Superficial ecosystem similarities *vs* autecological stripping: the "twin species" *Mesocyclops leuckarti* (Claus) and *Thermocyclops oithonoides* (Sars) - seasonal habitat utilisation and life history traits

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ABSTRACT

Mesocyclops leuckarti *and* Thermocyclops oithonoides*, among the most common European species of cyclopoid copepods, immigrated to central Europe from eastern refuges after the last glaciation.* M. leuckarti *arrived prior to* T. oithonoides*. In a border region of* T. oithonoides *in southern Norway, the species was found exclusively below the highest postglacial marine limit, whereas it had spread to other neighbouring lakes above the former marine limit close to its more central region of distribution in eastern Norway. The habitat of* M. leuckarti *is characteristically both littoral/profundal and planktonic, whereas* T. oithonoides *is a true planktonic species. The egg sacs of the larger species* M. leuckarti *protrude from its genital segment, likely increasing water friction.* M. leuckarti *has probably developed strategies to reduce predation on eggbearing females, such as staying in littoral, profundal or oxygen boundary regions where fish are either absent or experience hunting difficulties. We hypothesise that the numerical suppression of* M. leuckarti*, its sex ratio, the habitat distribution of adult females, and its life cycles in many eutrophic lakes, is strongly affected by fish predation.* M. leuckarti *is considerably larger than* T. oithonoides*; total body length: 1.0-1.3 mm vs 0.7-1.0, respectively. The negligibly coloured and smaller adult* T. oithonoides *may be outside the prey range for many fish species. In the lowland region, both species completed several numbers of reproductive cycles annually. There were various patterns of diannual and triannual life cycles. Some populations exhibited a conspicuously delayed revival from sediment diapause, others in eutrophic lakes developed slowly during the summer (probably due to naupliar competition from cladocerans), or stayed in the plankton during prolonged periods during autumn. At higher altitudes and in large cold lakes, one generation a year was recorded. In its northern range,* M. leuckarti *showed sediment diapause in all types of localities, even the deepest lakes, usually in the upper littoral region. In more shallow lakes, deeper diapause sites were observed.* T. oithonoides *diapaused in either the lower littoral, or the profundal regions.* M. leuckarti *showed different life cycles in localities within the same geographical region, especially in its southern range. In the shallow part of Bodensee in Germany it entered sediment diapause, whereas in the much deeper main basin it showed plankton diapause (also called "active diapause"). The period of diapause for* M. leuckarti *(especially in the sediment) decreased from north to south. At about 45° N, sediment and plankton diapause were non-existent, and the species exhibited continuous development, even with relatively low winter temperatures (in Lago Maggiore).* T. oithonoides*, whose southern distribution in western Europe extends to about 50° N, showed winter sediment diapause throughout its distribution, but frequently with a fraction of the local population in plankton diapause. The combined effects of these different abiotic and biotic parameters help explain the variations of life histories observed in the field.*

Key words: Mesocyclops leuckarti, Thermocyclops oithonoides, *life cycles, diapause, habitat selection*

1. INTRODUCTION

A basic familiarity with life cycles is a prerequisite for analysing life histories. A thorough understanding of autecology is furthermore important for analysing complex ecological systems. This is probably the background for the recent renewed interest in systematics and autecology. If nature is ordered hierarchically, one has to study it (or at least a part of it) hierarchically; if one level of the hierarchy is ignored, connections among the levels are lost. Systematic and taxonomic studies based on life cycles should be promoted; one cannot seriously describe a living species without a thorough knowledge of its life cycle.

The copepod order is one of the most numerous animal groups on the earth (Huys & Boxshall 1991). It ranges among the more conspicuous members of the aquatic biota and has diversified into a variety of habitats from interstitial sand to parasitic living, damp moss, subterranean localities and plankton. Cyclopoid copepods inhabit the above ecosystems as well. The Cyclopoida is by far the most successful inland-water group within Copepoda, in terms of the diversity within, and the geographical distribution of, their respective groups. Cyclopoid copepods form taxonomically a problematic and difficult group of animals, however. In plankton they are encountered both in neritic and epipelagic marine and freshwater environments, but are more diversely developed in freshwater. Planktonic cyclopoid copepods become progressively more carnivorous during their ontogenetic development. Since they are relatively unspecialised seizers, they will attack a variety of food-items from bacterial clumps, large algae and small zooplankton to underyearling (0[+]) fish. The animals deve-

lop and moult through many larval and juvenile stages (6 naupliar and 5 copepodids) before reaching adulthood, and therefore offer considerable practical and time consuming problems in ecological studies. Several cyclopoid species, similar in shape and size, often co-exist in the plankton. In a number of ecological studies, scientists have avoided the pelagic cyclopoids altogether, treating them as *Cyclops* spp., ignoring that several genera with a variety of life histories are thus being included in the category. Cyclopoid copepods have therefore never achieved a status as popular research animals, like e.g. the genera *Daphnia* spp. or *Chaoborus* spp. have. Nevertheless, several researchers have used cyclopoid copepods as test animals, notably in interesting studies on heritability, life history traits and diapause. The "twin species" *M. leuckarti* and *T. oithonoides* commonly coexist during similar periods in the plankton of temperate Palaearctic lakes. The genera *Mesocyclops* and *Thermocyclops* are usually observed sympatrically in most lakes all over the world. Many scientists underline the close taxonomic and ecological relationships of the species by continuing to place both within the genus *Mesocyclops*. In many quantitative ecological studies they are also treated together. Nevertheless, a whole array of ecological differences exist between the two species, and the aim of the present paper is to present and synthesise historical and new evidence for these facts.

1.1. Taxonomical overview

Along with the genus *Cyclops* O.F.Müller, 1785, the ecologically most important plankton genera of cyclopoids are *Mesocyclops* G.O. Sars, 1914 and *Thermocyclops* Kiefer, 1927. *Cyclops* is the dominant temperate genus, *Thermocyclops* the most conspicuous tropical, and *Mesocyclops* are found within both zoogeographical regions. The most important planktonic cyclopoid copepods were first described in the active taxonomic period in the last part of the 19th century, like the species in the present study: *Mesocyclops leuckarti* by C. Claus 1857 (as *Cyclops Leuckarti*) and *Thermocyclops oithonoides* by G.O. Sars 1863 (as *Cyclops oithonoides*). Sars later set up the genus *Mesocyclops* to include both species. Kiefer (1927) shortly after placed *T. oithonoides* in a separate subgenus under *Mesocyclops*, and later delimited *Thermocyclops* as a separate genus by using minute taxonomical criteria. Many systematisists and ecologists disagreed with Kiefer's view and still used *Mesocyclops* as the common genus for the two species. Sars, on the other hand, claimed that C.L. Koch[1] in the 1830s presented the first recognisable and thus valuable description of what we today classify as *M. leuckarti*, and Sars consequently used Koch's species name *M. obsoletus* (Koch). Kiefer (1928; 1978; 1981) also considered this species conspecific with *M. leuckarti*, but referred to Sars as its primary author (not the Koch authorship, which logically should have had priority). More ta-

xonomists expressed doubt concerning Koch's species descriptions, and in the list of species synonymous with *M. leuckarti*, both Rylov (1963) and Van der Velde (1984) explicitly wrote *M. leuckarti* non *C. obsoletus* Koch.

Nevertheless, both Sars and Kiefer agreed in what they considered "the remarkable cosmopolitan distribution of *M. leuckarti*". They were indeed "lumping" a number of species into the *M. leuckarti* concept. Paradoxically, Kiefer simultaneously acted as a considerable "taxonomic splitter" by creating the subgenus and later genus *Thermocyclops* from *Mesocyclops*, a process that started in 1927/1928.

Until the overripe revision of *Mesocyclops* by Kiefer in 1981 [only 3 years after completing his great account on freshwater copepods in the Binnengewässer 26, Part 2 in 1978, in which he still maintained the usual cosmopolitan approach of *M. leuckarti* (!)], the scientific community was living with the extreme cosmopolitan distribution of its primary species (see also Dussart & Fernando 1996; Dahms & Fernando 1993). Several other zooplankton, notably the cladoceran *Chydorus sphaericus*, also lost their cosmopolitanism in that period (Frey 1980, 1982). Kiefer (1981) delimited the geographical distribution of *M. leuckarti* to the Old World and West Asia, as shown on figure 1A. It is recently claimed that *M. leuckarti* is distributed in Lake Donghu (about 114 °E; Yufeng *et al*. 1999). For a current distribution of *M. edax* in North America, see Patalas (1986). The geographically more restricted distribution of *T. oithonoides* is shown in figure 1B. Many of the earlier "*M. leuckarti*" populations changed their nomenclature, even several times, in the turbulent after-

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[1] G.O. Sars seemed to rely strongly in the species descriptions of C. L. Koch. This was not the only case where he referred to Koch as the origin of the species description. In all the following cyclopoid species Sars claimed priority for Claus. Maybe the skilled taxonomist Sars identified some species characters several of the others were unable to recognise? Nevertheless, it is remarkable that Sars put so much stress upon Koch's original and often earlier descriptions, and considered these recognisable species. In the following, the Koch descriptions within Sars nomenclature are placed first, the original species name follows after: *Cyclops vulgaris* Koch - *Cyclops viridis* Fischer, *C. lucidulus* Koch - *C. vernalis* Fischer, *C. pulchellus* Koch - *C. bicuspidatus* Claus, *Mesocyclops obsoletus* (Koch) - *C. Leuckarti* Claus, *Pachycyclops signatus* (Koch) - *C. fuscus* Schmeil, *P. annulicornus* (Koch) - *C. albidus* Schmeil, *P. bistriatus* (Koch) - *C. distinctus* Richard, *Leptocyclops agilis* (Koch) - *C. serrulatus* Fischer. Even more remarkable is the addition Sars (1918, p. 211) made in his extremely detailed work on cyclopoid copepods, where he claimed *Cyclops pictus* Koch should have priority to *C. strenuus* Fischer : "As it appears to me beyond doubt, that Koch's species is the same as subsequently described by Fischer as *C. strenuus*, I think that, according to the rules of priority, the name proposed by the first named author must be retained for the present species".
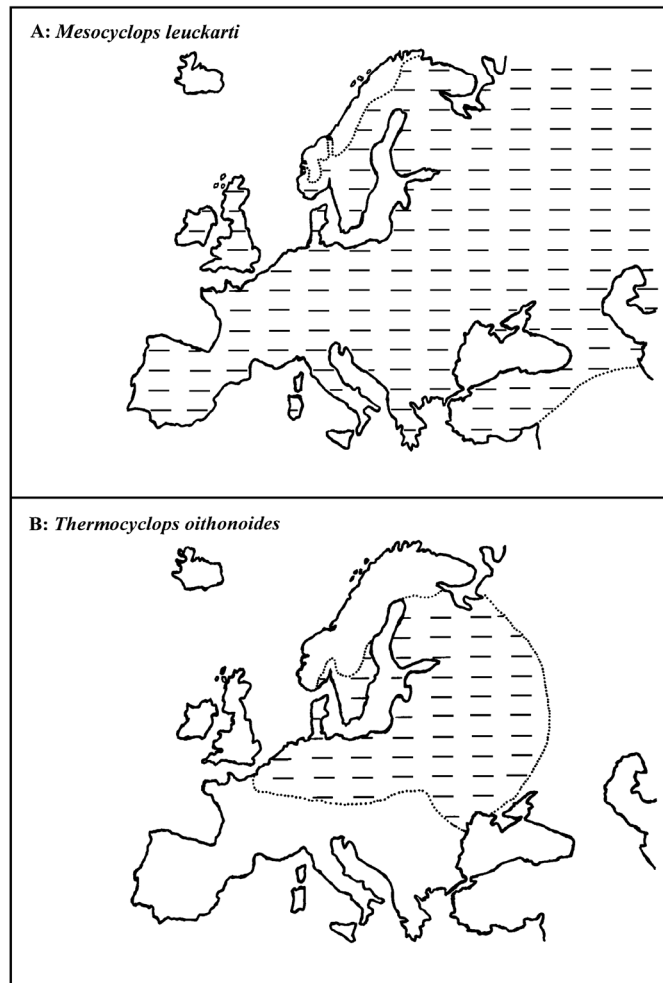
Fig. 1. The present zoogeographical distribution of *M. leuckarti* (A) and *T. oithonoides* (B). Mainly after Kiefer (1981), and papers referred to in the references. The exact boundaries of both species are uncertain due to too few samples and/or unsettled taxonomy, especially in the eastern regions.

math of Kiefer's revision, especially in Asia, Africa and Latin America. A good overview of Kiefer's thinking and viewpoints concerning cyclopoid systematics were presented in a somewhat hidden and largely unknown and little cited publication. Here he (Kiefer 1952) demonstrated an up-to-date knowledge concerning theories of taxonomy and systematics, including the continuous difficulties at species and subspecies levels (see also Einsle 1975; Nilssen 1979). Kiefer (1952) claimed to use the so-called evolutionary species concept, and was reluctant in utilising the subspecies concept for the various cyclopoid copepod species, and instead choose the concept "Rassenkreis"; a practical taxonomic translation would be a "collection of populations".

1.2. Ecological consequences of an unsettled taxonomy

A number of papers have been published on the ecology and life histories, especially of *M. leuckarti*, but also of *T. oithonoides*. The majority of these publications originates from the Old World, and therefore comprises the original *M. leuckarti* (Fig. 1A), and *T. oithonoides* (Fig. 1B). But other populations, like the one in Lake Kinneret, Israel, that has been intensively studied

the last decades (Gophen 1988), had its name changed to *M. thermocyclopoides* and thereafter to *M. ogunnus*. Likewise, the common *Mesocyclops* in the African great lake area is now *M. aequatorialis* (Van der Velde 1984). The Lake George (Uganda) *Thermocyclops* has changed from *T. neglectus* to *T. hyalinus consimilis*, according to Burgis (1970). It should be noted that both *T. consimilis* (Kiefer 1934) and T. neglectus (Sars 1909) are considered separate species by Kiefer (1978), and the common *Thermocyclops* in Lake George is according to Kiefer (1978), *T. crassus*.

The problem in identifying *M. leuckarti* and *T. oithonoides* is not straightforward, especially in Continental European lakes, where 3-6 cyclopoid copepods often coexist in the pelagial, and in which populations are dominated by larval and juvenile instars during much of the year. Analyses of life cycles is crucial in ecological research, and considering the 12 different developmental stages, the work often seems overwhelming or practically insurmountable (see Einsle 1989). It is easily understandable that even if rotifers and cladocerans are being counted and processed in detail, the cyclopoid copepods are very often referred to as Cyclo-

Mesocyclops leuckarti   *Thermocyclops oithonoides*
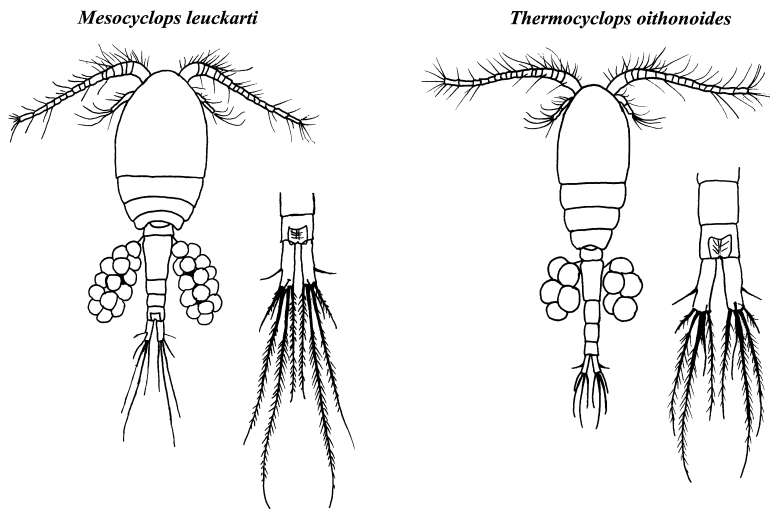
Fig. 2. Important species characteristics of *M. leuckarti* and *T. oithonoides*. Note position of egg sacs. Based on original drawings by Sars (1918, Plates 35, 36).

poidae indet., or *Cyclops* spp., the latter category usually including several species both of *Cyclops*, *Mesocyclops* and *Thermocyclops*. This is ecologically unfruitful, since in nearly 100% of the cases, cyclopoid copepods are present in the pelagial of most lakes all over the world.

More serious problems arise when the autecological details of the different species are concerned, and when the species are falsely identified. Figure 2 presents the most important "field" (stereomicroscopic) species characters of *M. leuckarti* and *T. oithonoides*. Notably are the shape of the furcal setae, their internal length relationships, the position and shape of the egg sacs of the gravid females, the general body shape, and the size of the animals. In addition, some ecological parameters are important, notably the altitude of the recorded site, the number of eggs per egg sac, and the habitat distribution of adult females and diapausing copepodids. *M. leuckarti* is considerably larger, by approximately 20-40 percent (total body length: 1.0-1.3 mm *vs* 0.7-1.0 for *T. oithonoides*), and thus more susceptible to fish predation, especially when carrying egg sacs. Other ecological features will be treated within the scope of this paper.

2. MATERIAL AND METHODS

The lakes sampled in Norway involved quantitative (lakes in Fig. 5; Fig. 6) and qualitative sampling (lakes in Fig. 3; Fig. 4) over the deepest parts of the lakes or the depth ranges where *M. leuckarti* and *T. oithonoides* were distributed. The plankton volume sampler was either Schindler/Patalas (10-20 l; Schindler 1969) or Blakar/van Dorn sampler (3-5 l; Blakar 1978). The bottom-sampling was done with a quantitative core sampler, either of the Kajak type (Ø: 7 cm; Kajak 1971) or the Skogheim/Ceev type (Ø: 7 cm; Skogheim 1979).

The qualitative sampling was performed with a plankton net (Ø: 25 cm) of mesh size 45 and 90 μm. Many of the publications by other authors referred to in this paper used plankton nets with different net sizes and/or volume samplers.

3. DISTRIBUTION: ZOOGEOGRAPHY, IMMIGRATION AND FAUNISTICS

3.1. General zoogeography

The general zoogeography of *M. leuckarti* and *T. oithonoides* is shown in Fig.1 A-B. It is evident that the two species, like the majority of freshwater species of Europe, immigrated from spatial refuges in the Ponto-Caspian region after the last Ice Age (Weichselian/Dryas; see Lattin 1967). It is also clear that *M. leuckarti* arrived prior to *T. oithonoides*, since there is no reason to suspect that the dispersal abilities of the species are so different as to have caused the considerable zoogeographical differences registered in countries with efficient dispersal barriers, i.e. Norway (see Figs 3-4), where both species have been investigated in detail. The zoogeographical region of overlap between the two species is delimited by southeastern Norway, southern Sweden and northern Finland, Russia (a not-yet-certain eastern distribution of the two species), Ukraine extending south to Odessa, from the Donau delta through northern Austria, southern Germany into France and up to Denmark (Fig. 1). The key-distribution area, where most research has been done on both species, encompasses Poland, Estonia, Germany, Finland and Norway. It is especially the ecology of *T. oithonoides* that is not so well known. *M. leuckarti* has been studied in a variety of environments, but details of their its cycle is still insufficiently known, especially habitat selection of the late copepodid and adult stages.
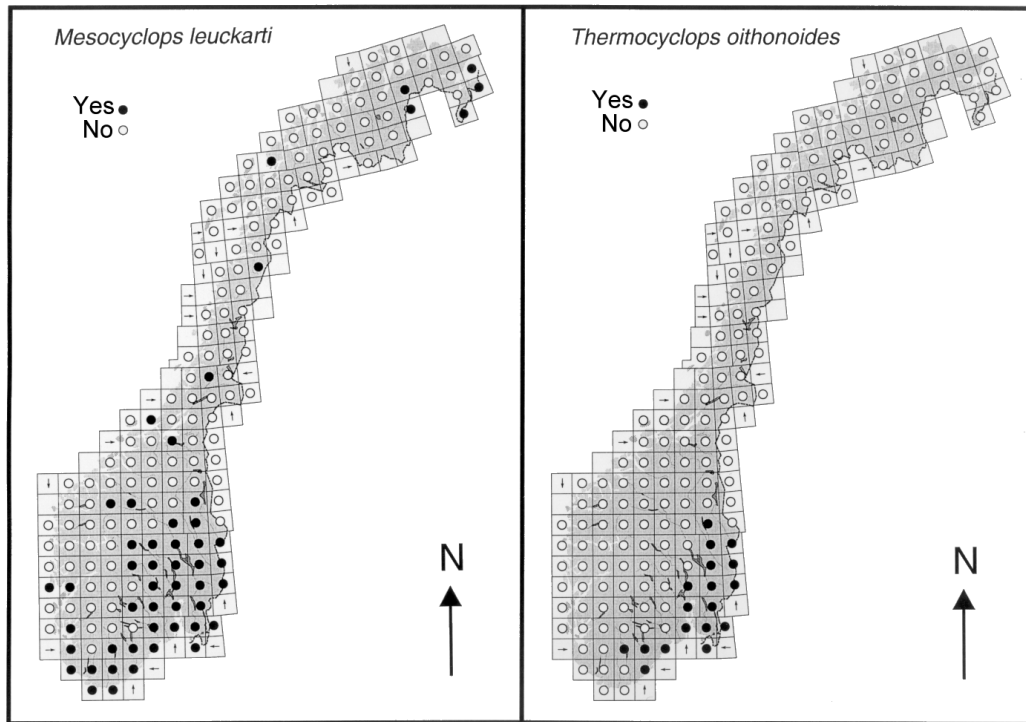
Fig. 3. Present distribution of *M. leuckarti* and *T. oithonoides* in Norway (reproduced from Walseng *et al*., unpubl. 2000).
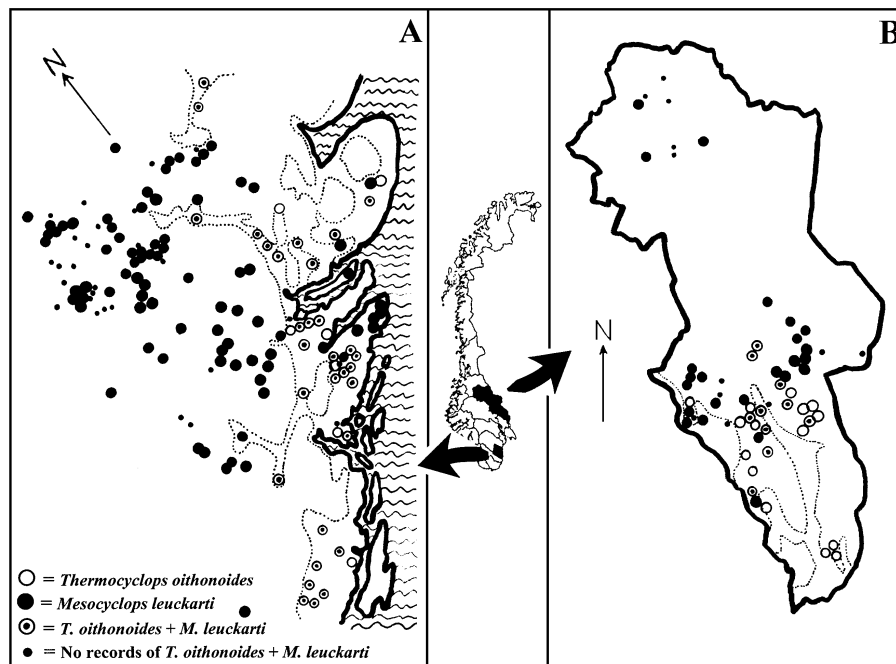

Fig. 4. Zoogeographical analysis of *M. leuckarti* and *T. oithonoides* from areas A & B. Dotted line indicates highest postglacial marine limit [in area A (about 100 m) and B (about 200 m) above present sea level]. Seventeen sites in the western part of area A derive from Halvorsen & Larsen (1998).

3.2. Distribution and habitat characteristics

a. Scandinavia/Norway

Zoogeography of *M. leuckarti* and *T. oithonoides* in Norway is shown in figure 3 (Walseng *et al.*, unpubl. 2000). *M. leuckarti* has been recorded all over Norway, nearly in all of the regions used for presenting its zoogeography (Aagaard & Dolmen 1996), whereas *T. oithonoides* was recorded only in the southeastern part (Fig. 3; Walseng *et al.*, unpubl. 2000). It should be noted, however, that *M. leuckarti* does not inhabit mountain regions in Norway (Eie 1974; Nilssen 1976), in agreement with similar conditions further south in Europe. Its distribution all over Norway may therefore be more apparent than real.

Because of its steep profile and variable geomorphology, Norway is an excellent country for studying immigration processes after the last Ice Age (Weichselian/Dryas) in Europe, which ended around 10,000 years ago. Of course, cyclopoid copepods possess very different dispersal mechanisms compared with freshwater fishes. Nevertheless, it is remarkable that *M. leuckarti* has a similar zoogeographical distribution to the Salmonidae in Norway (naturally occurring in most regions below a certain altitude), whereas *T. oithonoides* having arrived later, possesses a distribution comparable to the earliest Cyprinidae, or a zoogeographical area between that of the Eurasian Perch and the earliest Cyprinidae (Huitfeldt-Kaas 1924).

Two important areas of zoogeography of the two species have been investigated in detail for several years in Norway (Fig. 4). The southernmost area comprises an extreme western distribution of *T. oithonoides* and offers an altitudinal constraint to *M. leuckarti*. The other area presents the northernmost distribution of *T. oithonoides*, and as well an altitudinal constraint to *M. leuckarti*. These two areas is further shown in figure 4, where the geographical distribution of the two species are marked, together with altitudinal isoplots, marking the highest postglacial marine limit. *M. leuckarti* was found in most of the lowland localities, whereas *T. oithonoides* was restricted to the lowland and near-ocean sites (area A). *T. oithonoides* was found in lakes exclusively below the highest postglacial marine limit in area A, whereas *T. oithonoides* had spread to other neighbouring lakes above the former marine limit in area B . Coexistence of the two species was not uncommon, especially in the northernmost region, often co-occurring with heavy fish predation pressure.

The relationships of *M. leuckarti* and *T. oithonoides* to selected physical, chemical and biological parameters are presented in table 1. These relationships were slightly different in the two regions, and were therefore presented separately. The selected parameters included: altitude, acidity (pH), calcium content, total phosphorous concentrations, humic content, aluminium content (area A), and chlorophyll (area B). *M. leuckarti* is the

most tolerant of the two species, and able to endure hash environmental conditions. *T. oithonoides* was distributed at lower altitudes than *M. leuckarti*, especially in southern Norway, where *T. oithonoides* immigrated later. In both areas, *M. leuckarti* was tolerant to both acid, as well as eutrophic and alkaline environments, whereas *T. oithonoides* was absent at pH levels below 5.4. Both species were tolerant to humic environments (Tab. 1). *T. oithonoides* endured high fish predation better than *M. leuckarti* (Nilssen & Wærvågen, unpubl. data 1973-2000). Sandøy & Nilssen (1987) observed that liming had a very positive effect upon the abundance of *M. leuckarti*, and that reacidification immediately led to lower population numbers. Hessen & Nilssen (1983) investigated the other side of the pH spectrum (above pH: 9.0) in pelagic enclosures placed in the lowland, eutrophic Lake Gjersjøen. High pH favoured *M. leuckarti* over *T. oithonoides*, and *vice versa* for lower pH (Hessen & Nilssen 1983). Furthermore, high pH was characteristic during the eutrophic phase of the investigated lake, and *M. leuckarti* was the dominant cyclopoid during the peak eutrophic phase in the 1970s. With decreasing trophy, *T. oithonoides* is regaining abundance and is again becoming the dominant cyclopoid (Faafeng & Nilssen 1981).

Jørgensen (1972), in his comprehensive study on bog successions north of Oslo, found that *M. leuckarti* inhabited all localities from lakes to very shallow (not temporary) ponds, excluding wet bogs and bogs, and Nilssen (unpubl. data, 1980-84) found that the species inhabited the less saline rock pools (not temporary) close to Risør, in southern Norway. *T. oithonoides* was recorded in neither of these two areas. *M. leuckarti* was registered in four lowland ponds in east-central Norway (Elgmork 1964) and three humic ponds (Elgmork *et al.* 1990) near the timberline in boreal forests in south-central Norway. Furthermore, Jørgensen (1972) observed *M. leuckarti* in ten localities with pH between 4.2-4.5, but it was more common with a pH above 5.0, like in southern Norway (Nilssen 1974, 1980b; Hobæk & Raddum 1980). Jørgensen (1972) also recorded the plankton/littoral *M. leuckarti* from strongly coloured localities, but it was more common in lakes with higher calcium content, in accordance with Fryer's (1993) observations in northern England. *M. leuckarti* was also recorded and probably common in sewage-contaminated ponds in Norway (e.g. Källqvist *et al.* 1996).

Since the early 1970s Nilssen (partly unpubl., 1973-2000) has sampled or identified zooplankton in many localities, especially in southern and eastern Norway. From these studies it was evident that *M. leuckarti* was common in all sorts of habitats from small, oligosaline rock pools, ponds and littoral zones of lakes to large, lowland lakes. All trophic and predation patterns were included. *T. oithonoides* showed a more restricted distribution, being absent from the more shallow localities, more acidic environments, and being recorded only

Tab. 1. *Mesocyclops leuckarti* and *Thermocyclops oithonoides*: relationship to habitats and selected physical, chemical and biological parameters in areas A and B (in Fig. 4). Upper and lower extreme values are shown. - : no data.

	M. leuckarti	*T. oithonoides*	*M. leuckarti*	*T. oithonoides*
	Area A		Area B	
Altitude (m a.s.l.)	2-342	0.5-67	200-787	198-443
Acidity (pH)	4.6-7.0	5.8-6.8	4.9-8.5	5.4-7.1
Calcium (mg l^{-1})	0.1-10.2	1.5-5.2	1.9-39.0	1.4-32.0
Tot-P (µg l^{-1})	3.4-68.1	4.4-26.8	4.5-51.1	4.5-44.3
Humus (mg Pt l^{-1})	10-138	15-84	13-201	17-205
Aluminium (µg l^{-1})	16-250	16-139	-	-
Chlorophyll (µg l^{-1})	-	-	0.2-12.1	0.3-10.8

in lowland regions, below the postglacial marine limit. A special relationship to predation was found: *M. leuckarti* seemed strongly affected by intensive fish predation by cyprinids, if it did not obtain refuge from predation. In such circumstances, *T. oithonoides* seemed the most successful of the two. In a small, "shoe box"-shape, sheltered pond in southern Norway (l: 50 m, w: 5 m, d: 4 m) with steep rocky shores without a littoral area, the following species of cyclopoid copepods were found in dominance order: *T. oithonoides*, *C. strenuus*, *C. scutifer* and *M. leuckarti*. *T. oithonoides* was the dominant species of the two, probably because of the combination of high perch predation in the upper water masses, and the lack of a predation refuge for the vulnerable species, *M. leuckarti*. *C. strenuus* diapaused during summer and *C. scutifer* inhabited the deep, colder waters.

b. Estonia

Most lakes have been visited in Estonia for studying chemistry, phytoplankton, zooplankton and fish, and a detailed classification of lakes has been undertaken by Mäemets (1958; 1971; 1974). In nearly all types of lakes both *M. leuckarti* and *T. oithonoides* were important species (Mäemets 1958). The only exception was acid and coloured, shallow and dystrophic lakes, with Eurasian perch (*Perca fluviatilis*) and pike (*Esox lucius*), as the only fish species. This group of lakes was characterised by the scarcity of cyclopoids and the presence of the acid-tolerable, fish-predation-vulnerable, carnivorous calanoid *Heterocope saliens*, like in similar acidotrophic Norwegian lakes (Nilssen 1974, 1980b; Hobæk & Raddum 1980). Deeper and stratified humic lakes, with higher pH, had more cyclopoids. Here *M. leuckarti* dominated over *T. oithonoides*, which supports the former species' improved ability to withstand acidic environments. Lakes close to the sea, or recently isolated from the sea, contained *M. leuckarti* as the dominant species, while *T. oithonoides* was not recorded (Mäemets 1958). This contrasts with similar habitats in Norway, where *T. oithonoides* most commonly is observed in such localities (cf. Fig. 4). However, *M. leuckarti* can be found there as well, especially under more eutrophic

conditions, and when the invertebrate predator *Chaoborus flavicans* is common. Other species of cyclopoids in the extensive Estonian lake classification study were in decreasing order of abundance: *C. scutifer*, *C. kolensis*, *T. crassus* (= *T. hyalinus*), *C. abyssorum*, and *C. lacustris*. Lakes with *C. scutifer* as the characteristic species, harboured most cyclopoids. These lakes were furthermore eutrophic, and rich in lime (Mäemets 1958; 1971).

c. Poland

Poland is situated within the same biogeographical region as neighbouring Estonia. Pelagic plankton in Poland was studied regionally starting in the 1950s by Patalas & Patalas (1966) and continued by e.g. Karabin (1983), based on earlier zoogeographical studies by seniors as Litynski, Gajl, Kozminski, Rzoska and others. *M. leuckarti* and *T. oithonoides* were distributed over most of Poland, but their ecological parameters were slightly different. *T. oithonoides* dominated in mesotrophic environments, whereas *M. leuckarti* dominated in eutrophic, dystrophic and pond environments. The clearest differences were the pond and acid environments. The predominance of *M. leuckarti* in eutrophic lake sub-areas and localities (Szlauer 1958; Gieysztor 1959; Patalas & Patalas 1961; Hajduk 1966), ponds (Prószynska 1963; Kowalczyk 1969), and acid environments (Hajduk 1966) have later been noted by a number of authors. A similar distribution of *M. leuckarti* to Mäemets (1958) in oligosaline environments was recorded by Guttowa (1956). The dominating species in an estuarine area on the Baltic coast was *M. leuckarti*, whereas *T. oithonoides* was only recorded at one station. Saline inflow (transporting food elements?) furthermore stimulated egg production of *M. leuckarti*, and a sharp rise in abundance followed such saline inflow periods.

d. Russia

Rylov (1963) identified *M. leuckarti* in most of European Russia and Siberia, but this was prior to the taxonomical and zoogeographical revision by Kiefer (1981). Its eastern distributional limit remains uncertain from the present information available. The general habitat distribution of the two species was as recorded in

the aforementioned countries. Skadovski (1926) showed that the eggs of *M. leuckarti* can hatch at as low pH as 3.0, but the nauplii died rapidly at a pH below 4.5.

e. Germany

M. leuckarti is common over most of Germany, but does not penetrate into the high mountain areas of southern Germany (Kiefer 1978). Herbst (1951) found that *M. leuckarti*, together with *Eucyclops serrulatus*, were the most common copepods in small-sized environments, including perennial ponds, acid waters and brackish water, whereas *T. oithonoides* was not recorded. Maier & Buchholz (1996) reported that *M. leuckarti* was one of the most common species in gravel pits at all trophic levels, but also reported that *M. leuckarti* and *Eudiaptomus gracilis* were less common in the eutrophic group of the investigated lakes (also see Maier 1996). Both these epilimnetic species are highly susceptible to fish predation when carrying eggs; their distributional patterns in such lakes could therefore be due to fish predation, especially by juveniles (0^+). In Plöner lakes both species were recorded (Herbst 1955; Kiefer 1978). Furthermore, the habitat distribution of the two species was similar to Scandinavia, Estonia and Poland. *M. leuckarti* was often recorded in the littoral zone during summer (Herbst 1955), during the the so-called "clearwater phase".

f. UK and Ireland

Only *M. leuckarti*, not *T. oithonoides*, is recorded in the British Isles and Ireland (Eire), but *T. crassus* (= *T. hyalinus*) is found. *M. leuckarti* co-occurs with *C. abyssorum* in this region, but *M. leuckarti* tend to be distributed further south due to its warm-water and lowland preferences. In the region of the English Lake District they co-occur, however. In the British Isles, Gurney (1931-1933) described *M. leuckarti* as a species common both in ponds and in the plankton of lakes. Smyly (1957) recorded the species among macrophytes in moorland ponds near Windermere, but Fryer (1993) observed in Yorkshire that it was an "inhabitant of open water with a strong preference for large water bodies".

4. LIFE HISTORY TRAITS

4.1. Seasonal abundance and life cycles

a. Scandinavia and Norway

The generalised life cycle patterns of the two species, shown in figure 5, originate mainly from Norwegian sites. The main fraction of the species populations was present in the plankton from April/May to September/October (Elgmork 1964; Wærvågen 1985). Wintering in diapause, in copepodid stages IV-V, usually took place in the sediments. Alternatively, a small fraction of the populations (in Norway *T. oithonoides*) used the plankton as a diapausing habitat (also see Naess *et al.* 1993). This was denoted "active diapause" by Halvorsen

& Elgmork (1976), when analysing *C. scutifer* in two deep fjord-type lakes. *M. leuckarti* rested in shallow sediment areas, whereas *T. oithonoides* rested both in shallow and/or deeper areas (Elgmork 1958, 1964, 1973; Elgmork *et al.* 1990; Larsen 1982; Nyberg 1982; Sandøy 1984; Wærvågen 1985; Naess 1985; Demmo 1985; Brabrand *et al.* 1987). The intensity of diapause ("torpor") was usually not so deep in the two species, compared to *Cyclops* s. str., and the copepodids did not bury so deep into the sediments as the *Cyclops* s. str. species. In one investigated lake, *M. leuckarti* cop IV had significantly deeper torpor than cop V (Elgmork & Nilssen 1978; Elgmork 1996), but the knowledge of diapause development is much more restricted than for *Cyclops* spp. (cf. Elgmork & Nilssen 1978).

The most common life cycle of *T. oithonoides* was two or three generations a year. In the lakes where the species entered diapause in summer (Lake Vormelitjenn), it gave rise to only two generations a year, whereas in the localities where it entered diapause in autumn (Lake Bosviktjenn), it might produce three generations yearly. For a more comprehensive discussion see Naess *et al.* (1993). Elgmork (1958) suggested two yearly generations for *T. oithonoides* in a eutrophic lake (Lake Bergstjern), but it could also have a minor third generation, as observed in another eutrophic lake (Lake Gjersjøen; Brabrand *et al.* 1987). In Lake Créteil, France, diapause was terminated very late during summer, and the species was therefore able to produce only two generations annually (Lacroix & Lecher-Moutoué 1984). In some lakes (Lake Skuggetjenn) *M. leuckarti* produced both diannual and triannual life cycles, depending upon yearly variations in the habitat temperatures (Sandøy 1984). There were several patterns of diannual and triannual life cycles. Some populations of the two species exhibited a conspicuously delayed revival from sediment diapause (Lake Créteil: *T. oithonoides*), others in eutrophic lakes (*M. leuckarti*: Lake Mikolajskie, Lake Borrevann) developed slowly during the main summer (probably due to naupliar competition from cladocerans; Santer & Lampert 1995), and others stayed in the plankton during prolonged periods during autumn (*M. leuckarti*: Lake Borrevann). All these different selection pressures from abiotic and biotic parameters combine to produce the variable patterns of life cycles observed in the field.

M. leuckarti developed more rapidly than *T. oithonoides* both in laboratory and in field enclosures (Herzig 1983; Hessen 1982; Oksum-Eriksen 1982). More varieties were recorded in its life cycle patterns, from one to three generations (and probably more) a year (Elgmork 1964; Elgmork *et al.* 1990; Larsen 1982; Nyberg 1982; Papinska 1984; Sandøy 1984; Wærvågen 1985; Maier 1990; Halvorsen *et al.* 1996; Nilssen, unpubl.data 1979-1981). It is difficult, however, to identify single cohorts when they increase above three generations per year. Halvorsen *et al.* (1996) recorded two generations per
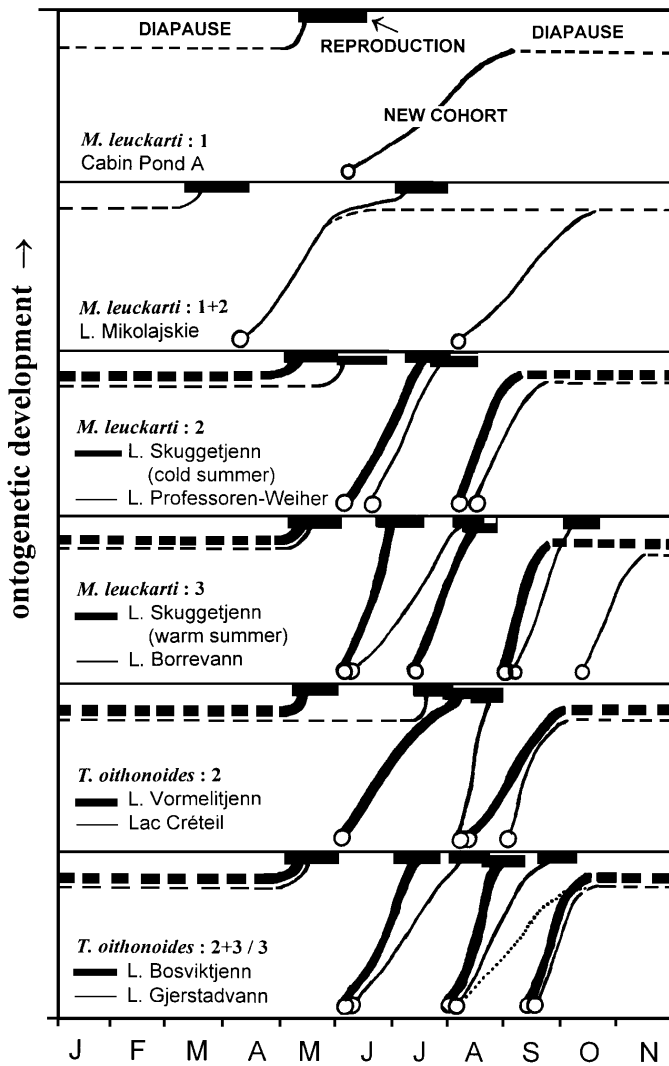
Fig. 5. Life cycles of selected populations of *M. leuckarti* and *T. oithonoides*; occurrence of different stages and rate of development (semi-diagrammatic). Legend to life cycles as in Cabin Pond A. The development patterns for the different populations are redraw from: Cabin Pond A (annual cycle: 1; Elgmork *et al.* 1990), Lake Mikolajskie (combination of annual and diannual cycles: 1 + 2, note the alternative routes of the early summer cohort; Papinska 1984), Lake Skuggetjenn (diannual or triannual, depending upon summer temperatures: 2 or 3; Sandøy 1984), Lake Professoren-Weiher (diannual cycle: 2; Maier 1990), Lake Borrevann (triannual cycle: 3; Nyberg 1982), Lake Vormelitjenn (diannual cycle: 2; Naess *et al.* 1993), Lac Créteil (diannual cycle: 2; Lacroix & Lecher-Moutoué 1984), Lake Bosviktjenn (triannual cycle: 3; Naess *et al.* 1993), Lake Gjerstadvann (combinations of diannual and triannual cycles: 2 + 3, dotted cohort: alternative diannual cycle; Wærvågen 1984). More details in the text.

year in Lake Randsfjorden, whereas in the shallower and warmer delta region, a combination of two and three generations per year predominated. Also with *M. leuckarti*, similar variations like the life cycle patterns of *T. oithonoides*, were recorded.

Adult females of *M. leuckarti* with egg sacs are more vulnerable to predation than earlier ontogenetical stages and males (see predation chapter; cf. Winfield & Townsend 1983), and will migrate from the plankton into shallow areas, often with dense macrophyte coverage. This is observed in many Norwegian lakes (Sandøy 1984; Sandøy & Nilssen 1987; Elgmork *et al.* 1990; Nilssen, unpubl. data 1979-1981). This is supposed to be a predation avoidance strategy of the species (cf. Winfield & Townsend 1983). However, this pattern is also found when no fish predators are present (Sandøy 1984; Elgmork *et al.* 1990; Nilssen, unpubl.data 1979-1981), suggesting that other selective factors may

also apply; abundant food and high temperatures. *M. leuckarti* has been found to utilize detritus as food (Papinska 1985), and maybe such shallow littoral zones offer additional periphytic and detritus food sources for the adults. Furthermore, the much higher temperatures offer more rapid development of the eggs and a possibility to produce more eggs at shorter time intervals (cf. egg development time; Taube & Nauwerck 1967; Herzig 1983). However, in a lake with very low fish predation, Larsen (1982) recorded adult females with eggs in the plankton, and the sex ratio was close to one most of the year. This indicates a considerable influence on fish predation on life history traits in many species populations of *M. leuckarti* (see Nilssen 1977; 1980a for a discussion on fish predation and life history patterns of other cyclopoid copepods). The behaviour in fish-less lakes may be due to a strong inherited characteristic, deeply rooted in the genotype of the species.

In Norwegian lakes both *M. leuckarti* and *T. oithonoides* inhabit the epilimnion, *T. oithonoides* seemed to be distributed slightly deeper in the watermasses than *M. leuckarti* (Wærvågen 1985). In lakes without *M. leuckarti*, *T. oithonoides* was found closer to the surface (Naess 1985; Demmo 1985). The plankton distribution is also reflected in the bathymetric depth distribution of the resting sediment stages, (cf. Fig. 6), where some Norwegian populations of the two species are shown together with some European populations. *M. leuckarti* selected generally the shallow littoral areas for sediment diapause. A striking exception was Lake Mikolajskie, where nevertheless the resting habitat selection differed strongly within various years (Papinska 1984), and as well included years with shallow habitat selection. *T. oithonoides* was distributed at deeper strata, in some lakes at maximum depths exclusively (Lakes Vormelitjenn and Gjerstadvann). In Lake Pääjärvi the maximum abundance of the two species occurred at similar depth (1-2 m), but only *T. oithonoides* was common at greater depths (Sarvala 1979). With sympatric occurrence of the two species, *M. leuckarti* was found in the shallow littoral, whereas *T. oithonoides* inhabited most depths, especially the deepest region (Fig. 6). Elgmork (1959; 1973) observed that resting copepodids accumulated near the chemocline in meromictic lakes, but also that some specimens penetrated the monimolimnion and was found at the deepest regions.

by filtrating with a 90 μm net, allowing *M. leuckarti* to develop alone with ample food, a full cycle was nearly completed in a little more than 2-3 weeks (Hessen 1982).

The reproductive patterns, including clutch sizes, of the two species contrast conspicuously. Egg sacs of *M. leuckarti* are larger, and contain more and smaller eggs (see Fig. 2). Czeczuga (1960) investigated this in several Polish lakes, and found interesting patterns. The present lakes were compared with some eutrophic European lakes (Fig. 7). Clutch size usually decreased from spring to summer and autumn, more pronounced in the predation-vulnerable species *M. leuckarti* than *T. oithonoides*. *M. leuckarti* exhibited a medium clutch size between 20-30, whereas *T. oithonoides* showed medium egg numbers between 7-15. In the oligotrophic Lake Gjerstadvann, both *M. leuckarti* and *T. oithonoides* produced comparable egg numbers to eutrophic lakes both in Norway and Europe. Since females with egg sacs use the littoral as an additional habitat in many European lakes, measurements on egg numbers of *M. leuckarti* are difficult available. The Estonian Lake Võrtsjärv, formed a conspicuous exception, since *M. leuckarti* exhibited low clutch sizes throughout the whole reproductive season.

The relationship to fish predators can be studied in neighbouring lakes in southern Norway where popula-
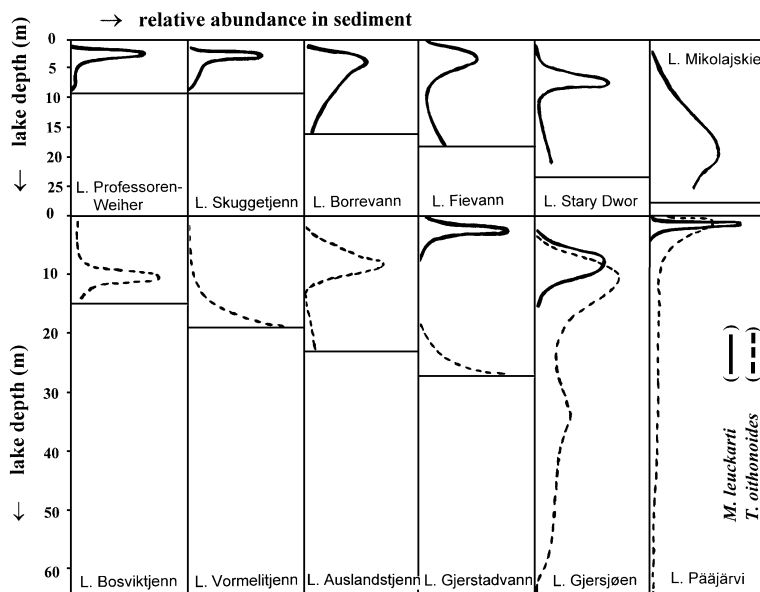
Fig. 6. Bathymetric distribution of the sediment resting stages in selected populations of *M. leuckarti* and *T. oithonoides* (relative abundance). Species legend as in Lake Pääjärvi. Maximum depth of the different lakes is shown. The curves for the different populations are redraw from: Lake Professoren-Weiher (Maier 1990), Skuggetjenn (Sandøy 1984), Lake Borrevann (Nyberg 1982), Lake Fievann (Larsen 1982; few samples, especially in littoral), Lake Stary Dwor (Szlauer 1963), Lake Mikolajskie (Papinska 1984; pattern differed conspicuously between years), Lake Bosviktjenn (Demmo 1985), Lake Vormelitjenn (Naess 1985), Lake Auslandstjenn (Wærvågen, unpubl. data 1980-85), Lake Gjerstadvann (Wærvågen 1985), Lake Gjersjøen (Brabrand *et al.* 1987), Lake Pääjärvi (Sarvala 1979). More details in the text.

Santer & Lampert (1995) presented clear evidence for a strong competition between larval stages of cyclopoid copepods and cladocerans. In enclosure experiments it was found that the two species developed slowly during the warm water period when cladoceran competitors were present (Hessen 1982; Oksum-Eriksen 1982). However, when the competitors where removed

tions are subject to contrasting predation patterns. In lakes with small populations of brown trout (Salmo trutta) as the only fish present, only *M. leuckarti* was found (Nilssen 1974; 1980a; unpubl.data, 1973-2000; Larsen 1982). When fish predation (either by Eurasian perch (*Perca fluviatilis*) or cyprinids) was intense, both species were found (Nilssen & Eie 1974; Nilssen &

Wærvågen unpubl.data 1973-2000). In eutrophic lakes with contrasting trophy and fish predation, the two species differed in their horizontal distribution in that *T. oithonoides* was able to better endure this predation (Bjørndalen & Warendorph 1982).

The above observations were also made in the other Scandinavian countries (Wesenberg-Lund 1904; Røen 1957; Nauwerck 1963; Hakkari 1969; Granberg 1970). Both Halme (1958) and Koski *et al.* (1999) recorded *T. oithonoides* in a freshwater-dominated coastal area in S Finland. Wesenberg-Lund (1904) stressed that in the predation-dense lakes in Denmark, *T. oithonoides* was the exclusive plankton representative, but under specific circumstances (eutrophy, large littoral or shallow areas) *M. leuckarti* might inhabit the plankton. Røen (1957), also observed that *M. leuckarti* and *T. oithonoides* occupied acidic environments (pH below 5.0), but only *M. leuckarti* was recorded in saline habitats. Rodhe (1941) found that *M. leuckarti* was generally distributed closer to the surface than *T. oithonoides* in three lakes in mid-Sweden. Sarvala (1979) reported that the onset of dormancy of the two species was gradually postponed from north to south, and that their reappearance in spring occurred later in the northern localities. Populations of *M. leuckarti* (where information was available) in large, big lakes in the same latitude behaved differently in that they disappeared later in autumn and revived later in spring than more shallow, smaller localities (Sarvala 1979). He (Sarvala 1979) also reported that the regularity of winter dormancy seemed to break down in southern Germany and Switzerland where benthic dormancy may or may not occur (Einsle 1964a; 1969a; Mittelholzer 1970), and in northern Italy where benthic dormancy was wholly absent (Smyly 1964). In Lago Maggiore two annual generations were produced (Ravera 1954).

b. Estonia

Cyclopoid copepods in the large, shallow and non-stratified Estonian Lake Võrtsjärv was investigated by Schönberg (1961). Both species, *M. leuckarti* and *T. oithonoides*, diapaused during winter as cop. IV-V. They were present in the plankton from April (*M. leuckarti*) or early winter (*T. oithonoides*). A fraction of the latter species was planktonic in an "active diapause" phase, like many other species populations (Naess *et al.* 1993). *M. leuckarti* disappeared from the plankton in September. *T. oithonoides* was still present at the final sampling date in November, supporting the above hypothesis concerning an alternative over-wintering habitat of *T. oithonoides*. The sex ratio of *M. leuckarti* was close to unity throughout the year, as observed in many other large lakes. Nevertheless, a considerable part of the population was always recorded close to the benthic region (Schönberg 1961), as observed elsewhere. The sex ratio of *T. oithonoides* in Lake Võrtsjärv was also close to unity throughout the year. *T. oithonoides* produced two generations a year, and *M. leuckarti* produced two full generations and one abbreviated cohort during one year; this latter behaviour has been suggested for both species in several European localities. The egg numbers of the two species decreased sharply from spring to summer. *M. leuckarti* produced about 24 eggs per egg-bearing female in spring, decreasing to 14 in summer. The numbers for *T. oithonoides* was 14 and 6, respectively (see also Fig. 7).

c. Poland

A number of studies have been performed on the
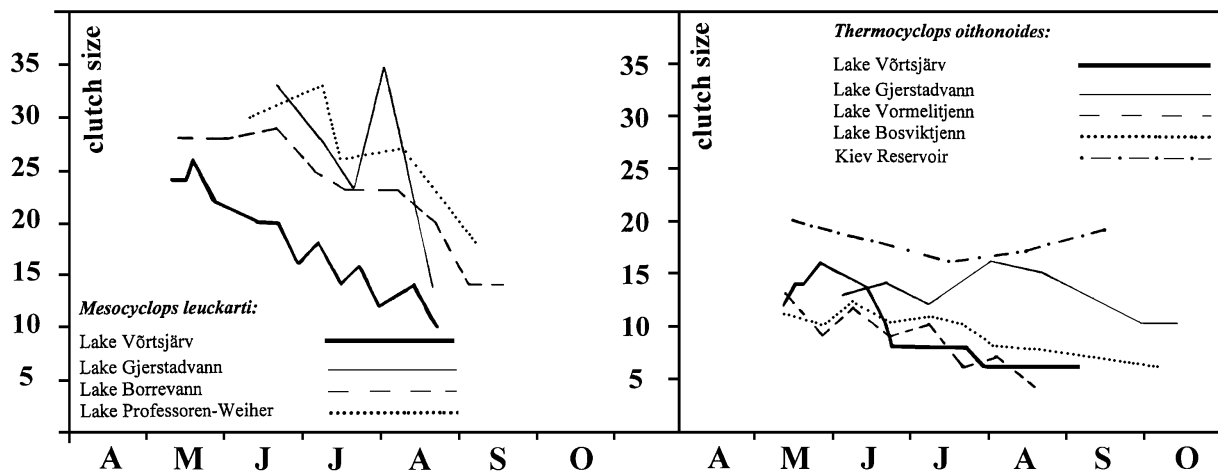
Fig. 7. Seasonal variation in clutch size (total eggs per egg-bearing females) of different populations of *M. leuckarti* and *T. oithonoides*. The curves for the different populations are redraw from: Lake Võrtsjärv (Schönberg 1961), Lake Gjerstadvann (Wærvågen 1985), Lake Borrevann (Nyberg 1982), Lake Professoren-Weiher (Maier 1990), Lake Vormelitjenn (Naess 1985), Lake Bosviktjenn (Demmo 1985), Kiev Reservoir (Zhdanova & Frinovskaya 1979). More details in the text.

two species in Poland, another "complicated cyclopoid country", with a long tradition in hydrobiology, including many studies of the two species. Patalas started an intensive study on habitat selection and life histories of Polish cyclopoids in the 1950s. This was the start of a modern plankton research tradition in that country, with a number of time-consuming quantitative zooplankton studies. Many of these included *M. leuckarti* and *T. oithonoides*, as in the 30 m-deep, eutrophic Lake Jeziorze. *T. oithonoides* appeared here earlier in the season (early March) and disappeared later (December/January) compared with *M. leuckarti* (early April, and late November, respectively). The abundance of the two species was similar, with *T. oithonoides* slightly more common. Other important cyclopoids were *C. abyssorum* and *C. kolensis* (Patalas 1956). A number of quantitative studies earlier and later supported this seasonal occurrence of the two species (Patalas 1954a; Patalas 1963; Patalas & Patalas 1961; 1968; Kowalczyk 1958; Szlauer & Widuto 1966), but in a few localities *M. leuckarti* occurred at the same time (Bittel et al. 1965) or even prior to *T. oithonoides*, like in Jeziorak (Zawislak & Bittel 1971) and some lakes in Libiszow/Lublin (Kowalczyk 1958), the ecological reasons for which will be discussed in the diapause section. In a few lakes both species were found in the plankton in small numbers during winter (Patalas & Patalas 1968).

In Polish lakes, *T. oithonoides* is usually distributed in deeper strata than *M. leuckarti* (Patalas 1954a), therefore Patalas (1963) called *T. oithonoides* a species characteristic for the lower epilimnion or metalimnion. Other studies have supported these observations (Bittel 1964; Szlauer & Widuto 1966). Patalas (1954a) registered, a slight diurnal vertical migration for the two species at different times of the year, in that they moved upward during the dark part of the 24 h period.

Papinska (1984; 1985) has published one of the most detailed studies on *M. leuckarti*. She (Papinska 1984) found that *M. leuckarti* formed dense sub-populations in the near-bottom layer (see also Papinska & Prejs 1979; Prejs & Papinska 1983), probably feeding on the detritus in the bottom sediments (Papinska 1985). Above the bottom sediments, *M. leuckarti* occurred most of the year. The life cycles of the 37 lakes in northern Poland she studied (Papinska 1984), had cohorts with two generations a year following three different life history patterns: one with a diapause (in cop. IV) lasting for about 9 months (June-March), a second without diapause, and a third with diapause (in cop. V) lasting for about 5 months (October-March).

d. Russia

Russia forms another centre of overlap between the two species. Their seasonal dynamics have been investigated by several authors. The findings are comparable to Poland and Estonia, but several populations of *M.*

leuckarti show an "active diapause" in the profundal habitats of some lakes in Ural (Ulomski 1953), and in the Rybinsk Reservoir (Monakov 1959). A considerable amount of work has been done in the former USSR on the feeding and diet of crustaceans (for reviews see Monakov 1972, 1976; Sushchenia 1975), but it is beyond the scope of this paper to summarise all this information. Monakov (1972, 1976) stated that the diet of *M. leuckarti* and *T. oithonoides* are similar, being composed by smaller crustaceans, protozoans and rotifers for late ontogenetical stages and adults. The seasonal occurrence and vertical distribution of the two species is simliar to earlier observations (River *et al.* 1982; Markevich *et al.* 1982; Stolbonuva 1985). The dominant life cycle of the two species was two generations annually (Rylov 1963; Alekseev 1987). Alekseev (1990) made a comprehensive study on diapause in crustaceans, including cyclopoids.

e. Germany, Switzerland and Austria

The ecology of the two species in Germany is similar to the findings from Scandinavia and Poland, but in southern Germany *M. leuckarti* is present both in the sediment and in the free water. Herbst (1955) found that for both these epilimnetic species, *M. leuckarti* was recorded above *T. oithonoides* in the Grosse Plöner See (see also Maier 1993). There was also a tendency for a more pelagic "active diapause" in *T. oithonoides* in this lake (Herbst 1955). Maier (1990) observed two annual generations of *M. leuckarti* in a small shallow, eutrophic lake. The distribution and annual cycle of *M. leuckarti* in Bodensee is an interesting case, with two different manifestations of diapause (Einsle 1964a). In the shallow Gnadensee (Untersee) it entered sediment diapause as cop V, whereas in the main, and very deep part of the lake (Obersee) it endured a planktonic diapause, so-called "active diapause" (Einsle 1964a; see also Kiefer & Muckle 1959; *M. bodanicola* = *M. leuckarti*). In the neighbouring lake to Gnadensee, Mindelsee, *M. leuckarti* is absent from the plankton only during mid-December to mid-January (Einsle 1964b; Einsle 1969a). Einsle (1964a) was not able to identify the number of cohorts during summer, but stressed the simularity of Smyly's (1961) observations of two generations a year. Even if *M. leuckarti* is distributed in the epilimnion, it showed considerable upwards vertical migration during the 24 h cycle (Einsle 1969b, 1987). The abundance of *M. leuckarti* during the period 1962-1986 was investigated by Einsle (1983, 1988), and showed a temporary decrease during the most intensive eutrophication period in the 1970s. *M. leuckarti* has now again increased its abundance, which could be due to decreased predation by *Cyclops vicinus* (Einsle 1983, 1988), and probably also to changes in fish predation with decreasing trophy.

The eutrophic Swiss Greifensee, with a maximum depth of only 32 m, is situated close to Zürich, whereas Viervaldstättersee, with a maximum depth of 214 m, is

close to Luzern. The life cycle of *M. leuckarti* in the two lakes differed in that it endured winter in sediment diapause in the shallow lake, but stays in the plankton in "active diapause" in the deepest lake (Mittelholzer 1970), comparable to the Bodensee population. He (Mittelholzer 1970), also reported a tendency of *M. leuckarti* to be distributed in the littoral areas. In Lake Biel (= Lac Neuchatel) the yearly abundance of *M. leuckarti* was similar to that in Bodensee (see Einsle 1964a), where the species overwintered in two fractions, one in the sediment and the other in the deep water above sediments (Stebler 1979).

In the large, but relatively shallow Ossiachersee in southern Austria, Wappis (1980) recorded sediment diapause in *M. leuckarti*, and it disappeared from the plankton during mid-winter. In the much deeper Attersee, Moog (1979) found only plankton diapause, and the species completed two generations a year.

Frenzel (1977) found in a eutrophic lake three yearly generations of *T. oithonoides* with a short, probably sediment diapause during mid-winter. A part of the population also inhabited the plankton during winter (Frenzel 1977). Advanced copepodid and adult stages partly inhabited the hypolimnion during the warm period, with a vertical migration towards upper strata during night for all stages (Frenzel 1977). A similar distributional pattern was found in Lake Stechlin (Kasprzak & Schwabe 1987), where, uncommonly, *M. leuckarti* was distributed below *T. oithonoides*. Such distribution could have been due be due to fish predation, but this was not reported.

f. The Netherlands and France

Vijverberg (1977) investigated the cyclopoids of the shallow Lake Tjeukemeer. He (Vijverberg 1977) did not report numbers of cohorts for *M. leuckarti*, but it was present in the free waters from March to October/November, and endured sediment diapause the rest of the year. Predation on females was probably keen during the period of maximum occurrence of fish fry in June-August (Vijverberg 1977). Vijverberg & Richter (1982) reported the conspicuous tendency of *M. leuckarti* to be distributed close to the bottom, an area which could not be sampled by their method. This could be corroborated by the composition of the major fish (bream, *Abramis brama*) diet, which contained a large number of adult copepods, including *M. leuckarti*.

T. oithonoides was also found in northern France. In Lake Créteil two generations a year were produced, with diapause mainly in the sediments, and a minor fraction in "active diapause" in the plankton (Lacroix & Lecher-Moutoue 1984). This population terminated diapause very late in the summer (Lacroix & Lecher-Moutoue 1984). Amoros (1973) found sediment diapause in *M. leuckarti* in three fishponds from October to April, and these populations produced probably 2-3 generations annually, if based upon his figures (Amoros

1973) and the findings of Lacroix & Lecher-Moutoue (1984).

g. UK

Several studies on *M. leuckarti* have been undertaken in the British Isles. Here, Fryer & Smyly (1954) published resting stages of cyclopoids without a cyst (a gelatinous sheat; see Birge & Juday 1908; Cole 1953; 1955) in the benthos of Esthwaite Water for the first time. *M. leuckarti* usually left the limnetic zone in winter and spent October to February/March dormant in the bottom sediments as parts of its life cycle (Smyly 1961; 1968). The species produced two generations during one year, with two egg-laying periods: April/May and June to August. In the colder, oligotrophic Loch Lomond, *M. leuckarti* produced one generation during one year, and diapause differed also from the most common types described (Chapman 1972). The species was observed in the plankton year-round. A small fraction rested in the sediment during winter, whereas the majority exhibited an arrested development similar to "active diapause" in the deep waters as copepodid stages IV/V (Chapman 1972). The initiation of dormancy coincided with the autumn circulation period and the associated temperature decrease, whereas the termination of the dormant period was not clearly related to any environmental change (Smyly 1961).

4.2. Trophic status, seasonal occurrence and ontogenetical 'bottle-necks'

Cyclopoid copepods exhibit eleven larval and juvenile stages and one adult stage. Many of the larval stages of summer species, like *M. leuckarti* and *T. oithonoides*, face dense competition from rotifers and especially cladocerans (summary by Nilssen 1978). In late spring and early summer, when cladocerans dominated the plankton, Santer & Lampert (1995) found that lakewater did not support nauplear growth. This can explain the considerable decrease in percentage of the naupliar fraction in lakes with increasing trophy, and thus higher competition from cladocerans (Patalas & Patalas 1961). This also seemed to be the reason for the marginal habitat selection of nauplii underneath the distribution of cladocerans during sympatric co-occurrence in the plankton (Patalas & Patalas 1961; Nilssen & Elgmork 1977; Nilssen 1977; Nilssen 1978). Santer & Lampert (1995) further found that development of *C. abyssorum* was retarded and that nauplii of two other *Cyclops* species died before they reached the first copepodid stage. They (Santer & Lampert 1995) were also able to culture the animals in the laboratory without an intervening diapause, as observed in the field. Hansen & Santer (1995) found that naupliar development time of *M. leuckarti* was inversely related to attractive food concentration. The competition between larval (nauplii) stages of cyclopoid copepods and cladocerans may explain the apparent paradoxical, early findings by Parker

(1960; 1961), that even predaceous and omnivorous co-pepods can be eliminated by herbivorous cladocerans through competition in early development stages of the copepods. Furthermore, it can also explain why *M. leuckarti* had difficulty establishing large populations in sewage-contaminated ponds when *Daphnia magna* dominated (Källqvist *et al.* 1996).

Vijverberg (1980) and Herzig (1983) have shown that both *M. leuckarti* and *T. oithonoides* are warm-water species; they develop comparably slower at low and more rapidly at high temperatures. *M. leuckarti* is an even more characteristic warm-water species than *T. oithonoides*. Accordingly, Smyly (1974) found that *M. leuckarti* developed very slowly at 4 °C with high egg mortality. Kiefer (1978) reported for *M. leuckarti* that eggs did not develop below 6 °C and that nauplii stagnated at a temperature below 8 °C. Jamieson (1980) was unable to hatch eggs at 6 °C and nauplii lowered to this temperature promptly died (probably another *Mesocyclops* species). Herzig (1983) indicated a genetic component in the embryonic development of *M. leuckarti*, but all populations developed rapidly at temperatures above 18 °C.

Cyclopoid copepods with their eleven larval and juvenile stages exhibit developmental or ontogenetical bottlenecks because of competition with specialised filter feeders at specific times of the year. A serious bottleneck possibly takes place after consumption of their yolk-supply, at approximately naupliar 2 stage, when the earlier naupliar stages have to start collecting their own food. Another susceptible stage is the conspicuous metamorphosis prior to copepodid I (see Twombly 1993; 1995), when a new way of collecting food must be initiated. Cladocerans during summer tend to displace the earlier ontogenetical stages of cyclopoid copepods to marginal habitats, often below the thermocline, or the specific cohort dies out altogether due to starvation. The frequent high death rate and/or variable death rates often found in pelagic copepods may be due to this serious competition. One strategy for the cyclopoid would be to suppress early spring growth of cladocerans by consuming juvenile cladocerans (Lampert & Schober 1978; Nilssen 1978; Santer 1993).

4.3. Life cycle and habitat selection of adult M. leuckarti *in littoral and profundal environments*

Already in 1863, Sars (1863) observed the main ecological differences between the two species, notably the ability of *M. leuckarti* to inhabit small ponds and ditches, in addition to lakes, and mentioned *T. oithonoides* as a true planktonic form. A number of other authors have later supported this view, and extended the habitat range of *M. leuckarti* to the littoral zone as well (Sramek-Husek 1948; Sladecek 1950; Straskraba 1963; Vranovsky 1964; Flössner 1967; Szlauer 1969; Mäemets & Haberman 1971; Zawislak & Bittel 1971; Eie 1974; Forro & Metz 1987; Vuille 1991; Spikkeland

1998). Litynski (1938) called *M. leuckarti* therefore an hemilimnetic form. Other authors have reported that *M. leuckarti* can occupy the near sediment region in large parts of lakes as well, not only the macrophyte-dominated littoral. For this reason, Sirkova & Mordukaj-Boltovski (1971) considered *M. leuckarti* as a member of the microbenthos, and it was one of the most important microbenthos species in all of several investigated lakes. Comita (1972) observed no planktonic adult females in the population of *M. edax* that appeared after the first of August. He (Comita 1972) ascribed this to their benthic habitat selection after that period, a spatial distribution also observed in other populations of the species (Moore 1939; Cole 1955; Carter 1974; Threlkeld & Dirnberger 1986). Other studies have stressed the benthic attraction of *M. leuckarti* (Vijverberg & Richter 1982; Papinska 1984), which may have serious consequences for many life history studies. By overlooking a part of the female population, both the egg stock and birth rates are underestimated, and the mortality rates of the adults overestimated.

In many investigations, adult females, often with eggs, were distributed close to the bottom (Vijverberg & Richter 1982), or in the littoral zone (Einsle 1972; Sandøy & Nilssen 1987; Jann & Bürgi 1988; Elgmork *et al.* 1990), especially in smaller bodies of water or localities with extensively developed littoral areas. In larger lakes without littoral or profundal refuges, or lakes with very low fish predation, adult females are present in the plankton and the sex ratio is on average close to unity (Ravera 1955; Larsen 1982). Einsle (1964b) seemed to have been the first to describe in detail this widespread phenomenon of planktonic disappearance of adult *M. leuckarti* females. He (Einsle 1964b) mentioned that after *M. leuckarti* terminated diapause and was present with copepodid V in the free waters, one should have expected a large number of adult females in the waters, but: "Ihre Zahl geht mit dem Anstieg der Erwachsenenkurve bis auf Null zurück(!)" ("The numbers went down to zero when adults should appear"). Shortly thereafter, Einsle (1970) reported the same observation in another lake, and eventually in his 1972 paper (Einsle 1972), he recorded the adult females in the littoral zone, but did not seem to be aware of the ecological importance of these findings. Later, a number of other authors have expressed difficulties to collect sufficient egg-bearing females in population studies of *M. leuckarti* (Sandøy 1984; Elgmork *et al.* 1990, Nilssen & Wærvågen, unpubl. observations 1979-1985).

This conspicuous habitat shift of adult females seems to be a common phenomenon. The reason for this may be several. Adult females with eggs are very susceptible prey for fish (see discussion under predation). To avoid or decrease this predation, adult females select the littoral area or regions close to the bottom as their preferred habitat. Additionally, and just as important, the littoral and profundal areas offer a variety of prey

species for invertebrate predators, like the predaceous adult females of *M. leuckarti* (body length 1.0-1.3 mm). These findings underscore the importance of sampling several environments, especially the sediment and littoral regions, in life history studies of many cyclopoid copepods. The above described behaviour could also be a strategy to reduce interspecific competition with other species through spatial niche segregation. It should be noted, however, that this habitat selection is not found in all types of lakes. In deeper lakes, with steep littoral zones or reduced macrophyte regions without shelter for predation, adult females with egg sacs are also present in the free waters, and the sex ratio here can be close to unity. Also, in some shallow lakes, like Võrtsjärv, Estonia, which can be considered as an extended littoral zone, females with eggs are also present in large numbers in the plankton, and sex ratio is close to unity (Schönberg 1961). Other species of *Mesocyclops* (e.g. *M. edax*) can also use the anoxic hypolimnion as a refuge for visual fish predation (Williamson & Magnien 1982). Other predation-vulnerable copepods, like *Heterocope saliens* can also aggregate in the littoral zone to avoid predation from pelagic fish species (Andersen & Nilssen 1984).

Smyly (1962), in his careful study on cop V of *M. leuckarti*, detected differences concerning many dormancy factors in two populations: dormancy differed throughout the season (see also Elgmork & Nilssen 1977), and it could be prevented altogether if the animals were offered ample food in the laboratory well before diapause.

4.4. Reproductive parameters: number and size of offspring

Number and size of offspring are important parameters in life history studies. Egg size and nauplius size are positively related (Cooney & Gehrs 1980). The general theory is, the larger the egg size (more energy allocated by adult females to single eggs), the greater changes there will be to overcome developmental bottlenecks, like these resulting from competition by filter feeding cladocerans. Burns (1988) found that egg size per se was not a good predictor of the relative abilities of the nauplii of different copepods to resist starvation, but that small clutches are composed of higher quality eggs than large clutches are. Differences in egg quality, as reflected in naupliar survival, may arise from differences among species in the composition of the stored reserves, which may also vary seasonally (Burns 1988).

Studies on such important life history parameters as above are remarkably rare with plankton animals (see Hutchinson 1951; 1967), but the early work of Czeczuga (1960) is a notable and classical exception. Czeczuga (1960) analysed numbers and size of eggs of a number of planktonic species of differing food patterns in 4 lakes of different nutrient levels. A number of interesting questions arise from his analysis, in addition to

those already commented upon by Hutchinson (1967). It seemed that *M. leuckarti* and *T. oithonoides* were using all available food during the spring outburst of algae, that is often dominated by attractive flagellates as food items (Santer & Lampert 1995), because egg numbers in spring animals did not increase even when conditions were getting more eutrophic. The size of the spring animals was also comparable throughout the trophic gradient. The summer situation was completely different. The animals were smaller, probably due to ontogenetical competition from cladocerans, and number of eggs were fewer, but they were generally larger; that was probably a strategy to allocate more energy to each single offspring, to decrease a possible effect of food bottleneck during summer. However, a predation effect was most probably also included, since egg carrying *M. leuckarti* are very susceptible to predation (see Fig. 2; and predation part). The smaller *T. oithonoides*, on the other hand, often seems outside the range of most fish predators (except for underyearlings), because nearly all cladocerans are more conspicuous prey than this species. The reproductive effort, as egg biomass in relation to body weight, increased for *T. oithonoides*, both in spring and summer cohorts, whereas no clear picture was evident for the predation vulnerable *M. leuckarti*, neither in the spring nor summer cohorts (Czeczuga 1960). Egg volumes in *T. oithonoides* were much higher in the spring cohorts compared with the summer cohorts. They were stable in the spring cohorts with increasing trophy, but increased in the summer cohorts with increasing trophy. For *M. leuckarti* the picture was less clear. Egg volumes of the spring cohorts decreased with eutrophication as in the summer cohorts. These findings may also indicate a different food saturation curve or different habitat distribution for nauplii of the two species. Clutch sizes of *M. leuckarti* was usually 20-35 eggs per ovigorous female and 6-20 for *T. oithonoides* (Czeczuga 1960; these numbers were similar to data in figure 7).

The evolutionary consequences of the above findings seem to be that during spring, non-predation vulnerable animals appear to be saturated with food (based on stable specific body size at that time), and more food does not lead either to larger animals, nor larger and more eggs. It should be added, however, that the spring animals partly subsist on food collected during late summer and autumn the previous year. In addition, diapause involves complex chemical and metabolic transformations within the animals' body, likely to influence the subsequent reproduction after a dormancy period. The prehistory of the spring animals is therefore important to study. The predation-vulnerable species, on the other hand, does not seem to grow larger under eutrophic conditions. Furthermore, it also allocates less energy for each single egg, maybe because food is always in access for their offspring under the more eutrophic environments.

4.5. M. leuckarti *and* T. oithonoides *as predators and prey*

Already in 1954, Patalas (1954b) stated that the biomass and yearly production of Crustacea should be considered as the remainder after satisfying the food requirements of the fish, both the underyearlings and adult fish (see also Bittel 1964). The cyclopoid copepods, especially the larger-sized species and/or those in late ontogenetical stages, are also vulnerable for fish predation, and many animals must adapt their life histories to this seasonal population stress (see extended discussion in Nilssen 1977; 1980a). Females of medium-sized cyclopoids, like *M. leuckarti*, when carrying large eggs sacs, are especially vulnerable to fish predation (see also Gliwicz 1967; Gliwicz & Rowan 1984). The egg sacs of *M. leuckarti* protrude from the genital segment in a characteristic manner (see drawing in Sars 1918; reproduced in figure 2, this paper). Such broad egg sacs offer much frictional resistance in the water, especially during periods with larger clutches (see Maier 1994). *T. oithonoides* has much smaller clutches than the former (Fig. 7). Even if *T. oithonoides* is a smaller-sized animal, it may be more mobile and more successful in escaping a predator. Therefore, it is not unexpected that *M. leuckarti* has developed additional strategies to reduce the mortality of eggbearing females, such as staying in the littoral, profundal or oxygen boundary regions where fish are either absent or experience hunting difficulties. Papinska (1985) demonstrated that the species utilise detrital food. It should be added that *M. leuckarti* adult females also seemed more predacious towards animal food than many other cyclopopid species (Hansen & Santer 1995; Hopp *et al.* 1997). The littoral areas offer a variety of animal food items and thus may be an additional habitat to a plankton-littoral species like *M. leuckarti*.

Hrbacek & Novotna-Dvorakova (1965) remarked that *M. leuckarti* was more frequently observed when fish stock decreased in four manipulated backwaters, especially when compared with *Thermocyclops* species, *T. oithonoides* and *T. crassus*. Studies on the relationships between the abundance, life cycles and life histories of cyclopoid copepods and fish are remarkably rare. This may partly be due to the fact that many papers maintain that "fish" (at summer sampling periods and above 20 cm body length) mainly consume cladocerans and benthos, and cyclopoid copepods are considered unimportant food items. Nevertheless, we hypothesise that the numerical suppression of *M. leuckarti*, the sex ratio, the habitat distribution of adult females, and the life cycles in many eutrophic lakes, is mainly an effect of fish predation, and 0^+ fish should be especially investigated with respect to this (see Guma'a 1977; Hansen & Jeppesen 1992). Adult planktivorous fish usually select cladoceran prey (see Nilssen 1977; 1978; Sanni & Wærvågen 1990), but 0^+ fish select a variety of prey, from algae and rotifers to cladocerans and copepods.

Especially the young fish may exert a considerable influence upon copepod abundance. Usually the largest copepods are the first to be selected, especially females with eggs (Langeland 1982). Podboltova & Potapova (1972) found that both *M. leuckarti* and *T. oithonoides* were consumed by fish, but *M. leuckarti* was more strongly selected than the smaller species by the vendace (*Coregonus albula*). Accordingly, Spanovskaja & Grygorash (1977) found that adult *M. leuckarti* was selected as planktivorous fish food, together with *Daphnia longispina* and *D. cucullata*. Nauplii and copepodid stages were not consumed (Spanovskaja & Grygorash 1977).

There will be a cost associated with producing large clutches of eggs in the presence of fish predation (Winfried & Townsend 1983; Vourinen *et al.* 1983; Hairston et al. 1983), especially in medium-sized copepods, like *M. leuckarti*. The large egg sacs of *M. leuckarti* in eutrophic lakes decrease the maneuverability of females (Winfried & Townsend 1983), and their success in such lakes is therefore considerably reduced when fish predators are abundant. Larger-sized egg-carrying species cannot occupy the epipelagic zone in freshwater, but survive instead by dwelling in the littoral and profundal habitats. Advanced copepodids of *M. leuckarti* have about a similar size to adult *T. oithonoides*. Therefore non-conspicuous, negligibly coloured and pigmented adult *T. oithonoides* of 0.7-0.8 mm total length may be outside the prey range for most fish species. They may be consumed by 0^+ fish (perch and roach), if they are forced to coexist in the same habitat, as observed in small enclosures (Ø 1.5 m, 4 m deep) sealed at the bottom (Hessen 1982).

Smyly (1980) reported a specific relationship between the invertebrate predator *Chaoborus flavicans* and the two cyclopoids, *C. abyssorum* and *M. leuckarti*. In tests with the two interacting cyclopoids, *C. abyssorum* outcompeted *M. leuckarti* when *Chaoborus* was absent but lost to *M. leuckarti* when *Chaoborus* was present. Smyly (1980) ascribed this to the swimming patterns of the two species; the "continuous" swimmer *C. abyssorum* was more conspicuous prey for *Chaoborus* than *M. leuckarti*, which in accordance with its more littoral-pelagic habitat distribution, interspersed short bouts of swimming with long periods of clinging to interfaces.

The most important food for *Mesocyclops* and *Thermocyclops* are rotifers and cladocerans, especially for the younger stages of the latter (Monakov & Sorokin 1959; Brandl & Fernando 1975; 1986; Karabin 1978; Williamson 1980; Papinska 1985). Monakov & Sorokin (1959) and Brandl & Fernando (1979) reported that juveniles of the plankton-littoral species *Diaphanosoma* (see Herzig 1984) and genus *Ceriodaphnia* were important food for advanced stages of *Mesocyclops*, and the same was found in Lake Kinneret (Gophen 1977) and Lake Donghu (Yufeng 1998). Fryer (1957a; 1957b)

has investigated the food collection mechanisms and food selection behaviour exhibited by several species of cyclopoid copepods. Fryer (1957a) claimed that *M. leuckarti* chiefly consumed crustaceans and rotifers. In this study, Fryer (1957a) lumped two species of *Mesocyclops* together; *M. leuckarti* from Loch Lomond and probably *M. aequatorialis* from Lake Nyasa. Smyly (1961) made some casual observations and found that *M. leuckarti* consumed young *Eudiaptomus gracilis*, *D. brachyurum* and *D. hyalina* in Esthwaite Water.

Usually, smaller-sized cyclopoids are less carnivorous than larger ones within the same biotop (Hopp et al. 1997; Brandl 1998). *M. leuckarti* seems to be more carnivorous than expected solely based on body size (Hansen & Santer 1995; Hopp *et al*. 1997), and even its smaller copepodids seem more carnivorous than similar-sized or even larger cyclopoids (Hansen & Santer 1995). *M. leuckarti* needed animal food to produce a high number of viable offspring (Hansen & Santer 1995; Hopp *et al*. 1997). This may partly be due to the temporal presence of the species, since it is present and reproduces during summer when algae is scarce or inedible and when protozoans, nauplii and rotifers are abundant. On the other hand, *Thermocyclops* spp. can do well on algae alone (Adrian & Frost 1993; Hopp et al. 1997), even if *T. oithonoides* has been reported to consume a lot of protozoans (Monakov 1972). Also when offered a dinoflagellate as food, *T. oithonoides* showed more "sloppy feeding" (killed the prey, but did not ingest it all) than *M. leuckarti* did (Santer 1996). Usually, when the two species coexist in the plankton the size relationship between *M. leuckarti* and *T. oithonoides* is 1.3 or more, a size difference that has been shown to facilitate coexistence in nearby species (see Hutchinson 1967).

4.6. Diapause and wintering

Diapause is a strategy for avoiding harmful conditions and synchronizing growth and reproduction with favourable biotic and abtiotic conditions in time and space. It is also a period for seasonal reduction of activity and for considerable restructuring of internal body biochemistry, morphology and anatomy. Transition of stored energy, most often triacylglycerol, in freshwater copepods (see Wierzbicka & Kenzierski 1970; Sargent 1978; Santer & Bolt 1998), may provide those copepods which spend late juvenile stages in diapause with readily available energy reserves for the deposition of several clutches of eggs after reproduction immediately following diapause termination.

Resting can take place in both cop. IV and V, the relative proportions between the two differs in the various investigations. Smyly (1968) found that less than 15% of the dormant population was in stage IV in British lakes, and both Nauwerck (1963) in Lake Erken and Szlauer (1963) in Stary Dwor Lake found stage V to be dominant. Elgmork (1964), on the other hand, found

more than 50% in cop. IV in small ponds in east-central Norway, and in Loch Lomond Chapman (1972) found around 40% cop. IV. The composition of animals in dormancy probably depends upon developmental patterns and ambient temperature in the habitat. It could also be a strategy to decrease competition by timing the life cycle for nauplii to avoid being predated by adults of other cyclopoid species, or to be present at maximum food availability during algal spring peak.

Wierzbicka (1974) observed that the freezing point depression (probably related to body triacylglycerol levels) of several species of diapausing cyclopoids was must higher than for active planktonic animals. Wierzbicka & Kedzierski (1964; 1970) also found that diapausing animals could withstand considerable anoxia and that they accumulated both oil and metabolic products (Wierzbicka 1972). Wierzbicka (1962) investigated the attraction of cyclopoid copepods of the genus *Cyclops* to the mud surface. All species used the sediment for feeding and burrowing and when it was removed they moulted and became adult. Their swimming feet were used to burrow, and could as well be described as "swimming and burrowing" feet (Wierzbicka 1962); the larger the species, the deeper it could penetrate into the mud.

In the majority of the investigated localities, both *M. leuckarti* and *T. oithonoides* disappeared from the plankton during winter. This seemed to be a more consistant life history trait in northern and high altitude lakes. Both species are mainly lowland and epilimnetic species. Even if wintering in sediment habitats is the most frequently reported form of diapause, alternative development paths are possible, but their evolutionary strategies remain unclear. The following summarises the observed patterns of wintering for the two species:

A. The whole population diapauses in the sediment as cop. IV and/or cop. V. The relationship between the two stages depends upon the speed of development in the plankton and age of the specimens prior to dormancy, affected by a combination of temperature and food (most northern and eastern populations, shallow lakes on the continental Europe).

B. As A above, but with a minor fraction of the population overwintering in the plankton, in "active diapause" (several northern and eastern populations; *T. oithonoides* in Lake Créteil). A greater tendency for "active diapause" (or plankton diapause) is observed in *T. oithonoides* compared with *M. leuckarti* in their area of overlap.

C. As A or B above, *M. leuckarti* is the first species of the two to diapause and the last to migrate into the plankton in spring (the majority of northern lakes); as A or B above, *T. oithonoides* is the first species to diapause and last to enter plankton in spring (some Polish populations); as A or B above, the two species diapause and enter plankton simultaneously (several Polish and Norwegian populations).

D. A large part of the species populations of either *M. leuckarti* or *T. oithonoides* overwinter in the plankton in "active diapause" as well as in the sediments (Bodensee, Lake Biel (= Lac Neuchâtel), Loch Lomond).

E. The entire population of either *M. leuckarti* or *T. oithonoides* overwinters solely in the plankton in "active diapause", in mainly copepodid IV and V stages, without any conspicuous ontogenetic development (Obersee (upper Bodensee), Attersee, Viervaldstättersee, some Russian sites).

F. The whole population overwinters in the plankton, but develops slowly during winter (Lago Maggiore).

The different observations concerning bathyographic habitat selection of diapause is difficult to explain in evolutionary terms at the present state of knowledge (Nilssen & Østdahl in prep.), but the time of spring revival in the plankton may partly be ascribed to temperature conditions at the selected diapause site. Fig. 6 shows the observations of different diapause habitats utilised by selected populations of *M. leuckarti* and *T. oithonoides*. In many cases, but not all, both species selected the more shallow part of the lake. However, in shallow lakes, the species often selected the deepest part. In deeper lakes, *M. leuckarti* selected more shallow areas, at a depth of only 0.5-2 meters. Littoral sites, as shallow ponds and lakes, follow more closely ambient air temperatures throughout the year. Gieysztor (1960) made a detailed study of this phenomenon, also involving diurnal measurements during different times of the year. Littoral areas, especially strata where *M. leuckarti* frequently diapause (Fig. 6), are subjected to much higher temperatures during spring conditions (up to 10 °C higher than in the pelagic epilimnion is common). High temperatures lead to earlier revival from diapause (Maier 1989, 1990).

We therefore hypothesise that in lakes where *M. leuckarti* is diapausing at shallow depths in the littoral zone (at 0.5-1.5 m depth), and *T. oithonoides* in the deepest region, *M. leuckarti* should have a selective time advantage over *T. oithonoides*, by exhibiting earlier diapause revival and faster ontogenetic development during spring. The greater the difference between the dormancy habitat temperature of the two species is, the greater the difference in diapause termination during spring will be. The time of spring arousal may also influence the time of the initiation of diapause in autumn, the relationship between cop. IV and cop. V in diapause, and the number of cohorts that can be produced during the pelagic phase.

Habitat selection of diapause may also be influenced by prey availability in any given specific part of the lake. Several species of cladocerans distribute their resting eggs in the littoral as well, like *D. brachyurum* (see Herzig 1984) and *Bosmina longispina*. Both cladocerans terminate egg diapause at times comparable to the carnivorous late copepodids of *M. leuckarti*. The latter thus have attractive prey with small body sizes available at a critical time during its ontogenetical development.

5. CONCLUSIONS

When superficially studied, *M. leuckarti* and *T. oithonoides*, among the most common European species of cyclopoid copepods, share a lot of common characteristics: body shape, diapause periods, presence in the plankton, geographical distribution, habitat selection, ontogenetic development patterns, and depth distribution. Nevertheless, a whole array of ecological differences exist between the two species, including these presented in this paper:

- The habitat of *M. leuckarti* is characteristically both littoral/profundal and planktonic, whereas *T. oithonoides* is a true planktonic species.

- *M. leuckarti* is considerably larger than *T. oithonoides*; total body length 1.0-1.3 mm vs 0.7-1.0, respectively.

- The negligibly coloured and smaller adult *T. oithonoides* may be outside the prey range for many fish species.

- Egg sacs of the larger species *M. leuckarti* protrude from its genital segment, likely increasing water friction.

- The numerical suppression of *M. leuckarti*, its sex ratio, the habitat distribution of adult females, and its life cycles in many eutrophic lakes, is probably strongly affected by fish predation.

- *M. leuckarti* has probably developed strategies to reduce predation on eggbearing females, such as staying in littoral, profundal or oxygen boundary regions where fish are either absent or experience hunting difficulties.

- In its northern range, *M. leuckarti* showed sediment diapause in all types of localities, even the deepest lakes, usually in the upper littoral region. In more shallow lakes, deeper diapause sites were observed.

- *T. oithonoides* diapaused in either the lower littoral, or the profundal regions.

- The period of diapause for *M. leuckarti* (especially in the sediment) decreased from north to south. At about 45 ° N, sediment and plankton diapause were non-existent, and the species exhibited continuous development, even with relatively low winter temperatures.

- *T. oithonoides*, whose southern distribution in western Europe extends to about 50 ° N, showed winter sediment diapause throughout its distribution, but frequently with a fraction of the population in plankton diapause.

- *M. leuckarti* most ptobably arrived prior to *T. oithonoides* after ice withdrawal from northern Europe, and was found at higher altitudes.

- In a border distributional region of *T. oithonoides* in southern Norway, the species was found exclusively below the highest postglacial marine limit, whereas it had spread to other neighbouring lakes above the former marine limit close to its more central distributional region in eastern Norway.

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