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The Effect of Latitude on the Biology of
the Genus Cyclothone (Pisces: Gonostomatidae)

by

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A thesis submitted to the University of Southampton
for the degree of Doctor of Philosophy

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

OCEANOGRAPHY

Doctor of Philosophy

THE EFFECT OF LATITUDE ON THE BIOLOGY OF
THE GENUS CYCLOTHONE (PISCES: GONOSTOMATIDAE)

by Douglas Scott McKelvie

Samples collected from the eastern North Atlantic between 10°N and 60°N were used to study the variability in aspects of the biology of the mesopelagic fish genus Cyclothone (Gonostomatidae). Intra- and interspecific differences in the maximum size, size at maturity, sex ratio, spawning period, egg size and fecundity were compared among populations from different latitudes.

Eight species were found to inhabit the sampled area. C. braueri and C. microdon had the most extensive ranges at the northern end of the transect and were most suitable for intraspecific comparisons. C. pseudopallida, C. pallida, C. livida, C. acclinidens, C. alba and C. obscura were primarily found at the southern extent of the transect.

Populations of C. braueri and C. microdon at low latitudes were generally smaller, reached maturity at a smaller size, spawned earlier in the year and probably spawned over a longer period than those at high latitudes. In both species, fecundity was highest at 40°N in the spring. The number of eggs found in females was lower both at other latitudes and other seasons. The results suggested that C. microdon may not spawn at the northern extent of its range.

Some characters, such as sex ratio and pre-spawning egg size, were similar among species. Within the shallow-living species, those at lower latitudes attained a larger maximum size, appeared to be longer lived and had a larger size at maturity. However, C. alba was an exception to these general patterns. Deep-living species showed similar trends however, maximum size did not appear to differ among species. Observed fecundity was lower among species at lower latitudes. Standard length and latitude were the best predictors of fecundity. Depth only indirectly affected fecundity in that larger individuals and species were usually found at greater depth.

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Chapter 1

INTRODUCTION

Many oceanic organisms are widely distributed, possibly due to the apparent lack of barriers to dispersal in the pelagic environment. Distributions of pelagic fish have been correlated with the water masses (e.g. Ebeling 1962, Ebeling and Weed 1963, Backus et al. 1965, 1969, 1970, 1977) but few species are limited to one water mass and some species are limited to smaller areas within a water mass (Haedrich and Judkins 1979). Populations of species whose distributions cross water mass boundaries could be subjected to different environmental conditions over the species range. Environmental differences could result in taxonomic and biological differences among populations of a single species.

Intraspecific differences in morphometric and meristic characters have been found among populations of a species at different locations (Badcock 1981, Badcock and Araujo in press, Johnson and Barnett 1972, 1975, Baird 1971, Badcock and Baird 1980). Some of these studies conclude that there are isolated populations within a species although there is clearly variation in the degree of localization necessary before populations differ at the specific level. Badcock and Araujo (in press) and Badcock (1981) recognize isolated, phenotypically different populations of a single species covering fairly expansive areas within the myctophids whereas Gibbs et al. (1983) suggest that within the genus Eustomias populations are very localized and endemism is high.

Although taxonomic and phenotypic differences have been noted few

attempts have been made to assess biological differences over the range of a widely distributed species. Karnella and Gibbs (1977) point out differences in the biology of Lobianchia dofleini between the eastern and western North Atlantic. But most studies are limited to restricted geographic areas such as Sagami Bay (Miya and Nemoto 1986a,b 1987a,b) or the Rockall Trough (Kawaguchi and Mauchline 1982,1987) and the species examined are locally abundant species although comparisons with other areas are possible (cf. Maurolicus muelleri Kawaguchi and Mauchline 1987). Comparisons among areas suggest that differences in variables such as size, lifespan, age and size at maturity, spawning time and fecundity can exist among populations of a single species.

The purpose of this study was to attempt to gain some insight into the broad scale variability of the breeding biology of widespread pelagic species in the eastern North Atlantic. The gonostomatid fish genus Cyclothone was chosen for detailed analysis for a number of reasons. Species within the genus are generally widespread (Badcock 1984) and extremely numerous, so suitable numbers are available for examination. The systematics are resolved with recent revisions by Mukhacheva (1974), Kobayashi (1973) and Badcock (1982). Other variables are available for comparative purposes such as depth range from samples obtained from mouth opening/closing nets fished in contiguous depth strata. In the eastern North Atlantic, closely related species overlap in their horizontal distributions allowing intraspecific differences to be compared with interspecific differences.

1.1 Review of the Biology of the genus Cyclothone

It has been suggested that the gonostomatid fish genus Cyclothone is the most abundant genus in the world ocean (Badcock 1982, Ahlstrom

1974). It is the most speciose and abundant genus within the family Gonostomatidae and is often the most abundant genus captured at meso- and bathypelagic depths (Mukhacheva 1964, Badcock 1982). There are 13 species worldwide, 10 of which are found in the Pacific Ocean (Mukhacheva 1964, Kobayashi 1973) and 9 in the Atlantic Ocean (Badcock 1982). Generally, species are widespread, 7 are common to both the Pacific and Atlantic Oceans. Four species, C. acclinidens, C. pallida, C. microdon, C. obscura, are common to the three major oceans (Marshall 1979). Few species are restricted to one water mass (Kobayashi 1973, Mukhacheva 1974) although C. pygmaea is restricted to the Mediterranean (Badcock 1984) and C. livida is thought to be associated with oceanic islands (Badcock 1984).

Species have been divided into groups based on a number of criteria. Taxonomically, Mukhacheva (1964) suggested a "signata" group (C. alba and C. signata), a "pallida" group (C. braueri, C. pseudopallida, C. pallida, and presumably C. parapallida (Badcock 1982)), and a "microdon" group (C. microdon, C. pacifica, C. acclinidens and C. obscura). Based on appearance and habitat there are two groups, a darker, deeper-living form characterized by C. microdon, C. pallida, and C. obscura and a lightly pigmented shallower-living form characterized by C. braueri, C. alba, and C. pseudopallida (Kobayashi 1973). Finally Badcock (1982) has separated the Atlantic species by their distributional patterns into temperate-subtropical (C. braueri and C. microdon), subtropical-tropical (C. pallida and C. pseudopallida), tropical (C. acclinidens, C. alba, C. parapallida, and C. obscura) and a pseudoceanic subtropical-tropical (C. livida).

As mentioned previously, species are generally widespread. Badcock (1982) qualifies his distributions by adding that these terms only represent the centres of abundance and that all species except C. parapallida and C. obscura can be taken anywhere between the equator and 60°N in the eastern North Atlantic. Marshall (1979) has pointed out that most of the deeper living forms seem to be more abundant in areas of eutrophic surface waters. Despite their occurrence over wide ranging physical conditions there has been little evidence of intraspecific variation (Kobayashi 1973, Mukhacheva 1974) except for a difference in the size of gill lamellae with differences in oxygen

concentration (Kobayashi 1973). Quero (1975) suggested there was significant variability within C. acclinidens to support an argument for another species, C. pseudoacclinidens, although this has been refuted (Mukhacheva in press, cited by Parin 1979, Badcock 1982).

All species have relatively discrete depth ranges (Mukhacheva 1964, DeWitt 1972, Badcock and Merrett 1976) although the depth range of some species changes with latitude (Badcock and Merrett 1977). The depth ranges of the species present in the eastern North Atlantic are given in Table 1. There is no evidence for daily vertical migration for those species studied (DeWitt 1972, Bond 1974, Badcock and Merrett 1976, 1977, Badcock 1984).

Structure within the depth distribution is complex. A size-depth relationship is evident both within and among species. Larger species are deeper living (Kobayashi 1973, Badcock 1984) and within a species larger individuals live deeper in the water column (DeWitt 1972, Kobayashi 1973, Bond 1974, Badcock and Merrett 1976, Roe and Badcock 1984). The larger, deeper living individuals of a species tend to be mature females whereas smaller less mature females are shallower and males and juveniles are in the upper limits of the species depth range (Badcock 1970, DeWitt 1972, Badcock and Merrett 1976, Roe and Badcock 1984, Miya and Nemoto 1986a,b 1987a,b). It appears that mature males go in search of females as a few mature males can be found at the depth of the mature females (Badcock and Merrett 1976). Also, the pronounced nasal rosette of mature males suggests some sort of olfactory cue is present to facilitate mate location by the males (Marshall 1967, Badcock and Merrett 1976) and males possess more red muscle than females allowing sustained movement when searching for a mate (Marshall 1971).

Most species are dioecious, however, two species C. atraria (Miya and Nemoto 1985) and C. microdon (Badcock and Merrett 1976) are protandrous hermaphrodites. Spawning probably occurs at depth with the eggs floating to the surface to hatch as larvae are found in the upper 100m of the water column (Gorbunova 1971, Loeb 1979). Metamorphosis is sudden and short and the post-larvae descend to adult depths (Badcock 1977). Estimates of the time to transformation and

subsequent migration to adult depths range from 2 to 6-7 months (Miya and Nemoto 1986a,b 1987a,b). All eggs are spawned at once (Badcock 1984) although there is one report that suggests intermittent ovulation through the spawning season by C. braueri (Spanovskaya and Grigorash 1978). Fecundity is size related, the larger females having more eggs (Badcock and Merrett 1976, Miya and Nemoto 1986a,b 1987a). Badcock and Merrett (1976) report latitudinal variation in the fecundity of C. braueri, the ovaries of females at more northern latitudes containing more eggs. The preovulation size of eggs in females close to spawning is about 0.5mm for those species studied (Badcock 1984).

Attempts to estimate ages of species of Cyclothone have been made by Miya and Nemoto (1986a,b 1987a,b) in a series of papers describing samples from Sagami Bay, Japan. They report that the smaller shallower species tend to be short lived, often only up to 2 years. The larger species tend to be longer lived, up to a maximum of 9 years for C. atraria (Miya and Nemoto 1987b).

Copepods and ostracods are the primary food items taken by Cyclothone (DeWitt and Cailliet 1972, Roe and Badcock 1984, Mauchline and Gordon 1983, Go and Badcock 1986). Prey items taken generally reflect the abundant copepods present within the depth range (Roe and Badcock 1984) with some indication of size selectivity (Gorelova and Tseitlin 1979, Roe and Badcock 1984, Go and Badcock 1986). All feeding studies have found empty stomachs to be predominant and no diel differences in stomach fullness suggesting a constant low level of feeding (Collard 1970, DeWitt and Cailliet 1972, Mauchline and Gordon 1983, Roe and Badcock 1984, Go and Badcock 1986).

Table 1. Depth ranges of species of Cyclothone present in the eastern North Atlantic. (from Badcock 1984).

Species	Min. Depth (m)	Max. Depth (m)
braueri	250	900
pseudopallida	300	900
livida	300	1250
acclinidens	300	1200
alba	300	600
microdon	500	2700
pallida	400	1000
obscura	900	3000

Chapter 2

METHODS

Samples for the study were obtained from collections at the Institute of Oceanographic Sciences (IOS). Samples chosen were from various years and were available at intervals of approximately 10 degrees of latitude in the region of 20 degrees west longitude from 60 to 10 degrees north in the spring (March to May) and 50 to 20 degrees north in the autumn (Sept. to Nov.) (Fig. 1, Appendix I).

Gear employed for capture of samples was either the RMT 1+8 midwater trawl (Baker et al. 1973) or the RMT 1+8M multi-net system (Roe and Shale 1979). Both are acoustically controlled mouth opening-closing nets. Only the catches of the larger net were used. This net has a mouth size of 8 square metres and a mesh size of 4.5mm. Depth of the net, water temperature, speed of the net through the water and whether each net is open or closed are all continuously telemetered to the ship during tows. These nets were towed through standard contiguous depth strata of 100m, from the surface to 1000m then 1000-1250m, 1250-1500m and 1500-2000m although the maximum depth was not the same for all stations (Appendix I). In most cases, both day and night tows were available for each depth stratum. For consistency only night tows were used at the shallower depths (above 1000m) although there is little difference in depth distribution between day and night samples of Cyclothone (Badcock and Merrett 1976).

All sampling devices are biased in some way and so give only a limited view of what is actually present (Angel 1977). This does not prohibit analysis, but conclusions need to be considered in the light

of the inherent biases involved. In fish collections, the sampling gear affects both the species composition and the size range of individuals captured. Larger nets decrease net avoidance resulting in an increase in the capture of rare fish as well as more individuals of common species (Harrisson 1967, Willis and Pearcy 1982, Kashkin and Parin 1983, Pearcy 1983). Net size also affects the size of fish captured, larger nets tend to catch larger fish (Harrisson 1967).

There are a number of facts that suggest that species of Cyclothone are relatively well sampled by the RMT8. The total number of specimens taken is high suggesting the RMT8 captures this group relatively well and the numbers are sufficient to give a good indication of the population structure. Avoidance is still possible (which could affect the overall estimations of density) but repeated tows are similar (IOS unpublished data) suggesting that comparative densities are probably accurate. Also, the avoidance capabilities of Cyclothone are probably low as they are small, lethargic, inactive fish as viewed from submersibles (Peres in Marshall 1960, Barham 1970).

The most likely area of bias is at the extremes of the size range of all species captured. The largest Cyclothone (60 mm) is well within the size range where a net of this approximate size is unlikely to be size selective (Harrisson 1967). However, the size at which juveniles are apparently recruited to the population will be affected by the smallest size fish the net retains. Previous studies suggest this size to be 10-12mm SL although it is impossible to tell whether all individuals this size are being retained (Badcock and Merrett 1976). Larvae are too small to be adequately sampled making it impossible for any quantitative analysis.

The samples available had been preserved in 10% formalin in seawater when collected and sorted and transferred to alcohol in the laboratory at a later date. The Cyclothone were identified, measured to the nearest 1mm., sexed and the females staged after Badcock and Merrett (1976) (Table 2). Stage allocations are based on actual microscopic histological changes in the gonad (Merrett 1971). However, three stages that are recognized by other workers as the growth phase (e.g. Hjort 1910) cannot be distinguished objectively by recognizable

histological changes and are grouped as stage III/V. This results in a prolonged period where the female can be staged as III/V. As stages are based on actual histological changes in the gonad they are a reliable method of staging gonads, particularly for large numbers of specimens (Erickson et al. 1985). Another possible method of classifying female reproductive stage, the gonosomatic index (Clarke 1984), was ruled out because of the inability to weigh gonads due to preservation and the small size of gonads in immature specimens.

Stage II of this classification was chosen to be the stage where females had reached maturity. Post-spawning females (stage VII/II) return to this stage before entering a second spawning period. Males were not staged because the presence of spermatozoa in the testes at all times made staging impracticable. The sizes at maturity for males could only be estimated from the size at which males become distinguishable from juveniles of indeterminate sex.

For stage III/V females the maximum diameter of a number of eggs were measured using an ocular micrometer and the minimum and maximum egg size were recorded. Use of maximum diameter measurements may help to reduce errors introduced through fixation and other shrinkage (Merrett 1971). Where possible, usually at egg sizes greater than 0.2mm, eggs were removed from stage III/V females and placed in Gilson's solution to aid separation and after two to four months were counted using a binocular dissecting microscope. For the purposes of this study, fecundity is defined as the number of eggs present in the ovary at any one time. Regression lines of fecundity versus standard length were fitted and comparisons of fecundities between areas were made using an analysis of covariance (ANCOVA, SAS 1985).

To allow comparisons, species counts were standardized to the number of fish per 1000 cu. m. of water filtered by the net. The volume of water filtered was available from flow meter readings for some tows and in others (Appendix I) was estimated from tow duration, size of the mouth opening of the net at depth and ship speed (Roe et al. 1980).

Biomass was estimated using a length/weight regression calculated

from samples of Cyclothone which were weighed and measured after being preserved. Shrinkage will have occurred in all fish measured but all specimens used had been preserved for greater than 3 years making it likely that the percentage shrinkage would be similar. Different species were used for the regression but no interspecific difference was found. Measurements were therefore pooled to calculate the regression equation. The equation used to estimate weight from the size of individuals was: $\log(\text{weight}) = 2.69 \log(\text{Standard length}) - 11.35$ (r-square=0.95, n=50).

Figure 1. Chart of the North Atlantic Ocean showing locations sampled. S=spring, A=Autumn.

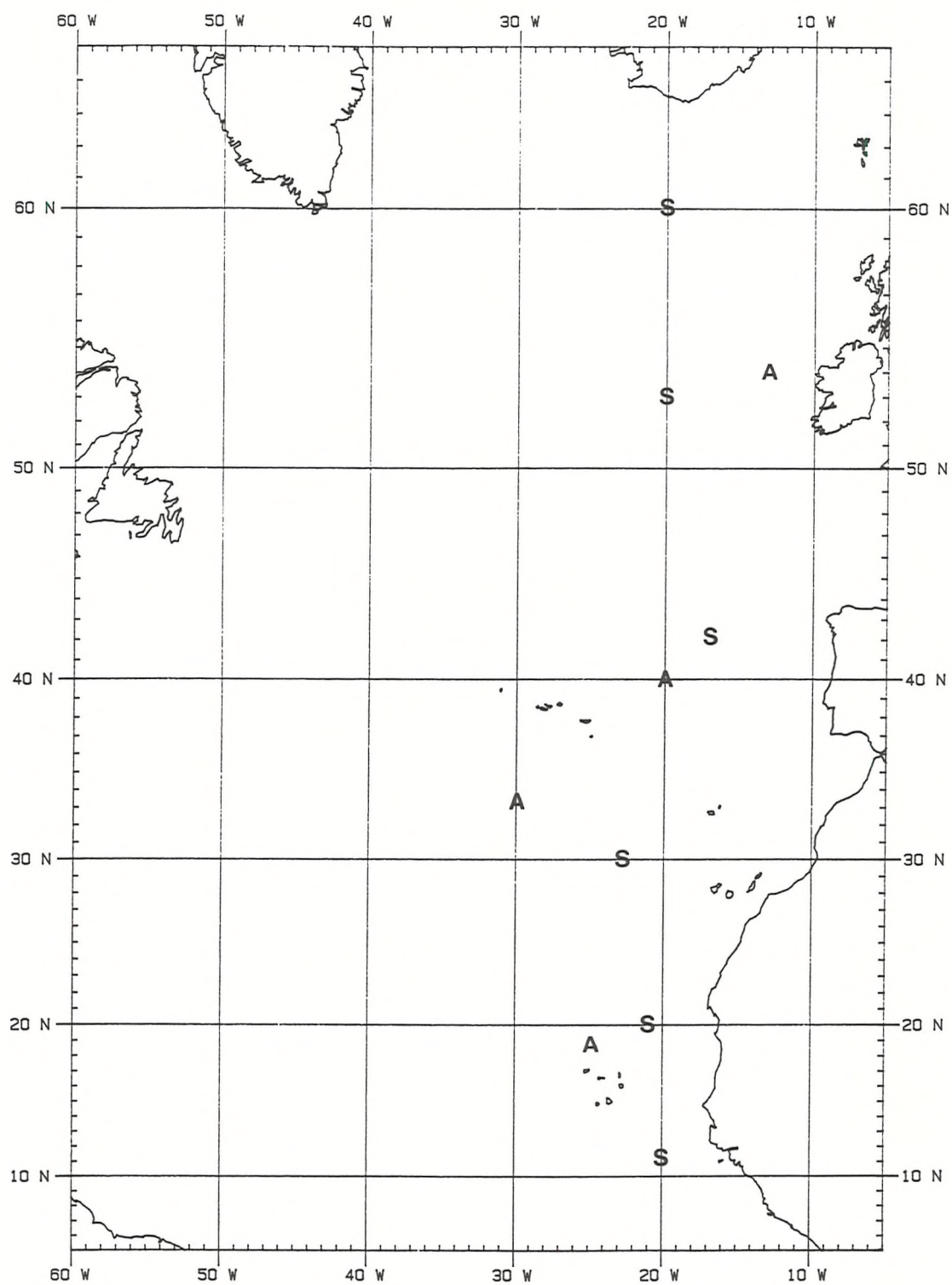


Table 2. Maturity stages used in classifying female Cyclothone (from Badcock and Merrett 1976).

Juvenile		sex indeterminant
Stage I	immature	ovaries small, compact; yolk absent from oocytes
Stage VII/II	spent/recovering	ovaries somewhat flaccid, larger than I; yolk absent from oocytes
Stage II	mature	ovaries firm, slightly enlarged; yolk granules present and chorion layer forming
Stage III/V	mature	ovaries firm and distended, eggs opaque; yolk vesicles readily apparent, chorion fully formed
Stage VI	spawning	ovaries extremely distended, eggs transparent, enlarged by liquid and freed from chorion
Stage VII	spent	ovaries extremely flaccid, enlarged empty sac or shrunk with enlarged central lumen

Chapter 3

RESULTS

3.1 Abundance and Distribution

A total of 28,896 fish were identified from 8 different species, Cyclothone braueri, C. microdon, C. pseudopallida, C. pallida, C. livida, C. acclinidens, C. obscura, and C. alba (Table 3). Of these, 28,061 were in a sufficiently good condition to allow measurement and determination of sex and stage of development.

Moving southwards from 60° North the number of Cyclothone per 1000 cubic metres increased gradually to 20 degrees north and then increased sharply at 10 degrees north (Fig. 2a). Density was slightly higher in the autumn, particularly at 30 and 20 degrees north. The rate of increase in density with decreasing latitude was greater in the autumn so that the greatest seasonal difference in density was at 20 degrees north. Conversely, there was little seasonal difference in density at 50°N and 40°N (Fig. 2a).

Although the density of individuals increased with decreasing latitude the biomass represented by these numbers decreased slightly or was constant to 30 degrees north, increased slightly to 20 degrees north and then rose sharply to 10 degrees north (Fig. 2b). At the more northerly stations biomass was higher in the spring than autumn (Fig. 2b). This was reversed at lower latitudes, particularly at 20°N, where the autumn biomass was greater. From 60°N to 30°N the slight increase

in density of fish was offset by a decrease in the biomass. The increase in density at 20°N and 10°N was reflected by a similar increase in biomass.

Biomass of most species present was much higher in spring than in autumn (Fig. 4). However, C. braueri showed little difference in biomass between the two seasons and was relatively constant over its range as compared to the other species present (Fig. 4) in spite of the large increase in density between 40 and 30 degrees north (Fig. 3).

The northern species were the most widespread. C. braueri and C. microdon were the predominant species both in total number and in frequency of occurrence. They were the most common species at 60, 50, 40, and 30 degrees north (Fig. 3 and Table 3). C. braueri extended as far as 20° north in the spring but not in the autumn collections. At the lower latitudes C. livida and C. pseudopallida were the most abundant at both times of year. C. acclinidens was most abundant at 10° north.

3.2 Species Accounts

3.2.1 Cyclothone braueri

Cyclothone braueri was the most widespread species, present from 20 to 60°N in the spring and at all autumn stations from 30 to 50°N. It was most abundant at 30°N at both times of the year (Fig. 3). It was the dominant species at mid-latitudes in the spring (Fig. 3a) and at the three northerly stations in the autumn (Fig. 3b). The biomass of C. braueri was relatively constant across the latitudes where it was distributed (Fig. 4).

Table 3. Number of specimens captured at each station sampled.

Station No.	Latitude ° N	C. braueri	C. microdon	C. pseudopalpida	C. pallida	C. livida	C. acclimens	C. obscura	C. alba	Total
Spring										
7709	60	280	1237	12	22	0	1	0	8	1560
7711	50	392	1084	7	20	2	1	0	8	1514
9801	40	503	427	5	6	0	0	0	2	943
7856	30	2432	883	105	64	3	1	2	0	3490
9541	20	377	0	49	96	621	55	71	6	1275
7824	10	0	0	1925	1052	3536	2755	378	994	10640
Autumn										
10105	50	271	220	3	1	0	0	0	2	497
7406	40	1361	1143	18	23	5	1	0	0	2551
10222	30	1082	390	33	49	3	1	0	0	1557
7089	20	3	0	1648	1031	1131	306	91	659	4869
Total		6701	5384	4805	2364	5301	3191	542	1679	28896

Figure 2. Distribution and abundance of Cyclothone in the eastern North Atlantic. a) Number per 1000 cubic m. b) Biomass per 1000 cubic m.

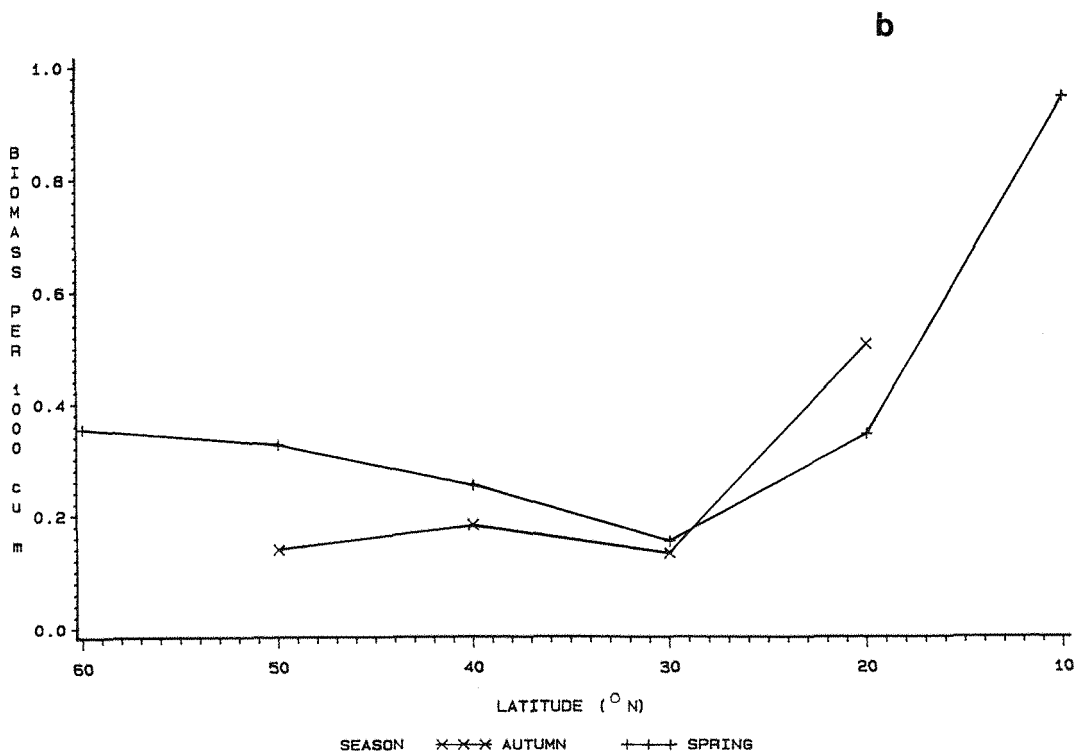
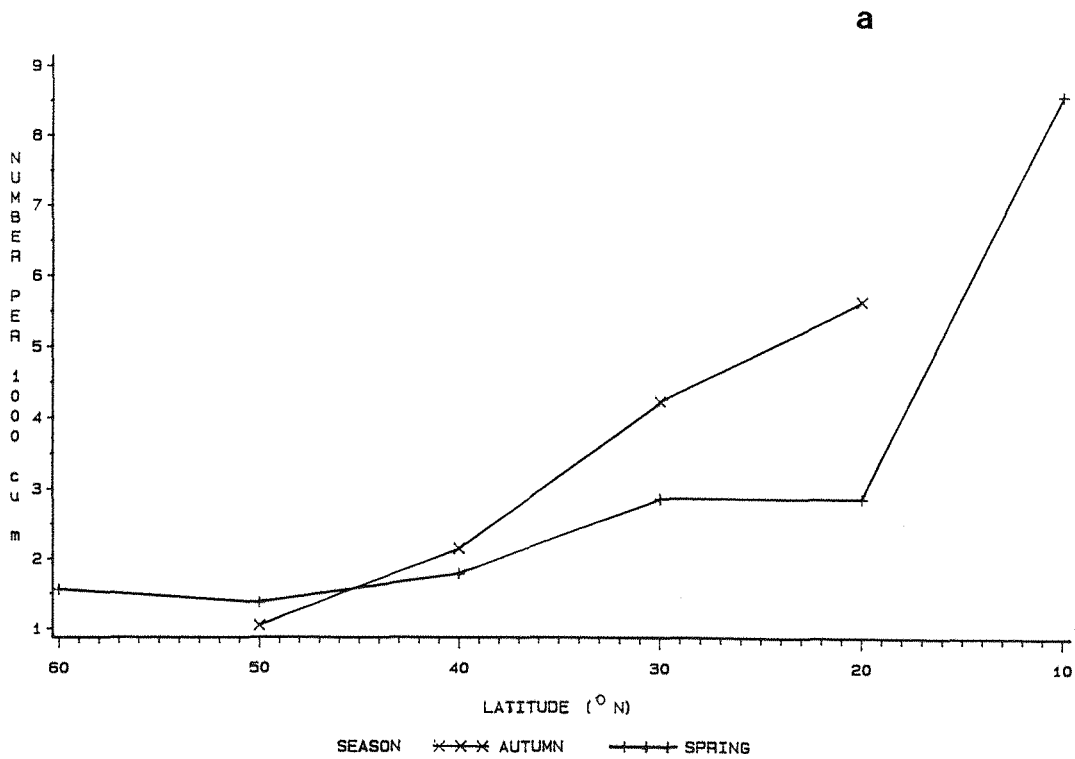


Figure 3. Number of Cyclothone at each latitude by species.
a) Spring, b) Autumn.

x = C. braueri
+ = C. microdon
□ = C. pseudopallida
◇ = C. pallida
△ = C. livida
▼ = C. acclinidens
✱ = C. obscura
● = C. alba

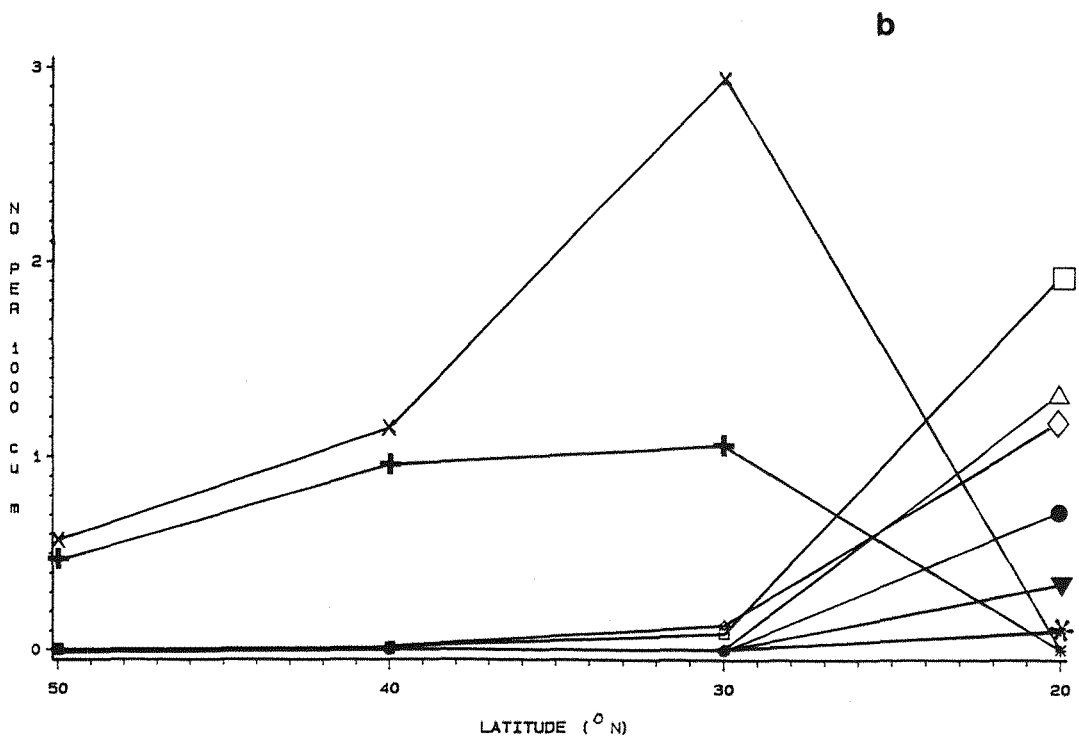
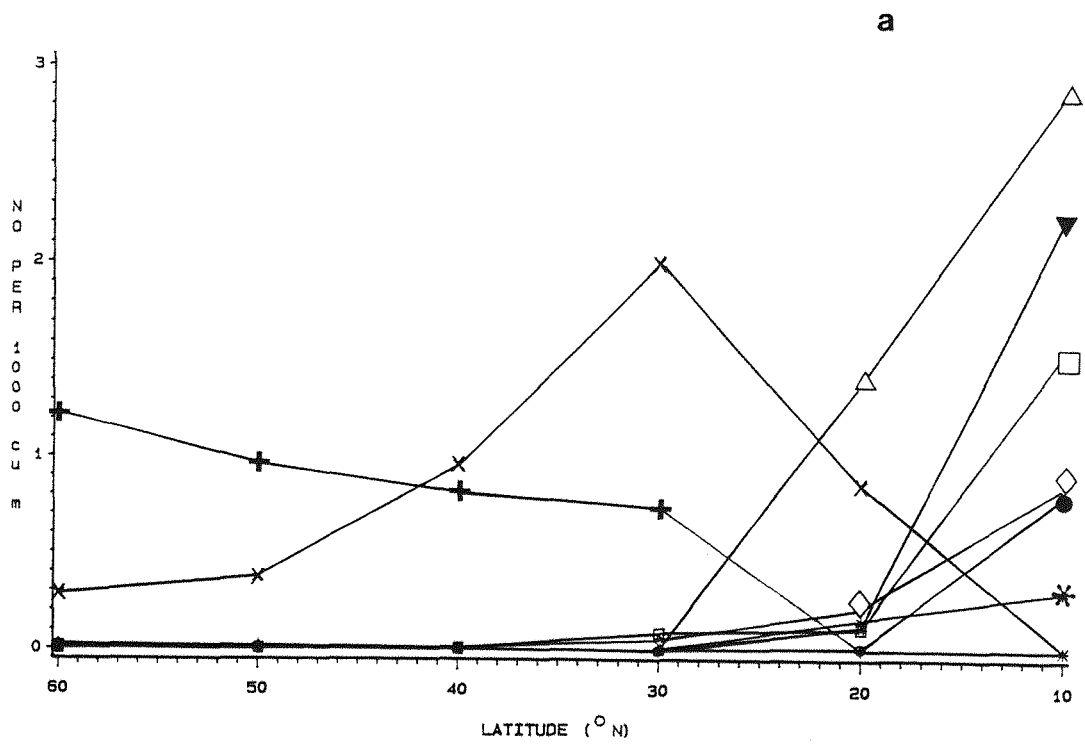
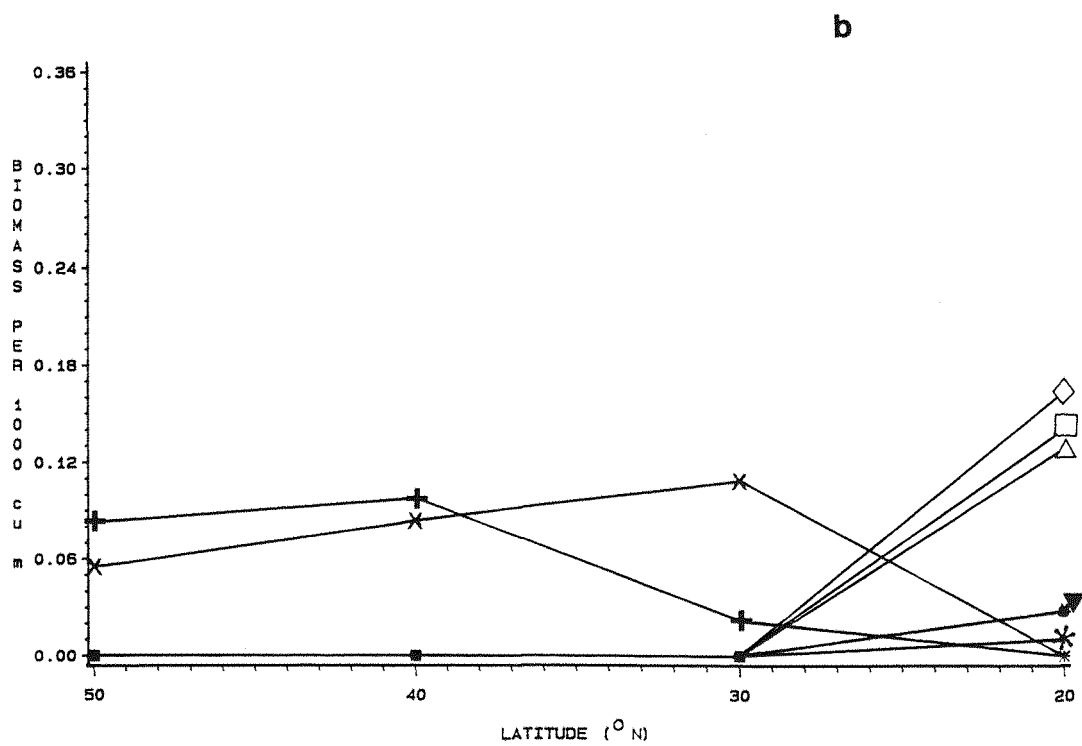
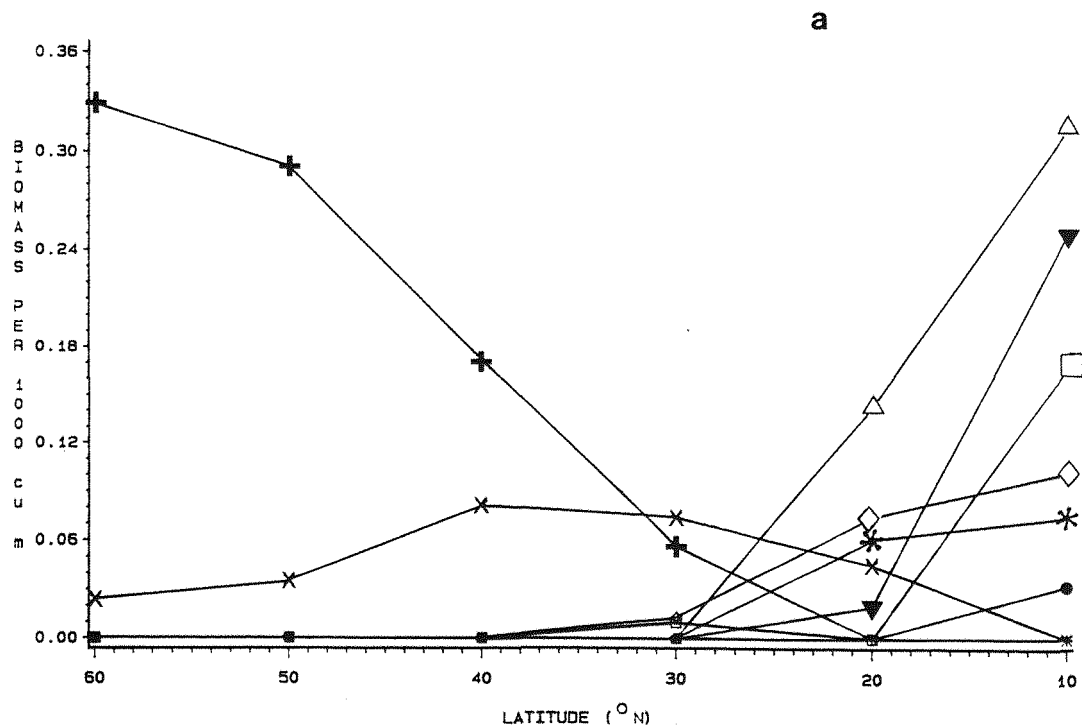


Figure 4. Biomass of Cyclothone at each latitude by species.

a) Spring b) Autumn.

- x = C. braueri
- + = C. microdon
- = C. pseudopallida
- ◇ = C. pallida
- △ = C. livida
- ▼ = C. acclinidens
- * = C. obscura
- = C. alba



3.2.1.1 60°N.

Stage II females predominated at 60°N in the spring with some stage III/V females present (Fig. 6a). Females were distributed between two peaks, immature stage I females at smaller standard lengths of 19-23mm SL and mature females at larger standard lengths (Fig. 5). Females were mature by 25mm SL and peaked in abundance at 30mm SL (Fig. 5). The few stage III/V females that were present had a maximum egg size of less than 0.2mm. Mature females were almost twice as abundant as males (males:females 1:1.9). Males made up approximately 30 percent of the population (Fig. 6a) and peaked in abundance at sizes similar to the stage I females (Fig. 5).

3.2.1.2 50°N.

In the spring, two peaks were present in the length frequency distribution of C. braueri at 50°N. The smaller, both in percent abundance and standard length, was comprised predominantly of males at 20mm SL with some stage I females up to 23mm SL (Fig. 7a). The larger peak was predominantly mature females at 30-32mm SL (Fig. 7a). Most females were mature by 25mm SL. Few juveniles or immature females were present (Fig. 8a). Stage III/V females were the most abundant group (Fig. 8a). Maximum egg size of these females was small with a peak at 0.22mm and a mean of 0.19mm ($s^2=0.002$ Fig. 9a) suggesting that they were not close to spawning. Stage II females were found throughout the adult size range suggesting either females were just progressing to stage III/V or that two age classes were overlapping and not readily distinguished by size.

Stage II females predominated in the autumn collections at 50°N (Fig. 8b). Two peaks were present in the length frequency distribution with males and some stage I females at 20mm SL and a larger peak of mature females at a mode of 32mm SL (Fig. 7b). Females were mature by

28mm SL and were more than twice as abundant as males (males:females 1:2.46). Most females had a largest egg of 0.18mm but a small number had more advanced eggs up to 0.3 and 0.34mm (Fig. 9b) which could be close to spawning. However, no spawning (stage VI) or spent (stage VII) females were found (Fig. 8b) and no juveniles were captured.

3.2.1.3 40°N.

A bimodal length frequency was evident at 40°N in the spring. The smaller peak in the length frequency was again predominantly males (Fig. 10a). The distribution of females suggested two groups, immature females at standard lengths of 19-26mm SL and a bimodal group of stage III/V females with peaks at 29 mm SL and 32 mm SL (Fig. 10a). Considering the range of sizes of stage III/V females (28-34mm SL) compared to other stations it appears that the bimodal shape is probably a sampling artefact. The majority of females were stage III/V (Fig. 11a) and had a maximum egg size of 0.3mm. Spawning was probably occurring as some individuals had eggs as large as 0.54mm (Fig. B12a) and stage VI females were present (Fig 11a). The lack of juveniles suggested spawning (Fig. 11a) had not been occurring for very long.

The length frequency of C. braueri at 40°N in the autumn was bimodal with the first mode substantially smaller than the second (Fig. 10b). The first peak was predominantly males, peaking in abundance at 18mm SL. The second peak of adult females was spread over a particularly large size range and the modal size was smaller than in the spring (25 mm SL). The maximum egg size of stage III/V females was highly variable with peaks at three sizes (Fig. 12b). These sizes appeared to represent females that were just maturing (<0.22mm), a smaller group approaching spawning (0.3mm) and a final group close to spawning (>0.4mm). The mean of the egg sizes was 0.27mm ($s^2=0.009$). Most stages were present at abundances less than 10 percent (Fig. 11b). The majority of adult females were still stage III/V in the autumn (Fig. 11b) suggesting a prolonged spawning period. The percentage of males

was very low resulting in an extremely skewed sex ratio of 8.5 females to every male.

3.2.1.4 30°N.

The length frequency distribution at 30°N in the spring was bimodal with the first mode larger than the second (Fig. 13a). The first mode was made up of stage I females and males at standard lengths around 17mm SL although stage I females reached larger sizes than did the males (Fig. 13a). The second mode was comprised of mature females. There was a lack of mature females greater than 30mm SL (Fig. 13a) and the modal size was small (23mm SL). The population was constituted by equal percentages of males, immature stage I females and stage III/V females (Fig. 14a). Mature females were more than twice as abundant as males (Table 4). Spawning was under way as both spawning (stage VI) and spent (stage VII) females were present (Fig. 14a) and some females had large eggs (Fig. 15a). Population egg sizes were spread over a wide range from 0.18 to 0.48mm (Fig. 15a mean=0.29, $s^2=0.005$) with a peak at 0.22mm and another peak at 0.38mm. The large size range with almost equal proportions from 0.26mm to 0.38mm could suggest a relatively prolonged spawning period with only a few females spawning at any one time.

Juveniles predominated in the autumn samples (Fig. 14b). They were mostly found at a size of 13mm SL (Fig. 13b). Mature females were present at about the same standard lengths as in the spring but stage I females were found at larger standard lengths of 18-24mm SL, approaching adult sizes (Fig. 13b). Males were scarce, making up less than 5 percent of the population, and this resulted in a sex ratio of 12.4 mature females to every male. Stage II was the predominant stage of mature females (Fig. 14b). Stage III/V females made up a larger proportion of each size class at the smaller standard lengths suggesting that the smaller females may spawn later in the season (Fig. 13b). Most females had eggs of 0.3mm and larger but the largest single size class was 0.22mm (Fig. 15b mean=0.29, $s^2=0.005$).

3.2.1.5 20°N.

Males had the higher mode at 18mm SL (Fig. 16) and the higher percent composition in the population (Fig. 17a) resulting in the lowest sex ratio in the species range (Table 4). Stage III/V was the predominant ovarian stage found although the percent composition of the three female stages was relatively even (Fig. 17a). Stage I females were present at a size range of 21 to 27 mm SL and peaked in abundance at 23 mm SL (Fig. 16). Mature females were most abundant at 27mm SL (Fig. 16). The mean egg size found among stage III/V females was 0.28mm ($s^2=0.004$) with a peak at 0.26mm (Fig. 17b). Some females seemed to be approaching spawning since they carried eggs of sizes up to 0.46mm. There were few indeterminant juveniles and those that were present were at the larger end of the size range (Fig. 16).

3.2.1.6 Latitudinal Comparisons

The same population structure was evident at all locations. Two peaks were present in the length frequency distributions made up of males and stage I females at smaller standard lengths and mature females at larger standard lengths (Figs. 5,7,10,13 and 16). The one exception to this rule was at 30°N in the autumn due to the presence of a large number of juveniles which added a third peak in the distribution (Fig. 13b). When present, immature females (stage I) were found either at standard lengths equal to those of the males or at low levels of abundance between the two peaks of males and mature females. At latitudes of 40°N and greater the first peak was always smaller than the second peak. At lower latitudes, the higher peak was found at the smaller standard lengths.

The lack of any modal structure within the adults of both sexes and

the absence of stage VII/II females suggests that C. braueri is a short lived species that spawns only once in its life span. Spawning appears to occur in the spring/summer period as this was the period when most females from the collections were stage III/V and egg sizes were the largest. Also, juveniles appeared in greater numbers in the autumn probably from eggs spawned in the spring (Fig. 13b). Recruitment of stage I females to the adult population occurred in the autumn as that was when they were found to be larger than males and approaching the sizes of the adult females. Males and stage I females appeared to be one year olds. Males probably died after spawning and females matured to spawn in their second year.

Although the above generalizations can be made, latitudinal differences among populations were found to exist in many of the characters examined.

The size distribution of the population was latitudinally dependent. Peak abundance occurred at lower standard lengths at lower latitudes for both males and females (Figs. 5,7,10,13 and 16). Maximum size, mean size and size at maturity all tended to decrease with decreasing latitude (Table 4). This resulted in the biomass of C. braueri remaining constant over latitude although density varied considerably (cf. Fig. 4).

In the spring, southerly populations were generally more advanced into the spawning season. Moving north to south the predominant stage of mature females changed from stage II to stage III/V at 40°N (Fig. 11). There was also a significant difference ($t=5.0$, $df=51$, $p<0.01$) in the mean of the maximum sized egg found in females between 50°N and 40°N (Figs. 9a and 12a). The populations at 30°N and 20°N in the spring had lower proportions of stage III/V females than at 40°N. However, there was a change in shape of the distribution of maximum egg sizes from a single peaked shape at 40°N to an almost bimodal shape at 30°N (Figs. 12a and 15a) suggesting some individuals with larger sized eggs were close to spawning and others were unlikely to spawn later. At 20°N spawning could be considered to be in winter/spring as it appeared as if spawning in the spring was almost completed. Recruitment from stage I females had begun as immature females were larger than the

males and approaching the adult sizes.

The same trend was evident in the autumn. Moving from 50°N to 40°N there was a large increase in the percentage of stage III/V females in the population at the expense of stage II females (Fig. 8b and 11b) so that more advanced stages of maturity were present at 40°N. Females tended to have larger eggs at 40°N as well (Figs. 9b and 12b). The population at 30°N in the autumn was very similar to that in the spring except for the large proportion of juveniles and slight differences in the relative abundances of stages II and III/V (Figs. 14a and 14b). The stage III/V females that were present at both times of the year had similar sized eggs (Figs. 15a and b, mean 30°N spring=0.28, 30°N autumn=0.29).

The data support the postulation that populations of Cyclothone braueri that are present at more southern latitudes tend to mature and spawn earlier and also spawn over a longer time than those further north. At 50°N spawning was just approaching in the spring and appeared to be completed by the autumn. At 40°N the spring samples taken were well into the spawning period with more stage III/V individuals and larger egg sizes and yet there were still some left to spawn in the autumn. The impression from 30°N was that spawning was very protracted almost to the point of being continuous so that almost equal percentages were present at the various maturity stages at both times of the year.

Females tended to have a larger maximum egg size at the lower latitudes at both times of the year. The means at 40°N, 30°N and 20°N were very similar but the variability differed, it was lowest at 50°N with a very peaked distribution of sizes (Figs. 9a and b). Even among the populations that appeared to be closest to spawning few females had very large eggs. The peaks in abundance usually occurred at 0.30mm or less (Figs. 9, 12a, 15b and 17b) with two exceptions at 30°N in the spring (Fig. 15a) and 40°N in the autumn (Fig. 12b). In those cases the largest peak was at 0.22mm or less. The implication of this is that spawning occurs in only a few individuals at a time rather than that mass spawning occurs in response to an environmental cue. This results in only a small proportion of the population of adult

females spawning at any one time during the spawning period.

Pre-spawning sex ratio was relatively constant at approximately 2 females for every male in the spring (Table 4). However, the sex ratio increased in the autumn in favour of females. There was also a decrease in the proportion of males in the population. At 50°N in the autumn the sex ratio was 2.5 females to every male and males made up close to 30 percent of the population (Fig. 8b) as they did throughout the spring (Figs. 6, 8a, 11a, 14a and 17a). At the other latitudes in the autumn the proportion of males was less than 10 percent (Figs. 11b and 14b) and the sex ratio showed a subsequent increase. There was also an increase in the number of juveniles present with respect to males in the autumn, particularly at the lower latitudes. These facts, linked with the lack of any seasonal decrease in the proportion of females, suggest that there is differential post-spawning mortality between males and females. The reduction in the proportion of males in the population in the autumn suggests that they die shortly after spawning leaving a predominance of females in the population until the effect is reversed by the later mortality among adult females and recruitment of juveniles to the adult male population.

Observed fecundity increased with standard length (Fig. 18). The number of eggs found in the ovaries of females ranged from 159 to 1096 (22-36mm SL). A significant regression was found when data for all stations were pooled regardless of latitude (Table 5). However, differences were found when fecundity was compared among stations. It was not possible to calculate regressions for stations at latitudes of 60 and 50°N because of a lack of samples. Where sample sizes were adequate only those at 30°N did not give a significant regression. The regression equations for the other locations are given in Table 5. Correlation coefficients were generally low indicating a lot of variability (Table 5). There was a significant difference in fecundity among the three stations for which regressions are reported (ANCOVA $F=105.26$, $df=(5,106)$, $p=0.01$). The fecundity at 40°N in the spring was significantly higher than both 40°N in the autumn ($p=0.0001$) and 20°N in the spring ($p=0.0002$). However, fecundity at 40°N in the autumn was lower than at 20°N in the spring ($p=0.0001$).

Figure 5. Length-frequency distribution by sex and stage of C. braueri at 60°N in the spring (n=275).

1= Juveniles

2= Males

3= I

4= II

5= III/V

6= VI

7= VII

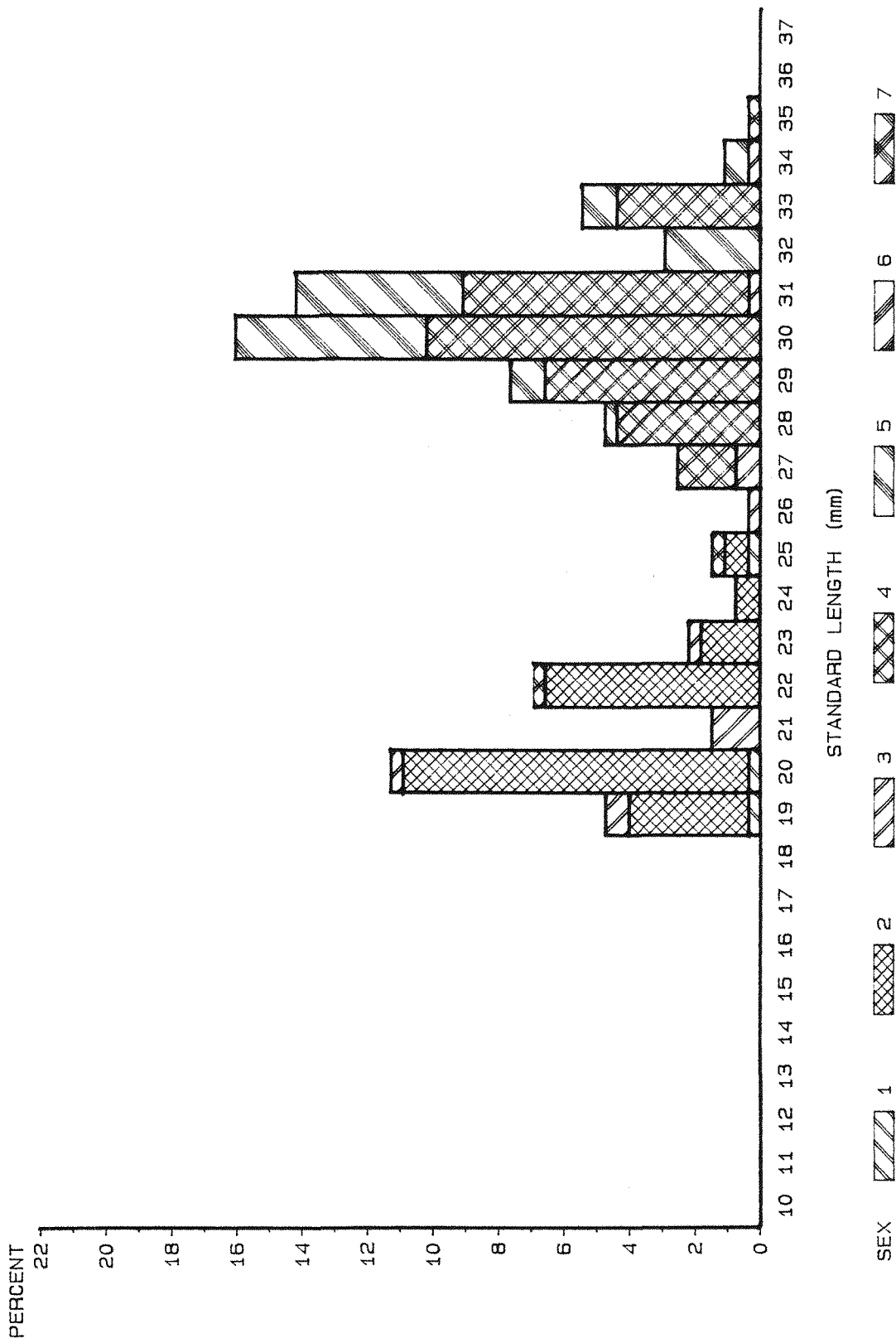


Figure 6. Percent abundance of each sex/stage of C.
braueri at 60° N (n=275).

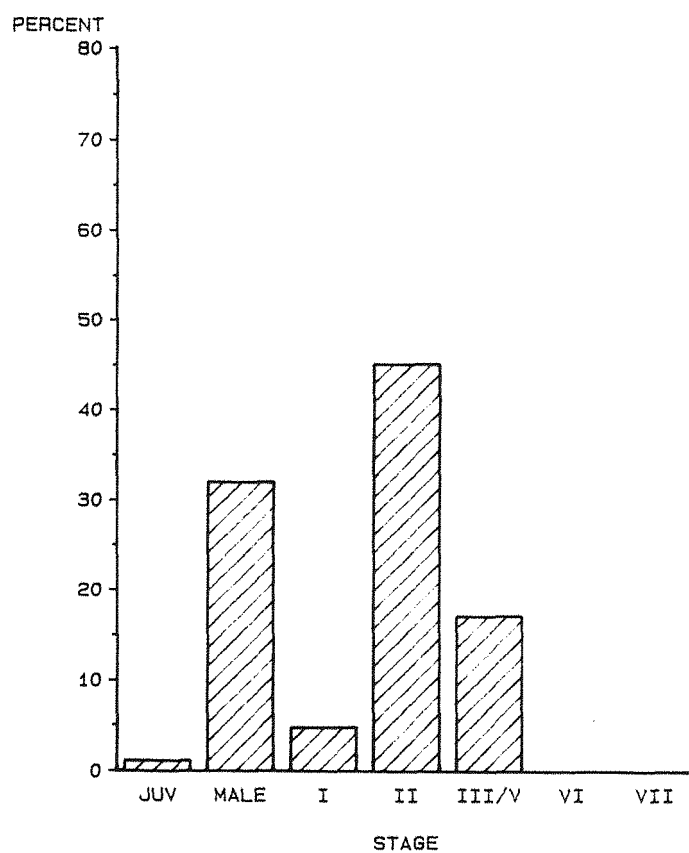
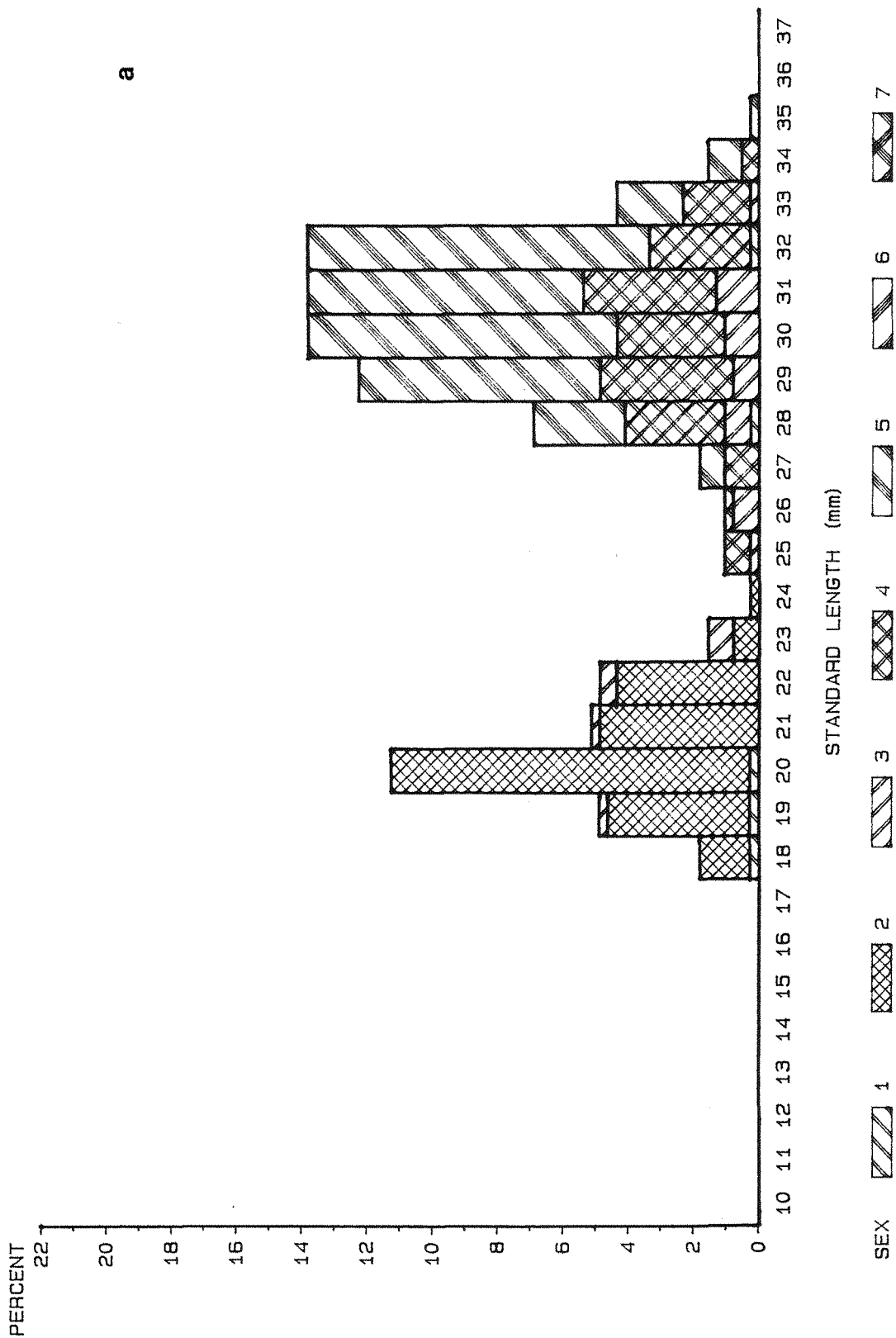


Figure 7. Length-frequency distribution by sex and stage of C. braueri at 50° N a) in the spring (n=392) and b) in the autumn (n=256).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII



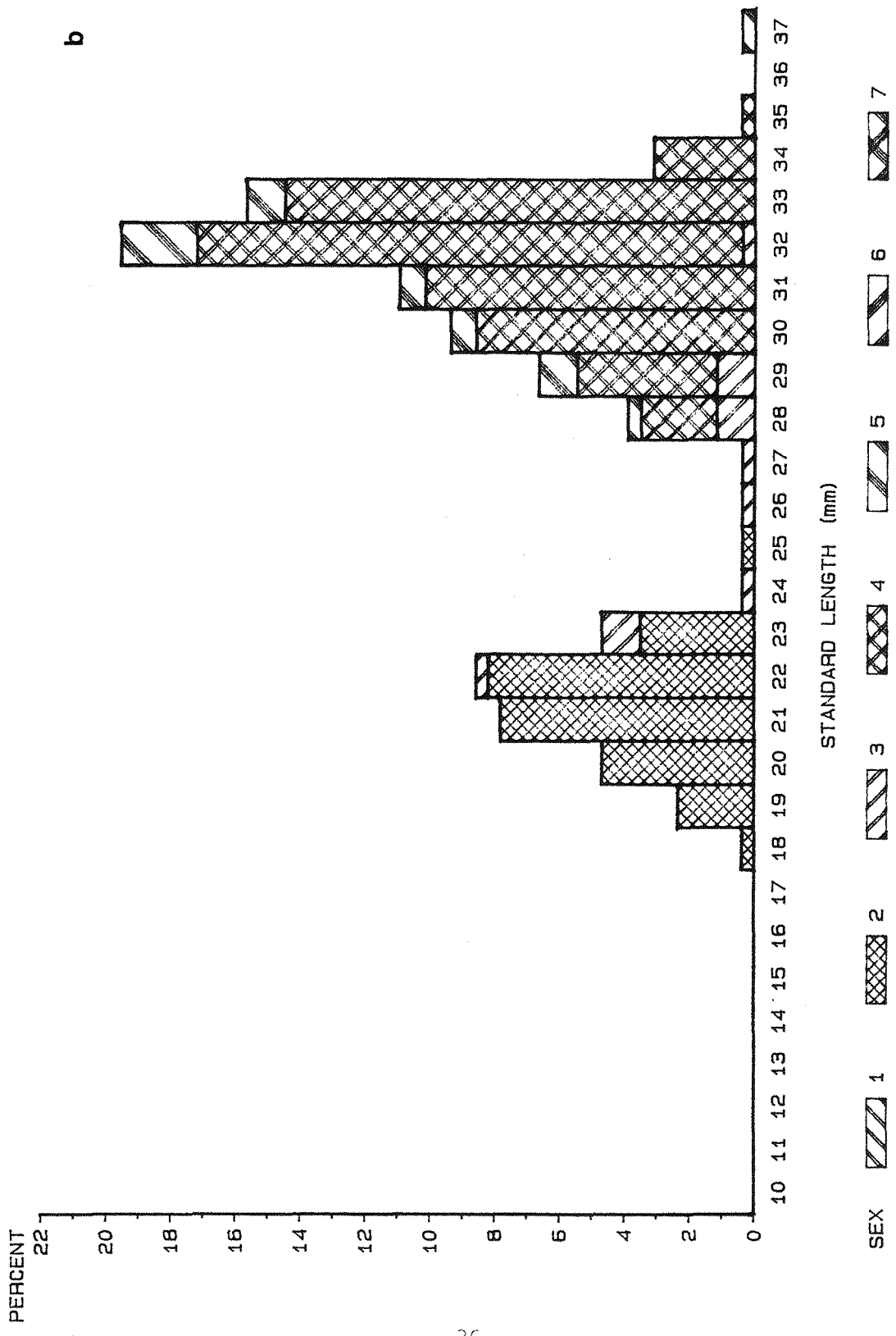


Figure 8. Percent abundance of each sex/stage of
C. braueri at a) 50°N in the spring (n=392)
b) 50°N in the autumn (n=256).

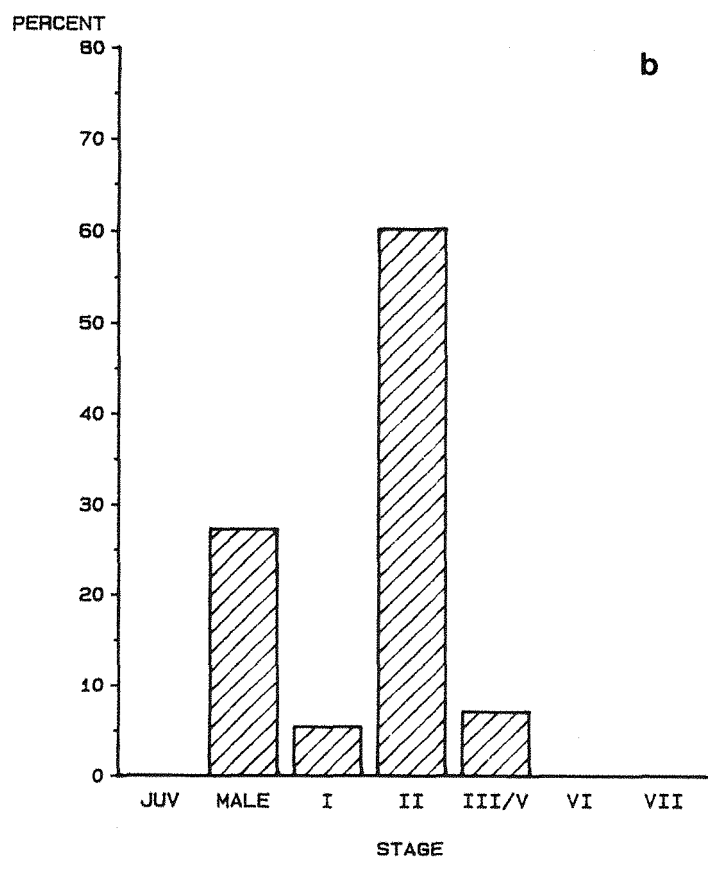
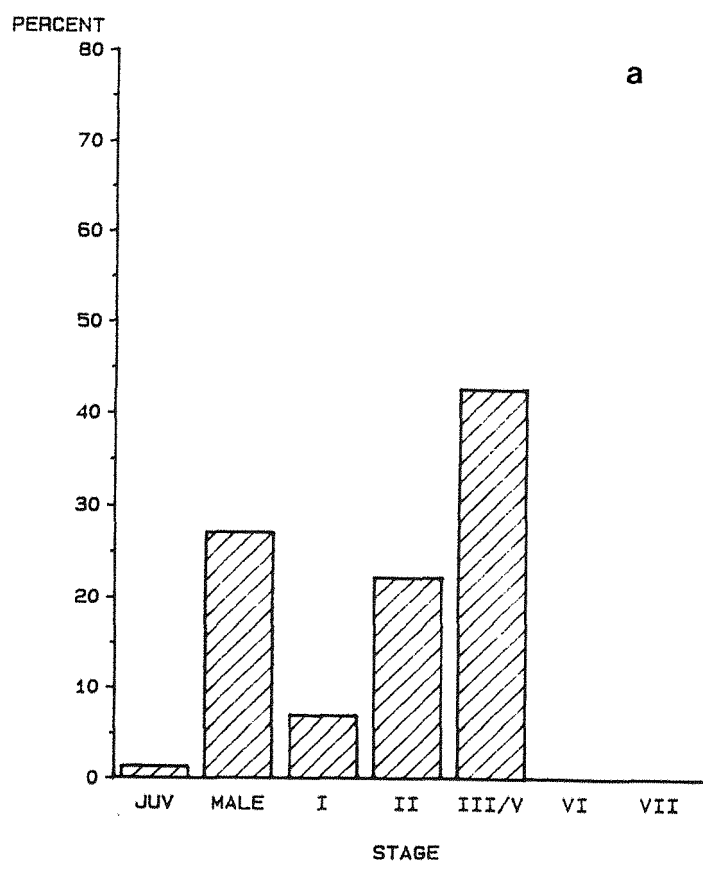


Figure 9. Size-frequency distribution of the maximum egg diameter in female C. braueri at 50°N in a) the spring (n=16) and b) the autumn (n=17).

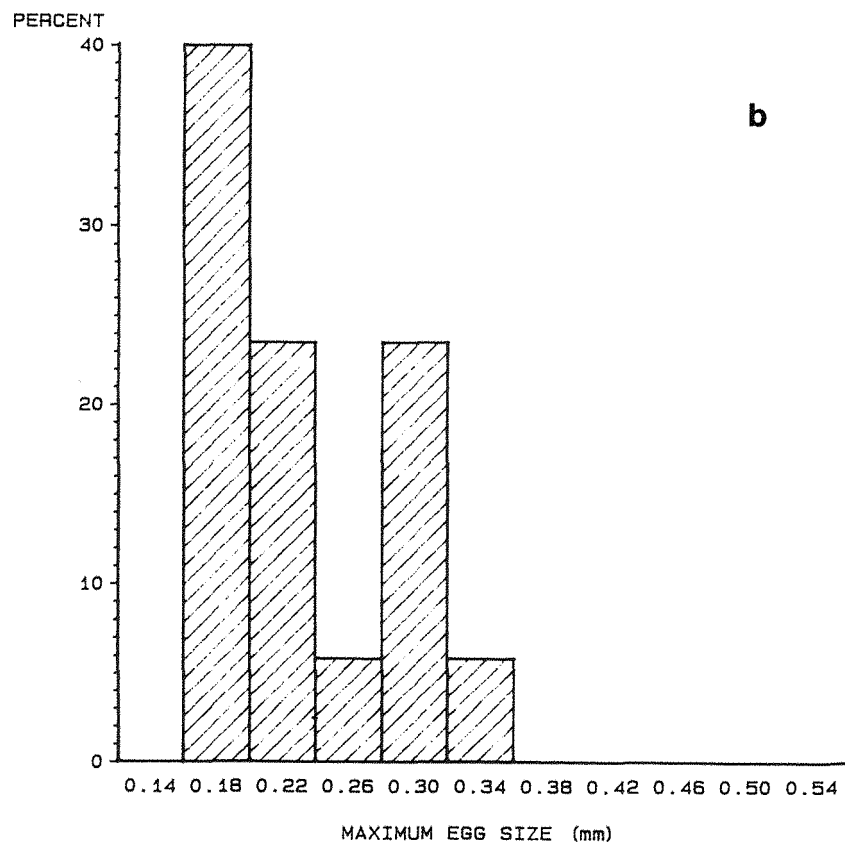
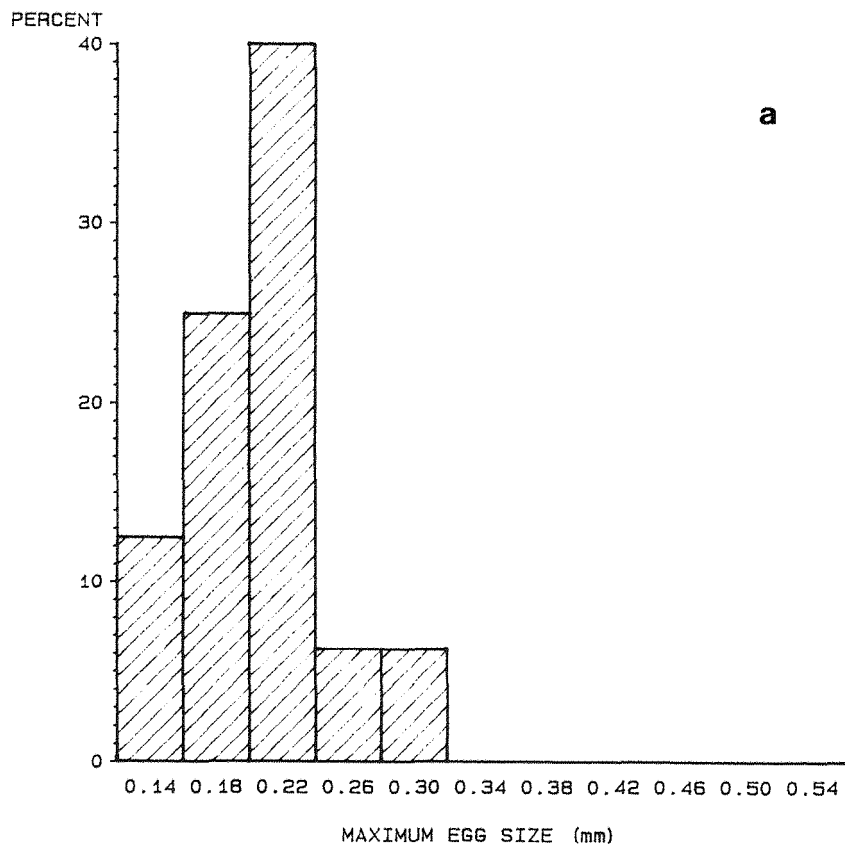
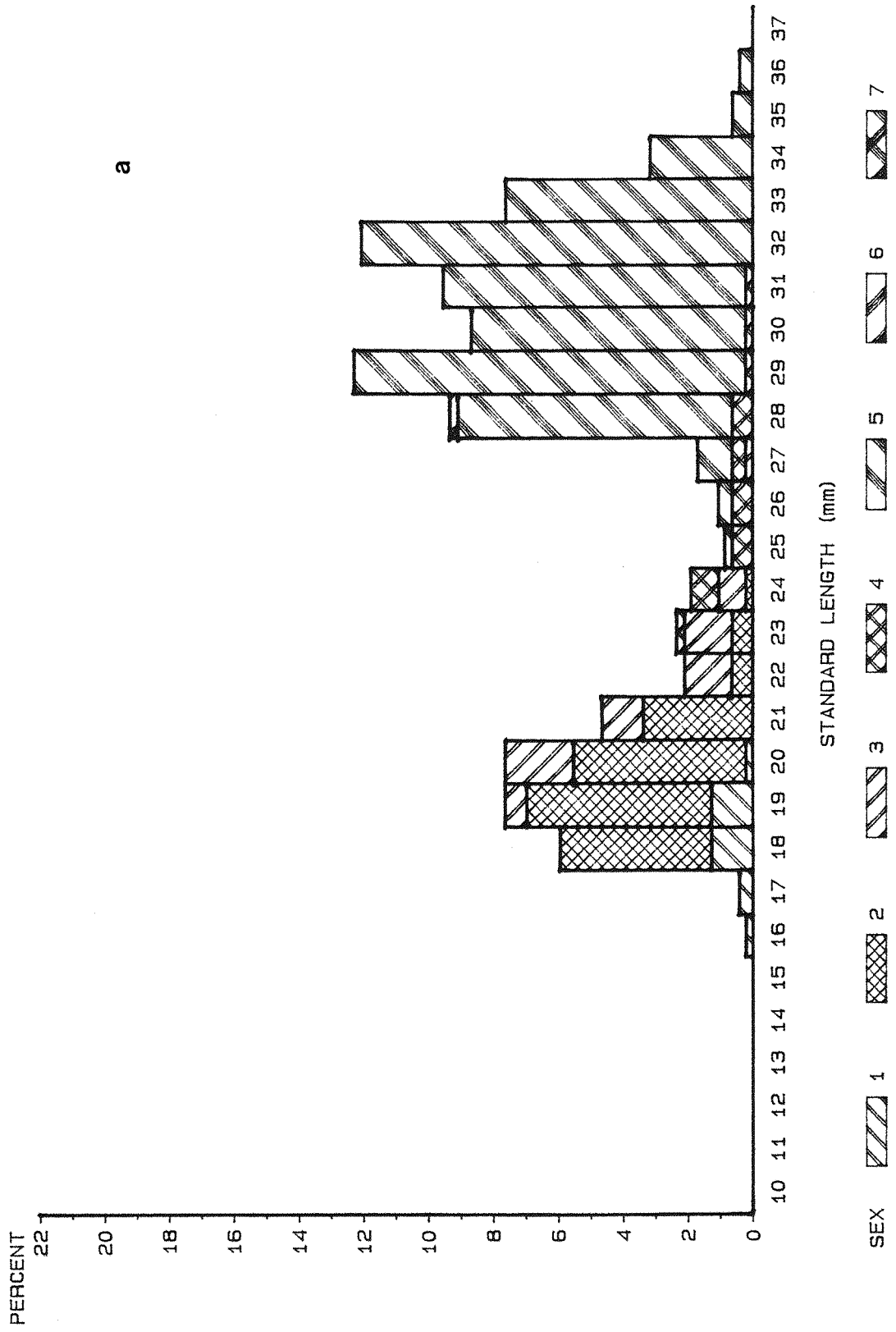


Figure 10. Length-frequency distribution by sex and stage of C. braueri at 40°N a) in the spring (n=473) and b) in the autumn (n=1361).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII



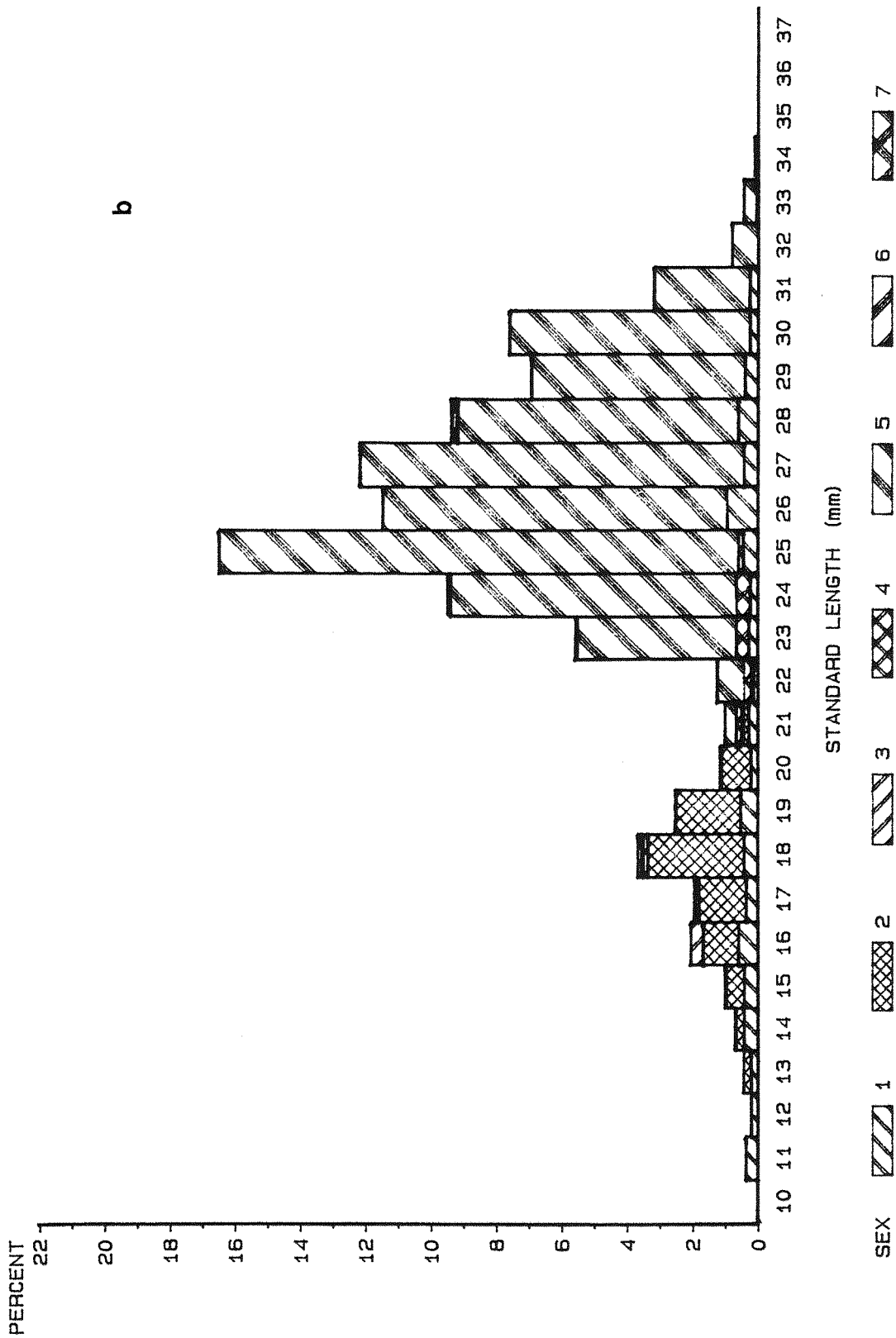


Figure 11. Percent abundance of each sex/stage of
C. braueri at a) 40°N in the spring (n=473)
b) 40°N in the autumn (n=1361).

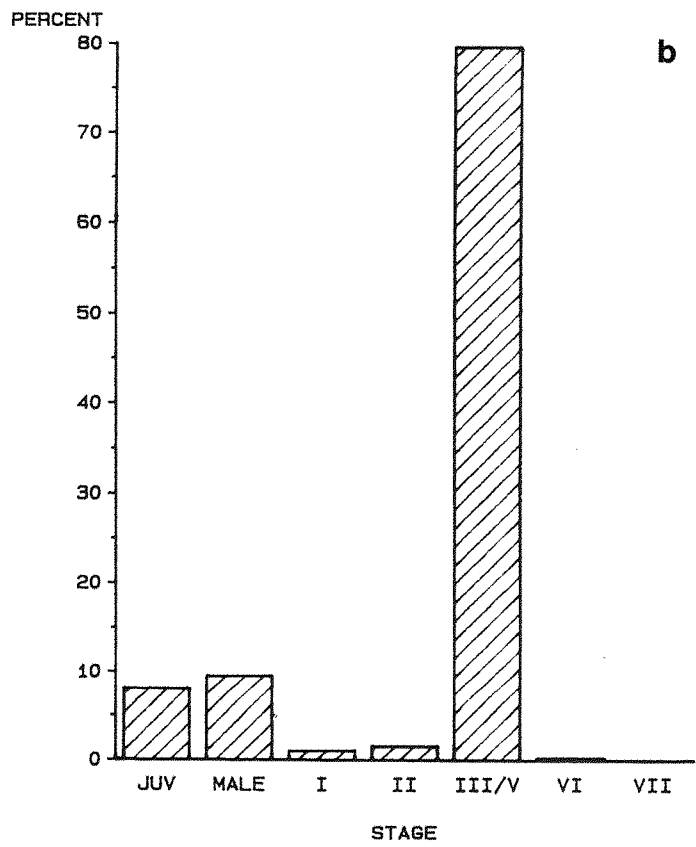
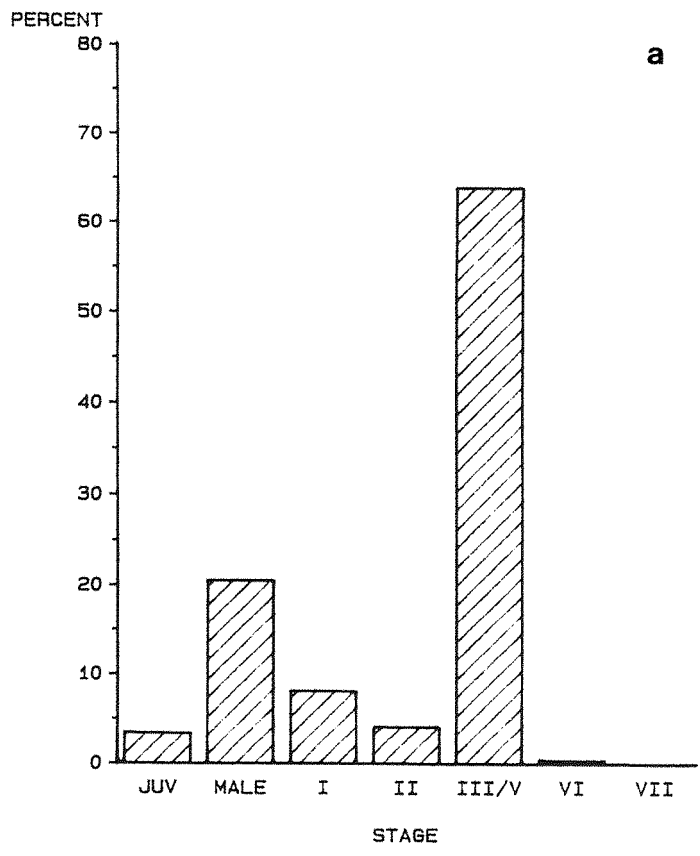


Figure 12. Size-frequency distribution of the maximum egg diameter in female C. braueri at 40° N in a) the spring (n=37) and b) the autumn (n=50).

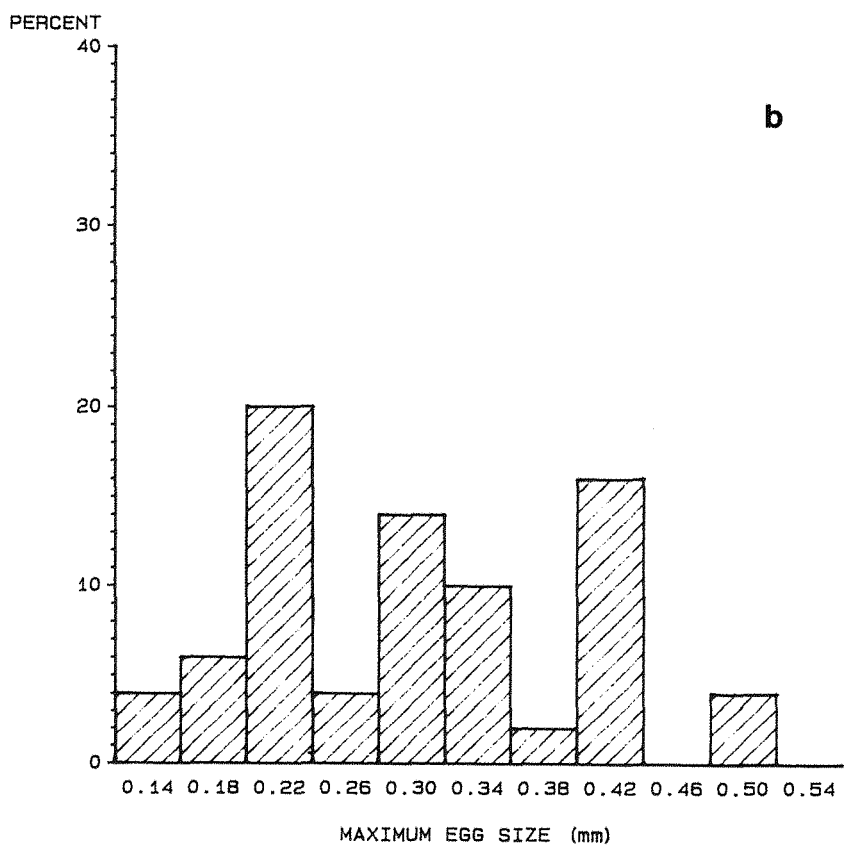
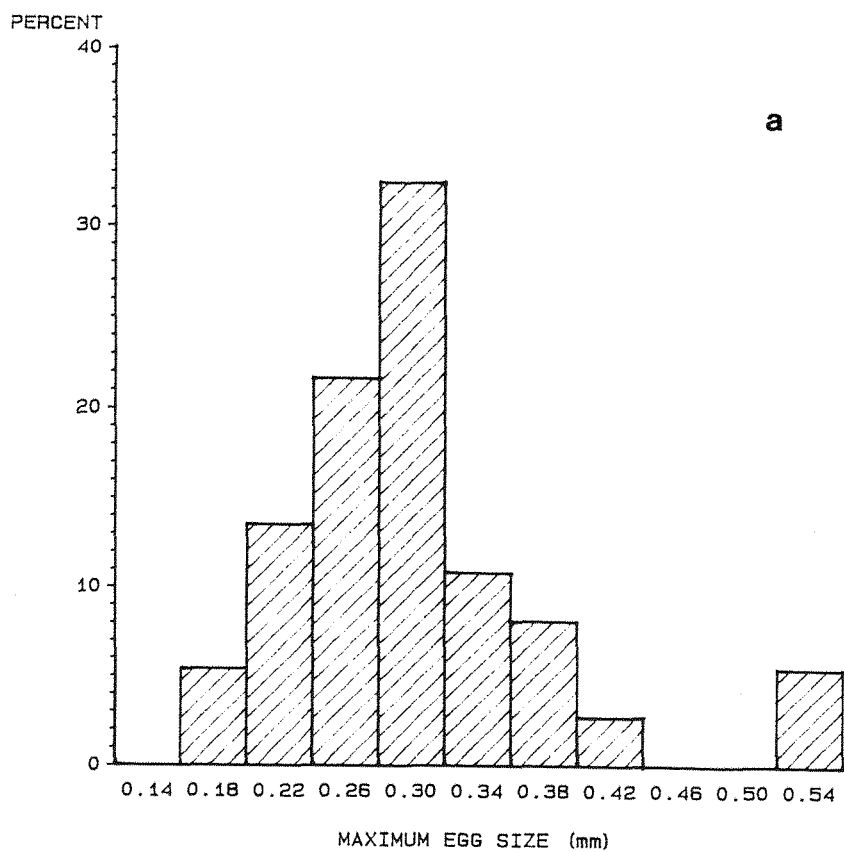


Figure 13. Length-frequency distribution by sex and stage of C. braueri at 30°N a) in the spring (n=2432) and b) in the autumn (n=1082).

1= Juveniles

2= Males

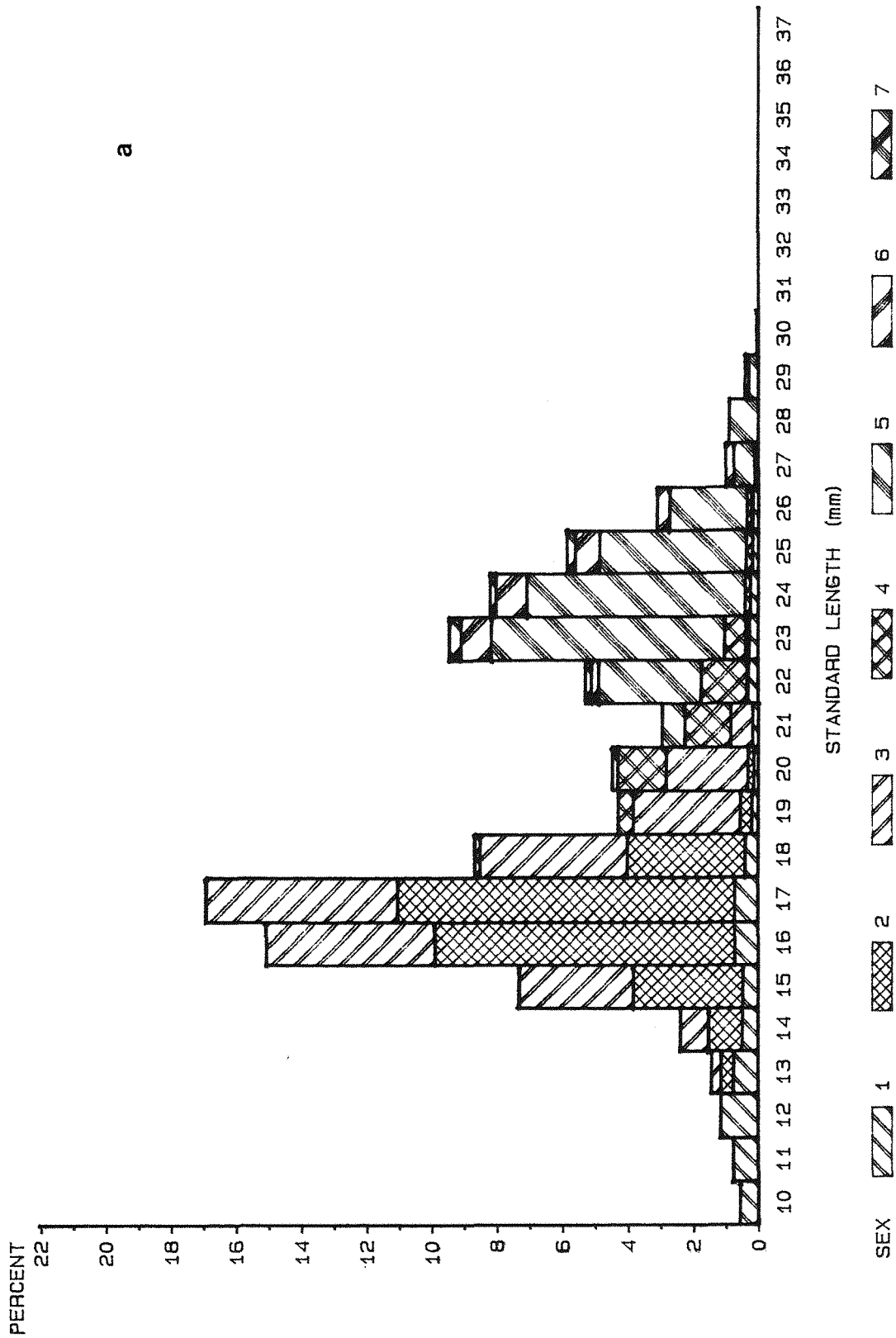
3= I

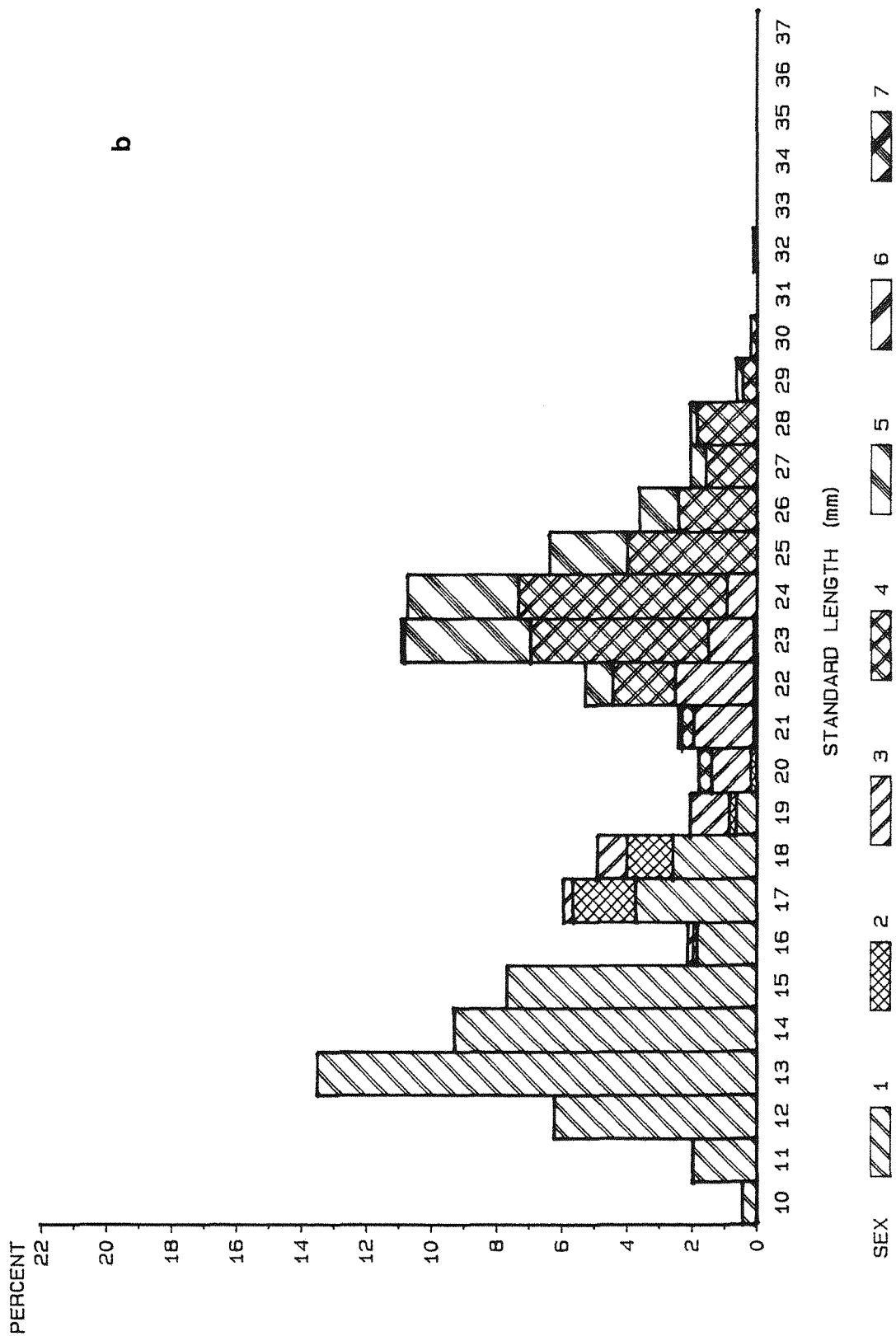
4= II

5= III/V

6= VI

7= VII





b

Figure 14. Percent abundance of each sex/stage of
C. braueri at a) 30°N in the spring (n=2432)
b) 30°N in the autumn (n=1082).

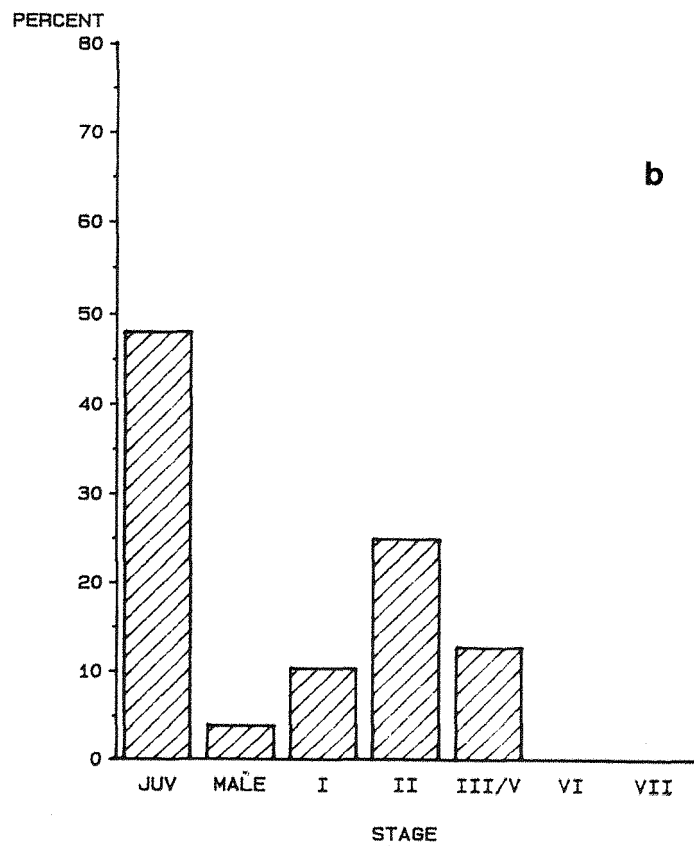
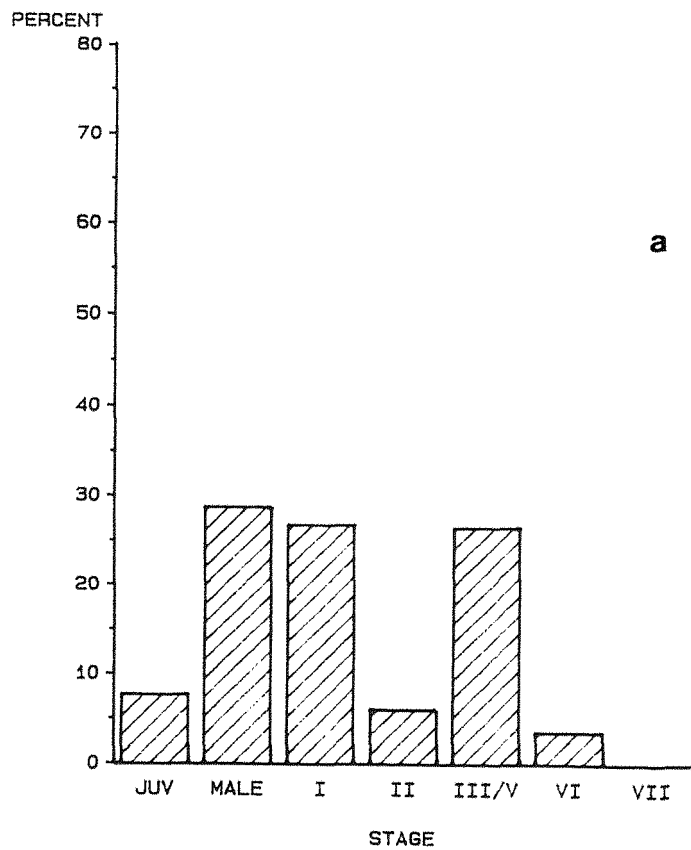


Figure 15. Size-frequency distribution of the maximum egg diameter in female C. braueri at 30°N in a) the spring (n=50) and b) the autumn (n=50).

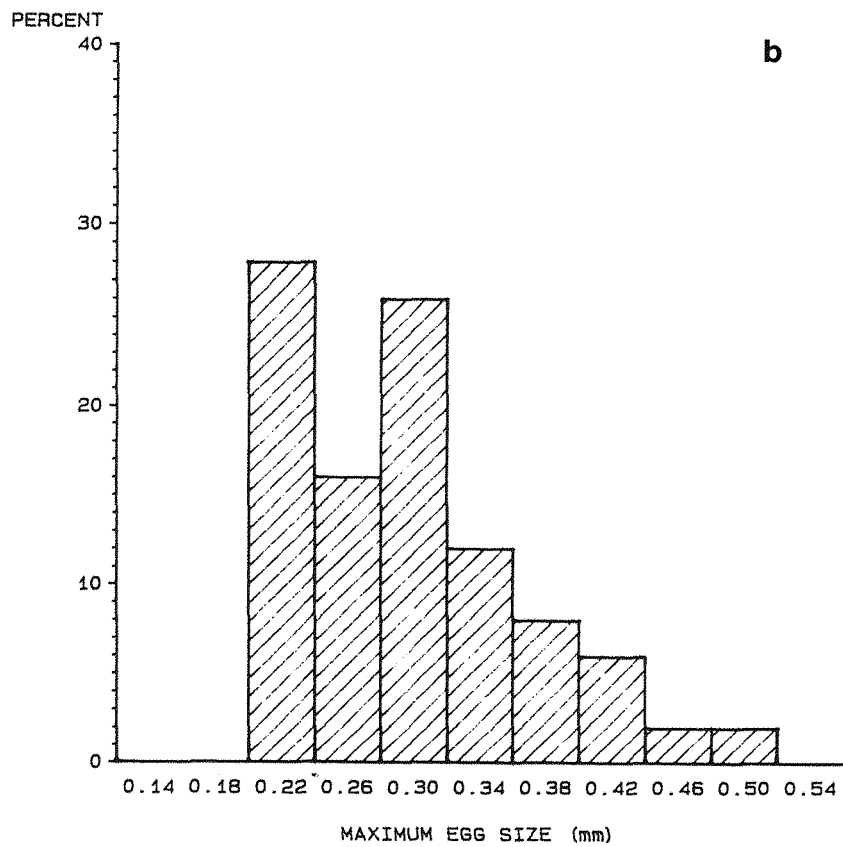
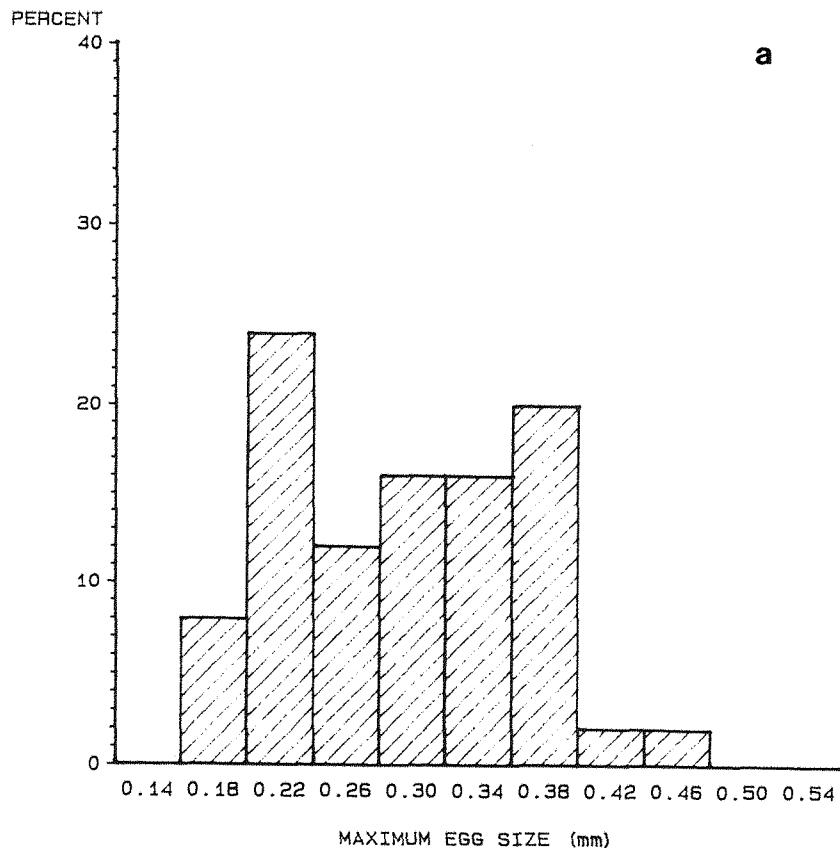


Figure 16. Length-frequency distribution by sex and stage of C. braueri at 20°N in the spring (n=352).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII

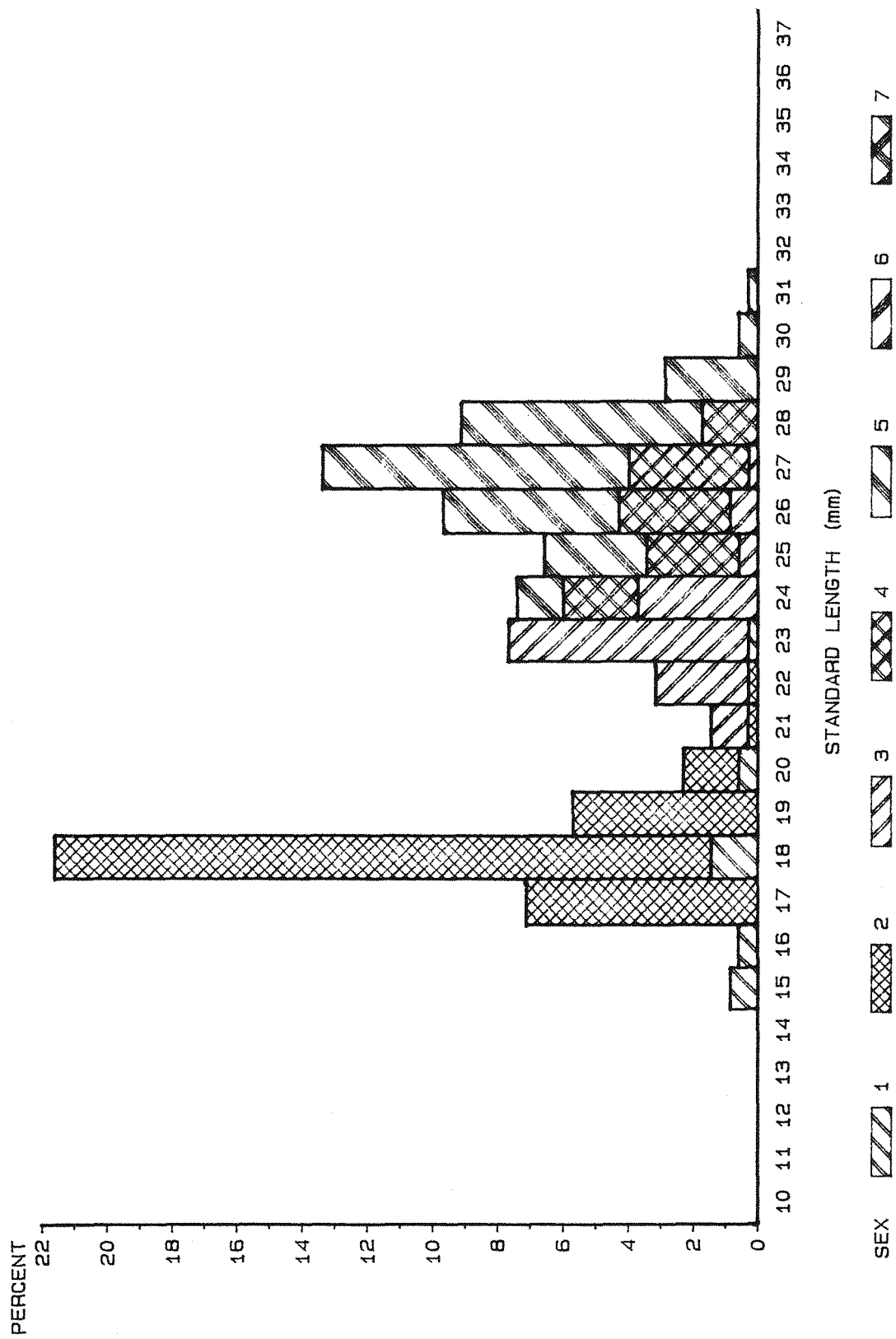


Figure 17. C. braueri at 20°N in the spring.

- a) Percent abundance by sex/stage (n=352) and
- b) the size-frequency distribution of the maximum egg diameter in females (n=50).

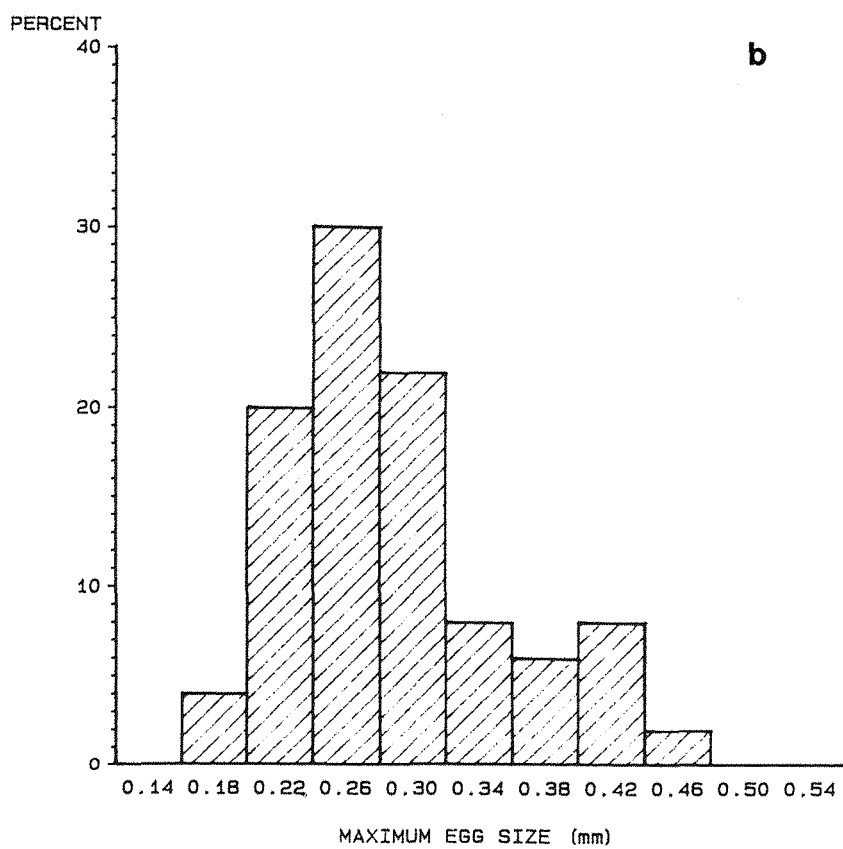
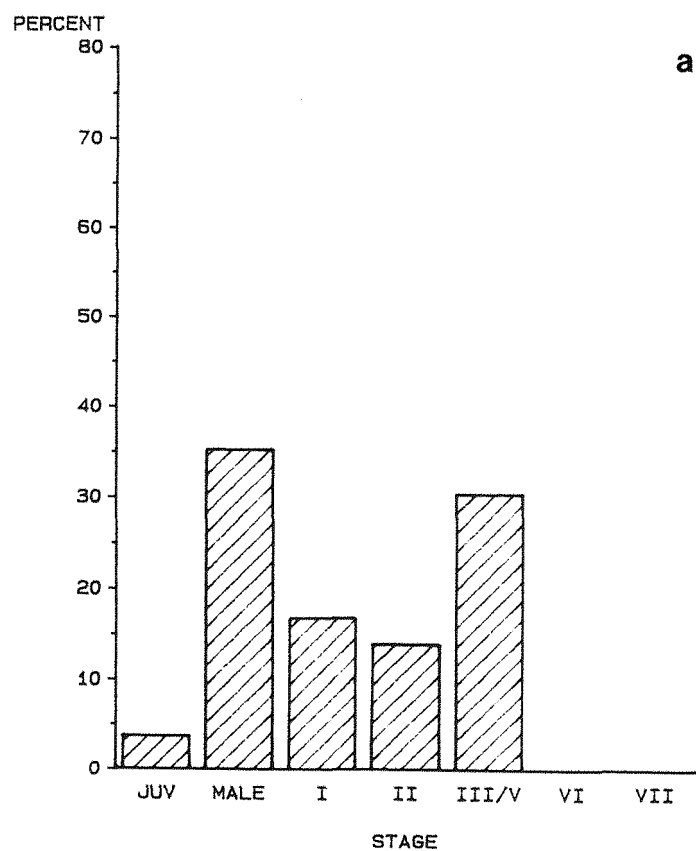


Table 4. Latitudinal and seasonal comparisons of Cyclothone braueri.

Latitude °N	Sex Ratio*		Size at Maturity (mm SL)		Max. Size (mm SL)	
	S	A	S	A	S	A
60	1.9		25		35	
50	2.4	2.5	25	28	35	37
40	3.7	8.5	24	22	36	34
30	2.2	12.4	19	20	29	32
20	1.7		22		31	

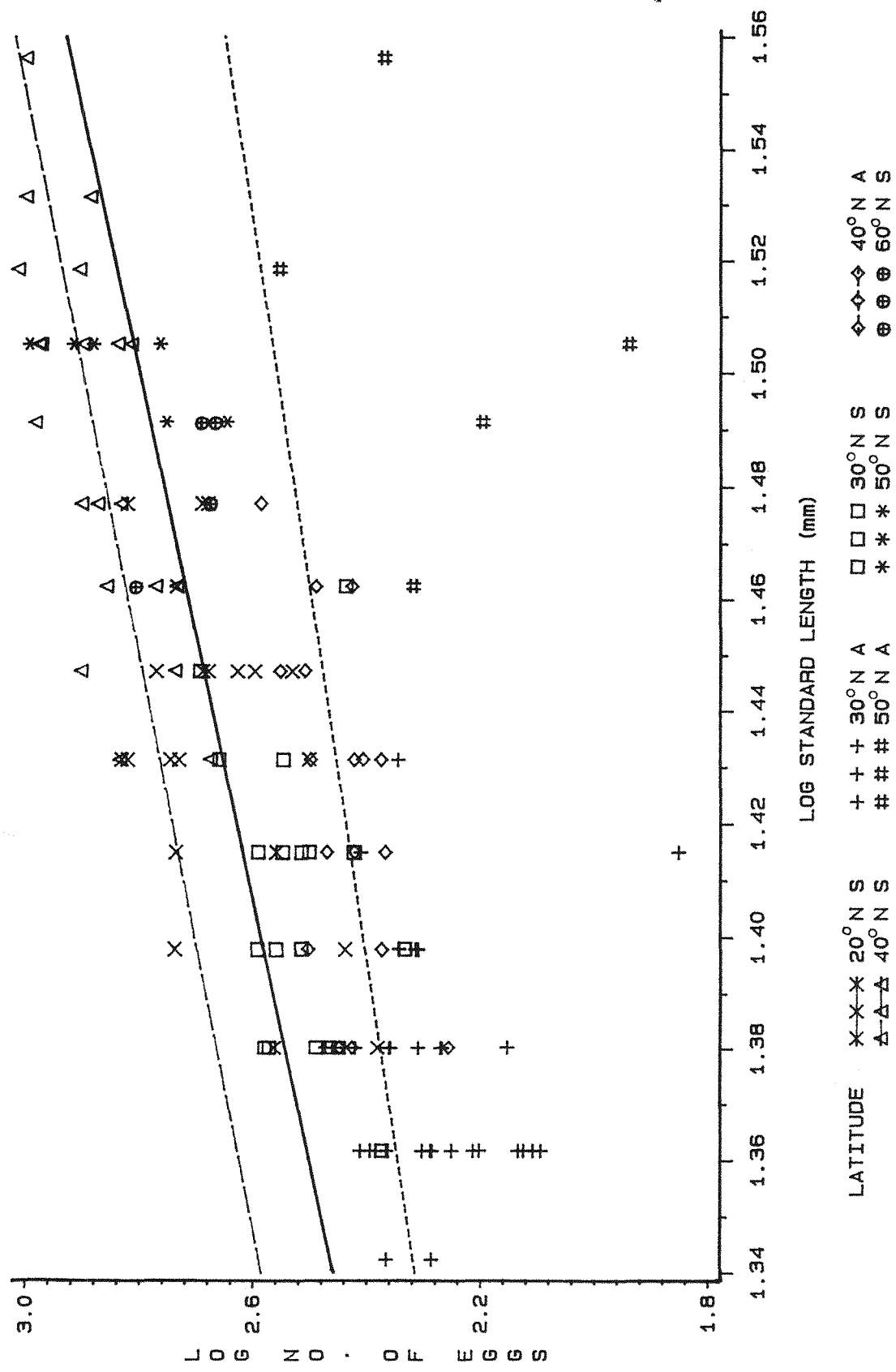
S=spring, A=autumn, *= expressed as number of females to each male.

Table 5. Regression equations of fecundity (F) vs standard length (mm SL) of C. braueri.

Location	Equation	p=	r ²	n	F
40°N S	$\log F = 2.16 \log SL - 0.32$	0.001	0.51	23	21.87
20°N S	$\log F = 2.14 \log SL - 0.41$	0.02	0.24	22	5.93
40°N A	$\log F = 1.53 \log SL + 0.26$	0.01	0.34	18	7.69
ALL	$\log F = 3.26 \log SL + 0.61$	0.001	0.67	112	220.64

S=spring, A=autumn, ALL= all stations combined

Figure 18. Log fecundity vs. log standard length for C. braueri. Regression lines are shown for stations where the regression was significant.



3.2.2 Cyclothone microdon

Cyclothone microdon was the predominant species at the northern extent of the sampled area. It was the most abundant species at 60 and 50°N in the spring and gradually decreased in importance until none were captured at 20°N (Fig. 3a and Table 3). A similar decrease in abundance was evident in the autumn although it was not as abundant as C. braueri at 50°N during that season (Fig. 3b). Although the density was relatively constant across the latitudes where it was taken (Fig. 3) the biomass was much higher at higher latitudes, particularly in the spring (Fig. 4).

3.2.2.1 60°N.

The population of Cyclothone microdon sampled at 60°N was dominated by a unimodal group of stage II females between 34 and 58mm SL with a peak at 44mm SL (Fig. 19). An overlapping group of stage I females was present at the lower end of this group from 30-42mm SL. Males were present in only very small numbers with a modal size of 28mm SL representing a sex ratio of one male to approximately 13 females. Size at maturity in the spring at this latitude occurred at 38-40mm SL. Protandrous hermaphrodites made up about 4% of the population at standard lengths of 28-38mm. Few gonad stages were present in any number other than stage II females (Fig. 20). The stage III/V females that were present were likely only just into that stage of maturity as the maximum egg size in their ovaries was approximately 0.1mm. The small size suggests they may be closer to stage II. There were very few juveniles present in the population (Fig. 20).

3.2.2.2 50°N.

Although the basic shape of the length frequency distribution at 50° N in the spring was bimodal, three groups could be distinguished (Fig. 21a). At the smallest standard lengths males were present at size of 24-34mm SL. Females were present in two overlapping groups of stage I females peaking at 38mm SL and more advanced stage II and III/V females with peak abundance at 44mm SL. Overall females were most abundant at 40mm SL. Stage II females were the predominant group present (Fig. 22a). Size at maturity of 40mm SL (Fig. 21a). Males were few in relation to females (1:9.3 males:females) and made up less than 6 percent of the population. Hermaphrodites were present in small numbers (<4%) at sizes of 30-38mm SL. There were few juveniles present (Fig. 22a). The mean of the maximum sized egg of the few stage III/V females was 0.2mm (n=7).

Autumn samples showed a picture of a population where spawning was probably complete. Few stage III/V females were present although spent (stage VII) and a relatively large proportion of spent/recovering (stage VII/II) females were captured (Fig. 22b). Stage II females predominated (Fig. 22b) and, together with other stages of mature females, were found at a range of standard lengths between 34 and 52mm although there were few adults at standard lengths larger than 46mm SL (Fig. 21b). There was a peak in the abundance of the mature females at 40mm SL with other lower peaks at 44mm SL and at 34mm SL, which was primarily immature females (Fig. 21b). There was the possibility of three overlapping size classes of females, stage I at 34mm SL, and mature females at 38-40mm SL and around 44mm SL (Fig. 21b). Few hermaphrodites were present (1.6%). The lack of juveniles would suggest that although spawning is completed the larvae have not yet descended from the epipelagic depths where the first part of the life history is spent. The sex ratio was heavily biased in favour of females (1:5.6 males:females). The males that were present were centred around a mode of 28mm SL (Fig. 21b).

3.2.2.3 40°N.

Spring populations of Cyclothone microdon at 40°N reflected a spawning population with both stage III/V and spent (stage VII) females present (Fig. 24a). The predominance of stage II females (Fig. 24a) and the proportion of females with small eggs (Fig. 25a) suggests that the majority of the population was still approaching spawning. A unimodal shape was present in the length frequency distribution with different stages abundant at different size intervals possibly suggesting different size classes. Adult females were distributed around a mode of 40mm SL (mean 40.5mm SL \pm 4.9) and there were few large females present (Fig. 23a). Stage I females were most abundant at 32mm SL and most had matured by 36mm SL although some were mature as small as 30mm SL. There were approximately 8 females to every male (Table 7). Male standard lengths ranged from 22-30mm SL (Fig. 23a). Hermaphrodites made up greater than 6% of the population. The lack of juveniles suggested spawning had not occurred for some time.

Juveniles predominated in the autumn samples (Fig. 24b) and were found in greatest numbers at standard lengths of 20 to 24mm (Fig. 23b). The presence of stage III/V and spent (stage VII) females indicated spawning was likely still occurring. Analysis of the maximum egg size in each female suggests that some females could have been approaching spawning (egg sizes approx. 0.3mm) but the majority had small eggs of 0.14-0.22mm (Fig. 25b). Adult females had a mean standard length of 37.1mm SL (\pm 7.7) with 34mm SL the most abundant size interval (Fig. 23b). It was difficult to isolate any separate size classes. The size at maturity was less than 34mm SL and some females were mature as small as 22 mm SL. Hermaphrodites were virtually absent from the population (Table 7). The sex ratio was skewed in favour of females (1:3.2 males:females), males making up less than 10 percent of the population (Fig. 24b).

3.2.2.4 30°N.

Juveniles predominated at 30°N during both times of the year when samples were taken. In the spring juveniles made up approximately 65% of the population (Fig. 27a). Together with a number of mature males of 20mm SL, they formed the largest peak in the population (Fig. 26a). The females that were present were mostly at stage III/V but in low numbers and scattered across the size range. All stages were represented except hermaphrodites (Fig. 27a). The presence of females in stages VI to VII/II indicates that spawning was occurring at this latitude in the spring. The maximum egg sizes of individual females confirms that spawning could be approaching for some individuals with egg sizes as large as 0.42mm diameter although the majority were probably in a pre-spawning condition with eggs of less than 0.3mm diameter (Fig. 28).

No adult females were present in the autumn (Fig. 27b and 26b). Juveniles were bimodally distributed with peaks at 14 and 18mm SL (Fig. 26b) and made up approximately 90 percent of the population (Fig. 27b). Males predominated at 20mm SL and had a mean size of 20.3mm SL \pm 1.4.

3.2.2.5 Latitudinal Comparisons

At northern latitudes the population generally consisted of a unimodal peak of adult females. Separate groups could be distinguished in this mode, primarily by stage of maturation. There appeared to be up to 3 size classes of females and one of males. If these were separate year classes a very low growth rate is indicated. Smaller individuals accounted for only a very small proportion of the catch of C. microdon at 60 and 50°N but were abundant at 40°N in the autumn. Although only one peak was present, the shape of the length frequency histogram at 50°N in the autumn could suggest underlying year classes that cannot be distinguished on the basis of size alone. At 30°N for both times of the year and at 40°N in the autumn there was

still only one size peak evident in the samples but this was at a much smaller standard length and was accounted for mainly by juveniles. It appears from this latitudinal series that adults and juveniles do not generally co-occur. Only at 40°N were both adults and juveniles found in large numbers and that was at different times of the year. Also, at no point did males make up a significant proportion of the total catch. Only at 30°N did males make up more than 10 percent of the total catch.

Comparison of length frequencies from the different latitudes suggests a shift towards a predominance of smaller individuals in the population with decreasing latitude both in the spring and in the autumn (Figs. 19,21,23 and 26). However, this is not reflected in the mean size of the separate stages. There was little change in the mean size of mature females (stage II+) with latitude (Table 6). There was no difference in the mean size of males between 60 and 40°N although the mean size at 30°N was significantly different from males at 40°N ($t=20.2$, $df=199$, $p<.001$) (Table 6). Size at maturity decreased with latitude (Table 7).

Seasonally, the mean size of mature females was significantly smaller in the autumn at 50°N ($p<.001$, $t=12.2$, $df=818$) and at 40°N ($p<.001$, $t=7.47$, $df=626$) (Table 6). This was primarily due to the lack of individuals at the larger standard lengths at 50°N as the modes were similar. Size at maturity of adult females was also slightly smaller in the autumn (Table 7). There was little seasonal difference in the size of males (Table 6).

More individuals were at advanced stages of maturity at lower latitudes. In the spring, there was a gradual shift from a majority of the mature females being classified as stage II at 60°N (Fig. 20) to the majority of mature females being classified as stage III/V at 30°N (Fig. 27). The size of eggs in mature females also suggested more advanced stages at lower latitudes at this time of year. The few egg sizes measureable at 60 and 50°N were all less than 0.2mm whereas at both 40°N and 30°N the eggs were larger in size (Fig. 25a and 28).

Spawning was more prolonged at lower latitudes with the population

at 40°N still spawning in the autumn whereas at 50°N spawning appeared to be finished. Few stage III/V females were present at 50°N as compared to 40°N (Fig. 22b and 24b), a larger proportion of stage VII and VII/II were present at 50°N and there were females with large eggs present at 40°N in the autumn (Fig. 25b) when all the eggs at 50°N were too small to be included in the analysis.

The sex ratio of Cyclothone microdon was high and variable over the latitudes examined (Table 7). The number of females for every male decreased with both latitude and season. The proportion of the population that were hermaphrodites decreased with advancing season (Table 7).

Fecundities ranged from 527 to 4391 (32-56mm SL). The highest fecundities were found at 40°N in the spring (Fig. 29). The number of eggs appeared to vary both with latitude and season. Counts were significantly lower at both 40°N in the autumn and 30°N in the spring (ANCOVA $F=21.67$, $df=(3,49)$, $p=0.01$). There was no significant difference between 40°N in the autumn and 30°N in the spring. Only a few fecundities were available from 50°N. They were randomly scattered between relatively high counts (48mm SL, 2905 eggs) and two of the lowest counts (43mm SL 200 eggs and 37mm SL 484 eggs). Correlation coefficients were higher at 40°N than at 30°N (Table 8).

3.2.3 Cyclothone pseudopallida

Cyclothone pseudopallida was found to have one of the most unpredictable distributions. It was present in very small numbers at most stations but was only abundant at 10°N in the spring and 20°N in the autumn (Table 3). At 20°N in the autumn it was the most abundant species (Fig. 3b). The total catch of C. pseudopallida was larger at 30°N than at 20°N in the spring (Table 3) but the nature of the sampling was such that the density at the two locations was comparable (Fig. 3a) although the biomass at 30°N was higher (Fig. 4a). The density and biomass at 10°N in the spring and at 20°N in the autumn

Figure 19. Length-frequency distribution by sex and stage of C. microdon at 60°N in the spring (n=1214).

- 1= Juveniles
- 2= Males
- 3= Hermaphrodites
- 4= I
- 5= II
- 6= III/V
- 7= VI
- 8= VII
- 9= VII/II

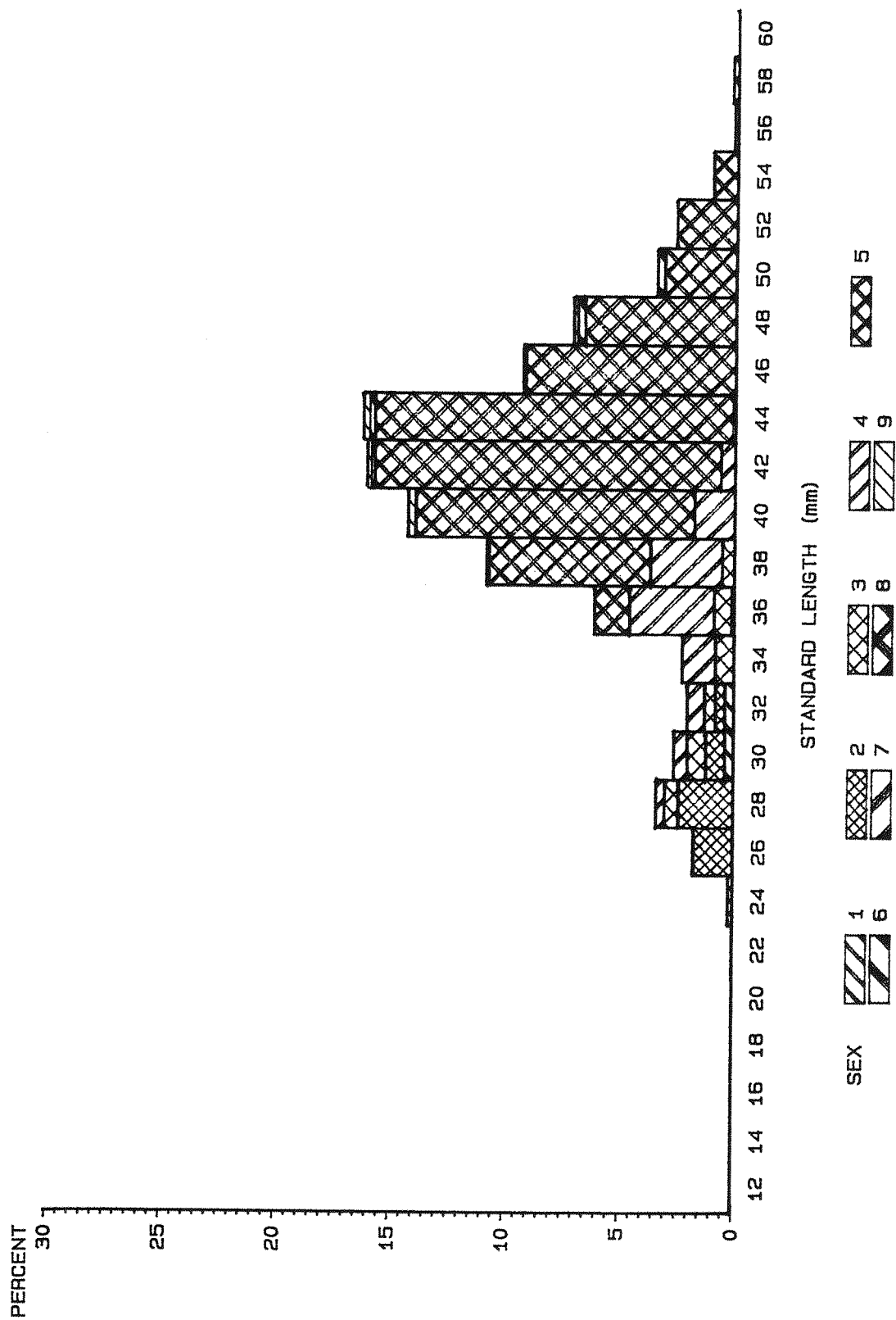


Figure 20. Percent abundance of each sex/stage of
C. microdon at 60°N in the spring (n=1214).

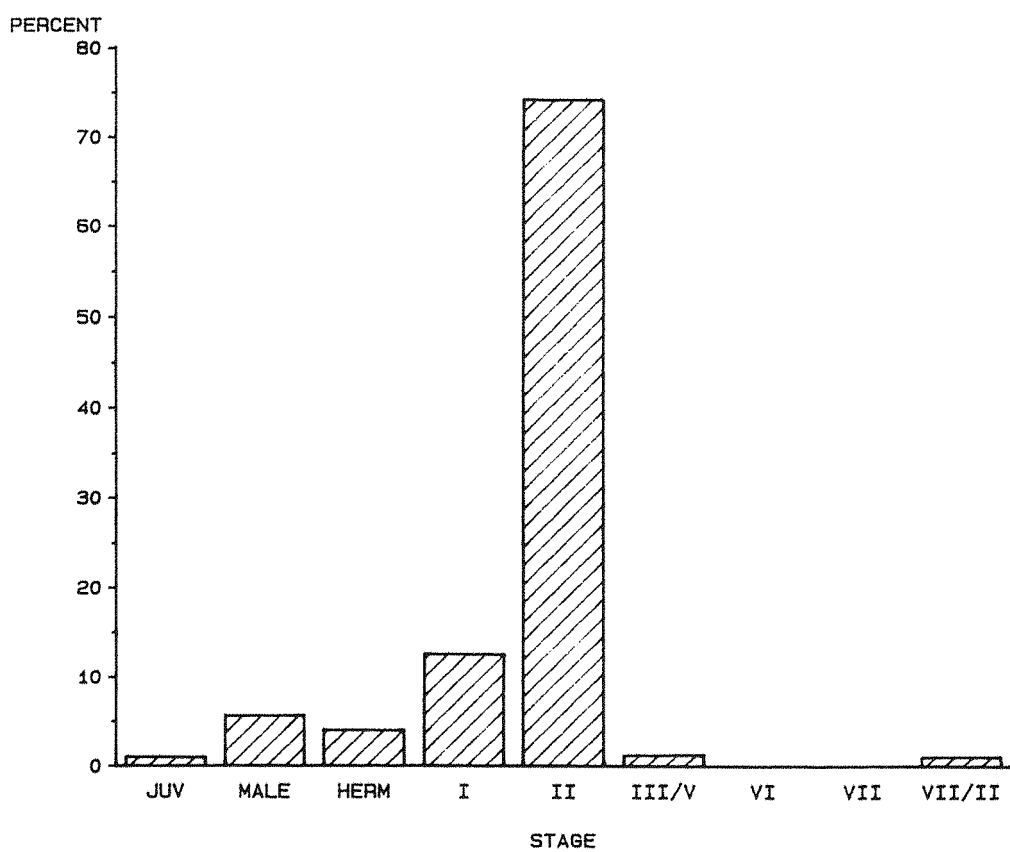
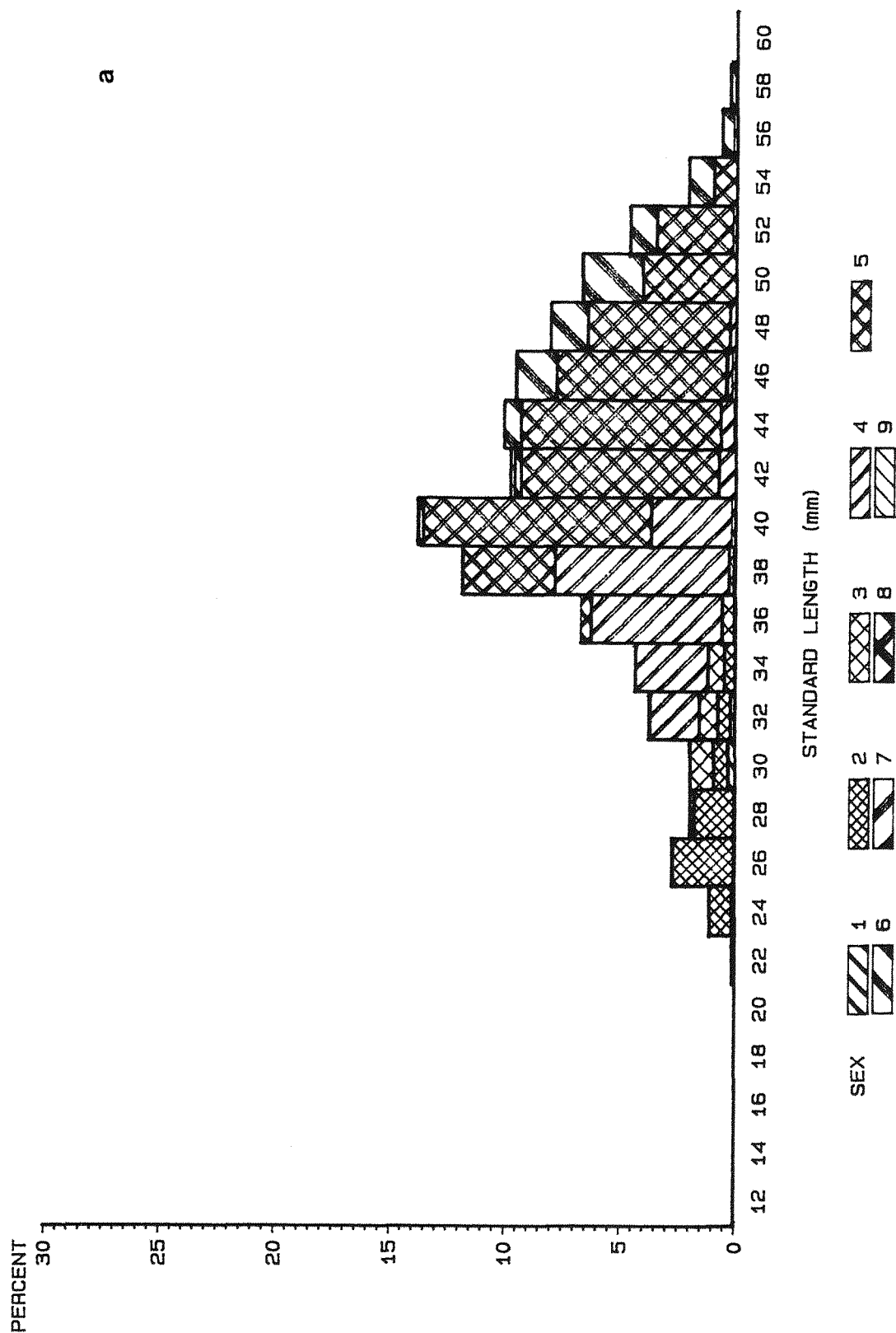
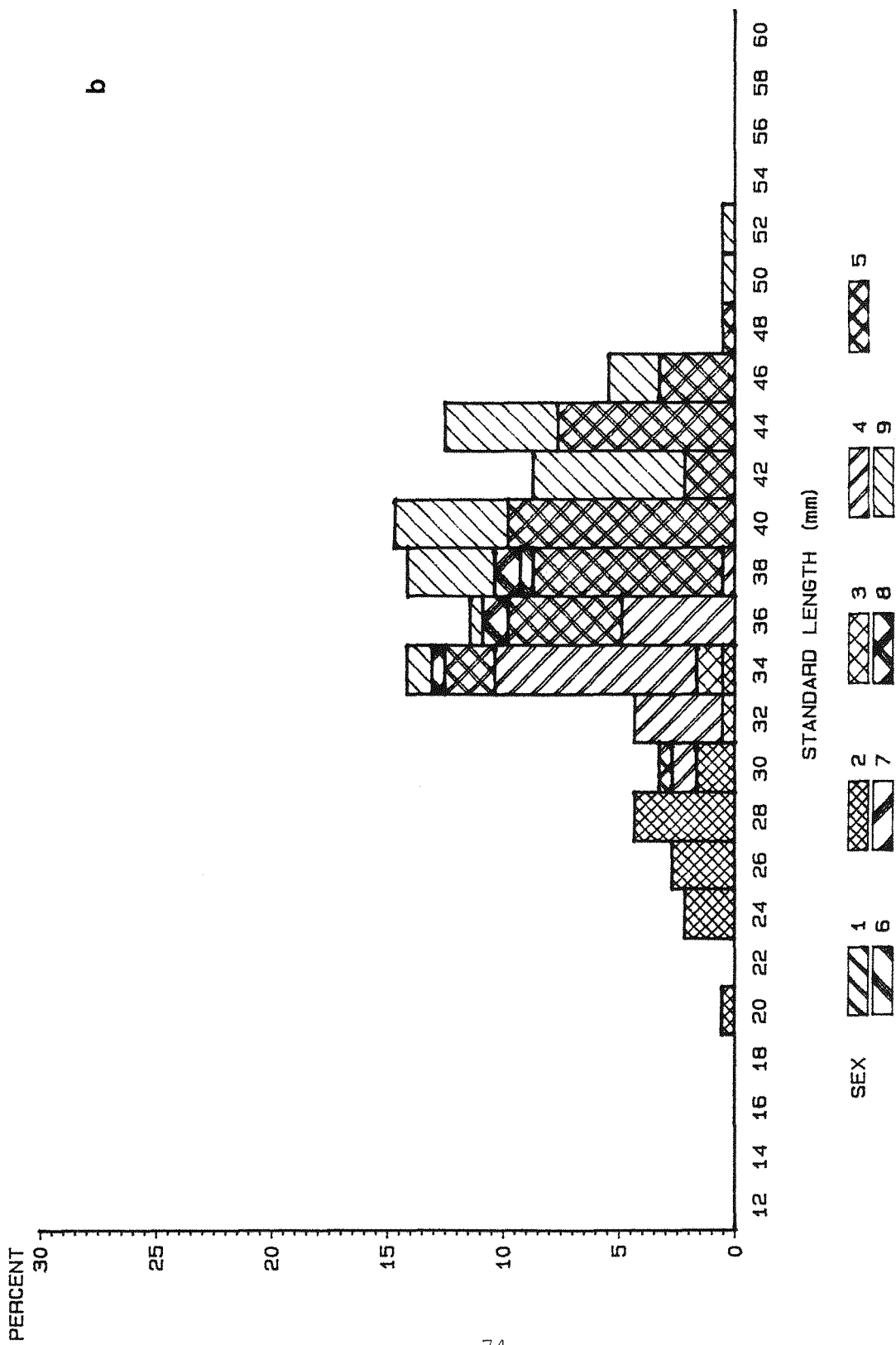


Figure 21. Length-frequency distribution by sex and stage of C. microdon at 50°N a) in the spring (n=1084) and b) in the autumn (n=184).

- 1= Juveniles
- 2= Males
- 3= Hermaphrodites
- 4= I
- 5= II
- 6= III/V
- 7= VI
- 8= VII
- 9= VII/II





b

Figure 22. Percent abundance of each sex/stage of
C. microdon at a) 50°N in the spring (n=1084)
b) 50°N in the autumn (n=184).

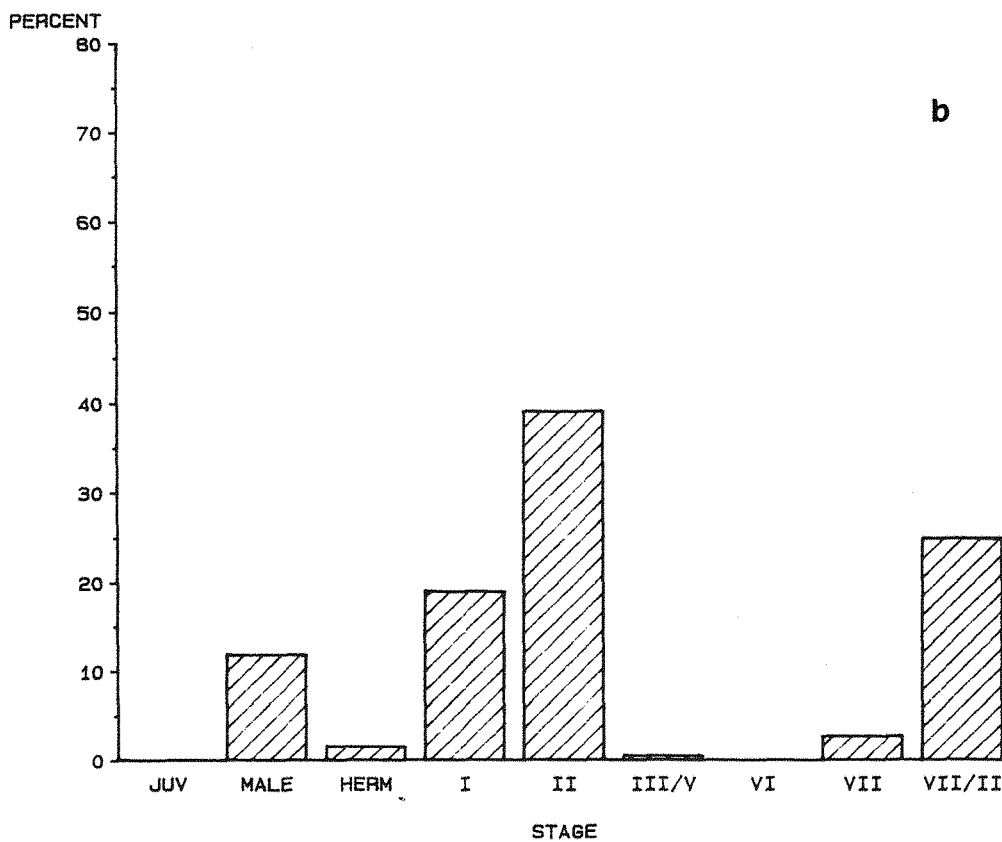
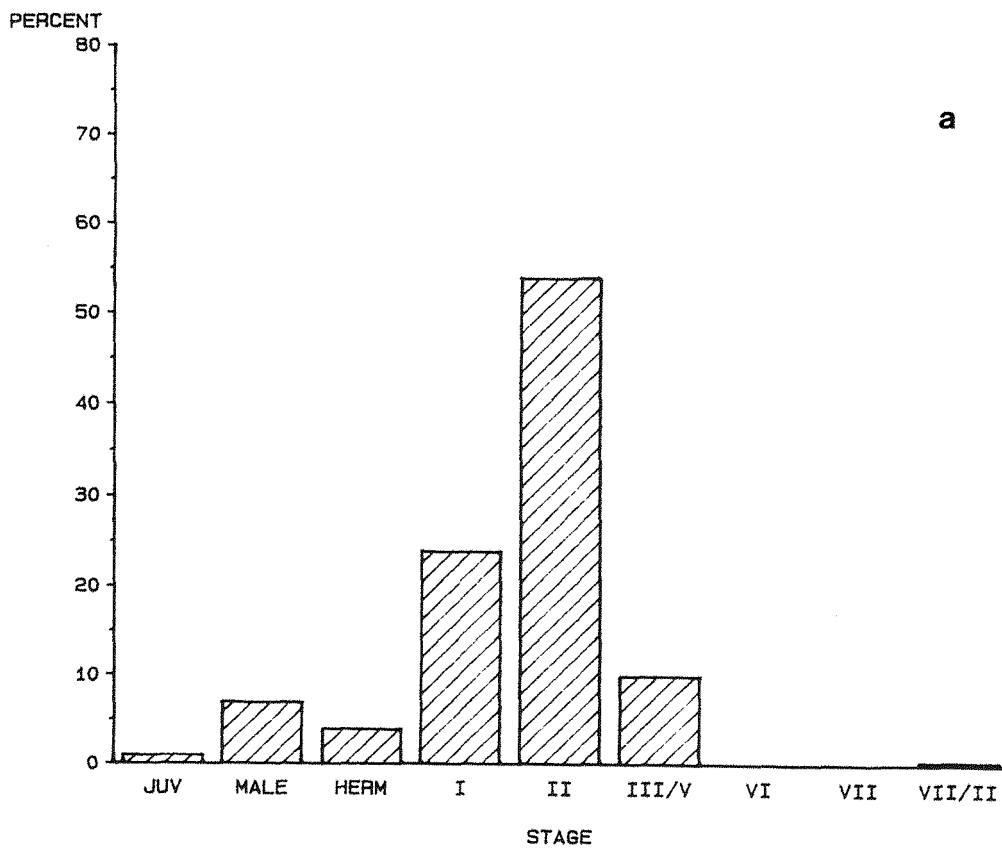
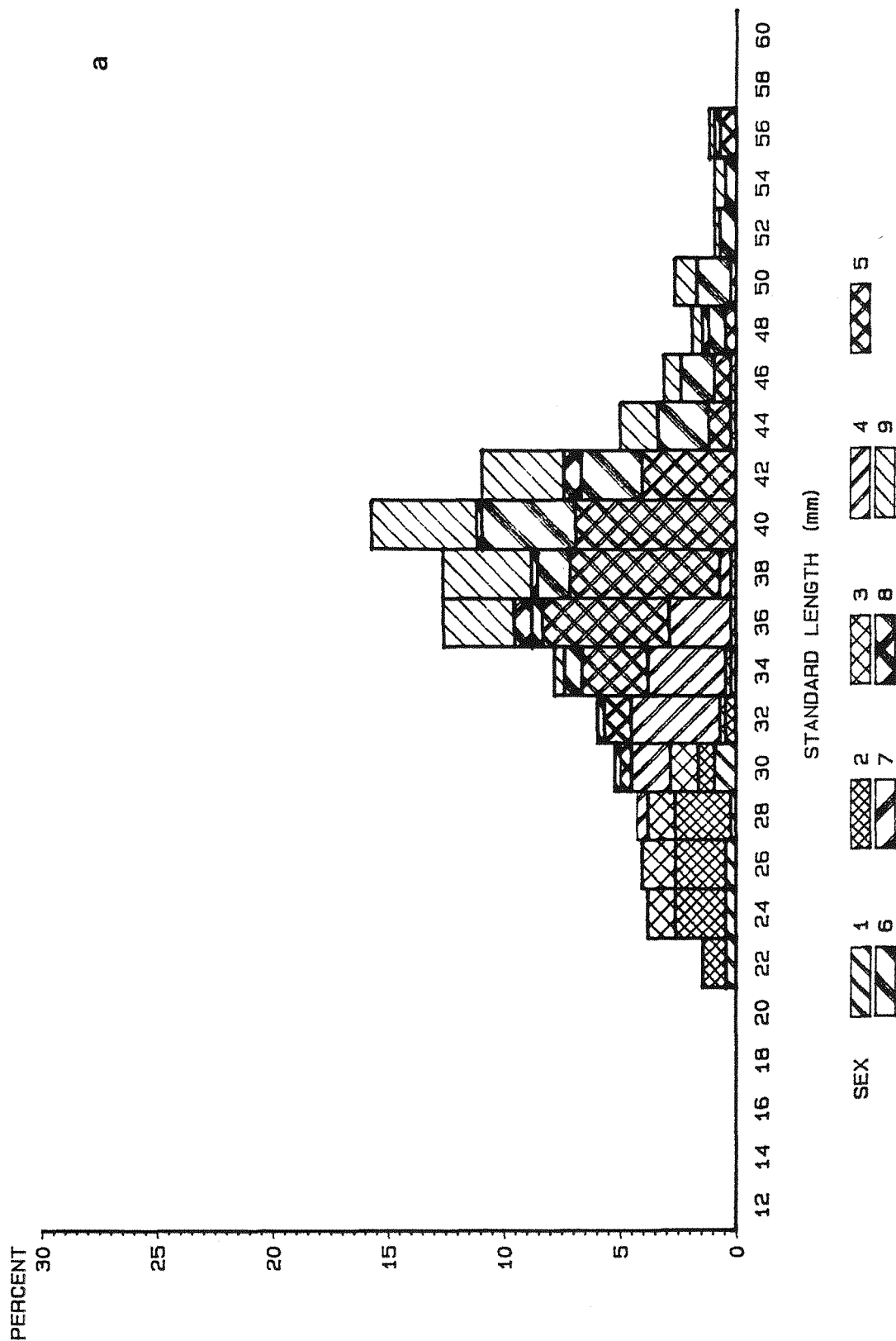
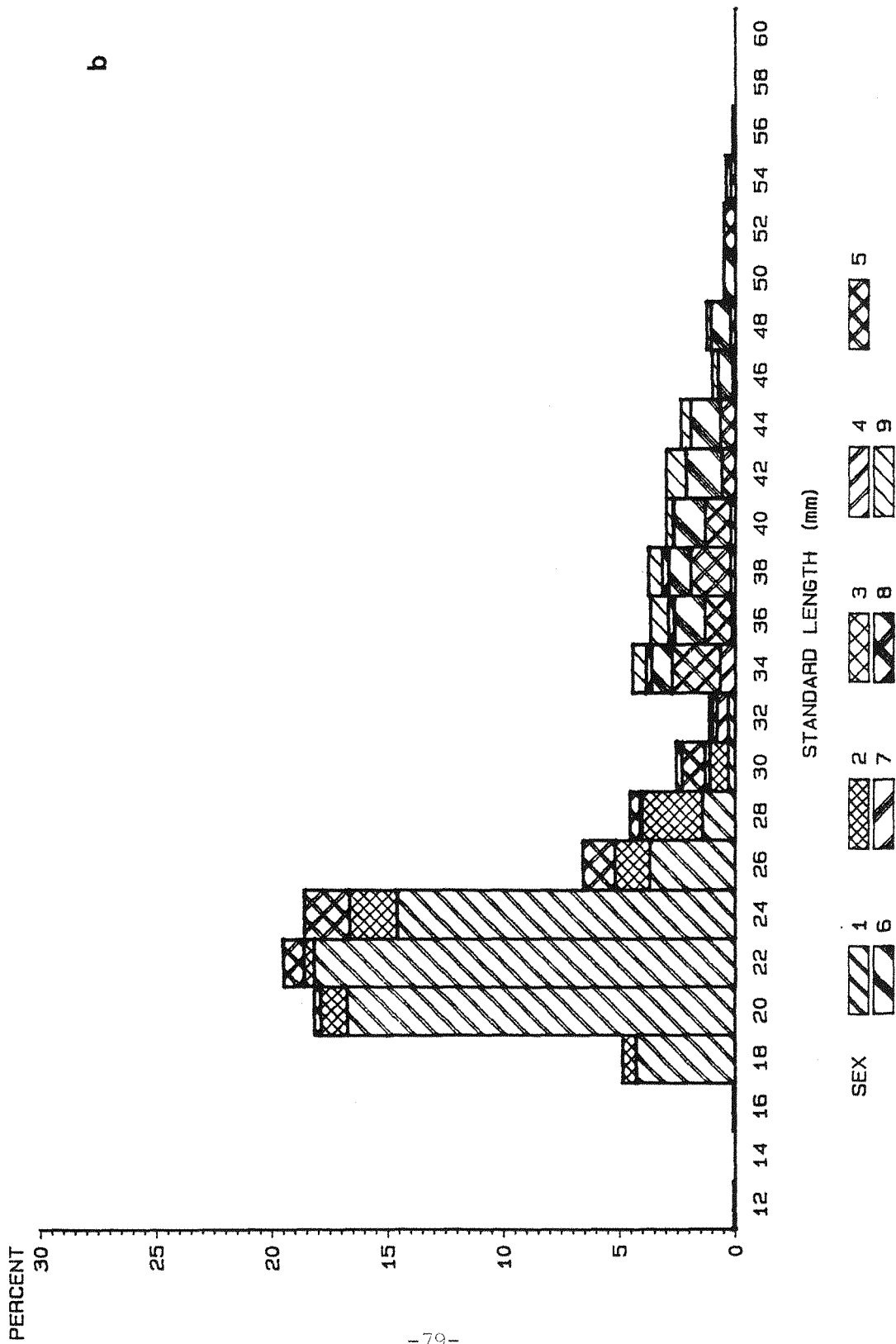


Figure 23. Length-frequency distribution by sex and stage of C. microdon at 40°N a) in the spring (n=421) and b) in the autumn (n=1142).

- 1= Juveniles
- 2= Males
- 3= Hermaphrodites
- 4= I
- 5= II
- 6= III/V
- 7= VI
- 8= VII
- 9= VII/II



a



b

Figure 24. Percent abundance of each sex/stage of C. microdon at a) 40° N in the spring (n=421) and b) 40° N in the autumn (n=1142).

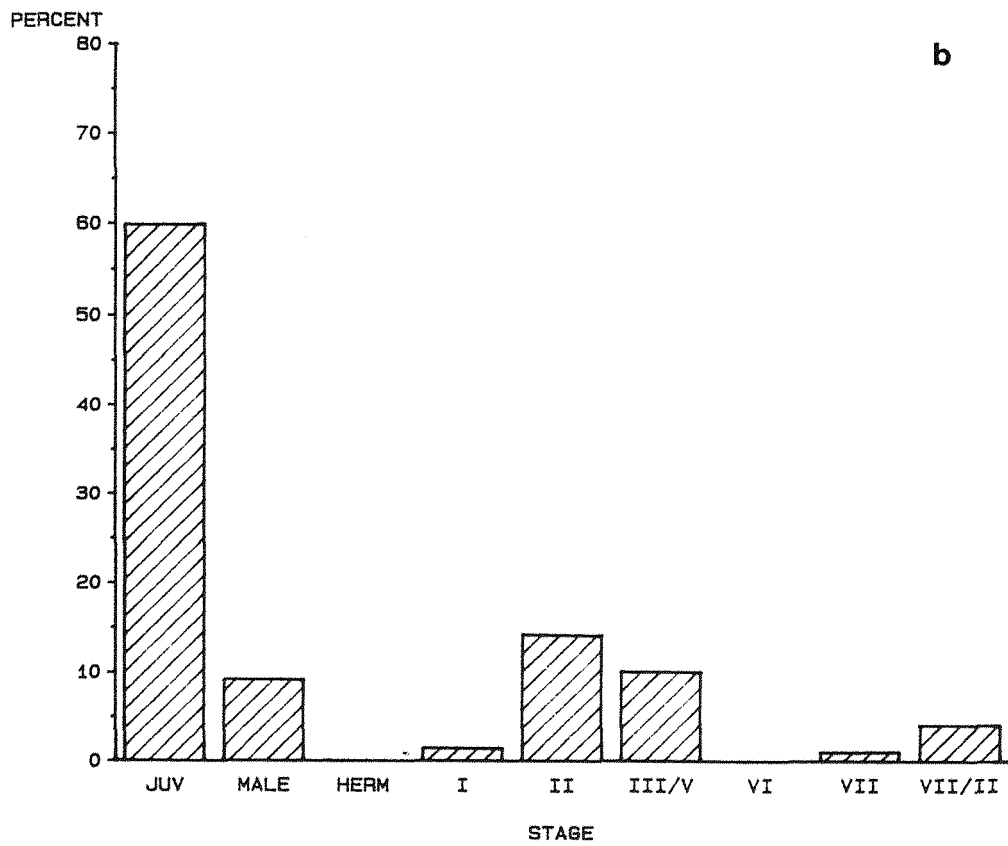
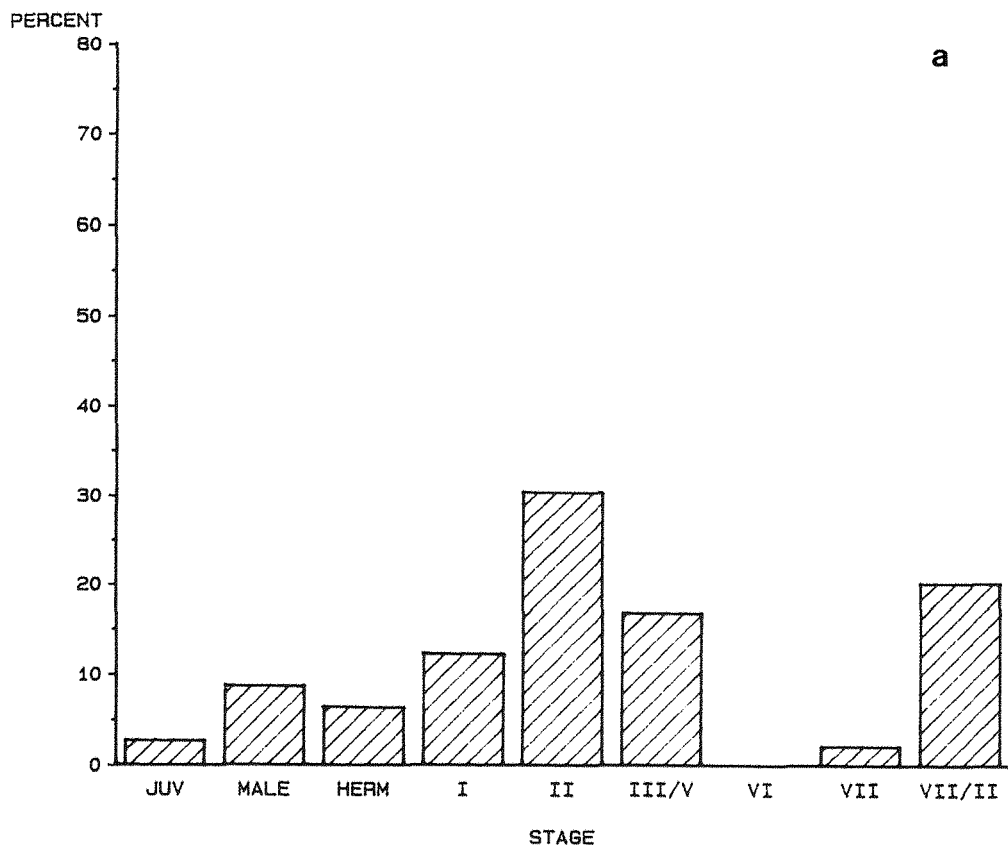


Figure 25. Size-frequency distribution of the maximum egg diameter in female C. microdon at 40°N in a) the spring (n=56) and b) the autumn (n=40).

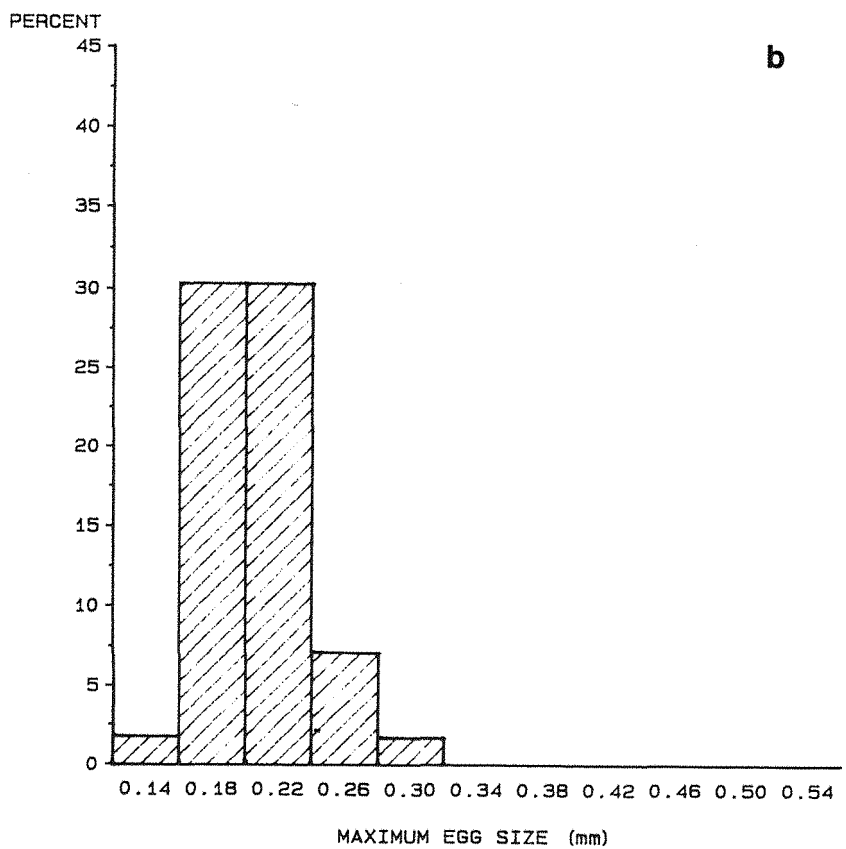
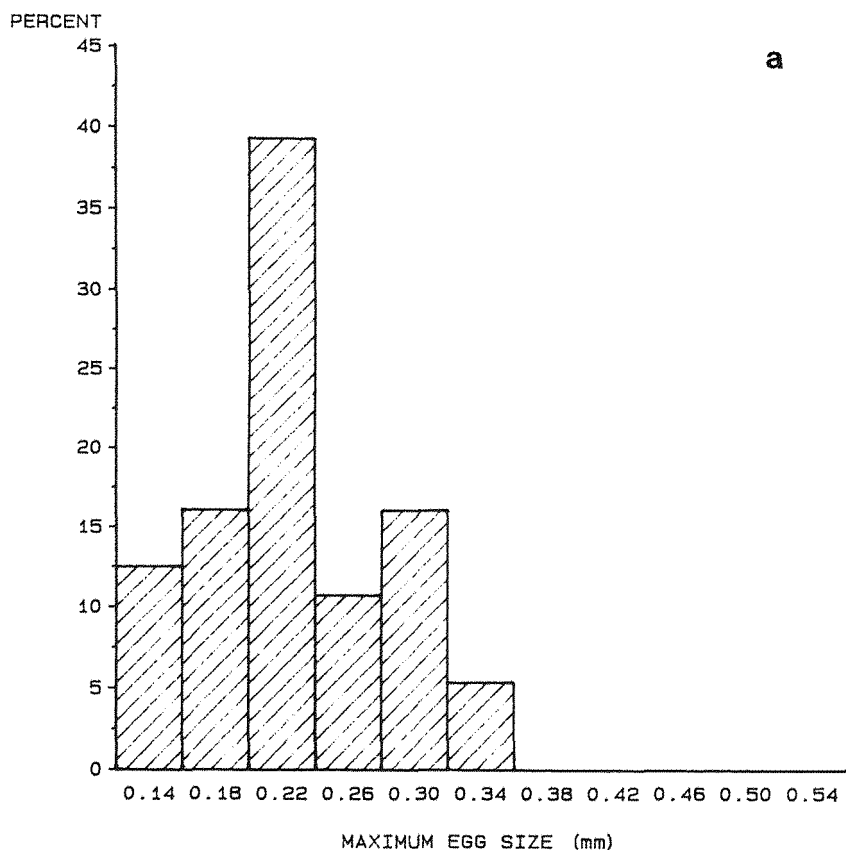
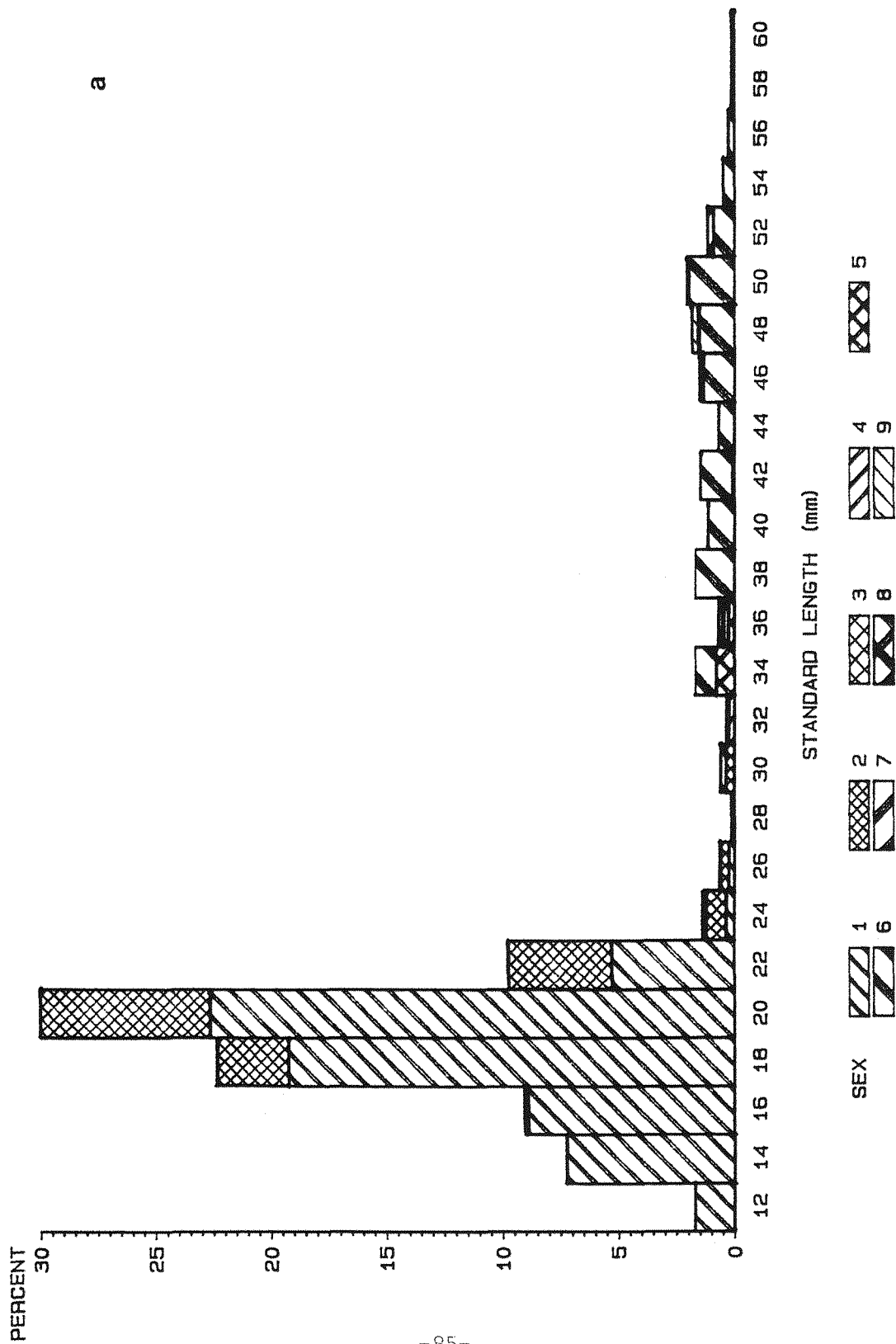
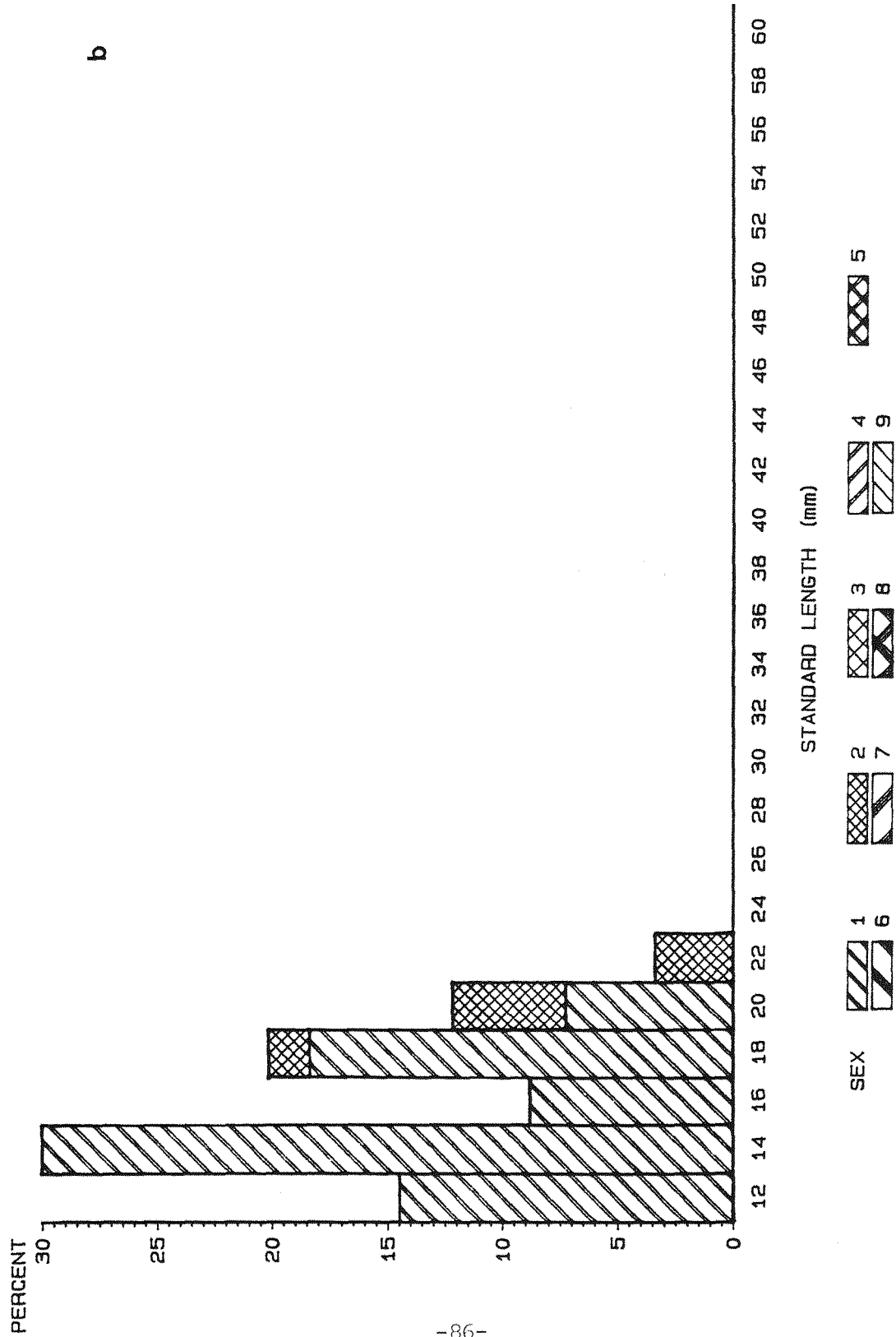


Figure 26. Length-frequency distribution by sex and stage of C. microdon at 30°N a) in the spring (n=874) and b) in the autumn (n=387).

- 1= Juveniles
- 2= Males
- 3= Hermaphrodites
- 4= I
- 5= II
- 6= III/V
- 7= VI
- 8= VII
- 9= VII/II





b

Figure 27. Percent abundance of each sex/stage of
C. microdon at a) 30°N in the spring (n=874)
and b) 30°N in the autumn (n=387).

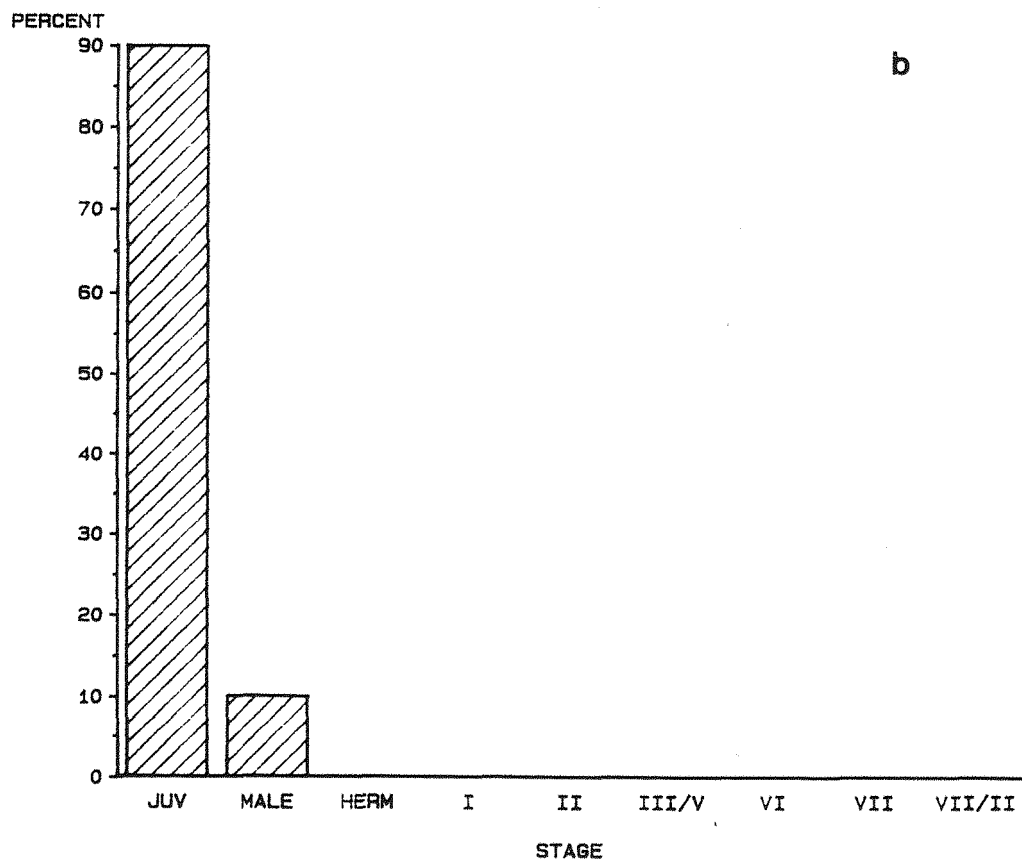
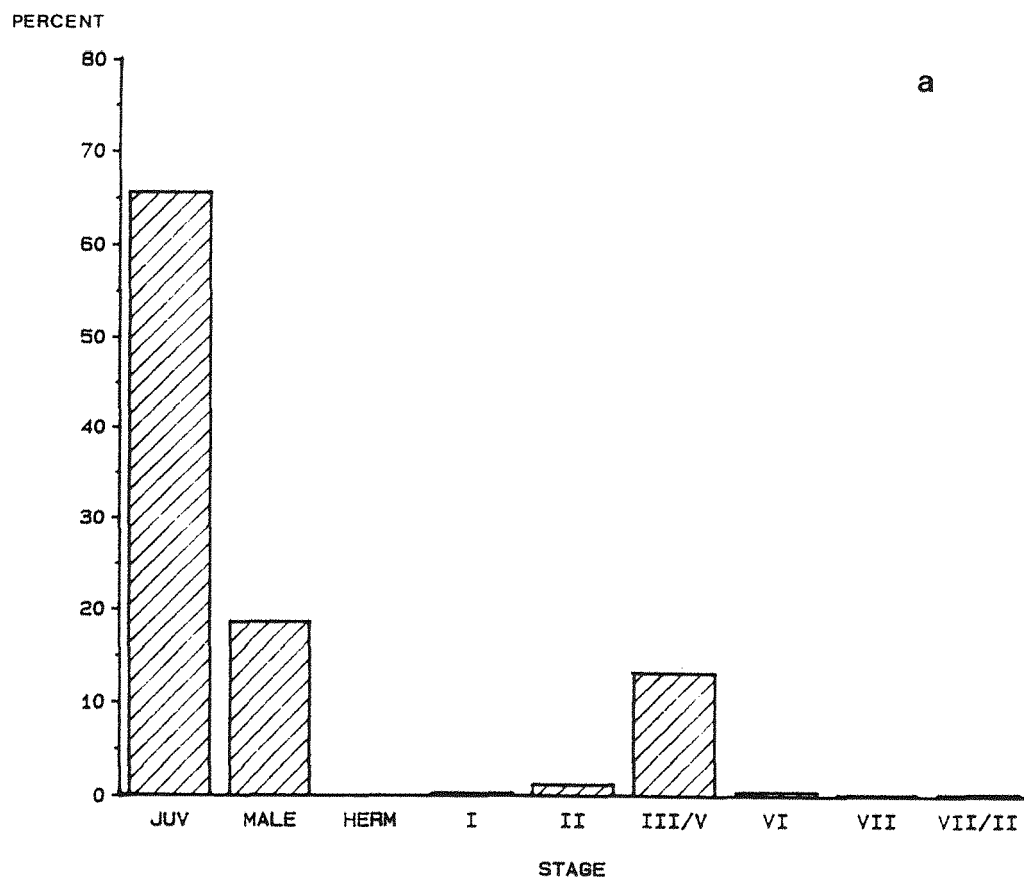


Figure 28. Size-frequency distribution of the maximum egg diameter of female C. microdon at 30° N in the spring (n=50).

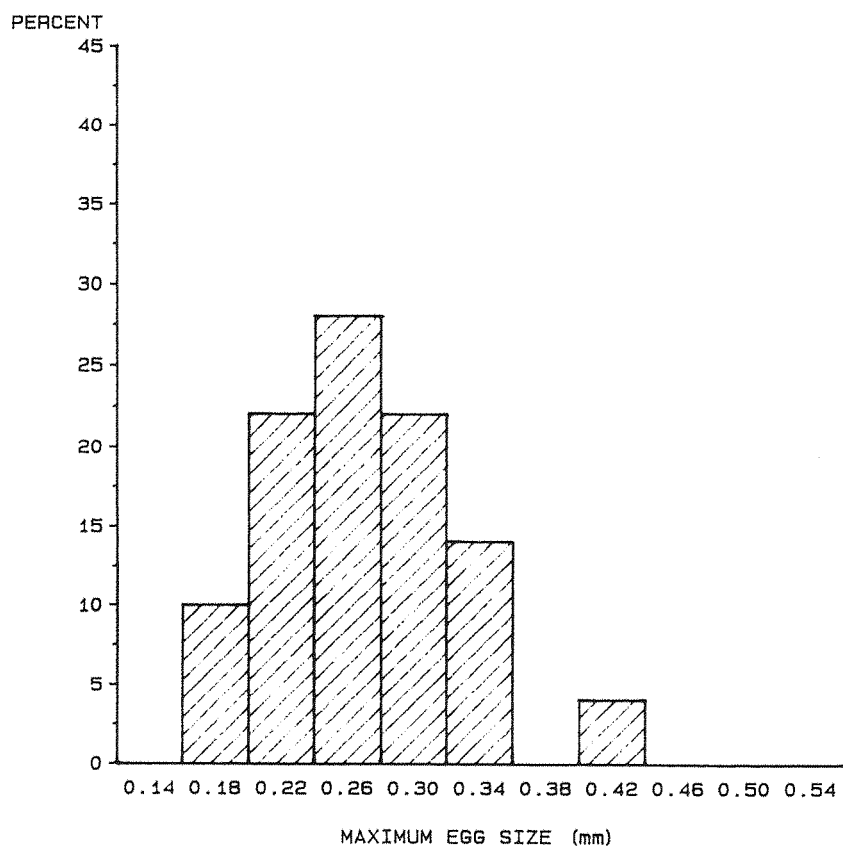


Table 6. Mean size (mm SL) and standard deviation of mature females (stage II+) and male Cyclothone microdon.

Lat. °N	Mature Females		Males	
	Spring	Autumn	Spring	Autumn
60	43.6 ±4.0		27.7 ±2.0	
50	45.1 ±4.6	40.5 ±3.7	27.7 ±2.9	27.0 ±2.9
40	40.5 ±4.9	37.1 ±7.7	26.2 ±2.7	25.2 ±3.6
30	43.6 ±6.9	-----	20.6 ±2.2	20.3 ±1.4

Lat.=latitude

Table 7. Size at maturity, sex ratio expressed as the number of females per males and percent abundance of hermaphrodites of Cyclothone microdon. Lat.=latitude S=spring A=autumn

Lat. °N	Maturity (mm SL)		Sex Ratio*		Hermaphrodites (Percent)	
	S	A	S	A	S	A
60	40		13.5		4.1	
50	40	38	9.3	5.6	4.0	1.6
40	38	34	7.9	3.2	6.4	0.1
30	34	--	0.8	---	0.0	0.0

*= expressed as number of females to each male

Figure 29. Log fecundity vs. log standard length for
C. microdon. Regression lines are shown
for stations where the regression was significant.

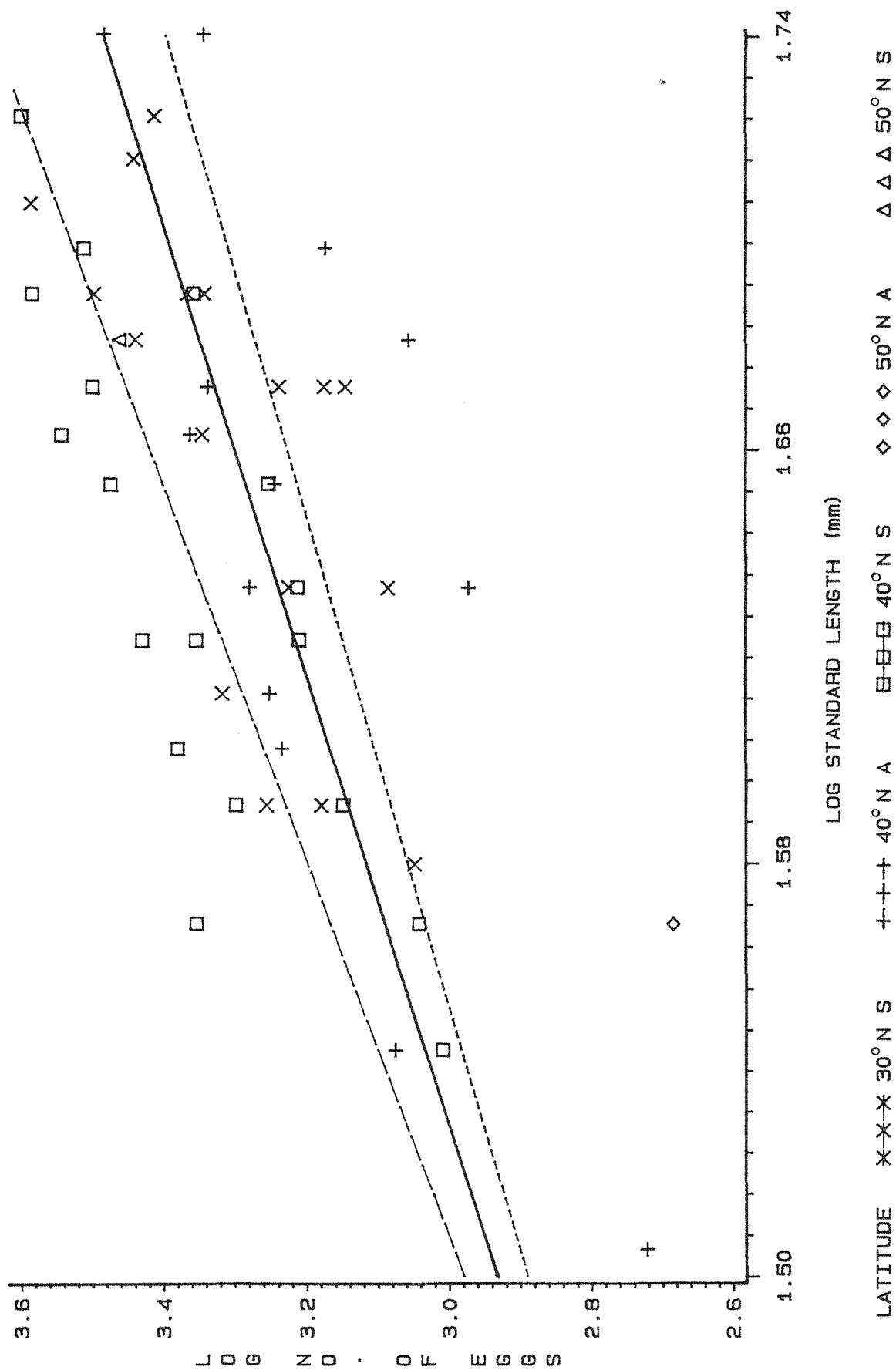


Table 8. Regression equations of fecundity (F) on standard length (mm SL) of C. microdon.

Location	Equation	p=	r ²	n	F
40°N S	$\log F = 3.0 \log SL - 1.56$	<.001	0.69	19	37.84
40°N A	$\log F = 2.5 \log SL - 0.82$.002	0.58	14	16.40
30°N S	$\log F = 1.7 \log SL + 0.5$.002	0.43	20	13.36
ALL	$\log F = 2.3 \log SL - 0.41$	<.001	0.41	53	35.12

S=spring, A=autumn

were very similar (Figs. 3 and 4).

3.2.3.1 30°N.

Three modes were evident in the length frequency of Cyclothone pseudopallida at 30°N in the spring (Fig. 30). The first mode at 20mm SL was made up of juveniles (Fig. 30). Their relatively large size suggests they had not recently been spawned. The second mode was predominately males of 26mm SL although some stage I females were present with a 24-26mm SL. Stage III/V was the predominant stage in the population (Fig. 31a) and these were the largest individuals present with a modal size of 36mm SL. A group of stage II females were found with a smaller size range between 30 and 34mm SL. Although stage III/V females were abundant the small eggs present suggested that the population was not close to spawning. The maximum egg diameter from all stage III/V females available was less than 0.22mm. Females were mature by approximately 28mm SL and were more than twice as abundant as males (males:females 1:2.8).

3.2.3.2 20°N.

No C. pseudopallida were captured at 20°N in the spring. The population in the autumn resembled a normal distribution although the sexes and maturity stages were not evenly distributed throughout the size range (Fig. 33). Juveniles predominated (Fig. 31b) and had a modal size of 22mm SL although they had a wide size range of 10-30mm SL (Fig. 33). Males were most abundant at a standard length of 26 mm SL and mature females were evenly distributed between 26 and 34mm SL (Mean 30.5 Fig. 33). However, the mature females could be split into a group of stage II females (mode 26-28mm SL, mean 26.8mm SL) and a group of stage III/V females (mode 34mm SL, mean 34.3mm SL). These two stages made up approximately equal proportions of the population (Fig.

31b). The size at maturation for females was 22mm SL and the sex ratio was 1.3 females for every male. The majority of the mature females had small eggs of 0.22mm but some females had eggs as large as 0.3mm (Fig. 32a). The population appeared to have been sampled well after spawning. The juveniles were probably just maturing to a point where their sex could be determined and recruitment to males and stage I females would occur as these three groups merge together at a standard length of 22-26mm (Fig. 33). Few large females were present.

3.2.3.3 10°N.

At 10°N the C. pseudopallida population was dominated by males and juveniles which together made up more than 60 percent of the total catch (Fig. 31c). Most of the juveniles were relatively large (mode 24mm SL, mean 23.3mm SL) and the males were more or less evenly distributed across a wide size range (28-34mm SL) (Fig. 34). Immature females (stage I) were found at similar sizes to the males. Size at maturation of females was approximately 32mm SL. Most of the mature females were stage II (Fig. 31c). The presence of stage VII females suggested spawning had occurred (Fig. 31c) although only in a small proportion of the population as the majority of stage III/V females had small immature eggs with only a limited number of individuals having eggs approaching a suitable size for spawning (Fig. 32b). The relatively large number of stage I females (Fig. 31c) was doubtless responsible for a sex ratio skewed in the favour of males (males: females 1:0.7). As these mature the sex ratio will probably be skewed in favour of females, as at other locations. Spawning at this station was considered to be completed. The low percentage of adult females with respect to males and stage I females could have resulted from post-spawning mortality. The lack of small juveniles suggested that the most recent hatch had not descended from the epipelagic depths where the early life history is spent.

3.2.3.4 Latitudinal Comparisons

C. pseudopallida appears to be a winter/spring spawner in the eastern North Atlantic. The spring samples were taken at the end of the spawning period. The autumn sample illustrated a population recovering from spawning and undergoing recruitment of the next generation.

Latitudinal comparisons were difficult because of the disjunct distribution. The mean size of females at 10°N was lower than at other latitudes, probably because of the lack of large individuals.

A comparison of the length frequencies suggested that three size classes of varying importance were present at different times of the year. Juveniles predominated at sizes of 20-22mm SL at both 30°N (Fig. 30) and 20°N (Fig. 33). The second class was made up of males and stage I and II females at approximately 26-28mm SL at all locations (Fig. 30, 33 and 34). The largest size class was most evident at 30°N at standard lengths of 36-38mm (Fig. 30) and was severely reduced in the autumn (Fig. 33). The mean size of mature females in the spring was 35.0 ± 3.2 mm SL and 37.1 ± 3.7 mm SL and in the autumn mean size was 30.5 ± 4.7 mm SL. The smaller size in the autumn resulted from post-spawning mortality of the larger females after the spring as well as an increase in the number of smaller mature females due to recruitment over the summer months.

Assuming a winter/spring spawning the first peak of juveniles at 16-24mm SL must represent the previous year's spawning and are therefore one year old. Males mature in their second year at sizes of 24-28mm SL, spawn and then die. Females reach stage I in their second year at sizes similar to those of males although some may begin to mature late in the year, possibly as a result of the extended spawning period. The adult females probably spawn twice in their life span at sizes of 30-34mm SL and 34-42mm SL.

The sex ratio varied with both season and latitude (Table 9). The

highest sex ratio found at 30°N in the spring is considered to represent the spawning sex ratio. At that time spawning had been completed but post spawning mortality had not yet occurred, leaving the population at approximately the spawning sex ratio. The 10°N sample was more advanced. There, post spawning mortality had taken place leaving few large females resulting in a lower proportion of mature females. In the autumn recruitment to the adult stages had begun thereby boosting the proportion of adults and increasing the sex ratio; presumably this reaches a maximum when recruitment is completed.

Fecundities ranged from 371 to 1850 (34-45mm SL, Fig. 35). A regression of fecundity on standard length was significant for only one station at 20°N in the autumn ($\log F = 4.08 \log SL - 3.57$, $F = 7.59$, $p = 0.02$, $n = 12$, $r = 0.43$). There did not appear to be any consistent pattern suggesting differences in fecundity between latitudes. At 10°N there was little increase in fecundity with standard length. The highest correlation coefficient was found when a regression was calculated on data pooled over all stations ($\log F = 3.51 \log SL - 2.64$, $F = 55.18$, $p = 0.0001$, $n = 38$, $r^2 = 0.61$).

3.2.4 Cyclothone pallida

Cyclothone pallida was found at all latitudes in at least small numbers but the centre of the distribution was at lower latitudes (Table 3). Although not particularly abundant with respect to many of the other species (Fig. 3) its large size meant a large contribution to the biomass, particularly at 20°N in the autumn (Fig. 4). Detailed analysis was only possible at 10°N in the spring and 20°N in the autumn because the number of individuals was low; though in addition some description was possible at 30 and 20°N in the spring.

3.2.4.1 30°N.

The population of Cyclothone pallida at 30°N in the spring had a number of modes at different standard lengths each mode characterized

Figure 30. Length-frequency distribution by sex and stage of
C. pseudopallida at 30°N in the spring (n=105).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII

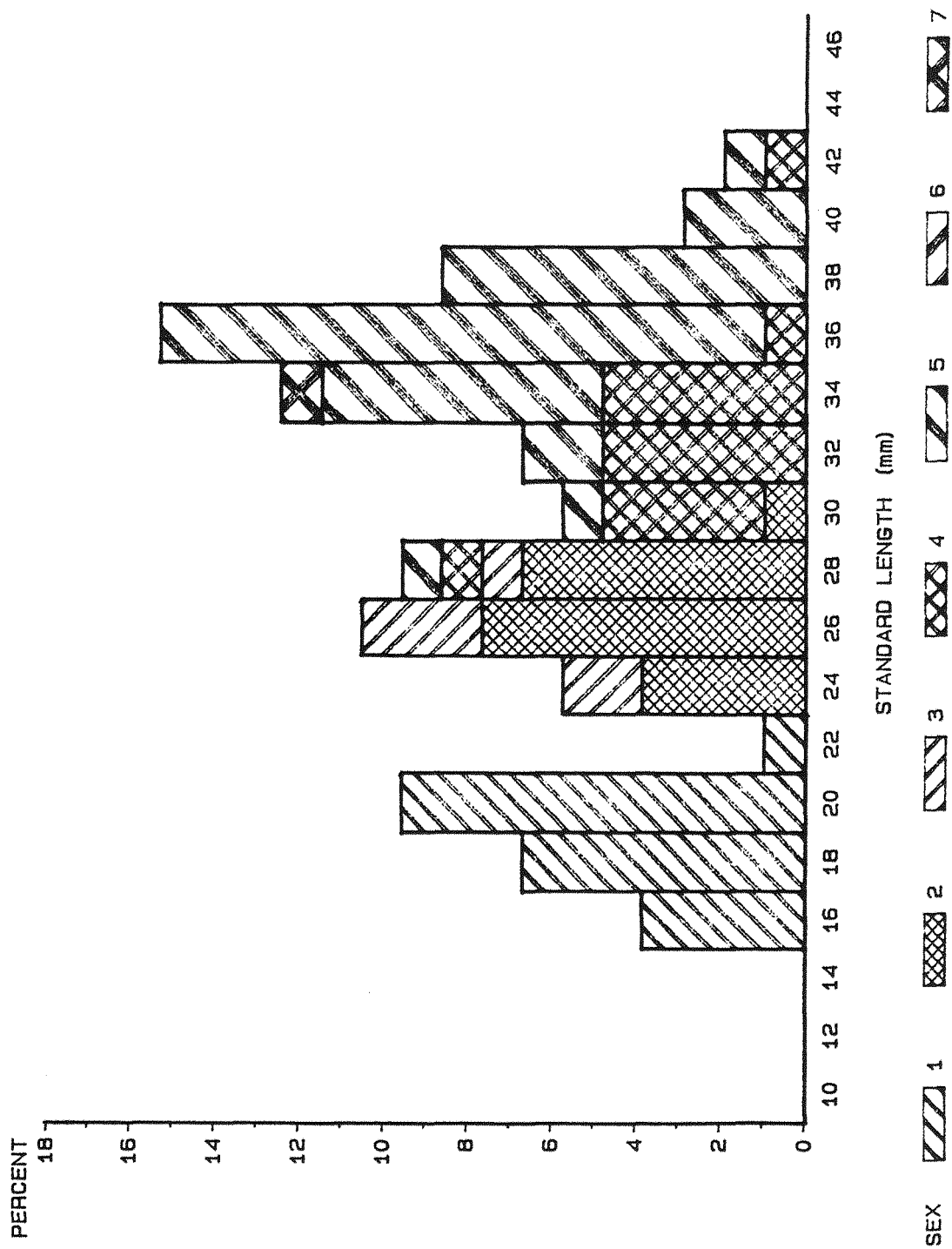
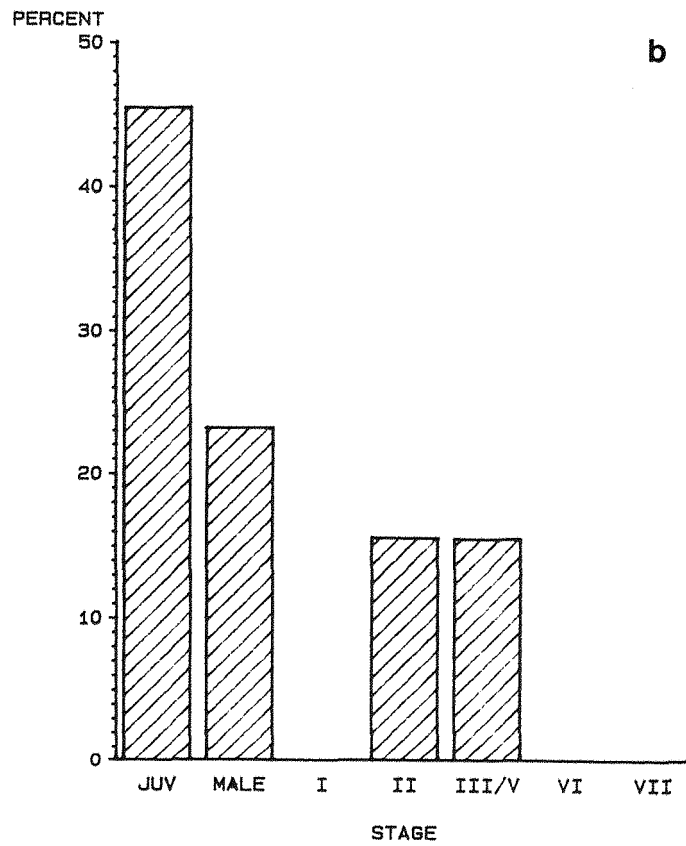
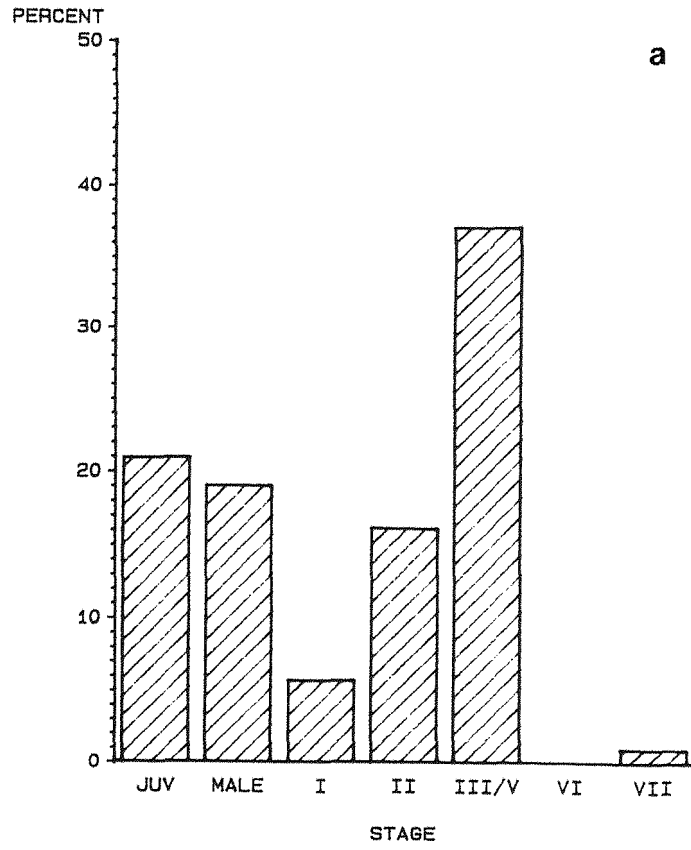


Figure 31. Percent abundance of each sex/stage of C. pseudopallida at a) 30°N in the spring (n=105) b) 20°N in the autumn (n=1649) and c) 10°N in the spring (n=1790).



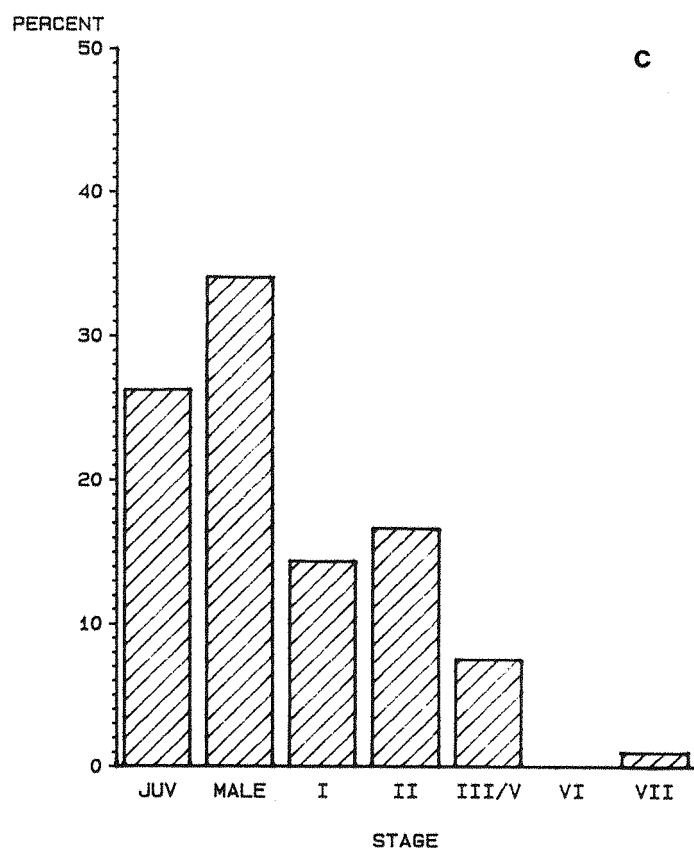


Figure 32. Size-frequency distribution of the maximum egg diameter of female C. pseudopallida at
a) 20°N in the autumn (n=50) and b) 10°N in the spring (n=57).

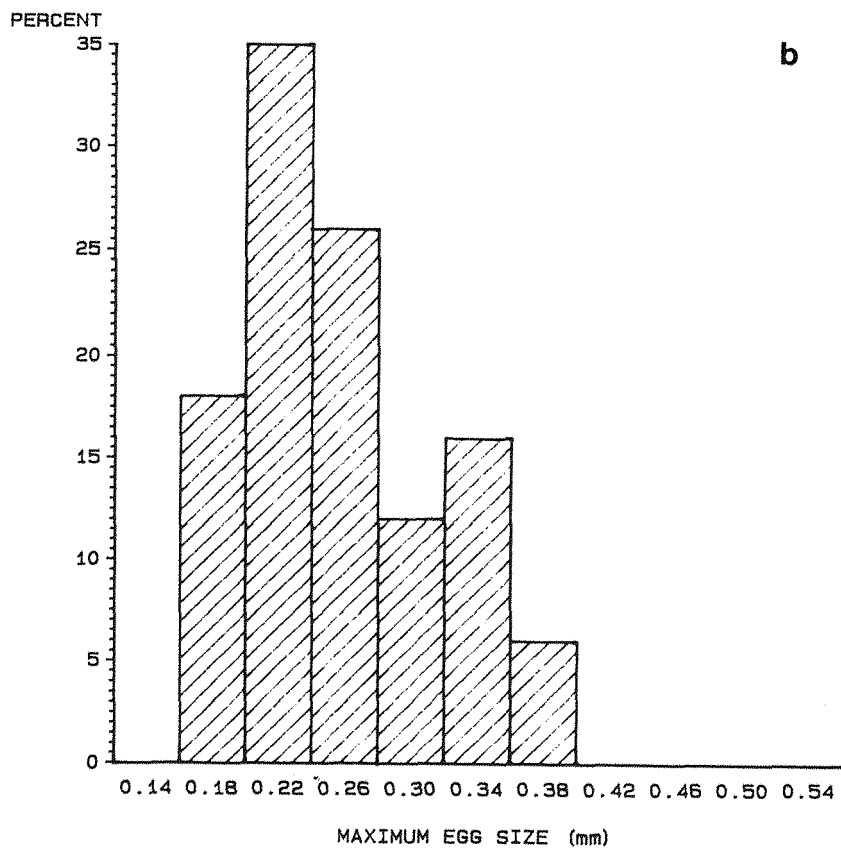
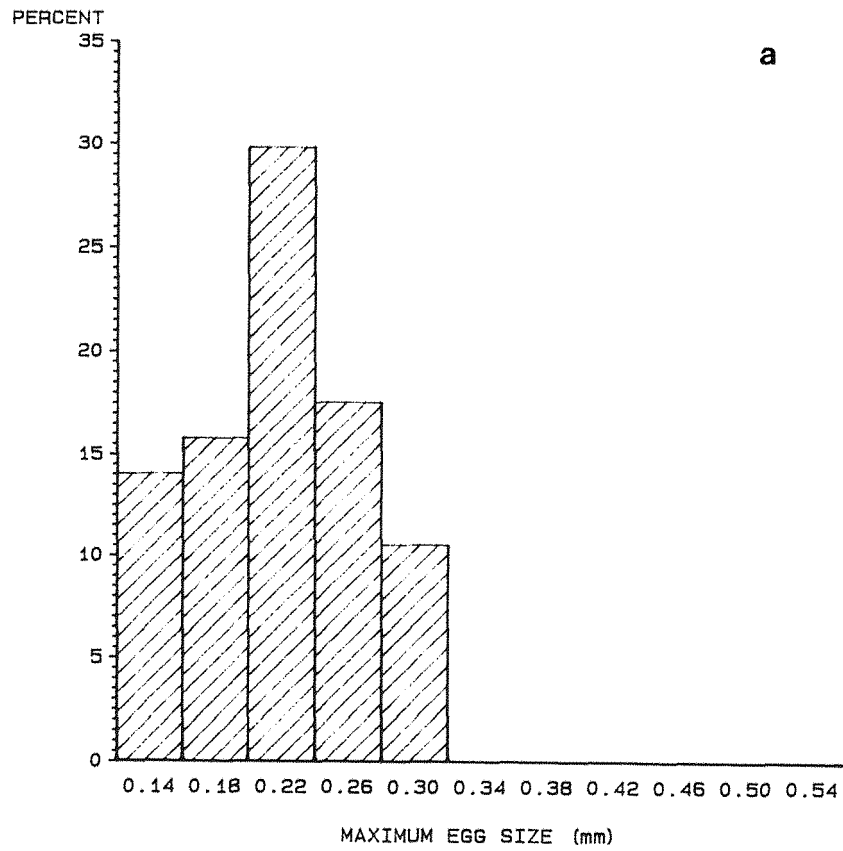


Figure 33. Length-frequency distribution by sex and stage of C. pseudopallida at 20°N in the autumn (n=1649).

1= Juveniles

2= Males

3= I

4= II

5= III/V

6= VI

7= VII

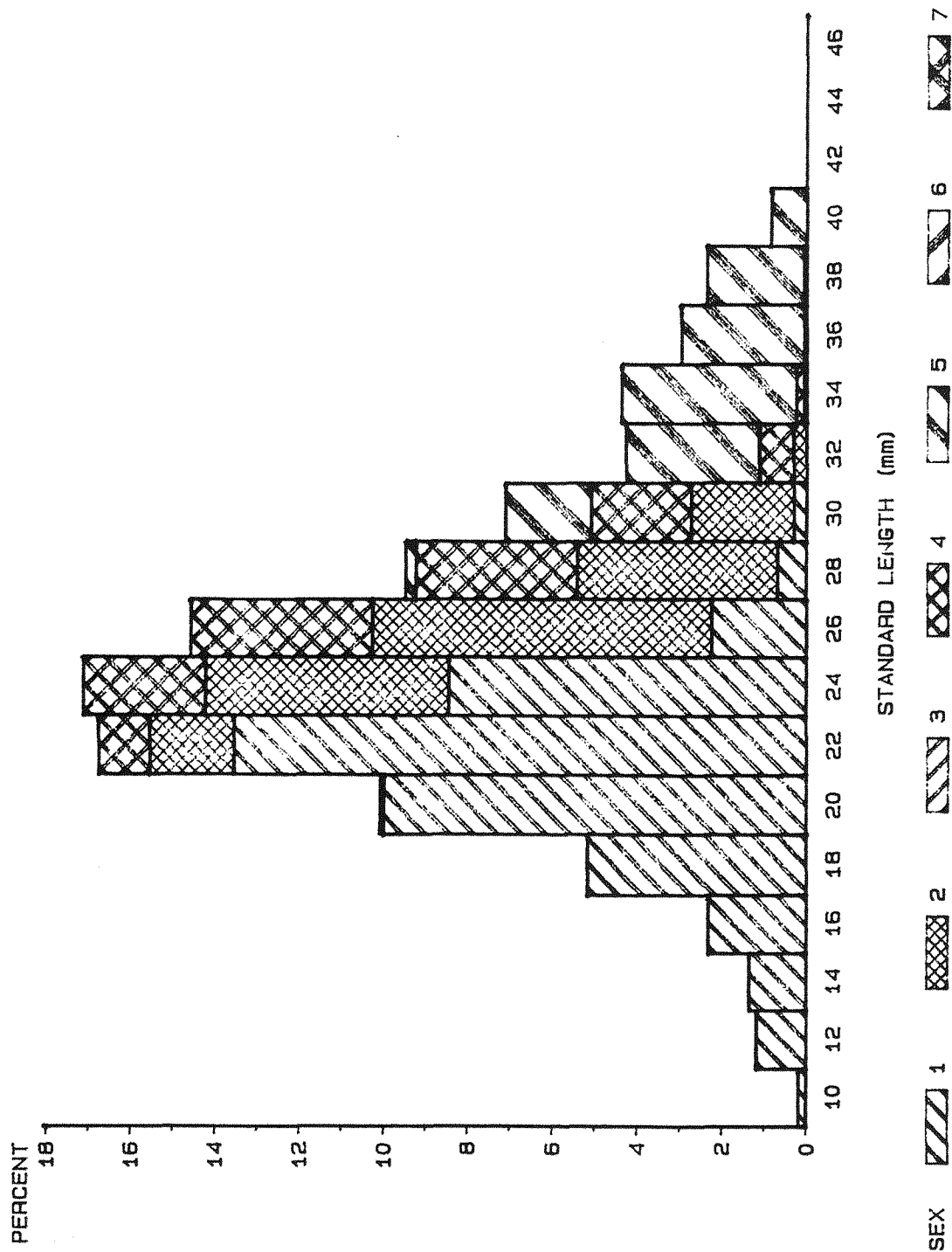


Figure 34. Length-frequency distribution by sex and stage of C. pseudopallida at 10°N in the spring (n=1790).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII

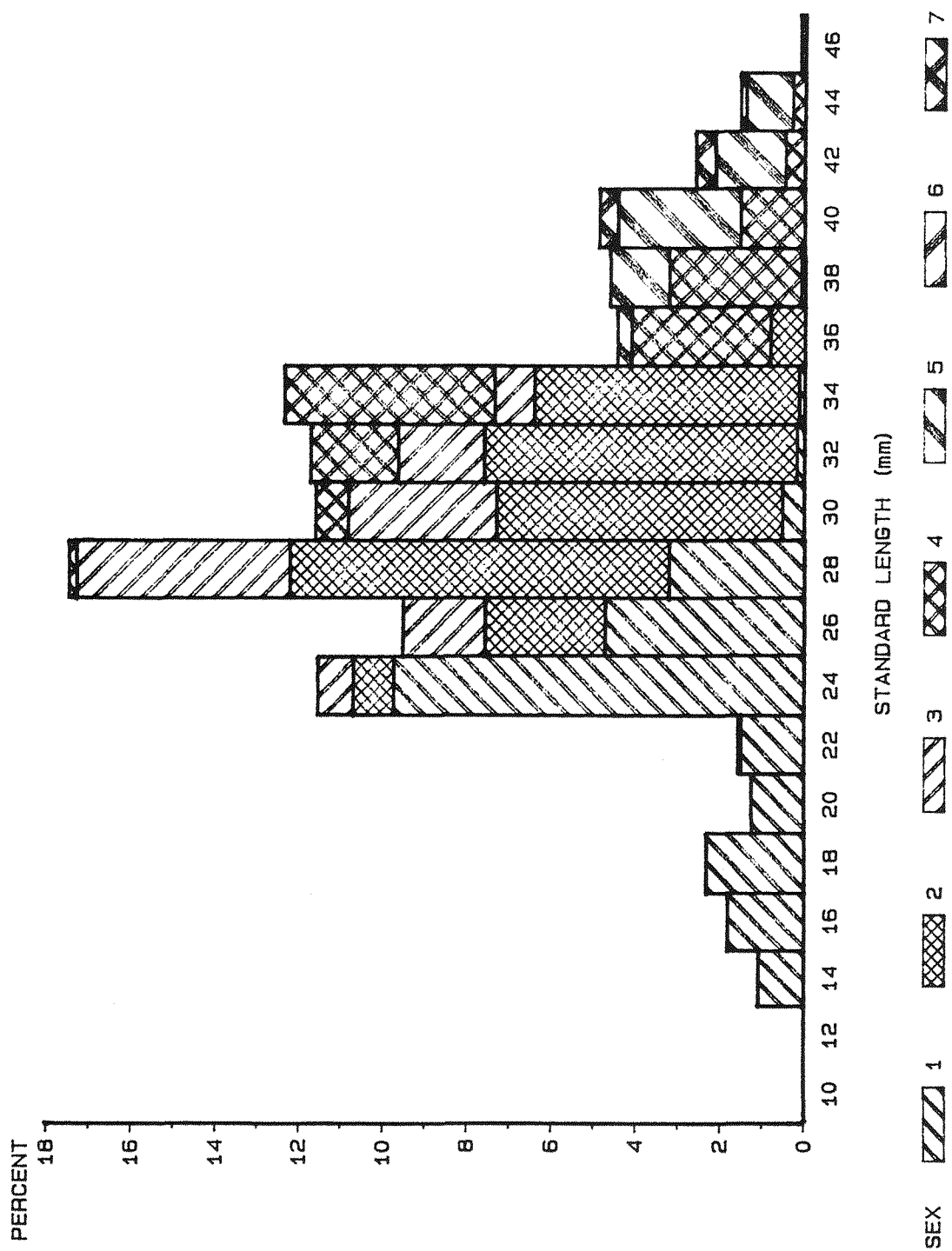


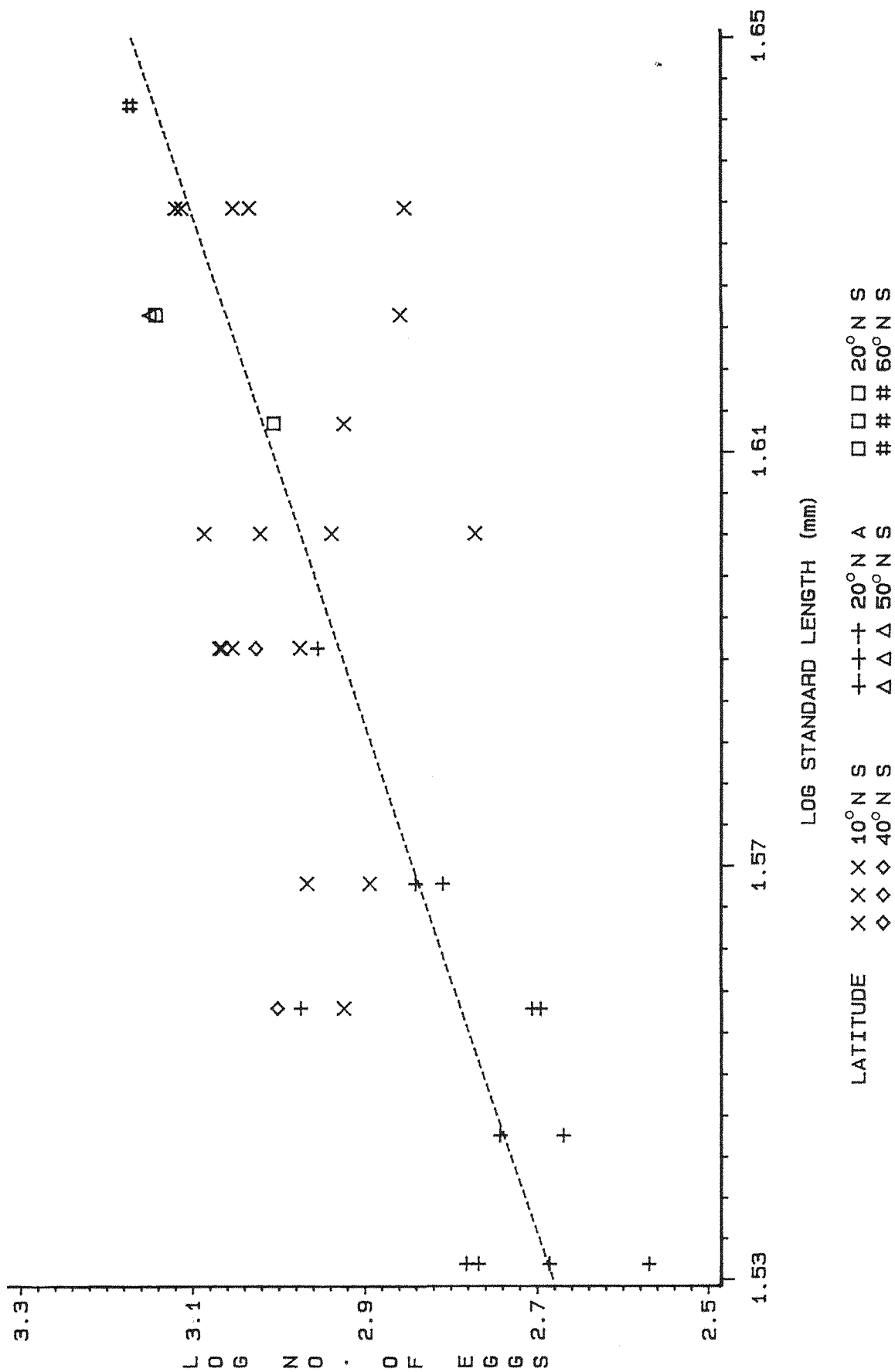
Table 9. Sex ratio, expressed as the number of females for each male, and size at maturity of females of Cyclothone pseudopallida.

Lat. °N	Sex Ratio M:F=1:X		Maturity (mm SL)	
	S	A	S	A
30	2.8		28	
20		1.3		22
10	0.7		32	

S=spring, A=autumn, Lat.=latitude

Figure 35. Log fecundity vs. log standard length for
C. pseudopallida. Regression lines are
shown for stations where the regression was
significant.





by various stages of maturation (Fig. 36). Juveniles were present in two groups with modes of 20mm SL and 30mm SL, males at 28mm SL and the largest mode at 36mm SL, stage I females at 30mm SL and 42mm SL, stage II females at 44-46mm SL and stage III/V females at 52mm SL with small peaks at 60 and 64mm SL (Fig. 36). All females were mature by 44mm SL. Males were the predominant sex/stage although the stages were comprised of relatively equal proportions (Fig. 37). The majority of females were stage III/V (Fig. 37) but the egg sizes of this group were all very small (<0.2mm) indicating spawning was not likely to occur for some time. The sex ratio between males and mature females was even (1:1).

3.2.4.2 20°N.

Fewer modes were evident in the population from 20°N in the spring (Fig. 38a). Stage III/V females predominated (Fig. 39a) with a mode at 52mm SL (Fig. 38a). The maximum egg size suggests that some individuals were approaching spawning as most stage III/V females had a largest egg of 0.3mm (Fig. 40a). The size at maturity of females at this location was 42mm SL. The modal size of males was 36mm SL (Fig. 38a) and they were outnumbered by mature females by greater than 3 to 1 (Table 10). Juveniles were present in two groups at 14-18mm SL and 30-32mm SL although in low numbers at both sizes (Fig. 38a). Immature females were most abundant at 38mm SL (Fig. 38a).

Juveniles predominated in the population in the autumn (Fig. 39b). They had a bimodal distribution with peaks at 18 and 24mm SL (Fig. 38b). Males made up a small proportion of the population and most were present at a standard length of 32mm (Fig. 38b). Females matured at approximately 32-34mm SL and were all stage III/V by 40mm SL and peaked in abundance at 46mm SL (Fig. 38b). Females at this stage had small eggs in the ovaries, over 90% of them less than 0.22mm (Fig. 40b). The sex ratio was 2.4 mature females for every male.

3.2.4.3 10°N.

Juveniles predominated in the population at 10°N in the spring (Fig. 42a). Two peaks in juvenile abundance were evident at 14-18mm SL and 28-30mm SL (Fig. 41). Females were present in three groups stage I, stage II and stages III/V-VII/II. Males were present at a modal size of 34mm SL at numbers less than half as abundant as mature females (male:female 1:2.2). Adult females matured at approximately 44mm SL although mature females could be found as small as 38mm SL (Fig. 41). Females were most abundant at a standard lengths around 50mm (Fig. 41). Most of the stage III/V females had relatively small eggs (Fig. 42b) suggesting no spawning was occurring. The presence of spent/recovering females (stage VII/II) suggest that spawning had occurred in the recent past (Fig. 42a).

3.2.4.4 Latitudinal Comparisons

Comparing samples from 30°N and 20°N in the spring an increase in the proportion of the population at stage III/V suggests that the females at 20°N were closer to spawning (Fig. 36 and 38a). The egg sizes in the population further support this as at 30°N eggs were generally less than 0.26mm although the sample size was small. Females at 20°N in the spring had maximum egg sizes larger than that with a mode at 0.3mm (Fig. 40a). Moving further south to 10°N spawning appeared to be close to completion, some stage VII/II females were present and except for a small percentage most of the stage III/V females were not close to spawning as indicated by the smaller egg sizes (Fig. 42b) and the high abundance of juveniles. In fact, the population at 10°N most resembles that at 20°N in the autumn in terms of shape of the length frequency distribution (Figs. 38b and 41), proportion of individuals in the various sex/stage categories (Figs. 39b and 42a), egg sizes of stage III/V females (Figs. 40b and 42b) and in the sex ratios (Table 10).

A spawning period of winter/spring is most consistent with the data obtained. Egg size at 20°N in the spring could suggest either a spring/summer or winter/spring spawning as the small size could be

interpreted as approaching or completed spawning. However, at 10°N in the spring the presence of large numbers of juveniles and the size of eggs is consistent with a view that spawning has recently finished. These juveniles can be traced to a slightly larger standard length in the autumn at 20°N. The large size range of juveniles suggests an extended spawning period.

There does not appear to be any change in size with decreasing latitude. Although the relative heights of the peaks change, the standard lengths where peaks occur was relatively constant (Figs. 36, 38 and 41). There was no change in size at maturity with latitude although indications were that it did decrease seasonally (Table 10). Similarly, there was some seasonal reduction in size at 20°N (Fig. 38a and b). Sex ratio differences were difficult to interpret. The even ratio at 30°N could be due to the small sample size at that location. The sample size at 20°N in the spring was not large either but it does appear that the number of females to males decreased both with latitude to 10°N and to 20°N in the autumn (Table 10).

Juveniles first appeared in the population at standard lengths of 10-12mm. A second peak in juvenile abundance was found at 26-30mm, and probably represents the previous year's spawning. The overlap in size of juveniles, adult males and stage I females indicates that this is the size at which juveniles are recruited to the population. Such an overlap was most obvious at 20°N in the autumn (Fig. 38b).

Males probably only spawn once as they were found to be present in only one mode up to sizes of 32-36mm, only slightly larger than their size at recruitment to the adult population. Males appeared to spawn for the first time in their second year. Females spend one year as juveniles reaching sizes of approximately 30mm SL. Two year old females are mostly stage I and reach sizes of up to 42mm SL. A small proportion could begin to mature in their second year as stage II females were found as small as 42mm SL. Females spawn at sizes of between 42 and 50mm SL although it was difficult to tell how many size classes were represented in the samples in this range. Females spawned at least twice as stage VII/II females were found. Sizes up to 60mm SL could represent up to a 4th or 5th year of life and 2 to 3

spawnings in that period. The sex ratio suggests that females do not live longer than this as longer lived females would be likely to cause a more skewed sex ratio in favour of females.

Females with eggs of a size suitable for counting were not abundant. Only 68 fecundity counts were made from all the stations ranging from 907 to 3733 (41-63mm SL). Overlap among stations and variability within stations were high but it appeared that fecundities were higher at mid-latitudes (Fig. 43). Fecundity increased with standard lengths although the high variability resulted in low correlation coefficients (Table 11). Regressions were calculated for two stations as well as for all counts regardless of locality (Table 11). There was no significant difference between the two stations.

3.2.5 Cyclothone livida

Cyclothone livida was only infrequently captured at latitudes greater than 20°N (Table 3). It was one of the most abundant in terms of both density and biomass at both 20°N and 10°N (Figs. 3 and 4). Seasonally, C. livida was equally abundant during spring and autumn at 20°N (Fig. 3).

3.2.5.1 20°N.

Three main groups were evident from the length frequency distribution of Cyclothone livida at 20°N in the spring (Fig. 44a). The smallest group was made up of juveniles with a peak in abundance at 15mm SL although the mean was slightly higher (17.8 +4.2mm SL). Males were distributed over a wide range from 21 to 30mm SL with the main peak in abundance at 25mm SL. Stage III/V females were the most abundant in the population (Fig. 45a) and were present at a modal size of 33mm SL (Fig. 44a). A size class of mature females was also present

Figure 36. Length-frequency distribution by sex and stage of C. pallida at 30°N in the spring (n=64).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII/II

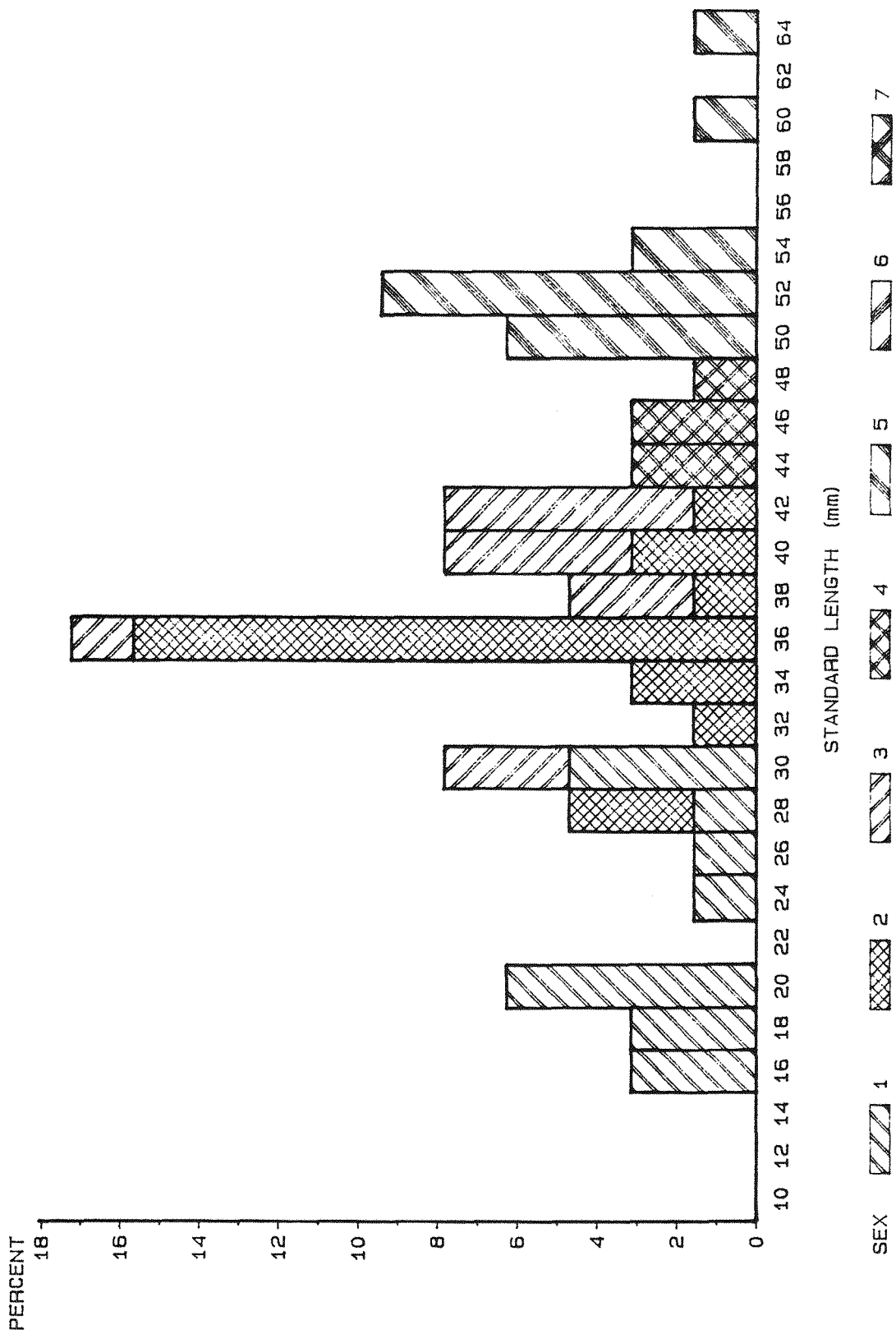


Figure 37. Percent abundance by sex/stage of C. pallida
at 30°N in the spring (n=64).

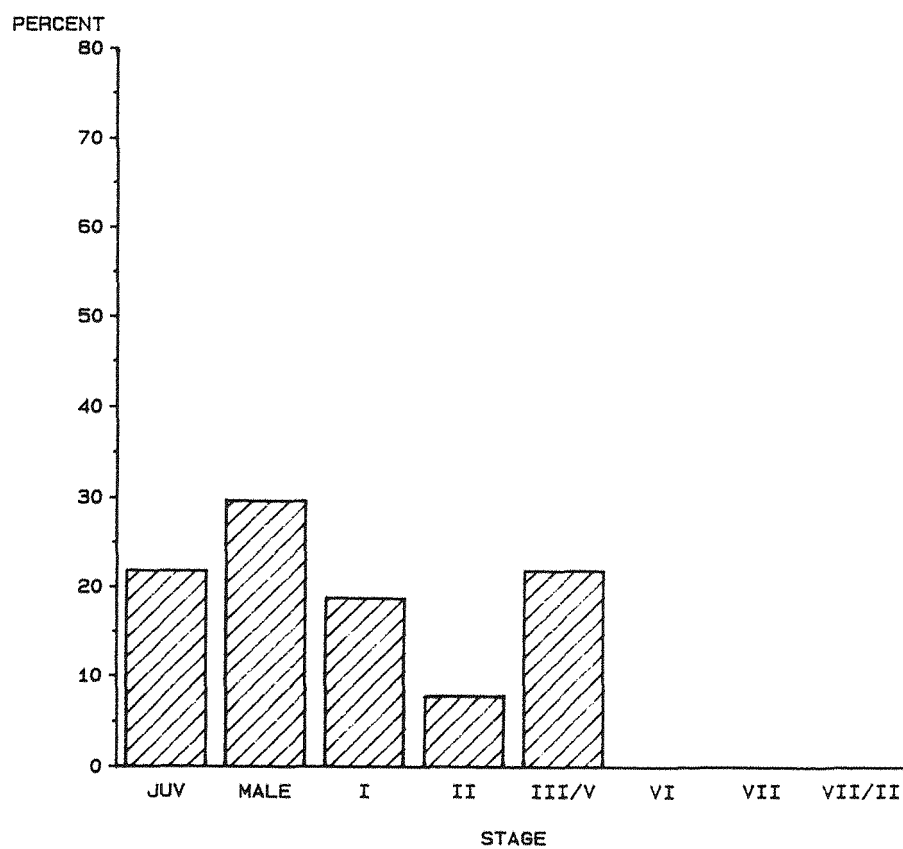
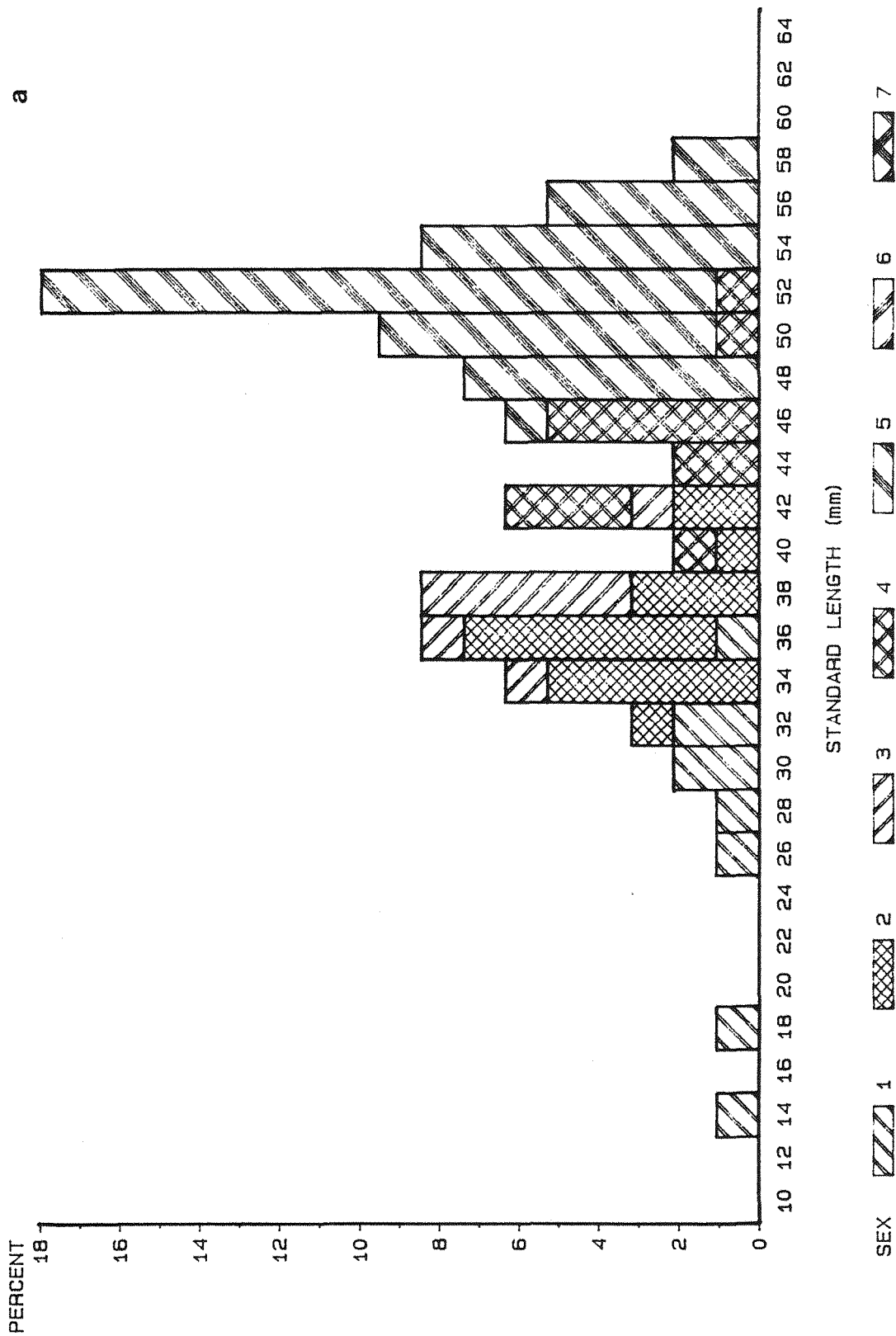


Figure 38. Length-frequency distribution by sex and stage of C. pallida at a) 20° N in the spring (n=95) and b) 20° N in the autumn (n=1031).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII/II



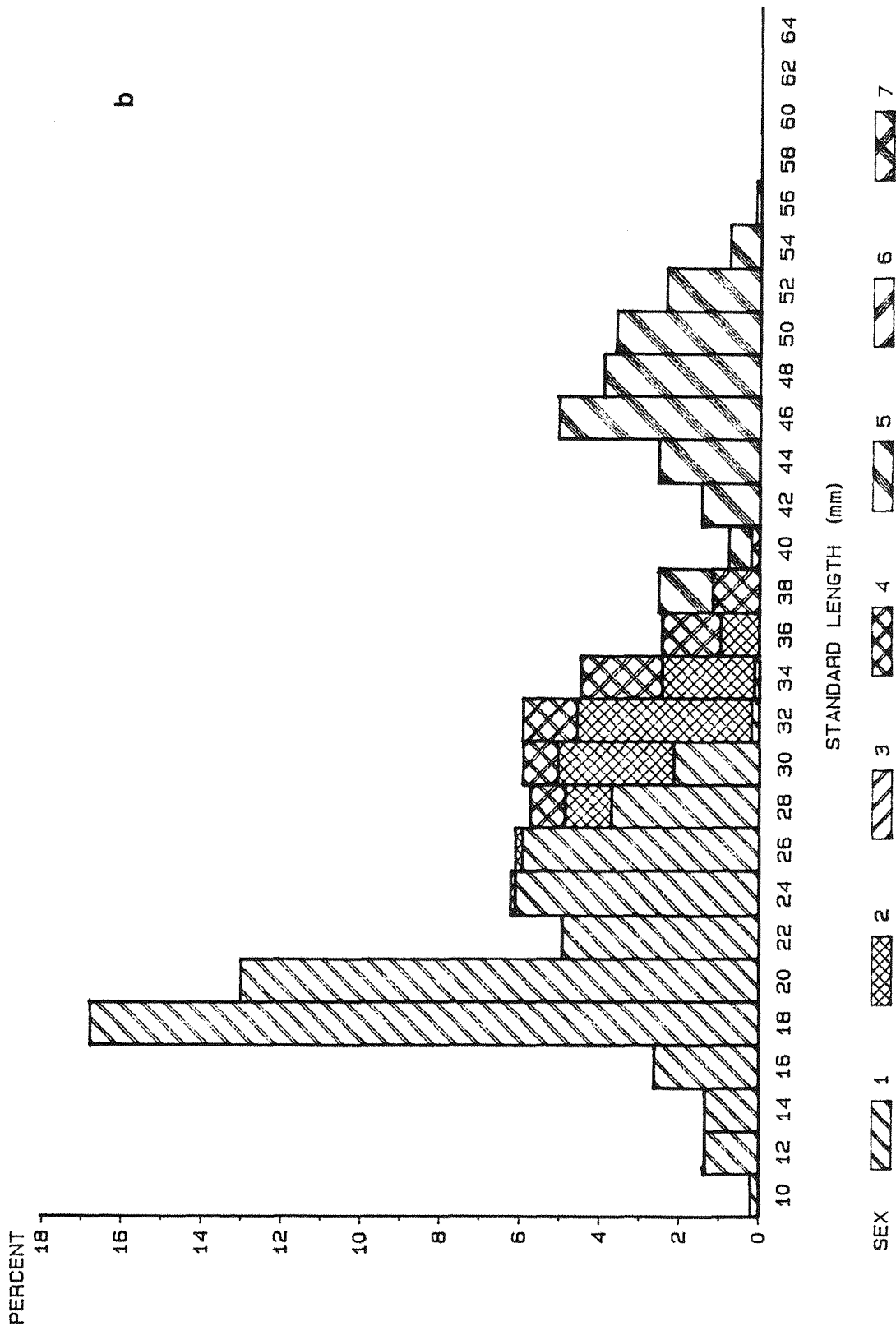


Figure 39. Percent abundance by sex/stage of C. pallida
at a) 20°N in the spring (n=95) and b) 20°N in the
autumn (n=1031).

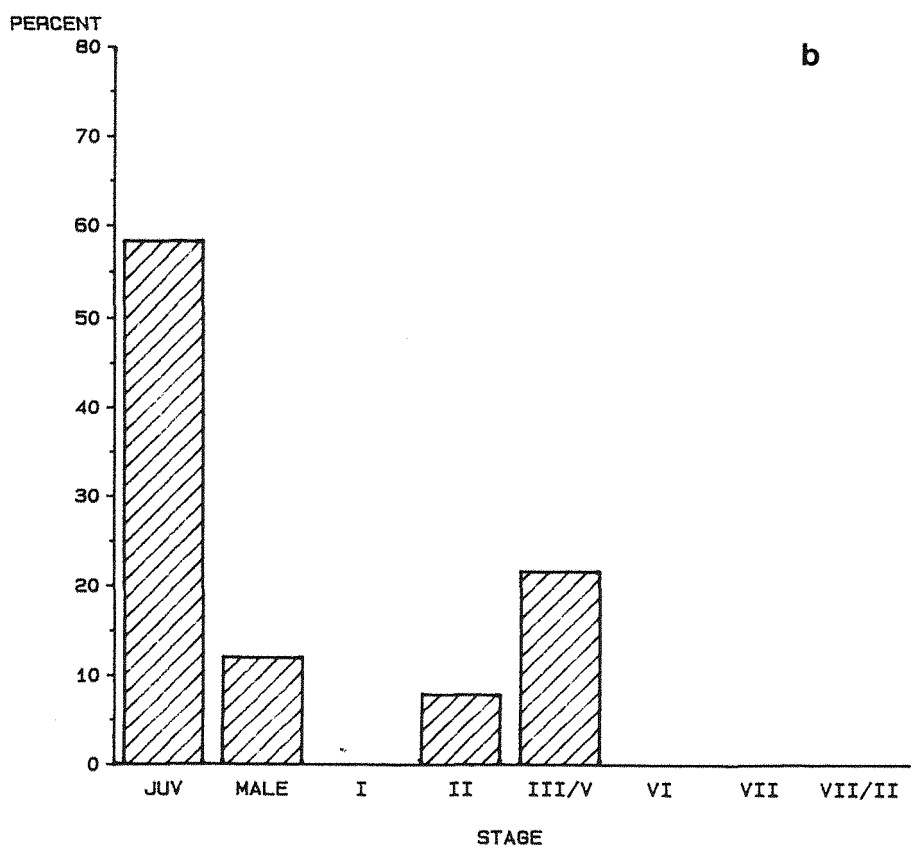
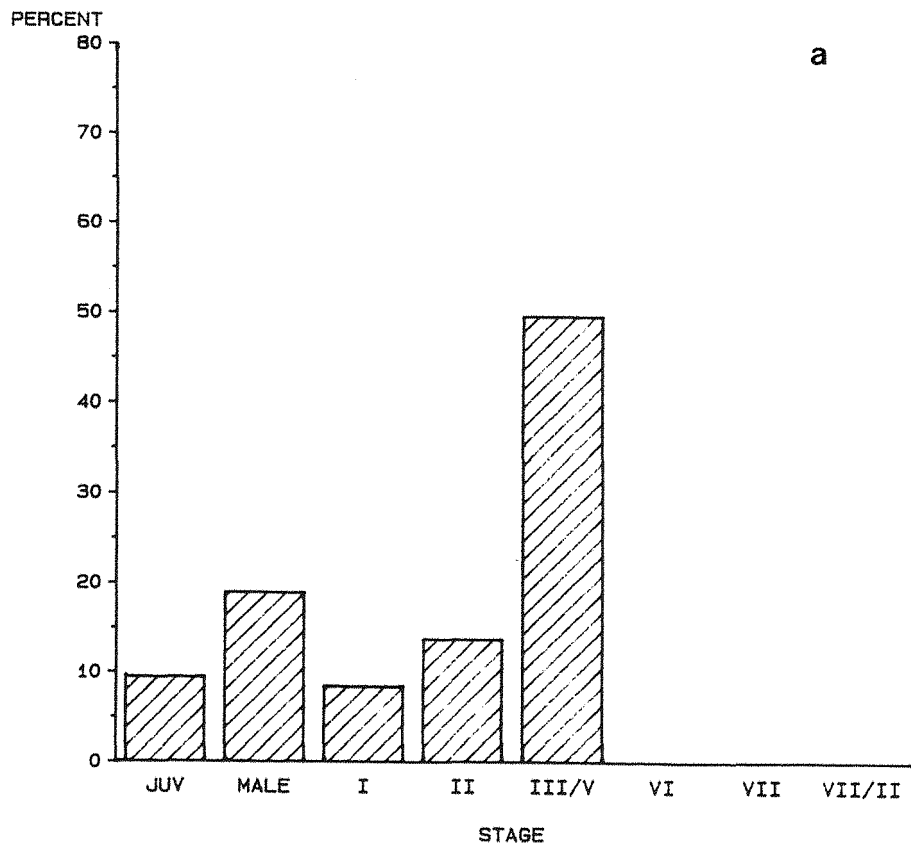


Figure 40. Size-frequency distribution of the maximum egg diameter in female C. pallida at 20°N in
a) the spring (n=43) and b) the autumn (n=43).

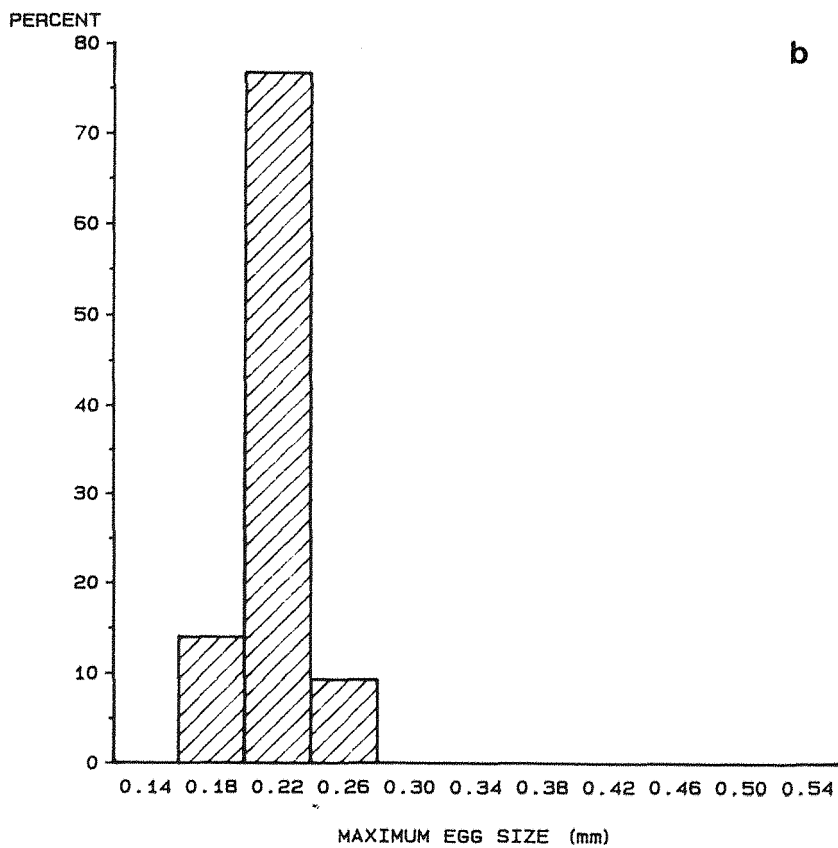
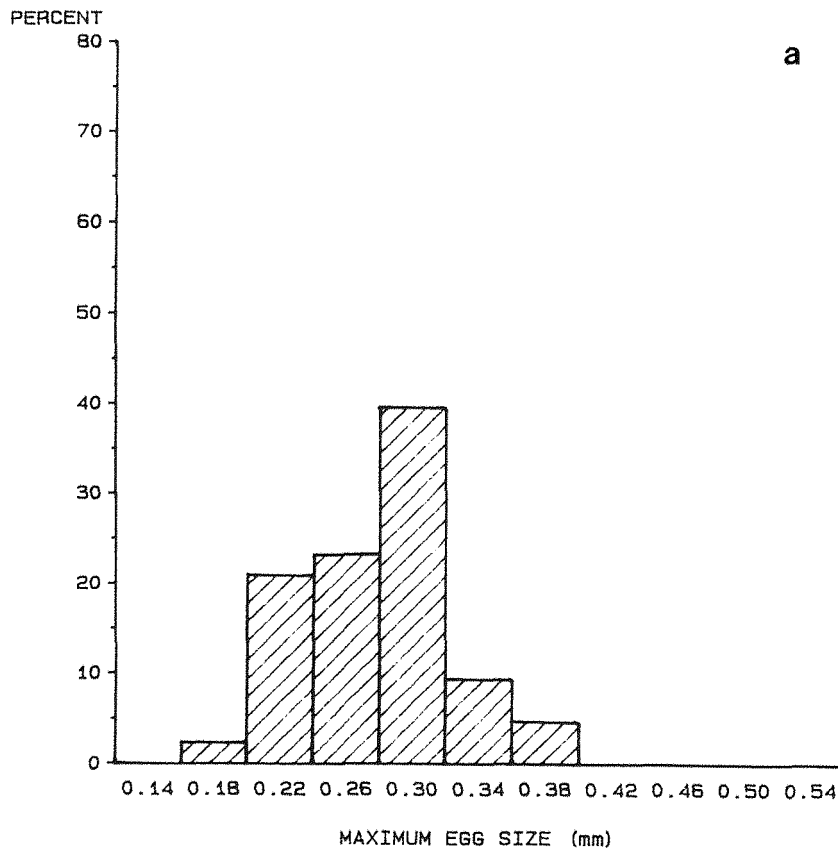


Figure 41. Length-frequency distribution by sex and stage of C. pallida at 10°N in the spring (n=1043).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII/II

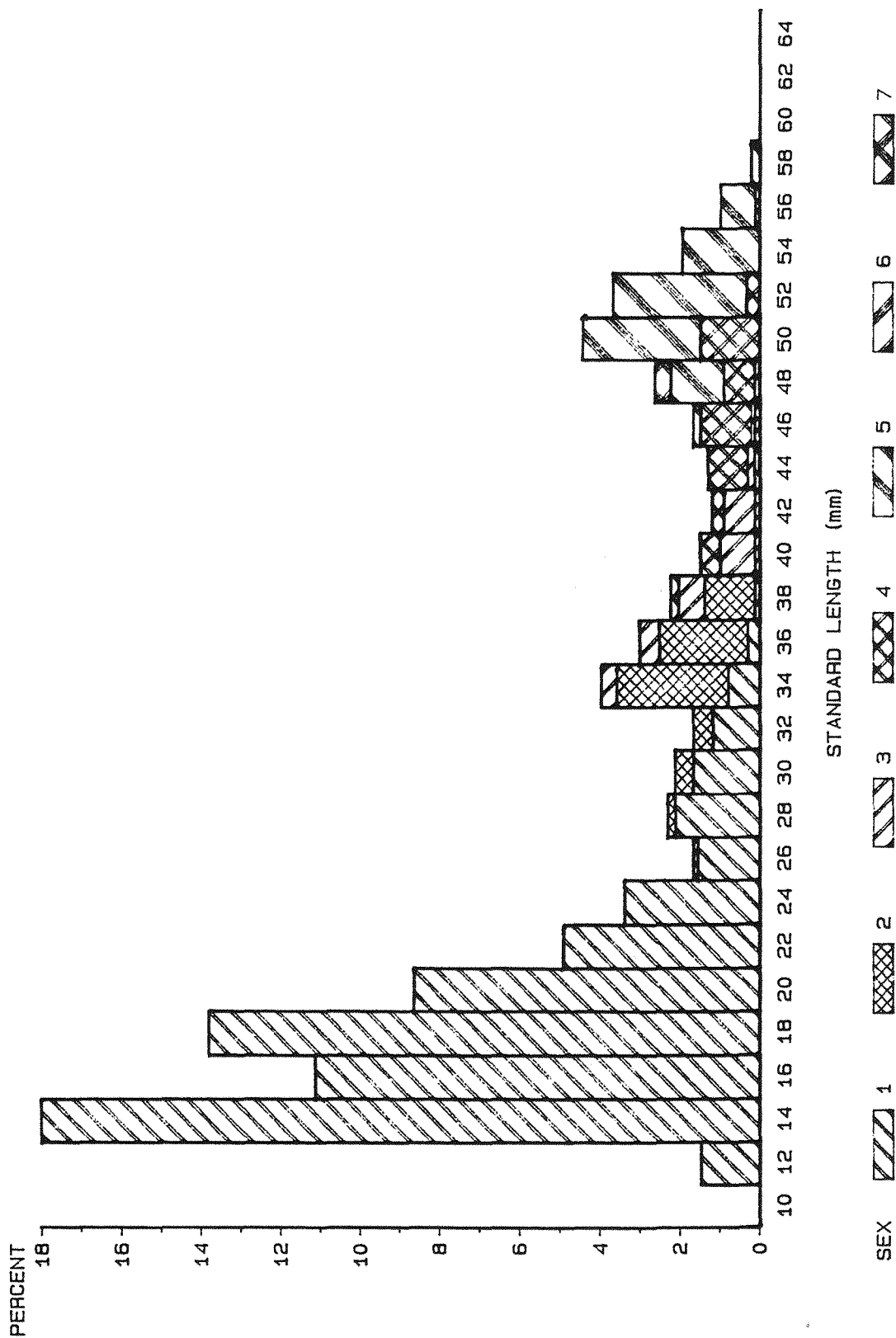


Figure 42. C. pallida at 10°N in the spring.
a) Percent abundance by sex/stage (n=1043) and
b) the size-frequency distribution of the
maximum egg diameter in females (n=35).

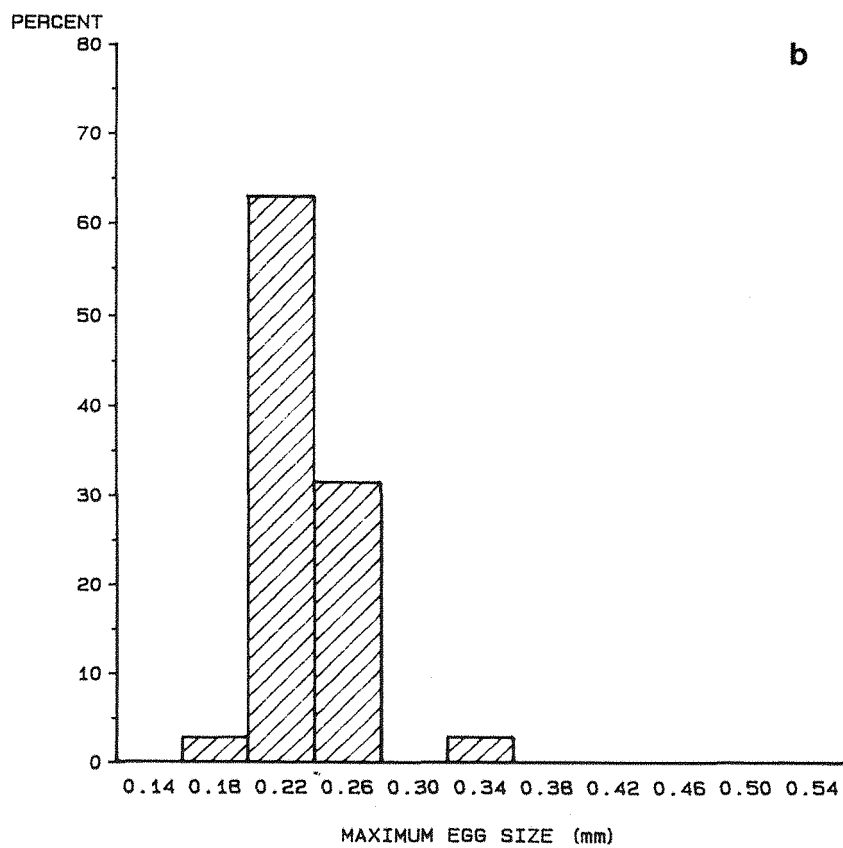
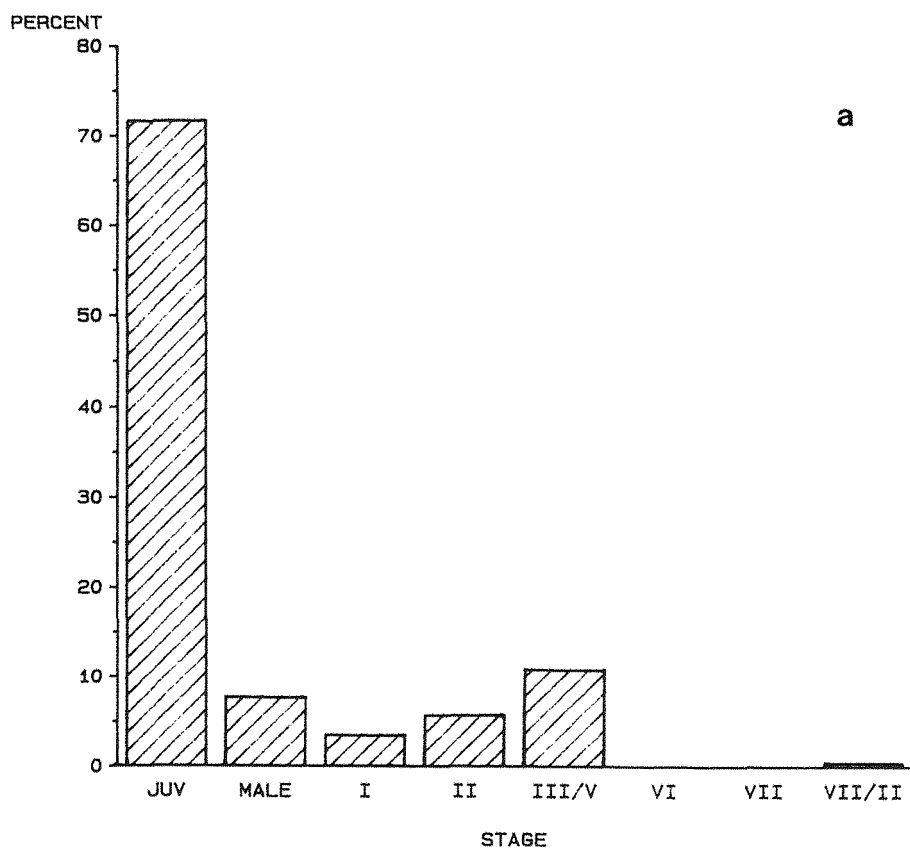


Table 10. Sex ratio, reported as number of females to every male, and size at maturity of Cyclothone pallida.

Lat. °N	Sex ratio M:F=1:X		Size at Maturity (mm SL)	
	S	A	S	A
30	1.0		44	
20	3.3	2.4	42	32
10	2.2		44	

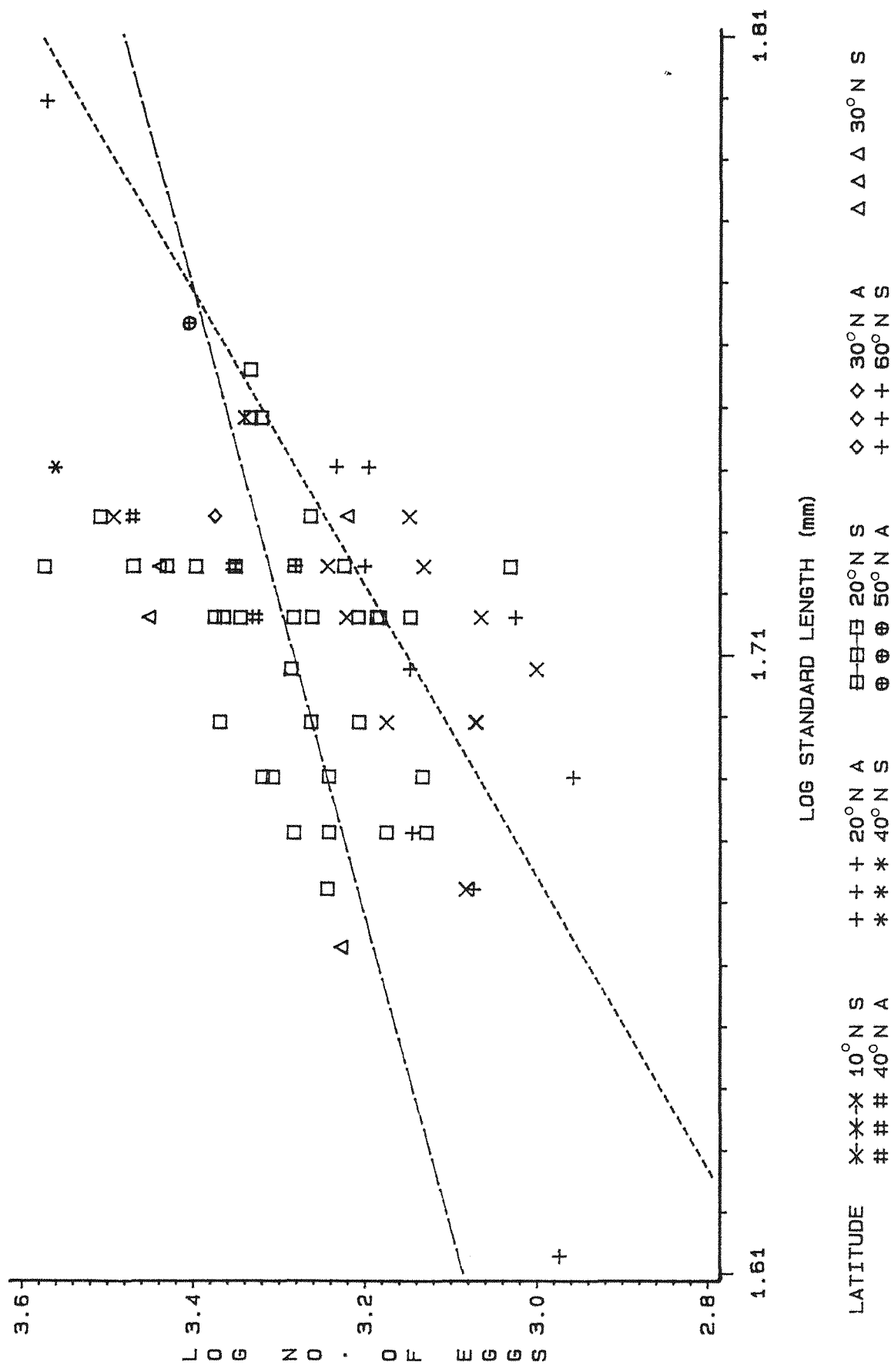
S=spring, A=autumn, Lat.=latitude

Table 11. Regressions of fecundity (F) on standard length (mm SL) of C. pallida.

Location	Equation	p=	r ²	n	F
ALL	$\log F = 2.94 \log SL - 1.78$.0001	0.3	68	28.15
20° N S	$\log F = 1.99 \log SL - 0.12$	0.03	0.14	35	5.17
10° N S	$\log F = 4.26 \log SL - 4.12$	0.03	0.39	12	6.40

S=spring

Figure 43. Log fecundity vs. log standard length of
C. pallida. Regression lines are shown
for stations where the regression was significant.



at small sizes of 27-31mm SL. At this time of the year the size at maturity was found to be 27mm SL and the sex ratio was 1.6 mature females for every male. Approximately 85 percent of the females were stage III/V (Fig. 45a). Spawning was probably in progress. Spent females (stage VII) were present, although only in small numbers (Fig. 45a), and the mature females had relatively large maximum egg sizes, the majority up to 0.42mm (Fig. 46a).

A similar population structure was found in the autumn samples. Males were the most abundant group making up greater than 35% of the population (Fig. 45b) and had a modal size of 25mm SL (Fig. 44b). Stage III/V females had a peak abundance at 33mm SL (Fig. 44b), similar to the spring. Juveniles were present at a low abundance at a much smaller size than the spring collection (mode 12mm SL mean 15.4 ± 3.5 mm SL). Greater than 97 percent of the females were at stage III/V in the maturation process (Fig. 45b) although most females had a small maximum egg size with only a few having egg diameters of 0.42mm (Fig. 46b). Some females were mature by 23mm SL but most females were not mature until 28mm SL or greater.

3.2.5.2 10°N.

The highest number of Cyclothone livida were taken at the 10°N station (Table 3). Three major peaks were evident in the length frequency histogram (Fig. 47). The largest single peak was at 18mm SL and was comprised of juveniles (mean 18.24 ± 2.45 mm SL). A group of juveniles was present at lower standard lengths (14mm SL) but the abundance was low (Fig. 47). Males were the most abundant overall (Fig. 48a) and had a mean size of 24.6 ± 2.1 mm SL and a mode of 24mm SL. There were more males than mature females (males:females 1:0.6). A small number of stage I females were present at standard lengths similar to the males. The third peak was primarily made up of stage III/V females but also contained some stage II, spent and spent/recovering females (stages VII and VII/II). The modal size of this group was 33-34mm SL (Fig. 47). Females were mature by a size of

27mm SL although most mature females were larger than 30mm SL.

Females of all gonadal stages were present including spawning (VI) and spent (VII) although stage III/V was most abundant (Fig. 48a). Eggs of stage III/V females showed a large variability in size (Fig. 48b mean=0.4 $s^2=0.01$). Some of the females had very large eggs greater than 0.6mm suggesting spawning was occurring (Fig. 48b).

3.2.5.3 Latitudinal Comparisons

The major difference in the population structure of C. livida among the three stations sampled was the presence of a large group of juveniles of indeterminant sex at sizes of 17-20mm SL at 10°N (Fig. 47) which were not present at 20°N in either the spring (Fig. 44a) or autumn (Fig. 44b). This difference was also reflected in the percent composition by sex/stage as stage III/V predominated at 20°N at both times of the year (Fig. 45a and b) but males and juveniles predominated in the samples from 10°N in the spring (Fig. 48a). Spent females were most abundant at 10°N.

The largest eggs were found in the spring samples (Fig. 46a and 48b) and there was no significant difference between the maximum egg sizes at 20°N in the spring and 10°N. The mean egg size in the autumn at 20°N (Fig. 46b) was significantly smaller than at both spring stations (20°N spring, $t=8.67$, $df=104$, $p<0.01$ and 10°N spring, $t=11.19$, $df=101$, $p<0.01$).

The data were consistent with a winter/spring spawning period. Spawning was occurring in the spring samples as the egg size of females was relatively high. The population at 10°N in the spring was slightly more advanced towards the end of the spawning period because of the larger numbers of stages VI and VII females. Also, the higher percentage of juveniles could be due to larvae from the earliest spawning beginning to descend to adult depths while the larger juvenile peak at approximately 17-20mm SL represents the next years

recruitment to the adult population. In the autumn the population was approaching the next spawning as most adult females had reached stage III/V but egg sizes were still small compared with the spring values.

If, as stated above, two year classes of juveniles were present at 10°N then males and stage I females were likely to be two years old, based on the modal structure. The smaller maximum size of males relative to females is likely to result from the females living longer than males. Males only live for two years whereas females live at least three years and possibly four. During this time the latter are presumed to spawn twice as peaks were evident at 28mm SL and 34mm SL. Some stage VII/II females were found. The difference in life span contributes to the skewed sex ratio found at all stations.

The number of eggs found in maturing females was unpredictable. Regressions of fecundity on standard length were not significant. At standard lengths below approximately 33mm SL the number of eggs was generally size related varying from 110 to 1010 (29-38mm SL, Fig. 49). At these sizes the greatest number of eggs were found in fish from 20°N in the spring. Above 33mm SL there was no relationship with size or latitude.

3.2.6 Cyclothone acclinidens

Sampling to 10°N only just entered the range where Cyclothone acclinidens was abundant. Only low densities were encountered at 20°N in both the spring and autumn (Fig. 3a and b). These numbers did not represent much of the biomass of Cyclothone present (Fig. 4a and b). At 10°N C. acclinidens was second in density and biomass to C. livida (Fig. 3a and 4a). One C. acclinidens was taken at each of the other latitudes, although not always in both seasons (Table 3).

Figure 44. Length-frequency distribution by sex and stage of C. livida at a) 20°N in the spring (n=611) and b) 20°N in the autumn (n=1123).

1= Juveniles

2= Males

3= I

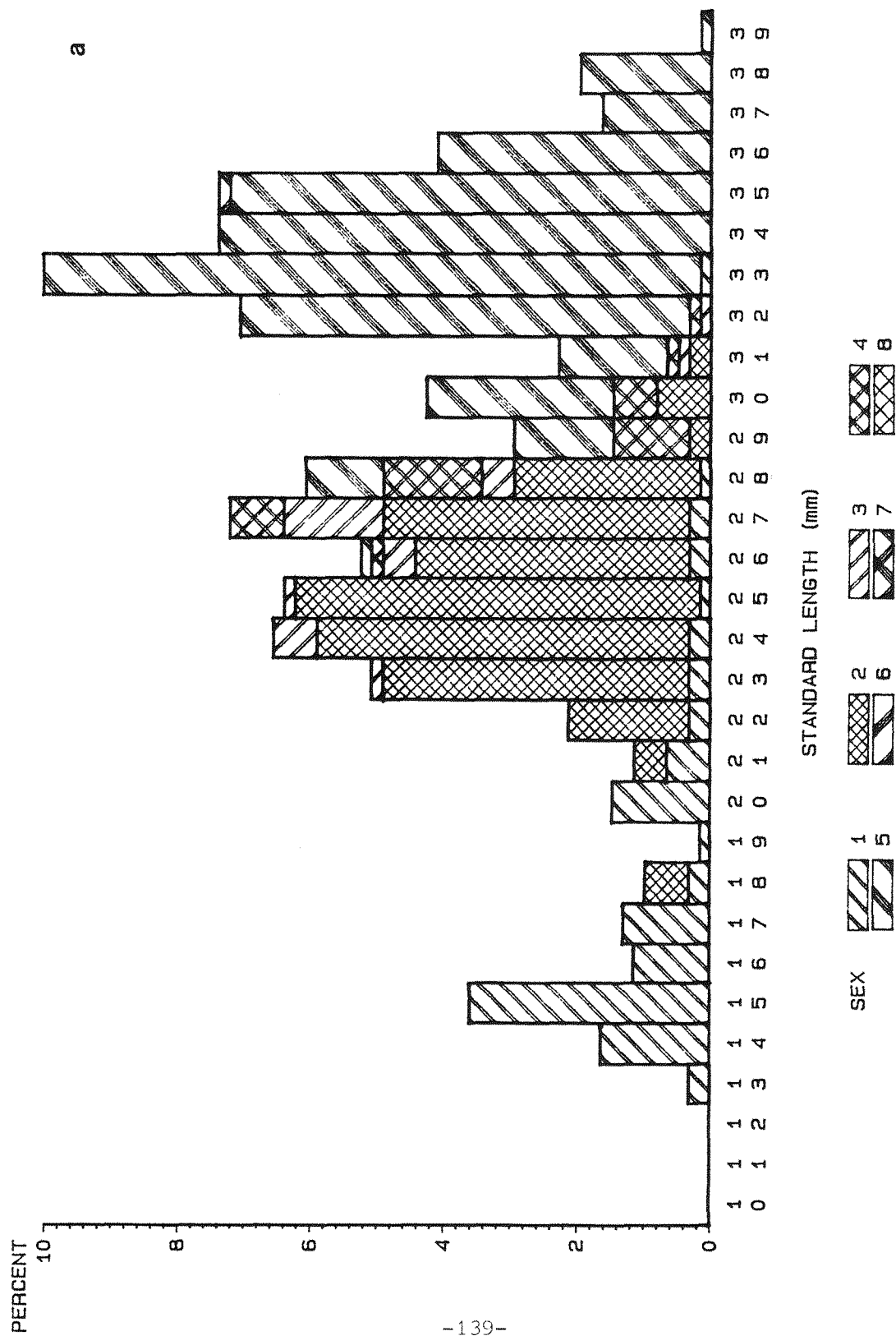
4= II

5= III/V

6= VI

7= VII

8= VII/II



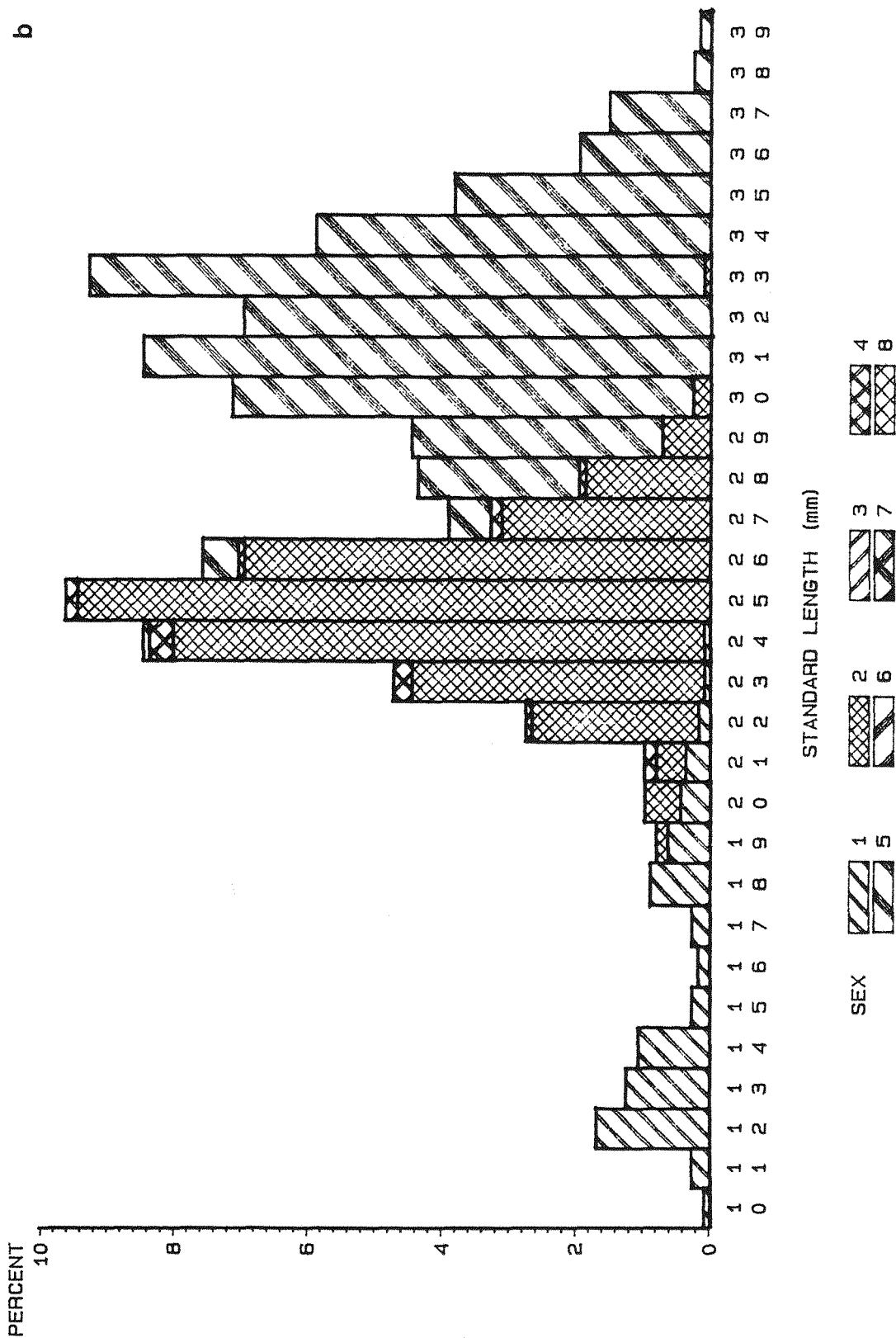


Figure 45. Percent abundance of each sex/stage of C.
livida at a) 20°N in the spring (n=611) and
b) 20°N in the autumn (n=1123).

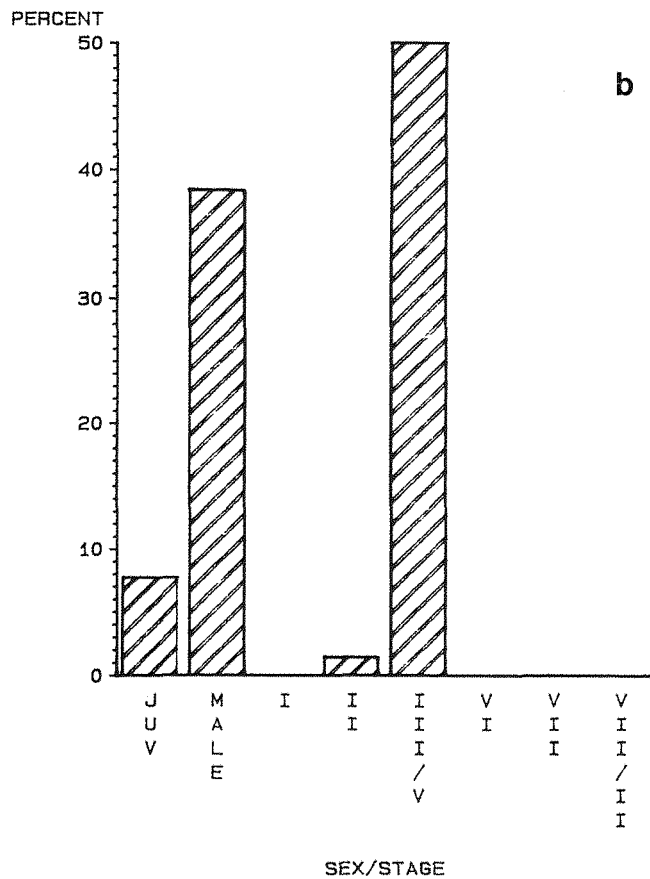
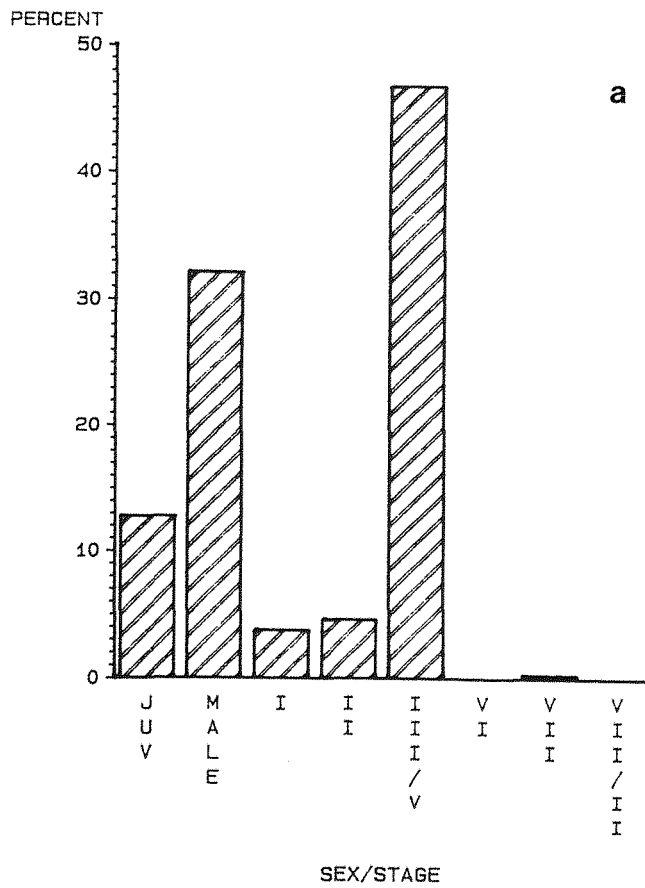


Figure 46. Size-frequency distribution of the maximum egg diameter in female C. livida at 20°N in
a) the spring (n=47) and b) the autumn (n=56).

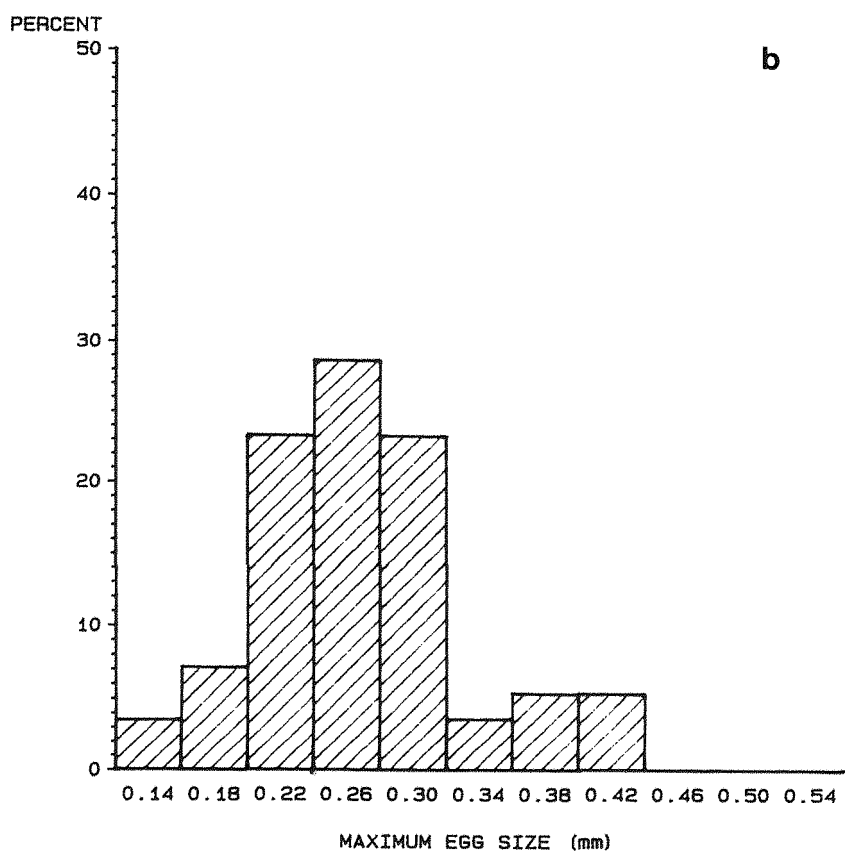
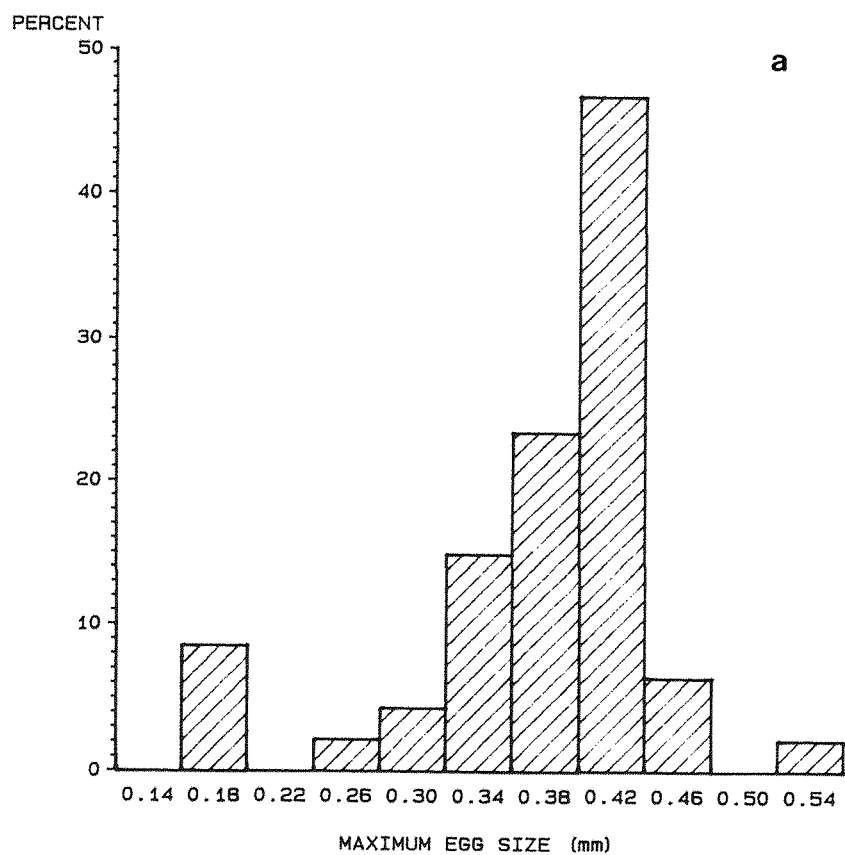


Figure 47. Length-frequency distribution by sex and stage
of C. livida at 10°N in the spring
(n=3531).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII
- 8= VII/II

Figure 48. C. livida at 10°N in the spring.
a) Percent abundance by sex/stage (n=3531) and
b) the size-frequency distribution of the
maximum egg diameter in females (n=50).

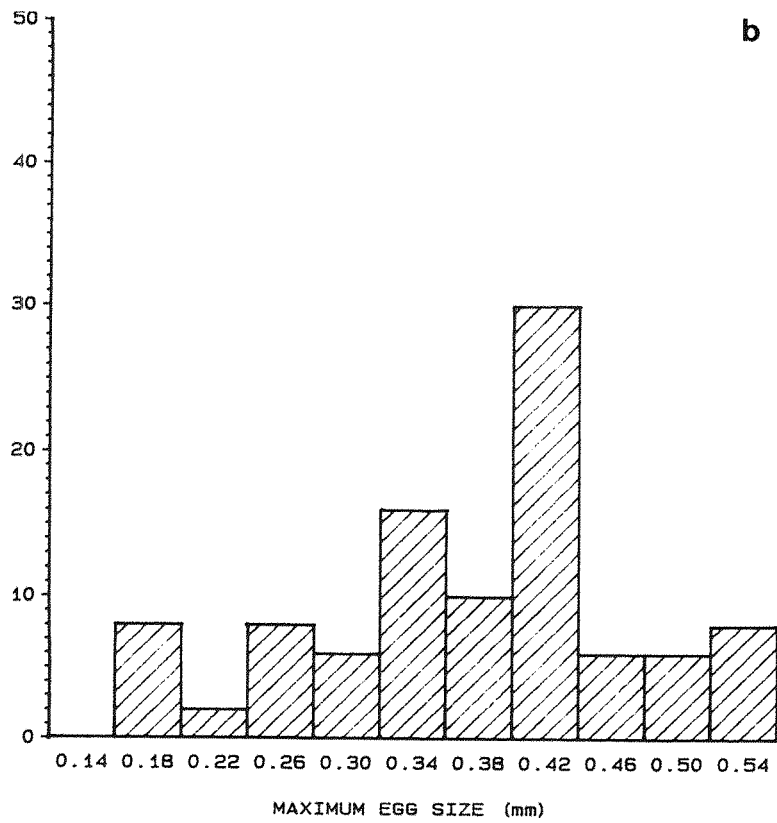
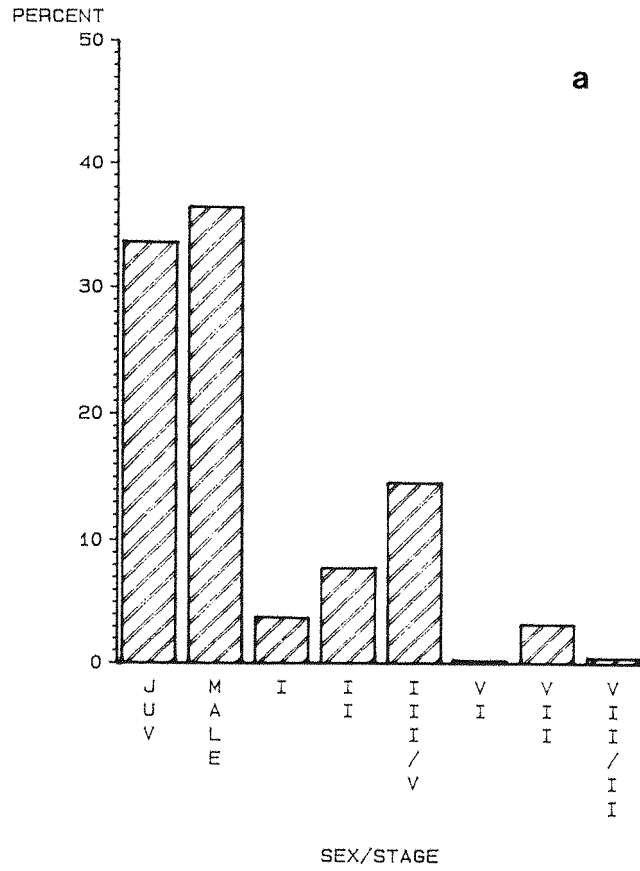
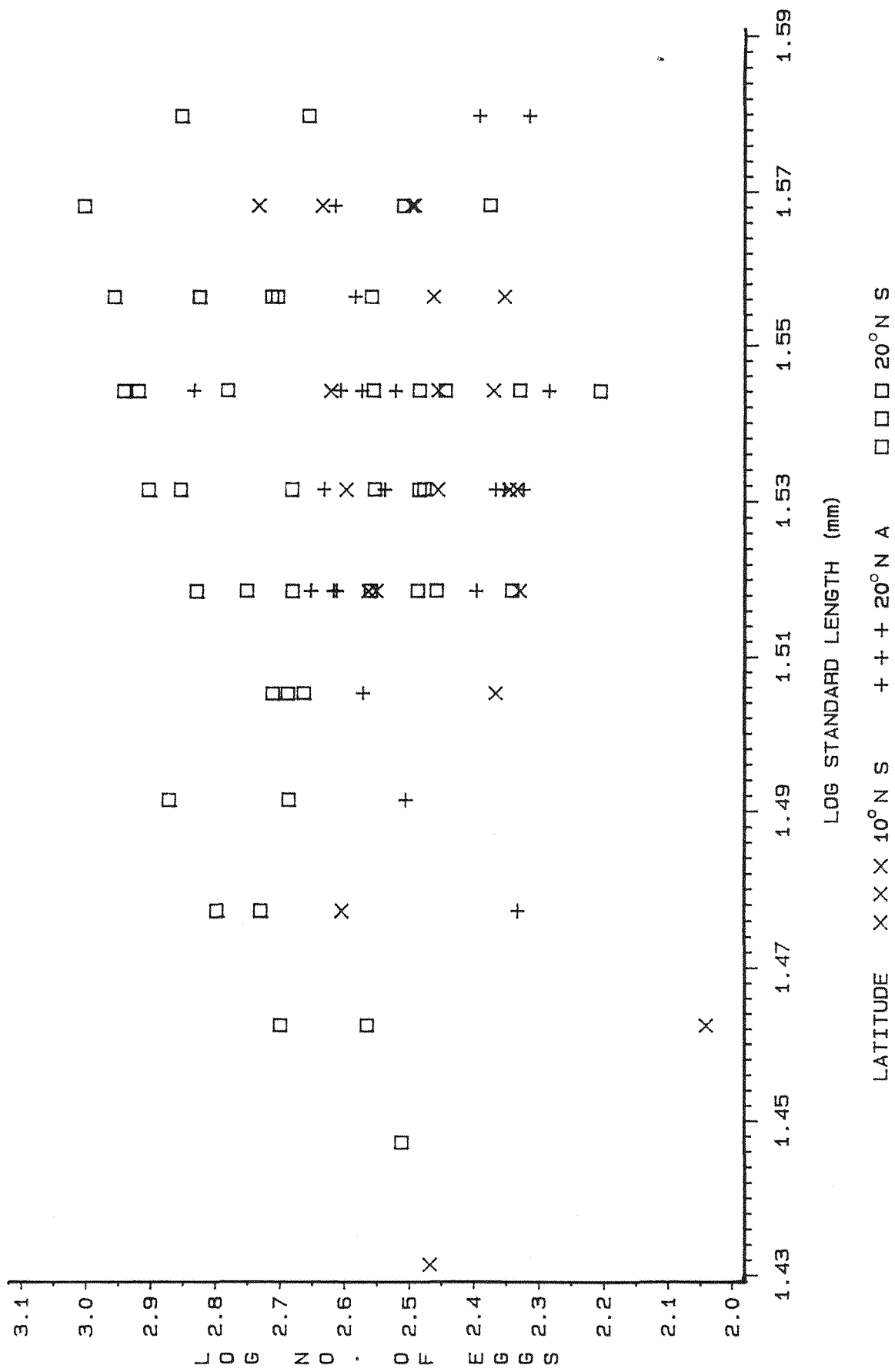


Figure 49. Log fecundity vs. log standard length of
C. livida.



3.2.6.1 20°N.

The number of individuals captured at 20°N in the spring was quite small (n=55). Of this number 50 percent were stage III/V females (Fig. 51a). These tended to be present, along with stage II females, in two peaks of adult female abundance at 35 and 38mm SL (Fig. 50). Mature females were over four times more abundant than males (males:females 1:4.1) although this could be due to the small sample size. Females were mature by approximately 31mm SL. Immature females (stage I) were present in very small numbers at 25 and 30mm SL (Fig. 50). Very few juveniles were present in the collections (Figs. 50 and 51a). The mean of the largest egg in females was 0.27mm (var=0.004) with two peaks at sizes of 0.22mm and 0.3mm (Fig. 51b). This could suggest an extended spawning period. Some females had eggs as large as 0.42mm suggesting a proportion of the population was close to spawning although no spent (stage VII) or spent/recovering (stage VII/II) females were present (Fig. 51a). Few juveniles or small males were captured.

Stage III/V was still the most frequent female stage present in the autumn although juveniles were the most abundant group in the whole population (Fig. 53a). Juveniles were widely distributed in size ranging from 12mm SL up to 28mm SL. They peaked in abundance at 18 to 21mm SL (Fig. 52). Female maturation occurred at a size of approximately 26mm SL although stage II females were found as small as 23mm SL (Fig. 52). Most mature females had relatively small eggs present in the ovaries (Fig. 53b) with a mean size for the population of $0.23\text{mm} \pm 0.003$. A small proportion of the mature females had eggs as large as 0.34mm. A few spent females were found at larger standard lengths (Fig. 52). Males were separable from juveniles at standard lengths of 23-24mm and were most abundant at 25mm SL (Fig. 52). The sex ratio of males to females was 1:1.68.

3.2.6.2 10°N.

At 10°N the abundance of individuals was relatively evenly distributed among the sex/stage categories except for the spawning and spent stages (Fig. 55a). Mature females outnumbered males by approximately 1.8 to 1. Most females were not mature until standard lengths of 32-33mm SL and peak abundance of mature females was found at 34mm SL (Fig. 54). Although spawning (stage VI) and spent (stage VII) females were present (Fig. 55) few females actually had eggs large enough to be considered close to spawning, most eggs being less than 0.3mm (Fig. 55b). The other gonad stages were found at separable size intervals, juveniles were prevalent at 23mm SL, males at 27mm SL and immature females (stage I) were most abundant at 30mm SL (Fig. 54). These three stages merged together at standard lengths of 22-26mm suggesting that this is the size range at which juveniles begin to be recruited to the adult population.

3.2.6.3 Latitudinal Comparisons

A number of factors point to a prolonged spawning period likely to start in late winter and finishing in early autumn for C. acclinidens. Spawning was underway in the spring as a few females had relatively large eggs and some spawning and spent females (stage VI and VII) were found at 10°N (Fig. 54). However, the lack of juveniles, particularly at the smaller standard lengths suggested spawning had not been underway for long in a large proportion of the population. The variability in the egg size of females examined supports the theory of a prolonged spawning period (Fig. 51b, 53b and 55b). The presence of stage III/V females in the autumn with eggs up to 0.34mm further suggests some spawning had yet to occur. The early start to spawning was apparent from the large number of juveniles around 18mm SL in the autumn; these juveniles being likely to have come from eggs spawned in winter or early spring (Fig. 52). Few females had large eggs at any one time; which is consistent with asynchronous spawning.

Latitudinal comparisons were not readily available as C. acclinidens

was not distributed over a wide enough range in suitable numbers.

The prolonged spawning period would make size classes difficult to isolate. However, it appeared that males and stage I females were likely to be one to two years old depending on the length of time spent as juveniles. As juveniles were found at sizes as large as 24mm SL it seems likely that they were one year old making males and stage I females two years old. Males did not appear to live longer as no other size classes were evident and they were not present over a wide size range. Assuming stage I females were two years old, females mature during their third year at sizes of approximately 28-30mm SL. A larger group of females at sizes of around 38mm SL at 20°N in the spring suggests a second year of spawning may occur.

Regressions of log fecundity against log standard length were calculated for both the spring samples. There was no significant difference between the two stations so the results were pooled. The resulting regression was significant ($\log F = 3.54 \log SL - 2.68$, $F = 11.84$, $n = 36$, $p = 0.002$) although the correlation coefficient was very low ($r^2 = 0.26$ Fig. 56). Fecundities ranged from 245 to 1191 (32-39mm SL).

3.2.7 Cyclothone alba

Cyclothone alba was taken in very small numbers at most latitudes (Table 3). It was only found in large numbers at 10°N and 20°N in the autumn. Even at these two stations the density and biomass was low relative to that of the other species (Fig. 3 and 4).

3.2.7.1 20°N.

Juveniles made up more than 50 percent of the Cyclothone alba population at 20°N in the autumn (Fig. 58a) and were present at a range of standard lengths with a mode at 15mm (Fig. 57a). No immature females were present and most of the mature females were stage III/V

Figure 50. Length-frequency distribution by sex and stage of C. acclinidens at 20°N in the spring (n=55).

1= Juveniles

2= Males

3= I

4= II

5= III/V

6= VI

7= VII

8= VII/II

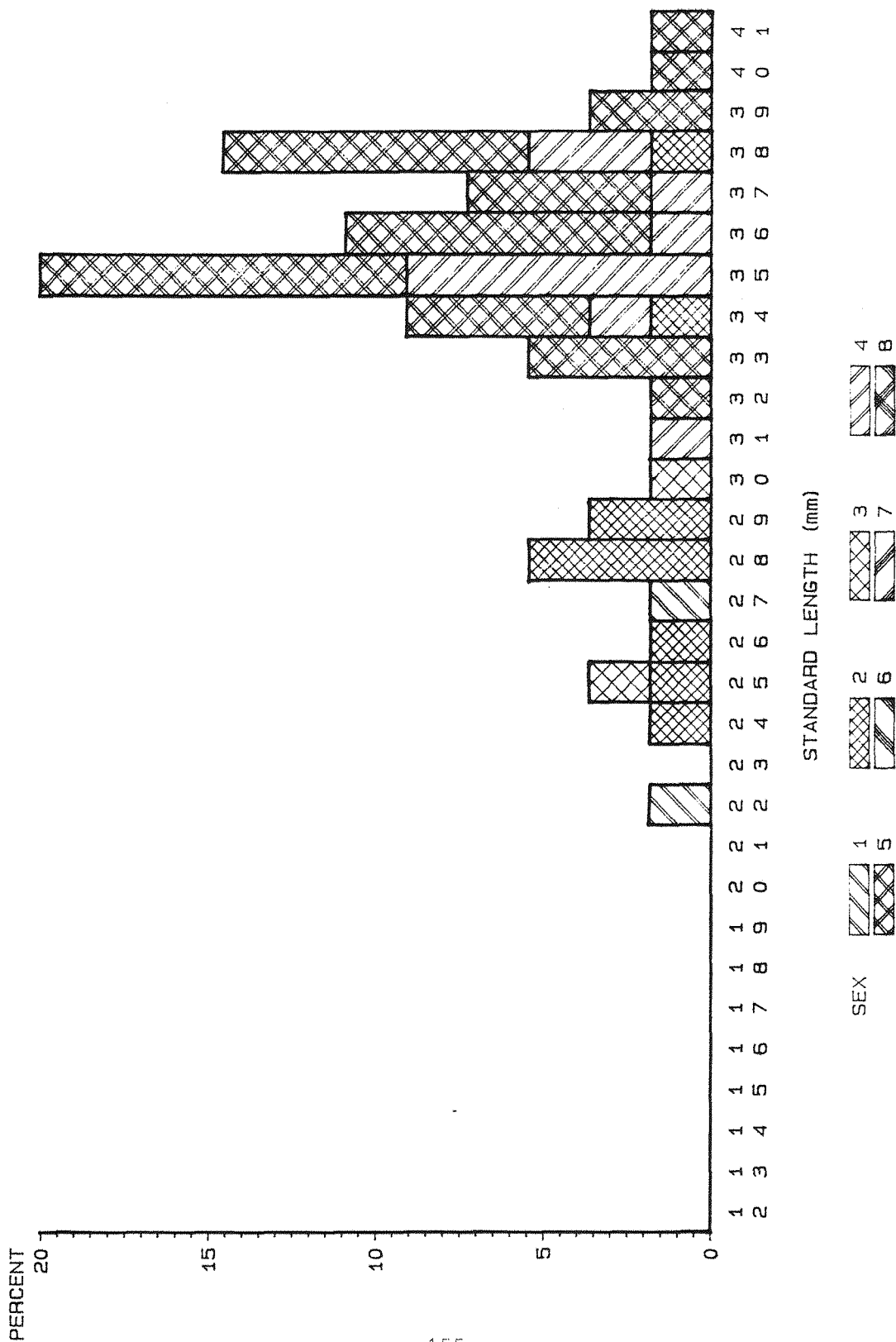


Figure 51. C. acclinidens at 20°N in the spring.
a) Percent abundance by sex/stage (n=55) and
b) the size-frequency distribution of the
maximum egg diameter in females (n=27).

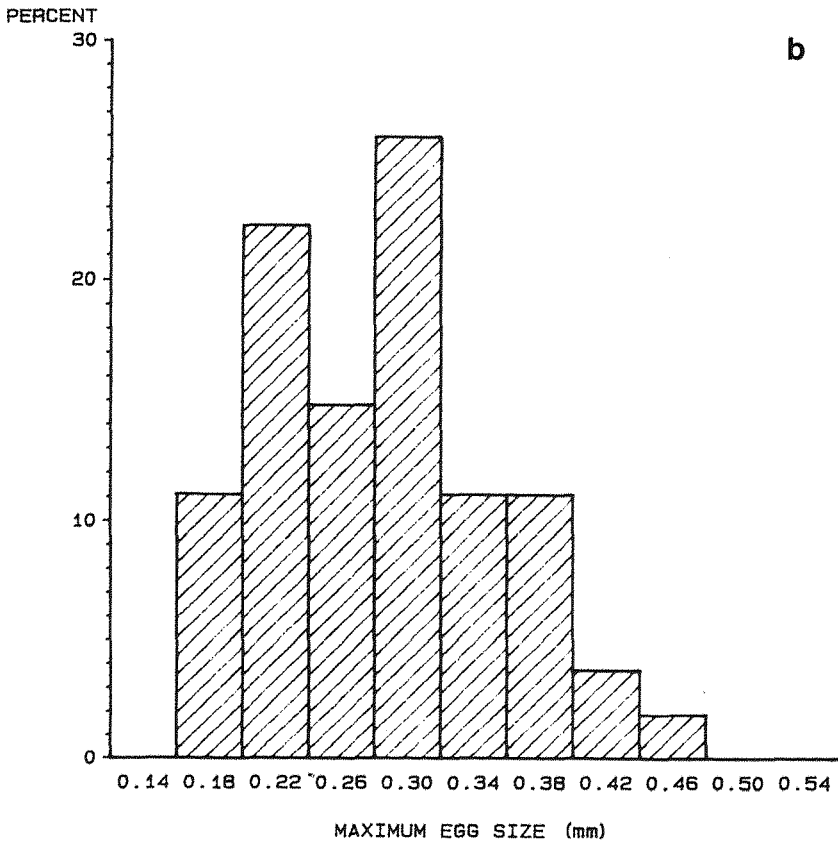
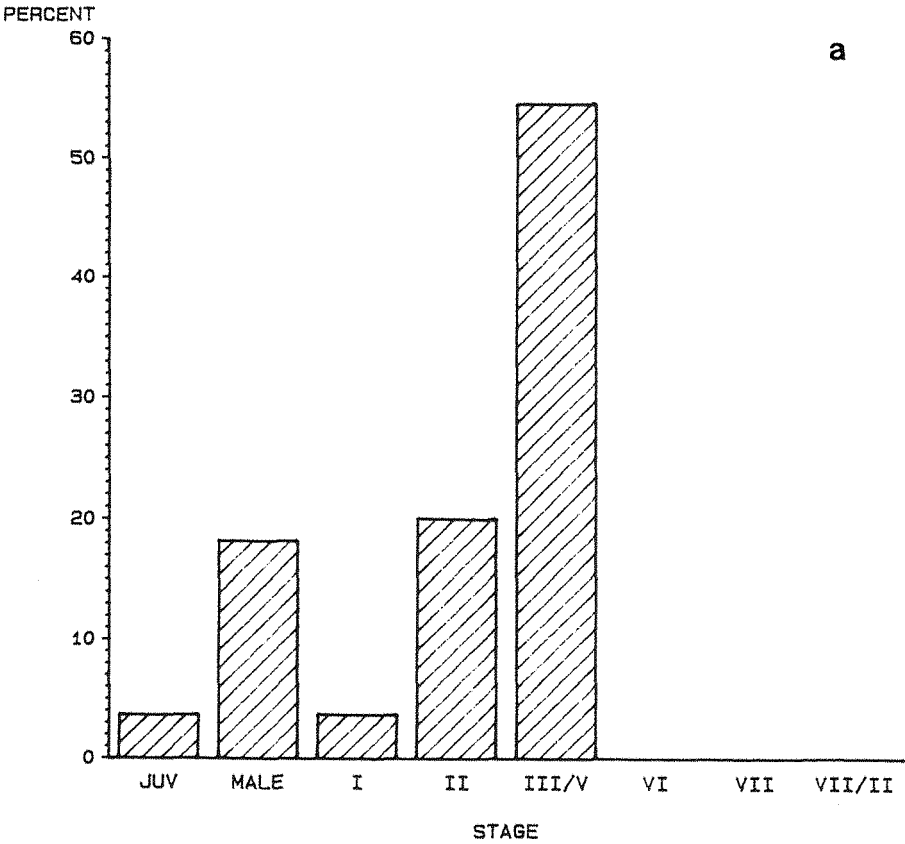


Figure 52. Length-frequency distribution by sex and stage of C. acclinidens at 20°N in the autumn (n=306).

1= Juveniles

2= Males

3= I

4= II

5= III/V

6= VI

7= VII

8= VII/II

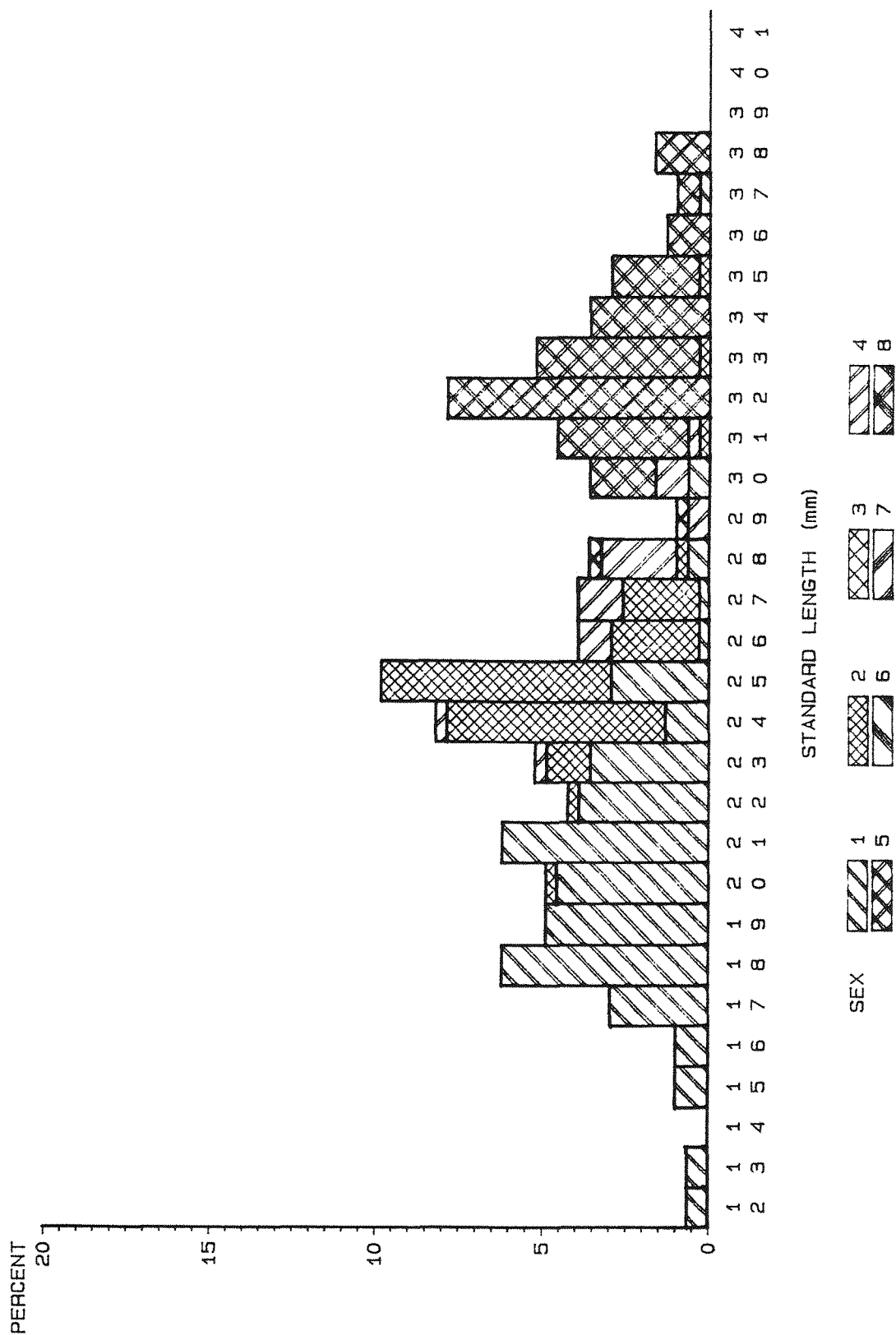


Figure 53. C. acclinidens at 20°N in the autumn.
a) Percent abundance by sex/stage (n=306) and
b) the size-frequency distribution of the
maximum egg diameter in females (n=19).

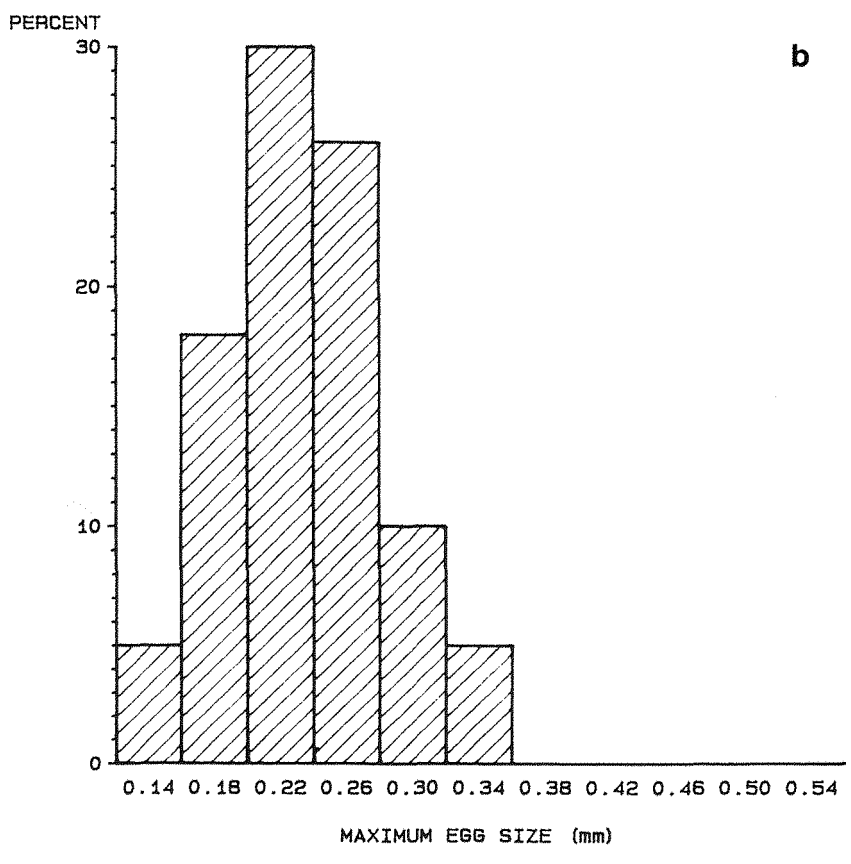
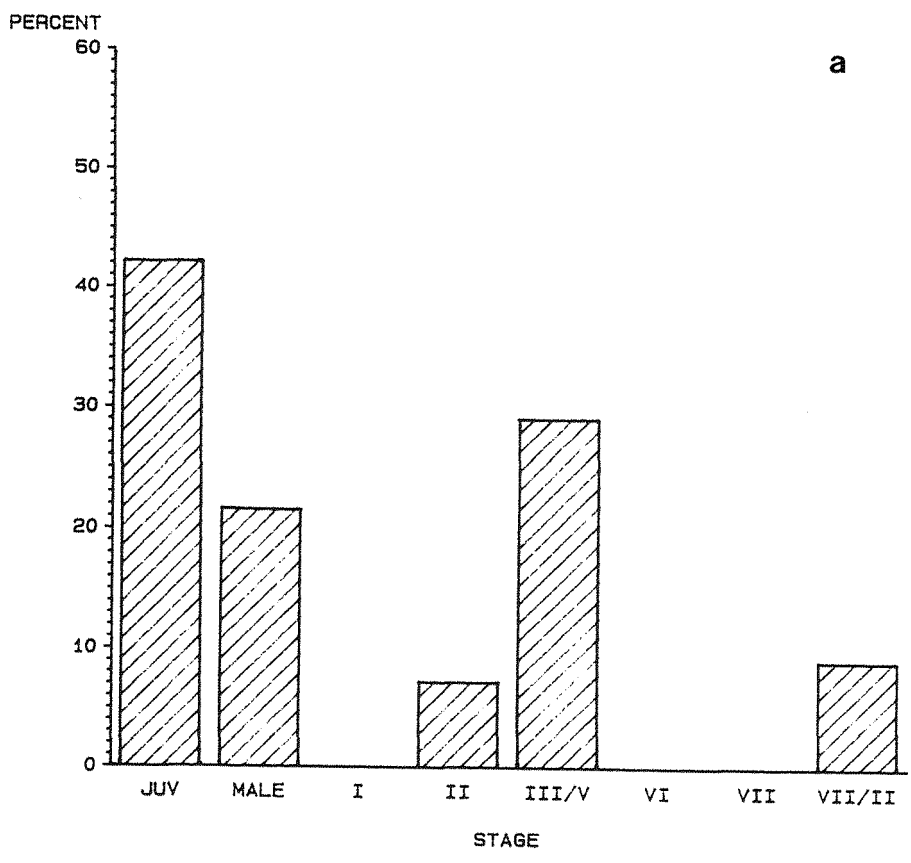


Figure 54. Length-frequency distribution by sex and stage of C. acclinidens at 10°N in the spring (n=2749).

1= Juveniles

2= Males

3= I

4= II

5= III/V

6= VI

7= VII

8= VII/II

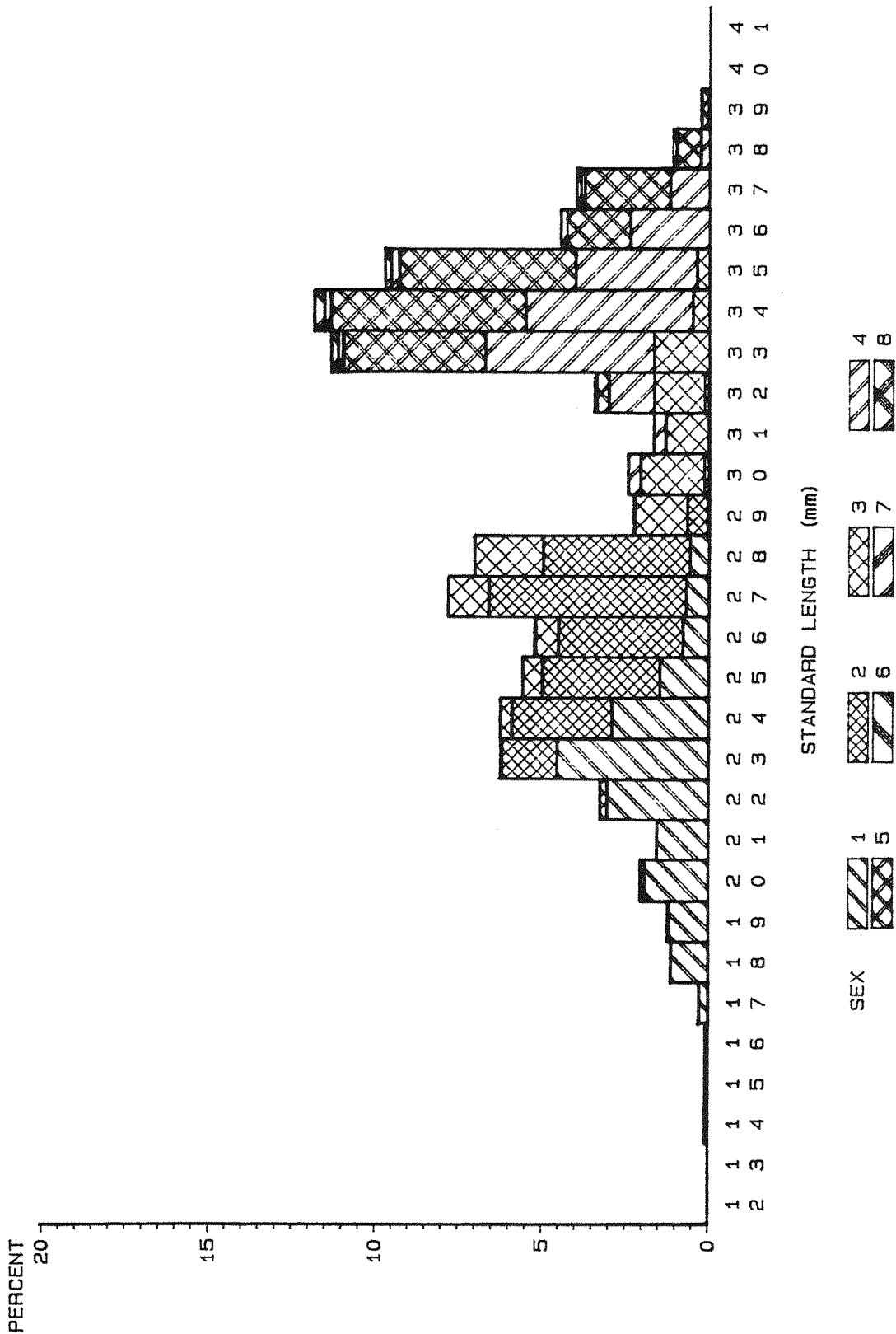


Figure 55. C. acclinidens at 10°N in the spring.
a) Percent abundance by sex/stage (n=2749) and
b) the size-frequency distribution of the
maximum egg diameter in females (n=49).

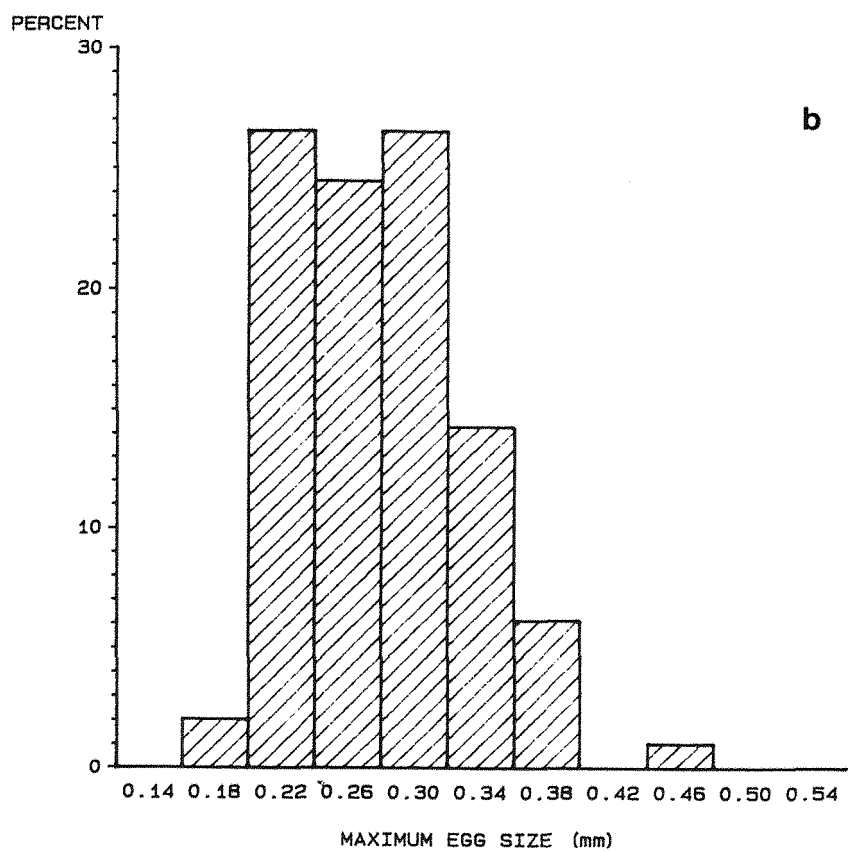
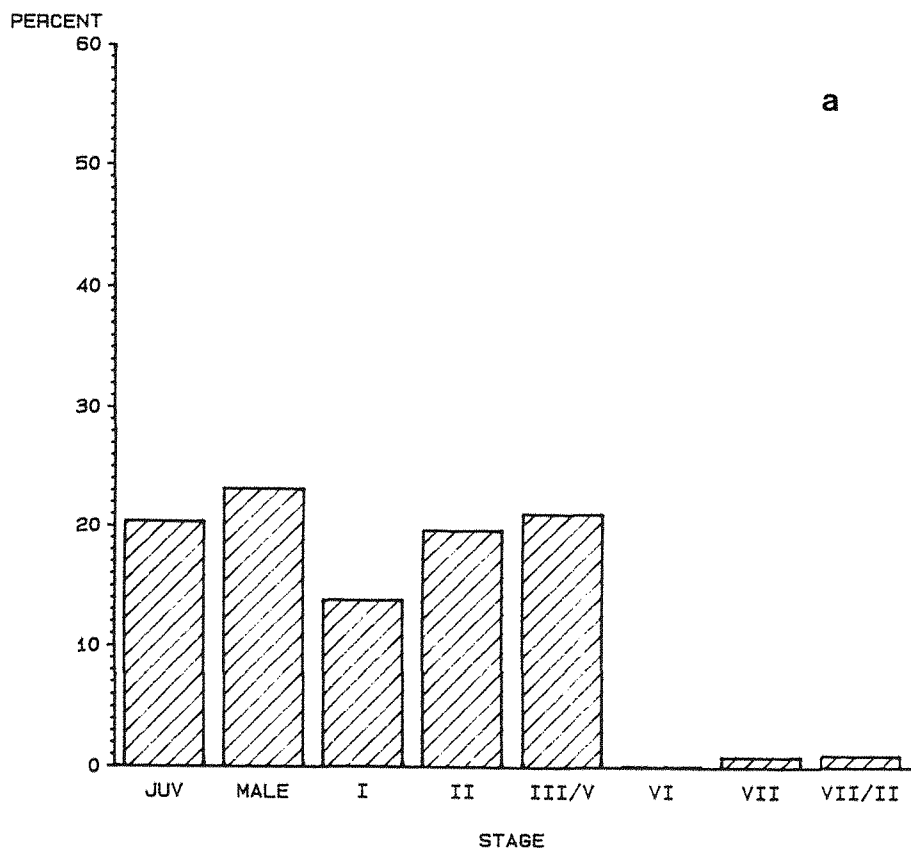
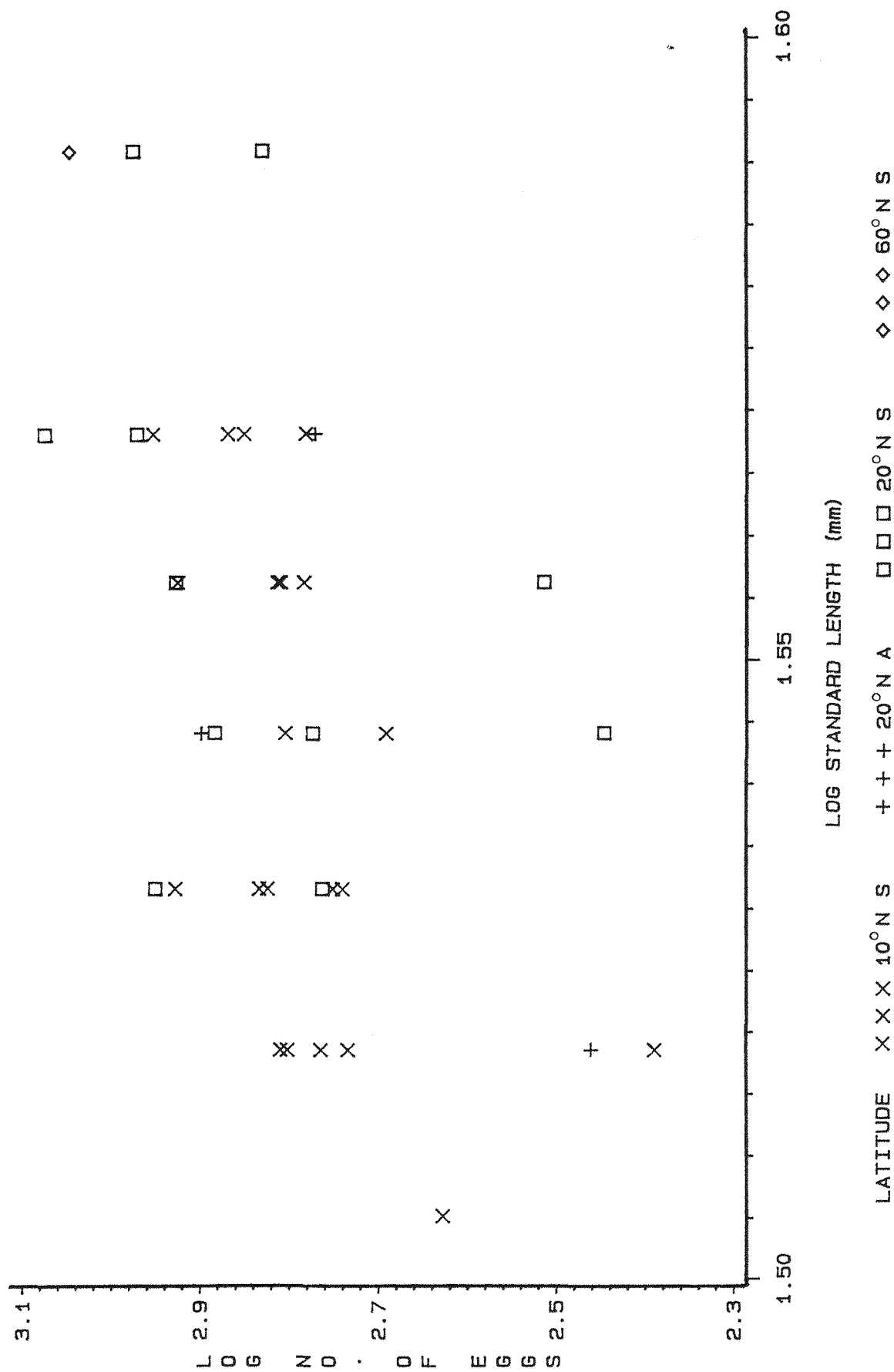


Figure 56. Log fecundity vs. log standard length of
C. acclinidens.



(Fig. 58a). Females were generally mature by 19mm SL. Maximum egg size of mature females was diverse with modes at 0.22mm and 0.4mm and a mean size of 0.32mm ($s^2=0.007$ Fig. 59a). The mean standard length of mature females was 24.18mm ($s^2=1.32$). The number of mature females for every male was greater than two (male:females 1:2.3) with males primarily found at standard lengths of 18mm (Fig. 57a).

3.2.7.2 10°N.

Juveniles and stage III/V females of Cyclothone alba were co-dominant in the spring at 10°N (Fig. 58b). Juveniles peaked in abundance at 15 and 18mm SL and stage III/V females were most abundant at a standard length of 27mm (Fig. 57b). The egg size of stage III/V females was variable with peaks at 0.22mm and 0.4mm and a mean size of 0.32mm (variance=0.009 Fig. 59b). Females reached maturity at standard lengths of 23mm. Males peaked in number at 20mm SL (Fig. 57b) and were more than three times less abundant than mature females (males:females 1:3.6).

3.2.7.3 Latitudinal Comparisons

The populations at 20°N and 10°N were similar. Three peaks in abundance were present in the length frequencies at both locations (Fig. 57a and b). The two peaks at the lower end of the size range occurred at the same standard lengths although the percentage contribution to the population differed. The peak of mature females was present at a larger standard length at 10°N than at 20°N. Similarities were also present in the proportion each sex/stage contributed to the population. At both locations juveniles and stage III/V females were most important. There were only slight fluctuations in all categories (Fig. 58a and b).

There was no significant difference in the mean of the maximum egg size of females in the population between the two stations. Both distributions of egg sizes showed peaks at 0.22mm and 0.4mm (Fig. 59a and b).

The results were consistent with a population undergoing continuous spawning. Patterns appear to be the same regardless of the season, both in population structure and in the egg size of females.

Juveniles appeared to be recruited to the adult male population at sizes as small as 14mm SL. The two peaks of juveniles at 15 and 18mm SL could represent males and females respectively. There was no indication of females spawning more than once and there was only one size class of females present. The skewed sex ratio must result from males being very short lived as there was little indication of the females living through two age classes.

There were no differences in the number of eggs present in females from the two latitudes so the results were pooled. The log-log regression of fecundity on standard length was significant ($\log F = 3.44 \log SL - 2.59$, $F = 24.35$, $p = 0.001$, $n = 41$) although there was a lot of variability about the line ($r^2 = 0.38$, Fig. 60). Counts ranged from 98 to 391 (23-29mm SL).

3.2.8 Cyclothone obscura

Few specimens of Cyclothone obscura were captured at latitudes other than 10°N (Table 3). Less than 100 were taken at both times of the year at 20°N. It was the least most abundant species at the southernmost stations during both the spring and the autumn (Fig. C3a and b). Due to its large size it comprised a greater biomass than C. alba at 10°N in the spring (Fig. 4a) but was lowest in biomass at 20°N in the autumn (Fig. 4b).

Figure 57. Length-frequency distribution by sex and stage of C. alba at a) 20°N in the autumn (n=659) and b) 10°N in the spring (n=784).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII

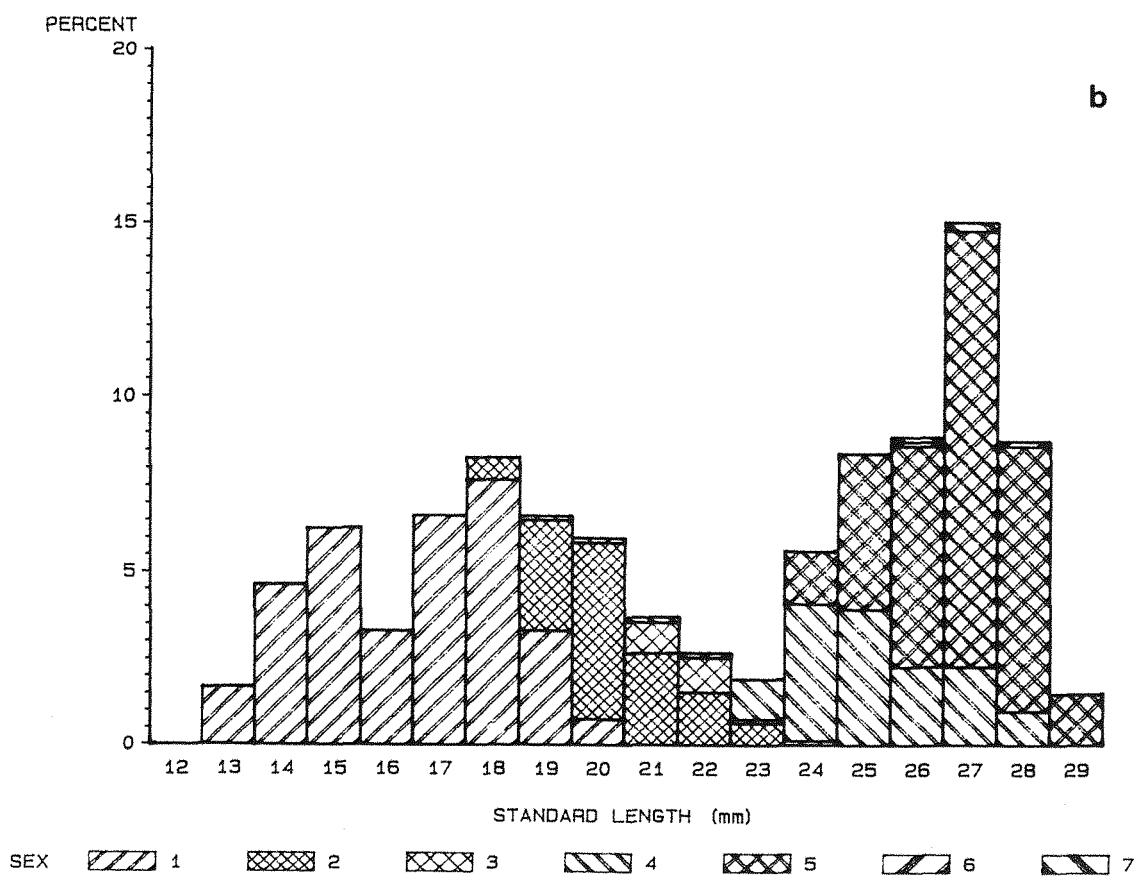
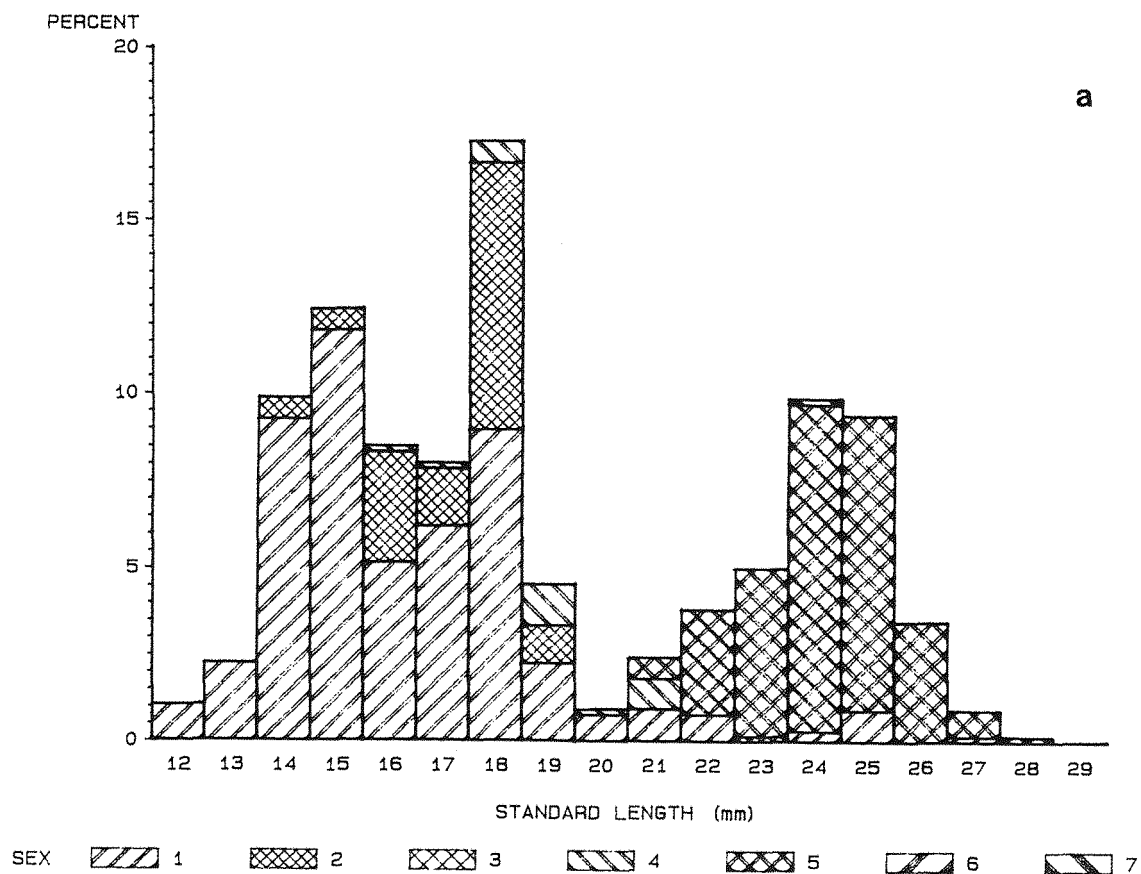


Figure 58. Percent abundance by sex/stage of C. alba
at a) 20°N in the autumn (n=659) and b) 10°N
in the spring (n=784).

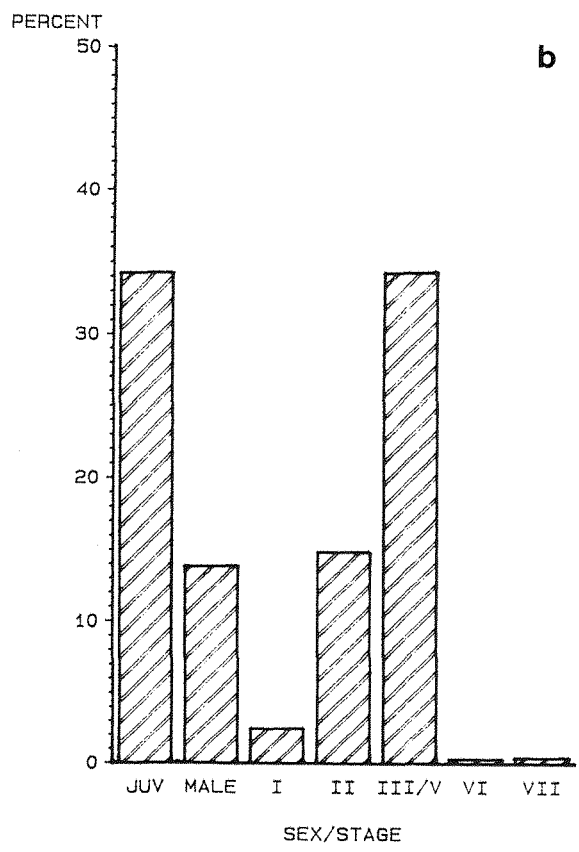
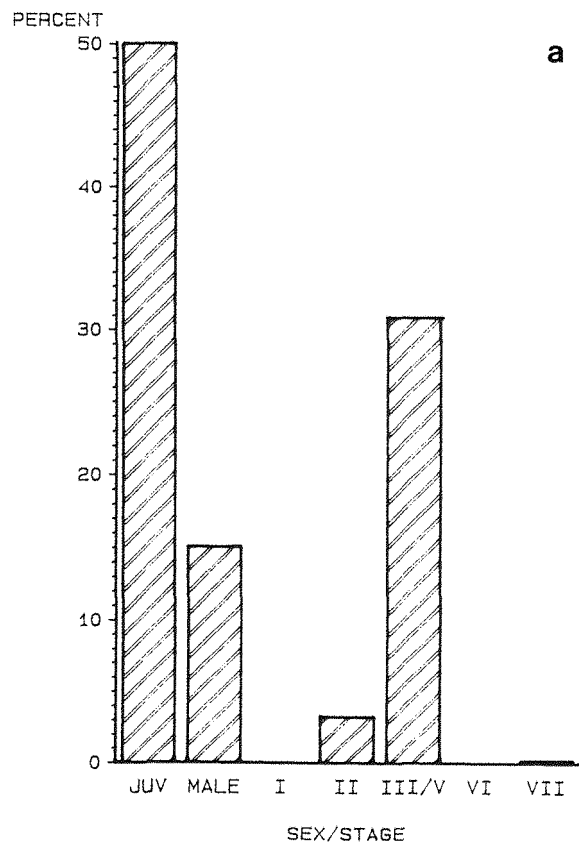


Figure 59. Size-frequency distribution of the maximum egg diameter in female C. alba at a) 20°N in the autumn (n=46) and b) 10°N in the spring (n=53).

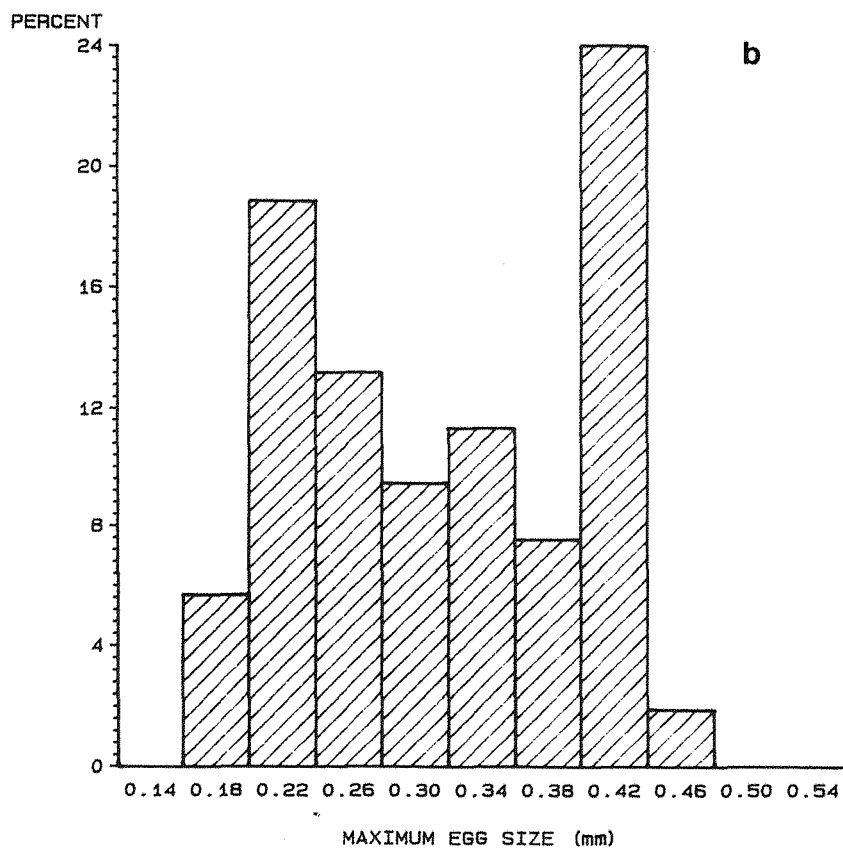
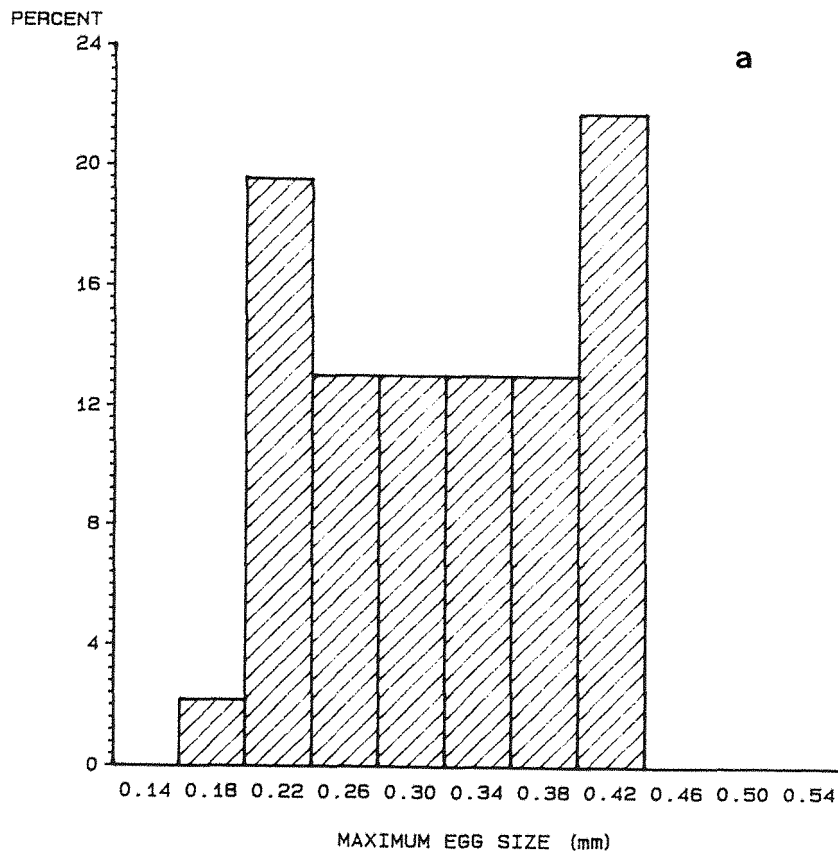
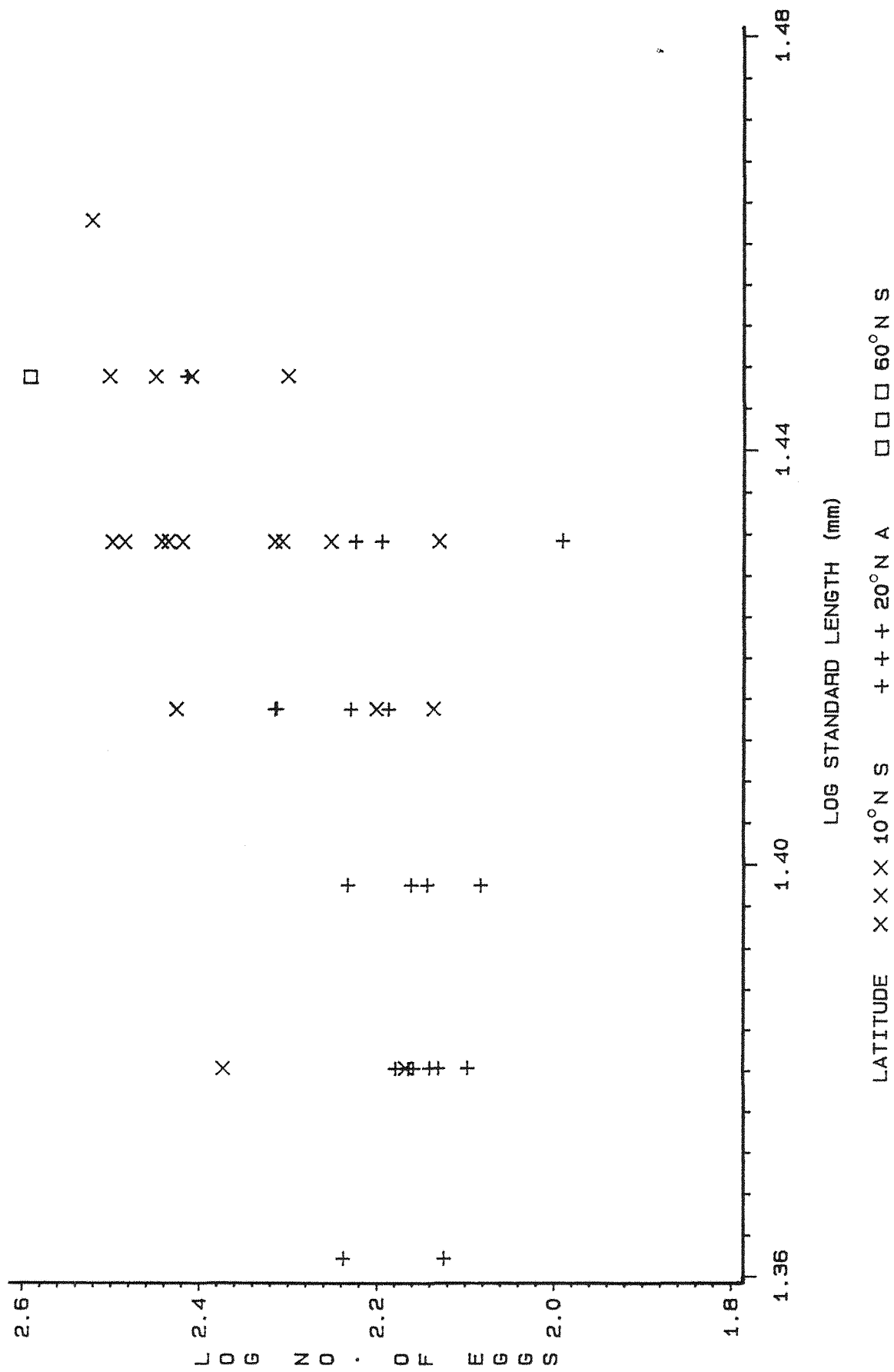


Figure 60. Log fecundity vs. log standard length of
C. alba.



3.2.8.1 20°N.

Of the low number of Cyclothone obscura taken at 20°N in the spring the majority were stage III/V females (Fig. 62a). These females had large eggs in their ovaries, the maximum being between 0.4 and 0.54mm (Fig. 63a) with a mean of 0.49mm (variance=0.001). All mature females were larger than 46mm SL with the greatest number found at standard lengths of 54-56mm (Fig. 61a). Immature females were present at sizes between 34 and 42mm SL. Males predominated at the smaller standard lengths with a mode of 38-40mm (Fig. 61a) and were less abundant than females (males:females 1:1.6). All other stages were only present in small numbers (Fig. 62a).

In the autumn, juveniles were the most abundant group (Fig. 62b). They were present over a wide range from 14-30mm SL but were most abundant at the lower extent of their size range (mode 16mm SL Fig. 61b). Few adults were present (Fig. 62b). Males and stage I females were most abundant between 36 and 40mm SL. Small peaks in the abundance of adult females were found at 48, 52 and 56mm SL (Fig. 61b). Males were only slightly more abundant than mature females (male:females 1:0.8).

3.2.8.2 10°N.

Three main groups were present in the Cyclothone obscura population at 10°N. Juveniles were the most abundant (Fig. 65a) and were relatively evenly spread over a range of standard lengths from 18-34mm SL (Fig. 64). The second group was predominantly males centred around standard lengths of 40mm with some stage I females (Fig. 64). The third group was made up of mature females at standard lengths of between 46 and 58mm with a mode at 54mm. These mature females were only slightly less abundant than males (males:females 1:0.94). A wide range of egg sizes were found in the stage III/V females (Fig. 65b). The mean population egg size was 0.32mm (variance=0.005).

3.2.8.3 Latitudinal Comparisons

The main difference among stations was the abundance and size of juveniles in the population. At 20°N in the spring few juveniles were present whereas in the autumn the sample was predominantly juveniles, primarily at the smaller end of the size range. At 10°N in the spring juveniles predominated however they were spread over an extensive size range.

These comparisons suggest a winter/spring spawning for C. obscura. Both spring samples had spent females present and females with large eggs. It was likely that females in the 10°N sample were more advanced to the point of almost completing spawning as stage III/V females made up a smaller proportion of the population and those that were present generally had small eggs. The large number of juveniles in the autumn sample probably represented young from the winter/spring spawning which had descended to adult depths. The few stage III/V females present had very small eggs. The wide range in lengths of juveniles was consistent with a prolonged spawning period and it seems that year round spawning in a proportion of the population may be possible.

The large variation in juvenile size at 10°N in the spring suggested a lengthy period as a juvenile. This and the large size at maturity suggested delayed maturation in C. obscura. Males were generally only present in one peak of abundance at all three stations. Up to three small peaks in female abundance were evident. Stage I females were present at sizes of 34-38mm SL, Stage II and III/V females at 48-50mm SL and a group of stage III/V females at 54-56mm SL. Age assessment is problematic as the large size range of juveniles makes it difficult to estimate how long it takes for maturation. The relatively limited size range of males suggests that it is unlikely that they survive more than one spawning period. Females spawn more than once and live a minimum of 2-3 years as adults.

The number of eggs found in females varied from 161-1001 (48-59mm SL, Fig. 66). A significant log-log regression was obtained between length and the number of eggs for samples at 10°N ($\log F = 3.31 \log SL - 3.16$, $F = 8.78$, $n = 19$, $p = 0.01$) although the correlation coefficient was very low ($r^2 = 0.34$). A significant regression was not obtained for the 20°N spring samples. There was no suggestion of any latitudinal effect on the number of eggs although a pooling of the two stations resulted in a lower correlation coefficient ($r^2 = 0.12$, $n = 33$, $F = 4.20$, $p = 0.05$, $\log F = 2.68 \log SL - 2.07$) rather than higher as might be expected from the increased sample size.

3.3 Interspecific Comparisons

Comparisons among species could most readily be made within the two naturally occurring groups, the small shallow-living species (C. alba, C. acclinidens, C. braueri, C. livida, C. pseudopallida) and the large deep-living species (C. microdon, C. obscura, C. pallida).

3.3.1 Shallow Species

Within the shallow group the maximum size attained by a species was latitudinally dependent. The maximum size attained by C. braueri was larger at more northerly latitudes (Table 12). However, among species the pattern was less obvious. Three species primarily found at lower latitudes than C. braueri (C. acclinidens, C. livida, C. pseudopallida) reached larger maximum sizes and one species (C. alba) had a smaller maximum size (Table 12). The complicating factor appeared to be depth. C. alba was the smallest species and was found at the shallowest depth range. The other four species all had overlapping depth ranges. Within these species the tendency was for the larger species to be found at lower latitudes, the opposite of the

Figure 61. Length-frequency distribution by sex and stage of C. obscura at a) 20°N in the spring (n=68) and b) 20°N in the autumn (n=91).

1= Juveniles

2= Males

3= I

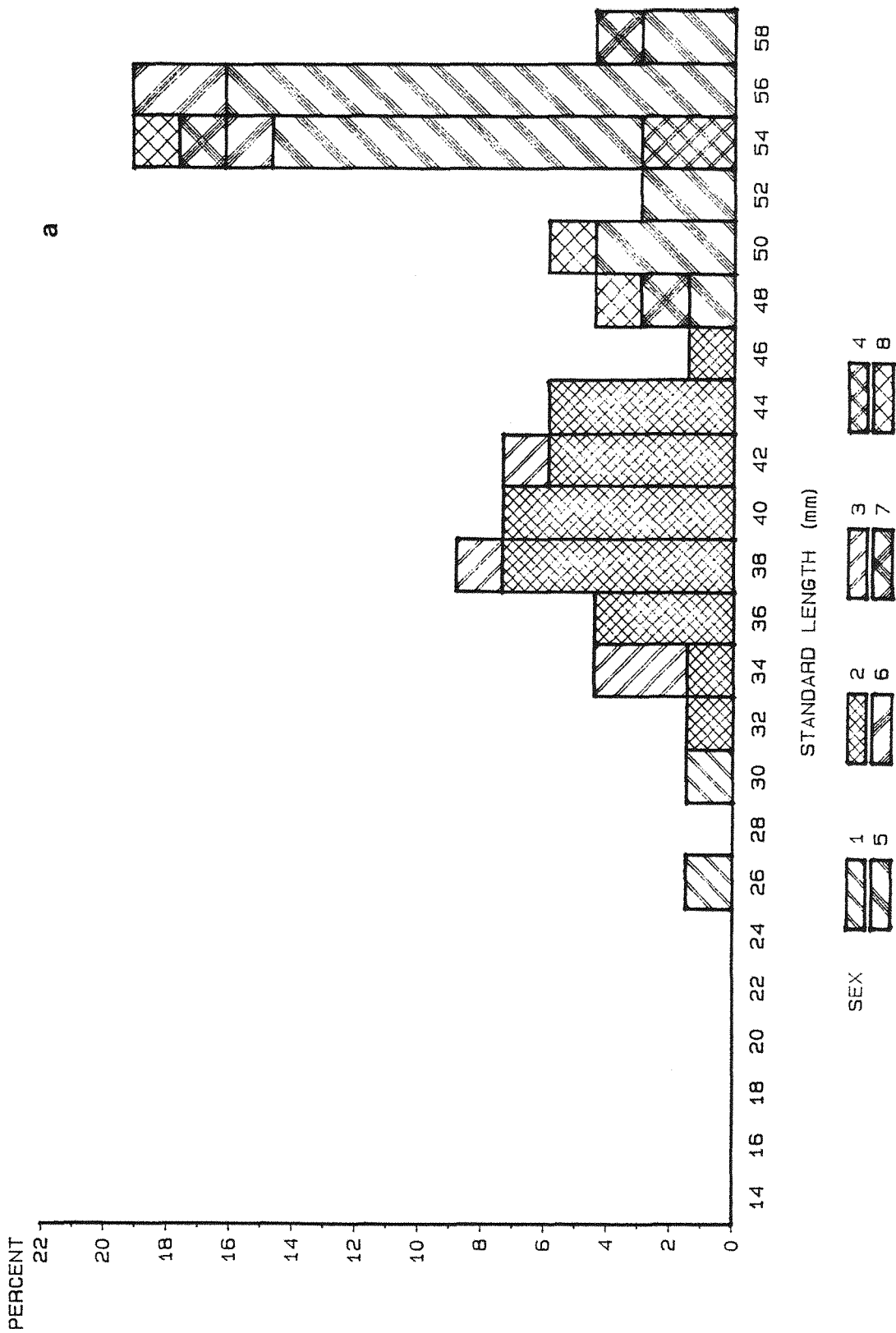
4= II

5= III/V

6= VI

7= VII

8= VII/II



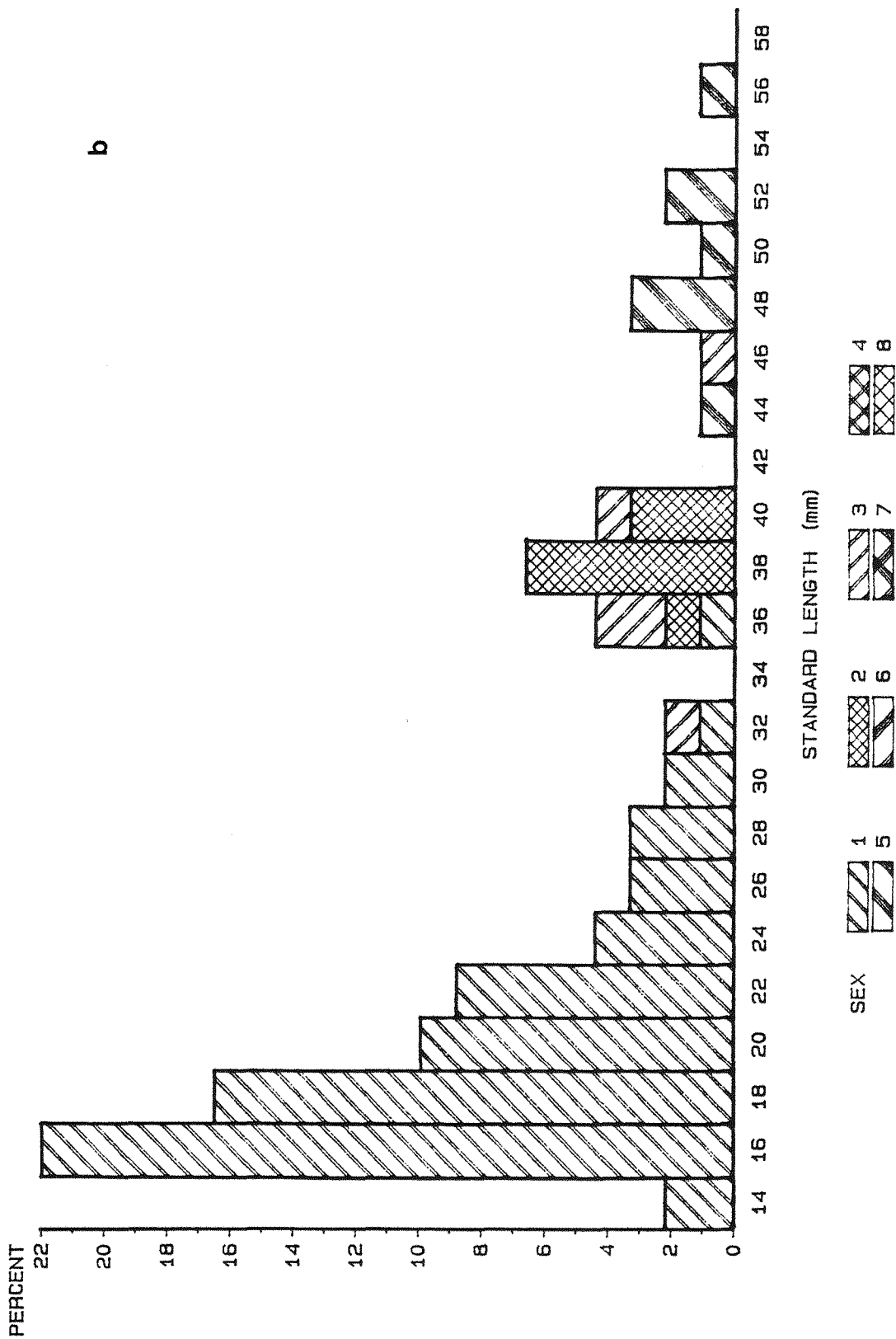


Figure 62. Percent abundance by sex/stage of C. obscura
at a) 20°N in the spring (n=68) and b) 20°N in the
autumn (n=91).

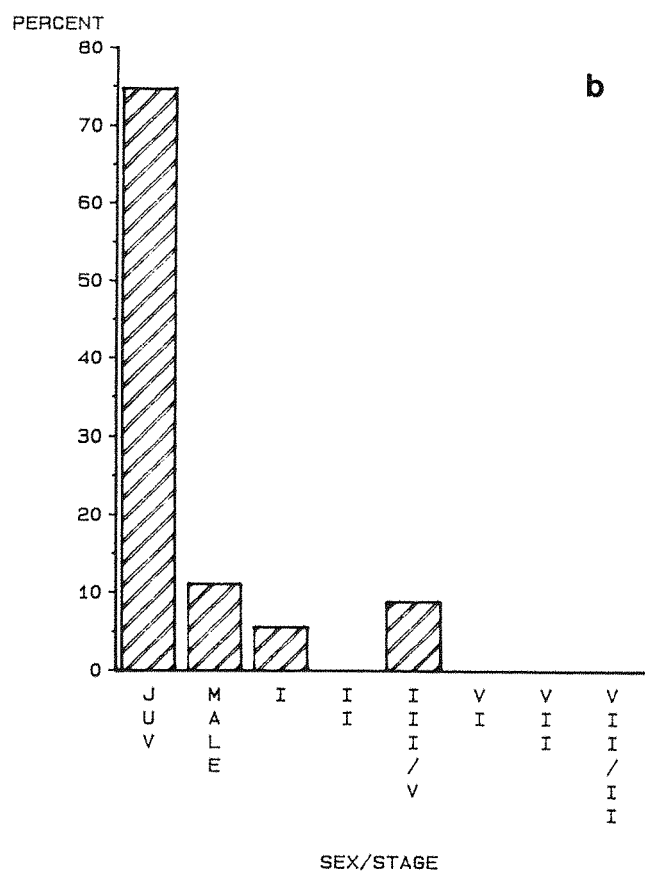
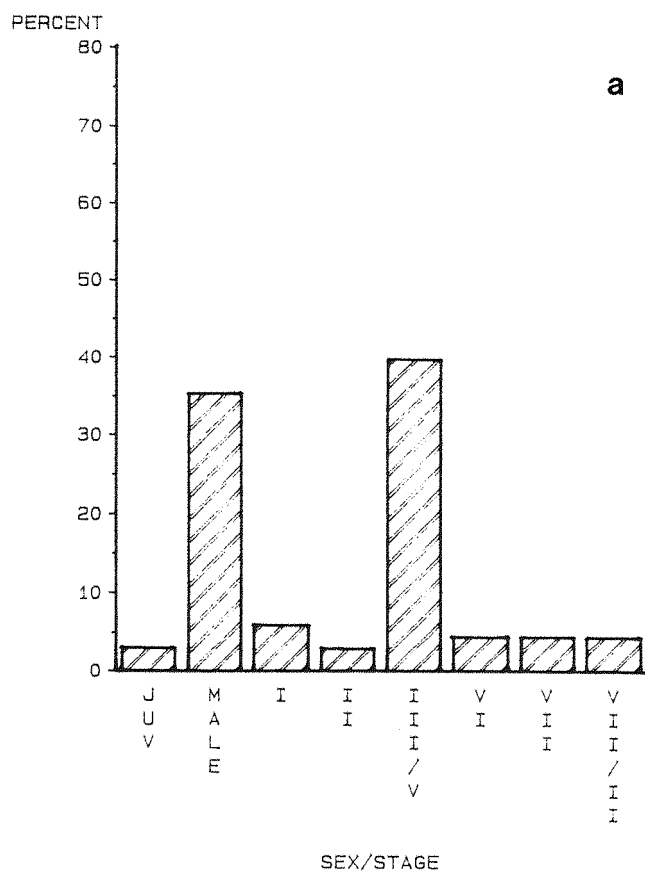


Figure 63. Size-frequency distribution of the maximum egg diameter in female C. obscura at 20°N in the spring (n=25).

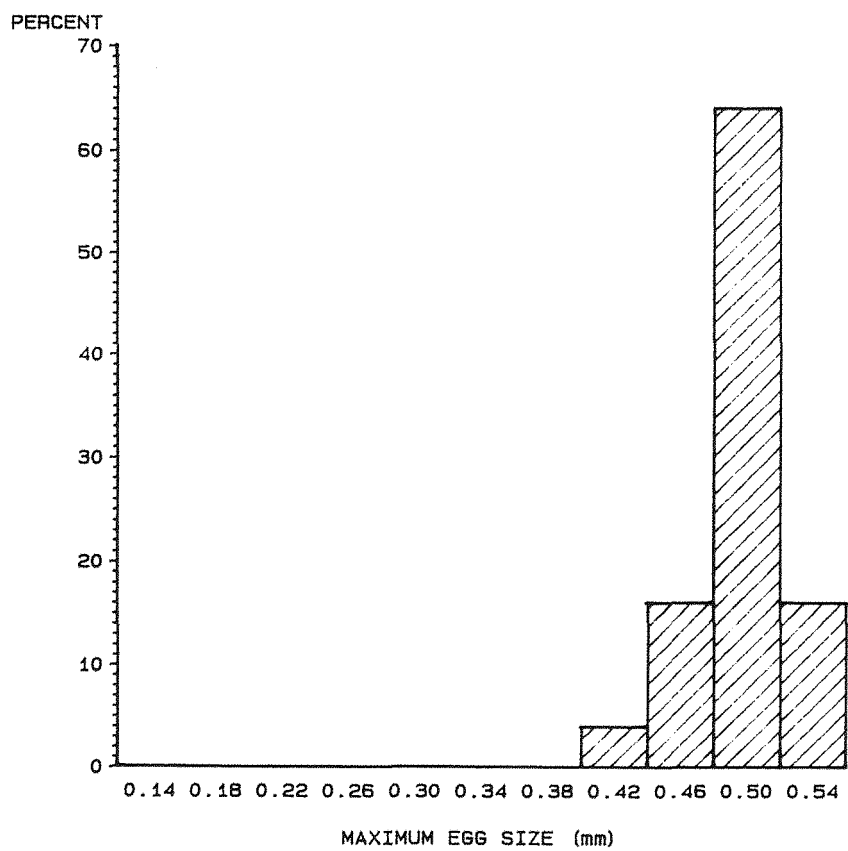


Figure 64. Length-frequency distribution by sex and stage of C. obscura at 10°N in the spring (n=378).

- 1= Juveniles
- 2= Males
- 3= I
- 4= II
- 5= III/V
- 6= VI
- 7= VII
- 8= VII/II

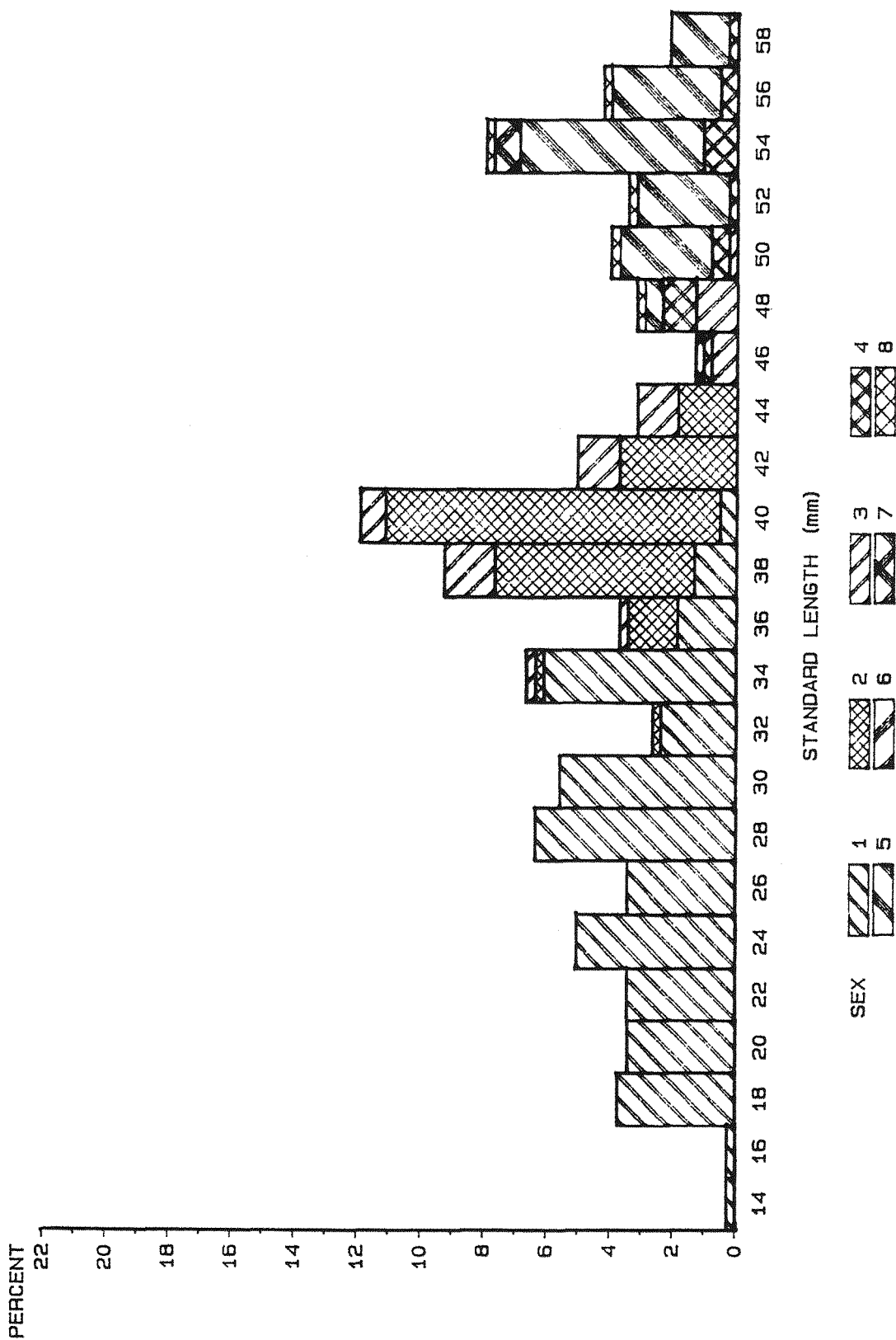


Figure 65. C. obscura at 10°N in the spring.
a) Percent abundance by sex/stage (n=378) and
b) the size-frequency distribution of the
maximum egg diameter in females (n=24).

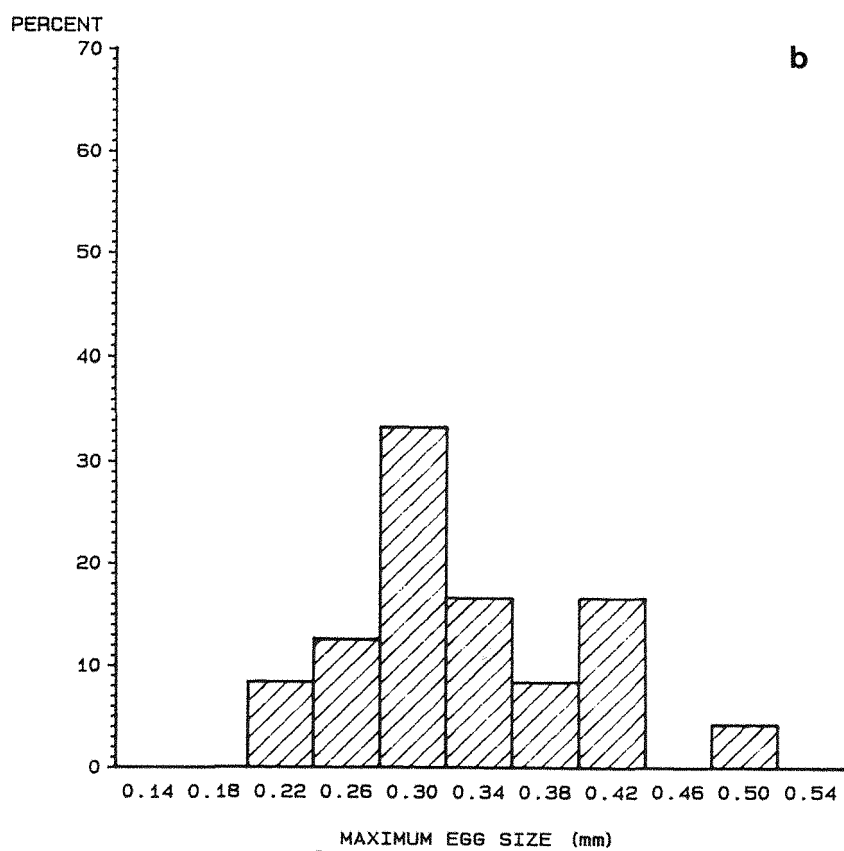
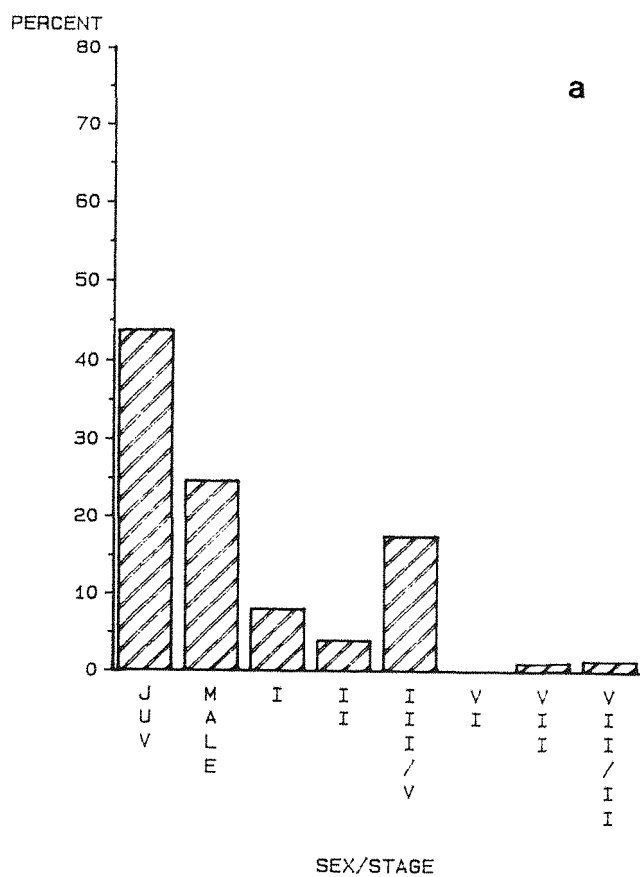
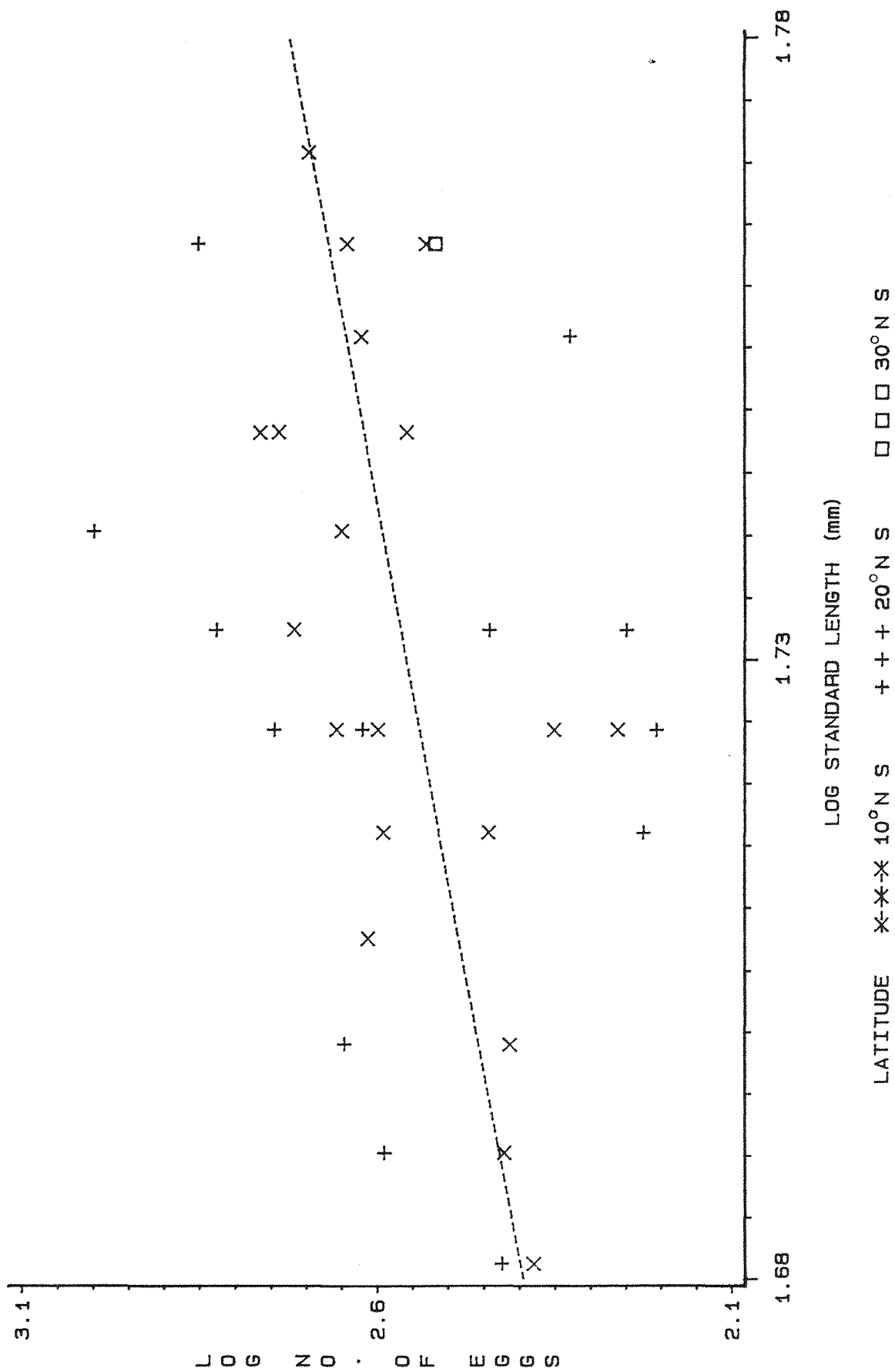


Figure 66. Log fecundity vs. log standard length of C. obscura. The regression line shown is the significant regression at 10°N in the spring.



pattern found within a species. The larger size was related to length of life. Species at lower latitudes appeared to be longer lived than those whose distributions were centred around higher latitudes (Fig. 67a).

Latitudinal differences were also evident in the size at maturity of females. The three species found at lower latitudes but similar depth ranges generally matured at larger standard lengths than the more northerly distributed species C. braueri (Table 13). A similar pattern was evident in the size at which males became distinguishable from juveniles (Table 14). In both cases the exception was the shallow living species C. alba which matured at smaller standard lengths despite its low latitude distribution.

The highest sex ratios in this group were found for C. braueri and C. alba, the species that spawned only once in their life span (Table 15). The other species had sex ratios of less than two females to every male.

A comparison of fecundities further confirmed the grouping among the shallow living species as there was a significant difference among the species (ANCOVA, $F=124.13$, $df=(5,305)$, $p<0.01$). C. braueri had the highest fecundities and the best correlation coefficient of all the species ($r^2=0.67$, Fig. 68, Table 16). Its fecundity was significantly different from that of all the other shallow species ($p<0.05$). There was no significant difference between the fecundities of C. acclinidens and C. pseudopallida, both of which had fewer eggs at a given standard length than did C. braueri. C. alba had the lowest fecundity and in this respect was significantly different from all the other shallow species ($p<0.05$).

It was difficult to compare the fecundity of C. livida with that of the other species because there was no relationship between fecundity and standard length. It did appear as if fecundities were similar to those of C. acclinidens and C. pseudopallida however there was a lot of variability, particularly at the higher standard lengths (Fig. 68).

There were some similarities among the species. In all the species

males appeared to spawn once and then die. There was no indication of any more than one year class in males. It is possible that males were longer lived but ceased to grow in their second year of maturity making them indistinguishable from males in their first year of maturity. However, that would be inconsistent with the skewed sex ratios evident in all the species. Males and stage I females were usually the same size suggesting similar growth rates are present in both sexes up to that point.

The above features result in the formation of three groups of species with slightly different strategies. At the northerly extent of the distribution of the genera C. braueri is semelparous. It reaches a smaller size and produces the most eggs of the shallow living species.

The second group was comprised of the three species at a similar depth range to C. braueri, C. acclinidens, C. livida and C. pseudopallida. These species delayed maturity and traded off a reduced fecundity for a slightly larger size, longer life span and iteroparity.

A third strategy appears to be undertaken by C. alba. At shallower depths it is able to spawn year round and matures very quickly but spawns only once in its lifetime. It produces the fewest eggs of the species considered, balanced by production of eggs throughout the year.

3.3.2 Deep Species

The same patterns were not evident in the larger deep-living species. There was no difference in the maximum size a species attained within or among species (Table 12) although species at lower latitudes appeared to be longer lived (Fig. 67a). However, there were differences in the size at maturity among the species. Females of species at lower latitudes matured at larger standard lengths (Table

13). It could be argued that C. microdon females mature at smaller size because they are protandrous hermaphrodites and therefore put energy that could go to growth to gonad production however, there was a similar reduction in the size at maturity between C. pallida and C. obscura. Also, there was an increase in the size at which males become distinguishable from juveniles with decreasing latitude (Table 14). This suggests that species at lower latitudes either grow faster and mature and spawn at the same time as those at northern latitudes or maturation and spawning is delayed at lower latitudes. The presence of more than one peak of juveniles generally found in the length frequency distribution of the southern species suggest the latter is the case.

Sex ratio also varied with latitude. The higher sex ratios were found in the species at higher latitudes (Table 15). C. microdon had the greatest female to male ratio followed by C. pallida and the lowest sex ratio for the deep group was present in C. obscura.

The fecundities of the three species were all significantly different from each other (ANCOVA, $F=231.83$, $df=(3,149)$, $p<0.05$). Fecundity was directly related to latitude among the species as C. microdon had the highest number of eggs followed by C. pallida and the lowest number in C. obscura (Fig. 68). Although the regressions were significant the variability was high as correlation coefficients were low (Table 16).

Trade offs between fecundity and other characteristics were evident among the deep-living species. At the higher latitudes C. microdon had the highest fecundity and the earlier maturation but it appeared as if only part of the population spawned more than once. C. pallida had a slightly lower fecundity and a later maturity and spawned at least twice in its lifetime. C. obscura had the lowest fecundity, delayed spawning possibly until its third year and spawns more than twice.

3.3.3 All Species

At lower latitudes, the spawning season appears to start earlier in the year and continue over a longer time period (Fig. 67b). At higher latitudes spawning occurs in the spring/summer period, possibly linked with a seasonal peak in food availability. The species whose distributions appear to be centred at the southern extreme of the sampled area (C. alba, C. obscura) could spawn all year round.

Although the smaller species had lower absolute fecundities, comparisons of the fecundities among all species showed similarities in relative fecundity between the deep living species and the shallow species by latitude (Fig. 68). There were significant differences in fecundities among the species (ANCOVA, $F=309.13$, $df=(8,455)$, $p<0.001$). There was no significant difference between the relative fecundities of C. braueri and C. microdon ($p<0.01$). Similarly, the relative fecundity of C. pallida was not significantly different from that of C. acclinidens and C. pseudopallida ($p<0.01$). C. alba and C. obscura did not have similar fecundities and had significantly fewer eggs at a given size than the above groups.

The relative unimportance of depth on fecundity was further supported by the results of a stepwise multiple regression. The most important factor in predicting fecundity regardless of species was standard length (partial $r^2=0.43$, $p=0.0001$, $F=338.92$, $df=1,450$). The only other variable that increased predictive ability was latitude (partial $r^2=0.12$, $p=0.0001$, $F=121.25$, $df=1,450$). Together these variables raised the correlation coefficient to 0.55 ($F=275.37$, $df=(2,449)$, $p=0.001$). Depth and season did not significantly increase the predictability of fecundity.

Table 12. Maximum size (mm SL) attained by each species at each latitude.

Species	Latitude ° N					
	60	50	40	30	20	10
braueri	35	37	36	32	32	
pseudopallida				42	40	46
livida					39	39
acclinidens					41	39
alba					28	29
microdon	54	58	56	60		
pallida				64	58	58
obscura					58	58

Table 13. Size at maturity (mm SL) of females of each species at each latitude.

Species	Latitude ° N					
	60	50	40	30	20	10
braueri	25	25	24	19	22	
pseudopallida				28	22	32
livida					27	27
acclinidens					31	28
alba					19	23
microdon	40	38	34	34		
pallida				44	34	44
obscura					48	48

Table 14. Size at maturity (mm SL) of males of each species at each latitude.

Species	Latitude ° N					
	60	50	40	30	20	10
braueri	19	18	15	14	17	
pseudopallida				24	22	24
livida					20	20
acclinidens					23	23
alba					14	18
microdon	19	20	21	18		
pallida				28	28	28
obscura					32	36

Table 15. Spring sex ratio, reported as the number of females for every male of each species at each latitude.

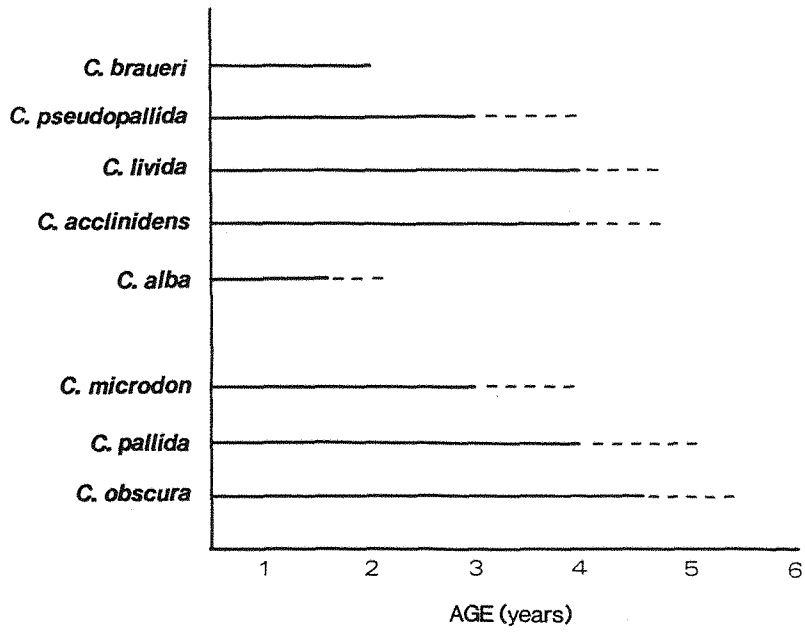
Species	Latitude ° N					
	60	50	40	30	20	10
braueri	1.9	2.5	3.7	2.2	1.7	
pseudopallida				2.8	1.3	0.7
livida					1.6	0.6
acclinidens					1.7	1.8
alba					2.3	3.6
microdon	13.5	9.3	7.9	0.8		
pallida				1.0	3.3	2.2
obscura					1.6	0.9

Table 16. Regressions of fecundity (F) on standard length (mm SL) for all species.

Species	Equation	r^2	p	n	F
braueri	$\log F = 4.08 \log SL - 3.26$	0.67	.0001	112	220.64
microdon	$\log F = 2.25 \log SL - 0.41$	0.41	.0001	52	35.12
pseudopallida	$\log F = 3.51 \log SL - 2.64$	0.61	.0001	38	55.18
acclinidens	$\log F = 3.54 \log SL - 2.68$	0.26	.002	36	11.84
pallida	$\log F = 2.94 \log SL - 1.78$	0.30	.0001	68	28.15
livida	no significant regression			84	
alba	$\log F = 3.44 \log SL - 2.59$	0.38	.0001	41	24.35
obscura	$\log F = 2.68 \log SL - 2.07$	0.12	.05	33	4.20

Figure 67. A schematic comparison of the trends in a) length of life of females and b) the timing and length of spawning season among species of the genus Cyclothone. Solid lines indicate probable periods and dashed lines indicate time periods suggested by the data but not confirmed.

a



b

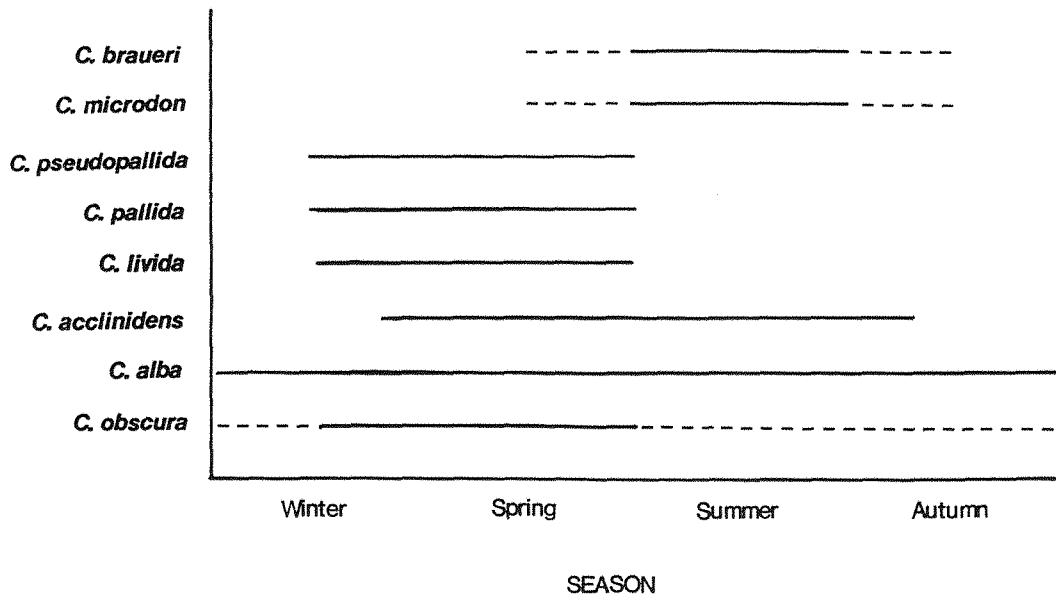
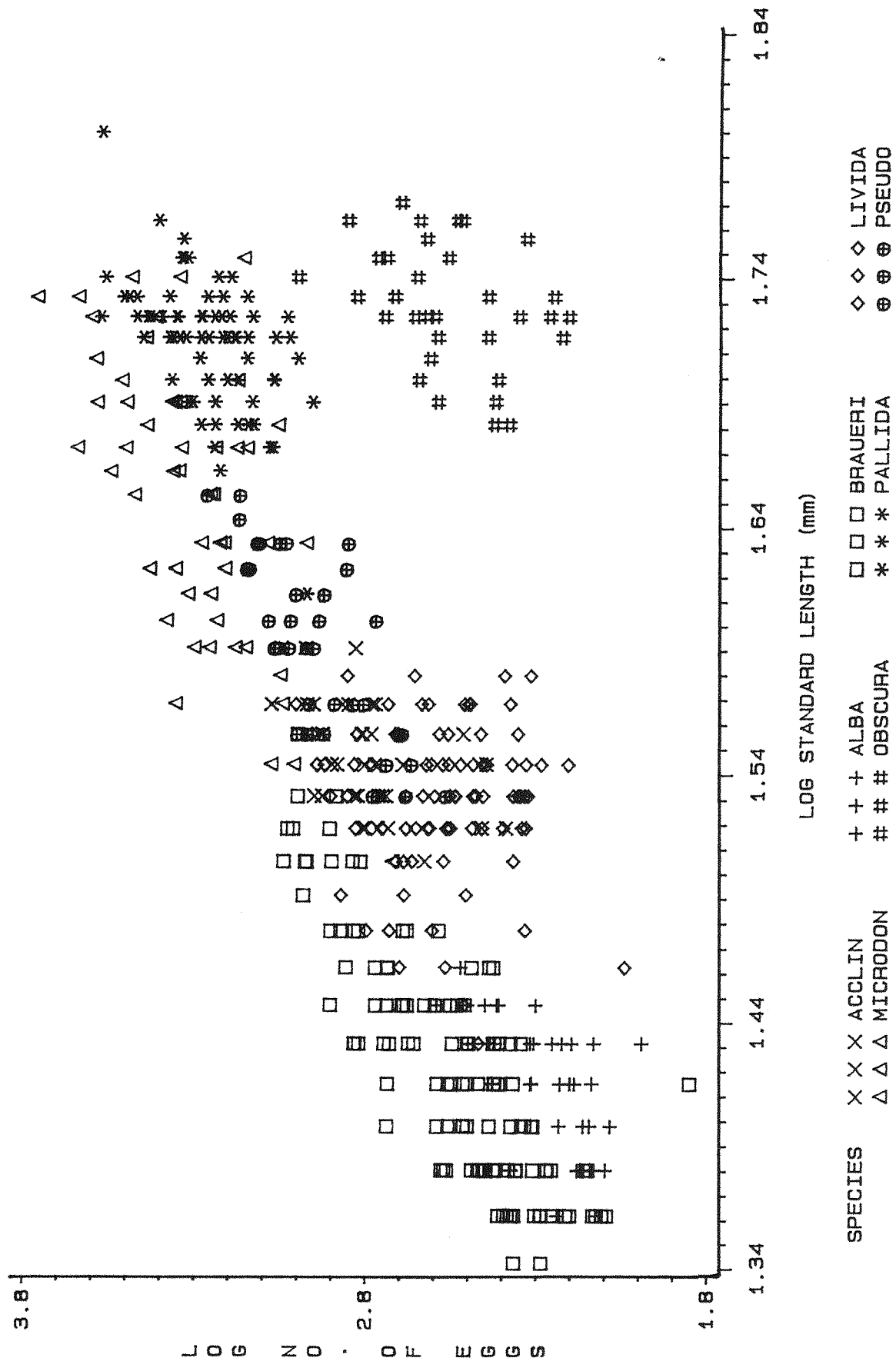


Figure 68. A comparison of the log number of eggs vs. the standard length of all species regardless of latitude.



Chapter 4

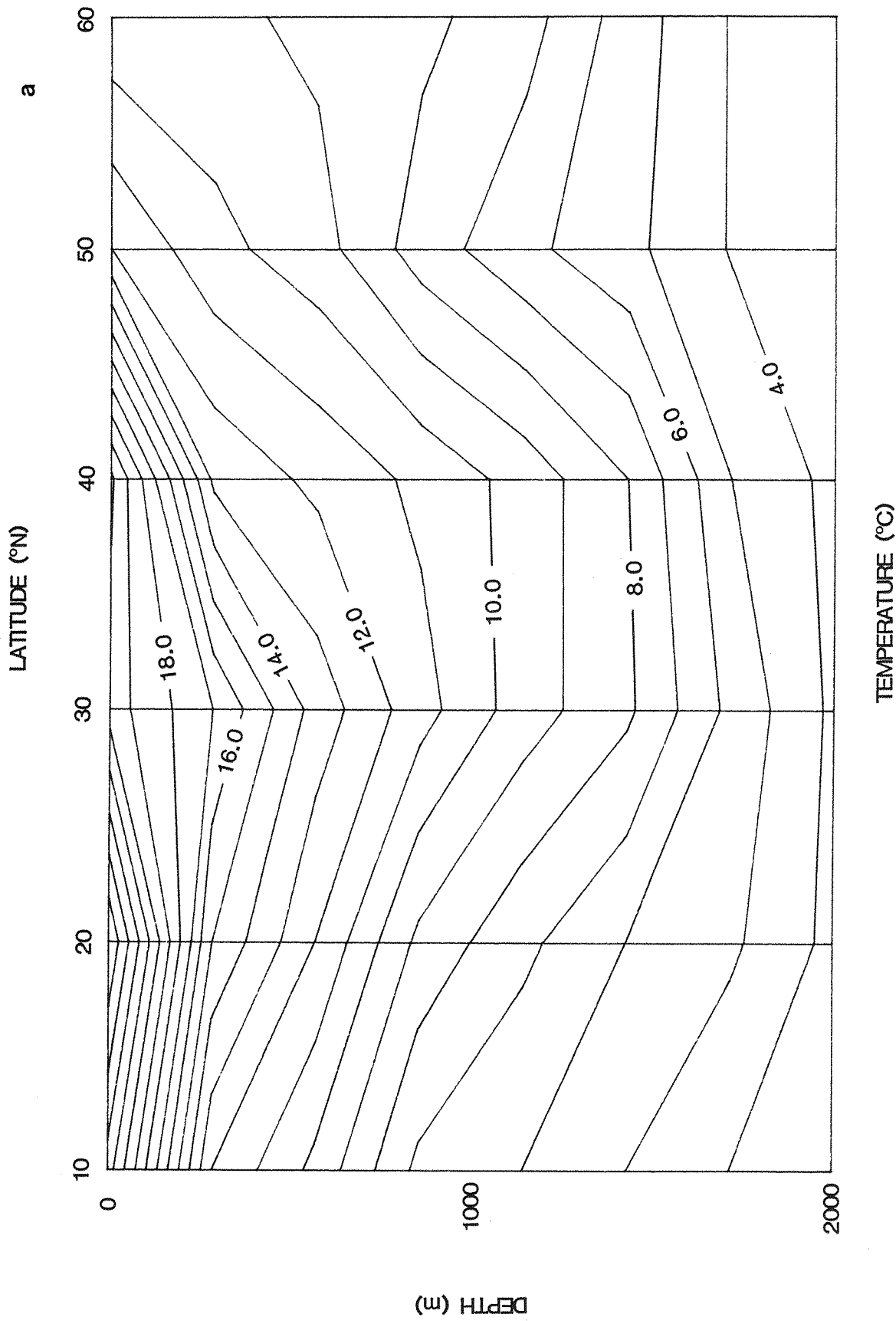
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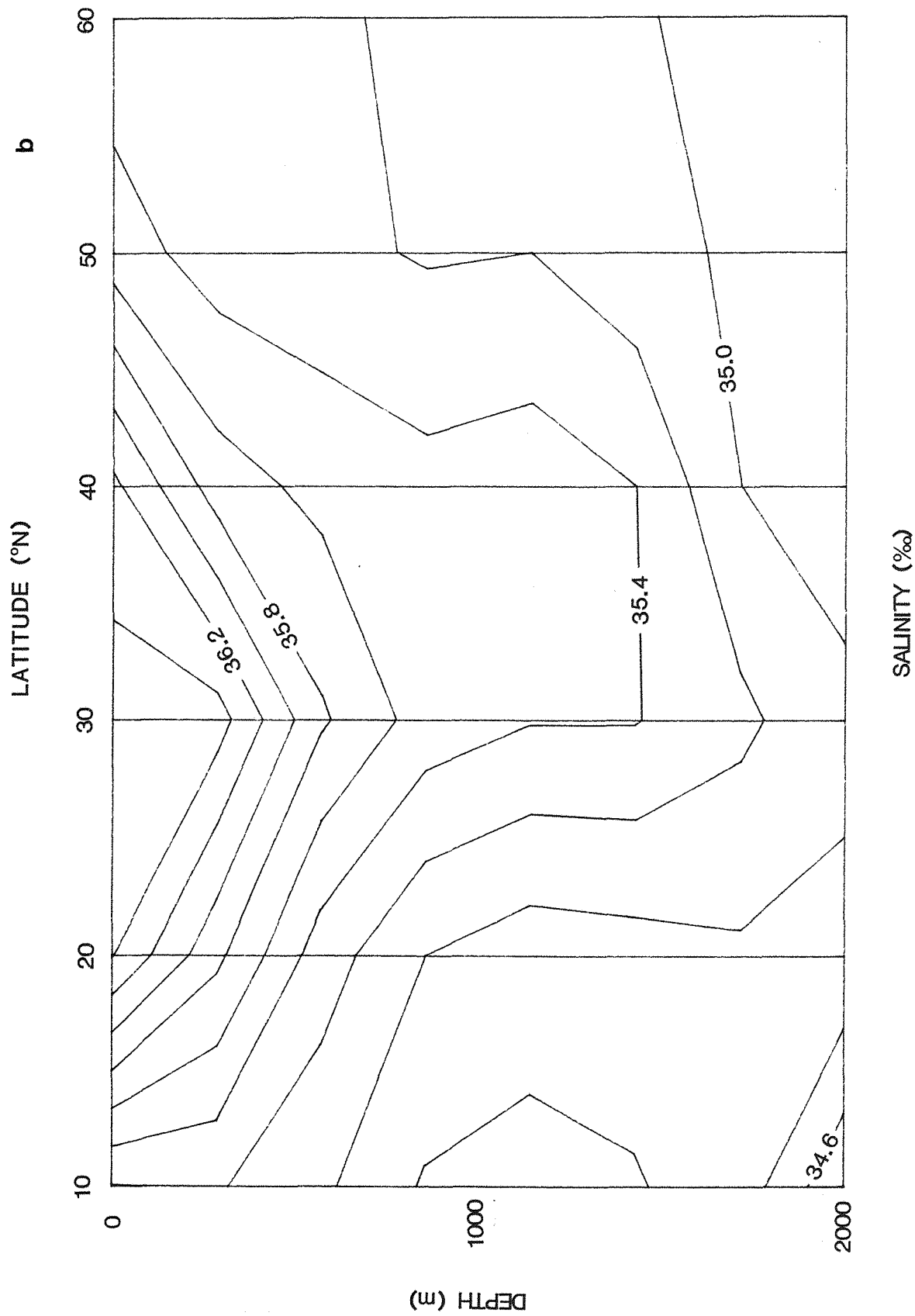
4.1 Environment

To analyse latitudinal variability in the biology of Cyclothone it is necessary to consider how the physical and biological variables change along the transect. The most obvious variables to examine are temperature and salinity. Temperature remains relatively constant at the depths which Cyclothone inhabit in the area, particularly below 1000m (Fig. 69a). At depths of 400-500m the warmest temperatures have been recorded at approximately 30°N with similar temperatures found at 10°N and 60°N. Salinity is very similar with the lowest values at the extremes of the transect and much higher values at mid-latitudes due to the influence of the Mediterranean Outflow (Fasham and Angel 1975, Fasham and Foxton 1979, Fig. 69b).

A combination of temperature and salinity can be used to define the different water masses in the area (Sverdrup et al. 1942). Three sections can be distinguished by an examination of the water masses. The boundaries dividing the sections are at latitudes of approximately 44°N and 18°N.

Figure 69. Contours of physical parameters along the transect.
a) Temperature vs. depth (contour interval 1°C).
b) Salinity vs. depth (contour interval 0.2‰).





The boundary at 44°N marks the northern limit of the subtropical gyre (Fasham and Foxton 1979). The North Atlantic Current splits at approximately this latitude and one branch moves north and the other south (Gould 1983). North Atlantic Central Water (NACW) predominates north of this boundary (Sverdrup et al. 1942). Below 1000m, North Atlantic Deep Water is found (Fasham and Angel 1975).

South of 44°N NACW still plays an important role (Sverdrup et al. 1942). However, the Mediterranean Outflow introduces enhanced variability in this area (Gould 1983). The core of this latter water mass occurs at a depth of approximately 1000m and it influences the water column between 500 and 1200m (Fasham and Foxton 1979, Gould 1983). Below this the water column is dominated by North Atlantic Deep Water (Fasham and Angel 1975). At depths less than 400m there is some mixing of South Atlantic Central Water with the NACW (Fasham and Angel 1975). Generally this section of the transect between 20°N and $44\text{--}45^{\circ}\text{N}$ is an area of mixing water masses.

At 18°N the boundary represents the northern edge of the South Atlantic Central Water at depths of less than 400m (Voituriez and Chuchla 1978). Below 400m, Antarctic Intermediate Water is found (Mamayev 1960, Fasham and Foxton 1979).

Mid-latitudes along this transect have been described as oligotrophic (Angel 1979) with higher surface productivity both at higher and lower latitudes (Koblentz-Mishke et al. 1970). Recent measurements suggest that primary production in the oligotrophic ocean may be higher than previously estimated (Pace et al. 1987). Merrett (1987) suggests that overall productivity in the eastern North Atlantic may be similar and the main difference between the two areas either side of 44°N is in the seasonality. At northern latitudes the productivity is highly seasonal (Colebrook and Robinson 1965, Robinson 1970, Colebrook 1979). At mid-latitudes the surface waters are permanently stratified implying less seasonality (Merrett 1987). Annual productivity south of 18°N is suggested to be similar to that of the northern extent of the transect (Koblentz-Mishke et al. 1970) although it differs in being constant with no seasonal peak (Williams 1984). However, at this longitude the area is near the area of high

productivity associated with the Guinea Dome (Voituriez and Dandonneau 1974) so productivity is probably higher than the generalized value suggested by Koblentz-Mishke et al. (1970).

The distributions of many groups of pelagic organisms have been related to the water masses in the eastern North Atlantic. The results indicate that faunal change occurs at 18°N (Backus et al. 1965, 1970, Foxton 1970, 1972, Fasham and Angel 1975, Badcock and Merrett 1977, Fasham and Foxton 1979) and at 44-45°N (Fasham and Angel 1975, Angel 1979, Fasham and Foxton 1979) coinciding with the boundaries of the water masses described above.

The northern zoogeographic boundary does not affect the distribution of Cyclothone although C. braueri did increase in abundance south of 40°N. Faunal change occurred at latitudes around 18°N where C. braueri and C. microdon give way to the more southerly distributed species. Biomass and density also underwent the greatest change at this latitude.

4.2 Species Accounts

4.2.1 C. braueri

A bimodal length frequency distribution is commonly reported for C. braueri (Jespersen and Taning 1926, Bond 1974, Zingone 1981, Badcock and Merrett 1976). Bond (1974) and Badcock and Merrett (1976) examined the sex and maturity of individuals within the population. They found the first peak to be made up of males and subadult females and the second peak to be mature females as was found in this study.

The presence of larger individuals at higher latitudes has been shown before (Koefoed 1960, Badcock and Merrett 1976). However, no latitudinal comparisons have been made with size at maturity. Other studies have been undertaken at latitudes equal to the lower latitudes of this study, Bond (1974) off Bermuda, Jespersen and Taning (1926) in the Mediterranean and Spanovskaya and Grigorash (1978) at 30°S in the Pacific. Size at maturity at these locations was 20-22mm SL similar to the 20mm SL found at the lower latitudes in this study.

Bond (1974) also found high seasonal variability in the sex ratio off Bermuda ranging from 1.2 females to every male to 19 females to each male. The larger range could be due to the fact that he did not distinguish immature and mature females past a category of subadult or adult. He did agree that the variation was due to males dying shortly after spawning. Badcock and Merrett (1976) found that if only stage VI females and mature males with enlarge nasal rosettes were included the ratio was approximately even. They even suggested the possibility that running ripe males were more abundant than ripe females as did Marshall (1967). Spanovskaya and Grigorash (1978) also suggest a 1:1 ratio in aggregations of fish close to spawning.

The variability in spawning period among published work is consistent with the dependence of spawning period on environment. Spring/summer spawning has been reported in the Mediterranean (Jespersen and Taning 1926, Zingone 1981). Goodyear et al. (1972) suggest that spawning time is even more localized in the Mediterranean as differences exist between the eastern and western sections. Off Bermuda, spawning occurs slightly sooner, starting in the winter and ending late in the spring (Bond 1974). In the south Pacific spawning is in the summer, beginning in January (Spanovskaya and Grigorash 1978). All studies report an annual period rather than year round spawning although it is generally agreed that spawning is protracted.

There is little agreement on the number of spawnings within the lifetime of a female. Badcock and Merrett (1976) concluded, as does the present study, that females spawn once, probably in the second year of their life. Bond (1974) concluded that the females spawned

twice at sizes represented by the two peaks in the length frequency distribution. However, mostly subadults and few adults were found at standard lengths where the smaller peak in abundance was found suggesting that if spawning occurs at this size it is only of very limited occurrence. Spanovskaya and Grigorash (1978) found evidence of more than one size class of egg in the ovaries of females and concluded from this that they spawned more than once a year but gave no indication of how many years this was repeated. The presence of two egg sizes in the ovaries does not necessarily prove that more than one spawning is likely to occur (Nikolsky 1963). Only one size class of egg was found within a female in this study as well as by Badcock and Merrett (1976). Badcock and Merrett (1976) also report that the ovaries of spent fish were empty sacs suggesting that all eggs within a female are spawned simultaneously.

Few fecundities have actually been reported. In all cases variability was high and regressions were not calculated. The ranges were usually comparable although they were not as broad as those found here as a result of the large area sampled (Table 17). Badcock and Merrett (1976) made latitudinal comparisons between 30°N and 42°N and found that fecundity was higher at 42°N where productivity was higher. The results of this study suggest fecundity peaks at this latitude and declines further north. There is some indication that C. braueri may extend the lower limits of its depth distribution at 40°N (Badcock and Merrett 1977).

4.2.2 C. microdon

Only two studies have placed boundaries on the spawning period of C. microdon. Bond (1974) reported that C. microdon spawned from January to June off Bermuda, a much earlier timing than that found here. Badcock (1984) suggests a period of summer to autumn in the eastern North Atlantic and Mediterranean, only slightly less extensive than the spring to autumn period that appeared to be the case in this study, possibly because of the larger geographical range over which

Table 17. Reported fecundities of C. braueri.

Size (mm SL)	Fecundity Range	Max. Egg Size (mm)	Reference
24-29	218-416	0.50	Badcock and Merrett 1976
-----	200-300	0.30	Jespersen and Taning 1926
30-35	1000	0.46	Murray and Hjort 1912
17-31	170-671	0.48	Spanovskaya and Grigorash 1978
24-36	163-1096	0.54	this study

samples were taken.

The prolonged spawning period is thought to be responsible for the lack of modality within the length frequency distribution (Bond 1974). Bond (1974) and Badcock and Merrett (1976) agreed that females live through at least two spawnings although Bond (1974) assumed the second spawning took place in the second year. Badcock and Merrett (1976) showed that spawning occurs later in life due to protandrous sex reversal.

In most species that undergo sex reversal from males to females the sex ratio is usually skewed in favour of males (Kawaguchi and Marumo 1967, Sadovy and Shapiro 1987). However, this is not the case with C. microdon where skewed ratios of three females to each male were also reported by Bond (1974). He postulated that this was due to the females being longer lived than males as he was unaware that sex reversal occurred in the species.

Although an increase in size with latitude was equivocal in this case, Spanovskaya and Lapin (1981) have found larger individuals at higher latitudes in the south Pacific. The reported size at maturity of 30mm SL at other locations (Koefoed 1960, Bond 1974, Spanovskaya and Lapin 1981) is lower than that found at all stations in this study.

Few fecundities have been measured. Badcock and Merrett (1976) found no relationship with length and no change with latitude with females having 2000-3000 eggs at size of 0.3mm. Murray and Hjort (1912) estimated as many as 10,000 eggs of 0.46-0.56mm from one specimen.

Although the distribution of C. microdon appears to be unaffected by the zoogeographic boundary reported at 44-45°N by Angel (1979) some differences appear to exist on either side of this latitude. At higher latitudes, C. microdon shows many of the characteristics that Zurbrigg and Scott (1972) claim suggest expatriation. Adults were larger, possibly due to somatic growth, no post-larvae (unpublished RMT-1 data) and relatively few juveniles were found, females with

ovaries generally only had small oocytes less than 0.2mm and such counts of eggs as were possible gave lower values than those at 40°N. Cyclothone microdon has been reported to be expatriate at higher latitudes in the South Atlantic (Spanovskaya and Lapin 1981). Another factor that could support expatriation at high latitudes was the scarcity of males at 50 and 60°N which reduces the spawning possibilities. The specimens at high latitudes also had large fat deposits in their body cavities which were not present at lower latitudes possibly suggesting that excess energy is stored for over-wintering rather than put into reproduction. The northerly flowing branch of the North Atlantic Current at this latitude (Gould 1983) could act as a mechanism to ensure constant recruitment from the south. Other species of fish (Kawaguchi and Mauchline 1982) and some crustaceans (Mauchline 1985,1986) have been suggested to be expatriates from samples north of 50°N. However, the highest densities of C. microdon were found at 60°N in the spring (Fig. 3). This suggests a large proportion of the breeding population could be lost unless there is some recruitment of these individuals back into areas where reproduction is possible. However, no mechanism is evident for transport of individuals to areas within the breeding range.

4.2.3 C. pallida

Miya and Nemoto (1987a) found a similar length frequency distribution for C. pallida as that found in this study. The size classes at the lower standard lengths are generally well represented whereas at higher standard lengths distribution is patchy with many size classes not represented or present at only low abundance (Miya and Nemoto 1987a, Fig. 2).

Miya and Nemoto (1987a) estimated that males did not mature until their third or fourth year and females did not mature until their fifth or sixth year, later than estimated here. They also concluded that females grew faster than males. In this study, males and stage I females were present at the same standard length. This suggests there

is no difference in age or growth rates of males and females and that differences in size were due to differences in life span. Females matured in their next year so that age at maturity of females was only one year more than that of males. Males appear to die after their first spawning as there was no evidence of more than one size class. The size at maturity reported in Sagami Bay (Miya and Nemoto 1987a, 40-45mm SL) and in other studies (Bond 1974, Badcock and Merrett 1976, Maynard 1982) was similar to that found in the spring although the size in the autumn was much lower than any previously reported.

Spawning time is related to location. A winter/spring spawning period was found in this study and was thought to be the case off Bermuda (Bond 1974). In Sagami Bay, Japan, spawning is later in the spring to summer period (Miya and Nemoto 1987a).

Sex ratios have only been reported off Bermuda. Bond (1974) found slightly higher sex ratios, the lowest was 2.3 females to each male and this varied to a high of 6.8:1 in the winter pre-spawning period. He concluded that the skewed sex ratio was due to the females being longer lived.

Fecundities in the eastern North Atlantic were similar to those found off Japan (Miya and Nemoto 1987a) however they conclude that there was no relationship between fecundity and standard length although they only had six counts. Those recorded off Hawaii (Maynard 1982) are similar to the lower fecundities found at the lower latitudes in this study.

4.2.4 C. pseudopallida

C. pseudopallida was found to have an earlier spawning period than in other areas. A peak of spawning in the summer months was found both off Bermuda (Bond 1974) and in Sagami Bay, Japan (Miya and Nemoto 1986a) as compared to the winter/spring suggested here. Maynard (1982) found no clear spawning season off Hawaii.

The size at maturity in the spring was similar to that found by Bond (1974, 28mm) and Miya and Nemoto (1986a, 30.7mm SL). However, mature females were found at sizes as small as 22mm SL in the autumn, much smaller than those reported in the literature.

There is general agreement that C. pseudopallida spawns more than once in its life span (Bond 1974, Badcock and Merrett 1976, Maynard 1982, Miya and Nemoto 1986a). Bond (1974) suggests that a second spawning takes place as early as the second year of life in females at sizes of 35+mm SL. As in this study, Miya and Nemoto (1986a) conclude that spawning is not reached until approximately age three, although some females may mature earlier (see 20°N autumn). There was no evidence of males living more than two years and spawning more than once whereas Miya and Nemoto (1986a) suggest that males live for up to three years. The shorter life in males is consistent with a sex ratio greater than 2:1 in favour of females.

As with the other species, the fecundities recorded here were similar to those found by Miya and Nemoto (1986a). Their results did suggest less variability ($r^2=0.784$) than was present in the eastern North Atlantic ($r^2=0.61$).

4.2.5 C. livida

This species has not been studied in any detail in the past. Badcock (1984) only reports that it is dioecious. The distribution of this species has been thought to be associated with oceanic islands (Badcock 1984) which could suggest that it is much more vulnerable to isolated local environmental fluctuations. This could account for the large amount of variation in fecundity.

4.2.6 C. acclinidens

The only other study that examined the biology of C. acclinidens was off Bermuda. Bond (1974) found a similar very prolonged spawning period from January to September. Females were mature at 30mm SL off Bermuda, similar to that from the spring samples but slightly larger than in the autumn. A skewed sex ratio was found (males:females, 1:2.7) which was approximately the same as sex ratios of C. acclinidens in the present study. Ripe females were present in Sagami Bay but population densities were so low that Miya and Nemoto (1987a) questioned whether reproduction occurred regularly because of the low probability of mate location.

4.2.7 C. alba

Maynard (1982) found no seasonal patterns in development and suggested there was no clear spawning period as indicated by the present study. However, Miya and Nemoto (1986b) report clear seasonality in the spawning of C. alba in Sagami Bay with spawning most likely between April and September. Bond (1974) had only small samples but suggested a summer spawning period. Miya and Nemoto (1986b) suggest the differences are due to the amount of seasonal variability in the surface waters where the larvae spend their early life. They suggest seasonal spawning occurs where there is seasonal variability in the surface waters, as off Japan, whereas off Hawaii surface waters are much more stable allowing continuous spawning.

Some factors were similar between this study and that of Miya and Nemoto (1986b). Size at maturity of females was the same as was the conclusion that this species is semelparous. Fecundities were higher both in Sagami Bay and off Hawaii (Maynard 1982). Miya and Nemoto (1986b) suggested that the similarity between the fecundities they found and those reported by Maynard (1982) indicated that fecundity was genetically controlled. This seems to be a rather hasty conclusion based on this premise alone.

Miya and Nemoto (1986b) suggest ages of up to two years and two spawnings in a lifetime. A single season and a one year lifespan seems more probable. C. alba appear to hatch at sizes of 3.5-6.0mm as that is the size they are first found in the plankton (Gorbunova 1971). Miya and Nemoto (1986b) suggest it takes 2-3 months to grow and descend to adult depths. The smallest size taken at adult depths is 10-12mm SL suggesting a growth of at least 4.0mm in 2-3 months. It seems unlikely that 14-15mm SL fish can be almost a year old as appears to be the suggestion of Miya and Nemoto (1986b). This would suggest a further growth of only approximately 4.0mm in the next 9-10 months. Perhaps ages were overestimated resulting in lower growth rates (see Growth and Age).

4.2.8 C. obscura

Bond (1974) suggested an autumn/winter spawning period for C. obscura although he based this on only 7 individuals. This conclusion differs from the winter/spring peak in spawning that was suggested here. Bond (1974) found the depth range off Bermuda to be between 1200 and 1700m. Badcock (1984) suggests C. obscura can be found as deep as 3000m. In the light of Bond's (1974) results, a maximum depth of sampling of 2000m in this study may not have missed a significant proportion of the population as was originally suggested (see Results). Although two of the other deep-living species are hermaphroditic (C. microdon, Badcock and Merrett 1976, C. atraria Miya and Nemoto 1985) there was no evidence of sex reversal in this species.

4.3 Spawning Season

Gjosaeter and Kawaguchi (1980) concluded that species at higher latitudes and shallower depths tend to have a better defined spawning season than species at lower latitudes and deeper depths. This seems to be true in Cyclothone. The spawning period appeared to be extended at lower latitudes within C. braueri. It was also more difficult to put estimated bounds on spawning periods in species at southern latitudes although this could be related to fewer locations being available for comparisons. At 10°N it appeared that C. alba spawned throughout the year and it also is possible that spawning occurs throughout the year in a small proportion of the population of C. obscura although the evidence is not conclusive. On the basis of the pattern of capture of Cyclothone larvae at 20°N, 20°W John (1986) has suggested that seasonal spawning is unlikely in that area.

Similar variations in spawning time have been noted in other widespread species. Maurolicus muelleri spawns over a 6 month period in the Rockall Trough as compared to a 5 months period off Norway and throughout the year in the Mediterranean (Kawaguchi and Mauchline 1987). Robertson (1976) also suggested that the duration of spawning season of M. muelleri varied with locality. Gjosaeter and Kawaguchi (1980) postulate that a greater variation in spawning time is evident in the gonostomatid fishes than in the myctophids.

Clarke (1973) suggested that spawning is timed to coincide with the seasonal peak in the abundance of zooplankton which could explain the longer spawning time at lower latitudes where there is less seasonality. Miya and Nemoto (1986b) suggest differences in spawning time among populations of C. alba are related to the seasonality of food availability for the larvae and juveniles. In the eastern North Atlantic there appears to be a lack of seasonality in production south of approximately 44°N (Merrett 1987). This makes it unlikely that

spawning time is co-ordinated with seasonal peaks in food availability alone. The possibility that C. microdon is expatriate north of 40°N, where production is seasonal, could be a reflection of its inability to adapt to a discrete pulse in food availability without other extraneous environmental cues.

There seems to be little indication of multiple spawnings within a season in mesopelagic fishes other than for C. braueri (Spanovskaya and Grigorash 1978) as mentioned previously. Clarke (1974) suggested it was possible in Gonostoma ebelingi and Badcock and Merrett (1976) for C. pseudopallida although evidence was lacking. Clarke (1984) found only circumstantial evidence for multiple spawning among 34 species near Hawaii. Considering that eggs in females tend to be approximately all the same size and that the ovaries of spent females are empty sacs rather than containing developing eggs, it seems unlikely that species of Cyclothone in the eastern North Atlantic are multiple spawners.

4.4 Fecundity and Egg Size

The egg size of Cyclothone (0.5-0.6mm diameter) is relatively small compared to most marine fishes as the smallest eggs known to produce viable larvae are 0.37-0.40mm, reported by Marshall (1971) in the genus Mytichthys. A spawning egg size of 0.5-0.6mm is common among many species of myctophids and within the genera Vinciguerria, Valenciennellus and Melamphaes (Clarke 1984). Egg size is related to the larval size at hatch (Ware 1975) so many mesopelagic larvae must also be of a similar size. This suggests that the larvae share the same environment as larval size is related to factors such as the size spectrum of food particles, the size and abundance of predators and the abundance of competitors (Svardson 1949). The similarity in egg size makes it easier to compare fecundities among species.

The highest fecundities among the species studied were found within species that occurred further north. C. braueri and C. microdon had the highest relative fecundities. Miya and Nemoto (1986b) report that C. braueri, along with C. alba, has the lowest fecundities among Cyclothone. The higher absolute fecundities appear to be related to size and latitude rather than depth suggesting that similar processes determine fecundity regardless of depth of occurrence.

The fecundities for species of Cyclothone found here are similar to those of many mesopelagic species that are approximately the same standard length (cf. Clarke 1984). Other species show indications of fecundity varying with habitat. Maurolicus muelleri has a higher fecundity in warmer regions where it is also smaller in size (Kawaguchi and Mauchline 1987). However, where fecundity is lower individuals have a higher reproductive lifespan, spawning more than once whereas females spawn only once where fecundity is higher, as in the Rockall Trough. Clarke (1984) found lower fecundities within individuals of a species where food concentrations were lower. Similarly, fecundity in Cyclothone could be related to food availability. The highest fecundities for C. braueri and C. microdon were found at 40°N which sustains a slightly higher biomass of prey items than at the other latitudes sampled (displacement volume of micronekton between 0 and 900m at 20°N=13.1, at 42°N=34 at 49°N=20.9, Angel and Baker 1982). Fecundity at higher latitudes could be also be affected by the more seasonal availability of prey (cf. Merrett 1987).

The wide variability in fecundity within a species at any one location and standard length could suggest that the number of eggs is sensitive to localized availability of resources (Hislop et al. 1978).

4.5 Sexual Dimorphism and Protandry

One factor common to all species of Cyclothone is sexual dimorphism with respect to size. In all species females are larger than males. Miya and Nemoto (1986b) state that sexual dimorphism results from two possible processes depending on the species, protandry or an earlier decline in growth rate among males. Badcock and Merrett (1976) and Marshall (1967) suggest the possibility that the sexual dimorphism is due to the males being shorter lived.

The results are not consistent with an early decline in growth rate among males. The first sexable peak (i.e. not juveniles) in all species was made up of males and stage I females. It is likely that these represent the same age class regardless of the length of time spent as juveniles suggesting a similar growth rate in males and females. Males matured at this age, spawned and died as there was never any indication of two size classes within the male population. Females did not mature until the following year and lived longer. The skewed sex ratios in favour of females are also consistent with females being longer lived (Bond 1974). Therefore the primary cause of sexual dimorphism appears to be longer lived females.

Ghiselin (1974) suggests two factors that increase the evolutionary pressure for smaller males, a sparse food supply and low density. A low food supply results in different strategies for the males and females. In fish, egg production is directly related to adult size (Nikolsky 1963) so egg production is maximized if females are large. In Cyclothone, females appear to put most of their energy into growth and egg production. These larger females have a reduced motility, possibly due to a lack of available energy. Male reproductive success is not size related so males mature early at a small size and therefore have more energy for movement and mate location. This is supported by the higher amounts of red muscle found in males as

compared to females (Marshall 1971). Both sexes reduce maintenance costs by progenesis, precocial maturation with adults retaining many 'larval' characters (Marshall 1984).

A second factor which can select for reduced size in males is low density. A low density increases the difficulty and increases the cost of finding a mate. The increased motility necessary for males increases their energetic requirements and a smaller size may allow more energy to be used in mate location as outlined above. As prey biomass decreases with depth (Angel and Baker 1982), males may occupy a shallower depth distribution (Badcock and Merrett 1976, Miya and Nemoto 1986a,b 1987a,b) to obtain sufficient energy to undertake mate location. The cost of this shallow depth distribution may result in a shorter lifespan, possibly due to an increased predation rate as a result of a higher concentration of predators at shallow depths.

Protandry probably evolved from sexual dimorphism rather than being the cause of it. According to Ghiselin (1974) hermaphroditism is a special case of sexual dimorphism. As outlined above, all male Cyclothone attain sexual maturity at a smaller size than do females, which are evidently older. Protandry is unlikely to cause the delay in maturation as suggested by Miya and Nemoto (1986b). It is more likely a character derived from delayed maturation. As mature males and females do not overlap in size to be a male first and then switch to being a female would maximise the possibilities of contributing genes to the next generation. It is not necessary to delay maturation further as overlap between the mature stages of the two sexes does not occur regardless of whether or not a species is protandrous.

Protandry can be explained by the size advantage model (Ghiselin 1969). In this model sex change is favoured when an individual's reproductive success is closely related to age or size and the relationship is different for each sex. For Cyclothone, large size in females allows an increased egg output but does not aid males in their competition to fertilize eggs. These factors favour an individual being a male first and a female second. The cost of sex reversal is in the energy cost required to mature twice and a possible loss in breeding time (Charnov 1982). These costs are reduced in Cyclothone as

males and females do not overlap in size so there is no loss in breeding time. However, it could result in a reduced growth rate as more energy is put into gonad production at a smaller size. This could contribute to the smaller size at maturity of the protandrous species C. microdon and C. atraria (approx. 40mm SL Miya and Nemoto 1987b) as compared to C. pallida and C. obscura. What cannot be deduced from this model is why the other species do not reverse sex as similar factors would seem to apply to all species.

4.6 Sex Ratio

Sex ratios skewed in favour of females are thought to maximise egg production (Ghiselin 1974, Clarke, T.A., 1983) and evolve as a response to low food availability (Mednikov 1961, Young et al. 1987). Cyclothone is similar to other species in that where females are more abundant than males the females are generally larger in size (Clarke, T.A., 1983, Young et al. 1987). The proximate cause of skewed sex ratios in Cyclothone is the longer lifespan of females (Bond 1974). There is variability among species both seasonally and latitudinally due to differences in spawning time but pre-spawning sex ratio generally appears to be approximately two females to every male. Other variations appear to be due to differences in the timing of post-spawning mortality between the sexes (Bond 1974, this study). The very high sex ratios found within C. microdon at the northern extent of the sampling area could be related to the possibility of expatriation.

4.7 Growth and Age

A comparison of growth rates found by Miya and Nemoto (1986a,b, 1987a) with those of other species reported by Childress et al. (1980) shows extremely slow growth rates compared to both mesopelagic and bathypelagic species. Considered in terms of their depth distribution and that they do not undertake vertical migration they should have relatively high growth rates (Childress et al. 1980). A maximum age for the larger species of 4-5 years which seemed possible for some species in this study rather than the 8-9 years suggested by Miya and Nemoto (1987b) would give equivalent growth rates to Stenobrachius leucopsarus and Triphoturus mexicanus (Childress et al. 1980, Figs. 1 and 2). It is possible that Miya and Nemoto (1986a,b, 1987a) could have overestimated the ages.

There must be some question as to the accuracy of their ages due to the techniques used. Miya and Nemoto (1986a,b 1987a) used a graphical method describe by Cassie (1954) to estimate ages from length frequency distributions. The main problem with this method is that it is not reproducible suggesting that some preconceived ideas about the biology is necessary (Macdonald and Pitcher 1979) or that much is dependent on interpretation. A problem specific to this case arises from the prolonged spawning periods reported for each species. This results in increased overlap in size between age classes. Length frequency analyses are best used when spawning occurs over a relatively short period (Pollock 1982) or when recruitment occurs in relatively discrete pulses (Grant et al. 1987). The prolonged spawning periods of Cyclothone and the resultant increase in overlap between age classes decreases the probability of accurately assessing age (Grant et al. 1987). Even the more advanced technique used for their study of C. atraria (Miya and Nemoto (1987b) based on Hasselblad (1966) is affected by these difficulties. Hasselblad (1966) admitted that estimation was difficult if the means of the size classes were separated by less than two standard deviation units. Grant et al. (1987) suggest this should be extended to three standard deviation units. Possible age classes of species of Cyclothone are not separated by this amount. Other problems with these techniques

include the necessity for large sample sizes (Cohen 1966, Macdonald and Pitcher 1979, Grant et al. 1987), the approximate number of age classes should be known Cohen (1966) and errors increase if the proportions in the age classes are not equal (Grant et al. 1987). Although the first criteria may be met the latter two cannot as independent estimates of age are not available and collection of some species are poorly represented at the larger size classes (e.g. C. pallida, this study and Miya and Nemoto 1987a).

Mauchline (1972) suggests that the growth rate of pelagic crustaceans is inversely proportional to latitude. The larger size attained by species with distributions centred around higher latitudes is thought to be due to a longer life span. The results suggest that growth rates in Cyclothone are lower at higher latitudes (see section 3.2.2.5). However, the maximum size of species at higher latitudes is either similar to, or lower than, the maximum size at low latitudes. Also, a longer life appears to occur in species at low latitudes.

These differences could be related to apparent differences in the growth rates of juvenile and larval Cyclothone species. At high latitudes, few juvenile size classes were evident. This suggests that at northern latitudes juveniles grow quickly, possibly maximising their energy intake during the seasonal peak in food availability. However, growth rate becomes greatly reduced in adults. At low latitudes there appears to be no ontogenetic difference in growth. Size classes of juveniles and adults were more or less equally well separated. In this way, growth rates at higher latitudes would be low, which is consistent with other studies (Mauchline 1972, Clarke, A., 1983) but maximum sizes could be similar due to the increased growth rate of juveniles at higher latitudes.

4.8 Life History Theory

Life history characteristics are thought to involve trade-offs among variables such as fecundity, size of offspring, reproductive lifespan, spawning season and spawning pattern (Mann and Mills 1979). Combinations of these variables result from variability in the survival of the juvenile and adult stages. If there is increased fluctuation in the mortality of immature fish then iteroparity is favoured to reduce the consequences of complete reproductive failure in one year (Murphy 1968). This results in reduced reproductive effort (reduced fecundity) in all individuals (Schaffer 1974). If the fluctuations occur in the adult population then reproductive effort is increased (increased fecundity) and a shorter lifespan is selected because of the decrease in probability of an adult surviving to breed in the next season (Schaffer 1974). This model has been termed bet-hedging (Stearns 1976).

Evidence suggests that most mesopelagic species at lower latitudes are smaller and shorter lived than those from temperate regions, and are semelparous (Mauchline and Fisher 1969, Clarke, T.A. 1973, Karnella and Gibbs 1977, Mauchline 1972,1977, Clarke, A. 1983,1987). In clupeoids, this pattern has been attributed to the stability of the tropics lowering the variability of juvenile survival (Murphy 1968). C. alba is the only species which fits this trend possibly because of its shallower depth range making it more susceptible to surface perturbations and variation and so more likely to experience selection pressures similar to those found in shallow-living fishes. The other species appear to be slightly larger, mature later, live longer and spawn more frequently than their temperate counterparts. According to the bet-hedging model this suggests either an increased variability in juvenile survival or a higher, more predictable, adult survival at lower latitudes. A number of points suggest variation in adult survival may be the case. It has been suggested that larval survival

should be enhanced at lower latitudes (Murphy 1968). Johnson and Barnett (1975) argue that egg size is genetically determined and that it should vary with productivity to maximize larval survival. This could be extended to suggest that since egg size in Cyclothone does not appear to vary with latitude, selective pressures on larvae are constant along the transect. Also, Johnson and Barnett (1975) concluded that there is no evidence of increased predation pressure on larval populations of midwater fishes in areas of higher productivity. These points suggest that variability in juvenile survival does not change along the transect examined. Adult survival could vary with the total production in surface waters as well as the seasonality of production (Merrett 1987).

In their study of growth, energy utilization and reproduction of pelagic fishes (Childress et al. 1980) divided the species they examined into two groups, mesopelagic migrators and bathypelagic non-migrators. Differences between the two groups were found in size, growth, length of life and reproductive lifespan. Cyclothone appears to be a link between these two groups. Although classified as a bathypelagic non-migrator by the criteria used by Childress et al. (1980) Cyclothone species tend to show more characteristics of the mesopelagic migrators such as small size, slow growth and repeated reproduction.

4.9 Dispersal and Gene Flow

The major problem with studies involving comparisons among geographic locations is that little is known about general dispersal, over time and space, of both adults and young. These factors must be considered since samples in the present study were only representative of a single location at a given time. As the larval phase is spent near the surface the young fish are probably dispersed over a

relatively large distance. This makes it unlikely that the smallest individuals captured at a given location were spawned from the adult fish surrounding them. Little is known about the dispersal distances of adults, partly because little is known about subsurface currents in the open ocean. From the few behavioural observations of the adults (Peres in Marshall 1960, Barham 1970) it appears they are not very motile suggesting they generally drift where the currents take them. The vertical distances that males must cover to locate a mate and their higher amounts of red muscle, suggests the smallest sizes are the most motile. The lack of meristic variation within a species of Cyclothone suggests gene flow is high since meristic variation in other species is thought to be genetic rather than ecophenotypic (Johnson and Barnett 1975, Johnson 1986). Therefore, isolated populations are unlikely even though the species is distributed over wide distances. If this is the case the intraspecific variation in this study suggests a degree of plasticity in the life history traits allowing individuals to make the most of the environment in which they find themselves.

Chapter 5

SUMMARY AND CONCLUSIONS

Differences exist in the biology of species of the genus Cyclothone among samples from different latitudes in the eastern North Atlantic. Intraspecific comparisons do not necessarily show the same trends as interspecific comparisons. Within a species, fecundity appears to peak at mid-latitudes and the maximum size attained by individuals, as well as the size at maturity, appears to be smaller at lower latitudes. Among species, fecundity is lower at lower latitudes but this appears to be offset by a longer life. Species whose distributions are centred at lower latitudes appear to mature at a larger size than species at higher latitudes.

These changes are linked with the known zoogeographic boundaries at 42°N and 18°N . However, these boundaries appear to affect the species within the genus in different ways. The zoogeographic boundary at approximately 42°N does not appear to affect species distributions, but either side of this latitude can be found differences in spawning time, fecundity, maximum size and other aspects of the biology of the species that cross it. The southern zoogeographic boundary at 18°N marks a complete change in the Cyclothone species present and separates the northern species from the southern species. This appears to be accompanied by changes in life-history strategies.

The results are limited by the practical difficulties of obtaining samples over a wide area and with suitable seasonal coverage. Although two sampling periods within the year is probably inadequate to accurately delimit the spawning period of a population, using a

range of variables such as size, stage of maturity and egg size of females in a comparative approach appears to have been successful for broad-scale comparisons.

Latitude is only a convenient method of marking where changes occur and is not a causative factor in itself. Although not exactly known, the ultimate cause appears to be related to both total production and food availability as well as the seasonal changes of these variables.

It is impossible to tell how large populations are or whether observed differences are controlled by environmental or genetic factors but, given the nature of dispersal and the possibilities for gene flow, environment would seem to play an important role in intraspecific variation within Cyclothone.

Chapter 6

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Appendix I. Station data.

Station	Lat. ° N	Long. ° W	Month	Max. Depth (m)	Gear
7709	60	20	4	2000	RMT8 *
7711	53	20	5	2000	RMT8 *
9801	42	17	5	2000	RMT8M
7856	30	23	5	2000	RMT8 *
9541	20	21	4	2000	RMT8 *
7824	11	20	3	2000	RMT8 *
10105	54	13	9	1500	RMT8M
7406	40	20	10	2000	RMT8 *
10222	33	30	10	1100	RMT8M
7089	18	25	11	1250	RMT8 *

* indicates estimated volume filtered