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Life history and population dynamics of *Daphnia* in seven ephemeral pools in Red Rock Canyon, Nevada

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LIFE HISTORY AND POPULATION DYNAMICS
OF *DAPHNIA* IN SEVEN EPHEMERAL POOLS
IN RED ROCK CANYON, NEVADA

by

Priscilla Kathleen Bowman

A thesis submitted in partial fulfillment
of the requirements for the degree of

Master of Science

in

Biological Sciences

Department of Biological Sciences
University of Nevada, Las Vegas
August 1996

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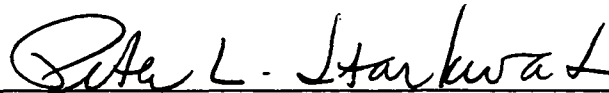
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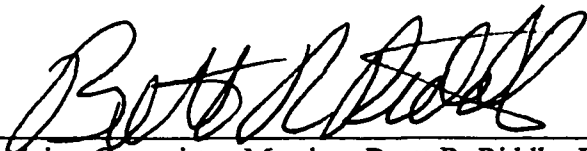
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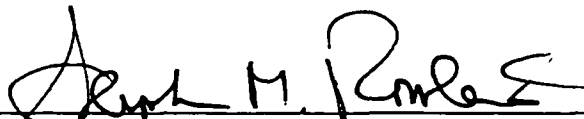
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August 1996

ABSTRACT

Seven ephemeral rock pools in Red Rock Canyon, Nevada were visited bimonthly over twelve months and sampled for resident zooplankton species. Population dynamics and life history characteristics of two *Daphnia* species, *D. pulex* and *D. obtusa* were analyzed with incidental attention given to an additional cladoceran, *Moina* sp. Aspects of the physical, chemical and biological environment were measured and evaluated. The behavior of these daphnid populations appears to be driven by the extreme seasonality of rock pool ecosystems between episodic disturbances of drought and deluge. No causal relationships between *Daphnia* population size or patterns of temporal change and abiotic factors appear to exist. The availability and duration of water limits population growth. When conditions are favorable, rapid population growth apparently occurs via obligate parthenogenesis. This is the first systematic study of any *Daphnia* species in the Mojave Desert, or in any ephemeral aquatic habitat within a desert region.

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INTRODUCTION

Background and Project Description

This study of the life history and population dynamics of *Daphnia* species in Red Rock Canyon Conservation Area will be the first in-depth examination of *Daphnia* population ecology in the Mojave Desert. In fact, this may be the first comprehensive study of desert *Daphnia* anywhere in North America, and perhaps world-wide.

Specifically, I intend the following:

1. To document patterns of population dynamics of *Daphnia* species in a system of seven ephemeral pools in Red Rock Canyon,
2. To evaluate the presence and timing of various life history stages of the two *Daphnia* species present,
3. To propose relationships between observed patterns and environmental factors, and
4. To interpret these patterns relative to *Daphnia* found in other high stress environments such as arctic and montane pools.

Several aspects of *Daphnia* ecology are significant to the above-stated goals.

These aspects include first, taxonomy, distribution, and habitat, with specific reference to small pond systems; second, anatomy and cyclomorphosis; and third, life history, energetics, reproduction, and seasonality. By way of introduction, these aspects will be discussed with reference to similar small pond or pool systems elsewhere.

Pools in Red Rock Canyon share some ecological similarities with coastal rock

pools in Scandinavia, tundra polygon pool systems in Alaska and the Canadian arctic, and to some montane pools. The central unifying feature shared by these pool systems is their short, very limited seasonality.

Taxonomy, Distribution, and Habitat

Daphnia, commonly known as water fleas, are microcrustaceans in the order Cladocera. The genus currently consists of 50 species with a world-wide distribution (Hebert 1987). This number of species is constantly under revision as new species are described.

Daphnia and *Ctenodaphnia* rank as two cladoceran subgenera according to Brooks (1957). The subgenus *Daphnia* has a wide geographic range and has been found in several zones including the Palearctic and Nearctic zones, and in the southern portion of the Ethiopian region (Hebert 1978). Most species of *Daphnia* living in temperate regions are pelagic, and small to medium-sized (Hrbacek 1987). *Ctenodaphnia* predominate in southern continents (Hebert 1978, 1984) and are large species living almost exclusively in temporary ponds (Hrbacek 1987). Hebert (1978) hypothesizes that this distributional pattern suggests a divergence between *Daphnia* and *Ctenodaphnia* before the division of Laurasia and Gondwanaland.

About ten *Daphnia* species are known to occur in Africa (Dumont 1980). Hebert (1977), in his revision of the taxonomy of Australian *Daphnia*, describes ten species, while Benzie (1986) states that six species of *Daphnia* occur on the Australian continent. Some measure of the confusion as evidenced by this disagreement in the number of species on any given continent is attributable to annual variation in gross morphological phenotype termed cyclomorphosis. Cyclomorphosis makes *Daphnia* species boundaries notoriously difficult to delimit because of these often drastic, seasonal alterations in appearance (Hebert 1977).

The two species of interest here are *Daphnia pulex (nevadensis)* and *Daphnia obtusa* because they were found in temporary pools in Red Rock Canyon Conservation Area, Nevada by Paul D. N. Hebert (P. D. N. Hebert, pers. commun. 1991). The presence of *D. obtusa* in North America has been the subject of some controversy. *D. obtusa*, previously thought to be absent from North America (Brooks 1957), has been demonstrated to be present (Schwartz et al. 1985). Schwartz et al. (1985) found that populations of *D. obtusa* are common throughout the midwestern United States. Using Brooks' (1957) criteria these two species would both be classified as *D. pulex*, but according to Schwartz et al. (1985), who investigated the occurrence of *D. obtusa* in North America, they can be distinguished by conventional morphological features. Scourfield (1942) and Johnson (1952) use features including: 1) a more pronounced antennular mound in *D. obtusa*; 2) fewer and smaller spines on the ventral margin of the carapace in *D. obtusa*, and 3) the presence of a set of fine setae on the middle portion of the inner lip of the ventral margin of the valves in *D. obtusa*. In addition, Schwartz et al. (1985) use a fourth difference suggested by Johnson (1952), the number of teeth in the middle pecten.

D. obtusa and *D. pulex* are found in other temporary environments. Hrbacek (1987) says that *D. pulex* is found in arctic ponds, along with a second related species, *D. middendorffiana*. *D. obtusa* and *D. pulex* are also found in arctic pools and lakes, as well as in temporary, high mountain ponds in California and Italy. *D. obtusa* is found in temporary pools in the Palearctic and Holarctic regions, and in New Zealand (Hrbacek 1987).

Curiously, arctic populations have many life history similarities to inhabitants of desert systems. *D. pulex*, *D. middendorffiana*, and a third species, *D. longiremis*, are the most widespread arctic species and are found in Alaska, Canada and Greenland, and likely in the Eurasian Arctic. Factors limiting their distribution are the extreme, seasonal variations in temperature and light, as lakes and ponds are ice-free for less than three months each year (Haney and Buchanan 1987). Other limiting factors in small ponds are invertebrate predators and food scarcity due to low primary productivity. Responses to all of these factors include melanic pigmentation, cyclomorphosis, facultative or obligate parthenogenesis, and the production of ephippial diapause embryos. Arctic species, like those in many other ephemeral habitats, are often asexual (Haney and Buchanan 1987). Beaton and Hebert (1988) state that arctic populations have completely abandoned sexual reproduction and reproduce by obligate parthenogenesis.

The taxonomic distribution of pigmentation, the presence of melanin, a dark brown or black pigment, in the cuticle of the exoskeleton of *Daphnia* is an area of dispute. *D. pulex* and *D. middendorffiana* from 11 ponds in the Canadian Arctic were examined and pigmentation was found in both species (Hebert and McWalter 1983). Haney and Buchanan (1987) discuss nine *Daphnia* species found in arctic lakes and ponds which occur in areas with permafrost. However, they state that *D. pulex* are incapable of producing carapace pigment. Arctic ponds which are shallow with high light penetration tend to have pigmented *D. middendorffiana*, and ponds that are humic-rich with low light penetration favor *D. pulex* (Haney and Buchanan 1987).

The melanization seen in arctic *Daphnia* may provide protection from

photodamage caused by short wavelength radiation (Hebert and McWalter 1983, Hebert and Emery 1990) and thus confer a fitness advantage. A high ultraviolet flux occurs in montane, alpine and desert environments, and cuticular pigmentation may prevent transmission of more than 90% of incident ultraviolet radiation through the cuticle (Hebert and Emery 1990). I occasionally observed pigmentation in specimens of *Daphnia* from Red Rock Canyon, raising the question of pigmentation as an obligate or phenotypically plastic characteristic, but that question is beyond the scope of this study.

Meijering (1975a) collected *Daphnia* from four ponds in Northwestern Canada. Pond temperatures, at the time of each visit, ranged from 8.4° C to 14.7° C depending on location and weather. Meijering found sympatric populations of *D. pulex* and *D. middendorffiana*. *D. pulex* males were found in three of the ponds located on the shore of the Arctic Ocean. He also found a ctenodaphnid, *D. magna*, far north of the Arctic Circle. As mentioned above, ctenodaphnids are usually found in the southern hemisphere though there are numerous European records (see below). Meijering states that the variability of *D. pulex* in growth, maximum body size, and other factors is the result of environmental conditions, the most important of which he felt was presumably the food supply.

Korpelainen (1989) studied 22 summer populations of *D. magna* in small rock pools in southern Finland. She found that monthly ratios of males to females ranged from 0.31 to 1.0, and that sex expression in *Daphnia* appears to be determined by interactive responses to environmental factors such as temperature, photoperiod, population density and food supply.

Other Scandinavian species found in northern Swedish lakes include the three

species *D. longispina*, *D. galeata* and *D. cristata* (Pejler 1973). Pejler found *D. longispina* in southern and central Sweden in pools and ponds. Hanski and Ranta (1983) studied three coexisting species of *Daphnia* (*D. longispina*, *D. magna*, and *D. pulex*) in rock pools on the Baltic islands off the south coast of Finland. They propose that interspecific competition influences extinction and colonization rates in their metapopulation model, wherein a metapopulation is defined as a regional population of a number of patchily distributed local populations.

Bengtsson (1986) feels that Hanski and Ranta (1983) overestimate the role of interspecific competition, colonization and extinction in species distribution, reminding us that there is little experimental or field evidence to support such models. Bengtsson (1986) suggests that local distribution patterns of *Daphnia* in rock pools, common in coastal areas of Finland and Sweden, depend more on species responses to abiotic factors such as salinity and food density, and that predators such as newts, fish and aquatic insects, if present, can easily drive *Daphnia* populations to extinction. Interspecific competition can be important, and should be incorporated in studies of metapopulation systems.

Montane habitats can have similar temporal features to those in arctic locations even in some equatorial regions. Green and Kling (1988) describe three species of montane *Daphnia* from 6 out of 37 lakes sampled in Cameroon, West Africa. All the lakes were at elevations over 1000 meters and at latitudes of 5-6° N. *D. obtusa* was found in one of the 37 lakes, *D. laevis* was found in the same lake plus two other lakes, and *D. rosea* was found in three other lakes. Daphnids were absent from the other 31

lakes. Populations were predominately female and only one male *D. laevis* was found. Similarly, I observed only females in Red Rock Canyon pools. Parthenogenesis is the predominant form of reproduction in most *Daphnia* populations (Hebert and Ward 1972).

Wiggins et al. (1980) propose a scheme for classification of temporary waters. Temporary pools in their typical form are an accumulation of surface water in an isolated basin. At no time during the year should this basin have a discrete inlet or outlet. Water should be entirely absent from a temporary pool for part of the year. Such a pool should not receive, by way of surface water connection, any animal inhabitants from an adjacent stream or pond.

Wiggins et al.'s criteria are very restrictive. As Williams (1985) points out in his discussion of temporary lentic waters in semi-arid and arid regions, no classification of temporary waters in temperate regions could be sufficiently comprehensive to categorize the range of conditions found in semi-arid and arid environments. For the most part Wiggins' scheme is too specific to be of general application. In fact, my pool system in Red Rock Canyon differs from Wiggins' strict criteria. I will discuss below the physical characteristics of my pools that are at variance with Wiggins' classification.

Wiggins et al. (1980) divide animals in temporary pools into four groups based on the method they use for tolerating or avoiding drought. *Daphnia* belong to the group which are year round residents incapable of active dispersal, and which avoid desiccation as resistant stages. Wiggins et al. (1980) state that successful pool inhabitants must synchronize their life histories with the annual cycle of the pool, and must adapt to summer dry periods and winter cold. When a cladoceran reproduces asexually it increases

its effectiveness in exploiting ephemeral habitats because a single propagule may begin a new population, and rapid population growth achieved by parthenogenesis is clearly an asset (Wiggins et al. 1980).

Williams (1975) discusses at great length patterns of sexuality, and, specifically, in the context of the interplay between sexual and asexual populations. He emphasizes the importance of facultative sexuality as a successful compromise between the genetic constraints of the limited variation of asexuality versus the ability of asexual populations to exploit habitats at the expense of sexual ones if habitats are temporally uniform. However, three species of the Order Cladocera (two *Daphnia* and one *Moina*) inhabit the same pools in Red Rock Canyon. Both *Daphnia* species appear to be obligate parthenogens, and *Moina* is sexual!

In the study of *Daphnia* thermal tolerances, six species from several geographic localities including the United States, Canada, England, Scandinavia and New South Wales were compared at three acclimation temperatures and showed marked variation in their ability to withstand acute temperature differences with *D. obtusa* having the highest tolerance and *D. pulex* the lowest (MacIsaac, Hebert, and Schwartz 1985).

Temperature extremes occur in arctic and desert habitats. Daphnids which inhabit shallow pools must have the ability to tolerate large and often rapid changes in temperature. While pools in the arctic freeze, I found that pools in the desert reach temperatures of 30°C. Desert pools are also reported to freeze (P. Starkweather, pers. commun. 1996). For 1991, Red Rock Weather Station (National Oceanic and Atmospheric Administration, Climatological Data Annual Summary, Nevada, 1991)

reported the minimum air temperature as -2.7°C and the maximum air temperature as 34.6°C .

Anatomy and Cyclomorphosis

All *Daphnia* have a common body plan which consists of a head with a large, prominent compound eye, two small first antennae on the ventral, anterior margin, and two large second antennae inserted near the posterior margin. Mouthparts are located near the ventral junction of the anatomical head and body. The thorax and abdomen are covered by a large, folded carapace which is open at the ventral margin. Internal organs such as the heart, esophagus, stomach, ovaries and brood pouch, as well as the legs and postabdominal process, are contained within or covered by the carapace (Pennak 1989).

The carapace has a dorsal spine of varying length which is usually intact in juveniles. I observed that young daphnids in Red Rock Canyon pools have a spine that is longer in proportion to their total body length than are the spines of adult daphnids. As discussed below, some species form longer dorsal spines in response to predation. I found that the dorsal spine is often broken off in varying amounts as the juveniles mature, and is sometimes broken off at the base of the carapace in adults. Whether the spine is regenerated after molting is unknown. Also this variation in dorsal spine length may well be a form of cyclomorphosis.

Cyclomorphosis, changes in morphology in response to seasonal and environmental cues, has been observed in both temperate and arctic *Daphnia* species. In arctic environments, *Daphnia pulex*, a species also found in Red Rock Canyon pools, has been found to display cyclomorphosis. *D. pulex* in arctic temporary pools near Turku, Finland developed spined morphs (Walls and Ketola 1989; Vuorinen, Ketola, and Walls 1989).

Cyclomorphosis also occurs in response to predation. A Manitoba, Canada population of *D. pulex*, in the presence of copepod predation, was found to produce predation-resistant clones which had a smaller body size in the second and third instars, but longer tail spines in each juvenile instar (Wilson and Hebert 1993). Vuorinen et al. (1989) suggest that induction of defensive spines in *Daphnia* may be common in the presence of all *Chaoborus* species.

Other morphological responses to predation include the production of toothed dorsal crests. In Wisconsin ponds, *D. pulex* neonates bearing a toothed dorsal crest, not present in the parents, are released from the brood pouch in response to chemical cues in the presence of the aquatic Dipteran larva *Chaoborus* (Havel 1985). *D. pulex* morphs possessing a toothed dorsal crest were superior to the typical morphs in escaping predation from *Chaoborus* larvae (Havel and Dodson 1984). Populations of *Daphnia pulex* have developed defenses in response to *Chaoborus* predation which include growth of a small, toothed neck spine (Ramcharan et al. 1992). Notonectid predators have also been found to induce crest development in four morphs in the *Daphnia carinata* King complex, and these morphs were less susceptible to predation than were those without a crest (Grant and Bayly 1981).

Another example of predator induced cyclomorphosis is the development of "helmets" where the head enlarges and becomes pointed achieving a bizarre appearance. *Daphnia longiremis* is commonly found in arctic Alaskan lakes in dimorphic states in response to a predaceous copepod, *Heterocope* (O'Brien et al. 1980). In a series of experiments, O'Brien et al. (1980) found that the helmeted morph was less vulnerable to

predation by *Heteroscope*. Mort (1986) notes that helmeted *Daphnia* are better at evading capture by *Chaoborus*.

Life History, Reproduction, Energetics and Seasonality

Daphnia life cycles vary among species and according to environmental conditions. Little information is available on chemical limiting factors in *Daphnia*. Most daphniads can withstand oxygen levels of less than 1.0 mg cm^{-1} (Pennak 1989). Chemical factors such as pH or calcium levels may or may not be influential. Most populations can withstand high concentrations of calcium (Pennak 1989). High calcium levels are likely found in Red Rock Canyon pools because the substrate of the Spring Mountains is Paleozoic limestone (Fiero 1986). Some species of daphnids live in acid and bog waters, but most live in water with a pH range of 6.5 to 8.5 (Pennak 1989).

Timing of life histories and reproduction is influenced by temperature as might be expected for these poikilothermic organisms. Temperature affects the length of a daphnid's life. According to Meijering (1972), *D. pulex*, a species found in Red Rock Canyon pools, can live up to nine months in the very cold lakes of Greenland. Maier (1993) determined through life table experiments that for *Daphnia obtusa*, another one of the species found in Red Rock Canyon pools, time from release from the brood pouch to first reproduction varied inversely with temperature from 77.9 ± 6.4 days at 2°C to 5.3 ± 0.4 days at 25°C . Maier found that *Moina brachiata*, however, had a much shorter time to the first reproduction of 9.0 days at 15°C to 1.3 days at 30°C with bigger clutches and higher birth rates. A *Moina* species is also present in Red Rock Canyon pools, and as discussed below, is found during the hottest months.

Temperature also affects the rate of parthenogenesis. *Daphnia* have been found to reproduce by parthenogenesis with temperature dependent rates. Occasionally males, or

resting eggs that develop after diapause, are produced (Threlkeld 1987). Threlkeld states that variation in egg development appears to be primarily under the control of physical aspects of the environment such as temperature, and that *Daphnia* generally age and die according to a temperature-dependent process.

During the life cycle of daphnids several instars, each followed by a molt, have been noted during the juvenile stages of *Daphnia* species with up to two adult instars (Pennak 1989). Most adults are parthenogenic females producing brood of up to 300 depending on the species and instar, but males can be produced in response to environmental stressors such as crowding of the females, reduction in available food, or unfavorable temperatures (Hebert 1978).

Eggs are released into the brood pouch where they develop. The young, when they are released, superficially resemble adults and grow through several juvenile instars with molts between instars, followed by one adolescent instar during which eggs develop in the ovaries. Adults may have several successive instars during which new clutches of eggs are released into the brood pouch. *D. pulex* may have three or four juvenile instars and as many as eight to twenty-five adult instars (Pennak 1989).

Daphnia also produce "resting eggs" in response to low food levels and under intense crowding (Carvalho and Hughes 1983). After pools freeze or dry, ephippia hatch. Ephippial eggs, or so-called "resting eggs," are one or two embryos enclosed in an ephippium which normally diapause when unfavorable conditions occur. Ephippia can colonize and refound populations by passive dispersal.

Resting embryos (ephippia) go through diapause, contributing to the survival of

the *Daphnia* populations through freezing, dry spells, or otherwise unfavorable pond conditions, and are then activated when conditions become favorable (Hebert 1978). Indeed, Meijering (1975b) states that the goal of a cladoceran's life cycle is the production of resistant resting eggs, and that in some time-niches the *Daphnia* population of a shallow pond may fail to reach the goal in a given space of time due to abnormally short pond durations.

Ephippia in arctic pools experience both darkness and freezing, and are then activated in the late spring when light and temperatures are favorable. Davison (1969) found that *D. pulex* eggs which were stored in the dark were activated by exposure to light. Chilling the ephippia resulted in an increased light requirement. In the Arctic, the strong seasonality is associated with a very brief period when *Daphnia* can grow and reproduce. The rest of the year, when ponds and lakes are frozen, is spent in diapause. Under these conditions populations may produce offspring capable of maximizing this capricious environment possibly by producing larger neonates (Schwartz 1984).

Daphnia are eurythermal (able to endure a broad range of temperatures) possibly because they experience such dramatic changes in temperature in their natural environments (Pennak 1989). While populations in more temperate environments have a longer period in which to grow and reproduce, and would have an opportunity to produce greater numbers of offspring, arctic studies show that pool water temperature is critical for the expression of the photoperiod control of reproduction (Stross 1969). Stross found that crowded females produce resting eggs at 20°C regardless of the photoperiod. Arctic pools visited by Stross fluctuate daily from a minimum of 5° to 12-15°C, and even during

July with 24 hours of daylight, females shift to producing broods of diapausing embryos.

Schwartz (1984) compared life history data from *D. middendorffiana* and other arctic species, with *D. pulex*, which he considers to be a temperate species. He found that *D. pulex* matures sooner, at a smaller size with more, smaller offspring during more adult instars than does *D. middendorffiana*. *D. pulex* also lives longer. Schwartz (1984) feels it should be possible to predict the life history of any *Daphnia* population given information concerning its local predators and the temperature regime. That may or may not be true.

Laboratory investigations of life history parameters of *Daphnia obtusa* and *Moina brachiata* showed that the two species have different temperature tolerances (Maier 1993). I found *D. obtusa* and a *Moina* species in my Red Rock Canyon pools. Maier (1993) found in his laboratory investigations that *D. obtusa* could tolerate a temperature range of 2° to 25°C while *M. brachiata* tolerated 15° to 30°C. Maier's laboratory investigations supported his field study findings. In a small temporary pond in South Germany, *D. obtusa* dominated during the spring, fall and winter, while *M. brachiata* dominated during warmer temperatures from May to October. In Red Rock Canyon pools in this study, *D. obtusa* also dominated in the spring while *Moina* sp. dominated during the summer.

In addition to its previously discussed impact on individual morphology, predation also has relevance with respect to patterning *Daphnia* life histories. Diapause can also be induced by the presence of predators (Slusarczyk 1995). Slusarczyk found that exudates released into the water by fish predators induced diapause in a population of *D. magna* from a lake in northern Germany. Known invertebrate predators are copepods,

notonectids, larvae of *Chaoborus*, and the flatworm, *Mesostoma*. As discussed above some *Daphnia* species exhibit different morphotypes in response to this predation pressure (Schwartz 1984). Vertebrate predators elicit the survival of small individuals, and invertebrate predators select smaller individuals with larger individuals surviving (Brooks and Dodson 1965). Paradoxically, instead of depressing populations of daphnids, Polishchuk (1995) found that invertebrate predation on young daphnids tends to increase the birth rate of *Daphnia*. By altering the size structure of the population so that there are more adults, per capita birth rate increases.

Predation can also influence the size of individuals in a *Daphnia* population. *D. pulex* from a small pond in Wisconsin were exposed to waterborne chemicals released from the backswimmer *Notonecta*, and phenotypic plasticity included rapid juvenile growth to a large size at the first reproduction (Black 1993). Spitze (1991) found that in the presence of *Chaoborus* predation, populations evolved towards a larger body size and earlier reproduction. Wilson and Hebert (1993) found that asexual populations of *Daphnia pulex* in Manitoba had predation-resistant clones that had a smaller body size in the second and third instars, but a consistently longer tail spine in every juvenile instar in response to copepod predation.

Individual daphnids as well as their eggs are vulnerable to copepods. Copepods prey on small-bodied species and on early instars. However large *Daphnia* species are vulnerable to predation by the early copepodite stages which invade brood chambers and feed on eggs and embryos (Gliwicz and Lampert 1994a, Gliwicz and Umana 1994b).

In addition to predators, parasites may also affect *Daphnia* life histories. Daphnids

are often found with a variety of epibionts attached to the heads and carapaces. *Daphnia* in Red Rock Canyon pools during the sampling year had epibionts attached including fungi, algae and rotifers. Epibionts reported in the literature include diatoms (Gaiser and Bachman 1993, Allen et al. 1993), diatoms and euglenoids (Chiavelli et al. 1993), and euglenoids, chlorophytes, and ciliates (Threlkeld and Willey 1993). Negative effects on population dynamics reported include impaired reproduction (Threlkeld and Willey 1993) and higher death rates (Allen et al. 1993).

Daphnia are planktonic suspension feeders; they feed on algae, bacteria, fungi, protozoa, and detritus (Hebert 1978). While algae and other protists have been thought to be the chief foods of *Daphnia*, bacteria and detritus are also important sources of food (Pennak 1989). Benthic food sources may be utilized by those pond species which can stir up food particles by scraping the bottom with their thoracic appendages (Lampert 1987). This behavior was shown experimentally in an aquarium with the species *D. magna* and *D. pulex* (Horton et al. 1979).

Temperature, in addition to its previously discussed effects on life history and reproduction in daphnids, also affects a daphnid's metabolism. Meijering's (1975b) studies of metabolic activity using heart rates of *Daphnia* populations in cold Arctic and central European biotopes showed that the heart rates of females in the arctic were a little slower than those of daphnids from temperate regions.

Some other physiological modulators of respiration are oxygen concentration, light, container size, and crowding (Lampert 1984). Oxygen is exchanged over the entire surface of a daphnid (Peters 1987) with especially high rates on limb surfaces as befits the

Branchiopoda. *Daphnia*, particularly those in small pools, are subject to highly variable oxygen regimes. *Daphnia* have a constant, flea-like, hopping motion. This motion allows them to change their position so that each new immediate environment has renewed food and available oxygen.

PRINCIPLE HYPOTHESES OF THIS STUDY

If similar to congeneric and conspecific populations in other ephemeral habitats, the life histories of *Daphnia* found in the temporary pools in Red Rock Canyon should respond as described below to considerable seasonal and annual variation in the length of time water is present in each pool, to temperature, oxygen, conductivity, and pH, and to the presence or absence of invertebrate predators.

The presence and timing of various life history stages, such as the production of ephippia, brood size and the size of the smallest ovigerous female, are likely related to these environmental variables. High temperatures in summer, evaporation of water from the pools with accompanying increased conductivity and a more alkaline pH, reduced oxygen tensions, crowding, and invertebrate predation are some of the potential primary effectors of life history patterns in Red Rock Canyon temporary pools.

My research objectives in this study are to test the following hypotheses relative to the life histories of *Daphnia* species found in the temporary pools in Red Rock Canyon.

Environmental effectors of *Daphnia* population size and population dynamics:

1. Pool depth

H_O There is no effect of pool depth on number or dynamic properties of *Daphnia* populations

H_A There is such an effect

2. Pool water temperature

H_0 There is no effect of pool water temperature on the number or dynamic properties of *Daphnia* populations

H_A There is such an effect

3. Pool water conductivity

H_0 There is no effect of pool water conductivity on the number or dynamic properties of *Daphnia* populations

H_A There is such an effect

4. Pool water pH

H_0 There is no effect of pool water pH on the number or dynamic properties of *Daphnia* populations

H_A There is such an effect

5. Pool water oxygen tension

H_0 There is no effect of pool water oxygen tension on the number or dynamic properties of *Daphnia* populations

H_A There is such an effect

6. Pool duration

H_0 There is no effect of pool duration on the number or dynamic properties of *Daphnia* populations

H_A There is such an effect

In addition, I will, as possible with the given data set, consider pool-to-pool and seasonal differences in the size of the smallest ovigerous female, brood size, and environmental effectors of *Daphnia* ephippial production. This information should be

important in determining the environmental factors underlying observed differences in reproduction between the two species of daphnids present in these pools.

METHODS AND MATERIALS

Site Description

The Red Rock Canyon Conservation Area is located approximately 33 km west of Las Vegas, Nevada at $36^{\circ} 9' N$ and $115^{\circ} 26' W$ (United States Department of the Interior Geological Survey, La Madre Mtn. Quadrangle, State of Nevada, 1972). I sampled seven temporary pools (Figures 1a and 1b) in the wash area of a canyon along the eastern base of the Red Spring Thrust (Fiero 1986), commonly known as the Calico Hills, in the Red Rock Canyon Conservation Area.

The Aztec Sandstone bluffs, above the area of the wash containing the pool system, reach an elevation of approximately 1418 meters. This site is at the second overlook on the 13 mile (21.6 km) Red Rock Scenic Drive. Access to the pool system is provided by an improved hiking trail down into the canyon below the scenic drive. The pools lie between an elevation of 1167 and 1183 meters.

These shallow pools are found in natural sandstone depressions along the path of water flow through the wash. The bottoms of the pools are of rocky cobble and sand derived from surrounding sand- and limestone strata. The collection sites are within about a 230 meter reach along a 20 meter elevation gradient at the base of the Calico Hills.

The pools are of various volumes and sizes (Table 1). They differ in their exposure to the sun because of their different locations and configurations. They are often short-lived and are dependent on unreliable, infrequent precipitation in the Spring Mountain Range (Figure 2).

MAP OF POOLS IN RED ROCK CANYON, NEVADA

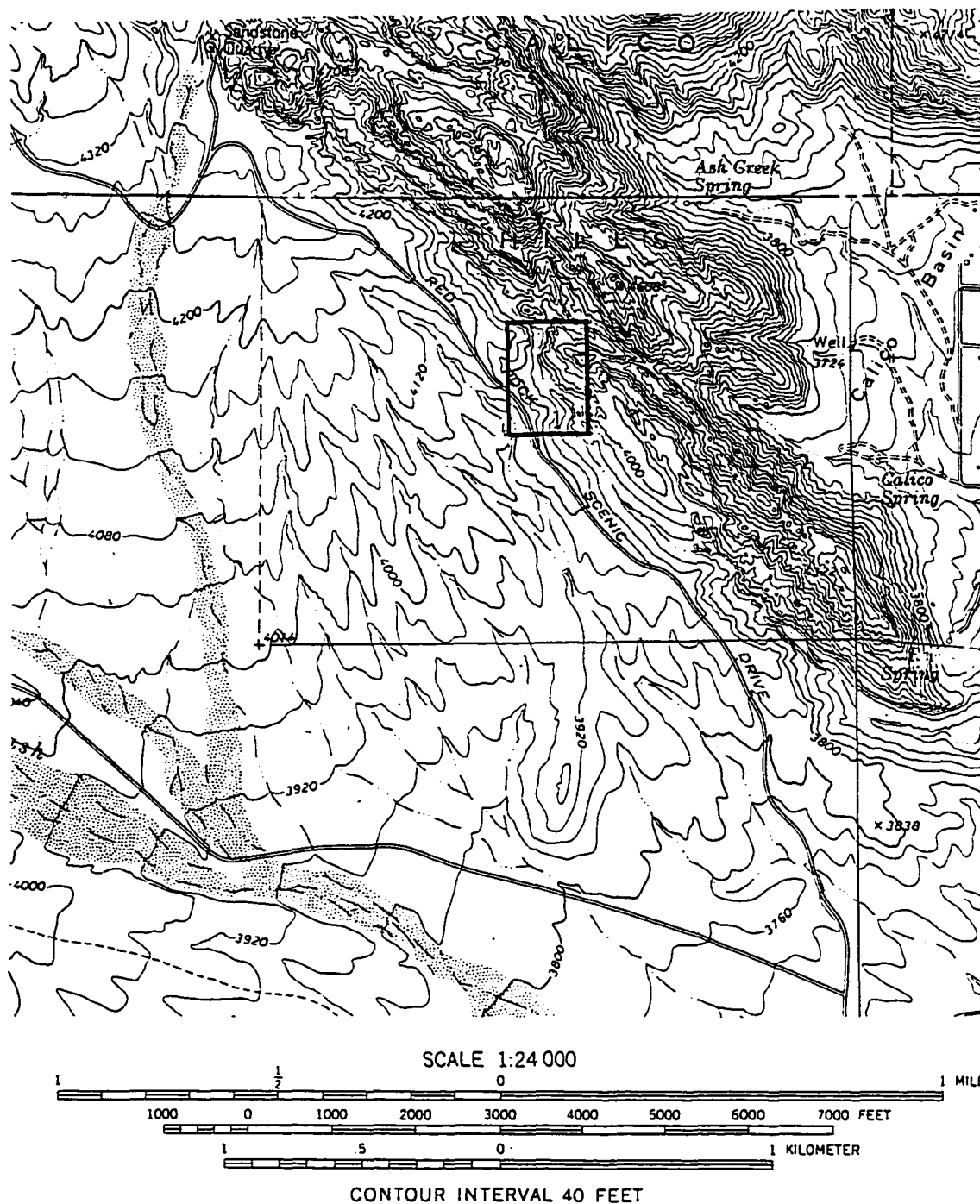


Figure 1: Topographic map of Red Rock Canyon, Nevada. The seven pools are located in the wash at the base of the Calico Hills. The boxed section contains the area where the seven pools are located. From the La Madre Mtn. Quadrangle, Nevada--Clark Co. (NW/4 Blue Diamond 15' Quadrangle) U. S. Geological Survey.

Table 1: Description of seven ephemeral pools in Red Rock Canyon, Nevada.

Pool #	Elev. in meters	Distance from Pool 1 in meters	Max. Depth in cms	Max. length in cms	Max. Width in cms	Dry during year	DESCRIPTION
1	1167	0	91	480	110	yes	Deep crevice between blocks of sandstone; midday sun
2	1169	5.4	55	330	175	yes	Shallow, oval; full sun all day
3	1175	153.9	64	320	280	yes	Shallow, circular, below sandstone cliff; full afternoon sun
4	1178	168.4	40	1200	200	yes	Long, shallow crevice between blocks of sandstone; shaded all day
5	1180	190.4	65	520	280	yes	Oval, beneath a block of sandstone to the north; full sun all day
6	1181	204.4	120	840	330	no	Deep, oval, extends back under a rock overhang; midday sun
7	1183	229.1	61	815	400	yes	Shallow, circular, below sandstone cliff; midday sun

Precipitation in cm During Two Weeks Before Sampling Dates

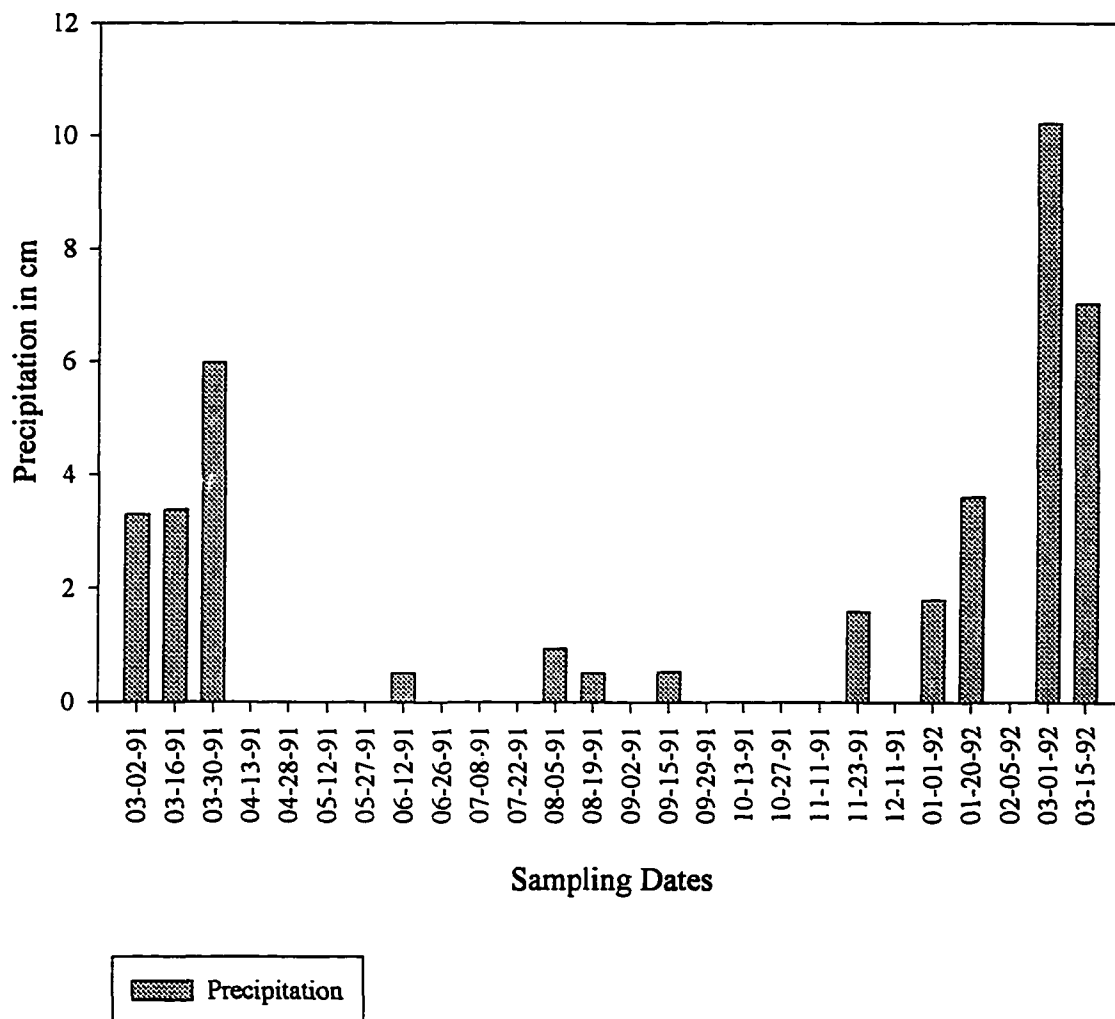


Figure 2: Precipitation in cm during two weeks before each sampling date recorded at the Red Rock Canyon Station 1 km away from sampling sites (from Climatological Data for Nevada from National Oceanic and Atmospheric Administration).

All pools are atypical according to the criteria of Wiggins et al. (1980) but because of their location in a wash these pools can receive species introduced by surface connections from pools upstream in the wash following rainfall. However, due to infrequent rainfall, the pools are isolated from each other for all but brief periods during the year. When abundant rainfall occurs the swift flowing water is like a river with all pools connected. The pools are deluged and scoured by these infrequent flash floods. When water stops running down the wash and collects and stands in the pools for a period of time, hatching of ephippia and/or production of eggs by any remaining daphnids allow *Daphnia* population growth.

During the twelve month collection period, all pools were dry at various times except Pools 1 and 6. These pools were designated as the most permanent. Pool 4 was the most productive (containing the largest number of daphnids per liter at any one time). Daphnids from these three pools were studied most closely with respect to biological and ecological (microlimnological) features.

General Community Structure

Occasionally fairy shrimps, Order Anostraca, tentatively identified as *Streptocephalus*, were present in Pools 3 and 4 during the summer and fall. A few clam shrimps, Order Conchostraca, were present in Pools 1, 2, and 4, but only during the summer.

Numerous copepods, both calenoid and diaptomid, (including the nauplius stages, copepodid stages and females with ovisacs) were present most of the sampling year in all of the pools.

Ostracods, small bivalved crustaceans also known as seed shrimp (Tressler 1959), were numerous in all pools throughout the year. At least two types were present, and the dominant type has been tentatively identified as *Cypria* sp. (F. W. Bachhuber pers. commun. 1996). Difficulty was encountered in species identification because the preservation technique utilized with the Cladocera was not conducive to the ideal preservation of ostracods. The preservation technique using sugar formalin (Haney and Hall 1973) made the shells soft, pliable, and difficult to open, and, consequently, hard to identify.

Various insects were present including notonectids and predacious diving beetles (Appendix I). Red water mites (order Acarina and tentatively identified as Trombiculidae) were also present (C. Murvosh pers. commun. 1996).

The only vertebrates noted in these pools during sampling trips were tiny (2.5 cm), red-spotted toads which were identified as *Bufo punctatis* (S. Hillyard pers. commun. 1991). Amphibian eggs were seen during the spring and summer, and numerous tadpoles

were found during the summer and fall. *B. punctatis* tadpoles scrape surfaces with their denticles. They then filter food particles from the turbid water. It is highly unlikely that they prey on daphnids (K. Hoff pers. comm. 1996).

I observed that water in the pools was clear after the pools were inundated and scoured by rainwater flowing through the wash. Sometimes, when water had been undisturbed for awhile, pool water was brown in color, opaque, and filled with debris. At other times the water took on a distinctive green coloration. At these times I observed free *Volvox* colonies and one-celled green algal epibionts. Algae was present in greatest numbers during late summer and early autumn. Water samples often contained so many *Volvox* colonies that when I examined the sample microscopically there were too many to count. I also saw algal epibionts attached to the heads and carapaces of the cladocerans.

Identification and Collection of Specimens

Using Brooks (1957) description of *D. pulex*, Hebert's revision of North American *Daphnia* (1993), Schwartz, Innes and Hebert's (1985) and Hebert's (CD-ROM in press) discussions of the morphological features that separate *Daphnia* species, I verified that the species in Red Rock Canyon were *D. pulex* and *D. obtusa*. In addition, I received type specimens of *D. pulex* from Dr. Hebert (which he designated as *D. nevadensis*, unpublished) and *D. obtusa* that he collected in Red Rock Canyon (P. D. N. Hebert, pers. commun. 1991). I used these specimens to compare and identify the individuals from Red Rock Canyon samples that I collected during the course of this study.

D. obtusa may be distinguished from *D. pulex (nevadensis)* by morphological features including the shape of the head, and presence of a pronounced antennular mound in *D. obtusa* (Figure 3) (Schwartz, Annes and Hebert 1985; P. D. N. Hebert, pers. commun. 1991). *D. pulex* generally has a concave area on the anterior part of the head (Haney and Buchanan 1987). As discussed above, Schwartz et al. (1985) demonstrated the presence of *D. obtusa* in North America when heretofore *D. obtusa* was not recognized in taxonomic surveys (Brooks 1957).

I visited and sampled the pools 26 times between March 3, 1991 and March 15, 1992 at approximately two week intervals. I collected all samples between 10 a.m. and 4 p.m. I obtained samples from the mid-point of each pool, and from about 10 to 30 cm below the surface when possible. The sampling depths differed due to variations in sizes of the pools and in the depths of the water in each pool from visit to visit. I decided not to

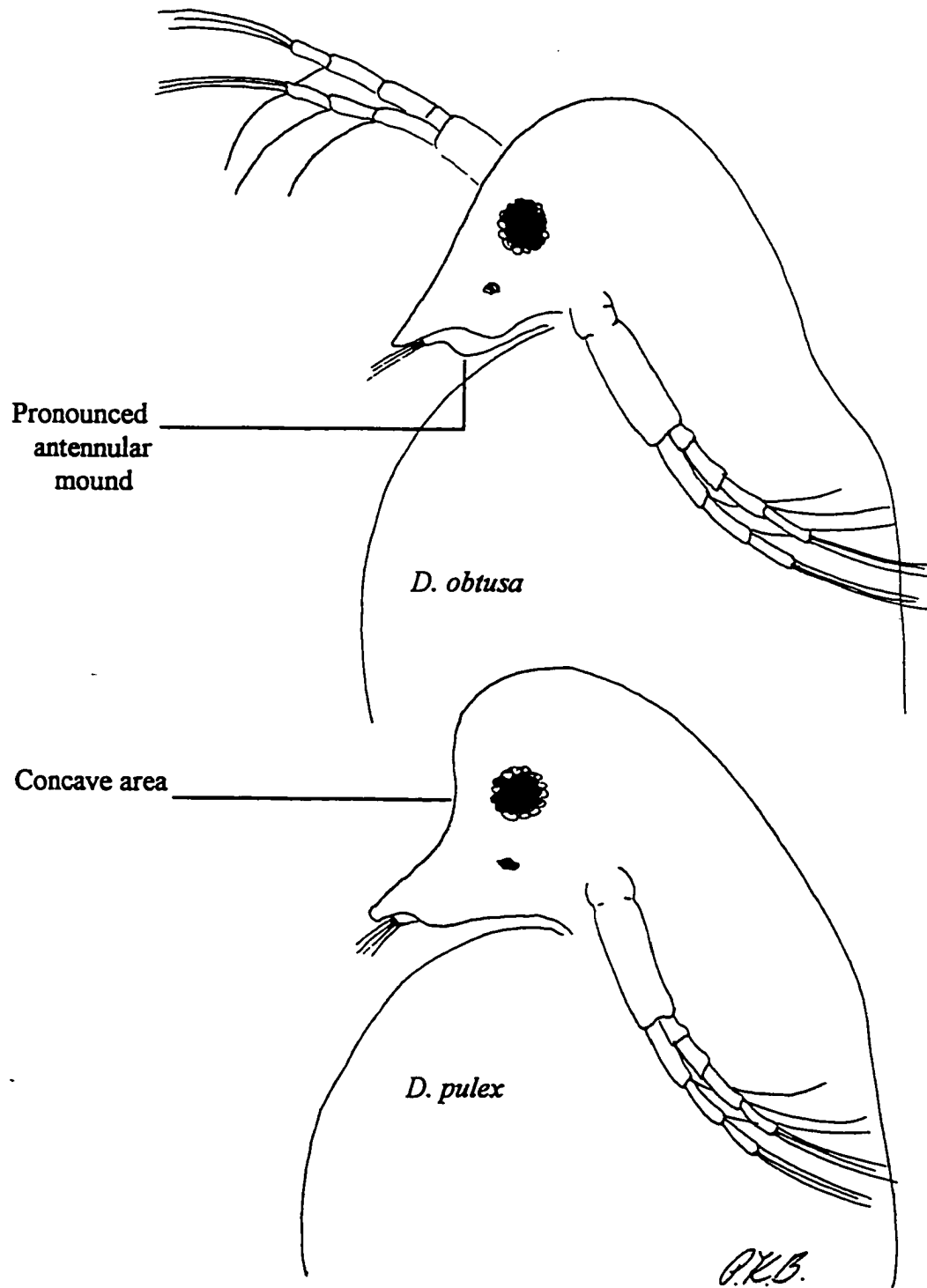


Figure 3: Morphological features used to distinguish *D. obtusa* and *D. pulex*.

use a plankton net because most pools were too shallow or small, and instead obtained samples with a 500 ml. open-mouthed, plastic bottle taped to a pole. Multiple samples were taken when possible, but in some cases would have depleted most, or all, of the remaining pool water when pool depth was low. Also, a significant proportion of the population would have been extricated each time I sampled. Therefore, this rigorous and unusual ecosystem demanded unusual responses in sampling methods. At each pool 1000 to 3000 ml of pool water (depending on the amount of water present) was poured through a Wildco plankton cup and backwashed through a 67 micrometer filter into a Whirlpak bag with about 150 mls of filtered pond water. I also obtained a 500 ml whole water sample from each pond removing a total of 750 mls of water from each pond at each visit.

I measured the depth of each pool in cms at each visit (Figures 4 to 10). I also measured the ambient temperature (Figure 11), and water temperature (Figures 12 to 18). Deluge disturbances (times when pools were full and overflowing due to flooding) and dessication disturbances (times when pools were dry or when water levels were less than 1 cm) are marked with arrows in the figures. Pool temperatures are generally associated with ambient temperatures, but more importantly the pools tend to change in unison (Figure 19).

I suspended the oxygen probe at mid-depth in each pool when the water was deep enough to do so, and measured oxygen in mg l^{-1} with a YSI Model 54A oxygen meter. I then calculated the percent saturation from mg l^{-1} , $^{\circ}\text{C}$ and elevation data (Figures 20 to 26). Low levels of oxygen saturation, probably due to high levels of heterotrophy, will be discussed below. Figure 27, which is a compilation of oxygen data, shows that in general

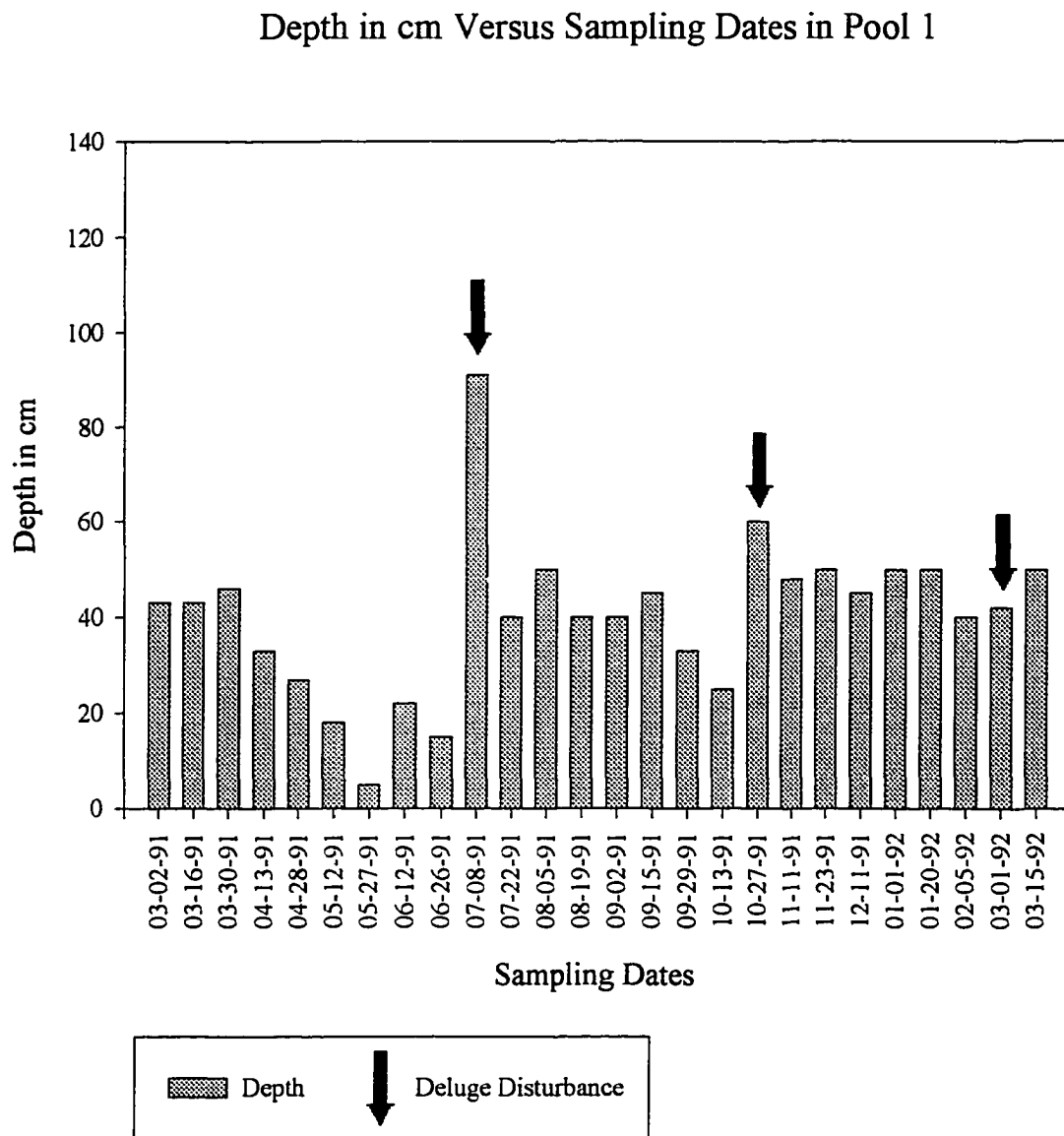


Figure 4: Relationship of depth in cm versus sampling dates in Pool 1.

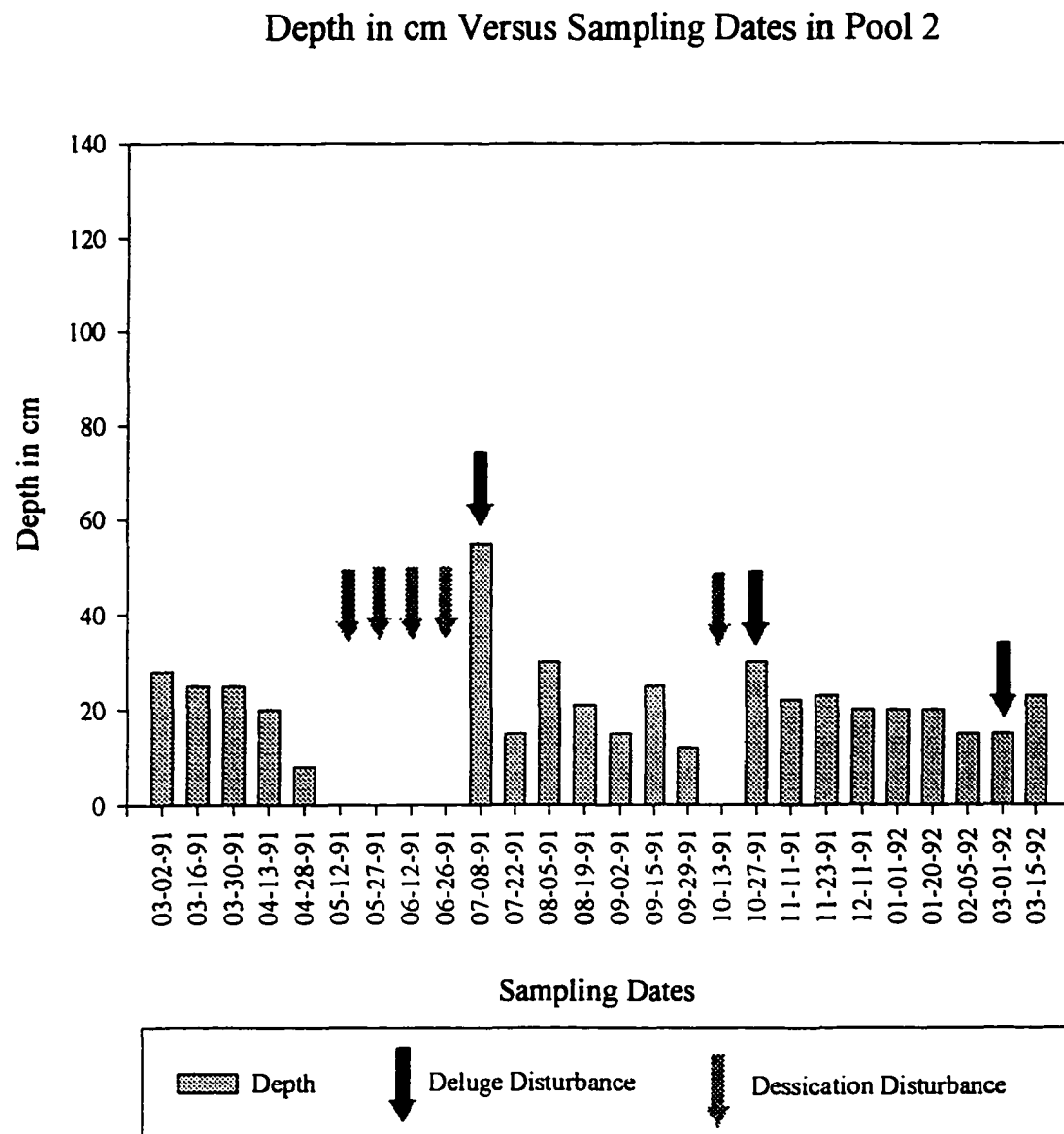


Figure 5: Relationship of depth in cm versus sampling dates in Pool 2.

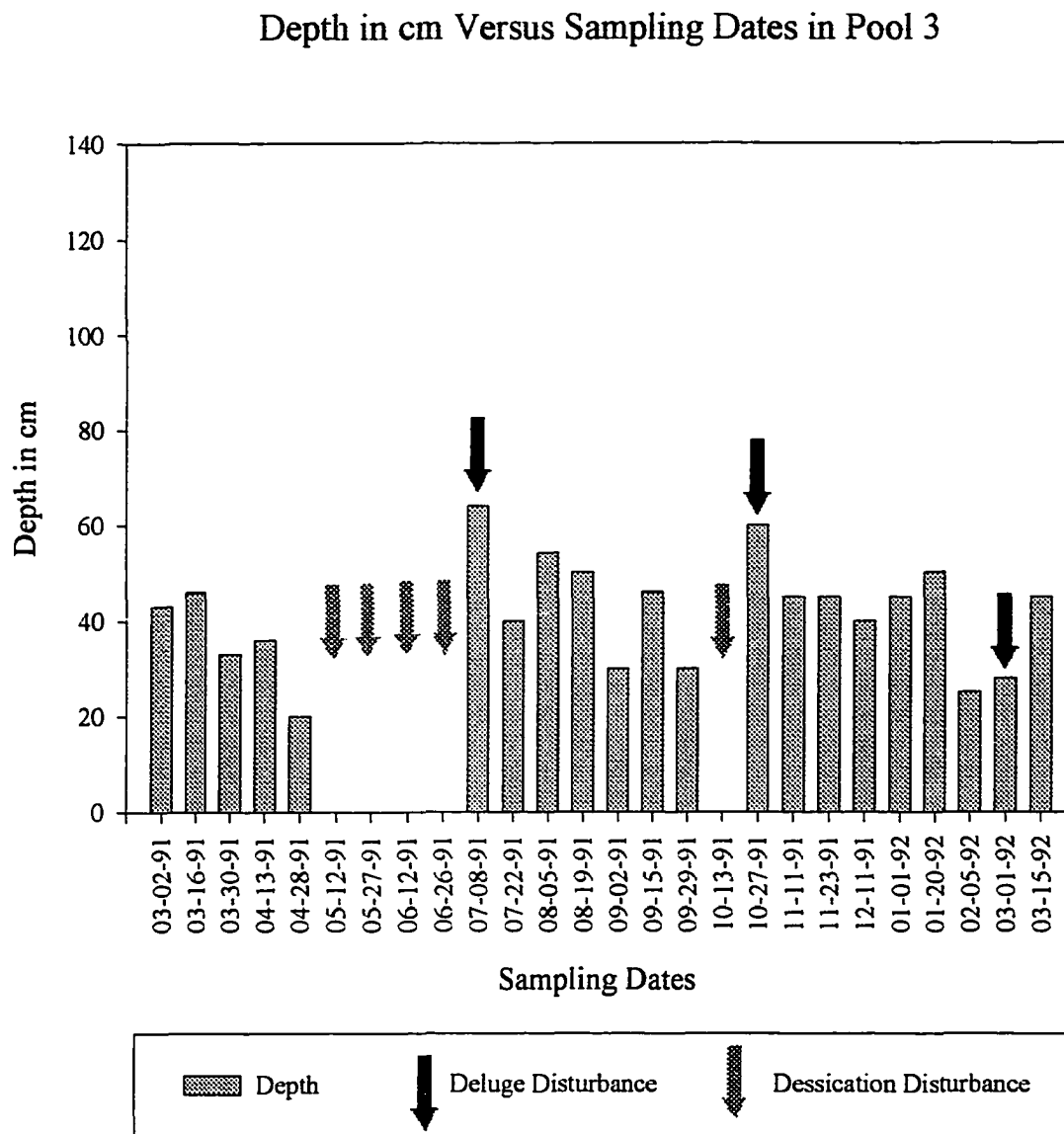


Figure 6: Relationship of depth in cm versus sampling dates in Pool 3.

Depth in cm Versus Sampling Dates in Pool 4

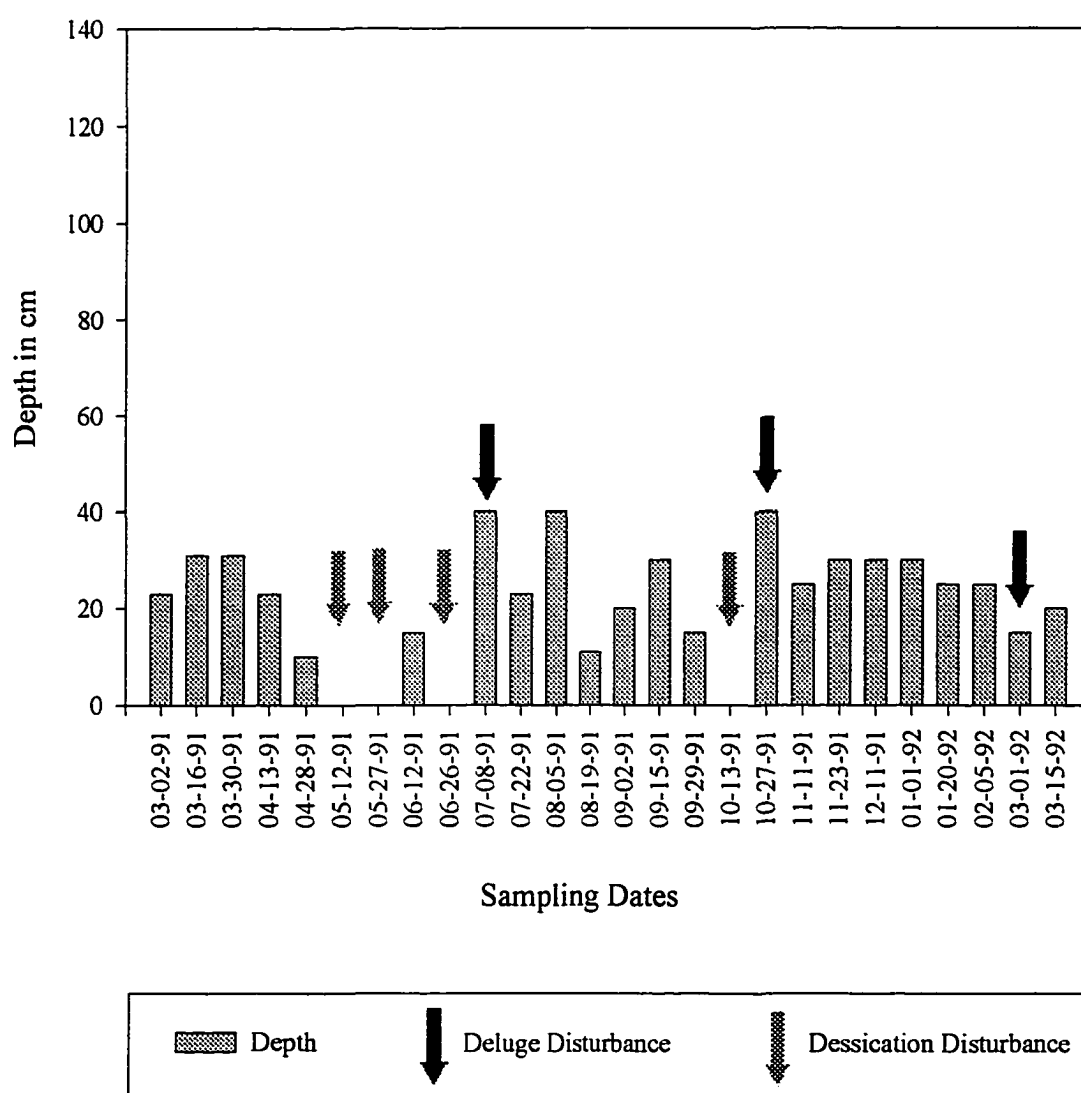


Figure 7: Relationship of depth in cm versus sampling dates in Pool 4.

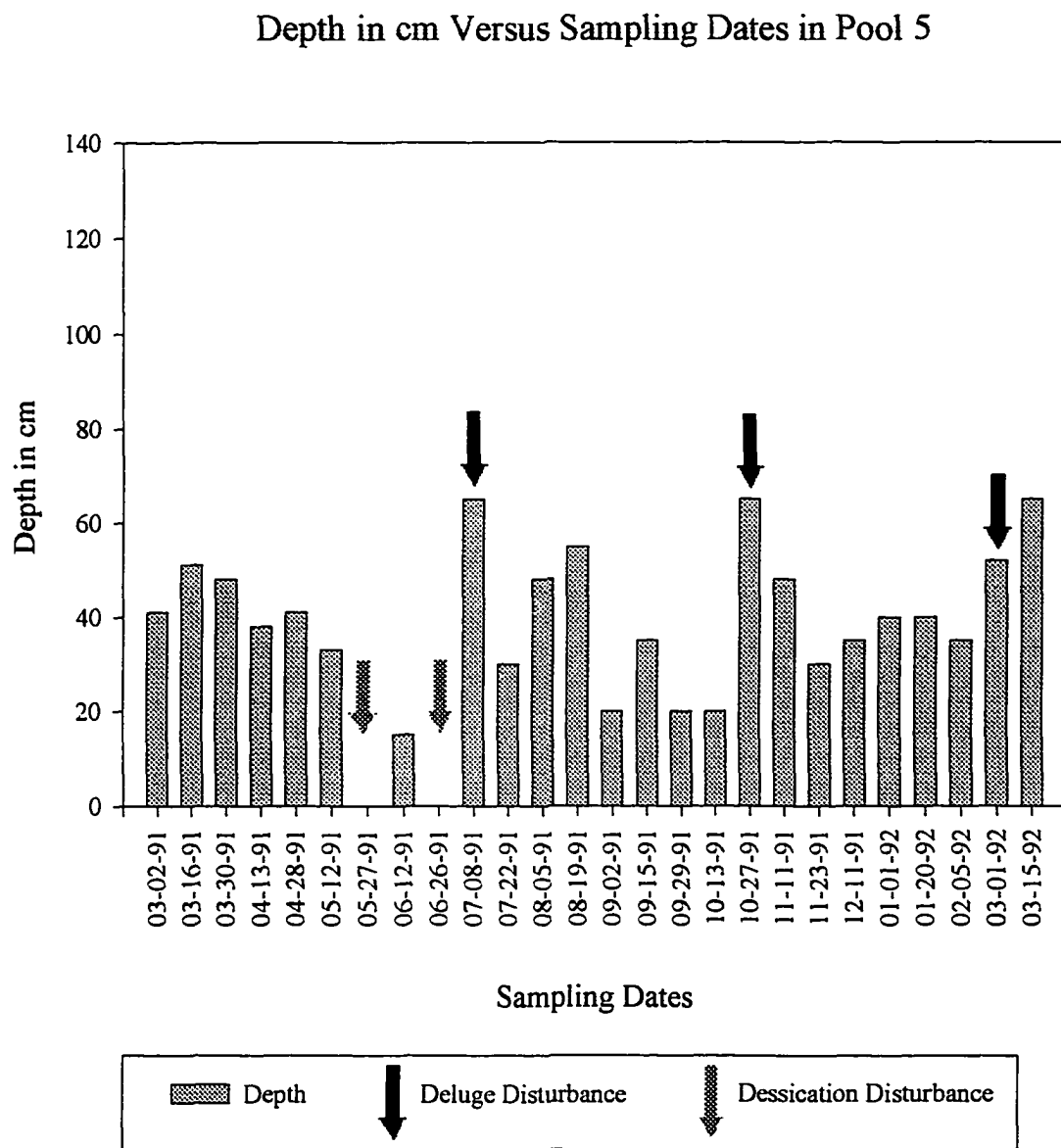


Figure 8: Relationship of depth in cm versus sampling dates in Pool 5.

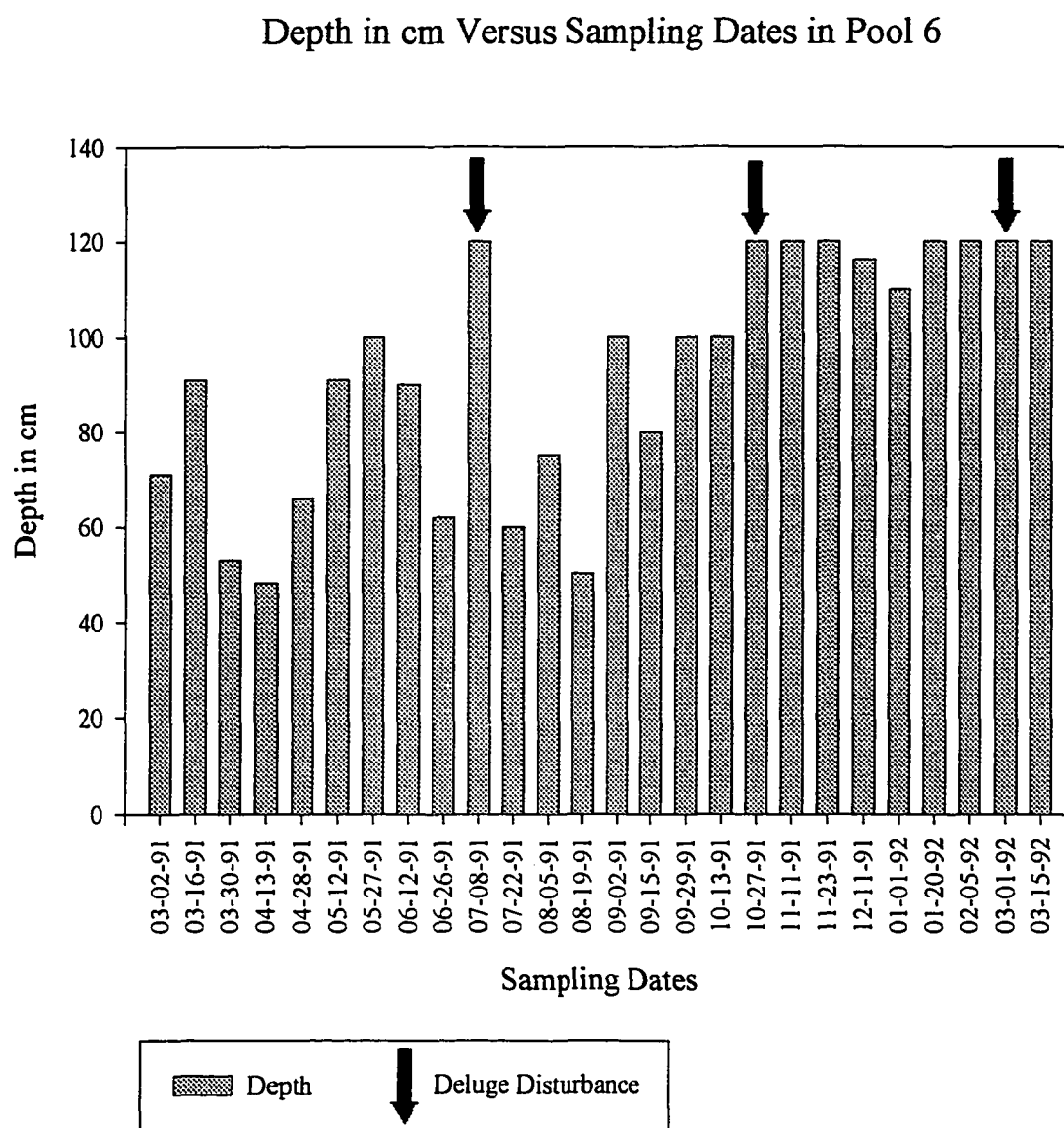


Figure 9: Relationship of depth in cm versus sampling dates in Pool 6.

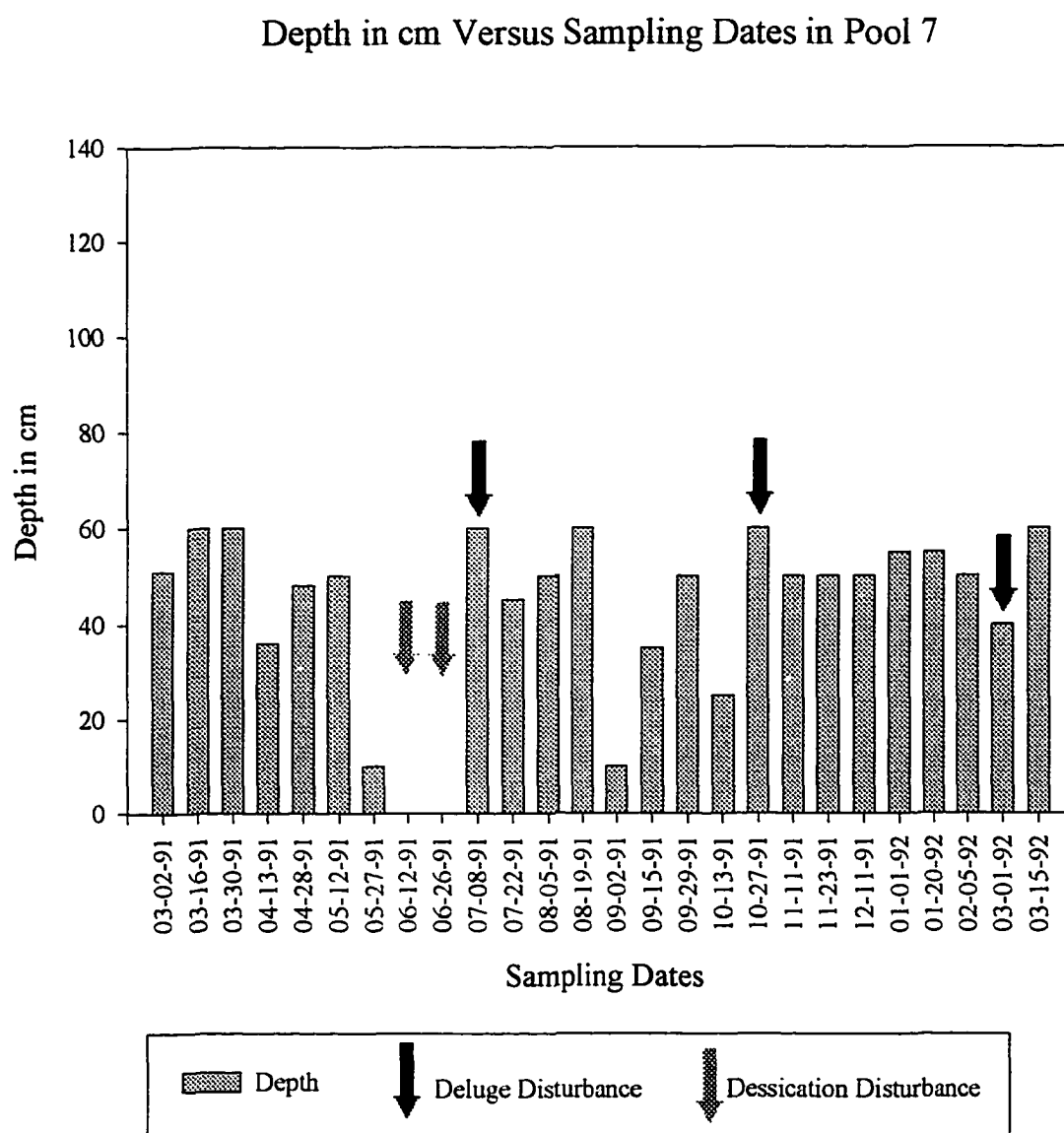


Figure 10: Relationship of depth in cm versus sampling dates in Pool 7. Pool 7, on 3-1-92, may have been measured in a shallow section due to difficult access because of flowing water in the area.

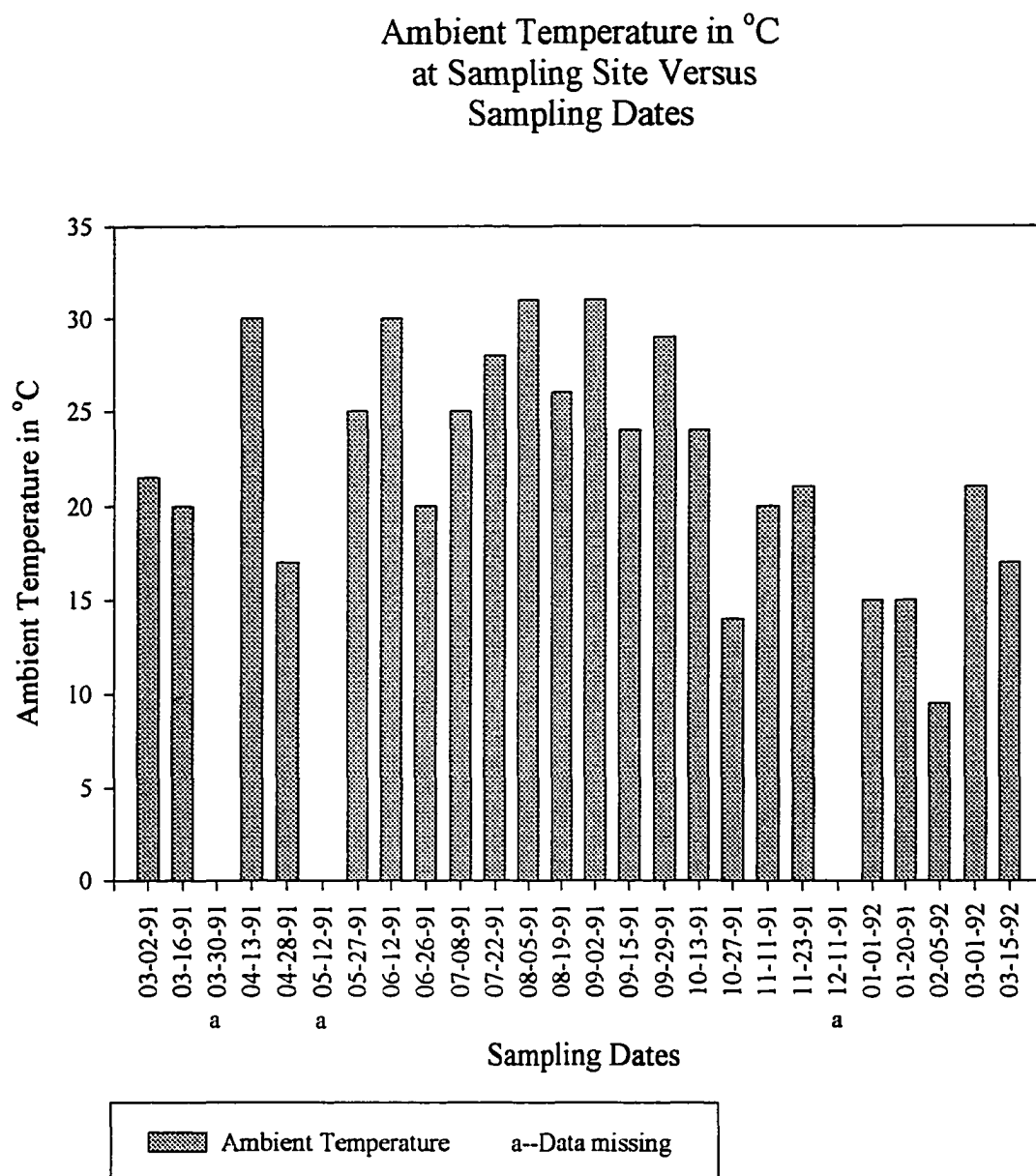


Figure 11: Relationship of the ambient temperature in °C at the sampling site versus the sampling dates.

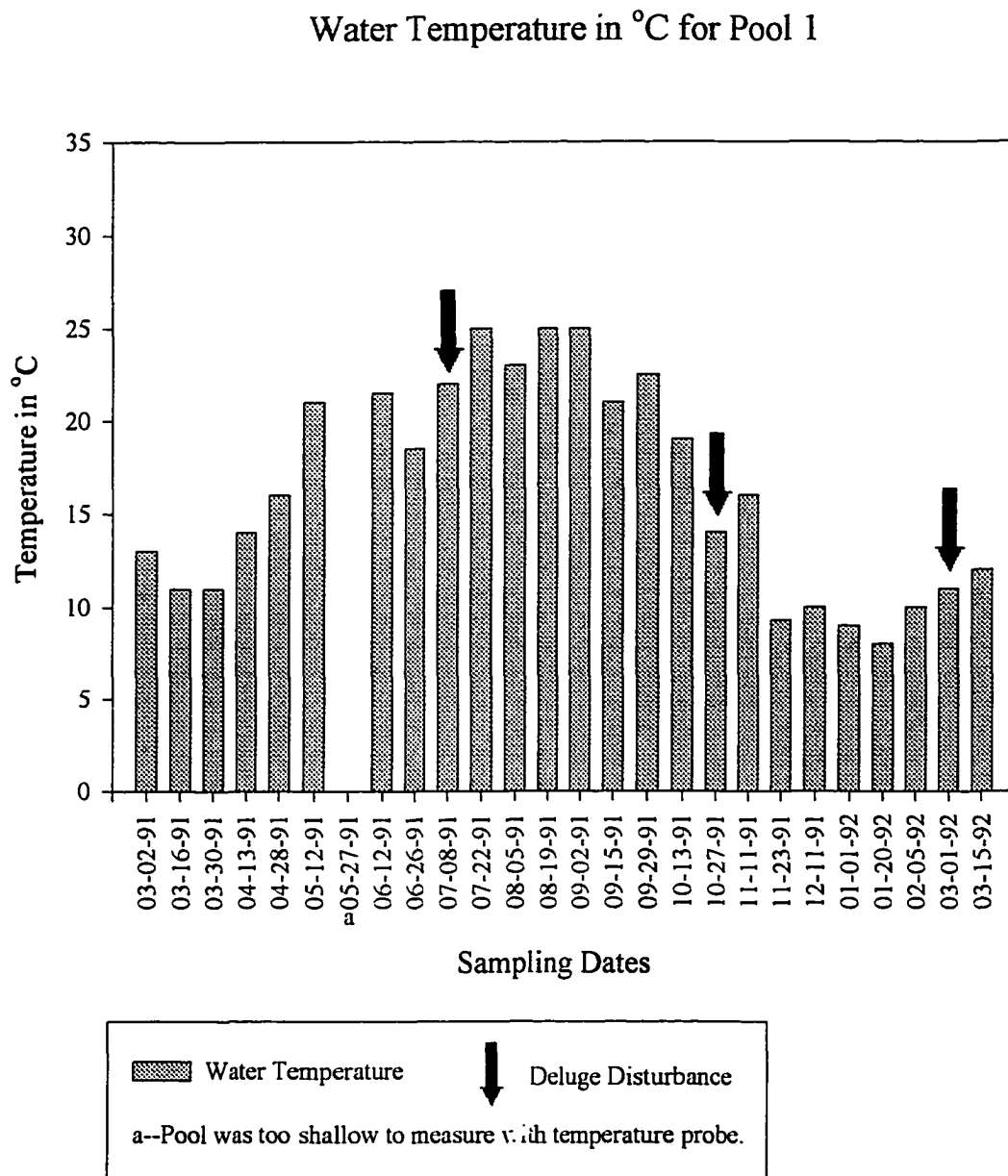


Figure 12: Water temperature in °C for Pool 1 during the sampling year.

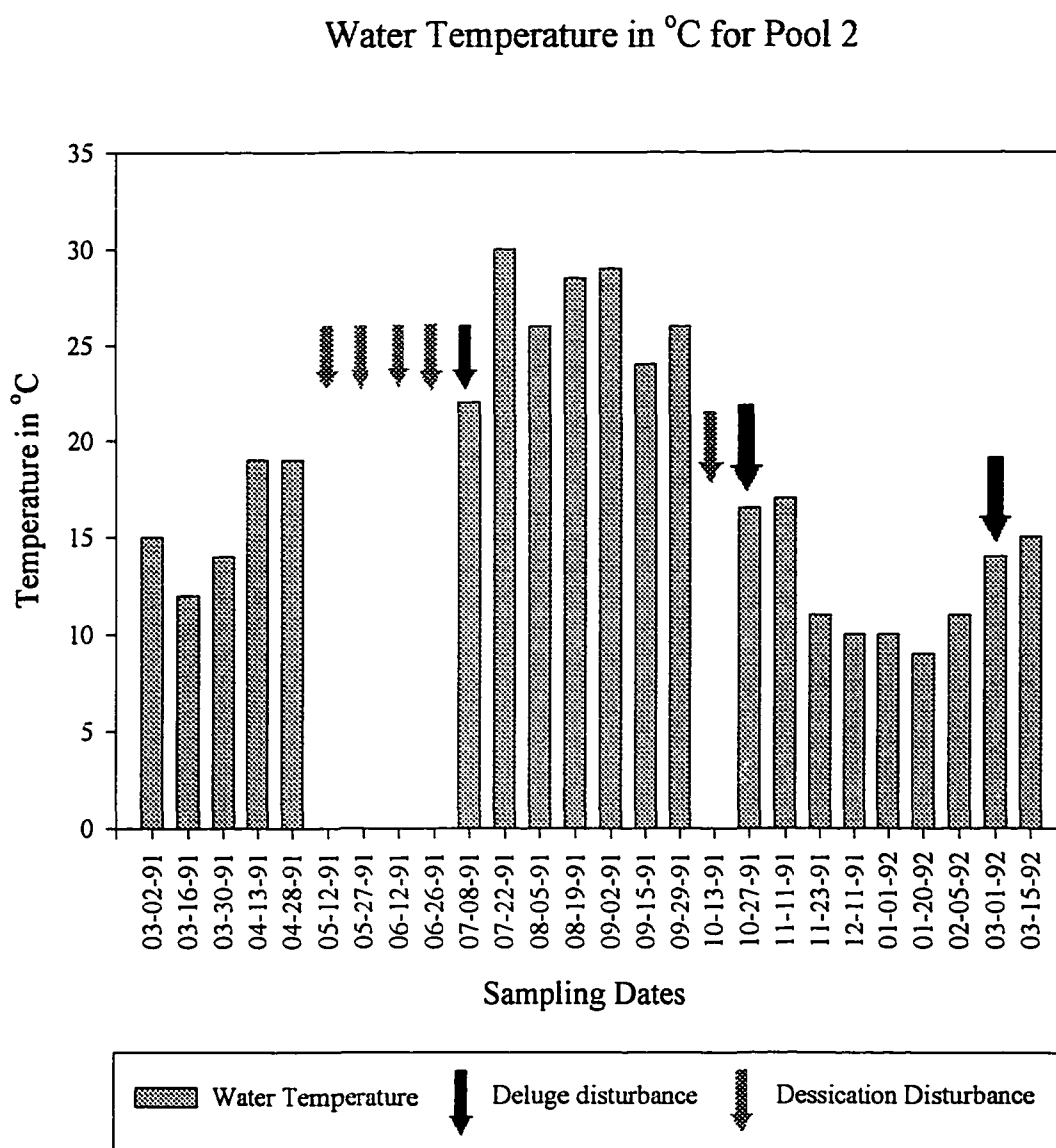


Figure 13: Water temperature in °C for Pool 2 during the sampling year.

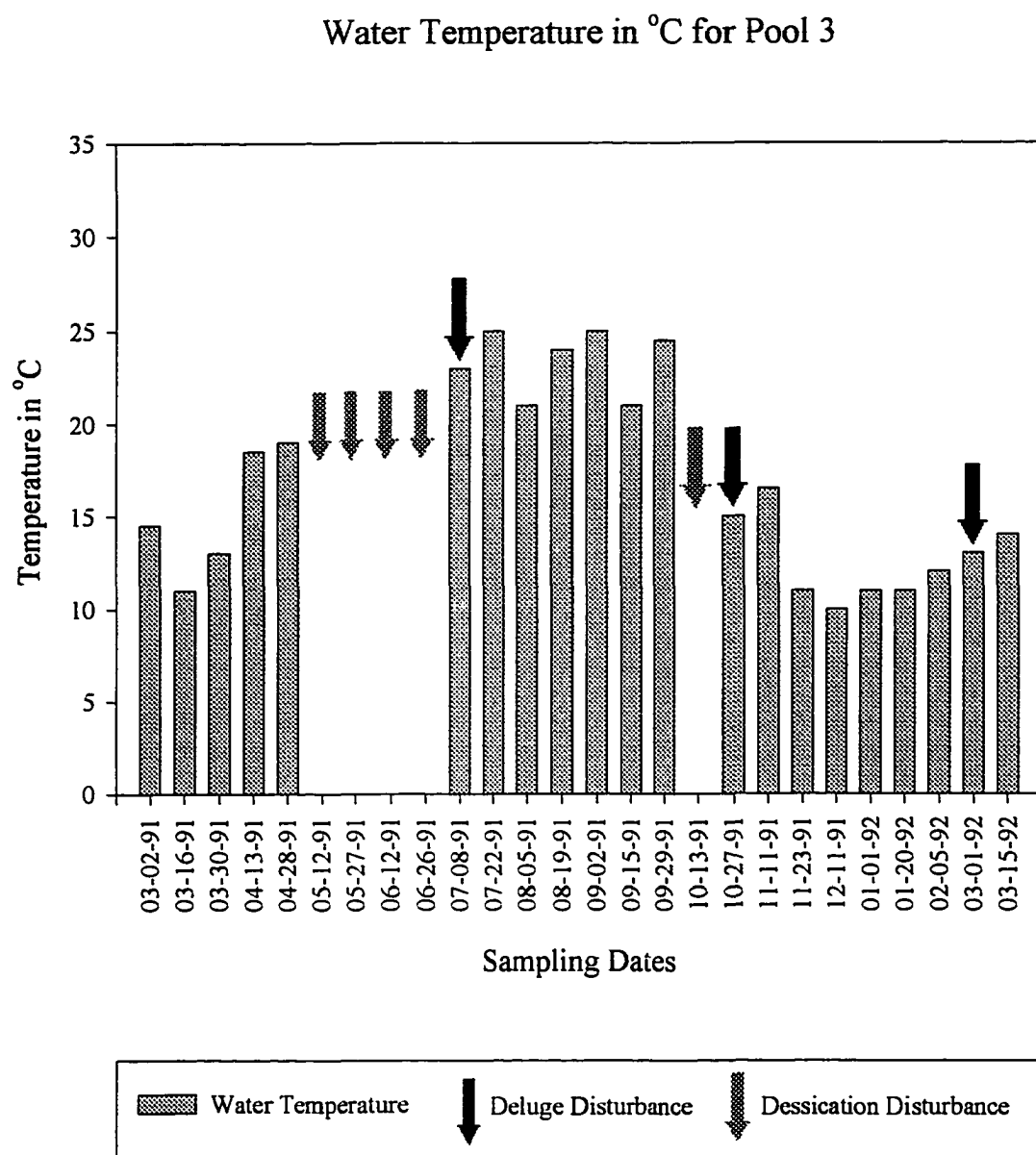


Figure 14: Water temperature in °C for Pool 3 during the sampling year.

Water Temperature in °C for Pool 4

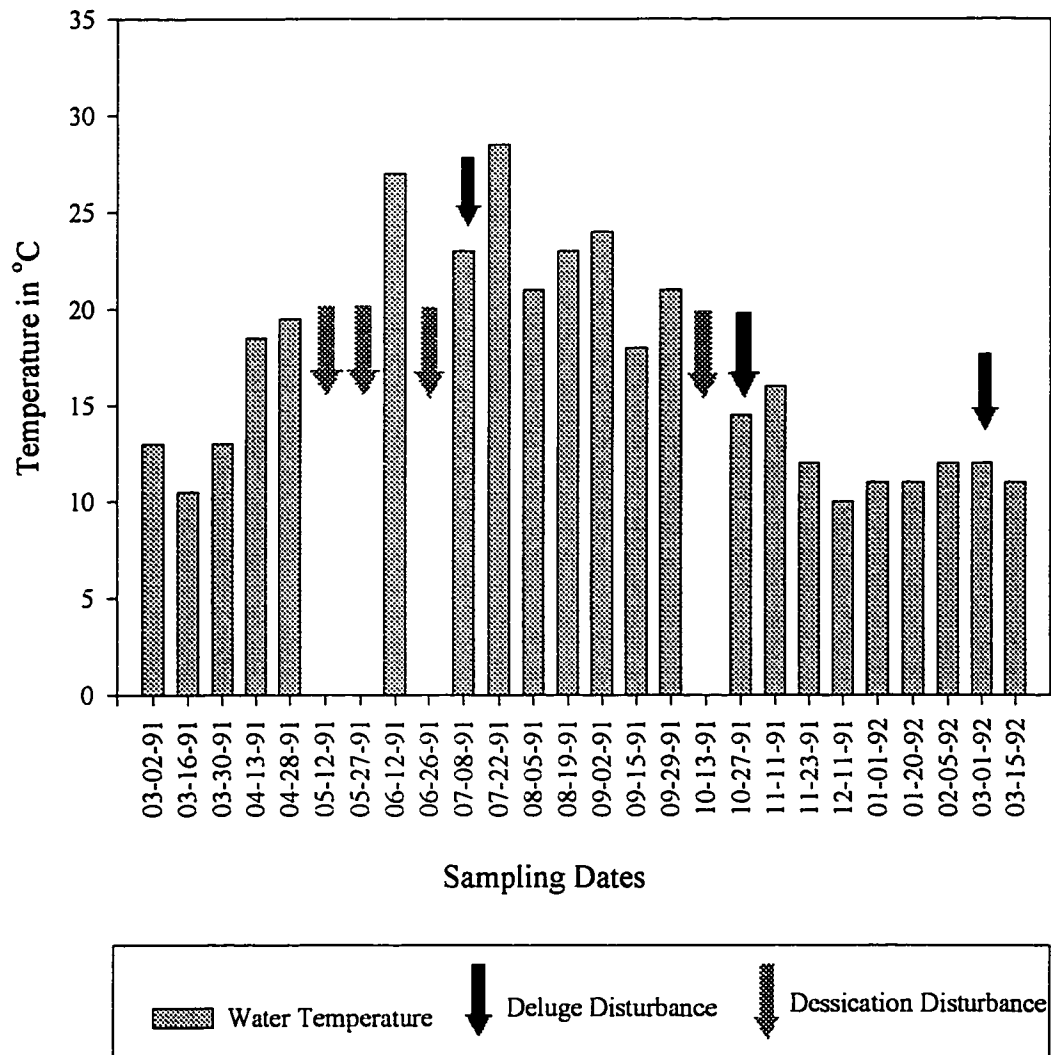


Figure 15: Water temperature in °C for Pool 4 during the sampling year.

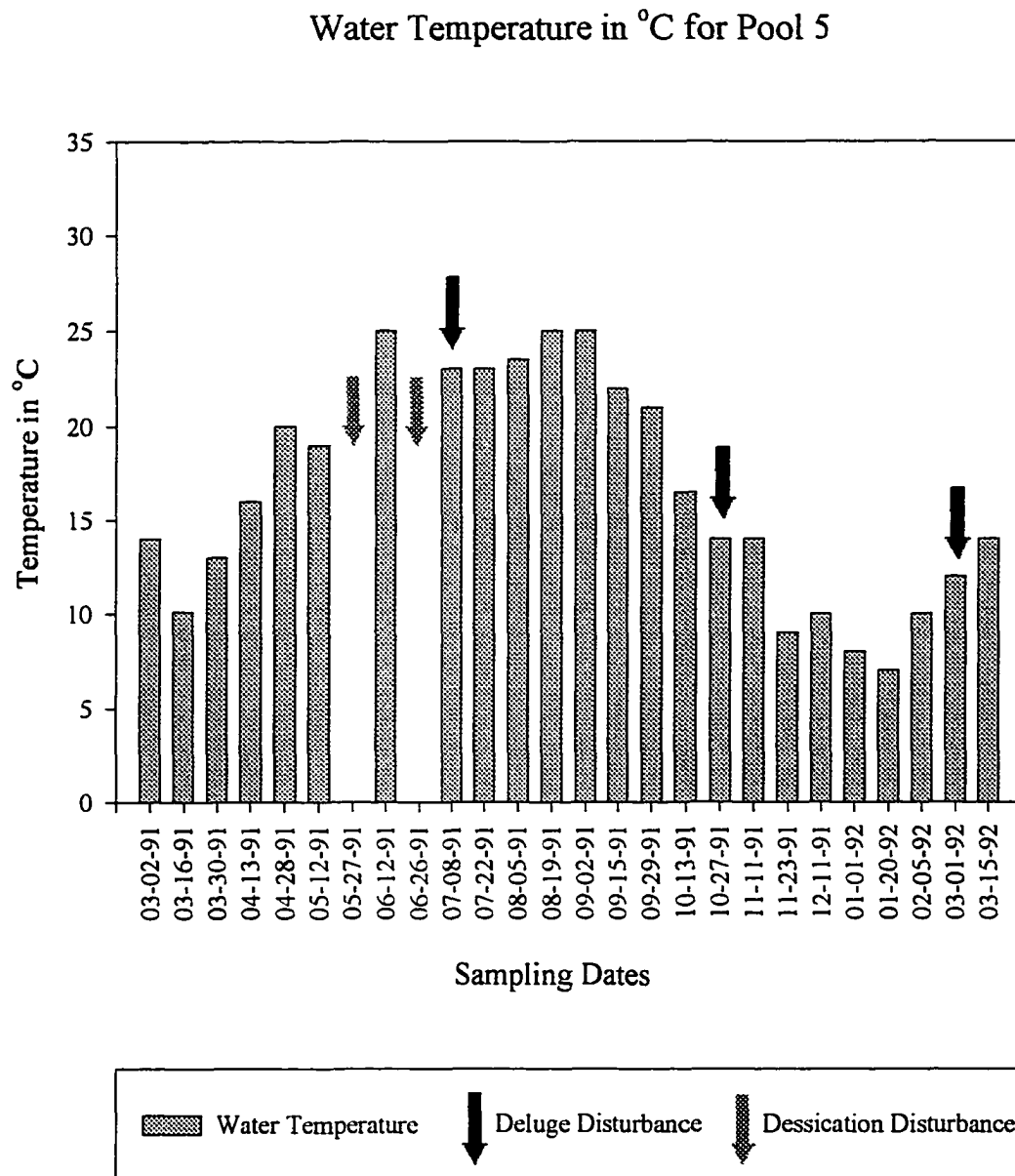


Figure 16: Water temperature in °C for Pool 5 during the sampling year.

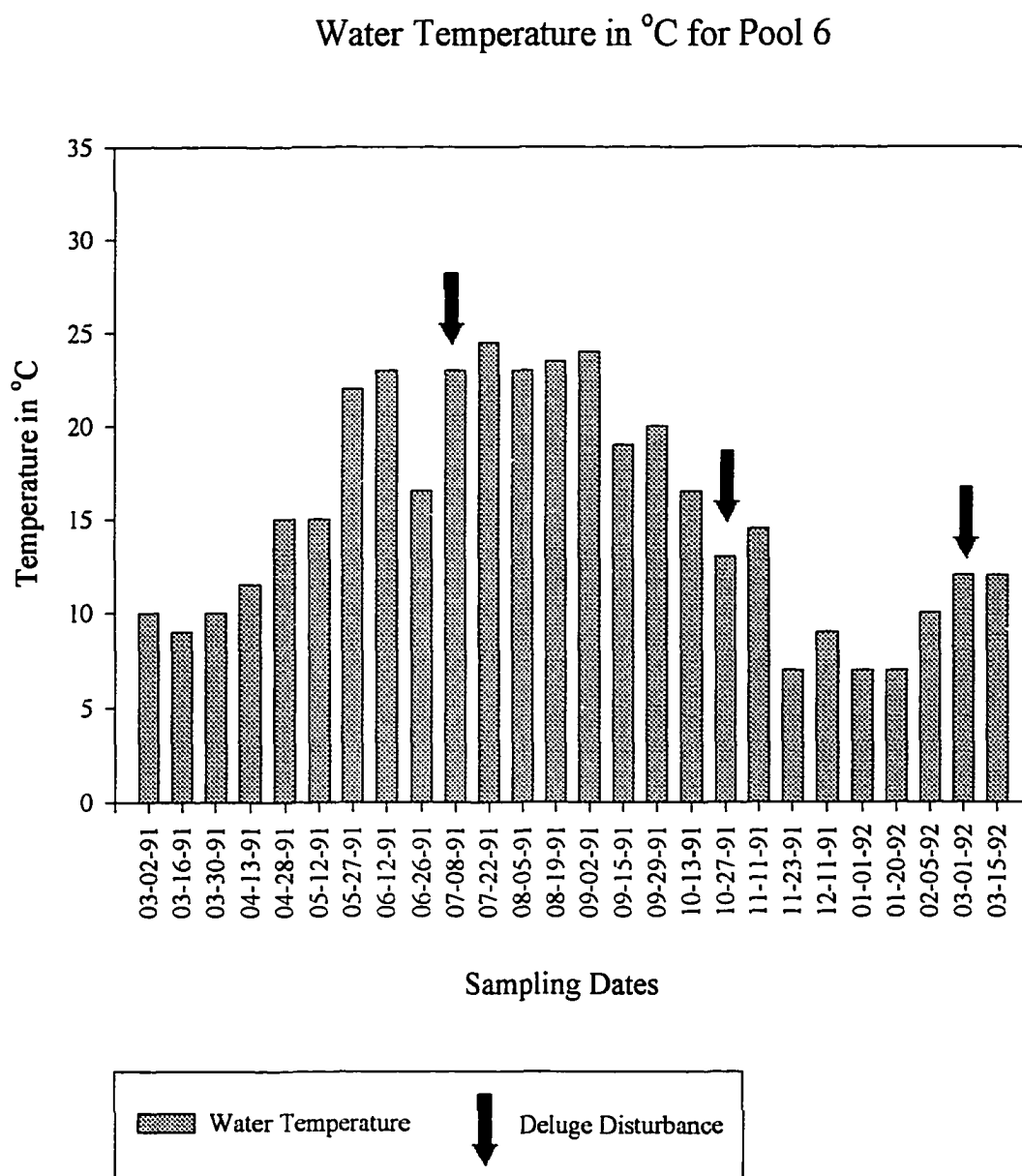


Figure 17: Water temperature in °C for Pool 6 during the sampling year.

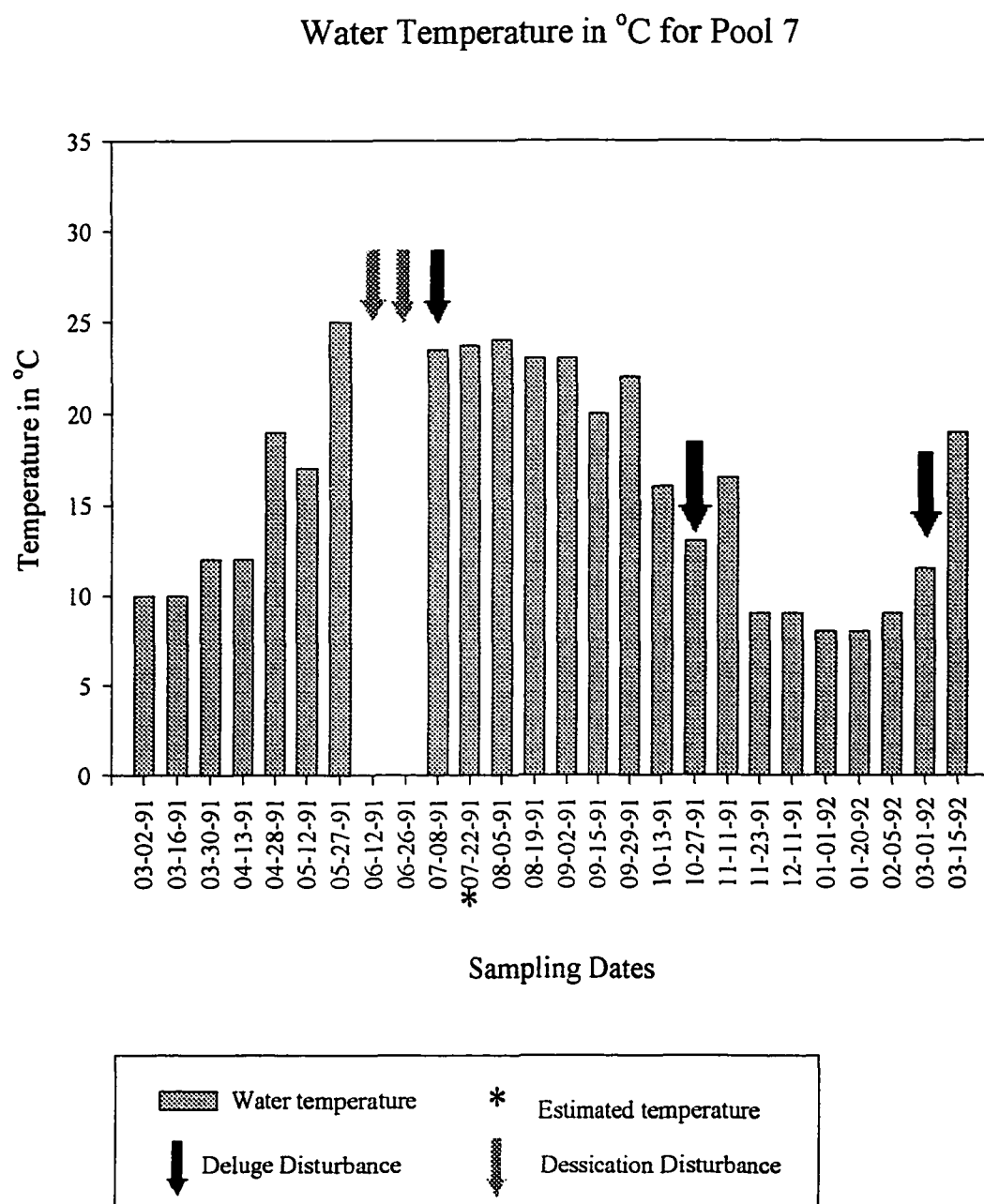


Figure 18: Water temperature in °C for Pool 7 during the sampling year.

Water Temperature for Seven Pools and
Ambient (air) Temperature in °C
Versus Sampling Dates

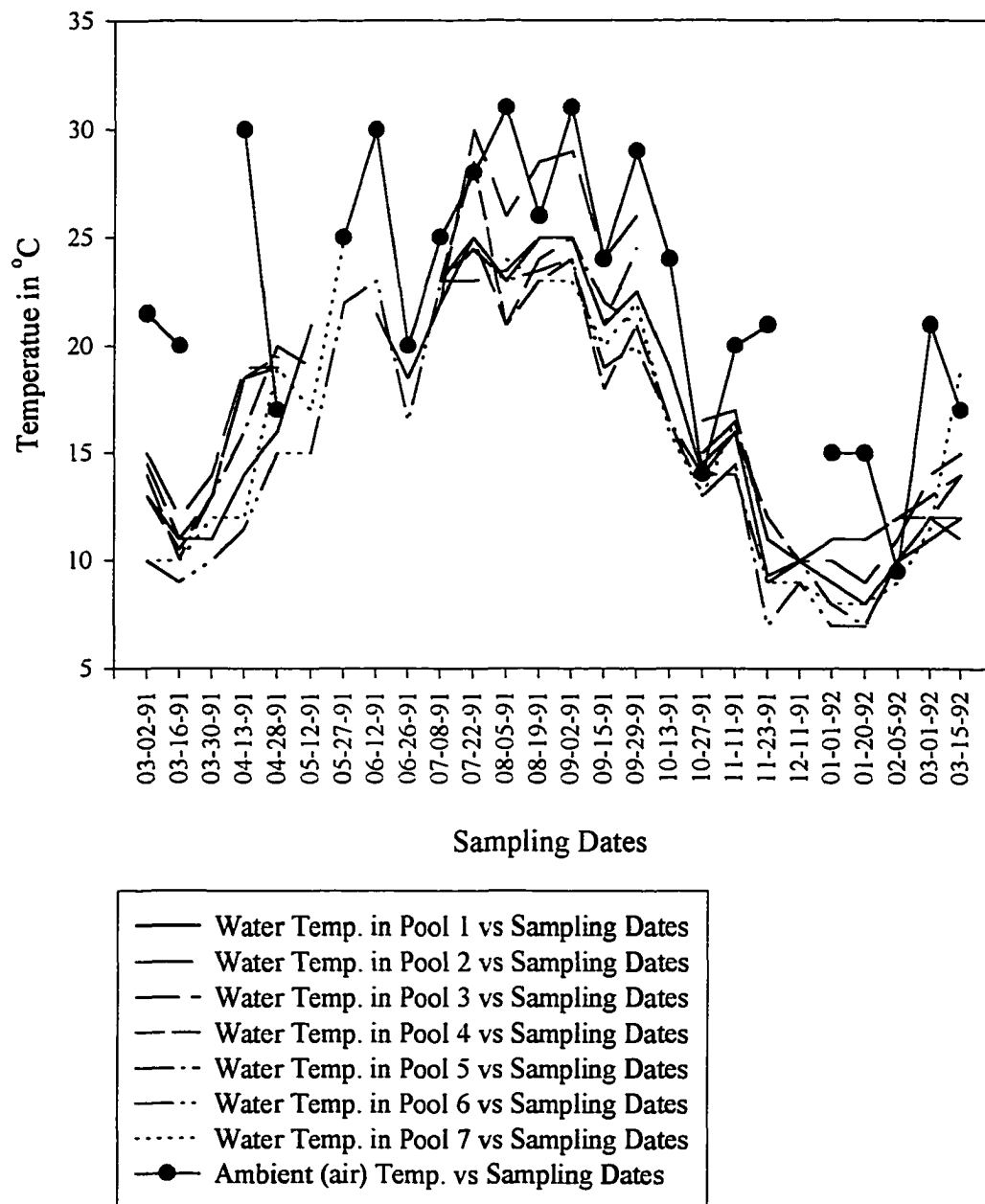


Figure 19: Relationship of water temperature for all seven pools and ambient (air) temperature in °C versus sampling dates. Missing values occur when pools are dry or when data are absent for that date.

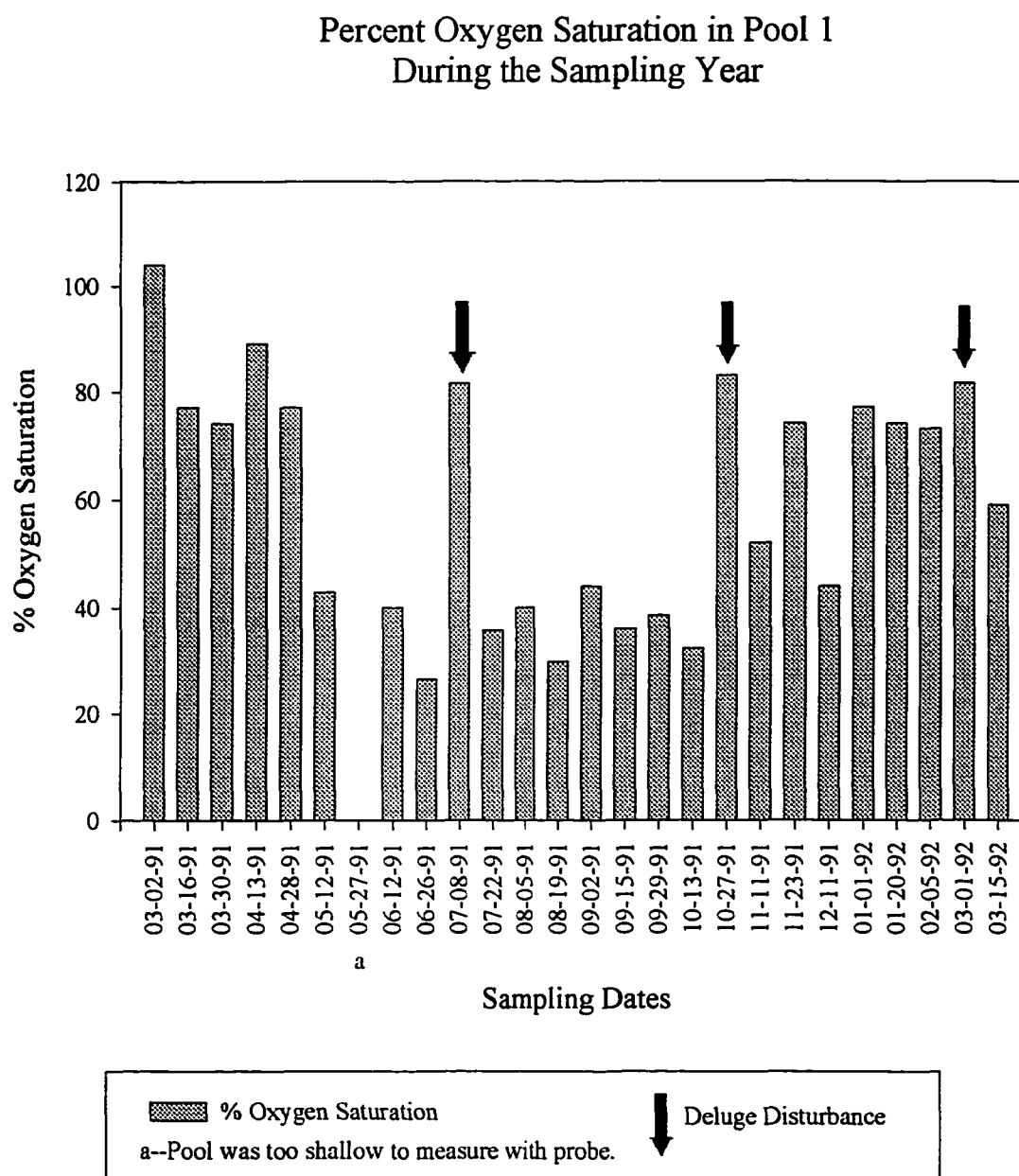


Figure 20: Percent oxygen saturation in Pool 1 during the sampling year.

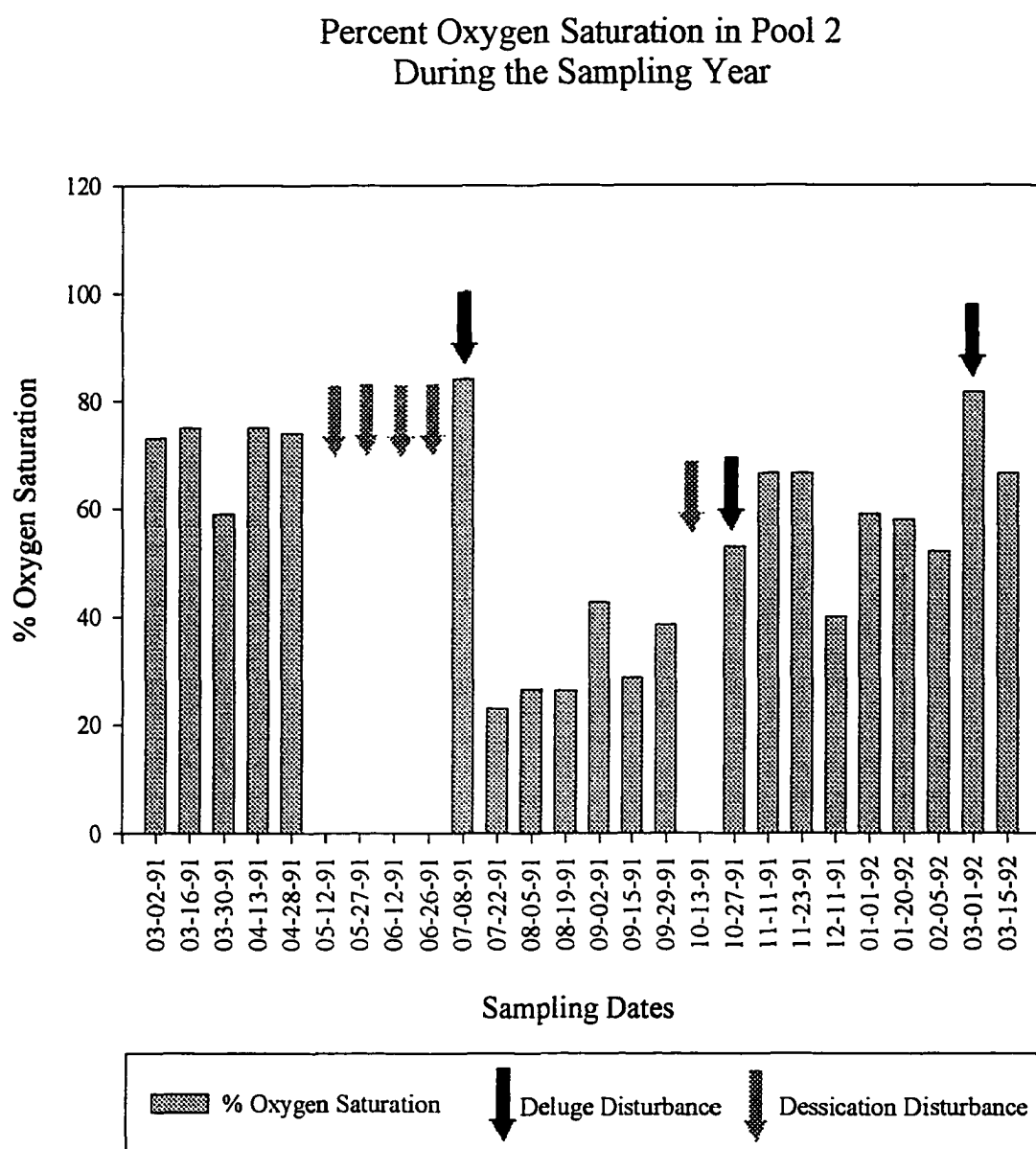


Figure 21: Percent oxygen saturation in Pool 2 during the sampling year.

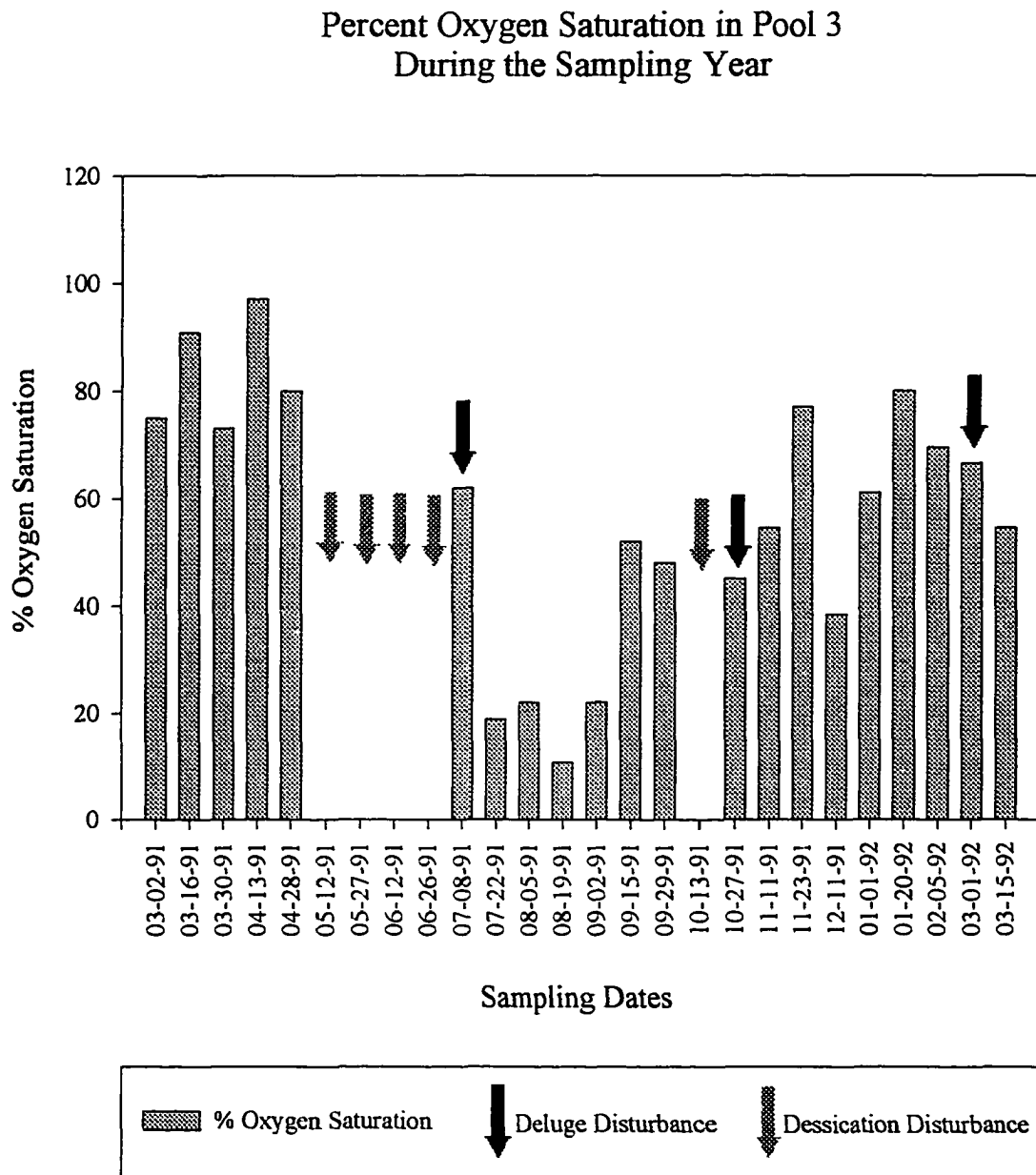


Figure 22: Percent oxygen saturation in Pool 3 during the sampling year.

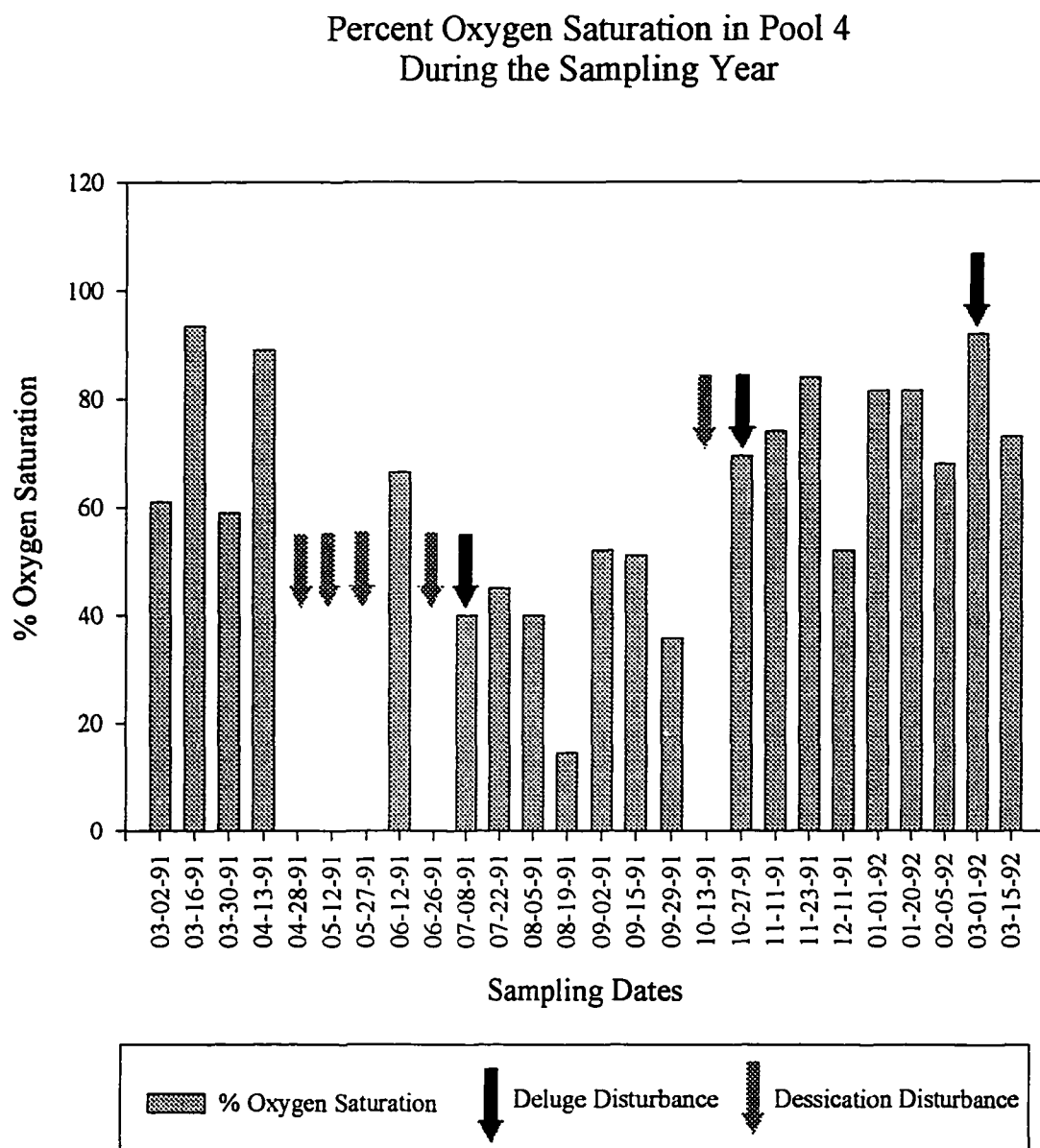


Figure 23: Percent oxygen saturaton in Pool 4 during the sampling year.

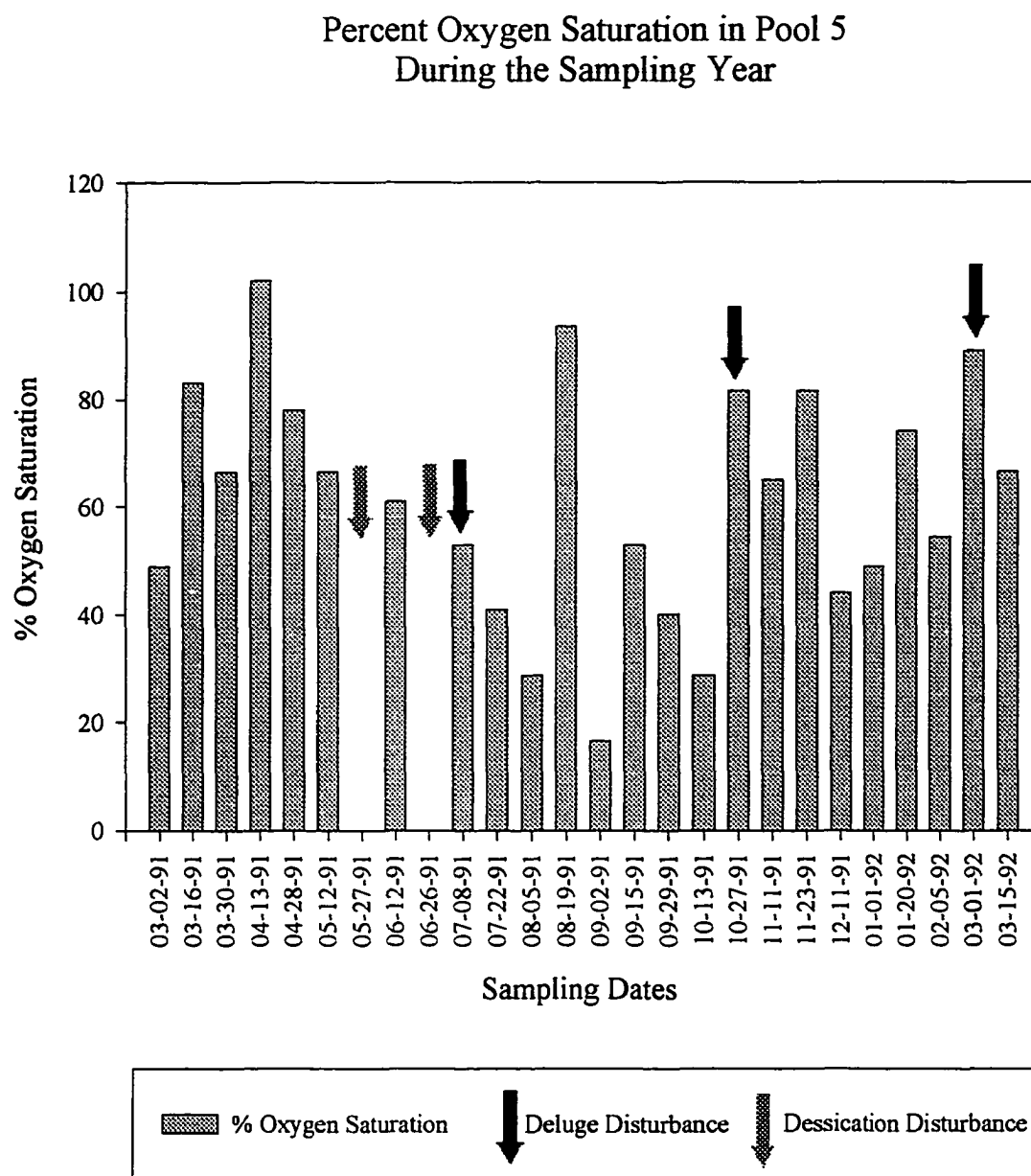


Figure 24: Percent oxygen saturation in Pool 5 during the sampling year.

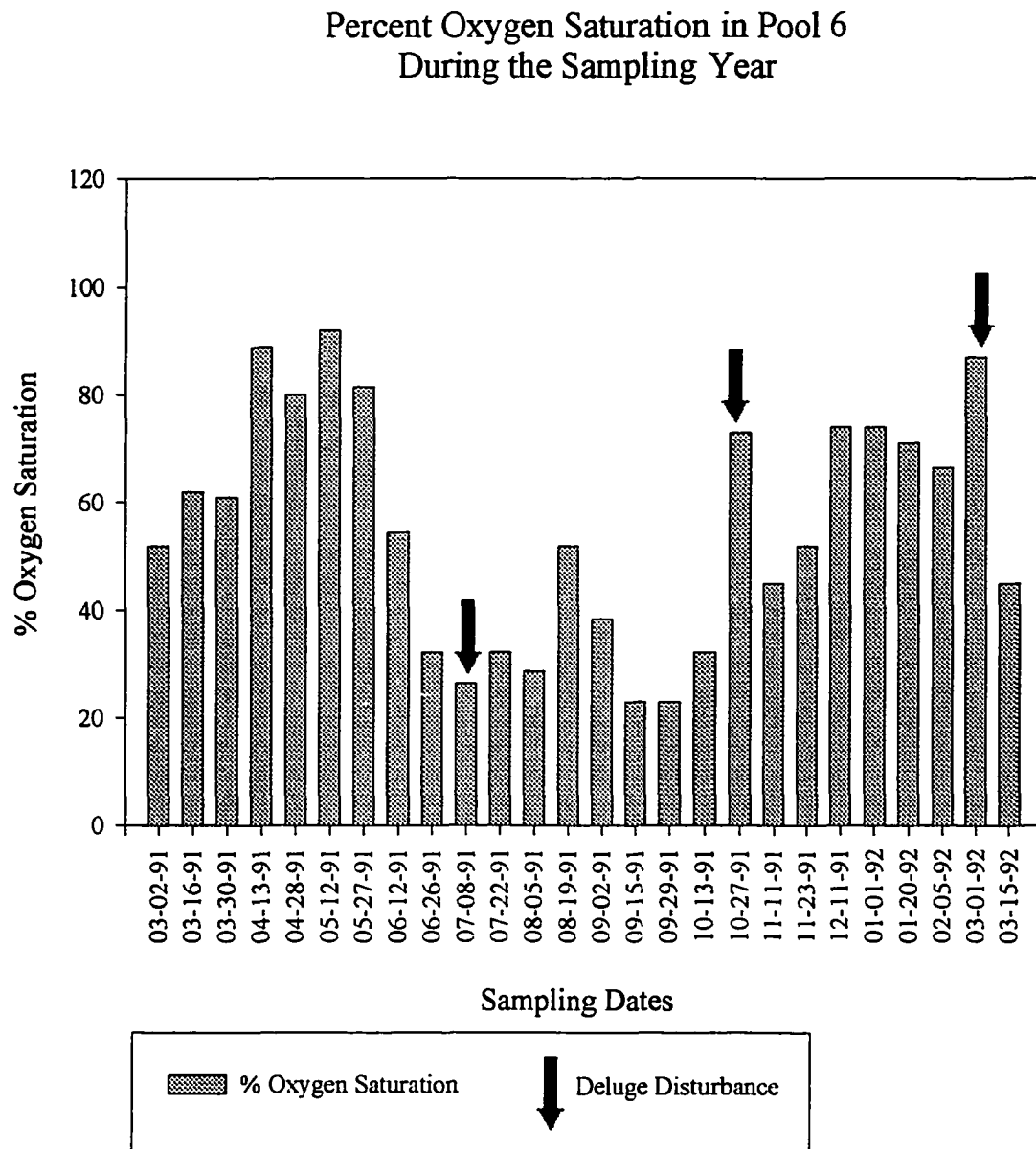


Figure 25: Percent oxygen saturation in Pool 6 during the sampling year.

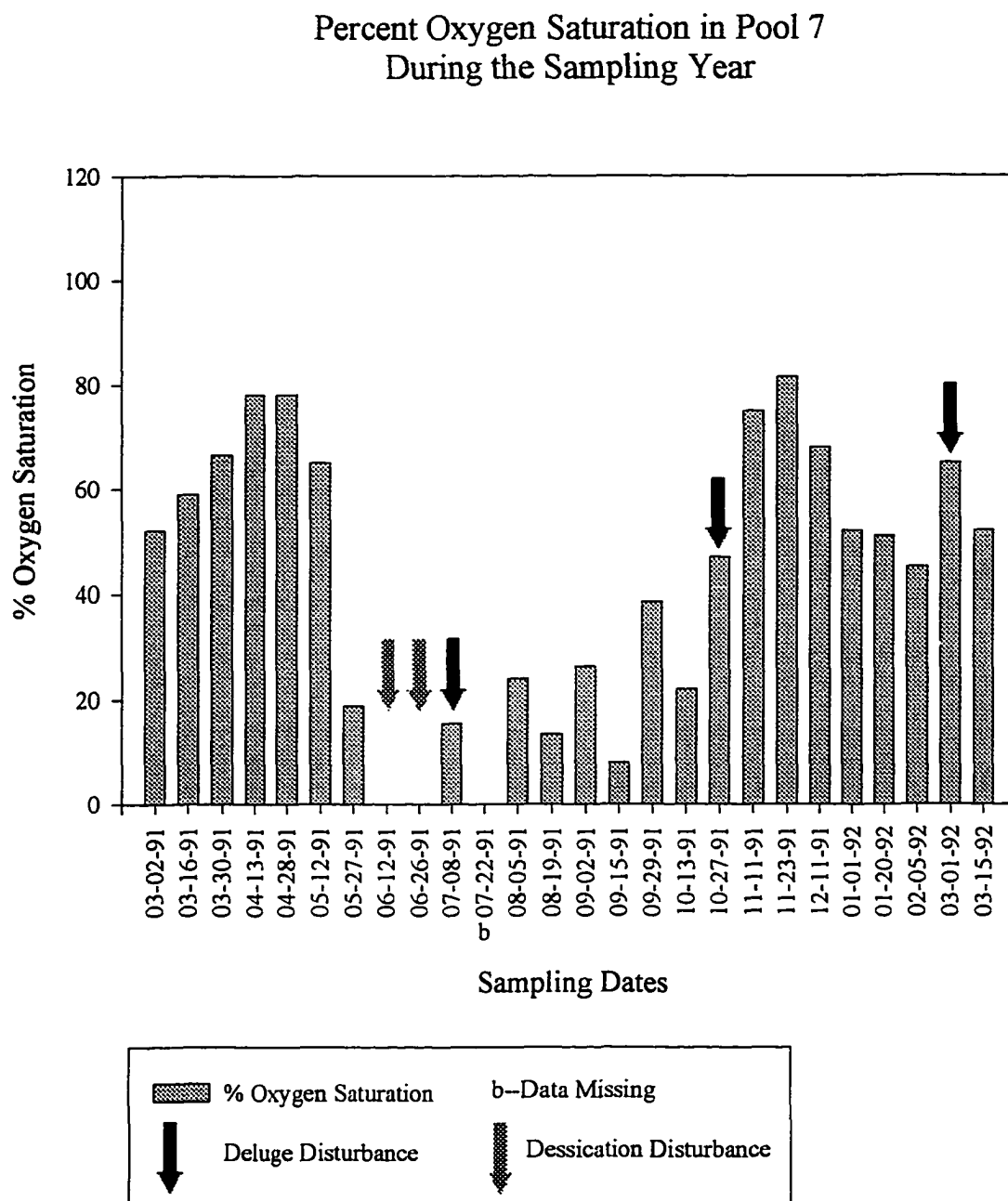


Figure 26: Percent oxygen saturation in Pool 7 during the sampling year.

oxygen levels seemed to change in unison.

I placed the samples in an ice chest until I returned to the laboratory. I then refrigerated the whole water samples at 4°C and incubated the filtered samples at 22°C until I examined and processed them later that day or the next morning.

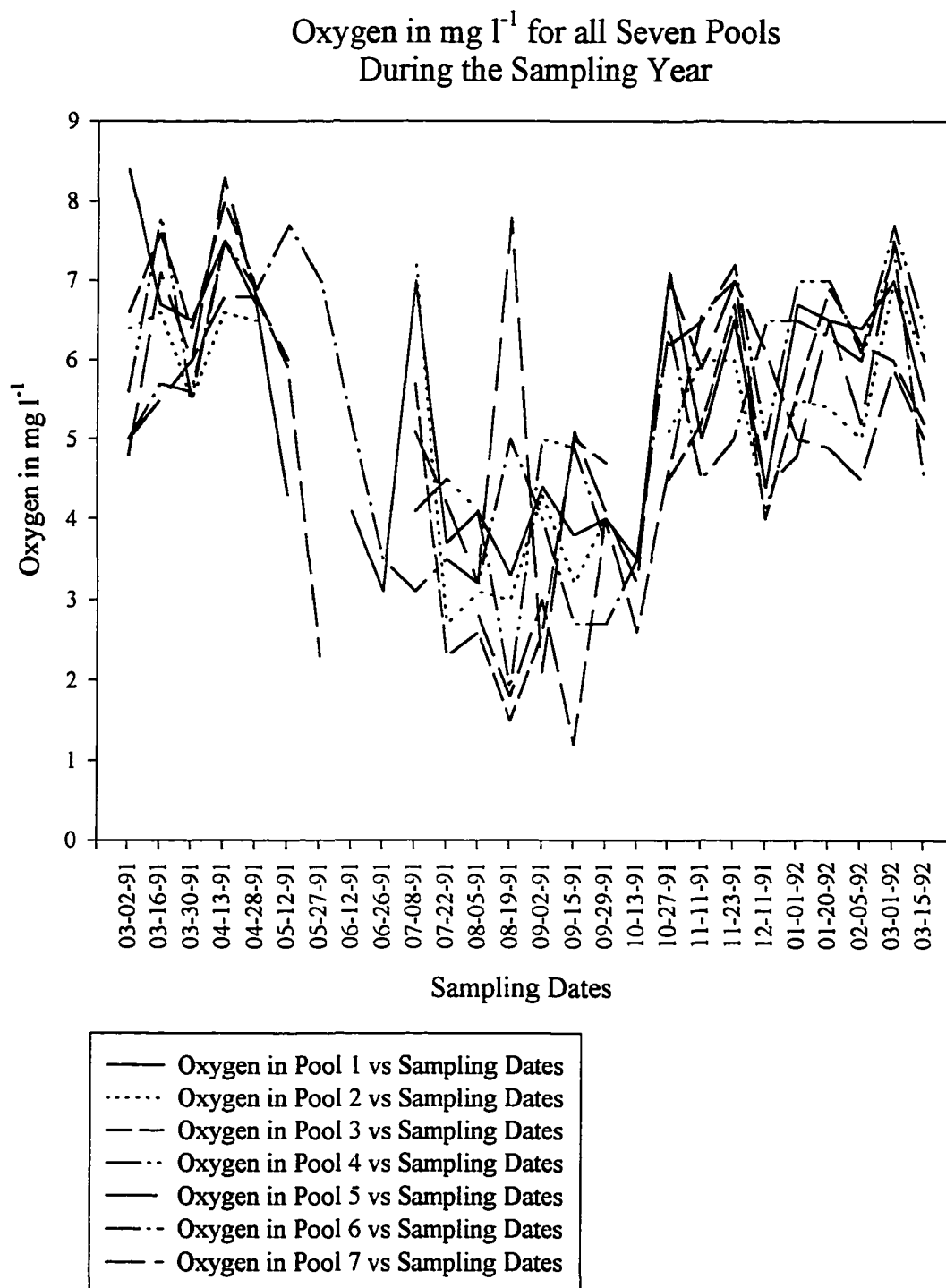


Figure 27: Relationship of oxygen in mg l^{-1} for all seven pools during the sampling year. Missing values are due to pool dessication or absence of data.

Laboratory Techniques

In the laboratory I observed the zooplankton with a Zeiss SR stereomicroscope for general features before preserving with a 4% sugar formalin solution, a special technique for Cladocera using chilled carbonated water to narcotize the *Daphnia* (Haney and Hall 1973). This technique purportedly prevents the *Daphnia* from ballooning and shedding their carapace with consequent loss of eggs. However, I occasionally found loose eggs and embryos in the preserved specimens. I then stored the specimens in capped bottles until I counted and measured them.

I measured pH using a Corning 240 pH meter (Figures 28 to 34). I measured conductivity in $\mu\text{S cm}^{-1}$ using a Corning PS-17 pocket-sized conductivity meter for the first five sampling dates, and when it became available on May 12, 1991, a Horizon Type 1484-10 conductivity meter (Figures 35 to 41). Measurements of conductivity on May 12, 1991 using both conductivity meters showed that the Corning pocket meter readings were about 25% lower than with the Horizon meter. Pooled conductivity data for all seven pools during the sampling year is summarized in Figure 42. Conductivity ran in concert in the pools especially around October. The single serious outlier is Pool 1 which on May 27, 1991 was so shallow that it produced an extremely high conductivity level on that date.

I calibrated the eyepiece micrometer in the Zeiss stereomicroscope using a Zeiss stage micrometer. I examined the contents of each specimen jar and identified and counted each individual of each species present. I identified the genus and species of the *Daphnia* present and measured the total length, and the length of the head and carapace.

pH of Pool 1 During the Sampling Year

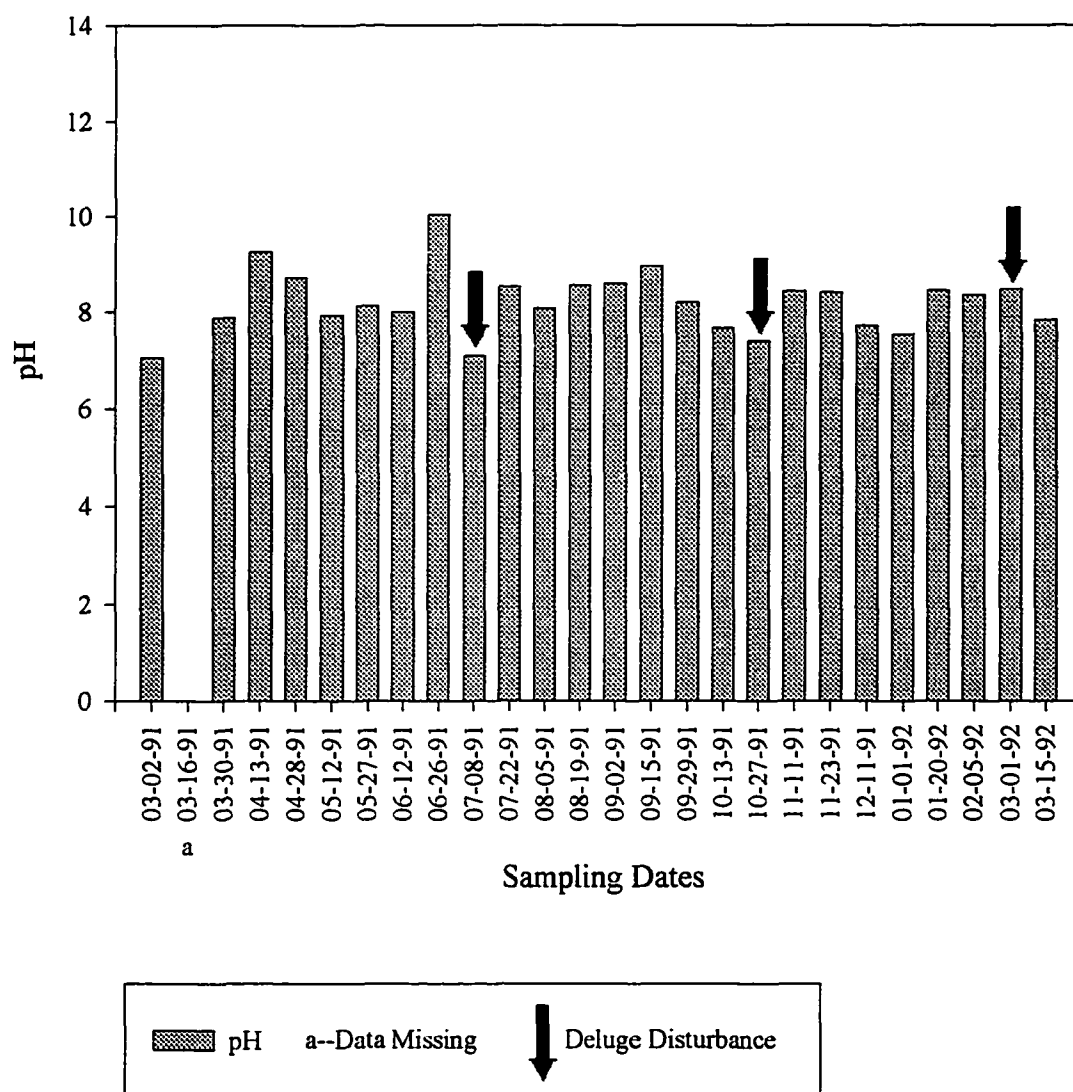


Figure 28: pH of Pool 1 during the sampling year.

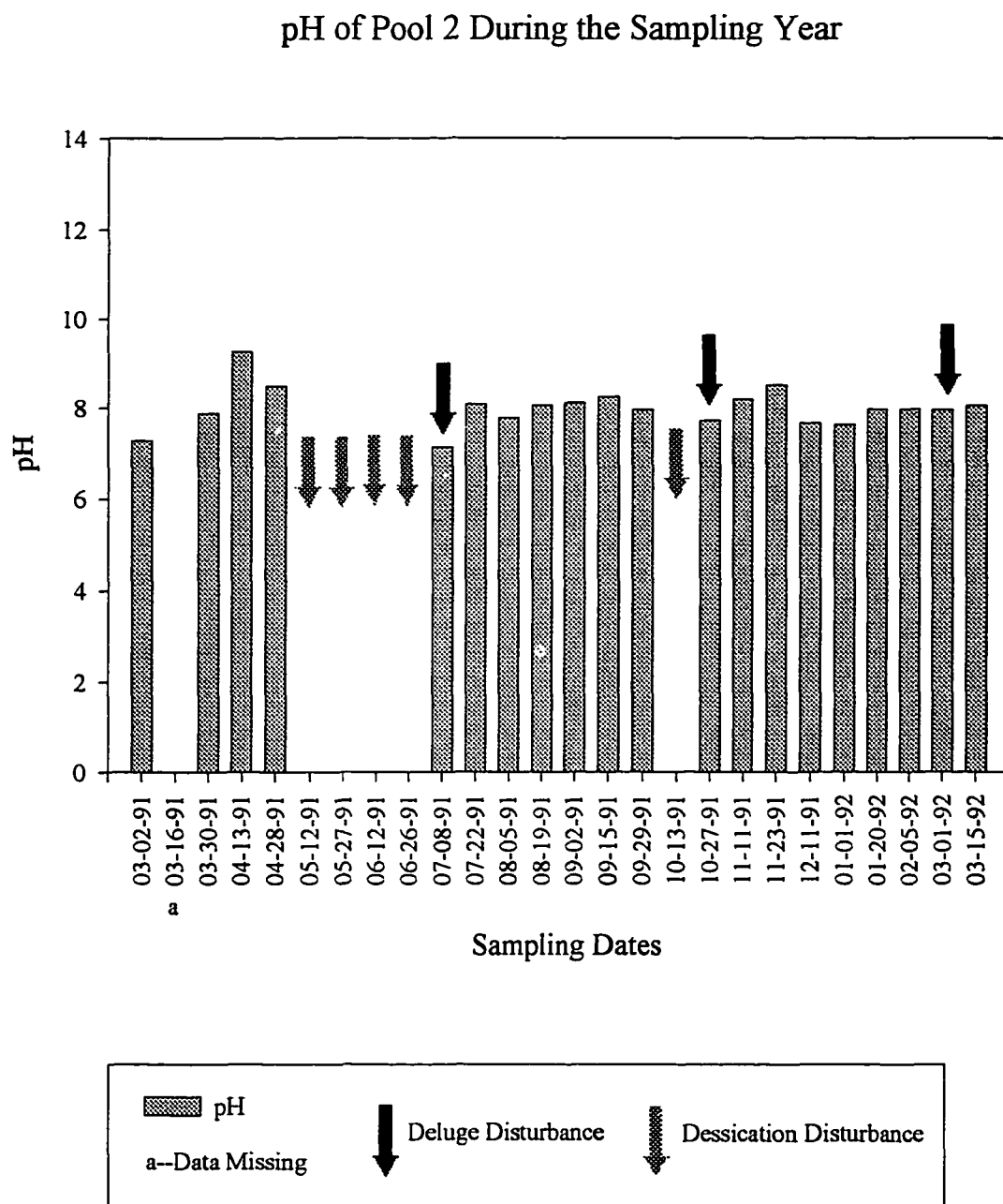


Figure 27: pH of Pool 2 during the sampling year.

pH of Pool 3 During the Sampling Year

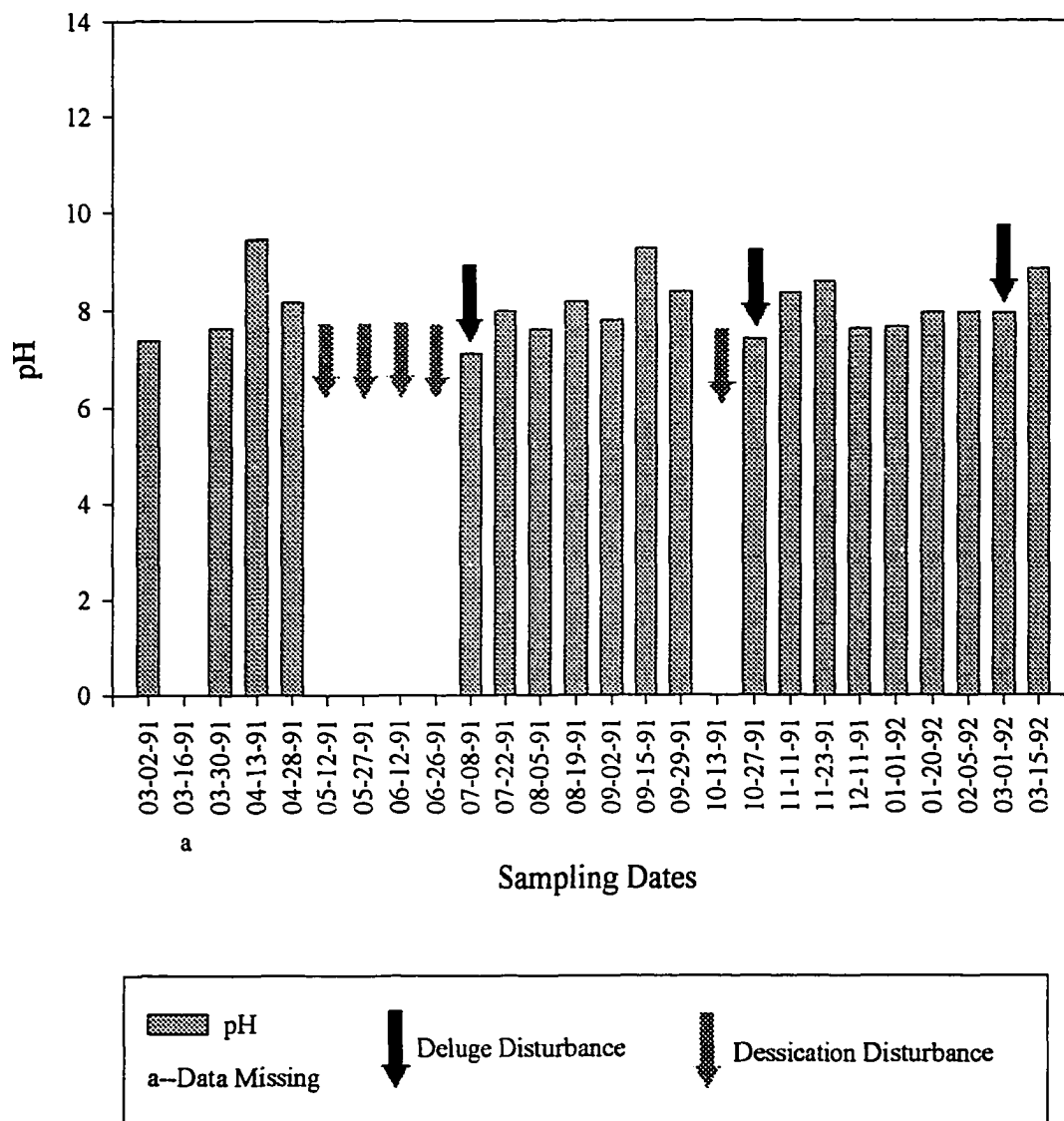


Figure 30: pH of Pool 3 during the sampling year.

pH of Pool 4 During the Sampling Year

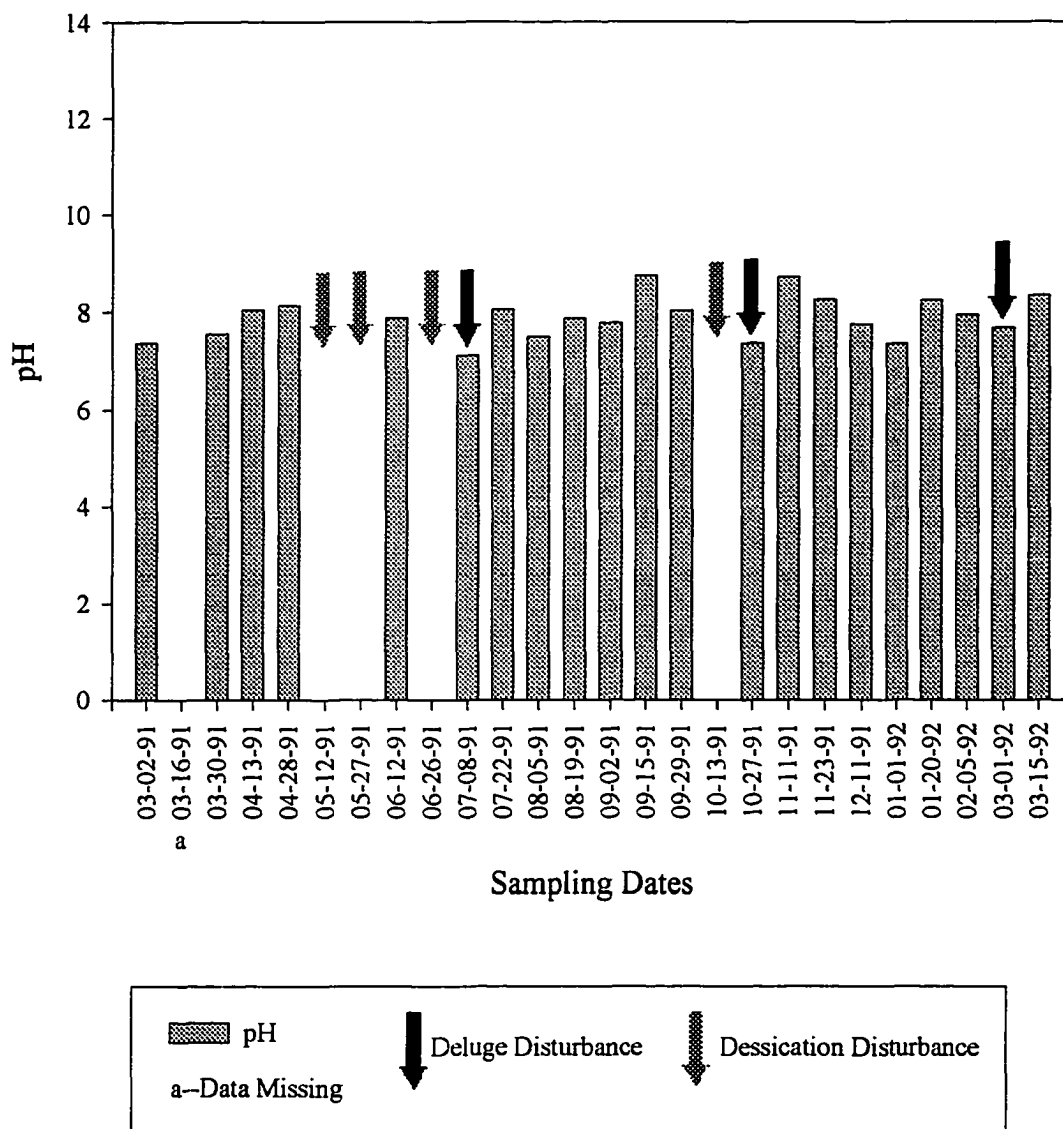


Figure 31: pH of Pool 4 during the sampling year.

pH of Pool 5 During the Sampling Year

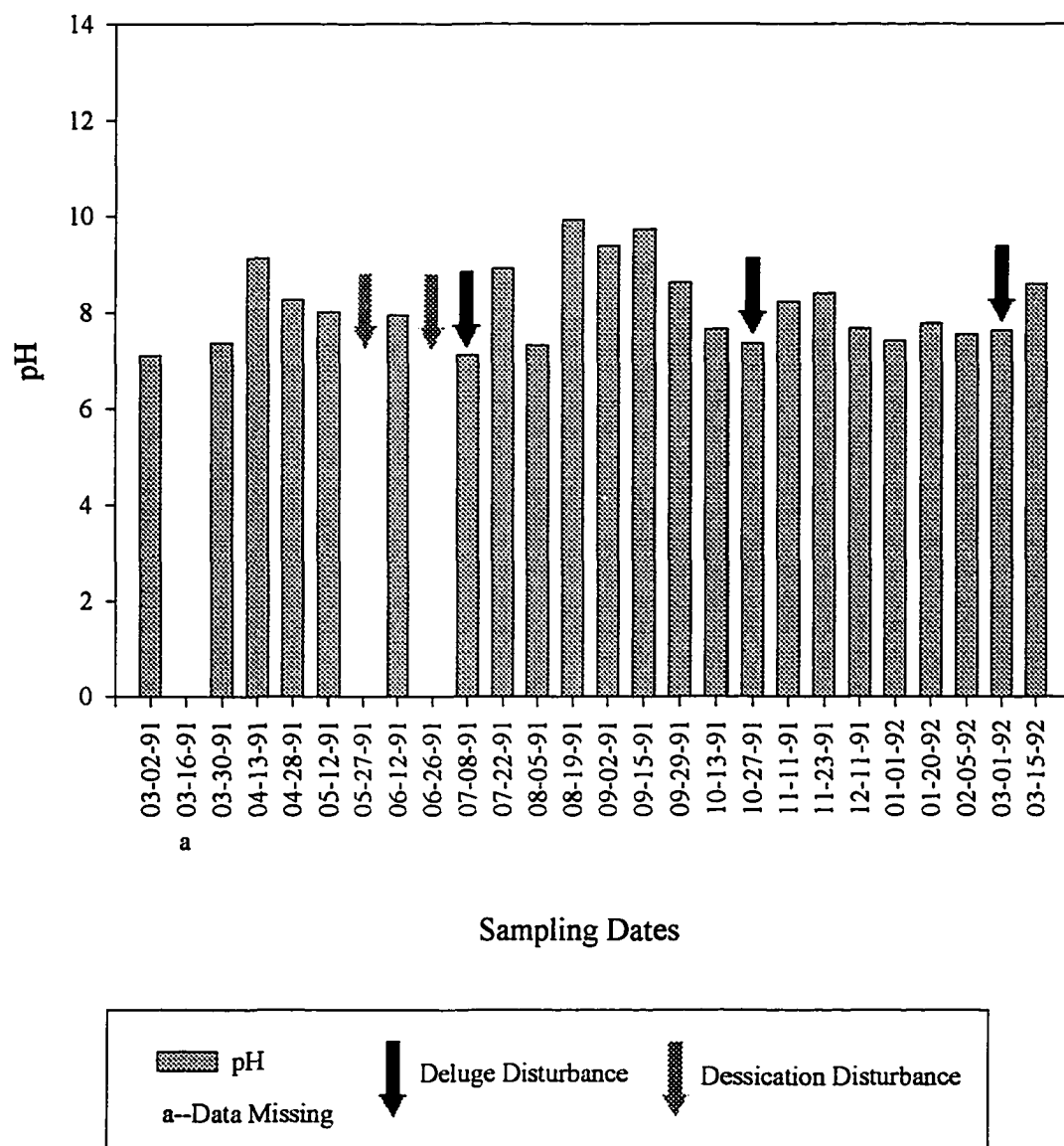


Figure 32: pH of Pool 5 during the sampling year.

pH of Pool 6 During the Sampling Year

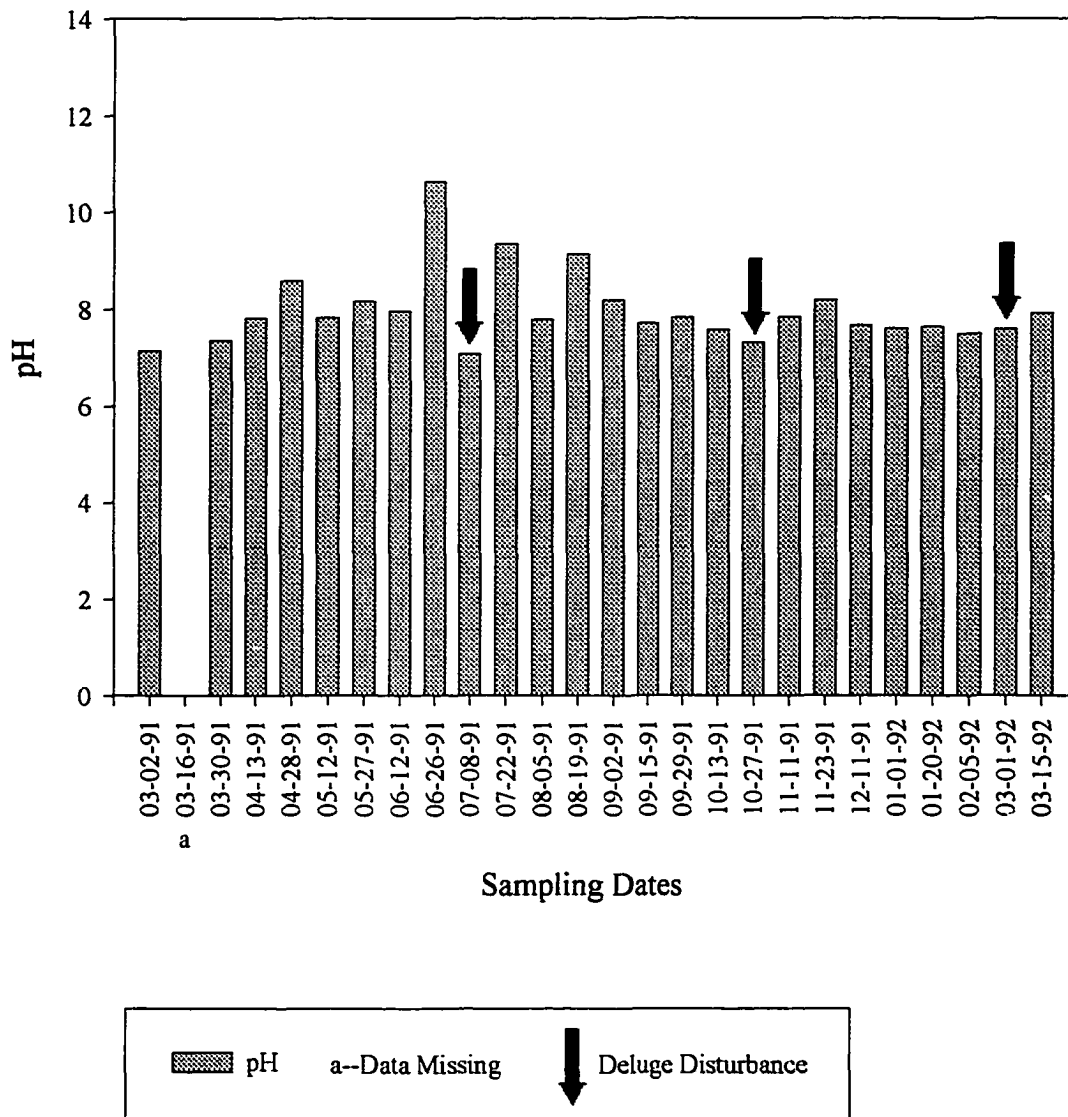


Figure 33: pH of Pool 6 during the sampling year.

pH of Pool 7 During the Sampling Year

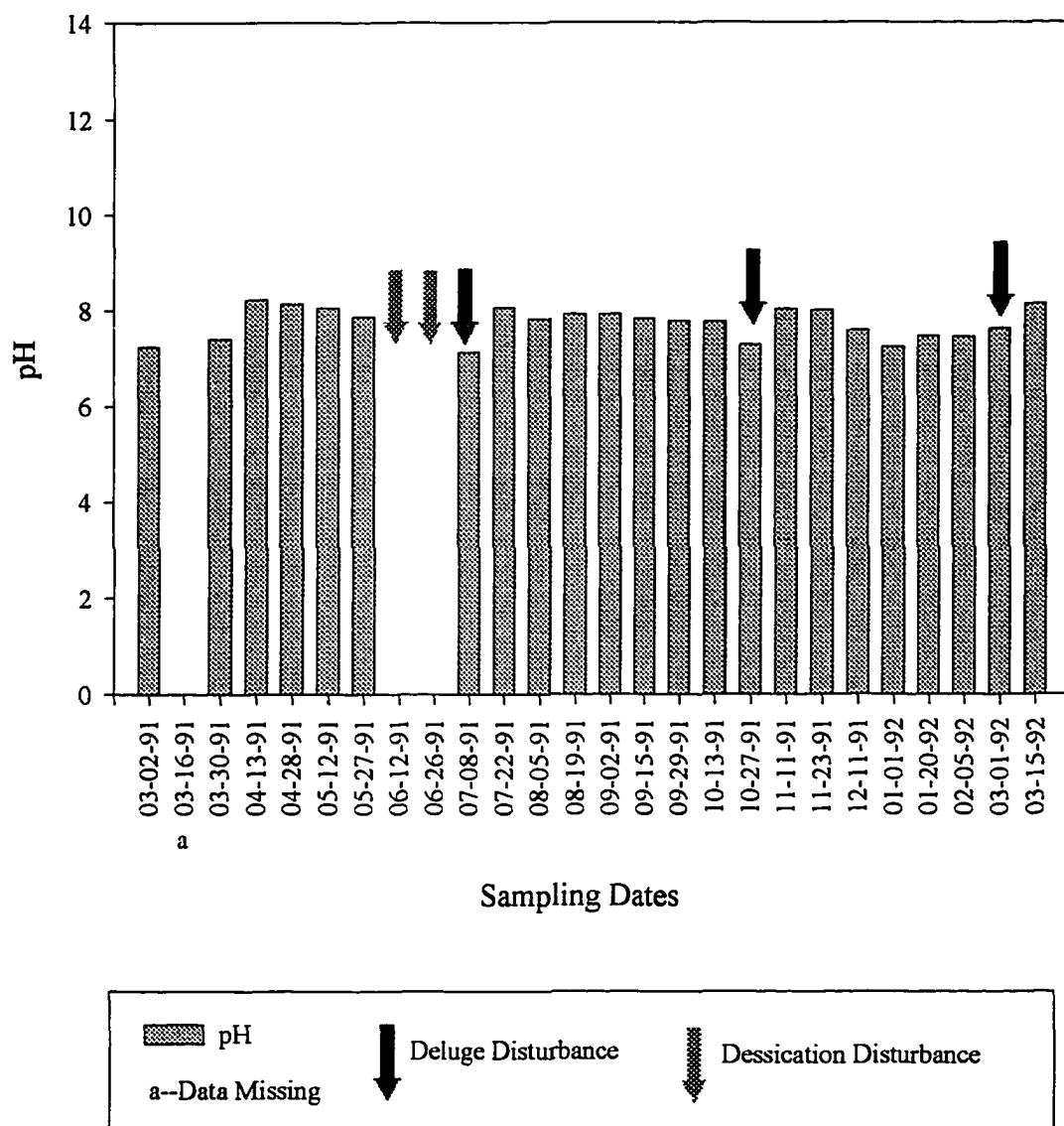


Figure 34: pH of Pool 7 during the sampling year.

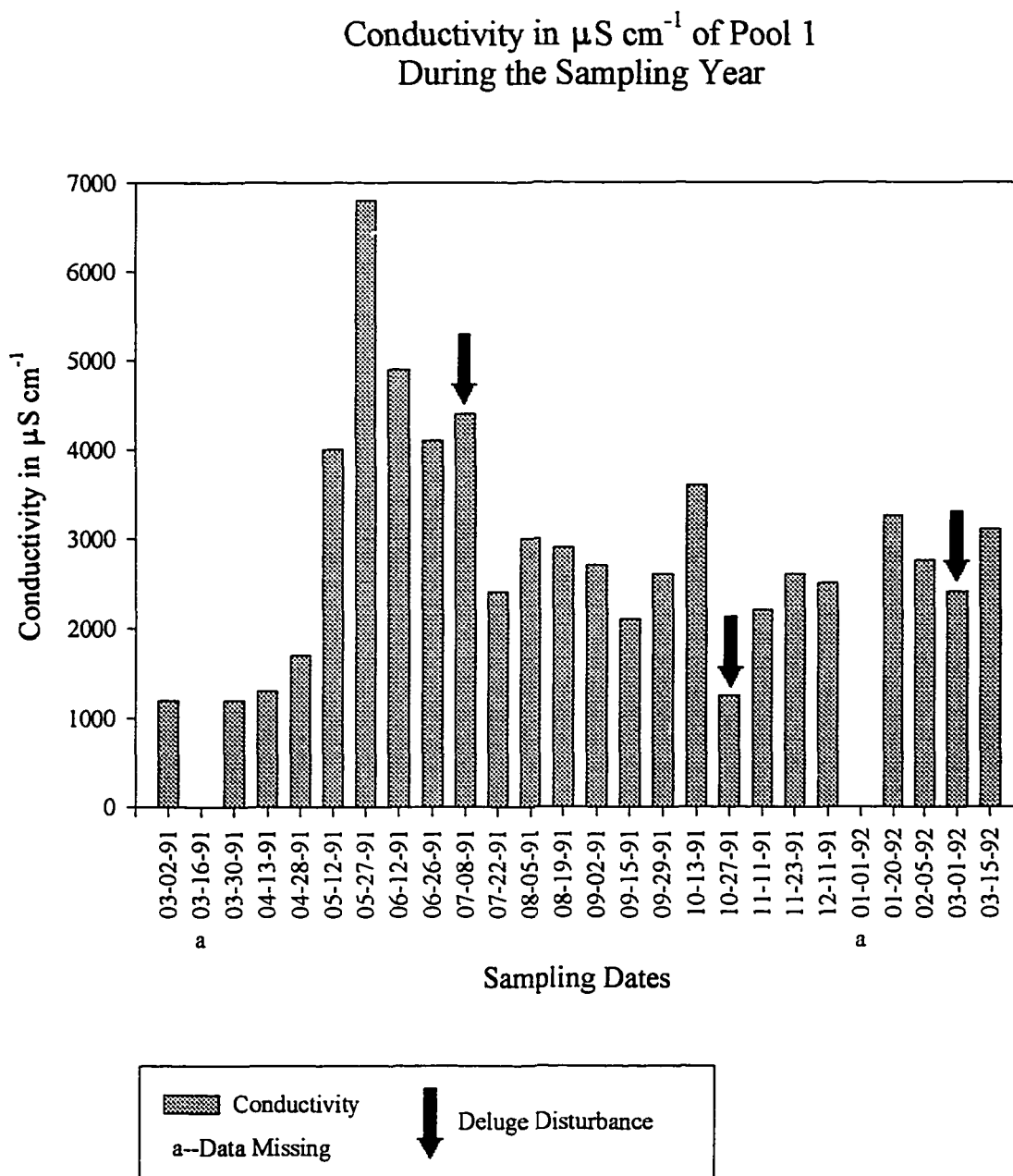


Figure 35: Conductivity in $\mu\text{S cm}^{-1}$ of Pool 1 during the sampling year.

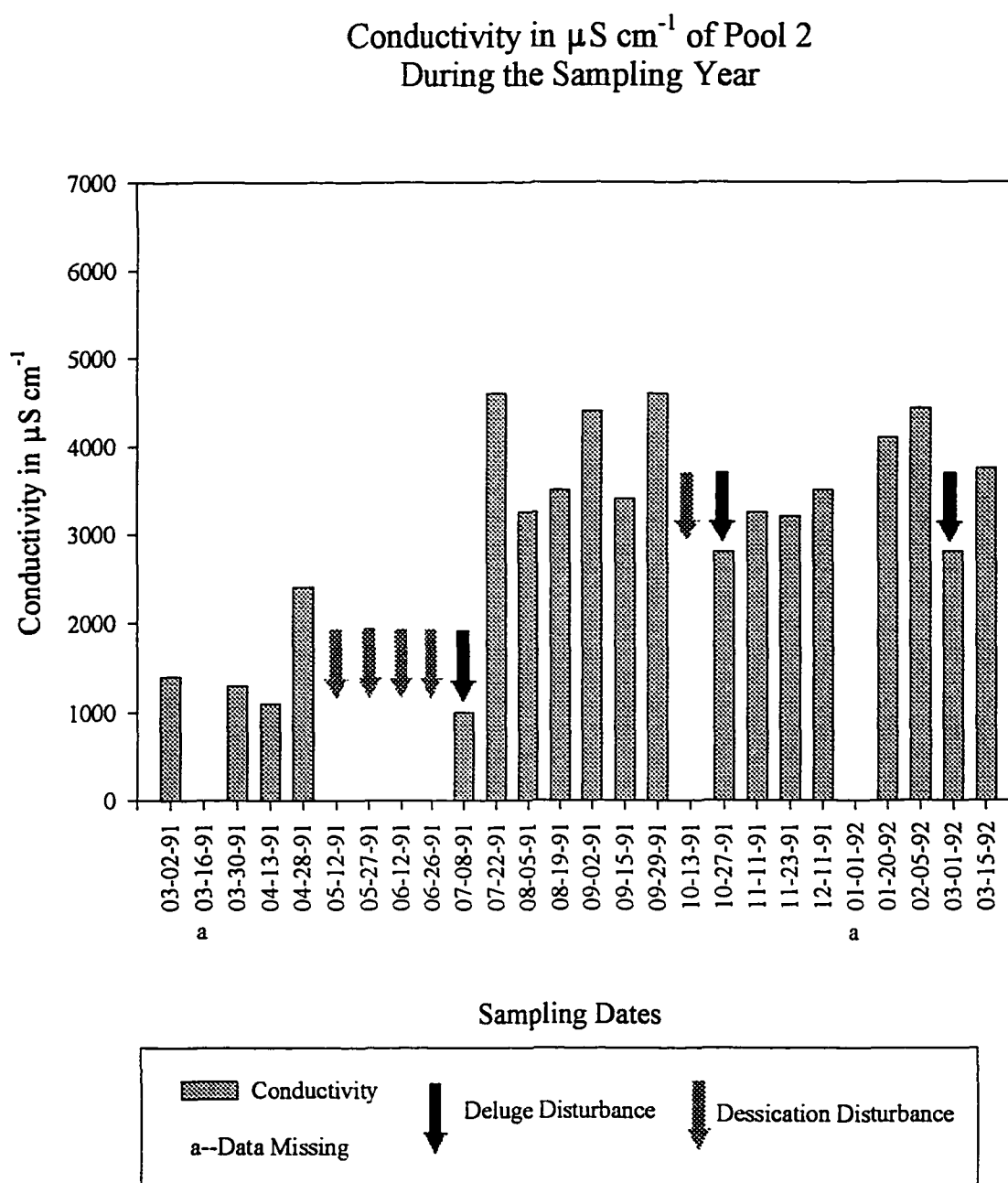


Figure 36: Conductivity in $\mu\text{S cm}^{-1}$ of Pool 2 during the sampling year.

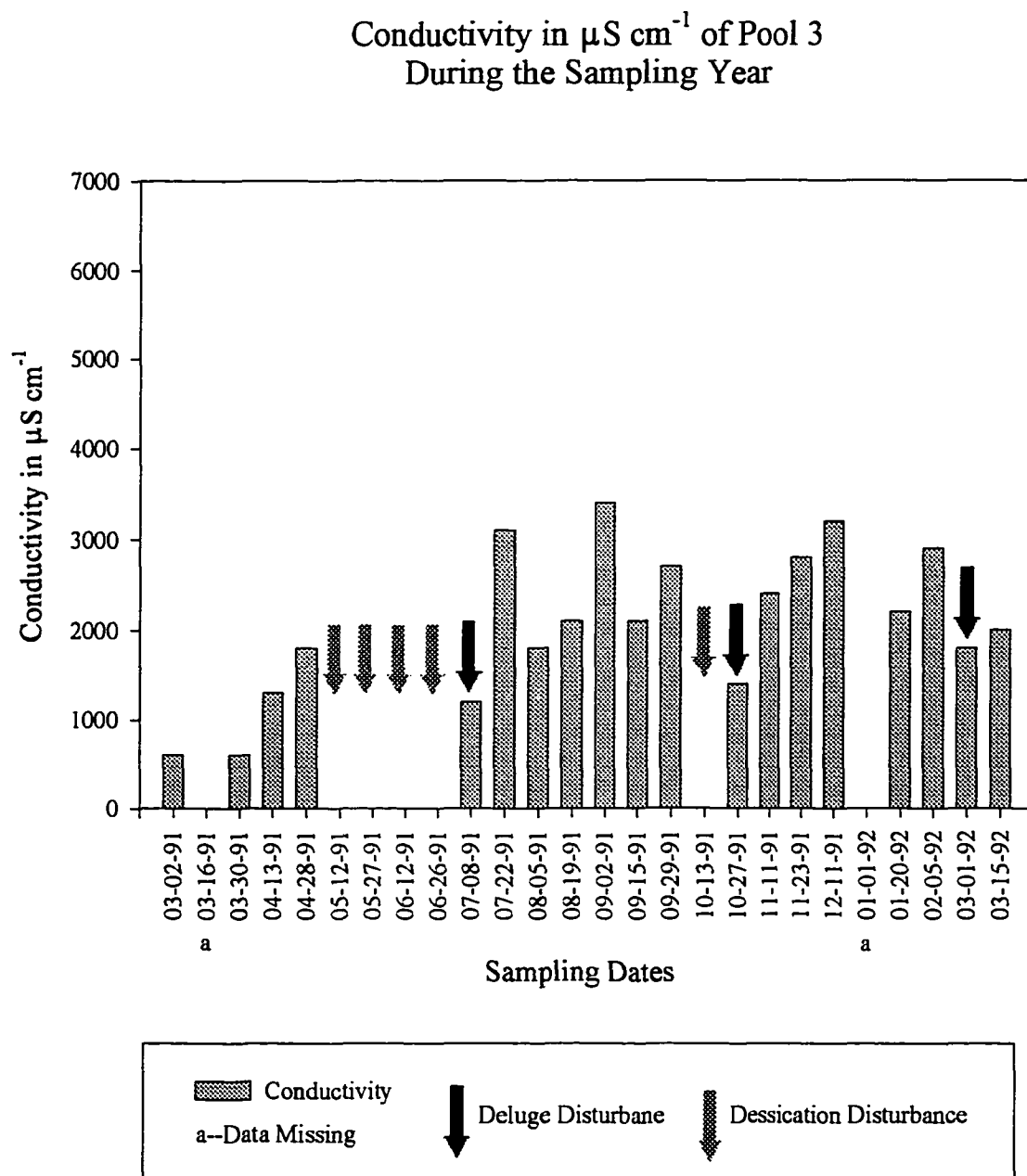


Figure 37: Conductivity in $\mu\text{S cm}^{-1}$ of Pool 3 during the sampling year.

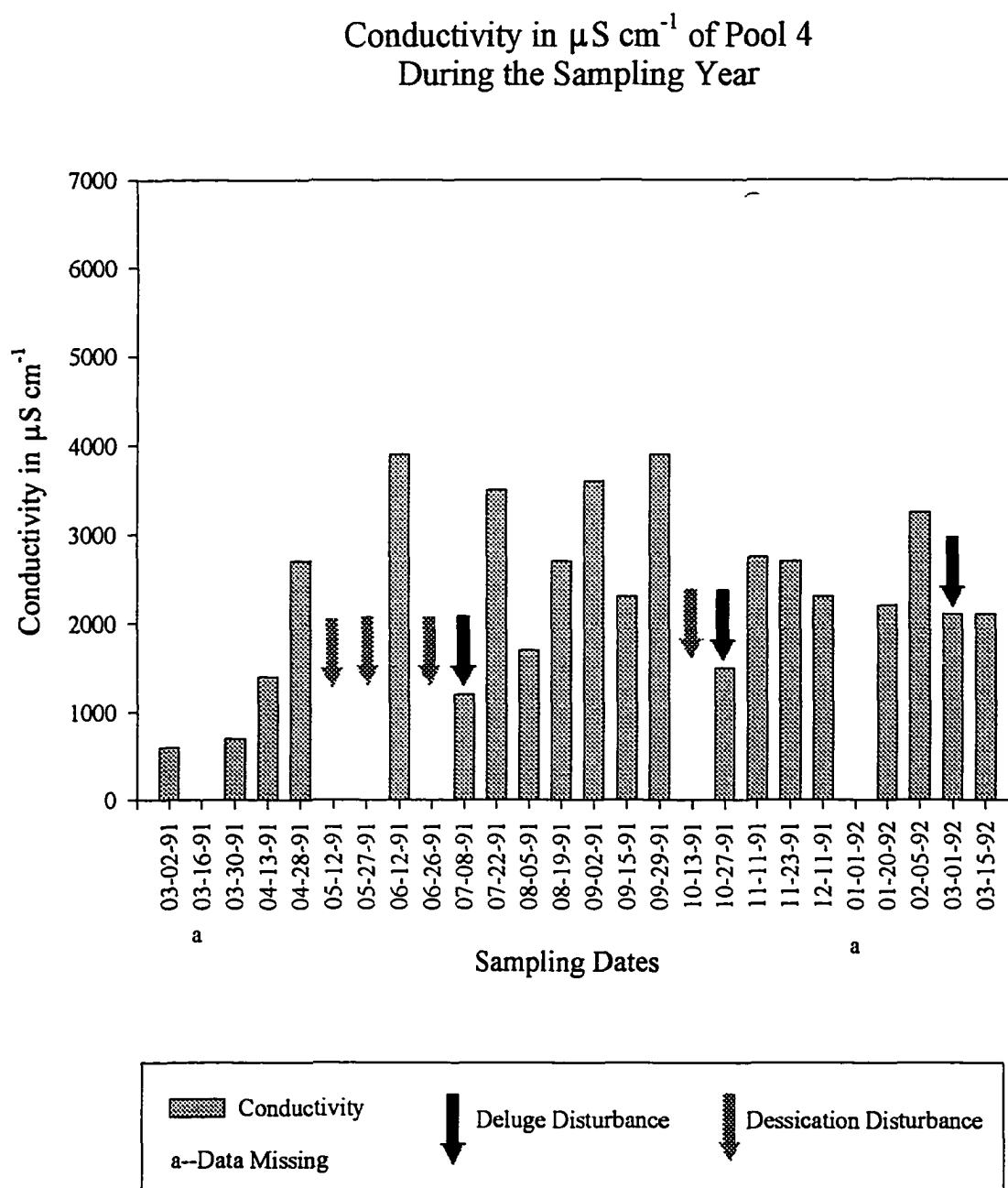


Figure 38: Conductivity in $\mu\text{S cm}^{-1}$ of Pool 4 during the sampling year.

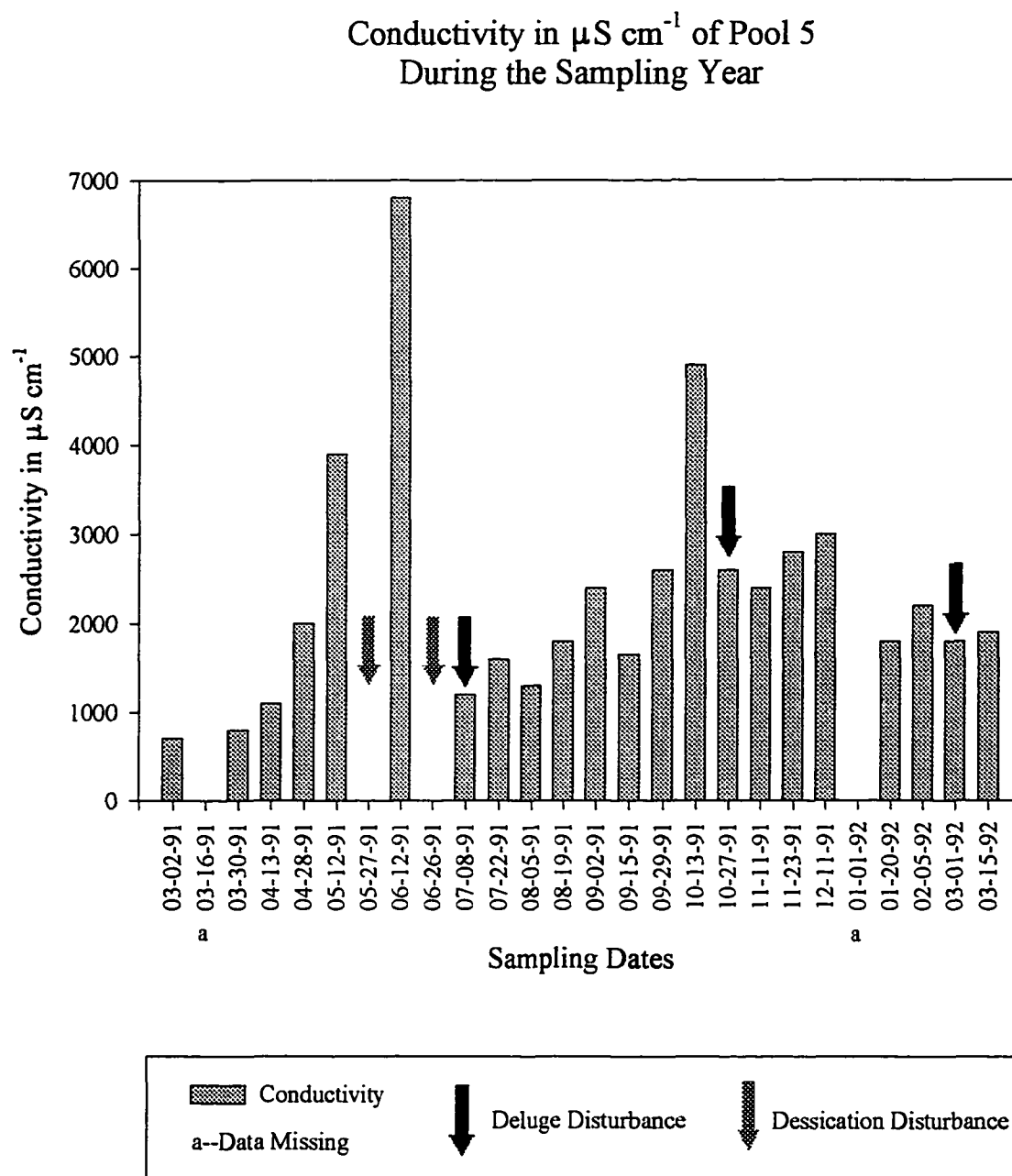


Figure 39: Conductivity in $\mu\text{S cm}^{-1}$ of Pool 5 during the sampling year.

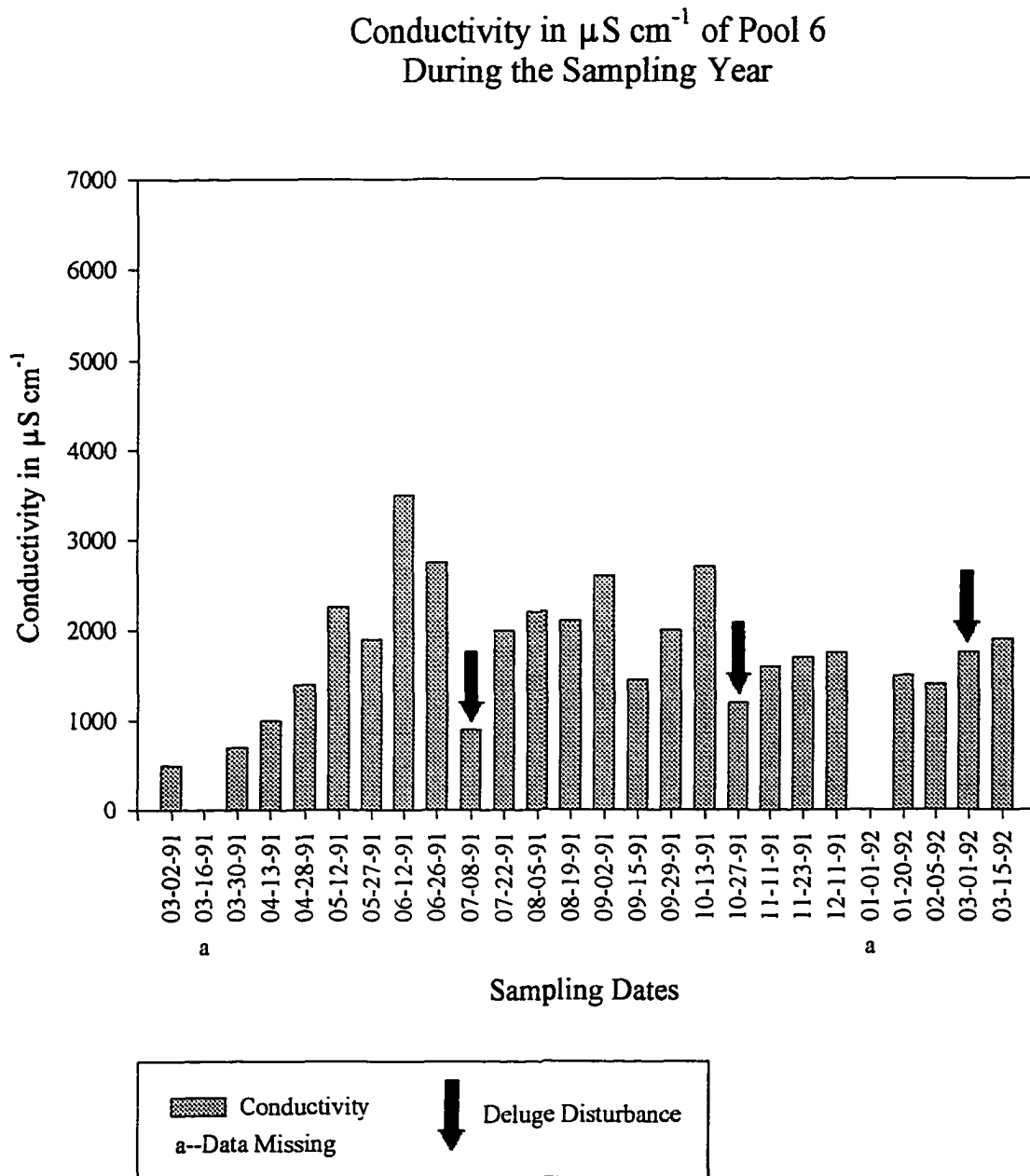


Figure 40: Conductivity in $\mu\text{S cm}^{-1}$ of Pool 6 during the sampling year.

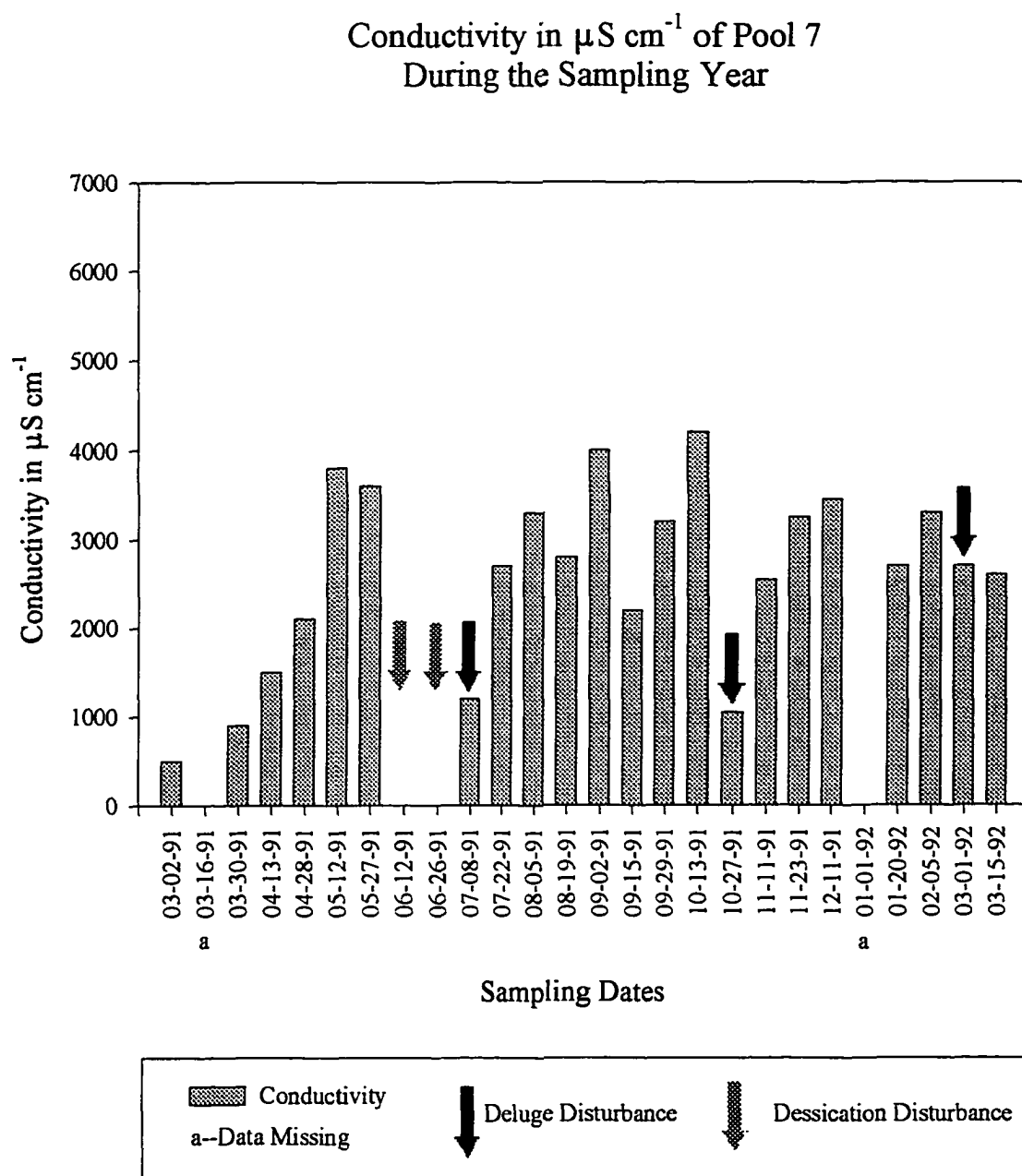


Figure 41: Conductivity in $\mu\text{S cm}^{-1}$ of Pool 7 during the sampling year.

Conductivity in $\mu\text{S cm}^{-1}$ of all Seven Pools
During the Sampling Year

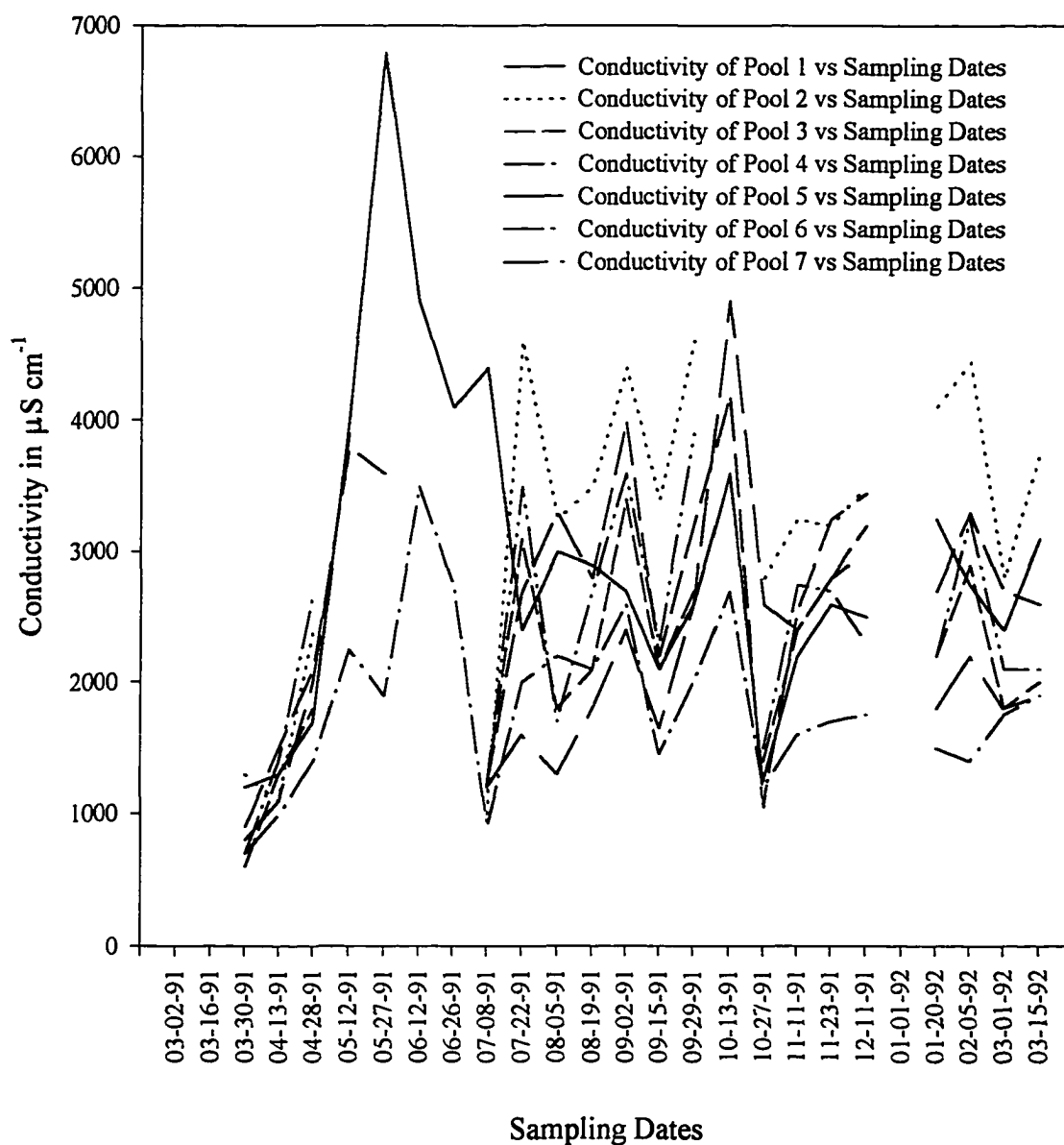


Figure 42: Relationship of conductivity in $\mu\text{S cm}^{-1}$ of all seven pools during the sampling year. Data missing on 3-16-91 and 1-20-92. Values on 3-2-91 would not graph due to absence of data on 3-16-91.

I found that *Daphnia* juveniles have a spine about one half the length of their body while adults have a much smaller spine in proportion to body length. Also the spine often appeared to be partially or totally broken off. Therefore, I determined that, in this study, total length was not a reliable measurement, and that the length of the head plus the carapace to the base of the posterior or caudal spine was the most useful.

I counted the number of eggs present in each individual, and noted whether an ephippium was developing. I also counted the number of loose eggs and loose ephippia present (see count data for each pool in Appendix II).

Statistical Treatment

I used SigmaPlot, Version 3, scientific graphing software (Jandel Scientific Software, Inc.). SigmaPlot uses a least squares method to select equation parameters to fit an equation to data, and calculates the correlation coefficient (r) when performing a linear regression. Specifically, it is the covariance divided by the product of the sample standard deviation. SigmaPlot reports the y-intercept, $b[0]$; the slope of the line, $b[1]$; and r^2 , which is the coefficient of determination and is a measure of the closeness of fit of a scatter graph to its regression line where $r^2=1$ is a perfect fit. The formula $y = mx + b$ is used to represent $b[1]$ and $b[0]$ for the slope of the line (m) and the y-intercept (b), respectively. The regression model is justified here since the measurement error associated with the various physical and chemical measurements is small relative to *Daphnia* population estimates.

Water temperatures were regressed against air temperatures. Annual abiotic factors such as pool depth, water temperature, conductivity, pH, and oxygen tension in mg l^{-1} are usually the driving forces of population dynamics in more permanent habitats such as ponds and lakes. The number of *Daphnia* present in each sample was regressed against each of these abiotic factors.

In an attempt to dissect the pool year into its principal parts, pool duration between episodes of dessication and/or deluge was determined for each pool. Each pool experienced the same deluge events and most pools experienced similar dessication disturbances. Three separate time periods between disturbances occurred for most pools. As previously discussed, Pool 6 was the least disturbed. To determine disturbance driving

of population dynamics, the number of *Daphnia* present was plotted against time (the duration of the pools in approximately two week units which was the time between sampling dates). The time periods for each pool were then combined and the number of *Daphnia* was regressed against the combined time periods.

The total number of *Daphnia* included both species, *D. obtusa* and *D. pulex*, which were pooled together because they are congeneric species and have ecological similarities in size and diet. Also, since both species had low population numbers for most of the year, it became necessary to pool them in order to have adequate numbers for statistical treatment. As seen in the count data in Appendix , total numbers of daphnids rarely exceeded 50 per sample on any one sampling date with no daphnids present on many dates.

An attempt was made to do an instar analysis of each daphnid species in Pools 1, 4 and 6. I started by listing the length of every individual in the sample on each sampling date to see the progression of instars over time. I found that the pools were disrupted too frequently by dessication and/or deluge to see this progression as populations at 200 l⁻¹ or more were not present at the next sampling date following flooding or dessication of the pool. The smallest ovigerous female, brood size and number of ephippia were determined by scanning count data from Pools 1, 4 and 6 for each sampling date. These pools were studied in depth and count data for these pools is given in Appendix III .

The smallest ovigerous female was determined by scanning count data for each sampling date. Attempts were made to correlate smallest ovigerous female with brood size and with abiotic factors, as listed in the hypothesis. These attempts were foiled by pool

disruptions and by the low numbers of daphnids present on most sampling dates.

Similarly, attempts to correlate brood size and ephippial production with abiotic factors faced the same difficulties.

RESULTS AND DISCUSSION

Annual Population Dynamics of Principal Cladocera in Each Pool

I found that Cladocera dominate the planktonic community of the rock pools studied in Red Rock Canyon with two species of *Daphnia* and one species of *Moina* present in these highly ephemeral pools (also called *tinajas*).

Pool temperatures indicate that two pool "seasons" exist. In some pools, the hot season and cool season were conveniently separated by periods of drying or flooding. Given warmer temperatures and equal seeding of *Daphnia* ephippia or immigrants, I would expect that summer would yield a faster turnover and therefore the opportunity for the development of a higher population size.

Daphnia in Red Rock Canyon possess two essential features. They are able to withstand the temporarily unfavorable conditions that exist in these pool systems when water is present, and they are able to synchronize their life cycles with the unreliable occurrence of water. By reproducing parthenogenically, *Daphnia* do not expend energy involved in sex (mate location/recognition) or in the production of males (Williams 1975). Paradoxically, *Moina* are able to persist in the same environment as a sexual species, even though they, too, resort to parthenogenesis.

Daphnia and *Moina* were occasionally present at the same time. Using Pennak's key (1989), I determined that the *Moina* species present in Red Rock Canyon most closely resembles *Moina macrocopa*. However, it may possibly be a new species (P. Starkweather, pers. commun. 1996). *Moina* appeared in all seven pools during the

summer, and inexplicably, in very small numbers in Pools 2 and 7 in February 1992 as discussed below. The number of *Moina*, when present, ranged from 1 l⁻¹ to 308 l⁻¹. Unlike *Daphnia*, both males and females were present in *Moina* samples, and females were often present with eggs or ephippia. Loose ephippia were also present in the samples. These *Moina* produce only one embryo per ephippium as opposed to *Daphnia* which produce two embryos per ephippium as discussed above.

Pool 1 was never dry during the year although water depth was very low in May. I found both species of daphnids in Pool 1 (Figure 43). Total *D. pulex* individuals found during the year ranged from 0-26 l⁻¹, while *D. obtusa* numbers ranged from 0-10 l⁻¹. *D. pulex* and *D. obtusa* were rarely present at the same time. A small bloom of *D. obtusa* occurred in May 1991 and August 1991, and again in January 1992. *D. pulex* was absent in the spring but appeared in August, September and October, with the largest numbers present in the winter during December 1991 and January 1992. Numbers of *Daphnia* individuals present in Pool 1 were never large. Eggs were produced in August and December by *D. pulex*. One or two ephippia were present in samples from August, September and October of 1991, and in January 1992.

Moina were not present in Pool 1 in March 1991, when I began sampling, until June 26, 1991, when suddenly the population increased to 268 individuals per liter (Figure 44). Notice that *Moina* peaks in between peaks of *D. obtusa* and *D. pulex* as in other pools. Pools were deluged at the next sampling date of July 8 with no *Moina* present, but by July 22, two weeks later, *Moina* had reached an abundance of 118 l⁻¹ in Pool 1. The numbers of *Moina* present were larger than the numbers of *Daphnia* by a factor of ten.

Number of *D. pulex* and *D. obtusa* Versus
Sampling Dates in Pool 1

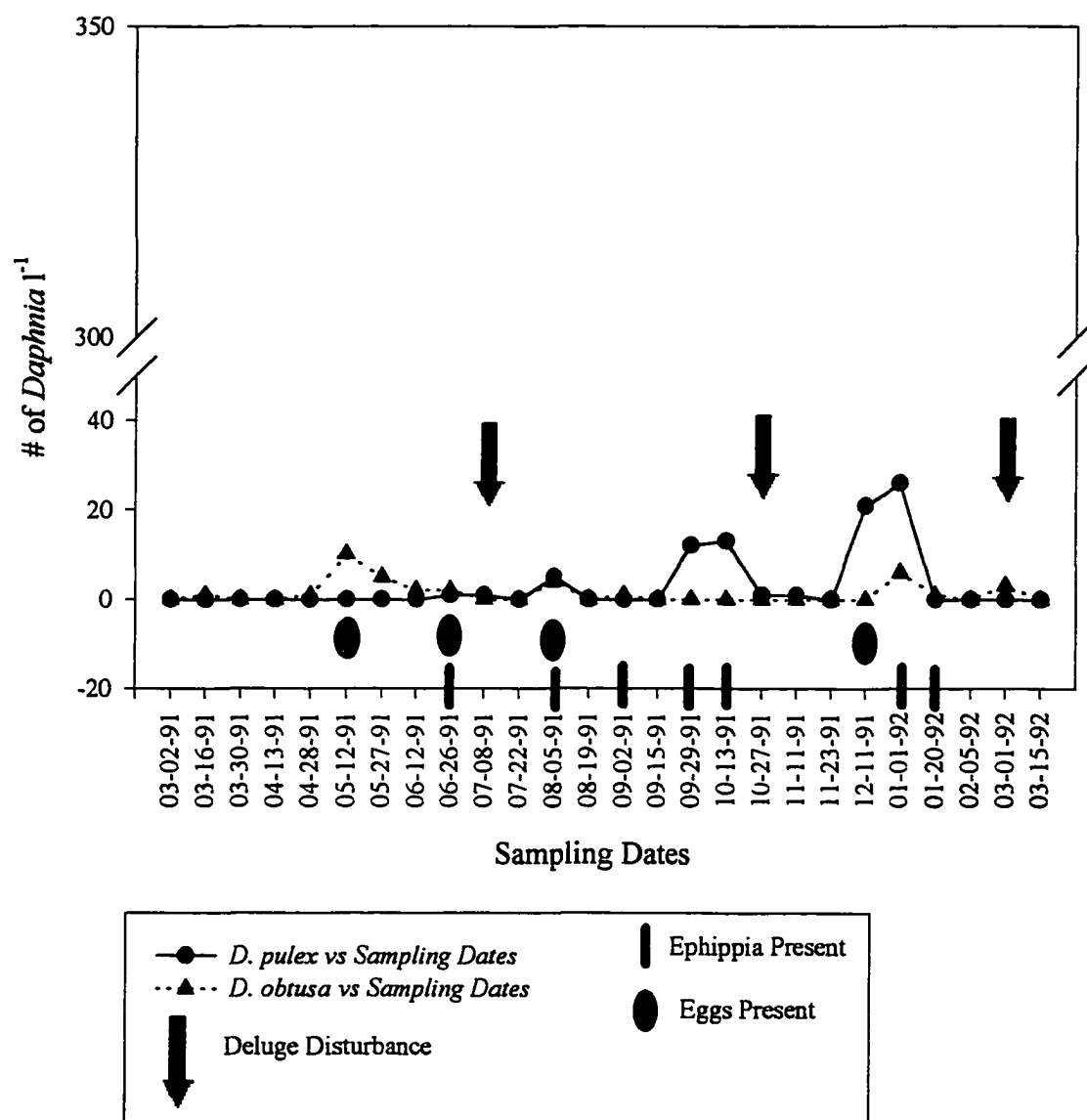


Figure 43: Number of *D. pulex* and *D. obtusa* versus sampling dates in Pool 1, showing dates when eggs or ehippia were present including those within each individual and those that were loose.

Number of *Moina* l⁻¹ Versus Sampling Dates in Pool 1

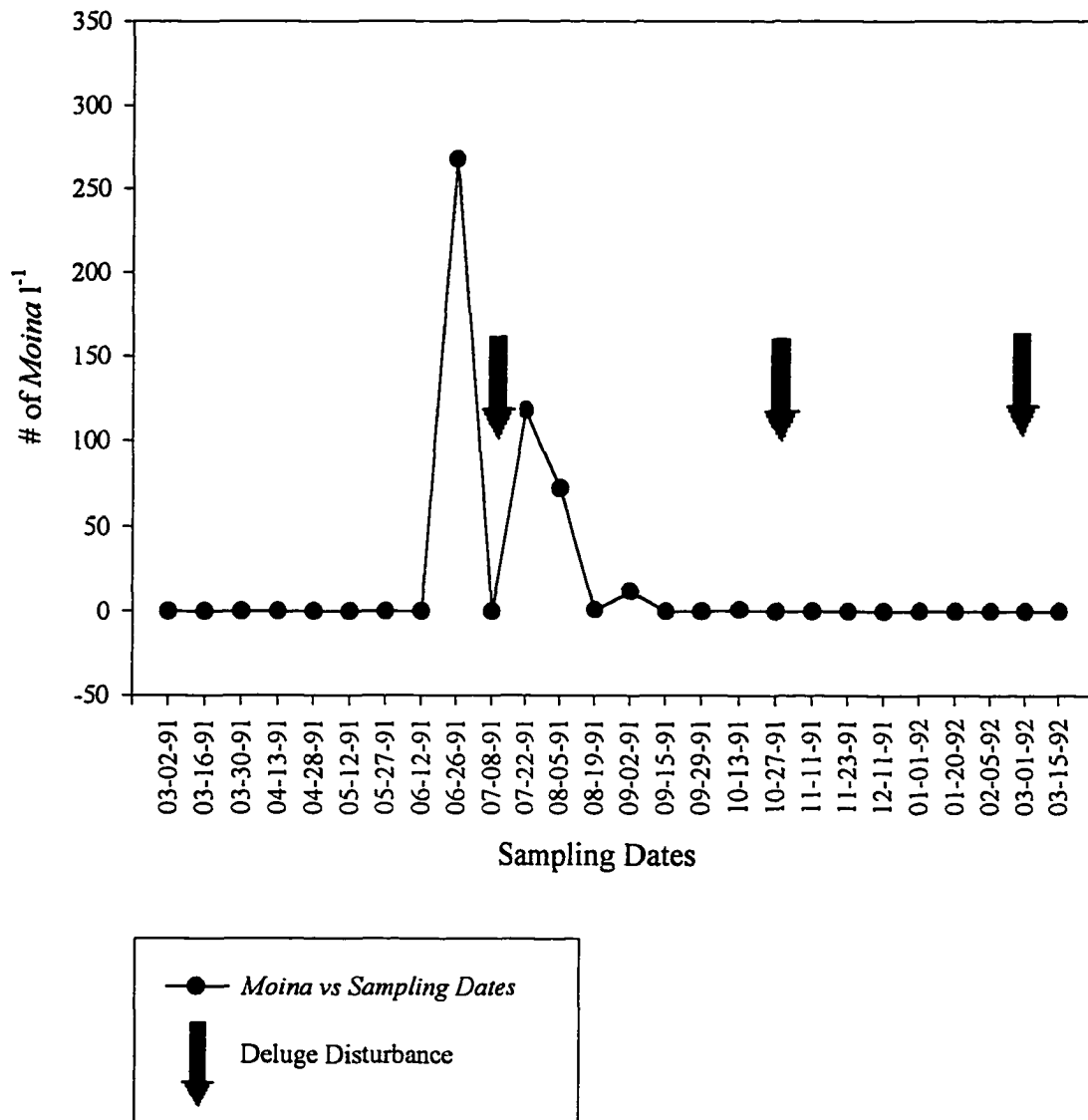


Figure 44: Number of *Moina* versus sampling dates in Pool 1.

Daphnia populations were usually suppressed when *Moina* was present. One factor that may account for the diminution in *Daphnia* numbers during the summer could be competitive exclusion by the incredible *Moina* numbers. Loss of *Moina* could allow the *Daphnia* populations to increase. However, they were occasionally found together in large numbers. Also, extremely warm pool temperatures during the summer probably limited the presence of daphnids, which appear to prefer cooler spring and fall conditions in this system. *D. obtusa* declined as summer approached, while *M. macrocopa* dominated during the summer months as water temperatures increased. These findings support Maier's (1993) study in which he found that *D. obtusa* died as water temperatures climbed above 25°C, whereas *Moina* sp. could tolerate water temperatures to 30°C. Daphnids can tolerate lower temperatures and they take longer to reach maturity and have smaller clutches (Maier 1993).

Higher reproductive rates in the summer turned out to be the case for *Moina* but not especially for *Daphnia*. *Daphnia obtusa* thrived in the spring, while *Daphnia pulex* appeared mainly in the fall as described for each pool below.

Pool 2 is the smallest, shallowest, most ephemeral pool and was dry on five of the sampling dates. Numbers of cladocerans present were accordingly low. *D. obtusa* were again present in the spring in very small numbers (2 l⁻¹) with small appearances in December 1991 and January 1992 (Figure 45). *D. pulex* appeared in the fall and winter, as they did in Pool 1, but the number of *Daphnia* never exceeded 8 l⁻¹. Eggs were produced in September and December. I found only one ephippium in the September sample when *D. pulex* were present. *Moina* numbers when present (Figure 46) ranged

Number of *D. pulex* and *D. obtusa* Versus
Sampling Dates in Pool 2

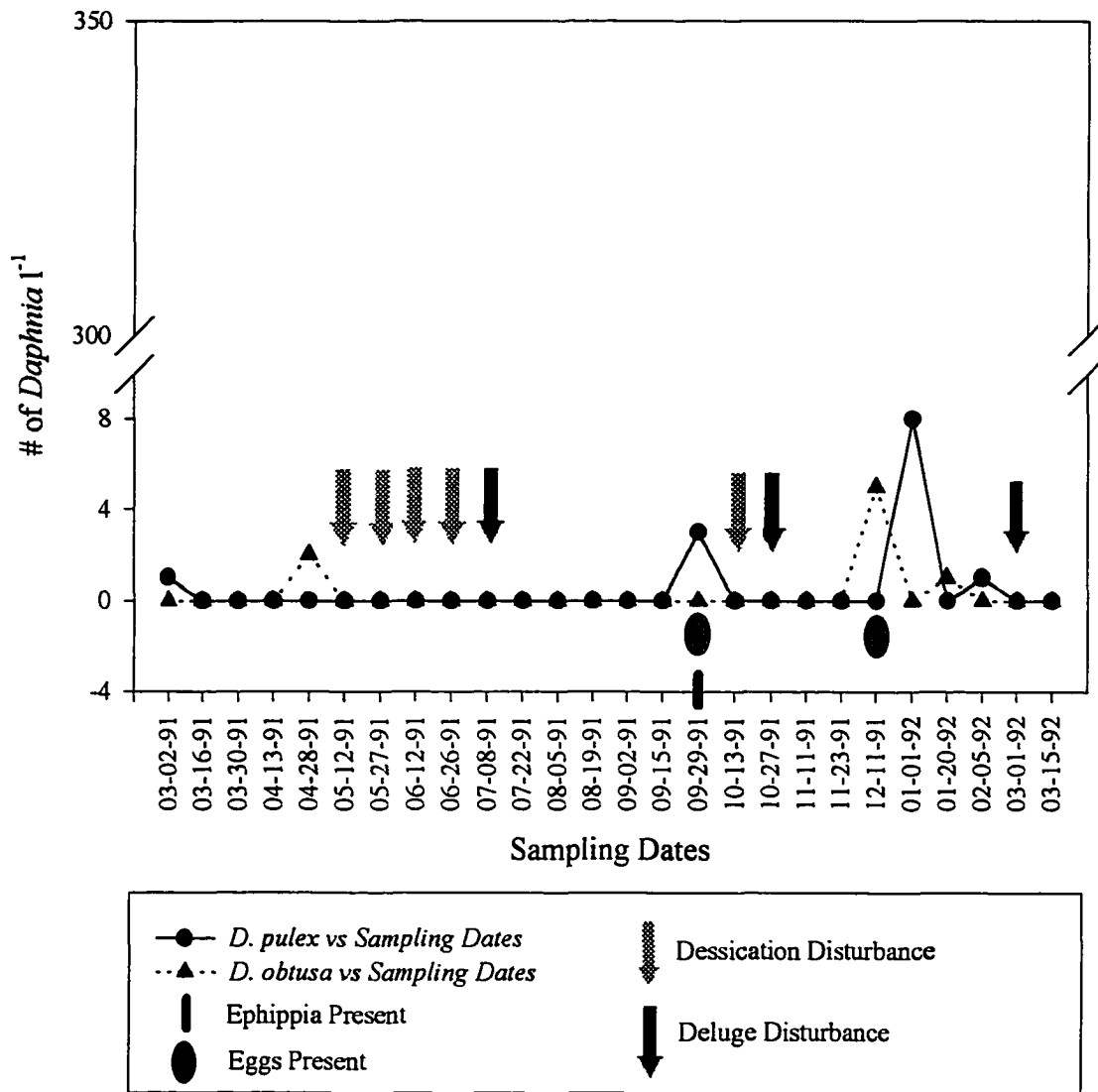


Figure 45: The number of *D. pulex* and *D. obtusa* versus sampling dates in Pool 2. Scale on y-axis varies from other pools due to low *Daphnia* counts in this pool.

Number of *Moina* l⁻¹ Versus Sampling Dates in Pool 2

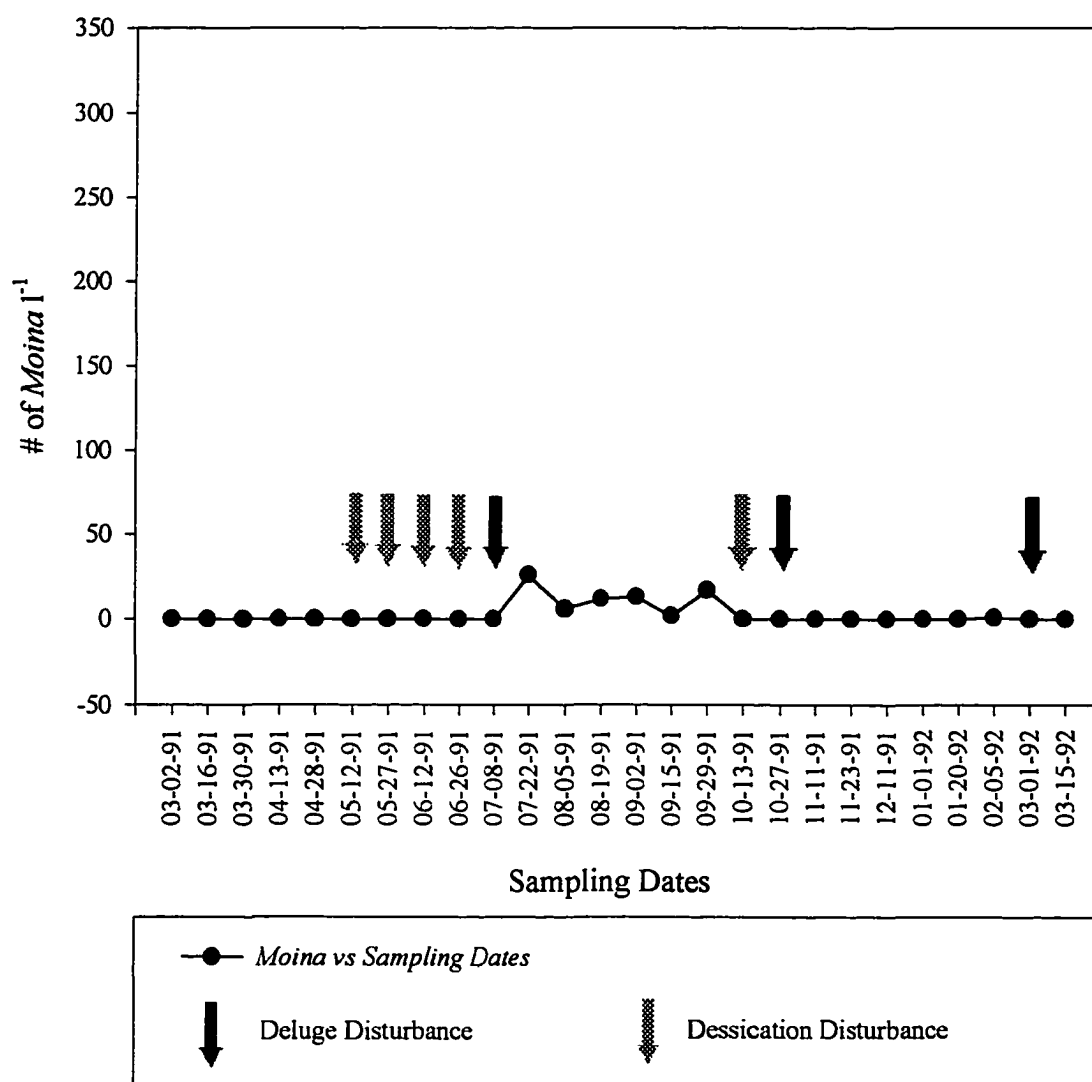


Figure 46: The number of *Moina* versus sampling dates in Pool 2.

from 1 to 26 l⁻¹. The first *Moina* appeared in July 1991 after the flooding event on July 8, and *Moina* were present in the summer during July, August, and September.

Pool 3 is a large, shallow pool, and like Pool 2, was dry on five sampling dates. *D. obtusa* was the first daphnid to appear with 89 l⁻¹ appearing suddenly in April (Figure 47). Pool 3 was dry in June and July, but refilled with July flooding. *D. pulex* appeared in September, but Pool 3 dried again in October. Following flooding in October, *D. pulex* peaked at 119 l⁻¹ in November, and were present until the pool was again deluged in March 1991. Large numbers of eggs were produced twice (107 per sample in November 1991 and 125 per sample in February 1992). I found very small numbers of ephippia in the samples (only 10 total for the whole year). *Moina* appeared in the summer in July, August and September when the pool refilled following two months of drought with numbers never exceeding 23 l⁻¹ (Figure 48).

Pool 4 is a very long, narrow pool in a fissure between blocks of sandstone and had only four dry periods, instead of five like Pools 2 and 3. *D. obtusa* appeared in the spring, as in Pools 1, 2, and 3, with 1 l⁻¹ on April 13, 1991 followed by a population explosion of 298 l⁻¹ two weeks later at the next sampling (Figure 49). However, the pool then dried and *D. obtusa* never fully recovered. In September, I found 8 l⁻¹ and then *D. obtusa* did not reappear during the sampling year. *D. pulex* appeared in late summer and fall in modest numbers (56 l⁻¹ on Sept 2 and 49 l⁻¹ on September 29). The pool then dried, and following refilling on October 27, one *D. pulex* was present in the sample (Figure 50). Two weeks later 11 ovigerous females were present in the sample along with 30 juveniles of various sizes (Figure 51). Ephippia, at 24 l⁻¹, were present in January 1992 while *D.*

Number of *D. pulex* and *D. obtusa* Versus
Sampling Dates in Pool 3

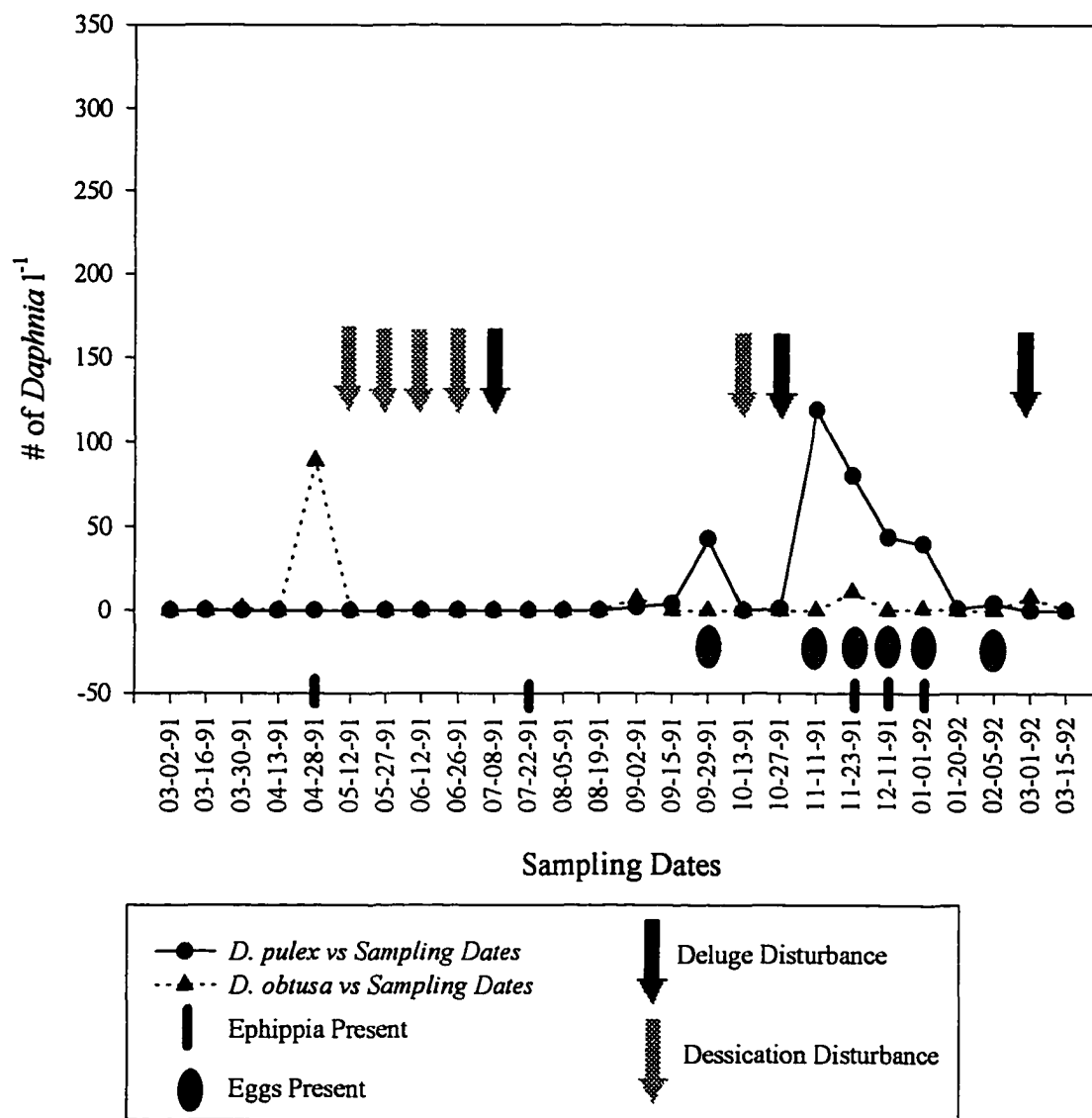


Figure 47: Number of *D. pulex* and *D. obtusa* versus sampling dates in Pool 3.

Number of *Moina* Versus Sampling Dates in Pool 3

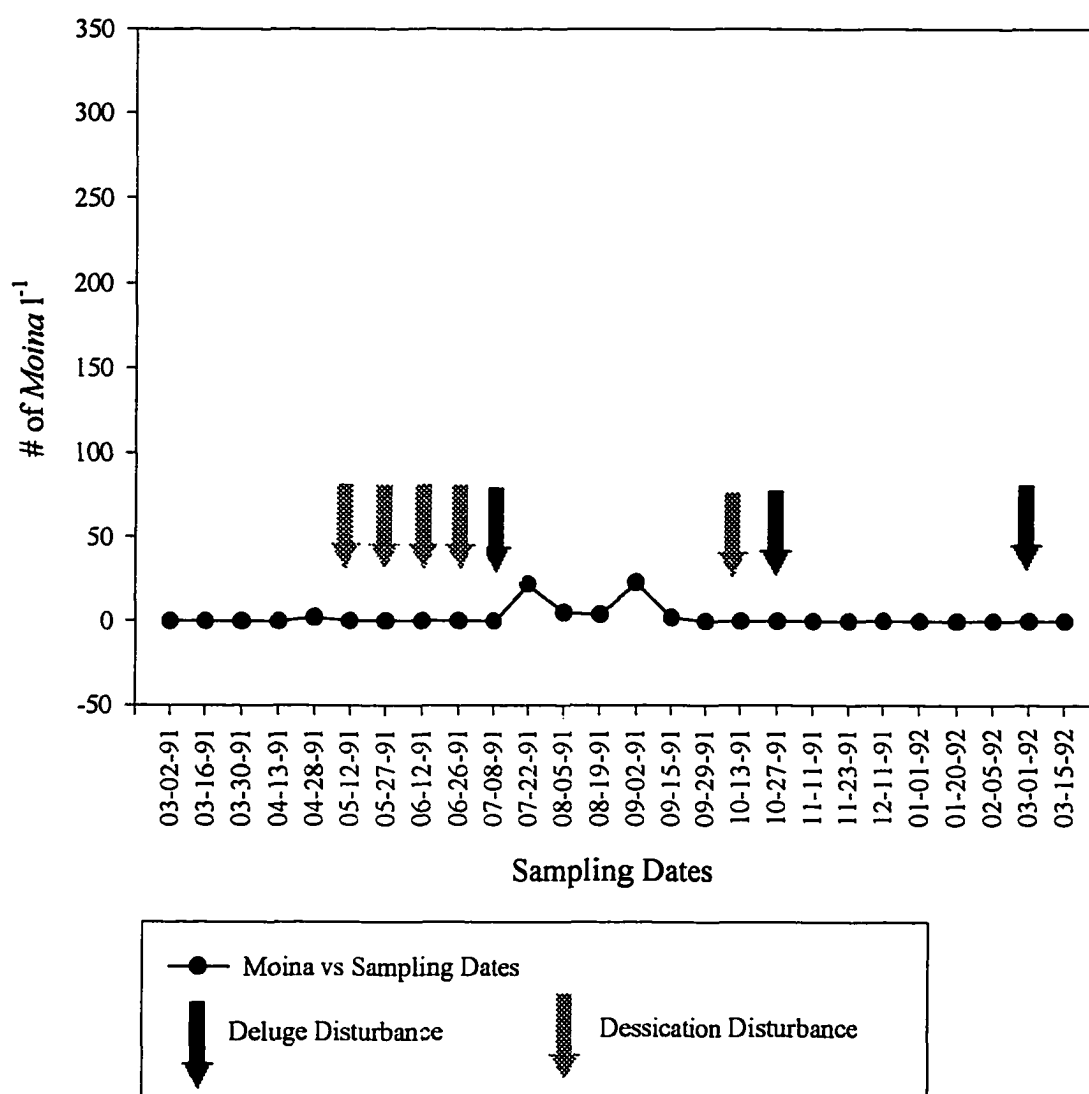


Figure 48: Number of *Moina* l^{-1} versus sampling dates in Pool 3.

Number of *D. pulex* and *D. obtusa* Versus
Sampling Dates in Pool 4

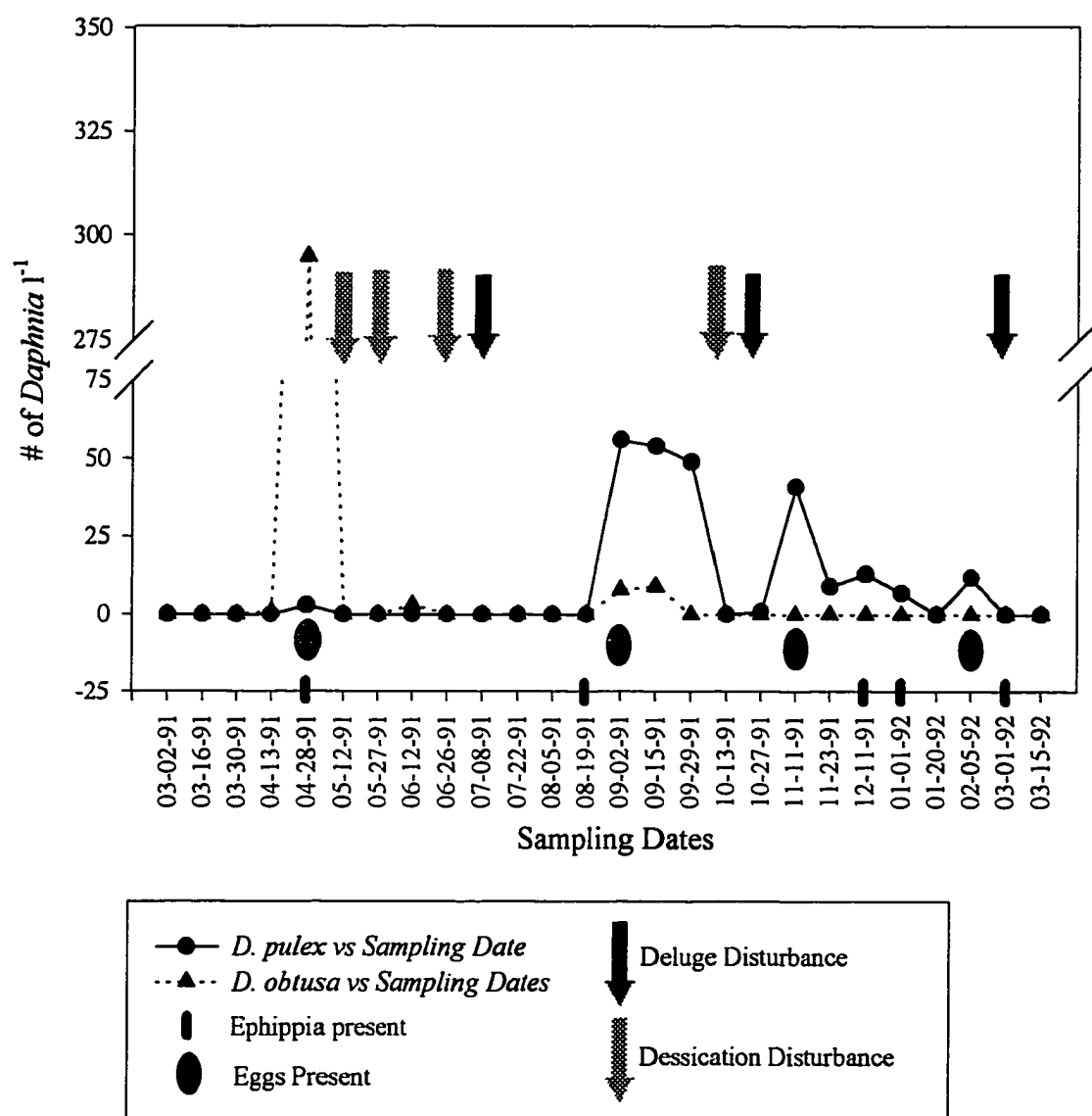


Figure 49: Number of *D. pulex* and *D. obtusa* versus sampling dates in Pool 4.

Number of *Moina* Versus Sampling Dates in Pool 4

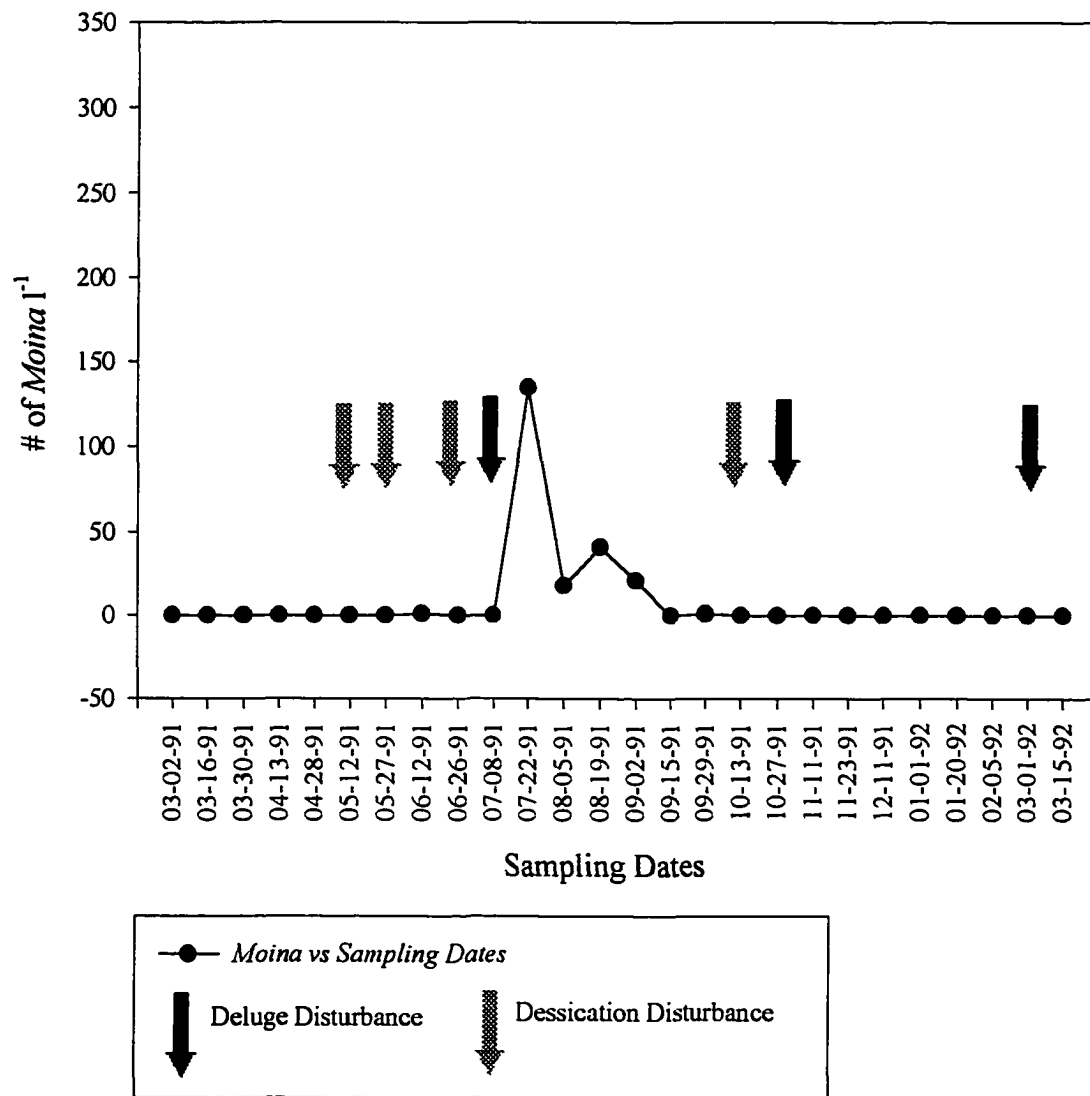


Figure 50: Number of *Moina* l^{-1} versus sampling dates in Pool 4.

pulex were present. *Moina* appeared, as in other pools in the summer after the pool refilled in July. Numbers were highest (135 l⁻¹) two weeks after filling on July 22, and, thereafter, ranged from 0 to 41 l⁻¹ until the pool dried in October.

Pool 5 is deeper and somewhat protected, so it had only two dry periods during the year, but experienced the same three deluge events that occurred for all pools. *D. obtusa* appeared in the spring in April at a maximum of 40 l⁻¹. The pool then dried, and when the pool refilled in June the population exploded to 251 l⁻¹. The pool dried again, and thereafter, numbers of *D. obtusa* remained low with an isolated, small (20 l⁻¹) peak in December. *D. pulex*, as in other pools, appeared in the fall with a peak of 68 l⁻¹ in September. Numbers dropped following flooding in October, and rebounded in the late fall and early winter. I found eggs produced by *D. obtusa* in the June 12 sample (216 l⁻¹), and by *D. pulex* in the November 11 sample. I saw only one ephippium during the whole year on July 22.

Daphnia in Pool 5 are an example of the remarkably prodigious developmental capacities of these animals in a desert system. In June, following a dry period in May, *D. obtusa* were able to undergo explosive growth. *Moina* appeared at 27 l⁻¹ in June. Then between two dry periods, and following flooding and pool refilling on July 8, they reappeared during the rest of July and August (Figure 52). *Moina* were then absent from samples for the rest of the sampling year.

Pool 6 is the most stable pool with no dry or low periods during the year. Its location, which protects it from the sun, and its depth and smaller relative surface area make it less subject to evaporation. *D. obtusa* appeared first in April at 28 l⁻¹, and then

Number of *D. pulex* and *D. obtusa* Versus Sampling Dates in Pool 5

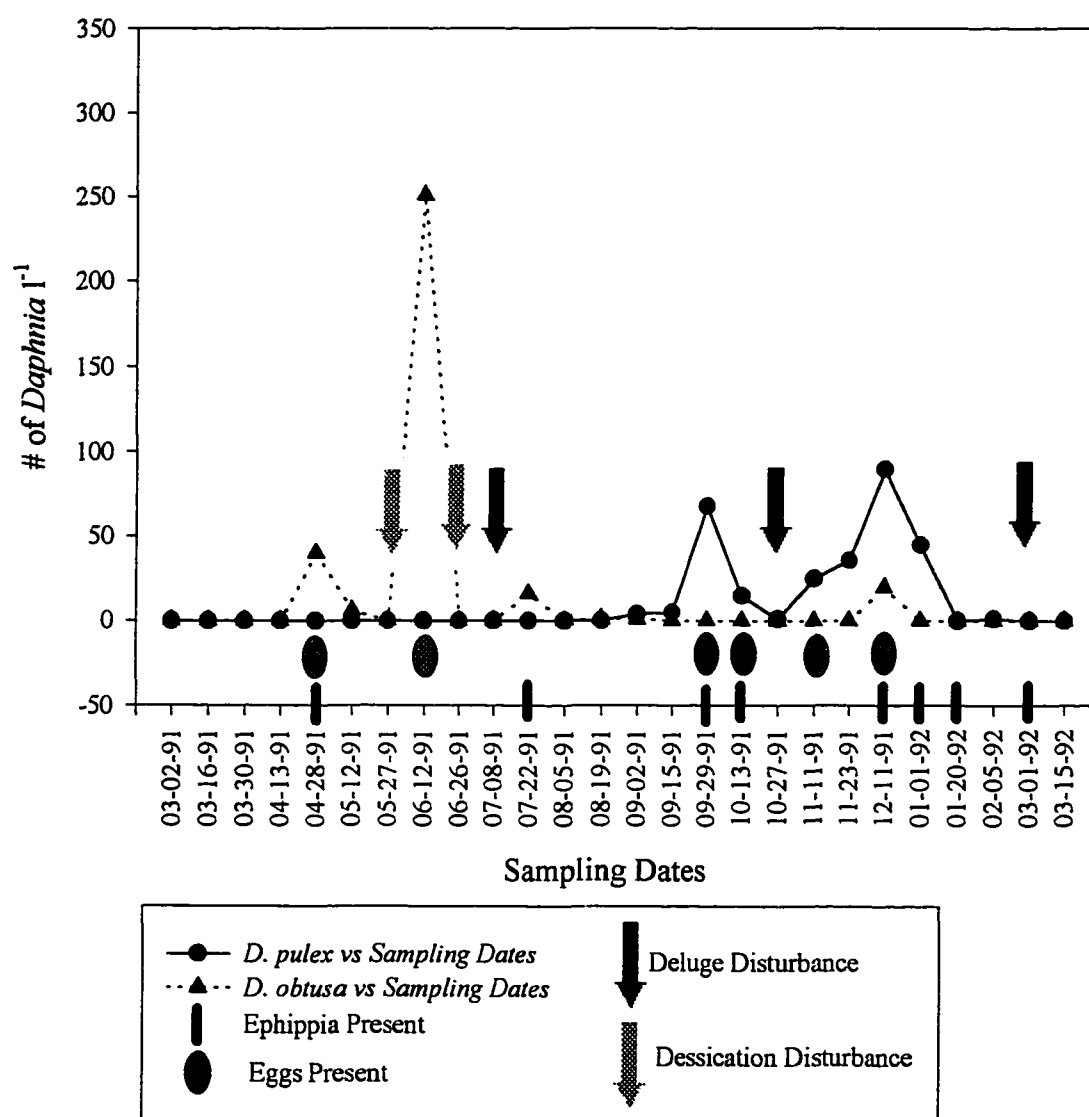


Figure 51: Number of *D. pulex* and *D. obtusa* versus sampling dates in Pool 5.

Number of *Moina* l⁻¹ Versus Sampling Dates in Pool 5

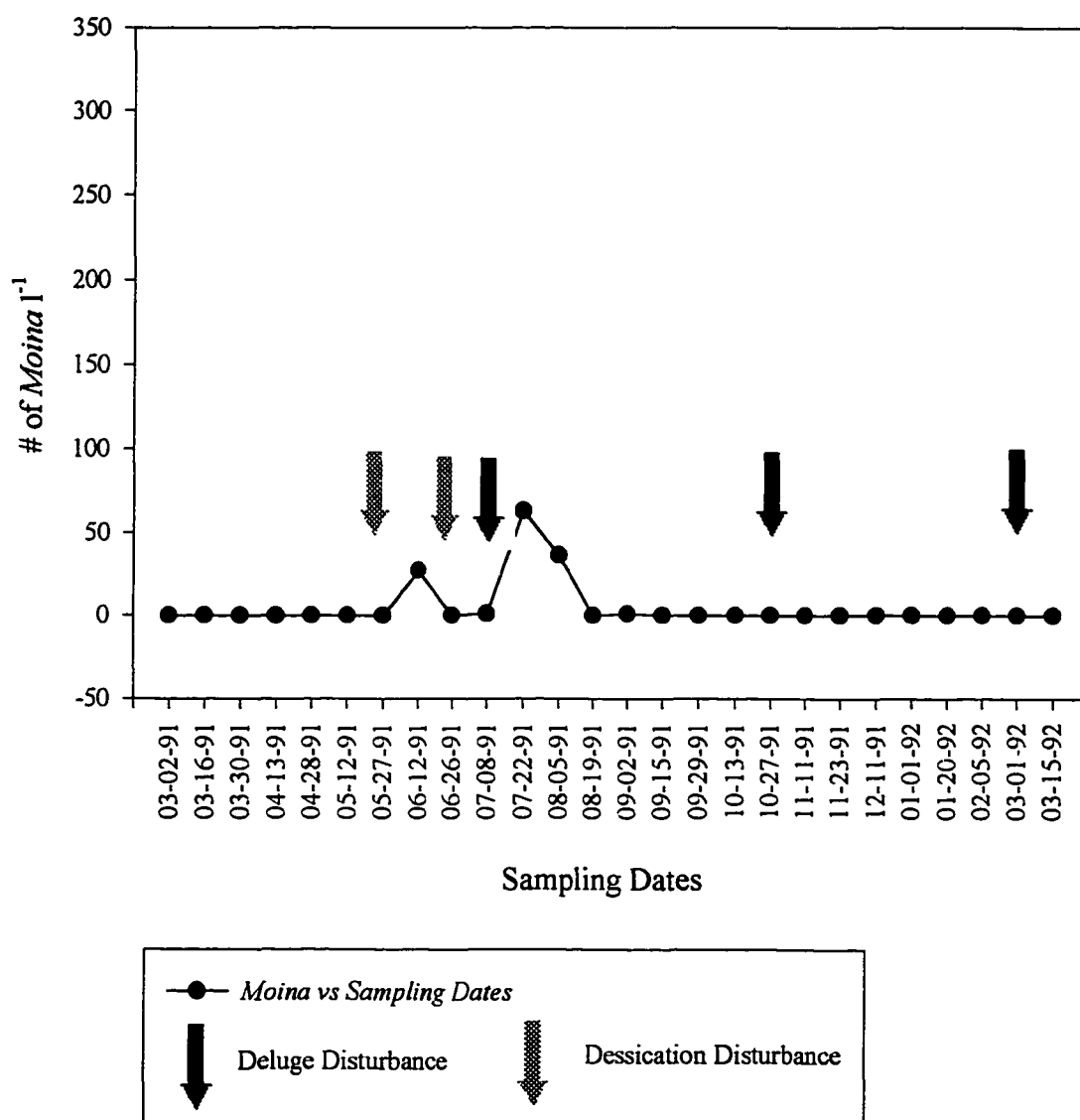


Figure 52: Number of *Moina* l⁻¹ versus sampling dates in Pool 5.

again in June at 18 l⁻¹, but were replaced by a large population (287 l⁻¹) of *D. pulex* in June (Figure 53). Numbers of both species declined following July flooding until *D. pulex* rebounded and persisted from September 1991 through January 1992. Egg and ephippia production were low throughout the year (only 35 eggs and 13 ephippia total for the whole year). I found *Moina* present in large numbers (308 l⁻¹) on June 26, but flooding on July 8 flushed out the pool (Figure 54). *Daphnia* and *Moina* were in concert during the year in this particular pool. While low numbers were present on July 22, and again on September 2, *Moina* then were absent the rest of the year.

In Pool 6 *D. pulex* appeared as early as June, whereas they were found in the fall in other pools. However, Pool 6 is an atypical pool in that it had lots of water during the whole sampling year. It is interesting to speculate what numbers *D. pulex* would have reached if the population (which reached numbers of 287 l⁻¹ prior to the July deluge event) had not been disturbed.

Pool 7, the uppermost pool, is a large, shallow circular pool which was dry only during the month of June. After flooding and refilling on July 8, it had water the rest of the sampling year. *D. obtusa* appeared in the spring starting in April and peaking in May at 204 l⁻¹ (Figure 55). The pool was dry during the next two sampling periods. Following refilling in July, and again in October, *D. pulex* appeared in low numbers (2 to 23 l⁻¹) during November, December, and January. *D. obtusa* also reappeared in low numbers during the same time period, but as *D. pulex* declined at the end of January 1992, they were replaced by *D. obtusa* in February. *D. obtusa* disappeared when flooding occurred on March 1, 1992. Egg production was highest (592 per sample) when *D. obtusa* was

Number of *D. pulex* and *D. obtusa* Versus
Sampling Dates in Pool 6

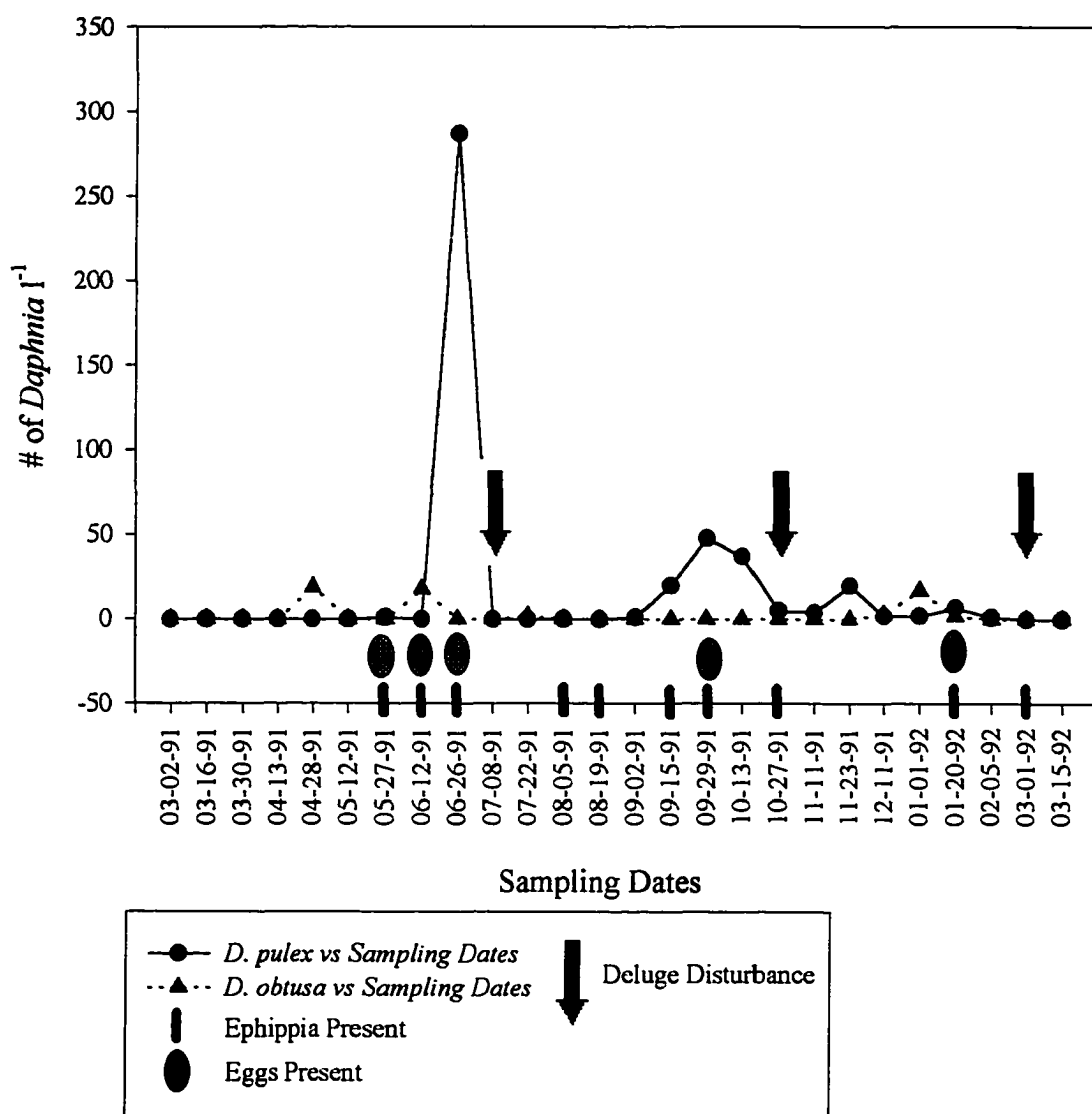


Figure 53: Number of *D. pulex* and *D. obtusa* versus sampling dates in Pool 6.

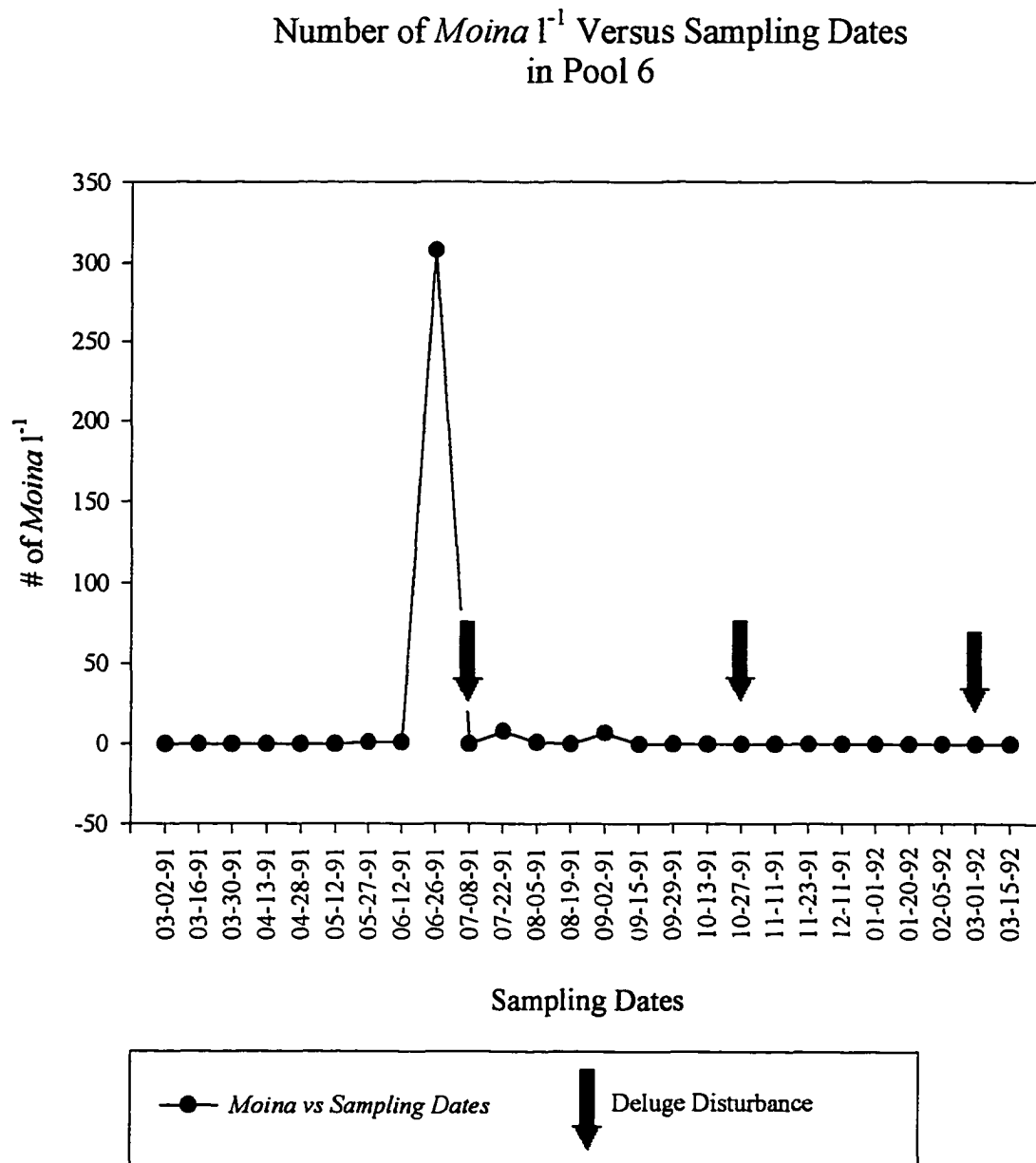


Figure 54: Number of *Moina* l⁻¹ versus sampling dates in Pool 6.

Number of *D. pulex* and *D. obtusa* Versus
Sampling Dates in Pool 7

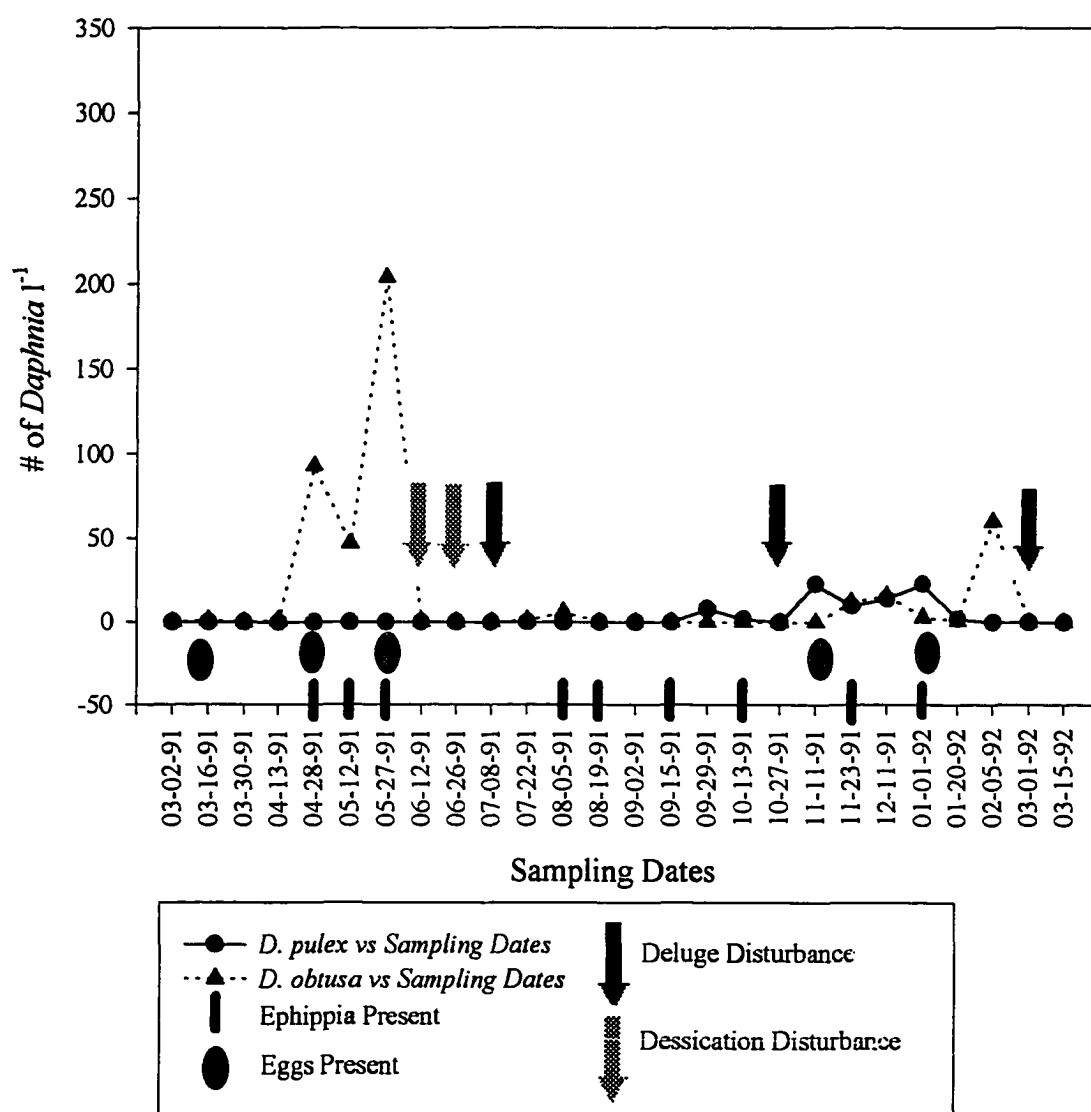


Figure 55: Number of *D. pulex* and *D. obtusa* versus sampling dates in Pool 7.

present in May 1991. Only 35 ehippia were present in samples for the whole year.

Moina did not appear in this pool in large numbers during the summer as in most other pools (Figure 56). The most I found were 7 l⁻¹ in August.

In these pools, long-term persistence of populations existed only in periods of relatively static conditions, or low water flow, which allowed animals to maintain their populations. I assumed, given the two week sampling intervals, that if water was present on two adjacent dates, it was present in between. It is possible, but not likely, that pools dried and refilled between sampling dates. It is more likely that pools were deluged during these intervals with possible scouring and washing away of populations.

In all pools, *D. obtusa* made initial appearances in April and May of 1991. They were then replaced by *Moina*, which had population explosions in midsummer with one exception that being in Pool 6. *D. obtusa* and *Moina* peaked at the same time in June. *Moina* appears to be a summer specialist as it was not found in any other season. *D. pulex* dominated during the fall and winter in all pools, although Pools 1, 2, 3, 5, and 7 also had small winter populations of *D. obtusa*.

Daphnia spp. have episodes of *D. pulex* dominance in the fall, and *D. obtusa* dominance in the spring, in some respects complimentary to each other. When *D. pulex* was high, *D. obtusa* was usually low and vice versa.

Moina population explosions can also be partly explained by behavioral differences between *Moina* and *Daphnia*. *Moina* allegedly browse as well as graze (P. Starkweather pers. commun. 1996), and productivity in these pools may be a surficial resource largely unavailable to *Daphnia*. *Moina* have summer peaks with a remarkable growth rate. The

Number of *Moina* Versus Sampling Dates in Pool 7

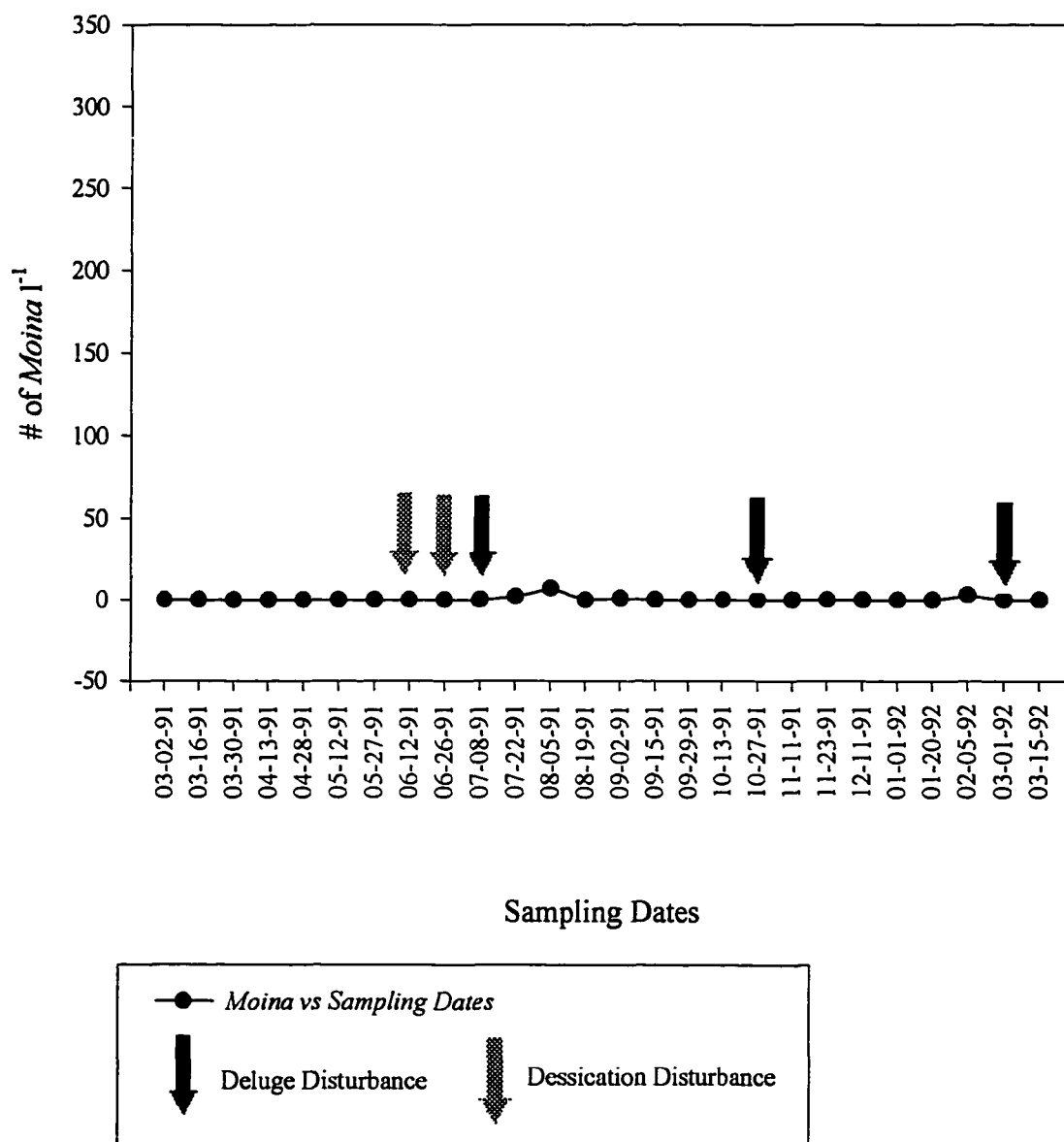


Figure 56: Number of *Moina* l^{-1} versus sampling dates in Pool 7.

full potential, of which, cannot be realized because on July 8, 1991, for example, *Moina* population size in Pool 1 was essentially unmeasurable because of flooding. Two weeks prior to this date, the population was huge, and two weeks after the flood it had rebounded.

The total number of *Daphnia* spp l⁻¹ in any one pool at any one time varied greatly from pool to pool with highs of 295 for *D. pulex* in Pool 6, and 295 for *D. obtusa* (see Appendix II for count data for all seven pools). At no time during the collection period did I find males present, so *Daphnia* species in Red Rock Canyon appear to be obligate parthenogens for both subitaneous eggs (embryos) and ephippial diapause eggs (embryos).

I did not find any obvious changes in morphology. Apparently, no seasonal or predator induction of cyclomorphosis exists in these *Daphnia*. Even though predators have been known to induce cyclomorphosis as discussed above, and known invertebrate predators were present in these pools, predators were few and infrequent, and appeared to have little, if any, impact on the daphnids in these pools.

Daphnia individuals varied in size from 0.3 mm to 3.2 mm in *D. obtusa* and from 0.4 mm to 3.5 mm in *D. pulex* (see Appendix III for *Daphnia* lengths and brood size for Pools 1, 4 and 6 for the sampling year). The smallest reproductive female was 0.8 mm in *D. obtusa* and 1.0 mm in *D. pulex*. The number of eggs per daphnid varied from 0 to 18 in *D. obtusa* and from 0 to 34 in *D. pulex*, but eggs may be expelled from the brood pouch during the preservation process and during manipulation during counting and measuring procedures. Therefore, the number of total eggs per liter, per sample was measured and this number varied from 0 to 590 (this includes loose eggs found in the sample). Both

daphnid species produced ephippia with two embryos. The number of ephippia per liter, per sample varied from 0 to 40. This includes individuals forming ephippia as well as loose ephippia found in the sample.

On life history grounds, in temporary pools with limited seasonality, reproducing earlier at smaller sizes is more efficient. However, size differences in zooplankton also affect their capacity to feed. In principle, large *Daphnia* (ie. *D. pulex*) should have dietary advantages because they can filter more water and can eat larger particles relative to smaller species (ie. *D. obtusa*) in terms of the size/efficiency hypothesis (Brooks and Dodson 1965, Hall et al. 1976). Competitively, large numbers of *D. pulex* could scavenge more effectively and strip the water of most particles so that the *D. obtusa* would have little nutritional resources unless they could also browse.

Dormancy enables *Daphnia* species in stressed environments to withstand unfavorable seasons (freezing, drying). In order to survive dessication disturbances, daphnids have to be in diapause stages. Timing of ephippial eggs is important. Early production of resting stages is beneficial because this ensures a pool of ephippia to endure dry periods and from which repopulation can occur after inundation. Ephippia in the samples reached highest numbers in Pool 1 (25) and Pool 6 (40) in June, and in Pool 4 (24) in January. Passive dispersal of ephippia allows the repopulation of pools in the pool system, particularly in an area such as Red Rock Canyon where pools periodically receive water from pools upstream in the wash during times of precipitation. These dessication and deluge events establish a temporal structure during the year which might lead one to believe that populations in these pools actually start and restart several times within the

year.

As previously discussed, *Daphnia* in arctic pools use the same strategy of apparently obligate parthenogenesis to make the most of a short period of favorable conditions. Obligately parthenogenic clones can take advantage of similar patterns that exist in their habitat year after year. As long as conditions do not change clones are genetically suited to their environment. The ability to switch between sexual strategies would enable a population to make the most of its habitat.

I often saw epibionts consisting of fungi, algae and rotifers attached to the heads and carapaces of both *Daphnia* and *Moina*. I saw free-swimming rotifers in the fresh samples but not in the preserved samples, possibly attributable to the special method and medium used to preserve the cladocerans. Delicate forms, such as ciliated protozoa and rotifers, may disintegrate in formalin solutions, and Lugol's solution is a preferred preservative for these forms (Wetzel and Likens 1991).

Allen and De Stasio (1993) found that an algal epibiont on *D. galeata mendotae* in Lake Mendota, Wisconsin in 1990 caused higher death rates which they attributed to added stress on individuals during the period of infestation. At other times I found rotifers attached to the heads and carapaces of these daphnids which can possibly affect population numbers of Red Rock Canyon *Daphnia*. When daphnids had large numbers of epibionts attached, they moved sluggishly and I also noticed more effluvia and dead daphnids in the sample.

Calanoid copepods are known predators of daphnids, and copepodite stages of *Acanthocyclops robustus* have been shown to invade brood chambers and eat *Daphnia*

eggs and embryos (Gliwicz and Umana 1994a). A few calanoid copepods were found in these pools. However, the presence of potential predators was intermittent, and they were present in such small numbers that it seems unlikely that they could have had a substantial impact on the dynamics of these systems. Also, as discussed above, paradoxically predators can induce larger populations, as well as cause lower population numbers.

As discussed above, vertebrates seem to have little or no impact on daphnids present in these pools. *Bufo punctatis* tadpoles are unlikely predators, and the only impact from larger vertebrates (sheep, burros, horses) would be due to the removal of water from the pools.

Pool Characteristics and Chronology

Precipitation in desert regions usually occurs during two periods rather than throughout the year as it does in other areas. Most precipitation occurs in the Great Basin during the winter (Evans and Thames 1981). Given normal winter precipitation patterns in the Spring Mountains, it is not surprising that all pools have water during winter months. The periods of winter inundation reflect, not necessarily a higher total precipitation rate, but less evaporation during cooler winter months. In the winter, more regionally uniform precipitation occurs in response to cyclonic storms as sequential fronts pass through the area with more correlation between winter rains and pond filling.

Precipitation as measured at the Red Rock Weather Station is independent of pool depth. However, the Red Rock Canyon weather station is located about one km from the collection sites, and rainfall is patchy in the Spring Mountains. For example, on July 8, 1991 I observed and made a notation that it was a warm, rainy day and that water was flowing rapidly down the wash connecting all the pools. Photographs (slides) taken that day show what looks like raging rapids with waterfalls from one pool running over into the next pool. Yet the Red Rock Weather Station recorded no precipitation for that day. Indeed, according to published data from that station, no precipitation occurred between June 1 and July 31, 1991 (National Oceanic and Atmospheric Administration Climatological Data for Nevada 1991). Assuming that the data provided by the Red Rock Weather Station are correct, it indicates a remarkable spatial heterogeneity of precipitation in the area during the time when all pools filled in July at a time when there was no recorded precipitation over the prior two week period.

Precipitation during two week periods between sampling dates varied from 0 to 10.21 cms (Figure 57), but not always with corresponding changes in the depths of the pools (Figure 58) as discussed below. During the study year I found that these pools had marked seasonal fluctuations in water level with five of the seven pools having periods where they were completely dry as a result of low precipitation, high temperatures, and high evaporation. These are truly ephemeral pools and the interplay between input and evaporative output is great. Clearly, as evaporation rates increased with the increase in ambient and water temperatures in the spring through April, May, and June, evaporation rates exceeded precipitation rates. Water reached higher temperatures in the shallower pools, particularly in Pool 2 which received full sun all day.

Pool depths varied from 0 to 120 cms with all pools except Pools 1 and 6 being dry during the sampling year. Pool 1 was extremely low only once, in May. Pools 1 and 6 showed most stability in water level, temperature, oxygen tension, conductivity and pH. Pools 1 and 6, as noted in Table 1, are in deep oval crevices under rock overhangs with only limited sun at midday. Lower evaporation rates explain the anomaly of Pools 1 and 6 relative to the other five pools.

All pools experienced three deluge events (July 8, 1991, October 27, 1991 and March 1, 1992) when all pools were full and overflowing. Pool 6 depths were the most consistent, ranging from a minimum depth of 48 cms to a maximum depth of 120 cms. Maximum depths occurred for most pools on July 8, 1991, when pools were overflowing and water was running rapidly down the wash in one continuous stream. However, by the time I reached the upper pools, water had stopped flowing. Therefore maximum depth for

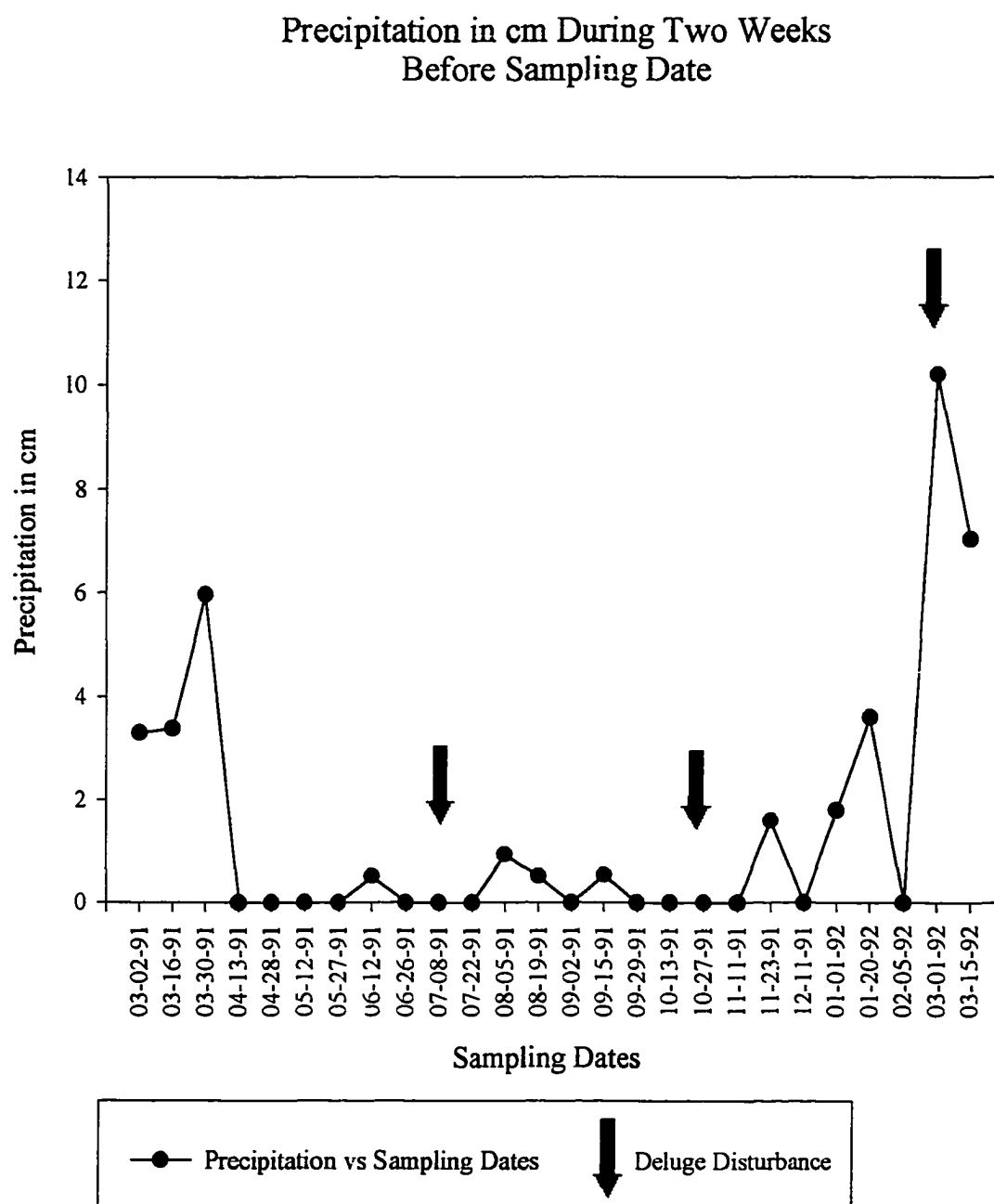


Figure 57: Relationship of precipitation in cm versus sampling dates.
Precipitation measurements were recorded from the Red Rock Canyon Station 1 km away from sampling site.

Depth in cm of all Seven Pools Versus Sampling Dates

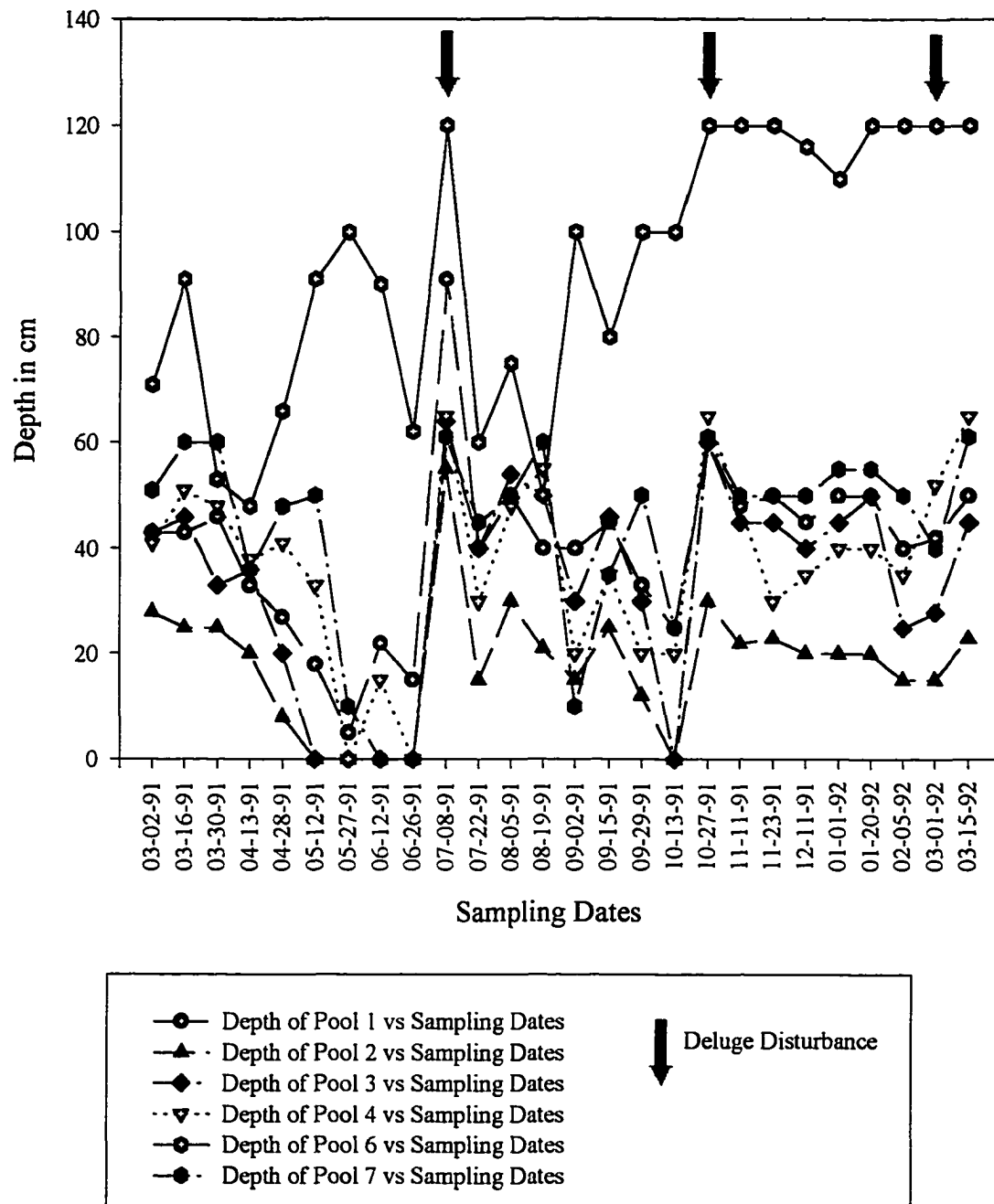


Figure 58: Relationship between depth in cm of all seven pools versus sampling dates during the sampling year.

Pools 5, 6, and 7 were recorded on two other known dates of flooding (October 27, 1991 and March 1, 1992) when upper pools were overflowing at the time of sampling. Also at times of flooding, pools were often difficult to access in order to measure them at midpoint and some inaccuracies may have occurred in gathering depth data.

Each pool behaves individually with respect to depth. The only time during the year when there is marked correspondence between precipitation and pool filling was in July 1991, and to a lesser extent, in October 1991 and March 1992. Most of the pools were maximally full in October and March from winter precipitation. In July and August, pools which had been dry in the spring filled with water reflecting increased summer precipitation. Pool depth in summer often seemed paradoxical because it did not seem like there was much precipitation recorded at the Red Rock Weather Station. Two reasons which account for this are 1) that the weather station is out on the bajada and collection sites are in a small canyon in the foothills, and 2) these pools can only get so full. They reach a maximum depth depending on the configuration of the pool basin and then they overflow downstream.

A related problem is that the pools occasionally filled even with no precipitation recorded at the Red Rock Weather Station. Again this reflects the extremely heterogeneous spatial array of rainfall factor. It may be that enough rainfall occurs in the mountains to increase the depth of some of the pools up the wash but not enough to overflow into lower pools.

A possibility for depletion of water from some pools, but not from others, is that large vertebrates such as bighorn sheep, wild burros and wild horses may use one or more

of the pools as sources of water. I saw many wild burros and one herd of about six to eight wild horses in Red Rock Canyon during the period of the study. Bighorn sheep are known to be present in this area (P. Starkweather pers. commun. 1996).

The number of *Daphnia* l⁻¹ was regressed against depth, and Pools 4, 5, and 7 showed modest relationships (Figures 59 to 65). The relationship between depth and population size shows five pools with a slight downward slope with regard to depth, and two, Pools 1 and 2, with no clear relationship. I anticipated a negative slope with these results assuming that with pool duration there would be a drop in water level and an increase in population numbers due to the amount of time for population development.

Air temperatures recorded at the Red Rock Weather Station (Figure 66) ranged from a low of -2.7°C to a high of 35.6 °C (National Oceanic and Atmospheric Administration, Climatologic Data, Nevada, February 1991-March 1992).

This is a desert habitat with a maximum midday annual temperature of 31.0°C and with an annual minimum of 9.5°C. Although there are anecdotal reports of these pools freezing in the winter as discussed above, the lowest pool water temperature that I encountered during midday was 7°C and the highest was 30°C. Pool water at 7°C may have cooled enough during the night to freeze, at least superficially.

High temperatures occurred in late spring, summer and early fall. Minimum temperatures occurred as expected during late fall, winter, and early spring. Average temperatures ranged from a low of 4.1°C in January 1992 to a high of 27.4°C in July 1991 (See Appendix V for complete air temperature data).

I recorded ambient temperature near Pool 1 at the time of sampling, and

Number of *Daphnia* l⁻¹ (2 species) Versus
Depth in cm in Pool 1

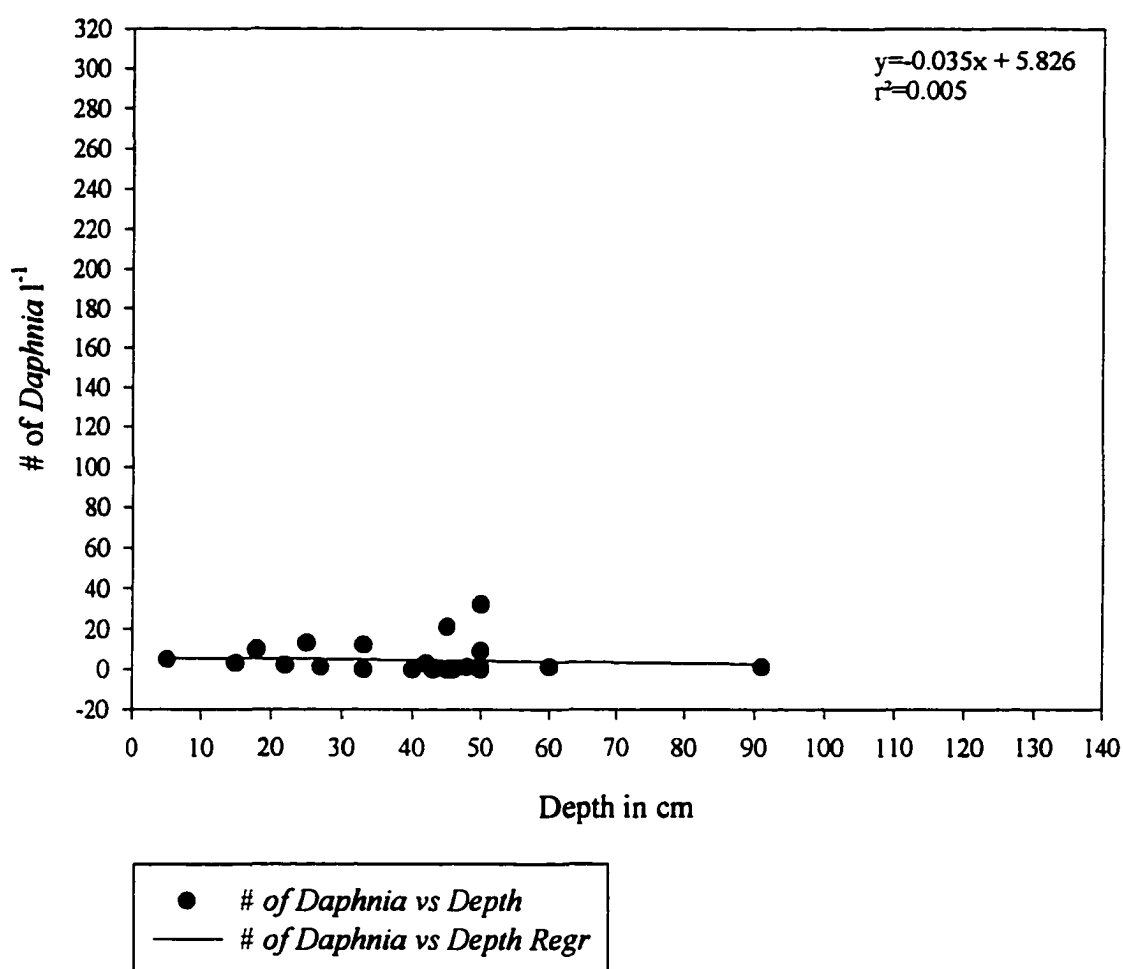


Figure 59: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus depth in cm in Pool 1, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Depth in cm in Pool 2

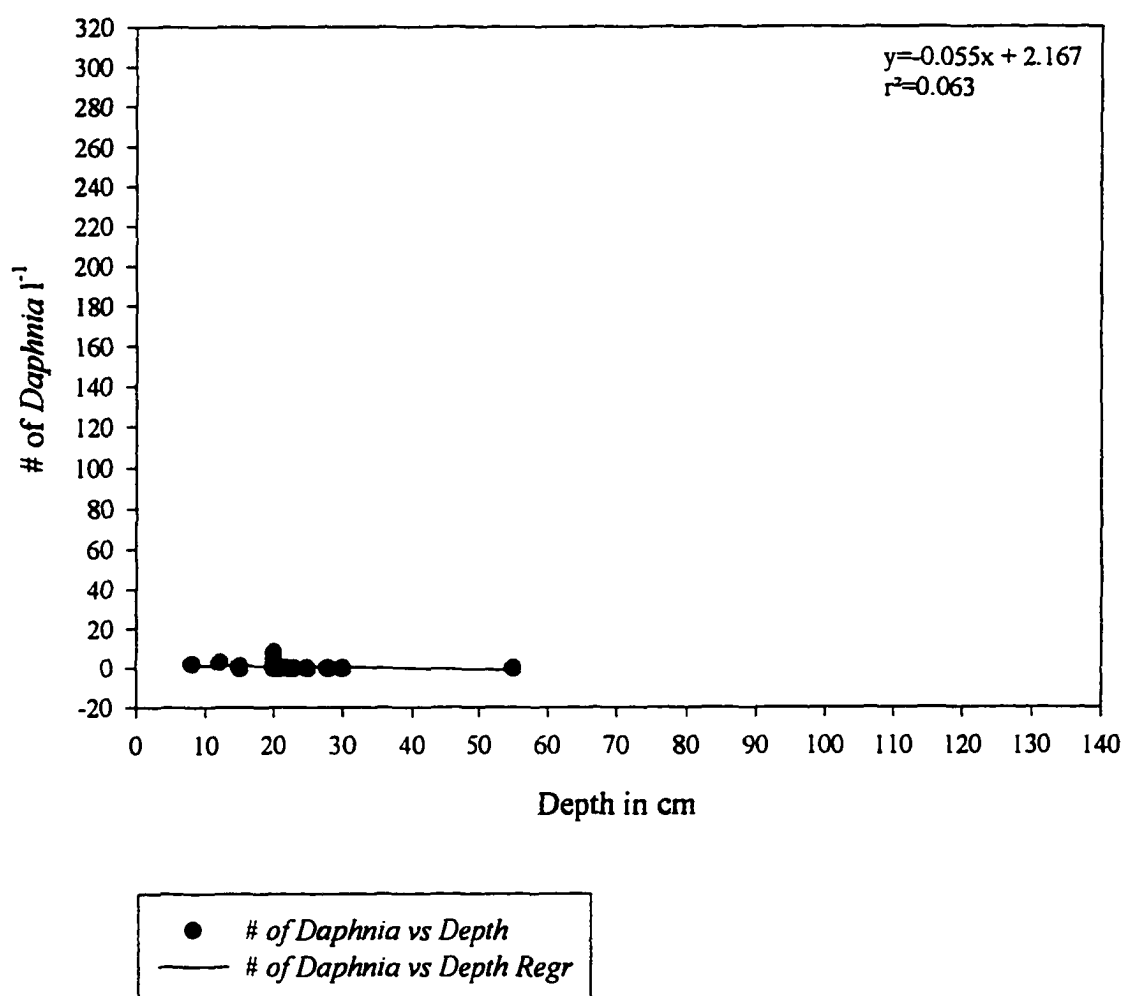


Figure 60: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus depth in cm in Pool 2, with individual data points and regression as shown.

Number of *Daphnia* liter⁻¹ (2 species) Versus
Depth in cm in Pool 3

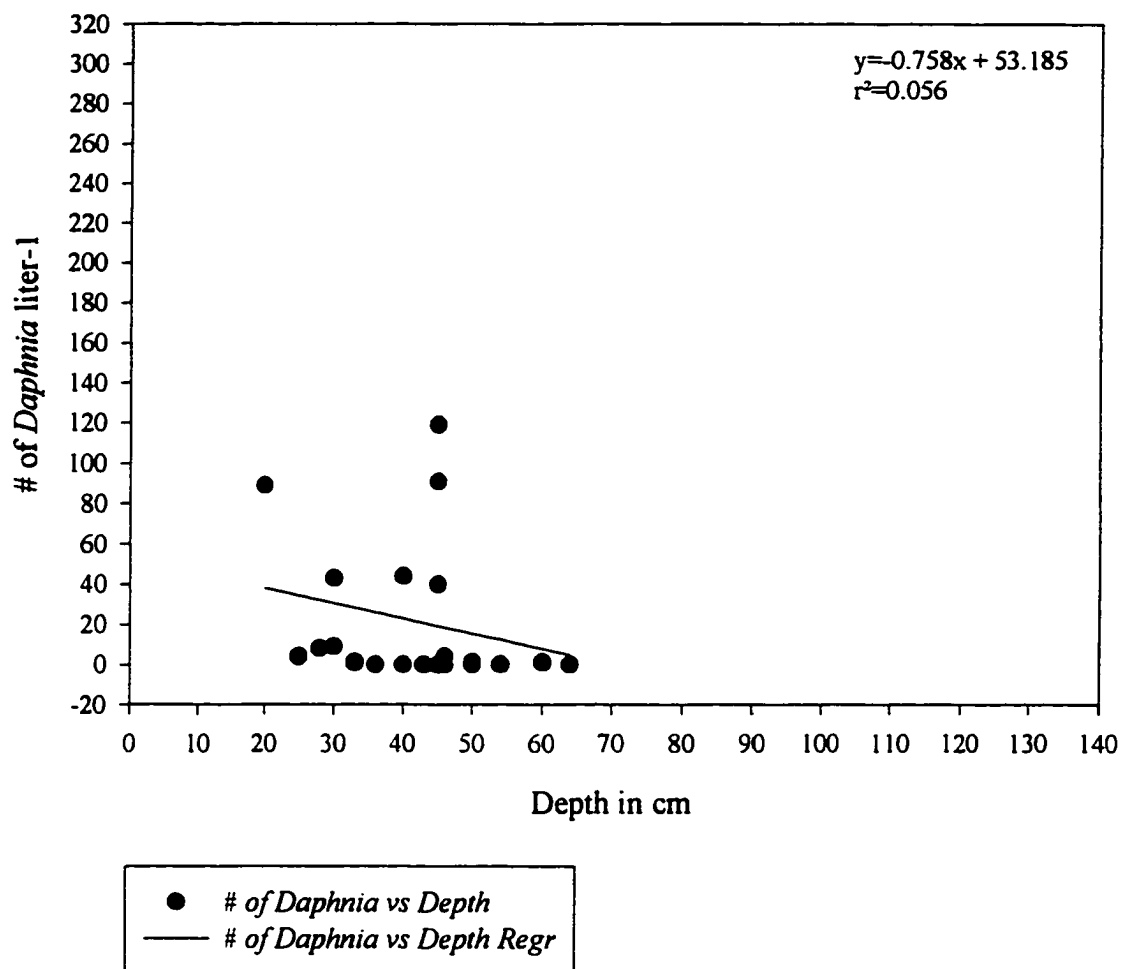


Figure 61: Relationship of the number of *Daphnia* liter⁻¹ (*D. pulex* and *D. obtusa*) versus depth in cm in Pool 3, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Depth in cm in Pool 4

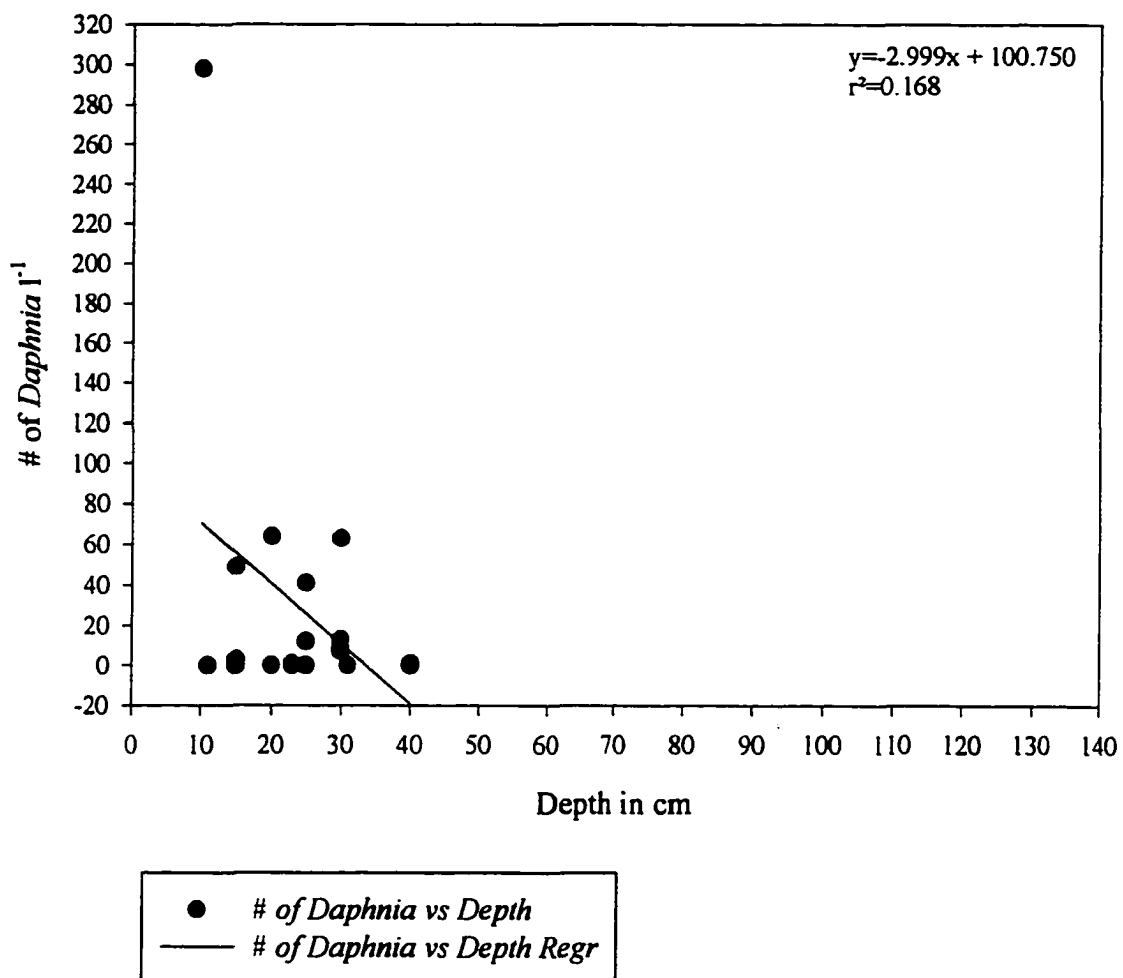


Figure 62: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus depth in cm in Pool 4, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Depth in cm in Pool 5

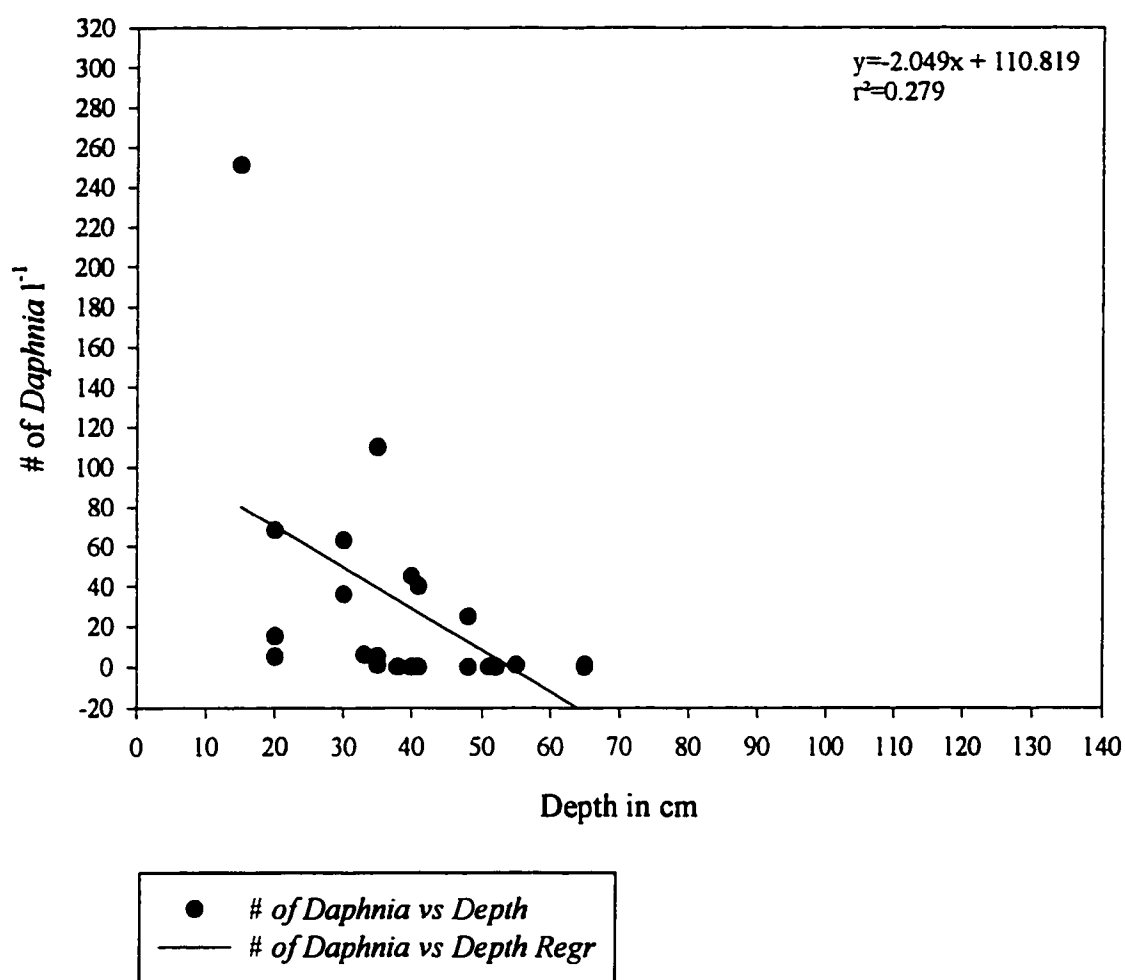


Figure 63: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus depth in cm in Pool 5, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Depth in cm in Pool 6

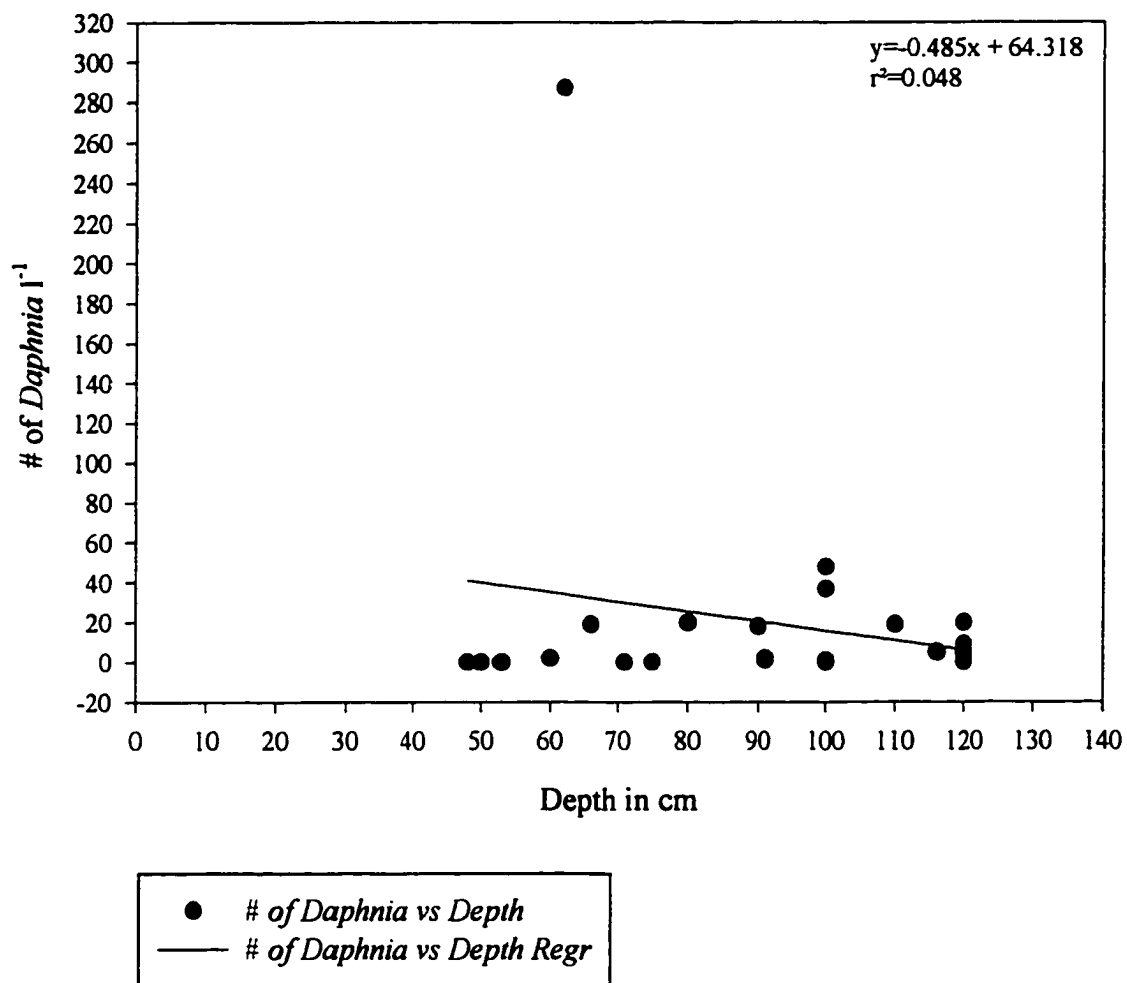


Figure 64: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus depth in cm in Pool 6, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Depth in cm in Pool 7

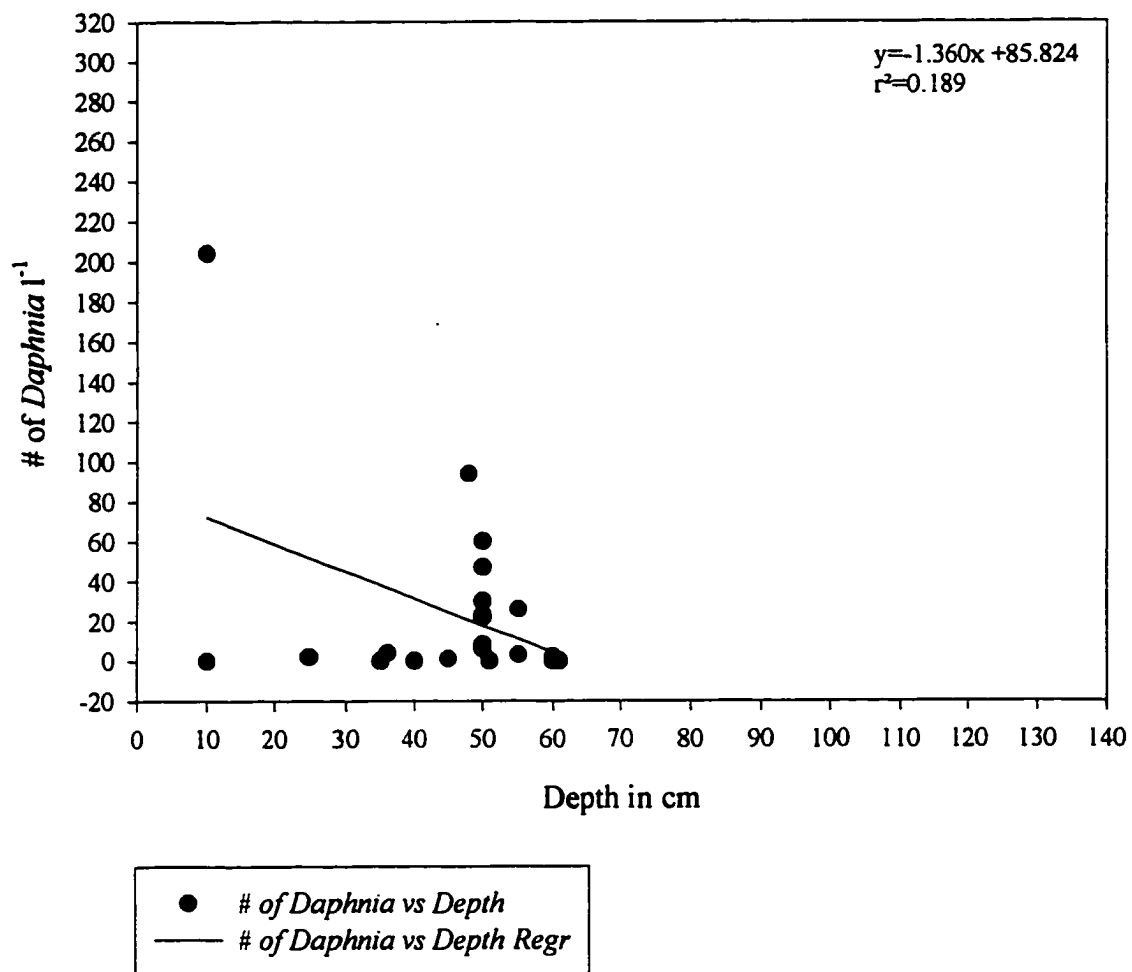


Figure 65: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus depth in cm in Pool 7, with individual data points and regression as shown.

**Monthly Air Temperatures in °C at Red Rock
Weather Station, Nevada During
the Sampling Year**

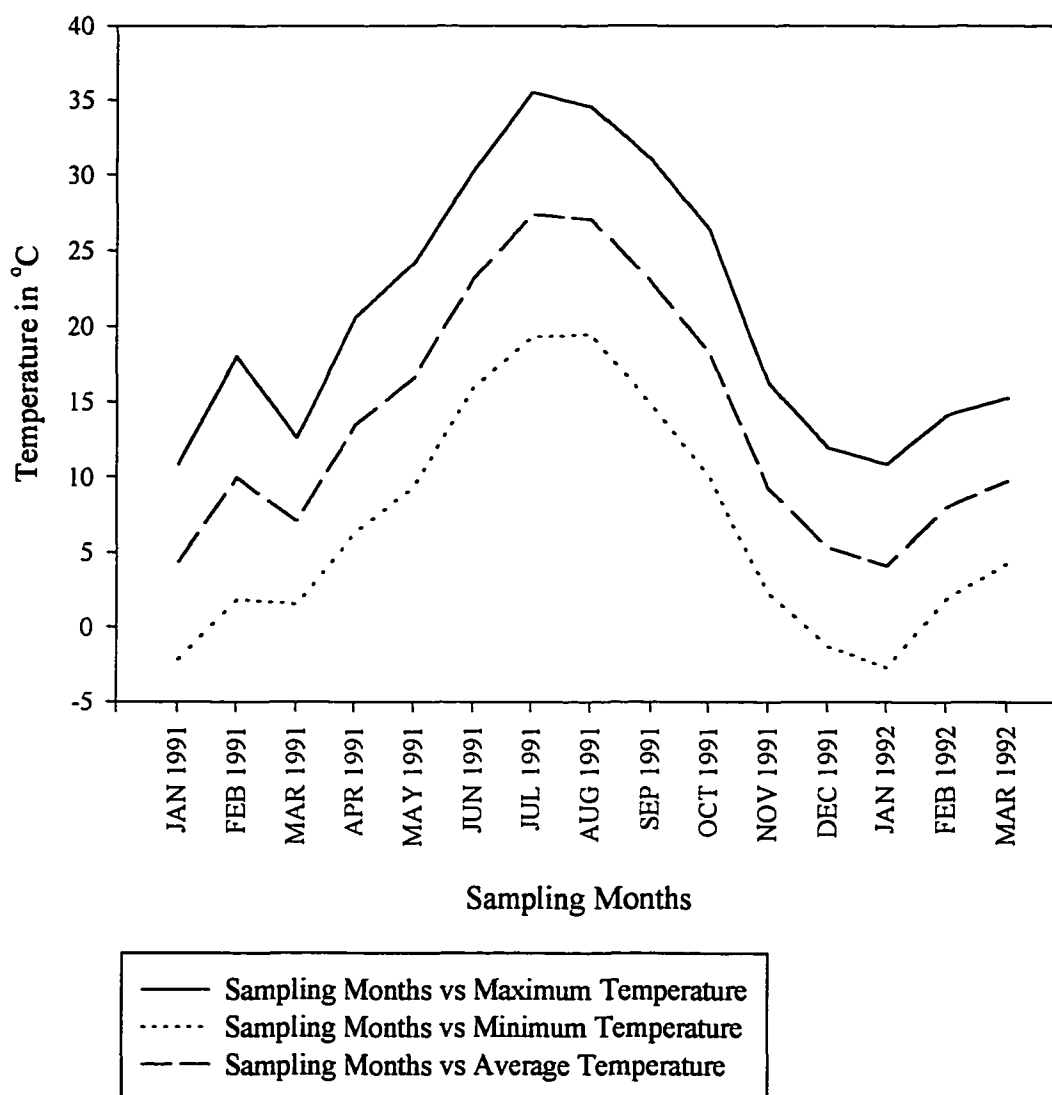


Figure 66: Monthly air temperature in °C at Red Rock Weather Station. Climatologic Data for Nevada from the National Oceanic and Atmospheric Administration.

temperatures ranged from 9.5°C to 31.0°C. Ambient temperatures were recorded between the hours of 10 a.m. and 4 p.m. Temperatures of pool water ranged from a low of 7.0°C in Pool 6 (deepest, least sunlight) to a high of 30.0°C in Pool 2 (smallest, shallowest, most sunlight). Water temperatures for each pool were regressed against the ambient temperature on each date and were correlated as expected (Figure 67). The uniqueness of Pool 2 is also reflected in Figure 67. Complete temperature data can be seen in Appendix V. Regression data for each pool appear in Table 2.

Also the number of *Daphnia* l⁻¹ was regressed against water temperature and appeared unrelated (Figures 68 to 74). This is not to say that temperature has no effect on which particular species of Cladocera is present at any given time, but rather that the physical variable of water temperature is not a physical variable which explains a substantial amount of the variability in the population sizes.

Oxygen values ranged from 1.2 mg l⁻¹ to 9.0 mg l⁻¹ (Appendix VI). Lowest values occurred in late summer, in general, in all the pools. However, each pool had its own cycle of high and low values which was probably determined by various factors, such as depth, temperature, bacterial activity, organic decomposition, and animal activity. Increasing sunlight during the summer with related algal blooms increased the amount of oxygen present during those blooms. Oxygen tension values dropped below 3.0 mg l⁻¹ only in the more ephemeral pools (Pools 2, 3, 4, 5, and 7). The most stable pools (Pools 1 and 6) maintained values between 3 and 9 mg l⁻¹ during the whole year.

The solubility of oxygen in water is influenced by temperature and air pressure. Oxygen was measured in mg l⁻¹ and % saturation was calculated using an Oxygen

Water Temperature in °C Versus Ambient Temperature in °C for all Seven Pools During the Sampling Year

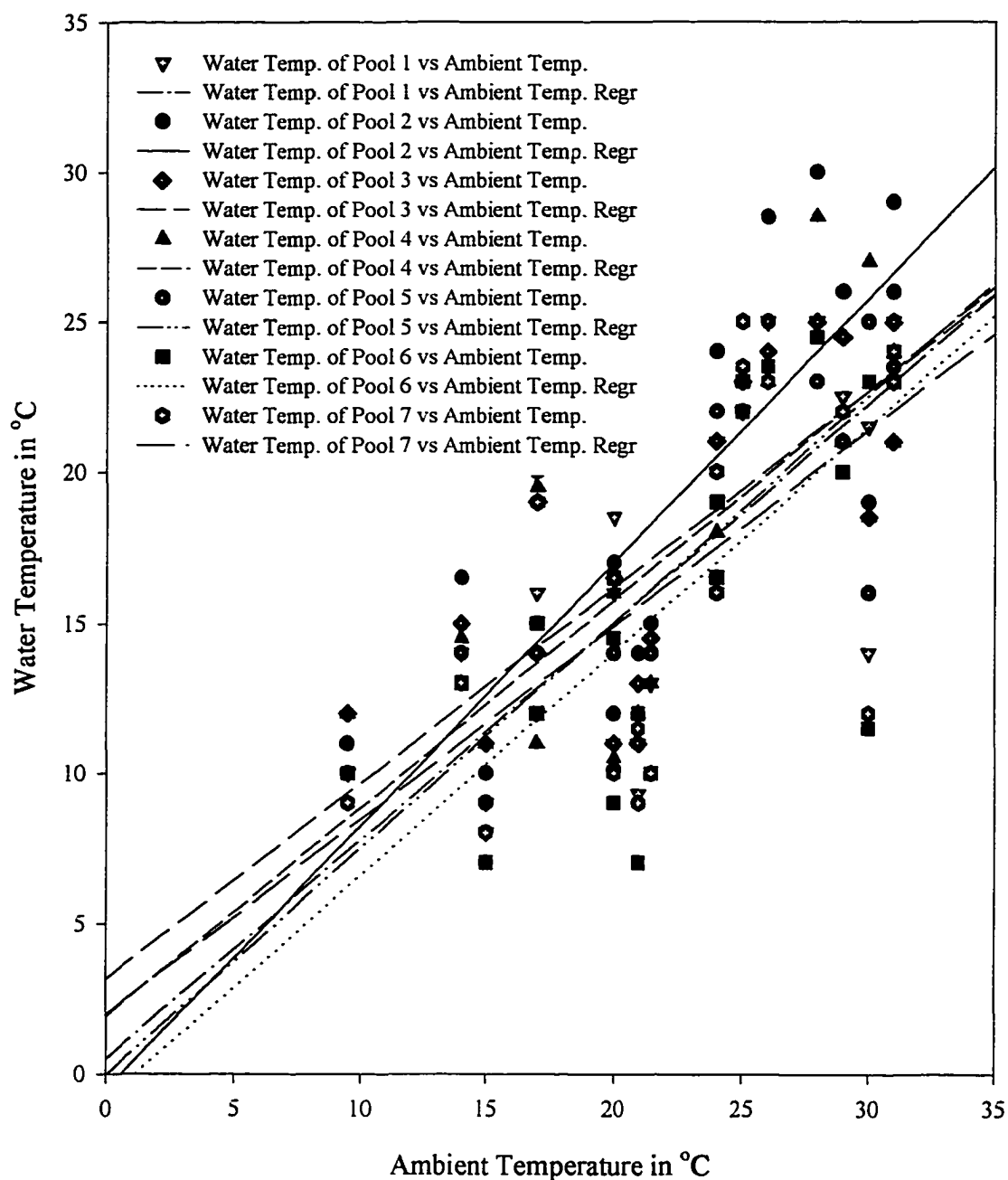


Figure 67: Relationship of water temperature in °C versus ambient temperature in °C for all seven pools during the sampling year.

Table 2: Regression coefficients for Figure 67. Water Temperature versus Ambient Temperature for all seven pools

Pool Number	Regression Coefficients	
	$y = mx + b$	r^2
Pool 1	$y = 0.73x + 0.51$	0.59
Pool 2	$y = 0.88x - 0.53$	0.64
Pool 3	$y = 0.65x + 3.15$	0.60
Pool 4	$y = 0.69x + 1.91$	0.59
Pool 5	$y = 0.75x - 0.04$	0.59
Pool 6	$y = 0.75x - 0.87$	0.53
Pool 7	$y = 0.65x + 1.96$	0.41

Number of *Daphnia* l⁻¹ (2 species) Versus
Water Temperature in °C in Pool 1

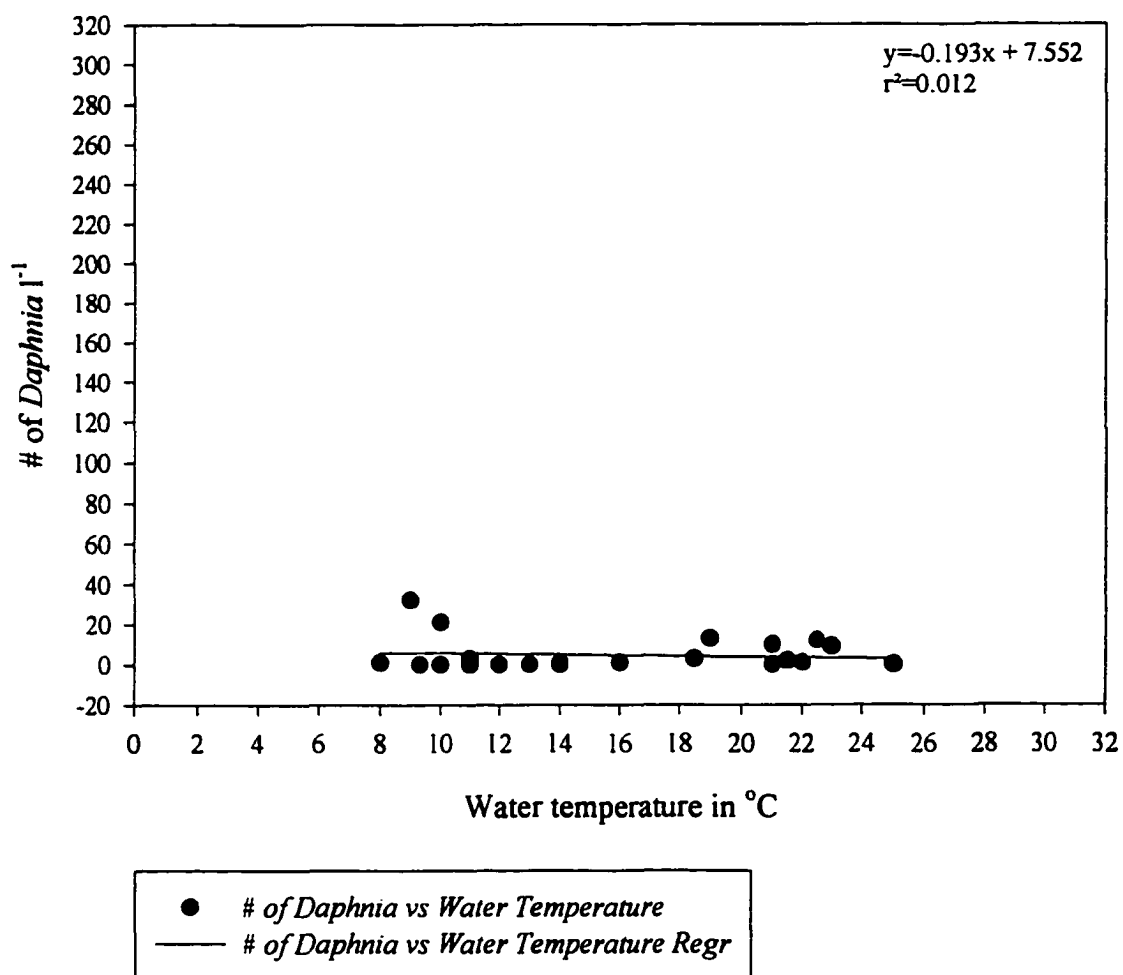


Figure 68: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus water temperature in °C in Pool 1, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Water Temperature °C in Pool 2

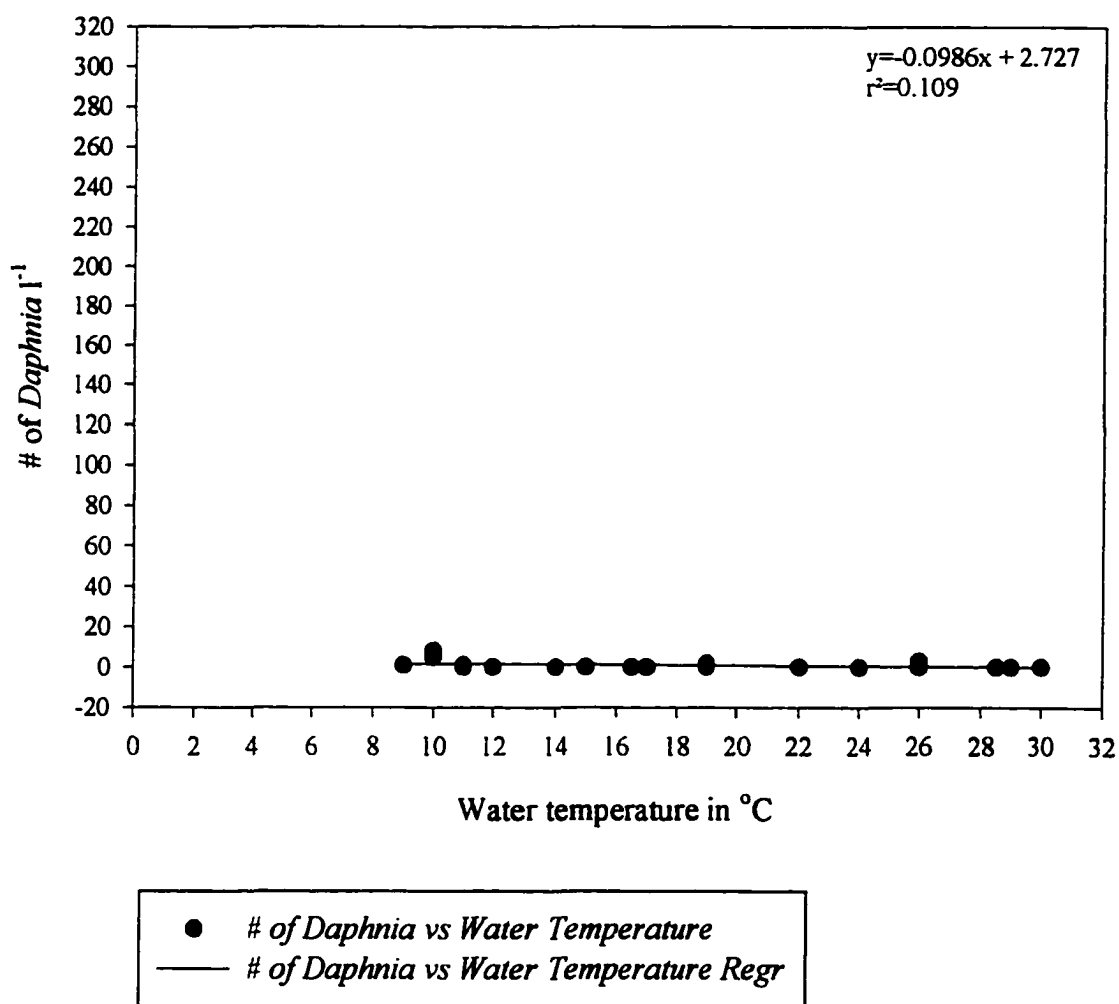


Figure 69: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus water temperature in °C in Pool 2, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Water Temperature °C in Pool 3

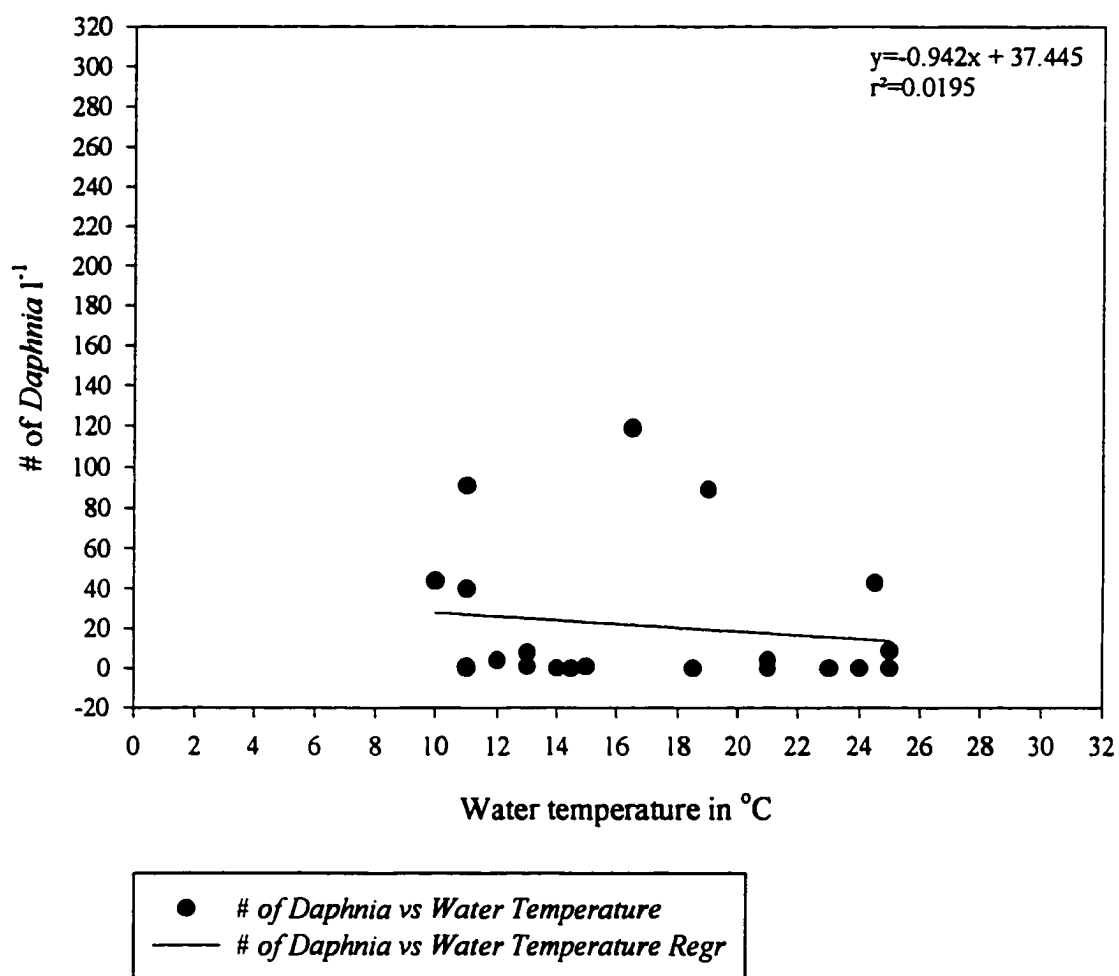


Figure 70: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus water temperature in °C in Pool 3, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Water Temperature in °C in Pool 4

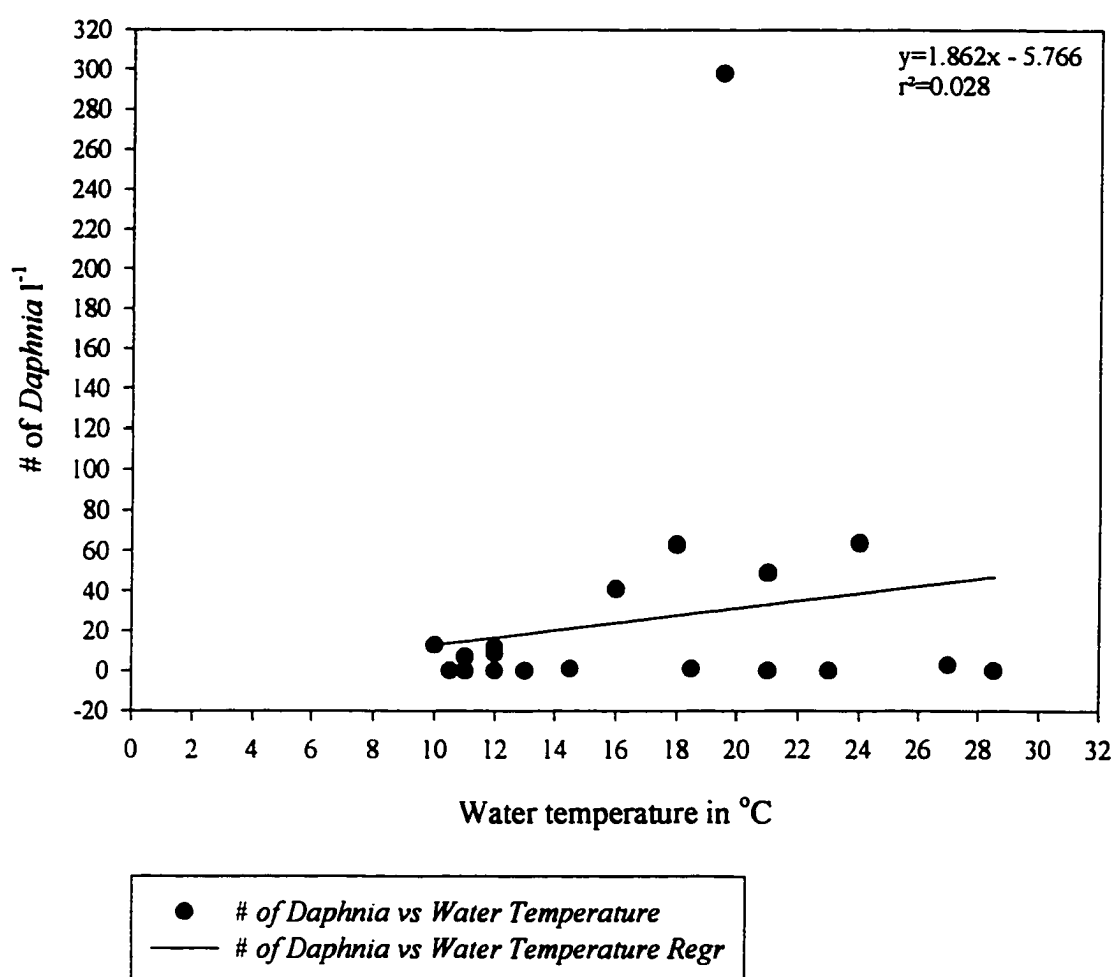


Figure 71: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus water temperature in °C in Pool 4, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Water Temperature in °C in Pool 5

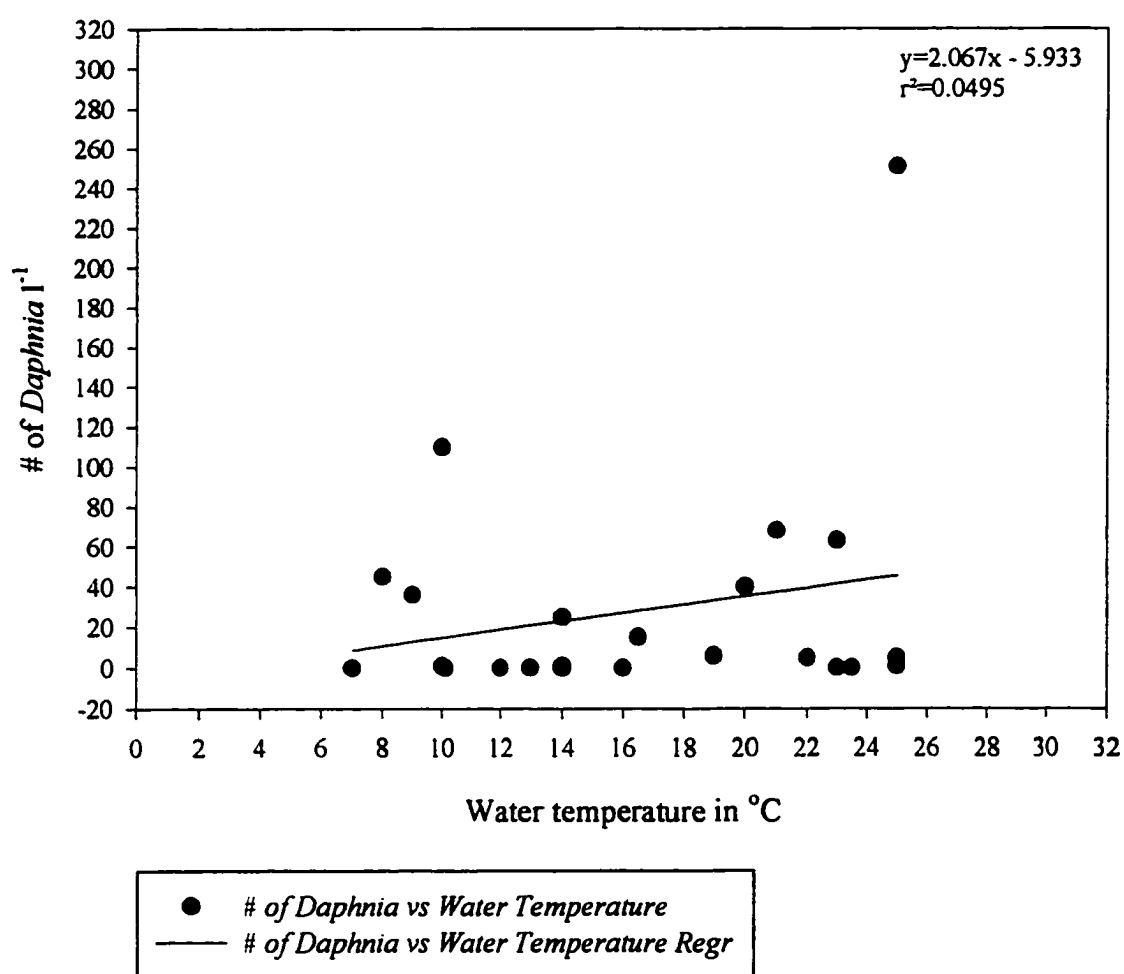


Figure 72: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus water temperature in °C in Pool 5, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Water Temperature in °C in Pool 6

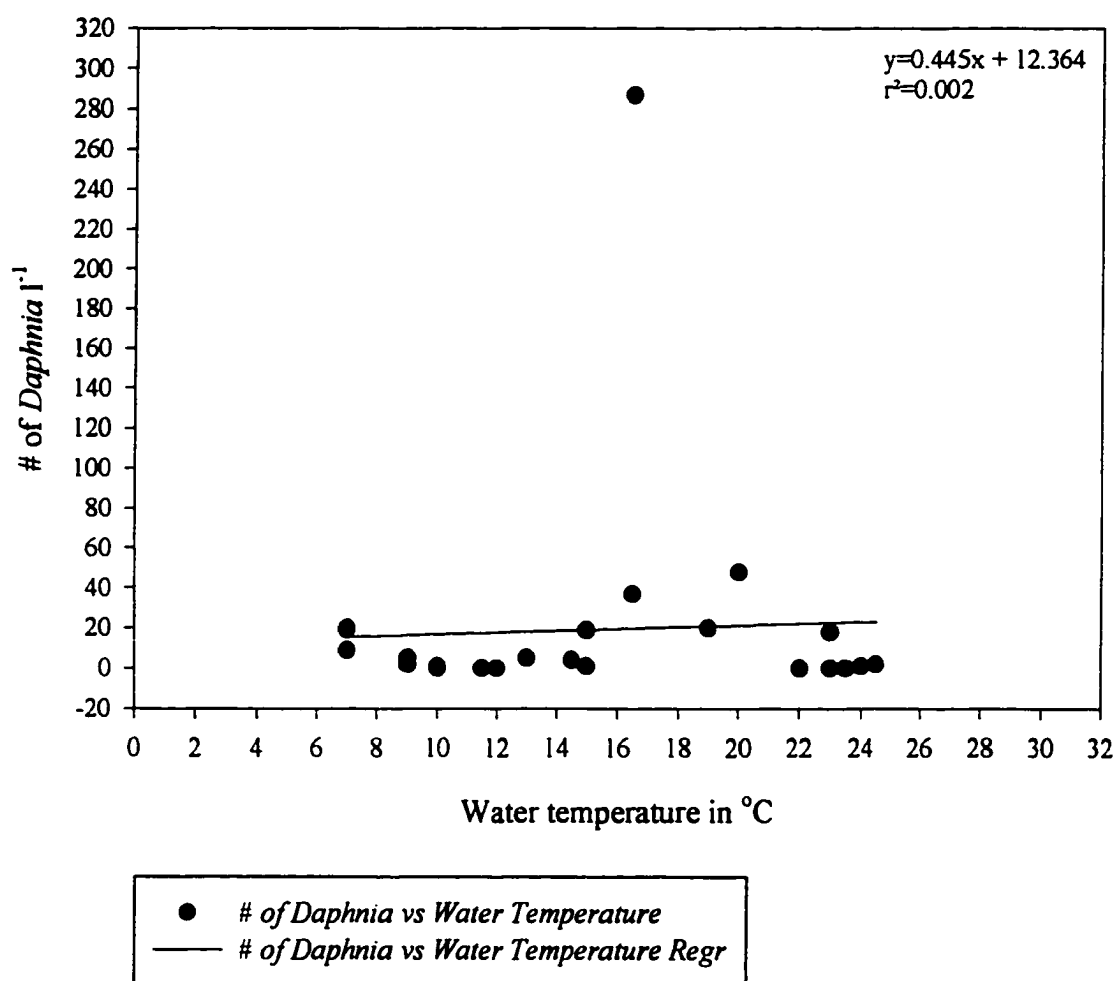


Figure 73: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus water temperature in °C in Pool 6, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Water Temperature in °C in Pool 7

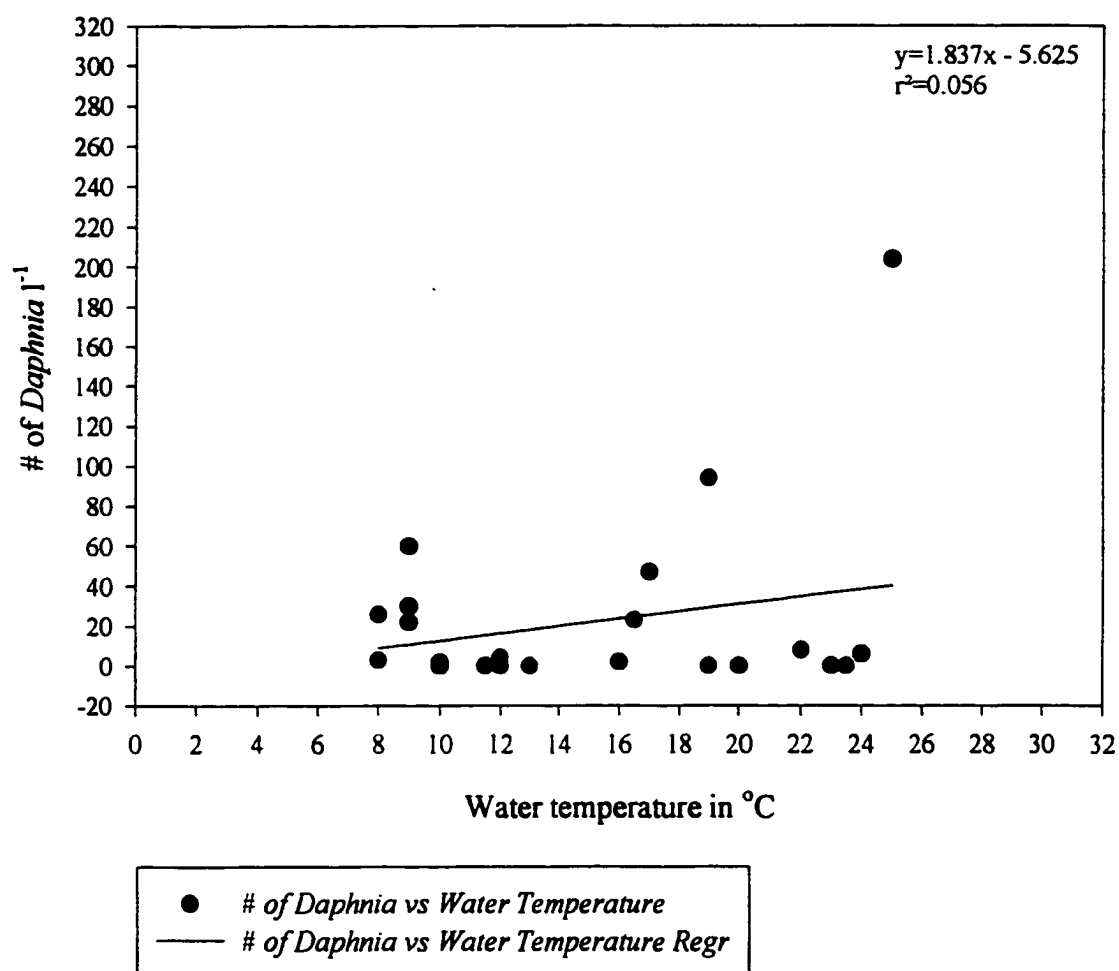


Figure 74: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obutsa*) versus water temperature in °C in Pool 7, with individual data points and regression as shown.

Saturation Nomograph (Wetzel and Likens 1991). Oxygen tensions were lowest during periods of high pool water temperatures. All of the pools in general had lower oxygen tensions during the summer than they did during the winter with low levels recorded at 2 to 3 mg l⁻¹. Pools routinely had an oxygen deficit as would be expected in a detritus rich system with high heterotrophic activity occurring. On the few occasions when pools were saturated, photosynthetic activity due to algal blooms was apparent, as in July. The number of *Daphnia* l⁻¹ was regressed against oxygen in mg l⁻¹ and inspection of these results clearly indicates that oxygen tension is not useful in explaining the number of *Daphnia* in these pools (Figures 75 to 81). There appeared to be no relationship in any of the pools.

Pool chemistry fluctuated after rainfall when pools that were usually small and shallow became inundated to overflowing with water flowing down through the wash, and with drying during periods of low precipitation and higher temperatures. The lowest pH was recorded after flooding, and the highest pH of 10.63 occurred when water in the pools was low and concentrated due to evaporation. Inexplicably, pH was not always correlated with depth.

A small month to month variation in pH values, always on the alkaline side of neutrality, ranged from 7.05-10.63 (see Appendix VII), but not always correlated with depth (Figures 82 to 88). Above neutral pH, as discussed above, can be largely explained by the limestone substrate of the Spring Mountains. Highest pH values in Pools 1 and 6 occurred on June 26, 1991 when all pools except Pools 1 and 6 were dry. A total of only 0.2 cms of rainfall was measured at the Red Rock Weather Station during April, May, and

Number of *Daphnia* l⁻¹ (2 species) Versus
Oxygen in mg l⁻¹ in Pool 1

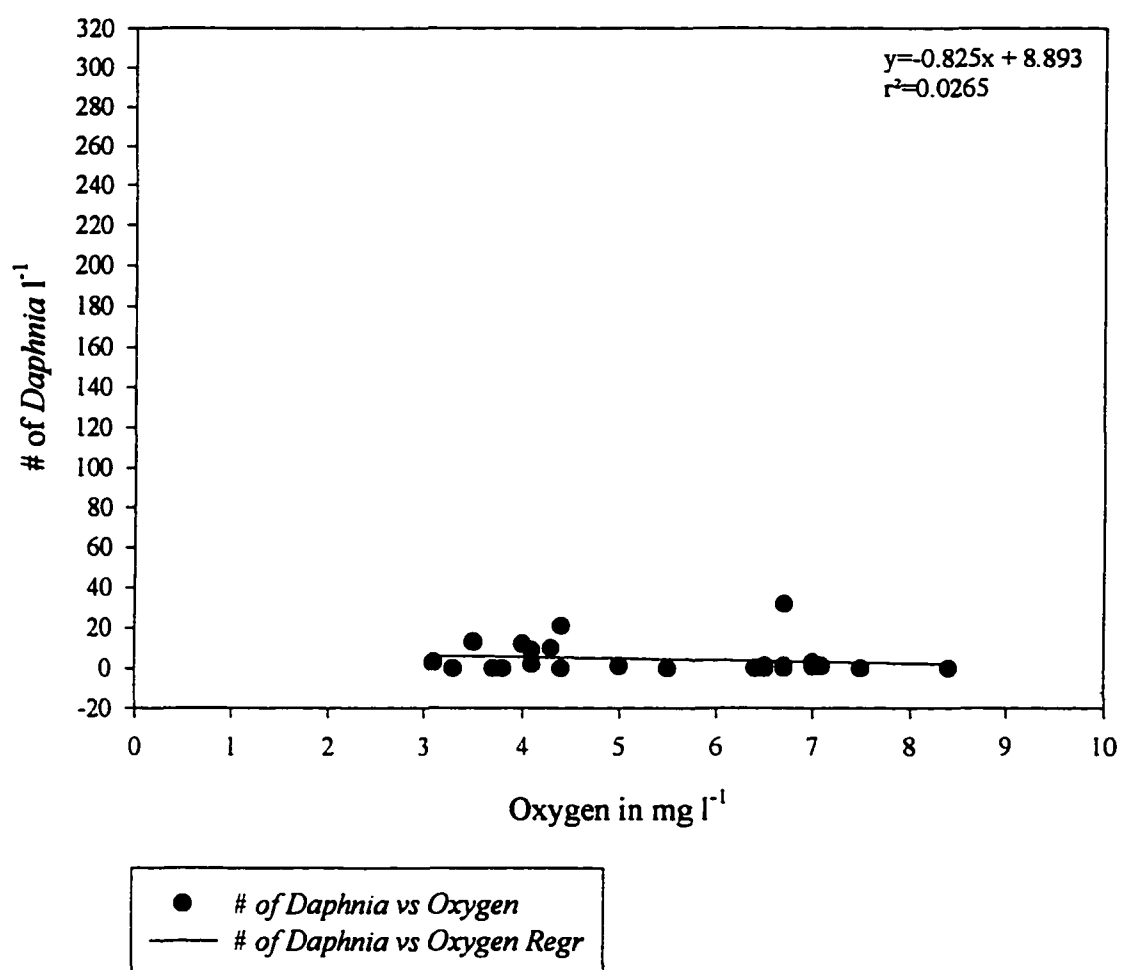


Figure 75: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus oxygen in mg l⁻¹ in Pool 1, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Oxygen in mg l⁻¹ in Pool 2

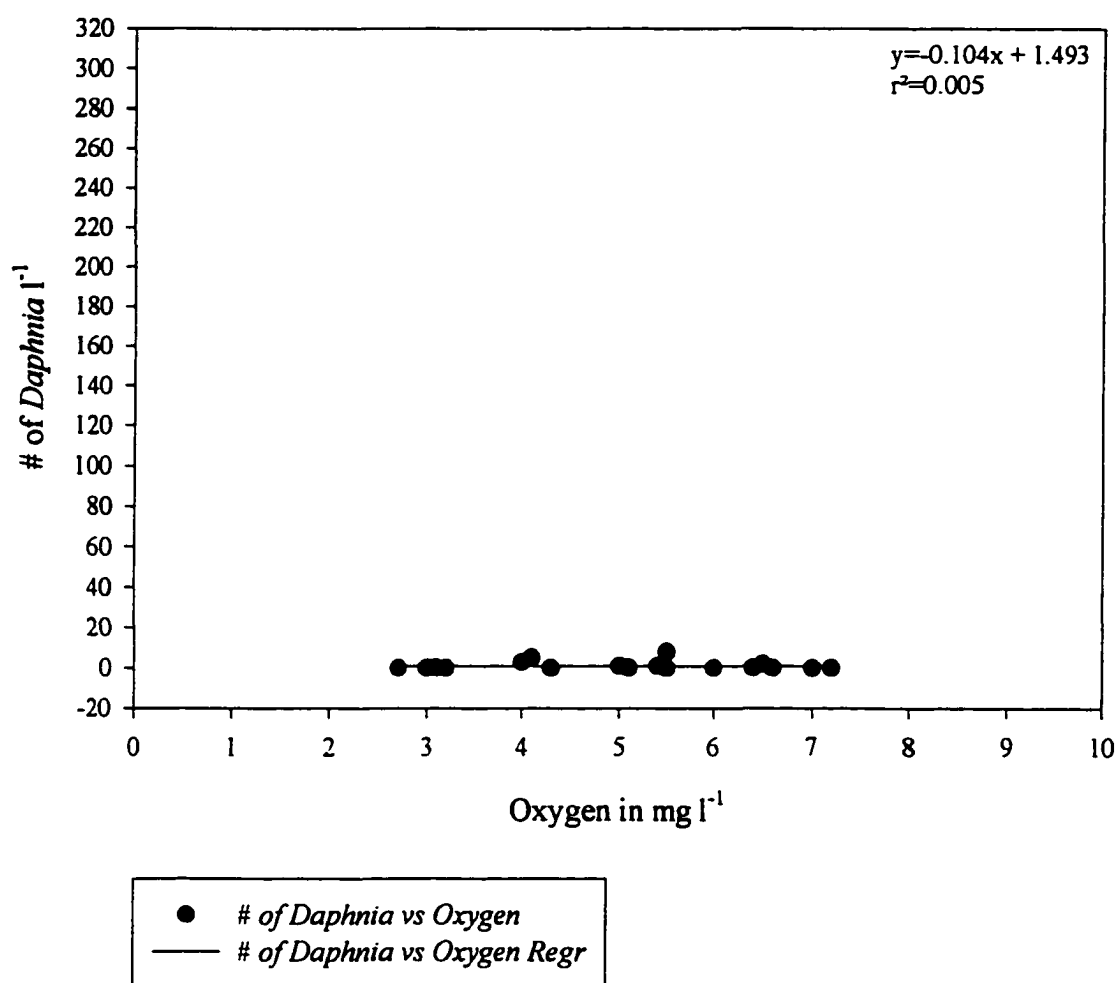


Figure 76: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus oxygen in mg l⁻¹ in Pool 2, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Oxygen in mg l⁻¹ in Pool 3

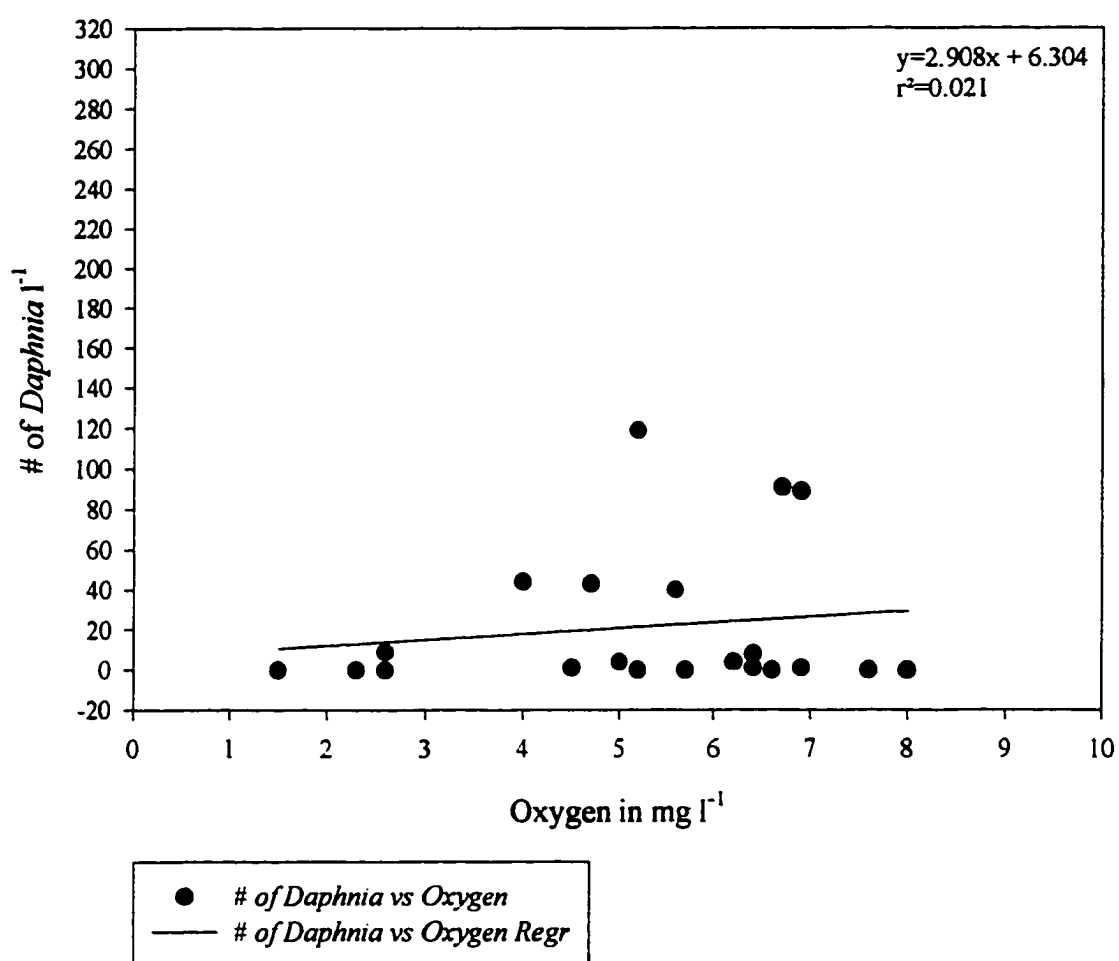


Figure 77: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus oxygen in mg l⁻¹ in Pool 3, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Oxygen in mg l⁻¹ in Pool 4

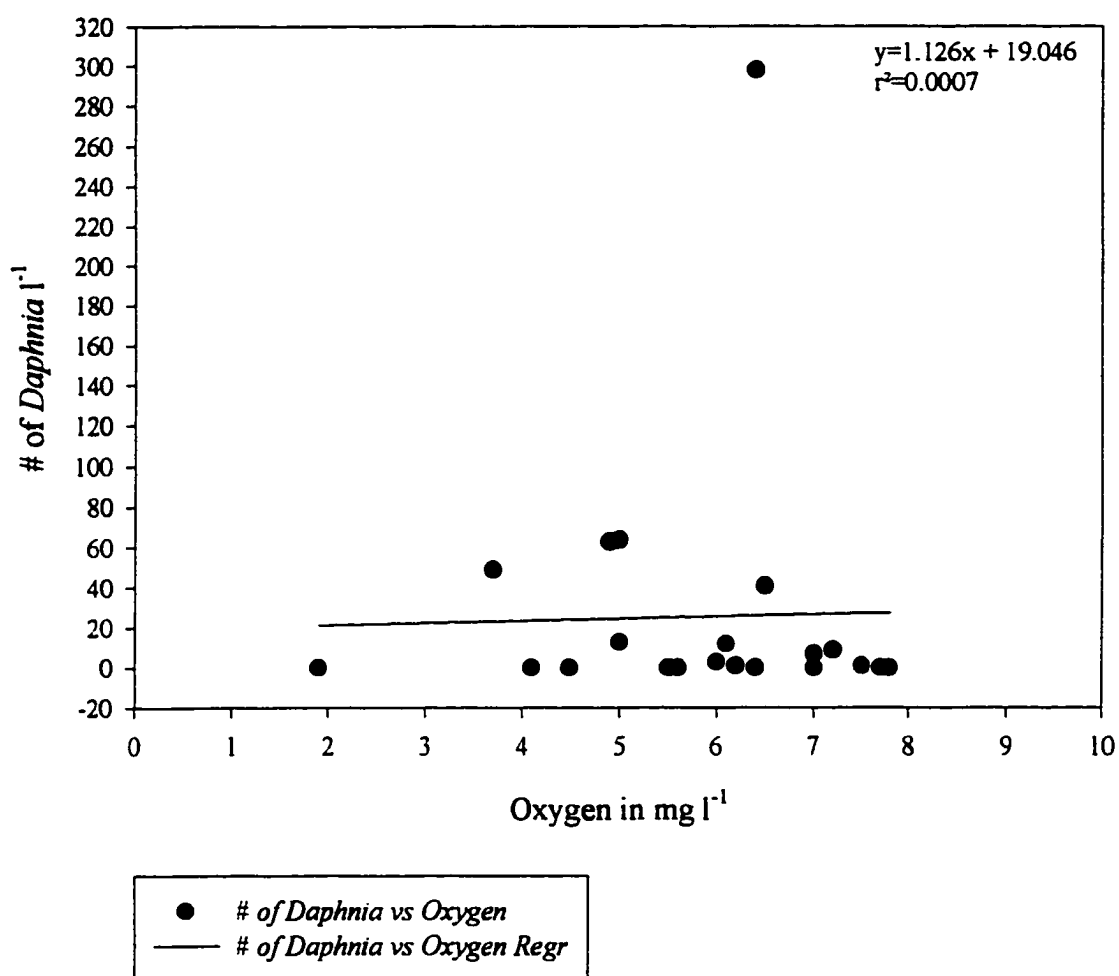


Figure 78: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus oxygen in mg l⁻¹ in Pool 4, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Oxygen in mg l⁻¹ in Pool 5

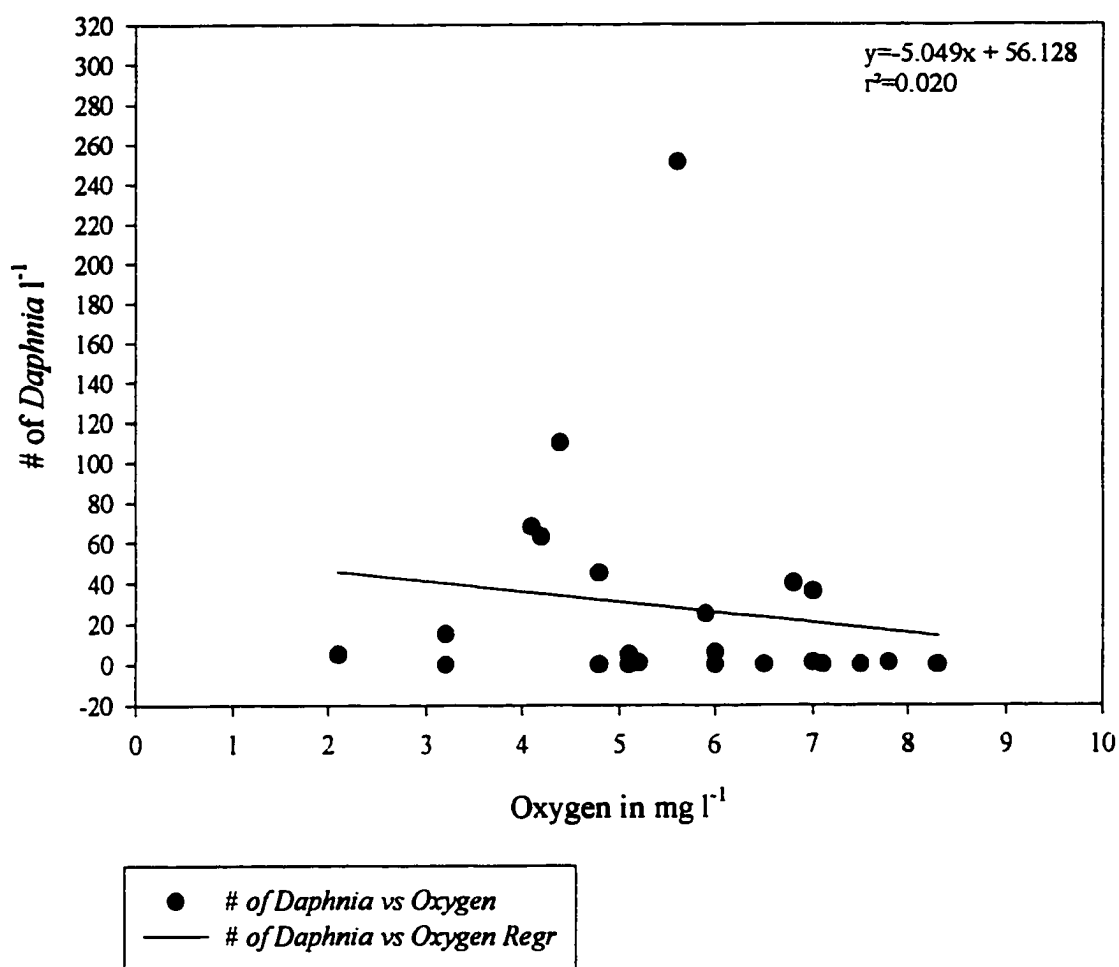


Figure 79: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus oxygen in mg l⁻¹ in Pool 5, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Oxygen in mg l⁻¹ in Pool 6

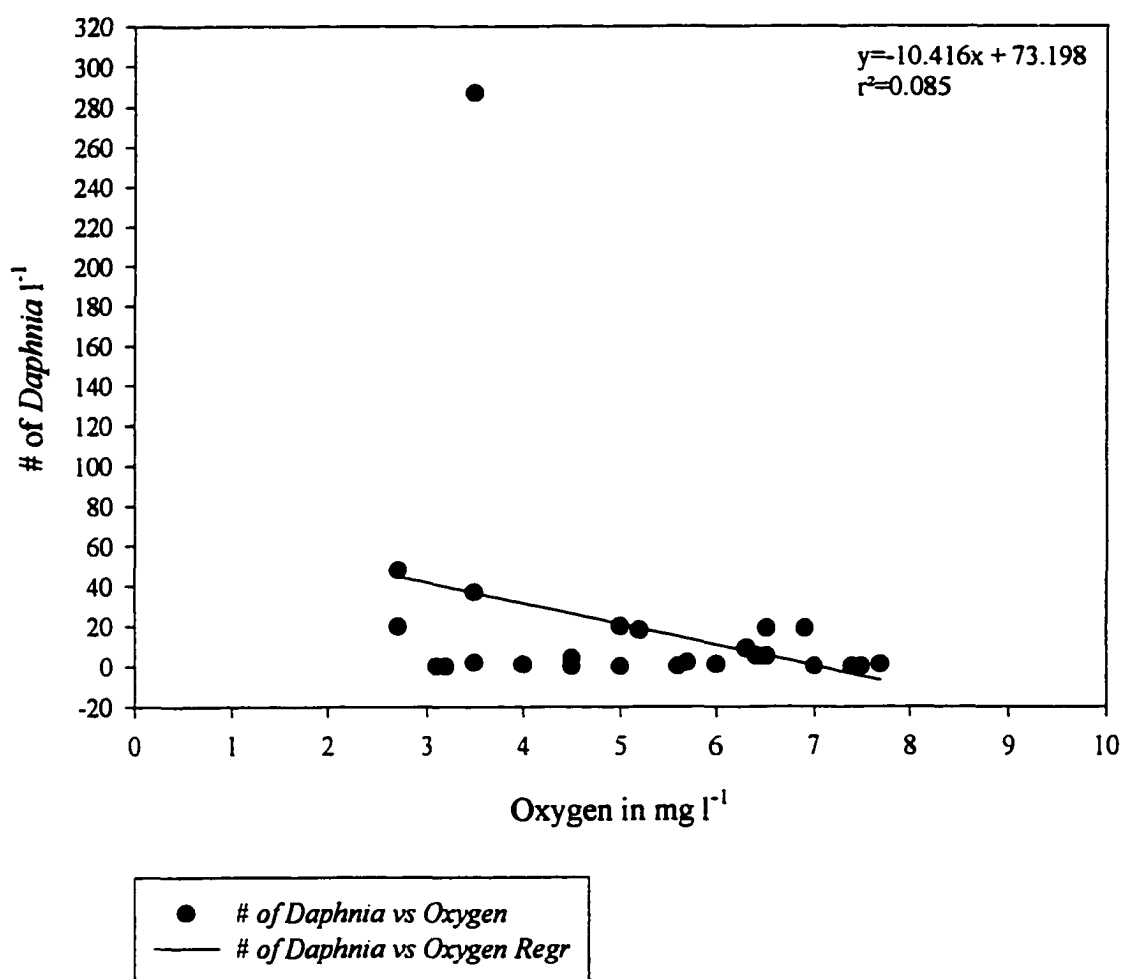


Figure 80: Relationship of the number of *Daphnia* liter⁻¹ (*D. pulex* and *D. obtusa*) versus oxygen in mg liter⁻¹ in Pool 6, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Oxygen in mg l⁻¹ in Pool 7

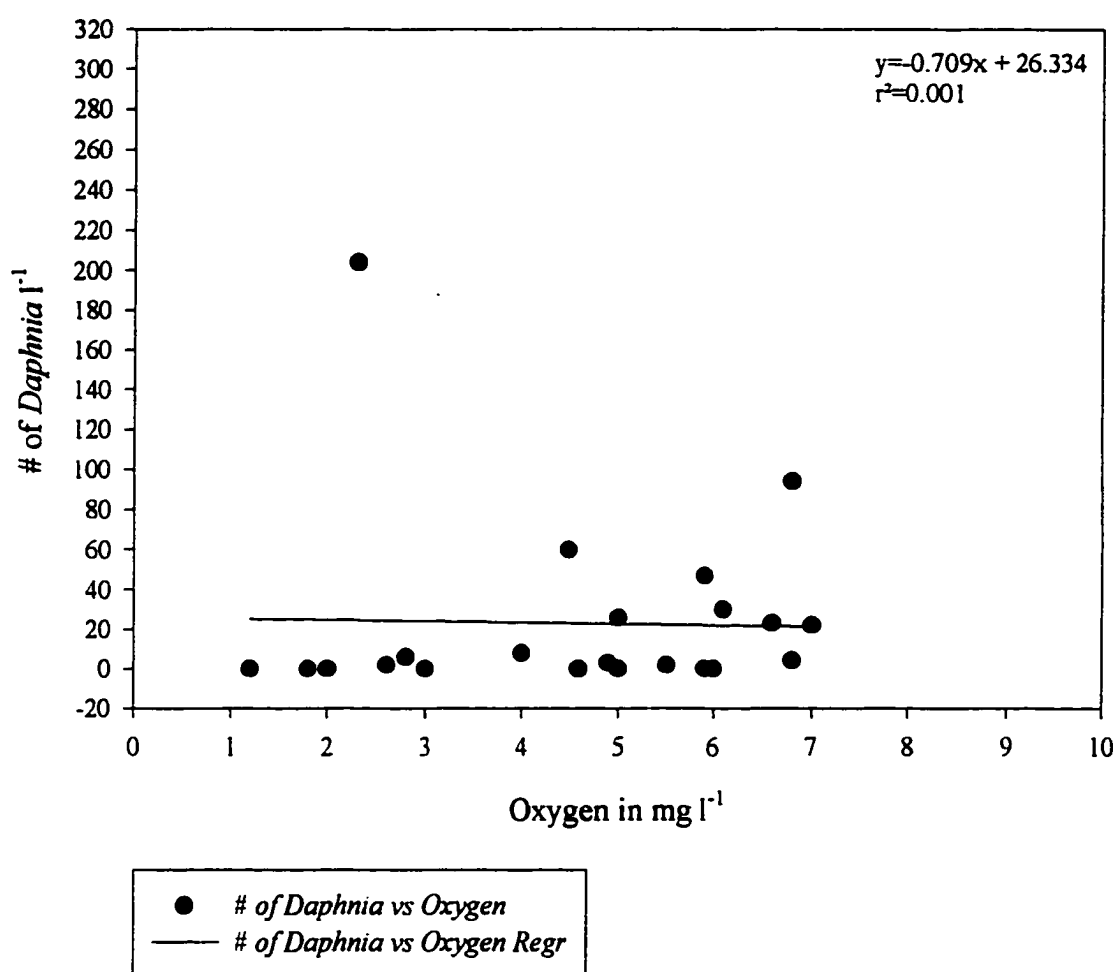


Figure 81: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus oxygen in mg l⁻¹ in Pool 7, with individual data points and regression as shown.

pH Versus Depth in cm in Pool 1

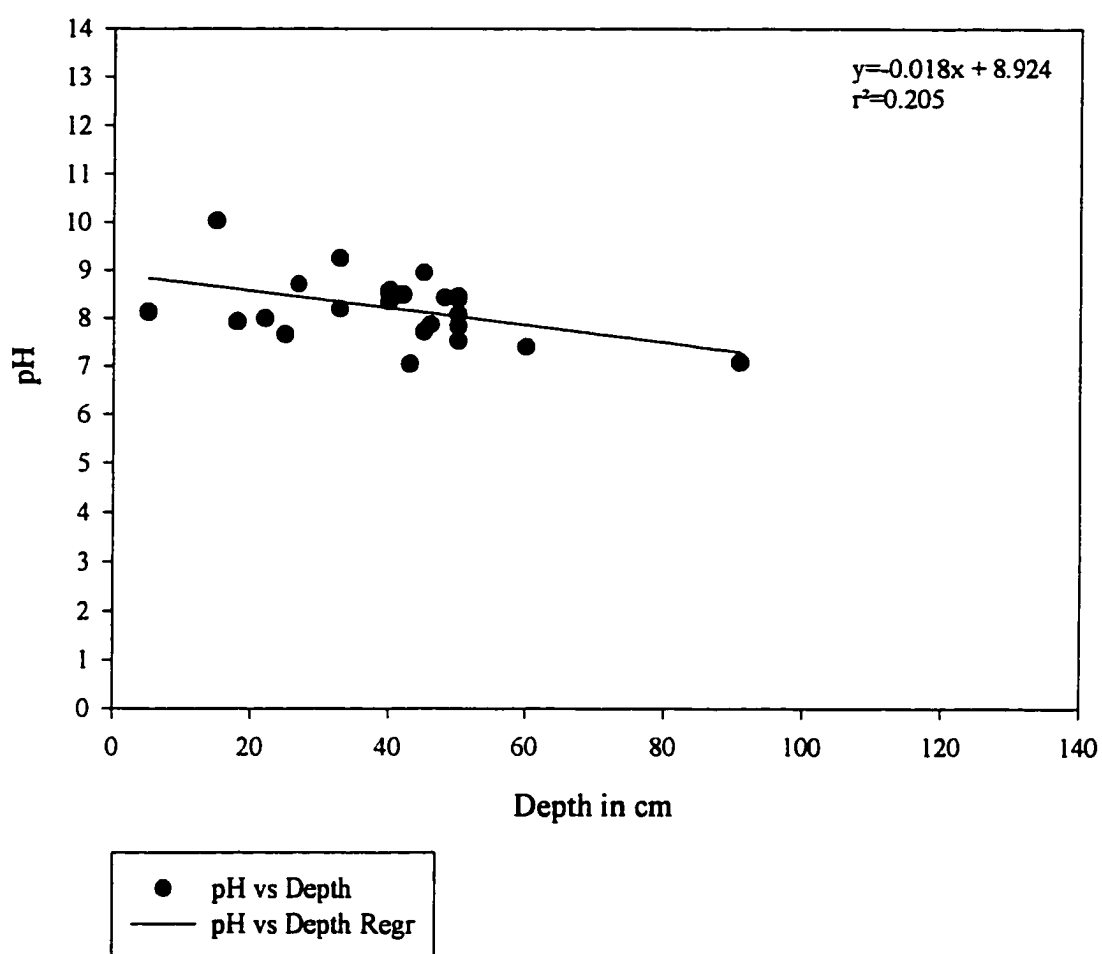


Figure 82: Relationship of pH versus depth in cm of Pool 1, with individual data points and regression as shown.

pH Versus Depth in cm in Pool 2

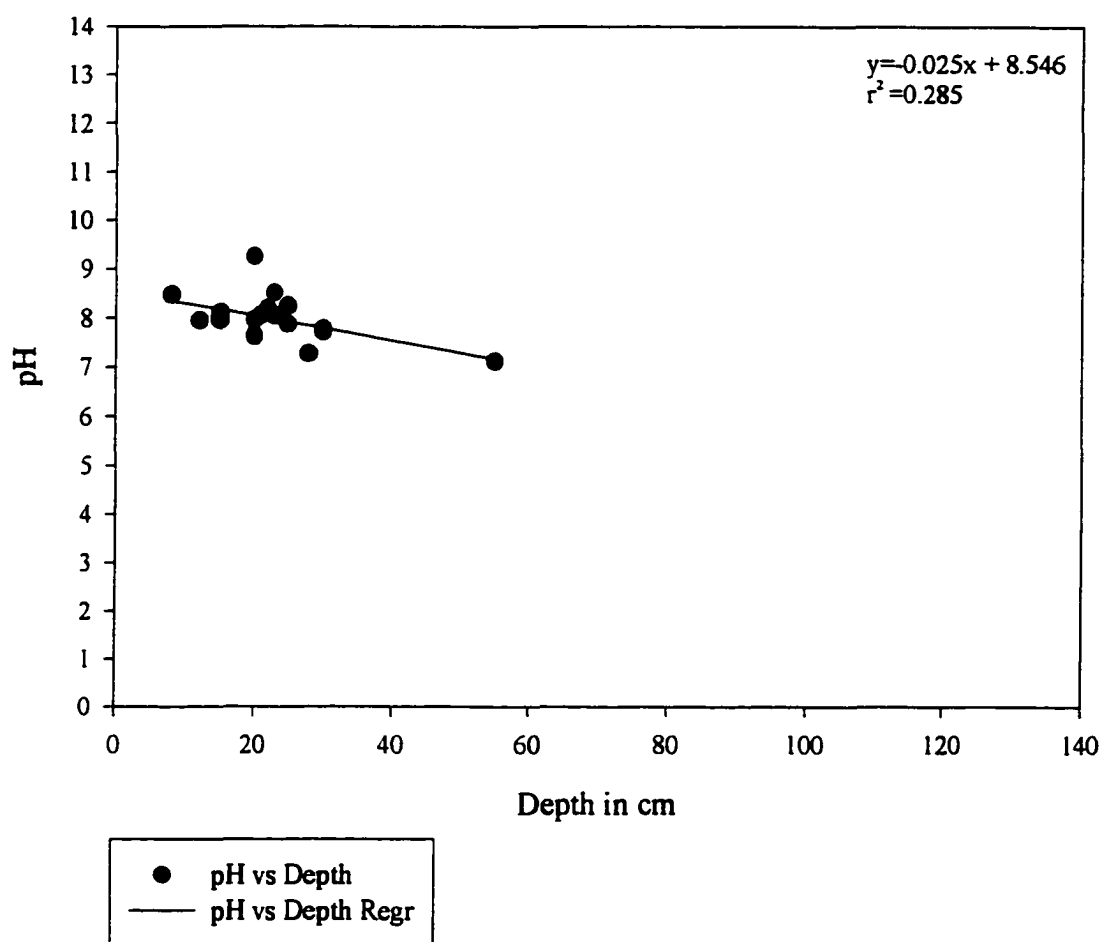


Figure 83: Relationship of pH versus depth in cm in Pool 2, with individual data points and regression as shown.

pH Versus Depth in cm in Pool 3

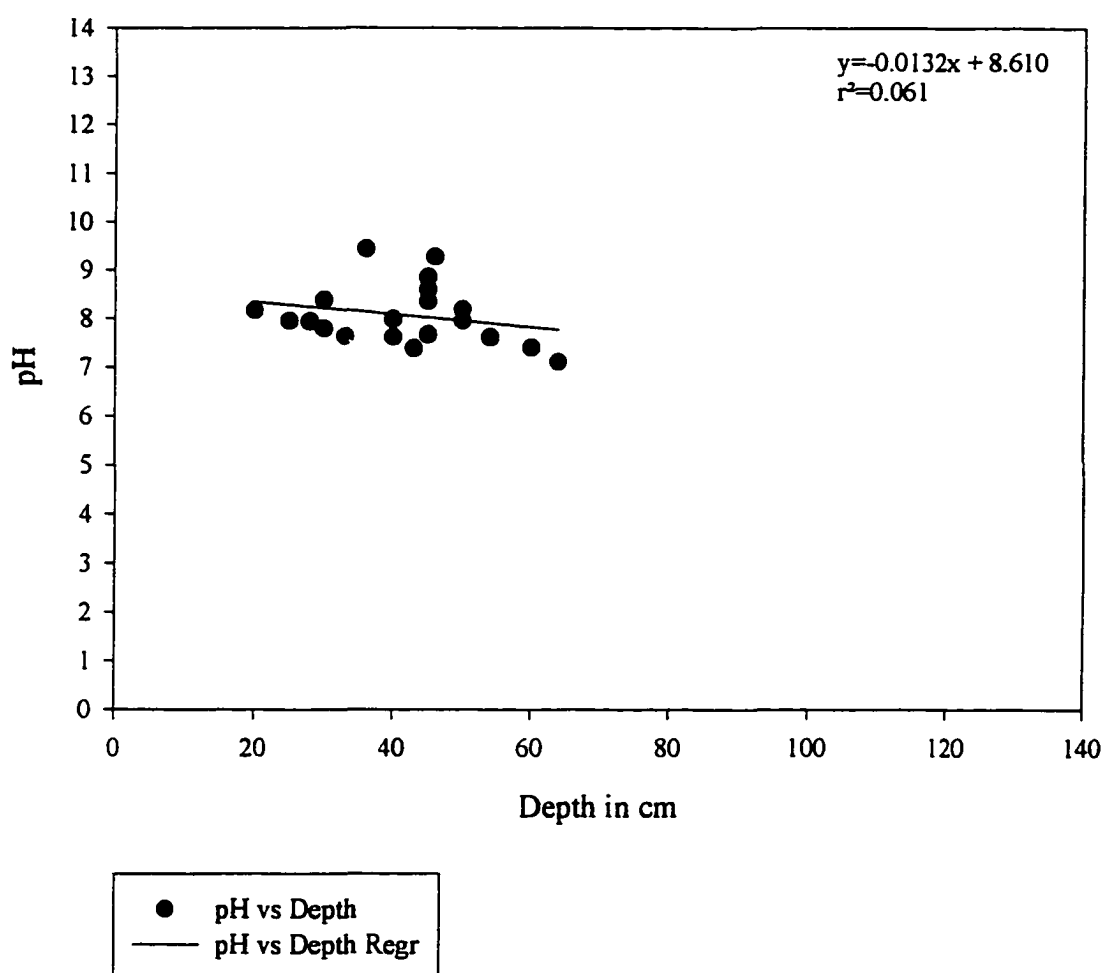


Figure 84: Relationship of the pH versus depth in cm in Pool 3, with individual data points and regression as shown.

pH Versus Depth in cm in Pool 4

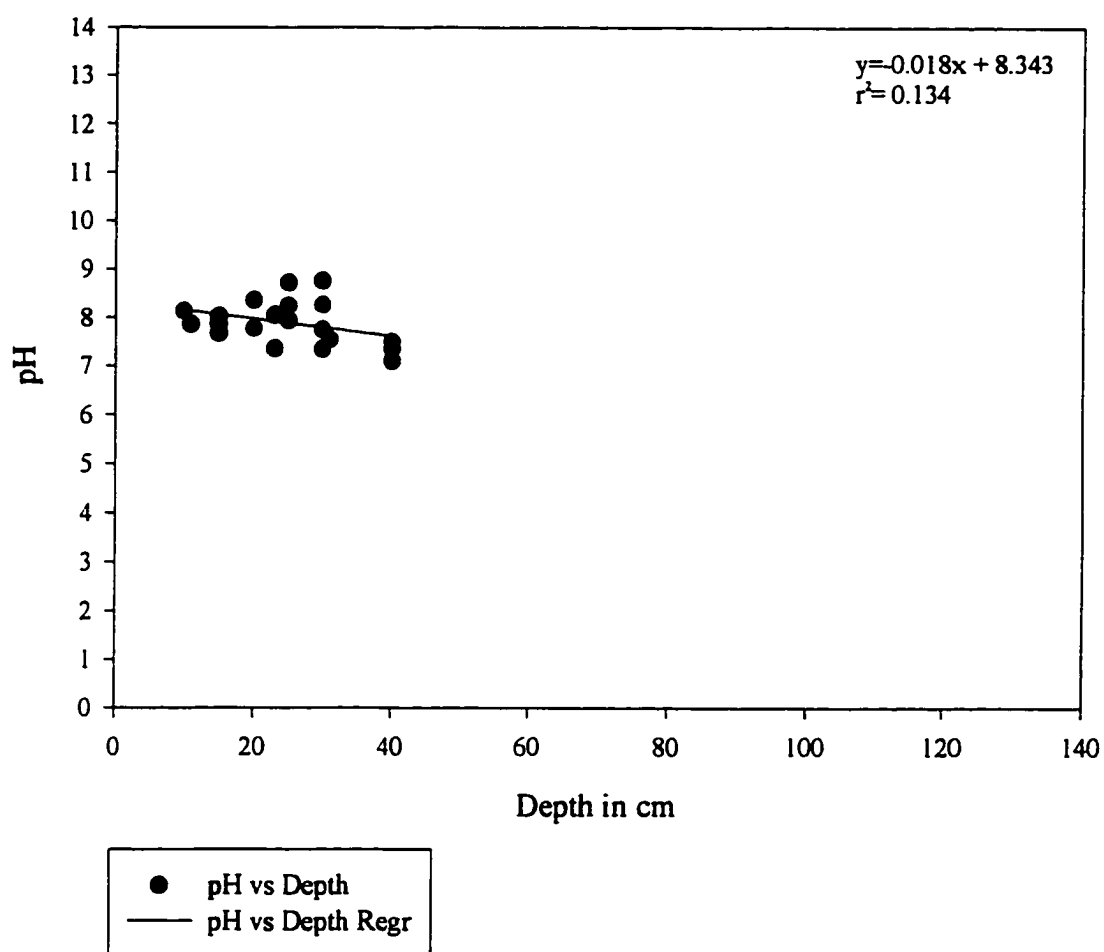


Figure 85: Relationship of pH versus depth in cm in Pool 4, with individual data points and regression as shown.

pH Versus Depth in cm in Pool 5

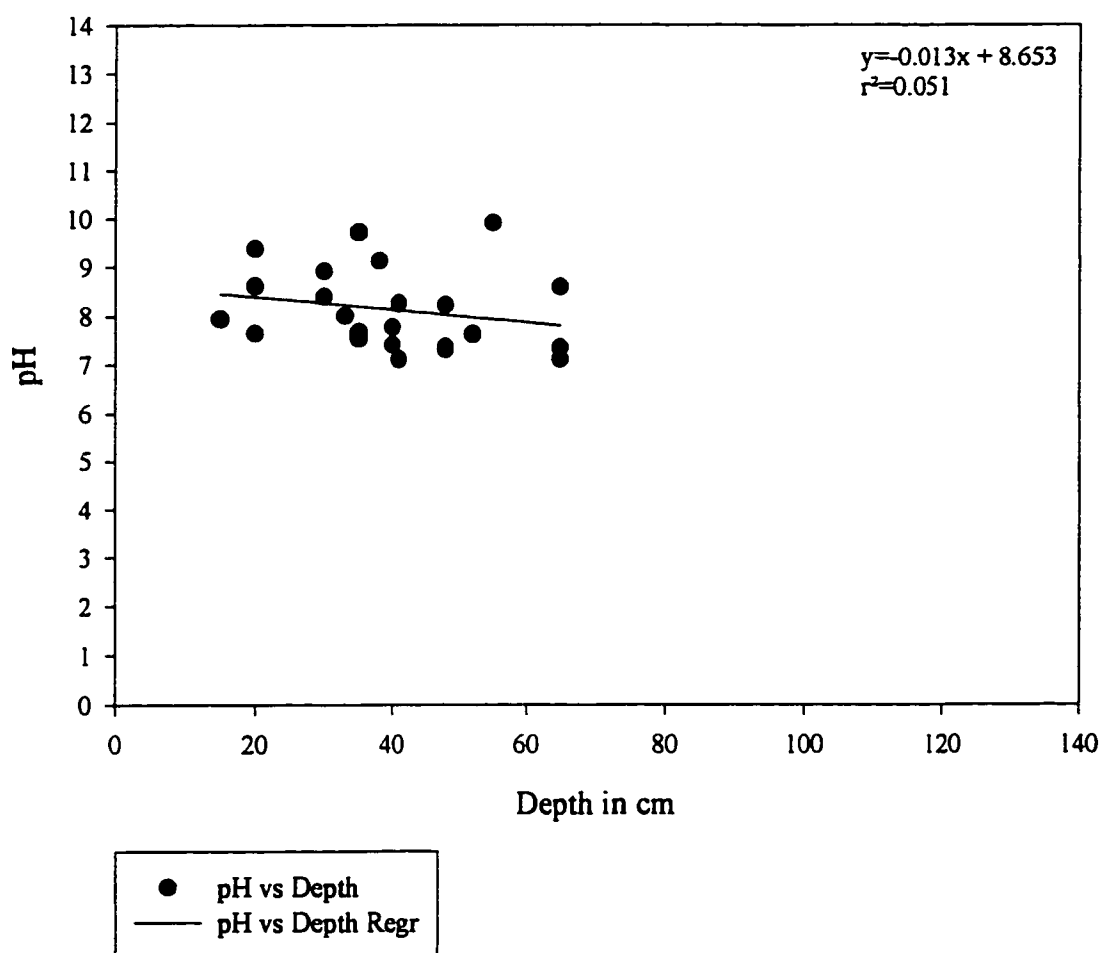


Figure 86: Relationship of pH versus depth in cm in Pool 5, with individual data points and regression as shown.

pH Versus Depth in cm in Pool 6

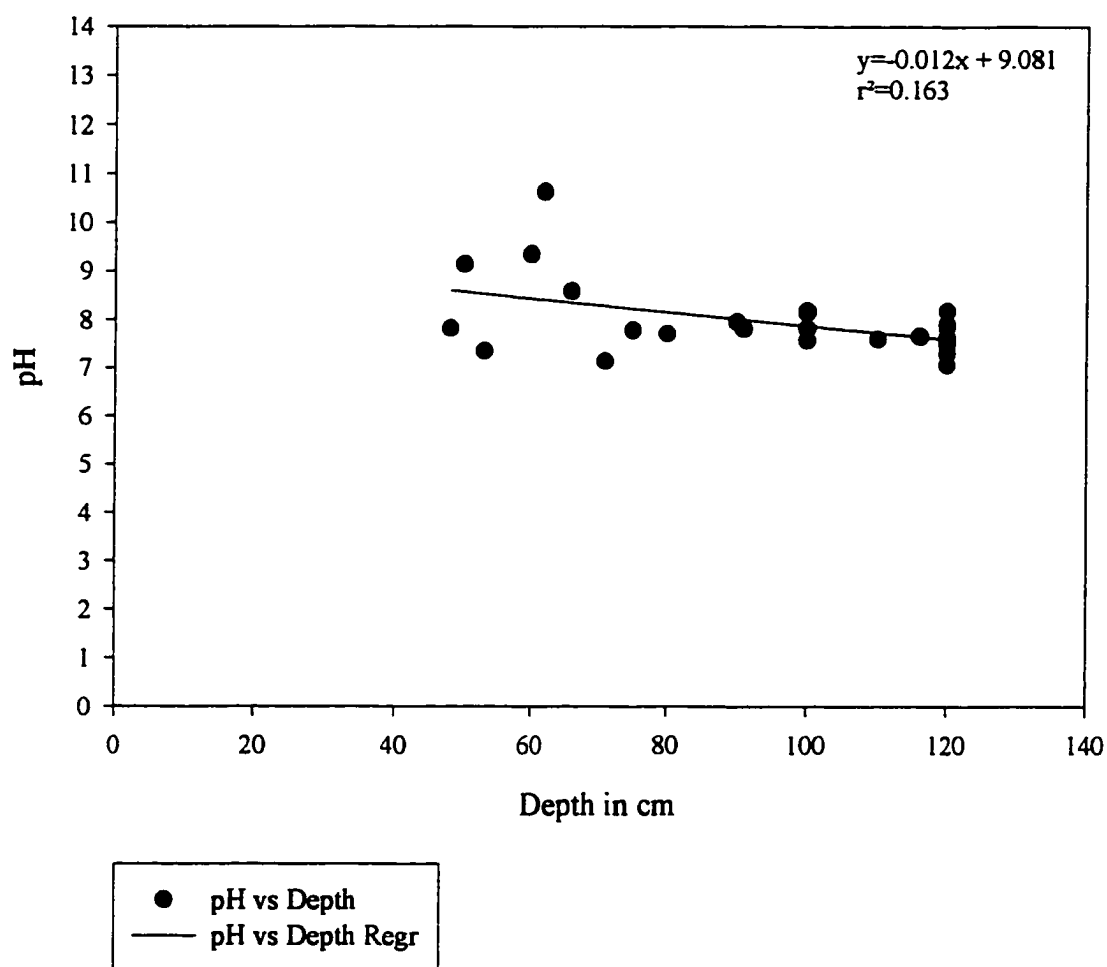


Figure 87: Relationship of pH versus depth in cm in Pool 6, with individual data points and regression as shown.

pH Versus Depth in cm in Pool 7

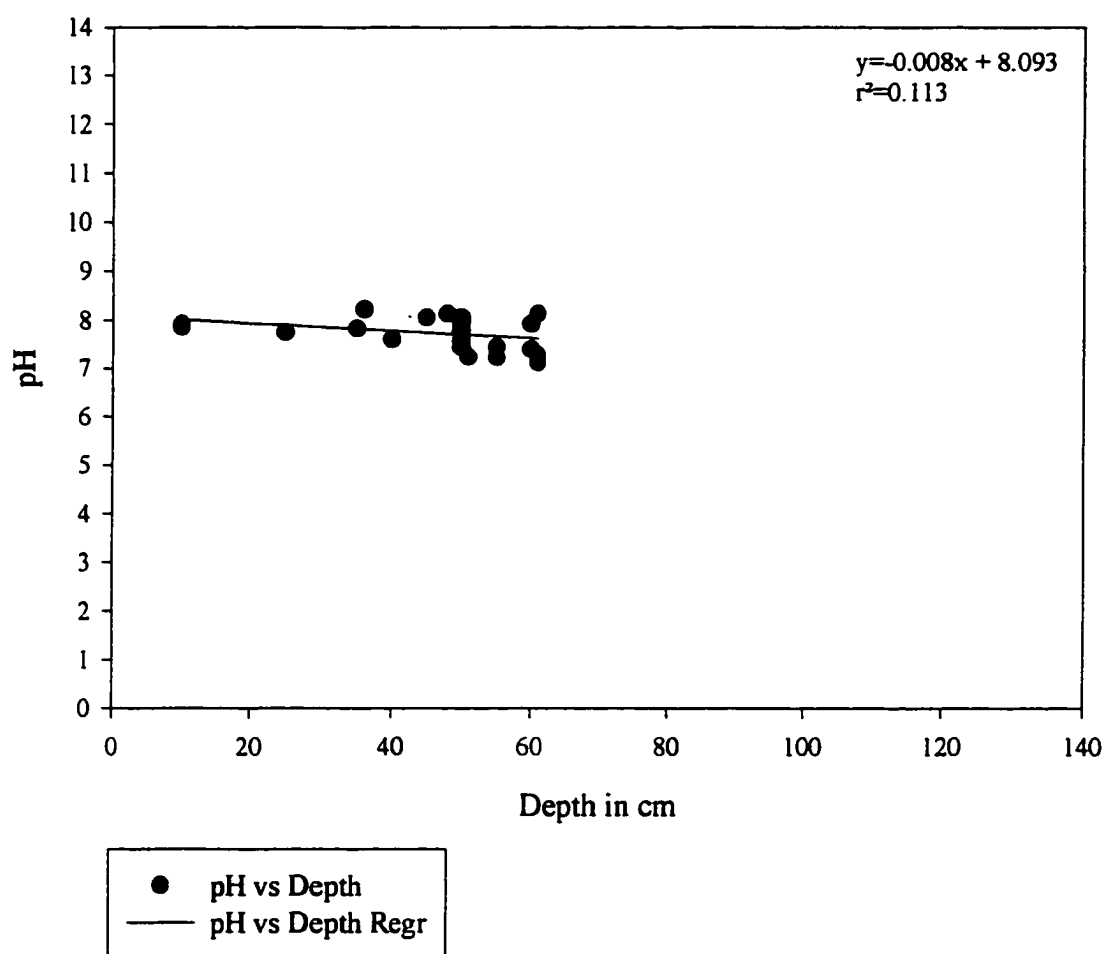


Figure 88: Relationship of pH versus depth in cm in Pool 7, with individual data points and regression as shown.

June combined. This lack of precipitation resulted in five pools drying and dissolved materials in the water of the two remaining pools becoming concentrated. Lowest pH values were measured in water samples collected on the day of flooding in July 1991 when pools were washed out with fresh water from recent precipitation. The relationship between pH and depth was modest, but always tending toward lowest pH with greatest depth. I have chosen not to regress the number of *Daphnia* l⁻¹ against pH since initial plots in many instances appeared to show a central tendency indicating that linear regression was inappropriate.

Conductivity, ranging from 500 to 6800 $\mu\text{S cm}^{-1}$, was linked to precipitation and evaporation with low levels appearing when the water was dilute and high levels appearing when the water was concentrated. Conductivity generally ran in concert in the pools especially around October. As previously discussed, Pools 1 and 6 are well-protected and consequently are the most constant and the most highly buffered because they are not subject to the same evaporation or percolation as the other five pools. Complete conductivity data are in Appendix VIII.

The number of *Daphnia* l⁻¹ was regressed against conductivity in $\mu\text{S cm}^{-1}$ for each pool (Figures 89 to 95). Little or no relationship was seen in all of the Pools except for Pool 5 which had a r^2 value of 0.54.

Highest conductivity values were measured on May 27, 1991 when Pools 2, 3, 4, and 5 were dry and Pools 1 and 7 were at their lowest depths for the sampling year. The relationship between conductivity and depth (Figures 96 to 102) was slightly more than for pH and depth. As expected, there was a negative relationship between pool depth and

Number of *Daphnia* l⁻¹ (2 species) Versus
Conductivity in $\mu\text{S cm}^{-1}$ in Pool 1

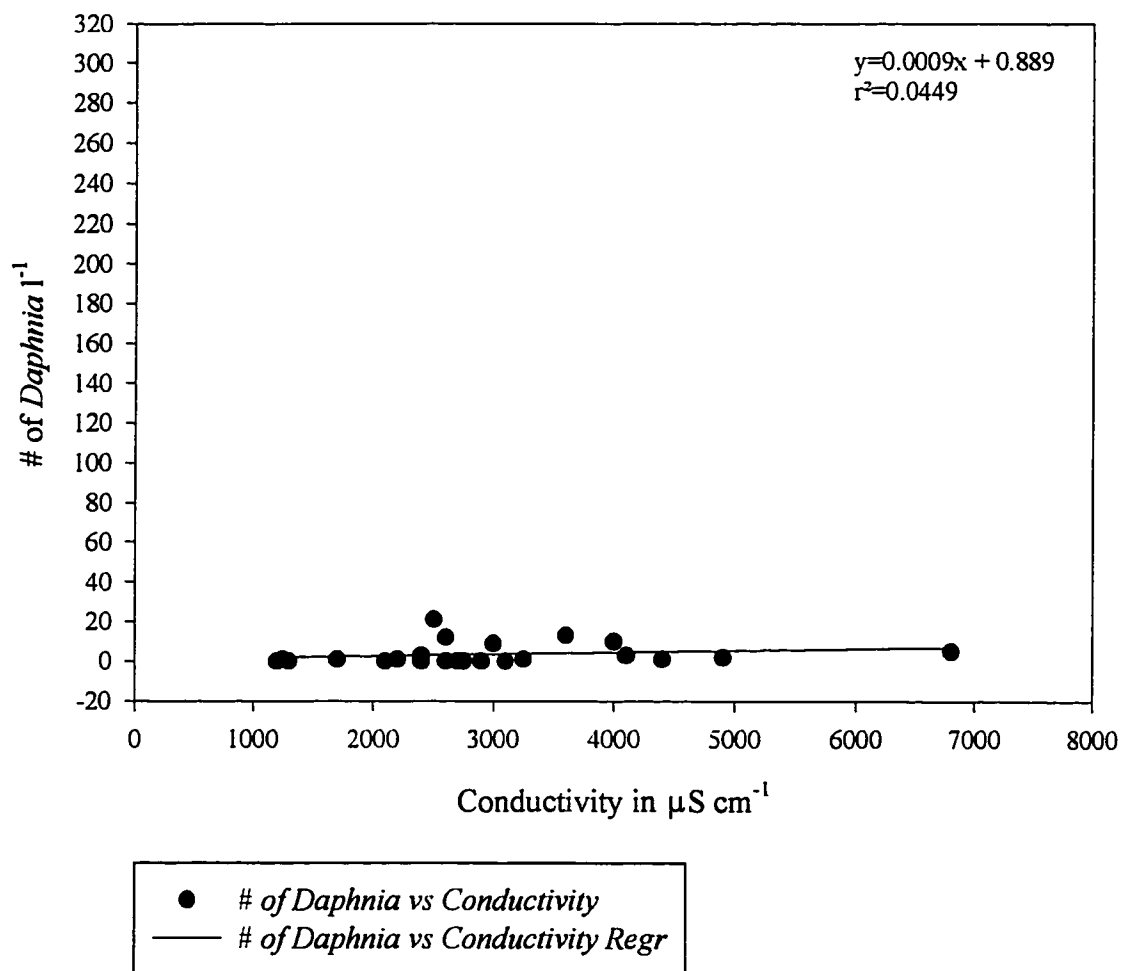


Figure 89: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus conductivity in $\mu\text{S cm}^{-1}$ in Pool 1, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Conductivity in $\mu\text{S cm}^{-1}$ in Pool 2

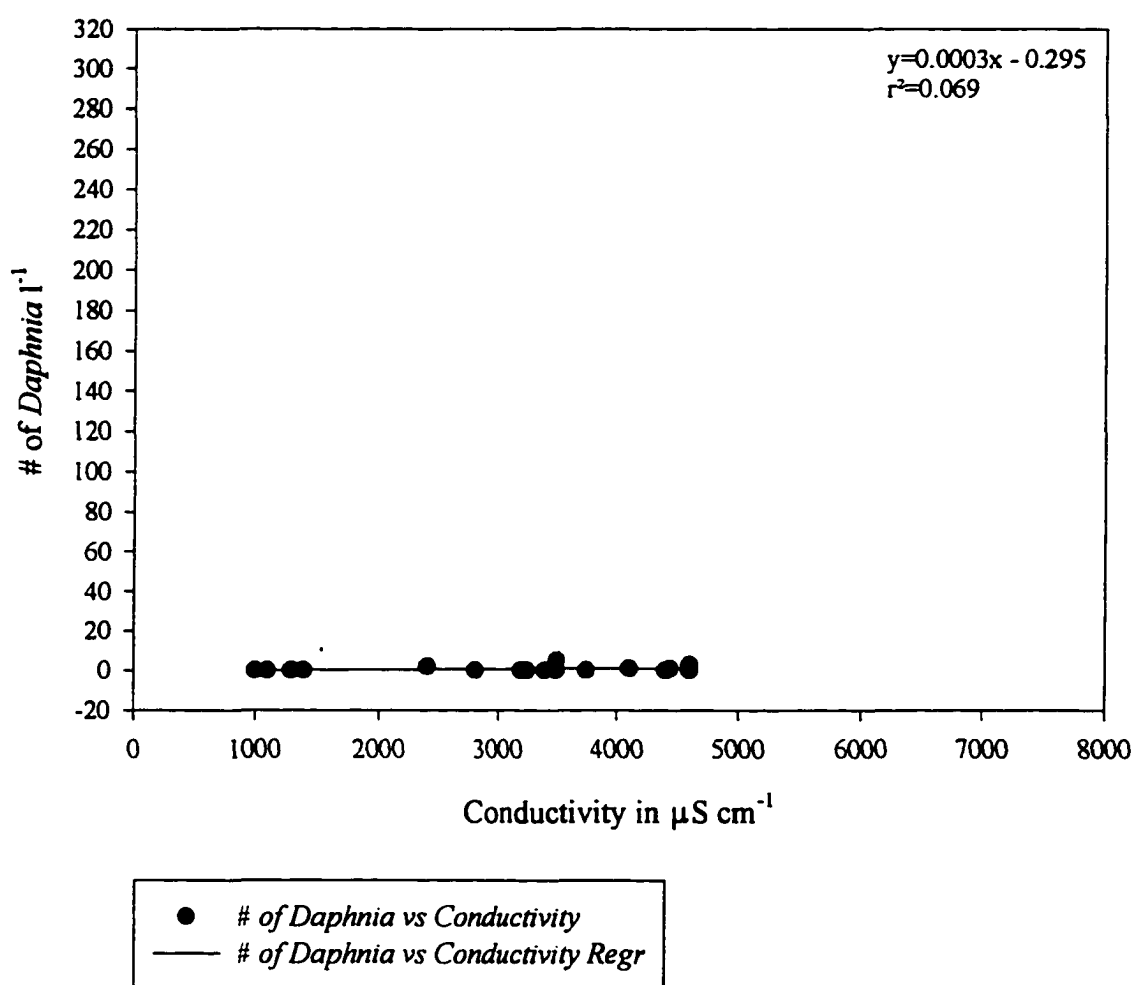


Figure 90: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus Conductivity in $\mu\text{S cm}^{-1}$ in Pool 2, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Conductivity in $\mu\text{S cm}^{-1}$ in Pool 3

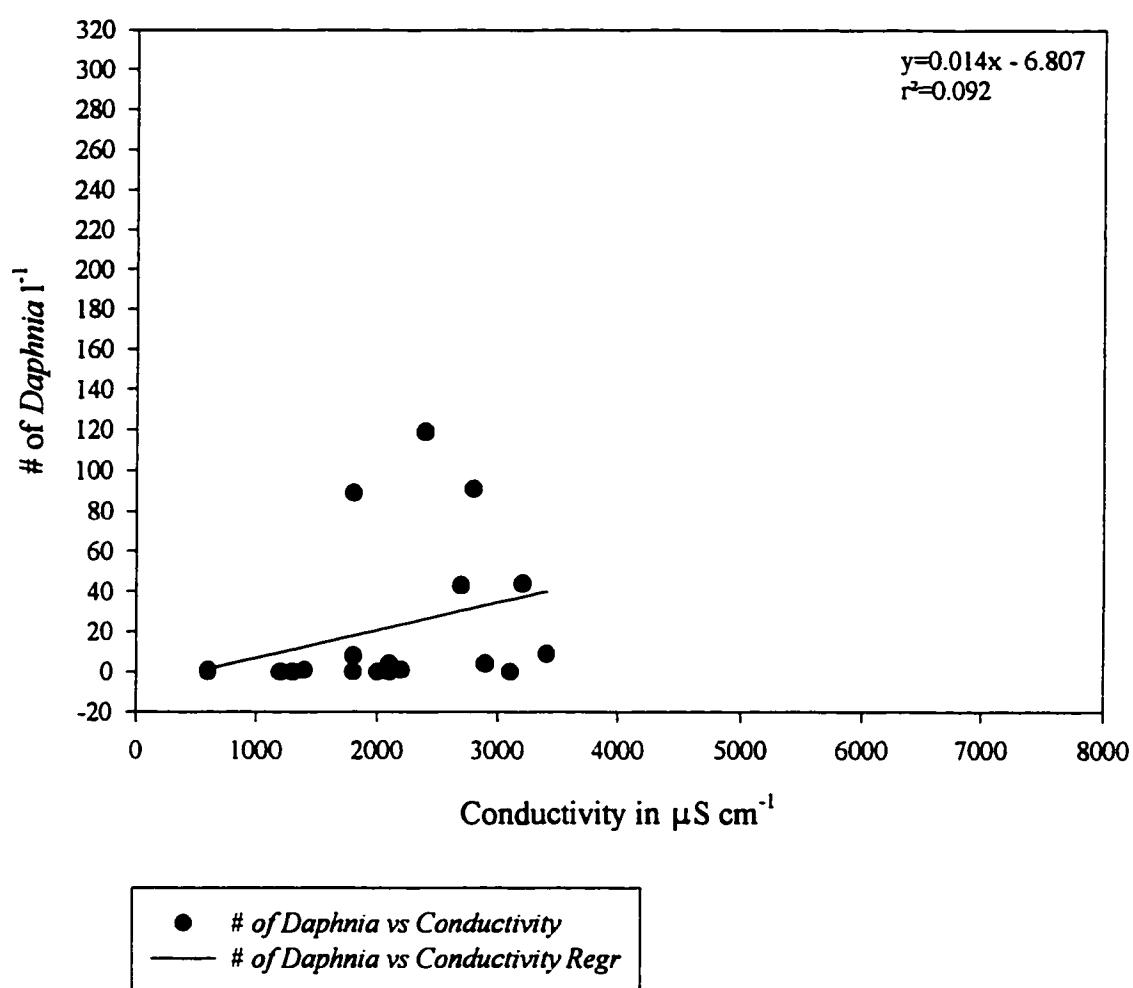


Figure 91: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus conductivity in $\mu\text{S cm}^{-1}$ in Pool 3, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Conductivity in $\mu\text{S cm}^{-1}$ in Pool 4

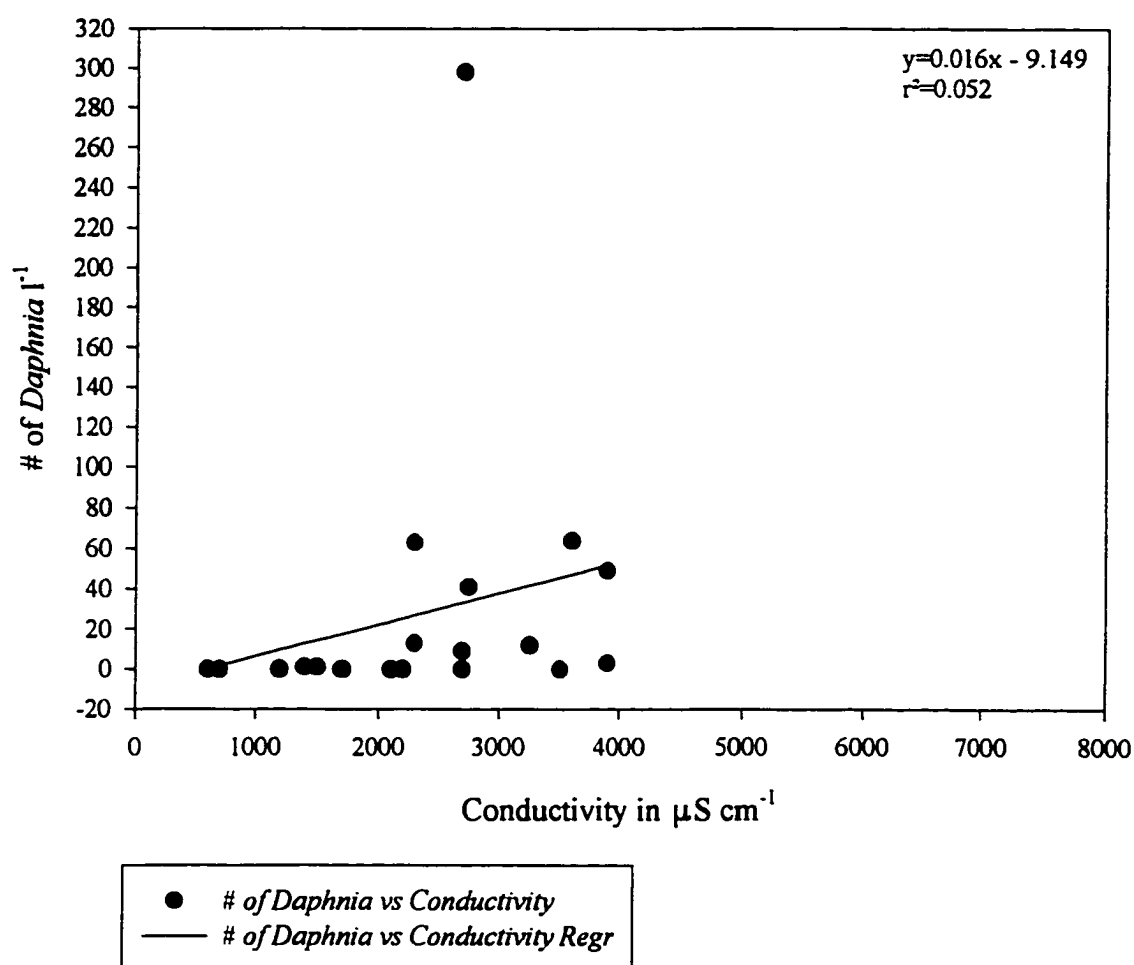


Figure 92: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obutsa*) versus conductivity in $\mu\text{S cm}^{-1}$ in Pool 4, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Conductivity in $\mu\text{S cm}^{-1}$ in Pool 5

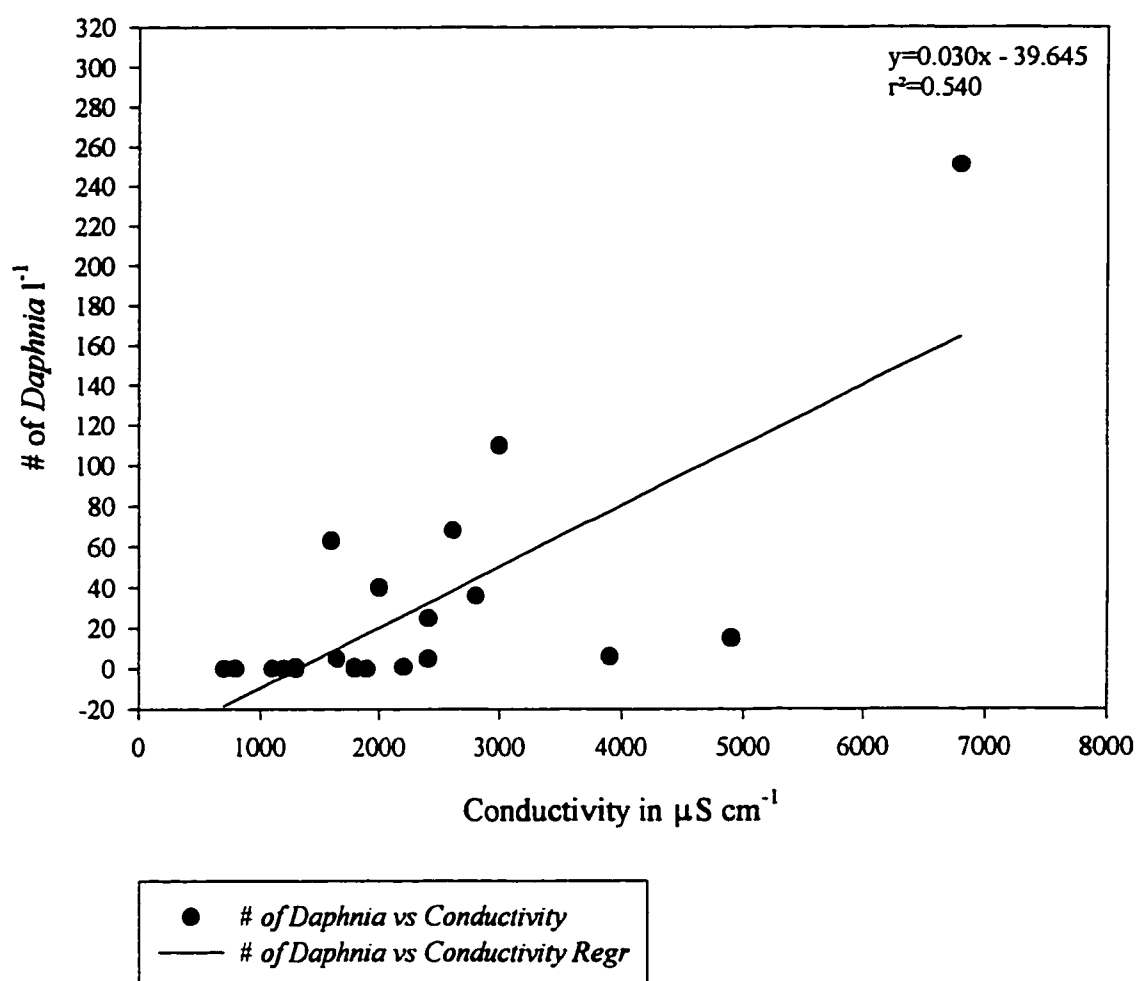


Figure 93: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obutsa*) versus conductivity in $\mu\text{S cm}^{-1}$ in Pool 5, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Conductivity in $\mu\text{S cm}^{-1}$ in Pool 6

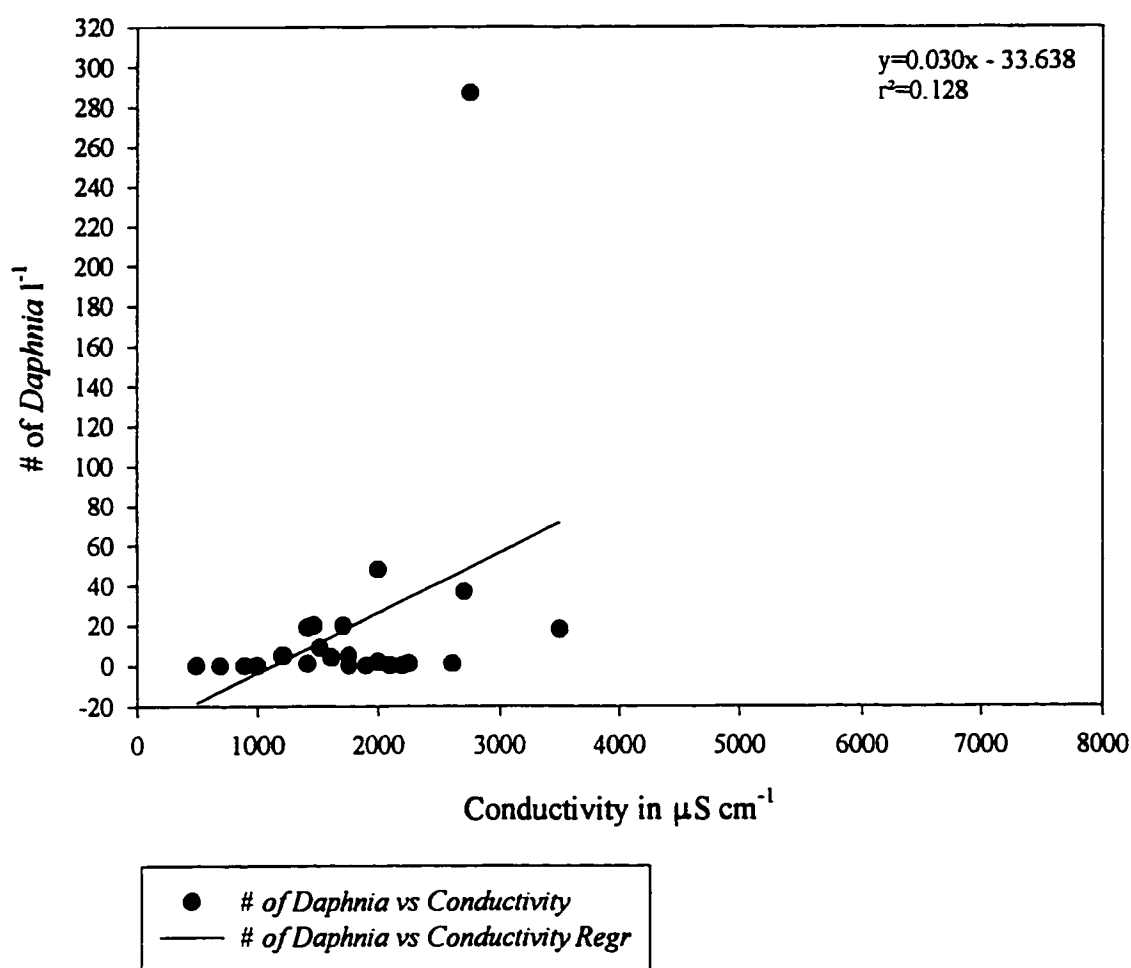


Figure 94: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus Conductivity in $\mu\text{S cm}^{-1}$ in Pool 6, with individual data points and regression as shown.

Number of *Daphnia* l⁻¹ (2 species) Versus
Conductivity in $\mu\text{S cm}^{-1}$ in Pool 7

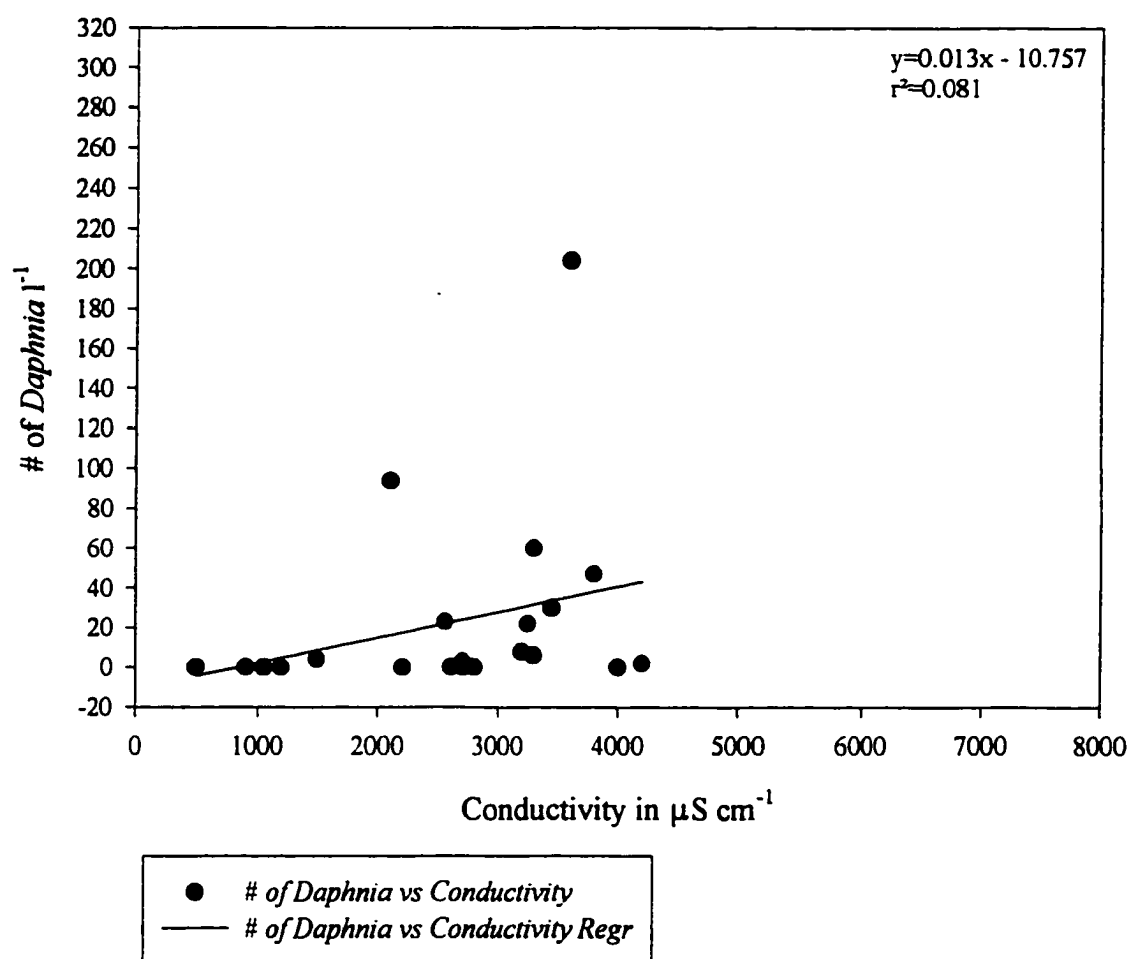


Figure 95: Relationship of the number of *Daphnia* l⁻¹ (*D. pulex* and *D. obtusa*) versus conductivity in $\mu\text{S cm}^{-1}$ in Pool 7, with individual data points and regression as shown.

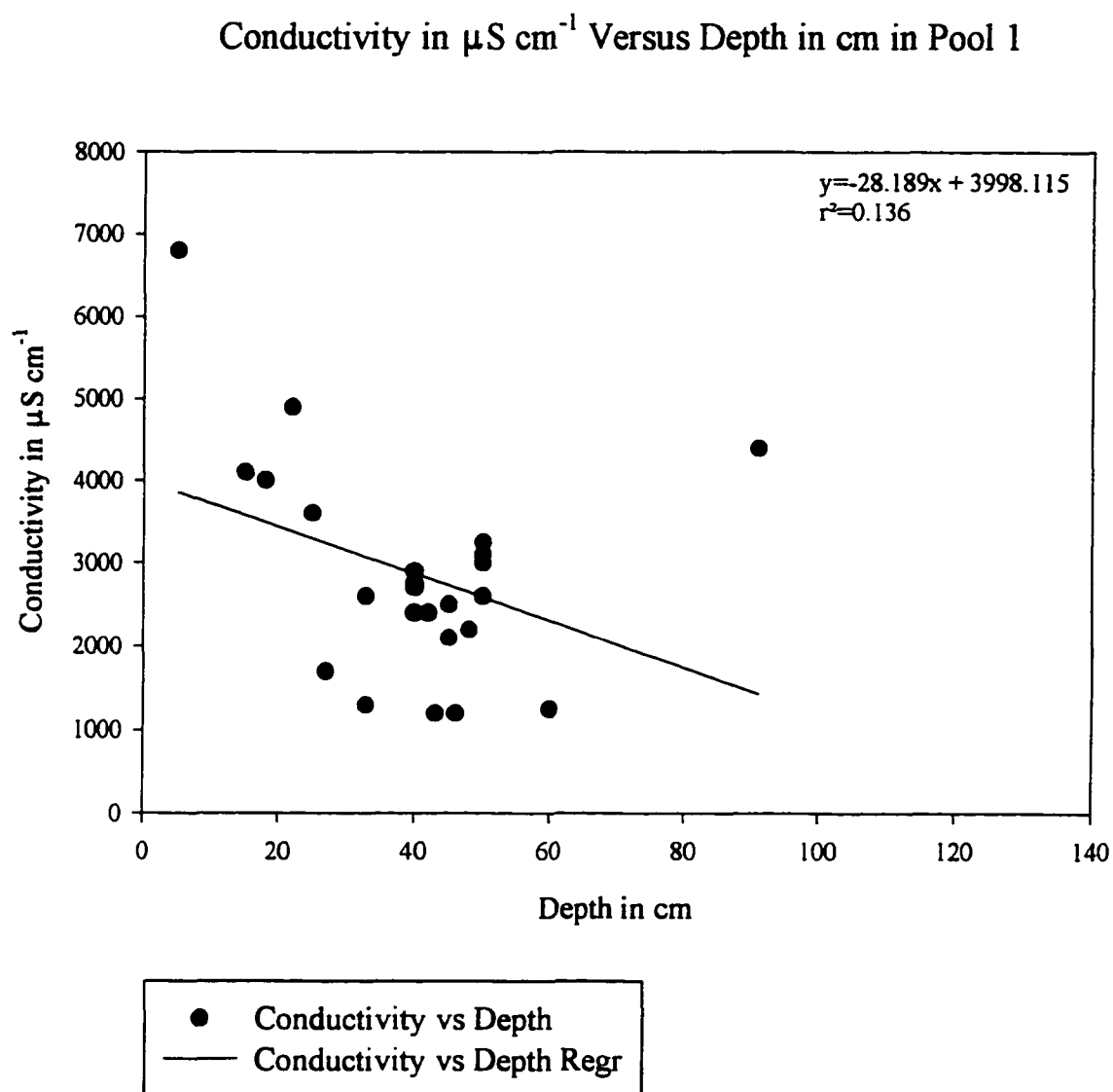


Figure 96: Relationship of conductivity in $\mu\text{S cm}^{-1}$ versus depth in cm in Pool 1, with individual data points and regression as shown.

Conductivity in $\mu\text{S cm}^{-1}$ Versus Depth in cm in Pool 2

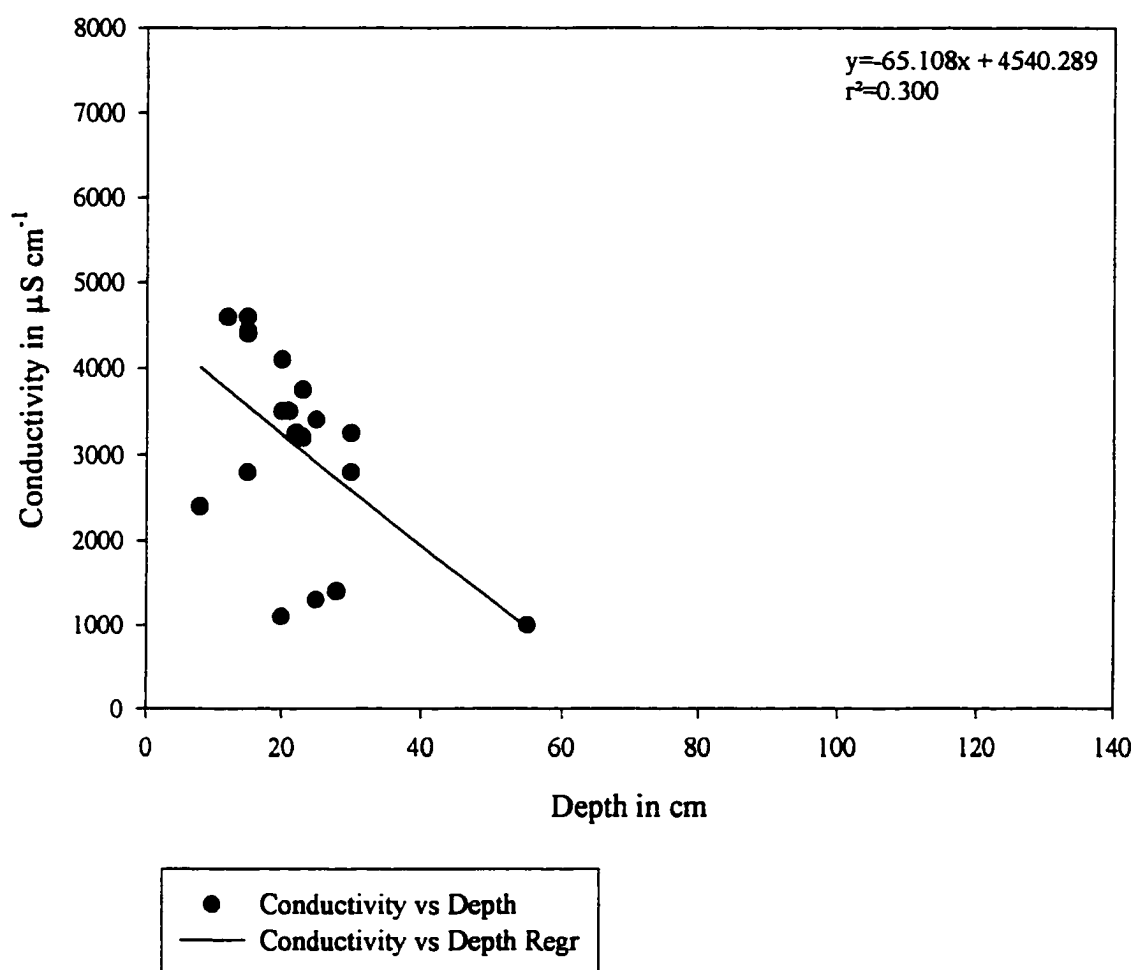


Figure 97: Relationship of conductivity in $\mu\text{S cm}^{-1}$ versus Depth in cm in Pool 2, with individual data points and regression as shown.

Conductivity in $\mu\text{S cm}^{-1}$ Versus Depth in cm in Pool 3

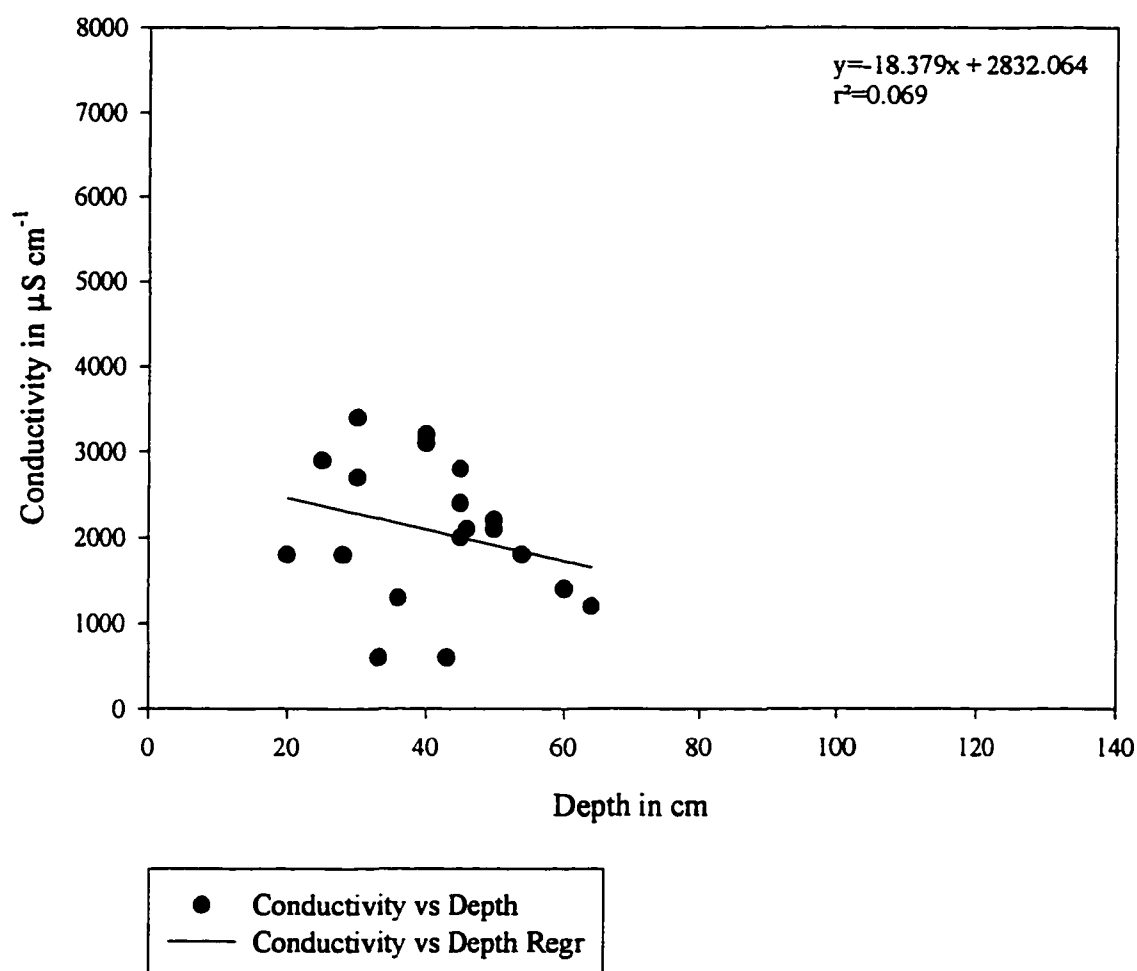


Figure 98: Relationship of conductivity in $\mu\text{S cm}^{-1}$ versus depth in cm in Pool 3, with individual data points and regression as shown.

Conductivity in $\mu\text{S cm}^{-1}$ Versus Depth in cm in Pool 4

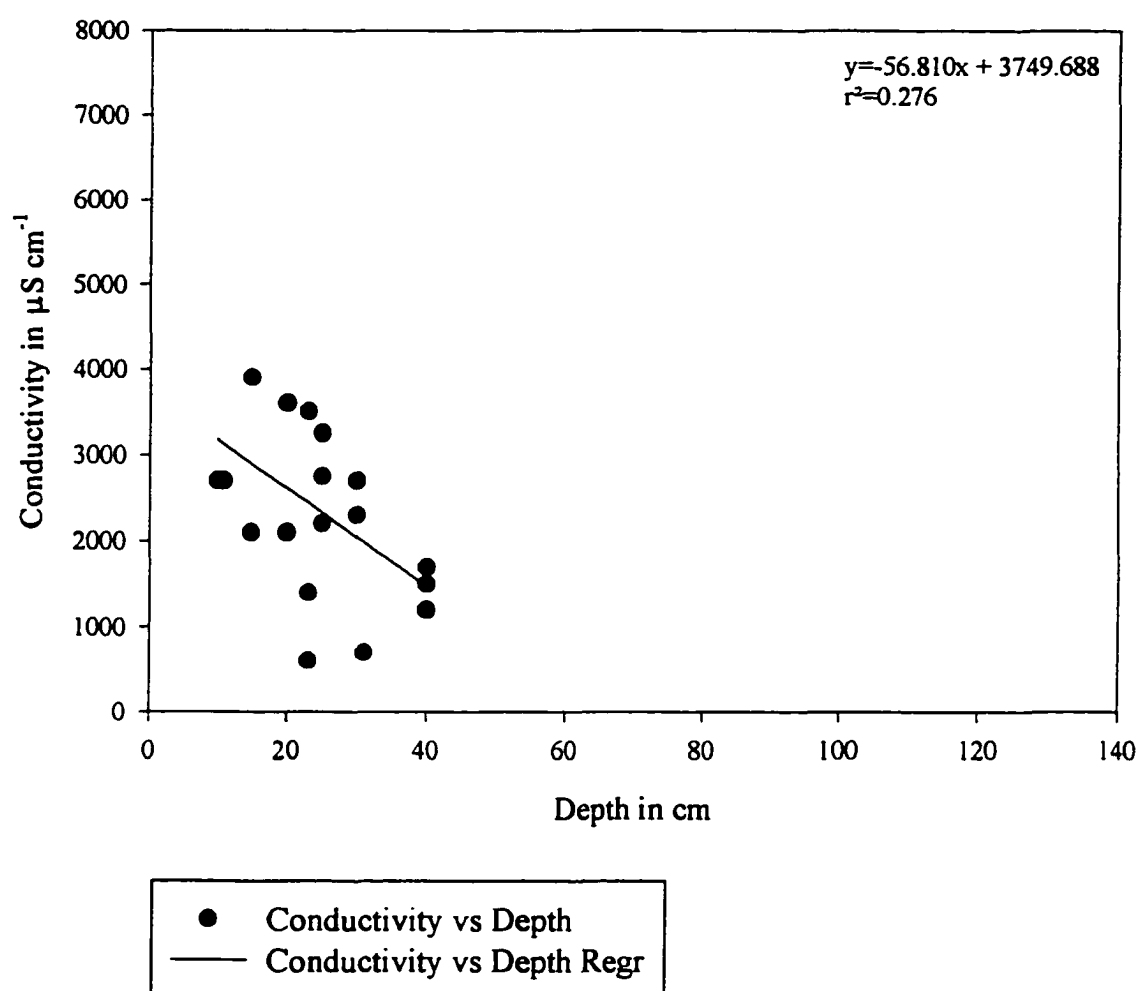


Figure 99: Relationship of conductivity in $\mu\text{S cm}^{-1}$ versus depth in cm in Pool 4, with individual data points and regression as shown.

Conductivity in $\mu\text{S cm}^{-1}$ Versus Depth in cm in Pool 5

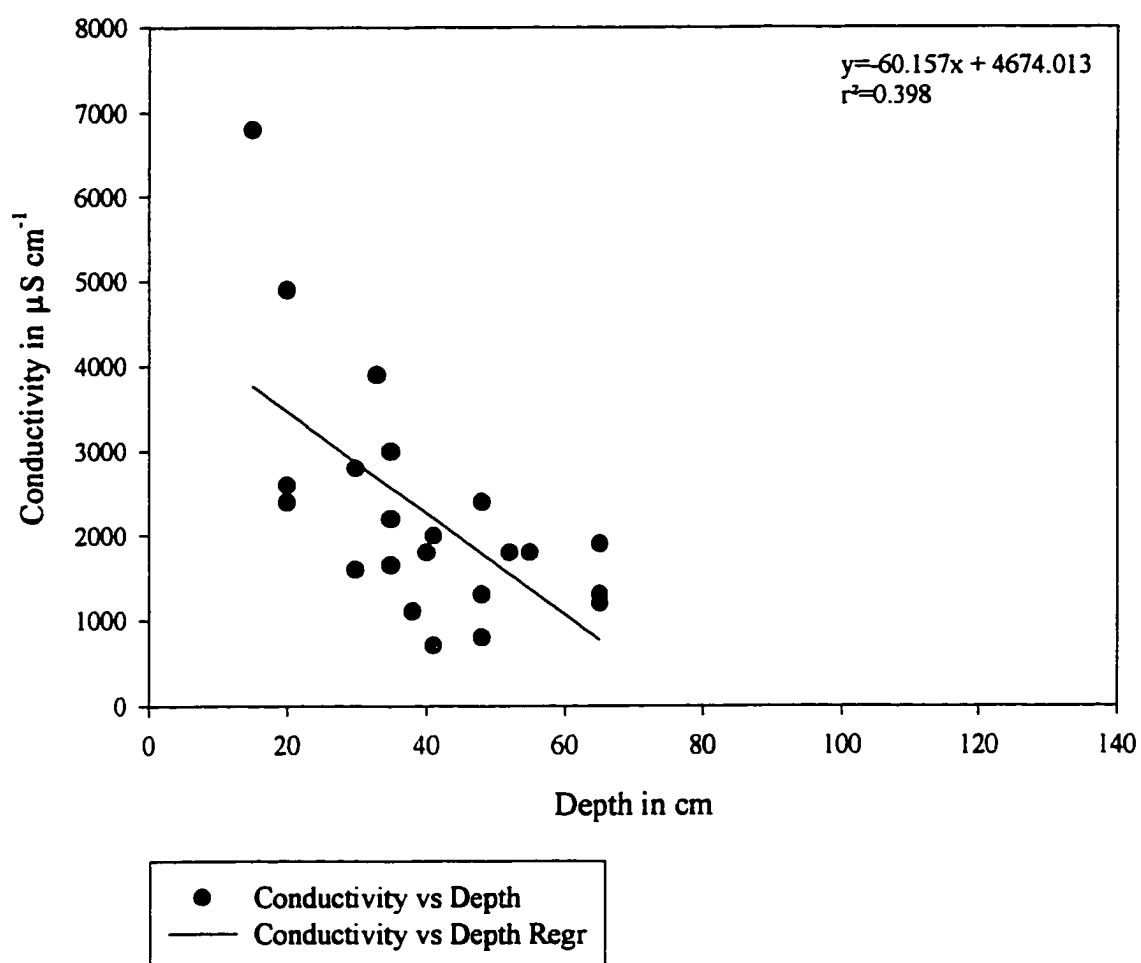


Figure 100: Relationship of conductivity in $\mu\text{S cm}^{-1}$ versus depth in cm in Pool 5, with individual data points and regression

Conductivity in $\mu\text{S cm}^{-1}$ Versus Depth in cm in Pool 6

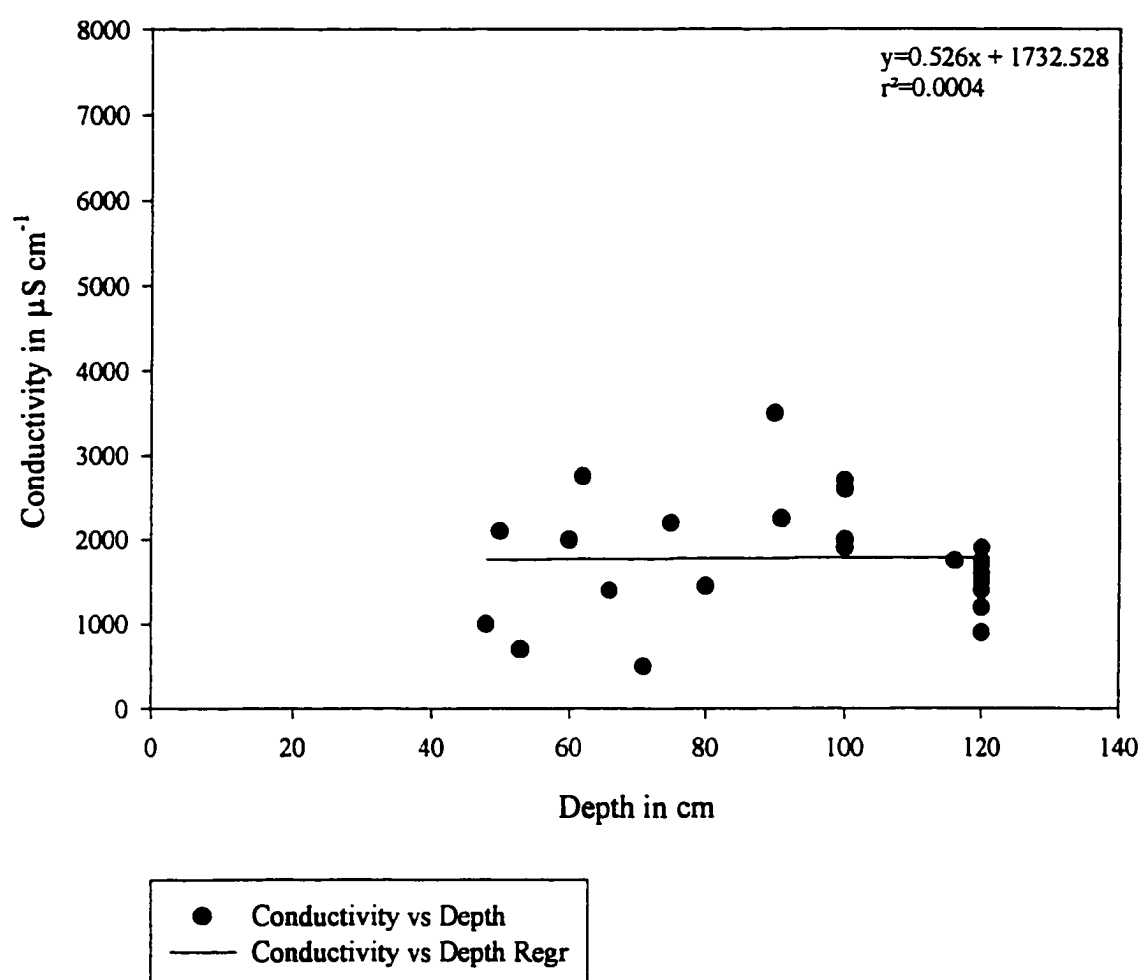


Figure 101: Relationship of conductivity in $\mu\text{S cm}^{-1}$ versus depth in cm in Pool 6, with individual data points and regression as shown.

Conductivity in $\mu\text{S cm}^{-1}$ Versus Depth in cm in Pool 7

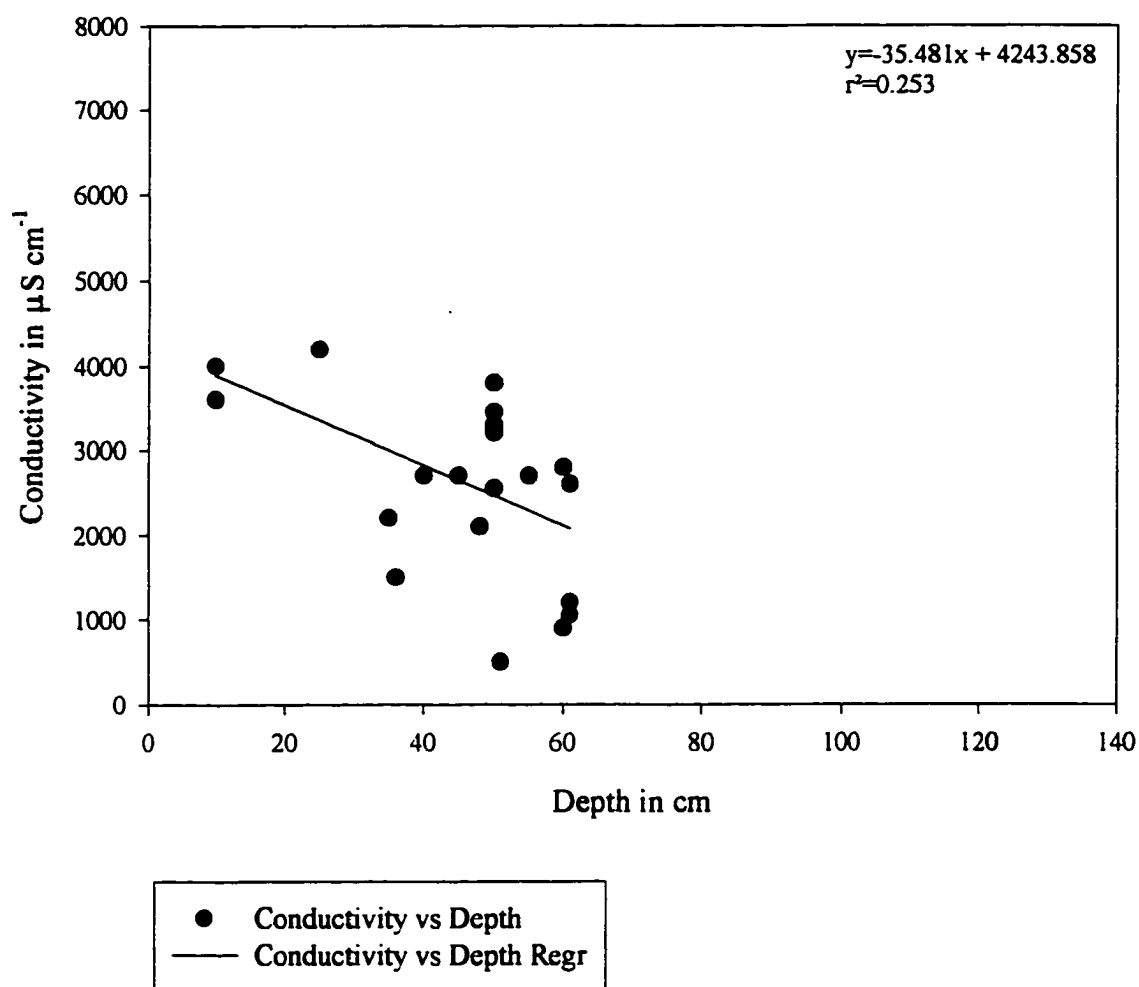


Figure 102: Relationship of conductivity in $\mu\text{S cm}^{-1}$ versus depth in cm in Pool 7, with individual data points and regression as shown.

conductivity, reflecting a strong concentration effect. This result is confirmed by examination of Pool 6, which did not dry during the year and which showed no discernible depth conductivity pattern. Conductivity and pH were not consistently related. I regressed pH against conductivity and found small and inconsistent r^2 values.

As was the case before for depth, I anticipated that conductivity would show a relationship for the number of *Daphnia* l⁻¹ since as pools become higher in conductivity it reflects long periods of evaporation, and therefore, duration. Pools 1 and 2 showed no relationship. There is a suggestion of a positive slope for conductivity and *Daphnia* density in Pools 3 through 7. However, the relationships may be driven by outlier points. The only convincing relationship is in Pool 5 where the r^2 reaches 0.54. Also when pool depth decreased, the density of *Daphnia* often increased.

It is likely that pH and conductivity are not causally related to the number of daphnids. It is more likely that as water remained in the pools for a period of time and depth decreased due to evaporation, daphnids were able to carry out their life cycles in spite of changes in pH and conductivity. It may be that in Pools 4, 5, 6 and 7 single outliers may have been unusually influential.

Relationship of Duration of Pools to
the Population Size of *Daphnia*

Long-term persistence of daphnid populations existed only in periods of relatively static conditions, or low water flow, which allowed animals to maintain their populations. I assumed, given two week sampling intervals, that if water was present on two adjacent dates, that it was present in between. It is possible, but not likely, that pools dried and refilled between sampling dates. It is more likely that pools were deluged during these intervals with possible scouring and washing away of populations.

To test whether the population size of daphnids is affected mainly by the duration time of the pools between disturbances, the number of *Daphnia* l⁻¹ per pool versus each period between drought and/or deluge disturbances was plotted for each period as discussed above. Each pool had three such periods (refer to previous figures where periods are located between drought and deluge disturbances and disturbances are indicated by arrows). Regressions were not done against each individual period because, in general, daphnid numbers were too low.

To obtain sufficient numbers for analysis all three periods were combined for each pool. The number of *Daphnia* l⁻¹ was regressed against all of the periods for each pool (Figures 103 to 130). Relationships between population size and length of duration of the pools were very modest. A single, descriptive factor that explains the dynamics and density of *Daphnia* in these pools remains unknown. It is most likely the case that this is an extremely stressful, complicated and rigorous system. This creates an irregular pattern of opportunity for population expansion that depends on a multiplicity of factors. Each of

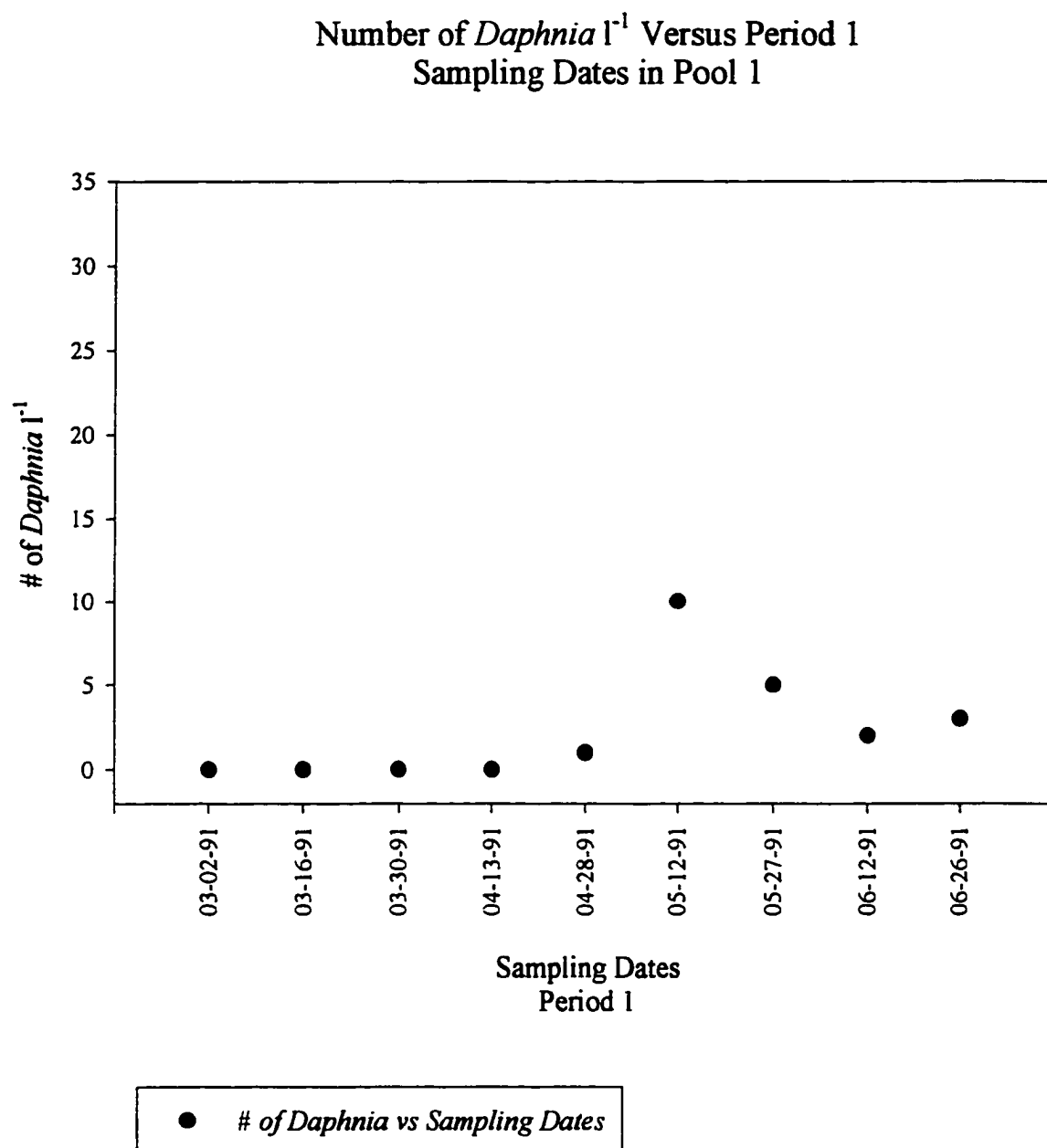


Figure 103: Relationship of the number of *Daphnia* l⁻¹ versus period 1 sampling dates in Pool 1, with individual data points as shown.

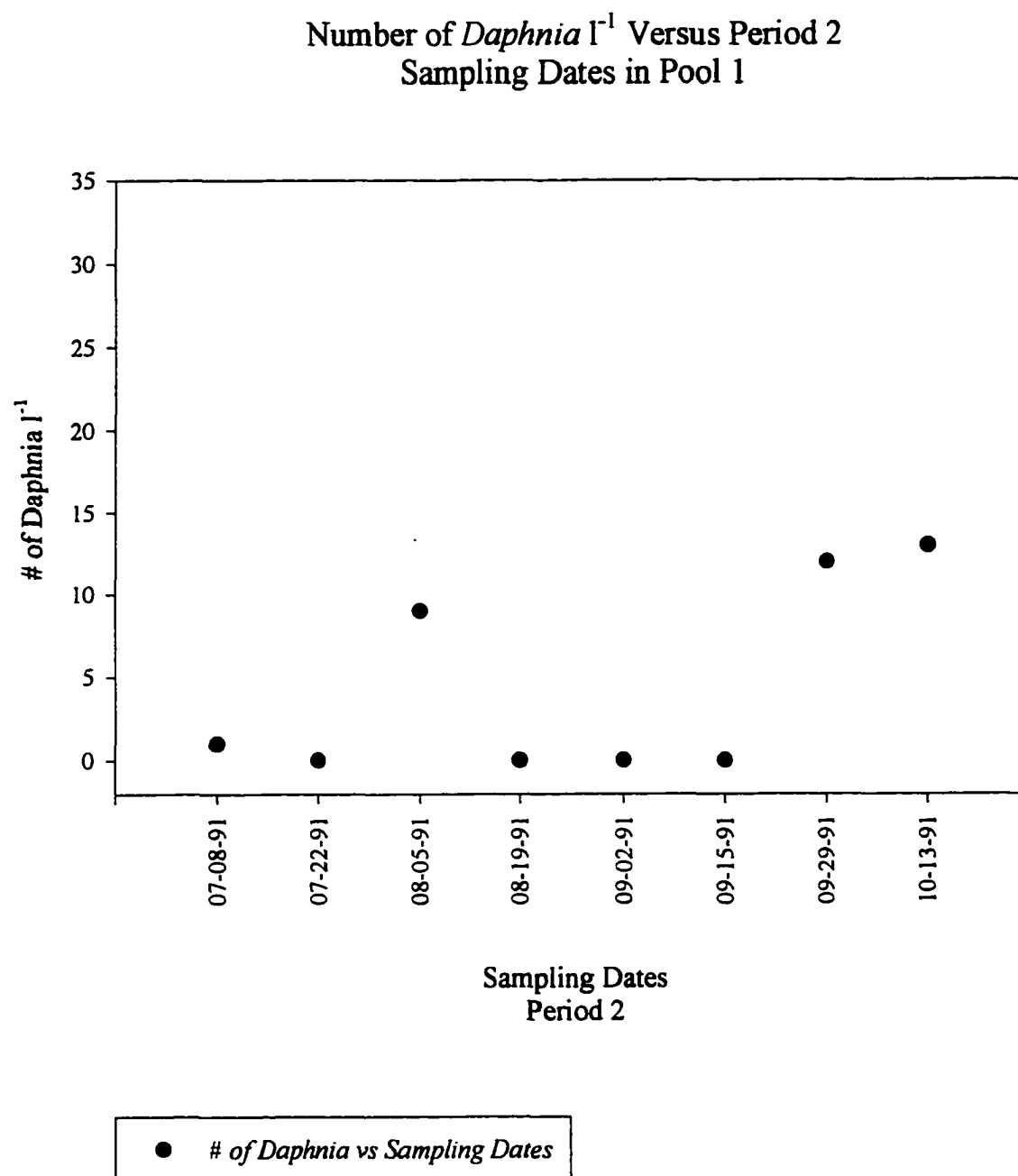


Figure 104: Relationship of the number of *Daphnia* l⁻¹ versus period 2 sampling dates in Pool 1, with individual data points as shown.

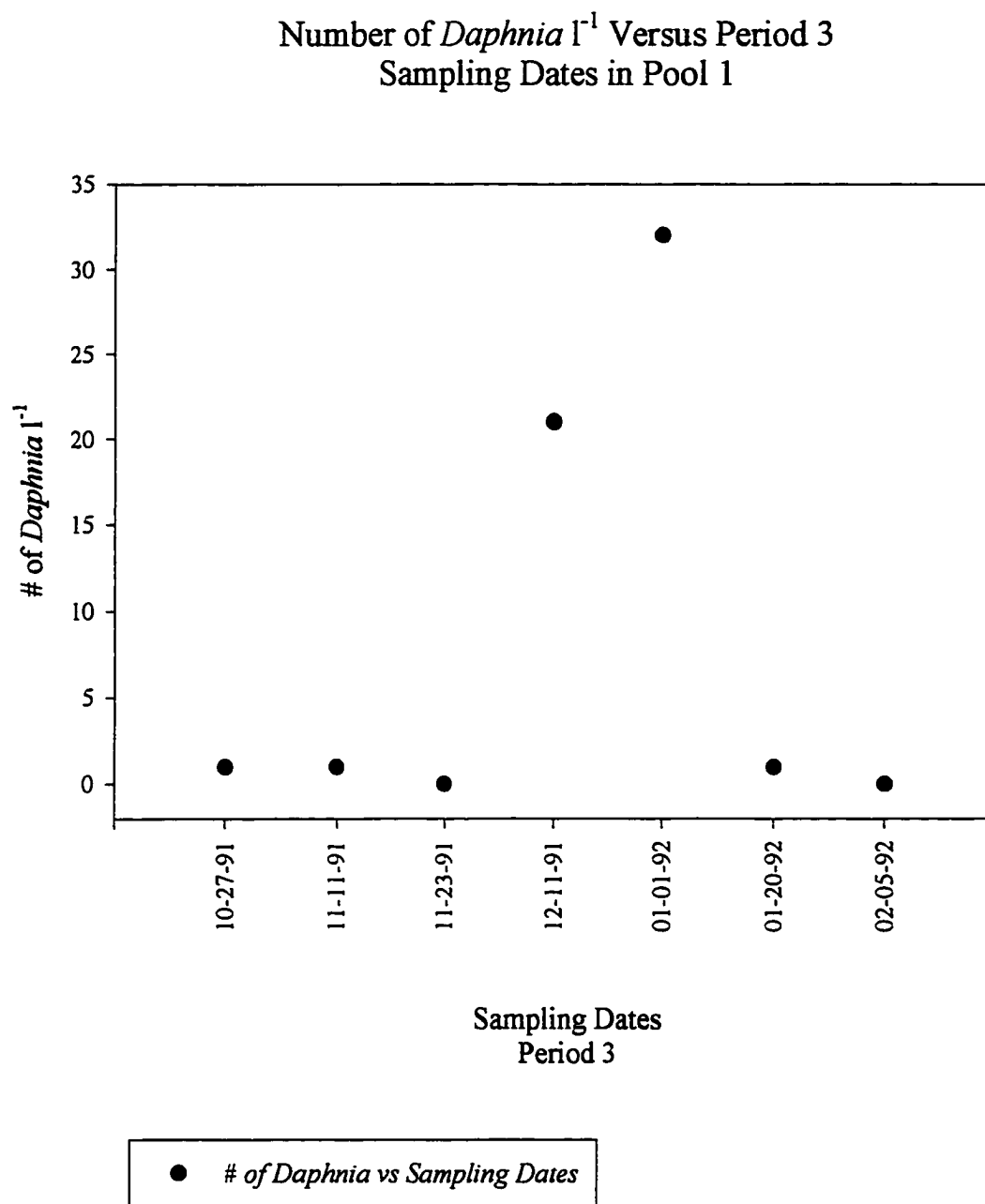


Figure 105: Relationship of the number of *Daphnia* l⁻¹ versus period 2 sampling dates in Pool 1, with individual data points as shown.

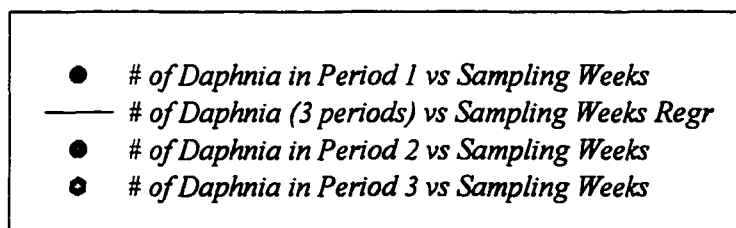
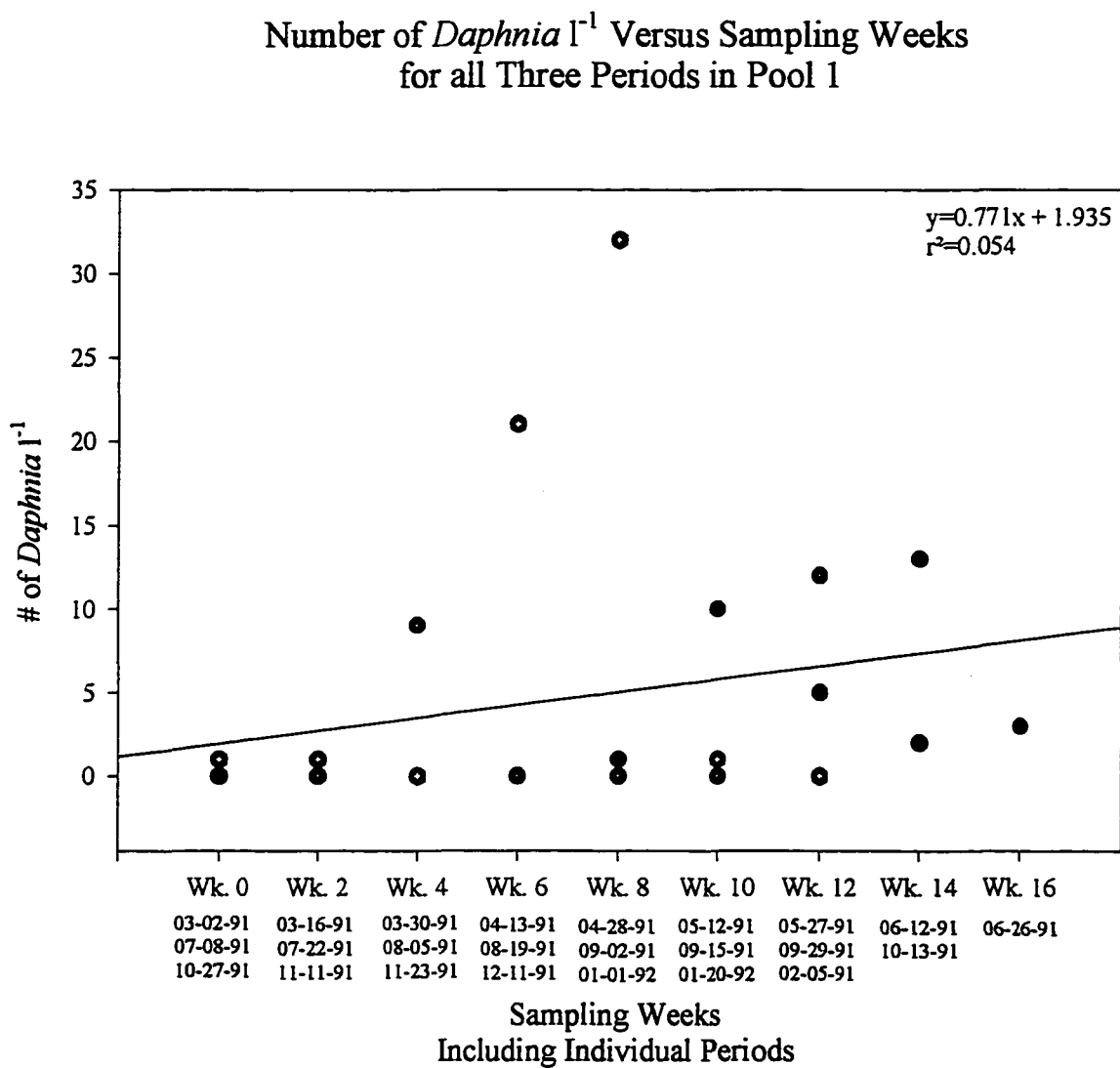


Figure 106: Relationship of the number of *Daphnia* l⁻¹, pooled for three periods, versus sampling weeks in Pool 1, with individual data points and regression as shown.

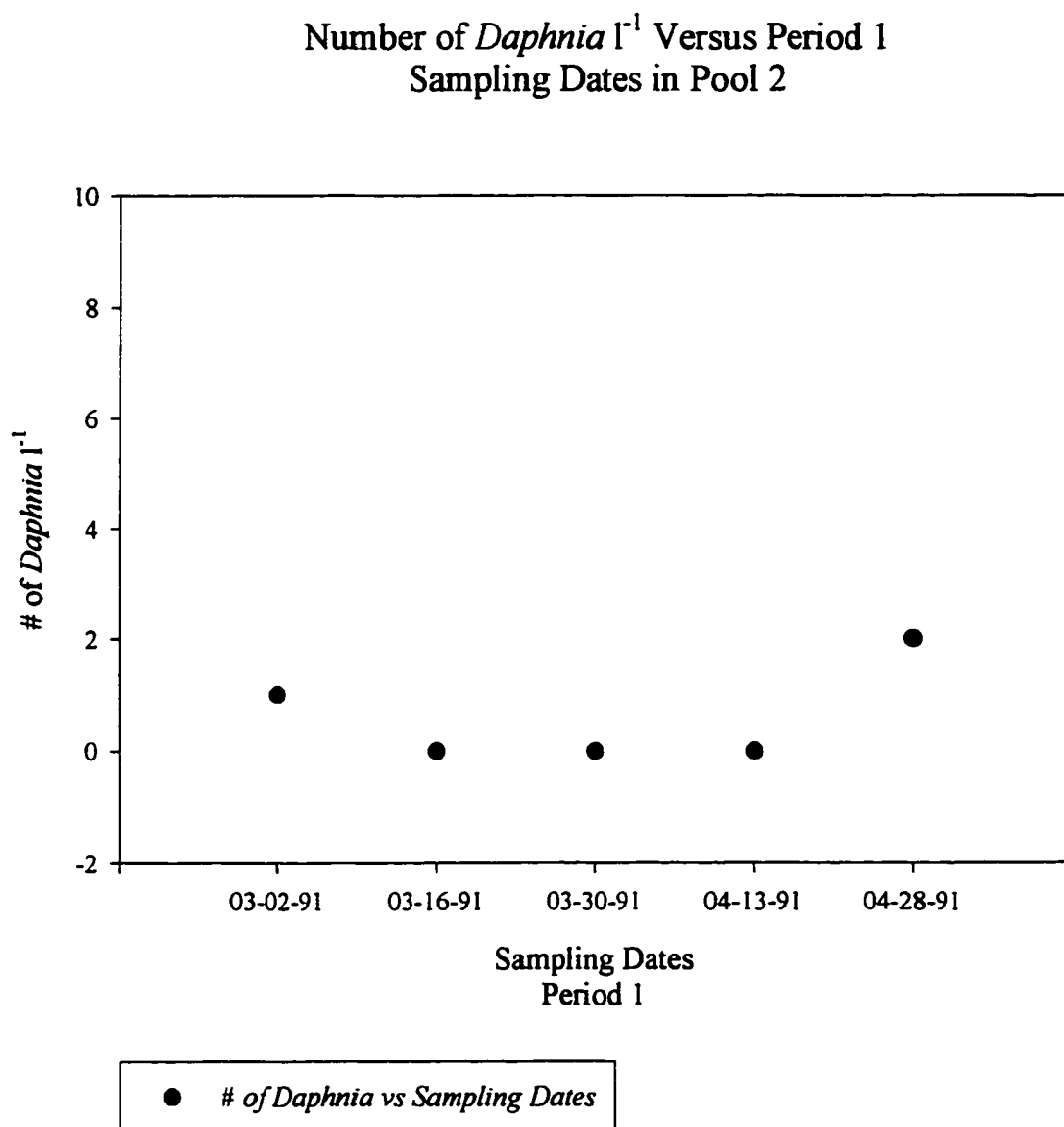


Figure 107: Relationship of the number of *Daphnia* l⁻¹ versus period 1 sampling dates in Pool 2, with individual data points as shown.

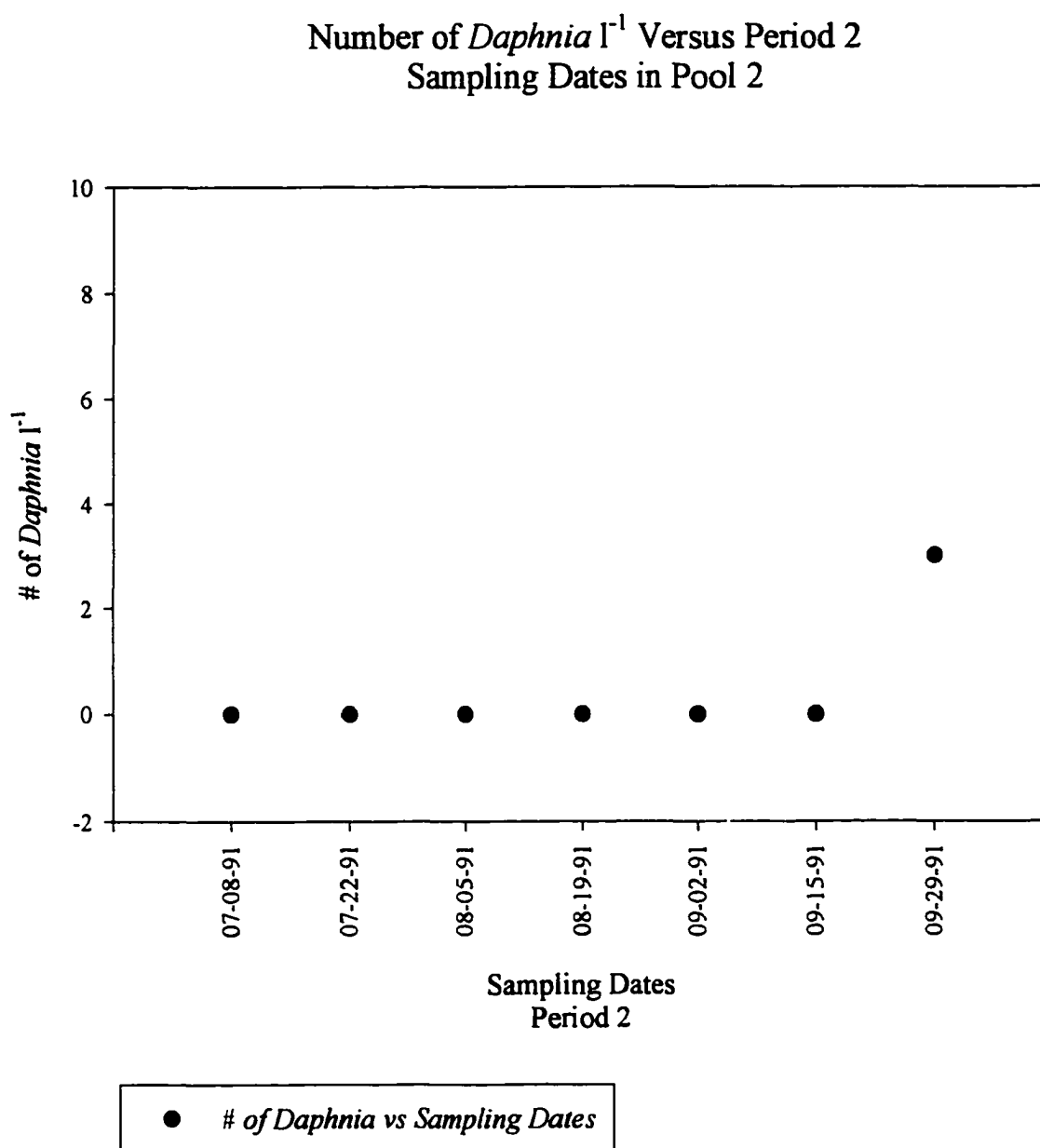


Figure 108: Relationship of the number of *Daphnia* l⁻¹ versus period 2 sampling dates in Pool 2, with individual data points as shown.

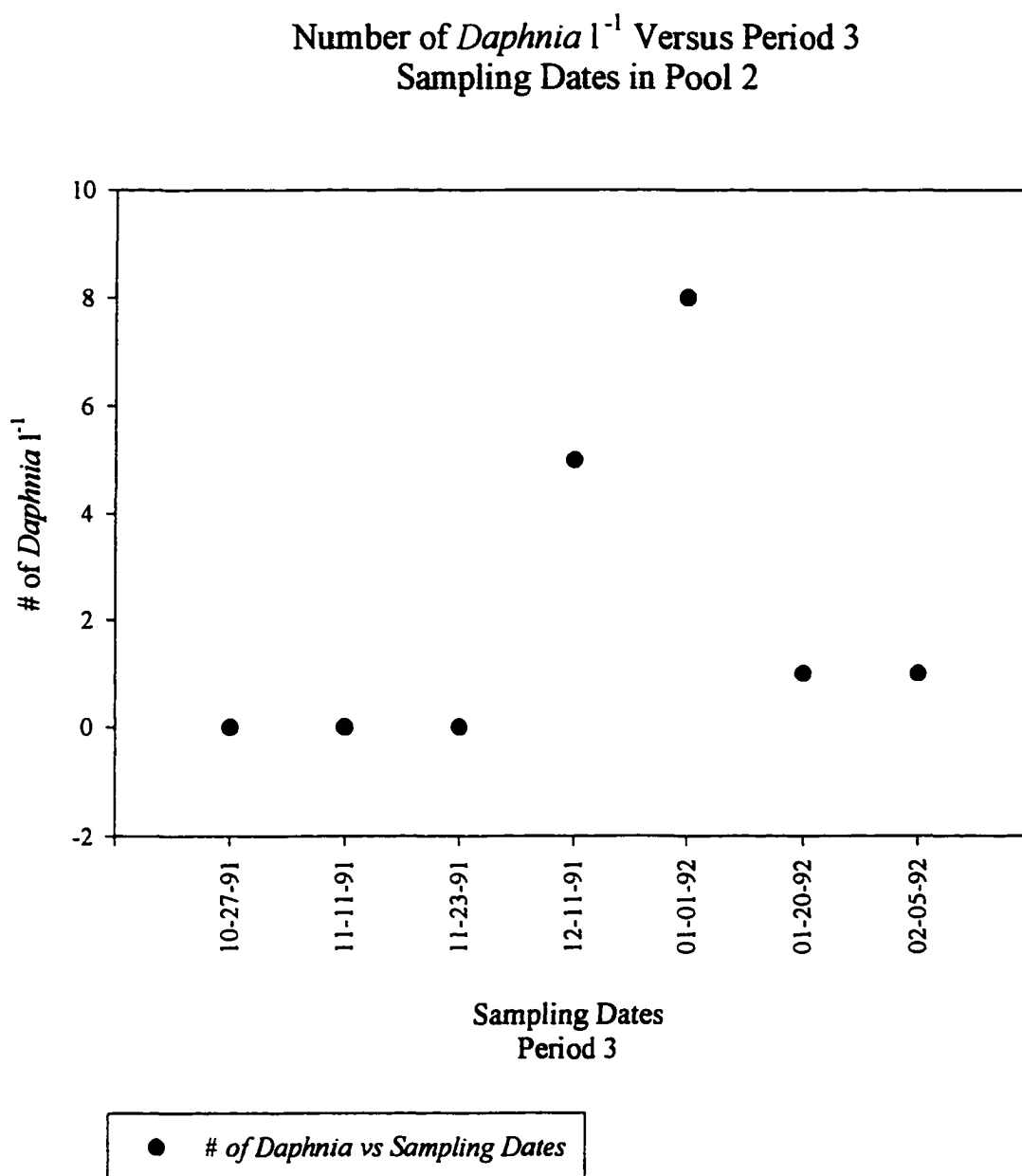


Figure 109: Relationship of the number of *Daphnia* l⁻¹ versus period 3 sampling dates in Pool 2, with individual data points as shown.

Number of *Daphnia* l⁻¹ Versus Sampling Weeks
for all Three Periods in Pool 2

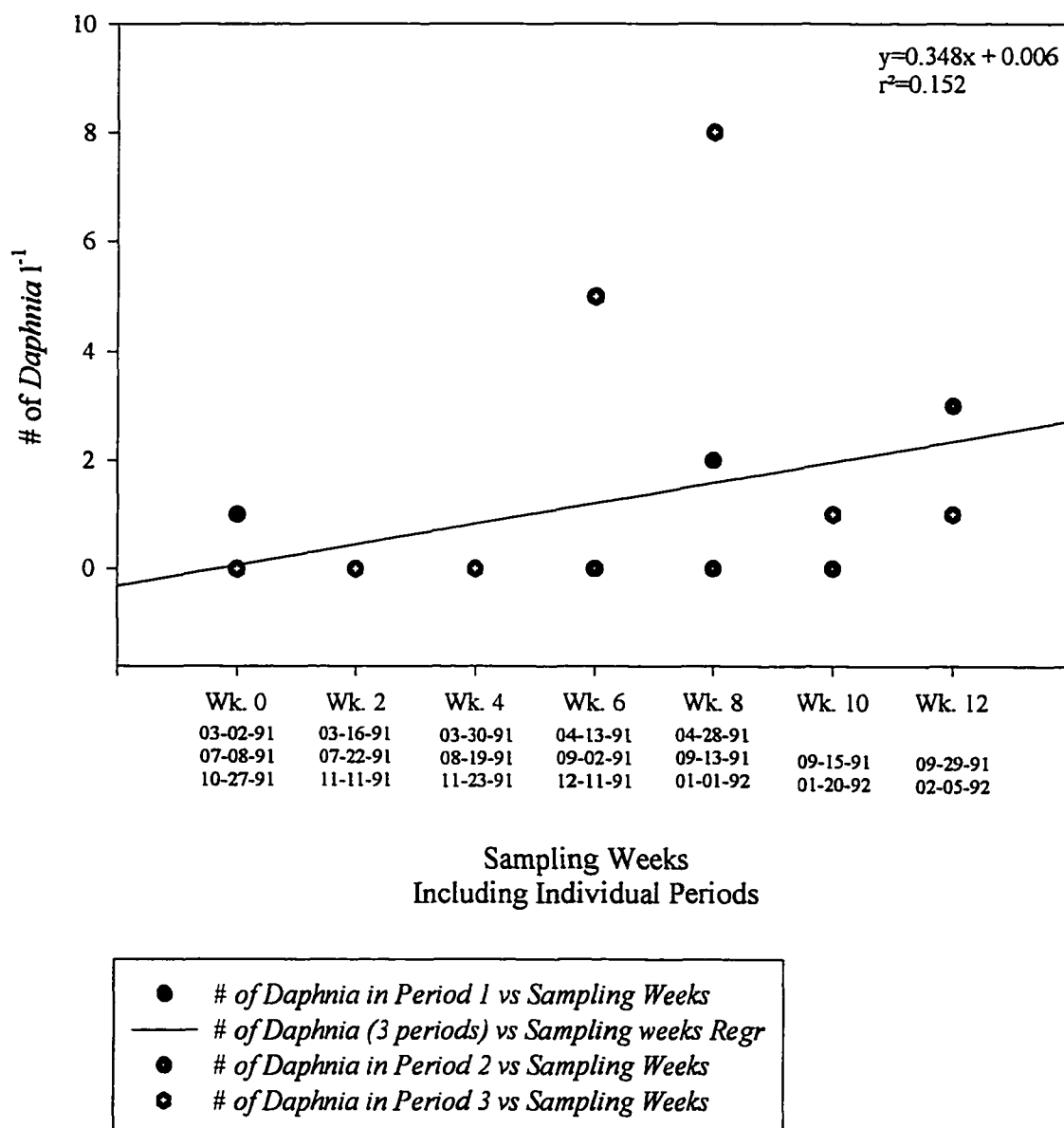


Figure 110: Relationship of the number of *Daphnia* l⁻¹, pooled for three periods, versus sampling weeks in Pool 2, with individual data points and regression as shown.

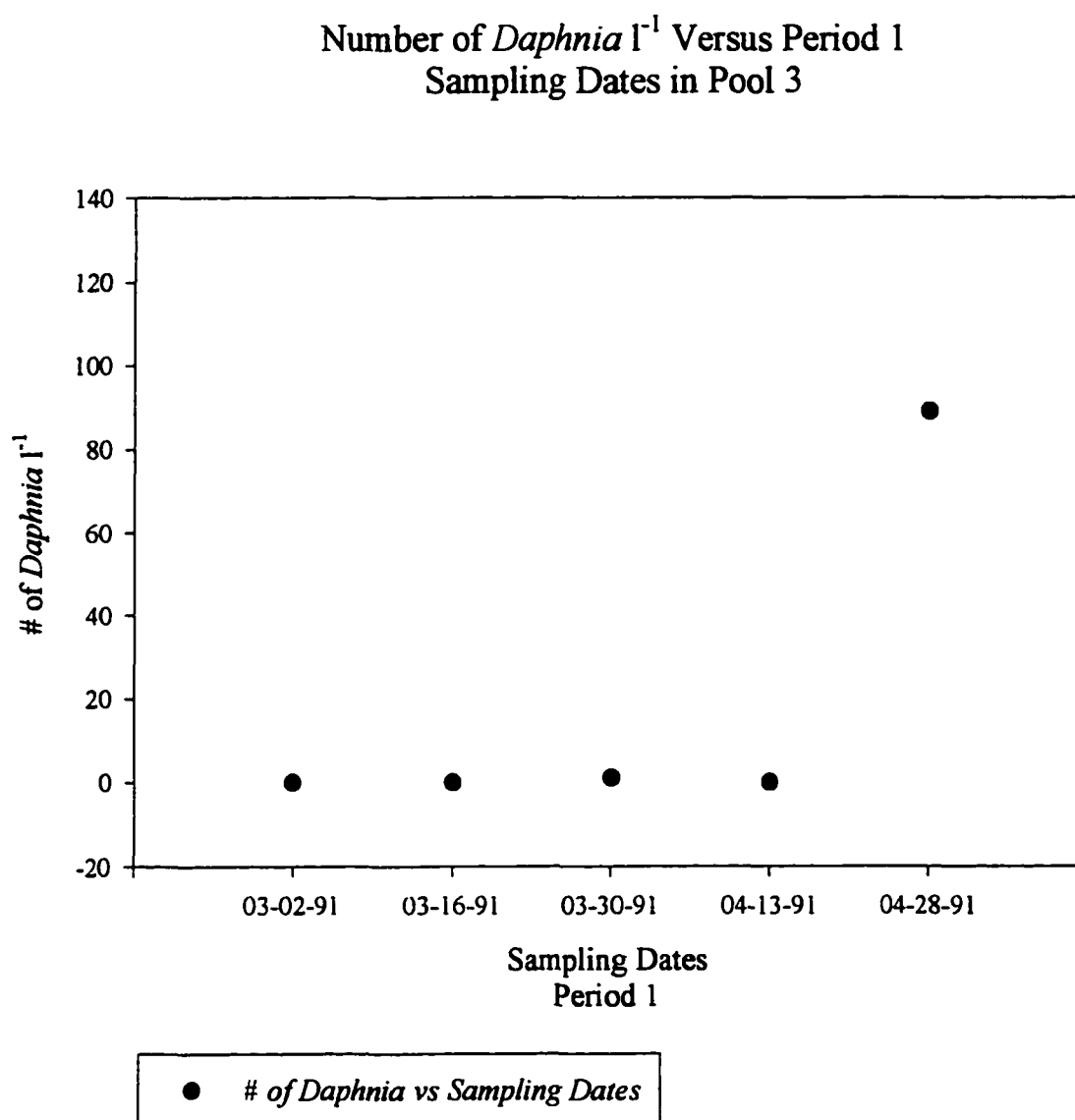


Figure 111: Relationship of the number of *Daphnia* l⁻¹ versus period 1 sampling dates in Pool 3, with individual data points as shown.

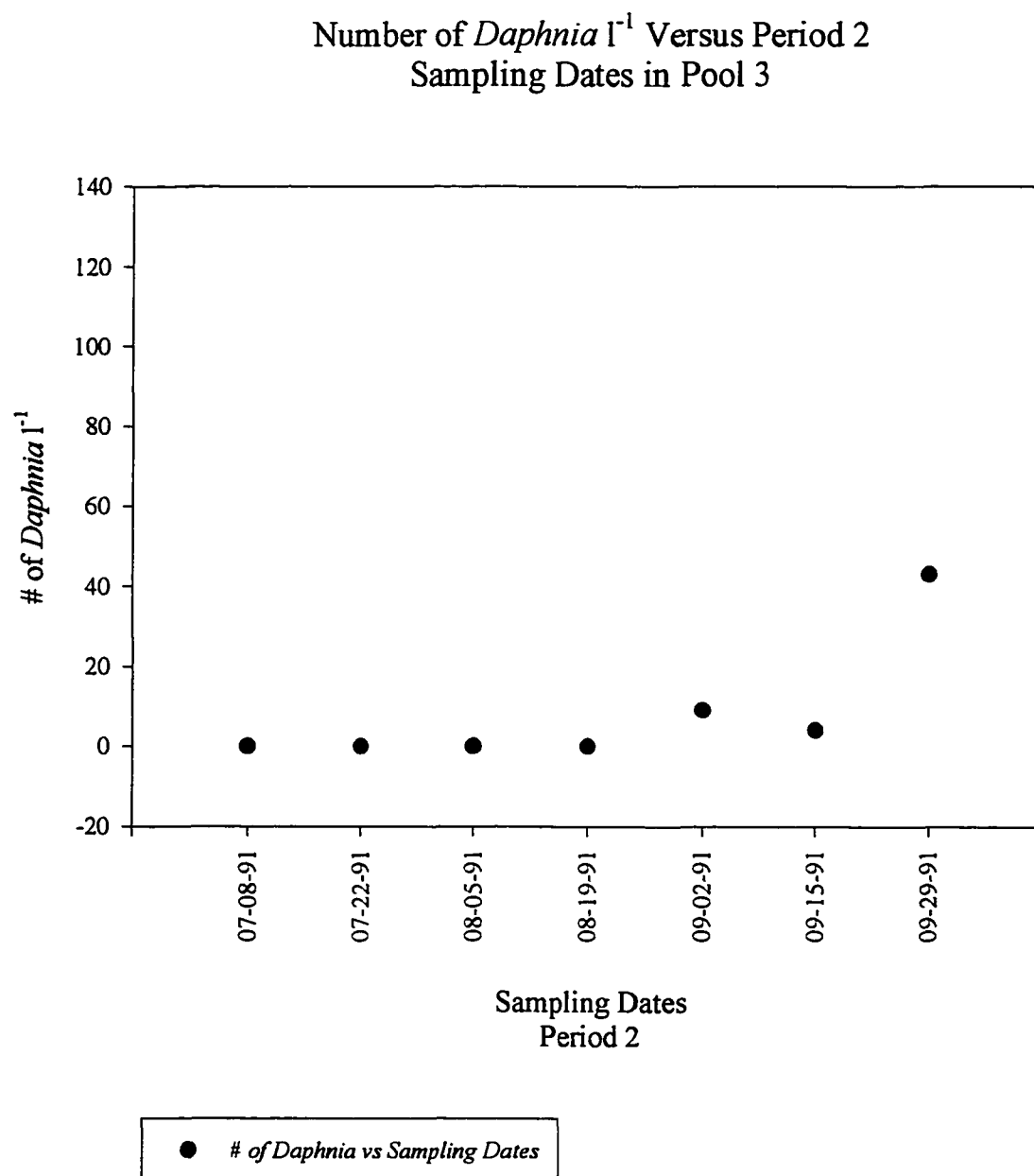


Figure 112: Relationship of the number of *Daphnia* l⁻¹ versus period 2 sampling dates in Pool 3, with individual data points as shown.

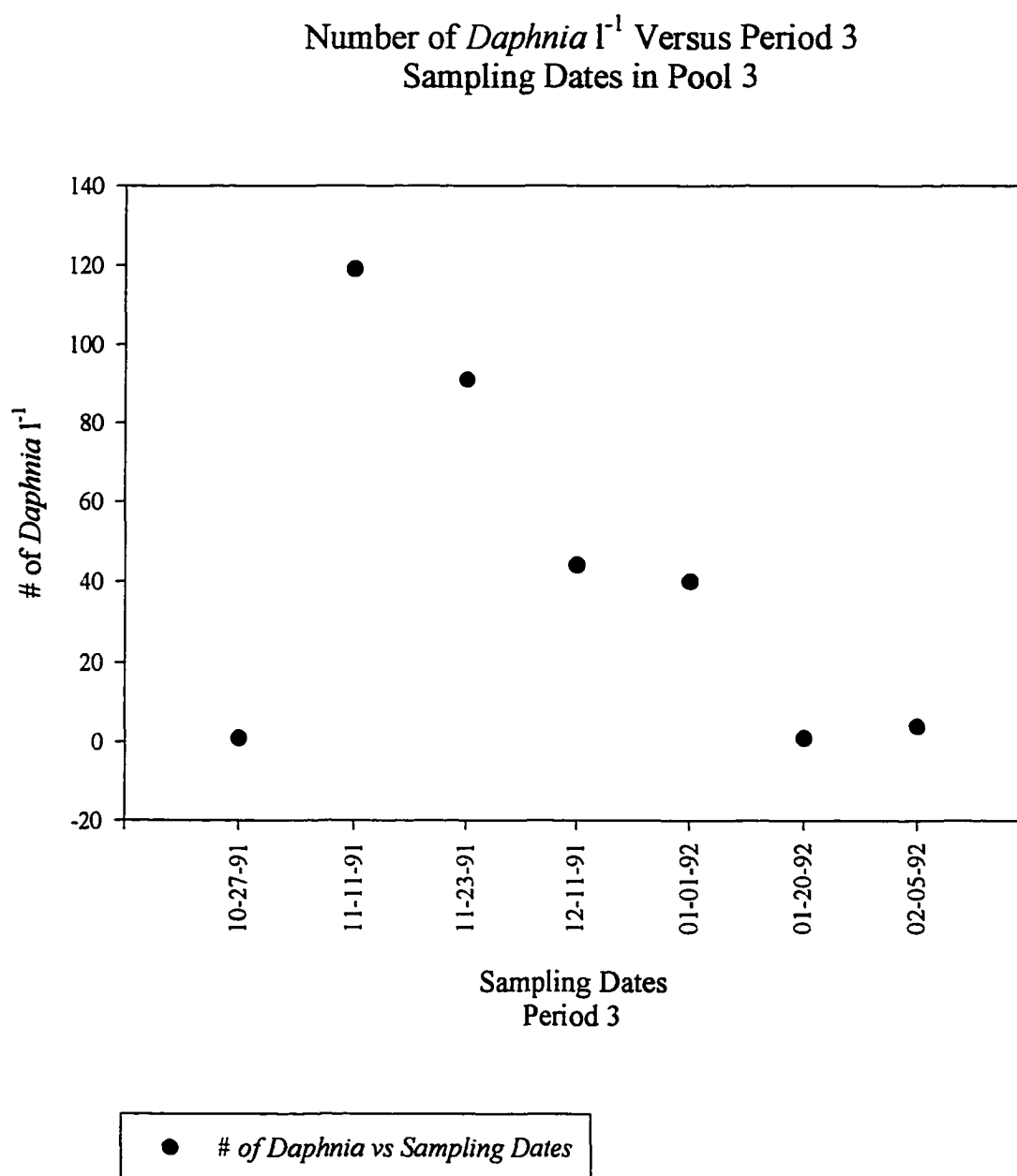


Figure 113: Relationship of the number of *Daphnia* l⁻¹ versus period 3 sampling dates in Pool 3, with individual data points as shown.

Number of *Daphnia* l⁻¹ Versus Sampling Weeks
for all Three Periods in Pool 3

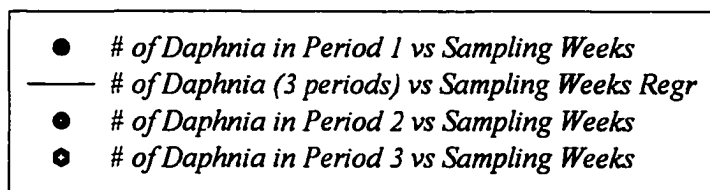
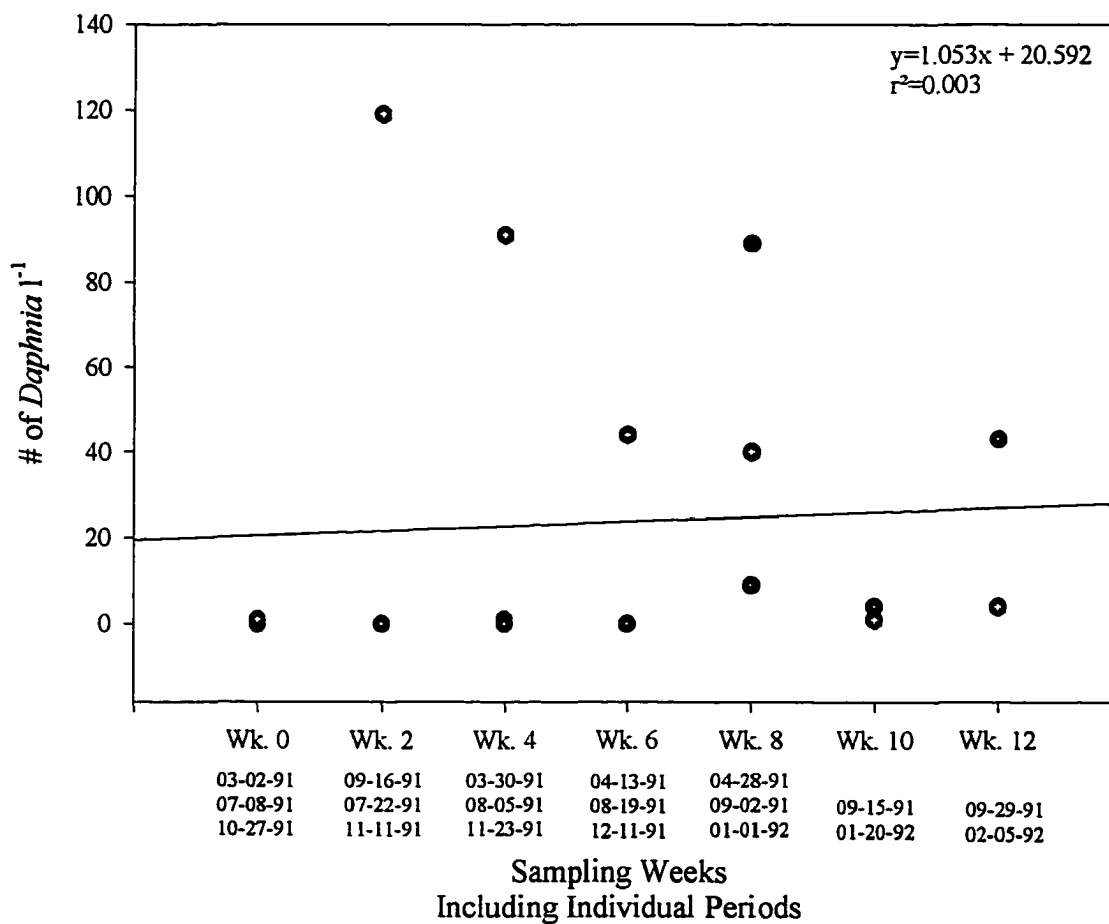


Figure 114: Relationship of the number of *Daphnia* l⁻¹, pooled for three periods, versus sampling weeks in Pool 3, with individual data points and regression as shown.

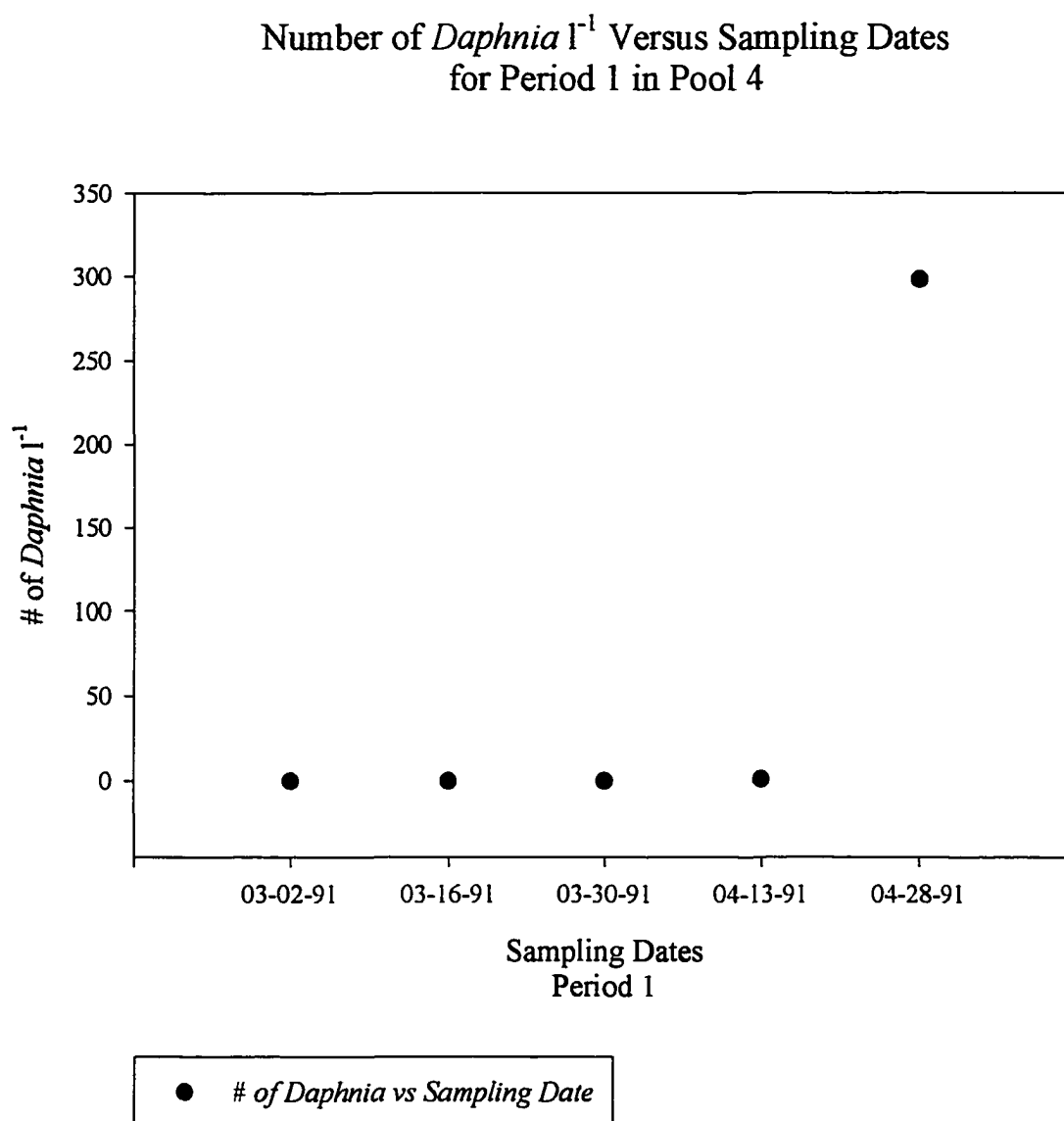


Figure 115: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 1 in Pool 4, with individual data points as shown.

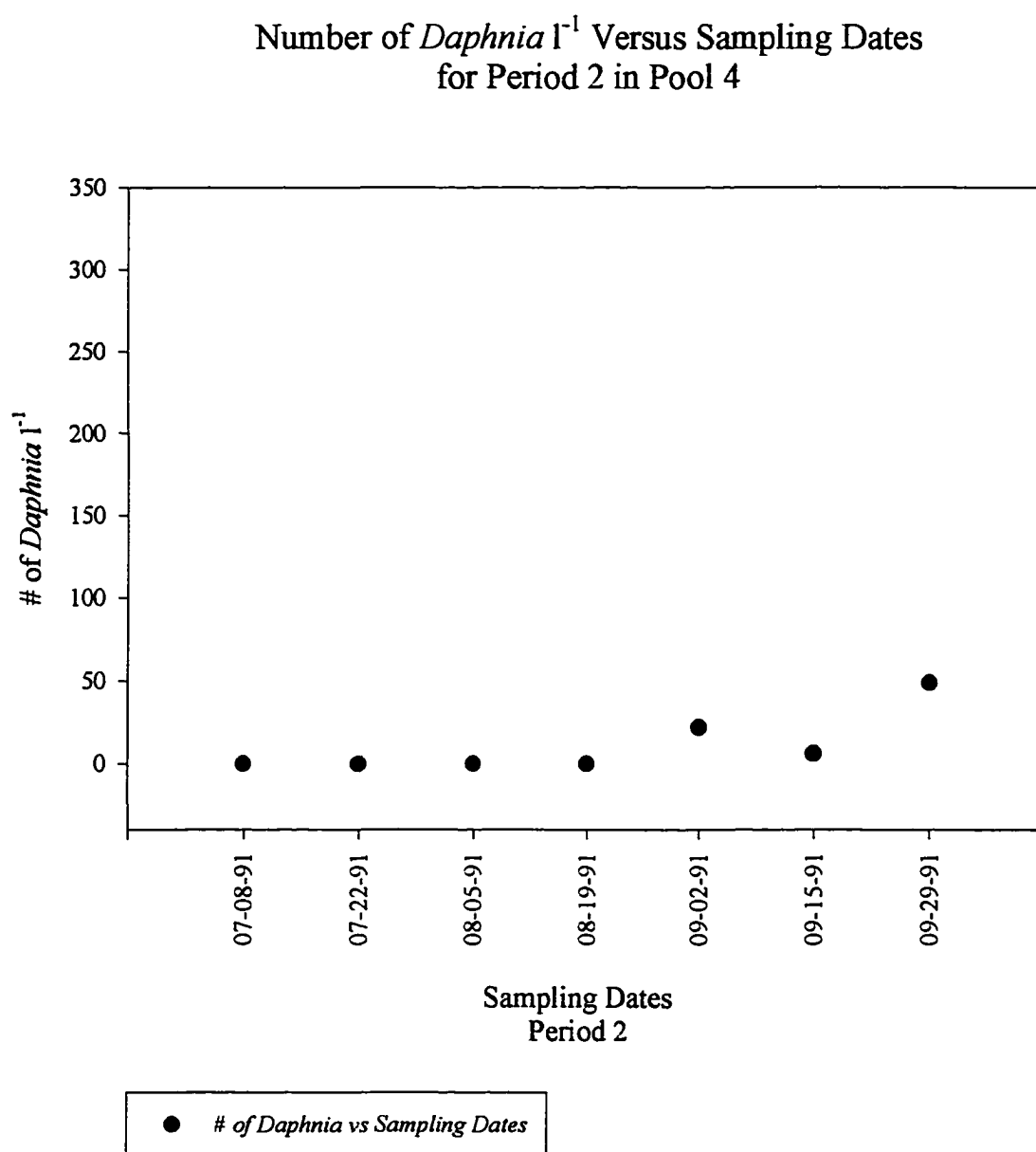


Figure 116: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 2 in Pool 4, with individual data points as shown.

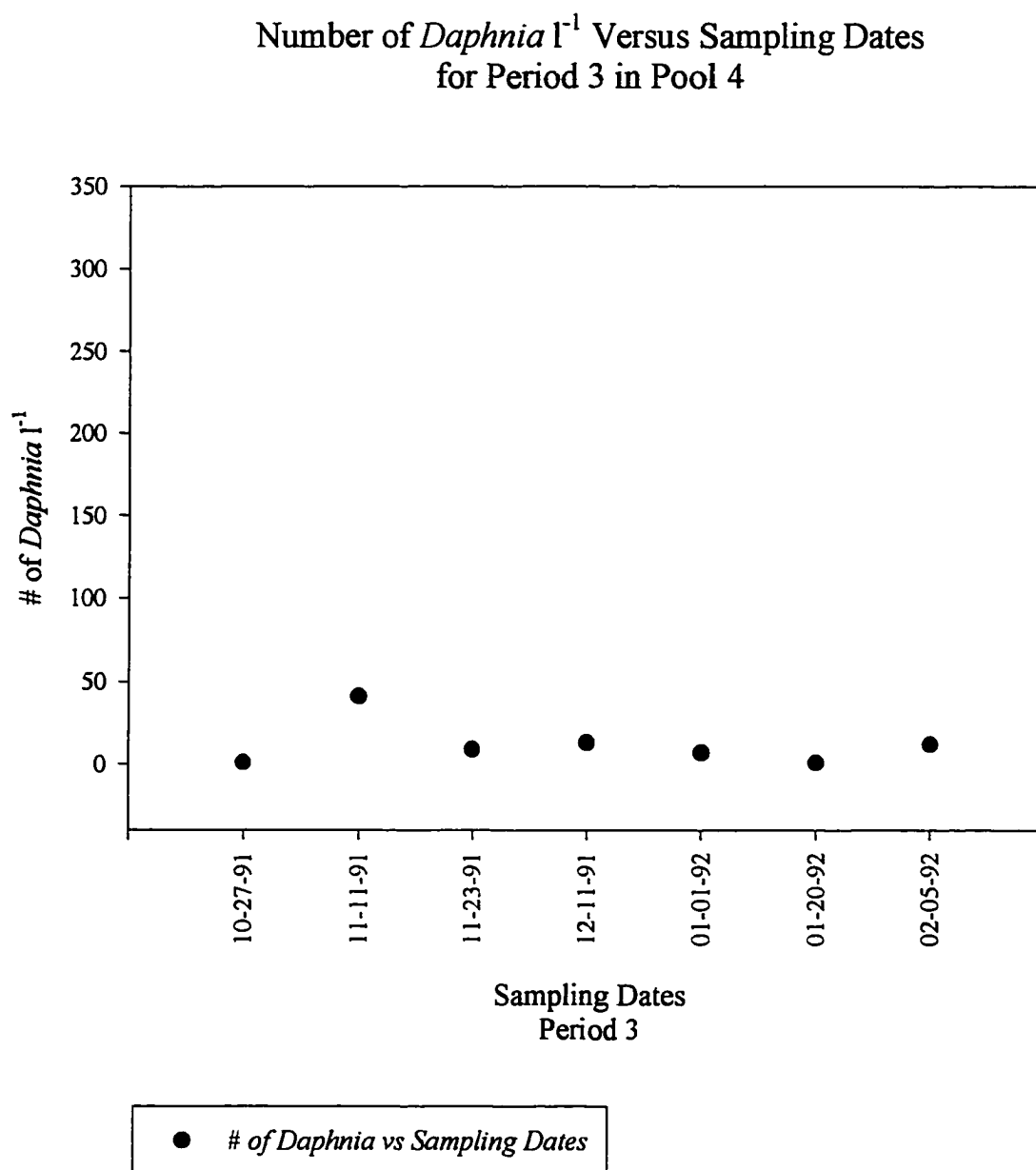


Figure 117: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 3 in Pool 4, with individual data points as shown.

Number of *Daphnia* l⁻¹ Versus Sampling Weeks
for all Three Periods in Pool 4

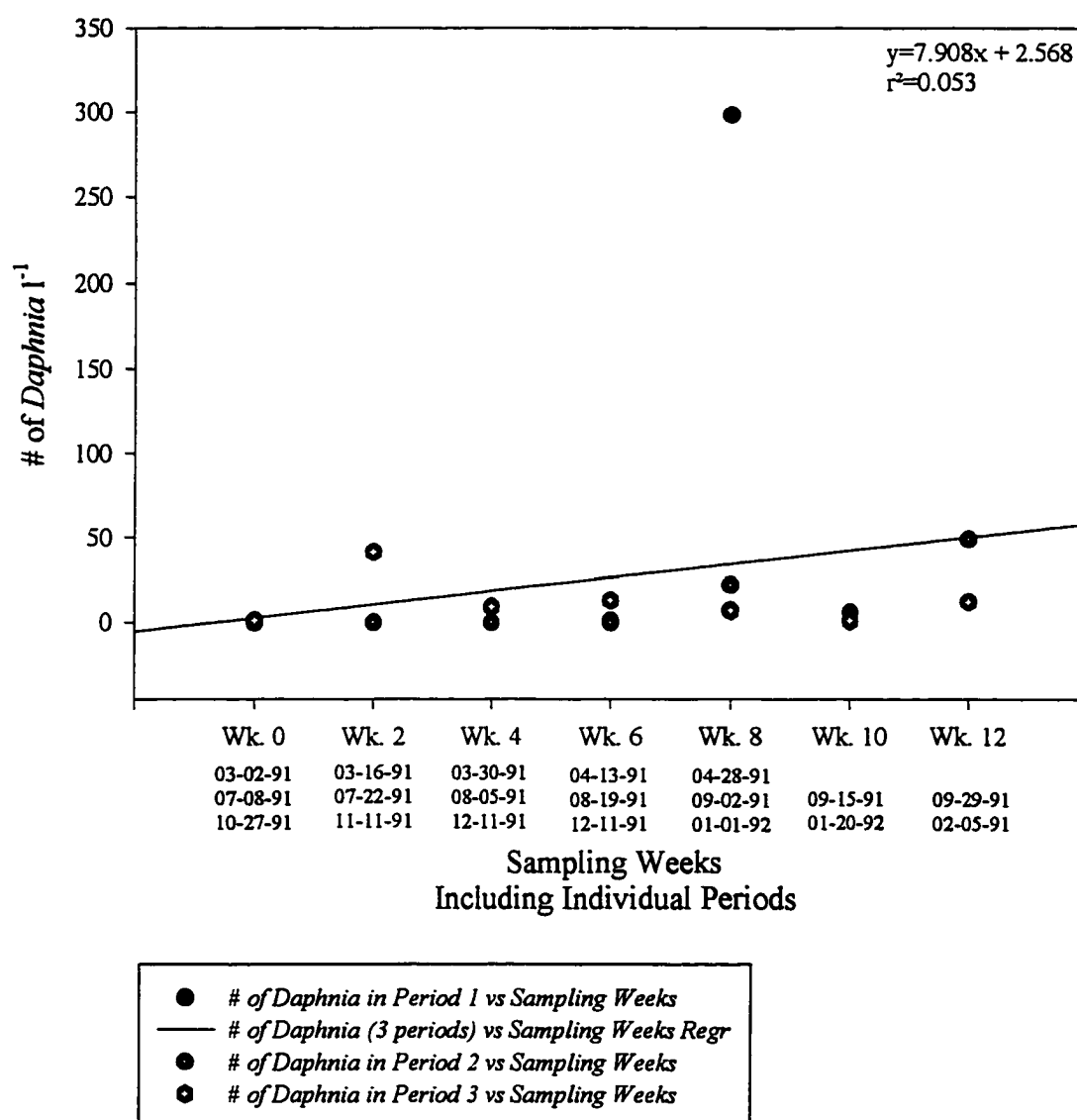


Figure 118: Relationship of the number of *Daphnia* l⁻¹, pooled for three periods, versus sampling weeks in Pool 4, with individual data points and regression as shown.

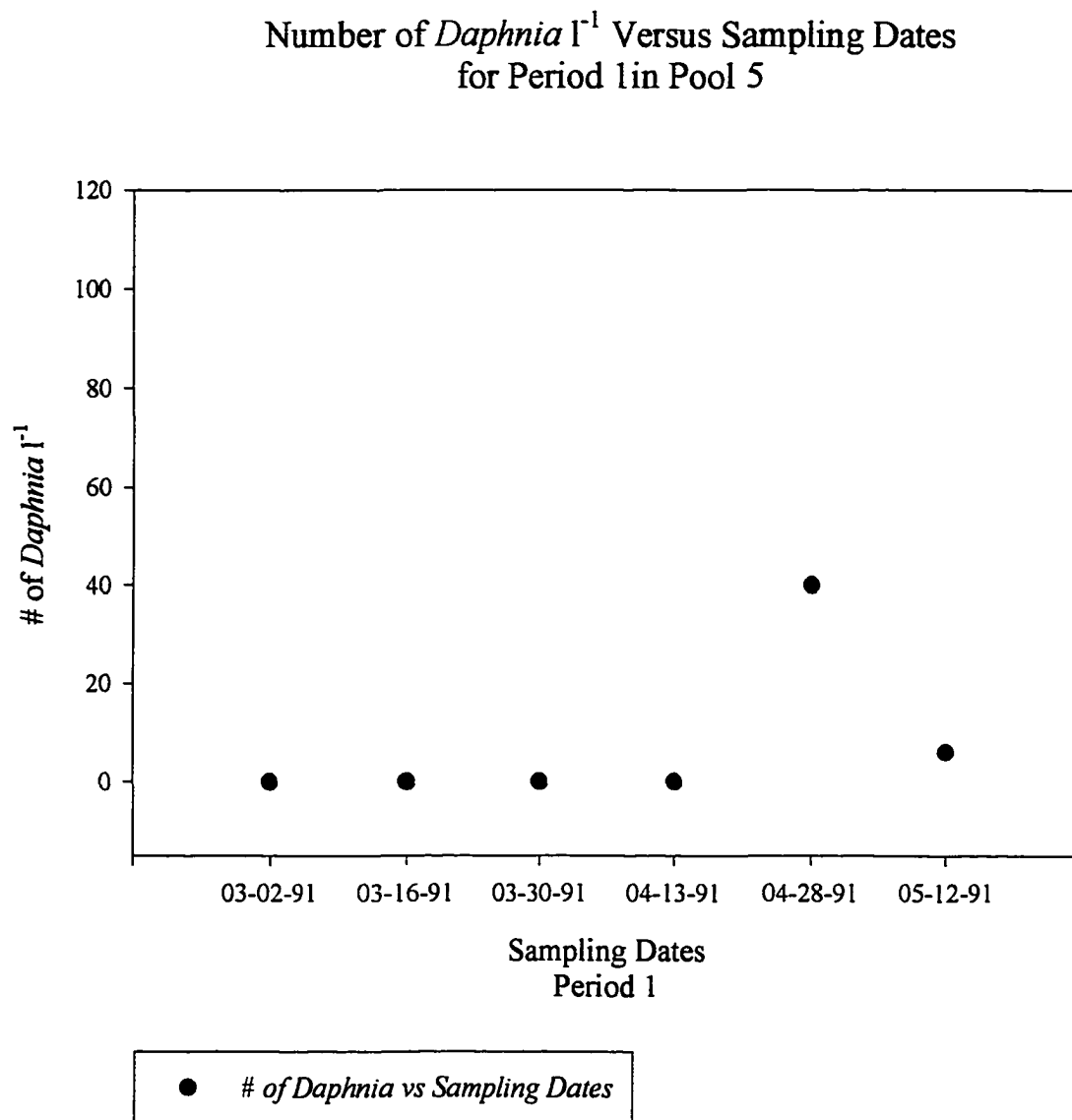


Figure 119: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 1 in Pool 5, with individual data points as shown.

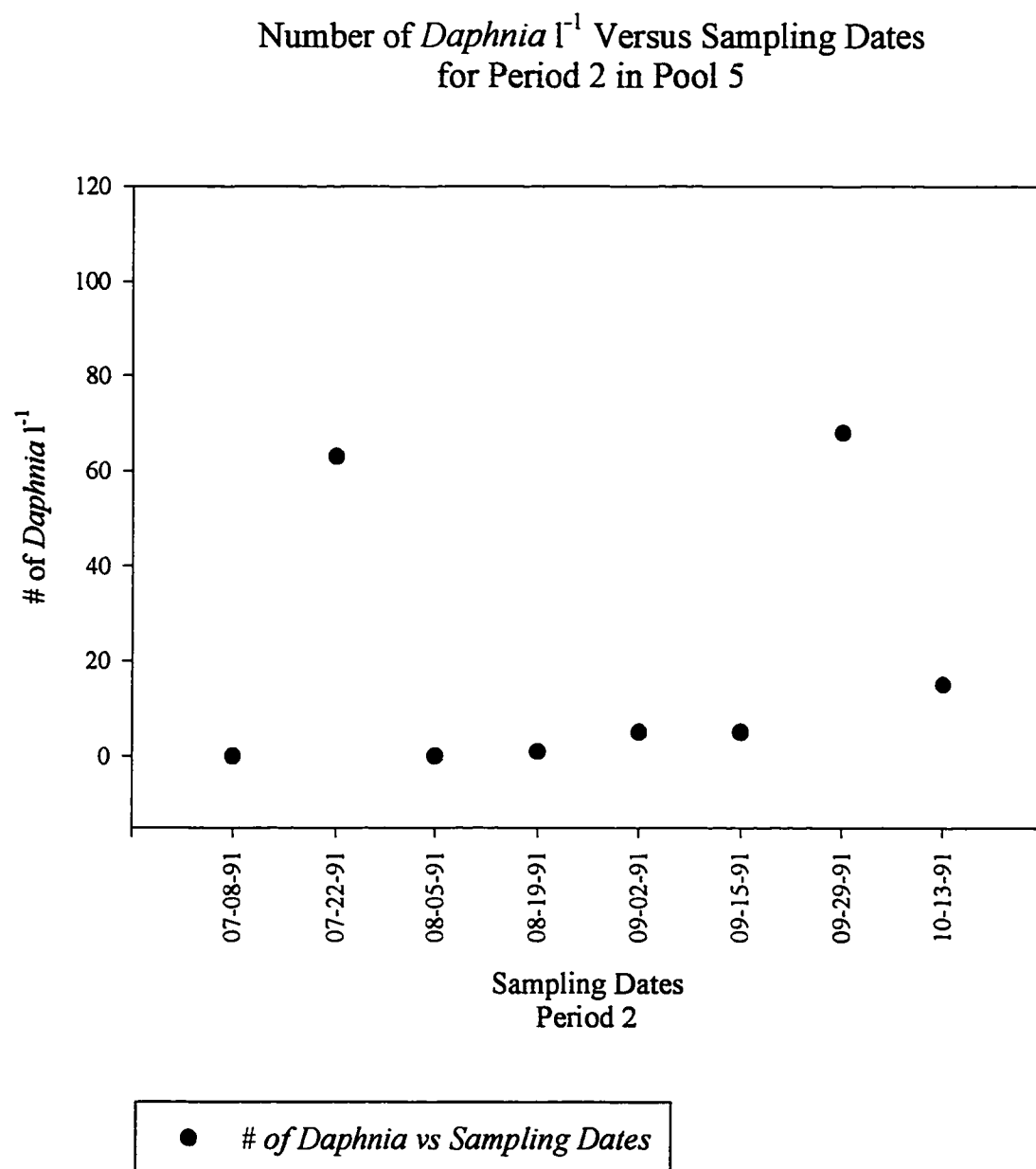


Figure 120: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 2 in Pool 5, with individual data points as shown.

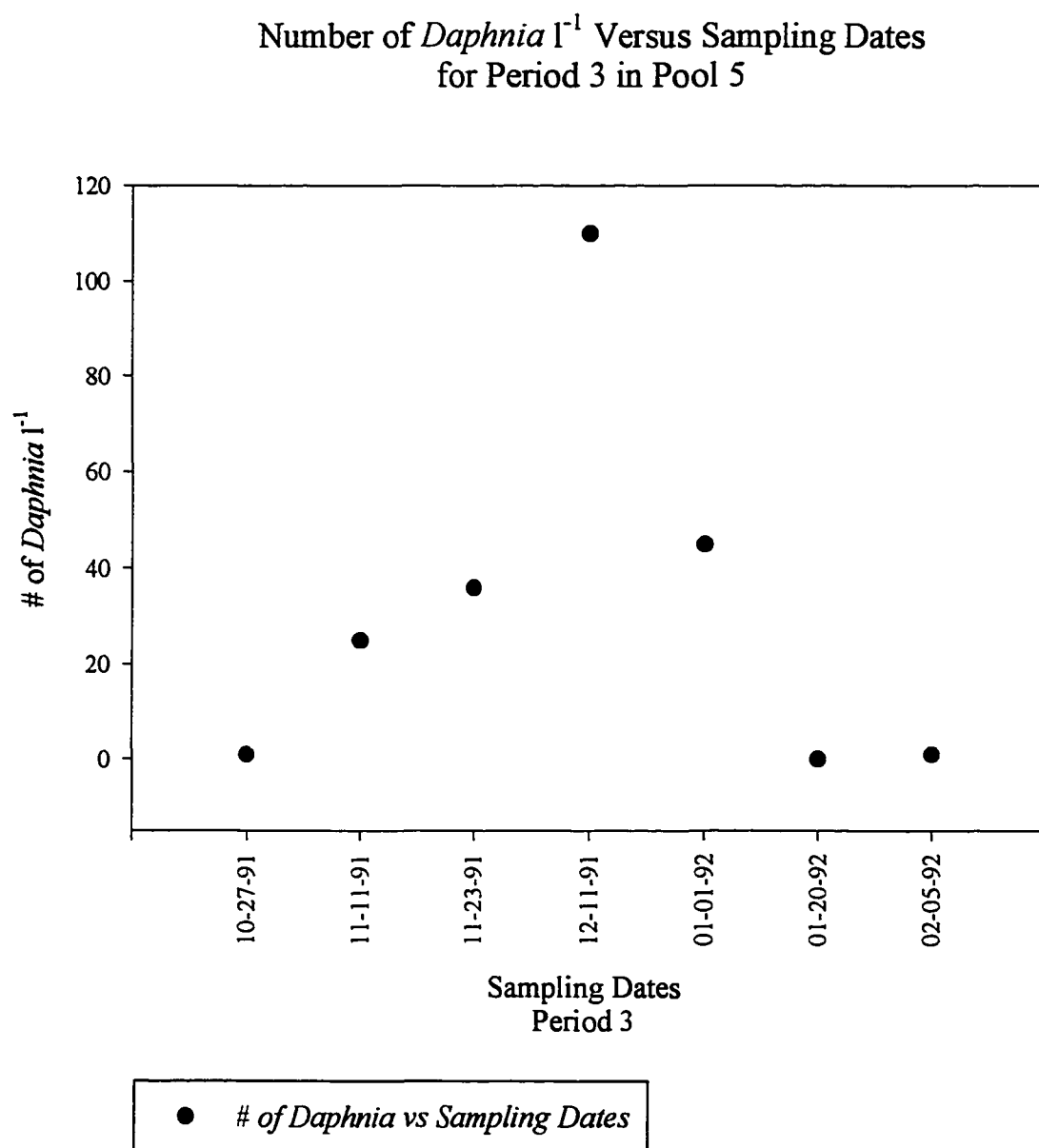


Figure 121: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 3 in Pool 5, with individual data points as shown.

Number of *Daphnia* l⁻¹ Versus Sampling Weeks
for all Three Periods in Pool 5

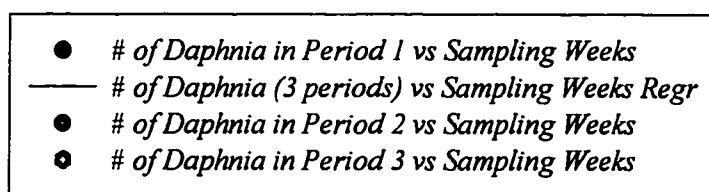
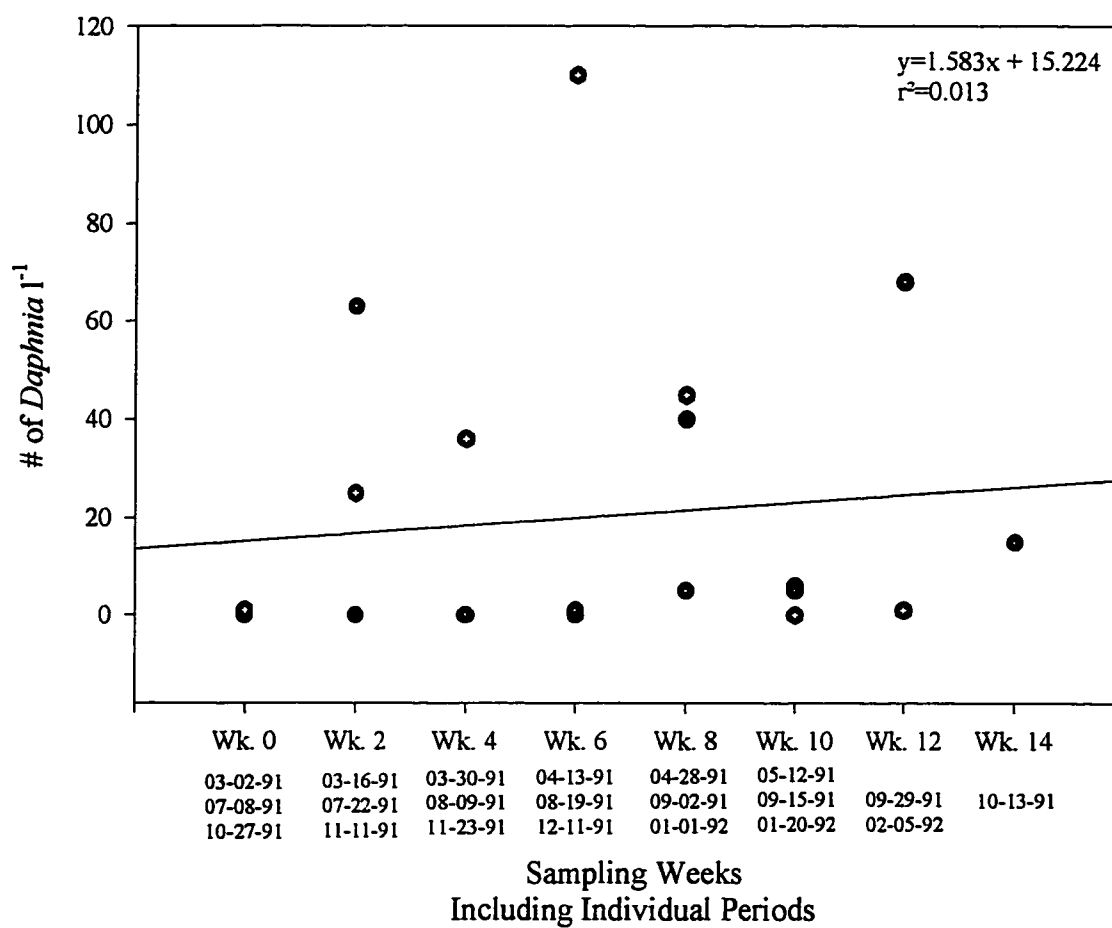


Figure 122: Relationship of the number of *Daphnia* l⁻¹, pooled for three periods, versus sampling weeks in Pool 5, with individual data points and regression as shown.

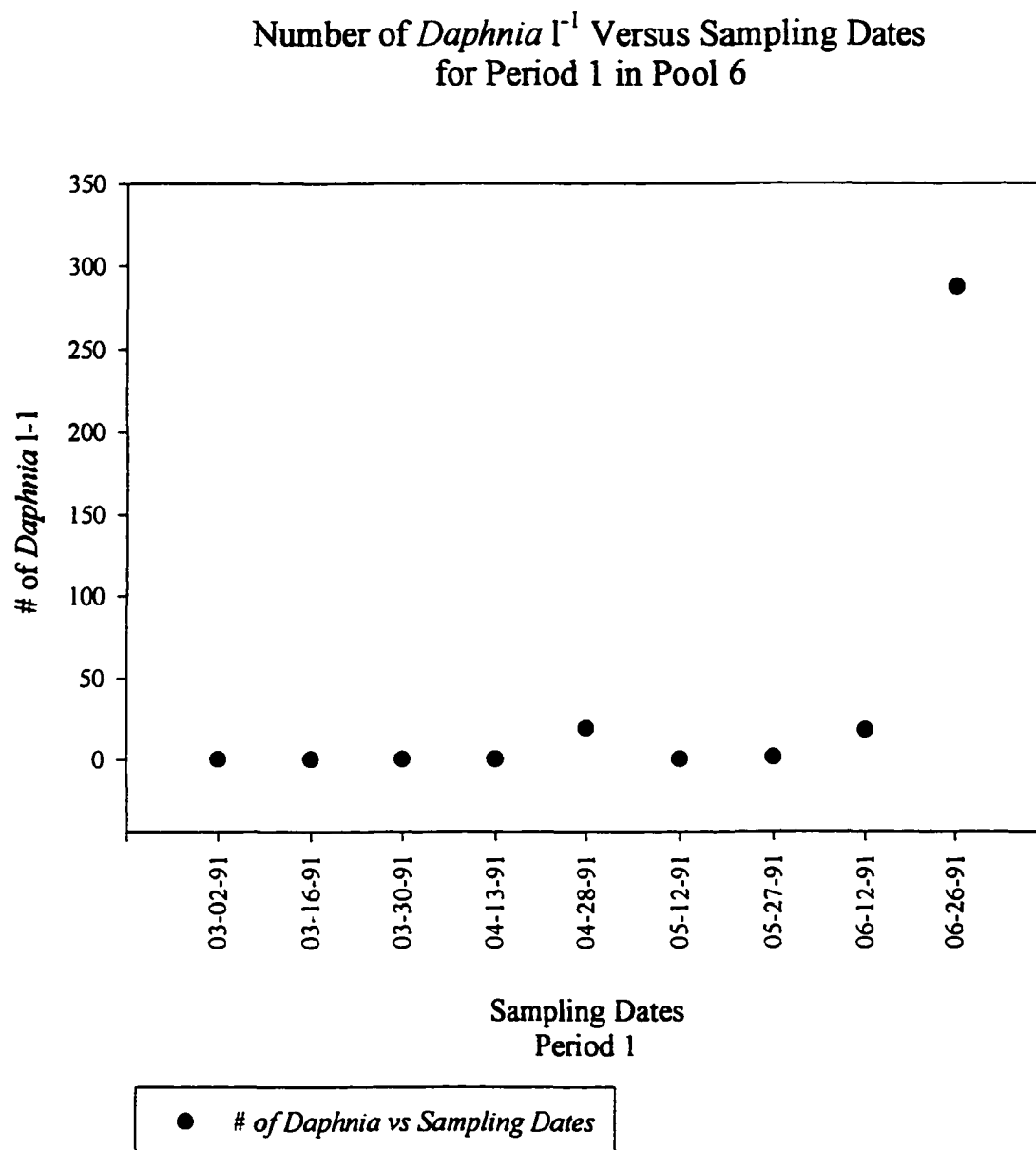


Figure 123: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 1 in Pool 6, with individual data points as shown.

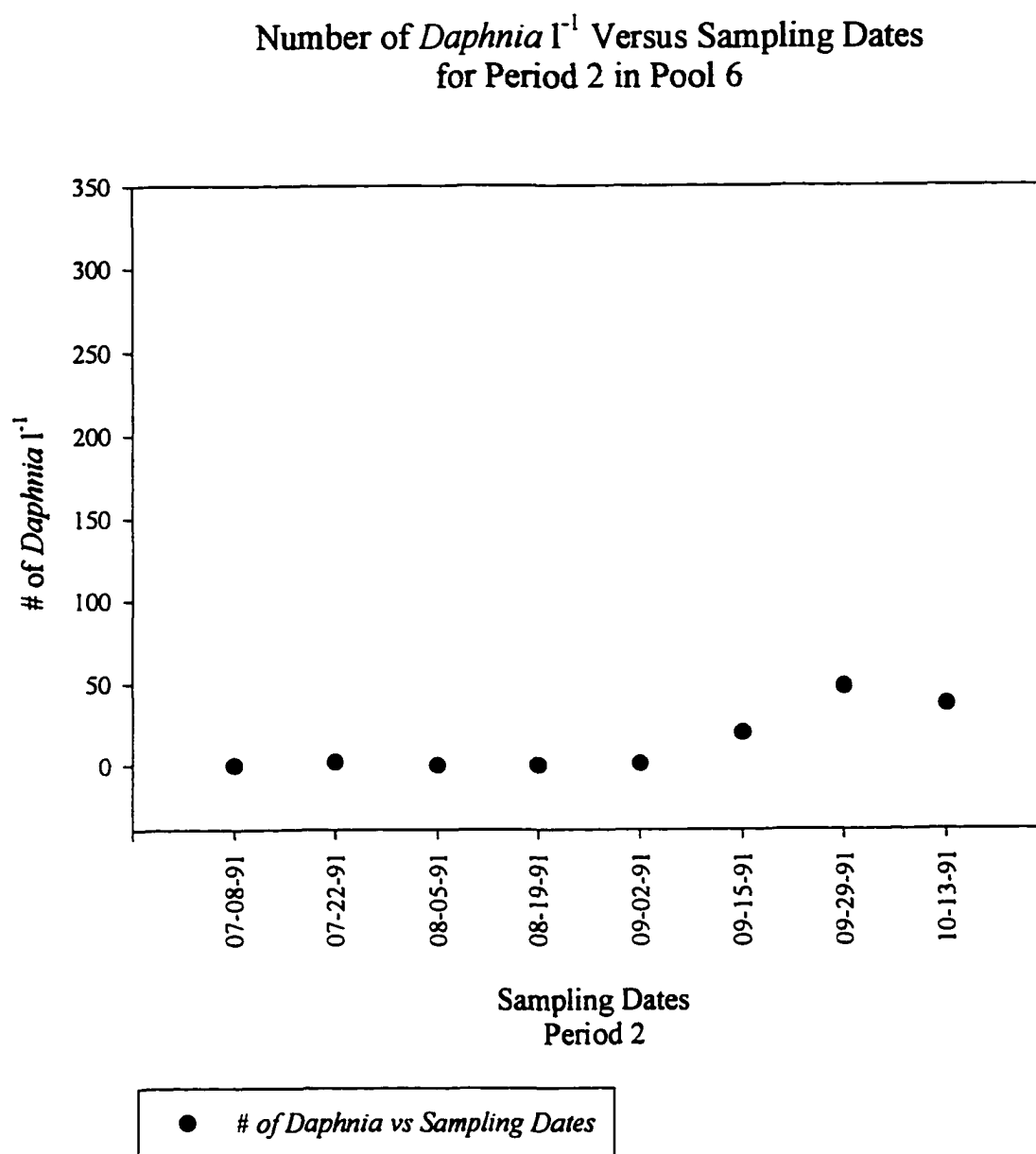


Figure 124: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 2 in Pool 6, with individual data points as shown.

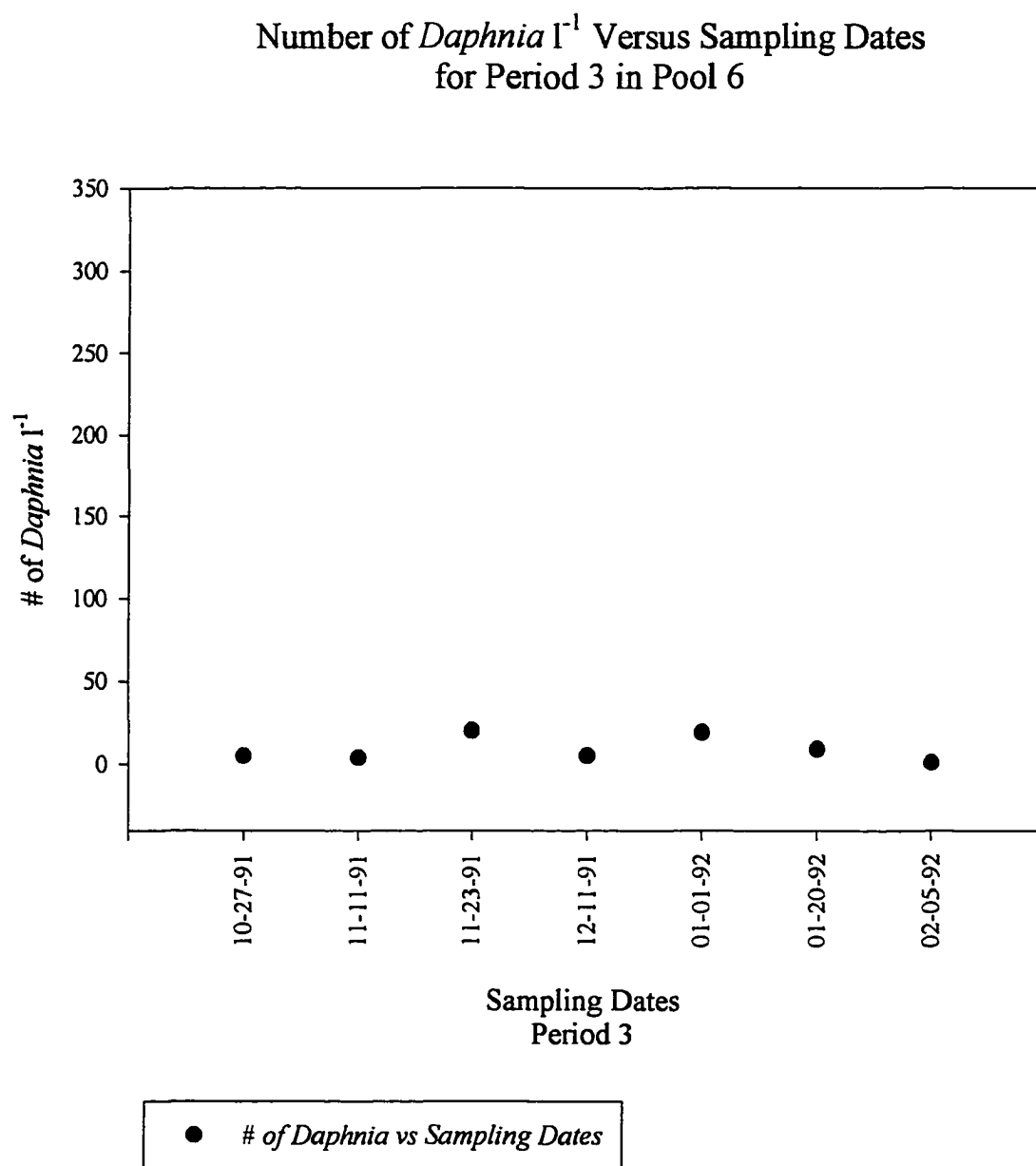


Figure 125: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 3 in Pool 6, with individual data points as shown.

Number of *Daphnia* l⁻¹ Versus Sampling Weeks
for all Three Periods in Pool 6

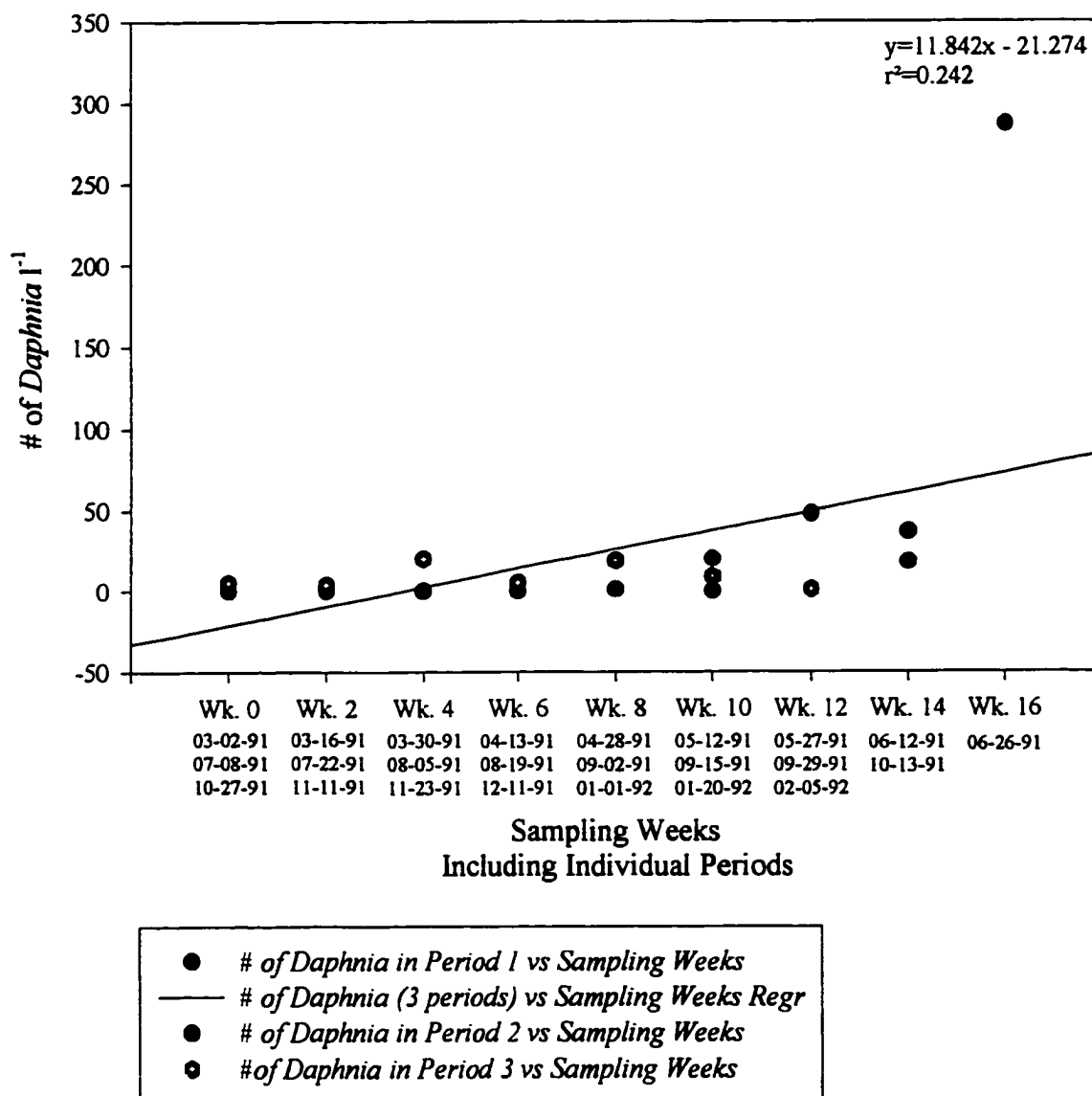


Figure 126: Relationship of the number of *Daphnia* l⁻¹, pooled for three periods, versus sampling weeks in Pool 6, with individual data points and regression as shown.

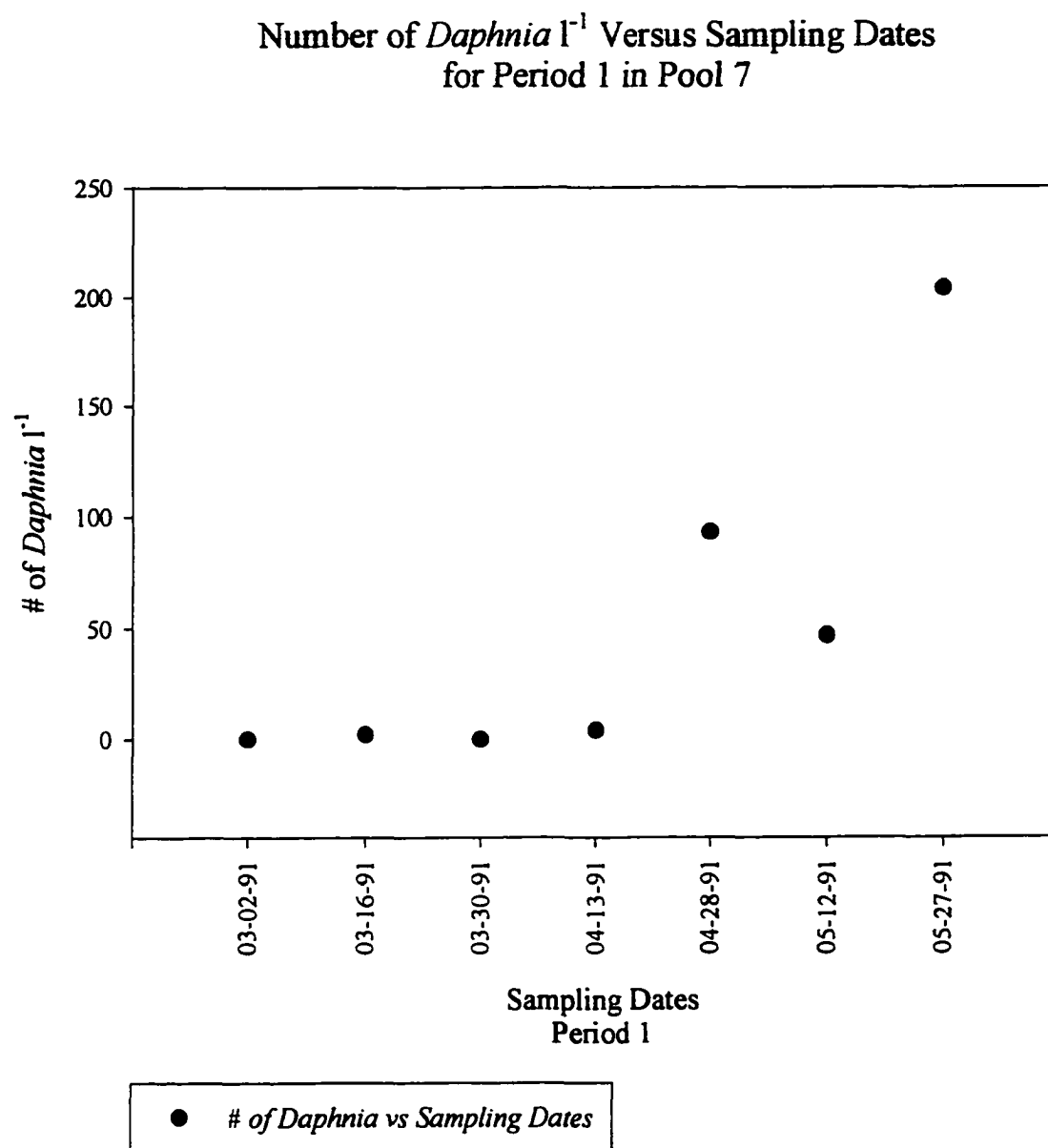


Figure 127: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 1 in Pool 7, with individual data points as shown.

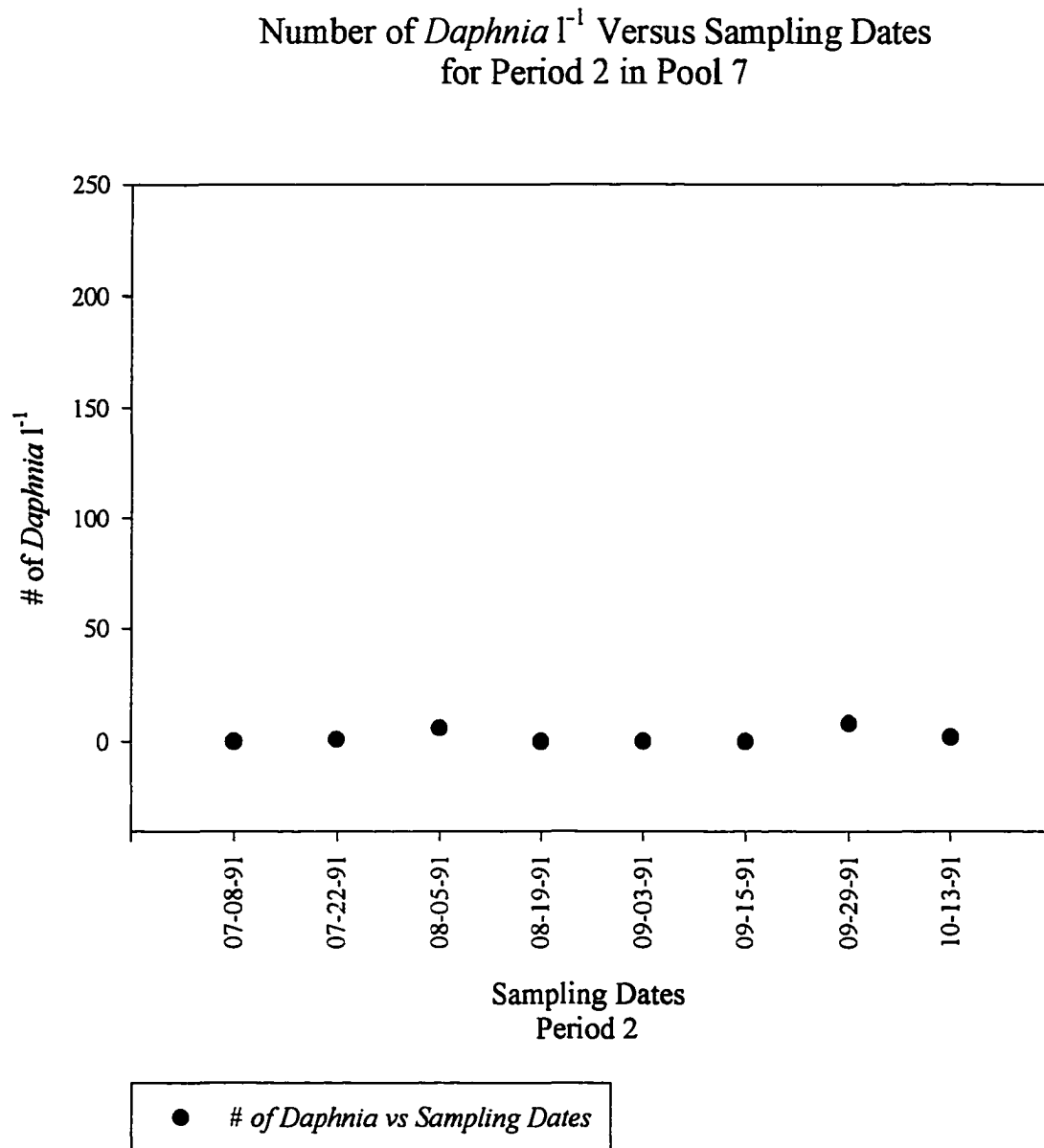


Figure 128: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 2 in Pool 7, with individual data points as shown.

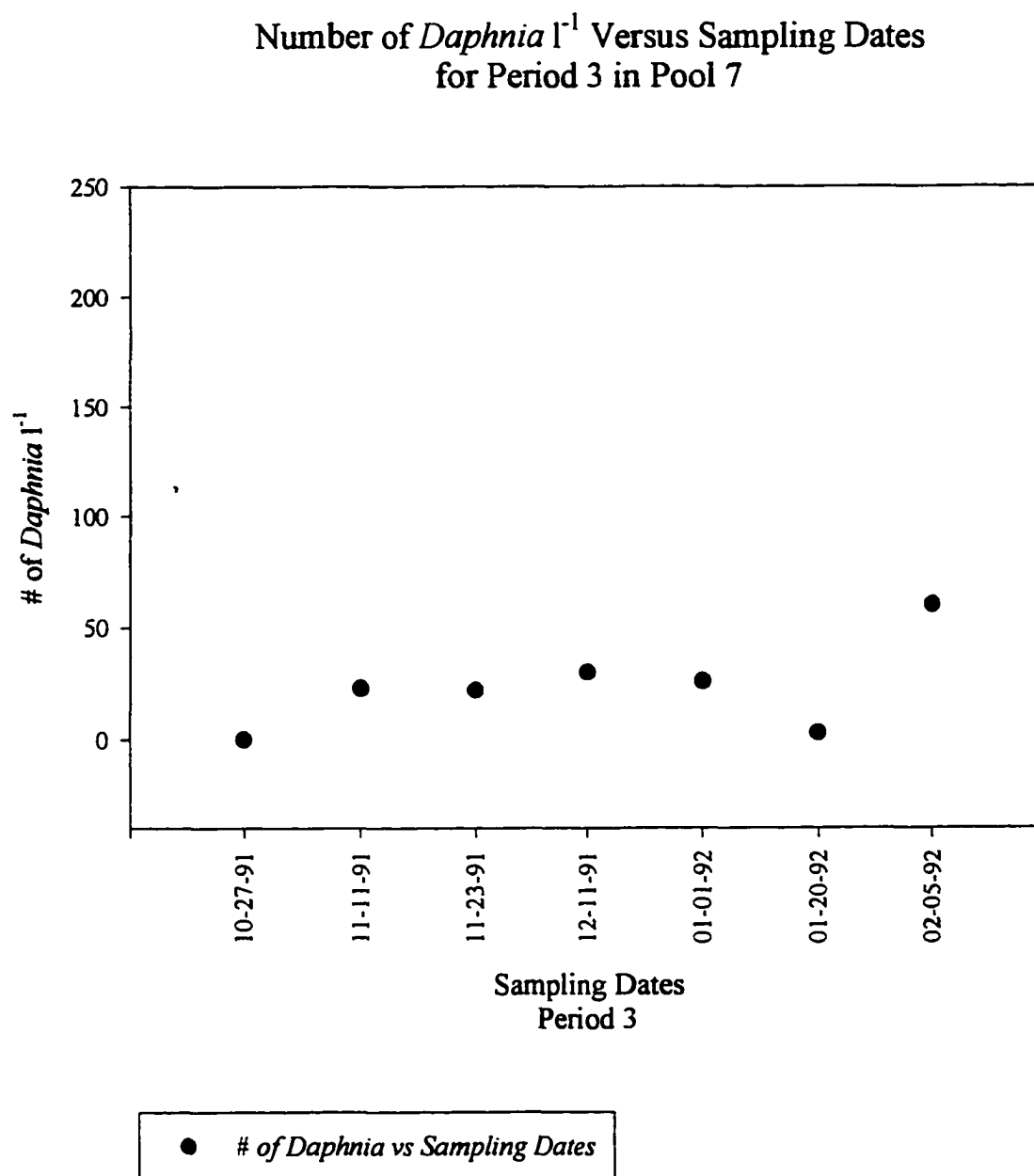


Figure 129: Relationship of the number of *Daphnia* l⁻¹ versus sampling dates for period 3 in Pool 7, with individual data points as shown.

Number of *Daphnia* l⁻¹ Versus Sampling Weeks
for all Three Periods in Pool 7

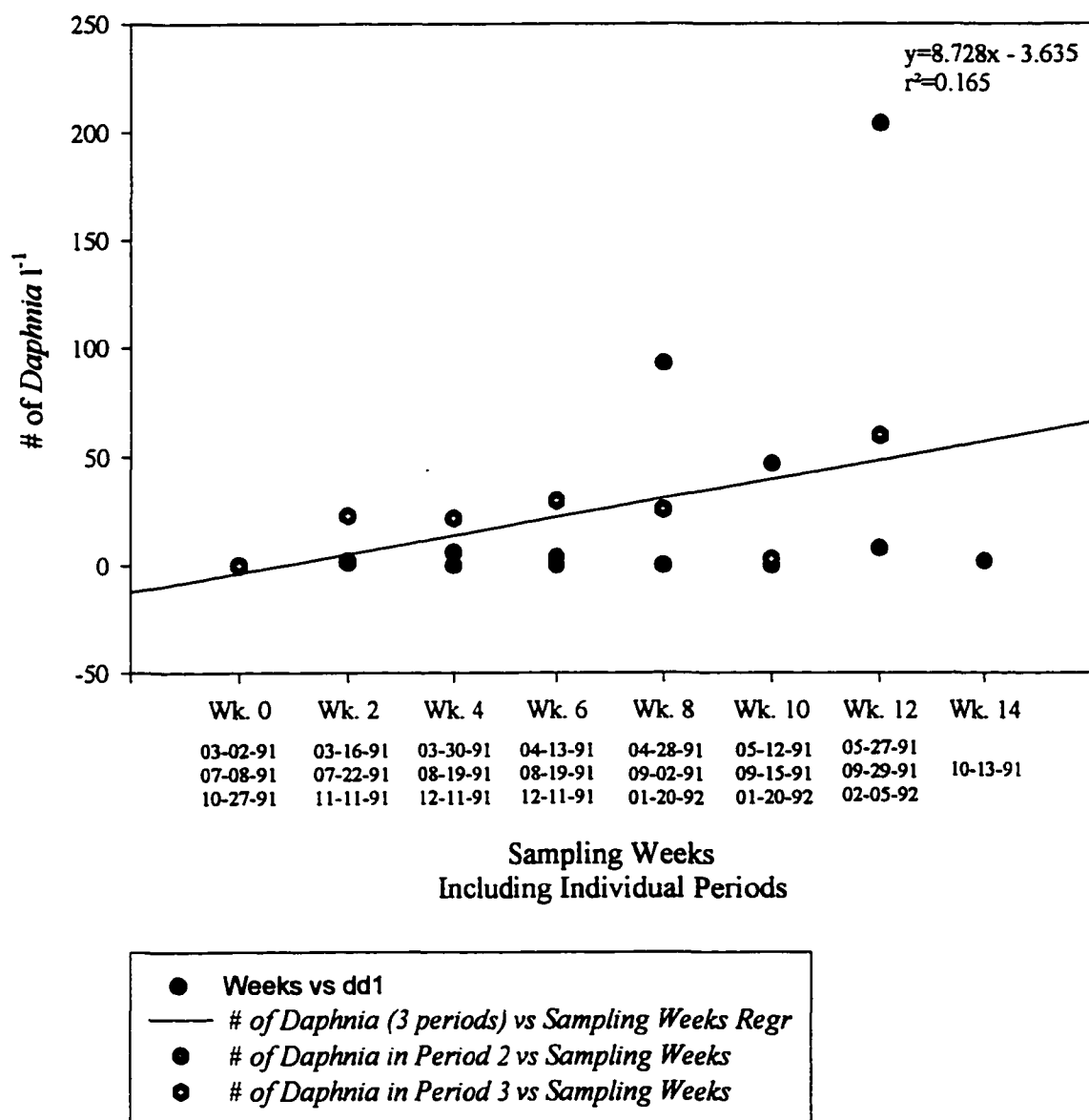


Figure 130: Relationship of the number of *Daphnia* l⁻¹, pooled for three periods, versus sampling weeks in Pool 7, with individual data pints and regression as shown.

these factors, including depth, temperature, oxygen, pH and conductivity, has been explored and discussed above. Each has been dismissed individually, but might be operating in concert. Multiple statistics were not performed because data are relatively low, and for good environmental reasons, without replication.

CONCLUSIONS

When I began this study I expected to find correlations between *Daphnia* population dynamics and abiotic factors (oxygen saturation, temperature, pH, conductivity and the depths of the pools) as has been found in the literature. However, in the Red Rock tinajas these factors appear to have little or no effect on the number of daphnids present on any given sampling date. That is not to say that the various Cladocera are independent of these physical factors; it is just that single factors cannot explain the behaviors of the cladocerans, although temperature appears to affect which cladoceran is present during any particular season. The complexity of the environment with its rigorous and stressful features is effectively exploited by the daphnids without reference to a single or paired environmental factor as explored above.

Further, while I expected to find a direct correlation between duration of the pools and numbers of daphnids present, here again, the temporal longevity of the pool did not appear to explain the *Daphnia* densities. Other factors such as preferred temperature regimes of the two different daphnid species, as well as possible interference and competition from another cladoceran, *Moina*, may complicate the findings. Clearly effectors of the wax and wane of populations exist as can be seen from the consistent seasonality of *D. obtusa* which predominates in spring, *Moina* which predominates in mid-summer, and *D. pulex* which predominates in late summer, although some of the factors may be endogenous. In an environment with such an extreme seasonal irregularity, there can be no annual reliance by cladocerans upon particular timing of seasonal

temperatures, and particularly of precipitation.

Accurate monitoring of precipitation at the sampling site was not possible because precipitation as measured at the Red Rock Weather Station on the bajada, about one km away from the pools, had little relationship to the depths of the pools. On July 8, 1991 and October 13, 1991, as previously discussed, I observed water everywhere indicating recent precipitation with pools overflowing and a river of water rushing down through the wash, yet no precipitation was recorded at the Red Rock Weather Station. On March 3, 1992, the Red Rock Weather Station did record precipitation with related filling of the pools. Precipitation on this date may have been more widespread and uniform than in the preceeding July and October deluge events. Future studies would be greatly enhanced by on site measurement of precipitation, but this is a national conservation area and gaining permission might be difficult. Also this is a very popular, highly used, recreation area with possible disturbance of any equipment left unattended.

While this is a preliminary study, and basic seasonal patterns exist, it is clear that to truly understand the intricacies of the dynamics of these *Daphnia*, a more closely arrayed sampling regimen is necessary, perhaps weekly or biweekly. These populations are subjected to unpredictable deluges, and populations which I found at or near maximum were washed away by flooding two weeks later. Even without accurate recording of precipitation, more frequent measurements of the depths of these pools would be an indication of deluge events that might not be witnessed otherwise.

Pools may have to be monitored for several years in order to determine true annual patterns of precipitation and temperatures, with accompanying flooding or drought, and

the effect of these patterns on population dynamics of the cladoceran inhabitants.

Although cladocerans are well adapted to these extreme conditions, they are decimated in one pool after another during deluge or drought, and have to restart their populations either by hatching of ephippia, or by reintroduction from another pool up the wash during periods of flooding. These unique organisms subsist under the most rigorous conditions in this truly ephemeral desert habitat, and are able to take advantage of brief periods of satisfactory conditions with large population explosions and the production of ephippia in order to persist until conditions again become favorable.

One problem to be considered for future research is in respect to sampling procedures. These pools are too small and too shallow for the use of a plankton tow net. By obtaining discrete samples from midpoint in each pool, a simple random sample is not obtained. These discrete samples may grossly over- or underestimate the true population size (Wetzel and Likens 1991). Taking 500 ml samples with a bottle attached to a pole from more than one spot in larger pools is more effective sampling than taking a single sample. It is difficult to know if sampling locations in each pool are biased because daphnids may be present in greater numbers in an area not sampled, such as near the bottom or edges of the pool. Also each time a sample is taken the population is reduced, which is not sound, ecologically speaking. Particularly in small, shallow pools, a tenth or more of the already taxed population may be removed with each sample. Every time a sample is taken the population clock is reset. Yet if samples were counted and then returned, the next sample might resample the same individuals. The problem becomes one of statistics versus ecology.

APPENDIX I

INSECT SPECIES PRESENT IN THE SEVEN POOLS DURING THE SAMPLING YEAR

ORDER	FAMILY	GENUS	SPECIES	COMMON NAME
Ephemeroptera	Leptophlebiidae			Mayfly larva
Odonata (Suborder Zygoptera)				Damselfly larva
Odonata (Suborder Anisoptera)				Dragonfly larva
Plecoptera				Stonefly larva
Thysanoptera	Thripidae			Thrips
Hemiptera	Notonectidae	<i>Notonecta</i>	<i>unifaciata</i>	Back swimmer
Homoptera	Cicadellidae			Leafhopper
Homoptera	Psyllidae			Jumping Plant Lice
Coleoptera	Chrysomelidae	<i>Agasicles</i>	sp.	Flea beetle
Coleoptera	Dytiscidae			Predacious diving beetle
Trichoptera	Limnephilidae	<i>Limnephilus</i>	sp.	Caddisfly larva
Diptera	Chironomidae	<i>Chironomus</i>	sp.	Midge larva
Diptera	Culicidae	<i>Culiseta</i>	<i>incidens</i>	Mosquito larva
Diptera	Culicidae	<i>Aedes</i>	<i>vexans</i>	Mosquito larva
Diptera	Dixidae			Dixid midge
Diptera	Tabanidae	<i>Tabanus</i>	sp.	Deer/horse fly larva

APPENDIX II

COUNT DATA FOR POOL 1 ON EACH SAMPLING DATE

Date	D. pulex	D. obtusa	* <i>Moin</i> <i>a</i> spp	<i>Daphnia</i> ephippia	smallest ovig. female in mm	*eggs in sample
03-02-91	0	0	0	0	0	0
03-16-91	0	0	0	0	0	0
03-30-91	0	0	0	0	0	0
04-13-91	0	0	0	0	0	0
04-28-91	0	1	0	0	0	0
05-12-91	0	10	0	0	1.3	4
05-27-91	0	5	0	0	0	0
06-12-91	0	2	0	0	0	0
06-26-91	1	2	268	25	1.5	3
07-08-91	1	0	0	0	0	0
07-22-91	0	0	118	0	0	0
08-05-91	5	4	72	2	1.6	7
08-19-91	0	0	1	0	0	0
09-02-91	0	0	12	1	0	0
09-15-91	0	0	0	0	0	0
09-29-91	12	0	0	2	0	0
10-13-91	13	0	1	1	0	0
10-27-91	1	0	0	0	0	0
11-11-91	1	0	0	0	0	0
11-23-91	0	0	0	0	0	0
12-11-91	21	0	0	0	1.7	10
01-01-92	26	6	0	1	0	0
01-20-92	0	1	0	1	0	0
02-05-92	0	0	0	0	0	0
03-01-92	0	3	0	0	0	0
03-15-92	0	0	0	0	0	0
Totals/yr	81	34	472	33	--	24

* Number of ephippia and eggs present in samples for each pool include those in individuals as well as loose ephippia and eggs.

COUNT DATA FOR POOL 2 ON EACH SAMPLING DATE

Date	<i>D. pulex</i>	<i>D. obtusa</i>	<i>Moina spp</i>	<i>Daphnia ephippia</i>	smallest ovig. fem. in mm	eggs in sample
03-02-91	1	0	0	0	0	0
03-16-91	0	0	0	0	0	0
03-30-91	0	0	0	0	0	0
04-13-91	0	0	0	0	0	0
04-28-91	0	2	0	0	0	0
05-12-91	DRY					
05-27-91	DRY					
06-12-91	DRY					
06-26-91	DRY					
07-08-91	0	0	0	0	0	0
07-22-91	0	0	26	0	0	0
08-05-91	0	0	6	0	0	0
08-19-91	0	0	12	0	0	0
09-02-91	0	0	13	0	0	0
09-15-91	0	0	2	0	0	0
09-29-91	3	0	17	1	1.2	3
10-13-91	DRY					
10-27-91	0	0	0	0	0	0
11-11-91	0	0	0	0	0	0
11-23-91	0	0	0	0	0	0
12-11-91	0	5	0	0	1.9	10
01-01-92	8	0	0	0	0	0
01-20-92	0	1	0	0	0	0
02-05-92	1	0	1	0	0	0
03-01-92	0	0	0	0	0	0
03-15-92	0	0	0	0	0	0
Totals/yr	13	8	77	1	--	13

COUNT DATA FOR POOL 3 ON EACH SAMPLING DATE

Date	<i>D. pulex</i>	<i>D. obtusa</i>	<i>Moina</i> spp	<i>Daphnia</i> ephippia	smallest ovig. fem. in mm	eggs in sample
03-02-91	0	0	0	0	0	0
03-16-91	0	0	0	0	0	0
03-30-91	0	1	0	0	0	0
04-13-91	0	0	0	0	0	0
04-28-91	0	89	0	2	0	0
05-12-91	DRY					
05-27-91	DRY					
06-12-91	DRY					
06-26-91	DRY					
07-08-91	0	0	0	0	0	0
07-22-91	0	0	22	2	0	0
08-05-91	0	0	5	0	0	0
08-19-91	0	0	4	0	0	0
09-02-91	2	7	23	0	0	0
09-15-91	4	0	2	0	0	0
09-29-91	43	0	0	0	1.6	2
10-13-91	DRY					
10-27-91	1	0	0	0	0	0
11-11-91	119	0	0	0	2.1	180
11-23-91	80	11	0	1	1.9	3
12-11-91	44	0	0	3	0	1
01-01-92	40	0	0	9	2.0	3
01-20-92	1	0	0	0	0	0
02-05-92	4	0	0	0	2.6	35
03-01-92	0	8	0	0	0	0
03-15-92	0	0	0	0	0	0

COUNT DATA FOR POOL 4 ON EACH SAMPLING DATE

Date	<i>D. pulex</i>	<i>D. obtusa</i>	<i>Moina</i> spp	<i>Daphnia</i> ephippia	smallest ovig. fem. in mm	eggs in sample
03-02-91	0	0	0	0	0	0
03-16-91	0	0	0	0	0	0
03-30-91	0	0	0	0	0	0
04-13-91	0	1	0	0	0	0
04-28-91	3	295	0	1	1.3	140
05-12-91	DRY					
05-27-91	DRY					
06-12-91	0	3	1	0	0	0
06-26-91	DRY					
07-08-91	0	0	0	0	0	0
07-22-91	0	0	135	0	0	0
08-05-91	0	0	18	0	0	0
08-19-91	0	0	41	1	0	0
09-02-91	56	8	21	0	1.0	8
09-15-91	54	9	0	0	0	0
09-29-91	49	0	1	0	0	0
10-13-91	DRY					
10-27-91	1	0	0	0	0	0
11-11-91	41	0	0	0	1.9	61
11-23-91	9	0	0	0	0	0
12-11-91	13	0	0	2	0	0
01-01-92	7	0	0	24	0	0
01-20-92	0	0	0	0	0	0
02-05-92	12	0	0	0	2.2	17
03-01-92	0	0	0	1	0	0
03-15-92	0	0	0	0	0	0
Totals/yr	228	315	217	29	--	226

COUNT DATA FOR POOL 5 ON EACH SAMPLING DATE

Date	<i>D. pulex</i>	<i>D. obtusa</i>	<i>Moina</i> spp	<i>Daphnia</i> ephippia	smallest ovig. fem. in mm	eggs in sample
03-02-91	0	0	0	0	0	0
03-16-91	0	0	0	0	0	0
03-30-91	0	0	0	0	0	0
04-13-91	0	0	0	0	0	0
04-28-91	0	40	0	3	1.7	31
05-12-91	0	6	0	0	0	0
05-27-91	DRY					
06-12-91	0	251	27	0	1.1	130
06-26-91	DRY					
07-08-91	0	0	1	0	0	0
07-22-91	0	16	63	1	0	0
08-05-91	0	0	36	0	0	0
08-19-91	0	1	0	0	0	0
09-02-91	4	1	1	0	0	0
09-15-91	5	0	0	0	0	0
09-29-91	68	0	0	2	1.3	5
10-13-91	15	0	0	1	1.6	4
10-27-91	1	0	0	0	0	0
11-11-91	25	0	0	0	1.9	33
11-23-91	36	0	0	0	0	0
12-11-91	90	20	0	3	1.9	4
01-01-92	45	0	0	9	1.6	12
01-20-92	0	0	0	2	0	0
02-05-92	1	0	0	0	0	0
03-01-92	0	0	0	1	0	0
03-15-92	0	0	0	0	0	0

COUNT DATA FOR POOL 6 ON EACH SAMPLING DATE

Date	<i>D. pulex</i>	<i>D. obtusa</i>	<i>Moina</i> spp	<i>Daphnia</i> ephippia	smallest ovig. fem. in mm	eggs in sample
03-02-91	0	0	0	0	0	0
03-16-91	0	0	0	0	0	0
03-30-91	0	0	0	0	0	0
04-13-91	0	0	0	0	0	0
04-28-91	0	19	0	0	0	0
05-12-91	0	0	0	0	0	0
05-27-91	1	0	1	4	1.7	6
06-12-91	0	18	1	1	1.6	11
06-26-91	287	0	308	40	1.8	10
07-08-91	0	0	0	0		0
07-22-91	0	2	8	0	0	0
08-05-91	0	0	1	1	0	0
08-19-91	0	0	0	4	0	0
09-02-91	1	0	7	0	0	0
09-15-91	20	0	0	2	0	0
09-29-91	48	0	0	5	1.3	5
10-13-91	37	0	0	0	0	0
10-27-91	5	0	0	1	0	0
11-11-91	4	0	0	0	0	0
11-23-91	20	0	0	0	0	0
12-11-91	2	3	0	0	0	0
01-01-92	2	17	0	0	0	0
01-20-92	7	2	0	2	1.3	4
02-05-92	1	0	0	0	0	0
03-01-92	0	0	0	1	0	0
03-15-92	0	0	0	0	0	0
Totals/yr	435	59	326	61	--	36

COUNT DATA FOR POOL 7 ON EACH SAMPLING DATE

Date	<i>D. pulex</i>	<i>D. obtusa</i>	<i>Moina</i> spp	<i>Daphnia</i> ephippia	smallest ovig. fem. in mm	eggs in sample
03-02-91	0	0	0	0	0	0
03-16-91	0	1	0	0	1.3	5
03-30-91	0	0	0	0	0	0
04-13-91	0	1	0	0	0	0
04-28-91	0	93	0	2	1.0	7
05-12-91	0	47	0	1	0	0
05-27-91	0	204	0	11	0.8	590
06-12-91	DRY					
06-26-91	DRY					
07-08-91	0	0	0	0	0	0
07-22-91	0	1	2	0	0	0
08-05-91	0	6	7	3	0	0
08-19-91	0	0	0	4	0	0
09-02-91	0	0	1	0	0	0
09-15-91	0	0	0	6	0	0
09-29-91	8	0	0	0	0	0
10-13-91	2	0	0	5	0	0
10-27-91	0	0	0	0	0	0
11-11-91	23	0	0	0	1.2	28
11-23-91	10	12	0	3	0	0
12-11-91	14	16	0	0	0	0
01-01-92	23	3	0	2	1.6	7
01-20-92	2	1	0	0	0	0
02-05-92	0	60	3	0	0	0
03-01-92	0	0	0	0	0	2
03-15-92	0	0	0	0	0	0
Totals/yr	82	445	13	37	--	627

APPENDIX III

DAPHNIA LENGTHS IN MM AND BROOD SIZE FOR POOL 1 DURING SAMPLING YEAR

Date	Length in mm	^a Eggs	Species
04-28-91	0.7	0	<i>D. obutsa</i>
05-12-91	0.5	0	<i>D. obutsa</i>
05-12-91	0.5	0	<i>D. obutsa</i>
05-12-91	0.7	0	<i>D. obutsa</i>
05-12-91	1.2	0	<i>D. obutsa</i>
05-12-91	1.3	1	<i>D. obutsa</i>
05-12-91	1.3	1	<i>D. obutsa</i>
05-12-91	1.3	2	<i>D. obutsa</i>
05-12-91	1.4	0	<i>D. obutsa</i>
05-12-91	1.4	0	<i>D. obutsa</i>
05-12-91	1.4	0	<i>D. obutsa</i>
05-27-91	0.8	0	<i>D. obutsa</i>
05-27-91	0.9	0	<i>D. obutsa</i>
05-27-91	1.0	0	<i>D. obutsa</i>
05-27-91	1.1	0	<i>D. obutsa</i>
05-27-91	1.1	0	<i>D. obutsa</i>
06-12-91	0.5	0	<i>D. obutsa</i>
06-12-91	0.8	0	<i>D. obutsa</i>
06-12-91	1.0	0	<i>D. obutsa</i>
06-27-91	1.4	0	<i>D. obutsa</i>
06-27-91	1.5	3	<i>D. pulex</i>
07-08-91	1.7	0	<i>D. pulex</i>
08-05-91	0.5	0	<i>D. obutsa</i>
08-05-91	0.6	0	<i>D. obutsa</i>
08-05-91	0.8	0	<i>D. obutsa</i>
08-05-91	0.8	0	<i>D. obutsa</i>
08-05-91	0.9	0	<i>D. pulex</i>
08-05-91	1.5	0	<i>D. pulex</i>
08-05-91	1.6	4	<i>D. pulex</i>

^a Loose eggs may have been present during the sampling year, besides those found in the *Daphnia* sampled, in Pool 1. Ehippia were not found in any of the *Daphnia* sampled. However, loose ehippia may have been present during the sampling year in Pool 1.

Date	Length in mm	Eggs	Species
08-05-91	1.6	0	<i>D. pulex</i>
08-05-91	1.7	3	<i>D. pulex</i>
09-29-91	1.1	0	<i>D. pulex</i>
09-29-91	1.1	0	<i>D. pulex</i>
09-29-91	1.2	0	<i>D. pulex</i>
09-29-91	1.2	0	<i>D. pulex</i>
09-29-91	1.2	0	<i>D. pulex</i>
09-29-91	1.3	0	<i>D. pulex</i>
09-29-91	1.3	0	<i>D. pulex</i>
09-29-91	1.3	0	<i>D. pulex</i>
09-29-91	1.3	0	<i>D. pulex</i>
09-29-91	1.4	0	<i>D. pulex</i>
09-29-91	1.4	0	<i>D. pulex</i>
09-29-91	1.6	0	<i>D. pulex</i>
10-13-91	1.3	0	<i>D. pulex</i>
10-13-91	1.3	0	<i>D. pulex</i>
10-13-91	1.4	0	<i>D. pulex</i>
10-13-91	1.6	0	<i>D. pulex</i>
10-13-91	1.7	0	<i>D. pulex</i>
10-13-91	1.7	0	<i>D. pulex</i>
10-13-91	1.9	0	<i>D. pulex</i>
10-13-91	2.0	0	<i>D. pulex</i>
10-13-91	2.2	0	<i>D. pulex</i>
10-13-91	2.2	0	<i>D. pulex</i>
10-13-91	2.3	0	<i>D. pulex</i>
10-13-91	2.3	0	<i>D. pulex</i>
10-13-91	2.4	0	<i>D. pulex</i>
10-27-91	1.9	0	<i>D. pulex</i>
11-11-91	1.0	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.7	0	<i>D. pulex</i>
12-11-91	0.8	0	<i>D. pulex</i>
12-11-91	1.0	0	<i>D. pulex</i>
12-11-91	1.0	0	<i>D. pulex</i>
12-11-91	1.0	0	<i>D. pulex</i>
12-11-91	1.0	0	<i>D. pulex</i>

Date	Length in mm	Eggs	Species
12-11-91	1.0	0	<i>D. pulex</i>
12-11-91	1.1	0	<i>D. pulex</i>
12-11-91	1.2	0	<i>D. pulex</i>
12-11-91	1.2	0	<i>D. pulex</i>
12-11-91	2.5	0	<i>D. pulex</i>
12-11-91	2.7	3	<i>D. pulex</i>
12-11-91	3.0	0	<i>D. pulex</i>
01-01-92	1.1	0	<i>D. obutsa</i>
01-01-92	1.1	0	<i>D. obutsa</i>
01-01-92	1.5	0	<i>D. obutsa</i>
01-01-92	1.7	0	<i>D. obutsa</i>
01-01-92	1.8	0	<i>D. obutsa</i>
01-01-92	3.3	0	<i>D. obutsa</i>
01-01-92	0.9	0	<i>D. pulex</i>
01-01-92	1.0	0	<i>D. pulex</i>
01-01-92	1.0	0	<i>D. pulex</i>
01-01-92	1.0	0	<i>D. pulex</i>
01-01-92	1.1	0	<i>D. pulex</i>
01-01-92	1.1	0	<i>D. pulex</i>
01-01-92	1.1	0	<i>D. pulex</i>
01-01-92	1.1	0	<i>D. pulex</i>
01-01-92	1.1	0	<i>D. pulex</i>
01-01-92	1.2	0	<i>D. pulex</i>
01-01-92	1.3	0	<i>D. pulex</i>
01-01-92	1.3	0	<i>D. pulex</i>
01-01-92	1.4	0	<i>D. pulex</i>
01-01-92	1.4	0	<i>D. pulex</i>
01-01-92	1.4	0	<i>D. pulex</i>
01-01-92	1.4	0	<i>D. pulex</i>
01-01-92	1.4	0	<i>D. pulex</i>
01-01-92	1.5	0	<i>D. pulex</i>
01-01-92	1.5	0	<i>D. pulex</i>
01-01-92	1.6	0	<i>D. pulex</i>
01-01-92	1.6	0	<i>D. pulex</i>
01-01-92	1.7	0	<i>D. pulex</i>
01-01-92	1.7	0	<i>D. pulex</i>
01-01-92	1.9	0	<i>D. pulex</i>
01-01-92	2.3	0	<i>D. pulex</i>
01-01-92	2.4	0	<i>D. pulex</i>
01-01-92	2.7	0	<i>D. pulex</i>
01-20-92	2.0	0	<i>D. pulex</i>
03-01-92	1.0	0	<i>D. obutsa</i>
03-01-92	1.1	0	<i>D. obutsa</i>
03-01-92	1.3	0	<i>D. obutsa</i>

***DAPHNIA* LENGTHS IN MM AND BROOD SIZE FOR
POOL 4 DURING SAMPLING YEAR**

[illegible]

* Loose eggs may have been present during the sampling year, besides those found from the *Daphnia* sampled, in Pool 4. Ehippia were not found in any of the *Daphnia* sampled. However, loose ehippia may have been present during the sampling year in Pool 4.

[illegible]

[illegible]

Date	Length in mm	Eggs	Species
04-28-91	0.8	0	<i>D. obtusa</i>
04-28-91	0.9	0	<i>D. obtusa</i>
04-28-91	1.0	0	<i>D. obtusa</i>
04-28-91	1.0	0	<i>D. obtusa</i>
04-28-91	1.0	0	<i>D. obtusa</i>
04-28-91	1.0	0	<i>D. obtusa</i>
04-28-91	1.0	0	<i>D. obtusa</i>
04-28-91	1.0	0	<i>D. obtusa</i>
04-28-91	1.0	0	<i>D. obtusa</i>
04-28-91	1.1	0	<i>D. obtusa</i>
04-28-91	1.3	1	<i>D. obtusa</i>
04-28-91	1.3	1	<i>D. obtusa</i>
04-28-91	1.4	0	<i>D. obtusa</i>
04-28-91	1.4	1	<i>D. obtusa</i>
04-28-91	1.5	0	<i>D. obtusa</i>
04-28-91	1.5	0	<i>D. obtusa</i>
04-28-91	1.6	2	<i>D. obtusa</i>
04-28-91	1.7	0	<i>D. obtusa</i>
04-28-91	1.7	0	<i>D. obtusa</i>
04-28-91	1.7	0	<i>D. obtusa</i>
04-28-91	1.7	0	<i>D. obtusa</i>
04-28-91	1.7	2	<i>D. obtusa</i>
04-28-91	1.7	7	<i>D. obtusa</i>
04-28-91	1.7	8	<i>D. obtusa</i>
04-28-91	1.8	0	<i>D. obtusa</i>
04-28-91	1.8	0	<i>D. obtusa</i>
04-28-91	1.8	6	<i>D. obtusa</i>
04-28-91	1.9	0	<i>D. obtusa</i>
04-28-91	1.9	2	<i>D. obtusa</i>
04-28-91	2.0	0	<i>D. obtusa</i>
04-28-91	2.0	6	<i>D. obtusa</i>
04-28-91	2.0	6	<i>D. obtusa</i>
04-28-91	2.0	13	<i>D. obtusa</i>
04-28-91	2.0	15	<i>D. obtusa</i>
04-28-91	2.1	4	<i>D. obtusa</i>
04-28-91	2.1	10	<i>D. obtusa</i>
04-28-91	2.5	0	<i>D. obtusa</i>
04-28-91	1.7	3	<i>D. pulex</i>
04-28-91	2.4	0	<i>D. pulex</i>
04-28-91	3.5	0	<i>D. pulex</i>
06-12-91	0.6	0	<i>D. obtusa</i>
06-12-91	0.7	0	<i>D. obtusa</i>
06-12-91	0.9	0	<i>D. obtusa</i>
09-03-91	0.6	0	<i>D. obtusa</i>
09-03-91	0.7	0	<i>D. obtusa</i>

Date	Length in mm	Eggs	Species
09-03-91	0.7	0	<i>D. obtusa</i>
09-03-91	0.7	0	<i>D. obtusa</i>
09-03-91	0.8	0	<i>D. obtusa</i>
09-03-91	0.9	0	<i>D. obtusa</i>
09-03-91	1.5	0	<i>D. obtusa</i>
09-03-91	1.6	0	<i>D. obtusa</i>
09-03-91	0.5	0	<i>D. pulex</i>
09-03-91	0.6	0	<i>D. pulex</i>
09-03-91	0.6	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.7	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.8	0	<i>D. pulex</i>
09-03-91	0.9	0	<i>D. pulex</i>
09-03-91	0.9	0	<i>D. pulex</i>
09-03-91	0.9	0	<i>D. pulex</i>
09-03-91	0.9	0	<i>D. pulex</i>
09-03-91	1.0	0	<i>D. pulex</i>
09-03-91	1.0	2	<i>D. pulex</i>
09-03-91	1.2	0	<i>D. pulex</i>
09-03-91	1.2	0	<i>D. pulex</i>
09-03-91	1.2	0	<i>D. pulex</i>
09-03-91	1.2	0	<i>D. pulex</i>
09-03-91	1.3	0	<i>D. pulex</i>
09-03-91	1.3	0	<i>D. pulex</i>
09-03-91	1.3	0	<i>D. pulex</i>
09-03-91	1.3	1	<i>D. pulex</i>

Date	Length in mm	Eggs	Species
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.6	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.7	0	<i>D. pulex</i>
09-15-91	0.8	0	<i>D. pulex</i>
09-15-91	0.8	0	<i>D. pulex</i>
09-15-91	0.8	0	<i>D. pulex</i>
09-15-91	0.8	0	<i>D. pulex</i>
09-15-91	0.9	0	<i>D. pulex</i>
09-15-91	0.9	0	<i>D. pulex</i>
09-15-91	0.9	0	<i>D. pulex</i>
09-15-91	0.9	0	<i>D. pulex</i>
09-15-91	0.9	0	<i>D. pulex</i>
09-15-91	0.9	0	<i>D. pulex</i>
09-15-91	0.9	0	<i>D. pulex</i>
09-15-91	0.9	0	<i>D. pulex</i>
09-15-91	1.0	0	<i>D. pulex</i>
09-15-91	1.1	0	<i>D. pulex</i>
09-29-91	0.6	0	<i>D. pulex</i>
09-29-91	0.6	0	<i>D. pulex</i>
09-29-91	0.6	0	<i>D. pulex</i>
09-29-91	0.6	0	<i>D. pulex</i>
09-29-91	0.6	0	<i>D. pulex</i>
09-29-91	0.6	0	<i>D. pulex</i>
09-29-91	0.6	0	<i>D. pulex</i>
09-29-91	0.6	0	<i>D. pulex</i>
09-29-91	0.6	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>

Date	Length in mm	Eggs	Species
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.7	0	<i>D. pulex</i>
09-29-91	0.8	0	<i>D. pulex</i>
09-29-91	0.8	0	<i>D. pulex</i>
09-29-91	0.8	0	<i>D. pulex</i>
09-29-91	0.8	0	<i>D. pulex</i>
09-29-91	0.8	0	<i>D. pulex</i>
09-29-91	0.8	0	<i>D. pulex</i>
09-29-91	0.8	0	<i>D. pulex</i>
09-29-91	0.8	0	<i>D. pulex</i>
09-29-91	0.9	0	<i>D. pulex</i>
09-29-91	0.9	0	<i>D. pulex</i>
09-29-91	0.9	0	<i>D. pulex</i>
09-29-91	1.0	0	<i>D. pulex</i>
09-29-91	1.0	0	<i>D. pulex</i>
09-29-91	1.0	0	<i>D. pulex</i>
09-29-91	1.0	0	<i>D. pulex</i>
09-29-91	1.0	0	<i>D. pulex</i>
09-29-91	1.0	0	<i>D. pulex</i>
09-29-91	1.0	0	<i>D. pulex</i>
09-29-91	1.0	0	<i>D. pulex</i>
09-29-91	1.1	0	<i>D. pulex</i>
09-29-91	1.1	0	<i>D. pulex</i>
09-29-91	1.1	0	<i>D. pulex</i>
09-29-91	1.1	0	<i>D. pulex</i>
09-29-91	1.2	0	<i>D. pulex</i>
09-29-91	1.3	0	<i>D. pulex</i>
09-29-91	1.3	0	<i>D. pulex</i>
10-27-91	1.5	0	<i>D. pulex</i>
11-11-91	0.5	0	<i>D. pulex</i>
11-11-91	0.6	0	<i>D. pulex</i>
11-11-91	0.6	0	<i>D. pulex</i>
11-11-91	0.7	0	<i>D. pulex</i>
11-11-91	0.7	0	<i>D. pulex</i>

Date	Length in mm	Eggs	Species
11-11-91	0.7	0	<i>D. pulex</i>
11-11-91	0.7	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.8	0	<i>D. pulex</i>
11-11-91	0.9	0	<i>D. pulex</i>
11-11-91	0.9	0	<i>D. pulex</i>
11-11-91	0.9	0	<i>D. pulex</i>
11-11-91	0.9	0	<i>D. pulex</i>
11-11-91	0.9	0	<i>D. pulex</i>
11-11-91	0.9	0	<i>D. pulex</i>
11-11-91	0.9	0	<i>D. pulex</i>
11-11-91	1.0	0	<i>D. pulex</i>
11-11-91	1.1	0	<i>D. pulex</i>
11-11-91	1.1	0	<i>D. pulex</i>
11-11-91	1.4	0	<i>D. pulex</i>
11-11-91	1.5	0	<i>D. pulex</i>
11-11-91	1.9	0	<i>D. pulex</i>
11-11-91	2.1	0	<i>D. pulex</i>
11-11-91	2.1	0	<i>D. pulex</i>
11-11-91	2.1	3	<i>D. pulex</i>
11-11-91	2.1	5	<i>D. pulex</i>
11-11-91	2.2	3	<i>D. pulex</i>
11-11-91	2.2	6	<i>D. pulex</i>
11-11-91	2.3	0	<i>D. pulex</i>
11-11-91	2.3	0	<i>D. pulex</i>
11-11-91	2.3	3	<i>D. pulex</i>
11-11-91	2.3	8	<i>D. pulex</i>
11-11-91	2.3	8	<i>D. pulex</i>
11-11-91	2.3	10	<i>D. pulex</i>
11-24-91	0.7	0	<i>D. pulex</i>
11-24-91	0.8	0	<i>D. pulex</i>
11-24-91	0.9	0	<i>D. pulex</i>
11-24-91	0.9	0	<i>D. pulex</i>
11-24-91	0.9	0	<i>D. pulex</i>
11-24-91	0.9	0	<i>D. pulex</i>
11-24-91	1.0	0	<i>D. pulex</i>
11-24-91	1.0	0	<i>D. pulex</i>
11-24-91	1.2	0	<i>D. pulex</i>

Date	Length in mm	Eggs	Species
12-11-91	0.8	0	<i>D. pulex</i>
12-11-91	0.9	0	<i>D. pulex</i>
12-11-91	0.9	0	<i>D. pulex</i>
12-11-91	1.0	0	<i>D. pulex</i>
12-11-91	1.2	0	<i>D. pulex</i>
12-11-91	1.4	0	<i>D. pulex</i>
12-11-91	1.4	0	<i>D. pulex</i>
12-11-91	1.4	0	<i>D. pulex</i>
12-11-91	1.6	0	<i>D. pulex</i>
12-11-91	1.6	0	<i>D. pulex</i>
12-11-91	1.7	0	<i>D. pulex</i>
12-11-91	1.7	0	<i>D. pulex</i>
12-11-91	1.7	0	<i>D. pulex</i>
01-01-92	1.3	0	<i>D. pulex</i>
01-01-92	1.7	0	<i>D. pulex</i>
01-01-92	1.9	0	<i>D. pulex</i>
01-01-92	1.9	0	<i>D. pulex</i>
01-01-92	1.9	0	<i>D. pulex</i>
01-01-92	2.0	0	<i>D. pulex</i>
01-01-92	2.5	0	<i>D. pulex</i>
02-05-92	0.6	0	<i>D. pulex</i>
02-05-92	0.6	0	<i>D. pulex</i>
02-05-92	0.8	0	<i>D. pulex</i>
02-05-92	0.8	0	<i>D. pulex</i>
02-05-92	1.0	0	<i>D. pulex</i>
02-05-92	1.0	0	<i>D. pulex</i>
02-05-92	1.1	0	<i>D. pulex</i>
02-05-92	1.3	0	<i>D. pulex</i>
02-05-92	1.3	0	<i>D. pulex</i>
02-05-92	1.7	0	<i>D. pulex</i>
02-05-92	2.2	3	<i>D. pulex</i>
02-05-92	2.6	14	<i>D. pulex</i>

**DAPHNIA LENGTHS IN MM AND BROOD SIZE FOR
POOL 6 DURING SAMPLING YEAR**

Date	Length in mm	^b Eggs	^b Ephippia	Species
04-28-91	0.6	0	0	<i>D. obtusa</i>
04-28-91	0.6	0	0	<i>D. obtusa</i>
04-28-91	0.6	0	0	<i>D. obtusa</i>
04-28-91	0.7	0	0	<i>D. obtusa</i>
04-28-91	0.7	0	0	<i>D. obtusa</i>
04-28-91	0.7	0	0	<i>D. obtusa</i>
04-28-91	0.7	0	0	<i>D. obtusa</i>
04-28-91	0.7	0	0	<i>D. obtusa</i>
04-28-91	0.7	0	0	<i>D. obtusa</i>
04-28-91	0.7	0	0	<i>D. obtusa</i>
04-28-91	0.7	0	0	<i>D. obtusa</i>
04-28-91	0.8	0	0	<i>D. obtusa</i>
04-28-91	0.8	0	0	<i>D. obtusa</i>
04-28-91	0.8	0	0	<i>D. obtusa</i>
04-28-91	0.8	0	0	<i>D. obtusa</i>
04-28-91	1.0	0	0	<i>D. obtusa</i>
04-28-91	1.0	0	0	<i>D. obtusa</i>
04-28-91	1.2	0	0	<i>D. obtusa</i>
05-27-91	1.7	6	0	<i>D. pulex</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.5	0	0	<i>D. obtusa</i>
06-12-91	0.6	0	0	<i>D. obtusa</i>
06-12-91	0.6	0	0	<i>D. obtusa</i>
06-12-91	0.7	0	0	<i>D. obtusa</i>
06-12-91	0.8	0	0	<i>D. obtusa</i>
06-12-91	0.8	0	0	<i>D. obtusa</i>

^b Loose ephippia and eggs may have also been present during the sampling year, besides those found in the *Daphnia* sampled, in Pool 6.

Date	Length in mm	Eggs	Ephippia	Species
06-29-91	1.2	0	0	<i>D. obtusa</i>
06-29-91	1.2	0	0	<i>D. obtusa</i>
06-29-91	1.2	0	0	<i>D. obtusa</i>
06-29-91	1.2	0	0	<i>D. obtusa</i>
06-29-91	1.2	0	0	<i>D. obtusa</i>
06-29-91	1.2	0	0	<i>D. obtusa</i>
06-29-91	1.2	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.4	0	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>
06-29-91	1.5	1	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>
06-29-91	1.5	0	0	<i>D. obtusa</i>

Date	Length in mm	Eggs	Ephippia	Species
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	2	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.3	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>

Date	Length in mm	Eggs	Ephippia	Species
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	present	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.8	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	present	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	present	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	present	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	1.9	0	0	<i>D. obtusa</i>
06-29-91	2.0	0	0	<i>D. obtusa</i>
06-29-91	2.0	0	0	<i>D. obtusa</i>
06-29-91	2.0	0	present	<i>D. obtusa</i>

Date	Length in mm	Eggs	Ephippia	Species
06-29-91	2.0	0	present	<i>D. obtusa</i>
06-29-91	2.0	0	0	<i>D. obtusa</i>
06-29-91	2.0	0	0	<i>D. obtusa</i>
06-29-91	2.0	0	0	<i>D. obtusa</i>
06-29-91	2.0	0	0	<i>D. obtusa</i>
06-29-91	2.0	0	0	<i>D. obtusa</i>
06-29-91	2.0	0	0	<i>D. obtusa</i>
06-29-91	2.0	0	present	<i>D. obtusa</i>
06-29-91	2.1	0	0	<i>D. obtusa</i>
06-29-91	2.2	0	0	<i>D. obtusa</i>
06-29-91	2.2	0	0	<i>D. obtusa</i>
06-29-91	2.2	0	0	<i>D. obtusa</i>
06-29-91	2.2	0	0	<i>D. obtusa</i>
06-29-91	2.3	5	0	<i>D. obtusa</i>
06-29-91	2.3	0	0	<i>D. obtusa</i>
06-29-91	2.3	0	0	<i>D. obtusa</i>
06-29-91	2.3	0	0	<i>D. obtusa</i>
06-29-91	2.3	0	0	<i>D. obtusa</i>
06-29-91	2.3	0	0	<i>D. obtusa</i>
06-29-91	2.3	2	0	<i>D. obtusa</i>
06-29-91	2.3	0	0	<i>D. obtusa</i>
06-29-91	2.4	0	0	<i>D. obtusa</i>
06-29-91	2.4	0	0	<i>D. obtusa</i>
06-29-91	2.4	0	0	<i>D. obtusa</i>
06-29-91	2.4	0	0	<i>D. obtusa</i>
06-29-91	2.4	0	0	<i>D. obtusa</i>
06-29-91	2.4	0	0	<i>D. obtusa</i>
06-29-91	2.4	0	0	<i>D. obtusa</i>
06-29-91	2.5	0	0	<i>D. obtusa</i>
06-29-91	2.5	0	0	<i>D. obtusa</i>
06-29-91	2.5	1	0	<i>D. obtusa</i>
06-29-91	2.5	0	0	<i>D. obtusa</i>
06-29-91	2.7	0	0	<i>D. obtusa</i>
06-29-91	2.8	0	0	<i>D. obtusa</i>
06-29-91	2.9	0	0	<i>D. obtusa</i>
07-22-91	0.5	0	0	<i>D. obtusa</i>
07-22-91	0.5	0	0	<i>D. obtusa</i>
09-03-91	**	0	0	<i>D. pulex</i>
09-15-91	0.8	0	0	<i>D. pulex</i>
09-15-91	0.8	0	0	<i>D. pulex</i>
09-15-91	0.8	0	0	<i>D. pulex</i>
09-15-91	0.8	0	0	<i>D. pulex</i>
09-15-91	0.8	0	0	<i>D. pulex</i>
09-15-91	0.9	0	0	<i>D. pulex</i>

** Measurement missing

Date	Length in mm	Eggs	Ephippia	Species
09-29-91	1.0	0	0	<i>D. pulex</i>
09-29-91	1.0	0	0	<i>D. pulex</i>
09-29-91	1.0	0	0	<i>D. pulex</i>
09-29-91	1.0	0	0	<i>D. pulex</i>
09-29-91	1.0	0	0	<i>D. pulex</i>
09-29-91	1.0	0	0	<i>D. pulex</i>
09-29-91	1.1	0	0	<i>D. pulex</i>
09-29-91	1.1	0	0	<i>D. pulex</i>
09-29-91	1.1	0	0	<i>D. pulex</i>
09-29-91	1.1	0	0	<i>D. pulex</i>
09-29-91	1.1	0	0	<i>D. pulex</i>
09-29-91	1.1	0	0	<i>D. pulex</i>
09-29-91	1.1	0	0	<i>D. pulex</i>
09-29-91	1.2	0	0	<i>D. pulex</i>
09-29-91	1.3	0	0	<i>D. pulex</i>
09-29-91	1.3	1	0	<i>D. pulex</i>
09-29-91	1.3	0	0	<i>D. pulex</i>
09-29-91	1.3	0	0	<i>D. pulex</i>
09-29-91	1.4	2	0	<i>D. pulex</i>
09-29-91	1.5	2	0	<i>D. pulex</i>
10-13-91	0.8	0	0	<i>D. pulex</i>
10-13-91	0.8	0	0	<i>D. pulex</i>
10-13-91	0.9	0	0	<i>D. pulex</i>
10-13-91	0.9	0	0	<i>D. pulex</i>
10-13-91	0.9	0	0	<i>D. pulex</i>
10-13-91	0.9	0	0	<i>D. pulex</i>
10-13-91	0.9	0	0	<i>D. pulex</i>
10-13-91	0.9	0	0	<i>D. pulex</i>
10-13-91	0.9	0	0	<i>D. pulex</i>
10-13-91	1.0	0	0	<i>D. pulex</i>
10-13-91	1.0	0	0	<i>D. pulex</i>
10-13-91	1.0	0	0	<i>D. pulex</i>
10-13-91	1.0	0	0	<i>D. pulex</i>
10-13-91	1.0	0	0	<i>D. pulex</i>
10-13-91	1.0	0	0	<i>D. pulex</i>
10-13-91	1.1	0	0	<i>D. pulex</i>
10-13-91	1.1	0	0	<i>D. pulex</i>
10-13-91	1.1	0	0	<i>D. pulex</i>
10-13-91	1.1	0	0	<i>D. pulex</i>
10-13-91	1.1	0	0	<i>D. pulex</i>
10-13-91	1.1	0	0	<i>D. pulex</i>
10-13-91	1.1	0	0	<i>D. pulex</i>
10-13-91	1.1	0	0	<i>D. pulex</i>
10-13-91	1.2	0	0	<i>D. pulex</i>
10-13-91	1.2	0	0	<i>D. pulex</i>

Date	Length in mm	Eggs	Ephippia	Species
10-13-91	1.3	0	0	<i>D. pulex</i>
10-13-91	1.3	0	0	<i>D. pulex</i>
10-13-91	1.3	0	0	<i>D. pulex</i>
10-13-91	1.3	0	0	<i>D. pulex</i>
10-13-91	1.3	0	0	<i>D. pulex</i>
10-13-91	1.3	0	0	<i>D. pulex</i>
10-13-91	1.3	0	0	<i>D. pulex</i>
10-13-91	1.4	0	0	<i>D. pulex</i>
10-13-91	1.4	0	0	<i>D. pulex</i>
10-13-91	1.6	0	0	<i>D. pulex</i>
10-13-91	1.6	0	0	<i>D. pulex</i>
10-13-91	2.0	0	0	<i>D. pulex</i>
10-13-91	2.1	0	0	<i>D. pulex</i>
10-27-91	0.7	0	0	<i>D. pulex</i>
10-27-91	0.8	0	0	<i>D. pulex</i>
10-27-91	0.8	0	0	<i>D. pulex</i>
10-27-91	0.8	0	0	<i>D. pulex</i>
10-27-91	0.8	0	0	<i>D. pulex</i>
10-27-91	1.4	0	0	<i>D. pulex</i>
10-27-91	1.5	0	0	<i>D. pulex</i>
10-27-91	1.6	0	0	<i>D. pulex</i>
10-27-91	1.7	0	0	<i>D. pulex</i>
11-11-91	0.6	0	0	<i>D. pulex</i>
11-11-91	0.6	0	0	<i>D. pulex</i>
11-11-91	0.6	0	0	<i>D. pulex</i>
11-11-91	1.3	0	0	<i>D. pulex</i>
11-24-91	0.7	0	0	<i>D. pulex</i>
11-24-91	0.7	0	0	<i>D. pulex</i>
11-24-91	0.8	0	0	<i>D. pulex</i>
11-24-91	0.8	0	0	<i>D. pulex</i>
11-24-91	0.8	0	0	<i>D. pulex</i>
11-24-91	0.8	0	0	<i>D. pulex</i>
11-24-91	0.8	0	0	<i>D. pulex</i>
11-24-91	0.8	0	0	<i>D. pulex</i>
11-24-91	0.8	0	0	<i>D. pulex</i>
11-24-91	0.9	0	0	<i>D. pulex</i>
11-24-91	0.9	0	0	<i>D. pulex</i>
11-24-91	0.9	0	0	<i>D. pulex</i>
11-24-91	1.0	0	0	<i>D. pulex</i>
11-24-91	1.0	0	0	<i>D. pulex</i>
11-24-91	1.0	0	0	<i>D. pulex</i>
11-24-91	1.0	0	0	<i>D. pulex</i>
11-24-91	1.0	0	0	<i>D. pulex</i>

Date	Length in mm	Eggs	Ephippia	Species
11-24-91	1.0	0	0	<i>D. pulex</i>
11-24-91	1.1	0	0	<i>D. pulex</i>
11-24-91	1.3	0	0	<i>D. pulex</i>
12-11-91	0.9	0	0	<i>D. obtusa</i>
12-11-91	0.9	0	0	<i>D. obtusa</i>
12-11-91	0.9	0	0	<i>D. pulex</i>
12-11-91	1.3	0	0	<i>D. pulex</i>
12-11-91	1.4	0	0	<i>D. pulex</i>
01-01-92	0.7	0	0	<i>D. obtusa</i>
01-01-92	0.7	0	0	<i>D. obtusa</i>
01-01-92	0.8	0	0	<i>D. obtusa</i>
01-01-92	0.8	0	0	<i>D. obtusa</i>
01-01-92	0.8	0	0	<i>D. obtusa</i>
01-01-92	0.8	0	0	<i>D. obtusa</i>
01-01-92	0.8	0	0	<i>D. obtusa</i>
01-01-92	0.8	0	0	<i>D. obtusa</i>
01-01-92	0.8	0	0	<i>D. obtusa</i>
01-01-92	0.9	0	0	<i>D. obtusa</i>
01-01-92	0.9	0	0	<i>D. obtusa</i>
01-01-92	0.9	0	0	<i>D. obtusa</i>
01-01-92	0.9	0	0	<i>D. obtusa</i>
01-01-92	1.0	0	0	<i>D. obtusa</i>
01-01-92	1.0	0	0	<i>D. obtusa</i>
01-01-92	1.0	0	0	<i>D. obtusa</i>
01-01-92	1.0	0	0	<i>D. obtusa</i>
01-01-92	0.9	0	0	<i>D. pulex</i>
01-01-92	0.9	0	0	<i>D. pulex</i>
01-20-92	0.8	0	0	<i>D. obtusa</i>
01-20-92	1.3	4	0	<i>D. obtusa</i>
01-20-92	0.8	0	0	<i>D. pulex</i>
01-20-92	1.2	0	0	<i>D. pulex</i>
01-20-92	1.2	0	0	<i>D. pulex</i>
01-20-92	1.3	0	0	<i>D. pulex</i>
01-20-92	1.4	0	0	<i>D. pulex</i>
01-20-92	1.5	0	0	<i>D. pulex</i>
01-20-92	1.8	0	0	<i>D. pulex</i>
02-05-92	0.8	0	0	<i>D. pulex</i>

APPENDIX IV

DEPTH IN CM FOR ALL SEVEN POOLS DURING THE SAMPLING YEAR

Date	Pool 1	Pool 2	Pool 3	Pool 4	Pool 5	Pool 6	Pool 7
03-02-91	43	28	43	23	41	71	51
03-16-91	43	25	46	31	51	91	60
03-30-91	46	25	33	31	48	53	60
04-13-91	33	20	36	23	38	48	36
04-28-91	27	8	20	10	41	66	48
05-12-91	18	DRY	DRY	DRY	33	91	50
05-27-91	5	DRY	DRY	DRY	DRY	100	10
06-12-91	22	DRY	DRY	15	15	90	DRY
06-26-91	15	DRY	DRY	DRY	DRY	62	DRY
07-08-91	91	55	64	40	65	120	60
07-22-91	40	15	40	43	30	60	45
08-05-91	50	30	54	40	48	75	50
08-19-91	40	21	50	11	55	50	60
09-02-91	40	15	30	20	20	100	10
09-15-91	45	25	46	30	35	80	35
09-29-91	33	12	30	15	20	100	50
10-13-91	25	DRY	DRY	DRY	20	100	25
10-27-91	60	30	60	40	65	120	60
11-11-91	48	22	45	25	48	120	50
11-23-91	50	23	45	30	30	120	50
12-11-91	45	20	40	30	35	116	50
01-01-92	50	20	45	30	40	110	55
01-20-92	50	20	50	25	40	120	55
02-05-92	40	15	25	25	35	120	50
03-01-92	42	15	28	15	52	120	40
03-15-92	50	23	45	20	65	120	60

APPENDIX V

MONTHLY AIR TEMPERATURES IN °C AT RED ROCK WEATHER
STATION, NATIONAL OCEANIC AND ATMOSPHERIC
ADMINISTRATION, CLIMATOLOGICAL DATA
FOR NEVADA

DATE	MAX TEMP °C	MIN TEMP °C	AVE TEMP °C
JAN 1991	10.89	- 2.11	4.39
FEB	18.06	1.89	10.00
MAR	12.61	1.56	7.11
APR	20.61	6.33	13.50
MAY	24.22	9.39	16.67
JUN	30.33	16.06	23.22
JUL	35.56	19.33	27.44
AUG	34.56	19.50	27.06
SEP	31.00	14.78	22.89
OCT	26.44	10.06	18.28
NOV	16.22	2.28	9.28
DEC	11.94	- 1.28	5.33
JAN 1992	10.89	- 2.67	4.11
FEB	14.11	1.94	8.06
MAR	15.28	4.28	9.78

**WATER TEMPERATURE IN °C FOR ALL SEVEN POOLS
DURING THE SAMPLING YEAR**

Date	Pool 1	Pool 2	Pool 3	Pool 4	Pool 5	Pool 6	Pool 7
03-02-91	13.0	15.0	14.5	13.0	14.0	10.0	10.0
03-16-91	11.0	12.0	11.0	10.5	10.1	9.0	10.0
03-30-91	11.0	14.0	13.0	13.0	13.0	10.0	12.0
04-13-91	14.0	19.0	18.5	18.5	16.0	11.5	12.0
04-28-91	16.0	19.0	19.0	19.5	20.0	15.0	19.0
05-12-91	21.0	DRY	DRY	DRY	19.0	15.0	17.0
05-27-91	**	DRY	DRY	DRY	DRY	22.0	25.0
06-12-91	21.5	DRY	DRY	27.0	25.0	23.0	DRY
06-26-91	18.5	DRY	DRY	DRY	DRY	16.5	DRY
07-08-91	22.0	22.0	23.0	23.0	23.0	23.0	23.5
07-22-91	25.0	30.0	25.0	28.5	23.0	24.5	**
08-05-91	23.0	26.0	21.0	21.0	23.5	23.0	24.0
08-19-91	25.0	28.5	24.0	23.0	25.0	23.5	23.0
09-02-91	25.0	29.0	25.0	24.0	25.0	24.0	23.0
09-15-91	21.0	24.0	21.0	18.0	22.0	19.0	20.0
09-29-91	22.5	26.0	24.5	21.0	21.0	20.0	22.0
10-13-91	19.0	DRY	DRY	DRY	16.5	16.5	16.0
10-27-91	14.0	16.5	15.0	14.5	14.0	13.0	13.0
11-11-91	16.0	17.0	16.5	16.0	14.0	14.5	16.5
11-23-91	9.3	11.0	11.0	12.0	9.0	7.0	9.0
12-11-91	10.0	10.0	10.0	10.0	10.0	9.0	9.0
01-01-92	9.0	10.0	11.0	11.0	8.0	7.0	8.0
01-20-92	8.0	9.0	11.0	11.0	7.0	7.0	8.0
02-05-92	10.0	11.0	12.0	12.0	10.0	10.0	9.0
03-01-92	11.0	14.0	13.0	12.0	12.0	12.0	11.5
03-15-92	12.0	15.0	14.0	11.0	14.0	12.0	19.0

** Data Missing

APPENDIX VI

OXYGEN TENSION IN mg l⁻¹ AND % SATURATION FOR ALL SEVEN POOLS DURING THE SAMPLING YEAR

DATE	POOL 1		POOL 2		POOL 3		POOL 4	
	mg l ⁻¹	%	mg l ⁻¹	%	mg l ⁻¹	%	mg l ⁻¹	%
03-02-91	8.4	104.0	6.4	75.0	6.6	75.0	5.6	61.0
03-16-91	6.7	77.0	6.6	91.0	7.6	91.0	7.8	93.5
03-30-91	6.5	74.0	5.5	73.0	6.4	73.0	5.5	59.0
04-13-91	7.5	89.0	6.6	97.0	8.0	97.0	7.5	89.0
04-28-91	6.7	77.0	6.5	80.0	6.9	80.0	DRY	DRY
05-12-91	4.3	42.8	DRY	DRY	DRY	DRY	DRY	DRY
05-27-91	**	**	DRY	DRY	DRY	DRY	DRY	DRY
06-12-91	4.1	40.0	DRY	DRY	DRY	DRY	6.0	66.5
06-26-91	3.1	26.5	DRY	DRY	DRY	DRY	DRY	DRY
07-08-91	7.0	81.5	7.2	84.0	5.7	62.0	4.1	40.0
07-22-91	3.7	35.7	2.7	23.0	2.3	18.8	4.5	45.0
08-05-91	4.1	40.0	3.1	26.5	2.6	22.0	4.1	40.0
08-19-91	3.3	29.8	3.0	26.3	1.5	10.7	1.9	14.5
09-02-91	4.4	44.0	4.3	42.8	2.6	22.0	5.0	52.0
09-15-91	3.8	36.0	3.2	28.7	5.0	52.0	4.9	51.0
09-29-91	4.0	38.5	4.0	38.5	4.7	48.0	3.7	35.7
10-13-91	3.5	32.3	DRY	DRY	DRY	DRY	DRY	DRY
10-27-91	7.1	83.0	5.1	53.0	4.5	45.0	6.2	69.5
11-11-91	5.0	52.0	6	66.5	5.2	54.5	6.5	74.0
11-23-91	6.5	74.0	6	66.5	6.7	77.0	7.2	84.0
12-11-91	4.4	44.0	4.1	40.0	4.0	38.5	5.0	52.0
01-01-92	6.7	77.0	5.5	59.0	5.6	61.0	7.0	81.5
01-20-92	6.5	74.0	5.4	58.0	6.9	80.0	7.0	81.5
02-05-92	6.4	73.0	5.0	52.0	6.2	69.5	6.1	68.0
03-01-92	7.0	81.5	7.0	81.5	6.0	66.5	7.7	92.0
03-15-92	5.5	59.0	6.0	66.5	5.1	54.5	6.4	73.0

** Data Missing

**OXYGEN TENSION IN mg l⁻¹ AND % SATURATION
FOR ALL SEVEN POOLS DURING
THE SAMPLING YEAR**

DATE	POOL 5		POOL 6		POOL 7	
	mg l ⁻¹	%	mg l ⁻¹	%	mg l ⁻¹	%
03-02-91	4.8	49.0	5.0	52.0	5.0	52.0
03-16-91	7.1	83.0	5.7	62.0	5.5	59.0
03-30-91	6.0	66.5	5.6	61.0	6.0	66.5
04-13-91	8.3	102.0	7.5	89.0	6.8	78.0
04-28-91	6.8	78.0	6.9	80.0	6.8	78.0
05-12-91	6.0	66.5	7.7	92.0	5.9	65.0
05-27-91	DRY	DRY	7.0	81.5	2.3	18.8
06-12-91	5.6	61.0	5.2	54.5	DRY	DRY
06-26-91	DRY	DRY	3.5	32.3	DRY	DRY
07-08-91	5.1	53.0	3.1	26.5	2.0	15.5
07-22-91	4.2	41.0	3.5	32.3	**	**
08-05-91	3.2	28.7	3.2	28.7	2.8	24.0
08-19-91	7.8	93.5	5.0	52.0	1.8	13.5
09-02-91	2.1	16.5	4.0	38.5	3.0	26.3
09-15-91	5.1	53.0	2.7	23.0	1.2	8.0
09-29-91	4.1	40.0	2.7	23.0	4.0	38.5
10-13-91	3.2	28.7	3.5	32.3	2.6	22.0
10-27-91	7.0	81.5	6.4	73.0	4.6	46.9
11-11-91	5.9	65.0	4.5	45.0	6.6	75.0
11-23-91	7.0	81.5	5.0	52.0	7.0	81.5
12-11-91	4.4	44.0	6.5	74.0	6.1	68.0
01-01-92	4.8	49.0	7.0	81.5	5.0	52.0
01-20-92	6.5	74.0	6.3	71.0	4.9	51.0
02-05-92	5.2	54.5	6.0	66.5	4.5	45.0
03-01-92	7.5	89.0	7.4	87.0	5.9	65.0
03-15-92	6.0	66.5	4.5	45.0	5.0	52.0

** Data Missing

APPENDIX VII

pH FOR ALL SEVEN POOLS DURING THE SAMPLING YEAR

Date	Pool 1	Pool 2	Pool 3	Pool 4	Pool 5	Pool 6	Pool 7
03-02-91	7.05	7.27	7.38	7.36	7.11	7.14	7.25
03-16-91	**	**	**	**	**	**	**
03-30-91	7.87	7.87	7.63	7.55	7.37	7.36	7.41
04-13-91	9.25	9.26	9.44	8.05	9.13	7.82	8.23
04-28-91	8.71	8.48	8.17	8.14	8.26	8.59	8.14
05-12-91	7.93	DRY	DRY	DRY	8.01	7.83	8.06
05-27-91	8.13	DRY	DRY	DRY	DRY	8.16	7.87
06-12-91	8	DRY	DRY	7.88	7.94	7.97	DRY
06-26-91	10.3	DRY	DRY	DRY	DRY	10.63	DRY
07-08-91	7.09	7.12	7.11	7.11	7.12	7.08	7.13
07-22-91	8.53	8.08	7.98	8.06	8.92	9.35	8.06
08-05-91	8.08	7.78	7.61	7.50	7.32	7.79	7.82
08-19-91	8.55	8.06	8.18	7.87	9.92	9.14	7.93
09-02-91	8.59	8.11	7.79	7.78	9.38	8.20	7.92
09-15-91	8.95	8.24	9.27	8.76	9.72	7.72	7.84
09-29-91	8.19	7.95	8.38	8.03	8.62	7.83	7.78
10-13-91	7.66	DRY	DRY	DRY	7.65	7.58	7.76
10-27-91	7.40	7.71	7.40	7.36	7.36	7.31	7.28
11-11-91	8.43	8.19	8.35	8.73	8.22	7.85	8.04
11-23-91	8.41	8.51	8.60	8.26	8.40	8.19	8.00
12-11-91	7.72	7.66	7.62	7.75	7.67	7.67	7.58
01-01-92	7.53	7.62	7.66	7.35	7.41	7.61	7.24
01-20-92	8.45	7.96	7.95	8.25	7.77	7.65	7.46
02-05-92	8.35	7.97	7.95	7.95	7.55	7.50	7.45
03-01-92	8.49	7.95	7.94	7.68	7.63	7.60	7.62
03-15-92	7.84	8.05	8.85	8.36	8.60	7.93	8.14

** Data Missing

APPENDIX VIII

CONDUCTIVITY IN $\mu\text{S cm}^{-1}$ FOR ALL SEVEN POOLS DURING THE SAMPLING YEAR

Date	Pool 1	Pool 2	Pool 3	Pool 4	Pool 5	Pool 6	Pool 7
03-02-91	1200	1400	600	600	700	500	500
03-16-91	**	**	**	**	**	**	**
03-30-91	1200	1300	600	700	800	700	900
04-13-91	1300	1100	1300	1400	1100	1000	1500
04-28-91	1700	2400	1800	2700	2000	1400	2100
05-12-91	4000	DRY	DRY	DRY	3900	2250	3800
05-27-91	6800	DRY	DRY	DRY	DRY	1900	3600
06-12-91	4900	DRY	DRY	3900	6800	3500	DRY
06-26-91	4100	DRY	DRY	DRY	DRY	2750	DRY
07-08-91	4400	1000	1200	1200	1200	900	1200
07-22-91	2400	4600	3100	3500	1600	2000	2700
08-05-91	3000	3250	1800	1700	1300	2200	3300
08-19-91	2900	3500	2100	2700	1800	2100	2800
09-02-91	2700	4400	3400	3600	2400	2600	41000
09-15-91	2100	3400	2100	2300	1650	1450	2200
09-29-91	2600	4600	2700	3900	2600	2000	3200
10-13-91	3600	DRY	DRY	DRY	4900	2700	4200
10-27-91	1250	2800	1400	1500	1300	1200	1050
11-11-91	2200	3250	2400	2750	2400	1600	2550
11-23-91	2600	3200	2800	2700	2800	1700	3250
12-11-91	2500	3500	3200	2300	3000	1750	3450
01-01-92	**	**	**	**	**	**	**
01-20-92	3250	4100	2200	2200	1800	1500	2700
02-05-92	2750	4440	2900	3250	2200	1400	3300
03-01-92	2400	2800	1800	2100	1800	1750	2700
03-15-92	3100	3750	2000	2100	1900	1900	2600

** Data Missing

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