AN ABSTRACT OF THE THESIS OF

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Title: The ecology of Lepidurus apus in Northern Utah and some limnological requirements for hatching.

Abstract approved _____ (Major Professor)

A survey of the major bodies of water, temporary and perennial, in the region of Northern Utah revealed a limited distribution of the Notostraca. Lepidurus apus (Linn.), the only representative found, was restricted to a single temporary shallow lake, Dry Lake, in the southern end of Cache County.

Dry Lake occupies a solution basin at 5,638 feet elevation, surrounded by mountains ranging from 6,500 to 7,900 feet in elevation.

The limnological succession of this lake during the tenure of L. apus showed a high rate of variation and wide ranges in temperature (-2° C to 31° C), dissolved oxygen (46% to 155% saturation), conductivity (1100-3400 mho), turbidity, and pH.

Laboratory incubation of the eggs of L. apus under a total of 120 different combinations of temperature and moisture pre-incubation treatments, disclosed the necessity of a pre-incubation freezing treatment to induce hatching. A pre-incubation drying treatment was not necessary for eggs incubated for 124 days but consistently produced significantly higher percentages of hatching in those

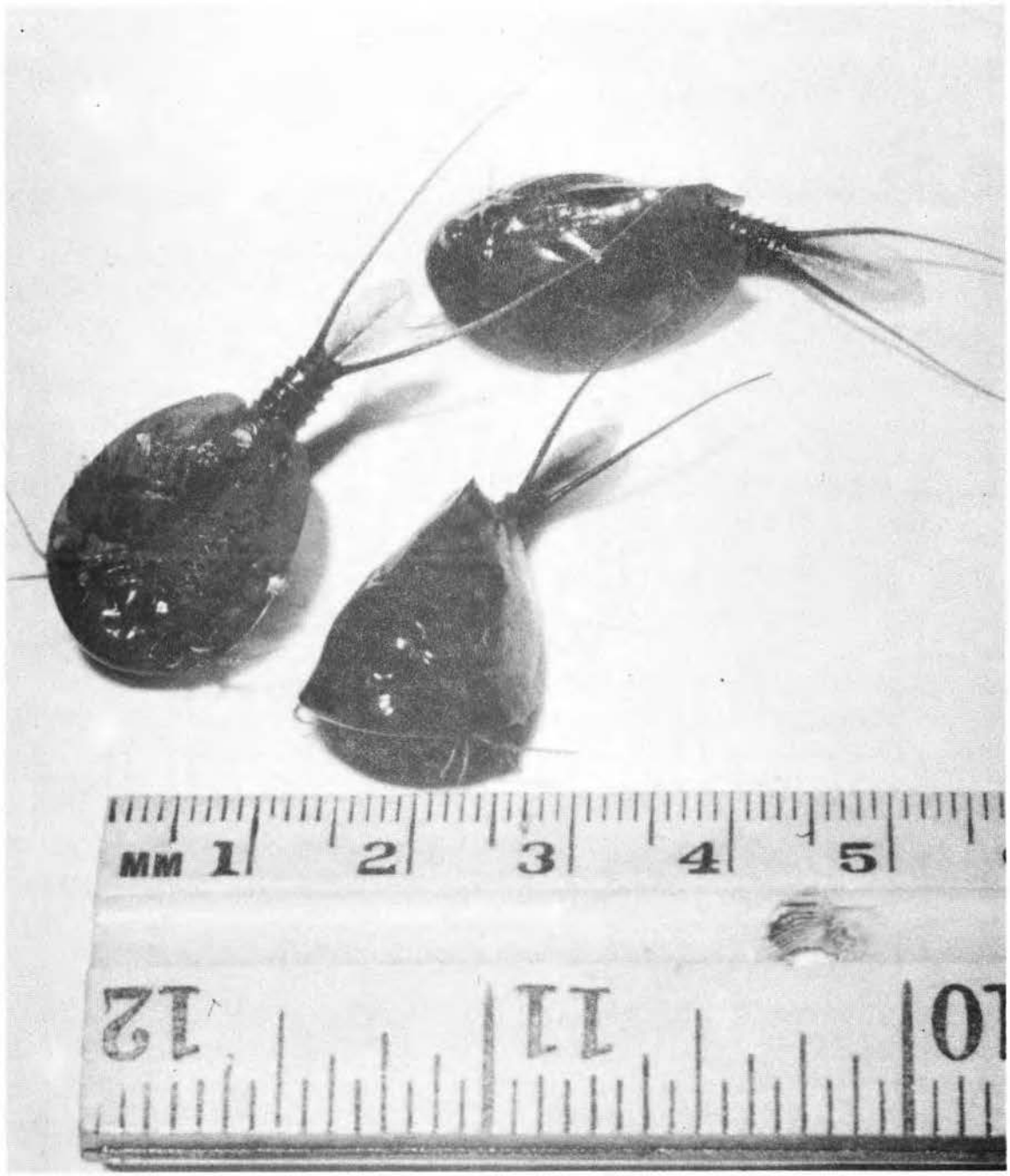
hatches dried at 18° C and 26° C. Eggs remained viable with but slight reduction in rate and percentage of hatching, even though they had undergone -20° C (rapid cooling) and 26° C (drying) pre-incubation treatments.

Pre-incubation freezing to -80° C, whether rapid or slow, reduced the percent hatch to a maximum of 12%. The 45° C drying for 48 hours permitted a maximum of 40% hatching and retarded significantly the hatching rate.

Sun-dried and wet eggs were subjected to -2° C for periods varying from 2 days to 37 days. One portion of these dried eggs was frozen in a dry state and another portion in a wet condition. Incubation of these eggs in pond water at 5° C, 10° C, 25° C, and 40° C produced hatching solely in the 10° C temperature among those sun-dried and frozen wet only. A 14 day duration of continuous cold was found to be a minimal requirement.

Eggs receiving the threshold duration of pre-incubation cold treatment required 14 days subsequent incubation at 10° C for hatching. Extension of the pre-incubation cold treatment up to 31 days resulted in a consequent reduction (not linear, however) of incubation time at 10° C from 14 to 7 days. Thirty-four and 37 days detention in the cold (-2° C) showed an increase to 10 days incubation time.

The eggs of L. apus can develop and hatch at -2° C, although at a greatly reduced rate.



Lepidurus apus (Linn.) X 2.5

THE ECOLOGY OF *LEPIDURUS APUS* IN NORTHERN UTAH AND SOME LIMNOLOGICAL REQUIREMENTS FOR HATCHING

by

Audrey Lee Braswell, jr.

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THE ECOLOGY OF *LEPIDURUS APUS* IN NORTHERN UTAH AND SOME LIMNOLOGICAL REQUIREMENTS FOR HATCHING

INTRODUCTION

Lepidurus and *Triops* are shield-bearing, fresh-water "tadpole shrimp", comprising the order Notostraca and are found primarily in vernal ponds or temporary rain pools throughout the world. They have been of particular interest to zoologists for several reasons; namely, geological antiquity, evolutionary stagnation, irregular but world-wide distribution, similarity of the two genera, and abnormal intra-specific variation. Geological antiquity is suggested by the existence of their fossil counterparts, found in strata of the lower Cambrian, which show very little morphological difference from the extant genera[1]. They appear to be in a state of evolutionary stagnation. They are of world-wide occurrence, but exhibit an unusual irregularity of distribution in the regions where they are found. This irregularity of distribution is somewhat enigmatic since "Their adaptation to a temporary habitat has enabled their drought-resistant eggs to become efficient agents of passive dispersal." (41, p. 84). The two genera, *Triops* and *Lepidurus*, are quite similar in most respects; the most obvious morphological distinction being possession of a supra-anal plate by *Lepidurus*. This apparent identity might suggest a commonality of ecological requirements, but only once have they ever been reported to occupy the same body of water (7, p. 587). Therefore

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1 Tasch (69) reviewed the genera which had been assigned to the Notostraca and concluded that *Apus* (syn. *Triops*) and *Lepidurus* are the only valid fossil genera of this order.

considerable interest has been shown in their respective ecologies without complete resolution of the problem.

Upon learning that Carrington had collected Lepidurus apus at Smithfield, Cache Valley, Utah, (59, p. 318), this author was desirous of conducting a three-phase study involving first, a survey of Notostracan distribution in the Northern Utah region; secondly, to determine, if possible, some of the ecological factors contributing to their unique distribution patterns; and finally, a laboratory phase in which the control of environmental conditions might identify some of the critical physical factors regulating the development of their eggs.

REVIEW OF THE LITERATURE

TAXONOMIC HISTORY AND DISTRIBUTION

First knowledge of the Notostraca, according to H.M. Fox (19, p. 693), resulted from a specimen collected in East Prussia by Herr Klein, the Stadt-Secretarius of Danzig. Klein sent his specimens with accompanying drawings to Johan Leonard Frisch who published a short account in 1732 of the "Flossfussiger See-Wurme mit dem Schild". Linnaeus in his Systema Naturae referred to Frisch's animal (illustrated Triops) as Monoculus Apus. Jacobus Theodor Klein then, in 1738, published his find, referring to the organism as the "Monoculus apus of Linnaeus". Later, Linnaeus, in his "Fauna Svecica", (19, p. 693) wrote: "Vidi animal siccum 1728 apud Studiosum Lundinensem qui ibidem captum narrabat" (a direct quotation from the actual plate of Frisch's (1732) Triops), thus providing reference to a previous collection at Lund in Sweden. It is not known, however, whether this latter reference concerned the collection of a Triops or Lepidurus, since both are found in Sweden (43, p. 54-85). "In an annotated copy of this edition of the 'Fauna Svecica', Linnaeus had stricken the words 'Vidi animal . . . narrabat' and substituted 'in fossis Lundinensibus. J. Leche' which is not explained" (19, p. 693). Schäffer's description of Apus (Triops) and its habits (67, p. 1-142) disclosed his knowledge of the difference between Triops and Lepidurus, referring to the latter as a "neue and bisher ganz und gar unbekannte Art" (19, p. 693); however, he referred to both forms as Apus cancriformis, thus supplying the generic and specific designation by which

Triops was to be known until the recent rejection of "Apus" in favor of Triops[2] Shrank, 1803 (34).

The identity and taxonomic designation of Lepidurus was thus masked through its confusion with Triops until 1801-1802 when Bosc and Latreille resegregated and designated them separately as Apus cancriformis (meaning Triops) and Apus productus (meaning Lepidurus). Finally, Leach[3] (36) advanced Apus productus to a separate genus, viz., Lepidurus, based upon the presence of a spatulate supra-anal plate extending backward from the telson between the two long filamentous furca. Numerous species have been described in these genera by various authors and an additional genus, Bilobus Sidorov, has been erected, but Folke Linder, (38) succeeded in resolving the Notostracan order to the two genera, Lepidurus and Triops. He based his reduction upon an examination of 109 United States National Museum lots comprised of more than 2,000 specimens carefully compared with about 3,000 specimens from 71 localities throughout the world. He concluded that all available specimens[4] of Lepidurus could be accurately classified into two main groups of species. Lepidurus apus, L. arcticus, L.

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[2] It is here noted that the Official List of Generic Names in Zoology in Opinion 502, p. 172, signed November 5, 1957, published January 24, 1958, under the Plenary Powers of the International Commission on Zoological Nomenclature validated "Lepidurus" at the expense of "Monoculus" and "Apus productus", and at the same time, "Triops" was retained while "Apus" was rejected.

[3] Lepidurus Leach, Dictionnaire des Sciences Naturelle, Vol. 1, p. 259, 1816.

[4] The type specimen of Lepidurus patagonicus was not available for Linder's scrutiny, but Longhurst (40, p. 48) later concluded, on the basis of Bruch's record and accompanying illustration, that it was unquestionably synonymous with L. apus.

couesii, L. kirkii, L. packardi, and L. viridis comprised one group characterized by fewer rings and legs, while his second group consisted of L. bilobatus and L. lynchi, these species demonstrating a more highly developed abdomen in the leg-bearing region. Continuing the trend for reduction of number of species, A.R. Longhurst (40, p. 49-54) further rearranged the speciation. On the strength of his analysis of preserved specimen from six major museums[5] of the world, his evidence derived from the growth and development of living animals, their cytology, reproduction, and protein specificity, he reduced Linder's eight species of Lepidurus to four and described a new species of Lepidurus from Russia. The listing of synonymies will not be included here, but his five species included L. arcticus (Pallas), L. lynchi Linder, L. bilobatus Packard, a comprehensive L. apus (Linn.) (syn. couesii), and L. batesoni sp. nov. with a strong suggestion of the likelihood of the eventual discovery of intergrades among the latter three genera, thus anticipating their synonymy.

Triops speciation was reduced by Longhurst (40, p. 41) to T. cancriformis, T. granarius, T. longicaudatus, and T. australiensis. Longhurst (40, p. 41-49) recorded Triops distribution to include many sites in Europe, Asia, North Africa, Balkans, and Asia Minor and Middle East to India for T. cancriformis; South Africa to China including India for T. granarius; while T. longicaudatus ranges from the Great Basin area of North America through Central and South America, West Indies, Hawaii, Japan, Galapagos Islands, and New Caledonia; and

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[5] British Museum of Natural History, United States National Museum, Muséum Nationale d' Histoire Naturelle, Western Australian Museum, Zoological Survey of India, Museo de Ciencias Naturalis.

T. australiensis occurred only in the drier regions of Australia.

In his monograph (40, p. 49-54), Longhurst reported the range of Lepidurus sp. to include Europe, North Africa, Palestine, Asia Minor, Russia, North and South America, New Zealand, Australia, Aleutians, Alaska to Labrador, Greenland, Iceland, Bear Island, Spitzbergen, Northern Palaearctic, Scandinavia to Siberia, and Australia.

Lepidurus apus (Linn.) has the largest range of any known Notostracan (40, p. 50), having been reported in Europe (excluding Britain), North Africa, Palestine, Asia Minor, Russia, North and South America, New Zealand, and Australia.

Collections of L. apus in North America have been reported from Medicine Hat, Alberta; Winnipeg, Manitoba; and Dufton, Saskatchewan (Johansen, 1921) in Canada, and eight localities in the United States (38, p. 35-38). The first American collection of L. apus was July, 1874, by Coues, a naturalist of the United States Northern Boundary Commission. He described them as occurring "in myriads in several small prairie pools from a hundred yards to a half mile or so wide, exactly on the Boundary line, 49° N., just on the west bank of Frenchman River, Montana." (58, p. 311-312). Packard reported a later collection of L. apus by Carrington who accompanied Hayden's United States Geological Survey (59, p. 318). He recorded "Several females with eggs were also obtained by C. Carrington . . . at Smithfield[6], Cache Valley, Utah. The specimens are in the museum of

[6] This author has good reason to question the accuracy of this reported locality as will be discussed in greater detail later.

Natural Sciences, Philadelphia . . ." (59, p. 318).

Collections in the United States National Museum representing other American localities include Idaho, 25 miles north of Ashton; Max, North Dakota; Davis, California; and Lassen County, California. More recently, Coopey (14) recorded the occurrence of L. lemmoni (syn. apus) in two separate localities in Oregon, i.e. Warner Valley Ponds, Lake County, near Plush in Warner Valley; and a second occurrence in Rocky Point Pond, Klamath County, 15 miles west of Klamath Falls. "Specimen have been found one mile north of Price, Utah in August, 1960, following heavy rains of that month in ponds of water that had been filled from run-off. Deer Season, 1961, specimens were obtained from temporary ponds on Hurricane Mesa, and in the country about ten miles south of Hurricane. I still have some of the specimens and if you are interested, would send them to you."[7] In personal conversation, J.H. Rumely reported a June 23, 1961, collection of "an unusual crustacean in the margin of a shallow stock pond east of Dog-Gun Lake, south of East Glacier, Montana". He and H. Picton found the organism in association with Carex sp., and the specimens were identified by this investigator as L. apus. The most recent record of collection of L. apus was by McCarraher (51) who found them in some prairie pools in Cherry County, Nebraska. This organism has undoubtedly been overlooked in many other temporary lakes and ponds of the Great Basin region of the United States. Its tenure is of short duration during the spring time when many of the lakes in the

[7] Personal correspondence, March 26, 1963, from Dr. Wesley P. Larsen, Associate Professor of Biology, College of Southern Utah, Cedar City, Utah.

higher altitudes are still inaccessible.

HABITAT

Frisch's account and description of his Monoculus apus (1732) has been followed by numerous records concerning the collection of the Notostraca with reference to the environments in which they were collected. Numerous natural historians have advanced a variety of conflicting theories concerning the habitat most favorable for either genus. Brauer (7, p. 588) reported in 1877 that L. apus could not survive water temperatures in excess of 14° C, thus substantiating Schaeffer's earlier designation of Lepidurus as the cold water form. Lundblad (43, p. 54-85) implied that Lepidurus required a pond or ditch which held water all winter, the organism making its appearance in early spring. Barnard's generalization that Lepidurus is found only in ponds which are permanent was disputed by Linder who indicated that he had "observed L. apus in several ponds which dry up every year." (38, p. 32). Wolf (82, p. 135-136) wrote that most investigators agreed on the requirement of a drying period for the eggs of L. apus and since adequate proof to the contrary was lacking, he would concur. He concluded that the respective distributions of Triops and Lepidurus would suggest a desiccation requirement for the eggs of both and a freezing requirement for the eggs of the latter to facilitate the bursting of the resting egg. But again the proof was lacking. Coues' Montana collection was from "prairie pools . . . of extensive, shallow sheets of sweet water with a little open space in the deepest part but mostly choked with luxuriant vegetation."

(58, p. 312). Berg (5, p. 233) failed to specify whether his Lepidurus patagonicus (syn. apus) collected by Illin near the Corcovado River in Patagonia, Argentina, came from a permanent or temporary pool. Coopey (14) recorded the collection of Lepidurus lemmoni (syn. apus) in two "cattle pools a few inches deep" at 4,300 and 4,500 feet in June of 1942 fifteen miles west of Klamath Falls, Oregon, at the base of the Cascade Mountains. His subsequent visit to the same ponds in 1944 found one of these ponds "dry from the previous summer", thus inferring its temporary nature; however, he didn't designate them specifically as temporary.

McCarraher (51) collected L. apus in Big Alkali Lake drainage, Nebraska, in prairie pools "usually temporary". Adult spawning pike entered, resulting in the temporary coexistence of 2.5" to 3.5" pike (Esox lucius) with Lepidurus.

Percival (61) noted the scantiness of relevant data on L. apus in reference to Linder's work North American Notostraca and mentioned a temporary pond on Marley's Hill near Christ Church, New Zealand, which annually dried up, but which supported a thriving population of L. kirkii (syn. apus). He reported that on very rare occasions a few triple-sized specimens were found in some permanent ponds of the same vicinity, but they were without progeny.

Longhurst cited personal correspondence from L. Glauert which included a distribution map of western Australia, showing the distribution of Lepidurus and Triops. Lepidurus appeared to be "restricted to the south-western coastal belt where there is regular winter rain and Triops to the arid interior where rainfall is . . . sparse."

(40, p. 35).

Desportes and Andrieux (17) collected L. apus from five "more or less temporary" ponds near Guilly, France, in 1936. Four of the ponds dried up annually while one fluctuated quite markedly in water level.

Rzóska (66, p. 272) reported some astonishing observations of extreme heat tolerance and rapid maturity of Triops granarius in tropical rain pools near Khartoum, Africa. The eggs from which these specimens were produced were definitely thoroughly desiccated prior to incubation in the intermittent puddles, having been subjected to July and August daytime temperatures of 37°-39° C.

There seems to be an infinity of conditions tolerated by the eggs of the various Phyllopods. Although Hay and Hay (27) hatched Eubranchipus vernalis from mud dried for 5 months, Avery (2) was unsuccessful in his attempts to hatch E. vernalis eggs after 26 days of drying, but the "wet" controls hatched. Castle (10) reported the hatching of a single E. vernalis January, 1938, from water in which gravid adult females had been cultured in March, 1937. This water had not frozen, nor had the water dried up.

Brauer, through experimental breeding of Lepidurus apus, concluded that its eggs were completely incapable of hatching after undergoing desiccation (7, p. 586-587). Barnard suggested the advisability of "confirmation of Brauer's results" and Fox (19, p. 697), by successfully incubating dried eggs in dried mud from New Zealand, confirmed the contrary, disproving Brauer's contention. Longhurst successfully repeated Fox's work (40, p. 36).

Bagatova (3) reported that the eggs of the autumnal generations of

Apus (syn. Triops) do not require drying and suggested the importance of oxygen supply as a factor in determining hatching. McNeill (52) collected Apus (syn. Triops) in central Australia, 800 feet up on Ayer's Rock which rises 1,180 feet above the sandy Spinifex Plains. He indicated that these rain pools certainly evaporate, resulting in a thorough desiccation of the eggs. He listed drying as a requirement for successful hatching.

Fox (19, p. 697) suggested the likelihood of two types of Phyllopod eggs - one type a regular summer hatching egg and one a resting type capable of withstanding extreme desiccation and freezing. As yet there are no reports of any experimental confirmation of this suggestion.

Through extensive experimentation with Chirocephalus diaphanus, a related "fairy shrimp" of the order Anostraca, Hall (24, p. 109) determined that, although the eggs subjected to 7 days of drying before incubation were retarded one day in their rate of development, normal development occurred during the drying treatment. Eggs subjected to somewhat longer periods of desiccation were found to require reduced incubation time before hatching, suggesting continual though retarded development during the dried state. In a later study (26), he concluded that eggs kept at near freezing temperatures developed at one-seventh the rate of those incubated in 15° C water, and water depth was shown to be a determining factor in rate of development, deeper water tending to retard development. The effect of water depth on the eggs of L. apus is not known.

Whitaker (81) subjected Artemia salina to conditions of extreme

cold (-190° C) for 24 hours and high vacuum (approximately 10^{-6} mm. Hg) for 6 months prior to incubation, and neither the rate of development nor the percentage hatching was impaired. Dempster and Hanna (16) obtained successful high percentage hatching of A. salina eggs which had been sealed in ampules under high vacuum for 4 years, while eggs preserved in screw-top jars failed to retain their viability.

Kanwisher (33), working in intertidal environments in the Woods Hole vicinity, observed that in situ temperature measurements ranged as low as -20° C, resulting in as much as 75% of the body water being frozen without deleterious effects on the intertidal organisms. These experiments involved primarily Mytilus, Modiolus, Littorina, and Crassostrea.

Coker and Addlestone (13, p. 71) noted a seasonal variation in the head morphology of the newborn of Daphnia longispina and traced this effect to temperature influences. Brooks (8, p. 446), working with Daphnia retrocurva and D. galeata, concluded that neonatae developing at temperatures below 7° C bear spikes; growth rate being maximal in the 6°-7° C range.

REPRODUCTION

L. apus is known to be bisexual, although there are northern genera in which the males are very rare or unknown (73). Desportes and Andrieux (17) concluded, on the strength of laboratory experimentation with L. apus of Guilly, France, that fertilization was absolutely obligatory since females isolated for 3, 5, and 6 days failed to fill their egg sacks. The same females, however, laid eggs

daily when returned to the presence of males. Chaigneau (11) obtained eggs from 6 of 25 isolated female virgins. He conceded this egg laying to be abnormal, since 5 of the 6 laid only once. In addition, they produced considerably smaller clutches (30-40 eggs less), and the eggs were found to be sterile. He contended, however, that it might also be possible under certain conditions to parthenogenetically induce development of these unfertilized eggs.

Longhurst (42), in the course of a discussion discounting parthenogenesis, indicated that Triops virgins will produce eggs but refuse to lay them unless they are fertilized. He cited deviations from this, however, in the case of isolated hermaphroditic females which did lay viable eggs. He found sperms in the long duct of all mature females.

Reports of male to female ratios of Lepidurus apus have varied drastically, ranging from 7 males in 999, according to Von Siehold, to Jézéquel's 323 males in 386 (73). Wolf (82, p. 138), reported L. lubboki to be completely without males. On the strength of his observations, Longhurst (41) advanced the generalization that Triops shows bisexuality in the South, irregular occurrence of males in mid-latitudes and hermaphroditism in the North. Main (46) maintained that males are more common in Triops than usually reported in the literature as a result of possible difference in mortality of the sexes, but that their life history should be better known in order to be sure. Desportes and Andrieux (17) contended that the method of capture definitely influences the sex ratio obtained. Zograf (83) indicated a tendency toward sex reversal in L. apus, because he found incipient

ovarian tetrads in the testes, but since they aborted, this was discounted by Longhurst (42).

Desportes and Andrieux (17) provided detailed observations and descriptions of copulation, fertilization, and egg-laying phenomena. They determined that eggs pass from the oviducts to the egg sacks invariably within 2 to 3 minutes after mating. Egg laying, then occurs within 6 to 12 hours or less; the female proceeding to deposit a clutch of an average of 70 to 90 eggs 6 to 8 mm. deep in the soft mud. Gaignonnière estimated egg clutches to contain 60 to 70 eggs and observed that they didn't bury the eggs in the mud (62). Longhurst (42) found Triops to extrude eggs immediately before ecdysis, attaching them with a sticky exudate to plants, stones, sand grains, and aquaria walls.

Goldschmidt (22) worked out the cytology of Lepidurus sp.[8], determining from 14 specimens that the haploid chromosome number was six. Moore had much earlier (1893) found Triops cancriformis somatic cells to be amitotic - (2n = 1). Longhurst (40, p. 34) set forth haploid chromosome numbers from testes smears of Triops species as four in all species except T. australiensis which was five. Both Goldschmidt (22) and Longhurst (40, p. 33) lamented the paucity of information concerning reproduction in Lepidurus apus.

Life cycles of Notostraca have been estimated to be varying lengths of time. Rzóska (66, p. 272) reported that Triops attained medium size in 7 days in a tropical rain pool near Khartoum. Wolf (82, p. 139), likewise, observing very rapid growth in L. apus, reported

[8] She speculated that these specimen were L. productus and Longhurst made the identification as L. apus lubbocki.

sexual maturity at 7 days and egg production at 2 weeks when organisms had attained a length of only 1½ cm. Life spans tend to vary in length, dependent upon the prevailing temperatures of the region. Most of the investigators reporting work with any of the Phyllopods, in general, cite high temperature as the lethal factor. These durations have shown a range from 11 days for Triops in temporary rain pools in North Africa (66, p. 272) to 3 months for L. apus near Angers (62). Wolf's (82, p. 138) findings of only one generation per year of L. apus was substantiated by Coopey's conclusion of the improbability of more than one generation per year, based on his Oregon collections (14). Coopey even suggested the necessity of an early development under the ice to accomodate one generation.

PALEONTOLOGY

The geological antiquity of the Notostraca is demonstrated by the discovery of their fossil counterparts in strata as ancient as lower Cambrian. Evolutionary stagnation is confirmed by the high degree of morphological correspondence of these fossils with the present day genera. Protocaris marshi is the oldest known Phyllopod and is found in the Olenellus zone of lower Cambrian (77, p. 574). Burgessa bella is considered by Walcott (76, p. 165) to be the fossil representative of Lepidurus from middle Cambrian. The likeness of the upper Cambrian Hymenocaris vermicaudata (77, p. 726) to present day Notostraca is most compelling! According to Longhurst (40, p. 39), Permian fossils were unmistakably identified as Notostracan carapaces by Guthörl in 1934. Various other forms, indisputably Notostracan, from upper

Triassic were identified by Trusheim (T. cancriformis) and Barnard (L. arcticus).

Bernard (6) and Lankester (35) each did some speculation regarding the relationship of the Phyllopods to simpler groups, viz., Chaetopoda, Limulus, Annelids, and Trilobites. They, however, assuming polar positions, were unable to come to any agreement on this relationship. Longhurst (39) has cited this long fossil record and the Notostracan's current lack of ecological competition as possibly related to the excessively high percentage of abnormalities or variations within the species.

ECOLOGY

Much of the reporting done on the ecology of Phyllopods has been of a "sketchy" nature with a very limited amount of data concerning the physical and chemical conditions which had prevailed in the habitat throughout the entire season. Without a knowledge of the sequence of events leading up to the conditions existing at the time of collection, one can accomplish very little ecologically. Brooks, in his impressive work with seasonal morphological changes in Daphnia galeata (8, p. 414), emphasized the imperative of sequential climatological data, as well as limnological information. Ordinarily the observers collected the organisms, noted sex ratio, recorded a few associated species, made record of the current temperature, then reported these observations as the ecology of the organism of special interest. There was also in evidence a distinct lack of succeeding collections at sufficiently short intervals to complete a history.

Campan (9, p. 96-97) stated that ostracods, copepods, and isopods constituted species associated with L. apus, while carnivorous larval culicides and aquatic coleoptera (Gyrinids, Dytiscids, and Hydrophilids) were predacious associates. McNeill (52) listed Branchinella and Limnadopsis in association with Triops. Packard (58) noted the presence of Lymnetis and luxuriant vegetation including Gramineae and Utricularia with Lepidurus apus. Wolf (82, p. 138) remarked that the cold water form, L. apus, fed on plankton and detritus including cannibalism and usually was succeeded by the warm water fairy shrimp. Rosenberg (63) collected Triops as a pest in rice fields. Bagatova (3, p. 165-176) found Triops a pest in the ponds used for rearing sturgeon. An adult Triops was seen to eat as many as 214 Daphnia or 130 chironomid larvae or even 8 sturgeon fry in a 24 hour period. McCarraher (51) found that predatory young pike, Esox lucius, grew much faster and larger when preying upon L. apus. Runnstrom (64) found L. arcticus in the stomachs of Characidae in lakes of the Scandinavian peninsula. Desportes and Andrieux (17) listed Daphnia and Chirocephalus diaphanus as nourishing cohabitants for L. apus.

In contrast to the foregoing a few more current studies have concentrated more on limnological data, an example of which is Coopey's survey of some ponds in Eastern Oregon (14). Branchinecta coloradensis, Lynceus brachyurus, Caenestheriella setosa, and sagebrush (Artemesia) were observed in association with L. apus in or near one pond by Coopey, while Eubranchipus serratus and Lynceus brachyurus were associates in another. His observations also included limnological data, viz., dissolved oxygen, free carbon dioxide, phenolphthalein

alkalinity in terms of carbonate, methyl orange alkalinity ($CaCo_3$), water temperature, and elevation.

Mattox and Velardo (49) collected reasonably complete limnological data in addition to extensive laboratory experimentation with Caenestheriella gynecia.

The most current ecological study of Notostraca was done by Rzóska (66, p. 265-286) who collected Triops cancriformis and Triops granarius[9] from rain pools of 7 days to 6 weeks duration near Khartoum in North Africa. His work included observations of latitude, climatology, fauna, limnological succession, and biological succession. Species in association with the Triops included Streptocephalus proboscideus, Streptocephalus vitreus, and Branchipus stagnalis of the Anostracans. The Conchostraca included Eocyzicus klunzingeri, Eocyzicus irritans, Leptestheria aegyptiaca, and Limnadia. Moina dubia, Metacyclops minutus, and Metadiaptomus mauretanicus were among the first to develop (within 24 hours of the falling of the rain), preceded only by red ciliates and nematodes. These shallow rain pools showed drastic and immediate limnological responses to the July to September weather, resulting in a wide range of fluctuation in water temperature (24° C - 36.5° C), pH (8.5 - 9.1), alkalinity (21.6 - 62.4), conductivity (140 - 1200 10^6 mho), dissolved oxygen (4.3 - 7.1 or 51% - 99% saturation), and phosphate content (.11 - 2.4). Air temperatures showed a diurnal range of 15° C (25° C - 39° C while

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[9] On at least one occasion, both species were collected in the same puddles by Rzóska. All specimens collected, however, were distinctly T. cancriformis or T. granarius, according to Longhurst's determination, with no intergrades (39).

relative humidity ranged between 30% - 41% midday during this period.

Biological succession proceeded as follows: Infusoria and nematodes, Moina, Metacyclops, Conchostraca, Rotatoria, Triops, Ostracada, and insect larvae; this succession varying only slightly from one pool to another.

It is expected that a study of Lepidurus apus, paralleling this recent work of Rzóska with Triops, will identify some of the ecological differences between the two genera.

METHODS AND MATERIALS

FIELD SURVEY

The initial phase of the project was to survey the Northern Utah area for the presence of the Notostraca, both *Lepidurus* and *Triops*. Maps of the area were obtained from the United States Department of Agriculture Forest Service, and the United States Geological Survey of the Department of the Interior. All ponds, rivers, lakes, and sloughs were noted, and, with the services of the Cache National Forest District Forest Ranger, Mr. Owen De Spain, additional unmapped cattle and sheep ponds in the forested area were added. With the assistance of the Cache County Agricultural agent, Mr. Lamont E. Tueller, additional farm ponds, conservation project ponds, and miscellaneous bodies of water of the agricultural area were added on the maps. The sites surveyed in the spring of 1961 are indicated on the map included in the Appendix.

In an attempt to insure that the survey could be completed during the limited tenure of the life span of the Notostraca, the higher elevations were reserved until last, since Coopey (14) found that life in those ponds at the higher elevations (7,000 feet) tended to be delayed compared to the lower elevations (4,000-5,000 feet) by at least a month or possibly two months. Collection procedure at each site involved numerous dips with a #20 dip net and examination of content. Whether Notostraca were observed or not, the contents of the hauls were preserved in vials with F.A.A. and labeled with the date and site for subsequent laboratory analysis. Allowing that they might

already have completed their brief spring tenancy in the pond, a pond-side mud specimen was taken to be incubated in the laboratory at a later date. Several of the ponds and lakes in the higher elevations were accessible by jeep only part of the way with a one to two mile hike for the remainder of the trip.

The extensive survey, in which the numerous lakes, ponds, rivers, and sloughs of the specified region were visited, disclosed Notostraca in only one lake in the entire region, Dry Lake, Cache Valley, Utah[10], and these were Lepidurus apus. No Triops species were found.

The collected pond-side mud samples experienced seasonal temperatures in the garage through the remainder of the summer and the following fall and winter. During this time they dried and froze as they would have in nature in order that they would be ready for hatching the next spring. The samples were incubated at 20° C in a 1:1 pond water and de-ionized water mixture, according to Longhurst's experimental findings with the incubation of Triops (40, p. 5). He theorized that the low osmotic pressure medium induced speedier hatching. Hall's results (24) with Chirocephalus diaphanus agreed in this respect. In order that these "eggs" might have the same period of rest or development as those in nature, the incubation was begun on May 3, 1962, which would allow an emergence time closely approximating that of

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[10] It was presumed that this lake, Dry Lake, Cache County, Utah, was the same site from which Carrington, according to Packard (58), had collected his L. apus. Packard listed the locality as "Smithfield, Cache Valley, Utah". The site of my collection is 23 miles southwest of Smithfield, Utah. There are 3 towns, all larger and older towns, closer to the lake than Smithfield, but having collected the valley comprehensively for this organism, I have concluded "Smithfield" to be in error.

those in nature.

The samples were placed in clean one-gallon jars contained in a 40 cm deep water bath thermostatically controlled at 20° C. Aeration was supplied individually to each jar through an extensive manifold system (see Figure 1) and the water bath was serviced by an individual heater and a one-quarter ton refrigeration system. Light was supplied from the regular incandescent lights in the laboratory, and no particular care was taken to regulate photoperiodism. Normal daily use of the laboratory and nightly disuse determined the lighting. Moore (54, p. 168) found light to have no appreciable effect upon the culture of Streptocephalus. The pH was maintained from neutral to slightly alkaline by the occasional addition of more water. Water conductivity was ignored, but water depth in the jars was maintained between 15 and 25 cm. at all times.

LIMNOLOGICAL METHODS

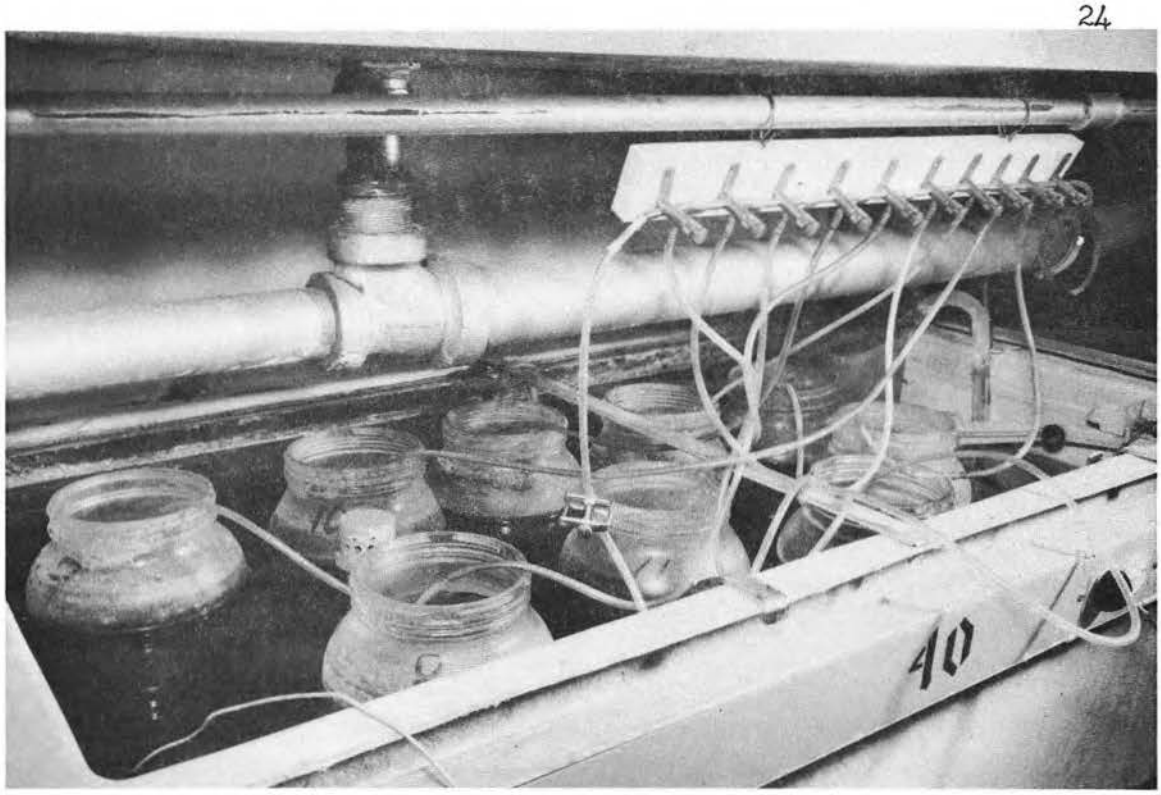
In order to obtain a more complete picture of the ecology of L. apus, visits to Dry Lake were commenced in the summer of 1961 and continued sporadically until April 15, 1962, when regular and frequent visits continued as recorded in Table 2.

Water temperatures were taken with a mercurial Weksler FPT field thermometer in the shade with the bulb submerged to a depth of 1 inch. Air temperatures were taken in the shade with a dry thermometer 3 feet above the ground.

Water samples for dissolved oxygen determination were in 100 ml. glass bottles with glass ground stoppers. Most samples were taken of

Figure 1. Water bath set-up for temperature regulation.

Figure 2. Rack for incubation of vials.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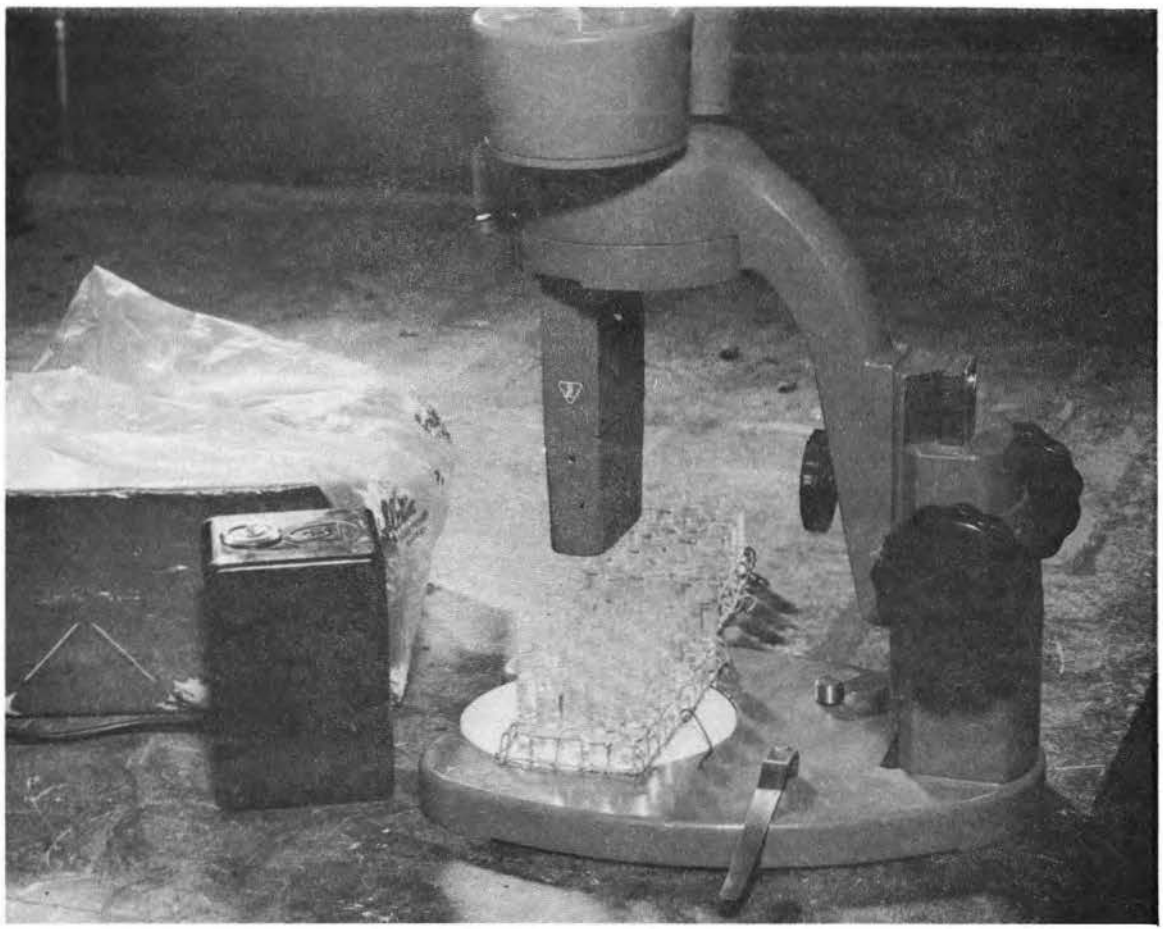

surface water, since the Lepidurus were seen to inhabit water of less than 3 inches in depth. The first three steps of the Winkler method were carried out in the field - addition of manganous sulfate, KOH-KI and sulfuric acid - after which the samples were taken to the laboratory for spectrophotometric analysis for dissolved oxygen with a Beckman spectrophotometer. Since the maximum depth of the lake never exceeded 5 feet and DO samples from various depths of the lake showed no appreciable variation, samples were restricted to the shallow edges of the lake.

The pH was ascertained through the use of an Analytical Measurement pocket hydrogen gas electrode pH meter. Again, the samples collected for testing were taken in very shallow water, usually less than 3 inches in depth. Conductivity was measured by a Solu Bridge conductance meter. Water samples were collected from shallow edges of the lake and held in a glass beaker into which the electrodes were submersed.

Turbidity determinations were made on the basis of measurement of the depth at which a shiny lid from a 3 inch tin can disappeared from view. The lid was lowered, noting the depth at which it disappeared, then raised until it reappeared and adjusted to an intermediate level and its depth measured and recorded. After the death of the Lepidurus, the water cleared to the extent that the lid probably would have been discernible from a much greater depth than 15 inches, but the water was no deeper than 15 inches by this time.

A variety of methods were attempted in an effort to avoid sample bias and to achieve representative sampling of the population for

density determination. Presence of a dense growth of Carex rendered the dip net technique ineffectual. A meter square frame was constructed of aluminum sheets 7 inches wide, forming, in effect, a bottomless and topless aluminum box 7 inches deep. Attempts were made at placing the frame down in random locations and counting the organisms trapped thereby, but the constantly changing bottom topography resulting from the gradually receding water level, as well as the Carex crop, rendered the frame procedure ineffectual. The shallowness of the water and interference of the vegetation precluded the use of bottles or jars. Finally, a count of the organisms visible at the water's edge in a 20 meter distance, during the time required to walk that distance, served as the index to population density. Dip net collections at any depth in excess of 2 to 3 inches showed greatly reduced numbers with negligible numbers of Lepidurus being captured in water deeper than 8 inches.

Representative fauna and flora were collected during each visit and identifications made. A sex ratio was computed for each collection of Lepidurus. Microscopic examination of gut content was made on a catch of 10 Lepidurus preserved in F.A.A. in the field.

EXPERIMENTAL METHODS OF HATCHING

Mere determination of the meteorological and limnological conditions prevalent at the collection site of an organism does not divulge an accurate representation of the requirements for hatching of its eggs. These field data established some broad boundaries within which the organism functions, but in order to ascertain more accurately the

exact limits of temperature and water requirements and the most productive sequence of treatments for the development of the Lepidurus egg, carefully measured and controlled environmental conditions were demanded.

Laboratory Explorations

Approximately 200 pounds of dry, lake-bed soil, presumed to contain Lepidurus eggs, was collected on July 28, 1961, 6 weeks after the water had evaporated. This soil was collected by shovel at random over a broad area of lake-bed and subsequently subjected to one hour's agitation in a one-fourth sack, paddle-type plaster mixer and stored dry at 60°-68° C in the basement. Numerous pilot experiments were carried out in an attempt to find out the most productive combination of temperature, time, and moisture requirements for egg development, most of which produced indefinite and unreliable results. It has since been determined that the area of the lake from which the soil was collected was the deepest portion of the lake, rarely, if at all, visited by the Lepidurus.

Another experiment was designed to determine whether or not the Lepidurus eggs would hatch in the same season in which they were laid. Since it was impossible to discern in situ whether the newly developing Lepidurus were from eggs of the current season or of the year before, they were cultured in the laboratory. In order to ascertain the effect of water temperature on the development of these eggs, 4 one-fourth meter heated and refrigerated aquaria were set up as water baths with an aquarium regulated to each of the following temperatures: 42° F,

68° F, 82° F, and 102° F (see Figure 1). On the premise that the resting eggs were laid in response to the onset of adverse environmental conditions (e.g. excessive temperature), it was postulated that eggs laid by Lepidurus and cultured at 42° F should hatch immediately. Further, those eggs obtained from the 82° and 102° F cultures would be the resistant "over-summering" type requiring a desiccation and freezing treatment, while eggs laid in water at 68° F were unpredictable.

Males and females (some gravid) of mixed sizes were collected May 1, 12, 19, and 20 from 40° to 55° F water and placed in about 50° F pond water in one gallon jars in each temperature bath and observed daily until July 1. Cultures were supplied with detritus and fed cultured infusoria, live Branchinecta, and live Daphnia collected from another reservoir (permanent) 3 miles south of Dry Lake. Longhurst (40, p. 5) had successfully cultured Triops on live Daphnia and Desportes and Andrieux (17) raised Lepidurus apus on Daphnia. Wolf's work (82, p. 140) supported the omnivorous feeding of Branchiopods and suggested the importance of dissolved organic nutrients. The latter was also stressed by Edmondson (18, p. 234). Again lighting was disregarded, cultures receiving only artificial light from the incandescent lamps lighting the laboratory when it was occupied.

The specimens survived for periods of time varying from 3 hours in the 102° F to 2 weeks in the 42° F with no hatching occurring in any, although many eggs were present. The cultures were left intact without hatching for 4 months, until September 28, at which time all the jars were placed into one water bath and kept at 68° F until the

following spring when those in nature hatched. Weaver (78) succeeded in breaking the 6 month resting requirement and hatched Eubranchipus vernalis by drying the eggs.

Since the exploratory incubation experiments with or without drying and/or freezing had yielded no reliable results, a comprehensive pre-treatment and hatching project was designed, utilizing the split-plot approach. This included a much greater variety of combinations of pre-treatment and incubation conditions.

Collection of Eggs

A copious supply (about 10,000) of Lepidurus eggs was collected June 16, 1962, when a knowledge of their laying habits had greatly simplified the collection process. Eggs in two categories were collected with small forceps and stored at room temperature in loosely corked vials. One collection of eggs was obtained by picking the clutches, already dried, from the exposed roots of Carex after the recession of the water. This group was designated "dry". The other group was collected while they were still submerged, never having been exposed to the air, and they were designated "wet". The "wet" eggs had never experienced any temperature below freezing. The "dry" eggs had been exposed in situ to the air during a period in which, on two occasions, 30° and 31° F night temperatures were recorded. Whether or not these eggs actually experienced a sub-freezing temperature is not known, but the negative is assumed.

All eggs were separated individually from the clutch in which they were originally laid and were then mixed well in order to

accomplish homogeneity in the egg stock. Some of the stock of eggs were observed to possess a secondary "shell" composed of a mixture of algal and fecal detritus while others were a brilliant orange color, devoid of such covering. Hall (26) found the presence or absence of this "shell" to be of no consequence whatsoever in the experimental hatching of Chirocephalus diaphanus.

Drying

In accordance with the sequence of events as they occur in nature, the eggs were first subjected to drying. Mathias (47, p. 63), in describing the conditions necessary to break the diapause of the resistant eggs of Eubranchipus stagnalis, recorded a requirement of 7 days drying at 17° C, or 4 days at 27° C, 2-3 days at 33° C, and only 1 day at 39° C. Weaver's work (78) confirmed this drying requirement. Hall (23), from one investigation, claimed that a drying period for Chirocephalus diaphanus eggs was unnecessary, but later recanted, asserting the necessity of a desiccation treatment.

Three thousand "wet" eggs were counted out on filter papers in Petri dishes, 600 per dish by actual count. Since the eggs are quite small, 0.35 mm. in diameter when wet, counting was accomplished by the use of a transparent plastic tube with a pipette attached. Eggs were drawn into the tube and counted with the aid of a binocular dissecting microscope. Excess water was pipetted from the filter papers and each Petri dish containing 600 eggs was placed in a different temperature chamber, July 6, 1962, for drying for 48 hours. Petri dish #1 was placed in a refrigerator at 6° C, #2 in a B.O.D. incubator at 18° C,

#3 in a B.O.D. incubator at 26° C, #4 in a thermostatically regulated Fischer oven at 45° C, and #5 Petri dish in a Cenco oven with the temperature ranging between 60°-70° C. The 6° C fraction did not dry at all. The other eggs, after drying were considerably reduced in size (0.2 mm. in diameter) and were counted dry with the aid of a camel's hair brush (1 hair) and a binocular dissecting microscope. Each egg, after drying, in addition to the observed shrinkage, was noted to have assumed a dark red color and to have a concavity on one side.

Freezing

Following this drying treatment, each of these five batches of eggs was fractionated by counting out 100 eggs into each of six 2-dram vials in preparation for six different cold treatments which were administered as described below.

One vial containing 100 eggs was taken from each of the five drying treatments, and these five vials then comprised an assortment of 500 eggs. Six such assortments were assembled, one of which was placed in a refrigerator at 5° C for 72 hours, and a second assortment was subjected to -2° C for 72 hours.

Rapid Cooling

Whitaker (81) subjected *Artemia* eggs to -190° C for periods of 7 and 24 hours with a very rapid rate of temperature change and noticed no impairment in percentage nor rate of excystment. Weaver (78) obtained hatching of *Eubranchipus vernalis* after quick freeze of eggs with dry ice and quick thaw at room temperature.

It is known (Table 1) that the eggs which provided the 1962 Dry Lake population had experienced a winter macrotemperature of -33° F. The actual microtemperature tolerated is not known, but in order to determine the range of tolerance, cooling to -80° C was provided in this laboratory experiment. Taylor's (70, p. 575) work with cell suspensions of chick embryo skin and human conjunctiva showed that the cooling rate down to -20° C was a highly critical factor in cell survival. His greatest percentage of survival was obtained in those cultures cooled in accordance with Figure 3 below.

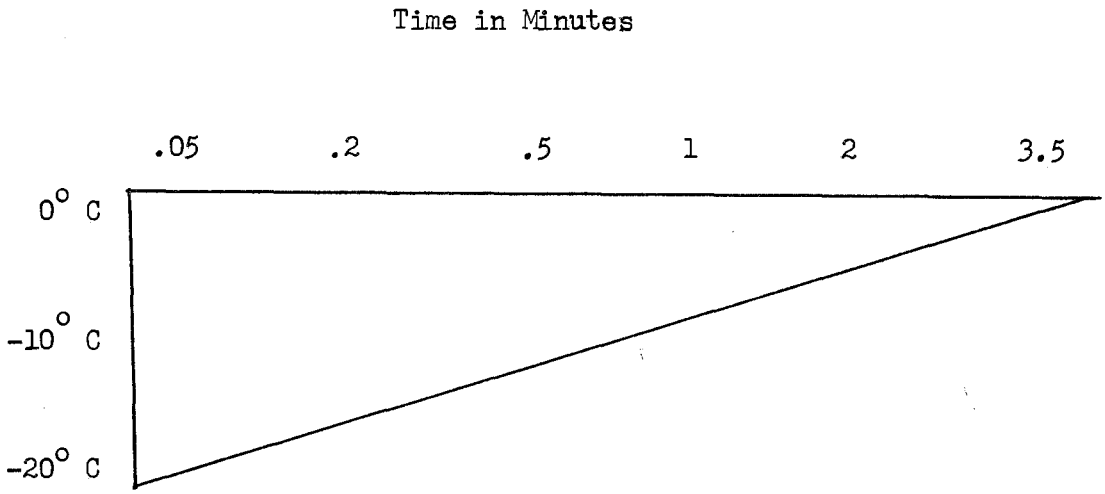

Figure 3. Detention time advocated for cooling live tissue. (After Taylor, 70, p. 575).

Luyet (44, p. 549) emphasized the importance of the cooling rate, stating that if crystallization can be supplanted by vitrification in cooling and warming, physical rupture can be avoided. The rate of cooling, as well as the temperature range, were controlled for the remaining four assortments of Lepidurus eggs.

Assortment #3 was plunged instantaneously from room temperature to a -20° C. Mazur (50, p. 610) established an arbitrary designation of "slow" cooling if the rate is less than 1° C per minute, and "rapid" cooling if the rate is greater than 300° C per minute. Although the microtemperature of the eggs was not known, the method of cooling provided reasonable assurance that the rate of cooling was "rapid". Since Meryman (53) found a 5% to 15% glycerine additive to preclude physical rupture in tissue culture of mammalian cells, the dried eggs were coated with a 5% glycerine and de-ionized water solution, after which they were hermetically heat-sealed, in one-quarter dram shell glass ampules and immersed quickly in a bath of dry ice and alcohol which had been stabilized at -20° C. They were then kept in a freezer at -20° C for 3 hours, after which the ampules were removed from the bath and warmed rapidly by immersion of the vials in a 40° C running water bath.

The 100 eggs in each vial of assortment #4 were transferred from their respective vials into five corresponding glass coverslip, sandwich cells containing a 5% glycerine solution. Each of the cells was constructed of a plastic ring 15 mm. in diameter and 1 mm. in thickness cemented to a glass coverslip. Eggs were added, and the top coverslip was cemented on. The five cells were then placed simultaneously on a block of dry ice and the second block of dry ice immediately placed on top, thus forming a dry ice sandwich with the cells (containing eggs) in between. These eggs were left at -78° C for 3 hours, after which the cells were removed and immediately warmed in 40° C water. They were then held at room temperature, having thus

accomplished rapid cooling and rapid warming.

Slow Cooling

The eggs in the five vials of assortment #5 were not coated with the 5% glycerine solution, but were placed in a -20° C refrigerator in an insulation of dry plastic bags which succeeded in retarding the cooling rate. They, likewise, experienced a 3 hour cold period and were subsequently allowed to air-cool at room temperature, thus accomplishing slow cooling and slow warming pre-treatment.

Assortment #6 was given the slow cooling treatment to -80° C and similarly warmed slowly to room temperature after 3 hours detention at the -80° C temperature. The eggs in these five vials were first coated with the 5% glycerine solution then heat-sealed (hermetically) in 5 one-fourth dram shell glass ampules. Slow cooling was accomplished by immersing the sealed vials in a 1,000 ml. beaker containing alcohol at room temperature. The beaker was very effectively insulated with a medium-expanded Styrene shipping and storage box. Crushed dry-ice and alcohol were poured gradually into the beaker at a controlled rate. After rapidly cooling the mixture to 0° C, the rate of cooling was carefully maintained at 1° C per minute to -20° C. At this point, by increasing the rate of addition of coolant mixture, the rate of cooling was increased to 2° C per minute until a -40° C temperature was achieved. A 3° C per minute cooling rate was observed between -40° C and -60° C, and a 6° C per minute rate on down to -80° C. This minimum temperature was maintained for 3 hours, after which the dry-ice was strained out, the alcohol allowed to warm, the ampules removed, and

air warmed to room temperature.

All six of the above described cold treatments were done on August 5, 1962, 30 days after the drying treatments. In this intervening time (30 days), all eggs were stored in lightly corked vials in the basement where the temperature ranged between 60° F and 68° F.

Incubation

Upon completion of the various cold treatments, the batches were again split into fractions which were each divided and incubated in pond water at four different temperatures ranging between -2° C and 40° C. Thus 120 different combinations of pre-treatment and incubation temperature were produced. Four $\frac{1}{4}$-inch mesh, hardware-cloth racks were fashioned (see Figure 2) like small test-tube racks, each to hold 30 one-quarter dram shell, short-form glass vials. Each hardware-cloth rack had 5 rows (A, B, C, D, and E) of vials, 6 vials per row, 25 eggs per vial (see Figure 7). All the 6 vials in row A contained eggs which had experienced 70° C drying, but the 25 eggs in vial #1, row A, had undergone a 5° C cold treatment; eggs in vial #2 had experienced a -2° C cold treatment; vial #3, -20° C (rapid cooling and rapid warming); vial #4, -80° C (rapid); vial #5, -20° C (slow cooling and warming); and vial #6, -80° C (slow).

All the 6 vials in row B contained eggs which had experienced a 45° C drying heat, but vial #1 had (as in row A) undergone 5° C cold treatment, vial #2, a -2° C cold and etc. Summarily, it could be stated that each row A, B, C, D, and E (vertical rows) represented a different drying temperature while each row 1, 2, 3, 4, 5, and 6

(horizontal rows) represented a different cold treatment.

The 40° C incubation temperature was provided by a thermostatically controlled Fischer oven, while the remaining three incubation temperatures were provided by thermostatically controlled, refrigerated chambers. Each rack of 30 vials was enclosed in a plastic bag, as a humidity chamber, for reduction of evaporation (see Figure 2). De-ionized water was added periodically to the humidity chamber, and it was necessary to make occasional additions of pond water to the vials containing the eggs in order to maintain a water depth between 20-25 mm.

Incubation was commenced on August 5, 1962, and daily observations were made for 6 weeks; twice weekly observations continued until 4 months had passed. At this time the visits were increased to every 48 hours. Careful scrutiny of each of the 130 vials was expeditiously accomplished by placing the vial racks (see Figure 2) on the stage of the binocular microscope and viewing the content of each vial without removal of the vial from its 30 vial rack.

Anticipating that the 10° C and 25° C incubation temperatures would be the most favorable, and likewise expecting that the 18° C would be the most favorable drying temperature, those fractions were split further on September 15. Twelve of the 25 eggs representing each cold treatment were incubated in 50% de-ionized water, with the expectation that these eggs should hatch first. Longhurst (38, p. 5) found that a low osmotic pressure medium effectively reduced incubation time of Triops. All other eggs were incubated in water obtained from the original habitat, Dry Lake. (See Figure 8 for time table of

treatments).

After 186 days of incubation at these various temperatures, all of the eggs were returned to a -2° C temperature chamber on February 16, 1963, and detained for 15 days. On March 3 they were replaced into their respective incubators at temperatures of -2°, 10°, 25°, and 40° C.

LABORATORY EXPERIMENT ON DURATION OF COLD

Both wet and dried eggs were taken from the stock collected from Dry Lake on August 18, 1962, which had been stored in the basement in lightly stoppered vials. On December 22, 1962, about 2,000 of these dry eggs and 2,000 wet eggs (group C) were placed in a -2° C refrigerator. One thousand of the dry eggs were left dry (group A) in the cold, while 1,000 were wetted (group B) at the time of introduction into the cold. After 96 hours of cold treatment, 40 eggs were withdrawn at 48 hour intervals from each group and transferred into pond water, each "40" being then incubated 10 eggs per vial at four different temperatures, viz. 5° C, 10° C, 20° C and 40° C. (See Figure 9). This treatment would show how much cold was required to scarify the eggs, as well as the time required for subsequent development and hatching of the eggs at the various temperatures.

Cooling was accomplished in unstoppered 2-dram vials and eggs were pipetted and counted as before into ¼-dram shell, short-form vials. The vials were again supported by ¼-inch hardware-cloth racks which were enclosed in plastic bags to reduce evaporation during incubation (see Figure 2).

After 12 days of transferring the eggs from the cold to the incubation chamber at 48 hour intervals (7 transfers), the transfer intervals were increased to 72 hours. Transfers at the 72 hour interval were continued for 24 days (8 transfers), well after hatching had commenced in earlier incubations, followed then by 3 transfers at 24 hour intervals. Incubations occurred in complete darkness, the eggs being exposed to light only during the transfer time.

OBSERVATIONS AND RESULTS OF EXPERIMENTATION

RESULTS OF FIELD SURVEY

The extensive survey in which the numerous lakes, ponds, rivers, and sloughs of the specified region were visited, disclosed Notostraca in only one lake in the entire region, Dry Lake, Cache Valley, Utah, and these were *Lepidurus apus*. No *Triops* species were found.

Daily observations of the incubated pond-side mud samples for the first three weeks showed no positive results until in the twenty-second day 2 small *Lepidurus* 0.4 cm. in length were observed in the sample from Dry Lake. In the remainder of the samples only algae and a succession of protozoa, rotifers, and snails were observed.

Since Notostraca were produced from the Dry Lake sample only, this negative laboratory result was considered to confirm the negative field results, concerning all bodies of water within the collected region, except Dry Lake. It must not be assumed that these other bodies never have contained Notostraca, nor should it be presumed that they will not in the future support them. One can only infer that if these waters contained Notostraca in the spring of 1961, they were in such small numbers that they both eluded capture and failed to produce a volume of eggs insuring collection in the random pond-side mud collections that were made. One could conclude the absence of the organisms with greater certainty if more frequent visits were made to each body of water during the spring for several years.

Dry Lake

Dry Lake, the only body of water in the collected region which produced Lepidurus, is an ephemeral round lake, 0.5 miles in diameter, 15.7 miles southwest of Logan, Utah, bisected by Highway 89-91. In the southern end of the Wellsville Range of the Wasatch Mountains, it lies intermediate between Cache Valley and Salt Lake Valley - 111° 58' west longitude and 41° 35' north latitude - in North Central Utah[11]. Lake Bonneville, a Quaternary lake of 19,500 square miles formerly occupied the entire region, the Wellsville mountain range being a peninsula and Cache Valley an embayment. The Dry Lake basin, a solution basin, was above the water level of Bonneville Lake and may or may not have been a small contemporary lake. Dry Lake basin sediments are immediately underlain with and surrounded by the Braser black shales and black phosphatic shales of the Upper Mississippian. Extensive convergent faulting (21, p. 13) in the immediate vicinity of the present lake initiated the gradual solution of the limestone sediment. This accounts for the depression which has subsequently become partially filled with a heavy black alluvial clay loam (57).

Currently, the elevation of the basin, mid-lake, is 5,638 feet, while the adjacent Cache Valley floor averages 4,500 feet. Mountain ridges surrounding the basin range from 7,900 feet on the west through 7,200 feet on the south and east and down to 6,500 feet on

[11] Information concerning location and elevations was taken from the Mt. Pisgah, Utah, quadrangle, topographic map, number 4130 - W 1115230/7.5 published by the United States Department of the Interior, Geological Survey, cooperating with the United States Department of the Army Corps of Engineers.

the north (see Figure 4). In addition to the rain, snow melt and drainage from the surrounding mountain sides, the lake is fed by numerous small springs. The lowest passes leading out of the basin are 5,720 feet on the north and 5,880 feet on the south, the only outlets being evaporation and one sink hole on the east border of the lake.

The area has an average annual rainfall of 18 inches per year with a winter and spring maximum, the majority of which falls as snow. This provides standing water in the basin from the time of the fall rains and snows throughout the winter and usually through July. An invigorating climate, characteristic of a mountain basin, prevails in this region with mean temperatures of 32.7 and 43.9° F in the spring and fall respectively. Winters are cold, with an average temperature of 19.6° F. Nighttime temperatures may dip below freezing any night of every month of the year. Daytime temperatures have never exceeded 96° F and the lowest recorded is -33° F, thus giving a range of 126° F[12]. The highest 1961 summer temperature in the vicinity was 96° F on August 8 (71) and the lowest winter temperature was -33° F, January 22, 1962 (72). Prevailing winds of the basin are from the west and southwest and commence around noon daily during the spring and early summer, but rarely exceed 20 miles per hour.

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[12] The climatological data used here were recorded at Hardware Ranch, a United States weather station of the same latitude, 41° 36' north and only 23' east of the Dry Lake area. The elevation, 5,580, is only 200 feet higher and the mountainous surroundings show a high degree of similarity. Observed temperatures of the Dry Lake vicinity, when compared with the Hardware Ranch Weather Station temperatures of the same dates show no more than 2°-4° variation. The length of the record is 7 years.

Figure 4. Aerial view of Dry Lake.
Viewer faces west. Salt Lake Valley is seen in the background, west of the Wellsville Mountains.

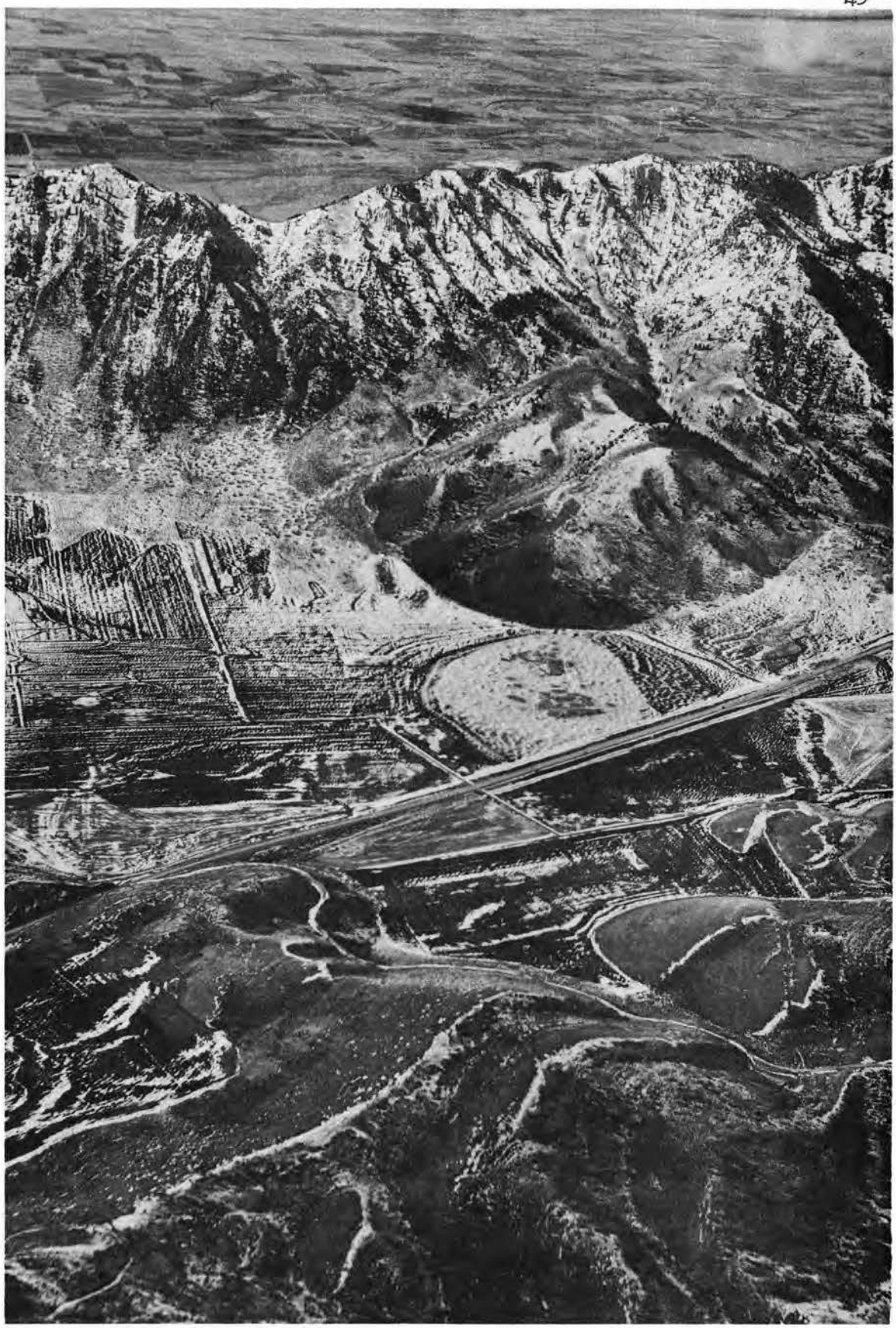

Table 1.. TEMPERATURE AND PRECIPITATION DATA FOR DRY LAKE AREA JUNE 1961 - JULY 1962[b]

Month		Total Precip	Day of the Month 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	Aver
Jun	Max		78	70	65	65	68			83	85	85	83	72	72	77	78	83	85	89	87	88	90	91	88	89	88	90	87	89	89	81		82.0
	Min		31	30	32	37	40			35	51	35	36	42	32	30	45	35	35	36	37	36	34	33	36	40	35	35	50	40	41	32		36.8
	H_2O	1.0		.1	.1	.2	.5																	T									
Jul	Max		82	89	87	72	83	88	88	89	90	89	84	83	86	85	88	92	93	87	86	87	89	87	90	89	91	89	88	90	91	89	89	87.4
	Min		34	30	36	36	37	42	44	37	31	36	34	36	33	44	37	41	41	37	37	47	47	35	40	49	59	46	55	43	44	48	46	40.7
	H_2O	-				.1																							-				.2	
Aug	Max		89	90	91	93	96	94	83	83	85	87	89	81	77	84	85	78	84	90	93	82	85	89	88	80	78	79	85	87	85	77		85.6
	Min		42	49	43	41	48	48	48	46	44	43	47	55	47	40	40	53	38	38	39	52	43	38	37	55	49	45	40	46				44.8
	H_2O	2.7					.5		.1					.4	.3			.4				.1				.1	.2	.6		T				
Sep	Max		76	75	64	72	77	80	81	78	70	71	75	65	70	78	79	78	75	60	56	57	48	50	54	56	60	64	69	70	51	60		67.3
	Min		51	38	23	24	26	30	29	29	45	38	39	32	22	21	33	35	40	40	40	39	33	35	24	26	22	27	19	35	32	30		31.9
	H_2O	1.9								T		.1		.1			T		T	.7	.5	.3	.1		.1						T			
Oct	Max		70	61	70	74	73	69	61	49	49	53	59	60	67	75	74	74	70	64	71	72		61	41	46	57	61	51	44	37	42	55	60.3
	Min		38	15	15	18	19	25	32	32	34	33	27	38	32	28	27	26	27	19	18	29		27	11	31	15	23	34	26	14	14	18	24.8
	H_2O	1.2							T			.1		T										.3					.1	.5	.1			
Nov	Max		44	40	39	46	42	45	51	56	56	58	52	39	42	45	38	37	32	37	41	37	38	40	55	50	48	45	51	49	51	49		45.1
	Min		27	10	9	15	9	10	12	15	17	18	24	21	10	14	24	20	15	4	4	22	19	5	17	16	24	32	31	17	16	30		16.9
	H_2O	.8	T	a	a	.1												T	T			.1	a	.3				.3						
Dec	Max		47	42	41	40	42	39	30	31	18	17	12	24	31	28	36	33	33	34	39	50	47	37	35	42	44	35	20	34	43	43	35	34.9
	Min		24	25	31	15	12	24	3	9	-4	-2	-2	1	15	8	16	9	20	21	16	32	25	7	3	6	14	6	-12	14	29	20	1	11.9
	H_2O	2.0	a	.1	.7					.2									.2		.1		.6				.1			.1				

T Trace, an amount too small to measure.
a Amount included in following measure, time distribution unknown.
- No record reported

Table 1. (Cont'd) TEMPERATURE AND PRECIPITATION DATA FOR DRY LAKE AREA JUNE 1961 - JULY 1962[b]

Month		Total Precip	Day of the Month																													Aver
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
Jan	Max		35	39	36	38	37	37	45	47	34	17	29	36	25	24	30	32	36	30	28	39	25	12	19	24	32	35	43	39	38	43	41	33.1
	Min		1	3	2	8	3	20	32	34	2	-9	-4	6	15	-10	7	-10	-5	6	16	18	-5	-33	-27	-18	-8	8	9	0	-5	0	-1	1.8
	H_2O	1.5						.2	.2	.1					.1					.1	.2	.6												
Feb	Max		41	44	46	50	50	47	47	46	45	45	54	42	47	49	44	42	39	40	37	36	34	39	36	32	31	16	17	25				40.0
	Min		-1	2	4	11	9	6	29	26	32	35	35	34	23	33	22	31	14	20	0	16	24	17	20	2	-3	6	-24	-19				14.4
	H_2O	3.1									.2	.2	.2	.4	.1	.1	.1	M	T	T		T	.1		.3									
Mar	Max		38	37	34	46	42	49	42	44	42	40	33	34	34	36	40	40	45	46	47	46	39	46	37	42	51	58	57	56	41	46	50	43.2
	Min		17	24	9	17	0	10	24	26	24	20	5	2	-11	-10	-6	-3	14	13	9	10	27	13	18	4	24	18	21	29	13	14	16	12.6
	H_2O	2.2		.2	.3			.1	.4	.1		.2											.4		.7								
Apr	Max		56	59	61	56	51	55	52	42	44	49	54	62	68	74	73	72	74	76	78	73	47	62	69	72	68	56	62	62	41	49		60.6
	Min		21	23	25	30	26	21	41	38	39	38	23	22	24	26	26	25	26	27	32	28	31	25	26	29	32	35	24	24	19	16		26.4
	H_2O	2.3					.1		.1		T											.1	M					.1		.7				
May	Max		62	65	70	71	72	76		77	73	73	67	70	57	55	52	59	51	63	71	70	51	56	65	60	55	61	57	55	60	69	67	63.7
	Min		20	19	34	37	33	34		35	37	30	40	29	37	31	30	30	35	28	31	32	31	38	27	40	35	34	40	32	35	31	40	32.8
	H_2O	2.7													.1	.1	.1	.1	.3			.1	.8	T		.1	.5	.1	.3	.1	.1			
Jun	Max		70	70	71	53	60	59	58	66	73	80	80	79	79	78	66	64	70	78	82	77	80	79	84	85	88	89	85	86	82	82		75.1
	Min		33	32	31	33	33	32	27	26	30	33	35	37	33	29	40	29	29	33	35	47	37	41	43	39	37	35	34	37	38	45		34.8
	H_2O	1.2				.6		.3	T							.1						.1												
Jul	Max		83	80	79	77	85	85	84	88	89	86	89	85	66	70	77	81	83	84	85	86	89	82	80	85	82	82	77	80	83	84	80	82.1
	Min		41	32	37	33	30	36	36	36	34	37	34	32	48	39	33	34	36	35	31	32	32	46	55	44	37	40	39	34	35	36	45	37.1
	H_2O	.9												T	.8	T																.1	

[b] For the source of these data see Bibliographic entry 71 and 72.

The mountains surrounding the lake are treeless except for small groves of stunted Acer pseudoplatanus, A. Negundo (Box Elder), Quercus Gamelii, Fraxinus sp., and Robinia sp. Celtis reticulata occupies the deep recesses and the well-protected northern slopes. The mountain slopes facing the small lake basin are covered with a thin mantle of soil and support a meager growth of Juniperous utahensis above which Juniperous scopulorum (see Figures 5 and 6) is found with some Pinus flexilis on the higher slopes (57).

The dominant plant residents of the lake itself include Carex sp., Polygonum sp., Alisma sp., Nitella sp., Typha latifolia, and Potamogeton sp. Carex is the dominant plant and occupies the entire inundated portion of the basin. It is harvested as a sedge hay in stages as the water recedes. Typha is restricted to several small areas spotted about the lake (see Figure 4).

LIMNOLOGICAL SURVEY OF DRY LAKE

The lake had dried up by June 14, 1961, and remained dry, exclusive of occasional dampening by intermittent rains, until December 19, when an unseasonal quick thaw occurred in the surrounding snow-covered mountain slopes, producing a lake over frozen ground. Subsequent subzero temperatures froze the lake for the winter. The final visit before the spring thaw was on April 15, 1962, at which time the ice was still 2 inches thick. By the next observation, May 1, Branchinecta shantzi was much in evidence and the females were trailing long, well-filled egg sacks. The neonatae Lepidurus were not nearly so numerous and were less than 2 mm. in length.

Figure 5. Dry Lake and sparsely wooded east slopes.

Figure 6. Dry Lake and gentle rolling east and north facing slopes.

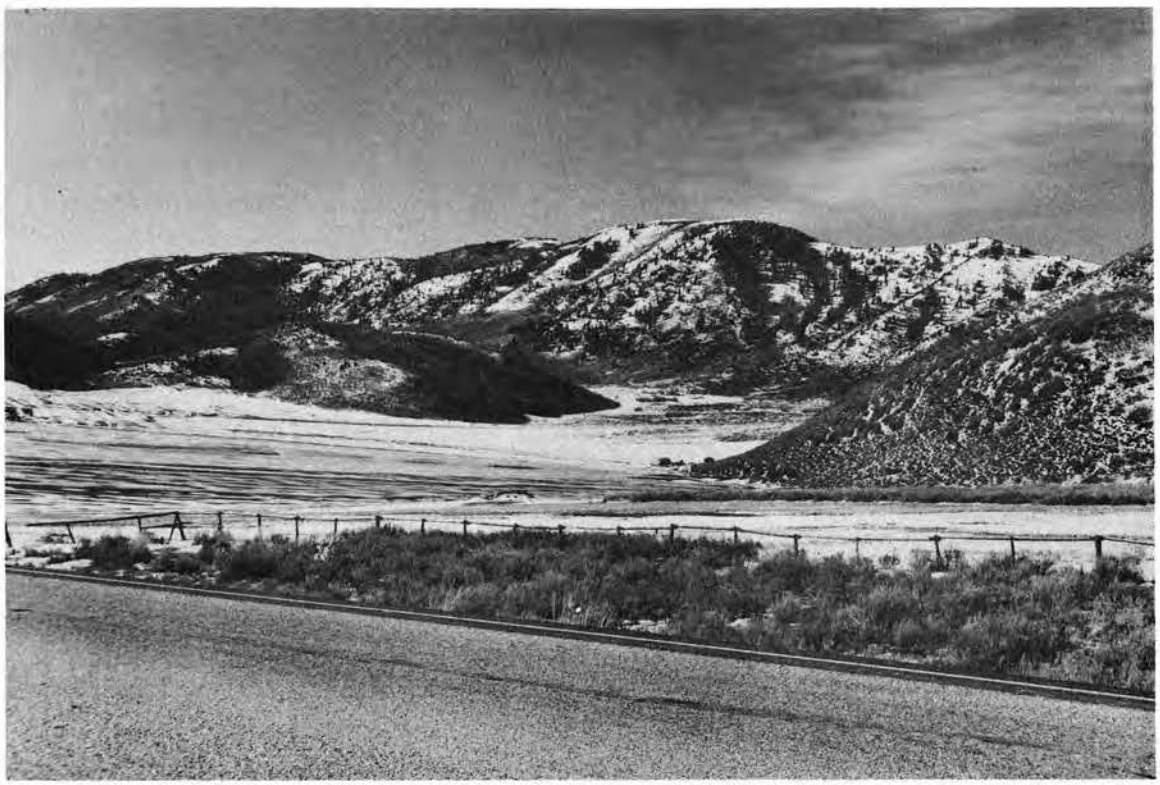

Table 2 contains a tabulated summary of the limnological data collected prior to, during, and just after the tenure of Lepidurus apus in Dry Lake. These data would be more valuable had they included chemical conditions during the earliest development of the faunal inhabitants. Greater consistency in the time of day of sampling would have reduced the amount of interpolation required to complete the limnological picture.

Table 2. Limnological Succession in Dry Lake, Spring, 1962

Date	Location	Depth	Time	Temperature Air °F	Air °C	Water °F	Water °C	Dissolved oxygen p pm	Dissolved oxygen cc/l	Dissolved oxygen % sat	pH	Cond	Turb	Pop/20 m
4-15-62			Frozen over											
5- 1-62	W	4"	12:00M	68	20	46	8							
5-12-62	W	4"	10:00AM	62	17	54	12							
5-19-62	W	4"	10:00AM	68	20	50	10							
5-20-62	W	4"	10:00AM	60	15.5	54	12							
5-30-62	W	3"	10:00AM	64	18	58	14	4.8	3.6	66			1"	60
5-30-62	W	3"	12:00M	70	21	74	24	9.1	6.3	110				38
6-10-62	W	S	4:00PM	75	24	82	28	3.7	2.5	49	7.6	2800	1"	21
6-12-62	W	S	4:00PM	80	27	85	29	8.3	5.8	105	7.6	3350	1.5"	12
6-14-62	W	S	4:00PM	76	24	85	29	8.65	6.0	110	7.6	2800	1.5"	14
6-16-62	W	S	3:00PM	63	17	80	27	10.7	7.5	132	8.8	2200	3"	9
6-21-62	W	S	5:00PM	68	20	84	29	13.4	7.8	155	8.8	2600	5"	6
6-22-62	EC	S	4:00PM	80	27	88	31				8.0	3400	8"	3
6-24-62	EC	S	4:00PM	88	31	92	33	9.7	6.7	135	8.0	3000	12"	1
6-29-62	EC	S	10:00AM	70	21	65	18	10.7	7.5	110	8.3	3100	15"	0
6-16-62	W	S	7:00AM	52	11	52	11						3"	
	E	S	8:00AM	54	12	52	11	9.3	6.5	83	9.2	1100	3"	
	E	S	9:00AM	60	16	60	16	9.7	6.8	97	7.4	1200	3"	
	E	S	10:00AM	62	17	64	18				7.0	1500	3"	
	E	S	11:00AM	68	20	70	21	9.3	6.5	105	8.0	1610	3"	
	E	S	12:00M	76	24	76	24				8.4	1800	3"	
	E	S	1:00PM	84	29	78	26	8.7	5.1	105	8.6	2000	3"	
	E	S	2:00PM	62	17	80	27						3"	
	E	S	3:00PM	63	17	80	27	5.4	3.9	70	8.8	2400	3"	9
	E	S	4:00PM	65	18	82	28						3"	

The collection data throughout one day was made in order to provide a more complete representation of succession throughout the day. (See Table 2).

The sex ratios observed in this population of L. apus are tabulated in Table 3 below.

Table 3. Sex Ratio of Lepidurus apus

Date	Males	Females	% Males	% Females	Total
5 - 19 - 62	18	5	78	22	23
6 - 12 - 62	26	44	37	63	70
6 - 14 - 62	42	44	49	51	86
6 - 16 - 62	43	71	38	62	114
6 - 21 - 62	34	38	47	53	72
Totals	163	202	45%	55%	365

No extensive collections were made to determine the beginning dates of the development of the various species of associated animals, but the following comprehensive list[13] included all species encountered in all the collections[14].

Coelenterata	-	Hydra utahensis
Bryozoa	-	Plumatella sp.
Annelida	-	Tubifex tubifex
	-	Hirudineans
Copepoda	-	Diaptomus shoshone

[13] Stanford, J.S., "An Ephemeral Lake", an unpublished paper delivered at the annual meeting of the Utah Academy of Science, Arts, and Letters, Utah State University, Logan, Utah, Spring, 1962.

[14] The most capable and willing assistance of Dr. J.S. Stanford, Prof. Emeritus of Zoology, Utah State University, Logan, Utah, in the identification of the above is gratefully acknowledged.

	-	Cyclops sp.
Eubranchiopoda	-	Branchinecta shantzi
Cladocera	-	Daphnia sp.
Ostracoda	-	Cypridopsis sp.
Hydracarina	-	Hydrachna sp.
Insecta	-	Aedes sp.
	-	Anax junius
	-	Callibaetis sp.
	-	Chironomus sp.
	-	Corixa sp.
	-	Dytiscus sp.
	-	Enallagma sp.
	-	Gerris sp.
	-	Hydrophilus triangularis
	-	Lestes uncatus
	-	Limnophila sp.
	-	Notonecta sp.
Gastropoda	-	Heliosoma sp.
	-	Lymnaea sp.
	-	Physa sp.
Polecypoda	-	Sphaerium sp.

The gut content of the L. apus was most difficult to identify and appeared to be composed primarily of detritus; however, legs of Branchinecta were distinguishable, as were some unidentifiable filamentous green algae.

Incidental Field Observations

Some interesting field observations on the behavior of the Lepidurus were made which might be of adaptive significance. While the Branchinecta were seen to expell their eggs at large, Lepidurus extruded its clutch, attaching them in discrete masses with a sticky exudate to the exposed roots of Carex. As the water level receded, reducing the depth of water above these roots, the gravid females sought out roots or dead stems near the shallow water's edge for attachment of their eggs. If Lepidurus should have two types of eggs, a summer hatching and a resting egg as suggested for Triops by Mathias

(47, p. 61), this might be ascertained through a comparison of the incubation results of the early eggs (those occurring high on the bank) and the late eggs (the lowest on the bank). This is not known. One might speculate that summer eggs are laid on the muddy bottom, while resting eggs are attached to roots at the shallow edge.

If the height of the "water column" above the egg (water depth) is critical for development of Lepidurus, as was found by Hall (26) with Chirocephalus diaphanus, then this practice of attaching eggs to fixed objects at the water's receding edge may have significance. When the lake is refilled during the succeeding season, the resting eggs, being attached at graduated levels on the graded bottom, will therefore be simultaneously subjected to a succession of graduated depths of water. Consequently not all the resting eggs would hatch at once, but hatching would occur serially as the lowering water level approached the threshold depth conducive to development. This was proposed by Simon in 1886 and cited by Desportes (17, p. 61). Hall (26) found that a 20 cm. water depth completely arrested egg development of Chirocephalus, while depths of 5 cm. to 15 cm. caused retardation directly proportional to water depth, 0.5 cm. being optimal depth. This requirement has not been worked out for Lepidurus.

Field collections of the clutches of Lepidurus apus eggs in Dry Lake disclosed a mean count of 41 eggs per clutch from 56 clutches counted. These eggs were collected dry after the water level had dropped exposing them to the air. This number is drastically below those numbers quoted for Triops by other investigators. Wolf (82, p. 139) advanced the number 300-400 for Triops; Bagatova (3), also for

Triops, recorded 590 eggs per laying (every third day). Researchers working with Lepidurus apus have counted smaller clutches, however, still considerably greater than the Dry Lake specimens. Desportes and Andrieux (17) reported 180 to be a large clutch with 70-90 eggs being average. Mathias (47, p. 57) quoted Gaignonnière's estimate of Lepidurus apus clutches to be 60-70. No particular significance should be attached to the fact that the clutches ranged between 12 and 69 eggs each, since there was no way of distinguishing between clutches of the very young and those of the most mature. Age of the female is a factor determining clutch size (17), the younger producing smaller clutches.

It is entirely possible that these clutches collected in Dry Lake might have contained more eggs originally with some eggs becoming dislodged from the initial mass through drying. Enumeration of eggs per clutch, while they are still in the egg sacks or after being laid but prior to undergoing drying, might possibly yield a more representative count.

Sex ratio of 45:55, males to females, observed in the Dry Lake population of Lepidurus (Table 3) was well within the expected range for this latitude as inferred from ratios derived by other investigators, viz., Desportes and Andrieux (17), Vandel (73) and Lubbock (1864), according to Desportes and Andrieux (17, p. 63). The disproportionate ratio of the first collection, May 19, showing 78% males was probably biased by the mode of collection. The sparsity of the population of sexually mature organisms resulted in the collector's resorting to dipping for a mating specimen as it would break the surface, causing

ripples. This predominance of males is in agreement, however, with Pelseneer's observation (60) that males are in the majority in the young stages and decrease in relative proportions as the season progresses. Main (46) proposed that a sample bias in favor of the males results from the males' preference for the open sunny areas, while the females sought out the shady places. This author interpreted the above mentioned observed ripples to result from the overt reaction of the male whose sexual aggressions had been repulsed either by another male or by an unreceptive pregnant female. This repulsion was described by Desportes and Andrieux (17).

Another incidental observation of the behavior of Lepidurus, which could possibly be of adaptive significance, was the strategic use of the convex lateral edge of the carapace. It was used very effectively by those specimens which found themselves in water too shallow to buoy them off the bottom. Likewise, the specimens trapped in isolated diminishing puddles, most efficiently forded through the connecting shallows by executing convulsive rocking movements, using the protruding abdominal extension and caudal plate to a decided advantage.

Although Lepidurus is the dominant aquatic organism and has adapted successfully, it is only one of a community of organisms similarly fitted to a highly specialized environment. In brief, this ephemeral lake and its unique limnological conditions could very well be succintly characterized as a compact ecosystem exhibiting quick changes, wide ranges, and localized successive instability to which a selected fauna has become peculiarly adapted.

Results of Experimental Methods of Hatching

Daily observation for the first 6 weeks disclosed nothing more than a succession of bacteria and algae, ciliates, flagellates, rotiferans, and one Cyclops sp.[15] A small amount of fungal mycelia were observed to be growing in a few of the vials, eking out a meager existence on the fecal and detrital "shells" of the "dirty" eggs. Twice weekly observations continued until on the morning of December 7, 1962, 124 days after commencement of the incubations, 3 eggs in the -2 C incubation chamber were observed to have hatched and numerous others had split the outer opaque detrital "shell". They were noticeably distended to an ellipsoidal configuration with a longitudinal diameter approximately twice that of the original spherical diameter. Movement of appendages was seen through the transparent "sac" and, by 4:00 p.m. of the same day, a total of 74 eggs, representing a variety of drying and cooling treatments, had hatched, 42 of which had undergone their first moult. Observations, including number hatched, number of moults, and number of "emergent" specimens, were subsequently made on alternate days until the field specimens in situ were observed to hatch in the ensuing spring. Figure 7 presents a graphic summary of pre-incubation treatments and the total percentages of eggs which hatched in each successful combination of conditions. Figure 8, by way of a time-line, gives the schedule of the treatments and hatching of the eggs.

The eggs in the -2° C and the 5° C (see Figure 7) cold treatment

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[15] It is interesting to note that this Cyclops hatched on the forty second day of incubation, after having been subjected to the slow freezing treatment at a minimum of -80° C for 3 hours then slowly warmed.

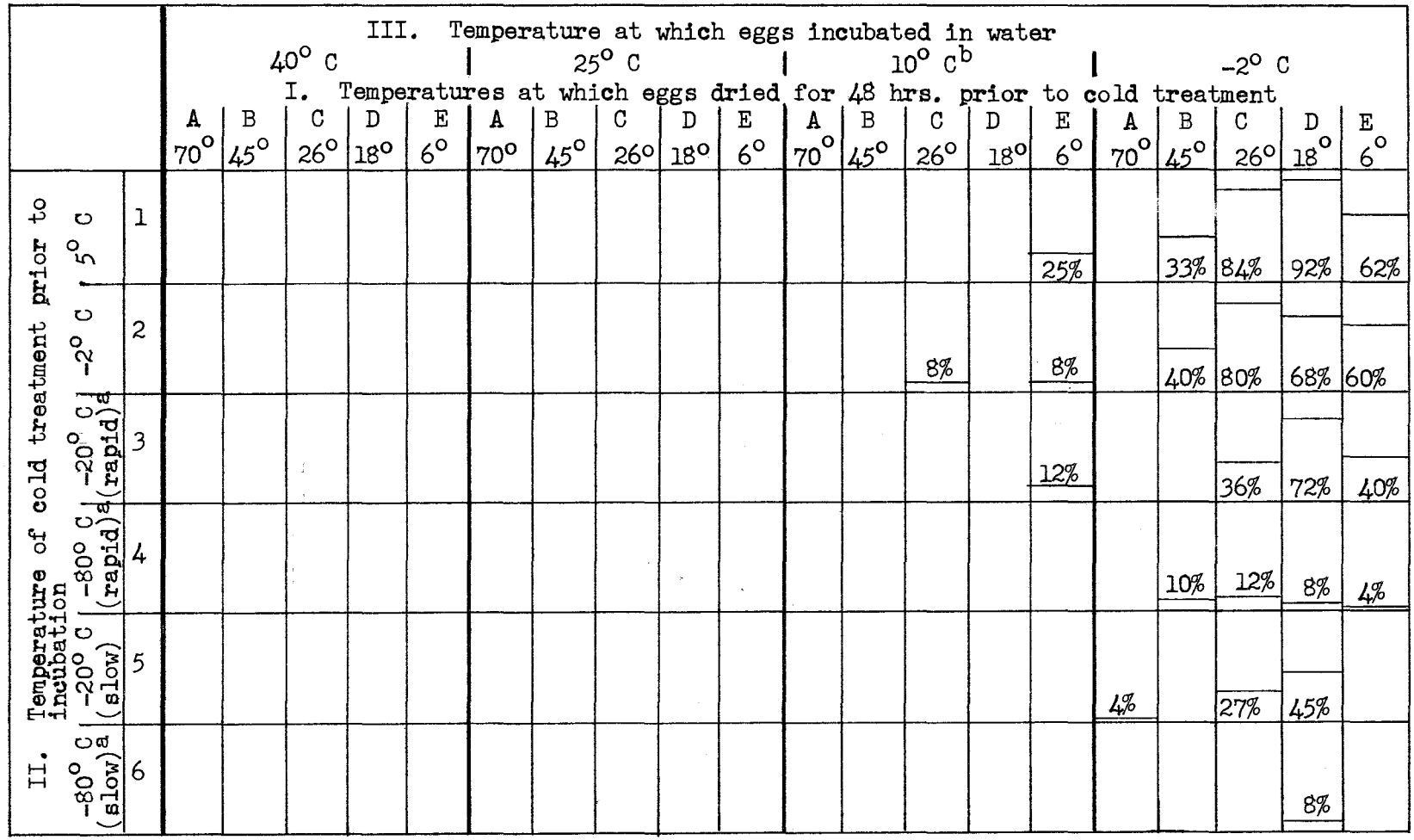

Figure 7. Results of laboratory incubation of eggs of Lepidurus apus.
Eggs were collected wet, June 16, 1962, and subsequently subjected to the above indicated treatments, viz., I, II, III. Ultimately, 25 eggs were incubated under the stipulated conditions. Darkened spaces indicate the hatching percentage as of the 240th day of incubation.
a. Eggs coated with 5% glycerine solution. b. Hatched only after a 15 day -2° C treatment (commenced on 186th day of initial incubation) followed by a 25 day incubation.

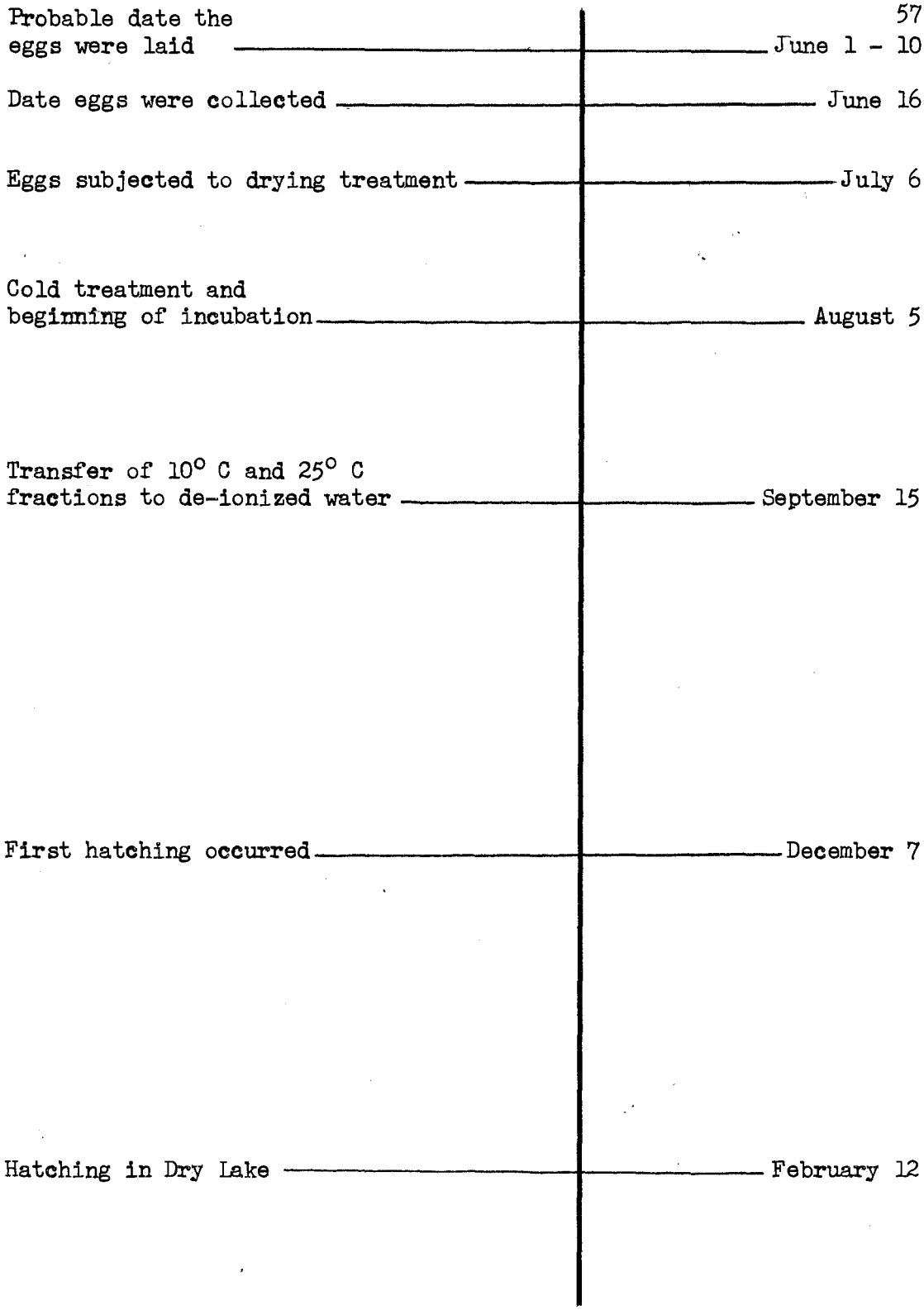

Figure 8. 1962-63 Time-line for eggs of L. apus, treatment, and hatching schedule.

produced the best percentage of hatching, but it should be noted here that the 4 month incubation temperature of -2° C would have completely over-shadowed both of these 3 day cold pre-treatments. The 18° C and 26° C drying treatment proved consistently advantageous in percentage hatch over the warmer drying temperatures, however, drying at 45° C (113° F) permitted 21 eggs of 150 to hatch. The 45° C dried, unfrozen eggs showed delayed hatching; 5 eggs of this group hatching only after 190 days of incubation. Drying at 18° C and 26° C proved significantly more productive of hatching than the 6° C drying temperature, which, incidentally, failed to accomplish drying. Forty-one eggs hatched which had never undergone any desiccation whatsoever. The experiment comparing the effects of osmotic pressure was ineffectual, since no eggs hatched in the temperatures involved.

One hatch was recorded in the vial of eggs which had been subjected to 70° C (150° F) for 72 hours and subsequently cooled slowly to -20° C, but this could possibly have been a contamination and is discounted for lack of other supporting hatches.

Although the percentages were quite low, (none over 12% per vial of 25 eggs), 9 hatches were recorded in the assortment of eggs which had been cooled rapidly to -80° C (-112° F). It seems almost inconceivable that hatching could have occurred in the -80° C (slow), and the fact that only 2 eggs did hatch reduces its significance. Figures 10 through 17 (Appendix) show a comparison of the results of the specific pre-incubation treatments.

Since hatching was restricted to the -2° C incubation batch with most of the cold and dry treatments producing <u>some</u> hatching, it was

theorized that duration of the sub-freezing temperature was the critical factor rather than the range of cold treatment. In Figure 9, the time-line graphically shows the time sequence for the duration of cold treatment experiments. Another incubation experiment was designed to discover what length of sub-freezing exposure time is required, and then what length of water incubation time is required at four different temperatures for hatching to occur.

Fifteen days of -2° C cold treatments of these eggs after the 186 day incubation resulted in a hatch of 12 eggs in the 10° C incubator only. Hatching commenced 22 days after the eggs were returned to the 10° C incubator among those batches indicated in Figure 7.

Results of Duration of Cold

Hatching occurred (see Table 4) solely in the "B" group (collected dry and rewetted at time of cold treatment), incubating at 10° C only. The first group to hatch enjoyed 30% hatching on the fourteenth day of incubation following 14 days of cold treatment. No hatching has occurred at any temperature among the eggs which experienced less than 14 days of sub-freezing temperature. Eggs spending more than the minimum requirement of 14 days in the cold, as a consequence thereof, required fewer days in the warmer incubation chamber, but this is not a linear relationship. A day spent in the cold, after satisfaction of the minimal 14 day cold treatment, is not as conducive to development as this day spent at the 10° C temperature. Between the range of 0 and 11 "extra" days of cold treatment, a cold day (-2° C) averages out 60% as effective as a 10° C day, while a 20% efficiency was shown between 11

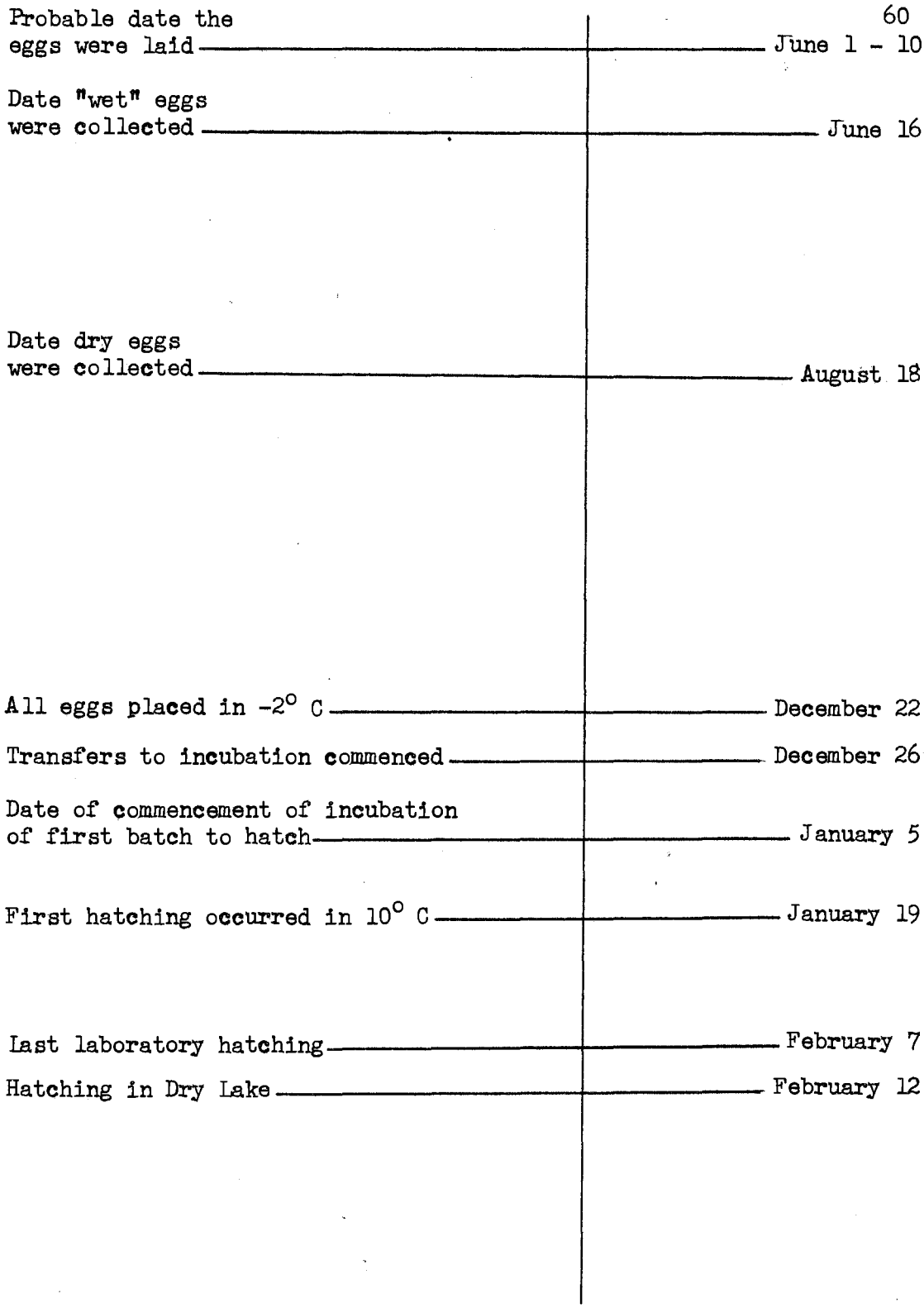

Figure 9. Time-line for duration of cold treatment experiments.

Table 4. Hatching Results of Duration of Cold Experiment

Transfer Numb	Date Incubated	Days at -2° C	Days at 10° C	Days Combined -2° and 10° C	Eggs Incubated	Eggs Hatched	Percent Hatched	Days in -2° C Excess of 14	Days in 10° C less than 14
1	12/26	4	a		10	0			
2	12/28	6	a		10	0			
3	12/30	8	a		10	0			
4	1/1	10	a		9	0			
5	1/3	12	a		10	0			
6	1/5	14	14	28	10	3	30%	0	0
7	1/7	16	a		10	0			
8	1/10	19	11	30	8	3	38%	5	3
9	1/13	22	9	31	8	5	63%	8	5
10	1/16	25	8	33	8	7	87%	11	6
11	1/19	28	7	35	7	4	56%	14	8
12	1/22	31	7	38	11	8	72%	17	8
13	1/25	34	10	44	9	1	11%	19	4
14	1/28	37	10	47	10	1	10%	23	4
15	1/31	40			10				
16	2/1	41			12				
17	2/2	42			9				
18	2/3	43			6				

[a] No hatching observed even though incubated for 7 months.

and 23 extra days of cold. An improvement in percent hatching with detention in the cold was noted in eggs detained up to 31 days. Detention in excess of 31 days has resulted in drastically reduced hatching. These eggs expanded as though they were emerging at the time when they would be expected to emerge, but they failed to hatch and instead turned a milky pink in color soon thereafter. The reason for this observed phenomenon is not presently known.

DISCUSSION

ECOLOGY

Although Lepidurus has been generally referred to as the "cold water form" by numerous investigators (Schaeffer, Brauer, Lundblad, Wolf, Longhurst, et al), this author's observations would perhaps suggest the advisability of qualifying this designation. Lepidurus were observed to thrive in profusion in temperatures considerably in excess of Brauer's 15° C maximum (7). Normal activity was seen frequently when the temperature had reached 20° to 25° C. As many as 25 Lepidurus were counted in a restricted area of 500 square yards in water of 3 inches depth which had attained a temperature of 31° C. This is only 5.5° C below the maximum temperature tolerated by Triops, the "warm water form", as reported by Rzóska (66, p. 281) in his North African work.

The wide diurnal range of temperature tolerated by Lepidurus is highly significant and undoubtedly has contributed toward its adaptation to this restricted ecological niche. Although actual measurements to that effect were not made, it is not at all inconceivable that the water temperature of some very small and shallow puddles, isolated by recession of the water, might experience diurnal ranges as great as 50° F. Five Lepidurus were seen to occupy an isolated footprint in which the water was three-quarters of an inch deep. While the air temperature remained constant, the temperature of this footprint water fluctuated as much as 4° F within 10 minutes in response to variation in insolation as a result of a passing cloud. Below

freezing temperatures at night are not at all uncommon in this vicinity during the time that the Lepidurus are present (see May and June maxima and minima, Table 1). Diurnal ranges of air temperatures approximated or exceeded 50° F on each of the following days in June, 1962: 10, 18, 19, 25, 26, 27, 28 (see Table 1); and since water temperatures were seen to consistently exceed the daytime air temperatures after 9:00 to 10:00 A.M. (Table 2), a 50° F range evidently was quite common. From these observations, it is evident that microclimatic data are much needed in the study of this organism.

Since the temporary pond habitat usually far outlasts the life of its Notostracan inhabitants, it is generally assumed that "heat death" accounts for an almost climactic and sudden disappearance of the Notostraca (7, p. 588; and 82, p. 138). The day after day high temperatures, peaking in the 28° to 30° C range, corresponded with the gradual extinction of Lepidurus in Dry Lake, but my observations fail to lend credence to any simultaneous dissolution of the population.

At maximum density of the Lepidurus, as observed on May 30, the water was truly a veritable "soup", Lepidurus and Branchinecta constituting the dominant residents. This bloom of Lepidurus, which peaked a few days after the Branchinecta peak, coincided with a decline in the Branchinecta population which would suggest either competition, with Lepidurus emerging as favored, or a predator-prey relationship. The latter was substantiated by the presence of Branchinecta leg parts in the gut of numerous Lepidurus. This predation could account in part for the demise of the Branchinecta, but no such predation could be established in connection with the subsequent dwindling of the

Lepidurus population. Campan (9, p. 96-97) considered the carnivorous larvae of Culicids and aquatic coleoptera, Gyrinids, Dytiscids, and Hydrophilids to be enemies of Lepidurus apus; Dytiscus, as well as Hydrophilus, were present, but never were they observed in sufficient numbers to accomplish any noticeable reduction in the adult Lepidurus population. Aedes larvae, in association, would more likely constitute a diet for these mature Lepidurus than a predaceous threat.

Conductivity and pH measurements, the slight, quick changes of the first notwithstanding, showed no significant changes concurrent with any unusual population fluctuations. Moderate to marked alkalinity is typical of these temporary pools and consistent with the findings of Coopey (14) and Rzóska (66, p. 270). This range of conductance (predominantly 2,000-3,000 mho's - see Table 1) is at great disparity with the range (100-700 mho's) obtained by Rzóska (66, p. 270) for Triops, but perhaps these diverse ranges may have generic uniqueness.

The dissolved oxygen content, being supersaturated for most determinations, was regarded as relatively unimportant, at least, not critical. Coopey (14) also found supersaturation in the Oregon ponds supporting Lepidurus. This supersaturated condition would be accounted for by the fact that temperatures rose rapidly, dense vegetation contributed toward an oxygen abundance, and the daily breeze whipped up small waves continuously, thus accomplishing thorough aeration of the shallow lake. The extreme turbidity of the water resulted from the agitation of silt and clay particles by the flailing appendages of the Branchinecta and Lepidurus. As the Lepidurus progresses along the bottom, the abdominal appendages are seen to touch the soil

lightly leaving a dual trail of silty, curling "exhaust". With the gradual diminution of the Notostracan population, the suspensoids settled leaving the water clear and untinted.

IMPLICATIONS OF LABORATORY HATCHING RESULTS

All incubation experiments attempted have indicated the necessity of a sub-freezing treatment of the eggs of Lepidurus apus to induce hatching. No eggs have hatched which had not previously undergone a minimum of 14 days of a continuous sub-freezing temperature. It is not known whether this cold treatment must be continuous. The Dry Lake habitat consistently provides sub-freezing treatment for a duration considerably in excess of this 14 day minimum, but so would all other ponds and lakes in the Northern Utah region. Eggs dried at 18° C and 26° C and subsequently experiencing temperatures slightly below freezing showed the best percentage of hatching. These conditions prevail at the Dry Lake habitat but also exist at other ponds visited in the survey.

Cooling rates in nature would be slower than any rates used experimentally and the ecological significance of the use of glycerine is limited. The lack of a control for the experimental use of glycerine limits the meaning of its application. Mazur's reference (50) to the importance of the preclusion of crystallization would not be applicable to eggs which had been dried and subsequently frozen; however, in nature they would be wetted prior to gradual cooling.

A prior drying treatment was not required for the hatching of eggs which were incubated at -2° C for 124 days, but only 2 eggs

(0.03%) hatched among the 700 "wet" eggs incubated in the "duration of cold" phase (wet eggs being those collected wet and kept wet). This inconsistency warrants further experimentation with the effects of drying.

Since in the duration of cold experiment no hatching occurred in that group of eggs which had been collected dry and chilled while dry, it appears that the presence of water in the egg during the cold treatment is necessary. The Dry Lake habitat consistently provides this needed water during the cold treatment.

In the duration of cold experiment, although the eggs had experienced the minimum 14 day sub-freezing treatment and had been dried, and then rewetted during the cold treatment, hatching occurred only in the 10° C (40° F) incubator. This indicates a need for a threshold warmth subsequent to the cold treatment in order that development might continue.

This 10° C minimum was substantiated by a subsequent experimentation. Seventy-five emergent eggs were collected from Dry Lake, February 10, 1963. These eggs were stored at -2° C for 6 days and showed no hatching. They were then divided among -2° C, 5° C, and 10° C. Within 24 hours of this transfer, 80% of the 10° C hatched while the 5° C required 7 days, and the -2° C had not hatched at all at the time of this writing (90 days).

Further confirmatory evidence of the requirement of both a cold treatment and a subsequent 10° C threshold incubation temperature was supplied through the successful hatching of the 10° C batch of eggs which had previously failed to hatch in 186 days of 10° C prior to

the cold treatment.

It is theorized that the shallowness of the water in the lake affords rapid daily warming in the early spring, thus providing this 40° F threshold temperature for the final hatching. Since 20-25 mm. of water depth was maintained in all incubated vials, the effect of water depth as observed by Hall (26) on the hatching of Chirocephalus diaphanus is not known. No attempt was made to measure the available oxygen, but this was maintained constant throughout all the incubator vials.

Bagatova's work (3) on the effect of available oxygen on hatching of the eggs of Apus cancriformis should be paralleled for Lepidurus apus.

The usual reason given for disappearance of Lepidurus apus - heat - should be re-examined in the light of these current observations. Brauer's 15° C maximum (7, p. 585) appears to be much too low. Longhurst's (40, p. 5) and Rzóska's (66, p. 274) finding regarding the favorable effect of low osmotic pressure on the hatching rate of Apus cancriformis needs yet to be confirmed for L. apus.

SUMMARY

Lepidurus apus was observed to have a limited distribution in Northern Utah, being restricted to a temporary shallow lake 15 miles southwest of Logan, Utah.

Drying was found to be unnecessary for hatching of eggs incubated at -2° C for 124 days.

Eggs subjected to 48 hours of 45° C drying and a 3 hour 80° C pre-incubation treatment hatched, but percentage and rate were significantly reduced.

Fourteen days constituted minimal duration of sub-freezing temperature required as pre-incubation cold treatment for hatching of sun-dried eggs of *L. apus*.

Fourteen days was minimal submersion time required for hatching of eggs which had received minimal (14 days) cold treatment.

Embryonic development does occur at sub-freezing temperature (-2° C) but at a slower rate.

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APPENDIX

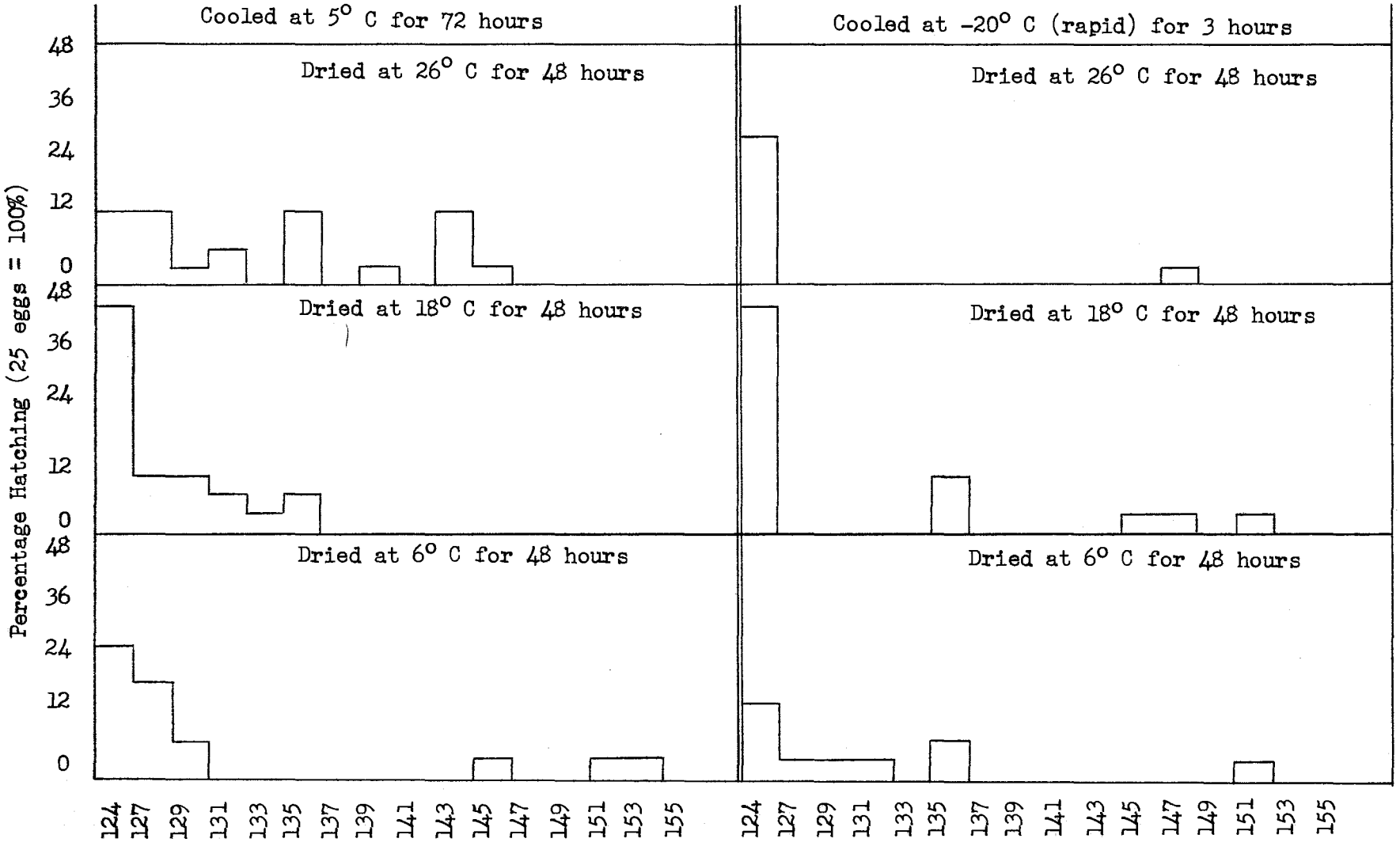

Figure 10. Days immersion required for hatching L. apus eggs after various pre-incubation treatments. Treatments yielding 12% or less total hatching were omitted from this graph.

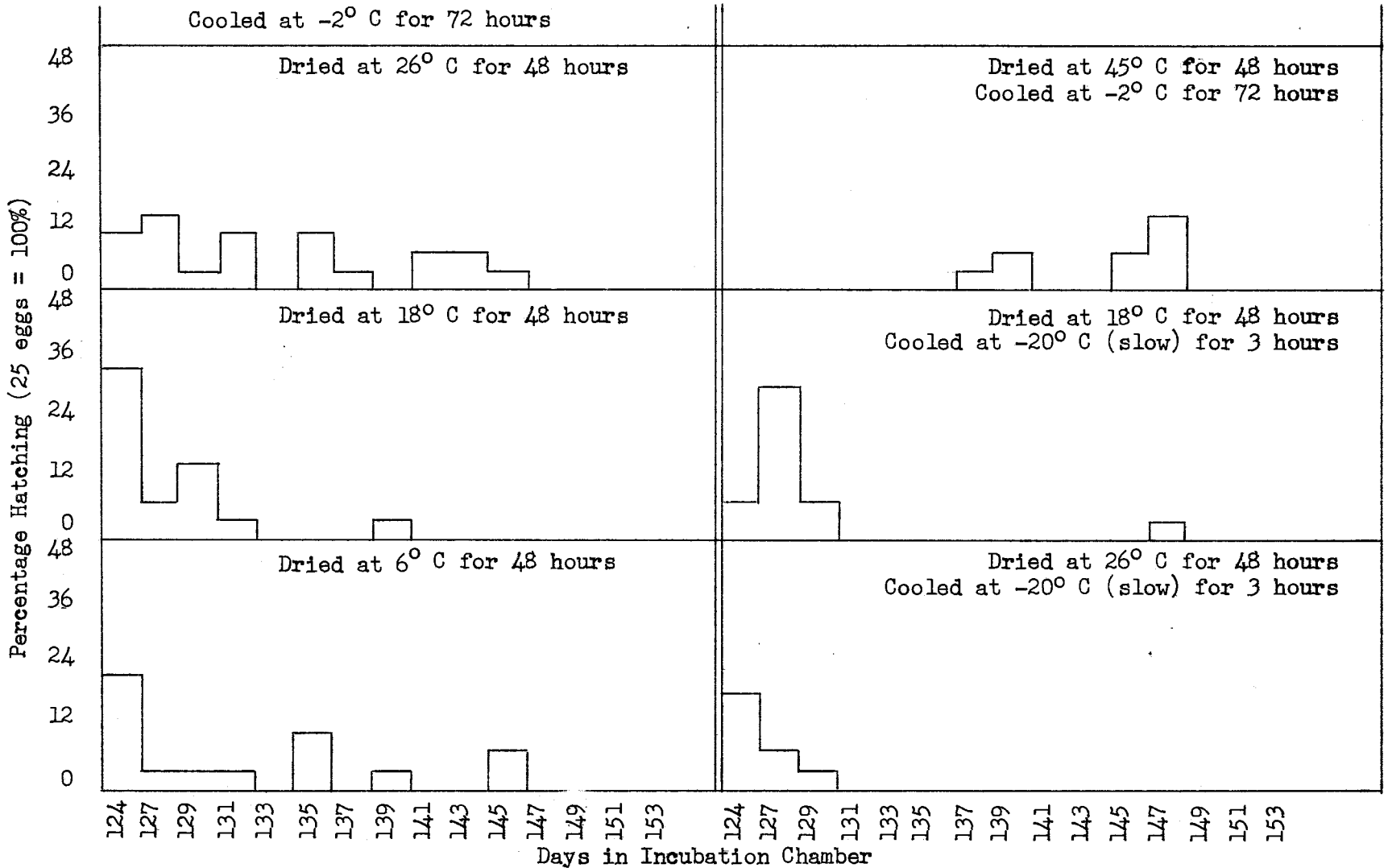

Figure 10. (Cont'd) Days immersion required for hatching of L. apus eggs after various pre-incubation treatments. Treatments yielding 12% or less hatching were omitted from this graph.

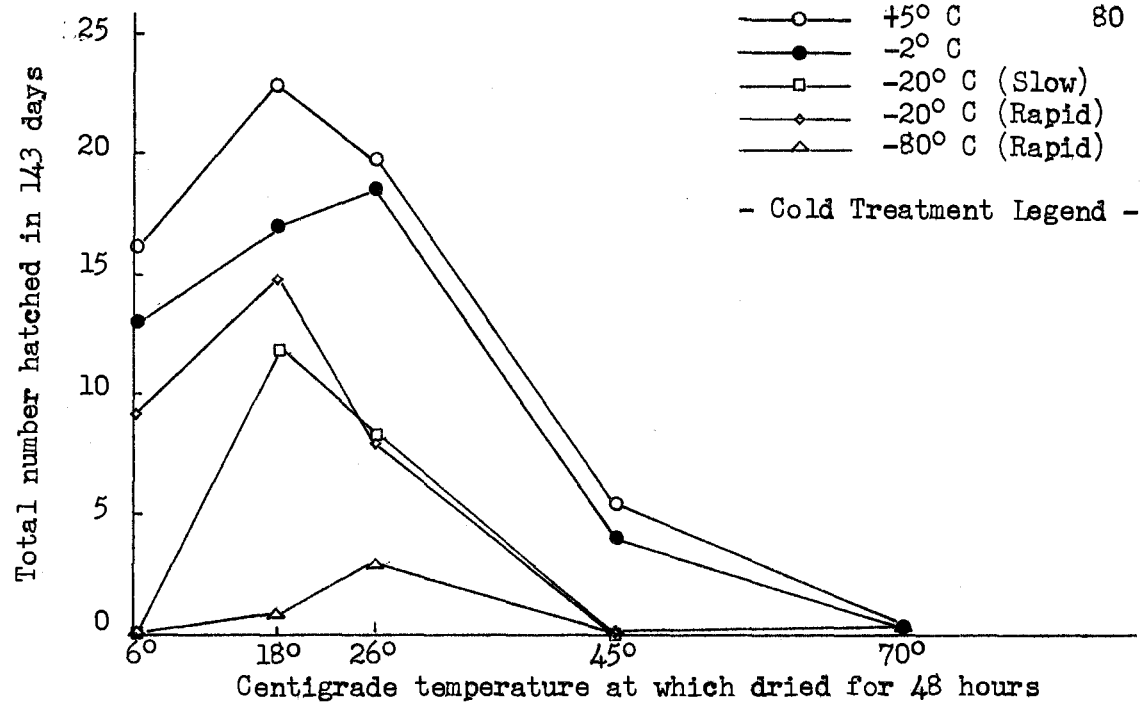

Figure 11. Total number hatched in -2° C incubation plotted according to drying temperature.

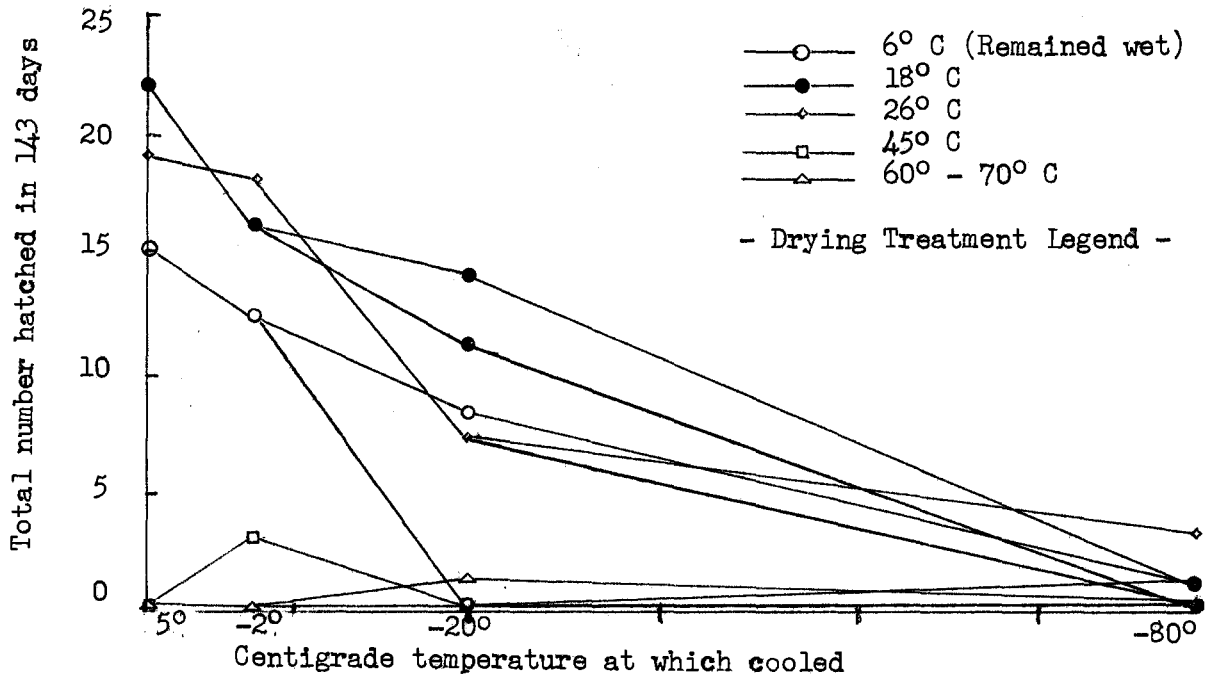

Figure 12. Total hatching in -2° C incubation plotted according to temperature at which eggs were cooled.

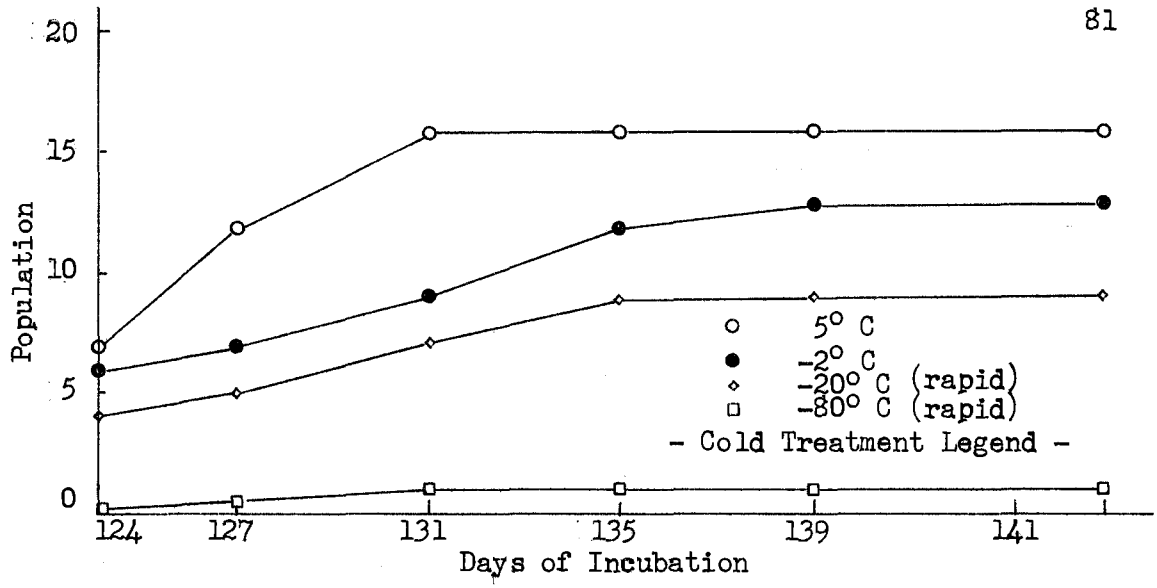

Figure 13. Population growth in eggs dried at 6° C for 48 hrs. (remained wet) and incubated at -2° C. No survival of any eggs frozen slowly in this undried sample.

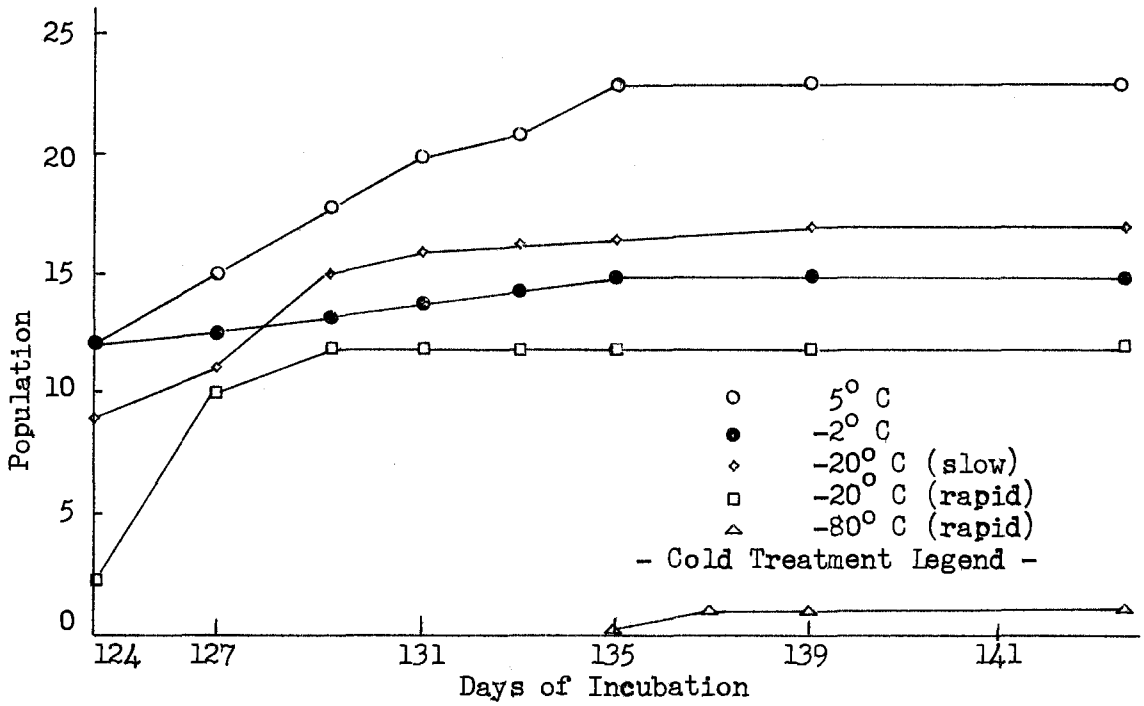

Figure 14. Population growth in eggs dried at 18° C for 48 hrs, cold treated, and then incubated at -2° C. No survival of any eggs frozen at -80° C (slow).

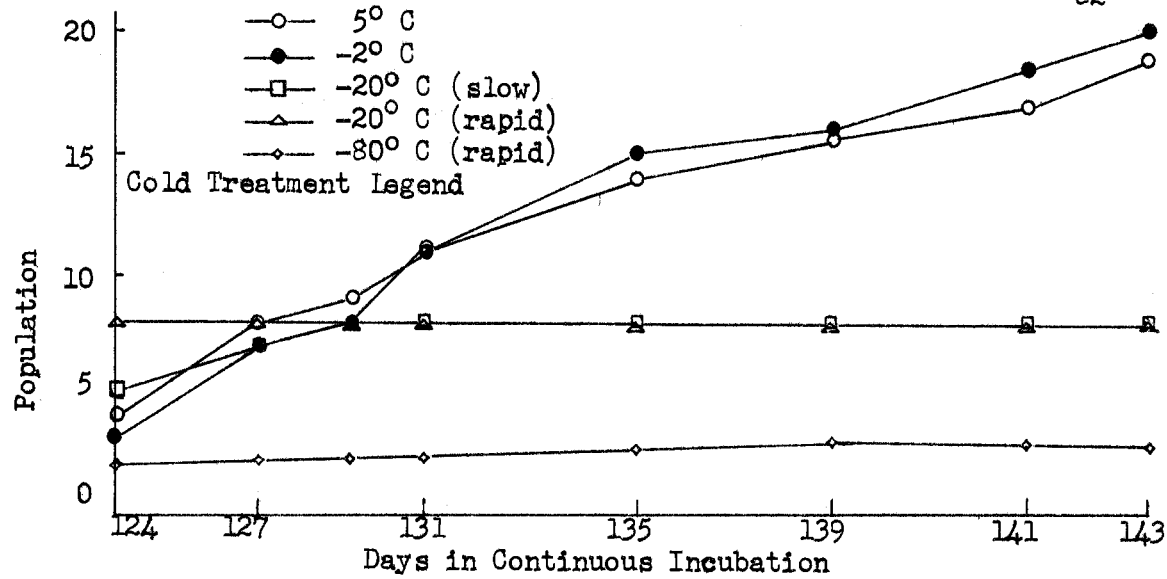

Figure 15. Population growth in eggs dried at 26° C for 48 hrs. and incubated in -2° C. No survival of eggs frozen -80° C (slow).

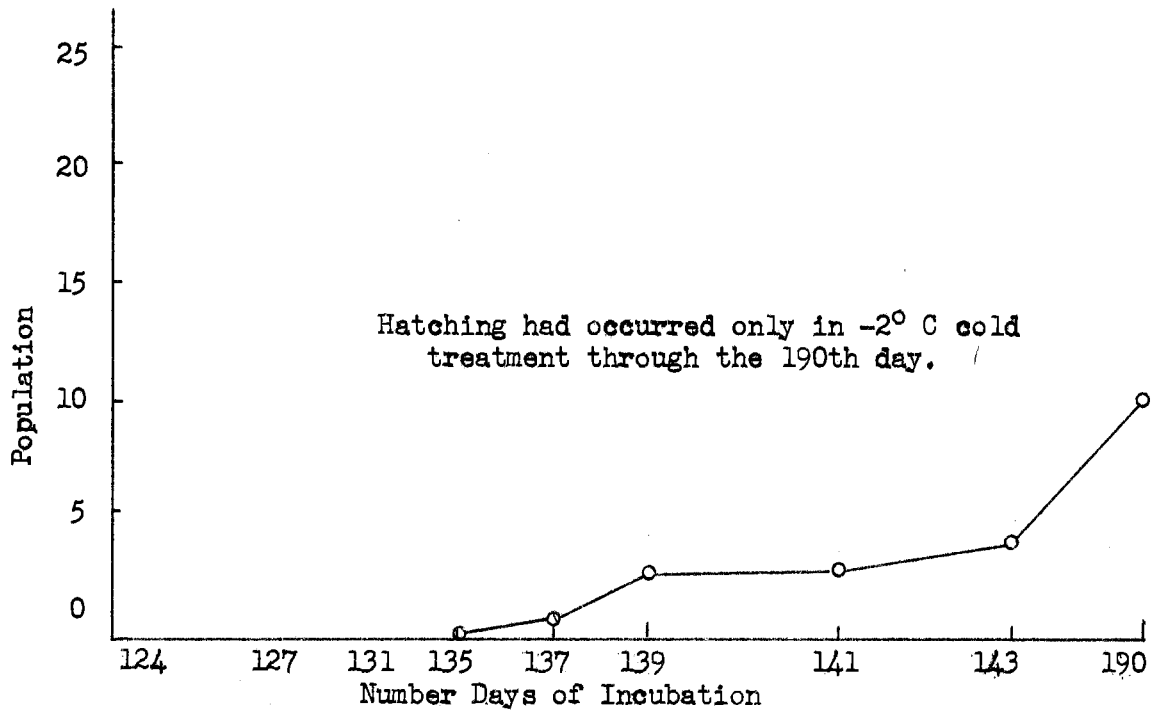

Figure 16. Population growth observed in eggs dried at 45° C for 48 hrs., cold-treated and incubated at -2° C.

U.S. DEPARTMENT OF AGRICULTURE

FOREST SERVICE

LOGAN RIVER & BLACKSMITH FORK AREAS

CACHE NATIONAL FOREST

1953

SCALE ½ 0 1 2 3 4 5 MILES

LEGEND

- NATIONAL FOREST BOUNDARY
- ADJACENT NATIONAL FOREST BOUNDARY
- MAIN MOTOR HIGHWAY
- GOOD MOTOR ROAD
- POOR MOTOR ROAD
- TRAIL
- RAILROAD
- TELEPHONE LINE
- TELEPHONE LINE ALONG ROAD
- ELECTRIC POWER TRANSMISSION LINE
- PIPE LINE OR CONDUIT
- SUPERVISOR'S HEADQUARTERS
- RANGER STATION
- GUARD OR RANGER STATION NOT PERMANENTLY OCCUPIED
- TRIANGULATION STATION
- HOUSE, CABIN OR OTHER BUILDING
- ELECTRIC POWER STATION
- RADIO STATION
- MUNICIPAL LANDING FIELD
- INTERMEDIATE LANDING FIELD
- BIRD REFUGE BOUNDARY
- U.S. ROUTE NUMBERS

Red numerals denote sites surveyed. DPSU/62
Circled numerals denote mud samples taken and cultured.
(13) Site of study material, Dry Lake