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On summer-breeding in populations of *Pontoporeia affinis* (Crustacea Amphipoda) living in lakes of North America

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Abstract

SEGERSTRÅLE, SVEN G.: On summer-breeding in populations of *Pontoporeia affinis* (Crustacea Amphipoda) living in lakes of North America. *Commentat. Biol. 44*, 18 pp. — In the amphipod *Pontoporeia affinis* Lindström, normally a winter-breeder, signs of reproduction outside the cold season have been observed in 6 lakes in North America. On the basis of a recent examination of material from the area, the author gives supplementary data on summer-breeding in some of these waters and presents evidence that this occurs in 5 additional lakes, including some of the Great Lakes. It is demonstrated that reproduction during the warm season is practically confined to the deep water. Recent experimental work suggests that in *P. affinis* the normal restriction of propagation to the cold season is due to the light factor, maturation of the gonads being induced by the decrease in illumination in late summer. Reproduction in the deep water during the warm season as well is concluded to be the result of weakening of the regulating effect of light below a certain level.

Introduction

As is well known, the amphipod *Pontoporeia affinis*, which is a glacial relict, has a wide distribution in the fresh waters of those parts of northern Eurasia and North America that were covered with ice during the Pleistocene glaciation.[1] In the latter area, with which the present paper is concerned, the crustacean occurs in large deep lakes and rivers in Canada and th United States (see, for instance, RICKER 1959, HENSON 1966). In many lakes the species is one of the main constituents of the bottom fauna and is a highly important food for fish (cf. MARZOLF 1965 a, HENSON 1966). A point of special interest is its abundance in several of the Great Lakes (maximum density observed: in L. Michigan 23 000, POWERS *et al.* 1967; in L. Ontario nearly 10 000, HILTUNEN 1969 b; in L. Huron 8 000, COOPER 1962). In these lakes *P. affinis* apparently plays an important role in the energy flow system as the species utilizes not only organic matter but also bacteria in the sediments (MARZOLF 1965 a, b).

In a number of North American lakes, besides the normal adult male, an aberrant form, f. *brevicornis*, has been found (SEGERSTRÅLE 1937, 1971 a) and in two lakes in the area even a second aberrant type of adult male

[1] For the taxonomic status of the *Pontoporeia* living in fresh waters of North America, see SEGERSTRÅLE 1971 a.

has recently been described under the name of f. *intermedia* (SEGERSTRÅLE 1971 a). Both forms exhibit signs of morphological reduction (neoteny; an especially marked feature is the shortening of the antennal flagella).

P. affinis is normally a winter-breeder (survey of extant data in SEGERSTRÅLE 1967). The reproductive cycle of this type may be exemplified by the following observations made in the Baltic Sea (coastal waters of southern Finland), where the biology of the species has been subjected to particularly detailed study (SEGERSTRÅLE 1937). Maturation of the ovaries commences in August; the first ovigerous females are found in the middle of November; the egg-laying period lasts about one month; embryonic development (the incubation period) takes *c.* four months (the temperature during the major part of this period does not exceed 2°C), the majority of the young leaving the brood-pouch of the mother in late March and April. The female produces only one brood and dies soon after the release of the young (last spent females caught in early July). During the course of the incubation period the mother undergoes a process of degeneration: her body becomes translucent, and gill pairs 1—4 become milky in colour and opaque; in spent females these gills have often broken off (other authors who have reported these signs of senescence are SAMTER & WELTNER 1904, LARKIN 1948, MATHISEN 1953). The strongly modified adult males, characterized especially by marked elongation of the antennal flagella, begin to appear some weeks before the first mature females (with fully developed oostegites) and are found for a few months only (the individual lifespan of the adult male, which has reduced mouthparts and does not take any food, seems to comprise only about one week). The male is semi-pelagic, rising high above the bottom at night in search of females (copulation, apparently without preceding precopula, apparently takes place during these nocturnal excursions into the free water in which the females also take part, although to a lesser extent; for the pelagic habit of the species, see also, for instance, MARZOLF 1965 b). The penultimate male stage, from which the adult form abruptly emerges is reached, in the Baltic study area concerned, about two months before the appearance of the first adult males; at 30—40 m depth, the young, hatched in spring, has by September attained a length of *c.* 4 mm.

Besides the normal linking of the breeding cycle to the cold season, indications that reproduction may also take place in summer are known from a number of lakes of North America and recently the same feature has been observed in Baltic waters (SEGERSTRÅLE 1967). The North American lakes concerned are Lake Cayuga (N.Y.), Great Slave Lake, Green Lake (Wisc.), Lake Huron, Lake Michigan, and Lake Nipigon.

As emerges from its title, the present paper aims at elucidation of this

aberrant feature, *i.e.* the summer-breeding of *P. affinis* in lakes of North America. The incentive for this study was a correspondence in 1963—65 between Dr. ROGER H. GREEN and myself concerning certain results of investigations carried out by him into the life-cycle of the amphipod under discussion in Lake Cayuga. The obvious occurrence, in this lake, of two distinct reproductive periods, the one starting in summer and the other in late autumn (cf. GREEN 1965, 1968), seemed to be of considerable interest, and I decided to subject the phenomenon to a general scrutiny, based on material from as many North American lakes as possible.

Material and methods

In recent years I have examined a large body of material of *P. affinis* collected from lakes of North America and received from various institutions and museums of the area. The collections comprise in total 362 samples, originating from 29 lakes. Of these, 24 have not previously been studied from the point of view of the breeding cycle of the species. The latter group comprises Lake Erie, Georgian Bay (connected with Lake Huron), Great Bear Lake, 19 lakes of the Algonquin Park area (Ont.), Lac la Ronge (Sask.), and Wollaston Lake (Sask.). The rest of the material refers to the following 6 lakes, for which earlier data on reproduction are also available: Lake Cayuga, Great Slave Lake, Green Lake, Lake Huron, Lake Michigan, and Lake Superior. Besides, published data are available from Lake Nipigon and Lake Washington. The total number of lakes for which conclusions on the reproduction cycle of *P. affinis* are possible thus amounts to 32. The largest collections were received from the following lakes (the institutions and colleagues who kindly arranged for dispatch of samples given in brackets): the Algonquin Park lakes (Ontario Dept. of Lands and Forests, Maple, Mr. N. V. MARTIN; National Museums of Canada, Ottawa, Dr. E. L. BOUSFIELD), Lake Erie, Lake Huron, Georgian Bay (Great Lakes Institute, Toronto, Prof. R. O. BRINKHURST), Great Bear Lake (Arctic Biological Station, Montreal, Dr. LIONEL JOHNSON), Lake Michigan, Lake Ontario, and Lake Superior (Bureau of Commercial Fisheries, Ann Arbor, Dr. J. K. HILTUNEN).[1]

On going through the material of *P. affinis* received, I noted the occurrence of certain categories which allow conclusions on the breeding

[1] Sincere thanks are also expressed to the following colleagues, who gave me the opportunity to examine, at their institutions, material of *Pontoporeia* in connection with a visit I paid to the Great Lakes region in October, 1966: Prof. R. O. BRINKHURST, Dept. of Zoology, University of Toronto; Dr. D. C. CHANDLER, Great Lakes Research Division, University of Michigan, Ann Arbor; Dr. J. W. MOFFETT, Bureau of Commercial Fisheries, Ann Arbor.

times of the species in the various lakes. By the term »breeding» is here meant the period of egg-laying, which is of relatively short duration in comparison with the reproductive period *sensu latiore*, which also includes the slow embryonic development and ends when the young leave the brood-pouch of the mother. The categories concerned (cats. 1—9) are listed below (among non-adult specimens only those of full-grown size, with a minimum length of 7 mm, are considered):

(1) young of the year, represented in late summer—autumn by a well defined numerous group of specimens 3—5 mm in length (indication of hatching in the spring of the same year and egg-laying in the preceding autumn),

(2) females, ovaries without signs of maturation (presence in summer of this category suggests breeding during the cold season),

(3) females, ovaries at an early stage of maturation (small eggs),

(4) females, ovarian eggs medium-sized or large,

(5) females, ovaries and oostegites fully developed (stage immediately before egg-laying),

(6) females with freshly deposited (yellowish, undifferentiated) eggs in brood-pouch,

(7) spent females (brood-pouch empty, gills 1—4 degenerating or lacking),

(8) males, penultimate stage (indication of breeding starting within a couple of months),

(9) adult males (indication of incipient breeding or this process having commenced at most a couple of months earlier).

Survey of the time of egg-laying in *Pontoporeia affinis* in North American lakes

Below, the results of the examination of the material received and earlier data on the incidence of breeding in *P. affinis* in the area under discussion are surveyed. Unless otherwise stated, the observations of the penultimate and adult stages of the male refer to the normal form (f. *filicornis*; cf. SEGERSTRÅLE 1971 a). Abbreviations of names of institutions mentioned: ABS = Arctic Biological Station, Montreal; BCFAA = Bureau of Commercial Fisheries, Ann Arbor; GLI = Great Lakes Institute, Toronto; NMC = National Museums of Canada, Ottawa; ODLF = Ontario Department of Lands and Forests, Maple. The lakes are given in alphabetical order.

Algonquin Park lakes

No literature records. Material examined: 26 samples (ODLF, NMC) from 19 lakes, V—XI, 1961, sampling depth about 30 m (verbal commun. by N. V. MARTIN; cf. MARTIN & CHAPMAN 1965).

Inferred time of egg-laying. Cold season in the following 17 lakes: Bob L., Gilmour L., Guthrie L., Kiosk L., Lake of Bays, Laurie L., Maple L., Minden L., Mink L., Muskrat L., Round L., Skeleton L., Talon L., Trout L. (N. Bay), Turtle L., Twelve-Mile L., White Partridge L. Cold season and summer in Greenleaf L. (VII: cats. 2,4) and Boshkung L. (VIII: cats. 1, 4, 6).

Cayuga

GREEN 1965, 1968. Sampling period: October 1963—September 1964, incl.; depth sampled: *c.* 100 m. Occurrence of gravid females: »— — — there are two distinct peaks, one starting in December and one starting in July» (1968: the majority of the females reproduce in the former period; cf. GREEN's Fig. 2). Adult males: »It is evident that each of the highest mature male peaks occurs about one month earlier than the high points of the gravid females peaks, or about the time of egg-laying.» Besides adult males of the normal type, one specimen of f. *brevicornis* was also caught in July (since then, this form has also been observed in September; SEGERSTRÅLE 1971 a).

Erie

No literature records. Material examined: 47 samples (most of them from GLI), 10—58 m, IV—XII, 1962—65.

Inferred time of egg-laying. Autumn—early winter, at greater depths also spring; evidence of this: presence of cat. 6 in several samples taken at 37—39 m in late April.

Georgian Bay

No literature records. Material examined: 53 samples (GLI), 23—135 m, V—IX, XI, 1964.

Inferred time of egg-laying. Autumn—early winter, at greater depths also summer; evidence of this:

month	*sampling depth (m)*	*categories*
V	70—100	4, 5, 8
VI	55—125	4, 5, 6, 8
VII	86—102	4, 9
VIII	116	6

Great Bear Lake

In LARKIN's paper of 1948, the time of reproduction is not discussed.

Material examined: 32 samples (ABS), 1—32 m, VII—IX, 1963—65. In most samples females of cat. 4 present, the rest belonging to cat. 2.

Females of the former type already to be found by the middle of July at 1.5—11.5 m. One sample, collected on 17 August, included an adult male of f. *intermedia* (SEGERSTRÅLE 1971 a).

Inferred time of egg-laying. Mainly September, also later in autumn. The occurrence of the *intermedia* male in the middle of August, suggesting an early start of breeding in the cold season, points to the possibility that the *P. affinis* population of the lake represents an aberrant race, whose males are of the *intermedia* type.

Great Slave Lake

LARKIN 1948. Depth range of sampling: 0—300 m. »In Great Slave Lake the larger part of the breeding season falls in the winter months. A few embryo bearing females were collected in the summer months, but they represent a small fraction of the total population.» It seems likely that these females belonged to the winter-breeding stock (cf. above, p. 4). By contrast, the fact that Larkin collected (in restricted numbers) females, 9.1 to 10.3 mm in length in late June at 40 to 60 m depth, which did not exhibit senescent characteristics but had enlarged brood-pouches, suggests that egg-laying also takes place to some extent in summer (LARKIN's interpretation, according to which these females were producing a second brood, cannot be upheld, since, throughout its range, *P. affinis* is known to breed only once and then die).

Material examined: 2 samples, without data on depth: »summer» 1946, cat. 7; August 1946, cat. 4.

Inferred time of egg-laying. Mainly autumn, also summer (indications of this confined to 40—60 m depth).

Green Lake

JUDAY & BIRGE 1927. Depth range of sampling, 10—68 m. »No egg-bearing females were found on November 22, 1922, but on January 30, 1923, 90 per cent of the sexually mature females had in their brood chambers eggs, all of which were in approximately the same stage of development. — — — Out of several thousand large specimens that were enumerated in the statistical work, only one female was found between July 1 and November 22 which carried eggs in the brood chamber; a female carrying 7 eggs in an early stage of development was observed on August 2, 1921.»

Material examined: 1 sample (U.S. Nat. Mus. Wash.), 25—28 m, VIII, 1922: cats. 2, 4, 5, 6; one adult male of f. *brevicornis.*

Inferred time of egg-laying. Mainly cold season, to some extent also late summer (of latter feature only one record with depth given: 25—28 m).

Huron (excl. Georgian Bay)

TETER 1960. 63 samples, 28 stations, 5.5—119 m, VI—X, 1952, 1956.

»*Pontoporeia* was carrying eggs in only one sample (station 65, August 3, 1956 [46 m]). In other samples it was possible to recognize a group of very small individuals of uniform size. They constituted 57 percent of all *Pontoporeia* in samples from station 64 [depth 33 m]. At this station they were about 2 millimeters long in June and about 3 millimeters in October. The rest of the *Pontoporeia* were of various sizes, but all were distinctly larger than the numerous small individuals. — — — Evidently *Pontoporeia* usually breeds once a year in Lake Huron and grows slowly. The major breeding season is in winter or early spring.«

COOPER 1962. »In spring, at the shallow 42-ft basin, two groups were noted: small young of the year, and large, mature, 1-year-old parents [mother animals are obviously meant]. At the 120-ft depth, three groups were found: small young of the year, medium-sized, immature, 1-year-old juveniles, and mature 2-year-old parents.«

Material examined: 57 samples (the majority from GLI), 17—148 m, VI—XI, 1956, 1963—64.

Inferred time of egg-laying. Autumn—early winter, to some extent also summer; evidence of this:

month	*depth (m)*	*categories*
VI	46—92	5, 6, 9
VII	60—83	4, 6
VIII	46	»females carrying eggs« (TETER, see above)

Lac la Ronge

No literature records. Material examined: 2 samples, without depth data, VIII, 1952. Cats.: 1, 2, 3.

Inferred time of egg-laying. Cold season.

Lake Washington

WALDRON 1953 (»*P. affinis* ssp. *erythrophthalma*«). Depth sampled: *c.* 60 m? »In this investigation it was found that mature males were present in the lake from December to June inclusive, while females with developing embryos in the brood pouch were collected between mid-January and the latter part of June. The first young-of-the-year were usually taken in March or April, and at the same time females with empty brood pouches were found. Mature males were not found in any of the collections gathered from Lake Washington during the months of July to November inclusive, and only one female carrying developing embryos was found after June. The majority of the young are released in the period from mid-March to the end of July, with the peak of hatching occurring in early June. — — — At

some time during the period from mid-November to early January the transition from the maturing to the mature form takes place.»

Inferred time of egg-laying. Mid- to late winter (+ spring?).

Michigan

SMITH 1874 (»*Pontoporeia hoyi*»). »Females carrying eggs were dredged by Dr. STIMPSON, in Lake Michigan, in 40 to 60 fathoms, off Racine, Wis., June 24, 1870, and with them the adult male form with long antennulae and antennae.» This form, which, according to SMITH, corresponded perfectly with the form of the European *P. affinis* figured and described by G. O. SARS in 1867, was obviously identical with the penultimate male stage (cf. SEGERSTRÅLE 1937). In the same collections from 40 to 60 fathoms depth off Racine SMITH also found an adult male of *P. affinis* (regarded by him as a separate species, *P. filicornis;* cf. SEGERSTRÅLE l.c. and 1971 a).

MARZOLF 1963. Study area: mouth of Grand Traverse Bay, N. E. Lake Michigan, 10 stations, 20.6—121 m, VI—VIII, 1961. »Collections of material from Lake Michigan in the present study show that mature males and ovigerous females are present in the early summer (sample No. 061661. 6 [June 6, stat. 5, *c.* 60 m]) and at no other time during the sampling period. No information is available from the present study as to the relative abundance of mature and ovigerous individuals during the winter, although the frequency of larger individuals did begin to increase in August. The relatively low frequency of newly hatched animals (1—2 mm in length) on June 16 [6?] and the major increase in this size class by July 7 indicates that the majority of the young are released during this time interval (Fig. 17).» These data suggest that (autumn—) winter is the main period of egg-laying but that this process also takes place in June at greater depths. MARZOLF 1965 b. »Larger individuals, predominantly adult and subadult instars» caught in tow-net samples above the bottom (42 m) in Grand Traverse Bay, August, 1963.

ALLEY 1968. »The brood chambers of the adult female amphipods, collected in the long-term study area, indicated that reproduction is completed by late May—early June at depths less than 35 m and beyond 35 m the amphipod populations breed intermittently throughout our sampling seasons» (1964: Aug.—Nov.; 1965: April—Nov.; 1966: March—Nov.). Details are given in Tables 2 and 3 from which, among other things, emerges that spent females were found, from *c.* 50 m depth downward, also in the months of July, August, and September.

Material examined: 102 samples from central and southern Lake Michigan (BCFAA) and 2 samples from Grand Traverse Bay (MARZOLF), 5.5—275 m, 1951—52, 1961—63, 1966.

Inferred time of egg-laying. Autumn—early winter, but at greater depths

also evidence of egg-deposition at the warm season. For ALLEY's results, see above; other indications:

month	*depth (m)*	*categories*
V	33—131	4, 5, 6, 9 (+ *brevicornis*, minimum depth 46 m)
VI	73—130	»females carrying eggs», 8, 9 (see SMITH above)
VI	60	6, 7, 9 (+ *brevicornis*, 84 m)
VI	*c.* 60	»mature males and ovigerous females» (MARZOLF 1963, see above)
VII	80	9
VIII	above 42	9 (MARZOLF 1965 b, see above)
VIII	178	9 (136 specimens, plankton sample, sent by MARZOLF)

Nipigon

ADAMSTONE 1928. Five adult males, f. *brevicornis* (cf. SEGERSTRÅLE 1937), caught in summer at a depth of more than 90 m, indicate breeding at this season.

Ontario

HILTUNEN 1969 b. 24 stations sampled in September, 1964, at 11—225 m depth. — — — the smallest (1 mm) were collected only in the deep area (91.5 m or more).»

Material examined: 21 samples (most of them from BCFAA), 11—183 m, II, IX, 1964.

Inferred time of egg-laying. Mainly cold season. No summer samples available, but the presence in September, at 90 m depth or more, of spent females (samples examined) and very small specimens (HILTUNEN) suggests egg deposition also in summer at greater depths.

Superior

SMITH 1874. »This species (»*P. hoyi*») was found in great abundance in the dredgings in Lake Superior in 1871, and occurred in every haul from 4 to 169 fathoms. — — — All the specimens dredged in Lake Superior were taken in August and the early part of September, and none of the females were carrying eggs during that time.»

SEGERSTRÅLE 1937. Five adult males, f. *brevicornis,* found in whitefish from Marquette Bay in December, 1929.

HILTUNEN 1969 a. »Three generations of *P. affinis* were present in the samples [June 23—26, 1964], but the size (age) groups could not always be distinguished. The presence of gravid females at station 53 (48 m) indicated that a fourth generation was about to emerge or that the timing between successive generations varied from station to station.»

Material examined: 18 samples (most of them from BCFAA and GLI), 17—182 m, VI—IX, 1959—64.

Inferred time of egg-laying. Cold season, but also summer (June—July); evidence of this:

month	*depth (m)*	*categories*
VI	38— 64	4, 5, 6
VII	64—135	4, 6
IX	64—181	7

Wollaston

No literature records. Material examined: one sample (NMC), collected »in summer», 1956; depth not given.

Inferred time of egg-laying. Autumn—winter.

Summary and discussion

The results of the present study on the time of reproduction in North American populations of *P. affinis* may be summarized as follows:

(1) As in other parts of the range of the species, egg-laying in the lakes in question takes place mainly in the cold season. In one of the lakes, *viz.* Great Bear Lake, reproduction seems to start as early as September (discussion p. 8).

(2) Besides this type of breeding there are, in a number of lakes in the area, also signs of propagation during the warm season. To the list of those lakes for which this feature is indicated by the earlier literature, *viz.* Cayuga, Great Slave Lake, Green Lake, Huron, Michigan, Nipigon, can now, on the basis of the present study, be added: two lakes of the Algonquin Park area, Erie, Georgian Bay, and Ontario. There is no evidence that the male form of *brevicornis* is exclusively linked with summer-breeding (cf. GREEN 1968).[1]

(3) The feature of summer-breeding is practically confined to greater depths (exception: Great Bear Lake; cf. p. 8). This tendency, already suggested by earlier observations in lakes of the area under discussion (note especially the data from L. Michigan), is clearly confirmed by the new material examined. The data concerned (including those published previously) are surveyed below:

[1] The data given by WALDRON for Lake Washington give no clear picture of the reproduction pattern in this lake (the observation of mature males from December to June inclusive is difficult to reconcile with the fact that only one female carrying developing embryos was caught after June).

lake	*upper limit of sampling range (m)*	*minimum depth (m) of egg-laying observed in the warm season*
Boshkung L.	*c.* 30	*c.* 30
Cayuga	*c.* 100	*c.* 100
Erie	10	37–39
Georgian Bay	23	56
Great Slave L.	0	40–60
Green L.	10	25–28
Greenleaf L.	*c.* 30	*c.* 30
Huron	5.5	46
Michigan	5.5	33
Ontario	11	90
Superior	7	38

Note. The observation of adult males (f. *brevicornis*) in L. Nipigon in summer at more than 90 m also suggests the occurrence of breeding at greater depths during the warm season in this lake.

GREEN, in his paper of 1968, discusses the existence of two separate breeding seasons observed by him in Lake Cayuga (see above, p. 5) and the other similar records from North American lakes known by that time. »A crucial question is whether the separation of times of reproduction was preceded by geographic isolation, or whether it arose within the lakes where it now occurs. SEGERSTRÅLE (1957) suggests that the relict species, including *P. affinis*, evolved and spread toward Europe and North America from a large ice lake in western Siberia, which was dammed up in front of the ice-cap of the penultimate glaciation and included trapped marine animals. KOZHOV has questioned the existence of such a lake, but, as far as North America is concerned, there seems to be little doubt that the presence of relicts in lakes of that continent is due to the sluicing-up effect of pro-glacial lakes (RICKER 1959, SEGERSTRÅLE 1962).»

As regards the existence of an ice-dammed lake in western Siberia at the time of the penultimate glaciation, the following postscript, added to a second printing (1967) of the present author's paper of 1966 may be inserted here: »At the time of writing this article, the present author was not aware of KOZHOV's comments on the supposed ice-lake in western Siberia (KOZHOV 1963). The existence of such an ice-lake had been concluded by PIROZHNIKOV on the basis of biological evidence and results obtained by Russian geologists (for instance, signs of a spillway at the head of R. TOBOL; cf. SEGERSTRÅLE 1957, p. 94). According to KOZHOV (p. 225), modern investigations in the West-Siberian Lowland reveal no trace of an extensive ice-dammed basin, neither are there any indications of an ancient run-off from it towards the Caspian Sea. However, KOZHOV admits that dammed glacial lakes, even very big ones, may have existed in North Siberia in Glacial times. Considering this, the present author is disinclined to abandon the essence of his view that Siberian ice-dammed waters played a role in the prehistory of the glacial relicts. On the contrary, he anticipates that future

geological research will provide evidence of the existence, somewhere in Siberia at the time of the penultimate glaciation, of proglacial waters, where the relict species evolved and from which they were able to spread along the margin of the ice-caps and, through overflow, southwards. Otherwise, the existence, on the one hand, of relicts, including some freshwater fishes of eastern origin, in lakes of the British Isles and, on the other, of a relict crustacean such as *Pallasea* in the North European region and the Caspian Sea, seem inexplicable (cf. SEGERSTRÅLE l.c.; EKMAN 1959).»

It may be added that the well-known authority on the zoogeography of the aquatic fauna of northern Soviet regions, E. F. GURYANOVA, in a recent paper (1970), also seems to reckon with the existence of an ice-dammed Siberian basin of the type suggested by PIROZHNIKOV and the present author (see footnote, p. 142, in her just-mentioned publication).

GREEN continues as follows: »A post-Pleistocene origin of *P. affinis* summer reproduction would mean that summer breeding began independently in several isolated lakes in North America. A Pleistocene origin, on the other hand, would have been aided by successive glacial invasions, with many separations and reconnections of melt waters and long periods of isolation in between. Such conditions would be ideal for geographic isolation, genetic differentiation and subsequent reproductive isolation in the classical manner (MAYR 1963).»

Since the appearance of GREEN's paper, observations have been made which clearly suggest that the reproductive cycle in *P. affinis* is regulated by environmental factors and thus support the first of the alternatives advanced by him, *viz.* that summer-breeding began independently in the various North American lakes concerned.

Recent experimental work carried out at the Zoological Station at Tvärminne, situated on the south coast of Finland, with material of the amphipod from the Baltic Sea, strongly suggest that maturation of the gonads and, as a consequence, restriction of the breeding period to the cold season, is induced by the decrease in light in late summer (SEGERSTRÅLE 1970). This conclusion is supported by the fact that, in Baltic waters, reproduction during the warm season — a feature unknown until recently (SEGERSTRÅLE 1967) — has been observed only at depths below 100 m, where practically dark conditions prevail or, at any rate, the annual fluctuations of illumination are largely smoothed out (material of *Pontoporeia* from the zone 60—100 m is lacking, but certain facts suggest that propagation outside the cold season commences near the lower limit of this zone).[1]

[1] It is of considerable interest that recent field observations and experimental studies on the reproductive cycle of the arctic-subarctic amphipod *Gammarus setosus* Dementieva which have been carried out by the Canadian zoologist V. J. STEELE have led to the same conclusion as that arrived at in my work with *Pontoporeia:* »Timing (of breeding) is evidently independent of temperature, but photoperiod has been found to affect the cycle (V. J. STEELE, unpublished observations)» (STEELE & STEELE 1970, p. 669).

As was mentioned above, in North American lakes breeding at the warm season also seems to be excluded from shallow water (exception: Great Bear Lake; for discussion, see p. 8). However, the minimum level of such reproduction has, in this area, in several cases been observed at considerable lesser depth than in Baltic waters, *viz.* in 6 lakes above 40 m, the minimum being 25—28 m (Green L. 25—28, Greenleaf and Boshkung L. *c.* 30, Michigan 33, Erie 37—39, Superior 38 m). This difference between the results from lakes of North America and the Baltic Sea seems to be explainable in one of the following alternative ways: (1) either the divergences concerned are genetically conditioned, or (2) there are differences in the transparency (light penetration) of the water in the two areas. As regards the first alternative, it should be borne in mind that the populations of *P. affinis* of the North American and Baltic regions are not quite identical from a morphological point of view (cf. SEGERSTRÅLE 1971 a). Furthermore, it is to be noted that, in Baltic waters, in the species *P. femorata*, which is closely related to *P. affinis* and is likewise mainly a winter-breeder, reproduction during the warm season (as in *affinis* restricted to deeper water) commences at a clearly higher level than in the latter species (SEGERSTRÅLE, 1967, 1971 c). As regards the second alternative, again, attention should be drawn to the results of recent studies on vision in *Pontoporeia*, which suggest that in fresh water, where the light is weaker in over-all transmission and, moreover, differs in its spectral composition from that of the brackish Baltic, the maximum depth at which illumination regulates the reproductive cycle of *P. affinis* may be less than in the latter area (cf. DONNER 1971). Furthermore, differences in transparency caused by variations in plankton production and in the amount of suspended particulate matter in the individual waters should be considered.

GREEN's observation that there are two distinct egg-laying periods in Lake Cayuga, one from December to April (corresponding to the normal pattern of breeding during the cold season) and the other (comprising a minor proportion of the population; cf. Fig. 2 in his paper of 1968) from July to September, deserves some comments.

We have to consider how we may account for such a distinct concentration of reproductive activity outside the normal period. The following tentative interpretation of the phenomenon is advanced. At the considerable depth, where GREEN collected his material in Lake Cayuga (*c.* 100 m) and where the light factor is apparently not efficient enough to cause an over-all restriction of the breeding cycle of *Pontoporeia* to the cold season, other, seasonally fluctuating environmental conditions contribute towards determining the timing of gonad maturation. Among such factors temperature seems to be excluded by the data given by GREEN, which indicate highly stable conditions in the bottom layers of the lake in the course of the year.

A more likely factor is fluctuation in the supply of food. For a number of aquatic invertebrates a close relationship between food and reproduction has been established or suggested (discussion in, for instance, GIESE 1959 a, b; as far as amphipods are concerned, the results obtained in studies on *Ampelisca macrocephala* are of special interest; KANNEWORFF 1965). In this connection the plankton production comes into the picture as a possible factor: on the one hand, that part of the plankton which, in due time, is deposited on the bottom is no doubt particularly valuable as food (as such or via bacteria) for substrate-feeders within the benthic fauna, among them *Pontoporeia*); on the other, marked seasonal fluctuations in the production of phytoplankton have been observed in the North American lakes (note, for instance, the occurrence of two distinct peaks in the course of the year in Lake Erie (CHANDLER 1944; cf. also HOLLAND's results obtained in Lake Michigan, 1969).

It is hoped that the present article will stimulate zoologists of North America to undertake a thorough analysis of the factors influencing the reproduction of *P. affinis* in their working area.

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