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OITHONA SIMILIS (COPEPODA: CYCLOPOIDA)
- A COSMOPOLITAN SPECIES?

DISSERTATION

Zur Erlangung des akademischen Grades eines Doktors der
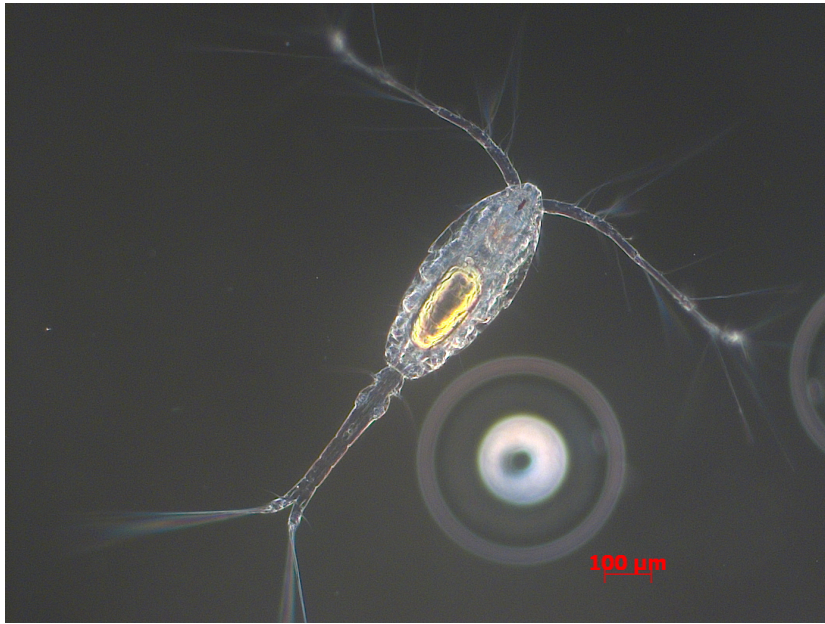Naturwissenschaften
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Für meinen Vater

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Summary

The present study investigated whether the cyclopoid copepod *Oithona similis* Claus 1866 is a cosmopolitan or a conglomerate of cryptic species. Adult and subadult females (C5 stages) of *O. similis* were closely examined morphologically and via DNA-barcoding from four study areas: the Arctic Ocean, the Southern Ocean, the North Sea and the Mediterranean Sea. Sampling was done during two expeditions with RV Polarstern in the Arctic Ocean (ARK XXIII-3, ARK XXV-1) and at one expedition in the Southern Ocean (ANT XXIV-2). Further samples from three stations in the North Sea and one station in the Mediterranean Sea were provided.

Based on the shape of the rostrum, body size and the formula and structure of the outer setae of the exopodits of the swimming legs, five different morphotypes were identified: *Oithona similis* (Arctic Ocean, Mediterranean Sea, North Sea, Southern Ocean), *O. atlantica* (Arctic Ocean), *O. frigida* (Southern Ocean), *O. nana* (North Sea) and *Oithona sp.* (North Sea). Via CO1-sequencing in total eight different haplotypes of *O. similis* were found in this study: "Osi ARK 1", "Osi ARK 2", "Osi ARK 3" (Arctic Ocean), "Osi ANT 1", "Osi ANT 2", "Osi ANT 3" (Southern Ocean), "Osi North Sea/ Med Sea" (North Sea, Mediterranean Sea) and "Osi Med Sea" (Mediterranean Sea). "Osi North Sea/ Med. Sea" is the only haplotype that was present at more than one of the sampling areas. In addition to the number of haplotypes, this clearly shows that *O. similis* is not a cosmopolitan but a conglomerate of cryptic species. Additionally to the *Oithona similis* groups, three other copepod species groups were identified morphologically as well as via sequencing: *O. frigida* (Ofr) in the Southern Ocean and in the North Sea *O. nana* (Ona) close to the island of Helgoland and *Oithona sp*. (Osp) close to the island of Sylt.

Oithona nana was chosen as the basis of a neighbor joining tree because it is not as closely related to *O. similis* as the other species are. Morphological differences regarding the appendages of the swimming legs of *O. frigida* and *O. similis* were obvious and were clearly reflected in the results of the CO1 sequences, as these haplotypes are each located on one of the two different main branches. The

differences reflected in the appendage structures of the swimming legs were also obvious between *O. similis* and *O. nana.* Another haplotype named *Oithona sp.* shares the swimming leg appendage structure with *O. nana,* but has a bended rostrum like *O. similis*. The differentiation between these species is also clearly reflected in their position in the neighbour joining tree as *Oithona sp.* is located on the same branch as *O. frigida*. Thus, *O. similis* and other *Oithona* species inhabiting the investigation areas can clearly be differentiated morphologically and genetically.

The genetical differences between haplotype "Osi ANT 1" that was found within the Weddell Gyre and the Polar Frontal Zone (PFZ) and "Osi ANT 2" from PFZ are considerable. The same applies to "Osi ANT 1" and the second PFZ haplotype "Osi Ant 3". Haplotype "Osi ANT 3" derives from the same branch in the neighbour joining tree as "Osi ANT 2", indicating a close relationship between these two haplotypes from the PFZ.

"Osi ARK 1" is widely distributed within the Arctic Ocean. "Osi ARK 2" and "Osi ARK 3", each represented by one female, were only found at a station above the Chukchi Plateau. An individual of "Osi ARK 1" was also caught at this station. The position of "Osi ARK 2" and "Osi ARK 3" in the neighbor joining tree indicates a close relationship between these two groups.

The haplotype "Osi ARK 1" derives from the same branch as the individuals of the haplotype "Osi ANT 1", but the distance between their branch-offs are quite huge. This also applies to the distances between this group and the two other groups from the Arctic Ocean. It can be assured that at least two different cryptic *O. similis* species occur in the Arctic Ocean.

The CO1- sequences of the *Oithona similis* haplotype containing individuals from two different places in the North Sea and the Mediterranean Sea differ from the sequences of the species sampled at the other regions. The fact that the same haplotype was found at different places in the North Sea as well as in the Mediterranean Sea shows that this species is widely distributed and might be quite flexible concerning environmental conditions. It is also possible that species of the genus *Oithona* are advected into the southern North Sea with Atlantic water.

A further haplotype of *O. similis* was sampled in the Mediterranean Sea. However, from the genetic aspect, the haplotypes found in that area are very different. The second Mediterranean one is genetically closer to the *O. frigida* haplotype than to any other *O. similis* haplotype.

Overall, almost no morphological differences were found within and between regions for individuals of the *Oithona similis* species groups from the Southern Ocean, the Arctic Ocean, the North Sea and the Mediterranean Sea. Exceptions are the individuals from the Arctic Ocean that were described as *Oithona atlantica*. One aim of this study was to examine whether possibly existing cryptic species in the nominal *O. similis* either show no morphological differences or only very slight ones that make it impossible to differentiate between them morphologically. Since the individuals that were described as *Oithona atlantica* prior to sequencing do not form an own haplotype, and as no other morphological differences within the *O. similis* individuals were found, this can be confirmed at least concerning the examined morphological characters.

Zusammenfassung

Die vorliegende Arbeit untersuchte die Fragestellung ob es sich bei dem cyclopoiden Copepoden *Oithona similis* Claus 1866 um einen Kosmopoliten oder mehrere unter diesem Namen zusammengefasste kryptische Arten handelt. Adulte und subadulte Weibchen (C5- Stadien) von *O. similis* aus vier Untersuchungsgebieten (Arktischer Ozean, Südlicher Ozean, Nordsee, Mittelmeer) wurden morphologisch und mittels "DNA-barcoding" genauer untersucht. Die Probennahme erfolgte während zwei Expeditionen mit FS Polarstern im Arktischen Ozean (ARK XXIII-3, ARK XXV-1) und einer Expedition im Südlichen Ozean (ANT XXIV-2). Weitere Proben von drei verschiedenen Stationen in der Nordsee und einer Station im Mittelmeer wurden zusätzlich zur Verfügung gestellt.

Anhand der Form des Rostrums, Körpergröße und der Anzahl und Beschaffenheit der äußeren Setae des Expoditen der Schwimmbeine konnten fünf verschiedene Morphotypen identifiziert werden: *Oithona similis* (Arktischer Ozean, Mittelmeer, Nordsee, Südlicher Ozean), *O. atlantica* (Arktischer Ozean), *O. frigida* (Südlicher Ozean), *O. nana* (Nordsee) und *Oithona sp.* (Nordsee). Im Verlauf dieser Arbeit wurden mittels CO1-Seqenzierung insgesamt acht verschiedene Haplotypen von *O. similis* gefunden: "Osi ARK 1", "Osi ARK 2", "Osi ARK 3" (Arktischer Ozean), "Osi ANT 1", "Osi ANT 2", "Osi ANT 3" (Südlicher Ozean), "Osi North Sea/ Med Sea" (Nordsee, Mittelmeer) und "Osi Med Sea" (Mittelmeer). "Osi North Sea/ Med Sea" ist der einzige Haplotyp, der nicht nur in einem Untersuchungsgebiet angetroffen wurde. Zusammen mit der Anzahl der Haplotypen zeigt dieses deutlich, dass *O. similis* kein Kosmopolit ist, sondern unter diesem Namen mehrere kryptische Arten zusammen- gefasst sind. Außer den *Oithona similis*-Gruppen wurden noch drei weitere *Oithona*- Artengruppen sowohl morphologisch als auch genetisch identifiziert: *O. frigida* (Ofr) im Südlichen Ozean und in der Nordseee: *O. nana* (Ona) nahe Helgoland und *Oithona sp.* (Osp) bei Sylt.

Als Basis eines "Neighbor joining" Baumes wurde *Oithona nana* ausgewählt, da diese Art nicht so nah mit *O. similis* verwandt ist wie die anderen untersuchten Arten. Morphologische Unterschiede bezüglich der Anhänge der Schwimmbeine von

O. frigida und *O. similis* waren eindeutig und spiegelten sich deutlich in den Ergebnissen der CO1-Sequenzen wider, da jeder dieser Haplotypen auf je einem der Hauptäste des Baumes lokalisiert ist. Auch zwischen den Arten *O. similis* und *O. nana* waren die Unterschiede bezüglich der Strukturen der Anhänge der Schwimmbeine eindeutig. Ein weiterer Haplotyp, *Oithona sp.*, weist die Anhang-Struktur der Schwimmbeine von *O. nana* auf, hat jedoch ein gebogenes Rostrum wie *O. similis*. Die Differenzierung zwischen diesen Arten zeigt sich auch deutlich in ihrer Position im „Neighbor joining" Baum. *Oithona sp.* ist auf demselben Ast lokalisiert wie *O. frigida*. *Oithona similis* und andere *Oithona*-Arten aus den Untersuchungsgebieten konnten deutlich morphologisch und genetisch unterschieden werden.

Die genetischen Unterschiede zwischen Haplotyp "Osi ANT 1", der sowohl im Weddell Wirbel als auch in der Polaren Frontzone (PFZ) gefunden wurde, und "Osi ANT 2" aus der PFZ sind deutlich. Dasselbe gilt für "Osi ANT 1" und den zweiten Haplotypen aus der PFZ: "Osi ANT 3". Haplotyp "Osi ANT 3" entspringt demselben Ast im "neigbor joining" Baum, wie "Osi ANT 2". Dies weist auf eine enge Verwandtschaft zwischen den beiden Haplotypen der PFZ hin.
"Osi ARK 1" ist im Arktischen Ozean weit verbreitet. "Osi ARK 2" und "Osi ARK 3", die nur aus je einem Weibchen bestehen, wurden nur an einer Station über dem Chukchi Plateau gefunden. Dort wurde ebenso ein Weibchen von „Osi ARK 1" gefunden. Die Positionen von "Osi ARK 2" und "Osi ARK 3" im „neighbor joining" Baum weisen auf eine enge Verwandtschaft zwischen beiden hin.
Die Verzweigung von "Osi ARK 1" entspringt demselben Ast wie "Osi ANT 1". Der Abstand zwischen ihren Abzweigungen ist jedoch sehr groß. Dies trifft auch auf die Abstände zwischen den Positionen von „Osi ARK 1" und den beiden anderen Gruppen aus dem Arktischen Ozean zu. Es kommen also mindestens zwei verschiedene kryptische *Oithona* similis-Arten im Arktischen Ozean vor.

Die CO1-Sequenzen des *Oithona similis* Haplotypen, der Individuen von zwei verschiedenen Orten in der Nordsee und aus dem Mittelmeer enthält, unterscheidet sich von den Sequenzen der Arten aus den übrigen Untersuchungsgebieten. Die Tatsache, dass derselbe Haplotyp sowohl an verschiedenen Orten der Nordsee als

auch im Mittelmeer gefunden wurde zeigt, dass diese Art weit verbreitet und sehr flexibel bezüglich Umweltfaktoren ist. Eine weitere mögliche Erklärung ist, dass Arten der Gattung *Oithona* mittels Atlantischem Wasser in die Südliche Nordsee transportiert werden. Im Mittelmeer wurde ein weiter Haplotyp ausgemacht. Vom genetischen Aspekt her sind diese beiden Haplotypen sehr verschieden. Der Zweite aus dem Mittelmeer ist enger verwandt mit *O. frigida* als mit einem der *O. similis* Haplotypen.

Insgesamt wurden fast keine morphologischen Unterschiede innerhalb der Untersuchungsgebiete und zwischen ihnen für Individuen der *Oithona similis* Gruppen aus dem Südlichen Ozean, dem Arktischen Ozean, der Nordsee und dem Mittelmeer gefunden. Die einzige Ausnahme sind Individuen aus dem Arktischen Ozean innerhalb „Osi ARK 1" die als *Oithona atlantica* beschrieben wurden. Ein Ziel dieser Untersuchung war zu untersuchen, ob potenziell existierende kryptische Arten innerhalb der nominalen Art *O. similis* entweder keine morphologischen Unterschiede zeigen oder nur sehr geringfügige, die es unmöglich machen die Arten morphologisch zu unterscheiden. Da die Individuen, die vor der Sequenzierung als *Oithona atlantica* erfasst wurden, keinen eigenen Haplotypen bilden und keine weiteren morphologischen Unterschiede innerhalb der *Oithona similis* Individuen gefunden wurden, kann dies zumindest für die untersuchten morphologischen Merkmale bestätigt werden.

1. Introduction

1.1 Cosmopolitan and Cryptic Species

The existence of cosmopolitan species, living in widely separated parts of the earth, is extremely interesting (Schmidt & Westheide 2000), since cosmopolitism is often hard or even impossible to explain. According to Fenchel and Finlay (2004), a pragmatic definition of a cosmopolitan species is that it occurs in at least two oceans or two biogeographical regions, and in both, the Northern and the Southern Hemisphere. Cosmopolitan marine species are found in the pelagos as well as in the benthos.

The presumed cosmopolitan distribution of meiofaunal taxa is under debate (Todaro et al. 1996). The reliability of species identifications from geographically distant areas is questioned, especially when made by different investigators using different methods (often low-resolution microscopy) and probable personal "instincts" to affiliate species with a given taxon (Todaro et al. 1996). On the one hand, careful morphological analysis has shown that some species with a presumed wide geographic range are actually composite assemblages of different species (see Todaro et al. 1996 and references therein). On the other hand, the use of highly reproducible techniques (e.g. high-resolution video microscopy) has confirmed that cosmopolitanism appears to be a widespread phenomenon among certain meiofaunal groups (Hummon 1994, Todaro et al. 1995). In many groups of marine organisms, wide geographic ranges have been uncritically accepted as the natural consequence of potentially broad oceanic dispersal (Knowlton 1993). Concerning the possible existence of cosmopolitans, it should be considered that the widely held opinion that marine environments are poorly supplied with effective isolating barriers has often proved untenable (Battaglia 1982). Powerful isolating barriers can be provided by a multiplicity of factors (hydrological differences, structure of coastline, presence of brackish-water lagoons and estuaries, current regimes, tides, etc.) that separately or jointly may favor or prevent interchange between populations (Battaglia 1982). According to Ward and Hirst (2007), real cosmopolitan species are not the rule within the plankton of the world`s oceans but rather exceptions. The majority of the plankton species has centers of distribution within ranges that alter in extent and

may often, but not always, be linked to particular physical features such as water masses (Ward & Hirst 2007).

Often cryptic species are used as equivalent to sibling species (Sáez & Lozano 2005). In other cases, it is specified that the term sibling connotes more recent common ancestors than cryptic, implying a sister-species relationship (Knowlton 1986). Sibling species are species that cannot or only hardly be distinguished based on morphological characters (Mayr 1942, Mayr & Ashlook 1991). However, even sibling species in the narrow sense often have minor morphological differences that in some case are subtle but diagnostic (Knowlton 1993). Many marine sibling species have substantial genetic differences (Knowlton 1993). Furthermore, marine sibling species are ubiquitous and appear to be common for a variety of marine invertebrates (Knowlton 1993). Such species are found from the poles to the tropics, in most known habitats and at depths ranging from intertidal to abyssal (Knowlton 1993). Cryptic species that do not show any morphological differences are either distinguished by e.g. chemical or behavioral mating signals, and/ or appear to show morphological stasis (Bickford et al. 2006). Documenting and measuring cryptic species diversity in the oceans has important ecological, evolutionary and conservation implications (Knowlton 1993, 2000, Mikkelsen & Cracraft 2001).

Marine cryptic species have been revealed by molecular and biochemical genetic analyses as well as interbreeding trials, and/ or detailed morphometry measurements (e.g. Frost 1974, Bucklin et al. 1996, Rocha-Olivares et al. 2001). These studies include some well-studied species of e.g. copepods such as *Calanus finmarchicus* (Hill et al. 2001) and some meiobenthic morphospecies previously regarded as cosmopolitan or as species with wide physiological tolerances (Rocha-Olivares et al. 2001, Bhadury et al. 2008, van Gaever et al. 2009). Thus, many cosmopolitan marine invertebrate taxa are actually complexes of sibling species and such species are now considered to have more limited geographic ranges (Rocha-Olivares et al. 2001). Each clade of a cryptic species is now considered to have more limited geographical ranges and smaller physiological tolerances (Montiel-Martínez et al. 2008). It is possible that cryptic speciation is even far more common than previously assumed

(Lee & Frost 2002). Thus, if the existence of cryptic biodiversity is not identified, it hampers the understanding of the evolutionary and ecological processes within a study. Correct species identification of microscopic organisms is therefore of prime importance (Castro-Longoria et al. 2003)

The cyclopoid copepod species *Oithona similis,* Claus 1866, has been described as cosmopolitan (e. g. Atkinson 1998, Peterson & Keister 2003, Hansen et al. 2004). Bigelow (1926) assumed that no other marine planktonic copepod exists over a wider range of temperature and salinity than this species. Thus, its wide range of tolerance for temperature and salinity is a possible explanation for its large area of distribution (Nishida 1985). However, the potential existence of morphologically distinct populations within the wide geographical range of *O. similis* needs further examinations (Nishida 1985). What is known about the life history of *O. similis* is full of contradictory information as will be shown in the following chapters. It is said to be a very flexible cosmopolitan species. On contrary, it might also be a conglomerate of several different cryptic species. Each of these species may actually be very stenoecious in contrast to their potentially similar or even identical morphology. If cryptic species really exist, we would have to draw a very different picture of *Oithona*`s life history, as in that case the known information would be for a species complex. For modellers, it is of great importance to define species-specific functional response equations for different environmental conditions.

Genetic examinations are one tool to see if there is more than one species within the nominal *Oithona similis*. However, genetic studies for this species are rather scarce. A recent study dealt with the molecular systematics based on 28s rDNA sequences of *Oithona similis*, *O. atlantica* and *O. nana* mainly from the Argentine Sea (Cepeda et al. 2012). In GenBank, unpublished partial sequences of a 28 s ribosomal RNA gene from Bisset et al. (2005) (1 sequence), Llinas et al. (2008) (1 sequence), Cepeda et al. (2009) (2 sequences), and of a 26 S ribosomal gene from Scorzetti (2008) (1 sequence) and one 18 S ribosomal RNA gene sequence (Wang & Sun 2010) are available in addition. Furthermore, sixteen unpublished partial sequences

of the mitochondrial CO1 gene of *O. similis* from the Chinese Sea can be found in GenBank (3: Sun et al. 2008 and 13: Lee & Lee 2011).

1.2. General introduction to the Copepoda

Copepods are small crustaceans with a typical length of 0.02-12 mm (Huys & Boxshall 1991). More than 10.000 species of free living or parasitic species inhabit fresh-, brackish- and marine water as well as terrestrial habitats (Huys & Boxshall 1991). Copepods evolved from benthic ancestors in the Palaeozoic about 200-400 million years ago and colonized the pelagial (Bradford-Grieve 2002). Typically, the zooplankton biomass in the contemporary ocean is dominated by copepods (Verity & Smetacek 1996). Worldwide copepods belong to the numerically most abundant and distributed group of marine animals (Humes 1994, Hansen et al. 2004). They might even be the most abundant metazoans on the planet (Humes 1994).

Within the marine copepods, pelagic, benthic and epibenthic species as well as species that live together with other organisms are found. Copepod vertical distributions cover all water layers, from the surface layers down to the abyssal zone (Bradford-Grieve et al 1999). Furthermore, copepods seem to be adapted to polar environments, as they form a huge part of the zooplankton in the Arctic Ocean as well as in the Southern Ocean (Conover & Huntley 1991), where they exhibit high biomasses (Ikeda 1985, Errhif et al. 1997). Consequently, these zooplankton organisms are an important component of marine food webs (Bradford-Grieve et al 1999) and can be considered as an especially successful group within the pelagic environment (Kiørboe 1997). Within the viscous, nutritionally dilute and perilous environment of marine zooplankton, copepods show many evolved exceptional and competent solutions to the main challenges of survival, feeding and reproduction (Kiørboe 2011).

Nine systematic orders of copepods are known: Platycopioida, Calanoida, Misophrioida, Harpacticoida, Monstrilloida, Mormonilloida, Gelyelloida, Cyclopoida, Siphonostomatoida and Poecilostomatoida (Bradford-Grieve et al 1999), with the former Poecilostomatoida now included in the Cyclopoida (Conway 2006). In terms of

their morphology, most planktonic copepods are very similar. They have a hydrodynamic elongated body with a well-developed musculature (Kiørboe 1997). This body shape allows fast escaping reactions (Ohman 1988). A further common attribute are antennules that are stretched out and have mechanosensorical hairs which enable them to perceive approaching predators (Yen et al. 1992).

The main food items of copepods are phytoplanktonic (Atkinson 1996, Gallienne & Robins 2001) and microzooplanktonic organisms (Atkinson 1996, Hansen et al. 2004). Most of the copepod species are omnivorous to a certain extent and prey on both groups of organisms (Kiørboe 1997). Generally, the clearing rates on mobile microzooplanktonic organisms are higher than for phytoplankton (Stoecker & Egloff 1987). The utility of the food depends on different characteristics of the prey, like abundance, shape, size and taste, but also on the behavior of the predator (Castellani et al. 2005). A preference for prey-particles with the dimension of nanoplankton (2- 20 µm) is well documented for many small copepod species (Fortier et al. 1994). Furthermore, protozoans can be an essential part of the food of marine copepods (Gifford & Dagg 1991). Thus, protozoans allow survival and reproduction of copepods independently of phytoplankton blooms (White & Roman 1992, Ohman & Runge 1994).

The food of copepods can be selective, diverse and differ regionally and temporally, as well as ontogenetically (Hirst & Bunker 2003). In general, copepods rather seem to limit the population of protozoans than to directly control the populations of small phytoplankton cells (Atkinson 1996). As food organisms, they are an important trophic link to marine carnivorous invertebrates and fishes (Gallienne & Robins 2001, Hirst & Bunker 2003) and even whales (Kiørboe 2011). Moreover, copepods are involved in carbonate export from the surface layers of the ocean to the bottom (Svensen & Nejstgaard 2003), by the migration in deeper layers and by the production of fecal pellets. Copepods graze on and modify fecal pellets of zooplankton organisms (see e.g. Reigstad 2000, Wexels Riser et al. 2001) and thus prevent sinking out of fecal pellets. "The export of biologically generated soft tissue (organic matter) and hard tissue (carbonate) to the deep ocean [is] collectively known

as the biological pump" (Palmer & Totterdell 2001). A part of the organic carbon from the surface layer may be transported into a depth of several hundred meters before its egestion or respiration takes place (Palmer & Totterdell 2001). It is also possible that the organism itself is preyed upon below the eutrophic layer (Palmer & Totterdell 2001).

Almost all copepods have twelve developmental stages: six naupliar stages, as e.g. identified for the genus *Oithona* (Murphy 1923), and six stages of copepodites, the sixth being the adult animal. The developmental time of the eggs depends on temperature and can extend from a one-day period up to several months. The duration of each naupliar stage is very short lasting from a few hours up to a few days. The period between the single copepodite stages can last much longer (Bradford-Grieve et al. 1999).

According to Kiørboe (2011), the success of copepods in marine waters has three main reasons. First, due to their torpedo shape and muscular body copepods are able to gain high velocity and to speed up (Kiørboe 2011). Their antennules bear sensors that are able to perceive information from huge distances and collect capable three-dimensional information concerning a prey`s, predator`s or mate`s identity, position and velocity (Kiørboe 2011). Thus, they enable reactions that are suitable and in time (Kiørboe 2011). The second reason is that they have exceptional escape jump ability compared to other organisms of the zooplankton (Kiørboe 2011). This is due to a binary impulsion mechanism that is present in many copepods (Kiørboe 2011). The "gearing of the swimming leg musculature" and the "impulsiveness of the jumps […] allow for an unusually high propulsion efficiency" (Kiørboe 2011). The third aspect is their feeding method: "scanning current feeding" and "ambush attack jumps" that are practiced by only very few other zooplankton organisms (Kiørboe 2011). "Smart technology, remote prey detection, utilized both in ambush and feeding-current feeding, releases copepods from the penalty of filtering sticky water. These, I believe, are the main reasons for the evolutionary success of pelagic copepods in the ocean" (Kiørboe 2011).

<u>1.3 Introduction to the genus *Oithona*</u>

The genus *Oithona* belongs to the order of cyclopoid copepods. These show high abundances in almost all environments of the ocean and often are the numerically dominant organism in the metazooplankton (e.g. Böttger-Schnack et al. 1989, Hay et al. 1991, Nielsen et al. 1993). In cold areas like the Arctic and in the temperate zone, *Oithona* is often the most present copepod genus in winter and shows reproduction in the upper water layers during the whole year (Kiørboe & Nielsen 1994, Uye & Sano 1995). *Oithona* is presumably the most abundant genus (Deevey 1948, Marshall 1949, Nishida 1985) with the widest distribution among copepods in the coastal waters as well as in the oceanic regions of tropical, temperate and polar waters (Nishida & Marumo 1982, Paffenhöfer 1993, Nielsen & Sabatini 1996, Atkinson 1998, McKinnon & Klumpp 1998).

<u>1.4 Feeding and role of *Oithona* spp in the food web</u>

In many planktonic systems, *O. similis* is highly abundant (Hirst & Ward 2008). Due to its numerical dominance (Nielsen & Sabatini 1996, Gallienne & Robins 2001), *O. similis* is one of the most important copepod species in the world (Gallienne & Robins 2001). The importance of *O. similis* is reflected in its high density, biomass and trophic role within the system (e.g. Fransz & González 1995, Metz 1996, Atkinson & Sinclair 2000). During its whole life span, it is an important predator as well as an important prey organism. In contrast to the nauplii of many other copepod species, the ones of *Oithona* spp. start to feed immediately after hatching (e.g. Uchima & Hirano 1986, Hirst & Ward 2008). However, Hirst and Ward (2008) observed an elevated mortality in the early stages, relative to the later naupliar and copepodite stages. These results likely reflect huge difficulties for the youngest nauplii to find sufficient food or to escape predation (Hirst & Ward 2008).

Whether the food spectrum changes in the nauplius and copepodid stages during growth is not known, but it is most likely. The naupliar stages of *O. similis* may be a major food source for fish larvae (Takahashi & Uchiyama 2007). All developmental stages of *Oithona* spp. are one of the most important sources of food for many

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ichthyoplankton organisms (Sánchez-Velasco 1998), particularly for the larvae of some commercially important species like cod, mackerel, seabream and hake (Young & Davis 1992, Reiss et al. 2005). In some cases, certain developmental stages of fish larvae feed almost exclusively on individuals of *Oithona* species (Porri et al. 2007).

Within a study of Nielsen and Sabatini (1996) in the North Sea, little temporal or spatial variability of the *Oithona* biomass was observed. Thus, Porri et al. (2007) suggested that *Oithona* could be a constant food source for ichthyoplankton and planktivorous fishes there. By preying on *Oithona* spp., carnivorous zooplankton like chaetognaths (Saito & Kiørboe 2001, Giesecke & González 2004) and jellyfish (Omori et al. 1995) make these small copepods also an important element in the structure of many food webs (Hansen et al. 2004). It is possible that small copepods like *O. similis* are a major food source for some seabirds in the open Southern Ocean (Dubischar et al. 2002). Hence, these copepod species may be a key element in the transfer of organic matter from the recycling pelagic community to the higher trophic food levels (Dubischar et al. 2002). On the whole, *O. similis* exhibits an omnivorous and/or detritivorous feeding (Petipa et al. 1970, Turner 1986, Paffenhöfer 1993, Atkinson 1998, Ashjian et al. 2003, Kattner et al. 2003, Reigstad et al. 2005). Furthermore, it has been shown that *O. similis* is an important link between microbial food webs and higher trophic levels (Nielsen & Sabatini 1996). It is therefore possible that *O. similis* benefits from increasing sea temperatures, particularly in high latitudes, where reduced ice cover is predicted to increase the prevalence of microbial recycling-based ecosystems (Hansen et al. 2003).

1.5. Geographic and vertical distribution of *Oithona similis*
Geographic distribution
Oithona similis is a cosmopolitan species (e.g. Fransz & Gonzalez 1997, Blain et al. 2001, Hansen et al. 2004) that is abundant in coastal and oceanic regions of the tropics, the temperate zone and also in polar waters (Sabatini & Kiørboe 1994).

In a study of Bernard (2002), *O. similis* and a small calanoid copepod species,

Ctenocalanus vanus, were most numerous, together contributing up to 85% (range 30 to 85%) to the total mesozooplankton abundances in the Polar Front. *Oithona similis* appears to be widely distributed (Conover & Huntley 1991) or ubiquitous (Atkinson 1998) and dominates the prevailing copepod assemblages in the Southern Ocean (Hopkins & Torres 1889, Metz 1996). Thus, *Oithona* spp. is undoubtedly important for the Antarctic ecosystem (e.g. Fransz 1988, Fransz & Gonzalez 1997, Atkinson & Sinclair 2000). This genus can in general temporarily dominate the metazooplankton of the mixed zone by numbers (e.g. Metz 1995, Fransz & Gonzalez 1995, Swadling et al. 1997). The Southern Ocean is inhabited by two species of the genus *Oithona*: *Oithona frigida* Giesbrecht 1902, and the smaller, numerically as well as according to its biomass dominant species *O. similis* (Metz 1996). *Oithona frigida* is an endemic species in the Southern Ocean (Rosendorn 1917). In the Arctic Ocean, *O. similis* is a dominant species as well (Richter 1994, Auel & Hagen 2002), being probably ubiquitous (Conover & Huntley 1991) as it is found in all Arctic water masses and near or even in the seasonal sea ice (Grainger & Mohammed 1986, Werner 2005). *Oithona similis* is one of the five dominant copepod species in the upper 100 m of the western Arctic Ocean (Ashjian et al. 2003) and in the Greenland Sea (Møller et al. 2006).

In the northern and southern parts of the North Sea and adjacent waters, *Oithona* spp. can contribute significantly to the copepod biomass (Hay et al. 1991, Nielsen et al. 1993, Kiørboe & Nielsen 1994). The biomass of *Oithona* spp. in the North Sea ranges between 1.0–1.4 g C m^{-2} year^{-1} (Tremblay & Roff 1983, McLaren et al. 1989) and 1.8–2.2 g C m^{-2} year^{-1} (Nielsen & Sabatini 1996). Hence, they contribute between 13 and 40% to the annual copepod production (Williams & Muxagata 2006). Sometimes *Oithona* spp. contribute as much as 50-70% to the copepod production in summer (Nielsen & Sabatini 1996). This depends on the region and on the associated calanoid species (Nielsen & Sabatini 1996).

The zooplankton community of the Mediterranean Sea is also dominated by copepods (e.g. Ross & Nival 1976, Dauby 1980, Razouls & Durand 1991). Small copepod species and juvenile stages of bigger copepods are important trophic links

between the classical and the microbial food webs (Roff et al. 1995, Wickham 1995, Calbet et al. 2000). These may be especially important in oligotrophic seas, like e.g. in most of the western Mediterranean Sea (Margalef 1985), as the relative size of primary consumers is expected to be smaller there (Chisholm 1992, Agawin et al. 2000) and the microbial organisms dominate (Gasol et al. 1997). Within coastal environments of the Mediterranean Sea, *Oithona similis* is very common (Castellani et al. 2005). This species is also found in open waters over a wide latitudinal range, but it prefers eutrophic conditions (Castallani et al. 2005). In oligotrophic seas, small-sized organisms (<1 mm) are an important fraction of the zooplankton community (Webber & Roff 1995, Mazzocchi et al. 2003).

Together with *Paracalanus* and *Clausocalanus*, *Oithona* is a dominant genus in the offshore waters of the Balearic Sea (Vives 1978, Fernandez de Puelles et al. 2004), the Ionian Sea (Mazzocchi et al. 2003), in the eastern Mediterranean (Siokou-Frangou et al. 1997), in coastal waters of the Gulf of Naples (Mazzocchi & Ribera d'Alcalà 1995), in the Bay of Tunis (Souissi et al. 2000), in the Gulf of Trieste (Specchi & Fonda-Umani 1983) and in neritic and open waters of the Gulf of Lion and in the Ligurian Sea (e.g. Kouwenberg & Razouls 1990, Licandro & Ibanez 2000, McGehee et al. 2004). In the Ligurian Sea, *Oithona similis* was mainly found in the epipelagic layer within the upper 50 m (Licandro & Icardi 2009). At a station in the Gulf of Naples, nine *Oithona* species were sampled by Mazzocchi & Ribera d´Alcalà during the year 1984 to 1990: *O. atlantica, O. akcipiens, O. longispina, O. nana, O. plumifera, O. setigera, O. similis, O. tenuis, and O. vivida* (Mazzocchi & Ribera d´Alcalà 1995). Within their samples *O. similis* was the dominant species during sampled years from 1984 to 1989. The only exception was 1990 when 50.1 % of the genus total numbers belonged to *O. nana* (Mazzocchi & Ribera d´Alcalà 1995).

Vertical distribution

Throughout the whole year, *Oithona similis* mainly remains in the upper 200 m of the water column of the Southern Ocean (e.g. Metz 1996, Atkinson 1998, Atkinson & Sinclair 2000). During observations in the Arctic, this species was also found close to the surface (Ashijan et al. 2003). However, *O. similis* inhabits all depths down to

4000 m (Rosendorn 1917). Compared to *O. similis, O. frigida* lives deeper in the water column (e.g. Rosendorn 1917, Hopkins & Torres 1988, Metz 1995) and seems to inhabit depths mainly below 200 m (Rosendorn 1917, Hopkins 1985 a), as already found by Giesbrecht who discovered this species in 1902. In contrast to females of *O. similis,* those of *O. frigida* were not found in the upper water layers (Metz 1995). Metz (1996) found adults of the genus *Oithona* in deeper water layers than the juveniles and supposed that this can be explained by the avoidance of predators. Dependent on the habitat and in accordance with the assumption that *O. similis* stays in the upper water layers during the whole year (Fransz & Gozalez 1995, Atkinson 1998, Atkinson & Sinclair 2000) and probably shows growth and reproduction there, the ability for exploiting low concentrations of food might be essential for this species (Atkinson 1998). Its demand of food seems to be large, thus this species would strongly be threatened by starvation. However, experiments hint on the ability to reduce its metabolism during longer times of starvation (Marshall & Orr 1966).

1.6. Morphology
1.6.1 General morphology of the Subclass Copepoda

Depending on species and habitats, the shape of copepods varies (Zhong et al. 1989). Figure 1 shows examples of copepod species of different orders. Free-swimming species generally have a cylindrical body with well-developed appendages and setae (Zhong et al. 1989). Copepod species that inhabit surface waters are rather transparent, colourless, or sometimes blue due to the presence of carotinoids within the cuticle (Zhong et al. 1989). Deep-water species can be colored red due to the presence of crusta (Zhong et al. 1989). There is no doubt that copepod shape and coloration are a manifestation of adaptation to the environment (Zhong et al. 1989).
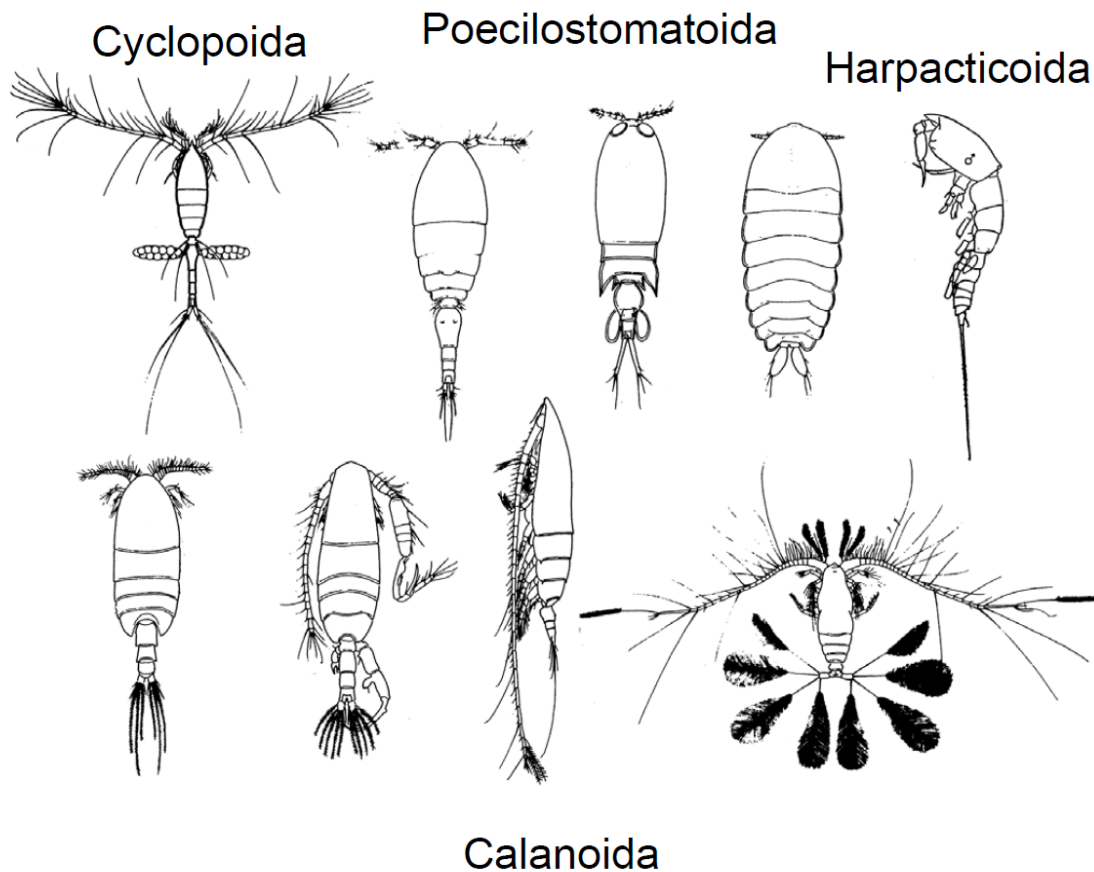
Fig. 1 Examples of morphological features from copepod species of the different orders (Hugget & Bradford-Grieve 2007)

Free-living copepods have a body with 16-17 somites (Zhong et al. 1989). However, less than eleven somites are often present due to fusion (Zhong et al. 1989). The copepod body is usually separated morphologically in two major divisions: prosome and urosome (Zhong et al. 1989, Bradford-Grieve et al. 1999). For an overview of an idealized copepod body see figures 2 and 3. The anterior part of the body is large and globular and the posterior one is narrower (Davis 1949). The anterior portion, the prosome, is further separated into two parts, the cephalosome and the metasome (Zhong et al. 1989). The frontal region of the prosome is covered by a dorsal cephalic shield (Bradford-Grieve et al. 1999). The cephalosome comprises the head that is a fusion of five somites with the first thoracic somite that bears the maxillipeds (Zhong et al. 1989, Bradford-Grieve et al. 1999). The posterior part of the prosome, the

metasome, consists of one to five free thoracic somites that usually have each a pair of pereiopods (swimming feet) (Zhong et al. 1989). Due to differences in the fusion of the metasome somites, interspecific distinctions in the number of free somites exist (Conway 2006). The head never has any segments, but may show a cervical groove in some species (Davis 1949). In many species the head is completely fused with the first pedigerous somite of the metasome, though they are completely separate in other species (Davis 1949, Bradford-Grieve et al. 1999). Anteriorly at the head (Davis 1949, Zhong et al. 1989) is the frontal plate (Zhong et al. 1989) where often one or more eyespots are found, and some species have large cuticulae lenses on its dorsal side (Davis 1949, Zhong et al. 1989). The anterior position of the head usually bears a rostrum ventrally (Davis 1949, Zhong et al. 1989) and a frontal organ with two sensory hairs (Davis 1949).

Copepod form – ventral view

Cephalosome

Rostrum

Aesthetasc

Antenna 1 (Antennule)

Labrum

Antenna 2 (Antenna)

Mandible

Maxilla 1 (Maxillule)

Maxilla 2 (Maxilla)

Maxilliped

Prosome

Coxa

Basis

Pedigerous somite 1

Exopod

Leg 1

Endopod

Leg 2

Pedigerous somite 3

Leg 3

Leg 4

Genital double-somite

Leg 5

Urosome

Anal somite

Caudal rami
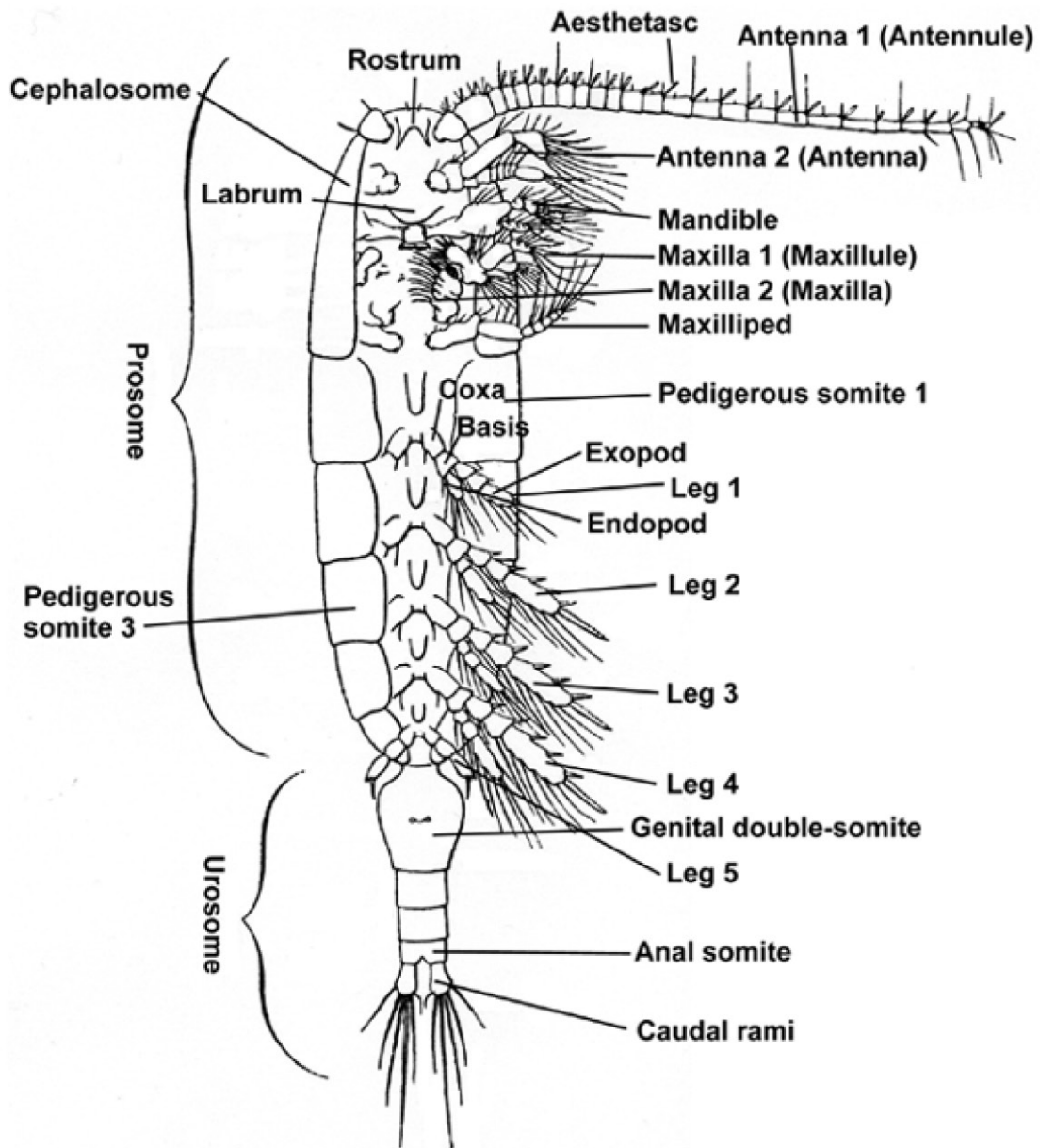
from Giesbrecht & Schmeil, 1898

Fig. 2 Ventral view of an idealized copepod (in Hugget & Bradford-Grieve 2007)

Copepod form – lateral view

Cephalosome (Ce)

Prosome (Pr)

Metasome (Me)

Urosome (Ur)

rostrum (Ro)
antennule (A1)
labrum
antenna (A2)
labium
mandible (Md)
maxillule (Mx1)
maxilla (Mx2) Mxp1*
maxilliped (Mxp) Mxp2*

leg 1 (P1)
leg 2 (P2)
leg 3 (P3)
leg 4 (P4)
leg 5 (P5)
genital somite (Gn)
anal somite (Ur4)
furca or caudal ramus (CR)

* used by some older works

crest   rostrum
cephalosome
prosome
pedigerous somites
pd 1
pd 2
pd 3
pd 4
pd 5
p1
p2
p3
p4
p5
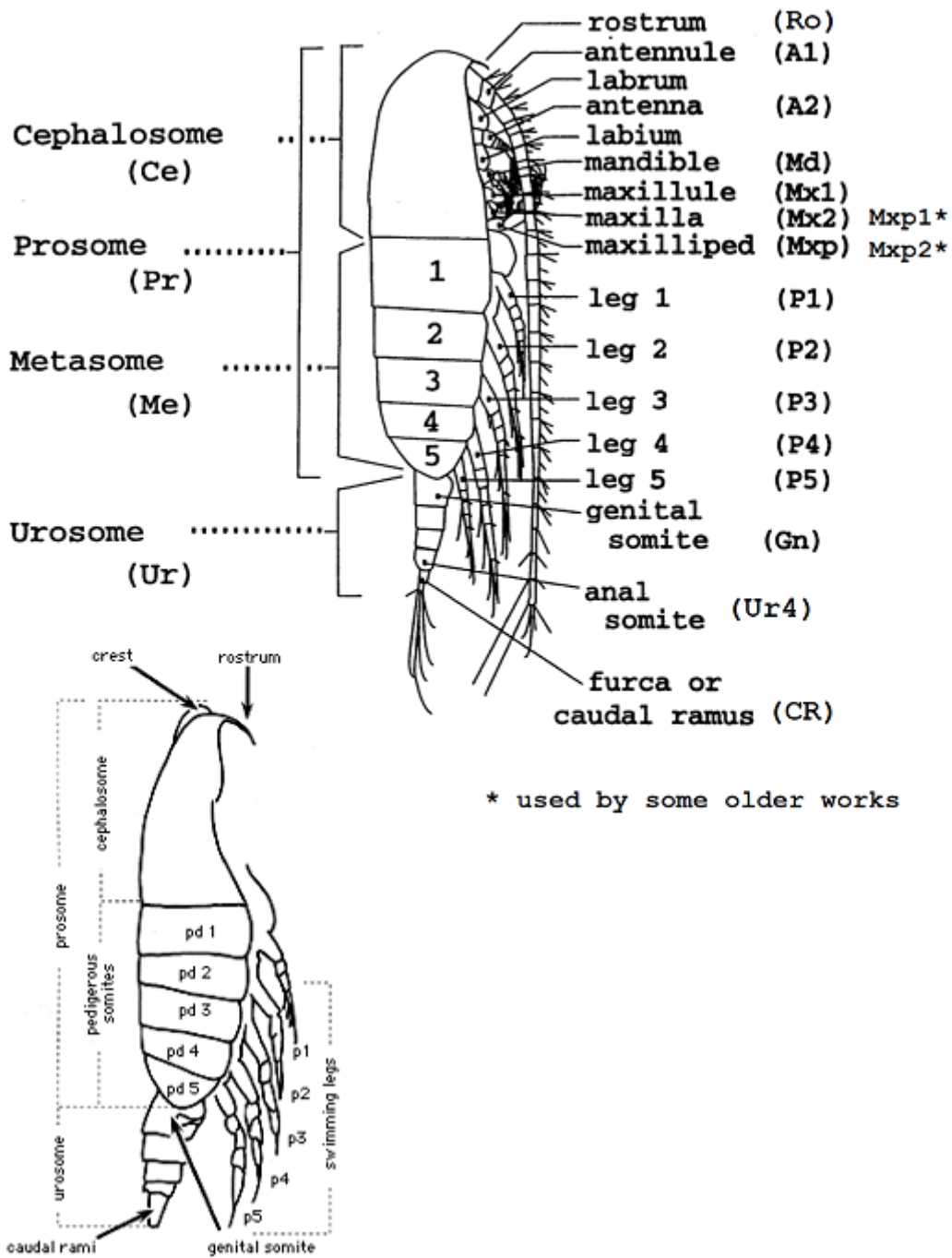swimming legs
urosome
caudal rami   genital somite

Fig. 3 Lateral view of an idealized copepod (Hugget & Bradford-Grieve 2007)

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The posterior portion, behind the body articulation (Zhong et al. 1989) is called the urosome (Davis 1949, Zhong et al. 1989). Calanoid copepods compared to cyclopoid and harpacticoid copepods have a different number of somites and thus a different point where the body articulates (Conway 2006). Figure 4 shows the major body articulation of different copepod orders. The urosome includes the abdomen and one or two (in the two suborders Harpacticoida and Cyclopoida; Davis 1949) somites of the thorax (Davis 1949, Zhong et al. 1989) that are fused with the abdomen (Zhong et al. 1989). The abdomen has a narrow and cylindrical shape and does not show any appendages (Zhong et al. 1989). Generally it has five somites, but in females the first two are normally fused to a genital somite (Zhong et al. 1989). This genital somite is usually swollen (Davis 1949), so that it appears as if they have at least one somite less in the urosome than the males (Conway 2006). In calanoids, it is the first somite of the urosome and shows the genital opening in both sexes (Conway 2006). However, in cyclopoid and harpacticoid copepods, this somite bears the fifth swimming feet while the following one is the genital somite (Conway 2006).

Major body articulation

PODOPLEAN COPEPODS   Cyclopoida Harpacticoida Poecilostomatoida   GYMNOPLEAN COPEPODS   Calanoida   ADULT
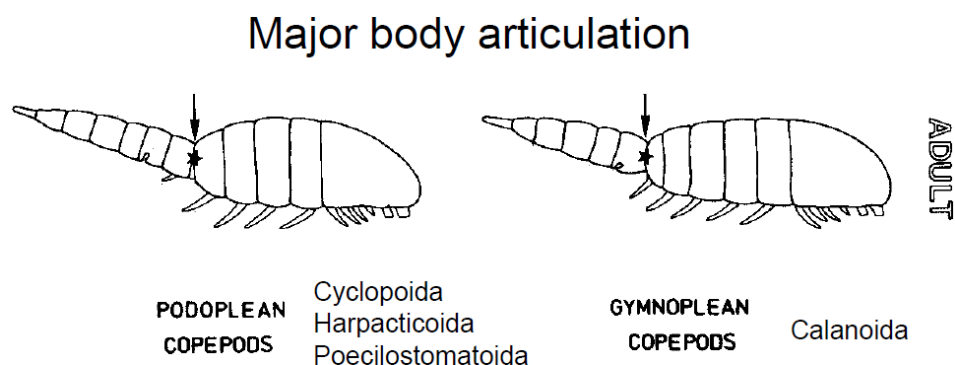
Fig. 4 Major body articulation of the different copepod orders
   (Hugget & Bradford-Grieve et al. 2007)

The last somite of the abdomen shows two appendages, named furcal (or caudal) rami (or furca; Zhong et al. 1989) (Davis 1949, Zhong et al. 1989). Each side of the anal opening bears one of these appendages that usually have terminal setae that help in flotation (Davis 1949). Some species have very greatly developed furcal setae (Davis 1949).

For the identification of copepod species, their appendages are very important. Thus, for this study, a detailed literature research on the morphological structures was necessary to identify the characteristics that could be used to distinguish between *Oithona* species. Copepods have eleven pairs of appendages which are either uniramous or biramous (Zhong et al. 1989). Generally the six pairs of appendages are modified into sense and feeding organs that are located on the head (Davis 1949): antennules, antennae, mandibula, maxillules, maxillae and the maxillipeds that are located on the first thoracic segment that is fused with the head (Zhong et al. 1989). The metasome further has five pairs of swimming legs (pereiopods; Zhong et al. 1989), one pair on each thoracic segment (Davis 1949, Zhong et al. 1989; see also figure 2).

The <u>first antennae</u> (antennules, Zhong et al. 1989) are located close to the tip of the copepod body. They are always uniramus and generally quite long (Davis 1949, Zhong et al. 1989). The antennules have numerous segments (Zhong et al. 1989), according to Davis (1949) up to twenty-five segments. However, the last two segments of the first antennae usually are fused and thus reduce the number of segments (Davis 1949). Females generally have symmetric first antennae, whereas one of them is modified to a grasping organ (Davis 1949) to copulate (Zhong et al. 1989) in the males of many genera. In males of *Oithona* and several other genera, both of the first antennae are geniculate (Davis 1949). The antennules are mainly balancing organs (Zhong et al. 1989). Their length and segment number are depending on the habitat (Zhong et al. 1989). For example, planktonic calanoid copepods have long and slender antennules with 23 to 25 segments, while benthic harpacticoid species have shorter antennules with five to nine segments (Zhong et al. 1989). Figure 5 shows a scheme of the first antennae of an idealized calanoid copepod.

Calanoid mouthparts

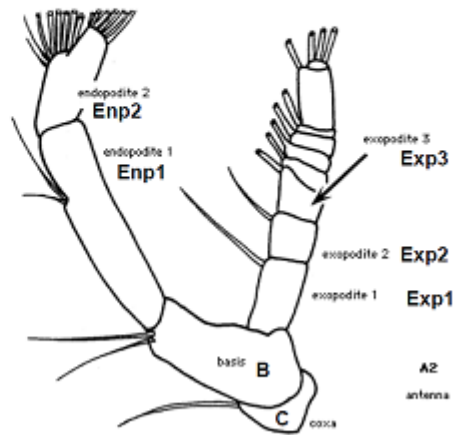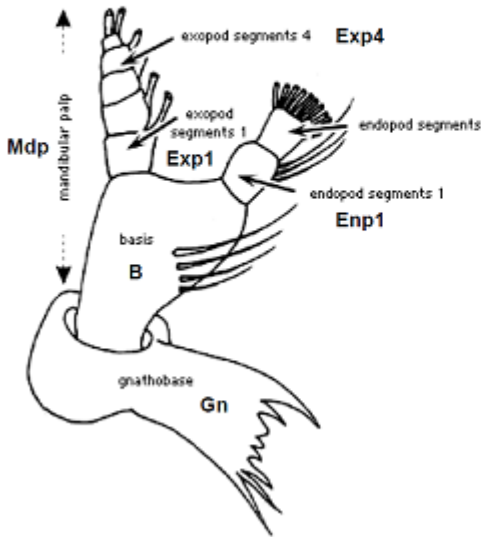## Antennule (A1)
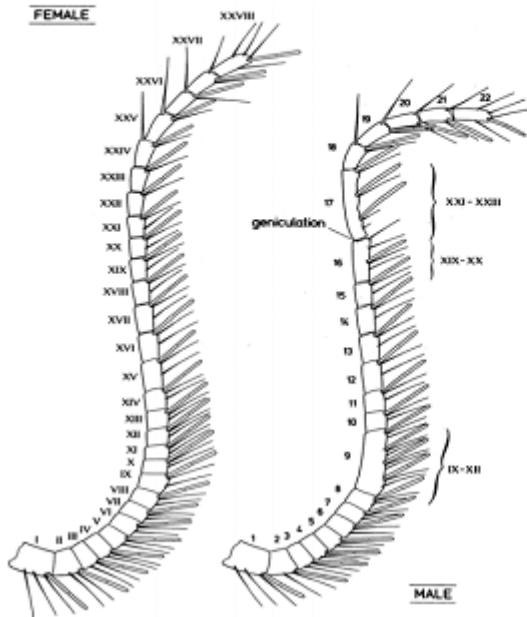
Antenna (A2)

Maximum 28 segments in female A1

Mandible (Md)

Maxillule (Mx1)

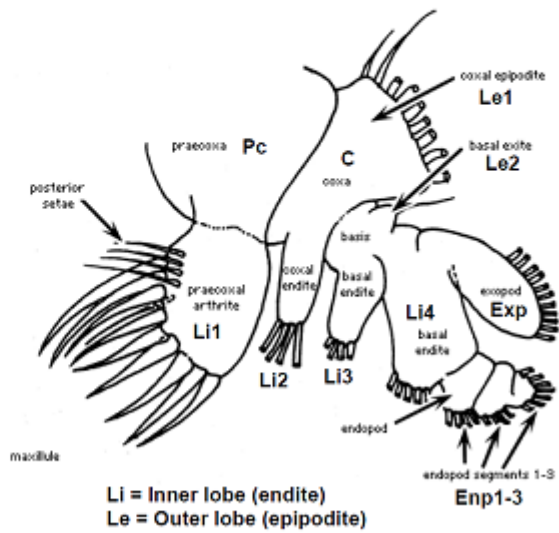Li = Inner lobe (endite)
Le = Outer lobe (epipodite)

Fig. 5 Schematic mouthparts of an idealized calanoid copepod (Huys & Boxshall 1991)

The paired second antennae are located posterior to the first ones (Davis 1949, Zhong et al. 1989). A scheme of a second antenna of an idealized calanoid copepod is shown in figure 5. The second antennae are shorter than the first ones and biramous (Zhong et al. 1989). Typically, they have a two-segmented basipod, a two-segmented endopod and an exopod with six or seven segments (Davis 1949). Thus, the second antennae are greatly modified in many individual genera and species and may in some cases be uniramous (Davis 1949). In many groups, such as cyclopoids, the exopodite is missing (Zhong et al. 1989). In males of e.g. the genus *Corycaeus* the second and not the first antennae are modified into grasping organs (Davis 1949).

A pair of mandibles (mandibula; Zhong et al. 1989) is located posterior to the second antennae (Davis 1949). They are located on either side of the mouth between the anterior and posterior labium (Zhong et al. 1989). Figure 5 shows a scheme of the mandible of an idealized calanoid copepod. The inner border of the basipod of the mandible shows teeth and this segment is called the masticatory portion of the mandible as it is used in the mastication of food (Davis 1949). Number and shape of teeth are variable depending on the different feeding habitats of the copepod species (Zhong et al. 1989). The mandibular palp is formed by the basis of the mandible and jointed exopod and endopod (that are mostly present; Davis 1949) (Davis 1949, Zhong et al. 1989), and bear setae (Zhong et al. 1989).

The appendages behind the mandibles are the first maxillae (maxillules; Zhong et al 1989). The pair of small and biramous maxillules is located beneath the mouth (Zhong et al. 1989). They are used to hold and manipulate food (Davis 1949). Furthermore, they are taste organs (Davis 1949). The protopod of the maxillule bears a (short; Davis 1949) exopodite and an endopodite (Davis 1949, Zhong et al. 1989) with setose lobes (Zhong et al. 1989). The first basipod segment consists of three inner and one outer lobe (Davis 1949) and bears serrated and stout spines (Zhong et al. 1989). It is called masticatory edge or gnathobase and a predation organ (Zhong et al. 1989). For morphological details see also figure 5.

The (second; Davis 1949) <u>maxillae</u> have only one branch (Davis 1949, Zhong et al. 1989). They are strongly developed in some species, while in others, they are small and insignificant or absent (Davis 1949). The maxillae generally comprise a protopod with two segments and an endopod with five segments that bears a series of setose endites (Zhong et al. 1989). A scheme of a maxilla of an idealized calanoid copepod can be seen in figure 6.

Calanoid mouthparts and swimming leg

Maxilla (Mx2)

Maxilliped (Mxp)
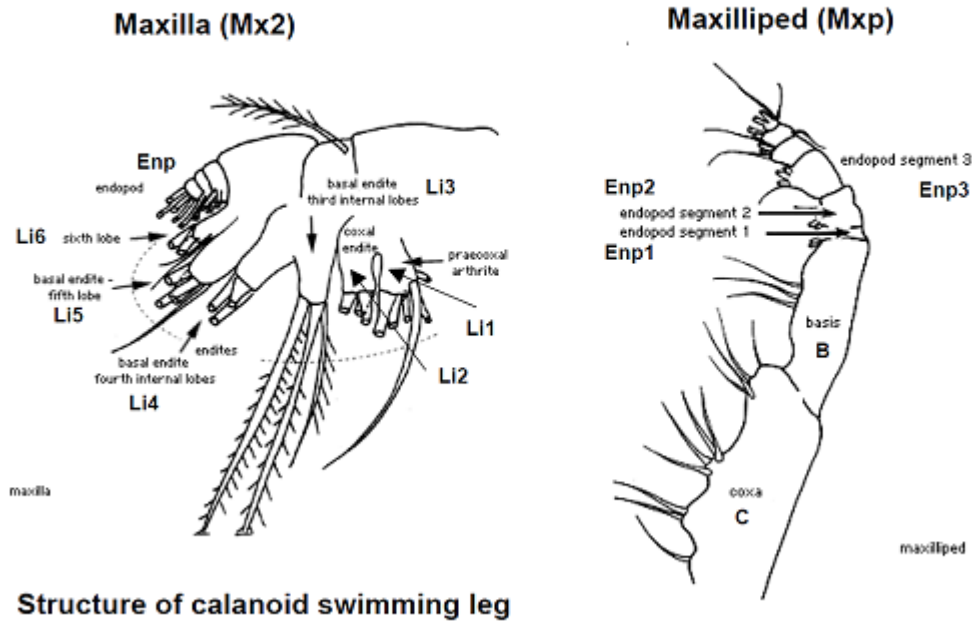
Structure of calanoid swimming leg

Structure of calanoid swimming leg. Basic copepod swimming leg, showing the maximum setation of a second leg.

Fig. 6 Schematic mouthparts and swimming feet of an idealized calanoid copepod (Huys & Boxshall 1991)

Located posterior to the second maxillae are the uniramous <u>maxillipeds</u> (Davis 1949). They are the first appendages of the thorax and modified as feeding organs (Zhong et al. 1989). Maxillipeds have two basal segments that are normally much larger than the other segments (Davis 1949). Furthermore, an endopod, consisting of several shorter segments, is attached to the distal end of the second basal segment (Davis 1949). The endopods have setae of various structures due to the different feeding habits of copepod species (Zhong et al. 1989). For example, carnivorous species have rather strong maxillipeds with stout spines like species of the genus *Euchaeta,* or claw-like one as in species of the genus *Oncaea* (Zhong et al. 1989). However, filter feeders have maxillipeds with many plumose setae (Zhong et al. 1989). An example of a maxilliped structure is shown in figure 6.

In general, copepods have five pairs of <u>swimming legs</u> (pereiopods; Zhong et al. 1989), each pair being attached to one thoracic segment (Davis 1949). The pereiopods are located below the sternite of the thorax somites (Zhong et al. 1989). Copepods within the suborder Calanoida have all their legs on the metasome. In the suborders Cyclopoida and Harpacticoida, the fifth pair of swimming legs is attached to the first segment of the urosome (Davis 1949). A few genera have a rudimentary sixth pair of feet (Davis 1949). They are located at the genital somite (Bradford-Grieve et al. 1999). In females, the sixth pereiopods constitute the opercula that closes off the paired genital aperture (Huys & Boxshall 1991). The first four pairs of swimming legs resemble each other (Davis 1949, Zhong et al. 1989). Figure 6 shows an example of a schematic swimming leg. These legs are almost identical in both sexes and symmetrically biramous (Zhong et al. 1989). Simultaneous movement is ensured through a chinious plate, "the coupler" that unites each pair of legs (Zhong et al. 1989). This intercoxal sklerite may be fused to the coxa (Bradford-Grieve et al. 1999). The pereiopods normally have two basal segments (Davis 1949, Bradford-Grieve et al. 1999): coxa and basis (Bradford-Grieve et al. 1999), an inner ramus (the endopod) and an outer ramus (the exopod) that are attached to the second basal segment (the basis) (Davis 1949, Bradford-Grieve et al. 1999). Both ramus bear setae and spines (Zhong et al. 1989, Bradford-Grieve et al. 1999).

The most generalized genus of the Copepoda is the genus *Calanus* (Davis 1949). In this genus, each exopod and endopod consists of three segments (Davis 1949). Though in most species, especially the endopods of the first and second legs show modified segmentations (Davis 1949). The female´s fifth swimming feet are normally extremely modified to primitive condition (Davis 1949). They are reduced in size, are often uniramus and extremely rudimentary, or even entirely absent (Davis 1949). Generally, in males, the structure of the fifth leg is more complex and better developed than in females (Zhong et al. 1989). Three types exist: biramous, uniramous or missing (Zhong et al. 1989). In the suborder Calanoida, the males usually have a highly developed fifth leg (Davis 1949). In some species, it is "modified into a complicated and powerful hand for the transference of spermatophores to the female during copulation" (Davis 1949). Especially for males the structure of the fifth swimming leg is extremely important for the determination of the species (Davis 1949, Zhong et al. 1989). However, in the orders Cyclopoida and Harpacticoida, the fifth legs are often rudimentary and therefore practically have no systematic value (Zhong et al. 1989).

1.6.1.1 Explanations and Abbrevations

According to Gardner & Szabo (1982) this thesis used the following terminology

Genital segment (gnst): The first segment of the urosome with the genital aperture, often with hairs, spines, flanges or bulges

Labrum: An upper lip that covers the mouth openings

Mandibles (md): Are paired mouthparts that are located posterior to the antennae

Maxillae (max 1, max 2): Are two pairs of mouthparts (mx1, max 2) that are located between the mandibles and maxillipeds

Maxillipeds (mxp): Are paired appendages located behind the second maxillae and prior to the first pair of swimming legs

Ornamentation: Occurrence of spines, hairs, or setae

Ovisac: a casing that contains the fertilized eggs and generally is attached to the genital segment

Prosome (pro): comprises head and thorax and is located anterior to the point of articulation of the urosome

Proximal: nearest to the point of origin

Ramus (pl. Rami): a branch that consists of one or more segments

Rostrum: a beak-like prolongation of the head

Seta: An elongated bristle

Setose: covered with setae

Setule: small, blunt seta often borne on a larger seta

Setulose: covered with setules

Spine: thorn-like projection with a defined point of attachment to the body

Spinifrom: drawn out to an acute point; in the shape of a spine

Spinulation: covering of small spines

Spinule: small spine

Spinulose: seta with small spines

Styliform: ending in a long, slender point

Thorax (th): the middle region of the body that bears the swimming legs

Total length: Means the distance between the apex of the head and the distal margin of the caudal rami

Urosome (ur): the abdomen; that part of the body that is located posterior to the major articulation and includes the genital segment

1.6.2 Order Cyclopoida

Cyclopoid copepods are characterized by small size (Wilson 1932, 1942, Gardner & Szabo 1982). Species of these orders all show the same segmentation of the body (Conway 2006). The body of adult cyclopoid copepods consists of a prosome with cephalosome and four pedigerous segments, and an urosome with six segments that are all free in males whereas in females only five are free (Conway 2006). The urosome is slender and elongated (Wilson 1932, 1942, Gardner & Szabo 1982), while the prosome is broader (Gardner & Szabo 1982, Zhong et al. 1989). Prosome and urosome are clearly distinct (Van Breemen 1908). Cyclopoid copepods have a very movable articulation between the last two trunk segments (Sars 1918, Zhong et al. 1989). The posterior of these segments is usually very small and tightly connected with the genital segment (Sars 1918, Wilson 1932). Thus at first sight, it seems likely that it belongs more properly to the posterior than to the anterior part of the body (Sars 1918). Consequently, the first segment of the urosome bears the fifth pair of legs which as a general rule is much reduced (Conway 2006). The fifth pedigerous segment first appears in the third copepodid stage (Conway 2006). Cyclopoid copepods more resemble calanoid than harpacticoid ones (Sars 1918). However, this articulation makes it easy to distinguish calanoid and cyclopoid copepods (Sars 1918).

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The antennules of cyclopoids are rather short (Brady 1883, Zhong et al. 1989) and scarcely longer than the cephalothorax (Brady 1883). They are generally shorter than the prosome (Gardner & Szabo 1982). Characteristic of males is that both antennules are modified to grasping organs (Brady 1883, Van Breemen 1908, Zhong et al. 1989). However, the anterior antennae of copepod species within the order Cyclopoida are usually more elongated than the ones in harpacticoid species (Sars 1918). Furthermore, they have more articulations (Sars 1918).

The antennae of cyclopoid copepods are generally uniramous (e.g. Brady 1878, Gardner & Szabo 1982, Zhong et al. 1989) without an exopod (Sars 1918). A slight rudiment of such a ramus can only be found in a few parasitic species (Sars 1918). The structure of antennules and antennae allows a jumpily swimming motion (Gardner & Szabo 1982).

Further characteristics of cyclopoid copepods are well developed mandibular and maxibular palps (Brady 1883). However, these are rudimentary in some species (Brady 1883).

In copepods of this order, the first four pairs of legs are equal (Brady 1883). They have two branches and are adapted for swimming (Brady 1883). Endopod and exopod of swimming legs one to four are trinomial or have a reduced number of segments (Van Breemen 1908). Leg number five is rudimentary (Brady 1883, Van Breemen 1908, Zhong et al. 1989), one or two-segmented (Zhong et al. 1989) and shows in most cases no difference between the sexes (Van Breemen 1908, Wilson 1932).

Females of this order bear their eggs in two ovisacs (e.g. Van Breemen 1908, Wilson 1932, Gardner & Szabo 1982) that are attached laterally or subdorsally at their surface (Wilson 1932, Zhong et al 1989).

<u>1.6.2.1 Family Oithonidae Dana 1853</u>

Species belonging to the *Oithonidae* are small sized (Zhong et al. 1989). Their slender cyclopiform body (e.g. Kiefer 1929, Zhong et al. 1989, Boxshall & Halsey 2004) has thin and transparent integuments (Sars 1918). Females reach total lengths of 0.36 to 1.9 mm while males are usually smaller and range between 0.37 and 1.24 mm (Nishida 1985).

Species of this family differ because they have a moderately dilated prosome, their urosome is long and slender (González & Bowman 1965, Zhong et al. 1989). The prosome has five somites (Nishida 1985), namely the cephalosome and four segments, each bearing a pair of swimming legs (Boxshall & Halsey 2004). At the lateral margin of the cephalosome, males of some *Oithona* species show paired flap organs (Boxshall & Halsey 2004). Prosome and urosome are clearly separated from one another (Zhong et al. 1989).

Oithonid species have a distinct head (Kiefer 1929) that exhibits a nauplius eye (Boxshall & Halsey 2004). The rostrum is variable (Boxshall & Halsey 2004) either pointed or curved and partly highly developed (Kiefer 1929). It can be directed anteriorly or ventrally but is often reduced (Boxshall & Halsey 2004).

The anterior antennae (antennules) of species within the family *Oithonidae* are very slender (Sars 1918, Kiefer 1929) and have long diverging setae in females (Sars 1918, Gonzalez & Bowman 1965). They have no aesthetascs, which are present in males (Gonzalez & Bowman 1965). Male antennules are more distinctly geniculate (Sars 1918) and modified as grasping organs (Kiefer 1929). The antennules have 10 to 15 segments (Zhong et al. 1989). In contrast, the posterior antennae are small (Sars 1918). They have between two and four segments (Kiefer 1929, Zhong et al. 1989) and are uniramous without an expopod (González & Bowman 1965, Zhong et al. 1989).

The well-developed mouth parts differ from those of other cyplopoids (Sars 1918). Partially mandibles and maxillae wear claw-like spines (Sars 1918).

The urosome of oithonids has five segments (Boxshall & Halsey 2004). In females, the genital and the first abdominal segment are fused to a genital double somite (Boxshall & Halsey 2004). On the double somite of the females paired genital apertures including copulatory pores and gonopores are located laterally (Boxshall & Halsey 2004). The abdomen has three further free segments (Boxshall & Halsey 2004). Males have a six-segmented urosome: five pedigerous, one genital and four free abdominal segments (Boxshall & Halsey 2004). The genital aperture of the males is paired and located ventrally (Boxshall & Halsey 2004).

The rami of oithonid swimming legs one to four are comparably slender and three-articulate (e.g. Gonzalez & Bowman 1965, Zhong et al. 1989, Boxshall & Halsey 2004) or less common, two-articulate (Kiefer 1929, Gonzalez & Bowman 1965, Boxshall & Halsey 2004), and edged with long setae (Sars 1918). The fifth pair is rudimentary (Sars 1918, Kiefer 1929) and partially coalescent with the corresponding segment (Sars 1918). Thus, it is only a small conical segment that shows one, two (Zhong et al 1989), three or four long setae (Boxshall & Halsey 2004). Two setae on the genital operculum of the two sexes represent the sixth leg (Boxshall & Halsey 2004).

Within this family, the caudal rami of females and males are different (Sars 1918). In males they have six setae (Boxshall & Halsey 2004). Moreover, females have paired egg sacs (Boxshall & Halsey 2004).

1.6.2.2 Subfamily *Oithoninae*

Typical for this subfamily is the rudimentary fifth foot (Kiefer 1929). Its ancient first limb is almost completely melded with the fifth thoracal segment and can only be recognized as small hump with one bristle (Kiefer 1929). The second limbs are better obtained, small and slender with one terminal bristle or, as in three species, with two bristles (Kiefer 1929). At least at the lateral limb of the fourth swimming feet one or more lateral spines are lacking or vestigial (Kiefer 1929).

This subfamily includes marine pelagic species and one freshwater species (Kiefer 1929).

1.6.2.3 Genus *Oithona* Baird 1843

Included in the genus *Oithona* are species with very different body sizes (Rosendorn 1917). Total lengths are ranging from 0.4 to 1.9 mm (Rosendorn 1917, Al Yamani & Prusova 2003). Characteristic of species within this genus is a slender body (Brady 1883, Sars 1918, Davis 1949) that shows thin and pellucid integuments (Sars 1918).

The slender prosome within this genus (Claus 1863, Gardner & Szabo 1982) is five-segmented (e.g. Wheeler 1901, Van Breemen 1908, Pesta 1920) and clearly separated from the urosome (Mori 1937). A well-marked structure defines the head from the first pedigerous segment (e.g. Claus 1863, Mori 1937, Zhong et al. 1989). The shape of the forehead is different in the sexes, usually sharp-pointed in females and rounded in males (e.g. Rosendorn 1917, Kiefer 1929, González & Bowman 1965). A rostrum can be present (Davis 1949) and may be useful for species identification (Al Yamani & Prusova 2003).

Species of the genus *Oithona* have long and slender first antennae with 10 to 15 segments (Brady 1883, Sars 1918) that reach the posterior margin of the prosome or are even longer (Gardner & Szabo 1982). In some species, the antennules of the females almost reach the end of the body (Kiefer 1929, Mori 1937) and show single very long bristles (Claus 1863). In males, they are modified to grasping organs (e.g. Claus 1863, Brady 1878, Mori 1937), each having one aestethasc at the end (Van Breemen 1908, Pesta 1920). Female antennules are lacking aestethascs (Van Breemen 1908, Wheeler 1901, Pesta 1920).

A further characteristic of this genus is that the second antennae consists of two segments (Van Bremen 1908, González & Bowman 1956), or in some species three, (Wheeler 1901, Kiefer 1929) and shows an abrupt bend in the middle (Sars 1918). The second antennae have no exopod (e.g. Wheeler 1901, Mori 1937, Al Yamani & Prusova 2003). According to Claus (1863), they have four segments. The last two

are attached to the basis in a geniculated joint and wear long and bent bristles (Claus 1863).

Species of this genus show an elongated and slender mandible (e.g. Brady 1883, Van Breemen 1908, Pesta 1920). It has two stout dentate apical spines and a jointed secondary branch, as well as a "ciliated wart-like marginal process" (Brady 1878). The basal part of the mandibular palp is greatly elongated, pediform and ends in two claw-like spines (Sars 1918). A very small setiferous appendage attached outside the basal part at some distance from its end forms the inner ramus (Sars 1918). The outer ramus is well developed, abruptly reflexed and consists of three to four joints that carry long plumose setae (Sars 1918). The endopod of the mandible has one somite (Kiefer 1929, González & Bowman 1956) while the exopod is three- (Kiefer 1929) to four-articulate (Kiefer 1929, González & Bowman 1956). The second basal somite has two terminal spines (Kiefer 1929, González & Bowman 1956, Al Yamani & Prusova 2003). In some species the exterior spine is reduced (Al Yamani & Prusova 2003). The mandibles of males are less strong than in females (Rosendorn 1917).

Characteristic for the genus *Oithona* is that endopod and exopod of the first maxillae are one-articulate (Wheeler 1901, van Breemen 1908, González & Bowman 1956). The maxillae are vigorous (Brady 1883, 1887). Their masticatory lobe is well defined and has a number of sharp claw-like spines (Wheeler 1901, Sars 1918). The spines are accompanied inside by the palp lamellar, a thick setiform appendage (Sars 1918) with two-branches (Brady 1878, 1883). The outer distal lobe of the maxilla is very small while the proximal lobe is well developed, recurved and shows long plumose setae at the tip (Sars 1918). In males, the first maxillae are weaker than in females (Rosendorn 1917).

The second maxillae and the maxilliped are slender (Wheeler 1901, Van Breemen 1908, Sars 1918) and elongated (Wheeler 1901, Sars 1918). They show strong spines (Van Breemen 1908). The endopod of the maxilliped has two somites (Van Breemen 1908). The anterior pairs of maxillipeds have five segments and the

posterior ones four (Sars 1918). Both carry long spines that are curved anteriorly (Sars 1918). Second maxillae and maxilliped do not show a strong sexual dimorphism (Rosendorn 1917). However, the maxilliped in males is slightly weaker developed (Rosendorn 1917).

The urosome of those species is elongate (Davis 1949, Gardner & Szabo 1982) with five segments in females and six in males (e.g. Van Breemen 1908, Mori 1937, Zhong et al. 1989). In the genus *Oithona*, the urosome is longer than one third of the total copepod length (Gardner & Szabo 1982). The second segment of the urosome forms the genital segment (Davis 1949, Zhong et al. 1989) that is usually swollen (Davis 1949) and the longest segment (Al Yamani & Prusova 2003). The genital opening of the females is located laterally (Wheeler 1901).

The basal part of the swimming legs is wide and oblate (Sars 1918). The rami are usually well-developed and subequal in size (Sars 1918). The endopods of the first swimming feet are three-articulate (e.g. Brady 1883, Mori 1937, Al Yamani & Prusova 2003). The exopods as well (Brady 1878, Kiefer 1929, González & Bowman 1956). In rare cases the endopod of the first foot has two segments (González & Bowman 1956). Inside the first joint of the outer ramus, swimming legs one to four have no distinctly developed setae (Sars 1918). However, the apical spine of this ramus is very slender and serrate outside (Sars 1918). In males, the spines of the outer edge are more consummately developed than in females (Sars 1918). Furthermore, the number of spines differs in some species as well from that of the females (Van Breemen 1908). In males, the swimming feet are less degenerated than in the females, and the shapes of the outer setae and the terminal spines show fundamental secondary sexual characters (Rosendorn 1917).

The fifth swimming feet are rudimentary (e.g. Claus 1863, Wheeler 1901, Mori 1937) and show two small setiferous papillae (Brady 1878, 1883, Al Yamani & Prusova 2003). In most species they are exactly alike in both sexes (Claus 1863, Rosendorn 1917, Sars 1918). The first limb is reduced to a small bump with one bristle (Kiefer 1929). The second limb is also small, with one (or in three species with two) terminal

spine(s) (Kiefer 1929). The sixth natatory feet are represented by one or two setae at the anterior part of the genital segment (Al Yamani & Prusova 2003).

The caudal rami are symmetrical (Zhong et al. 1989), short and in some cases heavily spread (Kiefer 1929). In females, they are intensely divergent (Sars 1918). Their two middle apical setae are much elongated and cross each other at the base (Sars 1918). In males, the furcal branches are not as spread as in females (Rosendorn 1917). They are shorter and have four bristles with the middle ones stronger and longer than the two others (Rosendorn 1917). A further difference between the sexes is that the outer setae of the furca are not placed above the middle of the margin, instead they are directly in the middle of the furcal margin and do not even reach the length of the furca in males (Rosendorn 1917).

Males are not known for all *Oithona* species yet (Kiefer 1929). The known males differ from their females in the urosome and the first antennae and show more secondary sexual characteristics, e.g. are their spines much more pronounced at the exopods of the swimming legs (Kiefer 1929). Comparative morphological examinations show that the specific differences of the female are partially compensated in the males (Rosendorn 1917). Thus, the attribution to a sex is not easy in some cases (Rosendorn 1917).

Rosendorn (1917) identified the female and males that belong together in the samples, when males and females of specific species were cosampled several times. The distinction depended on the relative size and thickness of both sexes, the relative number of bristles at the swimming legs and the same structure in the first leg and some single and specific characters that she found in both gender. However, the definite attribution was based on an extensive examination of the mouthparts, as both genders have the same number of setae at the mandibles and maxillae (Rosendorn 1917). This showed to which species they belong (Rosendorn 1917). Males of different species can be distinguished based on size and shape of the trunk, the structure of mandible and maxille, setae structure of the swimming legs and the shape of the abdomen (Rosendorn 1917).

The genus *Oithona* was established by Baird in 1843 (Claus 1863, Rosendorn 1917, Sars 1918) for the species *Oithona plumifera* from the tropical part of the Atlantic (Rosendorn 1917, Sars 1918) and *Oithona splendens* (Rosendorn 1917). *Oithona plumifera* characteristically has pinnate hairs on the swimming feet. "*Oithona* is distinguished from *Cyclopsina* by having a pair of short antennae situated immediately in front of the long pair" (Baird 1843). Baird believed that the first species of this genus is a "seawater louse" drawn by Slabber in 1778 (Rosendorn 1917). Baird named it *Oithona* and explained it like this: "Slabber in his work upon the microscopise gives a figure of ˈzeewater luisˈ, which very much resembles the species Cycloposina. I have therefore named it after him as its first observer: *Oithona* (Virgin of the wave)" (Rosendorn 1917). Later Dana described the genus *Scribella* that is identical with the genus *Oithona* (Claus 1863). He gave the first detailed description of this genus (Rosendorn 1917). Dana placed *Oithona* close to *Acartia* in the family of the *Calanida* (Claus 1863, Sars 1918).

Claus (1863) was of the opinion that the genus *Oithona* links the cyclopoid and calanoid copepods, but is much more connected to the genus *Cyclops* concerning the segmentation of the body and the viscera (Claus 1863). Starting with Claus remarks with regard to the relationship of the genus *Oithona* to *Cyclops*, *Oithona* was seen to belong to the order of Cyplopoida (Rosendorn 1917). Following the first description of *O. plumifera*, several species of the genus *Oithona* have been described from different parts of the ocean (Sars 1918). The first coherent basic description of the genus *Oithona* was done by Giesbrecht in 1892 ("Fauna und Flora von Neapel") with the eight species that he knew (Rosendorn 1917). Three of those were already known: *O. setigera* and *O. plumifera* (Dana 1852) and *O. similis* (Claus 1866) (Rosendorn 1917). *Oithona linearis*, *O. robusta*, *O. brevicornis*, *O. nana* and *O. hebes* were first described by Giesbrecht in 1892 (Rosendorn 1917). The number of species then increased to about three times of the eight species described by Giesbrecht (Rosendorn 1917). Nine of the species, including *O. helgolandica* Claus 1863 that were described until 1917 are no independent species (Rosendorn 1917). In 1908, Farran founded the genus *Paroithona* (Rosendorn 1917). Rosendorn (1917)

was of the opinion that *Paroithona* can only be a subgenus. A second subgenus is *Limnoithona* that was described by Burckhardt (1913) from the freshwater (Rosendorn 1917). Concerning the correct identification of some *Oithona* species, there is still considerable confusion because of the close relations or the difficulty in examining "such delicate and fragile animals" (Sars 1918).

Some of the most important characteristics belonging to cyclopoid copepods are present in *Oithona*: the geniculation of the first antennae in males, the posterior antennae without a secondary branch, the rudimentary fifth feet and the two ovisacs (Brady 1878). These characters all agree with *Cyclops* as well as the structure of the viscera (Brady 1878) and of the urosome (Claus 1863). The shape of the eye, the anatomy of the testes and ovaries and the development of two ovisacs ally to the genus *Cyclops* (Claus 1863).

Species of the genus *Oithona* are very numerous in the plankton of inshore waters throughout the world (González & Bowman 1956). This genus includes many species and "the characters used to separate some of the species are slight" (González & Bowman 1956). Furthermore, "some species have been described inadequately; e.g. such important characters as P5 and the terminal setae of the mandible have been omitted in some descriptions" (González & Bowman 1956). As a consequence the identification of a species is sometimes difficult (González & Bowman 1956).

1.7 DNA Barcoding

A widely used genetic method to detect crytpic phyto- and zooplankton species and, thus, to understand the role of cryptics in ecological and evolutionary processes, is DNA barcoding (e.g. Whiteman et al. 2004, Webb et al. 2006, Bucklin et al. 2007). DNA barcoding is based on the idea of sequencing a short, diagnostic segment of the DNA to discriminate species (Robba et al. 2006, Garros et al. 2008). It uses short sequences of one or a few genes, mostly from the mitochondrion, both to identify known species (Wong & Hanner 2008) and to discover new species (Mc Manus & Katz 2009). According to Mc Manus and Katz (2009), it is a comparatively simple, objective method, which can be applied to all developmental stages of a species and

also to parts of an organism. Hebert et al. (2003 a) proposed the use of a 650 bp 59 fragment of the mitochondrial cytochrome-c oxidase subunit 1 (CO1) gene as a reliable universal marker or 'DNA barcode' for global biological identification of animal species (Schander & Willasen 2005, Chantangsi et al. 2007, Radulovici et al. 2009).

Using this mitochondrial gene faces a number of advantages (Chantangsi et al. 2007). Among mitochondrial genes, CO1 is one of only two protein-encoding genes that are present in all eukaryotes (Chantangsi et al. 2007). CO1 has been used in a large number of vertebrate and invertebrate taxa and provides a reliable and accessible solution to the problem of species identification (Hebert et al. 2003 a, Rubinoff et al. 2006, Amaral et al. 2007) and offers the possibility to discriminate closely related species (Hebert et al. 2003 b, Hajibabaei et al. 2007). From various animal phyla it can easily be amplified using universal primers which are very robust (Hebert et al. 2003 a) and designed from conserved regions of the gene (Folmer et al. 1994, Saunders 2009). The mitochondrial genome evolves at a faster rate than the nuclear one (Hebert et al. 2003 b). Hence, mitochondrial genomic sequences at a particular region will be more informative in differentiating or distinguishing closely related species (Hebert et al. 2003 b) of a variety of animals (e.g. Floyd et al. 2002, Hebert et al. 2004 b, Ward 2009). CO1 is a good taxonomic marker for several terrestrial and aquatic invertebrates (Hebert et al. 2003 a, Hebert et al. 2004 a, Smith et al. 2005), fishes (Rock et al. 2008, Ward 2009), birds (Hebert et al. 2004 b, Ward 2009) as well as red and brown macroalgae, respectively (e.g. Robba et al. 2006, Kucera & Saunders 2008, Mc Devit & Saunders 2009). CO1 is not an all-purpose species diagnostic gene, however (Schander & Willassen 2005). Within the Cnidaria, for instance, low levels of variability and few distinctive features in CO1 are found (Hebert et al. 2003 a, b).

Barcode approaches may help to reveal cryptic species and thus to understand the role of cryptics in ecological and evolutionary processes (Whiteman et al. 2004). It is a valuable tool, especially when coupled with traditional taxonomic methods, and is

fundamental in revealing hidden diversity (Hebert et al. 2004 a). This technique has probably been the most widely applied molecular method for a closer identification of phyto- and zooplankton (e.g. Webb et al. 2006, Bucklin et al. 2007, Lin et al. 2008). According to McManus and Katz (2009), it is a comparatively simple, objective method which can be used for all developmental stages of a species, and which can also be applied to parts of an organism. DNA barcoding is a tool for assigning biological specimens to species (e.g. Hebert et al 2003 b, Schander & Williassen 2005, Borisenko et al. 2008).

Concerning the order of copepods, the mitochondrial cytochrome c oxidase subunit 1 gene is suitable for studies at species and population levels. Despite morphological similarity, copepods exhibit considerable base-sequence divergence in this gene (e.g. Folmer et al. 1994, Bucklin et al. 1999, Vestheim et al. 2005). According to Bucklin et al. (2003), it is possible to unambiguously discriminate even the most closely related species within the calanoid copepod families, Calanidae and Clausocalanidae, by using mt CO1 sequences. It is also possible to examine phylogenetic relationships among sibling and non-sibling species of different genera with this gene (e.g. Hill et al. 2001, Rocha-Olivares et al. 2001, Bucklin et al. 2003).

2. Aims of the thesis (Hypothesis)

Oithona similis shows a world-wide distribution and is therefore exposed to very different environmental conditions. Investigations on other assigned cosmopolitan marine invertebrate species (e.g. *Calanus finmarchicus*; Hill et al. 2001) showed that these are actually composed of cryptic species that are limited in their geographic ranges. This leads to the first hypothesis: (H1) *Oithona similis* is not a cosmopolitan, but a conglomerate of cryptic species. However, it is still mainly assumed that *O. similis* is a cosmopolitan species. I therefore propose that possibly existing cryptic species in the nominal *O. similis* either show no morphological differences or only very slight ones that make it impossible to differentiate between them morphologically (H2). For the investigation areas in this study additional *Oithona* species are described. Thus, I suggest that *O. similis* and further *Oithona* species

that inhabit the investigation areas can clearly be differentiated morphologically and genetically (H3).

3. Material and Methods

3.1. Investigation areas and sampling

To test whether *Oithona similis* is a cosmopolitan species or represents a complex of cryptic species, specimens of *O. similis* were closely examined from four study areas: the Arctic Ocean, the Southern Ocean, the North Sea and the Mediterranean Sea. These areas are inhabited by *O. similis* and four congeners: *O. frigida* (Southern Ocean), *O. atlantica* (Arctic Ocean), *O. nana* (North Sea) and *O. plumifera* (North Sea). There is great environmental heterogeneity between both polar oceans (Atkinson 1998). The North Sea and the Mediterranean Sea further represent different regions within the world-wide distribution of this species, especially with respect to the water temperature.

3.1.1 The Arctic Ocean
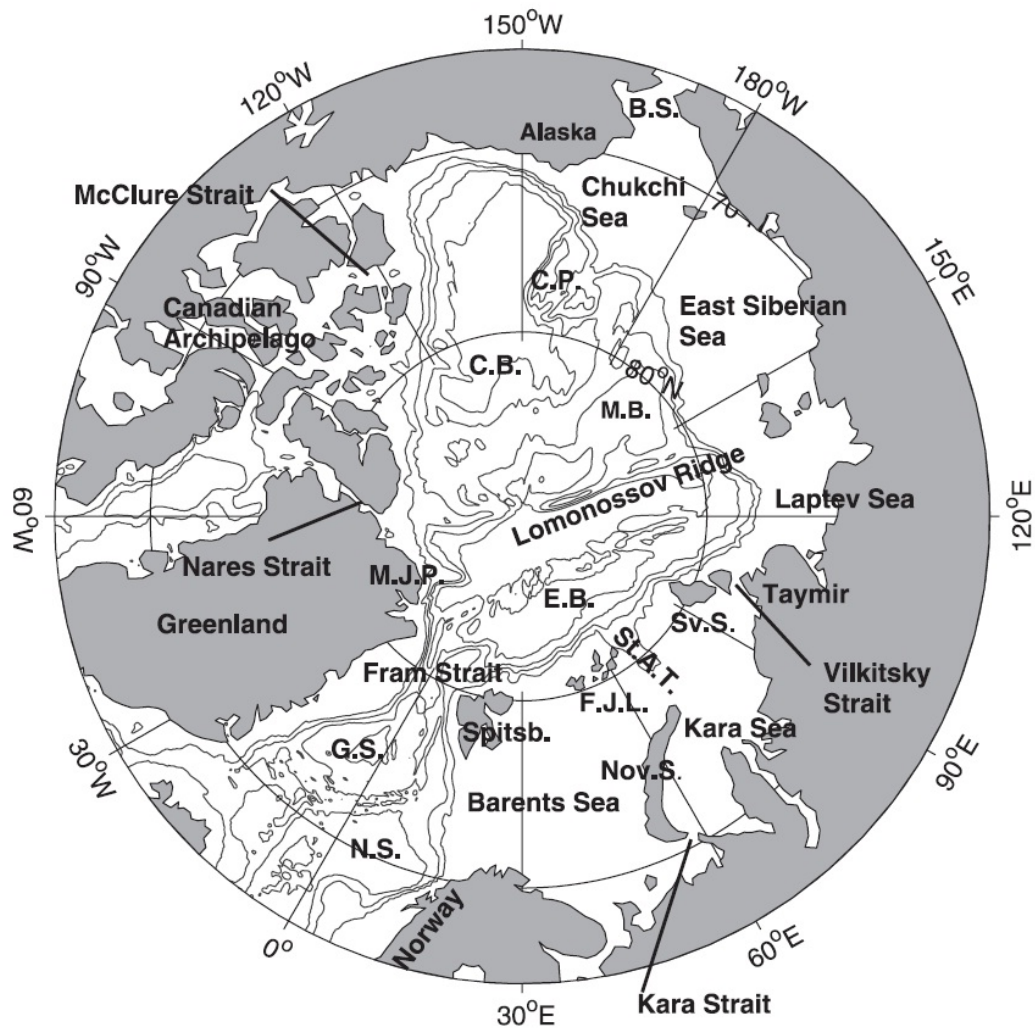
B.S.: Bering Strait
C.P.: Chukchi Plateau
E.B.: Eurasian Basin
F.J.L.: Franz Josef Land
G.S.: Greenland Sea
C.B.: Canadian Basin
M.B.: Makarov Basin
Nov.S.: Nowaya Semlya
N.S.: Norwegian Sea
St.A.T.: St. Anna Trough
Sv.S.: Svernaya Semlya
Spitsb.: Spitsbergen
M.J.P: Morris Jesup Plateau

Fig.7 The Arctic Ocean (Karcher & Oberhuber 2002)

The Arctic Ocean is enclosed by land masses and therefore the world`s largest mediterranean ocean (Foldvik & Gammelrod 1988). Approximately one-third of its

area is represented by shelf seas (Aagaard et al. 1981). An overview of the Arctic Ocean is shown in figure 7. The inner Arctic Ocean is divided into the major basins, the Canadian and the Eurasian Basin, by the Lomonosov Ridge (McLaughlin et al. 1996). The Canadian Basin is additionally split into the Canada and Makarov Basins by the Alpha-Medelev Ridge (McLaughlin et al. 1996). Further basins are partitioned via the Nansen-Gakkel Ridge: the Nansen and the Amundsen Basin (McLaughlin et al. 1996). Broad (600-800 km) and shallow (30-200 m) continental shelves that are mainly located north of Europe and Asia besides the Barents, Kara, Laptev and East Siberian seas, surround these basins (McLaughlin et al. 1996).

Waters from the North Atlantic and from the North Pacific are the main water sources entering the Arctic Ocean (McLaughlin et al. 1996). These waters become included in the large-scale circulation of the inner Arctic Ocean (McLauglin et al. 1996). Consequently, they undergo modifications caused by "air/sea/ice interaction, river inflow and exchange with surrounding shelves" (McLauglin et al. 1996). The Arctic Ocean itself is a supply of deep and intermediate waters to the Northern Hemisphere (Mauritzen 1996, Anderson et al. 1999). Via Fram Strait, the Arctic Ocean is connected to the Atlantic Ocean. This is the only deep-water connection to the Atlantic (Morison 1991) that is located between Greenland and Spitsbergen, with a sill depth of 2.600 m. Within the Fram Strait, the warm center of the Atlantic Water is conserved as it flows through deeper layers and thus looses a small amount of heat to the atmosphere (Beszczynska-Möller et al. 2011). Shallow connections to the North Atlantic are through the Davis Strait, west of Greenland and through the Barents Sea (Aagard & Carmack 1989). In the shallow Barents Sea, the Atlantic Water is strongly modified by the atmosphere (Beszczynska-Möller et al. 2011). There is a consolidation of both Atlantic water flows in the northern Kara Sea that proceeds in a frontier current alongside the border and ridges of the Arctic Basin (Aagaard 1989, Rudels et al. 1994). In the Arctic Ocean, sweeping transformations of water masses occur (Schauer et al. 2008). Thus, via cooling, freezing and melting as well as through an addition of river run-off, the warm Atlantic Water is modified to shallow Polar Water, ice and deep saline water (Schauer et al. 2008). The Atlantic

water loop through the Arctic is closed by a return flow of these waters southward across the Fram Strait and the Canadian Archipelago (Schauer et al. 2008).

The Bering Strait is the connection of the Arctic Ocean to the Pacific. The about 85 km wide and ca. 50 m deep Bering Strait is located at the distant end of the Pacific Ocean and is the only entrance for Pacific water into the Arctic Ocean (Aagard & Carmack 1989, Woodgate & Aagard 2005, Beszczynska-Möller et al. 2011). The inflowing Pacific water shows low salinity (Karcher & Oberhuber 2002). The main passage of Pacific water that is leaving the Arctic Ocean is the Canadian Arctic Archipelago (Karcher & Oberhuber 2002). The water mass exchange with the Pacific and Atlantic Ocean closely connects the Arctic Ocean with the global ocean system (Beszczynska-Möller et al. 2011).

The upper 500 m of the water column in the basins of the Arctic Ocean show a strong stratification (Rudels et al. 2004). Below the low saline polar mixed layer, a pycnocline is located (Rudels et al. 2004). Generally, the pycnocline between the polar mixed layer and the Atlantic layer is referred to as halocline (Coachman & Aagaard 1974). Showing a width of 150 m the halocline usually is about three times broader than the polar mixed layer (Rudels et al. 2004). The halocline exhibits salinity stratification and its temperatures in the upper part are close to freezing (Rudels et al. 2004). In contrast temperatures that are increasing towards the subsurface temperature maximum of the Atlantic layer cause a destabilizing thermocline at the base of the halocline (Rudles et al. 2004). The Atlantic layer contains water with temperatures above 0°C and could thus melt several meters of ice if it were to enter the polar mixed layer (Rudels et al. 2004). However, this is prevented by the halocline (Rudels et al. 2004). It operates as a shield between the surface mixed layer and the upward flux of heat and salt in the Atlantic layer that is located below (Shimada et al. 2005). During summer the melting of sea ice produces a surface layer of still lower salinity (Rudels et al. 2004). This causes a stratification of the polar mixed layer (Rudels et al. 2004). Ice formation, brine release and following haline convection removes this layer during winter (Rudels et al. 2004).

Through hydrologic cycling, the largest part of the Arctic receives a net overage of freshwater; a large amount of runoff that is discharged into the Arctic Ocean is included (Aagaard & Carmack 1989). Enduring and strong stratification is a precondition for significant ice formation in deep oceans (Aagaard & Carmack 1989). Ocean circulation influences the structure of the water temperature of the Arctic Ocean (Jinping et al. 2005). However, since the early 1990s a large-scale change to warmer terms comprising warmer Atlantic inflow has been recognized (Holliday et al. 2008, Schauer et al. 2008). This was further shown by infrequent warming of inflowing Pacific water, in particular in 2007 (Woodgate et al. 2010), penetrating aberrant warm water above Arctic shelves (Dmitrenko et al. 2010) flowing alongside the continental margin of the Arctic and into the Canada Basin (McLaughlin et al. 2009). This warming trend is expressed in a reduction of sea ice coverage, thickness and volume (Kwok et al. 2009). Furthermore, significant changes concerning the storage and distribution of freshwater in the Arctic Ocean have been recorded (see e.g. Rigor et al. 2002, Polyakov et al. 2008).
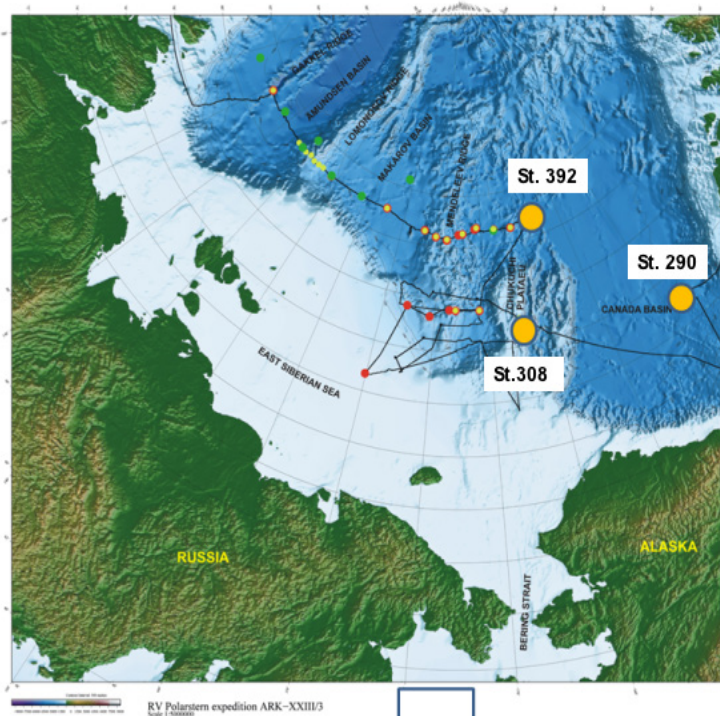
Fig.8 Sampling Area and location of the stations during the expedition ARK XXIII-3 in the Arctic Ocean

Sampling was conducted in the Arctic Ocean during two expeditions with RV Polarstern (ARK XXIII-3: 12.08.08-17.10.08, ARK XXIV-1: 10.06.10-29.06.10).

Individuals from the Arctic Ocean were sampled at two stations in the Canadian Basin and at an additional station at the Chukchi Plateau during ARK XXIII-3.
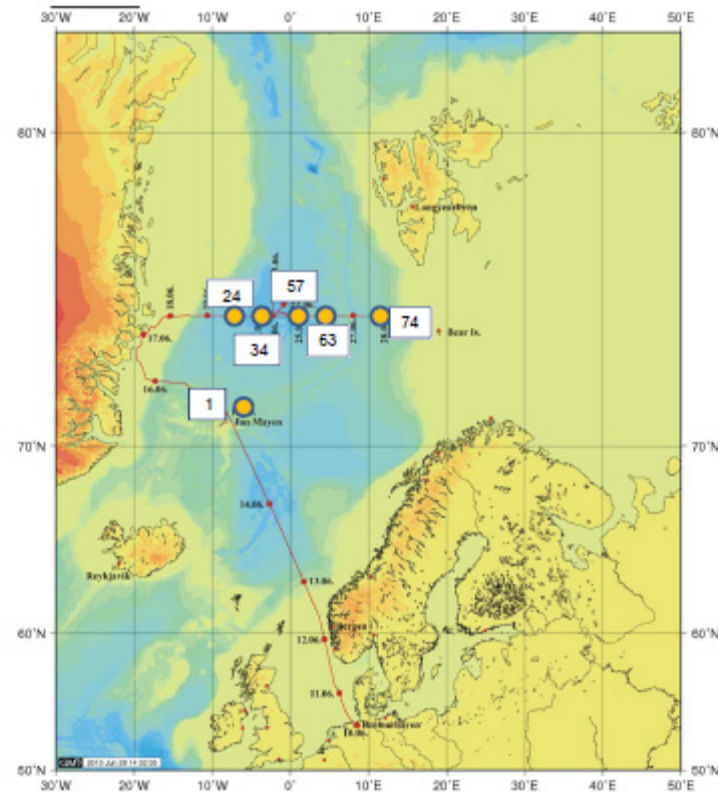
Fig. 9 Sampling Area and location of the stations during the expedition ARK XXV-1 in the Arctic Ocean

Further sampling in the Arctic Ocean was done at six stations during the expedition ARK XXV-1. For details see Figures 8 and 9.

3.1.2 The Southern Ocean

The Southern Ocean encompasses the entire oceanic region between the southern continent and the Subtropical Convergence, at about 40-50°S (Foldvik & Gammelsrod 1988). "[It] is the world's only zonal sea and with free boundaries to the north where it continues into the South Pacific Ocean, the South Atlantic Ocean and the Indian Ocean" (Foldvik & Gammelsrod 1988).

SLW	Surface Layer Water	NADW	North Atlantic Deep Water
SAMW	Subantarctic Mode Water	UPIW	Upper Intermediate Water, $26.8 \leq \sigma_\theta \leq 27.2$
RSW	Red Sea Water	LOIW	Lower Intermediate Water, $27.2 \leq \sigma_\theta \leq 27.5$
AABW	Antarctic Bottom Water	IODW	Indian Ocean Deep Water
NPDW	North Pacific Deep Water	BIW	Banda Intermediate Water
ACCS	Antarctic Circumpolar Current System	NIIW	Northwest Indian Intermediate Water
CDW	Circumpolar Deep Water		

Fig. 10 (Schmitz 1996) The schematics of the global overturning circulation. The wide, red arrow that is revolving Antarctica indicates the ACC (Rintoul 2006). Within each basin the zonally-averaged circulation is shown by arrows and for each water mass a different color is used (Rinoutl 2006). The deep ocean circulation is primarily connected to the upper ocean via water mass transformation in the Southern Ocean and a smaller contribution is provided from mixing at low latitudes (Rintoul 2006).

The bottom topography strongly affects the flow within all depths of the Southern Ocean (Rintoul et al. 2001). This ocean bears two main currents: a narrow one that borders on the Antarctic continent, the Coastal Current ("The East Wind Drift"), and the Antarctic Circumpolar Current (ACC) ("The West Wind Drift") (Deacon 1937). The eastward flow of the ACC dominates the general circulation of the Southern Ocean (Ward et al. 2002). Via its substantial eastward flow, the ACC links the ocean basins, "allowing the existence of a global-scale overturning circulation that carries most of the ocean heat transport" (Rintoul 2006). Thus, the ACC is the most important way

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for water mass exchange between the ocean basins (Rintoul 2006). A consequence of this basin interchange is that the regional large-scale ocean circulation and heat transport is converted to a global appearance (Rintoul 2006).

Figure 10 shows the west to east circulation of the ACC around Antarctica (Rintoul 2006). Within the ACC, several fronts that cover the whole depth and show high velocities, are interrupted by relatively quiet zones (Ward et al. 2002). In general, "[f]ronts are ubiquitous, robust circumpolar features of the Southern Ocean" (Sokolov & Rintoul 2002). Per definition a front is a sharp boundary among neighboring water masses (Bowman 1977). A further main factor within the dynamics of the ACC are eddies (Rintoul et al. 2001). Generally, eddy fluxes are very important for the dynamics and thermodynamics of the Southern Ocean (Rintoul et al. 2001). From north to south the fronts in the ACC are termed: Subantarctic Front (SAF), Polar Front (PF) and Southern ACC Front (SACCF) (Ward et al. 2002). The Southern Boundary (SACCB) delimits the ACC in the south (Orsi et al. 1995). The Subantarctic Front and the Polar Front are the two main fronts of the ACC (Orsi et al. 1995, Rintoul 2006). They consist of two or three branches that fuse and depart alongside the circumpolar trail of the current (Rintoul 2006).

The Polar Frontal Zone (PFZ) that is located in the ACC, is bordered by the Sub-Antarctic Front (SAF) in northward direction, and the Antarctic Polar Front (PF) in southward direction (Emery 1977, Hoffman 1985). Both cores exhibit high speeds (Emery 1977, Hoffman 1985). The Antarctic Polar Front (APF) is a physical frontier that is marked by obvious variations in water temperature and salinity (Honjo 2004). The PFZ further constitutes a shift from the warmer, less productive Sub-Antarctic Surface Waters (SASW) to the colder, more productive Antarctic Surface Waters (AASW) within the surface layer (Deacon 1983, Lutjeharms 1985). The SASW have their origin north of the SAF and the SASW originate south of the APF (Belkin & Gordon 1996, Ansorge et al. 1999, Froneman et al. 1999). The PFZ further conduces a significant biogeochemical boundary (Honjo 2004). A high extent of spatial and temporal changeability is suggested for the PFZ, including eddies and meanders in

both fronts (e.g. Legeckis 1977, Bryden 1983, Pakhomov & Froneman 1999). This variability is caused by interaction of the ACC and the bottom topography (Ansorge et al. 1999). The position of the PFZ is not stable and is shifted with time (Hoffman & Whitworth 1985). It is further strongly depending on the local bathymetry (Nowlin & Klinck 1986, Ansorge et al. 1999).

The zones of the Southern Ocean are created concentrically around the Antarctic continent (Orsi et al. 1995, Belkin & Gorden 1996). "Each zone maintains its unique physical properties" (Honjo 2004). The "zonally- average circulation" for each basin and their different layers are further shown in Figure 10 (Rintoul 2006). Altogether they form the "the global overturning or thermohaline circulation" (Rintoul 2006). Deep water that originates in the North Atlantic (NADW) is transported southward into the Southern Ocean. Via the ACC the NADW is brought eastwards (Rintoul 2006). It further expands towards the pole alongside "shoaling isopycnals to outcrop at the sea surface near Antarctica" (Rintoul 2006). Caused by interchanging of heat and humidity between ocean, atmosphere and sea ice the up welled deep-water near Antarctica is transduced to dense Antarctic Bottom Water or at lower latitudes to lighter intermediate waters (Rintoul 2006).

Via the new Southern Ocean water masses, oxygen-rich waters are carried into the interior and thus aerate about half of the volume of the global ocean (Rintoul 2006). A balance of the outflow of NADW is generated by the intermediate waters that are brought northwards into the Atlantic basin and thus close the overturning circulation in the Atlantic (Rintoul 2006). The global climate is influenced through the ACC and the Southern Ocean overturning circulation (Rintoul 2006). The ocean basins are linked and thus enable a "global-scale overturning circulation to exist" and supply "an oceanic teleconnection for the transmission of climate signals" (Rintoul 2006). The overturning circulation that is related to production and export of the NADW is finished through the transformation of deep to intermediate water via an interchange of air and sea in the Southern Ocean (Rintoul 2006). The water masses of the Southern Ocean further control "the ocean uptake of oxygen, carbon dioxide and heat" (Rintoul 2006).

A warming of the Southern Ocean was observed in recent decades (Gille 2002, Levitus et al. 2005). The biggest modifications of heat content within the oceans of the southern hemisphere shows the northern flank of the ACC (Rintoul 2006). Furthermore, in recent decades a significant freshening was noticed within certain sections of the Southern Ocean (Wong et al. 1999, Curry et al. 2003).
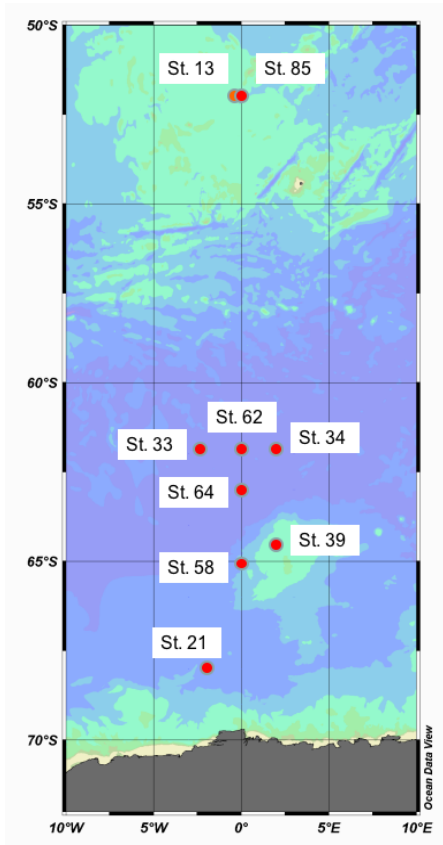
Fig. 11 Sampling area and location of the stations during the expedition ANT XXIV-2 in the Southern Ocean

Sampling in the Southern Ocean took place during the expedition ANT XXIV-2 (28.11.07-04.02.08) within two different water masses: the Weddell Gyre (at 7 stations) and the Polar Frontal Zone (2 stations). For details see fig. 11.

3.1.3 The North Sea
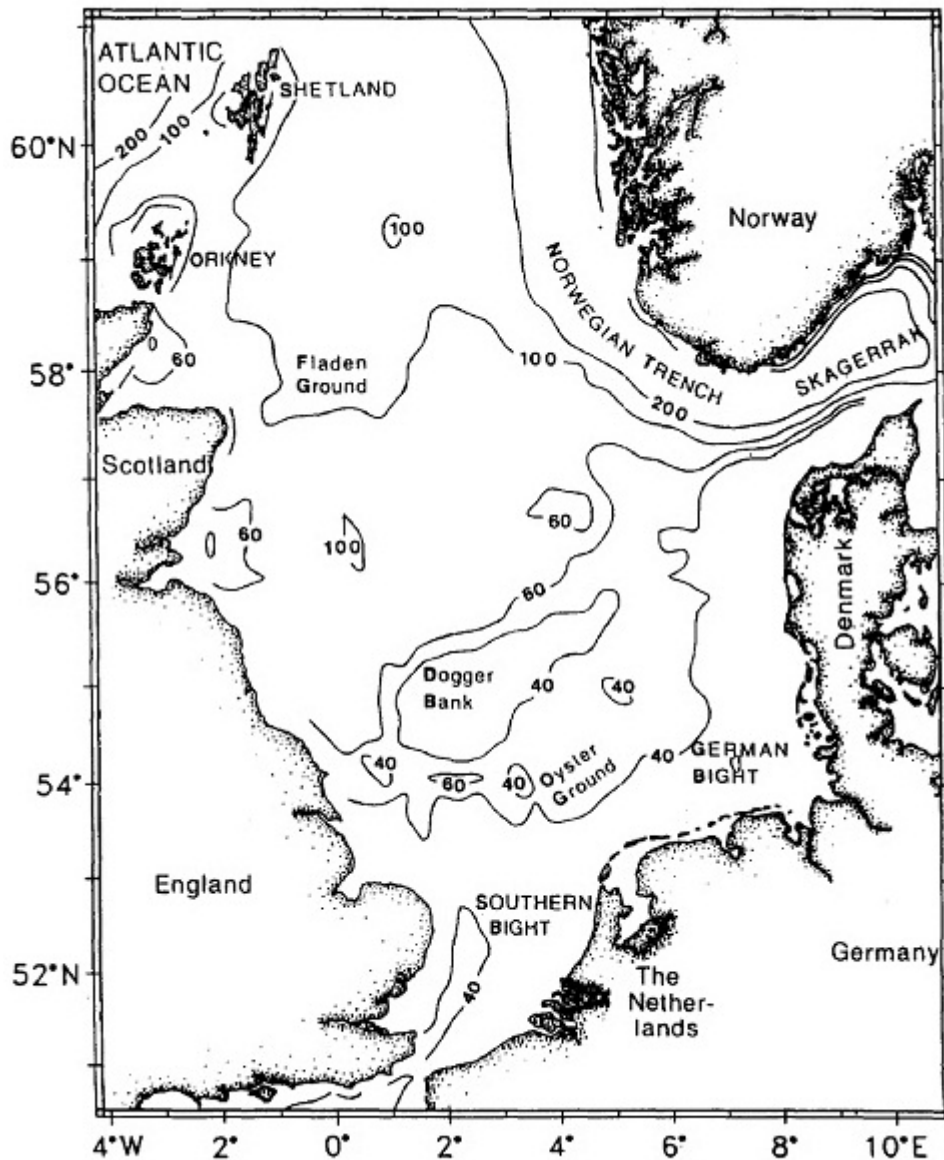
Fig. 12 Bathymetry of the North Sea after Sünderman 1994 (Krause et al. 1995)

The North Sea is located in the northern temperate climate zone (Banner et al. 1980). It encompasses a surface area of 575.300 km^2 (ICES 1983). Hence, it belongs to the world`s most extensive shelf seas (Huthnance 1991). Its bathymetry is shown in figure 12. The North Sea has a mean water depth of 100 m (Banner et al. 1980). It is influenced by the neighboring Atlantic Ocean and the marginal Baltic Sea (Krause et al. 1995). Through the English Channel (Dover Straits), Scottish

continental shelves and the Norwegian Sea, the North Sea water has connection to the Atlantic Ocean (Huthnance 1991). High saline water flows from the Atlantic Ocean through the English Channel to the south into the North Sea and via the Fair Isle Current and the Norwegian deep trench to the north (Krause et al. 1995). From the Baltic Sea low saline water enters the North Sea through the Kattegat-Skagerrak (Huthnance 1991, Krause et al. 1995). The rivers Elbe, Weser and Ems supply the main import of freshwater and nutrients into the North Sea (Krause et al. 1995).

Tidal motion is the central element within the dynamics of the North Sea (Otto et al. 1990). Thus, most of the variance in sea-surface elevation and currents within a large part of the North Sea is due to mainly semidiurnal tides (Huthnance 1991). Tides are important for intertidal systems (Otto et al. 1990). Their currents cause further horizontal and vertical exchange and have an impact on the bottom (Otto et al. 1990). Further effects are the transport via "rectified currents, the tidal residuals" (Otto et al 1990). The tide has also an impact on the carrying of plankton that performs vertical migration (Otto et al. 1990). Other components of the North Sea dynamics are effectively forced currents and related elevations within the extensive shallow waters (Huthnance 1991). These are the results of variations in atmospheric pressure and in particular strong winds (Huthnance 1991). Within some parts of the North Sea, these currents and their linked elevations may be comparable to the tidal motion or even larger (Huthnance 1991).
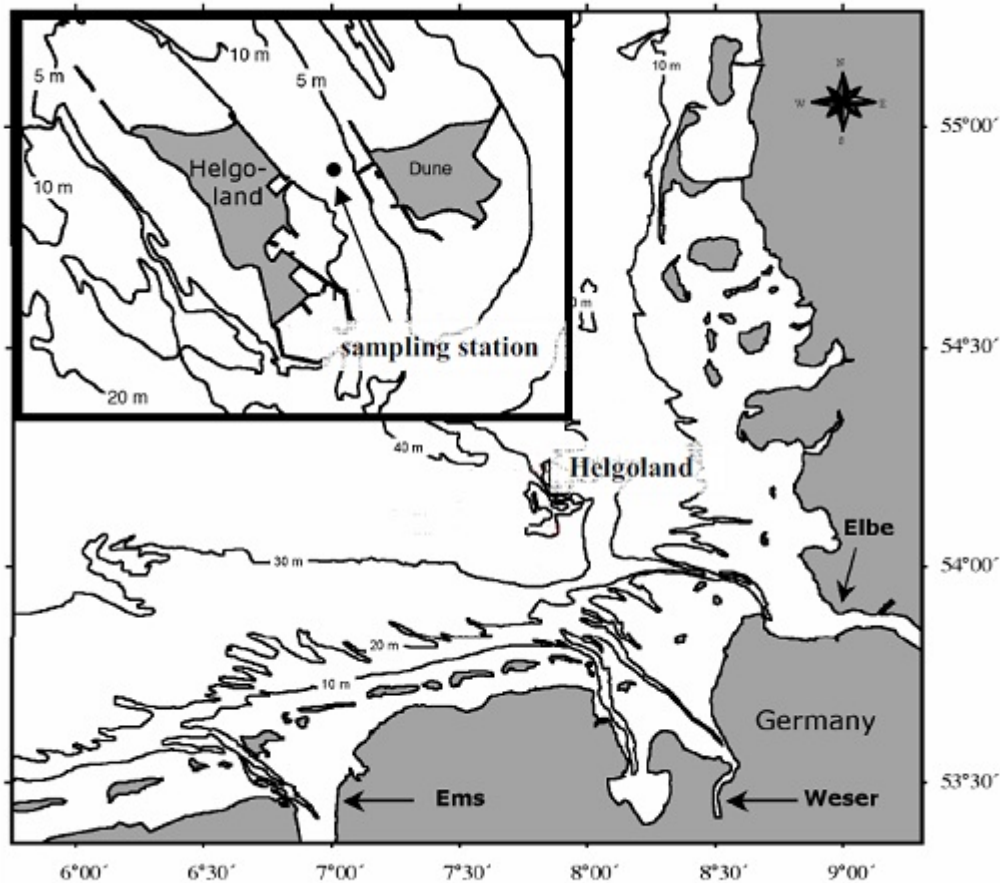
Fig. 13 The German Bight and Helgoland Island with the sampling station "Helgoland Roads" (Wesche 2007)

Copepods for this study were sampled during the expedition HE 302 with RV Heincke in April/May 2009 in the North Sea at station 56 by U. Tillmann. Further sampling of zooplankton in the North Sea was conducted by the crew of MB Aade with a plankton net (mesh size: 150 µm) close to the island of Helgoland at "Helgoland Roads" (54° 11.18' N; 7° 54.0' E; see fig. 13). This is a "hydrographically complex locality" (Greve et al. 2004) about 50 km offshore in the German Bight (Eilers et al. 2001). Sampling station characteristics are strong currents and thus no stratification (Radach et al. 1990). The German Bight is the southeastern part of the North Sea (Rachor 1990) and located at the very margin of the sea (Rachor 1990). It shows water depths mainly between 20 and 40 m (Rachor 1990, Otto et al. 1990). Its hydrography is influenced by Atlantic water, central North Sea water and coastal waters (Krause et al. 1995). It receives waters that originate mainly from western

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nearshore areas of the North Sea and is almost uncoupled from the oceanical waters of the northern North Sea, which are deep and effectively renewed by river runoff (Rachor 1990). During summer, the German Bight is strongly influenced by a freshwater inflow from the rivers Elbe and Weser (Halsband & Hirche 2004). An inflow of Atlantic water masses from the north and the English Channel arrives at the island Helgoland during autumn and winter (Goldberg 1973, Banner et al. 1980, Otto et al. 1990). A widespread feature of the German Bight is the incurrence of frontal zones caused by coinciding water masses of diverse origins (Otto et al. 1990). Forced by easterly wind stress there is a central North Sea bottom water upwelling that causes upwelling fronts in the west of the Helgoland (Krause et al. 1986).
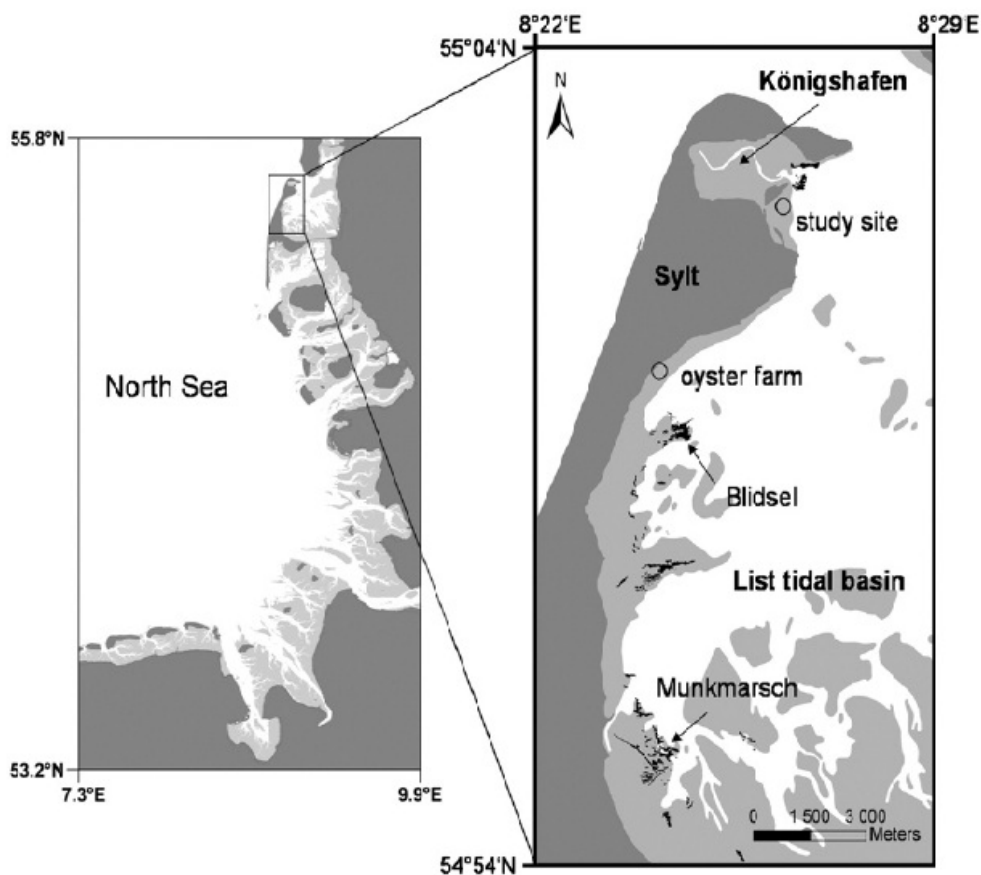
Fig. 14 The List Tidal Basin (Kochmann et al. 2008)

Another sampling station of this study in the North Sea is a fixed one (55°01.30 N, 08°27.10 E) that is located in the southernmost of three main tidal channels in the

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List Tidal Basin in the northern Wadden Sea (Martens & van Beusekom 2008). Sampling at this station was conducted by the crew of the "Mya". One semi enclosed bight within the North Sea is the List Tidal Basin that ranges 404 km^2 (Martens & van Beusekom 2008). Its connection to the open North Sea is limited to a single tidal inlet (Martens & van Beusekom 2008) with a width of 2.8 km (Diederich 2006). Laterally the basin is enclosed by two dams, one to the north and one to the south, that are connecting the island of Rømø and the island of Sylt (Martens & van Beusekom 2008). The mean water depth of the basin is 2.7 m (Loebl et al. 2007), but in the main tidal channel, the water depth reaches up to 40 m (Martens & van Beusekom 2008). Usually, the water column is homogenously mixed (Hickel 1980). The tides in the List Tidal Basin appear semidiurnal and have a mean range of about two metres (Martens & van Beusekom 2008). During the period of low tide, about 30% of the area is emerged (Martens & van Beusekom 2008).

3.1.4 The Mediterranean Sea
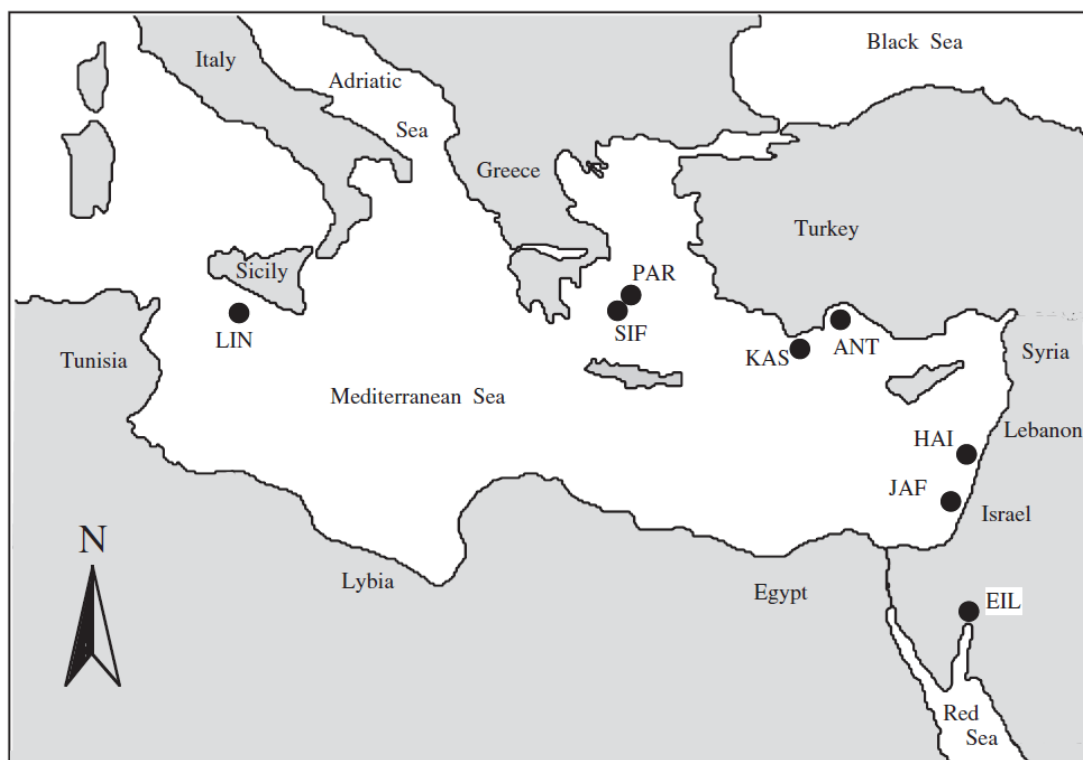
Fig. 15 The Mediterranean Sea (Azzurro et al. 2006)

A map of the Mediterranean Sea is shown in figure 15. The Mediterranean Sea is connected via the Strait of Gibraltar (15 km wide, 320 m max depth) to the Atlantic Ocean. Different sub-basins developed as consequence of complex geological events. The basins differ in their geo-morphological and hydrological features. The Eastern and the Western Basins are the two major sub-regions. They have two partly separated thermohaline cells. The Atlantic Ocean influences the Western region more directly than the Eastern one, the former being on average more productive than the latter.

The Mediterranean climate is influenced by the European and the Asian climate (Gómez & Gorsky 2003). In the Mediterranean Sea, thermal anomalies as well as changes concerning the circulation patterns occur (Maheras et al. 1999). They are influenced by the Sahara and the Atlantic Ocean (Maheras et al. 1999). The Mediterranean Sea is very receptive to heat or water budget fluctuations (Béthoux et al. 1999). The climate of the eastern and western basins is affected by different processes (Reddaway & Bigg 1996). Therefore, changes in the two basins are often uncoordinated (Reddaway & Bigg 1996).

In general, the Mediterranean Sea is considered a poor productive oligotrophic sea (Jacques & Tréguer 1986). Exceptions are some bays and ports where nutritional anthropic inputs may favor the growth of phytoplankton and zooplankton (Jamet et al. 2001). Characteristic of the Mediterranean Sea are shallow or very shallow straits (e.g. Gibraltar, Dardanelles, Silicily) that prevent a deep-water exchange with the neighboring ocean and between the deep sub-basins (Siokuou-Frangou et al. 2010). However, the deep waters are frequently formed autonomously in the western and eastern sub-basins of the Mediterranen Sea and renewed on a yearly basis and thus are well oxygenated (Hopkins 1978). The mixed layer depth decreases in winter, as a consequence of Atlantic water that flows into the Mediterranean basin and that adds a haline factor to the thermal contribution in stratification of large areas of the Southwest Mediterranean (D`Ortenzio et al. 2005). This water is frequently named Modified Atlantic Water (MAW) as it causes a proceeding eastward change in temperature and salinity characteristics (Siokou-Frangou et al. 2010). A further

characteristic of the Mediterranean Sea is the occurrence of stable or semi-permanent gyres in the sub basins (Robinson & Golnaraghi 1994). These gyres are generally depending on the topography (Robinson & Golnaraghi 1994).
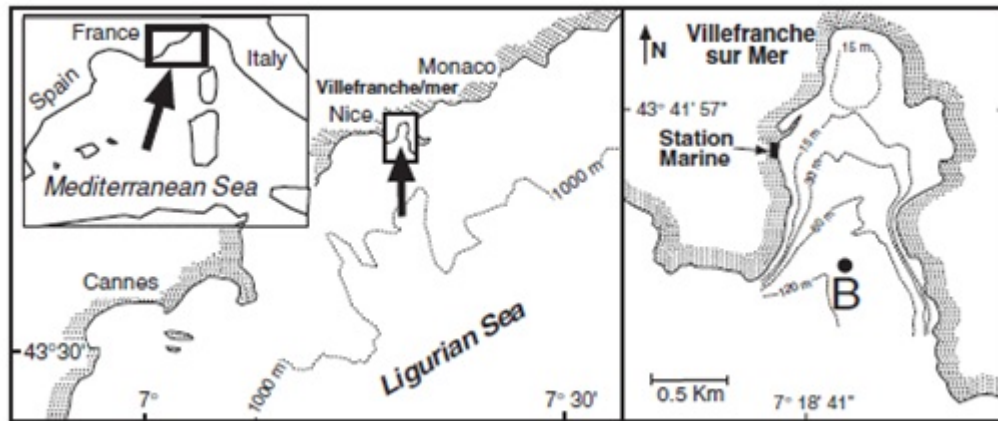
Fig. 16 Sampling area in the Mediterranean Sea (Gómez & Gorsky 2003)

The Ligurian Sea forms the northeastern part of the western Mediterranean and is bounded by the French coast (Provence, Corsica) and Italy (Boucher 1984). This Mediterranean basin is linked to the North Atlantic climate region (Mazzocchi et al. 2011). A cyclonic circulation at the surface is characteristic for the Ligurian Sea (Béthoux et al. 1982). This is the eastern part of the large cyclonic circulation of the northwestern Mediterranean Sea (Hopkins 1978 a). This cyclonic circulation encloses a central divergence that is characterized by dense and cold waters that are the result of upwelling very deep water masses (2000 m, Hela 1963). Offshore the western Ligurian-French coast, a thermohaline front, the Liguro-Provençal front, originates from the encounter of the faster flowing Ligurian current that flows counterclockwise from the eastern Ligurian Sea towards the Gulf of Lion and also from the weak currents in the central zone of the divergence (Boucher et al. 1987, Sournia et al. 1990). The Liguro-Provençal front may be impaired by such meanders and instabilities as anticyclonic eddies (Sournia et al. 1990, Pinca & Dallot 1997). Due to the complex hydrological system, the Ligurian Sea is less oligotrophic than other Mediterranean areas with the central zone of divergence being a highly productive zone in spring and strictly related to the beginning of the phytoplankton

bloom which is mainly composed of dinoflagellates (see Licandro & Icardi 2009 and references within). This feature affects the primary consumers as well as higher trophic levels comprising micronekton, molluscs, small fish and, in turn, large marine mammals that live in this area (Relini et al. 1994, Forcada et al. 1995, Pinca & Dallot 1997).

One station in the Mediterranean Sea was sampled for this study by S. Gasparini. Sampling was done at Villefranche sur Mer Point B (43° 41.10 ' N, 7° 18.94' E; see fig. 16) within the Ligurian Sea. Point B is a permanent coastal station with a water depth of about 80 m, and is located at the entrance of the Bay of Villefranche that is open towards the sea and exposed to wind (Nival & Corre 1976). To a great extent, the water circulation in the bay is goaded by the Northern Mediterranean Current (Molinero et al. 2005 a, b). The settings of the open Mediterranean further have a deep influence there (Molinero et al. 2005a, b). Atmospheric pressure, precipitation and temperature of the surface water in the Bay of Villefranche show a close interrelation with the North Atlantic Oscillation (NOA), an index of climate variation in the North Atlantic Ocean and surrounding continents (Molinero et al. 2005 a, b).

3.1.5 Sampling

At each station during the three expeditions with RV Polarstern a multinet (mesh size: 55 µm, opening size: 0.25 m^2) was deployed down to a maximum depth of 250 m. This kind of sampling is in accordance with the small size of the species that mainly lives within the epipelagic zone (see e.g. Metz 1995, Atkinson & Sinclair 2000, Ashjian et al. 2003). The samples at the other investigation areas were kindly provided by other people as described above. Hence, sampling within the North Sea and the Mediterranean Sea could not follow this scheme.

3.1.6 Preparation of the samples

For the genetic analyses, living adult and subadult females (C5 stage) of *Oithona* spp. were sorted from the samples at 4°C on board and were immediately transferred into absolute ethanol for later analysis. Following the published protocol for collection

and preservation of ZooGene samples, the ethanol was exchanged every 24 hours until it remained clear (http://www.zoogene.org/main/sample_preservation_protocol.html). Additional specimens were stored in formaldehyde (end concentration of 4%, buffered with hexamine) for morphological examinations. The samples from Helgoland Roads were treated the same way. Further samples were ethanol-preserved mixed zooplankton samples. All ethanol samples were kept cold at about 4-8°C until DNA extraction.

3.2 Morphological studies and literature research

For the morphological studies, all literature that was made available, mainly on *Oithona similis,* but also on *Oithona atlantica*, *Oithona frigida*, *Oithona helgolandica*, *Oithona nana* and *Oithona plumifera,* was studied. This study resulted in a card file showing all gained figures and descriptions of morphological structures for each of the species. Prior to the DNA extraction, formaldehyde preserved (end concentration of 4%, buffered with hexamine) individuals sampled in the respective investigation area were studied morphologically under an inverted microscope (Zeiss; Axiovert 40) with a magnification of 40. Whole animals as well as body parts were examined. At first, literature was studied to identify the characteristics that could be used to separate between the different species. It was very important to find remarkable characters that could be discovered and assigned easily to one species within seconds. This quick decision method was essential for dealing with the ethanol preserved individuals that had to be sorted under a microscope prior to the DNA extraction. The exposure to heat could have resulted in destruction of their DNA. To further prevent the DNA from destruction, the samples were kept on ice during the whole time, and ethanol preserved individuals were placed under a microscope that was equipped with a LED lamp.

Oithona atlantica, *O. frigida* and *O. nana* e.g. differ from *O. similis* in body size and the shape of the forehead (see figures 17-20 below and table 4 in the results). However, the size can vary (e.g. Van Breemen 1903, Dvoretsky & Dvoretsky 2009) and a variation of the rostrum shape has been reported as well (Früchtl 1924). Therefore, it was necessary to find a further characteristic that helps to clearly

determine an individual within seconds to either *O. similis* or one of the other species. The "number and shape of the setae externae at [the] outer branches of the swimming feets" (Van Breemen 1903) was a very supportive characteristic. A short view on the external spines of the exopodits of the swimming legs together with the body size and the shape of the rostrum, made it possible to decide within seconds which species the adult or subadult female belonged to. The most striking differences that are found when the exopods of *O. similis* are compared with the ones of the other three species are the number and structure of the setae of the third segments of swimming feet one to four (see figures 21-24 below). This kind of differentiation is in accordance with the observations by e.g. Giesbrecht (1893, 1902), Rosendorn (1917), Mori (1937), Nishida et al. (1977), Nishida (1985) and Bradford-Grieve et al. (1999). *Oithona plumifera* is not shown here as no individuals of this species were found within this study. However, it shares most structures with *O. atlantica* but shows remarkable "plumes".
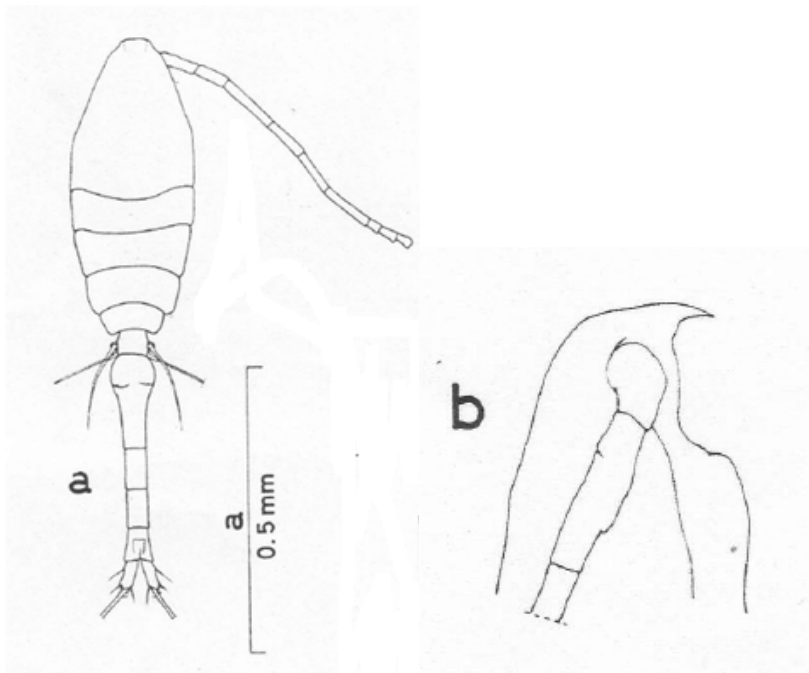
Fig. 17 *Oithona similis*: female dorsal view (a), female rostrum lateral view (b) (Nishida 1985)
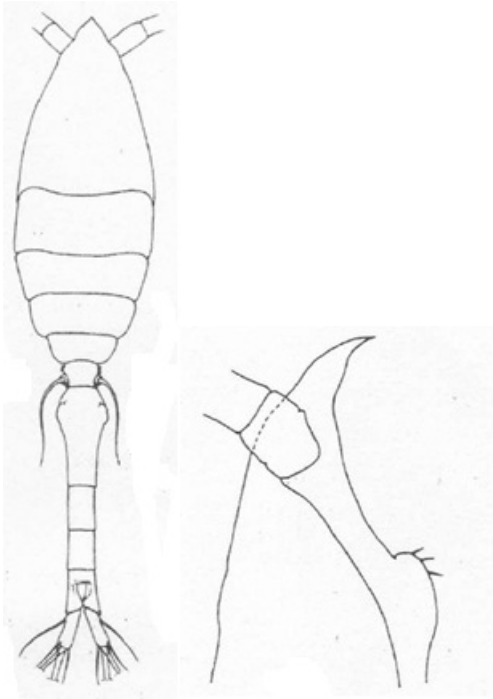
Fig. 18 *Oithona atlantica* female: dorsal view and rostrum lateral (Nishida 1985)
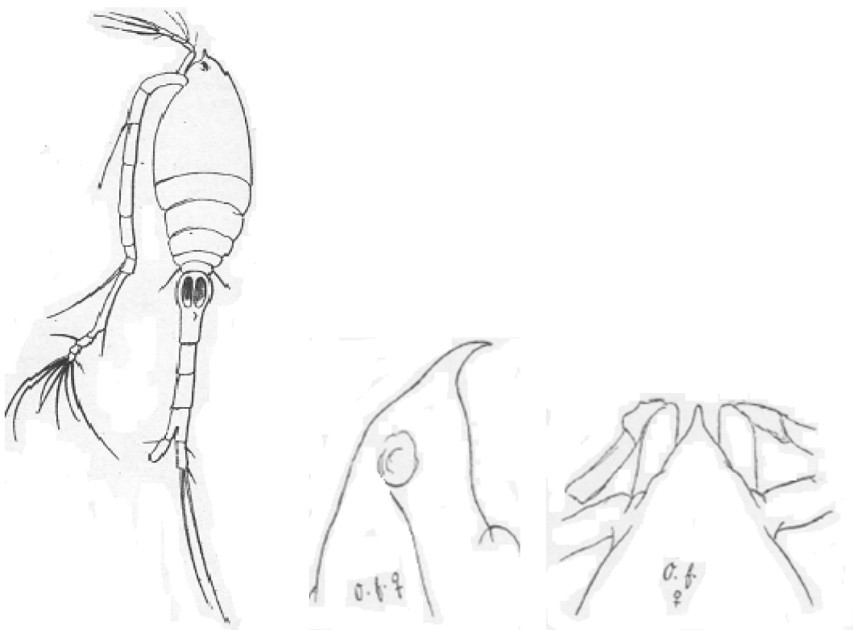
Fig. 19 *Oithona frigida* female dorsal view (Brady 1918), rostrum lateral, dorsal (Giesbrecht 1902)
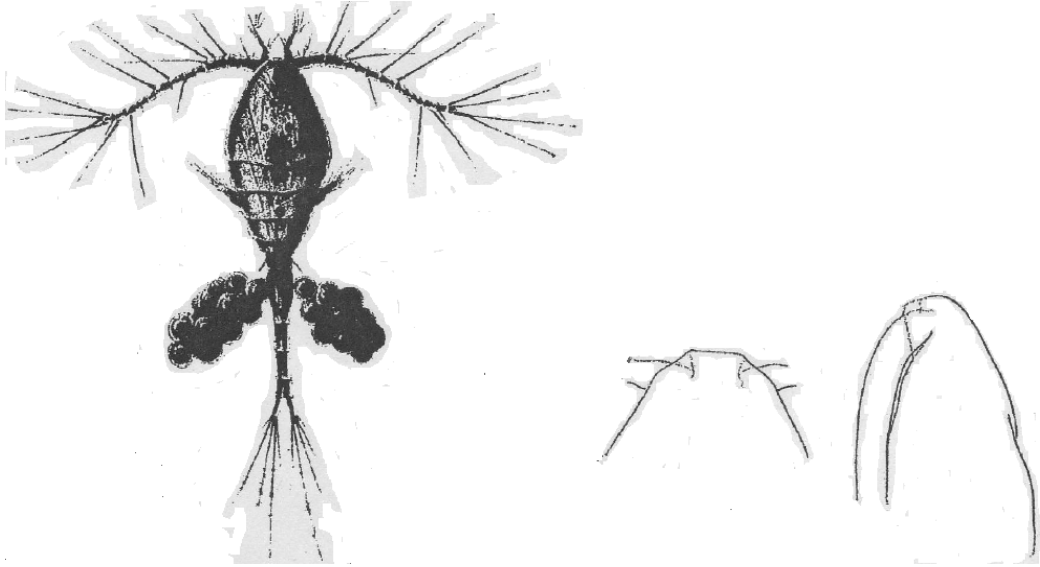
Fig. 20 *Oithona nana* female: dorsal, head dorsal and lateral (Giesbrecht 1893)
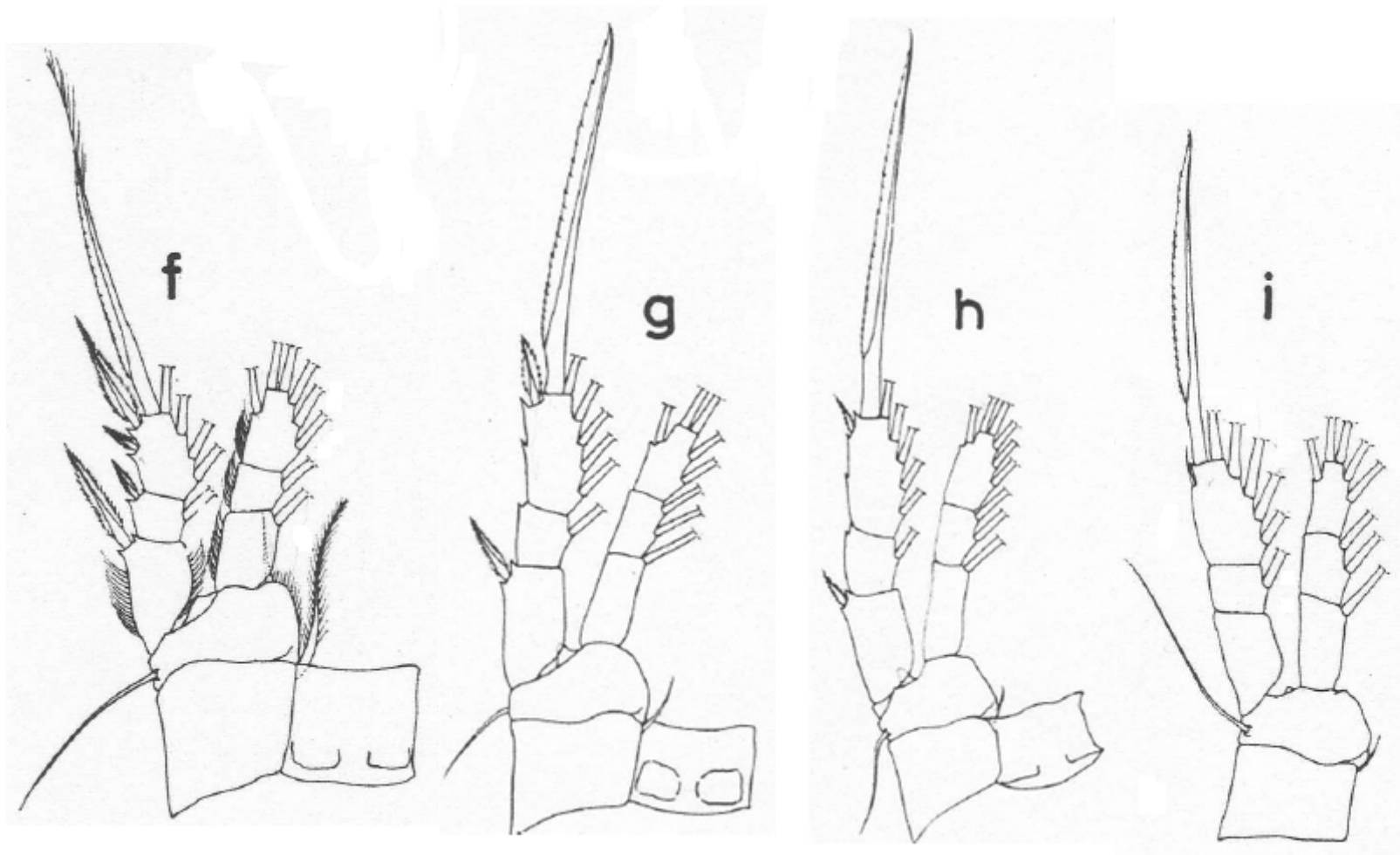
Fig. 21 *Oithona similis* female: leg 1 (f), leg 2 (g), leg 3 (h), leg 4 (i) (Nishida 1985)

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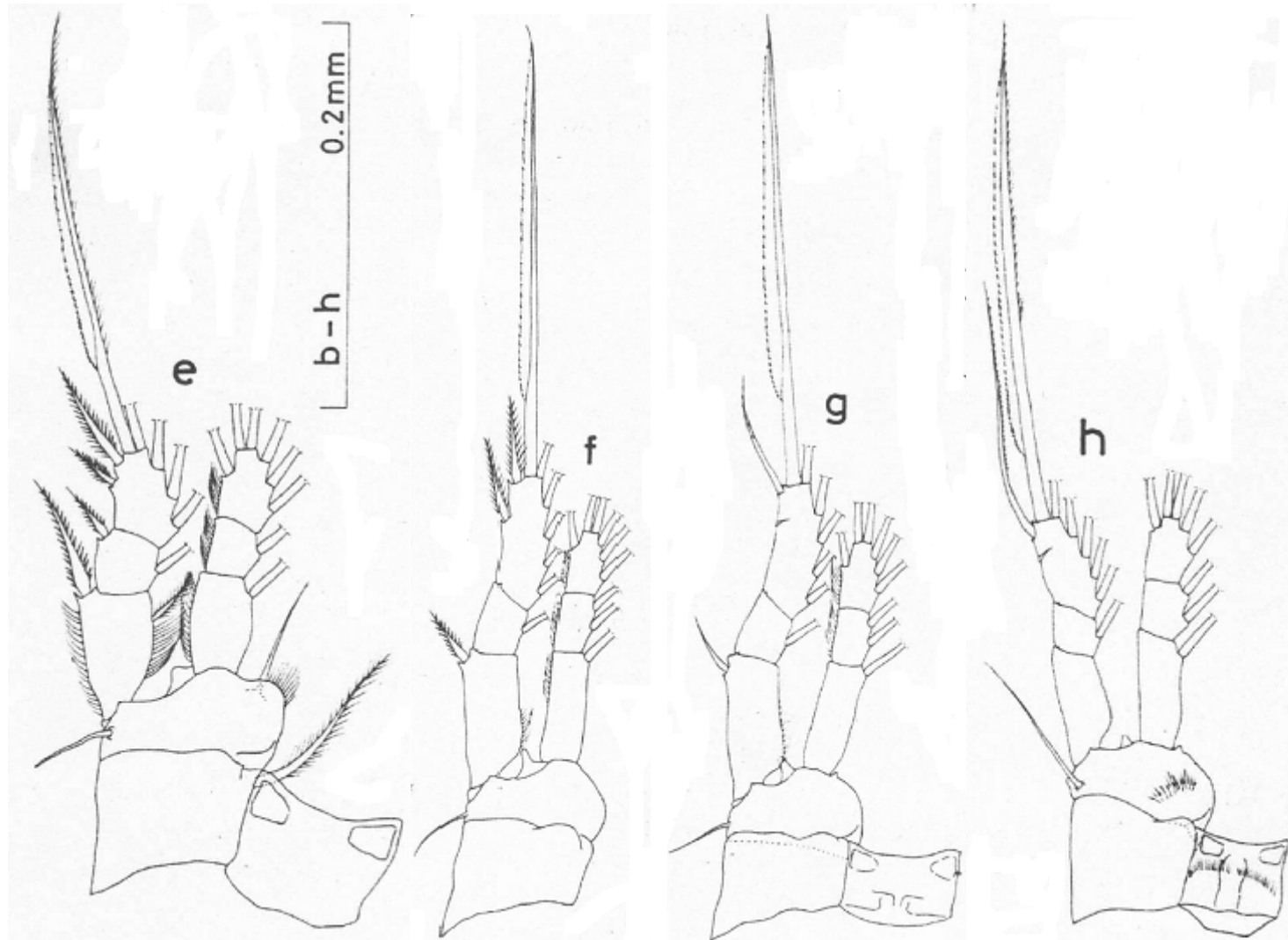
Fig. 22 *Oithona atlantica* female (e) leg 1, (f) leg 2, (g) leg 3, (h) leg 4 (Nishida 1985)
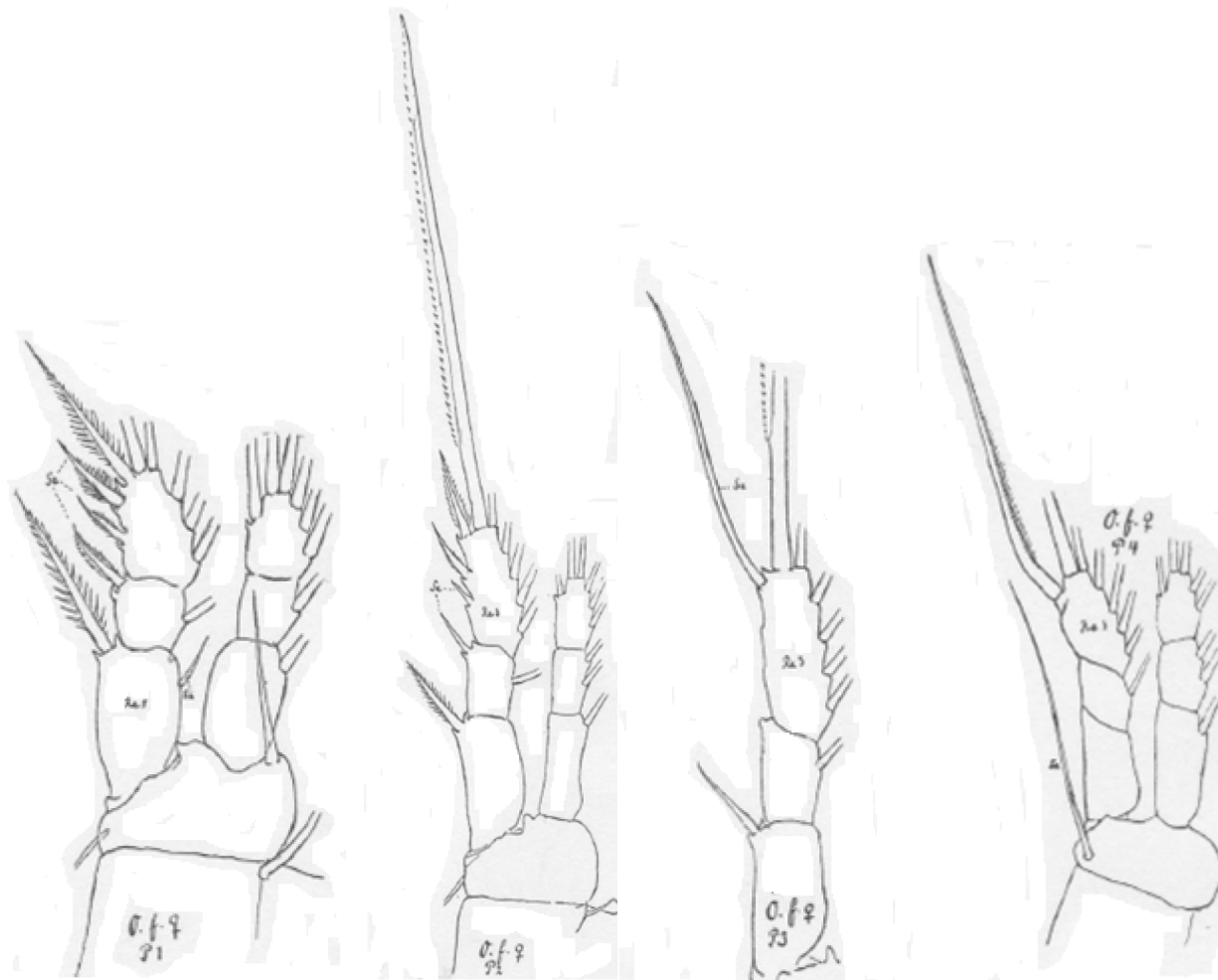
Fig. 23 *Oithona frigida* female leg 1, leg 2, leg 3, leg 4 (Giesbrecht 1902)
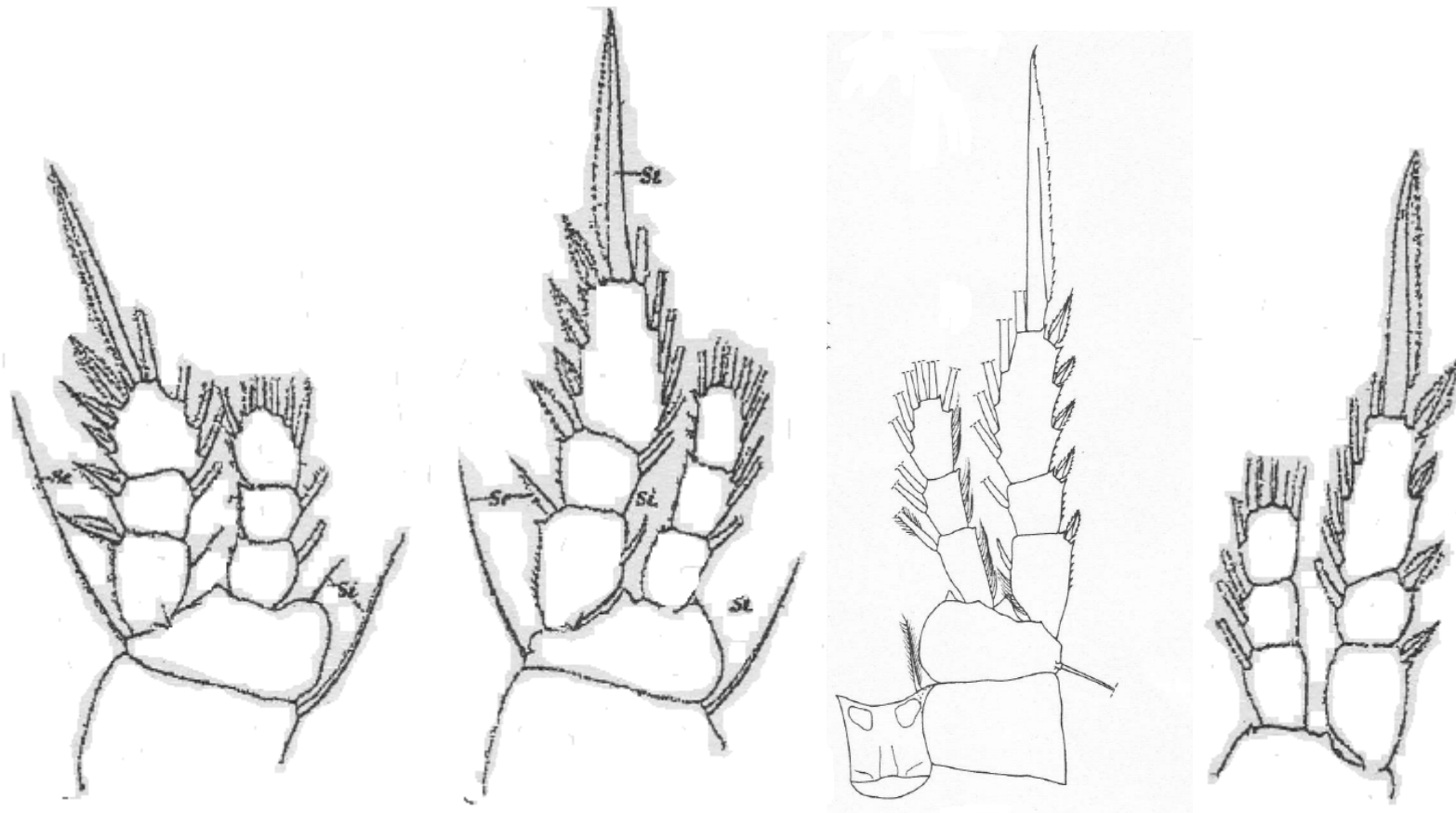
Fig. 24 *Oithona nana* leg 1, leg 2 (Giesbrecht 1893), leg 3 (Nishida 1985), leg 4 (Giesbrecht 1893)

3.3 Genetic examinations

Beside *Oithona similis*, *O. frigida*, an endemic species in the Southern Ocean, *O. atlantica*, found in the Arctic Ocean, and the two species *O. nana* and *Oithona sp.* from the North Sea were included in the genetic analyses in order to examine interspecific variability in the CO1 gene sequences. Following Bucklin (2000), the entire *Oithona* individuals were prepared for molecular analysis without DNA purification or extraction because of their small size (≤ 1 mm). The copepods were separated under an inverted microscope (Zeiss; Axiovert 40). Every single individual was transferred from absolute ethanol into a 1.5 mm cup containing 180 µl of pre-cooled ATL buffer and glass beads (diameter: 425-600 µm; Sigma G8772). Each cup was shaken on a vortexer at maximum speed for five minutes. The cups were horizontally fixed with tape. Afterwards, the samples were centrifuged for 10 minutes (16000 G). In the next step, 20 µl proteinase K were added. The samples were incubated over night in a thermo incubator (56°C; 550 rpm). The next day, purification was done following the instructions of the Qiagen Kit method for tissue. Then, 200 µl ATL buffer including 1 µl carrier RNA per 200 µl were applied. The samples were incubated for 10 minutes at a temperature of 70°C, before 200 µL ethanol were added. The samples were then eluted with 50 µl AE buffer. After the elution, 3 µL DNA of the samples were added to the PCR premix. Cytochrome C oxidase subunit 1 (CO1) was amplified using the universal primers HCO and LCO of Folmer et al. (1994). This primer pair consistently amplified a 710-bp fragment of CO1 across the broadest array of invertebrates (Folmer et al. 1994):

LCO1490: 5´ -ggtcaacaaatcataaagatattgg-3´;

HCO2198: 5´-taaacttcagggtgaccaaaaatca-3´

Table 1: PCR Premix for the primers of Folmer et al. (1994) and Machida et al. (2004)

	Stock	Final concentration	µl/sample
H20			16.35
10 x buffer	10 x	1 x	2.5
dNTP	2 mM	0.2 mM	2.5
HCO	100 µM	0.5 µM	0.125
LCO	100 µM	0.5 µM	0.125
Taq HM 5 Prime	5U/µl	0.03 U/µl	0.15
Betain	100x	1x	0.25
DNA			3

The PCR reaction program consisted of 2 minutes at 94°C, followed by 40 cycles of 20 seconds at 94°C, 10 seconds at 37°C and 50 seconds at 68°C. Upon completion of the 40 cycles, the program concluded with 8 minutes at 68°C and then held at 4°C. When LCO and HCO did not provide any bands on the gel, as it was the case in some individuals of *Oithona atlantica*, versatile primers for the CO1 genes based on highly conservative mitochondrial DNA regions [L1384-COI (GGT CAT GTA ATC ATA AAG ATA TTG G) X H2612-COI (AGG CCT AGG AAA TGT ATM GGG AAA)] were used (see Machida et al. 2004).

Table 2: For the further procedure the PCR premix was modified (see below)

	Stock	Final concentration	µl/sample
H20			11,1
5 x buffer	5 x	1 x	5
dNTP	10 mM	0,2 mM	0,5
HCO	100 µM	0,5 µM	0,125
LCO	100 µM	0,5 µM	0,125
Taq roust Kappa	5U/ µl	0,03 U/ µl	0,15
5 x Enhancer	5 x	1 x	5
DNA			3

Furthermore, the PCR conditions were also modified for the primer designed by Folmer et al. (1994). The new PCR reaction program consisted of 2 minutes at 95°C,

followed by 40 cycles of 20 seconds at 95°C, 20 seconds at 49°C and 2 minutes at 72°C. Upon completion of the 40 cycles, the programme concluded with 8 min at 72°C and then held at 4°C. For the primer used by Machida et al. (2004), the new PCR reaction programme consisted of 2 minutes at 95°C, followed by 35 cycles of 20 seconds at 95°C, 20 seconds at 51°C and 2 minutes at 72°C. Upon completion of the 40 cycles the programme concluded with 8 minutes at 72°C and then held at 4°C.

Samples that showed a positive reaction on the agarose gel were cleaned for sequencing. The first 148 samples were purified with the PCR purification KIT 28106 and eluted with 20 µL EB buffer. The following samples were purified with ExoSapit by using 5 µL of the PCR product adding 0.25 µL EXO I (Exonuclease I) and 1 µL SAP (shrimp alkaline phosphatase). The samples were incubated for 30 minutes at 37°C and then 15 minutes at 80 °C.

3.3.1 Sequencing

Cycle sequencing was done with the Big Dye Terminator of the cycle sequencing kit (ABI). Prior to sequencing with the ABI 3130XL sequencer, the samples were purified with the DyeEx Kit (Qiagen 63188). Sequence reads were proofread and contigs from both strands assembled in the program GeneMapper (ABI). The corrected sequences were aligned with the program Codon Code Alligner. Using Codon Code Alligner, ends were trimmed from the raw sequences. After trimming, forward and reverse sequences for each specimen were assembled. Each assembled contig was examined and edited by hand, and each sequence was checked for stop codons and quality.

The number of unique mitochondrial haplotypes was determined with the computer program MEGA 4. Following Saunders (2009), neighbour joining was used to provide a visual display of COI-5´ variation within and between species.

DNA-extraction, sequencing and analysis was done in cooperation with Andrea Eschbach and Christoph Held.

4. Results

4.1 Morphology of *Oithona similis*

4.1.1 Literature research

In this chapter, the results concerning body size and setae of the exopodits are presented. According to the literature, minimal sizes are 0.45 mm (*Oithona nana*), 0.6 mm (*O. similis*), 1.0 mm (*O. atlantica*) and 1.13 mm (*O. frigida*). Maximal sizes of these species are 0.8 mm (*O. nana*), 1.2 mm (*O. similis*), 1.4 mm (*O. frgida*) and 1.5 mm (*O. atlantica*). For further details see table 3 below.

Table 3 Bodysize of the females of the four *Oithona* species based on literature information

Species	Size [mm]	Reference
Oithona similis	0.73 - 0.8	Giesbrecht 1893
O. similis	0.73 - 0.8	Van Breemen 1903
O. similis	0.73 - 0.96	Van Breemen 1908
O. similis	0.78 - 0.95	Rosendorn 1917
O. helgolandica (=similis)	0.7 - 0.9	Sars 1918 (1913)
O. similis	0.73 – 0.96	Pesta 1920
O. helgolandica (=similis)	0.7 - 0.9	Campbell 1929
O. similis	0.86	Willey 1920
O. similis	0.76 - 1.0; usually 0.85 - 1.00	Farran 1929
O. similis	0.74 - 0.95	Kiefer 1929
O. similis	0.7 - 0.95	Wilson 1932
O. similis	0.73 - 0.96	Rose 1933
O. similis	0.9 - 0.93	Farran 1936
O. similis	about 0.8	Mori 1937
O. similis	0.69- 0.96	Davis 1949
O. similis	1.15 - 1.2	Vervoort 1951
O. similis	0.75 - 0.95	Vervoort 1957
O. similis	0.71 - 1.05	Tanaka 1960
O. helgolandica (=similis)	0.7	Gaudy 1963
O. similis	0.7 - 0.95	Kasturirangan 1963
O. similis	0.80 - 1.02	Tanaka 1964
O. helgolandica (=similis)	0.8	Ramirez 1966

Species	Size [mm]	Reference
O. similis	0.89 - 1.1	Pallares 1968
O. similis	0.7 - 0.8	Minoda 1971
O. similis	0.69 - 0.84	Nishida et al. 1977
O. similis	0.68 - 0.96	Nishida 1985
O. similis	0.8 - 0.92	Mazzocchi et al. 1995
O. similis	0.68 - 0.96	Chihara & Murano 1997
O. similis	0.68 - 0.96	Bradford-Grieve et al. 1999
O. similis	0.68 - 0.96	Hugget & Bradford-Grieve 2007
O. similis	0.76	Blachowiak-Samolyk et al. 2008
O. similis	0.6 - 0.75	Selifonova et al. 2008
O. similis	0.7 - 0.95	Perumal & Rajkumar
O. atlantica	1.0 - 1.16	Farran 1908
O. atlantica	1.0 – 1.15	Rosendorn 1917
O. atlantica	1 – 1.16	Früchtl 1923
O. atlantica	1.06	Kiefer 1929
O. atlantica	1.5	Gaudy 1963
O. atlantica	1.1	Wellershaus 1970
O. atlantica	1.11 - 1.29	Nishida et al. 1977
O. atlantica	1.14 - 1.43	Nishida 1985
O. atlantica	1.16 – 1.39	Mazzocchi et al. 1995
O. atlantica	1.14 – 1.43	Chihara & Murano 1997
O. atlantica	1.00 – 1.43	Bradford-Grieve et al. 1999
O. atlantica	1 - 1.43	Hugget & Bradford-Grieve 2007
O. frigida	1.2 – 1.35	Rosendorn 1917
O. frigida	1.3	Brady 1918
O. frigida	1.25 - 1.28	Farran 1929
O. frigida	1.2 – 1.35	Kiefer 1929
O. frigida	1.13 – 1.4	Vervoort 1957
O. frigida	1.3	Wellershaus 1970
O. frigida	1.23 - 1.24	Nishida 1985
O. frigida	1.20 – 1.24	Bradford-Grieve et al. 1999
O. nana	0.5 - 0.53	Giesbrecht 1893
O. nana	0.5 – 0.55	Van Breemen 1903
O. nana	0.7 - 0.8	Esterly 1905

Species	Size [mm]	Reference
O. nana	0.5 – 0.65	Van Breemen 1908
O. nana	0.59; 0.6	Burckhard 1913
O. nana	0.53	Rosendorn 1917
O. nana	0.5 – 0.53; 0.7 – 0.8	Pesta 1920
O. nana	0.55	Murphy 1923
O. nana	0.5 – 0.63	Früchtl 1924
O. nana	0.53 – 0.55; 0.62 – 0.69	Gurney 1927
O. nana	0.5 – 0.7	Kiefer 1929
Oithonina nana	0.5 – 0.65	Wilson 1932
Oithona nana	about 0.62	Mori 1937
O. nana	0.53 – 0.55; 0.62 - 0.69	Sewell 1947
O. nana	0.54 – 0.63	Marques 1951
O. nana	0.75	Grice 1960
O. nana	0.55 – 0.6	Björnberg 1963
O. nana	0.6	Gaudy 1963
O. nana	0.51 – 0.64	Tanaka 1964
O. nana	0.6 – 0.66	González & Bowman 1965
O. nana	0.5	Ramirez 1966
O. nana	0.53	Wellershaus 1970
O. nana	0.57 – 0.67	Marques 1974
O. nana	0.54 - 0.62	Nishida et al. 1977
O. nana	0.49 - 0.59	Nishida 1985
O. nana	0.49 – 0.62	Chihara & Murano 1997
O. nana	0.49 – 0.72	Bradford-Grieve et al. 1999
O. nana	0.45 - 0.55	Selifonova et al. 2008

Table 4 shows the formula of the external setae of the exopodits of *Oithona similis.* For legs one to three it is the same in all references: 1, 1, 2; 1, 0, 1; 1, 0, 1. For the fourth leg two variations exist: 0, 0, **0** (9 references) and 0, 0, **1** (19 references). For *O. atlantica*, three different formulae are mentioned that show differences at legs three and four: 1, 1, 2; 1, 0, 2; 1, 0, **1**; 0, 0, **1** (7 references), 1, 1, 2; 1, 0, 2; 1, 0. **2;** 0, 0, **1** (2 references) and 1, 1, 2; 1, 0, 2; 1, 0, **2**; 0, 0, **2** (1 reference). Two formulae of the external setae of the exopodits of *O. frigida* are described. Differences are shown in leg two: 1, 1, 3; 1, 1, **3**; 1, 0, 1; 0, 0, 1 (6 references) and 1, 1, 3; 1, 1, **2**; 1, 0, 1; 0,

0, 1 (5 references). *Oithona nana* is the only species with no variations in all cited references: 1, 1, 3; 1, 1, 3; 1, 1, 3; 1, 1, 2 (17 references). References that do not include the formulae for all four legs are additionally shown in table 4.

Table 4 Formula of the outer marginal spines of the exopodit of the female swimming legs (the source of information is color-coded, text references in red and references from drawn appendages in purple)

Reference	Name of the species	Leg 1 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 2 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 3 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 4 Number of external exopod spines Exp1, Exp2, Exp 3
Giesbrecht 1893	*O. similis* Claus 1866	1, 1, 2	1, 0, 1	1, 0 ,1	0, 0, 0
Wheeler 1901	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 0
Van Breemen 1903	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 0
Van Breemen 1908	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 0
Rosendorn 1917	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Sars 1918	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Pesta 1920	*O. helgolandica* (= *O. similis*)	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 0
Kiefer 1929	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Wilson 1932	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 0
Rose 1933	*O. helgolandica* (= *O. similis*)	1, 1, 2	1, 0, 1		0, 0, 0
Mori 1937	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Davis 1949	*O. helgolandica* (= *similis*)	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1

Reference	Name of the species	Leg 1 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 2 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 3 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 4 Number of external exopod spines Exp1, Exp2, Exp 3
Lindberg 1950	*O. similis*	1, 1, 2	1, 0, 1		
Lindberg 1955	*O. similis*	1, 1, 2	1, 0, 1		
Crisafi 1956	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Shen & Bai 1956	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 0
Tanaka 1960	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Kasturirangan 1963	*O. similis*	- , -, 2	-, -, 1	-, - , 1	-, - , 0
Pallares 1968	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Wellershaus 1970	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Bradford 1971	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Bradford 1972	*O. similis*		1, 0, 1		
Chen et al. 1974	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Nishida et al. 1977	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Dawson & Knatz 1980	*O. similis*	1, 1, 2	1, 0, 1		0, 0, 1
Shuvalov 1980	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Nishida 1985	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Zheng Zhong et al. 1989	*O. similis*				0, 0, 1 (after Zheng Zhong et al. 1965)
Mazzocchi et al. 1995	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1

Reference	Name of the species	Leg 1 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 2 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 3 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 4 Number of external exopod spines Exp1, Exp2, Exp 3
Chihara & Murano 1997	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Bradford-Grieve et al. 1999	*O. similis*	1, 1, 2	1, 0, 1	1, 0, 1	0, 0, 1
Rosendorn 1917	**O. atlantica Farran 1908**	1, 1, 2	1, 0, 2	1, 0, 1	0, 0, 1
Sars 1918	*O. spinirostris* (= *O. atlantica*)	1, 1, 2	1, 0, 2	1, 0, 2	0, 0, 1
Kiefer 1929	*O. atlantica*	1, 1, 2	1, 0, 2	1, 0, 2	0, 0, 1
Wellershaus 1970	*O. atlantica*	1, 1, 2	1, 0, 2	1, 0, 2	0, 0, 2
Bradford 1972	*O. atlantica*	1, 1, 2			
Chen et al. 1974	*O. plumifera* (= *O. atlantica*)	1, 1, 2	1, 0, 2	1, 0, 1	0, 0, 1
Nishida et al. 1977	*O. atlantica*	1, 1, 2	1, 0, 2	1, 0, 1	0, 0, 1
Björnberg et al. 1981	*O. atlantica*	1, 1, 2	1, 0, 2	1, 0, 1	0, 0, 1
Nishida 1985	*O. atlantica*	1, 1, 2	1, 0, 2	1, 0, 1	0, 0, 1
Mazzocchi et al. 1995	*O. atlantica*	1, 1, 2	1, 0, 2	1, 0, 1	0, 0, 1
Chihara & Murano 1997	*O. atlantica*	1, 1, 2	1, 0, 2	1, 0, 1	0, 0, 1
Bradford-Grieve et al. 1999	*O. atlantica*	1, 1, 2	1, 0, 2	1, 0, 1	0, 0, 1
Hugget&Bradford-Grieve 2007	*O. atlantica*	1, 1, 2	1, 0, 2	1, 0, 1	0, 0, 1

Reference	Name of the species	Leg 1 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 2 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 3 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 4 Number of external exopod spines Exp1, Exp2, Exp 3
Giesbrecht 1902	*O. frigida* **n.sp.**	1, 1, 3	1, 1, 3	1, 0, 1	0, 0 ,1
Rosendorn 1917	*O. frigida*	1, 1, 3	1, 1, 2	1, 0, 1	0, 0, 1
Kiefer 1929	*O. frigida*	1, 1, 3	1, 1, 2	1, 0, 1	0, 0, 1
Lindberg 1950	*O. frigida*	1, 1, 2	1, 1, 2		
Tanaka 1960	*O. frigida*	1, 1, 3	1, 1, 3	1, 0, 1	0, 0, 1
Wellershaus 1970	*O. frigida*	1, 1, 3	1, 1, 3/2	1, 0, 1	0, 0, 1
Bradford 1971	*O. frigida*	1, 1, 3	1, 1, 3	1, 0, 1	0, 0, 1
Shuvalov 1980	*O. frigida*	1, 1, 3	1, 1, 2	1, 0, 1	0, 0, 1
Björnberg et al. 1981	*O. frigida*	1, 1, 3	1, 1, 2	1, 0, 1	0, 0, 1
Nishida 1985	*O. frigida*	1, 1, 3	1, 1, 3	1, 0, 1	0, 0, 1
Bradford-Grieve et al. 1999	*O. frigida*	1, 1, 3	1, 1, 3	1, 0, 1	0, 0, 1
Giesbrecht 1893	*O. nana* **n. sp.**	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Van Breemen 1903	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Esterly 1905	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Van Breemen 1908	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Rosendorn 1917	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Pesta 1920	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Kiefer 1929	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2

Reference	Name of the species	Leg 1 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 2 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 3 Number of external exopod spines Exp1, Exp2, Exp 3	Leg 4 Number of external exopod spines Exp1, Exp2, Exp 3
Wilson 1932	*Oithonina nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Rose 1933	*Oithona nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Mori 1937	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Grice 1960	*O. nana*				1, 1, 2
Tanaka 1960	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
González & Bowman 1965	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Ramirez 1966	*O. nana*	1, 1, 3	-	1, 1, 3	1, 1, 2
Wellershaus 1970	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Nishida et al. 1977	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Dawson & Knatz 1980	*O. nana*	1, 1, 3	1, 1, 3		1, 1, 2
Ferrari & Bowman 1980	*O. nana*				1, 1, 2
Shuvalov 1980	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Nishida 1985	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2
Chihara & Murano 1997	*O. nana*	1, 1, 3	1, 1, 3	1, 1, 3	1, 1, 2

The numbers of inner marginal setae of the exopodit of the *Oithona similis* swimming legs differ for foot one (Table 5): 0, 1, **4**; 0, 1, 5; 0, 1, 5; 0, 1, 5 (nine references) and 0, 1, **5**; 0, 1, 5; 0, 1, 5; 0, 1, 5 (two references). For *O. atlantica* also two different formulae are shown: **0**, 1, 4; 0, 1, 5; 0, 1, 5; 0, 1, 5 (three references) and **1**, 1, 4; 0, 1, 5; 0, 1, 5; 0, 1, 5 (three references). Five cited

references refer to the following formula for *O. frigida*: 1, 1, 4; 0, 1, 5; 0, 1, 5; 0, 1, 5 and a schematic drawing of Björnberg et al. (1981) shows: 0, 1, 4 (**5**?); **0**, **0**, **4**; 0, 1, 5; 0, 1, **4**. *Oithona nana* is the only species with no variations in all cited references, also for the inner setae formulae: 1, 1, 4; 1, 1, 5; 1, 1, 5; 1, 1, 5 (six references). References, not including the formulae for all four legs, are additionally shown in Table 5.

Table 5 Formula of the inner marginal seta of the exopodit of the female swimming legs (the source of the information is color-coded: text references in red and references from drawn appendages in purple)

Reference	Name of the species	Leg 1 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 2 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 3 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 4 Number of inner marginal exopod setae Exp1, Exp2, Exp 3
Giesbrecht 1893	*Oithona similis* Claus 1866	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Van Breemen 1908	*O. similis*				0, 1, 5
Rosendorn 1917	*O. similis*	0, 1, 5	0, 1, 5	0, 1, 5	0, 1, 5
Sars 1918	*O. similis*	0, 1, 4	0, 1, 5		
Rose 1933	*O. helgolandica* (= *similis*)		0, 1, 5		
Mori 1937 (1964)	*O. similis*	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Davis 1949	*O. helgolandica* (= *similis*)	0, 1, 5	0, 1, 5	0, 1, 5	0, 1, 5

Reference	Name of the species	Leg 1 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 2 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 3 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 4 Number of inner marginal exopod setae Exp1, Exp2, Exp 3
Shen & Bai 1956	*O. similis*	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Crisafi 1959	*O. helgolandica* (= *similis*)	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Chen et al. 1974	*O. similis*	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Tanaka 1960	*O. similis*	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Bradford 1972	*O. similis*		0, 1, 5		
Chen et al. 1974	*O. similis*		0, 1, 5	0, 1, 5	0, 1, 5
Nishida et al. 1977	*O. similis*	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Dawson & Knatz 1980	*O. similis*	0, 1, 4		0, 1, 5	0, 1, 5
Gardner & Szabo 1982	*O. similis*		0, 1, 4 (after Rose 1933; but in Rose it is 0, 1, **5**)		
Nishida 1985	*O. similis*	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Zheng Zhong et al. 1989	*O. similis*				0, 1, 5 (after Zheng Zhong et al. 1965)
Mazzocchi et al. 1995	*O. similis*	0, 1, 4	0, 1, 5,	0, 1, 5	0, 1, 5
Chihara & Murano 1997	*O. similis*		0, 1, 5		
Bradford-Grieve et al. 1999	*O. similis*	?, 1, 4	1, 1, 5	1, 1, 5	0, 1, 5

Reference	Name of the species	Leg 1 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 2 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 3 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 4 Number of inner marginal exopod setae Exp1, Exp2, Exp 3
Rosendorn 1917	*O. atlantica* **Farran 1908**	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Sars 1918	*O. spinirostris* (=*atlantica*)	1, 1, 4	0, 1, 5		0, 1, 5
Bradford 1972	*O. atlantica*	?, 1, 4 (?)			
Chen et al. 1974	*O. atlantica*	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Nishida et al. 1977	*O. atlantica*	1, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Nishida 1985	*O. atlantica*	1, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Mazzocchi et al. 1995	*O. atlantica*	1, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Chihara & Murano 1997	*O. atlantica*				0, 1, 5
Bradford et al. 1999	*O. atlantica*	0, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Hugget & Bradford-Grieve 2007	*O. atlantica*	?, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Giesbrecht 1902	*O. frigida* **n. spec.**	1, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Rosendorn 1917	*O. frigida*	1, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Tanaka 1960	*O. frigida*	1, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Björnberg et al. 1981	*O. frigid*	0, 1, 4	0, 0, 4	0, 1, 5	0, 1, 4

Reference	Name of the species	Leg 1 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 2 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 3 Number of inner marginal exopod setae Exp1, Exp2, Exp 3	Leg 4 Number of inner marginal exopod setae Exp1, Exp2, Exp 3
Nishida 1985	*O. frigida*	1, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Bradford-Grieve et al. 1999	*O. frigida*	1, 1, 4	0, 1, 5	0, 1, 5	0, 1, 5
Giesbrecht 1893	***O. nana* n. spec.**	1, 1, 4	1, 1, 5	1, 1, 5	1, 1, 5
Esterly 1905	*O. nana*	-, - , 3			
Van Breemen 1908	*O. nana*				0, 1, 5
Rosendorn 1917	*O. nana*	1, 1, 4	1, 1, 5	1, 1, 5	1, 1, 5
Wilson 1932	*Oithonina nana*		1, 1, 5		
Rose 1933	*Oithona nana*				0, 1, 5
Mori 1937	*O. nana*	1, 1, 4	1, 1, 5	1, 1, 5	1, 1, 5
González & Bowman 1965	*O. nana*	1, 1, 4	1, 1, 5	1, 1, 5	1, 1, 5
Ramirez 1966	*O. nana*	0, 1, 5		1, 1, 5	1, 1, 5
Nishida et al. 1977	*O. nana*	1, 1, 4	1, 1, 5	1, 1, 5	1, 1, 5
Dawson & Knatz 1980	*O. nana*	1, 1, 4	1, 1, 5		0, 1, 5
Ferrari & Bowman 1980	*O. nana*				0, 1, 5
Nishida 1985	*O. nana*	1, 1, 4	1, 1, 5	1, 1, 5	1, 1, 5

4.1.2 Personal observations

Based on the shape of the rostrum, body size and the formula and structure of the outer setae of the exopodits of the swimming legs (see Figs. 21-24 and Tables 4 and 5), five different morphotypes were identified: *Oithona similis*, *O. atlantica*, *O. frigida*, *O. nana* and *Oithona sp.*. Individuals from the Arctic Ocean were identified as *O. similis* or *O. atlantica*. All specimens from the Mediterranean Sea showed the morphology of *O. similis*. Within the North Sea, individuals of three morphotypes were found: *O. similis* (HE 302; Helgoland), *O. nana* (Helgoland) and *Oithona* sp. (Sylt, List Basin). In this study, it was not possible to assign *Oithona sp.* to a specific known species. It shares the appendage structure of the swimming legs` exopodits of *O. nana* and shows a rostrum that is bended like the one of *O. similis* and can also only be seen from ventral or lateral view. In the Southern Ocean, two morphotypes were found: *O. similis* and *O. frigida*.

4.2. Genetics of *Oithona similis*

Sequences were gained from 163 individuals that were morphologically identified as *O. similis* prior to sequencing (71 from the Arctic Ocean, 83 from the Southern Ocean, 2 from the North Sea and 7 from the Mediterranean Sea). 19 individuals from the Arctic Ocean had the morphological appendage structure of the swimming legs of *O. atlantica*. Eight of the individuals that were sampled in the Southern Ocean were morphologically described as *O. frigida*. From the North Sea, 10 individuals were defined as *O. nana* and 9 copepods were named *Oithona sp*. prior to sequencing.

The distribution of the haplotypes is shown in figure 25 and Table 6. *Oithona similis* haplotypes were found in the Arctic Ocean (3 groups), the Southern Ocean (3 groups), the North Sea (1 group) and the Mediterranean Sea (2 groups). Within the Arctic Ocean, the biggest group (Osi ARK 1) includes mt CO1 sequences of 69 individuals that were described as *O. similis* and 19 copepods that were defined as *O. atlantica*. This group is widely distributed. It was found at all three stations in all depths of the expedition ARK XXIII-3 (as well as at all six stations sampled during the second expedition in the Arctic Ocean (ARK XXV-1). The two other groups (Osi ARK 2, Osi ARK 3) were only found at station 308 (ARK XXIII-3) in the upper 50 m of the

water column. These are each represented by just one female of the *O. similis* morphotype.

The three groups from the Southern Ocean only include individuals that were morphologically defined as *O. similis*. The first group (Osi ANT 1) is represented by 72 individuals and was found at the following stations of the expedition ANT XXIV-2: St. 21 (0-50 m, 50-100 m, 100-150 m, 200-250 m), St. 33 (0-50 m, 50-100 m, 100-150 m), St. 34 (0-50 m, 50-100 m, 100-150 m), St. 39 (0-50 m, 200-250 m), St. 58 (0-50 m), St. 62 (0-50 m, 50-100 m), St. 85 (100-150 m, 150- 200 m). The second group (Osi ANT 2) includes 19 copepods from the Southern Ocean and was only found at two stations namely at station 13 from 0-150 m depth and at station 85 within the upper 50 m of the water column. The third group (Osi ANT 3) consists only of one individual that was caught at station 13 between a water depth of 100 and 150 m.

In the North Sea, one haplotype (Osi North Sea/ Med.Sea) was found for *Oithona similis*. Eight individuals were sampled at two places in the North Sea close to the island of Helgoland (one female) and during an expedition of RV Heincke (one female) as well as in the Mediterranean Sea close to Villefranche (six individuals). In the Mediterranean Sea, a further haplotype (Osi Med. Sea) was detected. It is only represented by one specimen.

Additionally to the *Oithona similis* groups, three other copepod species groups were identified morphologically as well as via sequencing: *O. frigida* (Ofr) in the Southern Ocean, O. *nana* (Ona) (ten females) in the North Sea close to the island of Helgoland, and *Oithona sp.* represented by 9 individuals in the North Sea close to the island of Sylt. The *O. frigida* group consists of eight individuals that were sampled at five different stations during the expedition ANT XXIV-2: St. 13 (150-200 m), St. 33 (50-100 m, 100-150 m), St. 34 (100-150 m), St. 64 (200-250 m), St. 85 (100-150 m).

Table 6 Overview of the different haplotypes analyzed in the Arctic Ocean, Southern Ocean, Mediterranean Sea and North Sea

Abbreviation	Explanation
Osi ARK 1	*Oithona similis* Arctic Ocean Group 1
Osi ARK 2	*Oithona similis* Arctic Ocean Group 2
Osi ARK 3	*Oithona similis* Arctic Ocean Group 3
Osi ANT 1	*Oithona similis* Southern Ocean Group 1
Osi ANT 2	*Oithona similis* Southern Ocean Group 2
Osi ANT 3	*Oithona similis* Southern Ocean Group 3
Osi Med. Sea	*Oithona similis* Mediterranean Sea
Osi North Sea/Med Sea	*Oithona similis* North Sea, Mediterranean Sea
Ona	*Oithona nana*
Ofr	*Oithona frigida*
Osp	*Oithona sp.*
1; 290, 50	ARK XXIII-3, St. 290, 50-100 m
1; 290, 100	ARK XXIII-3, St. 290, 100-150 m
1; 308, 0	ARK XXIII-3, St. 308, 0-50 m
1; 308, 50	ARK XXIII-3, St. 308, 50- 100 m
1; 308, 100	ARK XXIII-3, St. 308, 100-250 m
1; 392, 0	ARK XXIII-3, St. 392, 0-150 m
2; 1, 0	ARK XXV-1, St. 1, 0-100 m
2; 24, 0	ARK XXV-1, St. 24, 0-100 m
2; 34, 0	ARK XXV-1, St. 34, 0-100 (200) m
2; 57, 0	ARK XXV-1, St. 57, 0-100 m
2; 63, 0	ARK XXV-1, St. 63, 0-100 m
2; 74, 0	ARK XXV-1, St. 74, 0-100 m
3; 13, 0	ANT XXIV-2, St. 13, 0-50 m
3; 13, 50	ANT XXIV-2, St. 13, 50-100 m
3; 13, 100	ANT XXIV-2, St. 13, 100-150 m
3; 13, 150	ANT XXIV-2, St. 13, 150-200 m
3; 21, 0	ANT XXIV-2, St. 21, 0-50 m
3; 21, 50	ANT XXIV-2, St. 21, 50-100 m
3; 21, 100	ANT XXIV-2, St. 21, 100-150 m
3; 21, 200	ANT XXIV-2, St. 21, 200-250 m
3; 33, 0	ANT XXIV-2, St. 33, 0-50 m

Abbreviation	Explanation
3; 33, 50	ANT XXIV-2, St. 33, 50-100 m
3; 33, 100	ANT XXIV-2, St. 33, 100-150 m
3; 34, 0	ANT XXIV-2, St. 34, 0-50 m
3; 34, 50	ANT XXIV-2, St. 34, 50-100 m
3; 34, 100	ANT XXIV-2, St. 34, 100-150 m
3; 39, 0	ANT XXIV-2, St. 39, 0-50 m
3; 39, 200	ANT XXIV-2, St. 39, 200-250 m
3; 58, 0	ANT XXIV-2, St. 58, 0-50 m
3; 62, 0	ANT XXIV-2, St. 62, 0-50 m
3; 62, 50	ANT XXIV-2, St. 62, 50-100 m
3; 64, 200	ANT XXIV-2, St. 64, 200-250 m
3; 85, 0	ANT XXIV-2, St. 85, 0-100 m
3; 85, 100	ANT XXIV-2, St. 85, 100-150 m
3; 85, 150	ANT XXIV-2; St. 85, 150-200 m
Point B	Mediterranean Sea
HE 302	North Sea
Helgol.	North Sea, close to the island of Helgoland
Sylt	North Sea, close to the island of Sylt
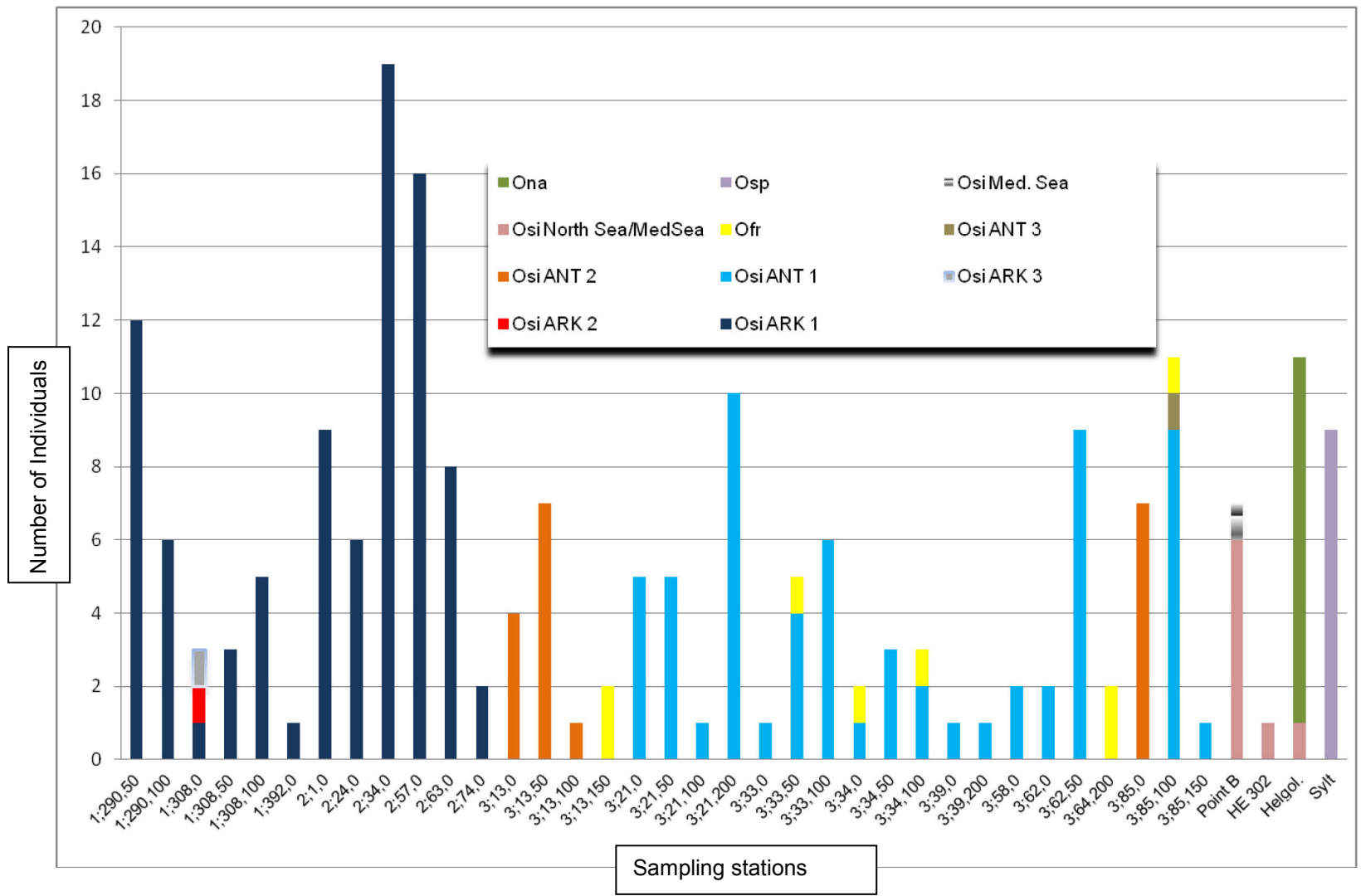
Fig. 25 Distribution of the different genetic haplotypes in the investigation areas

As basis of the neighbor joining tree, the species *Oithona nana* was chosen (see fig. 26). The tree has two main branches; the lower one is subdivided into three branches (see figs. 26, 26.3). One of these branches is formed by the second *O. similis* group from the Mediterranean Sea (see fig. 26.3). *Oithona frigida* forms the second branch and the sequences of the species *Oithona sp.* the third one (see fig. 26.3). The second main branch is divided into four branches (see figs. 26, 26.1, 26.2). The lowest one is subdivided into two branches, each one containing one of the two Arctic *O. similis* groups that are presented by one individual (see fig. 26.2). The second branch from below contains the *O. similis* group with individuals from the Mediterranean Sea and the North Sea (see fig. 26.2). The third one from below is divided in two branches (see fig. 26.2). The single individual from the Southern Ocean has its own branch next to the second group from the Southern Ocean. The uppermost branch is subdivided in two branches (see fig. 26.1, 26.2). One containing the first Arctic group (see fig. 26.1), and the other one formed by the first Southern Ocean group (see fig. 26.2).

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Fig. 26. Overview of the extraction consenus tree

Fig 26.1 Detail 1 of extraction consenus tree

OsiF1032_1 extraction
OsiF1056_1 extraction
OsiF1078_1 extraction
OsiF432_290_100m_1000bp_...
OsiF430_308_250m_1000bp_...
OsiF1040_1 extraction
OatF452_290_100m_1000bp_...
OsiF1213 extraction
OsiF914_57_100m_1000bp_...
OatF484ger_392_150m_100_...
OsiF1017_24_100m_1000bp_...
OsiF912_57_100m_1000bp_...
OsiF917_57_100m_1000bp_...
OsiF929_57_100m_Folmer_...
OatF467ger_308_50m_1000...
OatF946_C5_63_50m_1000b...
OsiF1006_74_100m_1000bp_...
OsiF915_57_100m_1000bp_...
OsiF918_57_100m_1000bp_...
OsiF937_63_50m_1000bp_K...
OsiF921_57_100m_1000bp_K_...
OsiF1020_24_100m_1000bp_...
OsiF1062_1 extraction
OsiF1033 extraction
OsiF1035_1 extraction
OatF455_290_100m_1000bp_...
OatF459_290_100m_1000bp_...
OsiF443_290_150m_1000bp_...
OsiF1052 extraction
OsiF1068_1 extraction
OatF932_57_100m_1000bp_...
OatF933_57_100m_1000bp_...
OsiF913_57_100m_1000bp_...
OsiF926_57_100m_1000bp_...
OsiF930_57_100m_1000bp_...
OsiF923_57_100m_1000bp_...
OatF934_57_100m_1000bp_...
OsiF919_57_100m_1000bp_...
OsiF920_57_100m_1000bp_...
OsiF911_57_100m_1000bp_...
OsiF957_63_50m_1000bp_K...
OatF941_63_50m_1000bp_K...
OatF940_63_50m_1000bp_K...
OsiF1019_24_100m_1000bp_...
OsiF1053 extraction
OsiF936_63_50m_1000bp_K...
OsiF948_63_50m_1000bp_K...
OsiF953_63_50m_1000bp_K...
OsiF954_63_50m_1000bp_K...
OsiF998 extraction 2
OsiF1030_1_1 extraction
OsiF1037_1 extraction
OsiF1039_1 extraction
OsiF1041_1 extraction
OsiF1045_1 extraction
OsiF1046_1 extraction
OsiF1047_1 extraction
OsiF1050_1 extraction
OsiF1054_1 extraction
OsiF1058_1 extraction
OsiF1072_1 extraction
OsiF1074_1 extraction
OsiF1075_1 extraction
OsiF1211_1 extraction
OsiF1212_1 extraction
OsiF1216_1 extraction
OsiF1049_1 extraction
OsiF1057_1 extraction
OatF450_290_100m_1000bp...
OatF451_290_100m_1000bp...
OatF453_290_100m_1000bp...
OatF454_290_100m_1000bp...
OatF458_290_100m_1000bp...
OatF460_290_100m_1000bp...
OsiF1016_24_100m_1000bp...
OsiF1024_24_100m_1000bp...
OsiF1043_1 extraction
OsiF1069_1 extraction
OsiF442_290_150m_1000bp...
OsiF428_308_250m_1000bp...
OsiF441_290_150m_1000bp...
OsiF1034_1 extraction
OatF434_308_250m_1000bp...
OatF444_290_150m_1000bp...
OsiF1044_1 extraction
OsiF440_290_150m_1000bp...
OsiF445_290_150m_1000bp...
OatF435_308_250m_1000bp...
OatF436_308_250m_1000bp...
OatF457_290_100m_1000bp...
OsiF431_290_100m_1000bp...

Osi ARK 1

51
53
53
52
52

100

51

86

100

56

100

100

100

51

100

Fig 24.2 Detail 2 of extraction consenus tree

0.06

Fig. 24.3 Detail 3 of the extraction consenus tree

100

100

Osp

100

51   Ofr

100

Osi Med. Sea

100

100
100
100
100
100

Ona

Osp_F1207 extraction
OspF1201 extraction
OspF1200 extraction
OspF1202 extraction
OspF1206 extraction
OspF1208 extraction
OspF1205 extraction
Osp_F1204 extraction
OspF1209 extraction
OspF1203 extraction
OfrF309_64_250m_Folmer ...
OfrF315_33_150m_Folmer ...
OfrF416ger_13_200m_Folm...
OfrF314_64-250m_Folmer ...
OfrF365_33_100_Folmer e...
OfrF384-C5-85_150m_Folm...
OfrF396_62_200m_Folmer ...
OsiF311ger_34_150m_1000...
OfrF413_13_200m_Folmer ...
Osi_F1180 extraction
OnaF1199 extraction
OnaF1198 extraction
OnaF1197 extraction
OnaF1196 extraction
OnaF1193 extraction
OnaF1192 extraction
OnaF480 extraction 2
OnaF479 extraction 2
OnaF437 extraction 2
OnaF438 extraction 2
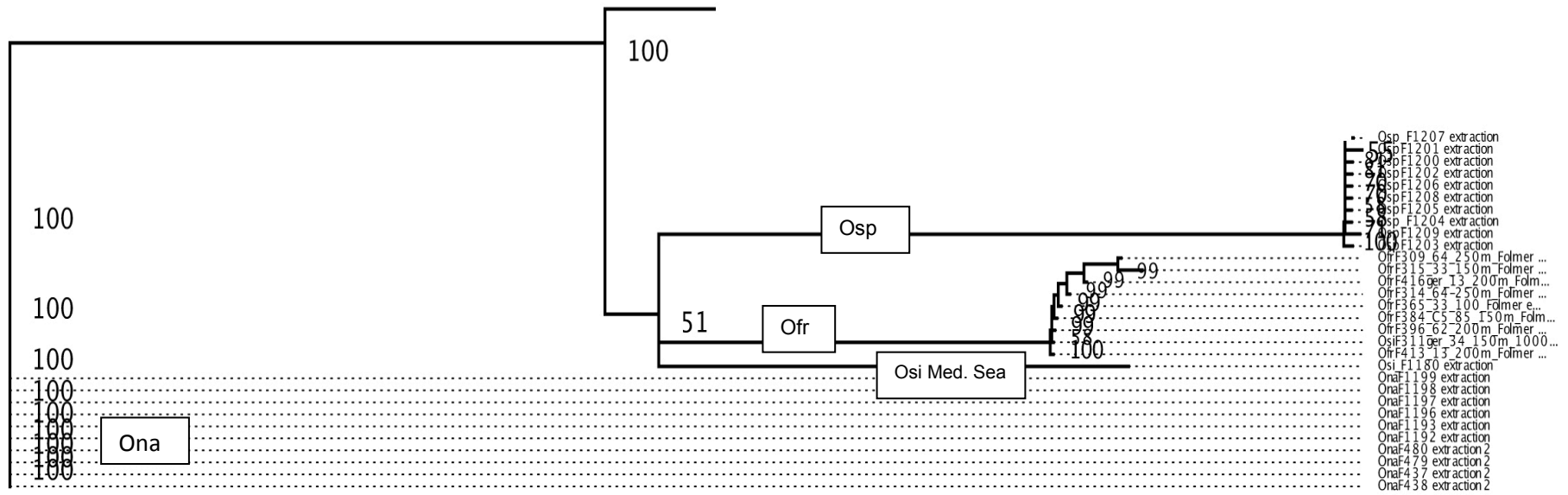
99   99

99

99

99

100

96

Table 7 shows the distribution of the individuals that belong to the haplotype "Osi ARK 1" from the Arctic Ocean according to the adjustment in the neighbor joining tree (see figs. 26, 26.1). Subadult females are referred to as C5. The table further shows the morphotype that was identified prior to sequencing.

Table 7 The distribution of the individuals of haplotype Osi ARK 1

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Area
Osi 1032	*Oithona similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1056	*O. similis*	St. 1, 0-100 m; ARK 25-1	71° 23.91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Osi F1078	*O. similis* (C5)	St. 1, 0-100 m; ARK 25-1	71° 23.91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Osi F432	*O. similis*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford See
Osi F430	*O. similis*	St. 308, 100-250 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Osi F1040	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	77° 59,95' N	3° 30.35' W	Greenland Sea
Oat F433	*O. atlantica*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Oat F452	*O. atlantica*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Osi F1213	*O. similis*	St. 308, 50-100 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Osi F914	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0,98' N	0° 59.47' E	Greenland Sea
Oat F484	*O. atlantica*	St. 392, 0-150 m; ARK 23-3	80° 27.90' N	158° 45.66' W	Canadian Basin/ Beauford Sea

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Area
Osi F1017	*O. similis*	St. 24, 0-100 m; ARK 25-1	74° 59.94' N	8° 1.03' W	Greenland Sea
Osi F912	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F917	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F929	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Oat F467	*O. atlantica*	St. 308, 0-50 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Oat F946	*O. atlantica* (C5)	St. 63, 0-50 m; ARK 25-1	74° 59.39' N	4° 50.07' E	Greenland Sea, close to Barents Sea
Osi F1006	*O. similis*	St. 74, 0-100 m; ARK 25-1	75° 0.06' N	11° 54.25' E	Norwegian Sea
Osi F915	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F918	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0,98' N	0° 59.47' E	Greenland Sea
Osi F937	*O. similis*	St. 63, 0-50 m; ARK 25-1	74° 59,39' N	4° 50.07' E	Greenland Sea, close to Barents Sea
Osi F921	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0,98' N	0° 59.47' E	Greenland Sea
Osi F1020	*O. similis*	St. 24, 0-100 m; ARK 25-1	74° 59,94' N	8° 1.03' W	Greenland Sea
Osi F1062	*O. similis*	St. 1, 0-100 m; ARK 25-1	71° 23,91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Osi F1033	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59,95' N	3° 30.35' W	Greenland Sea
Osi F1035	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59,95' N	3° 30.35' W	Greenland Sea
Oat F455	*O. atlantica*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Area
Oat F459	*O. atlantica*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Osi F443	*O. similis*	St. 290, 100-150 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Osi F1052	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30,35' W	Greenland Sea
Osi F1068	*O. similis*	St. 1, 0-100 m; ARK 25-1	71° 23.91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Oat F932	*O. atlantica*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Oat F933	*O. atlantica*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F913	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F926	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F930	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F923	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Oat F934	*O. atlantica*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F919	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F920	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F911	*O. similis*	St. 57, 0-100 m; ARK 25-1	75° 0.98' N	0° 59.47' E	Greenland Sea
Osi F957	*O. similis*	St. 63, 0-50 m; ARK 25-1	74° 59.39' N	4° 50.07' E	Greenland Sea, close to Barents Sea
Oat F941	*O. atlantica*	St. 63, 0-50 m; ARK 25-1	74° 59.39' N	4° 50.07' E	Greenland Sea, close to Barents Sea

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Area
Oat F940	*O. atlantica*	St. 63, 0-50 m; ARK 25-1	74° 59.39' N	4° 50.07' E	Greenland Sea, close to Barents Sea
Osi F1019	*O. similis*	St. 24, 0-100 m; ARK 25-1	74° 59.94' N	8° 1.03' W	Greenland Sea
Osi F1053	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F936	*O. similis*	St. 63, 0-50 m; ARK 25-1	74° 59.39' N	4° 50.07' E	Greenland Sea, close to Barents Sea
Osi F948	*O. similis* (C5)	St. 63, 0-50 m; ARK 25-1	74° 59.39' N	4° 50.07' E	Greenland Sea, close to Barents Sea
Osi F953	*O. similis*	St. 63, 0-50 m; ARK 25-1	74° 59.39' N	4° 50.07' E	Greenland Sea, close to Barents Sea
Osi F954	*O. similis*	St. 63, 0-50 m; ARK 25-1	74° 59.39' N	4° 50.07' E	Greenland Sea, close to Barents Sea
Osi F998	*O. similis*	St. 74, 0-100 m; ARK 25-1	75° 0.06' N	11° 54.25' E	Norwegian Sea
Osi F1030	*O. similis*	St. 24, 0-100 m; ARK 25-1	74° 59.94' N	8° 1.03' W	Greenland Sea
Osi F1037	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1039	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1041	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1045	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1046	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1047	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1050	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Area
Osi F1054	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1058	*O. similis*	St. 1, 0-100 m; ARK 25-1	71° 23.91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Osi F1072	*O. similis*	St. 1, 0-100 m; ARK 25-1	71° 23.91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Osi F1074	*O. similis*	St. 1, 0-100 m; ARK 25-1	71° 23.91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Osi F1075	*O. similis*	St. 1, 0-100 m; ARK 25-1	71° 23.91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Osi F1211	*O. similis*	St. 308, 50-100 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Osi F1212	*O. similis*	St. 308, 50-100 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Osi F1216	*O. similis*	St. 308, 50-100 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Osi F1049	*O. similis*	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1057	*O. similis*	St. 1, 0-100 m; ARK 25-1	71° 23.91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Oat F450	*O. atlantica*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Oat F451	*O. atlantica*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Oat F453	*O. atlantica*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Area
Oat F454	O. atlantica	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Oat F458	O. atlantica	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Oat F460	O. atlantica	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Osi F1016	O. similis	St. 24, 0-100 m; ARK 25-1	74° 59.94' N	8° 1,03' W	Greenland Sea
Osi F1024	O. similis	St. 24, 0-100 m; ARK 25-1	74° 59.94' N	8° 1.03' W	Greenland Sea
Osi F1043	O. similis (C5)	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F1069	O. similis	St. 1, 0-100 m; ARK 25-1	71° 23.91' N	8° 26.48' W	Greenland Sea close to Jan Mayen (volcanic island)
Osi F442	O. similis	St. 290, 100-150 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Osi F428	O. similis	St. 308, 100-250 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Osi F441	O. similis	St. 290, 100-150 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Osi F1034	O. similis	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Oat F434	O. atlantica	St. 308, 100-250 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Osi F444	O. similis	St. 290, 100-150 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Osi F1044	O. similis	St. 34, 0-100 (200) m; ARK 25-1	74° 59.95' N	3° 30.35' W	Greenland Sea
Osi F440	O. similis	St. 290, 100-150 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Osi F445	O. similis	St. 290, 100-150 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Area
Oat F435	*O. atlantica*	St. 308, 100-250 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Oat F436	*O. atlantica*	St. 308, 100-250 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau
Oat F457	*O. atlantica*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea
Osi F431	*O. similis*	St. 290, 50-100 m; ARK 23-3	75° 6.37' N	137° 2.00' W	Canadian Basin/ Beauford Sea

The distribution of the haplotype "Osi ANT 1" is shown in table 7.1. The order of the individuals equates to the one in the neighbor joining tree (see figs. 26, 26.2).

Table 7.1 The distribution of the individuals of haplotype Osi ANT 1

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Water mass
Osi F1141	*O. similis*	St. 62, 50-100 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre
Osi F385	*O. similis*	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F1168	*O. similis*	St. 21, 100-150 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F1156	*O. similis*	St. 33, 0-50 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Osi F1106	*O. similis* (C5)	St. 85, 150-200 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F1161	*O. similis*	St. 21, 50-100 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F1135	*O. similis*	St. 62, 50-100 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Water mass
Osi F317	*O. similis*	St. 33, 100-150 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Osi F322	*O. similis*	St. 21, 0-50 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddel Gyre (Coastal Current?)
Osi F1149	*O. similis*	St. 39, 0-50 m; ANT 24-2	64° 29.44' S	2° 50.73' E	Weddell Gyre
Osi F1165	*O. similis*	St. 21, 50-100 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F1166	*O. similis*	St. 21, 50-100 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F1125	*O. similis*	St. 34, 50-100 m; ANT 24-2	62° 0.05' S	3° 0.20' E	Weddell Gyre
Osi F1126	*O. similis*	St. 34, 50-100 m; ANT 24-2	62° 0.05' S	3° 0.20' E	Weddell Gyre
Osi F1137	*O. similis*	St. 62, 50-100 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre
Osi F1163	*O. similis*	St. 21, 50-100 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F1136	*O. similis*	St. 62, 50-100 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre
Osi F1139	*O. similis*	St. 62, 50-100 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre
Osi F1140	*O. similis*	St. 62, 50-100 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre
Osi F1142	*O. similis*	St. 62, 50-100 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Wedell Gyre
Osi F1138	*O. similis*	St. 62, 50-100 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre
Osi F319	*O. similis*	St. 33, 100-150 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Osi F321	*O. similis*	St. 33, 100-150 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre

Osi F330	*O. similis*	St. 21, 0-50 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Label	**Morphotype**	**St. Nr., depth interval; expedition**	**Position Latitude**	**Position Longitude**	**Water mass**
Osi F1115	*O. similis*	St. 34, 0-50 m; ANT 24-2	62° 0.05' S	3° 0.20' E	Weddell Gyre
Osi F318	*O. similis*	St. 33, 100-150 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Osi F328	*O. similis*	St. 21, 0-50 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F349	*O. similis*	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F323	*O. similis*	St. 21, 0-50 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F338	*O. similis*	St. 21, 0-50 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F343	*O. similis*	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F346	*O. similis*	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F347	*O. similis*	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F348	*O. similis*	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F399	*O. similis*	St. 33, 50-100 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Osi F1123	*O. similis*	St. 34, 50-100 m; ANT 24-2	62° 0.05' S	3° 0.20' E	Weddell Gyre
58 b	*O. similis*	St. 58, 0-50 m; ANT 24-2	65° 0.48' S	0° 0.96' W	Weddell Gyre
62 B1	*O. similis*	St.62, 0-50 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre
Osi F307	*O. similis*	St. 34, 100-150 m; ANT 24-2	62° 0.05' S	3° 0.20' E	Weddell Gyre

Osi F310	*O. similis*	St. 34, 100-150 m; ANT 24-2	62° 0.05' S	3° 0.20' E	Weddell Gyre
Osi F320	*O. similis*	St. 33, 100-150 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Label	**Morphotype**	**St. Nr., depth interval; expedition**	**Position Latitude**	**Position Longitude**	**Water mass**
Osi F325	*O. similis*	St. 21, 0-50 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F344	*O. similis*	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F345	*O. similis*	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F370	*O. similis*	St. 33, 50-100 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Osi F371	*O. similis*	St. 33, 50-100 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Osi F373	*O. similis*	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F375	*O. similis*	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F376	*O. similis*	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F383	*O. similis*	St. 33, 100-150 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Osi F386	*O. similis*	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F387	*O. similis*	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F388	*O. similis*	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F398	*O. similis*	St. 33, 50-100 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Osi F403	*O. similis* (C5)	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone

Osi F405	*O. similis*	St. 39, 200-250 m; ANT 24-2	64° 29.44' S	2° 50.73' E	Weddell Gyre
Osi F410	*O. similis*	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Osi F412	*O. similis*	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
Label	**Morphotype**	**St. Nr., depth interval; expedition**	**Position Latitude**	**Position Longitude**	**Water mass**
Osi F378	*O. similis* (C5)	St. 21, 200-250 m; ANT 24-2	67° 56.10' S	2° 58.31' W	Weddell Gyre (Coastal Current?)
62 b	*O. similis*	St. 62, 0-50 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre
58 a	*O. similis*	St. 58, 0-50 m; ANT 24-2	65° 0.48' S	0° 0.96' W	Weddell Gyre
Osi F350	*O. similis*	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone

The distribution of the specimens of the haplotype "Osi ANT 2" in the water masses of the Southern Ocean is shown in table 7.2. The labels are in the same order as in the neighbor joining tree (see figs. 26, 26.2).

Table 7.2 The distribution of the individuals of haplotype Osi ANT 2

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Water mass
Osi F418	*O. similis*	St. 13, 50-100 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
Osi F1087	*O. similis*	St. 13, 100-150 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
13 A1	*O. similis*	St. 13, 0-50 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
13 B1	*O. similis*	St. 13, 0-50 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Water mass
13 a	*O. similis*	St. 13, 0-50 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
13 b	*O. similis*	St. 13, 0-50 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
Osi F420	*O. similis*	St. 13, 50-100 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Water mass
Osi F421	*O. similis*	St. 13, 50-100 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
Osi F423	*O. similis*	St. 13, 50-100 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
Osi F424	*O. similis*	St. 13, 50-100 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
Osi F425	*O. similis*	St. 13, 50-100 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
Osi F426	*O. similis*	St. 13, 50-100 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
Osi F1097	*O. similis*	St. 85, 0-50 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F1098	*O. similis*	St. 85, 0-50 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F1099	*O. similis*	St. 85, 0-50 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F1093	*O. similis*	St. 85, 0-50 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F1095	*O. similis*	St. 85, 0-50 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F1096	*O. similis*	St. 85, 0-50 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone
Osi F1094	*O. similis*	St. 85, 0-50 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Frontal Zone

Table 7.3 contains the detailed sampling information for the single individual of the haplotype "Osi ANT 3" (see figs. 26, 26.2).

Table 7.3 The distribution of the individuals of haplotype Osi ANT 3

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Water mass
Osi F1092	*O. similis*	St. 13, 100-150 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone

The distribution of the specimens from the haplotype "Osi Nort Sea/ Med. Sea" is shown in table 7.4. The order of the labels is according to the one in the neighbor joining tree (figs. 26, 26.3).

Table 7.4 The distribution of the individuals of haplotype Osi North Sea/ Med. Sea

Label	Morphotype	Station	Area
Osi F1175	*O. similis*	Villefranche Point B	Mediterranean Sea
Osi F1189	*O. similis*	St. 56; HE 302	North Sea
Osi F1177	*O. similis*	Villefranche Point B	Mediterranean Sea
Osi F1182	*O. similis*	Villefranche Point B	Mediterranean Sea
Osi F1183	*O. similis*	Villefranche Point B	Mediterranean Sea
Osi F1184	*O. similis*	St. 56; HE 302	North Sea
Osi F439	*O. similis*	close to Helgoland	North Sea
Osi F1176	*O. similis*	Villefranche Point B	Mediterranean Sea
Osi F1179	*O. similis*	Villefranche Point B	Mediterranean Sea

The detailed sampling information for the single individual of "Osi ARK 2" (see fig. 26, 26.3) is presented in table 7.5.

Table 7.5 The distribution of the individuals of haplotype Osi Ark 2

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Area
Osi F462	*O. similis*	St. 308, 0-50 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau

Table 7.6 contains the detailed sampling information for the single individual of the haplotype "Osi ARK 3" (see figs. 26, 26.3)

Table 7.6 The distribution of the individuals of haplotype Osi ARK 3

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Area
Osi F463	*O. similis*	St. 308, 0-50 m; ARK 23-3	77° 5.11' N	164° 9.03' W	Chukchi Plateau

As shown in table 7.7, the haplotype Osp (see figs. 26, 26.3) was only sampled at the permanent station in the List Basin.

Table 7.7 The distribution of the individuals of haplotype Osp

Label	Morphotype	Station	Area
Osp F1207	*Oithona sp.*	close to Sylt	North Sea
Osp F1201	*Oithona sp.*	close to Sylt	North Sea
Osp F1200	*Oithona sp.*	close to Sylt	North Sea
Osp F1202	*Oithona sp.*	close to Sylt	North Sea
Osp F1206	*Oithona sp.*	close to Sylt	North Sea
Osp F1208	*Oithona sp.*	close to Sylt	North Sea
Osp F1205	*Oithona sp.*	close to Sylt	North Sea
Osp F1204	*Oithona sp.*	close to Sylt	North Sea
Osp F1209	*Oithona sp.*	close to Sylt	North Sea
Osp F1203	*Oithona sp.*	close to Sylt	North Sea

The detailed distribution of the morpho- and haplotype Ofr (see figs. 26, 26.3) in the Southern Ocean is shown in table 7.8.

Table 7.8 The distribution of the individuals of haplotype Ofr

Label	Morphotype	St. Nr., depth interval; expedition	Position Latitude	Position Longitude	Water mass
Ofr F309	*O. frigida*	St. 64 200-250 m; ANT 24-2	62° 0.94' S	0° 4.31' W	Weddell Gyre

Ofr F315	*O. frigida*	St. 33 100-150 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Ofr F416	*O. frigida*	St. 13, 150-200 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Frontal Zone
Ofr F314	*O. frigida*	St. 64 200-250 m; ANT 24-2	62° 0.94' S	0° 4.31' W	Weddell Gyre
Ofr F365	*O. frigida*	St. 33, 50-100 m; ANT 24-2	62° 0.69' S	2° 56.49' W	Weddell Gyre
Ofr F384	*O. frigida (C5)*	St. 85, 100-150 m; ANT 24-2	52° 1.15' S	0° 0.19' E	Polar Front Zone
Ofr F396	*O. frigida*	St. 62, 150-200 m; ANT 24-2	62° 59.85' S	0° 0.68' E	Weddell Gyre
Osi F311	*O. frigida*	St. 34 100-150 m; ANT 24-2	62° 0.05' S	3° 0.20' E	Weddell Gyre
Ofr F413	*O. frigida*	St. 13, 150-200 m; ANT 24-2	52° 2.16' S	0° 0.99' W	Polar Front

Table 7.9 contains the sampling information on the single female of "Osi Med Sea" (see figs. 26, 26.3).

Table 7.9 The distribution of the individuals of haplotype Osi Med. Sea

Label	Morphotype	Station	Area
Osi F1180	*O. similis*	Villefranche Point B	Mediterranean Sea

All individuals of the haplotype "O. na" (see figs. 26, 26.3) were sampled at Helgoland Roads as shown in table 7.10.

Table 7.10 The distribution of the individuals of haplotype O na

Label	Morphotype	Station	Area
Ona 1199	*O. nana*	close to Helgoland	North Sea
Ona 1198	*O. nana*	close to Helgoland	North Sea
Ona 1197	*O. nana*	close to Helgoland	North Sea
Ona 1196	*O. nana*	close to Helgoland	North Sea
Ona 1193	*O. nana*	close to Helgoland	North Sea

Ona 1192	*O. nana*	close to Helgoland	North Sea
Ona F480	*O. nana*	close to Helgoland	North Sea
Ona F479	*O. nana*	close to Helgoland	North Sea
Ona F437	*O. nana*	close to Helgoland	North Sea
Ona F438	*O. nana*	close to Helgoland	North Sea

5. Discussion

This chapter first deals with the scarcity of information on males within this study. Then, the results on morphology and genetics of the examined specimens are discussed. Further attention will be paid to a potential correlation of the results from the Arctic and Southern Ocean with hydrographic conditions. Finally, the methodological problems of the methods within this study will be addressed.

5.1 A sex-skewed species

This study concentrates on adult females and several C5-stages of females that could be identified additionally. Males were not included in the investigation as they were not found in the samples. One reason for the absence of males is that the sampling was not done quantitatively as the individuals for the examinations were picked out under a binocular and transferred alive via a pipette into ethanol. This method offers the best chance to get non-destructed DNA, but it does not include all individuals in a given sample. Moreover, within the oithonid species, males are less frequent than females (e.g. Van Breemen 1903, Boxshall 1977, Hirst & Ward 2008). The chance to miss the few males is therefore quite large. Highly skewed sex-ratios for adults of *Oithona similis* were found in Loch Striven, Scotland: 0.18 (Marshall 1949) and off Plymouth, English Channel (Digby 1950), and in Scoresby Sound, Greenland a ratio of 0.06 was determined (Digby 1954). Nishida et al. (1977) also "rarely collected males" within Suruga Bay and adjacent waters of Japan.

The genus *Oithona* is one of the most sex-skewed genera of the epipelagic copepods (Hirst & Kiørboe 2002, Kiørboe 2006). The reasons for this fact are not clear. It might be most probable that males are much more preyed upon than females

(Hirst & Ward 2008). This is explained by the general behavior in the water column. *Oithona similis* is an ambush feeder that detects its prey hydromechanically (Svensen & Kiørboe 2000, Saiz et al. 2003). Ambush predators hang quietly in the water column while they slowly sink and scan their surroundings for motile prey to attack it (Maar et al. 2006). Thus, the active mate finding behavior of the males is especially dangerous when compared to the passive behavior of the females (Hirst & Ward 2008). As consequence of their movements, encounter rates with predators may increase and these make males more visible and hydromechanically detectable for predators (Hirst & Ward 2008). It is likely that searching for a mate increases the rate at which males are preyed upon (Hirst & Ward 2008). Hence, Hirst and Ward (2008) suggested that not physiological longevity might be the primary cause of the strong sex ration skew in adult *Oithona* but predation. According to Hirst and Ward (2008), CV males and adult males of *O. similis* showed the highest mortality rates of any developmental stages.

Sex with mating has several advantages (Kiørboe 2011). It is helpful in removing harmful mutations and in fighting against diseases (Kiørboe 2011). Furthermore, mating enhances the potential for sexual selection and "promotion of 'good genes'" (Kiørboe 2011). However, the challenge is that males and females need to meet one another in a three dimensional environment (Kiørboe 2011). In general, the females produce pheromones that are explored by the males and guide their way to the female (Kiørboe 2011). It is not clear why males that may only be able to fertilize a small division of the females they meet, spend such an enormous attempt in high and continuous swimming velocities that enhance their risk to be captured (Kiørboe, 2011). One possible explanation might be that the males compete for "high-quality young females" (Kiørboe 2011). Both genders of *Oithona similis* seem to mainly inhabit the same water layers (see Metz 1996). Thus, one reason for the low number of males compared to females might be that the demand of males is not that huge because the encounter rate between males and females is sufficient to guarantee the sustainment of the population.

In this study the morphological examinations of size, whole body form, rostrum structure and the outer setae of the exopodits of the swimming legs showed five different morphotypes: *Oithona frigida* (Southern Ocean), *O. similis* (Arctic Ocean, Mediterranean Sea, North Sea, Southern Ocean), *O. atlantica* (Arctic Ocean), *Oithona sp.* (North Sea) and *O. nana* (North Sea). This method agrees with Van Breemen 1903: "the best way to differentiate between *O. nana* and *O. similis* is using their size, their general body shape as well as the existence or missing of a beaked rostrum, the length of their antennae compared to the cephalotorax as well as the number and shape of the setae externae at outer branches of the swimming feets." *Oithona nana* has a narrow head that is truncated anteriorly in dorsal view (Gubanova & Altukhov 2007). Its rostrum is blunt and not visible dorsally (Gubanova & Altukhov 2007). The rostrum is also helpful to differentiate between *O. similis* and *O. frigida,* because the forehead of *O. frigida* has a rostrum that can be seen from dorsal view while the one of *O. similis* is directed ventrally and cannot be seen in the dorsal view (Rosendorn 1917).

In my opinion, body size is a supportive criterion, but cannot be used as the only one because it is variable. For example, specimens of *O. similis* appear to grow larger in the North Sea in comparison to individuals that inhabit the Mediterranean Sea (Van Breemen 1903). Furthermore, according to Dvoretsky and Dvoretsky (2009), shape and size of the body of *O. similis* from the Arctic Ocean can vary particularly. This is in accordance with Shuvalov (1980) who suggested that *O. similis* in the Arctic Ocean is a polytypic species with different "groups or subpopulations". Measured lengths of the prosoma of *O. similis* females ranged from 450 to 570 µm in the Barents Sea (Dvoretsky & Dvoretsky 2009). These differences might be explained by two generations with one from the fall of the previous year that contained the large females (Dvoretsky & Dvoretsky 2009). For the White Sea female prosoma ranges of 660 to 790 µm in spring and 750 to 880 µm in fall were found (Shuvalov 1965 in Dvoretsky & Dvoretsky 2009 a).

The genus *Oithona* is a difficult one for copepodologist because of the small species size which makes it very hard to dissect single limbs (Van Breemen 1903). Further

problems provide meager descriptions of new species (Van Breemen 1903). In consequence of such reduced descriptions, several *Oithona* species are attributed as *Oithona similis*. Giesbrecht (1893) e.g. suggested that *O. helgolandica*, *O. spinifrons* and *O. pygmaea* could eventually be synonyms for *O. similis*. According to Van Breemen (1903) and Bourne (1889), a further *Oithona* species that was found close to Plymouth by Bourne and described as *O. spinirostris,* is in fact *O. similis*. The rostrum of *O. similis* has a small and ventrally straightened beak that cannot be seen from dorsal (van Breemen 1903). It is necessary to turn individuals of *O. similis* onto their side otherwise it is difficult or even impossible to see the bended rostrum (Van Breemen 1903). The bended rostrum should be considered as important feature, additionally to other characteristics that hint on *O. similis* (Van Breemen 1903). An example for a problematic description is the one of Boeck (1865) for *O. pygmaea* (Van Breemen 1903). In the description of Boeck (1865), it is only clear that *O. pygmaea* does not have the pointed rostrum of *O. spinifrons* or *O. spinirostris,* but not that it does not have a beak like *O. similis* (Van Breemen 1903). The confusion about this species might be an explanation for the fact that it is supposed to be a cosmopolitan but might indeed be an accumulation of several species grouped under one name.

A special case within the genus *Oithona* is the species *O. helgolandica* Claus 1863 that was supposed to be synonymous with *O. plumifera* or *O. similis* by other researchers (Van Breemen 1903). Van Breemen (1903) disagreed and suggested that it might be the same species as *O. nana*. Giesbrecht (1893) assumed that *O. helgolandica* and *O. spinirostris* are separate species (Van Breemen 1903). However, Giesbrecht (1893) thought that *O. helgolandica* might be the same species as *O. similis* (van Breemen 1903). Shuvalov (1972) shared this opinion. If this was true, Claus would have described one of his new found species twice with two different names within three years (Van Breemen 1903). Thus, according to Van Breemen (1903) is seems to be very unlikely that in 1866 Claus recognized *O. spinirostris* but not *O. helgolandica* in the species he described new as *O. similis*.

Van Breemen (1903) explained in his thesis that *Oithona helgolandica* and *O. nana* are the same species. They share for example the characteristic of relatively short

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first antennae (Van Breemen 1903). According to Claus, the antennae of *O. helgolandica* hardly reach the end of the thorax (Van Breemen 1903). Giesbrecht (1893) as well as Van Breemen (1903) described the antennae for *O. nana* as even shorter, not reaching the backmost part of the third thoracal segment (van Breemen 1903). Either way, the short first antennae indicate another species than *O. similis* (Van Breemen 1903). Especially because of this characteristic, Giesbrecht questioned that these two species are actually identical (Van Breemen 1903). Van Breemen (1903) critically compared his results with older works. He concluded that Cleve (1900, 1902, 1903) described at least partly individuals of *Oithona nana* as *O. similis* within parts of the North Sea. In his own samples at the same stations and taken with the same meshes, Van Breemen (1903) only caught individuals of *O. nana*. Furthermore, Van Breemen (1903) suggested that it might be possible that Timm (1896) described individuals of *O. nana* as *O. similis* in the southern North Sea. Van Breemen (1903) argued that according to Timm (1896), the individuals of *O. similis* close to Norway are slighlty larger than the ones from the southern North Sea. This might also be a normal size variation. However, there is a synonymy problem with this species (Fernández-Severini & Hoffmeyer 2005). This is further stressed by the fact that in Argentinean waters, *Oithona similis* has been cited as *Oithona helgolandica* (Fernández-Severini & Hoffmeyer 2005) following Ramírez (1966, 1970 a, b).

5.3 Genetics

Oithona similis is supposed to be a cosmopolitan species (e.g. Atkinson 1998, Peterson & Keister 2003, Hansen et al. 2004). This is astonishing because of the very different environmental conditions that a species with worldwide distribution has to cope with. It is therefore questionable whether *O. similis* is a true cosmopolite. Genetic examinations are suitable to answer this question. Genetic studies on *O. similis* are however scarce. To resolve the question whether *O. similis* is a cosmopolitan species, the principle of DNA barcoding (Hebert et al. 2003 a) was applied to individuals collected in four geographically different investigation areas. Mt CO1 was chosen as genetic marker for this study as it can discriminate even the most closely related species and resolve evolutionary relationships among species within a genus or among some genera (Hill et al. 2001). Identification of species

using DNA barcoding is based on the observation that intraspecific genetic divergence is usually lower than interspecific divergence (Meyer & Paulay 2005). Furthermore, DNA barcoding is useful to identify cryptic species in accordance with a critical taxonomic analysis (Groenenberg et al. 2009).

With sequencing, different haplotypes were found in the morphologically identical groups of *Oithona similis*: three groups in the Arctic Ocean, three groups in the Southern Ocean, one group in the North Sea and two groups in the Mediterranean Sea, of which one group was also found in the North Sea. In addition to the *Oithona similis* groups, three other copepod species groups were identified morphologically as well as via sequencing: *O. frigida* in the Southern Ocean, O. *nana* and *Oithona sp.* in the North Sea.

In this study, barcoding revealed indeed that *Oithona similis* is not a cosmopolitan species but a conglomerate of cryptic species. Within each of the four examination areas at least one cryptic species was found. With one exception, all of the haplotypes found in this study occur exclusively either in the North Sea, the Mediterranean Sea, the Arctic Ocean or the Southern Ocean. The exception is a species that was found at different places in the North Sea and within the Mediterranean Sea. Conglomerates of cryptic species are not unusual for copepods (e.g. Boileau 1991, Cervelli et al. 1995, Ganz & Burton 1995, Reid 1998). Individuals of the Mediterranean Sea sampled close to Nice were included in this work because the individuals that Claus used in 1886 for the first description of the new species *Oithona similis* also originated from there. Therefore, those samples offered the chance to find the *O. similis* that was first described by Claus in 1866 and compare it to potentially other species.

A general problem of this study is that the number of individuals in some of the found haplotypes is very small or they even consist of just one individual. This is a result of the whole working process from sampling to measuring. The number of individuals that were sampled largely differed between all sampling stations. Depending on the number of sampled individuals some of them were fixed in formaldehyde for morphological examinations. These animals could not be used for genetical

examinations anymore. Furthermore, many of the sampled individuals were often not in such a good condition and were therefore excluded from the genetic samples. A further problem was that not every single individual examined for the genetic work resulted in useful DNA. One single individual of course is not enough for a significant result but the findings may be used as a good indication.

For the Southern Ocean, within the nominal *Oithona similis*, three different haplotypes were found in this study: "Osi ANT 1", "Osi ANT 2" and "Osi ANT 3". "Osi ANT 1" is represented by 72 females and was found at the following stations of the expedition ANT XXIV-2: St. 21 (0-50 m, 50-100 m, 100-150 m, 200-250 m), St. 33 (0-50 m, 50-100 m, 100-150 m), St. 34 (0-50 m, 50-100 m, 100-150 m), St. 39 (0-50 m, 200-250 m), St. 58 (0-50 m), St. 62 (0-50 m, 50-100 m), St. 85 (100-150 m, 150-200 m). "Osi ANT 2" includes 19 copepods from the Southern Ocean and was only found at two stations namely at station 13 from 0-150 m depth and at station 85 within the upper 50 m of the water column. "Osi ANT 3" consists of one individual that was caught at station 13 between a water depth of 100 and 150 m. The genetical differences between the haplotypes "Osi ANT 1" and "Osi ANT 2" are considerable as well as for "Osi ANT 1" and "Osi Ant 3". The individuals from groups "Osi ANT 2" and "Osi ANT 3" are genetically closer.

During the expedition ANT XXIV-2, station 85 (52° 1.15´S; 0° 0.19 E) was done as a repetition of station 13 (52° 2.16'S; 0° 0.99`W). The sampling time between these two stations was an interval of 52 days. During this period, the temperature of the upper layer increased seasonally (pers. comm. V. Strass). Furthermore, the characteristics of the water masses in the deeper layers changed. This cannot be due to a seasonal signal (pers. comm. V. Strass). One possible explanation is a meridional shift of the Southern Ocean Polar Front meander. The stations 13 and 85 were localized at its northern flank. However, this explanation is only partially coherent. Temperature and salinity below the upper layer had changed reversely than would have been expected solely caused by a front shift. Hence, advective influences seem to be included as well (pers. comm. V. Strass). The appearance of one species in the upper 50 m (st. 85) and accordingly the upper 100 m (st 13) and the other species below 100 m agrees quite well with the depth of the upper layer (pers. comm. V. Strass).

Zooplankton species are able to find the circumstances they need to be successful in competing with other species (Longhurst 1985). In general, co-ocurring species ought to vary in the allocation of resources or otherwise separate seasonally (Halsband & Hirche 2001). Thus, it is possible that haplotype "Osi ANT 1" and haplotype "Osi ANT 2" both serve as indicators of different water masses and hydrological conditions (Raymont 1980). The fact that *Oithona* species live in diverse depth layers (Nishida & Marumo 1982) was also reported for the Eastern Mediterranean Sea at the basin level (Mazzocchi unpublished data in Mazzocchi & Ribera d'Alcalà 1995). Mazzocchi and Ribera d'Alcalà (1995) always observed differences in numbers of the distinct species when they found overlapping seasonal peaks of *O. nana, O. similis* and *O. plumifera.* The authors therefore suggested that ecological distinction exists among congener species.

One single female of haplotype "Osi ANT 2" was caught at station 13 between 100 and 150 m water depth. It cannot be said whether this female was caught at 100 m water depth or at 150 m, and if it was able to survive and reproduce below 100 m. It is therefore possible that the species distribution is the same at both stations. Both of the stations are within the PFZ, while the other seven stations, where the haptotype "Osi ANT 1" was caught, are located in the Weddell Gyre. Hydrographical data measured by Strass et al. during ANT XXIV-2 show a clear difference between the stations in the Polar Frontal Zone and the ones in the Weddell Gyre (figs. 27, 28). At stations 13 and 85, higher potential temperature and lower salinity values were measured than at the stations in the Weddell Gyre (figs. 27, 28).
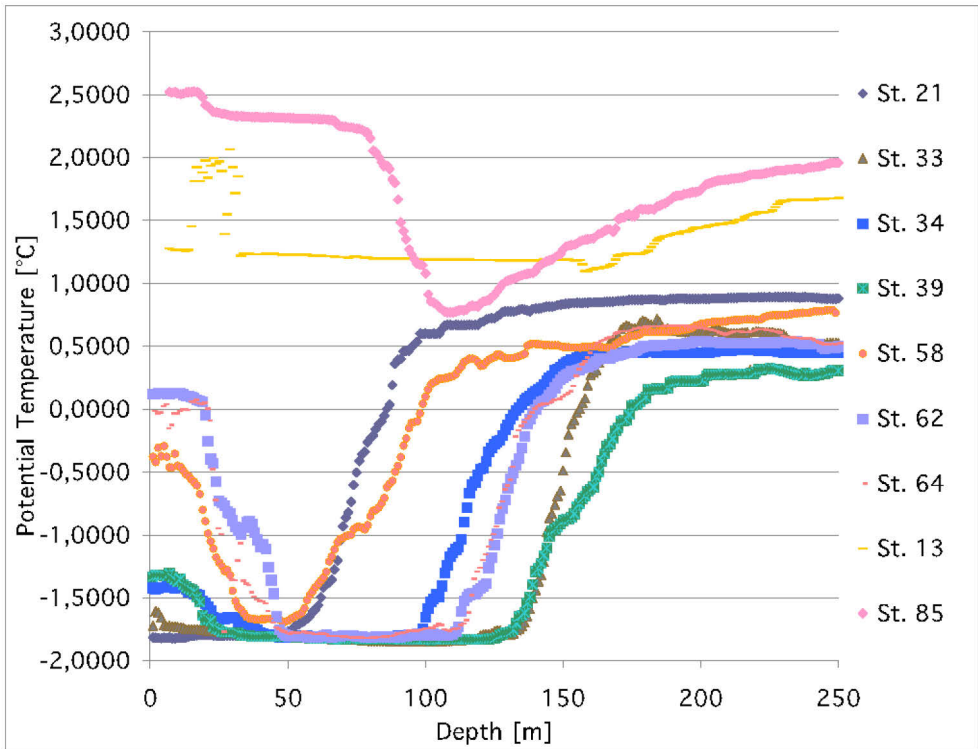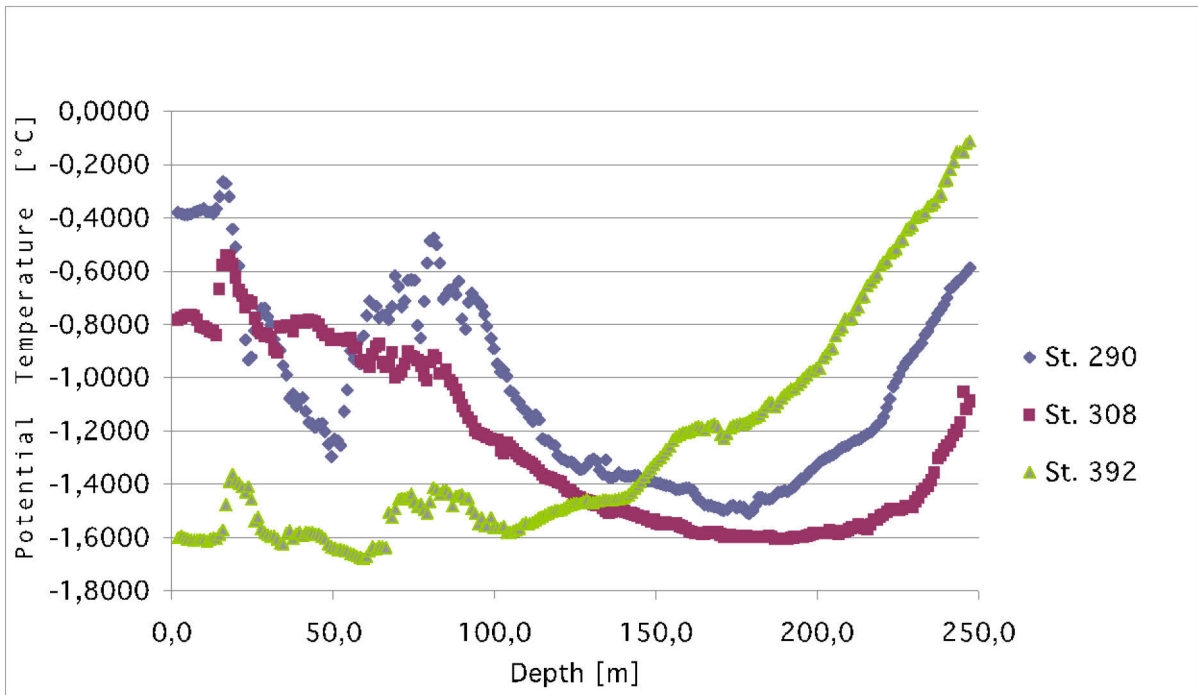
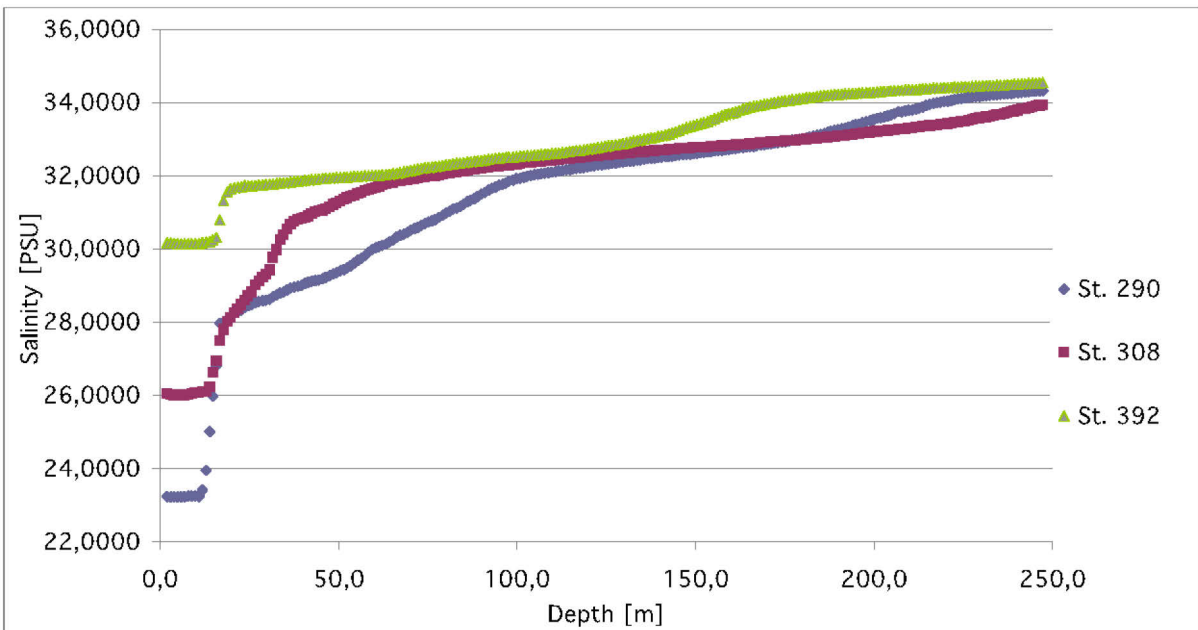Fig. 27 CTD-data of the potential temperature [°C] measured at the stations between 0-250 m during the expedition ANT XXIV-2 in the Southern Ocean (Strass 2010)
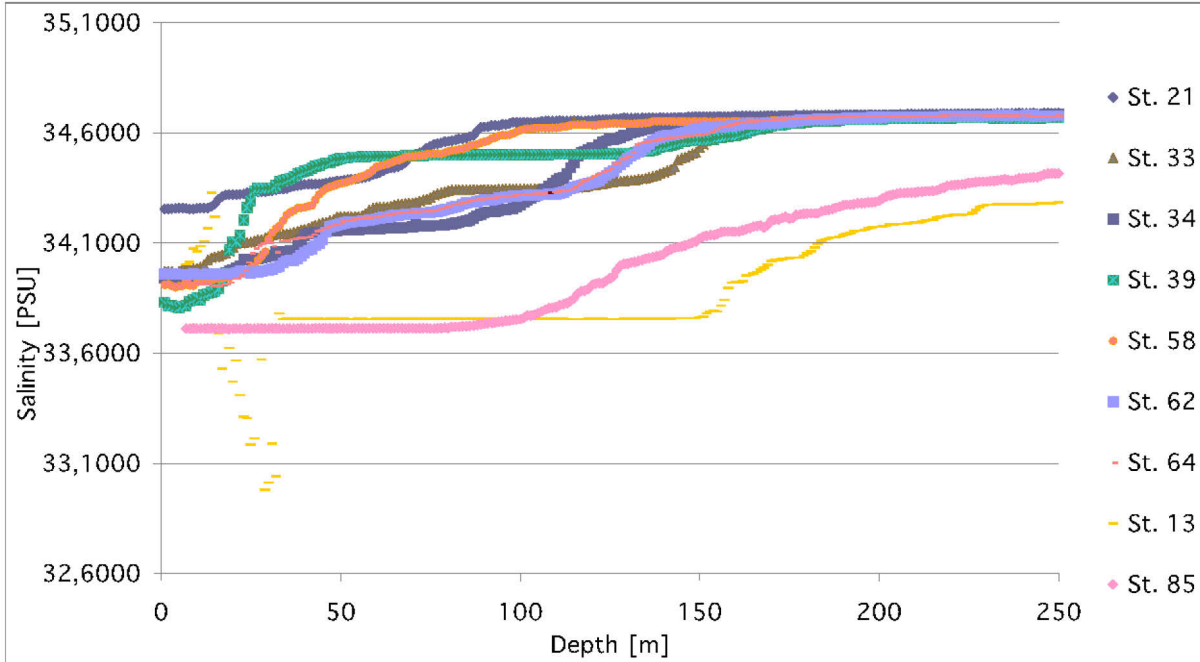
Fig. 28 CTD-data of the salinity [PSU] measured at the stations between 0-250 m during the expedition ANT XXIV-2 in the Southern Ocean (Strass 2010)

Hence, the haplotype "Osi ANT 1" could be more widespread, flexible and common within the Southern Ocean than "Osi ANT 2". The haplotype "Osi ANT 3" is represented by a single female that was sampled at station 13 between 100 and 150 m. This could indicate a third haplotype of *O. similis* that lives in the area of the Polar Front. This third haplotype derives from the same branch in the neighbour joining tree as haplotype "Osi ANT 2", indicating a close relationship between these two haplotypes from the PFZ.

The PFZ of the Southern Ocean is characterized by high physical and biological variability (Bernard & Froneman 2005). Meanders (e.g. Legeckis 1977, Lutjeharms 1990, Ansorge et al. 1999) and eddies (Bryden 1983, Ansorge et al. 1999, Froneman et al. 1999) are features of the two main fronts that are bounding the PFZ: the Subantarctic Front to the north and the Antarctic Polar Front to the south (Bernard & Froneman 2005). Plankton transfer via the major frontal systems is therefore facilitated (Bernard & Froneman 2005). Consequently, the zooplankton communities within the PFZ are very uneven and commonly include species from diverse origins that cover sub-tropic, sub-Antarctic and Antarctic species (Ansorge et al. 1999, Froneman et al. 1999, Pakhomov & Froneman 1999). This might explain the appearance of the different haplotypes at the stations in the PFZ.

In the Arctic Ocean, three haplotypes were detected within the nominal *Oithona similis*. Haplotypes "Osi ARK 2" and "Osi ARK 3" are each represented by a single female. These females were sampled in the upper 50 m of the water column at one station at the Chukchi Plateau. Their position in the neighbor joining tree indicates a close relationship between these two species groups. A further individual belonging to haplotype "Osi ARK 1" was sampled at the same station within the same water depth. The haplotype "Osi ARK 1" derives from the same branch as the individuals of the haplotype "Osi ANT 1", but the distance between their branch-offs are quite huge. This also applies to the distance between this group and the two other groups from the Arctic Ocean. It can be assured that at least two different cryptic *O. similis* species occur in that region. Thus, all three *O. similis* haplotypes are present at this station.

Hydrographical data measured by Rabe and Wisotzki (2010) during the expedition ANT XXIII-6 in the Arctic Ocean (figs. 29, 30) show no clear difference between the two stations in the Canada Basin and station 308 above the Chukchi Plateau. At station 290, the lowest temperature and salinity values were measured on average and the highest were measured at station 392. The potential temperature and salinity of station 308 ranges in between the data of the two other stations (figs. 29, 30). However, they are closer to the data of station 290 (for stations locations see section Material & Methods).

The occurrence of the two other haplotypes of *O. similis* above the Chukchi Plateau in 0-50 m water depth might be explained by their preference of low temperature and salinity found at this station (see figs. 29, 30). For the depth interval 0-50 m of station 290 in the Canada Basin, where even lower temperatures and salinity values are recorded by Rabe and Wisotzki (2010; figs. 29, 30), I have no CO1 sequence data of *Oithona* individuals. It might therefore be possible that these *Oithona* species could have been found at this station as well. This may be indicated by the absence of these haplotypes at station 392 where higher salinity values and temperatures occurred.

The two Sea Mountains forming the Chukchi Plateau extend 400 km in north-south and 250 km in east-west directions (Jinping et al. 2005). A basin with connections to the Canada Basin via three shallower valleys is located inside the Chukchi Plateau and has a maximum depth of 2100 m (Jinping et al. 2005). As a result, the deep water of the Chukchi Plateau is less exchangeable with the water outside (Jinping et al. 2005). Over the Chukchi Plateau in 30-40 m to below 100 m depth, waters seem to have Pacific origin and might have been reworked in the Chukchi Sea (Macdonald et al. 2002). This plateau has a complicated topography influencing the water that flows around it (Jinping et al. 2005). This is reflected in dynamical and complex temperature and salinity patterns (Jinping et al. 2005). Possibly these *Oithona* species are not found at the surrounding waters of the Canada Basin. This might be supported by flow and water exchange restriction through the complicated bottom topography of the Chukchi Plateau (Jinping et al. 2005).
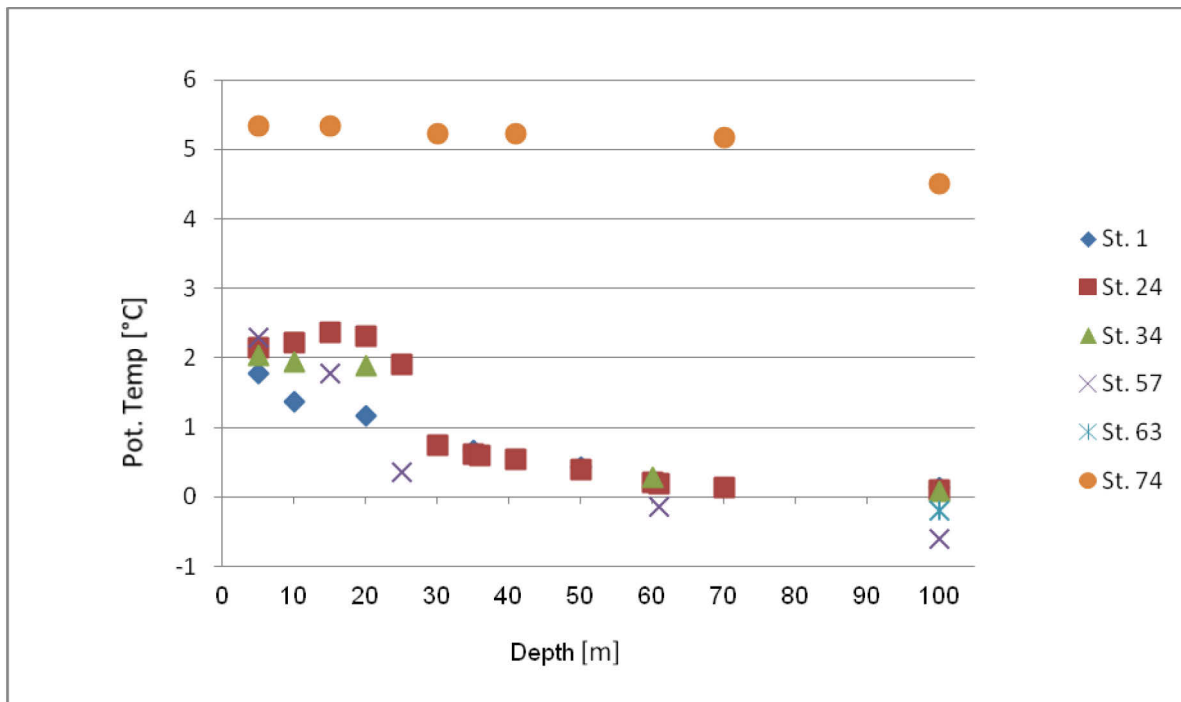
Fig. 29 CTD-data of the potential temperature [°C] measured at the stations between 0-250 m during the expedition ARK XXIII-3 (Rabe & Wisotzki 2010)

Fig. 30 CTD-data of the salinity [PSU] measured at the stations between 0-250 m during the expedition ARK XXIII-3 (Rabe & Wisotzki 2010)

The 88 individuals from group "Osi ARK 1" were sampled at all three stations of the expedition ARK XXIII-3 as well as at all six stations of the second expedition in the Arctic Ocean ARK XXIV-1. The preliminary CTD data on the potential temperature

and salinity for the stations 1, 24, 34, 57 and 63 of the expedition ARK XXV-1 mearured by Budeus et al. do not show any clear differences while station 74 has much higher values (about 3°C) for the potential temperature and also the highest salinity (figs. 31, 32). The fact that "Osi ARK1" was found at all these stations in the upper water layer shows that it is widely distributed within the Arctic Ocean and quite flexible concerning its range for the water temperature and salinity (see figs. 29-32).

Fig 31 CTD data of the potential temperature [°C] measured at the stations between 0-100 m during the expedition ARK XXV-1 (preliminary results from Budeus et al.)
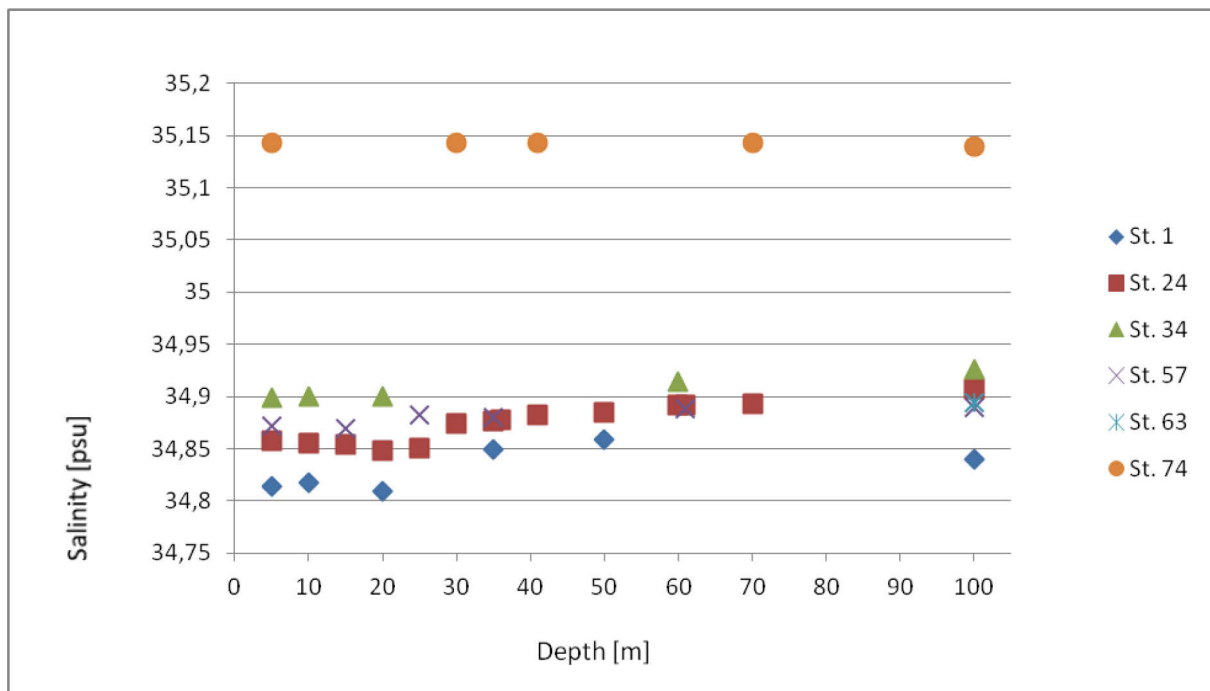
Fig 32 CTD data of the salinity [psu] measured at the stations between 0-100 m during the expedition ARK XXV-1 (preliminary results from Budeus et al.)

The CO1- sequences of the *Oithona similis* haplotype with individuals from two different places in the North Sea (one female from each sampling station) and the Mediterranean Sea (six individuals) differ from the sequences of the species sampled at the other regions. The fact that the same haplotype was found at different places in the North Sea as well as in the Mediterranean Sea shows that this species is widely distributed and might be quite flexible concerning environmental conditions. More individuals from the North Sea would need to be examined to confirm this status as well as to investigate whether this area is inhabited by more than one cryptic *O. similis* species. It is also possible that species of the genus *Oithona* are advected into the southern North Sea with Atlantic water as described for two congeners of *Centropages* (see Halsband & Hirche 2001 and references within).

A further haplotype of *O. similis* was sampled in the Mediterranean Sea. However, from the genetic aspect, the haplotypes found in that area are very different. The second Mediterranean one is closer to the *O. frigida* haplotype than to any other *O. similis* haplotype. This group is represented by one female. Unfortunately, it is not possible to say if one or even none of these two haplotypes represents the original *O.*

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similis that was first described by Claus in 1866 for this area, since a comparison with his material is not possible. However, more individuals from the Mediterranean Sea would help to get a better idea.

In total eight different haplotypes of *Oithona similis* were found via CO1 sequencing in this study. Except the one group with individuals from the North Sea as well as from the Mediterranean Sea, none of these groups was present at more than one of the sampling areas. In addition to the number of haplotypes, this clearly shows that *O. similis* is not a cosmopolitan but a conglomerate of cryptic species, which confirms hypothesis 1 of this study.

Three further haplotypes were identified*: O. frigida* (O fr.) in the Southern Ocean, *O. nana* (O. na) in the North Sea close to the island of Helgoland, and *O. sp*. in the North Sea close to the island of Sylt. The samples from the List Basin did not contain any individuals of *O. similis*, although it has been described to be frequent in this area (Kraefft 1910, Lücke 1912, Künne 1952). The *Oithona nana* haplotype was chosen as the basis of the neighbor joining tree because the relationship between *O. similis* and *O. nana* is not as close as it is between the other species. It was even supposed to regard *O. nana* as "the type of a separate, through nearly allied genus, for which the name *Oithonina* may be proposed" (Sars 1918). The genus name *Oithonina* was adapted by authors, for example, Wilson (1932, 1942) and Fagetti (1962). But the majority refers to it as a member of the genus *Oithona* (e.g. Rosendorn 1917, Kiefer 1929, Grice 1960).

The *Oithona frigida* group consists of eight individuals that were sampled at five different stations during the expedition ANT XXIV-2: st. 13 (150-200 m), st. 33 (50-100 m, 100-150 m), st. 34 (100-150 m), st. 64 (200-250 m), st. 85 (100-150 m). Except at station 33, all of these individuals were sampled between 100-250 m water depths. Mostly *Oithona frigida* and *O. similis* showed a distinct distribution in the water column with *O. similis* in the upper part (Hopkins 1985, Hopkins & Torres 1988, Metz 1995). This is not supported by the results of this study where both species were found together at most of the stations where *O. frigida* was sampled. However, overall, only a few individuals of *O. frigida* were found within this study that

concentrated on the main distribution area of *O. similis* (0-250 m water depth). Thus, if *O. frigida* would also prefer these water depths, much more individuals of this species would have been sampled through the expedition ANT XXIV-2. The haplotype *Oithona sp.* was only found close to the island of Sylt. It showed the closest genetic relationship with *O. frigida* and the second *O. similis* haplotype from the Mediterranean Sea.

5.4 Relation of genetics and morphology

In addition to the individuals that were morphologically described as *O. similis* prior to sequencing, four other morphotypes were included in this study: *O. atlantica*, *O. frigida*, *O. nana* and *Oithona* sp. The morphological identification of 19 individuals as *O. atlantica* in group "Osi ARK 1" cannot be adhered and most likely is a variation within this *O. similis* haplotype. Another possible explanation would be that *O. atlantica* is not an own species, but only a variation of the species *O. similis*. However, it is not possible to prove or disprove this theory by the means of the present study. Morphological differences regarding the appendages of the swimming legs of *Oithona frigida* and *O. similis* were obvious according to literature (e.g. Nishida 1985, Giesbrecht 1902). The morphological differences between these two species were clearly reflected in the results of the CO1 sequences, as these haplotypes are each located on one of the two different main branches. *Oithona frigida* females were found within the PFZ as well as in the Weddell Gyre. Thus, this species seems to be widely distributed within the Southern Ocean. The differences reflected in the appendage structures of the swimming legs were also obvious between *Oithona similis* and *O. nana.* Another haplotype named *Oithona* sp. shares the swimming leg appendage structure with *O. nana,* but has a bended rostrum like *O. similis*. The differentiation between these species is also clearly reflected in their position in the neighbour joining tree as *Oithona sp.* is located on the same branch as *O. frigida*. This confirms hypothesis 3, since *O. similis* and other *Oithona* species inhabiting the investigation areas can clearly be differentiated morphologically and genetically.

The single individual from "Osi ARK 1" that was sampled at station 308 in the upper 50 m of the water column was according to its appendages of the swimming legs

morphologically described as *O. atlantica* (Nishida et al. 1977). Further 18 individuals of this group shared this leg structure as well (sampled at the ARK XXIII-3 stations 290, 50-100 m, 308, 100-250 m, 392, 0-150 m and the ARK XXV-1 stations 57, 0-100 m; 63, 0-100 m). However, this was not the case for the other 79 individuals of this haplotype. They all shared the appendage structure described for *O. similis*. Thus, this might be just a morphological variation within this haplotype and it is not possible to differentiate between *O. similis* and *O. atlantica* by only concentrating on the appendage structure of the swimming legs.

A further haplotype of *Oithona similis* was sampled in the Mediterranean Sea. It also shares the appendages structure of the swimming legs of *O. similis*. Overall, almost no morphological differences were found within and between regions for individuals of the *Oithona similis* species groups from the Southern Ocean, the Arctic Ocean, the North Sea and the Mediterranean Sea. Exceptions are the individuals from the Arctic Ocean that were described as *Oithona atlantica*. Such differences do probably not exist despite the genetic divergence described above. This would not be surprising, as within the Crustacea most genetic analysis of species boundaries confirm the existence of cryptic species. Some of these are distinguished by surprisingly large genetic differences given their morphological similarity (e.g. Palumbi & Benzie 1991, Bucklin et al. 1995, Knowlton & Weight 1998, Sarver et al. 1998). Large genetic differences in phenotypically similar species could be explained by a rapid rate of molecular evolution or a slow rate of morphological divergence (Todaro et al. 1996). One aim of this study was to examine hypothesis 2: "possibly existing cryptic species in the nominal *O. similis* either show no morphological differences or only very slight ones that make it impossible to differentiate between them morphologically." Since the individuals that were described as *Oithona atlantica* prior to sequencing do not form an own haplotype, and as no other morphological differences within the *Oithona similis* individuals were found, hypothesis 2 can be confirmed at least concerning the examined morphological characters.

The distances in the neighbor joining tree support the conclusion that at least the two *Oithona similis* clusters of the Southern Ocean are reproductively incompatible. Bucklin et al. (1995) suggest that for copepods and other crustaceans reproductive

isolation may not require extensive morphological divergence. Hence, physiological, chromosomal and cytonuclear incompatibilities may be involved (Lee 2000, Willet & Burton 2001, Grishanin et al. 2006) as well as biological and behavioral ones. This is supported by other studies (e.g. Rocha-Olivares et al. 2001, Lee & Frost 2002, Thum & Harrison 2009). The development of specific subspecies can have other reasons like different biological niches. The phenomenon of the persistence of a standard morphology over vast periods of time during which much environmental change has taken place in spite of reproductive isolation is called morphological stasis (Wake et al. 1983). Reproductive isolation between genetically proximate and morphologically indistinguishable species indicates that morphological stasis reflects cryptic speciation within the copepod *Eurytemora affinis* (Lee & Frost 2002). This is reported for cyclopoid copepods (Dodson et al. 2003) and could even be common in many other free-living copepods (see Lee & Frost 2002 and references within, Dodson et al. 2003, Edmands & Harrison 2003). Despite or in addition to morphological stasis, cryptic species that do not show any morphological differences are distinguished by nonvisual mating signals (Bickford et al. 2006) such as chemical or hydrological signals.

In accordance with the results of the present study, detailed morphological studies (Lee & Frost 2002, Dodson et al. 2003) did also not detect any differences among genetically divergent and reproductively isolated lineages of copepods. Such observations indicate that copepod speciation can occur with little or no morphological change (Thum & Harrison 2009). Thum and Harrison (2009) state that rather slow morphological relative to molecular evolution may often occur with little or no morphological change in copepods. If copepod speciation indeed involves mechanisms that do not require morphological divergence, cryptic species may be the norm (Thum & Harrison 2009) or at least far more common than previously assumed for copepods (Lee & Frost 2002). Species estimates based on morphological differences may therefore drastically underestimate the true species diversity of copepods (Thum & Harrison 2009). However, morphology is only one small part of genetic expression. Physiology, behavior and feeding are a further expression of genetics. Hence, morphological changes can be the result of genetical ones but this is not always the case.

The outer appearance of a species does not always reflect genetical changes, morphological differences do therefore probably not exist despite genetic divergence (Thum & Harrison 2009) in the investigated *Oithona similis* species. However, Rocha-Olivares et al. (2001) e.g. have revealed morphological differences among genetically different lineages of harpacticoids that were previously considered a single copepod species. The morphological criteria that were used in this study might need additional factors to distinguish among the *Oithona* species. This is supported by the fact that some of the individuals belonging to the *O. similis* haplotype "Osi ARK 1" had the appendage structure that is attributed to *O. atlantica*. Another fact supporting this is that the two species *O. nana* and *Oithona sp.* have the same appendage structure at the exopods of their swimming legs, but differ in the structure of their rostrum. However, morphological differentiations at the swimming legs one to four were the only characters that could, besides the whole body structure, size and rostrum shape, be used for a quick species identification of the individuals that were sampled in this study. When using more subtle differences as criteria for the separation of copepod species, however, intraspecific variability has also to be considered (Montiel- Martínez et al. 2008).

5.5. Uncertainties

To relate genetic and morphological differences, it would be ideal to study DNA and morphology of the same specimen. In the present study, however, the whole animals were needed for DNA extraction. Thus, a future morphological study that concentrates on all structures of the individuals could only rely on individuals from the same station and depth. The problem is that we cannot rule out an overlap between the distributions of the different cryptic species. Hence, by coincidence a specimen of another cryptic species and not of the haplotype of interest could be described in a following morphological study. Morphological variation that might be found, could either correlate with the observed genetic differentiation or simply reflect phenotypic plasticity (Baker et al. 2007). Consequently, work on this small *Oithona* species as on other small animals, would benefit of a non-destructive DNA sampling technique that allows preserving the link between species morphology and DNA sequences (Ekrem & Willassen 2004). Quick high resolution photography and cinematography of the

whole body or body parts might be a helpful tool to determine the morphology of an individual haplotype. It is however not as precise as morphological work including the dissection of body parts. These body parts should additionally be photographed and drawn.

5.6 Flexibility of *Oithona similis*

Cyclopoids seem to be generalists as they can survive in a broad range of environmental circumstance caused by a narrow specialization (Paffenhöfer 1993). Species of the genus *Oithona* are successful colonizers of the Liguirian Sea and other parts of the Mediterraneas Sea in late autumn (Licandro & Icardi 2009). This might be possible because of their ability to survive and reproduce in the notably oligotrophic waters that are characteristic for this season (Licandro & Icardi 2009). *Oithona similis* is supposed to be extremely tolerant concerning diverse environmental conditions (Gallienne & Robins 2001). According to Dvoretsky and Dvoretsky (2009), differences within the morphological characteristics of adults, such as the prosome length of *O. similis*, are the result of the integrated effect of a series of changeable environmental variables including temperature, salinity and food levels during the development of the copepods. For individuals of *O. similis* in the Labrodor Sea, no relationship was found relating to water mass variability (Head et al. 2003). This is in contrast to descriptions of Richter (1994) and Gislason and Astthorson (2004). These authors characterize *O. similis* as a cold adapted species that occurs in highest numbers in the Greenland Sea and in cold waters in the region of Iceland. This is supported by a study of Blachowiak-Samolyk et al. (2008 a) who found the highest abundances of this species within ice-covered areas of Arctic water masses in the Barents Sea.

It would be very interesting to test the flexibility of *Oithona* individuals among several generations at different environmental conditions. However, this is problematic to implement as egg carrying females are needed. Otherwise successful mating has to take place. It cannot be ruled out that sampled males and females belong to different haplotypes that should not be mixed or also might not be able to reproduce successfully. It is also not clear whether males of the oithonids are less abundant than females due to predation or due to lower demand. The latter implies at least

only very few males within the offspring of one female or even none. Thus, the experiment might possibly stop after one generation due to a lack of males or due to unsuccessful reproduction. Furthermore such an experiment could only be used as implication owing to a quite small number of individuals that would be involved. A study of Ward and Hirst (2007) showed a range of 6 to 31 eggs per sack within *Oithona similis*. The offspring would have to be divided into groups to test the different environmental conditions and each group would at least need one surviving male. The best way to have environmental conditions close to nature would be a mesocosm, but it would be very difficult if not impossible to find such small specimens within a mesocosm. Such experiments are therefore very challenging and time consuming but should be worth the effort.

6. Conclusions and Perspectives

This study clearly shows that *Oithona similis* is not a truly cosmopolitan species, but a conglomerate of several cryptic species. Due to their clonal matrilineal transmission, mitochondrial traits are not directly linked to reproductive isolation and speciation events (Avise 1994). Hence, mt DNA sequence variation cannot be the sole basis to delimit or define species (Hill et al. 2001). Within copepods, the mt DNA gene seems to change rapidly (Burton et al. 2007). However, according to Hill et al. (2001), sequence variation in this gene is a diagnostic stable and accurate indicator for species identity (Hill et al. 2001). Consequently, such molecular data are useful for taxonomic identification and can be used as uniform standards of species' identification together with morphological, morphometric and ecological characters (Hill et al. 2001), geographic range description and ecological information (Bucklin et al. 2003). DNA barcoding can discover species by flagging cryptic ones, but more data than CO1 sequences are necessary for describing a new species (Radulovici et al. 2009). A new copepod species was, for example, determined by Ueda and Bucklin (2006). Their studies were induced by ecological information. After a closer examination, the authors found morphological traits that could separate a single species in two. This species level of divergence was confirmed by sequences of the mitochondrial cytochrome oxidase and the 16S ribosomal genes (Mc Magnus & Katz 2009). Such findings lead to the conclusion that in our case further examinations of

Oithona similis individuals from our chosen study areas are needed to decide whether the different clusters represent distinct species.

Cryptic species might differ in temporal and spatial patterns of distribution and abundance and in reproductive biology (cf. Bucklin et al. 1998). This implies the needed ability to distinguish the species at all life stages (cf. Bucklin et al. 1998). It is possible, for example, that the two cryptic species in our investigation areas may partition oceanographic habitats by depth or water mass preferences (Goetze 2003). If this is the case, some level of niche separation might occur (Bucklin et al. 2001, Mc Gillicuddy & Bucklin 2002). It is also possible that an overlap instead of niche preferences occurs. This could especially be possible for the cryptic species in the Arctic Ocean that were both found at one station in the upper 50 m of the water column. If the latter holds true, remains unclear, as this hypothesis is based on only two specimens.

If *Oithona similis* represents different species in the investigation areas, fundamental aspects of their geographic distribution, population ecology and life history should be re-examined as such published results may represent a species group rather than a single species. Thus, species could not be differentiated and would be mixed up. The species in that group may differ in temporal and spatial patterns of distribution and abundance, and in reproductive biology (cf. Bucklin et al. 1998). A failure to recognize such cryptic species would hamper studies of ecological and evolutionary processes in the sea (cf. Knowlton 1993, Castro-Longoria et al. 2003), as well as on marine bioinvasions (Bucciarelli et al. 2002). However, it is very complex and time consuming to verify the existence of such cryptic species complexes, as genetical, morphological and ecological investigations as well as reproductive isolation breeding trials would be essential (e.g. Lee 2000, Dodson et al. 2003). Hence, the possible existence of cryptic species should be kept in mind for future studies on *O. similis*.

If a species complex exists, every single *Oithona* species could have very different ecological requirements and therefore influence the system individually. Consequently, mixtures of unrecognized cryptic species could seriously confound

interpretations of present results (Knowlton 1993). There are for example still not many studies concerning the biology of small zooplankton species that are key organisms in the Mediterranean Sea (Licandro & Icardi 2000). More investigations dealing with their life cycles, behavior and physiological preferences will help to get a better understanding of their success in the pelagic system and to estimate their secondary production that is accessible for higher trophic levels (Licandro & Icardi 2009). Avoiding confusion caused by overlooked cryptic species is particularly important for abundant species (Knowlton 1993) like *O. similis*. This should be considered, although for the whole ecosystem the impact of one omnivorous ubiquitous species that is dominant and several cryptic species that are very stenoecious, might possibly be the same. Many complexes of sibling species offer the chance to test current evolutionary theories in ecology and behavioral biology (Knowlton 1993). There is an enormous difference in terms of evolutionary potential between a circumtropical species and a complex of many more geographically limited ones (Knowlton 1986). Furthermore, such information would enhance our understanding of the processes of speciation (Knowlton 1986). A study dealing with all these aspects for *O. similis* would be worth the effort.

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8 Appendix

Appendix Figure 1 Partial Sequences of 57 indiviuals of the neighbor-joining tree

Universität Bremen
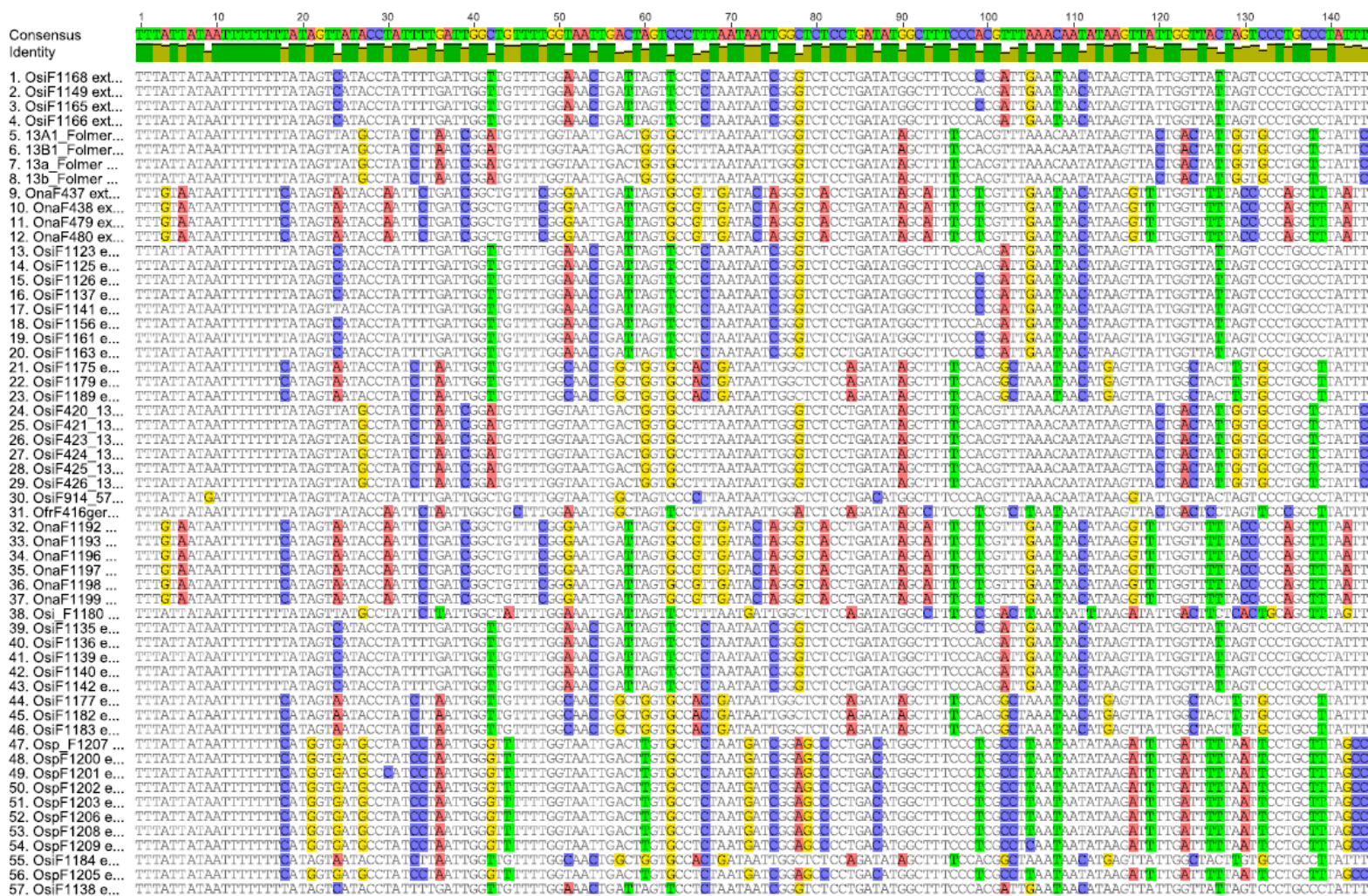
Name: Britta Wend-Heckmann   Datum: 05.02.2013

ERKLÄRUNG

Hiermit erkläre ich, dass ich die Doktorarbeit mit dem Titel:

Oithona similis (Copepoda: Cyclopoida) a cosmopolitan species?

selbstständig verfasst und geschrieben habe und außer den angegebenen Quellen keine weiteren Hilfsmittel verwendet habe.

Ebenfalls erkläre ich hiermit, dass es sich bei den von mir abgegebenen Arbeiten um drei identische Exemplare handelt.

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(Unterschrift)