

MOSQUITO BREEDING IN ALASKAN SALT MARSHES, WITH ESPECIAL REFERENCE TO *AÈDES PUNCTODES* DYAR

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In subarctic and temperate Alaska, settlements, salt marshes, and mosquitoes tend to occur wherever there is flat land at sea level. The mosquitoes, so far as known, are chiefly species of *Aedes* which breed in fresh water also. What the significance of these saline waters for mosquito control may be is a matter of uncertainty. In fact, few observations of mosquito larvae in subarctic salt marshes are recorded. Jenkins (1948) and Dr. Alan Stone (unpublished) of the Alaska Insect Project report *Aedes punctor*, *communis* and *flavescens* larvae in waters brackish to the taste. The former two species, they note, have shortened gills in the saline habitats, and among the full-grown "*punctor*" larvae, atypical open anal saddles are frequent. In temperate Scandinavia, Natvig (1948) reports *Aedes communis* from water of about 0.07% NaCl content. In North German coastal pools, *Aedes excrucians* is known to tolerate slightly brackish conditions (Martini, cited in Natvig, 1948).

The present preliminary study, reporting observations made during three seasons in two sharply different zoogeographical regions of Alaska lying about a thousand miles apart, indicates that a single species, *Aedes punctodes* Dyar, is the predominant mosquito larva of the salt-marsh habitats of both regions. The study provides a preliminary list of the other brackish species, and describes some typical larval habitats of these mosquitoes with reference to salinity and vegetation. Salinity tolerance of two of the principal larvae indicated by the field survey was checked experimentally in the laboratory. Unfortunately, identification of an Alaskan salt-marsh mosquito problem with *Aedes punctodes*, a rather distinct member of the perplexing *punctor* complex, does not make biological data available to the practical man. Knight

(1951) in proposing recognition of *punctodes* Dyar states that "no specific notes are available on its biology." Thus this paper introduces the larval ecology of *Aedes punctodes*.

PROCEDURE. Mosquito larvae, larger plants, periphyton, and salinity samples were collected at weekly intervals during May and June 1950, in 23 breeding areas of the Upper Cook Inlet marshes. The areas were selected and provisionally classified according to dominant larger plants. The beds of these plants corresponded, in general, to a certain salinity range though zonation was sometimes indefinite. The temperature of the surface water and the air, pH, color, and turbidity were recorded routinely. Occasional notes recorded the extent of the highest tides, changing light (shade) conditions, invasions of fish predators, etc. Salinities and larvae were determined in the laboratory. Experiments on larval salinity tolerance using mixtures of fresh and sea water proved impractical in natural pothole habitats. Therefore similar experiments were carried out in stender dishes in the laboratory. Salinities were determined to within about one part per hundred thousand by duplicate titrations with a standard solution of silver nitrate for chlorides, the end-point being indicated colorimetrically by potassium dichromate solution. The results have been expressed as parts per hundred thousand (ppht.) of chlorine so that even the lowest salinities are whole numbers. The computation of salinity, as defined by oceanographers, and the corresponding percentage of sea water can be made from these data (Muirhead-Thomson, 1951, p. 182), but the calculations with long decimals are tedious and the benefits dubious to mosquito workers.

Identification of larvae of the *punctor*

complex is subject to a certain error pointed out by Knight (1951) whose key was used for separating *punctor* and *punctodes*. He says: "an occasional *punctor* larva is found in the Fairbanks-Anchorage area which intergrades with the larvae of *punctodes*." Since about 90% of the larvae identified in this study belonged to these two forms or species, it is regrettable that there has not yet been sufficient time for the rearing in isolation of series of the two from the different types of salt-marsh habitats, for in this way the percentage of each species could be determined more accurately by habitat. However, since *punctor* predominated in the fresher habitats, *punctodes* in the more salt, and because specimens studied by Knight included associated larval exuviae and male genitalia from some of the marshes of this study, it was possible to make valid general conclusions from larval identifications.

SALT MARSHES AND LARVAL HABITATS. The ecological differences between these Alaskan salt marshes and those of warmer coasts are obviously considerable. In the Cook Inlet marshes, the larger plants—those excellent visible indicators of invisible salinity, tidal, and other differences—are dominated by a relatively small number of ubiquitous, tolerant species which presumably reflect the rigorous selection exercised by low temperatures as well as salt. The same may be said for the mosquitoes whose larval habitats are conveniently named after the weed beds where they are found. There are, nonetheless, in addition to the tolerant, primarily fresh-water plants which are adapted to withstand lower salinities, some true halophytes such as *Salicornia herbacea* L. But these salt plants are few and inconspicuous, and with reference even to the strictly coastal succulents, e.g., *Chrysanthemum arcticum* L., a beautiful daisy, they seem to represent northern as much as saline forms. And all of the mosquitoes, so far as known, belong to fresh-water species which are either quite resistant to salt, or, in the relatively few thousands of years since the glaciers retreated from the water front, have acquired a tolerance for salinity, pos-

sibly only in parts of their vast northern ranges. Farther south along the coasts of Washington and Oregon only *Aedes dorsalis* breeds in salt marshes (Stage *et al.*, 1952). Absence of competitive, obligatory salt-marsh mosquitoes may have been a factor which favored their invasion of salt marshes.

In the regions studied, the titrations proved that five more or less conspicuous vegetation zones are correlated with certain salinity ranges. The larval identifications further proved that the mosquito habitats within each zone differed consistently from those of other zones and that stations of the same habitat type harbored similar assemblages of larvae in the different marshes. This is the basis for the classification given, while the reason for its usefulness is the ease with which anyone may use it. Unfortunately, nevertheless, the types of habitat are composite. Preliminary study of the microbiotas, especially algae which include indicator organisms more sensitive than the larger plants or mosquitoes, show that the *Carex* and *Myrica* types should be subdivided. These three types support different microbiotas to a degree which is not permissible for mosquito habitats of the same type. At this early stage of the study and for the use of mosquito workers who must make field surveys with the naked eye rather than the compound microscope the simpler, though imperfect, preliminary classification which follows is preferable:

TYPES OF BRACKISH MOSQUITO HABITATS OF THE UPPER COOK INLET: (1) *Triglochin* Type: Salinity, Range, 330.5-844.4, Average 631.4; Dominant Plant, *Triglochin maritima* L.; pH, Range, 6.5-8.6, Average, 7.46; Water Color, none to brown; Light Condition, open; Surface Temperature, warm, Index,* 14.4 degrees C.; Other Conspicuous or Abundant Plants, *Plantago maritima* L. *juncooides* (Lam.) Hult., *Potentilla Anserina* L., *Scirpus validus* Vahl., *Glaux maritima* L., *Salicornia herbacea* L.

(2) Brackish *Carex* Type: Salinity, Range, 192-700.4, Average, 397.4; Domi-

* Averages, June 5-8.

nant Plant, *Carex lyngbyei* Hornem.; pH, Range, 5.8-8.1, Average, 6.75; Water Color, none-straw; Light Condition, partly shaded; Surface Temperature, medium, Index, 11.8 degrees C.; Other Plants, *Potentilla Anserina*, *Eleocharis kamschatica* (C.A. Mey.) Kom., *Chrysanthemum arcticum* L., *Plantago maritima juncoides*, *Triglochin maritima*, *Iris setosa* Pall., *Scirpus validus*.

(3) Fresh-water *Carex* Type: Salinity, Range, 5.1-91.9, Average 45.4; Dominant Plant, *Carex lyngbyei*; pH, Range, 6.3-7.0, Average, 6.62; Water Color, none-pale brown; Light Condition, partly shaded; Surface Temperature, medium, Index, 13.3 degrees C.; Other Plants, *Myrica Gale* L., *Scirpus validus*, *Potamogeton filiformis* Pers., *Potentilla Anserina*, *Salix* prob. *nana*, *Rumex fenestratus* Greene.

(4) *Myrica* Type: Salinity, Range, 8.0-57.5, Average, 30.9; Dominant Plant, *Myrica Gale*; pH Range, 6.2-7.0, Average 6.62; Water Color, none-brown; Light Condition, shaded; Surface Temperature, cold, Index, 8.2 degrees C.; Other Plants, *Calamagrostis canadensis* (Michx.) Beauv., *Iris setosa*, *Salix* prob. *nana*, *Rumex fenestratus*.

(5) Seepage Type: Salinity, Range, 23.5-65, Average, 38.6; Dominant Plant, uncertain, varies, *Caltha palustris asarifolia* (DC) Hult.; pH, Range, 6.8-7.6, Average, 7.05; Water Color, straw; Light Condition, open; Surface Temperature, warm, Index, 15 degrees C.; Other Plants, *Equisetum arvense* L., *Rumex fenestratus*, *Iris setosa*, *Dodecatheon macrocarpum* (Gray) Knuth.

MOSQUITOES. General. Twelve, or about half of all the species of mosquitoes known to occur in Alaska, were found breeding in Upper Cook Inlet saline marshes, viz.: *Aedes punctodes*, *punctor*, *hexodontus*, *impiger*, *communis*, *excrucians*, *pionips*, *flavescens*, *cinereus*, *Culiseta impatiens*, *alaskaensis*, and *morsitans*. The first two are of overwhelmingly greater importance than the others, however, and as a result of their abundance the data for these two are especially instructive. For instance, their distribution with reference to types

of habitats in the salt marshes is illustrated by analysis of 55 collections of large larvae. In the collections from the most saline waters (*Triglochin* Type), *punctodes* predominated; in those from the freshest waters (*Myrica* Type), *punctor* predominated; and in the intermediate salinities, intermediate mixtures of the two species occurred. The breakdown by percentages of these collections with (1) *punctodes* numerically dominant, (2) the two species about equally numerous and (3) *punctor* most numerous, by habitat type follows:

- (A) *Triglochin* Type—91% *punctodes*, 9% subequal, 0% *punctor*; and note that 90% of the predominant *punctodes* class had no *punctor* larvae.
- (B) Brackish *Carex* Type—76% *punctodes*, 12% subequal, 12% *punctor*;
- (C) Fresh *Carex* Type—46% *punctodes*, 16% subequal, 38% *punctor*;
- (D) *Myrica* Type—26% *punctodes*, 21% subequal, 53% *punctor*; and note that 41% of the *punctor* class had no *punctodes*, although most of these same stations yielded *punctodes* on other dates.

The other ten species of mosquitoes differ obviously in both larval salinity tolerance and in practical importance (adult abundance); but more data are needed to rule out variables affecting both. Yet it is reasonable to propose tentatively that four other *Aedes*, viz. *impiger*, *excrucians*, *flavescens*, and *communis* are the species of secondary importance in both regards. *Impiger* and *communis* are apparently less salt-tolerant, but they occur more frequently than the other two, especially in *Myrica* potholes. *Excrucians* and *flavescens* seem to be definitely salt-tolerant (both occurring in 500-800 ppht.), but they were relatively less common.

Reduction of gills. As appears to be universally true for salt-marsh mosquitoes, on the whole the Alaskan saline larvae have smaller gills than fresh-water species. (How this relates to a water-regulatory function need not concern us here.) It is

especially noteworthy that these particular northern species which "spill over" from fresh-water habitats are also invariably provided with relatively smaller gills in the brackish habitats than is characteristic of them in fresh water. The phenomenon of gill reduction relates similarly to all four instars, and individual variation in gill size for a species at a time and place is usually quite limited. There is also a considerable degree of correlation of gill reduction with salinity increase across a typical salt marsh within a single species. Thus the gill ratios—length of gill/length of dorsal saddle—of 4th instar *punctodes* from *Myrica* Type stations with a mean salinity of 30.9 average 1/1, while the comparable figure for *Triglochin* Type stations with a mean salinity of 631.4 is only about 6/10. The average ratio for the huge *punctodes* population on Mendenhall Flats, 5/10, probably represents the most characteristic size for the species in coastal waters. Thus the average reduction of gills is not nearly as great as for *Aedes sollicitans* and *detritus* of North Atlantic salt marshes, which are both more restricted to salt habitats and presumably geologically older salt-marsh breeders. Finally, striking contrasts in gill development were noted in comparing bog larvae with the same species from salt marsh, e.g.: *communis* from bogs—25/10, from salt-marsh—3/10–15/10; *impiger* from bogs—28/10, from salt-marsh—5/10–14/10; *flavescens* from fresh water (Stage *et al.*, 1952)—20/10, from salt-marsh—2/10.

Notes on Species. *Aedes punctodes* Dyar. These larvae were as abundant as *punctor* on the Upper Cook Inlet marshes in the four principal habitat types *in toto*. *Punctodes*, however, is the only species which thrives in the most saline waters (1,000 ppht.). Myriads of the newly hatched larvae appeared about the last of April. A few old larvae were still present in August. The anal gills are blunt, relatively short; the ratio is quite variable, 2/5–1/1.

Aedes punctor (Kby.). These larvae characterize the fresher habitats and are,

so far as is known, about equal numerically to *punctodes* on the marsh as a whole, being relatively less common in saltier types of marshes, e.g. Mendenhall Flats, Southeastern Alaska. The earliest larvae appear about a week later than *punctodes* because of the earlier melting of pools in the open, salt *Triglochin* zone. Some larvae linger until August, acquiring coats of vorticellids, especially heavy on the gills. *Punctor* gills are more pointed, attenuate, and longer than *punctodes* in the same collection; the ratio is usually over 12/10, ranging from 5/10 to 15/10 in salt marshes.

Aedes hexodontus Dyar. This is a doubtful record from a single *Myrica* pothole.

Aedes impiger (Wlk.). The species was taken in all five habitat types but was common chiefly in *Myrica* potholes associated with *communis* and, of course, *punctor* and *punctodes*. Some eggs hatch even earlier than *punctor* (as first noted by Dr. Sailer of the Alaska Insect Project), and there are small larvae present from mid-April to July. The gills are variable, budlike to long; the ratio is from 3/10 to 13/10, averaging about 6/10.

Aedes communis (DeG.). Larvae were taken in all four major habitat types, but they occur especially in *Myrica* potholes. They were almost invariably associated with *impiger*, *punctor* and *punctodes*. Like *impiger*, *communis* eggs may hatch as early as mid-April in small melt holes in the ice. The anal gills are quite variable, short to long, usually attenuate; the ratio is 3/10 to 15/10, averaging about 13/10. In collections in which both occur, *communis* has much longer gills than *impiger*.

Aedes excrucians (Wlk.). The larvae are characteristic of the deeper water of Fresh and Brackish *Carex* Type marshes but also occurred in one *Triglochin* Type station with an average salinity of 830. The smallest (2d instar) larvae collected were taken from the middle of May to the end of June. The apex of the dorsal saddle is peculiar in these brackish *excrucians*

in possessing spinelike denticles. The gills vary greatly, from budlike to attenuate; the ratios range from 2/10 to 14/10, averaging about 1/1.

Aedes pionips Dyar. This common species of fresh water is evidently of no importance in salt marshes, being scarce in a single collection of the Fresh *Carex* Type and in one *Myrica* pothole in late May and early June. The gills are rather attenuate; the ratios are 11/10 (*Myrica*) and 9/10 (Fresh *Carex*).

Aedes flavescens (Müller). Although the adults occurred in large numbers on two of the study marshes, only a few *flavescens* larvae were dipped, always in Brackish *Carex* Type stations early in June. The gills are minute, budlike, almost globular; the average ratio was 2/10.

Aedes cinereus (Meigen). The unmistakable larvae of this species of the 2d instar were present in a single collection of the Brackish *Carex* Type. The gills are attenuated; the ratio was 11/10.

Culiseta impatiens (Wlk.). Fourth stage larvae were taken a total of only three times in Fresh and Brackish *Carex* Type stations, but the rafts and small larvae were not infrequently collected, though never in the *Triglochin* Type habitat. Perhaps this exceedingly common Alaskan fresh-water mosquito is at an early stage of developing resistance to salt.

Culiseta alaskaënsis (Ludl.). Like *impatiens*, this species is presumably only adventitious in saline waters. It was collected (1st-3d instars) in one Brackish and one Fresh *Carex* Type station associated with its congeners, *impatiens* and *morsitans*.

Culiseta morsitans (Theob.). The 4th instar of this species was not found in other saline waters than the exceptional *Carex* stations where a few *C. impatiens* and *alaskaënsis* were its associates. The striking circumstance that all three *Culiseta* developed to the 3d or 4th instar, so far as is known, only in the same two identical stations may be meaningful.

Salinity tests. The degree of salt tolerance of larval *Culiseta impatiens* and *alaskaënsis* was determined approximately in

the laboratory. Sibs from individual rafts of these easily reared mosquitoes were simply placed in graded salinities and survival after 96 hours was noted. In general the *impatiens* larvae failed to molt with the controls and all died in the four days in water more saline than 200. For *alaskaënsis* the same was true for salinities exceeding only 50. The field-collected *Aedes* larvae, however, were less satisfactory to work with, surviving well regardless of salinity, only sometimes in large pans. As a result the data were variable and inconsistent. The adaptation of mosquito larvae to increasing salinity discovered by Wigglesworth (1933) was not the important disturbing factor, however. For example, "unadapted" 4th instar *communis* larvae and pupae from interior Alaska were compared with similar coastal larvae and pupae. Both lots were collected in *Myrica* potholes, the former of fresh water, the latter having about 55 ppht. chlorine. Of the interior *communis*, 90% pupated and emerged in test salinities of 20 to 500. In fact the most saline vessel increased from about 500 to about 700 and yet 80% pupated and emerged from it. For coastal *communis* larvae, which seem to have been less robust, about 10% less pupated and emerged from the same salinities. The pupae from the two sources were similarly quite salt-resistant. From the interior, 90% emerged (80% in the most saline: 500), while for the coastal pupae 65% emerged. Thus regardless of previous experience large larvae and pupae of this species tolerated about 500. The salt tolerance of *punctodes* might be greater since that species occurs naturally in higher salinities. The *punctodes* tests were ten series of 240 larvae each, and different instars were studied as they became available on the Mendenhall Flats where *punctodes* occurred in nearly pure culture. Both tides and heavy rains there led to wide fluctuations of the salinities from which the experimental larvae were taken. Unfortunately the variable results are difficult to condense or generalize upon. An attempted summary follows:

- (1) 1st instar taken in 12 ppt., tested in high salinities only, gave:
- for 640 (after 96 hours)—40% (survival)
 - for 835—10%
 - 900—1,000—1%. These larvae were not fed.
- (2) 1st instar (same source), fed ground whole wheat bread, gave:
- 695—60%
 - 855—50%
 - 900—1,000—8½%. However, except for (a), these larvae did not molt with the low-salinity controls.
- (3) 1st instar larvae from a salt habitat, 530, fed as above:
- 135—500—90%
 - 605—40%
 - 625—70%
 - 760—60%
- These larvae seemed to show adaptation, but of 30 at 605—760 only 3 survived for 10 days.
- (4) Tests with 2d instar larvae were unsuccessful; the larvae died in controls and test salinities alike.
- (5) 3d instar taken in 180:
- 395—560—25%
 - 70—260—56%
- (6) 4th instar taken in 6 (after rains):
- 460—20%
 - 295—335—17½%
- Pupation and emergence were normal for only one class, the (b).
- (7) No other data on pupae than 6 (b) immediately above.

While these few and variable results scarcely permit general conclusions on the salt tolerance of *punctodes*, it is probably significant that there were almost invariably individual larvae, even of the delicate 2d instar, which survived 10—30 days in test salinities up to 1,000. This species is difficult to rear in small vessels. It is not improbable that the positive results (survival of a few) are more significant in relation to salt tolerance than the high mortalities. Viewed in this way the experiments do not appear completely at

variance with field data showing great numbers of *punctodes* larvae at 700—800. However, there was neither molting nor growth manifested by many of these long-term survivors, and they were usually noticeably less active than is normal. If *communis* be regarded as just as salt-tolerant as *punctodes* on the basis of these preliminary findings, then the females have not acquired the habit of ovipositing as far out on the marsh as *punctodes*.

NATURAL CONTROL. Natural control of mosquitoes by predaceous insects is negligible on these Alaskan salt marshes. *Carex* marshes, however, support consequential numbers of dytiscid beetles and their larvae after about mid-June, and the doughty predatory midge larvae of *Eucorethra underwoodi* Underwood and *Mochlonyx* sp. clear certain potholes of wigglers. In the main, however, insect predators are too few or too late to effect a noticeable reduction of *Aedes* larvae.

On the other hand, predation by fishes, which is of no practical significance in Alaskan fresh-water mosquito breeding, is of the greatest importance in some saline mosquito habitats. The northern sticklebacks, *Gasterosteus aculeatus* L., and to a very much lesser extent, *Pungitius pungitius* (L.), spawn in the *Triglochin* and Brackish *Carex* Type habitats, access being provided especially by tidal bores in the Upper Cook Inlet. These bores, occurring in connection with the 30—35 foot spring tides resemble small tidal waves 1—12 feet high. The salinity* of the new water is not excessive and there is no evidence of mosquito mortality in flooded pools. The fish and their fry, nevertheless, eliminate all wigglers from the depressions in which they spawn. This phenomenon is an annual one and it was observed not only in the Upper Cook Inlet in 1950 and 1951 but also on the Mendenhall Flats in 1952. In the latter location, the sticklebacks, all *G. aculeatus*, came in when peak numbers of larvae were in the 4th instar

* Cook Inlet water average salinities, 1950: May 12—940; May 23—1172; May 29—1220; June 5—1042; June 16—342; June 24—677. The summer freshening represents glacial melt.

and the voracity of the fish was dramatically demonstrated by the disappearance of mosquitoes in stickleback pools. The outer half, approximately, of the marsh was affected. In larviciding, care should be taken to insure proper timing by tide tables and perhaps by low dosages to spare these useful little fish.

PARASITES AND ATTACHED ORGANISMS. Coatings of vorticellids crowded especially on the gills have been mentioned for *Aedes punctor* larvae in *Myrica* potholes. These stalked peritrichs evidently belong to a single nonparasitic species characteristic of mosquito larvae in shaded, nearly fresh, saline habitats. A few instances were noted for larvae from the most dense *Carex* Type stations. Since Kudo warns that specific determination is very difficult in this group it must suffice to note a similarity to *Vorticella alba* Fromentel. The following *Aedes* larvae were hosts: *punctor*, *punctodes*, *communis*, *impiger*, and *pionips*. Another attached organism occurring on *Aedes punctor* and *flavescens* in a single collection is an asterisk-shaped water mold, apparently not parasitic. In fresh-water habitats somewhat above the high tidal limits (Southeastern Alaska) mermithid parasites, probably identical to the worms described by Stabler (1952) for other mosquito hosts, were locally common chiefly in the thoraces of large *Aedes* larvae: *impiger*, *cinereus*, *punctor*, *communis*. They were not found in any species in saline waters, however.

DISCUSSION. The data of this paper were selected as representative, so far as is known, of salt marsh mosquito breeding in the subarctic and temperate regions of Alaska. To what extent the generalizations apply to Aleutian or arctic marshes is uncertain. A reduction in number of mosquito species northward into the arctic or westward out the Aleutian chain comparable to that which occurs in the fresh-water habitats may be conjectured. Of more immediate value than further distribution data are answers to basic life-history questions, e.g. to what extent are

the adult habits of these salt-marsh mosquitoes unlike those of the fresh-water species with which they are identified, or, in a larger sense, are not the salt forms distinct races? In consideration for its preponderant importance on the marshes, the biology of adult *punctodes* deserves early study. If, unlike fresh-water *punctor*, the adult is not a forest mosquito, *punctodes* may disperse quite differently. This would also possibly enable it to exist on the treeless Aleutians and far into the arctic.

SUMMARY. Mosquitoes breeding in salt marshes were studied in two widely separated regions of Alaska, one subarctic, the other temperate. With reference to the former region, five types of larval habitats based chiefly on salinity and zones of plants are proposed: (1) *Triglochin*; (2) Brackish *Carex*; (3) Fresh *Carex*; (4) *Myrica*; (5) Seepage.

Twelve species of northern fresh-water mosquito larvae were collected in these brackish habitats, of which six species of *Aedes* are of chief importance, viz.: *punctodes* Dyar, *punctor* (Kby.), *impiger* (Wlk.), *communis* (DeG.), *excrucians* (Wlk.), and *flavescens* (Müller).

Aedes punctodes, which is shown to be the principal Alaskan salt-marsh mosquito, predominates especially in the more saline waters, while the closely related *punctor* prefers the least brackish.

An attempt, only partly successful, to determine approximately the salt tolerance of *punctodes* and *communis* larvae in the laboratory suggests resistance to salinities equivalent to 500 parts per hundred thousand of chlorine, at least.

Predation by the stickleback, *Gasterosteus aculeatus* L., is shown to be significant in the natural control of *punctodes*.

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