

## FISHERIES RESEARCH BOARD OF CANADA

Translation Series No. 2521

The life cycle of Neurodiaptomus angustilobus Sars  
(Copepoda, Calanoida) in lake Dal'nee (Kamchatka)

by I. I. Kurenkov

Original title: Zhiznennyi Tsikl Neurodiaptomus angustilobus  
Sars (Copepoda, Calanoida) V Ozere Dal'nem (Kamchatka)

From: Izvestiya Tikhookeanskogo Nauchno-Issledovatel'skogo  
Instituta Rybnogo Khozyaistva i Okeanografii (TINRO)  
(Proceedings of the Pacific Scientific Research Institute  
of Marine Fisheries and Oceanography), 78 : 156-170, 1970

Translated by the Translation Bureau (CLA)  
Foreign Languages Division  
Department of the Secretary of State of Canada

Department of the Environment  
Fisheries Research Board of Canada  
Marine Ecology Laboratory  
Dartmouth, N. S.

1973

24 pages typescript

Russian

English

I. I. Kurenkov

THE LIFE CYCLE OF Neutrodiaptomus angustilobus Sars (Copepoda,  
Calanoida) IN LAKE DAL'NEE (KAMCHATKA)

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Calanoida) V OZERE DAL'NEM (KAMCHATKA)

Izvestiya tikhookeanskogo nauchno-issledovatel'skogo  
instituta rybnogo khozyaistva i okeanografii

REFERENCE IN ENGLISH - RÉFÉRENCE EN ANGLAIS

Journal of the Pacific Ocean Scientific Research  
Institute of Fisheries and Oceanography

PUBLISHER - ÉDITEUR	DATE OF PUBLICATION DATE DE PUBLICATION			PAGE NUMBERS IN ORIGINAL NUMÉROS DES PAGES DANS L'ORIGINAL
	Not available	YEAR ANNÉE	VOLUME	ISSUE NO. NUMÉRO
PLACE OF PUBLICATION LIEU DE PUBLICATION	(USSR)	1970	78	-
				NUMBER OF TYPED PAGES NOMBRE DE PAGES DACTYLOGRAPHIÉES
				24

REQUESTING DEPARTMENT  
MINISTÈRE-CLIENT Environment

TRANSLATION BUREAU NO.  
NOTRE DOSSIER NO 143643

BRANCH OR DIVISION  
DIRECTION OU DIVISION Fisheries Res. Brd.  
Marine Ecology Laboratory  
Bedford Institute of Oceanography  
Dartmouth, N.S.

TRANSLATOR (INITIALS)  
TRADUCTEUR (INITIALES) C. La.

PERSON REQUESTING  
DEMANDÉ PAR Dr. G. Harding

YOUR NUMBER  
VOTRE DOSSIER NO Nov. 22, 1972

DATE OF REQUEST  
DATE DE LA DEMANDE

UNREVISÉ TRANSLATION  
For information only  
TRADUCTION NON REVISÉE  
Information seulement



CLIENT'S NO. N <sup>o</sup> DU CLIENT	DEPARTMENT MINISTÈRE	DIVISION/BRANCH DIVISION/DIRECTION	CITY VILLE
	Environment	Office of the Editor Fisheries Res. Brd.	Dartmouth, N.S.
BUREAU NO. N <sup>o</sup> DU BUREAU	LANGUAGE LANGUE	TRANSLATOR (INITIALS) TRADUCTEUR (INITIALES)	
143643	Russian	C.La.	APR 26 1973

Izvestiya tikhookeanskogo nauchno-issledovatel'skogo instituta  
ribnogo khozvaistva i okeanografii (Journal of the Pacific Ocean  
Scientific Research Institute of Fisheries and Oceanography),  
Vol. 78, 1970, pp. 157-169 (USSR)

THE LIFE CYCLE OF Neutrodiaptomus angustilobus Sars (Copepoda,

Calanoida) IN LAKE DAL'NEE (KAMCHATKA) **NEDITED TRANSLATION**

By I.I. Kurenkov

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The present work represents one section of a general study 157\*  
of the ecosystem of Lake Dal'nee carried out in past years by a  
number of researchers (Krogus, Krokhin, Menshutkin, 1969). The basic  
principle of the work is the study of the trophic relationships of the  
biological cycle and the productivity of an ecosystem. To solve these  
problems, the production of the organisms which are the largest and  
most important food source must be determined; this necessitates  
knowing the biological cycles of these organisms well and having an  
idea of the quantitative indices of their development, growth, popu-  
lation dynamics and reproduction. The present study is devoted to  
the examination of several of these indices for N. angustilobus -  
one of the most important food sources for young red salmon in Lake Dal'nee.

\*Numbers in the right-hand margin indicate the corresponding pages  
in the original.

### Material and Methodology

Samples of plankton collected in Lake Dal'nee between October 1965 and October 1968 served as the research material. A majority of the samples were obtained in a period of five days in summer and ten to fifteen days in winter. In the winters of 1965-66 and 1967-68, the frequency of collection was irregular. In summer, the period of most rapid changes in the plankton's growth processes, the samples were gathered more often, sometimes daily. A total of more than 250 samples were collected and processed.

Sampling was done in the pelagic zone of the lake, in the centre or one-third of the distance along its long axis, in the area of the source of the Dal'nyaya River (the western end of the lake). The horizontal distribution of plankton in the lake was uneven; as it varied somewhat under the wind's influence. Therefore the position of the station to some extent affected the representivity of the quantitative indices of the samples; but in general, the deviations were relatively small, as demonstrated by control samples taken from different parts of the lake.

An overwhelming majority of the samples were taken during the evening, with the sun roughly at the same distance above the horizon. The same Juday net was always used with an aperture diameter of 18.0 cm., gauze No. 55. All catches were complete, and with a few exceptions, were made in the 0-37 metre layer.

The samples were fixed with formalin in the usual manner.

In 1965 and 1966 at each station, the nets were raised once,

but later, two or three times. The samples were processed by the standard method, with piston pipettes of 0.5, 1 and 5 ml. used, depending on the abundance of the various stages of the crustaceans.

All the crustaceans, except the nauplii, were divided into stages. The adults were often counted as a whole; the females were defined by the level of preparedness for reproduction (by the state of sexual products, the presence of spermatophores in the genital segment) and the number of barren and oviferous females was noted. To determine fertility, the number of eggs in the egg sacs was counted (for 10-20 females per sample).

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While working, I benefited by consultation with and advice of F.V. Krogus, E.M. Krokhin, V.V. Menshutkin and G.G. Vinberg and also the friendly aid of B.P. Kozhevnikov and laboratory assistant L.V. Palivoda, to whom I am deeply grateful.

#### Distribution of N. angustilobus

Published data about N. angustilobus is extremely sparse. There is only information about its morphology and location in a few regions of its geographic range.

On the Eurasian continent the species was first described as Diaptomus angustilobus by G.O. Sars (Sars, 1898) from a lake in the Yana River basin near Verkhoyansk. The description contained a few inaccuracies which were corrected by V.M. Rylov (1930) (from specimens from lakes at the mouth of the Yenisei). But this author's work too contains slight discrepancies compared to our data.

The morphological proximity of N. angustilobus to the American N. tyrelli (Poppe) at one time misled S.S. Smirnov, who was identifying

planktonic crustaceans of Lake Dal'nee, with the result that N.tyrelli was mistakenly assigned to the hydrofauna of Kamchatka (Rylov, 1940).

The species was also found in the lower reaches of the Lena River (Pirozhnikov, Shul'ga, 1957), but there are no other mentions of it on the continent. It can only be surmised that its geographic range covers broad areas of Eastern Siberia, at least from the Yenisei to the Pacific Ocean, where it is found in latitudes from the mouth of the Anadyr' River (and perhaps even the Chukotka) to Okhotsk (in the Amur basin and on Sakhalin, although this species has never been discovered there despite the frequent collection of hydrobiological samples).

The species is also found on the North Kurile Islands where, as in Kamchatka, it is very common in freshwater lakes (Kikuchi, 1936; Mijadi, 1937; Ueno, 1938).

Beyond the Asian continent and the Kurile Islands, it is also known on Bering Island as Diaptomus ambiguus from Lilljeborg's description (Lilljeborg, 1887). Subsequently, with advances in synonymy, this species will in all probability be known by this name, since Lilljeborg's account was written ten years before Sar's.

On the Pribilof Islands this species was described by Juday and Muttkowski (Juday and Muttkowski, 1915) as Diaptomus pribilofensis. According to E.V. Borutsky (personal communication) these last two species are synonymous.

The species is also known in Alaska and Canada as D. pribilofensis Juday and Muttkowski (Wilson and Yeatman, 1959). A diagram in the referenced material leaves no doubt that this is identical to the Asian species.

On Kamchatka, N. angustilobus is very widely scattered (Kurenkov, 1967) and, with Cyclops scutifer Sars and Daphnia longiremis Sars, forms the basic pelagic complex of crustaceous plankton. It is found in the largest lakes, such as Kronotskoe (more than 200 sq. km.) and also in the small ones with an area of a few hectares (especially in lakes formed in the craters of extinct volcanoes). It is possible that, in order to live, the species needs a significant part of the lake's water balance to be contributed by ground waters, since it is not found in floodplain and tundra lakes with little ground-water supply. At the same time, it is not found in many of Kamchatka's lakes which appear to have all the conditions for its existence and where its usual pelagic companions live.

It is not found in relict lakes either, except the large brackish Lake Nerpich'ee (found in only one sample). However, it was noted in brackish water in the Lena estuary by P.L. Pirozhnikov and E.L. Shul'ga (1957).

The water in all the lakes where we found N. angustilobus (except Lake Nerpich'ee) belonged to the hydrocarbonate class, characterized by high transparency and relatively low temperatures (no more than 20°C at the surface and considerably less in the hypolimnion). According to all the data, the species also avoids lakes with an appreciable humic acid content. In all the lakes studied in Kamchatka where we found Neutrodiaptomus, the pH varied from 6.8 to 9.5.

Obviously the species is well adapted to low temperatures, as seen in the timing of reproduction to coincide with the period of the minimum temperatures, which in Lake Dal'nee at the 40-metre level are 1.5 to 3.0°.

Data on the distribution and population dynamics of N. angustilobus in Lake Dal'nee were collected by E.M. Krokhin (1948) for a number of years. B.P. Kozhevnikov studied the characteristics of the summer vertical migrations of the crustaceans. This exhausts all the published information on the biology of this species.

#### Life Cycle

Lake Dal'nee is inhabited by a monocyclic population of N. angustilobus, whose reproduction takes place in the first half of the calendar year - from the beginning of January to the middle of August.

The first nauplii appear in February. At the end of June the transformation into the first copepodid stage begins. Since reproduction continues until August, nauplii are present in the lake until the end of that month. The copepodid period occupies a large part of the development time; crustaceans of these stages are found in the plankton from June until April, with the entire population made up of copepods (mainly in the fifth stage) in the middle of this period (October-November). The first adults appear in December and begin reproduction in January. This process is presented schematically in Fig. 1.

Let us examine the development of the crustaceans by phases. Reproduction. Reproduction begins when the adults become stronger after the final moulting. The difference in the ratio of the sexes at the beginning and end of the reproductive period is only slight (close to 1:1 and only towards the end of reproduction do the females begin to predominate).

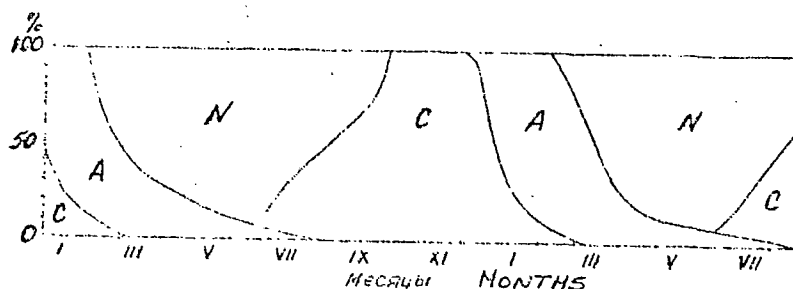


Рис. 1. Сезонные изменения в развитии популяции *N. angustilobus* в оз. Дальнее.  
 А - взрослые особи, N - науплии, C - копепода I-V стадий.

Fig. 1. Seasonal changes in the development of the *N. angustilobus* population of Lake Dal'nee  
 A - Adult N - Nauplii C - Copepods in Stages I-V

All the data show that the mating process of *N. angustilobus* does not differ from that of other representatives of this species. The incubation time can vary significantly with the water temperature, about which more will be said below.

After each mating, the female generates one unpaired egg sac in which the eggs are clearly seen, greenish at the beginning of incubation and black later. By the end of incubation, the female is obviously ready to produce new eggs, but without a repetition of mating these are not extruded and sacs are not generated.

In an aquarium with no males, females lived in such a condition for weeks, but when males were added, all the females proved to be oviferous on the next morning.

Spermatophores form very quickly; one male can fertilize up to at least ten females during three days.

Duration of incubation. To determine the length of time for eggs to mature under various temperatures, we kept oviferous females under aquarium conditions. Part of these were kept in a laboratory at room temperature, and the rest in 3-litre containers covered by two

layers of very thick gauze were placed in the river at its source from the lake. The daily water temperature here varied from 7 to 10°. Filtered lake water was poured into the containers. As food we supplied a culture of Scenedesmus and Chlorella, in a concentration which produced a barely noticeable greenish hue in the water in the aquarium tanks. This concentration of algae was higher than in the lake; therefore we assumed that the crustaceans experienced no food deficiencies.

We succeeded in completing tests with only thirteen specimens, twelve of which produced very close results. Since it was not possible to ensure complete temperature equality, a small discrepancy in results was quite natural. The average length of incubation at a temperature of 17-18° was 4 days.

We assumed that changes in the duration of incubation followed Krog's "normal curve" and, using the temperature correction found in the literature for relating the exchange values to 20° (Vinberg, 1956), we calculated our hypothetical curve within the limits of 2-20°. Points corresponding to the results of our experiments were plotted on this curve. Like most researchers, we used as indices not duration in days (D), but the reciprocal of this value  $\frac{1}{D}$ , i.e. the speed of development.

The fit of the curve appeared to be satisfactory. We compared this curve with similar ones obtained for Calanoida by other authors (Elster, 1954; Eichhorn, 1957) and those combined into a single diagram in the work of W.T. Edmundson, G.W. Comita and G. Anderson (1962). Although all the curves are

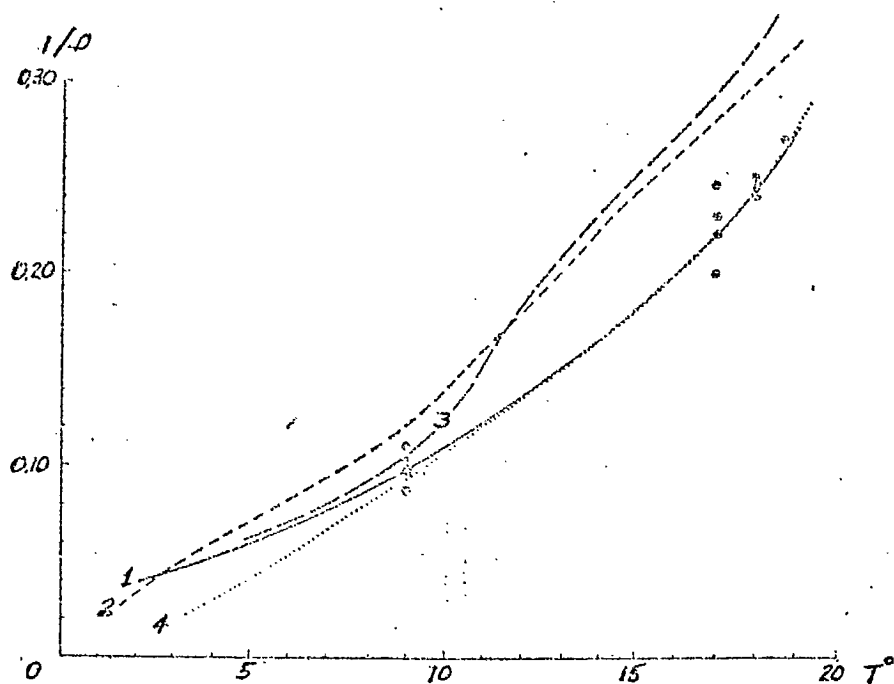


Рис. 2. Зависимость между скоростью эмбрионального развития и температурой у некоторых Каланоид:

1 — *N. angustilobus* (точки — результаты отдельных опытов); 2 — *Mixodiaptomus lacinatus*; 3 — *Eudiaptomus gracilis*; 4 — *Acanthodiaptomus denticornis*; № 2—4 — по Edmondson et al. (1957).

Fig. 2. Relationship between the speed of embryonic development and temperature for various Calanoida: 162

1. *N. angustilobus* (dots- results of separate experiments)
2. *Mixodiaptomus lacinatus*
3. *Eudiaptomus gracilis* No. 2-4 according to Edmondson et al (1957)
4. *Acanthodiaptomus denticornis*

similar (Fig. 2), the upper two for *E. gracilis* and *M. lacinatus* (curves 2 and 3) are noticeably different from the others, while a third, for *Acanthodiaptomus denticornis* (curve 4) almost coincides with ours. There is a discrepancy only in the lower part of the curve (below 8-9°), that is, in the section which was not corroborated by experimental data in our case.

The duration of incubation at various temperatures (taken from the curves) and a number of other calculated values, about which more will be said later, are presented in Table 1, A. 161

Table 1. Relationship between temperature and the duration of the various stages of the development of N. angustilobus (in days)

Зависимость между температурой и продолжительностью различных этапов развития N. angustilobus (в сутках)

Температура, град. 1	Инкубационный период (А) A	Перерыв между икредами (Б) B	Науплиальный период (В) V	Копеподидный период (Г-V ст.) G	Средняя жизнь взрослой особи (Д) D
2	25	7,5	101	350	
3	22	7,1	90	312	180
4	19	6,7	79	275	
5	17	6,0	70	241	147
6	15	5,2	61	213	
7	13	4,5	53	185	
8	11,6	4,0	48	162	
9	10,0	3,5	40	143	
10	8,9	3,0	36	125	75
11	8,0	2,7	32	112	
12	7,2	2,4	29	101	
13	6,5	2,2	25	91	
14	5,8	2,0	23	81	
15	5,2	1,8	21	73	44
16	4,8	1,6	19	67	
17	4,4	1,5	17,5	61	
18	4,0	1,4	16,0	55	
19	3,6	1,3	14,6	51	
20	3,3	1,1	13,3	47	28

1. Temperature (in degrees)                      V. Naupliar period  
 A. Incubation period                                G. Copepodid period (Stages I-V)  
 B. Interval between egg-layings                D. Length of adult life

In aquariums at 17-18° the interval between two consecutive periods of incubation of egg sacs lasted over a day (about 30 hours) and for specimens in the river containers, three days or a little more. This indicates that in this case too, the change in the relationship between the length of the interval and the temperature corresponds to the "normal curve". We also calculated such a relationship from the approximate data available to us (Table 1, B).

If the crustaceans had begun reproduction simultaneously, it would have been easy to prove how accurate our calculations were, since the sequence of incubations would have been accessible to direct observation. However the process of maturing (the transition from the fifth stage to the adult) is greatly prolonged, and in winter

takes almost three months. The gradual involvement of the adults in reproduction conceals the overall picture of the order of replacement of egg sacs. The calculation of oviferous and barren females (Fig. 3, A) shows that the ratio changes appreciably during the reproductive period, and it is possible to trace, although not very precisely, four periods of increase in the relative number of oviferous females. At winter lake temperatures of about 2° (Fig. 3, B) the period of one laying with an interval takes 30-35 days. Consequently, during the reproductive period, the great bulk of the females succeed in bearing 4-5, and some 5-6, egg sacs. As will be discussed further in greater detail, this assumption is confirmed by the existence of very distinct periods of the appearance of copepods in the first stage in the lake's pelagic zone. Usually there are five or six of these periods.

Figure 3. Fertility of female N. angustilobus

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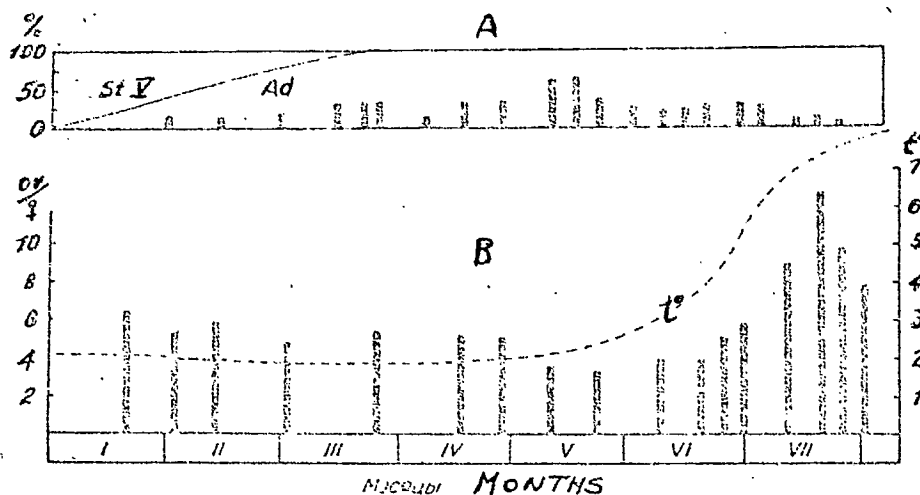


Рис. 3. Плодородность самок *N. angustilobus*:

A -- процентное соотношение яичных (столбики) и пустых самок в пробах за 1966 г.;  
 B -- количество яиц в одном яичном мешке самки (столбики) и средняя температура (t°)  
 40-метрового слоя воды.

- A. Percentage of oviferous (bars) and barren females in 1966 samples  
 B. Number of eggs in one egg sac (bars) and average temperature (t°)  
 of the 40-metre layer of water

Fertility. During the reproductive period the fertility of the females is not constant. From January to April the number of eggs in one egg sac changes very little (usually 4-6). In May it decreases 163 approximately one and a half times, but after ice break-up on the lake it quickly increases. In mid-July the average number of eggs reaches a maximum (12-13), but then declines and by the beginning of August has again fallen to 4-5 (Fig. 3, B). In all probability, the increase and decrease in fertility is related not to temperature, but to a change in food conditions. In May, before ice break-up, the situation is at its worst, and the crustaceans look "emaciated". This phenomenon was noted by A.P. Shcherbakov (1967) for the Diaptomus of Lake Glubokoe. The crustaceans are transparent, completely devoid of fatty inclusions. But already at the beginning of July their appearance has changed noticeably; small orange fat drops form under their body covering. The reason for such a rapid qualitative change is the increase, following quickly upon ice break-up, in the population of the highly nutritious diatom Stephanodiscus Hantzschii - the basic food, not only of Neurodiaptomus, but also other pelagic crustaceans and even many rotifers.

The fertility of the crustaceans declines at the end of the growth period of Stephanodiscus at the end of July and beginning of August, although the water temperature remains at roughly the same level. This confirms the prime role of the food factor in the changing fertility, as Edmondson (Edmondson et al, 1962) has noted for a series of other representatives of Calanoida.

This does not preclude that the decline in fertility is due

as well to the ageing of the females, the first generation of which are beginning to disappear at this time. A similar phenomenon was also noted by the above authors for Diaptomus sicilis in Lake Lenor. It is possible that the time of disappearance of the crustaceans from Lake Dal'nee, coinciding with a sharp deterioration in their food supply, is biologically expedient and results from the population's adapting to this change.

Proceeding from the approximate dates of egg-bearing, changes in fertility and the number of females, we calculated the average number of eggs produced by the females during the life of one year-class of Neurodiaptomus. We note that this value does not represent the "potential fertility" (Mazepov, 1963), when the elimination of females is not considered. It is more correct to call it "real fertility", as all necessary parameters for the calculation are taken from the actual state of the population. This latter is important for the future calculations of production.

We assumed that each female, surviving from maturation to the end of its year-class, produced annually five, and in 1965 six, egg sacs (judging by the six appearances of copepods in the first stage). We arbitrarily took the period of first bearing to be three months, taking into account the long interval for the change from the fifth stage to the adult. The determination of the number of crustaceans and weight of the eggs (on the basis of which calculation of the biomass was made) will be described below. The results of the computations (Table 2) showed that the real fertility of females in the years studied varied from 25 to 30 eggs per female, and the number of eggs in the plankton was approximately 13 to 21 thousand per cubic metre of water.

Table 2. Fertility of females, number and biomass of the eggs of *N. angustilobus* in Lake Dal'nee

Плодородность самок, численность и биомасса яиц <i>N. angustilobus</i> в оз. Дальнем													
Периоды посквп	Сроки посквп	1966 г.			1967 г.			1967 г.			1968 г.		
		n	M	N	n	M	N	n	M	N	n	M	N
1	I-III	4,0	500	3 600	5,5	900	4 950	4,5	1 500	6 750	4,0	860	3 440
2	IV	3,5	700	2 450	5,5	800	4 400	5,0	900	4 500	4,0	1 000	4 000
3	V	3,0	500	1 500	3,5	750	2 600	4,6	700	3 200	3,5	1 000	3 500
4	VI	4,2	350	1 470	5,0	700	3 500	4,5	600	2 700	4,2	1 000	4 200
5	VII	10,2	300	3 020	9,0	500	450	10,0	400	4 000	9,0	700	6 300
6	VIII	6,0	150	900									
3	Всего...	30,9		12 940	28,5		19 950	28,6		21 150	24,7		21 400
4	Биомасса яиц, мг/м <sup>3</sup>			18,1			27,9			29,6			30,0

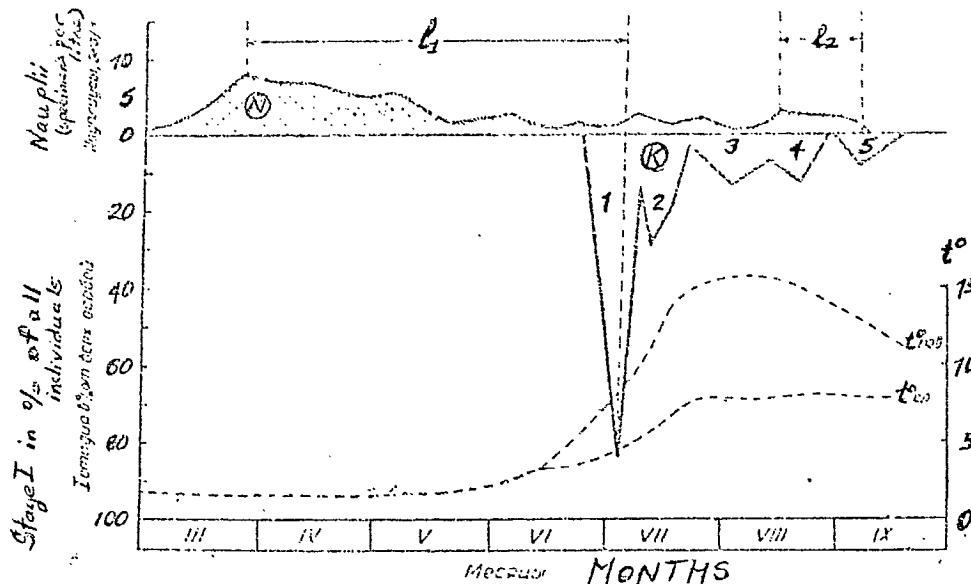
1. No. of laying n. Number of eggs per female  
 2. Periods of laying M. Average number of females per cubic metre  
 3. Total N. Number of eggs per cubic metre  
 4. Biomass of eggs (mg./cu.m.)

#### Duration of Development of Nauplii and Copepods

The duration of development of the nauplii from hatching out of the eggs to the transformation into the first stage was determined in two ways: by a comparison of the time between the maximum number of nauplii and the first copepodid stages in the samples, considering the water temperature at the time; and immediate retention of the nauplii as they hatched in aquariums at fixed temperatures.

The first calculation was done on the basis of the appropriate graphs for 1967 (Fig. 4). The diagram shows the change in numbers, first in the naupliar period, and then in the first copepodid stage. The number of specimens per litre is shown on the ordinate of the first graph and on the second, the percentage of the first stage compared to the total number of crustaceans in all copepodid stages. Such plotting allows us to observe more distinctly the

Fig. 4. Determination of the duration of development of nauplii (1967)



N - Number of nauplii (specimens per litre)

K - Number of copepodids of Stage I (in % of all copepodids of Stages I-V)

1-5 - Serial numbers of generations

l - Periods of development of the nauplii

appearance, length of existence in the plankton and sequence of the groups of crustaceans in the first stages, which are consecutively developing generations shown on the graph as five separate peaks.

We assume that the maximum peak in the number of nauplii, found in the 26 March sample, must correspond to the peak in the first copepodid generation, occurring on 3 July. In other words, this is the crest of the population density wave which extends over 100 days ( $l_1$ ).

During most of this time, the temperature at the forty-metre water level remained even ( $2.8^\circ$ ), and it rose noticeably only at the end of the period, with the result that the average temperature of this layer was  $3.2^\circ$  for the hundred day period.

From ice break-up and the beginning of warming up, we

considered the temperature, not of the entire depth, but only of the surface layer since, as is well known, the nauplii are primarily concentrated there.

Unfortunately there are no well-marked peaks in the numbers of nauplii in the growth period following the first, and we cannot assume with sufficient assurance that they correspond to the second, third and fourth generations. Such a comparison is possible only for the last, or fifth, generation. It is quite obvious from the graph that the nauplii population curve declines in the first ten days of August, corresponding to the formation of the fourth peak of the copepodids. Following this, a new peak in the nauplii curve begins to form with the maximum on 16 August. In the first ten days of September, the nauplii of this last generation completely change into the copepodid stage. The difference in time ( $l_2$ ) is 24 days in all. The average temperature of the surface layers of water in this warmest period of the hydrobiological year was  $14.6^\circ$ . For other years, the curves of the changes in nauplii numbers do not show sufficiently distinct peaks, particularly in the winter, and we are unable to verify the conclusions with these data.

In summer, when samples were collected more frequently, the development period of the last generation ( $l_2$ ) was traced more clearly : in 1965, 18 days (with an average temperature of  $14.3^\circ$ ); in 1966, 15 days (at  $15^\circ$ ); in 1968, 25 days (at  $14^\circ$ ). The possible error here is  $\pm 4$  days.

To test these results, nauplii were kept in aquariums. Several oviferous females were placed in three-litre containers. In two days

(3-4 August) nauplii hatched from a majority of the eggs. All the females were removed and the containers with the nauplii were suspended at the source of the Dal'naya River, with their tops above the water level and covered with thick gauze. The water temperature changed three times a day. During the first 15 days, the crustaceans were not disturbed, and after this the contents of the containers were examined under a microscope once every two days.

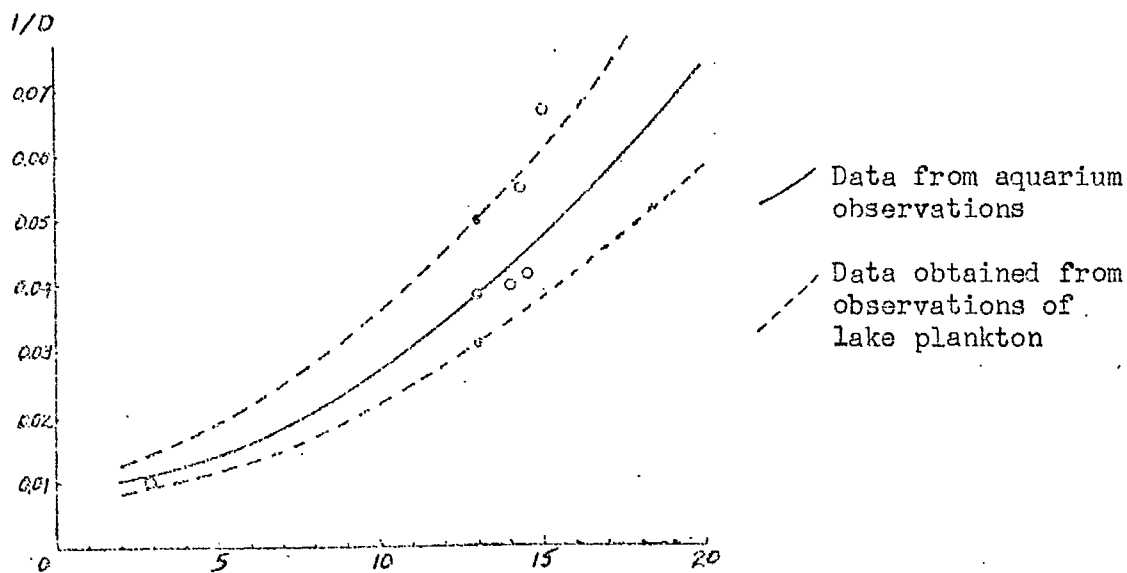
The first copepodid was discovered on 23 August.

The subsequent transition of the nauplii into the copepodid stage continued until 1 September, but occurred mainly from 28 to 30 August. If the average date of change is taken to be 29 August, then the average period of development at a mean temperature of  $13^{\circ}$  is 26 days, with a minimum of 20 and maximum of 30.

With these data, as in the first case when the incubation period was determined, a Krog "normal curve" was calculated (Fig. 5). On this graph we plotted the points produced by calculating the duration of development of the nauplii ( $l_1$  and  $l_2$ ). It is obvious that four of the five points are within the limits of the trend line. Only the fifth point (for 1966) lies below it, the one which was obviously obtained as a result of incorrect determination ( $l_2$ ) due to chance deviation of the N curve (Fig. 4), resulting in a decrease in the development period. Therefore it is possible to conclude that, within the limits of the accuracy of the analyses, the results of the observations are sufficiently confirmed experimentally.

Data on the nauplii development period in relation to temperature, calculated from the graph, are listed in Table 1, V.

Diagram 5. Relationship between the speed of development of the nauplii and the temperature



Information in the literature on the duration of the nauplii's development almost coincides with ours. Thus for E. gracilis and E. graciloides, this period is 10 to 20 days (Malovitskaya, 1965). It must be noted however, that at lower temperatures both species require a longer growth period than N. angustilobus.

This is probably related to the great adaptability of Neutrodiaptomus to low temperatures. As already stated, this species exists for a prolonged time, grows and even reproduces in winter at an underice temperature of 1.8 to 3°.

To determine the duration of development of the copepodids, we used the graphic method as for the nauplii. We calculated the average temperature of the 40-metre layer in winter and the 20-metre for the period of existence of the epilimnion, since vertical migrations of the crustaceans in general do not go beyond the boundaries of this layer.

The duration of development of the first generation can be observed clearly enough (150-160 days), but it is considerably more difficult for the last. Examining a large quantity of data, we discovered specimens in the fifth stage even in June. In all probability, they belonged to the last generation whose growth generally takes place at low temperatures (averaging about 4°) and continues for 280 to 300 days.

The relationship between the duration of development and temperature for three years was highly satisfactory, although for the last generation it is very arbitrary and calculated only for two year-classes (1965-66 and 1966-67) (Table 1, G).

Unfortunately, confirming these conclusions experimentally has not been successful as yet.

The life time of the adult crustaceans remains to be determined. 167

As already stated, the first individuals in this stage appear in the lake at the end of December and are seen until mid-August. However it must be remembered that this basic group is composed of varying ages from five consecutive generations.

As the feasible period of existence of adults of one (the first) generation, we took the interval of time from the beginning of maturing to the first signs of the males dying off. The latter is possible to determine from the ratio of males and females in the samples. When kept in aquariums the males die somewhat earlier than the females, therefore a change in the sex ratio of the adult portion of the population (noted in the second half of June) is the signal that the first generation is beginning to disappear.

The common life span of adults is about 240 days, but of the first generation (on the basis of the foregoing indications)-180 days; a significant part of this time the crustaceans live at very low temperatures (2-3°). Individuals from the four following generations grow more quickly since their development more often occurs during the period of higher temperatures. The results of an approximate calculation of changes in the life span of mature individuals at various temperatures (roughly of the average for males and females) are shown in Table 1, D. The ratio of the duration of the basic developmental stages of Neutrodiaptomus at different temperatures (egg : nauplius : copepod : mature) is 1 : 4 : 13 : 8, and for the post-embryonic stages - 1 : 3.5 : 2.1.

For E. gracilis and E. graciloides (Wutrich, 1948; Malovitskaya, 1965) the ratio of the same stages is somewhat different, 1 : 1.7 : 8 and 1 : 2.5 : 10, that is, it differs significantly from what we obtained, showing the ecological variation in representatives of the different species of Jalanoida. There is a particularly large variation in the life span of the adults. A possible explanation for this is that in M.L. Malovitskaya's experiments the adult crustaceans were kept in aquariums and our observations were made under natural conditions.

#### Conclusions

1. Neutrodiaptomus angustilobus Sars is very widely distributed in the northern part of Siberia, Kamchatka, the Northern Kurile, Komandorsky and Pribilov Islands and also in Alaska and Canada. However, information about its biology is practically non-existent in the

literature. In different regions of its geographical area, this species was described as new and therefore is now designated by three synonyms.

2. The species lives mainly in lakes of secondary oligotrophic or mesotrophic types and varying sizes. It avoids humic water and is rarely found in salty estuary lakes.

3. In Lake Dal'nee, there is one monocyclic population. Its reproduction begins in January and ends in August, after which the adults die. Nauplii are present in the plankton from February until the beginning of September. The first copepodids are noted at the end of June with the maximum number observed in July. The first adults appear in December and in March, practically the entire population is made up of mature crustaceans. The average duration of the post-embryonic period under natural conditions is about sixteen months.

4. During their lives, females produce 5 to 6 egg sacs. The number of eggs per sac varies, averaging about 4 in the winter, 10 in the summer and 5 to 6 at the end of their life. The number of eggs per sac reaches its maximum during the lake's "flowering" with Diatomus (Stephanodiscus), the basic food of the crustaceans. In all, a female produces 25 to 30 eggs. The length of incubation at a temperature of 10° is 9 days, with an interval of 3 days between layings.

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5. Observations of the lake population and experiments in aquariums demonstrated that the relationship between the rate of growth and temperature for the bulk of the crustaceans of various stages followed Krog's "normal curve", but some variation from the mean was characteristic of individual specimens even from one laying.

## Bibliography

1. Vinberg, G.G. 1956. The Metabolic Rate and Food Requirements of Fish. Minsk, BGU.
2. ----- (Editor). 1968. Methods of Determining the Production of Water Fauna. Minsk, "Vysheishaya Shkola".
3. Kozhevnikov, B.P. 1968. On the Problem of the Daily Vertical Migration of Zooplankton in Lake Dal'nee. TINRO Journal, Vol. 64.
4. Krogus, F.V.; Krokhin, E.M.; Menshutkin, V.V. 1969. Associated Pelagic Fish of Lake Dal'nee (Experiment in Cybernetic Model-building). Leningrad, "Science".
5. Krokhin, E.M. 1948. Paratunsky Lakes (Hydrography, Hydrology, Biology). Author abstract for the Geographical Institute, USSR Academy of Science.
6. Kurenkov, I.I. 1967. List of the Aquatic Invertebrates of the Inland Waterways of Kamchatka. TINRO Journal, Vol. 62.
7. Mazepova, G.F. 1963. Biology of the Pelagic Crustaceans Cyclops kolensis Lill in Lake Baikal. Works of the Limnological Institute, Vol. 1 (XXI).
8. Malovitskaya, L.M. 1965. Observations on the Life Cycle of Eudiaptomus gracilis Sars and E. graciloides Lill in the Rybinsky Reservoir. Works of the Institute of the Biology of Inland Waters. USSR Academy of Science, Issue 8 (11).
9. Meshkova, T.M. 1953. Zooplankton of Lake Sevan. Works of the Sevan Hydrobiological Station, Vol. 13.
10. Pirozhnikov, P.L. and Shul'ga, E.L. 1957. General Outline of the Zooplankton of the Lower Lena River. Works of the All-Union Hydrobiological Society, Vol. VIII.
11. Rylov, V.M. 1930. Freshwater Calanoida of the USSR. A Guide to Freshwater Organisms of the USSR. Issue 1. USSR Academy of Science, Leningrad.
12. ----- 1940. Free-Living Swimming Crustaceans. Freshwater Life in the USSR. Vol. 1. USSR Academy of Science, Moscow-Leningrad.
13. Shcherbakov, A.P. 1967. Lake Glubokoye. Moscow, "Science".

14. Eichhorn, R. 1957. Population Dynamics of the Calanoid Copepods in the Titi and Feld Lakes. Arch. für Hydrobiol., Suppl., 24,2.
15. Edmondson, W.T.; Comita, G.W.; Anderson, G. 1962. Reproductive Rate of Copepods in Nature and its Relation to Phytoplankton Population. Ecology, 43,4.
16. Eister, H.I. 1954. Population Dynamics of Eudiaptomus gracilis Sars and Heterocope borealis Fish in Lake Constance (Upper Lake). Arch. Hydrobiol., Suppl., 20, 4.
17. Juday, C. and Muttkowski, R.A. 1915. Entomostraca from St. Paul Island, Alaska. Bulletin of the Wisconsin Natural History Society, New series V, XIII (1).
18. Kikuchi, K. 1936. Freshwater and Brackish Water Calanoid Copepoda of Japan with Notes in their Geographical Distribution. Biogeographical Society of Japan, Vol. 6, No. 29.
19. Lilljeborg, W. 1887. On the Entomostraca collected by Mcleondard Stejenger on Bering Island, 1882-1883. Proceedings of the US Natural Museum, Vol. 10.
20. Mijadi, D. 1937. Limnological Survey of the North Kurile Islands. Arch. für Hydrob., XXXI.
21. Sars, G.O. 1898. The Cladocera, Copepoda and Ostracoda of Jana Expedition. Ann. Zool. Mus. Russ. Akad. Wiss., III.
22. Ueno, M. 1938. Inland Water Fauna of the Kurile Islands. Bulletin of the Biogeographical Society of Japan, Vol. 8, No. 1.
23. Wilson, M.S. and Yeatman. 1959. Free-Living Copepoda. Freshwater Biology. Ed. by W.T. Edmondson. 2nd edition, New York.
24. Wutrich, M. 1948. Study of the Development of the Nauplii of Diaptomus gracilis Sars and Diaptomus lacinatus Lill. Swiss Zoological Review, No. 55.

## ЛИТЕРАТУРА

1. Винберг Г. Г. 1936. Интенсивность обмена и пищевые потребности в Минске, БГУ.
2. Винберг Г. Г. [Ред.] 1953. Методы определения продукции водных животных. Минск, «Высшая школа».
3. Кожеевников В. П. 1938. К вопросу о суточных вертикальных миграциях зоопланктона оз. Дальнего Нев. ТИИРО, т. 64.
4. Крогнус Ф. В., Крехин Е. М., Меньшуткин В. В. 1969. Сообщество пелагиальных рыб оз. Дальнего (опыт кибернетического моделирования). М., изд. «Наука».
5. Крехин Е. М. 1942. Иратунские озера (гидрография, гидрология, биология). Автореф. дисс. Ин-т географии АН СССР.
6. Куренков И. П. 1937. Список водных беззвероных внутренних водоемов Камчатки. Изв. ТИИРО, т. 62.
7. Мазасова Г. Ф. 1963. Биология планктонического рачка *Cyclops kolensis* Lill' в оз. Байкал. Тр. лимнологич. ин-та, т. 1 (XXI).
8. Маловидская Л. М. 1955. Наблюдения над живущим личинком *Eudiaptomus gracilis* Sars и *E. graciloides* Lill' Рыбинского водохранилища. Тр. Ин-та биологии внутр. вод. АН СССР, вып. 8(11).
9. Менькова Т. М. 1953. Зоопланктон оз. Севан. Тр. Севанской гидробиол. станции, т. 13.
10. Нироджиков П. Л. и Шульга Е. Л. 1957. Основные черты зоопланктона низовья р. Мезь. Тр. Всес. гидробиол. об-ва, т. VIII.
11. Рылов В. М. 1939. Пресноводные Calanoida СССР. Определители организмов пресных вод СССР. Вып. 1. Б., АН СССР.
12. Рылов В. М. 1949. Свободноживущие плеснолюбные ракообразные. Жизнь пресных вод СССР. Т. 1. АН СССР. М.—Л.
13. Щербачев А. П. 1937. Озеро Глубокое. М., изд. «Наука».
14. Eichhorn R. 1957. Zur Populationsdynamik der Calaniden Copepoden in Titisee und Feldsee. Arch. fur Hydrobiol., Suppl., 24, 2.
15. Edmondson W. T., Comita G. W., Anderson G. 1962. Reproductive rate of Copepods in Nature and its relation to phytoplankton population. Ecology, 43, 4.
16. Eister H. I. 1954. Uber die Populationsdynamik von *Eudiaptomus gracilis*. Sars und *Heterocope borealis* Fish. in Bodensee—Obersee. Arch. Hydrobiol., Suppl., 20, 4.
17. Juday C. and Mullikowski R. A. 1915. Entomostraca from St. Paul Island, Alaska. Bull. Wisconsin Nat. Hist. Soc., New ser. V, XIII(1).
18. Kikuchi K. 1936. Fresh—Water and Brackish—Water Calanoid Copepoda of Japan with notes on their geographical distribution. Biogeograph. Soc. Japan, vol. 6, No 29.
19. Lilljeborg W. 1887. On the Entomostraca collected by Mcleopard Stejneger on Bering Island 1882—1883. Proc. of U.S. N. Museum, vol. 10.
20. Mijadi D. 1927. Limnological survey of the North Kurile Islands. Arch. fur Hydrob., XXXI.
21. Sars G. O. 1898. The Cladocera, Copepoda and Ostracoda of Jana Expedition. Ann. Zool. Mus. Russ. Akad. Wiss., III.
22. Ueno M. 1938. Inland water fauna of the Kurile Islands. Bull. Biogeogr. Soc. Japan, vol. 8, No 1.
23. Wilson M. S. and Yeatman. 1959. Free living Copepoda. Fresh—Water Biology. Ed. by W. T. Edmondson. 2nd Edit. N—Y.
24. Wutrich M. 1938. Etude du developpement des nauplii de *Diaptomus gracilis* O. Sars et *Diaptomus laciniatus* Lill. Revue Suisse. Zool., No 55.

THE LIFE CYCLE OF NEUTRODIAPTOMUS ANGUSTILOBUS SARS  
(COPEPODA, CALANOIDA) IN LAKE DAL'NEE (Kamcharka)

I. I. Kurenkov

Summary

The biological cycle was traced of a pelagic crustacean very common in the lakes of Kamcharka, an important food organism of the local planktophagous fishes. Data are presented on the geographical distribution and ecology of the species. The periods of embryonal and post-embryonal development were followed and the relation of this development in all its stages with temperature was established.