

AN ABSTRACT OF THE THESIS OF

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Title: BIOLOGICAL STUDIES ON SALDULA PALUSTRIS  
(DOUGLAS) WITH EMPHASIS ON FACTORS INFLUENCING  
WING PIGMENTATION (HETEROPTERA:SALDIDAE)

Abstract approved: Redacted for Privacy  
Dr. J. D. Lattin

The life history and wing pattern variation of the intertidal shore bug, Saldula palustris (Douglas), were studied in field and experimental populations from June 1970 until February 1972.

The study site was an estuarine salt marsh on Yaquina Bay near Toledo, Oregon. The insects live below mean high water level and are regularly submerged by the tide for up to ten hours. Behavior of S. palustris upon submergence is well adapted to the intertidal habitat.

Overwintering occurs in the adult stage and adults migrate from the intertidal area in late fall. The reproductive period begins upon their return in February with mating, egg development, and oviposition and ends in September with cessation of these activities. The first adults of the spring generation appear in mid-May. There

are three generations a year and reproductive diapause in fall and winter is facultative.

Mean adult wing darkness (based on percent dark area in wing membrane) in field collections varied from palest in mid-summer (45-50% dark) to darkest in late fall (65-70% dark). Males and females were in general not significantly different in wing darkness.

Wings of females are longer (and wing membrane area larger) than those of males. Maximum wing lengths were found in adults collected during the spring and late summer. Wing darkness was not associated with wing size in each sample but correlations over time, related to the emergence of the different generations, were observed. Aging had no effect on the extent of pigmentation in adult wings.

Temperature effects on the insects were investigated in some detail since previous reports showed that temperature was a major factor influencing the life history and morphological variation of insects. Developmental threshold temperatures, determined in the laboratory for S. palustris (10° C for embryonic development and hatching, 15° C for development to adult), were correlated with mean field temperatures and the first and last appearance of the various developmental stages in the field in spring and fall.

Temperature had the greatest effect on resulting adult wing darkness during the third and fourth nymphal stages, cooler

temperatures producing darker adults. Similarly, cool rearing temperatures produced significantly darker fifth instar cuticles if the nymphs were subjected to the lower temperature prior to the fifth instar. As with adults, nymphs do not darken after hardening following the moult.

Adults reared from the fourth instar stage on a black substrate had significantly darker wings than adults reared from similar age on a white substrate.

Biological Studies on Saldula palustris (Douglas) with  
Emphasis on Factors Influencing Wing Pigmentation  
(Heteroptera:Saldidae)

by

Mary Wilford Stock

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BIOLOGICAL STUDIES ON SALDULA PALUSTRIS (DOUGLAS)  
WITH EMPHASIS ON FACTORS INFLUENCING WING  
PIGMENTATION (HETEROPTERA:SALDIDAE)

INTRODUCTION

This investigation focuses upon variation in wing pigmentation in a population of Saldula palustris (Douglas) on the coast of Oregon. This insect was selected for study because it exists in dense populations in coastal salt marshes; it represents a taxonomic group in which forewing pigmentation is known to be extremely variable; and, being intertidal in habitat, is subjected to unusual environmental conditions which can influence the life history and morphological variation of the insect.

Members of the family Saldidae, commonly known as shore-bugs, are worldwide in distribution. They are small, oval, flattened insects with large, prominent eyes. Most species are inconspicuous inhabitants of the margins of fresh, alkaline, and saline bodies of water. Saldids are often referred to as semi-aquatic insects and species within the family range in habitat from terrestrial to almost completely aquatic. A few species, such as Saldula orthochila (Fieber) are completely terrestrial. Others are found below the high-tide line along oceans and estuaries and are regularly submerged by the tide. Members of the genera Saldula Van Duzee, Aepophilus

Signoret, Orthophrys Horvath, Salduncula Brown, and several others, are intertidal in habitat; some living on wave-washed exposed rocky shores, others in protected estuarine salt marshes, as does S. palustris in Oregon.

Environmental factors affecting intertidal organisms are extremely variable (MacDonald, 1969). The unique interaction of tidal submergence and exposure with diurnal and seasonal fluctuations of oceanographic and climatic variables affects many aspects of the life history and morphology of the insects. Thus, intertidal insects such as S. palustris present a variety of interesting biological and taxonomic problems to the investigator.

The Saldula pallipes-palustris species complex has confused the systematic heteropterist for some time and many synonyms have resulted because of its extreme variability. In Europe, S. palustris is exclusively halophilous, inhabiting estuarine mud flats, while S. pallipes (F.) is usually found inland. In North America, many specimens collected at inland locations have been identified as S. palustris (Chapman, 1962; Brooks and Kelton, 1967; Schuh, 1967).

Morphologically, the two species have been separated with some success in Europe by characters of the male genitalia and by use of the eunomic wing series for the forewings or hemelytra (Wagner, 1950; Cobben, 1960a). Saldid wings are usually black with a more or less extensive pattern of pale markings. Wing 'eunomy' involves

arrangement of wings in a series from darkest to lightest and is based on the idea that the pattern of pigmentation of the forewing is consistent within a species and varies from light to dark in a regular manner. The presence of morphological transitional phases in different geographic regions of the New World, however, makes differentiation difficult and there is evidence that the species complex here is not the same as in Europe (Cobben, 1960b).

Geographic differences in wing pigmentation have been noted in several species of Saldidae from both the Old and New World. For example, a north-south gradient in pigmentation, the palest forms predominating in southern Europe, is seen in S. palustris, S. arenicola (Scholtz), and S. opacula (Zetterstedt) (Cobben, 1959). Variability within a population at the same locality is expressed by a range of pigment variants in which a restricted section of the economy is dominating. Populations separated from each other by a few miles may have other dominating pigment variants. Cobben (1959) attributed these differences to sensitivity of developmental stages to macro- and micro-environmental factors.

In other insects, such variability has been related to diverse conditions of the external environment (e. g., temperature, humidity, background color, predator selection, crowding) as well as to the physiology of the insect itself (e. g., sexual maturity, metabolic differences, aging, parasites).

Geographic differences in pigmentation in Collembola (Rapoport, 1969), Nabis spp. (Heteroptera:Nabidae) (Harris, 1928), Perillus bioculatus (F.) (Heteroptera:Pentatomidae) (Knight, 1924), Eutettix tenellus (Bak.) (Homoptera:Cicadellidae) (Harries and Douglass, 1948), and many others, have been attributed primarily to temperature differences, cooler temperatures favoring deposition of melanic pigmentation. Humidity is believed related to geographical differences in pigmentation in some groups (Dobzhansky, 1933; Slater and Knopf, 1969) but most studies show that temperature has a greater effect. The effect of temperature during development on wing patterns in Lepidoptera is well-known (e. g., Oliver, 1970).

Background color is known to influence degree of pigmentation in certain Corixidae (Heteroptera) (Popham, 1941, 1943; Brown, 1946) and Acrididae (Orthoptera) (Faure, 1932).

Many of the differences reported (e. g., relative darkness of males, overwintered and parasitized insects) have been related to a slower rate of metabolism favoring deposition of melanic pigmentation.

As with all biological phenomena, a great number of factors can influence variation observed in a single phenotypic character such as degree of pigmentation. For example, pigmentation in Collembola and several other invertebrate species results from interaction of ground color, temperature (including solar radiation,

latitude, and altitude), rainfall and humidity, and type of pigment (Rapoport, 1969). In Eurydema oleracea (L.) (Heteroptera: Pentatomidae), there are cyclic changes in adults sampled in the field, individual variation, and a marked tendency for males to be more melanic. These cyclic changes are overlain by variation from place to place and year to year, temperature and humidity both being operative factors (Southwood and Leston, 1959).

According to Dobzhansky (1933), analysis of the mechanism of formation of geographic races and species ought to begin with study of the behavior of the single characters distinguishing the different forms from each other. Only then can one study the interaction of the unit-characters in complex systems representing the types with which taxonomy is primarily concerned. Such study of infraspecific variation of characters is included as the first level of "gamma taxonomy" by Mayr (1969, p. 15) and is the first step towards causal interpretation of organic diversity. Similarly, understanding the relative influence of each of the various environmental and genetic factors influencing the character precedes study of the complex interactions between these factors.

The principal objectives of this study are to (1) describe the life history of the insect, and (2) to define annual variation of wing pigmentation in the field and in experimental populations, especially as related to temperature effects during development.

TAXONOMY OF SALDULA PALUSTRIS (DOUGLAS)

Saldula pallipes (Fabricius) was a well-recognized species in Europe when Douglas first described S. palustris in England in 1874. Not all workers considered S. palustris a valid species (e. g., Brown, 1948) because of difficulties in morphological and habitat differentiation. For these reasons, some authors still refer to the two species as the S. pallipes-palustris complex (e. g., Schuh, 1967).

In 1949, Drake described S. fernaldi from coastal mud flats in Newfoundland. Drake and Hottes (1950) reported examining specimens of this species collected from tidal mud flats along the west coast of North America, including Oregon. Drake (1952) mentioned the presence of this species in Alaska.

In 1962, Drake suppressed fernaldi as a synonym after examining more specimens of S. palustris from Europe and both inland and coastal North America. Nevertheless, in view of the geographic discontinuity between European and Pacific coast S. palustris and the unanswered question of habitat requirements, the status of the species from coastal Oregon is still a problem. As a step towards clarification of this problem, taxonomic characterization of the coastal Oregon species identified as S. palustris was initiated.

Geographic Considerations

Evidence indicates that S. palustris on the Pacific coast is an exclusively halophilous species. Work described here demonstrates that the insect is well-adapted to the intertidal habitat. I have

collected the species along the entire length of the Oregon coast. No specimens of S. palustris were found above the area of the Alsea River (Figure 6, p. 20) affected by tides when this river was surveyed in early September 1971. Examination of the Oregon State University collection of several thousand Saldidae from the Pacific coast states (Oregon, Washington, and California) revealed no specimens of S. palustris from other than coastal localities.

### Morphology

Difficulty in finding adequate characters for separating species has created much confusion in the taxonomy of Saldidae. The taxonomy of this family still relies heavily on the generic concepts of Reuter (1912) although several authors (e. g., Usinger, 1956; Cobben, 1959) have pointed out that the system is inadequate. Characters which Reuter considered most important (e. g., length of inner cell of wing membrane) are often unreliable in the sense that they are seen in different genera. The genus Saldula Van Duzee is particularly heterogenous and includes "groups which morphologically and geographically shade off into one another so that no sharp criteria for genus or even subgenus divisions can be chosen" (Cobben, 1959, p. 306).

Saldula palustris (Figure 1) is easily separated from other coastal Oregon species by its large size and dense golden pubescence on the anterior half of the forewings. Characters of male genitalia and wing pigmentation have also been found useful by various

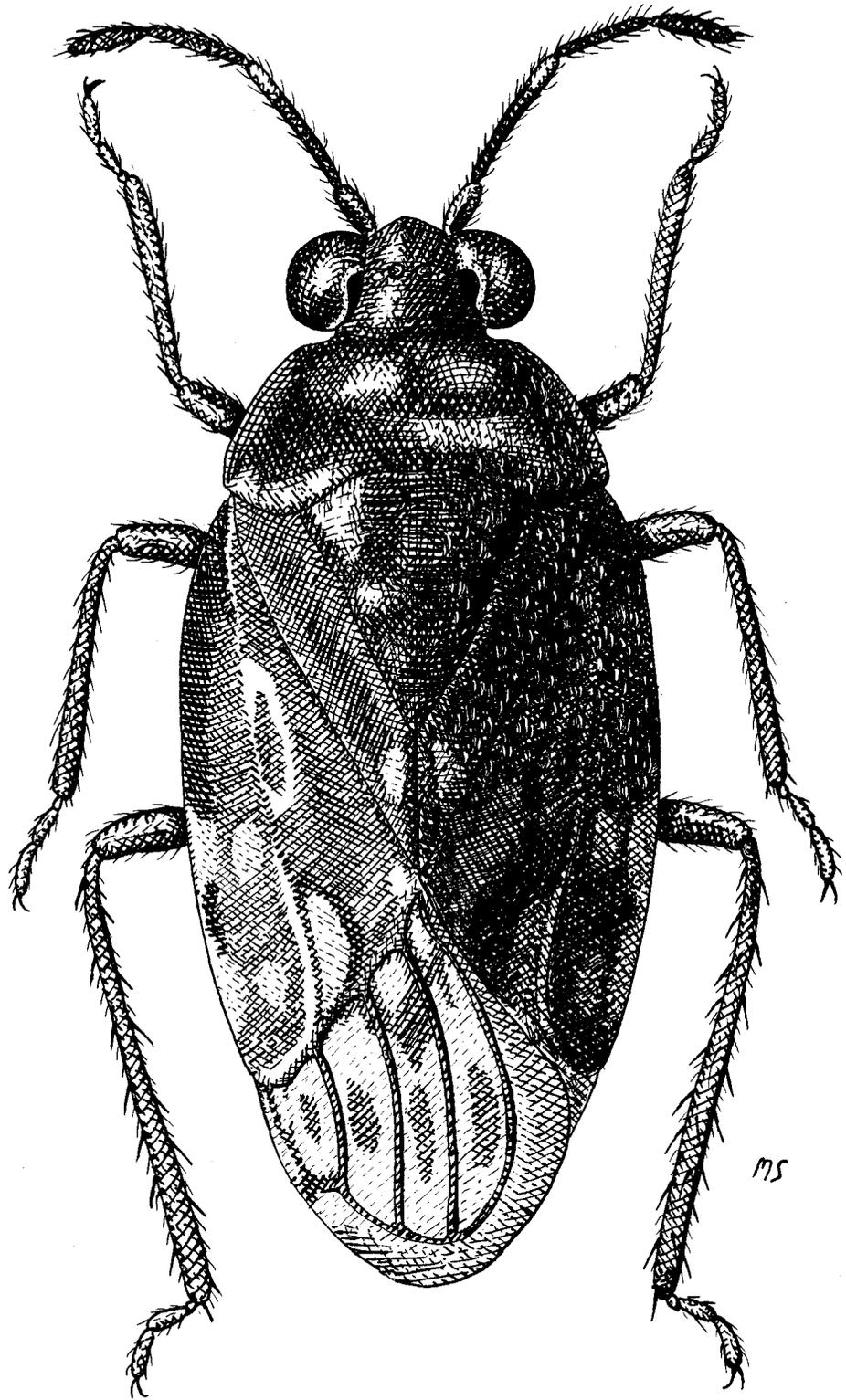


Figure 1. Dorsal view of Saldula palustris (Douglas).

investigators (see below) in identification of S. palustris. In initial attempts to characterize the Oregon species, attention was focused on these four characters and specimens of S. palustris and S. pallipes from Europe (the Netherlands) and Oregon were compared.

Male Genitalia. For examination of genital structures, the posterior abdominal segments were removed, cleared in hot 10% potassium hydroxide for 15 minutes and dissected. Parts were mounted on slides and drawn with the aid of a microprojector.

Although some authors (Usinger, 1956; Brooks and Kelton, 1967) found characters of the male genitalia of little use in differentiation of species, Cobben (1960a) described species-distinguishing characters in the male genitalia of S. palustris. Differences in length of the hairs on the processus sensualis of the parameres ("claspers") of the male are used to differentiate S. palustris from S. pallipes in Europe, the former having short hairs and the latter long hairs (Figure 2a, b). Cobben (1960b) used this character and wing-pattern eunomy to designate Caribbean specimens as S. 'palustris' (Figure 2c). Schuh (1967) found no differences in the parameres of Great Lakes specimens which appeared to be S. palustris and S. pallipes by their wing patterns.

This character does not appear reliable in differentiating the Oregon species. In my dissections, all parameres of Oregon S. palustris had long hairs on the processus sensualis (Figure 2g)

Figure 2. Parameres of male S. palustris, S. pallipes, and S. fernaldi, showing differences in length of hairs on processus sensualis (p. s.). Drawings not to scale.

- a. European S. palustris (after Cobben, 1960a).
- b. European S. pallipes (after Cobben, 1960a).
- c. Caribbean S. 'palustris' (after Cobben, 1960b).
- d. European S. palustris (my dissections).
- e. European S. pallipes (my dissections).
- f. S. fernaldi (after Drake and Hottes, 1950).
- g. Oregon S. palustris (my dissections).
- h. Oregon S. pallipes (my dissections) showing long- and short-haired conditions found.



although European specimens had the short hairs as described by Cobben (Figure 2d). Parameres of S. fernaldi were illustrated with long hairs by Drake and Hottes (1950) (Figure 2f) but the source of the specimen from which the drawing was made was not stated. Dissected specimens of European S. pallipes had long hairs (Figure 2e) as described by Cobben but only five of nine Oregon specimens of S. pallipes that were dissected had long hairs (Figure 2h).

Other features of the male genitalia (e. g., the penisfilum, shape of the aedeagus and the median sclerotized structure of the aedeagus) and the subgenital plate of the female appear similar in both European and Oregon S. palustris.

Pubescence. Type of pubescence is considered a reliable specific character by some authors (e. g., Brooks and Kelton, 1967). Drake and Hottes (1950, p. 56) distinguished S. fernaldi from S. pallipes by its "larger size and the longer, denser, golden pubescence on the hemelytra". Such dense golden pubescence, continuous across the anterior half of the hemelytra, is a conspicuous and unique characteristic of Oregon S. palustris. In European S. palustris, the golden pubescence is visible along the clavus and exocorium but not on the endocorium<sup>1</sup> (i. e., the golden hair is interrupted by a V-shaped wedge up the middle of the corium). Similar interruption of

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<sup>1</sup>See Figure 3 for terminology of wing regions.

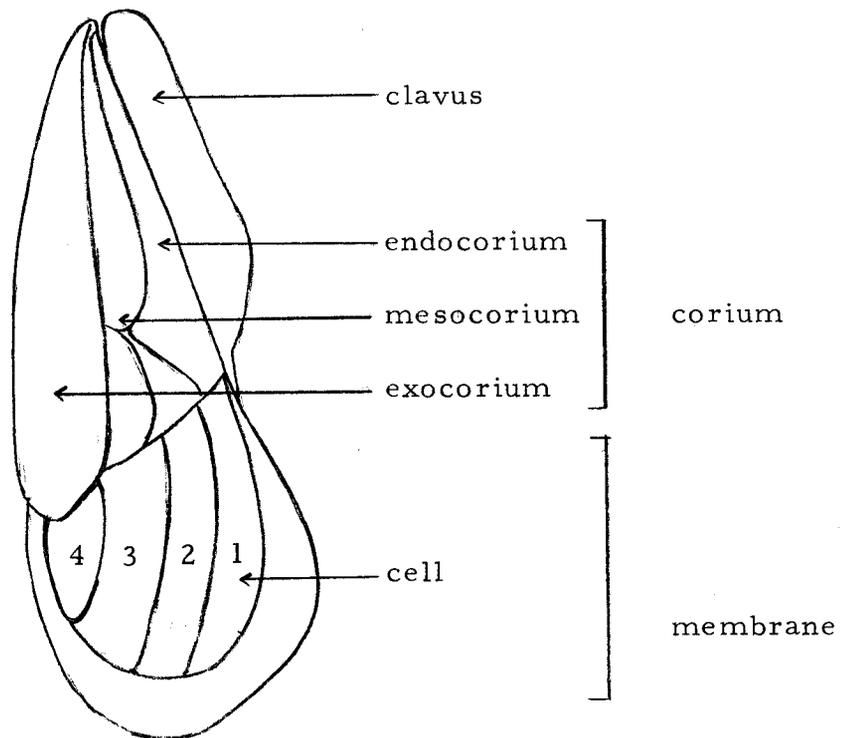


Figure 3. Left wing of *S. palustris*.

the golden pubescence is seen in Oregon S. pallipes.

Wing Pattern Eunomy. Although the extremely variable hemelytral pattern of Saldidae is considered an unreliable specific character by some authors (e. g., Brooks and Kelton, 1967), both Wagner (1950) and Cobben (1960a, b) found establishment of a eunomic series for the wing useful for species definition. Wagner (1950) considered the pale or dark types of the hemelytra the only single certain differentiating character between European S. palustris and S. pallipes. Cobben (1960a) clarified Wagner's work further and added other defining characters.

Two wing pattern characters (Figure 4) appeared consistently in both Oregon and European S. palustris and were not seen in Oregon and European S. pallipes. A distinct curved pale strip (Figure 4a) is present in the distal half of the corium. This strip is merged with the two white spots of the exocorium only in very pale specimens. A characteristic pale marking (Figure 4b) is also seen along the edge of the exocorium of S. palustris. This marking is often separated into two markings in darker individuals. In Oregon specimens, orange coloration of this second marking is common in S. palustris but not S. pallipes.

These two wing markings are useful in differentiating Oregon S. palustris from S. pallipes.

Size. Large size (about 4.7 mm) is a conspicuous character of

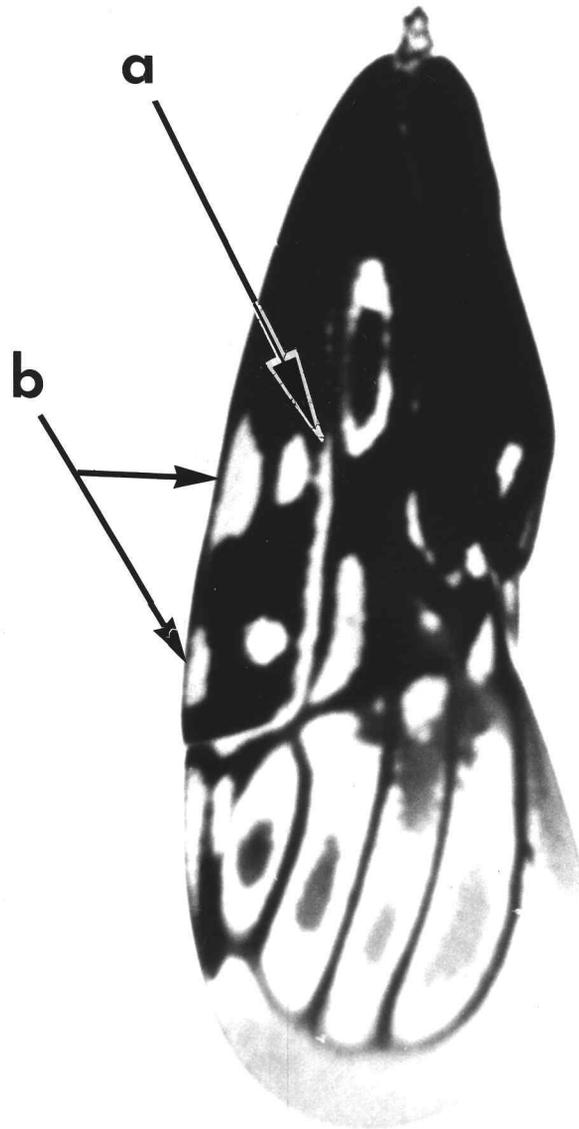


Figure 4. Two wing pattern characteristics of Oregon S. palustris.

Oregon S. palustris in comparison with other coastal Oregon species. However, because there is much infraspecific variation (geographic and seasonal) of size in insects, this character is probably not valid for comparison of European and Oregon S. palustris. My measurements do support literature reports that in North America, S. palustris is generally larger than S. pallipes (e. g., Chapman, 1962; Brooks and Kelton, 1967) and that in Europe, S. palustris is somewhat smaller (usually less than 4 mm long) than S. pallipes (Cobben 1960a).

Other Characters. Foretibial and antennal markings, and spines on the hind femora were not conspicuously different in the groups compared.

Brooks and Kelton (1967) used the callosities of the head (Parsons, 1961) as species-differentiating characters for Canadian S. palustris and S. pallipes but Oregon species could not be distinguished on this basis. The callosities of both European species appeared narrower and longer than those of Oregon species but since extent of pigmentation of these structures varies, actual size and shape were difficult to distinguish.

Spots along the sides of the femora (characteristic of Saldula species in general) were observed in all specimens but appeared more distinct, numerous, and regular in Oregon S. palustris than any other group.

A structure on the side of the abdomen of male Saldidae, originally described as a stridulatory organ (Drake and Hottes, 1951), is used during mating to grasp the edge of the female forewing (Cobben, 1957). This grasping organ bears a series of peg- and/or spine-like structures, the number of which is highly variable within and between species. S. palustris has 16 to 22 (Cobben, 1957).

The structure may have value in distinguishing species, however, when it has been studied in more detail. Electron scanning techniques reveal details of structure (e. g., V-shaped sculpturing of the pegs) not previously described (Figure 5).

Although systematic definition of Oregon S. palustris cannot be attempted until further studies are completed, characters of intertidal habitat, large size, continuous golden pubescence on the hemelytra, and long hairs on the parameres, throw considerable suspicion upon identification of this species with either European or inland North American S. palustris. Detailed morphological and distributional comparison of the Pacific coast S. palustris with specimens from the Atlantic coast, Alaska, and inland Canada and the United States, and examination of type specimens of S. palustris, S. pallipes, and S. fernaldi, would enable clarification and definition of the status of this species.

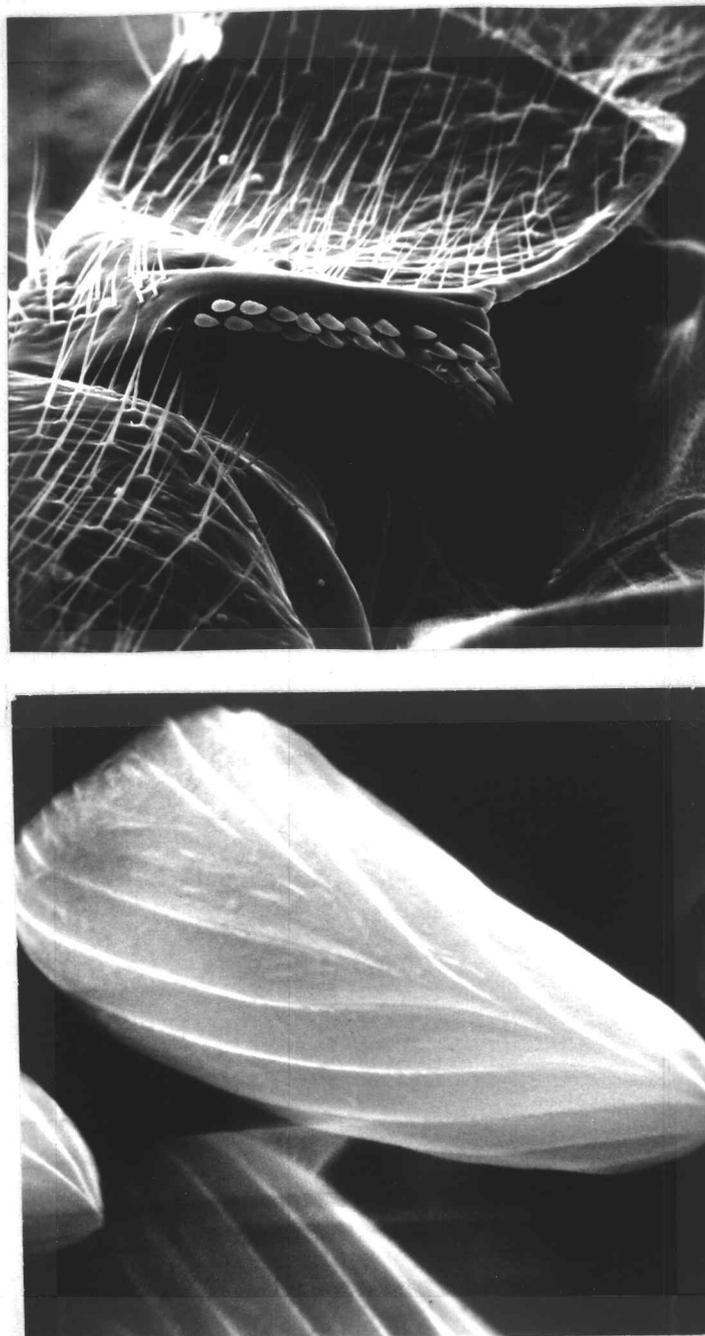


Figure 5. Left grasping organ of a male S. palustris. View is from the anterior end of the insect; lateral margin of second connexival segment bearing the organ is towards the right. Top micrograph (293X) shows entire structure. Lower micrograph (6805X) shows details of structure of a single peg. (Electron scan micrographs by A. Soeldner, Oregon State University.)

## STATISTICAL METHODS

In work described in the following pages, most data were analyzed with the aid of the Oregon State University CDC 3300 digital computer, using \*SIPS (Statistical Instruction Programming System). Some calculations were done on a Monroe Epic Calculator. Tests used are described by Snedecor and Cochran (1967) and Sokal and Rohlf (1969).

Significant differences between samples at the 95% and 99% levels of confidence are indicated in text, tables and figures with asterisks, (\*) and (\*\*), respectively.

Most differences between means were tested with a two-tailed Student's T-test. For longer series of samples (Figures 23 and 27), the least significant difference (LSD) was determined for the 95% and 99% levels and is indicated on the figure as two vertical bars showing difference required for significance at that level.

F-tests, correlation coefficients, and binomial tests were also employed.

## LOCATION AND DESCRIPTION OF THE STUDY AREA

The population of S. palustris described in this report inhabits the edge of an intertidal salt marsh on the east side of Yaquina Bay, 0.1 miles south of the Toledo airport (Figure 6). The area is located at 44° 35' N 47" N., 123° 56' 10" W. latitude (U. S. C. G. S.<sup>2</sup> map no. 6055). Yaquina Bay is an estuary lying on the western side of the central Oregon Coast Range. The estuary extends from its mouth at the Pacific Ocean near 44° 37' N. latitude to its upper limit near Elk City, about 23 miles inland. Toledo, Oregon is a channel distance of about ten miles inland on this estuary.

The climate of the Yaquina Bay area is characterized by extremely dry summers and wet winters. The mean annual rainfall is about 68 inches with approximately 70% of the rain occurring November through March (Holbrook, 1970). Air temperatures are mild and rather uniform; mean annual temperature is about 10°C.

A map of the area (Figure 7) was made by driving wooden stakes in along the water line at high tide and at four consecutive hours after high tide on September 1, 1970 and at low tide the following morning. The stakes, representing equal tidal elevations, were located vertically and horizontally with a K & E transect. Contour lines, corresponding to actual tide levels on that day, were then drawn on the map.

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<sup>2</sup>United States Coast and Geodetic Survey.

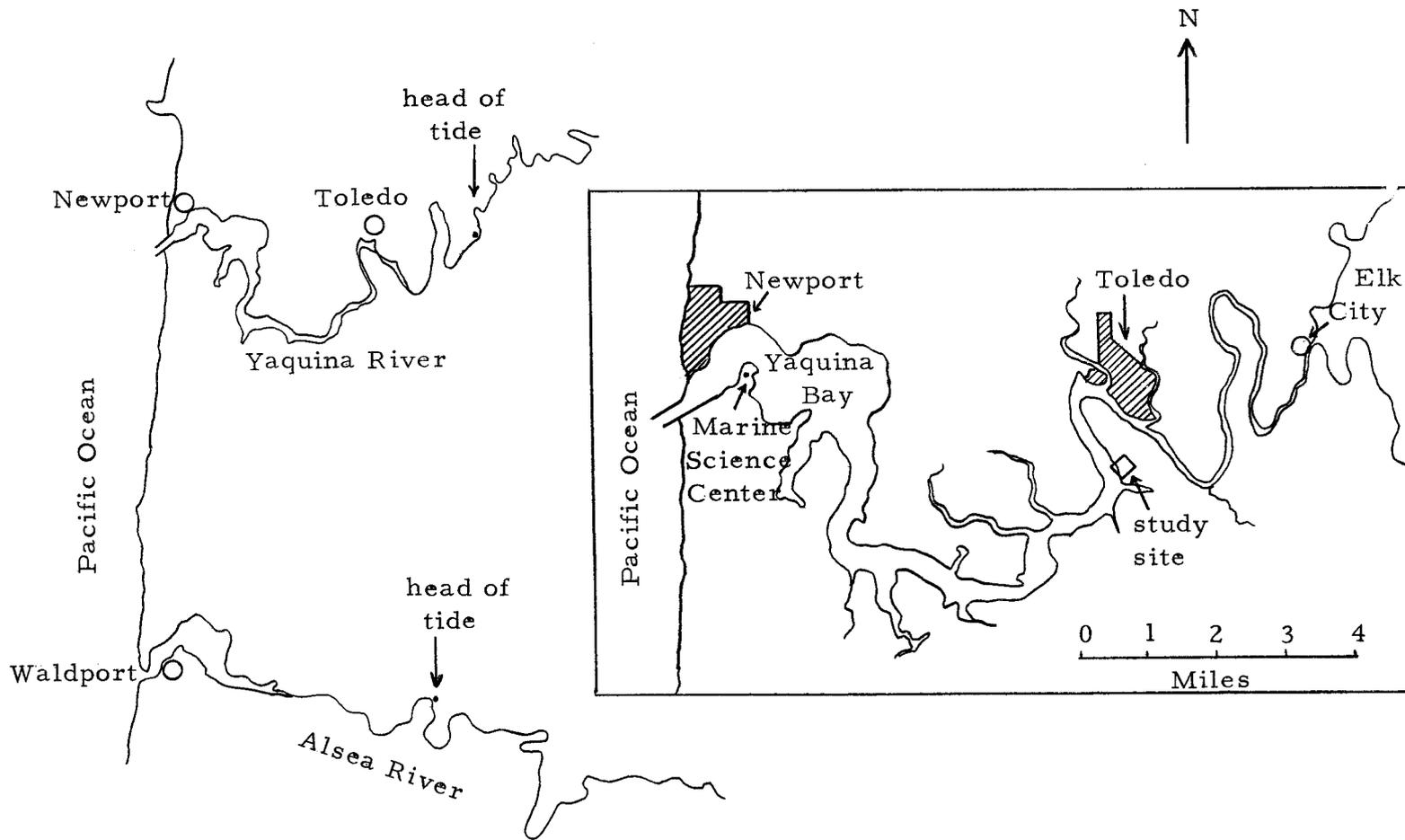


Figure 6. Location of study site on Yaquina River estuary at the Oregon coast.

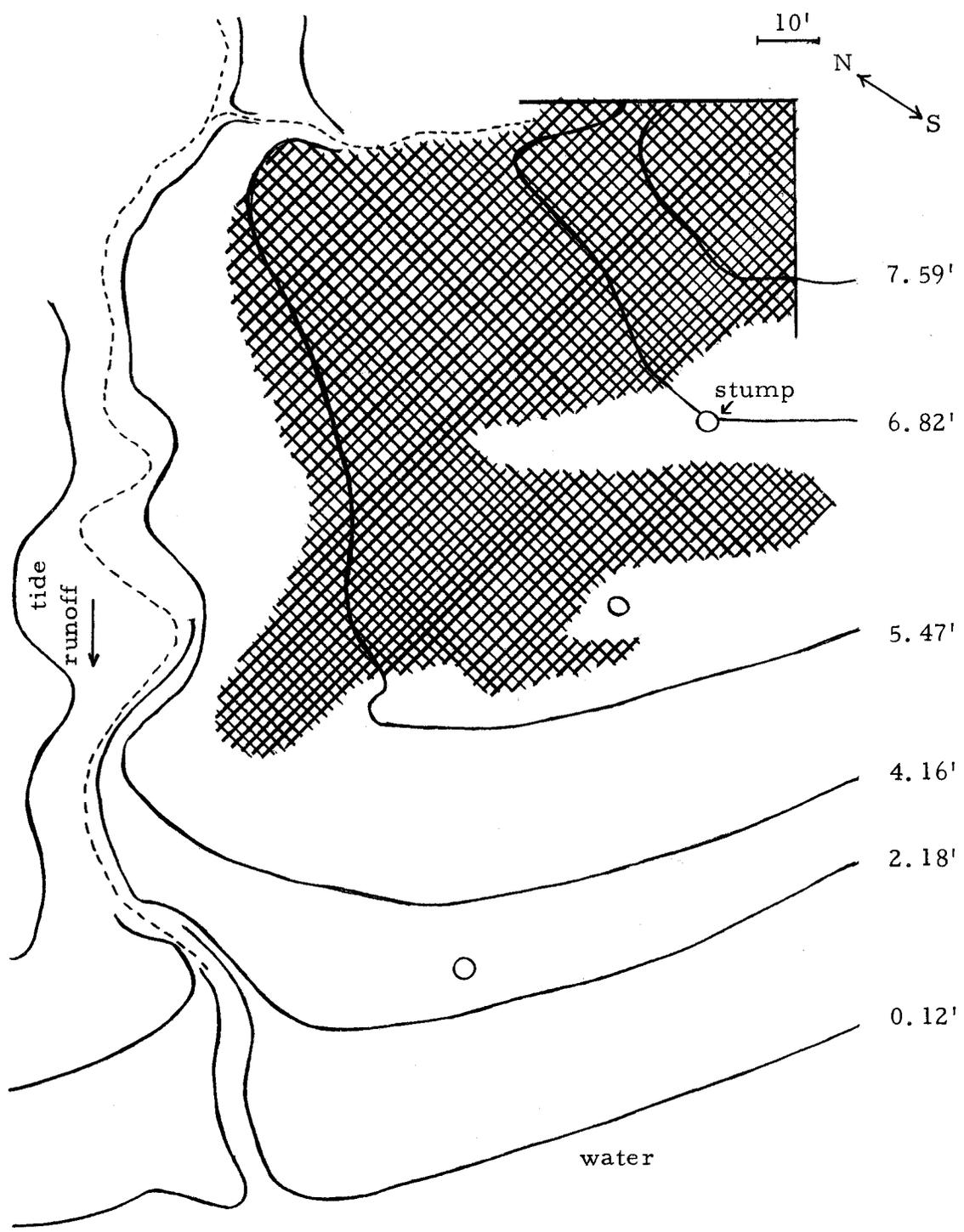


Figure 7. Map of study area showing vegetation (cross-hatched region) and lines of equal tidal elevation (feet above MLLW or 0.0 tide level).

Most of the insects were found between 5.50 and 7.50 feet above 0.0 tide level (mean lowest low water or MLLW along the Pacific coast). This region is almost entirely below the 7.40 foot mean high water mark (U. S. C. G. S., 1935) and is covered and uncovered by the tide at least once a day. Photos taken on November 8, 1970 (Figure 8) show the area at various stages of tidal submergence.

Density of vegetation over the area varies seasonally, being sparse from mid-September until early May and then growing up rapidly to cover much of the area during the summer months (Figure 9). The predominant vegetation is salt grass (Distichlis spicata (L.) Greene) and tufted hair grass (Deschampsia caespitosa (L.) Beauv.) (Figure 10a), both family Graminaceae. The seaward margin of vegetation is characterized by seaside arrow grass (Triglochin maritima (L.), family Juncaginaceae) (Figure 10b). A layer of algae (Cladophora gracilis (Griffiths) Kuetz) covers portions of the area during the summer. (Reference source for most plant names was Peck, 1961.)

Figure 8. Exposure of the study site by outgoing tide, November 8, 1970. Open waters of Yaquina Bay are to the left in the photos. Area inhabited by the insects is seen only in middle and bottom photos. In the top photo, the water line is at about the 7.5 foot level; in the middle photo, about the 5.0 foot level; and in the bottom photo, low tide or about 0.0 feet.



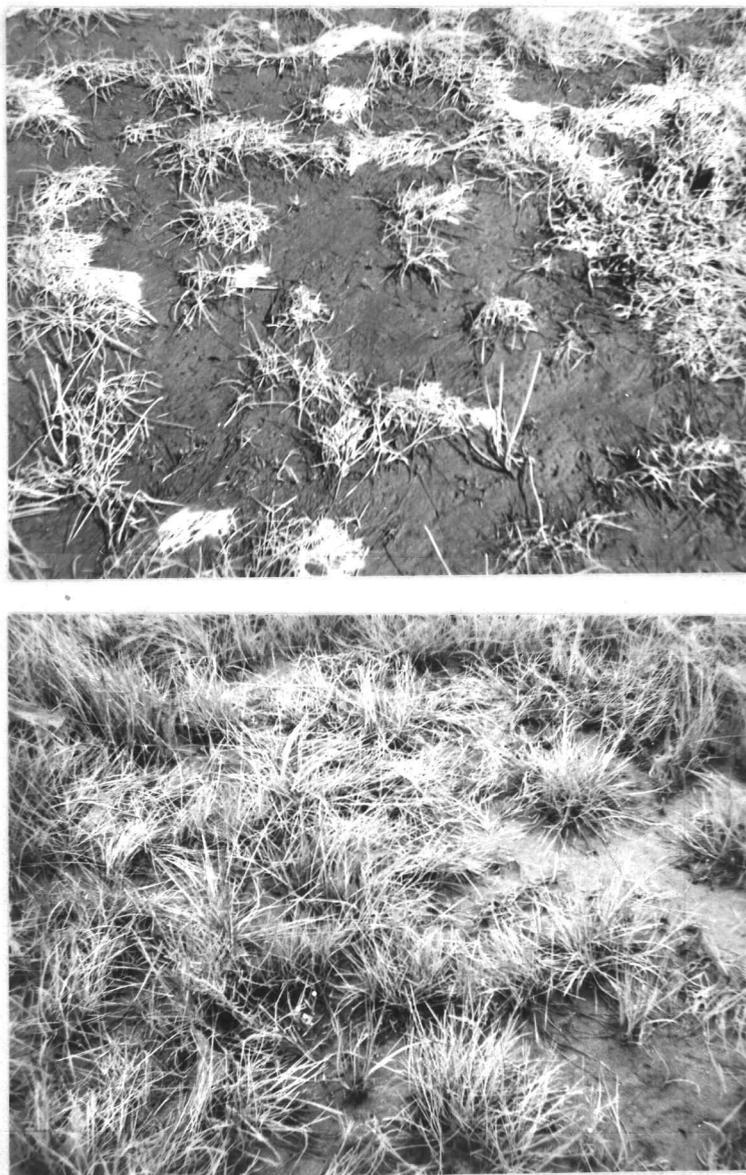


Figure 9. Seasonal variation in vegetation cover at study site. Photos show the predominating cover, salt grass (*Distichlis spicata* (L.) Greene), as it appeared October to April (top) and May to September 1971 (bottom). Photos show an area of about six square feet.



Figure 10. Other vegetation at the study site during summer 1971.

- a. (top) Tufted hair-grass (Deschampsia caespitosa (L.) Beauv. ).
- b. (bottom) Seaside arrowgrass (Triglochin maritima (L. )).

## BIOLOGICAL STUDIES

Literature

In general, female Saldidae lay eggs in spring and early summer. The eggs are elongate and without micropylar processes or a distinct cap and are deposited singly at the base of clumps of grass and other vegetation or in firm moist soil. Most species insert their eggs in such a way that only a small anterior part of the egg is exposed to free air or water. The eggs need saturated conditions for normal development but are not affected adversely by submer-sion (Cobben, 1968). Incubation time varies from four days at constant 30° C for Saldula spp. (Cobben, 1968) to nine months for Salda littoralis (L.) when eggs overwinter (Jordan and Wendt, 1938). The five nymphal stages or instars require about one month to develop (Wiley, 1922). Nymphs are oval in outline like adults but have two-segmented tarsi instead of three (the first being very small in both stages). Saldid nymphs are characterized by a single dorsal scent gland that opens between the third and fourth abdominal terga (Figure 13). Wiley (1922) described development of S. pallipes as including an egg incubation period of about 12 days and five nymphal stages lasting 4, 3, 3, 2 to 3, and 4 days, respectively.

In the few species whose biology is known, diapause ranges

from obligatory (e. g., eggs of S. littoralis, second instars of Chiloxanthus pilosus (Fallén) to facultative, where deposition of diapause eggs or egg development and oviposition itself depends to varying degrees on changing environmental conditions. The four Saldula spp. of the saltatoria-pallipes group in Europe hibernate, often far from their breeding places, as adults with undeveloped ovaries (Cobben, 1968).

### Field Studies

During warmer months of the year (June to September), adult insects were collected with a standard 12-inch insect net moved slowly back and forth across the ground. In cooler weather (October to May, with daytime temperatures below about 18° C), adult insects would not fly readily when disturbed so could be collected with an aspirator directly from the ground. Insects for experimental work were kept alive temporarily in large, cotton-plugged vials containing strips of damp paper towelling. Other specimens were preserved in 70% ethyl alcohol.

From June until December 1970, field collections of adults were made approximately once every two weeks. In both winter 1970-71 and 1971-72, no saldids were present in the area during the few weeks of late December and early January, even on unusually warm and sunny days. Attempts to find the insect during this period

both in the area and in adjacent regions were unsuccessful. Starting from the time when adults reappeared in the study area in late January 1971, collections were made at intervals of one week or less. Although the insects were seen pairing from January until September, no nymphs appeared until mid-April. Differences in overall wing coloration (not extent of wing pigmentation) distinguished overwintered from spring-generation adults from the time of the first emergence of the spring generation of adults in mid-May until all overwintered adults had died (late June).

Development of ovaries of dissected females, sex ratios, wing pigmentation and size, were some parameters measured for each collection.

Ovary Development. Female Saldidae have two laterally-placed ovaries of the acrotrophic type, each consisting of seven ovarioles (Carayon, 1950). Twenty to 25 freshly-killed or alcohol-preserved females from each field collection were dissected, ovary development noted, and eggs counted. The maximum number of mature eggs found in a single female was 26. The extent of the reproductive period of the insect is indicated by the frequency of dissected females found to contain mature eggs at different times of year (Figure 11). These data indicate that oviposition could take place throughout the February to mid-September period, even though nymphs did not appear in the field until mid-April. Although some saldids (e. g., Saldula

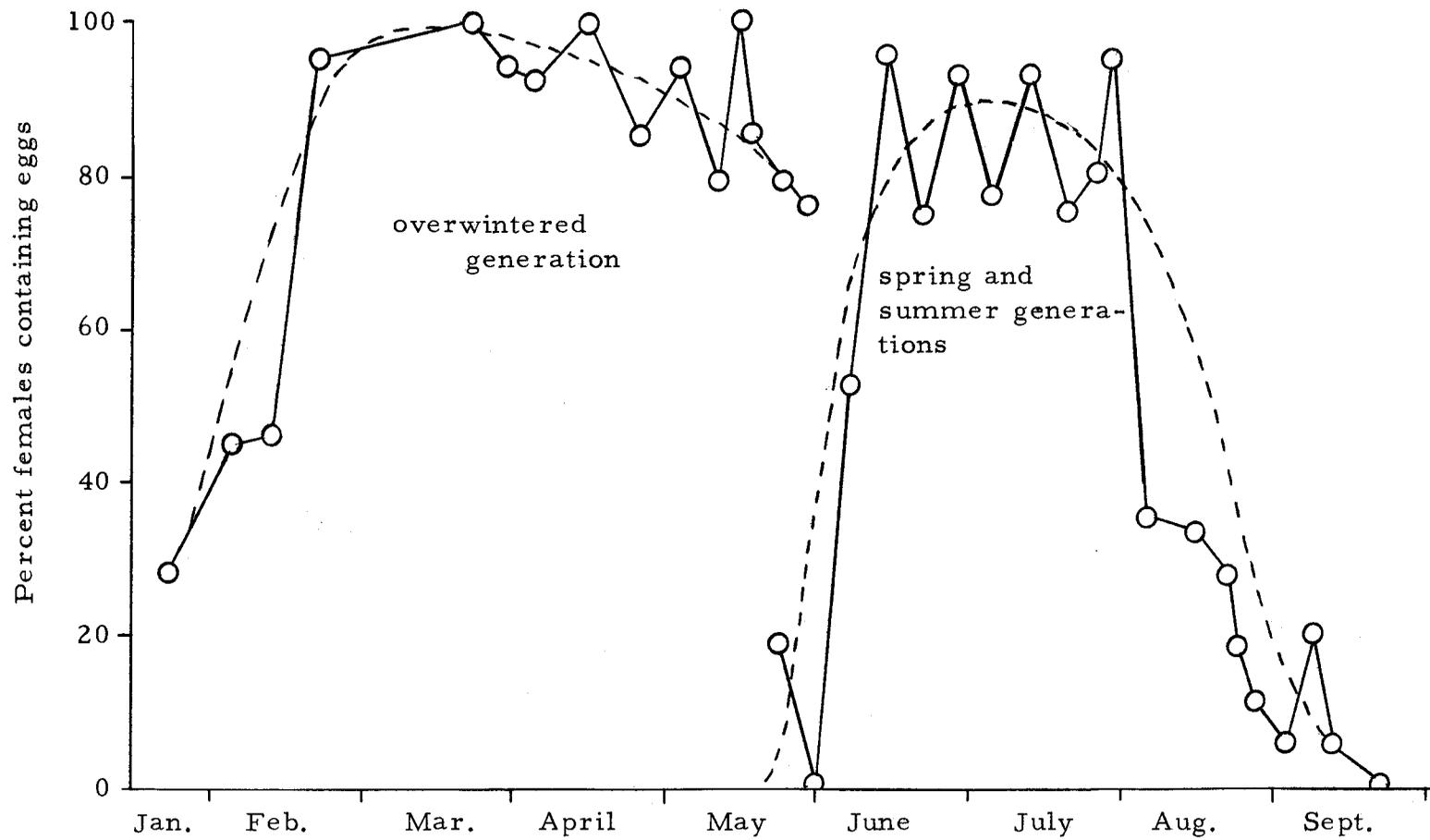


Figure 11. Percent females containing eggs in field collections, 1971.

orthochila (Fieber) are known to retain mature eggs within their bodies (Cobben, 1968), the demonstrated sensitivity (described below) of egg development and oviposition to even a few hours of warm temperature during this period, indicated that eggs were being deposited.

Comparison of groups of females preserved immediately upon collection in the field with females kept alive one to three days at room temperature (about 24° C) before preservation (Table 1) demonstrated that eggs matured rapidly in response to warm temperatures during the reproductive period of the year. After this time, warm temperatures had no immediate effect on egg development although longer periods at warm temperatures eventually induced oviposition in females collected any time during the late fall. Specimens collected in November and kept in the laboratory at 24° C, began to mate five days after collection and nymphs emerged within ten days, a normal incubation time for this temperature. Females collected during late January and early February oviposited in the laboratory within a day. Thus, there was no evidence of an obligatory reproductive diapause in this insect.

Table 1. Comparison of egg numbers in females preserved at collection in the field with females kept alive 1-3 days at 24° C.

Collection date	Time preserved	No. females	No. eggs/female
March 10, 1972	at collection	21	10.76
	1 day later	21	18.14**
August 6, 1971	at collection	21	2.9
	1 day later	21	11.1**
September 20, 1971	at collection	21	0
	3 days later	15	0

Sex Ratios. Sex ratios from field collections (Figure 12) suggest that females were either less abundant or significantly less active and therefore less susceptible to collection by net in the summer months than males. Netted field samples of adults contained a significantly (\*) low proportion of females to males although aspirated samples collected at the same time had a female:male ratio not significantly different from 1:1. This observation could be related to high numbers of eggs per female (increased weight) and the more active mating behavior of males during this time. Sex ratios of insect populations reared in the laboratory from either nymphs collected at various times of year or from eggs were not significantly different from 1:1.

Mating. Mating was observed in the field population throughout the late-January to September reproductive period and the procedure

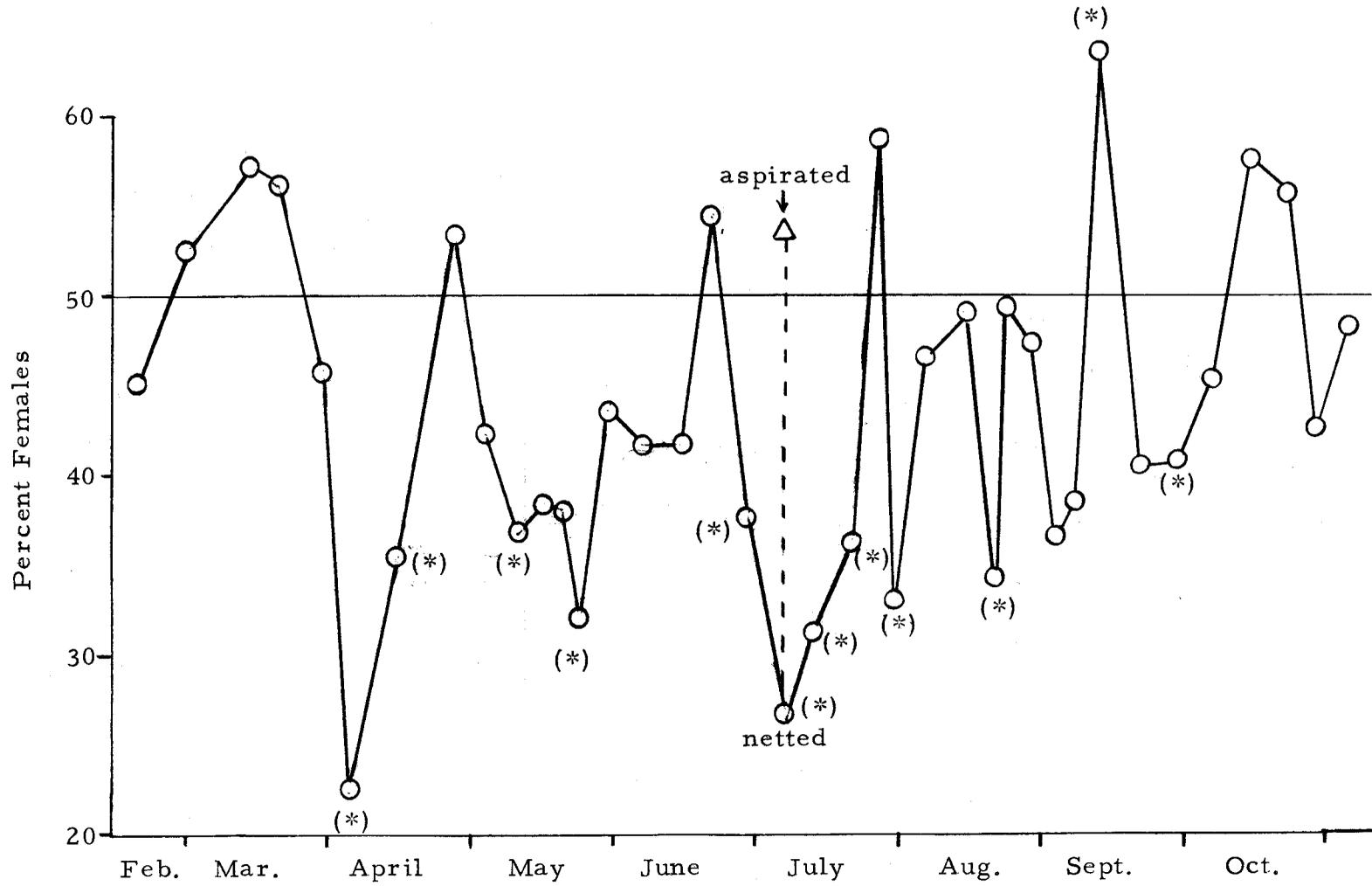


Figure 12. Percent females in field collections of adults, February to November 1971.

was similar to that described by Ekblom (1926) and Cobben (1957). The insects were extremely abundant in the area during this time and actively roamed about, especially on warm days, although flight activity was rarely observed. Encounters between two or more of the *saldids* was common. When the insects came within approximately two inches of each other, the male ran rapidly toward and leaped upon the female, grasping her and placing himself on one side of her at an oblique angle with his body on the same plane as the female. The pair remained in this position for five to ten minutes. In laboratory studies, both males and females were observed to pair repeatedly over a short period of time. However, active mating behavior early in the year and the 1:1 male to female ratio in field populations at this time suggest that the females did not overwinter in the fertilized state.

One striking characteristic of mating behavior in this species is that males were apparently unable to distinguish other insects when more than a few inches away. Within this distance they seemed almost completely unable to distinguish between males, females, or even *saldids* and other species until pairing was attempted. When two males met, there was a brief flurry of activity and the two usually separated immediately. I have observed in the laboratory, however, that in about one-third of the male-male encounters, the uppermost male did not jump off the other immediately but rather

appeared to assume the correct mating angle for a few seconds. Males also attempted pairing with mating pairs and with insects of other species (such as mudflat beetles (Coleoptera:Heteroceridae)). Kellen (1960) reported similar behavior in Omania (Heteroptera: Omaniidae) and suggested that this might be a type of recognition pattern, rather than a strictly mating-oriented response.

Parasites. On three occasions, nematode parasites of the family Mermithidae were found in the abdominal cavities of dissected adult females. No other parasites were seen.

Nymph Populations. Nymph populations were sampled at two-week intervals from June until October 1970 and at one-week intervals from their first appearance on April 15 until mid-October 1971. The sampling unit was a seven-inch length section of 12-inch diameter aluminum irrigation pipe. One edge was filed sharp and two handles were riveted one inch below the unsharpened top edge. In sampling, the pipe was set down, rotated slightly to cut through the grass, and all nymphs within the unit aspirated and counted according to nymphal stage. The five instars were separated primarily by size and relative development of the wing pads (Figure 13). Data on relative density and age structure of the nymph population (Figures 14 and 15) show three peaks of nymph numbers during the year (May, July, and August). Differences in height of the peaks for consecutive instars in May (Figure 15) probably reflect both increasing duration of the

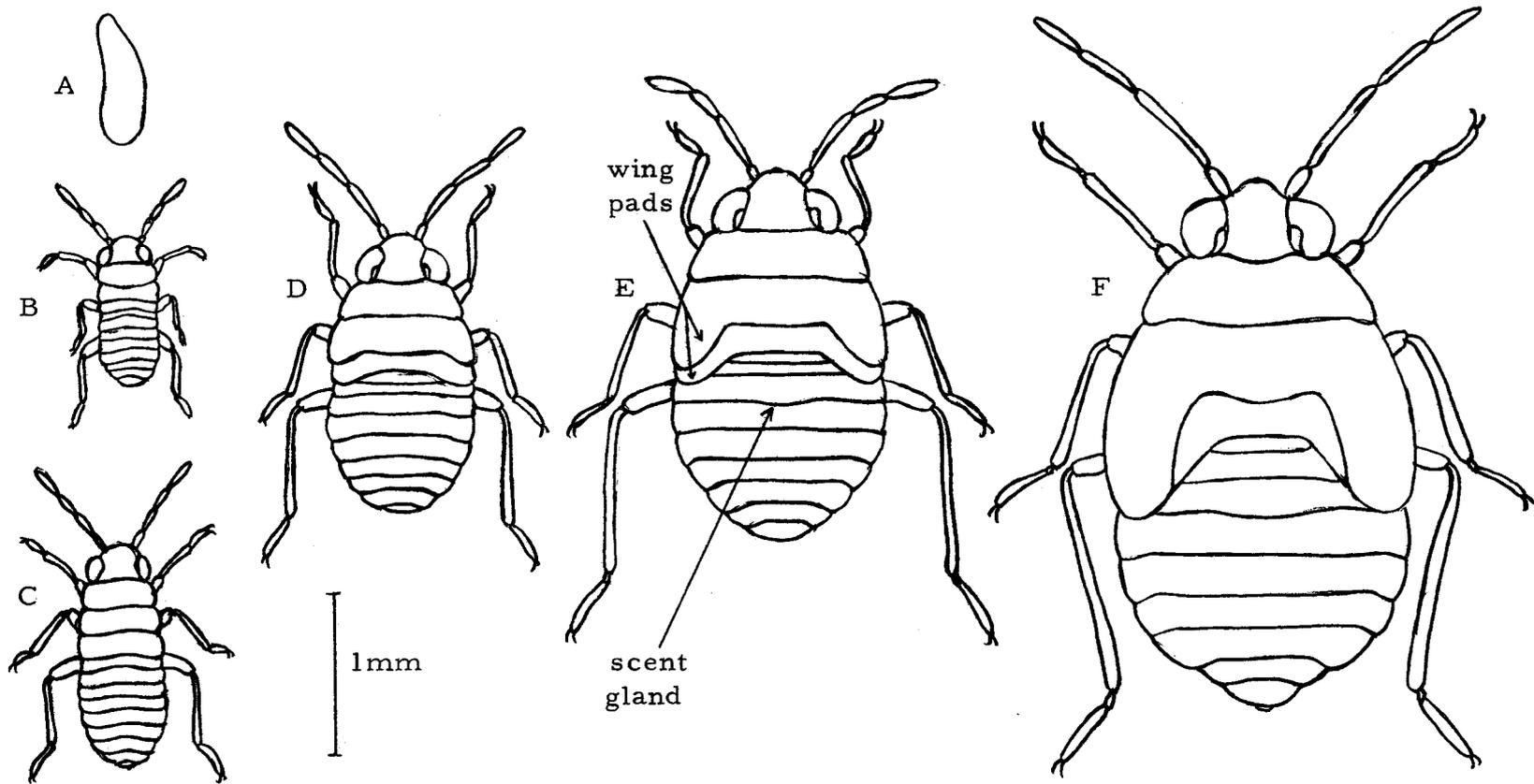


Figure 13. Immature stages of Saldula palustris (Douglas). A. Egg. B-F. Nymphs of five consecutive instars.

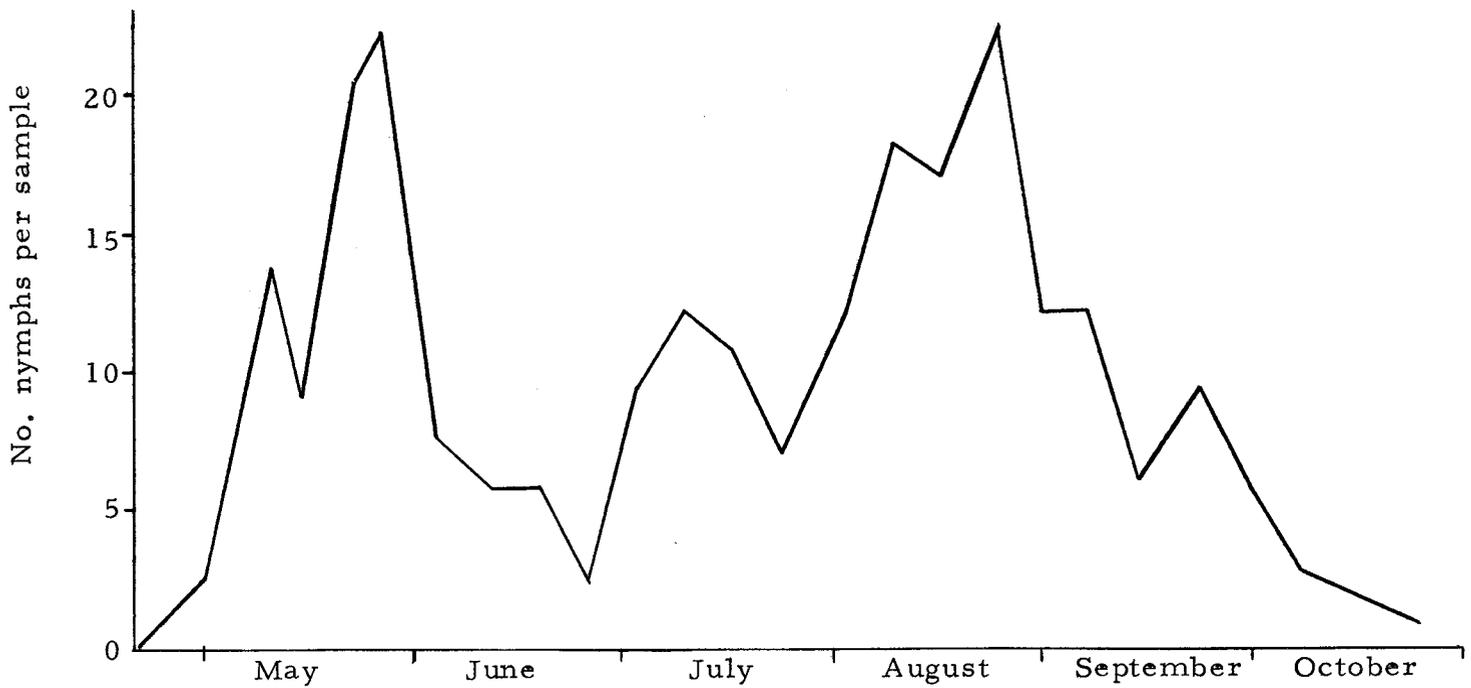


Figure 14. Total number of nymphs per sample (1971).

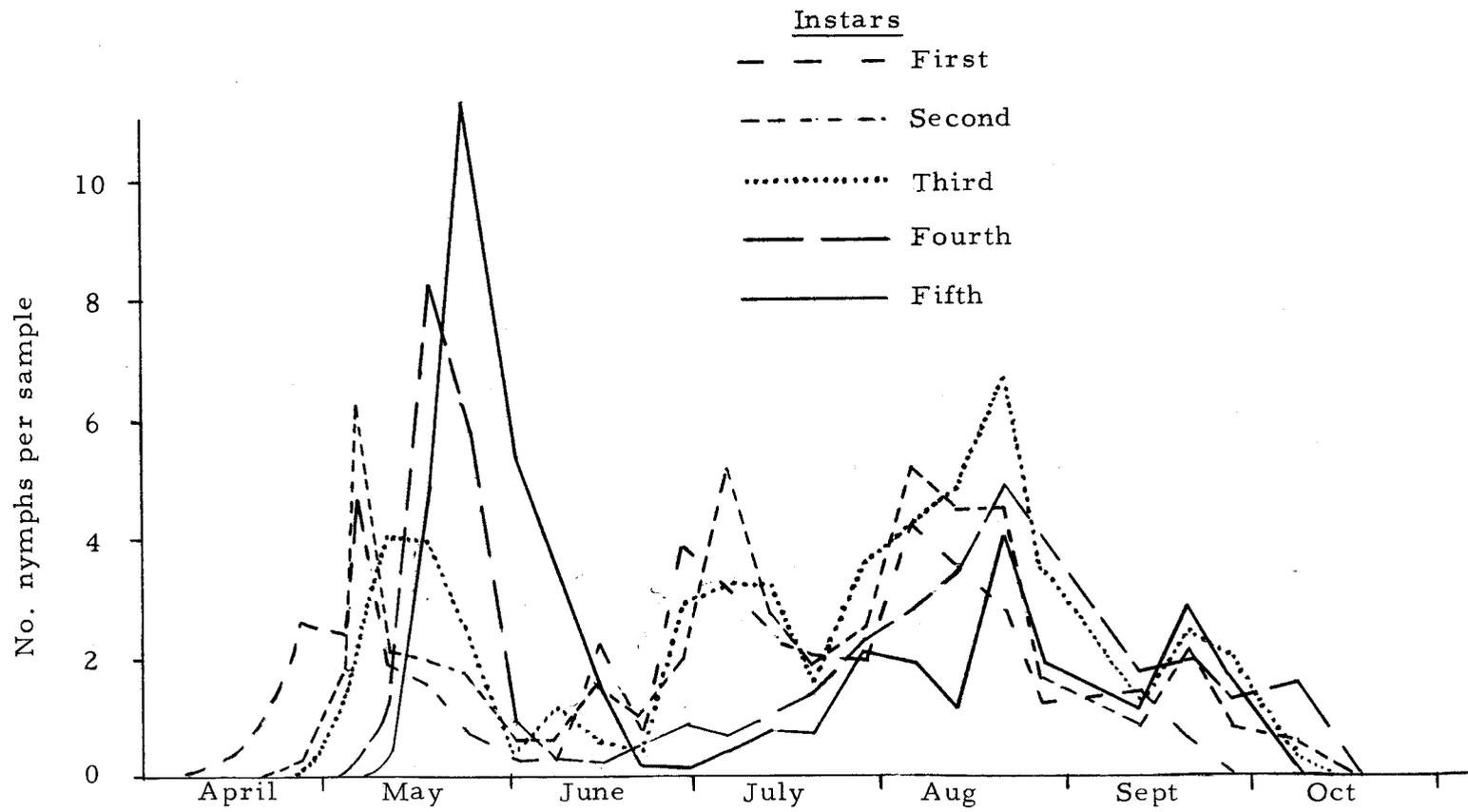


Figure 15. Age structure of nymph population, 1971.

older nymphal stages and the greater possibility of overlooking the smaller nymphs during sampling.

Some fifth instars were found in the field as late as November but these died and did not develop into adults even at warm laboratory temperatures. No nymphs were found in the spring until emergence of the spring generation.

Nymph Distribution. Three surveys of nymph distribution over the entire study area were made on September 2, 1970 and on May 11 and July 25, 1971 (Figure 16). The September survey showed a preponderance of young nymphs at lower tidal elevations and older ones at higher levels. Distribution at the time of the May survey was generally the same. On July 25, however, the nymphs were more evenly distributed over the area and there was a much higher percentage of older nymphs at lower tidal elevations. The possible relationship of these differences to environmental phenomena is discussed on page 62.

Feeding. Saldidae are generally considered predators and scavengers but actual records of feeding activity in the field are rare. In the laboratory, saldids have been fed on katydids, flies, cicadelids, and mirids (Hungerford, 1919; Wiley, 1922; Usinger, 1956; Schuh, 1967). I reared S. palustris on houseflies. Schuh noted that saldids in the laboratory were unable to catch live insects but Hungerford believed that they did capture living insects on occasion

September 2, 1970

May 11, 1971

July 25, 1971

Instar

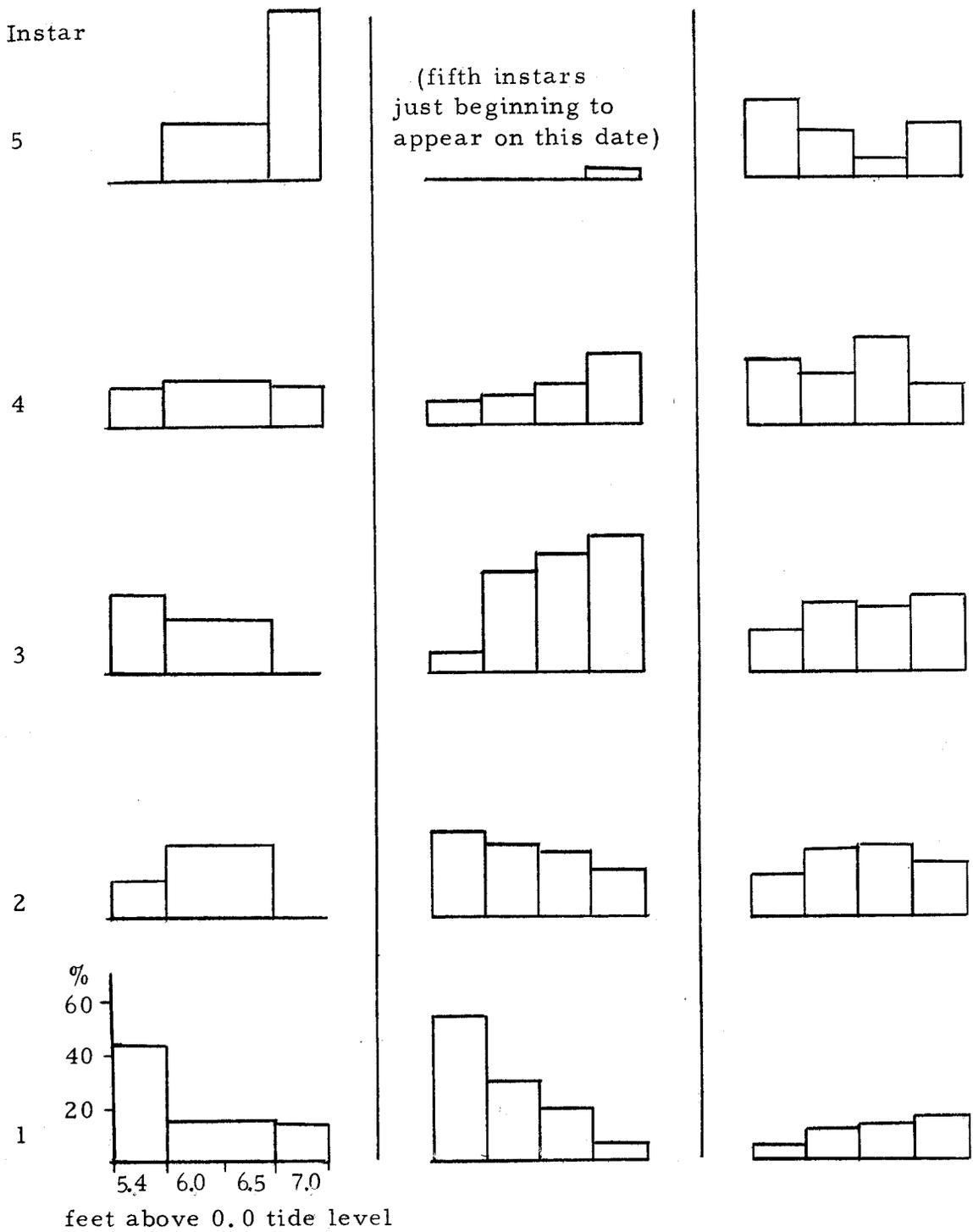


Figure 16. Distribution of nymphs over study area. (Height of bar shows percent of all nymphs collected at that tide level.)

in the field. The active foraging behavior of saldids is well-known.

Ekblom (1926) and Lindskog (1968) observed S. saltatoria (L.) preying upon different kinds of Diptera larvae living in the surface layers of the soil. The prey was found by probing in the soil with the proboscis. When a larva was found, the insect repeatedly inserted the proboscis into it, "at the same time hopping round about so as to avoid violent contorsions of the larva" (Ekblom, 1926, p. 61).

Ekblom suggests that there might be a powerful toxic effect of saliva since the larva died within a few minutes. He also mentions noticing unsuccessful and clumsy efforts of the insects to stalk flies and other small mobile animals above the ground. Lindskog (1968) observed saldids feeding on worms (Enchytraeidae) and midges (Chironomidae). The saldids attacked midges resting upon the ground. Associated copepods, collembolans, and mites have been mentioned as possible prey by several authors. Hungerford (1919) reports that Pentacora signoreti (Guérin) will feed on members of its own species

The primary activity of S. palustris in the field on most days was mating and perhaps some of the "stalking" behavior noted in the literature was actually mate-seeking. In September 1971 (at the end of the reproductive period) I saw for the first and only time what appeared to be the systematic "probing" of the mud with the proboscis that had been described by other workers.

On several occasions, adults appeared to chase nymphs. Only

on two occasions was feeding actually observed in the field. Once an adult aggressively attacked and fed on a third instar. On another occasion, a fourth instar attacked a very active small amphipod (Orchestria sp., Crustacea). The nymph inserted its proboscis repeatedly into the amphipod. When the amphipod retreated into a small pit in the sand, the nymph circled the pit and came forward three times to insert the proboscis. Finally, the nymph fed for about ten minutes, left and walked about, then returned and fed for another five minutes. When the nymph left, the crustacean was dead and quite flat.

The most common associated animals in the study area are small red mites (Centrotrombidium sp., family Johnstonianidae); beetles of the families Carabidae (Bembidion sp.), Heteroceridae, and Staphylinidae (Carpelimus sp.); many species of Diptera; small oligochaete worms (very abundant at the bases of salt-grass tufts); and numerous spiders of the families Lycosidae (wolf spiders) and Micryphantidae. Under laboratory conditions, saldids of all ages were put together with a range of other species from the study area. The only feeding activity observed was cannibalistic. Adult saldids aggressively captured and fed on second and third instars on three occasions. In other laboratory work, feeding of both adults and nymphs upon moulting individuals was very common.

In the field, S. palustris probably feeds on amphipods, Diptera

larvae, and members of its own species. Craig (1970) observed feeding behavior of the intertidal staphylinid beetle (Thinopinus pictus Leconte) upon amphipods. He concluded that although the amphipods did not appear numerous, they provided a regular supply of food for the beetles. Similarly, S. palustris might regularly feed upon amphipods in the field.

Predators. At another field site, I saw ants captureing saldid nymphs and once observed a wolf spider apparently feeding on an adult saldid in my study area. In the laboratory, one of the small micryphantid spiders captured and fed on a third instar. When saldids were reared outdoors, similar small spiders occasionally invaded the rearing containers and consumer many of the nymphs therein. For these reasons, and because of their abundance in the study area during the entire year, these spiders are probably one of the chief predators upon saldid nymphs. The flocks of shore birds observed following the water line as the tide receded during the summer, fed on what appeared to be a moving prey which they could see a foot or more away. Since saldids do not recover immediately from tidal submergence (see page 52) and are not distributed as far down in the intertidal zone as the birds were usually observed feeding, the birds were probably not feeding on the insects.

## Laboratory Studies

Methods. In order to rear S. palustris under controlled conditions that approximated temperatures at the cool and warm ends of the temperature range during the reproductive period of the year, two Sherer-Gillett growth chambers were utilized. In each chamber, a regime of alternating temperatures was established in order to more closely approximate natural differences between day and night temperatures. The cool chamber had night temperatures of 13° C and day temperatures of 21° C. The warm chamber was 21° C at night and 29° C during the day. In both chambers, daylength was set at 16 hours so that the average daily temperature in the cool chamber was 18° C, and in the warm chamber, 26° C.

To provide some insects with temperatures approximating actual field conditions for the particular time of year, a screened enclosure was built and placed outdoors on the roof of the five-story building which contains the Entomology Department. The lid of the enclosure was painted white and all sides were screened for free circulation of air. The unit had legs and was set in the water (about four inches deep) covering the roof. For these reasons, cool temperatures approximating those at the study site were maintained, even on very warm summer days.

Rearing containers were polyethylene refrigerator containers of various sizes with a half-inch of cotton and a half-inch of plaster

of paris and charcoal mixture in the bottom. The small amount of charcoal in the plaster increased porosity of the substrate and gave it a neutral gray color. Holes in the bottom allowed water to enter when the containers were set in a large tray of water. The plaster substrate and pieces of gray blotter paper (propped against the sides of the container to provide moulting and oviposition sites) could thus be kept saturated at all times and the humidity in the containers maintained at a high level. Centers of the lids were cut out and either fitted with a piece of plastic screening or placed over a laboratory tissue laid over the top of the container. Some plaster smeared up the sides when making the containers also provided vertical surfaces which the insects prefer for moulting and resting. Using a plaster substrate, rather than sand, restricted oviposition to the pieces of blotter paper. Initially, the plaster and blotter paper were moistened with clean sea water. Only distilled water was used in the trays from then on to prevent buildup of salts in the containers.

Attempts to control fungus growth by incorporating Nipagen or Captan fungicide, at reportedly non-toxic concentrations, into the plaster was associated with high nymph mortality and were discontinued. Since the containers were flexible, old plaster-cotton substrates could be removed; the container washed and refilled with fresh substrate when necessary. For some experiments, substrate color was varied from white (plaster only) to almost black (plaster

with a great deal of charcoal).

Freshly-killed houseflies were given to the insects as food every other day.

Cannibalism, especially upon moulting individuals, was a problem in laboratory cultures. In an attempt to reduce mortality by cannibalism and to rear insects individually for various reasons, some containers were made with four-inch sections of glass tubing set into the plaster before it hardened. One insect was placed in each tube. Mortality was very high in populations kept in separate tubes, however, so this practice was discontinued.

The best methods for reducing mortality by cannibalism were (1) avoidance of overcrowding the rearing containers, (2) frequent feeding, and (3) separation of age groups (all stages seem to attack younger stages). Blotter paper containing eggs was removed at two-day intervals and put into a separate container. Mortality of young nymphs was also reduced by minimized handling; i. e., moving them on the blotter paper or very gently with a wet brush rather than with an aspirator.

Development. Total generation time (from newly-emerged adult to newly-emerged adult offspring) was about 33 days in the warm chamber and 93 days in the cool chamber. Development from egg to adult took about 28 and 82 days, respectively.

Development of eggs from adults collected during the summer

months took about 10 days in the warm chamber and 24 days in the cool chamber. Development of eggs from adults collected in February and placed in the warm chamber took only about 7.5 days, however. If these eggs were placed in the cool chamber within 24 hours of oviposition, nymphs appeared in about 14 days.

Total nymphal development time was 18 to 21 and 55 days, respectively. Approximate lengths of stadia in the warm chamber were: first, 1-2 days; second, 2-4 days; third and fourth, 3-4 days each; and fifth, 4-5 days.

Figure 17 shows time from nymph emergence to the adult moult in groups of insects switched at different stages in development to the cool chamber from the warm chamber. Differences in development time prior to the adult moult were related to the age at which the nymphs were switched to the cool chamber. The data suggest that cool temperatures affected nymphal development times in a stepwise, rather than linear, fashion. Cool temperatures appeared to have little effect (in terms of slowing development) on the insects once they reached the fifth instar stage.

S. palustris could be reared from egg to adult at temperatures of 10° C (night), 18° C (day) (an average of 15° C) while insects reared at constant 15° C developed much slower and mortality at or soon after moulting to adults was near 100%. This observation supports reports that development of insects is faster at alternating

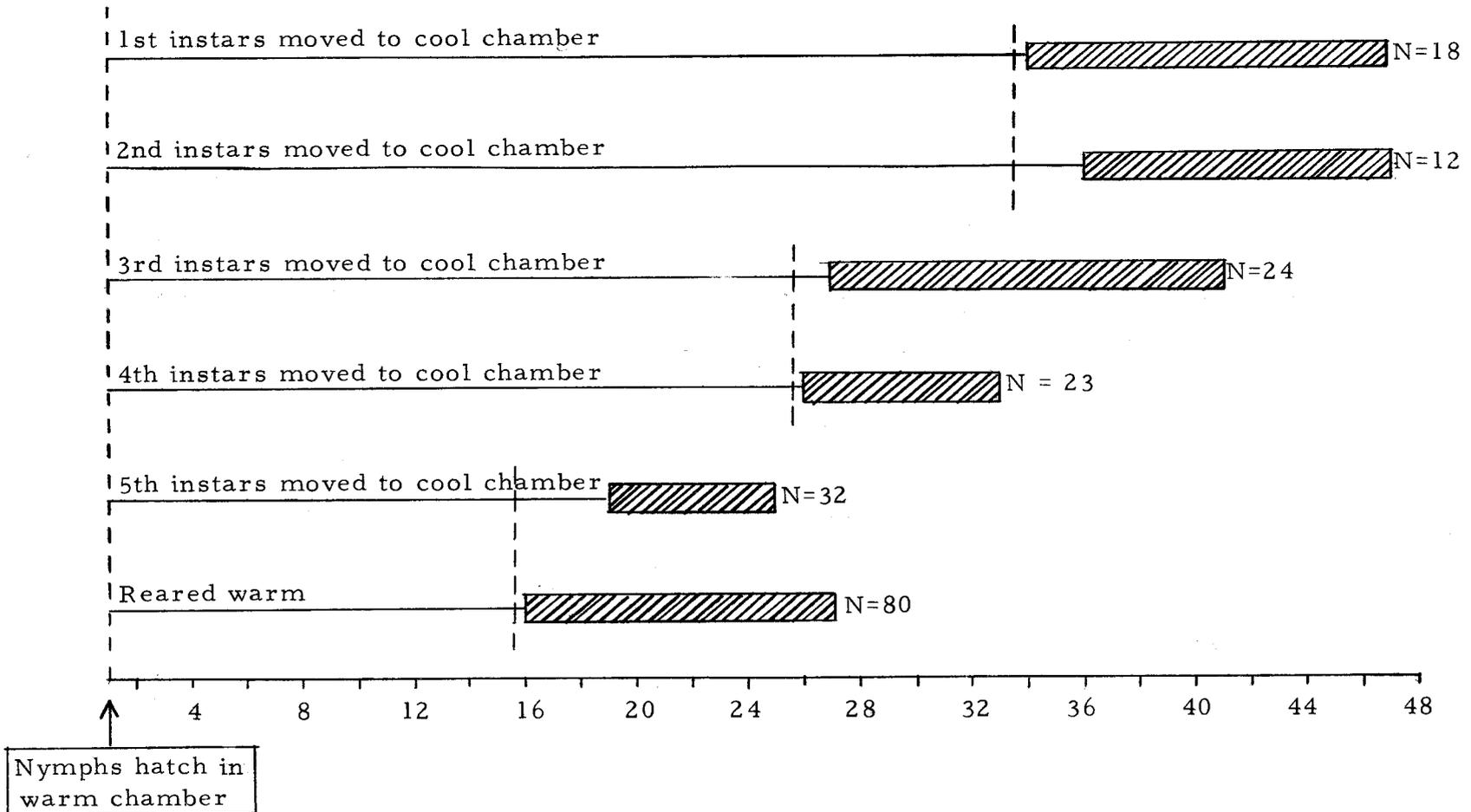


Figure 17. Time (in days) from emergence of nymphs to the adult moult in groups of *S. palustris* moved at different ages from the warm to the cool growth chamber. (Bar shows time from first to last adult moult for the group, N = total number of adults.)

temperatures than at thermally equivalent constant temperatures (Huffaker, 1944; Richards, 1957). It also indicates that the threshold (minimum) temperature for normal development to the adult stage in S. palustris is about 15°C.

There is a series of threshold temperatures for development of a species (Richards, 1957). For example, in Oncopeltus sp. (Heteroptera: Lygaeidae), the threshold temperature for egg development to the blastoderm stage is 5°C; to hatching, 15°C; and to the adult, greater than 17°C. In S. palustris, eggs were deposited and nymphs hatched at an average temperature of 10°C (alternating day and night temperatures) but all nymphs died before reaching the second stadium. Therefore, the hatching threshold for this species is about 10°C, while the threshold temperature for development through the nymphal stages is probably a few degrees higher than this.

The average lifespan of adults reared from fifth instars in late August was about 14 days (a maximum of 40 days) in the warm chamber, and 25 days (a maximum of 80 days) in the cool chamber. In the warm chamber, adults deposited eggs for about 33 days; in the cool chamber, 60 days. Several hundred overwintered adults, collected in mid-February and placed in the warm chamber, began active oviposition immediately and lived a maximum of 25 days.

## THE INTERTIDAL HABITAT

Only a few families of insects occupy the intertidal habitat on a worldwide basis and the Saldidae is one of these (Evans, 1968). Insects are generally believed to be primitively terrestrial. Semi-aquatic groups such as the Saldidae are of particular interest as showing possible methods by which colonization of the water might have occurred. Because of fluctuating tide levels, existence in the intertidal zone is more conducive to initial aquatic adaptation than one at margins of non-tidal freshwater bodies (Brown, 1948). Although only a few species are known to be exclusively intertidal (e. g., Paralosalda innova Polhemus and Evans, Aepophilus bonnairei Signoret, and all species of the genus Salduncula Brown and members of the closely related family Omaniidae), many others are subjected to tidal submergence occasionally or regularly. Some species reported able to withstand tidal submergence are Halosalda lateralis (Fallén), Chiloxanthus pilosus (Fallén), Chartoscirta cocksii (Curtis), Salda littoralis (L.), S. buenoi (McD.), Saldula setulosa Puton, S. pilosella Thomson, S. saltatoria (L.), S. woodwardi Drake, S. pallipes, and S. palustris (although records on the last two species are mixed).

Nymphs and adults of S. palustris are able to withstand at least

14 hours submergence (Brown, 1948)<sup>3</sup> which is comparable to China's (1927) report that A. bonnairei can easily survive 12 hours submergence between the two low tides. S. palustris nymphs can withstand longer submergence than adults. This has been attributed to the more delicate and hydrophile integument of the nymphs which allows them to utilize water-dissolved oxygen by cutaneous respiration and the ability of the adults to retreat to some extent before the incoming tide. Submerged adults are believed to depend upon atmospheric oxygen held in bubbles on their relatively pilose bodies or beneath the hemelytra (Woodward, 1958). There is no appreciable bubble retention by nymphs. A. bonnairei, which has gone furthest in adaptation to subaquatic life, has diverged in several ways from typical saldid structure. Woodward (1958) suggests that the soft cuticle of this insect may be related to cuticular respiration during submergence and provides the insect with greater potentialities for becoming truly aquatic in all stages.

In general, however, saldids have no obvious structural adaptations for submergence but are adapted physiologically and behaviorally to temporary underwater existence. This change of habit, not yet accompanied by morphological changes, is characteristic of aquatic adaptation in nearly every insect group (Brown, 1948).

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<sup>3</sup>Brown's work was done on S. palustris which he considered only a "dark form" (p. 180) of S. pallipes.

Woodward (1958) suggested that the habit of retreating under vegetation and stones when disturbed could be regarded as a preadaptive characteristic of salinids from which other habits suited to intertidal life might have developed.

At the study site, behavior of S. palustris nymphs upon submergence was very similar to that described by Brown for S. palustris and by Southwood and Leston (1959) for H. lateralis. The insect held firmly to the substrate or vegetation as it was submerged by the incoming tide and remained immobile. When the initial turbulence passed, it sometimes walked slowly along, until a more suitable place (such as a pit in the ground or a lower location on the vegetation) was found. There it remained quiescent until the tide receded. If washed to the surface it struggled actively until it encountered emergent vegetation or a projection and then climbed down beneath the water to remain quiescent near its base.

Brown compared behavior of H. lateralis and S. palustris upon submergence. These two species differ in distribution within the intertidal zone; H. lateralis lives near the top of this zone while S. palustris extends its range far down into the intertidal zone. When submerged in experiments, H. lateralis became restless and appeared to search for a means of escape whereas S. palustris by contrast either remained at rest or "moved about in a leisurely

manner, giving one the impression that it was in their nature to be submerged" (Brown, 1948, p. 184). Specimens of H. lateralis became completely torpid within a half-hour while S. palustris remained capable of activity for four to 14 hours. When removed from the water after 14 hours, only half of the H. lateralis recovered but all S. palustris recovered, including the torpid ones, within three and one-half hours.

Brown also noted that adult S. palustris are more resistant to desiccation than nymphs. In my studies, I also found this to be true. A group of nymphs of all ages put in a dry container died in direct relation to their age; the first instars within four hours, all fifth instars by 23 hours, and the single adult (which had been teneral at the beginning of the observation period) died at 26 hours. Eggs are very resistant to desiccation, however. A group of eggs allowed to become completely dry for two days in the laboratory produced nymphs and adults after similar development time as a control group of eggs which had been kept moist.

## TIDE AND TEMPERATURE ANALYSES

The salt marsh is subjected to tidal action and the resulting alternation of periods of submergence and exposure. Both the frequency and the duration of these periods change with elevation, producing a vertical zonation of environmental conditions across the marsh surface (Doty, 1946; MacDonald, 1969).

At any one level, both tidal and diurnal climatic rhythms are affecting the environment and have a combined effect on the life of the insects. While the area is submerged, the environment shares the physical and chemical characteristics of the estuary water. When exposed, the area is affected by climatic variables such as air temperature, radiation, and precipitation. Additional environmental variation results from seasonal fluctuations of these variables (MacDonald, 1969).

I have attempted to develop a simple model for the study site during 1971 that will enable description of tidal cycles in relation to the submergence and exposure of the insects within the intertidal zone. Incorporation into the model of air and soil surface temperatures permitted evaluation of daily temperatures to which the insects were subjected during their development. The insects live in the 'boundary layer'; the skin of air within 2 mm of the ground (Lowry, 1969, p. 41) and soil surface temperatures can be used to

approximate temperatures to which the insects are subjected when they are not covered by the tide.

Approaches to formulation of this type of model vary from simple to extremely complex. The simplest approach is to consider the soil surface region (where the insects live) as very near the air temperature when it is exposed, disregarding surface heating, cooling, and saturation effects. At the other extreme is a model involving an energy balance for the soil surface and includes consideration of many other meteorological and heat transfer phenomena. In initial attempts to correlate biological and physical phenomena, the simpler approach is recommended (Lowry, personal communication). I have, however, incorporated certain corollary assumptions and considerations into the data to make the model as realistic as possible, given the limitations (of time, information, and ability) at hand.

### Tides

At the study site, maximum water temperatures (up to 22° C) are reached during July and remain high until mid- to late August. Minimum water temperatures (7 to 8° C) occur during December and January (Manske, 1968). Coastal upwelling, which markedly lowers water temperatures at the coast and lower estuary during the summer, only extends five to six miles upstream and does not affect water temperature at the study site.

One of the chief characteristics of the tide along the Pacific coast of the United States is diurnal inequality; i. e., the difference in heights of successive high tides or low tides. The largest inequality is in the low tides (U.S.C.G.S., 1971). Predicted tide levels are published annually for Newport, Oregon. These predictions take into account seasonal variation in sea level (usually less than 0.5 foot) and river level (with allowances representing average flooding and drought conditions). Unusual flooding (as during January and March 1971) or droughts (October 1971) or changes in winds or barometric pressure at the coast sometimes create considerable deviation from predicted tide levels. Records of actual tide levels at the Oregon State University Marine Science Center (Figure 6) at Newport were obtained from the National Oceanic and Atmospheric Administration in Maryland (NOAA, 1972). After correcting these data to the 0.0 MLLW reference level, tide times and levels at Toledo (Appendix I) were determined using U.S.C.G.S. (1971) locality corrections. The amplitude of the tidal cycle is greater at Toledo (high tides 0.1 foot higher and low tides 0.2 foot lower) and there is a lag in time for the tides (high at Toledo is 45 minutes later than Newport and low, 57 minutes later).

Methods for calculating the height of tide at any time are based on the assumption that the rise and fall conform to simple sine curves (U.S.C.G.S., 1971). For simplicity of data manipulation,

this assumption was used to calculate tide levels between consecutive high and low tides (Appendix II).

For analysis of submergence and exposure times at different vertical elevations at the study site, the model (A) can be visualized as a tidal curve with an abscissa of 24 hours and an ordinate of height in feet above 0.0 foot tide level for the Pacific coast (Figure 18a).

Tolerance to Submergence. The large differences between levels to which two successive low tides fall along the Pacific coast result in distinct zonation of intertidal flora and fauna (Doty, 1946). Zone limits are correlated with critical tide levels where sudden increases (often two- or three-fold) occur in maximum duration of either continuous submergence or continuous exposure. Changes of this magnitude are sufficient to account for the abrupt restrictions in vertical range observed in intertidal organisms susceptible to drowning or desiccation. Doty (1946) correlated upper limits of certain algal zones with levels where maximum time of emergence from the water sharply increased, thus exposing the plants to desiccation and sun-killing. For S. palustris, determination of maximum submergence times at levels at and below the level of the insect population gives an indication of the tolerance of the insects to submergence and sub-aquatic life. Maximum submergence times were calculated according to model A (with the Fortran program in Appendix III) and

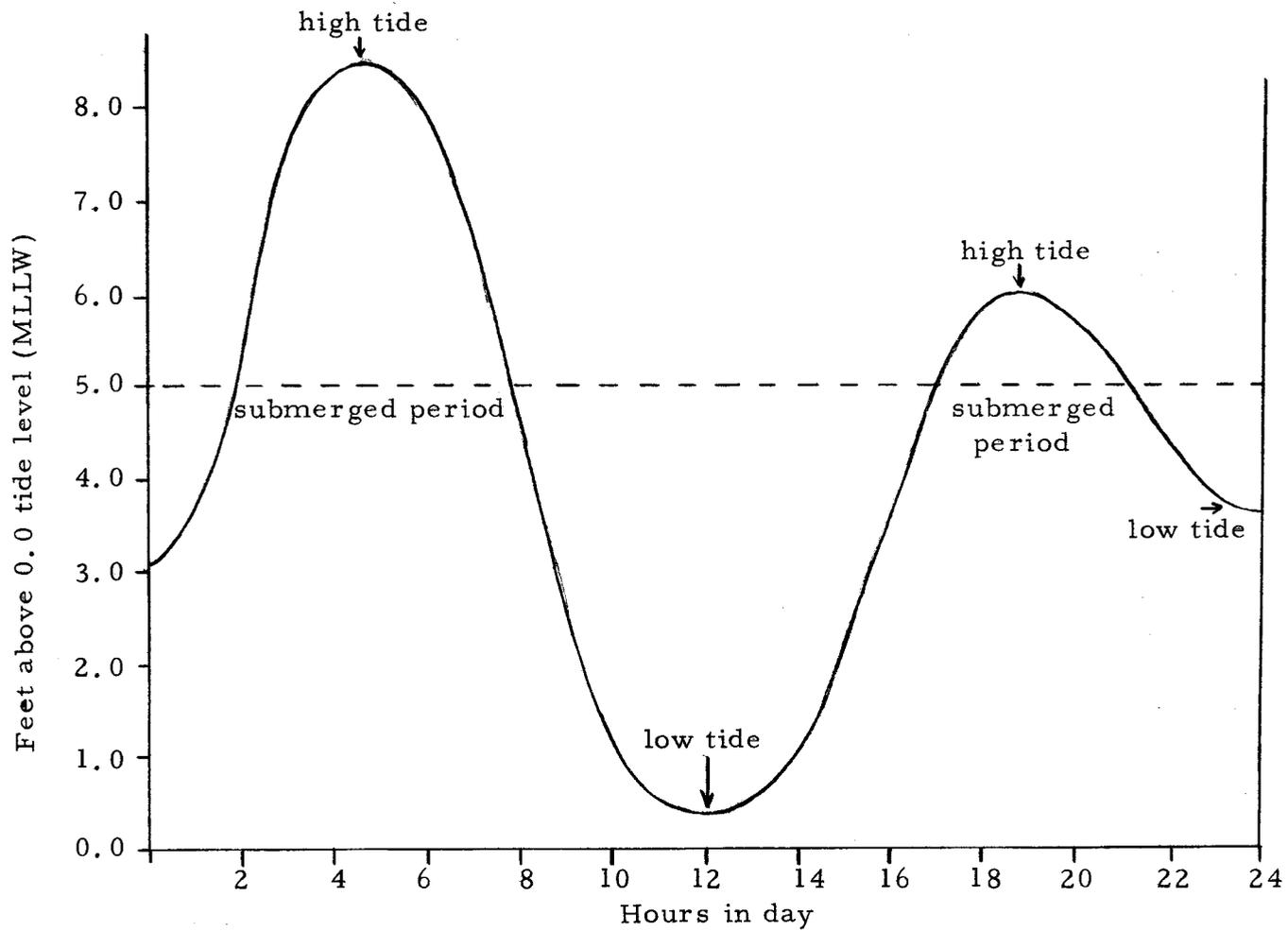


Figure 18a. Tidal submergence at the 5.0 foot tide level.

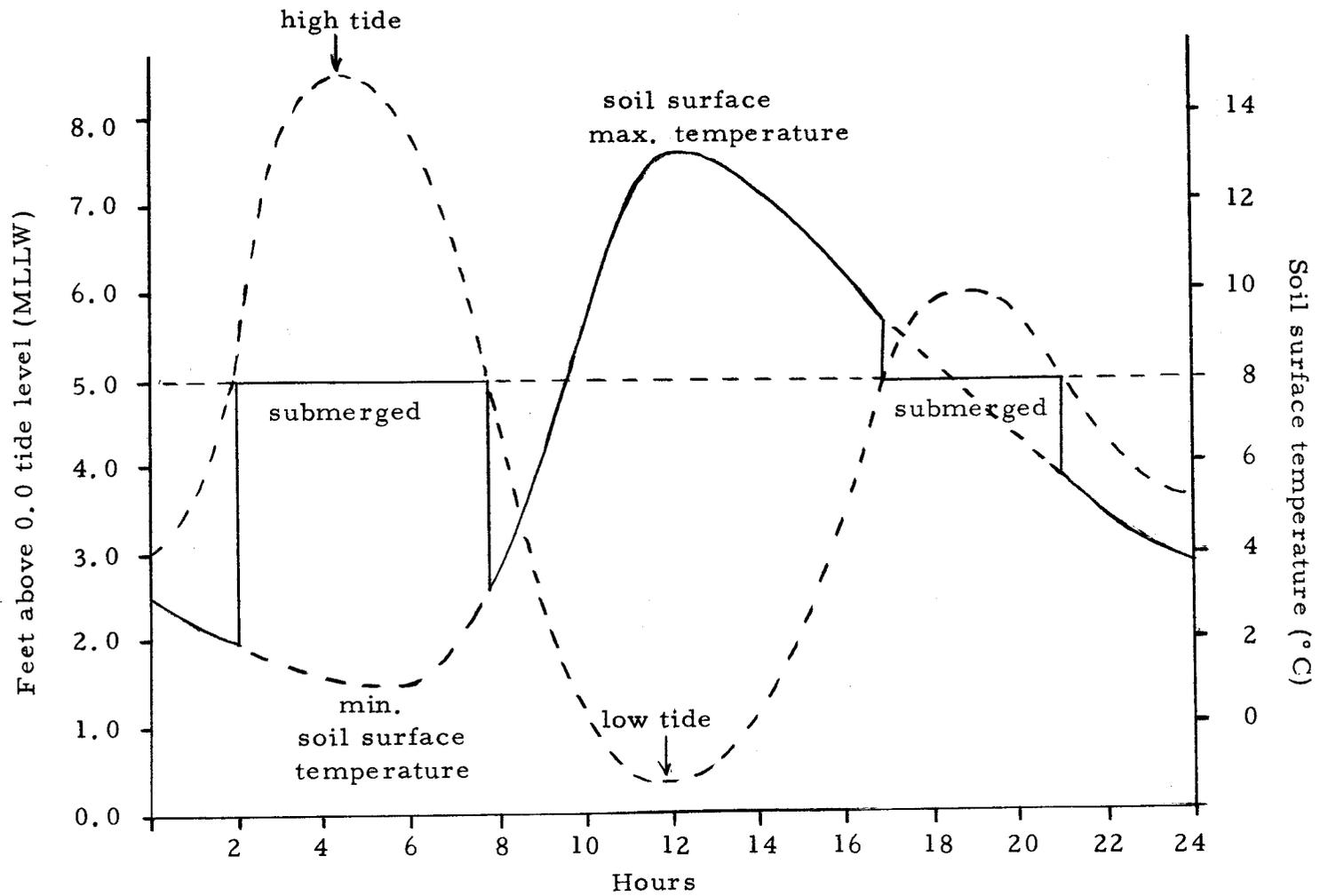


Figure 18b. Method for calculating mean temperature affecting insects for each day.

the single maximum submergence time for each month (March to October 1971) was determined for several vertical tide levels. The general pattern of these data are shown in Figure 19.

The insects and vegetation do not extend below the five foot tide level (Figure 7). Below this level (from about 4.5 to 5.0 feet), length of maximum single submergence time doubles from about eight to nine hours to 17 to 18 hours. This critical tide level at 4.5 to 5.0 feet resulted from unusually high low tides which occurred several times during 1971 (e. g., March 6, 4.58 feet; April 16, 4.95 feet; August 30, 4.67 feet). Mean low water at the study site is 1.1 feet (U. S. C. G. S., 1935). When these tides occur, the area below this level is continuously submerged from the previous low to the following low tide.

The insects are therefore well-adapted to submergence for up to nine or ten hours but may not be able to tolerate submergence for periods of 17 to 18 hours.

Percent of Day Submerged. Determination of the total percent of time submerged during a 24-hour period at any tidal level was based on summation of separate periods of submergence for that day (Appendix VI). Cyclic changes in percent of day submerged are related to changes in tidal heights during the spring-neap tide cycle (Figure 20).

Cyclic changes in distribution of the intertidal staphylinid

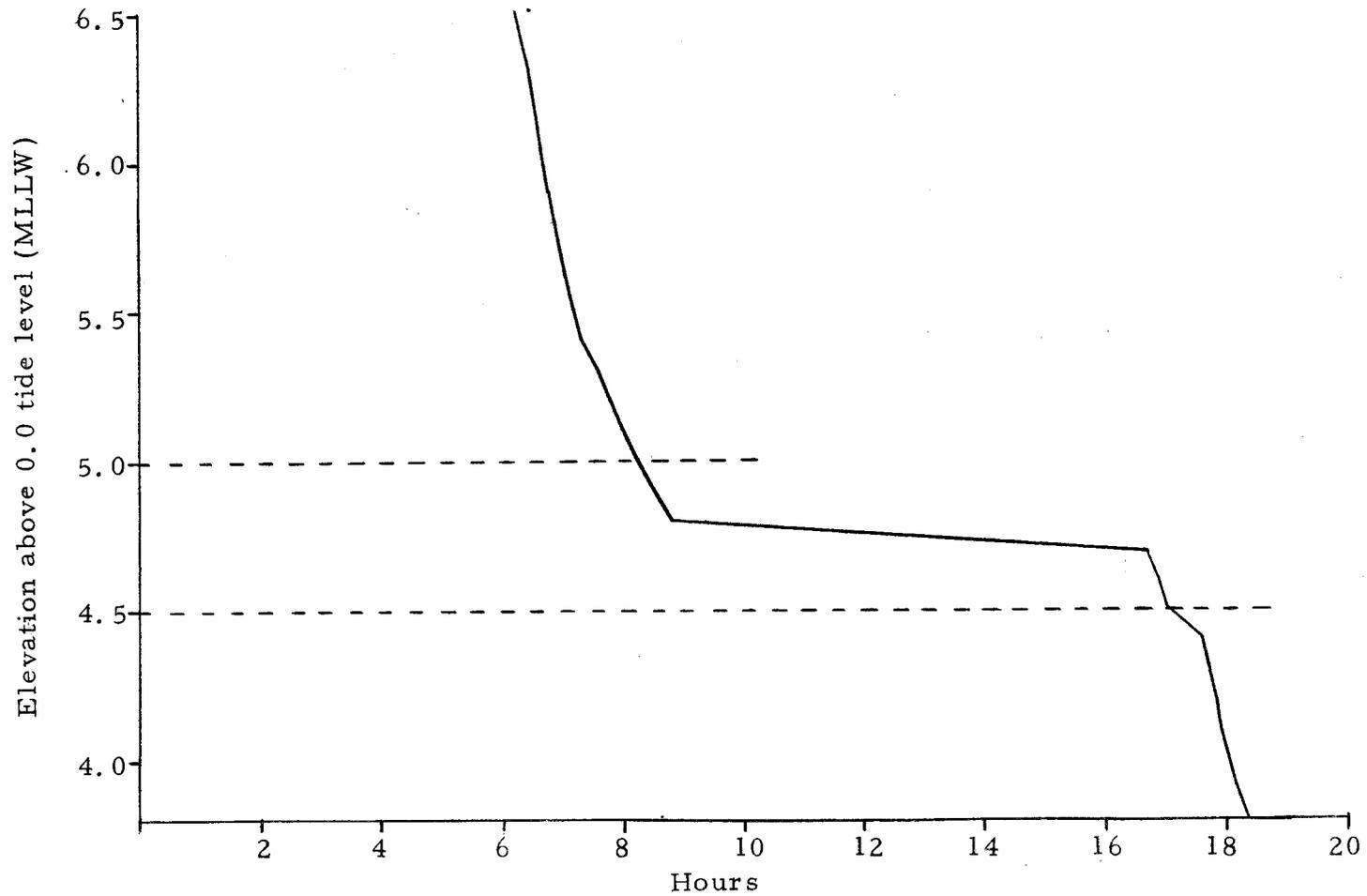


Figure 19. Maximum continuous submergence time at the study site, March to October 1971.

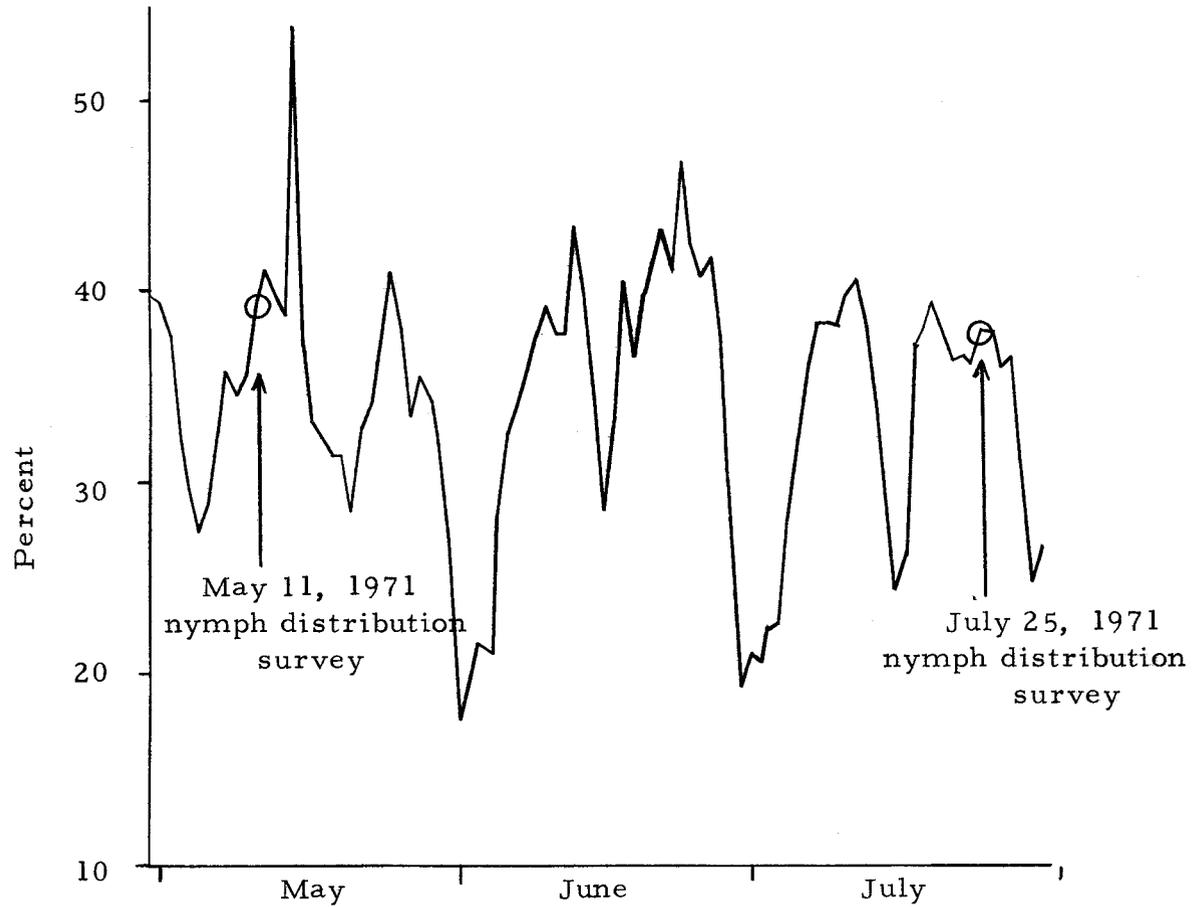


Figure 20. Total percent of day submerged at the 5.47 foot tide level (see also Figure 7).

beetle Thinopinus pictus Leconte were correlated with such tidal rhythms (Craig, 1970). Landward distribution of the beetles is restricted by their preference for certain levels of moisture. Seaward extension of the population is related to their preference for soft sand (the sand is more hard-packed towards the ocean). As a result of these preferences, cyclic displacement of the beetle population occurs. Correlation between landward-seaward distribution and spring-neap tidal cycles has also been reported for some intertidal crustaceans (Bowers, 1964; Hamner, Smyth, and Mulford, 1969).

Differences observed in distribution of populations of nymphal S. palustris at the study site (page 38) might be related to tidal cycles but sufficient data is not available to determine this. Dates of the 1971 distributional surveys are indicated on Figure 20 but no obvious differences can be seen in tidal cycles relative to nymph distribution on these dates.

Differences in nymph distribution might be related to the distribution of vegetation which was much more extensive over the area in July than in May (Figure 9).

The period of time submerged during the daylight hours (6 AM to 6 PM) was also calculated since the insects are diurnal and submergence during this time would disrupt their activity patterns. Figure 21 shows percent of the daylight hours submerged at two tidal levels: 5.47 feet (near the lower distributional limits of the

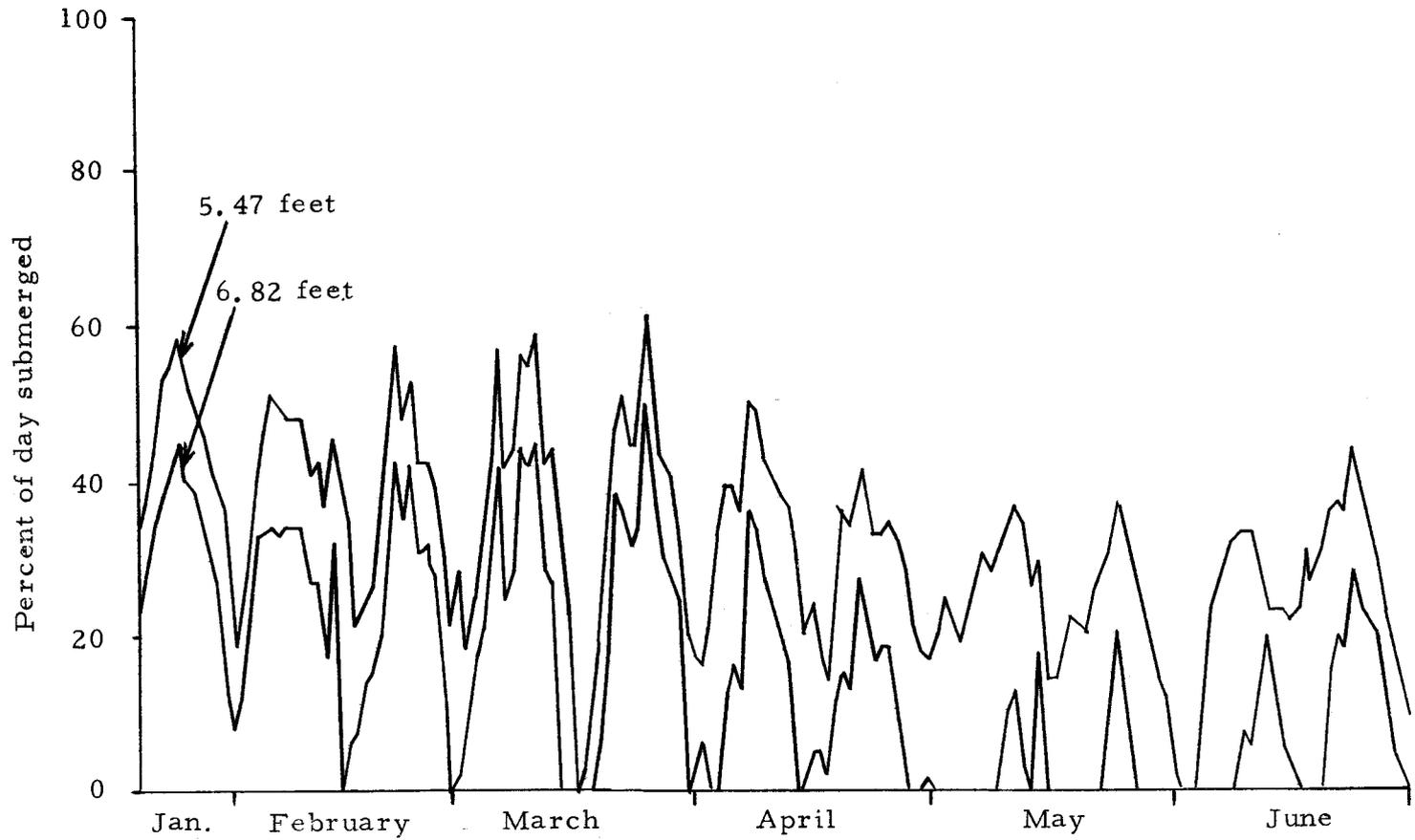


Figure 21. Percent of day (6 AM to 6 PM) submerged at 2 tidal elevations in study area (see also Figure 7).

insect population) and 6.82 feet (near the upper limits) (Figure 7). In addition to cyclic changes related to spring-neap tide cycles, there is a trend towards decreasing percent daytime submergence (to zero on many days) in late spring and summer. This trend is related to changes during the spring and fall of the time of the lowest spring tides in each cycle. During the summer months these low tides occur between about 4 and 8 AM while in the winter months they occur in the evening between about 6 and 9 PM (Thum, 1972). Thus, the area is exposed a greater percent of the time during the daylight hours during the summer.

### Temperature

The climate of the Yaquina Bay area is characterized by marked wet and dry seasons. At Newport, for example, seasonal fluctuations of precipitation during 1971 ranged from less than 1.2 inches in July to 20 inches in December. The Yaquina Bay area is also marked by warm summers and mild winters, having a mean annual temperature of about 10°C.

Sorting out data for temperatures affecting the insects when they were not submerged was a difficult task. Newport is the source of much weather data but a fog bank affects that town during much of the summer, creating cooler temperatures than Toledo. The Marine Science Center, slightly south of Newport, is less affected by

the coastal fog and data obtained there approximate conditions at Toledo more closely. Again, applicability to the study area of daily maximum and minimum temperatures recorded at Toledo (at the Georgia-Pacific paper mill) had to be assessed. I recorded soil surface temperature as well as air temperatures at one and six inches distance from the surface with a thermistor thermometer at the study site at approximately one-week intervals during 1971.

Both night and day temperature extremes occur at the ground surface since the surface is the most active heat exchanger in the soil-air system (Lowry, 1969). Time of minimum temperature at the ground surface is approximately one hour before sunrise and maximum temperature occurs about noon (Lowry, personal communication). On cloudy days the amplitude of the temperature wave is less at any given level as a consequence of reduced rate of input of solar heat at the surface and less effective, less vigorous, convective and conductive linkages between the surface and other levels (Lowry, 1969).

Digby (1955) stressed the importance of radiation levels on temperatures affecting small insects and consequently their activity. When insects are heated by the sun, their temperature is greater than air temperature by an amount called the temperature excess. Variation in temperature excess with radiation strength is approximately linear for small insects. The heating effect of metabolism

is less important compared with that of the sun as size decreases. For these reasons, heating of the soil surface relative to radiation levels has been emphasized in development of the tide-temperature model. The assumption is made that the insects, being very small and poikilothermic, are directly subject to external temperatures and have negligible regulatory control.

Approximation of daily maximum and minimum temperatures for the exposed soil surface (so that a temperature curve for each day could be calculated) resulted from (1) definition of air maximum and minimum temperatures for the study site and (2) evaluation of the relationship of air temperature to soil surface temperature based on radiation and precipitation level data for each day. Details of this procedure are given in Appendix IV and resulting daily maximum and minimum soil surface temperatures are found in Appendix V. During warmer months, mid-day soil surface temperatures can be almost 6°C higher than measured air temperatures at the study site.

For evaluation of temperatures affecting the insects, the model (B) consists of a second curve (for exposed soil surface temperature) superimposed on the tide curve and a second ordinate of degrees centigrade (Figure 18b). For simplicity of programming, it was assumed that the temperature of the exposed soil surface goes directly to water temperature upon submergence and directly to exposed soil surface temperature when the tide recedes. Mean daily

temperatures (Figure 22 a, b) were then calculated (with the Fortran program in Appendix VI).

The change in time of occurrence of the lowest spring tides from evening to morning takes place at the time of the vernal equinox (about March 21). During the summer, then, the intertidal zone is exposed to atmospheric heating during a greater percent of the morning hours and this change is reflected in increased mean daily temperatures after this time (Thum, 1972).

Approximate temperature thresholds for development, determined in the laboratory for S. palustris (page 48), corresponded to changes in mean daily temperature calculated for insects in the field.

The effects of heat summation or day-degrees on insect development are well-known. According to Allee et al. (1949, p. 111), a "day-degree represents one degree of mean temperature above the ecological zero lasting for one day". For S. palustris, mean temperatures of about 10° C are "ecological zero" since minimum mean temperature for egg development is about 10° C and temperatures greater than this are necessary for further development. The first nymphs of the year appeared after a period of about a month of average daily temperatures fluctuating above the 10° C level. The first adults appeared after mean daily temperature began to rise above the 15° C level. There is also a correspondence between decreasing mean daily temperatures in August and September with

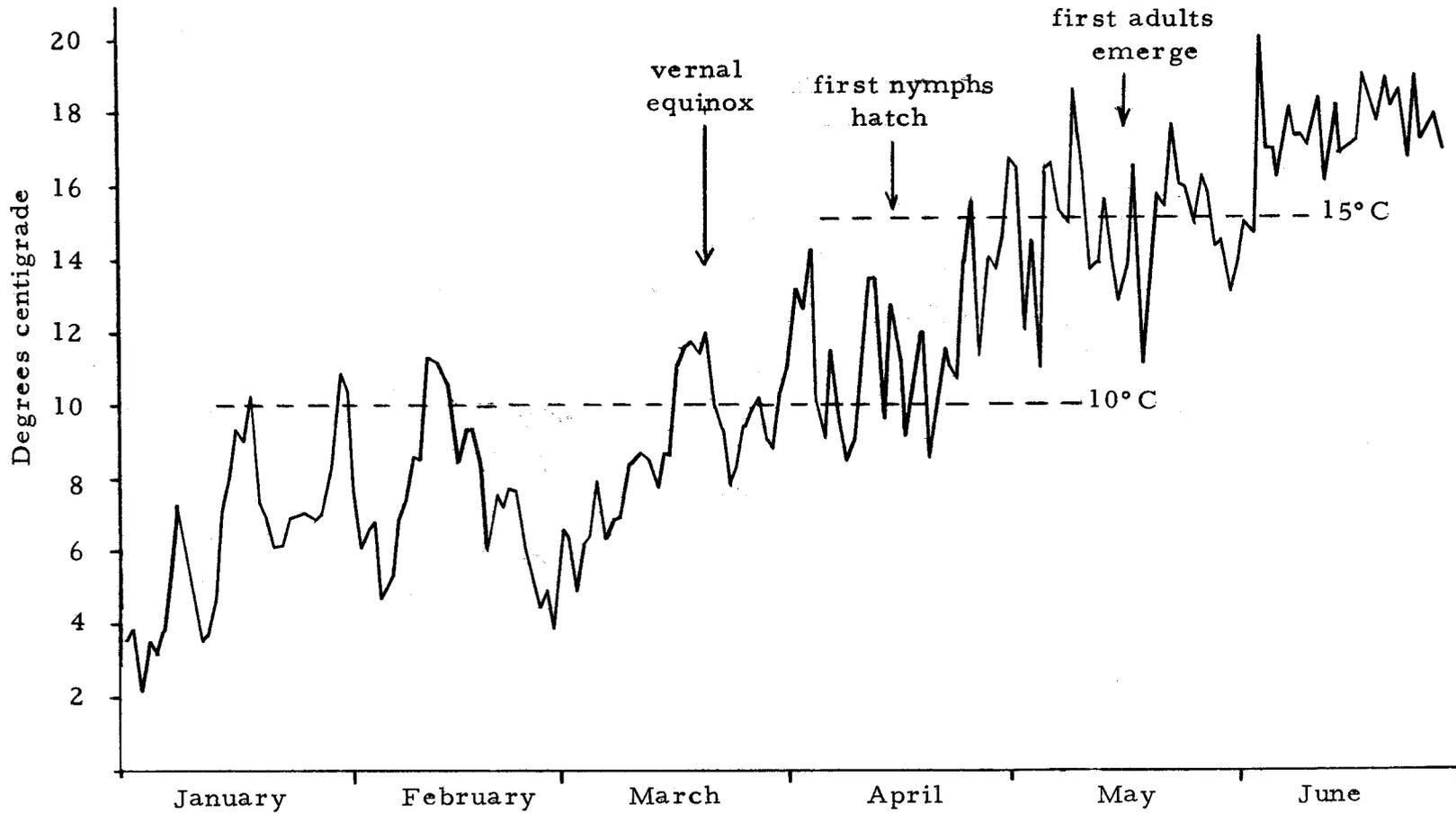


Figure-22a. Mean daily temperatures affecting insects, January to June 1971.

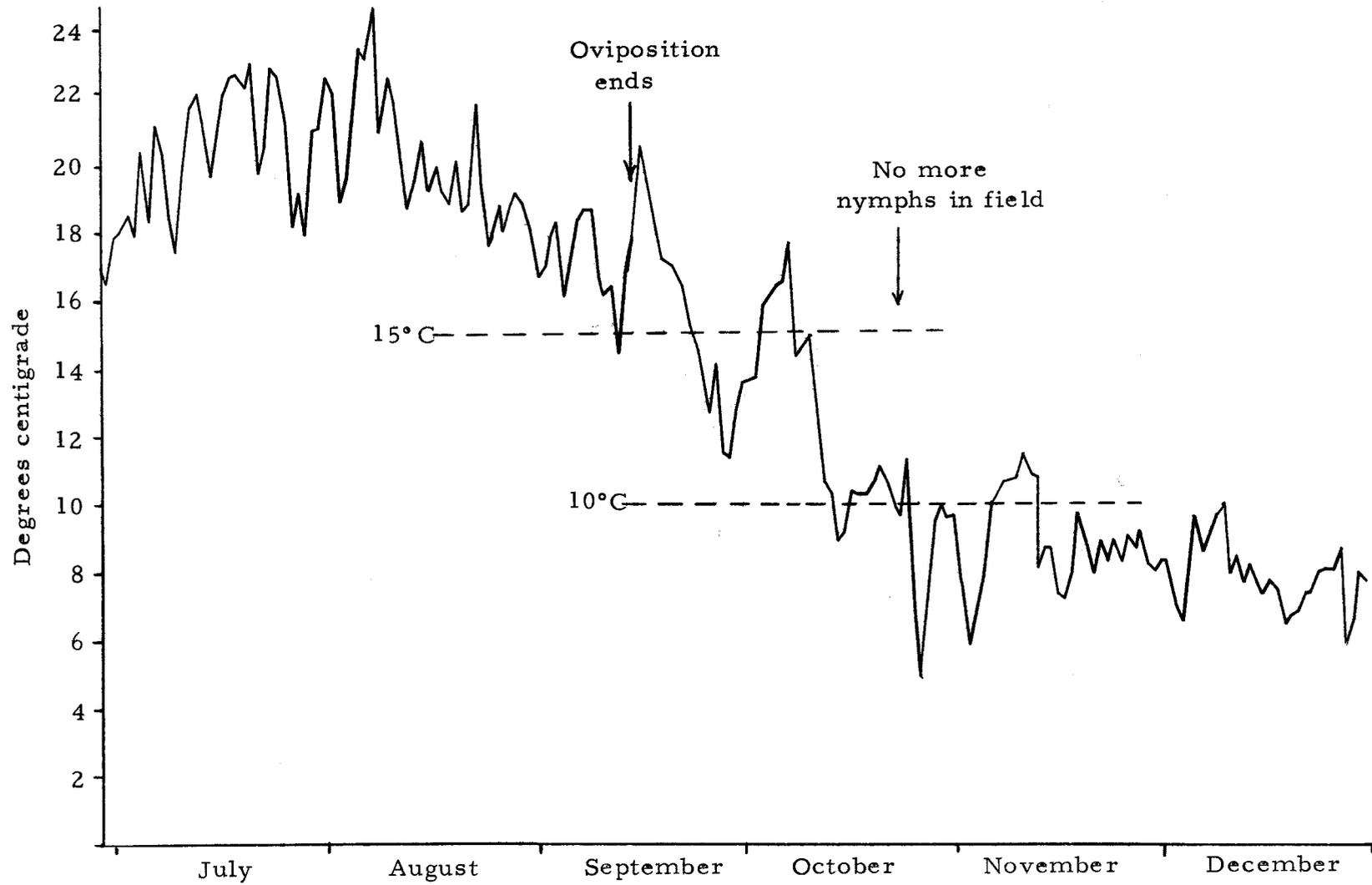


Figure 22b. Mean daily temperatures affecting insects, July to December 1971.

the ending of reproductive activity.

Mean daily temperatures of over 27°C in the growth chambers were found to be near the upper extreme for normal development and activity of these insects, even when humidity was maintained at a high level. Mean daily temperatures never rose above 24°C in the field during 1971.

## WING PIGMENTATION

The forewings or hemelytra of Saldidae have a thickened basal region divided into a clavus and corium and a thin apical membrane which, in S. palustris, has four long closed veins (Figure 3). The hemelytra of most species are predominantly black with pale markings; the clavus and corium having a greater percentage of dark area than the membrane. Differences in darkness between regions of the wing are probably a result of greater concentration of dark pigmentation in the darker areas. The palest areas are translucent, often faintly amber-colored. The conspicuously white spots in the distal exocorium of some wings probably result from structural differences in the cuticle rather than actual white pigmentation (Richards, 1967).

Some uncertainty has existed as to the applicability of the term "melanin" to dark pigments in insect cuticle. As in vertebrate skin, one is dealing with the reaction of tyrosine derivatives to give melanoproteins. In at least some cases, the dark color of insect cuticles can be removed or decreased in intensity by treatment with ethylene chlorhydrin (2-chloro-ethanol), a known solvent for vertebrate melanins (Richards, 1967). Insect melanin, however, is usually diffuse rather than granular as in vertebrate skin. It is generally believed that quinones, derived from tyrosine in the blood, tan the proteins in the outer procuticle after the moult, producing exocuticle

(sclerotization or hardening). This process is usually associated with darkening which may be a result of tanning alone (probably depending on the type of bond between the protein chains) but may also involve the polymerization of excess quinones to form melanin (Chapman, 1969).

The extent of area covered by black pigmentation in saldid hemelytra is defined before the hardening process has finished. In teneral individuals, when the wing is still very soft and flexible, the pattern of pigmentation is already clearly marked in pale gray. In Pentacora signoreti (Guérin), darkening of the hemelytra first appears in the anal corner of the mesocorium and along the clavus, expanding to the lateral mesocorium, leaving certain light spots open, and then over the exocorium (Cobben, 1960b). Darkening of hypodermal coloration in the wings of Perillus bioculatus (F.) (Heteroptera: Pentatomidae) begins at the apex of the corium (Knight, 1924). The direction of darkening of the wing is probably related to patterns of blood circulation in the wings at this time (Yeager and Hendrickson, 1934; Uvarov, 1966).

Wings of S. palustris are fully pigmented within 15 hours after the adult moult at 24° C.

#### Wing Pattern Development

Development of the layers of the cuticle involved in formation

of wing patterns has been described by Schatz (1952) and Richards (1967). Following the moult, the soft procuticle differentiates into one or more layers of other histological types; exocuticle, mesocuticle, and endocuticle. The exocuticular layer may be hardened, hardened and darkened, or blackened (melanized). The end result is the common cuticle which, in Mallory Triple-stained sections, is amber (sclerotized and non-staining exocuticle) in the outer portion, red (mesocuticle) in the central layers, and blue (endocuticle) in the inner layers. The relative development of these three components varies from one species to the next and from one area to another in the cuticle of a single individual, resulting in differences in hardness and darkness from one area to the next (Richards, 1967). Additional dark pigment (melanin), if present, usually forms a band somewhere in the exocuticle or throughout the exocuticle.

Hemelytra from teneral and darkened S. palustris, removed at intervals during the first day after the adult moult, were preserved, sectioned, and stained with Mallory's Triple for histological examination. Wings were fixed for 24 hours in modified Zenker's fixative and then transferred to 70% ethyl alcohol. Extremely soft teneral wings were preserved for an initial five minutes under a cover slip to prevent folding of the wing during fixation. The standard paraffin imbedding method was followed except that cedar oil was used in clearing from 95% ethyl alcohol to avoid the possible hardening action

of absolute alcohol. Wings were infiltrated and embedded in Paraplast and sectioned at six to ten microns.

After staining, two distinct layers were visible in wings removed within the first two hours after the moult; outer mesocuticle (red) and inner endocuticle (blue).

In fully hardened and darkened wings, two conditions were seen along wing sections through the corium. In some areas, hardened exocuticle (amber), mesocuticle (red), and endocuticle (blue) were clearly visible. In the majority of the section, however, only two layers were seen; an outer black layer (melanized exocuticle) and an inner blue endocuticle. The three-layered areas were probably pale markings in the wing pattern while the predominating two-layered dark regions were pigmented areas of the wing pattern. Shattering of the wing during sectioning prevented exact location of wing areas in these preparations.

#### Methods of Measurement

The left hemelytron of freshly-killed or alcohol-preserved adults were removed with fine forceps and laid in rows on a thin layer of fresh Hoyer's medium on a microscope slide. More than 50 wings could be mounted on one slide. A small amount of Barber's relaxing fluid, brushed on the wing-hinge, aided removal of wings from dried insects. After drying for a day, wings adhere to the

slide and are not displaced from the rows when more medium and the coverslip is applied.

Several methods were evaluated for rapid and accurate quantification of the extent of wing pigmentation. Some possibilities were; (1) the method of giving numerical values to several areas of the wing according to darkness (Uvarov, 1966; Willis, 1967; Slater and Knop, 1969); (2) manual methods including masking of images with a punched IBM card (Rohlf and Sokal, 1967), use of transparent film with dots overlying the image and counting dots, cutting out regions of the wing on photocopies and weighing the dark and light portions; and (3) mechanical methods of optical scanning and use of the computer digitizer or the densitometer (a type of light meter).

For reasons of relative accuracy, simplicity, speed, objectivity, and low cost, the following method was chosen and used. A large wing image was projected vertically from the slide in a Leitz Prado microprojector onto heavy vellum tracing paper taped to a piece of plate glass. Using a K & E planimeter, total area of the wing image and area covered by pale markings was measured. Percent pigmented area (percent "darkness") was then calculated for each wing. Initially, this method was used for the entire wing. Later, comparisons showed that wing membrane darkness was highly correlated ( $r = .96$  to  $.99$ ) with total wing darkness and showed greater amplitude of variation between samples. Therefore, only

wing membrane darkness was calculated for each wing. This saved time and expressed variation more clearly than if the entire wing had been measured.

### Bilateral Symmetry

With the exception of wing-edge transparency seen in overwintered insects (page 80) and aberrant venation (page 101), both left and right wings of individual S. palustris were identical in extent and type of pigmentation when measured by the above method.

### Wing Darkness in Field Collections

Initially, all males in a sample were compared to females for differences in mean darkness. In field collections from March 2, 1970 (\*) and May 11, 1971 (\*) (overwintered), and August 13 (\*), August 21 (\*\*), and September 4 (\*\*), 1971 (spring and summer generations), females were significantly paler than males. Since more than 100 samples were compared, such a number of statistically significant differences is not greater than could be expected by chance. For this reason, wing darkness values for males and females were pooled in analysis of other experimental and field data. F-tests showed no consistent differences in variability between darkness of males and females from field collections.

Mean wing darkness for field samples collected June 1970 to

December 1971 varied in both years from palest in mid-summer (45-50% dark) to darkest in late fall and winter (65-70% dark) (Figures 23 and 24). Mean wing darkness of ten adults reared in the roof insectary from fifth instars collected each week during the summer (1971) corresponded to changes in wing darkness observed in field collections of adults (also Figure 23). Changes in mean darkness of these adults reared from nymphs preceded similar changes in field populations. Therefore, variation in mean wing darkness of field samples probably resulted from incorporation of newly-emerged darker or paler groups of adults into the field population rather than changes in adults already in the field. Although sample sizes were small, females emerging from fifth instars collected in late July were significantly (\*) paler than males. This might be related to differences in darkness between males and females in field samples during August.

### Aging

From the first appearance of new adults in the spring (around mid-May, 1971) until the time when all overwintered adults had died (late June, 1971), the two generations were easily distinguished. New adults had a grayish ('teneral') caste to the dark parts of the wing whereas wings of overwintered adults were distinctly yellowed in pale areas and dark parts were browner than in new wings. Similar

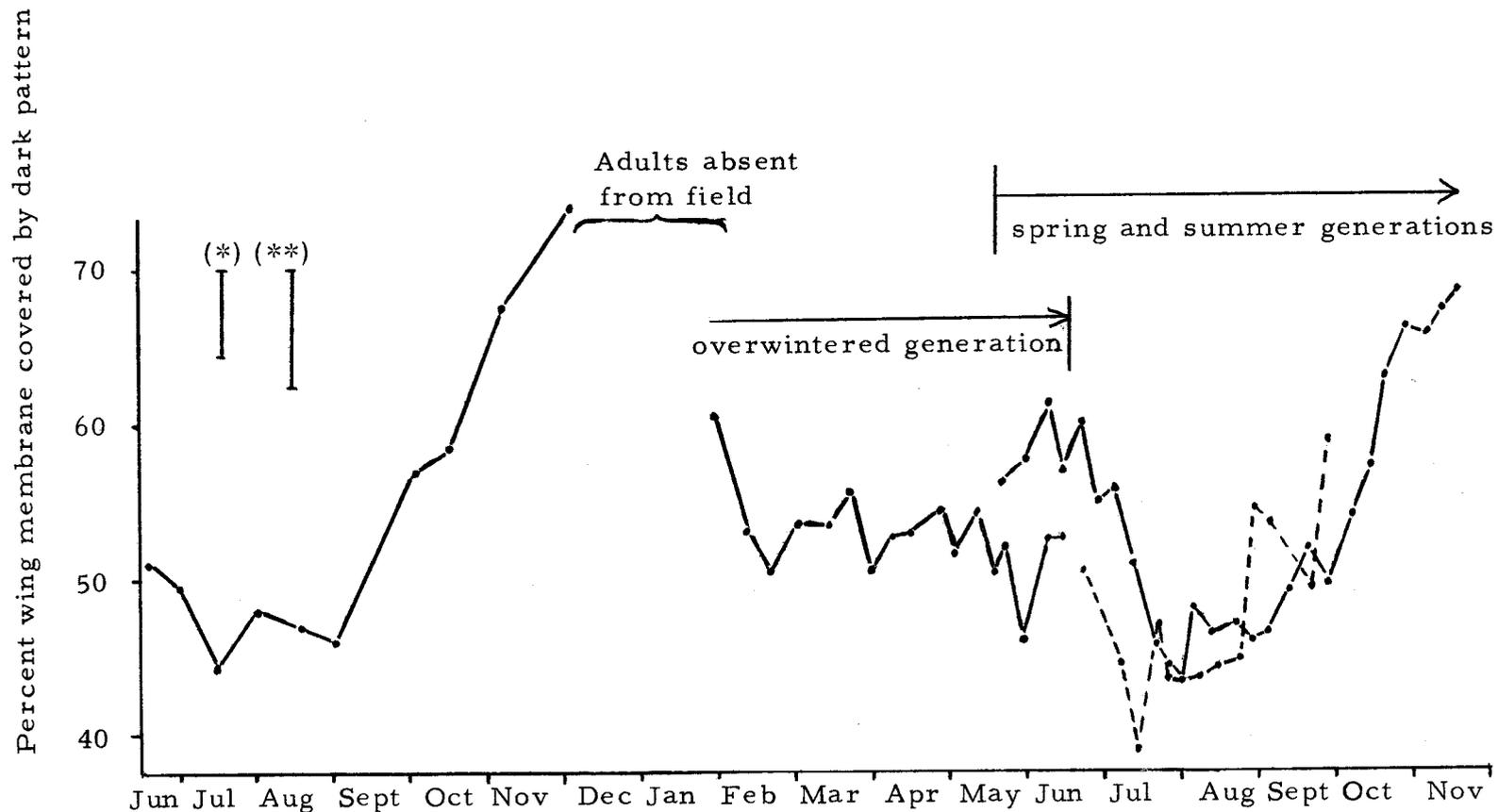


Figure 23. Mean wing darkness in field samples from June 1970 to November 1971.  
 (- - - - = darkness of adults reared from 5th instars collected June - September, 1971.)

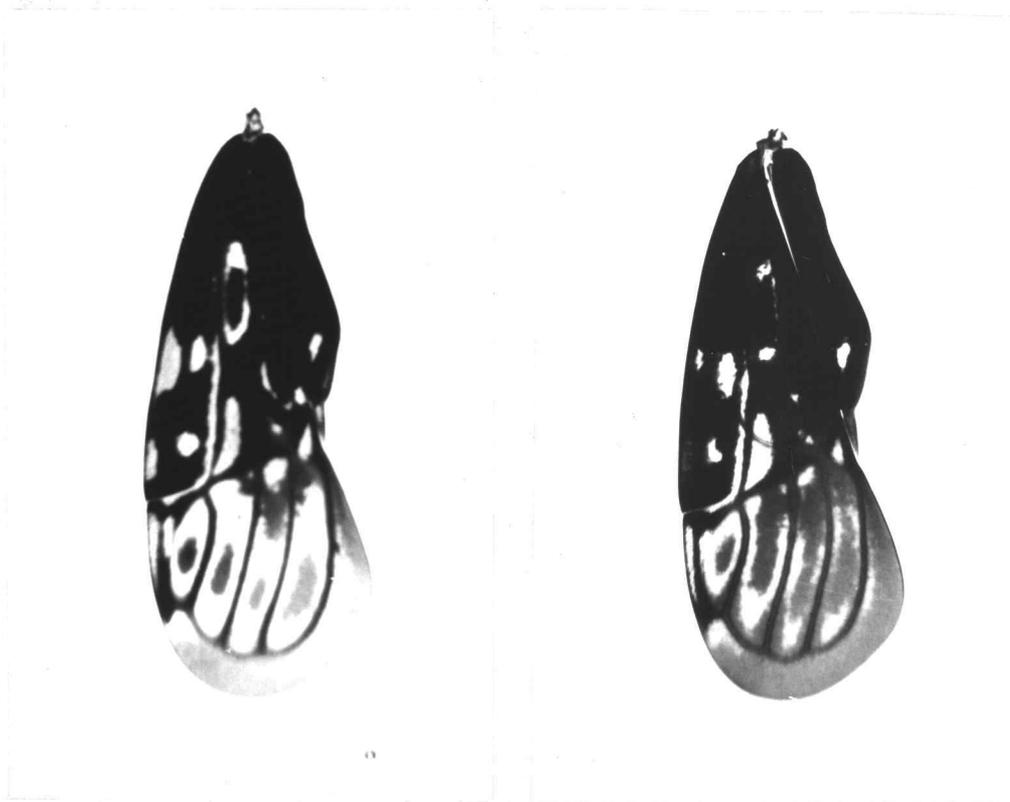


Figure 24. Wings showing pigmentation typical of S. palustris collected in July and August (46% dark) and November 1971 (right, 70% dark).

differences were seen in wings from late spring and early summer collections at other locations. Cobben (1960a) also noted yellowing of pale sections of wings with age. Lindskog (1968) reported that in S. saltatoria, overlap between overwintering adults and the new imaginal generation in the spring is small and survivors of the overwintered generation are recognizable by their "rugged appearance and the dull colour of the hemielytra" (p. 470).

In addition, old wings were often ragged at the distal ends and had miscellaneous very small dark spots ("age spots") in normally pale areas of the membrane. Commonly, a spot was evident in cell 3 above the large pigmented area in the cell (Figure 25). These small dark spots probably developed during the overwintering period and were not present on the wings at the time of adult emergence. In February and March collections, over 75% of more than a hundred wings examined had such spots. Almost all wings from overwintered adults collected in early May had spots while almost no wings from adults collected from late June until December (non-overwintered adults) had these spots. There was a slightly higher percentage of females with spots than males.

Many overwintered adults were also characterized by lack of pigmentation and often complete transparency of the inner or more posterior parts of one or both wing membranes. This condition was more or less extensive over the membrane and was sometimes



Figure 25. Typical "age spot" (indicated by arrow) seen in wings of overwintered adult S. palustris.

associated, in extreme cases, with absence of the end of the wing. Such anomalies could be associated with difficulty in removing wings from the cast skin when moulting at cooler temperatures. The inner wing tips are last to be removed from the old skin during the adult moult and interference with blood circulation during the moult could result in disturbances of pigmentation in these areas. Body movements as in struggling always upset the normal circulation to the elytra of the roach (Yeager and Hendrickson, 1934). When a region of the elytron is injured, the injured region becomes isolated from blood circulation. Such circulatory interference would account for transparency of ragged wings near torn parts.

The general extent of dark cuticular pigmentation over the wing, however, is not likely to change during the lifetime of an individual insect. Melanins are insoluble, highly stable pigments and can be expected to stay where formed (Richards, 1951). The final darkness of adult or nymph cuticle is acquired during the few hours following the moult and is not changed by age, temperature, or other factors (Knight, 1924; Popham, 1943; Harries and Douglass, 1948; Corbet, 1962). Accounts of darkening of insects just before and during overwintering (Southwood and Leston, 1959) probably refer to either darkening of hypodermal coloration with age or the emergence of darker individuals in late fall.

A study concluding that black pigmentation is produced as a

result of physical exertions in gregarious hoppers (Acrididae) (Hussin and Mathur, 1936) demonstrated this change over a period of five nymphal stages and did not suggest that any change took place within a stadium, between moults. Also, only darkening from green to black was investigated. Corbet (1962) reported that dragonfly nymphs can become darker at a moult but not paler. The appearance of a large black spot on acridid wings over several months (Burtt and Uvarov, 1944) is the only clear account of what appears to be development of cuticular melanization associated with aging. No reports of reduction in melanic pigmentation have been found.

According to the literature, then, reduction of melanic pigmentation is not to be expected in individuals as they age. However, since mean wing darkness (Figure 23) decreased in late winter when overwintered adults returned, the effect of aging on darkness was investigated in three groups of adults collected in the field February 12, June 15, and August 6, 1971 (Table 2). No significant differences were found between groups killed upon collection on these days and aged groups. Therefore, aging of adult wings is probably not related to the decrease in mean darkness of field samples in late winter.

Table 2. Comparison of mean wing darkness of field adults preserved at collection and 1 to 3-1/2 months later.

Date collected	Temperature maintained	Date preserved	Mean darkness	S. D.	N	T
12 Feb. 71		12 Feb. 71	52.81	12.54	11	-1.174
12 Feb. 71	10° C average	17 May - June 3	58.76	11.23	11	
15 June 71		15 June	53.85	5.69	13	(all less than 0.6)
15 June 71	(outdoor temp.)	13-21 July	55.73	16.86	13	
15 June 71	(outdoor temp.)	13-21 July <sup>a/</sup>	55.18	4.74	13	
6 Aug. 71		6 August	48.21	7.91	20	1.13
6 Aug. 71	18° C average	8 September	45.70	5.99	20	

<sup>a/</sup> (died before being preserved)

### Wing Darkness and Reproductive Condition

Seasonal differences in wing darkness have been associated with differences in reproductive activity of summer and overwintering generations of the pentatomid Eurydema oleracea (L.) (Poisson, 1951) and other insects. However, comparison of egg numbers in female S. palustris collected during 1971 revealed no significant correlations. This is not unexpected since the studies previously described (p. 30 and 83) demonstrated that (1) ovariole development in these insects is under short-term environmental control during much of the year (i. e., there is no clearcut distinction between reproducing and non-reproducing generations), and (2) adult wing darkness does not change with age.

### Temperature During Development and Wing Darkness (Laboratory Studies)

Insects were reared in the cool and warm growth chambers through one to one and one-half generations and switched at various stages in their development to the contrasting temperature regime (Table 3). Data in the right half of Table 3 (C) show that mean darkness of adults reared from eggs in the chambers falls into two general categories (40-43% and 49-56%) depending upon the temperature to which the insects were subjected during the latter half of their

Table 3. Comparison of mean wing darkness of adults subjected during development to varying regimes of warm (W) and cool (C) temperatures (read across).

Sample No.	Date coll.	Developmental stages																
		A				B (parental generation)			C (offspring)									
		3	4	5	adult	Mean darkness	s. d.	N	eggs	1	2	3	4	5	mean adult wing darkness	s. d.	N	
1	7-25-71	→	W	W	W	W	43.30	10.73	14	W	W	W	W	W	W	41.59	4.88	15
2	7-25-71	→	W	W	W	49.61	7.90	23	W	W	W	W	W	W	40.08	6.61	10	
3	7-25-71	→	W	W		40.43	8.49	71	W	W	W	W	W	W	43.38	6.11	14	
4	8-19-70	→	W	W					→	W	W	W	W	W	42.63	9.34	24	
5	8- 6-71	→	W	W	W	43.48	8.31	26	W	W	W	W	W	W	40.35	4.01	6	
6	9- 8-71	→	W	W	W	42.36	7.98	20	W	W	W	W	W	W	40.58	6.63	18	
7	8- 6-71	→	W	W	W	43.48	8.31	26	W	W	W	C	C	C	54.80	8.69	19	
8	9- 8-71	→	W	W	W	42.36	7.98	20	W	W	W	C	C	C	48.97	8.61	12	
9	8- 6-71	→	W	W	C	48.31	6.74	12	C	C	C	C	C	C	55.84	5.14	8	
10	7-25-71	→	C	C	C	56.15	5.85	14	C	C	C	C	C	C	52.63	9.16	13	
11	7-25-71	→	C	C		48.13	5.02	29	C	C	C	C	C	C	52.81	8.43	11	
12	8-19-70	→	C	C					→	C	C	C	C	C	51.70	6.74	43	
13	8- 6-71	→	C	C		48.21	7.91	20	C	C	C	C	C	C	53.86	10.72	11	
14	8- 6-71	→	C	C		48.21	7.91	20	C	C	C	W	W	W	42.38	5.09	11	
15	8- 6-71	→	C	C		48.21	7.91	20	W	W	W	W	W	W	41.54	8.48	12	
16	8- 6-71	→	C	C	W	54.57	10.09	32	W	W	W	W	W	W	40.45	6.98	36	

nymphal development. Temperature effects during development of the parental generation (A) were not related to offspring darkness.

Mean darkness of the parental generation (B) was not correlated with offspring darkness. This is seen most clearly by comparison of parental and offspring darkness in samples 5 and 7, 6 and 8, and 13 to 15.

In order to assess temperature effects during the last three nymphal instars, data in A and B of Table 3, plus additional data, were compiled and analyzed in more detail.

Initially, all data from adults reared from field-collected nymphs were separated according to (1) collection date, (2) age at collection, (3) rearing temperature, and (4) age of adults when killed. As in other aging experiments described, no significant differences were found between samples separated on the basis of (4) so this data was pooled.

All field nymphs in this analysis were collected from July 25 to September 8, 1971 (data from the two 1970 samples seen in Table 3 were not used). When nymphs from different dates of collection were compared (Table 4), the only consistent difference seen is in relative darkness of adults from field nymphs collected July 25. There are still the expected differences relative to temperature between groups collected on this date.

Table 4. Comparison of mean wing darkness of adults reared at warm and cool temperatures from nymphs collected on different dates during summer 1971.

Rearing temp.	Age (instar) when collected	Date coll.	Mean adult wing darkness	s. d.	N	T
warm	3rd	7-25-71	43.30	10.73	14	.467
	3rd	8- 6-71	41.47	8.79	11	
warm	4th	7-25-71	49.61	7.90	38	-2.18*
	4th	8- 6-71	45.01	8.08	23	
	4th	9- 8-71	42.36	7.98	20	
cool	4th	7-25-71	60.28	5.57	7	-2.071*
	4th	8- 6-71	54.57	10.09	32	

Finally, all data from adults reared from similar stage at the same temperature were pooled (Table 5).

Table 5. Mean wing darkness of adults from nymphs, field-collected at different ages, reared at warm and cool temperatures.

Starting age (instar)	WARM			COOL		
	N	Mean wing darkness	s. d.	N	Mean wing darkness	s. d.
1st	3	32.39	5.77	5	62.66	11.99
3rd	25	42.49	9.76	14	56.15	5.85
4th	81	45.66	8.36	41	55.35	9.71
5th	71	40.43	8.49	29	48.13	5.03

Comparison of mean darkness values in Table 5 (Table 6) shows that all adults reared from nymphs at warm temperatures were significantly (\*\*) paler than adults reared from nymphs of the same age at cool temperatures (Table 6a).

Although sample sizes are small, adults reared from first instars were significantly paler than adults reared from third (\*), fourth (\*\*), or fifth (\*) instars at warm temperatures. Adults reared from first instars in the cool chamber were only significantly (\*) darker than adults from fifth instars in this chamber.

Adults reared from fourth instars in the warm chamber were darker (\*\*) than adults from fifth instars in the same chamber (Table 6b), but this could be a result of the relative darkness of all adults from the July 25 sample of fourth instars.

Adults from fifth instars in the cool chamber were paler (\*\*) than adults from either third or fourth instars in the same chamber (Table 6c). Difference in darkness between this group and adults reared in the warm chamber was not great (Table 6d).

Prior to collection, these insects had developed during the warmest part of the season. Therefore, most attention was focused on results from nymphs reared in the cool chamber. These data indicate that temperature had a greater effect on resulting adult wing pigmentation during the third and fourth instar stages than during the fifth.

Table 6. T-test values for comparison of means of wing darkness shown in Table 5.

	Groups compared	T-value	d. f.
a.	1st W vs. 1st C	4.79**	6
	3rd W vs. 3rd C	-5.46**	37
	4th W vs. 4th C	-5.45**	120
	5th W vs. 5th C	-5.61**	98
b.	3rd W vs. 4th W	-1.47	104
	3rd W vs. 5th W	.94	94
	4th W vs. 5th W	3.82**	150
c.	3rd C vs. 4th C	.37	53
	3rd C vs. 5th C	4.40**	41
	4th C vs. 5th C	4.06**	68
d.	5th C vs. 3rd W	-2.60*	52
	5th C vs. 4th W	-1.87	108

Mean daily temperatures of about 26°C in the warm growth chamber produced lighter-winged adults than were found in the field at any time. However, the darkest-winged adults (over 90% dark) were found in field collections during late fall (November) when mean daily temperatures were below those in the cool growth chamber (Figure 26).

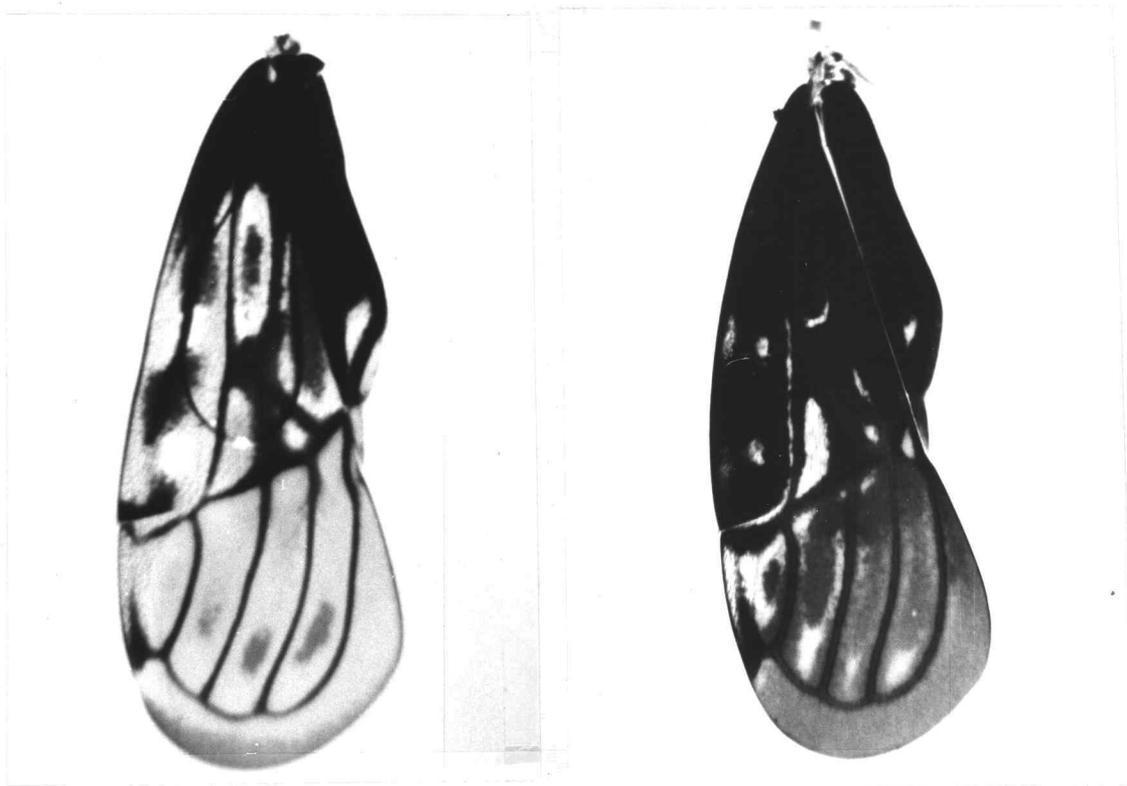


Figure 26. Extremes of pigmentation seen in S. palustris wings.

Left wing (14% dark) is from insect reared in warm growth chamber (mean temperature 26°C).

Right wing (92% dark) is from insect field-collected in November 1971.

## NYMPH COLOR

Live nymphs in the field are extremely variable in color even within the same age group at the same time of year. The range in darkness (from pale yellowish-tan to black) was believed related to darkness of the nymph's cuticle. This was tested by comparing darkness of live nymphs with darkness of the cuticle shed during the adult moult. Seven cast fifth instar skins, ranging from almost transparent ("1") to nearly black ("7"), were mounted in sequence on a slide and used as a reference standard to compare darkness of cast skins from field and experimental insects. As expected, the darkness of living nymphs is directly related to cuticle darkness. Sixty-two live fifth instars selected as "dark" in the field produced a mean cuticle darkness of 6.03 (st. dev. = .65) against this standard while 118 "pale" nymphs gave a mean cuticle darkness of 3.28 (st. dev. = .91). There was no difference in darkness between the sexes.

Nymph cuticle darkness was compared (see below) to rearing temperature, and sex and wing darkness of emerging adults.

### Rearing Temperature

Data on darkness of cast fifth instar skins (Table 7) from adults shown in Table 5 shows that cuticle darkness of fifth instars was only affected if previous instars had been exposed to cool

temperatures. (Again, the prior development of these nymphs at warm temperatures in the field makes data from the cool chamber of greater interest.) This observation corresponds to Corbet's (1962) report that darkening of the nymphal cuticle in Odonata by deposition of melanin can only occur within three hours after ecdysis and to other literature and experiments mentioned previously.

Table 7. Effects of rearing temperature on darkness of the cast fifth instar cuticle from field-collected third, fourth and fifth instars.

Starting age (instar)	WARM			T	COOL		
	N	s.d.	Mean darkness of cast skin		Mean darkness of cast skin	s.d.	N
3rd	26	1.13	3.08	$\leftarrow (-3.90^{**}) \rightarrow$	4.06	.84	49
4th	154	1.27	3.34	$\leftarrow (-4.84^{**}) \rightarrow$	4.20	1.07	56
5th	124	1.15	3.66	$\leftarrow ( .70 ) \rightarrow$	3.54	1.11	60

#### Sex of Adults

When data on nymph color from fifth instars collected July through September 1971 was pooled, it was found that pale nymphs resulted in a significantly (\*) high proportion of females to males (70.1%). Numbers of females from dark nymphs was low (37.5%) but the difference was not quite significant at the 95% level.

Wing Darkness of Adults

Comparison of mean wing darkness of adults reared in the roof insectary from pale and dark fifth instars (Table 8) indicates that extremes in nymph darkness are associated with similar variation in wing darkness of adults.

Table 8. Comparison of mean wing darkness of adults reared at outdoor temperatures from pale and dark fifth instars, field-collected 1971.

Nymph color	July 27-29		August 27	
	Pale	Dark	Pale	Dark
N	28	15	4	5
Mean wing darkness in adults	42.51	53.00	39.17	54.62
s. d.	6.35	6.69	7.52	6.06
T	-5.03**		-3.33*	

## SUBSTRATE COLOR

Groups of field-collected pale and dark fourth and fifth instars were reared on black and white substrates in the cool chamber. Table 9 shows mean wing darkness of adults produced. Adults reared from fourth instar nymphs on black substrates are significantly darker than those reared on white. No such differences are seen in adults reared from the fifth instar on black substrates. It appears that nymph darkness is related to adult wing darkness in these samples also but analysis of variance shows no significant differences based on nymph color in either group and no significant interaction between the two factors. Further work on substrate effects at both cool and warm temperatures is necessary.

Table 9. Comparison of wing darkness of adults reared in the cool chamber from pale and dark fourth and fifth instars on black and white substrates.

Nymph age (instar)	Substrate	Nymph color	N	s. d.	Mean adult wing darkness	T
4th	black	dark	13	7.69	59.15	2.60*
	white	dark	12	6.35	51.83	
	black	pale	7	4.35	56.55	3.24**
	white	pale	11	6.06	48.58	
5th	black	dark	11	8.71	50.80	.23
	white	dark	11	6.90	51.56	
	black	pale	19	5.97	48.18	.02
	white	pale	17	7.85	48.13	

## WING SIZE

Figure 27 shows mean forewing membrane area for males and females from field collections. In all cases, female wings were significantly (usually \*\*) larger than male wings. In both sexes there appeared to be a reduction in wing size of adults emerging during September and October.

Wing size variation in Heteroptera has been associated with temperature effects during development. Harris (1928) reported that some species of Nabidae from southern localities have better developed wings than those from more northern localities and suggested that temperature might play an important part in wing development in these insects. Brinkhurst (1959) demonstrated that cold temperatures affecting adult female Gerridae during the winter resulted in short-winged offspring. Southwood (1961) cited further instances of temperature effects on wing development in Heteroptera.

An attempt was made to determine if the changes in wing size during the year in S. palustris were correlated to similar changes in body size. If not, more clues to temperature effects on wings during development might be obtained. Head width (across the widest part of the eyes) was taken as an expression of body size of the insect. If head width is a stable indicator of body size and if wing size fluctuates only as body size fluctuates throughout the year, a ratio

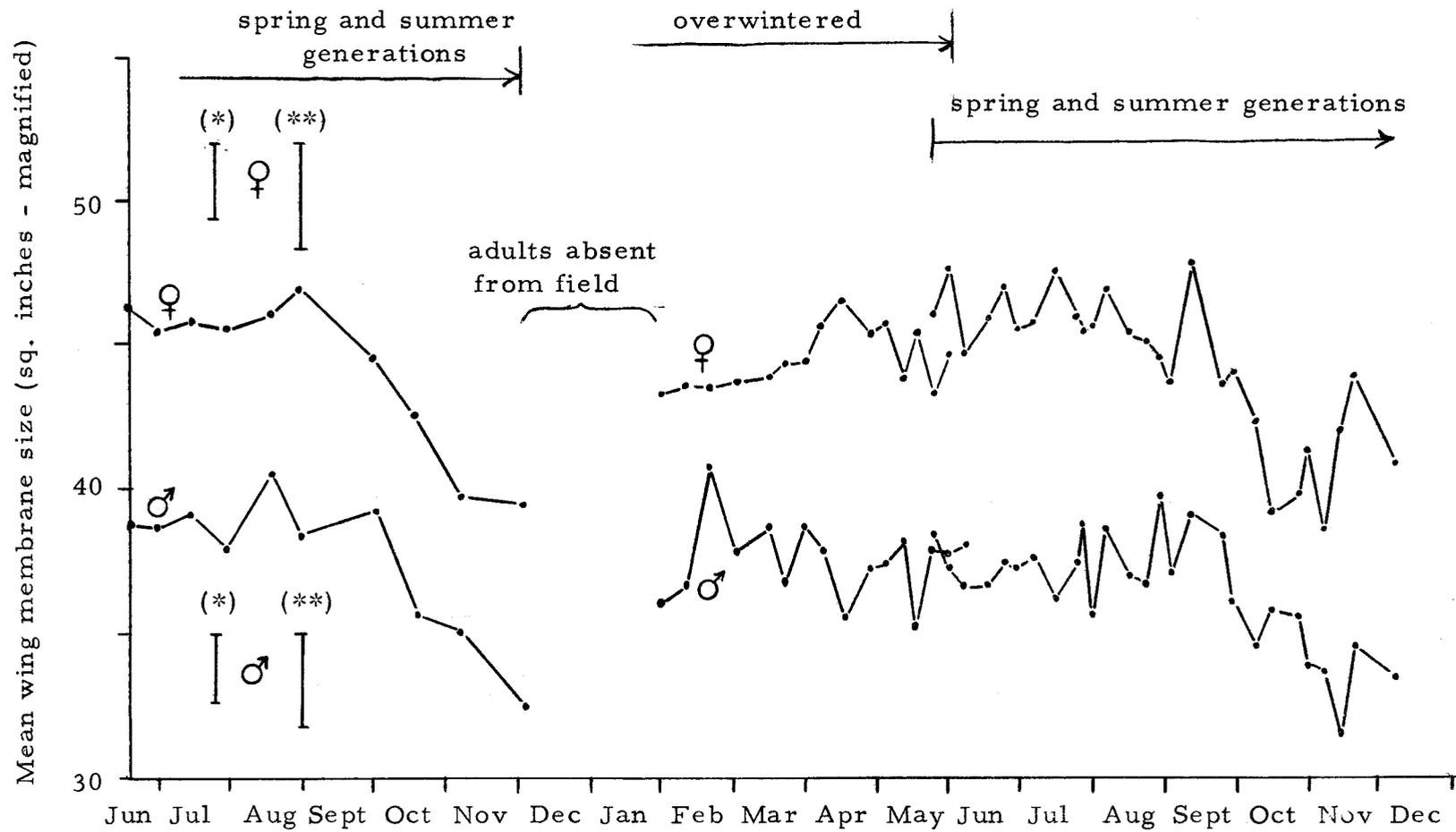


Figure 27. Mean wing membrane size in field samples from June 1970 to December 1971.

of forewing length divided by head width (averaged for each collection) would remain constant. Increase in size of this ratio would mean that wings are longer relative to body size and a decrease in the ratio would mean wings are shorter relative to body size. Ratios for ten males and ten females from field collections throughout the entire collecting period (1970 to 1971) are shown in Figure 28. Male wings were shorter relative to body size than female wings in almost all collections. Separate analysis of head width and wing length measurements showed that variability in wing length accounts for the fluctuations seen in Figure 28.

Female wings were long relative to body size during late August and September and also during the spring months. There was a decrease in wing length in late fall and mid-summer.

Fluctuations in length of male wings were not as conspicuous but there did seem to be a definite decrease in early summer and another in late fall. Maximum length of male wings corresponded to maximum length of female wings in the spring.

These fluctuations corresponded to the emergence of spring and summer generations of adults and suggest that in this species, the influence of cool temperatures during development is manifested in relative shortness of adult wings.

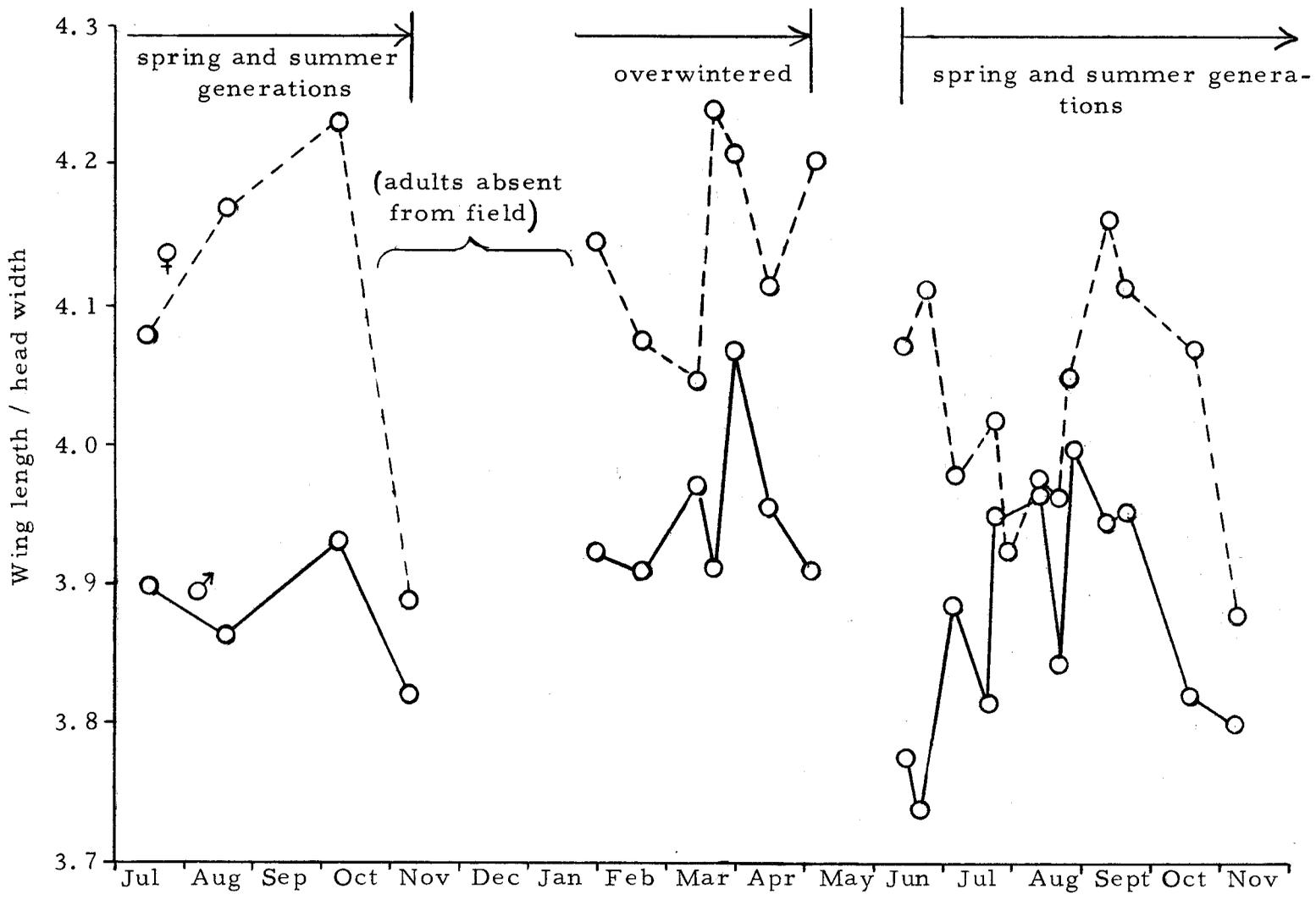


Figure 28. Wing length/head width ratios from field-collected adults, 1970 to 1971.

Wing Darkness vs. Wing Size

Wing darkness was compared to wing size in males and females of 57 field collections; a total of 114 correlation coefficients calculated. Ten significant correlations (6\*, 4\*\*, 8 negative, 2 positive) were observed but there was no apparent relationship between sex, time of year, and direction of correlation. Seasonal relationships were seen, however, between wing darkness and size and are believed related to the emergence of different adult generations.

## WING VENATION

Adventitious crossveins and other venational anomalies have been reported in other species of Saldidae (Cobben, 1960a, b) and are common in field and experimental populations of S. palustris (Figure 29). Adventitious crossveins can be induced by heat treatment of Drosophila pupae (Milkman, 1962; Milkman and Hille, 1966; Thompson, 1967). Supernumerary veins in Glossina spp. have been associated with seasonal temperature increases in the field (Glasgow, 1960). As in Glossina, certain types of crossveins are more common than others in S. palustris and bilateral symmetry of the feature is very rare. (I saw only one case of bilateral symmetry of a venational anomaly.) Further analysis of crossvein types and frequencies in field and experimental populations of S. palustris could give more insight into both temperature sensitivity of wings during development and taxonomy of the species. Welch (1960) found that differences in frequencies and types of crossvein anomalies in Glossina morsitans confirmed evidence of taxonomic subunits within the species. Sondhi (1963) showed that the veins of Drosophila wings could behave as independent units under modifying environmental influences such as temperature and may have different periods of sensitivity during development to these environmental influences since they are affected by different genes.



Figure 29. Adventitious crossvein in cell 4 of S. palustris wing.

## SUMMARY

The life history and wing pigmentation variation of the intertidal shore-bug Saldula palustris (Douglas) was studied in field and experimental populations from June 1970 until February 1972. The field study site was an estuarine salt marsh on Yaquina Bay near Toledo, Oregon. The insects live below the mean high water level and are regularly submerged by the tide for up to ten hours at a time. Behavior of S. palustris upon submergence is well-adapted to intertidal existence.

Overwintering occurs in the adult stage and adults migrate from the intertidal area in late fall. The reproductive period begins upon their return in February with mating, egg development and oviposition, and ends in September with cessation of these activities. The first adults of the spring generation appear in mid-May. There are three generations a year. There is a facultative reproductive diapause with egg development under short-term environmental control during most of the year.

Mating behavior, parasites, feeding, and predators of S. palustris are discussed. Intraspecific predation is common in this species. Spiders may be the main predators at the study site.

Mean daily field temperatures were calculated by integration of tide cycle and water temperature data with soil surface temperature

curves for each day during 1971. Threshold temperatures determined in the laboratory for S. palustris (10° C for embryonic development through hatching, 15° C for development to the adult stage) were correlated with mean field temperatures and the first and last appearance of the various developmental stages in the field in spring and fall.

Mean adult wing darkness (based on percent wing membrane area covered by dark patterning) in field collections varied from palest (45-50% dark) in mid-summer to darkest (65-70% dark) in late fall. Males and females were in general not significantly different in wing darkness and reproductive condition of females was not correlated with wing pigmentation levels. Females were larger than males and female wings longer relative to body size. Wing length in field collections was greatest during early spring and later summer. Correlations of wing length and wing darkness over time, related to the emergence of different generations during the season, was observed. The darker, shorter-winged adults developed during the cooler months of the year (spring, late summer) while paler, longer-winged forms developed during the warmer early summer months.

Histological differentiation of wing pigmentation patterns following the adult moult is described. Aging of adults had no effect on overall extent of wing pigmentation but other effects of aging

(e. g., small age spots, yellowing of pale areas of the wing) were observed.

Laboratory studies demonstrated that temperature during nymphal development had significant effects on adult wing darkness. Cooler temperatures, especially during the third and fourth instar stages, produced darker adults. Similarly, cool rearing temperatures produced significantly darker fifth instar cuticles if the nymphs were subjected to the lower temperature prior to the fifth instar. As with adults, nymphs did not darken after hardening following the moult.

A slower rate of metabolism resulting from low temperatures has been associated with greater deposition of melanic wing pigmentation in other insects. The effects of temperature on histological differentiation of wings in S. palustris nymphs and on overall metabolic or developmental rate were considered. Data on length of nymphal life of groups of nymphs switched at various stages of development from warm (26°C) to cool (18°C) temperature regimes suggest that there are three phases within the nymphal period that are unequally affected by temperature.

Adults reared from the fourth instar stage on a black substrate had significantly darker wings than adults reared from similar age on a white substrate.

Adventitious crossveins are common in field and experimental

populations of S. palustris and also may be related to temperature effects during development.

## DISCUSSION

In this study, emphasis was placed on the interrelated environmental parameters of temperature and tides which were believed to have a major effect on seasonal biological and morphological patterns exhibited by S. palustris. Field and experimental work have delimited certain aspects of the insect's range of tolerance and sensitivity to these environmental variables.

Various key events in the life history of the insect (e. g., nymph and adult emergence in the spring, end of reproductive activity in the fall) were closely related to temperature conditions in the field.

Seaward distribution of the insects in the intertidal zone is undoubtedly limited, directly or indirectly, by tide levels. S. palustris is probably limited in its ability to withstand regular submergence periods of greater than ten hours. More directly, distribution of the insects appeared most closely related to distribution of the salt-marsh vegetation in the seaward direction. The grasses provide shade and high humidity near the ground during summer months, clinging sites during tidal submergence, and possible oviposition sites. Major factors limiting seaward distribution of intertidal plants include submergence and salinity.

High moisture requirements may be an important factor limiting landward distribution of S. palustris since nymphs are extremely

susceptible to desiccation.

Long-term adaptation might involve the evolution of broader tolerances to the major limiting forces of the environment or the retention of narrow tolerances by the evolution of some means of changing the limits of tolerance from season to season (Watt, 1969). The latter type of adaptation is often manifested by either genetic polymorphism or alteration of phenotype from season to season with associated changes in the limits of tolerance.

Environmentally-controlled alterations of phenotype, such as appeared in S. palustris, give flexibility of response in the variable intertidal environment. For example, rapid response of ovarial development to temperature changes could be an adaptation of this type, having high selective value in areas where there might be considerable yearly variation in the time of onset of suitable temperature levels for completion of the life cycle. This feature of S. palustris (and many other members of the Saldidae) could also be related to the successful invasion of northern regions by these insects.

Other seasonal alterations of phenotype were seen in wing pigmentation and size variation over the year.

Beginning from the time adults become numerous in the field (during mid-February), mean wing darkness remained at about the 50 to 55% level until the first emergence of the spring generation in

mid-May. During the same period, wing length relative to body size was at a maximum.

Following emergence of spring-generation adults in mid-May, mean wing darkness of field samples increased to about 55 to 60% dark and wing length decreased. These changes are believed related to cool temperatures during development of the spring generation.

A sharp decrease in mean wing darkness in July and increase in wing length in July and August corresponded to the emergence of the first group of summer generation adults from eggs laid by the spring generation and which developed at relatively warm temperatures.

This marked but continuous seasonal shift in phenotype is common in species with overlapping generations and contrasts to more sharply-defined seasonal dimorphism seen most often in species with discrete generations (Oliver, 1970). Overlap between generations of S. palustris made differentiation of these generations difficult. Observed development times in the laboratory relative to temperature conditions at the study site suggest that there was sufficient time for some early eggs deposited by the summer generation to hatch and develop. Nymphal population levels, reproductive periods, and the time of emergence of the summer generation, also suggest the presence of a third generation. Overwintering adults were individuals emerging in late August and September in both second and third

generations. These insects, having been exposed to cooler temperatures during nymphal development, have darker, shorter wings than those emerging earlier in the summer.

The sharp decrease in wing length of collections from mid-September to November and the immediate increase when the insects reappeared in February suggest earlier migration of long-winged adults from the study site. Similarly, increase in mean wing darkness in late fall and relative paleness of collections in February indicate that migration of paler forms in late September and October preceded migration of darker forms.

Lindskog (1968) demonstrated that migration of S. saltatoria away from water in fall is based on a reversal of humidity response which is positive during reproductive periods and becomes negative at the end of the reproductive period. The reproductive period of S. palustris begins in February with mating and egg development and ends in September with cessation of these activities. Migration of S. palustris and associated changes in wing pigmentation and size in collections at the study site after the end of this reproductive period could have resulted from a similar change in response to some environmental stimulus (e. g., temperature, photoperiod).

Migration of S. palustris is probably not a specific adaptation to the intertidal zone but rather reflects an adaptation of the family as a whole since the majority of species live near inland waters

subject to freezing and flooding during the winter months.

Identification of the selective forces related to natural variation, such as observed in the wings of S. palustris, is a difficult task and very few such identifications have been made (e. g., Kettlewell, 1961). Natural selection rarely can be defined as acting directly on an easily discernible morphological character.

Differences in wing size, especially in dimorphic forms, are often associated with differences in development of the hind (flight) wings and have been related to flight ability and migration in certain Heteroptera (e. g., Brinkhurst, 1959; Drake, 1961). It has also been suggested that wing size differences are related to differences in cold-resistance (since shorter-winged forms cannot fly to a more favorable habitat in winter) (Ekblom, 1941) or simply to differences in rate of hardening of the expanding wings after the moult at different temperatures (van den Heuval, 1963).

Seasonal variation in wing darkness could be related both to indirect environmental effects on the wings and on selective forces, such as predation or thermoregulatory differences, acting directly on wing pigmentation differences.

Although Saldidae are occasionally described as cryptic (Southwood and Leston, 1959; Cobben, 1960b) evolution of actual cryptic resemblance to the background depends upon selection by a visual predator (Portmann, 1959). In Corixidae, predator selection by

fish has influenced development of a cryptic response (Popham, 1941). Certain spiders, such as those found associated with S. palustris in the field, are visual predators but their relationship to the substrate-matching response observed in the insects is not known. Corbet (1957) suggested that nymphal pigmentation in dragonfly larvae represents an adaptation to reduce cannibalism by older larvae, presumably the main predators. Again, the relationship of intraspecific predation in S. palustris to the substrate-matching response observed has not been established.

Large insects (e. g., locusts) with dark coloration may have a considerable advantage over lighter insects in terms of energy absorption from the sun. However, since variation in body temperature from variation in darkness is almost negligible in smaller insects (Digby, 1955), darkness is unlikely to be a thermoregulatory adaptation in S. palustris.

Investigation of developmental aspects and the degree of experimental modificability of wing pigmentation in S. palustris wings may lead to greater understanding of environmental effects on morphological variation. The developmental morphology of wings of hemimetabolous insects is a relatively unexplored subject although it has been studied in some detail in holometabolous groups.

The pupal stage of the Holometabola is regarded as equivalent to, and derived from, the last larval instar of hemimetabolous insects.

(Hinton, 1963). However, although the majority of wing development takes place just prior to pupation and during early pupal life in most species of Holometabola, there is a progressive development of the wings of hemimetabolous insects beginning early in nymphal life. Some studies (Holdsworth, 1942) suggest that histological development of wings (e. g., formation of blood lacunae) occurs much earlier in the Hemimetabola than the Holometabola.

Studies on the effects of external stimuli during development on adult characters of various insects (e. g., diapause, wing pigmentation and size) have delimited periods of sensitivity for determination of these features. Variation often exists between species in developmental stage affected and duration of the sensitive period. For example, experiments with Lepidoptera show that final determination of wing pigmentation is established early in the pupal stage and in some species can be directly influenced by temperature effects during that time (Kolyer, 1969, 1970). In other species of Lepidoptera, photoperiod length during the larval stage controls final deposition of pigment during the early pupal stage (Watt, 1969; Oliver, 1970).

In some insects, an environmentally-controlled genetic switch mechanism determines adult phenotype at a very specific stage in development (Stanley, 1935; Brinkhurst, 1959) and discontinuous variation of adult phenotypes is seen.

More commonly, the sensitive period extends over a longer

period of time (sometimes the entire developmental period is included) with some stages having greater sensitivity (e. g., van den Heuval, 1963). In insects with overlapping generations, this type of sensitivity is manifested as gradations of phenotype over the year.

In S. palustris, wing darkness is established prior to the adult moult even though the feature is not manifested visibly until this time. The extent of pigmentation does not change over the adult life and experiments substantiate previous reports of the stability of melanic pigmentation in the cuticle. Similarly, pigmentation of the exocuticle of nymphs does not change after the moult.

The sensitive period for determination of wing darkness in S. palustris extends over the first four nymphal stages but the third and fourth instars appear most critical. Differences in temperature and substrate color during the fifth instar did not affect final wing darkness of the adult but had significant effects during earlier stages of development.

Relative sensitivity of the third and fourth instars to external stimuli could result from effects on histological differentiation of the wings during this period or effects on other physiological factors such as metabolic rate.

Extrapolation from information that (1) the pupa and fifth instar are considered homologous; (2) wing pigmentation in holometabolous insects is established early in the pupal stage; and (3) histological

differentiation of wings of hemimetabolous insects takes place earlier than in holometabolous insects; it could be argued that maximum development of wings and establishment of wing pigmentation levels probably takes place in the third and fourth stadia of this insect. Since temperature effects on the later pupal stages of holometabolous insects have no effect on adult wing patterns, it seems reasonable that environmental effects during the last instar of Hemimetabola such as S. palustris would also have no noticeable effect on adult wing patterns.

Differential effects of temperature on development rate (Figure 17) suggest that the temperature effects on adult wing pigmentation might be attributed to overall differences in sensitivity to temperature during different phases of nymphal development. Harries (1944) carried out a more detailed study of this type on the beet leafhopper Eutettix tenellus (Bak.) and demonstrated the presence of two or more phases within the nymphal stage that are unequally affected by different temperatures. Huffaker's comment (1944, p. 5) that "the value of a degree is not developmentally equivalent everywhere in the biokinetic scale" seems relevant here. Huffaker also notes that straight-line relationships have no basis, either theoretically or empirically, in explaining biological phenomena.

A great deal of work remains to be done to clearly define sensitive stages to environmental stimuli and their effect on

morphological characters of wing pigmentation, size, and venation. Determination of the mechanism by which environmental stimuli are translated into phenotypic variation would be a further step. For example, in Corixidae, degree of pigmentation was found to be under the control of the nervous system acting through certain areas of the eyes (Popham, 1941, 1943).

Another factor which has not been considered is the effect of maternal aging on offspring phenotype. Some preliminary but inconclusive data on consecutive groups of offspring from the same population of adult S. palustris suggest that wing size and darkness may also be partly related to age of parents.

Lees (1955) cites several instances where incidence of offspring diapause is related to maternal age. Raychaudhuri and Butz (1965) found that duration of the larval stage of Tribolium confusum (Coleoptera: Tenebrionidae) was altered in a cyclic manner with increasing age of parents. These authors observed "that the effects of parental age upon the life cycle of the progeny of T. confusum are not a single longitudinal mechanism but a complex one" (p. 540).

Additional investigation of the effects of maternal aging and other factors mentioned above would give further depth to understanding of the complex variety of phenomena which are interrelated and manifested in wing pigmentation variation of S. palustris.

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## APPENDICES

## APPENDIX I

Tide Data for Toledo, Oregon 1971

THA = time of first high tide of day.  
HHA = height (in feet above 0.0 tide level) of first high tide.  
TLA = time of first low tide.  
HLA = height of first low tide.  
THB = time of second high tide.  
HHB = height of second high tide.  
TLB = time of second low tide.  
HLB = height of second low tide.

(a -3.0 in the time and height columns for a second high (or low) tide indicates that there is no second high (or low) tide that day.

DW = temperature of estuary water in degrees centigrade.

DAY: day 1 is January 1, 1971; day 365 is December 31, 1971.

THA	HHA	TCA	HCA	THB	HHR	TBR	HBR	OW	DAY
10.00	10.00	10.00	10.00	10.00	10.00	21.65	-1.56	7.5	
4.05	7.96	10.05	2.43	15.55	7.95	22.15	-1.39	7.5	1
4.85	7.95	10.75	1.69	16.45	6.96	23.05	-0.53	7.5	2
5.65	8.03	11.85	1.03	17.75	5.83	23.65	.44	7.5	3
6.35	7.75	13.15	.54	19.15	5.18	-3.00	-3.00	7.5	4
7.05	8.01	.55	1.42	20.45	4.86	14.75	-0.10	7.5	5
8.15	8.00	1.55	2.33	22.25	5.19	15.25	-0.73	7.5	6
8.65	8.13	2.65	2.89	23.35	5.81	15.45	-1.37	7.5	7
10.05	8.79	4.05	3.37	-3.00	-3.00	17.35	-1.29	7.5	8
.15	6.92	5.05	3.93	10.85	9.43	18.25	-0.85	7.5	9
.95	7.76	5.95	4.22	11.35	9.87	18.95	-0.77	7.5	10
1.45	7.95	6.75	4.35	12.25	9.95	19.45	-0.82	7.5	11
2.15	7.95	7.25	3.96	13.05	9.89	20.25	-0.43	7.5	12
2.55	8.31	8.05	4.14	13.45	9.40	20.75	-0.48	7.5	13
3.25	8.25	8.65	3.89	14.35	8.89	20.65	1.25	7.5	14
3.35	11.76	9.25	5.05	14.85	10.99	22.15	2.39	7.5	15
4.05	9.22	9.95	4.02	16.25	9.01	22.25	2.93	7.5	16
4.45	9.13	10.95	3.54	15.65	7.14	22.85	2.55	7.5	17
5.05	8.74	11.75	2.95	17.35	6.36	22.95	3.15	7.5	18
5.55	8.67	12.75	2.66	18.75	5.56	23.95	3.34	7.5	19
6.45	7.85	14.25	1.42	20.65	4.81	-3.00	-3.00	7.5	20
7.45	7.89	.75	3.53	21.95	4.82	15.25	.50	8.0	21
8.15	8.06	1.85	3.76	22.85	5.55	16.15	-0.02	8.0	22
9.25	8.43	3.35	3.98	23.75	6.18	17.25	-0.80	8.0	23
10.15	8.17	4.55	3.99	-3.00	-3.00	17.75	-0.85	8.0	24
.55	7.18	5.15	4.00	11.05	9.63	18.45	-1.60	8.0	25
1.15	7.23	6.25	3.16	11.85	9.46	19.35	-2.49	8.0	26
1.75	7.44	6.95	2.26	12.75	9.52	19.85	-2.53	8.0	27
2.35	7.75	7.85	1.55	13.65	9.22	20.45	-2.39	8.0	28
2.85	8.29	8.75	1.00	14.55	8.60	21.05	-1.71	8.0	29
3.55	8.67	9.65	.73	15.45	7.87	21.65	-0.86	8.0	30
4.25	8.82	10.55	.49	16.45	7.00	22.45	.45	8.0	31
4.85	8.89	11.55	.31	17.55	6.09	23.05	1.41	8.0	32
5.45	8.34	12.75	-0.12	18.95	5.02	-3.00	-3.00	8.0	33
6.45	8.11	.05	2.17	20.65	5.31	14.15	-0.10	8.5	34
7.65	8.54	1.05	3.90	22.25	5.72	15.35	-0.07	8.5	35
8.65	8.00	2.65	3.83	23.15	6.02	16.45	-0.59	8.5	36
9.65	8.19	3.75	3.68	24.05	6.48	17.15	-0.92	8.5	37
10.75	8.29	4.85	3.44	-3.00	-3.00	17.85	-1.14	8.5	38
.65	6.69	5.85	3.01	11.65	8.42	18.75	-1.10	8.5	39
1.25	6.39	6.55	2.79	12.25	8.53	19.15	-0.53	8.5	40
1.65	7.66	7.05	2.98	12.85	8.55	19.85	-0.95	8.5	41
2.15	7.22	7.85	1.93	13.45	7.97	20.15	-0.63	8.5	42
2.55	7.73	8.45	2.06	14.15	7.89	20.75	.07	8.5	43
3.05	7.72	8.95	1.67	14.75	7.31	21.15	.64	8.5	44
3.45	8.14	9.35	2.02	15.65	8.13	21.75	2.06	9.0	45
3.75	8.33	10.35	2.17	16.15	6.72	22.15	2.43	9.0	46

4.55	8.40	11.05	1.96	17.05	6.28	22.85	3.14	9.0	47
4.75	8.25	11.85	1.72	18.05	5.57	23.15	3.55	9.0	48
5.45	8.79	13.15	1.79	19.45	5.20	-3.00	-3.00	9.0	49
6.25	7.42	.15	3.81	21.35	4.89	16.25	.42	9.0	50
7.65	7.19	1.35	3.70	22.45	5.60	15.35	-0.20	9.0	51
8.75	7.40	2.45	4.05	23.35	6.39	16.45	-0.52	9.0	52
10.15	8.90	4.95	4.06	23.95	6.60	17.45	-0.89	9.0	53
10.85	8.78	5.45	2.97	-3.00	-3.00	18.05	-1.28	9.5	54
.65	7.11	6.15	2.74	11.95	9.79	18.85	-1.12	9.5	55
1.35	8.55	7.05	1.65	12.95	8.61	19.25	-2.02	9.5	56
1.75	7.81	7.55	-0.04	13.75	8.88	20.05	-1.30	9.5	57
2.25	9.36	8.65	-0.17	14.55	8.39	20.55	-0.56	9.5	58
2.85	9.22	9.25	-0.99	15.45	7.20	21.25	-0.20	9.5	59
3.45	8.58	9.95	-1.51	16.35	6.17	21.65	.89	9.5	60
4.25	8.60	10.95	-0.08	17.25	6.48	22.55	2.74	9.5	61
4.95	8.54	12.15	.35	18.75	5.80	23.75	3.71	9.5	62
5.75	8.35	13.75	.43	20.25	5.53	-3.00	-3.00	10.0	63
7.05	7.49	1.05	3.83	21.85	5.70	14.55	.02	10.0	64
8.35	7.56	2.55	3.87	22.85	6.97	15.75	.51	10.0	65
9.75	8.81	4.05	4.58	23.65	6.48	17.05	0	10.0	66
10.55	7.65	4.85	2.92	-3.00	-3.00	17.45	-0.43	10.0	67
-3.00	-3.00	5.65	2.62	11.25	8.01	18.05	.28	10.0	68
.55	7.76	6.15	2.95	12.15	9.63	18.95	.80	10.5	69
.95	8.13	6.85	2.11	13.25	9.43	19.25	2.38	10.5	70
1.15	9.33	7.45	3.33	13.45	9.35	20.25	2.09	10.5	71
1.55	8.69	7.95	1.33	14.05	8.02	19.85	1.59	10.5	72
2.35	9.28	8.85	2.19	14.55	7.89	20.15	2.67	10.5	73
2.45	8.52	9.25	.57	15.25	6.81	20.95	1.98	10.5	74
2.85	7.76	9.45	.17	15.85	6.15	21.25	2.05	10.5	75
3.45	7.54	10.25	-0.08	16.55	5.36	21.95	2.53	11.0	76
3.85	7.37	11.15	.03	18.05	4.97	22.75	3.18	11.0	77
4.65	7.30	12.25	.32	19.15	5.08	23.85	3.81	11.0	78
5.65	7.27	13.25	.34	20.85	5.39	-3.00	-3.00	11.0	79
6.95	7.24	1.95	4.02	21.65	6.18	14.85	.16	11.0	80
8.65	8.35	2.75	4.21	22.65	7.35	15.95	.41	11.0	81
9.65	8.51	4.15	3.66	23.15	7.81	16.85	-0.19	11.0	82
10.85	8.43	5.05	2.31	23.85	8.40	17.55	-0.64	11.0	83
11.75	9.98	6.05	1.17	-3.00	-3.00	18.05	-0.06	11.5	84
1.05	11.58	5.65	3.57	12.45	10.73	19.05	1.05	11.5	85
.95	10.20	7.25	.17	13.55	9.22	19.45	1.00	11.5	86
1.65	10.25	8.25	-0.80	14.35	8.55	20.15	1.46	11.5	87
2.05	10.29	9.05	-1.12	15.35	8.22	21.05	2.73	11.5	88
2.85	10.17	9.95	-0.63	16.11	7.66	21.75	2.98	11.5	89
3.55	9.16	10.75	-1.02	17.55	6.36	22.45	3.23	11.5	90
4.35	8.33	11.75	-0.41	18.55	6.06	23.25	3.74	11.5	91
5.35	7.45	12.85	-0.17	19.95	5.71	-3.00	-3.00	12.0	92
6.75	6.64	.75	3.53	21.15	5.85	13.85	.07	12.0	93
8.05	6.46	2.35	3.24	21.95	6.39	15.15	.28	12.0	94
9.25	6.98	3.65	3.14	22.65	7.15	16.05	.76	12.0	95
10.15	7.12	4.55	2.72	23.25	7.31	16.85	.73	12.0	96

11.05	7.13	5.35	1.96	23.75	7.95	17.55	.98	12.0	97
12.25	8.61	5.85	2.26	-3.00	-3.00	18.15	1.88	12.0	98
.05	8.55	6.35	1.75	12.45	8.44	18.55	2.36	12.5	99
.45	8.36	7.15	.81	13.55	7.93	19.05	2.41	12.5	100
.85	9.09	7.65	.30	13.85	7.72	19.35	2.36	12.5	101
1.25	8.76	8.05	-0.26	14.35	7.43	19.75	2.85	12.5	102
1.75	8.94	8.65	-0.27	15.15	7.19	20.35	3.20	12.5	103
2.15	8.75	9.25	-0.35	15.85	6.64	21.05	3.31	12.5	104
2.85	8.31	9.85	-0.57	16.85	5.99	21.55	3.58	12.5	105
3.55	8.12	10.75	.40	17.65	6.84	22.45	4.95	13.0	106
4.25	8.53	11.85	.57	18.85	5.97	-3.00	-3.00	12.5	107
5.35	7.04	.25	3.94	19.95	5.98	13.95	-0.13	12.5	108
6.85	6.76	1.55	3.64	21.15	6.91	14.15	.26	12.5	109
8.15	7.10	2.55	3.34	21.75	7.17	15.05	0	13.0	110
9.65	7.39	3.85	1.74	22.45	8.12	15.95	-0.02	13.0	111
10.75	7.95	4.75	1.07	23.15	8.92	16.95	.67	13.5	112
11.65	7.69	5.65	-0.20	23.65	9.08	17.65	.75	13.5	113
12.65	7.39	6.35	-1.71	-3.00	-3.00	18.25	.77	13.5	114
.35	9.41	7.25	-2.42	13.55	7.43	18.95	1.55	13.5	115
.95	9.50	7.95	-2.70	14.35	7.45	19.75	2.01	13.5	116
1.55	9.41	8.65	-2.51	15.25	7.01	20.55	2.41	14.0	117
2.25	9.94	9.45	-2.07	16.25	6.77	21.35	2.91	14.0	118
3.25	8.50	10.35	-1.31	17.25	6.64	22.35	3.41	14.0	119
4.05	7.95	11.51	-0.62	18.15	6.46	23.55	3.72	14.0	120
4.75	7.42	12.25	.07	19.25	6.59	-3.00	-3.00	14.0	121
6.15	6.31	.65	3.70	20.05	6.65	13.35	.54	14.5	122
7.45	6.17	2.15	3.12	20.95	6.84	13.95	.88	14.5	123
8.55	5.93	3.05	2.52	21.75	6.95	14.95	1.01	14.5	124
9.75	5.88	3.95	1.76	22.15	7.32	15.75	1.26	14.5	125
10.75	6.02	4.75	1.03	22.65	7.48	16.75	1.58	15.0	126
11.55	6.33	5.45	.33	23.15	8.09	16.95	1.99	15.0	127
12.25	6.53	6.05	-0.07	23.55	8.13	17.85	2.28	15.0	128
12.95	6.53	6.65	-0.89	-3.00	-3.00	18.25	2.43	15.0	129
.05	8.28	7.15	-1.26	13.65	6.64	18.85	2.76	15.0	130
.65	8.49	7.65	-1.31	14.35	6.97	19.45	3.27	15.5	131
1.15	8.77	8.45	-1.20	15.15	7.04	20.25	3.65	15.5	132
1.75	8.74	8.95	-1.22	15.75	6.83	20.75	3.60	15.5	133
2.35	8.53	9.75	-1.07	16.75	6.81	21.65	3.74	15.5	134
3.45	8.55	10.65	.22	17.55	7.82	23.35	4.76	16.0	135
4.15	7.31	11.55	-0.76	18.55	6.22	23.55	2.79	16.0	136
5.25	6.63	12.25	-9.53	19.25	6.65	-3.00	-3.00	16.0	137
6.55	6.31	1.15	2.53	20.25	7.20	13.25	-0.11	16.5	138
7.95	6.05	2.45	1.74	21.05	7.73	14.15	.20	16.5	139
9.25	6.97	3.45	.45	21.55	8.09	15.25	.69	16.5	140
10.55	6.17	4.35	-0.80	22.35	8.59	16.25	1.08	16.5	141
11.55	6.50	5.25	-1.76	23.05	8.99	16.95	1.58	17.0	142
12.75	6.65	6.05	-2.47	23.75	9.23	17.95	2.00	17.0	143
13.55	7.01	6.85	-2.86	-3.00	-3.00	18.45	2.50	17.0	144
.55	9.55	7.65	-2.46	14.35	7.51	19.55	3.02	17.0	145
1.25	9.48	8.45	-2.37	15.15	7.10	20.35	2.86	17.5	146

1.95	8.69	9.25	-2.42	15.85	6.65	20.95	2.68	17.5	147
2.75	7.34	9.85	-1.95	16.65	6.48	22.05	2.77	17.5	148
3.55	7.42	10.65	-1.21	17.35	6.46	22.95	2.85	17.5	149
4.35	6.55	11.35	-0.37	18.35	6.52	-3.00	-3.00	17.5	150
5.45	5.98	.15	2.69	19.05	6.46	12.35	.20	18.0	151
6.45	5.23	1.35	2.29	19.75	6.75	13.05	.78	18.0	152
7.85	5.08	2.15	1.88	20.35	7.04	13.75	1.52	18.0	153
9.15	5.17	3.15	1.36	21.15	7.37	14.65	2.07	18.0	154
10.25	5.42	4.15	.59	21.65	7.60	15.65	2.45	18.5	155
11.25	5.75	4.95	-0.01	22.25	7.87	16.05	2.69	18.5	156
12.15	6.11	5.55	-0.57	22.85	8.23	17.25	3.03	18.5	157
12.75	6.24	6.15	-1.15	23.45	8.44	17.85	3.08	18.5	158
13.45	6.47	6.65	-1.67	23.95	8.65	18.35	3.28	19.0	159
14.25	6.78	7.45	-1.79	-3.00	-3.00	19.15	3.40	19.0	160
.85	9.03	8.25	-1.71	14.85	6.90	19.85	3.32	19.0	161
1.55	8.76	8.75	-1.83	15.45	6.88	20.55	3.14	19.0	162
2.15	8.59	9.45	-1.75	16.25	7.05	21.55	3.09	19.0	163
3.25	8.38	10.15	-1.03	16.95	7.54	22.55	2.89	19.5	164
4.05	7.51	11.05	-0.89	17.75	7.43	23.85	2.19	19.5	165
5.25	6.63	11.75	-0.37	18.55	7.45	-3.00	-3.00	19.5	166
6.55	5.73	.75	1.21	19.15	7.78	12.75	.40	20.0	167
7.95	5.79	2.05	.70	20.25	8.60	13.55	1.58	20.0	168
9.45	6.27	3.05	.31	20.95	9.11	14.45	2.72	20.0	169
10.65	6.35	4.25	-0.50	21.85	9.29	15.75	2.94	20.0	170
11.55	6.73	4.95	-1.24	22.55	9.50	16.45	3.26	20.0	171
12.55	7.14	5.85	-1.75	23.45	9.61	17.65	3.47	20.5	172
13.65	7.47	6.75	-1.95	-3.00	-3.00	18.35	3.57	20.5	173
.15	9.55	7.55	-2.09	14.25	7.37	19.15	3.24	20.5	174
.95	9.39	8.15	-1.80	15.05	7.93	20.05	4.16	20.5	175
1.65	9.41	8.85	-1.27	15.55	7.59	20.75	3.27	20.5	176
2.25	8.55	9.35	-0.86	16.05	7.44	21.65	3.07	21.0	177
3.35	7.84	9.95	-0.36	16.75	7.39	22.35	2.84	21.0	178
3.85	6.78	10.65	.21	17.45	7.18	23.35	2.41	21.0	179
4.85	5.36	11.15	.66	18.05	6.97	-3.00	-3.00	21.0	180
5.75	5.25	.45	1.97	18.55	7.01	11.75	1.30	21.0	181
6.95	4.33	1.95	1.48	19.05	7.15	12.75	2.00	21.0	182
8.55	4.51	2.55	.94	19.95	7.06	13.45	2.45	21.0	183
10.05	4.73	3.25	.34	20.85	7.37	14.45	2.93	21.5	184
10.65	5.18	4.25	-0.26	21.55	7.77	15.55	3.19	21.5	185
11.95	5.66	4.95	-0.74	22.25	8.23	16.25	3.40	21.5	186
12.45	6.06	5.85	-1.30	23.15	8.52	17.25	3.33	21.5	187
13.05	6.49	6.45	-1.76	23.75	8.84	17.95	3.22	21.5	188
13.75	6.93	7.25	-2.06	-3.00	-3.00	18.75	3.23	21.5	189
.55	9.27	7.85	-2.05	14.55	7.12	19.65	2.74	22.0	190
1.36	9.05	8.35	-2.10	15.05	7.54	20.65	2.35	22.0	191
2.25	8.91	9.15	-1.88	15.65	7.83	21.55	1.91	22.0	192
3.14	8.12	9.85	-1.33	16.45	8.02	22.35	1.40	22.0	193
4.14	7.22	10.55	-0.63	17.14	8.08	23.45	.89	22.0	194
5.14	6.28	11.05	.19	17.95	8.14	-3.00	-3.00	22.0	195
6.45	5.63	.55	.41	18.55	8.33	11.95	1.26	22.0	196

7.85	5.21	1.65	.02	19.45	8.32	13.05	2.25	22.0	197
9.25	5.42	2.75	-0.59	20.45	8.42	13.85	2.98	22.0	198
10.55	6.14	3.85	-0.99	21.25	8.78	15.35	3.51	22.0	199
11.75	6.64	4.85	-1.15	22.55	9.06	16.55	3.63	22.0	200
12.35	6.82	5.75	-1.50	23.25	9.11	17.55	3.33	22.0	201
13.25	6.96	6.65	-1.77	-3.00	-3.00	18.45	2.87	22.5	202
.05	8.78	7.15	-1.94	13.85	7.01	19.25	2.56	22.5	203
.85	8.59	7.85	-1.81	14.45	7.15	19.75	2.36	22.5	204
1.45	8.38	8.45	-1.37	14.95	7.40	20.45	2.17	22.5	205
2.25	7.11	8.95	-0.83	15.35	7.45	21.15	2.07	22.5	206
2.85	7.11	9.35	-0.29	15.85	7.49	21.95	1.82	22.5	207
3.55	6.73	9.95	.47	16.55	7.56	22.55	1.86	22.5	208
4.35	6.32	10.25	1.43	16.85	7.66	23.55	1.82	22.5	209
5.28	5.72	11.15	2.21	17.45	7.54	-3.00	-3.00	22.5	210
6.35	5.19	.35	1.57	18.35	7.52	11.65	2.78	22.5	211
7.95	5.18	1.85	1.20	19.15	7.57	12.55	3.53	22.5	212
9.45	5.21	2.65	.75	19.95	7.75	13.75	3.81	22.5	213
10.65	5.55	3.85	.22	20.95	7.98	14.45	3.94	22.5	214
11.25	6.13	4.45	-0.28	21.85	8.51	16.05	3.91	22.5	215
11.95	6.51	5.35	-0.87	22.75	8.86	17.05	3.58	22.5	216
12.65	6.32	5.95	-1.42	23.55	9.19	17.95	2.95	22.5	217
13.75	7.43	6.75	-1.94	-3.00	-3.00	18.75	2.33	22.5	218
.35	9.24	7.55	-2.09	13.85	7.89	19.55	1.65	22.5	219
1.35	9.12	7.95	-1.74	14.65	8.43	20.35	1.05	22.5	220
2.25	8.65	8.55	-1.39	15.05	8.71	21.15	.52	22.5	221
3.15	7.99	9.25	-0.53	15.65	8.99	22.15	.24	22.5	222
4.05	7.26	10.05	.58	16.35	9.03	23.15	.09	22.5	223
5.05	6.42	10.55	1.55	17.05	8.80	-3.00	-3.00	22.5	224
6.25	5.78	.15	-0.05	17.85	8.50	11.35	2.53	22.5	225
7.85	5.49	1.15	-0.08	18.95	8.38	12.35	3.37	22.5	226
9.25	5.37	2.55	-0.21	20.15	8.10	13.15	3.72	22.0	227
10.55	6.14	3.55	-0.53	21.15	8.09	15.45	3.49	22.0	228
11.55	6.40	4.85	-0.93	22.35	8.22	16.55	3.19	22.0	229
12.25	6.72	5.55	-1.16	13.15	8.43	17.25	2.74	22.0	230
12.65	7.21	6.15	-1.20	-3.00	-3.00	18.15	2.49	22.0	231
.05	8.56	6.85	-0.81	13.15	7.54	18.85	2.20	22.0	232
.75	8.57	7.35	-0.49	13.75	7.91	19.45	1.96	22.0	233
1.25	8.20	7.75	-0.10	14.15	7.86	20.15	1.36	22.0	234
1.95	7.63	8.35	.07	14.45	7.74	20.75	1.02	22.0	235
2.65	7.11	8.65	.65	14.85	7.75	21.25	.82	22.0	236
3.15	6.60	9.05	1.24	15.25	7.59	21.85	.72	21.5	237
4.15	5.94	9.55	1.78	15.85	7.67	22.65	.95	21.5	238
4.85	5.65	9.85	2.70	16.25	7.73	23.75	1.22	21.5	239
5.85	5.40	10.75	3.40	16.95	7.53	-3.00	-3.00	21.5	240
7.15	5.25	.65	1.20	18.05	7.64	11.35	4.00	21.0	241
9.05	5.84	1.95	1.10	19.35	8.01	12.95	4.67	21.0	242
9.95	6.30	2.95	.95	20.45	8.19	14.55	4.44	21.0	243
10.75	7.37	3.75	.78	21.75	8.95	16.05	4.63	20.5	244
11.55	7.21	4.95	-0.23	22.45	8.79	16.95	3.14	20.5	245
11.95	7.52	5.55	-1.05	23.45	9.03	17.65	2.10	20.5	246

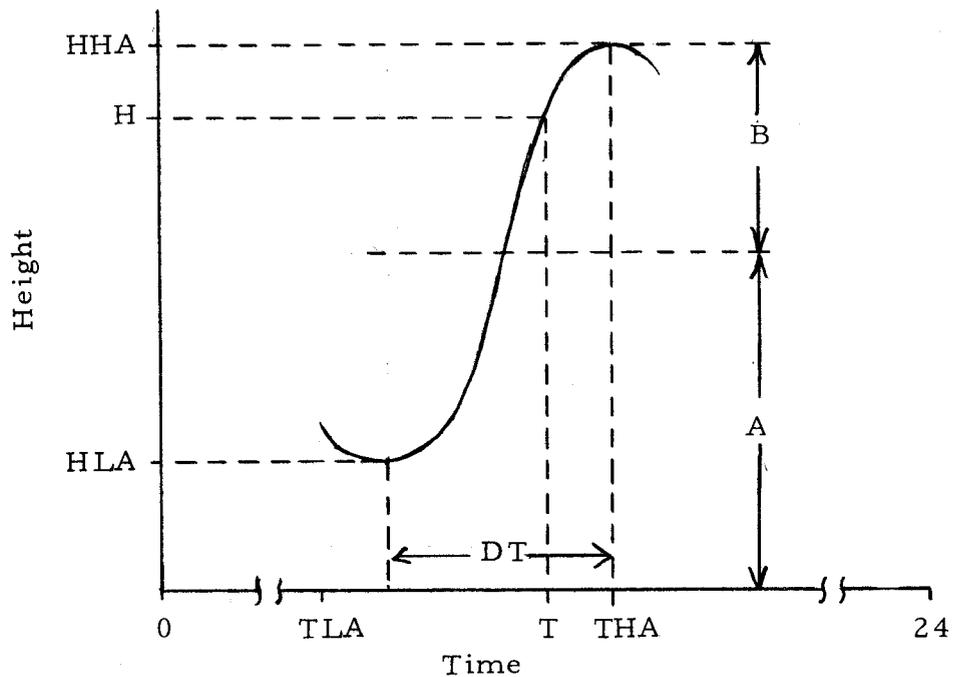
12.65	8.28	6.15	-1.23	-3.00	-3.00	18.55	1.35	20.0	247
.35	9.22	6.95	-0.96	13.25	8.87	19.25	.24	20.0	248
1.25	8.91	7.45	-0.84	13.85	9.15	19.95	-0.61	20.0	249
2.15	8.35	8.15	-0.24	14.35	9.27	20.65	-0.97	19.5	250
3.05	7.92	8.85	.75	15.05	9.54	21.65	-0.96	19.0	251
3.95	7.32	9.55	1.73	15.85	9.40	22.65	-0.52	19.0	252
5.05	6.75	10.15	2.90	16.45	8.92	23.75	-0.25	19.0	253
6.35	6.09	11.45	3.21	17.45	9.07	-3.00	-3.00	19.0	254
7.75	5.72	.85	-0.25	18.45	7.51	12.65	3.46	18.5	255
8.95	5.51	2.35	-0.36	19.95	6.78	14.35	3.06	18.5	256
10.15	5.76	3.45	-0.75	21.15	7.04	15.55	2.69	18.0	257
10.95	6.35	4.05	-0.67	22.25	7.36	16.35	2.29	18.0	258
11.55	6.85	4.95	-0.54	23.05	7.62	17.25	1.93	18.0	259
12.05	7.25	5.65	-0.31	23.85	7.81	17.85	1.54	17.5	260
12.55	7.72	6.25	.01	-3.00	-3.00	18.55	1.14	17.5	261
.45	7.98	6.75	.41	12.95	7.98	19.15	.68	17.0	262
1.15	7.71	7.25	.76	13.35	8.01	19.55	.34	17.0	263
1.75	7.38	7.75	1.09	13.75	8.09	20.25	.16	17.0	264
2.45	7.19	8.25	1.89	14.05	8.32	20.85	.26	17.0	265
3.15	7.06	8.45	2.49	14.45	8.27	21.35	.30	16.5	266
3.65	6.63	9.25	3.02	15.05	8.18	22.05	.52	16.5	267
4.65	6.39	9.55	3.69	15.75	8.20	22.75	.99	16.5	268
5.55	6.17	10.15	4.18	16.15	7.87	23.85	.87	16.5	269
7.05	5.76	11.15	4.24	17.25	7.38	-3.00	-3.00	16.0	270
8.45	6.37	1.15	.96	18.55	7.61	12.75	4.81	16.0	271
9.35	6.34	2.45	.94	20.05	7.62	14.65	4.37	16.0	272
10.05	6.89	3.35	.30	21.25	7.62	15.65	3.01	16.0	273
10.65	7.39	4.15	-0.32	22.25	7.87	16.55	1.75	15.5	274
11.25	7.97	4.95	-0.68	23.45	8.12	17.25	.51	15.5	275
11.85	8.67	5.45	-0.62	-3.00	-3.00	18.15	-0.65	15.5	276
.25	8.22	6.25	-0.33	12.45	9.27	18.85	-1.56	15.5	277
1.15	8.25	6.95	.48	13.05	9.77	19.75	-1.94	15.0	278
2.05	8.04	7.75	1.14	13.65	9.76	20.45	-2.20	15.0	279
2.95	7.63	8.45	1.83	14.35	9.72	21.25	-1.80	15.0	280
3.85	7.28	9.25	2.69	15.15	9.28	22.15	-1.20	15.0	281
4.95	6.84	10.05	3.28	16.05	8.45	23.35	-0.67	15.0	282
6.15	6.50	11.25	3.49	16.75	7.67	-3.00	-3.00	14.5	283
7.35	6.21	.35	-0.19	18.15	6.90	12.55	3.55	14.5	284
8.35	6.26	1.65	.09	19.45	6.63	13.95	3.23	14.5	285
9.45	6.64	2.55	.31	20.95	6.44	15.35	2.58	14.5	286
10.25	6.99	3.55	.37	22.05	6.94	16.25	2.12	14.0	287
10.85	7.41	4.35	.80	22.95	6.83	17.05	1.37	14.0	288
11.35	7.59	5.25	.82	23.75	6.93	17.75	.71	14.0	289
12.25	7.83	5.55	1.11	-3.00	-3.00	18.25	.20	14.0	290
.35	7.15	6.25	1.66	12.25	8.29	18.75	.27	14.0	291
1.05	7.86	7.05	3.31	12.45	9.00	19.25	-0.01	14.0	292
1.75	7.46	7.25	2.52	12.85	8.55	19.85	-0.55	13.5	293
2.25	7.00	7.65	2.89	13.45	8.57	20.35	-0.37	13.5	294
2.75	7.21	8.25	3.54	13.85	8.62	21.05	-0.26	13.5	295
3.65	7.02	9.15	3.74	14.55	8.51	21.75	-0.23	13.5	296
4.55	6.41	9.55	3.87	15.05	7.94	22.35	-0.07	13.0	297
5.15	6.17	10.35	3.92	15.85	7.41	23.45	.33	13.0	298

6.35	6.13	11.45	3.90	16.65	6.91	-3.00	-3.00	13.0	299
7.45	6.17	.45	.26	18.35	6.30	17.15	3.45	13.0	300
8.25	6.20	1.65	-0.15	19.55	6.00	14.25	2.50	13.0	301
9.15	6.70	2.35	-0.30	21.15	6.34	15.15	1.40	12.5	302
9.75	8.05	3.35	.18	22.25	6.90	16.25	.55	12.5	303
10.45	8.61	4.15	.50	23.25	7.66	17.15	-0.52	12.5	304
11.05	9.29	5.05	1.13	-3.00	-3.00	17.95	-1.90	12.5	305
.25	7.35	5.85	1.08	11.95	9.56	18.65	-2.66	12.0	306
1.15	7.35	6.55	1.54	12.45	9.74	19.45	-3.03	12.0	307
2.05	7.70	7.35	2.16	13.05	9.62	20.15	-3.15	12.0	308
2.95	7.11	8.05	2.28	13.95	9.21	21.05	-2.74	12.0	309
3.75	7.06	8.95	2.90	14.75	8.94	21.65	-1.53	12.0	310
4.75	7.31	10.05	3.38	15.55	8.19	22.85	-0.84	12.0	311
5.75	7.13	11.15	3.87	16.65	7.86	23.55	.58	11.5	312
7.05	7.80	12.45	4.43	18.15	7.62	-3.00	-3.00	11.5	313
7.65	7.62	.55	1.30	19.15	6.88	13.65	3.65	11.5	314
8.55	7.38	1.65	1.64	20.35	6.69	14.75	3.14	11.0	315
9.15	8.30	2.55	2.25	21.55	7.21	15.65	2.67	11.0	316
9.55	8.80	3.55	3.24	22.65	7.11	16.45	2.06	11.0	317
10.45	8.00	4.45	2.50	23.45	6.52	16.95	.49	11.0	318
10.85	8.17	4.65	2.46	24.05	6.53	17.55	-0.43	11.0	319
11.15	8.02	5.25	2.55	-3.00	-3.00	18.25	-1.03	11.0	320
.65	6.33	5.95	2.51	11.75	8.04	18.65	-1.57	10.5	321
1.45	6.31	6.55	2.72	12.25	8.19	19.55	-1.66	10.5	322
2.05	6.46	7.15	2.90	12.95	8.31	20.05	-1.65	10.5	323
2.95	6.54	7.75	3.25	13.45	8.51	20.65	-1.37	10.5	324
3.55	6.60	8.25	3.42	14.05	8.36	21.25	-1.27	10.0	325
4.15	6.43	9.35	3.45	14.75	7.85	21.85	-0.73	10.0	326
5.15	6.86	10.25	4.17	15.75	7.99	22.95	.02	10.0	327
5.95	7.48	11.45	3.89	16.65	7.26	23.75	.41	10.0	328
6.45	7.23	12.45	3.18	18.05	6.95	-3.00	-3.00	10.0	329
7.35	8.46	1.05	1.72	19.15	6.84	13.75	2.92	9.5	330
7.85	8.54	1.55	1.40	20.95	7.22	14.75	1.78	9.5	331
8.85	9.87	2.65	2.69	22.15	7.67	15.95	1.09	9.5	332
9.55	9.49	3.65	3.08	23.25	6.93	16.85	-0.83	9.5	333
10.45	9.72	4.25	2.56	-3.00	-3.00	17.75	-2.07	9.5	334
.35	7.45	5.35	3.02	11.35	10.43	18.55	-1.69	9.0	335
1.15	8.36	6.45	3.90	11.95	10.72	19.25	-2.34	9.0	336
2.25	8.47	7.35	4.24	12.85	11.15	20.05	-2.47	9.0	337
2.85	7.92	7.95	3.30	13.65	10.02	20.85	-1.41	9.0	338
3.45	8.35	8.75	3.76	14.25	9.63	21.55	-1.31	9.0	339
4.25	7.79	9.75	3.24	15.25	7.92	22.35	-1.21	9.0	340
4.95	7.02	10.45	2.74	16.15	6.90	23.05	-0.45	9.0	341
5.85	7.39	11.75	3.49	17.45	6.94	23.75	1.53	8.5	342
6.35	7.74	13.05	2.99	18.15	6.27	-3.00	-3.00	8.5	343
7.25	8.14	.65	2.11	19.65	5.83	14.35	2.73	8.5	344
8.05	7.85	1.55	2.40	22.05	6.71	15.05	2.15	8.5	345
8.65	8.35	2.65	4.21	21.95	5.92	15.95	1.99	8.5	346
9.25	8.29	3.25	3.25	23.45	6.79	16.95	.54	8.0	347
9.85	8.93	4.35	4.50	23.85	6.74	17.45	.51	8.0	348



## APPENDIX II

Method for Determining Time at Which a Given Tide  
Elevation (H) is Submerged



$$A = \frac{HHA + HLA}{2}$$

$$B = \frac{HHA - HLA}{2}$$

$$DT = THA - TLA$$

$$H = A + B \sin \left[ \frac{\pi}{DT} \left( T - \left( TLA + \frac{DT}{2} \right) \right) \right]$$

$$T = \frac{DT}{\pi} \arcsin \left( \frac{H-A}{B} \right) + TLA + \frac{DT}{2}$$

## APPENDIX III

Fortran Program for Calculating Total Submergence  
Times at a Given Tidal Elevation

```

PROGRAM DOTY
DIMENSION THA(400),HHA(400),TLA(400),HLA(400),THB(400),
1HHB(400),TLB(400),TCA(400),HLB(400),TUA(400),TCB(400),
1TUB(400),TCC(400),TUC(400),DW(400),PER(400),RPER(400),
1S1(400),S2(400),S3(400),TSM(1200)
PI=3.1416
1  FORMAT(8F6.2,F5.1)
   READ(35,1)(THA(I),HHA(I),TLA(I),HLA(I),THB(I),HHB(I),
1TLB(I),HLB(I),DW(I),I=1,367)
   REWIND35
   DO 5300 M=0,15
   XM=M
   H=7.0+0.1*XM
   WRITE(10,15) H
15  FORMAT(#1#,6X,#H=#,F6.2)
   N=0
   DO 300 I=306,335
   IF(THA(I).GT.TLA(I))GO TO 100
C  STATEMENTS UP TO 100 = FIRST HI BEFORE FIRST LO
   IF(HHA(I).LT.H)GO TO 40
   IF(HLB(I-1).GT.H).GO TO 42
   A=(HHA(I)+HLB(I-1))/2.
   B=(HHA(I)-HLB(I-1))/2.
   DT=THA(I)+(24.-TLB(I-1))
   XT=(PHI(H,A,B)/PI)*DT+(TLB(I-1)+DT/2.)
   TCA(I)=XT-24.
   IF(TCA(I).LT.0.0)TCA(I)=0.0
   GO TO 43
42  TCA(I)=0.0
43  CONTINUE
   IF(HLA(I).GT.H)GO TO 45
   A=(HHA(I)+HLA(I))/2.
   B=(HHA(I)-HLA(I))/2.
   DT=TLA(I)-THA(I)
   TUA(I)=-PHI(H,A,B)*DT/PI+(THA(I)+DT/2.)

```

```

GO TO 50
40 TCA(I)=-5.
TUA(I)=-5.
50 IF(HH3(I).LT.H)GO TO 55
A=(HH3(I)+HLA(I))/2.
B=(HH3(I)-HLA(I))/2.
DT=TH3(I)-TLA(I)
TCB(I)=(PHI(H,A,B)/PI)*DT+(TLA(I)+DT/2.)
GO TO 60
45 TUA(I)=-5.
TCB(I)=-5.
60 IF(TLB(I).LT.0.0)GO TO 65
C SECOND LO TIDE PRESENT:
IF(HL3(I).LT.H)GO TO 75
TUB(I)=-5.
TCC(I)=-5.
TUC(I)=24.
GO TO 95
75 A=(HH3(I)+HL3(I))/2.
B=(HH3(I)-HL3(I))/2.
DT=TL3(I)-TH3(I)
TUB(I)=-PHI(H,A,B)*DT/PI+(TH3(I)+DT/2.)
GO TO 80
55 TCB(I)=-5.
TUB(I)=-5.
IF(TLB(I).GT.0.0)GO TO 80
TCC(I)=-5.
TUC(I)=-5.
GO TO 95
80 IF(HHA(I+1).LT.H)GO TO 85
A=(HHA(I+1)+HL3(I))/2.
B=(HHA(I+1)-HL3(I))/2.
DT=THA(I+1)+(24.-TL3(I))
TCC(I)=(PHI(H,A,B)/PI)*DT+(TL3(I)+DT/2.)
IF(TCC(I).LT.24.)GO TO 90
TCC(I)=-5.

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TUC(I)=-5.
GO TO 95
90 TUC(I)=24.
GO TO 95
85 TCC(I)=-5.
TUC(I)=-5.
GO TO 95
C NO SECOND LO TIDE:
65 IF(HLA(I+1).GT.H)GO TO 70
A=(H4B(I)+HLA(I+1))/2.
B=(H4B(I)-HLA(I+1))/2.
DT=TLA(I+1)+(24.-THB(I))
TUB(I)=-PHI(H,A,B)*DT/PI+(THB(I)+DT/2.)
IF(TUB(I).GT.24.)TUB(I)=24.
TCC(I)=-5.
TUC(I)=-5.
GO TO 95
70 TUB(I)=24.
TCC(I)=-5.
TUC(I)=-5.
95 CONTINUE
GO TO 250
C STATEMENTS 100 TO 250 = FIRST LO BEFORE FIRST HI
100 IF(HLA(I).LT.H)GO TO 105
TCA(I)=0.0
TUA(I)=-5.
TOB(I)=-5.
GO TO 138
105 CONTINUE
IF(H4B(I-1).LT.H) GO TO 107
A=(H4B(I-1)+HLA(I))/2.
B=(H4B(I-1)-HLA(I))/2.
DT=TLA(I)+(24.-THB(I-1))
XT=-PHI(H,A,B)*DT/PI+(THB(I-1)+DT/2.)
TUA(I)=XT-24.
IF(TUA(I)-0.0)107,107,108

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107 TCA(I)=-5.
    TUA(I)=-5.
    GO TO 109
108 TCA(I)=0.0
109 IF(H4A(I).LT.H)GO TO 110
    A=(H4A(I)+HLA(I))/2.
    B=(H4A(I)-HLA(I))/2.
    DT=THA(I)-TLA(I)
    TCB(I)=(PHI(H,A,B)/PI)*DT+(TLA(I)+DT/2.)
138 IF(H4B(I).GT.H)GO TO 115
    A=(H4B(I)+HLB(I))/2.
    B=(H4B(I)-HLB(I))/2.
    DT=TLB(I)-THA(I)
    TUB(I)=-PHI(H,A,B)*DT/PI+(THA(I)+DT/2.)
    GO TO 130
110 TCB(I)=-5.
    TUB(I)=-5.
130 IF(T4B(I).LT.0.3)GO TO 150
C SECOND HI TIDE PRESENT:
    IF(H4B(I).LT.H)GO TO 135
    A=(H4B(I)+HLB(I))/2.
    B=(H4B(I)-HLB(I))/2.
    DT=T4B(I)-TLB(I)
    TCC(I)=(PHI(H,A,B)/PI)*DT+(TLB(I)+DT/2.)
    GO TO 140
115 TUB(I)=-5.
    TCC(I)=-5.
    IF(T4B(I).GT.0.0)GO TO 140
    TUC(I)=24.
    GO TO 250
140 IF(H4A(I+1).GT.H)GO TO 145
    A=(H4B(I)+HLA(I+1))/2.
    B=(H4B(I)-HLA(I+1))/2.
    DT=TLA(I+1)+(24.-THB(I))
    TUC(I)=-PHI(H,A,B)*DT/PI+(THB(I)+DT/2.)
    IF(TUC(I).GT.24.)TUC(I)=24.

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      GO TO 250
145   TUC(I)=24.
      GO TO 250
135   TCC(I)=-5.
      TUC(I)=-5.
      GO TO 250
C     NO SECOND LO TIDE PRESENT
150   IF(H+A(I+1).LT.H) GO TO 151
      A=(H+A(I+1)+HLB(I))/2.
      B=(H+A(I+1)-HLB(I))/2.
      DT=T+A(I+1)+(24.-TLB(I))
      TCC(I)=(PHI(H,4,B)/PI)*DT+(TLB(I)+DT/2.)
      IF(TCC(I)-24.) 160,151,151
151   TCC(I)=-5.
      TUC(I)=-5.
      GO TO 250
160   TUC(I)=24.
250   CONTINUE
      PER(I)=((TUA(I)-TCA(I))+(TUB(I)-TCB(I))+(TUC(I)-TCC(I)))/.24
      XCA=TCA(I)
      XUA=TUA(I)
      XCB=TCB(I)
      XUB=TUB(I)
      XCC=TCC(I)
      XUC=TUC(I)
      IF(XCA.EQ.-5.0) GO TO 255
      IF(XCA.LT.6.0) XCA=6.0
255   IF(XUA.EQ.-5.0) GO TO 260
      IF(XUA.LT.6.0) XUA=6.0
260   IF(XCB.EQ.-5.0) GO TO 265
      IF(XCB.LT.6.0) XCB=6.0
265   IF(XUB.EQ.-5.0) GO TO 270
      IF(XUB.LT.6.0) XUB=6.0
270   IF(XCB.GT.18.0) XCB=18.0
      IF(XUB.GT.18.0) XUB=18.0
      IF(XCC.GT.18.0) XCC=18.0

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IF (XUC.GT.18.0) XUC=18.0
RPER(I) = ((XUA-XCA) + (XUB-XCB) + (XUC-XCC)) / .12
300 CONTINUE
2   FORMAT(6X, #HOURS SUBMERGED BETWEEN EXPOSURES#)
3   FORMAT(6X, #DAY  S1      S2      S3      SUB. HOURS#)
4   FORMAT(6X, I6, 3F6.2, 10X, F6.2)
WRITE(10,2)
WRITE(10,3)
DO 4200 I=326,335
IF (RPER(I).NE.0.0) GO TO 430
S1(I)=0.0
GO TO 4170
430 IF (RPER(I).NE.100.0) GO TO 435
S3(I)=24.+S3(I-1)
S3(I-1)=0.0
GO TO 4172
435 IF (TAC(I).NE.24.) GO TO 470
IF (TCC(I).GT.0.0) GO TO 450
IF (TCB(I).GT.0.0) GO TO 440
S3(I)=24.-TCA(I)
GO TO 4172
440 S3(I)=24.-TCB(I)
S2(I)=0.0
GO TO 453
450 S3(I)=24.-TCC(I)
IF (TUR(I).GT.0.0) GO TO 460
S2(I)=0.0
453 IF (TUA(I).GT.0.0) GO TO 455
S1(I)=0.0
GO TO 4200
455 IF (TCA(I).EQ.0.0) GO TO 457
S1(I)=TUA(I)-TCA(I)
GO TO 4200
457 S1(I)=S3(I-1)+TUA(I)
S2(I-1)=0.0
GO TO 4200

```

```

460 IF(TCB(I).GT.0.0)GO TO 465
S2(I)=0.0
IF(TCA(I).GT.0.0)GO TO 462
S1(I)=S3(I-1)+TUB(I)
S3(I-1)=0.0
GO TO 4200
462 S1(I)=TUB(I)-TCA(I)
GO TO 4200
465 S2(I)=TUB(I)-TCB(I)
GO TO 453
470 IF(TUB(I).NE.24.)GO TO 480
IF(TCB(I).GT.0.0)GO TO 475
S3(I)=24.-TCA(I)
GO TO 4172
475 S3(I)=24.-TCB(I)
S2(I)=0.0
IF(TUA(I).GT.0.0)GO TO 478
S1(I)=0.0
GO TO 4200
478 IF(TCA(I).GT.0.0)GO TO 479
S1(I)=S3(I-1)+TUA(I)
S3(I-1)=0.0
GO TO 4200
479 S1(I)=TUA(I)-TCA(I)
GO TO 4200
480 IF(TCA(I).NE.0.0)GO TO 4110
IF(TUA(I).GT.0.0)GO TO 485
IF(TUB(I).GT.0.0)GO TO 490
S1(I)=S3(I-1)+TUC(I)
S3(I-1)=0.0
GO TO 4170
490 S1(I)=S3(I-1)+TUB(I)
S3(I-1)=0.0
S2(I)=0.0
GO TO 4185
485 S1(I)=S3(I-1)+TUA(I)

```

```

S3(I-1)=0.0
IF(TCB(I).GT.0.0)GO TO 4175
S2(I)=0.0
GO TO 4185
4110 IF(TCA(I).EQ.-5.)GO TO 4150
IF(TDA(I).GT.0.0)GO TO 4115
IF(TUR(I).GT.0.0)GO TO 4120
S1(I)=TUC(I)-TCA(I)
GO TO 4170
4120 S1(I)=TUB(I)-TCA(I)
S2(I)=0.0
GO TO 4185
4115 S1(I)=TUA(I)-TCA(I)
IF(TCB(I).GT.0.0)GO TO 4175
S2(I)=0.0
GO TO 4185
4150 S1(I)=0.0
IF(TCB(I).GT.0.0)GO TO 4175
S2(I)=0.0
GO TO 4195
4170 S2(I)=0.0
4171 S3(I)=0.0
GO TO 4200
4172 S1(I)=0.0
S2(I)=0.0
GO TO 4200
4175 IF(TUR(I).GT.0.0)GO TO 4180
S2(I)=TUC(I)-TCB(I)
GO TO 4171
4180 S2(I)=TUB(I)-TCB(I)
4185 IF(TCC(I).GT.0.0)GO TO 4195
GO TO 4171
4195 S3(I)=TUC(I)-TCC(I)
4200 CONTINUE
DO 4210 I=306,335
N=N+1

```

```

TSM(N)=S1(I)
N=N+1
TSM(N)=S2(I)
N=N+1
4210 TSM(N)=S3(I)
CONTINUE
NXX=N+4
DO 5200 K=1,NXX
DO 5200 I=1,N
TISM=TSM(I)
IF(TISM.GE.TSM(I+1)) GO TO 5200
TSM(I)=TSM(I+1)
TSM(I+1)=TISM
5200 CONTINUE
WRITE(10,4)(I,S1(I+1),S2(I+1),S3(I+1),TSM(I-304),I=305,334)
5300 CONTINUE
STOP
END

```

```

FUNCTION PHI(H,A,B)
ANG=(((H-A)/B)/SQRT((1.-((H-A)/B)**2)))
PHI=ATAN(ANG)
RETURN
END

```

## APPENDIX IV

Method for Approximating Daily Maximum and Minimum  
Soil Surface Temperatures at the Study Site

(Most records are in °F so conversion to °C was done at the end.)

1. After appraisal of records of (a) total daily radiation at the Marine Science Center and Astor Experiment Station (NOAA, 1971a), (b) general distribution and amount of daily rainfall at various coastal locations (NOAA, 1971b), and (c) hourly precipitation during each day at Newport (NOAA, 1971c), each day was classified as "+" (sunny or high radiation levels during the day) or "-" (overcast or low radiation during the day).

2. Comparison of daily maximum and minimum temperatures from the Georgia Pacific Company at Toledo with (a) max-min records from several other coastal and estuarine locations (NOAA, 1971b), and (b) my temperature records for the study area, with consideration of (c) the relative location and geography of the study site region, led to general acceptance of the Toledo data for maximum and minimum air temperatures for the study site.

As a result of the Newport fog bank and coastal upwelling which have a cooling effect on stations directly at the coast, maximum air temperatures of 10° F or more higher at Toledo are to be expected. Winter minimum temperatures for each day are very similar at Newport and Toledo. Some modifications were made to the Toledo temperature data when values appeared wildly inconsistent with these considerations.

3. Comparison of maximum air temperature with soil surface temperatures that I recorded throughout the year on different types of days (e. g., very sunny, hazy, overcast, and pouring rain) led to the following simplified formula for computing soil surface (boundary layer) maximum temperature for each day:

(1) Jan., Feb., Nov., Dec.

Soil surface maximum is considered equal to air maximum on both + and - days.

(2) Mar., Oct.

Soil surface maximum is 3° F higher than air maximum on + days and equal to air maximum on - days.

(3) Apr., Sept.

Soil surface maximum is 5° F higher than air maximum on + days and equal to air maximum on - days.

(4) May, June, Aug.

Soil surface maximum is 5° F higher on both + and - days.

(5) July

Soil surface maximum is 9° F higher than air maximum on + days and 5° F higher on - days.

4. During the night, soil surface temperature is probably near wet-bulb temperature. The average difference between minimum dry- and wet-bulb temperature at coastal locations (Pacific Northwest River Basins Commission, 1969) is approximately 1° F and this amount was subtracted from air minimum temperature to get soil surface minimum temperature one hour before sunrise each day.

5. The two temperatures for each day were converted to °C.

6. A sine curve was used to interpolate exposed soil surface temperatures between the daily maximum and the minimums on either side.

## APPENDIX V

Temperature of Soil Surface at the Study Site

- TMIN = time of minimum temperature for the day (one hour before sunrise).
- DMIN = minimum temperature in degrees centigrade.
- DMAX = maximum temperature in degrees centigrade.
- DAY: day 1 is January 1, 1971; day 365 is December 31, 1971.

TMIN	DMIN	DMAX	DAY					
6.82	-1.7	8.3			6.20	5.0	12.8	67
6.82	-3.9	6.7	1		6.17	3.9	12.8	68
6.82	-4.4	7.8	2		6.15	3.9	12.2	69
6.82	-4.4	4.4	3		6.12	-1.7	9.4	50
6.82	-5.0	7.2	4		6.08	-1.7	12.8	51
6.82	-3.3	5.6	5		6.07	2.8	8.9	52
6.82	-2.8	5.6	6		6.03	4.4	10.0	53
6.82	2.2	7.2	7		6.02	5.0	10.0	54
6.82	6.1	8.9	8		5.98	1.1	7.8	55
6.80	5.0	7.2	9		5.95	.6	6.7	56
6.80	-0.6	7.2	10		5.92	-1.7	5.6	57
6.80	-2.2	3.9	11		5.90	-1.1	5.6	58
6.78	-2.2	3.3	12		5.87	-3.3	5.0	59
6.78	-0.6	5.6	13		5.83	-3.9	10.6	60
6.77	-0.6	11.1	14		5.82	1.7	7.8	61
6.77	8.3	11.7	15		5.78	-0.6	5.6	62
6.75	8.9	13.3	16		5.75	-0.6	7.8	63
6.75	9.4	11.1	17		5.72	.6	7.8	64
6.73	8.9	16.1	18		5.70	3.9	10.0	65
6.72	1.7	10.0	19		5.67	0	7.8	66
6.70	1.1	10.0	20		5.63	.6	11.7	67
6.70	1.7	7.8	21		5.60	2.8	8.9	68
6.68	1.7	7.2	22		5.58	5.0	8.9	69
6.67	5.0	7.8	23		5.55	5.0	10.6	70
6.67	5.0	7.2	24		5.52	1.7	13.3	71
6.65	6.7	8.3	25		5.49	2.8	12.8	72
6.63	1.1	12.8	26		5.45	1.1	10.0	73
6.62	1.7	12.2	27		5.43	0	13.9	74
6.60	1.7	12.2	28		5.40	0	13.9	75
6.58	1.7	12.8	29		5.37	-1.1	10.4	76
6.57	8.3	17.2	30		5.33	-1.7	20.0	77
6.55	5.6	16.7	31		5.30	.6	18.9	78
6.52	3.3	10.6	32		5.28	1.7	18.3	79
6.50	1.1	8.3	33		5.25	.6	18.9	80
6.48	1.1	10.0	34		5.22	6.7	11.7	81
6.45	-1.1	11.1	35		5.18	5.6	12.2	82
6.43	-1.1	7.2	36		5.15	1.7	10.6	83
6.42	-1.7	10.0	37		5.12	3.9	9.4	84
6.40	-1.1	13.9	38		5.08	2.2	10.0	85
6.37	0	13.9	39		5.07	6.1	11.1	86
6.35	5.0	12.8	40		5.03	7.2	12.2	87
6.33	5.6	11.7	41		5.00	3.9	11.1	88
6.32	6.1	18.9	42		4.97	1.7	11.1	89
6.30	10.0	16.7	43		4.93	.6	14.4	90
6.27	7.2	16.7	44		4.90	2.8	16.1	91
6.25	5.0	11.7	45		4.87	.6	21.7	92
6.22	3.9	11.7	46		4.85	.6	21.7	93
					4.78	2.8	25.0	94

4.78	3.9	14.4	95	3.60	10.0	20.6	145
4.75	2.8	13.9	96	3.58	8.3	18.3	146
4.72	3.3	17.4	97	3.57	8.3	20.6	147
4.68	5.6	12.2	98	3.57	10.0	20.0	148
4.67	1.7	10.0	99	3.55	6.1	18.3	149
4.63	1.7	12.2	100	3.53	6.1	18.9	150
4.60	1.1	16.7	101	3.52	7.8	17.2	151
4.57	4.4	21.7	102	3.52	8.3	18.3	152
4.53	6.7	21.7	103	3.50	7.8	22.8	153
4.52	2.2	12.2	104	3.50	8.9	21.6	154
4.48	3.3	18.3	105	3.48	9.4	20.4	155
4.45	3.3	15.0	106	3.47	10.6	21.7	156
4.42	3.9	10.6	107	3.48	9.4	22.8	157
4.40	1.1	16.1	108	3.47	8.9	21.1	158
4.37	3.9	17.8	109	3.47	9.4	25.9	159
4.33	.6	11.1	110	3.47	9.4	22.8	160
4.32	1.7	15.0	111	3.45	9.4	22.8	161
4.28	3.9	18.3	112	3.45	7.8	22.2	162
4.27	3.3	16.1	113	3.45	8.9	25.6	163
4.23	5.6	13.3	114	3.45	7.2	19.4	164
4.20	4.4	23.3	115	3.45	6.1	25.1	165
4.18	4.4	26.7	116	3.45	5.0	25.0	166
4.15	6.7	12.8	117	3.45	7.2	25.6	167
4.12	6.1	19.4	118	3.45	8.9	22.8	168
4.10	6.7	18.3	119	3.45	13.3	23.9	169
4.07	6.1	20.0	120	3.45	10.6	24.4	170
4.05	6.7	24.4	121	3.45	9.4	23.9	171
4.02	9.4	23.9	122	3.45	10.6	26.1	172
4.00	6.7	15.6	123	3.47	10.6	23.9	173
3.98	6.1	22.2	124	3.47	6.1	27.2	174
3.97	3.9	15.6	125	3.47	7.2	19.4	175
3.95	5.0	26.7	126	3.48	9.4	26.1	176
3.92	8.3	25.1	127	3.48	6.7	21.7	177
3.88	6.7	25.0	128	3.50	6.1	23.9	178
3.85	3.9	25.0	129	3.50	3.9	26.1	179
3.83	5.0	33.3	130	3.50	6.1	27.2	180
3.82	6.7	26.7	131	3.52	7.2	25.0	181
3.80	3.9	20.0	132	3.52	7.2	28.3	182
3.78	3.9	20.0	133	3.53	6.1	28.9	183
3.77	3.9	23.9	134	3.53	5.0	28.9	184
3.75	3.9	16.7	135	3.55	10.6	22.8	185
3.73	3.3	15.6	136	3.55	8.3	30.6	186
3.72	6.7	18.3	137	3.57	5.0	27.8	187
3.70	6.7	25.0	138	3.58	7.2	32.8	188
3.68	5.0	13.9	139	3.60	11.7	27.2	189
3.67	3.9	19.4	140	3.60	11.1	21.1	190
3.65	6.7	23.3	141	3.62	11.1	20.0	191
3.63	7.8	21.1	142	3.63	8.3	27.2	192
3.62	8.3	26.7	143	3.65	8.3	30.6	193
3.60	9.4	21.1	144	3.67	12.2	31.1	194

3.67	11.7	31.7	195	4.60	11.7	29.0	245
3.68	9.4	30.9	196	4.62	7.8	26.7	246
3.70	8.9	33.9	197	4.63	10.6	27.2	247
3.72	9.9	34.4	198	4.65	6.1	23.3	248
3.73	11.7	32.8	199	4.67	6.1	27.2	249
3.75	13.9	33.9	200	4.68	6.1	27.2	250
3.77	10.6	35.0	201	4.72	12.2	26.1	251
3.78	11.1	35.6	202	4.73	10.6	27.2	252
3.80	10.6	25.0	203	4.75	10.6	21.7	253
3.82	13.9	26.1	204	4.77	7.2	25.0	254
3.83	11.1	33.9	205	4.78	8.3	25.6	255
3.85	12.2	31.7	206	4.80	5.6	22.2	256
3.87	12.2	28.3	207	4.82	5.0	27.8	257
3.88	12.2	20.0	208	4.85	6.1	29.9	258
3.92	12.2	23.9	209	4.87	15.0	29.4	259
3.92	12.8	21.1	210	4.88	13.9	31.1	260
3.93	15.0	27.8	211	4.90	5.6	32.8	261
3.95	13.3	28.3	212	4.92	11.7	26.7	262
3.97	15.6	30.6	213	4.93	6.1	30.9	263
3.98	11.7	31.7	214	4.97	6.7	29.4	264
4.00	10.0	24.4	215	4.98	5.6	26.1	265
4.03	12.2	25.0	216	5.00	9.4	20.6	266
4.05	12.8	29.4	217	5.02	9.4	18.9	267
4.07	10.0	37.8	218	5.03	8.9	18.3	268
4.08	12.2	33.9	219	5.07	5.0	17.2	269
4.10	15.0	36.7	220	5.08	9.4	21.1	270
4.12	15.0	25.0	221	5.10	4.4	15.0	271
4.15	15.0	30.6	222	5.12	4.4	14.4	272
4.17	13.9	29.4	223	5.13	4.4	19.4	273
4.18	13.9	23.9	224	5.17	7.2	19.4	274
4.20	17.9	23.9	225	5.18	6.7	20.6	275
4.22	9.4	29.9	226	5.20	7.8	21.0	276
4.25	12.2	29.4	227	5.22	6.7	27.2	277
4.27	10.0	26.7	228	5.25	9.4	26.7	278
4.28	10.0	28.9	229	5.27	9.4	27.2	279
4.30	10.0	29.4	230	5.28	8.9	27.8	280
4.32	14.4	25.0	231	5.30	9.4	31.1	281
4.33	13.9	25.6	232	5.33	10.0	17.8	282
4.37	11.7	23.9	233	5.35	10.6	20.6	283
4.38	8.3	27.2	234	5.37	7.2	23.9	284
4.40	8.3	32.2	235	5.38	7.2	21.7	285
4.42	15.0	24.4	236	5.42	4.4	15.0	286
4.43	8.3	23.9	237	5.43	4.4	15.0	287
4.47	10.6	28.9	238	5.45	.6	15.6	288
4.48	10.6	26.1	239	5.48	-1.1	17.2	289
4.50	11.1	27.2	240	5.50	3.3	16.1	290
4.52	12.8	26.1	241	5.52	4.4	13.9	291
4.53	13.3	23.9	242	5.55	3.9	12.8	292
4.55	12.2	21.7	243	5.57	3.9	15.6	293
4.58	11.7	16.7	244	5.58	3.3	16.7	294

5.62	6.7	13.3	295	6.40	5.6	10.0	331
5.63	2.8	13.9	296	6.42	6.7	11.1	332
5.65	1.7	14.4	297	6.43	6.1	9.4	333
5.68	6.7	13.3	298	6.47	3.3	11.1	334
5.70	.6	11.7	299	6.48	5.0	11.1	335
5.72	-2.8	9.4	300	6.50	5.6	14.4	336
5.75	-2.2	11.7	301	6.52	-1.1	12.2	337
5.77	2.2	12.8	302	6.53	-0.6	9.4	338
5.78	3.3	14.4	303	6.55	3.3	10.0	339
5.82	5.0	11.7	304	6.57	8.9	12.8	340
5.83	7.2	11.7	305	6.58	3.9	12.8	341
5.85	2.8	12.2	306	6.60	3.9	13.9	342
5.88	-2.8	10.0	307	6.62	6.1	13.3	343
5.90	-2.2	10.6	308	6.63	5.0	14.4	344
5.93	-1.7	12.2	309	6.65	3.9	10.0	345
5.95	4.4	15.0	310	6.67	3.9	12.2	346
5.97	3.3	14.4	311	6.68	3.9	10.0	347
6.00	5.0	14.4	312	6.68	5.0	12.2	348
6.02	7.2	12.2	313	6.70	2.2	12.8	349
6.03	8.9	11.7	314	6.72	5.0	10.0	350
6.07	8.9	15.6	315	6.73	3.9	12.8	351
6.08	5.0	16.7	316	6.73	3.9	13.3	352
6.10	2.8	8.9	317	6.75	.6	11.1	353
6.13	4.4	11.7	318	6.75	2.8	11.1	354
6.15	4.4	13.3	319	6.75	2.2	11.1	355
6.17	.6	12.8	320	6.77	1.7	12.2	356
6.20	1.1	12.8	321	6.78	1.1	11.1	357
6.22	1.1	12.8	322	6.78	2.2	12.8	358
6.23	7.2	13.3	323	6.80	1.7	12.8	359
6.25	5.6	12.8	324	6.80	.6	12.8	360
6.28	2.8	11.1	325	6.80	1.1	15.0	361
6.30	5.0	12.8	326	6.82	.6	7.2	362
6.32	5.0	10.6	327	6.82	1.7	10.0	363
6.33	2.8	12.8	328	6.82	3.9	12.8	364
6.37	3.9	10.0	329	6.82	5.0	12.8	365
6.38	4.4	11.7	330	6.82	1.7	8.9	

## APPENDIX VI

Fortran program for calculating percent of total 24-hour period submerged (PER); percent of day 6 AM to 6 PM submerged (RPER); and mean temperature at the soil surface (TEMP) for each day.

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PROGRAM CTIDES
DIMENSION THA(400),HHA(400),TLA(400),HLA(400),THB(400),
1HHB(400),TLB(400),TCA(400),HLB(400),TUA(400),TCB(400),
1TUB(400),TCC(400),TUC(400),DW(400),PER(400),RPER(400),
1EA(400),EB(400),EC(400),ED(400),EE(400),EF(400),TEMP(400),
1TMIN(400),DMIN(400),DMAX(400)
PI=3.1416
H=TTYIN(4HH= )
WRITE(10,7) H
7   FORMAT(/5X,#H=#,F6.2/)
1   FORMAT(8F6.2,F5.1)
2   FORMAT(/5X,#TCA TO TUC = TIMES COVERED AND UNCOVERED BY TIDE#)
9   FORMAT(6X,#PER = PERCENT OF ENTIRE DAY UNDER WATER#)
10  FORMAT(6X,#RPER = PERCENT OF DAY 5 A.M. TO 5 P.M. UNDER WATER#)
12  FORMAT(6X,#TEMP = MEAN TEMPERATURE FOR INSECTS OVER ENTIRE DAY#/)
3   FORMAT(6X,#DAY  TCA   TUA   TCB   TUB   TCC   TUC   PER   RPER
1EA   EB   EC   ED   EE   EF   TEMP#)
4   FORMAT(3X,I6,6F6.2,2F7.2,7F6.2)
READ(35,1)(THA(I),HHA(I),TLA(I),HLA(I),THB(I),HHB(I),
ITLB(I),HLB(I),DW(I),I=1,367)
READ(40,8)(TMIN(I),DMIN(I),DMAX(I),I=1,367)
8   FORMAT(F4.3,2F5.0)
REWIND40
WRITE(10,2)
WRITE(10,9)
WRITE(10,10)
WRITE(10,12)
WRITE(10,3)
REWIND35
DO 1600 I=2,366
IF(THA(I).GT.TLA(I))GO TO 100
C   STATEMENTS UP TO 100 = FIRST HI BEFORE FIRST LO
IF(HHA(I).LT.H)GO TO 40
IF(HLB(I-1).GT.H) GO TO 42
A=(HHA(I)+HLB(I-1))/2.

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B=(H4A(I)-H4B(I-1))/2.
DT=THA(I)+(24.-TLB(I-1))
XT=(PHI(H,A,B)/PI)*DT+(TLB(I-1)+DT/2.)
TCA(I)=XT-24.
IF(TCA(I).LT.0.0)TCA(I)=0.0
GO TO 43
42 TCA(I)=0.0
43 CONTINUE
IF(H4A(I).GT.H)GO TO 45
A=(H4A(I)+H4A(I))/2.
B=(H4A(I)-H4A(I))/2.
DT=TLA(I)-THA(I)
TUA(I)=-PHI(H,A,B)*DT/PI+(THA(I)+DT/2.)
GO TO 50
40 TCA(I)=-5.
TUA(I)=-5.
50 IF(H4B(I).LT.H)GO TO 55
A=(H4B(I)+H4A(I))/2.
B=(H4B(I)-H4A(I))/2.
DT=THB(I)-TLA(I)
TCB(I)=(PHI(H,A,B)/PI)*DT+(TLA(I)+DT/2.)
GO TO 60
45 TUA(I)=-5.
TCB(I)=-5.
60 IF(TLB(I).LT.0.0)GO TO 65
C SECOND LO TIDE PRESENT:
IF(H4B(I).LT.H)GO TO 75
TUB(I)=-5.
TCC(I)=-5.
TUC(I)=24.
GO TO 95
75 A=(H4B(I)+H4B(I))/2.
B=(H4B(I)-H4B(I))/2.
DT=TLB(I)-THB(I)
TUB(I)=-PHI(H,A,B)*DT/PI+(THB(I)+DT/2.)
GO TO 80

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55   TCB(I)=-5.
      TUB(I)=-5.
      IF(TLB(I).GT.0.0) GO TO 30
      TCC(I)=-5.
      TUC(I)=-5.
      GO TO 95
80   IF(H4A(I+1).LT.H) GO TO 35
      A=(H4A(I+1)+HLB(I))/2.
      B=(H4A(I+1)-HLB(I))/2.
      DT=T4A(I+1)+(24.-TLB(I))
      TCC(I)=(PHI(H,A,B)/PI)*DT+(TLB(I)+DT/2.)
      IF(TCC(I).LT.24.) GO TO 90
      TCC(I)=-5.
      TUC(I)=-5.
      GO TO 95
90   TUC(I)=24.
      GO TO 95
85   TCC(I)=-5.
      TUC(I)=-5.
      GO TO 95
C    NO SECOND LO TIDE:
65   IF(HLA(I+1).GT.H) GO TO 70
      A=(HHB(I)+HLA(I+1))/2.
      B=(HHB(I)-HLA(I+1))/2.
      DT=TLA(I+1)+(24.-THB(I))
      TUB(I)=-PHI(H,A,B)*DT/PI+(THB(I)+DT/2.)
      IF(TUB(I).GT.24.) TUB(I)=24.
      TCC(I)=-5.
      TUC(I)=-5.
      GO TO 95
70   TUB(I)=24.
      TCC(I)=-5.
      TUC(I)=-5.
95   CONTINUE
      GO TO 250
C    STATEMENTS 100 TO 250 = FIRST LO BEFORE FIRST HI

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100 IF(HLA(I).LT.H) GO TO 105
    TCA(I)=0.0
    TUA(I)=-5.
    TCB(I)=-5.
    GO TO 133
105 CONTINUE
    IF(HHB(I-1).LT.H) GO TO 107
    A=(HHB(I-1)+HLA(I))/2.
    B=(HHB(I-1)-HLA(I))/2.
    DT=TLA(I)+(24.-THB(I-1))
    XT=-PHI(H,A,B)*DT/PI+(THB(I-1)+DT/2.)
    TUA(I)=XT-24.
    IF(TUA(I)-0.0) 107,107,108
107 TCA(I)=-5.
    TUA(I)=-5.
    GO TO 109
108 TCA(I)=0.0
109 IF(HHA(I).LT.H) GO TO 110
    A=(HHA(I)+HLA(I))/2.
    B=(HHA(I)-HLA(I))/2.
    DT=THA(I)-TLA(I)
    TCB(I)=(PHI(H,A,B)/PI)*DT+(TLA(I)+DT/2.)
138 IF(HLB(I).GT.H) GO TO 115
    A=(HHA(I)+HLB(I))/2.
    B=(HHA(I)-HLB(I))/2.
    DT=TLB(I)-THA(I)
    TUB(I)=-PHI(H,A,B)*DT/PI+(THA(I)+DT/2.)
    GO TO 130
110 TCB(I)=-5.
    TUB(I)=-5.
130 IF(THB(I).LT.0.0) GO TO 150
C SECOND HI TIDE PRESENT:
    IF(HHB(I).LT.H) GO TO 135
    A=(HHB(I)+HLB(I))/2.
    B=(HHB(I)-HLB(I))/2.
    DT=THB(I)-TLB(I)

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TCC(I)=(PHI(H,A,B)/PI)*DT+(TLB(I)+DT/2.)
GO TO 14J
115  TUR(I)=-5.
      TCC(I)=-5.
      IF(THB(I).GT.0.0)GO TO 140
      TUC(I)=24.
      GO TO 25J
140  IF(HLA(I+1).GT.H)GO TO 145
      A=(HLB(I)+HLA(I+1))/2.
      B=(HLB(I)-HLA(I+1))/2.
      DT=TLA(I+1)+(24.-THB(I))
      TUC(I)=-PHI(H,A,B)*DT/PI+(THB(I)+DT/2.)
      IF(TUC(I).GT.24.)TUC(I)=24.
      GO TO 250
145  TUC(I)=24.
      GO TO 250
135  TCC(I)=-5.
      TUC(I)=-5.
      GO TO 250
C    NO SECOND LO TIDE PRESENT:
150  IF(HHA(I+1).LT.H)GO TO 151
      A=(HHA(I+1)+HLB(I))/2.
      B=(HHA(I+1)-HLB(I))/2.
      DT=THA(I+1)+(24.-TLB(I))
      TCC(I)=(PHI(H,A,B)/PI)*DT+(TLB(I)+DT/2.)
      IF(TCC(I)-24.)16J,151,151
151  TCC(I)=-5.
      TUC(I)=-5.
      GO TO 250
160  TUC(I)=24.
250  CONTINUE
      PER(I)=((TUA(I)-TCA(I))+(TUB(I)-TCB(I))+(TUC(I)-TCC(I)))/.24
      XCA=TCA(I)
      XUA=TUA(I)
      XCB=TCB(I)
      XUB=TUB(I)

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XCC=TCC(I)
XUC=TUC(I)
IF(XCA.EQ.-5.0)GO TO 255
IF(XCA.LT.6.0)XCA=6.0
255 IF(XJA.EQ.-5.0)GO TO 260
IF(XJA.LT.6.0)XJA=6.0
260 IF(XCB.EQ.-5.0)GO TO 265
IF(XCB.LT.6.0)XCB=6.0
265 IF(XJB.EQ.-5.0)GO TO 270
IF(XJB.LT.6.0)XJB=6.0
270 IF(XCB.GT.13.0)XCB=13.0
IF(XJB.GT.13.0)XJB=13.0
IF(XCC.GT.13.0)XCC=13.0
IF(XJC.GT.13.0)XJC=13.0
RPER(I)=((XUA-XCA)+(XUB-XCB)+(XUC-XCC))/.12
CONTINUE
C INTEGRATED AIR-WATER CURVES
IF(PER(I).NE.0.0)GO TO 1050
T1A=0.0
T2A=TMIN(I)
T3A=0.0
T4A=0.0
T1B=TMIN(I)
T2B=12.
T3B=0.0
T4B=0.0
T1C=12.
T2C=24.
T3C=0.0
T4C=0.0
GO TO 1400
1050 IF(PER(I).NE.100.0)GO TO 1100
T1A=0.0
T2A=0.0
T3A=0.0
T4A=0.0

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T18=J.J
T28=J.J
T38=J.J
T48=J.J
T10=J.J
T20=J.J
T30=J.J
T40=J.J
GO TO 1400
1100 CONTINUE
C EARLY MORNING
T1A=J.J
IF(TCA(I).GE.TMIN(I))GO TO 1110
IF(TCA(I).NE.-5.)GO TO 1130
T2A=TCB(I)
1125 IF(TUB(I).GE.TMIN(I).OR.TUB(I).EQ.-5.)GO TO 1180
T3A=TUB(I)
T4A=TMIN(I)
GO TO 1200
1110 T2A=TMIN(I)
GO TO 1180
1130 IF(TCA(I).NE.0.0)GO TO 1160
IF(TJA(I).EQ.-5.) GO TO 1133
IF(TJA(I).LT.TMIN(I)) GO TO 1140
1133 CONTINUE
IF(TUB(I).GE.TMIN(I)) GO TO 1135
T1A=TUB(I)
T2A=TMIN(I)
GO TO 1180
1135 T2A=J.J
GO TO 1180
1140 T1A=TJA(I)
IF(TCB(I).GE.TMIN(I))GO TO 1150
T2A=TCB(I)
GO TO 1125
1150 T2A=TMIN(I)

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GO TO 1180
1160 T2A=TCA(I)
IF(TJA(I).GT.TMIN(I))GO TO 1180
T3A=TJA(I)
IF(TCB(I).GE.TMIN(I))T4A=TMIN(I)
IF(TCB(I).LT.TMIN(I))T4A=TCB(I)
GO TO 1200
1180 T3A=0.0
T4A=0.0
1200 CONTINUE
C LATE MORNING
IF(TJA(I).GT.TMIN(I))GO TO 1210
IF(TJA(I).EQ.TCA(I))GO TO 1230
IF(TJA(I).EQ.-5.)GO TO 1220
IF(TJA(I).LT.TMIN(I)) GO TO 1230
1210 IF(TCA(I).GT.TMIN(I))GO TO 1215
IF(TUA(I).GE.12.0)GO TO 1225
T1B=TUA(I)
IF(TCB(I).EQ.-5.0.OR.TCB(I).GE.12.0)GO TO 1218
IF(TUB(I).GE.12.0)GO TO 1219
T2B=TCB(I)
T3B=TUB(I)
T4B=12.0
GO TO 1300
1218 T2B=12.
GO TO 1240
1215 T1B=TMIN(I)
T2B=TCA(I)
IF(TUA(I).GE.12.0)GO TO 1240
T3B=TUA(I)
T4B=12.
GO TO 1300
1219 T2B=TCB(I)
GO TO 1240
1220 IF(TUB(I).GE.12.0.OR.TUB(I).LE.TMIN(I))GO TO 1225
T1B=TUB(I)

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T2B=12.
GO TO 1240
1225 T1B=1.0
T2B=1.0
GO TO 1240
1230 CONTINUE
IF(TC2(I).EQ.-5.) GO TO 1235
IF(TC3(I).LE.TMIN(I))GO TO 1220
IF(TC3(I).GE.12.0.OR.TC3(I).EQ.-5.)GO TO 1235
T1B=TMIN(I)
T2B=TCB(I)
IF(TUB(I).GE.12.0.OR.TUB(I).EQ.-5.)GO TO 1240
T3B=TUB(I)
T4B=12.
GO TO 1300
1235 T1B=TMIN(I)
T2B=12.
GO TO 1240
1240 T3B=1.0
T4B=1.0
1300 CONTINUE
C AFTERNOON AND EVENING
IF(TUB(I).NE.24.)GO TO 1320
1305 IF(TC3(I).GT.12.)GO TO 1315
T1C=1.0
T2C=1.0
GO TO 1395
1315 T1C=12.
T2C=TCB(I)
GO TO 1395
1320 IF(TJC(I).NE.24.)GO TO 1350
IF(TJ3(I).NE.TCC(I))GO TO 1325
GO TO 1305
1325 IF(TC3(I).NE.TUB(I))GO TO 1330
T1C=12.
T2C=TCC(I)

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```

GO TO 1395
1330 IF(TCB(I).GT.12.)GO TO 1340
IF(TUB(I).GE.12.) T1C=TUB(I)
IF(TUB(I).LT.12.) T1C=12.
T2C=TCC(I)
GO TO 1395
1340 T1C=12.
T2C=TCB(I)
T3C=TUB(I)
T4C=TCC(I)
GO TO 1400
1350 IF(TUC(I).NE.-5.)GO TO 1370
IF(TCB(I).GT.12.)GO TO 1360
IF(TUB(I).GE.12.) T1C=TUB(I)
IF(TUB(I).LT.12.0) T1C=12.0
T2C=24.
GO TO 1395
1360 T1C=12.
T3C=TUB(I)
T4C=24.
GO TO 1400
1370 IF(TUB(I).NE.TCC(I))GO TO 1375
T1C=0.0
T2C=0.0
GO TO 1390
1375 IF(TCB(I).NE.TUB(I))GO TO 1380
T1C=12.0
T2C=TCC(I)
GO TO 1390
1380 CONTINUE
IF(TUB(I).GE.12.) T1C=TUB(I)
IF(TUB(I).LT.12.) T1C=12.
T2C=TCC(I)
1390 T3C=TUC(I)
T4C=24.0
GO TO 1400

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```

1395 T3C=.0
      T4C=.0
1400 CONTINUE
C     EARLY MORNING
      A=(D1AX(I-1)+DMIN(I))/2.
      B=(D1AX(I-1)-DMIN(I))/2.
      DT=12.+TMIN(I)
      EA(I)=A*(T2A-T1A)+B*DT/PI*(COS(PI/DT*(T2A+(12.-DT/2.)))
1-COS(PI/DT*(T1A+(12.-DT/2.))))
      EB(I)=A*(T4A-T3A)+B*DT/PI*(COS(PI/DT*(T4A+(12.-DT/2.)))
1-COS(PI/DT*(T3A+(12.-DT/2.))))
C     LATE MORNING
      A=(D1AX(I)+DMIN(I))/2.
      B=(D1AX(I)-DMIN(I))/2.
      DT=12.-TMIN(I)
      EC(I)=A*(T2B-T1B)-B*DT/PI*(COS(PI/DT*(T2B-(TMIN(I)+
1DT/2.)))-COS(PI/DT*(T1B-(TMIN(I)+DT/2.))))
      ED(I)=A*(T4B-T3B)-B*DT/PI*(COS(PI/DT*(T4B-(TMIN(I)+
1DT/2.)))-COS(PI/DT*(T3B-(TMIN(I)+DT/2.))))
C     AFTERNOON AND EVENING
      A=(D1AX(I)+DMIN(I+1))/2.
      B=(D1AX(I)-DMIN(I+1))/2.
      DT=12.+TMIN(I+1)
      EE(I)=A*(T2C-T1C)+B*DT/PI*(COS(PI/DT*(T2C-(12.+DT/2.)))
1-COS(PI/DT*(T1C-(12.+DT/2.))))
      EF(I)=A*(T4C-T3C)+B*DT/PI*(COS(PI/DT*(T4C-(12.+DT/2.)))
1-COS(PI/DT*(T3C-(12.+DT/2.))))
      TEMP(I)=(EA(I)+EB(I)+EC(I)+ED(I)+EE(I)+EF(I)+

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1PER(I)*.24*DN(I))/24.
  J=I-1
  WRITE(10,4)J,TCA(I),TUA(I),TCB(I),TUB(I),TCC(I),TUC(I),PER(I),
1RPER(I),EA(I),EB(I),EC(I),ED(I),EE(I),EF(I),TEMP(I)
  WRITE(10,13)T1A,T2A,T3A,T4A,T1B,
1T2B,T3B,T4B,T1C,T2C,T3C,T4C
13  FORMAT(3(/10X,4F7.2)//)
1600 CONTINUE
    STOP
    END

FUNCTION PHI(H,A,B)
ANG=(((H-A)/B)/SQRT((1.-((H-A)/B)**2)))
PHI=ATAN(ANG)
RETURN
END

```

APPENDIX VII

Percent Wing Darkness in Field Collections June 1970 to December 1971

June 18	July 1	July 7	Aug 2	Aug 18	Sept 2	Oct 3	Oct 17	Nov 8
43.50	48.15	48.16	45.28	33.89	45.29	57.00	52.92	63.04
67.30	54.22	36.21	56.83	27.49	38.75	62.93	60.59	60.37
52.58	39.19	40.19	42.97	46.21	50.62	56.64	58.35	56.58
56.69	32.08	61.56	54.54	43.25	48.62	66.82	59.80	54.45
41.99	37.95	37.66	51.84	43.62	44.44	58.82	56.21	85.46
52.27	59.97	39.08	31.30	35.15	46.11	89.65	45.75	63.68
58.13	55.17	47.53	38.65	57.15	48.07	48.71	57.33	73.03
34.45	40.06	39.01	43.19	43.73	46.26	57.08	64.30	67.19
36.08	50.21	41.39	55.09	38.46	46.89	52.96	52.93	54.47
53.83	52.24	34.76	42.72	54.37	38.35	55.22	61.23	61.57
53.74	48.27	40.70	55.79	37.30	47.46	63.96	72.04	84.25
49.86	56.19	56.92	35.02	45.16	44.88	53.06	49.52	59.21
43.18	47.86	60.57	56.70	49.74	43.73	53.31	63.01	82.16
55.41	55.00	42.51	40.65	45.27	47.70	59.76	62.21	66.82
46.24	66.31	41.20	49.65	47.15	51.78	63.95	54.44	74.54
59.14	47.42	45.53	50.38	52.88	38.84	54.68	54.45	57.98
54.15	47.56	36.62	57.31	51.08	54.31	51.16	56.68	61.70
45.78	44.96	55.01	46.72	55.69	41.81	53.78	54.13	55.47
56.64	42.07	47.47	44.14	45.50	44.98	44.42	59.57	59.84
57.00	66.55	49.00	57.34	52.61	49.67	40.82	50.60	88.29
50.60		50.09		31.53			55.49	38.32
35.50		38.36		44.73			58.90	68.70
49.72		41.59		54.80			51.22	66.90
55.94		46.25		43.02			51.26	70.24

Appendix VII (Cont.)

	June 18	July 1	July 7	Aug 2	Aug 18	Sept 2	Oct 3	Oct 17	Nov 8
	56.72		31.36		48.99			53.87	73.62
	56.95		45.42		41.77			59.68	63.24
	51.92		47.29		48.51			57.82	88.11
	45.53		30.89		46.42			67.55	81.15
	52.59		36.11		52.09			58.73	58.02
	43.88		52.22		54.38			62.94	66.72
	50.85		56.58		44.60			69.26	61.15
	60.85		36.34		53.29			70.82	64.85
	65.74		50.78		44.89			60.14	70.74
	41.39		43.82		53.68			54.62	83.92
	47.43		43.89		51.12			84.36	65.90
	82.34		43.89		46.94			52.56	71.19
	44.58		54.88		52.98			51.99	59.31
	51.79		39.91		46.40			62.20	85.71
	53.15		46.69		50.32			52.38	
	53.19		38.23		55.55				
Mean	50.97	49.57	44.39	47.81	46.79	45.93	57.24	58.51	67.57
St. Dev.	7.46	9.01	7.61	7.92	6.97	4.26	9.98	7.29	11.23

Appendix VII (Cont.)

Dec 4	Jan 31	Feb 12	Feb 21	Mar 2	Mar 14	Mar 21	Mar 30	Apr 6	Apr 15	
57.31	64.75	30.84	44.58	32.75	43.71	43.24	34.01	62.14	47.89	
91.15	63.28	47.22	63.68	43.89	59.98	87.03	42.13	54.18	51.86	
74.31	73.89	71.50	59.01	48.16	53.44	55.46	59.01	48.15	48.18	
64.69	56.00	45.26	41.76	51.36	57.72	35.45	65.85	59.78	57.82	
91.36	64.15	58.41	35.90	47.75	52.09	51.44	45.85	61.11	62.96	
73.03	59.89	38.48	62.78	66.09	53.05	49.17	60.98	57.12	53.05	
49.88	45.99	49.00	44.40	45.43	54.90	49.81	49.93	45.98	45.15	
88.27	72.88	64.55	44.56	47.32	53.54	52.69	34.82	41.09	52.30	
84.40	70.02	62.87	54.18	48.88	39.66	45.91	49.03	40.83	48.73	
63.62	63.70	47.95	52.39	41.53	76.74	53.48	32.33	43.18	55.74	
	51.05	54.03	60.53	50.69	74.21	58.83	45.36	54.29	46.39	
	82.57	63.55	42.94	55.39	44.38	46.59	56.32	60.02	59.29	
	85.65	55.01	58.16	75.80	61.66	53.16	61.78	37.40	54.58	
	50.95	46.29	49.21	49.15	48.59	69.94	56.03	83.58	73.75	
	56.73	64.71	45.75	78.49	42.07	54.08	41.49	41.80	55.38	
	52.54	58.31	48.50	52.51	36.38	60.70	56.36	40.12	44.76	
	50.50	58.90	45.88	64.70	53.04	46.58	49.65	67.65	41.49	
	56.65	38.31	50.10	64.45	55.74	45.21	49.94	47.41	57.37	
	78.61	47.97	55.39	38.65	48.89	88.68	62.21	41.47	59.29	
	51.35	56.67	49.04	68.93	57.55	65.85	57.77	66.29	43.58	
Mean	73.80	62.56	52.99	50.44	53.60	53.40	55.66	50.54	52.68	53.00
St. Dev.	14.77	11.52	10.40	7.62	12.30	10.15	13.51	9.96	12.02	7.68

Appendix VII (Cont.)

Apr 27	May 4	May 11 Old	May 18 New	May 18 Old	May 24 New	May 24 Old	June 1 New	June 1 Old	June 8 New	June 8 Old
66.25	63.34	59.67	47.39	34.55	64.64	49.67	61.29	32.02	60.29	45.91
49.46	45.38	43.61	53.72	47.13	64.36	56.67	62.76	51.04	51.19	54.98
50.26	40.98	46.64		56.39	52.46	48.77	49.87	53.43	55.89	49.24
49.56	56.53	46.92		43.31	58.68	55.25	63.87	46.36	46.16	58.78
59.68	45.17	50.88		42.82	51.51	47.67	50.77	52.54	63.37	52.80
44.37	54.67	47.42		59.40	55.69	46.52	62.96	40.39	76.69	53.97
51.24	44.56	55.42		61.86	59.89	54.45	66.09	35.14	55.90	52.25
61.57	57.20	54.01		45.59	54.06	46.84	54.08	43.54	49.31	
46.76	45.07	49.40		62.11	55.71	61.29	57.54	54.15	67.56	
77.72	63.30	49.36		46.69	55.66	65.60	47.00	47.72	53.65	
63.30	48.09	73.41		42.82	58.73	55.06	53.84	46.14	77.81	
69.53	47.71	47.53		57.41	57.23	41.88	51.80		59.41	
41.16	48.11	56.51		46.83	56.32	50.21	56.68		60.15	
38.69	55.30	59.32		54.04	53.73	43.09	35.52		68.85	
66.27	67.60	47.46		48.85	53.60	59.19	50.00		60.93	
49.88	45.35	48.50		48.32	57.35	54.10	58.38		64.80	
54.79	50.70	65.05		40.55	52.16	56.53	58.35		52.35	
61.97	59.22	60.18		50.32	51.54	52.79	65.55		62.02	
39.41	38.73	66.41		70.55	61.15	43.17	58.38		70.89	
44.29	55.28	56.80		43.92	51.99	41.01	68.18		69.47	
Mean										
54.31	51.66	53.77	50.55	50.16	56.32	51.99	56.64	45.68	61.33	52.56
St. Dev.										
10.94	7.95	7.51	4.48	8.81	3.98	6.29	7.83	7.37	8.76	4.12

Appendix VII (Cont.)

June 15		June	June	July	July	July	July	July	Aug
New	Old	22	28	6	13	20	25	29	6
49.51	49.08	63.53	51.83	60.54	49.00	44.34	51.13	48.09	48.25
64.46	55.82	67.54	46.00	59.90	57.07	40.63	36.75	49.31	42.72
48.03		62.56	73.16	57.13	45.75	47.42	36.28	32.07	48.42
55.53		67.91	58.16	51.29	64.10	51.19	54.43	29.76	36.02
55.79		57.58	52.69	50.04	34.44	41.93	26.35	51.84	55.58
55.70		51.62	60.28	56.07	45.90	31.36	65.79	42.94	39.76
55.06		42.31	65.63	68.54	53.33	36.71	31.24	33.52	57.85
56.49		50.47	49.39	48.21	40.27	51.61	41.61	32.58	57.70
60.16		60.77	45.23	41.44	62.14	43.50	17.12	33.41	38.70
42.60		53.57	47.65	58.40	37.75	33.84	35.31	38.08	55.77
56.65		60.53	62.16	47.25	63.03	48.62	47.59	64.88	43.84
88.53		62.96	43.03	68.54	55.32	54.63	53.90	46.38	58.43
51.05		68.21	53.68	69.39	49.34	53.85	54.92	43.45	58.86
58.04		55.74	53.96	47.48	42.40	29.76	40.69	46.62	34.66
59.19		36.57	62.37	59.55	51.89	57.61	49.56	36.47	44.32
42.54		65.20	51.90	65.52	54.18	81.91	55.87	39.50	54.79
58.85		66.38	49.88	57.71	47.37	35.73	41.39	49.99	41.55
52.43		71.28	68.05	39.02	62.28	38.50	59.93	46.09	50.12
60.08		48.01	41.88	57.28	50.63	49.83	46.82	49.67	59.01
62.21		81.91	64.13	49.34	54.71	39.43	42.09	55.94	47.83
Mean									
56.64	52.45	59.73	55.10	55.63	51.04	45.63	44.44	43.53	48.21
St. Dev.									
9.52	4.77	10.57	8.84	8.75	8.48	11.71	11.93	9.11	7.91

Appendix VII (Cont.)

	Aug 13	Aug 21	Aug 27	Sept 4	Sept 12	Sept 20	Sept 28	Oct 7	Oct 14
	38.87	39.12	51.27	39.26	47.87	58.24	39.27	57.01	60.93
	51.79	40.51	42.60	44.97	44.35	33.67	55.37	77.58	58.05
	41.79	34.53	47.11	55.17	49.43	52.48	50.76	50.89	50.94
	34.73	47.95	33.14	53.16	31.88	54.76	32.38	56.37	51.10
	35.30	45.55	41.30	45.06	48.71	53.71	50.34	53.06	72.12
	50.57	31.29	36.57	43.96	55.88	49.40	37.61	48.43	47.94
	40.43	51.04	35.15	37.65	51.32	47.44	46.78	51.71	68.15
	44.80	31.35	52.29	40.89	47.89	63.75	50.80	50.43	54.00
	36.40	44.07	42.04	44.01	55.27	36.51	44.30	48.91	46.90
	54.70	52.46	45.19	19.48	52.13	45.84	52.56	52.28	58.85
	50.09	47.40	40.92	47.12	44.43	38.98	56.98	41.92	71.17
	51.53	54.05	50.22	60.12	48.76	46.55	55.22	52.33	53.16
	54.65	57.91	45.44	51.08	50.66	51.54	53.14	64.00	52.12
	55.05	59.83	53.68	43.06	54.71	57.86	53.89	38.95	60.94
	66.89	57.06	44.56	52.47	51.21	53.51	43.69	64.76	76.19
	45.20	54.68	53.08	45.63	45.30	48.54	56.55	47.56	53.59
	42.86	37.82	52.64	45.91	62.43	47.16	52.26	61.59	57.91
	43.46	49.63	54.89	53.33	22.61	61.74	53.91	47.10	33.51
	50.63	53.39	36.02	54.23	68.25	69.01	54.89	46.22	54.26
	42.57	47.09	45.23	52.59	51.99	61.58	47.84	62.64	64.78
Mean	46.62	46.84	45.17	46.46	49.25	51.61	49.43	53.69	57.33
St. Dev.	8.10	8.69	6.71	8.67	9.59	9.10	6.82	8.97	9.97

## Appendix VII (Cont.)

	Oct 22	Oct 28	Nov 6	Nov 13	Nov 18	Dec 7
	52.01	63.82	65.37	89.85	45.93	63.32
	70.66	56.20	58.69	58.14	62.34	75.83
	63.56	44.76	65.37	56.99	69.26	52.76
	55.42	70.78	62.89	56.07	62.87	50.36
	66.65	71.97	64.02	65.81	59.66	77.98
	53.78	53.02	49.71	68.75	75.60	
	49.34	58.41	67.02	75.89	51.60	
	77.22	66.05	56.88		87.51	
	63.59	86.98	64.78		72.11	
	64.89	67.98	69.40		75.29	
	76.46	59.48	68.77		62.94	
	66.56	68.34	57.84		74.89	
	76.22	74.63	65.60		66.58	
	69.62	65.99	83.93		82.46	
	58.19	71.76	76.94		86.30	
	53.34	70.21	64.80		77.83	
	61.82	67.55	79.46		67.19	
	64.29	68.20	60.78		56.95	
	57.06	57.99	67.20		63.02	
	63.75	73.68	62.53			
Mean	63.22	65.89	65.60	67.36	68.49	64.05
St. Dev.	8.26	9.13	7.83	12.27	11.17	12.73