# Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions

## Padmini Dalpadado, Nina Borkner, Bjarte Bogstad and Sigbjørn Mehl

*Themisto abyssorum* and *Themisto libellula* were the dominant amphipod species observed in the central and the northern Barents Sea during 1984–1996. *T. abyssorum* was predominant in the subarctic waters, *T. libellula* in the Arctic waters. A third species, *Themisto compressa,* was rare and was restricted to the Atlantic waters. Our study showed peak abundances of *T. abyssorum* and *T. libellula* in summer and in early autumn. High abundances were usually associated with Polar Front waters. *T. libellula* has a more near surface distribution than *T. abyssorum*.

Followed by a decrease in the capelin stock from 1985–1987 there was an increase in the abundance of *Themisto abyssorum* and *T. libellula*, probably due to the reduced grazing pressure from capelin (*Mallotus villosus*). In the mid-1980s and 1990s when the capelin stock was at extremely low levels, cod (*Gadus morhua*) switched from capelin to alternative prey such as amphipods and krill. Detailed analysis of amphipods in the cod stomachs from 1984–1999, showed that cod fed mainly on *Themisto* spp., especially on *T. libellula*. *Themisto* species were consumed by most age groups of cod.

With an increase in the capelin stock from 1987–1991, a corresponding decrease in the abundance of *Themisto abyssorum* and *T. libellula* was observed. During 1993–1996 when the capelin stock again was at low levels, the abundance of these two amphipod species increased. The increase in abundance was less pronounced in the mid-1990s for *T. libellula* probably owing to higher grazing pressure from cod and other predators such as harp seal (*Phoca groenlandica*) and arctic sea birds. The stock size of cod in the mid-1990s was about twice the amount as in the mid-1980s. These results illustrate strong predator-prey interactions between macrozooplankton species as amphipods and capelin and cod in the Barents Sea. The amphipod populations in the Barents Sea appear to be to a large extent controlled by predation.

Keywords: amphipods, distribution, abundance, predator-prey interactions, Barents Sea.

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## Introduction

In general, amphipods are ranked third in numerical abundance of zooplankton, far exceeded by copepods and krill (Bowman, 1960). Members of the hyperiid amphipod genus *Themisto* (a senior synonym of *Parathemisto*) (Bowman *et al*., 1982), overwhelmingly dominate the cooler epipelagic amphipod fauna, and their importance in the north Atlantic has been documented (Dunbar, 1957, 1964). Of the three commonly found amphipods, *T. compressa* (Goes) and *T. abyssorum* (Boeck) are regarded as subarctic species,

whereas *T. libellula* (Mandt) is described as both arctic and subarctic (Dunbar, 1964). *T. libellula* can be regarded as a good indicator of the presence of Arctic water (Dunbar, 1964). Other amphipods, as *Hyperia* and *Gammarus,* are occasionally found in the Barents Sea (Dunbar, 1964). Gammarideans, *G. wilkitzkii*, *Onisimus* spp. and *Apherusa glacialis* dominate the invertebrate ice fauna in the Barents Sea (Syvertsen *et al.*, 1990).

The information on life cycle of amphipods is scarce. Bogorov (1940) reports a two-year life cycle for *Themisto abyssorum* in the Barents Sea. *T. libellula* can live up to two years in Hudson Bay, and in the waters of

southeast Baffin Island (Dunbar, 1957). *T. compressa* has a one year life cycle in the 0–20°E sector of the southern ocean (Kane, 1966). Laboratory studies based on intermoult period and moult increment of *Themisto japonica* (10–17 mm) from the Japan Sea indicate a life cycle of 333–593 days at 1°C and 195–347 days at 5°C (Ikeda, 1990).

Amphipods are important food of many fishes, sea birds and mammals in the Barents Sea. Studies by Lund (1981) and Ajiad and Pushchaeva (1992) show *Themisto abyssorum* and *T. libellula* to be important food in the diet of Barents Sea capelin (*Mallotus villosus*). Cod (*Gadus morhua*) which is the main predator on capelin in the Barents Sea ecosystem, switched to macro-zooplankton such as amphipods and krill when capelin stock was rather low (Bogstad and Mehl, 1997; ICES, 2000). Bowman (1960), Lønne and Gulliksen (1989), Lydersen *et al.* (1989), Nilssen *et al.* (1991, 1992), and others have shown polar cod (*Boreogadus saida*), ringed seal (*Phoca hispida*), harp seal (*Phoca groenlandica*) and many sea birds to feed heavily on *T. libellula*.

In the period 1979–1984 the zooplankton biomass showed several fold variation among years in the central Barents Sea (Skjoldal and Rey, 1989). The fish resources in the Barents Sea have also shown dramatic changes since 1983 (Gjøsæter, 1998). Skjoldal and Rey (1989) interpret these changes to be mainly due to biological interactions, such as predation and food limitation. Different advective transport from year to year from the Norwegian Sea to the Barents Sea may also determine the zooplankton abundance in the Barents Sea (Skjoldal and Rey, 1989; Giske *et al.*, 1998). Many of the advection studies in the Barents Sea are focused on the copepods, *Calanus finmarchicus*. Studies by Tande and Slagstad (1992), Slagstad and Tande (1996) and Giske *et al.* (1998) have shown that the advection of *Calanus* spp. from the Norwegian Sea might govern the amount of *Calanus* in the Barents Sea.

Though the general zoogeographical distribution of amphipods is known, there is limited information on the vertical distribution patterns as well as long time-series abundance estimates within the Barents Sea. The current study was conducted to gain more knowledge on the geographical and seasonal variation in abundance and distribution of amphipods in the central and northern Barents Sea. We also examine the interactions between amphipods and their major fish predators, with special emphasis on cod.

## Materials and methods

The present study is based on the samples of amphipods collected during several cruises to the Barents Sea from 1984–1996 (Figure 1). The sampling area covered 70°N–80°N and from 9°E–50°E. Material from 202 stations from several cruises is included in the current investigation. A MOCNESS sampler (Wiebe *et al.*, 1985) with a 1-m$^2$ mouth opening was used to collect the material for the present study. The towing speed of the boat was approximately 1.5 knots. The MOCNESS sampler was equipped with nine nets made of 180 μm (333 μm prior to 1991) nylon mesh netting. It was fished obliquely, allowing up to eight depth strata to be sampled. At most stations the MOCNESS nets were towed in oblique hauls from 200–175, 175–150, 150–125, 125–100, 100–75, 75–50, 50–25, and 25–0 m depth. The volume of the water filtered in each stratum varied from 100–600 m$^3$.

The zooplankton samples were usually separated into two halves. One half was preserved in 4% formaldehyde and the second half was used for dry weight estimates. The preserved half of the MOCNESS sample was used for species identification. Amphipods in the preserved half were identified to species and the number in each sample or sub-sample was recorded. Sub-samples were obtained by using a Motoda plankton splitter (Motoda, 1959). From both halves, the biomass per cubic meter in the depth range sampled and per square meter when integrated over the depth range, was calculated. Only the most commonly found hyperiid amphipod genus *Themisto* was taken into consideration in our study. The total length of amphipods [from the front of the head to the tip of the longest uropod (Dunbar, 1957)] was measured to the nearest mm below.

Since 1984, an extensive cod stomach sampling program has been carried out in the Barents Sea by the Institute of Marine Research (IMR), Bergen, Norway and the Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO) in Murmansk, Russia (Mehl and Yaragina, 1992). On average, about 8000 individual stomachs have been analyzed annually in the period 1984–1999. In cod stomachs, fish prey and shrimps were identified to species level at all times except when stomach contents were in an advanced state of digestion. A detailed description of methods of analysis is given by Mehl (1989). Krill, amphipods and other smaller organisms were species identified only when time and state of digestion permitted. Therefore, in the figures presenting cod stomach contents, in this study, several categories of amphipods are named varying from the general term "amphipods" to the species level. Cod stomach data presented in this paper is extracted from the joint Norwegian-Russian stomach data base. Partial stomach fullness indices (PFI) were calculated to allow comparison of quantities of prey in the stomachs of predators of various sizes (Lilly and Fleming, 1981).

A CTD drop sonde was used to obtain salinity and temperature data at MOCNESS stations. Salinity and temperature values at depths of 10, 50, 100, 200 and 500 m were used to classify sampling stations into
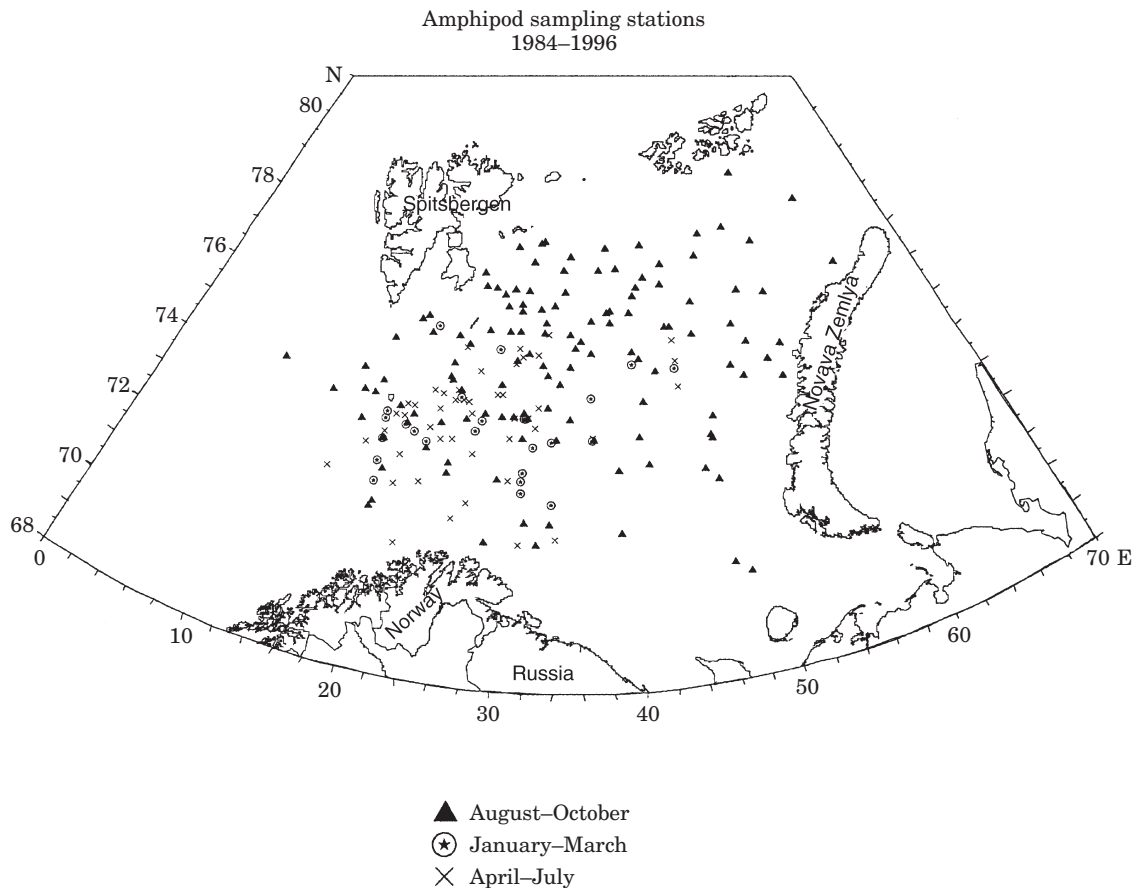
Amphipod sampling stations
1984–1996



▲ August–October
✸ January–March
✕ April–July

Figure 1. Location of MOCNESS stations during 1984–1996.

different water masses. The abundance (indiviudals m$^{-2}$) and density (ind. m$^{-3}$) of amphipods estimated in MOCNESS profiles were classified with reference to three water masses Arctic, North Atlantic and Polar Front as defined by Loeng (1991).

## Results

### Horizontal distribution

Horizontal distributions of *Themisto abyssorum* and *T. libellula* based on average numerical abundance (ind. m$^{-2}$) from all cruises are given in Figures 2 and 3, respectively. The interpolated distribution patterns of amphipods were visualized using Arc View spatial analyst (ESRI, 1996). These figures show average abundance within 1 km by 1 km grids during the study period. The interpolation was done using the griding technique Inverse Distance Weighting (IDW). Tables 1–3 show the mean density (ind. m$^{-3}$), abundance (ind. m$^{-2}$) and length for *T. abyssorum*, *T. libellula* and *T. compressa*, respectively.

*Themisto abyssorum* and *T. libellula* were the dominant amphipod species found in the central and the northern Barents Sea (Figures 2 and 3; Tables 1–3). The third species, *T. compressa* was scarce and was restricted to the Atlantic waters (Table 3). In the Arctic waters, the abundance of *T. abyssorum* was comparatively low (mean of all cruises, 5.8 ind. m$^{-2}$). In the Atlantic and Polar Front regions the abundance of this species varied from 0–269 ind. m$^{-2}$ with an average of 17.8 ind. m$^{-2}$ (Table 1). High abundances, up to 269 ind. m$^{-2}$ of this species was found in deep waters (300–400 m) south and south east of Svalbard Bank.

The distribution of *Themisto libellula* seems to be closely related to the different water masses in the Barents Sea (Figure 3). *T. libellula* was absent in about 81% of the stations taken between 70–76°N (Atlantic waters). In the area of the Polar Front, close to 76°N and between 30–32°E, high abundances up to 430 ind. m$^{-2}$ were recorded. The highest abundances of *T. libellula* were taken in the May–June 1987 and July 1988 cruises. More than 40% of the individuals taken in these two cruises were small (4–8 mm). *T. libellula* were recorded
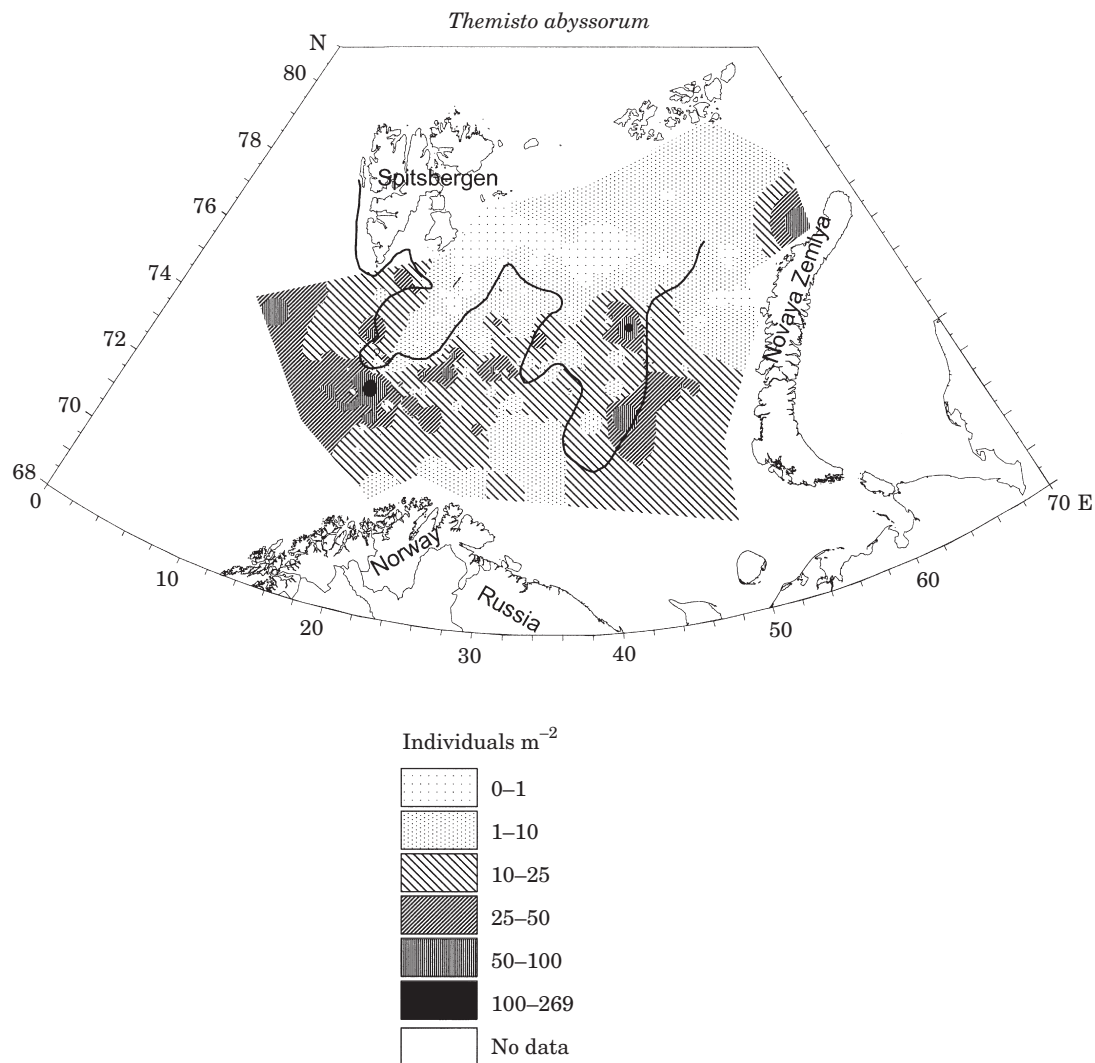
Figure 2. *Themisto abyssorum*. Horizontal distribution in the Barents Sea, based on average numerical abundance (ind. m$^{-2}$) from all cruises during 1984–1996. The thick solid line indicates the Polar Front. Note that samples were not obtained outside the shaded areas and the figure therefore does not show the total distribution area in the Barents Sea.

from all stations in the Arctic waters. The average abundance for all cruises for Arctic waters was 16.8 (range 3.9–30.8 ind. m$^{-2}$).

*Themisto compressa* was very seldom observed and was restricted to Atlantic waters. The abundances of this species were rather low, with an average of all cruises being 0.67 ind. m$^{-2}$. *T. compressa* was absent in the Arctic waters (Table 3).

## Density

The numerical densities of *Themisto abyssorum*, *T. libellula* and *T. compressa* are summarized in Tables 1–3.

Density of *T. abyssorum* in the Arctic water masses (0.018 ind. m$^{-3}$) was much lower than in Atlantic and Polar Front regions. The mean density of all cruises in Atlantic and Polar Front waters was 0.076 and 0.056 ind. m$^{-3}$, respectively (Table 1). The highest densities (>0.30) for this species were observed in July 1988 and September–October 1995 in the Atlantic waters and in July and October 1988 and in September 1994, in the Polar Front waters.

*Themisto libellula* from Arctic waters had a mean density of 0.106 ind. m$^{-3}$. In the Atlantic and Polar Front region the average density was 0.034 ind. m$^{-3}$ (Table 2). Maximum density for this species was
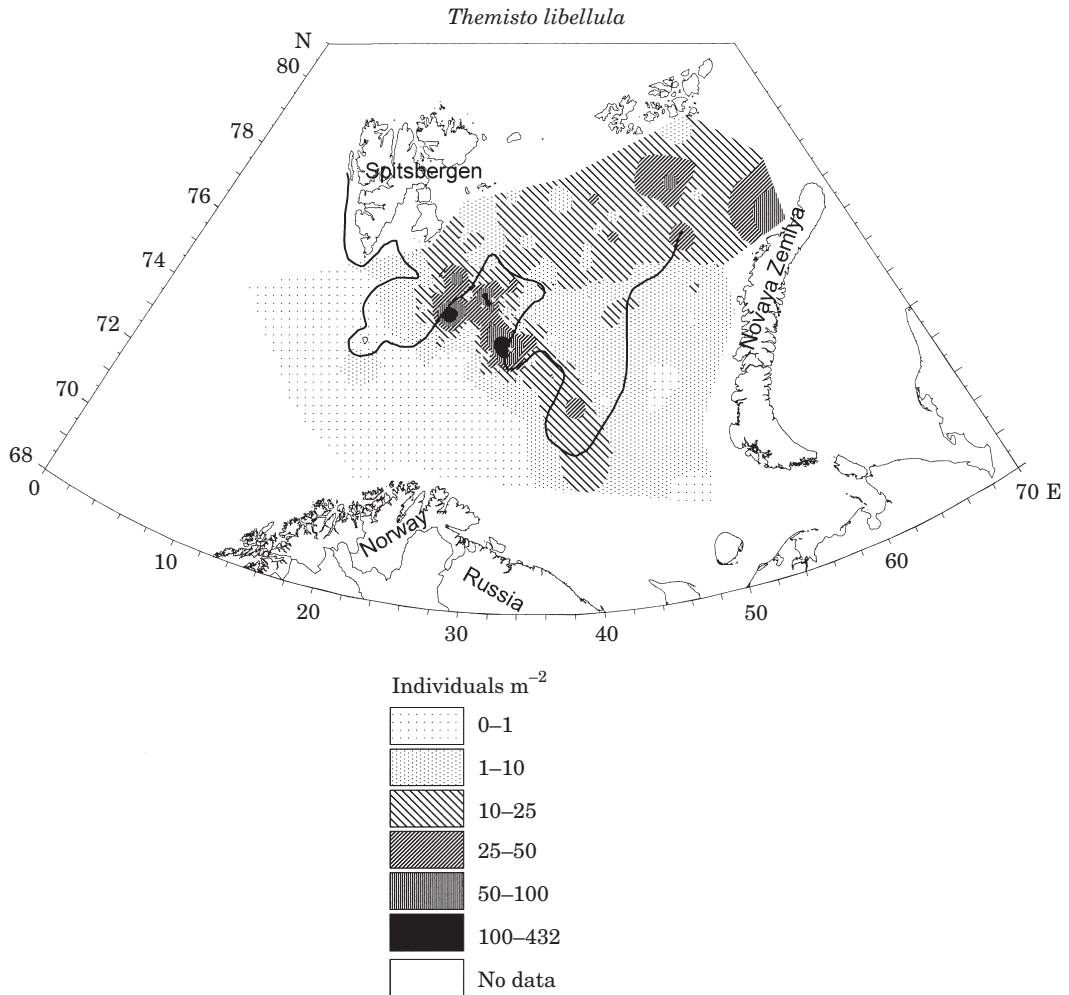
Themisto libellula



Figure 3. *Themisto libellula*. Horizontal distribution in the Barents Sea, based on average numerical abundance (ind. m$^{-2}$) from all cruises during 1984–1996. The thick solid line indicates the Polar Front. Note that samples were not obtained outside the shaded areas and the figure therefore does not show the total distribution area in the Barents Sea.

observed in August 1985 with 0.28 ind. m$^{-3}$. Very low densities of *T. compressa,* were observed, usually below 0.01 ind. m$^{-3}$ in the area investigated.

## Vertical distribution

Figure 4 shows the density of *Themisto libellula* and *T. abyssorum* against the water depth at sampling stations for two time periods, June–August and September–October.

In June–August, the highest densities of *Themisto abyssorum* were at deeper waters, at depths of 250–425 m. In September to October period a more even depth distribution, between 100–400 m was observed. *T. libellula,* on the other hand seem to prefer more shallow waters. This species was most abundant at depths above

300 m. Shallower depths in the Barents Sea are associated with colder Arctic waters. The densities of *T. libellula* below 300 m water depth was very low (<0.05 ind. m$^{-3}$)

Plots of densities of *Themisto abyssorum* and *T. libellula* against mean sampling depths for MOCNESS nets at selected stations from a selected cruise in 1996 are given in Figure 5. The highest densities of *T. abyssorum* were taken at depths below 200 m. The maximum densities of *T. libellula* were recorded from the upper 55 m. Data from a cruise in May–June 1987 also show that very high densities, up to 1.4 individuals m$^{-3}$ of *T. libellula* were taken in the upper 40 m. Data from most cruises showed this distribution pattern, indicating that *T. abyssorum* has a deeper distribution than *T. libellula*. Most of the *T. libellula* taken in the upper 50 m were

Table 1. *Themisto abyssorum*. Means and standard deviation (s.d.) of density (ind. m$^{-3}$), abundance (ind. m$^{-2}$) and total length (mm) observed during different cruises between 1984 and 1996 in Atlantic (NAW), Polar Front (PFW) and Arctic (AW) water masses.

| Type | Year | Month | Stations | Ind. m$^{-3}$ | | Ind. m$^{-2}$ | | Length (mm) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Mean | s.d. | Mean | s.d. | Mean | s.d. |
| AW | 1984 | Aug | 5 | 0.012 | 0.015 | 2.724 | 3.631 | 5.700 | 0.436 |
| AW | 1985 | Aug | 4 | 0.003 | 0.002 | 0.562 | 0.620 | 5.867 | 1.102 |
| AW | 1987 | Sep | 5 | 0.026 | 0.039 | 29.500 | 53.473 | 5.150 | 0.778 |
| AW | 1988 | July–Sep | 6 | 0.003 | 0.005 | 0.485 | 0.665 | 8.000 | 2.598 |
| AW | 1990 | Sep | 2 | 0.000 | 0.000 | 0.000 | 0.000 | | . |
| AW | 1992 | Sep | 7 | 0.018 | 0.011 | 3.294 | 1.894 | 7.271 | 2.248 |
| AW | 1993 | Aug–Sep | 2 | 0.006 | 0.001 | 1.020 | 0.057 | 7.305 | 2.044 |
| AW | 1994 | Sep | 1 | 0.000 | . | 0.000 | . | | . |
| AW | 1995 | Sep | 4 | 0.003 | 0.003 | 0.473 | 0.562 | 9.000 | 1.414 |
| AW | 1996 | Sep | 9 | 0.049 | 0.108 | 7.632 | 21.308 | 5.500 | 1.500 |
| | | | **45** | **0.018** | **0.051** | **5.821** | **20.570** | **6.760** | **1.944** |
| NAW | 1984 | Aug | 1 | 0.005 | . | 0.978 | . | 4.300 | . |
| NAW | 1985 | Jan | 1 | 0.006 | . | 1.434 | . | 10.000 | . |
| NAW | 1986 | May | 1 | 0.002 | . | 0.160 | . | 8.000 | . |
| NAW | 1987 | Jan–Sep | 6 | 0.035 | 0.026 | 9.340 | 7.018 | 8.742 | 3.574 |
| NAW | 1988 | Mar–Oct | 5 | 0.130 | 0.170 | 39.900 | 51.488 | 7.750 | 2.917 |
| NAW | 1989 | Jan–May | 8 | 0.050 | 0.031 | 14.751 | 10.908 | 10.300 | 1.108 |
| NAW | 1990 | Sep | 2 | 0.063 | 0.058 | 15.815 | 11.816 | 8.900 | 0.707 |
| NAW | 1991 | Jan–Jun | 7 | 0.007 | 0.015 | 2.716 | 6.235 | 10.300 | 3.843 |
| NAW | 1992 | Sep–Oct | 5 | 0.076 | 0.042 | 26.718 | 18.187 | 9.604 | 1.032 |
| NAW | 1993 | June–Sep | 13 | 0.052 | 0.051 | 14.740 | 16.006 | 6.485 | 2.200 |
| NAW | 1994 | Sep | 4 | 0.200 | 0.111 | 59.530 | 40.800 | 8.945 | 0.630 |
| NAW | 1995 | Sep–Oct | 7 | 0.178 | 0.205 | 62.540 | 96.746 | 8.453 | 1.509 |
| NAW | 1996 | Sep | 4 | 0.083 | 0.040 | 24.210 | 12.340 | 8.418 | 0.930 |
| | | | **64** | **0.076** | **0.104** | **23.824** | **40.397** | **8.437** | **2.371** |
| PFW | 1984 | May–Jun | 6 | 0.017 | 0.029 | 3.408 | 5.622 | 5.800 | 1.609 |
| PFW | 1985 | Jan/Aug | 11 | 0.035 | 0.047 | 6.587 | 7.377 | 7.945 | 1.957 |
| PFW | 1986 | Apr–May | 5 | 0.005 | 0.006 | 0.634 | 0.793 | 10.200 | 1.225 |
| PFW | 1987 | Feb–Sep | 12 | 0.009 | 0.010 | 2.660 | 3.921 | 8.156 | 2.854 |
| PFW | 1988 | Mar–Oct | 10 | 0.146 | 0.142 | 38.434 | 37.422 | 7.700 | 2.937 |
| PFW | 1989 | Jan–May | 3 | 0.073 | 0.065 | 18.120 | 15.362 | 10.500 | 0.458 |
| PFW | 1990 | Sep–Oct | 2 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| PFW | 1991 | Jan–Jun | 2 | 0.003 | 0.004 | 0.535 | 0.757 | 12.700 | . |
| PFW | 1992 | Sep–Oct | 9 | 0.020 | 0.024 | 3.786 | 5.136 | 8.400 | 2.156 |
| PFW | 1993 | Aug–Sep | 9 | 0.056 | 0.079 | 8.241 | 9.590 | 7.671 | 1.499 |
| PFW | 1994 | Sep | 12 | 0.161 | 0.185 | 31.798 | 31.417 | 7.176 | 1.304 |
| PFW | 1995 | Sep | 4 | 0.007 | 0.012 | 1.820 | 3.160 | 5.800 | 0.283 |
| PFW | 1996 | Sep | 8 | 0.028 | 0.044 | 5.540 | 7.427 | 8.106 | 1.825 |
| | | | **93** | **0.056** | **0.103** | **11.927** | **21.484** | **8.014** | **2.228** |

juveniles (<8 mm). Adults were usually found at depths between 100 m and 250 m.

## Importance of amphipods in the cod diet

Figure 6 shows the annual food consumption of cod during 1984–1999 (from Bogstad and Mehl, 1997; updated by ICES, 2000). Cod is a major predator in the Barents Sea ecosystem and consumes many ecologically and commercially important prey species. Capelin is a major prey of cod and in some years the cod can consume up to three million metric tons of capelin (Bogstad and Mehl, 1997). During periods with very low capelin abundance cod switched to alternative prey, e.g. zooplankton. The amount of krill and amphipods

increased in the diet of cod during 1986–1988 and 1994–1997 (Figure 6), corresponding to periods of low capelin abundance. During these periods cod consumed up to one million tonnes of amphipods annually.

Detailed analysis of cod diet into species level during 1984–1989 showed, that in most years the main amphipod species consumed were, *Themisto abyssorum* and *T. libellula*. In this paper we have presented 1988 and 1994, two years with high abundance of amphipods in cod stomachs, as examples. Locations of cod stomachs from these two years are presented in Figure 7. Figures 8 and 9 show the partial stomach fullness indices (PFI) expressed as a percentage for different age groups of cod for 1988 and 1994. In 1988, both *T. libellula* and *T. abyssorum* was consumed by most age groups of cod,

Table 2. *Themisto libellula*. Means and standard deviation (s.d.) of density (ind. m$^{-3}$), abundance (ind. m$^{-2}$) and total length (mm) observed during different cruises between 1984 and 1996 in Atlantic (NAW), Polar Front (PFW) and Arctic (AW) water masses.

| Type | Year | Month | Stations | Ind. m$^{-3}$ | | Ind. m$^{-2}$ | | Length (mm) | |
|------|------|-------|----------|------|------|------|------|------|------|
| | | | | Mean | s.d. | Mean | s.d. | Mean | s.d. |
| AW | 1984 | Aug | 5 | 0.078 | 0.041 | 13.085 | 4.584 | 16.680 | 3.021 |
| AW | 1985 | Aug | 4 | 0.282 | 0.378 | 30.795 | 27.741 | 15.150 | 0.889 |
| AW | 1987 | Sep | 5 | 0.057 | 0.045 | 11.636 | 7.968 | 21.860 | 3.722 |
| AW | 1988 | July–Sep | 6 | 0.168 | 0.187 | 25.303 | 14.691 | 16.720 | 4.591 |
| AW | 1990 | Sep | 2 | 0.095 | 0.014 | 16.505 | 6.088 | 26.050 | 0.495 |
| AW | 1992 | Sep | 7 | 0.035 | 0.039 | 5.930 | 6.293 | 18.780 | 4.344 |
| AW | 1993 | Aug–Sep | 2 | 0.024 | 0.031 | 3.885 | 5.028 | 17.630 | 7.255 |
| AW | 1994 | Sep | 1 | 0.028 | . | 5.960 | . | 18.830 | . |
| AW | 1995 | Sep | 4 | 0.057 | 0.018 | 11.203 | 3.685 | 24.518 | 1.382 |
| AW | 1996 | Sep | 9 | 0.133 | 0.127 | 24.977 | 25.958 | 20.620 | 3.785 |
| | | | **45** | **0.106** | **0.150** | **16.810** | **17.111** | **19.473** | **4.487** |
| NAW | 1984 | Aug | 1 | 0.000 | . | 0.000 | . | . | . |
| NAW | 1985 | Jan | 1 | 0.000 | . | 0.000 | . | . | . |
| NAW | 1986 | May | 1 | 0.001 | . | 0.070 | . | 7.000 | . |
| NAW | 1987 | Jan–Sep | 6 | 0.001 | 0.003 | 0.435 | 0.944 | 23.400 | 4.808 |
| NAW | 1988 | Mar–Oct | 5 | 0.002 | 0.003 | 0.460 | 1.029 | 7.300 | . |
| NAW | 1989 | Jan–May | 8 | 0.006 | 0.014 | 1.507 | 3.972 | 18.250 | 10.253 |
| NAW | 1990 | Sep | 2 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| NAW | 1991 | Jan–Jun | 7 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| NAW | 1992 | Sep–Oct | 5 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| NAW | 1993 | June–Sep | 13 | 0.001 | 0.004 | 0.299 | 0.835 | 9.833 | 1.041 |
| NAW | 1994 | Sep | 4 | 0.003 | 0.005 | 0.570 | 1.140 | 17.800 | . |
| NAW | 1995 | Sep–Oct | 7 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| NAW | 1996 | Sep | 4 | 0.004 | 0.006 | 1.005 | 1.503 | 20.000 | 1.414 |
| | | | **64** | **0.002** | **0.006** | **0.425** | **1.560** | **15.408** | **7.096** |
| PFW | 1984 | May–Jun | 6 | 0.025 | 0.044 | 4.794 | 8.500 | 12.433 | 10.017 |
| PFW | 1985 | Jan/Aug | 11 | 0.019 | 0.029 | 3.604 | 5.234 | 21.075 | 7.846 |
| PFW | 1986 | Apr–May | 5 | 0.000 | 0.000 | 0.000 | 0.000 | 17.000 | . |
| PFW | 1987 | Feb–Sep | 12 | 0.286 | 0.507 | 68.988 | 133.807 | 12.960 | 8.174 |
| PFW | 1988 | Mar–Oct | 10 | 0.105 | 0.091 | 25.539 | 22.143 | 11.188 | 7.038 |
| PFW | 1989 | Jan–May | 3 | 0.019 | 0.024 | 42.412 | 71.661 | 16.150 | 15.344 |
| PFW | 1990 | Sep–Oct | 2 | 0.001 | 0.002 | 0.220 | 0.311 | 27.000 | . |
| PFW | 1991 | Jan–Jun | 2 | 0.007 | 0.002 | 1.625 | 0.049 | 16.700 | 15.839 |
| PFW | 1992 | Sep–Oct | 9 | 0.025 | 0.065 | 3.570 | 9.098 | 24.260 | 1.950 |
| PFW | 1993 | Aug–Sep | 9 | 0.022 | 0.027 | 2.324 | 2.744 | 18.375 | 2.116 |
| PFW | 1994 | Sep | 12 | 0.012 | 0.020 | 2.868 | 5.225 | 22.781 | 3.377 |
| PFW | 1995 | Sep | 4 | 0.040 | 0.030 | 5.358 | 2.451 | 17.210 | 6.109 |
| PFW | 1996 | Sep | 8 | 0.055 | 0.069 | 10.020 | 12.286 | 22.427 | 2.560 |
| | | | **93** | **0.065** | **0.201** | **15.824** | **53.321** | **18.073** | **7.634** |

though the amount of *T. libellula* was higher in age groups 3–5. These age groups dominated the cod stomach samples in 1988. In 1994, *T. abyssorum* was mainly consumed by younger age groups of cod, where as *T. libellula* was consumed by older cod.

The length frequency distributions of *Themisto libellula* and *T. abyssorum* consumed by cod during 1988 are shown in Figure 10(a) and in the MOCNESS in Figure 10(b). In 1994, very few amphipods length measurements were made in cod stomachs, therefore they are not presented in this paper. The length frequncy distributions in 1988 show cod to prefer larger individuals of both *Themisto* species. This is clearly evident for *T. libellula*. In the cod stomachs *T. libellula* larger than 35 mm dominated (45%) whereas in the MOCNESS samples very few in these size classes were observed.

## Interactions between amphipods and fish (capelin, cod)

The mean abundance of *Themisto libellula* and *T. abyssorum* observed in each year from 1984–1996 together with the stock size of capelin and cod is shown in Figure 11. The capelin and cod data are extracted from Gjøsæter (1998), and Bogstad and Mehl (1997) (updated by ICES, 2000), respectively. The figure shows that during periods with extremely low capelin biomass,

Table 3. *Themisto compressa*. Means and standard deviation (s.d.) of density (ind. m$^{-3}$), abundance (ind. m$^{-2}$) and total length (mm) observed during different cruises between 1984 and 1996 in Atlantic (NAW), Polar Front (PFW) and Arctic (AW) water masses.

| Type | Year | Month | Stations | Ind. m$^{-3}$ | | Ind. m$^{-2}$ | | Length (mm) | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Mean | s.d. | Mean | s.d. | Mean | s.d. |
| AW | 1984 | Aug | 5 | 0 | | 0 | | | |
| AW | 1985 | Aug | 4 | 0 | | 0 | | | |
| AW | 1987 | Sep | 5 | 0 | | 0 | | | |
| AW | 1988 | July–Sep | 6 | 0 | | 0 | | | |
| AW | 1990 | Sep | 2 | 0 | | 0 | | | |
| AW | 1992 | Sep | 7 | 0 | | 0 | | | |
| AW | 1993 | Aug–Sep | 2 | 0 | | 0 | | | |
| AW | 1994 | Sep | 1 | 0 | | 0 | | | |
| AW | 1995 | Sep | 4 | 0 | | 0 | | | |
| AW | 1996 | Sep | 9 | 0 | | 0 | | | |
| | | | **45** | **0** | | **0** | | | |
| NAW | 1984 | Aug | 1 | 0.000 | . | 0.000 | . | . | . |
| NAW | 1985 | Jan | 1 | 0.007 | . | 1.780 | . | 13.100 | . |
| NAW | 1986 | May | 1 | 0.000 | . | 0.000 | . | . | . |
| NAW | 1987 | Jan–Sep | 6 | 0.015 | 0.022 | 4.218 | 6.231 | 13.133 | 0.321 |
| NAW | 1988 | Mar–Oct | 5 | 0.004 | 0.007 | 1.398 | 2.014 | 12.050 | 2.333 |
| NAW | 1989 | Jan–May | 8 | 0.001 | 0.002 | 0.435 | 0.695 | 13.933 | 1.290 |
| NAW | 1990 | Sep | 2 | 0.009 | 0.011 | 2.130 | 2.489 | 13.650 | 1.909 |
| NAW | 1991 | Jan–Jun | 7 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| NAW | 1992 | Sep–Oct | 5 | 0.004 | 0.003 | 1.358 | 1.204 | 11.250 | 0.500 |
| NAW | 1993 | June–Sep | 13 | 0.001 | 0.002 | 0.275 | 0.780 | 9.750 | 0.354 |
| NAW | 1994 | Sep | 4 | 0.004 | 0.004 | 1.455 | 1.685 | 11.400 | 1.980 |
| NAW | 1995 | Sep–Oct | 7 | 0.012 | 0.014 | 4.439 | 5.923 | 11.165 | 1.348 |
| NAW | 1996 | Sep | 4 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| | | | **64** | **0.004** | **0.009** | **1.392** | **3.124** | **12.072** | **1.656** |
| PFW | 1984 | May–Jun | 6 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| PFW | 1985 | Jan/Aug | 11 | 0.004 | 0.006 | 0.709 | 1.013 | 12.58 | 0.766 |
| PFW | 1986 | Apr–May | 5 | 0.000 | 0.000 | 0.010 | 0.022 | . | . |
| PFW | 1987 | Feb–Sep | 12 | 0.006 | 0.015 | 1.981 | 4.604 | 10.9 | 3.996 |
| PFW | 1988 | Mar–Oct | 10 | 0.002 | 0.005 | 0.880 | 2.092 | 11.9 | 0.283 |
| PFW | 1989 | Jan–May | 3 | 0.004 | 0.007 | 1.155 | 2.000 | 6.8 | . |
| PFW | 1990 | Sep–Oct | 2 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| PFW | 1991 | Jan–Jun | 2 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| PFW | 1992 | Sep–Oct | 9 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| PFW | 1993 | Aug–Sep | 9 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| PFW | 1994 | Sep | 12 | 0.002 | 0.004 | 0.177 | 0.413 | 11.7 | 0.424 |
| PFW | 1995 | Sep | 4 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| PFW | 1996 | Sep | 8 | 0.000 | 0.000 | 0.000 | 0.000 | . | . |
| | | | **93** | **0.002** | **0.007** | **0.495** | **1.907** | **11.508** | **2.308** |

amphipod abundance was high. The highest average amphipod abundance, close to 70 ind. m$^{-2}$, was observed at time periods with extremely low capelin abundance. The very low abundance of *T. libellula* (0.4 ind. m$^{-2}$) in 1986 is due to that samples were only available from Atlantic waters.

There was a subsequent strong decrease in the abundance of both amphipod species with the increase in the capelin stock in the late 1980s. The abundance of *Themisto libellula* was still low in the mid-1990s even after the decline in the capelin stock, indicating a slow recovery for this species. In periods with low capelin abundance the predation pressure from cod and other major predators of capelin on zooplankton increased.

This may explain the slow recovery of *T. libellula* as compared to *T. abyssorum* in the mid-1990s.

## Statistical analysis

*Abundance of* T. libellula *vs.* T. abyssorum *for each year, and water mass*

Paired-comparison t-tests (SAS Institute Inc., 1990) were used to compare abundance estimates of *Themisto abyssorum* and *T. libellula* based on samples taken at the same MOCNESS stations, for each year (Table 4). A t-test was performed to test the hypothesis that the true mean of this difference is 0. The abundance of these two species in the three water masses were compared for each
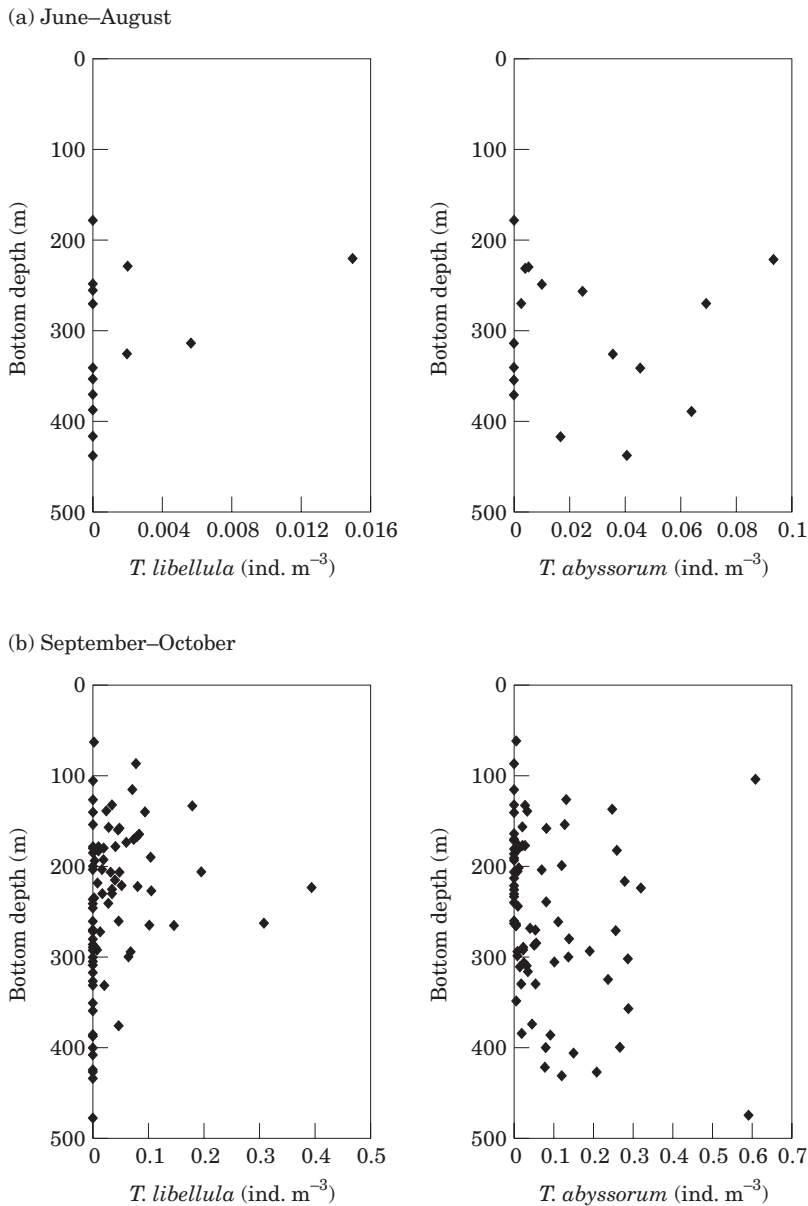
(a) June–August



(b) September–October



Figure 4. *Themisto libellula* and *T. abyssorum.* Mean numerical density (ind. m$^{-3}$) in relation to bottom depth in vertical profiles. (a) June–August, (b) September–October.

year separately. It is seen that the hypothesis of equal means should be rejected (at a 5% rejection level) in about 31% of the year/watermass combinations. The abundance estimates of *T. abyssorum* and *T. libellula* from the Polar Front are different only in 7.6%, those from the Arctic waters in 44.4%, and those of the Atlantic waters in 50%, of the years. When pooling the data from the each watermass type (Table 4, bottom row) the hypothesis that the abundance estimates of the two species are equal must be rejected both for the Arctic and Atlantic water masses.

*Amphipod abundance vs. capelin and cod stock size*

Regression analysis between mean annual amphipod abundance (unweighted mean of all stations during the year) and capelin stock size showed negative slopes indicating an inverse relationship between the amphipod abundance and the capelin stock size (Table 5, Figure 12). The relationship was not significant for *Themisto libellula* (p=0.078), but significant for *T. abyssorum* (p=0.047) at the 5% level. Amphipod data from 1986 was left out in the regression as the mean abundance for this year was not only based on a few stations, but also

(a) *T. libellula*
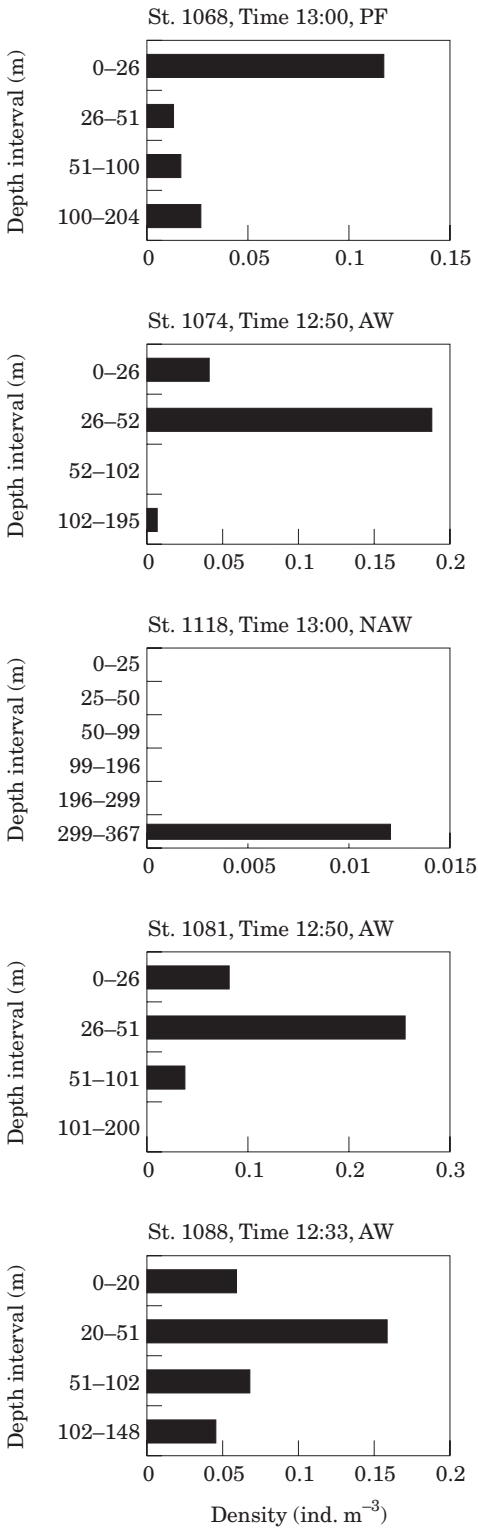
(b) *T. abyssorum*
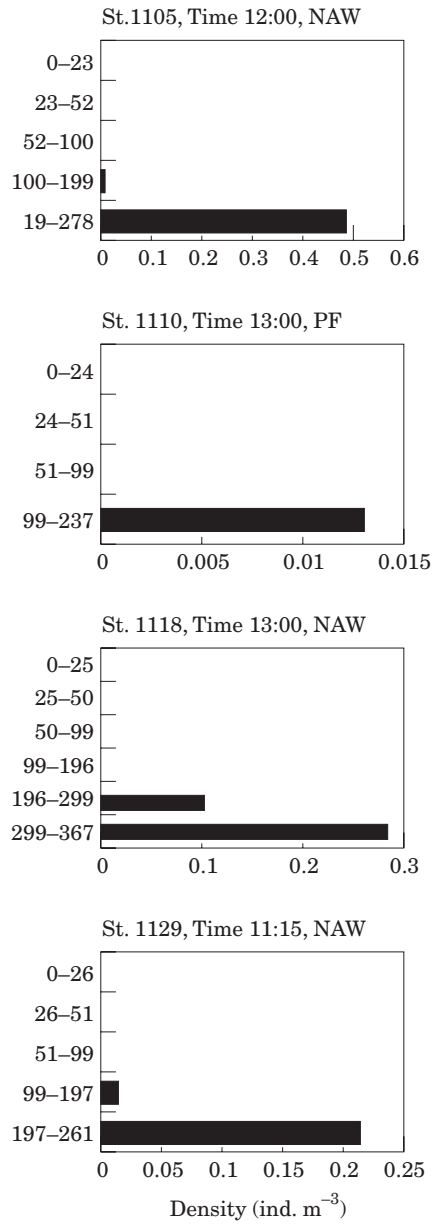


Figure 5. (a) *Themisto libellula* and (b) *T. abyssorum.* Numerical density (ind. m$^{-3}$) in relation to mean MOCNESS net sampling depth in a cruise in September 1996. PF=Polar Front waters, NAW=North Atlantic waters, AW=Arctic waters.
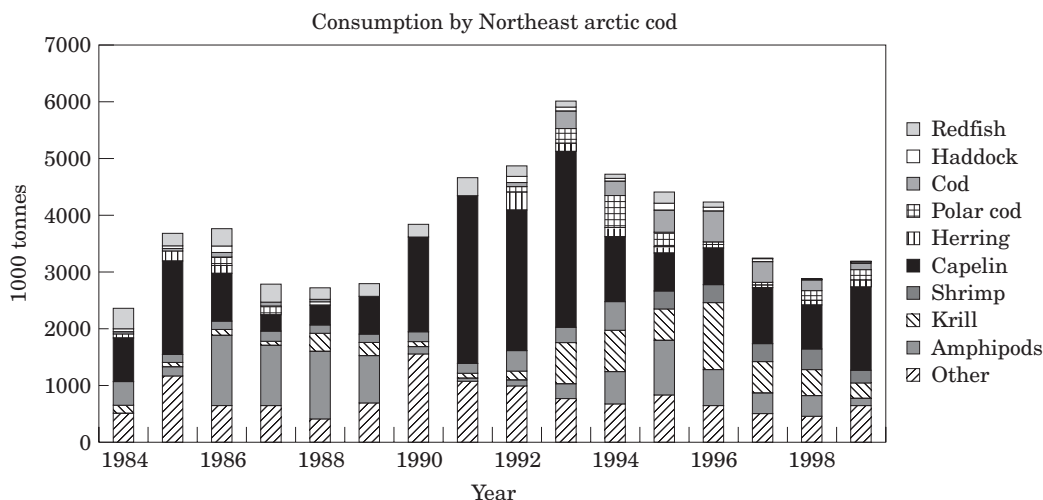
Figure 6. Annual food consumption by Northeast arctic cod (in thousand tonnes) in the Barents Sea during 1984–1999. (from Bogstad and Mehl, 1997; updated by ICES, 2000).

as these stations were from similar locality. The values of the coefficient of determination ($r^2$) in the regressions were low, indicating that factors not included in the regression analyses also are of major importance for determining the amphipod abundance.

The relationship between cod stock size and *T. libellula* abundance also gave negative slope (Figure 13), although insignificant, indicating a possible inverse relationship between cod and *T. libellula* (p=0.082). No significant correlation between the abundance of *T. abyssorum* and of cod was observed.

## Discussion

### Geographical distribution

Three species of the genus *Themisto*, (*T. abyssorum, T. libellula* and *T. compressa*) were recorded in this study. Of these, *T. abyssorum* predominated in the subarctic waters and *T. libellula* in the Arctic waters. *T. compressa* was rare and restricted to the warmer Atlantic waters in the south western Barents Sea with comparatively low abundance. The distribution patterns of *Themisto* spp. from the North Atlantic, given by Bogorov (1940), Bowman (1960) and Dunbar (1957, 1964), are similar to our observations. According to Schneppenheim and Weigmann-Haass (1986) *Themisto compressa* (Goes) until recently referred to as *Parathemisto gaudichaudii* or *Themisto gaudichaudii* and the Antarctic *T. gaudichaudii* (Guérin) are distinct and valid species. In most stations, *T. libellula* were distributed in the upper layers (<50 m) compared to *T. abyssorum* (>200 m), indicating a shallower distribution for *T. libellula*. Studies by Bradstreet (1976) also indicate a deeper distribution pattern for *T. abyssorum* than *T. libellula*. In Alaskan waters, Wing

(1976) found *T. libellula* to vertically migrate 150–200 m each night with a significant part of population in the upper 50 m.

Very few amphipod species other than *Themisto* species were observed in the Barents Sea during the study period. However, close to the ice edge *Gammarus wilkitzkii* was also found together with *T. libellula*. *G. wilkitzkii* is commonly associated with the undersurface of the ice, and regarded as a herbivore (Dunbar, 1964).

In our study the highest abundances of *T. libellula* and *Themisto abyssorum* were recorded in the summer and autumn respectively. Bogorov (1940) found the highest abundances of *T. abyssorum* in the Barents Sea in late summer whereas studies by Wing (1976) in Alaskan waters showed peak abundances of *T. libellula* in late spring and early summer. The highest concentrations of *T. libellula* were observed close to the Polar Front region in May–June 1987 and July 1988. Most of the *T. libellula* taken in these two cruises (93% and 42%, respectively) were between 2–8 mm. In the Arctic waters very few individuals below 8 mm were present. Though the time of reproduction may vary between water masses, our observations seem to indicate that breeding of this species occurs close to the productive Polar Front Region. Dunbar (1964) reports that since the food supply is rather poor in the Arctic Ocean, *T. libellula* may not breed in the main body of the Arctic zone. He suggests the center of production of this species to lie in the peripheral waters of the Arctic zone.

MOCNESS samples showed that *Themisto libellula* can grow up to 45 mm in total length (TL), with the largest individuals in Arctic waters. *T. abyssorum* is comparatively smaller, with a TL of up to 16 mm. The size distribution of amphipods in cod stomachs versus in MOCNESS seems to indicate, a preference towards

(a)

Cod stomach samples



(b)



▲ September–October
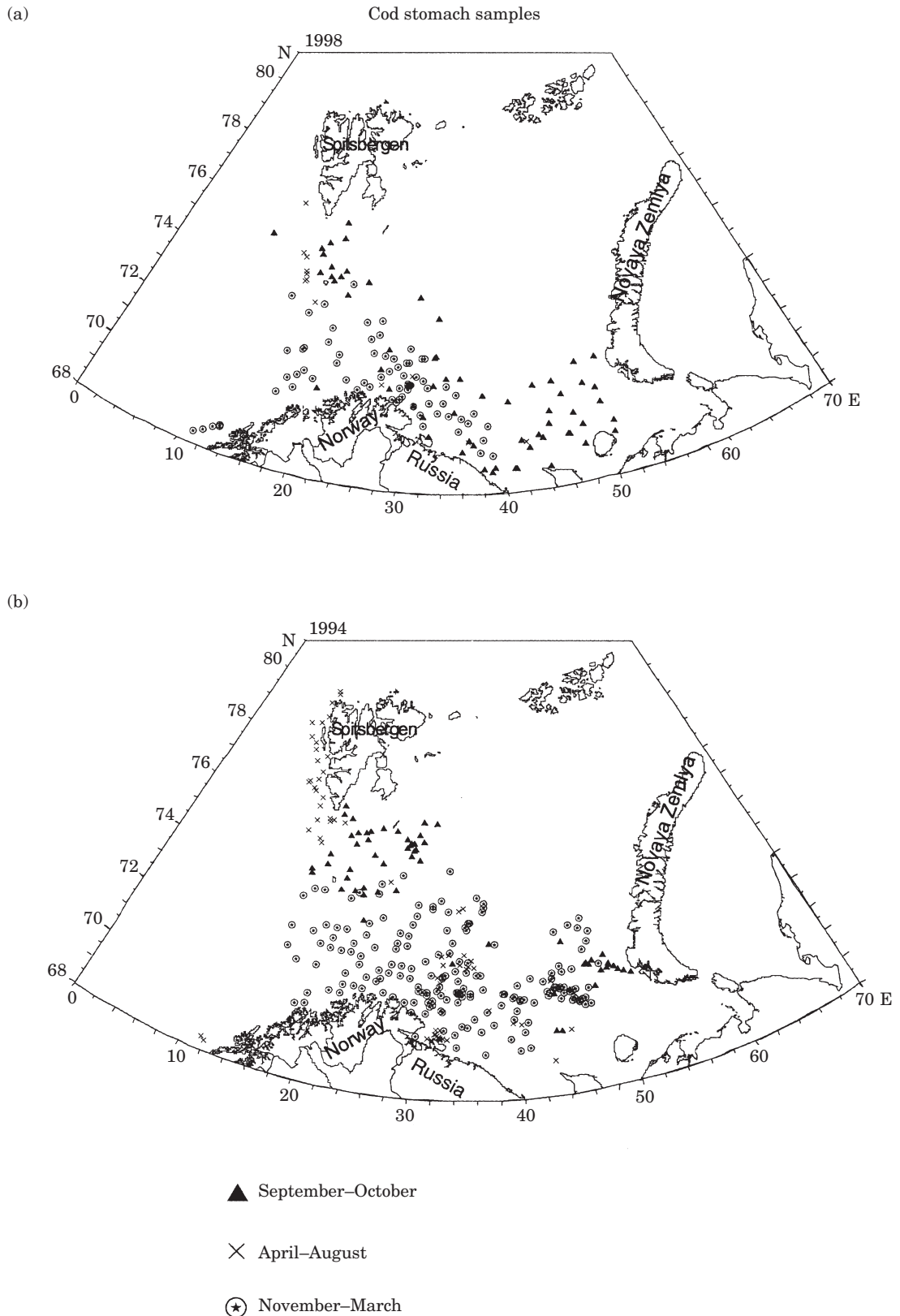
✕ April–August

⊛ November–March

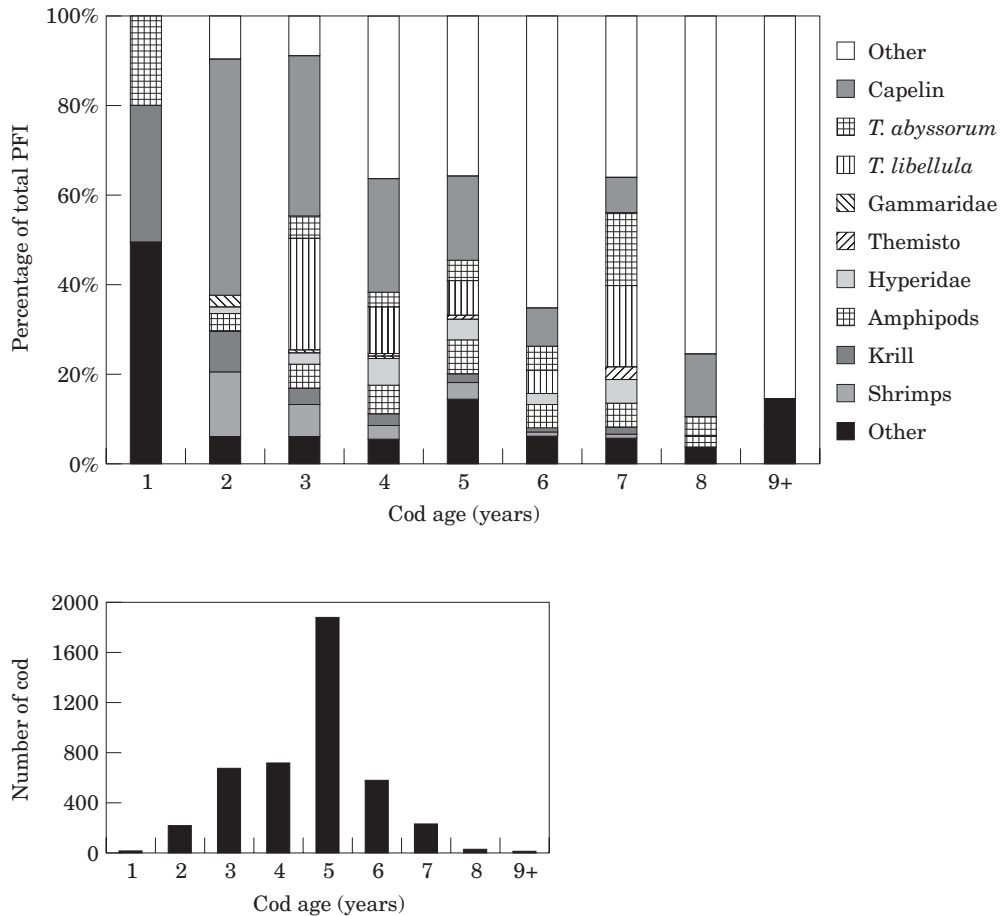Figure 7. Location of cod stomach samples from (a) 1988, (b) 1994.

Figure 8. Proportion of total Partial fullness index (PFI) in different age groups of cod in 1988. In the legend the group ''other'' includes prey other than shown in the figure as well as unidentified prey items. The age distribution of cod samples in 1988 is also illustrated.

larger *T. libellula* by cod. In cod stomachs, *T. libellula* larger than 35 mm dominated the diet where as very few individuals of this size was observed in the MOCNESS. Cod stomachs and MOCNESS samples were not taken at the same time and place, also the possible underestimation of larger amphipods in the MOCNESS make the data not directly suitable for selectivity studies. The reason for not encountering the largest individuals of *T. libellula* in the MOCNESS samples could be avoidance.

Avoidance, the active swimming of zooplankton out of capture of net, is the most serious bias affecting the catch of the larger meso- and macrozooplankton (Sameoto *et al.*, 2000). Our 1 m$^2$ MOCNESS samples are likely to have underestimated the abundance of the amphipods but the extent is not known. Wiebe *et al.* (1982) compared 1 m$^2$ and 10 m$^2$ MOCNESS for sampling of the krill *Nematocelis megalops* (15–25 mm). The number of krill caught in their study was much lower in the daytime than in the night samples, particu-

larly for the 1 m$^{-2}$. This indicates visual avoidance of macrozooplankton like krill during the daytime. These authors did not find any marked difference on the size frequency distribution of *N. megalops* in the two different size MOCNESS nets.

One would expect visual avoidance to be largest in the daytime and in the summer time and minimum in the late autumn/winter when the day and night differences in the Barents Sea light conditions are rather small. In the present study the highest abundances of *T. libellula* were recorded in the May–July where as for *T. abyssorum* the highest abundances were observed in late summer and in autumn. From our data it is difficult to interpret visual avoidance of *Themisto* spp. as one should expect, out of the two species, *T. libellula* to be less abundant in summer due to their larger size and consequently higher avoidance rate. However, looking at the size distribution of *T. libellula* in cod stomachs vs. in the MOCNESS samples, we see that the larger ones (>25 mm TL) is not present in the MOCNESS. This may be interpreted
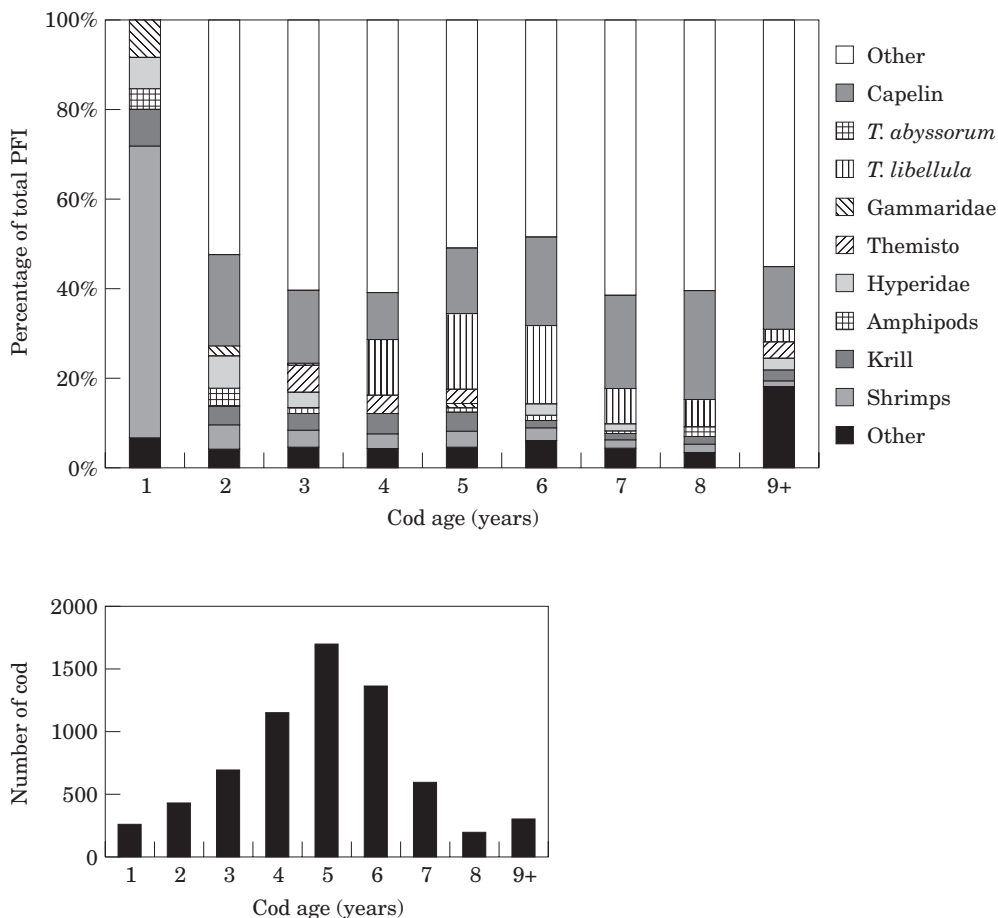
Figure 9. Proportion of total Partial fullness index (PFI) in different age groups of cod in 1994. In the legend the group "other" includes prey other than shown in the figure as well as unidentified prey items. The age distribution of cod samples in 1994 is also illustrated.

as the underestimation of larger *T. libellula* by the MOCNESS or that cod selectively feed on larger ones.

Apart from visual avoidance, the vertical distribution can also determine the extent to which amphipods are being sampled. We have operated the MOCNESS to within 20–30 m from the bottom for safety reasons, and may have missed the near bottom concentrations. This would have led to underestimations of amphipod abundance; especially of *T. abyssorum,* which has a deeper distribution (>200 m) than *T. libellula*.

Bradstreet and Cross (1982) in describing the trophic relationships at ice edges in the Canadian High Arctic, showed *Themisto* spp. to be an important component of the zooplankton fauna. The present study also shows that amphipods are dominant in the Arctic water masses of the Barents Sea. *Themisto* spp. are mainly carnivorous and feed on copepods, fish larvae, euphausiids etc. (Bigelow, 1926; Dunbar, 1964; Sheader and Evans, 1975). Scott *et al.* (1999) report *T. libellula*

from the marginal ice zone of the Barents Sea feed extensively on copepods. They can also feed on microalgae (Wing, 1976; Bradstreet and Cross, 1982).

## Predator-prey interactions

Amphipods are major prey of sea birds, harp seals and ringed seals. Harp seal is the most abundant seal species in the Barents Sea. The diet of harp seal from northern packed-ice areas to the south of Kvitøya and Viktoria Island during September 1991, consisted of 79.7% *Themisto libellula* in numbers and 28.7% in biomass (Nilssen *et al.*, 1991, 1992). The Barents Sea harp seal stock consumes about 300 000 tonnes of *Themisto* annually (Nilssen *et al.*, 2000). In their study, the consumed biomass of *Themisto* accounted for about 10% of the total consumption estimates. *Themisto libellula* is also a key prey species for several species of high arctic sea birds in the northern Barents Sea areas (Mehlum and

T. libellula                                   T. abyssorum

(a) Cod stomachs



(b) MOCNESS



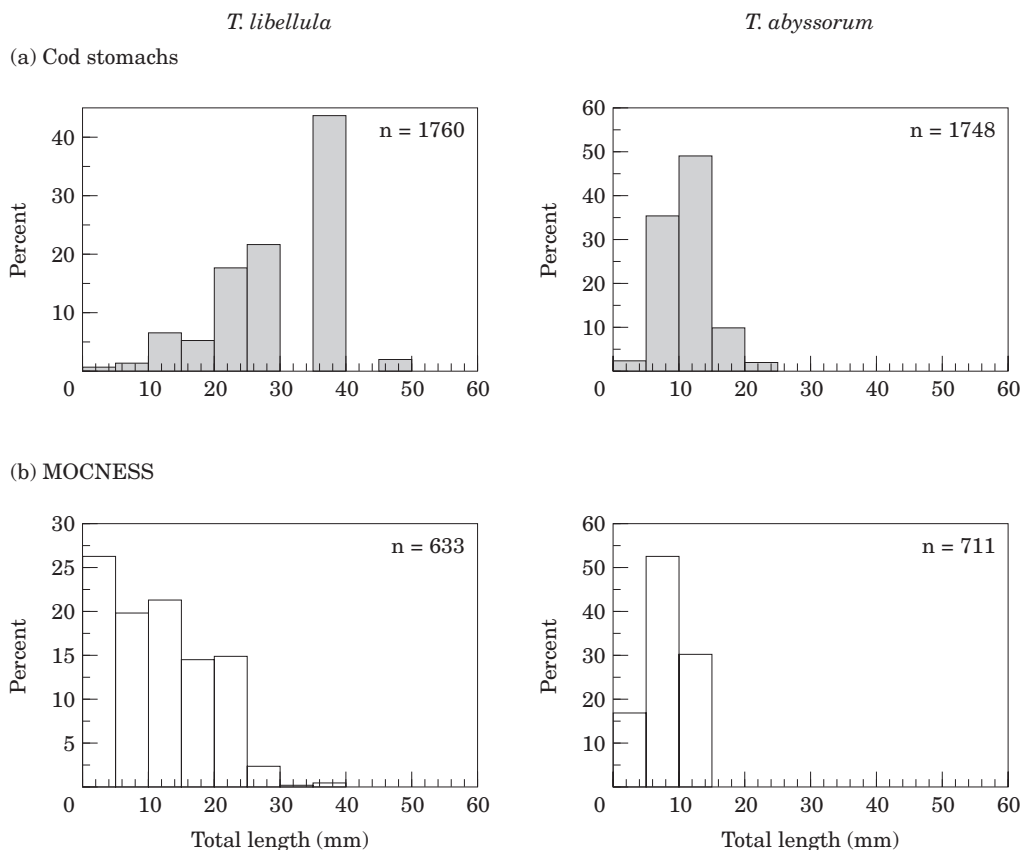Total length (mm)                              Total length (mm)

Figure 10. Length distribution of *Themisto libellula* and *T. abyssorum* in (a) cod stomachs, and (b) in MOCNESS samples, in 1988.

Gabrielsen, 1993). In the marginal ice zone east of Svalbard (north western Barents Sea), large groups of Brünnichs's guillemots, *Uria lomvia*, the most common of the sea birds in the Barents Sea, have been observed to forage mainly on *Themisto libellula* (Mehlum and Gabrielsen, 1993).

*Themisto spp*. are important food also of many commercial fish species in the Barents Sea as capelin, polar cod, Greenland halibut (*Reinhardtius hippoglossoides*), haddock (*Melanogrammus aeglefinus*) and cod (Ponomarenko and Yaragina, 1979; Lund, 1981; Burgos and Mehl, 1987; Haug *et al*. 1989; Ajiad and Gjøsæter, 1990; Lønne and Gulliksen, 1990; Ajiad and Pushchaeva, 1992; Bogstad and Mehl, 1997). Of these species, capelin and cod are the most abundant ones and thus they probably have the largest impact on the *Themisto* populations. The predation on *Themisto* species by cod has been described above. Studies by Lund (1981) show that the caloric importance of *T. abyssorum* and *T. libellula* in the diet of Barents Sea capelin (13–16 cm) can vary from 0.8–41.8%. The highest values were observed in autumn and the lowest in spring. Ajiad and Pushchaeva (1992) also showed the

importance of *T. abyssorum* and *T. libellula* (14.5% by weight) in the diet of 9–12 cm capelin.

A study by Panasenko (1981) showed that in mid-August capelin fed intensively on concentrations of larger plankton as krill and amphipods, which at this time of the year kept mainly to the near bottom concentrations. Lund (1981) also showed that predation on amphipods by capelin was highest in autumn. He suggests capelin to feed most intensively during daytime in autumn. Our MOCNESS data taken during daytime in September seem to indicate *T. abyssorum* to have a deeper distribution (>200 m) than *T. libellula*. Feeding pattern of capelin suggested by Panasenko (1981) and Lund (1981) seem to point out capelin to feed more on *T. abyssorum,* which were more deeply distributed than *T. libellula*. Statistical analysis carried out in the present study showed abundance of both *Themisto* species to be negatively correlated to the capelin stock size, with higher significance level for *T. abyssorum* than for *T. libellula.* These results seem to indicate capelin to feed more on the smaller size *T. abyssorum* during the autumn.

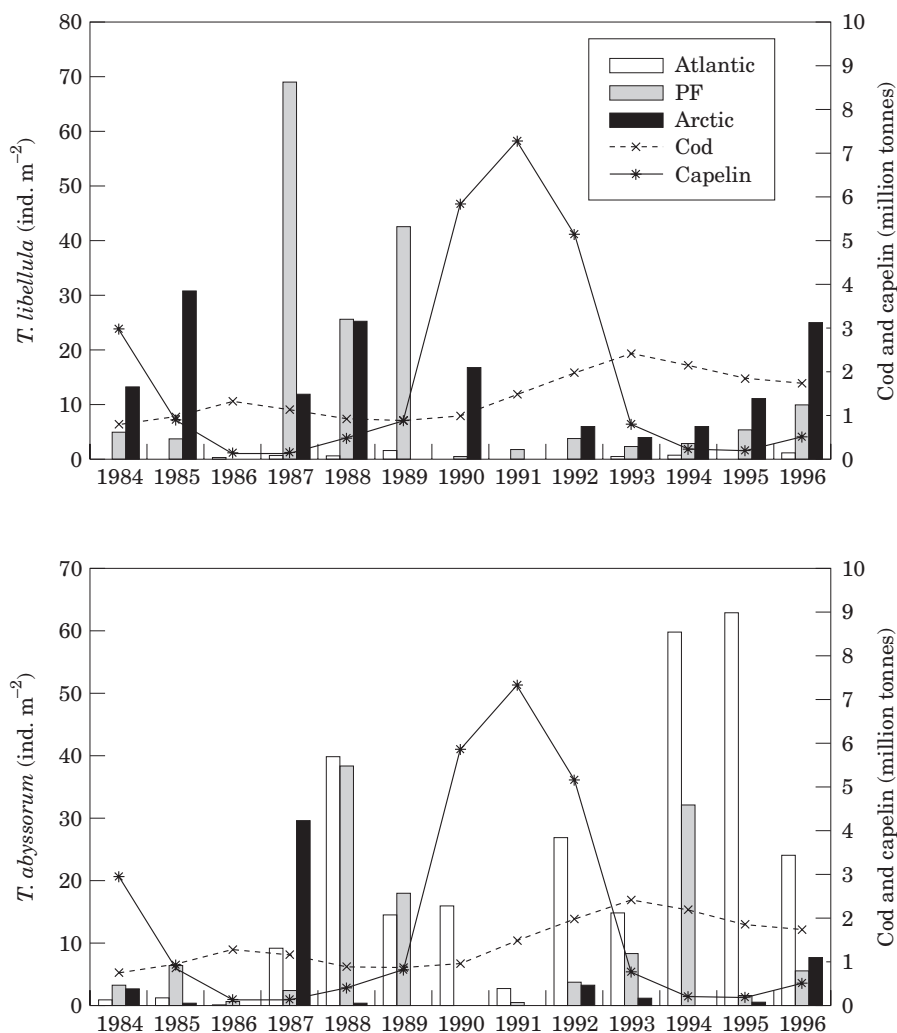In the Barents Sea, the feeding areas of capelin and cod overlap with the distribution areas of amphipods.

Figure 11. Variation in abundance (ind. m$^{-2}$) of amphipods in different water masses from 1984–1996, and the stock size of cod and capelin (million tonnes). Cod and capelin data are respectively from Bogstad and Mehl (1997), and Gjøsæter (1998).

During the feeding period of capelin, in summer and autumn, the main distribution of cod is restricted to 70–75°N and 15–45°E where as capelin is mainly distributed between 74–79°N and 15–50°E (Bogstad and Mehl, 1997; Gjøsæter, 1998). During the summer, capelin performs feeding migrations to the central and northern parts of the Barents Sea, and its distribution is northernmost in September–October. The older individuals stay further north and in colder waters than the younger ones. Many studies have shown the importance of amphipods in the diet of capelin, which is the major planktivore in the Barents Sea ecosystem. Statistical analysis confirmed that the abundance of both *Themisto* species are negatively correlated to the capelin stock size, with a lower significance level for *T. libellula* than for *T. abyssorum*. The amphipod data are mainly from late

summer and autumn, and therefore, the abundance data represent what is left after capelin feeding.

When the capelin stock was at low levels, the abundance of these two amphipod species increased, probably owing to the reduced grazing pressure. Dalpadado and Skjoldal (1996) also observed an inverse relationship between krill and capelin biomass in the Barents Sea. The high abundance of large zooplankton prey such as krill and amphipods probably contributed to the high growth rate of capelin and to the rapid recovery of the capelin stock (Skjoldal *et al.*, 1992). These results indicate that capelin exercise strong feedback control on the system through its predation pressure on zooplankton.

Cod >25 cm, which is mainly a piscivore, feeds very little on zooplankton when capelin is available. Studies by Steele and Lilly (1999) in the northwestern Atlantic

Table 4. Paired comparison T-test between abundance (ind. m$^{-2}$) estimates of *T. abyssorum* and *T. libellula* taken at the same MOCNESS stations for each year, and watermass. The significance probability is given for the three water masses for each year, plus total biomass estimates for the years combined. N is the number of stations. Significant probabilities below 0.05 are set in boldface. PFW=Polar Front water, AW=Arctic water, NAW=North Atlantic water.

| Year | PFW N | Prob>\|T\| | AW N | Prob>\|T\| | NAW N | Prob>\|T\| |
|---|---|---|---|---|---|---|
| 1984 | 6 | 0.689 | 5 | **0.010** | 1 | . |
| 1985 | 11 | 0.302 | 4 | 0.121 | 1 | . |
| 1986 | 5 | 0.149 | | | 1 | . |
| 1987 | 12 | 0.115 | 5 | 0.479 | 6 | **0.022** |
| 1988 | 10 | 0.386 | 6 | **0.008** | 5 | 0.156 |
| 1989 | 3 | 0.676 | | | 8 | **0.017** |
| 1990 | 2 | 0.500 | 2 | 0.162 | 2 | 0.309 |
| 1991 | 2 | 0.274 | | | 7 | 0.293 |
| 1992 | 9 | 0.956 | 7 | 0.393 | 5 | **0.030** |
| 1993 | 9 | 0.095 | 2 | 0.572 | 13 | **0.007** |
| 1994 | 12 | **0.013** | 1 | . | 4 | 0.064 |
| 1995 | 4 | 0.285 | 4 | **0.014** | 7 | 0.138 |
| 1996 | 8 | 0.449 | 9 | **0.010** | 4 | **0.039** |
| All years | 93 | 0.521 | 45 | **0.003** | 64 | **0.0001** |

Table 5. Mean annual amphipod abundance and capelin and cod stock size. The capelin biomass estimates are acoustic abundance estimates, while the cod stock biomass is calculated using virtual population analysis.

| Year | *T. libellula* (ind. m$^{-2}$) | *T. abyssorum* (ind. m$^{-2}$) | Capelin (Tonnes $\times 10^6$) | Cod (Tonnes $\times 10^6$) |
|---|---|---|---|---|
| 1984 | 17.88 | 7.11 | 2.96 | 0.78 |
| 1985 | 34.40 | 8.58 | 0.86 | 0.98 |
| 1986 | 0.07 | 0.79 | 0.12 | 1.32 |
| 1987 | 81.06 | 41.50 | 0.10 | 1.14 |
| 1988 | 51.30 | 78.82 | 0.43 | 0.92 |
| 1989 | 43.92 | 32.87 | 0.86 | 0.88 |
| 1990 | 16.73 | 15.82 | 5.83 | 0.98 |
| 1991 | 1.63 | 3.25 | 7.29 | 1.49 |
| 1992 | 9.50 | 33.80 | 5.15 | 1.97 |
| 1993 | 6.51 | 24.00 | 0.80 | 2.39 |
| 1994 | 9.40 | 91.33 | 0.20 | 2.18 |
| 1995 | 16.56 | 64.83 | 0.19 | 1.85 |
| 1996 | 36.00 | 37.38 | 0.50 | 1.74 |

also show the importance of amphipods in the cod diet. Their study also indicate that cod of all sizes fed on amphipods. Predation by cod and other predators such as harp seals and arctic birds on amphipods, especially, *Themisto libellula,* at time periods of low capelin abundance may further influence the interrelationships between amphipods and capelin. The results from the Barents Sea indicate *Themisto* populations to be controlled to a large extent by predation. *Themisto* spp., especially pelagic *T. libellula* plays a key role in the Arctic ice edge food web, in serving as a link between the copepods and other smaller planktonic forms and many vertebrates.

Studies by Bogorov (1940), Dunbar (1964) and Borkner (in prep.) in the Barents Sea show *Themisto*

species to reproduce in the Barents Sea. Borkner found females bearing eggs of both *T. libellula* and *T. abyssorum. Themisto* spp are viviparous and the females release young of 2–3 mm in size. We found young (2–3 mm) of both *Themisto* spp. in the Barents Sea. Though some of the evidences point out that *T. libellula* and *T. abyssorum* may reproduce in the Barents Sea, very little is known about the type of species and the amounts, advected from the Norwegian Sea. Climatic variations as temperature may also play an important role on the distribution and abundance of amphipods. If the inflow of warmer Atlantic water to Barents Sea is quite large, this will most probably have consequences on the spatial distribution and abundance of the arctic species, *T. libellula*. These factors may have contributed to the
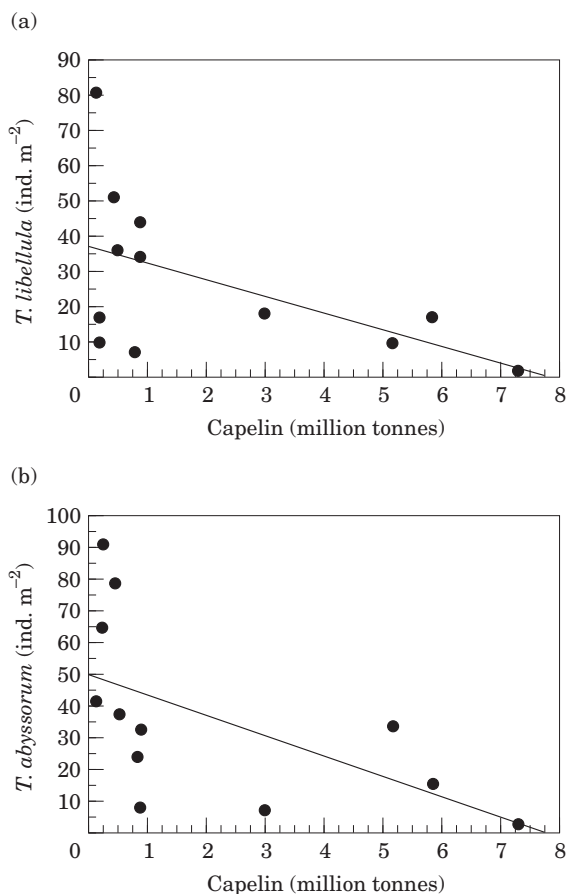
(a)



(a)



(b)



Figure 12. Regression analysis between capelin stock size and (a) *T. libellula* (y=37.074 − 4.767x; r²=0.278) and (b) *T. abyssorum* (y=50.209 − 6.483x; r²=0.338) abundance.

(b)
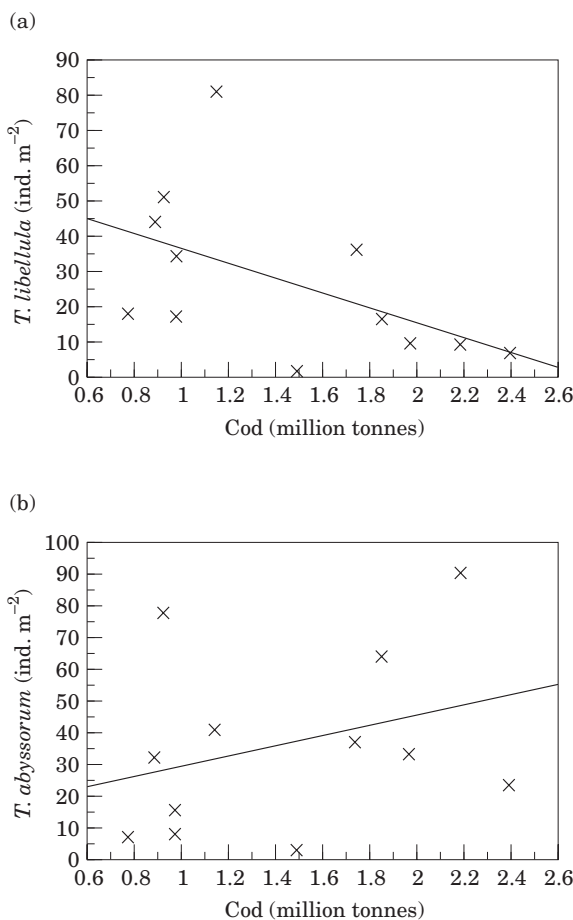


Figure 13. Regression analysis between cod stock size and (a) *T. libellula* (y=57.783 − 21.302x; r²=0.272) and (b) *T. abyssorum* (y=12.996+16.378x; r²=0.106) abundance.

variations in amphipod abundance in the Barents Sea, but the extent is not known. The importance of these factors on amphipod stocks needs to be quantified by model studies. Future investigations should be focused on estimating the absolute abundance and production of amphipods as well as on estimating the consumption of amphipods by capelin in the Barents Sea. Improved sampling procedures of amphipods, e.g. better spatial and temporal coverage, as well as better sampling equipment are essential for such studies.

## Acknowledgements

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