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FLOATING AND SEXUALITY IN LABORATORY POPULATIONS OF HYDRA LITTORALIS.

The University of Michigan, Ph.D., 1969
Zoology

University Microfilms, Inc., Ann Arbor, Michigan

FLOATING AND SEXUALITY IN LABORATORY POPULATIONS OF *HYDRA LITTORALIS*

by

Uzi Ritte

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in
The University of Michigan
1969

Doctoral Committee:

Professor Lawrence B. Slobodkin, Chairman
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ABSTRACT

FLOATING AND SEXUALITY IN LABORATORY POPULATIONS OF HYDRA LITTORALIS

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Characteristically, hydra are sessile animals that reproduce asexually by budding, but free floating and sexual reproduction are not uncommon in the laboratory as well as in nature. Both have been interpreted as escape mechanisms (in space, in the case of floating, or in time, in the case of sexuality), occurring in response to some changes in the environment, although no agreement has yet been reached about the exact nature of the factors involved. The purpose of the present study was to see the effect of several variables--in particular density and the availability of food--on the appearance of floating and sexuality under laboratory conditions, to find out what are the relations between the two responses, and to suggest a possible role for these responses in the dynamics of hydra populations in nature.

Hydra populations were maintained for 150 days under all possible combinations of 5 food levels and 3 volumes of water. Total population

size and the frequency of budding, sexuality and floating were recorded daily. Floating hydra were removed daily from 3 out of the 5 populations' kept at each set of conditions. In addition, short term experiments were carried out in which the effects of density, previous presence of hydra in the water, starvation, sexuality and depth of water on rates of floating were studied separately.

In very shallow water floating seems to be not an escape response, but a part of the regular movements of hydra around their dish. In deeper water floating is a special kind of movement, probably indicating an attempt to leave the population, but serving two different functions, depending on the environmental conditions. Under favorable conditions, floating is a dispersal mechanism, undertaken mostly by young individuals shortly after detachment. When the conditions deteriorate, floating becomes an escape response. The exact nature of the changes involved is not known, but they can be caused by the presence of a large number of hydra in the water; the higher the density, the earlier do these changes occur. The changes can probably come also from sources different from the hydra themselves. Partial starvation is necessary for floating to take place.

In populations kept at constant densities and food levels the appearance of floating is correlated with the appearance of sexuality, and both show rhythmic changes in frequency. No corresponding fluctuations in the external conditions could be identified, suggesting that the cycles are due to rhythmical physiological changes in the hydra themselves.

The high rates of floating and sexuality occur at about the same time, but sexual individuals float less frequently than non-sexual ones. Floating and sexuality are probably two mutually exclusive responses to the same environmental changes. Some hydra stop budding, become sexual and produce new, and potentially better adapted genotypes that remain dormant until the conditions become favorable again, while others maintain their capacity to bud and leave the population by floating. When the conditions become totally inhospitable the entire population floats away.

The temporary nature of hydra populations is indicated by many field observations. Floating hydra were collected in planktonic samples, and a few individuals were shown to migrate large distances. A more direct study of floating and sexuality in the field will have to await development of better techniques for collecting and censusing.

ACKNOWLEDGEMENTS

I am indebted to many people for their contributions at different stages of my work. Dr. Lawrence B. Slobodkin was a constant source of stimulation, encouragement, help and advice. Drs. Nelson G. Hairston, Frederick E. Smith and David G. Shappirio were generous in their help throughout the entire study, while the manuscript itself has benefited from the comments by Drs. Hairston, Smith and James N. Cather. Dr. Helen Forrest-Mantell kindly identified the hydra, and supplied other useful information.

My work was greatly aided by discussions with and advice from Robert Colwell, Mary Colwell, James Farris, Douglas Futuyma, Dan Gill, Douglas Gill, Adam Łomnicki, Uriel Safriel and John Vandermeer. Skilled technical help was received from Mary Benisek, Toni Hall, Nancy Houston and Yossef Loya.

Could I have followed the example set by Janet Rupp and Louis Martonyi, my work would have finished much earlier.

All the efforts involved in initiating the work and bringing it to its completion were fully shared by my wife, Shlomit, who has helped in more ways than she will admit.

Financial support was received from the Department of Zoology,

Horace H. Rackham School of Graduate Studies and the International Center of The University of Michigan, and from NSF grant GB-1595 to L. B. Slobodkin.

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INTRODUCTION

Laboratory cultures of hydra often include some individuals which are not firmly attached to a solid surface, but float freely, attached by their foot to the surface of the water, with the body and tentacles hanging down (Fig. 1). This behavior, which is contrary to the expected sessile mode of life of coelenterate polyps, has attracted the attention of several workers.

First among them was Abraham Trembley (1744), whose work was aimed at finding whether green hydra were plants or animals. A part of his work--in which he established hydra as an excellent organism for the study of regeneration--was devoted to movements. Trembley found that hydra, unlike plants, do move around ("seven or eight inches of road make a nice summer day for the polyps"), and, according to him, the surface of the water is just another surface they use for their movements. In an attempt to explain the forces that maintain the hydra at the surface, Trembley found that the hydra hangs down from the bottom of a shallow depression, with the basal part of the body, the foot, completely dry, protruding out into the air. This he considered necessary for floating--the hydra will stay at the surface as long as its foot is dry and sticking out. The only way for the hydra to reach the surface is, according to Trembley, by climbing up a wall. Once near the surface,



Figure 1. Floating hydra

(from Trembley, 1744)

the hydra attaches itself to the wall by means of its tentacles, pushes its foot out of the water, and when the foot becomes dry the hydra moves the tentacles away from the wall and remains floating. If one wants to induce hydra to float he has only to keep the hydra out of the water long enough for the foot to dry out. Upon returning to the water, if the foot remains outside, the hydra will stay at the surface. There the hydra either moves around, eventually reaching a wall and becoming attached to it, or it can anchor itself by means of its tentacles to some solid objects inside the water, and thus remain in one location.

Another attempt to explain the forces that operate to keep hydra suspended from the surface of the water was published by Scourfield (1901). He claims to see minute strands and irregular masses of gelatinous substance running from the basal disc to the surface film. This substance, which is produced by the disintegration of the outer ends of the large ectodermal cells of the basal disc, is water repellent, and as such causes the formation of minute capillary depressions. The surface film bounding a capillary depression is known to exert an upward pull on the object against which it is formed, and this is how the relatively heavy hydra succeeds to hang on to the surface.

The adaptive, rather than the technical, aspect of floating is discussed by Wilson (1891), in a general study of the movements of hydra. According to him hydra usually move not at random, but toward the sources of light and oxygen. As a result they tend to aggregate on the lit side of the aquarium, not far from the surface of the water. This is a highly adaptive behavior, because the food organisms that hydra

feed upon also tend to aggregate in that part of the aquarium, and, in brown hydra, it can be the first step of an interesting cycle: "If now the aquarium be allowed to stand for a long time undisturbed (the water remaining unchanged, but maintained at a constant level), until the food supply----becomes scanty, a very interesting series of movements may be observed-----. After a prolonged stay near the surface the animal detaches itself from the glass, and with tentacles widely outstretched sinks slowly to the bottom, often floating for a time at the surface before the descent. Arrived at the bottom, it slowly crawls once more to the light side, gradually----reascends to the surface, ultimately sinks again to the bottom, and so on.----The duration of the cycle----may be only one or two days, or it may be as many weeks". Every time the hydra is at the bottom it gorges itself with the sediment there, and eventually discharges the innutritious refuse. Hydra can live on this diet for a long time, indicating that enough food, like diatoms or bacteria, can be extracted from the mud. Green hydra do not sink to the bottom as often or as regularly, probably because of the additional energy they can derive from their symbionts.

Thus, according to Wilson, floating is a part of a cycle of movements, the function of which is to bring the hydra from near the top of the water to the bottom, where, in difficult times, food can be found. The hydra do not remain for a long time free at the surface, and the whole cycle is initiated only when the water is not changed for some time, and food becomes scarce.

A third way of attachment to the surface is mentioned by Wagner

(1905): "----a large air-bubble was attached to the basal disc, and this bubble apparently kept the Hydra afloat. It was, moreover, far from easy to remove this bubble or to break it. It seems to be surrounded by a tough substance".

A gas bubble is also discussed by Kepner and his co-workers (Kepner and Miller, 1928; Kepner and Thomas, 1928), who describe another mechanism used by hydra to reach the surface, in addition to climbing up the walls--direct floating. Their study was initiated by the observation that sometimes hydra which are lying on the bottom of the dish without being attached to it are seen to build a gas bubble at the foot region. The bubble increases in size until it lifts the animal to the surface of the water, with the basal end directed up. A detailed histological study of the foot region has shown that while the ectoderm and endoderm of the lateral part of the basal region are very similar to the same cells higher up, the cells of the basal disc itself are different. When a hydra is preparing to become attached to the substrate, all of the ectodermal cells of the basal disc are involved in mucus secretion and contain, in their distal sections, mucus granules. If, however, a gas bubble is produced, only the peripheral cells of the basal disc are involved in producing mucus, and this mucus forms a sac into which the ectoderm cells of the central region discharge gas. The discharge of gas continues until the bubble becomes large enough to lift the animal.

The endodermal cells of the basal disc are more slender and their cytoplasm is denser than that of the cells of the lateral endoderm. They contain many food vacuoles, and appear larger and more active in speci-

mens that are involved in gas secretion. Also, in these specimens the mesoglea of the basal disc becomes swollen and vacuolated. All this suggests that gas secretion is an energy requiring process, and the endoderm of the basal disc is differentiated so that it can supply the required energy when needed.

With regard to what happens to the hydra once it reaches the surface, Kepner and Miller disagree with Wagner: "When the bubble encounters the surface film of the water, its wall ruptures and forms a somewhat circular disc of mucus, that is closely applied to the surface film of the water to form a raft by which the polyp hangs. Wave-action will destroy this raft and then the specimen will sink. Or the hydra may abstract itself from the raft of mucus and sink".

No calculations are made to estimate the size of bubble needed to carry a hydra to the surface of the water, but according to data published by S. R. Williams (1900) the specific gravity of hydra is so close to that of water (green hydra-1.0095; brown hydra-1.0115) that a relatively small bubble will suffice.

Kepner, Miller and Thomas, like most workers before them, did not consider the factors that may cause hydra to float. This question arises especially after it is realized that floating is not just a continuation of the regular movements of hydra on solid surfaces. If hydra reach the surface of the water by actively producing gas bubbles, there must be some conditions that initiate the process of gas secretion, and the adaptive significance of this phenomenon should also be considered.

These subjects are dealt with in a recent study of floating behavior

by Łomnicki and Slobodkin (1966) who, by measuring floating rates at different levels of density and starvation tried to determine the conditions under which floating takes place. Floating is considered to be a rapid way for the hydra to leave their population, and the following general suggestions are made:

1. Hydra that receive no food or only small amounts of food float much more than hydra fed to excess. At low food levels there is no apparent effect of variations in the exact amount of food on floating rate.

2. The low floating rate of well-fed hydra is relatively constant for all densities (from 1 to 64 hydra per 20 ml water), while floating of hungry animals is related to density: the higher the density (up to a certain level), the higher is the rate of floating. At high densities the trend is reversed, and floating rate decreases with increased densities.

3. Floating is a response not to the actual presence of other hydra in the immediate environment, but to changes in the water, possibly caused by the presence of hydra. That such changes in the quality of the medium--so-called conditioning--are involved is demonstrated by comparing two groups of hydra, one introduced into water that had already contained hydra, and another introduced into water kept for the same length of time without containing any hydra.

4. Water is conditioned to the same degree by starved and well-fed hydra; the differences in the rates of floating between the two groups are due to differences in their response to conditioning.

As will be shown later on, not all of Łomnicki and Slobodkin's data, at least as presented in their paper, support these suggestions,

but the general relationship between floating, starvation and crowding is established. Wilson also saw a connection between floating and hunger, but according to him floating is a part of the movements within the boundaries of the population, while Łomnicki and Slobodkin consider floating to be an escape mechanism.

A second aspect of the biology of hydra, also supposed to be influenced by environmental conditions, is sexual differentiation. Tannreuther (1908) writes that "the condition necessary for the appearance of sexual organs has long been a question of much interest, especially among scientific investigators". This interest became even greater in the last 60 years, but the problem is still far from being resolved.

The literature is full of conflicting reports, but a summary of these reports published by Park, Sharpless and Ortmeyer (1965) indicates that some degree of consistency exists in the results of both field observations and experiments in the laboratory. In laboratory studies 6 species have been reported to develop gonads in response to a drop in temperature, while in 4 other species a rise in temperature is responsible for the appearance of sexuality. In almost every species the results are confirmed by at least two independent studies. Other factors have also been associated with sexuality in the laboratory. Nussbaum (1909), for example, claims that starvation leads to the development of males, while excess feeding causes the appearance of females. Whitney (1907) got sexuality only after the hydra were

transferred from a low temperature to a higher one and also did not receive any food. Loomis (1954a, 1964) accepts the notion that stagnation of the medium or crowding are involved in sexual differentiation (Grosz, 1925). Most studies, though, see in temperature, or, more specifically, in change of temperature, the primary factor behind sexuality.

Field studies do not contradict this idea. Twelve out of the 14 North American species for which there exists information about sexuality in the field (Park et al., 1965) develop gonads only in the spring or in the fall, when significant changes in the ambient temperature occur. Burnett and Diehl (1964) suggest that photoperiod may be associated with the seasonality of gonad development, and Griffin and Peters (1939) say about their species (H. oregona) that "sexual reproduction is related in a significant way to the drying up of the pond", presumably by an increase in pH.

Several laboratory studies have indicated that sexuality may also appear without any apparent change in environmental conditions (Grosz, 1925; Hyman, 1928, 1929). It is interesting to note that Hydra littoralis, about which most of these reports were made, has been reported from the field to have sexual forms all year round.

Assuming that some changes in the water are responsible for sexual differentiation, attempts have been made recently to distinguish chemically between water in which sexual forms do and do not appear. Most active in this area was Loomis, who accumulated a large amount of interesting data. But, contrary to his hope that the study will reveal

one factor which is the primary cause of sexuality, no such factor has yet been identified.

Originally (Loomis, 1954a), it was suggested that a low oxygen tension is responsible for sexual differentiation. In a later paper oxygen was ruled out as a causative factor (Loomis & Lenhoff, 1956). The evidence then indicated that another gas, which is secreted by the hydra themselves, is involved, that the gas is produced mostly in the period following feeding (a period in which respiration is highly increased), and that crowding is important because the concentration of gas has to reach a threshold in order to be effective, and the quantity produced by one hydra is not enough. The gas was identified as CO_2 (Loomis, 1957), and was even nicknamed "sex gas" (Loomis, 1959). Sexuality was shown to appear in hydra introduced into water in which other hydra had already become sexual, water that was connected by a gas-bridge to cultures containing sexual hydra, and even water in which the pCO_2 was artificially elevated. An additional factor was shown to be involved when it was found that running water, even with a high concentration of CO_2, fails to induce sexuality (Loomis, 1961). This was interpreted as meaning that high CO_2 is necessary but not sufficient, and that the accumulation of another substance, probably also produced by the hydra themselves, is needed. In its most recent version (Loomis, 1964) the theory still maintains that sexuality cannot be induced without crowding, but the primary factor is no longer CO_2. Loomis talks in general terms about cyclic feedback induction by microenvironmental enrichment, but he cannot say

anything more specific beyond suggesting that some components of the Krebs cycle may be of importance.

The various revisions of Loomis' theory occurred whenever his own findings did not support a previous version. Loomis consistently ignores or dismisses reports by others that suggest that his whole approach may be wrong. Both crowding and CO_2 concentrations were shown, under controlled conditions, not to be correlated with sexual differentiation in hydra derived from the same stock of H. littoralis used by Loomis himself (Park, Mecca & Ortmeyer, 1961, 1964). Temperature changes are not considered by Loomis to be of importance, but Park, Sharpless and Ortmeyer (1965) demonstrate that an increase in temperature induces sexuality, and that the percentage of hydra that become sexual goes up as the magnitude of the change in temperature increases. Moreover, the original description of H. littoralis (Hyman, 1934) limits its distribution to areas of swift currents, a fact that is confirmed by later observations (Hyman, 1938). In spite of the fact that such conditions do not facilitate the accumulation of whatever is needed, according to Loomis, to cause sexuality, sexual individuals were collected in these areas of rapid movement of the water.

Park, Sharpless and Ortmeyer present a hypothesis which is consistent with their findings, and which involves internal changes rather than chemical changes in the surrounding medium. According to this hypothesis H. littoralis contains two antagonistic substances--an initiator, which induces sexual differentiation, and an inhibitor, which

acts on the initiator. Normally the two are in equilibrium, and the initiator is blocked by the inhibitor. The inhibitor, though, is more temperature sensitive than the initiator, and when the temperature rises more of the inhibitor is destroyed relative to the initiator, resulting in sexual differentiation. The higher the temperature, the more rapid will be the destruction of the inhibitor, and more hydra will turn sexual.

The hypothesis of Park and her co-workers is not only consistent with data about induction of sexuality in H. littoralis, but also with a more general theory of cell differentiation in hydra, which has been developed mainly by Burnett, based on ideas first suggested by Brien. The gonads in hydra arise as a result of differentiation of interstitial cells, and it was Brien's idea that these cells undergo differentiation in response to some internal cue, specific for each type of tissue the interstitial cells differentiate to, and probably also specific for each species of hydra. In Brien (1960) we find the suggestion that "there is [sic] produced in the tissues of the hydra biochemical modifications responsible for the evolution of interstitial cells into germinal cells".

Burnett (1961) claims that the signal for differentiation does not lie in the type of stimulating substance, but rather in its quantity. According to him hydra contain an inducer which is probably of neurosecretory origin (Burnett & Diehl, 1964), the concentration of which shows a gradient extending from the hypostomal region, where it is produced, down toward the foot. The inducer seems to be identical

with the growth stimulator, the substance responsible for the axial polarity of hydra. The differentiation of interstitial cells into the various cell types depends on the relative concentrations of the inducer, and an inhibitor, produced by the dividing cells in the hypostomal region (Burnett, 1966). The inhibitor leaks into the medium and can accumulate there. Sexual differentiation occurs when for some reason the secretion of the inducer is stopped, which can probably be caused in different species by different factors. When this happens the regular growth processes, budding in particular, are slowed down or stopped completely, and the interstitial cells differentiate into gonads. The type of gonad that develops depends on the exact amount of inducer present. If enough inhibitor has accumulated in the water it can block the effect of the inducer and thus lead to sexual differentiation, even when the inducer is still being produced.

Another question which is asked with respect to sexuality is its effect, after its appearance, on population growth. As was already mentioned, the development of gonads in any individual hydra is often associated with a cessation of the process of asexual budding. What happens to the hydra after the gonads have developed is a matter of discussion and disagreement, which to a certain extent may be due to differences between the various species. Brien (1960) claims that during sexual differentiation all of the interstitial cells form gonads, and as a result there is no source of cells to replace discharged nematocytes, and feeding eventually becomes impossible so that "maintained sexuality results ultimately in death".

Burnett (1961), on the other hand, reports that a reduced number of interstitial cells can always be found in sexually differentiated hydra. This may explain Loomis and Lenhoff's (1956) finding that hydra remain sexual for a relatively long time, as long as the conditions that led originally to sexual differentiation are maintained. They feed, although their metabolic rate is much lowered, and even produce buds that become sexual while still attached to their parents. A possible explanation for the sexual differentiation of buds is given by Tannreuther (1916). His observations indicate that the development of gonads on buds is not due to differentiation of the interstitial cells of the buds themselves, but to migration of sexually differentiated cells from the parent to the bud, where they keep increasing in number and form gonads. Daily observations of individual hydra (Park, 1961) show that a hydra can remain in a sexual stage for a period of over 100 days, and there is no difference in budding rates between asexual and sexual individuals.

The various theories that connect the initiation of sexuality to a change in the equilibrium between substances that reside in the hydra themselves are consistent both with the reports about sexuality arising spontaneously in laboratory cultures, and also with the reported cases of rhythmicity in sexual differentiation. This phenomenon has been reported by Itô (1952) in H. magnipapillata, Park (1961) in H. littoralis, and Tardent (1966) in H. attenuata. Some cultures kept by Park showed for more than one year somewhat regular changes in the frequency of sexuality. The length of each "cycle" varied from about 20 to about

40 days, and the frequency of sexuality increased and decreased regularly over a rather wide range, from as low as 0% to as high as 50% in one case, or from 35% to 80% in another. Daily changes of water did not affect the rhythmical pattern. Individual hydra were also shown to undergo regular changes between asexual and sexual phases, with extreme variability in duration of sexual and asexual periods (from 1 to 100 days) for any given hydra and from hydra to hydra. No satisfactory explanation is available for the causes of such "cycles".

Both floating behavior and sexual differentiation can be interpreted as escape behavior (Slobodkin, 1962, 1968). The information about both is, as we have seen, quite confusing, but both have been suggested, at least by some, to be a response to changes in environmental conditions. The general impression is that both could be eventually tied into a unified theory of regulation, on the level of the individual as well as the population. Łomnicki and Slobodkin's conditioning of the water, Loomis' enrichment of the environment and Burnett's inhibitor which leaks out of the body, if they correspond at all to the real situation, may all be different interpretations of the same phenomenon. Even if they are completely independent of each other, they all suggest that a change in the medium may play an important role, directly as the primary factor or indirectly as the intermediate between the primary factor and the hydra, in determining the dynamics of the population--whether the hydra will reproduce or not, whether they will reproduce asexually or sexually, and whether they will stay where they are or

migrate to some other place.

The aim of the present study is to try and establish more exact relations between floating, sexuality, and some environmental conditions that are of ecological importance, to see whether the various reactions to environmental conditions are correlated to each other, and to consider the adaptive significance of escape mechanisms in hydra. No attempt was made to identify the exact environmental factors involved.

MATERIALS AND METHODS

All the hydra used during the course of the entire study belong to one clone of Hydra littoralis, derived from a single individual which was selected at random from a stock culture of unknown origin that had been maintained for several years by L. B. Slobodkin. A clone was used in order to eliminate the possibility that differences in results are due to genetic differences rather than differences in treatment. Because of technical limitations it was impossible to control the genetic factor, and it was decided, therefore, to remove it completely from the design, in spite of the need for more data about genetic variability in hydra (Lashley, 1915). A discovery of genetically determined differences in floating behavior, for example, would have been of great interest.

The medium used for maintaining the stock and performing the experiments was Loomis' "Littoralis (L) solution" (Loomis, 1953), containing 0.35g NaCl, 0.07 g $CaCl_2$ and 0.01 g $NaHCO_3$ per liter of demineralized distilled water. The solution was prepared from stock solutions, following the recommendations made by Loomis, in quantities of 1-4 gallons, according to the demand. This meant that different preparations could have been used on different days of one experiment, but, on the other hand, each preparation was used within a few days after it was made. The L-solution, which serves as artificial pond water, will be referred to in the description of the various experiments as water.

The stocks were kept in open finger bowls, and all the experiments were conducted either in Pyrex beakers of various sizes or in 100 x 20 Pyrex petri dishes, all covered to minimize evaporation and contamination by dust. Changing water involved transferring the hydra to a clean dish with a fresh supply of water. The dishes were washed with Microsolv detergent (Microbiological Associates, Inc., Bethesda, Maryland), rinsed several times in tap water followed by demineralized distilled water, and then air dried.

Throughout the study all the hydra were housed in an Environ-Room (Lab-Line Instruments, Melrose Park, Illinois), set at a constant temperature of 18°c and constant humidity of 85%. Fluctuation around these values was very small. Uniform fluorescent light was turned on continuously. All of the handling of the animals, setting up the experiments and collecting the data were done inside the room, so that the hydra were never exposed to conditions other than the ones existing inside. Each newly made preparation of L-solution was also kept in the room for at least 24 hours before it was used.

Artemia eggs, from the San Francisco Bay area, were hatched daily, and the nauplii were used as food. Nauplii from eggs collected in the Great Salt Lake proved to be harmful to the hydra. Hatching occurs at room temperature within 24-48 hours after the eggs (1/8 teaspoon) are spread over the surface of an 80-100 fold dilution of a saturated NaCl solution in water (about 750 ml), placed in a shallow Pyrex baking tray (3 qts. size). The Artemia can be easily collected

after they aggregate at an illuminated corner of their dish. Feeding is done immediately after all traces of salt are washed away by rinsing the Artemia several times with distilled water and L-solution, through a fine mesh net. Only actively swimming nauplii were given as food, and each feeding session lasted 1-2 hours, during which the dishes were kept in the dark to assure random distribution of Artemia. All of the uneaten Artemia, most of which are dead after a 2 hour stay in fresh water, were removed soon after feeding was over. According to Loomis and Lenhoff (1956) hydra eat as much as they can utilize rather early in the feeding period, so that the purpose of the quick removal of the uneaten food is mostly to prevent harmful effects of the dead Artemia on the hydra.

All contact with the hydra and their food was done by means of glass micropipettes that were changed frequently and kept in hot water when not in use.

Only hydra hanging freely from the surface of the water were counted as floating.

Further details are given in the descriptions of the individual experiments.

EXPERIMENTAL WORK

The experiments to be described can be divided into two major groups:

1. Short term experiments, of several days' duration, in which rates of floating were studied in relation to several parameters.

2. Long term experiments, to see the population consequences of the removal of floating hydra.

Experiments of the first kind are described and discussed in great detail by Łomnicki & Slobodkin (1966)[1] and the purpose of repeating them here was (1) to find out whether their results can be confirmed, (2) to establish the exact relationships between floating and environmental conditions for the clone used in the long term experiments, (3) to observe the appearance of sexuality and see its effect on floating, and (4) to study factors other than crowding and starvation that may suggest themselves, in the course of the long term experiments, as relevant to the determination of the rate of floating.

The major effort in the present study was devoted to the long term experiments, as these seem crucial for the understanding of the ecological significance of floating, and only a small number of such experiments, limited both in range of conditions and duration, are reported by L&S.

Most of the experiments were designed on the assumption that L&S's conclusions are correct. First to get started were the long-term ex-

[1]Because of the frequent references to their paper, Łomnicki and Slobodkin will be referred to in the following text as L&S.

periments. Reviewing the data and checking the validity of the conclusions had to wait until the long-term experiments were completed. As is often the case, some of the experiments seem now, in view of the results, irrelevant and unnecessary. A use of this hindsight will have to wait for future studies, however, and for the present work an effort was made to use all the available data.

Each of the experiments will be described and discussed separately. The order of presentation does not follow the classification to short and long term experiments, but is aimed at achieving some kind of a logical sequence. A general discussion will follow.

I. THE EFFECT OF CROWDING ON THE RATE OF FLOATING.

This is a repetition of L&S's initial experiment, in which the relationship between crowding and floating was established. In their experiment 7 levels of crowding were compared--1, 2, 4, 8, 16, 32 and 64 hydra per 20 ml of water. A constant number of hydra--sixty-four--was used for each level, with the amount of water varying according to the desired density. Not all 64 animals of a given density were kept in one container--each container had only 20 ml of water, so that the number of containers varied from 64--each containing one hydra--for the lowest density, to 1--containing all 64 hydra--for the highest density. All hydra were placed on the bottom of their dish at the beginning of the experiment, and were left, without handling or feeding, for 5 days. The number of floating hydra was recorded every day. Two controls--"fed" and "mock fed"--were also established, but those will be referred to later, as they are not necessary for demonstrating the relationship between crowding and the rate of floating.

L&S present the results of this experiment in their Figure 1. For each density the daily numbers of floating animals are combined, and the result--given as a fraction of 320 (= 5 x 64), which is the highest possible number of floating hydra during the 5-day period--is used as a measure of the floating rate at that density.

The only clear trend in the curve of floating rate vs. density is the decline in floating at levels of crowding above 16 hydra per 20 ml water. At densities below 16 hydra per 20 ml there is some indication of an increase in floating with an increase in density, but the changes are

rather small, from about 55% in the density of 1 hydra per 20 ml to less than 70% in 8 hydra per 20 ml. The value of 16 hydra per 20 ml is also within this range. Judging from these values alone--as evidently was done by L&S--the statement that "there is an apparent optimum [?] floating rate of intermediate crowding levels" can be challenged.

It is also doubtful whether the sum of the daily counts of floating hydra should be used as a measure of the rate of floating. On the assumption that floating is a response to conditioning of the water and to the level of starvation of the hydra themselves, we can expect the number of floating hydra to increase (or, at least, not to stay constant) from day to day. The shape of the curve of daily changes may be more meaningful than the sum of all the values of each curve, which is equivalent to the average rate of floating during the 5-day period, and for which similar values can be obtained from curves of completely different shapes. Curves for the different densities can be reconstructed from Figure 2 of L&S, and these indicate that the different densities vary only in the speed at which they reach the peak in floating activity. Differences between the different densities exist mainly in the first 3 days, with the intermediate densities (in this case 4-8 hydra per 10 ml) reaching values of 70-80% floating as soon as day 2 or 3, while lower or higher densities reach similar values later. Once the maximum value has been reached, there is no decline in the percent floating, so that toward days 6 or 7 most densities have similar high rates of floating. It would be interesting to find out whether the data used for Figure 2 of L&S, which were collected from an experiment very much

like the one described above, will yield a curve similar in shape to that of Figure 1. The raw data are unavailable, and Figure 2 itself is too generalized.

Ia. Equal number of hydra in all densities.

Experimental design

The experiment involved six levels of crowding--1, 2, 4, 8, 16 and 32 hydra per 20 ml, with the 32 animals used for each density distributed between the appropriate number of 50 ml beakers, each containing 20 ml water. Each level of crowding was replicated twice, and each beaker was kept for 8 consecutive days, without handling or feeding of the hydra. Only non-budding, non-sexual hydra were chosen to start the experiment, but a few did develop buds during the 8 days of the experiment.

Results

The daily counts of floating hydra are summarized in Table 1. Higher numbers of floating hydra do occur in the higher densities, but the major differences seem to exist between the lowest densities on one hand, and the intermediate and high ones on the other. Within the second group the difference is mainly with respect to the time it takes to reach the maximum values of floating.

Summing the values of the first 5 days of each density, and combining the replicates, we get the following values (the percentages are calculated from the maximum possible total of 64 x 5 = 320 hydra), which are equivalent to the values used by L&S in their Figure 1:

Table 1. Number of hydra (out of a total of 32) floating on successive days after beginning of experiment. Each value is the sum of floating animals in all beakers of a given density, separately for each replicate.

Density (number of hydra per 20 ml)	Replicate	Days after beginning of experiment							
		1	2	3	4	5	6	7	8
1	1	2	0	1	2	2	2	5	5
	2	7	4	4	3	4	7	11	9
2	1	9	2	2	4	4	4	5	6
	2	7	4	4	3	8	21	22	21
4	1	1	0	0	7	8	14	12	10
	2	1	4	10	13	17	25	25	27
8	1	1	1	1	5	11	14	12	11
	2	3	3	14	25	28	26	29	23
16	1	3	3	2	7	16	15	17	24
	2	4	11	22	29	27	25	22	24
32	1	3	6	15	8	7	19	20	22
	2	11	24	23	23	22	23	23	24

density (number of hydra per 20 ml):	1	2	4	8	16	32
sum of floating hydra during the 5 day period:	29	47	61	92	124	142
percent floating during the 5 day period:	9.1	14.7	19.1	28.8	38.8	44.4

Even if we accept these values as meaningful for measuring the rates of floating, L&S's suggestion of a maximum ("optimum") floating rate of intermediate densities cannot be supported. The values here keep increasing as the density goes up.

Ib. Equal number of dishes in all densities.

The difference between the results reported by L&S and the results of experiment Ia can be due to any of several reasons--different strains (or species) may have been used, the physiological condition of the animals may have been different, etc. One other possibility suggested itself when it was realized that in experiment Ia the variations between beakers with exactly the same conditions were often very large. The 32 hydra kept at a density of 16 per 20 ml, for example, occupied 2 separate beakers, each containing 16 hydra, and it was not unusual to find in one beaker 3 floating hydra while the other had, on the same day, 12 hydra which were floating. Among the 4 beakers containing 8 hydra each, a range of 0 to 6 floating hydra was also quite frequent. This indicates that local conditions in any one beaker, apart from the controlled parameters like volume of water or number of hydra, may be very important in triggering floating behavior (it may be, for

example, that not all hydra condition the water to the same degree, and the presence of a specially active "conditioner" will lead to an exceptionally high number of floaters in its dish). A more acceptable explanation is, of course, random variation. If enough replicates are available for each density, the extremes on one side of the mean can be cancelled by the extremes to the other side, but the higher densities had only 1 or 2 replicates, and there is no way to be sure how close their values were to the mean.

Experimental design

Experiment Ia was redesigned, therefore, this time using a constant number of beakers at each density, and varying the total number of hydra kept at each density accordingly.

The range of densities was the same as in experiment Ia, again using 50 ml beakers, each containing 20 ml of water. Ten such beakers were used for each level of crowding. The number of hydra subjected to each density varied from 10 in the lowest density (1 hydra per beaker) to 320 in the highest (32 per beaker). All other conditions were identical to those of Ia. The experiment was done twice.

Results

The daily means and standard deviations of floating hydra per beaker are given in Table 2. In Table 3 each mean is given as a fraction of the total number of hydra in the beaker, so that floating rates in different densities can be compared. This comparison can best be made using Figure 2, in which the average daily means (percents of total) are plotted as a function of time, for each density

Table 2. Floating of hydra on successive days after beginning of experiment, as a function of density; each value is the mean and standard deviation of 10 beakers kept under identical conditions. The two replicates are listed separately.

Density (hydra per 20 ml)	Replicate	Days after beginning of experiment 1	2	3	4
1	1	0.0	.10± .32	0.0	0.0
	2	.10± .32	.20± .42	0.0	0.0
2	1	.30± .48	.20± .42	.10± .32	.30± .67
	2	.50± .53	.20± .42	0.0	0.0
4	1	.70± .48	.40± .52	.40± .52	1.10±1.10
	2	.70± .67	.30± .48	.60± .52	.50± .85
8	1	.80± .63	.70± .67	2.20±1.55	4.50±1.96
	2	1.30±1.42	1.00±1.33	2.80±2.62	4.50±2.46
16	1	3.30±2.50	1.50±1.78	9.60±2.88	11.50±3.06
	2	3.80±3.33	6.00±3.30	11.40±3.57	12.20±1.69
32	1	3.70±3.89	10.00±7.59	18.90±6.31	11.50±3.98
	2	2.40±1.71	20.70±4.55	13.20±5.25	11.60±5.66

Density (hydra per 20 ml)	Replicate	Days after beginning of experiment 5	6	7	8
1	1	.10± .32	.10± .32	.10± .32	.10± .32
	2	.40± .52	.40± .52	.30± .48	.10± .32
2	1	.20± .42	.30± .48	.60± .84	.50± .71
	2	.40± .52	.50± .53	.60± .70	.80± .42
4	1	1.40± .84	1.90± .74	1.50± .85	1.70±1.25
	2	1.20± .92	1.70±1.34	1.80±1.03	2.30±1.42
8	1	4.60±1.17	5.20±1.48	4.70±1.77	4.00±1.25
	2	4.40±1.51	4.30±1.23	3.80±1.69	3.70±1.95
16	1	10.80±1.93	9.50±2.01	9.00±2.49	7.80±1.81
	2	11.30±2.87	10.90±2.23	10.40±2.12	8.30±2.75
32	1	17.70±3.02	18.20±3.79	17.40±3.63	17.00±2.54
	2	20.10±2.60	18.90±3.93	19.40±3.69	19.50±2.07

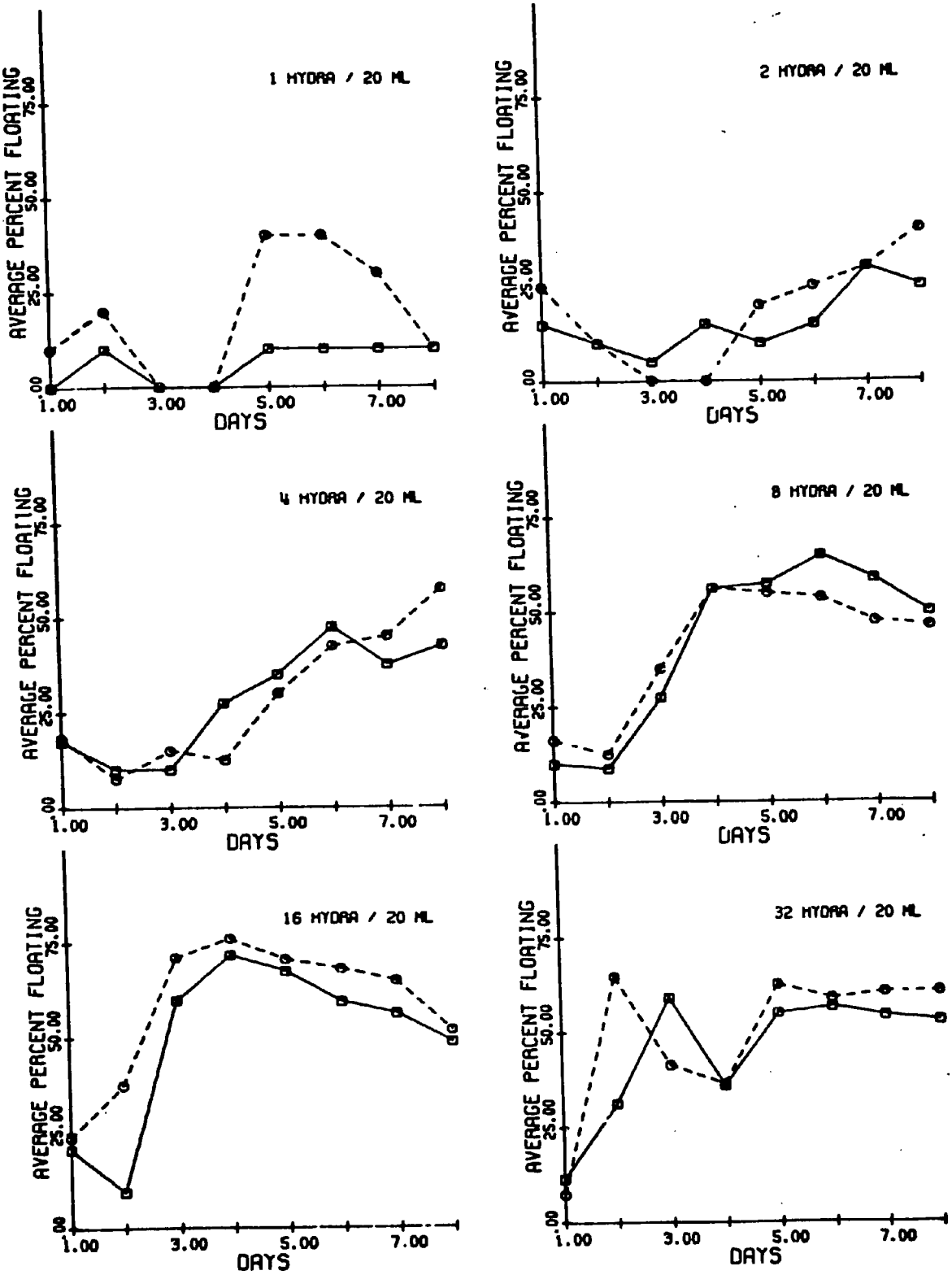
Table 3. Floating of hydra on successive days after beginning of experiment, as a function of density; each value is the average percent floating at a given density on a given day. The two replicates are listed separately.

Density (hydra per 20 ml)	Replicate	Days after beginning of experiment 1	2	3	4
1	1	0.0	10.0	0.0	0.0
	2	10.0	20.0	0.0	0.0
2	1	15.0	10.0	5.0	15.0
	2	25.0	10.0	0.0	0.0
4	1	17.5	10.0	10.0	27.5
	2	18.5	7.5	15.0	12.5
8	1	10.0	8.75	27.5	56.25
	2	16.25	12.50	35.0	56.25
16	1	20.6	9.4	60.0	71.9
	2	23.75	37.5	71.25	76.25
32	1	11.6	31.25	59.1	35.9
	2	7.5	64.7	41.25	36.25

Density (hydra per 20 ml)	Replicate	Days after beginning of experiment 5	6	7	8
1	1	10.0	10.0	10.0	10.0
	2	40.0	40.0	30.0	10.0
2	1	10.0	15.0	30.0	25.0
	2	20.0	25.0	30.0	40.0
4	1	35.0	47.5	37.5	42.5
	2	30.0	42.5	45.0	57.5
8	1	57.5	65.0	58.75	50.0
	2	55.0	53.75	47.5	46.25
16	1	67.5	59.4	56.25	48.75
	2	70.6	68.1	65.0	51.9
32	1	55.3	56.9	54.4	53.1
	2	62.8	59.1	60.6	60.9

FIGURE 2. FLOATING AS A FUNCTION OF TIME (AT SIX DIFFERENT DENSITIES)

SOLID LINE = REPLICATE 1
DASHED LINE = REPLICATE 2



separately.

In most cases there is a good agreement between the two sets of replicates. At the lowest density one replicate shows a large increase in the rate of floating compared to the other set, which remains constantly low, but toward the end of the experiment both sets show low rates.

In the density of 1 hydra per beaker floating is constantly low, around 10% (ignoring the rise and decline in one replicate). The two densities of 2 and 4 hydra per beaker remain on a low level for 3 or 4 days, and then the frequency of floating increases constantly, reaching 30-40% on day 8 at the density of 2 hydra per beaker, and 50-60% at that of 4 per beaker. At higher densities there are rapid increases in the frequency of floating almost from the beginning, with the hydra kept at a density of 8 per beaker reaching the maximum on day 4, those kept at 16 per beaker on day 3, and those kept at 32 per beaker reaching a somewhat lower level on day 2.

Discussion

Although the results are not in contrast with those reported by L&S, it seems that the interpretation should be modified. L&S measure the rate of floating as the total number of floating hydra during the entire length of the experiment, and base their conclusions on such measures, but these values can be expected to be meaningful for comparisons only if the curves of floating as a function of time for all densities are parallel to each other. Figure 2 shows that this is not the case.

Except for those of the lowest densities, the curves in Figure 2 have two more or less distinct parts--an initial part in which floating rate increases with time, and a second part in which floating, having reached some maximum value, remains at that level or even declines. The day on which the switch is made from the first part to the second is different in the different densities.

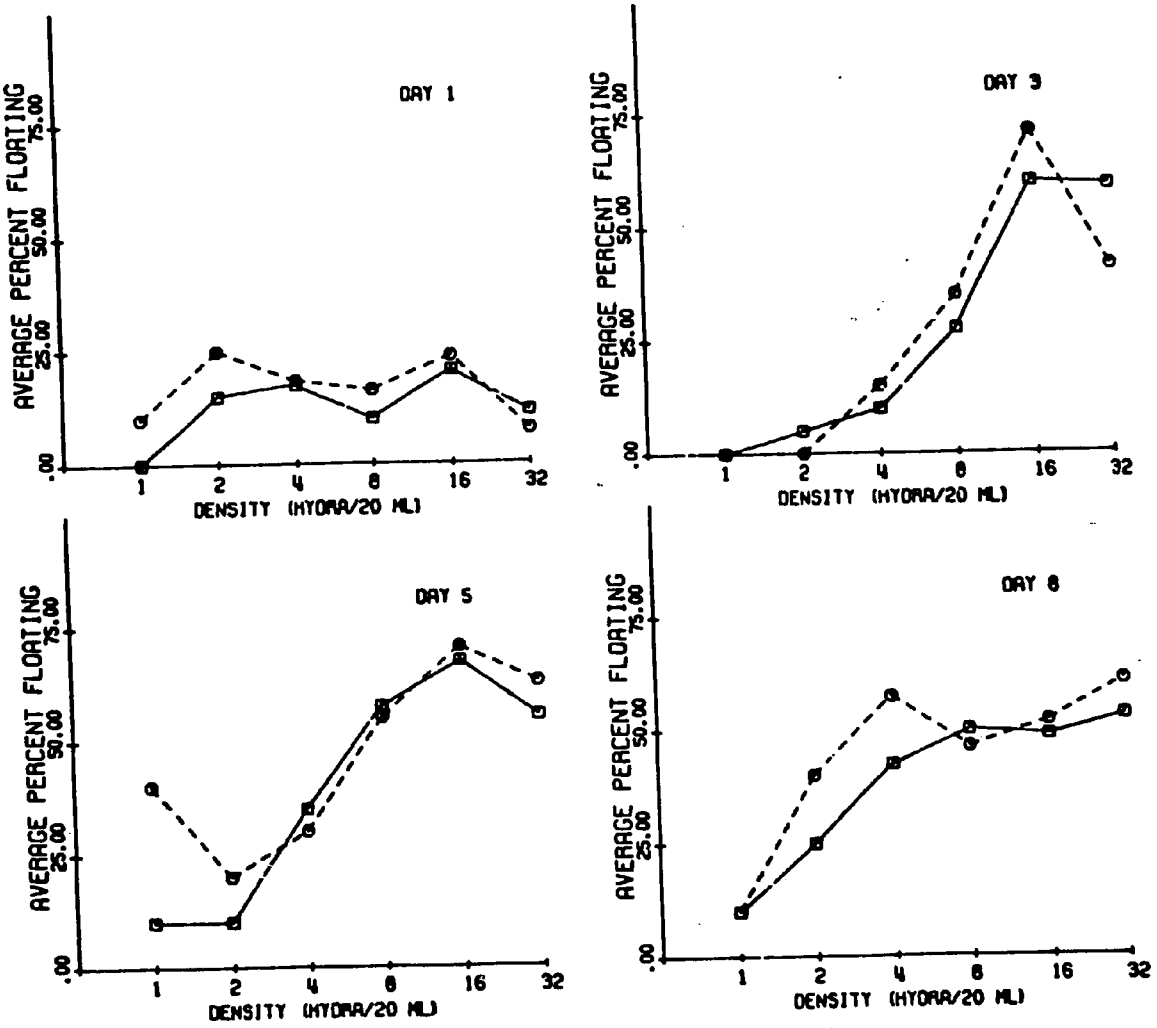
The dependence of floating on density is limited only to the initial part of the experiment, before the maximum rate of floating has been reached. The lower the density, the longer it takes the hydra to reach the maximum rate of floating, so that initially relatively more animals float at the higher densities. But as floating rates in more densities reach maximum values, the differences between densities become less apparent. This is clearly demonstrated in Figure 3, where floating rates are plotted as a function of density for 4 different days. On day 3 the two highest densities show floating rates of about 60%, while on day 5 the three highest, and on day 8 the four highest densities have similar high rates of floating.

We can conclude, then, that the upper limit of the rate of floating, the highest percent of hydra found floating together in one dish, is not a function of density, at least under the design of the present experiment, which is also the design used by L&S--the hydra being kept for several days in a relatively small volume, without food or change of water. In the 3 highest densities--8, 16 and 32 hydra/20 ml--the highest measured percentages of floating were 65.0, 76.25 and 64.7, re-

FIGURE 3.

FLOATING AS A FUNCTION OF DENSITY
(ON FOUR DIFFERENT DAYS)

SOLID LINE = REPLICATE 1
DASHED LINE = REPLICATE 2



spectively, and the average levels of floating, after the initial increase, were close to these values.

It is impossible to say what controls the maximum rate of floating. The shape of the dish or the depth of the water may be very important. Starvation is probably not a primary factor, because the level of starvation is the same in all densities, while the rate of floating does show significant variation, at least initially. It can be, of course, that starvation becomes more and more important toward the second half of the experiment, as the animals become hungrier, while in the first part, as long as the hydra have enough food reserves, they respond to the level of conditioning.

In some densities, especially the high ones, there is some decline in floating rates after the maximum has been reached. Such a decline may be due to two factors--hydra may sink back to the bottom after floating for some time, or they may move across the surface to the side of the beaker and become attached to the wall. The two possibilities have been reported by previous workers. Counts of hydra sitting on the bottom and on the walls suggest that the second alternative takes place more often than the first. The urge to "walk around" seems to increase as the number of other hydra in the dish increases, probably in an effort to avoid physical contacts with other hydra. When many hydra are floating, some physical contacts will be made at the surface, leading to "wanderings" across the surface of the water that may end with some hydra becoming permanently attached to the wall. This is probably more important in the higher levels of crowding, where the

initial burst of floating activity is quickly checked, and the floating level stabilizes according to the equilibrium between the tendency to avoid physical contacts and the tendency of many hydra to move to the surface of the water.

Individual dishes, supposedly identical, often show a wide range of variation in floating rates, suggesting the existence of a major random component among the factors responsible for floating. The rates of floating in the second replicate of both experiments Ia and Ib are higher than those of the first replicate. This suggests that slight variations in the water or in the physiological condition of the hydra themselves (the 2 replicates were not performed simultaneously) can also affect the results.

II. FLOATING AS A RESPONSE TO CONDITIONING.

If, as claimed by L&S, the rate of floating is a function of density, or, in other words, the level of crowding somehow regulates floating behavior, there must be a way for hydra to "measure" the level of crowding around them. L&S show that the effect of crowding is mediated through conditioning of the medium. Floating rates in water that had already contained hydra are higher than the rates of similar hydra introduced to unconditioned water. But the data of L&S reveal some inconsistencies that are ignored by the authors. In their design conditioning was done by groups of 4 hydra, each kept for 5 days in 10 ml water. At the end of the conditioning period the hydra used for the conditioning were removed, and replaced by other groups of 4 so-called test-hydra. Similar groups were introduced as controls to units of 10 ml water that were kept for the same 5 days without containing any hydra. The following table gives the frequency of floating among test hydra introduced to conditioned water (column A), hydra introduced into non-conditioned water that was kept in the same containers for 5 days (column B), and hydra introduced at a density of 4 per 10 ml into fresh water (column C):

day	A	B	C
1	.38	.09	.30-.40
2	.54	.40	.60-.70
3	.74	.56	.70-.80
4	.72	.65	.70-.80
5	.78	.72	.80-.90
6	.77	.78	.80-.90

[The values in columns A and B are calculated from L&S's Table I,

and those in column C are estimates based on L&S's Figure 2.]

There is no real difference between the floating rate of hydra introduced to conditioned water (A) and hydra introduced to fresh, non-conditioned water (C). It looks as if the difference between columns A and B is not due to increased rate of floating caused by conditioning, but rather to the initially reduced rate of floating of hydra introduced into the control containers.

According to L&S the rate of floating is a function of the degree of conditioning of the medium, which in turn is a function of the density of hydra and the length of time the hydra have been in the water. They suspect, therefore, that the rate of floating, when the test hydra are introduced in groups of 4 into 10 ml of conditioned water, is higher than expected, because in addition to the conditioner released by the conditioning hydra, the test animals add their own. There is nothing in the data to suggest that the floating rate was higher than expected, but to remove any doubt L&S repeated the experiment, using only one test animal per 10 ml instead of four. The values they got are as follows (columns A, B and C have the same meaning as above):

Day	A	B	C
1	.86	.11	.20-.30
2	.78	.22	.30
3	.69	.19	.40-.50
4	.78	.31	.50
5	.72	.25	.50-.60
6	.81	.31	.60-.70

As with 4 test animals/10 ml, floating rate in the control (column B) is much below the rate of floating in water which was just introduced

into the plastic compartments (column C). The results in column A are completely unexpected, although nothing is said about it by L&S. The experiment was repeated in order to remove possible effects of additional conditioning by the test animals, but now the floating rates, starting from day 1, are at least as high as the floating rates in the last days of the first run, when the supposed effect of the additional conditioning must have been maximal.

One possible explanation suggests itself in spite of L&S's statement that "all test animals [in both runs] had been subjected to circumstances that elicited a high floating rate immediately before the beginning of the test period". As mentioned in the paper, the test animals in the first run were taken from the stocks, while the test animals in the second run were selected from among the hydra used for the conditioning. This means that in the second run the test animals had not eaten for at least 5 days prior to the beginning of the test period, while the test animals in the first run were probably not as starved. It is very likely that the high rate of floating in the second run is a result of the degree of starvation of the test animals, as well as the conditioning of the water.

In short, L&S's results are not very conclusive. Conditioning is shown to have an effect on floating in some cases, but the exact relations between the two have yet to be worked out. The aim of experiment II is to confirm that floating is increased by previous conditioning, and to see whether the effect of conditioning is a function of density.

IIa. Floating in conditioned and non-conditioned water.

Experimental design.

The basic design is the same as that of L&S, with differences in the densities used. Ten 50 ml beakers, with 20 ml of water each, were used for conditioning, and 10 served as non-conditioned controls. Conditioning was done by keeping 16 hydra for 5 days without food in each of the 10 beakers. The control beakers contained water but no hydra for the same 5 days. Four hydra, newly taken from the stock cultures, were introduced into each of the 20 beakers after the conditioning animals were removed, and were left without food for 3 days.

All hydra were non-budding and non-sexual. The experiment was done twice.

Results and discussion.

The results of the experiment are given in Table 4.

Floating rates during conditioning were very close to the values obtained in experiment Ib for the same density of 16 hydra/20 ml (Table 3).

The test animals floated much more in the conditioned than in the non-conditioned water. The frequency of floating in the control beakers was within the range of values found in experiment Ib for the density of 4 hydra/20 ml. Floating in the conditioned water was much higher; it also kept increasing during the 3 days of observation, coming close, on day 3, to the maximum rate of floating shown by the conditioning animals. The fact that the high rate of floating was not reached immedi-

ately means either that the response to the conditioning takes a few days, or that there was an additional response to the presence of the test animals themselves.

IIb. Conditioning as a function of density.

Demonstrating that conditioned water causes an increase in floating rates is not enough to prove the dependence of floating on density. It has to be shown that the rate of floating of the test animals will vary according to the density used during conditioning, meaning that conditioning is an additive process and that floating is not a reaction to conditioning in general, but to the exact degree of conditioning or amount of conditioner in the medium.

Experimental design.

Ten 50 ml beakers, each containing 20 ml water, were used for each level of density during conditioning, which lasted 5 days. Seven levels were used, including a non-conditioned control--0, 1, 2, 4, 8, 16 and 32 hydra/20 ml. After the 5 days all the conditioning hydra were removed, and 4 hydra, taken from the stock cultures, were introduced for 3 days into each beaker. Only non-budding non-sexual hydra were used.

Results and discussion.

The results are given in Table 5.

The floating rates can be divided into two groups--one including hydra in non-conditioned water and in water conditioned by 1 hydra/20 ml, and the other including all the rest. In the first group floating rate is

Table 4. Floating in conditioned (by 16 hydra/20 ml for 5 days) and non-conditioned (control) water. Rates are given for 3 successive days after introduction of test hydra. Numbers are sums of floating hydra in all 10 beakers; in parentheses--percent floating out of a total of 40.

	Conditioned water		Control	
Day	Run 1	Run 2	Run 1	Run 2
1	16 (40.0)	14 (35.0)	3 (7.5)	8 (20.0)
2	24 (60.0)	22 (55.0)	2 (5.0)	4 (10.0)
3	31 (77.5)	23 (57.5)	3 (7.5)	8 (20.0)

Table 5. Floating among test hydra introduced into water with different levels of conditioning. Ten beakers were used for each level, and 4 test hydra were introduced into each beaker and watched for 3 days. The values are percent floating among a total of 40 animals.

Level of conditioning (hydra/20 ml)	Percent floating		
	Day 1	Day 2	Day 3
0	17.5	17.5	17.5
1	22.5	12.5	12.5
2	35.0	32.5	30.0
4	35.0	30.0	30.0
8	40.0	37.5	35.0
16	30.0	37.5	35.0
32	32.5	32.5	32.5

slightly higher than the rates of the control group in experiment IIa. In the second group the floating rate, in all levels of conditioning, is roughly the same as the rate on the first day of the test period in conditioned water in IIa, but, in contrast to that experiment, the rates here remain constant for all 3 days.

Why this is so is not clear, and no satisfactory explanation is available. It may be that the conditions of different experiments are not as similar as expected, because of unobservable physiological differences between the animals, or between the preparations of Artificial Pond Water. The fact that the values of the first day of the test period are similar in both experiments supports the suggestion that on the first day we see a response to the already existing conditioning of the water, while the later increase (in experiment IIa) is caused by the action of the test animals themselves. For some reason this increase did not appear in experiment IIb.

Like experiment IIa, IIb confirms the role of conditioning in triggering floating behavior, but no effect of density is apparent. In experiment Ib we saw that after several days floating rates become identical in most densities. We then suggested that the difference between the densities is in the time it takes to reach maximum floating. If the rate of floating is a response to the level of conditioning, we can now suggest that the same level of conditioning can be achieved by all densities, with the higher densities reaching it earlier, and most densities--under the present experimental design--reaching it in 5 days. This means that conditioning is a qualitative change. It can also be a quantitative change--

something accumulating in the water--but once the quantity of the conditioning factor passes a certain saturation level, the response is the same regardless of the exact amount.

A better understanding of the role of conditioning can be gained from an experiment that was not done in the present study--measuring floating rates in water conditioned not only by different densities, but also for different lengths of time.

III. LONG-TERM POPULATION STUDIES.

Introduction

L&S conclude in their paper that floating is a response of hungry hydra to crowding. Furthermore, they suggest that the rate of floating is a function of the degree of crowding, which is indicated by the amount of conditioner in the medium. If this is the case, floating immediately suggests itself not only as an important factor in the dynamics of hydra populations in nature, but also as a potential density-dependent mechanism for maintaining the population size at a constant level.

Although our knowledge about the ecology of hydra is very limited, it is not unreasonable to consider the total amount of hydra in a body of water to be divided into smaller or larger, but distinct, aggregates, each derived asexually from one or a few founders. Each such aggregate can be considered to be a population which, because of the ability of hydra to float and thus migrate away from it, is not as closed as is expected from a population of sessile organisms.

Assuming that L&S's findings are correct, and that their results were derived from only a limited range of conditions, we can build an hypothesis about the role of floating in the dynamics of such hydra populations. This hypothesis is not stated explicitly in L&S's paper, but all their arguments, especially in the discussion, strongly suggest that is more or less what they have in mind. The hypothesis is as follows: Hydra stay at one place as long as the conditions in this place are favorable. For the favorability of a place there are two measures,

which under most conditions are independent of each other--the amount of food that a hydra gets and the degree of conditioning of the water around it. The tendency to float increases as the favorability of the environment declines. The best environment, which the hydra is least likely to leave, is one in which there is plenty of food and a low density of hydra. The worst combination of conditions exists when a very dense population does not get any food, and then floating occurs at a high frequency. It may be that hungry hydra float regardless of density, or that well-fed hydra do not float even at very high densities, but it is also likely that combinations of starvation and low density or abundance of food and very high densities lead to rates of floating which are intermediate between the ones at the two extremes mentioned above. Within that intermediate range we can expect that addition of food will reduce the tendency to float at a given density, and an increase in density will increase the tendency to float at a given food level. Floating can be kept at a minimum at any given density, within that intermediate range, by giving each hydra enough food to counteract the effect of crowding.

A hydra that floats away either finds a new empty place to settle down and starts a new population, or is washed away by waves or currents and eventually disappears. The hydra that do not float are also affected by floating, because each floating hydra reduces the level of crowding in the remaining population. This may have two consequences, both working in the direction of reducing the rate of floating--a reduc-

tion in the level of conditioning and an increase in the amount of food that each hydra is getting. (The reduction in the amount of conditioner will probably not have an immediate effect. To get any effect of conditioning at all the substance which is responsible for conditioning has to accumulate around the hydra without immediately diffusing into tne entire lake. This can happen if the substance is not of a small molecular size, and if there are no currents. For this reason the conditioner can be expected to be there even after some of the hydra that produced it had left, so that floating may continue at the previous rate for quite some time. Hopefully, the conditioner will eventually diffuse out of the area, or will become somehow inactivated, without an equal amount being produced to replace it.)

Under normal conditions floating is the only way for a hydra population to lose some members. Addition of new individuals to the population occurs as a result of budding. New members increase the density, which leads to higher rates of floating. The availability of food plays here a double role--both the production of buds and the rate of floating depend on the amount of food that each hydra receives.

At equilibrium, when population size is relatively constant, with relatively constant food level and degree of mixing of the water around the hydra, the increase in the population due to budding equals the loss due to floating. With a constant food supply, as the population is growing, more and more hydra share the food. When the equilibrium level is reached, the amount of food that each hydra is getting is exactly

enough to compensate for the tendency to float as dictated by the density. Addition of new individuals above the equilibrium level (we must assume that the amount of food needed to produce a bud is smaller than the amount needed to prevent floating) will both increase the density and reduce the amount of food available to each hydra, so that floating will occur, returning the population to its equilibrium level. The bigger will the departure from equilibrium be, the higher is the floating rate expected to be. Thus, floating acts as a regulatory valve, achieving a constant population size by maintaining a balance between the level of crowding, an increase in which increases the tendency to float, and the availability of food, an increase in which reduces the tendency to float.

All this, of course, is highly simplified and generalized. Conditions in the field are never so constant. This should not mean, though, that the hypothesis cannot apply to natural populations. The parameter which is expected to vary when conditions change is population size at equilibrium, but the maintenance of that equilibrium will be achieved by the same mechanism as suggested above.

A check of the validity of the hypothesis can be more easily made in the laboratory, where constant conditions can be maintained for very long periods of time. This was the aim of the experiments to be described in the present section, which involve growing populations, with replicates, at various combinations of food level and volume of water, and studying the effect of the removal of floating hydra on the growth and dynamics of these populations. This design was also used, on a very preliminary scale, by L&S. Only after all the data had been col-

lected and analyzed it was realized that a different design would have given much better results without changing the amount of work involved.

The two factors which affect, according to the hypothesis, the rate of floating, are the amount of food available to each hydra and the density of the population. The experiment, of course, has to be designed in such a way that the hypothesis could be proved or disproved according to the results. The best test would involve setting various combinations of previously determined food levels (per individual) and densities, predicting which combinations are going to be stable and which are not, and following the populations to see whether the predictions are confirmed. But for this we have to know already the exact relationship between density and food level, while we do not even know yet if there exist such equilibrium densities.

For the time being we have to resort to a test which involves predetermined values of only one factor, and letting the population adjust the value of the other, by removing floating animals until an equilibrium stage is reached. The factor which can be more easily pre-determined is the availability of food per hydra. For each such food level we can start populations at different initial densities, and see what happens when floating hydra are removed. The volume in which each population is maintained is not changed, as is the amount of food given daily to each of the non-floating hydra. If the hypothesis is correct, we should find that (1) each population does eventually stabilize at a constant level of density, (2) the equilibrium densities of all populations of any given food level are the same, and (3) the equilibrium densities increase with

an increase in the daily ration of food per hydra. If there is no correlation between equilibrium densities and food level we can conclude that the availability of food does not play an important role in determining floating rates.

The experiments to be described here did not use this approach. Neither the availability of food per hydra nor the density were kept constant throughout the experiment. It can even be said that all populations were started at identical initial conditions, because what was kept constant were the total amount of food available to the population as a whole and the volume in which the population was maintained, and each population was started with one individual. The initial conditions of all populations can, therefore, be described as abundance of food and very low density. Differences between the conditions in which the populations are kept should become more pronounced as the populations grow, mostly because the higher food levels can support higher numbers of hydra, and higher numbers mean, at equal volumes of water, higher densities. What may prevent the buildup of these higher densities is the fact that floating hydra are always removed, so that, in a sense, we are letting the population "choose" the combination of food availability (per individual) and density at which floating rate equals budding rate, and this may be the same combination in all populations. One potential variable that, under the present design, may be of significance, is the fraction of the total daily food requirement per hydra which is met under the various conditions. As long as the density is low relative to the

amount of food in the dish, each hydra is expected to eat as much as it wants. At high food levels the equilibrium density may be such that the remaining hydra will never lack food. At low food levels, on the other hand, it may be that food becomes a limiting factor at the population size at equilibrium. In general, though, predictions are difficult, if not impossible, to make, and the rest of the discussion of these experiments will have to be postponed until after the results are analyzed.

A preliminary idea about the support the results give to the hypothesis can be derived from L&S's paper. As mentioned earlier, they used a similar approach in a few experiments that are summarized in their Table V. In addition to maintaining constant the total amount of food given to the population as a whole (only one quantity, 200 Artemia/ day, was used) and the volume in which each population was kept (either 100 ml or 1000 ml), they added two more variables--initial population size (1, 50 or 100 hydra) and the frequency at which floating hydra are removed (once every 1 or 2 days). They also counted the amount of food left uneaten every day, to get an estimate of the average amount of food consumed by each hydra. The only supporting evidence that the results give to their hypothesis is the demonstration that by removing the floating hydra the populations remain at a relatively constant level. The claim about floating being a density-dependent phenomenon cannot be supported at all. Four populations were kept at 100 ml water, but their levels at equilibrium varied from 6.96 to 30.69 hydra, with the other two being 8.46 and 20.55. It is interesting to note that the amount

of food consumed by each hydra was rather close for all 4 populations--8.2, 8.1, 7.4 and 5.2 Artemia/hydra/day. Average floating rates were also close to each other--17%, 21%, 14% and 21%, with no relation to the average population size or density. Even more surprising is the fact that at 1000 ml water population size at equilibrium was 10.33 hydra, average floating rate was 15% and food level was 7.5 Artemia/hydra/day. It looks as if all hydra, at least under L&S's set of conditions, got as much food as they wanted (there were always Artemia left uneaten), and that floating rate does not depend on density. Judging from these results we may suggest that population size (or density) is determined by the rate of floating, rather than floating being influenced by density.

The present work included, in addition to the open populations, from which the floating hydra were removed, a set of closed populations, where floaters were not removed. These control populations were grown at all combinations of food level and volume used for growing the open populations. The original aim of having closed populations was to compare the effect of living in open versus closed populations on the hydra themselves. As it turns out, the closed populations present an opportunity to check the hypothesis from an additional point of view.

The central point of L&S's hypothesis is the relationship between floating and density. In the open population this point is looked at only indirectly, because densities and food levels vary from day to day, and the major key to the confirmation of the hypothesis lies in the average population size at equilibrium, and its relations to external conditions.

The closed populations, on the other hand, are expected to grow until food becomes a limiting factor, and the final size reached by each population is largely a function of the amount of food available (Slobodkin, 1964). After these stationary stages are reached we have a series of populations of different densities, each maintained for a long period of time at constant levels of food and density. A comparison of floating rates at the various densities can show directly whether or not floating is a function of density. The advantages of this method over the approach used in experiment I are that here the hydra remain at a constant level of hunger from day to day, and long-term trends, if present, can also be studied.

A second escape mechanism which can be studied in these populations is sexuality. The appearance of sexuality is not expected to affect the final population size, because no loss of hydra is involved (unless Brien's claim about the eventual death of sexual individuals is correct). But sexuality can affect growth rates, as it was shown to be correlated with a reduction in budding, and most interesting will be the relationship between sexuality and floating. The results should contain information about such questions as the tendency to float among sexual and non-sexual hydra, and the relation between floating rates and frequency of sexuality.

Methods and experimental design

The ranges of conditions used in experiment III involved all 15 possible combinations of 5 food levels and 3 volumes of water. The

food levels were 20, 40, 80, 150 and 300 Artemia/day, and the populations were kept in 20, 40 or 80 ml water, in Pyrex petri dishes. Five populations were started at each combination, two of which were closed, with no removal of the floaters ("A" populations), the other three being open, with floating hydra removed every day before feeding ("B" populations). The name of each population is composed of several parts, the first referring to the number of Artemia given daily, the second to the volume, and the third says whether the population is closed (A) or open (B) and which replicate it is among the populations grown under the same set of conditions. Population 150 40 B2, for example, is the name of the second replicate of the open populations receiving 150 Artemia/day and kept at 40 ml water. Reference to groups of populations will be made using only the criterion according to which they are grouped. Thus, population 150 40 B2 can be said to belong to the "B" populations (open), the 150a/d populations (those receiving 150 Artemia/day), or the 40ml populations (those kept at 40 ml).

All populations were started with one non-budding and non-sexual hydra.

As one of the major objectives of the study was to find out whether the open populations stabilize around a constant level of population size, it was necessary to maintain the populations for a rather long period of time. On the basis of pilot experiments it was decided to keep each population for 150 days. Because of technical limitations not all populations could be handled together, and the experiment was divided into

two separate parts. The first part involved all of the 300a/d and 150a/d populations, and the second part all the others. Each population was started on a different day, to spread somewhat the effort involved in handling the populations. More importantly, if some cyclic or rhythmical phenomena are observed, it enables the separation of cycles that are caused by unknown cycles in the environment (these should show parallel effects at the same dates on different populations regardless of age) from cycles that are caused by internal factors, probably in relation to the age of the population (and which, therefore, will show different effects on different populations at any particular date).

Because of uncontrollable circumstances, the first half of the study had to be stopped before the populations reached the planned age of 150 days. One population out of a total of 75 (population 300 20 B2) was eliminated after 86 days because of a contamination that killed all the hydra.

Tables 6 ("A" populations) and 7 ("B" populations) list all the populations that were established in the course of the study, together with the date of initiation of each population, the date of termination and the age of the population on its last day.

One combination of food level and volume--80 Artemia/day and 80 ml of water--was used in an additional, smaller experiment in which open populations were established at initial high densities. The purpose of this experiment was to see whether the populations that start at a high level stabilize around the same density as the open populations

Table 6. A list of the closed ("A") populations established in experiment III.

Population name	Day of initiation	Day of termination	Age (in days) at termination
20 20 A1	Nov. 30, 1967	Apr. 28, 1968	150
20 20 A2	Dec. 3, 1967	May 1, 1968	150
20 40 A1	Nov. 17, 1967	Apr. 15, 1968	150
20 40 A2	Nov. 18, 1967	Apr. 16, 1968	150
20 80 A1	Oct. 29, 1967	Mar. 27, 1968	150
20 80 A2	Nov. 1, 1967	Mar. 30, 1968	150
40 20 A1	Oct. 29, 1967	Apr. 27, 1968	150
40 20 A2	Dec. 2, 1967	Apr. 30, 1968	150
40 40 A1	Nov. 13, 1967	Apr. 11, 1968	150
40 40 A2	Nov. 14, 1967	Apr. 12, 1968	150
40 80 A1	Oct. 28, 1967	Mar. 26, 1968	150
40 80 A2	Oct. 31, 1967	Mar. 29, 1968	150
80 20 A1	Nov. 28, 1967	Apr. 26, 1968	150
80 20 A2	Dec. 1, 1967	Apr. 29, 1968	150
80 40 A1	Nov. 11, 1967	Apr. 9, 1968	150
80 40 A2	Nov. 12, 1967	Apr. 10, 1968	150
80 80 A1	Oct. 29, 1967	Mar. 27, 1968	150
80 80 A2	Oct. 30, 1967	Mar. 28, 1968	150
150 20 A1	Mar. 6, 1967	June 11, 1967	97
150 20 A2	Mar. 7, 1967	June 12, 1967	97
150 40 A1	Mar. 6, 1967	June 14, 1967	100
150 40 A2	Mar. 7, 1967	June 14, 1967	99
150 80 A1	Mar. 6, 1967	June 16, 1967	102
150 80 A2	Mar. 7, 1967	June 18, 1967	103
300 20 A1	Jan. 31, 1967	June 19, 1967	139
300 20 A2	Feb. 1, 1967	June 21, 1967	140
300 40 A1	Jan. 31, 1967	June 22, 1967	142
300 40 A2	Feb. 1, 1967	June 23, 1967	142
300 80 A1	Jan. 31, 1967	June 24, 1967	144
300 80 A2	Feb. 1, 1967	June 25, 1967	144

Table 7. A list of the open ("B") populations established in experiment III.

Population name	Day of initiation	Day of termination	Age (in days) at termination
20 20 B1	Dec. 6, 1967	May 4, 1968	150
20 20 B2	Dec. 9, 1967	May 7, 1968	150
20 20 B3	Dec. 12, 1967	May 10, 1968	150
20 40 B1	Nov. 21, 1967	Apr. 19, 1968	150
20 40 B2	Nov. 24, 1967	Apr. 22, 1968	150
20 40 B3	Nov. 27, 1967	Apr. 25, 1968	150
20 80 B1	Nov. 8, 1967	Apr. 6, 1968	150
20 80 B2	Nov. 9, 1967	Apr. 7, 1968	150
20 80 B3	Nov. 10, 1967	Apr. 8, 1968	150
40 20 B1	Dec. 5, 1967	May 3, 1968	150
40 20 B2	Dec. 8, 1967	May 6, 1968	150
40 20 B3	Dec. 11, 1967	May 9, 1968	150
40 40 B1	Nov. 20, 1967	Apr. 18, 1968	150
40 40 B2	Nov. 23, 1967	Apr. 21, 1968	150
40 40 B3	Nov. 26, 1967	Apr. 24, 1968	150
40 80 B1	Nov. 5, 1967	Apr. 3, 1968	150
40 80 B2	Nov. 6, 1967	Apr. 4, 1968	150
40 80 B3	Nov. 7, 1967	Apr. 5, 1968	150
80 20 B1	Dec. 4, 1967	May 2, 1968	150
80 20 B2	Dec. 7, 1967	May 5, 1968	150
80 20 B3	Dec. 10, 1967	May 8, 1968	150
80 40 B1	Nov. 19, 1967	Apr. 17, 1968	150
80 40 B2	Nov. 22, 1967	Apr. 20, 1968	150
80 40 B3	Nov. 25, 1967	Apr. 23, 1968	150
80 80 B1	Nov. 2, 1967	Mar. 31, 1968	150
80 80 B2	Nov. 3, 1967	Apr. 1, 1968	150
80 80 B3	Nov. 4, 1967	Apr. 2, 1968	150
150 20 B1	Mar. 8, 1967	June 10, 1967	94
150 20 B2	Mar. 9, 1967	June 10, 1967	93
150 20 B3	Mar. 10, 1967	June 10, 1967	92
150 40 B1	Mar. 8, 1967	June 10, 1967	94
150 40 B2	Mar. 9, 1967	June 10, 1967	93
150 40 B3	Mar. 10, 1967	June 10, 1967	92
150 80 B1	Mar. 8, 1967	June 10, 1967	94
150 80 B2	Mar. 9, 1967	June 10, 1967	93
150 80 B3	Mar. 10, 1967	June 10, 1967	92
300 20 B1	Feb. 7, 1967	June 6, 1967	119
300 20 B2	Feb. 8, 1967	May 5, 1967	86
300 20 B3	Feb. 9, 1967	June 6, 1967	117
300 40 B1	Feb. 7, 1967	June 7, 1967	120
300 40 B2	Feb. 11, 1967	June 7, 1967	116
300 40 B3	Feb. 9, 1967	June 7, 1967	118
300 80 B1	Feb. 7, 1967	June 8, 1967	121
300 80 B2	Feb. 8, 1967	June 8, 1967	120
300 80 B3	Feb. 9, 1967	June 8, 1967	119

which start at an initial size of 1 and grow at the same combination of external conditions. The three populations included in this study--the "C" populations--were all kept for 63 days, from July 30 through Sept. 30, 1968. Population 80 80 C1 had an initial size of 200 hydra (80 non-budding and 120 budding), 80 80 C2 got started with 100 hydra (40 non-budding and 60 budding), and the initial size of 80 80 C3 was 50 (20 non-budding and 30 budding). All were non-sexual.

All populations were fed once a day, usually in the afternoon. Before feeding the volume was reduced to 20 ml in all dishes. A counted number of Artemia was added to each dish, and the hydra were left in the dark for a period of 1 to 2 hours. After eating the hydra were rinsed twice in clean water, and then transferred to a clean petri dish with the appropriate amount of water. All the hydra were placed on the floor of the dish, and those which had bubbles attached to their feet were carefully separated from the bubbles. No counts of leftover Artemia were made, but in the second part of the experiment (the 20a/d, 40a/d and 80a/d populations) it was noted whether or not Artemia were left at the end of the feeding session. If less than 10% of the introduced Artemia were left it was recorded as total consumption.

Censusing was done before the food was introduced, and the removal of the floating hydra from the "B" and "C" populations was also done at that time. Each population was counted every day, except for the "A" populations of which complete counts were made every few days after the growth phase was over. In the 20a/d, 40a/d and 80a/d

"A" populations the numbers of floating hydra were recorded daily. During the counts the hydra were sorted into 4 categories--non-floating non-sexual, non-floating sexual, floating non-sexual, and floating sexual. For each category a distinction was made between hydra with 0, 1 or 2 buds. An IBM card containing the daily readings in the 12 categories was punched for each population. Because of the very low occurrence of hydra with 2 buds the hydra carrying 1 or 2 buds were later lumped into a single group of budding hydra, so that the final classification involved 8 categories. All the analysis of the data was done using the IBM cards; details of the analysis will be given together with the results.

The floating hydra which were removed daily were weighed by means of a Cahn Gram Electrobalance (Model G). Before weighing the hydra were put on aluminum foil pans, 12 mm in diameter, and dried overnight under a desk lamp. The pans were made out of "Chef-Foil" aluminum wrap (Anaconda Aluminum), that was found to be resistent to corrosion. Five out of 10 pans kept in a petri dish served as blanks to correct for daily differences in the weights of the pans. The hydra were weighed in groups of 1-4 per pan, with each group containing hydra of roughly equal sizes, all belonging to the same category of the same population.

All the hydra, floating and non-floating, of all populations were weighed one day after the last feeding.

The results are presented and discussed separately for the "A",

"B", and "C" populations. Several aspects of the populations, in addition to floating rates and sexuality, are also treated in the discussion.

The "A" populations

The daily readings for each population, instead of being presented in long tables, are summarized in two plots, made by the CALCOMP plotter at the University of Michigan Computing Center, from the data on the punched cards. One plot is that of the growth curve of the population, and the other presents the occurrence of sexuality and the frequency of floating during the entire experiment, both measured as percents of total population size. The values in the curve of sexuality are the percentages for the days when complete censuses were made. The histogram-like curve of floating is based on averages of successive 10-day periods, because the variation in floating rates from day to day made it difficult to distinguish any trends in curves showing daily values. The averages in the curves of the 20a/d, 40a/d and 80a/d populations are each based on 10 readings; for each day for which total counts are not available, floating rate is calculated from the number floating on this day and the value of total population size on the next total census. This does not introduce much error, because the populations show, after the end of the growth period, very small variations in total counts. For the 150a/d and 300a/d populations daily readings of floating are not available, and the averages are based on as many values as the number of total counts made during each 10-day period. The number of such counts (and the number of values used in calculating the 10-day averages of floating rates) is as follows:

Periods	Number of counts
days 1-10; 11-20; 21-30; 31-40	10
41-50	7-8
51-60; 61-70	3
71-80; 81-90; 91-100; 101-110; 111-120	1-2

All the plots are given in Appendix A. All curves are plotted at the same scale, except for the growth curves of the 300a/d populations, which had to be drawn on a smaller scale because of space limitations.

Growth curves

The growth curves of the "A" populations can all be described generally as S-shaped, with an initial lag period, usually short, followed by a growth period and a more or less long period of steady state. Similar results are reported by Slobodkin (1964). In contrast to most other cases of S-shaped growth curves, where reaching the upper asymptote means reaching an equilibrium between the number of newborn and the number of dying animals, at the upper asymptote of hydra populations no new individuals are added, and there are no deaths. Slobodkin (1964) implies that deaths do occur, but there was nothing in the present work to indicate that this was the case here. Remains of dead hydra were often found in sick or contaminated cultures, and it is hard to believe that all dead hydra always disintegrated before the daily censuses. Budding rates were zero or very close to zero in all populations after the final level of population size had been reached, and no oscillations of the type expected when there is a turnover of individuals existed. The small variations in total counts were caused mostly

by errors in counting and by occasional losses of hydra during the transfer to clean dishes. These may also be the reasons for the fluctuations in Slobodkin's populations. Initial increases to levels much higher than the final size, followed by major declines, as seen in many of Slobodkin's populations, were never observed.

The final size reached by a population with a limited supply of food is, of course, a function of the amount of food. Slobodkin (1964) estimates that in H. littoralis the ratio between the number of hydra at the final population size and the number of Artemia in the daily food ration is roughly 1:1. A distinction has to be made, though, between the final size reached by a growing population and the maximum size that can be maintained by a given amount of food. The amount of food required for maintaining a single hydra is a function of the size of that hydra, and the number of hydra maintained by a given amount of food depends on the size of the animals. If a hydra population is given as many Artemia as there are hydra in the population, the hydra will probably lose weight until they reach a size that can be maintained by an average of one Artemia a day. If, on the other hand, a growing population is given a constant amount of food, budding will cease before population size reaches a value equal to the number of Artemia in the daily ration. At that stage each hydra will get enough food to maintain itself, but there will not be enough extra food for production of new buds. The population can still grow a little, because some hydra may occasionally get Artemia in a number large enough to produce a bud, but this will result in the

food being distributed among a larger number of hydra, so that the chances of another hydra getting enough food to produce a bud will be reduced, and the population growth will eventually stop completely at a level well below the maximum that can be maintained. The weights of the hydra at that time will be intermediate between the minimal weight necessary for budding and the weight of a very starved hydra.

Slobodkin (1964) found that in growing populations the same population size is reached, for a given amount of food, regardless of the initial size. One other factor that should be considered, in light of Burnett's model of the regulation of growth and differentiation, is the volume in which the population is maintained. Volume may be important if, as suggested by the model, budding depends, among other things, on the concentration of an inhibitor to cell division in the budding region. Normally the inhibitor, which is produced in the hypostome, leaks out before it reaches the budding region, and buds can be produced. If, however, the density of hydra is high, the inhibitor can accumulate in a significant quantity in the medium, and thus affect from the outside the production of buds. Among populations receiving the same amount of food, growth should stop earlier at the populations kept at smaller volumes, and the final size reached by these populations should be lower.

The final size maintained by a population at the steady state stage will be referred to as the K value of the population. For each population it was calculated as the mean of all total counts starting from an arbitrarily chosen day, on or before which population growth seemed to

have stopped. The sharp declines seen in the growth curves of the 150a/d and 300a/d populations were probably caused by carelessness during the handling of the populations, and the values of these parts of the curves were not included in the calculation of K (they were used in the calculation of the rates of floating and sexuality). The first days of the periods used for the calculation of K are given in Table 8, and the K values themselves are listed in Table 9.

The K values can be compared in two directions--across each line of Table 9, to test for the effect of volume, and down each column, to see whether the dependence of K on food level is linear or not.

The comparisons across the lines were done by a one way Analysis of Variance, one for each line The F ratios are as follows:

Food level (Artemia/day)	F (2, 3)	p
20	0.44	$p > .10$
40	13.47	$.05 > p > .025$
80	6.22	$.10 > p > .05$
150	1.63	$p > .10$
300	55.49	$.005 > p$

The only strong indication of a difference between the 3 volumes exists in the highest food level. The trend is as predicted--the lower the volume (the higher the density), the lower is the final population size. At all other food levels the density is probably not high enough to have any effect.

The check for linear relationship between food level and density was done by fitting a linear regression line between the K values and the food levels, separately for each volume, excluding the K values of the

Table 8. Population age (in days) at which each "A" population reached its final steady-state size. K values were calculated as means of all total counts from these days through the end of the experiment (except for a few last counts for some of the 150 a/d and 300 a/d populations.

Population	Age (in days)	Population	Age (in days)
20 20 A1	117	150 20 A1	68
20 20 A2	105	150 20 A2	70
20 40 A1	94	150 40 A1	61
20 40 A2	80	150 40 A2	74
20 80 A1	65	150 80 A1	68
20 80 A2	45	150 80 A2	70
40 20 A1	66	300 20 A1	70
40 20 A2	70	300 20 A2	73
40 40 A1	55	300 40 A1	77
40 40 A2	45	300 40 A2	73
40 80 A1	62	300 80 A1	74
40 80 A2	47	300 80 A2	76
80 20 A1	78		
80 20 A2	81		
80 40 A1	50		
80 40 A2	49		
80 80 A1	60		
80 80 A2	56		

Table 9. K values of the "A" populations (2 replicates at each combination of food level and volume).

Food level (Artemia/day)	Volume 20 ml		40 ml		80 ml	
20	11.54	11.59	14.00	11.89	13.53	10.53
40	19.90	21.24	22.21	21.08	24.58	24.07
80	47.29	53.40	44.86	44.57	41.91	38.18
150	91.25	90.71	92.22	93.80	91.63	94.33
300	197.40	188.56	216.67	228.50	247.00	246.29

highest food level, where the additional factor of density may have an effect. Setting X to be the food level and Y the K value, the three equations were found to be

at 20 ml $Y = -1.8 + .623X$
at 40 ml $Y = -2.2 + .624X$
at 80 ml $Y = -2.3 + .616X.$

Both slopes and Y intercepts are very close to each other, indicating that the relationship between food level and K is the same in all volumes. The Y intercepts are not far from the expected value, which is zero, and the fit of the line to the points is excellent, as shown by the following Analyses of Variance:

20 ml

Source	df	SS	MS
due to regression	1	7667.35	7667.35
deviation about regression	6	45.88	7.65
Total	7	7713.23	

$F(1, 6) = 1002.76$

40 ml

Source			
due to regression	1	7686.59	7686.59
deviation about regression	6	44.08	7.35
Total	7	7730.67	

$F(1, 6) = 1046.33$

80 ml

Source	df	SS	MS
due to regression	1	7497.09	7497.09
deviation about regression	6	143.97	23.99
Total	7	7641.06	

$F(1, 6) = 312.45$

The K values of the 300 a/d populations, as expected, do not fit the regression lines, but the deviations are not in the expected direction. The expected K values of the 300a/d populations, calculated from the regression equations, together with the observed values, are as follows (see also Fig. 4):

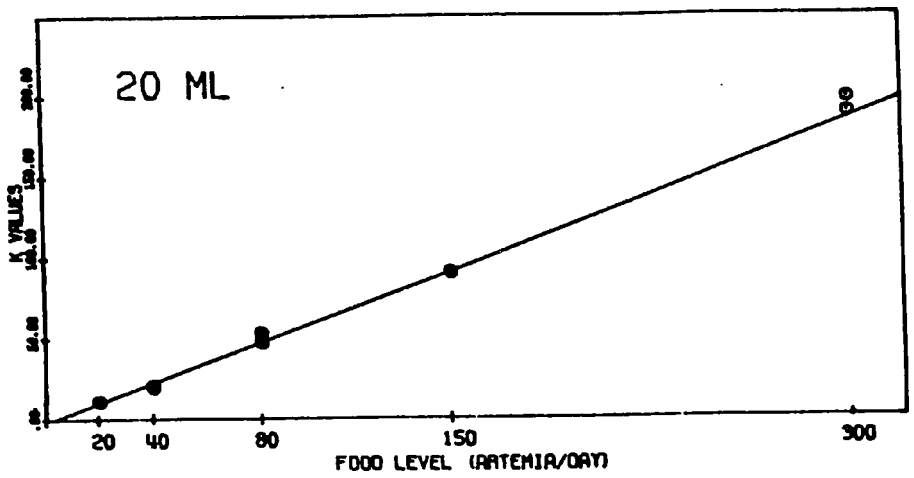
	K values		
		Observed	
Volume	Expected	K_1	K_2
20 ml	185.09	197.40	188.56
40 ml	185.05	219.67	228.50
80 ml	182.48	247.00	246.29

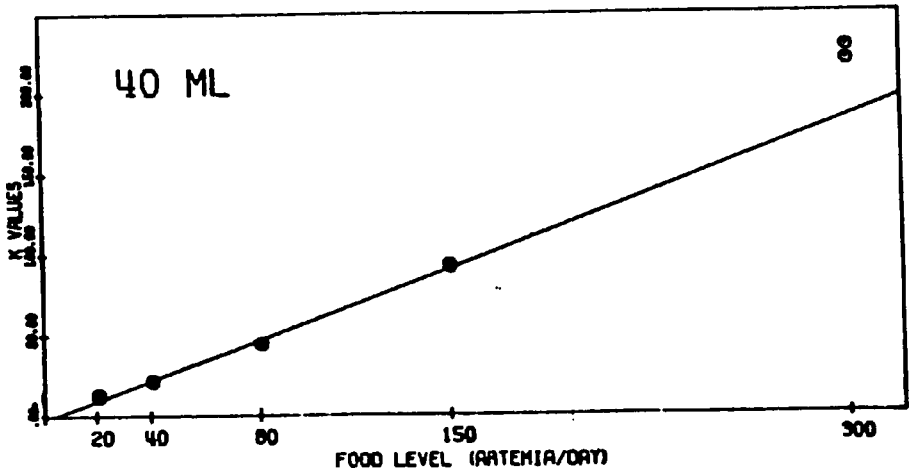
The closest fit is expected to be in the 80ml populations, where the effect of density is the smallest. The other values should fall below their respective expected values, with the K values of the 20ml populations deviating more than those of the 40ml populations. Here the situation is reversed--the best fit is shown by the 20ml populations, with the values of the other populations being larger than their expected values, and the largest deviations shown by the 80ml populations.

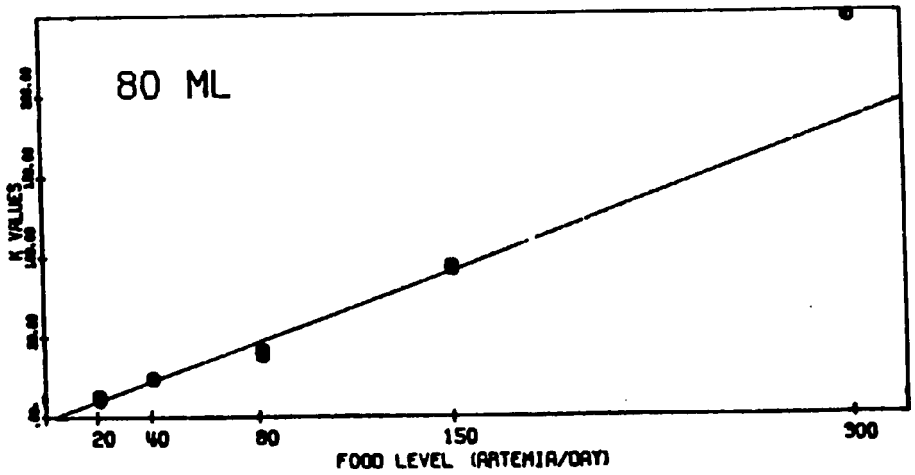
One possible explanation for this is that the ability of hydra to overcome the effect of the inhibitor can be increased by an increased amount

FIGURE 4. K VALUES OF THE 'A' POPULATIONS AS A FUNCTION OF FOOD LEVEL

THE K VALUES OF THE POPULATIONS RECEIVING 300 ARTEMIA/DAY (OPEN CIRCLES) WERE EXCLUDED FROM THE CALCULATION OF THE REGRESSION LINES







of food. At the high food levels we can expect a few hydra, especially those sitting in the area where the Artemia are introduced, to grab a relatively high number of Artemia before they disperse all over the dish and are caught by the other hydra. The higher is the total number of Artemia introduced into a dish, the higher is the number of Artemia that one hydra may catch by chance. A bud will be produced if a sufficient amount of Artemia will be caught by one hydra for a sufficient number of days. Indeed, more budding hydra were observed in the steady-state stage of the 300a/d populations than in all other populations. When the density of hydra in the dish reaches a level at which the concentration of the inhibitor is large enough to prevent budding even by the hydra that gets the highest amount of food, budding will stop and the populations will remain at a constant size. We can say, therefore, that the effect of the inhibitor is a function not only of density, but also of the amount of food consumed by individual hydra in the populations.

A comparison of the growth periods of the various populations may also be of interest. Floating occurs also during the growth period, and if a relationship exists between growth rate and floating rate, we may learn something about the factors responsible for floating. In addition, the appearance of sexuality may be a function of the growth rate. Even if no such relations exist, the growth rate itself can serve as an indicator of the amount of food consumed by the hydra, and reveal apparent cases of food limitation even when not all the Artemia are consumed.

Growth rates were calculated using the logistic equation. This equation approximates rather well the actual growth curves of many of the populations, and it can be easily handled mathematically. No claim is made here that the logistic equation is the correct way to describe population growth of hydra, but it can certainly serve for comparing the populations with each other.

In the logistic equation growth rate is measured by r, the innate rate of increase. The equation is

$$\frac{dN}{dt} = rN \frac{K-N}{K} ,$$

where N is the population size at time t and K is the final size reached by the population. After integration and taking logarithms the equation becomes one of a linear regression of the logarithm of $\frac{K-N}{N}$ against time--

$$\ln \left[\frac{K-N}{N}\right] = a - rt.$$

r is the negative of the slope of the regression line.

When the population grows exactly according to the logistic equation, fitting a regression line to any part of the growth curve should result in the same slope. This was found not to be the case for the hydra populations. The entire growth period of a population usually could not be used, because it often included segments that clearly did not fit the logistic equation. An objective method for selecting an r value that best describes the growth of the population had to be used.

Only the part of the growth curve describing active population growth was used for the calculation. Eliminated from the calculation were the part used for the calculation of K, where hardly any increase in population size took place, together with the first 20 days of the growth curve, where differences in the history of the hydra used for starting the populations might have had an effect. The K value of each population was calculated prior to the calculation of r. The selected section of active growth was then divided into overlapping segments, each containing 10 successive values of total counts. Days on which no total counts were made were skipped. The following were calculated for each of these segments:

1. r, or the negative of the regression coefficient of $\ln(\frac{K-N}{N})$ against t.
2. a, or the intercept of the regression line with the Y axis.

These two values can now be used for generating an expected growth curve. N_o, the expected population size on day 20, is found using the equation

$$N_o = \frac{K}{(\text{antilog } a+1)} ,$$

and then the entire expected growth curve is generated by means of the recurrence equation

$$N_{t+1} = \frac{N_t e^r}{1+N_t (e^r - 1)/K} .$$

For each day for which there exists a total count we can now calculate the squared deviation of the logarithm of the observed population size from the logarithm of the expected, and the mean of all the squared deviations is a measure of the goodness of fit of the expected growth curve to the observed.

After the process is completed for all the segments of 10 successive counts, the r value that gives the smallest mean squared deviation is selected as the r which best describes the growth curve of the population.

The r values of all "A" populations, as listed in Table 10, do not show much variation. One exception are populations 20 20 A1 and 20 20 A2, with r values which are much below the rest. These are the populations that reached their K values at a very late date. It is difficult to understand why, if this is a result of the effect of volume, the effect does not appear in the populations receiving more food and reaching higher densities. Difficulties in catching enough Artemia should exist also in the 20a/d populations kept at higher volumes. Apart from these 2 populations, for all other food levels there is no effect of volume (density) on growth rate, so that differences in floating rates--within each food level--cannot be associated with differences in the rate of growth. The changes in r with food level are due to differences in the amount of food available to the hydra at the initial parts of the growth curve, but here too the changes are not consistent for the whole range of food levels. Because of this the subject of growth rate will not be considered in subsequent discussions, and to finish

Table 10. Growth rates (r values) of the "A" populations. There are 2 replicates of each combination of food level and volume.

Food level (Artemia/day)	Volume 20 ml	40 ml	80 ml
20	.012	.061	.073
	.024	.097	.085
40	.104	.097	.097
	.085	.121	.097
80	.085	.109	.097
	.077	.109	.109
150	.158	.170	.158
	.145	.158	.121
300	.121	.120	.133
	.145	.121	.133

the discussion here a brief comparison of the results of the present study with those of others will now be made.

The calculation of growth rates by other workers was always based on exponential growth, observed for short periods of time when the density is low and food is abundant. Turner (1950) and Loomis (1954b) base their estimates on the time needed for the population to double itself, and Loomis estimates that the maximum rate of growth achieved by H. littoralis under optimum physical conditions and intensive feeding is $r = 0.44$. Stiven (1962a) criticizes Loomis' approach, and bases his own calculations on Cole's (1960) adaptation of Thompson's generation law to immortal animals like hydra. Stiven's values fall below those of Loomis, and show variation according to temperature and food level. The r values reported here for 18°C seem to fit the trend reported by Stiven for H. littoralis. Schroeder (1969) calculated r values, also using the equation of exponential growth, for H. pseudoligactis under various feeding conditions, and reports a range from 0.0 to 0.28. The range in Table 10 is well within these limits.

Daily consumption of food

Only indirect information is available about the amount of food consumed daily by the hydra. If force-fed, hydra will eat 20 Artemia or more. L&S report that when food is abundant, and the hydra do their own catching, they stop after 6-8 Artemia. This may have been true also here, but no direct counts were made. Estimates of the mean number of Artemia caught per hydra can be given only for the periods when all the Artemia in the dish were caught; no data about

this are available for the 150a/d and 300a/d populations. On days when some Artemia were left in the dish we cannot say that food was not a limiting factor, because if a few Artemia are left with only a few hydra present in the dish, the Artemia can easily escape being caught. This may be the reason for the tendency of the r values to increase with an increase in the food level (Table 10), but its effect is obviously not large.

Table 11 includes, for each population, the day on which food first became completely consumed (and remained so until the end of the experiment), and lists, for each such day, the population size, the ratio between that size and the K value, and the food consumption per hydra.

In general, at least in the 20a/d, 40a/d and 80a/d populations, food becomes totally consumed when the population reaches a level which is roughly one half of its final size. A trend can be seen in the 40a/d and 80a/d populations--in the populations kept at the smaller volumes total consumption of food is achieved by a number of hydra which is smaller than the one needed for total consumption in high volumes. As this cannot be due to differences in volume during feeding (this volume was the same for all populations), it may be that volumes, although they do not have an effect on K or r, do cause some differences in the size of individual hydra, or the number of Artemia they catch per day. These differences disappear when the K values are reached.

A trend can also be seen in the time it takes the population to

Table 11. "A" populations--the days on which food became totally consumed, and some information about the populations on these days.

Population	Day	Population size (N)	N/K	Food level (Artemia/day)/N
20 20 A1	65	6	.52	3.3
20 20 A2	80	6	.52	3.3
20 40 A2	30	6	.43	3.3
20 40 A2	30	6	.50	3.3
20 80 A1	40	8	.59	2.5
20 80 A2	30	6	.57	3.3
40 20 A1	25	8	.40	5.0
40 20 A2	30	10	.47	4.0
40 40 A1	35	11	.50	3.6
40 40 A2	35	12	.57	3.3
40 80 A1	40	13	.53	3.1
40 80 A2	35	13	.54	3.1
80 20 A1	30	20	.42	4.0
80 20 A2	30	17	.32	4.7
80 40 A1	40	25	.56	3.2
80 40 A2	35	20	.45	4.0
80 80 A1	50	33	.79	2.4
80 80 A2	50	32	.84	2.4

reach the size that completely consumes all the food, relative to the time it takes it to reach its final size. The ratio between the first and the second is larger for the populations kept at higher volumes.

These two trends, if they are real, may be due not to the direct effect of density, but to differences in the appearance of sexuality, as will be seen later on.

Mean food consumption, when food first becomes completely consumed, varies from 2.4 to 5.0 Artemia/hydra/day. Although most populations roughly double their size during the period of total food consumption, most of the new individuals already exist as buds before this period is reached. The frequency of budding individuals remains relatively high (varying from one third to two thirds of the population) until the beginning of the period of total food consumption or shortly thereafter. After that the frequency of budding is very low (hardly ever more than 10%, and most of the time zero). We can conclude, therefore, that a hydra needs at least 5 Artemia/day in order to produce buds. A more exact statement cannot be made without better information.

One purpose of the present study is to establish the relation between the two escape mechanisms of hydra, floating and sexuality, and the environmental factors of availability of food and density. As suggested earlier, the "A" populations give us an opportunity to do so, because after the K level has been reached, each population remains for a long time at constant, and known, levels of feeding and density. Table 12

Table 12. The availability of food to individual hydra (Artemia/hydra/day) in all "A" populations at the level of K. There are 2 replicates for each combination of total daily food supply and volume.

Total food level (Artemia/day)	Volume 20 ml		40 ml		80 ml	
20	1.73	1.73	1.43	1.68	1.48	1.90
40	2.01	1.88	1.80	1.90	1.63	1.66
80	1.69	1.50	1.78	1.79	1.91	2.10
150	1.64	1.65	1.63	1.60	1.64	1.59
300	1.52	1.59	1.37	1.31	1.21	1.22

Table 13. The density (hydra/ml) in all "A" populations at the level of K. There are 2 replicates for each combination of food level and volume.

Total food level (Artemia/day)	Volume 20 ml		40 ml		80 ml	
20	.58	.58	.35	.30	.17	.13
40	1.00	1.06	.56	.53	.31	.30
80	2.36	2.67	1.12	1.11	.52	.48
150	4.56	4.54	2.31	2.35	1.15	1.18
300	9.87	9.43	5.49	5.71	3.09	3.08

contains the values of food level per hydra (total food level/K) for all populations, and the density values (in hydra/ml) are listed in Table 13.

In spite of the 5 different food levels that were used, the hydra of all populations received, at the K levels, roughly the same amount of food. The values in Table 12 vary from 1.21 to 2.01 Artemia/hydra/day. As these values are well below the amount of food a hydra will eat if food is unlimited, we can regard all hydra as being in a stage of starvation, and because of the small variation in the individual values, we can even consider all hydra to be at the same degree of starvation. The "A" populations, therefore, when compared at the level of the K values, do not present an opportunity to see the effect of different levels of starvation on floating and sexuality.

The situation is different as far as density is concerned. As can be seen in Table 13, the density values vary within a range of almost 2 orders of magnitude. If density has an effect on floating, it should become apparent after we group the populations into 7 groups, each with a different level of density. The groups are as follows, arranged in the order of increasing densities (first number--food level; second number--volume):

1. 20-80
2. 20-40; 40-80
3. 20-20; 40-40; 80-80
4. 40-20; 80-40; 150-80
5. 80-20; 150-40; 300-80

6. 150-20; 300-40

7. 300-20

The 15 combinations of food level and volume are reduced now, if we consider the factors which are assumed to affect escape behavior, to 7 different densities and one level of starvation.

Sexuality

The only generalization that can be made about the appearance of sexuality (see curves in Appendix A) is a negative one--the frequency of sexuality does not stay constant even under conditions of constant food level and density, and the shape of its frequency curve does not seem to correlate with the conditions under which the population is grown. There is a surprising similarity in the shapes of the curves of replicate populations, which supports the idea that sexuality is, at least in part, a function of some environmental conditions, but none of the conditions that were under control can be shown to have varied, both within the duration of the 150 days of a given population and between populations, in a way that may suggest an explanation for the observed trends.

The most striking feature of the frequency curves of sexuality is their regularity. There are no significant short-term fluctuations, which is partly due, of course, to the fact that it takes some time for gonads to develop, and maybe even longer to disappear. Fluctuations do exist, however, on a long-term scale, and the frequency of sexuality hardly ever stays constant for more than a few days. Periods of constant increase in the frequency of sexuality alternate with periods of

constant decline, which gives to many of the frequency curves a cyclical shape, very similar to the results reported by Park (1961).

All of the sexual individuals in all the populations were males.

The differences between the various populations can best be expressed in terms of the number of peaks in the sexuality curve, the time of occurrence of the peaks and troughs, and the values of the frequency of sexuality at these extremes.

Four of the hydra used for starting a population--the two replicates of both the 20-20 and 20-80 populations--became sexual a few days after the beginning of the experiment. It is interesting that when this happened in one population it also occurred in its replicate, but in all these cases the hydra lost their sexuality very quickly and they will not be considered in the rest of the discussion. Ignoring these initial short peaks, it can be said that the earliest day of appearance of sexuality was day 16, in population 80 20 A2, the latest one was day 57, in population 20 80 A1, while in most populations sexuality was first observed 25-40 days after the beginning of the experiment. The number of peaks is 2 or 3, easily distinguishable in most populations. The 150a/d populations show only one peak, but they were kept for only 100 days, a period during which many of the other populations also had just one peak.

A summary of the appearance of sexuality is given in Table 14. It includes, for each population, the day of first appearance, the number of peaks, the frequency of sexuality at each peak and the day (or days) of its occurrence, and the frequency of sexuality at the lowest point be-

Table 14. Sexuality in the "A" populations.

Population	Day of 1st appearance of sexuality	Number of peaks	1st peak day(s)	1st peak % sexual	Trough % sexual	2nd peak day(s)	2nd peak % sexual	Trough % sexual	3rd peak day(s)	3rd peak % sexual	Trough % sexual
20 20 A1	26	3(?)	35-56	100.0	40.0	70	100.0	33.3	129	75.0	8.3*
20 20 A2	19	3	46-57	100.0	50.0	87	100.0	45.5	126	83.3	9.1*
20 40 A1	30	2(?)	54	100.0	36.4	118-136	100.0	14.3*			
20 40 A2	23	2	51-66	100.0	33.3	114-126	100.0	8.3*			
20 80 A1	57	2	80	85.7	21.4	134-137	100.0	23.1*			
20 80 A2	43	2	58-65	100.0	0.0	122-125	100.0	8.3			
40 20 A1	20	2(?)	45-48	100.0	35.0	78-93	94.7	0.0**			
40 20 A2	30	2(?)	60	46.7	31.6	84 or 108-117	81.8-85.0	0.0**			
40 40 A1	32	2	55-67	80.0	21.7	115	91.3	4.4*			
40 40 A2	33	2	54	100.0	57.1	102-105	100.0	22.7			
40 80 A1	47	2	52-59	13.6	0.0	143	33.0	0.0*			
40 80 A2	42	2	65	87.0	16.0	119	92.0	8.0			
80 20 A1	27	3(?)	51	100.0	53.9	93	97.8	57.1	135	66.7	14.2*
80 20 A2	16	3(?)	48	85.7	61.2	90-93	88.5	52.7	132	72.2	0.0*
80 40 A1	32	3	65	95.1	61.4	101-110	95.6	68.1	137	91.8	61.2*
80 40 A2	30	3	58	97.6	62.0	106	97.8	74.5	133	93.6	48.9*
80 80 A1	49	2	78	95.2	27.5	117-126	92.7	43.2			
80 80 A2	36	3	62	91.9	48.7	92	89.5	64.1	131	92.3	53.9*
150 20 A1	40	1	54	92.4	7.6						
150 20 A2	34	1	56	88.9	6.7*						
150 40 A1	33	1	57-75	86.0	1.3*						
150 40 A2	32	1	67	87.1	0.0*						
150 80 A1	26	1	61	85.1	8.3						
150 80 A2	29	1	49	87.5	20.8*						
300 20 A1	38	2	63	87.7	3.1	105	81.7	0.0**			
300 20 A2	40	2	62-65	85.9	1.1	97	89.7	0.0**			
300 40 A1	35	2	60	92.4	64.3	92	83.6	0.0*			
300 40 A2	34	2	61-65	86.5	42.3	111	71.4	0.0*			
300 80 A1	30	2	56	88.8	59.3	98	90.2	1.3*			
300 80 A2	37	2	62	85.6	62.7	97	99.9	5.6*			

*on last day of experiment.
**occurred before the last day of experiment, but remained unchanged until the end.

tween peaks. In most cases there was no difficulty in determining the number of peaks; a question mark near this number in Table 14 indicates uncertainty about the interpretation of the curve, usually because of the existence of relatively large random fluctuations. In many of the populations sexuality disappeared almost completely toward the end of the 150 day period. This seems to be associated with the appearance of depression in these populations, a subject which will be discussed later on.

If the sexuality curves are grouped into the 7 density levels, no within-group consistency or between-group trend becomes apparent. It is also interesting to note that the days on which food became totally consumed, or the days on which the K values were reached, cannot be determined from the sexuality curves, in which the trends seem to be independent of density.

In most food levels (total supply to the whole population), the volume seems to have an effect on sexuality, but not in the same direction in all food levels. Among the 20a/d populations, a higher volume is associated with a reduction in the total occurrence of sexuality. At lower volumes the peaks are taller and wider, and the troughs are not as deep as in the higher volumes. Deeper troughs also occur in the higher volumes of the 40a/d and 80a/d populations, although the difference between the volumes is not as pronounced as in the 20a/d populations. In one population--40 80 A1 (high volume)-- sexuality occurred at a very low level, but also had 2 peaks, as in the other populations. The 150a/d populations, maintained for only 100 days, do not show dif-

ferences in the total frequency of sexuality, except for the possibility that the peaks become wider with an increase in volume. This is in contrast with the trends in the lower food levels, but is consistent with the trend in the 300a/d populations, where the populations grown in 80 ml have higher and wider peaks, and much higher troughs, than the populations grown in 20 ml.

It is rather doubtful that all these differences are significant enough to contribute to our understanding of the effect of environmental conditions on sexual differentiation. Even if they are, we cannot suggest a factor that might be responsible for them. The reversed trends in the 20a/d, 40a/d and 80a/d populations on one hand, and the 150a/d and 300a/d populations on the other, may be due to the fact that the experiments were conducted at different times, or to the fact that in lower food levels volumes by themselves are important while in the higher food levels density plays a larger role. That density has an effect only at the highest food level was demonstrated already by the K values.

Another aspect of sexuality that seems to be affected by volume, or a combination of volume and density, is the time it takes a hydra, when the population becomes sexual, to develop gonads. If the growth curve of a population is plotted together with a curve of only the sexual individuals in the population, the initial parts of the two curves often parallel each other. This means that all new hydra in the population become sexual the same number of days after becoming independent, and the time it takes the gonads to develop is measured by the distance between

the two parallel curves. No cases of buds with gonads were observed in the present study.

The distances (in days) between the two curves are listed, for all the populations in which the curves are parallel, in Table 15. The effect of volume is clear--in the 20a/d, 40a/d and 80a/d populations it takes a hydra longer to develop gonads if the population is maintained at a higher volume, while the opposite is true for the 150a/d and 300a/d populations. As above, in the first group the volume itself (or the height of the water column) may have an effect, while in the second group density seems to overweigh the effect of volume. In the cases of non-parallel curves it is impossible to estimate the time needed for the development of gonads, because sexuality first appears at a late stage of the growth curve, and the hydra stay non-sexual for a while after becoming independent.

It should be emphasized that Table 15 deals with an aspect of sexuality which is different from the one discussed earlier. Previously we talked about the induction of sexuality being independent of density. The values in Table 15, as well as the information about the total occurrence of sexuality, refer to the time it takes a hydra to develop gonads and to remain sexual after conditions that induce sexuality have been established.

Although the appearance of sexuality cannot be shown to be a function of density, sexuality seems to have an effect on density, at least temporarily, by affecting the growth curve. In many populations reach-

Table 15. The time (in days) needed for the development of gonads after a bud is detached in an environment that induces sexuality. Estimates are based on the distance between the growth curve and the sexuality curve in all the "A" populations in which these two curves are parallel. (n.p. = the curves are not parallel).

Population	Time
20 20 A1	5-6
20 20 A2	5-6
20 40 A1	10-12
20 40 A2	10-12
20 80 A1	n.p.
20 80 A2	n.p.
40 20 A1	11
40 20 A2	n.p.
40 40 A1	15
40 40 A2	15
40 80 A1	n.p.
40 80 A2	n.p.
80 20 A1	9
80 20 A2	9
80 40 A1	12
80 40 A2	12
80 80 A1	n.p.
80 80 A2	20
150 20 A1	15
150 20 A2	18
150 40 A1	12
150 40 A2	16
150 80 A1	12
150 80 A2	12
300 20 A1	18-20
300 20 A2	15-18
300 40 A1	15-20
300 40 A2	12-18
300 80 A1	10-13
300 80 A2	10-13

ing the level of K involves a 2-step growth, with the rate of growth declining considerably somewhere along the period of active growth. This period of reduced growth, or in some cases of complete cessation of growth, is always associated with the first peak of sexuality. This can be seen most clearly in the following populations: 20 20 A1 and A2, 20 40 A1 and A2, 40 20 A1, 80 20 A1, 150 20 A1 and A2 and all the 300a/d populations, and to a lesser extent in all other 40ml populations. The rest of the populations do not show any break in the growth curve, and in them the first peak of sexuality is always reached when the population is already at its K level.

This phenomenon is consistent with the findings that budding is slowed down, or is completely stopped, when the hydra become sexual. At that time the hydra convert more of their food supply into their own tissues, and not enough is left for the production of buds. When the frequency of sexuality declines, energy is again available for bud production, and the population starts growing again. This is true, though, only for the first appearance of sexuality. The later peaks, that appear when the population is at a constant level with food limitation, cannot involve shunting of energy from bud production to sexuality, and the development of gonads is probably done at the expense of other metabolic activities.

The differences in the population size when food first becomes totally consumed can now be suggested to be a result, at least partially, of the differences in the frequency of sexuality in the different populations. If

the frequency is high, fewer animals are needed for the complete consumption of the total supply of food.

Floating

Any trend that may exist in the curve of daily floating rates of any population is to a large extent obscured by the high degree of variability in floating rates on successive days. It was already noted in the short term experiments (see experiment I, for example) that different groups of hydra kept under identical conditions showed very different floating rates. This was found to be true also for the "A" populations, where floating rate on any day did not have to depend on the number of floaters on the previous day, because after each daily feeding all the hydra were placed back on the floor. Even during periods of no change in population size and average amount of food available to each hydra the number of floating hydra varied markedly from day to day. The high and low rates occurred in the different populations on different days, so that the fluctuations cannot be attributed to differences in the quality of the water.

A careful examination of the curves reveals, though, that there is a tendency for higher values to occur more often at certain segments of the 150 day periods, and attempts were made to reduce the "noise" and make the trends more obvious. Selection of specific days at constant intervals and averages of 5 day and 10 day periods produced smoother and more consistent curves, and the method finally adopted was the one using 10-day averages. This way no readings are ignored,

and the gaps that appeared in the frequency curves using 5-day averages were avoided. Ten day averages were used for drawing the histogram-like curves presented in Appendix A.

Like the sexuality curves, the curves of floating do not show an overall dependence of floating rate on density. No pattern appears if the curves are grouped according to the 7 density levels. No relationship exists between the floating rate of a particular 10-day period and the average population size at that period. The trends in many populations, grown under different combinations of food level and density, are similar to each other, with the replicates showing in most cases almost identical curves.

A striking feature of many of the curves of floating is the apparent rhythmicity in floating activity. In all the populations that show significant rates of floating (that is, all populations except the 80ml populations receiving 20, 40 or 80 Artemia/day) the curves of floating show an initial increase in the 10-day averages until a peak is reached, no later than the 6th 10-day period (days 51-60), and sometimes as early as the third period (days 21-30). The peak is followed immediately by a decline, followed by one or more peaks roughly equal in magnitude to the first one. The 150a/d populations have one peak, which is due to the shorter length of time in which these populations were kept. Floating, like sexuality, disappeared almost completely toward the end of the experiments, probably also because of the appearance of depression.

The averages of floating that constitute the peaks are listed in Table

16, together with the periods in which they occurred. In a few cases the selection of peaks was rather arbitrary, but it is believed that on the whole the table presents a picture consistent with the general shape of the curves.

As in the sexuality curves, the shapes of the curves of rates of floating do not correspond to changes in population size, and instead of limiting ourselves to the periods of the K levels we can consider the entire curve of each population. The variation in time in the tendency to float may be due to changes in the amount of some factor which induces floating, or in the response to this unknown factor. To make the comparison of the various populations more meaningful, we will limit the discussion to the maximum values of the 10-day averages, as listed in Table 16. This way it can be said that the populations are compared at periods where the induction of floating or the response to the inducing factor were at their maximum.

As stated earlier, the averages of the periods of maximum floating do not show an overall correlation with density. Some trends are revealed if the populations are grouped according to the volume in which they were kept. For each volume, an increase in total food supply means an increase in density. Comparing floating rates in the different food levels, therefore, enables us to study the effect of density on floating, separately for each volume.

In the 20ml populations floating is roughly the same for the 3 lowest food levels (densities), and higher in the 150a/d and 300a/d popula-

Table 16. Average floating rates (percent of total population size) of the "A" populations at periods of maximum floating. The periods in which these maximum values were reached are also listed. An asterisk denotes uncertainty about the second peak.

	1st peak		2nd peak	
Population	Ave. % floating	Period (days)	Ave. % floating	Period (days)
20 20 A1	24.0	31-40	24.3	81-90
20 20 A2	30.0	21-30	19.0	71-80
20 40 A1	45.0	41-50	39.5	91-100
20 40 A2	37.0	61-70	39.2	81-90
20 80 A1				
20 80 A2				
40 20 A1	21.3	21-30	17.9	81-90
40 20 A2	20.2	21-40	22.3	71-80
40 40 A1	26.1	51-60	22.2	91-100
40 40 A2	32.5	41-60	32.7	91-100
40 80 A1				
40 80 A2				
80 20 A1	29.5	31-40	22.8	71-80
80 20 A2	22.2	41-50	27.2	71-80
80 40 A1	29.6	41-50	37.7	91-100
80 40 A2	38.9	51-60	30.9	91-100
80 80 A1				
80 80 A2				
150 20 A1	44.8	41-50		
150 20 A2	48.8	41-50		
150 40 A1	39.4	31-40		
150 40 A2	32.7	41-50	34.1*	71-80
150 80 A1	18.2	31-40		
150 80 A2	22.9	41-50		
300 20 A1	34.0	51-60	30.1	91-100
300 20 A2	34.9	51-60	16.1	101-110
300 40 A1	34.4	41-50	23.8*	91-100
300 40 A2	35.3	51-60	21.4	101-110
300 80 A1	34.1	41-50	19.1*	81-90
300 80 A2	36.9	41-50	13.5*	81-90

tions, more so in the 150a/d populations. All the 40ml populations show about equal floating rates. A clear effect of density exists in the 80ml populations--hardly any floating at all occurs at the 3 lowest densities, rates of 18% and 23% occur in the 150a/d populations, with the highest rates--34% and 37% occurring in the 300a/d populations. Because of the different rates in similar densities kept at different volumes we must conclude that the effect of volume is achieved not through the number of hydra per unit volume but by the depth of the water in the dish. It seems that within the range of densities used in the present experiment floating occurs in water 6 mm deep (the 40ml populations) at the same rate regardless of density, that at the smallest depth of 3 mm (the 20ml populations) floating is largely a function of depth but at high densities there is an additional effect of density, while in the deepest dishes, with a depth of 12 mm (the 80ml populations) floating is almost completely a function of density. In these populations there is no floating at low densities, and hydra start floating when the density is about 1 hydra/ml or more, with the rate of floating increasing as the density goes up. In smaller depths density has an effect only if its level is high enough to increase the density-independent rate dictated by the depth of the water.

It is difficult to compare these results withthe ones of the short term experiments. Here we talk only about maximum rates, which occur in response to an unknown factor. In most of the time floating occurred at much lower rates. It is not known whether or not the

hydra in the short-term experiments were in a state of maximum tendency to float, or what is the importance of the fact that the hydra in the present experiment were fed daily, while in experiments I and II no food was given. It seems, though, that under the conditions of the short term experiments the maximum rate of floating was also determined by the depth of the water, or the shape of the container.

The short term experiments involved hydra that were roughly of equal physiological state. Although this could not be determined directly, an effort was made to select hydra of equal size and equal condition with respect to budding. The long term populations, on the other hand, contained hydra of different ages and budding conditions. One attempt to see whether the physiological condition has an effect on floating was done by comparing floating rates among non-budding and budding indivduals. This was achieved by means of a sign test. For every day on which (1) floating occurred and (2) the population had both non-budding and budding individuals the rate of floating was calculated separately for the non-budding and the budding. If budding animals floated relatively more than the non-budding, a + was scored for that day. If non-budding floated more than budding, a - was scored, and a 0 was scored if floating rates in both groups were the same. The sign test involves counting the +'s and -'s of each population, and calculating a χ^2 according to the formula

$$\chi^2 = \frac{(|n_1 - n_2| - 1)^2}{(n_1 + n_2)} ,$$

where n_1 is the number of +'s and n_2 is the number of -'s. A χ^2 value of 3.84 or more indicates that the difference between the two is significant at the 5% level, and if the value is 6.63 or higher the significance is at the 1% level. The results of the tests are given in Table 17. In most populations the number of -'s is significantly larger than the number of +'s, and even in the cases where the difference is not significant the -'s outnumber the +'s. This strongly suggests that a condition of budding reduces the tendency to float.

Floating and sexuality

Floating among non-sexual and sexual hydra was also studied. Floating rates were calculated separately for non-sexual and sexual individuals, for all days on which floating occurred, and a sign test was performed for each population, using the same equation as above. The results are given in Table 18. As can be seen from the table, floating was much more frequent among the non-sexual hydra in the 150a/d and 300a/d populations. In the populations of lower food levels the number of -'s is also usually higher than the number of +'s. The reason that the differences are not significant may be partly due to the fact that in some populations (the 80ml ones) floating was generally very infrequent, and partly to the very high frequency of sexuality in many of the other populations. The tendency is still very much in the direction of floating being more common in non-sexual than in sexual individuals.

If we consider both floating and sexuality to be escape mechanisms, employed in response to some changes in the environment or to some

Table 17. The results of sign tests for differences in the frequency of floating of non-budding and budding hydra in the "A" populations. The + column gives the number of days on which floating rate was higher among the budding, and the - column gives the number of days on which floating rate was higher among the non-budding.

Population	+	-	χ^2
20 20 A1	2	5	0.57
20 20 A2	1	7	3.12
20 40 A1	1	11	6.75**
20 40 A2	4	9	1.23
20 80 A1	1	4	0.80
20 80 A2	0	3	1.33
40 20 A1	2	10	4.08*
40 20 A2	3	9	2.08
40 40 A1	4	22	11.12**
40 40 A2	4	20	9.37**
40 80 A1	1	7	3.12
40 80 A2	0	10	8.10**
80 20 A1	4	17	6.86**
80 20 A2	5	13	2.72
80 40 A1	11	25	4.69*
80 40 A2	8	21	4.97*
80 80 A1	1	15	10.56**
80 80 A2	1	20	15.43**
150 20 A1	9	22	4.65*
150 20 A2	6	23	8.83**
150 40 A1	6	28	12.97**
150 40 A2	11	24	4.11*
150 80 A1	9	32	11.80**
150 80 A2	5	34	20.10**
300 20 A1	9	25	6.62*
300 20 A2	12	19	1.16
300 40 A1	12	20	1.53
300 40 A2	9	28	8.76**
300 80 A1	10	31	9.76**
300 80 A2	5	26	12.90**

*Significant at the 5% level.
**Significant at the 1% level.

Table 18. The results of sign tests for the differences in the frequency of floating of non-sexual and sexual hydra in the "A" populations. The + column gives the number of days on which floating rate was higher among the sexual, and the - column gives the number of days on which floating rate was higher among the non-sexual.

Population	+	-	χ^2
20 20 A1	9	17	1.88
20 20 A2	4	25	13.79**
20 40 A1	16	19	0.11
20 40 A2	11	21	2.53
20 80 A1	5	1	1.50
20 80 A2	1	0	0.0
40 20 A1	10	16	0.96
40 20 A2	10	11	0.0
40 40 A1	17	19	0.03
40 40 A2	16	18	0.03
40 80 A1	0	5	3.20
40 80 A2	5	8	0.31
80 20 A1	15	20	0.46
80 20 A2	7	25	9.03**
80 40 A1	23	22	0.0
80 40 A2	23	23	0.02
80 80 A1	9	17	1.88
80 80 A2	9	13	0.41
150 20 A1	2	20	13.14**
150 20 A2	5	21	8.65**
150 40 A1	8	20	4.32*
150 40 A2	7	21	6.04*
150 80 A1	9	24	5.94*
150 80 A2	3	28	18.58**
300 20 A1	3	21	12.04**
300 20 A2	3	18	9.33**
300 40 A1	3	24	14.81**
300 40 A2	2	25	17.93**
300 80 A1	8	25	7.76**
300 80 A2	3	23	13.88**

*Significant at the 5% level.
**Significant at the 1% level.

internal changes that are influenced by environmental factors, then the results in Table 18 indicate that these two mechanisms may be mutually exclusive, at least partially. When an escape mechanism is called for, the individual hydra is given a choice between leaving the population by floating, or becoming sexual and staying in the population. Some, of course, become sexual and float, but the tendency to float is higher if the hydra is not sexual.

As we have seen, maximum rates of sexuality or floating do not persist for a long time even when the conditions that existed when they were first reached seem not to have changed. The first increase in the frequency of floating or sexuality must be a response to some gradual change in the environment. Sexuality tends to reach 100% at the peak; the maximum rate of floating seems to be determined by the shape of the dish, or the depth of the water, or, in some cases, by density. What causes the declines after the peaks have been reached, and the additional increases and declines, is not known. No apparent changes, with or without rhythmicity, occur in the environment after the K level has been reached. This opens the possibility that what is changing, maybe rhythmically, is the way in which the hydra interpret the environment. What at one time seems to call for escape behavior is, after some time, considered normal and acceptable until another change occurs, and escape behavior becomes again more frequent. It is fully realized that this suggestion does not increase the understanding of the factors responsible for floating or sexuality, but it offers a new direction for further studies in the future.

The last question to be asked about the relationship between floating and sexuality was whether the conditions that lead to escape behavior are the same for floating and sexuality. In other words--is there a correlation between the peaks and troughs in the sexuality curves and those in the corresponding curves of floating rates. Examination of the curves, which, for each population, appear on the same graph (Appendix A), suggests that such a correlation may indeed exist. The 20ml, 40ml and 80ml populations, for which data on floating are available for every day, were chosen for a statistical examination of the question.

The two curves (floating rate and sexuality) of each population were divided into 30 segments of 5 days each, and the average percent floating and average percent sexuality were calculated for each such period. Averages had to be used because of the large variation in the daily rates of floating. A correlation coefficient was then calculated between floating rates and sexuality rates of the same 5-day periods (column A in Table 19). The average floating rate of every 5-day period was also separately correlated with the average percent sexuality in the next three 5-day periods (columns B, C, and D in Table 19, arranged in order of increasing time interval between the two correlated periods), because of the possibility that the peaks and troughs of sexuality lag behind those of floating, due to the fact that gonads do not appear or disappear instantaneously. Each correlation coefficient in the table is accompanied by the corresponding F ratio of the Analysis

Table 19. Correlation coefficients between the average floating rate at any 5-day period and the average percent sexuality of the same 5-day period (column A), and of the 3 next 5-day periods (columns B, C, and D). The F ratios are the result of an Analysis of Variance around the regression of sexuality rates against floating rates.

	A			B			C			D		
Population	r(df=28)	F(1, 28)	p	r(df=27)	F(1, 27)	p	r(df=26)	F(1, 26)	p	r(df=25)	F(1, 25)	p
20 20 A1	0.28	2.39		0.42*	5.82	.01-.025	0.63**	16.92	.005	0.68**	22.05	<.005
20 20 A2	-0.91	0.23		0.11	0.33		0.36	3.93	.05-.10	0.46**	6.80	.01-.025
20 40 A1	0.22	1.43		0.24	1.61		0.31	2.76		0.27	2.01	
20 40 A2	0.33	3.54	.05-.10	0.42*	5.91	.01-.025	0.53**	10.12	.005	0.65**	18.52	<.005
20 80 A1	-0.20	1.17		-0.28	2.29		-0.24	1.67		-0.25	1.64	
20 80 A2	-0.32	3.25	.05-.10	-0.21	1.32		-0.14	0.50		-0.61	0.09	
40 20 A1	0.34	3.71	.05-.10	0.56**	12.37	<.005	0.72**	28.60	.005	0.73**	29.04	<.005
40 20 A2	0.16	0.72		0.30	2.65		0.45*	6.47	.025-.05	0.49**	7.81	.005-.01
40 40 A1	0.37*	4.49	.025-.05	0.53**	10.79	<.005	0.64**	18.40	.005	0.59**	13.63	<.005
40 40 A2	0.41*	5.70	.01-.025	0.55**	11.93	<.005	0.65**	18.70	.005	0.62**	15.91	<.005
40 80 A1	-0.16	0.70		-0.16	0.69		-0.14	0.54		-0.17	0.74	
40 80 A2	-0.19	1.08		-0.16	0.76		-0.11	0.31		-0.13	0.46	
80 20 A1	0.14	0.57		0.38*	4.54	.025-.05	0.66**	20.64	.005	0.76**	34.65	<.005
80 20 A2	0.37*	4.31	.025-.05	0.52**	9.75	<.005	0.69**	24.10	.005	0.70**	24.01	<.005
80 40 A1	0.32	3.17	.05-.10	0.47**	7.69	.005-.01	0.56**	11.80	.005	0.54**	10.47	<.005
80 40 A2	0.43*	6.22	.01-.025	0.58**	13.62	<.005	0.71**	26.45	.005	0.73**	29.12	<.005
80 80 A1	0.58**	14.19	<.005	0.63**	17.46	<.005	0.60**	14.64	.005	0.45*	6.26	.01-.025
80 80 A2	-0.30	2.68		-0.30	2.74		-0.26	1.92		-0.17	0.72	

* = significant at the .05 level.
** = significant at the .01 level.
p = the probability of getting the F ratio only because of chance. When no value is given the probability is larger than 0.1.

of Variance that checks the relative amounts of variation in the rates of sexuality that can be explained by regressing them linearly against the rates of floating.

Table 19 shows that singificant correlation does exist between floating rates and sexuality, in particular if the floating rate is correlated with the rate of sexuality 5-10 days later on. The prominent exceptions are the 80ml populations, in which hardly any floating occurred. We can conclude, then, that the two escape mechanisms are probably triggered by the same changes in environmental conditions or in the interpretations of these conditions.

In summary, our data suggest that floating and sexuality are two types of response to some change in the environment. Responding in one way usually reduces the probability of the same hydra responding in the other way, but the two types of response appear together in the population. An alternative explanation, that the rate of floating is determined by the frequency of sexuality--the higher the rate of sexuality the lower is the rate of floating--demands a negative correlation between the two, which cannot be demonstrated. After the first peak of the escape behavior is reached, in response to some changes in the environment, the frequency of the escape mechanism shows regular up and down changes, with the peaks being up to 40 days apart. These "cycles" are probably due to periodic internal changes in the hydra. It is also suggested that a distinction be made between the causes of escape behavior in general and the factors determining the magnitude of

the response at its peak, which, in the case of floating, may be solely due to the shape of the dish.

Two apparent differences exist between floating and becoming sexual. Floating seems to be an immediate response, while sexuality develops gradually. Hydra that initially respond by floating later become sexual if they are not removed from the population. Sexuality is also a phase which can remain for some time after the conditions that triggered it disappear, while there was no indication that hydra enter a "floating phase". Although no direct observations were made, the impression was that the "decision" by a hydra to float is not dependent on whether or not it floated one day earlier. The second difference is in the relative frequency of the two responses, and is probably a result of the first difference. When sexuality appears, it very often involves all the hydra in the dish. Floating, on the other hand, always involves only a part of the population, at least if the water is replaced every day, with the probability of floating varying in time but rarely reaching very high values.

Depression

In addition to floating and sexual differentiation, another possible response to environmental conditions is reported in hydra. This is the phenomenon of depression, and it will be brielfly discussed here because of its appearance in most of the "A" populations toward the end of the 150-day period. No data will be given about its frequency or exact time of occurrence, because no notes were taken about it at the

time. In general, the description in Hyman (1928) applies well to the "A" populations.

Depression is a state in which hydra stop feeding, showing persistent contraction of the body and tentacles. Often hydra recover from depression, but if it continues for a long time the tentacles break and vanish and the body diminishes to a small round ball, without a mouth. Recovery from advanced states of depression seems impossible.

Many factors were reported as causing depression (review in Hyman, 1928): long continued rich feeding, extremes of temperature, lack of oxygen or fouling of the water, transfer to clean fresh water and infestation with protozoan symbionts. Hyman rules out only the last factor, and states that "the primary cause of depression is a general lowering of the physiological processes, or more briefly, a condition of senescence".

This interpretation caught the attention of those interested in the question of immortality and aging in hydra (for an interesting example of the controversy see Brien, 1953, Stiven, 1962b and Forrest, 1963a). Turner (1950) reports rhythmicity in the appearance of depression, which he considers to be temporary senescence. He also believes that depression plays an important role in the dynamics of hydra in nature.

The present work cannot contribute to a better understanding of the phenomenon. Protozoa indeed seem not to be involved. No case of irreversible depression was observed, but "cycles", as reported

by Turner, were also not observed. In many cases the experiment was terminated before the hydra recovered from the depression. It should be noted that during depression escape behavior--both floating and sexuality--becomes virtually non-existent. Turner suggests that the main reason for mortality during depression in nature is the inability of the hydra at this stage to perform vertical migrations.

Weights

The number of animals in a population is not always a good measure of population size or density, in particular for comparative studies. In an animal like hydra, with a highly variable individual weight, biomass should also be considered. A certain amount of food can support many individuals of small size, or fewer individuals of larger size, but in both cases the total biomass is the same. The way the total biomass is divided among individual hydra may be a function of the volume in which the population is grown, and populations that have different densities when density is measured as numbers of animals per unit of volume may be found to be identical if total biomass is considered.

These considerations, together with the hypothesis that density is important in determining floating rates, led to the weighing of all the populations at the end of the experiment. No hydra could be weighted while the experiments were going on, because weighing a hydra means that it is removed from the population, and as a result no information is available about changes in biomass during population growth. The data on weights will be presented and discussed briefly, although the

main issue in weighing the hydra--correlating floating rates and biomass--no longer seems relevant.

The total weights on the last day of each population are listed in Table 20. The weights are given separately for non-sexual and sexual hydra (all non-budding). Apart from differences in volume and density, other factors may be of importance in determining the average weights in a particular population. Among them: 1. Hydra in a state of depression may have different weights than normal hydra, and the weighing was done when many--but not all--of the populations had at least some individuals in a state of depression. 2. It is clear from Table 20 that the average weight of sexual hydra is larger than that of non-sexual. If the switch from sexuality to non-sexuality and vice versa involves a change of weight, some differences between the populations may be due to differences in position along the range between non-sexuality and sexuality. 3. Not all populations were weighed after 150 days. Nothing more specific can be said about these factors, and they will not be dealt with in the rest of the discussion.

The comparison of the different populations is made easier if each population is represented by an overall average weight of a hydra on the day the population was weighed. The values for the various populations are listed in Table 21. The variance is rather large, sometimes even between replicates, but if the weights are divided into 3 groups, according to the volumes in which the populations are kept, the groups include populations with decreasing average weights as the volume goes

Table 20. Dry weights (in micrograms) of the "A" populations on last day of experiment. Each population is divided into two groups--non-sexual and sexual[1]--and the weights are given separately for each group.

	Non-sexual			Sexual		
Population	Total weight	Number of individuals	ave. weight	Total weight	Number of individuals	Ave. weight
20 20 A1	372	10	37.2	78	2	39.0
20 20 A2	387	10	38.7	56	1	56.0
20 40 A1	354	12	29.5	65	2	32.5
20 40 A2	438	11	39.8	40	1	40.0
20 80 A1	294	10	29.4	73	3	24.4
20 80 A2	323	10	32.3	51	2	25.5
40 20 A1	719	20	36.0			
40 20 A2	689	22	31.3			
40 40 A1	675	22	30.7	38	1	38.0
40 40 A2	396	14	28.3	266	8	33.3
40 80 A1	583	24	24.3			
40 80 A2	447	24	18.6	27	1	27.0
80 20 A1	1299	41	31.7	241	7	34.4
80 20 A2	1482	54	27.4			
80 40 A1	443	19	23.3	782	30	26.1
80 40 A2	628	24	26.2	717	23	31.2
80 80 A1	462	18	25.7	682	25	27.3
80 80 A2	403	18	22.4	541	21	25.8
150 20 A1	1864	72	25.9	446	13	34.3
150 20 A2	1809	73	24.8	183	6	30.5
150 40 A1	2023	77	26.3	48	1	48.0
150 40 A2	1681	78	21.6			
150 80 A1	1233	59	20.9	544	24	22.7
150 80 A2	1613	60	26.9	448	16	28.0
300 20 A1	6160	183	33.7			
300 20 A2	6209	189	32.9			
300 40 A1	5838	194	30.1			
300 40 A2	5829	181	32.2			
300 80 A1	6203	230	27.0	50	3	16.7
300 80 A2	5687	200	28.4	415	12	34.6

[1] Only non-budding hydra are included in the table. In addition to them there were a few budding non-sexual--2 in 300 40 A1, 3 in 300 40 A2 and 1 each in 150 80 A2 and 300 80 A1, as well as 3 budding sexual--1 in 150 80 A1 and 2 in 300 80 A2.

Table 21. Total and mean dry weights (in micrograms) of all the "A" populations on the last day of experiment.

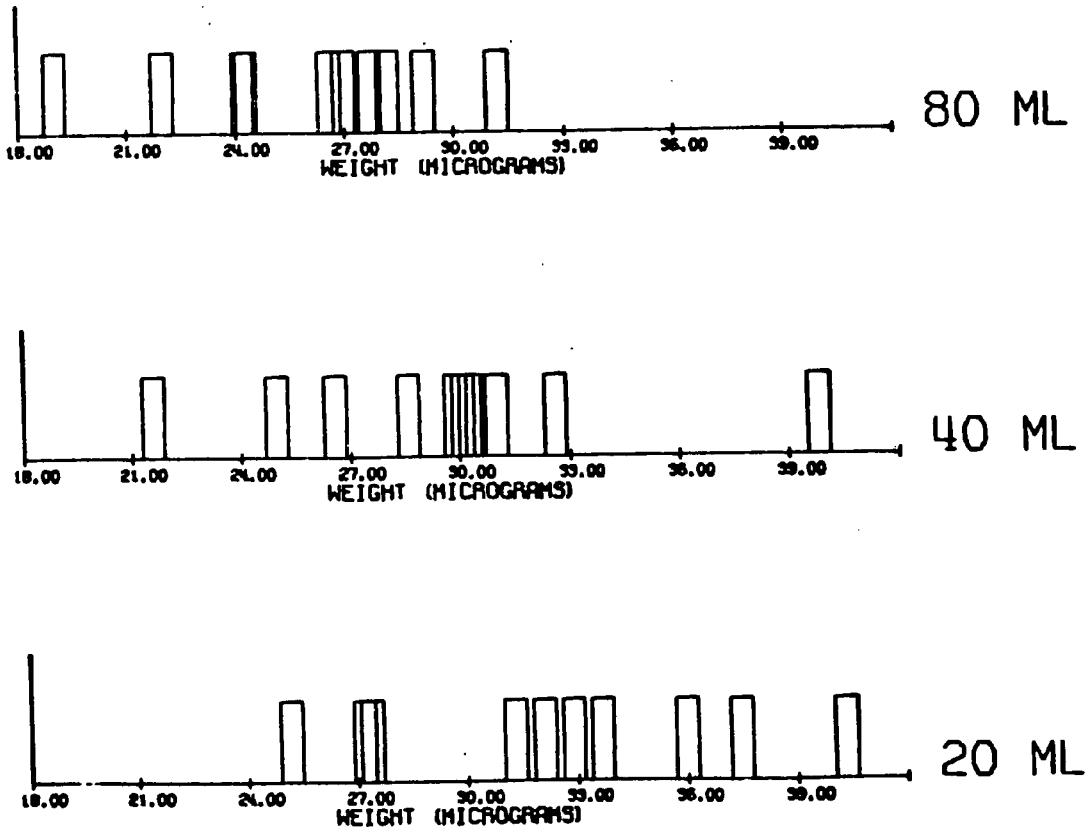
Food level (Artemia/day)	20 ml			40 ml			80 ml		
	Total weight	number of individuals	Average weight	Total weight	number of individuals	Average weight	Total weight	number of individuals	Average weight
20 A1	450	12	37.5	419	14	29.9	367	13	28.2
A2	443	11	40.3	478	12	39.8	374	12	31.2
40 A1	719	20	36.0	713	23	31.0	583	24	24.3
A2	689	22	31.3	662	22	30.1	474	25	19.0
80 A1	1540	48	32.1	1225	49	25.0	1144	43	26.6
A2	1482	54	27.4	1345	47	28.6	944	39	24.2
150 A1	2310	85	27.2	2071	78	26.6	1824	84	22.0
A2	1992	79	25.2	1681	78	21.6	2134	77	27.7
300 A1	6160	183	33.7	5939	196	30.3	6314	234	27.0
A2	6209	189	32.9	6001	184	32.6	6199	214	29.2

Table 22. Total biomass (dry weight, in micrograms) of all "A" populations at the K level. There are 2 replicates in each combination of volume and food level.

Total food level (Artemia/day)	Volume					
	20 ml		40 ml		80 ml	
20	432.8	467.1	418.6	473.2	381.5	328.5
40	716.4	664.8	688.5	634.5	597.3	457.3
80	1518.0	1463.2	1121.5	1274.7	1114.8	924.0
150	2482.0	2285.9	2453.1	2026.1	2015.9	2612.9
300	6652.4	6203.6	6656.0	7449.1	6669.0	7191.7

FIG. 5. DISTRIBUTION OF AVERAGE WEIGHTS OF HYDRA IN THE 'A' POPULATIONS, FOR EACH VOLUME SEPARATELY

EACH BAR REPRESNTS ONE POPULATION. ALL HYDRA WERE WEIGHED ON THE LAST DAY OF EXPERIMENT



up (see Fig. 5).

This tendency is consistent with the inhibitor hypothesis, but the hypothesis also requires that the total biomass will be the same for a given food level in all volumes. Multiplying the average weight of a hydra by the K value of its population we get an estimate of the total biomass of the population at the steady-state stage. These weights are given in Table 22. Here also the variance between replicates is sometimes very large, but several suggestions about the data can be made.

It seems that density has an effect on the efficiency of the utilization of the food. The 300a/d populations have relatively much more biomass per unit of food than the populations in the other food levels. Why should high density have such an effect is not known. It is interesting to note that the 300a/d populations were also the only ones to show an effect of volume (density) on the number of hydra. In the lower food levels no effect of density on the number of hydra could be shown, but volume does seem to have an effect on the weight of the hydra--the weights of the hydra in the 80ml populations are smaller than those in the other populations of the same food level, in spite of the fact that in all volumes the average amount of food available to each hydra was roughly the same. Again, no satisfactory explanation is available, although the fact that in the lower volumes the hydra stay for longer periods of time in a sexual state may be of relevance.

The "B" Populations

The "B", or open, populations were grown under the same combinations of food level and volume as were the "A" populations. Floating hydra were removed every day. There were 3 replicates in each of the 15 combinations, making a total of 45 populations. The growth curves--a summary of the daily counts--and the frequency curves of floating and sexuality of all the populations can be found in Appendix B. These curves, unlike those of the "A" populations, include, in addition to the daily total counts, the numbers of floating hydra that were removed daily.

The shapes of the growth curves are not consistent for all combinations of food level and volume, but the within-replicates similarity is striking. In all populations there are rather extended periods of steady state, when the population fluctuates around a horizontal line, the fluctuations varying in magnitude in the different combinations of food and volume.

Differences among the "B" populations exist both in the period before the steady state is reached, and in the ability of the populations to remain at the average size of the steady state--the K level--until the end of the 150-day period.

The populations can be divided into 3 groups according to the shape of the curve before the K value is reached: (1) A gradual increase until the population levels off at the K level. Examples--the 20-20, 40-80 and 80-80 populations. Two of the latter (B1 and B2) have a very prolonged growth period, but the K level is eventually reached.

(2) Hardly any increase at all, with the K value remaining very close to 1. Examples - the 20-20, 20-40 and 40-40 populations. In one case - population 20 40 B2 - there was only one animal in the dish on the last day of the experiment. (3) A rapid increase, reaching population sizes well above the K value, followed by an equally quick decline and stabilization around the K level. This type of curve is seen mostly in the 300a/d populations, and to a lesser extent in some of the 150a/d populations.

Once the K level is reached, most populations remain in that level until the end of the experiment. Some populations, however, increase again in size after some time, usually reaching another level of steady state, higher than the first one. Examples can be seen in the 20-20, 40-20 and especially in the 80-20 populations, but also in some other cases. These secondary steady states, whenever they occurred, were not included in the calculation of the K values.

The similarity between the steady state of an "A" population and a "B" population does not extend beyond the fact that in both the population levels remain more or less constant. In the first case the steady state is a result of the absence of a turnover in the population--there are no births and no deaths. In the second, there is a balance between the number of hydra that are added to the population as a result of budding and the number of individuals that are lost because of floating. The hydra in these two types of conditions are obviously of very different physiological states--in the "A" populations they are rather

starved, while in the "B" populations they get enough food to produce buds throughout the entire steady state period.

As in the "A" populations, the K values of the "B" populations are measured as the mean population size during the steady state period. In the selection of the period the average of which serves as the K value of a population, the initial growth period and the period of secondary increase have to be eliminated. Usually it was not difficult to decide when the first levelling at the K level occurred, and ignore the values previous to this point. The identification of the end of the period in which a constant level of K was maintained was more problematic, because of the fact that some fluctuations around the mean always occurred, and it was difficult to decide what was the last day on the curve that can be still included in the period of regular fluctuations. An examination of the frequency curves of floating and sexuality revealed that they can be used to reduce the error in making these cuts. When a secondary increase occurs in a population it means either that the rate of budding increases without a corresponding increase in the rate of floating, or that there is a reduction in the rate of floating while the budding proceeds as before, at least for a while. The frequency curves show that the latter is the case. Average floating rates remain relatively constant for the entire steady state period. If there is a secondary increase, floating frequency goes down abruptly. In most cases the same transition point marks also a change in the sexuality curve, and this point was chosen, whenever there was a seconary increase, as the end of the steady state

period.

The periods used for the calculation of the K values are listed in Table 23, and the K values themselves are given in Table 24. The relations between K values, food levels and volumes are shown graphically in Figures 6 and 7. Figure 6 shows the relation between K and volume, separately for every food level. The trend is identical in all five food levels--the lowest K is always in the 40ml populations, and the highest in the 80ml ones. Looking at the relations between K and food levels (Figure 7), we find that in general K values increase with the food level. The curves of the 20ml and 80ml populations tend to level off at the higher food levels, while the curve of the 40ml populations starts, at the lowest food levels, with a horizontal section.

Because of the direct effect of floating on the K values of the "B" populations, further discussion of the K values will be delayed until the rates of floating are considered.

The r values of the "B" populations were calculated using the same equations as in the "A" populations. The fit of the expected growth curves to the observed is, of course, not as good as in the "A" populations, but the r values can still serve for comparing the different populations.

The r values, each with the growth period from which it was calculated, are listed in Table 25. The missing values belong to the populations in which the K values were close to 1. The growth rates of the

Table 23. The periods of steady state in the "B" populations. The K value of each population is calculated as the mean population size during that period.

Population	Period (first day-last day)	Population	Period (first day-last day)
20 20 B1	1-100	80 80 B1	91-130
20 20 B2	1-110	80 80 B2	91-135
20 20 B3	1-85	80 80 B3	51-140
20 40 B1	1-130	150 20 B1	42-95
20 40 B2	1-150	150 20 B2	42-94
20 40 B3	1-130	150 20 B3	42-93
20 80 B1	16-140	150 40 B1	42-95
20 80 B2	41-150	150 40 B2	42-94
20 80 B3	51-150	150 40 B3	42-93
40 20 B1	51-100	150 80 B1	42-95
40 20 B2	51-110	150 80 B2	42-94
40 20 B3	41-100	150 80 B3	42-93
40 40 B1	1-150	300 20 B1	70-120
40 40 B2	1-130	300 20 B2	70-86
40 40 B3	1-120	300 20 B3	70-118
40 80 B1	51-150	300 40 B1	60-121
40 80 B2	51-150	300 40 B2	60-117
40 80 B3	41-125	300 40 B3	60-119
80 20 B1	41-100	300 80 B1	50-122
80 20 B2	51-100	300 80 B2	50-121
80 20 B3	41-95	300 80 B3	50-120
80 40 B1	21-150		
80 40 B2	21-115		
80 40 B3	21-110		

Table 24. K values of the "B" populations. The values of each of the 3 replicates of any combination of food level and volume are given together with their average ($\bar{K}$).

Food level (Artemia/ day)	Repli-cates	20 ml K values	$\bar{K}$	40 ml K values	$\bar{K}$	80 ml K values	$\bar{K}$
20	B1	1.69	1.56	1.37	1.53	3.16	4.95
	B2	1.52		1.60		4.47	
	B3	1.48		1.61		7.21	
40	B1	3.26	3.95	1.73	1.60	12.68	8.97
	B2	4.73		1.58		8.83	
	B3	3.85		1.48		5.40	
80	B1	7.05	9.38	3.16	3.41	16.52	15.70
	B2	10.74		4.14		17.51	
	B3	10.36		2.94		13.06	
150	B1	12.72	13.88	11.09	9.63	23.94	22.05
	B2	21.68		6.66		19.42	
	B3	12.52		11.13		22.79	
300	B1	19.27	18.98	19.68	16.68	21.25	26.25
	B2	16.94		13.19		28.44	
	B3	20.73		17.17		29.07	

FIGURE 6. K VALUES OF THE 'B' POPULATIONS AS A FUNCTION OF VOLUME

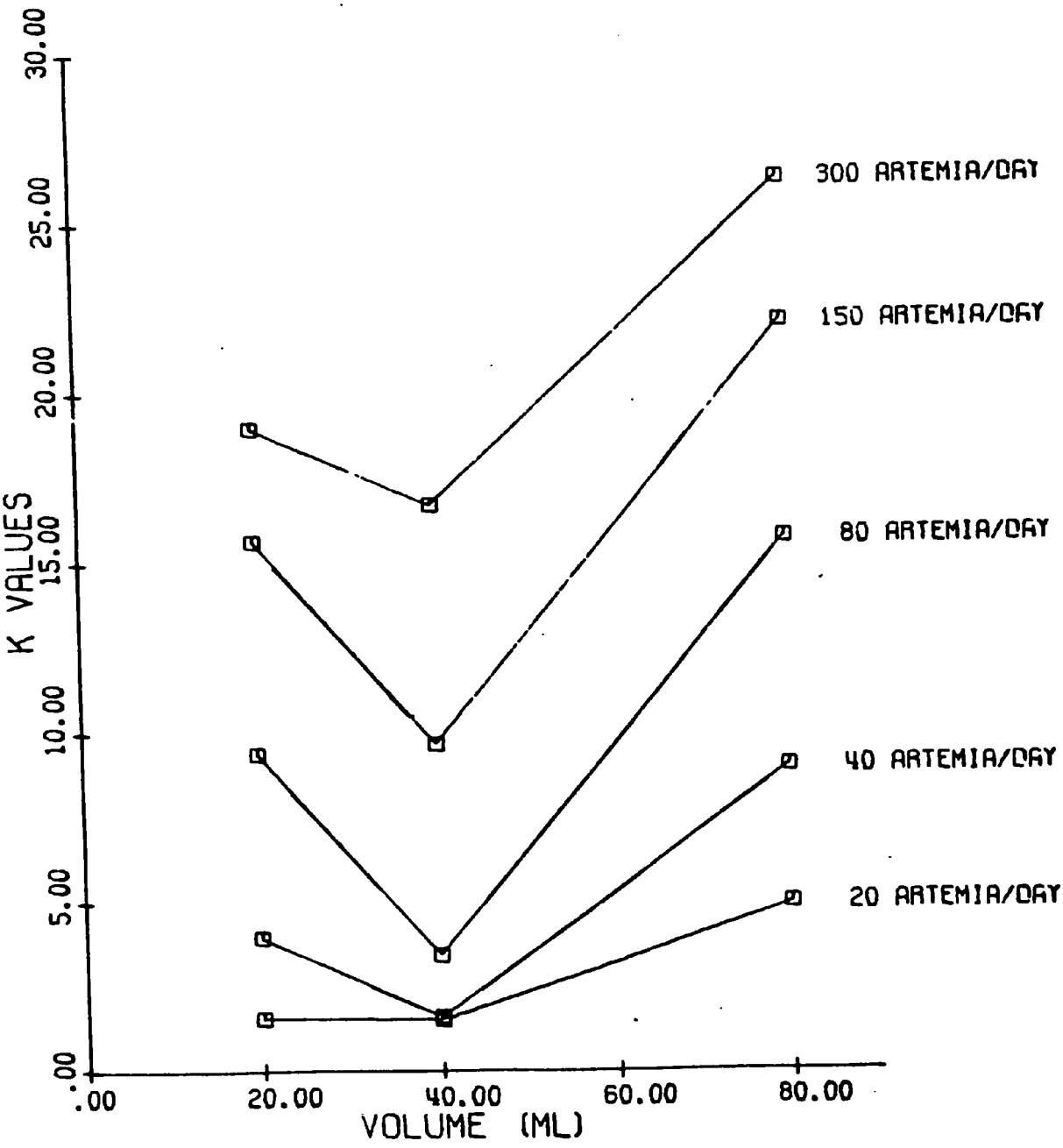
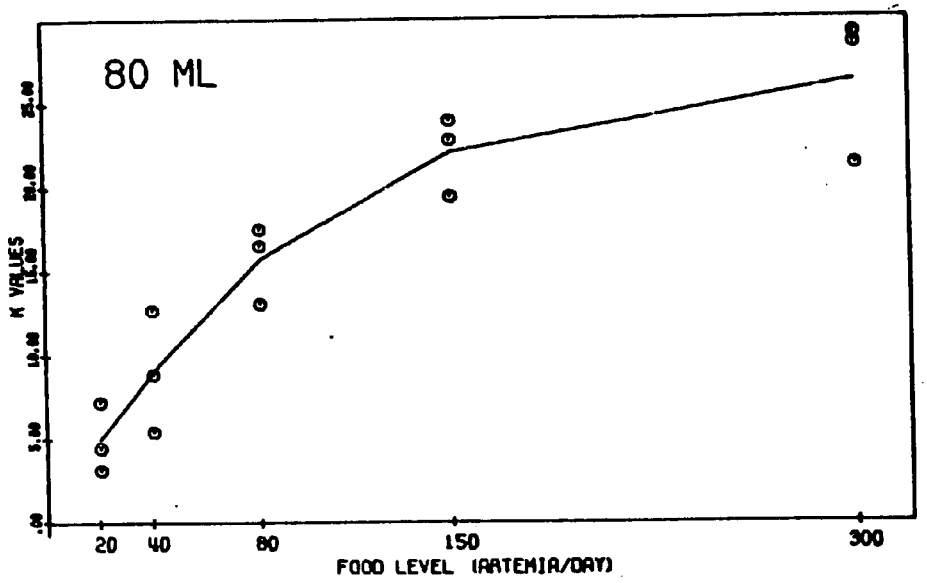
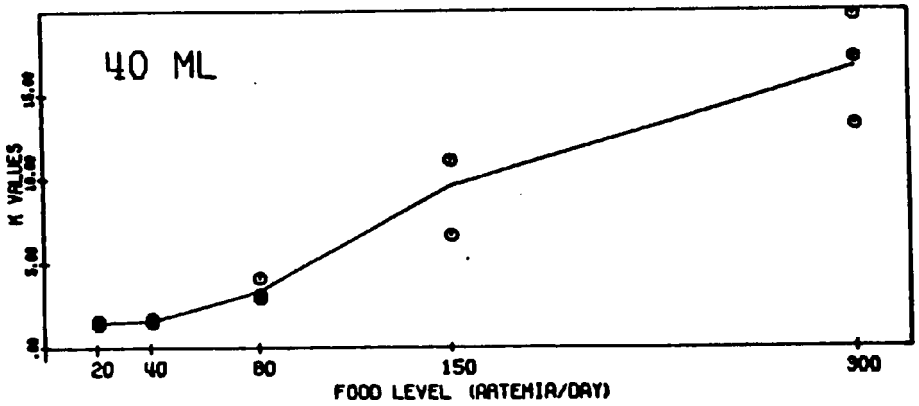


FIGURE 7. K VALUES OF THE 'B' POPULATIONS AS A FUNCTION OF FOOD LEVEL

LINES CONNECT AVERAGE K'S OF EACH FOOD LEVEL





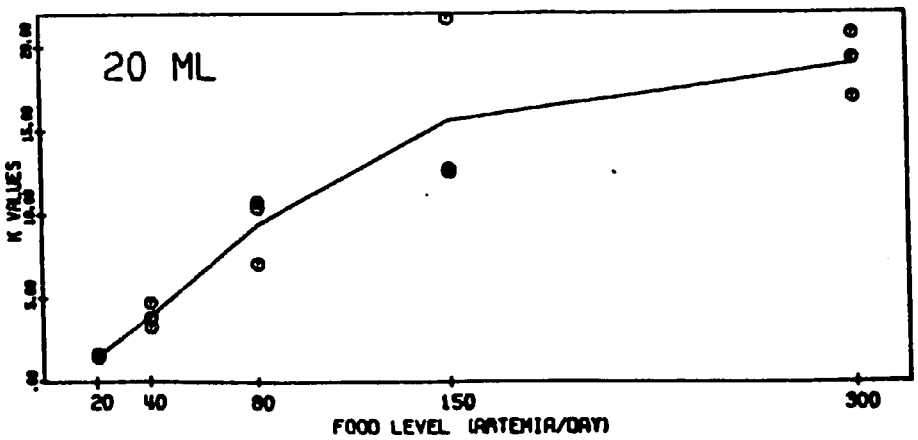


Table 25. The r values of the "B" populations. The growth periods, on which the calculations of r were based, are also listed.

Population	r	Growth Period (days)
20 20 B1	-	
20 20 B2	-	
20 20 B3	-	
20 40 B1	-	
20 40 B2	-	
20 40 B3	-	
20 80 B1	0.067	1-37
20 80 B2	0.062	1-39
20 80 B3	0.077	1-54
40 20 B1	0.012	1-55
40 20 B2	0.040	1-57
40 20 B3	0.057	1-42
40 40 B1	-	
40 40 B2	-	
40 40 B3	-	
40 80 B1	0.060	1-53
40 80 B2	0.066	1-55
40 80 B3	0.081	1-38
80 20 B1	0.047	1-62
80 20 B2	0.054	1-59
80 20 B3	0.058	1-57
80 40 B1	0.133	1-24
80 40 B2	0.103	1-33
80 40 B3	0.116	1-24
80 80 B1	0.042	1-88
80 80 B2	0.045	1-91
80 80 B3	0.091	1-54
150 20 B1	0.050	1-42
150 20 B2	0.109	1-31
150 20 B3	0.124	1-36
150 40 B1	0.158	1-28
150 40 B2	0.188	1-24
150 40 B3	0.169	1-29
150 80 B1	0.156	1-29
150 80 B2	0.101	1-40
150 80 B3	0.137	1-36
300 20 B1	0.135	1-36
300 20 B2	0.167	1-31
300 20 B3	0.159	1-33
300 40 B1	0.177	1-32
300 40 B2	0.170	1-34
300 40 B3	0.178	1-31
300 80 B1	0.145	1-32
300 80 B2	0.179	1-31
300 80 B3	0.172	1-31

150a/d and 300a/d populations are as high as the highest rates of the corresponding "A" populations. The growth curves of these "B" populations show that in them floating did not start until the peak of population size was reached, so that during the growth periods there was no difference between the "A" and "B" populations of the two highest food levels. The slightly higher r values of the "B" populations, compared to the "A" populations, are probably a result of the choice of K values for the calculations. The "B" populations of the lower food levels grow much more slowly, which is a result of the fact that floating occurred, and floaters were removed, during the entire growth period.

The availability of food

In most populations food was very abundant during the period of steady state. As can be seen from Table 26, the hydra got, in these periods, more than enough food for maintenance and budding. Even at the highest K values, relative to the amount of food (the 80ml populations of the lower food levels), there is still enough food per hydra to keep on budding, sometimes at a lower rate.

Under these conditions food very rarely becomes totally consumed, strongly suggesting that in most populations there was no food limitation during the period of steady state. Total consumption of food usually occurred in the populations that had secondary increases, after the initial period of steady state (the K level) was over. The only populations where total consumption of food occurred starting from the middle of the K level itself were the 20-80, 40-80 (except 40 80 B3) and the 80-80

populations.

Table 27 lists the populations in which food limitation occurred, together with information about the time food started to be totally consumed, the food level (per hydra) at that time, and the food level (per hydra) at the highest population size reached by each population. These last values are not as low as the ones that existed is the "A" populations, but they come very close.

Lacking more specific knowledge about the exact food consumption by individual hydra, the only conclusion we can draw from the information in Tables 26 and 27 is that as long as the rate of floating equals the rate of budding, the populations are maintained at a level that does not lead to food limitation.

Floating

Curves of the frequency of floating--presented as averages of 5-day periods--are given in Appendix B. In contrast to the "A" populations, the average rates of the "B" populations tend to remain relatively constant for long periods of time, and also there are no major differences between the various combinations of food level and volume. The averages of 5-day periods usually range between 0 to 20%, and there are no clusters of higher or lower values in different parts of the curves, except for the populations in which there was a secondary period of increase. These increases were always associated with a large decline in the rates of floating toward the end of the experiment.

Limiting ourselves, for the time being, to the periods of steady

Table 26. The availability of food (Artemia/hydra/day) during the periods of K of the "B" populations.

Food level (Artemia/ day)	Repli- cates	Volume 20 ml	40 ml	80 ml
20	B1	11.8	14.6	6.3
	B2	13.2	12.5	4.5
	B3	13.5	12.4	2.8
40	B1	12.3	23.1	3.2
	B2	8.5	25.3	4.5
	B3	10.4	27.0	7.4
80	B1	11.3	25.3	4.8
	B2	7.4	19.3	4.6
	B3	7.7	27.2	6.1
150	B1	11.8	13.5	6.3
	B2	6.9	22.5	7.7
	B3	12.0	13.5	6.6
300	B1	15.6	15.2	14.1
	B2	17.7	22.7	10.5
	B3	14.5	17.5	10.3

Table 27. Cases of food limitation in the "B" populations. The populations in which the food was never totally consumed are not included.

Population	Day on which food first became totally consumed	Food level (*Artemia*/hydra/day) on that day	Minimal food level reached by the population
20 20 B1	110	5.0	2.5
20 20 B2	110	5.0	2.2
20 20 B3	95	5.0	2.5
20 80 B1	110*	5.0	2.2
20 80 B2	115*	4.0	2.9
20 80 B3	100*	3.3	2.2
40 20 B1	120	5.7	4.4
40 20 B2	120	4.0	3.1
40 20 B3	130	5.7	4.4
40 80 B1	60*	3.1	2.2
40 80 B2	100*	4.4	3.3
40 80 B3	130	4.0	3.1
80 20 B1	105	7.3	2.6
80 20 B2	100	8.0	2.4
80 20 B3	90	5.3	2.4
80 80 B1	80*	5.7	4.0
80 80 B2	80*	5.3	4.4
80 80 B3	80*	5.7	3.8

*Within the initial period of steady state.

state, we have to conclude that in spite of the differences in total food supply, volume of water, and density, there is no corresponding variation in floating rates.

As was pointed out earlier, the "B" populations are not well designed for checking the validity of the hypothesis that floating is a density-dependent phenomenon. By starting all populations with one animal, with an abundance of food and very low density, the variety of environmental conditions, required for comparing rates of floating, may not be achieved. Nevertheless, the "B" populations do contain some relevant information. First of all, by the removal of floating hydra the populations maintain relatively constant densities, at least for a while, as required by the hypothesis. Secondly, there are consistent trends in the relation of the K values to food level and volume (Figures 6 and 7). This is in contrast to L&S's results, but their populations were maintained for only short periods of time.

Floating itself has to be looked at from a point of view different from the one used in the case of the "A" populations. In the "A" populations partly starved hydra were maintained at constant densities, and floating was measured among the same hydra day after day. By calculating averages it was possible to eliminate the extreme values of the rates of floating, and the averages of the different populations can be compared. In the "B" populations, on the other hand, floating hydra are removed. The rates of floating that affect the population curve are therefore the maximum, rather than the average ones. Even if high rates of floating occur only rarely, every time a relatively large num-

ber of hydra are found floating they are removed from the population. The random component in rates of floating plays here a very significant part, and, as can be seen from the growth curves, floating can reach, on some days, rates as high as 80% or more. (On rare occasions, when a population had only very few individuals, all the hydra in the dish were found floating. In order to keep the population going, no hydra were removed on these days). The total numbers of hydra that are removed because of floating may be more meaningful for comparing the different populations than rates of floating.

In the density which is kept constant by the removal of floating hydra, the number of floaters roughly equals the number of new individuals that are added by budding. It is conceivable that the number of floating hydra is determined not by the density of the population but by the rate of budding in the population. We have seen already that non-budding individuals tend to float more often than hydra with buds. That this is true also for the "B" populations can be seen in the results of the sign tests, comparing floating among non-budding and budding hydra (Table 28).

It is very likely that young individuals, after detachment, float more readily than older hydra of larger size. The tendency to float appears when a certain ratio is established between the population size and the amount of food supplied to the population. At that point all new additions to the populations will tend to float, and even if they do not float right after becoming detached they will eventually float and be removed. With the random component of floating, and the occasional

Table 28. The results of sign tests for differences in the frequency of floating of non-budding and budding hydra in the "B" populations. The + column gives the number of days on which floating rate was higher among the budding, and the - column gives the number of days on which floating rates were higher among the non-budding.

Population	+	-	χ^2
20 20 B1	3	3	0.17
20 20 B2	0	6	4.17*
20 20 B3	3	5	0.13
20 40 B1	1	7	3.12
20 40 B2	2	3	0.0
20 40 B3	3	2	0.0
20 80 B1	2	11	4.92*
20 80 B2	0	7	5.14*
20 80 B3	0	3	1.33
40 20 B1	5	10	1.07
40 20 B2	8	5	0.31
40 20 B3	6	19	5.76*
40 40 B1	4	12	3.06
40 40 B2	1	19	14.45**
40 40 B3	0	11	9.09**
40 80 B1	0	14	12.07**
40 80 B2	3	24	14.81**
40 80 B3	0	22	20.05**
80 20 B1	9	36	15.02**
80 20 B2	11	34	10.76**
80 20 B3	5	28	14.67**
80 40 B1	11	25	4.69*
80 40 B2	11	22	3.03
80 40 B3	8	28	10.03**
80 80 B1	2	54	46.45**
80 80 B2	8	41	20.90**
80 80 B3	3	60	49.78**
150 20 B1	15	25	2.02
150 20 B2	14	33	6.89**
150 20 B3	11	22	3.03
150 40 B1	10	38	15.19**
150 40 B2	8	34	14.88**
150 40 B3	10	34	12.02**
150 80 B1	2	46	38.52**
150 80 B2	9	45	22.69**
150 80 B3	6	50	33.02**
300 20 B1	36	37	0.0
300 20 B2	25	23	0.02
300 20 B3	29	42	2.03
300 40 B1	20	49	11.36**
300 40 B2	13	45	16.57**
300 40 B3	17	49	14.56**
300 80 B1	14	65	31.65**
300 80 B2	13	70	37.78**
300 80 B3	14	74	39.56**

*Significant at the 5% level.
**Significant at the 1% level.

floating of older, budding individuals, the populations will fluctuate around a relatively constant value.

In contrast to the hypothesis that floating is affected by density, the "B" populations suggest that density is affected by floating. This is demonstrated very well by the 20-80 populations. The K values of populations B1, B2 and B3 are 3.16, 4.47 and 7.21, respectively. If floating is a density-dependent behavior, we would expect to see the highest floating rates in B3. The growth curves of the 3 populations show that B1 has the highest frequency of floating, both in terms of total number of floaters and percent floating relative to total population size. In B3, on the other hand, floating is rather infrequent.

We can conclude, then, that in the "B" populations floating is undertaken mostly by newly detached individuals, possibly in response to some environmental conditions. This response can be inhibited by a large enough supply of food, and this is why older hydra do not float very often. The younger hydra probably float before they have a chance to eat enough, so that shortage of food is involved in floating although food is not a limiting factor.

The overshoots of the growth curves of the 300a/d populations may be connected to the food factor. When food is extremely abundant the conditions leading to the floating response may develop later than in the other populations, and in the meantime the populations manage to grow very rapidly.

Some populations hardly increase above the level of one individual.

This happens only in the lower food levels, mostly in the 40ml populations, but also in the 20ml ones. Here the depth of the water probably plays the most important role in causing floating, and almost every hydra, regardless of its physiological condition or food level will float sooner or later. The frequencies of floating among budding and non-budding hydra in these populations are not different from each other (see Table 28).

The occurrence of secondary growth periods, caused by a sudden reduction in floating activity, can be compared to the fluctuations in floating activity observed in the "A" populations (not to the cases of depression). It is interesting to note that these reductions in the rate of floating occurred, in the "B" populations, only in relatively few cases, and almost exclusively in the 20ml populations. Again, no satisfactory explanation is available, except for the general suggestion that some changes in the interpretation of the environment by the hydra take place. What is the physiological meaning of these changes we do not know. The hydra in the "B" populations keep budding very actively, indicating that at least from that point of view there is no deterioration of the metabolic state.

Sexuality

Because of the removal of floating hydra, some of which may be sexual, the frequency curves of sexuality (see Appendix B) are not as regular as in the "A" populations. Table 29 summarizes the occurrence of sexuality. In the three lower food levels its frequency is rather high,

Table 29. The occurrence of sexuality in the "B" populations. The frequency of sexuality is estimated by the amount of time that each population contained sexual individuals, and the number of sexual hydra during the periods of its occurrence.

Population	First day of appearance of sexuality	Frequency of sexuality[1]
20 20 B1	5	h.
20 20 B2	29	h.
20 20 B3	25	h.
20 40 B1	21	h.
20 40 B2	37	h.
20 40 B3	40	h.
20 80 B1	50	m.
20 80 B2	51	m.-h.
20 80 B3	76	h.
40 20 B1	27	m.-h.
40 20 B2	5	h.
40 20 B3	30	m.-h.
40 40 B1	23	h.
40 40 B2	36	h.
40 40 B3	48	h.
40 80 B1	56	h.
40 80 B2	52	h.
40 80 B3	41	m.-h.
80 20 B1	34	m.
80 20 B2	27	m.
80 20 B3	31	m.
80 40 B1	52	h.
80 40 B2	30	m.-h.
80 40 B3	50	m.-h.
80 80 B1	43	m.-h.
80 80 B2	40	m.-h.
80 80 B3	38	m.-h.
150 20 B1		v.l.
150 20 B2		v.l.
150 20 B3		v.l.
150 40 B1	39	l.
150 40 B2		v.l.
150 40 B3	38	l.
150 80 B1	32	m.
150 80 B2	36	m.
150 80 B3	26	m.
300 20 B1	41	l.
300 20 B2		v.l.
300 20 B3		v.l.
300 40 B1	38	l.
300 40 B2	39	l.
300 40 B3	40	l.
300 80 B1	34	l.-m.
300 80 B2	36	l.-m.
300 80 B3	34	l.-m.

[1] h. = high m. = medium
l. = low v.l. = very low

sometimes with the populations kept at smaller volumes having higher frequencies than those kept under the same food level but at larger volumes. In the two higher food levels sexuality is much less common, with the populations that are kept at higher volumes having higher frequencies. Similar trends were seen in the "A" populations, but the various explanations that can be suggested are, at the present level of understanding, nothing more than an intellectual exercise.

Table 30 contains the results of sign tests, showing that in the "B" populations, as in the "A" populations, non-sexual hydra float more readily than sexual ones.

The vast majority of the sexual hydra were males, but on a few occasions some hydra developed eggs. When this happened, it usually involved more than one hydra in a population, suggesting that the type of gonads that develop is influenced by the environment.

The appearance of female gonads in what seems to be a male clone of Hydra littoralis is in contrast to the official characterization of H. littoralis as a dioecious species (Forrest, 1963b). According to Dr. Forrest (personal communication), however, a distinction should be made between "dioecious" and "strictly dioecious", and as members of a "dioecious" species male H. littoralis can be expected occasionally to develop eggs.

Weights

All floating hydra were weighed immediately after their removal from the population. No consistent changes in weights occurred as

Table 30. The results of sign tests for differences in the frequency of floating of non-sexual and sexual hydra in the "B" populations. The + column gives the number of days on which floating rate was higher among the sexual, and the - column gives the number of days on which floating rates were higher among the non-sexual.

Population	+	-	χ^2
20 20 B1	3	11	3.50
20 20 B2	1	10	5.82*
20 20 B3	3	10	2.77
20 40 B1	0	17	15.06**
20 40 B2	1	13	8.64**
20 40 B3	0	12	10.08**
20 80 B1	1	8	4.00*
20 80 B2	1	9	4.90*
20 80 B3	0	2	0.50
40 20 B1	2	19	12.19**
40 20 B2	3	15	6.72**
40 20 B3	2	21	14.09**
40 40 B1	2	18	11.25**
40 40 B2	0	18	16.06**
40 40 B3	2	11	4.92*
40 80 B1	4	8	0.75
40 80 B2	5	16	4.76*
40 80 B3	2	20	13.14**
80 20 B1	8	33	14.05**
80 20 B2	8	37	17.42**
80 20 B3	2	31	23.76**
80 40 B1	4	25	13.79**
80 40 B2	3	28	18.58**
80 40 B3	3	28	18.58**
80 80 B1	5	43	28.52**
80 80 B2	2	41	33.58**
80 80 B3	8	52	30.82**
150 20 B1	6	12	1.39
150 20 B2	2	24	16.69**
150 20 B3	6	16	3.68
150 40 B1	8	35	15.72**
150 40 B2	3	12	4.27*
150 40 B3	13	22	1.83
150 80 B1	4	43	30.72**
150 80 B2	5	42	27.57**
150 80 B3	10	43	19.32**
300 20 B1	22	42	5.64*
300 20 B2	8	11	0.21
300 20 B3	6	21	7.26*
300 40 B1	12	49	21.25**
300 40 B2	8	23	6.32*
300 40 B3	15	45	14.02**
300 80 B1	13	65	33.35**
300 80 B2	16	61	25.14**
300 80 B3	16	62	25.96**

*Significant at the 5% level.
**Significant at the 1% level.

the populations grew older. Table 31 includes, for each population, the total dry weight of the hydra that were removed during the 150 day period, and the average weight of floating hydra in that population. The majority of floaters in most populations were of the non-budding, non-sexual category. The table includes information only about the 20a/d, 40a/d and 80a/d populations; the other populations were not kept for 150 days, and it is also suspected that some of the weights recorded from these populations have a large component of error.

In general, the average weights of the floating hydra are very close to those of the corresponding "A" populations, with the same tendency of the weights of the 80ml populations to be lower than those of the populations kept at smaller volumes.

The non-floating hydra were weighed on the last day of the experiment, and the weights are given in Table 32. The weights of the hydra that did not float are, as can be seen by comparing the values in Tables 31 and 32, much higher than those of the hydra that floated. This is the case even in the populations that showed the secondary increase, which, on the last day of the experiment, must have had hydra that weighed less than the non-floaters during the K period.

For a more complete analysis of the data, aimed at estimating the efficiency of utilization of the energy supplied to a population, some information about actual food consumption by the hydra must be available. In the meantime we can only point out that the amount of hydra tissue which is removed as a result of floating--which is roughly

Table 31. Total and average dry weights (in micrograms) of floating hydra, removed over a period of 150 days from the 20a/d, 40a/d, and 80a/d "B" populations.

Population	Number of hydra removed					Total weight	Average weight
	Non-budding non-sexual	Budding non-sexual	Non-budding sexual	Budding sexual	Total		
20 20 B1	13	1		2	16	480	30.0
20 20 B2	14		1		15	416	27.7
20 20 B3	10	2	1	2	15	502	33.5
20 40 B1	19	1			20	489	24.5
20 40 B2	16	2	1		19	555	29.2
20 40 B3	14	3			17	492	28.9
20 80 B1	20	2	2	1	25	554	22.2
20 80 B2	14		2		16	344	21.5
20 80 B3	7		2		9	196	21.8
40 20 B1	20	5	1	1	27	966	35.8
40 20 B2	18	4	1	5	28	946	33.8
40 20 B3	24	4	1	2	31	1060	34.2
40 40 B1	23	4		2	29	1000	34.5
40 40 B2	28	2	1		31	1009	32.5
40 40 B3	22		2		24	830	34.6
40 80 B1	22		7		29	729	25.0
40 80 B2	25	1	6	2	34	854	25.1
40 80 B3	33	3	1		37	838	22.6
80 20 B1	44	10	6	3	63	2457	39.0
80 20 B2	53	9	5	6	73	2702	37.0
80 20 B3	55	4	7	2	68	2149	31.6
80 40 B1	38	11	2	3	54	2248	41.6
80 40 B2	39	12	2	6	59	2484	42.1
80 40 B3	40	7	2	5	54	2074	38.4
80 80 B1	72	1	11	1	85	2048	24.1
80 80 B2	60	6	7	3	76	2089	27.5
80 80 B3	75	2	15	3	95	2411	25.4

Table 32. Total and average dry weights (in micrograms) of the non-floating hydra, on the last day of the 20a/d, 40a/d, and 80a/d "B" populations.

	Number of hydra					Total	Average
Population	Non-budding non-sexual	Budding non-sexual	Non-budding sexual	Budding sexual	Total	weight	weight
20 20 B1	7				7	448	64.0
20 20 B2	8				8	442	55.3
20 20 B3	6				6	330	55.0
20 40 B1	3		1		4	187	46.8
20 40 B2	1				1	12	12.0
20 40 B3	5				5	222	44.4
20 80 B1	6	1	1		8	276	34.5
20 80 B2			4	2	6	252	42.0
20 80 B3	5		4		9	295	32.8
40 20 B1	7				7	367	52.4
40 20 B2	13		1		14	574	41.0
40 20 B3	7	2			9	406	45.1
40 40 B1	1		1		2	56	28.0
40 40 B2	5			1	6	259	43.2
40 40 B3	5	1			6	299	49.8
40 80 B1	11		2		13	420	32.3
40 80 B2	6	1	4	1	12	342	28.5
40 80 B3	8	2	2		12	440	36.7
80 20 B1	31				31	1242	40.1
80 20 B2	34				34	1406	41.4
80 20 B3	29	1			30	1339	44.6
80 40 B1	3		2		5	204	40.8
80 40 B2	3	2	1		6	349	58.2
80 40 B3	6	3	2		11	494	44.9
80 80 B1	13	1	4	3	21	706	33.6
80 80 B2	5	1	12	1	19	739	38.9
80 80 B3	4		7	2	13	538	41.4

equivalent to the amount of tissue produced by budding--is proportional to the amount of food given to the population. The differences in weights between floaters and non-floaters support the suggestion that the newly formed hydra are the ones that float away. This suggestion does not imply that the non-floating hydra are always the same individuals. Occasionally a budding hydra does float, or a newly detached individual stays in the dish long enough to gain weight, start budding and lose the tendency to float, but tne turnover among the non-floating members of the population is very slow. The association of the weights of hydra with the tendency to float may also explain why in the "A" populations, where the average weights were similar to those of the floating hydra of the "B" populations, the probability of floating is the same for all the members of a population.

The "C" Populations

If the K value of an open population is influenced by a combination of environmental factors, then the population should stabilize, at the same combinations of these factors, around the same K, regardless of its initial size. The long-term experiments were originally intended to see the effect of total food supply and volume of water on the K values. One combination out of the 15 used for the "A" and "B" populations--that of 80 Artemia/day and 80 ml water--was chosen for studying the effect of daily removal of floating hydra on populations with initial sizes which are above the K level maintained by the 80-80 "B" populations. Three populations were established under these conditions--80 80 C1, with an initial size of 200; 80 80 C2, with an initial size of 100; and 80 80 C3, with an initial size of 50 hydra. The "C" populations were handled exactly like the "B" populations, with the exception that no weighing was done. The populations were maintained for 63 days.

Results and discussion

The changes in population size, separately for each population, together with the number of floating hydra that were removed each day, are shown in the plots in Appendix C. A plot of the frequency of sexuality in each population is also included in the Appendix. The scaling of the time axis is different in the two types of plots.

Each population started with an increase in population size, a result of detachment of some of the buds that were carried by the hydra on day 1. But the increase did not last more than one day, be-

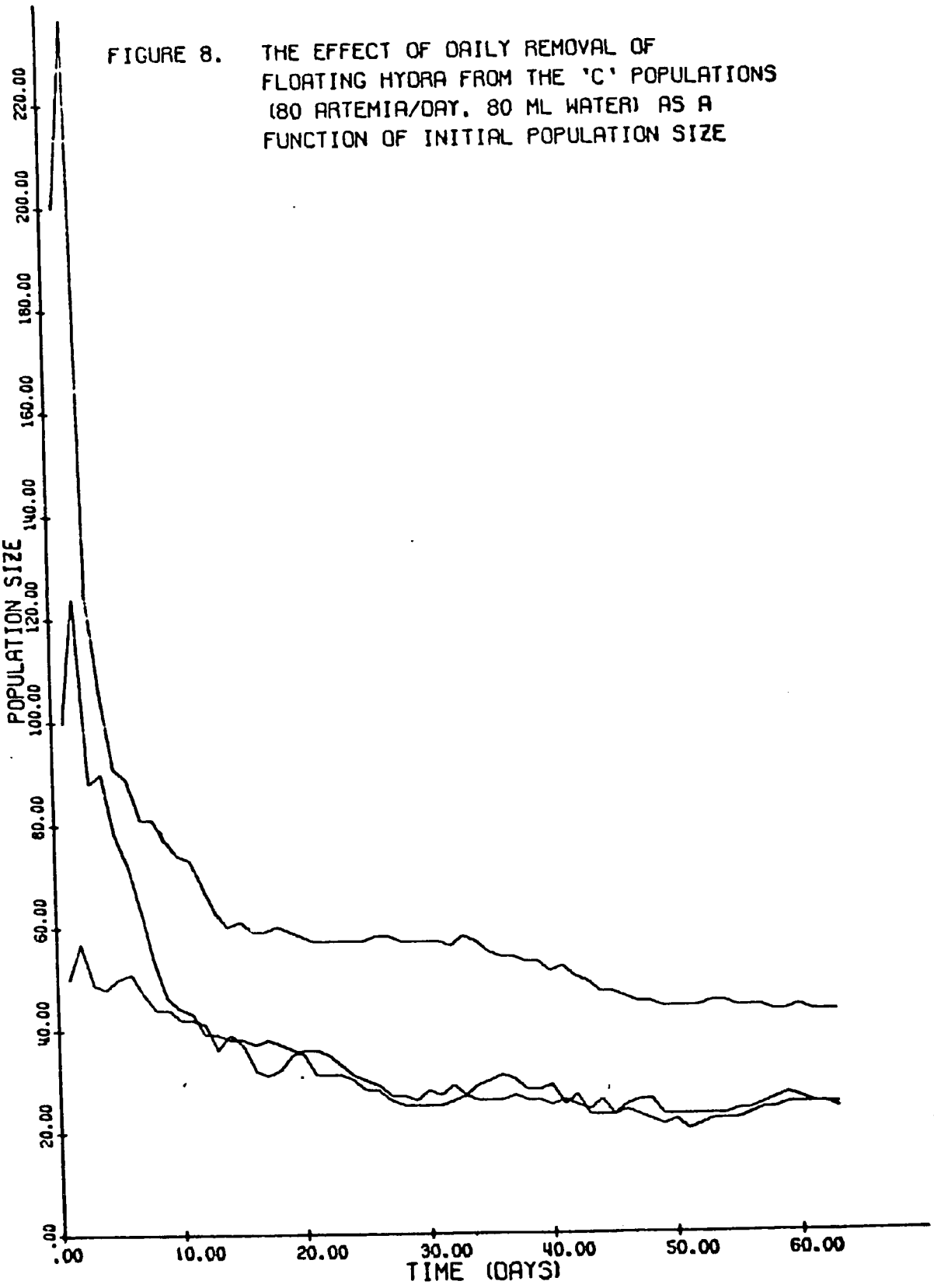
cause each population included on day 2 a large number of floaters that were removed: 56.5% in population C1, 42% in C2 and 33% in C3. The rate of floating remained relatively high for a few days, resulting in a rather quick decline in population size until about day 20, when the populations levelled off. Populations C2 and C3 remained around a constant level from about day 25 on, while C1 declined slowly until about day 40, when a steady state was reached. The changes in the 3 populations are plotted together in Figure 8, which shows that the initial population size has an effect on the level around which the population stabilizes.

The K values of the 3 populations are as follows:

Population	K
80 80 C1	44.7 (days 44-63)
80 80 C2	25.7 (days 25-63)
80 80 C3	24.6 (days 27-63)

The K level reached by the 80 80 C1 population is close to the K values of the "A" populations of the same combination of food level and volume--41.9 and 38.2. Floating in the 80ml "A" populations was affected by density--it became significant only in the high densities of the 150a/d and 300a/d populations. This suggests that in the 80 80 C1 population floating occurred in response to density until the population reached a size of about 45 individuals, when density was not high enough to induce floating, and the amount of food given to each hydra was not large enough to cause, by budding, an increase in population size.

FIGURE 8. THE EFFECT OF DAILY REMOVAL OF FLOATING HYDRA FROM THE 'C' POPULATIONS (80 ARTEMIA/DAY, 80 ML WATER) AS A FUNCTION OF INITIAL POPULATION SIZE



The 80 80 C2 and C3 populations stabilized at lower levels, slightly above those maintained by the corresponding "B" populations, the K values of which were 16.5, 17.5 and 13.1. The reason for the difference between the K values of C1 on one hand and C2 and C3 on the other hand is not clear; the initial sizes of populations C2 and C3, or their initial densities, somehow made the conditions such that hydra floated even when the populations reached sizes of 40 or even less.

That differences existed between the conditions of C1 relative to C2 and C3 can also be seen by comparing the sexuality curves of the 3 populations. Cycles, with peaks roughly 30 days apart appear in all of them, but the 2 peaks and the trough of C1 are much lower than those of the other two populations. Whatever the reason for these differences, here again we see the correlation between the conditions that regulate sexuality and those that induce floating. If sexuality reaches higher frequencies, it probably means that the environment is less favorable, and indeed in these populations floating occurs at lower densities.

The steady state sizes of populations C2 and C3 enable some hydra to get enough food to produce buds, and, as in the "B" populations, the steady state in them means that a balance exists between budding rate and the rate of floating. On the last day of the experiment (day 63) the frequency of budding hydra was 4.7% in population C1, 16.7% in C2 and 24.0% in C3.

Sign tests for differences in the rates of floating among non-sexual vs. sexual and non-budding vs. budding gave similar results as in the

"A" and "B" populations. The frequency of floating among non-sexual was significantly higher in all 3 populations compared to its frequency among sexual hydra (χ^2 values are 6.25 in C1, 9.82 in C2 and 7.22 in C3), and non-budding floated much more readily than budding hydra (χ^2 = 24.30 in C1, 15.75 in C2 and 29.26 in C3).

IV. THE EFFECT OF SEXUALITY AND STARVATION ON CONDITIONING AND FLOATING

Introduction

The hypothesis about the role of density and starvation in determining floating rates suggests that floating is a function of both the level of starvation of the hydra and the degree of conditioning of the water. Experiment IV was performed in order to get more data that can help in the interpretation of the results of the long term experiments, which were performed on the assumption that the hypothesis was correct. In particular it was suspected that different levels of conditioning are achieved not only by different densities but also by hydra of different metabolic conditions that may arise in the course of the long term experiments. Hydra of various metabolic conditions can also be expected to react differently, by floating at different rates, to the same level of conditioning.

Experimental design

All conditioning was done by groups of 16 hydra, kept in 20 ml water in 50 ml beakers for 5 days. These hydra will be referred to as the conditioning hydra. Floating was measured for 3 successive days in hydra (test hydra) introduced in groups of 4 into each beaker.

Four types of hydra were used both as conditioning hydra and test hydra--unfed non-sexual, unfed sexual, fed non-sexual, fed sexual. All 16 possible combinations of conditioning hydra and test hydra were performed, each involving 20 beakers with conditioned water and 20 control beakers.

All hydra--non-sexual and sexual--were selected from the stocks. They all did not have buds when the experiments were started, but many of the fed hydra developed buds in the course of the experiment. If a bud became independent it was removed from the dish. The hydra that had to be fed were removed from their beakers each day, fed for one hour, washed and returned, with as little water as possible, to their original beakers.

Results

Floating among fed hydra, non-sexual and sexual, was very low, both in conditioned and unconditioned water. Floating of test hydra in the control beakers was also very low. The values are very close to the ones reported by L&S (their Figure 1) and in Experiment I above, and will not be given here.

Table 33 contains the rates of floating among unfed non-sexual and sexual hydra, in water conditioned by hydra of all 4 metabolic conditions. Each value is the sum of the numbers of floating hydra in the 20 beakers. Floating is lower in water conditioned by fed hydra, in particular when the test hydra were sexual, and also in sexual compared to non-sexual hydra in all 4 types of conditioned water, but various chi-square tests did not reveal any significant differences. The differences between non-sexual and sexual hydra are consistent with the results of the long term experiments.

It was shown in experiment IIb that different densities during conditioning do not lead to different levels of conditioning. The results of

Table 33. Floating of unfed hydra in water conditioned by hydra of 4 different metabolic conditions. Conditioning was done by groups of 16 hydra, kept for 5 days in 20 ml water. The test hydra were introduced in groups of 4 into each beaker. Each number is the sum of the numbers of floaters in 20 beakers, out of a total of 80 hydra.

	Non-sexual			Sexual		
Conditioning hydra	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3
unfed non-sexual	30	46	54	29	38	50
fed non-sexual	21	27	49	15	19	30
unfed sexual	26	41	53	20	33	43
fed sexual	31	39	38	15	21	31

Experiment IV present evidence that hydra of different metabolic conditions also do not cause differences in the level of conditioning, at least as measured by the rate of floating in the conditioned water.

L&S's experiment in which rates of floating were compared between unfed and fed hydra involved a second control, referred to as "mock fed". It consisted of hydra that were not fed, but were removed daily for one hour or so into other dishes, like the hydra that received food during the experiment. The most important aspect of this control is that in the "mock fed" group all the floating hydra were put back every day on the bottom of their dish. When the hydra are not disturbed throughout the experiment it is impossible to tell whether the number of floating hydra on a later day is a response to conditions in the dish on that day, or a result of floating on previous days, with hydra remaining at the surface once they reach it. According to L&S there are no differences in the rate of floating in their two groups of "starved" and "mock fed" hydra. A repeat of this experiment, using densities of 16 hydra per 20 ml water in 50 ml beakers (10 replicates of each set) confirmed that the rate of floating among the hydra that were resettled on the floor every day was only slightly lower than the rate among hydra that were not disturbed. As the rates of floating do not decrease in time if the water is not changed, we can conclude that under such conditions the fact that floating hydra are not resettled every day does not have a signficant effect on the results. The lower rates of floating among fed hydra can be attributed solely to the availability of food.

V. THE EFFECT OF THE DEPTH OF THE WATER ON FLOATING RATES.

The long term experiments suggest that the shape of the dish, in particular the depth of the water, may play an important role in determining the rate of floating. The following experiment was designed to further check this point, which was not dealt with in any of the short term experiments described earlier, all of which involved 50 ml beakers, each containing 20 ml of water.

Experimental design

The only variable in Experiment V was the shape of the dish, or the depth of the water. Sixteen hydra were kept in 20 ml water in all the dishes, so that volume of water and density of hydra were kept constant. Four types of dishes were used--50 ml beakers, 150 ml beakers, 250 ml beakers and petri dishes, and the depth of the water in them was 19 mm, 10 mm, 7 mm and 3 mm, respectively. The experiment was run twice, each run including 10 dishes of each kind.

Sixteen non-budding, non-sexual hydra were introduced into each of the dishes, and the daily numbers of floaters were recorded for 5 days.

Results and discussion

The results are summarized in Table 34 and Figure 9. The shape of the dish is very clearly shown to have an effect on the rate of floating--the deeper the water is, or the smaller is the surface area of the water (or the floor area of the dish), the higher is the rate of floating.

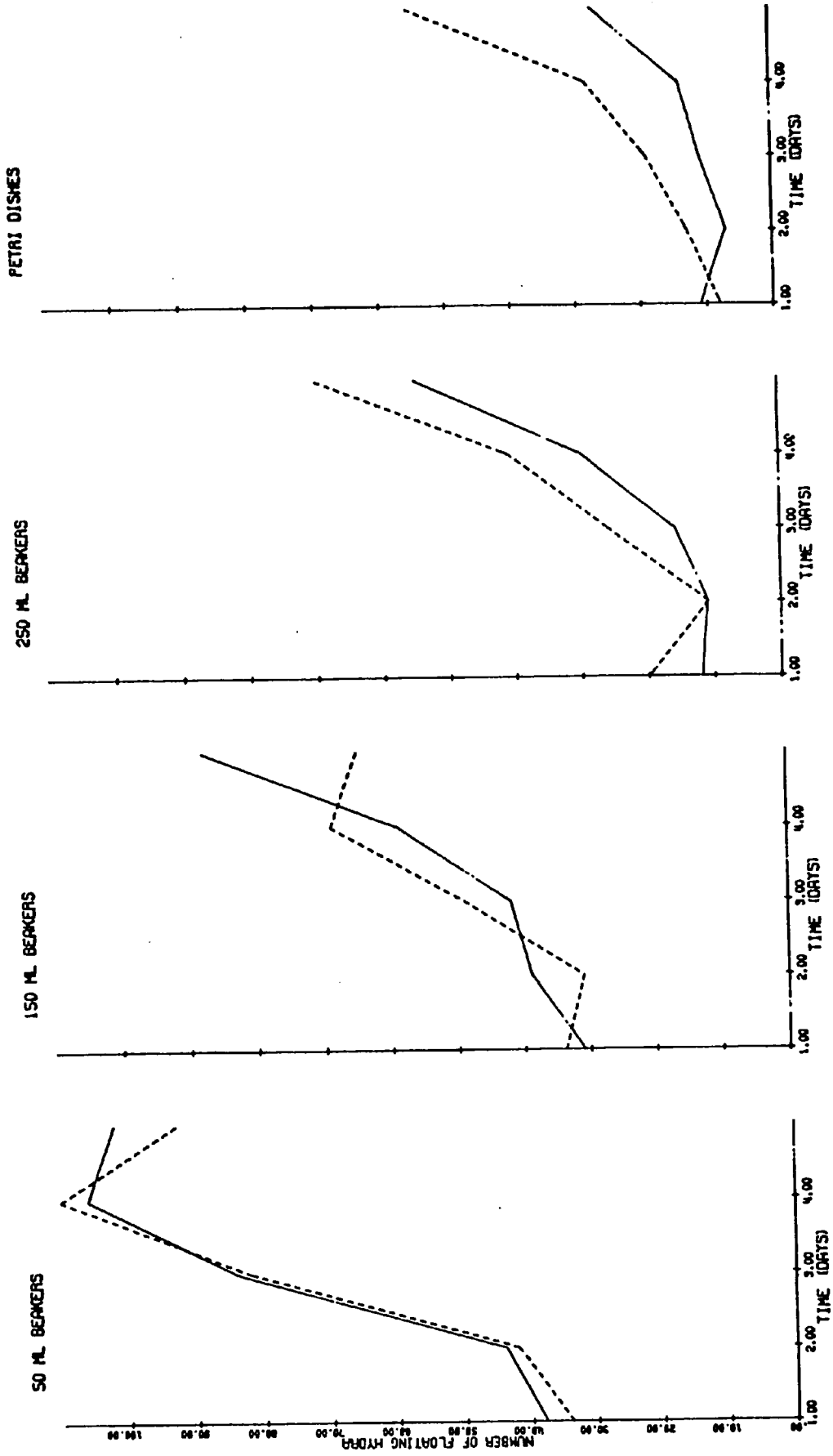
Table 34. The effect of the depth of the water or other factors related to the shape of the dish on the rate of floating of hydra, introduced in groups of 16 into 20 ml of water. The experiment was repeated twice, each time involving 10 dishes of each type, and the values in the table are the sums of the numbers of floating hydra in all 10 dishes, out of a total of 160.

Type of dish		Days 1	2	3	4	5
50 ml beakers (19 mm deep)	Run 1	38	44	84	106	102
	Run 2	34	42	82	110	93
150 ml beakers (10 mm deep)	Run 1	31	39	42	59	88
	Run 2	34	31	49	69	65
250 ml beakers (7 mm deep)	Run 1	12	11	16	30	55
	Run 2	20	11	26	41	70
petri dishes (3 mm deep)	Run 1	11	7	11	14	27
	Run 2	8	13	19	28	55

FIGURE 9. THE EFFECT OF THE SHAPE OF THE DISH ON FLOATING.

FOUR TYPES OF DISHES WERE USED, EACH CONTAINING 16 HYDRA IN 20 ML WATER

SOLID LINE - RUN 1; DASHED LINE - RUN 2. THERE WERE 10 DISHES OF EACH TYPE IN EACH RUN



What is the cause of this trend is not known. The distance from the surface may be important, but it is unlikely that in depths that do not exceed 19 mm there is a shortage of oxygen at the bottom. The ratio between the area of solid surfaces (floor and walls) and the surface area is probably more important, but it is difficult to suggest a specific reason. Other observations indicate that there is usually no relation between the number of floaters and the number of hydra sitting on the walls, so that considering floating as only a continuation of the crawling up the walls can be ruled out.

The trend in the results of Experiment V is in disagreement with the results of the long term experiments, where the highest rates of floating occurred in the 40ml populations, which were kept in water of intermediate depth. The disagreement between the two is most probably due to the fact that in the long term experiments the hydra were introduced into their dishes immediately after a feeding session. Direct observations, for more than 24 hours, of recently fed hydra, showed that for one or two hours after the introduction into their dishes the hydra perform intensive movements, including moving around the dish. Many of the movements involved stretching the tentacles, holding on to some object, and then contracting the body and bringing the foot closer to the hypostome. In water which is deeper than the height of the hydra, the tentacles can only become attached to the floor or to the walls. In shallower water the hydra can reach the surface of the water with their tentacles, hold on to it and then lift the foot and remain suspended at the

surface. In other cases one hydra would grab another and lift it to the surface, leaving it there. In the petri dishes that contained 20 ml of water (3 mm deep) many of the hydra that reach the surface at this time return later to the bottom by similar methods. In dishes containing 40 ml of water the return to the bottom is more difficult, and many of the hydra stay at the surface. After about two hours the movements in the dishes cease, and real, direct floating starts only after 12 or more hours.

Hydra that are found floating 24 hours after the introduction to the dish include those that reached the surface by floating directly from the bottom, and those that reached the surface after climbing a wall, as a part of the regular movements around the dish. It looks as if in the 40ml populations of the long term experiments the second component was most important.

The same explanation does not seem to hold for the results of Experiment V, but it can generally be concluded that the shape of the dish in some way affected the rates of floating also in the present experimental design.

GENERAL DISCUSSION

The significance of emigrations

In hydra, which is a sessile animal, the distinction between animals that are in the process of leaving their population and those that are not is relatively unambiguous, if we equate the phenomenon of floating with migratory behavior (Łomnicki and Slobodkin, 1966). All hydra which are found floating can be considered as migrants, in contrast with those which remain attached to the substrate. This distinction between migrants and non-migrants is much more complicated when most other animals are considered, because of the fact that animals regularly spend a great deal of their time on the move. It is often difficult to distinguish between routine movements, within the boundaries of the "home" area--in search for food or mate, for example--and movements which result in a departure from the regular "home".

Disagreements exist with respect to the way animal movements should be classified and the way the various categories can be distinguished from each other. In addition, those authors who concern themselves with the problem of the causes, effects and the adaptive value of migratory movements often disagree with each other, even when they use identical definitions for the various kinds of movements. The following survey of the field of migratory behavior and its evolution is necessary before an attempt can be made to look at the floating behavior of hydra in a more general context.

Heape (1931) and Elton (1930) seem to be the first to deal extensively

with the phenomenon of animal movements--mostly migrations--on a general-theoretical basis. The points of view of the two authors differ widely from each other (in neither book is there a reference to the other; Elton's book was published between the time of Heape's death and the posthumous publication of his book): Heape looks at the problem as a part of the general field of reproductive physiology, while Elton considers mostly the ecological and evolutionary implications of migration.

Heape devotes a great deal of attention to definitions, and tries to classify and sub-classify animal movements both according to their causes and their effects. Most of the changes in definitions after the publication of Heape's book involve reductions of the number of recognized categories, by rejecting some as non-valid and sometimes lumping the others into a smaller number of units.

According to Heape, four kinds of movements should be recognized:

1. Emigrations--"movements which entail change of environment, but which do not involve return to the original area of habitat".

2. Migrations--"movements which impel migrants to return to the region from which they have migrated".

3. Nomadism--"life of roaming or wandering", either "over a definite area or territory" or "without recognizing any boundaries to the wanderings".

4. Diffusion--a definite movement which is possible only when the neighboring territory is available for occupation. In contrast to migration, contacts with the original population are not severed.

The further classification of migratory movements according to causes is based on Heape's idea that there are two primary, primitive systems in the body--the digestive system, whereby the life of the individual is maintained and its growth assured, and the reproductive system, which is responsible for the continuance of the race. As such, both systems control not only their immediately related activities, namely nutrition and reproduction, but also all other activities that might be related to their objectives, including migratory movements.

Emigration can be one of the following:

1. Alimental emigration, for the purpose of finding a better supply of food or water.

2. Climatic emigration, prompted by a desire to escape from rigorous to a more congenial climatic environment; may be a special case of (1).

3. Mass emigration, essentially induced by overpopulation and performed by a surplus population. The main incitement to such an exodus appears to be want of food, and in all cases all emigrants, sooner or later, die. As for the evolution of mass emigration, Heape has a problem: "I know of no reasonable explanation of its conduct, while the evolution of the habit in animals is entirely beyond my comprehension".

All emigrations, regardless of the size of the emigrating group, are considered to be due to the need of the individual, and even cases when the individual does not seem to benefit at all from the fact that he became migratory do not cause Heape to suggest another alternative.

Three incentives are also recognized for migration:

1. Alimental migration.

2. Climatic migration.

Both (1) and (2) are prompted by the need of the individual, and the only differences between them and alimental and climatic emigrations lie in the fact that migrations are followed, after a certain period of time, by a return to the original "home", and the choice in migrations of routes and destination seems to be determined by instincts.

3. Gametic migration, undertaken for the production of the young and for their nurture, i.e. for the preservation of the species. This is the only type of migration that Heape considers to be tied to racial necessity rather than individual needs. No obvious reason suggests itself for this idea, except for the fact that Heape believes that the reproductive system--the function of which is, as we have seen, to serve the species rather than the individual--is responsible for initiating gametic migrations.

Elton (1930) sees in migration (synonymous with Heape's emigration) one of the most important ecological factors, particularly with respect to population dynamics. Migration is even suggested as a probable key to the success of contemporary populations and communities, as animals with the ability to migrate do not have to stay in one place if the conditions become unfavorable.

Elton considers animal migration to be one of the biological processes that cannot be expected to be explained satisfactorily by

Darwinian natural selection. When trying to explain the evolution of migration, one easy, and seemingly logical, alternative to classical natural selection is to base an argument on the suggestion that a population with migration will be favored over a population without it ("it pays not to have all your eggs in one basket"). This idea, however, does not appeal to Elton, who suggests that a better one lies in the possibility that natural selection is not the only mechanism in operation in nature:

> [we can talk also of] selection of the environment by the individual, a process mainly accomplished by migration. This migratory behaviour seems to require the existence of a definite awareness of unharmonious relations with the environment, a certain ability to choose what are the optimum or at any rate the most comfortable surroundings for the species. (pp. 89-90). The migratory impulse, and more especially the sense of harmony which actuates it, is a fundamental property of animal organisms which has emerged gradually into higher activity with the increased motility and mental organization of animals. (p. 53).

For some reason Elton does not mention the possibility that this "sense of harmony" must have evolved by the process of natural selection.

Now, after the acquisition of the migratory impulse, migration can serve an ecological function:

> Probably the connection between migratory behaviour in relation to the suitability of the animals' surroundings, and the regulation of numbers in the community, will by now have become pretty obvious. When the population increases seriously far above its optimum, there is a shifting of the animals to other places, so that the abnormal density is relieved. If the density is great over a wide area the local shifting may grow into a great stream of migrants, travelling in a body to distant regions. ----If the population is less than it might be, the gaps soon fill in from the outside by a similar process of

> adjustment. Migration in response to an innate sense of harmony with the habitat makes possible a solution of the animal population problem. (p. 61)

In summary, both Heape and Elton can be said to have recognized the importance of animal migrations, the apparent correlation that exists, in many cases, between migratory behavior and unfavorable environmental conditions (like lack of food, inclement weather or overcrowding), and the difficulties that arise when trying to explain the evolution of migration, assuming that the above correlations are correct and meaningful. The suggestions they make to overcome these difficulties should probably be judged relative to the status of biology at that period; a great deal of credit should be given to the fact that they, especially Elton, realize what the difficulties are.

Later studies added much more information about the occurrence of migrations, but it seems that a consensus about their causes and adaptive significance has not yet been achieved. Regular, seasonal, two-way migrations of entire populations, as known in birds and fish, are usually excluded from the discussions. In these two-way migrations the act of migrating is easily identifyable, and the selective value is also agreed upon. This is not the case, however, with one-way migrations (emigrations, according to Heape). Among the questions that are asked are the following: Can we, and should we, distinguish between dispersal movements, that result in increasing the area occupied by the populations, and migrations, that involve departure from the population? Is there a difference between the rather frequent, small-scale migrations,

usually involving relatively small numbers of animals, and the more spectacular mass emigrations or irruptions? Is migration a genetically determined response to some environmental conditions, or does it operate irrespective of the environment?

Different authors give different answers to these, and other, questions, and different answers lead, of course, to different explanations of the evolution of migrations. When reviewing some of the ideas in this field it should be kept in mind that we are not looking for the one theory that will make all others wrong. What is true for one species does not necessarily mean that it has to be true for all others. Some ideas will have to be rejected, but the real truth may very well be a synthesis of all the other suggestions, or lie somewhere among them.

The question with the smallest amount of mutual agreement is also the question that is most relevant to the problem of the evolution of migrations: do animals migrate in response to some immediate environmental cue, or is migration independent of the environment? Most studies give an affirmative answer to the first part of the question, but here again there is disagreement as to what are the specific factors responsible for migration. The two main suggestions are: 1. overpopulation. 2. shortage of food or water or some climatic or other change in the physical environment.

Suggestions in favor of overcrowding being the primary cause of animal migrations have been made by many authors. Indeed, for many years this has been the obviously accepted theory, and many reviews

of the subject do not even bother to support it with references to specific cases. Actually, a closer look at the literature reveals that this idea was presented mostly in such general reviews, while the number of original works in which the idea is suggested after a careful analysis of specific cases is rather limited.

Abbott (1951), summarizing the migration of the Painted Lady butterfly, Vanessa carduii, in southwestern United States, concludes that population pressure is the most likely cause of migration. A similar suggestion is made by Fraser (1943), regarding the dragonfly Sympetrum fonscolombii. Kluijver (1951) looked for, but did not find, good evidence that higher rates of emigration are tied--in the great tit Parus major--to high densities. Nevertheless, he did not want to rule out this possibility, explaining that this may still be the case, except that objective reasons prevent his data from showing it. This did not prevent Mayr (1952), in his review of Kluijver's paper, from stating that "at high population densities high productivity may produce heavy emigration (apparently induced by overpopulation)----. Similar correlations between high population density and emigration have been established by many authors for various species of vertebrates and invertebrates".

Kettlewell (1947) was evidently, but not explicitly, of the same opinion, as he tried to demonstrate that a very simple genetic model can explain why some, but not all, members of a population will leave at periods of high density.

Most other authors, even when correlations between high densities and migrations can be demonstrated, are reluctant to suggest high density to be the cause of migration, as this implies that the aim of migration is to reduce the density in the remaining population. If this were the case, one can expect a very strong and quick selection against the carriers of the tendency to migrate. We cannot expect a character to be advantageous if its carrier sacrifices itself in favor of somebody else who does not have that character (and therefore does not migrate). Kettlewell later (1952) realized this fact, and to make his model more meaningful he added to it heterozygote superiority and limited the model only to two-way migrations.

The problem of matching the ideas of natural selection with a possible mechanism for the evolution of migratory behavior exists only if one accepts the assumptions of a causal relationship between overcrowding and migration, and of migration being an adaptation for keeping the population size at an optimum. This has been recognized by many people, but the efforts to solve the problem concentrated around two different strategies: attacking the assumptions about the meaning and function of migration, or accepting these assumptions and attacking the relevance of Darwinian natural selection, as we find in the following passage from Cloudsley-Thompson (1957):

> Another weakness----is in the assumption that natural selection acts upon the individual rather than the population. Indeed, if it were so, the problem of emigration would be inexplicable, for----very few of the migrants survive; yet, the migratory instinct persists despite continual heavy selection against it----This apparent paradox can be resolved only by supposing that natural

selection plays upon populations as a whole.

The most eloquent advocate of this idea is Wynne-Edwards (1962):

> In any confined area the build-up of numbers is typically more or less gradual, and the decline sudden: when the time comes, emigration, and mortality caused by stress, parasites and predators, combined in varying proportions, sometimes remove the surplus so fast that the event is described as a crash----Under such conditions discharging the surplus, to a distance at which its demands can no longer be felt, is the way to protect the habitat from damage and to safeguard the continued survival of the stock left behind. As a group-manoeuvre its survival value is obvious. The emigrants may all in fact perish after they leave the habitat--their fate being a matter of indifference so far as the immediate future of the local population is concerned. Students who have not recognized the over-riding power of group-selection have sometimes wondered why, since so many of the emigrants usually succomb, selection has not long ago eliminated the inclination to emigrate, by constantly wiping out the individuals that responded to it. We can possibly obtain a truer perception of the problem by regarding the kind of emigration at present under discussion as being the result of an automatic social guillotine. ----The inclination to comply at all times with the rules of the social code----will be neither stronger nor weaker in those chopped off than in those that remain behind, and will not therefore be under selection: but any stock in which this safety-valve device decayed and ceased to function would soon overtax its habitat and be exterminated. (p. 471)
>
> [Emigration] is an almost universally available means of rapidly reducing population-density in any area where the optimum has been exceeded. For this it is an ad hoc remedy capable of being invoked immediately by the animals themselves, without depending in the least on any outside agency like parasites or predators. ----Emigration-pressure, that is to say, is density-dependent, and ceases to be felt at or below the optimum density level. (p. 480)

A more easily acceptable way to avoid the problem of the evolution of migration as a mechanism for the regulation of population size is, of course, not to consider migration as such a mechanism, or not to see in overcrowding the cause of migration. These are, indeed, the main arguments in the criticism of Wynne-Edward's ideas, as presented at great length by G. C. Williams (1966) and Lack (1966). Moreover, these two assumptions are rejected not only because they lead to the difficult-to-accept theory of group selection, but also because many authors, independently of the argument against group selection, simply considered them to be wrong, even if they saw in the environment the cause of migration.

C. B. Williams (1957), after more than forty years of study of migrations in insects, mostly butterflies, concludes that in spite of the fact that the environment is responsible for migration, it is not overcrowding that causes it. Even in migratory species great abundance need not result in migration. Williams mentions one case where no migration was observed in the pierid Glycesthia aurota at a time when an enormous local abundance of larvae brought about an almost complete defoliation of the food plants. Another interesting example is supplied by Danais plexippus, where the fall migration is initiated by scattered individuals, and only as they move south their numbers keep growing, until huge swarms are formed, and at that stage migration stops. The spring migration starts only after the instinct for gregariousness is lost.

Williams does not suggest a definite environmental factor which is responsible for migration. Climatic conditions are mentioned as the most probable. The assumption that most, if not all, migrants are lost, and the populations are re-established from the few that stay behind, presents the same difficulty we had before--how is the migratory behavior maintained under such a strong selection pressure? Williams, toward the later part of his career, became more and more convinced that true emigrations do not exist, and there is always a return of some of the migrants, or their descendants, to their original habitat and their original population.

An interesting relationship between migration and density is described by Milne (1960), in the Garden Chafer, Phyllopertha horticola. In this beetle there is very little immigration if local density is high, and most eggs will then be laid at the same place where the parents were born. If the density is low, however, the females do not get fertilized, and they fly away in search for mates. The environmental factor which is most important in causing migration in the Garden Chafer is lack of males, which is a result of undercrowding, not overcrowding.

In several cases lack of food is suggested as the cause of migration. Food can become scarce not only because of climatic or other external reasons. If the population reaches a high level relative to the amount of the available food, the scarcity of food, rather than the density of the population as such, can cause some, or all, members of the population

to migrate. This possibility is suggested by Lack (1954, 1966), who points out that we have to assume that not all migrants are lost--some of them find suitable places and settle down successfully.

Support of a part of this theory is given by Strecker (1954). House mice that were kept in an unconfined area, but with a limited supply of food, started to migrate after the population grew to a certain level, when the shortage of food started to be felt.

Water shortage can also cause migrations. Kennedy, Lamb and Booth (1958) have shown this to be the case in the appearance of winged, migratory individuals in the aphid Aphis fabae. Interestingly, the first signs of water shortage that lead to migration initially cause an increase in the nutritive value of the phloem sap. It is concluded that the intervals in the uptake of the sap, rather than its quality, are responsible for migration in this species.

A completely different approach is to consider migration not to be a response to any immediate environmental condition.

That this is the case is suggested, for example, by Andrewartha and Birch (1954). For them migration is only a special case of dispersal movements, which have been shown repeatedly to be independent of environmental conditions. In response to the continuously changing pattern of suitable places in which to live, each species has a characteristic "innate tendency toward dispersal", which is responsible for both short-range and long-range movements.

Most other workers in the field of animal movements prefer to maintain the distinction between dispersal and migration. Good experimental evidence in support of this distinction is given by Sakai, Narise, Hiraizumi and Iyama (1958), who demonstrate, in Drosophila, the existence of two kinds of movements--"random migration", independent of density, and "mass migration", that starts only when population density reaches a certain level. These two kinds of movements are genetically determined, independently of each other. There are demonstrable differences between different genetic strains with respect to the level of random migration, the percent population taking part in mass migrations, and the density threshold at which mass migration first appears. The causal relationship between higher densities and mass migrations is doubtful, particularly because of the fact that at all densities above the threshold the percent of migrants remains constant.

A more recent school of thought also considers migration separately from dispersal movements, but sees in it a built-in mechanism that operates in particular stages of the life cycle, or in particular seasons of the year, regardless of the physical conditions of the environment or the density of the population.

The origins of these ideas can probably be traced to the attempts to redefine migratory movements. For many years suggestions have been made to classify, and identify, migratory movements not according to their outcome, but rather according to the behavior of the migrating animal itself. C. B. Williams (1958) elaborates his idea of migra-

tion being a self-propelled, self-directed flight -- "movement determined by the insect itself, which instead of being haphazard in direction is straightened-out so as to result in a change of habitat". This definition does not cover many migrating animals, including insects. Not all stages of the migratory movements are necessarily actively performed by the migrating animal, and during some parts of its migration the animal rarely has control over the direction of the flight.

Johnson (1960) tries to replace Williams' behavioral definition with a physiological one. If the assumption that migration is caused by a deterioration of environmental conditions is correct, migrating insects are expected to show some signs of physiological stress. Johnson finds--in the cases that he studied--that the opposite is true. According to him migratory flights appear to be made primarily by newly emerged adults, at the end of the teneral period after moulting from the previous instar, and as soon as the insects have full capacity for flight. Usually these exodus flights are made by the animals without reference to each other. Mass migrations are not related to the size of the population, the immediate food supply or space; neither is behavioral synchronization responsible for the formation of the aggregates. In many species rhythms of emergence are known, and these rhythms cause many young adults to reach flight-maturity, and actually take off, at the same time. In Johnson's words, "I see migration as an evolved adaptation [for recolonization] rather than as a current reaction to adversity".

This idea is further elaborated by Kennedy (1961), who also sees in migration a mechanism for colonization rather than escape from adverse conditions. Any adult, before reproduction, can be a good colonizer. Kennedy suggests that migrations are not limited only to young adults, but are performed by all pre-reproductive stages. The suggestion is supported by Dingle's work (1965) on the milkweed bug, Oncopeltus fasciatus. The "straightening out" feature of migratory movements, as suggested by Williams, is correct, but not because of an internal sense of direction. Rather, it is an outcome of the fact that the migrating animal does not pay any attention to stimuli that under other conditions will cause it to stop moving--food or a mate. The migratory behavior of pre-reproductive adults is "persistent, straightened-out movement that is accompanied by and dependent upon the maintenance of an internal inhibition of those 'vegetative' reflexes that will, eventually, arrest movement. Conversely, the locomotor reflexes (or other reflexes securing displacement) cannot for some while be inhibited by stimuli that do promptly inhibit them at other times".

The physiological changes responsible for this may be accompanied by a deterioration of the general physiological condition of the animal; this deterioration (which was suggested for migrating animals by some authors, but denied by Johnson) should be considered as a preparation for migration, not as its cause.

How can the evolution of migration as an adaptation for colonization

be explained? A survey done by Southwood (1962), covering many groups of terrestrial arthropods, indicates the existence of a strong correlation between the presence, in a species, of migratory behavior (as distinguished from trivial movements), and the type of habitat this species occupies. The same conclusion is reached in many groups, when a comparison is made between migratory and non-migratory species--migratory species tend to occupy more temporary habitats in comparison to their non-migratory relatives. The level of migratory behavior is positively correlated with the degree of impermanence of the habitat, and the prime evolutionary value of migration lies in the colonization of changing or temporary habitats. Not many cases are known of migrations from permanent habitats, while movements within the habitat are more likely to be closely related to overcrowding, and it may be that from such movements migration has evolved.

Migration, with all its physiological and behavioral features is maintained in spite of enormous losses of individuals en route, including entirely abortive movements by large numbers of individuals, because in the long run some migrants find what they require, while those who stay behind are eventually wiped out when their habitat changes.

Another phenomenon which is associated with temporary habitats is diapause. Whether diapause or migration are selected as a way to survive unfavorable conditions depends to a large extent on the nature of the changes in the habitat. If the change is temporary and reversible,

diapause may be the way to cope with it. An irreversible change can be avoided only by migration. Sometimes this "either-or" relation between diapause and migration seems to be violated--when animals have to migrate to the site of their diapause. This can be considered, however, as an example of the regular to-and-fro migrations, because the diapause is later followed by a return flight to the original habitat.

We have seen that wide disagreements exist between workers in the field of animal emigrations. This is probably due to difficulties, on the part of many workers, to distinguish between primary and secondary causes, primary and secondary effects, and even between causes and effects in general. The most acceptable interpretation of one-way migrations is the one that considers colonization to be of prime evolutionary value, especially for inhabitants of temporary or changing habitats. The fact that the habitat is temporary is recognized, no doubt, by the occurrence of changes in the past. The animals that could not react to these changes, by migrating, for example, were selected against. The species that today occupy temporary habitats must have evolved the ability to react to possible changes. Some of them do not migrate before a change has actually happened, and the physiological welfare of the animals has been affected. Their study will suggest that migration is a direct response to environmental deterioration. Others do not wait for a change to occur, and they include migration in their normal "repertory". A study of these spe-

cies will suggest that migration is independent of the environment. An interesting "gradient" of the tendency to migrate--from facultative migration, depending on the environment, to obligatory migration, that occurs regularly without regard to the environment, is described in closely related species of aphids by Shaposhnikov (1960). It has to be remembered, however, that regardless of its immediate cause the prime purpose of migration is finding a more suitable site, and regardless of the dangers that sometimes lead to death of entire migrating populations, for members of some species it is better, in the long run, to have, and use, the ability to migrate. It is also conceivable that, regardless of its long-term advantage, a secondary effect of migration may very well be a lowering of all kinds of undesirable effects caused by overcrowding, to the immediate benefit of the migrating animals, and those that stay behind as well. In cases where, on one hand, the physiological condition of the individual is affected by crowding, and, on the other hand, the physiological condition serves for triggering migratory behavior, the interaction between these two relationships may cause migration to appear as a mechanism responsible for maintaining a constant population size.

Non-obligatory sexuality

All the cases of emigration of animals, regardless of their causes and direct or indirect consequences can be considered as a kind of escape behavior. Sexuality, on the other hand, cannot, in most animals, be included in that category. Sex is generally an integral part of reproduction in animals, and all the species that have either only

sexual reproduction or a regular and predictable alternation between sexual and non-sexual modes of reproduction can be excluded from our discussion. Only in the relatively few species that normally reproduce asexually or parthenogenetically, with sexual forms appearing irregularly, in response to some environmental cues, can we consider sexuality to be an escape mechanism. In these species sexual reproduction results not only in new genetic combinations, but the products of this reproduction, instead of following a definite time table of development, often remain in a dormant stage, or diapause, until the environment again becomes favorable. While emigrations are examples of escape in space, the appearance of sexuality in normally asexual species is an escape through time, with the animals not necessarily leaving, in a physical sense, their immediate environment (Slobodkin, 1968).

The factors responsible for the appearance of sexuality in normally asexual or parthenogenetic animals have been a matter of discussion not only in the case of hydra. For good and comprehensive reviews of the subject reference should be made to the papers of Shull (1929) and Suomalainen (1950). The common denominator of the various explanations, which are often contradictory even when the same species is discussed, is that a change in the level of a factor, rather than its absolute level, causes the appearance of sexual forms. It may even be that a significant change in any of several environmental factors can induce sexuality.

The adaptive significance of this phenomenon is obvious. If the animals get along well in the present set of conditions, there is no need to leave the area or to form dormant stages. A change in the environment may signal a deterioration of its fitness, and formation of more resistant dormant stages, which also include new and possibly better adapted genetic combinations, is the way of responding to it. As in the case of emigrations, if the change in the environment is seasonally predictable, the dormant stages, and the switch from an asexual to a sexual mode of reproduction, will be incorporated into the normal life cycle of the species.

More careful studies make the relation between environmental factors and the appearance of sexuality more difficult, rather than easier, to understand. An attempt to identify the chemical responsible for the appearance of sexuality in the rotifer Asplanchna (Gilbert, 1967, Gilbert and Thompson, 1968) has shown that the substance is a dietary component which cannot be correlated with any of the ecologically important parameters. Gilbert does not claim that the relation between population size or the condition of the abiotic environment and sexual differentiation is fortuitous, but a satisfactory explanation has yet to come.

Floating and sexuality in hydra

Although the available information about the ecology of hydra in nature is very incomplete, all the reports suggest that floating may play a very important role in determining the distribution of hydra and their abundance in any location. Because of technical problems all cen-

suses describe only hydra which are attached to some natural or artificial substrate, but the characterization of the hydra population as "a population which is in part attached, in part floating and drifting free in the water, and in part related to the surface film" (Welch and Loomis, 1924) can probably apply to most hydra populations. It is very difficult to determine how many hydra exist without being attached to some solid object, but some hydra are always found in plankton samples, and the implication of the observed drastic changes in numbers of attached hydra is that at certain periods floating may involve entire populations.

Such migratory behavior is expected, as we have seen, to be associated with temporary habitats. And, indeed, changes in abundance and general occurrence of hydra, indicating that the suitability of their habitat is very unstable, are frequently observed by those who collect hydra in the field. Dr. Helen Mantel (Forrest) states (personal communication): "For more than fifteen years I collected hydras regularly from more than 25 localities in New Jersey throughout the year, and from some of them more often than once a week for long periods. The variation and succession of species I found could not be explained only by changes in behavior. For example, there was a mill pond where hydras were always present, but in which a different species seemed to take over dominance nearly every year, sometimes alone, sometimes with one or two other species. In many cases a species would be present in greater or lesser abundance for one to five years and would then disappear, not to be found again. At another collecting

spot, two species were found constantly present over a five year period, after which one died out and was replaced by two others, both of which disappeared again in two years".

Following is a short review of the relevant information of four more quantitative long term field studies of hydra populations.

Welch and Loomis (1924) report that in seven years of observation of H. oligactis in Douglas Lake, Michigan, the populations, found on the vegetation, reached their peaks in spring and early summer, and then disappeared completely from the surface water after a decline period of variable length. Movements, rather than mortality, seemed to be responsible for the disappearance of hydra, and the authors conclude, after measuring various environmental factors and analyzing their effect in laboratory conditions, that temperature is the most important factor, if not the only one. They suggest that the hydra migrate to the bottom, but they could not find any evidence for that.

A study of two species (H. (Pelmatohydra) oligactis and H. (P.) pseudoligactis) in the same lake (Miller, 1939) has shown that the increase in late spring and early summer and the subsequent decline are true only for the hydra found on the emergent vegetation, mostly bulrush, Scirpus validus. Usually the hydra do not disappear completely from the surface water, and a further decline occurs in winter. Similar fluctuations, but on a different time table, involve the hydra on submergent vegetation, and there the population becomes very sparse in winter. Populations on artificial racks below the surface show the same

trends as those on the bulrushes, with racks located more deeply getting hydra later in the summer. No hydra could be collected from the bottom. Miller rejects temperature as the factor responsible for the mass movements, and also rules out wave action. Free hydra were collected only rarely, but their existence is assumed because of cases of tranfer of hydra from one rack to another, and Miller suggests that the movements are initiated by the hydra themselves. The factor responsible for the hydra leaving their substrate is, according to Miller, the accumulation of organic material (mostly diatoms and algae) on their supports, which is most significant in the middle of summer. As evidence, Miller states that disappearance of hydra involves only those sitting on older bulrushes, and any young plant, as long as it is clean, immediately becomes covered with hydra, even when the decline on the older plants is at its peak. Extreme temperatures, unfavorable local chemical conditions, protozoan parasites (Hydramoeba hydroxena) and some carnivorous flatworms cause some mortality, but neither can completely eliminate a population. Food is always available, and there are always enough apparently suitable places to become attached to. Migration, then, is a most important factor, caused, according to Miller, by the accumulation of unfavorable material on the places of support.

Bryden (1952), in a study of H. oligactis in Kirkpatricks Lake, Tennessee, found that migration was responsible for changes in abundance in the summer and fall, while other factors, probably temperature,

caused declines during the winter. The hydra are most abundant on an emergent plant, Dianthra americana, increasing in numbers from June until September, when they reach a peak density of 40-60 per liter. In October, with the first frosts that kill the Dianthra, the hydra move to the bottom and undercuts along the shore, where increases in the density of hydra occur throughout the fall. During the winter the hydra at the bottom decline, and they reappear on the plants as these start growing again in June. The vertical and horizontal distribution of hydra in the Dianthra beds is not uniform, indicating that many sections are unsuitable for the hydra. Hydra are also found on submerged branches of trees, and it was found that some species of trees, like willows and maples, carry many hydra, while others, like oaks and sycamores, carry none. Empty plates in the water accumulate hydra, which must have reached them by drifting freely in the water. Hydra dyed with Nile blue sulfate were found to migrate hundreds of feet. Hydra are assumed to be selective in their choice of substrate, and the disappearance of suitable supports is the most important factor in causing migrations. Other factors, like low temperatures and lack of food in late winter are sources of mortality.

Mass migrations are also reported by Griffing (1965), in a study of H. oligactis and H. pseudoligactis in Pickerel Lake, Michigan, in which seasonal changes in distribution, similar to the ones reported in the previous papers, were found. This study adds an interesting aspect to the phenomenon--the two species migrate in opposite vertical direc-

tions at the same time. In early spring the two species occupy both the thermocline and epilimnion, but later in the spring H. oligactis disappears from the epilimnion and increases significantly in the thermocline, while H. pseudoligactis moves from the thermocline to the epilimnion. This again indicates selection of habitat by the hydra, with different preferences for the two species. Griffing reports more rapid fluctuations than in the previous studies, but a general decline, also a result of migration, occurs throughout the summer.

None of these four studies devotes a great deal of attention to the occurrence of sexual forms in nature, and the possible relationship between it and the periods of mass migrations. The rest of the discussion will be devoted to an effort to combine the field observations with the results of the laboratory studies reported earlier, so that some idea can be gained about the role and meaning of escape mechanisms in hydra populations in nature.

The laboratory studies gave, as we have seen, somewhat confusing and contradictory results. In some cases floating is not correlated with density, in others it is. Feeding sometimes prevents floating, and in other times floating has no relation to the level of feeding. Conditions that on one day lead to floating, or the appearance of sexual forms, on other days fail to do both. Some clarification may be achieved if we realize that the results are influenced to a large extent by the experimental design, that different hydra may react differently to the same set of conditions, and that floating, as we measure it, may be a result

of several independent activities.

Hydra reach the surface either by direct floating, or by moving up the walls and detaching when they reach the top. In very shallow water they can also reach the surface with their tentacles, hold on to the surface film and then lift themselves. This last possibility was probably of great importance in many of our experiments, but its relevance to natural situations is minimal, because hydra are rarely found right below the surface.

Moving up the walls and detaching at the surface is of greater relevance, and this is a phenomenon which is mostly associated with well fed hydra. Ewer (1946a, b) has shown that in well fed populations newly detached buds, if they are not immediately fed, keep for 3 days a geonegative response, which causes them to move away from their parents and up the walls, regardless of the direction of light, the pH or the availability of oxygen. This is a normal dispersal mechanism, insuring colonization of empty favorable areas, associated with the temporary nature of the habitats occupied by hydra. Indirectly, it also prevents overcrowding. This situation is similar to the one achieved by many of the "B" population, where the numbers of floaters roughly equal the numbers of newly formed buds, with the rates of floating not showing any relation to density. In nature hydra are regularly found in plankton samples, and under normal conditions these may be the dispersing young. This can also explain the relative absence of sexual individuals from the floating hydra in the "B" populations, as young hydra do not

usually have gonads, and the sexual members of the population are older and well fed.

When the conditions deteriorate, as was the case in the "A" populations, floating affects all the individuals of the population. Sexuality also increases in frequency as the conditions become unfavorable.

As long as the hydra can survive in their original location, floating does not affect all of them. The frequency of floating is probably a function of the degree of severity of the environment, which, in the case of the 80ml "A" populations was associated with density (it has to be remembered, though, that the "A" populations were kept in highly unnatural conditions as far as floating was concerned, because the floating hydra were forced to stay in the population day after day). The reason that not all hydra float when the conditions start deteriorating is that floating hydra are exposed to great uncertainties about survival and finding a suitable place to settle down. As long as the hydra can survive in their old place, and there is a chance that the environment will return to its previous conditions, or at least not deteriorate further, some animals stay behind.

Another case of correlation between formation of new genetic recombinants and migratory behavior is reported from migratory locusts by Nolte (1967, 1968). Here migration is also supposed to be induced by high densities, through a gaseous pheromone, resembling in some ways the conditioning of water by hydra. Nolte found that the pheromone not

only induces the development of migratory forms, but also increases significantly the number of chiasmata in the meiotic divisions of the migrating individuals, leading to an increase in the kinds of recombinants which will be produced when the migrants reach their destination.

The increase in the crossover rate in locusts is analogous to the increase in the frequency of sexuality in hydra, but in locusts the increase is found in the migrants, while in hydra sexual forms do not float as much as non-sexual ones. This disagreement is only superficial. In both cases the migrating individuals have to be in maximum reproductive capacity, and in hydra this is associated with asexual forms. The direction of movement of hydra, in contrast to that of locusts, is random, and a successful migrating hydra may find itself all alone in its new location. Gonads will not be of much use in such cases, while the ability to start budding quickly is of great importance. The sexual hydra, on the other hand, tend to stay behind, and they respond to the possibility of the environment becoming totally unfavorable by producing zygotes of as many genotypes as possible, some of which may be adapted to the new conditions immediately, while others remain dormant until the conditions become more favorable.

If the conditions become totally unfavorable, as when no suitable supports can be found (Miller, 1939), all the hydra that will not leave will die, and the population will disappear completely.

What constitutes an optimal environment for hydra, or by what

criteria hydra measure the favorability of their environment, probably varies from species to species and from lake to lake. Conditioning of the water by the hydra themselves may play a role, but overcrowding as such does not seem to be involved. Clemens (1922), for example, reports a huge concentration of H. oligactis along a 15 mile stretch of the north shore of Lake Erie in the summer of 1920, with densities that exceed by far those reported from other studies. But in all cases we can expect the conditions not to remain favorable for very long, and when this happens escape behavior will appear.

The apparent cycles in escape responses are not easy to explain. It was already suggested that some changes in the way hydra interpret their environment may occur, so that what on one day is considered unfavorable on another day becomes acceptable. On the other hand, it may be that for escape responses to occur the hydra must be in good physiological conditions, and that temporary periods of decline in their physiological welfare, similar to the temporary periods of senescence associated with depression, occur in hydra.

Escape mechanisms, then, are important in population dynamics of hydra in nature. Field evidence suggests that hydra have a patchy distribution, and each population will stay at one place as long as the conditions are favorable. The density of the population is determined by many factors--temperature, food, parasites, predators and the presence of other species--but escape behavior, which serves normally for dispersal and colonization, also plays an important part. When

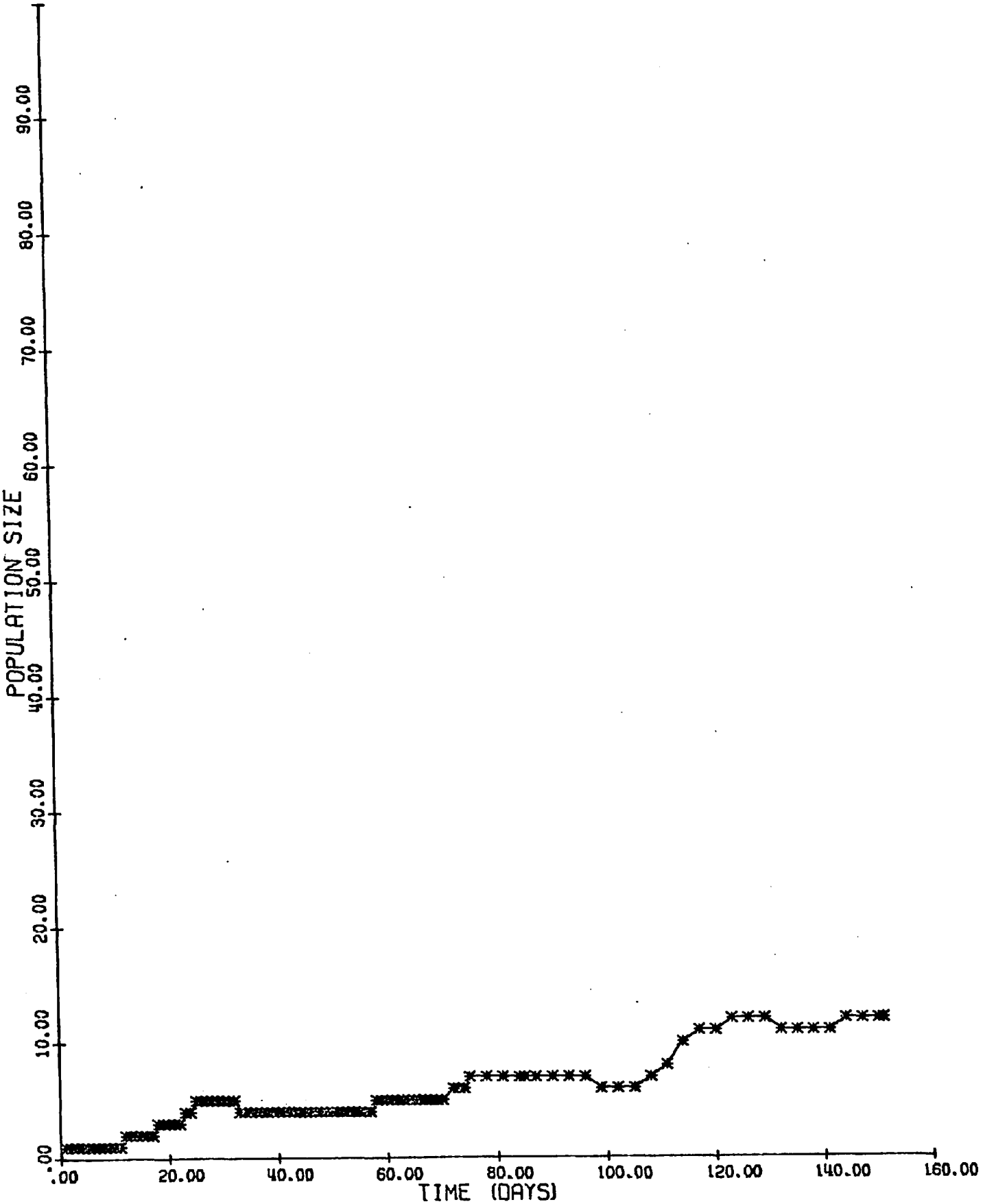
conditions deteriorate more hydra will utilize floating for leaving the population, while others will become sexual and produce dormant stages, possibly better adapted genetically. In extreme cases the whole population may take off and move away.

APPENDIX A

Growth curves (curve 1) and curves of the frequency of floating and sexuality (curve 2) of all "A" (closed) populations of the long term experiments. The following table gives for each curve the page on which it can be found.

Population	Curve 1	Curve 2	Population	Curve 1	Curve 2
20 20 A1	181	182	80 40 A2	211	212
20 20 A2	183	184	80 80 A1	213	214
20 40 A1	185	186	80 80 A2	215	216
20 40 A2	187	188	150 20 A1	217	218
20 80 A1	189	190	150 20 A2	219	220
20 80 A2	191	192	150 40 A1	221	222
40 20 A1	193	194	150 40 A2	223	224
40 20 A2	195	196	150 80 A1	225	226
40 40 A1	197	198	150 80 A2	227	228
40 40 A2	199	200	300 20 A1	229	230
40 80 A1	201	202	300 20 A2	231	232
40 80 A2	203	204	300 40 A1	233	234
80 20 A1	205	206	300 40 A2	235	236
80 20 A2	207	208	300 80 A1	237	238
80 40 A1	209	210	300 80 A2	239	240

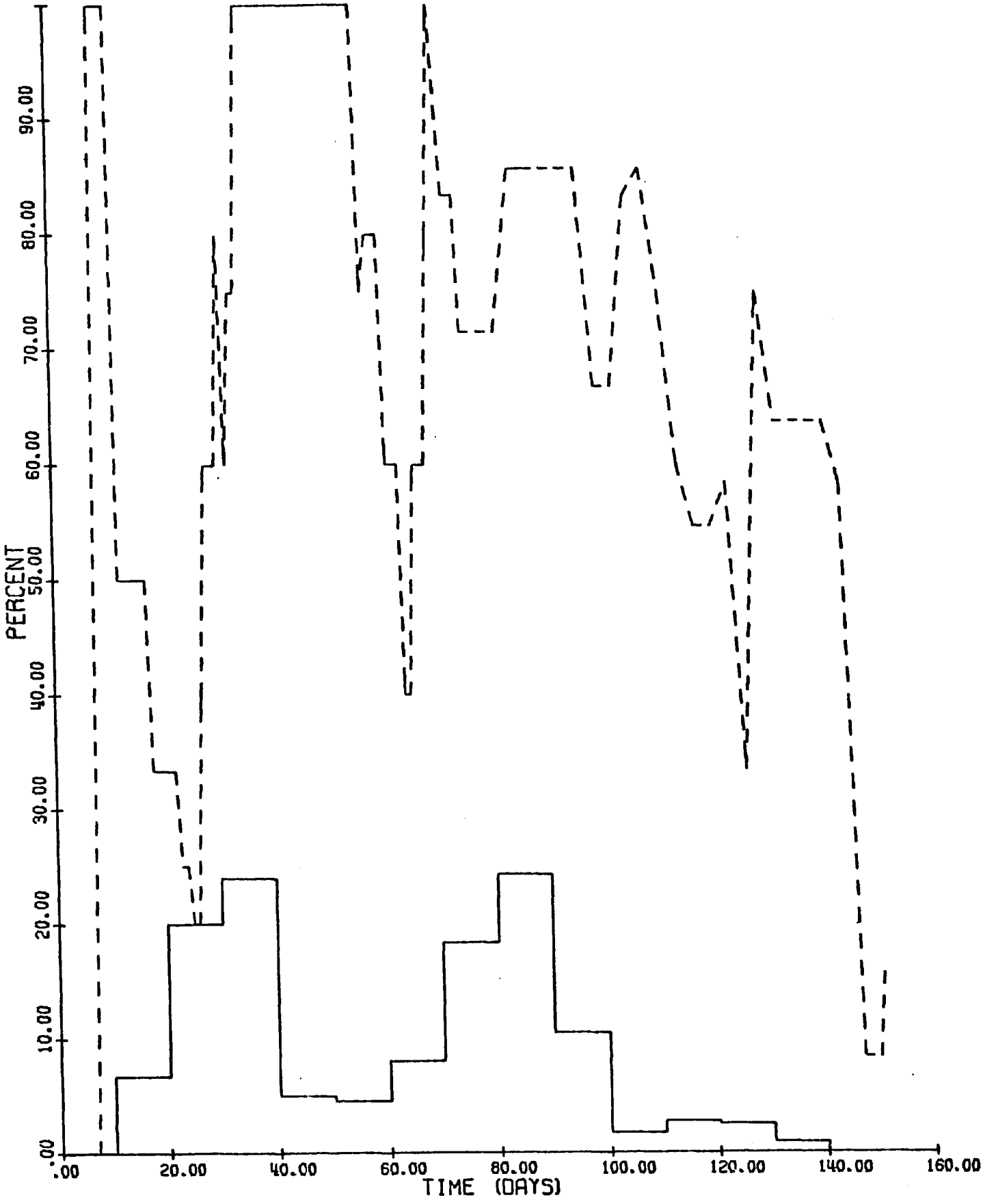
POPULATION 20 20 A1 - GROWTH CURVE



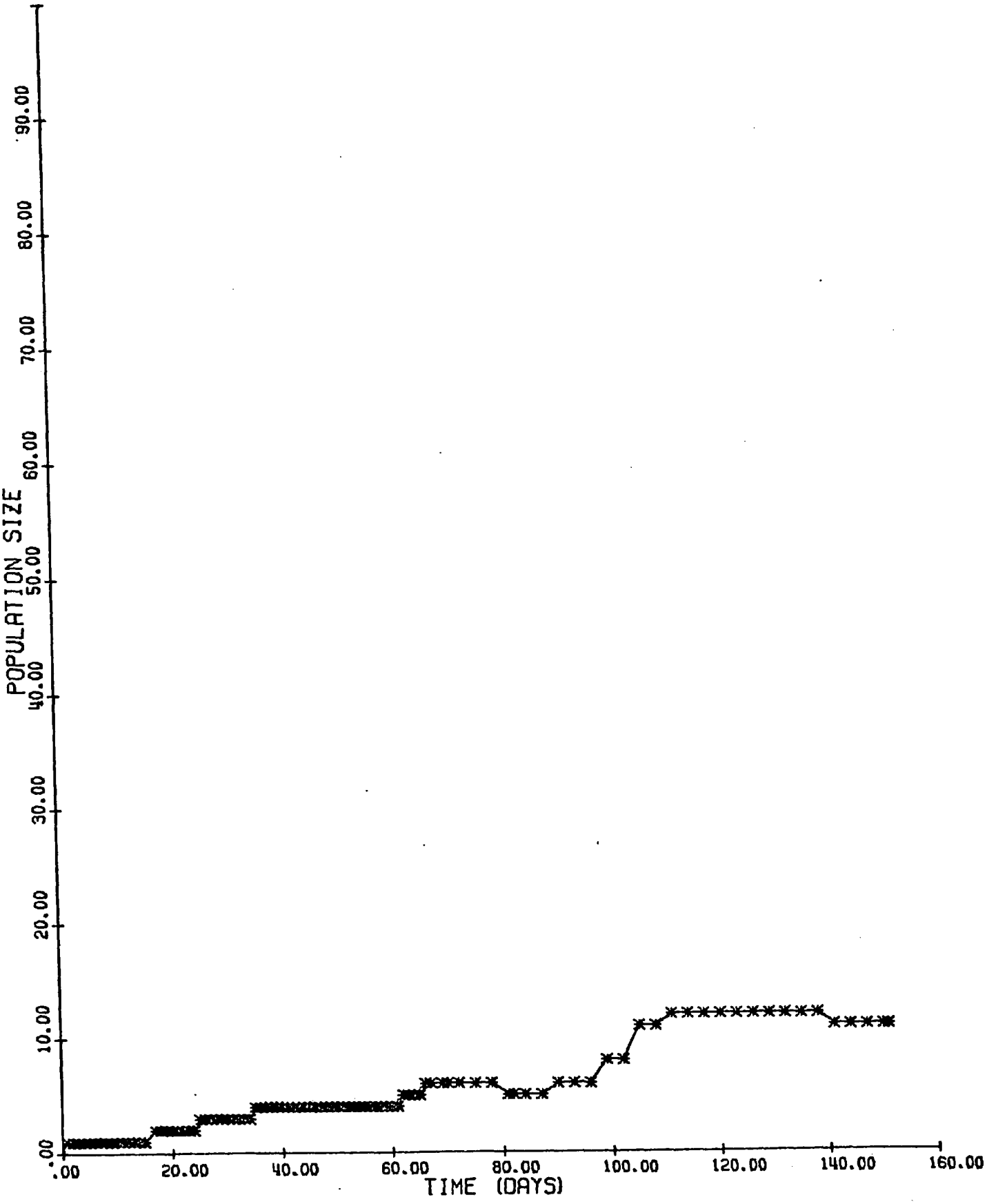
POPULATION 20 20 A1 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



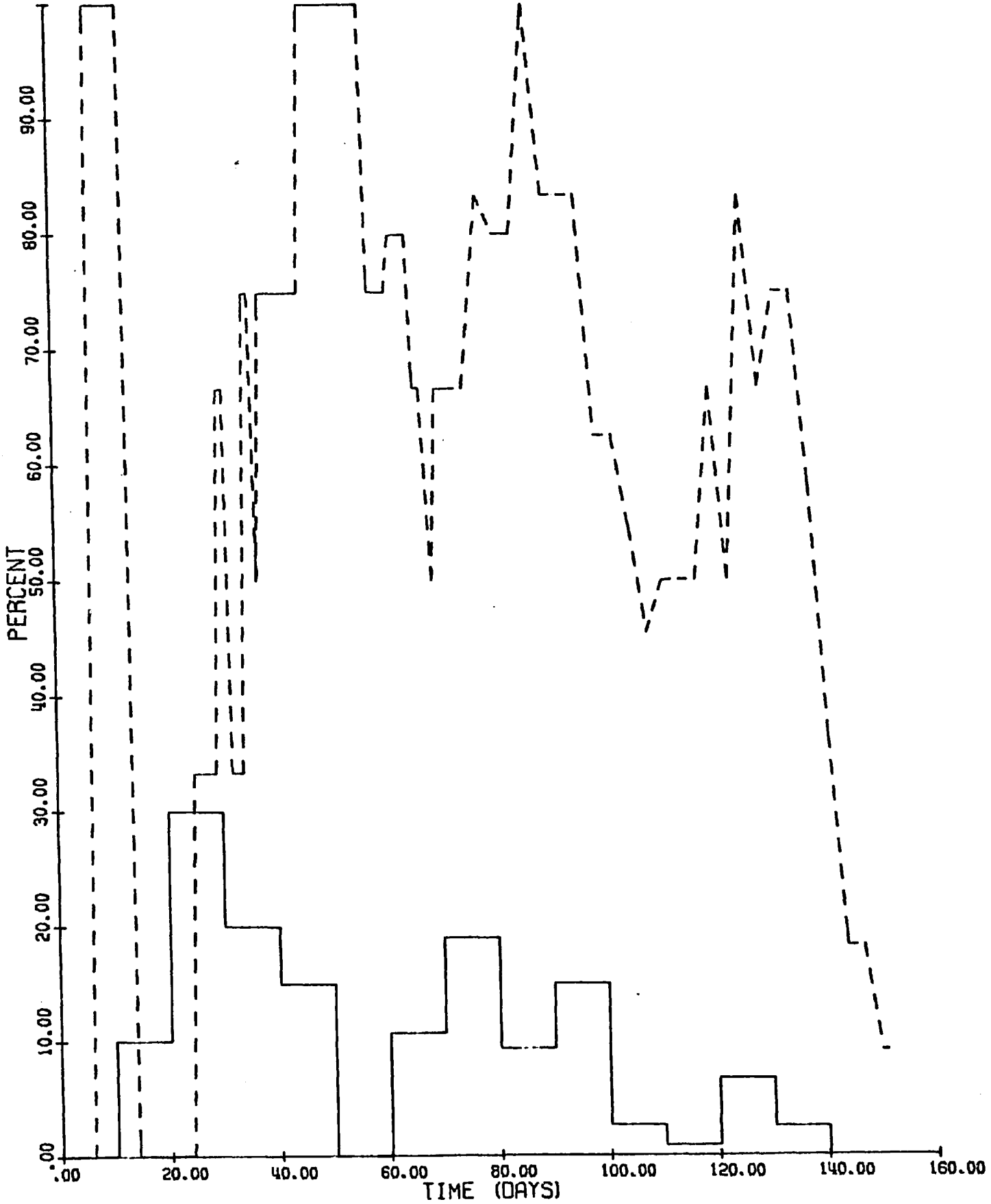
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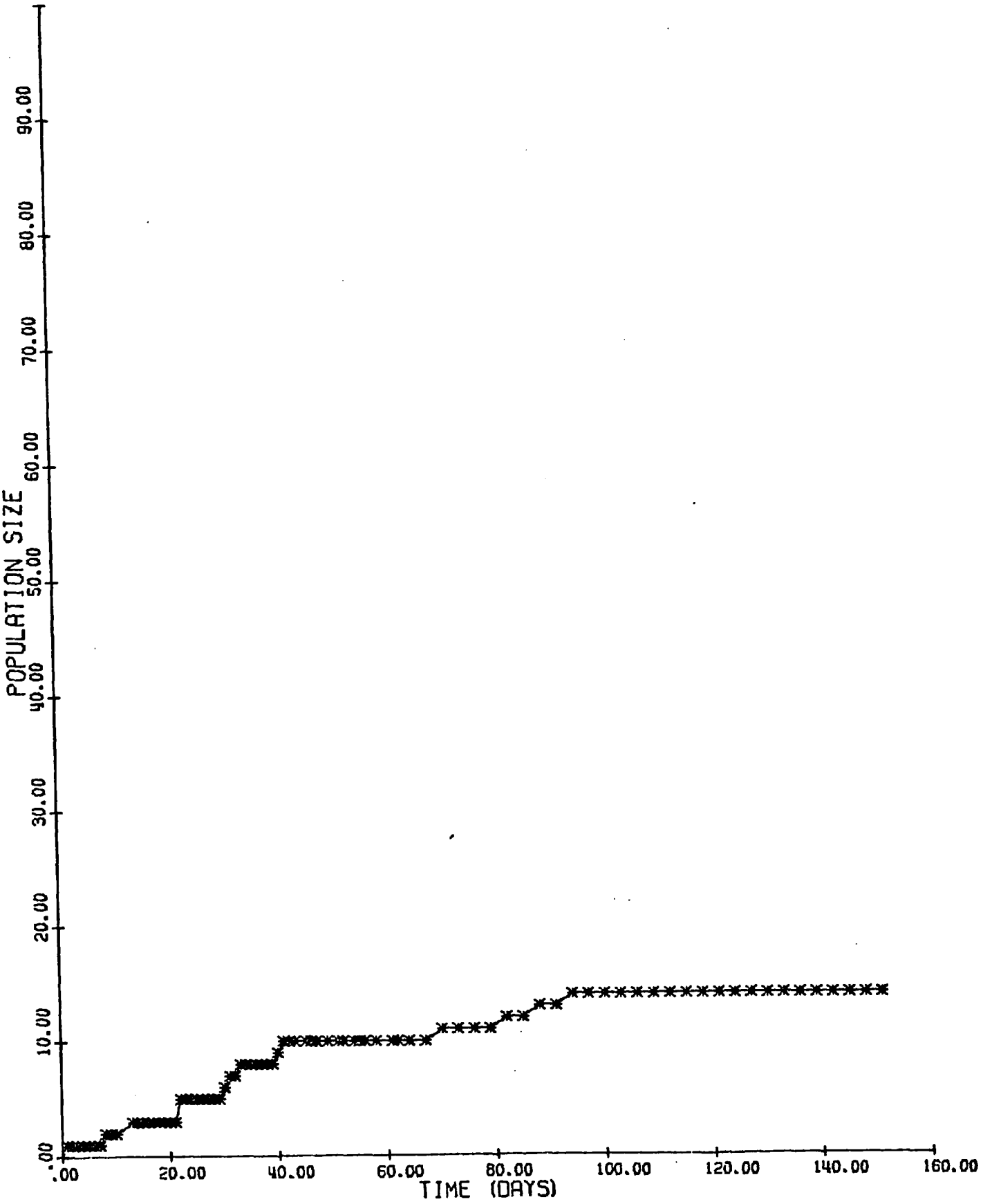
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FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



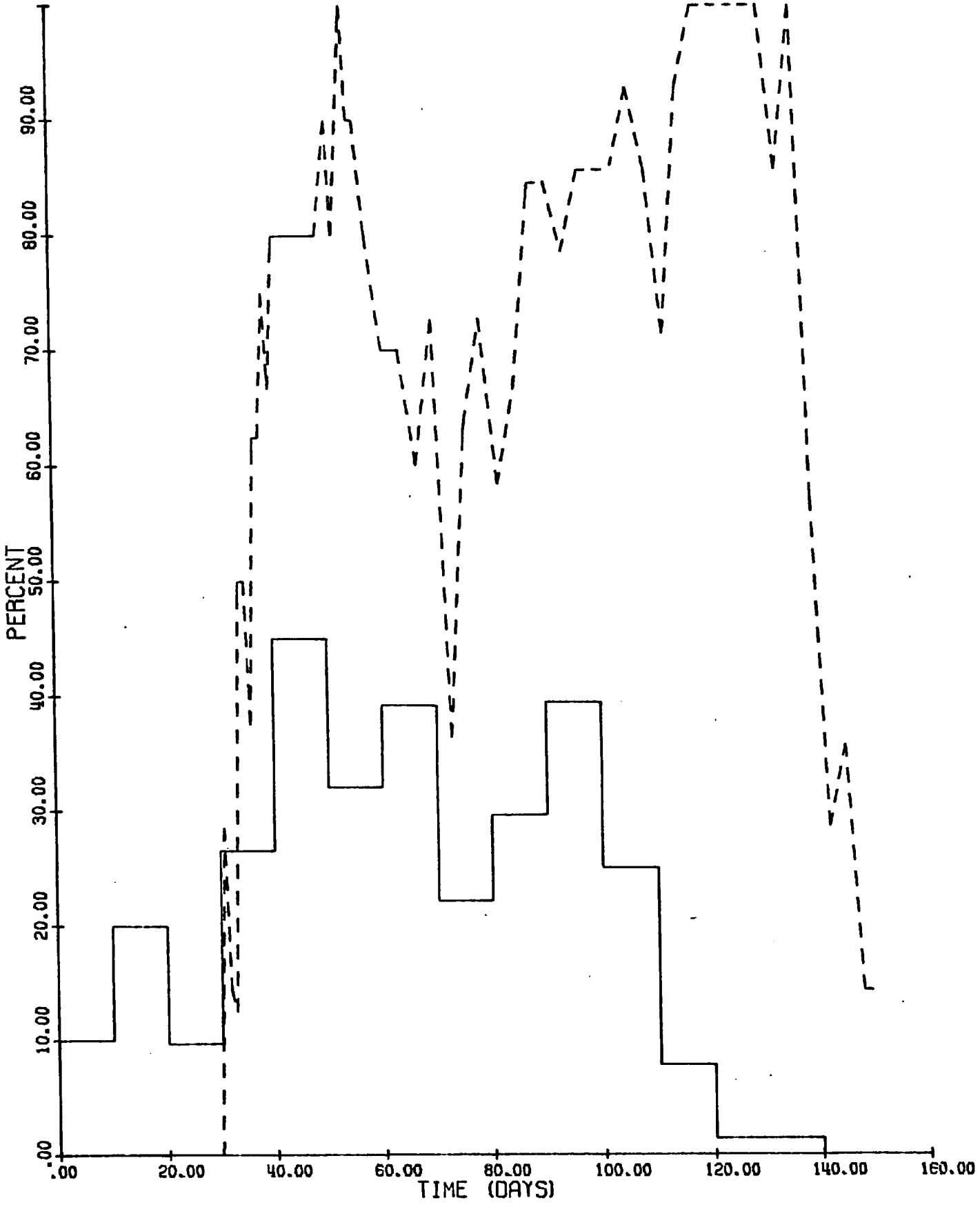
POPULATION 20 40 A1 - GROWTH CURVE



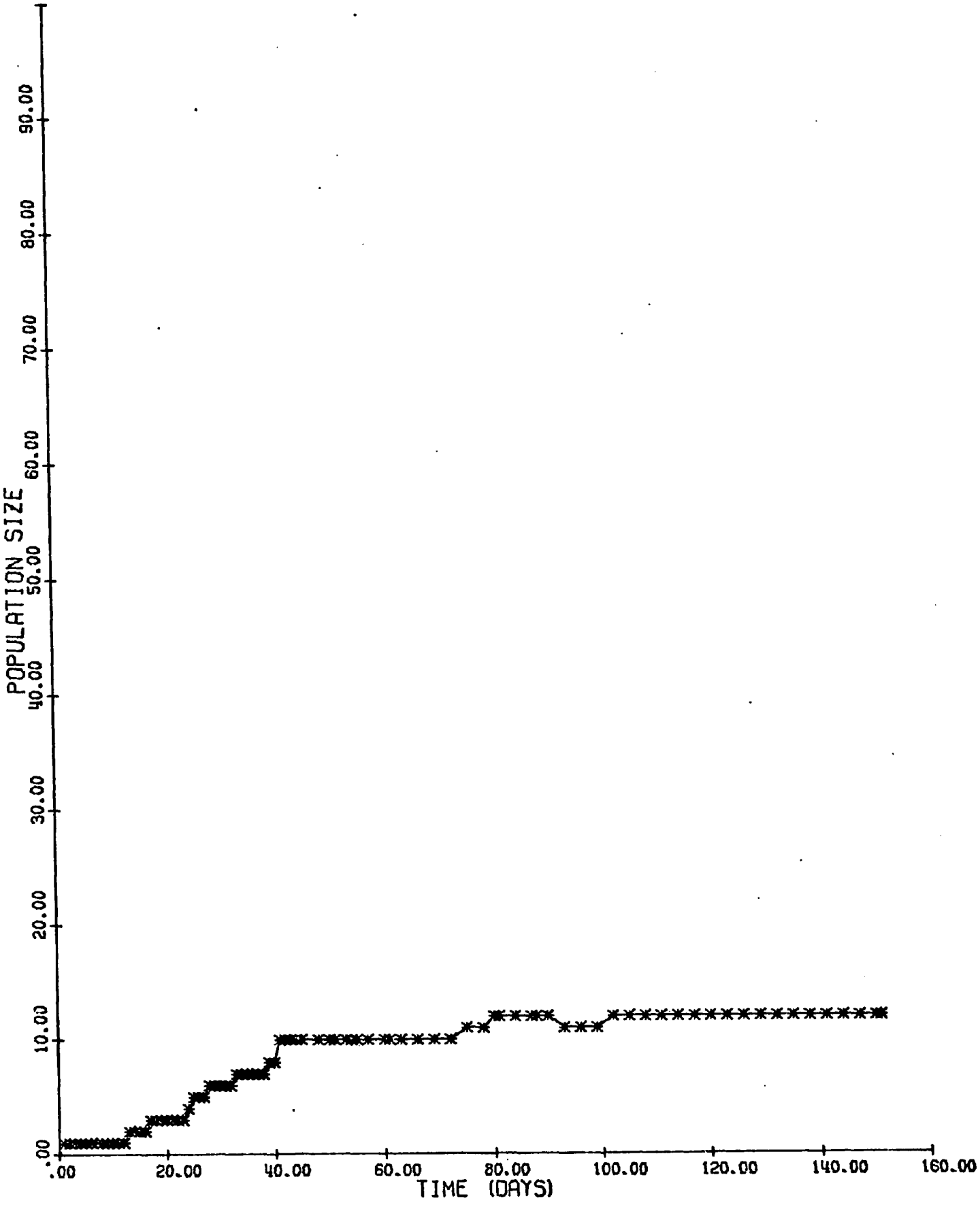
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



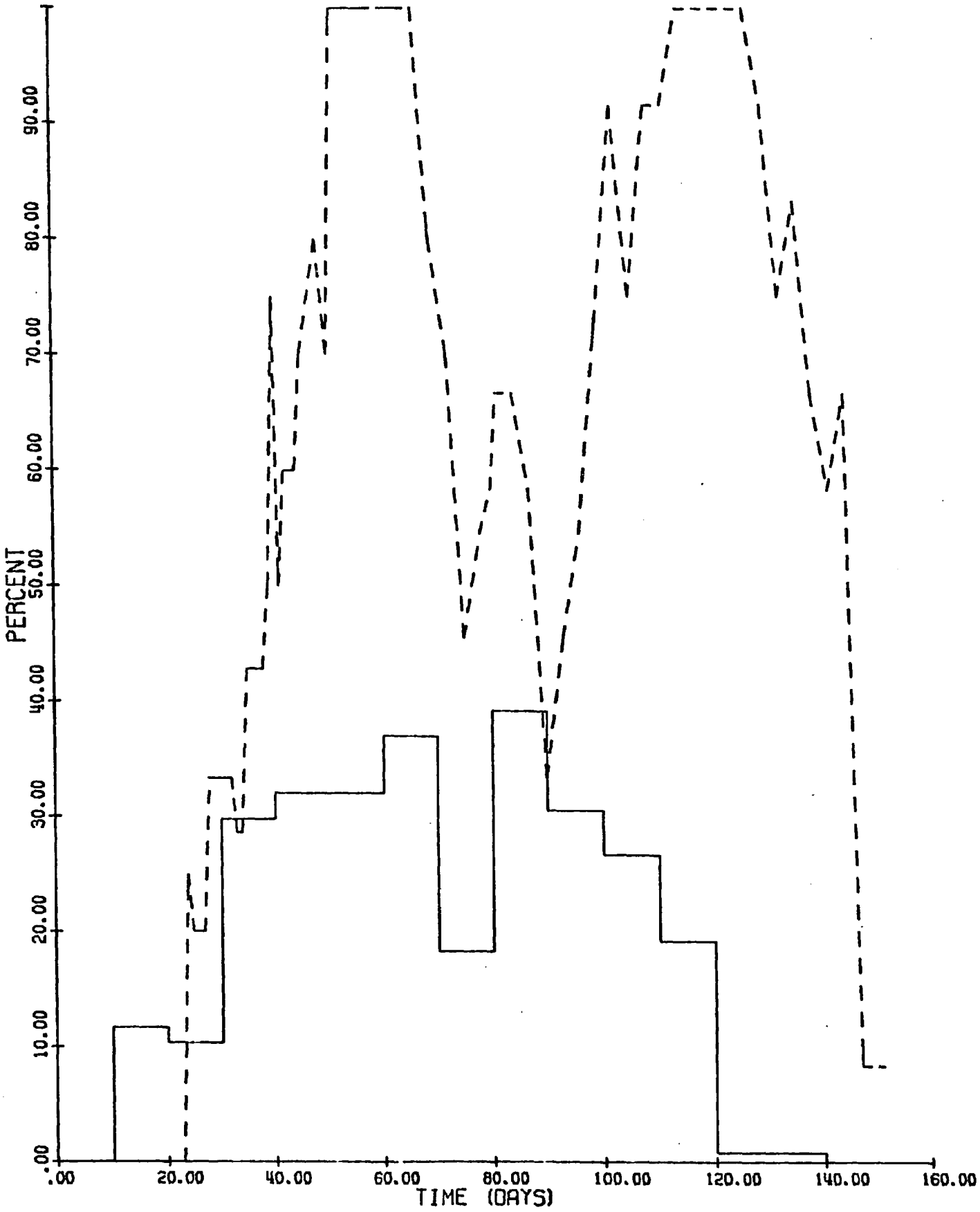
POPULATION 20 40 A2 - GROWTH CURVE



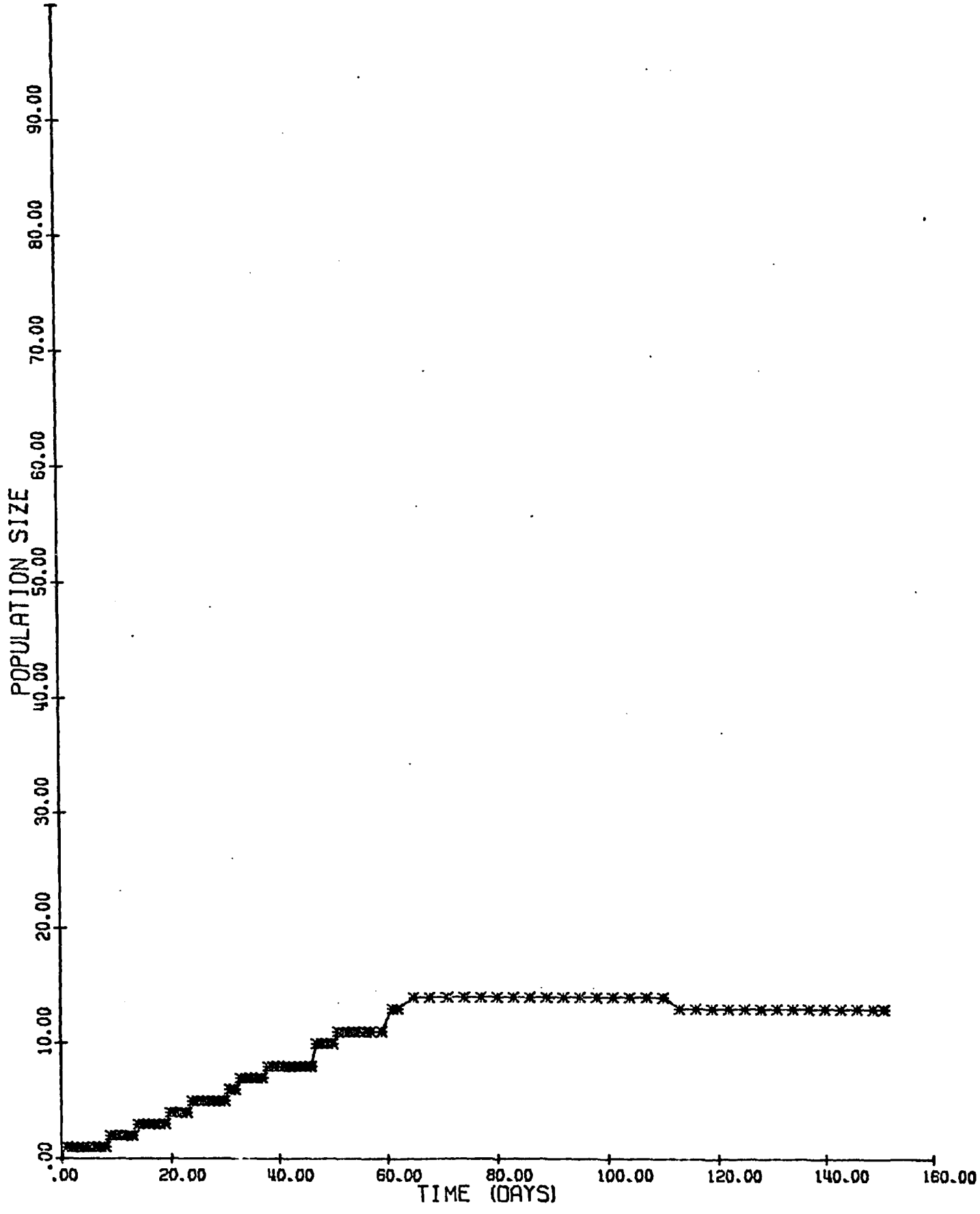
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



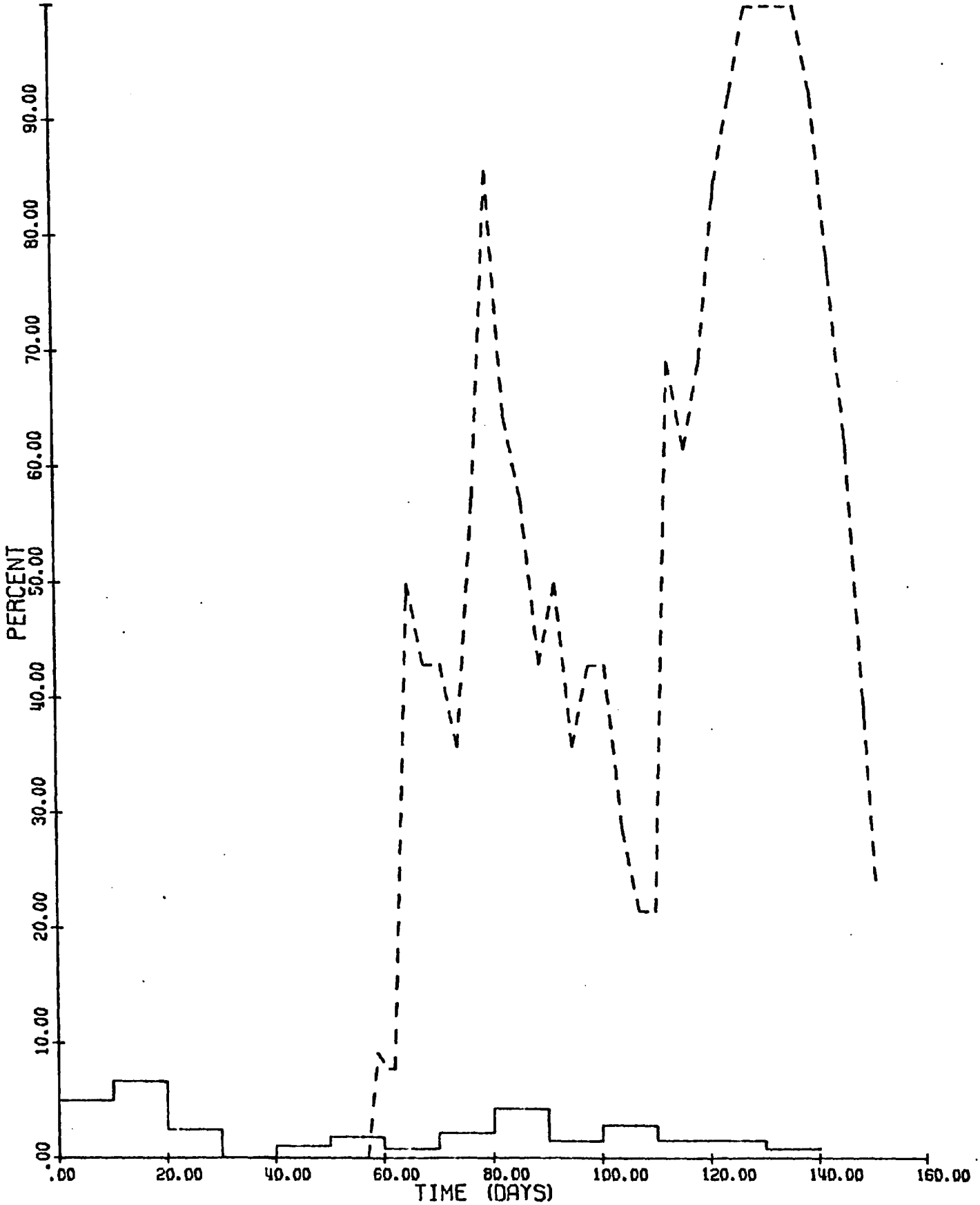
POPULATION 20 80 A1 - GROWTH CURVE



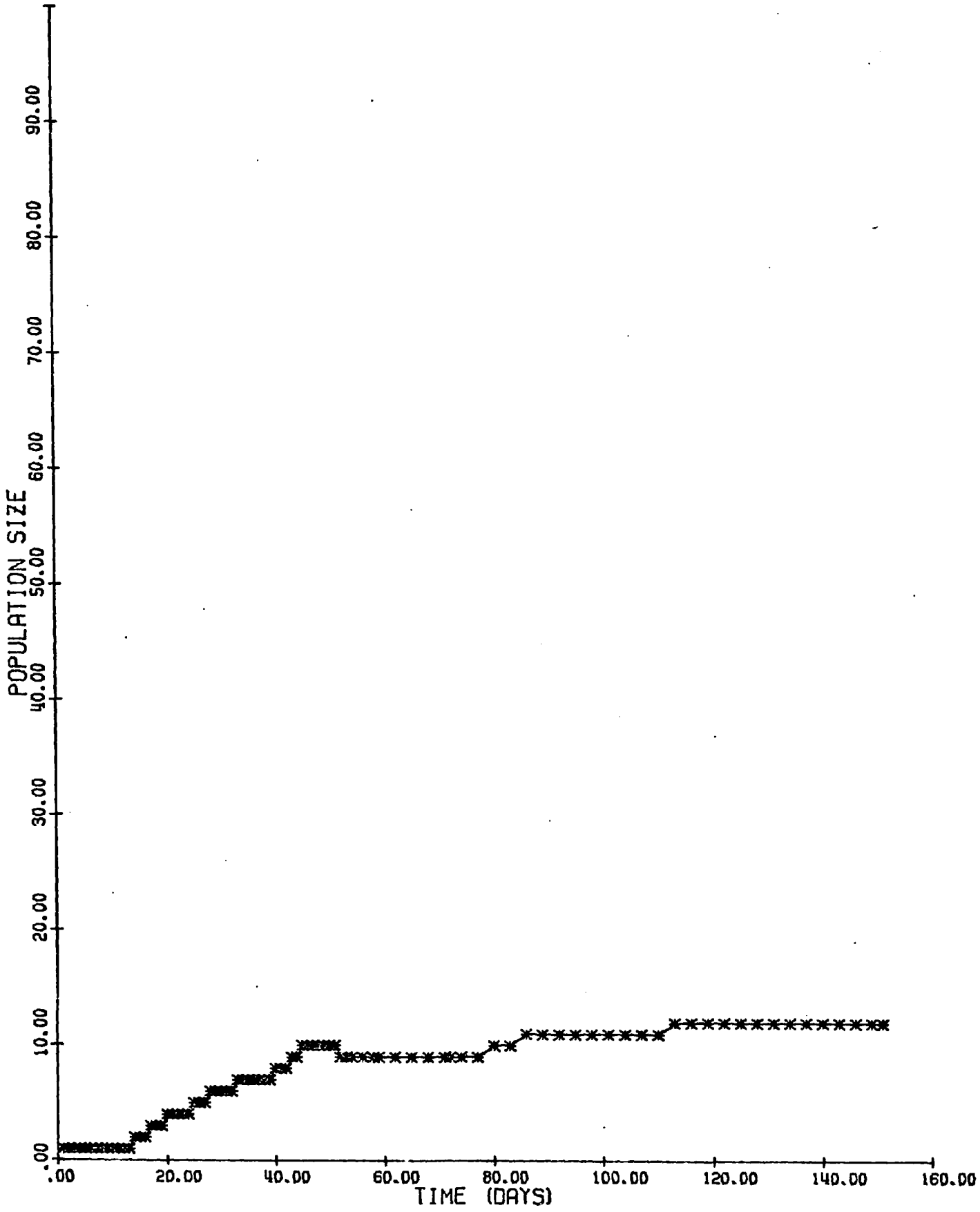
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



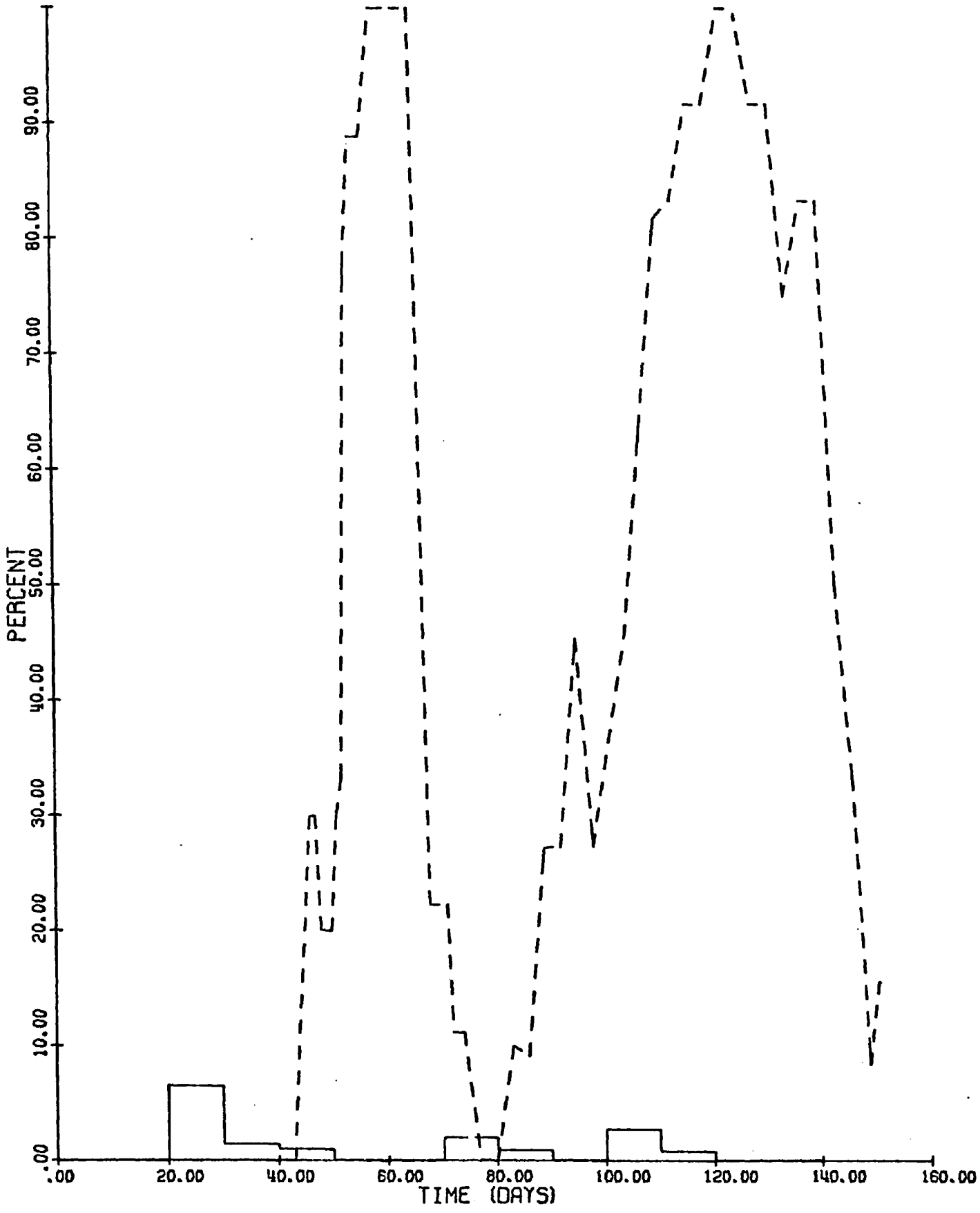
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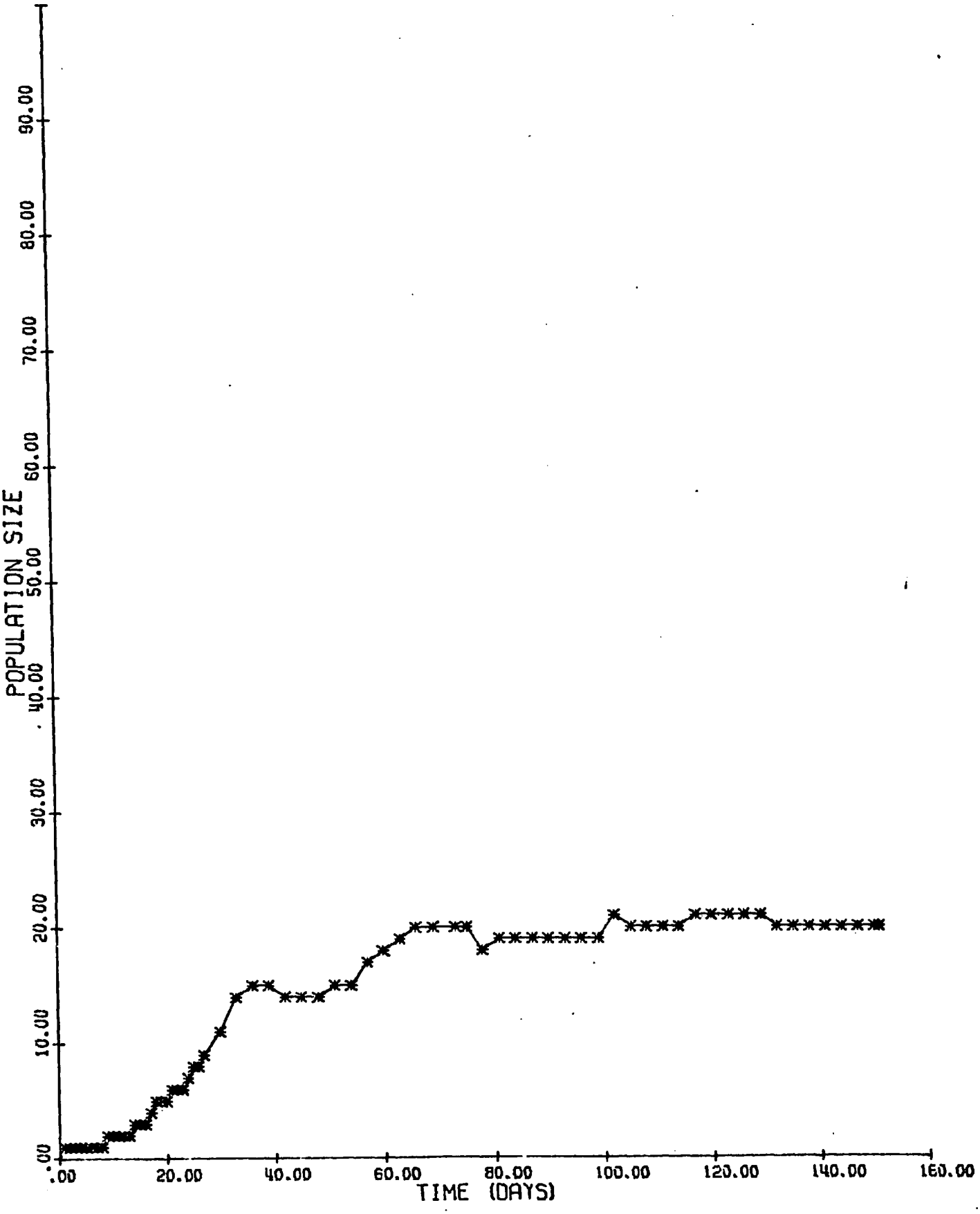
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



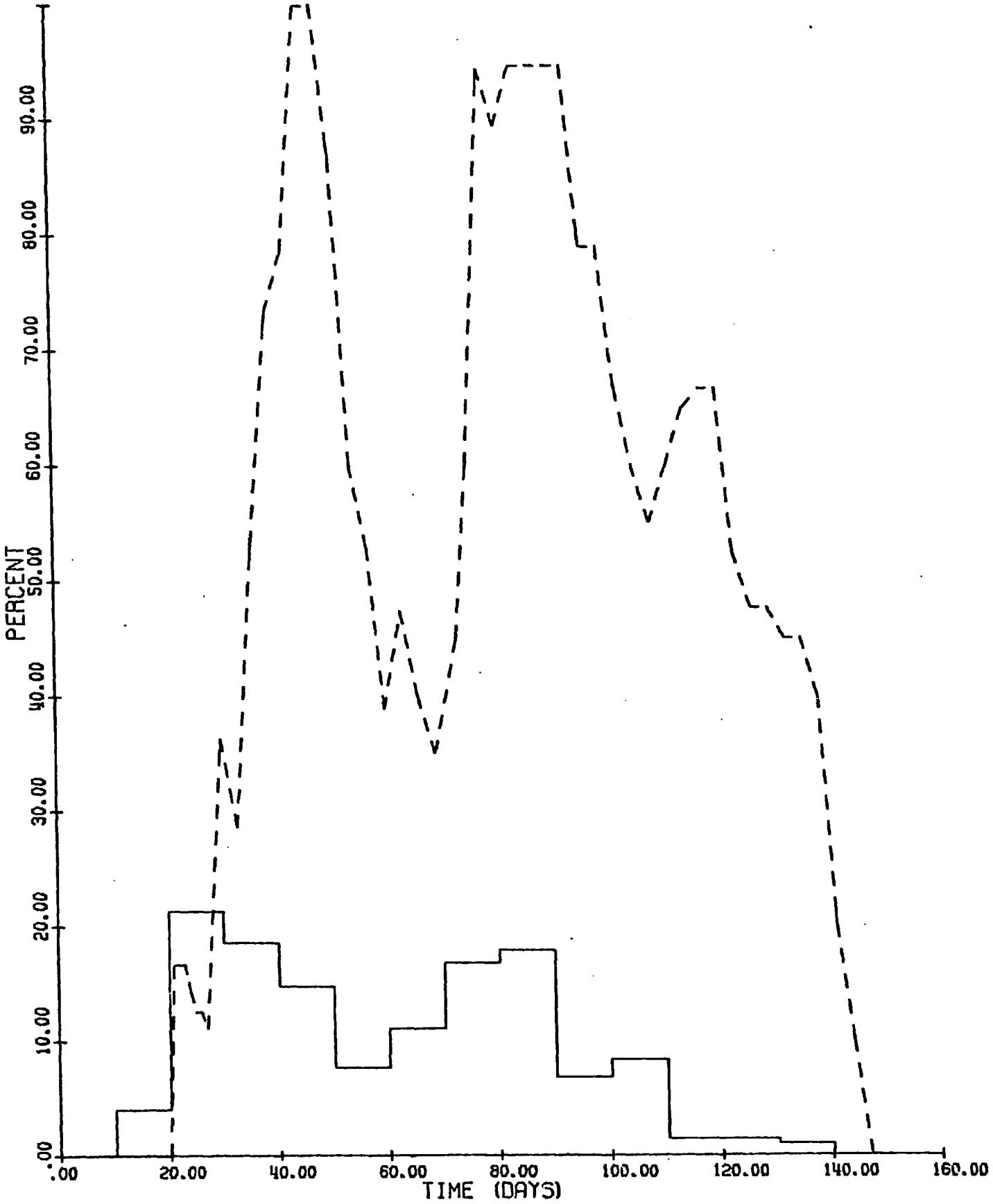
POPULATION 40 20 A1 - GROWTH CURVE



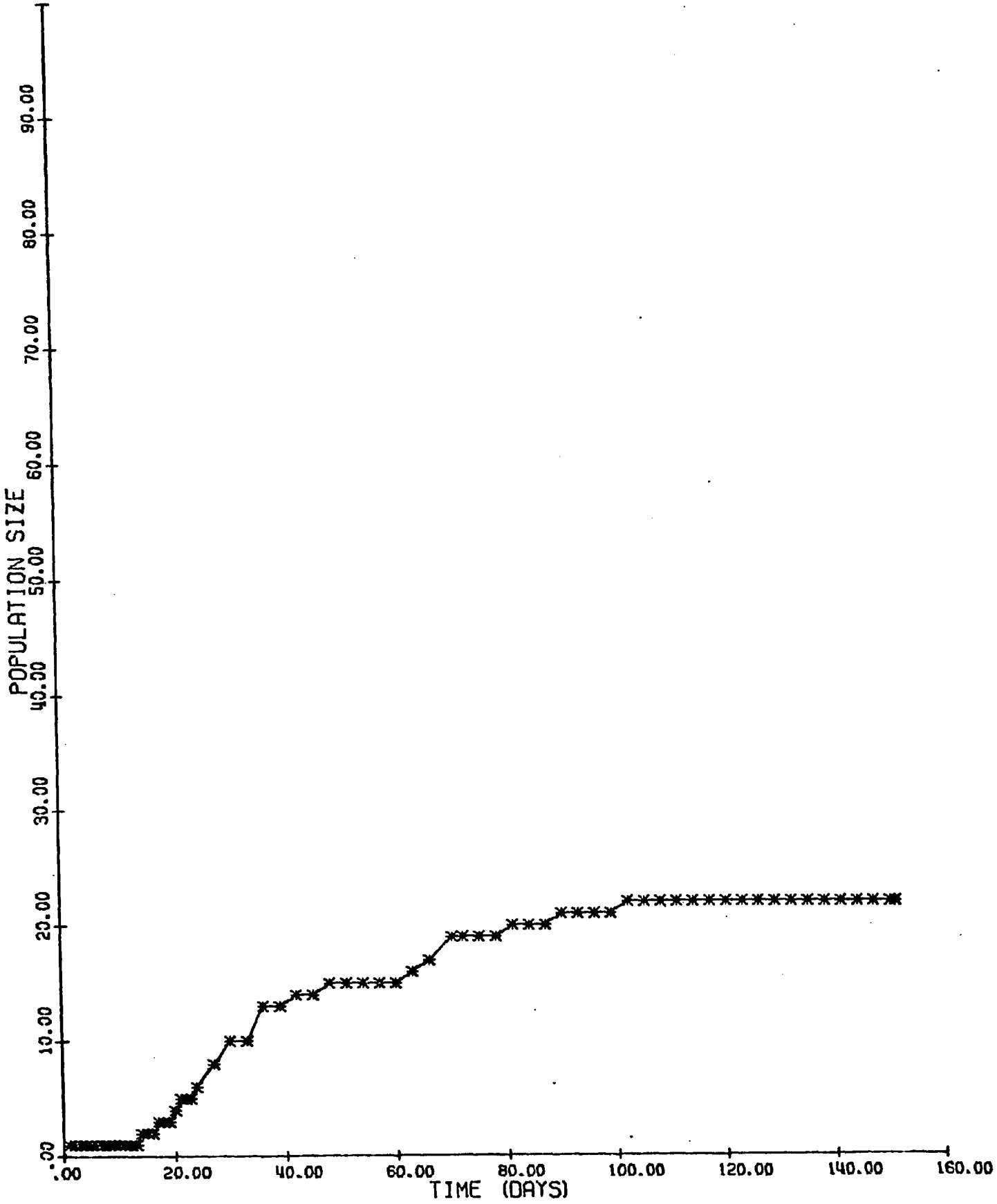
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



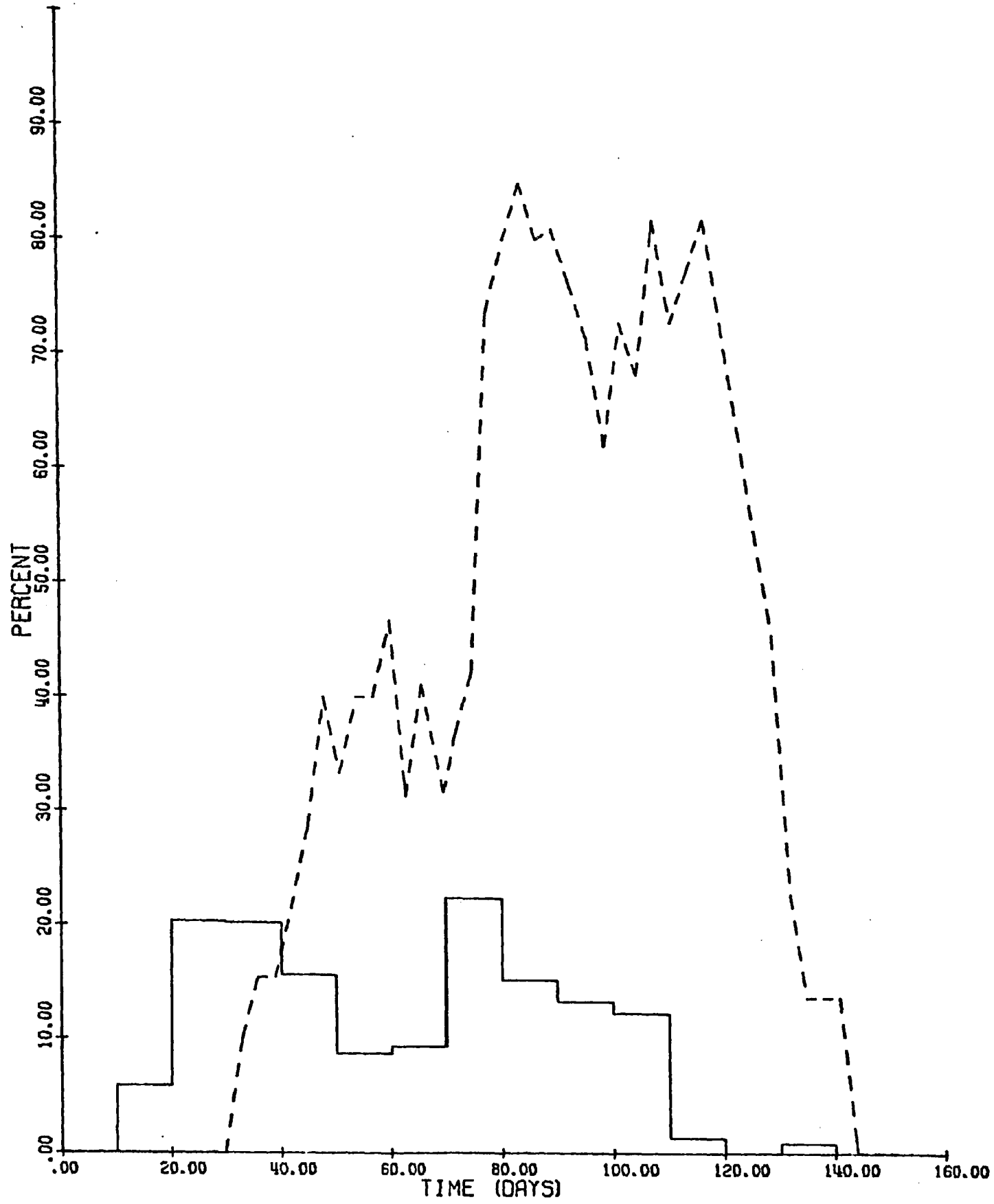
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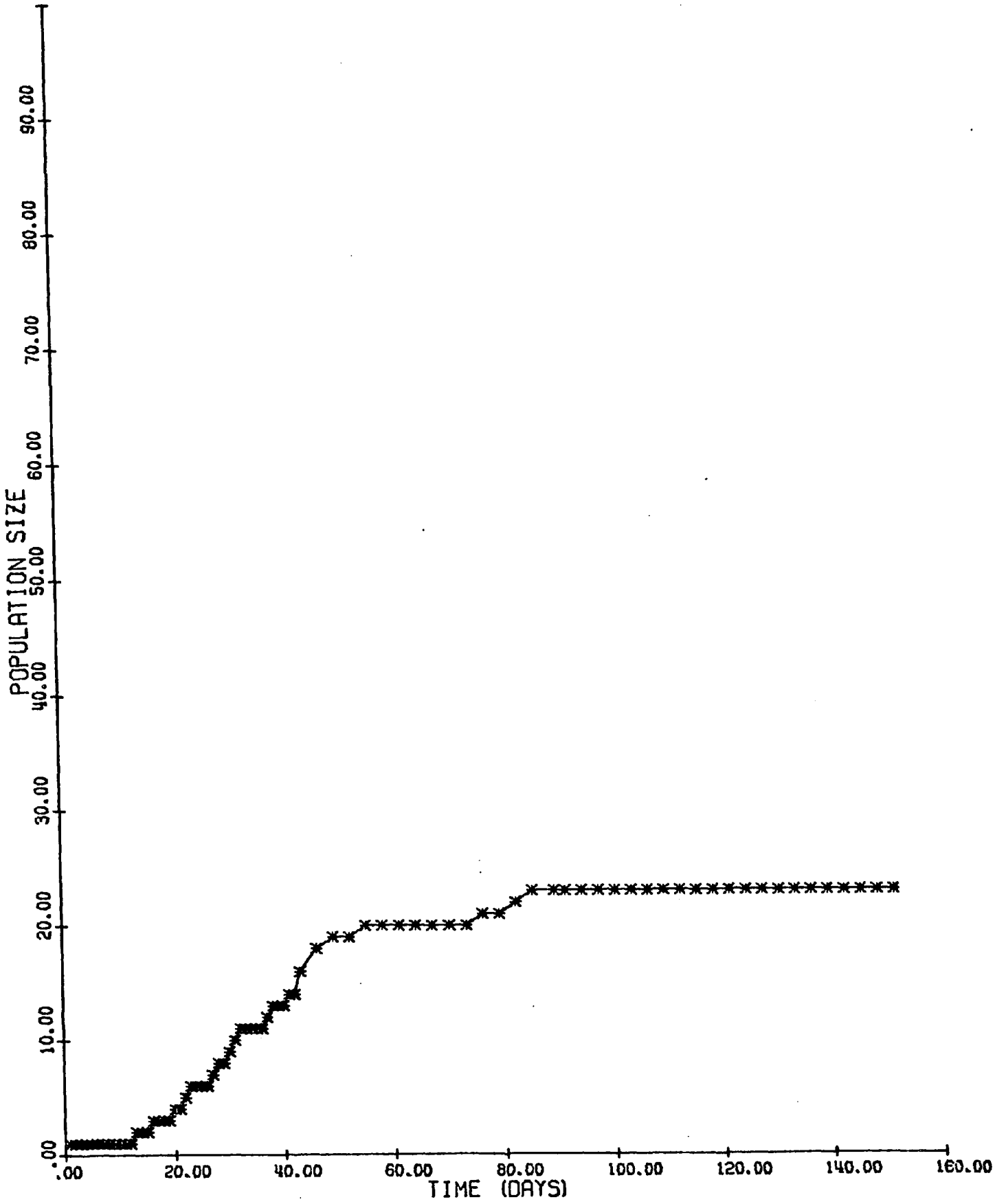
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



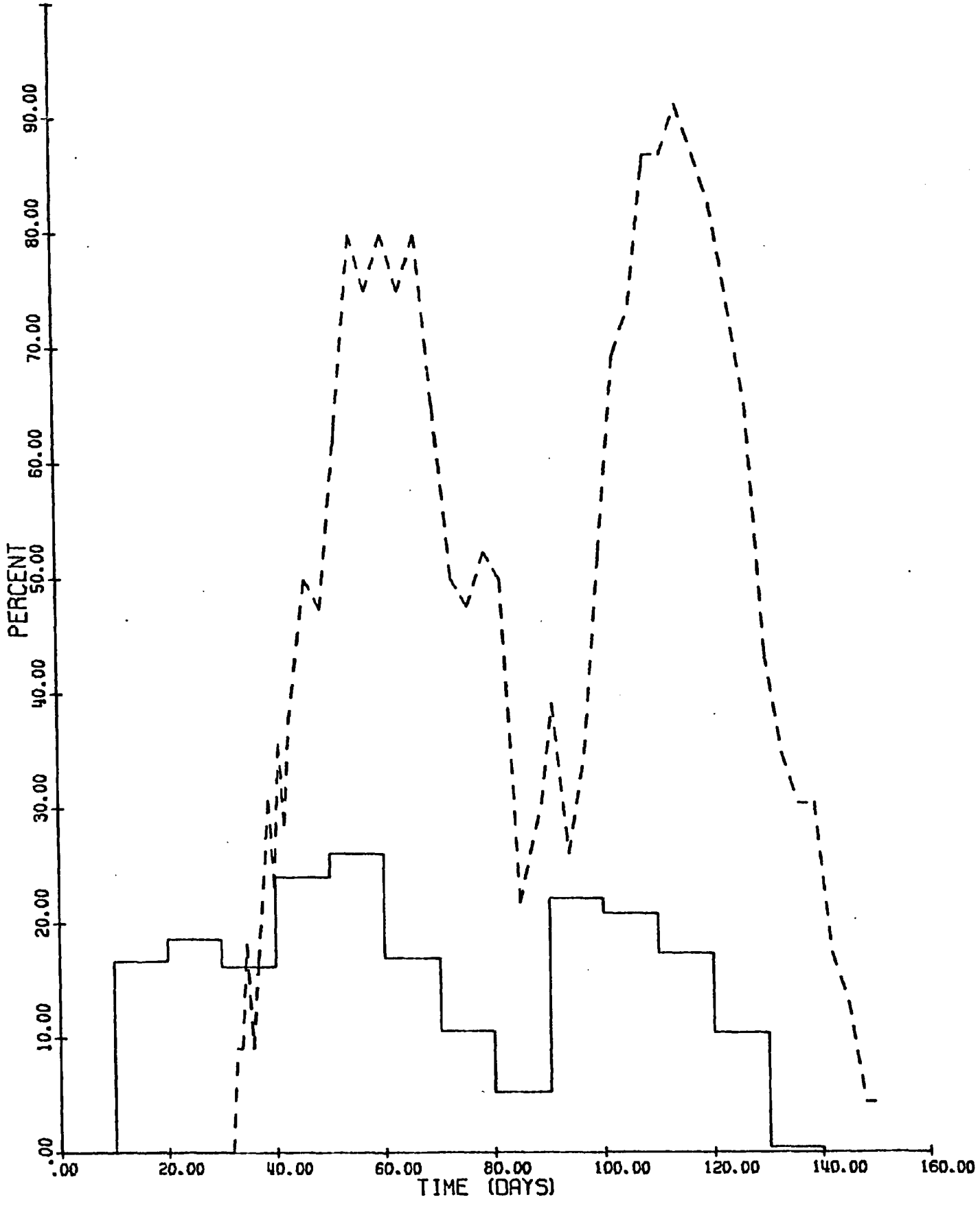
POPULATION 40 40 A1 - GROWTH CURVE



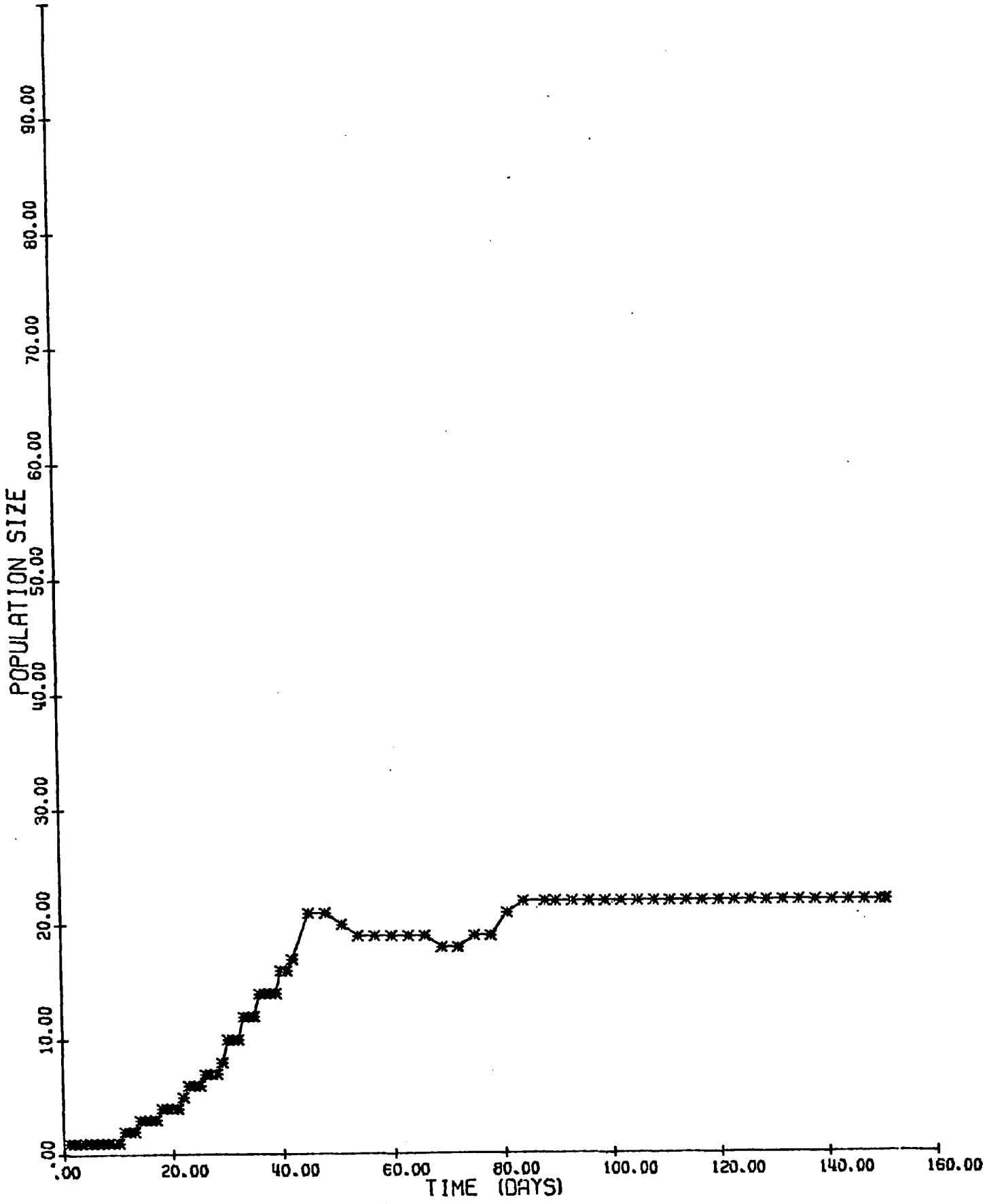
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



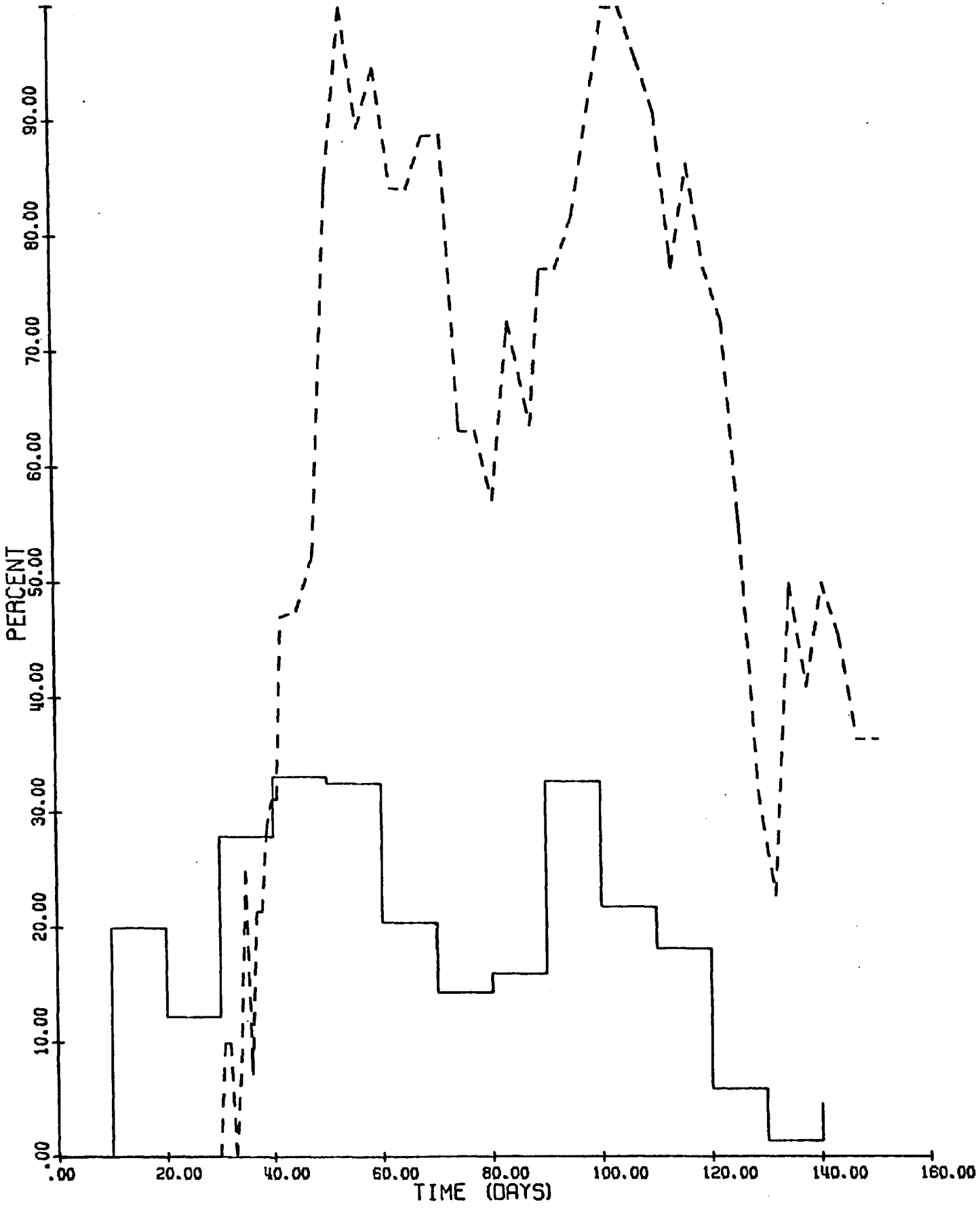
POPULATION 40 40 A2 - GROWTH CURVE



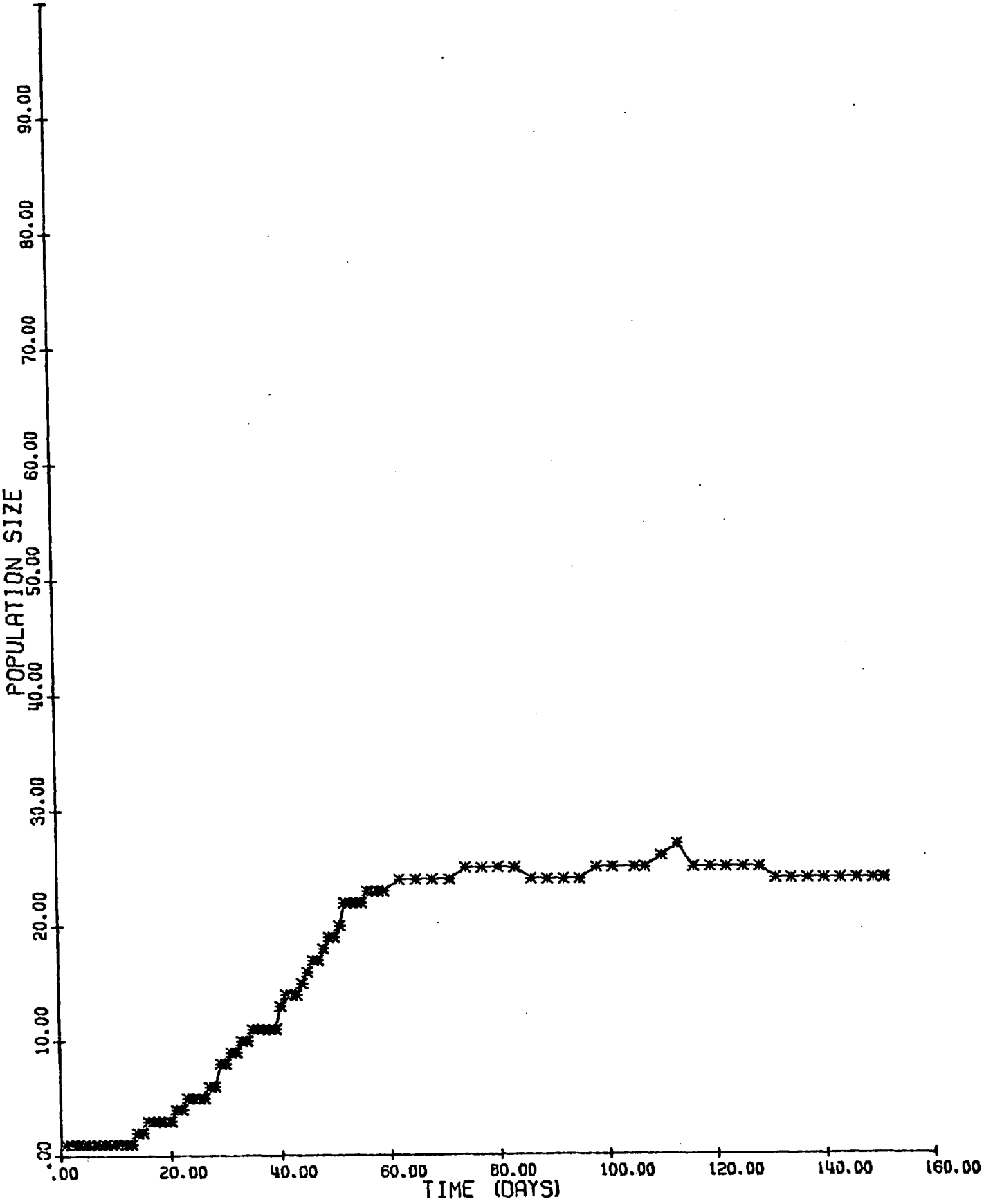
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



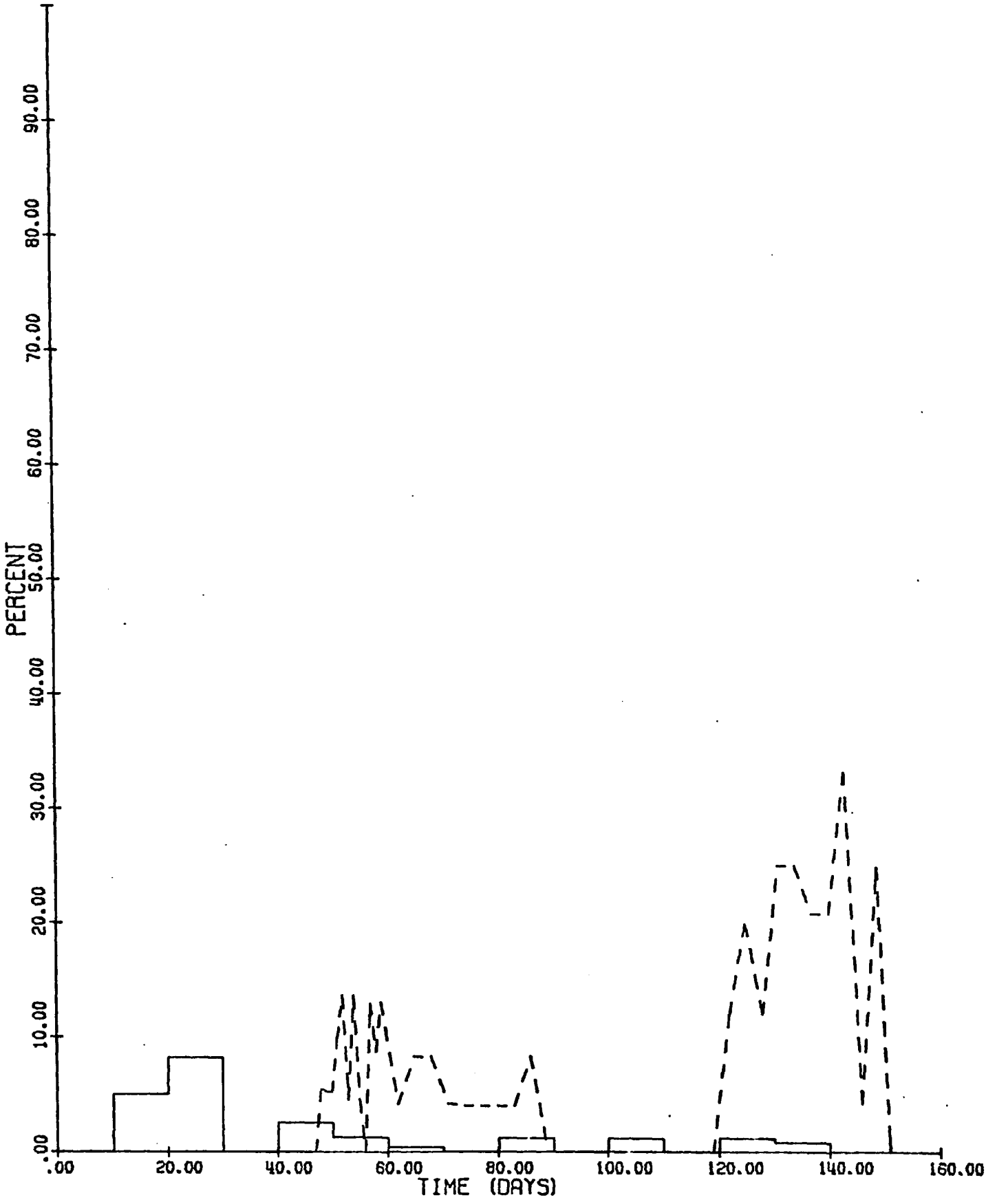
POPULATION 40 80 A1 - GROWTH CURVE



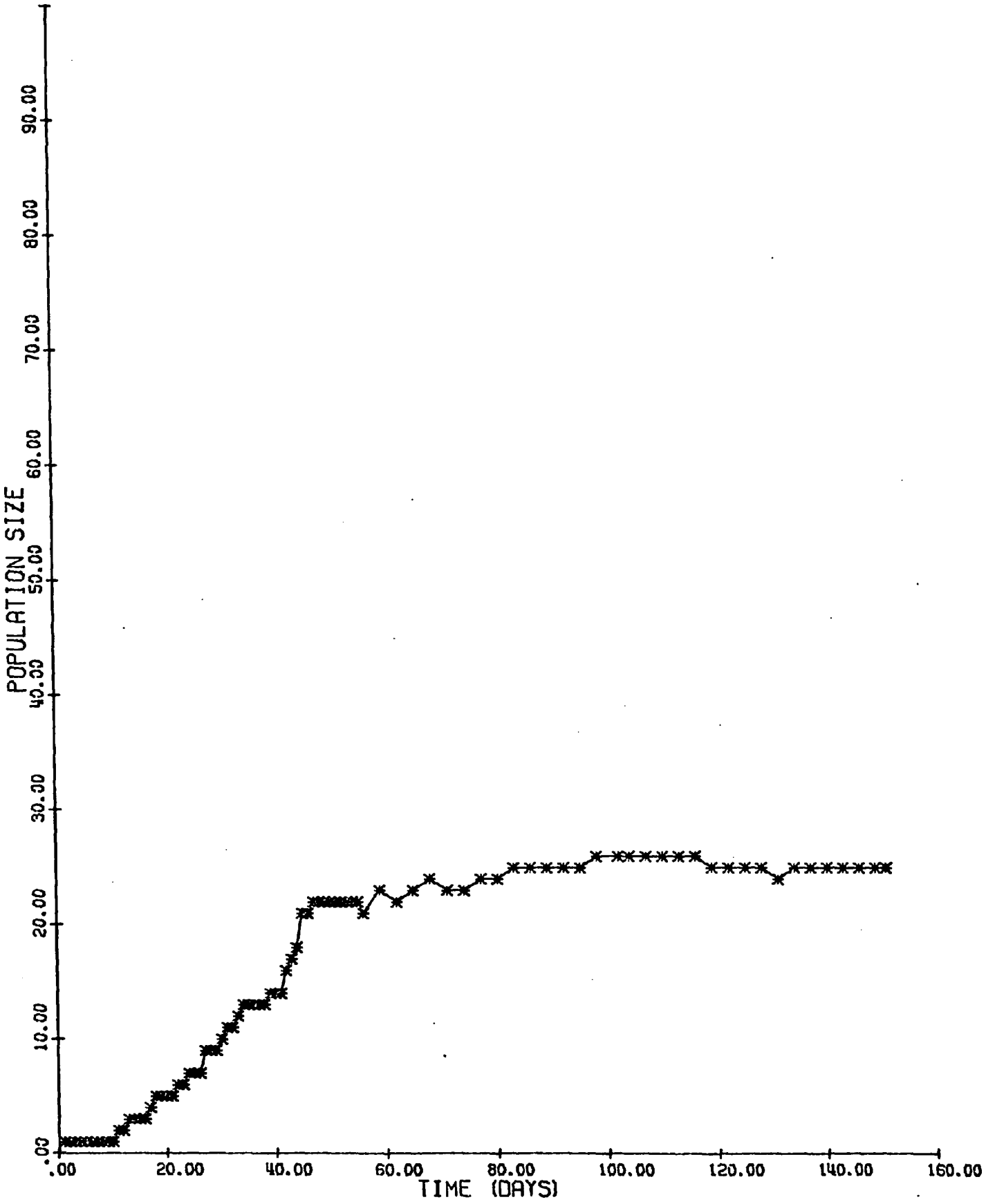
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



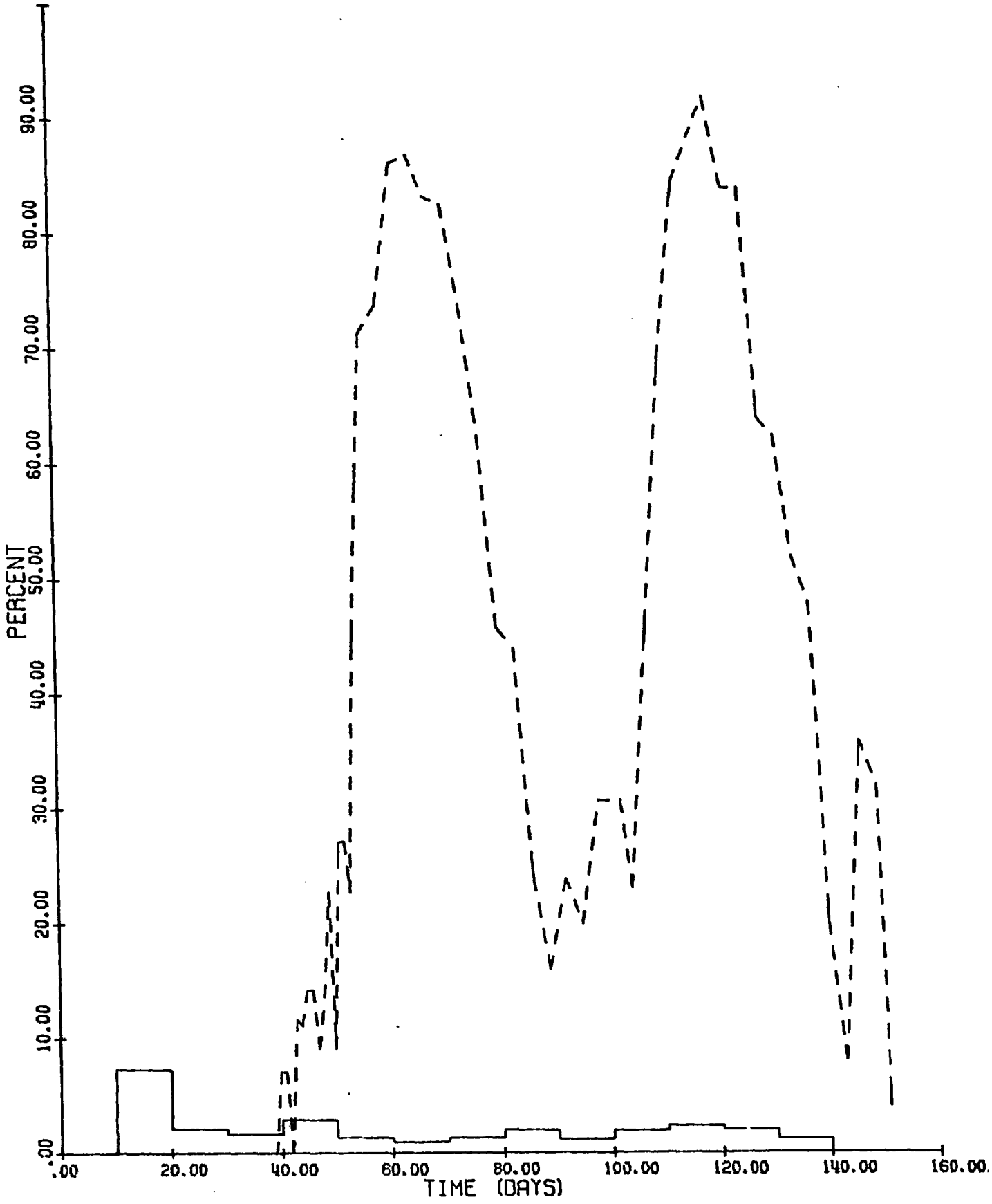
POPULATION 40 80 A2 - GROWTH CURVE



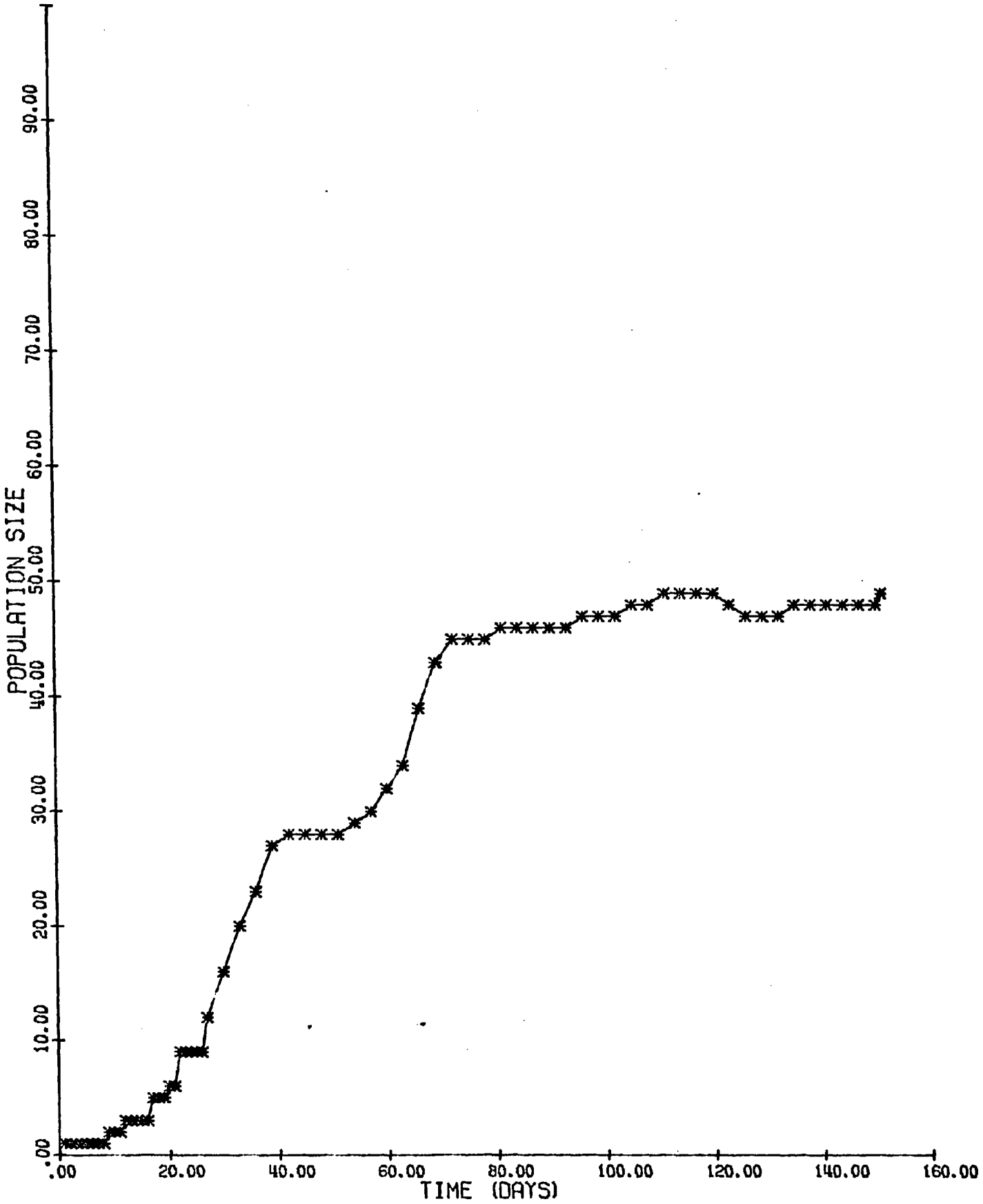
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



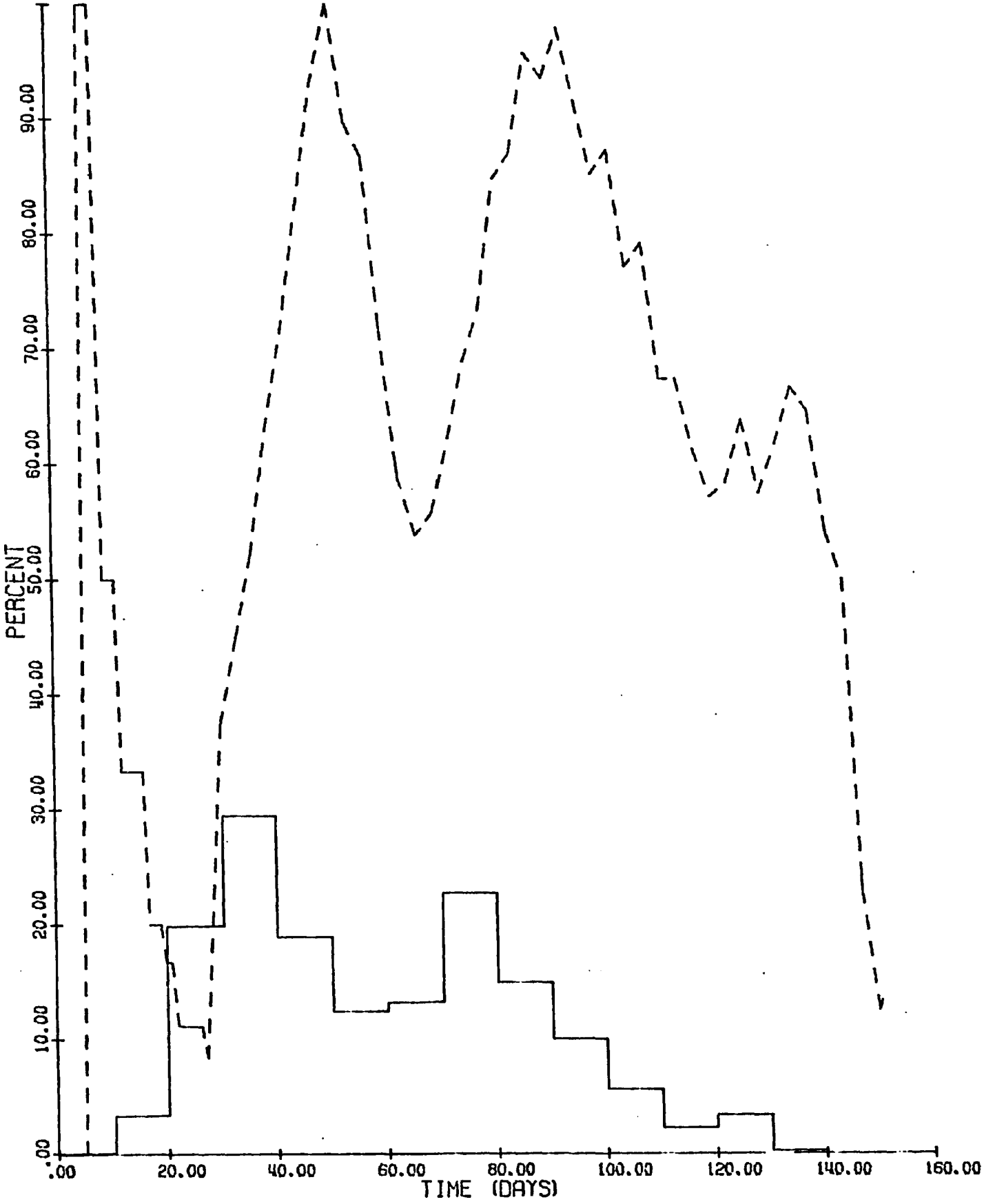
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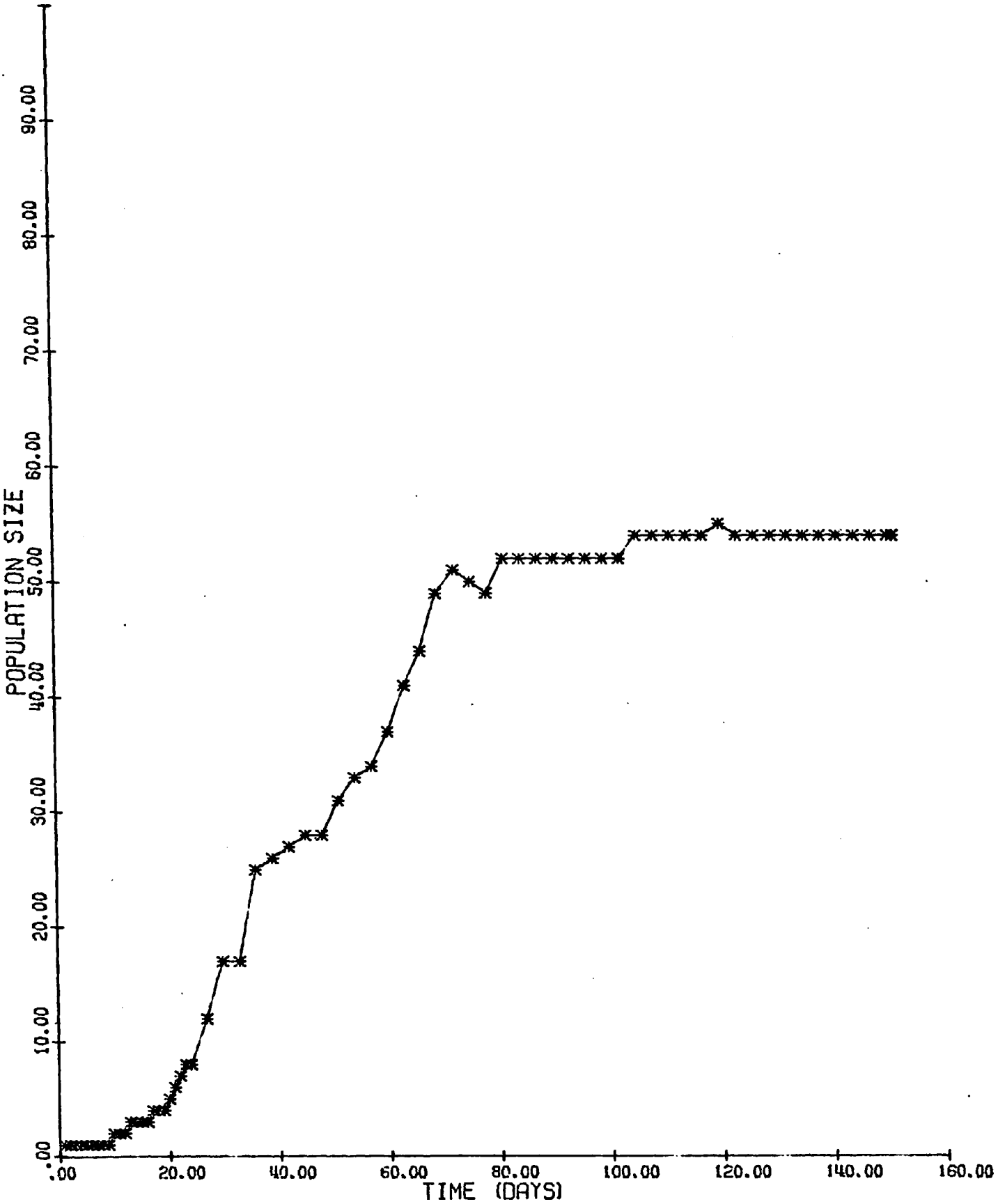
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



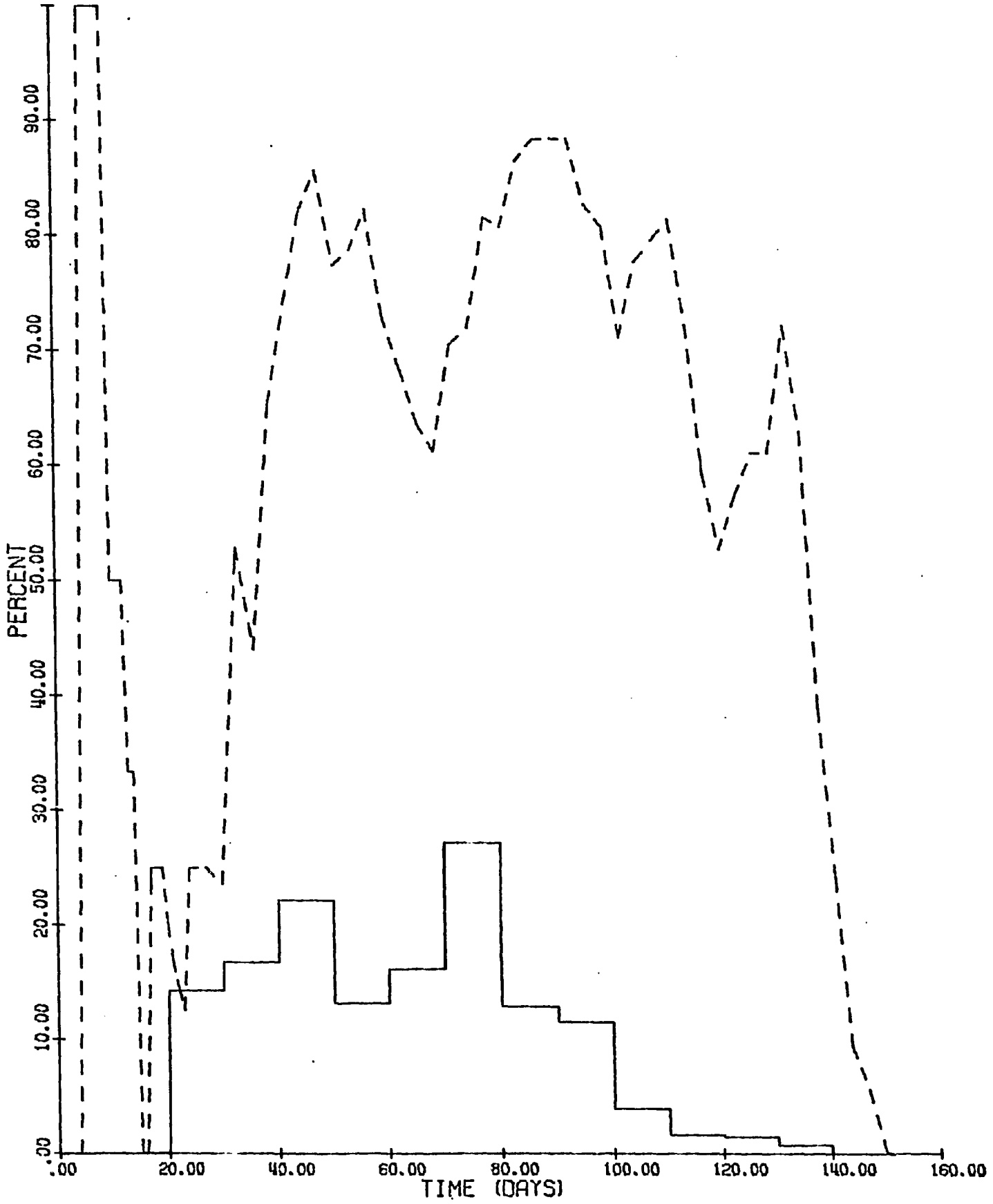
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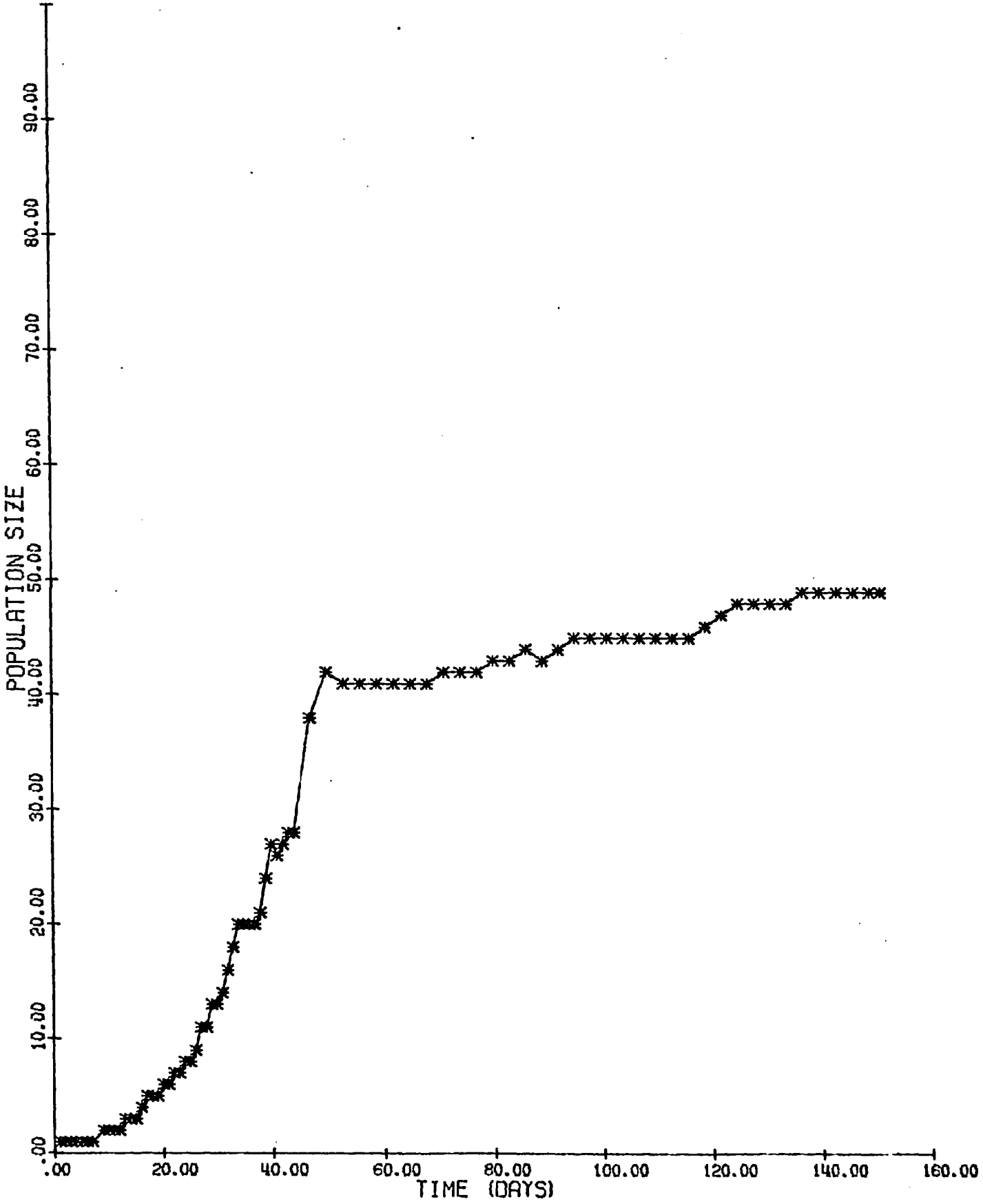
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



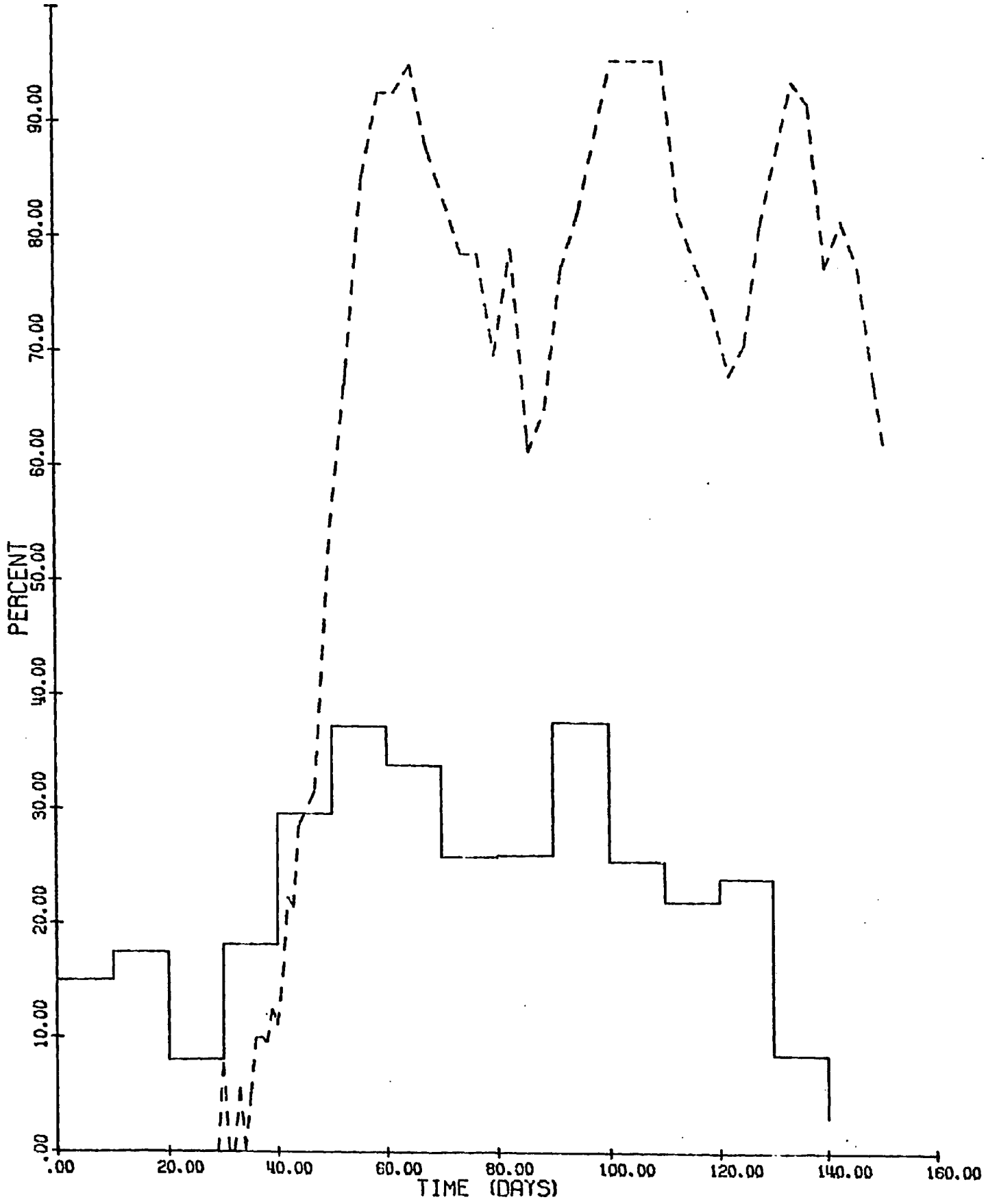
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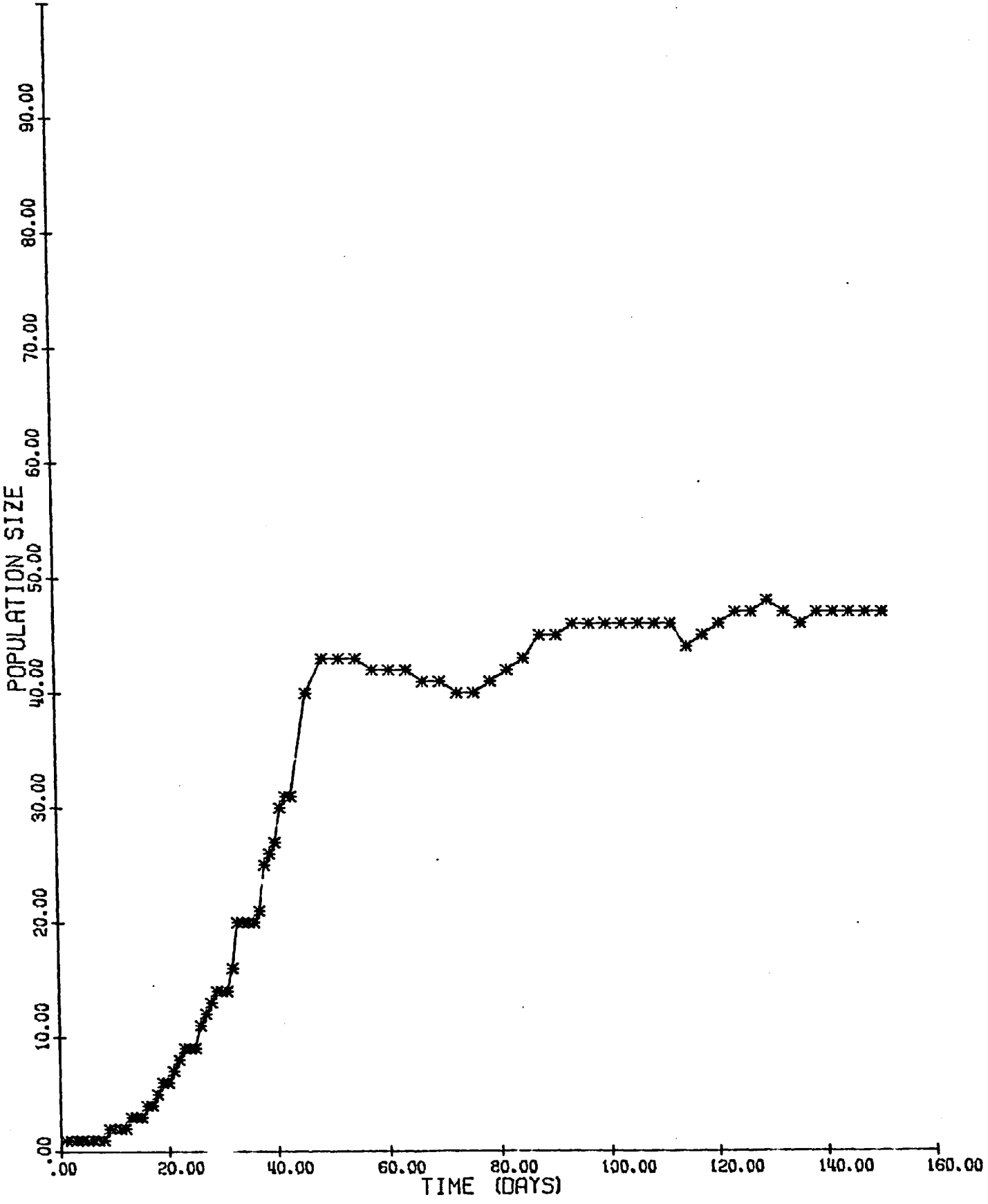
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



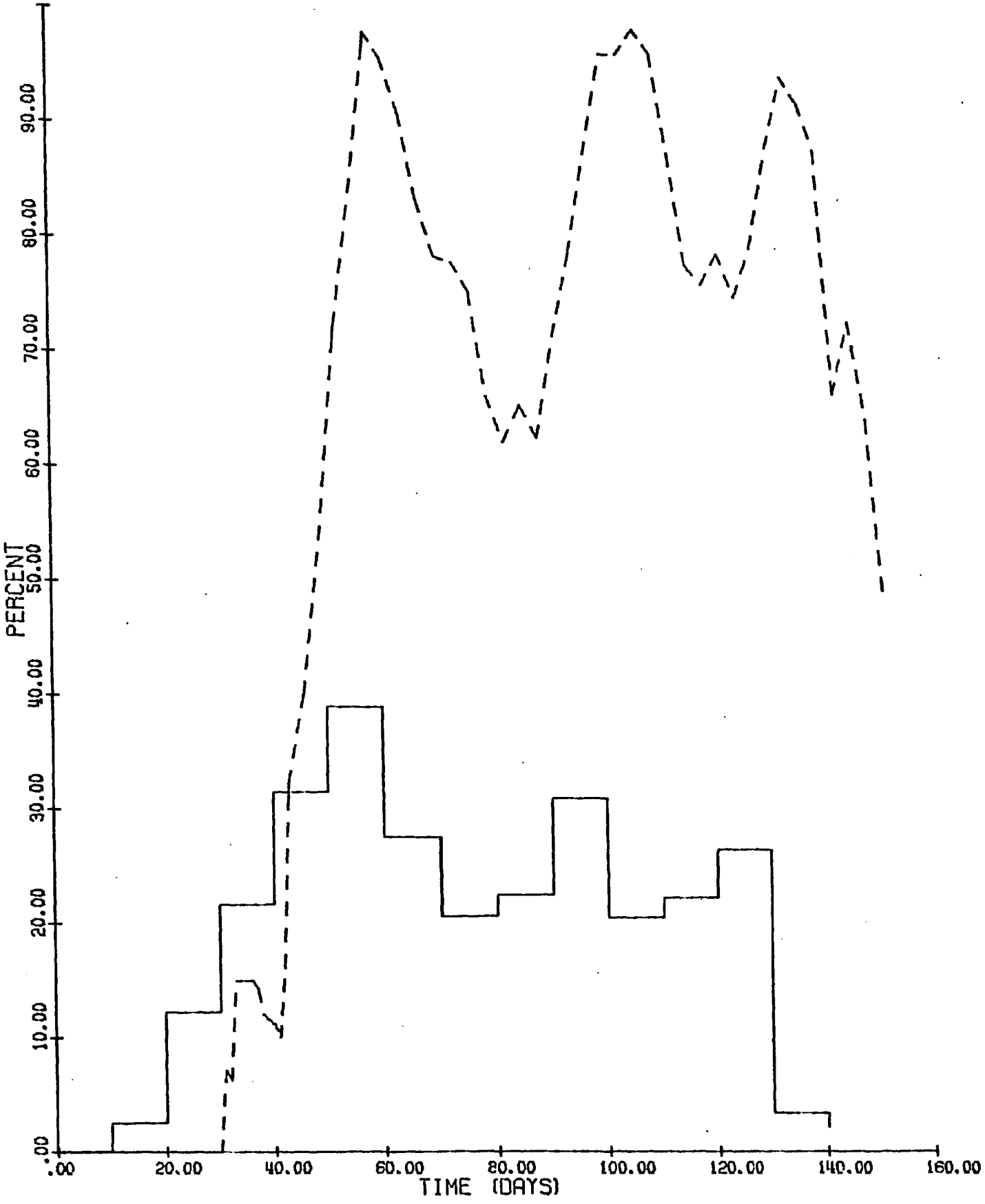
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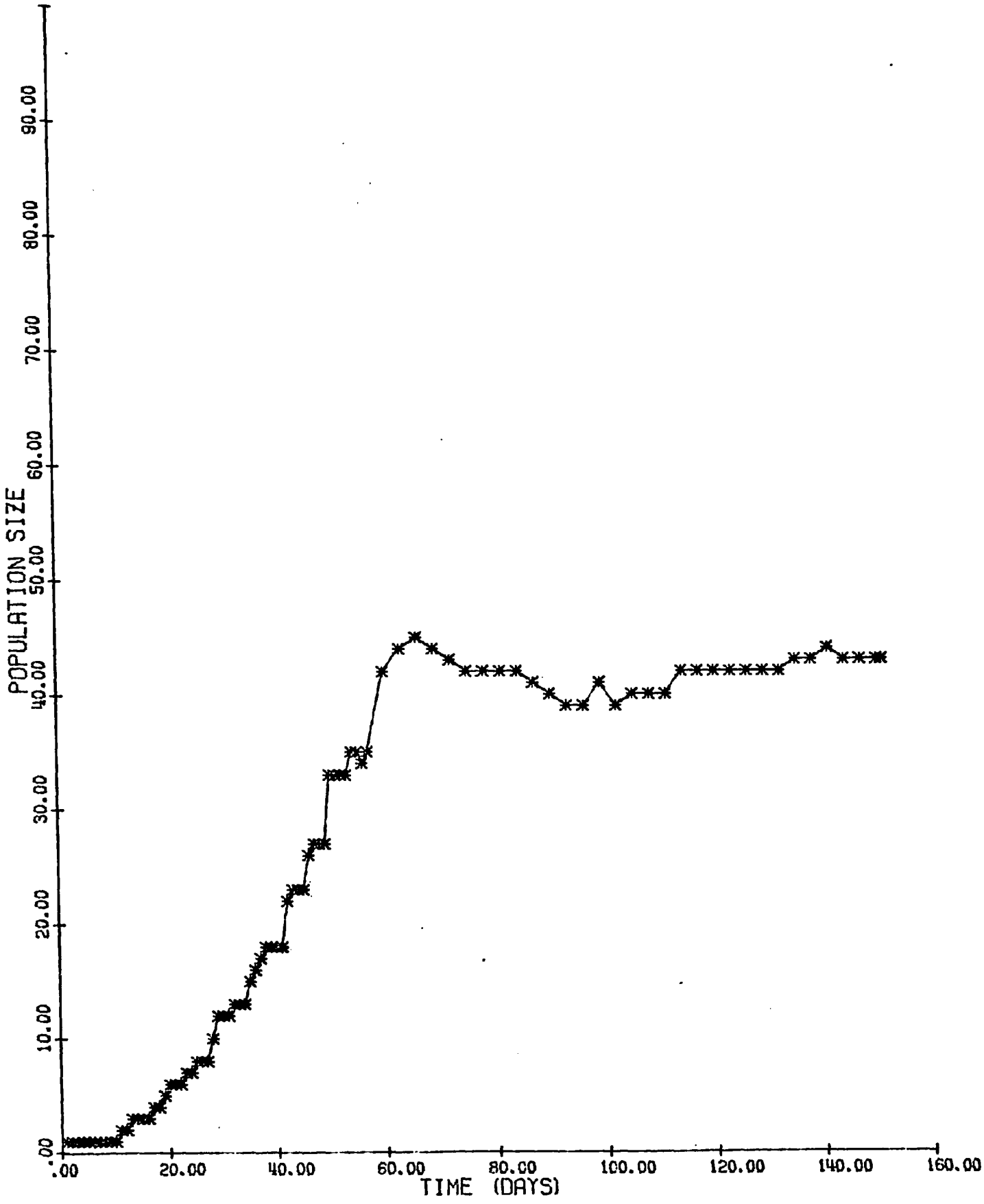
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



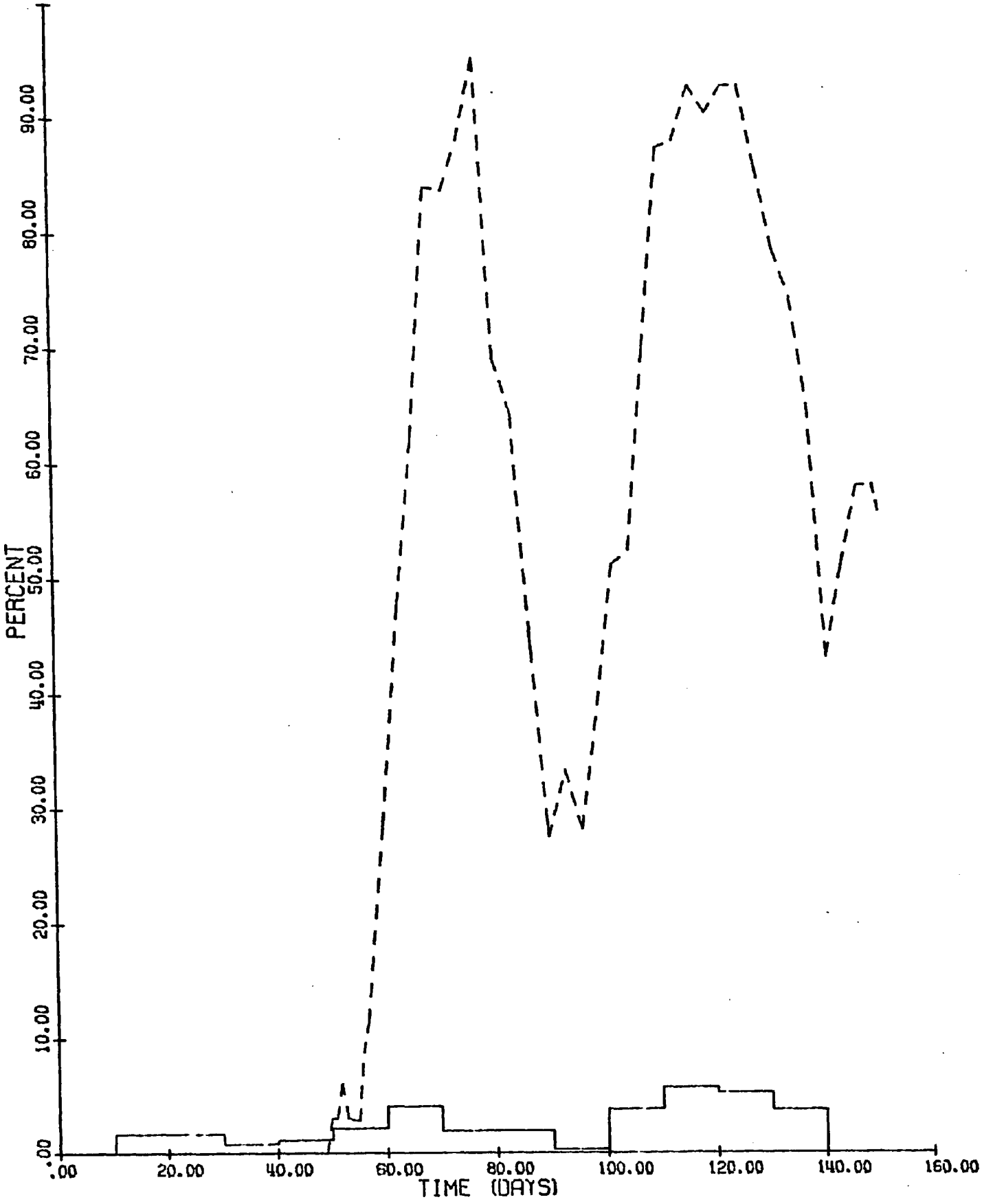
POPULATION 80 80 A1 - GROWTH CURVE



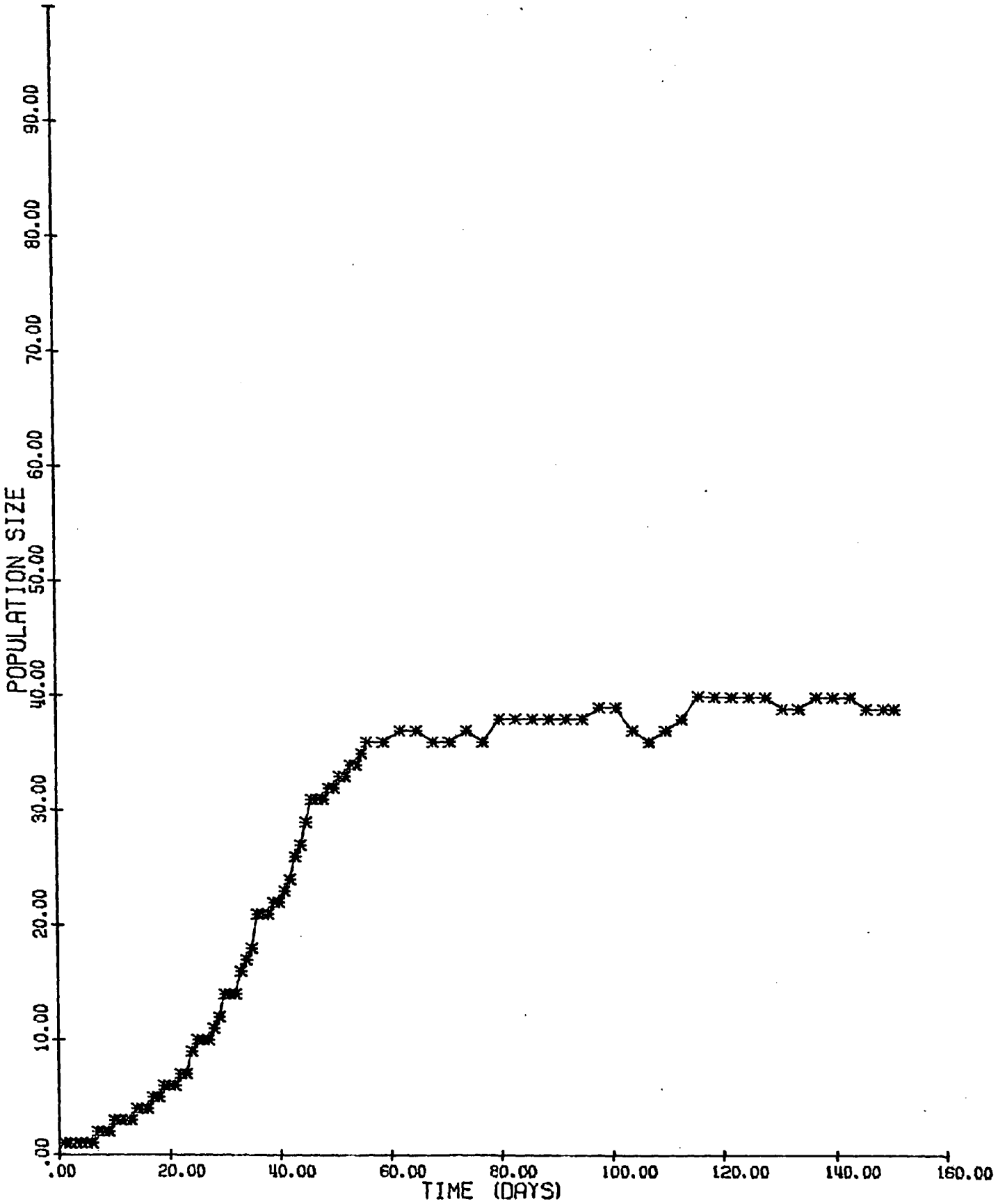
POPULATION 80 80 A1 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



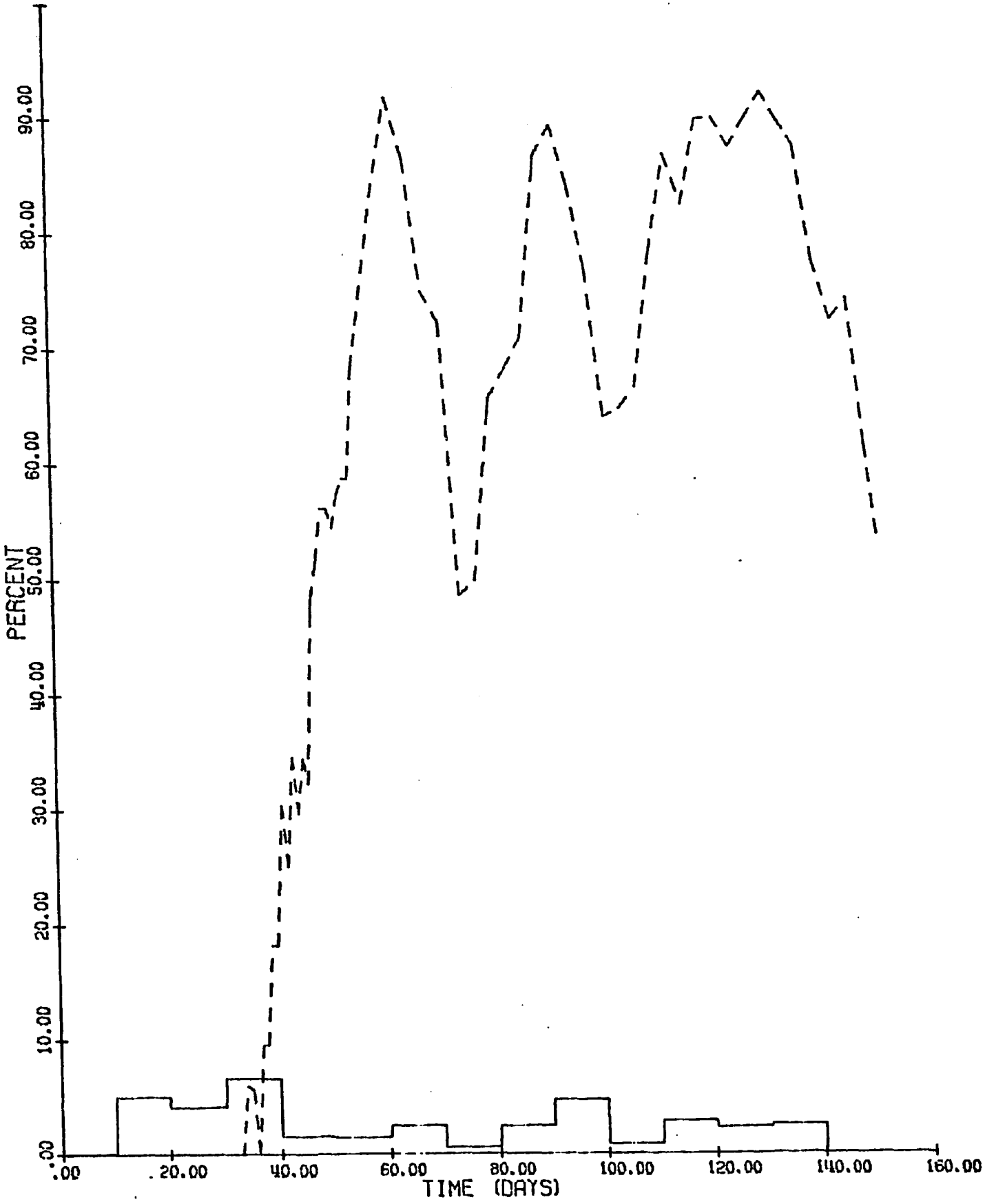
POPULATION 80 80 A2 - GROWTH CURVE



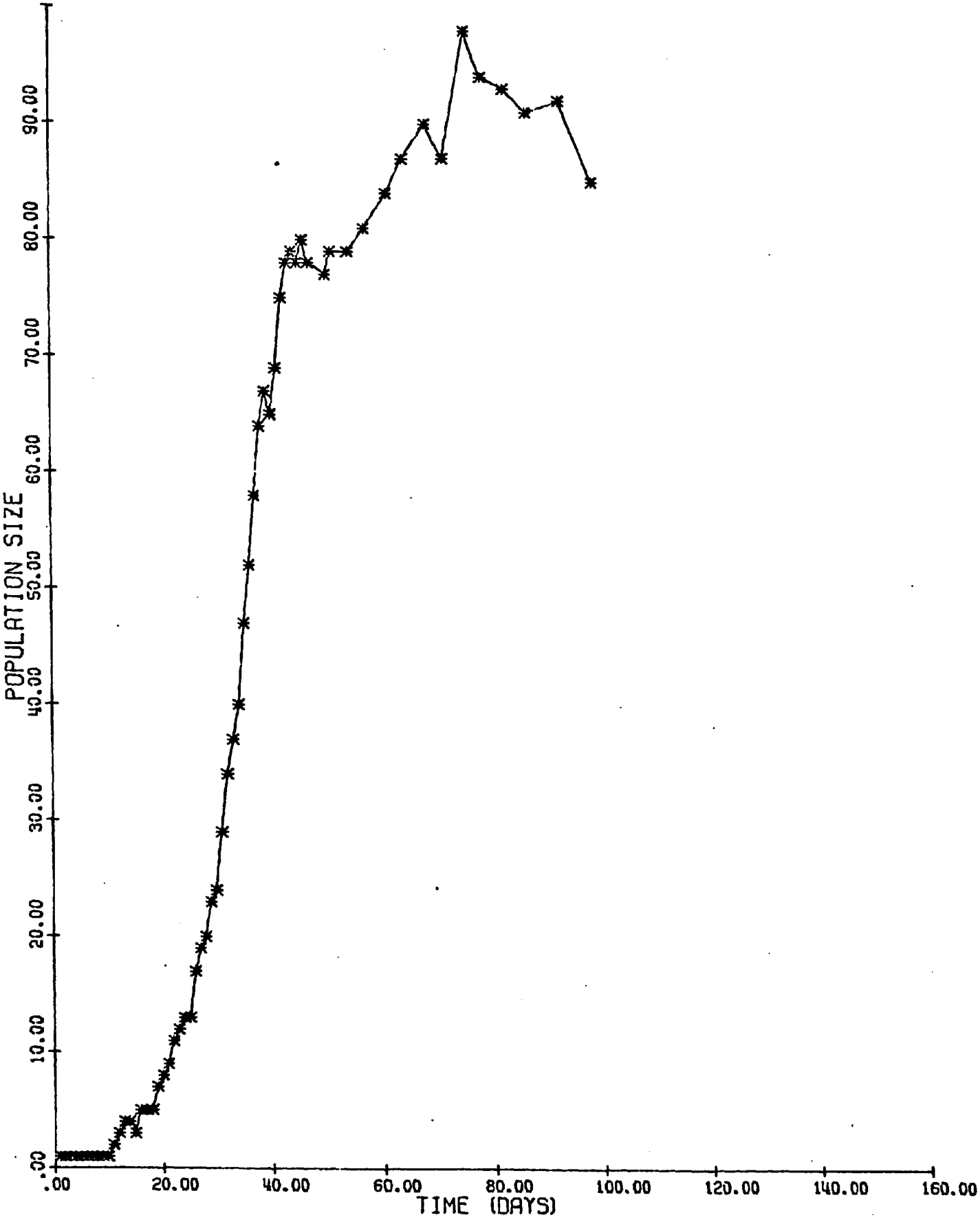
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



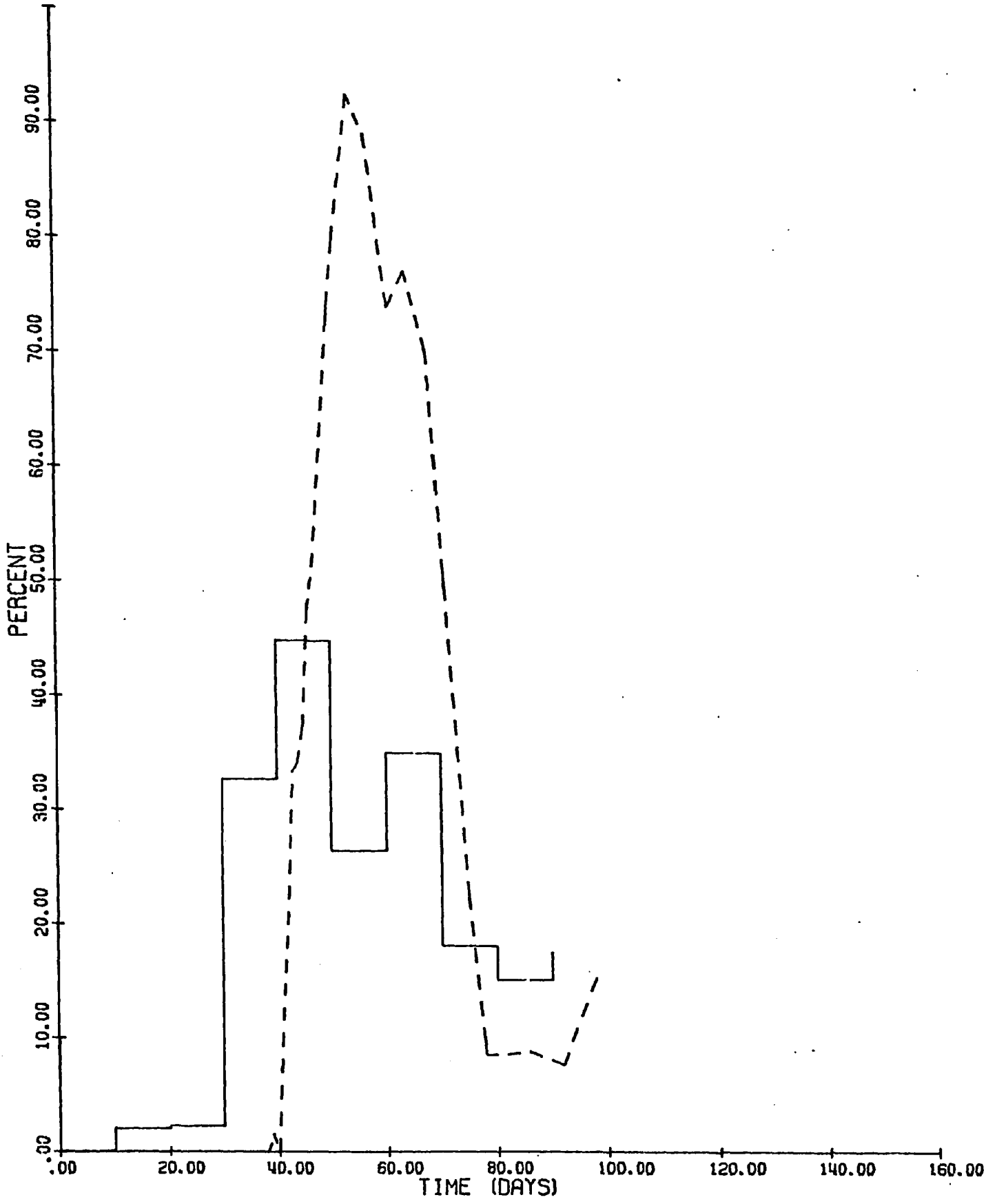
POPULATION 150 20 A1 - GROWTH CURVE



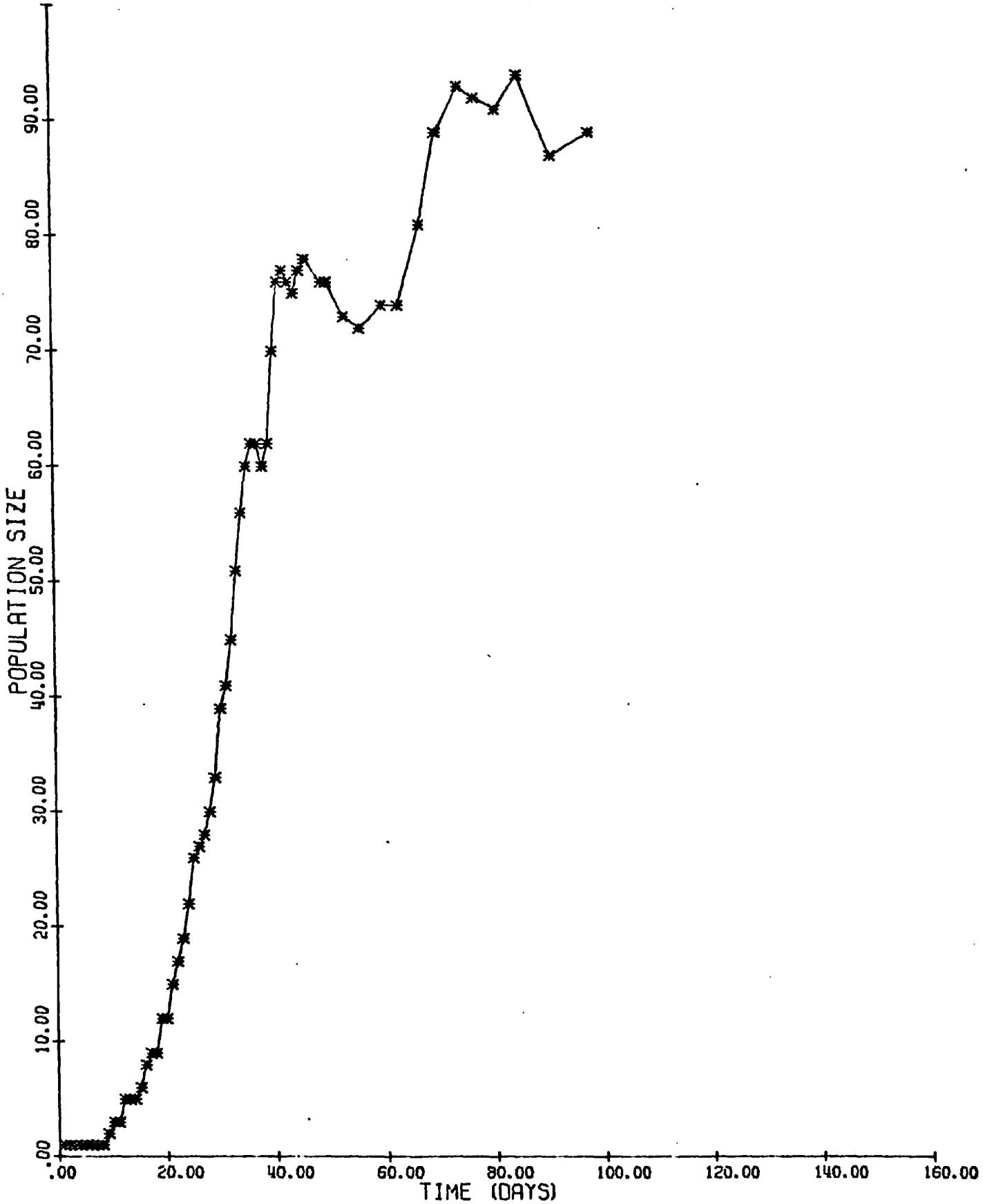
POPULATION 150 20 A1 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE: AVERAGES OF 10-DAY PERIODS)



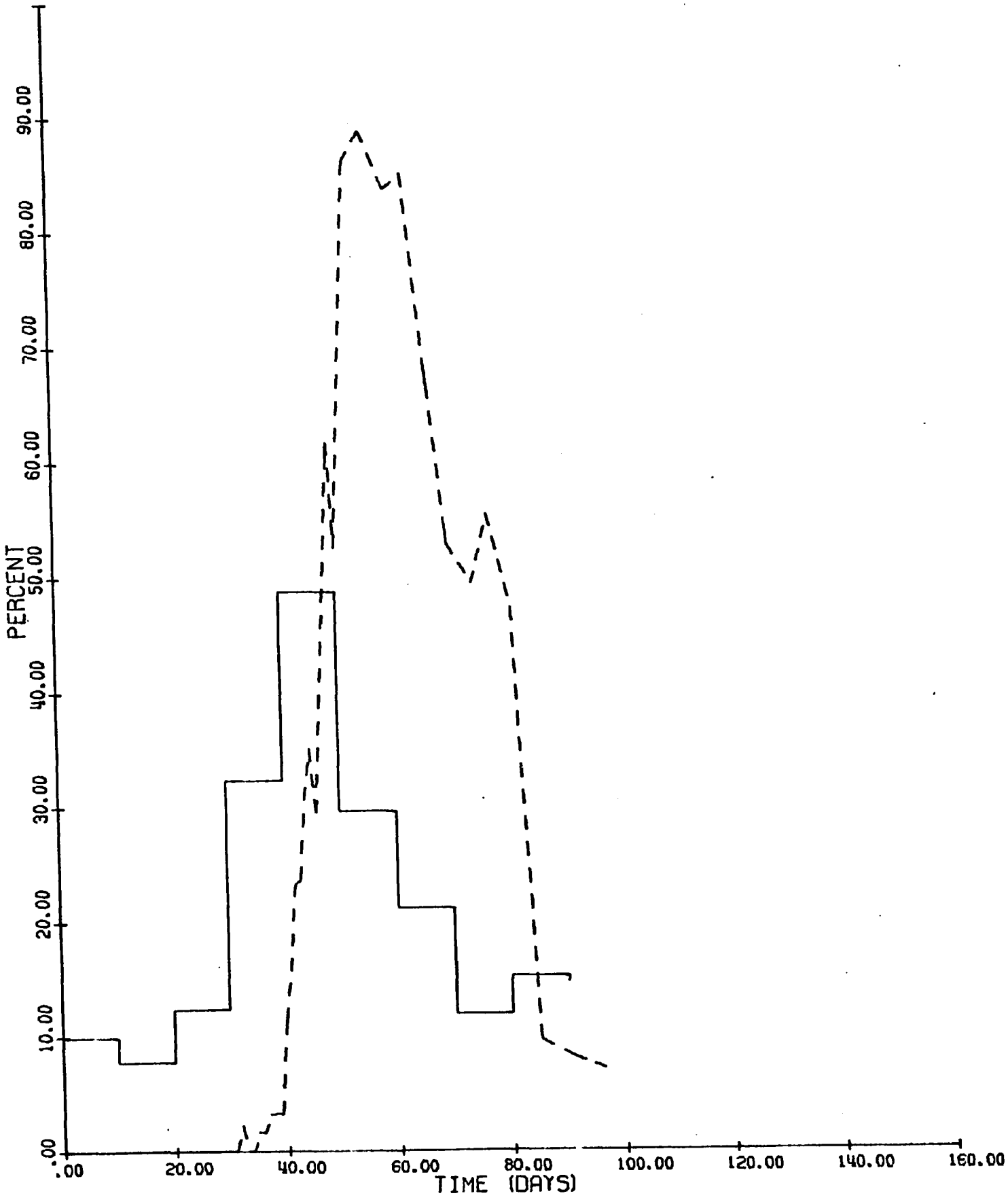
POPULATION 150 20 A2 - GROWTH CURVE



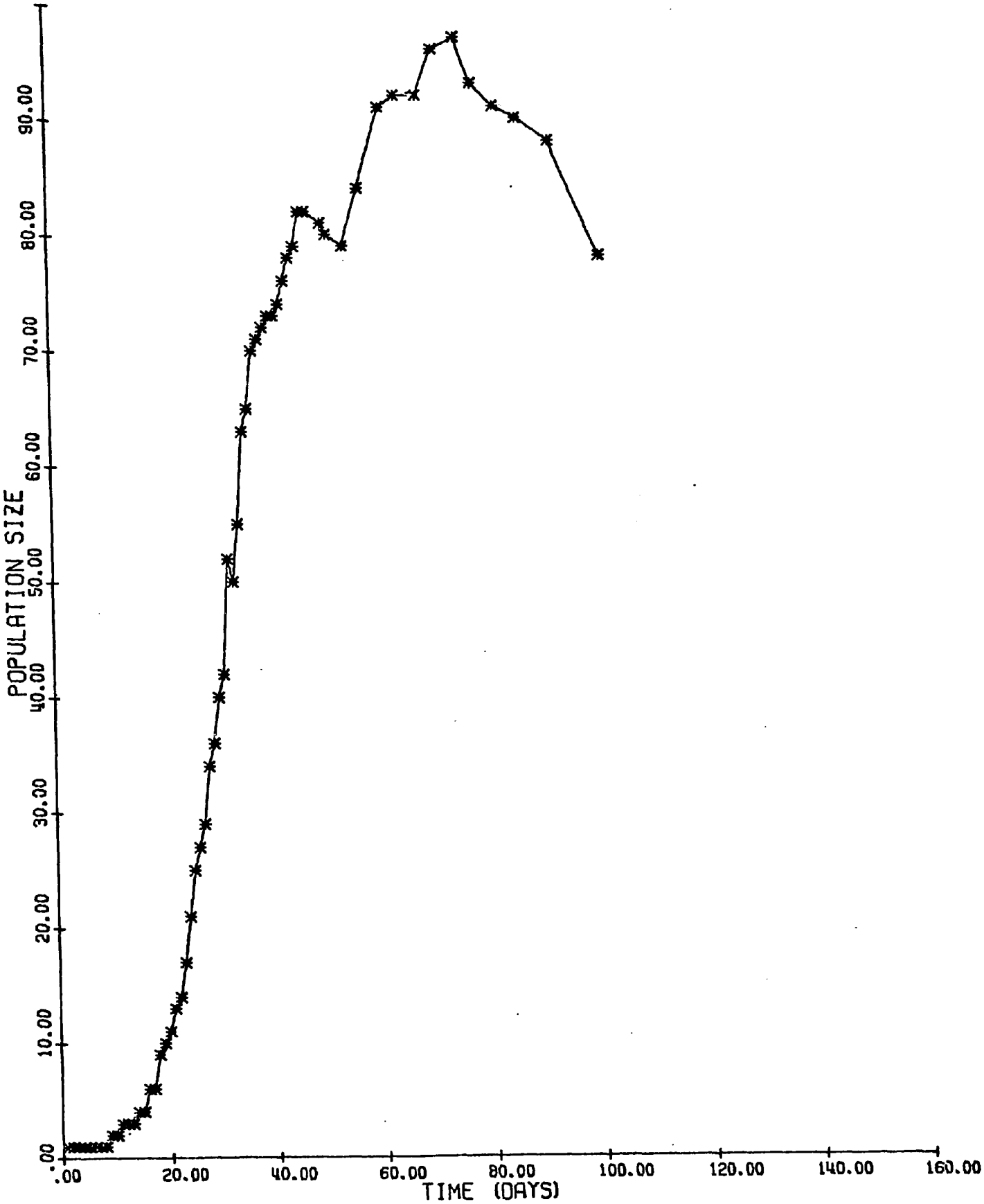
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PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



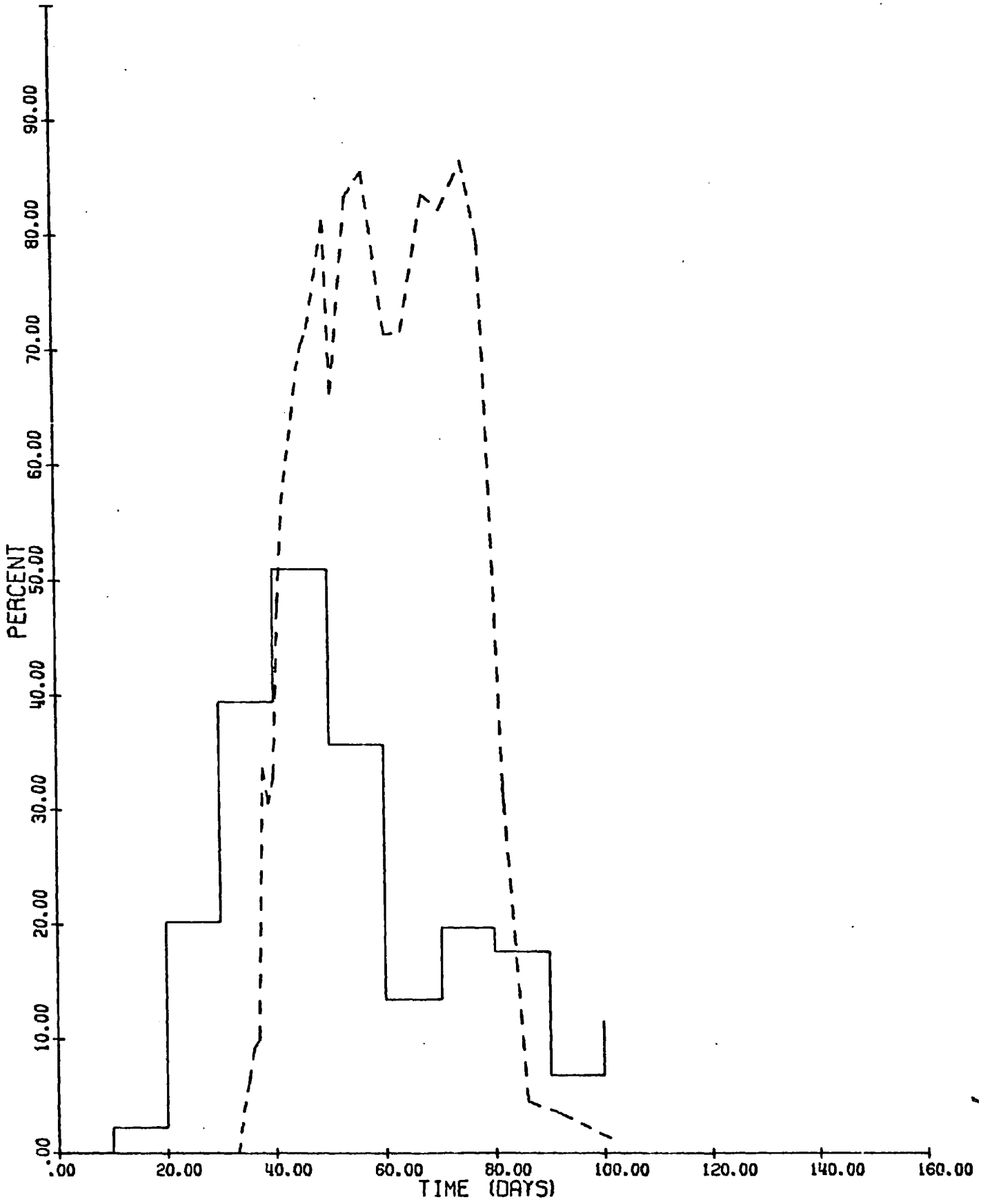
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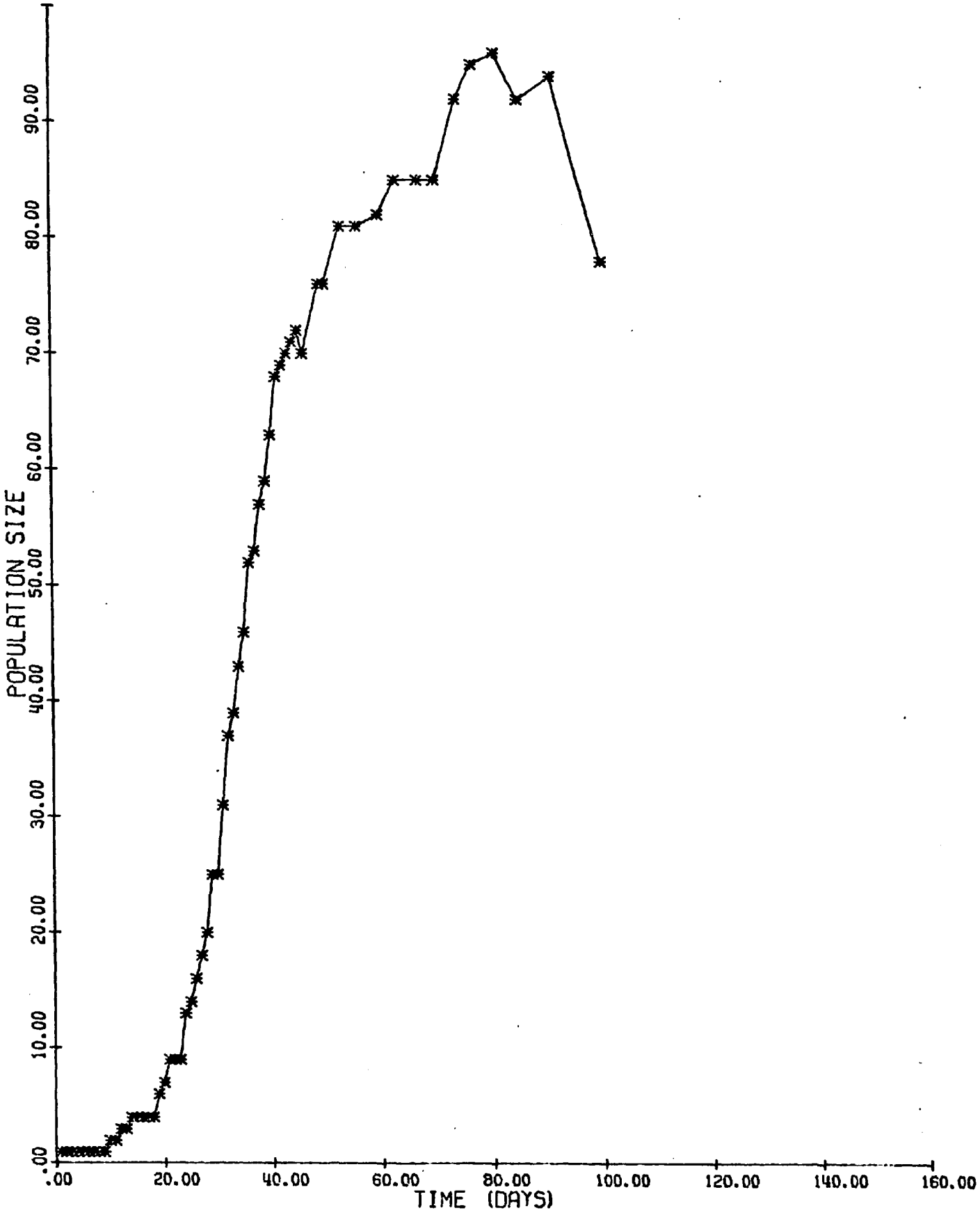
POPULATION 150 40 A1 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



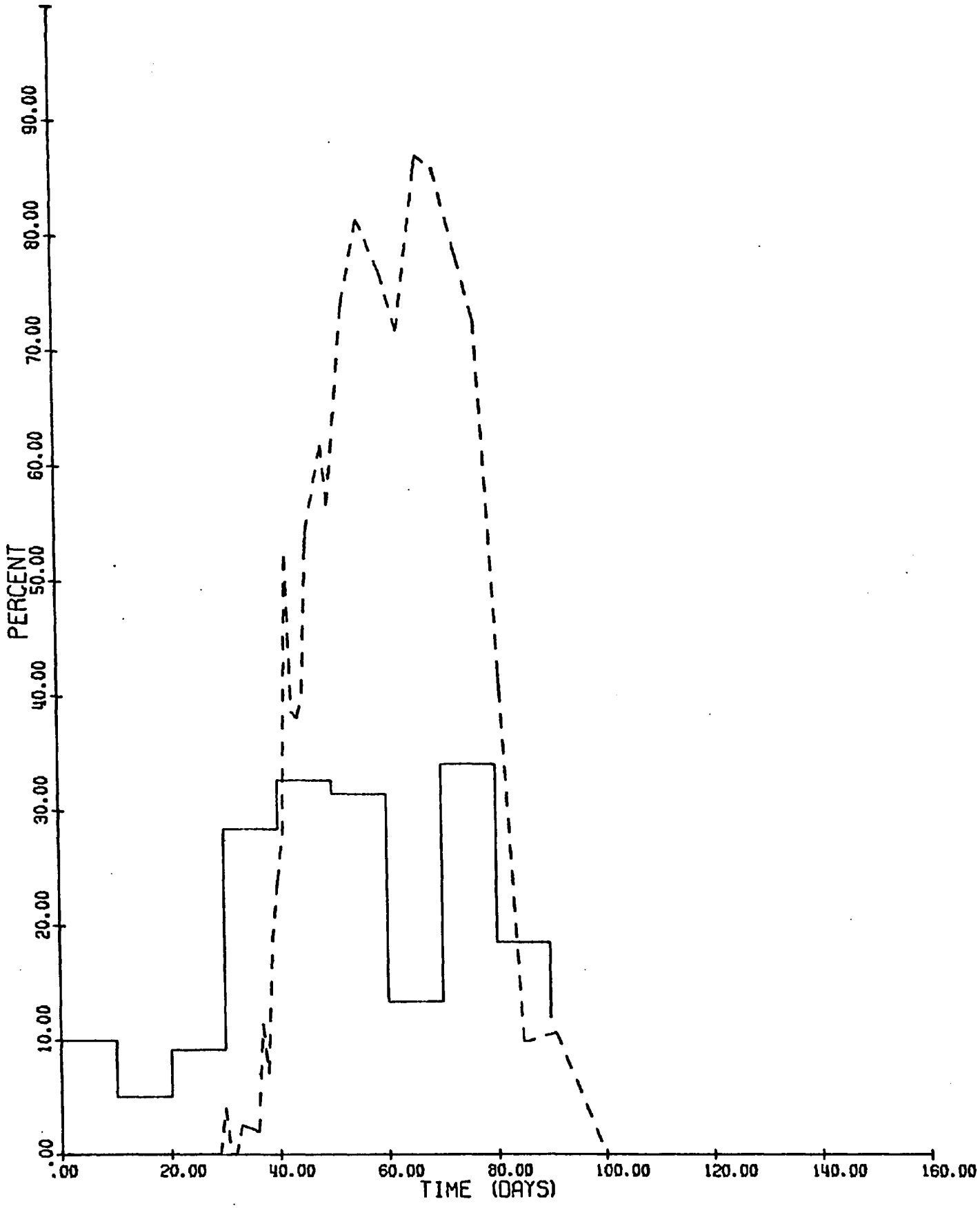
POPULATION 150 40 A2 - GROWTH CURVE



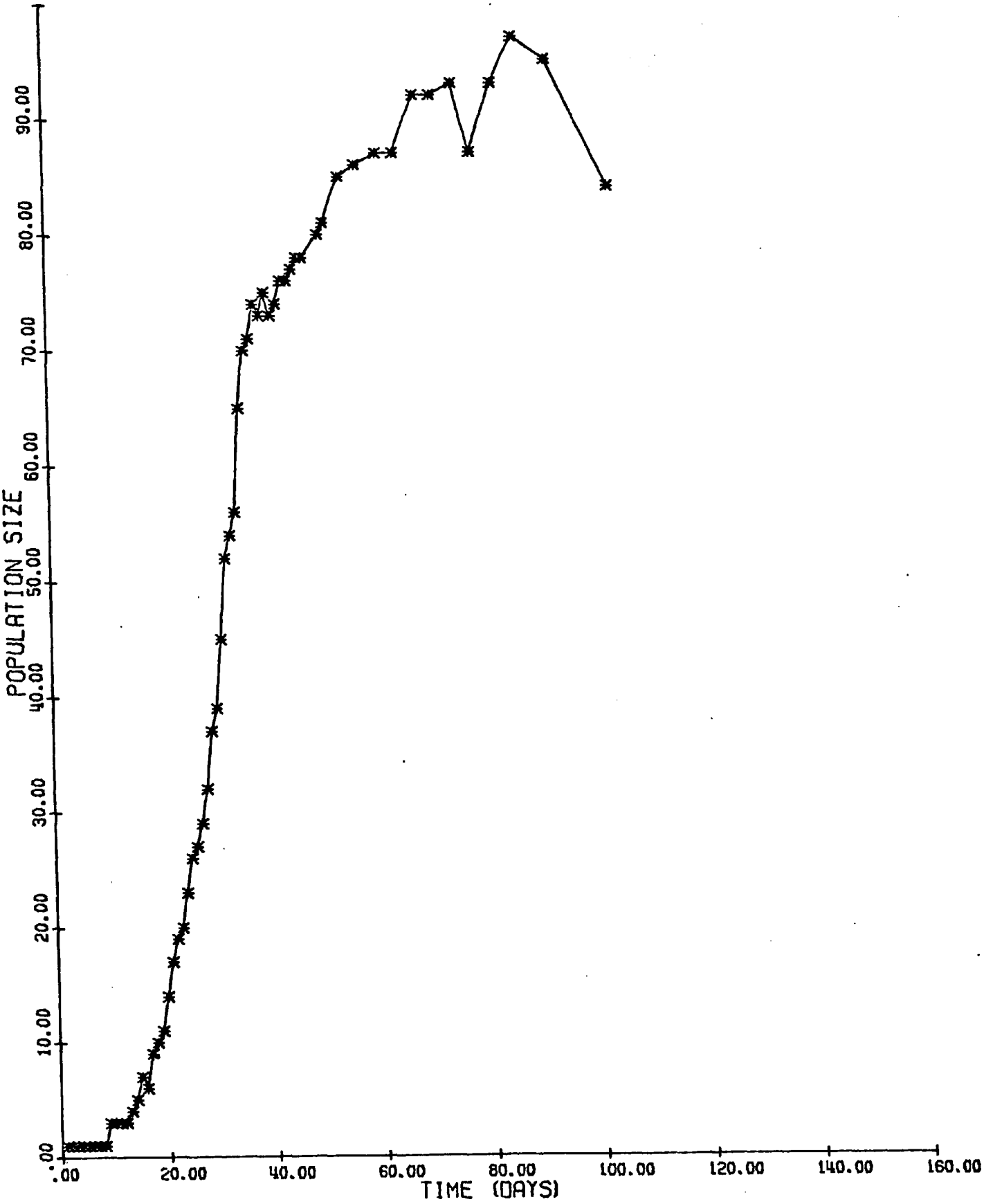
POPULATION 150 40 A2 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



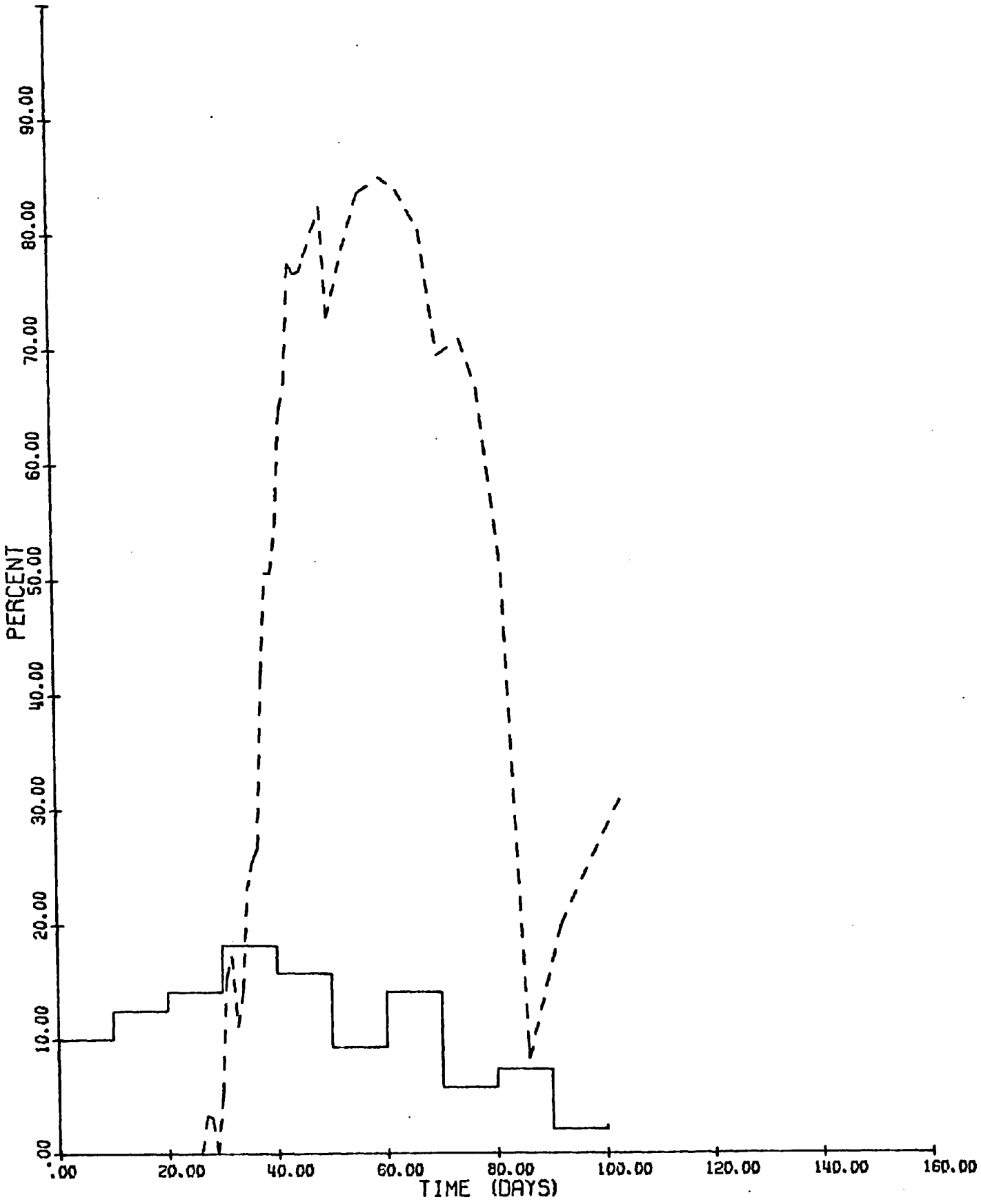
POPULATION 150 80 A1 - GROWTH CURVE



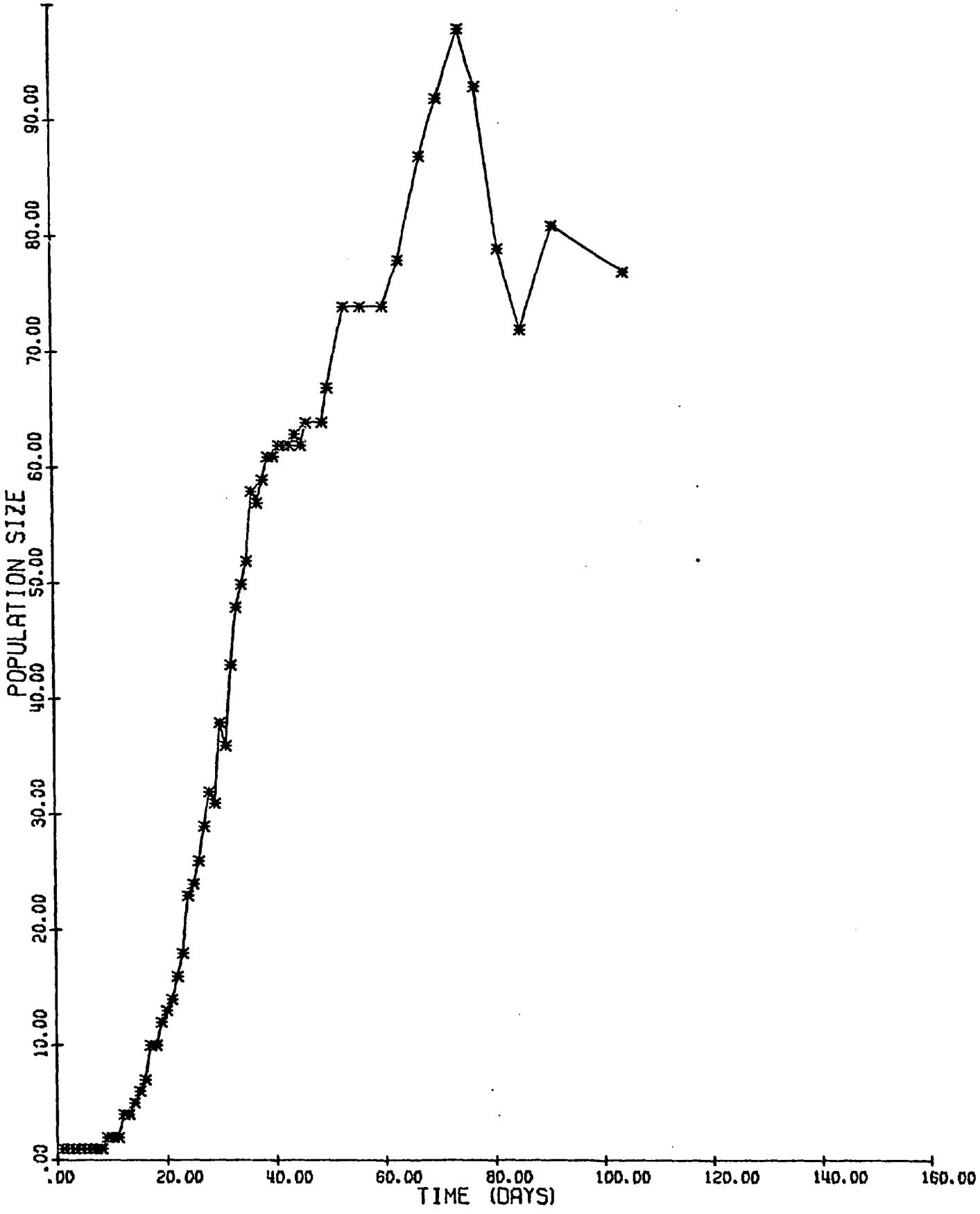
POPULATION 150 80 A1 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



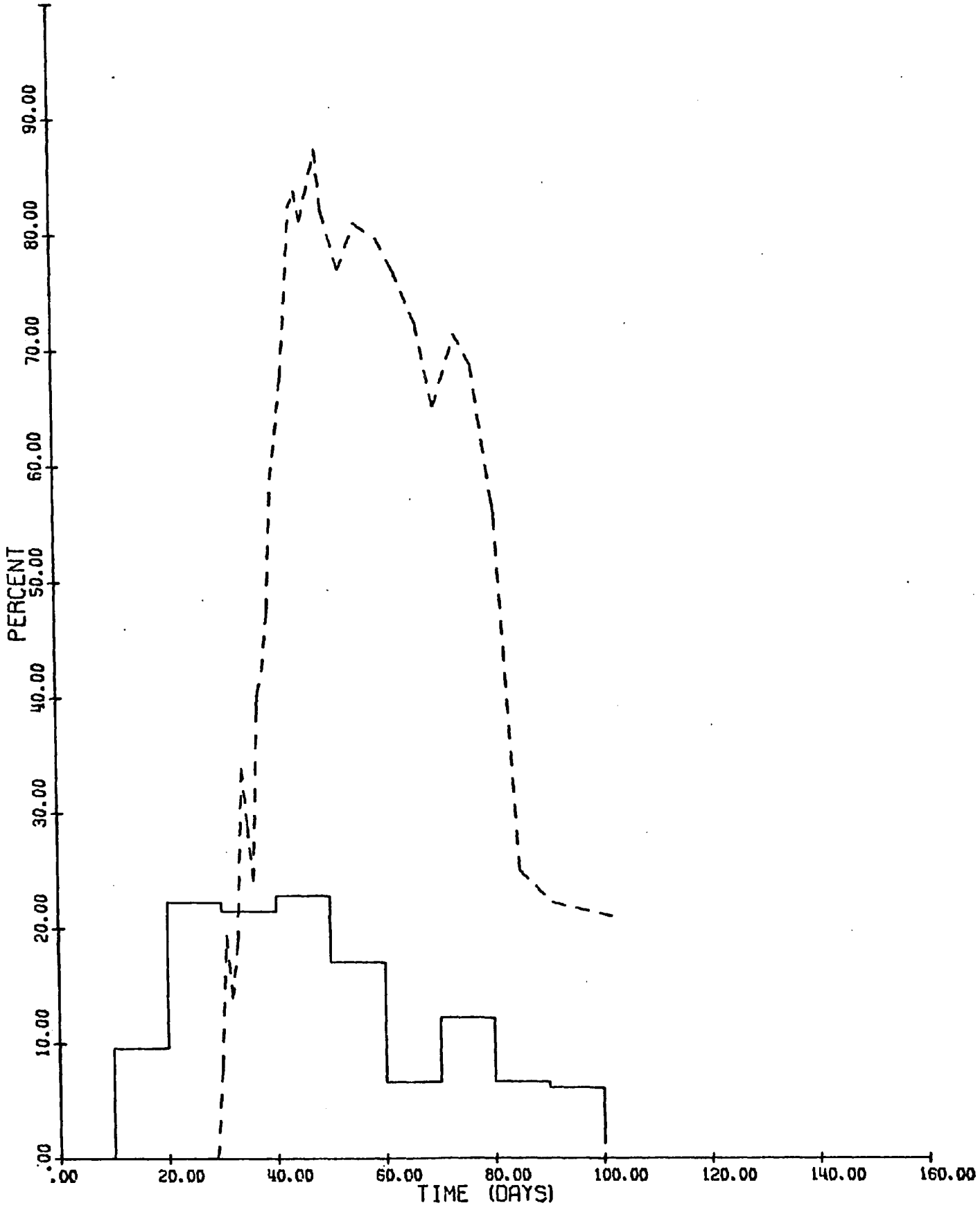
POPULATION 150 80 A2 - GROWTH CURVE



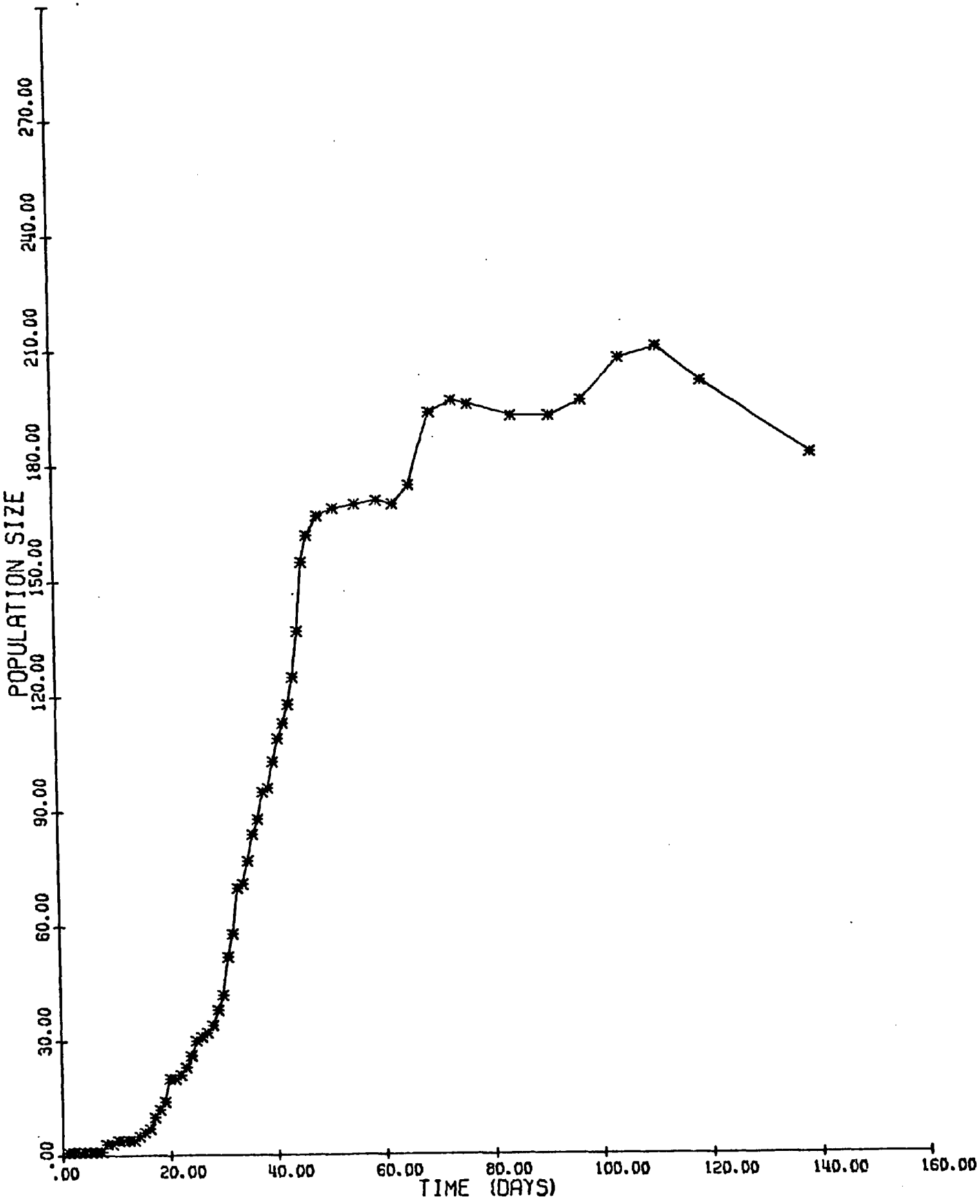
POPULATION 150 80 A2 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



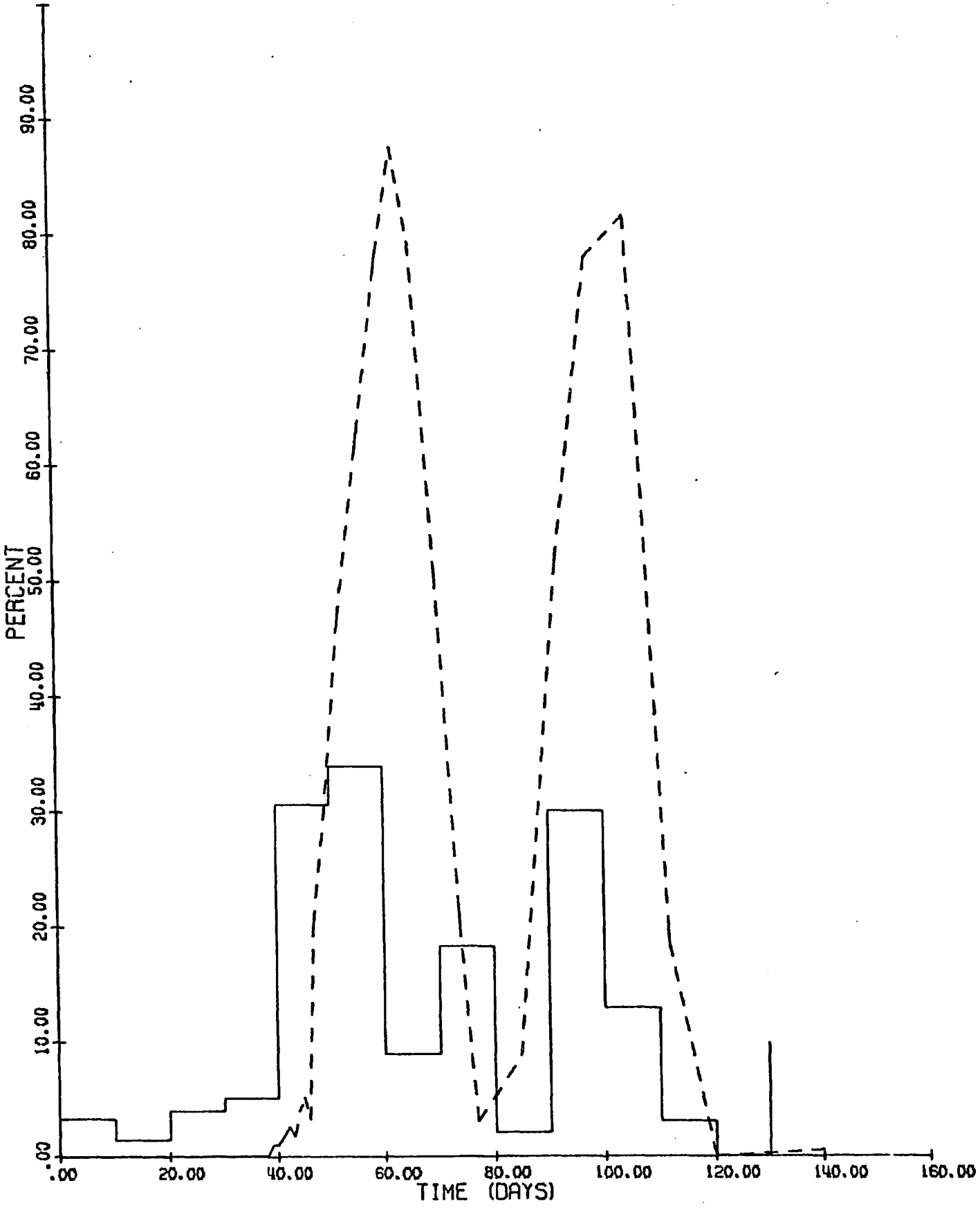
POPULATION 300 20 A1 - GROWTH CURVE



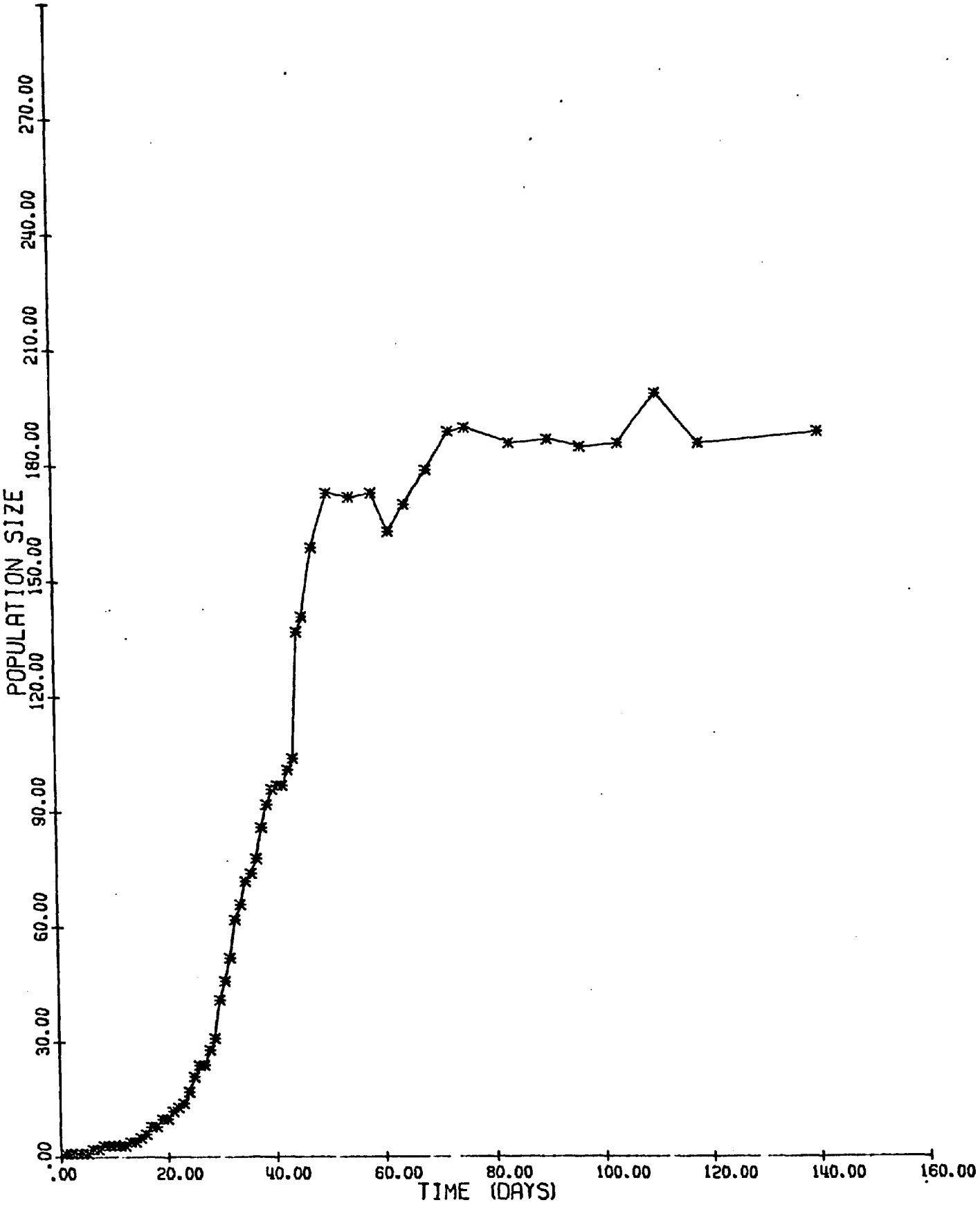
POPULATION 300 20 A1 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



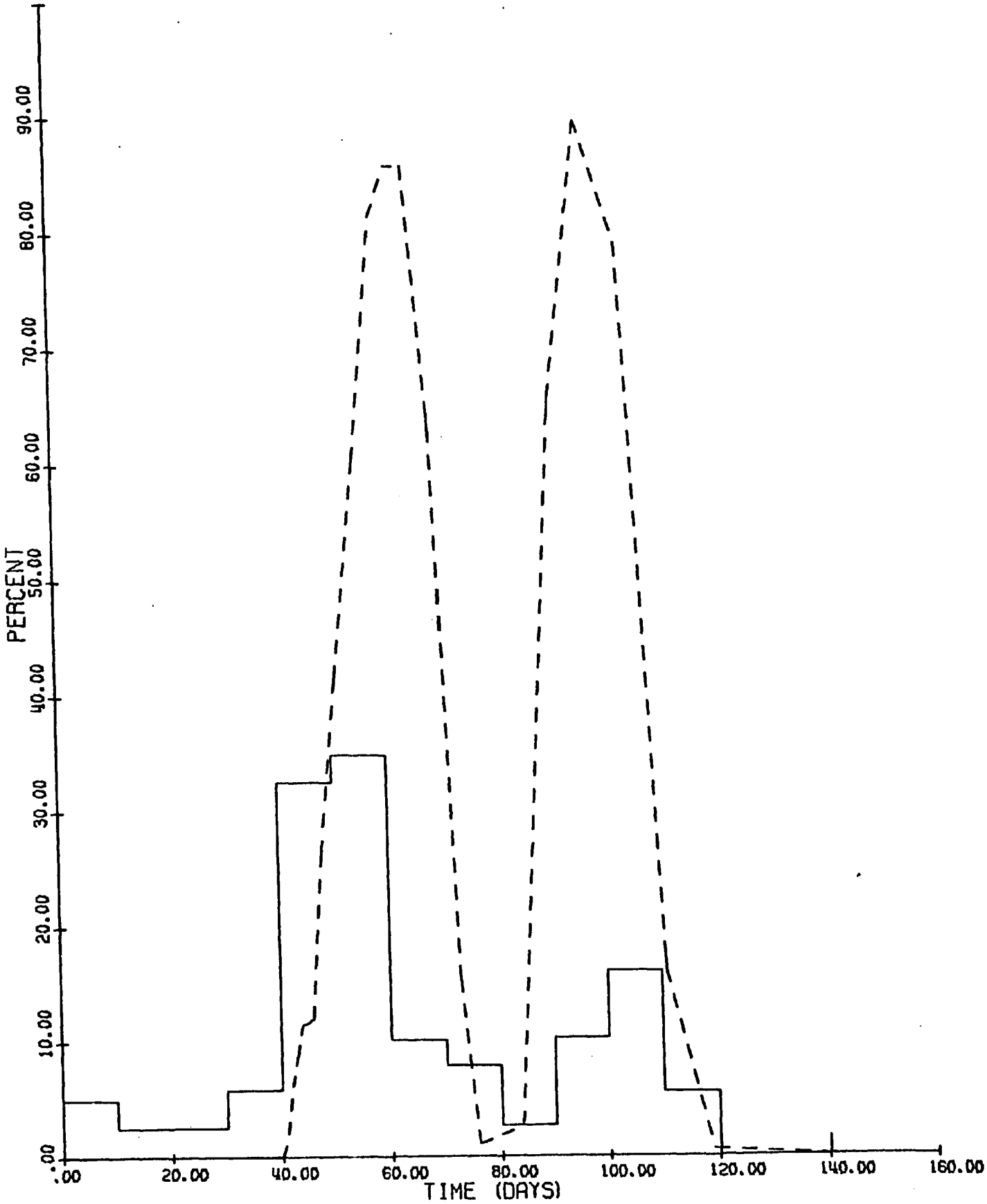
POPULATION 300 20 A2 - GROWTH CURVE



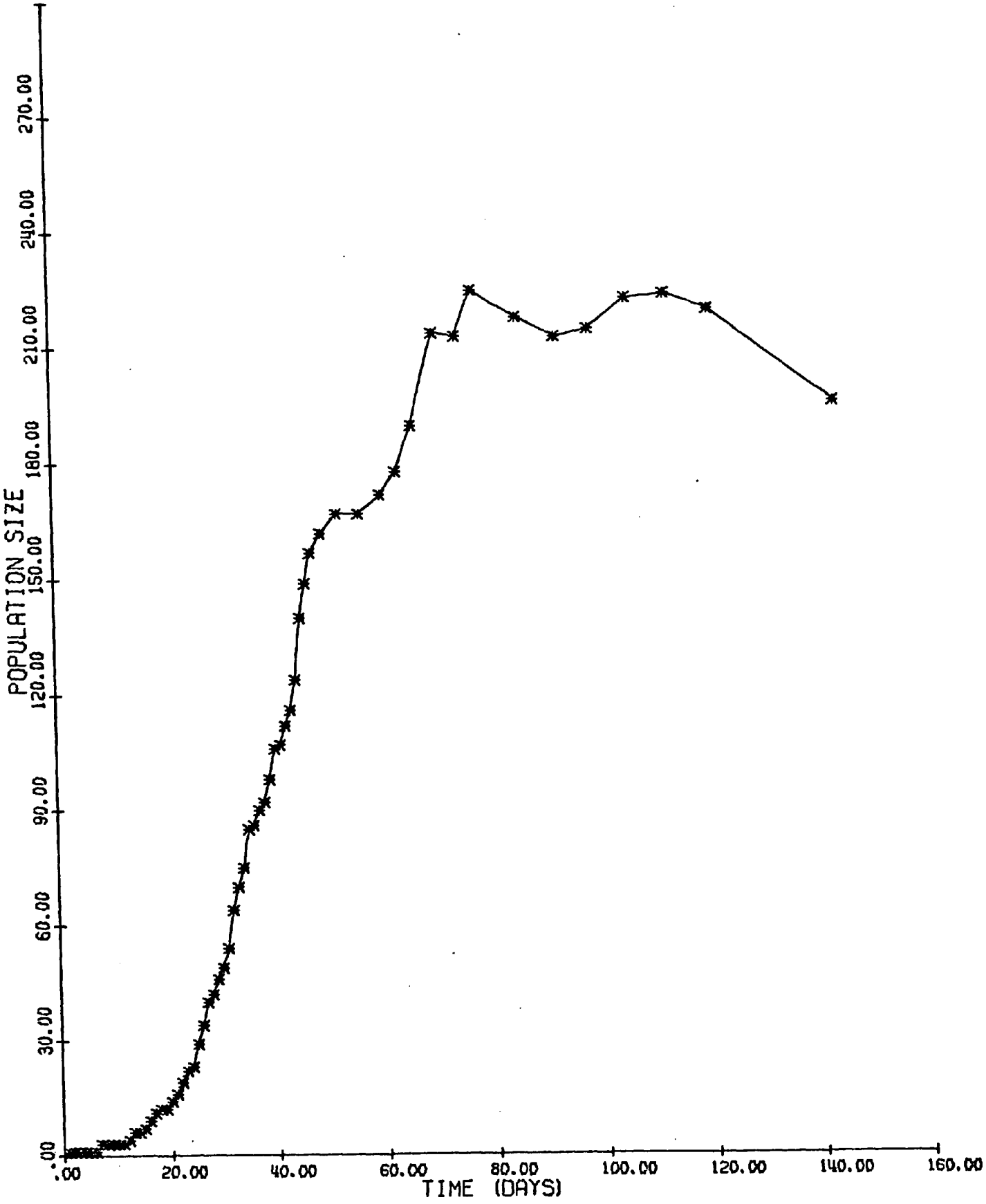
POPULATION 300 20 A2 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



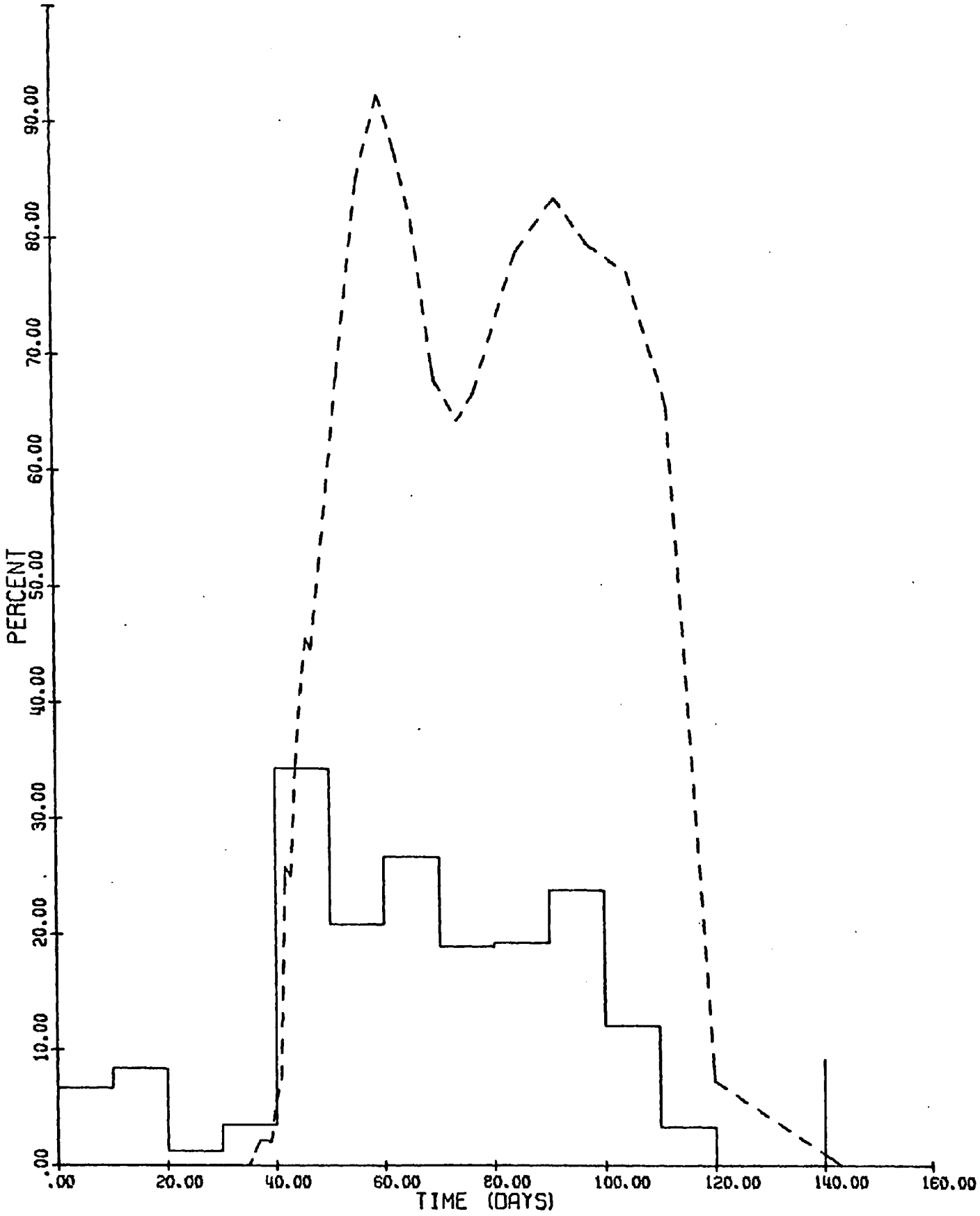
POPULATION 300 40 A1 - GROWTH CURVE



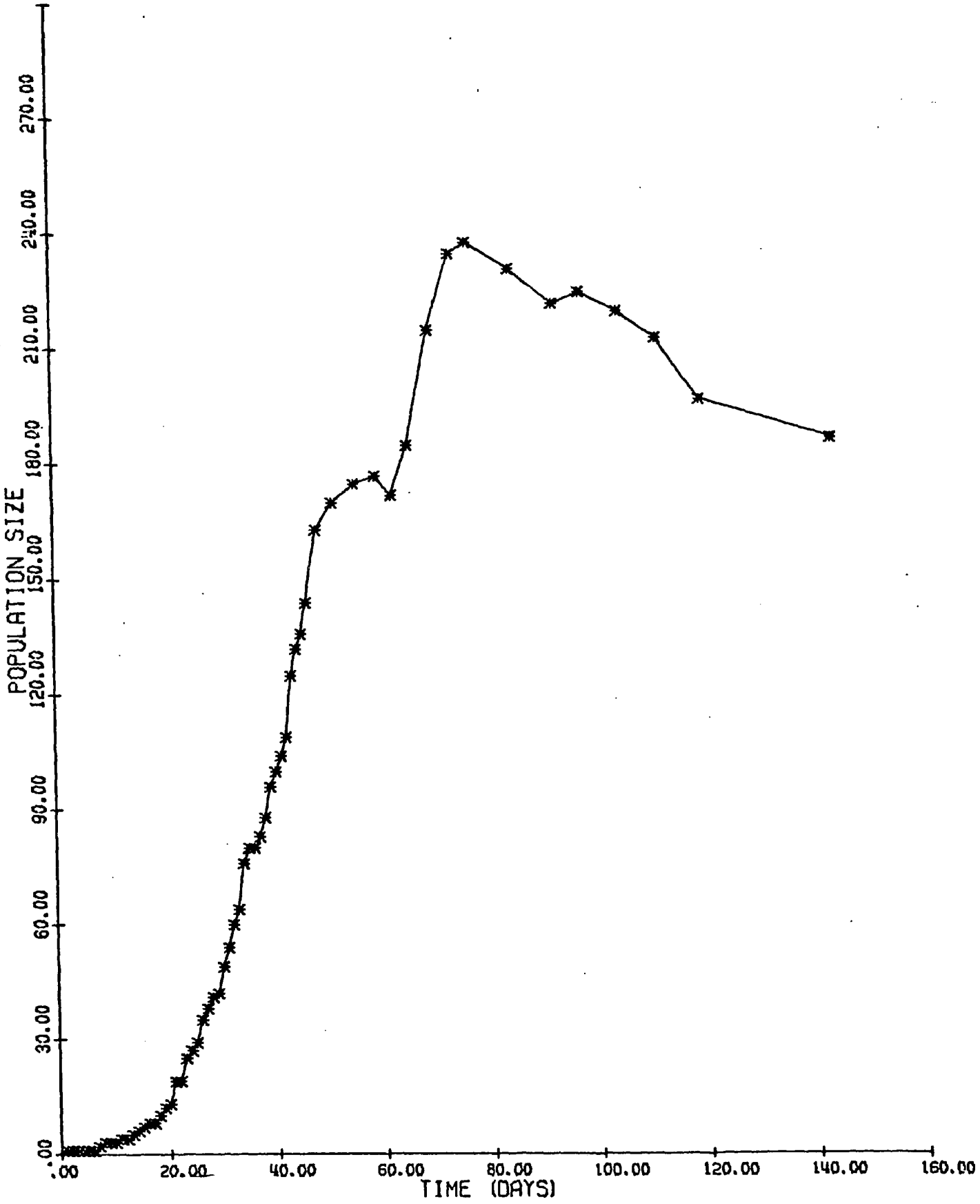
POPULATION 300 40 A1 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



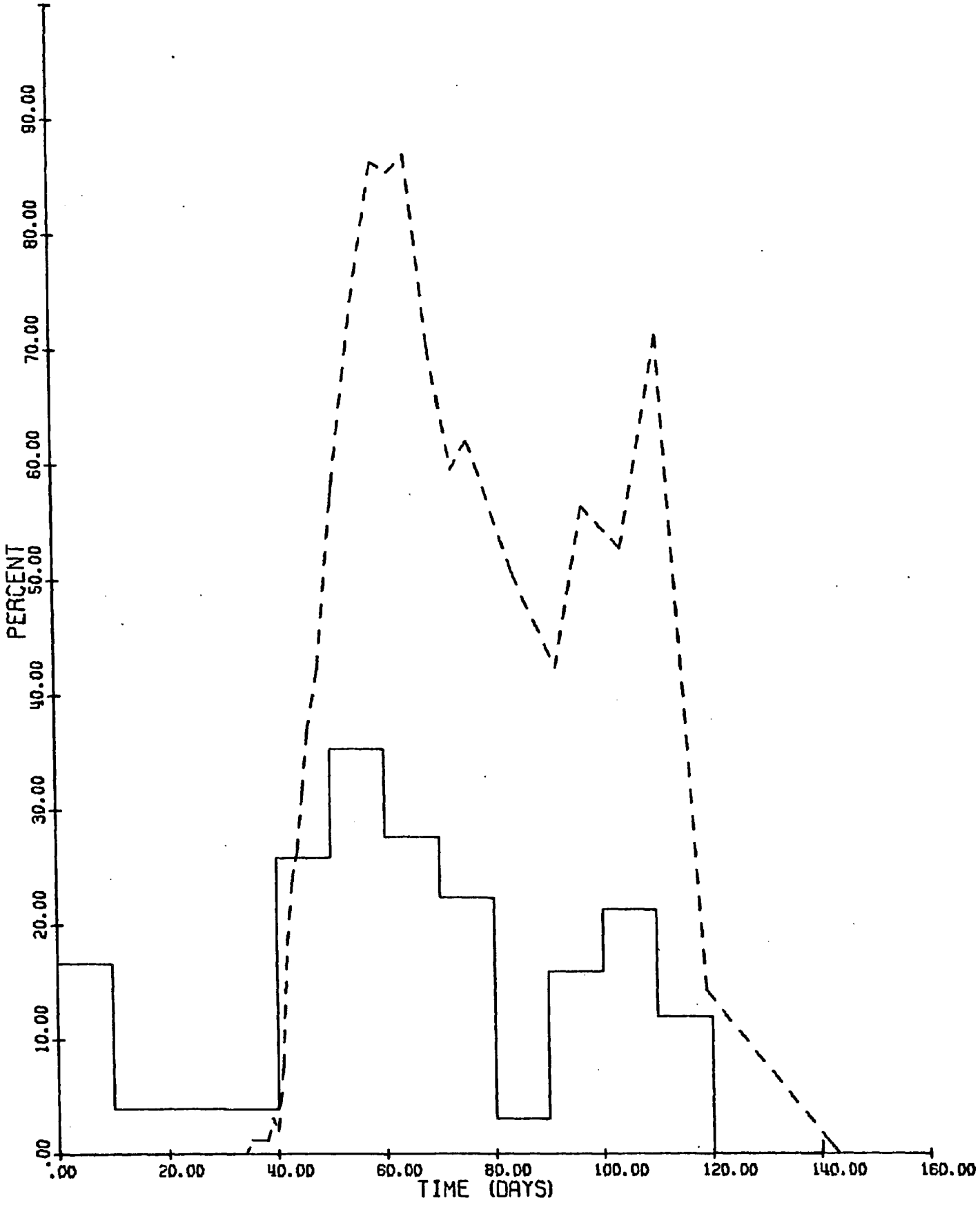
POPULATION 300 40 A2 - GROWTH CURVE



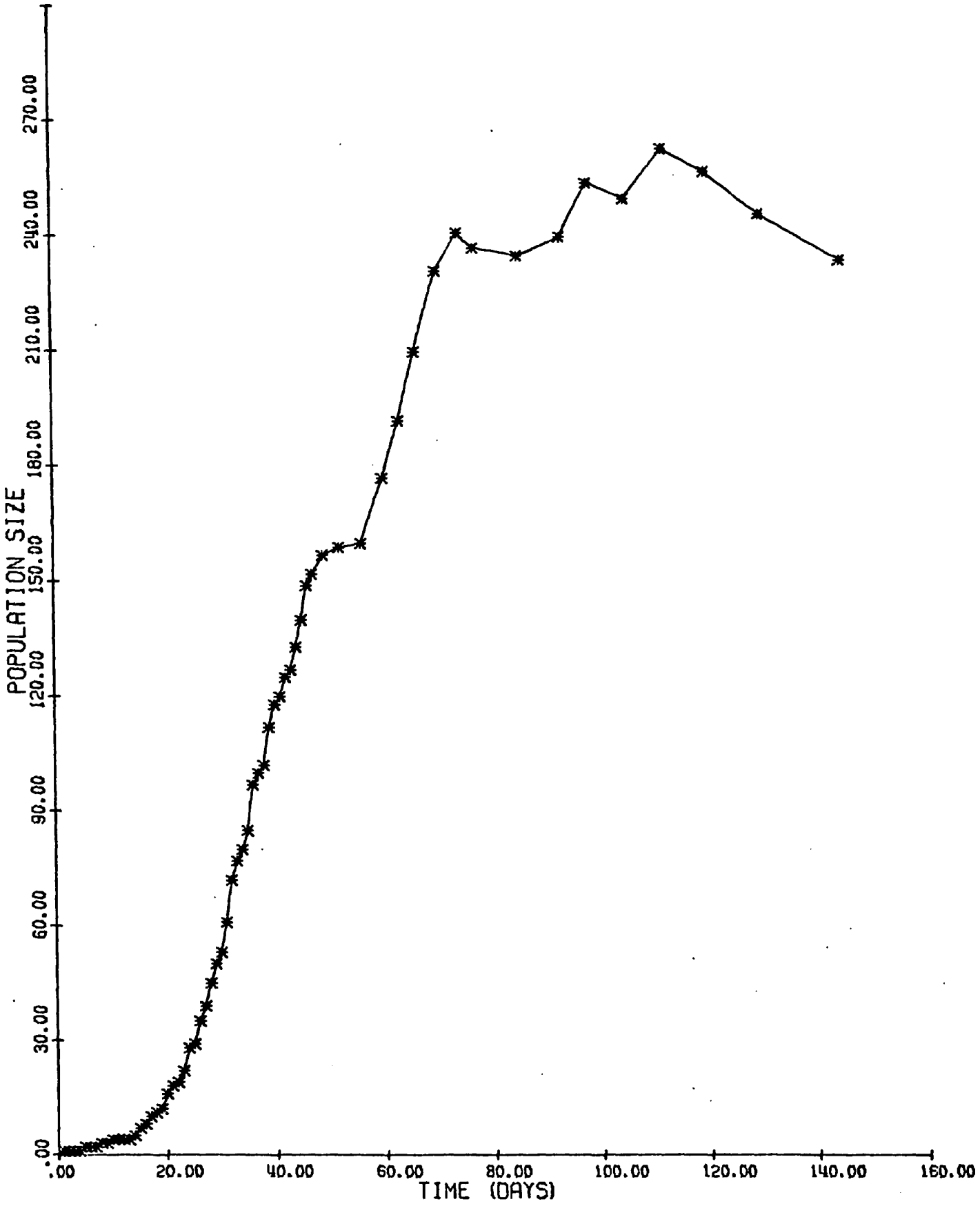
POPULATION 300 40 A2 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



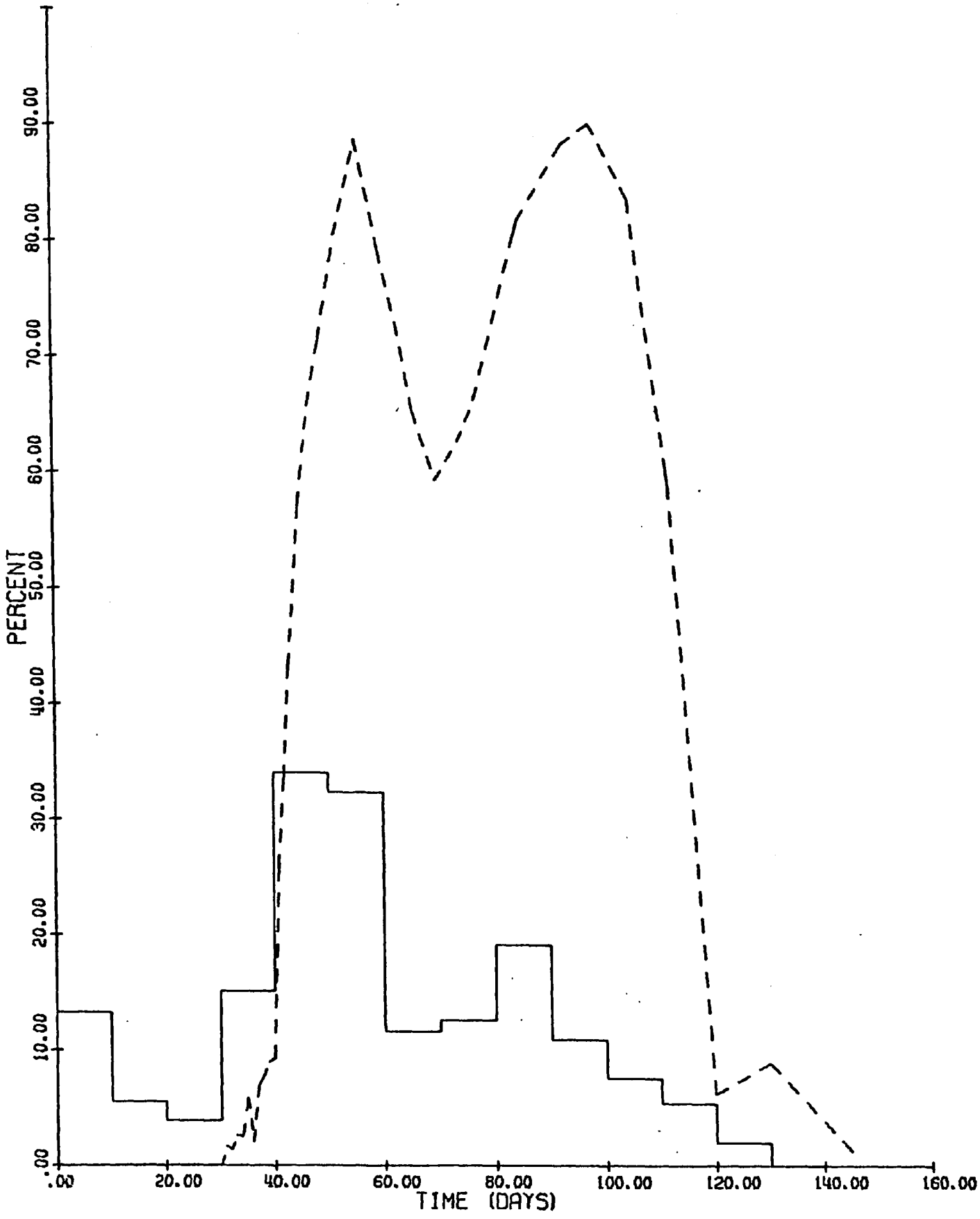
POPULATION 300 80 A1 - GROWTH CURVE



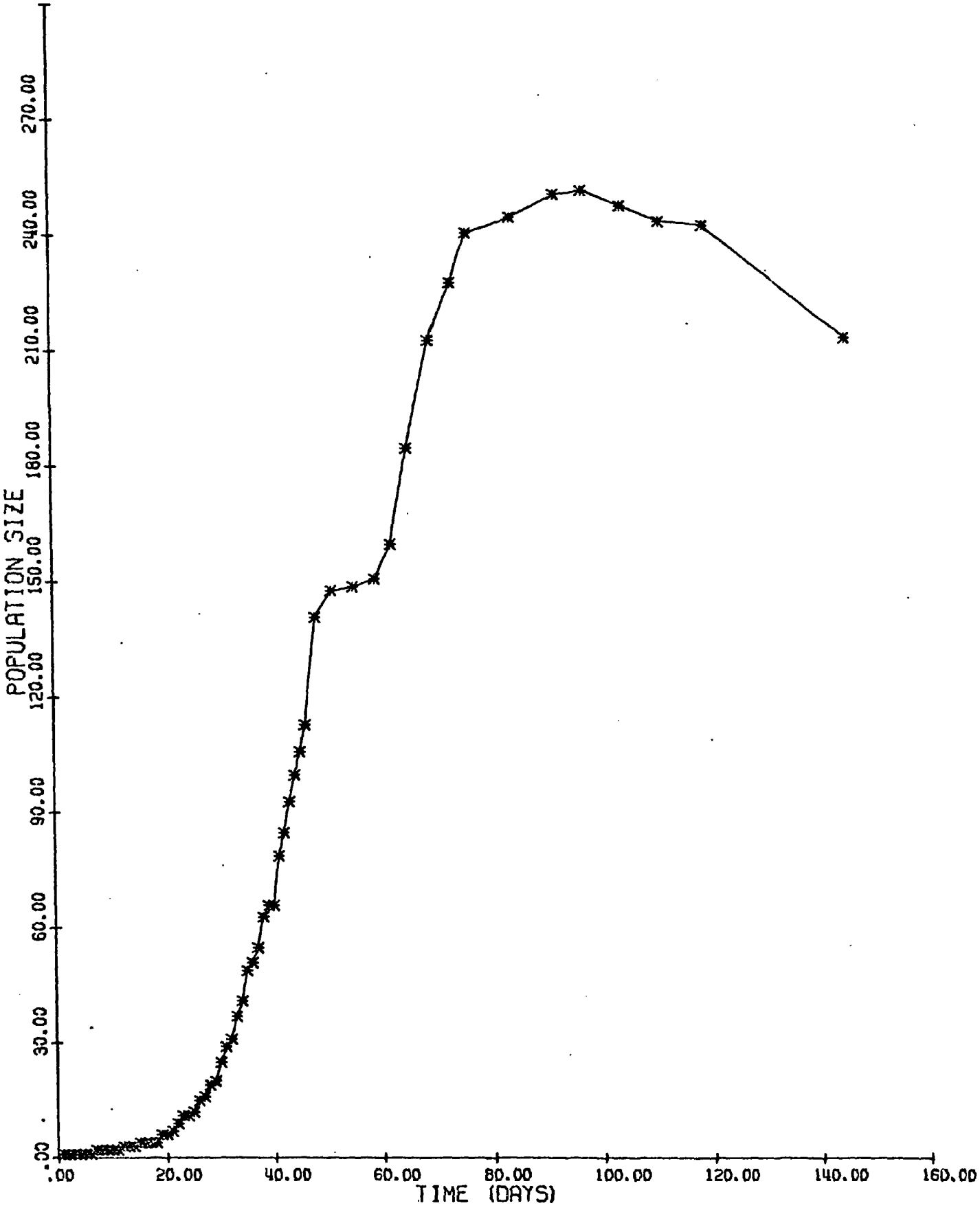
POPULATION 300 80 A1 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 10-DAY PERIODS)



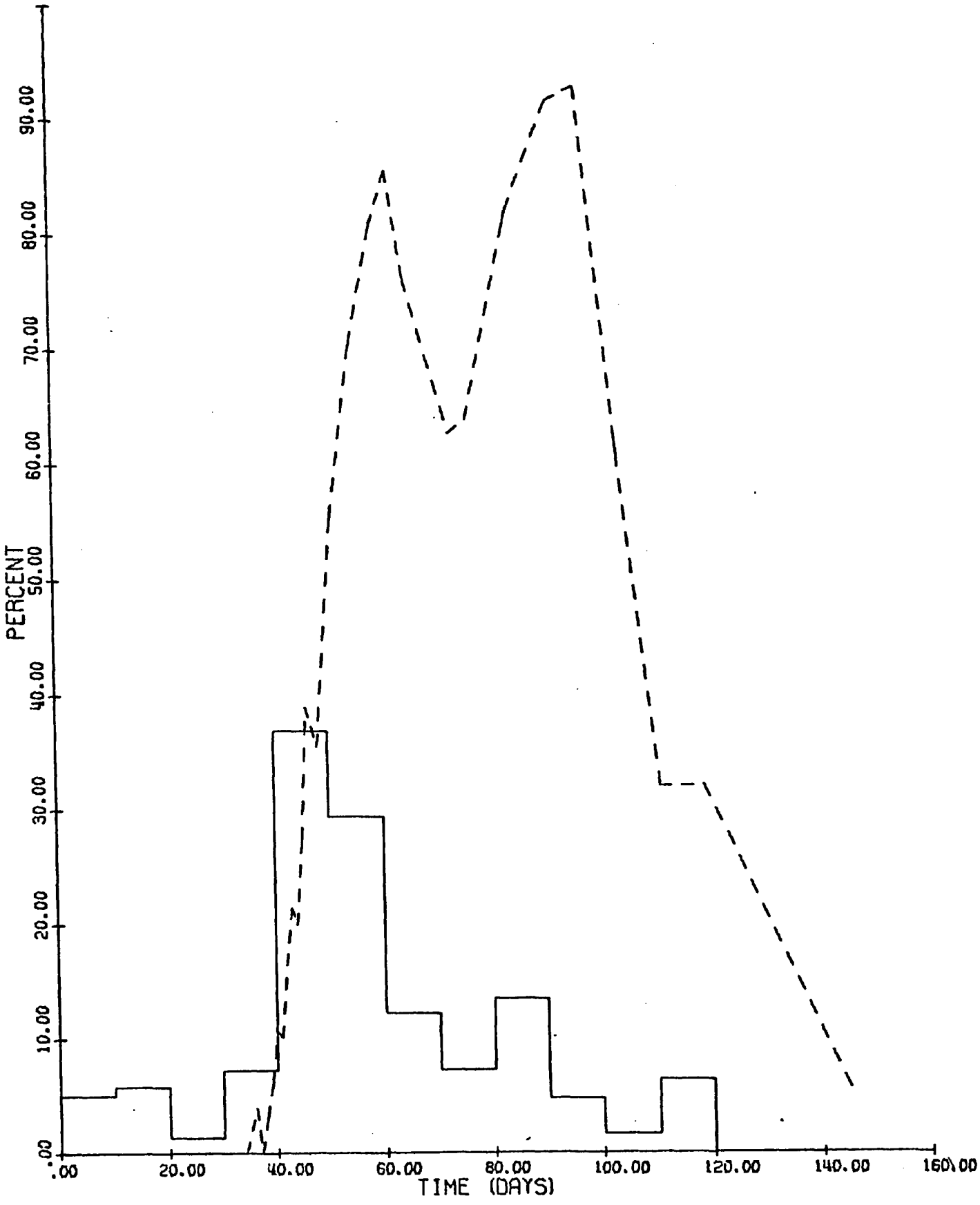
POPULATION 300 80 A2 - GROWTH CURVE



POPULATION 300 80 A2 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE: AVERAGES OF 10-DAY PERIODS)



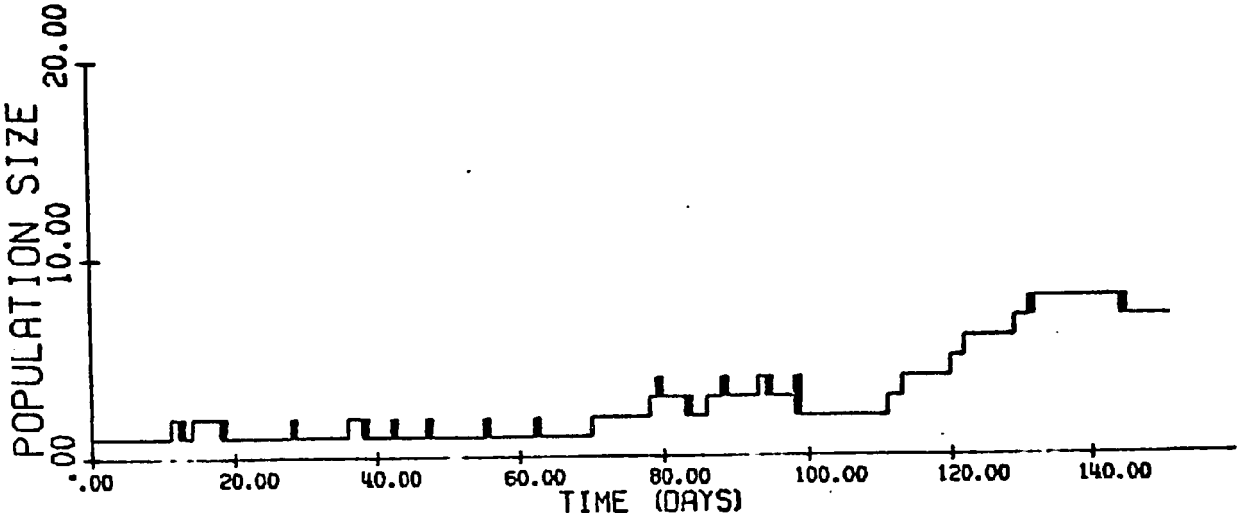
APPENDIX B

Growth curves (curve 1) and curves of the frequency of floating and sexuality (curve 2) of all "B" (open) populations of the long term experiments. The following table gives for each curve the page on which it can be found.

Population	Curve 1	Curve 2
20 20 B1	242	243
20 20 B2	242	244
20 20 B3	245	246
20 40 B1	245	247
20 40 B2	248	249
20 40 B3	248	250
20 80 B1	251	252
20 80 B2	251	253
20 80 B3	254	255
40 20 B1	254	256
40 20 B2	257	258
40 20 B3	257	259
40 40 B1	260	261
40 40 B2	260	262
40 40 B3	263	264
40 80 B1	263	265
40 80 B2	266	267
40 80 B3	266	268
80 20 B1	269	270
80 20 B2	271	272
80 20 B3	273	274
80 40 B1	275	276
80 40 B2	277	278
80 40 B3	279	280
80 80 B1	281	282
80 80 B2	283	284
80 80 B3	285	286
150 20 B1	287	288
150 20 B2	289	290
150 20 B3	291	292
150 40 B1	293	294
150 40 B2	295	296
150 40 B3	297	298
150 80 B1	299	300
150 80 B2	301	302
150 80 B3	303	304
300 20 B1	305	306
300 20 B2	307	308
300 20 B3	309	310
300 40 B1	311	312
300 40 B2	313	314
300 40 B3	315	316
300 80 B1	317	318
300 80 B2	319	320
300 80 B3	321	322

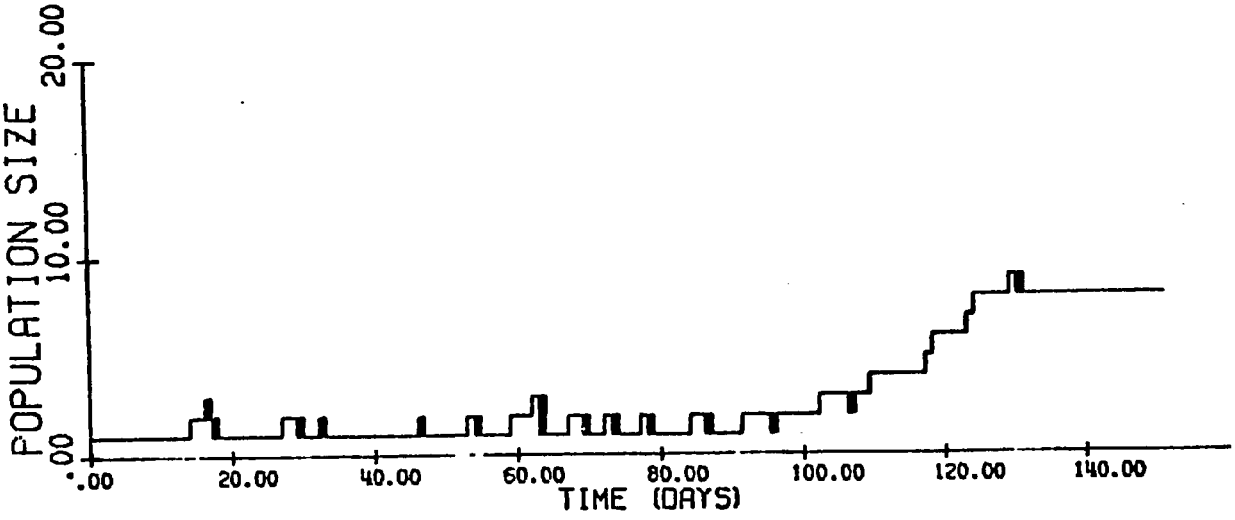
POPULATION 20 20 B1 - GROWTH CURVE

SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 20 20 B2 - GROWTH CURVE

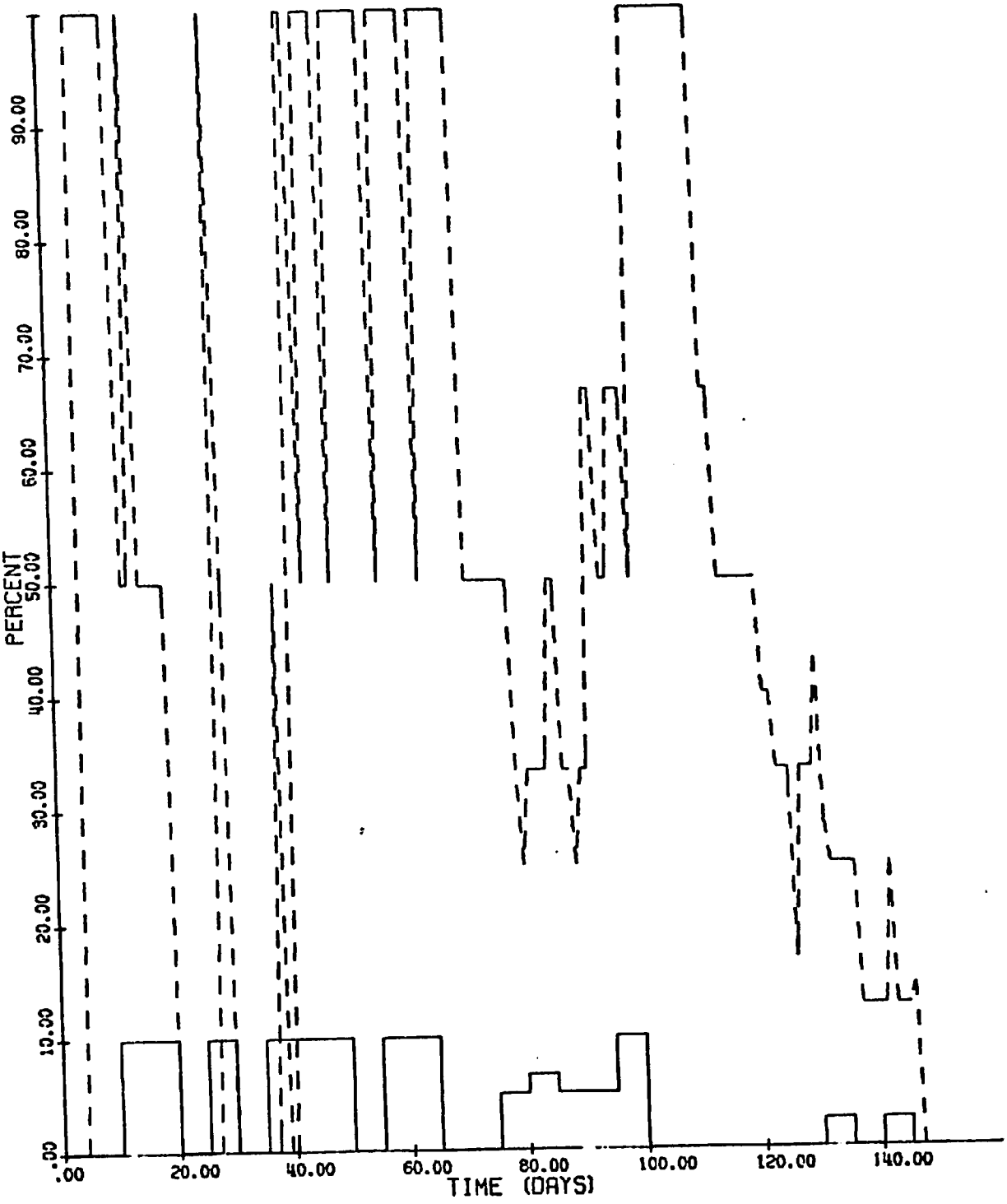
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 20 20 B1 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

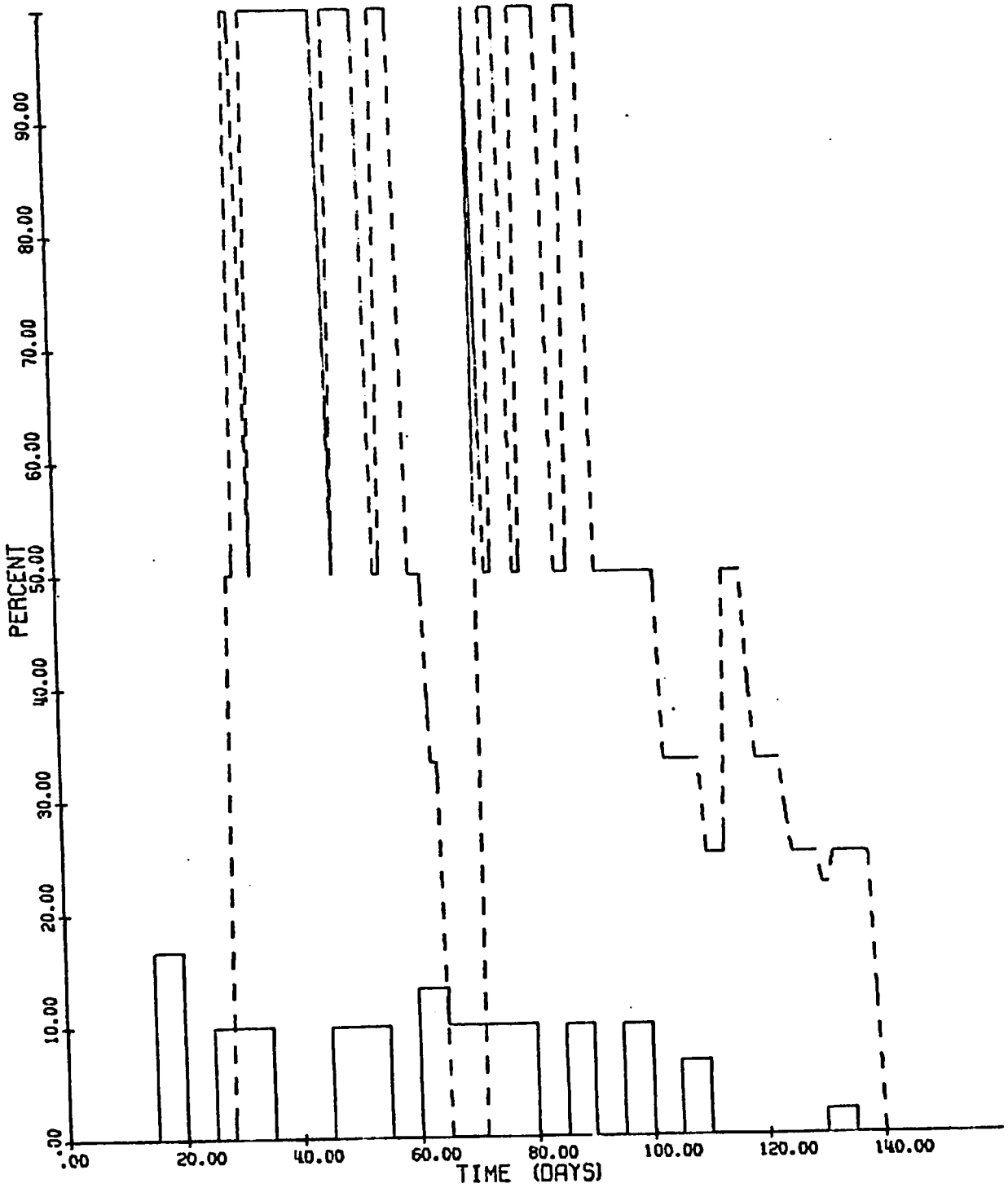
FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 20 20 82 -

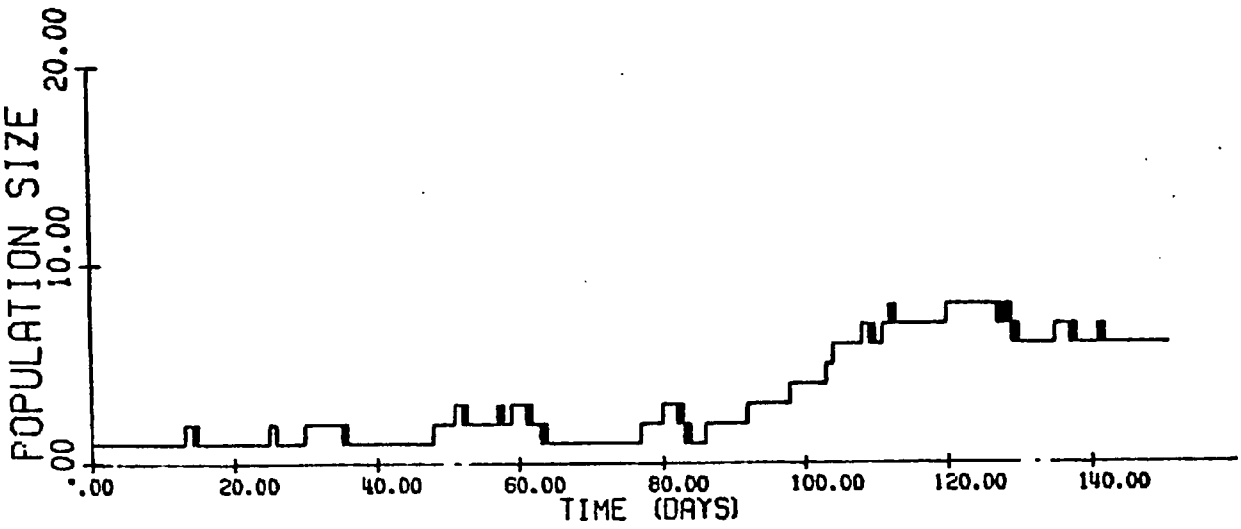
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



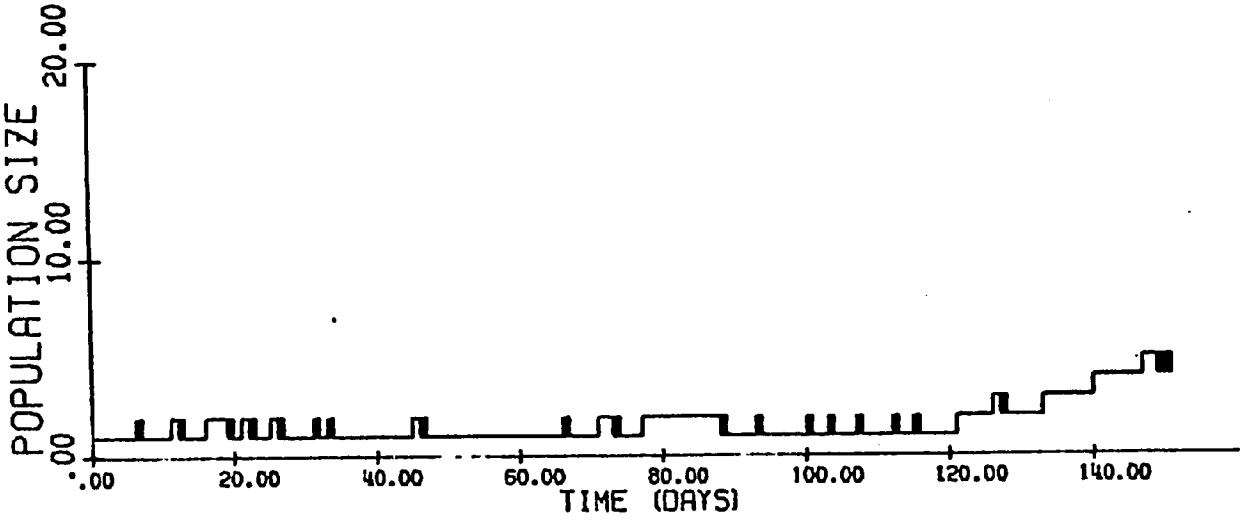
POPULATION 20 20 B3 - GROWTH CURVE

SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 20 40 B1 - GROWTH CURVE

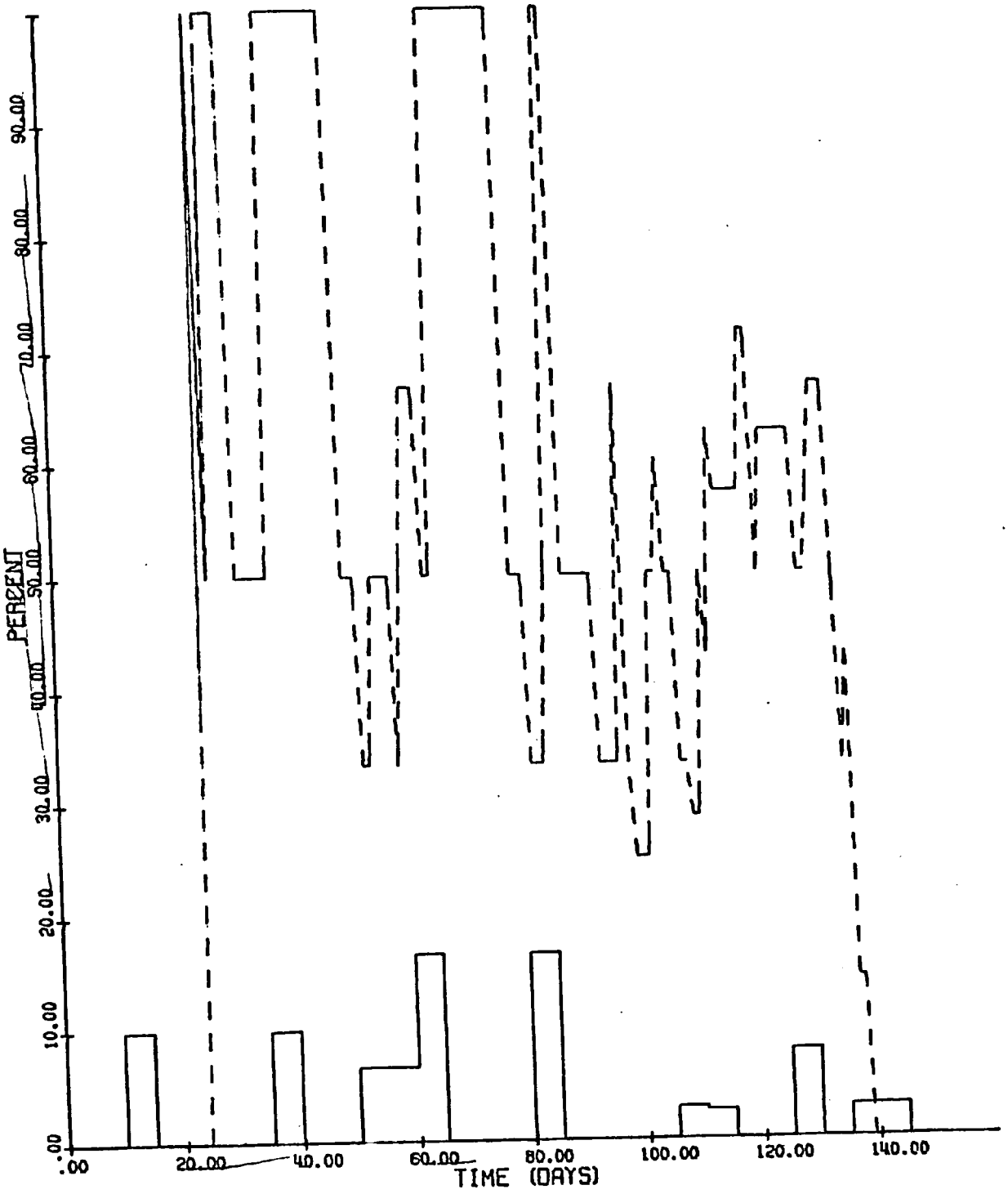
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 20 20 83

PERCENT SEXUAL HYDRA (DASHED LINE) AND

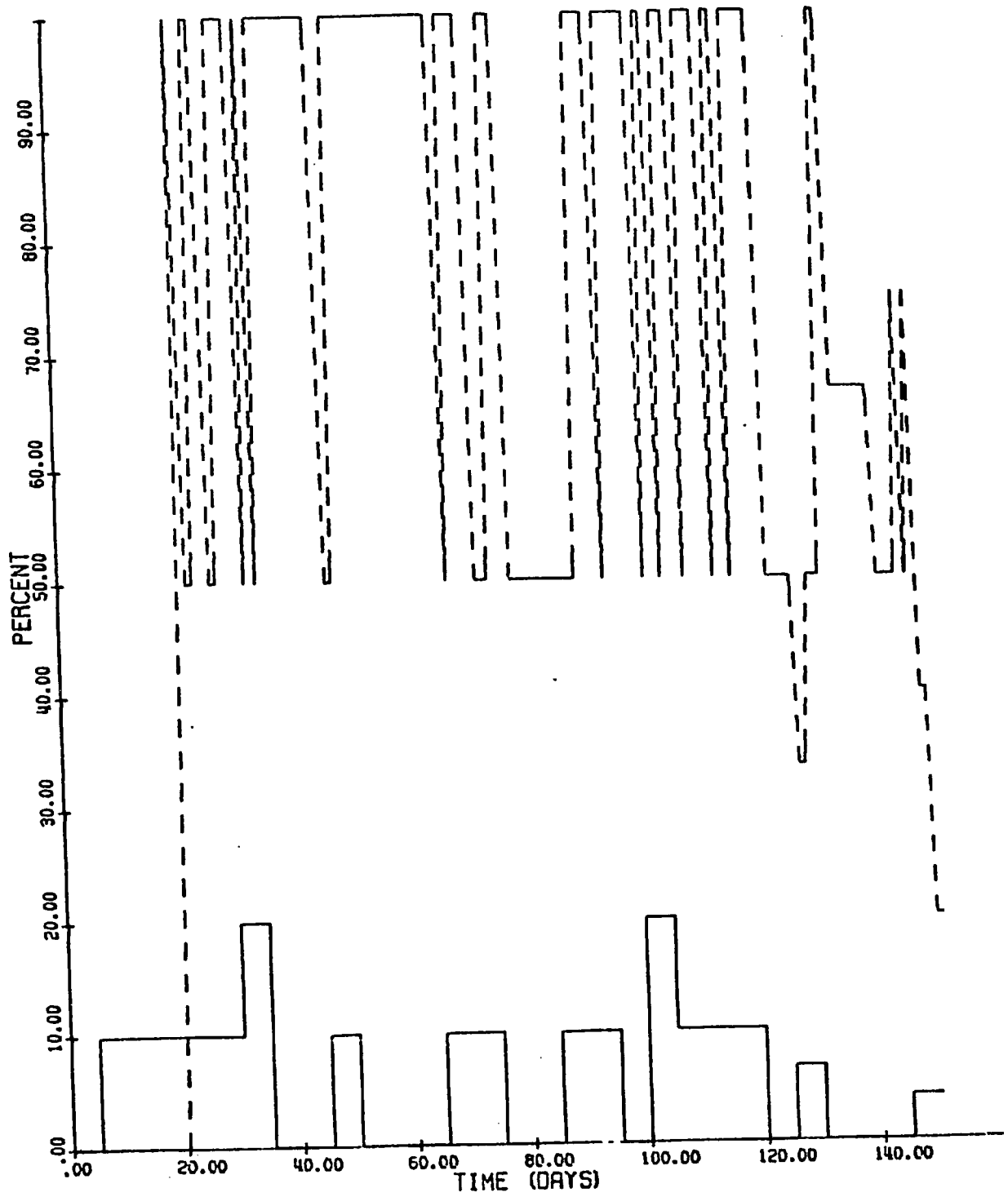
FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 20 40 B1 -

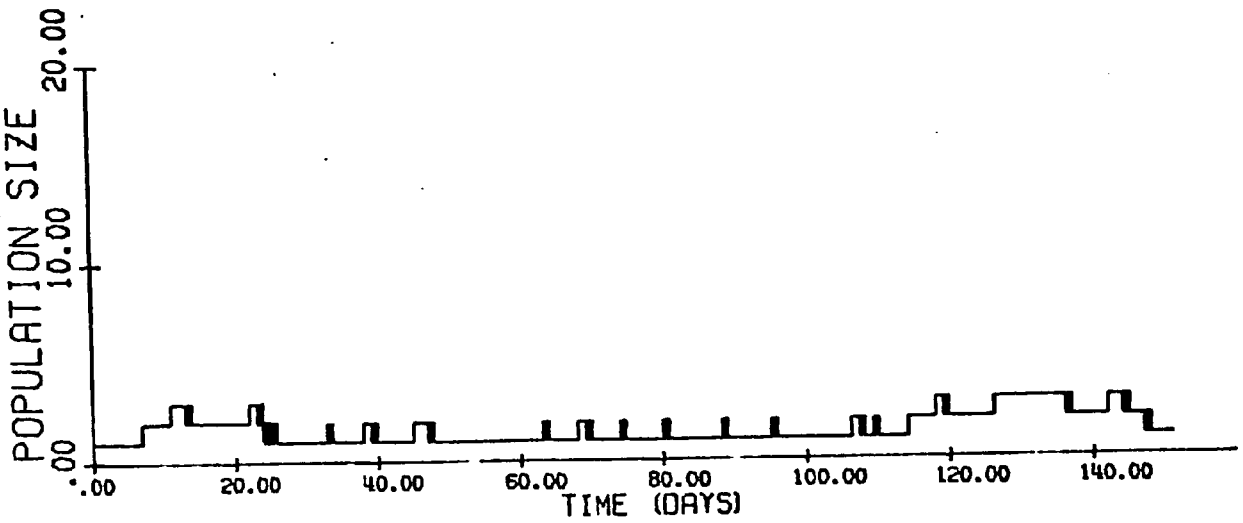
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



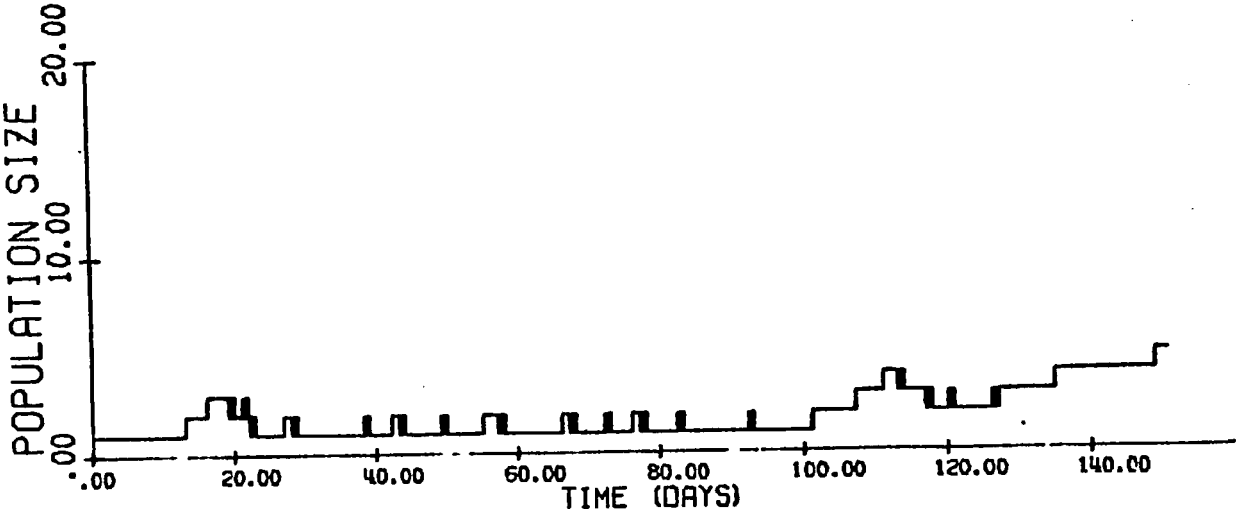
POPULATION 20 40 B2 - GROWTH CURVE

SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 20 40 B3 - GROWTH CURVE

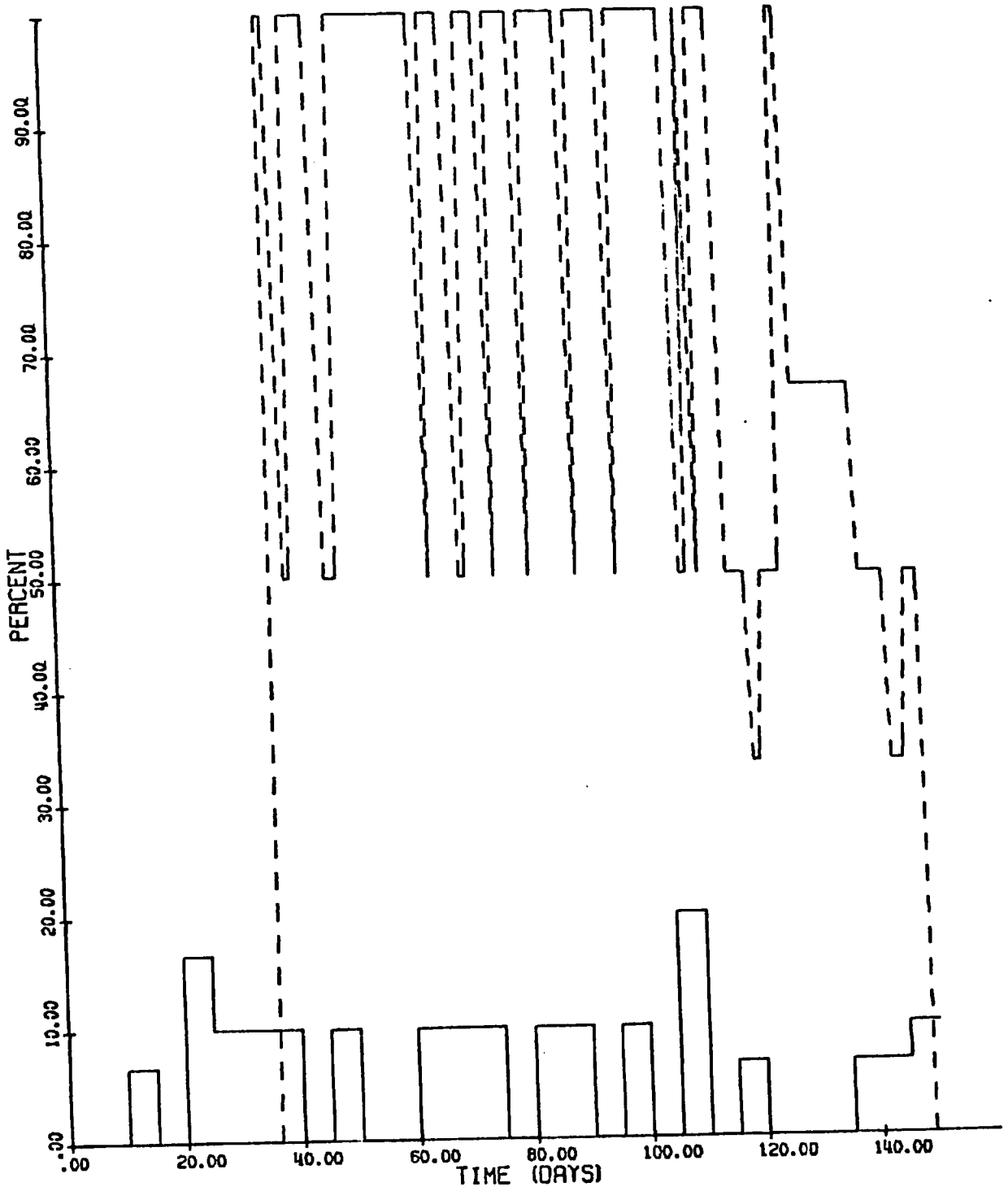
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 20 40 82 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

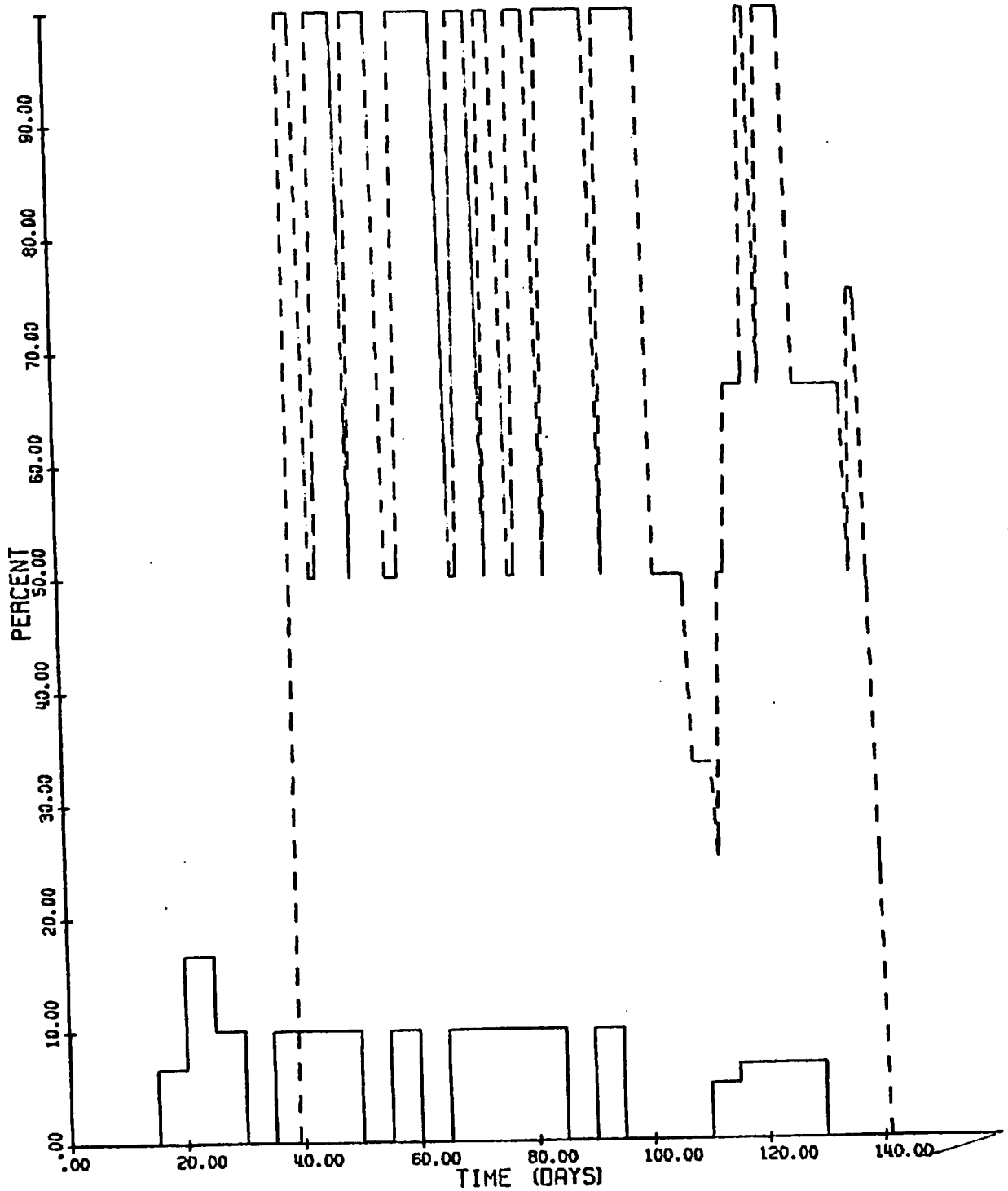
FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 20 40 83

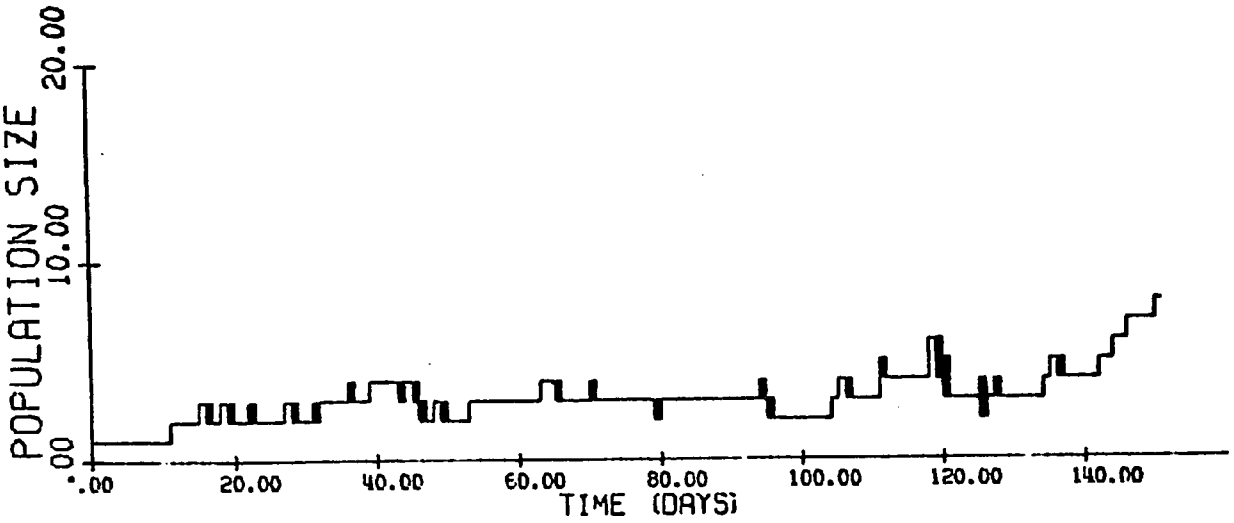
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE) AVERAGES OF 5-DAY PERIODS)



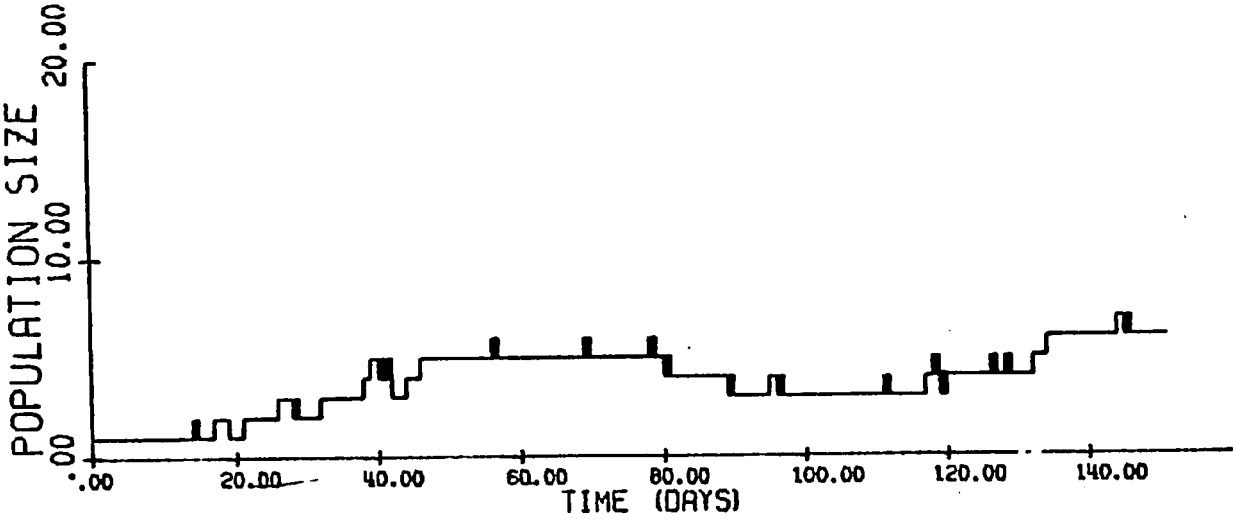
POPULATION 20 80 B1 - GROWTH CURVE

SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 20 80 B2 - GROWTH CURVE

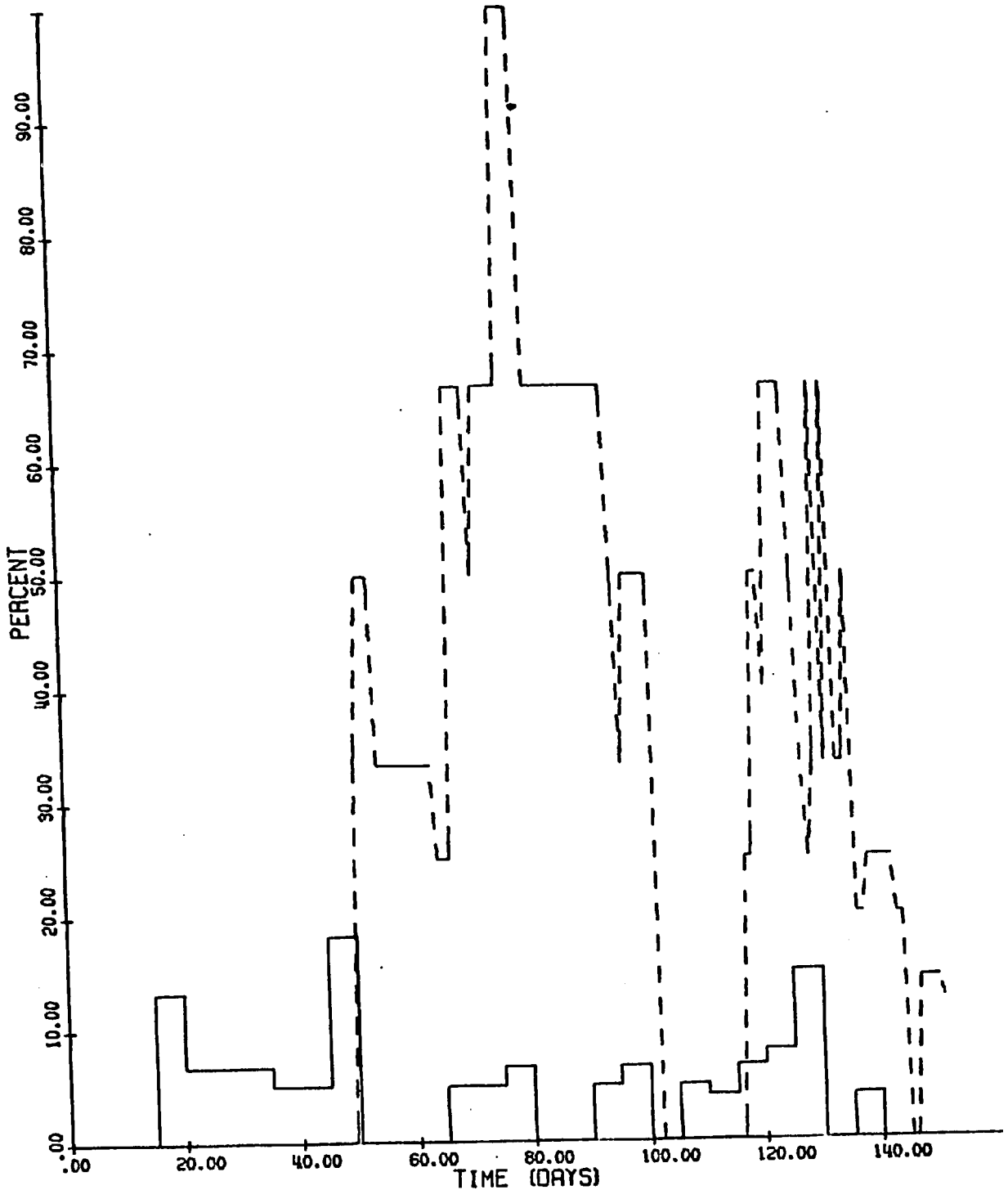
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 20 80 81 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

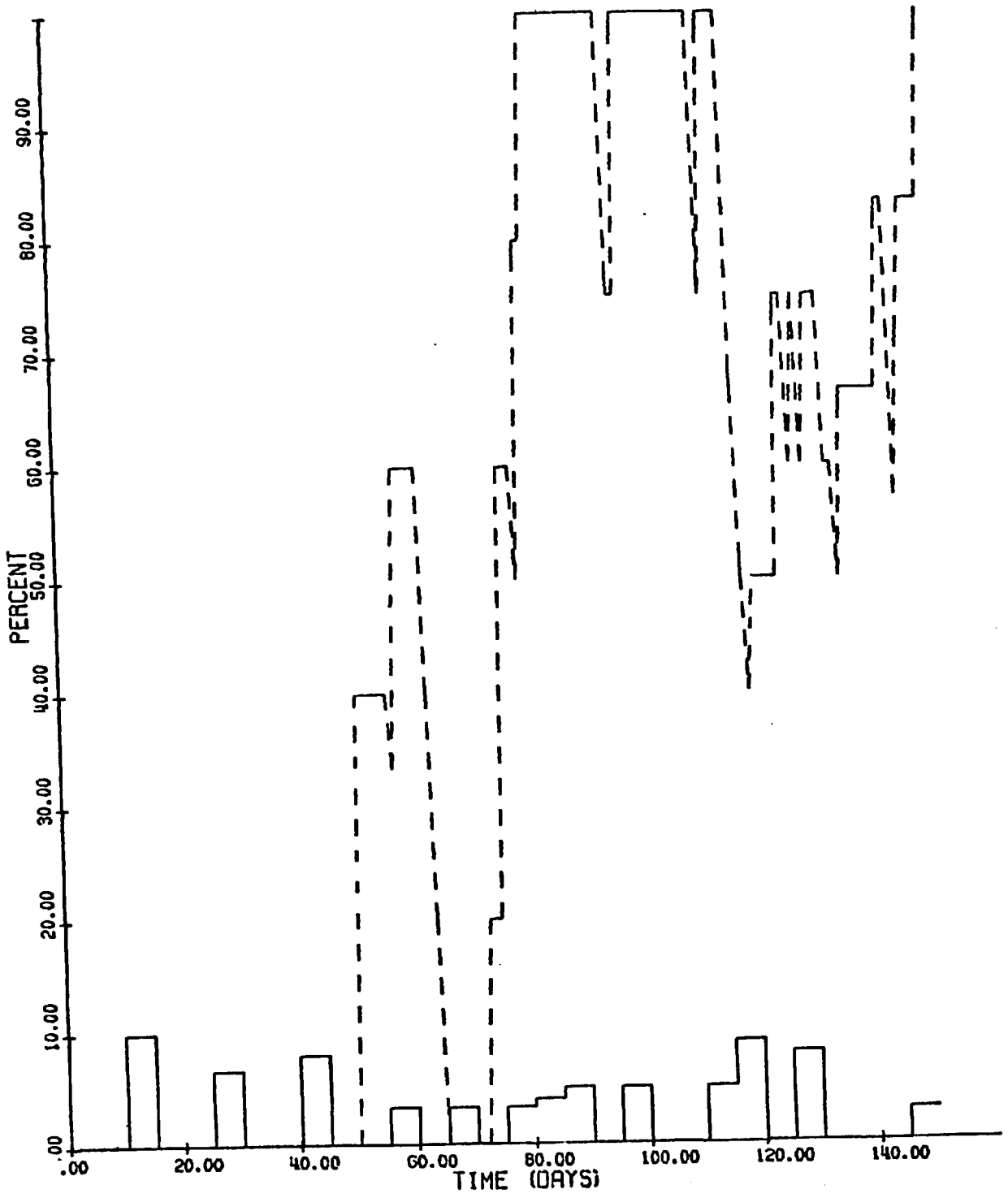
FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 20 80 82 -

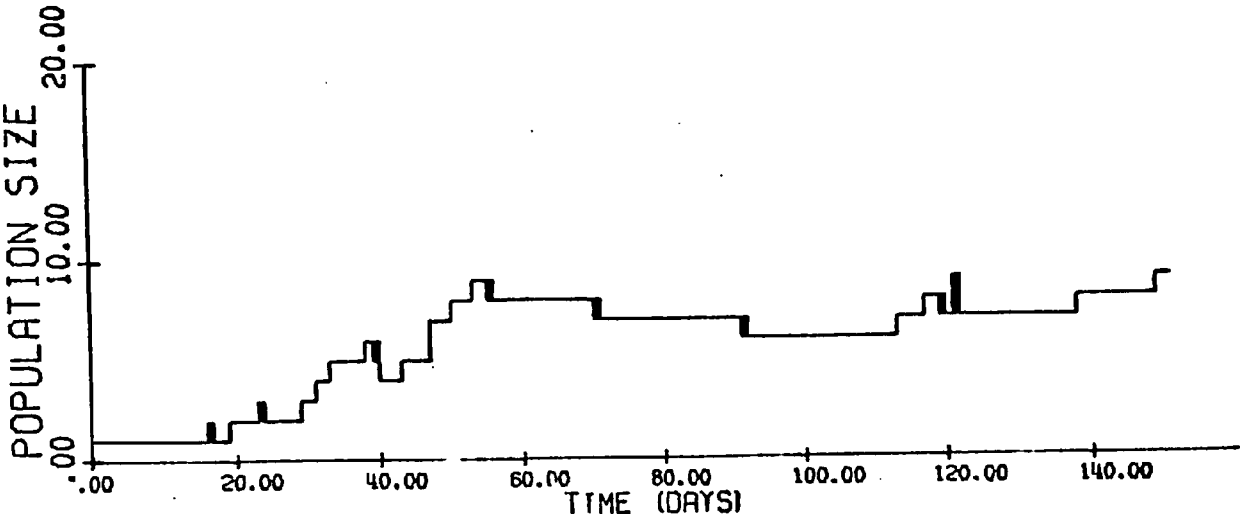
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



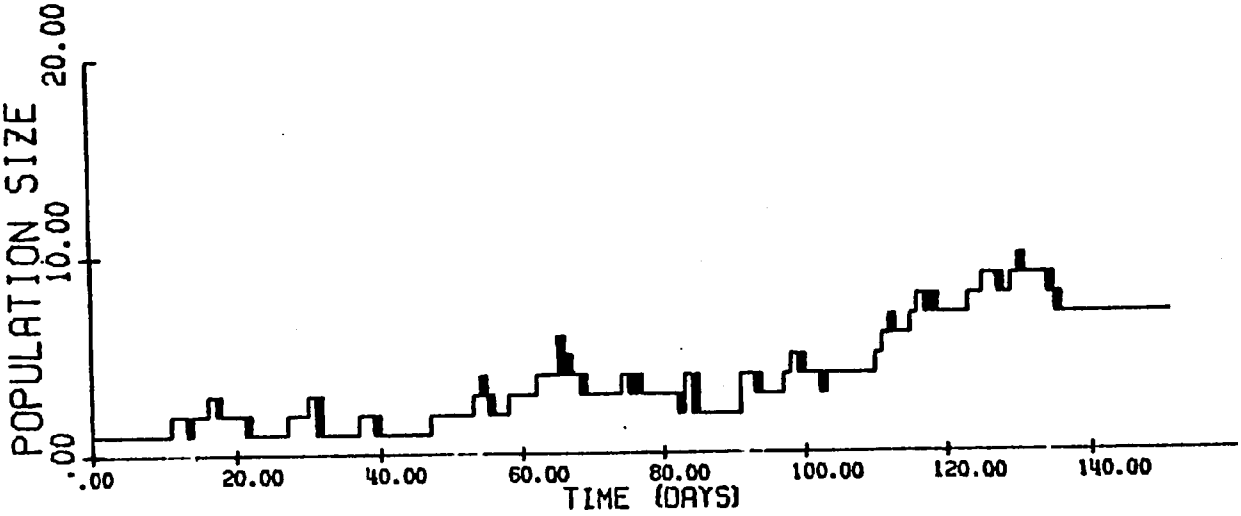
POPULATION 20 80 B3 - GROWTH CURVE

SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 40 20 B1 - GROWTH CURVE

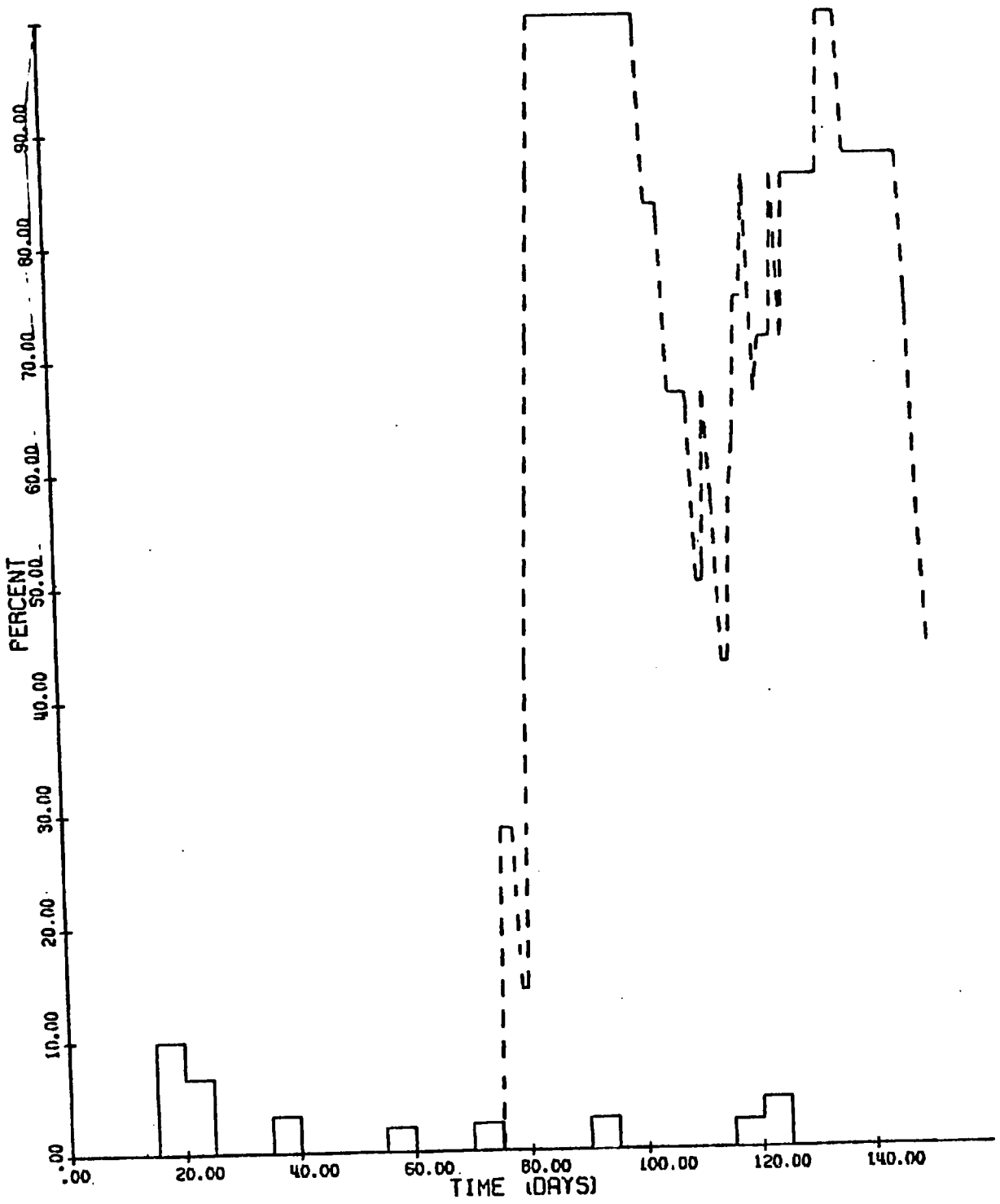
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 20 80 83 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

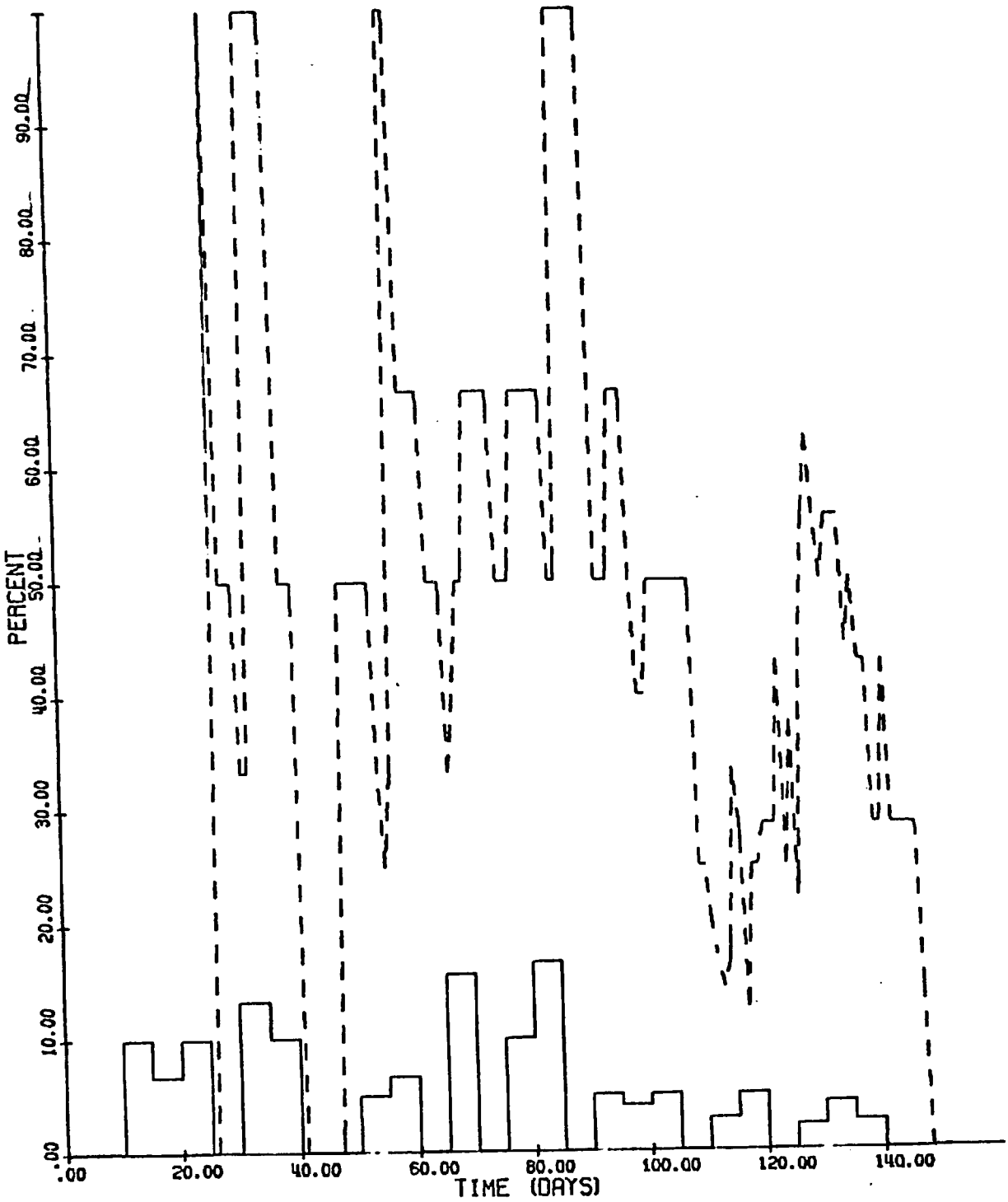
FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 40 20 81 -

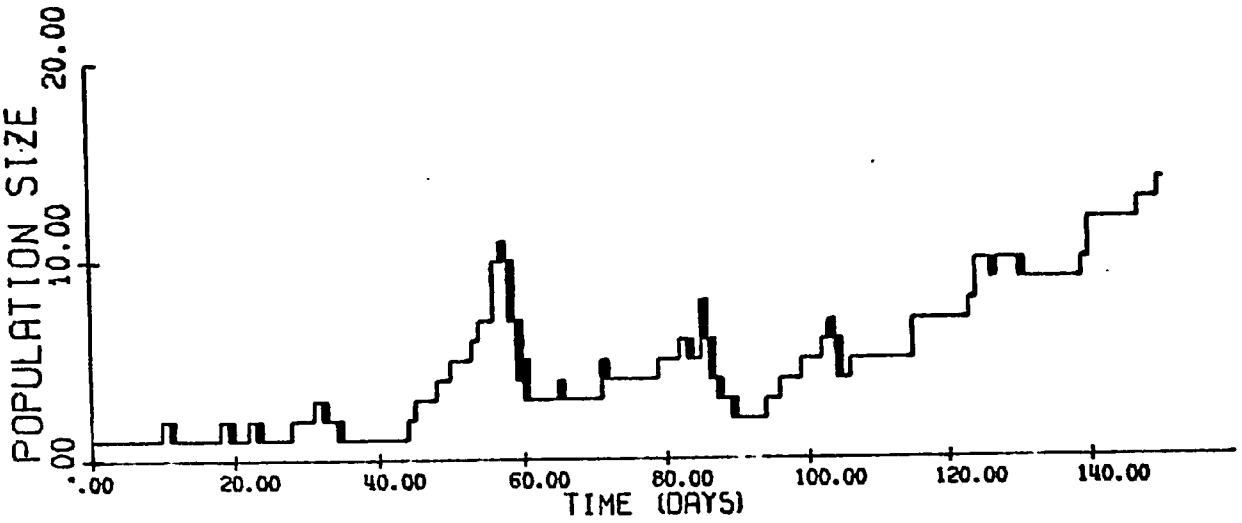
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



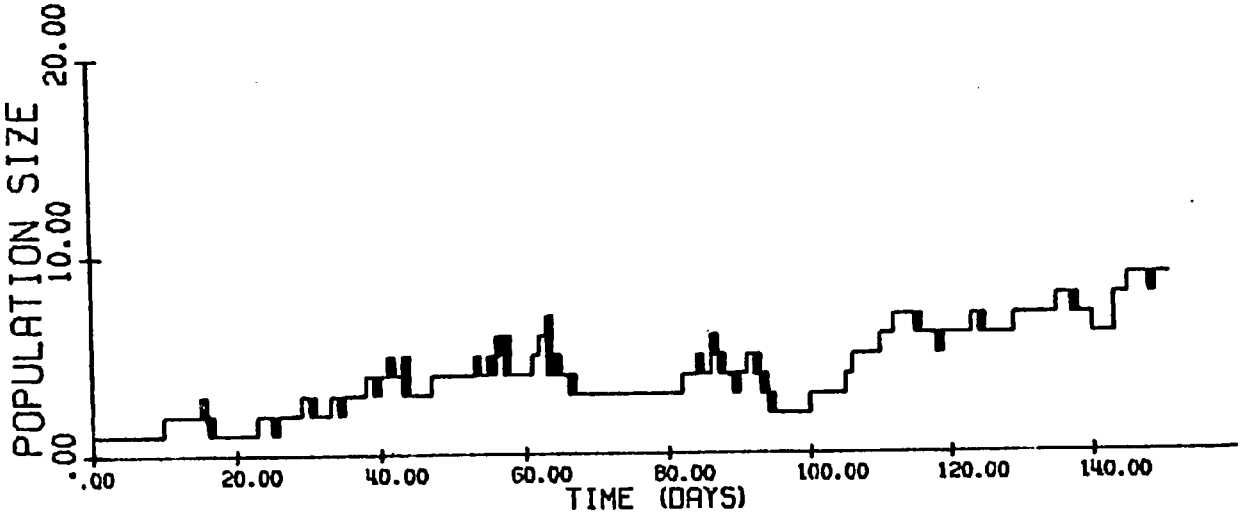
POPULATION 40 20 B2 - GROWTH CURVE

SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 40 20 B3 - GROWTH CURVE

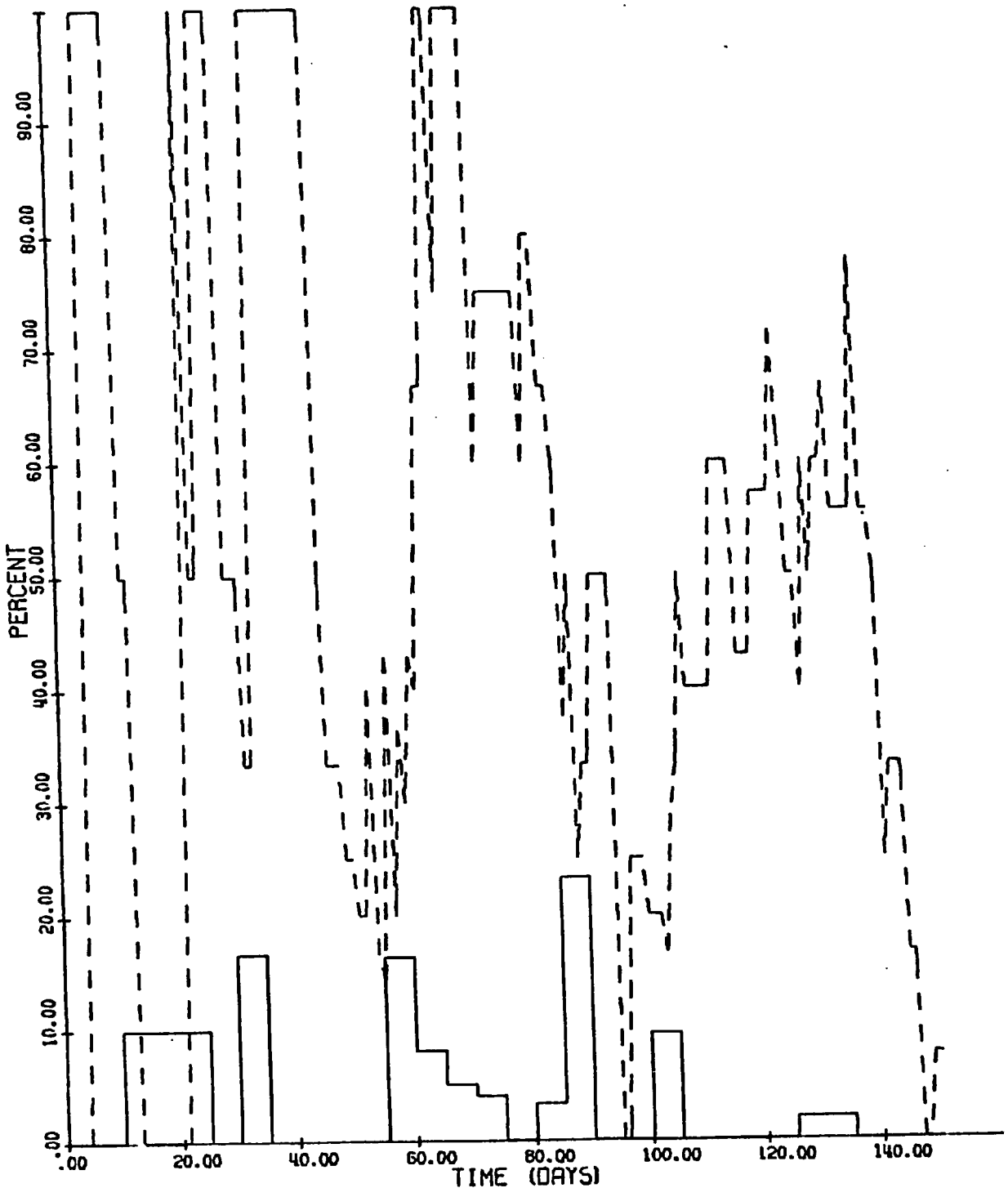
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 40 20 82 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

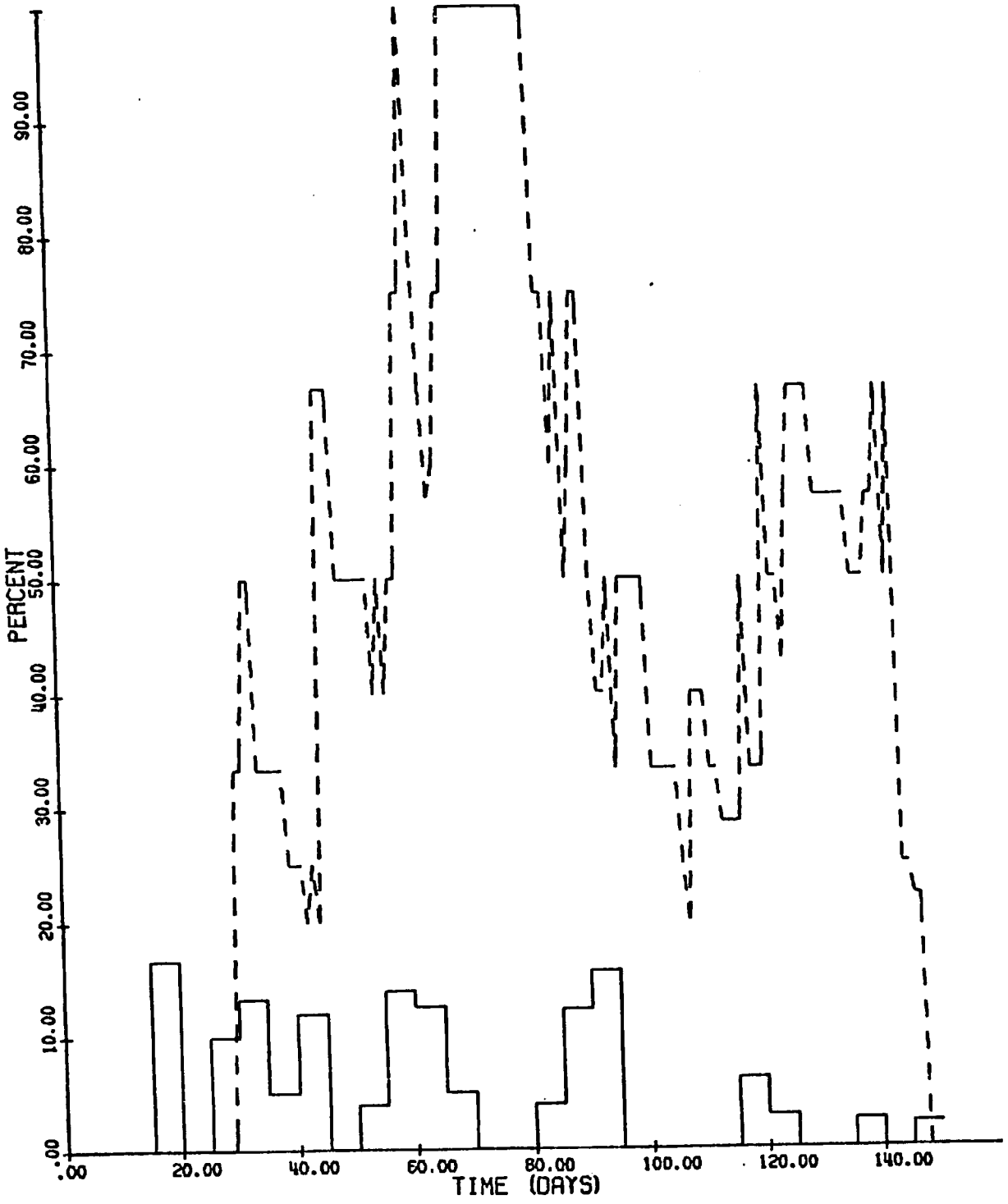
FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 40 20 83 -

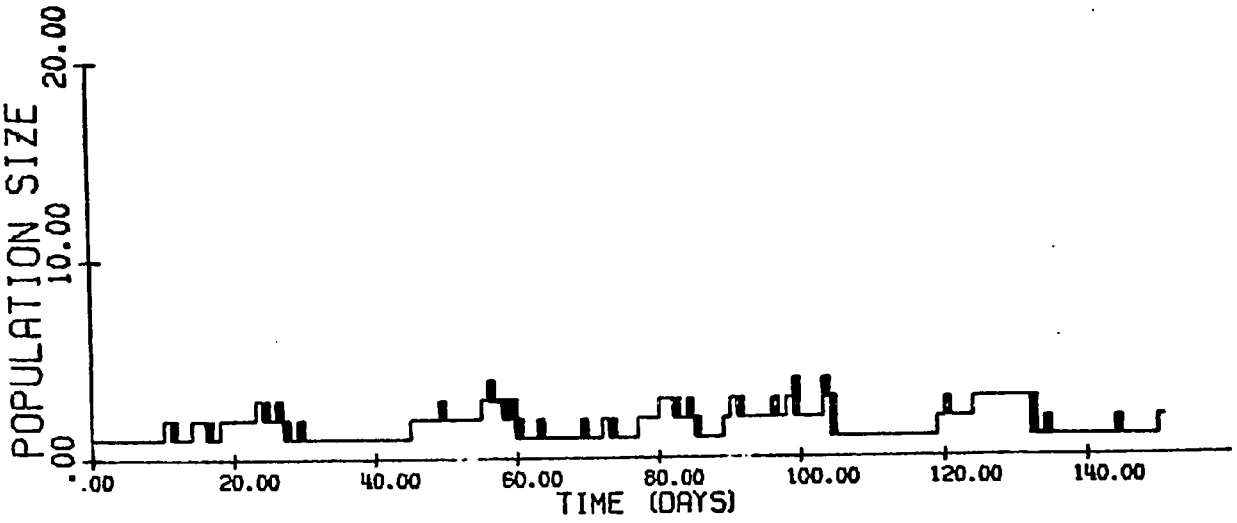
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



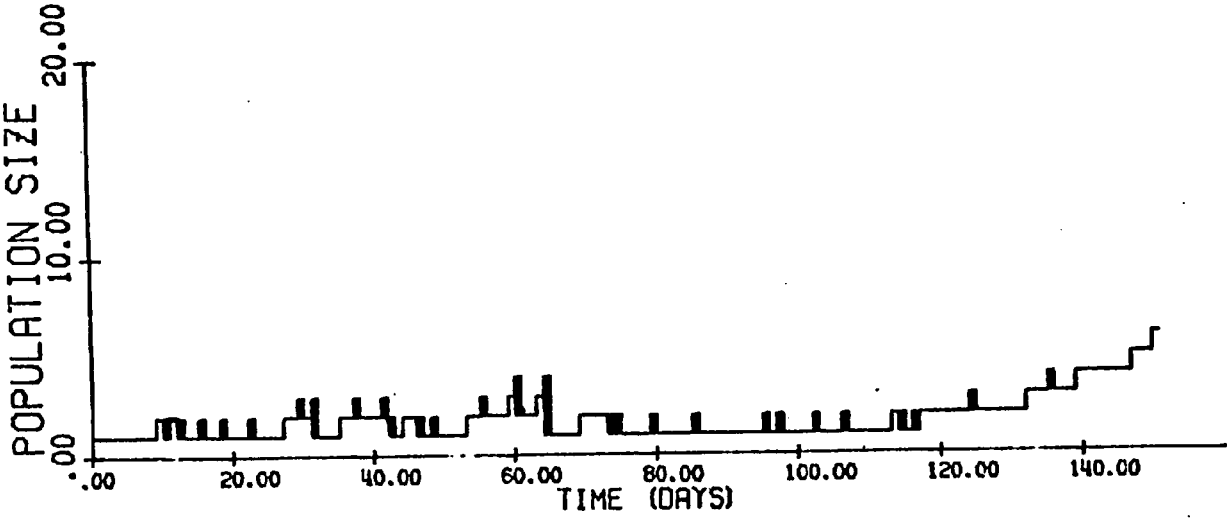
POPULATION 40 40 B1 - GROWTH CURVE

SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 40 40 B2 - GROWTH CURVE

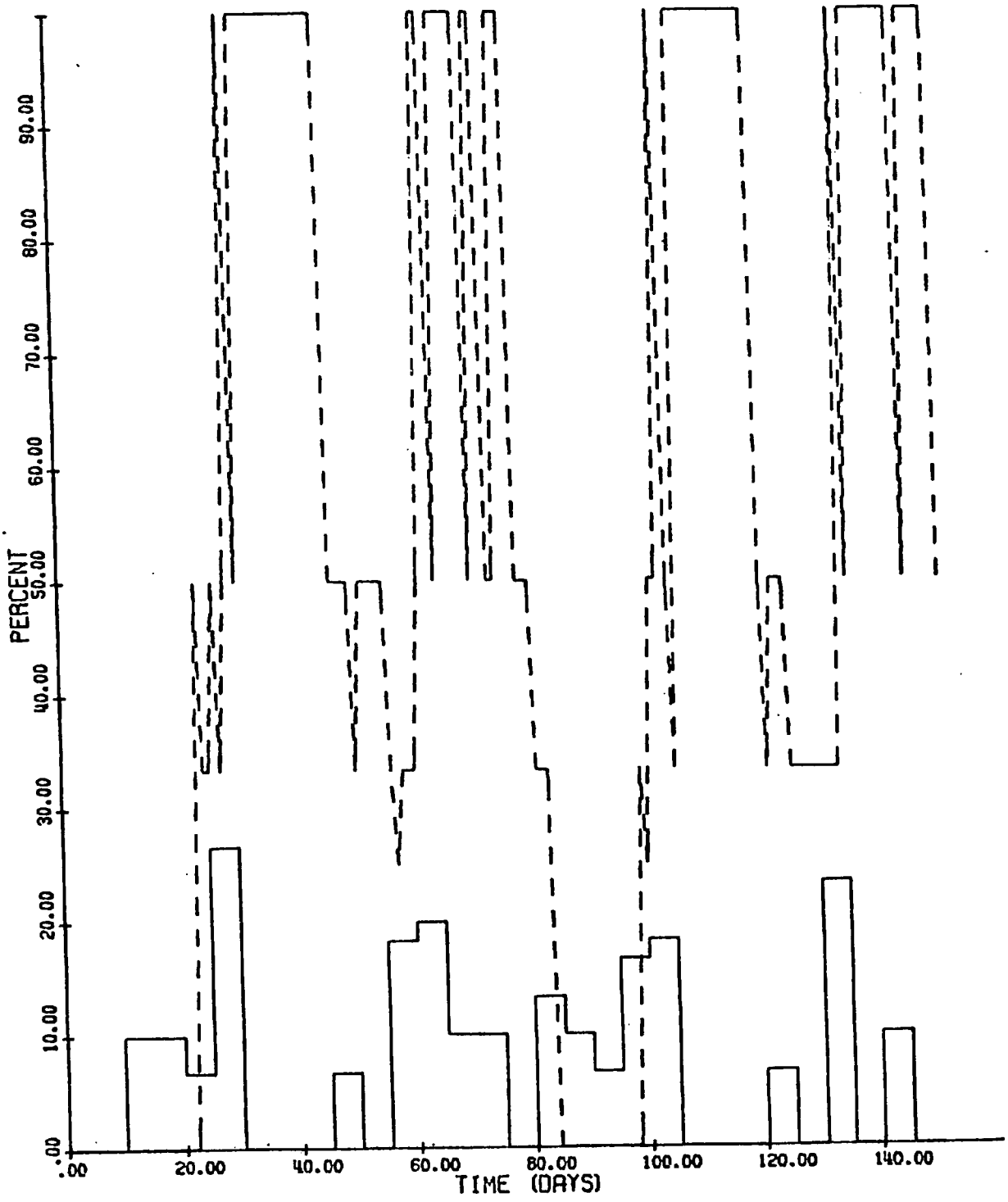
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 40 40 B1

PERCENT SEXUAL HYDRA (DASHED LINE) AND

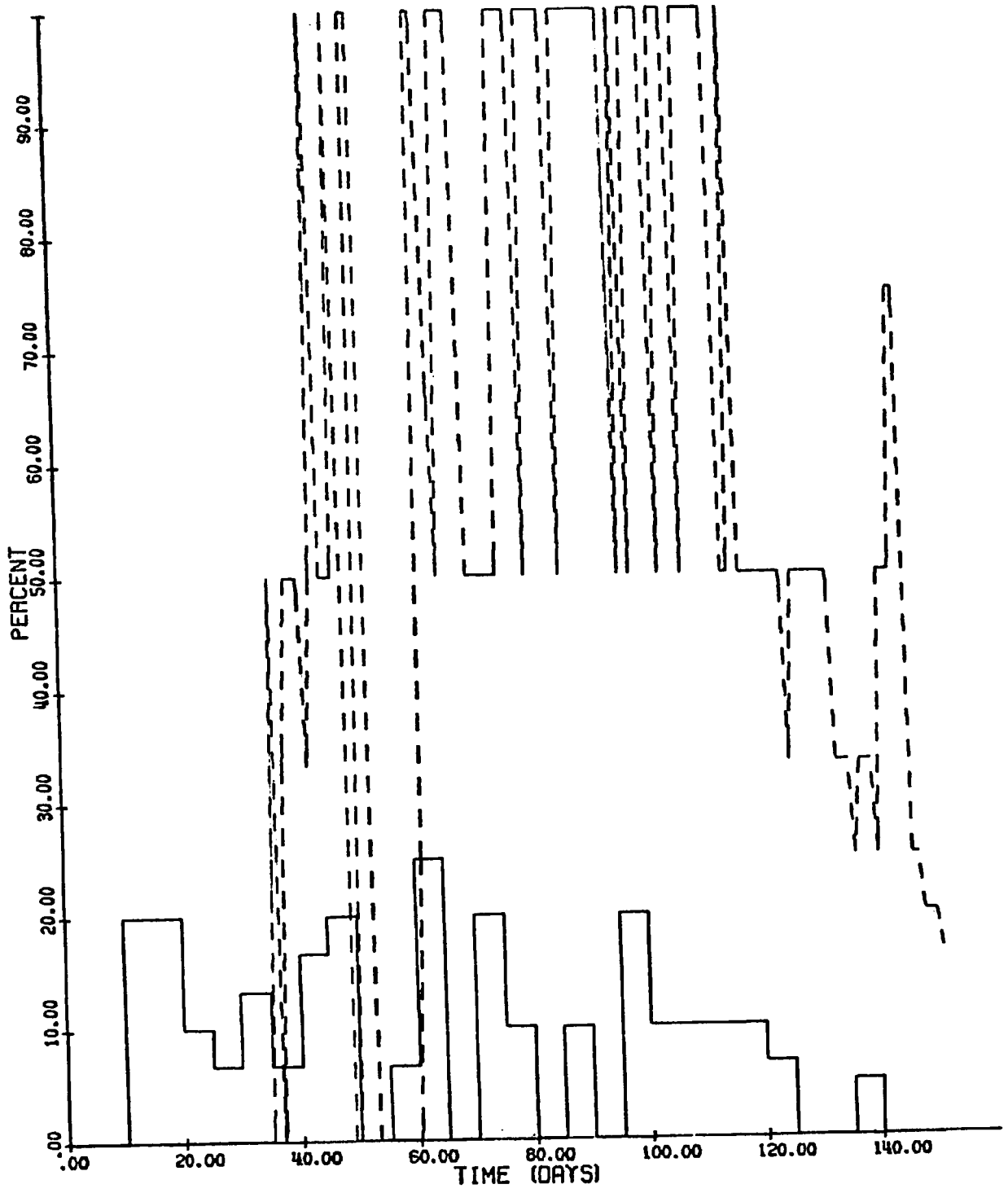
FLOATING HYDRA (SOLID LINE, AVERAGES OF 5-DAY PERIODS)



POPULATION 40 40 B2 -

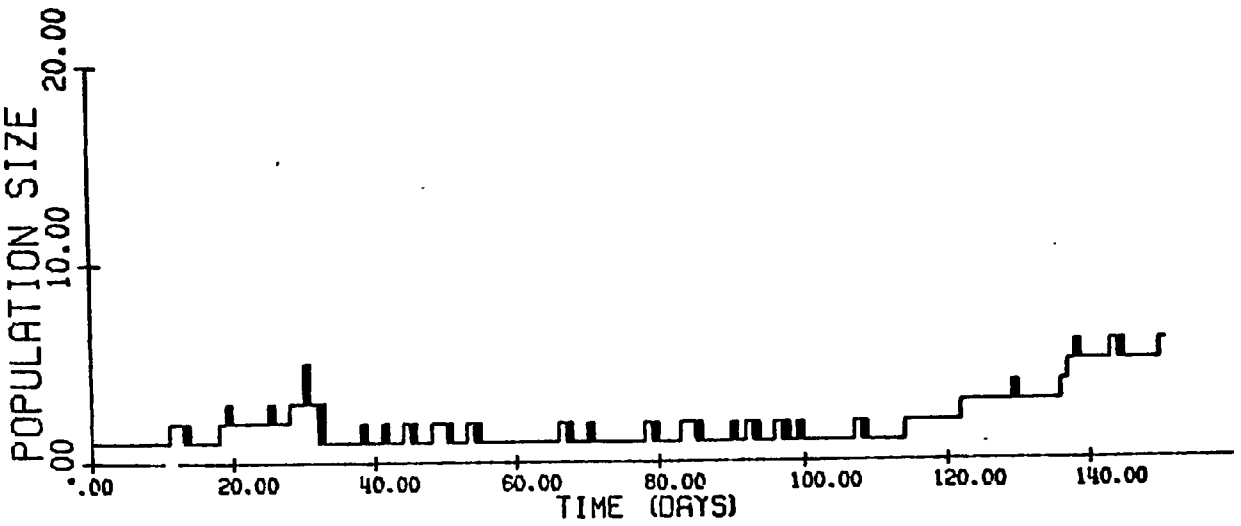
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



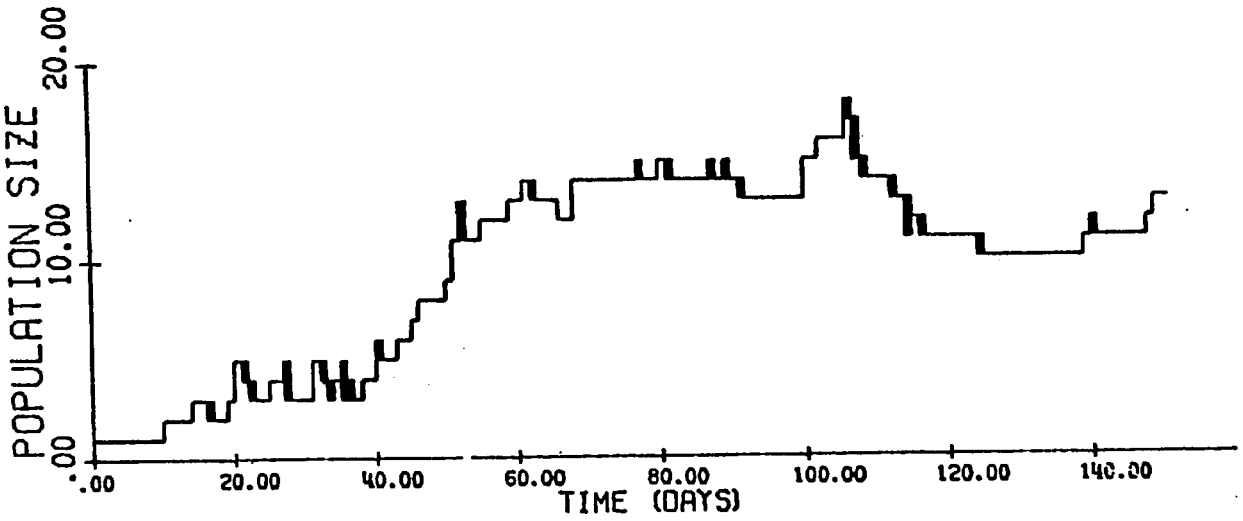
POPULATION 40 40 B3 - GROWTH CURVE

SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 40 80 B1 - GROWTH CURVE

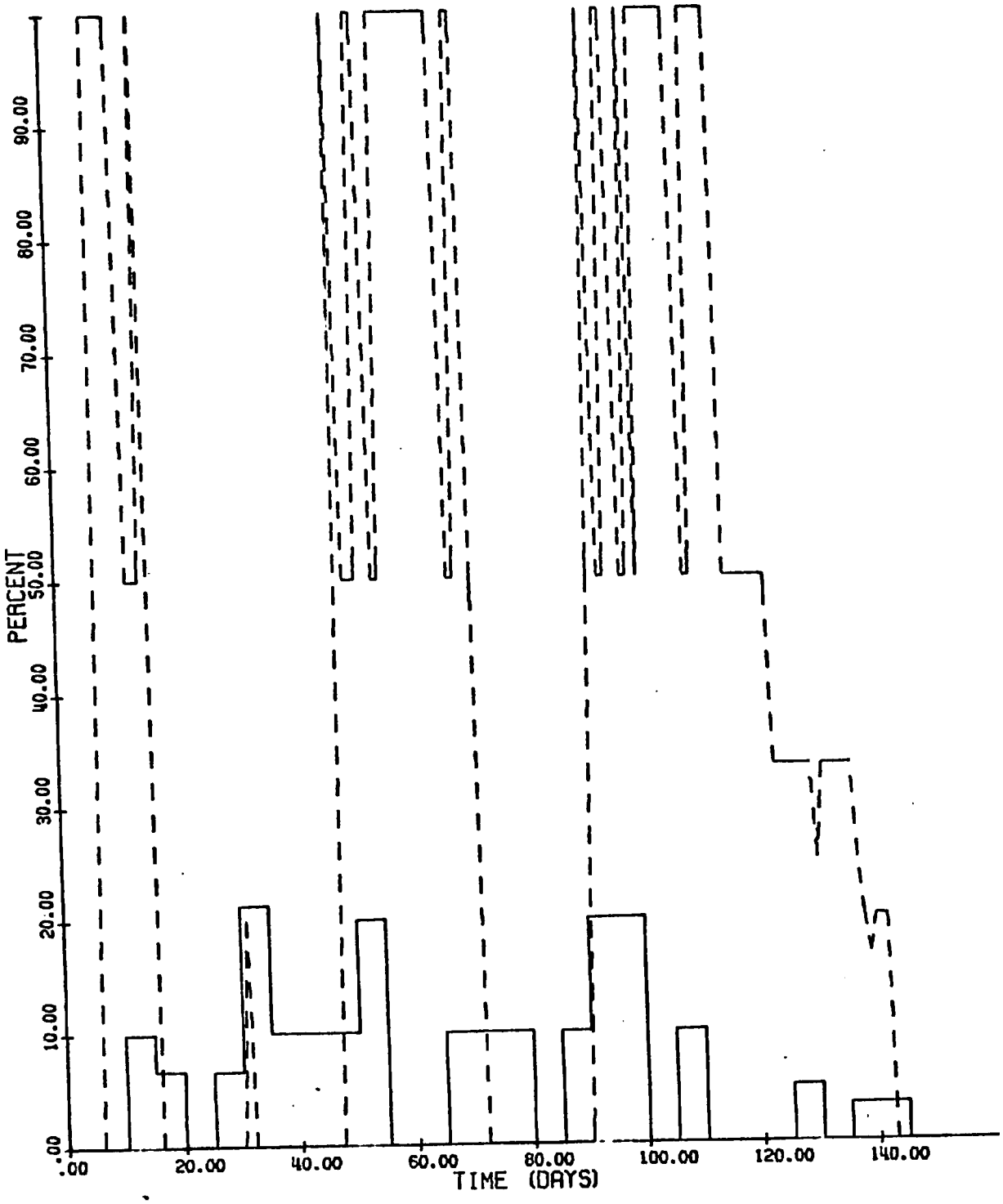
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 40 40_B3 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

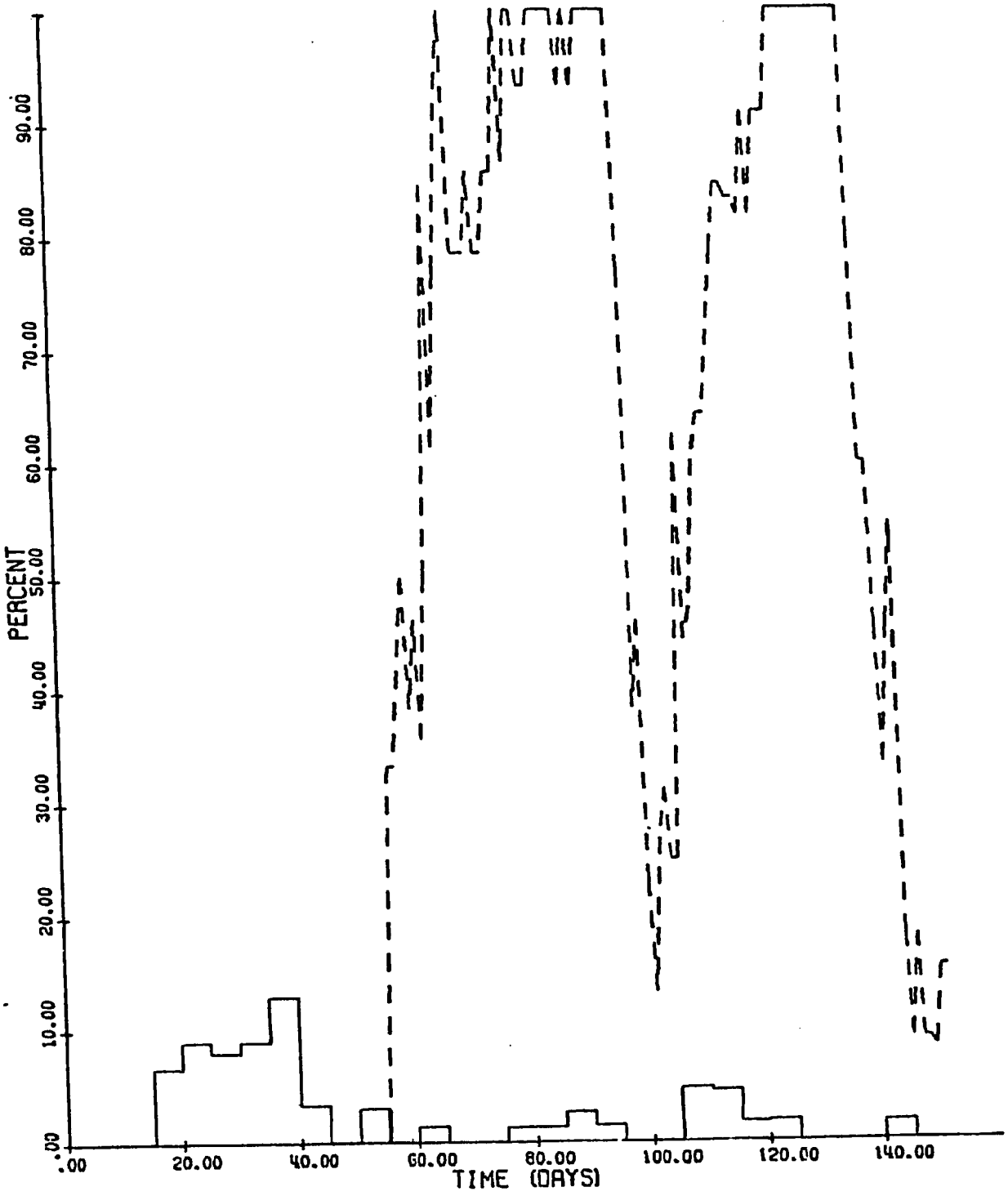
FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 40 80 81 -

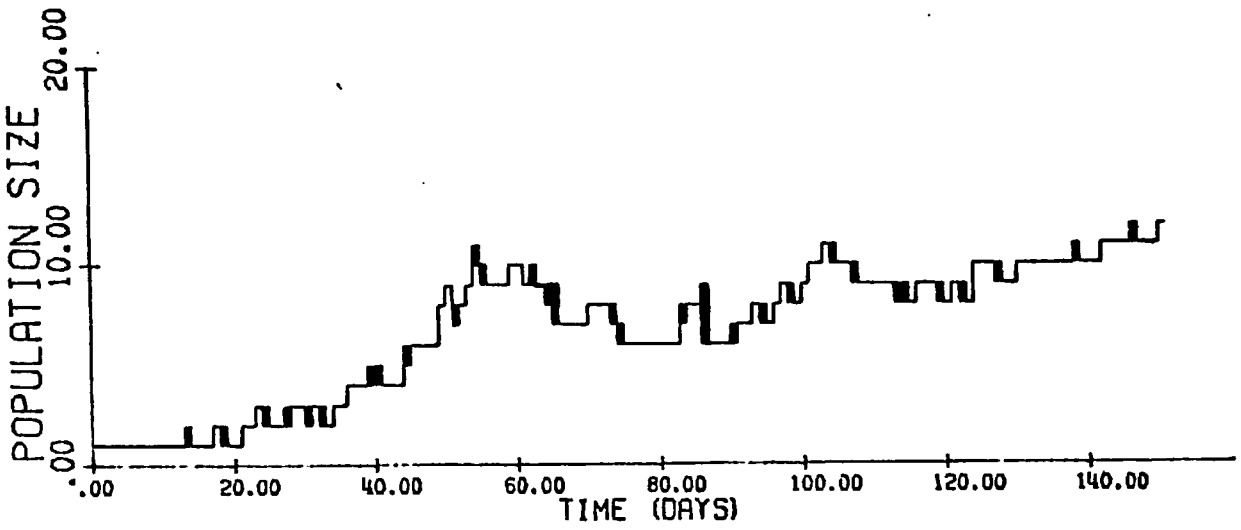
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



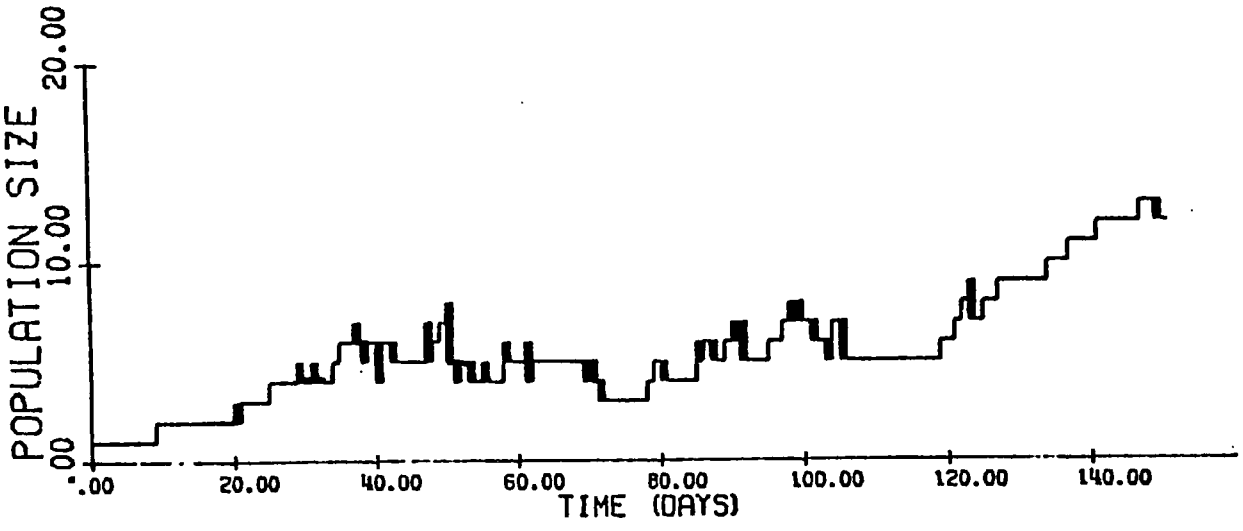
POPULATION 40 80 B2 - GROWTH CURVE

SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 40 80 B3 - GROWTH CURVE

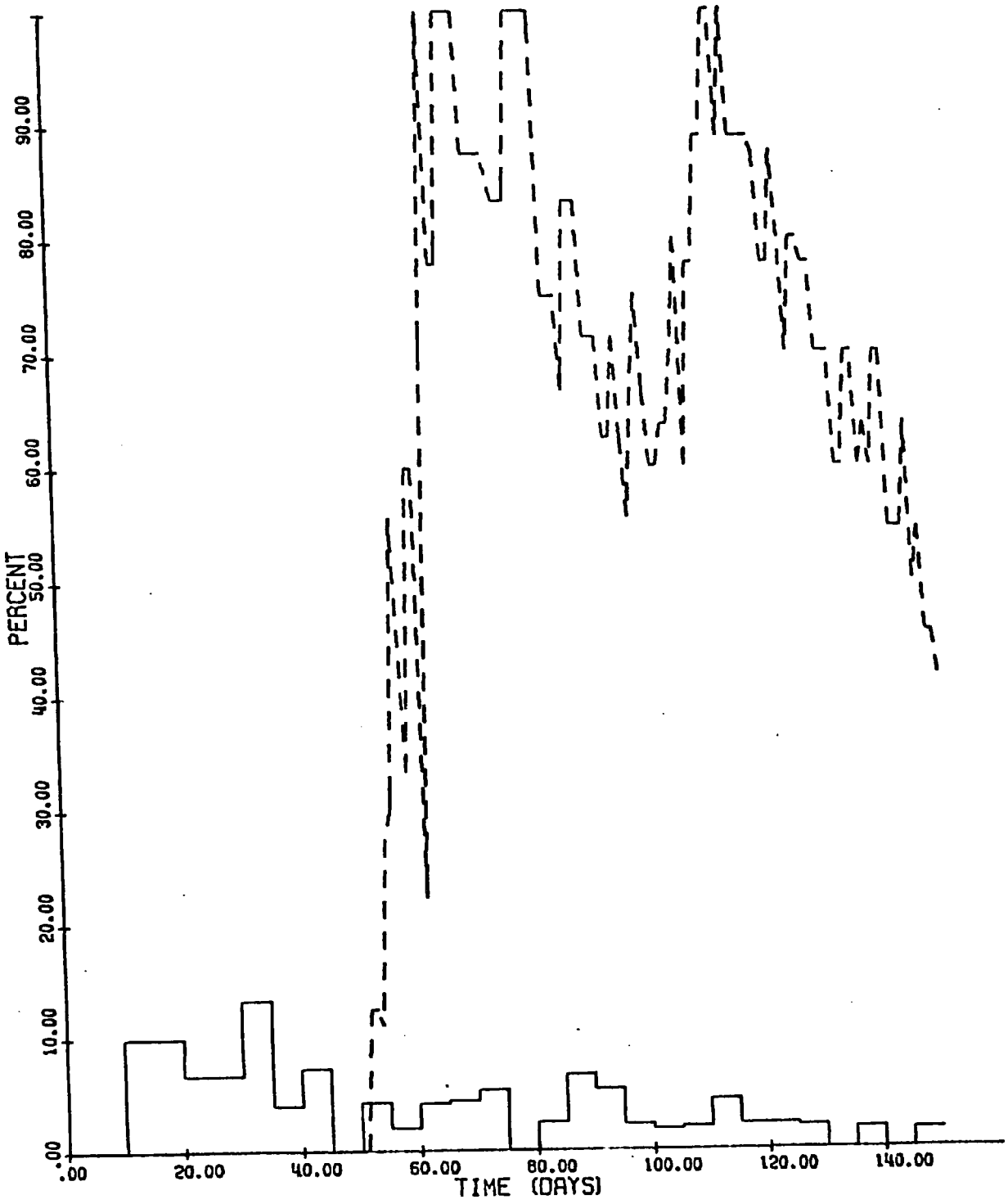
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 40 80 82 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

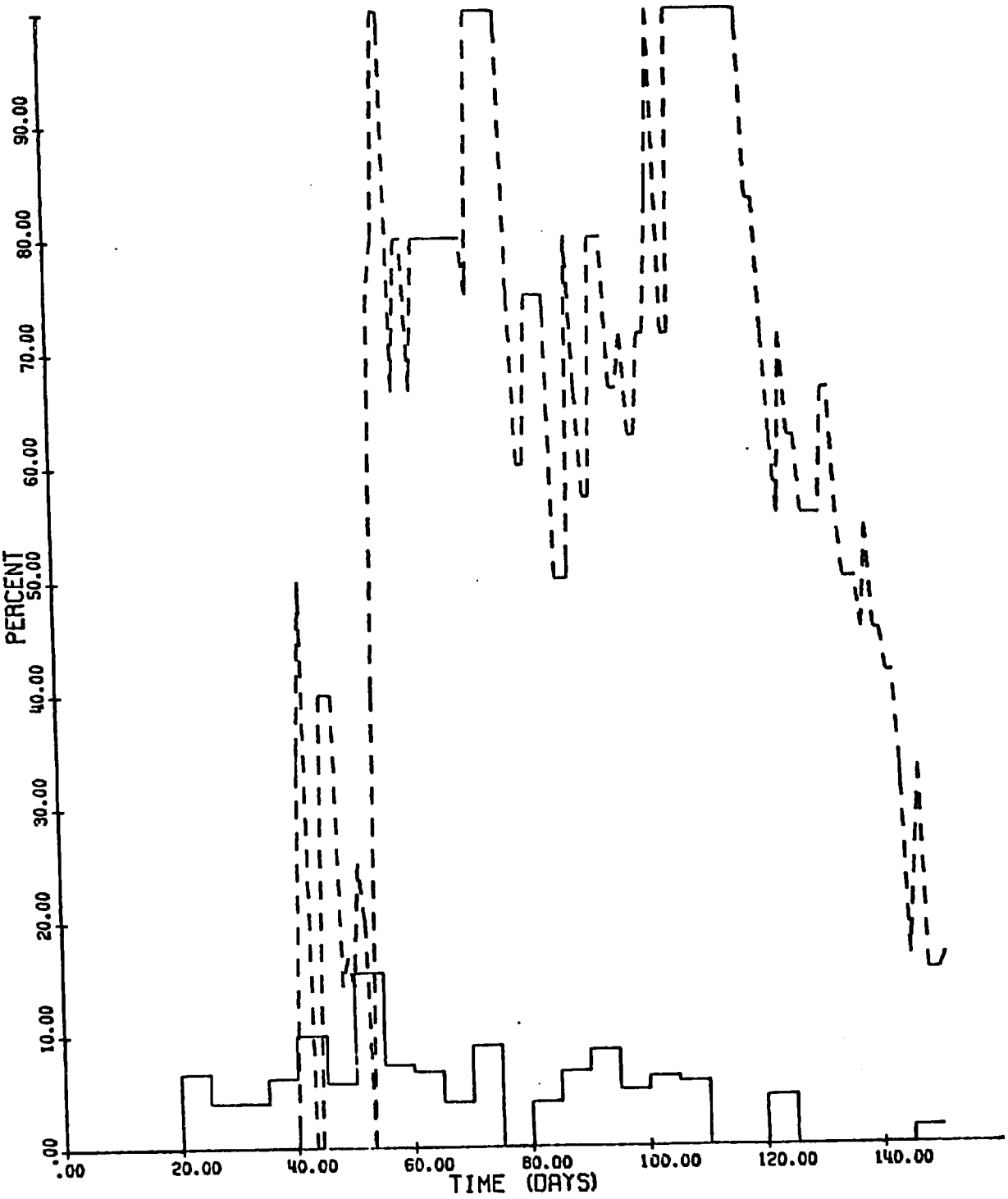
FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 40 80 83 -

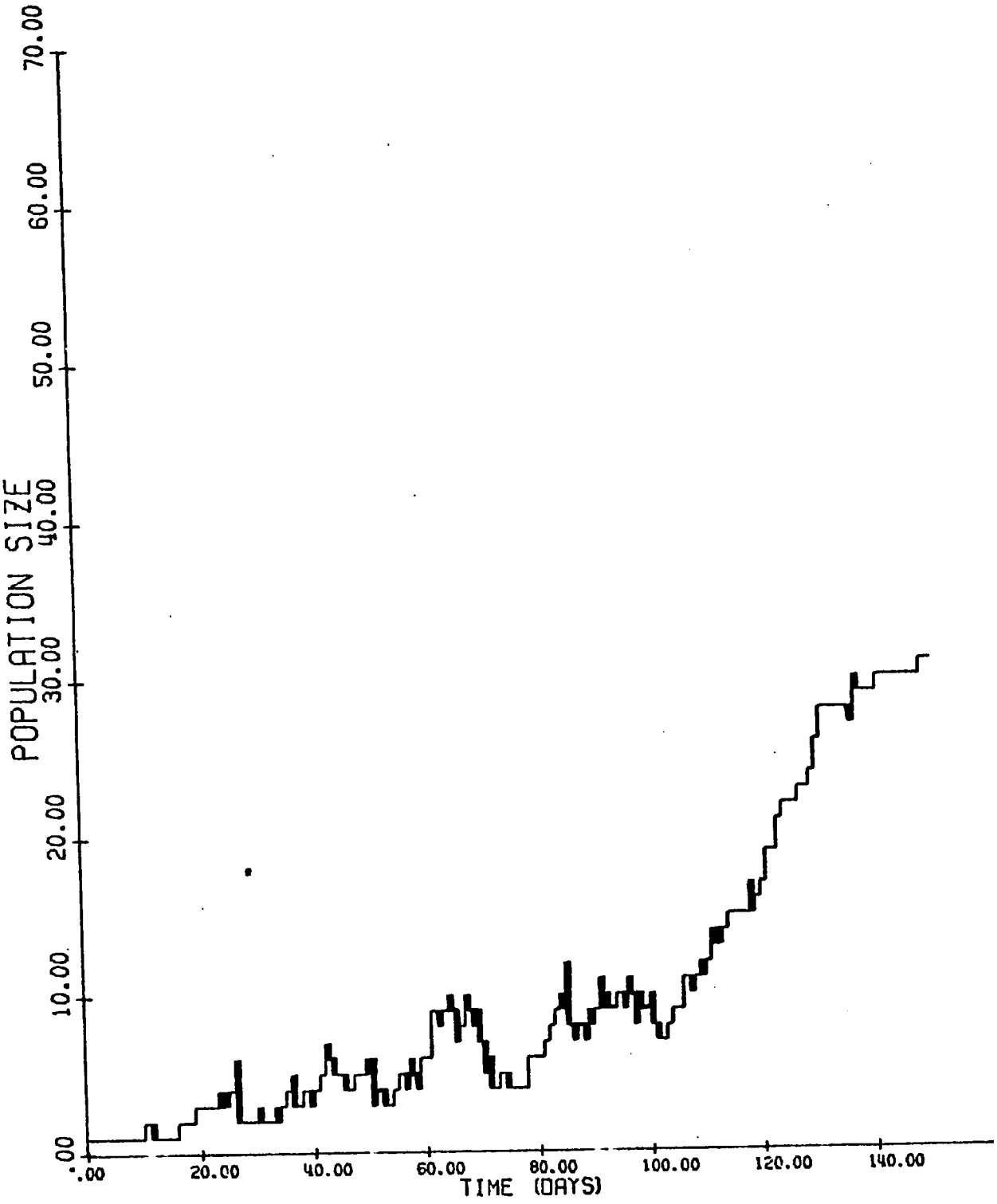
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 80 20 81 - GROWTH CURVE

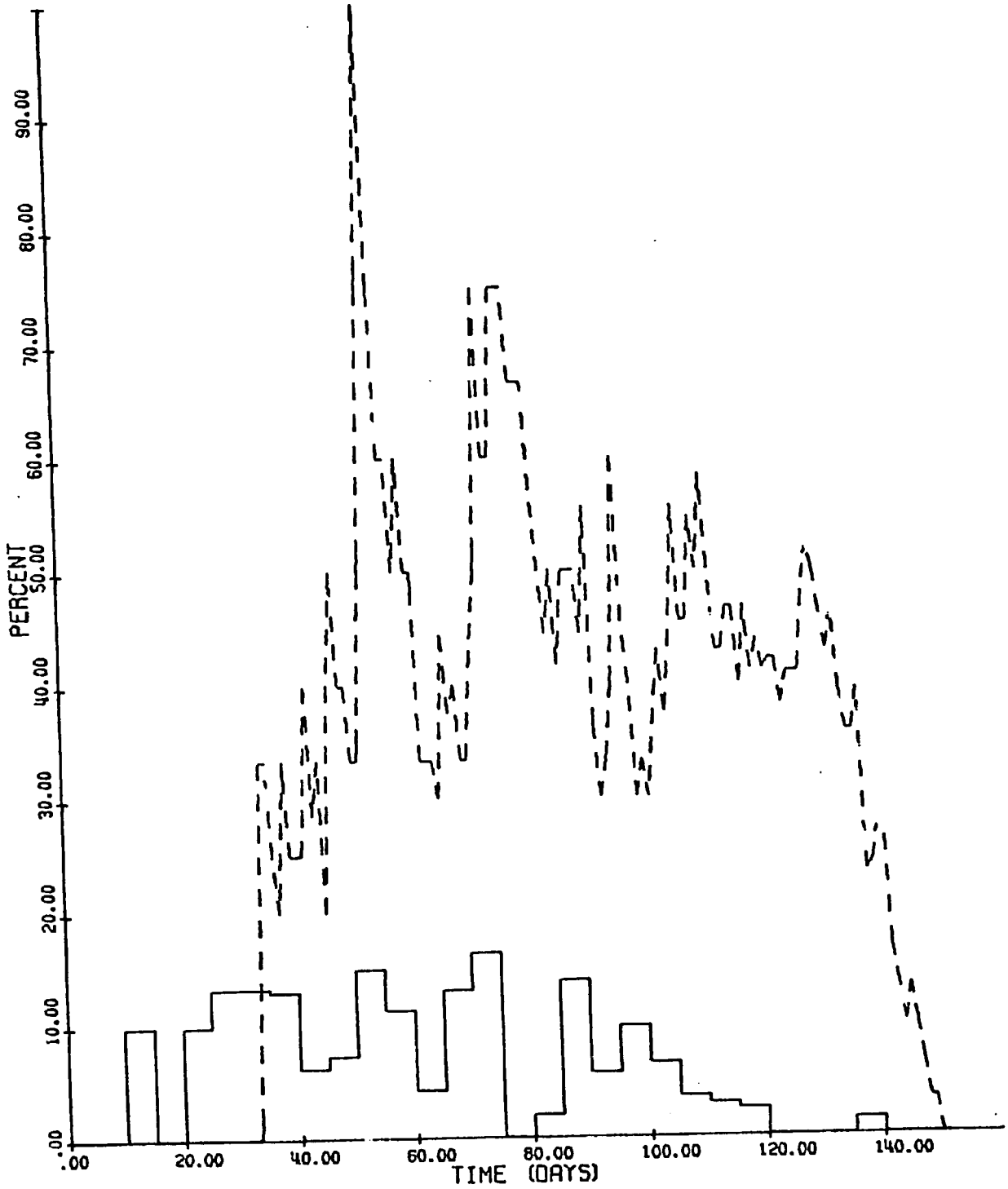
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 80 20 81 -

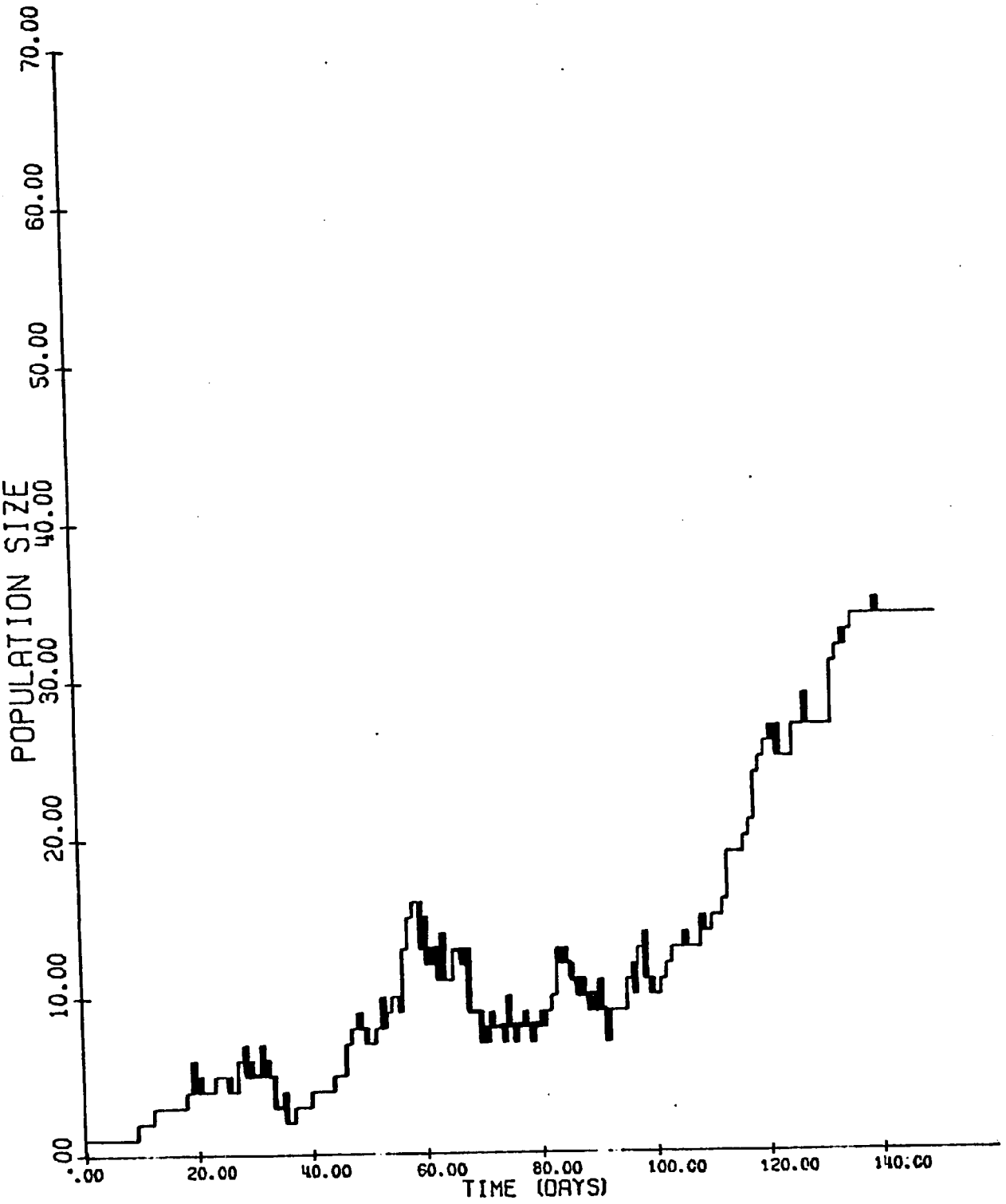
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE: AVERAGES OF 5-DAY PERIODS)



POPULATION 80 20 82 - GROWTH CURVE

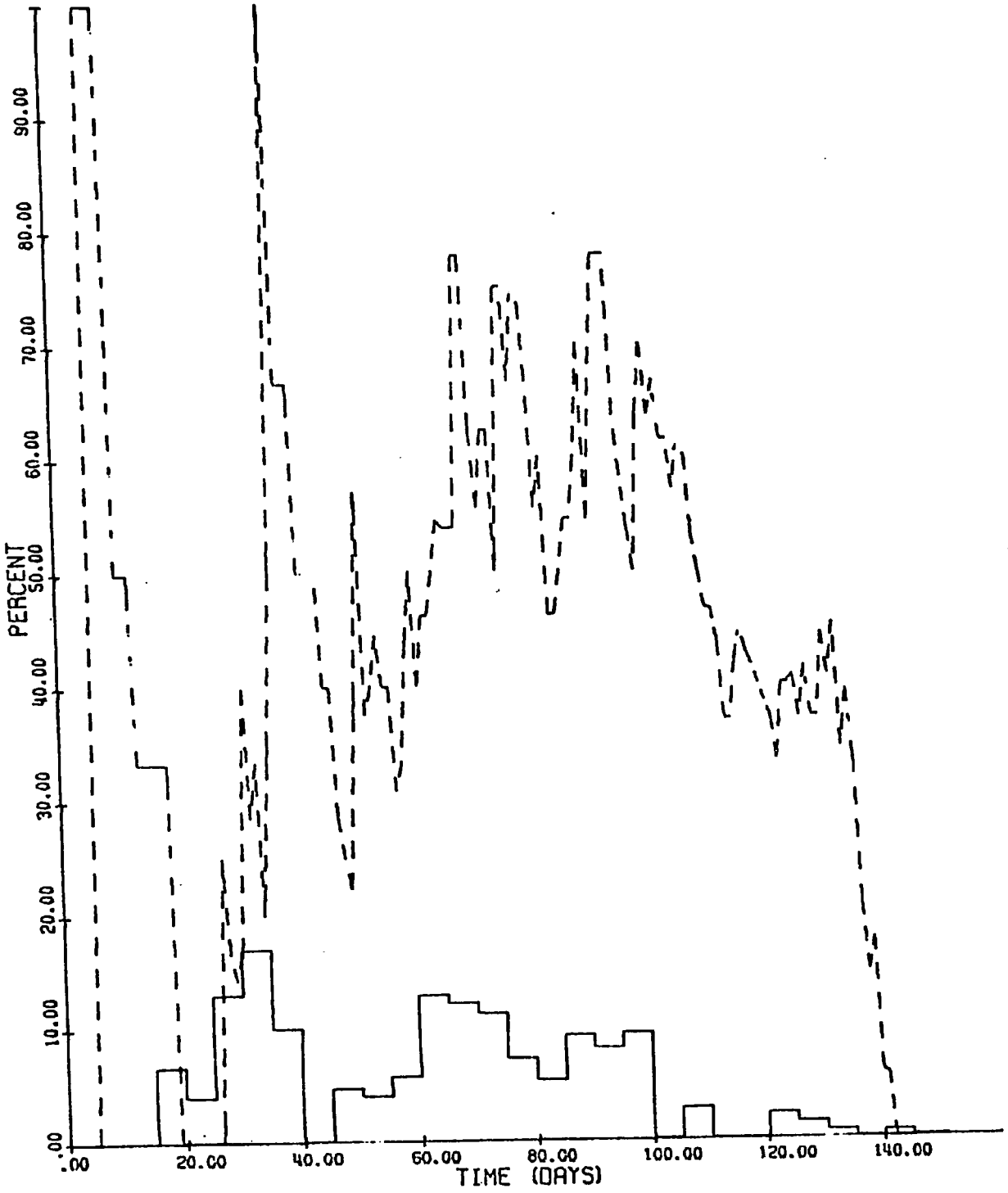
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 80 20 82 -

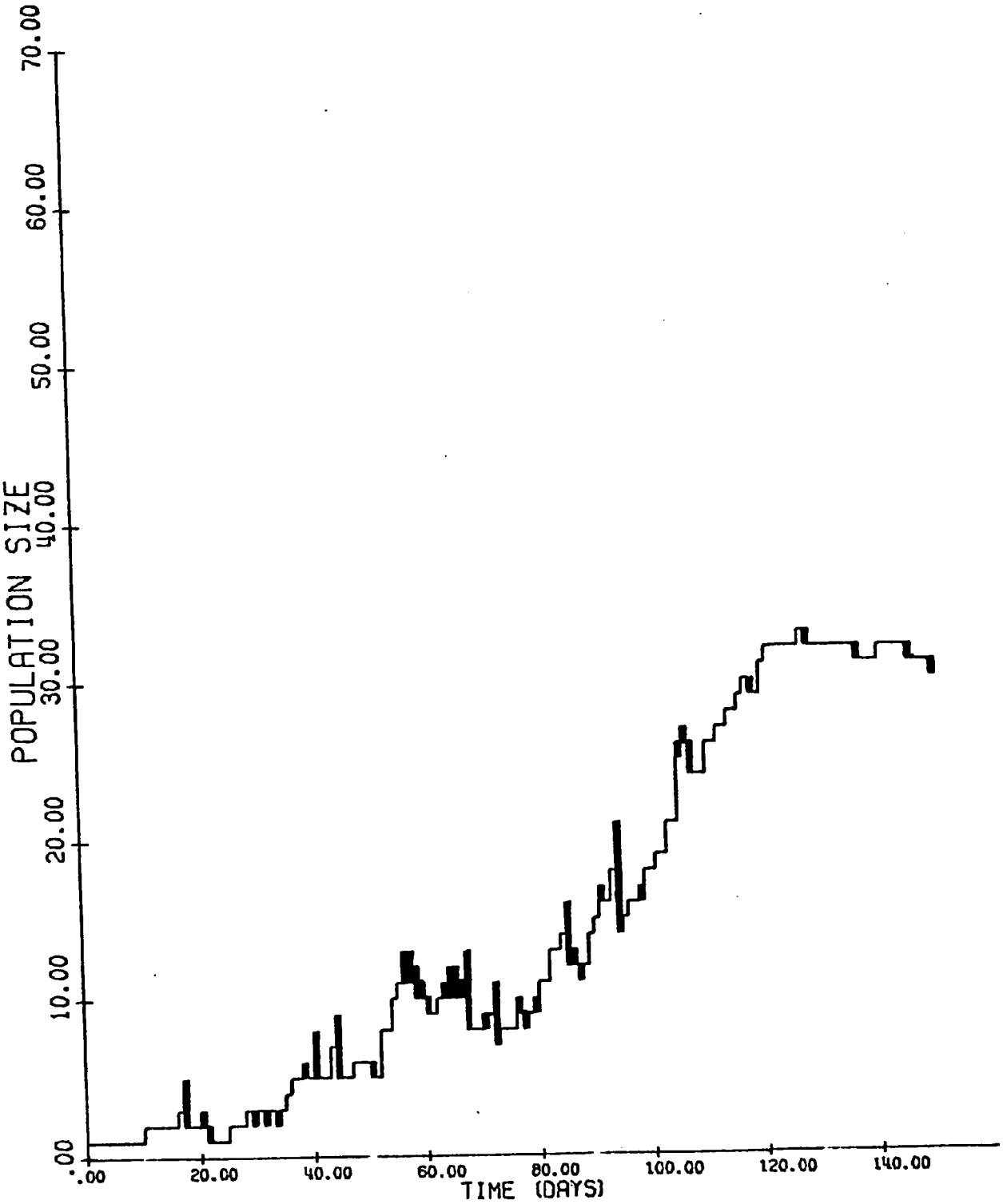
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 80 20 83 - GROWTH CURVE

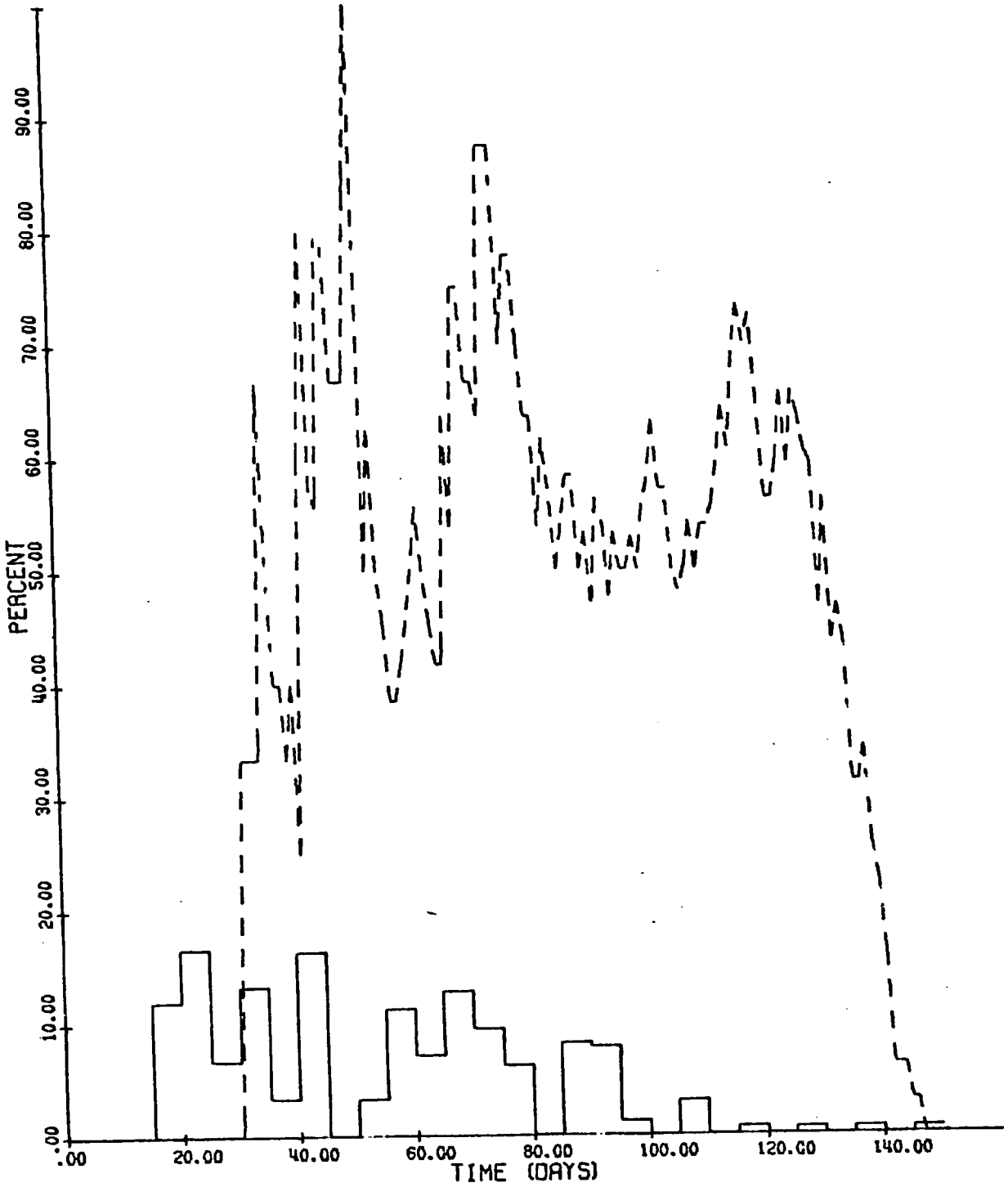
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 80 20 B3 -

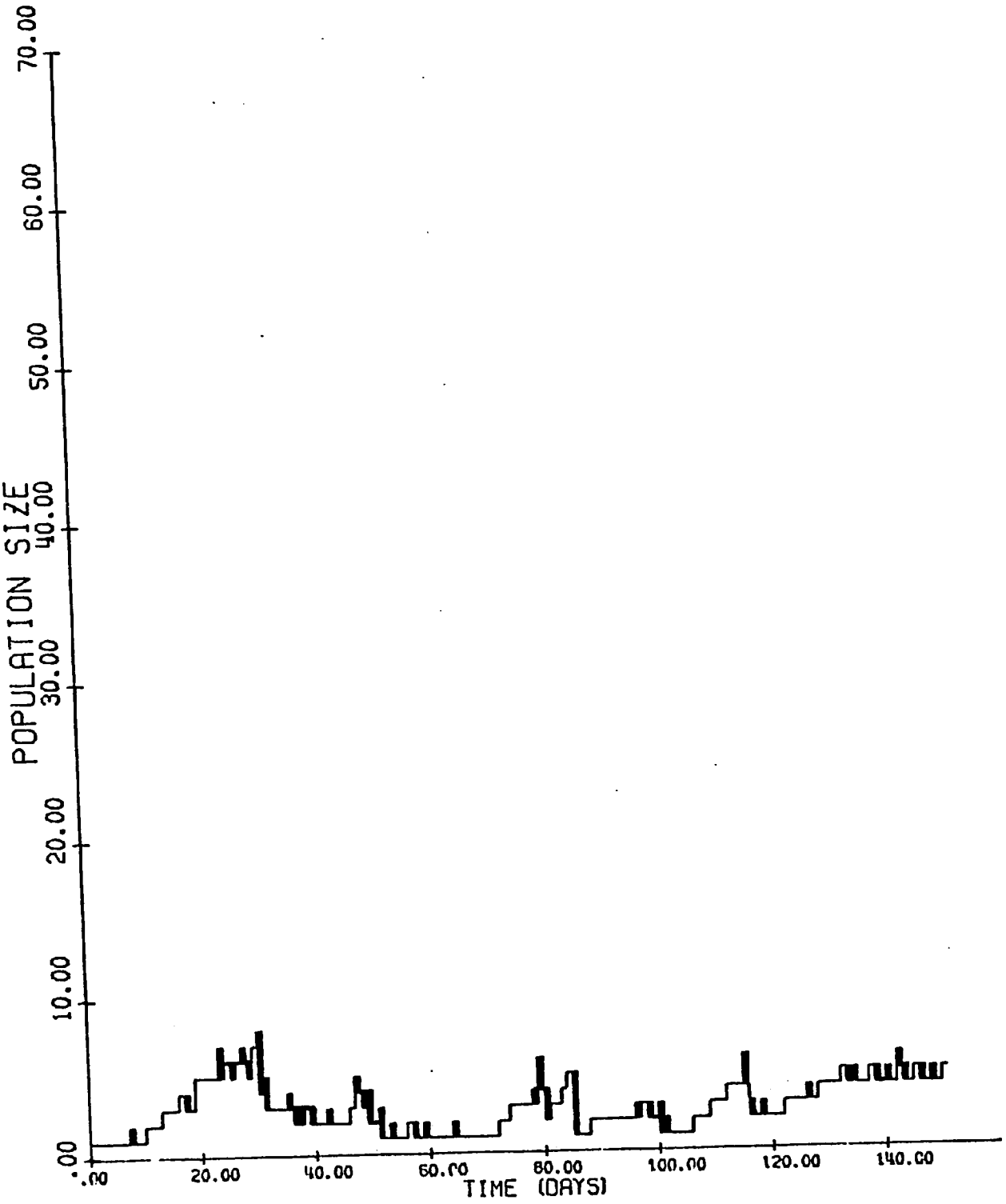
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 80 40 81 - GROWTH CURVE

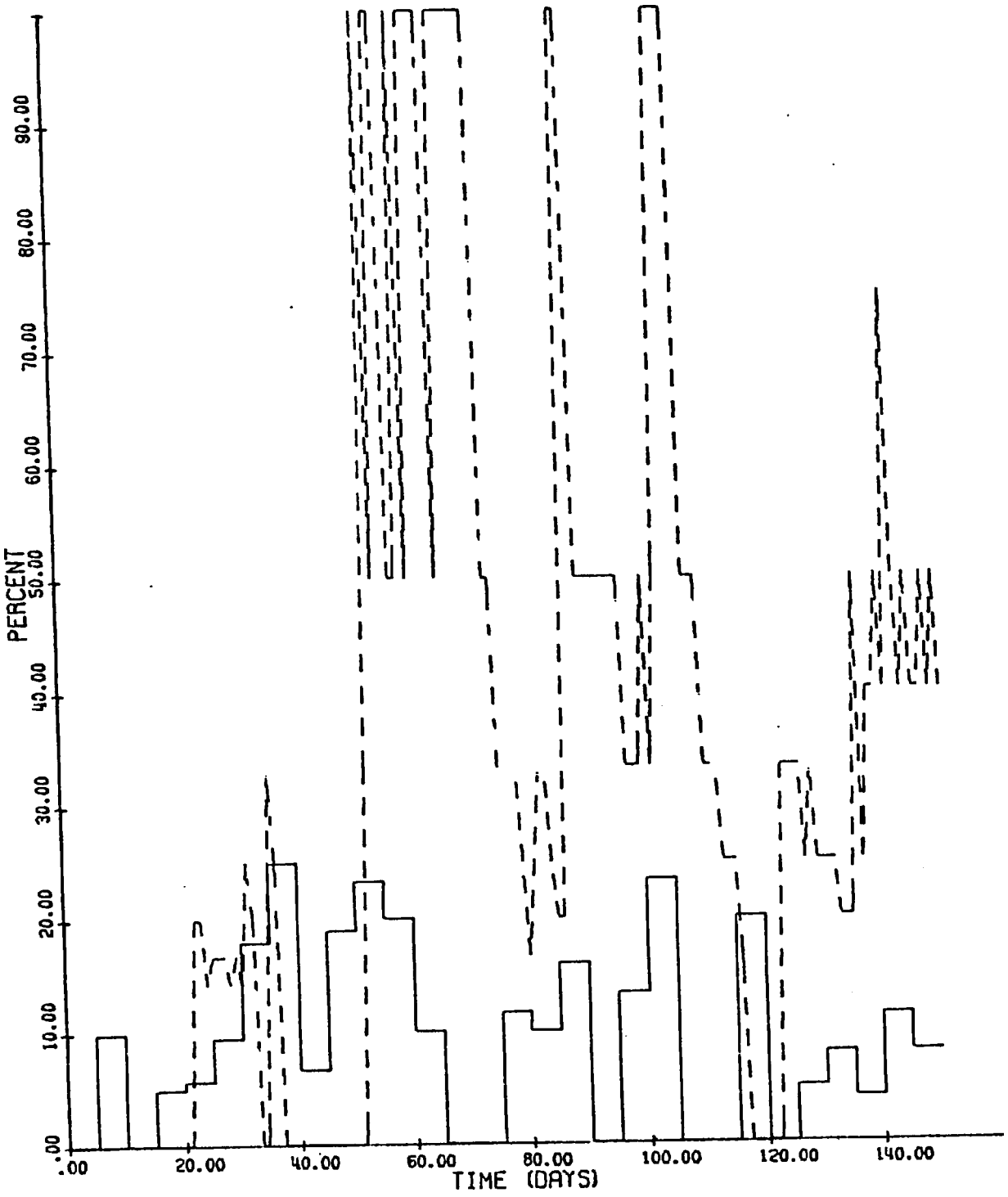
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 80 40 81 -

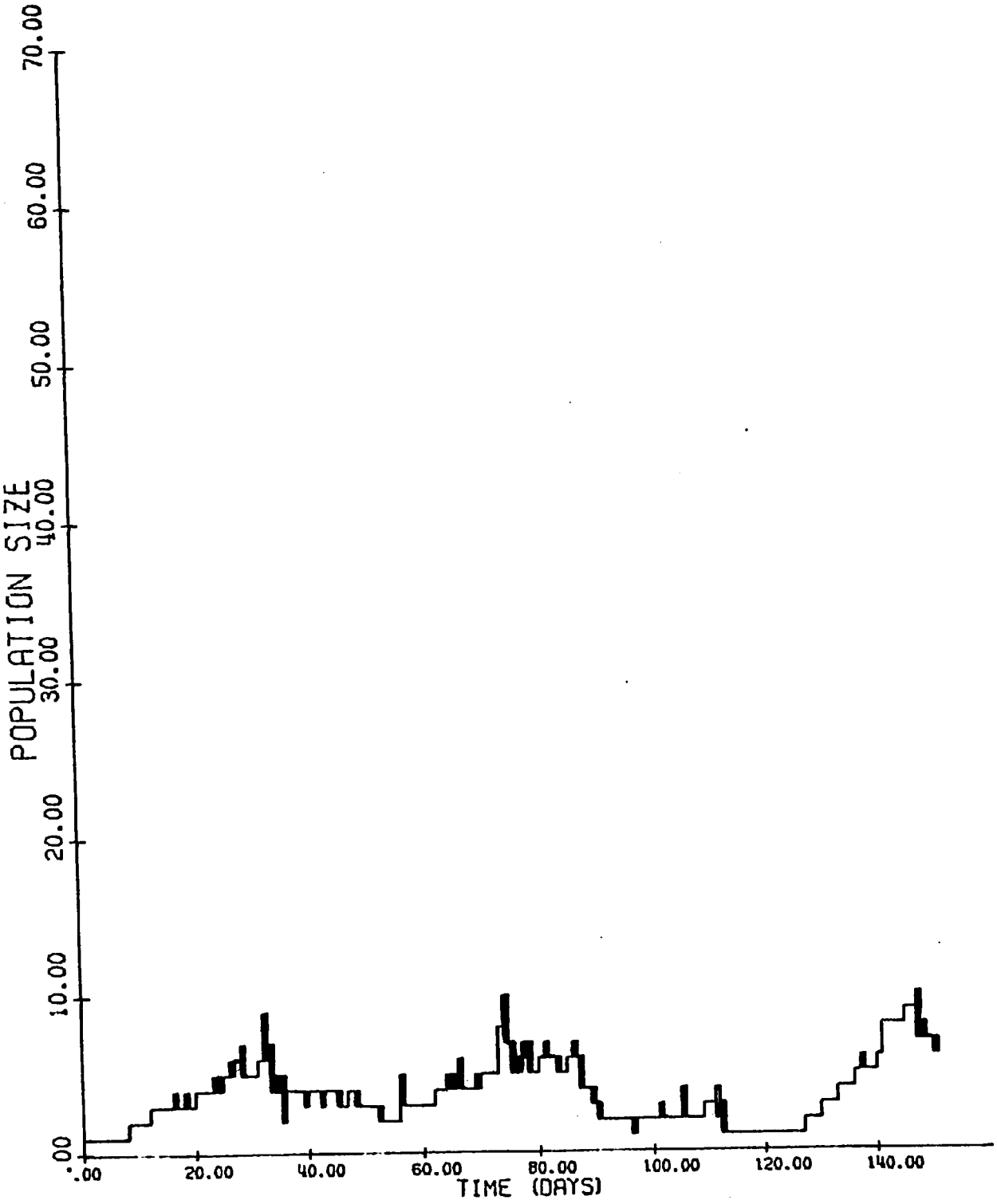
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 80 40 82 - GROWTH CURVE

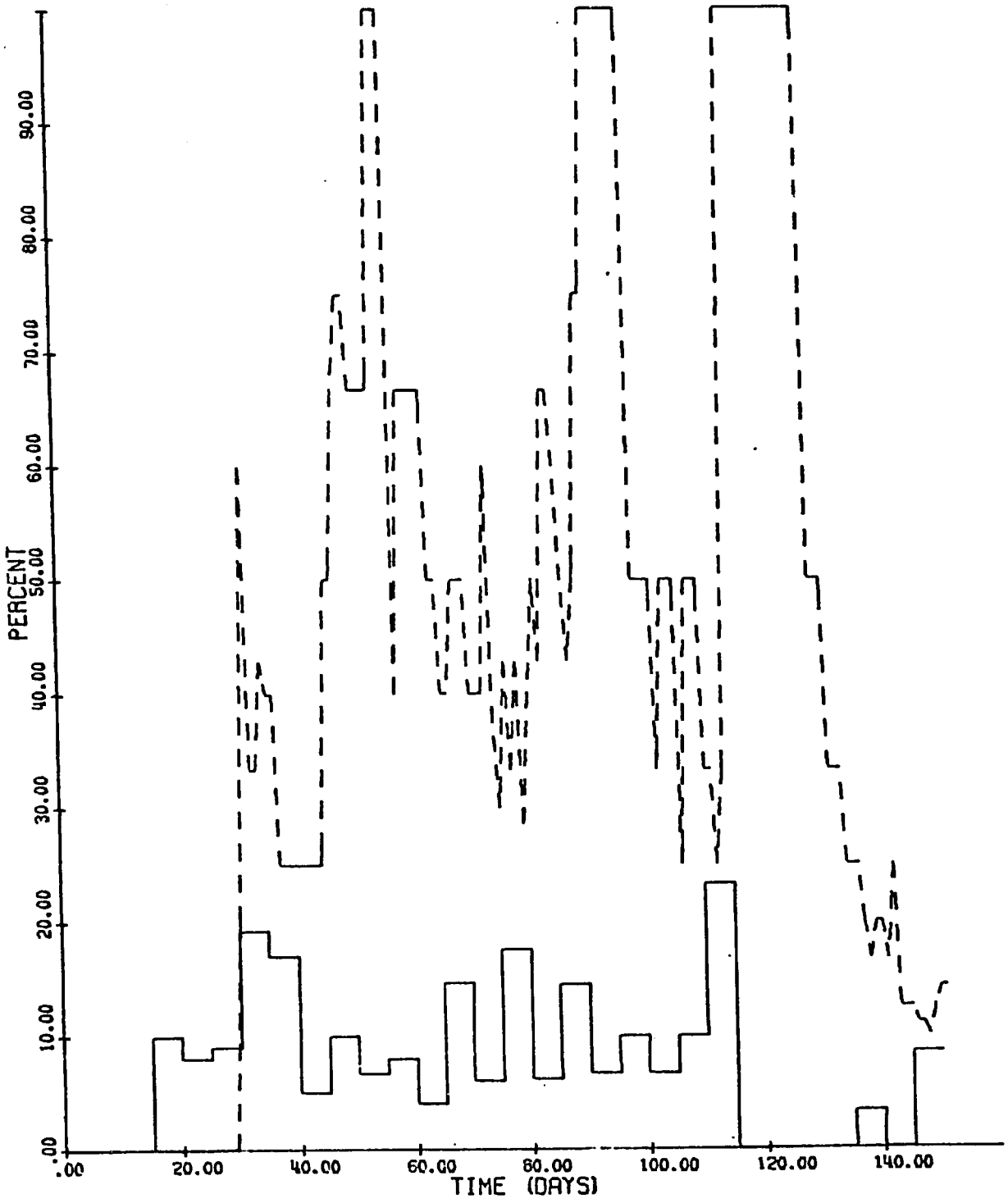
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 80 40 82 -

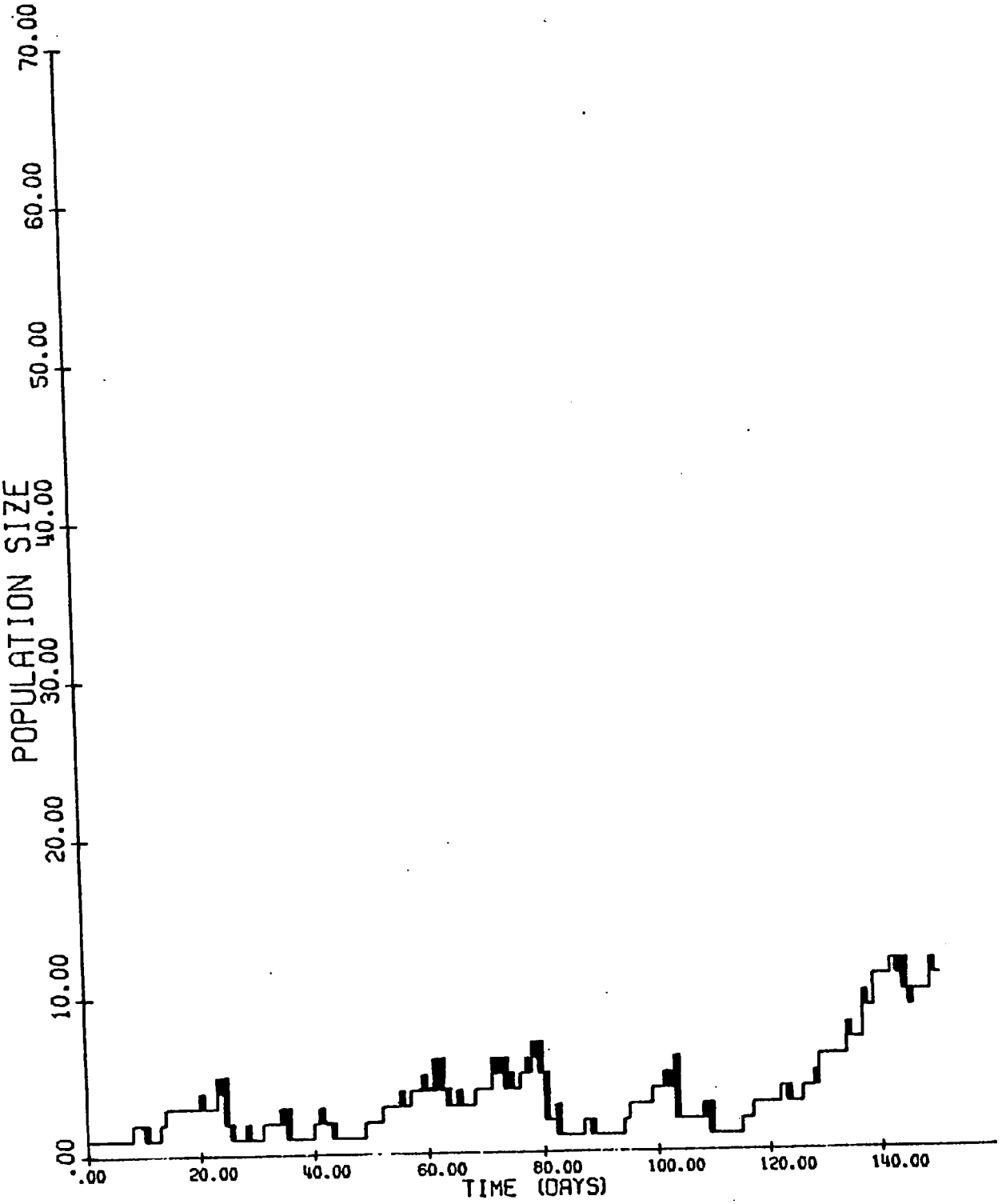
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 80 40 83 - GROWTH CURVE

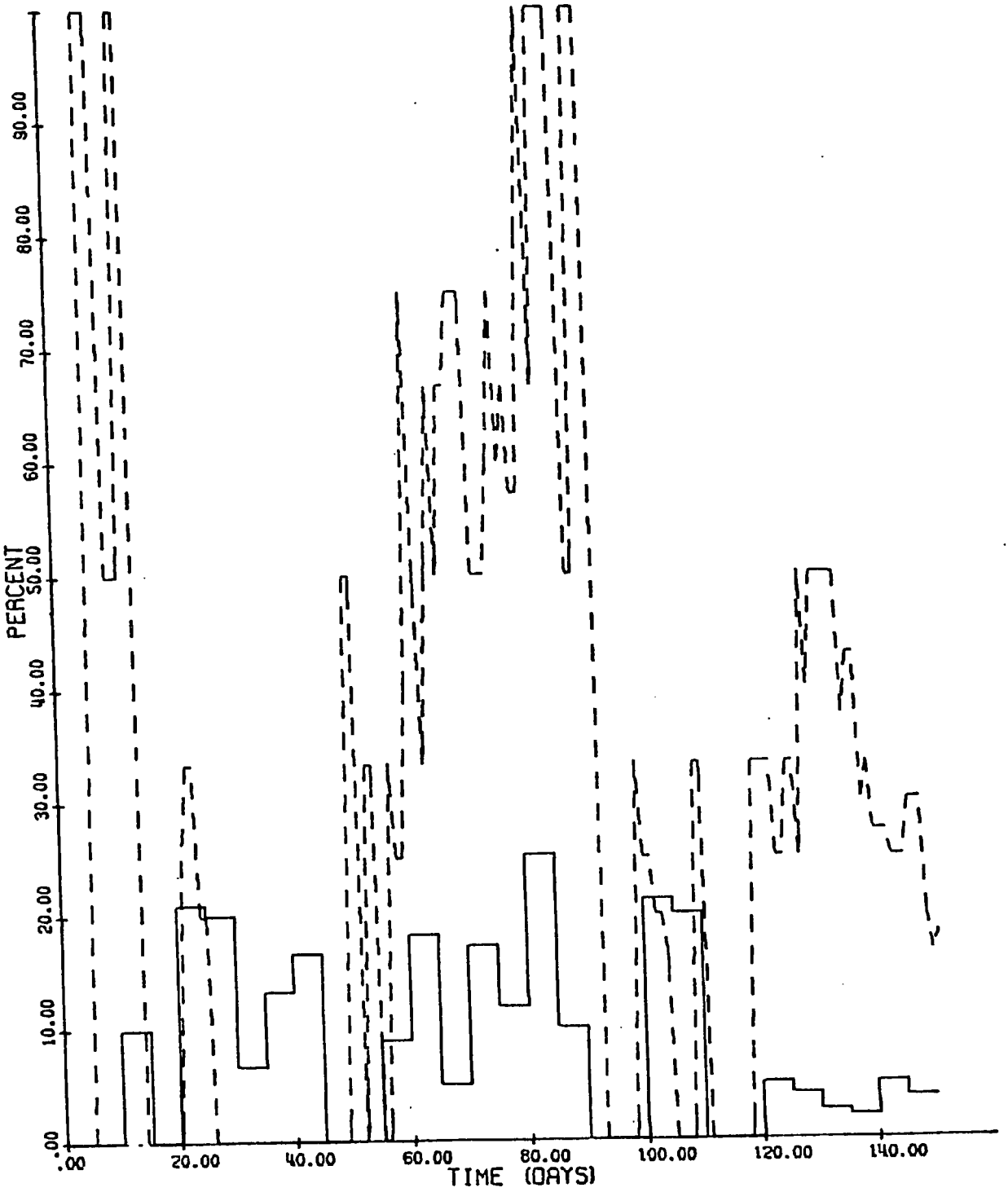
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 80 40 83 -

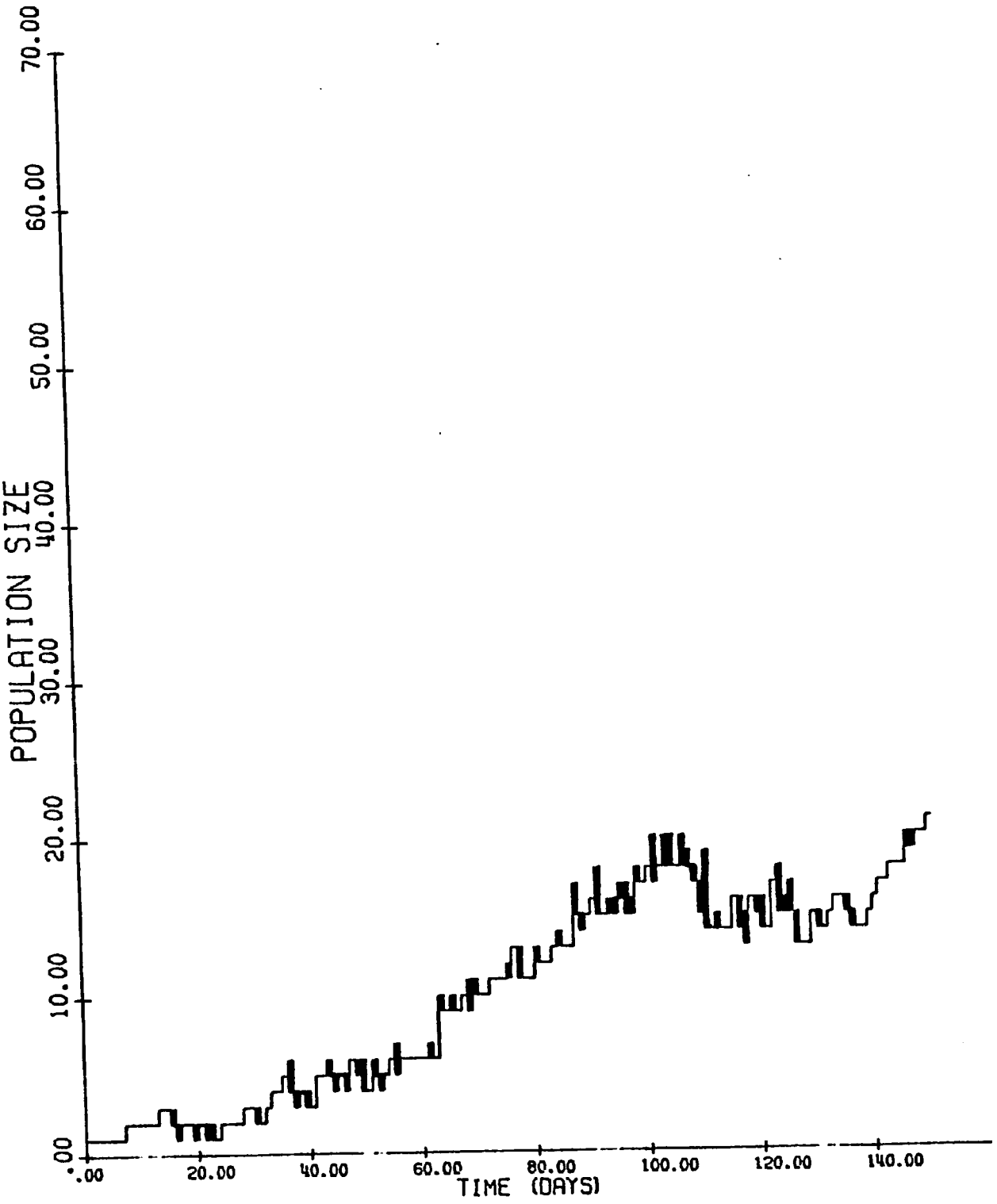
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE: AVERAGES OF 5-DAY PERIODS)



POPULATION 80 80 81 - GROWTH CURVE

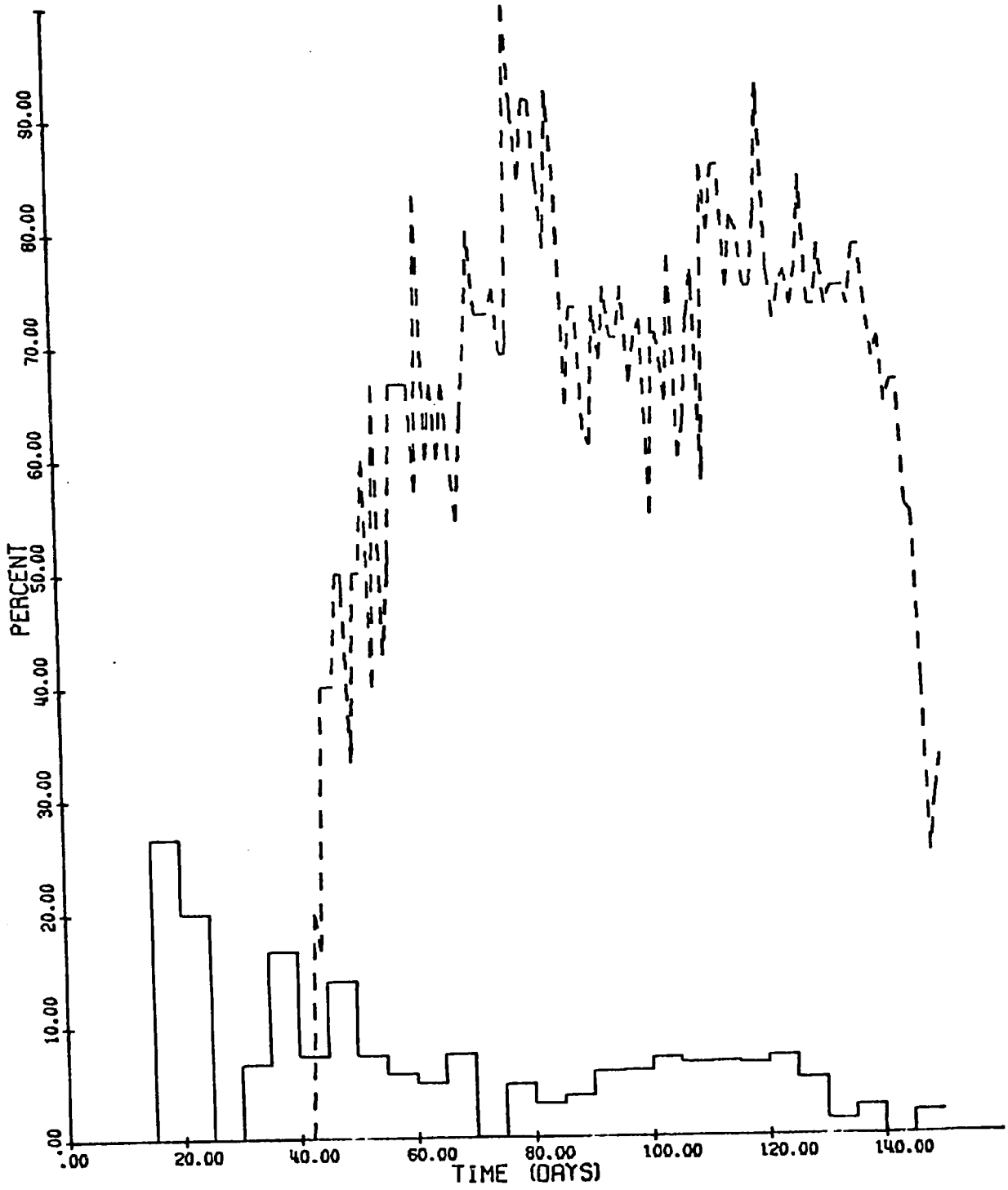
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 80 80 81 -

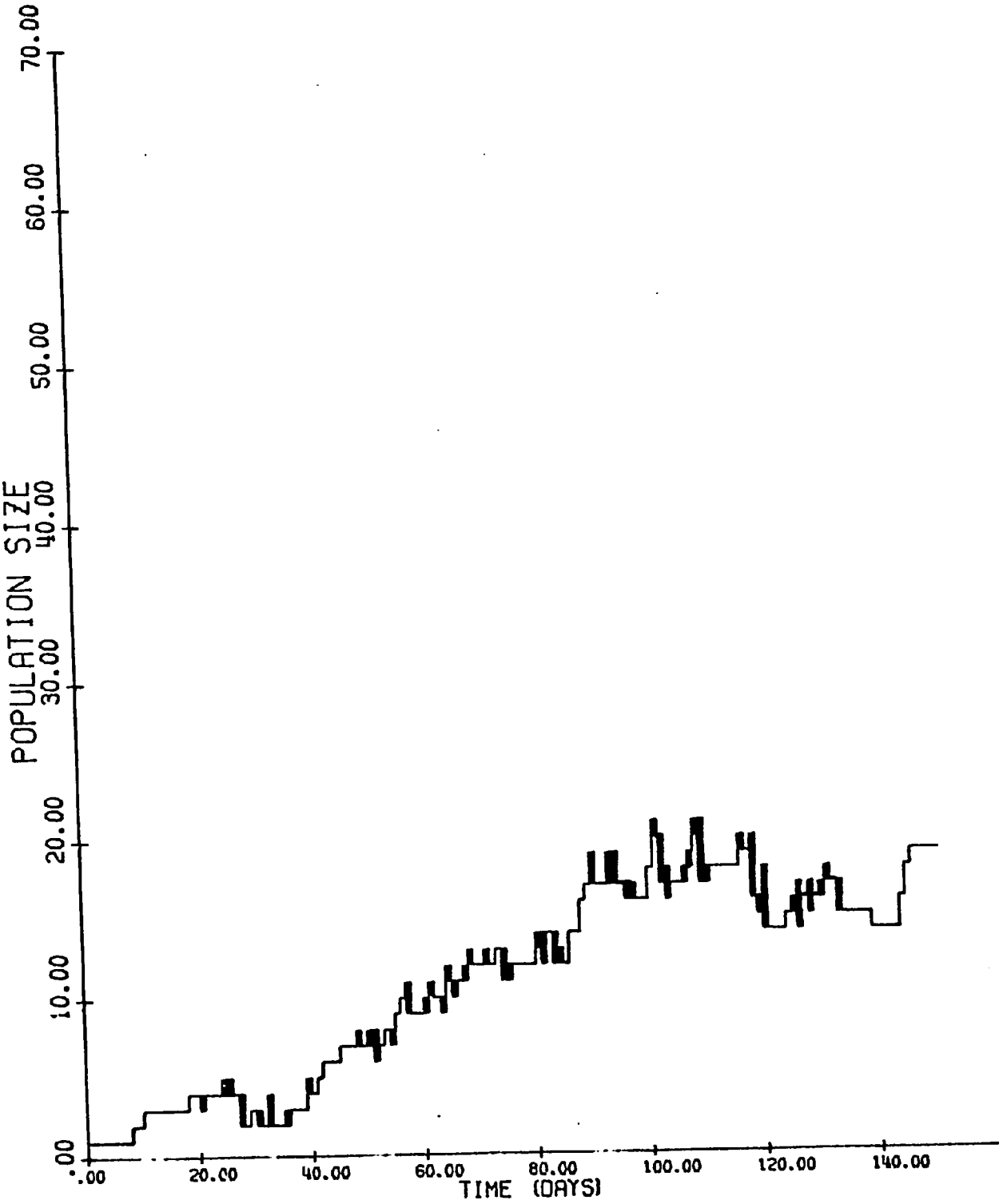
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 80 80 82 - GROWTH CURVE

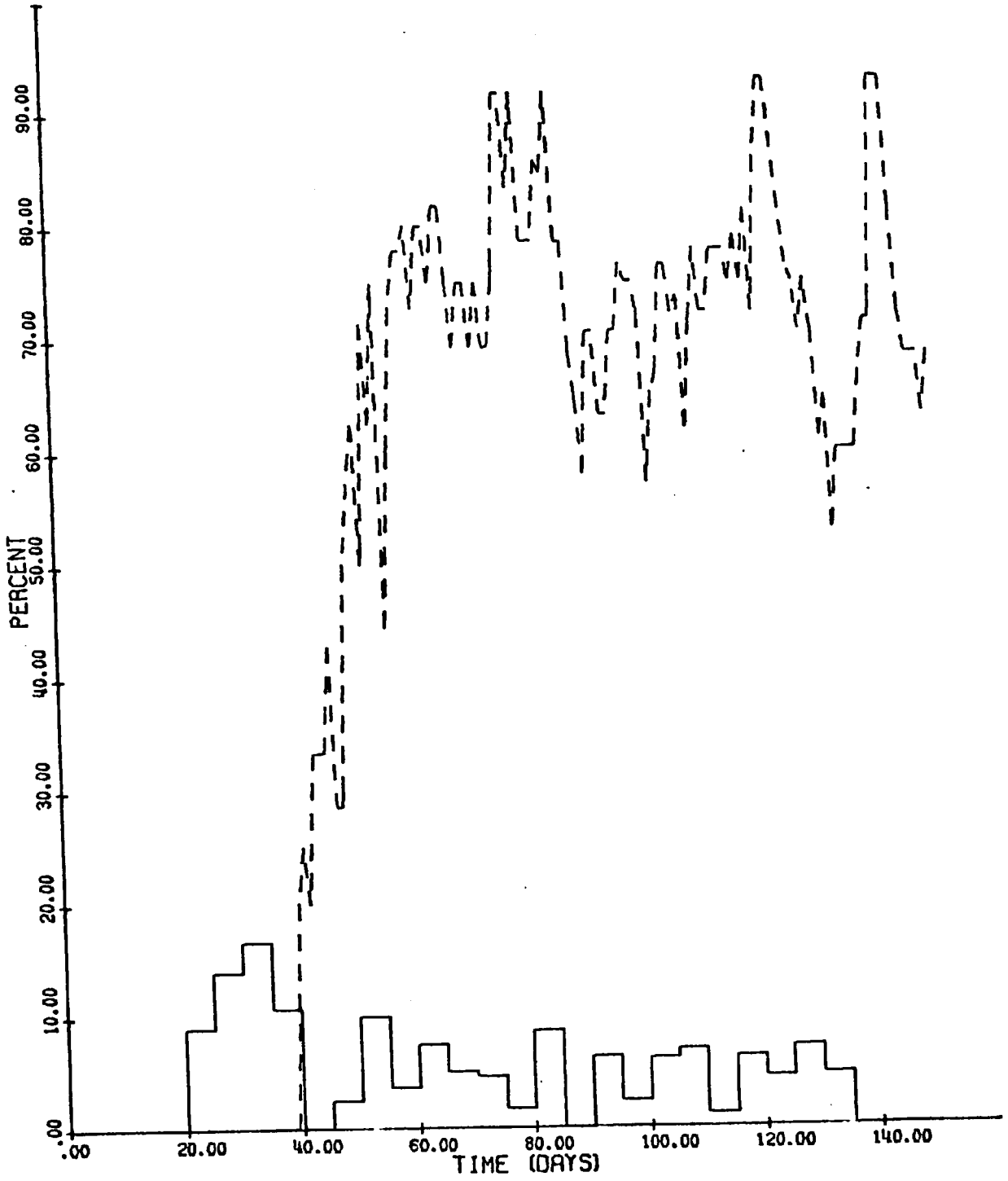
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 80 80 82 -

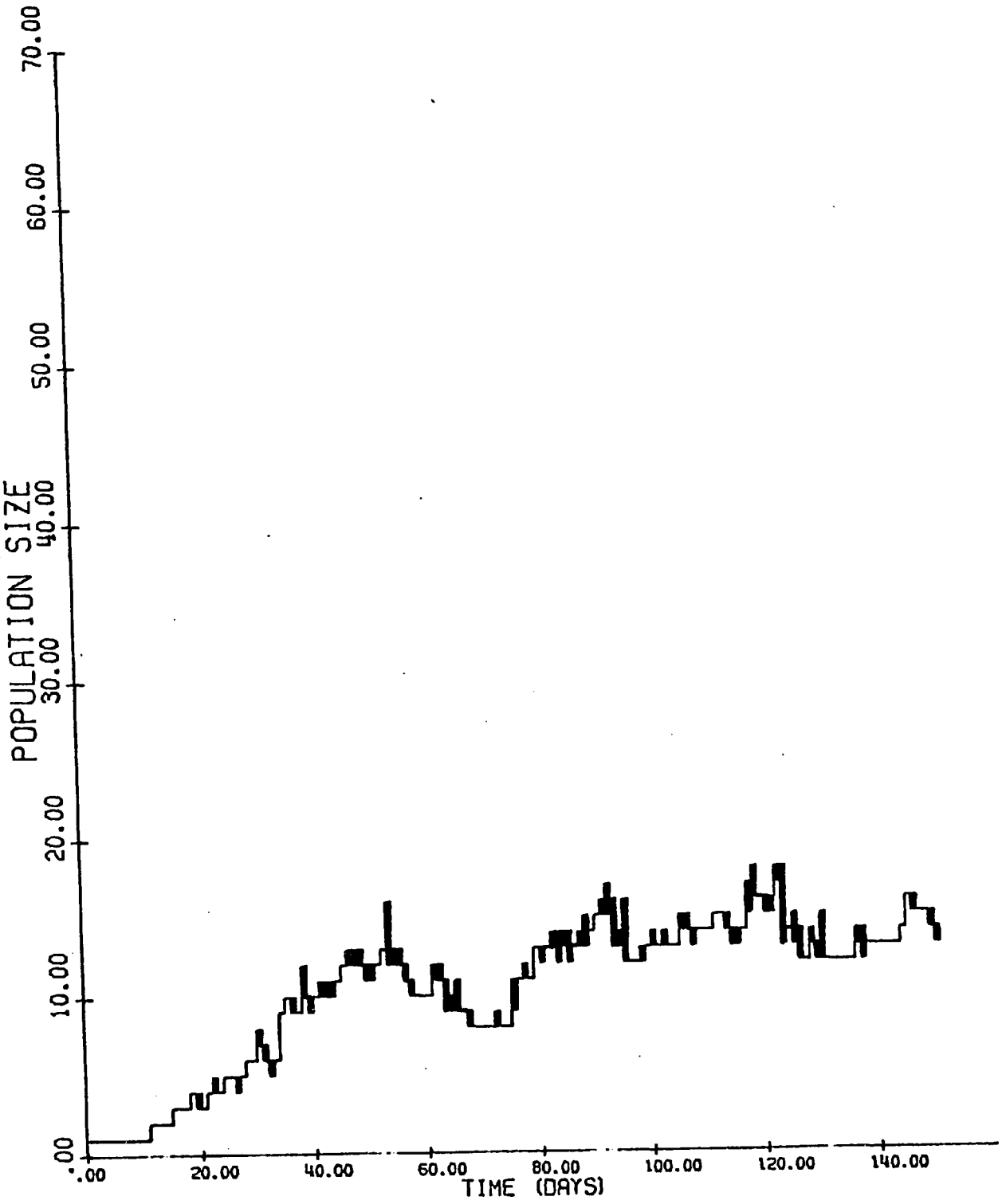
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 80 80 B3 - GROWTH CURVE

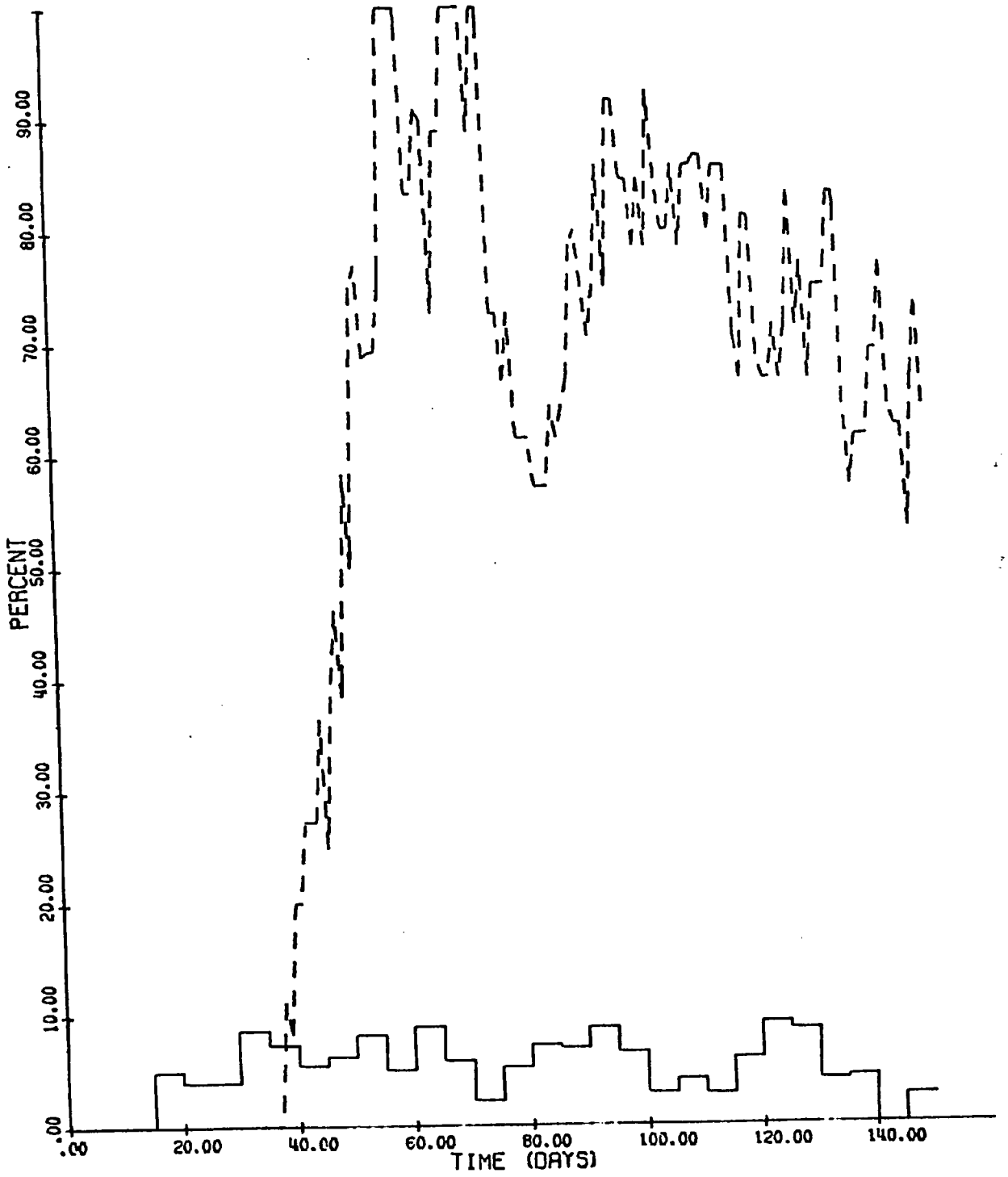
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 80 80 83 -

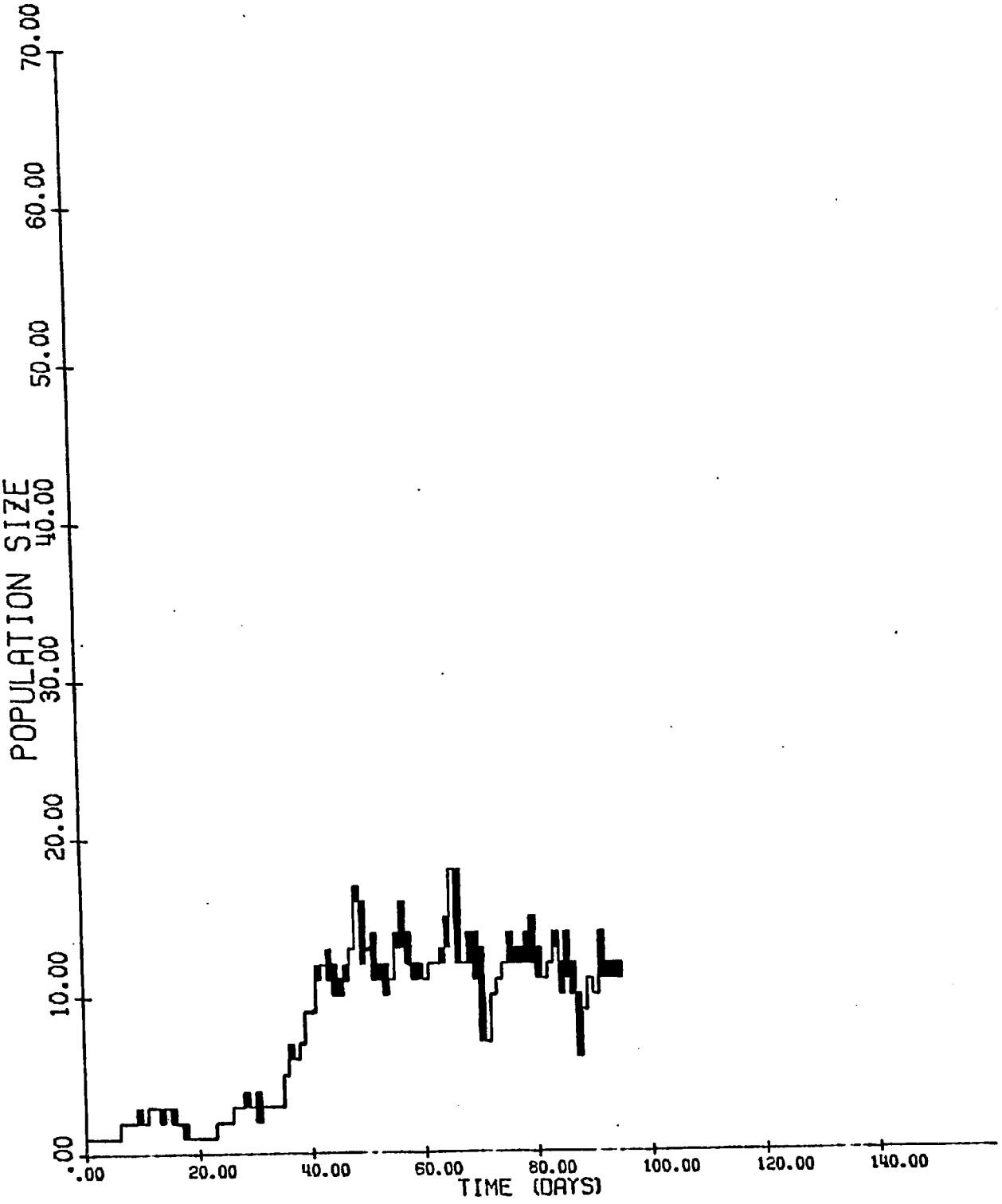
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 150 20 B1 - GROWTH CURVE

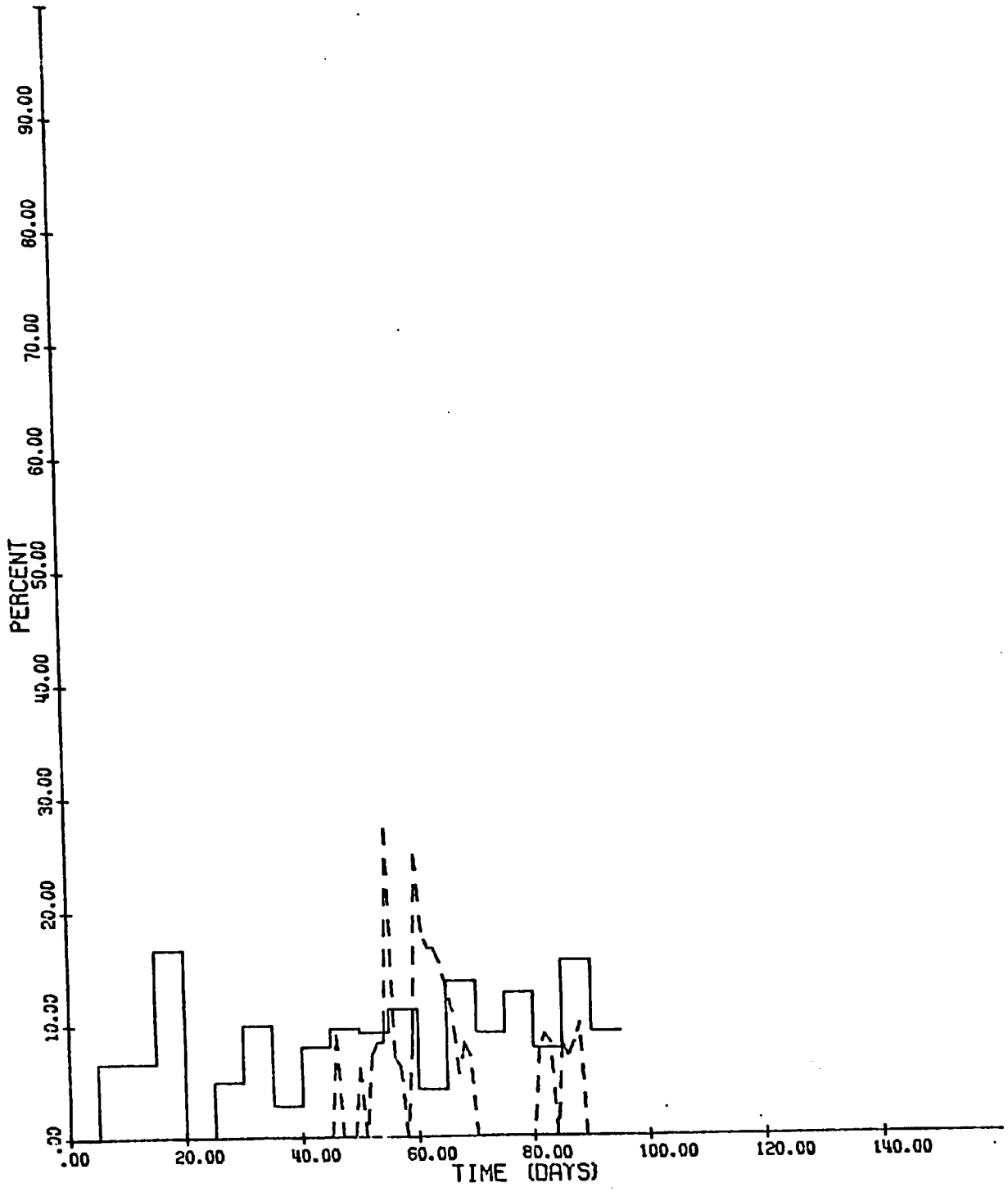
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 150 20 B1 -

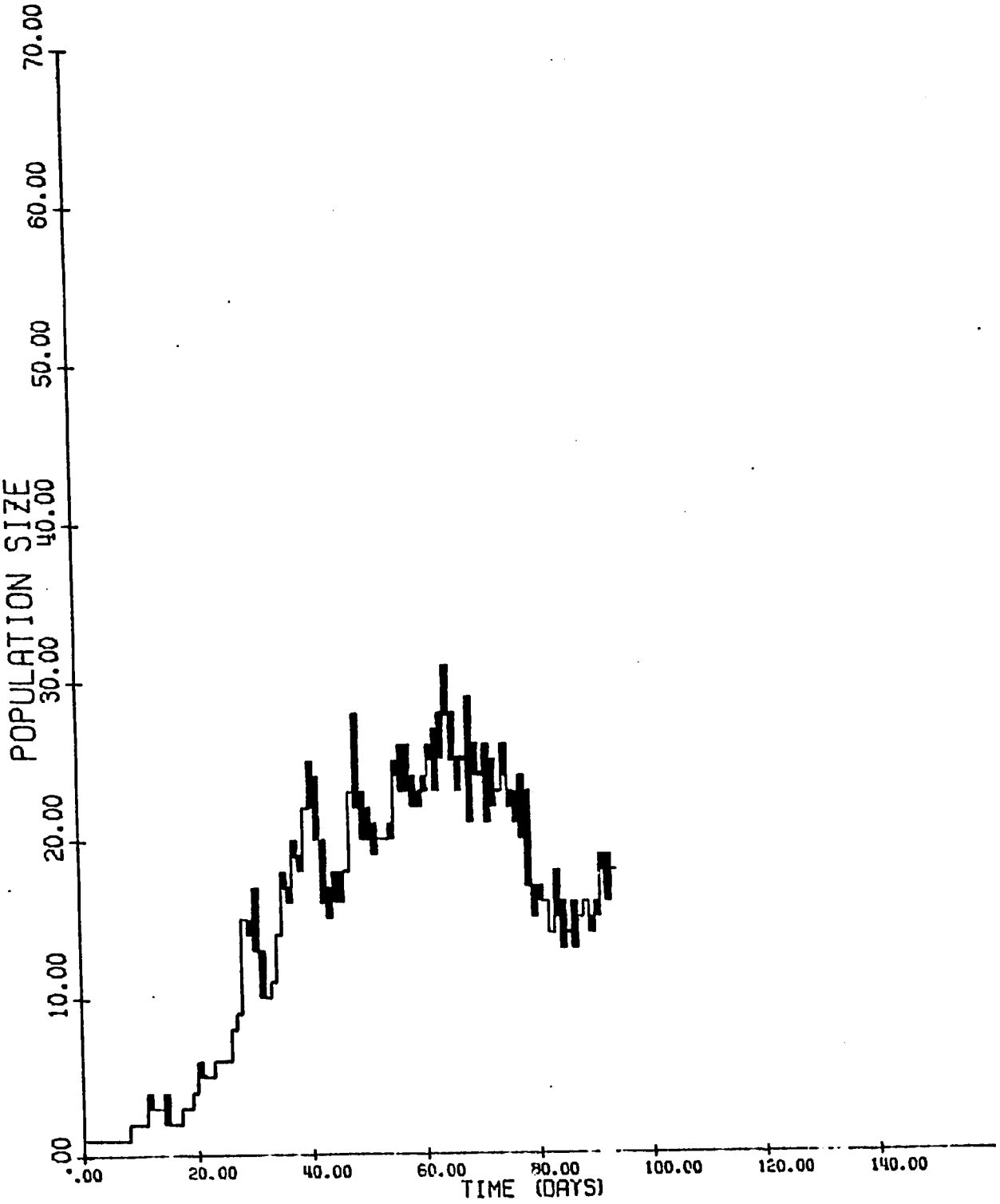
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 150 20 B2 - GROWTH CURVE

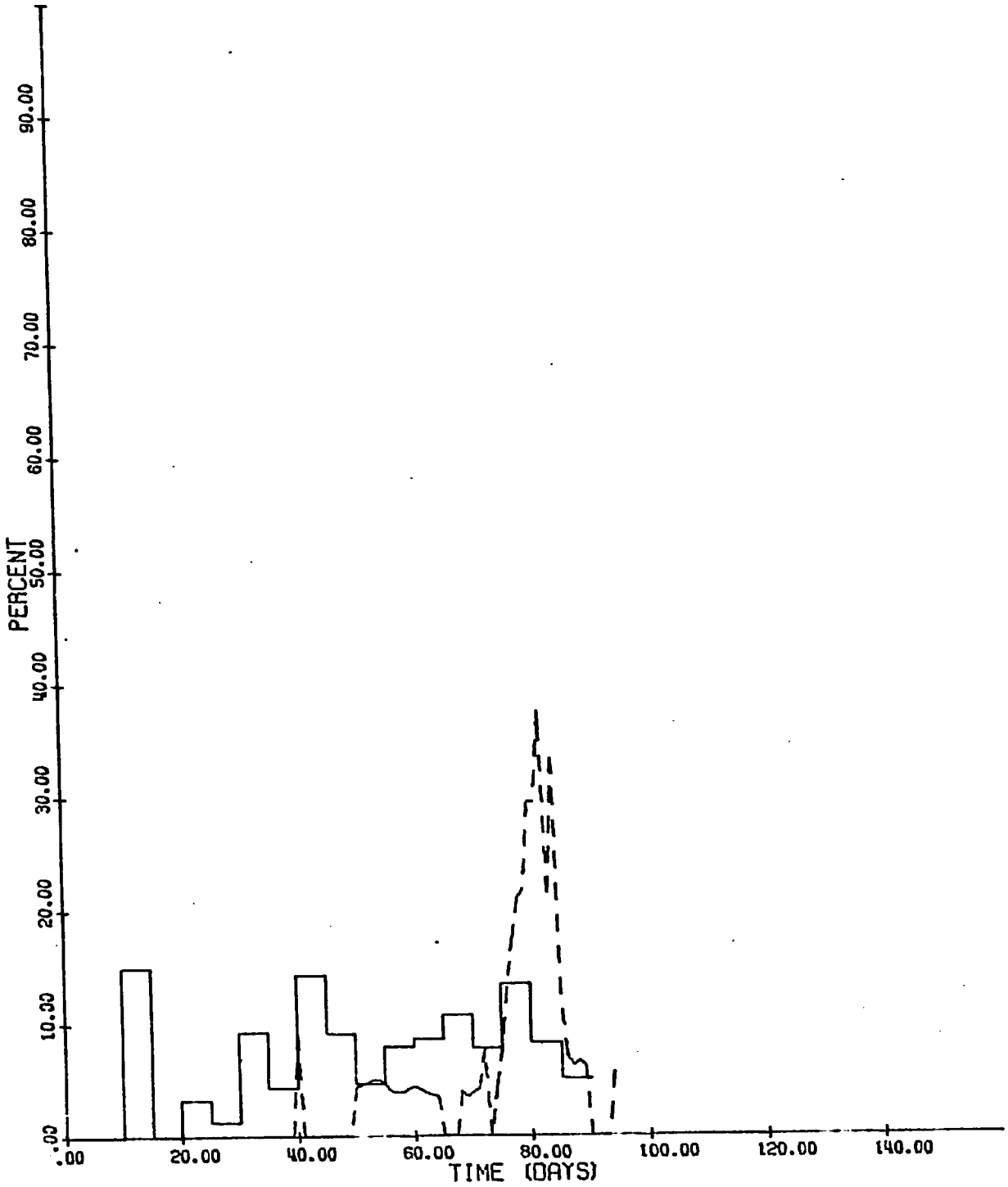
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 150 20 82 -

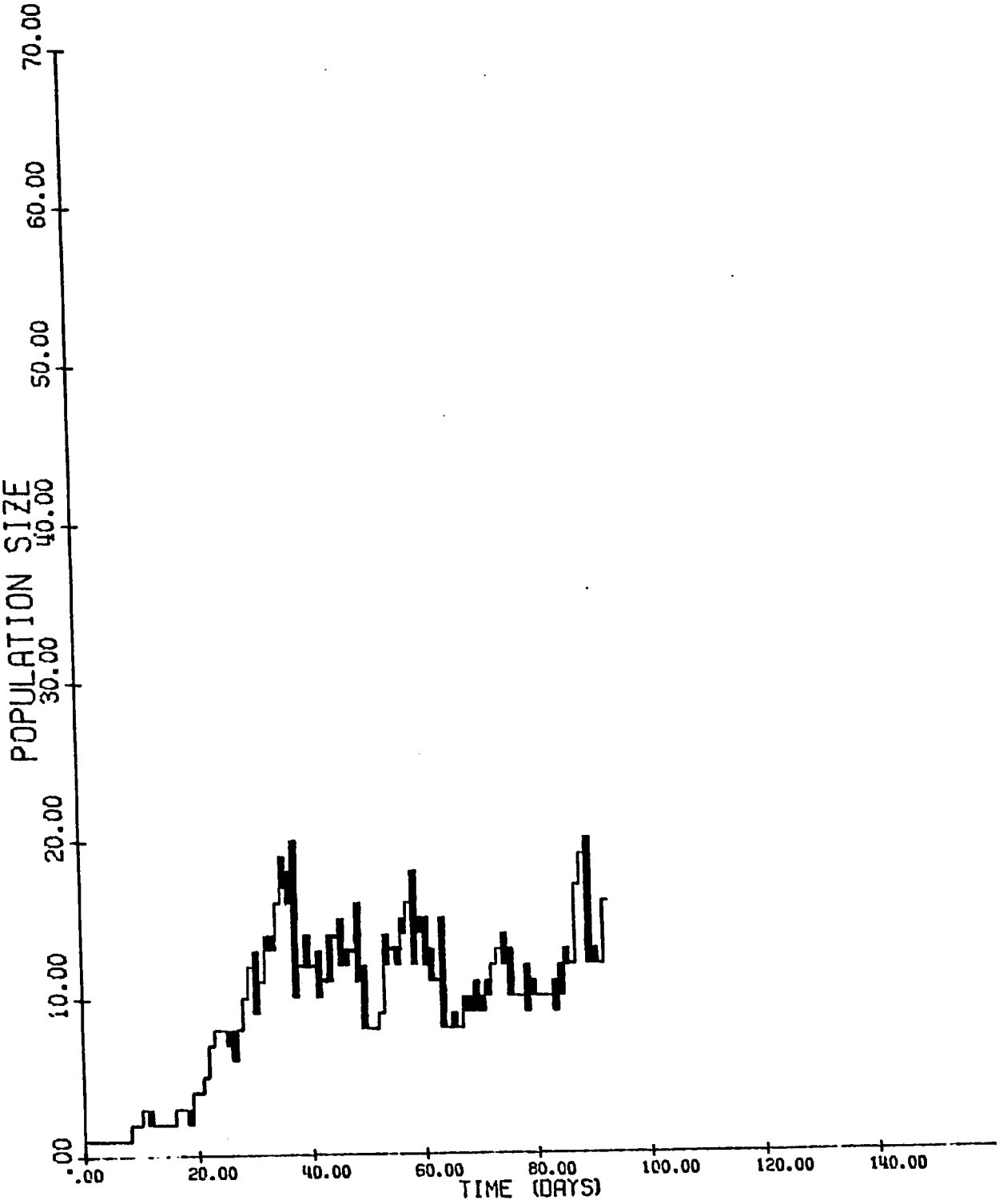
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 150 20 B3 - GROWTH CURVE

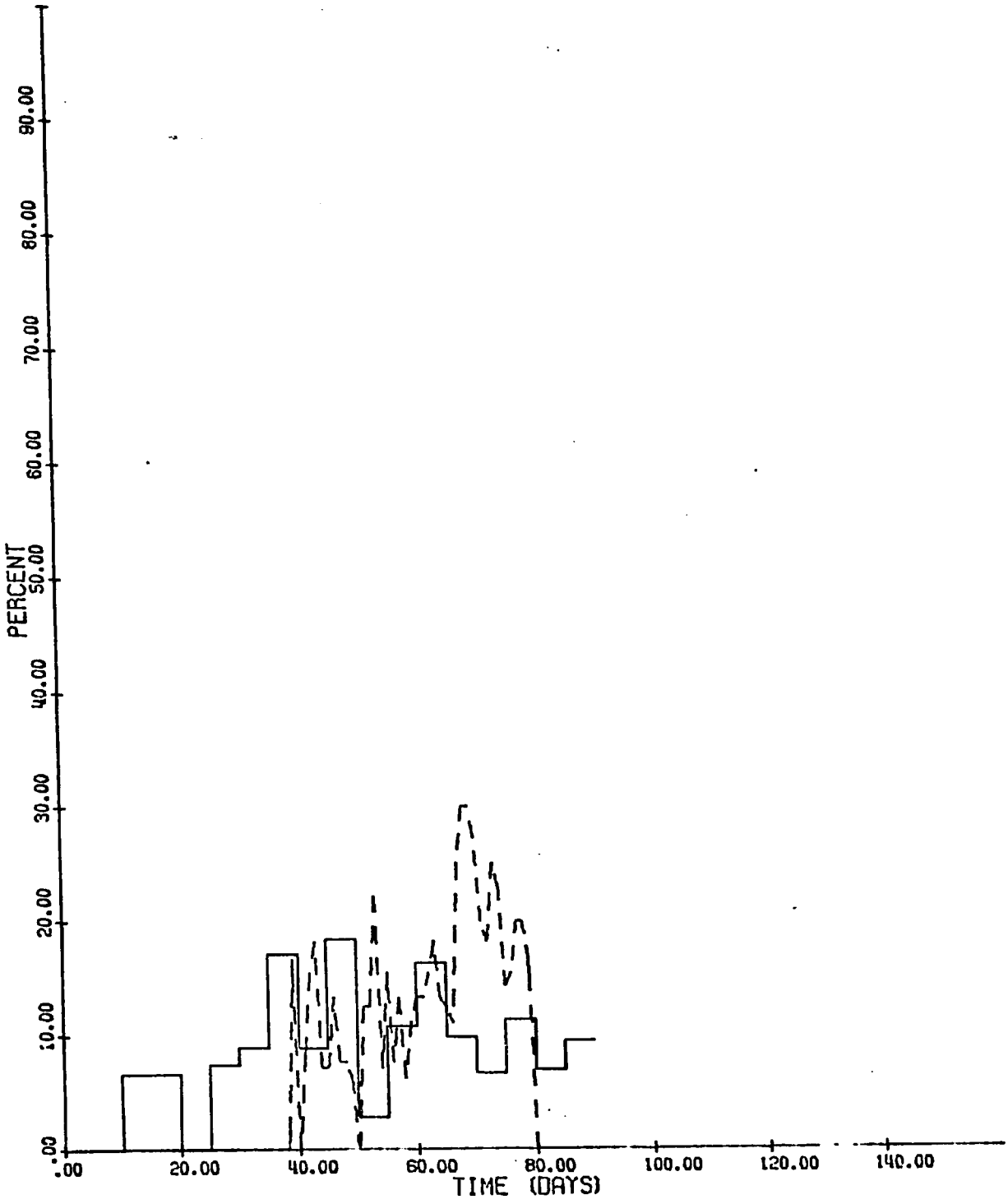
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 150 20 83 -

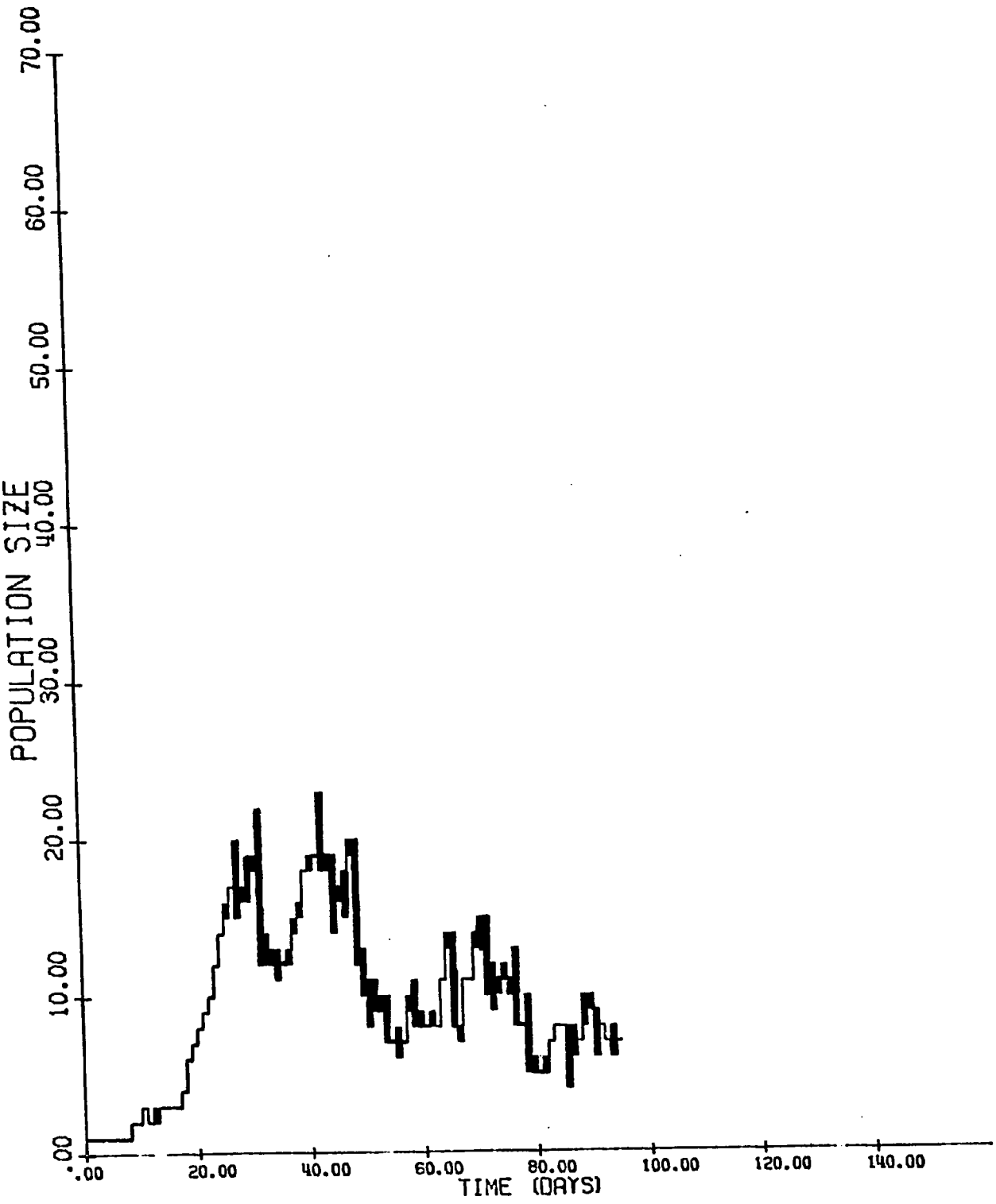
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE: AVERAGES OF 5-DAY PERIODS)



POPULATION 150 40 B1 - GROWTH CURVE

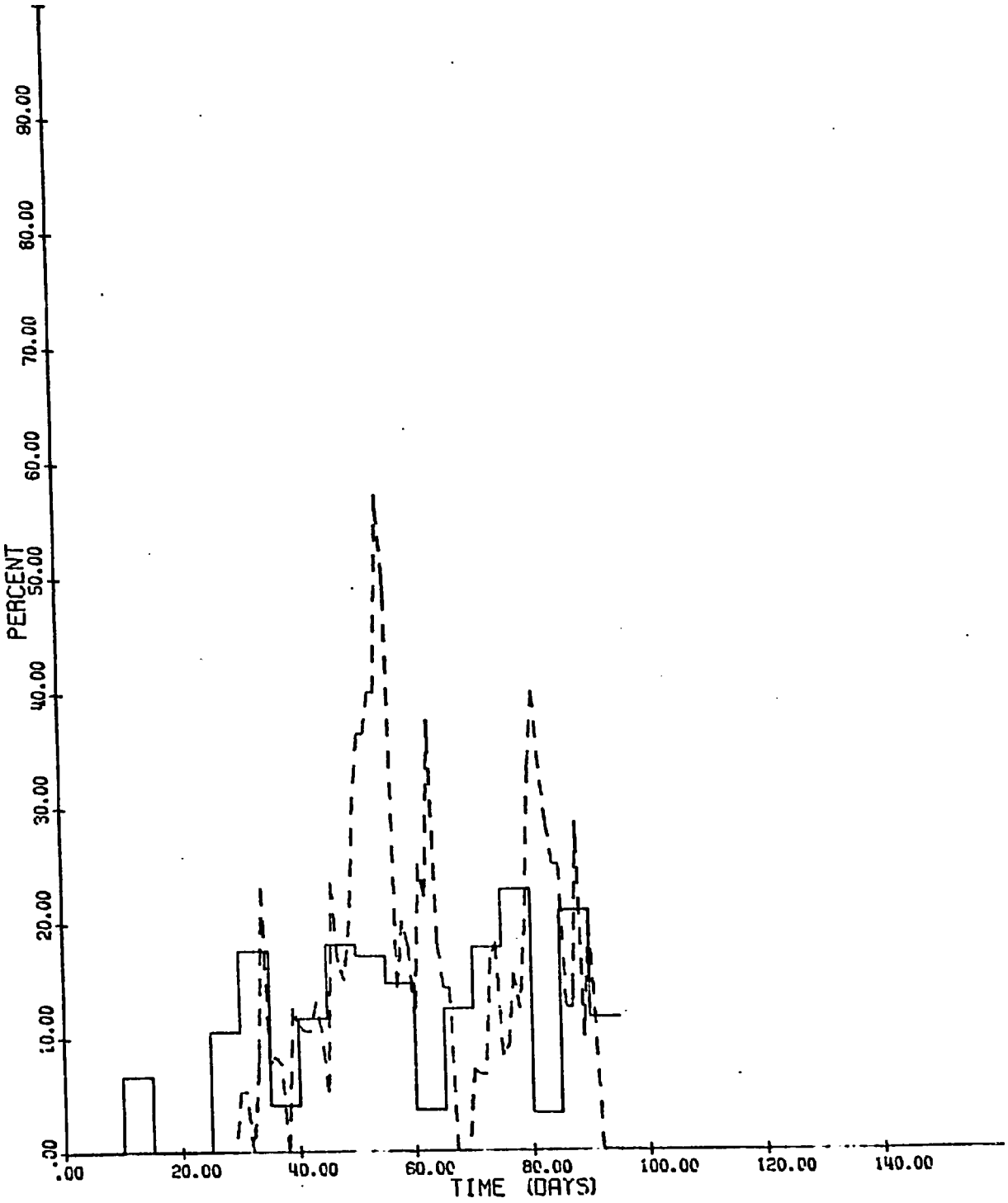
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 150 40 81 -

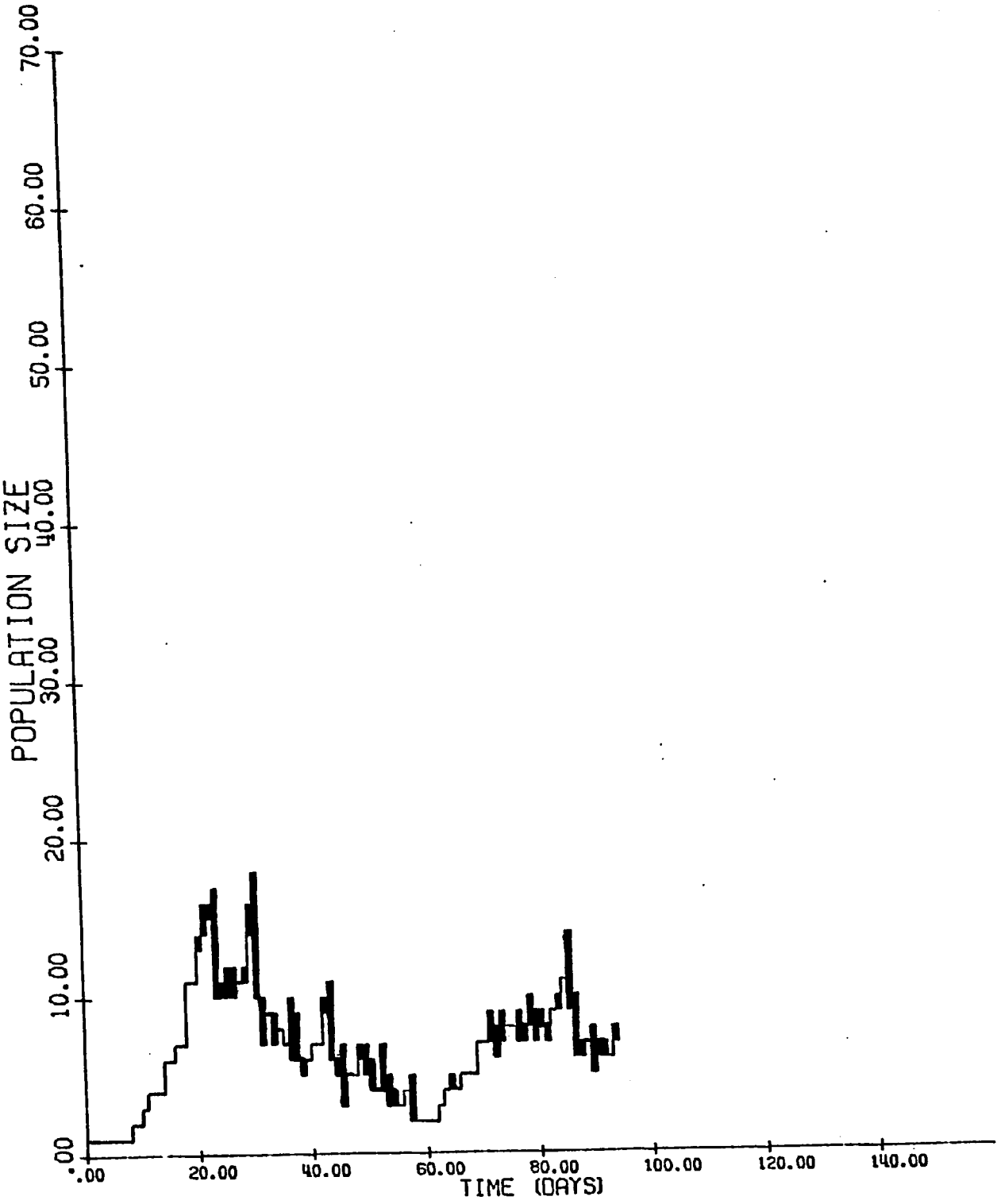
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 150 40 82 - GROWTH CURVE

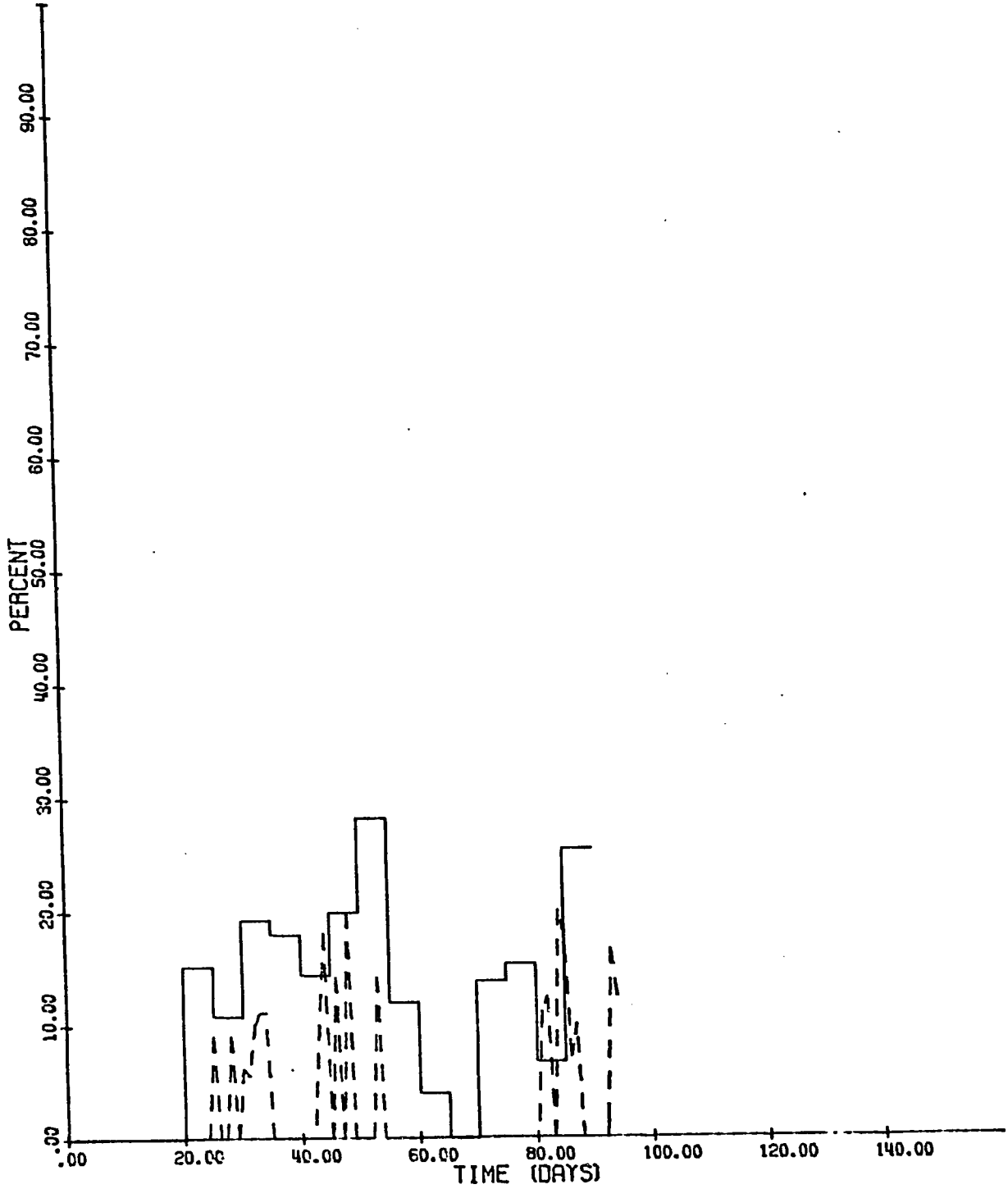
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 150 40 B2 -

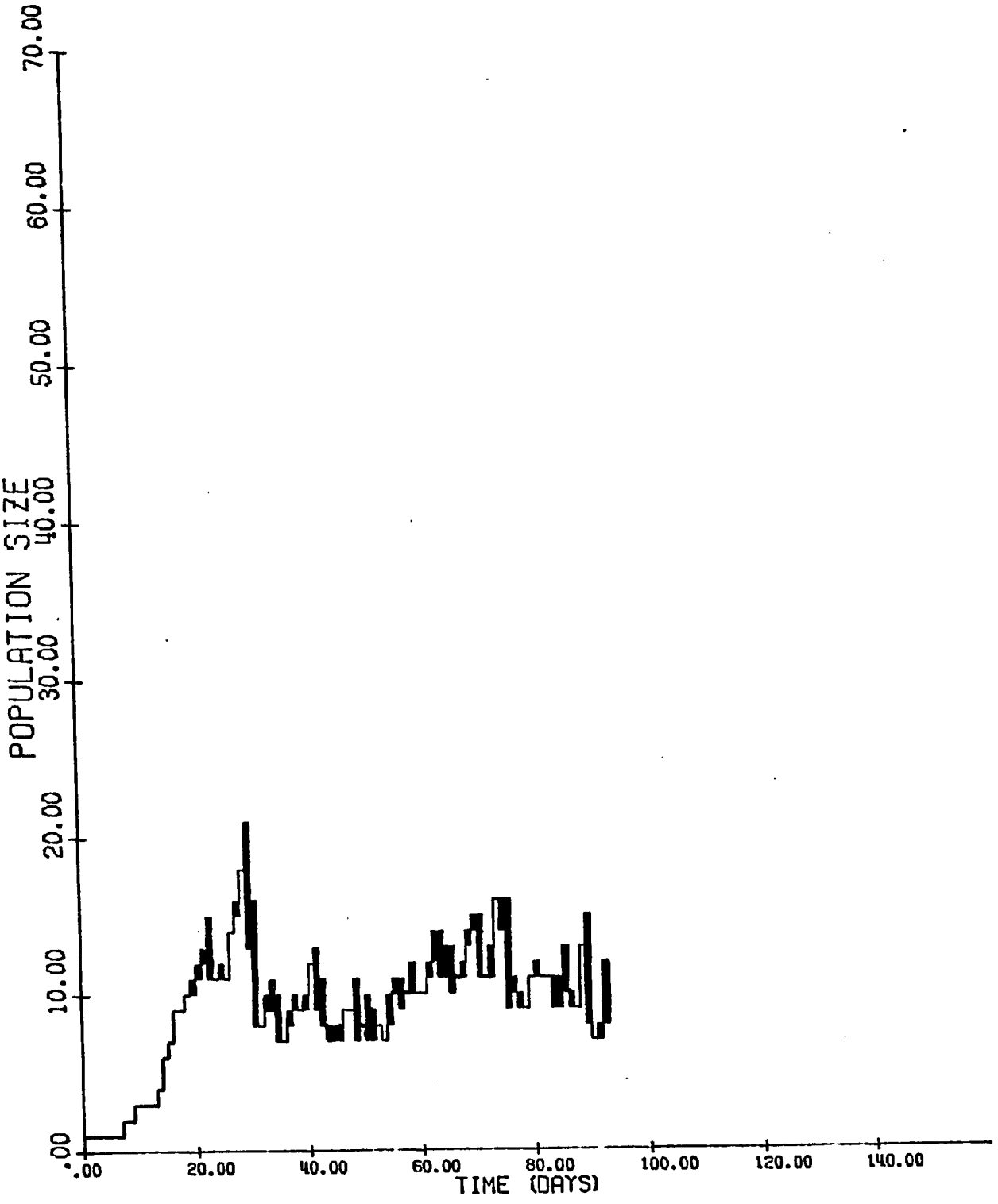
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLIB LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 150 40 B3 - GROWTH CURVE

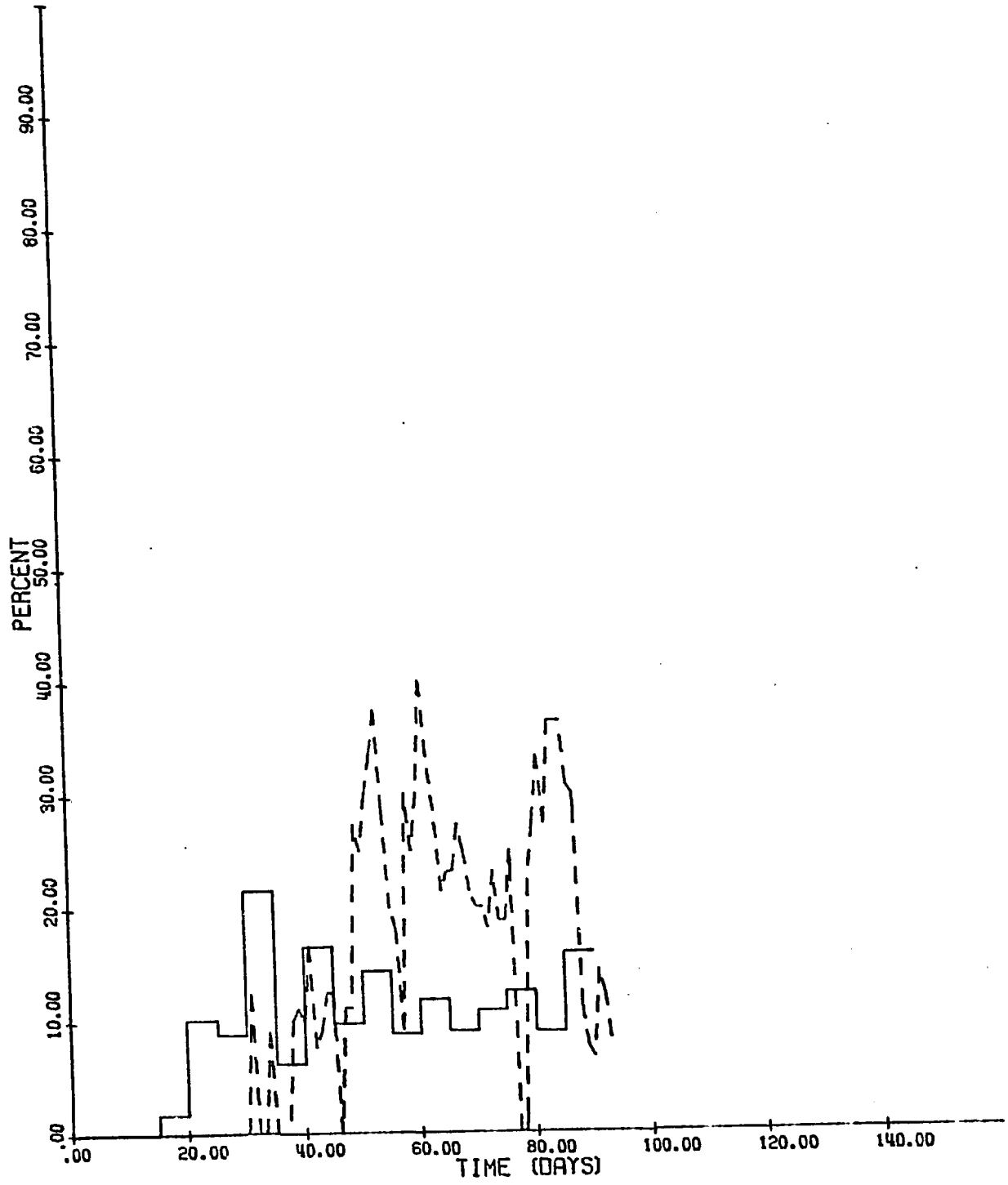
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 150 40 83 -

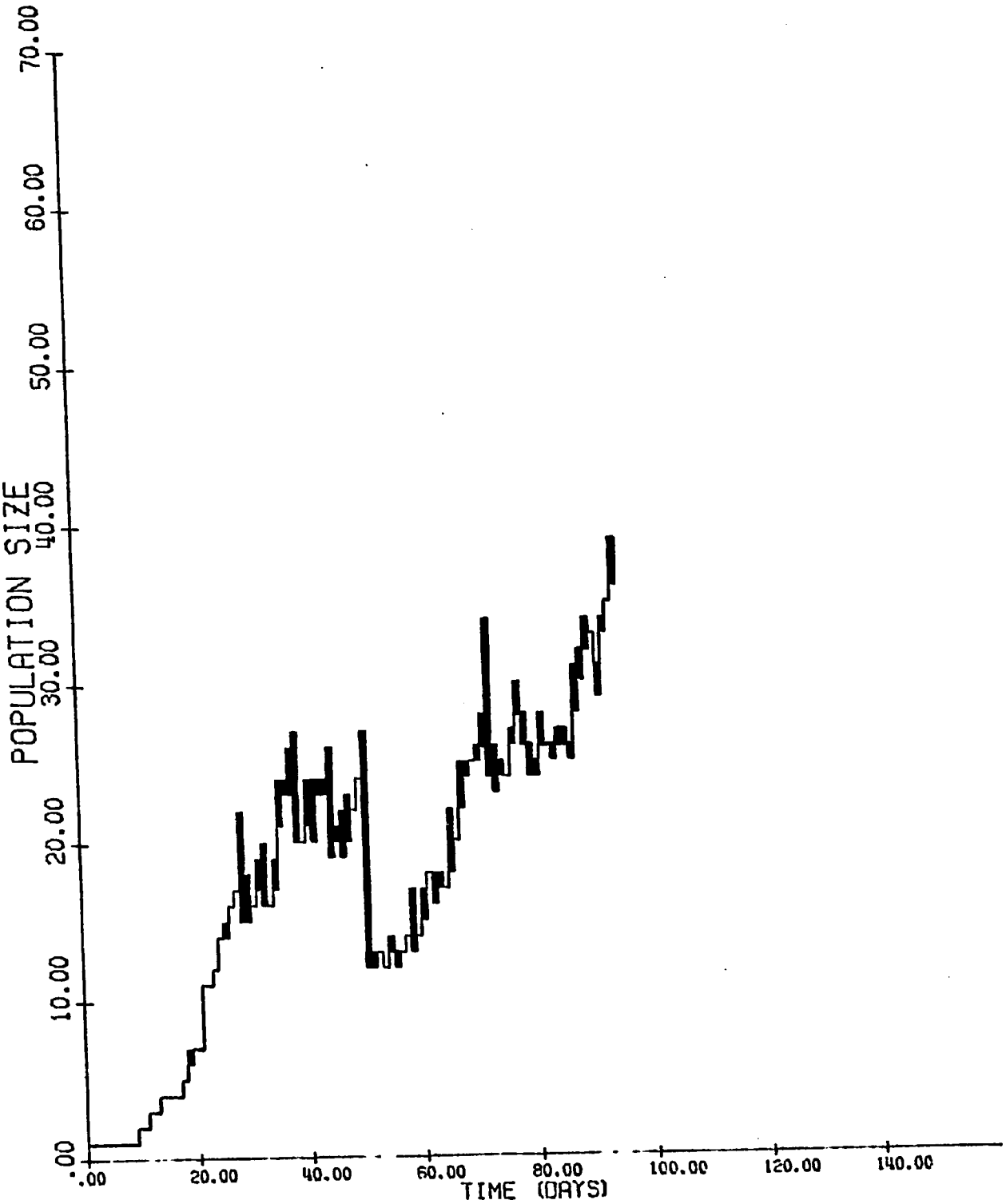
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE: AVERAGES OF 5-DAY PERIODS)



POPULATION 150 80 B1 - GROWTH CURVE

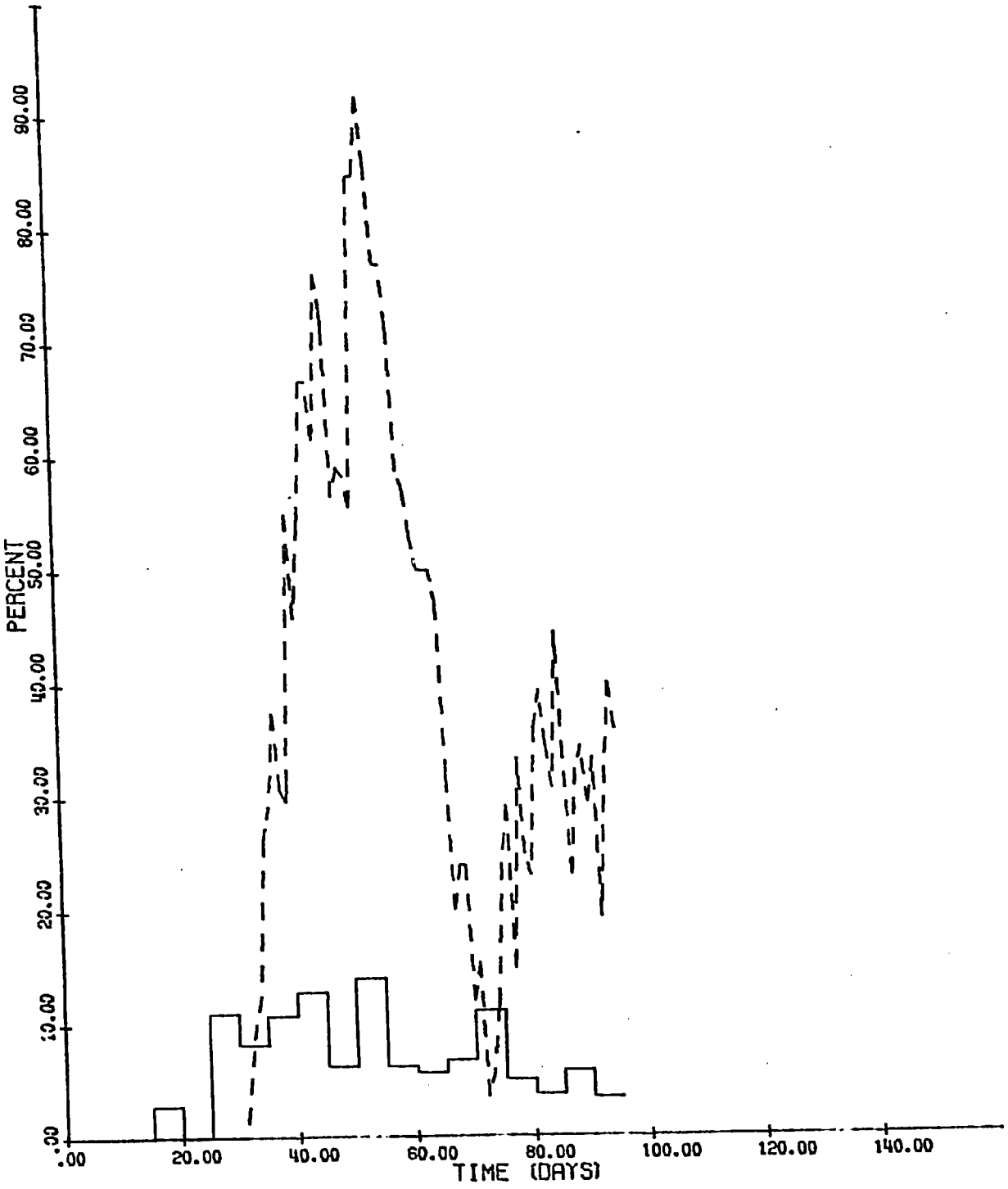
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 150 80 81 -

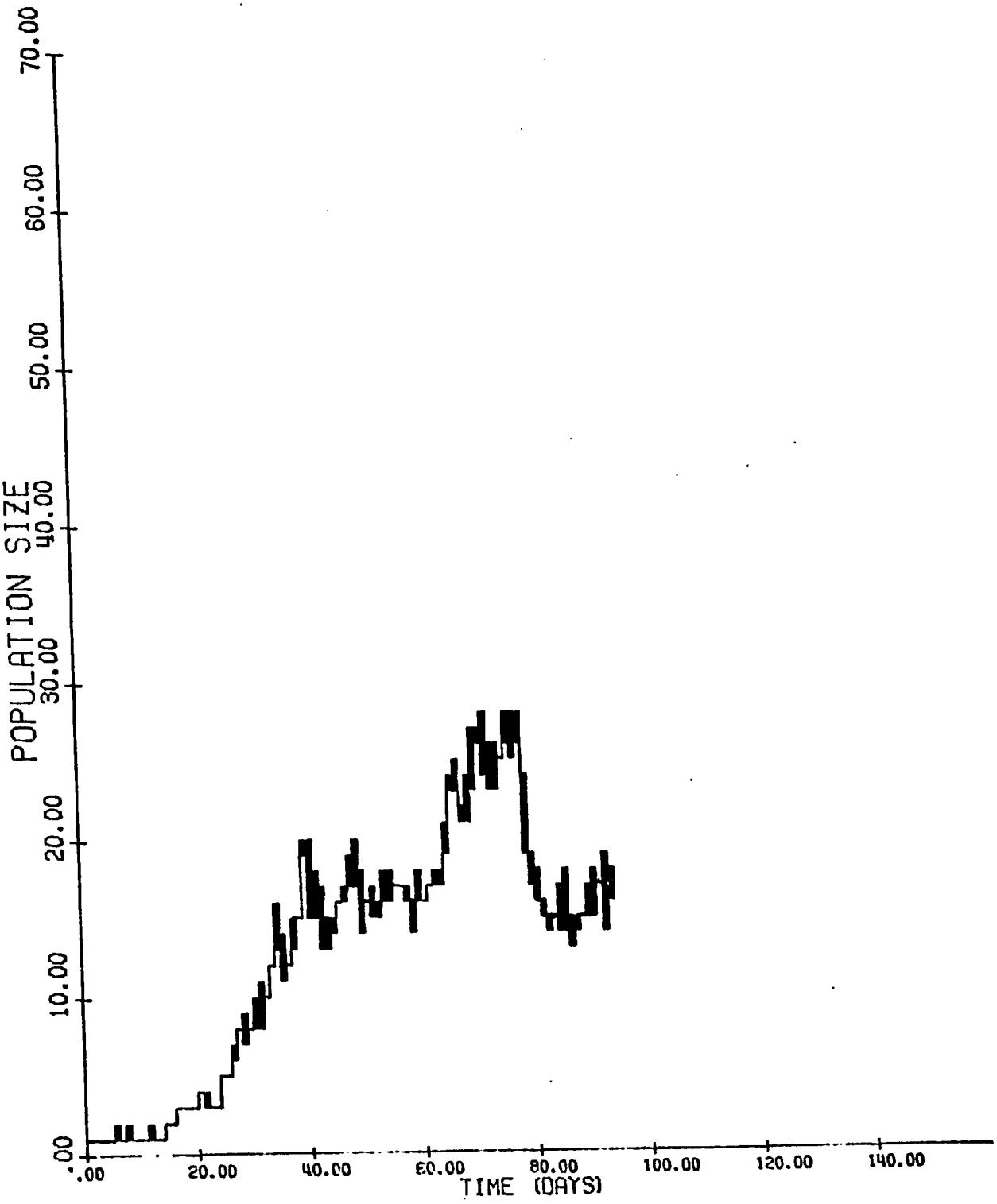
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 150 80 82 - GROWTH CURVE

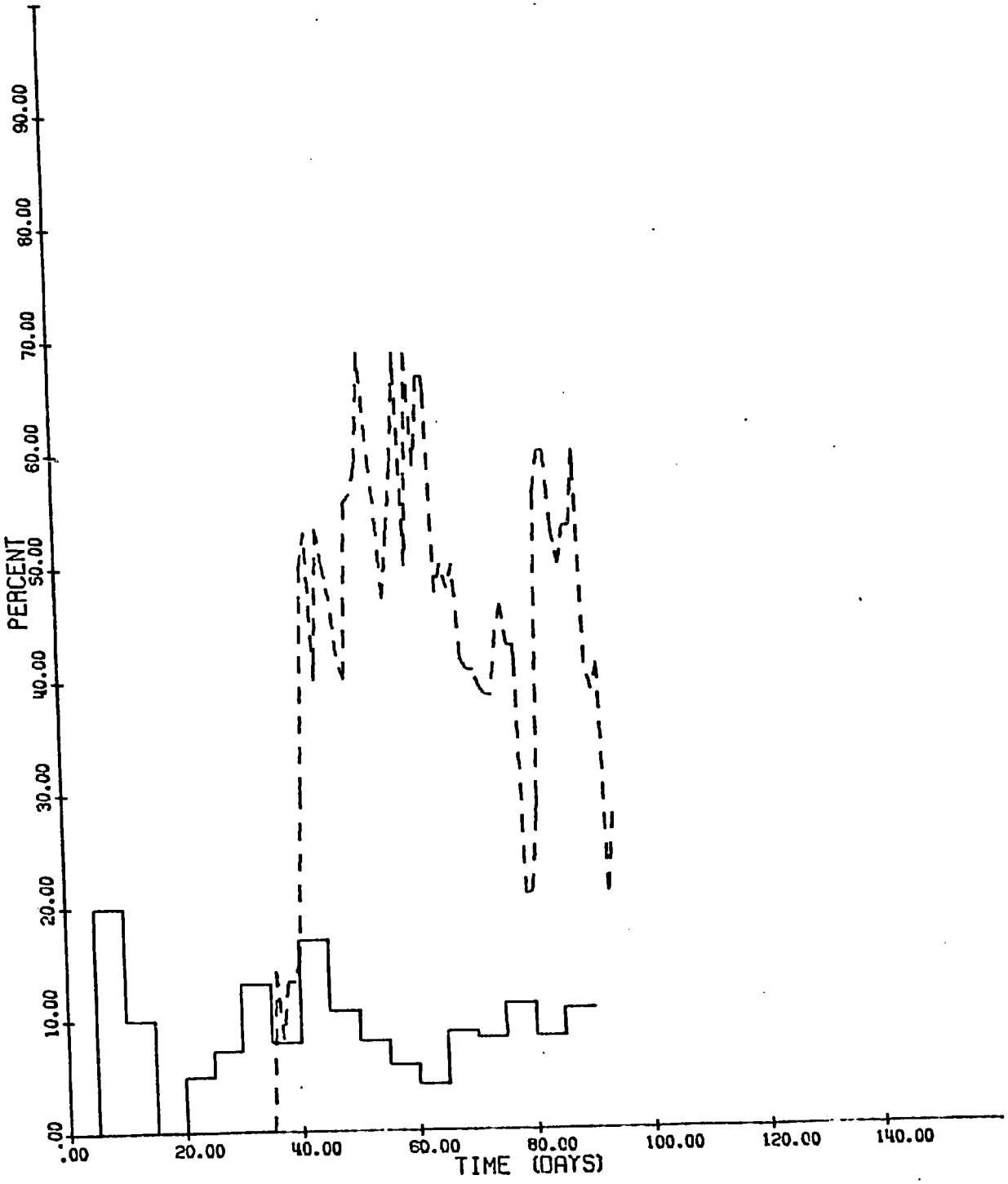
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 150 80 82 -

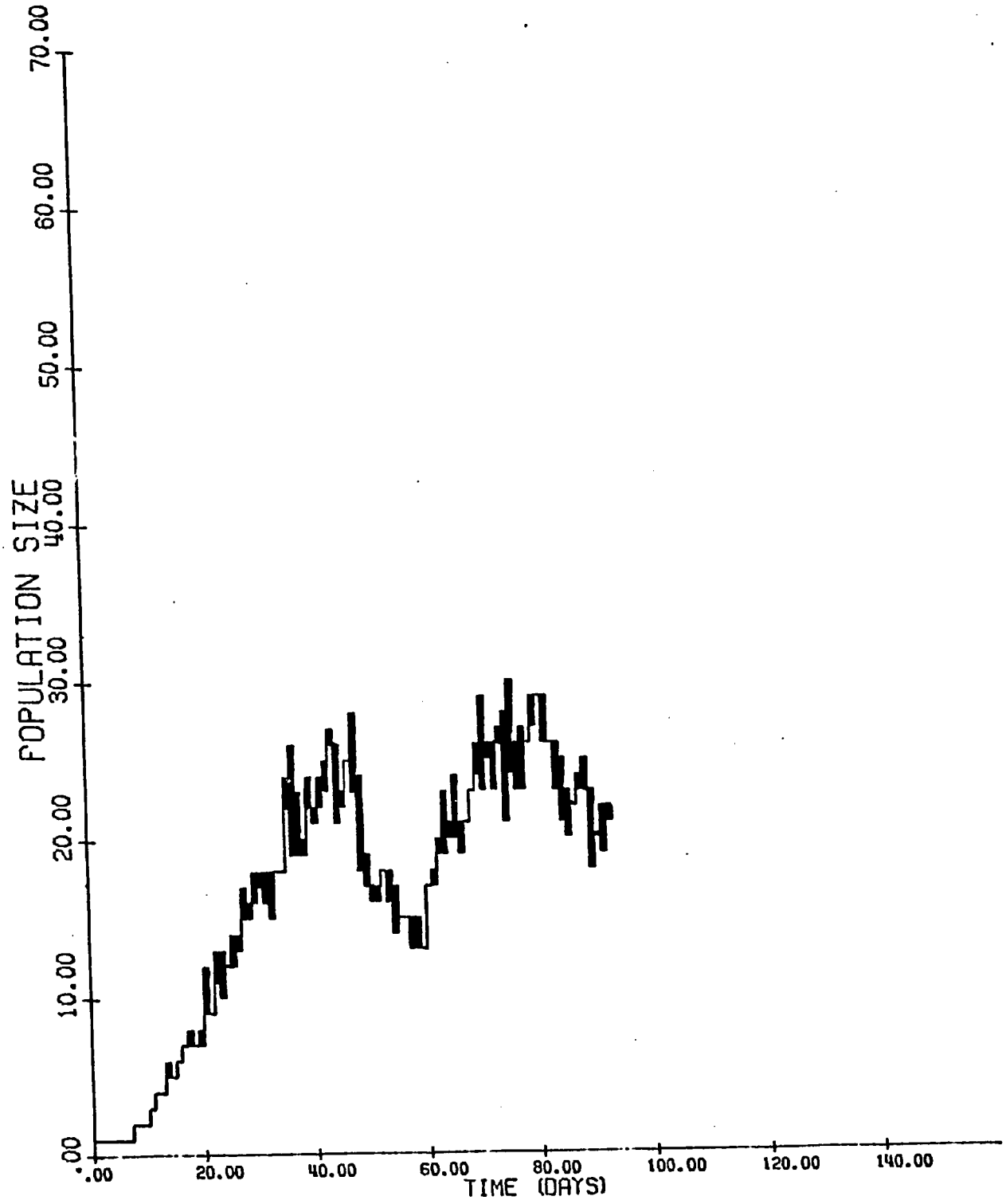
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 150 80 83 - GROWTH CURVE

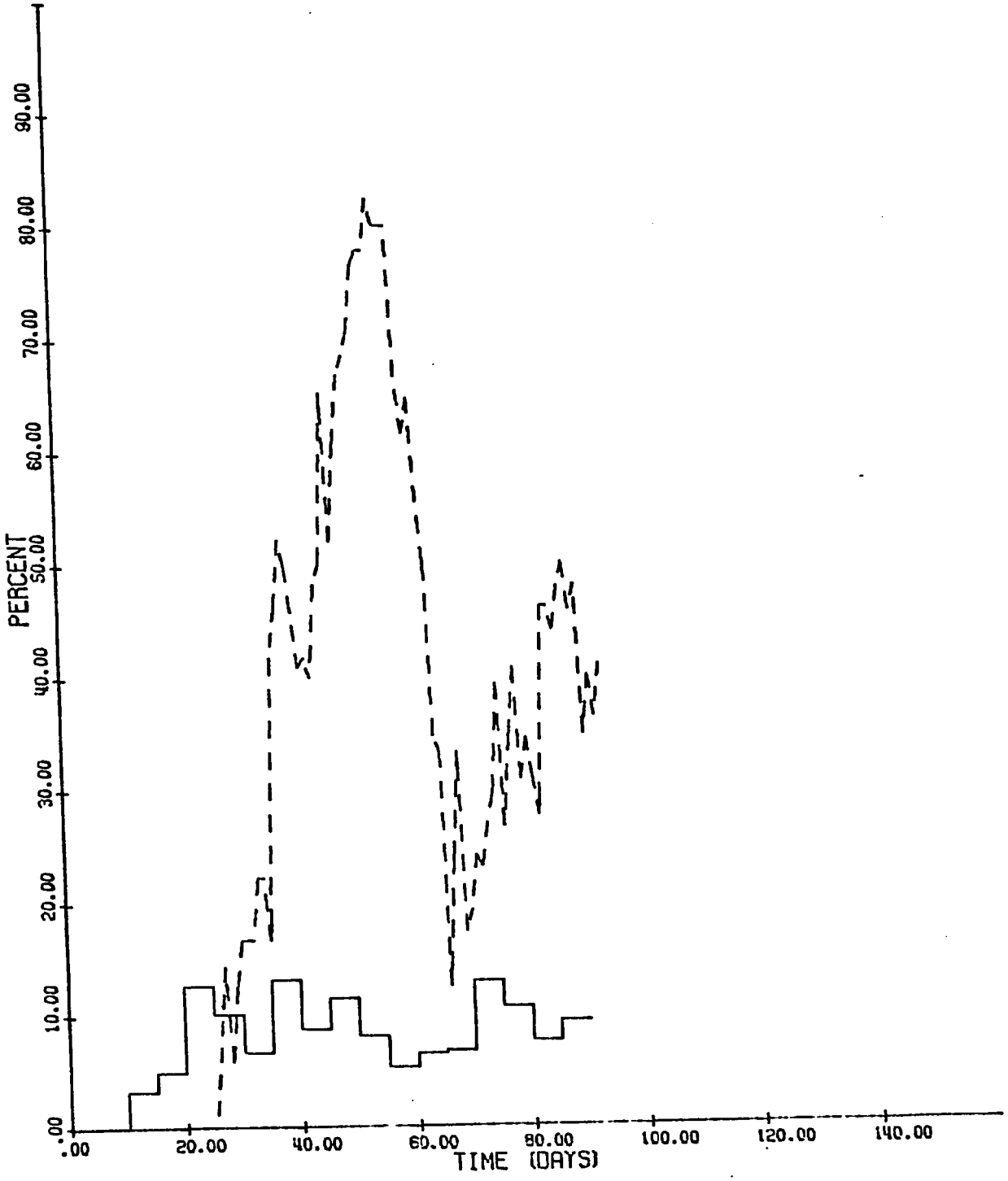
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 150 80 83 -

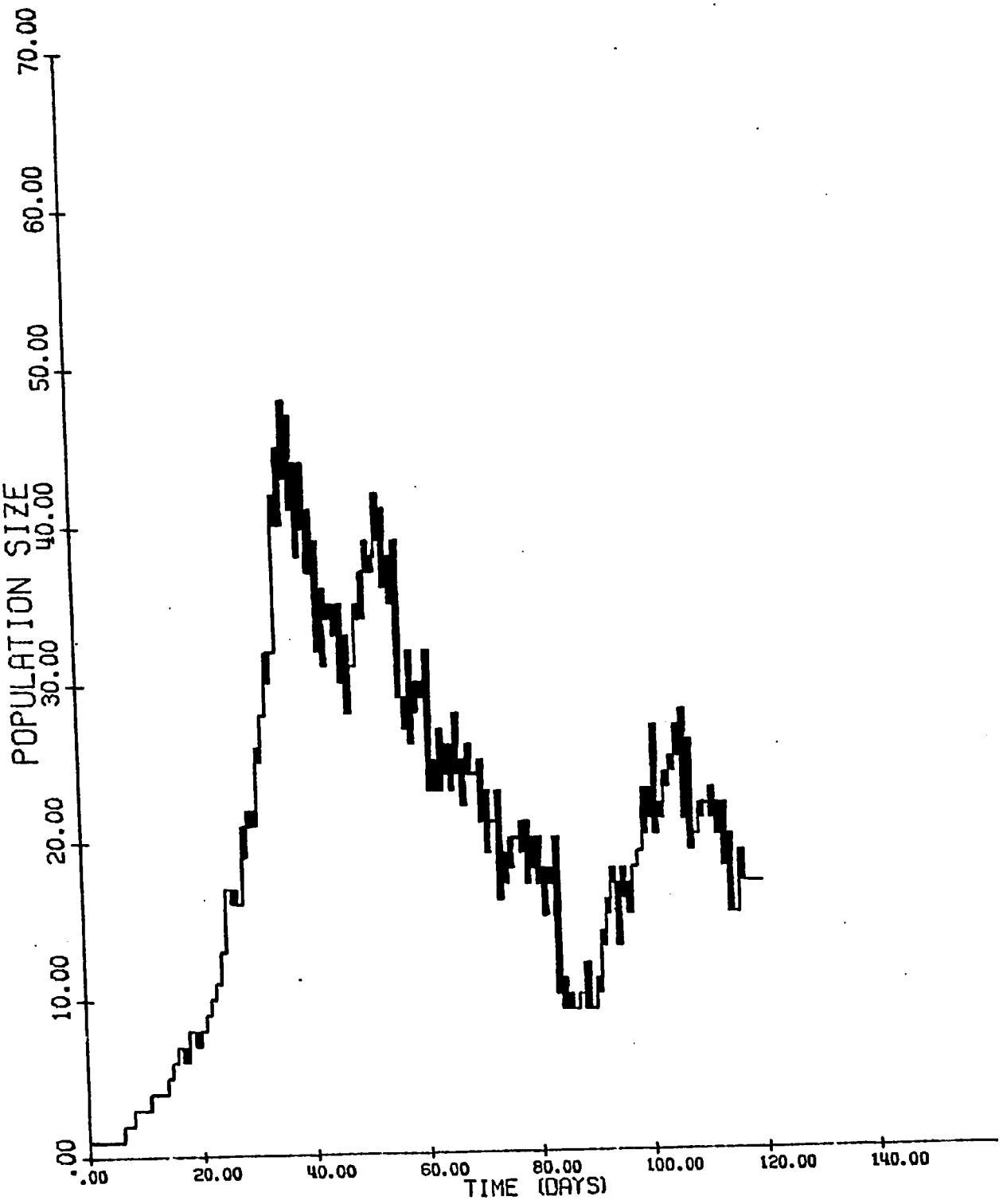
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 300 20 B1 – GROWTH CURVE

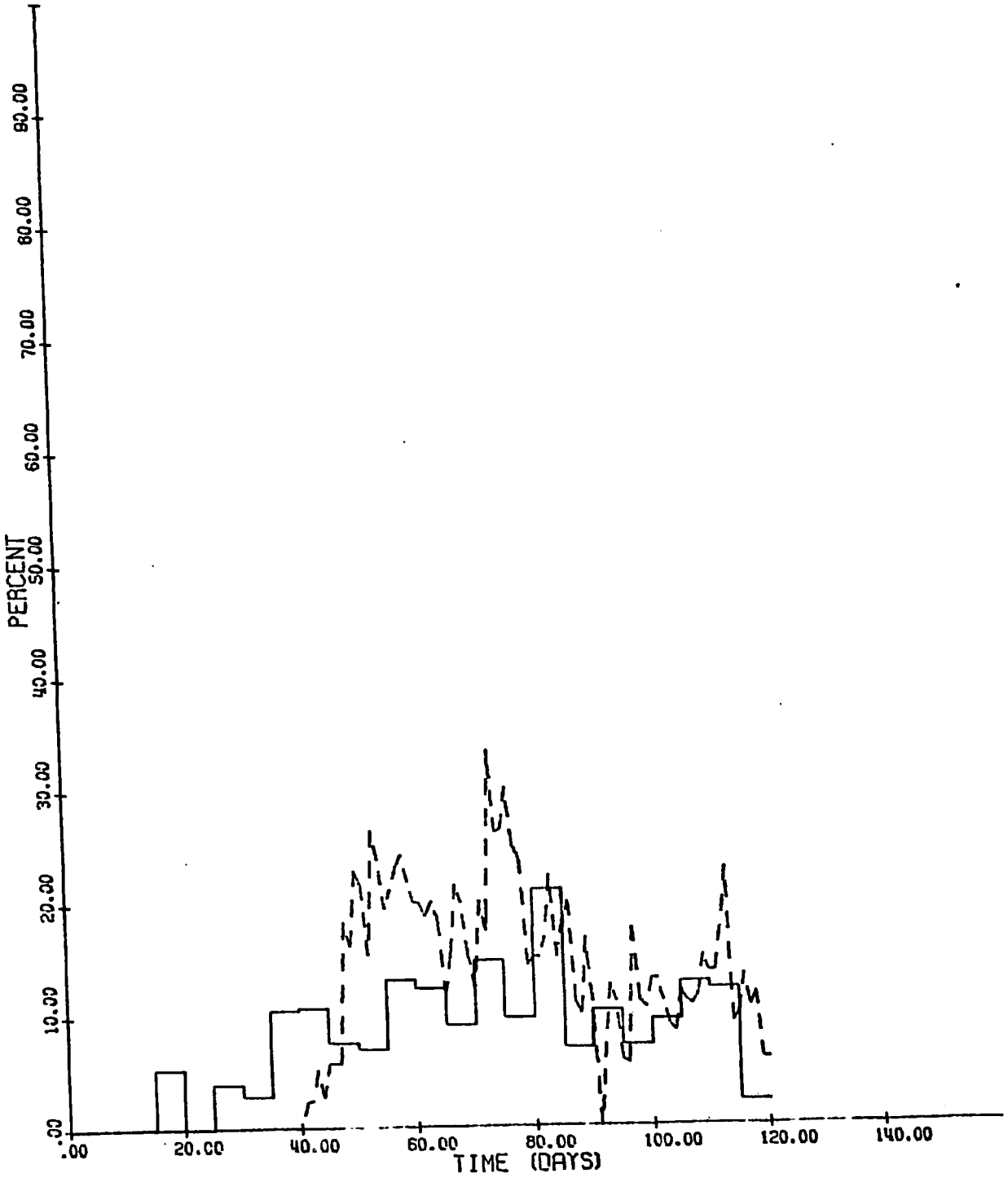
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 300 20 B1 -

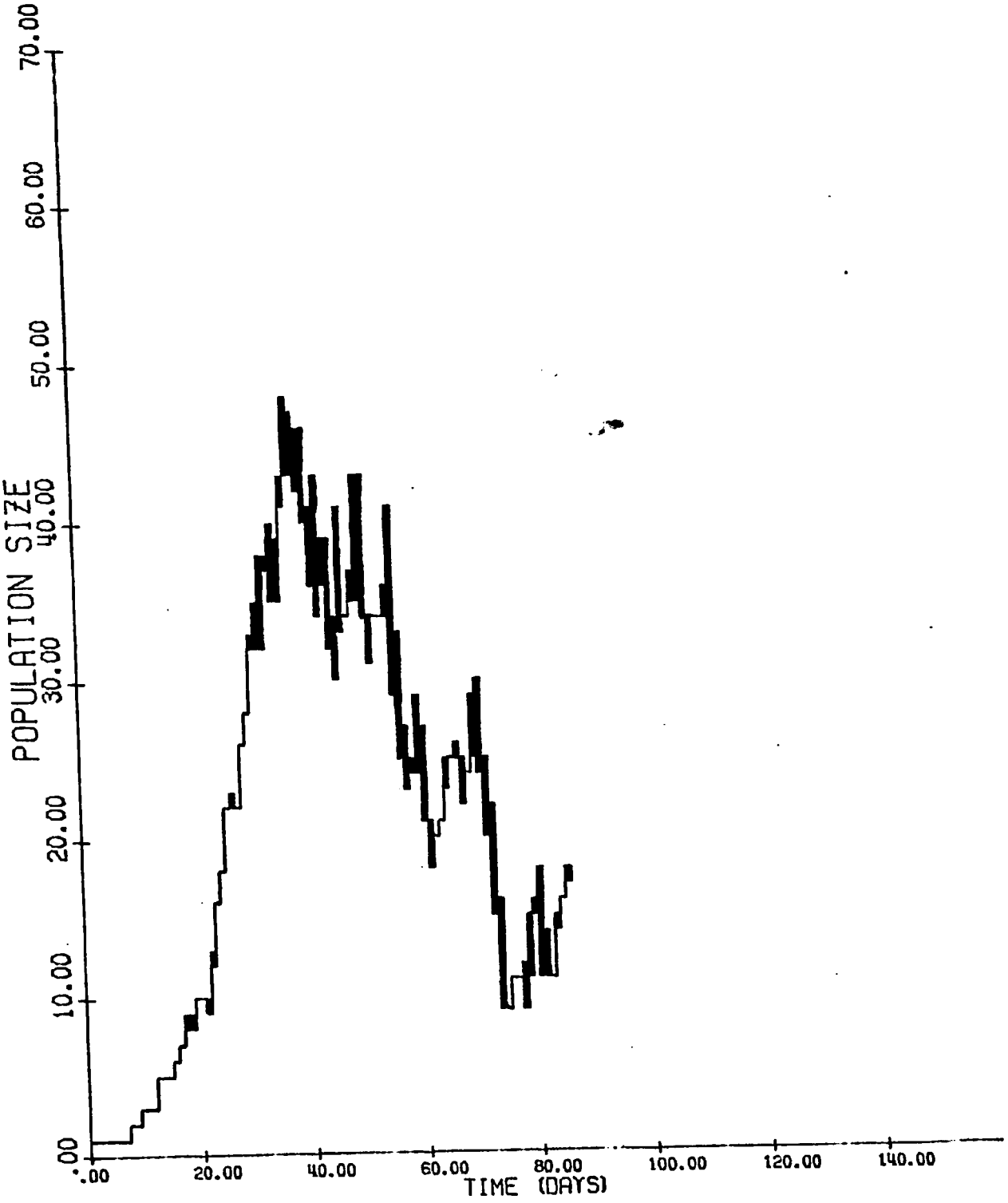
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE: AVERAGES OF 5-DAY PERIODS)



POPULATION 300 20 B2 - GROWTH CURVE

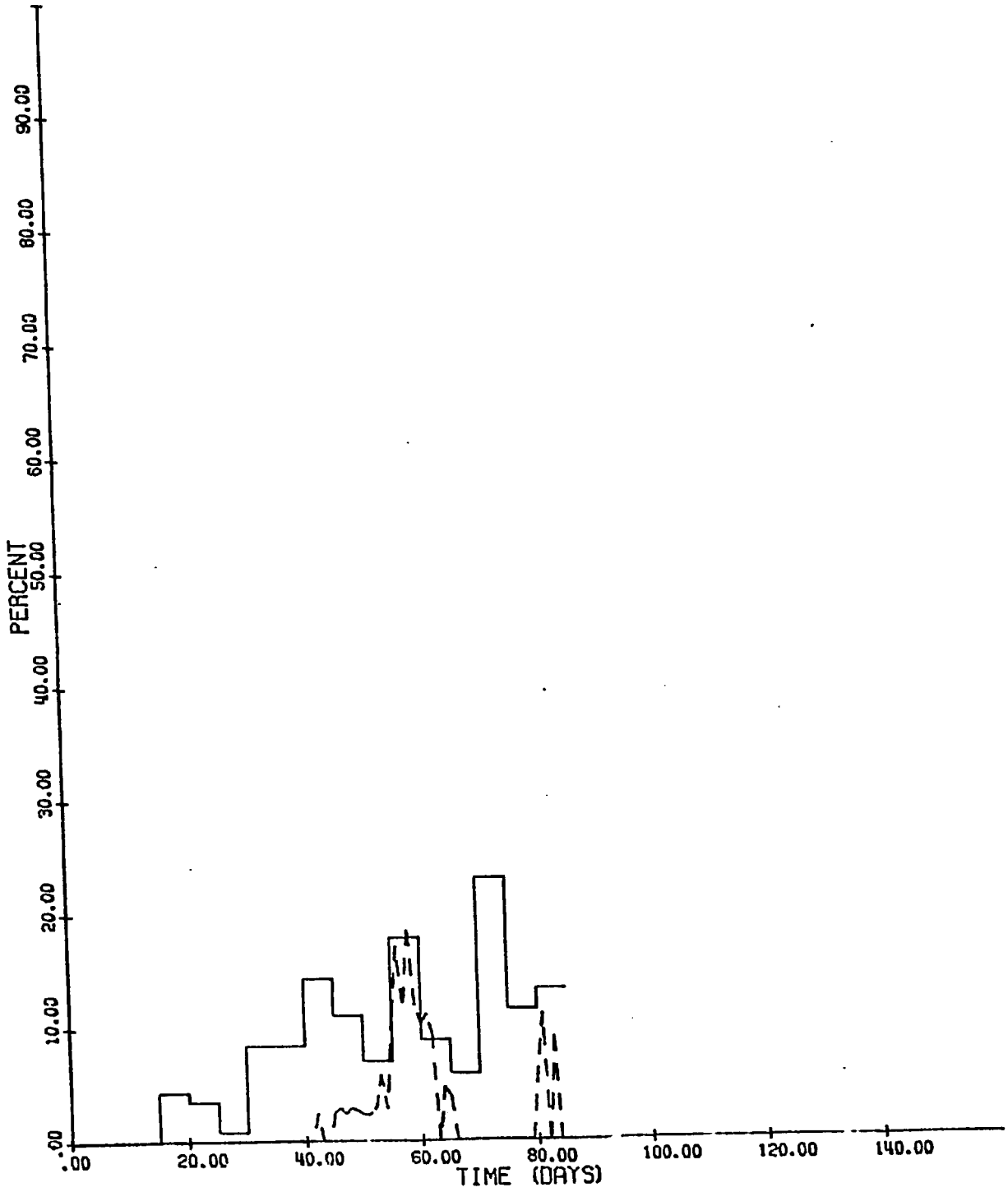
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 300 20 82 -

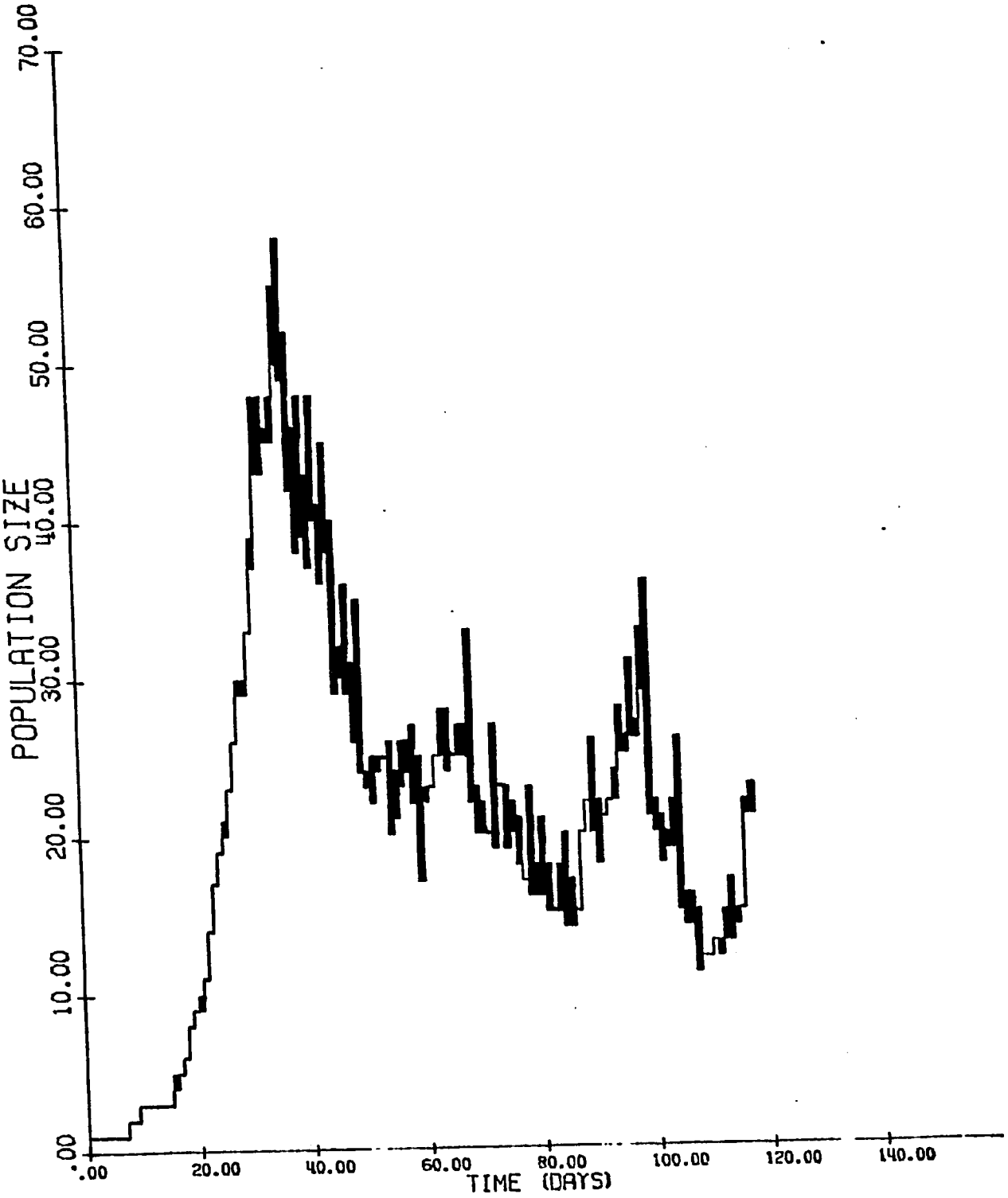
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 300 20 B3 - GROWTH CURVE

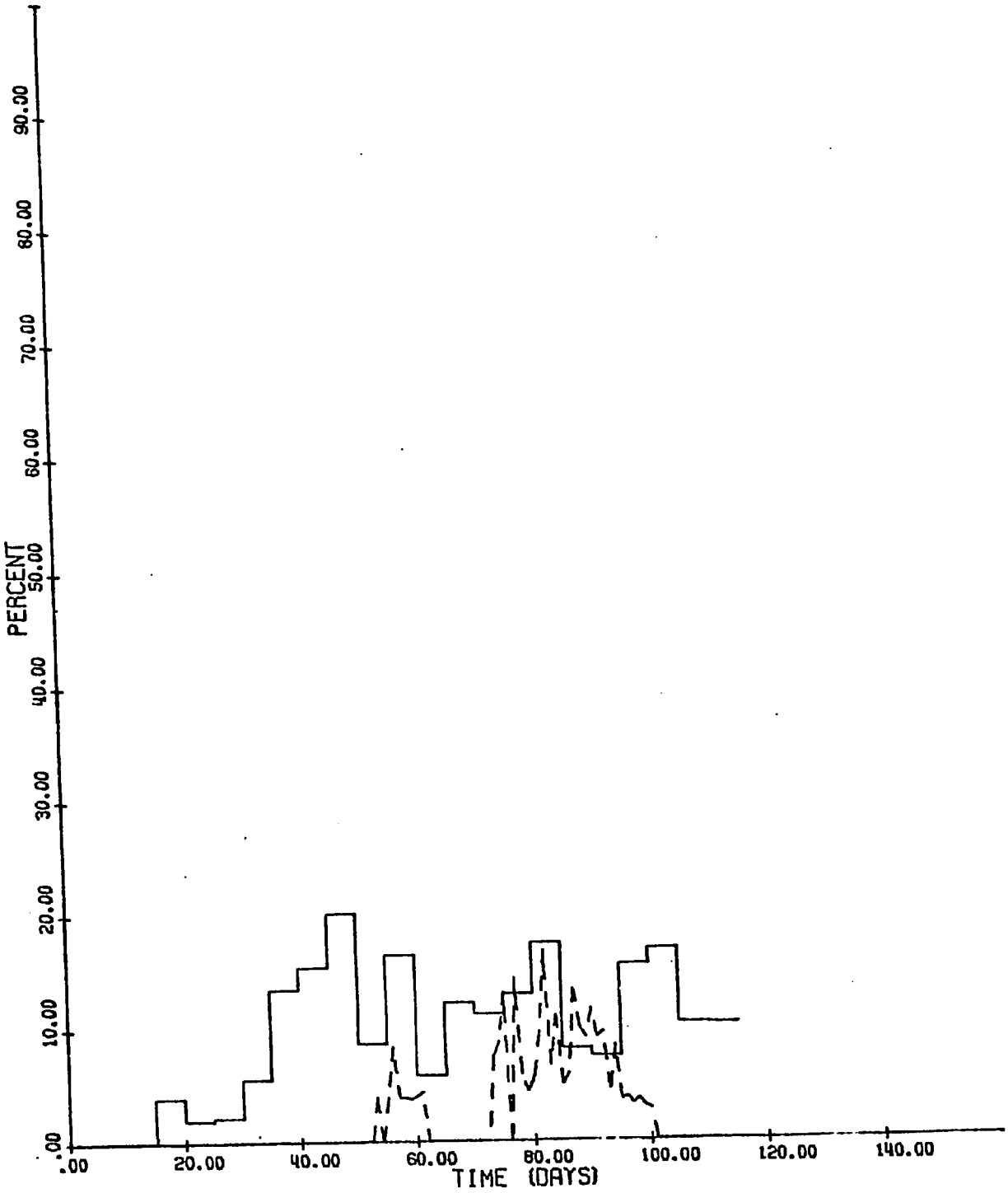
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 300 20 83 -

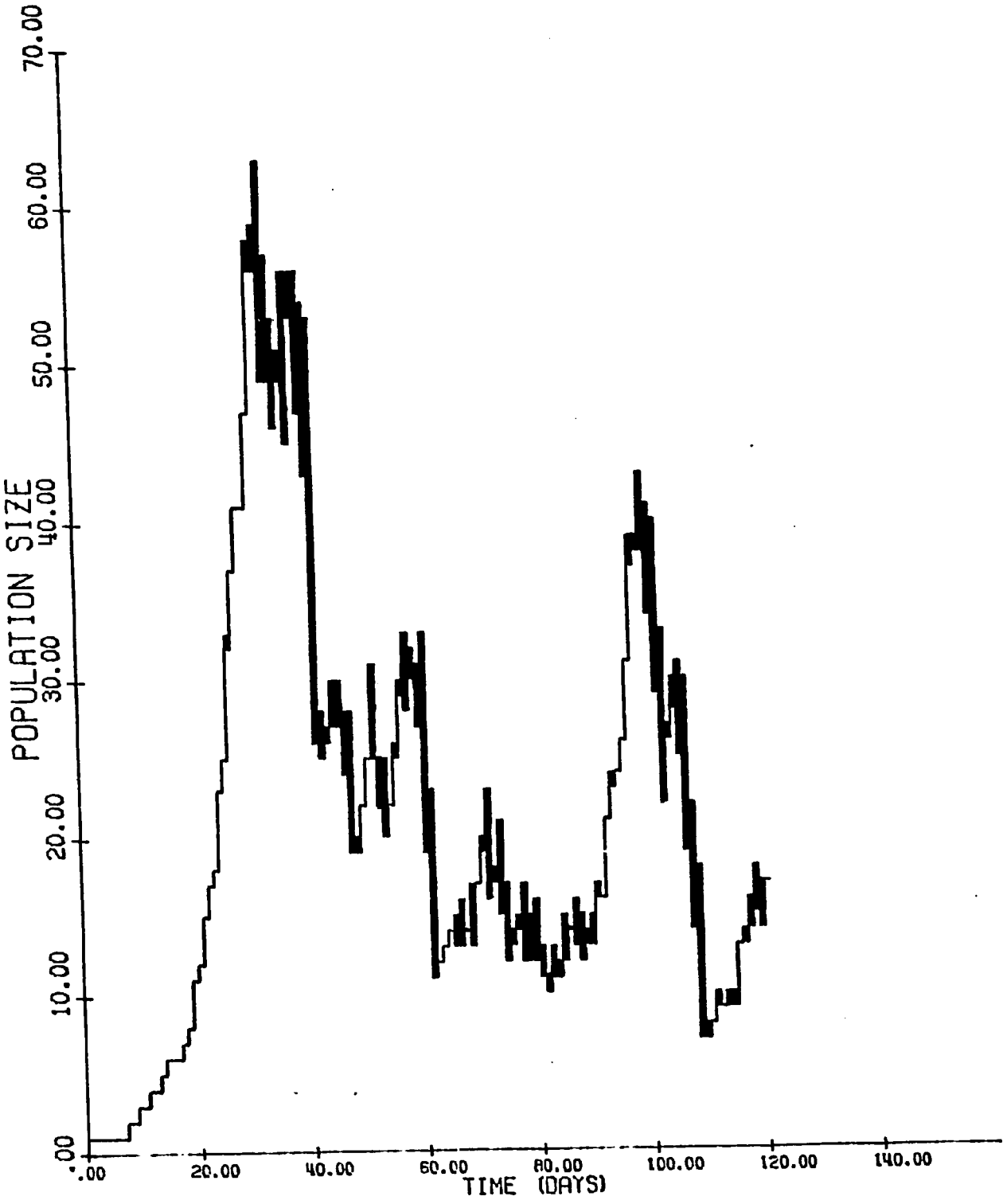
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 300 40 B1 - GROWTH CURVE

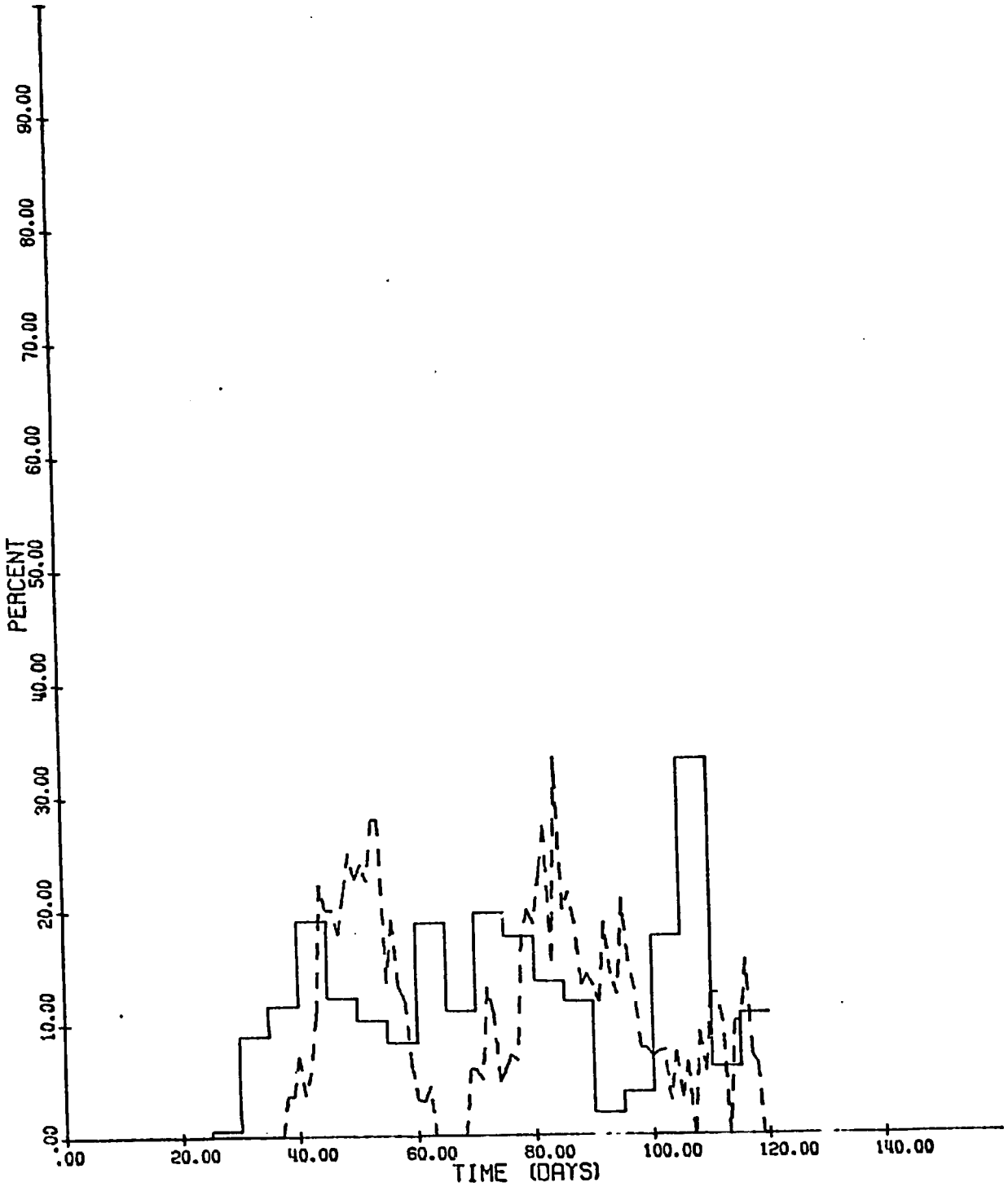
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 300 40 B1 -

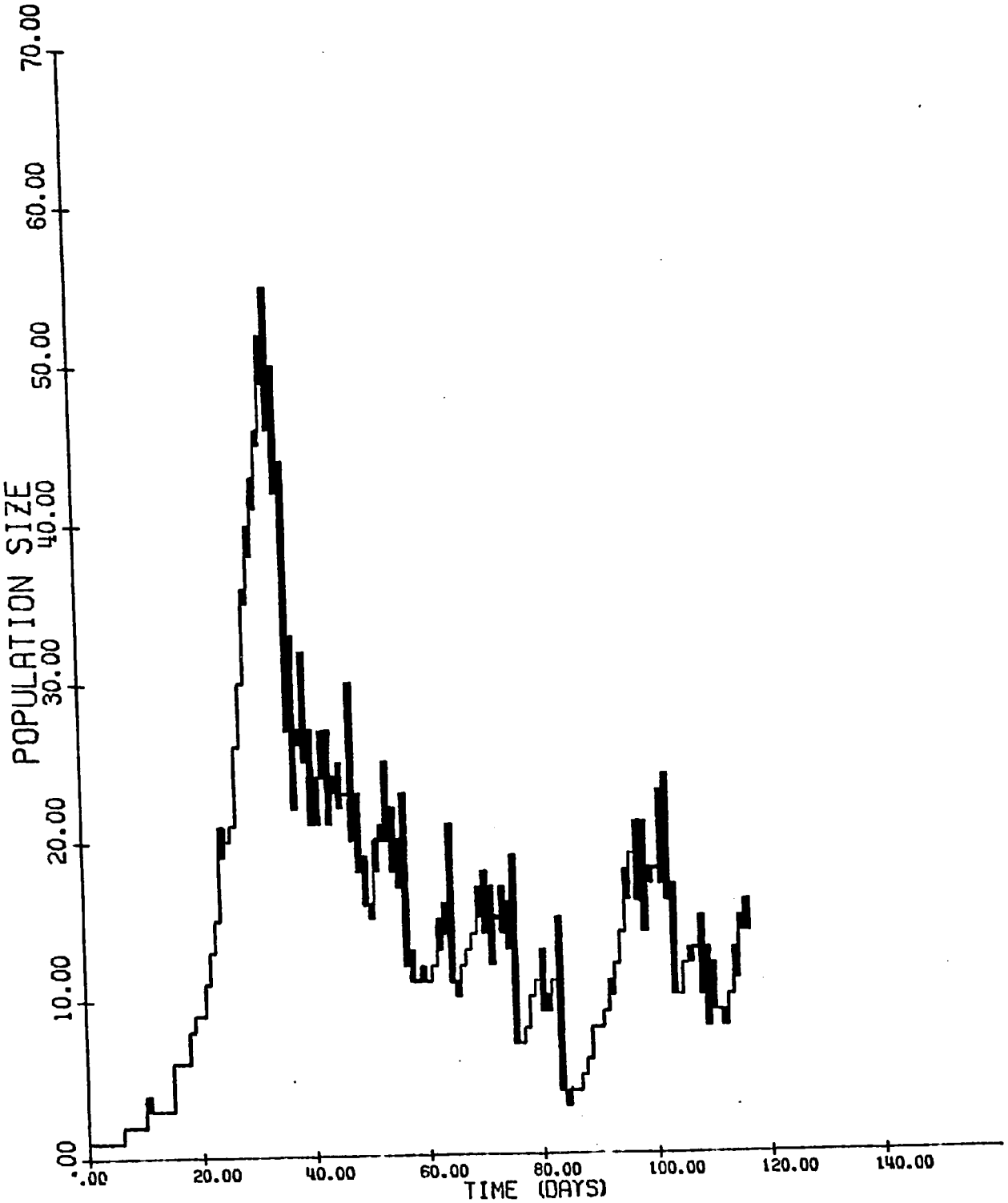
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 300 40 B2 - GROWTH CURVE

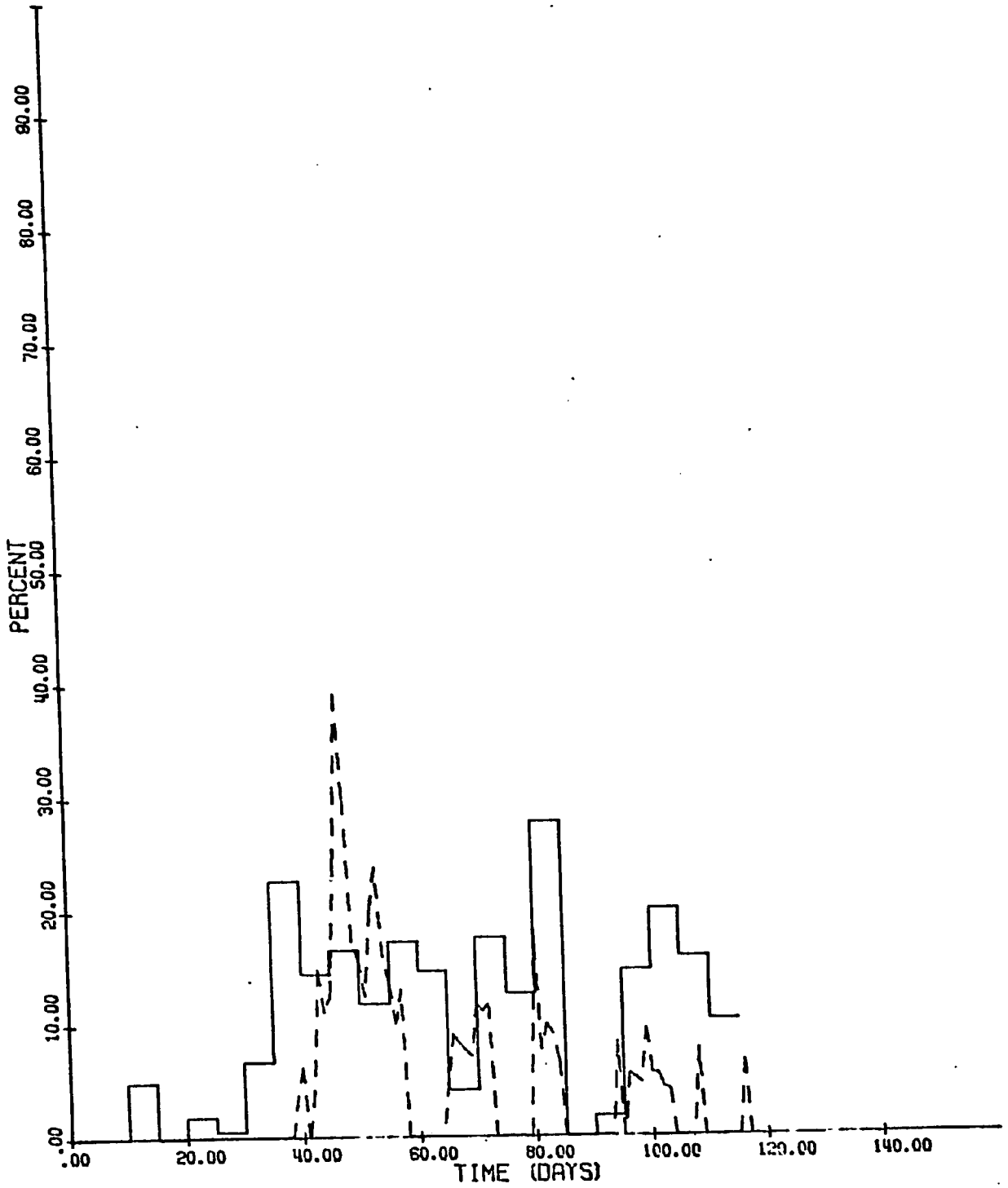
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 300 40 82 -

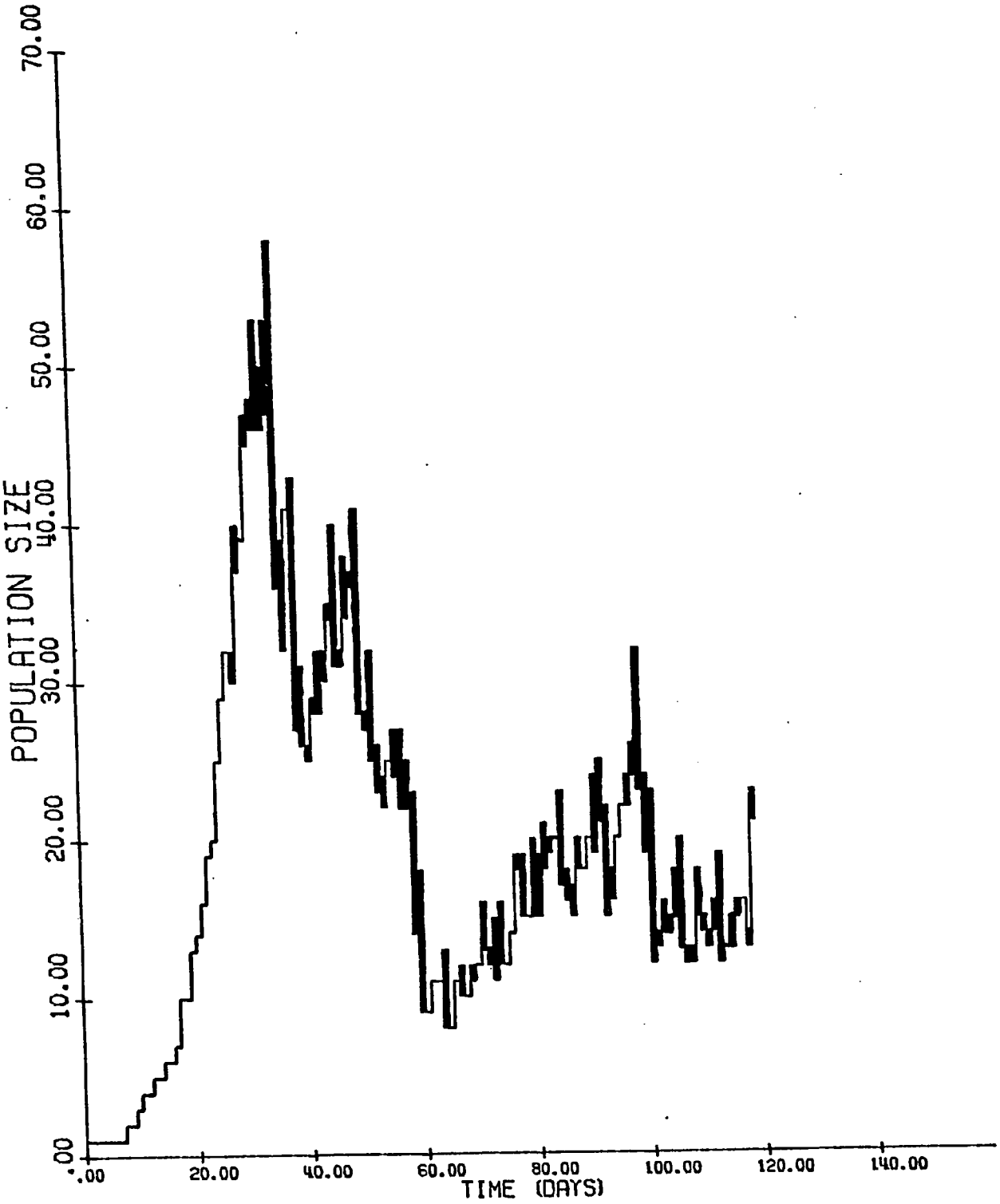
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 300 40 83 - GROWTH CURVE

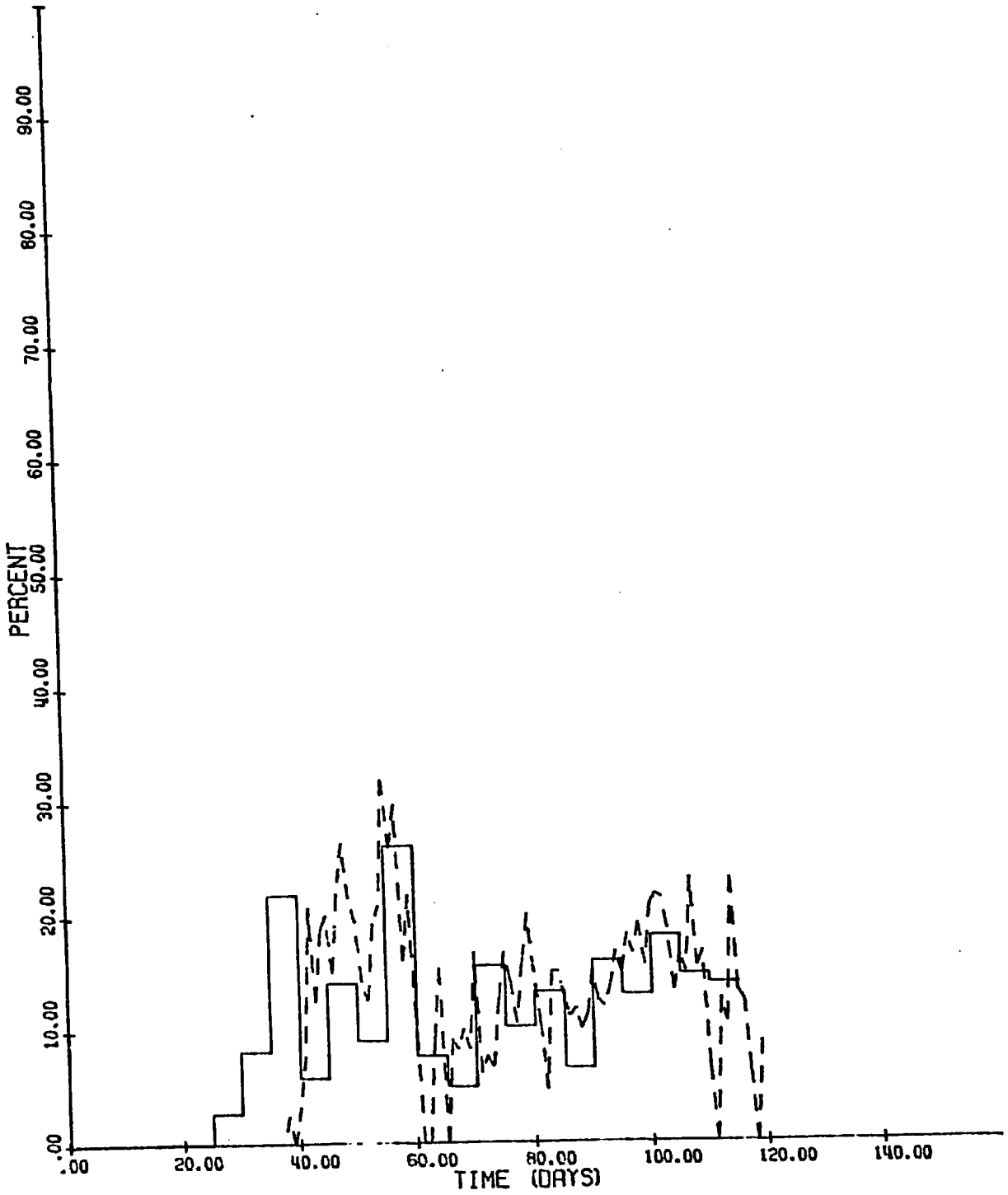
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 300 40 83 -

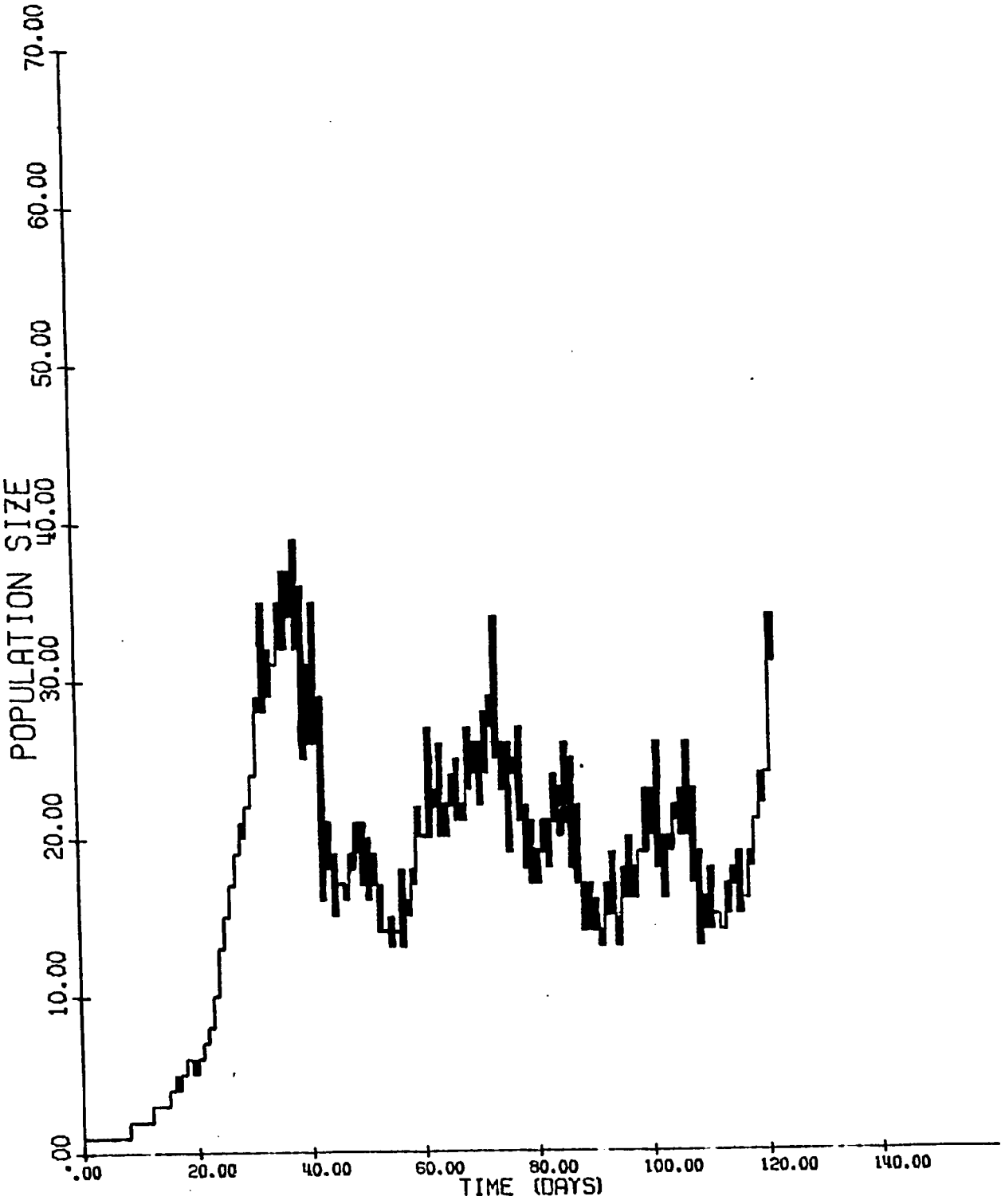
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE: AVERAGES OF 5-DAY PERIODS)



POPULATION 300 80 B1 - GROWTH CURVE

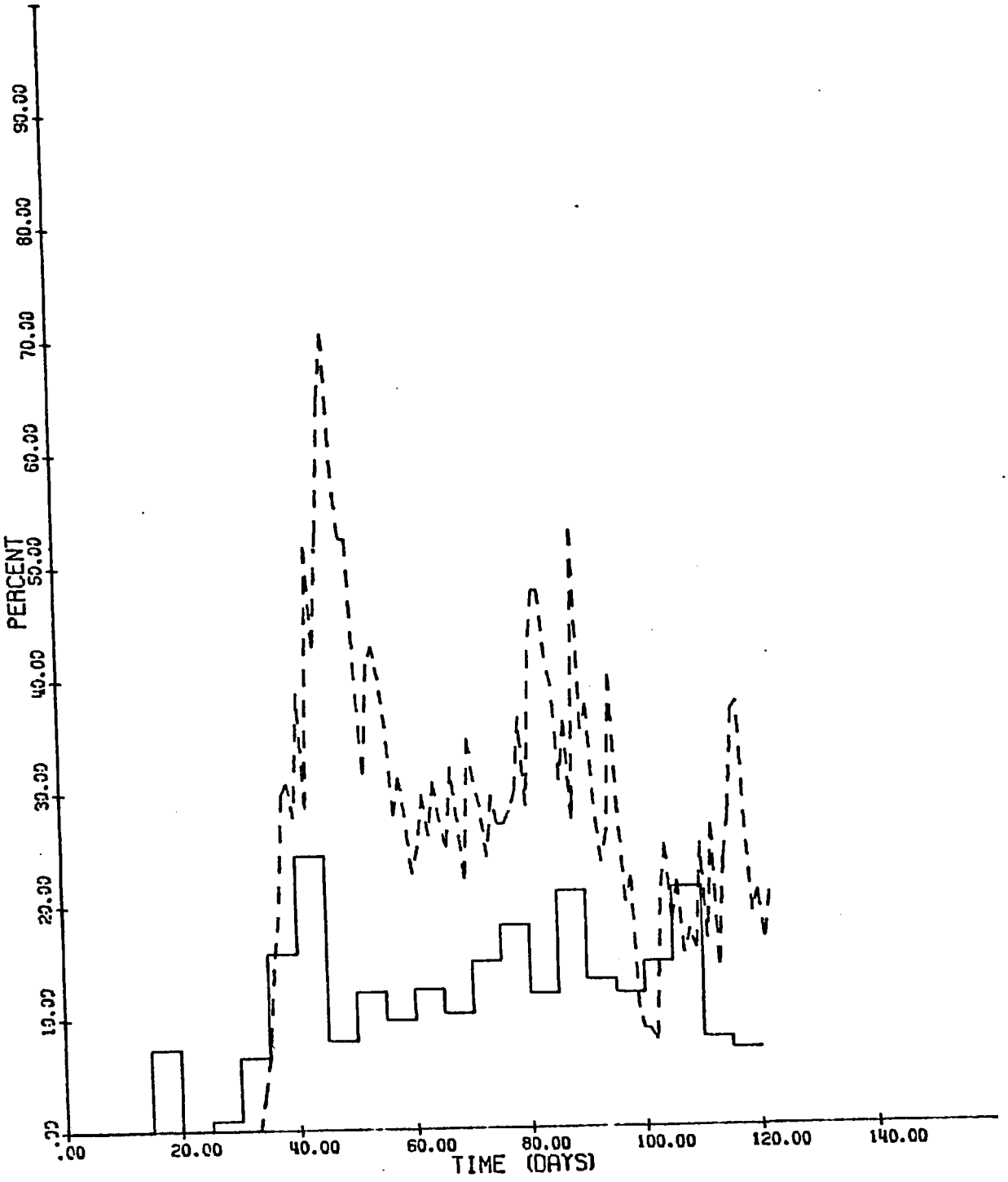
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 300 80 81 -

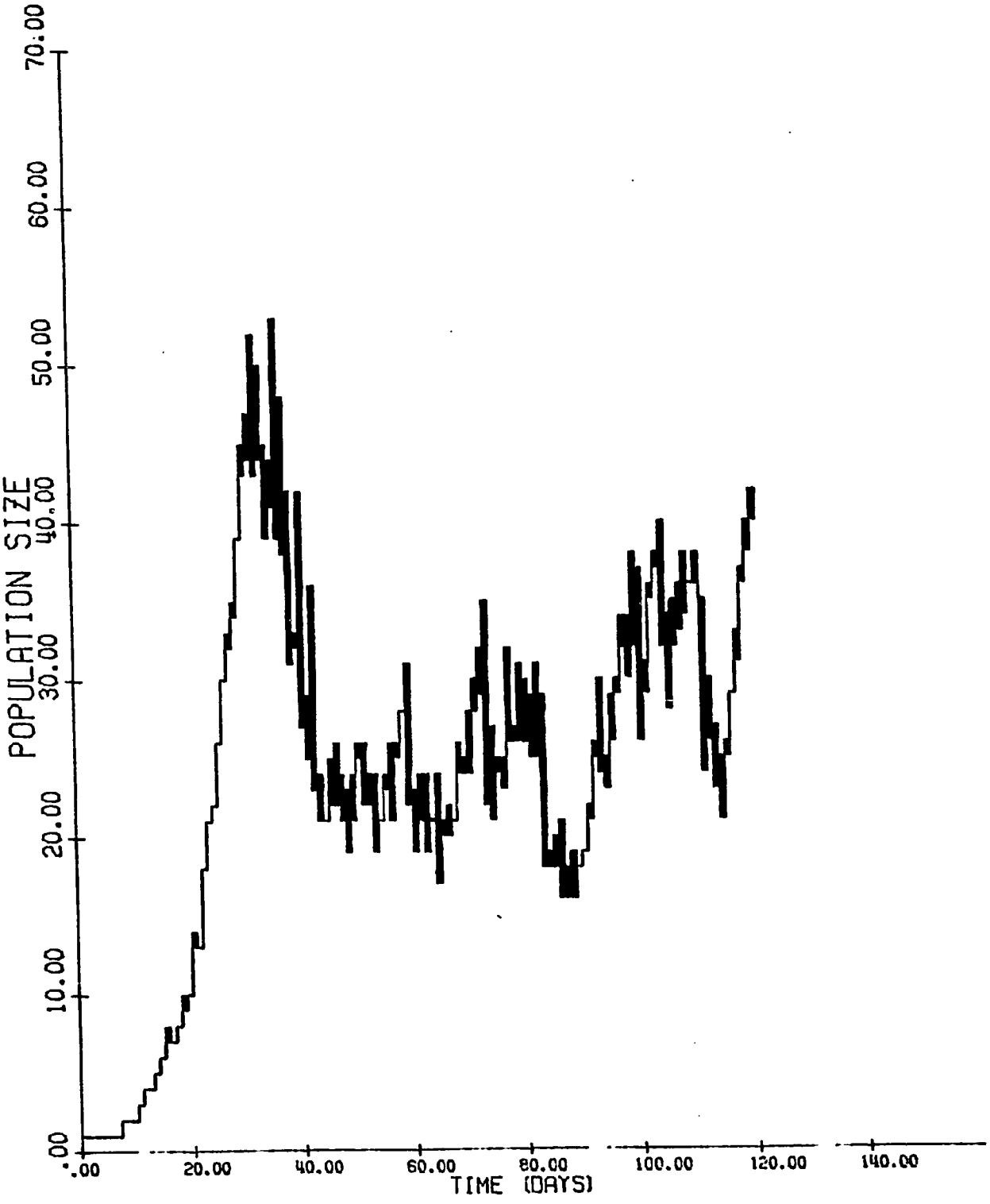
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE: AVERAGES OF 5-DAY PERIODS)



POPULATION 300 80 B2 - GROWTH CURVE

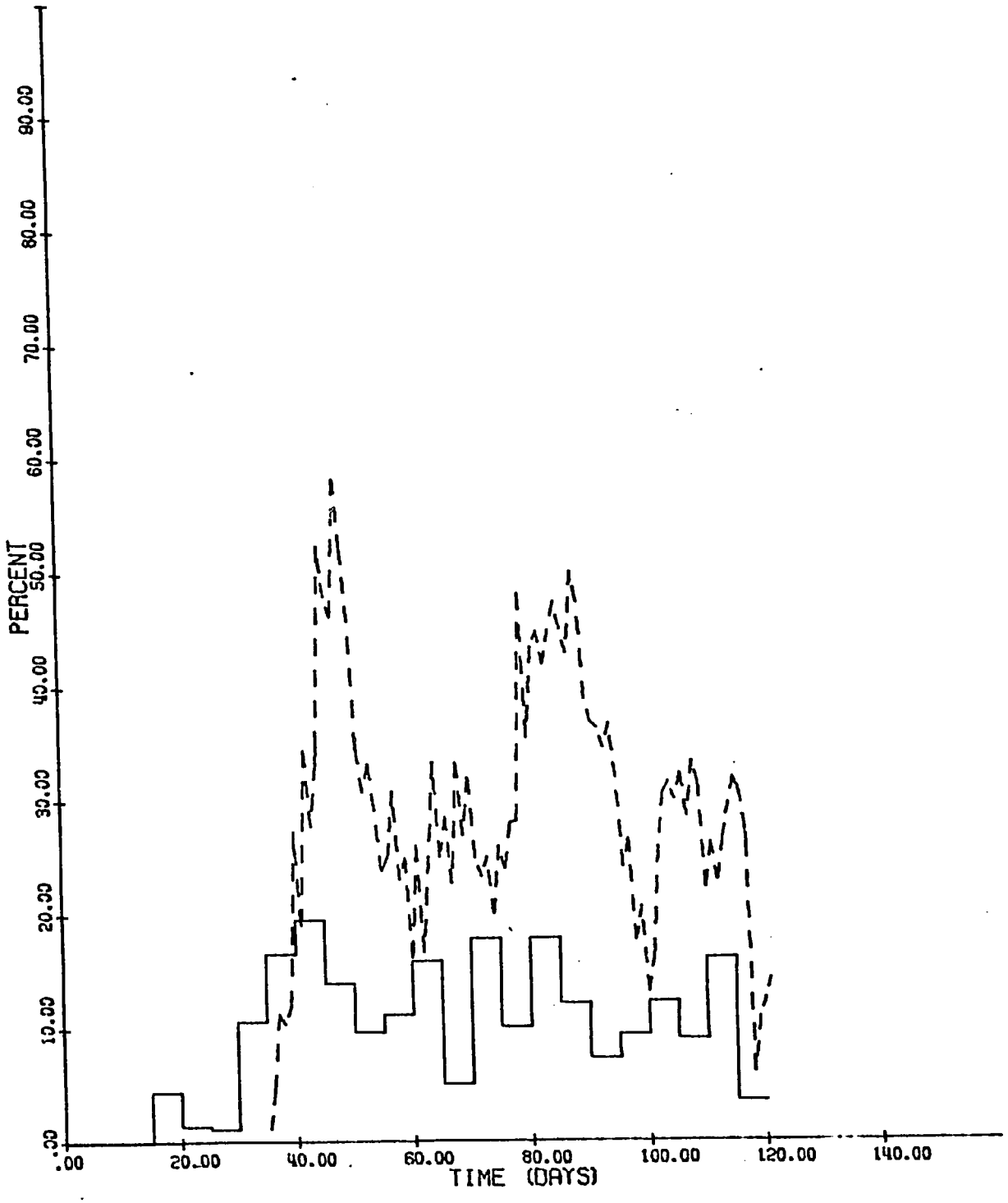
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 300 80 82 -

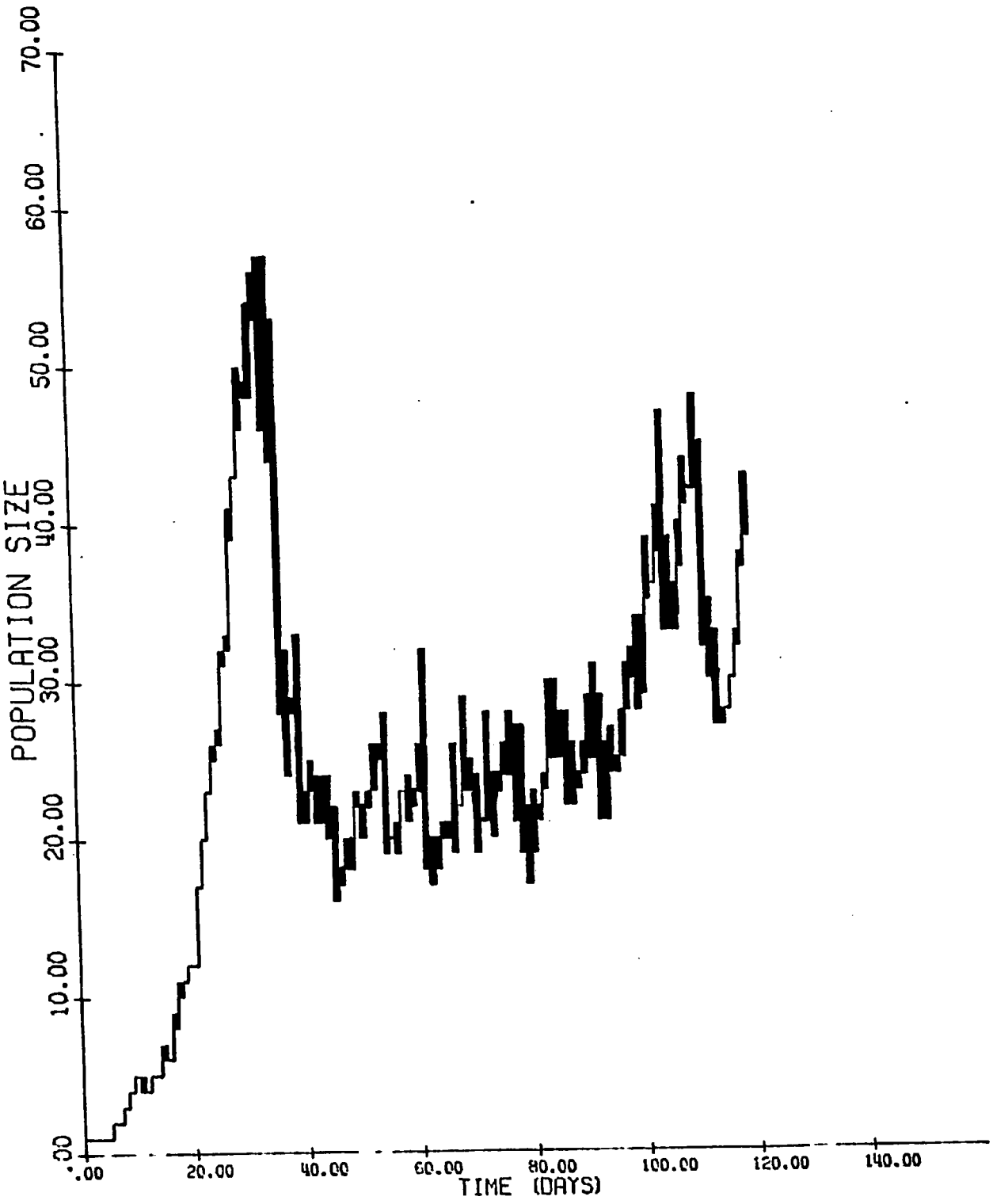
PERCENT SEXUAL HYDRA (DASHED LINE) AND

FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



POPULATION 300 80 B3 - GROWTH CURVE

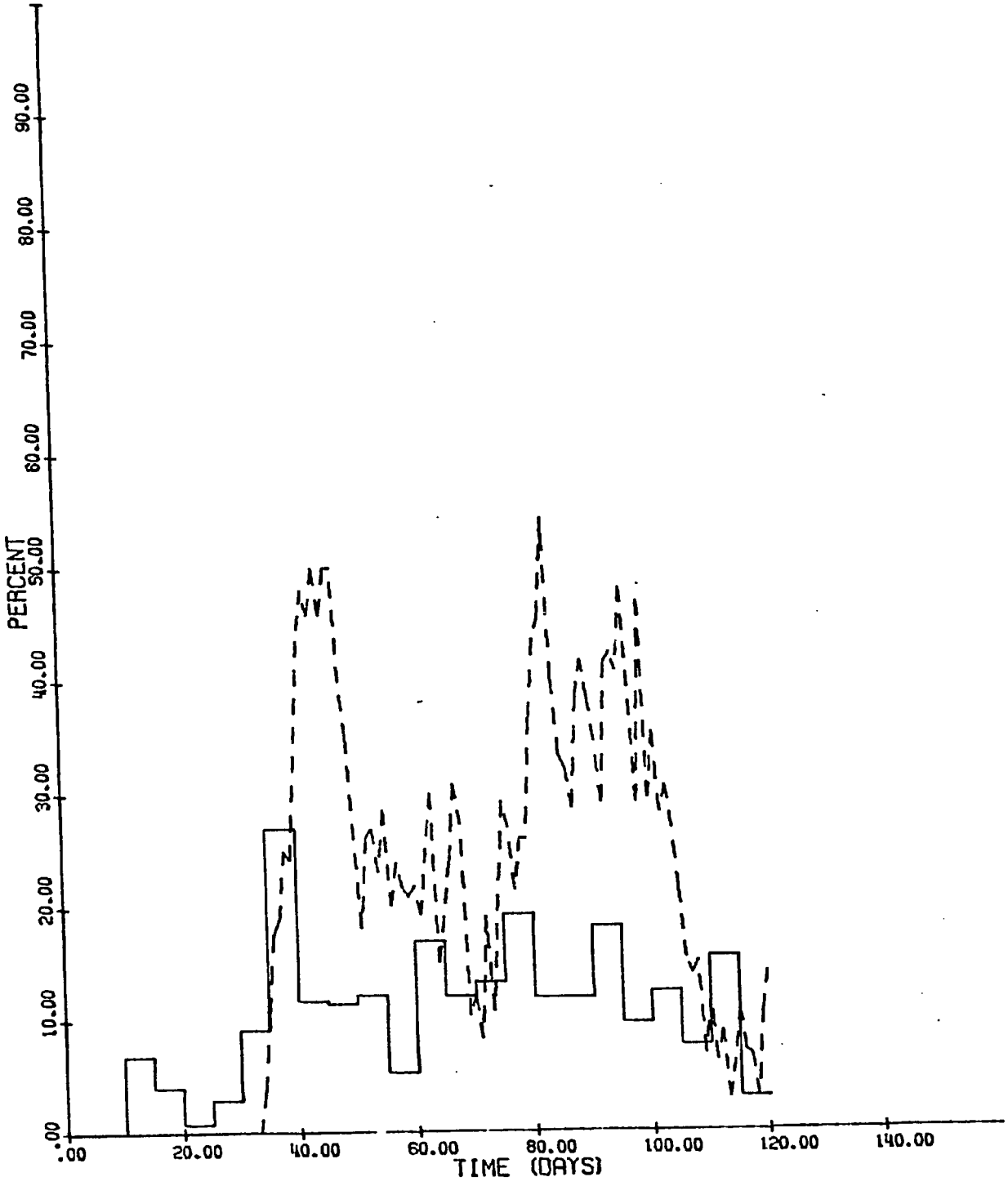
SOLID AREAS INDICATE FLOATING HYDRA, REMOVED DAILY



POPULATION 300 80 83 -

PERCENT SEXUAL HYDRA (DASHED LINE) AND

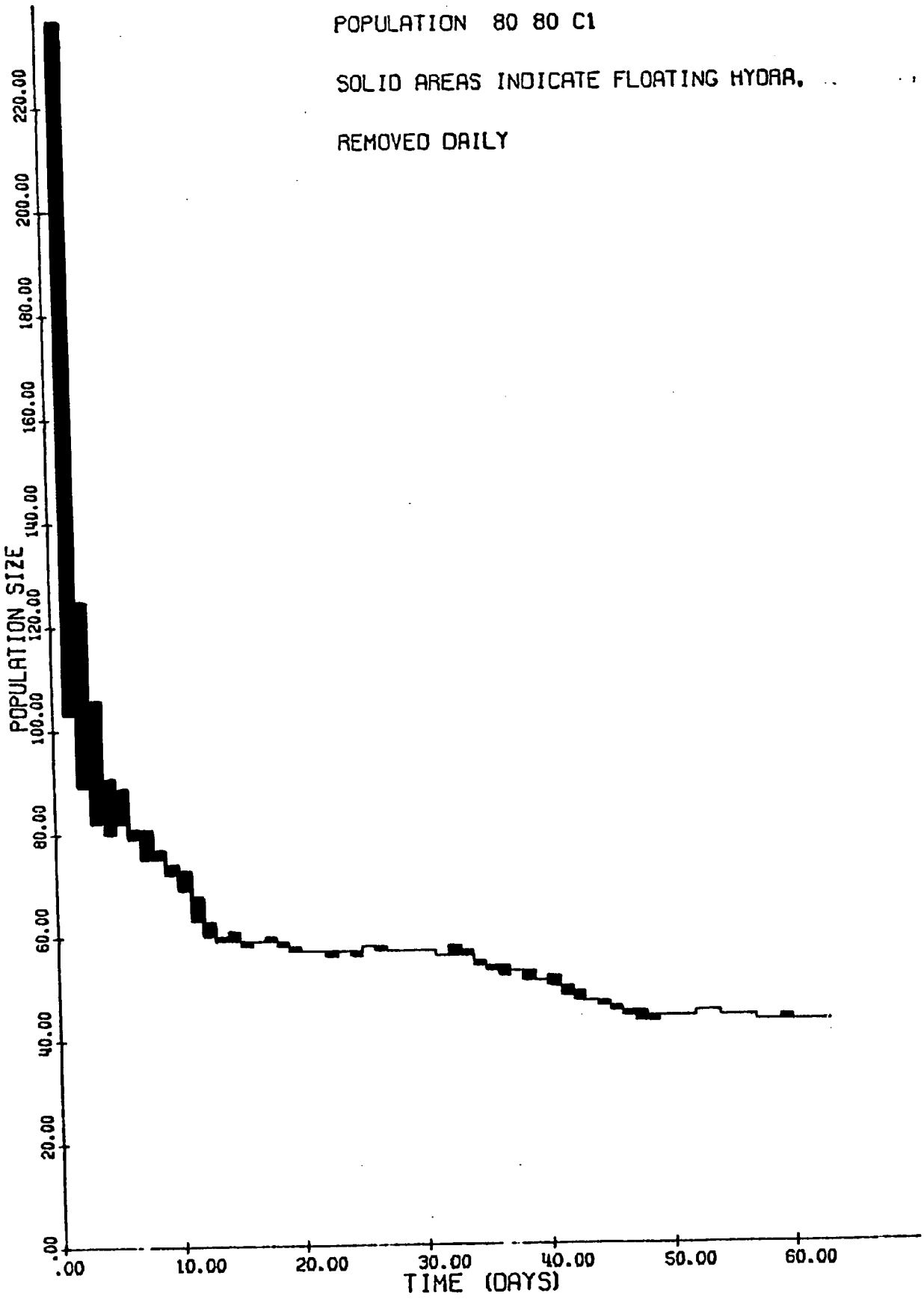
FLOATING HYDRA (SOLID LINE; AVERAGES OF 5-DAY PERIODS)



APPENDIX C

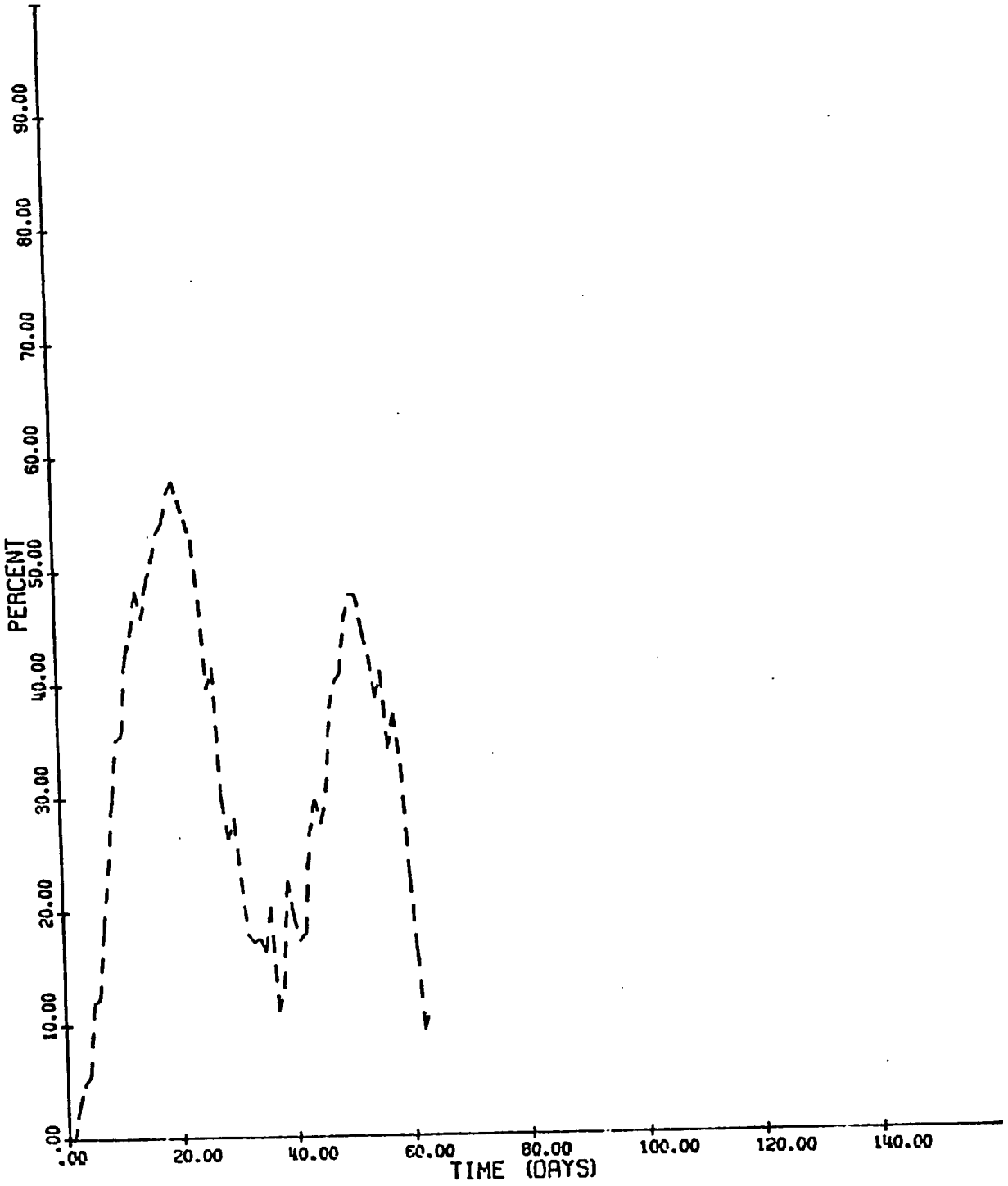
Curves of the changes in population size (curve 1) and the frequency of sexuality (curve 2) of the "C" populations. The following table gives for each curve the page on which it can be found.

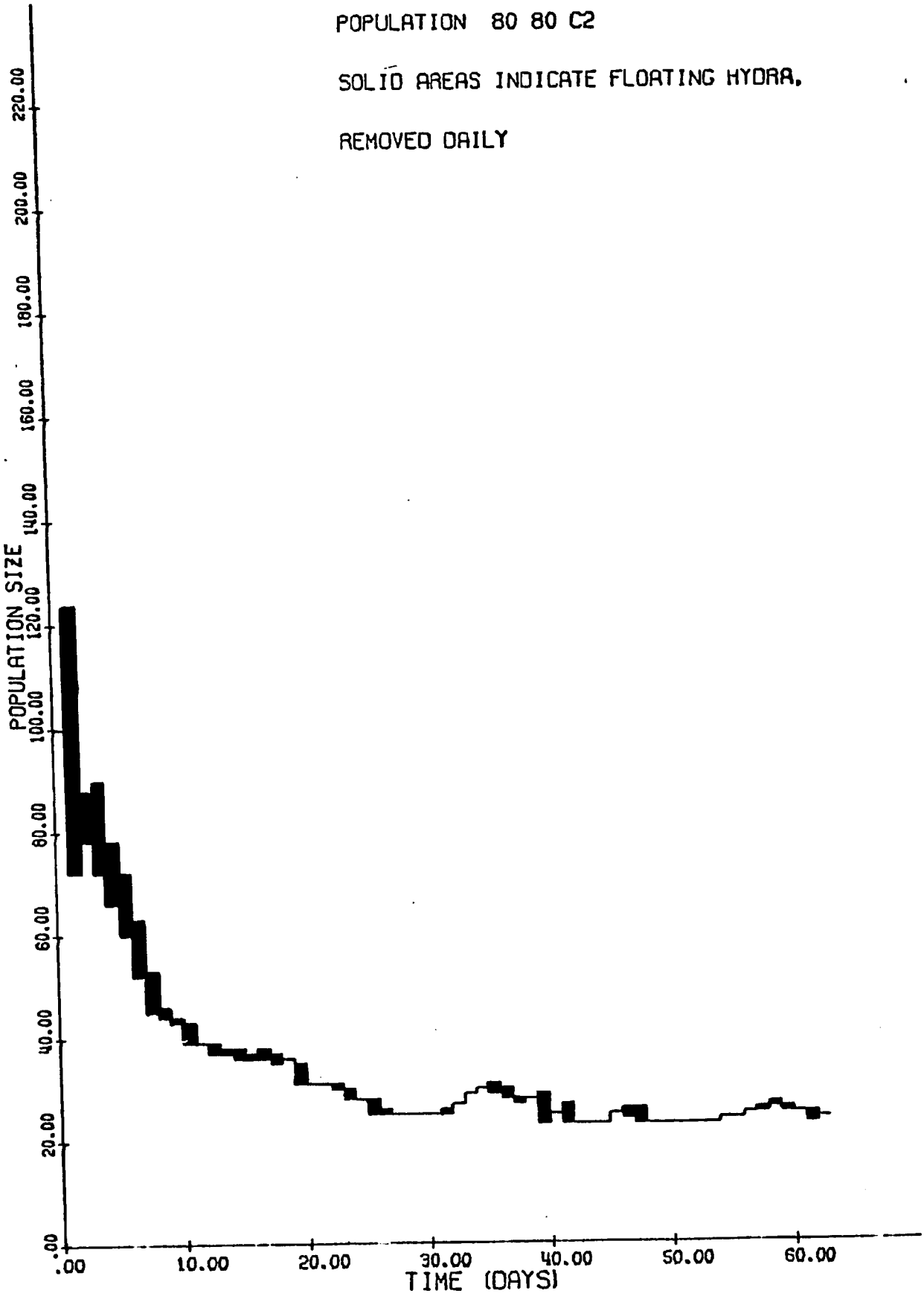
Population	Curve 1	Curve 2
80 80 C1	324	325
80 80 C2	326	327
80 80 C3	328	329


POPULATION 80 80 C1
SOLID AREAS INDICATE FLOATING HYDRA.
REMOVED DAILY
POPULATION SIZE
.00
20.00
40.00
60.00
80.00
100.00
120.00
140.00
160.00
180.00
200.00
220.00
.00
10.00
20.00
30.00
40.00
50.00
60.00
TIME (DAYS)

POPULATION 80 80 C1 -

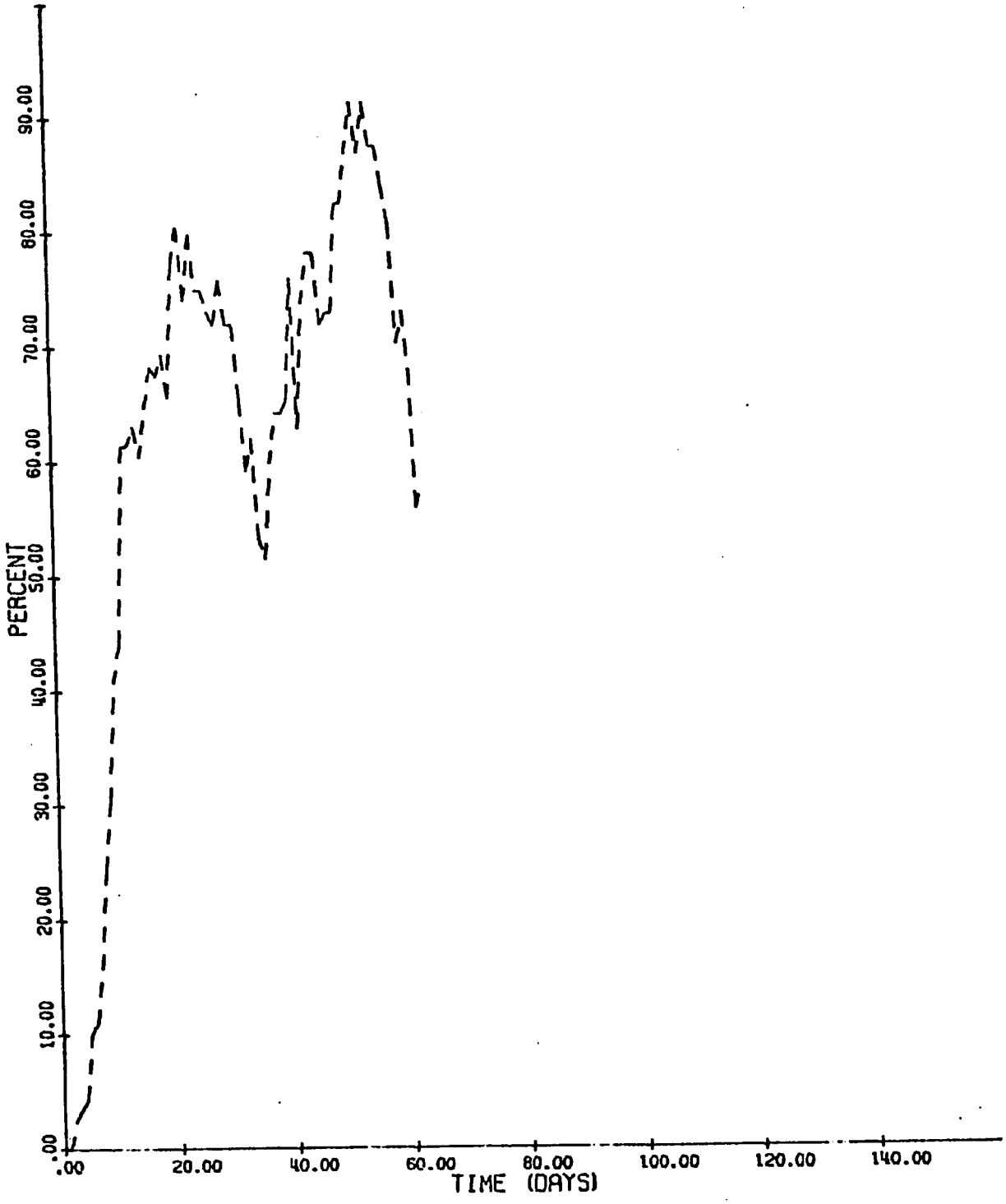
PERCENT SEXUAL HYDRA

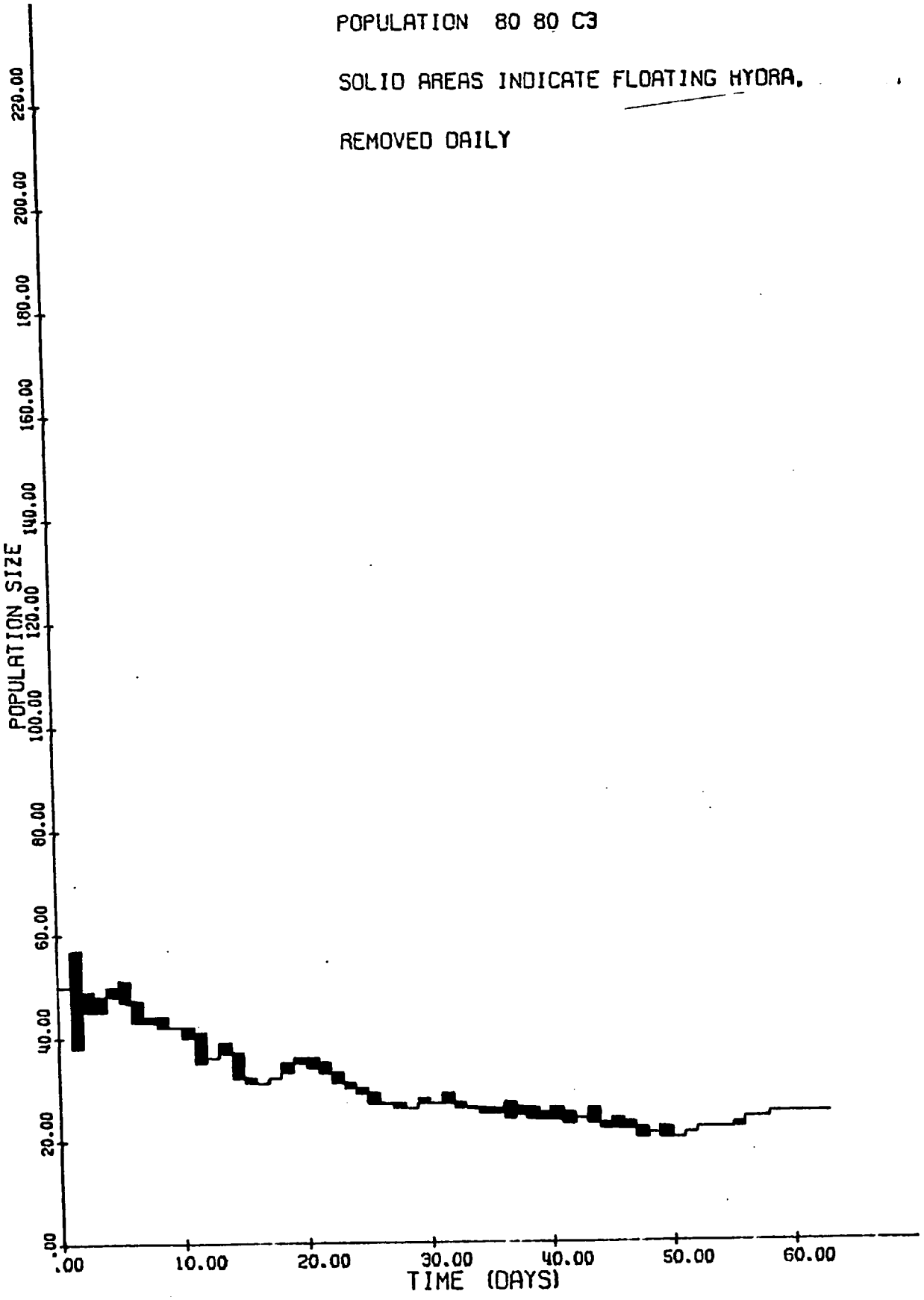



POPULATION 80 80 C2
SOLID AREAS INDICATE FLOATING HYDRA.
REMOVED DAILY
POPULATION SIZE
.00
20.00
40.00
60.00
80.00
100.00
120.00
140.00
160.00
180.00
200.00
220.00
.00
10.00
20.00
30.00
40.00
50.00
60.00
TIME (DAYS)

POPULATION 80 80 C2 -

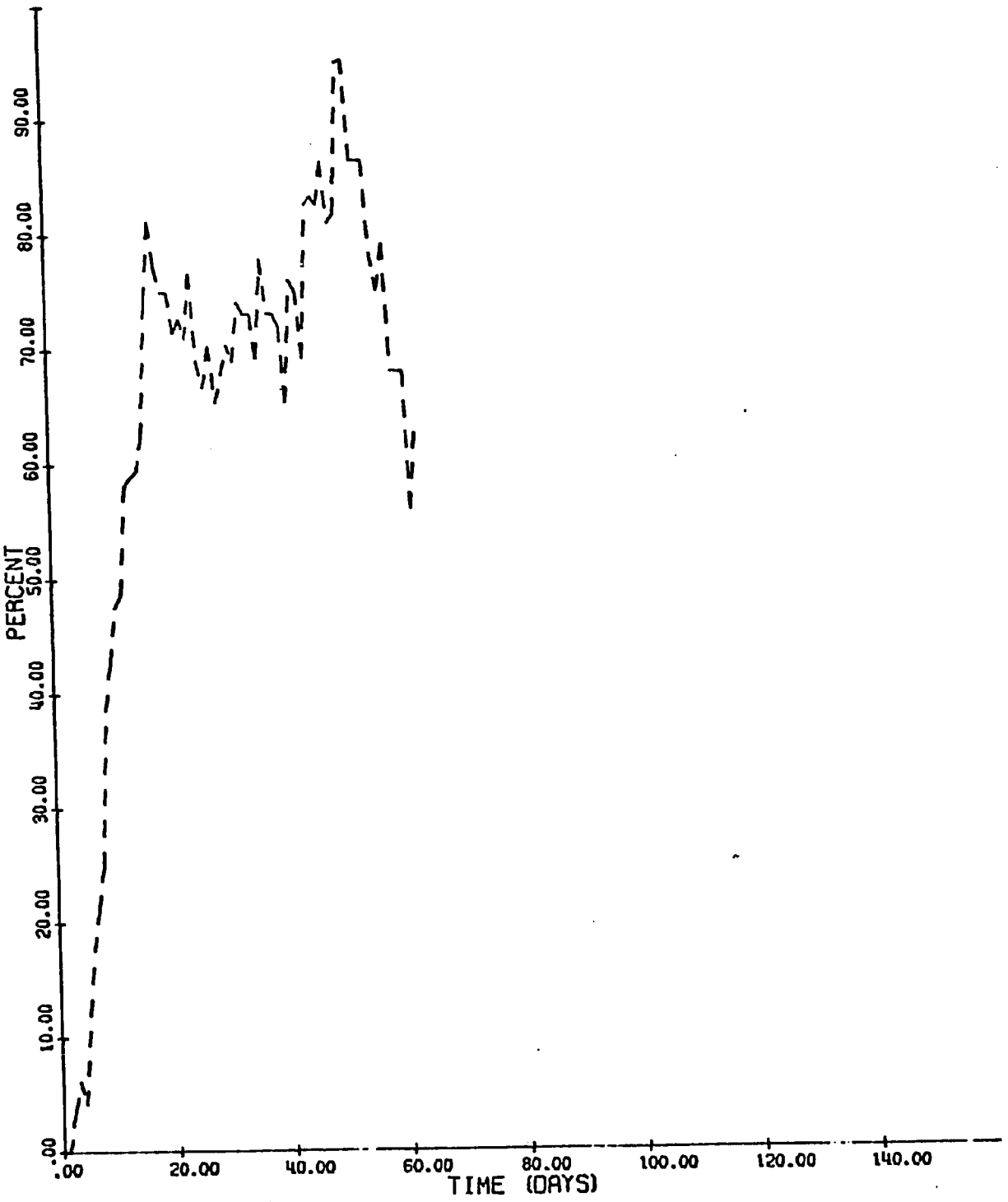
PERCENT SEXUAL HYDRA




POPULATION 80 80 C3
SOLID AREAS INDICATE FLOATING HYDRA.
REMOVED DAILY
POPULATION SIZE
220.00
200.00
180.00
160.00
140.00
120.00
100.00
80.00
60.00
40.00
20.00
.00
.00
10.00
20.00
30.00
40.00
50.00
60.00
TIME (DAYS)

POPULATION 80 80 C3 -

PERCENT SEXUAL HYDRA



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