Predatory zooplankton on the move:

Themisto amphipods in high-latitude marine pelagic food webs

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ABSTRACT

Hyperiid amphipods are predatory pelagic crustaceans that are particularly prevalent in high-latitude oceans. Many species are likely to have co-evolved with soft-bodied zooplankton groups such as salps and medusae, using them as substrate, for food, shelter or reproduction. Compared to other pelagic groups, such as fish, euphausiids and soft-bodied zooplankton, hyperiid amphipods are poorly studied especially in terms of their distribution and ecology. Hyperiids of the genus *Themisto*, comprising seven distinct species, are key players in temperate and cold-water pelagic ecosystems where they reach enormous levels of biomass. In these areas, they are important components of marine food webs, and they are major prey for many commercially important fish and squid stocks. In northern parts of the Southern Ocean, *Themisto* are so prevalent that they are considered to take on the role that Antarctic krill play further south. Nevertheless, although they are around the same size as krill, and may also occur in swarms, their feeding behaviour and mode of reproduction are completely different, hence their respective impacts on ecosystem structure differ. *Themisto* are major predators of meso- and macrozooplankton in several major oceanic regions covering shelves to open ocean from the polar regions to the subtropics. Based on a combination of published and unpublished occurrence data, we plot out the distributions of the seven species of *Themisto*. Further, we consider the different predators that rely on *Themisto* for a large fraction of their diet, demonstrating their major importance for higher trophic levels such as fish, seabirds and mammals. For instance, *T. gaudichaudii* in the Southern Ocean comprises a major part of the diets of around 80 different species of squid, fish, seabirds and marine mammals, while *T. libellula* in the Bering Sea and Greenland waters is a main prey item for commercially exploited fish species. We also consider the ongoing and predicted range expansions of *Themisto* species in light of environmental changes. In northern high latitudes, sub-Arctic *Themisto* species are replacing truly Arctic, ice-bound, species. In the Southern Ocean, a range expansion of *T. gaudichaudii* is expected as water masses warm, impacting higher trophic levels and biogeochemical cycles. We identify the many knowlegde gaps that must be filled in order to evaluate, monitor and predict the ecological shifts that will result from the changing patterns of distribution and abundance of this important pelagic group.

KEYWORDS

Hyperiidea, biogeography, range shifts, food web, life cycle, Antarctic krill, salps, climate change

CONTENTS

1. BACKGROUND

Five major groups of zooplankton are characteristic of high-latitude oceans, copepods, soft-bodied zooplankton (e.g. tunicates, cnidarians), pelagic amphipods, euphausiids and chaetognaths (Longhurst, 1985). Of these groups, amphipods are amongst the least known (e.g. Murphy et al., 2007). Unlike the chaetognaths and euphausiids that comprise relatively few species with little variation in morphology and feeding behaviour, pelagic amphipods are highly diverse. This is reflected in their wide range of feeding habits, which is as diverse as that of copepods, and comprises carnivory, omnivory and even herbivory in certain developmental stages. There are also parastic and commensal forms. Such varying lifestyles is manifested in pronounced morphological diversity which is comparable to that of cnidarians. This diversity is far from being fully described and understood and deserves much greater attention.

The Hyperiidea represent the most dominant group of pelagic amphipods, comprising exclusively pelagic species. They are believed to be the most ancient amphipod colonizers of the pelagic realm, as opposed to the Gammaridea, of which only about 30% of the species inhabit the pelagial which they colonized much later in evolutionary history (Vinogradov, 1999a). Hyperiids span the size range of around 2 mm adult size to a maximum of 10 cm recorded for the genus *Megalanceola* (Zeidler, 1992). They contribute up to 20% of all zooplankton biomass in some regions, but generally are in about the same range as other so-called raptorial planktonic predators: the chaetognaths, which in total comprise 4% of the global ocean's zooplankton biomass (Longhurst, 1985). So far, 286 hyperiid species belonging to 32 families and 77 genera (De Broyer, 2010) have been described from the open ocean, the majority of which inhabit the epipelagic zone, however several are mesopelagic and deep-water species (Vinogradov, Volkov & Semenova, 1996; Vinogradov, 1999a).

Recently their phylogenetic relationships have been invesigated with modern molecular tools which confirmed the presence of two monophyletic groups: the Physosomata, mainly confined to bathypelagic depths and the Physocephalata, inhabiting primarily epi- and mesopelagic depths (Hurt, Haddock & Browne, 2013). This independent radiation, segregated on the bathymetric scale, is reflected in the morphological characteristics of both groups. Whilst the Physosomata often show an overall reduction in the size of the head and eyes relative to the body as well as a cryptic coloration typical of deep-sea organisms, most Physocephalata have large heads and eyes relative to their body length and are often transparent (Hurt et al., 2013). Despite these generalizations, the range in variation of hyperiid morphology can reach bizarre proportions in some highly specialised species and contrasts with the relatively similar body shapes across an order of magnitude size scale in other pelagic crustacea: copepods, euphausiids and decapods. Many species may have coevolved alongside large-volume zooplankton, in particular cnidarians that themselves exhibit a broad range of body plans. Indeed, hyperiids are considered as an entirely pelagic group but are described as having a "quasi-benthic lifestyle" where soft-bodied (often lumped under the term gelatinous) zooplankton such as salps and jellyfish function as moving substrate. These are often indispensable to the completion of the hyperiid's life cycle for shelter, reproduction, food and predator avoidance (Laval, 1980). Many reports exist on a commensal or parasitic relationship with ctenophores, cnidarians and salps (e.g. Harbison, Diggs & Madin, 1977; Gasca & Haddock, 2004). The co-evolution with other plankton can also be illustrated by the example of two Antarctic *Hyperiella* species that carry live pteropods (*Clione* and *Spongiobranchaea*) on their backs, holding these between their elongated pereopods as an efficient chemical defence against fish predators (Havermans et al., 2018).

Soft-bodied zooplankton are classically regarded as a trophic 'dead end' in the pelagic food web: even though the disparate groups, e.g. cnidarians and tunicates, that fall in this category can build up an enormous biomass very rapidly by asexual reproduction, few pelagic predators seem to benefit from their abundances. However, this is contested; besides a relatively small number of specialists on a soft-bodied plankton diet (e.g. Harbison, 1993; Mianzan et al., 1996), a majority of predators use soft-bodied zooplankton as part of their diet (Arai, 2005) as so-called 'survival-food' when preferred prey items are limited (e.g. anchovies feeding on salps, Mianzan et al., 2001). Hyperiid amphipods, with their grappling and tearing mouthparts, are particularly well adapted to feeding on soft-bodied zooplankton and parasitizing them for completing (part of) their life cycle. This is confirmed by a high predation pressure on hydromedusae by hyperiids (e.g. Mills, 1993). Regional studies have clearly demonstrated a relationship between the distribution of several species of hyperiids and the presence of salps (e.g. Young, 1989) and other groups (e.g. radiolarians, ctenophores, siphonophores, e.g. Colebrook, 1977). Burridge et al. (2017) linked the distribution and diversity of hyperiids sampled throughout the Atlantic with those of soft-bodied zooplankton. On the other hand, the importance of parasitic hyperiids has recently been emphasized as an important energy transfer pathway, with fish preying on hyperiids within jellyfish and hence, as a hitherto unstudied link between the so-called trophic dead end and fishes in pelagic ecosystems (Riascos et al., 2012). In the context of hypothesized synergistic events of the overfished fish stocks and increasing blooms of soft-bodied zooplankton, these interactions in the shape of parasitism, commensalism and predation urgently need a more concentrated research effort.

Hyperiid amphipods of the genus *Themisto* Guérin, 1825 (a senior synonym of *Parathemisto*, Bowman et al., 1982) play an important role in high-latitude and temperate waters where they often represent a major trophic link between zooplankton secondary production and higher trophic levels such as squid, fish, seabirds and marine mammals (see section VI in this review). *Themisto* amphipods are believed to be voracious visual predators using their large compound eyes to detect and feed upon meso- and macrozooplankton in the epipelagic layer. *Themisto* feeds upon the most abundant zooplankton species in the water column and can control the mesozooplankton standing stock. However, a phytoplankton diet has been proposed for the juvenile life stages (see section IV). The genus is currently represented by seven species (Zeidler, 2004): ***T. gaudichaudii*** Guérin, 1825, the most abundant amphipod in the southern hemisphere, ***T. japonica*** (Bovallius, 1887) and ***T. pacifica*** (Stebbing, 1888) from North Pacific waters and ***T. australis*** (Stebbing, 1888) from the colder waters of the Southwest Pacific and ***T. libellula*** (Lichtenstein in Mandt, 1822), ***T. compressa*** Goës, 1865 and ***T. abyssorum*** (Boeck, 1871), which inhabit temperate Atlantic and Arctic waters. *T. gaudichaudii* was previously believed to be an amphitrophic species, occurring in both hemispheres, but has been revised to comprise *T. gaudichaudii* in the southern hemisphere and *T. compressa* in the northern hemisphere (Schneppenheim & Weigmann-Haas, 1986). Synonymized species are *T. bispinosa* Boeck, 1871 that is now accepted as *T. compressa* and *T. gracilipes* (Norman, 1869), now *T. gaudichaudii*. However, records of *T. gracilipes* north of the Southern Ocean, such as those in Australian and New Zealand waters, may refer to *T. australis*.

Climate change, proceeding at an unprecedented pace, is currently redistributing life on Earth (Pecl et al., 2017). Warming of the upper ocean layer and the atmosphere have altered sea ice extent and seasonal dynamics in the Arctic (Screen & Simmonds, 2010; Stroeve et al., 2014), and similar changes are observed in the Atlantic sector of the Southern Ocean, the western Antarctic Peninsula and Bellingshausen Sea (Meredith & King, 2005; Gille, 2008; Whitehouse et al., 2008; Stammerjohn et al., 2012). This has a strong impact on stocks of key pelagic species such as Antarctic krill (*Euphausia superba* Dana, 1850). In light of these environmental changes, range expansions or shifts in the polar pelagic realm are ongoing or predicted for some species whilst others, e.g. ice-dependent species, are undergoing poleward range contractions. Within the SW Atlantic sector of the Southern Ocean, a decline of Antarctic krill densities is hypothesized (although still debated) concomitant with an increase in salps (mainly *Salpa thompsoni* Foxton, 1961), which is often attributed to bottom-up factors such as alterations in summer phytoplankton blooms and winter sea-ice extent (Loeb et al., 1997; Atkinson et al., 2004; Meyer, 2012). In the Arctic Ocean and surrounding seas, changes in the distributional range of *Themisto libellula* have also been reported (Marion et al., 2008; Volkov, 2012), while *T. compressa* has recently invaded the Arctic Ocean in the Fram Strait (Kraft et al., 2013). Hence, in order to make reliable predictions of the consequences of such distributional shifts and the effects of environmental changes, we feel a stock-take of the information available on *Themisto* amphipods is urgently needed, as well as highlighting what needs to be studied to determine the future status and role of this key group in global plankton communities. Therefore, we will discuss the knowns and known unknowns of *Themisto* amphipods regarding distributional patterns, life history traits, feeding habits and their role in regional food webs and biogeochemical cycles and develop hypotheses on their ecology and biology based on literature and observations. In doing so, we provide both the current status of this group and move towards predicting the consequences of range shifts of *Themisto* species for high-latitude ecosystems.

2. DISTRIBUTIONAL PATTERNS AND SPECIES ZONATION OF *THEMISTO*

Distributional ranges of macrozooplankton are often linked with oceanographic features and the distribution of their major prey, or both. Some species, such as *Themisto libellula* and *T. abyssorum*, are assumed to be indicators of particular water masses: *T. libellula* is a typical species of cold Arctic waters in different sub-Arctic regions, whilst *T. abyssorum* is more associated with warmer Atlantic waters (e.g. Mumm et al., 1998; Dalpadado, 2002; Volkov, 2012). Nonetheless, *T. libellula* is not only thriving in the Arctic but also in its marginal seas (Fig. 1), where water layers < 3°C are present throughout summer, including the Bering and Okhotsk seas, as well as in southern Alaskan fjords, Prince William Sound and the Gulf of St Lawrence (Marion et al., 2008; Pinchuk et al., 2013). In the southern Alaskan fjords, as well as in Prince William Sound, no extensive cold layers persist, and also in the Bering Sea, the upper layers are 9°C in the coldest years and 14°C in the warmest (Pinchuk et al., 2013). *T. libellula*'s upper lethal temperature (at which 50% of the animals die) has been experimentally determined to be 9.4°C for the Canadian Arctic populations (Baffin Bay), whereas it is between 13 – 15°C for individuals of Alaskan populations (Percy, 1993). This shows that some populations are physiologically adapted to warmer waters by shifting their thermal ranges (Percy, 1993), which may be the case for other geographic populations as well.

Similarly, *Themisto abyssorum* is also found in the Arctic Barents Sea, although in tenfold lower abundances than in waters of Atlantic origin (e.g. Dalpadado, 2002), indicating a broad temperature tolerance. However, contrary to *T. libellula*, it is absent from the Bering Sea and Pacific (Fig. 1). The species supposedly prefers deeper waters (> 50m), mostly linked to the presence of deep Atlantic water in the Arctic Ocean, possibly explaining its absence in the shallow Bering Sea. However, surface records of this species also exist (Dalpadado, 2002; Havermans C., unpublished data), and it is likely that other bottom-up or top-down factors are having an impact on *T. abyssorum*'s realized distribution.

Themisto australis is present in the southwestern Pacific, but seemingly absent from the eastern part (Fig. 2), the reasons for which being still unclear. Both *T. compressa* and *T. gaudichaudii* are characterized by a very wide distribution encompassing both polar and temperate regions (Figs. 1 and 2). *T. compressa* is distributed in the western Atlantic from 40°N to about 66°N in the Davis Strait whilst, in the eastern Atlantic, it can be found as far north as the northern Barents Sea (79°N), down to about 30°N off the Moroccon coast. It is also present in the Mediterranean Sea from Gibraltar to about 24°W.

In the southern Atlantic and Southern Ocean, *Themisto gaudichaudii* can be found in waters to the North and South of the Polar Front. The species occurs in waters from subzero temperatures around the Antarctic Peninsula and Weddell Sea (66 – 70°S) to as far north as the Benguela upwelling system (Kane, 1966, Auel & Ekau, 2009) and the Patagonian shelf and coast (Ramírez & Viñas, 1985; Padovani et al., 2012) (Fig. 2). *T. gaudichaudii* is regarded as a species typical of the warmer (surface) waters of the Antarctic (Mackintosh, 1934) and is more common in the northern Scotia Sea to as far south as the Bransfield Strait (Jażdżewksi & Presler, 1988). In contrast to the high abundances of *Themisto* species observed throughout Arctic water masses, Southern Ocean distributions seem to be very patchy with only particular areas harbouring high amphipod concentrations. This can be explained by the fact that the Southern Ocean itself is a mosaic of high and low productivity regions, with the coastal and continental shelf zones being amongst the most productive (Constable, Nicol & Strutton, 2003). The Antarctic Polar Frontal (APF) Zone, situated between the Polar and sub-Antarctic fronts is also characterized by an elevated primary production and intense eddy and frontal activities (Constable et al., 2003). In both areas, *T. gaudichaudii* has high abundances, e.g. around South Georgia, the Kerguelen, Heard, Crozet and Prince Edward Islands, and in the APF zone (Ealy, 1954; Kane, 1966; Labat, Mayzaud & Sabini, 2005; Pakhomov & Froneman, 1999; Froneman, Pakhomov & Treasure, 2000; Watts & Tarling, 2012). Whether these patchy distributions can be linked with temperature, particular prey abundances or concentrations of predators needs to be further examined.

The interesting feature of the distribution of *Themisto* species is that it extends across several latitudinal zones of prey species. In the case of *T. gaudichaudii*, its southern range overlaps with the northern range of *Euphausia superba* and covers the ranges of the euphausiid species *E. frigida* Hansen, 1911 , *E. triacantha* Holt & Tattersall, 1906, *Thysanoessa macrura* G.O. Sars, 1883 and *T. vicina* Hansen, 1911 (Brinton, 1985). Furthermore, several *Themisto* species have overlapping geographic distributions. This is the case for example for *T. libellula*, *T. abyssorum* and *T. compressa* in the Arctic Ocean and shelf seas (Fig. 1), for *T. libellula* and *T. pacifica* in the Sea of Okhotsk (Gorbatenko, Grishan & Dudkov, 2017) and for *T. pacifica* and *T. japonica* in the western sub-Arctic Pacific (Bowman, 1960; Yamada, Ikeda &Tsuda, 2004). Where distributions overlap, each species occupies a distinct ecological niche. For instance, both the sub-Arctic boreal *Themisto abyssorum* and the high-Artic *T. libellula* are present sympatrically in the Arctic Ocean and surrounding seas, but they feed on different prey (Auel et al., 2002; Kohlbach et al., 2016).

Nevertheless, the genus *Themisto* is in urgent need of a taxonomic revision and the biogeographic limits of the species must be tested with molecular tools. *T. gaudichaudii* has been shown to consist of at least three distinct genetic lineages throughout the Atlantic sector of the Southern Ocean (Havermans C. et al., in preparation) and in-depth population genetic studies should be carried out to evaluate the extent of gene flow between these populations. Within the Southern Ocean at least two morphospecies have been distinguished (Zeidler & De Broyer, 2014). Populations along the Patagonian shelf consist of *T. gaudichaudii* (Havermans C. et al., in preparation), whilst the populations from the Benguela upwelling system have not yet been revised according to their differing morphology and genetic connectivity. The morphological differences between *T. pacifica* and *T. japonica* are minute (Yamada et al., 2004) and only a century after their description has a study pinpointed characters allowing immature specimens of these two species to be distinguished from each other (Yamada &

Ikeda, 2004). Furthermore, several characters used to distinguish mature adults of both species (Yamada et al., 2004) are also prone to vary according to sex and developmental stage (e.g. length of second antennae), which may lead to further identification errors. Within *T. libellula*, several distinct genetic lineages have been revealed, linked to regional variation (Tempestini et al., 2017). Only after the genus *Themisto* has been thoroughly revised with an integrative approach combining morphology and genetics, can further conclusions be made regarding species' zonation and distributional patterns.

3. LIFE-HISTORY TRAITS AND SMALL-SCALE DISTRIBUTIONAL PATTERNS OF *THEMISTO*

3.1. Life cycles of the different *Themisto* species

In the genus *Themisto*, the number of generations per year decreases with increasing latitude: the respective boreal and Arctic species *T. libellula* and *T. abyssorum* have one generation every year or every two years, whilst warmer-water species such as *T. japonica*, *T. pacifica* and *T. compressa* have several generations per year (Ikeda, Hirakawa & Imamura, 1992) (Table 1). This does not hold true for *T. gaudichaudii*, for which the number of generations varies throughout its distributional range. Around South Georgia, it has two recruitment events per year (Watts & Tarling, 2012) but only one around the sub-Antarctic Kerguelen Islands (Labat et al., 2005). However, this statement is subject to the validity of the current species delimitation (see above). *Themisto* populations off South Africa have a life cycle of less than a year and females become mature when reaching 6 mm of length (Siegfried, 1965) whilst in Antarctic waters, *T. gaudichaudii* grows to a larger size with a maturity of around 12 mm or more, displaying slower growth rates (Barnard, 1932). Hence, it has been argued that growth and maturation rates depend on food availbaility and temperature (Sheader, 1981; Auel & Ekau, 2009). Breeding periods and number of generations per year also differ amongst sympatric species. *T. libellula* has a prolonged breeding period from January to March, however, breeding females have been recorded as early as July to September in Svalbard fjords (Dale, 2006). *T. libellula* females release juveniles in a time frame (March to May) matching the spring blooms in the Marginal Ice zones of the Arctic Ocean (Dalpadado, 2002). In the Bering Sea, this peak release occurs much later in June (Pinchuk et al., 2013). *T. abyssorum*, strongly associated with the Atlantic inflow in the Arctic, breeds later and over a shorter time period (May and June) (Dalpadado et al., 1994; Dalpadado, 2002). For *T. japonica*, experimentally determined life cycles varied with temperature and almost doubled in duration upon exposure to waters at 1°C compared to those at 5°C (Ikeda, 1990). Individuals of *T. libellula*, as a typical Arctic species, appear to be smaller in Atlantic waters (Dalpadado, 2002). Hence, growth and maturation rates depend on temperature and food availability (Sheader, 1981; Yamada et al., 2004; Auel & Ekau, 2009). In most species, peaks of hatched juveniles seem to be synchronized with the increase of seawater temperatures in spring and its associated phytoplankton blooms followed by increases in zooplankton abundances (e.g. *T. gaudichaudii*, Labat et al., 2005; *T. libellula*, Noyon, Gasparini & Mayzaud, 2009). This timing allows juveniles, reported to feed both herbivorously as well as on mesozooplankton (see below), to take advantage of increased food supply and pass through the more vulnerable life stages quickly.

3.2. Do *Themisto* species swarm?

Themisto amphipods are very motile and have been reported to occur in large swarms (e.g. Vinogradov et al., 1982). Net catch data reported hundreds of *Themisto* individuals per square meter (e.g. *T. abyssorum*: 269 ind.m^{-2}, Dalpadado, 2002; *T. japonica*: 622 ind.m^{-2}, Ikeda et al., 1992). However, more research is needed to find out whether these high densities represent just locally aggregating individuals feeding upon patchily distributed prey or true schooling behaviour (Hamner, 1984). For the hyperiids *Hyperoche* and *Themisto*, Westernhagen & Rosenthal (1976) suggest chemical or visual detection of copepod prey, but they hypothesize that predation depends on random encounters, therefore requiring a minimum density of prey. Hence, active hunting of copepods may be facilitated by the formation of swarms. Swarms have also been suggested to be linked to certain reproductive stages. Anecdotal underwater observations around the sub-Antarctic Snares Islands have reported the occurrence of *T. gaudichaudii* and *T. australis* in loose swarms in the neuston layer (down to 3 m depth) (Fenwick, 1973). Camera images from subsurface layers in the Fram Strait showed many but rather spaced out encounters of *T. libellula* (Havermans C., unpublished data). From submersibles, near-bottom swarms of hundreds of *T. abyssorum* mature females have been observed several times at 1700 m depth. Acoustic records have shown diel vertical migrations of swarms of zooplankton, including *T. gaudichaudii*, that forage in near surface waters at night and descend to the seafloor after sunrise (Pakhomov & Froneman, 1999). The swarming or aggregating habit of *Themisto* may explain its dominant role in the macrozooplankton compared with other hyperiids with similar morphological and ecological traits. Two other abundant hyperiid species in the Southern Ocean are *Cyllopus lucasii* and *Primno macropa*. In common with *Themisto*, they are good swimmers, and are not commensal or parasitic on soft-bodied zooplankton (Zeidler & De Broyer, 2014). Logically, species adapted to a commensal life style depend on their host and remain solitary rather than form dense aggregations. However, *P. macropa* and *C. lucasii* are not known to swarm (Vinogradov, 1999b) but can still be found in sufficient biomass to represent a major food source for top predators (Zeidler & De Broyer, 2014). Combining optical with advanced acoustic methods may be pivotal for understanding to what extent swarming occurs in pelagic amphipods and its selective advantage over the more solitary lifestyles of other hyperiid species.

3.3. Vertical distributions and diel migrations: do all species exhibit the same patterns?

Diel vertical migrations (DVM), of ascent at night and descent during the day, have been well documented for *Themisto* species (Ikeda et al., 1992). It is yet unknown what triggers the diel vertical migration of *Themisto* species. If these migrations are determined by the vertical distribution of their prey, in this case copepods, would *Themisto* feed on these during diurnal aggregation at depth, by looking upward, or chasing them in the surface layer at night? *Themisto* species are assumed to be visual predators based on the large size of their eyes, but they are still capable of capturing copepods during imposed periods of darkness when kept in aquaria (Pakhomov & Perissinotto, 1996). The optical structure of *Themisto*'s eyes, in comparison to other hyperiids, reveals an increased resolution particularly in the forward-pointing part of the lower eye (Land, 1989). Hence, *Themisto* not only uses the dorsal upward looking direction but, in addition, has enhanced visual acuity looking forwards (Land, 1989). This, together with a better understanding of its hunting habits, could provide an answer to the questions above.

Whether the ascent to surface layers during the night is a consistent pattern for all *Themisto* species across regional populations still needs to be ascertained. For instance, *T. gaudichaudii* has been reported at the surface during day time: e.g. off Terra Nova (Barnard, 1930), as well as along the Patagonian shelf (Havermans C., unpublished data). In many sampling localities in New Zealand and sub-Antarctic waters, *T. australis* was not found in any catch at the surface at night but was there during day time, rising to the surface in the afternoon (Fenwick, 1978). Also a large portion of the *T. compressa* population spent more time in surface layers, independent of day/night time (Lampitt et al., 1993). Similarly, in the shelf regions of the Prince Edward Islands, part of the *T. gaudichaudii* population did not display a clear diel vertical pattern and remained in the upper 100 m whereas another fraction of the population descended to depths between 200 – 400 m (Pakhomov & Froneman, 1999). This was also visible in the acoustic record, where small swarms occurring between 50 and 100 m tended to descend after sunrise, to greater depths, sometimes to the shelf floor (Pakhomov & Froneman, 1999). A sinking behaviour towards deeper depths straight after feeding may also explain these descents, similar to the satiation sinking behaviour discovered for Antarctic krill (Tarling & Thorpe, 2017). In another study, nighttime abundance of *T. gaudichaudii* was consistently higher than day time levels on the Prince Edward Islands' shelf, and no vertical variation in distribution between size classes was observed (Pakhomov & Froneman, 1999). Juveniles and immatures of *T. japonica* migrate to depths of 150 – 200 m at daytime, whereas smaller size classes of the co-occurring *T. pacifica* stay in shallower waters both at night- and daytime. Furthermore, in both species, a segregation exists between mature males and females (Yamada et al., 2004). For *T. japonica*, males were never found in daytime samples, indicating a deeper descent (beyond 500 m) and an ascent during daytime to depths < 100 m (Yamada et al., 2004). Between these two species, the extent of vertical migration, as well as the daytime distribution depth, also differ, as a function of the superior swimming abilities of *T. japonica* and a higher risk of predation associated with its larger body size (Yamada et al., 2004). Hence, there is much variation in DVM behaviour between *Themisto* species and even between regional populations of the same species. Furthermore, we presently have little understanding of what triggers DVM in *Themisto*. A more frequent use of opening/closing nets will decrease the uncertainties about the precise depth distributions of the different species.

3.4. Local and regional segregation of juveniles, males and females

Many hyperiid species are known to form single-sex swarms, particularly during the reproductive period, but *Themisto* species were considered to be one of the exceptions in forming mixed swarms during this time (Laval, 1980 and references therein). However, both for *T. gaudichaudii* and *T. libellula*, several authors have reported males to be absent, or only present in low densities in their samples (Barnard, 1930, 1932; Schneppenheim & Weigmann-Haass, 1986), which may indicate separate swarms outside reproductive periods. For *T. japonica* and *T. pacifica*, males and females show distinct, but overlapping, vertical distributions (Yamada et al., 2004). Active migrations associated with growth stages have also been proposed (e.g. Labat et al., 2005). In Toyama Bay in the Sea of Japan, adult females only appeared in spring (Ikeda et al., 1992). In Arctic Kongsfjorden where a year-round presence of *T. libellula* has been recorded, mature females have never been caught, however, juveniles are found in high abundances (Noyon et al., 2011). Vast numbers of *T. compressa* (then: *Parathemisto gaudichaudii*) were found washed upon the shore of Northeast England, turning the beaches white, which consisted of females carrying young, eggs, and many recently hatched juveniles (Gray & McHardy, 1967). These examples may corroborate other previous findings (Labat et al., 2005; Noyon et al., 2011) that females release their brood nearshore, entering bays or fjords and subsequently leaving these “nursery” areas. Around Svalbard, first- and second-year specimens of *T. libellula* have been found in different fjords (Noyon et al., 2011) and, for *T. gaudichaudii* in the Kerguelen archipelago, younger individuals dominate the sheltered sites between the islands and segregate from larger-sized individuals offshore (Labat et al., 2005).

Themisto juveniles seem to be segregated vertically, being distributed in the top 100 m layer (daytime: 0 – 100 m, nighttime: 0 – 50 m, e.g. Yamada et al., 2004) and, in some cases, appear not to perform DVM, possibly because of surface layer temperatures (Ikeda et al., 1992). Size segregation may avoid competition or cannibalism on newly hatched juveniles. A geographic separation of recruitment/nursery areas from the feeding grounds of mature individuals, known to be the case for Antarctic krill (Meyer et al., 2017), may enhance recruitment success and dispersal dynamics of the different populations. Investigations of patterns of gene flows may be one means of determining whether such segregation is also commonly prevalent in *Themisto* species.

3.5. Commensalism or parasitism on soft-bodied zooplankton

In many species, the use of a planktonic host is assumed to ensure food availability when juveniles hatch. In other species, juveniles are capable of catching pelagic prey directly upon release from the brood pouch: *Hyperoche medusarum* (Krøyer, 1838) juveniles immediately prey on herring larvae when leaving the the marsupium, as observed in aquaria (von Westernhagen & Rosenthal, 1976). They have been observed clinging onto herring larvae, after having grasped them by the tail, and then sinking together to the bottom where they continue feeding on them (von Westernhagen & Rosenthal, 1976). Juveniles of *Themisto pacifica* have been collected from medusae (*Calycopsis nematomorpha* Bigelow, 1913) in the sub-Arctic Pacific Ocean (Renshaw, 1965). Juveniles of the same species have been reported to infest *Aequorea* medusae, living inside their stomachs where they feed on partially digested prey, whilst larger individuals have been found burrowed in the jelly or grazing on subumbrellar structures (Mills, 1993). Similarly, *T. australis* was associated with the scyphozoan *Cyanea capillata* (Linnaeus, 1758). The amphipods did not seem to feed on the jellies but rather use them as a substrate to attach to (Condon & Norman, 1999), likely facilitating dispersal. Some salps (*Pegea*, *Iasis*) collected in the Atlantic were covered with recently hatched *Themisto* juveniles, which has been interpreted as a close association between juveniles and salps (Madin & Harbison, 1977). Despite these observations, this relationship is thought to be much more tenuous than most other interactions documented for hyperiids (Zeidler & De Broyer, 2014) and many authors argue that *Themisto* release juveniles into the pelagic environment without the presence of a host (e.g. Dunbar, 1957; Siegfried, 1965; Kane, 1963, 1966). After hatching, juveniles likely colonize the salps independently, to which they commonly attach using their pereopods as shown in Fig. 3c. In other hyperiids, the females actively find salps or other gelatinous zooplankton and demarsupiate their brood into their tissues. This does not seem to be the case for most *Themisto* species, with the potential exception of *T. pacifica*, of which specimens were found inside medusae. In the Southern Ocean, at a sampling site where hundreds of *T. gaudichaudii* juveniles were recovered, salps were absent. On the contrary, where many adults were found, salps densities were high (Havermans, Schöbinger & Schröter, 2017). This observation does not support the hypothesis that salps are hosts for juvenile stages but adults likely feed on salps. However, an algal bloom was observed at the site where juveniles were abundant (Havermans et al., 2017), which supports their herbivorous feeding habits and the synchronization of juvenile hatching and spring blooms, observed for *Themisto* species (e.g. Dalpadado, 2002).

4. ***THEMISTO*'S FEEDING ECOLOGY**

4.1. From herbivory to carnivory: which trophic niches do *Themisto* species occupy?

Themisto amphipods are believed to be roving predators, feeding on the most abundant taxa in the water column. In the southern hemisphere, gut content analyses of *T. gaudichaudii* have shown that it feeds non-selectively and opportunistically, on copepods, chaetognaths, euphausiids and pteropods, amongst other taxa (Siegfried, 1965; Hopkins, 1985; Gibbons, Stuart & Verheye, 1992; Pakhomov & Perissinotto, 1996). In the Benguela Upwelling system, it was shown to consume the most abundant copepod and chaetognath species (Gibbons et al., 1992). Nonetheless, other studies focusing on the feeding dynamics of *T. gaudichaudii* are surprisingly scarce: two studies have been carried out in nearshore waters of (sub-) Antarctic islands (Pakhomov & Perissinotto, 1996; Froneman et al., 2000), one study was done off the West Coast of South Africa (Siegfried, 1965) and one in the Polar Frontal

Zone (Lange, 2006). Virtually nothing is known about *T. gaudichaudii*'s feeding ecology elsewhere, e.g. on the Patagonian shelf.

Salps have been reported in gut contents of *Themisto gaudichaudii* collected near the Antarctic Peninsula (Hopkins, 1985), and on the basis of its well-suited grappling appendages it has been hypothesized that the species is a major predator of salps more widely (Smetacek, Assmy & Henjes, 2004). Unfortunately, conventional gut content analyses with microscopy often fail to find soft-bodied zooplankton due to their rapid degradation in the stomach and lack of hard features for identification (Arai et al., 2003). Feeding experiments of *T. gaudichaudii* have shown that adults feed on salps, particularly on their stomachs (see Fig. 3d), a habit which may be held responsible for the presence of biomarkers for herbivory in adult *Themisto* (e.g. Stowasser et al., 2012). Based on both morphological stomach analyses and stable isotopes, Kruse et al. (2015) hypothesized an extensive feeding of *T. gaudichaudii* on salps in the Polar Frontal zone. *Salpa thompsoni* DNA has also been successfully amplified from stomach contents of *T. gaudichaudii* sampled in the Polar Frontal Zone (Havermans C., unpublished data). During an *in-situ* iron-fertilization experiment carried out in the same region, *T. gaudichaudii* was the dominant macrozooplankton species that colonized the fertilized patch, showing a two-fold higher abundance within the patch (Mazzocchi et al., 2010). *T. gaudichaudii* may have been attracted to the phytoplankton bloom within the patch to prey on salps, which would explain the low numbers of salps observed. In this case, *Themisto* would form an efficient link between the gelatinous and muscular food chains (Verity & Smetacek, 1996).

The position of *Themisto* species in Arctic food webs is better understood, particularly in the European Arctic. Trophic studies have been carried out both in open waters (Fram Strait, Auel et al., 2002; Kohlbach et al., 2016) and coastal regions (Svalbard fjords, Noyon et al., 2009, 2011) as well as in temperate ecosystems (Gulf of St. Lawrence, Marion et al., 2008). Both *T. libellula* and *T. abyssorum* are known to feed predominantly on copepods. Only one account of feeding on gelatinous zooplankton has been reported for Arctic species, despite "jellies" being ubiquitous and occurring in high abundances (e.g. Rascoff et al., 2010). Only one specimen of *T. abyssorum* investigated from slurpgun samples taken with submersibles had a jellyfish tentacle in its stomach (Vinogradov, 1999b). Despite their co-occurrence, *T. abyssorum* and *T. libellula* populations occupy distinct ecological niches. *T. libellula* feeds on herbivorous copepods that are dependent on the cryo-pelagic pathway involving ice algae (sympagic diatoms) (Auel et al., 2002; Kohlbach et al., 2016). By contrast, *T. abyssorum*'s feeding involves a more variable, less ice-dependent, trophic pathway where a variety of mesozooplankton grazing on flagellates and *Phaeocystis* seems to be the main prey (Auel et al., 2002; Kohlbach et al., 2016). Biomarker analyses indicated a higher trophic level for *T. abyssorum* than *T. libellula*, suggesting greater feeding on omnivorous and carnivorous prey (Auel et al., 2002). *T. libellula* seems to prefer copepodite stages CIII of *Calanus* species but can also feed on smaller copepods such as *Oithona* and *Pseudocalanus* species, when abundances reach a certain threshold (Noyon et al., 2009). In the St Lawrence system, stomach content analyses indicate feeding on copepodite stages CIV and CV of *Calanus finmarchicus* (Gunnerus, 1770), complemented by euphausiids, chaetognaths, amphipods and mysids (Marion et al., 2008). In the North Atlantic, *T. abyssorum*'s diet, investigated with molecular methods, consisted mainly of crustaceans but detritus also appeared to be an important food source (Olsen et al., 2013). *T. compressa* and *T. abyssorum* have both been hypothesized to feed on particles in the water column. In the Arctic, *T. libellula* and *T. abyssorum* accumulate high amounts of wax esters (> 40% of total lipids), with their proportion increasing with individual size (Auel et al., 2002). This contrasts with *T. gaudichaudii*, which has virtually no wax esters (0.1%). Despite the comparatively more complete knowledge of *Themisto* feeding ecology on the Northern hemisphere, the scarcity of reports of feeding on gelatinous zooplankton should not be taken as evidence of its absence in *Themisto* diet due to the high probability of false negatives until investigated with methods that are not misled by the absence of persistent hard structures identifiable in amphipod stomachs.

4.2. Do functional morphologies indicate distinct prey preferences in *Themisto*?

In the pelagic realm, there are two kinds of predators: engulfers (e.g. fish) and grapplers (e.g. cephalopods). *Themisto* belongs to the latter type. As well as using its appendages to grapple and manipulate prey items, aquarium observations have shown that *T. gaudichaudii* uses its posterior long legs (pereopods) to manoeuvre: for stopping, turning sharply or making movements towards food items in immediate proximity (Kane, 1963). The grasping and holding on of prey is mainly achieved by the posterior pereopods, in particular the fifth pair, which is longer than the others (Nemato & Yoo, 1970). In the case of *T. gaudichaudii*, *T. australis* and *T. libellula*, the fifth pereopods also have well-developed spines and setae along their anterior edges. The third and fourth pereopods are generally characterized by sickle-shaped terminal segments apparently used to hold the prey (as seen in Fig. 3a, b) and to direct food items towards the gnathopods (Nemato & Yoo, 1970) that tear apart pieces and push them towards the mouthparts (Kane, 1963). *T. gaudichaudii* is capable of hooking onto larger prey such as small fish (Kane, 1963) and euphausiids and to start feeding on their stomach content while attached (Havermans C., unpublished data). The long and spiny fifth pereopods of *T. gaudichaudii*, used for grasping prey, are supposedly linked to feeding on larger prey items (see below).

When comparing the mouthparts of *Themisto pacifica* to those of the gammarid-type pelagic predator *Cyphocaris challengeri* Stebbing, 1888, Haro-Garay (2003) found that the mandibular palps of *T. pacifica* appeared weaker and the toothed, more comb-like incisors indicated a less pronounced predatory lifestyle suggesting a diet that combines microphagous and carnivorous feeding. Investigating the functional anatomy of mouthparts as well as the alimentary canals may reveal more about feeding habits than the actual gut content analyses regarding the prevalence of soft-bodied zooplankton in the diet (Coleman, 1994). When comparing internal foreguts of gammarids and hyperiids, Coleman (1994) noted an impressive variation in morphologies as well as several presumed adaptations to handle larger food particles in the latter group, likely for feeding on larger gelatinous zooplankton. Therefore, a comparative analysis of the mouthparts of the different *Themisto* species may give insights into the importance of salps or other gelatinous zooplankton in their respective diets. One caveat here is that it is at present unknown to what extent non-exclusive feeding on gelatinous zooplankton requires adaptations of external and internal functional morphology of *Themisto* and what those may look like.

Within several species, e.g. *Themisto gaudichaudii* (Schneppenheim and Weigmann-Haass, 1986) and *T. compressa* (Stephensen, 1924; McHardy, 1970; Sheader, 1975), both "long-legged" and "short-legged" morphs, differing in the length of the fifth pereopod, have been observed to occur in sympatry. Experiments have shown that these different morphs arise depending on temperature and nutrition (Sheader, 1975). Phylogeographic analyses have shown that these morphs are independent of the different mitochondrial DNA lineages observed and that the ratio of the fifth versus the sixth pereopod decreases with increasing latitude (and hence decreasing temperature) (Havermans C., unpublished data). Within populations in the Southern Ocean, these two morphs have been linked to different feeding strategies. Recent findings confirm that long-legged *bispinosa* morphotypes feed on a slightly higher trophic level than short-legged *compressa* morphotypes and it is hypothesized that the length of the pereopod plays a role in the efficiency with which bigger types of prey are caught (Kruse et al., 2015).

4.3. Herbivory? Grazing by juveniles and feeding on prey stomach contents by adults

Some trophic studies of *Themisto gaudichaudii* based on stable isotope analyses of the pelagic food web confirmed a high degree of omnivory (Gurney et al., 2001), whereas others place adults of this species at similar trophic levels to herbivorous zooplankton (Stowasser et al., 2012). Gut content analyses of *T. gaudichaudii* and *T. japonica* juveniles revealed significantly higher pigment concentrations than in adults' stomachs and hence juveniles are believed to feed substantially on phytoplankton (Siegfried, 1965; Nemoto & Yoo, 1970; Hopkins, 1985; Sugisaki et al., 1991). In the faecal pellets of *T. compressa* from the Northeast Atlantic, a marine snow signature was clearly distinguished by Lampitt et al. (1993). In incubation experiments, *T. compressa* individuals also fed to a great extent on aggregates (Lampitt et al., 1993). For *T. japonica*, results suggest that feeding behaviour switches from herbivory to carnivory as they grow (Sugisaki et al., 1991). The time of hatching of the juveniles also often matches with the onset of the spring bloom, e.g. for *T. libellula* in the Arctic (Dalpadado, 2002). Nelson et al. (2001) revealed a source of phytoplankton present in the fatty acid profiles of both juvenile and adult *T. gaudichaudii*. Large amounts of phytoplankton pigments were also reported in the gut contents of adult *T. gaudichaudii*, however, it remains unclear whether these were ingested by *Themisto* themselves or originated from digested prey (Pakhomov & Perissinotto, 1996). Indeed, adults have been observed to feed preferably on stomach contents of salps, euphausiids and conspecifics (Havermans et al., 2017; Figs. 3d, e, f).

4.4. Explaining *Themisto*'s visits to the seafloor

Various observations on migrations by adults to the deep-sea floor (depths around 1000 – 3000 m) have been reported for the northern *Themisto* species, *T. abyssorum* and *T. libellula*. These were explained by the animals feeding on detritus or phytoplankton (Vinogradov, 1999b and references herein). Furthermore, in Svalbard waters, *T. libellula* seems to be the major food item of the Atlantic spiny lumpsucker (*Eumicrotremus spinosus* (Fabricius, 1776)), a slow-moving benthic fish that is unlikely to prey upon fast-swimming migrating amphipods in the water column (Berge & Nahrgang, 2013). Apparently, *T. libellula* migrates to the bottom during the day where it aggregates, as was observed by submersible imaging (Vinogradov, 1999b) and temporarily makes up a major component of the hyperbenthos. This may also be the case for *T. gaudichaudii*, since individuals have been collected by epibenthic sled catches at depths of more than 3000 m in the Polar Frontal Zones (Havermans C., unpublished data). On the shelf around the Prince Edward Islands, *T. gaudichaudii* has frequently been sampled with near bottom trawls (Pakhomov & Froneman, 1999). Also *T. japonica* adults have been recorded at depths of 3000 m (Semenova, 1974). Hence, feeding by juveniles and adults on phytoplankton in the water column or on the deep-sea floor should be further explored given that it may have profound implications for pelago-benthic coupling processes and the biological pump. Migrations to the seafloor can also stem from moulting and reproductive behaviour including the release of juveniles by brooding females (see above).

5. *THEMISTO*, DRESSED FOR SUCCESS?

Themisto's omnivorous and flexible feeding habits alone do not justify its abundance and status as the most abundant of the pelagic amphipods found in temperate or high latitude oceans. Other hyperiids seem to be equally voracious predators, for example, *Hyperoche medusarum* from the Pacific appears to have a similar diet composition and raptorial behaviour as *T. gaudichaudii*, feeding on a variety of mesozooplankton such as copepods, juvenile decapods, euphausiids, medusae and clupeid fish larvae. The latter appears to be its preferred prey and it exerts a high predation pressure on newly hatched herring larvae and hence herring stocks in British Columbia waters (von Westernhagen & Rosenthal, 1976). Why *Themisto* alone reaches these high biomass levels needs further consideration:

5.1. A body fit for hunting and escaping?

Studying morphological differences and similarities between zooplankton species, i.e. identifying features retained from ancestors versus unique adaptations newly evolved within *Themisto*, is one way to consider the influence of competition and the ability to colonize new niches, amongst other processes. In the case of *Themisto*, one could argue that its morphology reflects a development towards a shrimp-like morphotype. Within the genus, species bear a well-developed fan-like urosome that reaches its maximum in *T. libellula* and *T. gaudichaudii* that could provide a tail-flip escape response capability as seen in euphausiids and decapods. However, the urosome appears to function more as armour, given that the amount of muscle tissue it contains appears insufficient to provide a strong tail-flip. *Themisto* differs from all other hyperiids in that it bears many spines on the dorsum and urosome (posterior part, in particular on the uropods), which could provide protection from predation. When feeling threathened, *T. gaudichaudii* spreads its spiny uropods upwards, which may indicate they serve as a primary defence apparatus (Fig. 4). Despite their armour, *Themisto* amphipods are fast swimmers: swimming speeds of 30 cm.s^{-1} have been measured for *T. japonica* (Hiroki, 1988). Nonetheless, *Themisto* seems to escape less from predators compared to euphausiids and chaetognaths (Volkov, 2012). Most other hyperiid amphipods lack conspicuous morphological attributes such as spines which would ward off predators. For the many hyperiid species associated with, and often residing inside, soft-bodied zooplankters, a smoother body surface facilitates the interactions of juveniles or adults with their hosts. The dorsal spines on the back of *T. gaudichaudii* and *T. australis* compared with the absence of spines in *T. abyssorum* and *T. pacifica* may reflect different predator avoidance strategies or interactions with hosts. Variation in diet and predation pressure may account for the intra-specific occurrence of morphotypes with and without dorsal spines (e.g. in *T. gaudichaudii*, Havermans C., unpublished data).

5.2. Adaptations to life in the mesopelagial

The highly developed eyes of many hyperiidean species suggest selection for finding their transparent, widely scattered prey. Nevertheless, it is often the case that one cannot see without being seen and the large eyes of *Themisto* must be visible to predators. However common in pelagic animals (Buskey, 1992), bioluminescent properties have not yet been reported from *Themisto* amphipods, but its dark coloration and opacity could reduce its detectability by predators in deeper waters, contrary to the epipelagic waters. Pelagic taxa are transparent in shallower waters and become more opaque in the deep, with colorations turning to uniform black (fish) or scarlet red (crustaceans) and with reduced reflectance over the gut to mask their bioluminescent prey. Forms of *T. gaudichaudii* with different pigments (from partly transparent to almost totally brown) have been discovered at sampling sites in close proximity to each other (Havermans C., unpublished data). They may be linked to different stages after moulting, turning darker with time. At hatching, juveniles appear to be almost completely transparent except for pleonites covering the stomach region (which are light brown) and the eyes (Havermans C., unpublished data), which may protect them from predation after release from the brood pouch, after which they seem to remain in the surface layer.

6. UP THE FOOD CHAIN: THE IMPORTANCE OF THEMISTO FOR HIGHER TROPHIC LEVELS

6.1. *Themisto* sustaining a variety of top consumers in polar and boreal food webs

Environmental change has winners and losers and *Themisto* are considered to be the major replacement of krill both in the Arctic (e.g. Dalpadado et al., 2001) and the Southwest Atlantic Ocean (Padovani et al., 2012). A list of predators of the different *Themisto* species worldwide has been compiled (Supplementary Material, Table S1), demonstrating their major importance as key species for higher trophic levels such as fish, seabirds and marine mammals in boreal and polar food webs. In the adjacent seas and gateways of the Arctic Ocean, *T. abyssorum* and *T. libellula* are the main prey of birds, fish, whales and seals (Supplementary Material, Table S1). In the Bering Sea, *T. libellula* sustains commercially important fish stocks such as the walleye pollock, the Pacific herring and cod, and the most commonly exploited salmonid species (Fig. 5a). The species varies in abundance from year to year due to natural climatic oscillations. In colder waters, it reaches enormous numbers, being a major prey item for several of these fish species and impacting the entire food web structure (Volkov, 2012; Pinchuk et al., 2013). Also on the Greenland shelf and in the Barents Sea, *T. libelulla* is preyed upon by fish stocks such as capelin, Atlantic cod and Greenland halibut (Fig. 5b). Similarly, *T. gaudichaudii* along the Patagonian shelf and around the Falkland Islands has also been referred to as the krill of the northern Southern Ocean and supports millions of tons of commercially exploited fish and squid (Arkhipkin et al., 2012, Padovani et al., 2012, Arkhipkin, 2013) (Fig. 6a). Across the whole Southern Ocean, *T. gaudichaudii* comprises a major share of the diet of at least 80 different species of squid, fish, seabirds and marine mammals (Supplementary Material, Table S1, Fig. 6b).

6.2. *Themisto* amphipods are not the preferred food of all predators

Compared to euphausiids, hyperiid amphipods have a tough exoskeleton, which is reflected when comparing the chitin content of *Euphausia superba* and *Themisto gaudichaudii* (Ikeda, 1974). This may serve both for feeding by providing a stiff skeleton to exert strength, with the long pereopods serving as lever arms to rip off pieces of soft-bodied plankters, as well as to deter predators which prefer to feed on the “muscular” food chain and not the “armoured” one. The known predators of *T. gaudichaudii* are summarized in Table S1. Certain species appear actively to avoid eating *Themisto* when encountering them. For instance, although humpback (*Megaptera novaeangliae*, Clapham, 2002; Findlay et al., 2017) and fin whales (*Balaenoptera physalus*, Aguilar, 2002) do consume *T. gaudichaudii*, other baleen whales do not, including blue whales and minke whales, which appear to avoid *Themisto* swarms despite high abundances in their feeding grounds (Kawamura, 1994). Observations from the *Discovery Reports* state that: "the whales caught at South Georgia (excluding the Sperm Whale, *Physeter macrocephalus*) feed exclusively on *Euphausia superba* and have no other food whatever in their stomachs apart from a few specimens of the amphipod *Euthemisto*, which is so abundant in the plankton round South Georgia that the whales can hardly help swallowing a certain quantity" (Mackintosh & Wheeler, 1929).

7. IMPACTS OF ONGOING AND ANTICIPATED RANGE SHIFTS IN BOTH HEMISPHERES

7.1. Range shifts in the Arctic and adjacent oceans

In the last decades, range shifts have been observed for *Themisto* species in the northern hemisphere as a likely consequence of environmental changes. In the Fram Strait, the temperate species, *T. compressa*, started to appear in high abundances in the long-term sediment trap record in 2004 and a reproductive event in the region was first documented in 2011 (Kraft et al., 2012, 2013, Schröter et al., submitted). Furthermore, *T. abyssorum* has become more abundant whilst *T. libellula* has decreased, both in the Barents Sea and Fram Strait (the Atlantic gateway to the Arctic, CAFF, 2017). Other – less monitored regions – of the Arctic are likely undergoing similar changes. An expansion of the range of *T. abyssorum* and a corresponding range contraction of *T. libellula* is very likely to be a manifestation of the ongoing Atlantification of the Arctic with corresponding reduced levels of sea-ice (Overland & Wang, 2013; Polyakov et al., 2017). *T. libellula* depends on the cryo-pelagic pathway involving ice algae and herbivorous copepods (Auel et al., 2002; Kohlbach et al., 2016) and is likely to suffer from these changes. In contrast, *T. abyssorum* and *T. compressa* may benefit due to their shorter life cycles and a more varied diet (Auel et al. 2002; Kohlbach et al., 2016). These shifts in distributional range and abundance may cause difficulties for higher trophic levels specializing on *T. libellula*, which is larger than *T. abyssorum* and *T. compressa*. Top predators that rely on larger sized prey, such as little auks (*Alle alle*) that specialize on feeding on only the largest *T. libellula* size class (Lønne & Gabrielsen, 1992), face an uncertain future if climate change leads to a shift towards equally nutritive but smaller *Themisto* in the near future.

Nevertheless, climatic shifts have also allowed *Themisto libellula* to inhabit new environments. For instance, since the 1990s, *T. libellula* appeared in the Gulf and Estuary of St. Lawrence where it had not been recorded before and it is now an abundant full-time resident of the system (Marion et al., 2008). In the Bering Sea, *T. libellula* has periodically spread further south with the southward inflow of colder northern waters, whilst in years characterized by a higher inflow of Pacific waters, the species disappears again (Volkov, 2012). These changes impact trophic pathways in these waters: when *T. libellula* is present, the major fish species (Pacific herring *Clupea pallasii*, Pacific cod *Gadus macrocephalus* and juvenile pink, chum and sockeye salmon *Oncorhynchus* spp.) switch from piscivory to planktivory (Pinchuk et al., 2013). In the southeastern Bering Sea shelf ecosystem, it is believed that *T. libellula* was once an ever-present key component of the system but now is only present in cold years (Pinchuk et al., 2013). Combined, these examples highlight the importance of these amphipods to entire Arctic food webs and emphasise the need to predict their response to rapid ongoing changes of the Arctic system.

7.2. *Themisto* in the Southern Ocean

Themisto is an opportunistic predator and may impact the abundances and recruitment of both krill and salps through consumption of the smaller larval stages. For example, in waters around South Georgia, *T. gaudichaudii* can consume up to 70% of daily secondary production (Pakhomov & Perissinotto, 1996) – over 200 krill larvae per square metre per day – and by doing so, can significantly influence the local recruitment of Antarctic krill (Tarling et al., 2007). Salps are also part of *Themisto*'s diet, as demonstrated by Kruse et al. (2015) with stomach content analyses and by Havermans et al.

(2017) with experimental observations. Hence, changes in the distributional range and abundance of *T. gaudichaudii* may represent a significant top-down control of other biomass dominant species.

Mackey et al. (2012) took a climatic envelope approach to considering historical and present-day abundance distributions of a number of macrozooplankton species in the Atlantic sector of the Southern Ocean, including that of *Themisto gaudichaudii*. Historical distributions were determined from *Discovery Investigations* records (1925 – 1951), from which species-specific temperature-envelope models were determined. Projections to the present day were made through assuming a 1°C increase in upper water column temperature over the past 70 years (a conservative estimate based on measured changes over that time by Meredith & King, 2005 and Whitehouse et al., 2008). From being limited to mostly the northern sections of the Atlantic sector in the *Discovery* era, temperature envelope projections predict *T. gaudichaudii* establishing itself even in the vicinity of the Antarctic Peninsula. Indeed, recent macrozooplankton surveys at the Peninsula report *T. gaudichaudii* as a minor component of the total catch (Ross et al., 2008, Loeb et al., 2009, Steinberg et al., 2015). A continued upward trend in abundances of *T. gaudichaudii* in southern parts of the Southern Ocean may have direct predatory impacts to both Antarctic krill and salps to go alongside the environmental pressures on these biomass dominant species. The further impacts to krill-consuming higher predators may also be profound. Even though some krill consumers can efficiently switch from a krill-based to an amphipod-based diet in years of low krill availability (e.g. Macaroni penguins *Eudyptes chrysolophus*), most species seem to be truly krill-dependent for their breeding success and even adult survival, which was shown to be the case for the black-browed and grey-headed albatrosses (*Thalassarche* spp.), the Gentoo penguin (*Pygoscelis papua*) and the Antarctic fur seal (*Arctocephalus gazella*) (e.g. Croxall, Reid &Prince, 1999; Forcada et al., 2005). The limited palatability of *T. gaudichaudii* as a food source for some baleen whale species (Kawamura, 1994) may also limit their population recovery in these regions.

7.3. Implications for the biological carbon pump and biogeochemical cycling

Zooplankton may play an important role in the biological pump by the vertical flux of particulate organic matter (POC) in the form of both faecal pellets, moults and dead bodies that sink to the ocean floor (Turner, 2015). However, the faecal pellet production of pelagic amphipods remains largely unstudied. Lampitt et al. (1993) studied the presence of marine snow derived from zooplankton faecal pellets, focusing on *Themisto compressa* (a key species of the Northeast Atlantic). A large variety of material in the pellets was noted from black, densely packed material to white, apparently empty “ghost” pellets. Sinking rates were in the range of 108 and 215 m day^{-1}, depending on size (Lampitt et al., 1993).

In our own observations of faecal pellet production by *Themisto libellula* from the Arctic, faecal pellets of individuals that had been feeding on copepods consisted of rather loose and fluffy orange-coloured material (Fig. 7). They easily fell apart and were prone to degradation by other organisms, in contrast to the compact faecal pellets of copepods and euphausiids and the large fast-sinking pellets of salps. In several instances, we observed *T. libellula* individuals feeding on their own faeces (coprophagy, Fig. 8). The faecal pellet produced was transferred from the urosome to the gnathopods after the individual had swirled on its axis several times and then bent its body so that the faecal pellet could be grasped by the feeding appendages directly from the posterior part of the body. This handling and ingestion of own faecal material could explain why the pellets are very loose and occur in aggregates. The partial degradation of pellets into smaller, slow-sinking pellets (called coprorhexy) will affect the vertical flux as they can be more easily degraded by other organisms (Iversen & Poulsen, 2007). Also the fate of limiting micronutrients (e.g. iron in the Southern Ocean) during the passage of food through the gut remains unexplored in amphipods. As shown for Antarctic krill (Schmidt et al., 2016), the breaking down and release of iron by grazers feeding on primary producers could be an important means of sustaining productivity in iron deplete regions such as the Southern Ocean.

8. Conclusions

(1) We compiled existing knowledge on the distributions of the different *Themisto* species which dominate boreal and polar pelagic ecosystems. In the northern hemisphere, boreal, sub-Arctic and Arctic species often show overlapping distributions whereas, in the southern hemisphere, one species i.e. *T. gaudichaudii*, dominates, while the distribution of *T. australis* is more restricted. There is a strong relationship between the geographic limits of a number of *Themisto* species and water mass boundaries such that *Themisto* species can be used as water mass indicators. *Themisto* species also exhibit fluctuations in abundance as a consequences of natural climate oscillations, and are likely to be impacted by ocean warming.

(2) At a smaller scale, *Themisto* species exhibit distinct diel vertical migration patterns; patterns vary even within populations, with segregation according to sex and age being evident in both vertical and horizontal scales. Nearshore areas may function as "nursery" areas, where females release their brood from their brood pouch, as is evident in *T. libellula* and *T. gaudichaudii*. In contrast to other hyperiids, *Themisto* species seem to be less dependent on soft-bodied zooplankton as hosts, but rather use them as food, e.g. salps in the Southern Ocean. However, *T. pacifica* and *T. australis* use jellies as a holdfast during several life stages.

(3) *Themisto* is not an exclusive carnivore as previously suggested, but feeds on a variety of food types, displaying detritivorous, herbivorous and carnivorous feeding habits. Juveniles benefit from algal blooms after their release, whereas adults also feed on algal fluff and detritus on the seafloor. This previously underestimated flexibility further contributes to the ever-growing importance of *Themisto* in a changing ocean. These hitherto unconsidered trophic links also change our view on the trophic role of *Themisto* species, although further quantification of these feeding habits is now required.

(4) Through reviewing the available literature, we demonstrate that *Themisto* is a major trophic link in boreal and polar food webs, sustaining a variety of predators, of which many are commercially exploited. Both in the Arctic and Antarctic, many fish, bird and marine mammal species are dependent

on *Themisto* as prey. Nevertheless, it may not always be a preferred prey and its consumption as a secondary prey item can indicate stress within regional food-webs.

(5) The distributional ranges of *Themisto* appears to be changing in line with environmental shifts. The consequences of the replacement of the larger, lipid-rich *T. libellula* by the smaller and less nutritious sub-Arctic and temperate species *T. abyssorum* and *T. compressa* in the Arctic will significantly impact fish, whale and seabird populations. In the Southern Ocean, a poleward range expansion of *T. gaudichaudii* will generate an overlap of distribution with Antarctic krill and salps which may impact their levels of recruitment. However, the consequences remain hypothetical and will depend on the feeding habits and prey preferences of *Themisto*. Hence, a better understanding of the biology of this key pelagic group is crucial to predicting its future impact on food web structure, energy flow and biogeochemical cycles.

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FIGURE LEGENDS

Figure 1. Occurrence maps of *Themisto* species from the northern hemisphere: *T. libellula* (Tli), *T. abyssorum* (Tab), *T. compressa* (Tco), *T. japonica* (Tja), *T. pacifica* (Tpa).

Figure 2. Occurrence maps of *Themisto* species from the southern hemisphere: *T. gaudichaudii* (Tga) and *T. australis* (Tau).

Figure 3. Documented feeding of a) *T. libellula* on an ostracod; b) on a pteropod (*Limacina*); c) *T. gaudichaudii*'s typical position when holding onto a salp or siphonophore; d) *T. gaudichaudii* specimens were observed at several instances to feed directly on the salp's stomach content; e) behavioural observations documented cannibalism of *T. gaudichaudii*: it was observed attacking other individuals of a similar size class and starting to feed on them and in particular the stomach region; f) When *Themisto* was placed in an aquarium together with large individuals of Antarctic krill (> 5 cm), it predominantly fed on the head, in particular the eyes, as well as on the stomach region.

Figure 4. a) When feeling threathened, *T. gaudichaudii* spreads its uropods upwards, which is likely serving as a primary defence apparatus. b) Its spiny urosome, or posterior part offers protection from predation, and is a distinguishing character from other abundant hyperiid species.

Figure 5. *Themisto libellula* as major prey item for a variety of top consumers, many of which are of commercial importance, in a) the Bering Sea and b) the Greenland and Barents seas.

Figure 6. *Themisto gaudichaudii* as major prey item for a variety of top consumers, many of which are of commercial importance, in a) the Southwest Atlantic Ocean (Patagonian shelf and slope and Falkland Islands) and b) the Scotia Sea and Antarctic Peninsula region.

Figure 7. Faecal pellets produced by an individual of *Themisto libellula*.

Figure 8. The phenomenon of autocoprophagy was observed several times when keeping *T. libellula* in aquaria. A swirling movement was carried out to produce the faecal pellet (indicated with a black

arrow) and subsequently transfer it from its position between the uropods to the mouthparts and gnathopods.

SUPPORTING INFORMATION

Table S1: Importance of *Themisto* species as major prey in the diet of cephalopods, fish, birds and marine mammals. A non-exhaustive list compiled from literature. Predator species followed by an * represent a species at the basis of a (major) commercial fishery, raised for aquaculture, or an important bycatch species. Past fisheries are indicated by their time span between brackets. Abbreviations: NZ – New Zealand, SA – South Africa.

Table 1. Life-history characteristics of the different *Themisto* species from distinct geographic areas, including the life cycle and the number of generations per year.

Species	Geographic distribution	Life cycle	Generations yr^{-1}	References
T. gaudichaudii	Kerguelen Islands	-	one	Bocher et al., 2001, Labat et al., 2005
	0-20°E sector SO	1 year		Kane, 1966
	South Georgia region	-	two	Watts & Tarling, 2012
	Off W coast South Africa	-	several	Siegfried, 1965
T. libellula	Fram Strait – Greenland Sea	4 years	one	Kraft, 2010
	Northern and central Barents Sea	Up to 3 years	one	Dalpadado, 2002
	Eastern Barents Sea	2 years		Koszteyn et al., 1995
	Hudson Bay, SE Baffin Island	Up to 2 years		Dunbar, 1957
	NW Greenland Sea	2-3 years		Koszteyn et al., 1995
	Greenland Sea, Fram Strait	At least 3 years		Auel & Werner, 2003
	Baffin Bay	1 year	-	Dunbar, 1946
T. abyssorum	Western and southern Barents Sea	Up to 2 years		Bogorov, 1940; Koszteyn et al., 1995
	Northern and central Barents Sea	1 (-2) years	one	Dalpadado, 2002
	NW Greenland Sea	2 years	-	Koszteyn et al., 1995
	Greenland, Norwegian, Barents seas	1 year	one-two	Koszteyn et al., 1995
	Gulf of St Lawrence	1 year	one	Hoffer, 1971
T. compressa	North Sea		several	Sheader, 1981
	Fram Strait – Greenland Sea	2 years	two	Kraft et al., 2013
T. japonica	Japan Sea	195-593 days		Ikeda, 1990
	southern Japan Sea		three	Ikeda et al., 1992
	Western North Pacific	8.5 – 12 months	-	Yamada et al., 2004
T. pacifica	Western North Pacific		four	Yamada et al., 2004
	Southeastern Alaska		four-five	Wing et al., 1976

Figure 1.

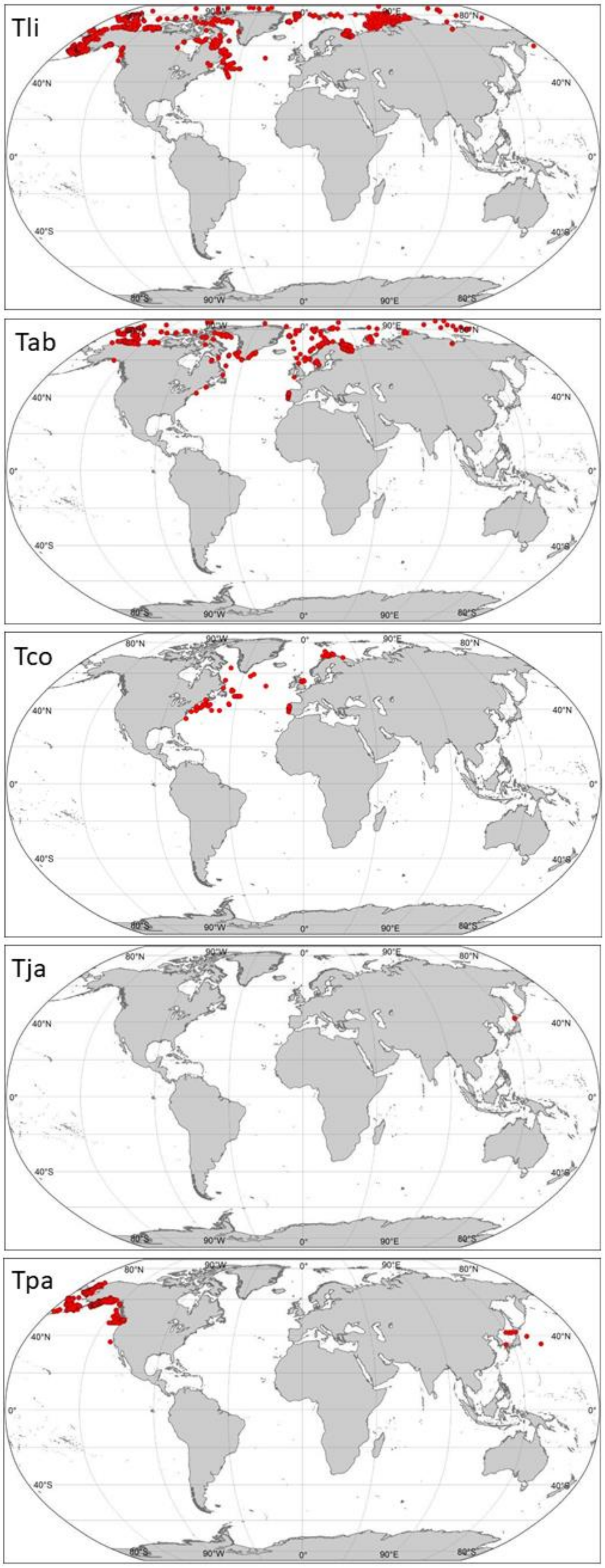
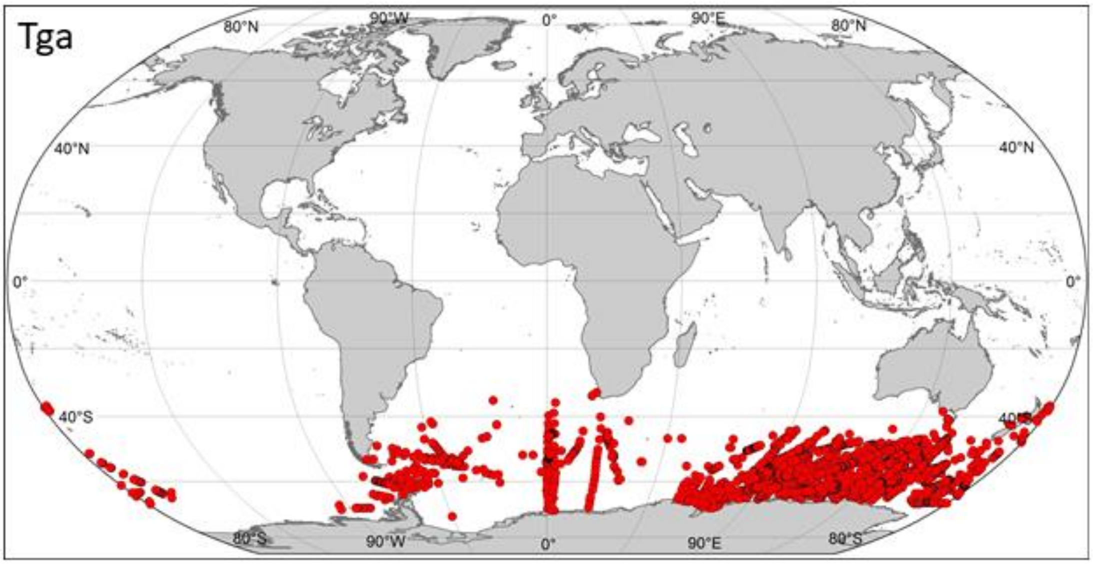


Figure 2.



Tga
80°N
90°W
0°
90°E
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40°S
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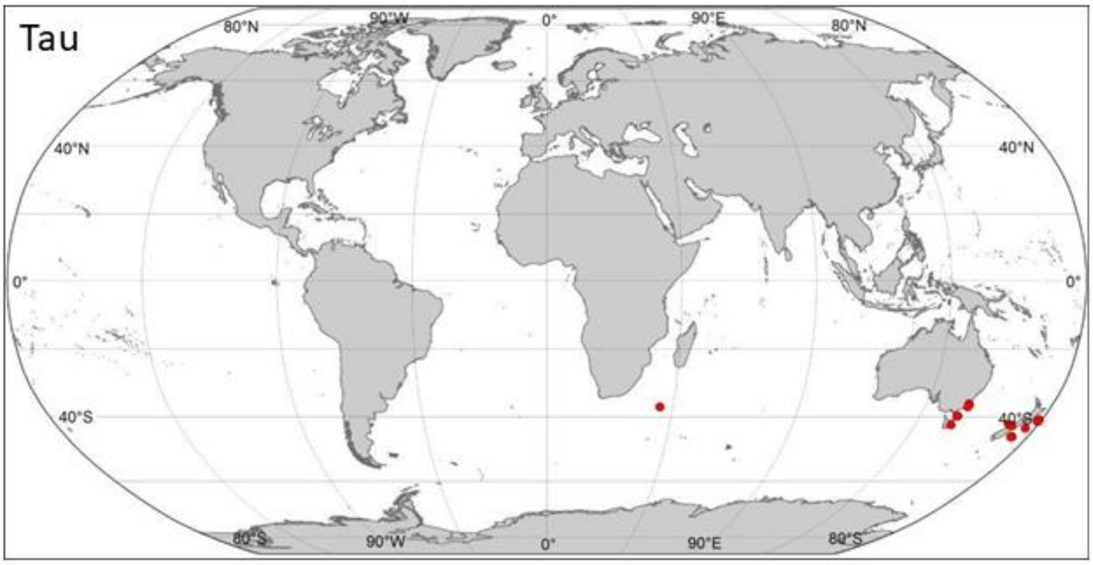
90°E
80°S



Tau
80°N
90°W
0°
90°E
80°N
40°N
40°N
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0°
40°S
40°S
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90°W
0°
90°E
80°S

Figure 3.

Figure 4.

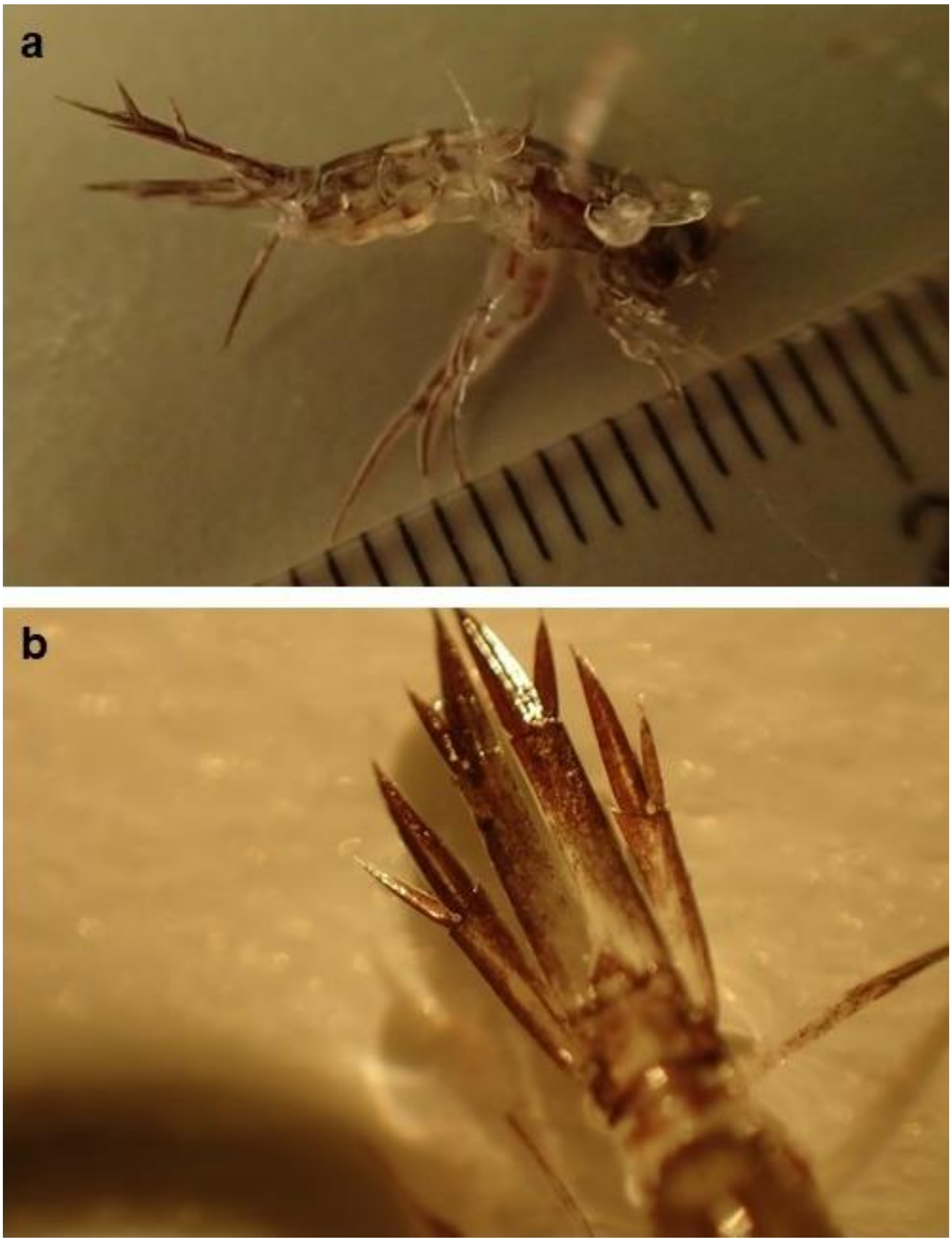
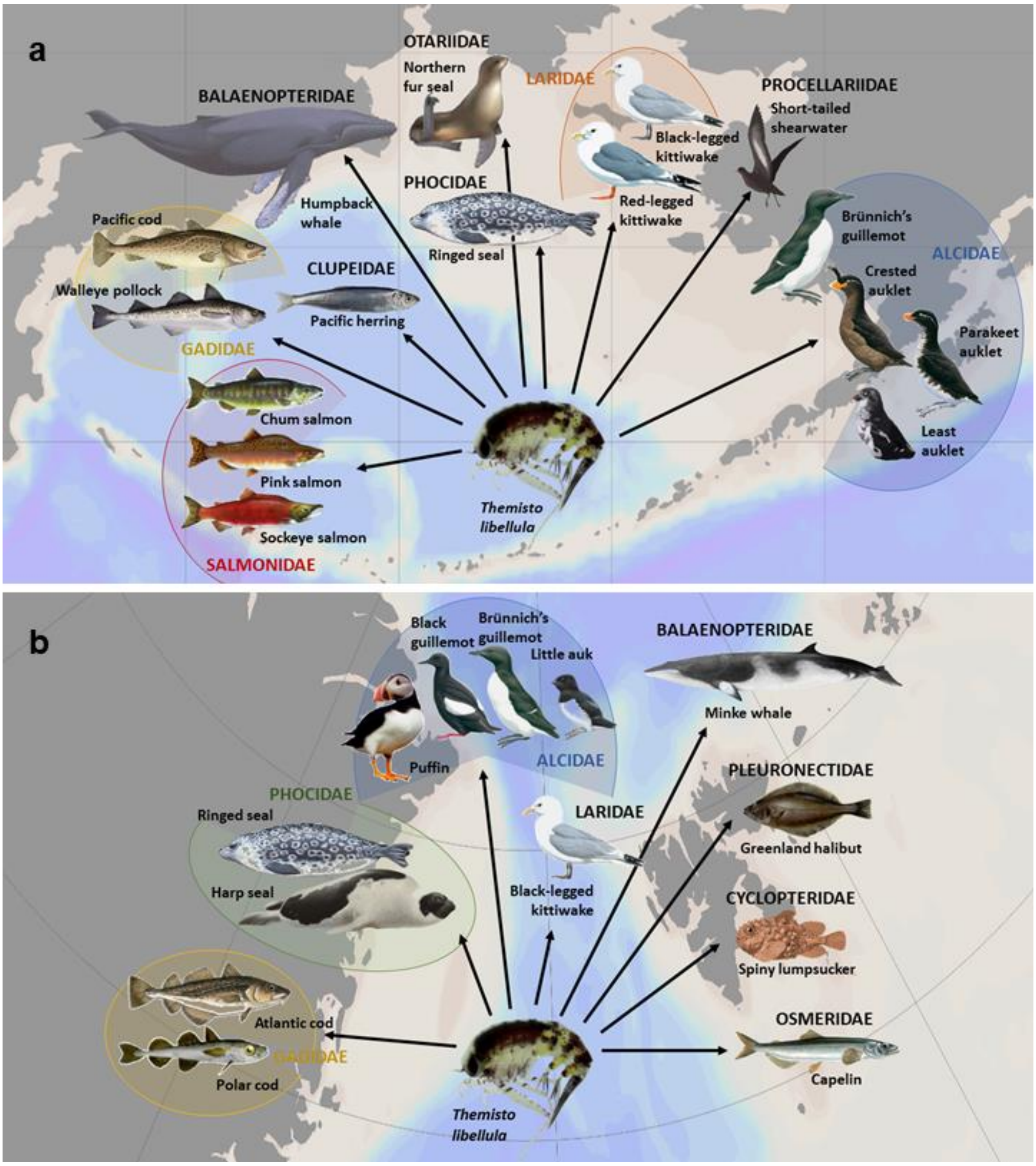


Figure 5.



a
OTARIIDAE
Northern fur seal
BALAENOPTERIDAE
LARIDAE
PROCELLARIIDAE
Short-tailed shearwater
Black-legged kittiwake
Red-legged kittiwake
PHOCIDAE
Humpback whale
Ringed seal
Pacific cod
Brünnich's guillemot
ALCIDAE
Crested auklet
CLUPEIDAE
Walleye pollock
Pacific herring
Parakeet auklet
GADIDAE
Chum salmon
Least auklet
Pink salmon
Themisto libellula
Sockeye salmon
SALMONIDAE
b
Black guillemot
Brünnich's guillemot
Little auk
BALAENOPTERIDAE
Minke whale
Puffin
ALCIDAE
PLEURONECTIDAE
PHOCIDAE
LARIDAE
Ringed seal
Greenland halibut
Harp seal
Black-legged kittiwake
CYCLOPTERIDAE
Spiny lumpsucker
Atlantic cod
GADIDAE
OSMERIDAE
Polar cod
Capelin
Themisto libellula

Figure 6.

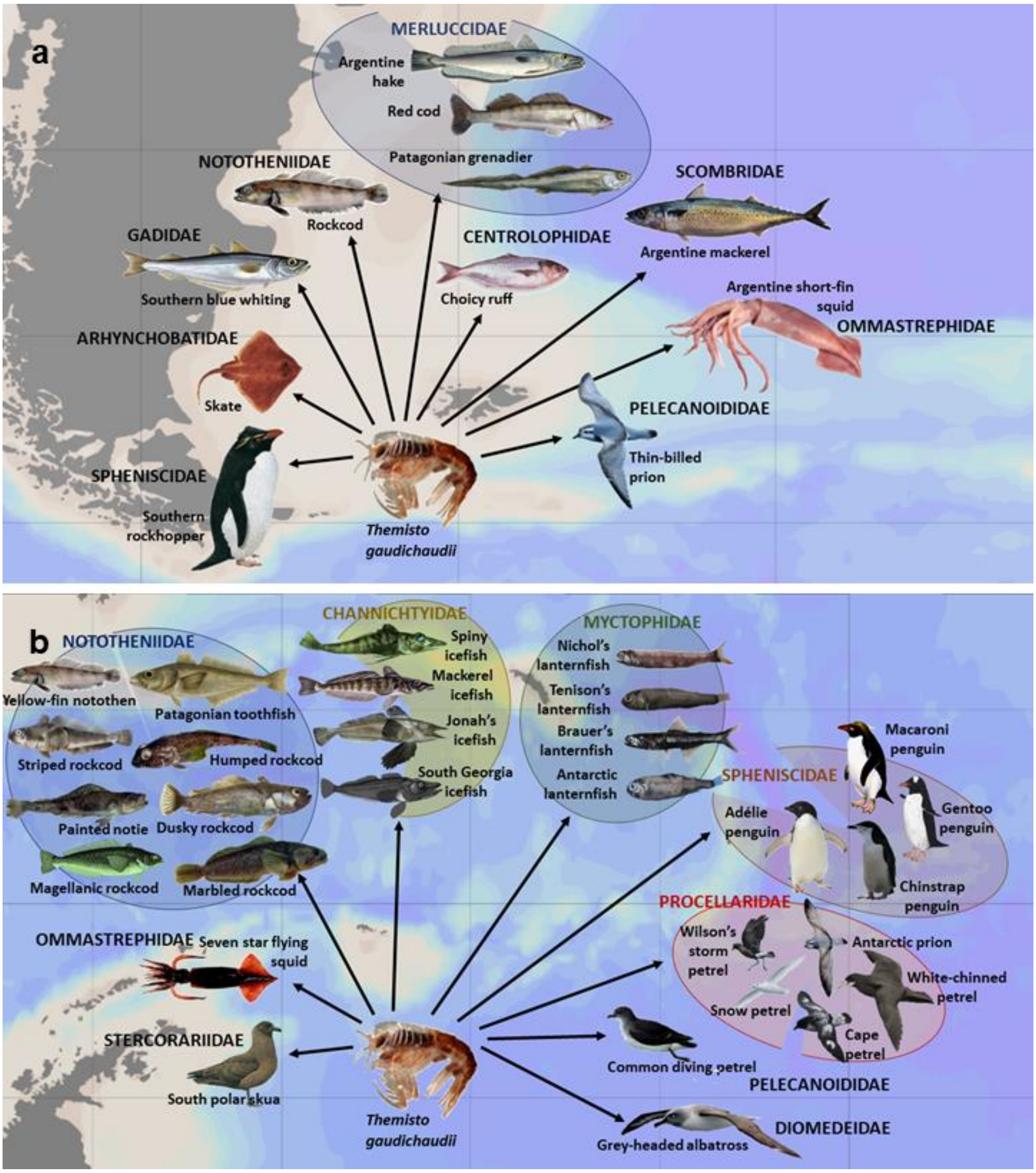

a
MERLUCCIDAE
Argentine hake
Red cod
Patagonian grenadier
NOTOTHENIIDAE
Rockcod
SCOMBRIDAE
Argentine mackerel
GADIDAE
Southern blue whiting
CENTROLOPHIDAE
Choicy ruff
Argentine short-fin squid
OMMASTREPHIDAE
ARHYNCHOBATIDAE
Skate
PELECANOIDIDAE
Thin-billed prion
SPHENISCIDAE
Southern rockhopper
Themisto gaudichaudii
b
NOTOTHENIIDAE
Yellow-fin notothen
Patagonian toothfish
Striped rockcod
Humped rockcod
Painted notie
Dusky rockcod
Magellanic rockcod
Marbled rockcod
CHANNICHTYIDAE
Spiny icefish
Mackerel icefish
Jonah's icefish
South Georgia icefish
MYCTOPHIDAE
Nichol's lanternfish
Tenison's lanternfish
Brauer's lanternfish
Antarctic lanternfish
SPHENISCIDAE
Macaroni penguin
Adélie penguin
Gentoo penguin
Chinstrap penguin
PROCELLARIDAE
Wilson's storm petrel
Antarctic prion
White-chinned petrel
Snow petrel
Cape petrel
OMMASTREPHIDAE
Seven star flying squid
STERCORARIIDAE
South polar skua
Themisto gaudichaudii
Common diving petrel
PELECANOIDIDAE
Grey-headed albatross
DIOMEDEIDAE

Figure 7.

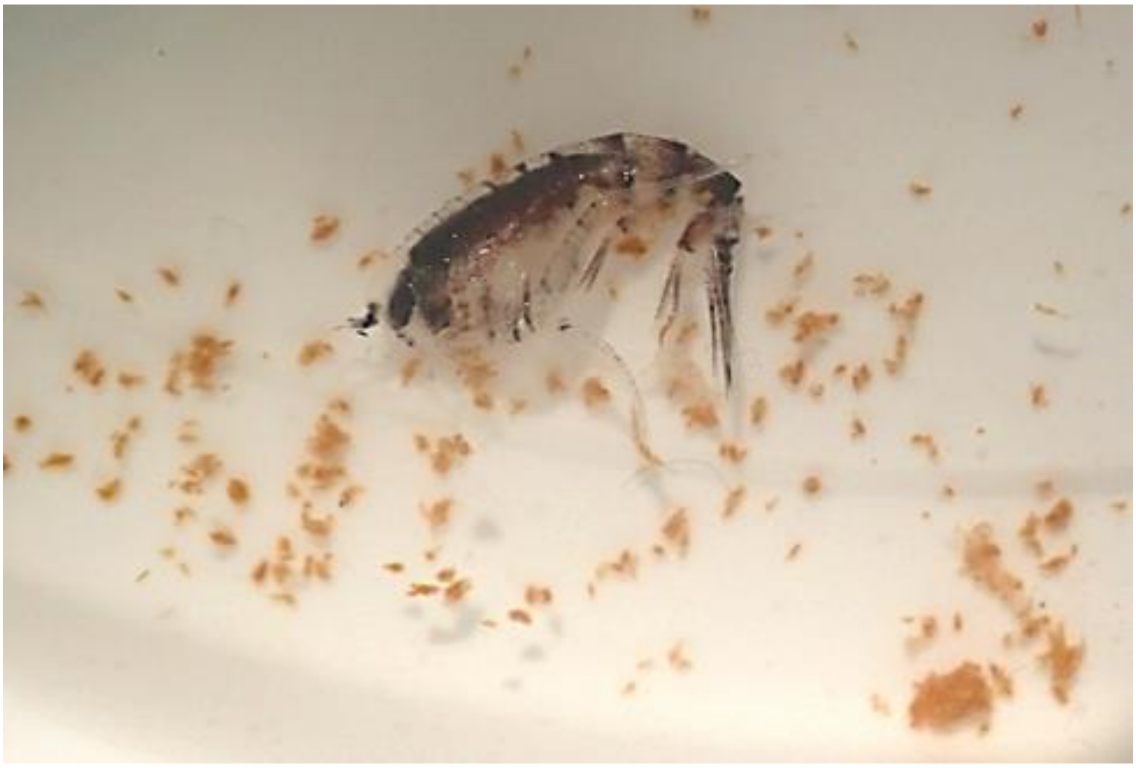
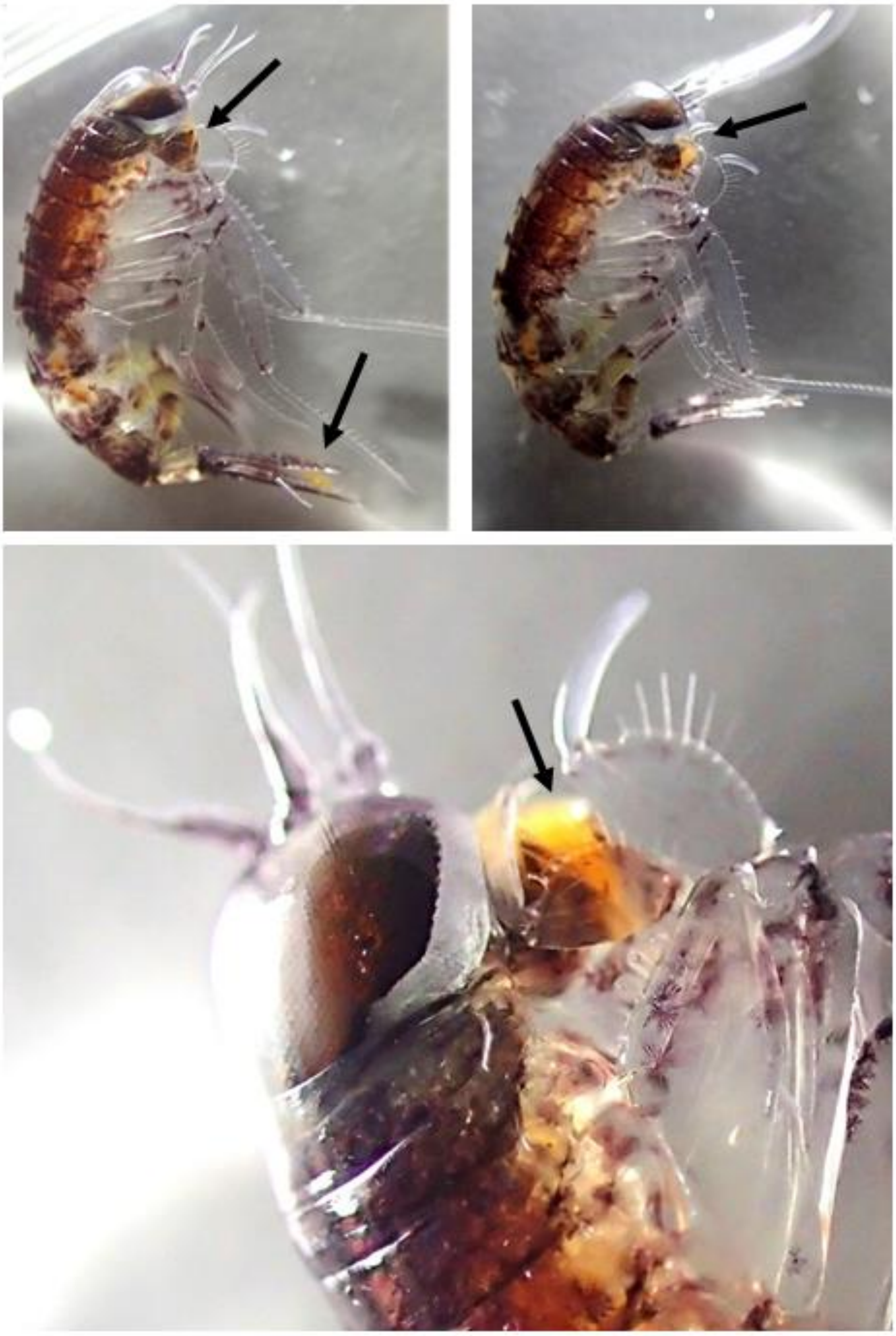


Figure 8.



Predatory zooplankton on the move: *Themisto* amphipods in high-latitude pelagic food webs

Advances in Marine Biology

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Supporting Information

Table S1: Importance of *Themisto* species as major prey in the diet of cephalopods, fish, birds and marine mammals. A non-exhaustive list compiled from literature. Predator species followed by an * represent a species at the basis of a (major) commercial fishery, raised for aquaculture, or an important bycatch species. Past fisheries are indicated by their time span between brackets. Abbreviations: NZ – New Zealand, SA – South Africa.

Species	Region	References
Themisto gaudichaudii		
Cephalopods		
OMMASTREPHIDAE		
Illex argentinus (Argentine shortfin squid)*	Southern Patagonian Shelf	Ivanovic & Brunetti, 1994
Illex argentinus (Argentine shortfin squid)*	Falkland Islands	Mouat et al., 2001; Laptikovsky, 2002
Martialia hyadesi (Seven star flying squid)*	South Georgia	Dickson et al., 2004
Martialia hyadesi (Seven star flying squid)*	NE Falkland Islands	González et al., 1997
CRANCHIIDAE		
Galiteuthis glacialis	South Shetlands	Nemoto et al., 1985
ONYCHOTEUTHIDAE		
Onykia ingens (Greater hooked squid)	Falkland Islands	Phillips et al., 2003
*Kondakovia longimana (*Giant warty squid*)*	Southern Ocean (90°-50°W)	Nemoto et al., 1985
Fish		
NOTOTHENIIDAE – Cod icefishes		
Gobionotothen gibberifrons (Humped rockcod)	South Georgia	Targett, 1981; Jażdżewski & Presler, 1988
Gobionotothen gibberifrons (Humped rockcod)	southern Scotia Sea	Rembiszewski et al., 1978
Gobionotothen gibberifrons (Humped rockcod)	South Orkneys	Targett, 1981
Gobionotothen gibberifrons (Humped rockcod)	Bransfield Strait	Jażdżewski & Presler, 1988
Notothenia rossii (Marbled rockcod)	South Georgia	Hoshiai, 1979; Jażdżewski & Presler, 1988
Notothenia rossii (Marbled rockcod)	Heard & McDonald Islands	Williams, 1983
Notothenia coriiceps (Black rockcod)	McDonald Island	Williams, 1963
Notothenia microlepidota (Small-scaled cod)	Campbell Plateau (NZ)	Clark, 1985
Paranotothenia magellanica (Magellanic rockcod)	Scotia Sea	Rembiszewski et al., 1978
Lepidonotothen larseni (Painted notie)	South Georgia	Targett, 1981; Jażdżewski & Presler, 1988
Lepidonotothen larseni (Painted notie)	South Orkneys	Targett, 1981
Trematomus hansoni (Striped rockcod)	South Georgia	Jażdżewski & Presler, 1988
Trematomus lepidorhinus (Slender scalyhead)	Western Ross Sea	Takahashi & Nemoto, 1984
Trematomus newnesi (Dusky rockcod)	South Orkneys	Targett, 1981
Dissostichus eleginoides (Patagonian toothfish)*	Shag Rocks & South Georgia	Collins et al., 2007
Patagonotothen ramsayi (Rock cod)*	Southern Patagonian Shelf	Padovani et al., 2012
Patagonotothen ramsayi (Rock cod)*	Falkland Islands	Laptikhovsky & Arkhipkin, 2003
Patagonotothen guntheri (Yellow-fin notothen)*(1978-1990)	Shag Rocks & South Georgia	Collins et al., 2008
Pleuragramma antarctica (Antarctic silverfish)	Ross Sea	Takahashi & Nemoto, 1984; La Mesa et al., 2004
CHANNICHTYIDAE – Icefishes		
Chaenodraco wilsoni (Spiny icefish)	Joinville Island	Kock et al., 2004
Champsocephalus gunnari (Mackerel icefish)*(1975-1990)	Shag Rocks, South Georgia	Kock et al., 1994; Jażdżewski & Presler, 1988
Neopagetopsis ionah (Ionah's icefish)	Scotia Sea	Rembiszewski et al., 1978
Pseudochaenichthys georgianus (South Georgia icefish)	South Georgia	Clarke et al., 2008
MERLUCCIIDAE		
Merluccius capensis and *M. paradoxus* (Cape Hakes)*	Benguela Upwelling System	Pillar & Barange, 1997
Merluccius hubbsi (Argentine hake)*	Southern Patagonian Shelf	Padovani et al., 2012
Merluccius hubbsi (Argentine hake)*	Southwest Atlantic Ocean	Angelescu & Cousseau, 1969
Merluccius hubbsi (Argentine hake)*	San Gorge Gulf	Temperoni et al., 2013
Salilota australis (Red Cod)*	Falkland Islands	Arkhipkin et al., 2001
Macruronus magellanicus (hoki, Patagonian grenadier)*	Southern Patagonian Shelf	Padovani et al., 2012
Macruronus magellanicus (hoki, Patagonian grenadier)*	Southwest Atlantic	Giussi et al., 2016
Macruronus magellanicus (hoki, Patagonian grenadier)*	Falklands Isl./Islas Malvinas	Brickle et al., 2009
Macruronus novaezelandicae (hoki)	Campbell Plateau (NZ)	Clark, 1985
MACROURIDAE – grenadiers or rattails		

Lepidorhynchus denticulatus (Javelin fish)	Campbell Plateau (NZ)	Clark, 1985
Malacocephalus laevis (Armed grenadier)	W coast SA, Agulhas Bank	Anderson, 2005
Coelorinchus braueri (Shovelnose grenadier)	W coast SA, Agulhas Bank	Anderson, 2005
Coelorinchus matamua (Mahia whiptail)	W coast SA, Agulhas Bank	Anderson, 2005
Coelorinchus simorhynchus	W coast SA, Agulhas Bank	Anderson, 2005
Coryphaenoides striaturus (Striate whiptail)	W coast SA, Agulhas Bank	Anderson, 2005
Lucigadus ori (Bronze whiptail)	W coast SA, Agulhas Bank	Anderson, 2005
Nezumia micronychodon (Small-tooth grenadier)	W coast SA, Agulhas Bank	Anderson, 2005
Nezumia umbracincta	W coast SA, Agulhas Bank	Anderson, 2005
Macrourus carinatus	Southwest Atlantic	Giussi et al., 2010
ARHYNCHOBATIDAE		
Bathyraja spp. (Skates)*	Falkland Isl./Islas Malvinas	Brickle et al., 2003
ARGENTINIDAE		
Argentina elongata (Silverside)	Campbell Plateau (NZ)	Clark, 1985
CENTROLOPHIDAE - Medusafishes		
Seriolella porosa (Choicy ruff)*	Southern Patagonian Shelf	Padovani et al., 2012
GADIDAE – Codfishes		
Micromesistius australis (Southern blue whiting)*	Southern Patagonian Shelf	Padovani et al., 2012
Micromesistius australis (Southern blue whiting)*	Campbell Plateau (NZ)	Clark, 1985
Micromesistius australis (Southern blue whiting)*	Falkland Islands	Brickle et al., 2009
SCOMBRIDAE		
Scomber japonicas marplatensis (Argentine mackerel)*	Argentine Sea	Angelescu, 1979
Allothunnus fallai (Slender tuna)*	S Pacific, S Peru current	Yatsu, 1995
MYCTOPHIDAE – Lanternfishes		
Electrona antarctica (Antarctic lanternfish)	northern Scotia Sea	Shreeve et al., 2009
Electrona antarctica (Antarctic lanternfish)	South Georgia	Rowedder, 1979
Metelectrona herwigi (Herwig lanternfish)	Sub-Tropical Front	Pakhomov et al., 1996
Protomyctophum choriodon (Gaptooth lanternfish)	36-51°S	Pakhomov et al., 1996
Gymnoscopelus braueri (Brauer's lanternfish)	northern Scotia Sea	Jażdżewski & Presler, 1988; Shreeve et al., 2009
Gymnoscopelus nicholsi (Nichol's lanternfish)	Scotia Sea	Rembiszewski et al., 1978
Gymnoscopelus nicholsi (Nichol's lanternfish)	Sub-Tropical Front to APF	Pakhomov et al., 1996
Protomyctophum tenisoni (Tenison's lanternfish)	Scotia Sea	Rembiszewski et al., 1978
NOTACANTHIDAE		
Notacanthus sexspinis (Spiny-back eel)	W coast SA, Agulhas Bank	Anderson, 2005
OPHIDIIDAE – Cusk eels		
Genypterus blacodes (Pink cusk-eel)	Falkland Islands	Nyegaard et al., 2004
SERRANIDAE		
Lepidoperca aurantia (Orange Perch)	Chatman Rise, NZ	Horn et al., 2013
Birds		
SPHENISCIDAE – Penguins		
Eudyptes chrysolophus (Macaroni penguin)	South Georgia	Croxall et al., 1997, 1999; Waluda et al., 2012
Eudyptes chrysolophus (Macaroni penguin)	Crozet Islands	Ridoux, 1994
Eudyptes chrysolophus (Macaroni penguin)	Marion Island	Brown & Klages, 1987
Pygoscelis adeliae (Adélie penguin)	King George Island	Volkman et al., 1980; Jażdżewski, 1981
Pygoscelis adeliae (Adélie penguin)	Adélie Land	Ridoux & Offredo, 1989
Pygoscelis adeliae (Adélie penguin)	Laurie Island, S Orkneys	Libertelli et al., 2003
Pygoscelis adeliae (Adélie penguin)	Shirley Island, E Antarctica	Kent et al., 1998
Pygoscelis antarcticus (Chinstrap penguin)	King George Island	Volkman et al., 1980; Jażdżewski, 1981
Pygoscelis papua (Gentoo penguin)	Kerguelen Islands	Bost et al., 1994; Lescroël et al., 2004
Pygoscelis papua (Gentoo penguin)	South Georgia	Williams, 1991, Xavier et al., 2018
Pygoscelis papua (Gentoo penguin)	Heard Island	Ealey, 1954; Green & Wong, 1992
Pygoscelis papua (Gentoo penguin)	Kerguelen Islands	Bost et al., 1994
Eudyptes chrysocome chrysocome (Southern rockhopper)	Tierra del Fuego	Schiavini & Raya Rey, 2004
Eudyptes chrysocome (Rockhopper penguin)	Kerguelen Islands	Bocher et al., 2001; Tremblay & Cherel, 2003
Eudyptes chrysocome (Rockhopper penguin)	Heard Island	Ealey, 1954
Eudyptes chrysocome (Rockhopper penguin)	Macquarie Island	Horne, 1985
Eudyptes schlegeli (Royal penguin)	Macquarie Island	Horne, 1985
STERCORARIIDAE – Skuas		
Stercorarius maccormicki (South polar skua)	Ant. Peninsula, S Scotia Sea	Reinhardt et al., 2000
PELECANOIDIDAE		
Pelecanoides urinatrix (Common diving petrel)	Kerguelen Islands	Bocher et al., 2000, 2001
Pelecanoides urinatrix (Common diving petrel)	Crozet Islands	Ridoux, 1994
Pelecanoides urinatrix (Common diving petrel)	South Georgia	Reid et al., 1997
PROCELLARIDAE		
Pachyptila belcheri (Thin-billed prion)	Falkland Islands	Quillfeldt et al., 2010, 2011
Pachyptila belcheri (Thin-billed prion)	Kerguelen Islands	Bocher et al., 2001; Cherel et al., 2002a
Pachyptila desolata (Antarctic prion)	Kerguelen Islands	Bocher et al., 2001; Cherel et al., 2002a
Pachyptila desolata (Antarctic prion)	South Georgia	Croxall et al., 1997, 1999
Pachyptila salvini (Salvin's prion)	Crozet Islands	Ridoux, 1994
Pachyptila turtur (Fairy prion)	Crozet Islands	Ridoux, 1994
Pachyptila crassirostris (Fulmar prion)	Heard Island	Ealey, 1954
Procellaria aequinoctialis (White-chinned petrel)	Marion Island	Cooper et al., 1992
Procellaria aequinoctialis (White-chinned petrel)	Crozet Islands	Ridoux, 1994; Catard et al. 2000; Connan et al. 2007
Procellaria aequinoctialis (White-chinned petrel)	South Georgia	Berrow et al., 2000
Pterodroma mollis (Soft-plumaged petrel)	Crozet Islands	Ridoux, 1994
Daption capense (Cape petrel)	Crozet Islands	Ridoux, 1994
Daption capense (Cape petrel)	South Orkneys, Signy Isl.	Fijn et al., 2012

Halobaena caerulea (Blue petrel)	Crozet Islands	Ridoux, 1994
Halobaena caerulea (Blue petrel)	Kerguelen Islands	Bocher et al., 2001; Cherel et al., 2002b
Halobaena caerulea (Blue petrel)	Marion Island	Steele & Klages, 1986
Puffinus tenuirostris (Short-tailed shearwater)	Bruny Island, Tasmania	Weimerskirch & Cherel, 1998; Connan et al., 2010
Fulmares glacialoides (Antarctic fulmar)	Adélie Land	Ridoux & Offredo, 1989
Pagodroma nivea (Snow petrel)	Adélie Land	Ridoux & Offredo, 1989
Pagodroma nivea (Snow petrel)	South Orkneys, Signy Isl.	Fijn et al., 2012
HYDROBATIDAE – Storm petrels		
Oceanites oceanicus (Wilson's storm petrel)	Crozet Islands	Ridoux, 1994
Oceanites oceanicus (Wilson's storm petrel)	South Georgia	Croxall et al.,1988
Fregetta tropica (Black-bellied storm petrel)	Crozet Islands	Ridoux, 1994
DIOMEDEIDAE – Albatrosses		
Thalassarche chrysostoma (Grey-headed albatross)	Crozet &, Kerguelen Islands	Ridoux, 1994; Cherel et al., 2002c
Thalassarche chrysostoma (Grey-headed albatross)	South Georgia	Xavier et al., 2003
Thalassarche chrysostoma (Grey-headed albatross)	Marion Island	Connan et al., 2014
Thalassarche melanophrys (Black-browed albatross)	Kerguelen Islands	Cherel et al., 2000; 2002c
Thalassarche melanophrys (Black-browed albatross)	Diego Ramirez Isl, Chile	Arata & Xavier, 2003
Phoebetria fusca (Sooty albatross)	Marion Island	Cooper & Klages, 1995
Phoebetria palbeprata (Light-mantled sooty albatross)	Marion Island	Cooper & Klages, 1995
Phoebetria palbeprata (Light-mantled sooty albatross)	Macquarie Island	Green et al., 1998
Marine mammals		
PHOCIDAE – True seals		
Mirounga leonina (southern Elephant Island)	Macquarie Island	Green & Burton, 1993
OTARIIDAE – Eared seals		
Arctocephalus gazella (Antarctic fur seal)	Kerguelen Islands	Lea et al. 2002, 2008
BALAENOPTERIDAE – Rorquals		
Balaenoptera borealis (Sei whale)	Polar Frontal zone	Nemoto, 1970
Balaenoptera borealis (Sei whale)	Sub-Antarctic 170°W-170°E	Nemoto, 1962
Balaenoptera borealis (Sei whale)	Indian sector SO	Bottino, 1978
Themisto libellula		
Fish		
CLUPEIDAE		
Clupea pallasii (Pacific herring)*****	SE Bering Sea	Pinchuk et al., 2013
GADIDAE – Codfishes		
Gadus macrocephalus (Pacific cod)*****	SE Bering Sea	Pinchuk et al., 2013
Gadus chalcogrammus (Walleye pollock)*****	Bering Sea	Yoshida, 1984; Pinchuk et al., 2013
Boreogadus saida (Polar cod)	W Barents Sea, Svalbard	Lønne & Gulliksen, 1989
Boreogadus saida (Polar cod)	Canadian Beaufort Sea	Majewski et al., 2016
Boreogadus saida (Polar cod)	NE Greenland	Christiansen et al., 2012
Gadus morhua (Atlantic cod)*****	Barents Sea	Bogstad & Mehl, 1997
Arctogadus glacialis (Arctic cod)	NE Greenland (polynya)	Süfke et al., 1998; Christiansen et al., 2012
SALMONIDAE – Salmons		
Oncorhynchus keta (Chum salmon)*****	Bering Sea	Pinchuk et al., 2013
Oncorhynchus keta (Chum salmon)*****	Sea of Okhotsk	Karpenko et al., 2007
Oncorhynchus nerka (Sockeye salmon)*****	Bering Sea	Pinchuk et al., 2013
Oncorhynchus gorbuscha (Pink salmon)*****	Bering Sea	Pinchuk et al., 2013
Oncorhynchus gorbuscha (Pink salmon)*****	Sea of Okhotsk	Karpenko et al., 2007
Salvelinus alpinus (Arctic char)*****	Baffin Island	Moore & Moore, 1974
Salmo salar (Atlantic salmon)	Canadian high Arctic	Neilson & Gills, 1979
OSMERIDAE		
Mallotus villosus (Capelin)*****	Barents Sea	Lund, 1981; Ajiad & Pushaeva, 1991
PLEURONECTIDAE – Righteye flounders		
Reinhardtius hippoglossoides (Greenland halibut)*****	Greenland waters	Smidt, 1969; Haug et al. 1989; Michalsen et al., 1998
Reinhardtius hippoglossoides (Greenland halibut)*****	Kara Sea	Dolgov & Benzik, 2017
CYCLOPTERIDAE		
Eumicrotremus spinosus (Spiny lumpsucker)	Svalbard waters	Berge & Nahrgang, 2013
Birds		
ALCIDAE – Auks		
Uria lomvia (Brünnich's guillemot)	Gulf of Anadyr, N Bering Sea	Ogi & Hamanaka, 1982
Uria lomvia (Brünnich's guillemot)	E Bering Sea	Hunt et al., 1981
Uria lomvia (Brünnich's guillemot)	W Barents Sea (ice-covered)	Lønne & Gabrielsen, 1992
Uria lomvia (Brünnich's guillemot)	Svalbard, Barents Sea	Lydersen et al., 1989
Cepphus grylle (Black guillemot)	W Barents Sea (ice-covered)	Lønne & Gabrielsen, 1992
Cepphus grylle (Black guillemot)	Svalbard, Barents Sea	Lydersen et al., 1989
Aethia pusilla (Least auklet)	St Lawrence Island, Alaska	Bédard, 1969
Aethia cristatella (Crested auklet)	St Lawrence Island, Alaska	Bédard, 1969
Aethia psittacula (Parakeet auklet)	St Lawrence Island, Alaska	Bédard, 1969
Alle alle (Little Auk)	W Barents Sea (ice-covered)	Lønne & Gabrielsen, 1992
Alle alle (Little Auk)	W Barents Sea, Svalbard	Lydersen et al., 1989; Steen et al., 2007
Alle alle (Little Auk)	W Greenland	Pedersen & Falk, 2001
Alle alle (Little auk)	Bear Isl., Barents Sea	Weslawski et al., 1999
Fratercula arctica (Puffin)	W Barents Sea, Svalbard	Lydersen et al., 1989
PROCELLARIIDAE (puffins)		
Puffinus tenuirostris (Short-tailed shearwater)	NE Bering Sea shelf	Ogi et al., 1980
Puffinus tenuirostris (Short-tailed shearwater)	E Bering Sea	Hunt et al., 1981

LARIDAE		
Rissa tridactyla (Black-legged kittiwakes)	E Bering Sea	Sinclair et al., 2008
Rissa tridactyla (Black-legged kittiwakes)	Svalbard	Lydersen et al., 1989
Rissa tridactyla (Black-legged kittiwakes)	W Barents Sea (ice-covered)	Lønne & Gabrielsen, 1992
Rissa brevirostris (Red-legged kittiwakes)	E Bering Sea	Sinclair et al., 2008
Marine mammals		
PHOCIDAE – True seals		
Phoca hispida (Ringed seal)	Canadian High Arctic	Bradstreet & Finley, 1983
Phoca hispida (Ringed seal)	Point Barrow, Alaska	Lowry et al., 1978
Phoca hispida (Ringed seal)	Canadian Western Arctic	Smith, 1987
Phoca hispida (Ringed seal)	Canadian Eastern Arctic	Dunbar, 1941; McLaren, 1958
Phoca hispida (Ringed seal)	Svalbard fjord	Weslawski et al., 1994
Phoca hispida (Ringed seal)	NW Greenland	Vibe, 1950
Phoca hispida (Ringed seal)	Kara Sea	Chapskii, 1940
Phoca hispida (Ringed seal)	Chukchi Peninsula	Fedoseev, 1976
Phoca hispida (Ringed seal)	Alaskan and Canadian Arctic	Dehn et al., 2007
Phoca hispida (Ringed seal)	Bering Sea	Lowry et al., 1982
Phoca hispida (Ringed seal)	Barents Sea	Whatne et al., 2000
Erignathus barbatus (Bearded seal)	Alaskan and Canadian Arctic	Dehn et al., 2007
Phoca largha (Spotted seal)	Alaskan and Canadian Arctic	Dehn et al., 2007
Pagophilus groenlandicus (Harp seal)	Barents Sea	Lydersen et al., 1991, Nilsen et al. 1991,1992, 1995
Pagophilus groenlandicus (Harp seal)	NW, central W Greenland	Finley et al., 1990; Kapel, 2000
Pagophilus groenlandicus (Harp seal)	Greenland Sea, E Greenland	Enoksen, 2014
OTARIIDAE – Eared seals		
Callorhinus ursinus (Northern fur seal)	E Bering Sea Shelf	Harry & Hartley, 1981
BALAENOPTERIDAE – Rorquals		
Megaptera novaeangliae (Humpback whale)	Bering Strait, Chukchi Sea	Tomilin, 1957
Balaenoptera acutorostrata (Minke whale)	Barents Sea	Haug et al., 1993
Balaena mysticetus (Bowhead whale)	Beaufort Sea	Lowry & Frost, 1984; Lowry et al., 2004
Themisto abyssorum		
Squid		
OMMASTREPHIDAE		
Todarodes sagittatus (European flying squid)*****	North Norwegian waters	Breiby & Jobling, 1985
Fish		
OSMERIDAE		
Mallotus villosus (Capelin)*****	Barents Sea	Lund, 1981; Ajiad & Pushaeva, 1991
GADIDAE – Codfishes		
Gadus morhua (Atlantic cod)*****	Barents Sea	Bogstad & Mehl, 1997
Arctogadus glacialis (Arctic cod)	NE Greenland (polynya)	Süfke et al., 1998; Christiansen et al., 2012
Boreogadus saida (Polar cod)	NE Greenland fjords	Christiansen et al., 2012
Boreogadus saida (Polar cod)	Canadian Beaufort Sea	Majewski et al., 2016
MYCTOPHIDAE – Lanternfishes		
Lampanyctus macdonaldi (MacDonald's lanternfish)	Greenland Sea	Klimpel et al., 2006
Birds		
ALCIDAE – Auks		
Alle alle (Little auk)	W Spitsbergen fjord	Steen et al., 2007
Alle alle (Little auk)	Bear Isl., Barents Sea	Weslawski et al., 1999
Themisto australis		
Fish		
MACROURIDAE – grenadiers or rattails		
Lepidorhynchus denticulatus (Javelin fish)	Chatman Rise, NZ	Stevens & Dunn, 2011
Coelorinchus oliverianus (Hawknose grenadier)	Chatman Rise, NZ	Stevens & Dunn, 2011
Birds		
PELECANOIDIDAE		
Pelecanoides urinatrix urinatrix (Common diving petrel)	SE Australia	Schumann et al., 2008
PROCELLARIIDAE		
Puffinus tenuirostris (Short-tailed shearwater)	Bruny Island, Tasmania	Weimerskirch & Cherel, 1998
Puffinus griseus (Sooty shearwater)	New Zealand	Cruz et al., 2001
Themisto pacifica		
Squid		
OMMASTREPHIDAE		
Todarodes pacificus (Japanese common squid)*****	Sea of Japan	Okiyama, 1965; Uchikawa & Kidokoro, 2014
GONATIDAE		
Berryteuthis anonychus (Minimal armhook squid)	NE Pacific	Uchikawa et al., 2004
Fish		
SALMONIDAE – Salmons		
Oncorhynchus kisutch (Coho salmon)*****	Northern California current	Brodeur, 1989; Brodeur et al., 2013
Oncorhynchus mykiss (Steelhead salmon)	Northern California current	Brodeur et al., 2013
Oncorhynchus gorbuscha (Pink salmon)*****	Offshore Japan Sea	Fukataki, 1967
Oncorhynchus masou (Masu salmon)*****	Offshore Japan Sea	Fukataki, 1969
Oncorhynchus spp.	Central Gulf of Alaska	Kaeriyama et al., 2004
Oncorhynchus keta (Chum salmon)*****	Aleutian Basin	Kosenok & Naidenko, 2008

Oncorhynchus keta (Chum salmon)*****	Central Bering sea	Sakai et al., 2012
GADIDAE – Codfishes		
Gadus macrocephalus (Pacific cod)*****	Eastern coast N Japan	Yamamura, 1993
Gadus chalcogrammus (Alaska/Walleye pollock)*****	Off Iwate, E Japan	Fujita et al., 1995
Gadus chalcogrammus (Alaska/Walleye pollock)*****	Gulf of Alaska	Brodeur, 1998
Gadus chalcogrammus (Alaska/Walleye pollock)*****	Northern Japan	Yamamura et al., 2002
MACROURIDAE – Grenadiers		
Albatrossia pectoralis (Giant grenadier)	NW Pacific	Chuchukalo & Napazakov, 2012
MYCTOPHIDAE – Lanternfishes		
Stenobrachius leucopsarus (Northern lanternfish)	Central Bering Sea	Tanimata et al., 2008
Stenobrachius leucopsarus (Northern lanternfish)	Western North Pacific	Moku et al., 2000
Stenobrachius leucopsarus (Northern lanternfish)	Northern California current	Suntsov & Brodeur, 2008
Tarletonbeania crenularis	Northern California current	Suntsov & Brodeur, 2008
Diaphus theta (California headlightfish)	Western North Pacific	Moku et al., 2000
Diaphus theta (California headlightfish)	Northern California current	Suntsov & Brodeur, 2008
SEBASTIDAE – Rockfishes		
Sebastes entomelas (Widow rockfish)	Off Oregon	Bosley et al., 2014
Sebastes flavidus (Yellowtail rockfish)	Off Oregon	Bosley et al., 2014
Sebastes crameri (Darkblotched rockfish)	Off Oregon	Bosley et al., 2014
GONOSTOMATIDAE		
Sigmops gracilipes	NW North Pacific	Uchikawa et al., 2001b
BATHYLAGIDAE		
Leuroglossus schmidti (Northern smoothtongue)	Sea of Okhotsk	Beamish et al., 1999
Themisto japonica		
Fish		
SALMONIDAE – Salmons		
Oncorhynchus spp.	Central Gulf of Alaska	Kaeriyama et al., 2004
Oncorhynchus keta (Chum salmon)*****	Sea of Okhotsk	Karpenko et al., 2007
Oncorhynchus keta (Chum salmon)*****	Bering Sea	Karpenko & Koval, 2007
Oncorhynchus gorbuscha (Pink salmon)*****	Sea of Okhotsk	Karpenko et al., 2007
STERNOPTYCHIDAE		
Maurolicus japonicus (North Pacific lightfish)	Pacific coast N Japan	Uchikawa et al., 2001a
GADIDAE – Codfishes		
Gadus chalcogrammus (Alaska/Walleye pollock)*****	Northern Japan	Yamamura et al., 2002
Gadus macrocephalus (Pacific cod)*****	Eastern coast N Japan	Yamamura, 1993
GONOSTOMATIDAE		
Sigmops gracilipes	NW North Pacific	Uchikawa et al., 2001b
MYCTOPHIDAE – Lanternfishes		
Stenobrachius leucopsarus (Northern lanternfish)	Western North Pacific	Moku et al., 2000
Diaphus theta (California headlightfish)	Western North Pacific	Moku et al., 2000
CYCLOPTERIDAE		
Eumicrotremus asperrimus (Spiny lumpfish)	NW Sea of Japan	Antonenko et al., 2008
HEMITRIPTERIDAE		
Blepsias cirrhosis (Silverspotted sculpin)	Sea of Okhotsk	Kolpakov & Dolganova, 2006
PLEURONECTIDAE – Righteye flounders		
Hippoglossoides dubius (Flathead flounder)	Japan coast	Kimura et al., 2004
***Themisto* sp./spp.**		
Fish		
PLEURONECTIDAE		
Reinhardtius hippoglossoides (Greenland halibut)*****	West Greenland	Pedersen & Riget, 1993
Reinhardtius hippoglossoides (Greenland halibut)*****	Barents Sea	Nizovtsev, 1991
SEBASTIDAE – Rockfishes		
Sebastes spp. (Redfish)	West Greenland	Pedersen & Riget, 1993
HEXAGRAMMIDAE		
Pleurogrammus monopterygius (Atka mackerel)	Aleutian Islands	Yang, 1999
SQUALIDAE		
Squalus acanthias (Spiny dogfish)	South Island, NZ	Hanchet, 1991
CLUPEIDAE		
Clupea harengus (Atlantic herring)*****	Western Norwegian Sea	Dalpadado et al., 2000
MYCTOPHIDAE – Lanternfishes		
Lampanyctus macdonaldi (MacDonald's lanternfish)	Greenland Sea, Irminger Sea	Kimpel et al., 2006
SCIAENIDAE – Croakers		
Larimichthys polyactis (Small yellow croaker)*****	Central Yellow Sea	Xue et al., 2005

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