

Reproduction and growth of the Arctic hyperiid amphipod *Themisto libellula* Mandt

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Summary. The hyperiid amphipod, *Themisto libellula*, is abundant in Arctic seas and is an important prey for fish, birds and mammals. Characterization of its life cycle has been hampered by the lack of winter collections. In this study, that portion of the hyperiid population inhabiting the upper 30 m of the water column in Frobisher Bay was sampled periodically in winter, spring and summer during five consecutive years. In one year the winter and spring collections included large numbers of ovigerous females. These samples provide new information about timing of reproduction, size at maturity, fecundity, embryonic development, hatching, release and rate of growth of *T. libellula* in the Arctic. The average length of the ovigerous females was 23.3 mm. This and the summer growth rate of about 6 mm/month indicates that they can reproduce when one year old. Eggs are laid prior to early February, and although some young may be released from the marsupium as early as mid-March, most are liberated during April and May. The fecundity is significantly correlated with female length and an average 23 mm long individual had 275 embryos. The size-specific fecundity is similar to that of hyperiids from temperate and subtropical waters.

Introduction

The planktonic hyperiid amphipod, *Themisto libellula* (Mandt), is important in the marine ecosystems of Arctic and subarctic seas, where its pivotal role in the food chain has been compared to that of euphausiids in temperate and Antarctic waters (Dunbar 1942, 1946, 1957). This large, carnivorous amphipod forms a significant trophic link between smaller zooplankton and many species of marine and anadromous fish (Grainger 1953; Bradstreet and Cross 1982; Loenne and Gulliksen 1989), seabirds (Bradstreet 1980; Bradstreet 1982; Bradstreet and Cross 1982; Gaston et al. 1985) and mammals (Dunbar 1941a; Maclaren 1958; Lowry and Frost 1984).

Themisto libellula also occurs in the Bering Sea (Bowman 1960), and north Pacific, although the population inhabiting the coastal embayments and sounds of south-

eastern Alaska, in the vicinity of Juneau (Wing 1976), may be a relict since they appear to be absent from the intervening Gulf of Alaska (Bowman 1960). Only the populations inhabiting the coastal waters of southeastern Baffin Island (Dunbar 1942, 1946, 1957) and southeastern Alaska (Wing 1976) have been studied in any detail. The information available suggested that the life histories of the animals in these two areas were very different. In southeastern Alaska *T. libellula* had a one year life cycle, matured at 19–21 mm, seldom exceeded 25 mm, reproduced when one year old and then died. In contrast, in Baffin Island waters they appeared to have a two year life span, matured at a much larger size (> 35 mm), reached lengths of up to 46 mm and had an “alternating or two-phase” breeding cycle in which immediately adjacent age cohorts were essentially genetically separated (Dunbar 1946). These pronounced differences were attributed to the influence of latitudinal gradients in habitat temperature on physiological processes (Wing 1976) similar to that reported in other zooplankton (Bogorov 1940; Dunbar 1941b; Einarsson 1945; Digby 1954) and other polar invertebrates (Arnaud 1977). The habitat temperature in eastern Arctic waters is consistently several degrees lower than that in southeastern Alaska.

However, information about the life cycle of *T. libellula* in Arctic waters has been derived largely from samples collected during the summer, supplemented by a few partially digested samples from seal stomachs during the winter (Dunbar 1946, 1957). As the peak of reproductive activity takes place in winter, it was recognized by Dunbar (1957), and subsequently reiterated by Bowman (1960), that more winter collecting was necessary to substantiate the initial conclusions. However, in the ensuing years little further attention has been paid to the biology of *T. libellula* in the Arctic in spite of growing evidence of its importance in marine food chains.

During a study of the macrozooplankton community in Frobisher Bay, Southeastern Baffin Island, samples were collected in the upper 30 m of the water column at various times throughout the year. Some of the winter and spring collections included large numbers of ovigerous

T. libellula. These samples, while probably not encompassing the whole population and all the life history stages of the species, nevertheless provide hitherto unavailable information about the reproductive season, size at maturity, embryo development and rate of growth of *T. libellula* in arctic waters, as well as the first estimates of its fecundity. This permits a reexamination of the purported differences in the life histories of the eastern Arctic and Southeastern Alaskan populations.

Material and methods

Meaningful comparisons of zooplankton abundance at different times of the year requires a method of sampling that can be used in all seasons. Collecting when the sea is covered by ice has long posed problems for marine biologists studying large zooplankton in the Arctic. Vertical hauls sample relatively small volumes of water and rarely yield adequate numbers of animals. For this study modified plankton nets were moored at different depths in the strong tidal currents generated by the very large semidiurnal tides (11 m). Their construction, deployment and effectiveness are described elsewhere (Percy et al. 1988; Percy 1989). Briefly, they consisted of 0.5 m ring nets (1 mm mesh) with a stiff mesh entrance cone in the mouth leading into a 6 cm diameter entrance tube to minimize the likelihood of escape of animals from the net during periods of slack water. A fibreglass rod kept the net extended and a plastic fin oriented it in the current. Typically three nets were suspended by swivel hooks on a line at 1, 15 and 30 m depths, in winter through a hole in the ice and in summer beneath a moored float. They were usually retrieved within 24 h.

The net array was deployed 63 times between February and September from 1981 to 1985 (11 in 1981; 21 in 1982; 10 in 1983; 11 in 1984; 10 in 1985) at stations 1 or 5 (Percy 1989), located on the eastern side of inner Frobisher Bay with depths of about 40 and 50 m, respectively. Twelve sets of zooplankton samples were collected at station 1 (mostly during 1981) while 51 sets were taken at station 5. Nets were not equipped with flow meters during the first five deployments in 1981, so these collections serve only to confirm the presence of *Themisto* and provide some information about the size distribution of the population. Detailed information about individual collections is tabulated in Percy et al. (1988). The nets were also occasionally deployed singly at 15–20 m depth to collect *Themisto* for physiological studies. Gravid females found in these collections were preserved individually and also used for the analysis of fecundity.

The nets were usually deployed near the peak amplitudes in the lunar tidal cycle when currents were maximal. Velocities of 20–30 cm/s throughout the water column are typical at this station (Grainger pers. commn). Samples from nets that filtered less than 100 m³ of water were excluded from the analysis. During a deployment, the nets at 1 m depth filtered an average volume of 700 m³ (SD = 385 m³, n = 28), those at 15 m filtered 544 m³ (SD = 279 m³, n = 36) and those at 30 m filtered 635 m³ (SD = 334 m³, n = 30).

Zooplankton were preserved in 5% buffered formaldehyde. Eggs and embryos can be lost from the marsupium once the pleopods cease beating (Sheader 1977), so each ovigerous female was immediately removed from the sample and preserved separately. Abundances were calculated as the number of animals/100 m³ at each of the three collecting depths. To facilitate comparisons between seasons, abundances were integrated to a depth of 50 m and expressed as the number of animals/10 m². This calculation assumes that the density of organisms at a particular sampling depth is representative of their density half way to the nets immediately above and below, or to the bottom (≈ 50 m) in the case of the deepest net. The abundance estimates derived from the passive net collections should only be considered indicative of relative changes in population density.

The total lengths of fully extended animals were measured to the nearest 0.1 mm from the front of the head to the tip of the longest uropod, using micrometer calipers and an illuminated magnifier. Embryos were flushed out of the marsupium to estimate fecundity. The maximum diameter of each of 10 embryos per marsupium was measured to the nearest 0.01 mm with an optical micrometer. No correction was made for possible shrinkage following preservation. A subsample of the embryos was then mounted in glycerine on a microscope slide and their developmental stage assessed. Weight-specific reproductive output (total weight of the embryos as a percentage of the weight of the adult without embryos) was estimated for four freshly-collected gravid females, 26–28 mm in length, collected in mid-March. Embryos were carefully removed from the brood pouch and embryos and females were drained and weighed to the nearest 0.01 mg.

Results

Study area and abundance

Frobisher Bay is covered by landfast ice from late November until late July. A maximum ice thickness of 1.5–2.0 m is reached by late May. Semidiurnal tides with peak amplitudes of 11 m generate strong currents, ensuring thorough mixing and rapid flushing of surface waters (Grainger 1975). Details of oceanographic conditions at stations 1 and 5 are presented elsewhere (Grainger 1971a; Percy and Fife 1985a). *T. libellula* frequented the upper 50 m of the water column throughout the year (Fig. 1). However, the abundance in the summer (August) was usually one to two orders of magnitude greater than in the winter (February–March). In early August the abundance in the upper 50 m typically ranged from 50 to 250 animals/10 m², while in winter there were usually fewer than 5

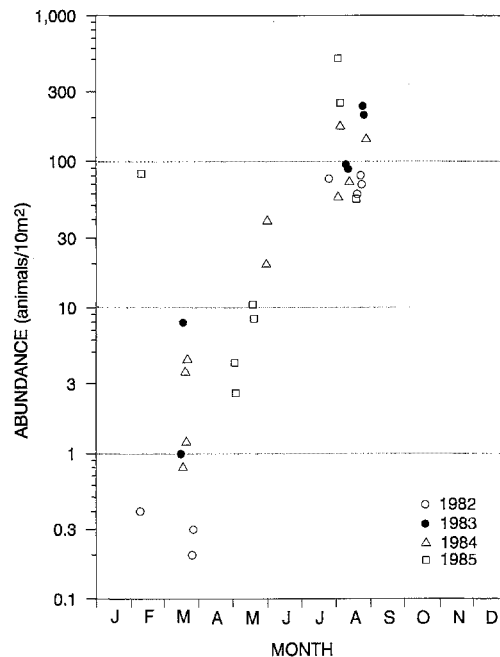


Fig. 1. Abundance of *T. libellula* in the upper 50 m at station 5 during different seasons and years

animals/10 m². A notable exception occurred in 1985 when *T. libellula* were almost as abundant in February as in the summer. It was in this collection and those of the subsequent three months that virtually all of the gravid females were found.

Size distribution and growth

In February the population consisted almost exclusively of animals 18 to 25 mm in length (Fig. 2). A small number of juveniles < 4 mm first appeared in the samples in March. Their numbers steadily increased during the ensuing months and peaked during the second half of May. The release of young ceased in June, for by July there were no longer any of the very smallest (≈ 2 mm) animals present in the collections. From July onwards the average length of the juveniles increased steadily and this cohort constituted the bulk of the population for the remainder of the summer. Substantial numbers of animals > 20 mm were still present in May, but after July they were virtually non-existent in the samples. By late August the largest of the young-of-the-year cohort were approaching the size (≈ 17 mm) at which the sexes are externally distinguishable by the lengthening of the second antenna in males and

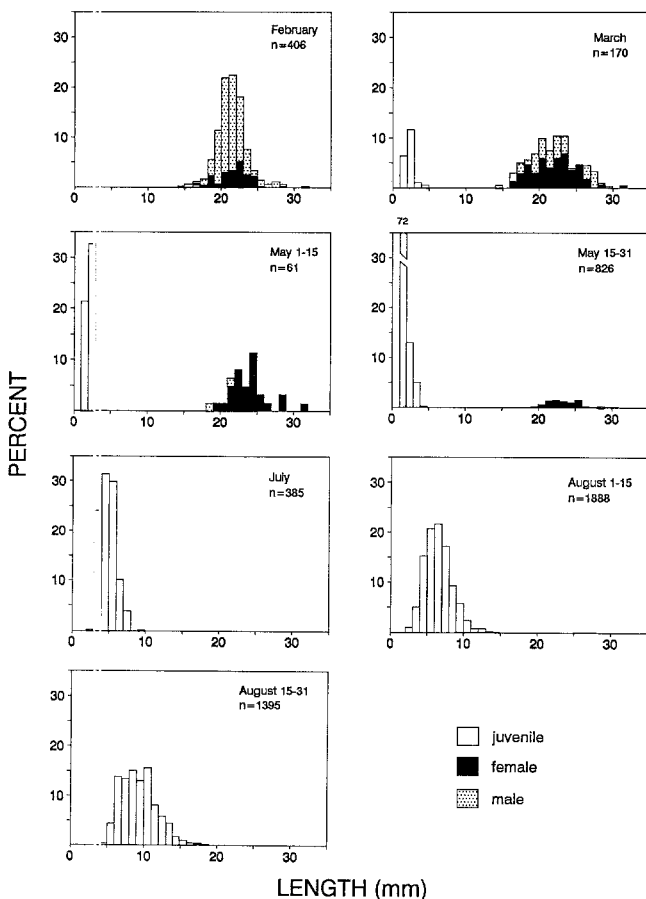


Fig. 2. Size frequency distributions of *T. libellula* in upper Frobisher Bay. Results from 1982–1985 combined

the development of brood lamellae in females (Dunbar 1940, 1957).

Growth was estimated by plotting the mean lengths at different times of the year of both the juvenile and adult cohorts (Fig. 3). The length of the adult cohort increased consistently from February (≈ 20 mm) until at least early August (≈ 29 mm) at a rate of about 1.5 mm/month. During 1984 and 1985 the rates of growth of the adult cohorts were similar (slope of the regression 0.042 and 0.039, respectively) and the differences in length between 1984 and 1985 are not statistically significant ($F=0.01$, $p>0.93$). For the combined 1984 and 1985 data the regression equation of length (L) on Julian day (D) is $L=0.043D+18.9$ ($r=0.93$, $p<0.01$, $n=9$). Not enough adults were collected in August to assess their growth during the summer.

There was little change in the mean length (≈ 2.5 mm) of the juvenile cohort between March and late May ($L=2.44-0.0008D$; $r=-0.054$, $p>0.1$, $n=6$). However, between late July and late August the mean length rose from about 5.5 mm to over 11 mm ($L=0.181-32.89D$; $r=0.84$, $p<0.01$, $n=11$). The variation in the growth rate of juveniles during July and August in different years is summarized in Table 1. The mean rate was 5.67 ± 1.47 mm/month and the slowest growth was half that of the fastest. However, in three of the years the growth was similar, averaging just over 6 mm/month.

Reproductive cycle

Gravid females were not found in the near surface waters of Frobisher Bay during the winter and spring every year. Between 1982 and 1984 only one such female was obtained

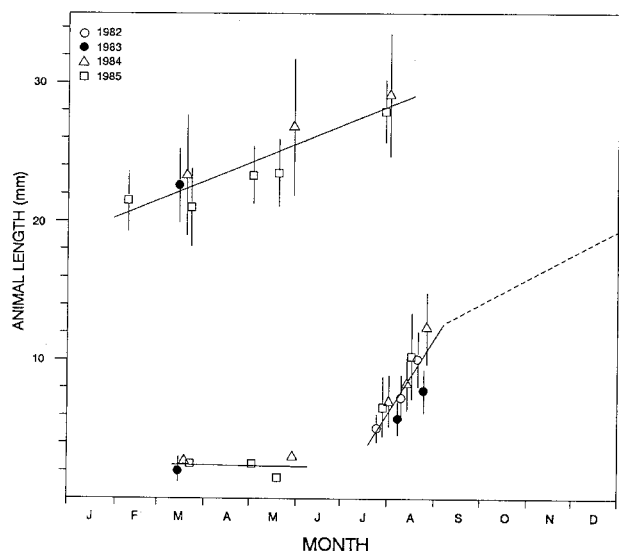


Fig. 3. Growth of juvenile (lower lines) and adult (upper line) cohorts of *T. libellula* during different years. Vertical lines through points are standard deviations. Solid lines are least square regressions for adjacent data points. Dashed line indicates expected growth during winter months

even though animals were regularly collected in late winter and early spring (Fig. 1). In marked contrast, a total of 186 gravid animals were obtained from 13 collections between February 4 and May 29, 1985. Only 84 of these were preserved individually and thus suitable for the fecundity analysis. Of these, 34 were collected from 4–20 February, 23 from 13–20 March, and 27 from 3–29 May. The highest proportion occurred in February, when over half the females were carrying embryos. This declined to about 40% by mid March and to 30% by the third week in May.

Fecundity and embryo development

The average length of all the gravid females was 23.3 ± 1.8 mm, with most being 22 to 25 mm long (Fig. 4). The smallest was 20.3 mm and the largest 32.4 mm. The weight-specific reproductive output of females carrying stage a₁–a₂ embryos (Table 2) in mid-March was 14.5 ± 2.2% (weight of brood = 28.7 ± 6.8 mg; weight of female without embryos = 197.4 ± 17.9 mg, n = 4).

In both February and March the fecundity was significantly correlated with animal size (Fig. 5). The regressions of brood size (BS) on female length (L) for each of those two months were not significantly different (ANCOVA p < 0.05), so a common regression was calcu-

Table 1. Growth rates of the juvenile cohort of *T. libellula* during July and August in different years

Year	Date	n	Mean length (mm) ± S.D.	growth rate (mm/month)
1982	Jul 24	358	5.07 ± 0.99	5.82
	Aug 19	594	10.12 ± 2.00	
1983	Aug 9	636	5.83 ± 1.19	3.57
	Aug 25	543	7.74 ± 1.54	
1984	Aug 2	409	6.99 ± 1.81	6.42
	Aug 27	191	12.33 ± 2.62	
1985	Aug 2	437	6.63 ± 2.14	6.87
	Aug 18	56	10.30 ± 3.10	

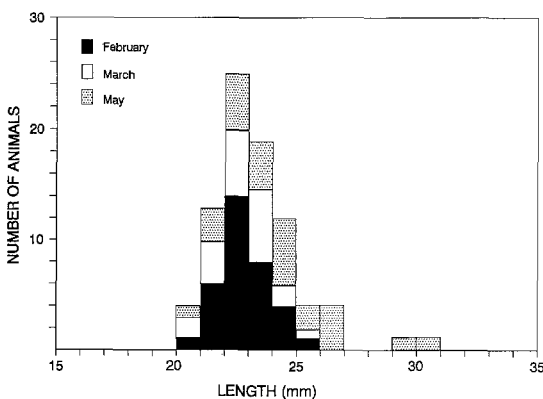


Fig. 4. Size frequency distributions of ovigerous *T. libellula* during February, March and May of 1985

Table 2. Developmental stages of *Themisto libellula* while present in brood pouch

- a. *Stages within egg membrane*
 - a₁ Undifferentiated cell mass with no trace of caudal furrow.
 - a₂ Caudal furrow developing but no distinguishable limb buds.
 - a₃ Limb buds distinguishable, endopodite and exopodite of pleopods unsegmented with no distal spines.
- b. *Post hatching stages*
 - b₁ Body tightly curled in embryonic position with urosome close to head, endopodite and exopodite of pleopods unsegmented, no distal spines on endopodite and exopodite of pleopods, no setal tuft on dactyls of pereopods 5–7.
 - b₂ Body partially uncurled, endopodite and exopodite of pleopods with 2 podomeres, no distal spines on endopodites and exopodites of pleopods, no bifid spine on endopodite of pleopods, no setal tuft on dactyls of pereopods 5–7.
 - b₃ Body completely uncurled, endopodite and exopodite of pleopods with 3 podomeres, distal spines on endopodites and exopodites of pleopods, bifid spine present on endopodite of pleopods, setal tuft present on dactyl of pereopods 5–7.

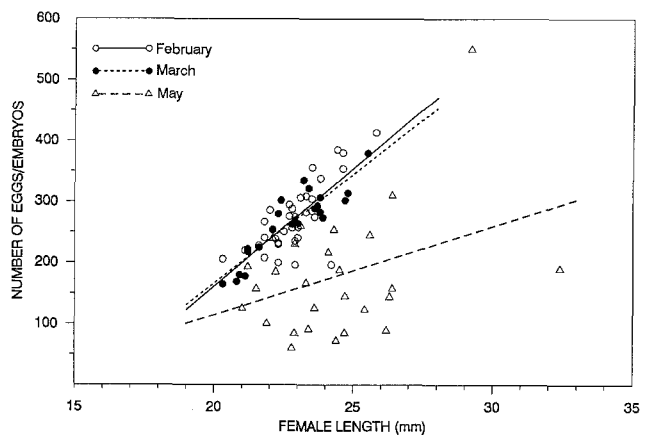


Fig. 5. Relationship between brood size and body length for *T. libellula* during February (r = 0.74, n = 33, p < 0.001), March (r = 0.90, n = 21, p < 0.001) and May (r = 0.39, n = 18, p > 0.1) of 1985

lated: BS = 37.2L – 579.3 (n = 54, r = 0.81, p < 0.001). This regression indicates that in February–March an average 23 mm long female had about 275 embryos. The minimum number observed in the samples was 165 and the maximum 413. In May the relationship between length and embryo number was no longer significant (p > 0.05). The mean number of embryos estimated for a 23 mm female was lower (177), and the observed range in brood size (60–550) was more than double that observed in February–March.

There was no significant relationship between the diameter of embryos and the length of the female in either the February (F = 0.13, p > 0.7) or March (F = 0.57, p > 0.4) samples. The mean embryo diameter in February (535 ± 24 μm, n = 34) was not significantly different (F = 0.18, p > 0.6) from that in March (547 ± 35 μm, n = 22), so a common mean (540 ± 29 μm) was calculated. The criteria used to assess embryo development are summarized in

Table 2. During February, all of the embryos were spherical or slightly oval and consisted of a mass of seemingly undifferentiated cells, containing distinct oil globules of varying sizes, and enclosed within an egg membrane (Table 3). About 40% of them showed the beginnings of the caudal furrow that eventually delineates the cephalic and posterior body rudiments (Sheader 1977). There was no trace of limb buds or other recognizable structures. By mid-March, almost all the embryos were still within the egg membrane, but in most the caudal furrow was well developed. One third of the broods had begun to develop rudimentary, but recognizable, limb buds, and one brood had even hatched. By early May, all of the embryos had hatched. Over three quarters of these were still in the early post hatching stage (b_1) with bodies still tightly curled. About 10% had moulted to stage b_2 and a similar proportion had moulted to stage b_3 , were fully uncurled, had spines on the pleopods, characteristic setal tufts on the dactyls of the perieopods and 3 podomeres on each pleopod ramus. This was the latest stage observed in the marsupium. The mean extended body length of 10 stage b_3 animals taken from the marsupium of each of 10 randomly selected females during May was 2.22 ± 0.10 mm (min. = 1.99 mm, max. = 2.46 mm, $n = 100$). This was not significantly different ($T = 1.15$, $p > 0.25$) from the mean length (2.19 ± 0.15 mm; min = 1.97, max. = 2.73, $n = 63$) of a sample of free-living juveniles collected at the same time. These also had 3 podomeres on the pleopod rami. Gravid animals, bearing stage b_3 embryos, collected on May 10 and 19, 1985 and kept in the laboratory, released young within 24 h. Six subsamples consisting of 200 juveniles each, collected within 4 h of release, had average wet and dry weights per individual of 96.5 ± 40.0 μg and 23.8 ± 8.3 μg , respectively.

Discussion

Although *T. libellula* inhabits the upper 30 m of the water column in Frobisher Bay throughout the year, the abundance in winter is typically less than 5% that of peak densities in summer. In the central Arctic Basin, concentrations of *T. libellula* near the surface in winter were similarly found to be about 3% of those in summer (Mel'nikov 1989). The rapid increase in numbers in the spring is largely attributable to the recruitment of newly-

released juveniles. As their number increased in spring, the number of adults declined sharply and were virtually absent after May. It has been suggested that they are semelparous and die immediately after reproducing (Dunbar 1957; Wing 1976), although other species of hyperiids may breed several times during their life span (Kane 1963).

By late August the population appeared to have reached its peak, and in early September the abundance in Frobisher Bay and adjacent coastal waters began to decline (Dunbar 1946, 1957; Percy and Fife 1985a) towards its midwinter minimum. Dunbar (1946) speculated that this was a consequence of either predation by seals or, more likely, offshore transport by surface currents. However, migration of the animals into deeper water as they mature or with the onset of winter may also occur. In *T. libellula* (Wing 1976) and other *Themisto* species (Bigelow 1926; Bousfield 1951; Williams and Robins 1981) adults live at greater depths than juveniles. There is no information about seasonal vertical movements of *Themisto* in eastern Arctic waters, but it migrates to deeper water in winter in other areas. In southeastern Alaskan waters, for example, the population resided largely in the upper layers during early summer, but descended to 200–300 m during the fall and winter (Wing 1976). Similarly, a review of zooplankton data from the central Arctic basin led Grainger (1989) to conclude that several species, including *T. libellula*, concentrate in the upper 50 m (Arctic surface water) during the summer and then descend to below 200–300 m (Atlantic water) during the winter.

Themisto were unusually abundant in the upper 30 m in Frobisher Bay during the winter and spring of 1985. The fact that almost all the gravid females were obtained during this one period suggests that reproduction in near-surface waters may not be the normal situation. It may be that there was an advection of a deeper dwelling population of mature females into the bay at this time. Nevertheless, the collections thus obtained have provided worthwhile information about its life cycle and reproductive biology in Arctic waters.

Some caution is called for in interpreting the size frequency data because of the possibility of size bias inherent in sampling a highly mobile species with a passive collecting system. However, intensive sampling with towed 1 m ring nets during several open water seasons (Percy and Fife 1985b) yielded a pattern of size frequency distribution during July and August similar to that illustrated in Fig. 2.

Perhaps the most unexpected finding of this study is that Arctic populations of *T. libellula* mature and reproduce at a much smaller size than previously thought. Some ovigerous females were just over 20 mm long and most were only 22–25 mm in length. This contrasts with an earlier finding of Dunbar (1946) that in autumn rudimentary brood lamellae were present only in animals greater than about 25 mm in length. He further reported that a few gravid specimens found in the stomachs of seals in March ranged in length from 35 to 46 mm and concluded that this was the size at which they first reproduced. Similarly, in the Belle Isle Strait region of southern Labrador between July and September not a single sexually mature specimen was collected even though some

Table 3. Number of ovigerous *T. libellula* with broods in various stages of embryonic development at different times between February and May

Date	Developmental stage					
	a_1	a_2	a_3	b_1	b_2	b_3
Feb. 4		1				
Feb. 13–16	19	12				
Mar. 13	2	12	7	1		
Mar. 20		1				
May 3–4				6	2	1
May 19–21				7		1
May 29				1		

were up to 25 mm in length, leading Bousfield (1951) to conclude that *T. libellula* does not mature "until the animal becomes quite large". Since such a larger size was probably unattainable within one year it was concluded that they reproduced only when at least two years old. However, the finding, in seal stomachs in February, of a few *Themisto* as small as 20 mm bearing oostegites, led Dunbar (1957) to suggest that "although it is improbable that many of the juveniles of the year breed in the following winter, some apparently do". Our results tend to confirm this speculation.

The estimated growth rate of *Themisto* suggests that it can probably attain breeding size within a year. Juvenile *T. libellula* were released from the brood pouch, chiefly during April–June, at a mean length of about 2.2 mm. This is only slightly larger than the size at release (1.8–1.9 mm) of specimens from southeast Alaskan waters (Wing 1976) and is comparable to that observed in *T. gaudichaudi* (Kane 1963). From March through May there was no change in the mean length of the juvenile cohort, presumably because of the continuing release of large numbers of juveniles. Only upon termination of brood release in late May did the length of the juvenile cohort begin to rise. During July and August in three years they grew at a rate of about 6 mm/month, while in one year they grew at only half this rate. From size frequency distributions of animals collected during the open water season at Lake Harbour, Dunbar (1946) concluded that in the eastern Arctic juveniles grew only about 3 mm/month. This is comparable to the lower rate observed in the present study. In contrast, during May and June *T. libellula* in the Gulf of Alaska grew at an average rate of 5.7 mm/month (Wing 1976), similar to the mean rate found in this study. Thus, the difference between the earlier growth rate estimates of the eastern Arctic and southeast Alaskan populations may not be attributable to a geographic gradient in physiological processes (Wing 1976) but rather to normal year to year variation.

Although the summer growth rates in the two areas were similar there was a time lag in the seasonal change in modal length of the Arctic population (Fig. 6). The Alaskan

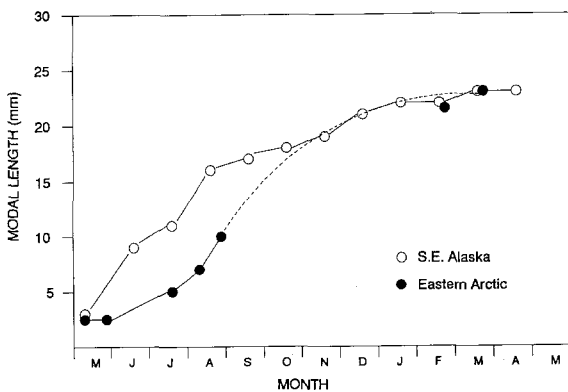


Fig. 6. Modal lengths of size frequency distributions of *T. libellula* at different times of the year in S.E. Alaska (after Wing 1976) and eastern Arctic. Dashed line indicates expected growth rate

animals grew rapidly in May and this was sustained into early August, after which the rate declined sharply. In contrast the eastern Arctic animals began rapid growth only in July, some two months later. This probably reflected differences in the timing of the spring blooms and in seasonal temperature cycles in the two areas. In S.E. Alaska the bloom peaked in late April/May (Wing 1976), while in the eastern Arctic it peaked some two months later in late July/August (Grainger 1971a, b). By the end of August the length of the juvenile cohort in the eastern Arctic was about 10 mm. In order to develop into the gravid 23 mm cohort present in February the Arctic populations must have grown more rapidly during the fall than their Alaskan counterparts. This seems reasonable given the lag in the seasonal production cycle and probably in prey abundance. In the surface waters in Frobisher Bay, potential prey biomass (mesozooplankton) typically falls to about 40% of the summer peak during September and then gradually declines by about 5%/month through the fall and into the winter (Grainger 1971b).

There appears to be little if any difference between the southeast Alaskan (Wing 1976) and eastern Arctic populations in terms of annual growth rate and size or age at initial maturity. However, the more important question about the proportion of the population that breeds at the end of the first year remains to be answered. It may be that some of the females breed after the first year and then die (Dunbar 1957; Wing 1976) while others breed only at the end of the second year. Such a pattern has been reported in gammaridean amphipods (Sainte-Marie and Brunel 1983; Siegfried 1985). It is also possible that females reproduce after one year and then again the following year. This appears to occur in other species of *Themisto* (Siegfried 1965) and the females seem to moult to an immature condition and overwinter between broods (Kane 1963; Evans 1968). Either pattern could give rise to the three-cohort size frequency distribution that Dunbar (1957) attributed to a "two phase" breeding cycle.

In southeast Alaskan waters the first ovigerous females of *T. libellula* were collected in March and none were encountered after May (Wing 1976). In the waters of southeastern Baffin Island *T. libellula* also breeds chiefly during the winter and spring. Dunbar (1946) thought it possible that in the Arctic reproduction extended through much of the year; however, intensive sampling over a number of years during July, August and September using both passive and towed nets failed to yield gravid animals (Percy and Fife 1985a). No zooplankton collections have been made between October and February (because of the hazards of working on newly formed sea ice in the fall and the inadequate day length for carrying out field work in mid-winter) so the date of initiation of egg laying is unknown. However, all of the embryos present in mid-February were undifferentiated and at an early stage of development. The general pattern of development was similar to that described for *T. gaudichaudi* (Kane 1963; Shearer 1977). By mid-March considerable development had occurred and rudimentary limb buds were observed in many of the embryos. Although the embryos within any given marsupium were at a comparable state of development, there was a great deal of variation among different

broods. Some juveniles were also being released from the marsupium at this time as evidenced by the presence of free-living animals of ≈ 2 mm in length in the March net collections. This release of young from the brood pouch continued through April and probably peaked during May. The reduction and greater variability in the fecundity of ovigerous females collected in May clearly reflected the fact that most of the broods were by then fully developed and young were being released. This was also reflected in the rise in the proportion of small juveniles in the zooplankton collections during May.

There is no information about what these young fed upon during the weeks or months prior to the blooms of phytoplankton (Grainger 1971a) and zooplankton (Grainger 1971b) in the water column during July and August. Dunbar (1957) suggested that they may subsist on leptopelic detritus. There was no evidence that they parasitize gelatinous zooplankton as do many hyperiids (Laval 1980). Neither was there any evidence that they congregated at the ice water interface to feed on the sub-ice (epontic) biota as do several species of gammarid amphipods (Grainger and Hsiao 1982). Unlike these gammarids (Aarset and Aunaas 1987; Shea and Percy 1990) *T. libellula* is poorly adapted physiologically (Aarset and Aunaas 1987) to cope with the osmotic stresses characteristic of the epontic habitat. Grainger et al. (1985) also found no *T. libellula* associated with the sub-ice community, though they were present deeper in the water column. Nets deployed within 1 m of the ice did not collect significant numbers of *Themisto* (Percy et al. 1988). Although divers in the central Arctic Basin observed swarms of *T. libellula* just beneath the ice during both summer and winter (Mel'nikov 1989), these only occurred in "hydrologically calm zones" in the lee of ice keels, and dispersed when exposed to currents. There was no indication that they were feeding on sub-ice biota. Similar swarm formation would be unlikely in Frobisher Bay given the high current velocities and the even topography of the undersurface of the landfast ice.

In amphipods, as in other invertebrates, the number of young produced usually varies directly with the size of the female (Sheader and Chia 1970; Myers 1971; Sheader 1977). Fecundity is clearly related to length in *T. libellula*, ranging from about 165 eggs in a 20 mm animal to over 600 in a 32 mm animal. The eggs are relatively large in keeping with the fact that the embryos are retained in the marsupium during a lengthy period of direct development. Polar invertebrates are generally considered to be more K-strategists in respect to reproduction than their temperate or tropical counterparts (Arnaud 1977; Clarke 1979). In other words, they usually produce a small number of eggs but their investment per offspring is high because these eggs are large. However, a comparison of the fecundity-size relationship of various species of hyperiids from different regions (Fig. 7) provides no evidence that polar species, and in particular *T. libellula*, have fewer offspring per brood than non-polar species. The equation for the linear regression of brood size (BS) on length (L) for the 17 hyperiids is $BS = 17.54L - 49.58$ ($r = 0.79$, $p < 0.01$). Logarithmic transformation of the data did not improve the fit. Size at maturity rather than latitude seems to be the

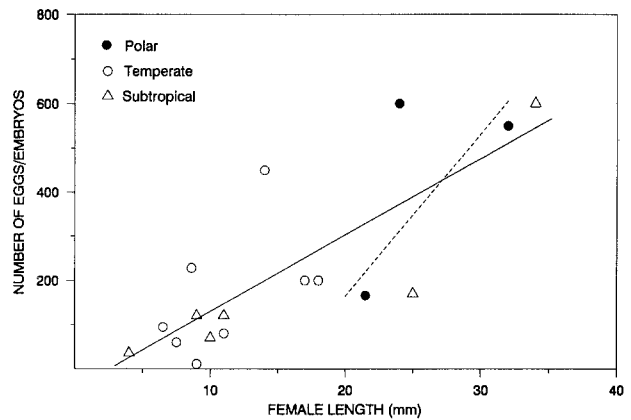


Fig. 7. Relationship between the maximum reported brood size and adult body length of hyperiids from polar, temperate and subtropical waters. The solid line is the least square regression for all 17 species. The data is derived from Behning 1939; Bowman 1960; Dudlich 1926; Evans 1968; Harbison 1976; Laval 1968; Laval 1980; Metz 1967; Percy, this study; Percy unpubl; Sheader 1977; Siegfried 1965; Westernhagen 1976; White and Bone 1972. The dashed line is the February-March regression for *T. libellula* derived from Fig. 5

principal factor influencing fecundity. The number of broods produced during the life cycle also influences the number of eggs per brood as well as the egg size in gammaridean amphipods (Sainte-Marie 1991). However, too little reliable information is available about the number of broods produced by hyperiids to determine if a similar phenomenon occurs.

Although much has been learned about the biology of *T. libellula* during its first year there is still little information about its subsequent fate. Elucidation of the complete life history has been hampered by an inability to collect larger animals with conventional plankton nets. This may account for their apparent absence in southeastern Alaska waters, where the largest animal encountered was 29.5 mm (Wing 1976). The largest animal collected during the present study was a 33 mm long specimen obtained in late August. Furthermore, in several years of intensive sampling in Frobisher Bay with 1 m towed ring nets the largest animal collected was only 34.6 mm, again in late August. This is approaching the bottom of the size range (35–46 mm) of the mature and gravid amphipod remains found in seal stomachs in March by Dunbar (1946). The growth rate data and the seasonal pattern of size frequency distributions indicate that these animals could not have attained this size in a single year but were more likely at least two years old. A report of animals up to 60 mm long (Bovallius 1889) suggests that some may live even longer. Dunbar (1957) felt that the larger animals might simply reside at depths beyond the reach of his sampling gear. However, this seems unlikely since sampling with 1-m ring or bioness nets as deep as 485 m in outer Frobisher Bay and in adjacent areas of eastern Hudson Strait failed to capture any of the larger specimens (Percy and Fife 1985a; Percy unpublished). Net avoidance can be a major problem in sampling large highly mobile hyperiids (Laval 1980) and this may be an important consideration

in relation to larger *Themisto*. Until effective means are found for sampling these older animals a full understanding of the life history of *T. libellula* will continue to elude us.

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