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Seasonal Changes in Populations of Corixidae and Notonectidae  
(Hemiptera: Heteroptera) in New Zealand

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*Abstract*

THE life cycles and changing population structure of flight polymorphic species of Corixidae and Notonectidae are described. The two families have very similar life cycles with one and a part second generation each year, and respond similarly to changing habitat conditions in the development of the different morphs. Normal bugs develop in early and mid-summer and flightless ones predominantly towards the end of summer.

INTRODUCTION

THERE are surprisingly few published accounts of the biology of the Corixidae and Notonectidae in New Zealand although there is a large literature from studies in other parts of the world, especially Europe where they have been a popular group. Myers (1926) has given brief notes on the habits of the two families in New Zealand in an account of the biology of the Heteroptera. The paper by Marples (1962) gives little new information, but that by Barclay (1966) is valuable for showing precisely when larvae first appeared in a temporary pond near Auckland. The most complete study of the Corixidae is still that of Young (1959) which considered the habitats of the various species, growth, life cycles and some anatomy, especially in relation to flight polymorphism. Parts of this thesis have appeared in papers on migration (Young 1962a) and taxonomy (Young 1962b).

Polymorphism for flight with a normal flying morph and one or more flightless morphs in which at least the indirect flight musculature is reduced and often the wings also modified is widespread in the aquatic and semi-aquatic Heteroptera and is often related to habitat stability. Within the Corixidae and Notonectidae flightlessness most commonly results from failure of the flight muscles to develop, but in a few species the wings are also reduced. The flightless morph has reduced thoracic pigmentation and may be smaller than the normal morph but is otherwise similar. Young (1965b) described the several morphs of the polymorphic species of British Corixidae and much of this account applies equally well to both the Corixidae and Notonectidae in New Zealand. The descriptions of the morphs used in the present paper follows the scheme outlined there.

The polymorphism is environmentally determined, at least to the extent that larvae, and in some species newly moulted imagines, developing to the flightless morph can be switched back to normal development. In the laboratory moderate temperatures have been found effective in controlling development in this way and

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the whole cycle of development can be related to seasonal temperature changes with some success (Young, 1965a). In neither species considered in the present paper can mature imagines switch from one morph to another.

In the present paper the changes occurring over a single year in populations in three habitats are examined. It describes the first year of what was to have been an intensive, long term study of the control and development of flight muscle polymorphism in the Notonectidae but pollution of the main study habitat at Kainga at the end of the first summer prevented this study from developing. The results are given here simply as an account of the changes observed with little attempt at interpretation. It is hoped that further suitable populations will develop to allow the work to continue in the future.

#### DESCRIPTION OF THE HABITATS

The populations studied were in three habitats, a pond and drainage channel at Kainga and the lagoon at Leithfield. The pond is the easternmost of a series of abandoned shingle pits lying close to the south bank of the Waimakariri River 10 miles north of Christchurch (NZMS 1, S76: 023697). It is L shaped with a length over the curve of 70 metres and an area of 3,000 square metres. There are shelving beaches extending to two or three metres in the south and east but elsewhere the bank plunges steeply to depths over five metres. Much of the bed and vegetation is covered by a thick layer of rusty silt which appears to have prevented extensive colonisation by corixids. The drainage channel runs out of the pond to the east. It has a uniform width of seven metres and is mostly between 30 and 50cm deep. Until cleared in December, 1964, it was almost choked with weed and debris.

The pond contained only one species of notonectid, *Anisops assimilis* White, and very low numbers of the corixid *Sigara arguta* (White). The channel held large numbers of *S. arguta*. Each habitat therefore contained essentially a single dominant species. This has advantages in easing identification of the earlier stages of the life cycle but has shortcomings in the loss of comparative information where responses to changing conditions might be expected to vary among different species.

Leithfield Lagoon is a long, narrow lagoon lying behind the sand dunes at Leithfield, 27 miles north of Christchurch (NZMS 1, S68: 115953). Most of the edge is rimmed with dense stands of *Typha muelleri*, but where this is broken *Ranunculus* sp., *Myriophyllum* sp., *Potamogeton cheesemani* and *Elodea canadensis* run out into the deep water. Collecting was confined to the southern end of the lagoon away from the *Typha* and in a pond in the southwest corner that became separated from the main lagoon as the water level fell in summer.

The lagoon held enormous numbers of *A. assimilis* and *S. arguta*. In the deeper water the primitive corixid *Diaprepocoris zealandiae* Hale was also very common. Collections from this area allow comparison with those from the Kainga pond and channel and also demonstrate differences in response to changing conditions of species in each family, here occupying the same general habitat and subject to similar environmental conditions.

#### SAMPLING THE POPULATIONS

##### THE POND AND CHANNEL AT KAINGA

During late winter when the study began there was little aquatic vegetation and it was not too difficult to devise a sampling method of standard sweeps at a series of stations, typical of the different zones around the pond, to obtain a measure of population size and distribution. In this period two sweeps of two metres each using a 'D' net with the top edge of the net just touching the surface were made at each station. The notonectids taken were counted and after the numbers of the

two morphs had been determined from external pigmentation differences they were released back into the pond. Very few bugs were found in the deeper water away from the bank and the whole population appeared to be readily sampled from the shore. During summer, however, the important part of the year for the study of the polymorphism, the population became broken into local swarms dotted through the vegetation and became almost impossible to sample quantitatively. During this period only broad indications of changing population size were obtained. Most collections for the analysis of changing structure of the population came from two areas. The first was about the mid-point of the inner side of the curve of the pond where the bank dropped away sharply under water and where the bugs clung closely to the shore edge (the deep area). The second was along the southern edge where the beach shelved out gradually to no more than half a metre deep three metres from the shore (the beach area). Notonectids were dispersed throughout the clear water patches among the vegetation over the whole of this beach.

Sampling stations for *S. arguta* were also established in the channel from the pond but were abandoned after clearing when reduced numbers of bugs required more extensive netting.

#### LEITHFIELD LAGOON

No attempt was made in this habitat to estimate numbers of any of the species there. Collections were taken by sweep netting, along the edges of the weed for *A. assimilis* and through the vegetation and along the bottom for *S. arguta* and *D. zealandiae*.

First and second instar larvae of both *A. assimilis* and *S. arguta* tend to congregate in the shallowest, most sheltered water often partly separated from the rest of the larval population and are not adequately sampled in general sweep netting. Moreover, nets fine enough to retain these stages move too slowly through the water to catch the older ones. This failing has been recognised in the account and analysis of changes in the life cycle stages has been confined to the later larval stages and imagines. To a certain extent also, netting for the faster swimming imagines tends to miss the younger larvae. For this reason comparison between numbers of larvae and imagines in the population, although useful for a general summary of the development of the adult population, cannot be drawn too finely. These shortcomings in sampling technique would need to be overcome in a more detailed study of the life history.

#### THE LIFE CYCLES OF THE TWO SPECIES

Corixids and notonectids pass through five larval stadia before moulting to the imago. The last moult is followed by the teneral period in which the flight musculature develops fully and the cuticle hardens and darkens. This period may be prolonged in cold conditions or when food is restricted. The bugs are active throughout the teneral period but flight cannot occur until the flight musculature matures. This delay in ability to fly ensures that even in habitats where emigration is taking place the normal morph is recorded in regular sampling.

In New Zealand the two families overwinter as adults, although in the north of the country larvae from one year may persist far into the winter. Ovarian growth in overwintering corixids begins about the shortest day, varying from habitat to habitat, and may even precede it by as much as three weeks in some habitats about Christchurch. Oviposition begins during the coldest part of the year in late winter, often while the ponds are ice-covered. The testes in corixids are inactive in early spring and sperm for the fertilisation of eggs laid at this time is stored overwinter in the seminal vesicles of the male. Transfer of sperm to the spermathecae of the female takes place as the eggs are developing in the ovaries and mostly before the first eggs ripen.

The annual cycle of ovarian and testis development in *Sigara* is shown in Fig. 1. The ovarian cycle shows development beginning about the shortest day with regression in January and February. It is plotted as the percentage of adults in the sample on each date containing enlarged egg rudiments or ripened eggs. The broad bands indicate the extent of variability of development among the habitats within a few miles of Christchurch. In general the early habitats also maintain mature animals longer into the autumn. The eggs are laid soon after maturing. The male cycle is indicated by volume changes in the testis and seminal vesicle. The movement of sperm to the seminal vesicle is clearly indicated. Growth of ovaries shown in October and November is that occurring in bugs of the new generation. Ovarian development occurs later in the spring in the Notonectidae and in *Diaprepocoris* but is otherwise similar.

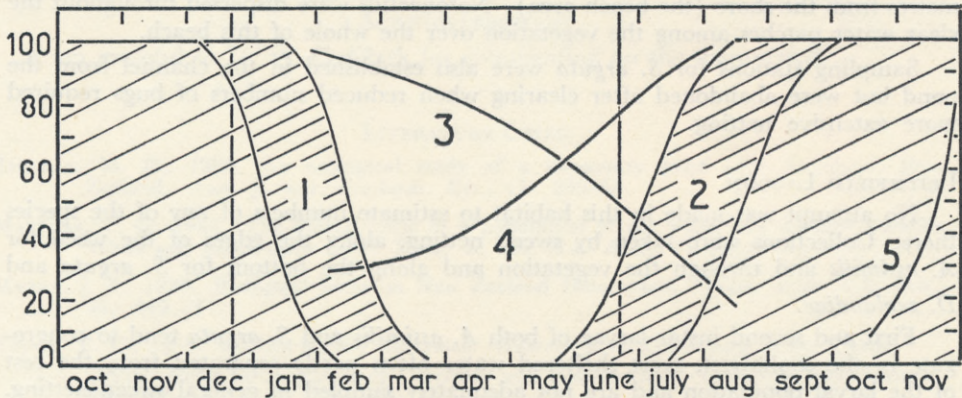


FIG. 1.—The annual cycle of ovarian and testis development in the Corixidae. (1 and 2). The regression and development of ovaries of overwintering bugs; plotted as the percentage of animals in samples from different habitats with at least enlarged egg rudiments. The zones at the start and close of the breeding period indicate the variability found in habitats about Christchurch. (3). The volume of the testes in overwintering bugs. (4). The volume of the seminal vesicles in overwintering bugs. (5). Ovarian developments in bugs of the new generation.

#### THE LIFE CYCLE OF *A. assimilis*

*The cycle in the Kainga Pond.* Larvae first appeared in this habitat on November 3, and as only 68 of 476 eggs dissected from the tissue of *Potamogeton* stems on this date were "eyed" and only 12 ready to hatch few would have hatched before this. The earliest of these larvae moulted to the imago by December 7. Overwintering bugs persisted among the new generation adults until mid-December. Two estimates from sampling on October 15 and November 10, gave population totals for the pond of 4,785 and 5,105 adults respectively. This number had fallen to about 3,000 by late November and to fewer than 1,500 in the first week of December. Continuation of this trend would lead to collapse of the overwintering population by about the middle of December; and in fact few were found after this in the collections.

All bugs moulting to adult before the end of January began ovarian development and continued laying eggs until mid-February. Those becoming adult after January failed to start growth so that as in the Corixidae in England there is one and a part second generation each year. Larvae occurred until the end of April, but made up only a small part of the population after March.

Until February 5, the frequencies of each larval instar in the samples taken from the two sampling stations in the pond, separated by less than 15 metres, were very similar and immediately preceding this date there had been a fall in the numbers of the third and fourth instars and a subsequent rise in the numbers of the fifth instar. From this time on the samples in the two areas differed markedly

(Fig. 2). In the deep water area the incidence of fifth instar larvae continued to increase steadily. In the shallow beach samples, however, this build up of the fifth instar was broken at first by a rapid increase in the third instar and then later the fourth instar. It is known from dissection that eggs were being laid in both areas through January but their resultant impact on the structure of the larval population was apparently greater in the shallower and warmer part of the pond than elsewhere.

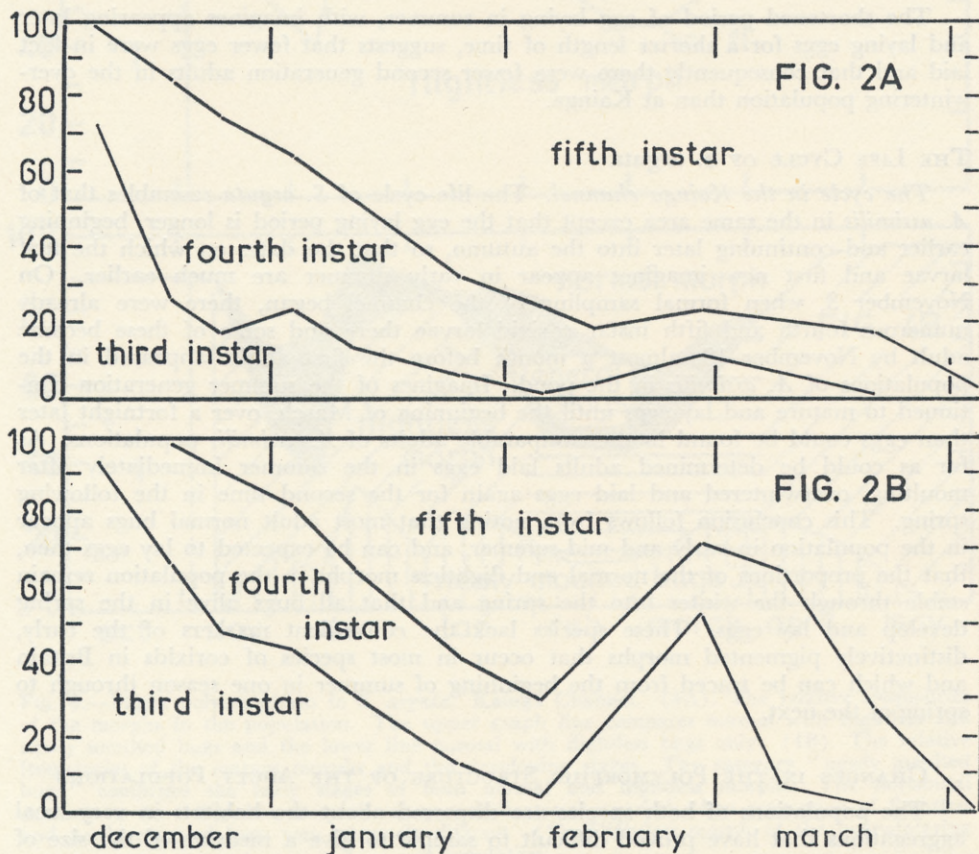


FIG. 2.—Relative frequencies of larval instars in the *A. assimilis* population at Kainga. Calculated from samples taken from the deep water bank (2A) and the shallow beach (2B). See text for further details.

These differences in the larval population within the same general habitat point to variation in environmental features along the pond margin and to restricted movement about the pond by what would be expected to be a mobile species well able, by virtue of its pelagic habits, to roam widely. The possibility of similar variation in life history phenomena needs to be borne in mind when sampling variable or extensive aquatic habitats. As a general rule series of collections taken from different parts of these habitats should be considered separately, at least until they have been examined for uniformity. The water cover of aquatic habitats masks the same variability found in terrestrial ones and the two should be sampled similarly.

*The cycle in Leithfield Lagoon.* Small numbers of imagines of the new generation were found in this habitat on December 23 but they did not become abundant until the first week of January. This point of the cycle was therefore two to three

weeks later than in the Kainga pond. The same sort of variation among populations in the same area has been found before (Young, 1965a). The most usual explanation is that it is the result of temperature differences during the egg and larval growth period, but such differences were not obvious in the present study. As at Kainga the early imagines laid eggs to give second generation adults in late summer. Egg laying was, however, not as prolonged and few mature bugs of either morph contained eggs after mid-January.

The shortened period of egg laying in summer, with imagines appearing later and laying eggs for a shorter length of time, suggests that fewer eggs were in fact laid and that consequently there were fewer second generation adults in the overwintering population than at Kainga.

#### THE LIFE CYCLE OF *S. arguta*

*The cycle in the Kainga channel.* The life cycle of *S. arguta* resembles that of *A. assimilis* in the same area except that the egg laying period is longer, beginning earlier and continuing later into the autumn, so that the dates on which the first larvae and first new imagines appear in early summer are much earlier. On November 3, when formal sampling of the channel began, there were already numerous fourth and fifth instar corixid larvae there and some of these became adult by November 10, almost a month before the first adults appeared in the populations of *A. assimilis* in the pond. Imagines of the summer generation continued to mature and lay eggs until the beginning of March, over a fortnight later than eggs could be found in the comparable adults of *A. assimilis* populations. As far as could be determined adults laid eggs in the summer immediately after moulting, overwintered and laid eggs again for the second time in the following spring. This conclusion follows from noting that most adult normal bugs appear in the population in early and mid-summer, and can be expected to lay eggs then, that the proportions of the normal and flightless morphs in the population remain stable through the winter into the spring and that all bugs alive in the spring develop and lay eggs. These species lack the convenient markers of the early, distinctively pigmented morphs that occur in most species of corixids in Britain and which can be traced from the beginning of summer in one season through to spring of the next.

#### CHANGES IN THE POLYMORPHIC STRUCTURE OF THE ADULT POPULATIONS

The populations of both species are dispersed about the habitats in very local aggregations that have proved difficult to sample to give a measure of the size of the whole population and an accurate impression of the change in numbers during the season. In this first year no attempt was made to estimate the size of the population by mark and recapture methods. This failure to obtain population numbers means that the analyses were restricted to examination of the relative frequencies of the adult morphs and their developmental stages in the samples.

The analyses show the structure of the population at the date of collection, and because it is possible to recognise developmental stages of each morph, the way the structure is changing through recruitment. It is worth noting that the structure of each sample is the result of all the changes occurring in the population up to the time of collection. It has developed from the accumulative effects of differential recruitment of the various morphs on the one side and the effects of migration and death of bugs on the other. To determine actual recruitment of morphs at each sampling date requires analysis of recently moulted adults, or some equivalent stage. The year can be usefully divided for the examination of the structure of the adult population into four periods as follows:

The expected structure of the population and the changes possible in each period are summarised in Table I. From this summary it can be seen that the

TABLE I.—Summary of the changes that can be expected in the population during the year.

Period of the year	Stages present in the population	Migration possible?	Larval recruitment to adult population?	Possible changes to population	Stable groups to act as population size markers or indicators of migration of normal morph
1 Overwintering period (May-July)	Overwintering adults, no eggs or larvae	No	No	Loss through death	Numbers of all morphs stable
2 Spring to early summer (July-November)	Overwintering adults, eggs and larvae	Yes	No	Changes possible in the numbers of the normal morph through migration. Loss through death of both morphs	Numbers of the flightless morph provide basis of estimating changes in that of the normal morph
3 Summer and Autumn (November-April)	Overwintering adults at the start of the period. Eggs, larvae and teneral and mature adults of the new generations	Yes	Yes	Recruitment of new imagines from larvae. Loss of the overwintering imagines. Migration of the normal morph	No stable groups
4 Late autumn (April-May)	Overwintering adults only	Yes	No	Migration of the normal morph	Numbers of the flightless morph stable

(1) The overwintering period during which the structure is stable, little migration is likely and there is no recruitment from a larval population.

(2) The early spring period beginning when migration of the normal morph becomes possible, some time in late July or August and continuing until the first larvae moult to adult in November or December. There may be differential survival of the morphs over this period.

(3) The summer and early autumn period when the population is being radically affected by death of the overwintering population and by recruitment of new imagines from larvae. Migration both into and away from the habitat is also possible.

(4) The late autumn period beyond which recruitment of new imagines, invariably flightless, may occur but while migration is still possible.

flightless morph provides a marker against which to measure migration of the normal morph in periods 1, 2 and 4. This requires nothing more than direct comparison of the frequencies of the two morphs during flight periods. It can be used in the same way on occasions during period 3 when there is no larval recruitment, as in the drying pond at Leithfield, or when recruitment can be allowed for. This technique for measuring the extent of migration is only possible if the two morphs survive similarly during most of the year. However, there is now considerable evidence both from the present study and in the earlier ones (Young, 1965a) that

this is so. (In practice movement of normal bugs during the usual dispersal phase in early spring is difficult to detect from changing proportions of the flying and flightless morphs (Young, 1966) but emigration away from recognisably unfavourable or deteriorating conditions in summer is readily demonstrated.)

In the third period, during summer, and the longest of the four, there is heavy recruitment from the larval population, loss of the overwintering imagines through death, and migration of normal bugs. This complex period, however, lacks any natural indicator through which changes in population size or structure can be assessed. The numbers of both morphs increase through the period and the distinctly pigmented early morphs that could be used in this way in corixid populations in England make up either too small a part of the population here to be useful, or, as in the Notonectidae, are apparently lacking altogether. Even so, some interpretation of the changing structure is still possible from the way the polymorphism develops in the population.

The most important features for the analysis of the developing population structure are as follows. Firstly, the period in which recruitment of imagines is occurring can be defined by recognising late fifth instar larvae and newly moulted imagines. Secondly, overwintered bugs, through differences in cuticle, pigmentation and fat bodies remain recognisably distinct from the new imagines in early summer and the collapse of their numbers is easily followed. Thirdly, the changing proportions of the morphs over a long period, generally a steady build up in the frequency of one at the expense of the other, give a fair, overall picture of the way recruitment has been occurring—assuming all the time there has been negligible change in the numbers of the normal morph through migration or differential mortality. Fourthly, in both the Corixidae and the Notonectidae teneral bugs developing to the normal morph are easily recognisable through their intermediate pigmentation and muscle development and provide a certain indication of the recruitment of this morph. Fifthly, in the Notonectidae, but alas not clearly in most corixid species, the two morphs are separable on the basis of differences in the appearance of the indirect flight muscles from the end of the last larval stadium. This last finding provides a powerful tool for the interpretation of changes occurring in notonectid populations not generally available in studies of corixids. Similar information for the Corixidae on the identify of the morphs being recruited to the population has been determined elsewhere by holding collections of late instar larvae in cages in the habitat until the two morphs as adults became separable by inspection. The most critical pointers for the analysis are the last two listed because they define the periods in which the various morphs are developing and allow correlation of development of the polymorphism with physical or climatic factors in the environment.

#### THE POLYMORPHISM OF *A. assimilis*

The following mature morphs and developmental stages are recognisable in populations of this species; remembering that it is analysis of the immature stages that contributes most to the success of attempts to interpret the changes found.

*Normal and flightless morphs as late fifth instar larvae.* The development of the indirect flight musculature in the two morphs diverges during the fifth stadium. In the normal morph the muscles grow steadily through the stadium whereas in the flightless one it scarcely enlarges from its condition at the start of the stadium. By the end of the stadium the two morphs are perfectly distinct in this species, the muscles completely fill the mesothorax of normal bugs but remain as thin slivers of tissue, well separated by the fat body in flightless bugs. As growth takes place through the stadium, the morphs may be confused unless examination is confined to the end of the stadium. Analysis of these late-instar larvae also ensures that only those larva very soon to moult to adult are considered, increasing the precision



for dating recruitment of the morphs determined into the adult population. The most useful criterion for indicating maturity of the larvae is that of the presence of a brown patterning in the folds of the pronotal and mesonotal tissue of the imago where it lies crumpled beneath the larval cuticle.

*Newly moulted imagines.* These are uniformly white with the wings soft and opaque. The normal and flightless morphs can be readily distinguished. In normal bugs the width of the median dorsal longitudinal muscles is about equal to the gap between them; in flightless bugs the muscles are less than half as wide as the gap.

*Teneral imagines of the normal morph.* A transitional stage between newly moulted and mature in which the muscles complete development and the pigmentation of the thoracic nota deepens from the white of newly mounted bugs to the black of mature bugs.

The teneral development of *A. assimilis* differs from that of *Sigara*, in a number of respects.

At moulting the cuticle is soft and opaque white, but within several hours becomes firmer and more transparent so that the tissues show beneath. The abdominal venter, thoracic sternites and leg bases are the first parts to darken. This occurs very soon after moulting and corresponds to the rapid pigmentation of the wings and pronotal disc found in the Corixidae. The relation between swimming posture in the water and the areas of first pigmentation on the body is most striking in these two families: in each the uppermost surface darkens first even though this is the ventral side in the Notonectidae, which swim upside down, and not the dorsal one as in other bugs normally oriented.

The way the pigment develops in the cuticle of the mesonotum is as described for corixids (Young, 1965c) except that the final stages, in which the pigment is intensified from an earlier uniform, light colouring, occurs in the reverse order, with the anterior areas completed first. From moulting, light colouring appears first on the posterior mesonotum and the insertion areas of the lateral dorsal longitudinal muscles before forming further anteriorly over the insertion areas of the median muscles. For a short period the whole surface is uniformly lightly pigmented. Darkening then begins, and is most intense, on the muscle insertion areas along the anterior and anterolateral border of the mesonotum spreading only gradually back over the rest of the surface. The flight muscles, already partly enlarged at moulting, are fully developed by the time the posterolateral areas are first pigmented but before any pigment shows on the insertion areas of the median muscles. Development of the muscles in relation to pigmentation is thus similar to that of *Sigara scotti* (Fieber) (Young 1965c, p. 162) but more advanced relative to pigmentation than *S. arguta*.

*The normal morph.* The flight muscles are fully developed and the cuticle of the mesonotum and metanotum uniformly darkened.

*The flightless morph.* The muscles are not enlarged from their condition at moulting. The pigmentation is variable but the thoracic nota are rarely much darkened.

The morphology and pigmentation of the mature morphs has been described by Young (1962b, p. 364).

#### THE POPULATIONS IN THE KAINGA AND LEITHFIELD HABITATS

The development of the overwintering adult population of this species is first described from collections made along the deep water bank at the Kainga pond. This cycle of development is considered typical for this species in moderately favourable habitats and is compared with the collections from the shallow beach area of the same pond, in which the life cycle was somewhat different, and from two parts of Leithfield Lagoon.

The changing frequencies of mature bugs of the two morphs taken from Kainga are shown in Fig. 3a. From a start about the middle of December, when the two morphs in the new population were equally common, the numbers of normal bugs increased (migration of the flightless morph was impossible and death unlikely at this stage), followed from the end of January by a steady increase in the flightless morph.

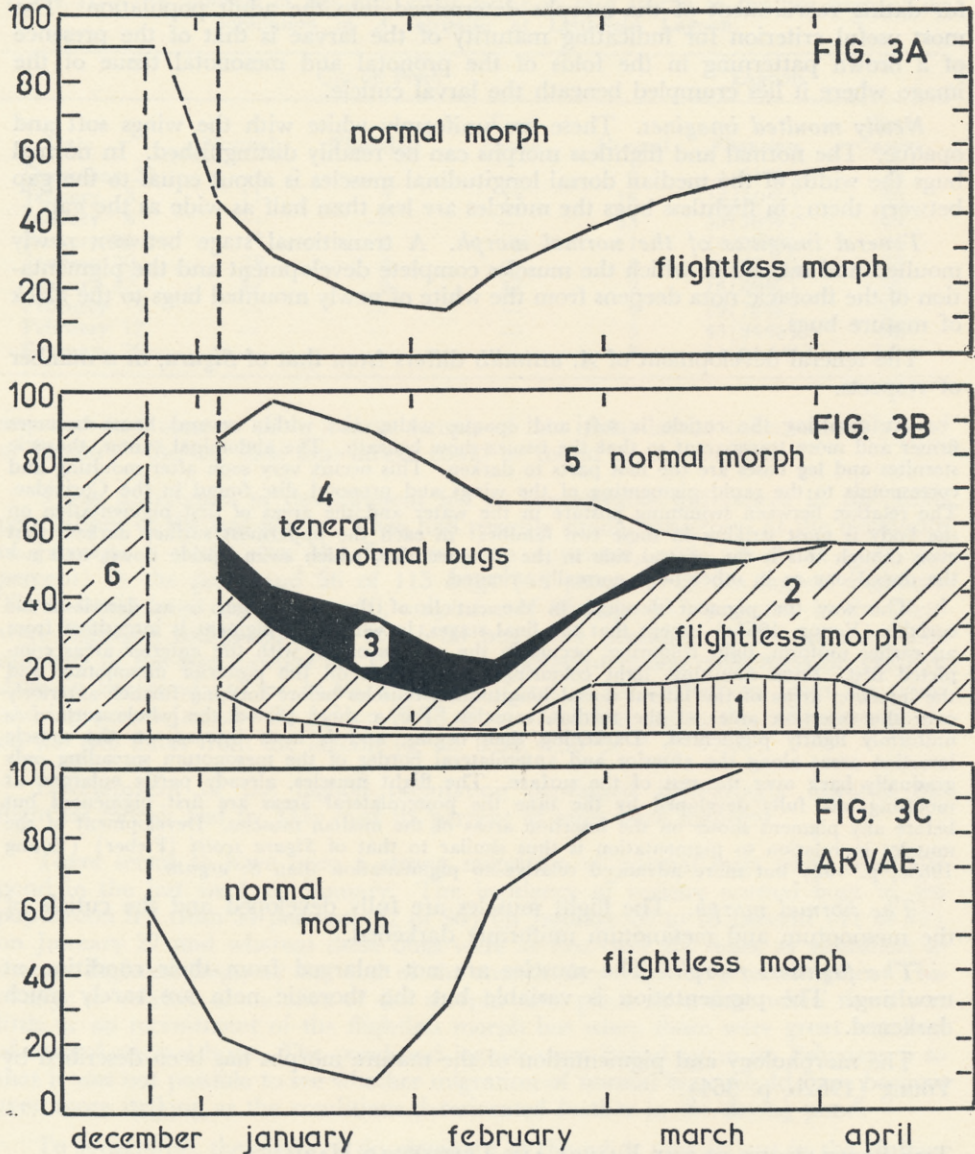


FIG. 3.—Flight polymorphism in *A. assimilis*. Kainga Pond. (3A). The relative frequency of each of the two morphs in the population. (3B). The relative frequencies of the mature morphs and developmental stages in the population. (1) newly moulted flightless bugs, (2) the mature flightless morph, (3) newly moulted normal bugs, (4) teneral normal bugs, showing development of flight musculature from moulting, (5) the mature normal morph and (6) flightless morph of the overwintering population. (3C). The relative frequencies of the two morphs in samples of late fifth instar larvae. Separation of the morphs was based on differences in the amount of flight muscle development.

The changes over summer are shown in greater detail in Fig. 3b, confirming that although both normal and flightless bugs were moulting to adult through December and January, the normal morph predominated and a major part of the total adult population in January and early February was made up of the teneral stage of this morph. The high incidence of teneral bugs indicates that the overall

change in the proportions of the mature morphs seen above occurred through recruitment from larvae and not through migration. From mid-February, an increasing proportion of newly moulted imagines were flightless and lifted the part occupied by this morph from about 13 percent at the start of February to over 50 percent in May.

The switch in the development of the morphs from predominantly flightless to normal to flightless again is confirmed also from the examination of larvae about to moult to adult (Fig. 3c). The incidence of the flightless morph in the samples of this stage, over 60 percent in mid-December, falls steadily to 9 percent towards the end of January and rises to 100 percent in March. The preponderance of flightless bugs in the collections after mid-February lets one conclude that the overall increase in the incidence of the flightless morph in the adult population was through larval recruitment, and not through loss of the normal morph by emigration.

Except after mid-March, and perhaps at the beginning of summer, the two morphs were developing together throughout summer in this population.

This cycle of development was paralleled almost exactly in the populations along the beach of the pond even though the influence of the second larval generation was more pronounced there and presumably made up a greater part of the adult population later in the year. Throughout summer the collections of late instar larvae were similar. For example, on February 26, 51 of 62 larvae (82 percent) from the deep water and 58 of 68 larvae (85 percent) from the beach were the flightless morph. It was not surprising therefore, to find that at the end of summer, when differences between the populations in different parts of the pond could be expected to show most clearly, the proportions of two morphs were almost identical with 54 percent of bugs flightless from the deep water and 52 percent flightless from the beach.

In general the habitat features that led to differences in the life cycles in the parts of the pond did not affect the development or the ultimate structure of the polymorphism of the adult population. At Leithfield Lagoon, however, where marked differences appeared in the parts of the habitat over summer, similar life cycle divergences to those described above were associated with changes in the development of the polymorphism. In this habitat a section of the initially unbroken population was cut off in a shallow bay from the rest of the lagoon as the water level dropped through summer. The animals there experienced much higher water temperatures, larval growth was faster, and most adults developed to the normal flying morph. This is a similar situation to that described in a population of *Sigara scotti* (Fieber) in England (Young, 1965a, p. 374) and as in that situation shows clearly the effects of environmental factors in the control of the polymorphism.

On January 27, over a month after the populations separated, fifth instar larvae made up 78 percent of the last three instars in the pond but less than 11 percent of the same stages in the lagoon. This difference, which became even more pronounced later in the summer, indicates not only a different rate of larval growth, with faster growth in the pond, but also changed breeding success there as well. Few larvae were present in the pond after February 5 even though large numbers of adults persisted through summer and many contained mature eggs until late January. In the main population in the lagoon larvae were common until April.

The numbers of late fifth instar larvae developing to each morph in the pond and lagoon are compared in Table II. In the main population the development of the morphs seen at this stage parallels that found in the Kainga population during the same period and shows a steadily increasing tendency towards the development of the flightless morph. By the end of January most bugs were developing in this way. By contrast, in the cut-off pond there were few developing flightless bugs at

TABLE II.—The numbers of late fifth instar larvae of each morph in the two parts of the population of *A. assimilis* at Leithfield Lagoon.

Date	Cut-off Pond			Lagoon		
	Normal	Flightless	Total larvae	Normal	Flightless	Total larvae
December 23	—	—	—	9	4 (31%)	13
January 3	11	2	13	16	16 (50%)	32
January 6	—	—	—	33	33 (50%)	66
January 11	5	0	5	11	14 (56%)	25
January 20	19	5	24	6	16 (68.5%)	19
January 27	42	0	42	2	16 (89%)	18
February 5	—	—	—	8	29 (78%)	37
February 12	—	—	—	3	45 (94%)	48
February 26	—	—	—	3	51 (94.5%)	54

any time and none at all in a large sample of late instar larvae collected at the end of January—the last date that larvae could be found in any number.

These differences in development led to considerable differences in the adult populations of the two places. They had roughly similar structures at the beginning of January, a week after the first imagines appeared, with 18 of 52 bugs (35 percent) in the pond and 56 of 115 bugs (48 percent) in the lagoon flightless. Three weeks later on, January 20, only nine of 96 bugs (9.5 percent) in the pond were flightless compared with 45 of 83 bugs (54 percent) in the lagoon. The numbers of the two morphs are significantly different in the collections on the two dates in the pond ( $\chi^2 = 14.40$ ,  $P < .001$ ) and in the collections from the pond and lagoon on January 20 ( $\chi^2 = 42.48$ ,  $P < .001$ ) but not in the collections made on the two dates from the lagoon ( $\chi^2 = 0.58$ ,  $0.50 > P < 0.30$ ).

Development of the lagoon population continued increasingly towards the flightless morph and by May over 95 percent of bugs were flightless.

There seems to have been a strong migration of normal bugs away from the pond in the last week of January. The incidence of mature normal bugs in the population fell from 54 percent (52 of 96) on January 20 to 16 percent (11 of 70) on January 27 and whereas these bugs were at first over six times as abundant as mature flightless bugs, by the end of the month they were only as common. This change in relative abundance of the morphs took place at a time when there was little or no recruitment of the flightless morph but when there were great numbers of teneral normal bugs. The pond and lagoon were linked again on February 5 so that it was not possible to see whether migration of normal bugs would have become even more striking as the conditions deteriorated further in the drying pond.

To summarise, the cycles of development of the adult populations in the Kainga pond and Leithfield Lagoon were similar with predominantly normal development in early and mid-summer and flightless development at the end of summer, excepting that in the cut-off population at Leithfield most bugs developed to the normal morph in response to the unfavourable environmental conditions of the drying pond. At the end of summer the structure of the populations at Kainga and in the Lagoon at Leithfield were nevertheless quite different with only 54 percent of imagines flightless at Kainga compared with over 95 percent flightless at Leithfield. Although the two morphs occurred together in samples of late instar larvae throughout summer flightless development predominated earlier at Leithfield. Most bugs in these samples were flightless after mid-January at Leithfield but a similar incidence was not reached until nearly a month later, on February 10, at Kainga. Differential recruitment of the morphs seems the most likely explanation of the differences between the two overwintering populations.

THE POLYMORPHISM OF *S. arguta*

The morphs in this species, in common with most corixids, do not show clear differences at moulting to the imago so that analysis of the population is far more difficult than in *Anisops*. The category, newly moulted imagines, contains both normal and flightless bugs and provides no information of the way the polymorphism is changing. Mature normal bugs, and teneral bugs after some development, are clearly recognisable through their pigmentation and muscle development and can be readily sorted from the remainder of the sample. Flightless bugs have no such obvious differences from newly moulted imagines and the success of the analysis depends largely on the ability to identify them. They become recognisable from newly moulted bugs when the cuticle becomes hardened and brittle rather than flexible; or pigment, often rather blotched and uneven, develops over the mesonotum beyond the patterning arising soon after moulting; or the gonads enlarge and mature beyond the newly moulted condition; or the fat bodies in the thorax, which are at first pale and tenuous, enlarge and yellow as fat is deposited. When any of these features are found in bugs with undeveloped musculature it is generally safe to assume that the bug is flightless. Techniques of ageing based on growth patterns of the cuticle are inconvenient for routine analysis of large samples and moreover would not separate flightless bugs from teneral normal bugs during periods of slow teneral growth.

In practice the best method of identifying flightless bugs in summer, before cuticle or fat body differences develop, is by examination of the ovaries of female bugs and subsequent sorting of male bugs with similar pigmentation and overall appearance. The ovaries enlarge very quickly after moulting, at about the same rate as the flight muscles develop in normal bugs, so that bugs with enlarged ovaries and undeveloped musculature can be certainly identified as flightless. The comparable technique for the male is more difficult to use as the testes are well developed in moulting bugs and development is limited to growth of the accessory glands. Unfortunately ovarian development does not begin in moulting bugs through the full length of summer. In the Kainga pond no development occurred in bugs moulting to adult after February 5, and in Leithfield Lagoon there was none later than mid-January, even though bugs with gonads that had matured earlier continued to lay eggs until at least the end of February.

Thus to summarise, in early or mid-summer four groups of imagines can be distinguished; newly moulted bugs which will mature into one or other of the two morphs, a composite group of maturing and mature flightless bugs, which are generally not separable, and the teneral and mature normal bugs separable by differences in pigment and muscle development. After the end of January recognition of flightless bugs becomes more difficult, although mature bugs still carry ovarian eggs, and from the end of February only three groups are certainly recognisable: teneral normal bugs, mature normal bugs and all the remainder, comprising flightless bugs and newly moulted bugs of both morphs. These levels of working accuracy in the parts of the year have been acknowledged in the graphs showing population changes by combining the numbers of flightless and newly moulted bugs at the end of summer, even though some information is lost.

The pattern of the changing development of the morphs through the season, in contrast to simple analysis of structure at each date, is indicated by the change in the relative frequencies of the morphs with time, assuming limited migration and mortality, and the occurrence of the maturing stages of each of the morphs. For most of the year it is the occurrence and importance of teneral normal bugs that gives the most definitive indication of the development occurring in the population.

The following section describes briefly the characteristics of the four groups of imagines recognisable in populations in early and mid-summer.

*Newly moulted imagines.* At first these have a soft, white cuticle with opaque, thickened wings. Within a few hours, the dorsal exposed surface of the body, the wings and pronotal disc, are pigmented and over the following days pigment develops in the rest of the cuticle. It has not been possible to separate the two morphs at this stage in this species.

*Teneral imagines of the normal morph.* These bugs are recognisable from newly moulted imagines as soon as the flight muscles enlarge significantly. The stages in the development of pigment of the mesonotum are shown in Young (1965c, p. 160). Pigmentation of the mesonotum begins very soon after moulting to stage II, with light brown on the posterior half, and spreads anteriorly to cover the insertion areas of the lateral longitudinal muscles before covering the insertions of the median pair. The pigment later intensifies over the whole surface to dark brown or black. The muscles have not begun to enlarge by stage II but are fully grown by the end of stage III, before any pigment shows on the median areas of the mesonotal cuticle. Development of the muscle relative to pigmentation is therefore very similar to that in *Sigara dorsalis* (Leach) (Young, 1965c, p. 161).

*Normal morph.* This morph is easily recognised by its full pigmentation and flight muscle development.

*Flightless morph.* In this morph the flight muscles remain undeveloped and the pigmentation is lighter than normal with the thoracic cuticle only partly marked. The ways of recognising flightless from newly moulted imagines have been described earlier.

The normal and flightless morph of this species were described in detail by Young (1962b).

The collections in early and mid-summer from Leithfield were more difficult to sort and interpret than those from Kainga. There were fewer bugs in each sample, the development of ovaries in flightless bugs was more variable and led to doubt in the separation of the morphs and the widely fluctuating numbers of newly moulted imagines in the sample suggested that the method of sampling was inadequate during this period. From early February the numbers in the samples were greater and the proportions of the morphs were more constant between samples. This population is described in less detail in the text.

#### POPULATIONS IN THE KAINGA CHANNEL AND IN LEITHFIELD LAGOON

About December 12, soon after the first new generation imagines began to appear, the Kainga channel was cleared with a drag-line; this disrupted for a short time the development of the adult population.

The relative frequencies of the mature bugs of the two morphs and of mature normal bugs compared with flightless and newly moulted bugs taken together are shown in Fig. 4a. The graphs demonstrate the possible error arising from confusion of flightless with newly moulted bugs. The more detailed analysis of all imagines including the teneral stages appears in Fig. 4b.

The two analyses taken together indicate that an early development of the flightless morph soon gave way to the normal morph which continued through the drain-clearing until mid-March when flightlessness once more became dominant. Teneral normal bugs occurred from mid-November until the end of March and made up a substantial part of the adult population until mid-March. Flightless and newly moulted imagines are lumped from mid-February, because of the uncertainty of the identification of the mature flightless bugs after this date. However, most bugs of this composite grouping were considered to be flightless from the beginning of April.

The striking increase in the incidence of mature flightless bugs in the population following clearing suggests that large numbers of bugs flew from the habitat during and immediately after this upheaval.

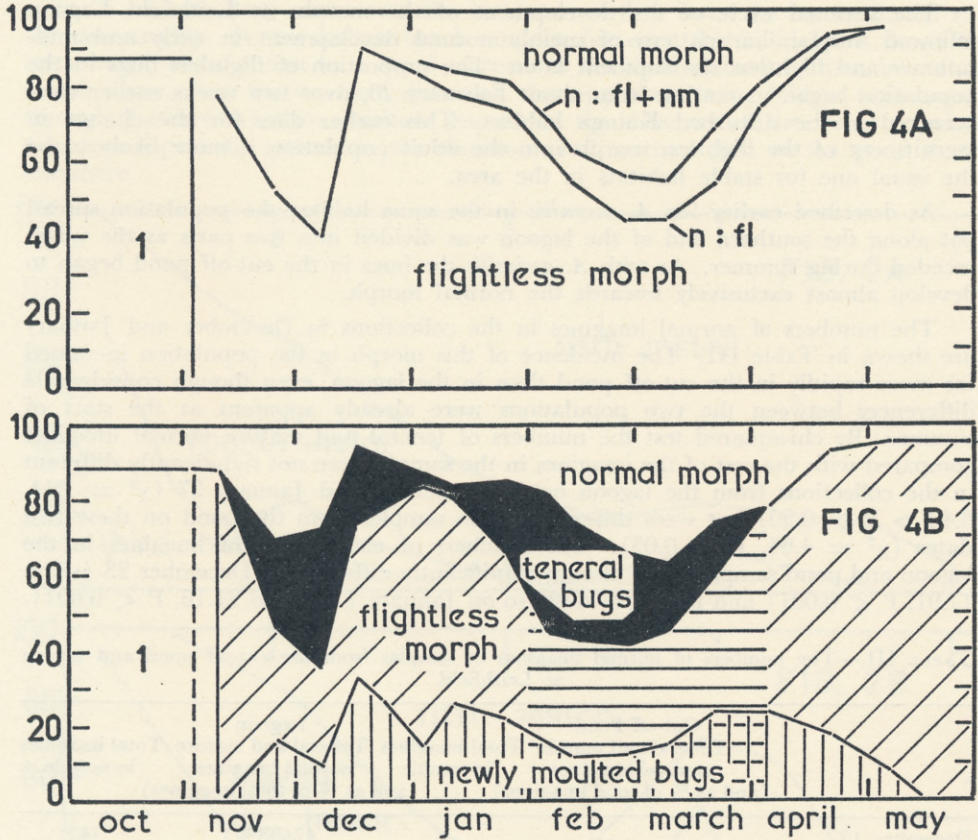


FIG. 4.—Flight polymorphism in *S. arguta*. Kainga Channel. (4A). The relative frequencies of the morphs in the population. The upper graph line compares normal with flightless and newly moulted bugs and the lower line normal with flightless bugs only. (4B). The relative frequencies of the mature morphs and the developing stages. The category "newly moulted bugs" comprises the early stages of both normal and flightless morphs. The horizontal shading in the "flightless morph" category indicates the period when separation of flightless and newly moulted bugs was extremely difficult. (1). Flightless morph of the overwintering population.

Clearing caused a drastic fall in numbers of all stages and fewer than 20 percent of the population was considered to have survived. There is no certain explanation for the low incidence of teneral normal bugs in the collections in early January, over a fortnight after the drain was cleared. Normal development dominated before clearing and could be expected to continue through December and January, especially as the habitat had been so badly disturbed.

During winter in 1964 the population was composed mainly of the flightless morph, remaining stable at about 88 percent of the population. At the end of summer in 1965 the new overwintering population, growing through drastically changed conditions at first following the clearing of the drain, had a similar structure with 92 percent of the bugs flightless. Clearly the recruitment of flightless bugs into the population towards the end of summer after the drain had re-settled was numerically much greater than that of normal bugs developing over a far longer period earlier in summer. The loss of normal bugs by flight in mid-summer would have also increased the difference between the numbers of the two morphs.

The seasonal cycle of the development of the morphs at Leithfield Lagoon followed the familiar pattern of mainly normal development in early and mid-summer and flightless development later. The proportion of flightless bugs in the population began increasing from about February 20, over two weeks earlier than occurred in the disturbed Kainga habitat. This earlier date for the change in recruitment of the flightless morph into the adult population is more likely to be the usual one for stable habitats in the area.

As described earlier for *A. assimilis* in the same habitat the population spread out along the southern end of the lagoon was divided into two parts as the water receded during summer. As with *A. assimilis* the bugs in the cut-off pond began to develop almost exclusively towards the normal morph.

The numbers of normal imagines in the collections in December and January are shown in Table III. The incidence of this morph in the population increased far more rapidly in the cut-off pond than in the lagoon, even though considerable differences between the two populations were already apparent at the start of summer. By chi-squared test the numbers of teneral and mature normal imagines compared with the rest of the imagines in the sample were not significantly different in the collections from the lagoon on December 23 and January 27 ( $\chi^2 = .044$ ,  $0.40 > P > 0.50$ ) but were different in the samples from the pond on these two dates ( $\chi^2 = 4.64$ ,  $P < 0.05$ ). The numbers of each group of imagines in the lagoon and pond samples were already significantly different on December 23 ( $\chi^2 = 11.91$ ,  $P < 0.001$ ) and more obviously so on January 27 ( $\chi^2 = 21.16$ ,  $P < 0.001$ ).

TABLE III.—The numbers of normal imagines in samples from the cut-off pond and lagoon at Leithfield.

	Cut-off Pond		Lagoon	
	Teneral and mature normal imagines (and as % of total imagines)	Total imagines in sample	Teneral and mature normal imagines (and as % of total imagines)	Total imagines in sample
December 17	—	—	47 (33%)	142
December 23	96 (67%)	143	64 (46%)	137
January 3	66 (65%)	102	39 (35%)	112
January 11	83 (74%)	111	35 (38%)	92
January 20	94 (82%)	115	73 (42%)	174
January 27	85 (80%)	107	33 (45%)	73

The changes in the development occurring within a generation in these two contrasting habitats by larvae from a common population demonstrate the effectiveness and advantages of a sensitive, environmentally determined polymorphism over a less flexible one more directly related to genetic factors and non-responsive within the life span of the animal.

At the end of summer the population at Kainga and the lagoon at Leithfield differed in the same way as found for *A. assimilis* in the same places: at Kainga over 90 percent of bugs were flightless, at Leithfield no more than 60 percent were flightless. Thus, in spite of the disturbance of clearing, Kainga was apparently a more favourable habitat for this species. Factors other than temperature, which was if anything lower in the lagoon, are thought responsible for this difference. At Leithfield the thick vegetation overlying the debris-covered bed seemed less suitable for corixids than the open silt areas in the Kainga channel but no examination of water or food quality was attempted.

#### COMPARISON OF THE LIFE CYCLES AND POLYMORPHISM OF *A. assimilis* AND *S. arguta*

The populations of the two species were in adjoining habitats at Kainga, but shared the same habitat and could be netted in the same sweeps of the net at



Leithfield. The separation of a part of the population of each species into the pond at Leithfield provided a useful comparison of their reaction to adverse conditions. The habits of these two species are clearly contrasted, with the notonectid pelagic and carnivorous and the corixid bottom-living and mainly herbivorous. They come closest together in weeded areas. At Leithfield dense breeding populations of *S. arguta* and *D. zealandiae* occur from time to time in beds of *Elodea* floating over several metres of water.

It is surprising nevertheless to find such similar biology in the two families, with almost identical life cycles and flight polymorphism. The differences between them, as exemplified by the two species examined, are less than those occurring among corixid species in England and lie in such fine points as the differences in teneral development, conditioned by swimming habit, and in the response to changing conditions in spring which cause the notonectid cycle to lag behind the corixid one. In summary the differences are of degree not kind.

At both Leithfield and Kainga the first imagines of *S. arguta* appeared almost a month earlier than the first ones of *A. assimilis* and a similar gap, at least for the larvae, is indicated for populations of the same two species at Auckland by Barclay (1966, pp. 248-49). At the other end of the season eggs develop longer into autumn in *S. arguta* than in *A. assimilis* but even though the corixid has a longer active reproductive period both species have a similar annual cycle of one and a part second generation each year.

The first imagines in summer in both species are predominantly flightless even though those of *A. assimilis* appear much later than those of *S. arguta* and would have developed under different conditions. It should be noted, however, that the initial determination of the polymorphism occurs during the early larval instars, developing under more similar conditions. This early flightless development is short-lived and in both species soon gives way to predominantly normal growth. Its presence in *A. assimilis* at Kainga was established unequivocally by examination of the only mature larvae in the population on December 23: 23 of 33 larvae were found to be the flightless morph. The switch to the development of the flightless morph in late summer, after the long mid-summer period of mainly normal development, showed in the adult populations at the same date in the two species, about the end of February. This correspondence suggests that the labile developing stages were responding similarly to the same factors in the environment. Furthermore the two species behaved similarly to the changed conditions of the cut-off pond. From a similar starting point at the end of December, 77 of 96 (86 percent) of *A. assimilis* imagines and 94 of 115 (81 percent) of *S. arguta* imagines in this population had developed to the normal morph a month later.

It is interesting to compare these cycles of development with that occurring in the populations of *D. zealandiae* at Leithfield. This species is undoubtedly a primitive corixid sharing features with the Notonectidae but differs from both species examined in the present study through having the wings reduced in the flightless morph. The normal flying morph is comparatively rare and there is some evidence that the control of the polymorphism has a more direct genetic factor than in the other species.

The life cycle of *D. zealandiae* was similar to the other species with first imagines appearing in mid-December and laying eggs for a time to give a partial second generation. Few bugs with developing eggs were discovered after the end of January. Teneral normal bugs occurred from late January until early March but even when most common, normal bugs, both teneral and mature, made up little more than 10 percent of the population and later in winter this figure had fallen to less than 3 percent. In contrast to the other species none of the normal bugs matured early enough in the summer to develop eggs and the first oviposition of this morph consequently must occur in the following spring.

From this and earlier studies it is considered that the most favourable habitats for a species have the highest incidence of flightlessness. On this criterion therefore Leithfield Lagoon seems a more favourable habitat for *A. assimilis* than for *S. arguta*. It was also more favourable for *A. assimilis* than the pond at Kainga where the population numbers fell drastically towards the end of summer through pollution of the habitat by rotting saw-dust. The clearing of the Kainga channel did not have any long-term effect on the make-up of the population of *S. arguta* there and the incidence of the flightless morph at the end of summer was higher in this place than in the lagoon, where the population was never imperilled. From knowledge of other corixid habitats it is considered that the bottom of the lagoon is too soft, with too much finely broken and rotting vegetation to be ideal for this species.

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