

## Chapter 2

# Does Predation Affect the Life Style of Freshwater Copepoda?

H.H. Mohammed<sup>1</sup>, S.D. Salman<sup>1\*</sup> and  
A.A.M. Abdullah<sup>2</sup>

Department of Marine Biology,  
Marine Science Centre, Basrah University, Iraq  
<sup>2</sup>Department of Fisheries and Marine resources,  
College of Agriculture, Basrah University, Iraq

### ABSTRACT

Quantitative water samples were collected from a pool at the University Campus of Garmat-Ali from August 1998 to July 1999. The diapause in *Apocyclops dengizicus* extended from mid August 1998 to the beginning of February 1999. While that of *Mesocyclops isabellae* occurred from January to the beginning of April 1999. The presence of *M. isabellae* in the water column was synchronized with the absence of *A. dengizicus*, which suggested a strategy of avoiding predation by *M. isabellae*. The diapause stage in *A. dengizicus* was CIV and individuals were found at 5 cm deep in the sediments whereas the diapause stages of *M. isabellae* were CIV and CV and were found at a

\* Corresponding author: E-mail: dr\_salmands@yahoo.com

depth of 20 cm in the mud. Quiescence is only exhibited by the last naupliar stage and all the copepodite stages including the adult of *M. isabellae*.

**Keywords:** *Diapause, Apocyclops dengizicus, Mesocyclops isabellae, Predation, Life cycle, Quiescence, Basrah.*

## Introduction

The ecosystem of ponds differs from lakes, rivers and any other aquatic habitat because it is rather small and shallow and there is a slight difference in temperature between the surface and the bottom, and is subjected to a complete dryness during summer when the temperature rises up to 35°C or it may be freezed when the temperature drops to -5 °C, thus, the organisms living in these aquatic habitats should be ecophysiologically adapted to the surrounding factors as well as having special strategies for growth, reproduction and life cycles enabling them to pass the unsuitable environmental conditions (Thompson and Coldrey, 1985).

The life cycles of many species of freshwater cyclopoid had been studied in details in various localities in the world and represented complex types including diapause and relatively long life cycles. It is well known that many zooplankton communities both in freshwater and in marine habitats are usually having short lives extending for one year at the most, for instance Protozoa, Rotifera and Cladocera are having a life span varying from a few days to one year (Elgmork, 1981). Longer generation times are found among Copepoda, for instance, in the temporary pools, they usually have a one year life cycle, whereas in some other species the life cycle may extends for two years or more as in *Cyclops scutifer* (Sars) of Lake Hazen in Iceland (McLaren, 1961), and in Kuril Lake (Nosova, 1970a,b), these localities are arctic or sub-arctic and the lakes are exposed to very low temperatures even during summer, for the same species, a three years life span was recorded in the sub-arctic lakes and cold high mountains of Norway (Halvorson, 1973) and in the Swidish sub-arctic lake, Latnjajaure (Nauwerck *et al.*, 1980), apparently without diapause.

The main reason for the prolonged life span in these localities is the low temperatures which in turn causes lowering of the rate of development, and many species exhibit one period of diapause or

sometimes two consecutive periods of diapause (Elgmork, 1981). The first report of diapause in freshwater Cyclopoida was that of Brige and Juday (1908) on *Cyclops bicuspedatus* which stimulated the interest in investigating this phenomenon in other species of Cyclopoida and several hypotheses attempting to explain the causes of the presence of the resting stages in these species, were put forward. In this respect many studies concerning the resting stage of *Mesocyclops leuckarti* Claus in Russia (Monakov, 1958), and of *Cyclops strenuus strenuus* Fisher in Norway (Elgmork, 1955) were carried out, followed by those of Smyly (1961) and Fryer and Smyly (1954) on *Mesocyclops leuckarti* (Claus) and those of Wierzbicka (1960, 1962) on *Cyclops bohater* Kezminski and *Cyclops vicinus vicinus* Uljanin. According to Elgmork (1980), "diapause" evolved to optimize reproduction and growth and to avoid food shortages and increased competition and predation.

The present article is aimed at understanding the tactics exhibited by the cyclopoids *Apocyclops dengizicus* and *Mesocyclops isabellae* to cope with each other and with the critical conditions imposed by a pool at Basrah, south of Iraq, an investigation conducted for the first time in such subtropical area.

## Materials and Methods

### Study Area

The sampling site is a shallow pool at the University Campus of Garmat-Ali. It represents a draining water surrounded by agricultural area and covered with water throughout the study period. The width of the pond is 1.5 m., the length is about 100 m and the depth is nearly 1m. The sediments of the pool are soft mud with sand and organic material there is no aquatic plant except a few *Phragmites australis* and two species of green algae *Cladophora* sp. and *Oscillatoria* spp. which covered a large area of the pond during winter and spring and considered as a good food for the nauplius stages of Cyclopoda. In addition there are some crustaceans and benthic animals like Ostracoda and Cladocera and the snail *Lymnaea tenera euphratica* (Mousson) and aquatic insects which represented the naiads and adults of Notonecta (Hemiptera).

In the sediment samples, meiofauna were found represented by species of Harpacticoida and larvae of *Chironomus* (Diptera).

## Sampling M

Quantitati  
every two wee  
July 1999. A pla  
10 cm with a ca  
was rinsed in th  
samples were f  
collected every

Resting sta  
of 30 cm and a  
insertion of the  
which was cut  
washing with  
mm, after filtr  
examined und  
*A. dengizicus* w  
*isabellae* were  
repeated for  
diapausing in

## Results

Figures 2  
copepodite s  
*dengizicus* and  
represented b  
copepodites  
population, w  
cent males (I  
population fro  
1999. In Febru  
column, wher  
females consti  
in March 1999  
and their num  
per cent cope  
the cease of sa  
of *A. dengizicus*

*M. isabellae*  
pool from Au



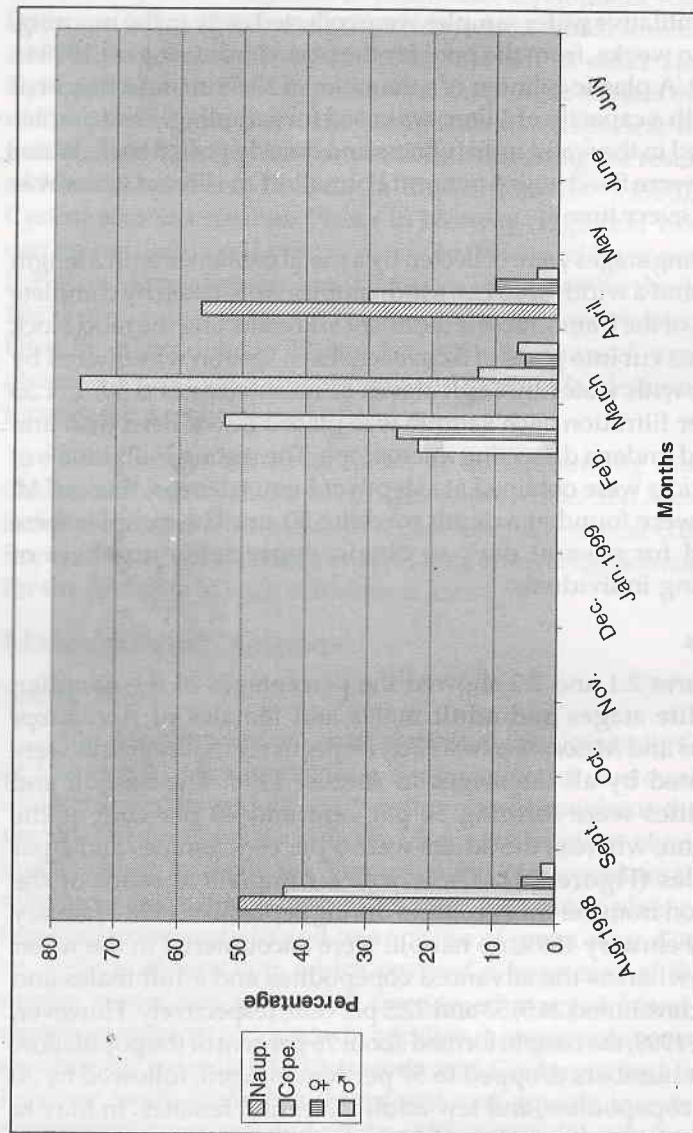


Figure 2.1: Percentage (per cent) of Nauplii Instars, Copepodite and Adults of *Apocyclops dengizicus* during August 1998–July 1999

Figure 2.1: Percentage (per cent) of Nauplii Instars, Copepodite and Adults of *Apocyclops dengizicus* during August 1998–July 1999

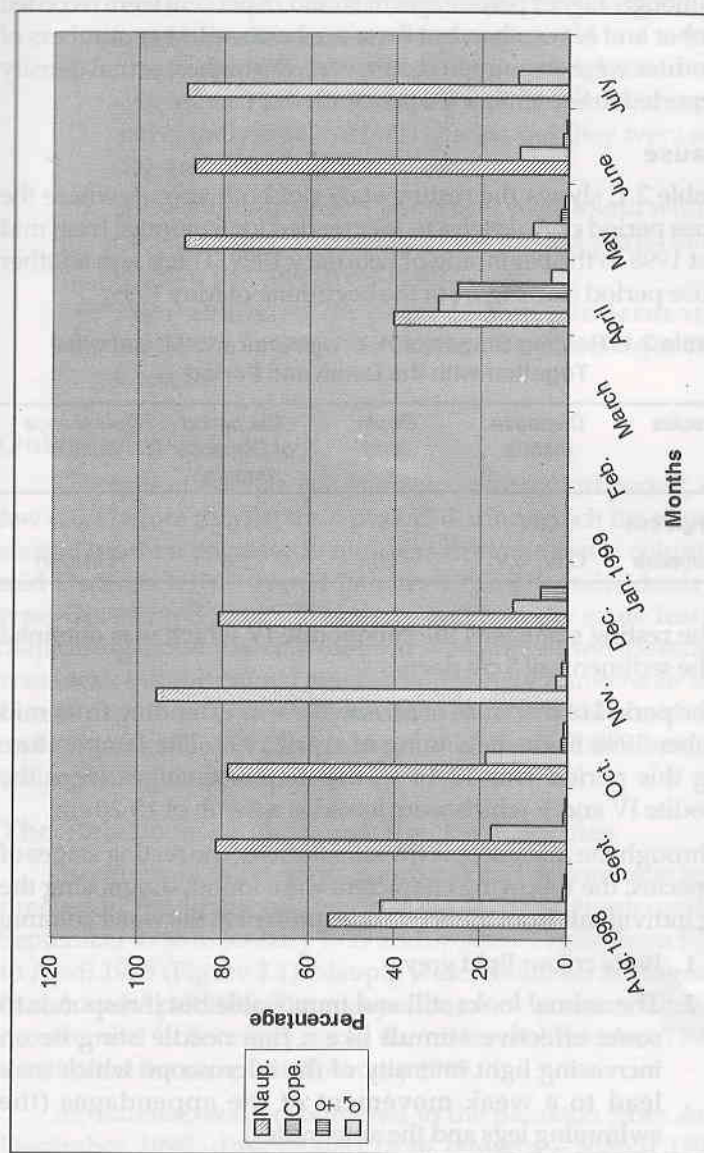


Figure 2.2: Percentage (per cent) of Nauplii Instars, Copepodite and Adults of *Mesocyclops isabellae* during August 1998–July 1999

in January, February and March 1999, and reappeared again from April through the end of sampling in July of the same year (Figure 2.2). Although, higher percentages of 96 and 76 per cent were recorded in October and November, but these are because lower numbers of copepodites were encountered, however, the highest actual density was reported in September (82 per cent).

### Diapause

Table 2.1, shows the resting stages of both species where the diapause period of *A. dengizicus* is extended for 6 months, from mid August 1998 to the beginning of February 1999. There was another diapause period starting from the beginning of May 1999.

**Table 2.1: Resting Stages of *A. dengizicus* and *M. isabellae* Together with the Depth and Period**

Species	Diapause Instars	Depth (cm)	The period of Diapause (month)	Quiescence Instars
<i>A. dengizicus</i>	C.IV	5	6	—
<i>M. isabellae</i>	C.IV, C.V	20	2.5	N.VI-C.VI

The resting stage was the copepodite IV which was obtained from the sediments of 5 cm deep.

The period of diapause of *M. isabellae* was extending from mid December 1998 to the beginning of April 1999. The temperature during this period was 12-14°C, the diapause stages were the copepodite IV and V which were found at a depth of 10-20 cm.

Through the microscopic investigations of the resting stages of both species, the following characters were found, diagnosing the resting individuals from the active ones present in the water column:

1. Body colour light grey.
2. The animal looks still and immovable but it responds to some effective stimuli like a fine needle sting or on increasing light intensity of the microscope which may lead to a weak movement of the appendages (the swimming legs and the antennules).
3. The intestine was empty of food particles.



4. The presence in *M. isabellae* of numerous oil droplets of varying sizes all over the body of the animal but were more concentrated in the cephalothorax, and pale yellow in colour, whereas, they were small in size and in addition to the pale yellow droplets there were bright red ones in *A. dengizicus*. However, these droplets can be observed in active individuals of both species, but they were small in size and few in numbers.
5. Some individuals of *A. dengizicus* were found with debris on their body, especially in the jointed parts, but in *M. isabellae* the body was clean.
6. The abdomen appeared bent underneath the cephalothorax, with the antennules extending to the body laterals.

### Quiescence

This type of dormancy was obtained for a short period, about a few days before the diapause period, during which the population started gradual decrease in numbers from the water column from mid December 1998 to mid January 1999. The individuals of this type were found near the bottom, and had the same features of diapausing individuals but the body was straight and the movement was weak but the animal was not completely immovable as in the case of diapause. The quiescence was observed only in *M. isabellae* and it includes the larval stages from N VI (in small numbers) to C VI (in large numbers).

### The Relationship Between the Two Species

Monthly plankton samples indicate that *A. dengizicus* was only present in the water column in August 1998, disappeared from September 1998 to January 1999 and appeared again from February to April 1999 (Figure 2.1). Nauplii were dominant in August 1998, March and April 1999. The copepodites were present in these three months and in February, so as the males and females. The males dominated the sample in February 1999.

*M. isabellae*, was encountered in the plankton from August – December 1998, disappeared from January – March 1999, and appeared again from April – the end of sampling in July 1999 (Figure 2.2). The nauplii dominated the plankton throughout the entire

sampling period, followed by the copepodites, the females and the males.

An obvious strong predator-prey relationship was observed in a laboratory experiments when putting the two species together in the same dish. It was noticed that *M. isabellae* is predating upon various stages of development of *A. dengizicus*. The predatory stages were C IV – C V of the former species, whereas the preys were the naupliar stages and the first three copepodite stages of the latter. Moreover, the predatory stages of *M. isabellae* were found attacking the advanced copepodites and adults of *A. dengizicus*, but were unable to ingest them. They captured them and released them again. All adults of the latter species were found dead after being attacked by *M. isabellae*.

## Discussion

The adaptive significance of diapause in the freshwater Cyclopoida is centered on two aspects, the escape from unfavourable environmental conditions, and the timing of the important events in the life cycle. The diapause is considered as the most tolerant stage to extreme environmental conditions like low temperatures, lack of oxygen and shortage of food. It is the only means of survival and may be regarded as a regulatory mechanism in the life history to secure survival during critical periods and catastrophes (Elgmork, 1980).

However, the influence of the abiotic factors on the diapause may be different, as it was found in certain species like *Cyclops vicinus* which can enter diapause in some lakes but, remains in the water column in others, although the environmental conditions are similar especially temperature (Maier, 1989; Hansen and Jappesen, 1992).

Danks (1987) generally defined dormancy as a "state of suppressed development" which is represented either by quiescence or diapause, and defined quiescence as "an immediate direct response to limiting factors, such as cessation of development if temperature falls below the developmental threshold, but immediate resumption of development if temperature rises above the developmental threshold". He also defined diapause as "a more profound interruption that routes the metabolic program of the organisms away from direct developmental pathway and into much clearly organized break development that not controlled simply by the direct action of developmental factors.



Most studies of dormancy in cyclopoids have not attempted to distinguish quiescence from diapause. These two forms of dormancy are some times confused with one another which may create problems in interpretation of the life histories. However, a distinction can be made between the two phenomena, as quiescence is characterized by being short and irregular and directly imposed by adverse environmental conditions, and is not limited to a special ontogenetic instar and may be repeated in the same individual, whereas, diapause is a response to predictable cyclic changes in the environment that occurs regularly in the seasonal cycle and manifests itself to a definite ontogenetic instar (Andrwartha, 1952; Elgmork, 1959; Mansingh, 1971).

Dormancy in cyclopoids may includes prolonged duration of juvenile instars (Smyly, 1962), cessation of feeding (Williamson, 1984), settlement to the bottom mud (Elgmork, 1962, 1996; Santer and Lampert, 1995), encystment (Cole, 1953) and reduced oxygen consumption (Watson and Smallman, 1971).

The diapause did not occur only in Cyclopoida but, also in other orders of Copepoda, Williamson and Coull (1992) and Fryer and Smyly (1954) reported the occurrence of diapause in the adult stage of Harpacticoida. Whereas, females of Calanoida produced resting eggs as cysts which tolerate and survive a long period of unfavourable conditions (Brewer, 1964).

The diapause may occur in summer (summer resting stage) initiated during the beginning of summer, or there may be a winter resting stage initiated in the autumn. In both cases the resting periods may extend to the next spring, thus, it may last for 10 months, often under severe abiotic conditions (Elgmork, 1967).

There are many reasons to cause diapause to occur in summer. It may be a response to avoid high temperatures or it may be behavioural, exhibited by species living in temporary ponds (Maier, 1989; Einsle, 1987; Hunt and Robertson, 1977; Munro, 1974), or it may be an escape from predation by fish during the winter (Nilssen and Elgmork, 1977).

The present results showed obvious fluctuations in the population densities of both *A. dengizicus* and *M. isabellae* during the study period, for when a sharp decline in numbers of the first species was reported, there was a gradual increase of the second species which reached a high density in September 1998 (371 ind./l) in

which time there was a complete absence of individuals of the first species from the water column.

The results obtained from the mud sediments showed the presence of *A. dengizicus* in a resting state at the copepodite IV, which is characterized by pale colour, empty gut and spreading of oil droplets in various parts of the body, these demonstrated in the literatures in different species of cyclopoids (Elgmork, 1959, 1962, 1998; Vijverberg, 1977). Moreover, clay particles and detritus were observed adhered to the body of the individuals. These were also observed by Elgmork (1981) in *Cyclops scutifer*, but were absent in other species or in individuals of the same species (Elgmork, 1998). Wierzbicka (1972) demonstrated physiologically that the gut is isolated from the environment by the formation of bungs which were considered as a metabolic products taking definite shapes like star, crystal or without a definite shape depending on the species. The chemical analysis of these bodies illustrates that they were derived from uric acid and they cast off through the vent after the end of the diapause period (Wierzbicka, 1972).

The results of the examination of the sediments illustrated that *M. isabellae* during the period of dormancy is represented by C IV and C V. This result is partly coincided with the result of Elgmork (1980, 1998) who indicated that the diapause is most frequently observed in C IV which in many species seems to be the only diapause stage, whereas, C V is the next frequent stage, however the diapause may also occurred occasionally in other instars.

It was found that the diapause instars in *Mesocyclops* were C IV and C V (Papinska, 1984; Elgmork, 1964; Elgmork *et al.*, 1990; Nauwerck *et al.*, 1980; Smyly, 1961). Moreover, the diapause instar may not be the same in every year like in *Acanthocyclops robustus* for instance, as in one year it may be C III and C IV, whereas in several other years the dormant stages were C IV and C V. This may be caused by the ice cover which may fluctuates from year to year by about 16–38 days (Vijverberg, 1977).

The present results indicate that both *M. isabellae* and *A. dengizicus* were present as a resting stage in the bottom of the pool, but there were no individuals in the slop of the pool. The resting individuals didn't penetrate to greater depth, but they are in relatively restricted areas of the pool's bottom. However, there were species present in the deepest part of the pond or lake, and in some other

species there:  
the lake lead  
*Cyclops scutif*  
individuals p

The hori  
the environn  
important fa  
the resting sta  
1961), while  
the slope of t  
to the fact th  
autumn turn  
oxygen defic  
of the anima

The pre  
of *A. dengizi*  
in *M. isabel*  
demonstrat  
as deep as 3  
were found  
copepods is  
period. In th  
may be con  
but changes  
as reviving  
especially  
(Elgmork,  
temperatur  
to an active  
that a rise  
apparent th  
by internal  
thus seems  
absence of

More  
of *M. isab*  
individual  
intensity o  
and a rep  
recorded.



species there seems a tendency to concentrate in the deepest part of the lake leading to tremendous numbers in restricted areas like in *Cyclops scutifer* which was found in a density of about 4 million individuals per m<sup>2</sup> in Norway (Elgmork, 1962).

The horizontal distribution of Cyclopoida may be affected by the environmental factors of which the oxygen may be the most important factor (Elgmork, 1967). In Esthwaite waters in England the resting stage of *M. leuckarti* was found in the deepest basin (Smyly, 1961), while in a lake in Poland the same species was confined to the slope of the basin (Szlaue, 1963). These differences may be due to the fact that the diapause in the lake in England started after the autumn turnover whereas, in Poland it starts before. Apparently the oxygen deficiency in the deepest areas is the key factor in the escape of the animals from these areas of the lake or pond (Szlaue, 1963).

The present results showed that the resting copepodite instars of *A. dengizicus* were found in depth of not more than 5 cm, whereas in *M. isabellae* the depth was 20 cm. However, Elgmork (1959) demonstrated that the resting stage of Cyclopoda have been found as deep as 30 cm. Generally, the majority of the resting individuals were found in the upper layer of the mud. An important aspect of copepods is the possible factors terminating and initiating the resting period. In the present study, it seems that the change in temperatures may be considered as an important factor especially in *M. isabellae*, but changes in other environmental conditions are usually important as reviving factors, and it seems that changes in temperature, especially rising temperature, act as arousing factor in the field (Elgmork, 1959; Smyly, 1961). Wierzbicka (1962) states that temperature has no significant effect in the emergence from a resting to an active state in the laboratory and surmises, as Szlaue (1963), that a rise in the oxygen pressure may have reviving effect. It is apparent that the resting conditions in *C. strenuus strenuus* terminated by internal physiological changes in a constant environment, there thus seems to be an internal clock that can awake the animals in the absence of environmental fluctuations (Elgmork, 1959).

Moreover cannibalism was observed to occur in the population of *M. isabellae*, whereby, individuals at stage C IV predating on individuals of C I and the naupliar stages of the same species. The intensity of predation was maximal when the temperature increases, and a repetitive incidence of the females predating on males was recorded.



Cannibalism was also noticed to occur at a very lesser extent in *A. dengizicus*, whereby adults were found attacking the naupliar stages, but at certain environmental stresses like the scarcity of food and increase of temperature.

Generally, *A. dengizicus* can not persist for long and reproduce successfully in the presence of *M. isabellae*, therefore, it develops the strategy of diapause to disappear from the water column while the latter is in abundance and reappeared again in the absence of *M. isabellae* (Figures 2.1 and 2.2).

The disappearance of *A. dengizicus* may be regarded as an escape from predation by *M. isabellae* during the presence of the latter, this phenomenon was quite apparent through a laboratory experiment done here demonstrating this relation between the two species. Nilssen and Elgmork (1977) presented some evidence that diapause in *C. abyssorum* may be regarded as an escape from predation by fish during the winter. Also in insects, diapause is considered to minimize the risk of predation (Southwood, 1978).

### Acknowledgements

We are grateful to Dr. M. Holynska of the Museum and Institution of Zoology, Warsaw, Poland for the identification of *M. isabellae*. H.H.M. would like to thank Prof. K. Elgmork of the Univ. Oslo, Norway for help with some important references.

### References

- Andrewartha, H.G., 1952. Diapause in relation to the ecology of insects. *Bil. Rev.*, 27: 50-107.
- Brewer, R.H., 1964. The phenology of *Diaptomus stagnalis* (Copepoda: Calanoida). The development and the hatching of the egg stage. *Physiol. Zool.*, 37: 1-20.
- Brige, E.A. and Juday, C., 1908. A summer resting stage in the development of the *Cyclops bicuspidatus* Claus. *Trans. Wis. Acad. Sci. Arts. Lett.*, 16: 1-9.
- Cole, G.A., 1953. Arrêt du développement chez les copepods. *Bull. Biol.*, 67: 276-287.
- Danks, H.V., 1987. Insect dormancy: an ecological perspective. *Biol. Surv. Canada*, 1: 439.

- Einsle, U., 1987. Zur Vertikale und derung planktischer Copepoden im Bodensee – Obersee. *Schweizerische Zeitschrift für Hydrologie*, 49: 303-315.
- Elgmork, K., 1955. A resting stage without encystment in the annual cycle of the freshwater copepod *Cyclops strenuus strenuus*. *Ecology*, 36: 739-743.
- Elgmork, K., 1959. Seasonal occurrence of *Cyclops strenuus strenuus* in relation to environment in small water bodies in Southern Norway. *Folia limnol. Scand.*, 11: 196 p.
- Elgmork, K., 1962. A bottom resting stage in the planktonic freshwater copepod *Cyclops scutifer* Sars. *Oikos*, 13: 306-310.
- Elgmork, K., 1964. Dynamics of Zooplankton communities in some small inundated ponds. *Folia limnol. Scand.*, 12: 1-83.
- Elgmork, K., 1967. On the distribution and ecology of *Cyclops scutifer* Sars in New England (Copepoda, Crustacea). *Ecology*, 48: 967-971.
- Elgmork, K., 1980. Evolutionary aspects of diapause in freshwater copepods. In Kerfoot, W.C. (ed.), *Evolution and Ecology of Zooplankton Communities*. Univ. Press, New England, p. 411-417.
- Elgmork, K., 1981. Extraordinary prolongation of life cycle in a freshwater planktonic copepod. *Holaric. Ecol.*, 4: 278-290.
- Elgmork, K., 1996. Variation in torpidity of diapause in freshwater cyclopoids. *Hydrobiologia*, 320: 63-70
- Elgmork, K., 1998. Diapause in the life cycle of *Cyclops scutifer* (Copepoda) in a meromictic lake and the problem of termination by an internal clock. *Arch. Hydrobiol. Spec. Issues. Advanc. Limnol.*, 52: 371-381.
- Elgmork, K., Halvorsen, G., Eie, J. and Longland, A., 1990. Coexistence with similar life cycles in two species of freshwater copepods (Crustacea). *Hydrobiologia*, 208: 187-199.
- Fryer, G. and Smyly, W., 1954. Some remarks on the resting stages of some freshwater cyclopoid and harpacticoid copepods. *Ann. Mag. nat. Hist.*, 7(12): 65-72.
- Halvorsen, G., 1973. Crustacean from the high mountain area Haradangervidda, South Norway. *Rapp. Høyfjellsokol. Forsk. Stn Finse, Norge*, 2: 1-17.

- Hansen, A.M. and Jeppesen, E., 1992. Life cycle of *Cyclops vicinus* in relation to food availability, predation, diapause and temperature. *J. Plank. Res.*, 14: 591-605.
- Hunt, G.W. and Robertson, A., 1977. The effect of temperature on the development time and brood size of *Diaptomus pallidus* Herrick. *Hydrobiologia*, 61: 75-80.
- Maier, G., 1989. Variable life cycles in the freshwater copepod *Cyclops vicinus* (Uljanin 1875), support for the predator avoidance hypothesis? *Archiv. Hydrobiologie*, 115: 203-219.
- Mansingh, A., 1971. Physiological classification of dormancies in insects. *Can. Entomol.*, 103: 983-1009.
- McLaren, I.A., 1961. A biennial copepod from Lake Hazen, Ellesmere Island. *Nature*, 189: 774-779.
- Monakov, A.V., 1958. Some data on the biology of development and reproduction of *Acanthocyclops viridis*. *Dokl. Acad. Nauk. SSSR (Tran. Am. Inst. Biol. Sci.)*, 119: 613-616.
- Munro, I. G., 1974. The effect of temperature on the development of egg, naupliar and copepodite stages of two species of copepods *Cyclops vicinus* (Uljanin) and *Eudiaptomus gracilis* (Sars). *Oecologia*, 16: 355-367.
- Nauwerck, A., Duncan, A. Hillbricht-Ilkowska, A. and Larsson, P., 1980. Zooplankton. In: Le Cren E. D. and Lowe McConnell, R.H. (eds.). The functioning of freshwater ecosystems. *Cambridge Univ. Press. Cambridge*, p. 251-285.
- Nilssen, J.P. and Elgmork, K., 1977. *Cyclops abyssorum*, life cycle dynamics and habitat selection. *Mem. Idrobio.*, 34: 197-238.
- Nosova, I.A., 1970a. Life cycle of *Cyclops scutifer* Sars (Copepoda: Cyclopoida) from Kuril Lake (South Kamchatka) Instomosok. ryb. Knoz. Okeanogr., 3: 82-92 (Russian with English summary).
- Nosova, I.A., 1970<sub>b</sub>. Data on the reproduction and development of *Cyclops scutifer* Sars in Lake Kuril *Inst. morok. Ryb. Khoz. Okeanogr.*, 78: 171-185. (Russian with English summary). *Izv. Tikhookean. Nauchno.*
- Papinska, K., 1984. The life cycle and the zones of occurrence of *Mesocyclops leuckarti* Claus (Cyclopoida, Copepoda). *Eol. Pol.*, 32: 493-531.



- Santer, B. and Lampert, W., 1995. Summer diapause in cyclopoid copepods: adaptive response to a food bottleneck? *J. Anim. Ecol.*, 64: 600-613.
- Smyly, W.J., 1961. The life cycle of the freshwater copepod *Mesocyclops leuckarti* Claus, in Esthwaite water. *J. Anim. Ecol.*, 30: 153-169.
- Smyly, W.J., 1962. Laboratory experiments with stage V copepods of the freshwater copepod *Cyclops leuckarti* Claus, from Windermere and Esthwaite water. *Crustaceana*, 4(4): 273-280.
- Southwood, T.R.E., 1978. Habitat, the templet for ecological strategies. *J. Anim. Ecol.*, 46: 337-365.
- Szlauer, L., 1963. The resting stages of Cyclopoida in Stary Dwor Lake. *Pol. Arch. Hydrobiol.*, 1(24): 385-394.
- Thompson, G. and Coldrey, J., 1985. The pond. Toppan Printing Company: 256 pp.
- Vijverberg, J., 1977. Population structure, life histories and abundance of copepods in Tjeukemeer, the Netherlands. *Freshwater Biol.*, 7: 579-597.
- Watson, N.H. and Smallman, B.N., 1971. The role of photoperiod and temperature in the induction and termination of an arrested development in two species of freshwater cyclopoid copepods. *Can. J. Zool.*, 49: 855-862.
- Wierzbicka, M., 1960. *Cyclops bohater* Kozm dans le birtope. *Pol. Arch. Hydrobiol.*, 7: 143-156.
- Wierzbicka, M., 1962. On the resting stage and mode of life of some species of Cyclopoida. *Pol. Arch. Hydrobiol.*, 10: 215-229.
- Wierzbicka, M., 1972. The metabolic products of copepodites of various Cyclopoida species during their resting stage. *Pol. Arch. Hydrobiol.*, 19: 279-290.
- Williams-Howze, J. and Coull, B.C., 1992. Are temperature and photoperiod necessary cues for encystment in the marine benthic harpacticoida copepod *Heteropsyllus nunni* Coull. *Biol. Bull.*, 182: 109-116.
- Williamson, C.E., 1984. Laboratory and field experiment of feeding ecology of the cyclopoid copepode *Mesocyclops edax*. *Freshwater Biol.*, 14: 575-585.