Callibaetis floridanus (EPHEMEROPTERA: BAETIDAE) LIFE HISTORY AND PRODUCTION IN A WEST TEXAS PLAYA

THESIS

Presented to the Graduate Council of the
University of North Texas in Partial
Fulfillment of the Requirements

For the Degree of

MASTERS OF SCIENCE

By

Gregory Mark Anderson, B.S. Biol

Denton, Texas

May 1998

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A life history study of *Callibaetis floridanus* was conducted over the wet cycle of a playa on the Southern High Plains of Texas from June through September 1995. Abundance, recruitment, growth, development, voltinism, and production were investigated. *C. floridanus* reach great densities in playas. Fecundity was influenced by adult size. Sexual dimorphism and temperature influences on nymphal growth were analyzed. Development was very fast in playas resulting in a seasonal multivoltine life history. Secondary production was estimated at 11.7 $g/m^2/0.25yr$.

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CHAPTER I

INTRODUCTION

Playas

Playas are temporary wetlands that form in shallow, gently sloping basins. The basins flood when rainfall is sufficient. Playa basins have no surface outflow; water leaves the basins by evaporation or infiltration. Playas are perched wetlands because they have no influence from ground water. Water is held in playa basins by a layer of clay, which, when saturated, allows only very slow percolation.

Playas exist in plains and desert landscapes around the world, but they are most numerous and densely spaced on the Llano Estacado or Southern High Plains of west Texas (Osterkamp and Wood 1987). Texas High Plains contain about 20,000 playas (Bolen *et al.* 1989). When flooded, they are rarely deeper than a meter. Flooded basin diameters, generally 200-300 meters, range from under a hundred meters to tens of kilometers (Sublette and Sublette 1967, Reeves 1966).

Frequency of flooding and duration of water in playas is highly variable. Each year approximately a third of the Llano Estacado playa basins flood (Bolen *et al.* 1989). Flooding depends on the patchy precipitation of a semi-arid climate. Most wet cycles begin in late spring or summer. The length of the wet cycle is stochastic, being influenced by infiltration, evaporation, and rainfall frequency, duration, and intensity. Most playa basins are dry by fall or winter, and dry periods can last for many years. Dry playa basins can be recognized as gentle depressions in the landscape, blanketed by flood conditioned grasses. A few large, deep playas on the Llano Estacado are considered permanent water bodies.

Animal communities on the Llano Estacado use playas for water, food, and habitat. Only the Gulf Coast of Texas is more important than Southern High Plains playas to birds migrating in the central flyway. In wet years, as many as two million, or 40% of all waterfowl in the central flyway, overwinter in playas (U.S. Bureau of Reclamation 1982). Many other migratory birds use playas as resting points along their migration (Bolen and Gray 1988). In the absence of fish, amphibians reach great densities in playas. The Southern High Plains are home to 11 year-round resident bird species and 60 species of mammals (U.S. Bureau of Reclamation 1982). Playas have wetter soils than the surrounding upland and support more vegetational biomass, providing greater habitat value. Playas are especially important as habitat in the intensive sea of agriculture that is the Southern High Plains of today.

Loring et al. (1988) suggest that playas can exist as heterotrophic or autotrophic ecosystems. Litter, standing dead vegetation, and organic material transported from the watershed, support a quickly established heterotrophic ecosystem in a newly flooded playa. Microbial heterotrophs produce biomass when they are not energy limited by a lack of organic material. Production of bacterial biomass can deplete nutrients and limit algae growth. When organic carbon sources become limited, dying microbes release nutrients that can support algae and the system becomes more autotrophic. Chlorophyll *a* concentrations commonly increase over the wet cycle (Kennedy et al. 1996).

Playas support an active aquatic community of invertebrates. Kennedy *et al.* (1996) identified over 90 species of macroinvertebrates inhabiting playas, 90% of which were insects. Organisms inhabiting temporary pools often exhibit fast life cycles and desiccation resistant life stages.

Evolutionary and ecological strategies of animals in temporary pools are discussed by Wiggins *et al.* (1980). Organisms are divided into four groups based on their strategies for avoiding or tolerating drought. Group 1 includes permanent residents with desiccation resistant life stages. Group 2 consists of organisms with desiccation resistant life stages that are capable of aerial dispersion, but require water for oviposition. Group 3 is similar to group 2, but oviposition is independent of water. Group 4 organisms have no desiccation resistant life stages and must leave before onset of the dry phase. These organisms maintain populations in permanent water bodies. Williams (1985) constructed a fifth group, which includes organisms similar to group 4 that maintain populations by dispersion among temporary water bodies.

Invertebrate communities of Southern High Plains playas follow a pattern of development that is similar to temporary water bodies worldwide (Kennedy *et al.* in press, Lake *et al.* 1989). After flooding, the earliest colonizers are filter feeders and collector-gatherers, making use of allochthonous material that collects in the playa basin. Many of the early colonizers develop from desiccation resistant eggs or aestivating life stages; others aerially colonize shortly after flooding. Early playa communities are typified by crustaceans such as fairy shrimp (Anostraca), tadpole shrimp (Notostraca), and clam shrimp (Conchostraca), and mosquitoes (*Aedes sp.*). Small numbers of other playa inhabitants that later dominate the community such as *Callibaetis floridanus*

(Banks 1900), hydrophilid and dytiscid beetles, and oligochaetes are present early in a playa cycle. During the second month of playa succession, most crustaceans have completed their life cycles and disappeared from the community. Collector-gatherers continue to thrive, increasing in numbers and supporting predators. From mid phase of development to drying, oligochaetes are very important to the playa community. Predator numbers increase over time until the playa dries (Kennedy *et al.* in press). Figure 1 presents a conceptual model of nutritional resource categories and invertebrate feeding groups for playas modified from Merrit and Cummins (1984).

Beginning in the 40's and peaking in the 60's and 70's, playas have been modified to increase water longevity and, therefore, usefulness in irrigation and livestock watering (Steiert 1995). Modifications also keep the vast basins dry for agriculture. Dams across the basin or blocking inflows, or pits and trenches in the basin concentrate water and slow evaporation (Ward and Huddleston 1972). In some areas of the Llano Estacado as many as 85% of the larger playas have been modified (Bolen *et al.* 1979, Bolen *et al.* 1989). Modifications greatly reduce aquatic habitat. Natural playas have vast shallow littoral zones, but modified playas are reduced to cattle tanks with only marginal vegetation.

Playas are localized sites of ecological diversity and extremely important to the ecology of the Llano Estacado (Bolen *et al.* 1989, Sublette and Sublette 1967). Despite their importance, there has been little ecological research on playas. More research is needed to integrate playas with other wetlands (Bolen *et al.* 1989). Lack of research in playa ecology is due, in part, to the notorious unpredictability of wet cycles.

Callibaetis floridanus

Mayflies (Insecta: Ephemeroptera) represent the most ancient existing order of winged insects. Some 2000 species and 72 genera are recorded from lotic and lentic habitats worldwide for this hemimetabolous order (Brittain 1982, Edmunds 1984). Mayfly populations commonly account for a large portion of the biomass of aquatic invertebrate communities. Nymphs generally feed on plants and algae. As a major secondary producer, mayflies are an important link in the trophic structure of many aquatic ecosystems. Most mayfly nymphs and adults are prey for predators including fish, insects, birds, amphibians, and spiders (Borror *et al.* 1989).

Baetidae is the largest family of mayflies in North America (Borror et at. 1989). Baetids are commonly known as minnow mayflies. Adults are usually less than 15 mm long. Adult baetid hind wings are small or absent, and males' eyes have an upper turbinate portion.

Callibaetis is one of the most abundant and widespread of all Ephemeroptera genera (Check 1982, Lugo-Ortiz and McCafferty 1996, McCafferty and Waltz 1990). There are 15 species described from Middle and North America (Lugo-Ortiz and McCafferty 1996). *Callibaetis* is known for its tolerance of a wide range of environmental conditions and poor water quality (Check 1982, Lenat 1993). *Callibaetis* exhibits some of the shortest nymphal development times of all mayflies (Wiggins *et al.* 1980). Most species of *Callibaetis* are ovoviviparous, and eggs hatch within seconds of being oviposited in water (Berner *et al.* 1988). Female adult life span of ovoviviparous mayflies is longer than other mayflies allowing time, as the eggs develop, for wider dispersal (Berner 1941, Edmunds 1945, Wiggins *et al.* 1980). Despite the prevalence of *Callibaetis*, little work has been done with this genus due to difficulties such as poorly defined taxonomic characters and sexual dimorphism (Berner and Pescador 1988, Check 1982).

Callibaetis floridanus was described in 1900 (Banks). Nymphs and males were first described in 1941 (Berner). In 1963, Trost and Berner published a study on the life history, ecology, and behavior of *C. floridanus* in Florida. Check (1982) provided the first workable description of the species with a revision of North American *Callibaetis*. Life history, growth, and production were investigated in Virginia by Christman and Voshell (1992).

C. floridanus is distributed throughout the southeastern United States. Collections have been made as far north as Maryland, southern Indiana, southern Missouri, and southern Kansas (Check 1982). *C. floridanus* has also been reported in southeastern Iowa (Klubertanz 1995). They range west through south and east Texas in "small streams and swampy habitats" (McCafferty and Davis 1992) and playas of the Texas panhandle (Kennedy *et al.* 1996). *C. completa* is reported as synonymous extending the range south to Costa Rica and the Antilles (Lugo-Ortiz and McCafferty 1996, Travers 1938).

Lugo-Ortiz and McCafferty (1996) state that *C. floridanus* "has one of the widest ranges of habitat tolerances of any mayfly," possibly explaining its extensive distribution. Occurring in a wide range of lentic habitats including temporary ponds, roadside ditches, wetlands, and estuaries, nymphs generally live among submerged vegetation. Open water does not provide sufficient cover and food; mats of algae or floating macrophytes can obstruct oviposition (Berner and Pescador 1988).

C. floridanus exhibits a wide range of tolerance to pH, dissolved oxygen (DO), and temperature (Hubbard 1978). This tolerant mayfly has even been shown to inhabit brackish waters (Berner 1950, Berner and Sloan 1954, Sloan 1956). Normal rearing to emergence occurs with nymphs held in water at 12 parts per thousand salinity (Trost and Berner 1963). Trost and Berner (1963) collected *C. floridanus* from water with temperatures ranging from 1 to 34.5^{o}C. *C. floridanus* thrives in playas, which commonly exhibit DO levels below 1 mg/L (Kennedy *et al.* 1996, Loring *et al.* 1988).

Wide tolerances to physico-chemical parameters allow *C. floridanus* to flourish in niches that are unavailable to competing organisms. Sloan (1956) collected *C. floridanus* in great numbers from the two most extreme habitats of Florida springs: near the boil (where the DO is low (2.20 mg/L)) and in high chlorine estuary waters (where daily chlorine fluctuations are 1 to 5 parts per thousand). Sloan (1956) remarks that periodic fluctuation of salinity "is perhaps as important a barrier [to insect habitation] as concentration itself." Wide tolerances of *C. floridanus* may be related to the "importance," as Gibbs (1979) postulates, of an ovoviviparous naiad being able to survive adverse conditions, because ovoviviparous life cycles have no resistant egg stage.

Callibaetis is classified as herbivorous, feeding on diatoms and other algae (Edmunds *et al.* 1976). Cushing and Rader (1982) noted *Callibaetis* feeding almost exclusively on fine particulate organic matter. Trost and Berner (1963) report *C. floridanus* as a nonspecific plant feeder, eating mostly plant epidermis, but also algae. Trost and Berner analyzed mayfly food habits in a temporary pond that had recently filled. The flooded vegetation was primarily terrestrial and in the process of death and decay making the epidermis easier to graze. Playas provide an abundance of decaying terrestrial plant epidermis and epiphytic algae.

Examination of the Palmen body taken from an adult *Callibaetis sp.* indicated 16 instars (Taylor and Richards 1963). From rearing experiments, Trost and Berner (1963) reported nine to eleven instars for *C. floridanus*, with the most common number being ten. However, due to small early instar size, Trost and Berner (1963) admit "it was difficult to determine the number of molts with certainty".

Emergence occurs in late afternoon or early evening. For 2 to 10 minutes just prior to emergence, nymphal activity becomes erratic and concentrated near the water surface. The subimago emerges on to the surface of the water and flies to nearby vegetation. Sometime in the night, the subimago flies some 200 feet away from the water and waits until the subimaginal molt and mating flight the next morning (Trost and Berner 1963).

Trost and Berner (1963) described the mating flight of *C. floridanus* as occurring between 6:20 A.M. and 10:30 A.M., 20 to 30 minutes after the subimaginal molt. Mating flights occur over an open field. Males suddenly fly upward in a zigzag path to a height of 1 to 8 meters and begin rising and falling abruptly over vertical distances of several centimeters to over half a meter. Females then fly into the swarm and assume the rhythm of the flight. Males approach from below, using their turbinate eyes to find females. After copulation, females return to vegetation, while males are reported to reenter the swarm.

After the mating flight and generally within 21 hours of emergence, *C. floridanus* males die. Females, however, become quiescent prior to oviposition for five to seven or more days as the eggs develop (Trost and Berner 1963). Oviposition occurs in early morning (Trost and Berner 1963). Contact with water stimulates the eggs to hatch. Instant hatching of oviposited eggs allows nymphs to make immediate use of temporary habitats.

C. floridanus adults are not attracted to light traps. Frost (1967) reported one female subimago in nine years of light trapping in Florida. Kennedy *et al.* (1996) collected no *C. floridanus* in light traps near Amarillo, Tx.

Merickel and Wangberg (1981) reported an undesignated species of *Callibaetis* in two playas near Lubbock, Texas. *Callibaetis sp.* has also been reported in a playa near Las Cruces, New Mexico (Richardson 1971). Sublette and Sublette (1967) did not report *Callibaetis* in over twenty playas and ponds in the Southern High Plains, but they did identify *Cleon sp.*, perhaps misidentified.

C. floridanus is well adapted to temporary habitats, including playas. When a playa floods, terrestrial and wetland vegetation in the basin is flooded. Terrestrial vegetation begins to die and decay, providing an abundant food source. Ovoviviparity allows colonization and growth of mayflies among the dense submerged vegetation before many predators become established.

CHAPTER II

RESEARCH OBJECTIVES

The purpose of my research was to describe the ecology and life history of *Callibaetis floridanus* in a west Texas playa wetland. Specific objectives were to determine abundance, development rates, voltinism, and secondary productivity. *C. floridanus* is a dominant species providing a major trophic link in playa ecosystems. Little ecological research has been conducted on playas in general, and nothing has previously been published on *C. floridanus* life history in playas.

CHAPTER III

STUDY AREA

Two playas (referred to here as Playa 2 and Playa 7) were used in this investigation of *Callibaetis floridanus* life history. The study playas are in Carson County, Texas on the northern Llano Estacado about 20 miles northeast of Amarillo, Texas. Figure 2 shows the playas relative to the Llano Estacado and Amarillo.

The Llano Estacado is a semi-arid region. Average annual rainfall is 45 cm, but, typical of semi-arid climates, rainfall varies widely from year to year. Most precipitation occurs between May and September, generally as strong localized thunderstorms. High winds are common and annual evaporation is high (200-250 cm). Mean air temperatures are around 1-3^{o}C in winter and 25-28^{o}C in summer with 180-220 frost free days.

Playa 7 was investigated in 1994. Most other playas in the area, including Playa 2, were dry during that time. Playa 7 flooded during precipitation on August 2-3, 1994 and dried up in early November. *C. floridanus* nymphs from aquatic net samples were examined for developmental stage to assess development time. Playa 7 is at 101^{o}36' N longitude and 35^{o}15' W latitude. The watershed covers 2,654 ha. Landuse is 44% crop production, 33% rangeland, 20% Conservation Reserve Program, and 2% associated with residences and roads. The basin is modified with a small shallow trench at the basin margin and a pond on a small inlet ravine.

In 1995, Playa 2 was studied to assess population structure and production of *C. floridanus*. Playa 2 flooded due to rain on June 2-3, 1995. By early September, the playa consisted of isolated pools within the basin. Playa 7 also flooded in June 1995, but the basin was dry by August. Playa 2 lies at 101°35’ N longitude and 35°19’ W latitude. The watershed is approximately 1,114 ha. Landuse is about 40 percent grazed pasture, 10 percent industrial, 30 percent cultivated, and 20 percent grasslands (not grazed but periodically mowed). The basin has no modifications.

CHAPTER IV

METHODS AND MATERIALS

Physico-chemical Parameters

Water quality measurements of temperature, dissolved oxygen, pH, chlorophyll *a*, turbidity, and specific conductance were taken monthly over the wet periods of Playas 2 and 7. Late September, 1995, Playa 2 refilled, after drying in early September, and water quality measurements were taken on October 2. Full methodology disclosure and result analysis of water quality measures are presented in Kennedy *et al.* (1996). A total of 8 playa wet cycles, including Playa 7 in 1994 and Playa 2 in 1995, were measured in association with that study.

Collection Methods

Playa 7 was sampled qualitatively with an aquatic net, biweekly over the wet period in 1994. Development rates of *Callibaetis floridanus* were determined based on external developmental characteristics such as length and darkening of nymphal wing pads (Hutchinson 1993). Samples were fixed and preserved in Kahle's solution and transferred to 80% ethanol in the lab.

Three replicate quantitative depletion samples were taken from Playa 2 approximately weekly throughout the wet cycle from June through September 1995. One of eight sectors (N, NE, E, SE, S, SW, W, NW) was randomly selected by drawing chits from a cup for each depletion replicate. Weekly samples were taken due to fast development rates of *C. floridanus* in playas.

Depletion samples are taken by sectioning off an area (1 m^2) of the playa with four panels of plywood, and taking repetitive sweep samples over the entire area using a sweep net (approx. 250-350 um mesh). Each sweep from the depletion area was fixed and preserved with Kahle's solution and later transferred to 80% ethanol for long term preservation. Multiple samplings of the same area allow a catch-per-unit effort method to estimate abundance within the sampler.

To attract adults, a sheet of black plastic (5.5 X 6 m) was spread on the ground before sunrise. Females ready to oviposit came to the plastic where they were collected with an aspirator. Head widths and wing lengths were measured in the laboratory on an Olympus™ dissecting scope equipped with an Olympus™ Cue-2 Image Analyzer. Young produced by collected females were counted or used in rearing experiments. The plastic trap method was used to collect mayflies in west Texas (near Amarillo) and in north central Texas at the University of North Texas Water Research Field Station (near Denton). During collections, estimates of temperature and wind speed were noted.

Density of *Callibaetis floridanus*

The depletion sampling method is based on catch-per-unit effort theory. With each sweep, insects are removed from the area within the depletion sampler; each successive sweep collects a lower number of insects. An estimate of the actual number of insects within the depletion area can be calculated by linear regression using a maximum-likelihood estimation method (Maciena et al. 1993, Mahon 1980, Zippin 1958). This method for estimating populations was developed for fisheries but is suitable for aquatic invertebrate populations (Carle 1976, Carle and Strub 1978). Estimates were made with

Microfish™, a software program developed to estimate populations using a maximum-likelihood estimation method (Van Deventer and Platts 1985, Van Deventer and Platts 1989)

Size Class Analysis

Depletion samples were examined for all nymphal stages of the *C. floridanus* life cycle. Growth was measured in head capsule width. Head capsule measurements were used because they were reported by Trost and Berner (1963) as the least variable of possible size measurements including body, median filament, and cerci lengths. Christman and Voshell (1992) also used head widths in their study of *C. floridanus* production. Head width measurements were made with the Olympus™ Cue-2 Image Analyzer.

Kahle's solution, which was used to fix and preserve samples, contains ethanol and formalin, both of which have been shown to reduce the weight of specimens (Howmiller 1972, Leuven *et al.* 1985). Although Mason *et al.* (1983) showed no significant difference between the dry weights of preserved and unpreserved mayflies, biomass to head width relationship estimates were made with dry weight measurements of unpreserved individuals. A size range of live *C. floridanus* were collected, measured, dried, and weighed to develop a functional relationship between head capsule width and biomass. Drying was conducted in a drying oven at 105°C for at least 24 hours. Weights were taken on a Cahn™ C-31 microbalance. The data were Ln-Ln transformed to produce a functional relationship used for production calculations.

Productivity, mean standing stock biomass, and production to biomass (P/B) ratios were estimated via the size frequency method (Hamilton 1969, Hynes and Coleman 1968) using Christman and Voshell's (1992) size classes for *C. floridanus*. Benke's (1979) modification for multivoltine species was required, where the production value is multiplied by 365 days divided by the Cohort Production Interval (CPI) (Benke 1979). The CPI is equivalent to average larval development time in days; egg, pupal, and adult stages are not considered because they do not contribute to aquatic production. Because playas are temporary and Playa 2 was wet for one fourth of the year, the production estimate time unit is 0.25 yr. Benke's multiplier was calculated as 92 days, instead of 365 days, divided by nymphal development time because the wet cycle of the playa lasted about 92 days. Hamilton (1969) suggested keeping negative values in production estimates to avoid a positive bias. Negative values, however, were set to zero following Benke and Wallace (1980) because negative values are theoretically impossible.

Water temperatures were not continuously monitored during the study. Air temperature data from the National Weather Service was used as a guide to estimate accumulated degree-days in playas. Other researchers have found playa temperature to be closely related to air temperature (Sublette and Sublette 1967). Degrees accumulated each day was calculated as the average of the maximum and minimum air temperatures.

Laboratory Growth Studies

First instar nymphs collected near Denton, Texas were reared to adults in tanks using sod from a dry playa basin as substrate. Tanks were placed at different temperatures in three Precision™ Low Temperature Incubators (model 818). Temperatures (18°C, 23°C, and 28°C) were chosen to be within tolerable range for *C. floridanus* and representative of playa temperatures. After emerging subimagoes were allowed to molt, then imagoes and subimago exuvia were collected with an aspirator. Development times were used to construct a degree-day model.

CHAPTER V

RESULTS AND DISCUSSION

Physico-chemical Parameters

Playa 7 in 1994 and Playa 2 in 1995 had physico-chemical parameter levels within ranges recorded for playas (Curtis and Beierman 1980, Kennedy *et al.* 1996, Loring *et al.* 1988, Sublette and Sublette 1967). Table 1 presents average water quality measurements for Playa 7 in 1994 and Playa 2 in 1995. In playas, water temperatures fluctuate widely through the seasons and on a daily bases. On September 02, 1995, temperature in Playa 2 increased by over 11°C from 18.3°C at 9:30 a.m. to 29.4°C at 5:00 p.m. Due to the shallow depth and great surface area, playa temperatures are strongly influenced by air temperatures (Sublette and Sublette 1967). The shallow water column in a playa is well mixed by the strong winds typical of the High Plains, but sharp gradients in temperature and DO can develop owing to the great turbidity that sometimes exists. Dissolved oxygen levels in playas can be very low and fluctuate widely due to high winds, photosynthesis, and biological oxygen demand of decaying organic matter. Conductivity can increase over the wet cycle, but a slight decline is often seen toward the end of the cycle (Loring *et al.* 1988). The trend of increasing conductivity is not universal, being influenced by evaporation, transpiration, infiltration, precipitation, and perhaps even usurpation by biological production. Values of pH, ranging from 6.5 to slightly over 8, usually fall between 7.2 and 7.5 (Sublette and Sublette 1963, Kennedy et al. 1996). When algae are prevalent, a diel cycle in pH can be discerned

(Kennedy et al. 1996). Phytoplanktonic biomass can represent a substantial autotrophic energy source for playa ecosystems (Loring et al. 1988). Chlorophyll *a* concentrations can reach over 30 mg/L (Kennedy et al. 1996). Kennedy *et al.* (1996) presents results of water quality measurements from the wet cycles of Playa 7 in 1994, Playa 2 in 1995, and 6 other playas in 1995.

Populations and Development

Callibaetis fits into the fourth and fifth strategies of tolerance/avoidance for organisms inhabiting temporary water bodies proposed by Wiggins *et al.* (1980) and Williams (1985). Populations are maintained in permanent water bodies or by dispersion among temporary pools. After a playa floods, gravid *Callibaetis floridanus* immigrate from established populations to colonize the new habitat.

Little information is available on how far gravid *Callibaetis* travel to oviposit. *C. floridanus* have been reported to be quiescent while eggs incubate (Trost and Berner 1963). However, *Callibaetis* is one of the few baetid genera of Pacific Islands, indicating that great distances are, at least, occasionally traveled (Edmunds 1972).

C. floridanus abundance estimates from depletion samples in Playa 2, 1995, are shown in Figure 3. Initial densities are low. Small early populations are probably a result of low densities of immigrating *C. floridanus* during this early colonization phase.

Populations of *C. floridanus* peaked on July 7, 1995, approximately one month after flooding. Increases in density are attributable to continued ovipositing of gravid females that have either immigrated to or emerged from the playa. Abundance decreased after July 7 and increased twice over the next two months (Figure 3). The drop in density during July is probably due to emergence. *C. floridanus* never reach the same density, presumably because of the large predator populations that develop in playas. Trost and Berner (1963) included a table showing that *C. floridanus* numbers decrease in the presence of predators.

Trost and Berner (1963) reported a change in the maximum size of the population as a unit. Through the wet cycle of Playa 2, maximum head capsule width decreased. Figure 4 illustrates the frequency distribution of head capsule widths for each sampling date. In the later part of the playa cycle, mature nymphs were smaller. Average air temperatures increased through the wet cycle, probably effecting the change in nymphal size (Sweeney 1984). Maximum and minimum temperature as well as precipitation data over the wet cycle of Playa 2 in 1995 are presented in Table 2 (National Weather Service).

Flooding date is the earliest possible start of nymphal development. *Callibaetis* oviposition requires water. Time that passes from playa flooding to emergence must be equal to, or greater than, minimum time requirements for nymphal development under environmental constraints of the playa.

Mature nymphs were first collected in Playa 2 on June 23, 1995, which was 21 days after the playa flooded. It is not known when oviposition occurred. 21 days is probably an overestimate of development time due to delayed oviposition and low immigration. During this early colonization phase, there were probably few large populations of *C. floridanus* established nearby to serve as sources of a large oviposition event. The wet cycle began early in the growing season (June), and air and water temperatures were low. Monthly average temperatures from May to July, 1995, were lower than a 42 year average compiled from 1948 - 1990 (National Weather Service).

During a preliminary study in 1994, a large oviposition event was witnessed at Playa 7. This large oviposition provided an excellent opportunity to get an estimate of playa development time that would not be overestimated by a lag between flooding and the start of a large, easily sampled, relatively synchronous population. Playa 7 flooded during storms on August 2-3, 1994. On the morning of August 6, thousands of female mayflies littered the surface as evidence that a large generation of nymphs began development shortly after the playa flooded.

C. floridanus development in Playa 7, 1994, was very fast. Mature nymphs with darkened wing pads were collected on August 15, only 14 days after the playa flooded. This is a conservative estimation of development time; development might have been shorter but could not have been longer.

During the 14 day development period in Playa 7, 1994, average temperature was about 23°C, totaling 324 accumulated degree-days (ADD). Other studies for eastern populations of *C. floridanus* have reported longer development times. A minimum time from oviposition to subimaginal emergence was reported as 27 days at about 30°C (810 ADD) and 60 to 75 days at 19°C (1140-1425 ADD) by Trost and Berner (1963). Christman and Voshell (1992) reported a much slower development rate of 77 days at 30°C (2310 ADD), attributing the slow development to "low food quality or quantity and lack of preferred habitat." Temperate aquatic insects typically have ADD requirements around 1300 degree-days, but some mayflies have developmental requirements of only 180-310 degree-days (Cummins 1974). Gray (1981) reports similar short development times for *C. montanus* and other mayflies in a lowland Sonoran Desert stream in Arizona. Rapid development is a common characteristic of insects that use temporary habitats (Wiggins *et al.* 1980).

C. floridanus has a seasonal multivoltine life history in playas of west Texas. *C. floridanus* has been reported as non-seasonal multivoltine in Florida (Trost and Berner 1963) and bivoltine in Virginia (Christman and Voshell 1992). Figure 5 shows an estimation of cohort development and emergence in Playa 2 (1995) based on degree-day requirements determined from Playa 7 (1994). The diagonal lines indicate cohort growth to emergence and are placed to link gaps in the population structure from sample date to sample date with consideration of the 324 degree-day developmental requirement. The first few generations are relatively distinct, but as the playa ages, the population becomes less synchronous. With developmental requirements of 324 degree-days in playas, *C. floridanus* could have produced at least 6 generations during the 2233 accumulated degree-days of Playa 2 in 1995.

Secondary Production

Head capsule width was a good indicator of nymphal dry weight. A highly significant regression of head capsule width to dry mass accounts for 99.3% of the variation: Ln(dry weight (mg)) = 3.343 (Ln(Head Capsule Width (um)) - 23.30 ($r^2 = 0.9931$, $p = 0.0001$, $N = 35$). The regression is illustrated in Figure 6.

C. floridanus is an important contributor to secondary production in playa ecosystems. Mean standing stock biomass was estimated as 0.199 g/m^2. Productivity was estimated at 11.7 g/m^2/0.25yr. Cohort production to biomass (P/B) ratio was 8.6. Table 3 illustrates the production calculations.

Cohort Production Interval (CPI) was determined based on the development in Playa 7 in 1994, when the circumstance of a large, early oviposition allowed a relatively precise measurement of 324 developmental degree-days. Accumulated degree-days over the 92 day wet period of Playa 2 was 2233 degree-days, yielding an average of 24.3 degrees per day, and CPI of 13.3 days. Benke's multivoltine modification calculates as 6.9.

Production estimates were based on 1/4 of a year because that was about the length of the wet cycle in 1995. This unit of time is more representative of playa wet cycle production than a full year. Extrapolated to 1 year, the production estimate is 46.8 g/m^2/yr. This value is meaningless except for comparison with seasonal production rates. Annual production of *C. floridanus* in west Texas playas is as variable as the playas themselves, depending on the length of the wet cycle. Even if a playa were flooded all year, production in the colder months would be much slower than the rate determined here. Most production estimates include data from a whole year, and, therefore, average in slower winter production rates. Average *C. floridanus* production in the Playa 2 basin for 1995 could be stated as an average of 4 seasons of production (3 seasons of which there was no production because the playa was dry) or 2.93 g/m^2/yr ((=11.7+0+0+0)/4). Even this conservative production estimate is relatively high.

Production of *C. floridanus* in west Texas was much greater than the production in Virginia (11.5 mg/sampler/yr) reported by Christman and Voshell (1992). Direct comparison of production rates is difficult due to the difference in spacial units. Christman and Voshell had a much longer CPI (175.5 days). Colder temperatures and poor habitat account for the reduced production.

There was good agreement between the P/B ratios of *C. floridanus* in west Texas and Virginia. Christman and Voshell (1992) report an annual P/B ratio of 16.4. Because *C. floridanus* exhibited a bivoltine life history in Virginia, the equivalent cohort P/B ratio is 8.2 and similar to the cohort P/B ratio in west Texas (8.6).

Production analysis is useful in determining the functional role of aquatic insects in ecosystems (Benke 1984). The only other production estimate of a playa invertebrate is for *Tropisternus lateralis nimbatus* (Say) (Coleoptera: Hydrophilidae). Cook (1997) estimated *T. lateralis* production at 1.31 g/m^2/0.25yr. This production value is directly comparable to the estimate for *C. floridanus* (11.7 g/m^2/0.25yr) because the units are identical. *T. lateralis* production was high but still much less than *C. floridanus* as would be expected because predatory *T. lateralis* occupies a higher trophic level.

CHAPTER VI

ANCILLARY STUDIES

Sexual Dimorphism

Sexual dimorphism is widespread in *Callibaetis* and reported by Trost and Berner (1963) for *Callibaetis floridanus*. One dimorphism is the turbinate eyes of adult males. As these eyes develop in male nymphs, head capsule width is affected. One of the densest samples, collected on 07July 95, was measured for head capsule widths, keeping track of the gender of larger nymphs. Nymphs with head widths over 1300 um were large enough to determine sex by the presence or absence of developing turbinate eyes. A highly significant difference between *C. floridanus* male and female nymphal head capsule widths over 1300 um was detected (Wilcoxon 2-sample test, $p = 0.0001$, $N = 256$). Figure 7 illustrates *C. floridanus* head capsule width difference between sexes.

Plastic Trap Collections

Gravid female *C. floridanus* were attracted to the plastic trap, apparently seeking water by visual cues. Schwind (1991) suggests that insects attracted to shiny surfaces key in on polarized light which reflects from the surface of water or smooth objects. The black plastic reflected and polarized light from the sky.

Number of gravid females attracted to the plastic trap was highly variable. During summer and fall of 1996, and spring, summer, and fall of 1997, 40 plastic trap method collection attempts were made. Figure 8 presents results of plastic trap method collection attempts with morning temperatures. Collection attempts near Amarillo, Tx. are indicated by an asterisk. Half of the time no mayflies were caught; another 25% of the time 1 or 2 were caught. More than two mayflies were collected on only 25% of the collection attempts. The largest collections were 22 mayflies on August 23, 1996, and 13 on June 20, 1997, both collections were made near Denton, Tx.

The only mayflies collected with the plastic trap method near Amarillo, Tx., were one gravid female each of two days out of 10 collection attempts. Although no more than one mayfly was collected per collection attempt in west Texas, if the area of plastic is extrapolated to the size of a playa, even 1 mayfly attempting to oviposit on the plastic is equivalent to thousands of mayflies on a playa. All collections of more than one mayfly, were made near Denton. Greater aerial density near Denton is expected due to the wetter climate and lower winds of north central Texas. Average wind speed throughout the collections was less than 5 mph near Denton and over 10 mph near Amarillo. Higher winds may have contributed to the infrequency of mayfly collections near Amarillo by blowing gravid females off the plastic before they were discovered and collected.

Temperature and number of mayflies collected with the plastic trap method were weakly correlated (Spearman rank correlation, $r = 0.61$, $N = 34$, $p = 0.0001$). Figure 9 plots number of mayflies collected against morning temperature. Numbers in the graph indicate multiple observations. Morning temperature data were not recorded during the early collections in 1996. Data with missing morning temperatures were not used in the correlation analysis.

Fecundity

Counting of eggs laid by females collected on the plastic showed the number of eggs carried to be variable. Egg counts ranged from 436 to 1074.

Adult size influences fecundity. A significant regression between number of eggs and wing length ((Number of Eggs = (Wing Length(um))(0.2627) - 1080.5; r^2 = 0.8376, N = 9, p = 0.0099)) explained 84 percent of the variation. Figure 10 shows the regression of fecundity on wing length. Wings were used as adult size measures instead of head capsule widths because they produced a regression with a higher coefficient of determination (r^2). Wing lengths are much larger than head widths, reducing measurement error. Head width and wing length of female adults were highly significantly correlated (Spearman rank correlation, r = 0.9916, N = 9, p = 0.0001). This correlation shows that head capsule width, as an indication of size, applies to adults as well as nymphs, and it can be assumed that larger nymphs yield larger adults with greater reproductive potential.

Rearing Studies

Incubator rearing of 1st instar nymphs from gravid females collected from the University of North Texas Water Research Field Station near Denton, Texas showed development rates similar to those reported by Trost and Berner (1963). At 18°C the median development time was 81.5 days, with a minimum of 68 days and a maximum of 104 days. Nymphs held at 23°C developed in 32 to 71 days with a median of 46 days. 28°C incubator tanks produced subimagoes in between 22 and 37 days with a median of 25 days. A degree-day model for these data is shown in Figure 11 with development rate plotted against temperature. A best fit line of the median development rates from 7 tanks is described by the equation: Development Rate = (0.0024)(Celsius Temperature) - 0.033. Minimum cardinal temperature is estimated at 13.75°C.

The apparent difference in development rates between the incubator reared mayflies from Denton and the field populations in west Texas could be evidence of genomic differences. West Texas mayflies may be more adapted for the ephemeral playa ecosystems. Another explanation, however, would be the incubator simulated habitat was poor and did not represent playa habitats. Limits on secondary production can be related to "food quality and quantity, temperature, habitat complexity, and biological interactions" (Benke 1984).

Head capsule widths of adults emerging from different incubator temperatures were significantly different (Females: Kruskal Wallis one-way multisample test, $N = 40$, $p = 0.0328$; Males: Kruskal Wallis one-way multisample test, $N = 38$, $p = 0.0099$). Figure 12 illustrates the size of adults reared at different temperatures. Males emerging from 18°C incubators were significantly larger than males emerging from 28°C incubators (Tukey multiple range test on ranked data, $N = 38$, $p < 0.05$). All other pairwise comparisons among males were not significant. Males reared at 18°C were not significantly different from males reared at 23°C probably due to small sample size. Despite small sample size and considerable overlap, a significant difference was detected between females reared at 18°C and females reared at 23 or 28°C (Tukey multiple range test on ranked data, $N = 40$, $p < 0.05$). Females from the 23 and 28°C tanks did not form statistically distinct groups.

Additional Note

A large emergence from Playa 7 was witnessed on September 6, 1996. It was a rainy evening; near sunset large numbers of mayfly subimagoes were noticed near the playa. Just after dark, in the grass emerging from the playa, a flashlight shone horizontally through the vegetation revealed the shining white wings of mayfly subimagoes. Densities were estimated to average 1 mayfly for every 2 m^2, with maximum densities of $3/m^2$ and minimum densities of at lease 1 in every 3 m^2. By 10:30 p.m., a walk into the playa revealed only 4 subimagoes, indicating that most had moved from the emergent playa grass.

CHAPTER VII

CONCLUSION

The objective of this study was to explore the life history of *Callibaetis floridanus* in a playa of west Texas. Density fluctuated through the wet cycle as cohorts emerged, and it decreased with higher predator density. Development required less than 14 days resulting in a multivoltine life history. Secondary production was high, estimated at 11.7 $g/m^2/0.25yr$.

C. floridanus exhibits many characteristics that are common to organisms that inhabit temporary habitats. Fast life cycles and high reproductive capability typify *C. floridanus* and other playa insects. *C. floridanus* is very important to playas, reaching high densities and transferring energy to higher trophic levels. Based on the dominant numbers and large production values of *C. floridanus*, they are a major foundation for predators such as *Tropisternus lateralis* that colonize playas.

Additional research on playa ecology is required to increase our understanding of playa ecosystems. Playas are unique systems with advantages for researchers. In particular, the ephemeral nature of playas, which has hampered many research ambitions because of its unpredictability, is helpful in determining development rates of aquatic organisms. Playas have received little attention although they are one of the most defining and important ecological features of the Southern High Plains.

Table 1. Average water quality measurements over the wet cycles of Playa 7 in 1994 and Playa 2 in 1995.

Playa 7 (1994)	17-Aug	03-Sep	17-Sep	01-Oct	15-Oct	29-Oct
Temperature (C)	19.3	21.4	16.5	13.5	9.6	7.0
DO (mg/L)	0.4	7.0	2.0	1.3	4.5	4.2
pH	6.7	7.4	7.3	7.6	7.6	7.8
Chl *a* (mg/m^3)	73.3	25.7	22.4	15.9	14.5	NA
Turbidity (NTU)	15.8	5.7	28.9	33.0	103.9	49.7
Conductivity (umho)	157	210	211	230	265	282
Playa 2 (1995)	11-Jun	08-Jul	04-Aug	02-Sep		30-Sep
Temperature (C)	14.9	22	21.5	18.5	Playa	16.8
DO (mg/L)	1.4	0.8	0.9	1.3	Dry	3.8
pH	7.1	6.8	7.0	7.3		7.1
Chl *a* (mg/m^3)	0.5	13.2	31.4	8.2		10.3
Turbidity (NTU)	69.5	10.3	13.1	14.1		128.3
Conductivity (umho)	NA	242	270	343		212

Table 2. Maximum and minimum temperatures and precipitation over the wet cycle of Playa 2 in 1995 (National Weather Service).

	Temperature (C)			Precip.
Date	Max	Min	Mean	(inches)
29May95	16.1	10.0	13.1	1.10
30May95	23.9	9.4	16.7	0.68
31May95	24.4	10.6	17.5	T
01Jun95	26.7	12.2	19.4	
02Jun95	26.7	14.4	20.6	0.18
03Jun95	20.6	13.9	17.2	0.64
04Jun95	24.4	13.3	18.9	T
05Jun95	26.1	13.3	19.7	0.02
06Jun95	33.9	14.4	24.2	
07Jun95	30.0	12.8	21.4	
08Jun95	31.7	17.2	24.4	
09Jun95	27.8	17.8	22.8	
10Jun95	17.8	10.0	13.9	0.06
11Jun95	23.3	9.4	16.4	
12Jun95	30.6	11.7	21.1	
13Jun95	34.4	16.1	25.3	
14Jun95	36.7	17.2	26.9	
15Jun95	33.3	17.2	25.3	
16Jun95	30.6	15.6	23.1	
17Jun95	26.7	15.6	21.1	
18Jun95	27.8	17.2	22.5	
19Jun95	30.0	16.7	23.3	
20Jun95	31.1	17.2	24.2	
21Jun95	31.1	17.2	24.2	0.06
22Jun95	31.7	13.9	22.8	
23Jun95	31.7	13.3	22.5	0.48
24Jun95	26.7	14.4	20.6	T
25Jun95	28.3	13.9	21.1	T
26Jun95	30.6	12.8	21.7	1.12
27Jun95	28.9	12.8	20.8	
28Jun95	32.8	16.7	24.7	0.14
29Jun95	22.2	14.4	18.3	0.01
30Jun95	23.3	13.3	18.3	
01Jul95	27.2	13.9	20.6	1.22
02Jul95	30.0	14.4	22.2	0.26
03Jul95	32.8	15.6	24.2	
04Jul95	27.8	15.0	21.4	
05Jul95	29.4	11.7	20.6	
06Jul95	31.7	15.6	23.6	
07Jul95	32.8	17.8	25.3	
08Jul95	33.9	17.2	25.6	
09Jul95	34.4	18.3	26.4	
10Jul95	36.1	17.2	26.7	
11Jul95	36.1	18.9	27.5	
12Jul95	36.1	17.8	26.9	
13Jul95	33.9	18.9	26.4	
14Jul95	33.9	18.9	26.4	
15Jul95	29.4	18.9	24.2	T
16Jul95	32.2	17.8	25.0	0.95
17Jul95	27.8	18.3	23.1	0.02
18Jul95	23.3	17.8	20.6	0.14
19Jul95	31.7	17.8	24.7	T
20Jul95	31.1	19.4	25.3	T
21Jul95	33.9	18.9	26.4	0.03
22Jul95	35.0	17.8	26.4	0.04
23Jul95	33.3	17.2	25.3	0.17
24Jul95	32.2	14.4	23.3	
25Jul95	36.7	17.2	26.9	
26Jul95	37.2	18.9	28.1	
27Jul95	40.0	20.0	30.0	
28Jul95	38.9	18.9	28.9	
29Jul95	37.2	18.3	27.8	
30Jul95	31.1	20.0	25.6	
31Jul95	30.6	16.7	23.6	0.02
01Aug95	20.6	14.4	17.5	T
02Aug95	23.9	16.7	20.3	T
03Aug95	31.1	17.2	24.2	
04Aug95	31.1	17.8	24.4	
05Aug95	34.4	18.3	26.4	0.20
06Aug95	35.6	16.1	25.8	
07Aug95	36.7	20.6	28.6	
08Aug95	35.6	20.0	27.8	
09Aug95	35.0	22.8	28.9	
10Aug95	35.0	18.9	26.9	
11Aug95	35.6	18.3	26.9	
12Aug95	36.1	18.9	27.5	
13Aug95	35.6	18.3	26.9	
14Aug95	33.3	18.9	26.1	1.95
15Aug95	28.3	18.3	23.3	0.03
16Aug95	31.7	19.4	25.6	
17Aug95	32.8	21.1	26.9	
18Aug95	32.8	17.8	25.3	
19Aug95	31.7	18.3	25.0	
20Aug95	32.2	18.9	25.6	
21Aug95	32.8	17.8	25.3	
22Aug95	32.2	18.3	25.3	
23Aug95	31.7	17.8	24.7	
24Aug95	32.2	17.8	25.0	
25Aug95	33.3	18.9	26.1	
26Aug95	33.3	18.9	26.1	
27Aug95	33.3	17.8	25.6	
28Aug95	33.3	17.8	25.6	
29Aug95	35.0	19.4	27.2	
30Aug95	35.6	20.6	28.1	
31Aug95	34.4	20.0	27.2	T
01Sep95	34.4	17.8	26.1	
02Sep95	35.0	16.1	25.6	

Table 3. Size frequency method production calculations for *C. floridanus* in Playa 2 in 1995.

Size Class	Annual Mean Density (#/m^2)	Mean Class Weight (mg)	Biomass (mg/m^2)	Number Lost (#/m^2)	Median Head Weight (mg)	Average Median Weight (mg)	Weight Loss (mg/m^2)	X 15 Size Classes (mg/m^2)	Negatives Set To Zero (mg/m^2)
I	0.76	0.010	0.01	NA	0.010				
II	2.08	0.020	0.04	-1.3	0.020	0.015	-0.02	-0.3	0
III	3.48	0.039	0.14	-1.4	0.040	0.030	-0.04	-0.6	0
IV	4.64	0.063	0.29	-1.2	0.064	0.052	-0.06	-0.9	0
V	7.76	0.105	0.81	-3.1	0.106	0.085	-0.27	-4.0	0
VI	9.88	0.163	1.61	-2.1	0.163	0.135	-0.29	-4.3	0
VII	11.48	0.249	2.86	-1.6	0.252	0.207	-0.33	-5.0	0
VIII	15.00	0.362	5.43	-3.5	0.362	0.307	-1.08	-16.2	0
IX	13.68	0.513	7.02	1.3	0.513	0.437	0.58	8.7	8.7
X	11.48	0.705	8.09	2.2	0.722	0.617	1.36	20.4	20.4
XI	10.80	0.955	10.32	0.7	0.954	0.838	0.57	8.5	8.5
XII	9.12	1.374	12.53	1.7	1.383	1.168	1.96	29.4	29.4
XIII	11.36	1.836	20.86	-2.2	1.820	1.602	-3.59	-53.8	0
XIV	37.32	2.588	96.59	-26.0	2.610	2.215	-57.51	-862.7	0
XV	10.20	3.159	32.23	27.1	3.094	2.852	77.35	1,160.2	1,160.2
				10.2		3.094	31.56	473.4	473.4
	Mean		Mean Standing						
	Density		Stock Biomass						1,700.6
	159/m^2		199 mg/m^2		Multivoltine Modification = 92/13.3				X 6.9
									11,724.2
			Annual Production = 11.7 g/m^2/0.25yr						

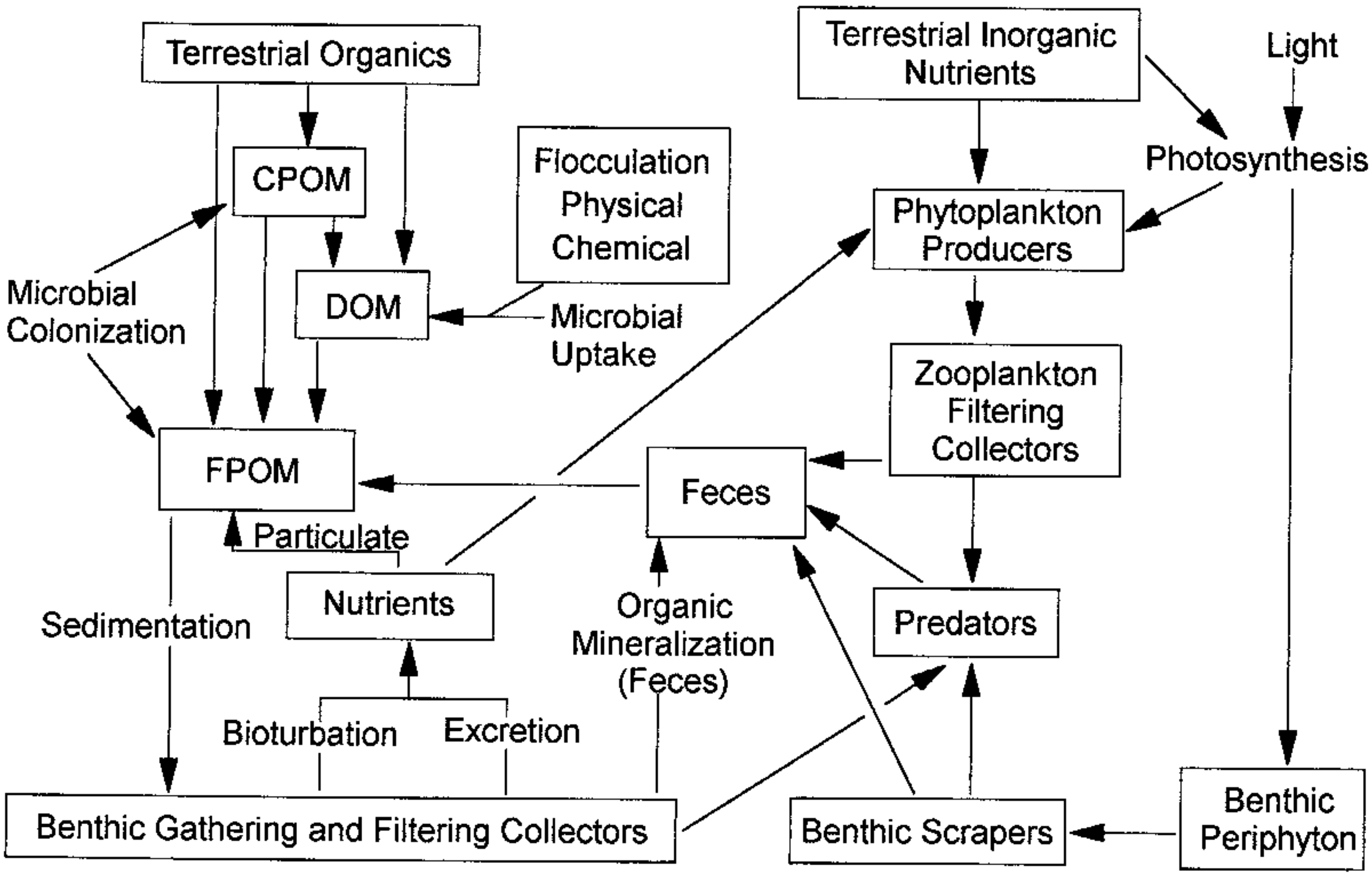


Figure 1. Conceptual model of nutritional resource catagories and invertebrate feeding groups for playas.

Figure 2. Study playas relative to Amarillo and the Llano Estacado.

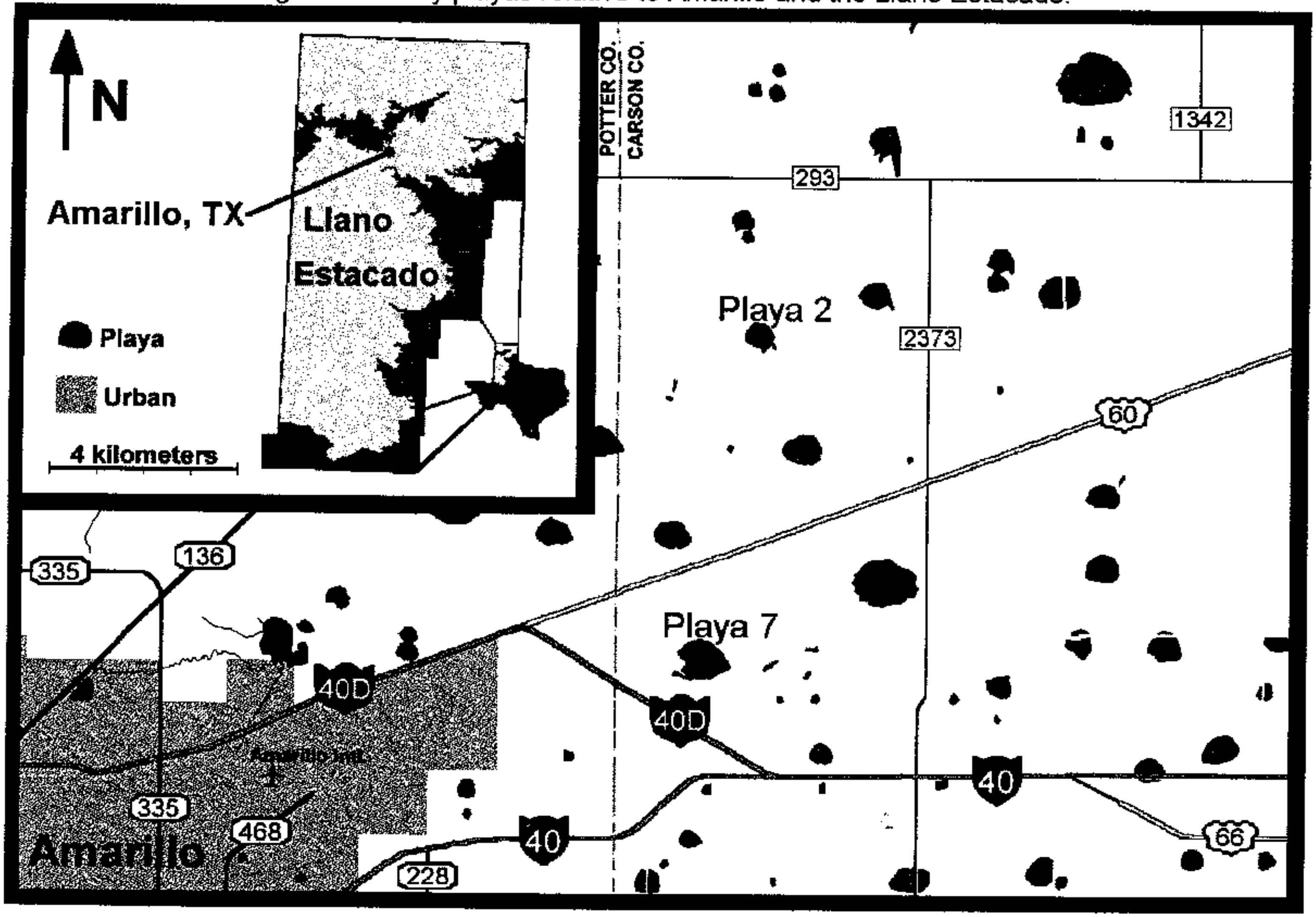


Figure 3. Average nymphal density and standard deviation from depletion samples.

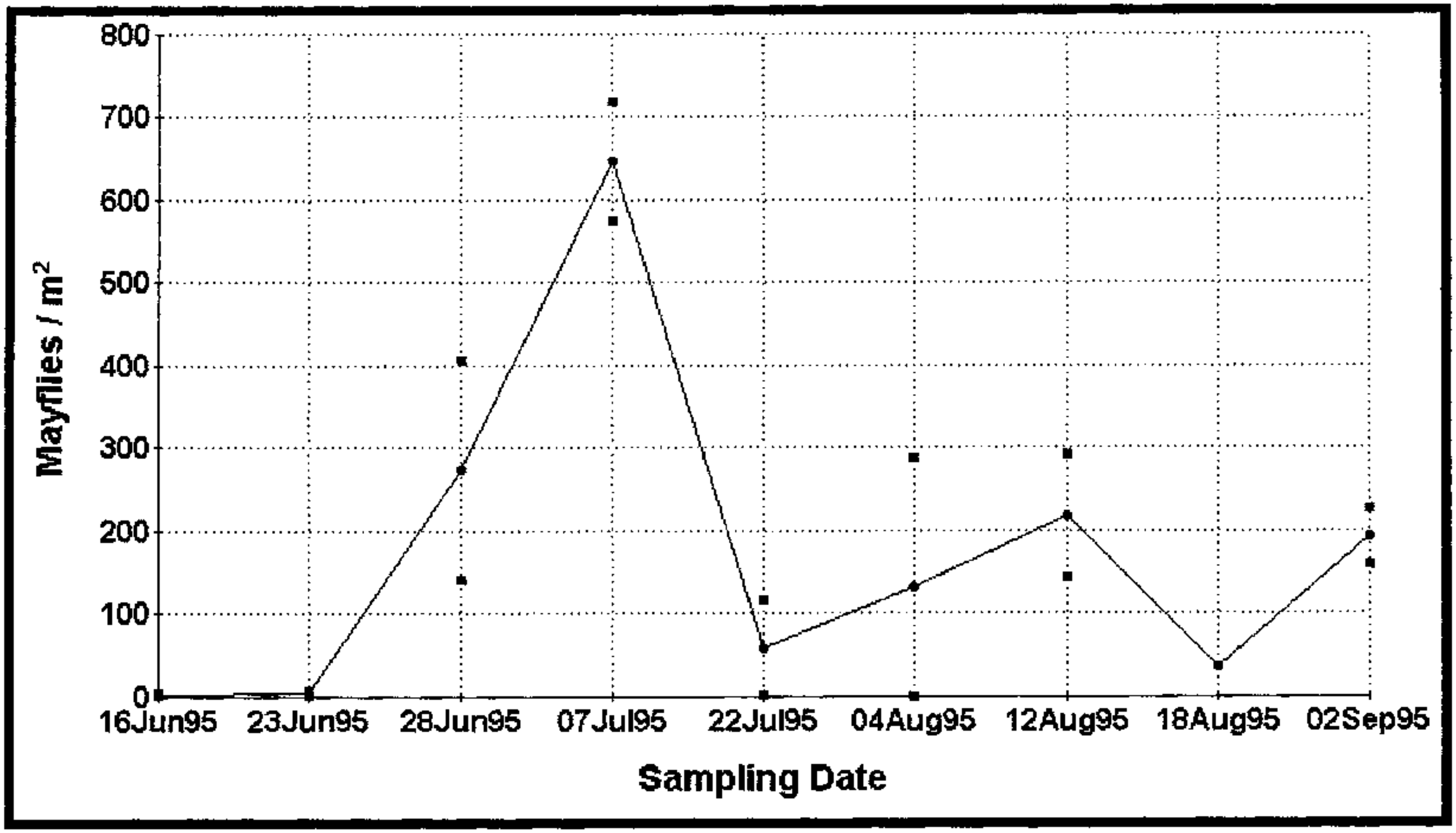


Figure 4. Head capsule width histogram for each sample date with mean density (#/m^2).

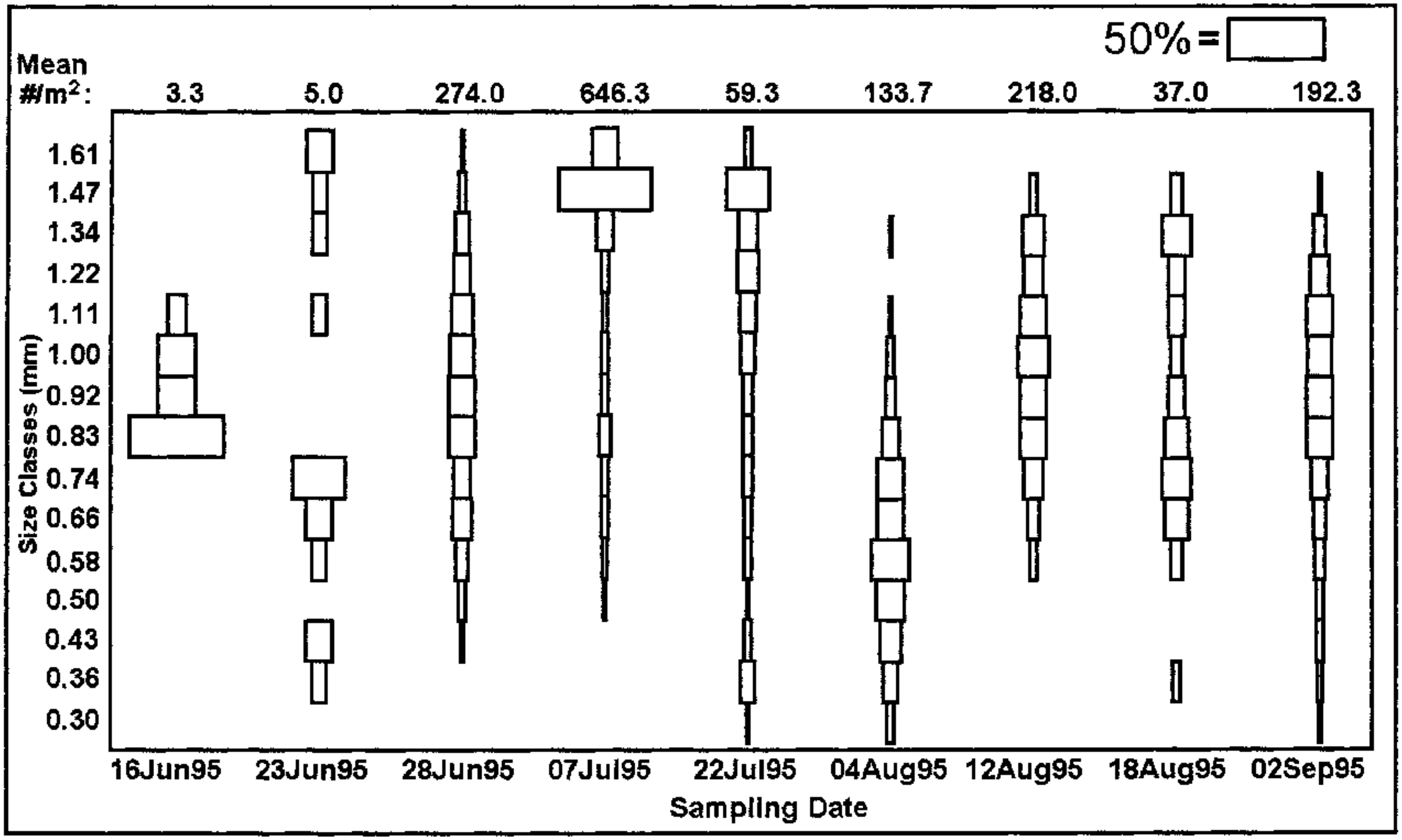


Figure 5. Size frequency distribution of *C. floridanus* spaced by date with cohort development and emergence lines based on accumulated degree-days.

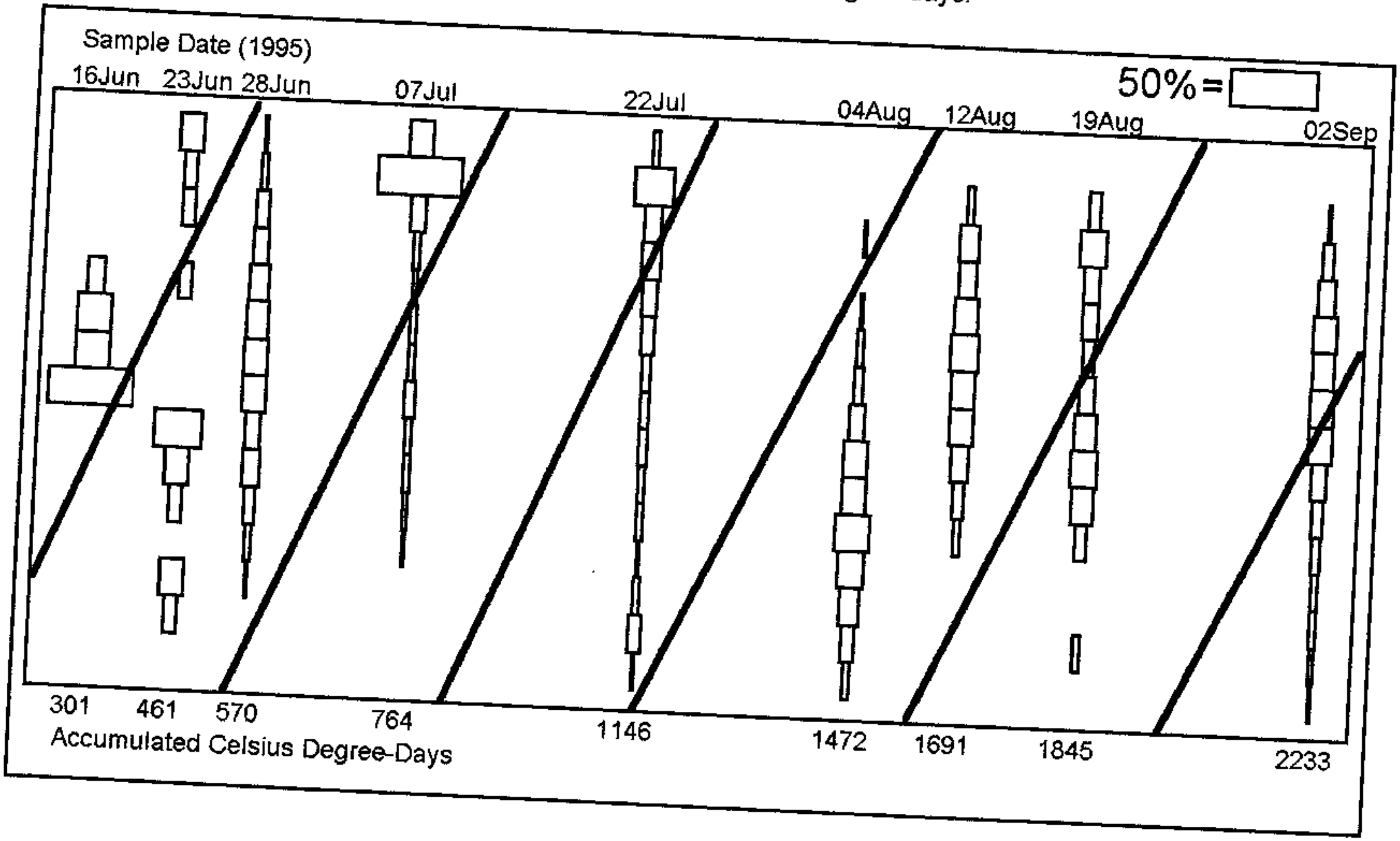


Figure 6. Ln-Ln regression of head width to dry mass (r^2 = 0.9931, p = 0.0001, N = 35).

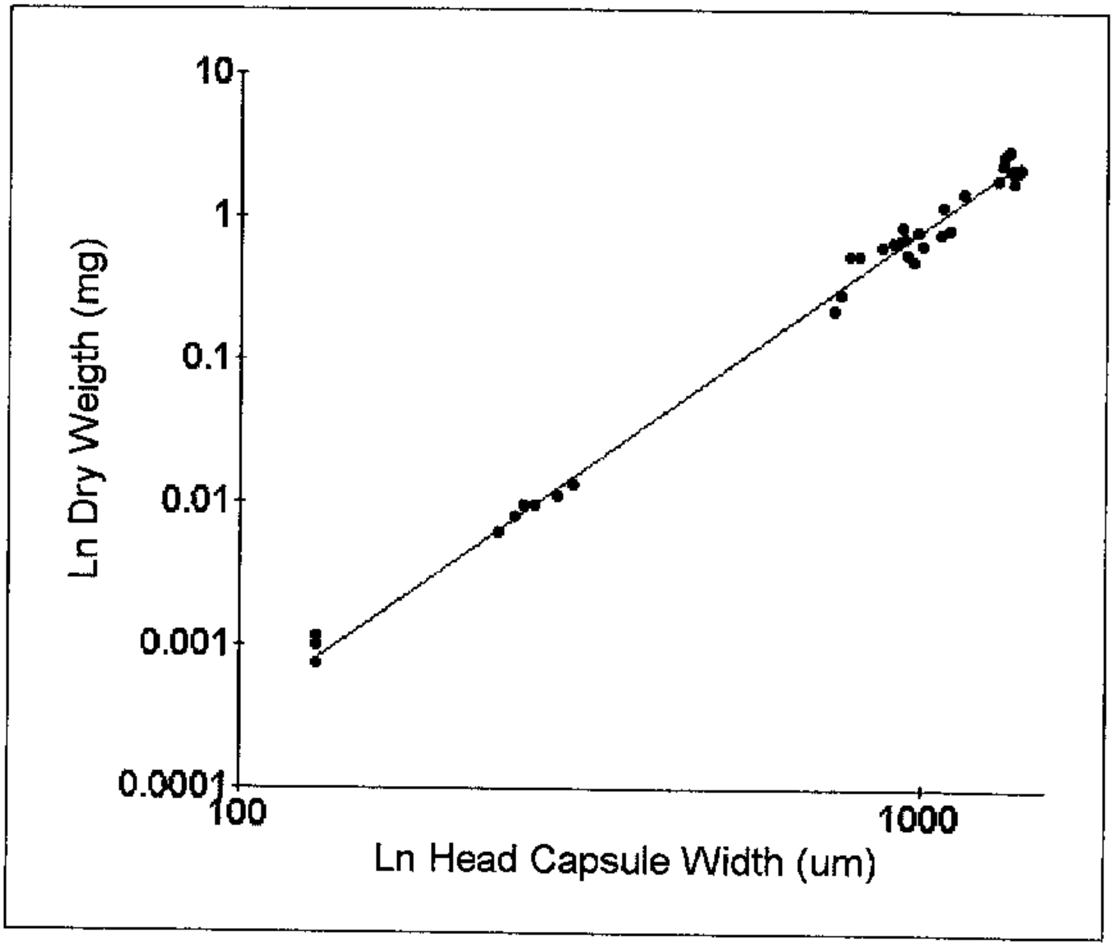


Figure 7. Sexual dimorphism in head capsule width frequency.

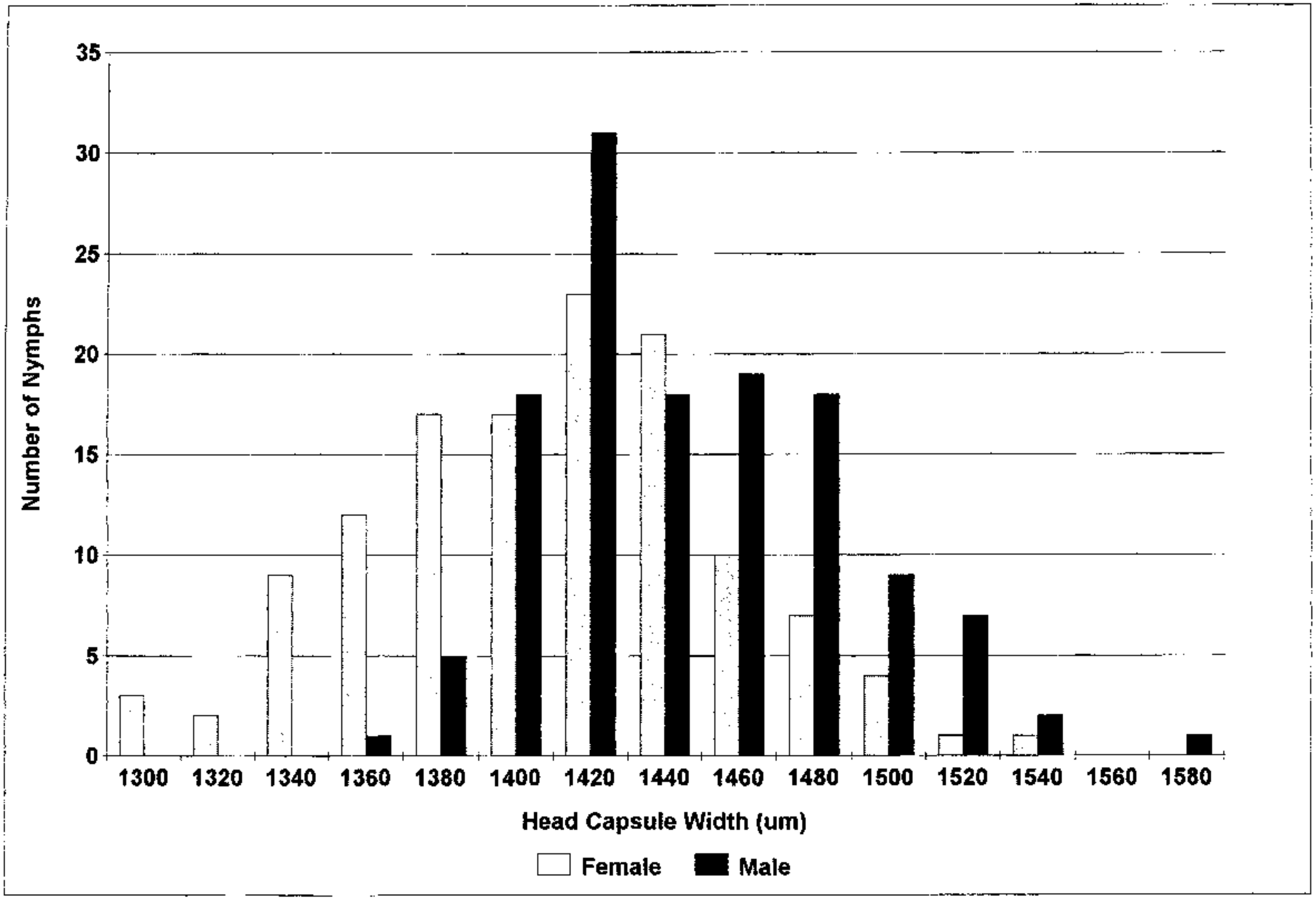
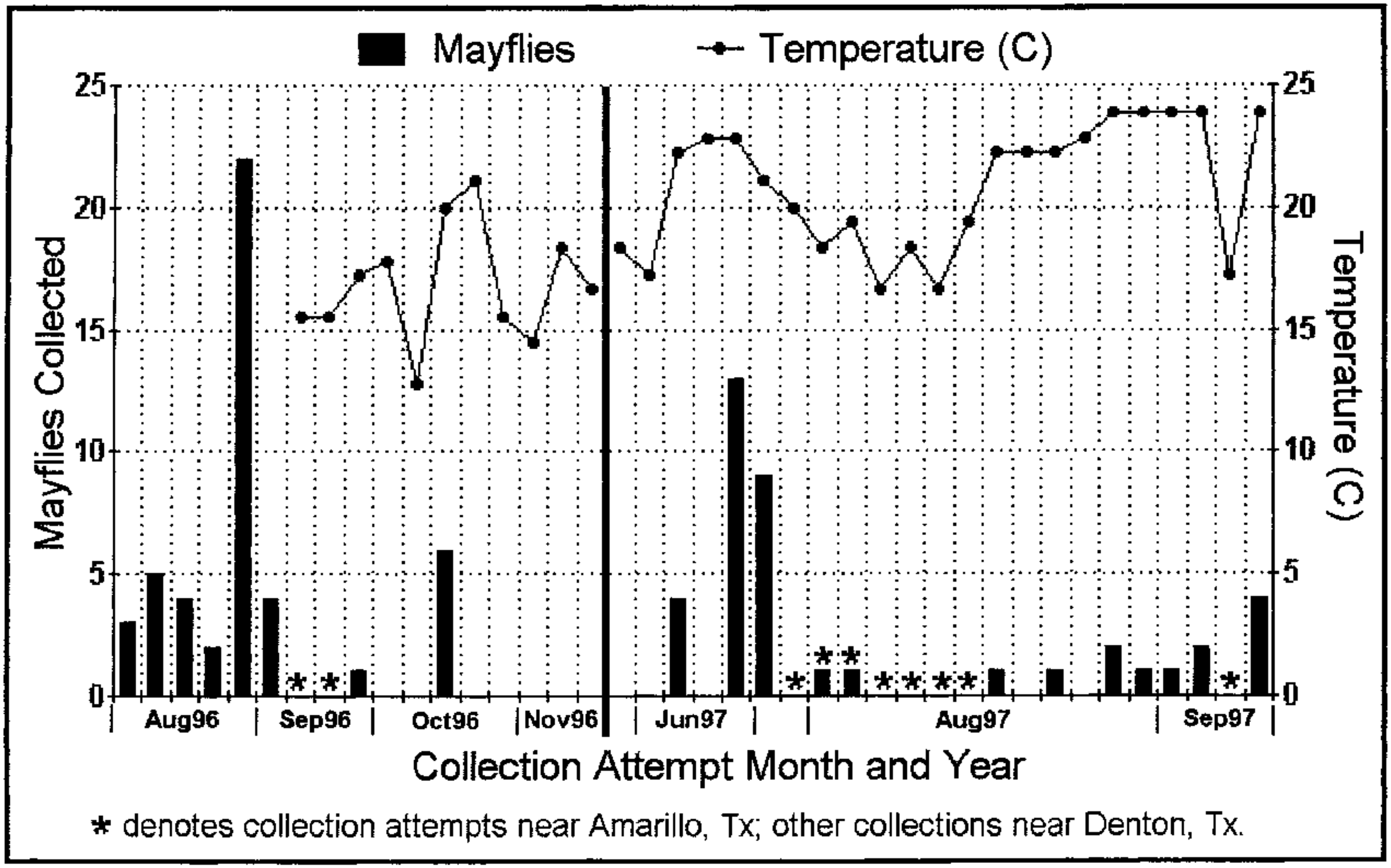


Figure 8. *Callibaetis floridanus* collections from polarizing black plastic with morning temperature and location.



* denotes collection attempts near Amarillo, Tx; other collections near Denton, Tx.

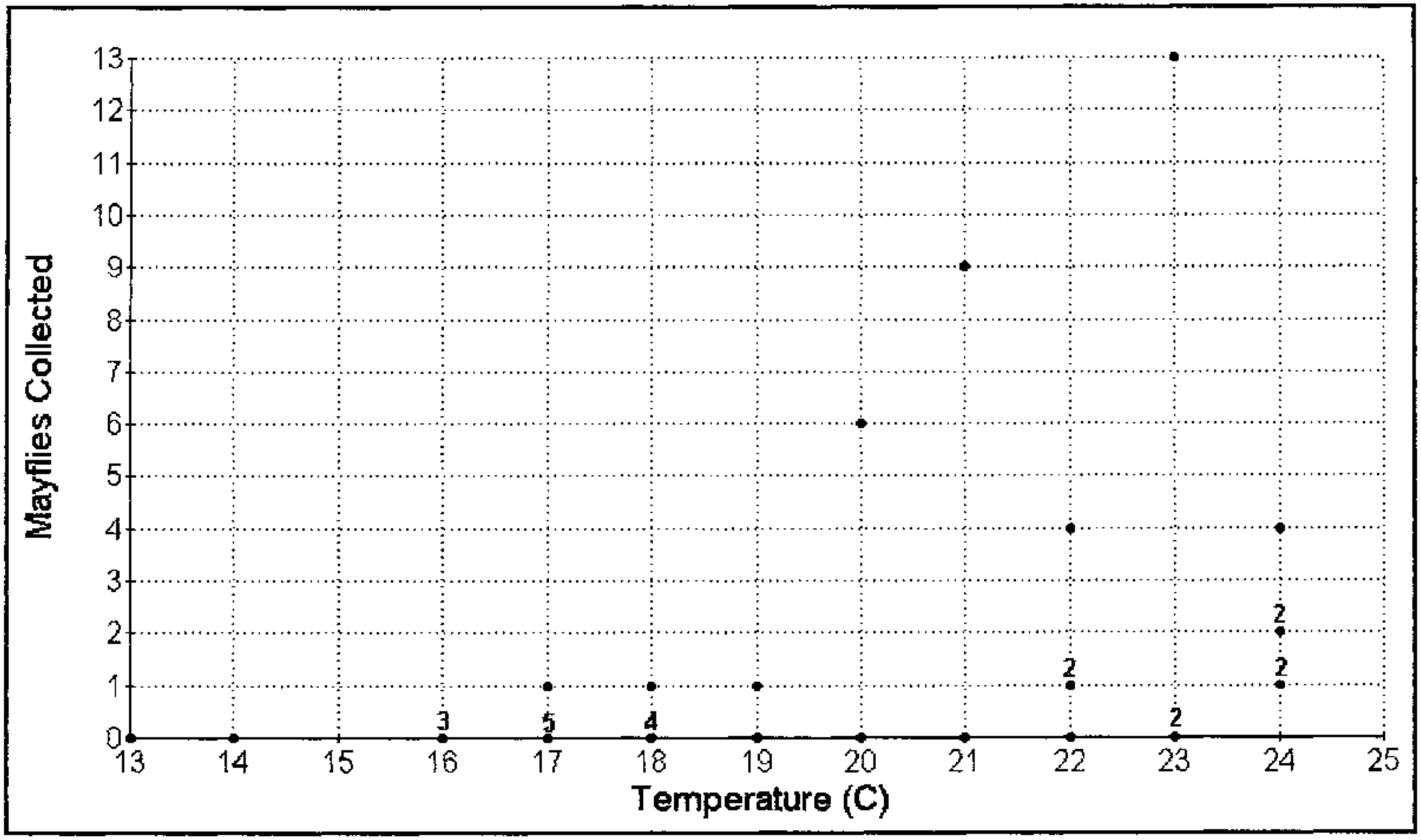


Figure 9. Number of mayflies collected at different morning temperatures. Numbers indicate multiple observations.

Figure 10. Regression of fecundity on wing length of gravid *C. floridanus* collected on from plastic trap ((Number of Eggs = (Wing Length(um))(0.2627) - 1080.5; $r^2 = 0.8376$, $N = 9$, $p = 0.0099$)).

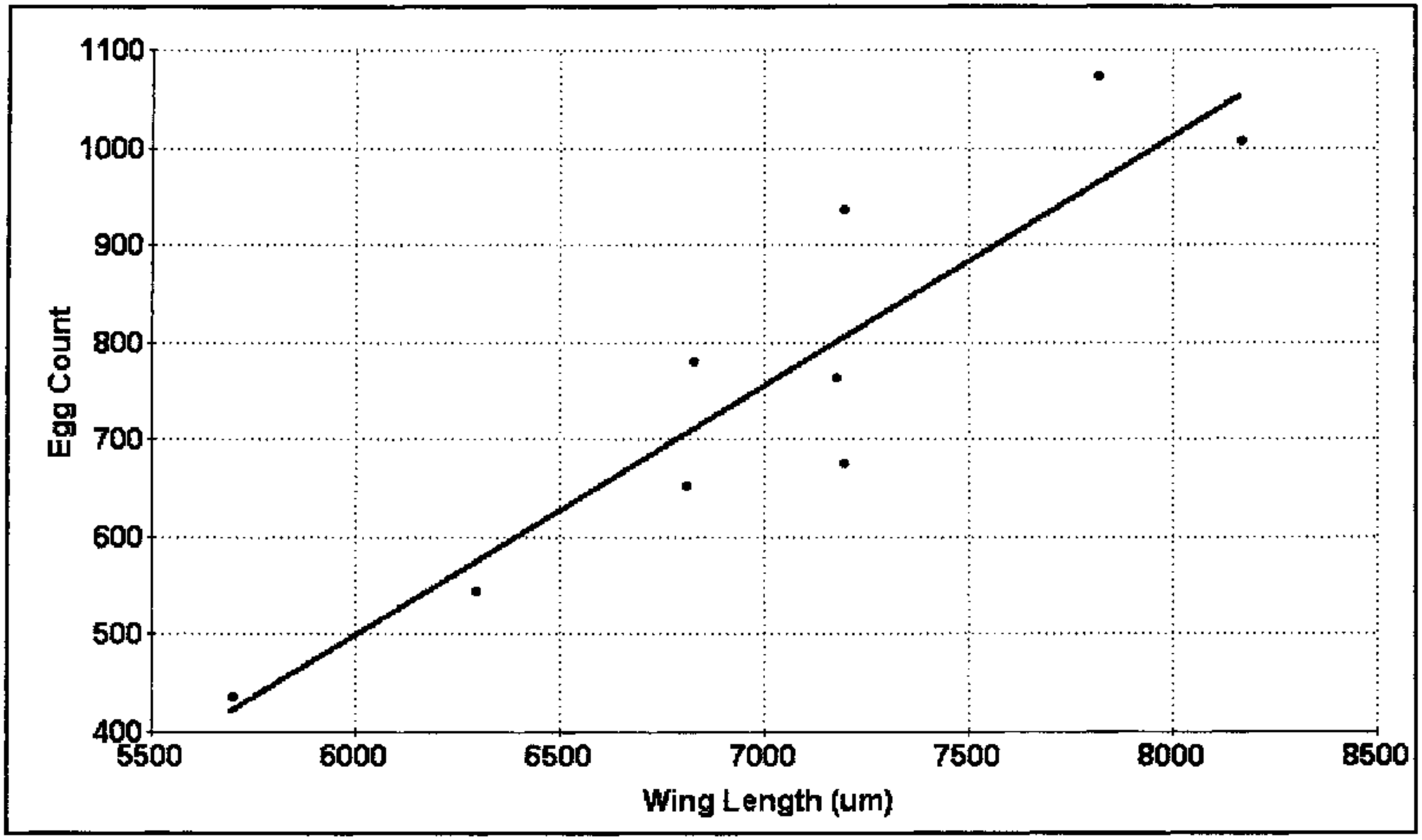


Figure 11. Degree-day model of *Callibaetis floridanus* development in incubators. Minimum cardinal temperature is estimated at 13.75°C

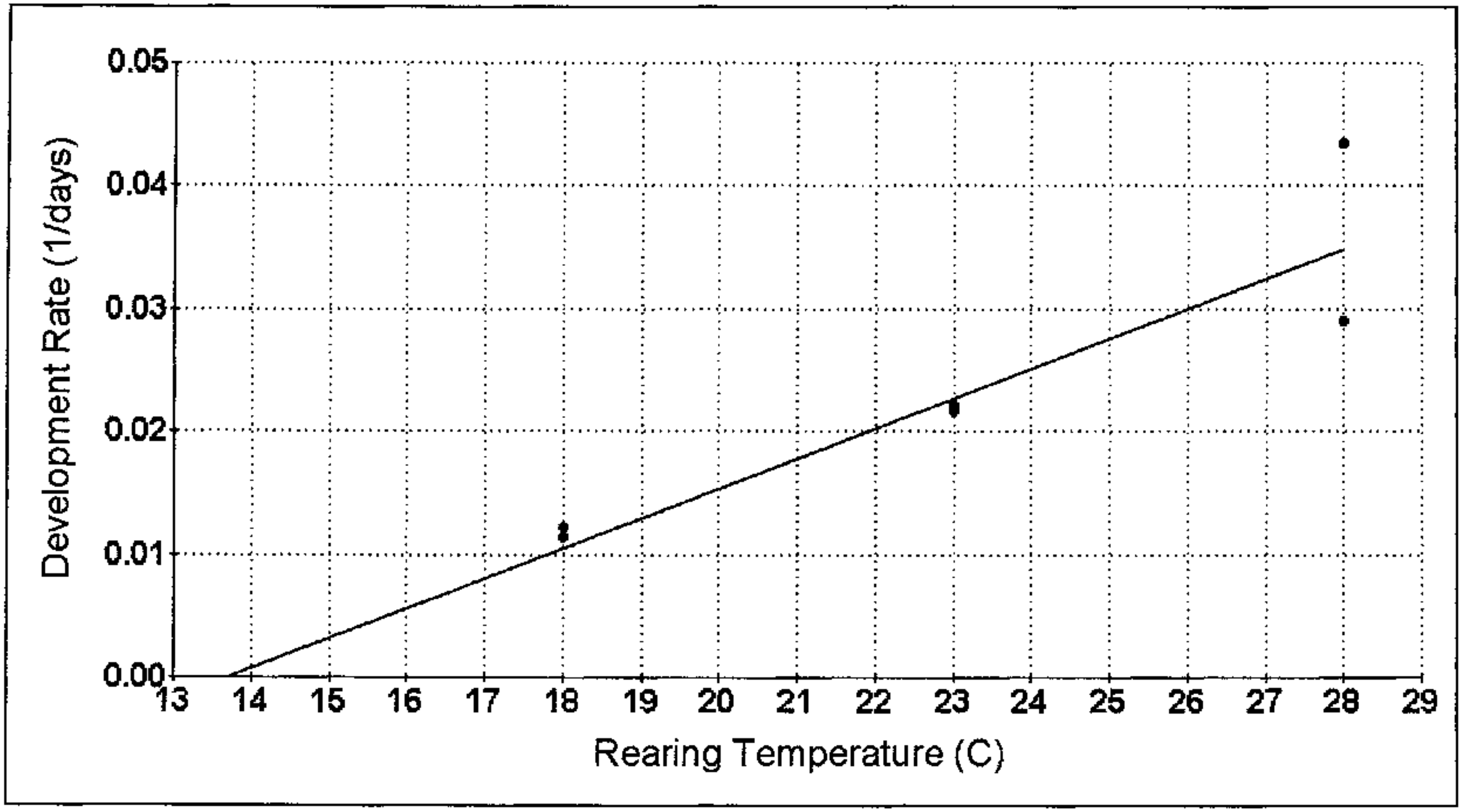
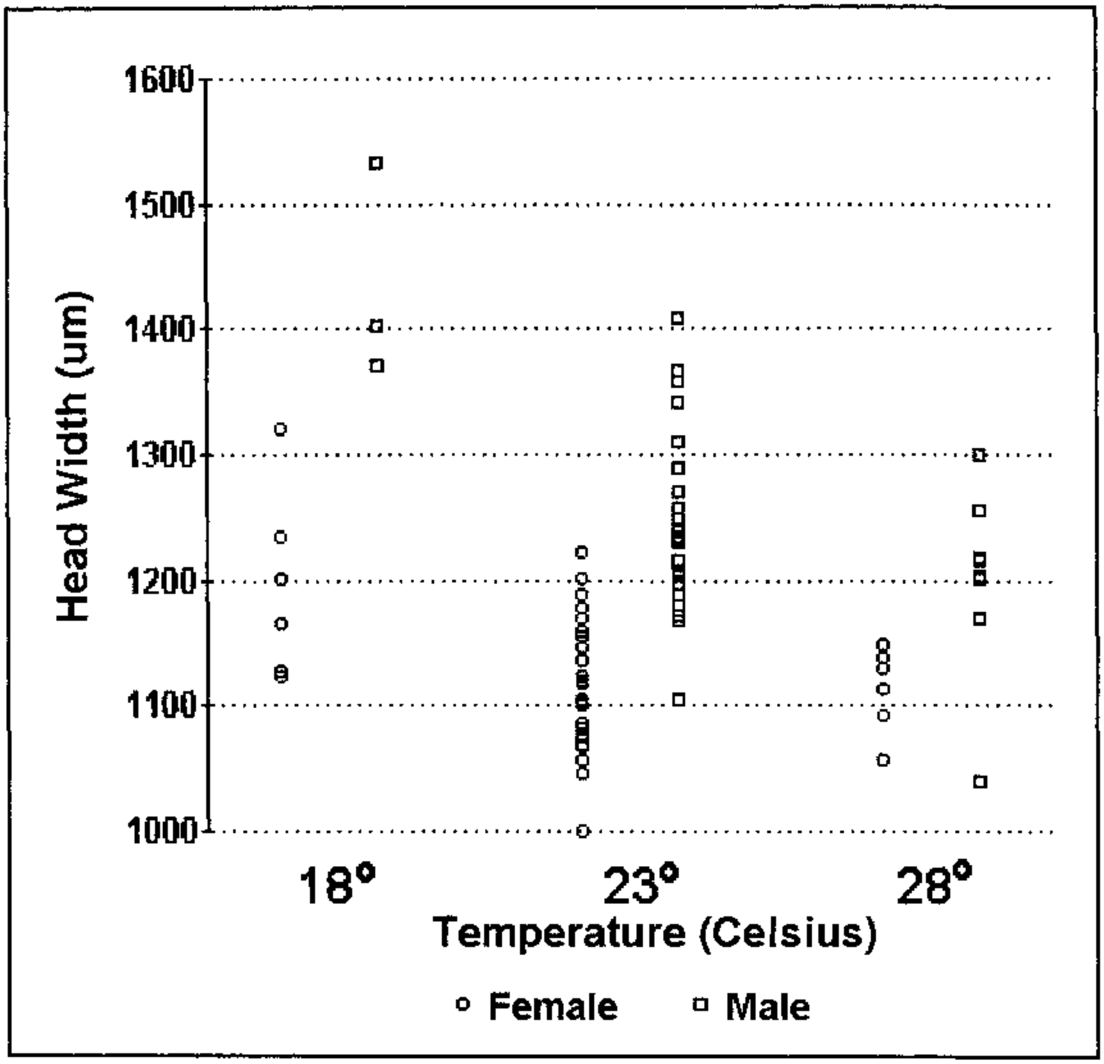


Figure 12. Head capsule width measurements from *C. floridanus* adults reared at different temperatures.



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