. Both sexes occurred for the most part throughout the year in the samples, with the restricted appearance of immature females (< 10 mm TBL) during July-August 2004 and September-October 2006 (Fig. 3.4). Females with large oostegites or bearing young were not observed in the traps, while fully mature males were regularly present.

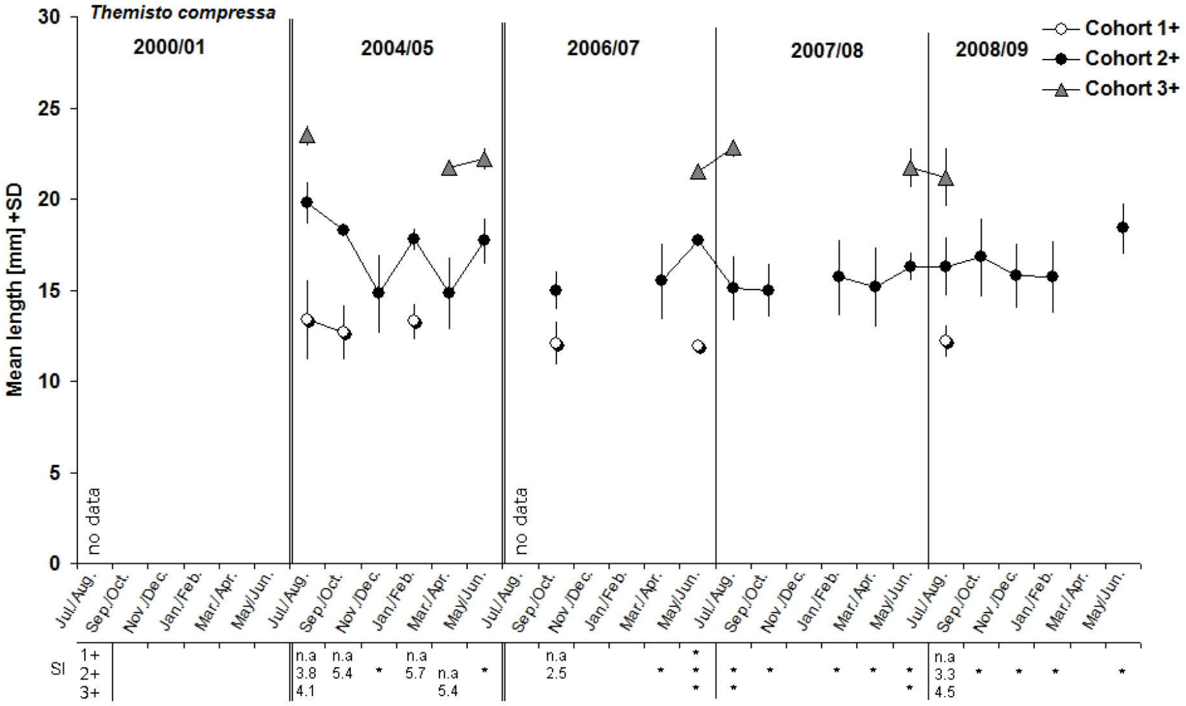

Fig. 3.7 Seasonal and interannual development of recognized cohorts for *Themisto compressa* in sediment trap samples during 2000-2009. Missing dots indicate absence of respective cohort. Separation indices (SI) of the cohorts are given; n.a = not applicable; * Too few individuals - not included in statistical analysis. No data present for July/August 2000 and 2006

Themisto libellula

In the case of the typically Arctic specialist *T. libellula*, the appearance of 1-4 cohorts could be observed during the two-month time frames from 2000 to 2009. The mean length of each cohort (including ranges) was recorded as follows: Cohort no. 0+ = 11.6 (4.4-15.9) mm, cohort no. 1+ = 22.1 (16.7-26.4) mm, cohort no. 2+ = 33.3 (27.5-38.2) mm, cohort no. 3+ = 44.3 (39.1-50.0) mm. The collective appearance of all four cohorts was restricted to the months September-October 2006 as well as January-February and May-June in 2007 (Fig. 3.8 and Table S3 in the Supplement). Immature and mature female individuals dominated the length-frequency distribution during most time frames (Fig. 3.5). With few exceptions, males were also collected year-round in the traps. For *T. libellula*, the maximum size of the observed male specimens was smaller (50.0 mm) compared to their female counterparts (56.7 mm) (Fig. 3.5). From December to June, small juveniles ~1 mm TBL and females with partly filled brood pouches could be observed in the traps. Since the collected juveniles were of the same developmental stage as the ones found in the brood pouch, it was assumed that they were released from the Marsupium of the female upon entering the trap. The other collected juvenile individuals had a TBL of more than 4 mm and were found scarcely in the samples. Their highest appearance occurred during May-June 2001 (5 specimens) and May-June in 2008 (4 specimens).

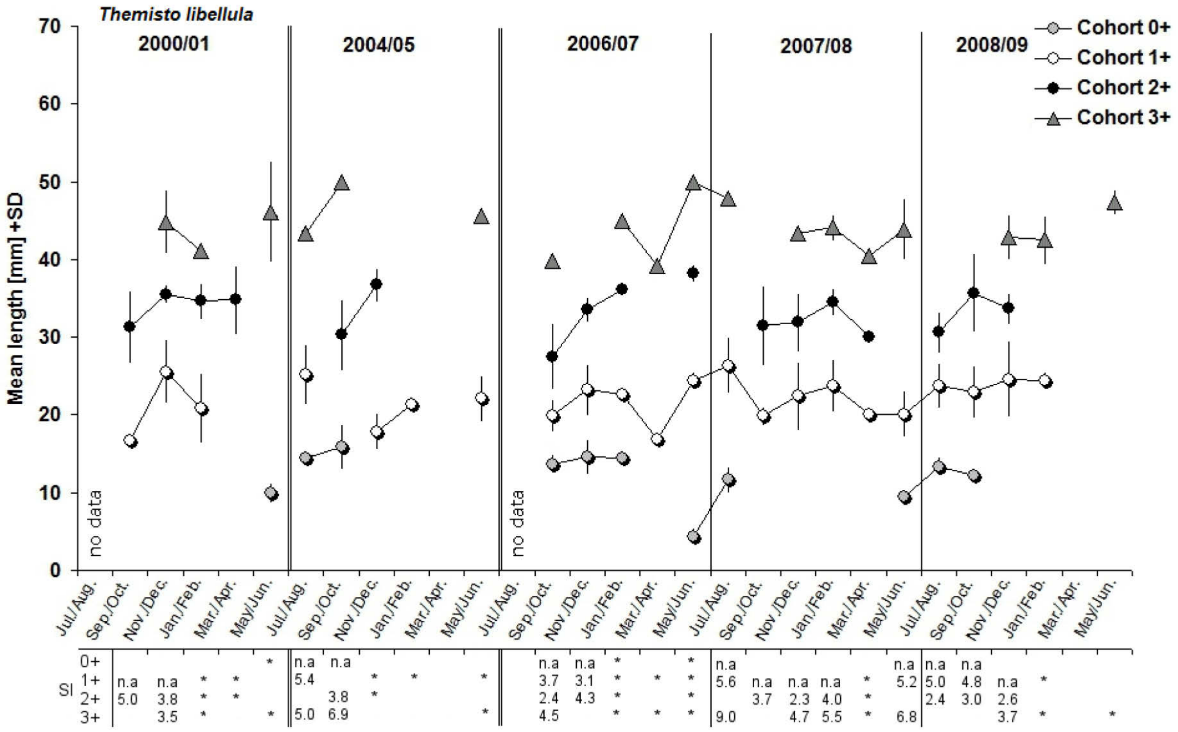

Fig. 3.8 Seasonal and interannual development of recognized cohorts for *Themisto libellula* in sediment trap samples during 2000-2009. Missing dots indicate absence of respective cohort. Separation indices (SI) of the cohorts are given; n.a = not applicable; * Too few individuals - not included in statistical analysis. No data present for July/August 2000 and 2006

Growth

The growth of *T. abyssorum*, *T. compressa* and *T. libellula* was best described by the Gompertz growth function (Fig. 3.9), indicating that the calculated asymptotic size is the largest for *T. libellula* ($L_{t\,\infty}$ = 60.00), followed by *T. abyssorum* ($L_{t\,\infty}$ = 35.50) and *T. compressa* ($L_{t\,\infty}$ = 28.75) (Table 3.3).

Table 3.3 Gompertz growth function parameters of *Themisto abyssorum*, *T. compressa* and *T. libellula* derived from the Gompertz growth model: $L_{t\,\infty}$ = asymptotic final length, k = growth constant, t^* = age of growth inflexion

Species	$L_{t\,\infty}$	**k**	t^*
T. abyssorum	35.50	0.60	0.91
T. compressa	28.75	0.56	0.71
T. libellula	60.00	0.62	1.11

The growth constants were k = 0.60, 0.56 and 0.62 for *T. abyssorum*, *T. compressa* and *T. libellula* respectively, and therefore highest for the largest Arctic species, *T. libellula*. The observed growth pattern suggests a division into two phases with an immature phase of rapid growth and a mature phase of slower growth, which also can be influenced by ecological and environmental parameters such as food availability and temperature. This development leads to a size overlap of *T. abyssorum* and *T. libellula* during the 0+ cohort stage, and of all three individuals including *T. compressa* during the 1+ cohort (Fig. 3.9). Within the 2+ age group, individuals of *T. libellula* have already grown larger compared to their subarctic and Atlantic congeners, which both had more similar size ranges.

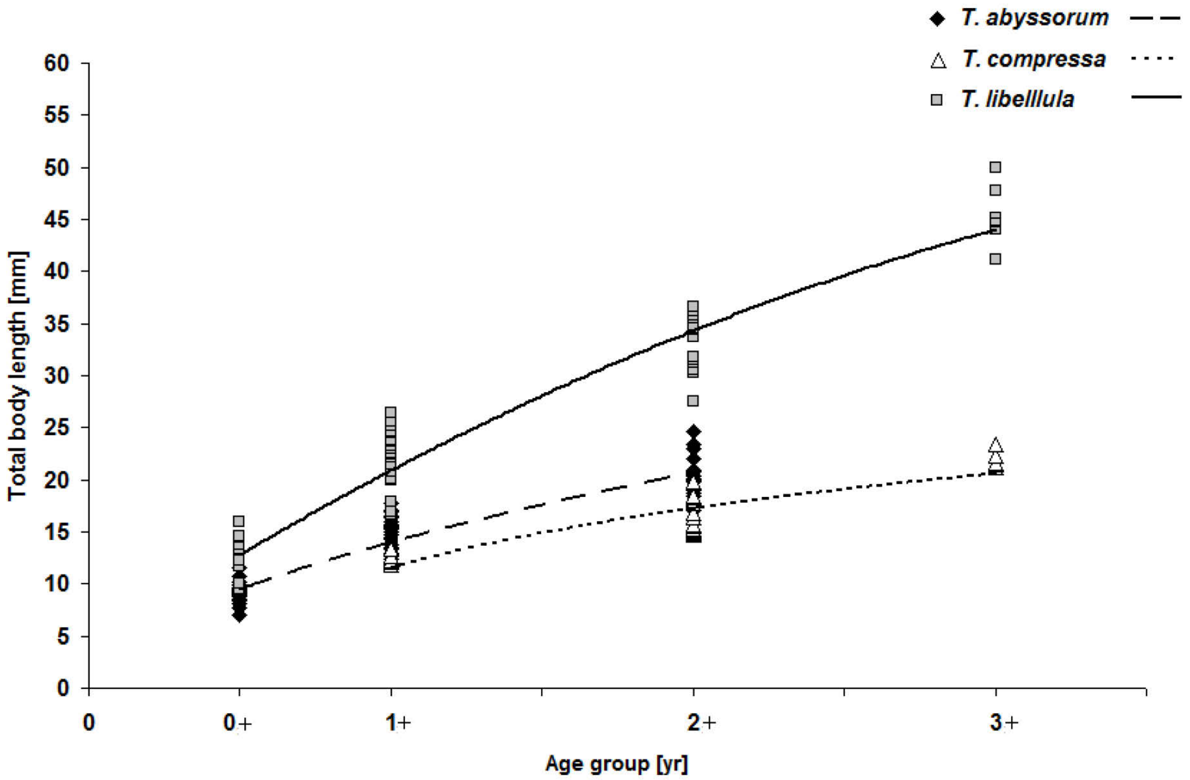

Fig. 3.9 Mean length of cohorts and fitted Gompertz growth function for *Themisto abyssorum*, *T. compressa* and *T. libellula* (genders combined); growth parameters are listed in Table 3.3

Discussion

The population structure and length-frequency distributions presented here for the three hyperiid amphipods *T. abyssorum*, *T. compressa* and *T. libellula* in the Fram Strait represent continuous multi-year information on the three species. Similar data were previously published mostly for the summer period, including data from the Barents Sea and Canadian Arctic (Dunbar 1957; Koszteyn et al. 1995; Dalpadado 2002); in the case of *T. compressa*, data were completely absent for this region. Our results show evidence of increasing pelagic amphipod populations in the eastern Fram Strait (Fig. 3.2), including the dominance of *T. abyssorum* in the traps with a mean contribution between 69.5 % and 82.6 % during a time span from November to June in all observed sampling periods (Table 3.2). The dominance of *T. abyssorum* likely reflects the prevailing influence of North Atlantic water masses in the upper part of the water column in the HAUSGARTEN area. Due to the lack of a full dataset on temperature and salinity at the position of the sediment traps, we refer to data obtained by moorings across the Fram Strait. This mooring line, located 20 km south of the HAUSGARTEN, was established in 1997 and has been operating since then (Beszczynska-Möller et al. 2011 accepted). Those authors describe the presence of warm water anomalies from 2005-2007, which were accompanied by a positive linear trend of 0.06°C/year in the Atlantic Water mean temperature for the time period 1997-2010. The effect of this trend could be that a community shift to the disadvantage of the typically Arctic species *T. libellula* is occurring, caused by increasing influence of warming Atlantic water and rising contribution of the subarctic species *T. abyssorum*. This development was suggested by previous studies for the Kongsfjorden area (Hop et al. 2006) and is discussed in detail by Kraft et al. (2011) for the eastern Fram Strait.

We are aware that it is unusual to address amphipod contributions from sediment traps in a qualitative and quantitative manner. However, there are other investigations like Seiler and Brandt (1997), Steinberg et al. (1998) and Makabe et al. (2010) who presented reliable information on zooplankton obtained with sediment trap samples. Furthermore, long-term data series for marine systems are scarce (Perry et al. 2004; Richardson 2008). It is expected that such data sets provide the best opportunity to identify the causes of community changes on a worldwide scale and in the Arctic region (Smetacek and Nicol 2005; Schiermeier 2007; Turner et al. 2007; Berge et al. 2009b), especially since the Arctic is an area of high political, economic and scientific interests. One tool for obtaining long-term data are sediment traps which have been used during the last 50 years in marine and limnic environments (e.g., Bloesh and Burns 1980; Peterson et al. 1993; Buesseler et al. 2007). Sediment trap studies led to new insights on particles and flux estimations from surface waters and enhanced our understanding of biogeochemical processes in the pelagic system (e.g., Bauerfeind et al. 2009). In this context, swimmers were more often than not considered a contamination (Karl and Knauer 1989; Michaels et al. 1990; Wakeham et al. 1993) and only few studies are known which exploited their composition patterns (e.g., Seiler and Brandt 1997; Willis et al. 2008; Makabe et al. 2010; Wallace et al. 2010).

With the sediment trap technique, the most apparent reasons for variability in the composition of swimmer collections are differences in location and depth of the deployed traps. In the present study, all presented data were collected at the same sampling position in the HAUSGARTEN area. However the trap depth varied between 190 and 280 m due to technical issues. In this context it should be noted that each of the three investigated species has different vertical distribution ranges. Among them, *T. abyssorum* has the widest range, as it is found in a water depth of 3000 m (Koszteyn et al. 1995; Vinogradov et al. 1996; Weigmann-Hass 1997), although no high abundances were usually recorded below 1000 m. From June to August, Dalpadado et al. (2001) recorded the highest densities of *T. abyssorum* at water depths of 250-425 m in the northern Barents Sea, and a more even distribution between 100-400 m during autumn. The vertical distribution capacity of the Arctic congener *T. libellula* is still subject to much discussion. While some authors (e.g., Weigmann-Haass 1997) described the distribution of *T. libellula* as no deeper than 500 m, Vinogradov et al. (1996) recorded the species with submersibles at about 1000 m water depth in Norwegian and Greenland Seas. Furthermore, Grainger (1989) observed high numbers of *T. libellula* in the upper 50 m of the water column during summer in the central Arctic Ocean and a shift toward high abundances at a water depth below 200-300 m in winter. In the southern Barents Sea, Dalpadado et al. (2001) found peak abundances of this Arctic specialist in the upper 300 m of the water column from May-July; maximum densities were caused by juveniles in the upper 55 m, and most adult individuals appeared at about 100-250 m. For *T. compressa*, vertical distribution data have been reported in only a few studies to date. Williams and Robins (1981) confined the appearance of this species to the upper 500 m water column of the North-East Atlantic, with its highest abundances (>3.7 ind. m^{-3}) occurring in the upper 10 m of the water column in August and September and the majority of juveniles found in 0-100 m water depth. Furthermore, a diel migration pattern of *T. compressa* was observed by Williams and Robins (1981): adult individuals were closer to the surface by night, when they migrated from more than 200 m depth to the upper 40 m of the water column. A diel vertical migration capacity was also recorded for *T. libellula* by Harvey et al. (2009) in the St. Lawrence marine ecosystem. There, the species migrated to the upper 30 m of the water column at night and to about 125 m water depth during the day, following the migration of its prey. The same phenomenon was also described by Wing (1976) for Alaskan waters, where *T. libellula* showed a vertical migration of 150-200 m each night. In addition, newer studies revealed that diel vertical migration behavior of zooplankton also occurred during the polar night (when no daylight is present in the Arctic winter) in open and ice-covered waters (Berge et al. 2009a). The causes of the seasonal and diel vertical migration behaviors among pelagic amphipods are thought to be the result of several intrinsic factors, e.g. migration and feeding habits, and their connection to the influence of abiotic parameters such as the distribution of different water masses. Considering the prevalence of Atlantic water in the upper 300 m of the HAUSGARTEN area and the seasonal and diel vertical migration capacity for *Themisto* species, it seems unlikely that a depth variation of 90 m between the sediment traps has a significant influence on this population study; however it still remains a possibility.

A clear advantage of the sediment trap technique seems to be the year-round recording of large adult *Themisto* specimens in general, including the appearance of *T. libellula* individuals up to 56.7 mm TBL (Fig. 3.5). To our knowledge, no published record of such large specimens is available for the Fram Strait. Respectively large individuals of *T. libellula* however have been sampled in the Fjords of Svalbard (up to 40-45 mm TBL; Weslawski et al. 2006; Noyon et al. 2011), the Gulf of St. Lawrence (up to 50 mm TBL; Marion et al. 2008) and the Barents Sea (up to 45 mm TBL; Dalpadado et al. 2008) (Table 3.4). Furthermore, Bovallius (1889) recorded that *T. libellula* may reach a maximum body length of 60 mm. However, most studies using traditional plankton nets, often with a mesh size below 500 µm, fail to sample large *Themisto* species due to their excellent swimming capacity and consequent active net avoidance, as suggested by several authors (e.g., Vinogradov 1999; Dalpadado et al. 2001; Dalpadado 2002). Similarly, *T. abyssorum* specimens of up to 25.5 mm TBL were collected during the present investigation; this measurement is up to ~4 mm larger compared to previous studies (Table 3.4). As indicated by previous life history data for *Themisto* amphipods (Table 3.4), it seems common that female individuals reach a larger size than their male counterparts. This observation also became apparent for *T. abyssorum* and *T. libellula* during the present study with size difference of the maximum TBL up to 4.7 and 6.7 mm, respectively (Fig. 3.3 and 3.5). In the case of *T. compressa*, females only showed a slightly larger body size with a difference up to 0.7 mm (Fig. 3.4).

Population structure and growth

In Arctic seas, marine invertebrates with a life span of several years have often been shown to develop separate, annual cohorts characterized by different age groups varying in size and sometimes also in spatial distribution (Dunbar 1957; Hargrave 1985; Weslawski and Legezynska 2002). For Arctic *Themisto* amphipods, this concept was highlighted by Weslawski et al. (2006), who compared the typically Arctic species *T. libellula* from Svalbard fjords with populations from *Themisto abyssorum* and *Themisto compressa* from the Southern Barents and Norwegian Sea. While the authors found the presence of at least three separate annual cohorts for *T. libellula*, a 1-year life span was hypothesized for *T. abyssorum* and *T. compressa*. In this context, it has been our interest to identify, follow and compare the cohort development of the three *Themisto* species from the same investigation area in the eastern Fram Strait in order to increase our understanding of their ecological interactions and possible life-cycle adaptations to the recorded temperature increase of Atlantic water inflow in the area from 1997-2010 (Schauer et al. 2004, 2008; Piechura and Walczowski 2009; Beszczynska-Möller et al. accepted).

In the process of the length-frequency analysis, repeating patterns in appearance of cohorts and the distribution of stages during the time periods 2000/01, 2004/05, 2006/07, 2007/08 and 2008/09 could be observed for the three *Themisto* species (Fig. 3.3, 3.4, 3.5). One conspicuous feature was the lack of newly-released juveniles in the sediment trap samples. This can be explained by the fact that female *Themisto* species have been observed to release their young exclusively within the upper 50 m of the water column, and that small juveniles do not appear to undergo vertical migration until they reach a certain size and respective maturity (Williams and Robins 1981; Ikeda et al. 1992; Dalpadado 2002; Yamada et al. 2004). This critical size for the onset of migration behavior was indicated in the present study to be ≥4.2 mm for *T. abyssorum* and ≥ 4.0 mm for *T. libellula*. In previous studies, small juveniles of both species were found throughout spring and summer in surface waters, with large numbers occurring predominantly during May and June (Dunbar 1957; Wing 1976; Percy 1993; Koszyten et al. 1995; Dalpadado 2002). The respective authors concluded that the breeding period for both species is prolonged. A prolonged breeding period may also lead to the appearance of overlapping size groups and lack of a consistent increase in length of the cohorts (Fig. 3.6, 3.7, 3.8); thus the ‘join-up’ of one cohort to another and the time frame in which these joins occur are difficult to identify. Therefore, it can be assumed that the mean lengths of the 0+ cohort for *T. abyssorum* and *T. libellula* presented in this study may be underestimates.

We observed a growth pattern for *Themisto* consisting of two phases with a more rapid growth during juvenile and immature stages and a slower growth of maturing individuals, which were also recorded by Noyon et al. (2011) for *T. libellula* in Kongsfjorden and Rijpfjorden. The authors proposed the explanation that individuals in their second year redirect energy investments towards lipid storage in order to secure e.g. their reproductive success. Our results showed generally few juveniles of *T. libellula*, with smallest individuals collected in May/June 2001, 2007 & 2008 (Fig. 3.8). Furthermore, we observed an increase in the mean length of the 0+ cohort from July to December during 2004, 2006 & 2008 for *T. abyssorum*. Larger juveniles occurred in May and the smaller ones from July to August (Fig. 3.6) for this species. These findings support the hypothesis of an earlier brood release of *T. libellula* compared to *T. abyssorum*, which was also suggested by Koszyten et al. (1995) and Dalpadado (2002) in the subarctic regions. For *T. compressa*, the total absence of juveniles (Fig. 3.4 and 3.7) and the low occurrences compared to *T. libellula* and *T. abyssorum* (Fig. 3.4) indicate its recent introduction into the open waters of the eastern Fram Strait (Kraft et al. 2011), and our respective conclusion that this north Atlantic species does not (as of yet) reproduce in high Arctic waters. Dalpadado (2002) found only a single egg-carrying female individual of *T. compressa* in the southern Barents Sea, which further supports the hypothesis that this species does not reproduce in the Arctic; however, sampling efforts in the 50-100 m of the water column of the Fram Strait are necessary to prove this aspect. Of the three studied species, a seasonal pattern in the ratio of male to female individuals could only be observed for *T. abyssorum*, with increased proportions of male specimens from January to April in the traps (Fig. 3.3).

Age-size relationship

The cohort analysis revealed during most two-month time periods the concurrent presence of three age groups of *T. abyssorum* (Fig. 3.6), implying a life span of two years for the species in the eastern Fram Strait. The results therefore support previous estimates of a 2-year life-cycle in the Central Arctic as well as in the Barents, Greenland and Norwegian Sea (Bogorov 1940; Bowman 1960; Koszteyn et al. 1995; Vinogradov et al. 1996). The population structure of *T. compressa* also showed the presence of up to three age groups at the same time, with the 0+ cohort being absent from the samples. One respective conclusion may be that *T. compressa* has a 3-year life-cycle, with reproduction in a more southern region and occasional northward migration. Northward migration of this species could be connected to the temperature increase in Atlantic water in the Fram Strait region as observed by Schauer et al. (2008) and Beszczynska-Möller et al. (accepted). A 3-year life-cycle in Arctic and subarctic regions for *T. compressa* would be much longer than a life span of up 10 months as suggested by Sheader (1981) in the North Sea, or its Antarctic counterpart *T. gaudichaudii* with a hypothesized 1-year life span (Kane 1966; Auel and Ekau 2009). Consequently, the concurrent presence of four cohorts for the typically Arctic specialist *T. libellula* indicates a life span of at least three years for the species in eastern Fram Strait. Such a prolonged life-cycle was also suggested by Auel and Werner (2003) for the northern Farm Strait and for the fjords Kongsfjord and Hornsund on Spitsbergen (Weslawski et al. 2006). Earlier investigations, including Dunbar's (1957) work in the Canadian Arctic as well as studies by Koszyten et al. (1995) and Daldadado (2002) in European Arctic waters indicated a 2-year life-cycle of *T. libellula* (Table 3.4). Neither authors, however, observed particularly large individuals with a total body length ≥ 50 mm in their samples, which were regularly present in our study (Fig. 3.5).

The maximum life spans presented here of two years for *T. abyssorum*, three years for *T. compressa* and at least three years for *T. libellula* indicate that all three species can be regarded as amphipods with a long lifetime. Such prolonged lifespans are rare among other *Themisto* species such as the Antarctic hyperiid *T. gaudichaudii* and the more temperate sympatric species *T. pacifica* and *T. japonica* (Table 3.4). In contrast, long life spans are quite common among polar gammarids, such as the well-known Arctic sympagic species *Gammarus wilkitzkii* or the benthic scavenging amphipod *Onisimus carius*, both with life-cycles of five years or more and a maximum recorded body size of 62.3 mm and 30.0 mm, respectively (Poltermann 2000; Nygard et al. 2009). In the present study, the Gompertz growth model best reflected the mean lengths of the respective cohorts obtained by the distribution analysis (Fig. 3.9). The model indicated an asymptotic final length of 35.5 mm for *T. abyssorum*, 28.8 mm for *T. compressa* and 60.0 mm for *T. libellula* (Table 3.3). The latter two calculations fit well with the observations (we found a TBL of 24.4 mm and 56.7 mm, respectively), while the largest recorded specimen of *T. abyssorum* was smaller, with a TBL of 25.5 mm. Within the here presumed life spans, *T. abyssorum* doubles its body length, whereas *T. libellula* growths by a factor of 3.5. Furthermore, the immature and adult recorded specimens of *T. compressa* increased in body length by the factor 1.5. Thus, the calculated growth rate is quite similar for all three observed species (k-values, Table 3.3) and in comparison with the above-mentioned Arctic gammarids, the three observed pelagic *Themisto* species grow much faster. However, when compared to their Antarctic counterpart, *T. gaudichaudii*, which has been shown to reach a size of ~20 mm within a time span of eight months (Watts and Tarling 2011), the observed growth of the three Arctic congeners seems relatively slow. At this point it should be noted that a direct comparison of growth parameters should always be treated with caution, as various methodological approaches in size determination and growth determination are used among the different studies.

In the northern hemisphere, crustaceans with a wider geographic distribution are expected to have a smaller size and shorter life-cycle in the southern parts of their distribution ranges, while northern populations attain their maximal size at an older age (K- versus *r*- strategy, respectively) (Steele and Steele 1975; Sainte-Marie 1991; Koszteyn et al. 1995; Weslawski and Legezynska 2002). In accordance with results mentioned above, this phenomenon is also shown by the *Themisto* amphipods in the eastern Fram Strait. Indeed, the Fram Strait also seems to represent the northernmost and recently-expanded geographical border for the North Atlantic species *T. compressa*. It seems that due to the influence and interaction of several water masses (WSC, EGC, RAC and eddies interconnecting the former) in the HAUSGARTEN, the investigation area is a mixing pool for typical K-strategists (*T. libellula*), the sub-arctic intermediate, *T. abyssorum*, and adapting, usually typically r-strategy specimens of the south such as the North Atlantic hyperiid *T. compressa*.

In spite of the increase in abundance of the three hyperiids, the seasonal and long-term size structure of these pelagic species seems to be consistent for the observed time period in the HAUSGARTEN region (Fig. 3.3-3.8). Consistency of size structure suggests a well-established coexistence mechanism for *T. abyssorum* and *T. libellula* in the area. This mechanism is supported by a different timing in brood release (Koszyten et al. 1995; Dalpadado 2002; present study) and seasonal vertical migration (Kraft et al. 2011) as well as the exploitation of varying food sources (Auel et al. 2002; Søreide et al. 2006; Dalpadado et al. 2008). Furthermore, diet variations among the different stages have been shown; for example small juvenile individuals of *T. libellula* are considered omnivores, feeding on algal matter and zooplankton, while adults are mostly carnivorous (Wing 1976; Fortier et al. 2001; Weslawski et al. 2006; Dalpadado et al. 2008; Noyon et al. 2011). Due to these differences in feeding ecology Weslawski et al. (2006) concluded that the annual cohorts of *Themisto* may function as separate species in an ecological sense. With the addition of a new taxonomic and possibly several ecological species due to the introduction of *T. compressa*, the pelagic amphipod community could shift towards dominance of smaller-sized, less energetic species population, consequently affecting lower and higher trophic levels. However, at the present stage, the ecological role of *T. compressa* in the Fram Strait cannot be determined yet, as its contribution to the whole pelagic amphipod community is still small in Arctic and subarctic waters. A continuation of sampling efforts will add to our understanding how this North Atlantic species may be integrated into the coexistence mechanism already existing between *T. abyssorum* and *T. libellula* or if it may even replace one or both species in a continuous warming Arctic Ocean.

Table 3.4 Life history parameters of *Themisto* amphipods

Themisto	**Location**	**Size classification [TBL, mm]**				**Generations**	**Life span**	**Reference**
		Min. adult	**Max. adult**	**Immature**	**Juvenile**	**year^{-1}**		
abyssorum	Arctic	10	21(♀)	6-9.9	2-5.9	0.5	up to 2 yrs	Bogorov (1940), Bowman (1960)
	Gulf of St. Lawrence	9(♀)	15(♀)			1		Hoffer (1972)
	Barents, Greenland & Norwegian Sea	11	18	>7-10	1-7	1-2	up to 2 yrs	Koszteyn et al. (1995)
	Arctic	10	21				2 yrs	Vinogradov et al. (1996)
	Barents Sea	≥11	18	9-11	2-8		1 yr	Dalpadado (2002), Dalpadado et al. (2001, 2008)
	Eastern Fram Strait	11.8(♀)	25.5(♀)	7.1-11.5	4.2-7.0	1	2 yrs	this study
*compressa**	North Sea	3(♀)	18(♀)			≤6	up to 10 months	Sheader (1977, 1981),
	North-East Atlantic	≥8	24.3	3<8	<3			Williams and Robins (1979, 1981)
	Barents Sea		17		<9			Dalpadado (2002)
	Eastern Fram Strait	10.2(♀)	24.4(♀)	8.8-10.0			up to 3 yrs	this study
libellula	Arctic	30(♂)	60(♀)			0.5-1		Bovallius (1889)
	Canadian Arctic	31(♂), 35(♀)	47		2-19	2	up to 2 yrs	Dunbar (1946, 1957)
	Southeastern Alaska	19(♂), 21(♀)	22(♂), 30(♀)		≥1.8	1	1 yr	Wing (1976)
	Southeastern Alaska		32.4(♀)		≥2.2		at least 2 yrs	Percy (1993)
	Barents, Greenland & Norwegian Sea	>20	31	10-19	2-9		up to 3 yrs	Koszteyn et al. (1995)
	Barents Sea	≥18	45	14-17	2-14		2 yrs	Dalpadado (2002), Dalpadado et al. (2001, 2008)
	Northern Fram Strait	21(♂)	39	10-20	5-10		at least 3 yrs	Auel and Werner (2003)
	Fjords of Svalbard	>19		12-19	<12		up to 3 yrs	Dale et al. (2006)
	Fjords of Svalbard	30	45	15-30	5-15	1	4 yrs	Weslawski et al. (2006)
	Gulf of St. Lawrence		50					Marion et al. (2008)
	Eastern Fram Strait	26.4(♀)	56.7(♀)	12.1-26.0	4.0-12.0		at least 3 yrs	this study
pacifica	Arctic	3.8(♂), 4.0(♀)						Bowman (1960)
	Southeastern Alaska	4.5(♂), 5.5(♀)	8(♂), 10(♀)		≥1.0	4-5	<1yr	Wing (1976)
	Northern Pacific Ocean & Bering Sea	4.5(♀)	8.5(♀)					Vinogradov et al. (1996)
	Western North Pacific	3.8(♂), 3.5(♀)				4		Yamada et al. (2004)
gaudichaudii	Antarctic / Sub-Antarctic		33			1	1 yr	Kane (1966)
	Antarctic Polar Front Zone	≥12	33.8		<12			Bocher et al. (2001)
	Beluga current System off Namibia	7	11				1 yr	Auel and Ekau (2009)
	Antarctic / South Georgia	≥9	25		<9	2		Watts and Tarling (2011)
japonica	Arctic	8.5	17					Bovallius (1889)
	Japan Sea	6(♂), 9(♀)	12(♂), 17(♀)		≥1.3	>3	up to 1.6 yrs	Ikeda (1990), Ikeda et al. (1992)
	Japan & Okhotsk Sea	9(♀)	17(♀)					Vinogradov et al. (1996)
	Western North Pacific	7.1(♂), 9.6(♀)					up to 1 yr	Yamada et al. (2004)

TBL = Total body length. * before the revision by Schneppenheim and Weigmann-Haass (1986) the species was named (*Para*)*Themisto gaudichaudii*.

Conclusion

Our study on the pelagic amphipod community at the long-term observatory HAUSGARTEN during the years 2000-2009 displayed a distinct trend towards increasing amphipod abundances and a continuous long-term size structure pattern among the three observed species. The multi-year length-frequency analysis in sediment traps indicated a life span of two years for *T. abyssorum*, three years for *T. compressa* and a life-cycle of at least three years for *T. libellula* in the eastern Fram Strait. Remarkably, regular occurrences of large specimens (up to 56.7 mm in total body length) of *T. libellula* were recorded in the sediment traps, which are usually failed to be sampled with traditional plankton nets till today in the Arctic region.

Acknowledgments

We thank the Arctic-lab team including C. Lorenzen, S. Murawski, N. Knüppel, S. Simon and D. Freese for the tedious work of picking out swimmers, and the AWI-zooplankton group of Polar Biological Oceanography for their helpful comments and support. We greatly acknowledge the crew of R/V *Polarstern* during the work at sea. Furthermore we thank three anonymous reviewers for their helpful comments that improved the initial manuscript.

References

Angel MV, Pugh PR (2000) Quantification of diel vertical migration by micronektonic taxa in the northeast Atlantic. Hydrobiologia 440(1-3):161-179.

Auel H, Ekau W (2009) Distribution and respiration of the high-latitude pelagic amphipod *Themisto gaudichaudii* in the Benguela Current in relation to upwelling. Prog Oceanogr 83(1-4):237-241.

Auel H, Harjes M, Da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25:374-383.

Auel H, Werner I (2003) Feeding, respiration and life history of the hyperiid amphipod *Themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. J Exp Mar Biol Ecol 296(2):183-197.

Bauerfeind E, von Bodungen B (2006) Underestimation of biogenic silicon flux due to dissolution in sediment trap samples. Mar Geol 226(3-4):297-306.

Bauerfeind E, Nöthig E-M, Beszczynska A, Fahl K, Kaleschke L, Kreker K, Klages M, Soltwedel T, Lorenzen C, Wegner J (2009) Particle sedimentation patterns in the eastern Fram Strait during 2000-2005: Results from the Arctic long-term observatory HAUSGARTEN. Deep-Sea Res I 56:1471-1487.

Beszczynska-Möller A, Fahrbach E, Schauer U, Hansen E (accepted) Variability of Atlantic water temperature and transport in the entrance to the Arctic Ocean in 1997-2010. ICES J Mar Sci.

Berge J, Cottier F, Last KS, Varpe Ø, Leu E, Soreide J, Eiane K, Falk-Petersen S, Willis K, Nygard H, Vogedes D, Griffiths C, Johnson G, Lorentzen D, Brierley AS (2009a) Diel vertical migration of Arctic zooplankton during the polar night. Biol Lett 5:69-72.

Berge J, Renaud PE, Eiane K, Gulliksen B, Cottier FR, Varpe Ø, Brattegard T (2009b) Changes in the decapod fauna of an Arctic fjord during the last 100 years. Polar Biol 32:953-961.

Bloesch J, Burns NM (1980) A critical review of sedimentation trap technique. Schweiz Z Hydrol 42(1):15-55.

Bocher P, Cherel Y, Labat JP, Mayzaud P, Razouls S, Jouventin P (2001) Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. Mar Ecol Prog Ser 223:261-276.

Bogorov VG (1940) Longevity and ecological characteristics of *Themisto abyssorum* in the Barents Sea. C R Acad Sci URSS XXVII:68-70.

Bovallius C (1889) Contributions to a Monograph of the Amphipoda Hyperiidea, Part I: 2. The Families Cyllopodidae, Paraphronimidae, Thaumatopsidae, Mimonectidae, Hyperiidae, Phronimidae and Anchylomeridae. Kongliga Svenska Vetenskapsakademiens Handlingar 22(7):1-434.

Bowman TE (1960) The pelagic amphipod genus *Parathemisto* (Hyperiidea: Hyperiidae) in the North Pacific and adjacent Arctic Ocean. Proc US Acad Sci 112(3439):343-392.

Brandt A (1997) Suprabenthic Peracarida (Crustacea, Malacostraca) sampled at 75 degrees N off East Greenland. Polar Biol 17(5):462-464.

Brey T (2001) Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2. WWW-Page, http://www.thomas-brey.de/science/virtualhandbook.

Buesseler KO, Antia AN, Chen M, Fowler SW, Gardner WD, Gustafsson O, Harada K, Michaels AF, Rutgers van der Loeff M, Sarin M, Steinberg DK, Trull T (2007) An assessment of the use of sediment traps for estimating upper ocean particle fluxes. J Mar Res 65:345-416.

Dale K, Falk-Petersen S, Hop H, Fevolden SE (2006) Population dynamics and body composition of the Arctic hyperiid amphipod *Themisto libellula* in Svalbard fjords. Polar Biol 29(12):1063-1070.

Dalpadado P (2002) Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. Polar Biol 25:656-666.

Dalpadado P, Ellertsen B, Melle W, Dommasnes A (2000) Food and feeding conditions of Norwegian spring spawning herring (*Clupea harengus*) through its feeding migrations. ICES J Mar Sci 58:876-895.

Dalpadado P, Bogstad B (2004) Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. Polar Biol 27(3):140-154.

Dalpadado P, Ellertsen B, Melle W, Skjoldal HR (1998) Summer distribution patterns and biomass estimates of macrozooplankton and micronekton in the Nordic Seas. Sarsia 83(2):103-116.

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58:876-895.

Dalpadado P, Yamaguchi A, Ellertsen B, Johannessen S (2008) Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55:2266-2274.

Dunbar MJ (1946) On *Themisto libellula* in Baffin Island coastal waters. J Fish Res Board Can 6:419-434.

Dunbar MJ (1957) The determinates of production in the northern seas: a study of the biology of *Themisto libellula* (Mandt). Can J Zool 35:797-819.

Dunbar MJ (1964) Serial Atlas of the marine environment. Folio 6. Euphausiids and Pelagic Amphipods. American Geographical Society, New York.

Fortier M, Fortier L, Hattori H, Saito H, Legendre L (2001) Visual predators and the diel vertical migration of copepods under arctic sea ice during the midnight sun. J Plankton Res 3:1263-1278.

Furevik T, Mauritzen C, Ingvaldsen R (2007) The flow of Atlantic Water to the Nordic Seas and Arctic Ocean. In: Ørbæk JB, Kallenborn R, Tombre I, Nøst Hegseth, E, Falk-Petersen S, Hoel AH (eds) Arctic–Alpine Ecosystems and People in a Changing Environment, Springer, Berlin, pp 123-146.

Grainger EH (1989) Vertical distribution of zooplankton in the central Arctic Ocean. In: Rey L, Alexander V (eds) Proceedings of the Sixth Conference of the Comité Arctique International 13-15 May 1985, EJ Brill, Leiden, The Netherlands, pp 48-60.

Hansen B, Østerhus S, Hátún H, Kristiansen R, Larsen KMH (2003) The Iceland-Faroe inflow of Atlantic water to the Nordic Seas. Prog Oceanogr 59:443-474.

Hargrave BT (1985) Feeding rates of abyssal scavenging amphipods (*Eurythenes gryllus*) determined in situ by time lapse photography. Deep-Sea Res 32:443-450.

Harvey M, Galbraith PS, Descroix A (2009) Vertical distribution and diel migration of macrozooplankton in the St. Lawrence marine system (Canada) in relation with the cold intermediate layer thermal properties. Progr Oceanogr 80:1-21.

Hoffer SA (1972) Some aspects of the life cycle of *Parathemisto abyssorum* (Amphipoda: Hyperiidea) in the Gulf of St. Lawrence. Can J Zool 50:1175-1178.

Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Søreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Prog Oceanogr 71:182-231.

Ikeda T (1990) A growth model for a hyperiid amphipod *Themisto japonica* (Bovallius) in the Japan Sea, based on its intermoult period and moult increment. Journal of the Oceanographical Society of Japan 46:261-272.

Ikeda T, Hirakawa K, Imamura A (1992) Abundance, population structure and life cycle of a hyperiid amphipod *Themisto japonica* (BOVALLIUS) in Toyama Bay, Southern Japan Sea. Bulletin of Plankton Society of Japan 39(1):1-16.

Kane JE (1963) Observations on the moulting and feeding of a hyperiid amphipod. Crustaceana 6:129-132.

Kane JE (1966) The distribution of *Parathemisto gaudichaudii* (Guer.), with observations on its life-history in the 0° to 20°E sector of the Southern Ocean. Discovery Rep 34:163-198.

Karl DM, Knauer GA (1989) Swimmers: a recapitulation of the problem and a potential solution. Oceanogr 2:32-35.

Knauer GA, Martin JH, Bruland KW (1979) Fluxes of particulate carbon, nitrogen and phosphorus in the upper water column of the northeast Pacific. Deep-Sea Res 26:97-108.

Koszteyn J, Timofeev S, Weslawski JM (1995) Size structure of *Themisto abyssorum* (Boeck) and *Themisto libellula* (Mandt) populations in European Arctic Seas. Polar Biol 15:85-92.

Kraft A, Bauerfeind E, Nöthig E-M (2011) Amphipod abundance in sediment trap samples at the long-term observatory HAUSGARTEN (Fram Strait, ~79°N/4°E) - Variability in species community patterns. Mar Biodiv 41:353-364.

Kremling K, Lentz U, Zeitzschel B, Schultz-Bull DE, Duinker JC (1996) New type of time-series sediment trap for the reliable collection of inorganic and organic trace chemical substances. Rev Sci Instrum 67:4360-4363.

Lampert DG (1960) The food of the redfish *Sebastes marinus* (L.) in the Newfoundland area. J Fish Res Board Can 23:235-243.

Lampitt RS, Wishner KF, Turley CM, Angel MV (1993) Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. Mar Biol 116(4):689-702.

LeBrasseur RJ (1966) Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J Fish Res Board Can 23:85-100.

Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin, 1773) in ice covered waters. Polar Biol 9:187-191.

Lydersen C, Gjertz I, Weslawski JM (1989) Stomach contents of autumn-feeding marine vertebrates from Honsund, Svalbard. Polar Res 25:107-114.

Makabe R, Hattori H, Sampei M, Ota Y, Fukuchi M, Fortier L, Sasaki H (2010) Regional and seasonal variability of zooplankton collected using sediment traps in the southeastern Beaufort Sea, Canadian Arctic. Polar Biol 33:257-270.

Marion A, Harvey M, Chabot D, Brêthes J-C (2008) Feeding ecology and predation impact of the recently established amphipod, *Themisto libellula*, in the St. Lawrence marine system, Canada. Mar Ecol Prog Ser 373:53-70.

Michaels AF, Silver MW, Gowing MM, Knauer GA (1990) Cryptic zooplankton “swimmers” in upper ocean sediment traps. Deep-Sea Res 37:1285-1296.

Noyon M, Narcy F, Gasparini S, Mayzaud P (2011) Growth and lipid class composition of the Arctic pelagic amphipod *Themisto libellula*. Mar Biol 158:883-892.

Nygard H, Vihtakari M, Berge J (2009) Life history of *Onisimus caricus* (Amphipoda: Lysianassoidea) in a high Arctic fjord. Aquat Biol 5(1):63-74.

Percy JA (1993) Reproduction and growth of the Arctic hyperiid amphipod *Themisto libellula* Mandt. Polar Biol 13:131-139.

Perry RI, Batchelder HP, Mackas DL, Chiba S, Durbin E, Greve W, Verheye HM (2004) Identifying global syncronies in marine zooplankton populations: issues and opportunities. ICES J Mar Sci 61:445-456.

Peterson ML, Hermes PJ, Thoreson DS, Hedges IH (1993) Field evaluation of a valved sediment trap. Limnol Oceanogr 38(8):1741-1761.

Piechura J (2004) The circulation of the Nordic Seas. In: Skreslet S (ed) Jan Mayen Island in Scientific Focus, Kluwer Academic Publishers, Netherlands, pp 91-99.

Piechura J, Walczowski W (2009) Warming of the West Spitsbergen Current and sea ice north of Svalbard. Oceanologia 51(2):147-164.

Poltermann M (2000) Growth, production and productivity of the Arctic sympagic amphipod *Gammarus wilkitzkii*. Mar Ecol Prog Ser 193:109-116.

Quadfasel D, Gascard J-C, Koltermann K-P (1987) Large-scale oceanography in Fram Strait during the 1984 marginal ice zone experiment. J Geophys Res 92: 6719-6728.

Richardson AJ (2008) In hot water: zooplankton and climate change. ICES J Mar Sci 65:279-295.

Ricker WE (1975) Computation and interpretation of biological statistics for fish populations. Bull Fish Res Board Can No 191.

Sainte-Marie B (1991) A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. Hydrobiologia 223:189-227.

Schauer U, Beszczynska-Möller A, Walczowski W, Fahrbach E, Piechura J, Hansen E (2008) Variation of Measured Heat Flow Through the Fram Strait Between 1997 and 2006. In: Dickson RR, Meincke J, Rhines P (eds) Arctic–Subarctic Ocean Fluxes, Springer, Netherlands, pp 65-85.

Schauer U, Fahrbach E, Osterhus S, Rohardt G (2004) Arctic warming through the Fram Strait: Oceanic heat transport from 3 years of measurements. J Geophys Res Oceans 109 (C6).

Schiermeier Q (2007) The new face of the Arctic. Nature 446:133-135.

Schneppenheim R, Weigmann-Haass R (1986) Morphological and electrophoretic studies of the genus *Themisto* (Amphipoda: Hyperiidea) from the South and North Atlantic. Polar Biol 6:215-225.

Seiler D, Brandt A (1997) Seasonal occurrence of planktic Crustacea in sediment trap samples at three depth horizons in the Greenland Sea. Polar Biol 17:337-349.

Sheader M (1977) Breeding and marsupial development in laboratory maintained *Parathemisto gaudichaudii* (Amphipoda). J Mar Biol Assoc UK 57(4):943-954.

Sheader M (1981) Development and growth in laboratory maintained and field populations of *Parathemisto gaudichaudii* (Hyperiidea, Amphipoda). J Mar Biol Assoc UK 61:769-787.

Skjoldal HR, Dalpadado P, Dommasnes A (2004) Food webs and trophic interactions. In: Skjoldal HR (ed) The Norwegian Sea Ecosystem, Tapir Academic Press, Trondheim, Norway, pp 447-506.

Smetaceck V, Nicol S (2005) Polar ocean ecosystems in a changing world. Nature 437:362-368.

Søreide JE, Hop H, Carroll ML, Falk-Petersen S, Hegseth EN (2006) Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Prog Oceanogr 71(1):59-87.

Sparre P (1988) Computer programs for fish stock assessment (LFSA) package of basic programs for IBM computers. FAO Fisheries Technical Paper, FAO, Rome.

Steele DH, Steele VJ (1975) Egg size and duration of embryonic development in Crustacea. Int Rev Gesamten Hydrobiol 60:711-715.

Steinberg DK, Pilskaln CH, Silver MW (1998) Contribution of zooplankton associated with detritus to sediment trap 'swimmer' carbon in Monterey Bay, California, USA. Mar Ecol Prog Ser 164:157-166.

Turner J, Overland JE, Walsh JE (2007) An Arctic and Antarctic perspective on recent climate change. Int J Climatol 27:277-293.

Vinogradov ME (1999) Deep-sea near-bottom swarms of pelagic amphipods *Themisto*: observations from submersibles. Sarsia 84:465-467.

Vinogradov ME, Volkov AF, Semenova TN (1996) Hyperiid amphipods (Amphipoda, Hyperidea) of the world oceans, Science Publishers Inc., Lebanon, USA.

Wakeham SG, Hedges JI, Lee C, Pease TK (1993) Effects of poisons and preservatives on the composition of organic matter in a sediment trap experiment. J Mar Res 51:669-696.

Wallace MI, Cottier FR, Berge J, Tarling GA, Griffiths C, Brierley AS (2010) Comparison of zooplankton vertical migration in an ice-free and seasonally ice-covered Arctic fjord: An insight into the influence of sea ice cover on zooplankton behavior. Limnol Oceanogr 55:831-845.

Watts J, Tarling GA (2011) Population dynamics and production of *Themisto gaudichaudii* (Amphipoda, Hyperiidae) at South Georgia, Antarctica. Deep-Sea Res II: doi:10.1016/j.dsr2.2011.05.001.

Weigmann-Haass R (1997) Verbreitung von Makrozooplankton in der Grönlandsee im Spätherbst 1988 (Crustacea: Ostracoda, Hyperiidea [Amphipoda], Euphausiacea). Helgolander Meeresun 51:69-82.

Weitkamp LA, Sturdevant MV (2008) Food habits and marine survival of juvenile Chinook and coho salmon from marine waters of Southeast Alaska. Fish Oceanogr 17(5):380-395.

Wencki K (2000) Interannual variability in the occurrence of *Themisto* (Amphipoda) in the north Norwegian Sea. Pol Polar Res 21:143-152.

Weslawski JM, Kwasniewski S, Stempniewicz L, Błachowiak-Samolyk K (2006) Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords. Pol Polar Res 27(3):259-278.

Weslawski JM, Legezynska J (2002) Life cycles of some arctic amphipods. Pol Polar Res 23(3-4):253-264.

Williams R, Robins D (1979) Calorific, ash, carbon and nitrogen content in relation to length and dry weight of *Parathemisto gaudichaudii* (Amphipoda: Hyperiidea) in the North East Atlantic Ocean. Mar Biol 52(3):247-252.

Williams R, Robins D (1981) Seasonal variability in abundance and vertical distribution of *Parathemisto gaudichaudii* (Amphipoda: Hyperiidea) in the North East Atlantic Ocean. Mar Ecol Prog Ser 4:289-298.

Willis K, Cottier F, Kwasniewski S, Wold A, Falk-Petersen S (2006) The influence of advection on zooplankton community composition in an Arctic fjord (Kongsfjorden, Svalbard). J Mar Sys 61(1-2):39-54.

Willis KJ, Cottier FR, Kwaśniewski S (2008) Impact of warm water advection on the winter zooplankton community in an Arctic fjord. Polar Biol 31:475-481.

Wing BL (1976) Ecology of *Parathemisto libellula* and *P. pacifica* (Amphipoda: Hyperiidea) in Alaskan waters. Northwest Fisheries Center Processed Report, Seattle.

Yamada Y, Ikeda T, Tsuda A (2004) Comparative life-history study on sympatric hyperiid amphipods (*Themisto pacifica* and *T. japonica*) in the Oyashio region, western North Pacific. Mar Biol 145(3):515-527.

Yamada Y, Ikeda T (2006) Production, metabolism and trophic importance of four pelagic amphipods in the Oyashio region, western subarctic Pacific. Mar Ecol Prog Ser 308:155-163.

Zeitzschel B, Diekmann P, Uhlmann L (1978) A new multisample sediment trap. Mar Biol 45:285-288.

Supplement

This supplementary material contains three additional tables.

Table S1 Length-frequency analysis of *Themisto abyssorum* during selected time periods from 2000 to 2009 indicating the count (N) and stage of collected individuals, separated cohorts and mean total body length

Table S2 Length-frequency analysis of *Themisto compressa* during selected time periods from 2004 to 2009 indicating the count (N) and stage of collected individuals, separated cohorts and mean total body length

Table S3 Length-frequency analysis of *Themisto libellula* during selected time periods from 2000 to 2009 indicating the count (N) and stage of collected individuals, separated cohorts and mean total body length

Table S1 Length-frequency analysis of *Themisto abyssorum* during selected time periods from 2000 to 2009 indicating the count (N) and stage of collected individuals, separated cohorts and mean total body length

Time period	N ♀	N ♂	N Juv.	N Total	Cohort no.	Count / Cohort	Mean length [mm]	SD	SI
Jul./Aug. 2000	n.d.	n.d.	n.d.	n.d.	-	-	-	-	-
Sep./Oct. 2000	12	1	5	18	0+	12	8.6	1.7	n.a.
					1+	6	13.8	1.5	3.2
Nov./Dec. 2000	32	1	3	36	0+	12	8.9	0.6	n.a.
					1+	19	12.9	2.2	2.8
					2+	5	19.8	0.7	4.6
Jan./Feb. 2001	11	3	-	14*	1+	8	12.6	1.8	*
					2+	6	17.0	0.6	*
Mar./Apr. 2001	11	2	-	13*	0+	4	10.2	0.9	*
					1+	3	13.4	0.6	*
					2+	6	17.1	1.4	*
May/Jun. 2001	34	3	-	37	0+	6	11.5	1.1	n.a.
					1+	30	17.8	2.2	3.8
					2+	1	24.6	-	4.9
Jul./Aug. 2004	180	21	3	204	0+	6	8.1	1.6	n.a.
					1+	86	13.8	1.8	3.4
					2+	112	17.5	1.5	2.2
Sep./Oct. 2004	74	5	12	91	0+	36	8.8	0.9	n.a.
					1+	49	12.3	1.8	2.6
					2+	6	19.1	1.2	4.6
Nov./Dec. 2004	50	5	11	66	0+	31	9.5	1.0	n.a.
					1+	34	14.4	2.4	2.9
					2+	1	22.0	-	5.2
Jan./Feb. 2005	24	14	-	38	0+	4	9.7	0.6	n.a.
					1+	34	15.4	1.9	4.6
Mar./Apr. 2005	119	26	-	145	1+	97	14.4	1.8	n.a.
					2+	48	18.4	2.0	2.1
May/Jun. 2005	235	30	-	265	1+	100	15.3	1.5	n.a.
					2+	165	18.9	2.3	2.1
Jul./Aug. 2006	n.d.	n.d.	n.d.	n.d.	-	-	-	-	-
Sep./Oct. 2006	54	5	6	65	0+	8	7.0	1.5	n.a.
					1+	57	12.9	2.0	4.4
Nov./Dec. 2006	9	2	2	13*	0+	9	9.3	1.2	*
					1+	3	15.0	2.0	*
					2+	1	18.8	-	*

Table S1 continued

Time period	N ♀	N ♂	N Juv.	N Total	Cohort no.	Count / Cohort	Mean length [mm]	SD	SI
Jan./Feb. 2007	42	9	3	54	0+	8	9.1	1.0	n.a.
					1+	41	14.7	2.1	3.6
					2+	5	21.0	0.9	4.1
Mar./Apr. 2007	22	15	-	37	0+	4	10.2	0.8	n.a.
					1+	31	17.0	1.6	5.7
					2+	2	23.0	0.5	5.5
May/Jun. 2007	288	21	1	310	0+	10	10.7	1.4	n.a.
					1+	235	15.9	2.0	3.0
					2+	65	20.1	1.6	2.3
Jul./Aug. 2007	111	11	8	130	0+	25	9.6	1.7	n.a.
					1+	105	15.5	2.3	3.0
Sep./Oct. 2007	102	9	39	150	0+	73	9.0	1.3	n.a.
					1+	77	15.6	1.7	3.3
Nov./Dec. 2007	21	3	42	66	0+	57	8.5	1.1	n.a.
					1+	3	11.8	2.0	2.2
					2+	6	17.7	0.9	4.1
Jan./Feb. 2008	16	3	1	18	0+	6	9.9	1.8	n.a.
					1+	12	16.5	2.7	2.9
Mar./Apr. 2008	90	23	0	113	0+	6	9.3	0.6	n.a.
					1+	107	13.4	2.7	2.5
May/Jun. 2008	509	30	1	540	0+	6	9.3	2.0	n.a.
					1+	485	16.4	2.2	3.4
					2+	49	20.8	1.2	2.6
Jul./Aug. 2008	620	85	3	708	0+	5	7.7	2.4	n.a.
					1+	697	16.9	2.5	3.8
					2+	6	24.7	0.6	5.2
Sep./Oct. 2008	189	27	1	217	0+	8	9.2	0.8	n.a.
					1+	122	13.5	1.8	3.2
					2+	87	19.9	1.8	2.2
Nov./Dec. 2008	28	2	5	35	0+	23	9.7	1.2	n.a.
					1+	11	14.7	1.8	3.4
					2+	1	23.4	-	7.5
Jan./Feb. 2009	12	5	-	17	1+	13	16.0	1.6	n.a.
					2+	4	19.0	1.0	2.3
Mar./Apr. 2009	4	-	-	4*	1+	4	15.9	1.4	*
May/Jun. 2009	582	46	2	630	1+	513	15.7	2.4	n.a.
					2+	117	20.3	1.4	2.1

Length frequency analysis with standard deviation (SD) and separation index (SI). Juv. = Juveniles; - = no individuals present; n.d. = no data; n.a. = not applicable; * Too few individuals - not included in statistical analysis

Table S2 Length-frequency analysis of *Themisto compressa* during selected time periods from 2004 to 2009 indicating the count (N) and stage of collected individuals, separated cohorts and mean total body length

Time period	N ♀	N ♂	N Juv.	N Total	Cohort no.	Count / Cohort	Mean length [mm]	SD	SI
Jul./Aug. 2004	25	5	-	30	1+	19	13.4	2.2	n.a.
					2+	6	19.8	1.2	3.8
					3+	5	23.5	0.6	4.1
Sep./Oct. 2004	18	2	-	20	1+	19	12.7	1.5	n.a.
					2+	1	18.3	-	5.4
Nov./Dec. 2004	3	2	-	5*	2+	5	14.8	2.2	*
Jan./Feb. 2005	11	5	-	16	1+	14	13.3	1.0	n.a.
					2+	2	17.8	0.6	5.7
Mar./Apr. 2005	17	4	-	21	2+	20	14.8	2.0	n.a.
					3+	1	21.7	-	5.4
May/Jun. 2005	3	10	-	13*	2+	11	17.7	1.3	*
					3+	2	22.2	0.6	*
Jul./Aug. 2006	n.d.	n.d.	n.d.	n.d.	-	-	-	-	-
Sep./Oct. 2006	39	2	-	41	1+	29	12.1	1.2	n.a.
					2+	12	15.0	1.1	2.5
Nov./Dec. 2006	-	-	-	-	-	-	-	-	-
Jan./Feb. 2007	-	-	-	-	-	-	-	-	-
Mar./Apr. 2007	2	1	-	3*	2+	3	15.5	2.1	*
May/Jun. 2007	1	2	-	3*	1+	1	11.9	-	*
					2+	1	17.7	-	*
					3+	1	21.5	-	*
Jul./Aug. 2007	6	2	-	8*	2+	6	15.1	1.8	*
					3+	2	22.8	0.5	*
Sep./Oct. 2007	6	0	-	6*	2+	6	15.0	1.5	*
Nov./Dec. 2007	-	-	-	-	-	-	-	-	-
Jan./Feb. 2008	12	1	-	13*	2+	13	15.7	2.1	*
Mar./Apr. 2008	5	0	-	5*	2+	5	15.2	2.2	*
May/Jun. 2008	4	3	-	7*	2+	5	16.3	0.8	*
					3+	2	21.7	1.1	*
Jul./Aug. 2008	25	16	-	41	1+	7	12.2	0.9	n.a.
					2+	32	16.3	1.6	3.3
					3+	2	21.2	0.6	4.5
Sep./Oct. 2008	6	4	-	10*	2+	10	16.8	2.2	*
Nov./Dec. 2008	9	-	-	9*	2+	9	15.8	1.8	*
Jan./Feb. 2009	6	2	-	8*	2+	8	15.7	2.0	*
Mar./Apr. 2009	-	-	-	-	-	-	-	-	-
May/Jun. 2009	4	6	-	10*	2+	10	18.4	1.4	*

Length frequency analysis with standard deviation (SD) and separation index (SI). Juv. = Juveniles; - = no individuals present; n.d. = no data; n.a. = not applicable; * Too few individuals - not included in statistical analysis

Table S3 Length-frequency analysis of *Themisto libellula* during selected time periods from 2000 to 2009 indicating the count (N) and stage of collected individuals, separated cohorts and mean total body length

Time period	N ♀	N ♂	N Juv.	N Total	Cohort no.	Count / Cohort	Mean length [mm]	SD	SI
Jul./Aug. 2000	n.d.	n.d.	n.d.	n.d.	-	-	-	-	-
Sep./Oct. 2000	21	9	-	30	1+	1	16.7	-	n.a.
					2+	29	31.3	4.7	5.0
Nov./Dec. 2000	17	6	-	23	1+	13	25.6	4.1	n.a.
					2+	4	35.5	1.2	3.8
					3+	6	44.8	4.1	3.5
Jan./Feb. 2001	6	2	-	8*	1+	4	20.8	4.5	*
					2+	2	34.6	2.3	*
					3+	2	41.1	1.1	*
Mar./Apr. 2001	1	2	-	3*	2+	3	34.8	4.4	*
May/Jun. 2001	4	1	5	10*	0+	6	10.0	1.3	*
					3+	4	46.1	6.5	*
Jul./Aug. 2004	69	9	-	78	0+	1	14.4	-	n.a.
					1+	76	25.2	3.9	5.4
					3+	1	43.3	-	5.0
Sep./Oct. 2004	118	33	1	152	0+	15	15.9	2.9	n.a.
					2+	136	30.3	4.6	3.8
					3+	1	50.0	-	6.9
Nov./Dec. 2004	10	-	-	10*	1+	9	17.9	2.4	*
					2+	2	36.7	2.2	*
Jan./Feb. 2005	1	1	-	2*	1+	2	21.4	0.5	*
Mar./Apr. 2005	-	-	-	-	-	-	-	-	-
May/Jun. 2005	3	-	-	3*	1+	2	22.1	3.0	*
					3+	1	45.6	-	*
Jul./Aug. 2006	n.d.	n.d.	n.d.	n.d.	-	-	-	-	-
Sep./Oct. 2006	80	16	-	96	0+	4	13.7	1.2	n.a.
					1+	16	19.9	2.1	3.7
					2+	72	27.5	4.3	2.4
					3+	4	39.8	1.1	4.5
Nov./Dec. 2006	18	2	-	20	0+	5	14.6	2.2	n.a.
					1+	7	23.2	3.3	3.1
					2+	8	33.6	1.6	4.3
Jan./Feb. 2007	5	-	-	5*	0+	1	14.4	-	*
					1+	1	22.6	-	*
					2+	1	36.2	-	*
					3+	2	44.9	2.6	*
Mar./Apr. 2007	2	-	-	2*	1+	1	16.9	-	*
					3+	1	39.1	-	*

Table S3 continued

Time period	N ♀	N ♂	N Juv.	N Total	Cohort no.	Count / Cohort	Mean length [mm]	SD	SI
May/Jun. 2007	1	6	2	9*	0+	2	4.4	1.1	*
					1+	2	24.4	1.1	*
					2+	3	38.2	1.1	*
					3+	2	50.0	1.1	*
Jul./Aug. 2007	192	6	2	200	0+	5	11.7	1.7	n.a.
					1+	194	26.4	3.6	5.6
					3+	1	47.8	-	9.0
Sep./Oct. 2007	98	31	-	129	1+	5	19.9	1.2	n.a.
					2+	124	31.5	5.1	3.7
Nov./Dec. 2007	39	9	-	48	1+	23	22.4	4.4	n.a.
					2+	23	31.9	3.8	2.3
					3+	2	43.3	1.1	4.7
Jan./Feb. 2008	13	3	-	16	1+	7	23.8	3.4	n.a.
					2+	3	34.5	1.8	4.0
					3+	6	44.1	1.7	5.5
Mar./Apr. 2008	5	1	-	6*	1+	2	20.0	1.1	*
					2+	1	30.0	1.1	*
					3+	3	40.4	1.1	*
May/Jun. 2008	48	3	4	55	0+	4	9.4	1.1	n.a.
					1+	47	20.1	3.0	5.2
					3+	4	43.9	4.0	6.8
Jul./Aug. 2008	394	65	-	459	0+	4	13.4	1.2	n.a.
					1+	421	23.7	2.9	5.0
					2+	34	30.6	2.7	2.4
Sep./Oct. 2008	94	44	-	138	0+	1	12.2	-	n.a.
					1+	25	23.0	3.4	4.8
					2+	112	35.7	5.1	3.0
Nov./Dec. 2008	37	15	-	52	1+	24	24.6	4.9	n.a.
					2+	26	33.7	2.0	2.6
					3+	12	42.9	2.9	3.7
Jan./Feb. 2009	8	2	-	10*	1+	2	24.4	1.1	*
					3+	8	42.5	3.1	*
Mar./Apr. 2009	-	-	-	-	-	-	-	-	-
May/Jun. 2009	4	-	-	4*	3+	4	47.3	1.6	*

Length frequency analysis with standard deviation (SD) and separation index (SI). Juv. = Juveniles; - = no individuals present; n.d. = no data; n.a. = not applicable; * Too few individuals - not included in statistical analysis

PUBLICATION II

Feeding in Arctic darkness: mid-winter diet of the pelagic amphipods *Themisto abyssorum* and *T. libellula*

Short communication

Angelina Kraft[a]*, Jørgen Berge[b,d], Øystein Varpe[c,e], Stig Falk-Petersen[c,d]

[a]Alfred Wegener Institute for Polar and Marine Research
Am Handelshafen 12,
27570 Bremerhaven, Germany
* Contact information:
E-mail: Angelina.Kraft@awi.de
Phone: + 49-471-48311085
Fax: + 49-471-48311149

[b]University Centre in Svalbard
P.O. Box 156
9171 Longyearbyen, Norway

[c]Norwegian Polar Institute
Fram Centre
9296 Tromsø, Norway

[d]Department of Arctic and Marine Biology
Faculty of Biosciences, Fisheries and Economics
University of Tromsø
9037 Tromsø, Norway

[e]Akvaplan-niva
Fram Centre
9296 Tromsø, Norway

Published in Marine Biology 160:241-248 (2013),

doi:10.1007/s00227-012-2065-8

Abstract

The pelagic amphipods *Themisto abyssorum* and *Themisto libellula* represent important links between the herbivore zooplankton community and higher trophic levels of the Arctic marine food webs. Large double structured eyes of both of these hyperiid species are assumed to be used for visual prey detection. However, no information is available on the feeding strategies of these visually searching predators for the period of the polar night, a time of year with no or very low levels of daylight. Here we report on the stomach and gut content of both *Themisto* species collected during a January expedition around Svalbard (78° to 81° N). Results indicate that *T. abyssorum* and *T. libellula* feed actively during the Arctic winter. The major food source of both amphipods consisted of calanoid copepods, most frequently *Calanus finmarchicus*.

Keywords: Amphipoda • Hyperiidea • *Themisto abyssorum* • *Themisto libellula* • Food sources • Arctic winter • visual feeding • predator prey interactions

Introduction

Two species of the hyperiid genus *Themisto*, *T. libellula*, a typical Arctic species, and its subarctic-boreal congener *T. abyssorum* occur in the open waters of the northern polar regions (Dunbar 1957; Koszteyn et al. 1995; Dalpadado et al. 2001; Dalpadado 2002). Both are epipelagic predators and considered to be visual feeders. In their adult life stage both feed on smaller mesozooplankton (e.g., Dalpadado et al. 2008) and act themselves as prey for marine vertebrates, e.g., polar cod, little auk and seals (Wing 1976; Falk-Petersen et al. 1987, 2004, 2009; Scott et al. 1999; Auel et al. 2002; Marion et al. 2008; Renaud et al. 2012). Thus both represent links between herbivore zooplankton and higher trophic levels in the Arctic marine food web.

Previous studies of their feeding ecology have focused on the larger one of the two, *T. libellula* (Auel et al. 2002; Dalpadado et al. 2008; Marion et al. 2008; Noyon et al. 2011, 2012). Findings included an increased storage of lipids of *T. libellula* in late summer and a diet dominated by copepodid stages III-IV of *Calanus* spp. (Scott et al. 1999; Dale et al. 2006). *T. abyssorum* on the other hand is known to have a more diverse diet including omnivorous prey such as appendicularians (Dalpadado et al. 2008).

Most of these investigations are based on spring or summer data. To our knowledge there is no published information on the food sources and feeding strategies of these predators during the Arctic winter. This period of the year, defined here as the time period when the Sun is more than 12° below the horizon, is perceived by humans as being continuously dark. Difficulties of obtaining winter samples in the Arctic Ocean are the likely reason for this scarce information (Dalpadado et al. 2008; Berge et al. 2009). Thus a good seasonal coverage is essential for a full understanding of zooplankton annual routines (Varpe 2012), including their feeding activity and potential role as predators, for instance on overwintering copepods.

The aim of this study was to identify whether the pelagic amphipods *T. abyssorum* and *T. libellula* feed during the Arctic polar night and if they do, what their dominant prey is.

Materials and methods

Investigation areas

T. abyssorum and *T. libellula* were collected during the ARCTOS Marine ecological research cruise with R/V *Helmer Hanssen* at sampling sites in Rijpfjorden (80°18’ N, 22°16’ E), Sofiadjupet (81°44’ N, 14°17’ E) and Isfjorden (78°16’ N, 15°33’ E), Svalbard, from 12 to 18 January 2012. The area around the archipelago of Svalbard is characterized as a transition zone between Atlantic and Arctic waters, with the West Spitsbergen Current as the main pathway of Atlantic water into the Arctic Ocean, running at its western coast. This is where the sampling site of Isfjorden is located, which is strongly influenced by the inflowing Atlantic water masses (Nilsen et al. 2008). North-west of Svalbard an eastward turning branch of the West Spitsbergen Current flows along the continental slope (Rudels et al. 1999) and keeps this area around the Sofiadjupet, the “Whalers Bay”, mostly ice free during winter time. Rijpfjorden is a broad shallow fjord located along the northern coast of Nordaustlandet and dominated by colder Arctic water.

Sampling and processing

Profiles of temperature, salinity and density at each sampling site were measured vertically using a Sea-Bird Electronics SBE 9 CTD sonde throughout the total water column. Water masses have been classified according to Baczewska et al. (2012) and references therein (Table 4.1). Daily data on down-welling irradiance (PAR, μmol m^{-2} s^{-1}) during the research cruise was provided from the Rijpfjorden Weather Station (80°13’ N, 22°28’ E) using a Kipp&Zonen PAR LITE Quantum Sensor on a Iridium Satellite System. A total of twelve Methot Isaac Kidd (MIK) hauls (3.14 m^2 opening, 1.5 mm mesh size) were carried out. The net was trawled for 10 min at a speed of ~1.5 knots. Three depth intervals were sampled, (20, 75 and 225 m in Rijpfjorden and 30, 60 and 225 m in Isfjorden), by doing separate hauls at each depth. Deck lights were switched on for the handling of the net winch, but these did not illuminate the net or the sampling area. Due to ice cover, no MIK tow was possible at Sofiadjupet. Instead, samples were collected using a vertically hauled WP3 net (1 m^2, 1.0 mm mesh size, 0-1200 m depth). At Sofiadjupet, only *T. abyssorum* was present in the net. Live individuals were immediately sorted from the catch and transferred into buckets with cold seawater. To avoid post-capture feeding, all examined specimens were immediately separated from other zooplankton after the samples were collected on deck. The collected specimens were identified according to species and stage and total body length was measured to the nearest mm (from the anterior side of the head to the tip of the third pair of uropods (Dunbar 1957)). After identification, all specimens were deep-frozen alive at -55° C as soon as possible (at latest within 4 h of capture) and transferred into a -80° C freezer after the cruise. Subsamples of 44 adult individuals of *T. abyssorum* (size range 8-15 mm) and 17 adult individuals of *T. libellula* (size range 20-32 mm) were selected for stomach and gut content analysis.

Table 4.1 Station and amphipod composition data at the three sampling sites in Rijpfjorden, Isfjorden and Sofiadjupet during the Arctic polar night

Station Position	Rijpfjorden 80°18’ N, 22°16’ E	Isfjorden 78°16’ N, 15°33’ E	Sofiadjupet 81°44’ N, 14°17’ E
Sampling Date	13.01.2012	17.01.2012	15.01.2012
Time interval (UTC)	1104-1232 h	1957-2300 h	0713-0900 h
Bottom depth (m)	278	269	2257
Sampling depth (m) / Water mass# Salinity (PSU) / Temperature (°C)	20 / Meltwater 34.24 / 0.36	30 / Meltwater 34.34 / -0.36	30 / Meltwater 33.98 / -1.85
	75 / Arctic Water 34.41 / 0.68	60 / Meltwater 34.23 / -1.12	500 / Arctic Deep Water 34.95 / 1.52
	225 / Arctic Water 34.57 / -1.26	225 / Mixed Fram Strait Water 34.63 / 1.89	1200 / Arctic Deep Water 34.91 / -0.26
Average PAR (µmol m^{-2} s^{-1} ±SD)*	DAY (0700-1900h): 6.49±4.08 NIGHT (1900-0700h): 7.58 ±6.03	-	-
Themisto abyssorum			
Depth [m] / Density (ind. 1000 m^{-3})	20 / 60.6	30 / 0.4	0-1200 / 13.3
	75 / 169.3	60 / 2.9	-
	225 / 23.1	225 / 1.8	-
Size (Total body length in mm ±SD)	11.9 ±2.6	12.7 ±1.7	
Themisto libellula			absent
Depth (m) / Density (ind. 1000 m^{-3})	20 / 16.1	30 / 5.1	-
	75 / 25.7	60 / 3.9	-
	225 / 6.7	225 / 0.0	-
Size (Total body length in mm ±SD)	26.0 ±5.5	22.7 ±4.5	-

*Average down-welling irradiance PAR (µmol m^{-2} s^{-1} ±SD) measured during day- and nighttime hours from 13 to 17 January 2012 at the Rijpfjorden Weather Station (80°13’ N, 22°28’ E) with an Iridium interface with CR1000 datalogger and Kipp&Zonen PAR LITE Quantum Sensor

#Dominant water mass at the three sampling sites and respective depths. Classification based on temperature and salinity (see Baczewska et al. 2012 and references therein)

SD = Standard deviation

Stomach and gut content analysis

At the home laboratory, the stomach and gut of each individual were carefully removed and placed in a solution of glycerin in water. The degree of fullness was classified according to Nakagawa et al. (2000) and Dalpadado et al. (2008), with stage 0: empty, stage 1: <25 % full, stage 2: 25-50 % full, stage 3: 51-75 % full and stage 4: 76-100 % full. The prey items were examined under a light microscope and grouped into different categories based on the work of Dalpadado et al. (2008) and modified by the inclusion of the groups: amphipod appendages, fecal pellets, eggs and the parasite *Ganymedes themistos*:

1.) Copepods (with the presence of mandibles and/or appendages)

2.) Amphipods (presence of appendages)

3.) Dinoflagellates

4.) Fecal pellets / digested green

5.) Eggs

6.) Parasite *Ganymedes themistos* (Prokopowicz et al. 2010)

7.) Unidentified

When whole prey individuals were found, their total body length was measured. All encountered copepod mandibles were photographed and their size recorded to the nearest µm (mandible width L1, given in Karlson and Båmstedt (1994)) using an inverted microscope (Zeiss IM40, magnification 60-400x) and the image analysis system AxioVision40 V4.7.1 (Carl Zeiss Imaging Solution GmbH). All copepod mandibles were identified to species and stage level when possible (Table 4.3), following the results of Karlson and Bamstedt (1994) and Dalpadado et al. (2008).

Results

Stomach and gut content - Themisto abyssorum

Thrity-two out of forty-four analyzed specimens of *T. abyssorum* possessed a full or partly filled stomach and gut (Fig. 4.1). In 16 cases, their diet consisted predominantly of copepod residues (Table 4.2). This included mandibles (Fig. 4.2a), antennae, fragments of prosomes and other body parts in various stages of digestion. Adult female and male individuals with a total body length of 11-15 mm had up to two copepods in their stomachs. The mandible width of the exclusively calanoid copepods varied from 50-175 µm. Examination of the mandibles showed that *Calanus finmarchicus* was the main prey species of *T. abyssorum* at Isfjorden and Sofiadjupet (Table 4.3). The copepodite stages CII, CIII, CV and adults of this species were identified. At Rijpfjorden, two of the three mandible samples were damaged and could not be identified to species level. Their blade widths of 140 and 138 µm indicate that they belonged to *C. finmarchicus* CV or *C. glacialis* CIII and CIV.

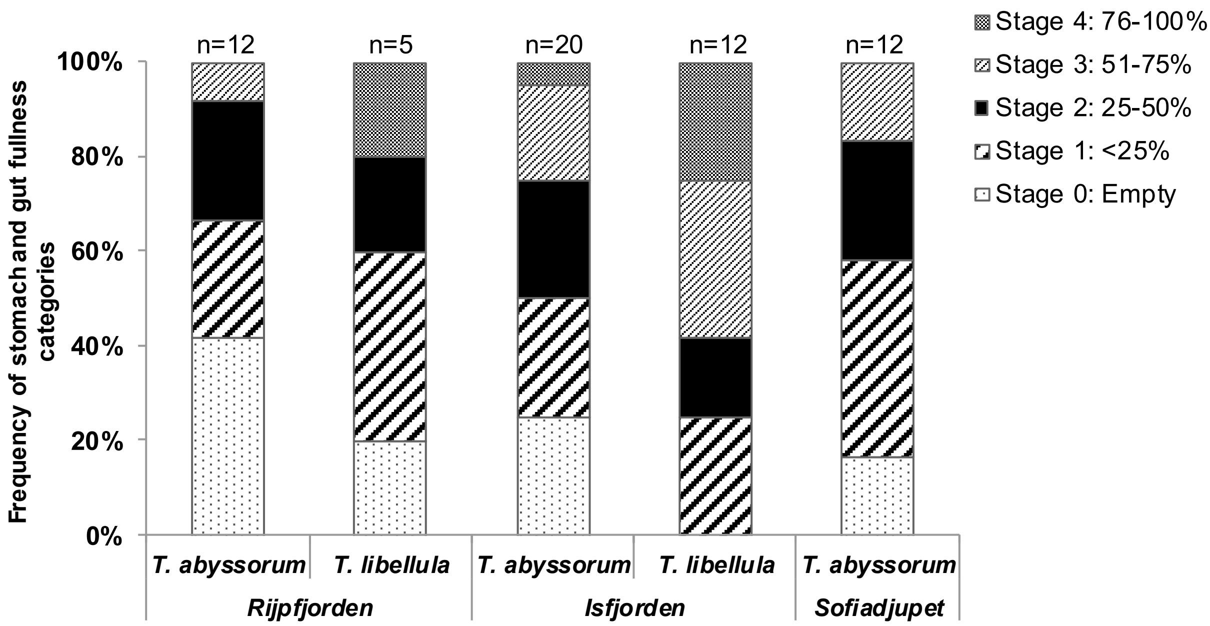

Fig. 4.1 Degree of gut fullness in percent for the hyperiid amphipod *Themisto abyssorum* and *Themisto libellula* at the three sampling sites in Rijpfjorden, Isfjorden and Sofiadjupet during the Arctic polar night

Other food components included fecal pellets and a gregarine parasite, which we identified as *Ganymedes* sp. according to its morphological structure (Fig. 4.2b). The stages of digestion varied from moderately digested material with good recognizable features of the preferred prey such as prosomes of calanoid copepods to heavily digested material consisting mainly of fecal pellets in the fore- and midgut of *T. abyssorum*. Individuals with empty stomach were also present at all stations; most of them, however, from the cold Arctic, Rijpfjorden (Table 4.2).

Table 4.2 Diet composition (% contribution of prey by numbers) for the hyperiid amphipod *Themisto abyssorum* and *Themisto libellula* at the three sampling sites in Rijpfjorden, Isfjorden and Sofiadjupet during the Arctic polar night

	Rijpfjorden		Isfjorden		Sofiadjupet
Prey item	*T. abyssorum*	*T. libellula*	*T. abyssorum*	*T. libellula*	*T. abyssorum*
Copepoda (fragments)	75.8	42.5	53.6	78.9	32.5
Amphipoda (fragments)	-	10.0	-	-	-
Dinoflagellates (whole)	0.7	-	0.4	0.8	-
Fecal pellets/digested green (fragments)	10.7	43.8	34.0	17.1	27.0
Eggs, full and empty (whole)	12.1	-	3.2	0.1	9.5
Ganymedes sp. (whole)	-	3.7	3.6	0.5	20.0
Unidentified (fragments)	0.7	-	5.2	2.7	11.0
Number of guts analyzed	12	5	20	12	12
Mean volume of gut content (mm³)	0.8	1.4	1.1	4.2	1.1

Stomach and gut content – Themisto libellula

In contrast to *T. abyssorum*, almost all examined individuals of *T. libellula* possessed a (partly) filled stomach and gut at the sampling sites Rijpfjorden and Isfjorden (Table 4.2, Fig. 4.1). Similar to its congener, its diet also consisted mainly of calanoid copepods, with up to three copepods per analyzed amphipod. This included CIV, CV or adult stages of *C. finmarchicus* (Fig. 4.3a), *C. hyperboreus* and *Metridia longa* (Table 4.3) with mandible widths from 117 to 240 µm. While adult female individuals of *T. libellula* with a total body length from 25 to 28 mm also possessed copepod appendages in their guts, intact mandibles were only found in the male specimens (total body length from 20 to 32 mm).

Table 4.3 Information on all encountered copepod mandibles in the digestive tract content of the analyzed hyperiids *Themisto abyssorum* and *T. libellula*

Species	Sex	Total body length [mm]	Wet weight [mg]	Mandible blade width [µm]	Species	Stage
Rijpfjorden						
T. abyssorum	M	13	25.1	140	*Calanus* spp.	-
T. abyssorum	F	10	22.4	146	*C. finmarchicus*	CV
T. abyssorum	F	11	31.1	138	*Calanus* spp.	-
Isfjorden						
T. abyssorum	M	11	30.4	175	*C. finmarchicus*	adult
T. abyssorum	F	15	58.3	50	*C. finmarchicus*	CII
T. libellula	M	27	176.3	185	*Metridia longa*	CIV
				174	*C. finmarchicus*	adult
T. libellula	M	20	74.3	122	*C. finmarchicus*	CIV
				117	*C. finmarchicus*	CIV
T. libellula	M	23	130.9	240	*C. hyperboreus*	CV
				135	*C. finmarchicus*	CV
				185	*C. finmarchicus*	adult
Sofiadjupet						
T. abyssorum	F	14	40.7	78	*C. finmarchicus*	CIII
				144	*C. finmarchicus*	CV

Other items found in the guts included fecal pellets and the gregarine *Ganymedes* sp. (Fig. 4.3b), probably *Ganymedes themistos* at both fjords. Also varying stages of digestion of the diet were seen, with a higher amount of heavily digested material (fecal pellets, Fig. 4.3c) at the sampling site of Rijpfjorden (Table 4.2). Due to the larger size of *T. libellula*, the mean gut content of this Arctic species was nearly three times higher compared with *T. abyssorum*, with an amount of 2.8 and 1.0 mm³, respectively.

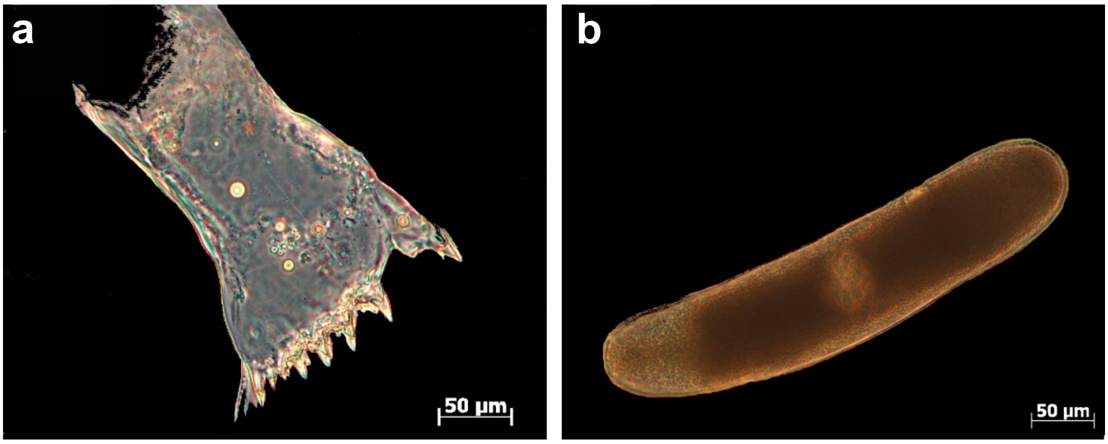

Fig. 4.2 a-b Stomach and gut contents identified from winter samples of *Themisto abyssorum*; (**a**) mandible *Calanus finmarchicus* CV; (**b**) marine gregarine trophozoite *Ganymedes*

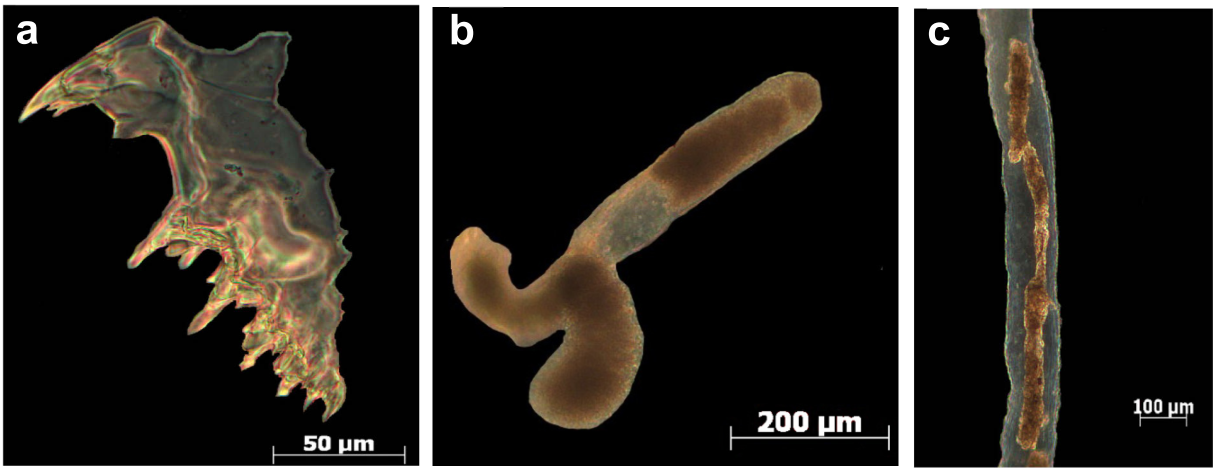

Fig. 4.3 a-c Stomach and gut contents identified from winter samples of *Themisto libellula*; (**a**) mandible *Calanus finmarchicus* adult; (**b**) marine gregarine trophozoite *Ganymedes*; (**c**) fecal pellet in mid-gut segment

Discussion

Within polar ecosystems sampling conditions are harsh and the investigation of zooplankton winter life-cycle strategies is a challenge in the total darkness of the polar night – a time period when the sun is continually located more than 12° below the horizon. During this study the only light source at all sampling sites was (beside the ship's deck lights) star and moonlight, with a mean irradiance of 6-7 PAR (Table 4.1, measured at the Rijpfjorden Weather Station). This is 100x less compared to the period of the midnight sun with a mean irradiance of ~600-700 PAR.

With the onset of shorter daylight periods in fall, many zooplankton species such as calanoid copepods are known to descend to deeper waters and enter a state of winter dormancy (diapause) (e.g., Hirche 1991, 1996; Kosobokova 1999; Wold et al. 2011). Other species such as the carnivorous hyperiid *Themisto* have been suggested to maintain their active mode of life also during the winter (e.g., Dale et al. 2006). However evidence on their feeding strategy has been missing.

Our study suggests active feeding in both species during the polar night. The food items identified consisted predominantly of calanoid copepods and did not differ substantially between the sampling sites. With adult and CV stages of *C. finmarchicus* found in the diet of both species (Table 4.3), our results indicate at least a partial overlap in terms of food sources. *T. libellula* also seemed to prey upon other copepod species such as *C. hyperboreus* and *Metridia longa*. The traditional analysis of digestive tract contents is used in numerous studies to give a first insight into the feeding modes of different species, including fish and zooplankton (e.g., Dalpadado et al. 2008). While the stomach and gut content analysis is expected to provide reliable qualitative results regarding the kind of prey, the semi-quantitative estimates using this method have to be treated with caution as predation rates may be over- or underestimated. This is due to the variable physical properties and thus differing digestion rate of the prey contents. In this study, the digestive tract content of both investigated amphipods showed moderately to advanced stages of digestion. With the known average digestion rate of *Themisto* to be 7.5-13 h (Pakhomov and Perissinotto 1996; Marion et al. 2008) we suggest that our results present a good qualitative assessment of the recent food uptake of *T. abyssorum* and *T. libellula* during the polar night.

Our results stand in contrast to two studies, which compared the feeding modes of *T. abyssorum* and *T. libellula* in Arctic waters during summer and fall (Auel et al. 2002; Dalpadado et al. 2008). Both studies suggested that their diet differed, with extensive feeding on copepods by *T. libellula* (also shown by e.g., Scott et al. (1999), Marion et al. (2008), Noyon et al. (2011, 2012)) and a broader food spectrum for *T. abyssorum*. The latter has been shown to possess a mixed diet by preying upon copepods as well as other zooplankton groups such as appendicularians (Dalpadado et al. 2008). The authors concluded that this mixed diet of *T. abyssorum* is a possible consequence of its broad vertical distribution in the water column (reaching down to 2000 m depth) and its association with warmer, Atlantic water (Koszteyn et al. 1995; Dalpadado 2002). Our study showed a rather similar diet composition with a clear dominance of calanoid copepods, indicating no difference in prey selectivity among the two species during winter. The diet appeared to be complemented by intraspecific cannibalism as well as the feeding on dinoflagellates. With the latter, however, it remains unclear if the amphipods fed directly upon them or if they were digested with the copepod prey. Also the origin of the ingested eggs remains unclear (Table 4.2).

Assemblages of lipid-rich calanoid copepods were present throughout the water column at the three sampling sites in January (personal observation), thus being available as a food source for *Themisto*. These populations were sampled with a multinet (Hydrobios, 0.25 m^2 opening, mesh size 200 μm) at five depths (260, 200, 100, 50 and 20 m) and will be analyzed for mesozooplankton species composition, vertical and size distribution (to be reported in a separate publication). The highest densities of *Themisto* were observed within the upper 75 m of the water column (Table 4.1). Therefore, the hyperiids may play a role in the control of mesozooplankton communities also during the Arctic winter.

The presence of the gregarine trophozoite *Ganymedes* sp., probably *G. themistos*, in both amphipod species was unexpected. While this parasite has been previously recorded and was newly described from *T. libellula* samples collected in the Canadian Arctic (Prokopowicz et al. 2010), to our knowledge our study is the first to document its appearance in *T. abyssorum* (Fig. 4.2b). Leander (2008) described the group of marine gregarines as single-celled, host-specific organisms, which inhabit the intestines of invertebrates and can reach large sizes. Because of this host-specificity we recognize the necessity to genetically compare the parasites in order to reach a reliable conclusion if the same species (*G. themistos*) infects both *Themisto* species. In our study most amphipod individuals, which contained *Ganymedes* in their digestive tract also had other food items (including copepod mandibles) present. Therefore we agree with Prokopowicz et al. (2010) that this trophozoite infection does not seem to have a significant impact on the feeding and survival of *T. libellula*. Furthermore we suggest that the same is also true for its congener *T. abyssorum*.

Our findings of active feeding raise questions concerning the mechanism that enables these supposedly visual predators to hunt during the polar night. A characteristic feature of hyperiid amphipods are the large, double structured eyes which possess special upward-pointing regions covering a narrow field of view (Land 1989, 2000). Land (2000) suggested that these regions are an adaptation to the task of detecting small objects against the dim down-welling light in the water column. As little down-welling light is available at high latitudes during the Arctic winter (with the exception of the periodic moonlight events) this part of the eye structure may only play a small part in the active foraging strategy of *Themisto* during this time of the year if at all. The lower part of the eyes is considered to be used to detect bioluminescent sources, whose brightness would show only little variation with depth (Land 1989, 2000). We found one specimen of a bioluminescent copepod in the digestive tract of the analyzed amphipods, *Metridia longa* (Table 4.3). There is the opportunity that *Metridia* itself could provide background illumination, a concept suggested for other visual predators, e.g. polar cod (*Boreogadus saida*) (Benoit et al. 2010). Berge et al. (2012) recently documented the presence of small bioluminescent dinoflagellates retaining metabolic rates that enable them to produce light also during the polar night. It is a possibility that *Themisto* uses this illumination to actively prey on copepods. Beside the visual aspect, feeding modes of hyperiids may also depend on mechanical, tactile and olfactory stimuli. Carnivorous zooplankton including copepods of the genus *Euchaeta*, scyphozoan jellyfish and siphonophores have been shown to use tactile stimuli over vision, tracking the vertical movements of their prey. This enables them to prey upon zooplankton equally well under darkness and daylight conditions (Hays 2003). However, because of the lack of investigations it still remains unclear to what degree tactile or other impulses such as olfactory or mechanical ones are important in the feeding strategy of *Themisto*. Our observations of active feeding during dark conditions suggest that alternatives to visual search may be more important than previously acknowledged. We suggest further studies, including controlled laboratory investigations, of the potential role of tactile or other prey search mechanisms in *Themisto* spp. in order to understand to what extent a pelagic predator relies on visual search.

Conclusion

Our results showed that the Arctic hyperiids *T. abyssorum* and *T. libellula* are active raptorial feeders during the polar night. The most important prey items consisted of calanoid copepods such as *Calanus finmarchicus*. In addition we present first evidence of a marine gregarine infection within the hyperiid *Themisto abyssorum*.

Acknowledgments

We greatly acknowledge Captain Hans Hanssen and the crew of the R/V *Helmer Hanssen* for their skillful work and support during the ARCTOS Marine ecological research cruise in January 2012. We thank Anette Wold, Clare Webster, Jordan Grigor and Malin Daase for their help with the sample processing on board. We acknowledge Angus Atkinson and two anonymous referees who greatly improved the original version of the manuscript. We also thank Gerhard Dieckmann for his valuable suggestions and proof reading. This work was partly financed by the Norwegian Research Council through the Circa Project.

References

Auel H, Harjes M, da Rocha R, Stubing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25:374-383.

Baczewska A, Blachowiak-Samolyk K, Angel M (2012) Distribution of pelagic Ostracoda (Crustacea) inhabiting the waters around Svalbard (Arctic Ocean: 76°36-81°50N). Hydrobiologia 688:75-92.

Benoit D, Simard Y, Gagne J, Geoffroy M, Fortier L (2010) From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. Polar Biol 33:1505-1520.

Berge J, Båtnes AS, Johnsen G, Blackwell SM, Moline MA (2012) Bioluminescence in the high Arctic during the polar night. Mar Biol 159:231-237.

Berge J, Cottier F, Last KS, Varpe Ø, Leu E, Soreide J, Eiane K, Falk-Petersen S, Willis K, Nygard H, Vogedes D, Griffiths C, Johnsen G, Lorentzen D, Brierley AS (2009) Diel vertical migration of Arctic zooplankton during the polar night. Biol Lett 5:69-72.

Dale K, Falk-Petersen S, Hop H, Fevolden SE (2006) Population dynamics and body composition of the Arctic hyperiid amphipod *Themisto libellula* in Svalbard fjords. Polar Biol 29:1063-1070.

Dalpadado P (2002) Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. Polar Biol 25:656-666.

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of *Themisto* (Amphipoda) spp in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58:876-895.

Dalpadado P, Yamaguchi A, Ellertsen B, Johannessen S (2008) Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55:2266-2274.

Dunbar MJ (1957) The determination of production in the northern seas: a study of the biology of *Themisto libellula* Mandt. Can J Zool 35:797-819.

Falk-Petersen S, Sargent JR, Tande KS (1987) Lipid composition of zooplankton in relation to the sub-arctic food web. Polar Biol 8:115-120.

Falk-Petersen S, Haug T, Nilssen KT, Wold A, Dahl TM (2004) Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. Polar Res 23:43-50.

Falk-Petersen S, Mayzaud P, Kattner G, Sargent J (2009) Lipids and life strategy of Arctic *Calanus*. Mar Biol Res 5:18-39.

Hays GC (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiologia 503:163-170.

Hirche HJ (1991) Distribution of dominant calanoid copepod species in the Greenland Sea during late fall. Polar Biol 11:351-362.

Hirche HJ (1996) Diapause in the marine copepod *Calanus finmarchicus*. Ophelia 44:129-143.

Karlson K, Båmstedt U (1994) Planktivorous predation on copepods. Evaluation of mandible remains in predator guts as a quantitative estimate of predation. Mar Ecol Prog Ser 108:79-89.

Kosobokova KN (1999) The reproductive cycle and life history of the Arctic copepod *Calanus glacialis* in the White Sea. Polar Biol 22:254-263.

Koszteyn J, Timofeev S, Weslawski JM, Malinga B (1995) Size structure of *Themisto abyssorum* Boeck and *Themisto libellula* (Mandt) populations in the European Arctic Seas. Polar Biol 15:85-92.

Land MF (1989) The eyes of hyperiid amphipods - relations of optical structure to depth. J Comp Physiol Sensory Neural Behav Physiol 164:751-762.

Land MF (2000) On the functions of double eyes in midwater animals. Philos Trans R Soc Lond Ser B-Biol Sci 355:1147-1150.

Leander BS (2008) Marine gregarines: evolutionary prelude to the apicomplexan radiation? Trends Parasitol 24:60-67.

Marion A, Harvey M, Chabot D, Brethes JC (2008) Feeding ecology and predation impact of the recently established amphipod, *Themisto libellula*, in the St. Lawrence marine system Canada. Mar Ecol Prog Ser 373:53-70.

Nakagawa Y, Endo Y, Taki K (2000) Diet of *Euphausia pacifica* Hansen in Sanriku waters off northeastern Japan. Plankton Biol Ecol 48:68-77.

Nilsen F, Cottier F, Skogseth R, Mattsson S (2008) Fjord–shelf exchanges controlled by ice and brine production: The interannual variation of Atlantic Water in Isfjorden, Svalbard. Continent Shelf Res 28:1838-1853.

Noyon M, Narcy F, Gasparini S, Mayzaud P (2011) Growth and lipid class composition of the Arctic pelagic amphipod *Themisto libellula*. Mar Biol 158:883-892.

Noyon M, Narcy F, Gasparini S, Mayzaud P (2012) Ontogenic variations in fatty acid and alcohol composition of the pelagic amphipod *Themisto libellula* in Kongsfjorden (Svalbard). Mar Biol 159:805-816.

Pakhomov EA, Perissinotto R (1996) Trophodynamics of the hyperiid amphipod *Themisto gaudichaudii* in the South Georgia region during late austral summer. Mar Ecol Prog Ser 134:91-100.

Prokopowicz AJ, Rueckert S, Leander BS, Michaud J, Fortier L (2010) Parasitic infection of the hyperiid amphipod *Themisto libellula* in the Canadian Beaufort Sea (Arctic Ocean), with a description of *Ganymedes themistos* sp n. (Apicomplexa, Eugregarinorida). Pol Biol 33:1339-1350.

Renaud P, Berge J, Varpe Ø, Lønne O, Nahrgang J, Ottesen C, Hallanger I (2012) Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*? Polar Biol 35:401-412.

Rudels BJ, Friedrich H, Quadfasel D (1999) The Arctic circumpolar boundary current. Deep-Sea Res II 46:1023-1062.

Scott CL, Falk-Petersen S, Sargent JR, Hop H, Lønne OJ, Poltermann M (1999) Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal ice zone of the Barents Sea. Polar Biol 21:65-70.

Varpe Ø (2012) Fitness and phenology: annual routines and zooplankton adaptations to seasonal cycles. J Plankton Res 34:267-276.

Wing BL (1976) Ecology of *Parathemisto libellula* and *P. pacifica* (Amphipoda: Hyperiidea) in Alaskan waters. Northwest Fisheries Center Processed Report, Seattle.

Wold A, Darnis G, Soreide JE, Leu E, Philippe B, Fortier L, Poulin M, Kattner G, Graeve M, Falk-Petersen S (2011) Life strategy and diet of *Calanus glacialis* during the winter-spring transition in Amundsen Gulf, south-eastern Beaufort Sea. Polar Biol 34:1929-1946.

PUBLICATION III

Amphipods in sediment traps of the eastern Fram Strait with focus on the life-history of the lysianassoid *Cyclocaris guilelmi*

Angelina Kraft[a]*, Edurad Bauerfeind[a], Eva-Maria Nöthig[a], Michael Klages[a], Agnieszka Beszczynska-Möller[a], Ulrich V. Bathmann[b]

[a]Alfred Wegener Institute for Polar and Marine Research
Am Handelshafen 12,
27570 Bremerhaven, Germany
* Contact information:
E-mail: Angelina.Kraft@awi.de
Phone: + 49-471-48311085
Fax: + 49-471-48311149

[b]Leibniz Institute for Baltic Sea Research Warnemünde,
D-18119 Rostock, Germany

Published in Deep-Sea Research Part I:
Oceanographic Research Papers 73:62-72 (2013),
doi:10.1016/j.dsr.2012.11.012

Abstract

Life-cycle characteristics of the free-swimming lysianassoid amphipod *Cyclocaris guilelmi* were investigated and compared to those of other regularly appearing amphipods in the Arctic deep-sea community. In this context we analysed time-series data of meso- and bathypelagic amphipods collected as swimmers in moored sediment traps from 2004-2008 at the deep-sea long-term observatory HAUSGARTEN (79° N/4° E) in the eastern Fram Strait, Arctic Ocean. Six mesopelagic and three bathypelagic deep-sea amphipod species regularly occurred in the traps. The lysianassoid *C. guilelmi* showed a stable interannual population size and seasonal peaks in its occurrence from August to February during the five-year sampling period. The investigation of its population structure and reproduction ecology indicated year-round breeding behavior of this species. Up to 4 cohorts consisting mainly of juvenile and female *C. guilelmi* were observed. We conclude that *C. guilelmi* plays an important role within the Arctic amphipod deep water community.

Keywords: Amphipoda • Lysianassoidea • life-cycle • swimmer • Arctic • mesopelagic • bathypelagic

Introduction

Meso- and bathypelagic organisms play an essential role in pelago-benthic coupling processes by altering organic matter on its way down to the seafloor (Mauchline 1972; Wassmann 1998; Gardner 1999). However, little is known about the biology and seasonal dynamics of zooplankton species living in deeper waters. Among deep-sea amphipods, lysianassoid species are known as an abundant and widely distributed taxa in polar Atlantic and Pacific Oceans (Lowry and Stoddart 1994, 2011) that dominate amphipod communities of the bathy- and mesopelagic zones (Barnard 1954; Blankenship et al. 2006). Lysianassoidea pursue a variety of life-styles; the group includes free-living detritivores as well as predators and scavengers. In the Arctic Ocean, almost no attention has been given to free-swimming, deep-water lysianassoids with the exception of few notes on their occurrence, geographical, and sometimes vertical distribution.

One of these, is the Arctic lysianassoid amphipod *Cyclocaris guilelmi* (Chevreux 1899), which has been observed at depths below 500 m in Arctic and subarctic waters (Stephensen 1935; Tencati 1970; Buchanan and Sekerak 1982; Grainger 1989; Seiler and Brandt 1997; Kosobokova et al. 1998, 2011; Bucklin et al. 2010; Lowry and Stoddart 2011). Gran (1902) even named the cold bottom layers of the Norwegian Sea the ‘Cyclocaris region’, implying *C. guilelmi* as the main planktonic organism in water depths from 1000 to 2000 m. However, recent sampling with modern plankton nets has not revealed high abundances of *C. guilelmi* (Tencati 1970; Buchanan and Sekerak 1982; Bucklin et al. 2010; Kosobokova et al. 2011). Reasons for this discrepancy are most likely that small nets and relatively shallow sampling depths do not efficiently capture these amphipods. Lysianassoid amphipods were usually collected via plankton nets or baited traps several hundred or even thousands of meters above the sea-floor (Barnard 1954; Brusca 1967; Birstein and Vinogradov 1970; Thurston 1976a, 1976b; Blankenship et al. 2006). In the study of Seiler and Brandt (1997), *C. guilelmi*, however, dominated the amphipod and the total zooplankton biomass collected in sediment traps deployed at water depths of ~1000 m in the Greenland Sea. There, the authors collected the species in comparatively large numbers (up to 3314 individuals per sampling year). Most studies of *C. guilelmi* were limited to determining its geographical and vertical distribution, thus no detailed studies of their population structure and reproduction exist (Fowler 1898; Stebbing 1906; Apstein and Brandt 1901; Gran 1902; Østvedt 1955; Johnson et al. 2001).

Time-series sediment traps are primarily used to gather information on vertical particle fluxes in the oceans (e.g., Bloesh and Burns 1980; Larsson et al. 1986; Buesseler et al. 2007). In addition to collecting passively sinking particles, different groups of zooplankton are routinely found in the traps. These so-called ‘swimmers’ are considered to actively enter the traps (Knauer et al. 1979; Karl and Knauer 1989; Lee et al. 1992). In contrast to episodic sampling with plankton nets, the use of sediment traps deployed year round can provide information on the seasonality of zooplankton in marine pelagic environments. In spite of the advantages of using sediment traps for long-term studies of zooplankton, little research has been done on swimmers collected in sediment traps in the past (Seiler and Brandt 1997; Steinberg et al. 1998; Willis et al. 2008; Makabe et al. 2010). In the eastern Fram Strait, Kraft et al. (2011) investigated the amphipod composition in sediment traps of the epipelagic zone (~300 m) over a 10-year period showing the seasonal pattern of the common amphipod genus *Themisto* (including the species *T. abyssorum*, *T. libellula* and *T. compressa*).

The aim of this study is to present results on amphipods collected with sediment traps in the mesopelagic and bathypelagic zone (down to 2700 m) in the eastern Fram Strait and identify the life-cycle characteristics of the species *C. guilelmi*, the dominant amphipod found in the sediment traps. Sediment traps were deployed at 800-1316 m and 2357-2370 m depth from 2004 to 2008. Our focus is the evaluation of seasonal and interannual patterns in *C. guilelmi* in comparison to other regularly appearing free-swimming amphipods in the deep sea. Furthermore, we investigate its population structure and reproduction ecology, and contribute new insights into the mesopelagic plankton community at the only deep-water connection between the North Atlantic and central Arctic Ocean.

Material and methods

Investigation area

Our main study site is the HAUSGARTEN, a long-term, deep-sea observatory located along a submarine projection of the Svalbard continental margin in the eastern Fram Strait (Fig. 5.1). A considerable exchange of oceanic water masses takes place in this important transition zone between the North Atlantic and the Arctic oceans, which result in heat and freshwater/salt fluxes (Quadfasel et al. 1987; Schauer et al. 2008). The main current system is represented by the northward-flowing West Spitsbergen Current (WSC) in the eastern part of the Fram Strait, which transports relatively warm Atlantic waters into the Arctic Ocean Boundary Current (Quadfasel et al. 1987; Manley 1995). In the west, the southward-flowing East Greenland Current (EGC) exports colder and less-saline Arctic waters out of the Arctic Ocean (Schauer et al. 2008). The upper ~700 m of the HAUSGARTEN are strongly influenced by Atlantic water of the WSC (Bauerfeind et al. 2009). Below the Atlantic water layer, low-temperature waters prevail, namely the Arctic Intermediate Water and Norwegian Sea Deep Water, the latter modified by deep water masses of polar origin (Schlichtholz and Houssais 2002). Another study site was located in the eastern Greenland Sea, where cold Arctic water of the EGC dominates the upper and Norwegian Sea Deep Water the deeper water columns (Fig. 5.1).

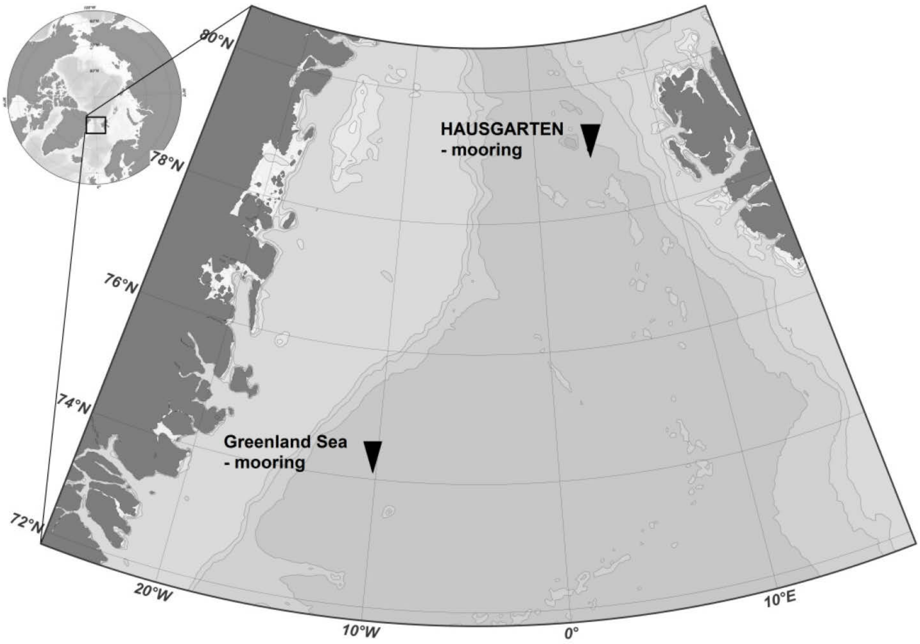

Fig. 5.1 The sediment trap mooring positions (inverted triangles) at the deep-sea long-term observatory HAUSGARTEN in the eastern Fram Strait and in the eastern Greenland Sea

Sediment trap sampling and treatment

Deep-sea mooring arrays equipped with sediment traps provide year-round information on particle fluxes and dominant zooplankton occurring between the central Arctic Ocean and the North Atlantic. In the HAUSGARTEN area, sampling took place in the mesopelagic (800 m), upper bathypelagic (1230-1316 m) and lower bathypelagic (2357-2370 m) water column from 2004-2008 (Table 5.1). Furthermore, we investigated samples from a sediment trap deployed at 2700 m depth in the eastern Greenland Sea from 2000-2001 and compared the results with those from the HAUSGARTEN area (Table 5.1). Samples were collected by modified automatic Kiel sediment traps with an aperture of 0.5 m^2 and 20 collection cups (Kremling et al., 1996). The automatic sampler was set to rotate every 7 to 17 days during the phytoplankton bloom period (May to September) and for longer intervals (up to 49 days) during the other months. Prior to deployment, collection bottles were filled with filtered sterile North Sea water and the salinity adjusted to 40 psu and poisoned with $HgCl_2$ with a final concentration of 0.14 %. At the home laboratory, swimmers were removed under a dissecting microscope (Olympus SZX10, magnification 20-50), separated into common systematic groups (Amphipoda, Chaetognatha, Copepoda, Ostracoda and Pteropoda) and stored refrigerated until further examination.

Table 5.1 Location, sampling time, water and trap depth of moored sediment traps analyzed for their amphipod compositions and size structure at HAUSGARTEN and in the Greenland Sea

Mooring period	Position	Lat. N	Long.	Water depth (m)	Trap depth (m)	No of samples
12.07.2004-19.08.2005	HAUSGARTEN	79°00.99’	04°20.62’ E	2584	800	20
23.08.2005-31.08.2006	HAUSGARTEN	79°01.01’	04°20.63’ E	2530	1230	17
05.08.2006-20.06.2007	HAUSGARTEN	79°00.83’	04°20.60’ E	2540	1300	20
21.07.2007-15.07.2008	HAUSGARTEN	79°00.82’	04°20.62’ E	2589	1316	18
23.08.2005-31.08.2006	HAUSGARTEN	79°01.01’	04°20.63’ E	2530	2357	19
21.07.2007-15.07.2008	HAUSGARTEN	79°00.82’	04°20.62’ E	2589	2370	20
18.09.2000-17.09.2001	Greenland Sea	74°23.93’	10°19.48’ W	3146	2700	20

All collected amphipods from HAUSGARTEN were identified to species level where possible, counted, and classified according to sex and stage. The total body length (TBL; accuracy 0.01 mm) of each collected *Cyclocaris* specimen was measured by image analysis using the cell^P software (Olympus Europa Holding GmbH) from the anterior side of the head to the tip of the third pair of uropods (Dunbar 1957; Hoffer 1972). Maturity was determined by the examination of secondary sexual characters such as the presence of oöstegites in females and the elongation of the second antenna with calceoli in males (Kane 1963; Tencati 1970). Small individuals without recognizable sexual features were recorded as juveniles. Females with developing eggs were carefully dissected and the number and diameter of the eggs recorded (Olympus SZX10, image analysis cell^P, accuracy 0.01 µm). The collected amphipods from the Greenland Sea were identified to species level and counted. Stage or size, were not determined because of their subsequent use for a different research project.

Water temperature

Continuous, daily measurements of water temperature (°C) were taken with temperature sensors on recording current meters (RCM, Aanderaa Data Instruments AS), fitted to the sediment trap moorings at HAUSGARTEN in the upper bathypelagic (1230-1316 m) and lower bathypelagic (2357-2370 m) zones during the sampling periods. No data were recorded in the mesopelagic zone from August 2004 to July 2006 due to the loss of the RCM. Furthermore, no temperature data are available for sampling locations from the Greenland Sea.

Data analysis

Amphipod abundance indices and length-frequency histograms were calculated for each month per mooring period (summer to summer). The dataset was normalized to ind. m^{-2} day^{-1}. For statistical analysis, the abundance data were transformed (log (x+1)) in order to meet the assumptions of normality. Significant differences in amphipod occurrences from the various years and water columns were tested using the Student's t test ($p<0.05$) included in the STATGRAPHICS centurion XVI software. Routines from multivariate statistics using the PRIMER v6 software package (Clarke and Gorley 2006; Clarke and Warwick 2001) were applied to visualize differences in amphipod collection and compositions for the respective sampling periods (years and months) and water columns (meso- and bathypelagic). The log (x+1)-transformed abundance data were used for a Bray-Curtis similarity analysis and visualized via an ordination biplot (nMDS, non-metric multi-dimensional scaling). An ANOSIM routine was applied to test for differences in the species composition from different years and sampling depths. In addition, a SIMPER routine was used to determine the contribution of individual species responsible for the grouping patterns on the nMDS plot.

Length-frequency distributions for each month were analyzed for normally distributed components (cohorts) according to Sparre (1988) and Dalpadado (2002) using Bahttacharya's analysis. During months with few recorded individuals (<15 counted specimens) the statistical testing could not be applied. In these cases, recorded length-frequencies were classified in cohorts on the basis of previous statistic results derived from the respective seasonal time-frames of other sampling years.

Results

Water temperature

The daily measurements indicated a variation of up to 0.38° C (-0.81 to -0.43 °C) in the upper bathypelagic zone, with a mean water temperature of -0.64° C during the 2006/2007 sampling period and -0.65 °C during the 2007/2008 sampling period. In the lower bathypelagic zone, the recorded water temperatures ranged between -0.84 to -0.77° C, with mean values of -0.79° C in 2004/2005, -0.79° C in 2005/2006, -0.78° C in 2006/2007 and -0.79° C in 2008/2009.

Amphipod identification

Specimens (2,770 total) belonging to nine different species were collected in the sediment traps samples from 2000 to 2008. Of these nine species, two occurred in both mesopelagic and bathypelagic sediment traps on a regular basis: the deep-water amphipod *Cyclocaris guilelmi* and the hyperiid *Themisto abyssorum*. The proportion of both accounted for 68.1-99.5 % of all identified specimens. Amphipods contributed between 1.9 and 23.3 % by number to the overall swimmer composition. Throughout the study period, *C. guilelmi* was found at all mooring stations and clearly dominated the species composition (Table 5.2, Fig. 5.2 a-b).

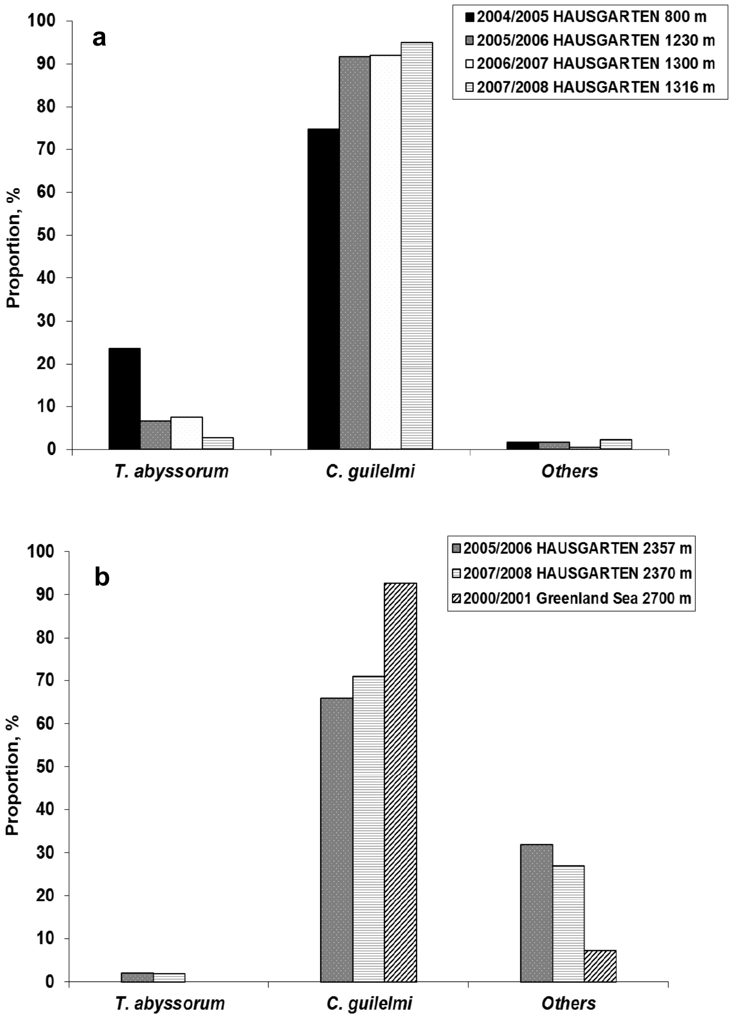

Fig. 5.2 a-b Relative contribution (%) of *Cyclocaris guilelmi*, *Themisto abyssorum* and other amphipod species to the total amphipod abundance in the mesopelagic (800 m) and upper bathypelagic (1230-1316 m) (**a**) and lower bathypelagic (2357-2700 m) (**b**) sediment traps

Table 5.2 Average yearly appearances of recorded amphipod taxa (ind. $m^{-2}d^{-1}$) in sediment traps during 2000-2008 at HAUSGARTEN and in the Greenland Sea

Year	2004/2005	2005/2006	2006/2007	2007/2008	2005/2006	2007/2008	2000/2001
Depth	800 m	1230 m	1300 m	1316 m	2357 m	2370 m	2700 m
Position	HAUSGARTEN	HAUSGARTEN	HAUSGARTEN	HAUSGARTEN	HAUSGARTEN	HAUSGARTEN	Greenland Sea
Type	Mesopelagic	Upper bathypelagic	Upper bathypelagic	Upper bathypelagic	Lower bathypelagic	Lower bathypelagic	Lower bathypelagic
Taxon							
Cyclocaridae							
Cyclocaris guilelmi (Chevreux 1899)	2.41	3.13	6.78	3.76	0.20	0.43	0.44
Cyphocarididae							
Cyphocaris bouvieri (Chevreux 1916)							<0.05
Eusiridae							
Eusirus holmii (Hansen 1887)	<0.05	<0.05					
Hyperiidae							
Themisto abyssorum (Boeck 1870)	1.17	0.19	0.55	0.11	<0.05	<0.05	
Themisto libellula (Lichtenstein 1822)	<0.05				<0.05		<0.05
Lanceolidae							
Lanceola clausi (Bovallius 1885)	<0.05	<0.05	<0.05	<0.05			<0.05
Lysianassidae							
Tryphosella sp. (Bonnier 1893)					0.12	0.12	
Stegocephalidae							
Andaniexis abyssi (Boeck 1871)				<0.05			
Uristidae							
Onisimus nanseni (Sars 1900)			<0.05				
Amphipoda indet.				<0.05			

In the mesopelagic and upper bathypelagic traps, the proportion of this species increased significantly (from 74.7 % in 2004-2005 to 91.7-95.0 % in 2005-2008, p=0.008), with no further significant changes in the later years (Fig. 5.2a). Of the other amphipod species, only *T. abyssorum* appeared in higher numbers (2.7-23.6 %). Rare species such as *Eusirus holmii* and *Lanceola clausi* were occasionally observed (Fig. 5.2a). A dominance of *C. guilelmi* (66.0-92.7 %) (Fig. 5.2b) also occurred in the lower bathypelagic traps. There, other species including the hyperiid *T. abyssorum*, as well as the deep-water genus *Tryphosella* sp. in the HAUSGARTEN area and *L. clausi* and *Cyphocaris bouvieri* in the Greenland Sea (Table 5.2) were also found.

Vertical distribution and seasonality

Significant differences in species occurrences between the meso- and bathypelagic traps were shown by a nMDS plot (Fig. 5.3). The amphipods *C. guilelmi*, *Tryphosella* sp., and *T. abyssorum* contributed most to this distinct separation between the two pelagic zones (SIMPER routine, contribution 64.8-87.1 %). A separate analyses showed no overall separation within the mesopelagic and upper bathypelagic traps (ANOSIM routine, Global *R* = 0.22, p = 0.001) and little separation between the sampling year 2004-2005 and the other years from 2005 to 2008 (*R* = 0.35-0.44, p = 0.001) (Fig. 5.3). However, a seasonally-based analysis resulted in a significant separation between the late fall/early winter (October to December) and spring/early summer months (April-June) (*R* = 0.61, p = 0.001). The SIMPER routine showed that *C. guilelmi* was responsible for this pattern, with a contribution of 63.72 %. Within the lower bathypelagic traps, no overall separation between the analyzed sampling years and stations was detected (ANOSIM, Global *R* = 0.26, p = 0.001) (Fig. 5.3). However, a significant difference between late fall/early winter (October to December) and the winter/spring months (January-June) was also observed (*R* = 0.41-0.51, p = 0.001). This separation was mainly caused by differences in the abundance indices of *C. guilelmi* (SIMPER routine, contribution 73.9-82.4 %).

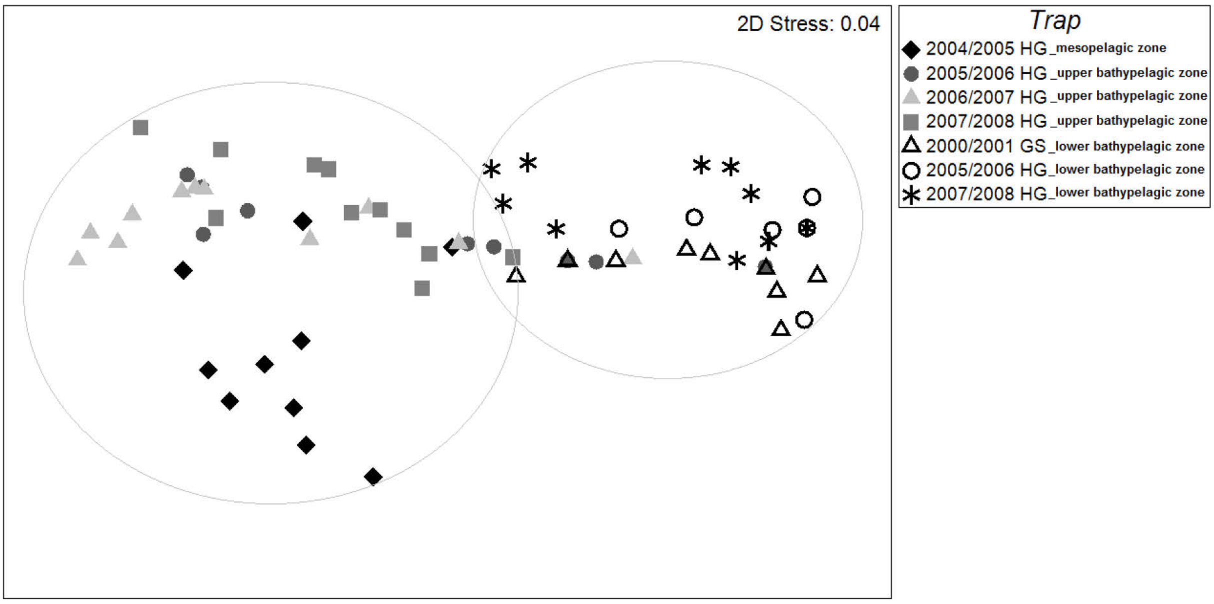

Fig. 5.3 Non-metric multi-dimensional scaling plots (nMDS) depicting the amphipod compositions from sediment trap samples in different mooring periods (2000/2001, 2004/2005, 2005/2006, 2006/2007, 2007/2008) and water depths at HAUSGARTEN and in the Greenland Sea. A stress value of 0.04 corresponds to a very good ordination of the two-dimensional data

Seasonal variation of amphipod abundance in the traps

The following results focus on a closer investigation of monthly abundance indices of the lysianassoid *C. guilelmi*. Overall, the occurrence of this species was higher in the mesopelagic and upper bathypelagic traps (Fig. 5.4 a-d), compared to the lower bathypelagic ones (Fig. 5.5 a-c). The first sampling period 2004-2005 at 800 m depth was characterized by the lowest abundance indices of *C. guilelmi* (Fig. 5.4a) compared to the following years 2005-2008 (Fig. 5.4b-d), where the sediment traps sampled at depths between 1230-1316 m. Interestingly, a seasonal signal in the abundance pattern of *C. guilelmi* could be observed in the deeper mesopelagic traps: starting in summer 2005, the lysianassoid showed significantly higher abundance indices ($p = 0.001$) in the first part of the sampling period until December, with lower abundance in the following spring and summer months (Fig. 5.4b). This seasonal pattern repeated itself in the next sampling periods of 2006-2007 (Fig. 5.4c) and 2007-2008 (Fig. 5.4d). In the Greenland Sea, few individuals of *C. guilelmi* were observed from October 2000 to June 2001 (Fig. 5.5a). Similarly low occurrences of this species were recorded in the bathypelagic zone in the HAUSGARTEN (Fig. 5.5b and c), where the highest abundance indices of *C. guilelmi* appeared in August, October and November 2007, respectively.

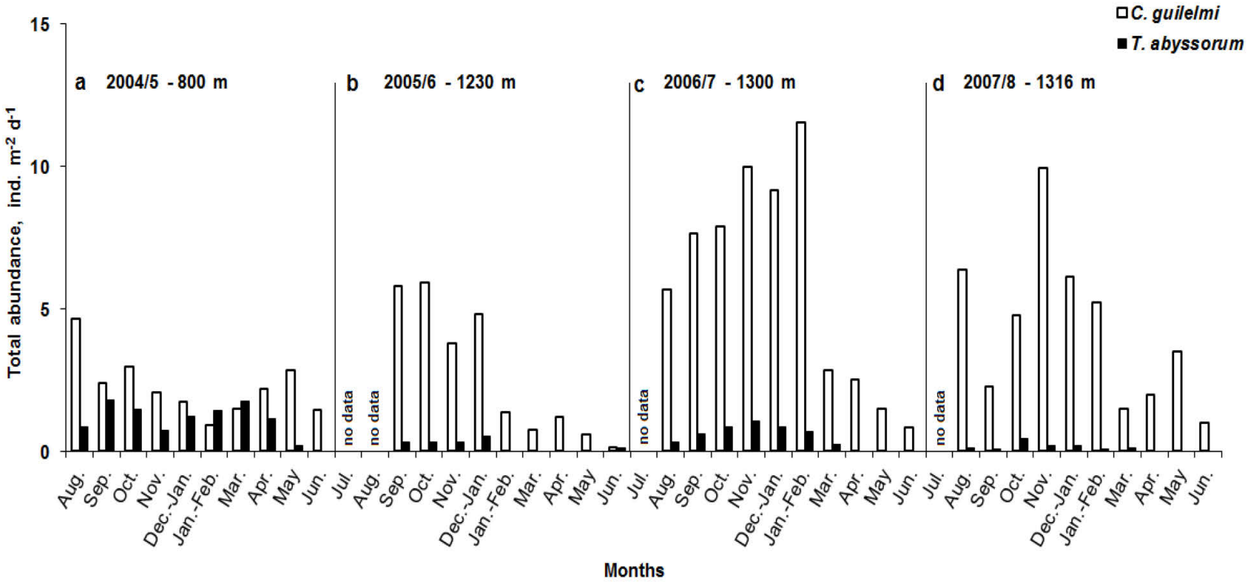

Fig. 5.4 a-d Monthly appearances (ind. $m^{-2}d^{-1}$) for *Cyclocaris guilelmi* and *Themisto abyssorum* from the mesopelagic und upper bathypelagic sediment traps at the central HAUSGARTEN mooring station during 2004-2008 at the respective water depths (m)

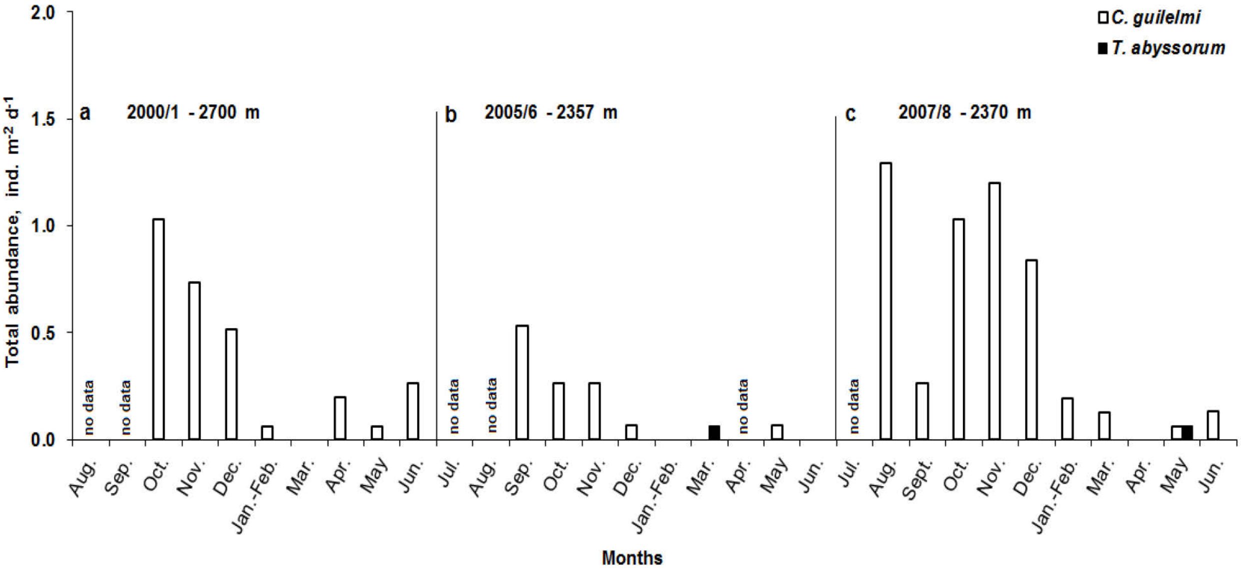

Fig. 5.5 a-c Monthly appearances (ind. $m^{-2}d^{-1}$) for *Cyclocaris guilelmi* and *Themisto abyssorum* from the lower bathypelagic sediment traps in the Greenland Sea at 2700 m during 2000/2001 (**a**) and at the central HAUSGARTEN mooring station during 2005-2008 (**b** and **c**) at the respective water depths (m)

Population structure

In most analyzed samples from the HAUSGARTEN mooring, female (Fig. 5.6A and 6B) or juvenile (Fig. 5.6C) individuals dominated the population structure of *C. guilelmi*. Males were only occasionally observed (Fig. 5.6D and 5.7). Females were most abundant in the samples in water depths of 800 m, 2357 m and 2370 m, while juveniles constituted most of the

C. guilelmi population in the upper bathypelagic traps during the 2005-2008 sampling period. In 2004-2005, 2005-2006, 2006-2007 and 2007-2008, the total body length of *C. guilelmi* in the mesopelagic and upper bathypelagic zone (with the ratio of mature females to males given in brackets) ranged from 5.0-27.1 mm (50:1), 5.0-28.2 mm (12:1), 4.4-28.5 mm (10:1) and 3.7-26.5 mm (17:1), respectively. In the lower bathypelagic zone the ratio was 3:1 during 2005-2006 and 14:1 during 2007-2008. Female individuals with developing eggs (oocytes) in a dorsally located ovary were observed in all traps (Fig. 5.6B). All females with growing oocytes showed oöstegites in different stages of development; however, no females with a full brood pouch were observed. In the mesopelagic and upper bathypelagic traps, the TBL of these females ranged from 19.6-26.8 mm (mean 22.7 mm), with a count of 13-45 (mean 28) eggs. The diameter of the recorded eggs varied between 134-588 (mean 299) µm. In the lower bathypelagic samples, females with developing oocytes had a similar size (range 20.0-28.5 mm, mean 23.7 mm TBL), with 17-77 (mean 40) eggs in the ovary. In these samples, the egg diameter varied from 94 to 300 (mean 197) µm.

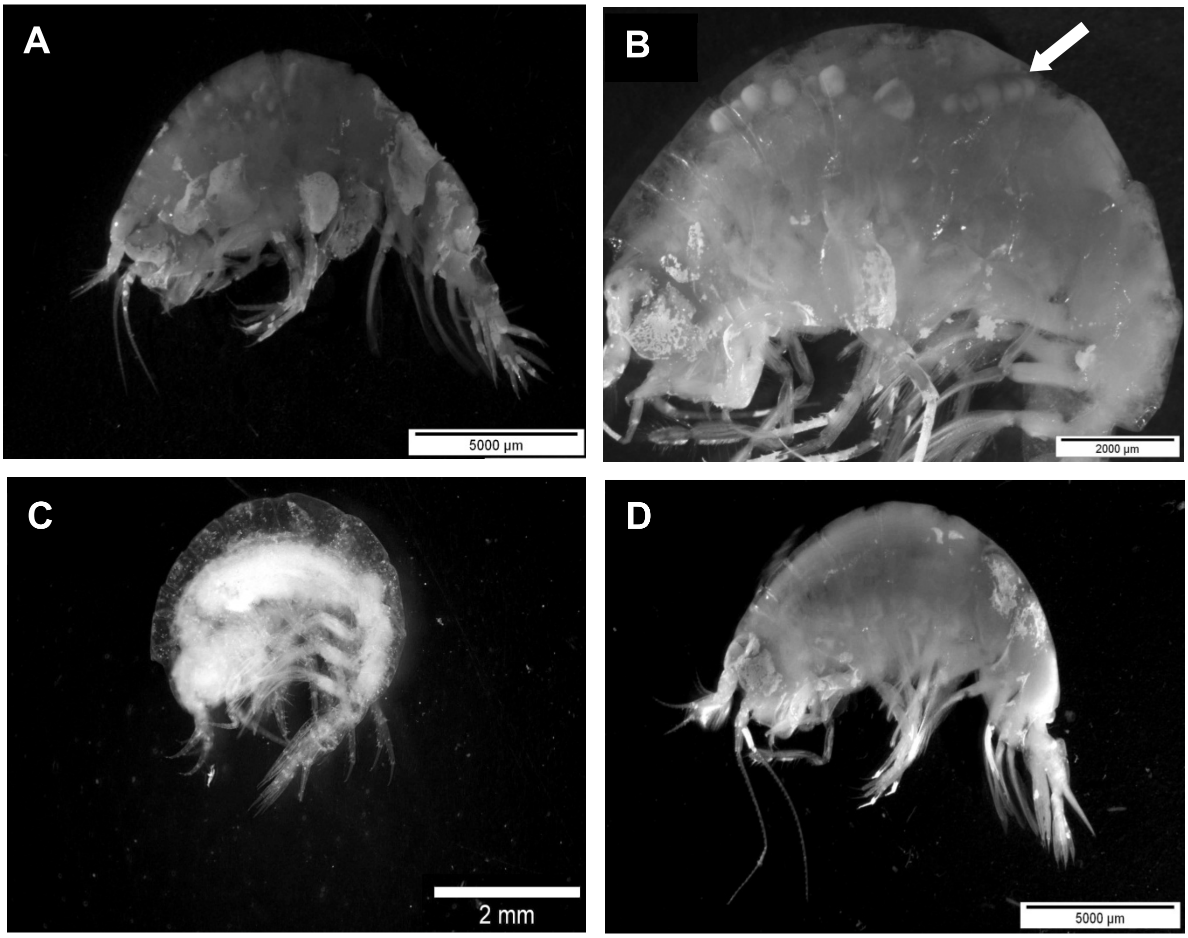

Fig. 5.6 A-D The deep-sea amphipod *Cyclocaris guilelmi* collected from sediment traps samples. A Female. B Female with developing oocytes in a dorsally located ovary. C Juvenile. D Male

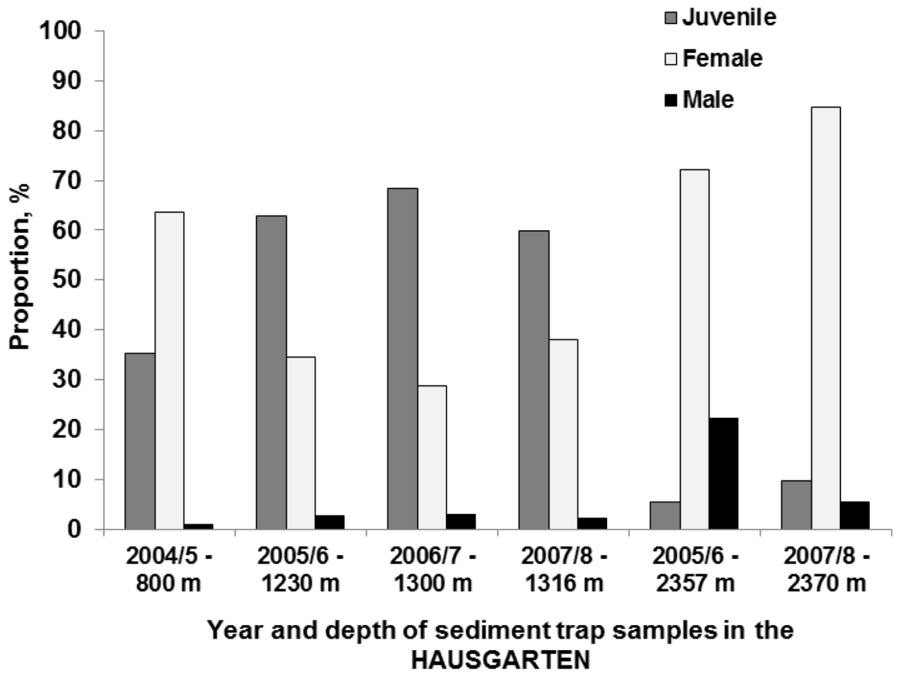

Fig. 5.7 Variation of recorded female, male and juvenile individuals of *Cyclocaris guilelmi* (in %) at the long-term deep-sea observatory HAUSGARTEN from 2004 to 2008

A detailed view of the seasonal population structure is given by the results of the statistical analysis of size groups within the length-frequency distributions of *C. guilelmi*: continuous time-series diagrams show the presence of four cohorts throughout most of the five-year sampling period in the mesopelagic and upper bathypelagic water column (Fig. 5.8). This indicated that juveniles (0+ cohort), immatures (1+ cohort) and mature individuals (2+ and 3+ cohort) were present at almost all studied time periods in the samples. Their appearance did not seem to be connected to a seasonal pattern: juveniles for example were present in all sampling months from August 2004 to June 2008 (with the exception of June 2006). The mean length (including ranges in brackets) for each detected size group was determined as follows: cohort no. 0+ = 7.4 (4.9-9.6) mm, cohort no. 1+ = 12.3 (9.4-15.9) mm, cohort no. 2+ = 17.9 (14.2-20.9) mm and cohort no. 3+ = 23.1 (18.5-27.8) mm. Most males were already fully mature when collected in the traps. Within the analyzed time-frames, mature male and female individuals of *C. guilelmi* attained a different maximum size, with the males being smaller (up to 22.8 mm) compared to their female counterparts (up to 28.5 mm).

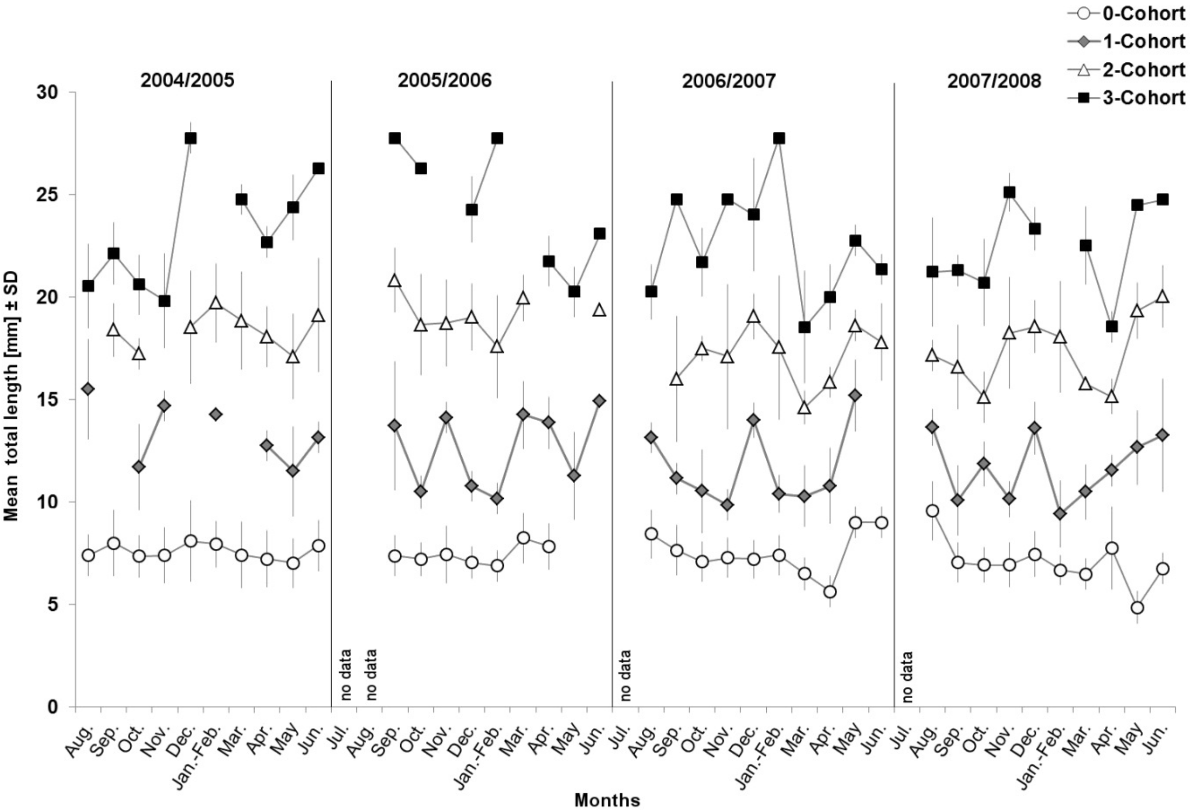

Fig. 5.8 Seasonal and interannual development of recognized cohorts of *Cyclocaris guilelmi* in mesopelagic and upper bathypelagic sediment trap samples during 2004-2008. Missing dots indicate absence of respective cohort. No data are available for July-August 2005, July 2006 or July 2007

Four cohorts were also recorded for *C. guilelmi* in the lower bathypelagic traps and showed a simultaneous appearance in the sampling months September 2005, August 2007 and October 2007 (Fig. 5.9). In the lower bathypelagic water column, females clearly dominated the population structure with only occasional occurrences of male and juvenile individuals. The mean length of each size class was 9.1 (8.2-9.7) mm for the 0+ cohort, 13.9 (12.3-15.2) mm for the 1+ cohort, 18.5 (16.5-19.8) mm for the 2+ cohort, and 23.1 (20.8-26.4) mm for the 3+ cohort. When compared to the mesopelagic and upper bathypelagic traps, the juveniles (0+ cohort) and immatures (1+ cohort) in the bathypelagic zone had a larger mean body size. Furthermore, adult specimens of *C. guilelmi* attained maximum size of 28.2 mm TBL for females and 24.5 mm TBL for males.

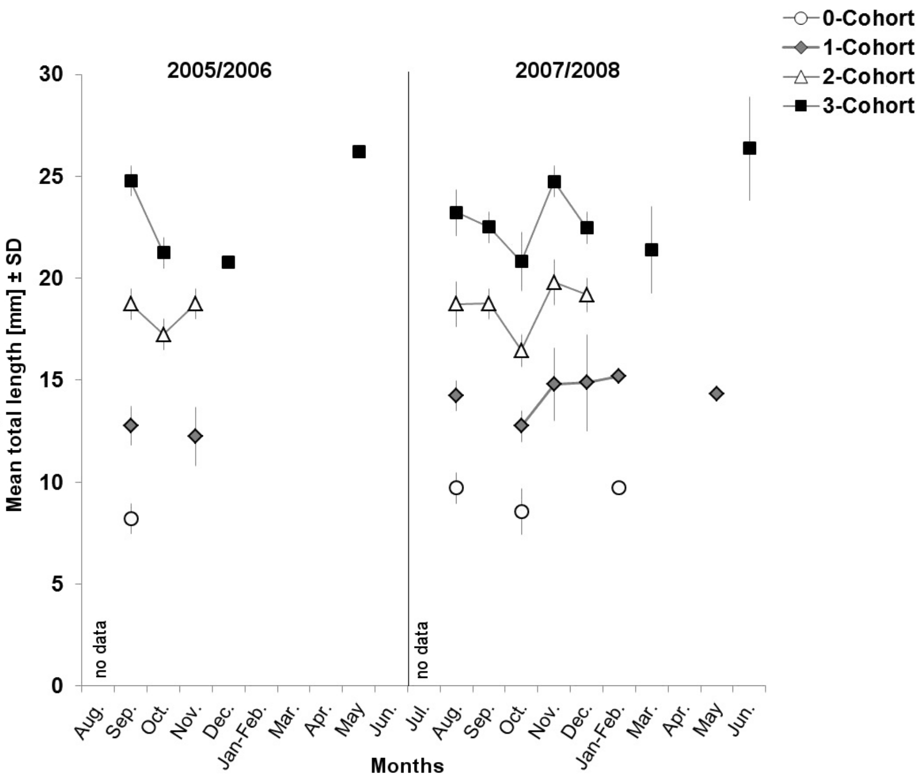

Fig. 5.9 Seasonal and interannual development of recognized cohorts of *Cyclocaris guilelmi* in lower bathypelagic sediment trap samples during 2005/2006 and 2007/2008. Missing dots indicate absence of respective cohort. No data are available for August 2005 and July 2007

Discussion

Long-term data-series for polar ecosystems are scarce and the year-round investigation of plankton communities and their respective life-cycle strategies is a challenge. In the Arctic, where little attention has been given to meso- and bathypelagic zooplankton, we show how seasonally recorded amphipod occurrences from sediment traps contribute new information on zooplankton life-cycle strategies, such as a year-round breeding behavior of the deep-water lysianassoid *Cyclocaris guilelmi*. While we are aware that the use of sediment traps does not provide a quantitative assessment of pelagic amphipod taxa, the seasonal and interannual patterns of free-swimming amphipods we observed are useful to infer general trends in their population development. We discuss these trends in more detail below, with special attention to *C. guilelmi,* the dominant amphipod species in terms of numbers and biomass.

Amphipod species in the meso- and bathypelagic zone of the Fram Strait

All nine amphipod taxa identified in the sediment traps (Table 5.2) have been previously recorded in the eastern Greenland Sea and the Fram Strait, but the lysianassoid amphipod *C. guilelmi* was clearly the dominant species in our traps (Fig. 5.2 a-b). *C. guilelmi* is sometimes mentioned in older scientific studies including references on Arctic Amphipoda (e.g., Fowler 1898; Sars 1900; Apstein and Brandt 1901; Gran 1902), but is seldom or not mentioned at all in more recent publications (Lee 1975; Hop et al. 2006; Bucklin et al. 2010; Kosobokova et al. 2011). These scarce observations of *C. guilelmi* are even more intriguing considering the fact that Gran (1902) named cold bottom layers of the Norwegian Sea the 'Cyclocaris region'. In Barnard (1959), *C. guilelmi* is regarded an Arctic deep-water form, also occurring in subarctic regions. As indicated by our results, as well as previous results of Seiler and Brandt (1997) for sediment trap samples from 1000 m in the Greenland Sea, this abundant lysianassoid amphipod may represent an important food source within the meso- and bathypelagic zones in the Fram Strait and Greenland Sea. Furthermore, *C. guilelmi* is characterized by large lipid deposits: during February 1993 in the central Arctic Ocean, Lee (1975) reported a total lipid content of 22 % dry mass (DM) for *C. guilelmi*, the highest compared to other common amphipod species (19 % DM for *T. abyssorum* and 14 % DM for *Hyperia galba*). Therefore, *C. guilelmi* may serve as a high energy food source for pelagic predators such as fish (e.g., *Reinhardtius hippoglossoides* and *Paraliparis bathybius*) (Bjelland et al. 2000) in deeper Arctic waters.

Besides *C. guilelmi*, few other amphipod species were observed: the hyperiids *Themisto abyssorum* and *T. libellula*, which are considered the most abundant amphipods in the epipelagic zone of Arctic waters, as well as the typically sympagic amphipod species *Eusirus holmii* and *Onisimus nanseni* (Bowman 1960; Holmquist 1965; Koszteyn et al. 1995; Dalpadado et al. 2001; Arndt and Beuchel 2006). Furthermore, the pan-oceanic species *Lanceola clausi* and the typical deep-water amphipods *Cyphocaris bouvieri*, *Andaniexis abyssi* and *Tryphosella* sp. were recorded in the sediment trap samples (Table 5.2).

Of the recorded species, the hyperiid *T. abyssorum* shows the largest vertical migration capacity in the Arctic region; while it is most abundant in the epipelagic waters down to 300 m in the Greenland and Norwegian Sea and in the eastern Fram Strait, it also is regularly observed in the meso- and bathypelagic water column down to 3000 m (Koszteyn et al. 1995; Vinogradov et al. 1996; Weigmann-Haass 1997; Dalpadado 2002; Kraft et al. 2011). These observations correspond well with our results. We found the highest abundance indices of *T. abyssorum* at 800 m depth and low occurrences in the upper bathypelagic zone at 1230-1316 m depth (Fig. 5.4 a-d). In the lower bathypelagic traps, the most frequent taxa beside *C. guilelmi* was *Tryphosella* sp., a well-known genus of lysianassoid amphipods which can be found from the infralittoral zone down to abyssal depths (Kilgallen et al. 2006). However, when compared to *C. guilelmi*, *Tryphosella* sp. appeared in low numbers in our study.

Overall, our observation of mesopelagic and bathypelagic free-swimming deep-sea amphipod species in the eastern Fram Strait and the Greenland Sea corresponded well with previous records on the zooplankton communities in the Fram Strait and the Norwegian Sea (Brandt 1997; Hop et al. 2006). This included a slight decrease in the number of observed amphipod species with increasing depth, a phenomenon also recorded by Dahl et al. (1976) and Brandt (1997) in the Norwegian Sea. Of the free-swimming amphipod taxa that were caught by sediment traps, only the lysianassoid *C. guilelmi* showed a distinct interannual and seasonal population pattern, which is discussed below.

Interannual and seasonal variation of occurrences of Cyclocaris guilelmi

C. guilelmi clearly dominated the amphipod composition at water depths of 800-2700 m in the HAUSGARTEN and the eastern Greenland Sea during this long-term study. Its abundance indices significantly increased from the first mooring period in 2004-2005 to the other sampling years 2005-2008. This pattern was most likely caused by differences in sampling depths of 800 and 1230-1316 m, respectively (Fig. 5.4a-d). In this context, depth-related variations in local circulation patterns could be responsible for the differences in abundance indices: at 800 m depth, the Norwegian Sea Arctic Intermediate Water is expected to be more strongly influenced by the Atlantic water masses of the WSC, which circulates in the upper water column. The resulting differences in water mass characteristics (with higher temperature and salinity at 800 m) might have caused the lower collection of *C. guilelmi* in 2004-2005. No changes in collection patterns were observed in the following years (2005-2008), which corresponds with the measured temperature at 1230-1316 m: no pattern of increase or decrease in the temperature of the Norwegian Sea Arctic Intermediate Water was recorded from August 2006 to July 2008, with values varying from -0.81 to -0.43° C. Within the Norwegian Sea Deep Water masses at a water depth of 2357-2370 m, the recorded range from August 2004 to July 2008 of water temperatures was with -0.84 to -0.77° C much smaller compared to the mesopelagic zone at 800 m. Likewise, we recorded no up- or downward trend in temperature and abundance indices during the measured time-frame at these depths.

C. guilelmi showed a distinct seasonality in its appearance, with the highest number of individuals recorded from August to February in the upper bathypelagic traps (Fig. 5.4b-d). Our results are in agreement with a previous study which also observed distinctly higher occurrence of *C. guilelmi* during winter compared to the summer months in sediment trap samples from the Greenland Sea (500-2300 m depth) (Seiler and Brandt 1997). Based on the observation of high numbers of *C. guilelmi* at 1000 m depth, the authors suggested that the species either had a patchy distribution by forming dense swarms, or was particularly attracted to sediment traps to feed. We agree with Seiler and Brandt (1997) that the seasonal pattern could be caused by a starvation-driven entering of the traps during winter. However, it remains unclear how seasonally variable food is for this carnivore species in the meso- and bathypelagic zone.

Population structure and reproduction ecology of Cyclocaris guilelmi

The dominance of juveniles in the upper bathypelagic samples (1230-1316 m) and their scarcity in the deeper bathypelagic traps (Fig. 5.7) represents an interesting finding, as it suggests an ontogenetic stratification of the population structure of *C. guilelmi* in the eastern Fram Strait. The majority of the population seems to inhabit, and as a consequence reproduce, in the upper bathypelagic zone. While migration or a permanent establishment of populations at shallower depths may occur (Fig. 5.4a), the significantly lower appearances of juveniles at 800 m points towards less favourable physical or ecological conditions for *C. guilelmi* in the lower mesopelagic zone. In the deeper bathypelagic regions (i.e., depths 2357-2370 m), an increase of hydrostatic pressure and a stronger food competition due to a higher proximity to benthic species may be two responsible factors that prohibit *C. guilelmi* from reproducing. This phenomenon of ontogenetic stratification in amphipod communities is not new, and found for example by Blankenship et al. (2006) in benthic deep-sea amphipods (*Scopelocheirus schellenbergi* and *Hirondellea dubia*) along the steep continental slopes at the Tongo and Kermadec trenches. Another explanation for the high occurrences of juveniles in the upper bathypelagic traps could be a reduced predation pressure by fish and other predatory animals, which is also considered a major driving force of the ontogenetic distribution in the deep-sea (Yamaguchi et al. 2004).

We suggest that the year-round presence of (small) juveniles infers a prolonged non-seasonal breeding of this species, possibly throughout the year. This hypothesis is supported by the year-round occurrences of four cohorts (Fig. 5.8 and 5.9) and the presence of females with developing eggs (Fig. 5.6B) at the two depth horizons. However, we observed no females with a full marsupium. The latter observation agrees with other studies which show that brooding lysianassoid deep-sea amphipods seem to actively avoid traps (e.g., Christiansen et al. 1990; Johnson et al. 2001). The sex ratios of *C. guilelmi* with female/male ratio of 50:1 to 3:1 clearly differed from the observations of other deep-sea amphipods, which include mainly benthic species, e.g. the lysianassoid *Uristes* sp. Within these amphipod populations the recorded ratio of females to males from baited traps was 1:1 (Klages et al. 2001; Blankenship et al. 2006). While a ratio of 3:1 was similar to the published data on typically epipelagic Arctic species like the genus *Themisto* (e.g., Yamada et al. 2004; Dale et al. 2006), the ratio of 50:1 as found at 800 m depth appeared particularly high (Fig. 5.7). This may support the assumption that *C. guilelmi* mainly reproduces in deeper regions. Also the implied continuous reproduction of *C. guilelmi* made the interpretation of the occurrence of annual cohorts difficult and leaves the question of a maximum life-span open.

Cyclocaris guilelmi – An important member of the pelagic ecosystem in the Fram Strait

As part of a polar pelagic community, the zooplankton composition in the Fram Strait has been reported to consist of 103 taxa, including 24 calanoid copepod species, 10 amphipod species, and 3 Euphausiacea (Hop et al. 2006). Three *Calanus* species (*C. finmarchicus, C. glacialis,* and *C. hyperboreus*) are considered key copepods, especially in the epipelagic zone. Other groups include the epipelagic amphipod species *Themisto libellula* and *T. abyssorum*, which predominantly prey on these copepods (Hop et al. 2006; Dalpadado et al. 2008; Noyon et al. 2009). In the meso- and bathypelagic zones, Fram Strait zooplankton are characterized by copepods such as *Augaptilus glacialis*, *Heterorhabdus compactus*, *Scaphocalanus brevicornis*, or the ostracods *Boroecia borealis* and *B. maxima* (Broms et al. 2004; Hop et al. 2006) as well as by the deep-water amphipod species presented in this study. While the structure of pelagic biota has been the subject of several studies in the Fram Strait (e.g., Smith 1988, 1990; Hirche et al. 1991; Hirche 1997; Auel et al. 2002) not much is known about the predator-prey relationships in the mesopelagic and bathypelagic zones of this sea passage and the Arctic basins in general (Kosobokova and Hirche 2000; Auel and Hagen 2002; Blachowiak-Samolyk et al. 2007). Søreide et al. (2003) suggested that the relative importance of predatory species in Arctic waters becomes greater during the winter months, as this is the time when herbivore and omnivore zooplankton taxa descend to depth. In Arctic pelagic waters, predatory species come mostly from two groups: amphipods and chaetognaths. In contrast to previous studies in the Fram Strait, where the dominant zooplankton predator in numbers and biomass was the chaetognath *Eukrohnia hamata* during spring and autumn (Blachowiak-Samolyk et al. 2007), scarce occurrences of chaetognaths (<0.05 ind. $m^{-2}d^{-1}$) were recorded in deep sediment traps year-round (E. Bauerfeind and E.-M. Nöthig, unpubl. data). We suggest that the relative high abundance indices and the presence of few other carnivore taxa in the meso- and bathypelagic in the sediment traps could indicate that *C. guilelmi* takes on the role of *Themisto* in the meso- and bathypelagic waters and actively preys on copepods. On the other end of the Arctic food web, *C. guilelmi* might also represent an important food source for deep-water fish species such as *Reinhardtius hippoglossoides* and *Paraliparis bathybius*, as reported in the eastern Norwegian Sea (Bjelland et al. 2000).

Conclusions

Our study on meso- and bathypelagic zooplankton at the long-term, deep-sea observatory HAUSGARTEN and in the Greenland Sea from 2004-2008 and 2000-2001, respectively, indicates that *Cyclocaris guilelmi* is an important member among the free-swimming deep-sea amphipods of the Arctic. We conclude that *C. guilelmi* undergoes a consistent long-term development during the observed time periods in both water layers, with regular seasonal peaks in occurrence from August to February. *C. guilelmi* performs a year-round reproduction, which stands in contrast to seasonally-timed broods of epipelagic amphipod species. Its population structure consists of at least four overlapping cohorts dominated by juveniles in the upper bathypelagic and females in the lower bathypelagic water column.

Acknowledgments

We greatly acknowledge the help of the Arctic-lab team including C. Lorenzen, S. Murawski and N. Knüppel for the tedious work of swimmer picking. We thank the AWI-zooplankton group of Polar Biological Oceanography for their helpful comments and support. Our thanks go also to the captain and crew of R/V *Polarstern* and R/V *Lance* for their skillful support during the work at sea and to our colleagues on board for their assistance. We also thank G. Dieckmann and K. Meyer for her valuable suggestions and proof-reading. Furthermore, we thank D. Steinberg and two anonymous reviewers for their helpful comments that greatly improved the first version of this manuscript. This work was financed by institutional funds of the AWI, Bremerhaven, and by the German Federal Ministry of Education and Research (project: 03F0629A).

References

Apstein C, Brandt KAH (1901) Nordisches Plankton: Zoologischer Teil: 3. Malacostraca. Lipsius and Tischer, Kiel, pp 589-722.

Auel H, Hagen W (2002) Mesozooplankton community structure, abundance and biomass in the central Arctic Ocean. Mar Biol 140:1013-1021.

Auel H, Harjes M, Da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25:374-383.

Arndt CE, Beuchel F (2006) Life history and population dynamics of the Arctic sympagic amphipods *Onisimus nanseni* Sars *and O. glacialis* Sars (Gammaridea: Lysianassidae). Polar Biol 29:239-248.

Barnard JL (1954) Four species of bathypelagic Gammaridea (Amphipoda) from California. Allan Hancock Foundation Occasional Paper 13:52-69.

Barnard JL (1959) Epipelagic and under-ice Amphipoda of the Central Arctic Basin. Geophys Res Papers 63:115-152.

Bauerfeind E, Nöthig E-M, Beszczynska A, Fahl K, Kaleschke L, Kreker K, Klages M, Soltwedel T, Lorenzen C, Wegner J (2009) Particle sedimentation patterns in the eastern Fram Strait during 2000-2005: Results from the Arctic long-term observatory HAUSGARTEN. Deep-Sea Res I 56:1471-1487.

Birstein Y, Vinogradov ME (1970) On the fauna of pelagic gammarids in the Kurile-Kamchatka area of the Pacific Ocean. Academy of Sciences of the USSR, Proceedings of the Shirshov Institute of Oceanology 86:419-438.

Bjelland O, Bergstad OA, Skjaeraasen JE, Meland K (2000) Trophic ecology of deep-water fishes associated with the continental slope of the eastern Norwegian Sea. Sarsia 85(2):101-117.

Blachowiak-Samolyk K, Kwasniewski S, Dmoch K, Hop H, Falk-Petersen S (2007) Trophic structure of zooplankton in the Fram Strait in spring and autumn 2003. Deep-Sea Res II 54:2716-2728.

Blankenship LE, Yayanos AA, Cadien DB, Levin LA (2006) Vertical zonation patterns of scavenging amphipods from the Hadal zone of the Tonga and Kermadec Trenches. Deep-Sea Res I 56(1):48-61.

Bloesch J, Burns NM (1980) A critical review of sedimentation trap technique. Schweizerische Zeitschrift für Hydrologie 42 (1):15-55.

Boeck A (1870) Crustacea Amphipoda borealia et arctica. Saerskilt aftrykt af Vidensk.-Selsk. Forhanlinger, 266 p.

Boeck A (1871) Die scandinaviske og arktiske Amphipoder. I. Hyperina. Christiana, pp. 76-94.

Bonnier J (1893) Les amphipodes du Boulonnais (1). Bulletin Scientifique de la France et de la Belgique 24:161-713.

Bovallius CEA (1885) On some forgotten genera among the Amphipodous Crustacea. Bihang till Kungliga Svenska Vetenskaps-Akademiens Handlingar 10(14):1-17.

Bowman TE (1960) The pelagic amphipod genus *Parathemisto* (Hyperiidea: Hyperiidae) in the North Pacific and adjacent Arctic Ocean. Proc US Acad Sci USA 112:343-392.

Brandt A (1997). Biodiversity of peracarid crustaceans (Malacostraca) from the shelf down to the deep Arctic Ocean. Biodiversity and Conservation 6:1533-1556.

Broms F, d'Udekem d'Acoz C, Hosia A, Isensee K, Macnaughton M (2004) The species composition, vertical distribution and abundance of zooplankton communities north west of Svalbard. Cruise Report, AB 320 Marine Zooplankton and Sympagic Fauna of Svalbard waters, 2004. The University Centre in Svalbard (UNIS), Longyearbyen.

Brusca GJ (1967) The ecology of pelagic Amphipoda, I. Species accounts – vertical zonation and migration of Amphipoda from the waters off Southern California. Pac Sci 21(3):382-393.

Buchanan RA, Sekerak AD (1982) Vertical distribution of zooplankton in Eastern Lancaster Sound and Western Baffin Bay, July - October 1978. Arctic 35(1):41-55.

Bucklin A, Hopcroft RR, Kosobokova KN, Nigro LM, Ortman BD, Jennings RM, Sweetman CJ (2010) DNA barcoding of Arctic Ocean holozooplankton for species identification and recognition. Deep-Sea Res II 57(1-2):40-48.

Buesseler KO, Antia AN, Chen M, Fowler SW, Gardner WD, Gustafsson O, Harada K, Michaels AF, Rutgers van der Loeff M, Sarin M, Steinberg DK, Trull T (2007). An assessment of the use of sediment traps for estimating upper ocean particle fluxes. J Mar Res 65:345-416.

Chevreux E. (1899) Sur quelques intéressantes espèces d'amphipodes provenant de la dernière campagne du yacht Princesse Alice. Bulletin de la Société Zoologique de France 24:147-152.

Christiansen B, Pfannkuche O, Thiel H (1990) Vertical distribution and population structure of the necrophageous amphipod *Eurythenes gryllus* in the West European Basin. Mar Ecol Prog Ser 66:25-45.

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial, PRIMER-E Ltd, Plymouth.

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition, PRIMER-E Ltd, Plymouth.

Dahl E, Laubier L, Sibuet M, Strömberg JO (1976) Some quantitative results on benthic communities of the deep Norwegian Sea. Astarte 5:61-79.

Dale K, Falk-Petersen S, Hop H, Fevolden SE (2006) Population dynamics and body composition of the Arctic hyperiid amphipod *Themisto libellula* in Svalbard fjords. Polar Biol 29:1063-1070.

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58:876-895.

Dalpadado P (2002) Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. Polar Biol 25:656-666.

Dalpadado P, Ellertsen B, Johannessen S (2008) Inter-specific variations in distribution, abundance and reproduction strategies of krill and amphipods in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55(20-21):2257-2265.

Dunbar MJ (1957) The determination of production in the northern seas: a study of the biology of *Themisto libellula* Mandt. Can J Zool 35:797-819.

Fowler GH (1898) Contributions to our knowledge of the plankton of the Faeroe Channel. No.VI. Description of a new mid-water tow-net. Discussion of the mid-water fauna (mesoplankton). Notes on *Doliolum tritonis* and *D. nationalis*, and on *Parathemisto abyssorum*. Proc Zool Soc Lond, pp 567-585.

Gardner WD (1999) Sediment sampling in surface waters. In: Hanson RB, Ducklow HW, Field JG (eds) The Changing Ocean Carbon Cycle: A midterm synthesis of the Joint Ocean Global Flux Study, Cambridge University Press, Cambridge, pp 240-281.

Grainger EH (1989) Vertical distribution of zooplankton in the central Arctic Ocean. In: Rey L, Alexander V (eds) Proceedings of the Sixth Conference of the Comité Arctique International 13-15 May 1985, EJ Brill, Leiden, The Netherlands, pp 48-60.

Gran HH (1902) Das Plankton des Norwegischen Nordmeeres von biologischen und hydrographischen Gesichtspunkt behandelt. Rep Norweg Fish Invest 2(5):1-222.

Hansen HJ (1887) Oversigt over de paa Dijmphna-Togtet indsamlede Krebsdyr. Dijmphna-Togtets Zoologisk-Botaniske Udbytte, Del II. Dijmphna-Togtets zoologiske udbytte, pp 183-286.

Hirche H-J, Baumann MEM, Kattner G, Gradinger R (1991) Plankton distribution and the impact of copepod grazing on primary production in Fram Strait, Greenland Sea. J Mar Sys 2:477-494.

Hirche H-J (1997) Life cycle of the copepod *Calanus hyperboreus* in the Greenland Sea. Mar Biol 128:607-618.

Hoffer SA (1972) Some aspects of the life cycle of *Parathemisto abyssorum* (Amphipoda: Hyperiidea) in the Gulf of St. Lawrence. Can J Zool 50:1175-1178.

Holmquist C (1965) The amphipod genus *Pseudalibrotus*. J Zool Systemat Evol Res 3:19-46.

Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Søreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Prog Oceanogr 71:182-231.

Johnson WS, Stevens M, Watling L (2001) Reproduction and development of marine peracaridans. Adv Mar Biol 39:105-260.

Kane JE (1963) Observations on the moulting and feeding of a hyperiid amphipod. Crustaceana 6:129-132.

Karl DM, Knauer GA (1989) Swimmers: a recapitulation of the problem and a potential solution. Oceanogr 2:32-35.

Kilgallen NM, Myers AA, McGrath D (2006) A review of the genus *Tryphosella* (Crustacea: Amphipoda) from Britain and Ireland, with the description of a new species *Tryphosella lowryi*. J Mar Biol Ass UK 86:1067-1081.

Klages M, Vopel K, Bluhm H, Brey T, Soltwedel T, Arntz WE (2001) Deep-sea food falls: first observation of a natural event in the Arctic Ocean. Polar Biol 24:292-295.

Knauer GA, Martin JH, Bruland KW (1979) Fluxes of particulate carbon, nitrogen and phosphorus in the upper water column of the northeast Pacific. Deep-Sea Res 26:97-108.

Kosobokova KN, Hanssen H, Hirche H-J, Knickmeier K (1998) Composition and distribution of zooplankton in the Laptev Sea and adjacent Nansen Basin during summer, 1993. Polar Biol 19(1):63-76.

Kosobokova K, Hirche H-J (2000) Zooplankton distribution across the Lomonosov Ridge, Arctic Ocean: species inventory, biomass and vertical structure. Deep-Sea Res I 47:2029-2060.

Kosobokova KN, Hopcroft RR, Hirche HJ (2011) Patterns of zooplankton diversity through the depths of the Arctic's central basins. Mar Biodiv 41:29-50.

Koszteyn J, Timofeev S, Weslawski JM (1995) Size structure of *Themisto abyssorum* (Boeck) and *Themisto libellula* (Mandt) populations in European Arctic Seas. Polar Biol 15:85-92.

Kraft A, Bauerfeind E, Nöthig E-M (2011) Amphipod abundance in sediment trap samples at the long-term observatory HAUSGARTEN (Fram Strait, ~79°N/4°E) - Variability in species community patterns. Mar Biodiv 41:353-364.

Kremling K, Lentz U, Zeitzschel B, Schultz-Bull DE, Duinker JC (1996) New type of time-series sediment trap for the reliable collection of inorganic and organic trace chemical substances. Rev Sci Instrum 67:4360-4363.

Larsson U, Blomqvist S, Abrahamsson B (1986) A new sediment trap system. Mar Ecol Prog Ser 31:205-207.

Lee RF (1975) Lipids of arctic zooplankton. Comp Biochem Physiol 51B:263-266.

Lee C, Hedges JI, Wakeham SG, Zhu N (1992) Effectiveness of various treatments in retarding microbial activity in sediment trap material and their effects on the collection of swimmers. Limnol Oceanogr 37:117-130.

Lichtenstein H (1822) *Parathemisto libellula*. In: Mandt MW (ed) Observationes in historiam naturalem et anatomiam comparatam in itinere Groenlandico factae. Inaug-diss Berlin, Guilelmus Mandt Beyenburgenis, 40 p.

Lowry JK, Stoddart HE (1994) Crustacea Amphipoda: Lysianassoids from the troptical western South Pacific Ocean. In: Crosnier A (ed) Résultats des Champagnes MUSORSTOM, Volume 12. Mémoires du Muséum National d'Histoire Nautrelle, Series A, Zoology 161:127-223.

Lowry JK, Stoddart HE (2011) The new deep-sea families Cebocaridae fam. nov., Cyclocaridae fam. nov. and Thoriellidae fam. nov. (Crustacea: Amphipoda: Lysianassoidea). Zootaxa 2747:53-68.

Makabe R, Hattori H, Sampei M, Ota Y, Fukuchi M, Fortier L, Sasaki H (2010) Regional and seasonal variability of zooplankton collected using sediment traps in the southeastern Beaufort Sea, Canadian Arctic. Polar Biol 33:257-270.

Manley O (1995) Branching of Atlantic Water within the Greenland-Spitsbergen Passage: an estimation of recirculation. J Geophys Res 100:20627-20634.

Mauchline J (1972) The biology of bathypelagic organisms, especially Crustacea. Deep-Sea Res 19:753-780.

Noyon M, Gasparini S, Mayzaud P (2009) Feeding of *Themisto libellula* (Amphipoda Crustacea) on natural copepods assemblages in an Arctic fjord (Kongsfjorden, Svalbard). Polar Biol 32(11):1559-1570.

Østvedt O-J (1955) Zooplankton investigations from weather ship M in the Norwegian Sea, 1948-49. Hvalr Skrift 40:1-93.

Quadfasel D, Gascard J-C, Kolermann K-P (1987) Large-scale oceanography in Fram Strait during the 1984 marginal ice zone experiment. J Geophys Res 92:6719-6728.

Sars GO (1900) The Norwegian North Polar Expedition, 1893-1896. Scientific results V. Crustacea 1-141.

Schauer U, Beszczynska-Möller A, Walczowski W, Fahrbach E, Piechura J, Hansen E (2008) Variation of Measured Heat Flow through the Fram Strait between 1997 and 2006. In Dickson RR, Meincke J, Rhines P (eds) Arctic–Subarctic Ocean Fluxes. Springer, Netherlands, pp 65-85.

Schlichtholz P, Houssais MN (2002) An inverse modeling study in Fram Strait. Part II: water mass distribution and transports. Deep-Sea Res II 46(6-7):1137-1168.

Seiler D, Brandt A (1997) Seasonal occurrence of planktic Crustacea in sediment trap samples at three depth horizons in the Greenland Sea. Polar Biol 17:337-349.

Smith SL (1988) Copepods in Fram Strait in summer: distribution, feeding and metabolism. J Mar Res 46:145-181.

Smith SL (1990) Egg production and feeding by copepods prior to the spring bloom of phytoplankton in Fram Strait, Greenland Sea. Mar Biol 106:59-69.

Søreide JE, Hop H, Falk-Petersen S, Gulliksen B, Hansen E (2003). Macrozooplankton communities and environmental variables in the Barents Sea marginal ice zone in late winter and spring. Mar Ecol Prog Ser 263:43-64.

Sparre P (1988) Computer programs for fish stock assessment (LFSA) package of basic programs for IBM computers. FAO Fisheries Technical Paper, Rome.

Stebbing TRR (1906) Amphipoda I. Gammaridea. Das Tierreich 21:1-806.

Steinberg DK, Pilskaln CH, Silver MW (1998) Contribution of zooplankton associated with detritus to sediment trap 'swimmer' carbon in Monterey Bay, California, USA. Mar Ecol Prog Ser 164:157-166.

Stephensen K (1935) The Amphipoda of N. Norway and Spitsbergen with adjacent waters. Tromso Museum Skrifter 3(1):1-140.

Thurston MH (1976a) The vertical distribution and diurnal migration of the Crustacea Amphipoda collected during the Sond Cruise, 1965. I. The Gammaridea. J Mar Biol Assoc UK 56:359-382.

Thurston MH (1976b) The vertical distribution and diurnal migration of the Crustacea Amphipoda collected during the Sond Cruise, 1965. II. The Hyperiidea and general discussion. J Mar Biol Assoc UK 56:383-470.

Tencati JR (1970) Amphipods of the central Arctic. In Leung YM, Kobayashi HA (eds) Taxonomic guides to Arctic zooplankton (I), Tech. Rep. 2. University of Southern California, Department of Biological Sciences, pp 3-37.

Vinogradov ME, Volkov AF, Semenova TN (1996) Hyperiid amphipods (Amphipoda, Hyperidea) of the world oceans. Science Publishers Inc., Lebanon, USA, 632 p.

Wassmann P (1998) Retention versus export food chains: processes controlling sinking loss from marine pelagic systems. Hydrobiologia 363:29-57.

Weigmann-Haass R (1997) Verbreitung von Makrozooplankton in der Grönlandsee im Spätherbst 1988 (Crustacea: Ostracoda, Hyperiidea [Amphipoda], Euphausiacea). Helgolander Meeresun 51:69-82.

Willis KJ, Cottier FR, Kwasniewski S (2008) Impact of warm water advection on the winter zooplankton community in an Arctic fjord. Polar Biol 31:475-481.

Yamada Y, Ikeda T, Tsuda A (2004) Comparative life-history study on sympatric hyperiid amphipods (*Themisto pacifica* and *T. japonica*) in the Oyashio region, western North Pacific. Mar Biol 145(3):515-527.

Yamaguchi A, Ikeda T, Watanabe Y, Ishizaka J (2004) Vertical distribution patterns of pelagic copepods as viewed from the predation pressure hypothesis. Zool Stud 43:475-485.

PUBLICATION IV

Lipids in Arctic pelagic amphipods – A comparison between summer and winter: do seasons matter?

Angelina Kraft[a]*, Martin Graeve[a], Dieter Janssen[a], Stig Falk-Petersen[b,c]

[a]Alfred Wegener Institute for Polar and Marine Research
Am Handelshafen 12,
27570 Bremerhaven, Germany
* Contact information:
E-mail: Angelina.Kraft@awi.de
Phone: + 49-471-48311085
Fax: + 49-471-48311149

[b]Norwegian Polar Institute
Fram Centre
N-9296 Tromsø, Norway

[c]Department of Arctic and Marine Biology
Faculty of Biosciences, Fisheries and Economics
University of Tromsø
N-9037 Tromsø, Norway

Submitted to Canadian Journal of Fisheries and Aquatic Sciences,

12. November 2012

Abstract

Polar regions are characterized by a strong seasonality in primary production and distinct fluctuations in food supply. The storage of food in form of lipids is expected to follow a seasonal pattern, however, year-round observations are lacking. We investigate seasonal variations of lipid classes and fatty acid compositions of four pelagic amphipods collected during summer, fall and winter expeditions to the Fram Strait and Svalbard archipelago (78° to 81°N). Our results showed a year-round dominance of wax esters and triacylglycerols over phospholipids for *Themisto abyssorum*, *T. libellula*, *T. compressa* and *Cyclocaris guilelmi*. High levels of the *Calanus*-markers 20:1 and 22:1 (both isomers) in all seasons indicated that all four species are part of the *Calanus*-based food web. Tracers of diatoms (16:1(n-7) and 20:5(n-3)), ice-algae (16:4(n-1)) and dinoflagellates (22:6(n-3)) indicated that the lipid-based energy transfer could be traced back to the respective algal sources. We highlighted that the lipid reservoir of these amphipods and their biochemical modifications seemed to buffer seasonal variations in available prey, and allow an active, predatory life-style year-round in Arctic waters.

Keywords: Lipids • Polar Regions • Trophic Relationships • Amphipods • Zooplankton

Introduction

For a long time the analysis of lipid compositions has been used to address food web relationships in marine ecosystems and for studying the life-cycle strategy of Arctic pelagic animals. Specific dietary components such as characteristic fatty acids are used to trace the energy transfer from primary producers to higher trophic levels, as they are believed to be incorporated, largely unmodified, into the lipid pool of the consumer (e.g., Sargent et al. 1976; Graeve et al. 1994a; Budge et al. 2002; Dalsgaard et al. 2003; Falk-Petersen et al. 2004; Lee et al. 2006). With seasonality being a crucial feature in structuring plankton communities, the investigation of temporal influences in the lipid-based energy flux at high latitudes is of fundamental importance (e.g., Falk-Petersen et al. 2000, 2007; Leu et al. 2006). In this context the dominance of biomarkers within the lipid class and fatty acid compositions can relay trophic information over a time scale of several weeks to months (Graeve et al. 1994a, 2005). Thus, this technique is considered to produce a prolonged understanding of trophic structure within pelagic ecosystems and stands in contrast to snapshot insights provided by the classical approaches such as gut content analysis (e.g., Stübing et al. 2003).

Pelagic zooplankton represent an extensively studied group with regard to their lipid- and biochemical composition (e.g., Graeve et al. 1994a; Falk-Petersen et al. 1999; Lee et al. 2006; Mayzaud et al. 2007). Especially the accumulation and role of lipids in the life-cycle of calanoid copepods and krill, which have been well documented in polar waters (Sargent and Henderson 1986; Quetin and Ross 1991; Hagen et al. 1996; Falk-Petersen et al. 2000, 2009; Pond and Tarling 2011). As a consequence, lipid-rich herbivorous zooplankton are exploited as a major energy source by higher trophic levels. The hyperiid amphipods of the genus *Themisto* are pelagic predators in the Arctic food web and form a link between herbivorous mesozooplankton (mainly calanoid copepods) and higher trophic levels (including planktivorous fish, seabirds and marine mammals) (Bradstreet and Cross 1982; Lønne and Gulliksen 1989; Dalpadado et al. 2000, 2001, 2008; Hobson et al. 2002; Dalpadado and Bogstad 2004; Noyon et al. 2009; Wold et al. 2011). Three species comprise the genus *Themisto* in northern latitudes: *T. libellula* (a typical large Arctic species associated to cold, polar water masses), its sub-arctic congener *T. abyssorum*, which is transported to the Arctic by inflowing North Atlantic water masses and *T. compressa*, a typical North Atlantic species with its major distribution area in the southern Norwegian Sea (Kraft et al. 2011). The ecology of the first two has been studied over the past decade with regard to their food sources, variations in distribution, reproduction strategies, abundances and summer lipid compositions (Bousfield 1951; Percy 1993; Koszteyn et al. 1995; Scott et al. 1999; Auel et al. 2002; Dale et al. 2006, Dalpadado et al. 2008; Marion et al. 2008; Noyon et al. 2009, 2011, 2012; Kraft et al. 2011, 2012a, 2012b).

Detailed investigations of the lipid class compositions of *T. abyssorum* and *T. libellula* during Arctic summer in the Fram Strait, Svalbard Fjords and central Arctic Ocean, indicated that dominant lipid classes in both species consisted of wax esters and triacylglycerols (Auel et al. 2002; Dale et al. 2006; Noyon et al. 2011). These lipid classes also represent the major energy storage in most Arctic calanoid copepods (Conover 1988; Lee et al. 2006; Falk-Petersen et al. 2009). While most studies highlighted the importance of winter investigations on lipid reserves (as they were suggested to play an essential role in the reproduction of hyperiid amphipods, Noyon et al. (2011)), to our knowledge a respective investigation of seasonal differences of lipid dynamics and feeding ecology has been missing so far.

The aim of this study was to investigate the seasonal lipid dynamics and feeding ecology of pelagic amphipods commonly found in the Fram Strait and Svalbard waters. We elucidate on feeding strategies of three epipelagic and one deep-water species associated with different water masses and depth zones. Specimens from different seasons (summer, fall and winter) were analyzed for their lipid class composition, fatty acid composition and gut content. This combination of seasonal information is expected to provide a conclusive understanding on seasonality in lipid composition and its effects on life strategy of these free-swimming predators.

Material and methods

Study area

Sampling sites were located around the archipelago of Svalbard and in the northern Fram Strait. Both areas are characterized as transition zones between Atlantic and Arctic water masses (Fig. 6.1). The Fram Strait, a sea-passage with a mean depth of ~ 2600 m, located west of Svalbard, represents the only deep connection between the central Arctic Ocean and its surrounding seas. Already the early pioneers in physical oceanography recognized the complex oceanographic features of this area, featuring the meridional hydrographic fronts of the cold polar current, on the Greenland side, and the warm Atlantic current, west of Svalbard (Helland-Hansen and Nansen 1909).

Characterized by a voluminous exchange between intermediate and deep oceanic water masses, the main current systems in this area are represented by the northward flowing West Spitsbergen Current (WSC), located over the upper shelf slope in the eastern Fram Strait, and the southward flowing East Greenland Current (EGC), with a core over the western shelf slope (Quadfasel et al. 1987; Schauer et al. 2008). While the WSC transports relatively warm Atlantic waters into the Arctic Ocean Boundary Current (Quadfasel et al. 1987; Manley 1995), the EGC in the west exports colder and less-saline Arctic waters out of the Arctic basins. In the northern Fram Strait, a complex bathymetry leads to a split of the WSC into three branches: one enters the central Arctic Ocean north of Svalbard, the second continues north- and farther eastward around the rim of the Yermak Plateau and the third recirculates to the west as the Return Atlantic Current directly in the strait or shortly north of it (Gascard et al. 1995; Schauer et al. 2008). In addition, transition zones with mixed water masses are formed along the WSC and EGC current systems (Piechura 2004). Below the relatively warm Atlantic water layer, low-temperature waters prevail, namely the Arctic Intermediate Water and Norwegian Sea Deep Water, the latter modified by Polar origin deep water masses (Schlichtholz and Houssais 2002). On the western and northern coast of the Svalbard Archipelago sampling sites are mainly influenced by the inflowing Atlantic water masses (Nilsen et al. 2008) and the eastward turning branch of the WSC, along the continental slope North-west of Svalbard, keeps these areas mostly ice-free during winter time (Rudels et al.

1999). Farther to the east broad, shallow fjords are located the northern coast of Nordaustlandet and are dominated by colder Arctic water masses (Fig. 6.1).

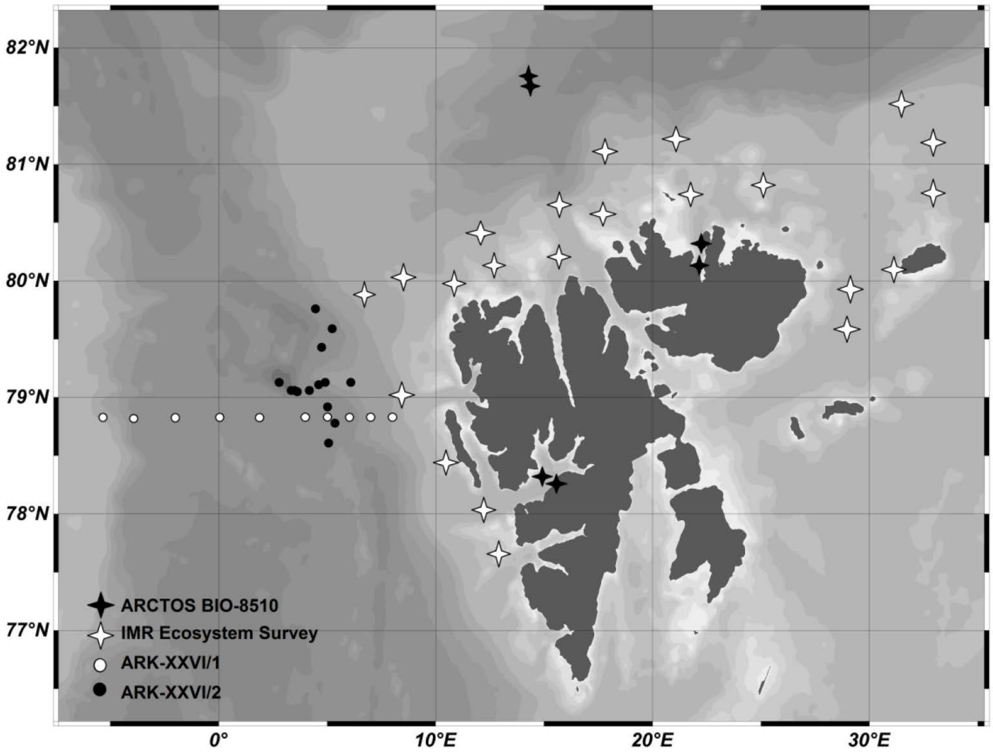

Fig. 6.1 Map of sampling stations in the eastern and across the central Fram Strait and around Svalbard, Arctic Ocean. Black stars: stations during the ARCTOS-BIO winter cruise in January 2012; white stars: stations during the IMR Ecosystem Survey cruise in August 2011; black circles: stations during the ARK-XXVI/2 expedition to the long-term observatory HAUSGARTEN in July and August 2011 the eastern Fram Strait; white stars: sampling stations on a 78°50’ N transect across the central Fram Strait (ARK-XXVI/1) in June and July 2011

Net sampling

Pelagic amphipods were sampled during four cruises at a total of 53 stations in the coastal waters of Svalbard and across the Fram Strait (Table 6.1). Summer samples were taken during the R/V *Polarstern* expeditions ARK-XXVI/1+2 during June, July and August 2011 in the northern Fram Strait. Sampling took place from the surface to 2000 m water depth at 24 stations along a 78°50’ N transect and at the long-term observatory HAUSGARTEN (Fig. 6.1). For sample collection, a large multinet (HYDRO-BIOS type Maxi with an aperture of 0.5m^2 and nine 1000 micron net bags) was hoisted at 0.8 m/s with stops at 1500 m, 1000 m, 800 m, 600 m, 400 m, 200 m, 100 m and 50 m. At shallower stations, the sampling depth was adapted accordingly. The volume of water filtered in each stratum varied from 344 to 1449 m^3. Additionally, large, fully mature specimens of *T. libellula* were caught in August 2011 around Spitsbergen on the R/V *Helmer Hanssen* during the ‘IMR Ecosystem survey’ cruise with a pelagic fish trawl, containing an aperture of 9 m and 10 mm mesh. Winter samples of *Themisto* and the deep-water amphipod *Cyclocaris guilelmi* were obtained during the ARCTOS "Polar night" research cruise with R/V *Helmer Hanssen* at six sampling sites located around Svalbard (Rijpfjorden, Sofiadjupet, and Isfjorden) in January 2012. During the winter cruise, sampling took place with a Methot Isaac Kidd (MIK; 3.14 m² opening and 1.5 mm mesh size) by trawling the net for 10 min with a speed of ~1.5 knots at three different depth intervals (20, 75 and 225 m in Rijpfjorden and 30, 60 and 225 m in Isfjorden). Due to ice cover, no MIK tow was possible at Sofiadjupet. Instead, samples were collected with a vertically hauled WP3 net (1 m², 1.0 mm mesh size, at 600-2000 m).

All collected material was immediately transferred into buckets with cold seawater and brought to a cooling container or cold room (4° C). All amphipods were sorted, determined to species level, counted and measured for their total body length (accuracy 1.0 mm, from the front of the head to the tip of the longest uropod (Dunbar 1957)). Maturity was determined by the examination of secondary sexual characters: female individuals were identified by the presence of oostegites among the inner coax margin of the anterior walking legs; males were identified by the presence of testes on the ventral side of the last segment of the thorax and a segmented, elongated second antenna (Dalpadado et al. 2008). Small individuals without recognizable sexual features were recorded as juveniles. Following identification, the specimens were quickly rinsed with Milli-Q water and deep-frozen alive at -80° C for lipid and gut content analyses.

Table 6.1 Station and sampling information during four research cruises to the Fram Strait and Svalbard in summer 2011 (ARK-XXVI/1, ARK-XXVI/2), fall 2011 (IMR Ecosystem Survey) and winter 2012 (ARCTOS BIO-8510)

Cruise	ARCTOS BIO-8510	IMR Ecosystem Survey	ARK-XXVI/1	ARK-XXVI/2
Number of stations	6	22	10	15
Month / Year	1 / 2012	8 / 2011	6 & 7 / 2011	7 & 8 / 2012
Bottom depth (m)	87-2417	80-850	685-2736	1284-5578
Sampling depth (m)	0-1200	0-100	0-2000	0-2000
Gear	MIK-net 1500 µm	Pelagic fish trawl 10000 µm	Multinet 1000 µm	Multinet 1000 µm

Analyses of dry mass, lipids and gut content

For the determination of dry mass (DM) and length-frequency, specimens of *Themisto abyssorum* (summer: n = 118, winter: n = 30), *T. libellula* (summer: n = 50, fall: n = 39, winter: n = 13), *T. compressa* (summer: n = 9, winter: n = 2) and *Cyclocaris guilelmi* (summer: n = 47, winter: n = 5) were lyophilized for 24 h and their weight determined on a

Satorius microbalance (Satorius micro 4504 MP8; accuracy 0.01 mg). Lipid classes and fatty acids were analyzed for a total of 52 individuals, including the species *Themisto abyssorum* (n = 12), *T. compressa* (n = 10), *T. libellula* (n = 21) and *Cyclocaris guillelmi* (n = 9). Analyzed specimens included adult female and male individuals that originated from water depths of 0 to 2000 m.

For lipid and fatty acid analyses, total lipids were extracted after Folch et al. (1957) three times with 3 mL dichloromethane:methanol (2:1, v/v) from single, lyophilized and homogenized individuals using a Potter homogenizer (Braun, Melsungen, Germany). The solvent was washed with 2 mL 0.88 % KCl solution before the mixture was centrifuged at low speed (2000 rpm). The lipid containing organic phase was separated and evaporated under nitrogen. The lipid extract was re-dissolved in dichloromethane and taken for analysis. All extracts were kept at -20° C for further analysis. The lipid classes were separated and identified according to Graeve and Janssen (2009) on a monolithic silica column (Chromolith®Performance-Si) using high performance liquid chromatography (HPLC, LaChromElite HPLC system) with an evaporative light scattering detector (ELSD). Total lipid content in terms of percent dry mass was calculated using the sum of neutral and polar lipids according to Lu et al. (2008).

For the gas-liquid chromatographic analyses of the fatty acids and fatty alcohols, aliquots of the total lipid extract were taken. Methyl esters of fatty acids were prepared by transesterification under nitrogen atmosphere with 3% concentrated sulfuric acid in methanol for 4 h at 80° C. The resulting fatty acid methyl esters and free fatty alcohols were extracted with hexane and their composition determined with a Hewlett Packard 6890 gas liquid chromatograph on a 30 m wall-coated capillary column (i.d. 0.25 mm, film thickness: 0.25 µm; liquid phase DB-FFAP) using temperature programming according to Kattner and Fricke (1986). Fatty acids and alcohols were quantified with an internal nonadecanoic acid methylester standard (FAME, Sigma-Aldrich, USA) and identified by comparing the retention time with those of standard mixtures. Based on fatty acid compositions, four biomarker ratios were calculated. These included the ratio of PUFA/SFA (polyunsaturated versus saturated fatty acids) and the quotient of the fatty acid isomers 18:1(n-9)/18:1(n-7). Both are used as relative indicators of carnivory in marine zooplankton (e.g., Graeve et al. 1997; Falk-Petersen et al. 2000; Nelson et al. 2001; Auel et al. 2002, Legezynska et al. 2012). To further differentiate between a diatom- and a flagellate-based diet composition, the ratios of EPA/DHA (eicosapentaenoic versus docosahexaenoic acid, 20:5(n-3)/22:6(n-3)) and 16:1(n-7)/16:0 were calculated (Graeve et al. 1994a; Nelson et al. 2001; Auel et al. 2002).

Routines from multivariate statistics using the PRIMER v6 software package (Clarke and Warwick 2001; Clarke and Gorley 2006) were applied to assess differences in lipid class composition between the different species (including the respective stages) and seasons. The data were left untransformed (Howell et al. 2003) and converted into similarity matrices using Euclidian distances as the metric. Similarity patterns in the data were visualized using a principal component analysis (PCA). Only results revealing a specific seasonal or stage related pattern in terms of lipid class distribution were shown in a PCA diagram.

For the assessment of their diet, the stomach and gut of *T. abyssorum* (n = 43), *T. libellula* (n = 40) and *C. guilelmi* (n = 18) were carefully removed and placed in a solution of glycerin in water. Their degrees of fullness were classified into four categories: empty, <25 % full, 25-50 % full, 51-75 % full and 76-100 % full according to Nakagawa et al. (2000) and Dalpadado et al. (2008). The prey items were examined under an inverted microscope (Zeiss IM40, magnification 60-400) with the image analysis system AxioVision40 V4.7.1 (Carl Zeiss Imaging Solution GmbH) and grouped into the following categories: Copepoda, Amphipoda, Chaetognata, Euphausiacea (all fragments or mandibles), dinoflagellates (whole), fecal pellets / digested green (fragments), eggs (whole, full or empty), the parasite *Ganymedes themistos* (Prokopowicz et al. 2010) and unidentified items. We identified the present copepod mandibles to the species level following the results of Karlson and Båmstedt (1994) and Dalpadado et al. (2008).

Results

Dry mass, length-frequency and gut content analysis

Biometric measurements were taken of different stages (females, males and juveniles) of the pelagic amphipods *Themisto abyssorum*, *T. compressa*, *T. libellula* and *Cyclocaris guilelmi*. We found a similar mean total body length and dry mass of *T. abyssorum* females and males during all seasons. Juvenile individuals were smaller in summer samples than in winter. Large adult specimens of *T. libellula* were sampled in fall. They contained a high dry mass and total lipid content (mean 23.5 %). *T. libellula* juveniles were only observed in summer (Table 6.2). No evidence of size reduction during the winter season was found among the investigated species. The mean total body length and dry weight of the North-Atlantic species *T. compressa* was similar during seasons. Male individuals of this species were larger and heavier than females. We found the same phenomenon to be the case in populations of the deep-water amphipod *C. guilelmi*, with the occurrence of large male individuals during summer and winter (Table 6.2, Fig. 6.2 a-d).

Table 6.2 Allometric characteristics of the four pelagic amphipod species *Themisto abyssorum*, *T. libellula*, *T. compressa* and *Cyclocaris guilelmi* sampled during summer 2011 (ARK-XXVI/1+2), fall 2011 (IMR Ecosystem Survey) and winter 2012 (ARCTOS BIO-8510) research cruises to the Fram Strait and Svalbard

Species	Stage	*n*	Total body length (mm ± SD)	Dry mass (mg ±SD)	Allometric relationships
Themisto abyssorum					
ARK-XXVI/1+2					
Summer	Juvenile	62	4.1 ±1.8	0.7 ±0.7	$DM = 0.0455L^{1.92}$ $r^2 = 0.9385$
	Female	40	14.9 ±2.6	9.5 ±4.2	
	Male	16	14.3 ±1.5	7.9 ±1.7	
ARCTOS Winter	Juvenile	6	7.2 ±1.1	3.0 ±1.0	$DM = 0.1093L^{1.67}$ $r^2 = 0.8758$
	Female	14	13.2 ±2.1	8.3 ±2.6	
	Male	10	13.5 ±1.7	8.6 ±1.6	
Themisto libellula					
ARK-XXVI/1+2					
Summer	Juvenile	32	7.3 ±1.6	1.3 ±0.9	$DM = 0.0056L^{2.65}$ $r^2=0.9358$
	Female	18	17.8 ±4.2	13.2 ±10.2	
	Male	-	-	-	
IMR Fall	Juvenile	-	-	-	$DM = 0.0028L^{2.99}$ $r^2 = 0.9546$
	Female	20	26.4 ±11.8	84.1 ±78.0	
	Male	19	26.9 ±8.2	70.2 ±54.6	
ARCTOS Winter	Juvenile	-	-	-	$DM = 0.00004L^{4.11}$ $r^2 = 0.7462$
	Female	6	29.8 ±3.9	51.3 ±24.3	
	Male	7	26.1 ±4.7	33.1 ±22.4	
Themisto compressa					
ARK-XXVI/1+2					
Summer	Juvenile	3	6.0 ±1.6	0.9 ±0.4	$DM = 0.0224L^{2.11}$ $r^2 = 0.9441$
	Female	3	12.0 ±0.8	5.0 ±0.6	
	Male	3	16.7 ±1.3	8.5 ±2.3	
ARCTOS Winter	Juvenile	-	-	-	-
	Female	1	13.0	5.1	
	Male	1	14.0	6.4	
Cyclocaris guilelmi					
ARK-XXVI/1+2					
Summer	Juvenile	25	5.6 ±1.3	0.9 ±0.7	$DM = 0.0068L^{2.72}$ $r^2 = 0.9206$
	Female	19	13.3 ±3.1	9.4 ±6.6	
	Male	3	17.0 ±0.8	16.0 ±2.7	
ARCTOS Winter	Juvenile	-	-	-	$DM = 0.0301L^{2.29}$ $r^2 = 0.8955$
	Female	4	11.5 ±0.9	8.1 ±1.4	
	Male	1	17.0	20.5	

Note: The sample sizes (*n*), total body length (mm ± standard deviation (SD)), dry mass (DM) (mg ± SD), and allometric relationships between total body length (L) and DM are reported, as are the regression coefficients (r^2). Dash (-) indicates that no individuals were sampled during the respective expedition

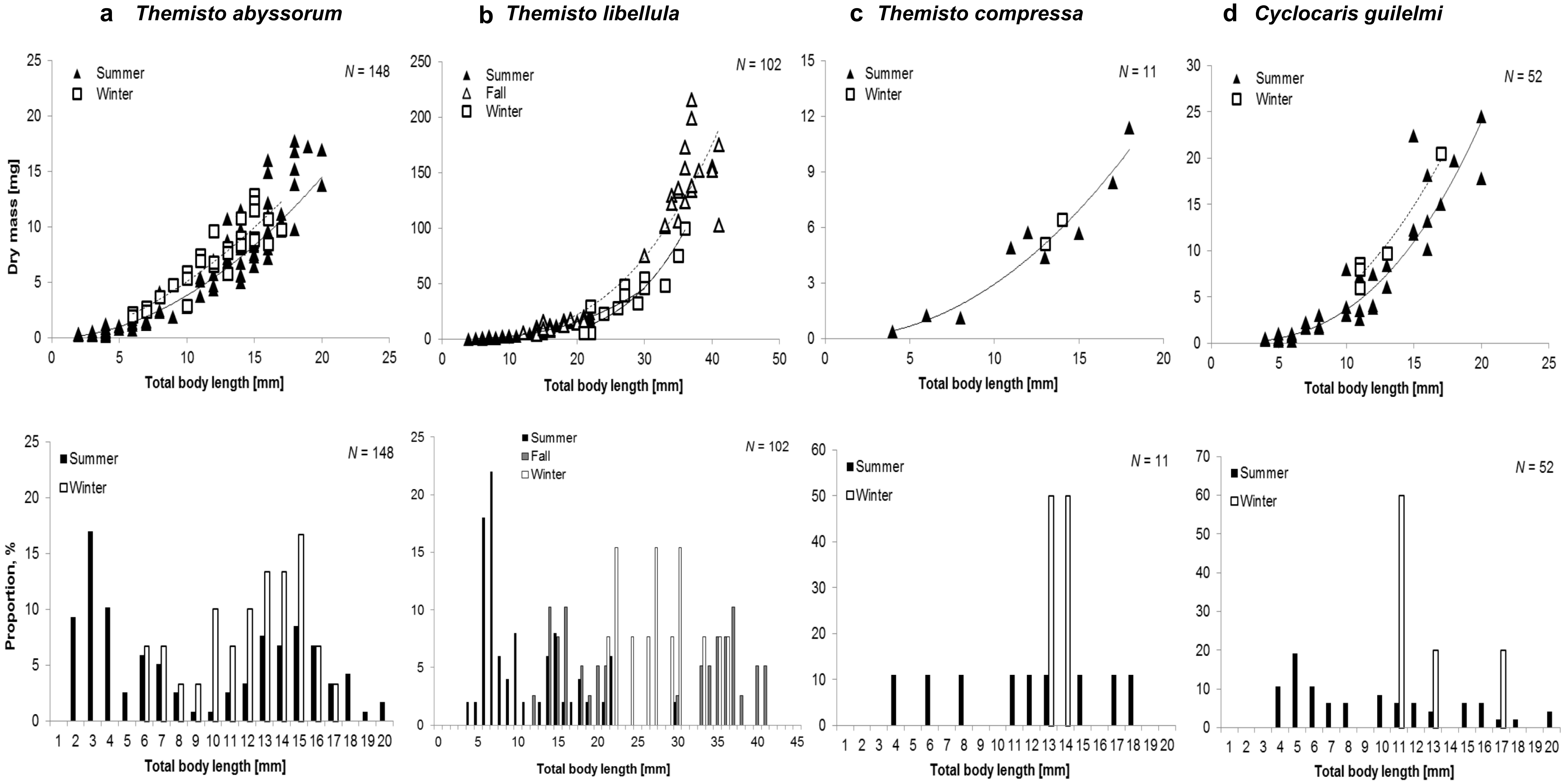

Fig. 6.2 a-d Allometric relationships between dry mass DM (mg) and total body length (mm) and the respective length-frequency distribution (proportion, %) of *Themisto abyssorum* (**a**), *T. libellula* (**b**), *T. compressa* (**c**) and *Cyclocaris guilelmi* (**d**) collected during four research cruises to the Fram Strait and Svalbard in summer 2011 (ARK-XXVI/1, ARK-XXVI/2), fall 2011 (IMR Ecosystem Survey) and winter 2012 (ARCTOS BIO-8510)

Forty-one out of forty-three analyzed specimens of *T. abyssorum* possessed a full or partly filled stomach and gut. The degree of gut fullness of most specimens ranged between 25-75 %. Abundant prey items were copepod residues (Table 6.3) in the form of mandibles, antennae, fragments of prosomes and other body parts in various stages of digestion. Examination of the mandibles showed that *Calanus hyperboreus* was the main prey species of *T. abyssorum* during the summer in the northern Fram Strait. Other identified copepod mandibles belonged to the species *Metridia longa* and *Paraeuchaeta norvegica*. Other food components included fecal pellets, eggs and a gregarine parasite. The parasite was identified as *Ganymedes* sp. (Table 6.3). The stages of digestion varied from moderately digested material with good recognizable features, e.g., the prosomes of calanoid copepods, to heavily digested material consisting of fecal pellets.

Calanoid copepods also were the most abundant prey items of *T. libellula* in the northern Fram Strait, and included the species *Calanus hyperboreus*, *Calanus glacialis* and *P. norwegica*. Additional abundant items included fecal pellets and the gregarine *Ganymedes* sp., probably *G. themistos*. Varying stages of digestion of the diet were observed. During fall, digested material and fecal pellets had a higher contribution (30.6 %) in the diet of *T. libellua*. As with the summer samples, remains of calanoid copepods constituted most of the stomach and gut content, including mandibles of the species *C. finmarchicus* and *C. glacialis*. Both *Themisto* species had small amounts of amphipod fragments in their guts, providing evidence of cannibalism. Because of the limited total sampling size of *T. compressa* (n = 11, Table 6.2), no stomach and gut content analysis was done for this species.

The stomach and gut content of the deep-water amphipod *C. guilelmi* was characterized by the dominance of copepod residues. Furthermore, mandibles of *C. hyperboreus* and unidentified fragments and mandibles of meso- and bathypelagic copepods were occasionally observed. Other prey items consisted of digested material, fecal pellets, and residues of amphipods and euphausiids. The euphausiids were exclusively found within the gut of *C. guilelmi* (Table 6.3).

Table 6.3 Diet composition (% contribution of prey by numbers) for the four pelagic amphipod species *Themisto abyssorum*, *T. libellula* and *Cyclocaris guilelmi* sampled during summer 2011 (ARK-XXVI/1+2) and fall 2011 (IMR Ecosystem Survey) research cruises to the Fram Strait and Svalbard

	ARK-XXVI/1+2 *T. abyssorum* (*n* = 43; *L* = 11.8)	*T. libellula* (*n* = 20; *L* = 24.2)	*C. guilelmi* (*n* = 18; *L* = 10.4)	IMR Ecosystem Survey *T. libellula* (*n* = 20; *L* = 21.3)
Prey item				
Copepoda (fragments)	63.6	69.7	66.1	50.5
Amphipoda (fragments)	0.3	1.1	2.2	1.2
Chaetognata (fragments)	-	0.2	-	-
Euphausiacea (fragements)	-	-	5.0	-
Dinoflagellates (whole)	<0.1	<0.1	-	2.0
Fecal pellets/digested green (fragments)	26.7	17.1	18.5	30.6
Eggs, full and empty (whole)	2.6	4.2	-	-
Ganymedes sp. (whole)	2.1	-	-	-
Unidentified (fragments)	4.4	7.5	8.2	15.7
Mean gut volume / content (mm^3)	0.7	1.3	0.9	1.1

Note: The sample sizes (*n*),and mean total body length (*L*) are reported. Dash (-) indicates that no evidence of the respective taxon was found in the stomach and gut content

Total lipid and lipid classes

The mean percentages of the seasonal total lipid content in the dry mass ranged from modest 8.0-13.3 % in *T. abyssorum*, 6.9-29.0 % in *T. compressa* and 7.9-23.5 % in *T. libellula* to a substantial 27.2-27.6 % in *C. guilelmi*. High standard deviations (Table 6.4) expressed a wide variation of the individual total lipid content of the investigated amphipods, with ranges of 4.3-22.0, 2.8-46.8, 2.8-46.8 and 7.3-48.4 %, respectively. While no differences in the share of total lipids in summer and winter samples of *C. guilelmi* were observed, *T. libellula* showed its highest content in fall (23.5 %). In contrast, the other *Themisto* species were richer in lipids during the winter period, with a mean total lipid content of 13.3 % for *T. abyssorum* and 29.0 % of *T. compressa* (Table 6.4).

The lipid class and fatty acid compositions of total lipid extracts, triacylglycerols and phospholipids showed large overlaps but also distinct species- and seasonal-dependent differences. Wax esters comprised the major lipid class in summer and winter samples of *T. libellula* (mean 50.5-76.7 %) and *C. guilelmi* (mean 60.4-84.0 %), as well as in summer samples of *T. compressa* (mean 46.1%). Triacylglycerols were the second most abundant lipid component in these three species. In *T. abyssorum*, triacylglycerols even represented the most prominent lipid class (mean 39.0-59.8 %) during both summer and winter. Polar lipids including the membrane components phosphatidylethanolamine and phosphatidylcholine accounted for the third most abundant lipid class (mean 2.2-12.2 %, with the highest values found in winter samples of *T. libellula*), followed by free fatty acids (mean 1.0-10.2 %) and cholesterol (0.2-3.8 %). The cell membrane component phosphatidylcholine dominated the polar lipid composition in all species, with high proportions in summer samples of *T. abyssorum* (mean 10.7 %) and winter samples of *T. libellula* (mean 9.9 %). The ratio phosphatidylethanolamine versus phosphatidylcholine was similar in all four species and seasons, with a mean range from 0.1 to 0.3 (Table 6.4).

The multivariate analysis of the lipid class composition revealed a clear season and-stage related biochemical gradient in the preference of storage lipids (wax esters vs. triacylglycerols) only within the typical Arctic amphipod *T. libellula*. The first principal component (PC1) accounted for 70.7 % of the total variation, with positive displacements caused by wax esters and negative displacements caused by higher shares of triacylglycerols. Using the suite of displayed lipid classes, it became apparent that sex specific differences in lipid composition exist in winter, with a preferred storage of triacylglycerols in *T. libellula* females (Fig. 6.3).

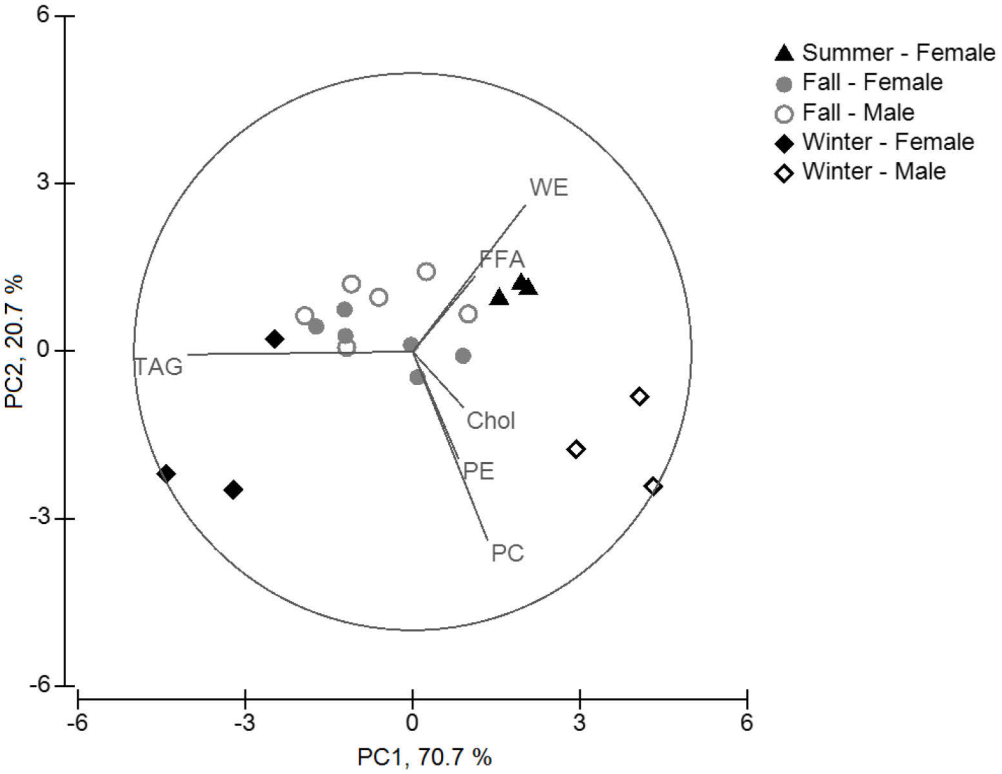

Fig. 6.3 Two-dimensional principal component analysis (PCA) of male and female individuals of the pelagic amphipod *Themisto libellula* in summer, fall and winter according to their lipid class composition, including wax esters (*WE*), cholesterol (*Chol*), free fatty acids (*FFA*), triacylglycerols (*TAG*), phosphatidylethanolamine (*PE*), and phosphatidylcholine (*PC*)

Table 6.4 Dry mass, lipid content and lipid class composition (mean ± standard deviation) of the amphipods *Themisto abyssorum*, *T. libellula*, *T. compressa* and *Cyclocaris guilelmi* sampled in summer 2011 (ARK-XXVI/1+2), fall 2011 (IMR Ecosystem Survey) and winter (ARCTOS BIO-8510) research cruises to the Fram Strait and Svalbard

	Dry Mass	Total lipid	Total lipid	Wax esters	Cholesterol	Free fatty acids	Triacylglycerols	Polar lipids		
								PE	PC	Ratio
	(mg)	(mg)	(% *DM*)	(% *TL*)	(% *TL*)	(% *TL*)	(% *TL*)	(% *TL*)	(% *TL*)	(% *TL*)
Themisto abyssorum										
ARK-XXVI/1+2 Summer (*n* = 6; *L* = 14.0)	9.0 ±1.1	0.7 ±0.3	8.0 ±3.0	37.3 ±13.9	3.8 ±3.2	8.3 ±3.3	39.0 ±20.9	0.9 ±0.8	10.7 ±8.3	0.1 ±0.0
ARCTOS Winter (*n* = 6; *L* = 13.0)	8.3 ±0.9	1.1 ±0.5	13.3 ±5.5	32.4 ±18.0	1.2 ±0.6	2.6 ±1.8	59.8 ±18.9	0.8 ±0.5	3.1 ±1.0	0.2 ±0.1
Themisto libellula										
ARK-XXVI/1+2 Summer (*n* = 3; *L* = 22.0)	20.1 ±2.4	2.3 ±0.8	11.1 ±3.6	76.7 ±3.7	0.7 ±0.1	4.9 ±1.4	14.6 ±2.2	0.2 ±0.2	2.9 ±0.5	0.1 ±0.1
IMR Fall (*n* = 12; *L* = 26.3)	77.4 ±65.0	18.5 ±15.6	23.5 ±5.1	60.5 ±6.5	0.4 ±0.3	1.7 ±1.9	34.9 ±7.8	0.5 ±0.5	2.0 ±1.7	0.2 ±0.1
ARCTOS Winter (*n* = 6; *L* = 30.2)	57.9 ±23.6	4.7 ±3.1	7.9 ±4.2	50.5 ±22.1	1.6 ±1.9	1.0 ±1.9	34.8 ±30.6	2.3 ±2.2	9.9 ±5.9	0.2 ±0.1
Themisto compressa										
ARK-XXVI/1+2 Summer (*n* = 8; *L* = 12.5)	4.5 ±2.1	0.3 ±0.3	6.9 ±3.5	46.1 ±18.9	0.8 ±1.6	4.7 ±3.9	39.3 ±18.2	1.5 ±2.2	7.7 ±5.8	0.2 ±0.3
ARCTOS Winter (*n* = 2; *L* = 13.5)	5.8 ±0.7	0.7 ±0.5	29.0 ±17.8	34.9 ±32.1	3.4 ±2.3	11.6 ±7.6	37.8 ±12.2	2.6 ±2.1	9.2 ±7.5	0.3 ±0.3
Cyclocaris guilelmi										
ARK-XXVI/1+2 Summer (*n* = 6; *L* = 14.0)	11.8 ±4.6	2.9 ±1.6	27.2 ±13.4	84.0 ±10.4	0.4 ±0.5	2.7 ±1.2	10.7 ±10.4	0.3 ±0.3	2.0 ±1.4	0.1 ±0.1
ARCTOS Winter (*n* = 3; *L* = 12.0)	9.2 ±0.6	2.5 ±1.1	27.6 ±13.7	60.4 ±20.2	0.2 ±0.2	10.2 ±2.3	25.9 ±15.8	0.3 ±0.2	3.0 ±1.8	0.1 ±0.0

Note: The proportions of the polar lipids phosphatidylethanolamine (PE) and phosphatidylcholine (PC) as well as the PE/PC ratio are indicated separately

Fatty acids, biomarkers and fatty alcohol composition

In all species and seasons, docosahexaenoic acid (DHA, 22:6(n-3)) and eicosapentaenoic acid (EPA, 20:5(n-3)) represented the two major PUFAs (mean 2.3-13.3 % and 2.3-13.5 % of total fatty acids, respectively) (Tables 6.5 and 6.6). Another PUFA frequently found in the samples was the flagellate marker 18:4(n-3), with a mean contribution of 1.2-7.0 %. The share of most identified PUFAs including DHA and EPA was distinctly higher in winter samples. The most frequent monounsaturated fatty acids (MUFAs) included 20:1(n-9) (mean 9.9-22.2 % of total fatty acids), 18:1(n-9) (7.6-21.5 %) and 16:1(n-7) (4.2-9.1 %). For the species *T. abyssorum*, *T. compressa* and *C. guilelmi*, the share of MUFAs was higher during the summer season. The principal SFAs in all samples were 16:0 (mean 6.6-21.3 % of total fatty acids), 14:0 (2.3-8.9 %), 18:0 (0.7-2.8 %), 17:0 (0.1-0.4 %) and 15:0 (<0.1-0.3 %). The overall SFAs contribution of *Themisto* was lower in winter (Table 6.6).

The observed EPA/DHA ratio was low (0.6-1.6), with small differences between summer and winter. Elevated values were found in the fall samples of *T. libellula* (Fig. 6.4). In general, *T. libellula* possessed the highest EPA/DHA ratios (0.8-1.6), while the ratio was lowest in the North-Atlantic species *T. compressa* (0.6-0.6) (Table 6.5). A strong seasonal gradient between summer and winter ratios of the 18:1(n-9)/18:1(n-7) biomarker in all four species could be observed, showing distinctly higher values in summer (6.8-7.9) (Fig. 6.4, Table 6.6). The reverse pattern was found with regard to the PUFA/SFA ratio, with higher values in *Themisto* and *C. guilelmi* in the winter/fall (2.0-2.3) versus the summer (0.9-1.6) samples. For the 16:1(n-7)/16:0 biomarker no seasonal trend could be observed. The proportion of the flagellate marker 18:4(n-3) increased towards winter in all species, with the highest contributions in *T. libellula* in fall (mean 7.0 % of total fatty acids) and *T. compressa* in winter (mean 7.2 %) (Table 6.6).

The fatty alcohol composition of the investigated amphipods consisted mainly of the long-chain monounsaturated 22:1(n-11) (mean 37.6-62.7 % of total fatty alcohols) and 20:1(n-9) (21.0-38.3 %). In *T. abyssorum*, *T. compressa* and *C. guilelmi*, the share of 20:1(n-9) was distinctly higher in winter samples. The opposing trend could be observed for 22:1(n-11). In the case of *T. libellula*, both fatty alcohols showed only slight variations between seasons. Short-chain saturated moieties such as 14:0 and 16:0 contributed with means of 1.7-18.0 % and 5.9-15.7 %, respectively, to the total fatty alcohol composition. In *T. abyssorum* the short-chain fatty alcohols showed strong seasonal variations, with a distinctly higher proportion of 14:0 and 16:0 in summer samples (Table 6.6).

Table 6.5 Trophic markers and ratios commonly determined in fatty acid profiles (Graeve et al. 1994a, 1994b, 1997; Falk-Petersen et al. 1987, 1998; Auel et al. 2002; Scott et al. 2002; Legezynska et al. 2012 and references therein)

Fatty acid	**Trophic marker**
16:0	Carnivory
16:1(n-7)	Spring bloom (Diatoms)
16:4(n-1)	Diatoms / Ice-algae
18:1(n-9)	Carnivory
18:2(n-6)	chlorophytes or cyanobacteria
18:4(n-3)	Flagellates / *Phaeocystis pouchetii*
20:1(n-9)	*Calanus* spp.
20:5(n-3)	Diatoms
22:1(n-11)	*Calanus* spp.
22:6(n-3)	Flagellates; e.g. presence of *Phaeocystis pouchetii* in the diet of *Calanus*
Fatty acid ratios	
18:1(n-9)/18:1(n-7)	High values (>3) as indicator for increasing carnivory in marine zooplankton
20:5(n-3)/22:6(n-3)	High ratio – diatom-originated diet; low ratio – flagellate-based diet
PUFA/SFA	Increasing value may be used as an indicator for dominance of carnivorous vs. herbivorous feeding; however also increases under starvation conditions
Fatty alcohol ratio	
22:1(n-11)/ 20:1(n-9)	Indicates different copepod species in diets of carnivore zooplankton; e.g. ~2:1 refers to *C. hyperboreus* and ~1.1:1 or less to *C. finmarchicus*

Table 6.6 Fatty acid and alcohol composition (mean ± standard deviation as percentage of total fatty acid or alcohols, respectively) of the four pelagic amphipod species *Themisto abyssorum*, *T. libellula*, *T. compressa* and *Cyclocaris guilelmi* sampled during summer 2011 (ARK-XXVI/1+2), fall 2011 (IMR Ecosystem Survey) and winter 2012 (ARCTOS BIO-8510) research cruises to the Fram Strait and Svalbard

	Themisto abyssorum		***Themisto libellula***			***Themisto compressa***		***Cyclocaris guilelmi***	
	ARK-XXVI/1+2	ARCTOS	ARK-XXVI/1+2	IMR	ARCTOS	ARK-XXVI/1+2	ARCTOS	ARK-XXVI/1+2	ARCTOS
	Summer (*n* = 6)	Winter (*n* = 6)	Summer (*n* = 3)	Fall (*n* = 12)	Winter (*n* = 6)	Summer (*n* = 8)	Winter (*n* = 2)	Summer (*n* = 6)	Winter (*n* =3)
Fatty acids									
14:0	6.0 ±2.5	5.1 ±1.8	8.9 ±2.2	6.4 ±1.8	3.6 ±1.1	5.0 ±2.0	4.9 ±3.2	2.3 ±1.7	3.2 ±0.3
15:0	<0.1	0.2 ±0.1	0.3 ±0.2	0.1 ±0.1	0.1 ±0.1	0.3 ±0.4	0.1 ±0.1	<0.1	0.1 ±0.0
16:0	17.1 ±4.6	11.6 ±1.1	16.5 ±2.8	9.9 ±1.9	11.3 ±1.1	21.3 ±6.4	11.8 ±0.2	6.6 ±2.0	10.6 ±4.3
16:1(n-7)	6.5 ±1.6	6.1 ±0.5	5.2 ±0.6	8.8 ±2.5	5.6 ±1.7	5.9 ±2.4	4.2 ±0.9	9.1 ±4.9	8.3 ±0.9
16:1(n-5)	0.3 ±0.1	0.4 ±0.2	0.3 ±0.2	0.4 ±0.1	0.3 ±0.1	0.2 ±0.1	0.4 ±0.1	0.2 ±0.1	0.5 ±0.1
16:2(n-4)	0.4 ±0.2	0.5 ±0.1	0.3 ±0.1	0.5 ±0.2	0.1 ±0.1	0.3 ±0.3	0.5 ±0.2	0.3 ±0.1	0.4 ±0.0
17:0	0.4 ±0.1	0.4 ±0.1	0.3 ±0.1	0.1 ±0.1	0.2 ±0.2	0.4 ±0.3	0.1 ±0.1	<0.1	0.1 ±0.0
16:3(n-4)	0.5 ±0.0	0.7 ±0.2	0.5 ±0.1	0.6 ±0.2	0.4 ±0.2	0.4 ±0.2	0.3 ±0.0	0.3 ±0.2	0.3 ±0.0
16:4(n-1)	0.2 ±0.2	0.3 ±0.2	0.6 ±0.1	1.0 ±0.5	0.9 ±0.5	0.1 ±0.2	0.2 ±0.2	0.5 ±0.3	0.2 ±0.1
18:0	1.7 ±0.2	1.2 ±0.4	0.9 ±0.2	0.7 ±0.3	1.0 ±0.3	2.8 ±2.0	1.3 ±0.3	0.7 ±0.2	0.8 ±0.2
18:1(n-9)	20.9 ±1.3	11.1 ±1.9	13.2 ±0.5	7.6 ±1.2	14.9 ±3.1	19.7 ±8.0	10.6 ±1.9	21.5 ±6.2	14.4 ±0.9
18:1(n-7)	2.7 ±0.5	2.2 ±0.5	2.0 ±0.4	1.8 ±0.4	3.1 ±0.8	2.5 ±0.6	2.6 ±1.5	2.8 ±0.9	2.9 ±0.8
18:2(n-6)	1.2 ±0.3	1.6 ±0.3	0.9 ±0.5	1.4 ±0.3	2.2 ±0.2	1.3 ±0.8	1.7 ±0.2	1.5 ±0.3	2.0 ±0.9
18:3(n-3)	0.8 ±0.3	1.7 ±0.4	0.5 ±0.4	1.3 ±0.8	0.9 ±0.5	0.7 ±0.8	2.0 ±1.3	0.6 ±0.3	1.5 ±1.1
18:4(n-3)	1.4 ±0.7	6.0 ±2.4	1.8 ±1.9	7.0 ±3.2	3.0 ±1.7	1.2 ±1.9	7.2 ±6.1	2.4 ±3.5	5.7 ±2.7
20:1(n-11)	3.7 ±1.7	2.6 ±1.2	6.1 ±0.0	2.5 ±1.0	3.4 ±1.5	3.4 ±1.6	2.2 ±0.2	4.6 ±2.9	2.4 ±0.6
20:1(n-9)	9.9 ±3.0	11.2 ±2.8	22.2 ±0.6	16.0 ±6.0	14.3 ±2.8	10.8 ±4.6	12.9 ±3.4	14.8 ±3.7	11.6 ±3.8
20:1(n-7)	0.7 ±0.2	1.9 ±0.6	0.7 ±0.2	0.9 ±0.1	1.0 ±0.2	0.8 ±0.5	0.9 ±0.0	1.7 ±0.6	1.5 ±0.4
20:4(n-6)	0.3 ±0.2	0.6 ±0.2	0.0 ±0.1	0.5 ±0.3	0.5 ±0.3	0.2 ±0.3	1.2 ±0.2	0.4 ±0.1	0.5 ±0.1
20:4(n-3)	0.4 ±0.3	1.1 ±0.1	0.2 ±0.2	5.0 ±5.1	4.7 ±4.5	0.2 ±0.3	6.6 ±6.1	0.4 ±0.3	0.7 ±0.1
20:5(n-3)	7.7 ±4.2	13.5 ±2.5	2.3 ±1.3	11.8 ±3.3	8.5 ±2.4	6.6 ±5.6	8.5 ±4.3	4.4 ±2.1	9.0 ±1.6
22:1(n-11)	6.0 ±2.6	4.3 ±1.2	10.2 ±0.6	4.5 ±3.1	6.2 ±5.3	6.0 ±2.8	4.7 ±4.2	15.7 ±4.9	9.4 ±3.5
22:1(n-9)	1.4 ±0.7	1.5 ±0.5	2.4 ±0.5	0.8 ±0.6	1.1 ±1.0	1.7 ±1.2	0.9 ±0.6	3.5 ±1.2	3.2 ±0.9
22:1(n-7)	0.2 ±0.1	0.3 ±0.3	0.4 ±0.2	0.9 ±2.2	0.1 ±0.1	0.2 ±0.1	0.2 ±0.2	0.4 ±0.1	0.4 ±0.1
22:5(n-3)	0.2 ±0.2	0.7 ±0.5	0.2 ±0.2	0.7 ±0.1	0.2 ±0.2	0.1 ±0.2	0.4 ±0.1	0.6 ±0.4	0.8 ±0.3
24:1(n-9)	0.7 ±0.2	0.4 ±0.2	0.9 ±0.1	0.5 ±0.1	0.7 ±0.5	1.0 ±0.6	0.4 ±0.0	0.8 ±0.4	0.6 ±0.1
22:6(n-3)	8.7 ±4.6	12.8 ±3.0	2.3 ±1.4	8.1 ±2.4	12.0 ±3.7	7.0 ±6.8	13.3 ±1.1	4.1 ±2.0	9.0 ±2.2

Table 6.6 continued

	Themisto abyssorum		***Themisto libellula***			***Themisto compressa***		***Cyclocaris guilelmi***	
	ARK-XXVI/1+2	ARCTOS	ARK-XXVI/1+2	IMR	ARCTOS	ARK-XXVI/1+2	ARCTOS	ARK-XXVI/1+2	ARCTOS
	Summer (n = 6)	Winter (n = 6)	Summer (n = 3)	Fall (n = 12)	Winter (n = 6)	Summer (n = 8)	Winter (n = 2)	Summer (n= 6)	Winter (n = 3)
Σ PUFA	21.8 ±9.3	39.5 ±5.6	9.5 ±6.0	38.1 ±5.4	33.4 ±3.8	18.1 ±15.8	42.0 ±8.2	15.5 ±8.2	30.1 ±7.0
Σ MUFA	53.0 ±5.8	42.0 ±5.7	63.6 ±2.2	44.6 ±8.4	50.6 ±4.1	52.1 ±10.6	39.8 ±11.0	74.9 ±9.6	55.1 ±8.4
Σ SFA	25.3 ±6.9	18.5 ±2.2	26.9 ±5.3	17.3 ±3.9	16.1 ±1.1	29.8 ±8.2	18.2 ±2.8	9.6 ±3.8	14.8 ±4.7
Fatty acids ratios									
18:1(n-9)/18:1(n-7)	7.9 ±1.3	5.4 ±1.6	6.8 ±1.1	4.6 ±1.4	5.0 ±0.8	7.9 ±2.6	5.5 ±2.4	7.9 ±1.6	5.3 ±1.0
20:5(n-3)/22:6(n-3)	0.9 ±0.1	1.1 ±0.1	1.0 ±0.1	1.6 ±0.6	0.8 ±0.3	0.9 ±0.2	0.6 ±0.3	1.1 ±0.2	1.0 ±0.1
PUFA/SFA	0.9 ±0.5	2.1 ±1.1	0.4 ±0.2	2.2 ±1.1	2.1 ±1.0	0.6 ±0.4	2.3 ±1.1	1.6 ±0.7	2.0 ±0.8
Fatty alcohols									
14:0	18.0 ±10.3	5.5 ±3.0	1.7 ±0.5	2.7 ±0.6	2.4 ±1.6	11.6 ±14.7	9.3 ±6.1	2.3 ±1.4	5.3 ±2.3
16:0	15.7 ±5.8	9.2 ±2.9	6.8 ±0.6	8.3 ±2.9	7.1 ±3.9	13.6 ±10.1	11.6 ±0.5	5.9 ±1.7	8.9 ±2.0
16:1(n-7)	0.5 ±0.6	0.6 ±0.6	1.2 ±0.3	2.8 ±1.3	1.6 ±0.8	0.8 ±1.3	1.5±1.5	0.7 ±0.4	1.6 ±0.5
18:1(n-9)	1.2 ±0.7	3,7 ±1.0	2.2 ±0.3	2.9 ±1.1	2.2 ±0.5	1.7 ±2.0	2.5 ±2.5	2.4 ±1.9	2.2 ±0.4
18:1(n-7)	1.4 ±1.2	2.5 ±1.0	1.0 ±0.0	1.4 ±0.4	1.4 ±0.1	1.0 ±1.5	0.8 ±0.8	1.5 ±1.0	2.0 ±0.5
20:1(n-9)	21.0 ±4.8	38.3 ±4.1	35.5 ±1.2	33.3 ±10.2	36.8 ±1.9	25.8 ±8.1	36.8 ±0.5	24.5 ±3.8	30.1 ±2.6
22:1(n-11)	42.2 ±12.2	40.2 ±7.0	51.7 ±1.3	48.7 ±12.3	48.6 ±4.5	45.5 ±17.4	37.6 ±1.3	62.7 ±7.0	50.0 ±5.1
Fatty alcohol ratio									
22:1(n-11)/ 20:1(n-9)	2.0 ±0.4	1.1 ±0.3	1.5 ±0.3	1.4 ±0.5	1.3 ±0.4	1.8 ±0.5	1.0 ±0.3	2.6 ±0.4	1.7 ±0.3

Note: The sample sizes (n), mean fatty acid composition (in percent of total fatty acids or alcohols ± standard deviation) and characteristic fatty acids and alcohol ratios are reported. PUFA: polyunsaturated fatty acids, MUFA: monounsaturated fatty acids, SFA: saturated fatty acids

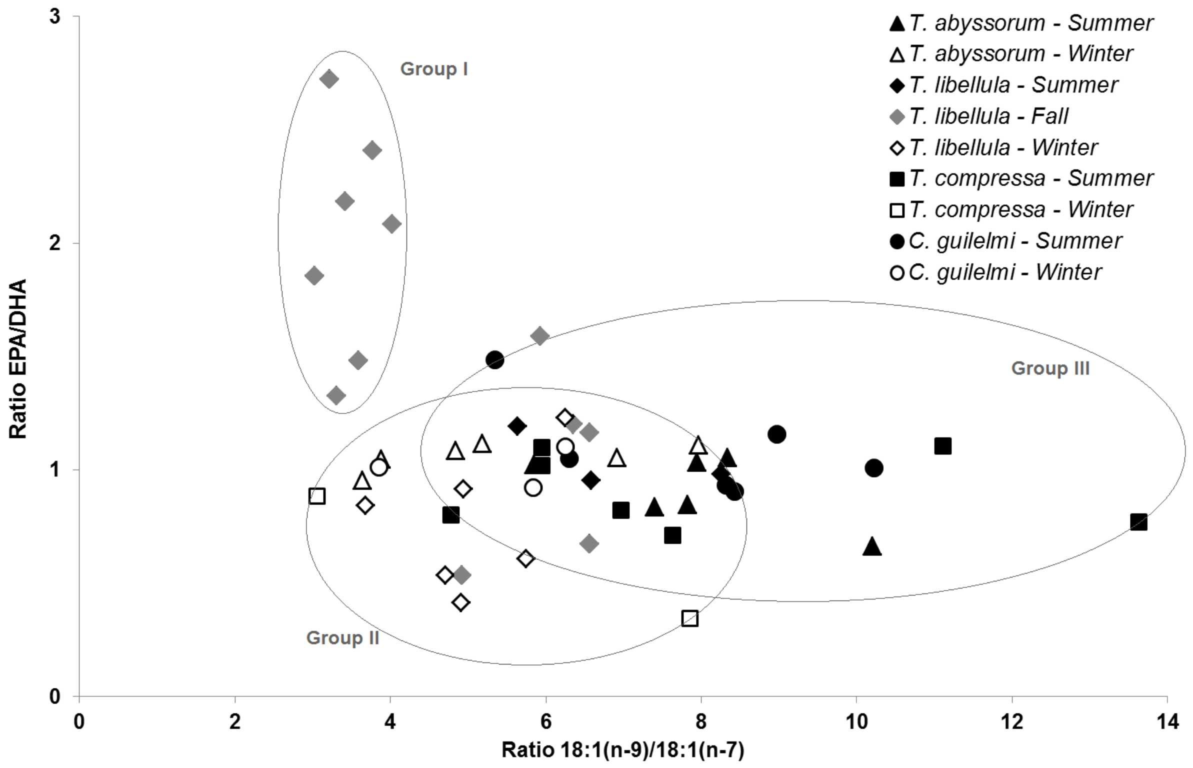

Fig. 6.4 Seasonal variation of the fatty acid biomarker ratios *EPA*/*DHA* (eicosapentaenoic versus docosahexaenoic acid, 20:5(n-3)/22:6(n-3)) and 16:1(n-7)/16:0 in the pelagic amphipods *Themisto abyssorum*, *T. libellula*, *T. compressa* and *Cyclocaris guilelmi*

Discussion

Lipids are of fundamental importance within high-latitude pelagic animals. Lipid reserves serve as energy sources to sustain them during the polar winter and reproduction periods, and provide hydrostatical uplift. This study presents a first evaluation of the influence of seasonality on lipid compositions in four free-swimming amphipods from varying ecological backgrounds, comparing Arctic (*Themisto libellula*), sub-arctic (*T. abyssorum*), North-Atlantic (*T. compressa*) and deep-water (*Cyclocaris guilelmi*) species. We found strong similarities in terms of lipid class composition and fatty acid signatures of the investigated amphipods, which reflected their common status as pelagic predators on mesozooplankton. In all species, the reliance on lipid reserves was high, and depot lipids such as wax esters and triacylglycerols dominated the lipid composition (Table 6.3). Within the genus *Themisto*, the total lipid and PUFA content increased during winter. All amphipods showed a primarily carnivorous diet with copepods as their preferred prey. We discuss the trophic status of these free-swimming predators in detail below.

Dry mass and total lipid content

In polar waters, lipids in crustaceans contribute as much as 48 % of the dry mass (Hagen et al. 2001), with high potential shares of neutral storage lipids such as wax esters or triacylglycerols (Falk-Petersen et al. 1987, 1999). The relative amount and composition of storage lipids may depend on the type of food, feeding history and life-cycle strategy of the respective species, as well as their biosynthesis from either dietary fatty acids or dietary proteins, carbohydrates or lipids (Pond et al. 2000; Pond 2012). Our results showed large individual ranges in total lipid content of adult specimens of *T. abyssorum*, *T. compressa*, *T. libellula* and *C. guilelmi*. Moreover, high total lipid contents were observed for the more boreal adapted species *T. abyssorum* and *T. compressa* in winter and the Arctic species *T. libellula* in fall (Table 6.4). Because individuals of a similar size range were analyzed between different seasons, an increase in lipid levels during winter might point towards an accumulation of energy reserves, or indicate that boreal species have been recently transported into high Arctic waters from more temperate regions.

The observed dry mass of adult *T. abyssorum* (mean 9.0 and 8.3 mg during summer and winter, respectively) and *T. libellula* (mean of 20.1, 77.4 and 57.9 mg in summer, fall and winter, respectively) were in good accordance with previous summer studies from the Fram Strait (Auel et al. 2002; mean dry mass 6.8-10.8 and 76.3-93.4 mg, respectively). The rather low mean total lipid contents of *T. abyssorum* and *T. libellula* in summer and winter (<15 %, Table 6.3) indicate an ecological status as active predators throughout the year. This status is further supported by evidence of active winter feeding of *Themisto* with copepods accounting for a substantial proportion of their diet during the polar night (Kraft et al. 2012b). With a total lipid content of 27.2 and 27.6 % in summer and winter, respectively, the deep-water species *C. guilelmi* had the highest observed lipid content in our study. This result is in line with the findings of Lee (1975) (22 % total lipid) from the central Arctic, where the author represented the only published data on lipid class and fatty acid compositions of *C. guilelmi*. Within *C. guilelmi*, the lack of a distinct trend in the total lipid content of summer versus winter samples indicated that their metabolic demands were sustained by year-round dietary input and the biochemical modification of internal reserves, rather than the depletion of the latter.

Lipid classes

In all amphipods, the outstanding dominance of storage lipids (particularly wax esters and triacylglycerols) over phospholipids, the major component of cell membranes, was obvious.

This phenomenon is frequently observed among zooplankton from polar regions. In a strongly seasonal driven environment with possibly long periods of limited food availability, the storage of long-term energy reserves are essential for survival. Especially wax esters which are important sources of metabolic energy and an adaptation to a highly seasonal food supply (e.g., Sargent and McIntosh 1974; Falk-Petersen et al. 1987; Lee et al. 2006; Noyon et al. 2011). While we cannot rule out that the investigated amphipods might be able to synthesize wax esters themselves, stomach and gut content analysis of this study (Table 6.3) and previous investigations (e.g., Dalpadado et al. 2008; Marion et al. 2008) have shown that they largely feed on copepods of the genus *Calanus*. *Calanus* copepods accumulate high amounts of wax esters which contain fatty acids and alcohols that are not found in phytoplankton or other particulate organic matter, e.g., the long-chain monounsaturated fatty acids 20:1(n-9) and 22:1(n-11) (e.g., Pascal and Ackman 1976; Hagen 1988; Albers et al. 1996).

A dominance of wax esters within the genus *Themisto* was previously described by Auel et al. (2002). The authors found wax ester proportions of 41-43 % of total lipid content in both *T. libellula* and *T. abyssorum*. In the fjords Kongsfjorden and Rijpfjorden (Svalbard, Norway) Noyon et al. (2011) observed proportions of wax esters ranging from 24.4 to 48.5 % for adult *T. libellula*. In our study the wax ester proportions of *T. libellula* were even higher, with means of 76.7, 60.5 and 50.5 % in summer, fall, and winter, respectively. In contrast, the observed wax ester contents in *T. abyssorum* were slightly lower (mean 37.3 and 32.4 % in summer and winter, respectively) (Table 6.4). Other studies also reported high shares of wax esters within *Themisto*, e.g., 46 % for *T. abyssorum* collected in April from Ullsfjord, Norway (Falk-Petersen et al. 1987).

One of our most outstanding results is the high wax ester content of the deep-sea amphipod *C. guilelmi* (mean 60.4-84.0 % of total lipids) (Table 6.4). This contribution of wax esters was distinctly higher than the only data recorded for this species (54 %, Lee 1975) and other published results of free-swimming amphipods in Arctic waters (Scott et al. 1999; Auel et al. 2002; Noyon et al. 2011; Prokopowicz 2011; Legezynska et al. 2012). Interestingly, this high contribution was more similar to that of scavenging amphipods of the deep-sea benthos, e.g. in *Eurythenes gryllus,* with a share of 70 % (Bühring and Christiansen 2001).

The high proportion of wax esters within Arctic amphipods is of special interest when we take note that this is not a bipolar phenomenon: many Antarctic species such as *Themisto gaudichaudii* have a very low wax ester content (mean 0.1 to 8.1 %; Reinhardt and Van Vleet 1986; Nelson et al. 2001). Our results show very high shares of wax esters within *T. compressa* (up to 67.0 % of total lipids). This is interesting given the fact that *T. compressa* and *T. gaudichaudii* were considered to be the same species until their separation in a northern Atlantic and southern Antarctic species in 1986 (Schneppenheim and Weigmann-Hass 1986). Since then, *T. gaudichaudii* has been subject to numerous studies, indicating a symbiotic life-style attached to gelatinous zooplankton (Madin and Harbison 1977). In contrast, a limited number of investigations of *T. compressa* suggested a free-swimming life-style, with sporadic occurrences in North Atlantic water masses in sub-arctic regions (Brandt 1997; Weigmann-Hass 1997; Dalpadado et al. 2001; Dalpadado 2002). Since 2004, we regularly observed this species in the Fram Strait, with its northernmost distribution at 81° N (Kraft et al. 2011, 2012a). To our knowledge, the presented lipid class and fatty acid compositions of *T. compressa* are the first to be published for individuals from Arctic waters. We suggest that the different share of wax esters of *T. gaudichaudii* and *T. compressa* reflects the differences in the life-style (symbiotic vs. pelagic) of both species.

Furthermore, Noyon et al. (2011) proposed that varying shares of wax esters have an important function fueling reproduction during late winter as part of the life-cycle strategy of *T. libellula*. The diminishment of wax ester reserves of *T. libellula* from summer towards fall, and even lower shares in winter (Table 6.4) support this hypothesis. Another reason of this pattern could be the decline of wax ester content of their major prey, calanoid copepods, in winter. During this time of the year calanoid copepods utilize metabolic energy for gonad development (Falk-Petersen et al. 1987).

In addition, our results might indicate a more complex functional role of wax esters besides their character as a metabolic energy reserve related to species ecology. For example, their function of buoyancy control was previously suggested by Auel et al. (2002) for the genus *Themisto*. Pond (2012) and references therein also discussed this function for polar zooplankton in general, with a special focus on copepods. In his review, Pond (2012) indicated that wax esters represent a highly pressure sensitive lipid component, and are of high importance in the diapause phase of copepods. Pond and Tarling (2011) showed that the diapause of the Antarctic copepod *Calanoides acutus* is initiated when a threshold of 50 % unsaturation in wax ester molecules (expressed by the number of double bonds between carbon atoms) is reached. Our recorded fatty acid compositions might provide evidence that wax esters are also used for buoyancy control in amphipods: while the total share of wax esters decreased from summer to winter in all species but *T. compressa* (Table 6.4), the share of the diatom biomarker 20:5(n-3) significantly increased in the winter in all studied amphipods (Table 6.6). According to Pond and Tarling (2011), this PUFA biomarker is considered a key factor controlling the pressure sensitivity of wax esters among polar zooplankton.

For the deep-water amphipod *C. guilelmi* we expected no significant seasonal differences in their lipid class composition as this species was shown to inhabit the meso- and bathypelagic zones of the northern Fram Strait and possesses a year-round reproduction-cycle (Kraft et al. submitted). While its total lipid content was similar in summer and winter, we observed a decrease of their wax ester proportion from 84.0 % in summer to 60.4 % in winter. The decrease was associated with high amounts of 20:5(n-3) (Table 6.4 and 6.6). This pattern might point to changes in the diet consumption of *C. guilelmi* in winter and/or a stronger buoyancy control by vertical migrations within the water column as a response to a shift in food availability. We conclude that wax esters are of high importance as a year-round long-term energy reserve for demanding metabolic processes such as reproduction and/or buoyancy aids within epi- and mesopelagic amphipods.

In *T. abyssorum*, triacylglycerols were the dominant lipid class with higher proportions in winter (mean 59.8 %), than in summer (39.0 %) (Table 6.4). Similar proportions of triacylglycerols were recorded by Auel et al. (2002) in the Fram Strait (23.0 %) and in the central Arctic Ocean (31.9 %). Next to wax esters, this lipid class represents the dominant form of metabolic energy storage in polar zooplankton groups including copepods (e.g., *Calanus propinquus*, Pond 2012), krill (e.g., *Euphausia superba*, Ju and Harvey 2004), and amphipods (e.g., *Anonyx nugax*, Legezynska et al. 2012). Triacylglycerols have been considered to be accumulated by year-round feeding organisms (e.g., Auel et al. 2002). This trait was recently confirmed by gut content analysis of winter samples for the hyperiids *T. libellula* and *T. abyssorum* (Kraft et al. 2012b). Being less sensitive to pressure changes, Pond (2012) suggested triacylglycerols represent the preferred form of storage by zooplankton species occupying the epipelagic zone, such as *C. proponquus.* This species also does not undergo diapause and maintains an active life-style throughout the winter. In this context, the amphipod *T. abyssorum* is known for a larger vertical distribution range than *T. libellula*, with vertical distribution depths of 3000 m and 1000 m, respectively (Vinogradov et al. 1996). However, as both species do feed actively in winter, we do not suggest that depth adaptation is the key to the higher proportion of triacylglycerols in *T. abyssorum*. Rather, a different life-cycle strategy with a later start of the reproduction period for *T. abyssorum* (May to July) than for *T. libellula* (February to May) (Koszteyn et al. 1995; Dalpadado 2002; Weslawski et al. 2006, Kraft et al. 2012a) might be connected to its higher share of triacylglycerols. *T. libellula* also showed a sex specific seasonality in triacylglycerol content, with highest proportions in female individuals (51.3-76.5 % in females, vs. 3.0-8.3 % in males) during winter (Fig. 6.3). Consequently, triacylglycerols seem to be of high importance for readily accessible short-term energy storage and have an important role in the reproduction ecology of hyperiid amphipods.

The phenomenon of differences in rates of deposition and mobilization of neutral lipids between male and female individuals was also observed in other crustaceans (e.g. in the krill species *Meganyctiphanes norvegica*), and can be considered to be of importance in the gonad development of the respective species (Falk-Petersen et al. 1981). The observed increase of triacylglycerol contributions in *C. guilelmi* in winter might point towards broader, possibly diet-induced factors (e.g., a shift from a copepod to an euphausiid/amphipod dominated diet), which are responsible for this pattern. An extensive storage of triacylglycerols has also been considered as an indication of winter feeding in other zooplankton species, e.g. the Antarctic krill *E. superba* (Hagen et al. 2001).

Fatty acids, fatty alcohols and biomarker ratios

Fatty acid profiles reflect a time-averaged feeding history of consumers and can be further modified by species-specific metabolic processes (Dalsgaard et al. 2003). Up to date, few studies include data on fatty acid compositions of polar zooplankton in the winter season (Torres et al. 1994; Ju and Harvey 2004; Kruse et al. 2010) and to our knowledge, the winter fatty acid profile of *Themisto* and *Cyclocaris* presented here are novel. Pelagic amphipods are commonly known for a mixed diet related to season, vertical and geographical distribution and prey abundance (e.g., Auel et al. 2002; Dale et al. 2006; Dalpadado et al. 2008; Kraft et al. 2012b). We expected their fatty acid profiles to consist of a mixture of accumulated and *de novo* synthesized fatty acids of their prey. Summer and winter profiles indicated that all studied species were part of the *Calanus*-based food web. This was shown by high levels of the *Calanus* biomarkers 20:1(n-9) and 22:1(n-11) in fatty acid and alcohol compositions (Table 6.6). C20 and C22 long-chain monoenes are typical components of herbivorous *Calanus* copepods (Sargent and Henderson 1986; Kattner and Hagen 1995; Hagen et al. 2000; Dalsgaard et al. 2003). Their accumulation takes place during brief, pronounced ice-algae and phytoplankton blooms in Arctic spring and summer, and consequently allows copepods to survive long periods of food shortage (Falk-Petersen et al. 1999). High proportions of monounsaturated C20 and C22 fatty acids and alcohols indicate that all four species have a high ability to efficiently absorb storage lipids from *Calanus* copepods.

Previous studies on CV and adult stages of *C. hyperboreus*, *C. glacialis* and *C. finmarchicus* from high Arctic waters revealed that these species can be distinguished on the basis of their share of 22:1(n-11) fatty alcohol in their wax ester composition (Falk-Petersen et al. 1987; Scott et al. 2002; Table 6.5). Consequently, high values of the fatty alcohol ratio 22:1(n-11)/20:1(n-9) within *T. abyssorum*, *T. compressa* and *C. guilelmi* (1.8-2.6; Table 6.6) serve as an indication for predominant feeding on *C. hyperboreus* in the northern Fram Strait. In contrast, the fall and winter sampling took place in shelf waters north of Svalbard, where *C. finmarchicus* and *C. glacialis* represent the dominant copepods in the upper 600 m of the water column (Rabindranath et al. 2011). Most interestingly, the values of the fatty alcohol ratio 22:1(n-11)/20:1(n-9) of the *Themisto* samples were lower in this area (1.0-1.4). Consequently, our results might reflect the different geographical distinction of calanoid copepods around Svalbard, with *C. hyperboreus* as the dominant species in the northern Fram Strait and *C. glacialis* and *C. finmarchicus* on Svalbard shelf areas.

Arctic spring blooms in cold, nutrient-rich waters have a high potential to support good nutritional quality with regard to fatty acid composition (including high levels of PUFAs) (Leu et al. 2006, 2011; Søreide et al. 2008, 2010). High proportions of fatty acids derived from phytoplankton can serve as an indicator for the beginning of food uptake of *Calanus* copepods (Falk-Petersen et al. 2009). The classical “spring bloom” may occur along the ice-edge as the sea-ice recedes during summer and autumn, or in openings in the ice cover any time between late March and October (Zenkevitch 1963; Falk-Petersen et al. 2007). Interesting results of this study were higher 22:6(n-3) fatty acid proportions in winter specimens, as a high DHA content has been related to an increased share of dinoflagellates and *Phaeocystis pouchetii* in the diet of *Calanus* (Scott et al. 2002). Furthermore, the combined increase of flagellate (18:4(n-3), DHA) and diatom (particularly EPA) markers in winter (Table 6.6, Fig. 6.4) suggested a higher turnover rate and preferential utilization of deposited lipids during the time of the polar night. Consequently, the seasonality of phytoplankton biomarkers in the summer and winter fatty acid profiles within *Themisto* and *Cyclocaris* could be induced by different phytoplankton diets of their preferred prey, *Calanus* copepods. This outlines the complexity of the trophodynamics of Arctic amphipods. That such a change in diet can be traced up the food web has been previously shown for higher trophic levels, e.g. in the case of juvenile cod in the North Sea (St John and Lund 1996). This could also imply that both photosynthetic systems, the typical high Arctic diatom system (Horner et al. 1992 and references therein) and a dinoflagellate-/*P. pouchetii* dominated one (Sargent et al. 1985), seem to be capable of providing the baseline energy reserves that can be found in higher trophic predators such as pelagic amphipods.

The complexity of fatty acid profiles in polar amphipods was also shown by the hyperiid *Themisto gaudichaudii*. In older studies, *T. gaudichaudii* was classified as an obligate carnivore based on biomarker and gut content analysis of individuals collected during the austral summer in waters around South Georgia and the South Shetland Islands (Pakhomov and Perissinotto 1996; Nelson et al. 2001). More recently, Richoux (2011) argued that contributions of more than 3 % of 18:2(n-6) in samples from the subtropical convergence zone might point towards a more omnivorous status of *T. gaudichaudii* than previously thought. Interestingly, our results also showed an increase of this marker in the winter samples of *Themisto* and *Cyclocaris*, with a similar range (1.6-2.2 %) in both species (Table 6.6).

In addition to the individual contribution of specific fatty acid markers, ratios are commonly used in order to address the trophic status of a species via its fatty acid profile (Table 6.5). For example, a high 18:1(n-9)/18:1(n-7) ratio is considered an indicator for carnivory, while an increase in the ratio of EPA/DHA points towards a shift from a flagellate towards a diatom based-diet (Graeve et al. 1994a, 1997; Auel et al. 2002). The respective increase of the 18:1(n-9)/18:1(n-7) biomarker ratio (Table 6.6) in summer might imply a stronger carnivory during this season for all observed amphipods. However, a distinct overlap in both ratios for all investigated species and seasons (Groups II and III, Fig. 6.4) also suggested that the fatty acid profile of an individual strongly depends on physiological needs and surrounding environmental conditions. Auel et al. (2002) suggested that a strong linkage to sympagic reproduction might be shown by high EPA levels (indicating the presence of ice-algae) and high EPA/DHA ratios. One interesting finding in this context was the respective separation of *T. libellula* individuals collected with a pelagic fish trawl in fall 2011 (Fig. 6.4). As a consequence of the large mesh size (10 mm), only large adult specimens were present in the trawl samples. Our results indicated a different trophic status of individuals caught during fall; higher proportions of diatom and flagellate biomarkers in their fatty acid profiles and the highest EPA/DHA ratio observed of all analyzed species and seasons further support this hypothesis (Fig. 6.4, Table 6.6).

Furthermore, a high PUFA/SFA ratio was observed within all investigated species; this phenomenon has been suggested as an indicator for carnivory in recent zooplankton feeding history (Cripps and Atkinson 2000). Our results indicating high ratios of PUFA/SFA for all species during winter seem to disagree with lower winter values of other markers for carnivory such as the fatty acids 16:0 and 18:1(n-9), and the increase of diatom (particularly EPA) and flagellate (18:4(n-3), DHA) markers at the same time (Table 6.6). One possible explanation of this contradiction might be based on the fact that phytoplankton marker fatty acids can be ingested directly via phytoplankton and particles or indirectly via zooplankton. While the flagellate 18:4(n-3) marker is typical for summer phytoplankton populations and indicates non-diatom input (Harrington et al. 1970; Graeve et al. 1994a, 1996) it can be also found in high levels in calanoid copepods (Graeve et al. 1994a; Kattner and Hagen 1995) and consequently can be transferred up the food web. Cripps and Atkinson (2000) also suggested that an increase in PUFA content might indicate starvation due to the depletion of triayclglycerol. However, no such depletion from summer to winter was shown in our results; on the contrary, distinctly higher levels of triacylglycerol of all amphipods (with the exception of *T. compressa*) were observed in winter (Table 6.4). In addition, the fatty alcohol compositions during both seasons were clearly dominated by the monounsaturated *Calanus* markers 20:1(n-9) and 22:1(n-11). Based on these results we suggest an intense feeding on copepods as the primary food source of *Themisto* and *Cyclocaris* during winter and a more diverse diet during summer. Consequently, our findings imply a vertical migration of *Themisto* during winter, as this hyperiid amphipod follows its main prey into deeper waters.

In summary, the presented emphasis on lipid class, detailed fatty acid and fatty alcohol compositions revealed relatively strong seasonal and minor inter-specific differences in feeding behavior and food sources of the investigated species. In contrast to most herbivore or omnivore zooplankton groups, which enter a state of dormancy or face starvation, these pelagic predators seem to continue a 'business-as-usual' mode during the polar winter. This overwintering strategy was first described by Torres et al. (1994) and is characterized by the absence of a reduction of the metabolic rate and an active feeding behavior throughout this season. Concerning *T. abyssorum* and *T. libellua,* this result stands in contrast to the overwintering strategy of their Antarctic congener *T. gaudichaudii*: the latter has been shown to reduce its metabolism and combusts body substance in order to cope with reduced food availability during the polar night (Torres et al. 1994).

To conclude, the analyzed lipid classes and fatty acid profiles of *Themisto* and *Cyclocaris* indicated that both genera are predominantly carnivore predators during summer and winter in the *Calanus*-based Arctic food web, with calanoid copepods as their main food source. Pronounced seasonal differences characterized their fatty acid composition, with an increasing contribution of polyunsaturated fatty acids during winter. As a part of the *Calanus*-based food web, the population dynamics of *T. abyssorum*, *T. compressa*, *T. libellula* and *C. guilelmi* might be vulnerable to shifts in abundance and distribution of *Calanus* species. Seasonal shifts in the geographical and vertical distribution of these copepods are also reflected in their gut content and fatty alcohol profile, with *C. hyperboreus* as the preferred prey of *Themisto* in the northern Fram Strait during summer and *C. fimarchicus* and *C. glacialis* as the major food sources on shelf regions north of Svalbard during fall and winter. Consequently, these pelagic predators would be affected by possible climate induced changes of the copepod community composition, seasonal vertical migration behavior and timing in reproduction of calanoid copepods. This also implies the importance of a future match between primary producers (either ice-algae or phytoplankton bloom or both), copepod life-cycles and their respective availability as a key food source for pelagic amphipods.

Acknowledgments

We thank the Captains and crews of R/V *Polarstern* and R/V *Helmer Hanssen* for their skillful support during the research cruises. We thank the Institute of Marine Research in Bergen, Norway, for the possibility to join the 'IMR Ecosystem survey' cruise in fall 2011. Furthermore we would like to thank our colleagues Jørgen Berge, Øystein Varpe, David Pond, Thomas de Lange Wenneck, Julio Enrices, Eike Stübner, Daniel Vogedes, Malin Daase and Nadine Knüppel for their assistance during the plankton hauls and in the lab. We also thank Ulrich V. Bathmann, Eva-Maria Nöthig, Eduard Bauerfeind, Barbara Niehoff, Mandy Kiel, Christiane Lorenzen, Ruth Alheit and Sandra Murawski who helped with cruise preparations for the cruises and/or during the biochemical analyses in the laboratory. We also thank Ben Lange for his valuable suggestions and proof-reading. This work was financed by institutional funds of the AWI, Bremerhaven, and by the German Federal Ministry of Education and Research (project: 03F0629A).

References

Albers CS, Kattner G, Hagen W (1996) The compositions of wax esters, triacylglycerols and phospholipids in Arctic and Antarctic copepods: evidence of energetic adaptations. Mar Chem 55:347-358.

Auel H, Harjes M, da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25:374-383.

Bradstreet MSW, Cross WE (1982) Trophic relationships at high Arctic ice edges. Arctic 35(1):1-12.

Bousfield EL (1951) Pelagic amphipoda of the Belle Isle Strait region. J Fish Res Board Can 8:134-163.

Budge SM, Iverson SJ, Bowen WD, Ackman RF (2002) Among and within species variability in fatty acids signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank, and southern Gulf of St. Lawrence. Can J Fish Aquat Sci 59:886-898.

Bühring SI, Christiansen B (2001) Lipids in selected abyssal benthopelagic animals: links to the epipelagic zone? Prog Oceanogr 50:369-382.

Brandt A (1997) Suprabenthic Peracarida (Crustacea, Malacostraca) sampled at 75 degrees N off East Greenland. Polar Biol 17(5):462-464.

Clarke KR, Gorley RN (2006) PRIMER v6: User Manual/Tutorial. PRIMER-E Ltd., Plymouth.

Clarke KR, Warwick RM (2001) Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E Ltd., Plymouth.

Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high-latitudes of the northern hemisphere. Hydrobiologia 167:127-142.

Cripps GC, Atkinson A (2000) Fatty acid composition as an indicator of carnivory in Antarctic krill, *Euphausia superba*. Can J Fish Aquat Sci 57:31-37.

Dale K, Falk-Petersen S, Hop H, Fevolden SE (2006) Population dynamics and body composition of the Arctic hyperiid amphipod *Themisto libellula* in Svalbard fjords. Polar Biol 29:1063-1070.

Dalpadado P, Ellertsen B, Melle W, Dommasnes A (2000) Food and feeding conditions of Norwegian spring spawning herring (*Clupea harengus*) through its feeding migrations. ICES J Mar Sci 58:876-895.

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58:876-895.

Dalpadado P (2002) Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. Polar Biol 25:656-666.

Dalpadado P, Bogstad B (2004) Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. Polar Biol 27(3):140-154.

Dalpadado P, Yamaguchi A, Ellertsen B, Johannessen S (2008) Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55:2266-2274.

Dalsgaard J, St John M, Kattner G, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:225-340.

Dunbar MJ (1957) The determination of production in the northern seas: a study of the biology of *Themisto libellula* Mandt. Can J Zool 35:797-819.

Falk-Petersen S, Gatten RR, Sargent JR, Hopkins CCE (1981) Ecological investigations on the zooplankton community in Balsfjorden, Northern Norway: seasonal changes in the lipid class composition of *Meganyctiphanes norvegica* (M. Sars); *Thysanoessa rashii* (M. Sars) and *T. inermis* (Krøyer). J Exp Mar Biol Ecol 54:209-224.

Falk-Petersen S, Sargent JR, Kande KS (1987) Lipid composition of zooplankton in relation to the sub-arctic food web. Polar Biol 8:115-120.

Falk-Petersen S, Sargent JR, Lønne OJ, Timofeev S (1999) Functional biodiversity of lipids in Antarctic zooplankton: *Calanoides acutus*, *Calanus propinquus*, *Thysanoessa macura* and *Euphausia crystallorophias*. Polar Biol 21:37-47.

Falk-Petersen S, Hagen W, Kattner G, Clarke A, Sargent J (2000) Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. Can J Fish Aquat Sci 57:178-191.

Falk-Petersen S, Haug T, Nilsen KT, Wold A, Dahl TM (2004) Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. Polar Res 23:43-50.

Falk-Petersen S, Timofeev S, Pavlov V, Sargent JR (2007) Climate variability and possible effects on Arctic food chains. The role of *Calanus*. In: Ørbæk J-B, Tombre T, Kallenborn R, Hegseth EN, Falk-Petersen S, Hoel AH (eds) Arctic-alpine ecosystems and people in a changing environment. Springer, Berlin, pp 147-166.

Falk-Petersen S, Mayzaud P, Kattner G, Sargent JR (2009) Lipids and life strategy of Arctic *Calanus*. Mar Biol Res 5:18-39.

Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for isolation and purification of total lipids from animal tissue. J Biol Chem 226:497-509.

Gascard JC, Richez C, Rouault C (1995) New insights on large-scale oceanography in Fram Strait: The West Spitsbergen Current. In: Smith W, Grebmeier J (eds) Arctic Oceanography: Marginal Ice Zones and Continental Shelves, Coastal Estuarine Stud., vol. 49. AGU, Washington DC, pp 131-182.

Graeve M, Hagen W, Kattner G (1994a) Herbivorous or omnivorous? on the significance of lipid composition as trophic markers in Antarctic copepods. Deep-Sea Res I 41:915-924.

Graeve M, Hagen W, Kattner G (1994b) Diet-induced changes in the fatty acids composition of Arctic herbivorous copepods: experimental evidence of trophic markers. J Exp Mar Biol Ecol 182:97-110.

Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? Polar Biol 18:53-61.

Graeve M, Albers C, Kattner G (2005) Assimilation and biosynthesis of lipids in Arctic *Calanus* species based on feeding experiments with a 13C labelled diatom. J Exp Mar Biol Ecol 317:109-125.

Graeve M, Janssen D (2009) Improved separation and quantification of neutral and polar lipid classes by HPLC-ELSD using a monolithic silica phase: Application to exceptional marine lipids. J Chromat B, Analyt Technol Biomed Life Sci 877:1815-1819.

Hagen W (1988) Zur Bedeutung der Lipide im antarktischen Zooplankton. Ber Polarforsch 49:1-129.

Hagen W, Van Vleet ES, Kattner G (1996) Seasonal lipid storage as overwintering strategy of Antarctic krill. Mar Ecol Prog Ser 134:85-89.

Hagen W, Kattner G, Friedrich C (2000) The lipid compositions of high-Antarctic notothenioid fish species with different life strategies. Polar Biol 23:785-791.

Hagen W, Kattner G, Terbrüggen A, Van Vleet ES (2001) Lipid metabolism of the Antarctic krill *Euphausia superba* and its ecological implications. Mar Biol 139:95-104.

Harrington GW, Beach DH, Dunham JE, Holz GG (1970) The polyunsaturated fatty acids of marine dinoflagellates. J Eukaryot Microbiol 17:213-219.

Helland-Hansen B, Nansen F (1909) The Norwegian Sea, its physical oceanography. Based on the Norwegian researches 1900-1904. Report on Norwegian Fishery and Marine-Investigations, Vol. 11, Bergen, Norway.

Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon J-M, Fortier M (2002) A stable isotope (δ13C, δ15N) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep-Sea Res II 49:5131-5150.

Horner R, Ackley SF, Dieckmann GS, Gulliksen B, Hoshiai T, Legendre L, Melnikov IA, Reeburgh WS, Spindler M, Sullivan CW (1992) Ecology of sea ice biota. 1. Habitat, Terminology, and Methodology. Polar Biol 12:417-427.

Howell KL, Pond DW, Billett DSM, Tyler PA (2003) Feeding ecology of deep-sea seastars (Echinodermata: Asteroidea): a fatty-acid biomarker approach. Mar Ecol Prog Ser 255:193-206.

Ju S-J, Harvey HR (2004) Lipids as markers of nutritional condition and diet in the Antarctic krill *Euphausia superba* and *Euphausia crystallorophias* during austral winter. Deep-Sea Res II 51:2199-2214.

Karlson K, Båmstedt U (1994) Planktivorous predation on copepods. Evaluation of mandible remains in predator guts as a quantitative estimate of predation. Mar Ecol Prog Ser 108:79-89.

Kattner G, Fricke HSG (1986) Simple gas-liquid chromatographic method for the simulataneous determination of fatty acids and alcohols in wax esters of marine organisms. J Chromatogr 361:263-268.

Kattner G, Hagen W (1995) Polar herbivorous copepods – different pathways in lipid biosynthesis. ICES J Mar Sci 52(3-4):329-335.

Koszteyn J, Timofeev S, Weslawski JM, Malinga B (1995) Size structure of *Themisto abyssorum* Boeck and *Themisto libellula* (Mandt) populations in the European Arctic Seas. Polar Biol 15:85-92.

Kraft A, Bauerfeind E, Nöthig E-M (2011) Amphipod abundance in sediment trap samples at the long-term observatory HAUSGARTEN (Fram Strait, ~79°N/4°E) - Variability in species community patterns. Mar Biodiv 41:353-364.

Kraft A, Bauerfeind E, Nöthig E-M, Bathmann UV (2012a) Size structure and life-cycle patterns of dominant pelagic amphipods collected as swimmers in sediment traps in the eastern Fram Strait. J Mar Sys 95:1-15.

Kraft A, Berge J, Varpe Ø, Falk-Petersen S (2012b) Feeding in Arctic darkness: mid-winter diet of the pelagic amphipods *Themisto abyssorum* and *T. libellula*. Mar. Biol. online first, doi:10.1007/s00227-012-2065-8.

Kruse S, Hagen W, Bathmann UV (2010) Feeding ecology and energetics of the Antarctic chaetognaths *Eukrohnia hamata*, *E. bathypelagica* and *E. bathyantarctica*. Mar Biol 157:2289-2302.

Lee RF (1975) Lipids of arctic zooplankton. Comp Biochem Phys B 51:263-266.

Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307:273-306.

Legezynska J, Kedra M, Walkusz W (2012) When season does not matter: summer and winter trophic ecology of Arctic amphipods. Hydrobiologia 684:189-214.

Leu E, Falk-Petersen S, Kwasniewski S, Wulff A, Edvardsen K, Hessen DO (2006) Fatty acid dynamics during the spring bloom in a High Arctic fjord: importance of Abiotic factors versus community changes. Can J Fish Aquat Sci 63(12):2760-2779.

Leu E, Søreide JE, Hessen DO, Falk-Petersen S, Berge J (2011) Consequences of changing sea ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. Prog Oceanogr 90:18-32.

Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin, 1773) in ice covered waters. Polar Biol 9:187-191.

Lu Y, Ludsin SA, Fanslow DL, Pothoven SA (2008) Comparison of three microquantity techniques for measuring total lipids in fish. Can J Fish Aquat Sci 65:2233-2241.

Madin LP, Harbison GR (1977) The associations of Amphipoda Hyperiidea with gelatinous zooplankton - I. Associations with Salpidae. Deep-Sea Res 24:449-463.

Manley O (1995) Branching of Atlantic Water within the Greenland-Spitsbergen Passage: an estimation of recirculation. J Geophys Res 100:20627-20634.

Marion A, Harvey M, Chabot D, Brethes JC (2008) Feeding ecology and predation impact of the recently established amphipod, *Themisto libellula*, in the St. Lawrence marine system, Canada. Mar Ecol Prog Ser 373:53-70.

Mayzaud P, Laureillard J, Merien D, Brinis A, Godard C, Razouls S, Labat JP (2007) Zooplankton nutrition, storage and fecal lipid composition in different water masses associated with the Agulhas and Subtropical Fronts. Mar Chem 107:202-213.

Nakagawa Y, Endo Y, Taki K (2000) Diet of *Euphausia pacifica* Hansen in Sanriku waters off northeastern Japan. Plankton Biol Ecol 48:68-77.

Nelson MM, Mooney, BD, Nichols PD, Phleger CF (2001) Lipids of Antarctic Ocean amphipods: food chain interactions and the occurrence of novel biomarkers. Mar Chem 73:53-64.

Nilsen F, Cottier F, Skogseth R, Mattsson S (2008) Fjord–shelf exchanges controlled by ice and brine production: The interannual variation of Atlantic Water in Isfjorden, Svalbard. Cont Shelf Res 28:1838-1853.

Noyon M, Gasparini S, Mayzaud P (2009) Feeding of *Themisto libellula* (Amphipoda Crustacea) on natural copepods assemblages in an Arctic fjord (Kongsfjorden, Svalbard). Polar Biol 32:1559-1570.

Noyon M, Narcy F, Gasparini S, Mayzaud P (2011) Growth and lipid class composition of the Arctic pelagic amphipod *Themisto libellula*. Mar Biol 158:883-892.

Noyon M, Narcy F, Gasparini, S., and Mayzaud, P. 2012. Ontogenic variations in fatty acid and alcohol composition of the pelagic amphipod *Themisto libellula* in Kongsfjorden (Svalbard). Mar Biol 159:805-816.

Pakhomov EA, Perissinotto R (1996) Trophodynamics of the hyperiid amphipod *Themisto gaudichaudii* in the South Georgia region during late austral summer. Mar Ecol Prog Ser 134:91-100.

Pascal JC, Ackman RG (1976) Long chain monoethylenic alcohol and acid isomers in lipids of copepods and capelin. Chem Phys Lipids 16:219-223.

Percy JA (1993) Reproduction and growth of the Arctic hyperiid amphipod *Themisto libellula* Mandt. Polar Biol 13:131-139.

Piechura J (2004) The circulation of the Nordic Seas. In: Skreslet S (ed) Jan Mayen Island in scientific focus. Kluwer Academic Publishers, Netherlands, pp 91-99.

Pond DW, Gebruk A, Southward E, Southward A, Fallick A, Bell M, Sargent J (2000) Unusual fatty acid composition of storage lipids in the bresilioid shrimp *Rimicaris exoculata* couples the photic zone with MAR hydrothermal sites. Mar Ecol Prog Ser 198:171-179.

Pond DW, Tarling GA (2011) Phase transitions of wax esters adjust buoyancy in diapausing *Calanoides acutus*. Limnol Oceanogr 56:1310-1318.

Pond DW (2012) The physical properties of lipids and their role in controlling the distribution of zooplankton in the oceans. J Plankton Res 34:443-453.

Prokopowicz AJ, Rueckert S, Leander BS, Michaud J, Fortier L (2010) Parasitic infection of the hyperiid amphipod *Themisto libellula* in the Canadian Beaufort Sea (Arctic Ocean), with a description of *Ganymedes themistos* sp n. (Apicomplexa, Eugregarinorida). Polar Biol 33:1339-1350.

Prokopowicz AJ (2011) Écophysiologie de l'amphipode *Themisto libellula* sur le plateau du Mackenzie et dans la Polynie du Cap Bathurst (mer de Beaufort, océan Arctique). Ph.D. thesis, Départment de Biologie, Université Laval, Québec.

Quadfasel D, Gascard J-C, Kolermann K-P (1987) Large-scale oceanography in Fram Strait during the 1984 marginal ice zone experiment. J Geophys Res 92:6719-6728.

Quetin LB, Ross RM (1991) Behavioral and physiological characteristics of the Antarctic krill, *Euphausia superba*. Am Zool 31:49-63.

Rabindranath A, Daase M, Falk-Petersen S, Wold A, Wallace MI, Berge J, Brierley AS (2011) Seasonal and diel vertical migration of zooplankton in the High Arctic during the autumn midnight sun of 2008. Mar Biodiv 41:365-382.

Reinhardt SB, Van Vleet ES (1986) Hydrocarbons of antarctic midwater organisms. Polar Biol 6:47-51.

Richoux NB (2011) Trophic ecology of zooplankton at a frontal transition zone: fatty acid signatures at the subtropical convergence, Southern Ocean. J Plankton Res 33(3):491-505.

Rudels BJ, Friedrich H, Quadfasel D (1999) The Arctic Circumpolar Boundary Current. Deep-Sea Res II 46:1023-1062.

Sargent JR, McIntosh R (1974) Studies on the mechanism of biosynthesis of wax esters in *Euchaeta norvegica*. Mar Biol 25:271-277.

Sargent JR, Lee RF, Nevenzel JC (1976) Marine waxes. In: Kolattukudy PE (ed) Chemistry and biochemistry of natural waxes. Elsevier, Amsterdam, pp 50-91.

Sargent JR, Eilertsen HC, Falk-Petersen S, Taasen JP (1985) Carbon assimilation and lipid production in phytoplankton in northern Norwegian fjords. Mar Biol 85:109-116.

Sargent JR, Henderson RJ (1986) Lipids. In: Corner EDS, O'Hara SCM (eds) The biological chemistry of marine copepods. Clarendon Press, Oxford, pp 491-531.

Schauer U, Beszczynska-Möller A, Walczowski W, Fahrbach E, Piechura J, Hansen E (2008) Variation of Measured Heat Flow Through the Fram Strait Between 1997 and 2006. In: Dickson RR, Meincke J, Rhines P (eds) Arctic–Subarctic Ocean Fluxes. Springer, Netherlands, pp 65-85.

Schlichtholz P, Houssais MN (2002) An inverse modeling study in Fram Strait. Part II: water mass distribution and transports. Deep-Sea Res II 46(6-7):1137-1168.

Schneppenheim R, Weigmann-Haass R (1986) Morphological and electrophoretic studies of the genus *Themisto* (Amphipoda: Hyperiidea) from the South and North Atlantic. Polar Biol 6:215-225.

Scott CL, Falk-Petersen S, Sargent JR, Hop H, Lønne OJ, Poltermann M (1999) Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal ice zone of the Barents Sea. Polar Biol 21:65-70.

Scott CL, Kwasniewski S, Falk-Petersen S, Sargent JR (2002) Species differences, origins and functions of fatty alcohols and fatty acids in the wax esters and phospholipids of *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* from Arctic waters. Mar Ecol Prog Ser 235:127-134.

Søreide JE, Falk-Petersen S, Hegseth EN, Hop H, Carroll ML, Hobson KA, Blachowiak-Samolyk K (2008) Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. Deep-Sea Res II 55:2225-2244.

Søreide JE, Leu E, Berge J, Graeve M, Falk-Petersen S (2010) Timing of blooms, algal food quality and *Calanus glacialis* reproduction and growth in a changing Arctic. Global Change Biol 16:3154-3163.

St John M, Lund T (1996) Lipid biomarkers: Linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. Mar Ecol Prog Ser 131(1-3):75-85.

Stübing D, Hagen W, Schmidt K (2003) On the use of lipid biomarkers in marine food web analyses: An experimental case study on the Antarctic krill, *Euphausia superba*. Limnol Oceanogr 48(4):1685-1700.

Torres JJ, Donnelly J, Hopkins TL, Lancraft TM, Aarset AV, Ainley DG (1994) Proximate composition and overwintering strategies of Antarctic micronektonic Crustacea. Mar Ecol Prog Ser 113(3):221-232.

Vinogradov ME, Volkov AF, Semenova TN (1996) Hyperiid Amphipods (Amphipoda, Hyperidea) of the World Oceans. Science Publishers Inc, Lebanon, USA.

Weigmann-Haass R (1997) Verbreitung von Makrozooplankton in der Grönlandsee im Spätherbst 1988 (Crustacea: Ostracoda, Hyperiidea [Amphipoda], Euphausiacea). Helgoländer Meeresuntersuch 51:69-82.

Weslawski JM, Kwasniewski S, Stempniewicz L, Blachowiak-Samolyk K (2006) Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords. Pol Polar Res 27:259-278.

Wold A, Jaeger I, Hop H, Gabrielsen GW, Falk-Petersen S (2011) Arctic seabird food chains explored by fatty acid composition and stable isotopes in Kongsfjorden, Svalbard. Polar Biol 34:1147-1155.

Zenkevitch L (1963) Biology of the seas of the UDSSR. Georg Allen and Unwin, London.

PUBLICATION V

Reproduction in a southern invader indicates community shift among Arctic zooplankton

Angelina Kraft[a]*, Eva-Maria Nöthig[a], Eduard Bauerfeind[a], David J. Wildish[b], Gerhard W. Pohle[b], Ulrich V. Bathmann[c], Agnieszka Beszczynska-Möller[a], Michael Klages[a]

[a]Alfred Wegener Institute for Polar and Marine Research
Am Handelshafen 12,
27570 Bremerhaven, Germany
* Contact information:
E-mail: Angelina.Kraft@awi.de
Phone: + 49-471-48311085
Fax: + 49-471-48311149

[b]Atlantic Reference Centre
Huntsman Marine Science Centre
1 Lower Campus Road
St. Andrews, New Brunswick E5B 2L7, Canada

[c]Leibniz Institute for Baltic Sea Research Warnemünde
18119 Rostock, Germany

Submitted to Nature Climate Change,

19. December 2012

Abstract

The Arctic Ocean is severely affected by climate warming, with clearly visible signs, such as the progressive decrease in Arctic sea-ice. On the biological side, community shifts in the trophic cascade caused by the advance of warm Atlantic waters have been documented by marine ecologists over the past two decades. Here, we present the first evidence of successful reproduction by a pelagic crustacean, the Atlantic hyperiid amphipod *Themisto compressa*, which has expanded its range from more southerly warmer waters. We observed 21 ovigerous females with fertilized eggs and recently hatched juveniles. The results were obtained after 12 years of long-term zooplankton observations near the Svalbard archipelago at the boundary between the central Arctic Ocean and the Greenland Sea in the eastern Fram Strait.

Main Text

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 x 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 (Strove et al. 2007; Wang and Overland 2009). With climate warming come new impacts on established Arctic ecosystems, including shifts among the marine communities. Published examples include the re-appearances of the blue mussel (*Mytilus edulis*) for the first time in the Arctic since the Viking Age, 1,000 to 1,300 BP (Berge et al. 2005) and the occurrence of three temperate euphausiids (*Thysanoessa longicaudata*, *Meganyctiphanes norvegica* and *Nematoscelis megalops*) in Kongsfjorden, West Spitsbergen, Svalbard (Buchholz et al. 2010). However, none of those southern invaders are considered reproductively competent in the Arctic, presumably because of the low temperature constraint (Berge et al. 2005; Dalpadado et al. 2008a, b; Buchholz et al. 2010). Reproductive competence for a given species might be established by observing a temporal sequence of egg maturation and recording the presence of live juveniles in the new environment. Such active 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 finding of a North Atlantic (Sheader 1981; Williams and

Robins 1981; Lampitt et al. 1993), free-swimming, open-water invader, which now successfully reproduces in high Arctic waters – the hyperiid amphipod *Themisto compressa*.

Since 2000, a long-term observatory has been maintained by the Alfred Wegener Institute 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 the observations in September 2000, pelagic amphipods of the genus *Themisto* (Hyperiidae) 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. The sampling site is located in the Fram Strait, an important transition zone, characterized by the 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, occupying the upper layer of 200 m, is present throughout the year. However, 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 et al. 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 (Schauer et al. 2008; Beszczynska-Möller et al. 2012). The highest recorded values of temperature and salinity in the core of Atlantic Water were observed in 2006 (Walczowski and Piechura 2007; Walczowski et al. 2012). Concomitantly a progressive reduction of sea-ice coverage and increased ice export through the Fram Strait has been observed since 2003 (Spreen et al. 2009).

Among Arctic macrozooplankton, pelagic amphipods act as predators on herbivorous zooplankters, forming a link to higher trophic levels as a food source for seabirds and marine mammals (Bradstreet and Cross 1982; Lønne and Gulliksen 1989; Hobson et al. 2002; Dalpadado and Bogstad 2004; Dalpadado et al. 2008b; Noyon et al. 2009). Our observations show that the North Atlantic invader *T. compressa*, which ranks third in frequency of appearances (individuals m^{-2} d^{-1}) compared to its sub-Arctic and Arctic relatives (*Themisto abyssorum* and *Themisto libellula*, respectively), has recently established an increasing, annually re-appearing population at higher latitudes. Furthermore, we record an increasing contribution of sub-arctic *T. abyssorum* and the temperate *T. compressa* to the zooplankton community over the last 8 years (Fig. 7.1).

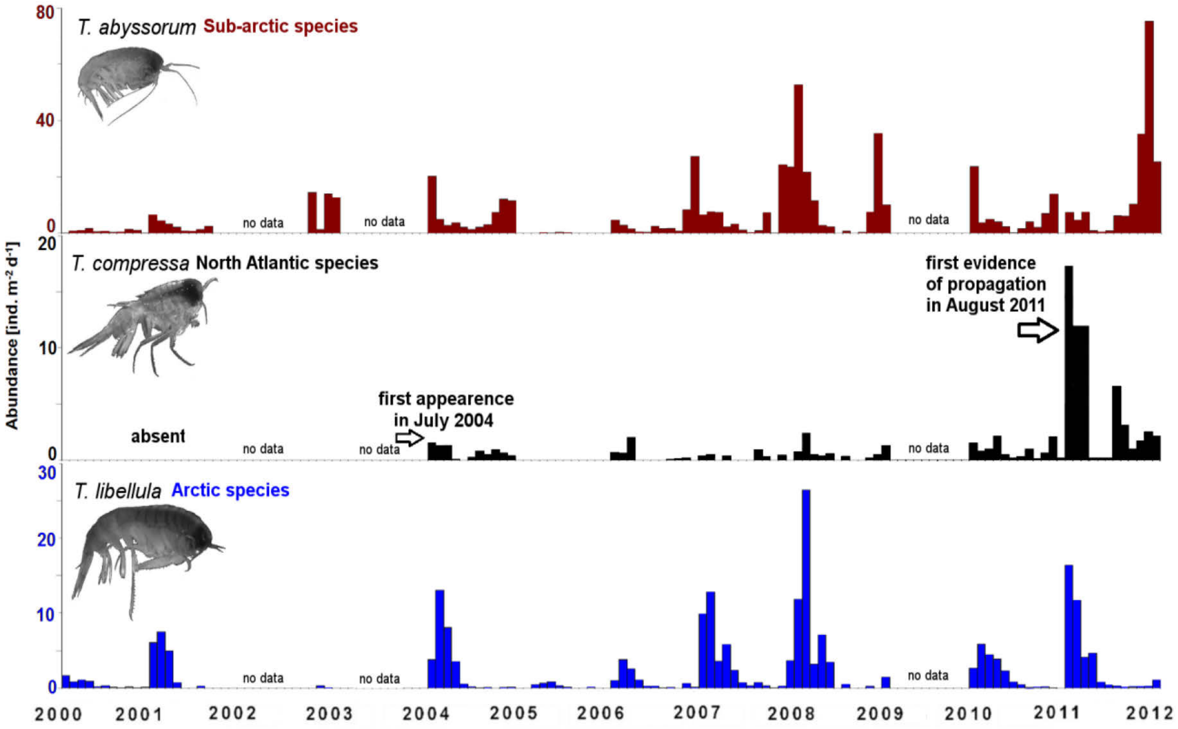

Fig. 7.1 Long-term progression of three different temperature-adapted species of free-swimming amphipods (genus *Themisto*, family Hyperiidae) in the northeastern Fram Strait, Arctic Ocean. While *T. abyssorum* and *T. libellula* are the well-known, actively breeding predators in high Arctic waters, the appearance of the typical North Atlantic species *T. compressa* at 79° N in summer 2004 was surprising. Even more so was the recording of ovigerous females in August 2011. Presumably, this north Atlantic species has recently established a small but stable population and inhabits the warm Atlantic current between 200 and 900 m depth in the northeastern Fram Strait

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 competence within *T. compressa*. Since the first appearance of this southern, temperate invader in 2004, no evidence of reproducing individuals or discovery of juveniles had been recorded for this North Atlantic species 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. 7.2). Later developmental stages of juveniles appeared in September and October 2011. With a presumed life span of up to two years in sub-arctic waters, up to three size cohorts with juveniles, sub-adults and adults were recorded from October 2011 onwards in the traps (Fig. 7.2). Mean current speed of ~13 cm s^{-1} in the core Atlantic water of the West Spitsbergen Current suggest that a passive transport of ovigerous females from North Atlantic breeding grounds, such as from the central Norwegian Sea, would take at least 150 days for organisms to reach the northeastern Fram Strait. Given an estimated egg incubation time of 1-2 months for females, the probability that the observed individuals originated from more southern habitats seems unlikely. Different stages of egg maturation were represented in samples from August to October 2011. Each female carried 23-56 fertilized eggs (mean diameter 125 µm) or newly hatched juveniles in their brood pouch (Fig. 7.2). 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, which allow the establishment of a stable population of this species in high Arctic waters, our findings provide the first evidence that this species has successfully reproduced in high Arctic waters. It supersedes recently published results of its non-reproducing state up to 2010 (Kraft et al. 2012).

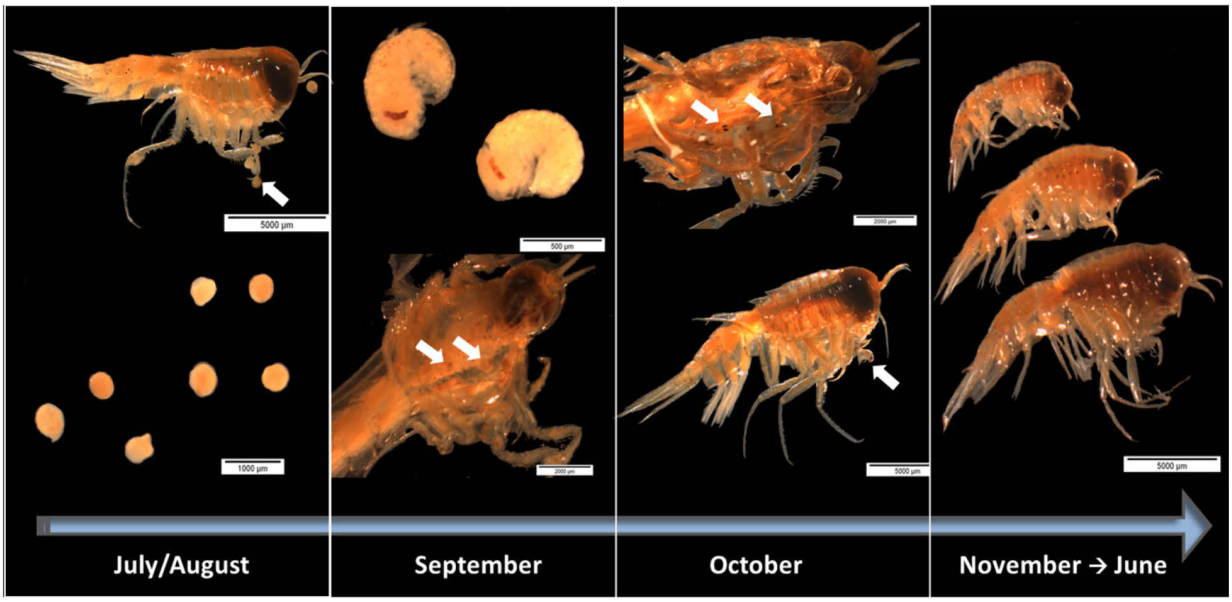

Fig. 7.2 Observations of 21 ovigerous individuals with fertilized eggs, as well as recently hatched juveniles, in the southern temperate invader *Themisto compressa* (Amphipoda, Hyperiidae) provide evidence of reproductive competence within this North Atlantic species at 79° N, 4° E. Later developmental stages of juveniles appeared in September and October 2011. With a presumed life span of up to two years in sub-arctic waters, up to three size cohorts with juveniles, sub-adults and adults were recorded from October 2011 onwards in moored sediment traps. Our findings provide the first evidence that this species has successfully reproduced in high Arctic waters

So far, the general assumption of 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 was 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 and Kosobocova 2007). Observations of full reproductive competence may thus serve to indicate a regime shift from Arctic to boreal conditions.

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 the dissipation of the energy flow by a higher diversity and abundance of small carnivorous zooplankton, and the resulting increased competition for habitat and food sources among cold-adapted taxa. Arctic top predators will have to adapt, as fishes, seabirds and marine mammals will have to adjust to a new diet, consisting not only of large Arctic zooplankters, such as *T. 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.

Acknowledgments

We thank N. Knüppel and C. Lorenzen (Alfred Wegener Institute for Polar and Marine Research) for lab assistance and the tedious work of swimmer picking, and K. Lochte (Alfred Wegener Institute for Polar and Marine Research) and J. F. Fife (St Andrews Biological Station, Department of Fisheries and Oceans, Canada) for very useful discussions and perspectives. This study is funded by the German Federal Ministry of Education and Research (project: 03F0629A).

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 twelve expeditions to the Arctic long-term HAUSGARTEN observatory in the northeastern Fram Strait. The mooring is located at 79°03’ N, 04°11’ E, with a sampling depth of 190-280 m. Water depth on location was 2567 m. Collector cups 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 10-16 days during times of high primary and secondary production (May-September), with longer sampling intervals (up to 32 days) 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 carried setae. Males were recognized by long, segmented antennae and considered mature when 13 or more segments were counted (Kane 1963).

References and Notes

NSIDC (National Snow and Ice Data Center) (2012) Arctic sea ice extent settles at record seasonal minimum. NSIDC Publication September 19, 2012, http://nsidc.org/arcticseaicenews/2012/09/arctic-sea-ice-extent-settles-at-record-seasonal-minimum/.

Berge J, Johnsen G, Nilsen F, Gulliksen B, Slagstad D (2005) Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. Mar Ecol Prog Ser 303:167-175.

Beszczynska-Möller A, Fahrbach E, Schauer U, Hansen E (2012) Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean, 1997–2010. ICES J Mar Sci 69:852-863.

Bradstreet MSW, Cross WE (1982) Trophic relationships at high arctic ice edges. Arctic 35:1-12.

Buchholz F, Buchholz C, Weslawski J (2010) Ten years after: krill as indicator of changes in the macro-zooplankton communities of two Arctic fjords. Polar Biol 33:101-113.

Dalpadado P, Bogstad B (2004) Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. Polar Biol 27:140-154.

Dalpadado P, Ellertsen B, Johannessen S (2008a) Inter-specific variations in distribution, abundance and reproduction strategies of krill and amphipods in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55:2257-2265.

Dalpadado P, Yamaguchi A, Ellertsen B, Johannessen S (2008b)Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55:2266-2274.

Gabric AJ, Qu B, Matrai P, Hirst AC (2005) The simulated response of dimethylsulfide production in the Arctic Ocean to global warming. Tellus B 57:391-403.

Hirche HJ, Kosobokova K (2007) Distribution of *Calanus finmarchicus* in the northern North Atlantic and Arctic Ocean - Expatriation and potential colonization. Deep-Sea Res II 54:2729-2747.

Hobson KA, Fisk A, Karnovsky N, Holst M, Gagnon JM, Fortier M (2002) A stable isotope (δ13C, δ15N) model for the North Water food web: implications for evaluating trophodynamics and the flow of energy and contaminants. Deep-Sea Res II 49:5131-5150.

Kane JE (1963) On the moulting and feeding of a hyperiid amphipod. Crustaceana 6:129-132.

Kraft A, Bauerfeind E, Nöthig E-M (2011) Amphipod abundance in sediment trap samples at the long-term observatory HAUSGARTEN (Fram Strait, ~79°N/4°E). Mar Biodiv 41:353-364.

Kraft A, Bauerfeind E, Nöthig E-M, Bathmann UV (2012) Size structure and life-cycle patterns of dominant pelagic amphipods collected as swimmers in sediment traps in the eastern Fram Strait. J Mar Sys 95:1-15.

Lampitt RS, Wishner KF, Turley CM, Angel MV (1993) Marine snow studies in the northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. Mar Biol 116:689-702.

Lenton TM (2012) Arctic Climate Tipping Points. In: Wassmann P, Lenton TM (eds) The Arctic in the Earth System perspective: the role of tipping points. Ambio, Springer Netherlands, vol. 41, pp 10-22.

Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. Polar Biol 9:187-191.

Manley O (1995) Branching of Atlantic Water within the Greenland-Spitsbergen passage: An estimate of recirculation. J Geophys Res 100:20627-20634.

Noyon M, Gasparini S, Mayzaud P (2009) Feeding of *Themisto libellula* (Amphipoda Crustacea) on natural copepods assemblages in an Arctic fjord (Kongsfjorden, Svalbard). Polar Biol 32:1559-1570.

Polyakov I, Timokhov L, Dmitrenko I, Ivanov V, Simmons H, Beszczynska-Möller A, Dickson R, Fahrbach E, Fortier L, Gascard J-C, Hölemann J, Holliday NP, Hansen E, Mauritzen C, Piechura J, Pickart R, Schauer U, Walczowski W, Steele M (2007) Observational program tracks Arctic Ocean transition to a warmer state. Eos Trans AGU 88:398-399.

Quadfasel D, Gascard JC, Koltermann KP (1987) Large-scale oceanography in Fram Strait during the 1984 marginal ice zone experiment. J Geophys Res-Oceans 92:6719-6728.

Reigstad M, Wassmann P, Wexels Riser C, Øygarden S, Rey F (2002) Variations in hydrography, nutrients and chlorophyll a in the marginal ice-zone and the central Barents Sea. J Mar Sys 38:9-29.

Saloranta TM, Haugan PM (2001) Interannual variability in the hydrography of Atlantic water northwest of Svalbard. J Geophys Res-Oceans 106:13931-13943.

Schauer U, Beszczynska-Möller A, Walczowski W, Fahrbach E, Piechura J, Hansen E (2008) Variation of Measured Heat Flow Through the Fram Strait Between 1997 and 2006. In: Dickson RR, Meincke J, Rhines P (eds) Arctic–Subarctic Ocean Fluxes, Springer, Netherlands, pp 65-85.

Sheader M (1981) Development and growth in laboratory-maintained and field populations of *Parathemisto gaudichaudi* (Hyperiidea: Amphipoda). J Mar Biol Ass UK 61:769-787.

Spreen G, Kern S, Stammer D, Hansen E (2009) Fram Strait sea ice volume export estimated between 2003 and 2008 from satellite data. Geophys Res Lett 36:L19502.

Stroeve J, Holland MM, Meier W, Scambos T, Serreze M (2007) Arctic sea ice decline: Faster than forecast. Geophys Res Lett 34:L09501.

Walczowski W, Piechura J (2007) Pathways of the Greenland Sea warming. Geophys Res Lett 34:L10608.

Walczowski W, Piechura J, Goszczko I, Wieczorek P (2012) Changes in Atlantic water properties: an important factor in the European Arctic marine climate. ICES J Mar Sci 69:864-869.

Wang M, Overland JE (2009) A sea ice free summer Arctic within 30 years? Geophys Res Lett 36:L07502.

Wassmann P, Duarte CM, Agusti S, Sejr MK (2011) Footprints of climate change in the Arctic marine ecosystem. Glob Change Biol 17:1235-1249.

Weslawski J, Wiktor J, Kotwicki L (2010) Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming. Mar Biodiv 40:123-130.

Weslawski JM, Kendall MA, Wlodarska-Kowalczuk M, Iken K, Kędra M, Legezynska J, Sejr MK (2011) Climate change effects on Arctic fjord and coastal macrobenthic diversity—observations and predictions. Mar Biodiv 41:71-85.

Williams R, Robins D (1981) Seasonal variability in abundance and vertical distribution of *Parathemisto gaudichaudii* (Amphipoda: Hyperiidea) in the North East Atlantic Ocean. Mar Ecol Prog Ser 4:289-298.

8. Synoptic discussion

Hyperiid species representing the order Amphipoda form important links between the herbivore zooplankton community and higher trophic levels of the Arctic marine food webs. The present study investigates the community patterns and life-cycle history of the epipelagic amphipod genus *Themisto* (**publications I, II, IV** and **V**) under the aspects of declining sea-ice cover and warming water temperatures. In additon, a first investigation of the ecological status (including reproduction and feeding strategies) of the deep-water amphipod *Cyclocaris guilelmi* was carried out (**publications III** and **IV**). The following sections combine the findings of the five research studies, and compare results and interpretation to the current knowledge published in the scientific literature. Thereby, the objectives of this thesis are addressed in three sections:

- section 8.1 explains the year-round life-cycle biology, population structure and biomass development of dominant amphipod taxa in the northern Fram Strait
- section 8.2 describes the trophic structure of pelagic amphipods and compares their lipid and gut content composition during different seasons, including the polar night
- section 8.3 highlights the species specific adaptations to their Arctic environment, and discusses the consequences of long-term shifts in amphipod compositions under the aspect of changing temperature and sea-ice properties

8.1 Community composition, life-cycle history and biomass estimations

As the annual Arctic summer sea-ice cover continues to reach new minima and average annual seawater temperature is warmer compared to about 50 years ago, one has to expect a biological answer to these changes at multiple levels, which includes the pelagic amphipod community. In order to understand biological consequences, a comprehensive view of the ecology of the involved species is needed. In comparison to calanoid copepods, which have been thoroughly investigated over the past 50 years (e.g., Jaschnov 1970; Conover 1988; Conover et al. 1988; Eilertsen et al. 1989; Hirche 1989, 1996; Hirche et al. 1994; Niehoff et al. 2002; Graeve et al. 2005; Daase et al. 2007; Falk-Petersen et al. 2007, 2009; Leu et al. 2011), studies describing the biology, distribution and appearances of pelagic Amphipoda in high Arctic ecosystems are rare. To address this issue, year-round population dynamics and life-cycle biology of dominant pelagic amphipods in a high Arctic ecosystem were studied.

Community composition

At the sampling sites across the open waters of the Fram Strait, around the Svalbard archipelago and in the fjords of Isfjorden and Rijpfjorden, pelagic amphipods were found to largely contribute to the zooplankton composition in this high-latitude ecosystem. With a total of 18 amphipod species found in moored sediment traps (**publications I and III**), and collected from the open water column by means of a Methot Isaac Kidd net (**publication II**), a large multinet and a pelagic fish trawl (**publication IV**), the reported species composition agrees with previous observations in these areas, as reviewed by Hop et al. (2006). An overview of the study sites and applied sampling methods is presented in Appendix A1, Tables 12.1 and 12.2.

The most abundant amphipods sampled belonged to the genus *Themisto*, family Hyperiidae, in epipelagic waters (*T. abyssorum*, *T. compressa* and *T. libellula*), while the deep-water amphipod *Cyclocaris guilelmi* (family Cyclocaridae) was most frequently sampled in meso- and bathypelagic waters. Interestingly, similar species compositions were found in multinet samples and in sediment trap samples as most of the collected taxa were sampled by both methods (Table 8.1). Exceptions were two hyperiids of the genus *Hyperia*, (*H. galba* and *H. medusarum*), which were mainly observed in the traps; the ice-amphipod *Apherusa glacialis*, which was exclusively found in nets, as well as the three bathypelagic amphipods *Tryphosella* sp., *Andaniexis abyssi* and *Astyra longipes*, which occurred either in the net or trap samples (Table 8.1).

An important finding of this thesis is the northward range expansion of the North Atlantic hyperiid *Themisto compressa*, which was continuously present in the sediment trap at 79° N staring July 2004 (**publication I**), and showed first evidence of breeding activity by summer 2011 (**publication V**). In this context, the North Atlantic origin of *T. compressa* is well established. Although not many published investigations of this species exist, it is in fact the dominant pelagic amphipod in the open waters of the North Atlantic (Sheader 1981; Williams and Robins 1981; Lampitt et al. 1993) and frequently collected by various plankton nets (including multinets and pelagic fish trawls) along the eastern coast of Canada (Fig. 8.1). With its appearance and established reproductive competence in Arctic waters, *T. compressa* would become an indicator for a regime shift in high Arctic ecosystems, which is discussed in detail in section 8.3.

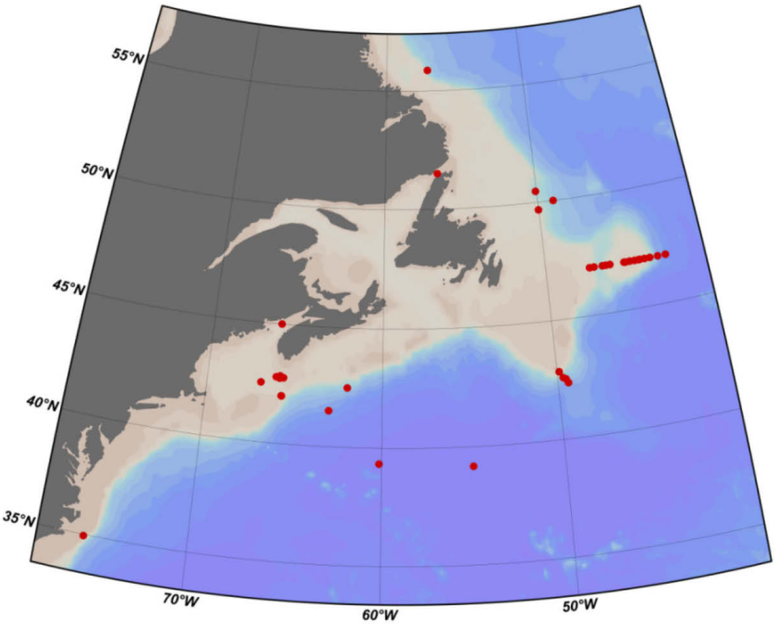

Fig 8.1 Sampling records of the pelagic hyperiid amphipod *Themisto compressa* from 1923 to 2008 in North Atlantic waters off the eastern coast of Canada (Source: Atlantic Reference Centre, St. Andrews Biological Station, St. Andrews, New Brunswick, Canada).

Life-cycle history

The life-cycles of *Themisto* spp. in the European Arctic has been the subject of strong debate in published literature. The life span of *T. libellula*, for example, has been reported to last from one (Dunbar 1957) to four years (Weslawski et al. 2006; Marion et al. 2008). With sediment traps collecting year-round samples of the zooplankton composition in the northern Fram Strait, I had the serendipitous opportunity to study and compare complete annual cycles of pelagic amphipod species. The results presented in **publication I** indicate a life span of two years for *T. abyssorum*, three years for *T. compressa* and at least three years for *T. libellula* in the northeastern Fram Strait (Fig 8.2). For all three species the observed growth patterns suggested a division into two phases, with an immature phase of rapid growth, and a mature phase of slower growth. The appearance of *T. libellula* specimens with a total body length of up to 56.7 mm suggested that *T. libellula* can prolong its life over more than three years. Furthermore, a detailed analysis of the inter-annual cohort pattern of *T. abyssorum* and *T. libellula* from 2000 to 2009 indicated that both species have developed a well-established co-existence mechanism, which includes a different timing of brood release (February to late April for *T. libellula* and May to late July for *T. abyssorum*) (**publication I**). Given their longevity in the waters around Svalbard, *Themisto* spp., but in particular *T. libellula*, are an important year-round food source for higher trophic levels such as fish and seabirds in high-latitude ecosystems. This status is confirmed by trophic investigations of fish stocks, e.g., the capelin (*Mallotus villosus*). In a recent study, Hedeholm et al. (2012) investigated the stomach and gut content of capelin stocks off the western coast of Greenland (from 66° to 72° N), and found that 18 % of capelin food sources were comprised of amphipods. The dominant amphipod found in capelin stomachs was *T. libellula*, followed by fewer individuals of *T. abyssorum* and *T. compressa.* Other food items included euphausiids (61 %) and copepods (10 %).

As reviewed in **publication I**, studies of *Themisto* spp. from different investigation areas show different life span maxima, generation times and sizes. I suggest that the adoption of a particular life history is not a fixed feature within *Themisto* spp., but strongly depends on local and geographic variants. The concept of life-cycle adaptation according to abiotic factors within amphipods is not new: it was suggested for gammarids, for example the intertidal species *Gammarus duebeni*, three decades ago (Wildish 1982). In a highly variable and seasonal environment, such as the one found in the northern Fram Strait, it can be expected that a two to three year life-cycle within an amphipod population may result in large inter-annual variations in abundances: the population can boom in good years and crash in bad ones, based on the availability on their food sources. Consequently, it can be expected that an amphipod population with a longer life-cycle, (namely *T. libellula*, **publication I**) has a better ability to withstand years with low food availability.

At greater water depths, the meso- and bathypelagic amphipod community in sediment trap samples (**publication III**) and plankton nets (**publication IV**) was shown to be dominated by the deep-water amphipod *Cyclocaris guilelmi*, a so far poorly investigated member among the free-swimming deep-sea amphipods in the Arctic. A high number of collected *C. guilelmi* individuals questioned its ecological importance among the deep-water zooplankton. With the first investigation of its population structure, the presence of four size cohorts including juveniles and ovigerous (egg-bearing) females was found in sediment trap samples from 2004 to 2008 (800-2700 m water depth). The year-round appearance of juveniles pointed to a prolonged breeding span of this species, possibly occurring throughout the year (**publication III**). Furthermore, this thesis first reported on the fatty acid composition of *C. guilelmi* and the status of this amphipod as a pelagic carnivore in the meso- and bathypelagic waters of the Fram Strait and north of Svalbard. Herewith, signals are that *C. guilelmi* fills the niche of *Themisto* spp. in the meso- and bathypelagic waters, feeding actively on calanoid copepods and other herbivore and carnivore zooplankton (**publication IV**).

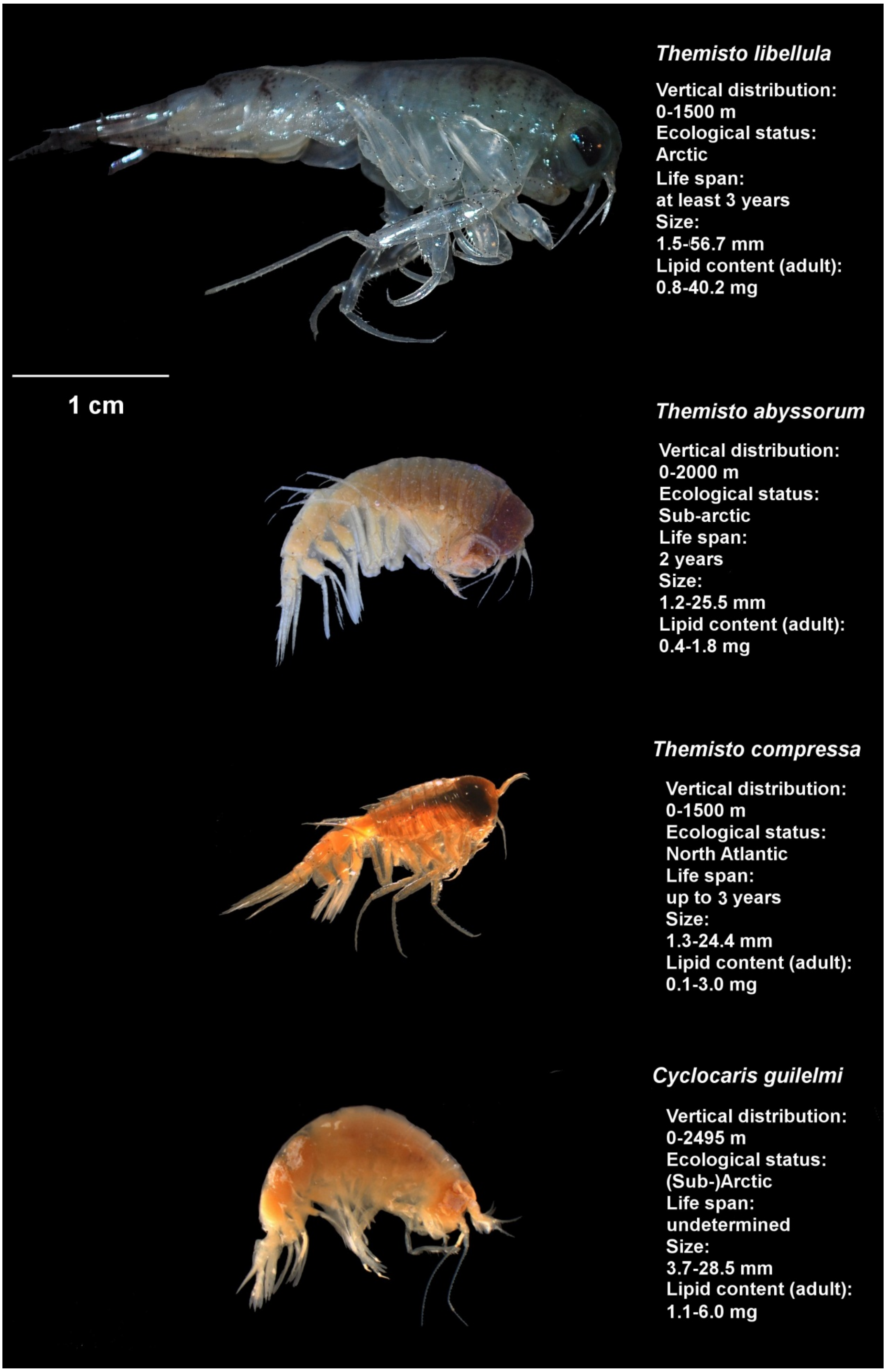

Fig. 8.2 A comparison of life history parameters of *Themisto libellula*, *T. abyssorum*, *T. compressa* and *Cyclocaris guilelmi* found during this study

Table 8.1 Records of amphipod species and depth distribution in plankton nets and sediment traps from high Arctic waters

Year Expedition	2011 ARK-XXVI/1	2011 ARK-XXVI/2	2011 IMR Survey	2012 ARCTOS-8510	Sediment Trap HAUSGARTEN (Year, month, depth)
Taxon					
Calliopiidae					
Apherusa glacialis (Hansen 1887)	-	400-2000 m	-	-	-
Cyclocaridae					
Cyclocaris guilelmi (Chevreux 1899)	400-2000 m	400-2000 m	-	-	2000-2012; year-r.nd; 280-2495 m
Cyphocarididae					
Cyphocaris bouvieri (Chevreux 1916)	1000-2000 m	-	-	-	2009-2012; Oct-May; 1313-2495 m
Eusiridae					
Eusirogenes arctica (Tencati 1968)	1000-1500 m	-			-
Eusirus holmi (Hansen 1887)	600-800 m	800-1000 m	-	-	2004-2012; year-r.nd; 190-1230 m
Gammaridae					
Gammarus wilkitzkii (Birula 1897)	-	0-600 m	0-100 m	-	2000-2012; year-r.nd; 190-280 m
Hyperiidae					
Hyperia galba (Montagu 1813)	-	-	-	0-60 m	2008-2009; year-r.nd; 201 m
Hyperia medusarum (Müller 1776)	-	-	-	-	2000-2001; year-r.nd; 280 m
Themisto abyssorum (Boeck 1870)	0-2000 m	0-2000 m	0-100 m	20-225 m	2000-2012; year-r.nd; 190-2495 m
Themisto compressa (Goës 1866)	0-50 m	0-600 m	-	60-225 m	2004-2012; year-r.nd; 190-1300 m
Themisto libellula (Lichtenstein 1822)	0-600 m	0-600 m	0-100 m	20-225 m	2000-2012; year-r.nd; 190-1250 m
Lanceolidae					
Lanceola clausi (Bovallius 1885)	200-2000 m	0-2000 m	-	-	2004-2012; year-r.nd; 190-2370 m
Lysianassidae					
Tryphosella sp. (Bonnier 1885)	-	-	-	-	2005-2012; year-r.nd; 2357-2495 m
Scinidae					
Scina borealis (G. O. Sars 1882)	600-800 m	-	-	-	2005; Jan-Feb; 280 m
Stegocephalidae					
Andaniexis abyssi (Boeck 1871)	-	-	-	-	2007; Dec; 1316 m
Stilipedidae					
Astyra longipes (Stephensen 1933)	1500-2000 m	1000-1500 m	-	-	-
Uristidae					
Onisimus glacialis (Sars 1900)	-	-	-	-	-
Onisimus nanseni (Sars 1900)	400-600 m	0-600 m	-	-	2006; Dec; 1300 m

Biomass estimates from sediment trap and multinet samples

Through 50 years of sediment trap based studies, collected zooplankton were considered a contamination (e.g., Karl and Knauer 1989; Wakeham 1993; Buesseler et al. 2007). However, more recent investigations indicated the usefulness of collected zooplankton from sediment traps, for example for the long-term exploration of species biomass and population dynamics (Seiler and Brandt 1997; Willis et al. 2008; Makabe et al. 2010; Kraft et al. 2011; **publications I, III-V**). When collected in sediment traps, the zooplankton are referred to as 'swimmers', as they are assumed to have actively entered the moored traps. Besides the obvious reasons for variability of swimmer biomass such as location and depth variations, one caveat of the sediment trap technique, when compared to plankton nets, is their restriction in terms of quantitative sample collection. A comparison of data from sediment traps with multinet records must take into account that multinet samples provide integrated data regarding the sampling depth (Richter 1994), whereas sediment traps are moored at a fixed depth in the water column. An exemplary comparison of copepod versus amphipod biomass from sediment trap and multinet samples (Appendix A2, Tables 12.4-12.6) addressed this issue.

In total, amphipods and copepods comprise about 80 % of the total macro- and mesozooplankton biomass collected in the sediment traps (Nöthig et al., unpublished data). Other zooplankton groups observed in sediment trap samples included, amongst others, pteropods, ostracods, euphausiids and chaetognaths, which had an average contribution of less than 20 % of the total swimmer biomass. An exemplary biomass calculation for the sampling period 2007-2008 showed an overall year-round ratio of 3:1 of amphipod (*Themisto* spp.) over copepod biomass collected in sediment trap samples at 190 m water depth (Appendix A2, Table 12.4). Interestingly, these findings agree with a study from Hirche et al. (1994), where the authors found a three times higher amphipod biomass than that of copepods (*Calanus hyperboreus* and *Paraeuchaeta* spp.) in RMT net samples in the Greenland Sea. While *Themisto* spp. have the highest share among the amphipod biomass, another predator rules the copepod biomass in the sediment traps: the carnivorous copepod *Paraeuchaeta norvegica* (Appendix A2, Table 12.4). *P. norvegica* is a widely distributed copepod in the Norwegian Sea, with its major vertical distribution at 400-500 m depth (Fleddum et al. 2001) and *Calanus* spp. being its major prey (Olsen et al. 2000). Similar results were also recorded by Seiler and Brandt (1997) in the Greenland Sea, where carnivorous crustaceans dominated the swimmer biomass in sediment traps deployed at 500, 1000 and 2300 m depth. Taken the above facts into account, it can be implied that the high biomass of carnivorous zooplankton (*Themisto* spp. and *P. norvegica*) in sediment traps might be caused by their attraction to the traps, as a location where potential food could be found. However, further investigations, for example by the provision of a recording camera system attached to the sediment trap funnel, are needed to address this hypothesis. From 2000 to 2012, the observed biomass of copepods and *Themisto* spp. showed high year-to-year variations (Fig. 8.3), with a trend towards an increase of the proportion of the sub-arctic hyperiid *T. abyssorum* and the North Atlantic *T. compressa* in the most recent sampling period 2011/12 (Appendix A2, Table 12.5).

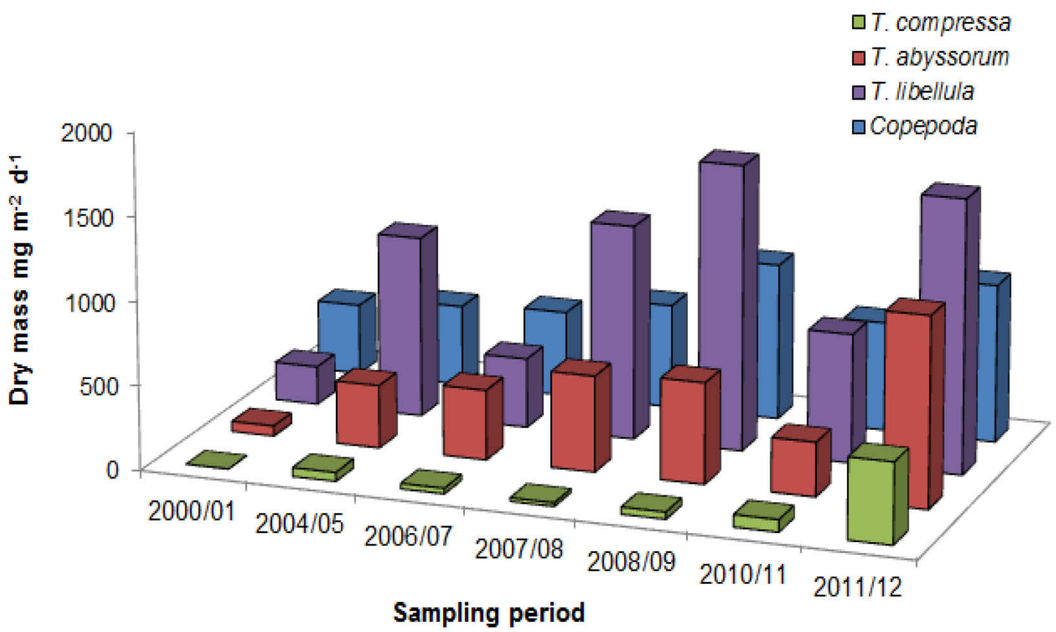

Fig. 8.3 Year-to-year variations of the estimated biomass development of dominant *Themisto* species and copepods recorded in the epipelagic sediment traps (190-280 m) at the HAUSGARTEN observatory (79°01’ N / 04°20’ E) in the northeastern Fram Strait, Arctic Ocean

In the multinet samples collected during June 2011, the total *Themisto* biomass ranged from 39.68-948.43 mg DM m^{-2} (or 0.20-2.17 mg DM m^{-3}) and depended on the sampling depth (Appendix A2, Table 12.6). The multinet results on biomass were in the same range as previously recorded in literature from the northern Fram Strait (0.25-1.05 mg DM m^{-3} in August 2000; Auel and Werner 2003), and in the north Norwegian Sea (0.59-1.31 mg DM m^{-3} in July 1993, 1996-1998; Wencki 2000). In multinet samples, the amphipod biomass in the upper 200 m was a factor 100 lower than the copepod biomass, while a ratio of ~1:1 was shown in a depth of 200-500/600 m (Appendix A2, Table 12.6). Most interestingly, the monthly mean amphipod biomass recorded in sediment traps (7.52-591.95 mg DM m^{-2} d^{-1}; Appendix A2, Table 12.4) has the same order of magnitude compared to the biomass estimates based on stratified multinet samples in the northeastern Fram Strait. However, as stated above, the biomass ratios (amphipods:copepods) differed between both methods. A possible explanation for the differences in amphipod and copepod biomass ratios from sediment traps and multinets is the absence of large *T. libellula* individuals in the multinet samples (**publication IV**). Amphipods with total body length of more than 35 mm are regularly absent in the samples of plankton nets such as MOCNESS, WP2, WP3, RMT and multinet (e.g., Wencki 2000; Dalpadado et al. 2001; Auel and Werner 2003). It was found that sediment traps (**publication I**) and pelagic fish trawls regularly collect such individuals with a dry mass up to 40.2 mg for *T. libellula* (**publication IV**), as does cod stomach sampling (Dalpadado et al. 2001).

On the background of biomass and life-cycle history of dominant pelagic amphipods in the northern Fram Strait established (**publications I and III**), the question of their trophic impact in a highly heterogeneous Arctic ecosystem remained unclear. Thus, the following section discusses and compares lipid classes, gut contents and fatty acid compositions of the four dominant pelagic amphipods during two strongly contrasting seasons, during the polar night and during midnight sun.

8.2 Trophic structure

Knowledge of predator-prey relationships is essential for understanding energy flows and its control mechanisms in marine ecosystems. The best-studied example of a pulsed Arctic food regime is that of calanoid copepods (genus *Calanus*). Calanoid copepods accumulate large proportions of lipids during the periods of elevated food supply in spring and early summer (e.g., Lee et al. 2006). Furthermore, calanoid copepods are capable to withdraw primary produced carbon from the open water column for several months (Mayzaud et al. 2007), or possibly even longer depending on the life span of the respective species. Most calanoid copepods store wax esters and fatty acids that originate from the photosynthetic processes of phytoplankton, mainly diatoms, ice-algae and dinoflagellates (Sargent and Henderson 1986). The lipids of calanoid copepods consist mainly of polyunsaturated fatty acids (PUFAs), including essential omega-3 fatty acids, which are of high importance in the reproduction, growth and physiology of all marine organisms (Pond et al. 1996). The transfer of particulate lipids to zooplankton largely depends on the trophic characteristics of the consumer (Mayzaud et al. 2007), and only neutral lipids such as triacylglycerols and wax esters are transferred directly via fatty acids from the prey to the consumer (Sargent and Henderson 1986).

The degree and nature of lipid accumulation varies with the adaptation of the zooplankton species: while wax esters are used for long-term energy storage and dominate in diapausing taxa, the metabolically less stable triacylglycerols are associated with short-term energy needs, e.g., during the time of oogenesis (Hakanson 1984, Conover 1988). The accumulated lipids allow the copepods to survive the winter in a non-feeding state at depth, the so-called 'diapause', and provide energy for later reproduction in spring (Conover and Huntley 1991; Falk-Petersen et al. 2009). This strategy makes them a valuable food source for predators, including pelagic amphipods.

Visible gut content

The life strategies of epipelagic amphipods include a seasonal vertical migration (**publication I**). Evidence for this migration behavior is provided by seasonal peaks in occurrences during early (May-June, *T. abyssorum*) and late summer (August-September, *T. libellula*), as well as by few collected individuals during the winter months in sediment trap samples at 190-280 m water depth in the northeastern Fram Strait. A seasonal vertical migration allows to maintain an active life-style throughout the dark periods of the Arctic winter, when *Themisto* spp. follow their main prey, calanoid copepods (**publication II**), to greater water depths. The qualitative and semi-quantitative analyses of *Themisto* spp. gut contents confirmed this feeding strategy and revealed new insights into the diet of pelagic amphipods.

Copepod remains were the main items found in the guts of the investigated *Themisto* species and made up between 50.5-69.7 % of the total food items in summer and fall (**publication IV**), and 32.5-78.9 % in winter (**publication II**). As in *Themisto* spp., the gut content of the deep-water species *C. guilelmi* was also characterized by the dominance of copepod remains. When not damaged, the encountered copepod mandibles could be identified to species and stage level (Fig. 8.4 a-d). Thereby, we followed the results of the only two available studies of mandible-based identification for Arctic and sub-arctic copepods, with exemplary drawings of mandibles of *Metridia longa* (Fig. 8.4 a, b; Dalpadado et al. 2008b) and *Calanus finmarchicus* (Fig. 8.4 c, d; Karlson and Bamstedt 1994). **Publications II and IV** indicate a similar diet composition of *T. abyssorum* and *T. libellula* during the Arctic summer and winter, as both species fed mostly upon calanoid copepods of the genus *Calanus*. Other identified components included fragments of amphipods and chaetognaths, as well as eggs, dinoflagellates, fecal pellets and parasites. The presence of amphipod remains in the gut contents of *T. abyssorum*, *T. libellula* and *C. guilelmi* (**publications II and IV**) provided evidence of cannibalism of these three amphipod species. With various stages of digested zooplankton remains in both, summer and winter samples, this study provided the first evidence that adult individuals of *T. libellula* and *T. abyssorum* can be considered opportunistic feeders during during both seasons, the polar night and midnight sun.

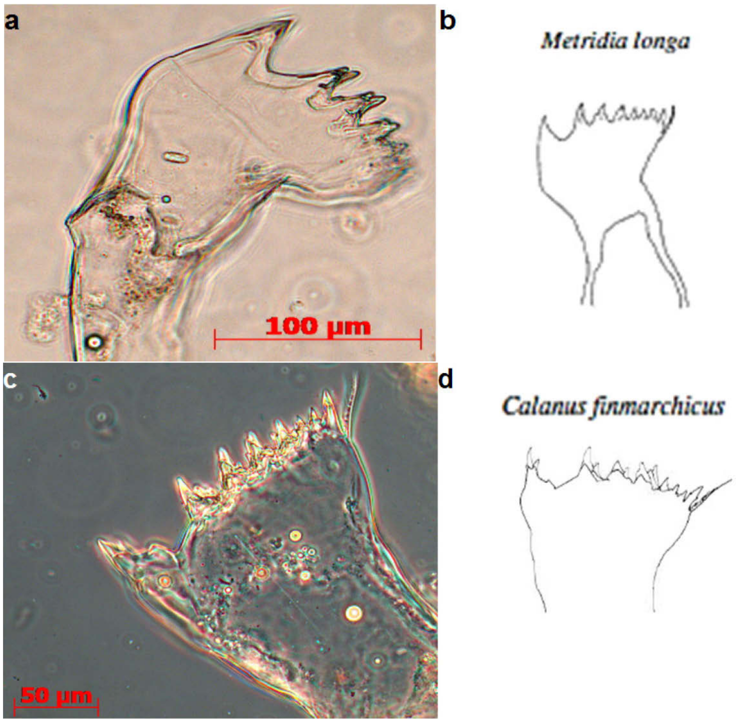

Fig 8.4 a-d Copepod mandibles. Mandible of *Metridia longa* (**a**) and *Calanus finmarchicus* (**c**) from the gut content of *Themisto libellula* and *T. abyssorum*, respectively. Drawing for the identification of *M. longa* (**b**) and *C. finmarchicus* (**d**) mandibles modified from Dalpadado et al. (2008b) and Karlson and Bamstedt (1994), respectively

Foraging strategies

The results of **publications II and IV** demonstrate that the pelagic amphipods *T. libellula* and *T. abyssorum* are active raptorial feeders throughout the year. This year-round feeding behavior raises questions of the respective foraging strategies which allow these predators an effective hunt during the polar night. Land (1989, 2000) and Warrant and Locket (2004) suggested that hyperiid amphipods possess large, doubled structured eyes which allow them to detect objects against dim, down-welling light (upper eye) as well as bioluminescent sources (lower eye). Because down-welling light during the Arctic winter is limited to periodic moonlight events, I suggest that the use of this upper part of the eye structure is not solely responsible for the active foraging and prey detection of *Themisto* spp. Throughout the world’s oceans, a wide variety of organisms from protists to vertebrates are recognized for their ability to produce light by bioluminescence. However, as reviewed by

Haddock et al. (2010), the majority of light emitted in the euphotic zone can be attributed to dinoflagellates and zooplankton. In the Arctic region, Berge et al. (2012) recently documented the presence of small bioluminescent dinoflagellates retaining metabolic rates that enable them to produce light also in times of the polar night. In Arctic winter, dinoflagellates have also been suggested to produce a bioluminescent signal to attract predators of their own predators (Haddock et al. 2010). This mechanism is known as the so-called ‘burglar alarm’. Consequently, it is a possibility that *Themisto* spp. uses light emitted by dinoflagellates to actively prey on calanoid copepods. Other than the visual foraging, feeding modes of hyperiid amphipods could also be influenced by mechanical, tactile and/or olfactory stimuli. In other carnivore zooplankton, such as copepods of the genus *Euchaeta*, scyphozoan jellyfish and siphonophores, the use of tactile stimuli over vision in order to locate prey has been further investigated (Hays 2003). Hays (2003) also showed that tactile stimuli, e.g. by physical contact, enables *Euchaeta* to prey upon zooplankton equally well under darkness and daylight conditions. However, I know of no experimental investigations which address this question in pelagic amphipods yet.

Parasites

Publications II and IV of this stuy illustrate that the digestive systems of one-third of the investigated individuals of *T. libellula* and *T. abyssorum* (including specimens collected with plankton nets as well as from sediment traps from the different investigation sites) were infected by gregarine apicomplexans of the genus *Ganymedes*. While this parasite was first described in the gut contents of *T. libellula* in sediment trap and plankton net samples from the Beaufort Sea in the Canadian Arctic (Prokopowicz et al. 2010), we provided first evidence for the appearance of *Ganymedes* in the guts of *T. abyssorum* in the European Arctic (**publications II and IV**). The genus *Ganymedes* belongs to the family Ganymedidae (Apicomplexa, Gregarinea, Eugregarinorida). This divers group is known to inhabit the intestines, coeloms and reproductive vesicles of marine, freshwater and terrestrial invertebrates (e.g., Huxley 1910; Levine 1977; Leander 2008). Abundant forms found in the gut content are trophozoites, the feeding stage of gregarines. Like most gregarines, the genus *Ganymedes* includes highly derived species with a well-adapted physiology and morphology. Typically, it has a flattened, crown-shaped structure at the anterior end of the trophozoite, the mucron, which is used to attach to the gut epithelium of the host (Leander 2008; Prokopowicz et al. 2010). Besides the visibility of mucrons, we observed similar morphological features of the parasite in both *Themisto* species. This included a single cell structure, an oval to rectangular shaped nucleus at the posterior end of the cells, and the presence of light brownish colored granules in the cytoplasm which suggested an accumulation of amylopectin (Fig. 8.5 a, b). Following the descriptions of Prokopowicz et al. (2010), the trophozoites from *T. libellula* and *T. abyssorum* were both identified as *Ganymedes themistos*. However, as host specificity is described as a key characteristic for the group of gregarines in general (Leander 2008), it is important that further investigations genetically compare individuals from the gut contents of *T. libellula* and *T. abyssorum* to verify this assumption.

With an infection rate of about one-third (29-40 %) of all analyzed *Themisto* spp. collected by plankton nets in winter (**publication II**), summer (only *T. abyssorum*, **publication IV**) and in sediment traps year-round (Appendix A3, Table 12.7), the question of the impact of *Ganymedes* on *Themisto* survival and mortality rate is on hand. Previous studies indicated that the effects of gregarine infections cover a wide range, from harmless commensalism to death (e.g., Jimenez et al. 2002). In marine ecosystems, the infection of crustaceans with parasites is a well-established phenomenon with high potential impact on ecosystem function and food web structure. Examples of large infection events leading to mass mortality of the target species have been shown in open marine waters (for example the mass mortality in the krill species *Euphausia pacifica, Thysanoessa spinifera*, and *Thysanoessa gregaria;* Gomez-Gutierrez et al. 2003) and in aquaculture farms, for example causing growth reduction and high mortality in cultured Pacific white shrimp, *Litopaneus vannamei* (Jimenez et al. 2002). A logical consequence of the presence of a parasite in the gut lumen would be the reduction of a host's ability to assimilate food, accompanied by a reduction of fitness (Siva-Jothy and Plaistow 1999; Takahashi et al. 2009, 2011). However, it also has been suggested that gregarines occupying the lumen of the gut are often harmless commensals (Jimenez et al. 2002). In the only other study which compared infection rates of *T. libellula* from plankton net samples with those from sediment traps, Prokopowicz et al. (2010), the authors found no significant difference of infection frequency between both methods. Furthermore, the authors concluded that individuals infected by gregarine individuals were in good health, and were recorded in the sediment traps during their vertical migrations. The results presented agree with the observations and conclusions of Prokopowicz et al. (2010), and I suggest extending this view also on the sub-arctic congener, *T. abyssorum*. Interestingly, no gregarines were found in the investigated individuals of *T. compressa* from sediment trap samples (Appendix A3, Table 12.7), a result which also points to a recent invasion of this North Atlantic hyperiid into the northern Fram Strait.

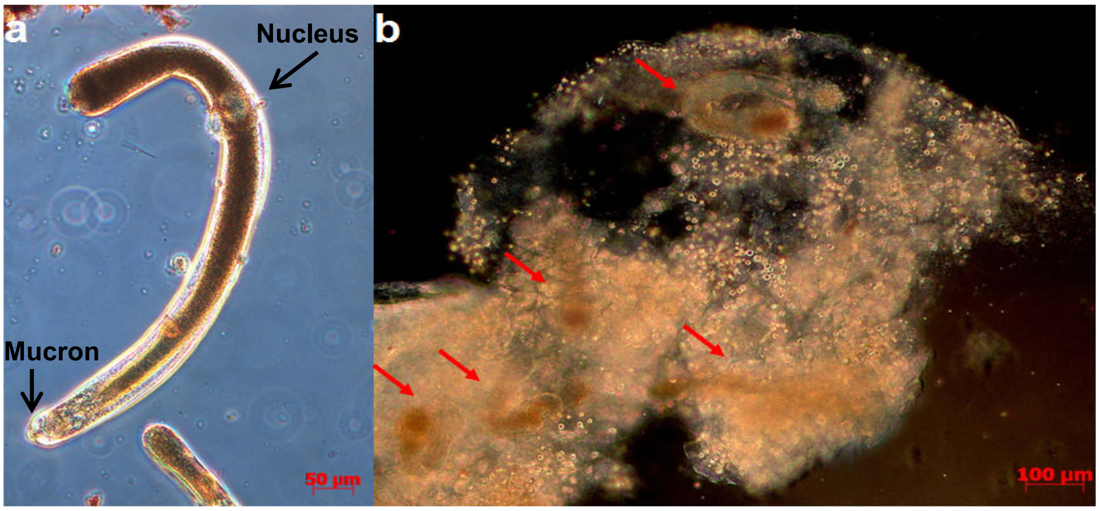

Fig 8.5 a-b Marine gregarine trophozite *Ganymedes* sp., probably *Ganymedes themistos* (**a**), found in summer and winter gut content samples of *Themisto libellula* (with a ball-shaped end on the bottom, the mucron, and an oval shaped nucleus), and in *T. abyssorum* (**b**; red arrows indicate *Ganymedes* individuals attached to gut epithelium). The mucron is used for attachment. The light brown color is most likely caused by an accumulation of amylopectin in the cytoplasm of the single-celled individuals

Lipid composition

Lipids are an effective adaptation to transfer metabolic energy up the food web (e.g., Falk-Petersen et al. 2004; Lee et al. 2006). The tracking of trophodynamic relationships with the use of lipid class and fatty acid profiles is an often-applied method to highlight predator-prey relationships in marine environments (e.g., Graeve et al. 1994a; Falk-Petersen et al. 2002, Dalsgaard et al. 2003). This method is based on the fact that the bulk of *de novo* biosynthesis of fatty acids takes place among the primary producers in marine systems, which consist mainly of diatoms, ice-algae and dinoflagellates in Arctic waters (Bradstreet and Cross 1982; Falk-Petersen et al. 1990, 2009; Carmack and Wassmann 2006). From the base of the marine food web, fatty acids are transferred to higher trophic levels and accumulate as major constituents of the lipid composition of practically all marine mammals (Sargent and Falk-Petersen 1988). However, as we go from herbivores to omnivores and consequently to carnivore zooplankton such as free-swimming amphipods, the markers of herbivory will blur, while other markers such as tracers of herbivorous calanoid copepods (C_{20} and C_{22} MUFAs) increase in importance (Graeve et al. 1994b; Dalsgaard et al. 2003).

In polar environments, herbivorous crustaceans (e.g., copepods) are confronted with strong seasonality of food supplies, and store large reserves of energy-rich lipids to cope with the energetic costs of offspring production and overwintering (Hagen and Auel 2001). In this context, different lipid classes are used for short- (triacylglycerols) and long-term (wax esters) energy storage. An outstanding result of **publication IV** is the observation of a particularly high wax ester content of *C. guilelmi* (mean 60.4-84.0 % of total lipids), which is distinctly higher compared to other published results for pelagic amphipods (including *Themisto* spp.), and much more similar to that of scavenging deep-sea species such as *Eurythenes gryllus* (e.g., Bühring and Christiansen 2001). This suggests that *C. guilelmi* successfully accumulates long-term lipid reserves throughout the year, with copepods as one possible food source. Consequently, the lipid class composition of *C. guilelmi* (**publication IV**) is an example for the fact that wax esters tend to replace short-term reserves as the major lipid class in animals originating from a greater water depth or at higher latitudes (Lee et al. 1971). Beside wax esters, the investigated amphipods stored short-term energy in form of triacylglycerols (TAGs) in different proportions, with increasing TAG contents in winter. Noyon et al. (2011) suggested a similar development for *T. libellula* in Kongsfjorden, Svalbard. The authors concluded that this increase is connected to a survival strategy, which allows *T. libellula* to cope with short periods of starvation. We agree with this hypothesis, and suggest that the increase in TAG levels observed for *T. abyssorum, T. libellula* and *T. compressa* may serve to provide energy for the active vertical migration during the winter, in order to follow copepod prey into deeper waters. This seasonal shift in lipid class proportions seems to be restricted to pelagic amphipod populations, as no such shifts were observed for example among sub-littoral communities in the Arctic region (Legezynska et al. 2012).

With a detailed analysis of the fatty acid profiles from summer and winter samples of *Themisto* spp. and *C. guilelmi*, we expected to gain new insight whether the respective feeding habits and survival strategies vary between 1. pelagic niche species with different water mass origins, and 2. seasons. With regard to the first point, we found a strong similarity in the fatty acid profile within Arctic, sub-arctic and Atlantic *Themisto* spp. and the deep-water amphipod *C. guilelmi*: all amphipods showed high levels of the *Calanus* biomarkers 20:1(n-9) and 22:1(n-11) in their fatty acid and alcohol composition (**publication IV**). The results of the fatty acid analyses indicated that all studied species are part of the *Calanus*-based food web and consequently pelagic predators. With regard to seasonal differences, the clearest fatty acid signal discovered in all investigated species was the increase of diatom markers (16:4(n-1) and 20:5(n-3)) and flagellate markers (18:4(n-3) and 22:6(n-3)) in the winter samples. The typical algal fatty acid markers are most likely digested indirectly via herbivorous copepods, which lead to the conclusion that *Themisto* and *Cyclocaris* exhibit a more intense feeding on *Calanus* during winter and share more diverse diet during summer (**publication IV**). Following the respective tracers of diatom fatty acid markers in importance were high levels of protozoan biomarkers. This result may serve to indicate the importance of dinoflagellates and ciliates in the feeding strategies of the ingested copepods, and agree with a recent review by Saiz and Calbet (2011). In their study the authors concluded that dinoflagellates and ciliates are important components of copepod diets in areas with low primary production and in the summer season. Most interestingly, the results of the fatty acid and fatty alcohol analyses with high levels of the *Calanus* biomarkers indicated that the North Atlantic hyperiid *T. compressa* seems to share the *Calanus*-based diet of *T. abyssorum* and *T. libellula* (**publication IV**); a finding which supports the suggestion of a successful adaptation of this southern invader to high-latitude habitats. Year-round observations of *T. compressa* in sediment trap samples in the northeastern Fram Strait (**publications I and V**), and its appearence in plankton net samples in Isfjorden, Svalbard, during winter (**publication IV**) further confirm this hypothesis. However, as the winter data are only based on two individuals of *T. compressa*, these results have to be seen as a first approach and should be interpreted with the respective caution. Thus, I recognize the need of further sampling efforts of *T. compressa* during the Arctic winter.

In contrast to our expectations, a high similarity was found in the lipid class composition of the epipelagic *Themisto* spp. and the deep-water amphipod *C. guilelmi* and (**publication IV**). This suggests that the epipelagic hyperiids and the meso- and bathypelagic predators follow a similar physiological strategy, with wax esters as preferred long-term storage molecules. From a bi-polar perspective, this similarity among Arctic pelagic amphipods is particularly striking. The circum-Antarctic congener *Themisto gaudichaudii* for example, which shares a similar morphology as *T. compressa*, has a low wax ester content of 0.1-8.1 % (Reinhardt and Van Vleet 1986; Nelson et al. 2001). This variation in lipid storage is also reflected in the life-history: while *T. gaudichaudii* forms a symbiotic commensalism with salps (Madin and Harbison 1977), *T. compressa* is a pelagic predator. Furthermore, the finding of a seasonal signal in the fatty acid profile of *C. guilelmi* was unexpected. On the basis of the previous results on its life history, with a year-round reproduction and a regular appearance throughout the sampling year in sediment traps (**publication III**), we expected a similar fatty acid composition of *C. guilelmi* during both seasons. However, the results of **publication IV** show an increase of *Calanus*-biomarkers in winter samples. For this finding, two possible explanations are presented: one, that *C. guilelmi* has a better access to calanoid copepods during winter as they migrate into deeper water layers during the phase of their diapause; two, that *C. guilelmi* actively feeds on higher trophic levels, such as *Themisto* spp.

The analyses of the gut content of *C. guilelmi* supported both feeding strategies, because copepod and amphipod were both present among the food items (**publication IV**).

To conclude, the findings discussed in this section indicate that a comprehensive analysis of gut contents, fatty acids, fatty alcohols and lipid class composition is needed to understand the complex trophodynamic interactions within pelagic amphipods. It is shown that *Themisto* spp. and *C. guilelmi* act as small predators in high Arctic waters, and seem to continue a 'business-as-usual'-mode (characterized by the absence of reduction of the metabolic rate and an active feeding behaviour; Torres et al. 1994) during the polar night. The fatty acid profiles of *T. abyssorum*, *T. libellula* and *T. compressa* indicated that the three species are predominantly carnivorous predators during summer and winter in the *Calanus*-based Arctic food web. Furthermore, I suggest that the deep-water species *C. guilelmi* possible takes over the trophic niche of *Themisto* spp. in meso- and bathypelagic waters as a carnivore crustacean. The presence of (ice) diatom markers such as 16:4(n-1) and 20:5(n-3), as well as flagellate markers such as 18:4(n-3) and 22:6(n-3) indicate that both photosynthetic systems, an ice-diatom and a dinoflagellate-/*Phaeocystis pouchetii* dominated one, are likely capable of providing the baseline energy reserves to sustain these higher trophic predators.

8.3 Adaptations to a polar environment

Trophic adaptations

A detailed analysis of the fatty acid profiles of the investigated genera *Themisto* and *Cyclocaris* showed the presence of ice-related diatom markers and flagellate markers (**publication IV**). However, no remarkable difference between the two genera was observed. This suggests that either the amphipods, or their respective prey, have established a mechanism to utilize energy sources from both types of phytoplankton groups. While phytoplankton and ice-algae serve as the main food source for herbivorous zooplankton in polar waters, herbivorous copepods represent in turn the main food source for many higher trophic levels, including the pelagic amphipods. With increasing light and sea-ice melt during spring, the stratification of nutrient-rich water masses initiates a short period of high primary production, when both ice-algae and pelagic phytoplankton bloom. This bloom period represents the main pulse of food energy for the entire pelagic ecosystem in Arctic waters. Potential changes of this regime, with an earlier retreat of sea-ice and changes in the timing of ice-algal and phytoplankton blooms, may affect the life-cycle strategies (e.g., reproduction times) and survival of the grazers including *Calanus* spp. and their predators. This match-mismatch hypothesis encompasses the reproductive success of grazers and predators relative to the food availability during critical life stages (Durant et al. 2005), and is gaining more attention because of the observed strong decrease in sea-ice cover in the central Arctic Ocean and the warming of the Atlantic inflow during the last decade (Durant et al. 2007). Because of the strong connection of pelagic amphipods to the *Calanus*-based food web in the Fram Strait and around the Svalbard archipelago implied in this study (**publications II and IV**), a potential mismatch between the appearance of herbivorous *Calanus* species and respective blooming scenarios might also disrupt the match between predatory amphipods and copepods as their prey. Because of the strong similarity of the diet of *Themisto* spp. implied in the findings of this thesis, I hypothesize that the predation pressure on calanoid copepods might remain stable, even if *T. libellula* might be replaced by smaller North Atlantic congeners, such as *T. compressa*. In a top-down dominated food web scenario, the size of fish stocks could also be negatively affected: the polar cod (*Boreogadus saida*), which prefers large Arctic zooplankters, such as *T. libellula* (Bogstad et al. 2011), will have to adapt to a new diet consisting of smaller temperate congeners.

Invasion from the south

In biological oceanography, the identification and classification of zooplankton groups according to their characteristic biology and their water mass affinity is a routine method to determine ecological situations (Harris et al. 2000). By applying this method, zooplankton compositions have been monitored over decades in temperate and tropical waters, while only few datasets convey long-term observation in polar environments such as the central Arctic Ocean and is surrounding seas (e.g., Brodeur and Ware 1992; Hays et al. 2005; Bauerfeind et al. 2009; Wassmann et al. 2011). In the past three decades, published short- and long-term records showed a shift in the zooplankton communities throughout the North Atlantic basin: this shift was characterized by large-scale northward spreads of warm-water calanoid copepod crustaceans (e.g., *Calanus helgolandicus*) and a decrease in the number of cold-water species in the eastern North Atlantic Ocean and European shelf seas (e.g., Beaugrand et al. 2002; Beaugrand 2004, 2009). In these studies, changes in sea-temperature were given as the most likely explanation. Thus, a warming inflow of Atlantic water (transported by the WSC) into the central Arctic Ocean may also lead to the breakdown of current barriers at gateways to high Arctic ecosystems, and consequently to the invasion of new species in these regions. However, one must distinguish whether an invasion is related to the relaxation of dispersal barriers, or to the establishment of new environments that allow the settling of boreal or sub-arctic species in an Arctic environment. Grebmeier et al. (2006)

described an example of a dispersal barrier breakdown in their study: the authors observed the disappearance of a near-bottom ''cold pool'' formed by wintertime sea-ice in the Bering Sea, which allowed the invasion of more southern pelagic species. On the other hand, examples of possible adaptations of boreal and temperate species to changing physical environments are more numerous and can be found at different trophic levels. Examples are the recent re-establishment of the blue mussel (*Mytilus edulis*) on the Svalbard archipelago (Berge et al. 2005), or the introduction and survival of Pacific salmon populations in the Beaufort Sea (Irvine et al. 2009). In general, a warming scenario of Arctic ecosystems is assumed to favor boreal species, with one example being the calanoid copepod *Calanus finmarchicus* (Daase et al. 2007; Falk-Petersen et al. 2007). This leads to the question whether a similar development is to be expected among the pelagic amphipod community. In **publication V**, evidence is presented for the reproductive competence of the southern invader *Themisto compressa* in the northeastern Fram Strait. Although the exact mechanisms of its successful settlement in this region are a subject of speculation, I suggest that this North Atlantic hyperiid was distributed with the recent warming events in 1999-2000 and 2005-2007 (Beszynska-Möller et al. 2012). This suggestion is supported by the first appearance of *T. compressa* at 79° N in July 2004 in sediment trap samples deployed at the deep-sea observatory HAUSGARTEN in the northeastern Fram Strait (Kraft et al. 2011). In the past fourteen years, continuous measurements of the Atlantic Water transported by the WSC through the Fram Strait have shown a considerable warming of about +1° C, with the trend overlaid by multi-year variability (Beszynska-Möller et al. 2012). Furthermore, *T. compressa* seems to have adjusted its growth rates (**publication I**), food source (**publications II and IV**) and time of brood production (**publication V**) to Arctic conditions, because its life-cycle characterisics are similar to the ones observed for the established Arctic and sub-arctic amphipods *T. libellula* and *T. abyssorum*, respectively, in the northeastern Fram Strait. One example in this context is the suggested life span of up to three years for *T. compressa*, which is in the same range as the life span of *T. abyssorum* (two years) and *T.libellula* (at least three years) (**publication I**).

In amphipod ecology, adjustments of body size, growth rate and timing of brood production are known to be the primary adaptations to their environment (Wildish 1982). An example of life history adaptations is described in the study of ten *Gammarus* species by Steele and Steele (1973, 1975). The authors showed that amphipods of the genus *Gammarus* can occupy an extensive geographic area, ranging from the North Pole to the Gulf of Mexico in the northwest Atlantic, because of their adaptations to different temperature regimes. Furthermore, the authors provided evidence that temperature is the fundamental function which controls the metabolic rate, body size and time of reproduction. Thus Arctic amphipods, such as the sympagic species *Gammarus wilkitzkii*, can grow to a large size and have a single, annual brood, which is produced to match the short productive season of high latitudes (Poltermann et al. 2000). Following the importance of temperature on the evolutionary ecology of amphipods, Morino (1978) suggested that distinctive life history adaptations exist for the climatic zones of the world; in this context, multi- and biannual species are found in polar and cold regions, annual species occupy temperate regions, and semiannual species inhabit tropical regions. In the present study, a prime example of Morino's hypothesis is *T. compressa*. In the North Sea, Sheader (1977, 1981) suggested a life span of up to ten months and up to six generations per year for this species, with a maximum size of adult females of 18 mm. We recorded females with a size of up to 24 mm and a life span of two to three years in the northeastern Fram Strait (**publication I**). As far as I am aware, intraspecific differences in size along a latitudinal gradient have been rarely documented in amphipods. One example is a study of two species of supralittoral talitrids along the Atlantic coast of North America (Wildish et al. 2011). In their study, the authors reported an intraspecific correlation between median body size and degrees of latitude north of the species *Platorchestia platensis* and *Orchestia grillus*. Following their conclusions, I hypothesize that the size differences of *T. compressa* from investigation areas in the North Sea and the northern Fram Strait might also be caused by genetic and/or phenotypic responses to the temperature gradients found in the waters from 55° N to 79° N.

Consequently, increasing seawater temperatures in combination with a northward shift of boreal and temperate species, such as *T. compressa* (**publication V**), could lead to an increase in biological competition (Grebmeier 2012), and to an decrease of the abundance of cold-water species that are unable to adjust quickly to warming waters (Bluhm et al. 2009; Weslawski et al. 2009, 2011; Somero 2012). In this thesis, no decrease in absolute numbers (**publication V**) or biomass (Fig. 8.3 and Appendix A2, Table 12.5) was observed for the Arctic species *T. libellula* in the northeastern Fram Strait. Not yet. However, a recent study from Dalpadado et al. (2012), covering a 25-year data series from the Barents Sea, showed a significant reduction in the abundance of *T. libellula* from 1984 to 2010, which the authors suggested to be correlated to a decreasing area of Arctic water masses. To conclude this section, I recommend a continuation of the monitoring of pelagic amphipod populations in the European Arctic, with special attention on the abundances and size structures of *T. libellula* and *T. compressa*. Both species may serve as biological indicators of future environmental modifications in the Arctic marine ecosystem off Svalbard.

9. Future perspectives

In this study I investigated life histories and population structures from the surface waters to the deep-sea, on the example of pelagic amphipods in an Arctic marine ecosystem. Facing the strong physical heterogeneity of the Arctic environment, such as the one found in the Fram Strait, predictions on the effects of global climate change (and warming) are a challenge. If climate-related changes have the capacity to alter an established ecosystem structure, the phyto- and zooplankton composition in high-latitude ecosystems could shift to a new structural state. While this thesis provided a first insight to the trophic relationships of pelagic amphipods as important year-round secondary consumers in a *Calanus*-based food web, it is of prime importance **to maintain and develop established long-term marine observatories, such as the HAUSGARTEN in the northeastern Fram Strait**, for monitoring possible ecosystem shifts. To further investigate the *in situ* behavior of pelagic amphipods, **a programmable camera and video recording system** attached to moored sediment traps would provide further knowledge of amphipod vertical migration patterns and swarming behavior, as well as their possible attraction to the traps.

During this study the emphasis on the lipid class, fatty acid and fatty alcohol composition and the respective food sources of *Themisto abyssorm*, *T. compressa*, *T. libellula* and *Cyclocaris guilelmi* showed strong similarities between epipelagic and deep-water amphipods. However, the actual feeding and foraging strategies of these predators and the role of visual versus tactile or mechanical stimuli is still object of speculation. In order to fully establish a clear understanding of amphipod year-round foraging behavior, I propose **controlled laboratory investigations of these pelagic predators including feeding experiments in both light and dark conditions**. Furthermore, **a study of their enzyme activity in combination with digestion rates should give new insights to the effectiveness of their energy uptake from the respective food sources**. The presented analysis of the lipid class composition showed that all investigated species share a high wax ester content, which serves for a long-term storage of metabolic energy. Thereby, the Arctic *Themisto* spp. strongly differed from their Antarctic congener, *T. gaudichaudii*, which contains close to no wax esters. In fact, the lipid composition of *T. abyssorum*, *T. compressa* and *T. libellula* was much more similar to that of the deep-water amphipod *C. guilelmi*. **A closer investigation of the evolutionary origin of the wax ester analogy between Arctic epi-, meso- and bathypelagic amphipods** could be of high interest to further improve our knowledge of the mechanisms governing the Arctic ecosystem as a whole. Such an understanding would build the basis to adequately predict changes in plankton communities, carbon fluxes and food web processes in the near future.

Another consequence of the presented results is a strong evidence of increasing contributions of boreal and North Atlantic amphipod species in the European sector of the Arctic within the upcoming decade. This development might cause **a higher abundance of smaller, less energetic prey species for higher trophic levels**, although the predation pressure on herbivores, in particular calanoid copepods, could remain stable. Or to end with a quote of Weslawski et al. (2009): "*Warming in the Arctic may result in the negative effects of increased biodiversity*".

10. References

Aarset AV, Aunaas T (1987) Physiological adaptations to low temperature and brine exposure in the circumpolar amphipod *Gammarus wilkitzkii*. Polar Biol 8:129-133.

Angel MV (1989) Vertical profiles of pelagic communities in the vicinity of the Azores front and their implications to deep ocean ecology. Progr Oceanogr 22:1-46.

Astthorsson OS, Gislason A (2003) Seasonal variations in abundance, development and vertical distribution of *Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis* in the East Icelandic Current. J Plankton Res 25:843-854.

Auel H, Harjes M, Da Rocha R, Stübing D, Hagen W (2002) Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biol 25:374-383.

Auel H, Werner I (2003) Feeding, respiration and life history of the hyperiid amphipod *Themisto libellula* in the Arctic marginal ice zone of the Greenland Sea. J Exp Mar Biol Ecol 296(2):183-197.

Bauerfeind E, Nöthig E-M, Beszczynska A, Fahl K, Kaleschke L, Kreker K, Klages M, Soltwedel T, Lorenzen C, Wegner J (2009) Particle sedimentation patterns in the eastern Fram Strait during 2000-2005: Results from the Arctic long-term observatory HAUSGARTEN. Deep-Sea Res I 56:1471-1487.

Beaugrand G, Reid PC, Ibanez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296:1692-1694.

Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog Oceanogr 60:245-262.

Beaugrand G (2009) Decadal changes in climate and ecosystems in the North Atlantic Ocean and adjacent seas. Deep-Sea Res II 56:656-673.

Berge J, Johnsen G, Nilsen F, Gulliksen B, Slagstad D (2005) Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. Mar Ecol Prog Ser 303:167-175.

Berge J, Batnes AS, Johnsen G, Blackwell SM, Moline MA (2012) Bioluminescence in the high Arctic during the polar night. Mar Biol 159:231-237.

Beszczynska-Möller A, Woodgate RA, Lee C, Melling H, Karcher M (2011) A synthesis of exchanges through the main oceanic gateways to the Arctic Ocean. Oceanogr 24(3):82-99.

Beszczynska-Möller A, Fahrbach E, Schauer U, Hansen E (2012) Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean, 1997–2010. ICES J Mar Sci 69:852-863.

Bluhm BA, Iken K, Mincks Hardy S, Sirenko BI, Holladay BA (2009) Community structure of epibenthic megafauna in the Chukchi Sea. Aquat Biol 7:269-293.

Bogstad B, Dalpadado P, Hop H, Orlova EL, Prokopchuk IP, Rudneva GB, Nesterova VN (2011) Feeding of polar cod (*Boreogadus saida*) in the Barents Sea related to food abundance and oceanographic conditions. In Proceedings of 15th Norwegian–Russian Symposium Climate Change and Effects on the Barents Sea Marine Living Resources, Longyearbyen, 7-8 September 2011, p 159.

Bourke RH, Newton JL, Paquette RG, Tunnicliffe MD (1987) Circulation and Water Masses of the East Greenland Shelf. J Geophys Res 92:6729-6740.

Bowman TE (1960) The pelagic amphipod genus *Parathemisto* (Hyperiidea: Hyperiidae) in the North Pacific and adjacent Arctic Ocean. Proc US Acad Sci 112(3439):343-392.

Bowman TE, Gruner HE (1973) The families and genera of Hyperiidea (Crustacea: Amphipoda). Smithsonian Contributions to Zoology 146:1-64.

Bradstreet MSW, Cross WE (1982) Trophic relationships at high Arctic ice edges. Arctic 35(1):1-12.

Brandt A (1997) Suprabenthic Peracarida (Crustacea, Malacostraca) sampled at 75 degrees N off East Greenland. Polar Biol 17:462-464.

Brodeur RD, Ware DM (1992) Long-term variability in zooplankton biomass in the subarctic Pacific Ocean. Fish Oceanogr 1:32-38.

Bühring SI, Christiansen B (2001) Lipids in selected abyssal benthopelagic animals: links to the epipelagic zone? Prog Oceanogr 50:369-382.

Buesseler KO, Antia AN, Chen M, Fowler SW, Gardner WD, Gustafsson O, Harada K, Michaels AF, van der Loeff MR, Sarin M, Steinberg DK, Trull T (2007) An assessment of the use of sediment traps for estimating upper ocean particle fluxes. J Mar Res 65:345-416.

Carmack E, Wassmann P (2006) Food webs and physical–biological coupling on pan-Arctic shelves: Unifying concepts and comprehensive perspectives. Prog Oceanogr 71:446-477.

Carmack E, McLaughlin F (2011) Towards recognition of physical and geochemical change in Subarctic and Arctic Seas. Prog Oceanogr 90:90-104.

Comiso JC (2003) Warming Trends in the Arctic from Clear Sky Satellite Observations. J Climate 16:3498-3510.

Comiso JC, Parkinson CL, Gersten R, Stock L (2008) Accelerated decline in the Arctic Sea ice cover. Geophys Res Lett 35:L01703.

Conover RJ (1988) Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere. Hydrobiologia 167/168:127-142.

Conover RJ, Bedo AW, Herman AW, Head EJH, Harris LR, Horne EPW (1988) Never trust a copepod - some observations on their behavior in the Canadian Arctic. B Mar Sci 43:650-662.

Conover RJ, Huntley M (1991) Copepods in ice-covered seas - Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas. J Mar Sys 2:1-41.

Cooney RT, Coyle KO, Stockmar E, Stark C (2001) Seasonality in surface-layer net zooplankton communities in Prince William Sound, Alaska. Fish Oceanogr 10:97-109.

Dalsgaard J, St. John M, Gerard K, Müller-Navarra D, Hagen W (2003) Fatty acid trophic markers in the pelagic marine environment. Adv Mar Biol 46:227-318.

Daase M, Vik JO, Bagøien E, Stenseth NC, Eiane K (2007) The influence of advection on *Calanus* near Svalbard: statistical relations between salinity, temperature and copepod abundance. J Plankton Res 29:903-911.

Dalpadado P, Borkner N, Bogstad B, Mehl S (2001) Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES J Mar Sci 58:876-895.

Dalpadado P (2002) Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. Polar Biol 25:656-666.

Dalpadado P, Bogstad B (2004) Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. Polar Biol 27:140-154.

Dalpadado P, Ellertsen B, Johannessen S (2008a) Inter-specific variations in distribution, abundance and reproduction strategies of krill and amphipods in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55:2257-2226.

Dalpadado P, Yamaguchi A, Ellertsen B, Johannessen S (2008b) Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. Deep-Sea Res II 55:2266-2274.

Dalpadado P, Ingvaldsen RB, Stige LC, Bogstad B, Knutsen T, Ottersen G, Ellertsen B (2012) Climate effects on Barents Sea ecosystem dynamics. ICES J Mar Sci 69:1303-1316.

Donnelly J, Torres JJ, Hopkins TL, Lancraft TM (1994) Chemical composition of antarctic zooplankton during austral fall and winter. Polar Biol 14:171-183.

Dunbar MJ (1946) On *Themisto libellula* in Baffin Island coastal waters. J Fish Res Board Can 6:419-434.

Dunbar MJ (1957) The determinates of production in the northern seas: a study of the biology of *Themisto libellula* (Mandt). Can J Zool 35:797-819.

Dunbar MJ (1964) Serial Atlas of the marine environment. Folio 6. Euphausiids and Pelagic Amphipods. American Geographical Society, New York.

Durant JM, Hjermann DO, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N, Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecol Lett 8:952-958.

Durant JM, Hjermann DO, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271-283.

Eiane K, Daase M (2002) Observations of mass mortality of *Themisto libellula* (Amphipoda, Hyperidae). Polar Biol 25:396-398.

Eilertsen HC, Tande KS, Taasen JP (1989) Vertical distributions of primary production and grazing by *Calanus glacialis* Jaschnov and *Calanus hyperboreus* Kroyer in Arctic Waters (Barents Sea). Polar Biol 9:253-260.

ERMS (2012) European Register of Marine Species. Online dataset, 07.12.2012, http://www.marbef.org/data/erms.php.

Falk-Petersen S, Hopkins CCE, Sargent JR (1990) Trophic relationships in the pelagic, Arctic food web. In: Barnes M, Gibson RN (eds) Trophic relationships in the marine environment. Aberdeen University Press, Aberdeen, pp 315-333.

Falk-Petersen S, Dahl TM, Scott C, Sargent J, Gulliksen B, Kwasniewski S, Hop H, Millar R (2002) Lipid biomarkers and trophic linkages between ctenophores and copepods in Svalbard waters. Mar Ecol Progr Ser 227:187-194.

Falk-Petersen S, Haug T, Nilsen KT, Wold A, Dahl TM (2004) Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. Polar Res 23:43-50.

Falk-Petersen S, Timofeev S, Pavlov V, Sargent JR (2007) Climate variability and possible effects on Arctic food chains. The role of *Calanus*. In: Ørbæk JB, Tombre T, Kallenborn R, Hegseth EN, Falk-Petersen S, Hoel AH (eds) Arctic-alpine ecosystems and people in a changing environment. Springer Verlag, Berlin, pp 147-166.

Falk-Petersen S, Haug T, Hop H, Nilssen KT, Wold A (2009) Transfer of lipids from plankton to blubber of harp and hooded seals off East Greenland. Deep-Sea Res II 56:2080-2086.

Fleddum A, Kaartvedt S, Ellertsen B (2001) Distribution and feeding of the carnivorous copepod *Paraeuchaeta norvegica* in habitats of shallow prey assemblages and midnight sun. Mar Biol 139:719-726.

Funder S, Goosse H, Jepsen H, Kaas E, Kjær KH, Korsgaard NJ, Larsen NK, Linderson H, Lysa A, Möller P, Olsen J, Willerslev E (2011) A 10,000-Year Record of Arctic Ocean Sea-Ice Variability - View from the Beach. Science 333:747-750.

Gascard JC, Richez C, Rouault C (1995) New insights on large-scale oceanography in Fram Strait: the Spitsbergen Current. Coast Estuar Stud 49:131-182.

Gomez-Gutierrez J, Peterson WT, Robertis A, Brodeur RD (2003) Mass mortality of krill caused by parasitoid ciliates. Science 301:339.

Graeve M, Hagen W, Kattner G (1994a) Herbivorous or omnivorous? on the significance of lipid composition as trophic markers in Antarctic copepods. Deep-Sea Res I 41:915-924.

Graeve M, Hagen W, Kattner G (1994b) Diet-induced changes in the fatty acids composition of Arctic herbivorous copepods: experimental evidence of trophic markers. J Exp Mar Biol Ecol 182:97-110.

Graeve M, Albers C, Kattner G (2005) Assimilation and biosynthesis of lipids in Arctic *Calanus* species based on 13C feeding experiments with a diatom. J Exp Mar Biol Ecol 317:109-125.

Grebmeier JM, Overland JE, Moore SE, Farley EV, Carmack EC, Cooper LW, Frey KE, Helle JH, McLaughlin FA, McNutt SL (2006) A Major Ecosystem Shift in the Northern Bering Sea. Science 311:1461-1464.

Grebmeier JM (2012) Shifting Patterns of Life in the Pacific Arctic and Sub-Arctic Seas. In: Carlson CA, Giovannoni SJ (eds) Annu Rev Marine Sci 4:63-78.

Haddock SHD, Moline MA, Case JF (2010) Bioluminescence in the sea. Annu Rev Marine Sci 2:443-493.

Hagen W, Auel A (2001) Seasonal adaptations and the role of lipids in oceanic zooplankton. Zoology 104:313-326.

Hakanson JL (1984) The long and the short term feeding condition in field-caught *Calanus pacificus*, as determined from the lipid content. Limnol Oceanogr 29:794-804.

Harris R, Wiebe P, Lenz J, Skjoldal R-H, Huntley M (eds) (2000) ICES Zooplankton methodology manual. Academic, London.

Hays GC (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiologia 503:163-170.

Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. Trends Ecol Evol 20:337-344.

Hedeholm R, Grønkjær P, Rysgaard S (2012) Feeding ecology of capelin (*Mallotus villosus* Müller) in West Greenland waters. Polar Biol 35:1533-1543.

Hirche H-J (1989) Egg production of the copepod *Calanus glacialis* – Laboratory experiments. Mar Biol 103:311-318.

Hirche H-J (1996) Diapause in the marine copepod, *Calanus finmarchicus* – A review. Ophelia 44:129-143.

Hirche H-J, Hagen W, Mumm N, Richter C (1994) The Northeast Water Polynya, Greenland Sea. III. Meso- and macrozooplankton distribution and production of dominant herbivorous copepods during spring. Polar Biol 14:491-503.

Holliday NP, Hudges SL, Bacon S, Beszczynska-Möller A, Hansen B, Lavin A, Loeng H, Mork KA, Østerhus S, Sherwin T, Walczowski W (2008) Reversal of the 1960s to 1990s freshening trend in the Northeast North Atlantic and Nordic Seas. Geophys Res Lett 35:L03614.

Hop H, Falk-Petersen S, Svendsen H, Kwasniewski S, Pavlov V, Pavlova O, Soreide JE (2006) Physical and biological characteristics of the pelagic system across Fram Strait to Kongsfjorden. Prog Oceanogr 71:182-231.

Huxley JS (1910) On *Ganymedes anaspidis* (nov. gen., nov. sp.) a gregarine from the digestive tract of *Anaspides tasmaniae* (Thompson). Q J Mircosc Sci 55:155-175.

Irvine JR, R.W. Macdonald, R.J. Brown, L. Godbout, J.D. Reist, E.C. Carmack (2009) Salmon in the Arctic and how they avoid lethal low temperatures. North Pac Anadromous Fish Comm 5:39-50.

Jaschnov VA (1970) Distribution of *Calanus* species in the seas of the Northern Hemisphere. Internationale Reveue der Gesamten Hydrobiologie 55:197-212.

Jimenez R, de Barniol L, Machuca M (2002) *Nematopsis marinus* n. sp., a new septate gregarine from cultured penaeoid shrimp *Litopenaeus vannamei* (Boone), in Equador. Aquac Res 33:231-240.

Karl DM, Knauer GA (1989) Swimmers: a recapitulation of the problem and a potential solution. Oceanography Magazine 2:32-35.

Karlson K, Bamstedt U (1994) Planktivorous predation on copepods. Evaluation of mandible remains in predator guts as a quantitative estimate of predation. Mar Ecol Prog Ser 108:79-89.

Klekowski RZ, Weslawski JM (1991) Atlas of the marine fauna of southern Spitsbergen, vol 2, Invertebrates: Part 1. Institute of Oceanology, Gdansk, 550 p.

Kosobokova KN, Hirche HJ, Hopcroft RR (2007) Reproductive biology of deep-water calanoid copepods from the Arctic Ocean. Mar Biol 151:919-934.

Koszteyn J, Timofeev S, Weslawski JM, Malinga B (1995) Size structure of *Themisto abyssorum* Boeck and *Themisto libellula* (Mandt) populations in the European Arctic Seas. Polar Biol 15:85-92.

Kraft A, Bauerfeind E, Nöthig E-M (2011) Amphipod abundance in sediment trap samples at the long-term observatory HAUSGARTEN (Fram Strait, ~79°N/4°E). Variability in species community patterns. Mar Biodiv 41:353-364.

Land MF (1989) The eyes of hyperiid amphipods - relations of optical structure to depth. J Comp Physiol Sensory Neural Behav Physiol 164:751-762.

Lampitt RS, Wishner KF, Turley CM, Angel MV (1993) Marine snow studies in the Northeast Atlantic Ocean: distribution, composition and role as a food source for migrating plankton. Mar Biol 116:689-702.

Land MF (2000) On the functions of double eyes in midwater animals. Philos Trans R Soc Lond Ser B-Biol Sci 355:1147-1150.

Leander BS (2008) Marine gregarines: evolutionary prelude to the apicomplexan radiation? Trends Parasitol 24:60-67.

Lee RF, Hirota, J, Barnett, AM (1971) Distribution and importance of wax esters in marine copepods and other zooplankton. Deep-Sea Res 18:1147-1165.

Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307:273-306.

Legezynska J, Kedra M, Walkusz W (2012) When season does not matter: summer and winter trophic ecology of Arctic amphipods. Hydrobiologia 684:189-214.

Levine ND (1977) Revision and checklist of the species (other than *Lecudina*) of the aseptate gregarine family Lecudinidae. J Protozool 24:41-52.

Leu E, Søreide JE, Hessen DO, Falk-Petersen S, Berge J (2011) Consequences of changing sea ice cover for primary and secondary producers in the European Arctic shelf seas: timing, quantity, and quality. Prog Oceanogr 90:18-32.

Lønne OJ, Gulliksen B (1989) Size, age and diet of polar cod, *Boreogadus saida* (Lepechin, 1773) in ice covered waters. Polar Biol 9:187-191.

Makabe R, Hattori H, Sampei M, Ota Y, Fukuchi M, Fortier L, Sasaki H (2010) Regional and seasonal variability of zooplankton collected using sediment traps in the southeastern Beaufort Sea, Canadian Arctic. Polar Biol 33:257-270.

Madin LP, Harbison GR (1977) The associations of Amphipoda Hyperiidea with gelatinous zooplankton - I. Associations with Salpidae. Deep-Sea Res 24:449-463.

Manley TO (1995) Branching of Atlantic Water within the Greenland-Spitsbergen Passage: An estimate of recirculation. J Geophys Res 100:20627-20634.

Marion A, Harvey M, Chabot D, Brethes JC (2008) Feeding ecology and predation impact of the recently established amphipod, *Themisto libellula*, in the St. Lawrence marine system, Canada. Mar Ecol Prog Ser 373:53-70.

Marques JC, Bellan-Santini D (1993) Biodiversity in the ecosystem of the Portuguese continental shelf: distributional ecology and the role of benthic amphipods. Mar Biol 115:555-564.

Mayzaud P, Laureillard J, Merien D, Brinis A, Godard C, Razouls S, Labat JP (2007) Zooplankton nutrition, storage and fecal lipid composition in different water masses associated with the Agulhas and Subtropical Fronts. Mar Chem 107:202-213.

Morino H (1978) Studies on the Talitridae (Amphipoda, Crustacea) in Japan. III. Life history and breeding activities of *Orchestia platensis* Krøyer. Publ Seto Mar Biol Lab 24:245-267.

Morison J, Kwok R, Peralta-Ferriz C, Alkire M, Rigor I, Andersen R, Steele M (2012) Changing Arctic Ocean freshwater pathways. Nature 481:66-70.

Nelson MM, Mooney, BD, Nichols PD, Phleger CF (2001) Lipids of Antarctic Ocean amphipods: food chain interactions and the occurrence of novel biomarkers. Mar Chem 73:53-64.

Niehoff B, Madsen SD, Hansen BW, Nielsen TG (2002) Reproductive cycles of three dominant *Calanus* species in Disko Bay, West Greenland. Mar Biol 140:567-576.

Noji TT (1991) The influence of macrozooplankton on vertical particulate flux. Sarsia 76:1-9.

Noyon M, Gasparini S, Mayzaud P (2009) Feeding of *Themisto libellula* (Amphipoda Crustacea) on natural copepods assemblages in an Arctic fjord (Kongsfjorden, Svalbard). Polar Biol 32:1559-1570.

NSIDC (National Snow and Ice Data Center) (2012) Arctic sea ice extent settles at record seasonal minimum. National Snow and Ice Data Center, Online Publication, 19.09.2012, http://nsidc.org/arcticseaicenews/2012/09/arctic-sea-ice-extent-settles-at-record-seasonal-minimum/.

Olsen EM, Jurstad T, Kaartvedt S (2000) The feeding strategies of two large marine copepods. J Plankton Res 22:1513-1528.

Pakhomov EA, Perissinotto R (1996) Trophodynamics of the hyperiid amphipod *Themisto gaudichaudii* in the South Georgia region during late austral summer. Mar Ecol Prog Ser 134:91-100.

Piechura J (2004) The circulation of the Nordic Seas. In: Skreslet S (ed) NATO advanced research workshop on Jan Mayen Island in scientific focus. Kluwer, pp 91-100.

Poltermann M, Hop H, Falk-Petersen S (2000) Life under Arctic sea ice - reproduction strategies of two sympagic (ice-associated) amphipod species, *Gammarus wilkitzkii* and *Apherusa glacialis*. Mar Biol 136:913-920.

Pond D, Harris R, Head R, Harbour D (1996) Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, UK. Mar Ecol Prog Ser 143:45-63.

Polyakov IV, Beszczynska A, Carmack EC, Dmitrenko IA, Fahrbach E, Frolov IE, Gerdes R, Hansen E, Holfort J, Ivanov VV, Johnson MA, Karcher M, Kauker F, Morison J, Orvik KA, Schauer U, Simmons HL, Skagseth O, Sokolov VT, Steele M, Timokhov LA, Walsh D, Walsh JE (2005) One more step toward a warmer Arctic. Geophys Res Lett 32:L17605.

Polyakov IV, Timokhov LA, Alexeev VA, Bacon S, Dmitrenko IA, Fortier L, Frolov IE, Gascard J-C, Hansen E, Ivanov VV, Laxon S, Mauritzen C, Perovich D, Shimada K, Simmons HL, Sokolov VT, Steele M, Toole J (2010) Arctic Ocean warming contributes to reduced polar ice cap. J Phys Oceanogr 40:2743-2756.

Prokopowicz, A.J., Rueckert, S., Leander, B.S., Michaud, J., and Fortier, L. 2010. Parasitic infection of the hyperiid amphipod *Themisto libellula* in the Canadian Beaufort Sea (Arctic Ocean), with a description of *Ganymedes themistos* sp n. (Apicomplexa, Eugregarinorida). Polar Biol 33:1339-1350.

Quadfasel D, Gascard JC, Koltermann KP (1987) Large-scale oceanography in Fram Strait during the 1984 marginal ice zone experiment. J Geophys Res-Oceans 92:6719-6728.

Rabindranath A, Daase M, Falk-Petersen S, Wold A, Wallace MI, Berge J, Brierley AS (2011) Seasonal and diel vertical migration of zooplankton in the High Arctic during the autumn midnight sun of 2008. Mar Biodiv 41:365-382.

Reigstad M, Wassmann P, Wexels Riser C, Øygarden S, Rey F (2002) Seasonal variation in hydrography, nutrients and suspended biomass in the marginal ice-zone and the central Barents Sea. J Mar Syst 38:9-29.

Reinhardt SB, Van Vleet ES (1986) Hydrocarbons of antarctic midwater organisms. Polar Biol 6:47-51.

Richter C (1994) Regional and seasonal variability in the vertical distribution of mesozooplankton in the Greenland Sea. Thesis, University of Kiel, pp 1-101.

Rudels B, Jones EP, Schauer U, Eriksson P (2004) Atlantic sources of the Arctic Ocean surface and halocline waters. Polar Res 23:181-208.

Sainte-Marie B (1991) A review of the reproductive bionomics of aquatic gammaridean amphipods: variation of life history traits with latitude, depth, salinity and superfamily. Hydrobiologia 223:189-227.

Saiz E, Calbet A (2011) Copepod feeding in the ocean: scaling patterns, composition of their diet and the bias of estimates due to microzooplankton grazing during incubations. Hydrobiologia 666:181-196.

Sakshaug E (2004) Primary and secondary production in the Arctic seas. In: Stein R, Macdonald RW (eds) The Organic Carbon Cycle in the Arctic Ocean. Springer, New York, pp 57-81.

Sargent JR, Henderson RJ (1986) Lipids. In: Corner EDS, O'Hara SCM (eds) The Biological Chemistry of Marine Copepods. Oxford Univ. Press, pp 59-108.

Sargent JR, Falk-Petersen S (1988) The lipid biochemistry of calanoid copepods. Hydrobiologia 167:101-114.

Satapoomin S (1999) Carbon content of some common tropical Andaman Sea copepods. J Plankton Res 21:2117-2123.

Schauer U, Beszczynska-Möller A, Walczowski W, Fahrbach E, Piechura J, Hansen E (2008) Variation of measured heat flow through the Fram Strait between 1997 and 2006. In: Dickson RR, Meincke J, Rhines P (eds) Arctic-Subarctic Ocean Fluxes: Defining the Role of the Northern Seas in climate. Springer Science + Business Media BV, Berlin, pp 385-404.

Schlichtholz P, Houssais MN (2002) An inverse modeling study in Fram Strait. Part II: water mass distribution and transports. Deep-Sea Res II 46(6-7):1137-1168.

Scott CL, Kwasniewski S, Falk-Petersen S, Sargent JR (2002) Species differences, origins and functions of fatty alcohols and fatty acids in the wax esters and phospholipids of *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* from Arctic waters. Mar Ecol Prog Ser 235:127-134.

Sheader M (1977) Breeding and marsupial development in laboratory maintained *Parathemisto gaudichaudii* (Amphipoda). J Mar Biol Assoc UK 57(4):943-954.

Sheader M (1981) Development and growth in laboratory maintained and field populations of *Parathemisto gaudichaudii* (Hyperiidea, Amphipoda). J Mar Biol Assoc UK 61:769-787.

Seiler D (1995) Jahreszeitliches Vorkommen von Crustacea aus Sinkstoffallenproben in drei Tiefenhorizonten der Grönlandsee. Diploma Thesis, Institut für Polarökologie an der Christian-Albrechts-Universität Kiel, 61 p.

Seiler D, Brandt A (1997) Seasonal occurrence of planktic Crustacea in sediment trap samples at three depth horizons in the Greenland Sea. Polar Biol 17:337-349.

Simpson SL, Batley GE, Stauber JL, King CK, Chapman JC, Hyne RV, Gale SA, Roach AC, Maher WA, Chariton AA (2005) Handbook for sediment quality assessment. Canberra, Australia: Environmental Trust, New South Wales Department of Environment and Conservation, Sydney, Australia.

Siva-Jothy MT, Plaistow SJ (1999) A fitness cost of eugregarine parasitism in damselfly. Ecol Entomol 24:465-470.

Soltwedel T, Bauerfeind E, Bermann M, Budaeva N, Hoste E, Jeaeckisch N, von Juterzenka K, Matthiessen J, Mokievsky V, Nöthig E-M, Queric NV, Sablotny B, Sauter E, Schewe I, Urban-Malinga B, Wegner J, Wlodarska-Kowalczuk M, Klages M (2005) HAUSGARTEN Multidisciplinary investigations at a deep-sea long-term observatory in the Arctic Ocean. Oceanogr 18:46-61.

Somero G. 2012. The physiology of global change: linking patterns to mechanisms. Annu Rev Mar Sci 4:39-61.

Spreen G, Kaleschke L, Heygster G (2008) Sea ice remote sensing using AMSR-E 89-GHz channels. J Geophys Res-Oceans 113:C02s03.

Steele DH, Steele VJ (1973) The biology of *Gammarus* (Crustcea, Amphipoda) in the northwestern Atlantic. VII. The duration of embryonic development in five species at various temperatures. Can J Zool 51:995-999.

Steele DH, Steele VJ (1975) The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. XI. Comparison and discussion. Can J Zool 53:1116-1126.

Steele M, Zhang J, Ermold W (2010) Mechanisms of summertime upper Arctic Ocean warming and the effect on sea ice melt. J Geophys Res 115:C11004.

Stroeve J, Holland MM, Meier W, Scambos T, Serreze MC (2007) Arctic sea ice decline: faster than forecast. Geophys Res Lett 34:L09501.

Stroeve J, Serreze M, Drobot S, Gearheard S, Holland M, Maslanik J, Meier W, Scambos T (2008) Arctic sea ice extent plummets in 2007. Eos 89:13-20.

Takahashi KT, Kawaguchi S, Toda T (2009) Observation by electron microscopy of a gregarine parasite of Antarctic krill: its histological aspects and ecological explanations. Polar Biol 32:637-644.

Takahashi K, Kawaguchi S, Kobayashi M, Toda T, Tanimura A, Fukuchi M, Odate T (2011) Eugregarine infection within the digestive tract of larval Antarctic krill, *Euphausia superba*. Polar Biol 34:1167-1174.

Tencati JR, Geiger SR (1968) Pelagic amphipods of the slope waters of Northeast Greenland. Journal of the Fisheries Research Board of Canada 25:1637-1650.

Tencati JR (1970) Amphipods of the central Arctic. In: Leung YM, Kobayashi HA (eds) Taxonomic guides to Arctic zooplankton (I), Tech. Rep. 2. University of Southern California, Department of Biological Sciences, pp 3-37.

Thomas JD (1993) Biological monitoring and tropical biodiversity in marine environments: a critique with recommendations, and comments on the use of amphipods as bioindicators. J Nat Hist 27:795-806.

Tomisch K (2012) Mesozooplankton in the Fram Strait: Distribution, abundance and species composition in a warming Arctic Ocean. Master Thesis, University of Bremen, pp 1-84.

Torres JJ, Donnelly J, Hopkins TL, Lancraft TM, Aarset AV, Ainley DG (1994) Proximate composition and overwintering strategies of Antarctic micronektonic Crustacea. Mar Ecol Prog Ser 113(3):221-232.

Vassilenko SV, Petryashov VV (eds) (2009) Illustrated keys to free-living invertebrates of Eurasian Arctic seas and adjacent deep waters, Vol. 1. Rotifera, Pycnogonida, Cirripedia, Leptostraca, Mysidacea, Hyperiidea, Caprellidea, Euphausiasea, Dendrobranchiata, Pleocyemata, Anomura, and Brachyura. Alaska Sea Grant, University of Alaska Fairbanks, 192 p.

Vinogradov ME, Volkov AF, Semenova TN (1996) Hyperiid amphipods (Amphipoda, Hyperidea) of the world oceans. Science Publishers Inc., Lebanon, USA, 632 p.

Vinogradov ME (1999) Deep-sea near-bottom swarms of pelagic amphipods *Themisto*: observations from submersibles. Sarsia 84:465-467.

Wakeham SG, Hedges JI, Lee C, Pease TK (1993) Effects of posions and preservatives on the composition of organic matter in a sediment trap experiment. J Mar Res 51:669-696.

Walczowski W, Piechura J (2007) Pathways of the Greenland Sea warming. Geophys Res Lett 34:L10608.

Walczowski W, Piechura J, Goszczko I, Wieczorek P (2012) Changes in Atlantic water properties: an important factor in the European Arctic marine climate. ICES J Mar Sci 69:864-869.

Walkusz W, Kwasniewski S, Falk-Petersen S, Hop H, Tverberg V, Wieczorek P, Weslawski JM (2009) Seasonal and spatial changes in the zooplankton community of Kongsfjorden, Svalbard. Polar Res 28:254-281.

Wang M, Overland JE (2009) A sea ice free summer Arctic within 30 years? Geophys Res Lett 36:L07502.

Warrant EJ, Locket NA (2004) Vision in the deep sea. Biol Rev 79:671-712.

Wassman P (2011) Arctic marine ecosystems in an era of rapid climate change. Progr Oceanogr 90:1-17.

Wassmann P, Duarte CM, Agusti S, Sejr MK (2011) Footprints of climate change in the Arctic marine ecosystem. Glob Change Biol 17:1235-1249.

Wencki K (2000) Interannual variability in the occurrence of *Themisto* (Amphipoda) in the north Norwegian Sea. Polish Polar Res 21:143-152.

Weslawski JM, Kwasniewski S, Stempniewicz L, Blachowiak-Samolyk K (2006) Biodiversity and energy transfer to top trophic levels in two contrasting Arctic fjords. Pol Polar Research 27(3):259-278.

Weslawski JM, Kwasniewski S, Stempniewicz L (2009) Warming in the Arctic may result in the negative effects of increased biodiversity. Polarforschung 78(3):105-108.

Weslawski J, Wiktor J, Kotwicki L (2010) Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming. Mar Biodiv 40:123-130.

Weslawski JM, Kendall MA, Wlodarska-Kowalczuk M, Iken K, Kedra M, Legezynska J, Sejr MK (2011) Climate change effects on Arctic fjord and coastal macrobenthic diversity-observations and predictions. Mar Biodiv 41:71-85.

Wildish DJ (1982) Evolutionary ecology of reproduction in gammaridean Amphipoda. Int J Inver Rep Dev 5:1-19.

Wildish DJ, Kraft A, Pohle GW, Lecroy SE (2011) Variation in body size of two species of supralittoral talitrids (Amphipoda, Talitroidea) from the Gulf of Mexico and Atlantic coasts of North America. Crustaceana 84:1243-1250.

Williams R, Robins D (1981) Seasonal variability in abundance and vertical distribution of *Parathemisto gaudichaudii* (Amphipoda: Hyperiidea) in the North East Atlantic Ocean. Mar Eco Prog Ser 4:289-298.

Willis KJ, Cottier FR, Kwasniewski S (2008) Impact of warm water advection on the winter zooplankton community in an Arctic fjord. Polar Biol 31:475-481.

Wold A, Jaeger I, Hop H, Gabrielsen GW, Falk-Petersen S (2011) Arctic seabird food chains explored by fatty acid composition and stable isotopes in Kongsfjorden, Svalbard. Polar Biol 34:1147-1155.

Woodgate RA, Weingartner T, Lindsay R (2010) The 2007 Bering Strait Oceanic heat flux and anomalous Arctic sea-ice retreat. Geophys Res Lett 37:L01602.

Acknowledgements

Albert Einstein said: "*Learn from yesterday, live for today, hope for tomorrow. The important thing is not to stop questioning*". During this thesis, I had the outstanding opportunity to learn, and to question. A chance I may have missed if not for the following people, who were my mentors, my supporters, my friends along the way:

I am deeply grateful to Dr. Eva-Maria Nöthig for her supervision of this thesis at the AWI. A big and heartfelt 'THANK YOU' for your support during the last three years: your scientific input, our fruitful discussions and your sound advice in all situations, which made the advance and fulfillment of this thesis possible.

I would like to express my gratitude to my supervisor Prof. Dr. Ulrich V. Bathmann for providing me with the opportunity to conduct my thesis. Thank you for your constructive input, your scientific guidance, encouragement and trust during this work.
I am also deeply grateful to PD Dr. Holder Auel for his willingness to evaluate this thesis.

Special thanks go to Dr. Eduard Bauerfeind for his support at the AWI and on board the R/V *Polarstern*. Thank you for your constructive scientific advice and for introducing me to all the new techniques, starting with the handling of sediment traps, all the way to presenting at international conferences.

Special thanks also to all the scientists, Captains and crews from the R/V *Polarstern* and the R/V *Helmer Hanssen* cruises, for offering helping hands during this thesis.

Furthermore I thank 'Team Canada':
Dr. David Wildish, for introducing me to the world of amphipods in the first place, and sharing his experience, knowledge and passion in this field;
Dr. Gerhard Pohle, Lou Van Guelpen and Mary Greenlaw, for giving me my first insight into zooplankton ecology at the Atlantic Reference Centre in St. Andrews, Canada;
You truly helped me in becoming what I am today: an 'Amphipodologist'. My heartfelt gratitude for that.

I would also like to thank all members of my ‘PhD-Committee’, and the people involved in the different aspects of a three year study:
Dr. Michael Klages and Dr. Hauke Flores, who contributed with discussions and advices to the advance of this thesis;
Dr. Jørgen Berge, Dr. Stig-Falk Petersen and Dr. Øystein Varpe for giving me the opportunity to participate at two Norwegian research cruises to the Arctic and their scientific advice and helpful input during my studies;
Dr. Martin Graeve and Dieter Janssen for constructive comments and discussions, and for their support with the lipid analyses;
Dr. Agnieszka Beszczynska-Möller for sharing her expert knowledge of oceanography.

To Dr. Svenja Kruse, Dr. Bettina Meyer, Dr. Barbara Niehoff, Kristin Hardge, Britta Wend, Estelle Kilias, Maria Winkler, Christian Wolf, Mar Fernandez-Mendez, Gastón Aguirre, Steffi Gäbler-Schwarz, Daniela Freese, Nadine Knüppel, Nicole Hildebrandt, Christiane Lorenzen, Sandra Murawski, Helga Mehl, Ruth Alheit, Mandy Kiel, Kirstin Meyer, Gordon Lax and Claudia Daniel: a big THANK YOU for your support during all the different phases of this thesis, during long office hours, on expedition, in the lab or during lunch breaks.

I thank the ‘Team of the Graduate School POLMAR’ for giving me support and advice along the way.

I thank Dr. Gerhard Dieckmann and Ben Lange for their help with all aspects of the English language and grammar, and their valuable advice with regard to preliminary manuscript versions.

Thanks also go to Dr. Malin Daase, Dr. Janne Søreide and Dr. Anette Wold, for all your help and support during my research stays in Norway.

Last but not least I’d like to thank my family, and my friends, for their support and interest in my work during the last three years; for being at my side and for giving me security during all the ups and downs. I thank Beate Brügging for her friendship, her understanding and the long talks we had together. My heartfelt gratitude also goes to my parents and Eric Diehl for their love and for giving me perspective.

Appendix A1-A3

A1. Field observations and analytical techniques

This appendix section contains an overview of the methods used for zooplankton field observations during this thesis. The mooring records for sediment trap sampling are listed in Table 12.1, the sampling methods to obtain plankton net samples in Table 12.2. A list of applied analytical techniques is given in Table 12.3. A detailed method description is included in the respective **publication (I-V)**.

Table 12.1 Location, sampling time, water depth and trap depth of moored sediment traps in the HAUSGARTEN and Greenland Sea analyzed for their amphipod composition

Mooring period	Lat. N	Long.	Water depth (m)	Trap depth (m)	No of samples	Publication
18.09.2000-17.09.2001	74°23.93’	10°19.48’ W	3146	2700	20	III
31.08.2000-14.08.2001	79°01.70’	04°20.86' E	2456	280	18	I, V
12.07.2004-19.08.2005	79°00.99’	04°20.62’ E	2584	280	20	I, V
12.07.2004-19.08.2005	79°00.99’	04°20.62’ E	2584	800	20	III
23.08.2005-31.08.2006	79°01.01’	04°20.63’ E	2530	1230	17	III
23.08.2005-31.08.2006	79°01.01’	04°20.63’ E	2530	2357	19	III
05.08.2006-20.06.2007	79°00.82’	04°20.50’ E	2540	230	20	I, V
05.08.2006-20.06.2007	79°00.83’	04°20.60’ E	2540	1300	20	III
21.07.2007-15.07.2008	79°00.82’	04°20.62’ E	2589	190	20	I, V
21.07.2007-15.07.2008	79°00.82’	04°20.62’ E	2589	1316	18	III
21.07.2007-15.07.2008	79°00.82’	04°20.62’ E	2589	2370	20	III
17.07.2008-18.07.2009	79°00.40’	04°20.00’ E	2557	201	20	I, V
10.07.2010-30.06.2011	79° 00.41'	04°19.90' E	2567	200	20	V
10.07.2011-30.06.2012	79° 00.40'	04°19.90' E	2555	200	20	V

Table 12.2 An overview of ship-based studies and used plankton nets which provided the data for this thesis

Cruise	Time	Ship	Field sampling method	Mesh size (µm)	Sampling depth (m)	Investigation area	Publi-cation
ARK-XXVI/1	15.06-13.07.2011	R/V *Polarstern*	Multinet	1000	0-2000	Fram Strait	IV
ARK-XXVI/2	13.07-03.08.2011	R/V *Polarstern*	Multinet	1000	0-2000	HAUSGARTEN, Fram Strait	IV
IMR Survey	09.08-24.08.2011	R/V *Helmer Hanssen*	Pelagic fish trawl	10000	0-100	Svalbard	IV
ARCTOS-8510	12.01-18.01.2012	R/V *Helmer Hanssen*	a) Methot Isaac Kidd net	1500	20-225	Rijpfjorden and Isfjorden	II, IV
			b) WP3 net	1000	0-1200	Sofiadjupet	

Table 12.3 A list of analytical techniques which were applied during this thesis

Analytical method	Method details	Publication or section
Amphipod composition	Species and stage identification based on morphological features	I-V
Abundance	Calculation of abundance indices (sediment trap method) and integrated values (net samples)	I-V
Length-frequency analyses	Measurements of total body length (mm) of each species and stage	I, III, IV
Cohort analyses	Identification of normally-distributed components in length-frequency distributions using Bahttacharya's analysis	I, III
Growth	Establishment of a growth function; Gompertz growth model	I
Biomass estimates	See Appendix A2	Synoptic discussion, section 8.1
Gut content analyses	Qualitative (prey item identification) and semi-quantitative (degree of fullness) investigation of amphipod gut contents	II, IV
Lipid analyses	Determination of total lipid content, lipid classes (HPLC analyses) and fatty acid profiles (GC analyses)	IV
Statistical analyses	Student's *t* test (univariate statistics); PCA, nMDS and SIMPER analyses (multivariate statistics)	I, III, IV

A2. Method description of biomass estimations in sediment traps and plankton nets

This appendix section describes the calculation of biomass estimates, which are discussed in section 8.1 of this thesis. The calculation of biomass for copepods was based on dry mass values which were published in Donelly et al. (1994), Richter (1994), Satapoomin (1999) as well as Kosobokova et al. (2007) and a stage specific analyses of the copepod composition (S. Fuhrmann, unpublished data) for the sampling year 2007-2008 in the epipelagic sediment trap (190 m water depth) from the HAUSGARTEN observatory (79°01' N / 04°20' E). The biomass calculation for *Themisto* spp. was determined from body length-frequency information (**publication I**) and length-to-weight functions (**publication IV**) obtained during this study. The detailed copepod and amphipod biomass for the sampling year from 2007 to 2008 is shown in Table 12.4.

Based on the 2007-2008 observation, a similar species, length and cohort composition was assumed for the copepod compositions in sediment trap samples from 2000 to 2012, and mean dry mass per individual and respective biomass was estimated for each mooring period within this time frame (Table 12.5). The same procedure was applied for the amphipod composition, with the respective *Themisto* species, which contributed more than 90 % of the total amphipod population (as shown for sampling period from 2000 to 2009 in **publication I**).

For a comparison of plankton net and sediment trap biomass estimations, the amphipod biomass from plankton nets was calculated for ranges of 0-200 m, 200-500/600 m and 500 / 600-1000 m water depth (Table 12.6). Calculations were based on dry mass of dominant amphipod and copepod species (> 95 % total contribution) from the HAUSGARTEN observatory (79°01' N / 04°20' E) and the northeastern Fram Strait (78°50' N / 01°45' E) obtained from stratified multinet samples (1000 µm mesh for amphipods and 150 µm mesh for copepods) in mg DM m^{-2} during June/July 2011. Data on copepod abundances were courtesy provided by Tomisch (2012).

Table 12.4 Biomass calculations (mg DM m^{-2} d^{-1}) based on dry mass of dominant amphipod and copepod species (> 95 % total contribution) from sediment trap samples at the HAUSGARTEN observatory (79°01' N / 04°20' E, 190 m sampling depth); a comparison of year-round sediment trap samples from 2007 to 2008 (mg DM m^{-2} d^{-1})

Sampling period 2007/08 190 m depth	**Month** Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	April	May	Jun	Year
Amphipoda												
Themisto												
abyssorum	70.97	50.14	11.72	9.90	5.04	2.03	7.79	48.86	1.38	255.54	108.64	572.02
compressa	5.16	0.00	2.66	0.00	0.00	0.00	6.86	2.42	0.00	4.62	0.00	21.72
libellula	515.82	190.27	252.60	90.42	43.77	30.78	45.50	18.62	6.14	25.41	61.87	1281.20
Total	**591.95**	**240.41**	**266.99**	**100.32**	**48.82**	**32.81**	**60.15**	**69.91**	**7.52**	**285.57**	**170.52**	**1874.94**
Copepoda												
Calanus												
finmarchicus	0.14	0.13	0.14	0.05	0.02	0.00	3.89	1.42	0.00	0.13	0.32	6.24
glacialis	5.88	0.38	0.31	0.00	0.01	0.00	2.55	2.33	0.00	0.20	0.21	11.88
hyperboreus	0.40	0.40	0.59	0.00	0.00	0.00	0.49	1.21	0.00	6.11	13.24	22.44
Gaetanus												
tenuispinus	0.71	0.00	2.86	4.65	2.35	4.11	0.00	0.00	0.00	0.37	0.00	15.04
Metridia												
longa	4.00	0.75	0.36	0.41	0.24	0.27	0.27	0.17	0.00	4.87	4.70	16.03
Paraeuchaeta												
norvegica	79.56	43.71	126.45	5.92	1.25	0.86	7.64	67.27	11.45	99.15	107.36	550.60
Total	**90.69**	**45.37**	**130.70**	**11.03**	**3.87**	**5.24**	**14.84**	**72.39**	**11.45**	**110.83**	**125.84**	**622.23**
Ratio [Amphipoda/ Copepoda]	**6.5**	**5.3**	**2.0**	**9.1**	**12.6**	**6.3**	**4.1**	**1.0**	**0.7**	**2.6**	**1.4**	**3.0**

Table 12.5 Mean daily biomass (mg DM m^{-2} d^{-1}) calculated on estimations of the mean dry mass (Factor DM ind^{-1}) and the recorded appearances of dominant amphipod and copepod species (> 95 % total contribution) collected in sediment trap samples from the HAUSGARTEN observatory from 2000 to 2012 (79°01' N / 04°20' E, 190-280 m sampling depth)

	Factor	Year													
	[DM ind^{-1}]	2000/01		2004/05		2006/07		2007/08		2008/09		2010/11		2011/12	
Appearance		ind m^{-2} d^{-1}	Biomass	ind m^{-2} d^{-1}	Biomass	ind m^{-2} d^{-1}	Biomass	ind m^{-2} d^{-1}	Biomass	ind m^{-2} d^{-1}	Biomass	ind m^{-2} d^{-1}	Biomass	ind m^{-2} d^{-1}	Biomass
Copepoda	0.629	675.92	**425.15**	769.60	**484.08**	816.33	**513.47**	990.25	**622.23**	1487.57	**935.68**	1035.07	**651.06**	1500	**943.50**
Themisto															
abyssorum	7.305	8.28	**60.51**	51.44	**375.79**	57.16	**417.62**	78.30	**572.02**	82.50	**602.70**	44.18	**322.79**	155.17	**1133.52**
compressa	8.59	0.00	**0.00**	6.09	**52.32**	3.80	**32.66**	2.52	**21.72**	4.86	**41.78**	8.52	**73.20**	56.06	**481.57**
libellula	41.686	5.52	**230.25**	25.96	**1082.26**	9.96	**415.56**	30.73	**1281.20**	40.92	**1706.11**	18.44	**768.78**	39.18	**1633.66**
Biomass ratio [Amphipoda/ Copepoda]			**0.7**		**3.1**		**1.7**		**3.0**		**2.5**		**1.8**		**3.4**

Table 12.6 Biomass estimations from stratified multinet in mg DM m^{-2} at the HAUSGARTEN observatory (79°01’ N / 04°20’ E) for amphipods, and at the northeastern Fram Strait (78° 50’ N / 01° 45’ E) for copepods, obtained during June/July 2011. Copepod data were courtesy provided by Tomisch (2012)

Sampling July 2011	ARK-XXVI/2		
0-1000 m depth	**Depth [m]**		
	0-200	200-600	600-1000
Amphipoda			
Themisto abyssorum	39.68	869.44	159.04
compressa	0.00	33.44	0.00
libellula	0.00	45.55	0.00
Total	**39.68**	**948.43**	**159.04**

Sampling June 2011	**Depth [m]**		
0-1000 m depth	0-200	200-500	500-1000
Copepoda			
Calanus			
finmarchicus	12310.61	221.90	130.39
glacialis	1101.29	0.00	9.19
hyperboreus	4034.75	94.11	150.20
Calanus spp. CI-CIII	410.70	0.90	2.25
Gaetanus brevispinus	0.00	2.82	0.00
tenuispinus	115.22	218.30	106.12
Heterorhabdus norvegicus	8.40	39.60	32.20
Metridia longa	190.69	202.29	61.13
Mircocalanus spp.	249.65	104.83	194.43
Microsetella spp.	1.81	0.00	0.02
Nauplii	108.09	3.18	6.91
Oithona similis	508.34	1.62	1.41
Onacaea spp.	33.22	7.98	30.21
Paraeuchaeta norvegica	124.47	71.19	23.36
Paraeuchaeta spp. CI-CIII	15.04	12.63	174.40
Pseudocalanus minutus	138.09	8.63	0.69
Scaphocalanus brevicornis	0.00	0.00	7.88
magnus	12.06	9.74	9.28
Scolecithricella minor	1.78	1.58	0.60
Spinocalanus spp.	0.00	2.46	5.98
Total	**19364.19**	**1003.76**	**946.63**

Ratio [Amphipoda/ Copepoda]	**0.002**	**1.0**	**0.2**

A 3. *Ganymedes* sp. infecton

This appendix section contains a list (Table 12.7) which shows the share of *Themisto* spp. infected with the gregarine *Ganymedes* sp. from gut content analyses of sediment trap samples from the central HAUSGARTEN station (79°01’ N / 04°20’ E).

Table 12.7 Percentage of individuals infected with the gregarine *Ganymedes* sp. from gut content analyses of sediment trap samples from the central HAUSGARTEN station (79°01’ N / 04°20’ E), 200 m water depth, from July 2010 to June 2012. n = number of investigated adult individuals

	Summer (May-July)		Fall (August-October)		Winter (November-January)		Spring (February-April)	
Themisto	No.	%	No.	%	No.	%	No.	%
abyssorum	n = 45	33.33	n = 45	39.87	n = 45	29.81	n = 45	37.95
compressa	n = 38	-	n = 25	-	n = 19	-	n = 25	-
libellula	n = 45	30.01	n = 45	35.57	n = 45	28.98	n = 45	29.22