BIOLOGY AND PRODUCTION OF

<u>Nyctiphanes</u> <u>australis</u> G.O. Sars,

IN THE COASTAL WATERS OF S.E. TASMANIA.

by

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Submitted in fulfilment

of the requirements for the degree of

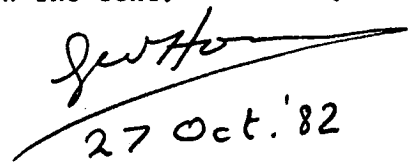Master of Science

UNIVERSITY OF TASMANIA

HOBART

October, 1982.

(conferred March 1983).

STATEMENT

Except as stated herein this thesis contains no

material which has been accepted for the award of

any other degree or diploma in any university.

To the best of my knowledge and belief this thesis

contains no copy or paraphrase of material previously

published and written by another person, except

where due reference is made in the text.

27 Oct.'82

CONTENTS

ABSTRACT

The euphausiid <u>Nyctiphanes australis</u> forms an important component of the zooplankton biomass in south-eastern Tasmanian coastal waters, particularly in Storm Bay where the species exists in high densities throughout most of the year. During the warmer spring and summer months, the standing crop of <u>N. australis</u> often exceeded the total copepod biomass. Rapid growth occurred throughout the year, with females reaching sexual maturity after 3 to 4 months. The total life span of <u>N. australis</u> is unlikely to exceed one year. The intermoult period increased exponentially with increase in body length and weight. Larvae moulted approximately every 2.5 to 3 days and large adults every 4 to 5 days at 15°C. A decrease in temperature from 15° to 10°C resulted in the intermoult period almost doubling. The mean weight of exuviae produced represented nearly 6% of the body dry weight of the individual. Continuous maturation of ova was observed, with an individual female capable of releasing a total of 1100 eggs in a life time. These are deposited as a series of batches into a pair of external ovisacs, every 30 days. The size of the batch of eggs was dependent on the size of the female. Stomach content analysis revealed that <u>N. australis</u> feeds on a broad spectrum of items, a large portion of which was detrital in origin. Monthly changes were observed in dietary components, which most likely reflects the availability of food items suspended in the water column (or settling at the sediment interface) at that particular time. There was little difference between the stomach contents of larvae and adults, despite the results of mouth parts analysis, which indicated that larvae are capable of utilizing a different food source. Two methods were used to calculate production of <u>N. australis</u>. An equation suited to animals with continuous release of larvae, gave a result of

78.29 mg m^{-3} yr^{-1}. A graphical method provided a comparable value

of 84.79 mg m^{-3} yr^{-1}. The calculated mean annual biomass was

5.39 mg m^{-3}, giving a P : B ratio, a measure of population turnover,

of 14.5. This value is much higher than previously recorded for

other euphausiid species. Moulting of euphausiids forms a significant

contribution of organic matter to detrital food webs. A value of

42.01 mg m^{-3} yr^{-1} was obtained for the production of exuviae. Egg

production was calculated to be between 1.41 and 4.22 mg m^{-3} yr^{-1}.

Thus, the total production integrated for the whole of Storm Bay,

was 124 mg m^{-3} yr^{-1} or 2,307 tonnes dry weight yr^{-1}, representing

an overall P : B ratio of 23.1.

ACKNOWLEDGEMENTS

I am extremely grateful to the following people and institutions for assistance and interest in this project :

Tasmanian Fisheries Development Authority, for the use of their patrol vessels F.P.V. "Freycinet" and F.P.V. "D'Entrecasteaux" skippered by Messrs. J. Woods and G. Darcey, respectively,

Skippers and crew of the Zoology Dept. vessel R.V. "Wobbegong", Messrs. R. Mawbey, B. Rumbold, R. Holmes, S. Reid,

Mr. A. Martin of the Marine Study Centre, Woodbridge, for the use of the F.R.V. "Penghana", skippered by Mr. S. Parkin,

Mr. J. MacGaughey for the use of his vessel "Impact" on several occasions, as well as for his keen interest in the study,

Messrs. N.G. Elliott, A.J. Dartnall, A.J. MacGifford, and W.L. Morgan for their assistance in the collection of field data,

Miss G.E. Fenton for helpful assistance and discussion,

Dr. D.P. Thomas of the Botany Dept., University of Tasmania for assistance in the identification of stomach contents,

Mr. S. Jager of Dover, for supplying the Mewstone Is. sample,

Mr. D. Mackinnon of the Marine Science Laboratories, Queenscliff, Victoria, for supplying the Pt. Phillip Bay sample,

Miss. H.P. Morton for both typing and proof-reading the text,

and to my fellow students and staff of the Zoology Dept. for their interest.

Special thanks are due to the following people :

My supervisor Dr. D.A. Ritz for his encouragement, advice, assistance and wit, as well as for giving me the opportunity to come to Tasmania to work on N. australis; Dr. R.W.G. White for his supervision in the absence of D.A.R.; and finally to my wife Karen, who not only assisted in the counting of the massive October 1980 sample, but also gave her unfading moral support throughout the study.

INTRODUCTION

Euphausiids occur in vast numbers in all oceans particularly in the
temperate and polar regions where they can represent as much as 30% of
the zooplankton biomass (Mauchline and Fisher, 1969). In tropical and
sub-tropical waters, euphausiids are known to comprise 8% of the total
macroplanktonic and micronektonic biomass (Roger, 1973b). Kulka et al.
(1982) claimed that euphausiids, together with copepods, form the bulk
of the marine zooplankton and as such are important links in the marine
food webs at intermediate trophic levels.

The importance of euphausiids in the diet of several species of whales
has long been recognised and Mauchline and Fisher (1969) noted that most
of the large marine predators, including commercially exploited species
of fish, feed directly or indirectly on euphausiids at some stage of
their lives. Considerable attention has, therefore, been given to the
trophic status of the euphausiids, as well as their general biology. A
detailed review of previous investigations was provided by Mauchline and
Fisher (1969), and has since been updated by Mauchline (1980).

Nyctiphanes australis is the most important neritic euphausiid in
south-east Australian waters (Blackburn, 1980; Dakin and Colefax, 1940;
Sheard, 1953,1965). Notably, it forms a very conspicuous component of
the zooplankton of Storm Bay, south-east Tasmania (Nyan Taw and Ritz,
1979), at times dominating the non-copepod zooplankton, both in terms of
numbers and biomass.

The species is known to be an important dietary component of several
species of commercial fish, e.g. barracouta Leionura atun (Blackburn,
1957), jack mackerel Trachurus declivis (Webb, 1976), Australian salmon
Arripis trutta (Malcolm, 1959), and skipjack tuna Katsuwonus pelamis
(unpublished observations). Blackburn (1957) proposed that fluctuations
in the success of the barracouta fishery in Bass Strait, were closely

linked with corresponding fluctuations in the availability of N. australis. The migratory mutton bird Puffinus tenuirostris is known to feed almost exclusively on this euphausiid while in the south-east Australian region (Morgan and Ritz, 1982).

The large numbers of predators that feed on N. australis indicates that this euphausiid occupies a key position in coastal food webs. A broad study was, therefore, instituted within the Zoology Department, University of Tasmania, to define the trophic status of N. australis. Part of this study is an investigation of the standing stocks and production of N. australis in south-east Tasmania and forms the basis of this thesis. In order to calculate production, aspects of the life history of the species, i.e. growth, moulting, and reproduction were examined. Definition of what a single species eats is also important when investigating food chains (Mauchline, 1977a). Thus, an examination of the dietary requirements of N. australis has also been included in the present study. Part of the work described in this thesis has been published (Ritz and Hosie, 1982).

PART ONE

LIFE HISTORY SECTION

CHAPTER 1

INTRODUCTION TO LIFE HISTORY SECTION

The genus Nyctiphanes is unique amongst the euphausiids in that all
4 species inhabit the shallow water neritic region, with limited geograph-
ical ranges (Talbot, 1974). Brinton (1962) noted that members of this
genus tended to be associated with regions of transition between warm and
cold currents, as well as areas of coastal upwelling. In Australian
coastal waters, N. australis is distributed between 31° and 44^OS latitude
and between 132° and 156^OE longitude (Blackburn, 1980). Markina (1976)
claimed that the range of the species extends as far as 125^OE longitude.
N. australis also occurs in coastal waters of New Zealand (Bartle, 1976;
Bary, 1956; Fenwick, 1976; Jillett, 1971).

Sheard (1953) considered N. australis to be sub-tropical with an
optimum temperature range between 12° and 18^OC. This species does, however,
experience wider ranges in temperature, varying from 9° to 21^OC, throughout
its distribution (Sheard, 1965). N. australis also tolerates a comparat-
ively wide span of salinity, ranging from 34.05 S^O/oo (Bary, 1956) to
35.59 S^O/oo (Sheard, 1965).

Nyctiphanes australis has been shown to undertake diurnal vertical
migration appearing in the surface at night (Bartle, 1976; Bary, 1956) and
swimming at greater depths during day possibly remaining close to the bottom.
Diurnal vertical migration is a common characteristic of euphausiids
(Berkes, 1976; Brinton, 1962; Fowler et al., 1972; Frost, 1932; Gros and
Cochard, 1978; Hickling, 1925; Hu, 1978; Lebour, 1925; Mauchline, 1965,1980;
Mauchline and Fisher, 1969; Roger, 1974, 1975; Sameoto, 1976a,1980).
Sheard (1953) noted that during winter adult N. australis tended to spend
most of the time at the bottom, with the larvae being somewhat more scattered
through the water column, but offered no supporting evidence. Blackburn
(1980) claimed on the other hand, that during winter in Tasmanian and
Victorian waters, all individuals over 5 mm in length showed the tendency

to remain at the bottom.

Like many other species of euphausiids, N. australis forms large dense aggregations or swarms, mainly during the period October to March. This behaviour has been linked with the breeding phase of the species (Sheard, 1953).

The life cycle of N. australis has been established by Sheard (1953) and reviewed by Fenton (1981) and Palmer (1978). The cycle is briefly summarised below. Eggs are deposited by the female into paired ovisacs attached to the last two thoracic legs, i.e. Nos. 6 & 7. The hatching stage is the pseudometanauplius which rapidly changes into a metanauplius. This stage is followed by 3 calyptopis stages often referred to as CI, CII, CIII and 3 furcilial stages, FI, FII, FIII (Sheard, 1953). Individuals then pass through post larval and adolescent stages before maturing as adults (Fig. 1.1). Each calyptopis stage represents 1 instar, while there are 6 possible instars in the FI stage, 15 in the FII and 7 in the FIII stages. The various instars of N. australis are illustrated in Palmer (1978). The larvae of N. australis do not necessarily pass through all the possible instars of the furcilial phase. In fact, various developmental pathways have been demonstrated to exist at different localities, and these may vary seasonally (Sheard, 1953).

Despite the previous studies reviewed above, comparatively little is known about important aspects of the life history of N. australis, such as growth, moulting and reproduction. Sheard (1953) did describe the growth of N. australis in terms of development of appendages in respect to size, but did not apply a time base to his data. Sheard speculated, however, that N. australis may take one year to mature, and that the breeding season was continuous, based on the presence of CI larvae all year round. Actual numbers were not presented, thus the duration of the breeding season and the main peaks of larval release are still to be accurately determined.

FIGURE <u>1.1</u> Life stages of <u>N. australis</u>. Size ranges of each stage is

shown. Note: the postlarva and adolescent are similar in

morphology.

Metanauplius
0.45 - 0.80 mm

Calyptopis I
0.80 - 1.28 mm

Calyptopis II
1.50 - 1.98 mm

Calyptopis III
1.50 - 2.55 mm

Furcilia I
1.82 - 3.43 mm

Furcilia II
2.25 - 4.55 mm

Furcilia III
3.18 - 6.60 mm

Postlarva   4.75 - 8.95 mm
&
Adolescent   6.55 - 11.63 mm

Female Adult with Eggs
11.00 - 20.75 mm
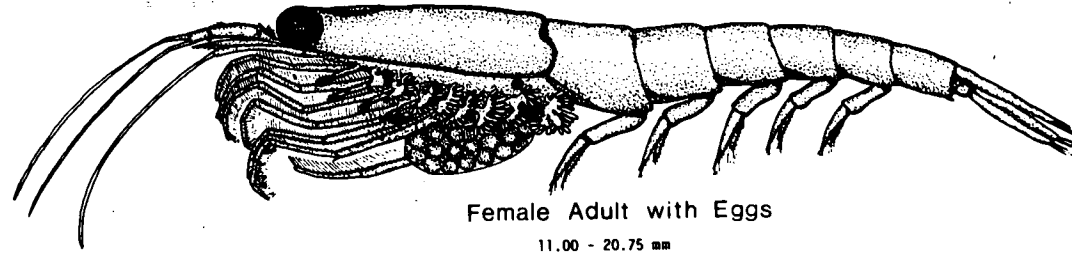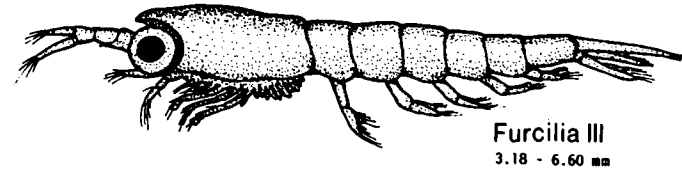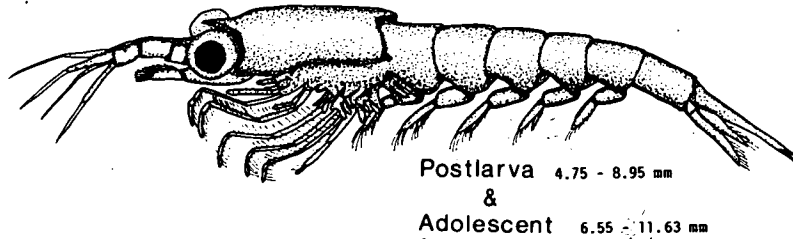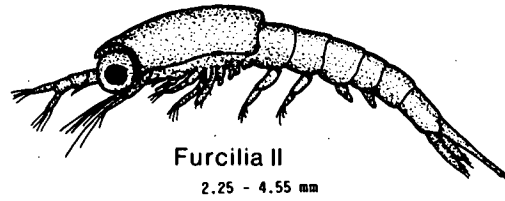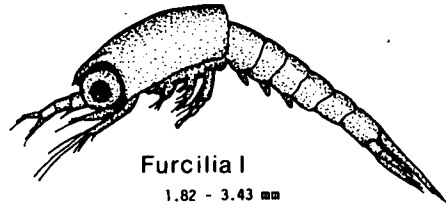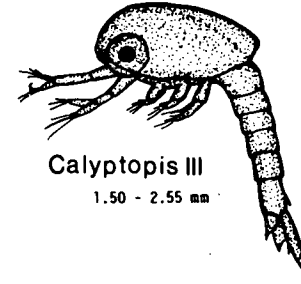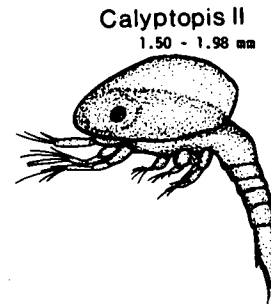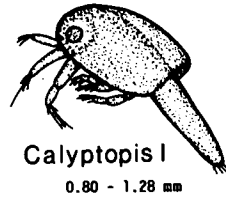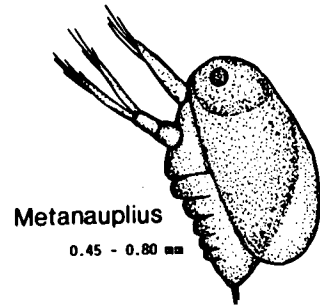
In this section, data on growth, moulting, breeding season and fecundity of N. australis are presented. These data, together with results described elsewhere in this thesis, were used to estimate production.

CHAPTER 2

ABUNDANCE, GROWTH AND MOULTING

2.1 Introduction

Growth data for euphausiids can often be determined directly from
size-frequency histograms by plotting the progressive change in mean
length against time. However, this method depends on the basic
assumption that the samples are taken from the same population (Falk-
Petersen and Hopkins, 1981). Mauchline (1977b) noted that repeated
sampling of discrete populations of oceanic euphausiids is generally
impossible. Growth can also be studied by simulating environmental
conditions in the laboratory (Mann, 1969). This method has the additional
advantage in allowing moulting to be monitored at the same time.

Previous studies into the growth of euphausiids have mainly centered
around species from temperate and cold water regions. In these areas
euphausiids typically exhibit a sigmoid growth curve (Mauchline, 1977b;
Mauchline and Fisher, 1969), i.e. very little growth occurs during winter
due to low sea temperatures, with accelerated growth during warmer summer
months. Zero growth rates during winter have, in fact, been recorded
for many temperate and Antarctic species (Clarke, 1976; Fowler et al.,
1971a; Jorgensen and Matthews, 1975; Kulka and Corey, 1978; Mauchline,
1966). Bamstedt (1976) actually recorded negative growth for an
overwintering population of Meganyctiphanes norvegica. As would be
expected, temperate euphausiids usually live longer than warm-water
species, often taking a full year to mature as a consequence of low
temperatures (Berkes, 1976; Mauchline, 1966, 1977b, 1980; Mauchline and
Fisher, 1969). In the colder Antarctic waters, Euphausia superba may
take up to 3 years to mature (Fevolden, 1979; Ivanov, 1970). Most
species of tropical euphausiids on the other hand, have life spans of
only 10 to 15 months (Roger, 1974).

Temperature is also a major factor affecting moulting. Euphausiids in general, show a clear trend for the intermoult period (IP) to increase with a decrease in temperature, which naturally corresponds with a slower growth rate (Fowler et al., 1971b, 1972; Lasker, 1966; Sameoto, 1976b). This is a feature that occurs in all crustaceans (Kurata, 1962). It has also been demonstrated that the IP increase with increase in body size, either length or weight, as well as successive moult number (Fowler et al., 1971b; Mauchline, 1977b; Murano et al., 1979). The resulting relationship is usually an exponential curve (Kurata, 1962; Mauchline, 1977b) i.e. the log of the duration of the IP increases with size. The curve, however, is shallow. Previous authors had earlier claimed that there was no discernible relationship between IP and size (Jerde and Lasker, 1966; Lasker, 1964, 1966; Paranjape, 1967). Fowler et al.(1971b) suggested, however, that any subtle changes in IP due to size were likely to be masked by the high temperature fluctuations which had occurred in those experiments. Moreover, only narrow size ranges had been examined. A clear exponential relationship between IP and size was demonstrated by Fowler et al. (1971b) for N. couchi. The relationships of IP with size and temperature have been reviewed in detail for several species of euphausiids by Mauchline (1977b), and for crustaceans in general by Kurata (1962).

Characteristics of the intermoult period have been reviewed by Mauchline (1980) for a number of euphausiids. It appears that a high frequency of moulting is a characteristic feature of all euphausiids (Paranjape, 1967). Jerde and Lasker (1966) recorded a narrow range of 4 to 7 days for the IP of adults from several species.

The weight of the exuviae expressed as a percentage of the body weight (percentage moult weight), is also well established for many euphausiids. Values have ranged from 3% for Euphausia superba (Clarke, 1976), to a mean value of 12.8% for Nyctiphanes simplex (Jerde and Lasker, 1966).

Growth in N. australis was determined, in the present study, by

following the progressive changes in a size-frequency histogram through time. Since there is no guarantee that the same population was sampled each time, laboratory growth experiments were undertaken to confirm the data used to produce the growth curve. At the same time moulting was monitored, to establish an accurate measure of the percentage moult weight, as well as relationships between size and temperature and the intermoult period. The collection and analysis of field data, as well as abundance of N. australis in Storm Bay, will also be discussed.

2.2 Methods. A : Collection and analysis of field data.

2.2.1 Field Sampling.

Storm Bay is located in south-eastern Tasmania (Fig. 2.1) adjacent to the mouth of the Derwent River, on which Hobart is located. Although it is a coastal body of water, at certain times of the year it experiences intrusions of sub-tropical and sub-antarctic oceanic water (Nyan Taw and Ritz, 1979). The bay is approximately $505 \times 10^6 \ m^2$ in area and the depth varies between 20m at Station SB9 to 70m at SB2, representing a volume of $18.54 \ km^3$ (Table 2.1).

The nine stations, forming a matrix of 10 x 10 nautical miles (16 x 16 km) were sampled monthly from December 1979 to March 1981, except for January and March 1980 which were missed due to bad sea conditions. Not all stations were sampled each month for similar reasons, and those that were are shown in Table 2.1. An unencased high speed plankton net (Lockwood, 1974) with 250 µm mesh was used (Fig. 2.2), which sampled all stages with the possible exception of the metanauplius. The net was fitted with a mouth-reducing cone which restricted the opening to $0.0314 \ m^2$. A General Oceanics, Inc. flowmeter was situated in the mouth of the net. The collecting bucket was angled at 90° to the longitudinal axis of the net, in order to reduce damage to the animals.

FIGURE 2.1 Storm Bay, south-eastern Tasmania, showing
station positions.

TABLE 2.1.   Stations sampled each month (X) and depth in metres at each station.

	STATION								
	SB1	SB2	SB3	SB4	SB5	SB6	SB7	SB8	SB9
DEPTH (metres)	50	70	44	37	44	35	21	25	20
MONTH									
December 1979	X	X	X	X					
February 1980	X	X	X	X	X	X	X	X	X
April 1980	X			X	X	X	X	X	X
May 1980	X			X	X	X	X	X	X
June 1980	X	X	X	X		X		X	X
July 1980		X	X	X		X	X	X	X
August 1980	X	X	X	X	X	X	X	X	X
September 1980			X			X		X	X
October 1980	X	X	X	X	X	X	X	X	X
November 1980			X			X	X	X	X
December 1980							X	X	X
January 1981				X	X	X	X	X	X
February 1981	X			X	X	X	X	X	X
March 1981	X	X	X	X	X	X	X	X	X

FIGURE 2.2   Unencased high speed plankton net. Size is indicated by

the 1 m rule in the foreground.
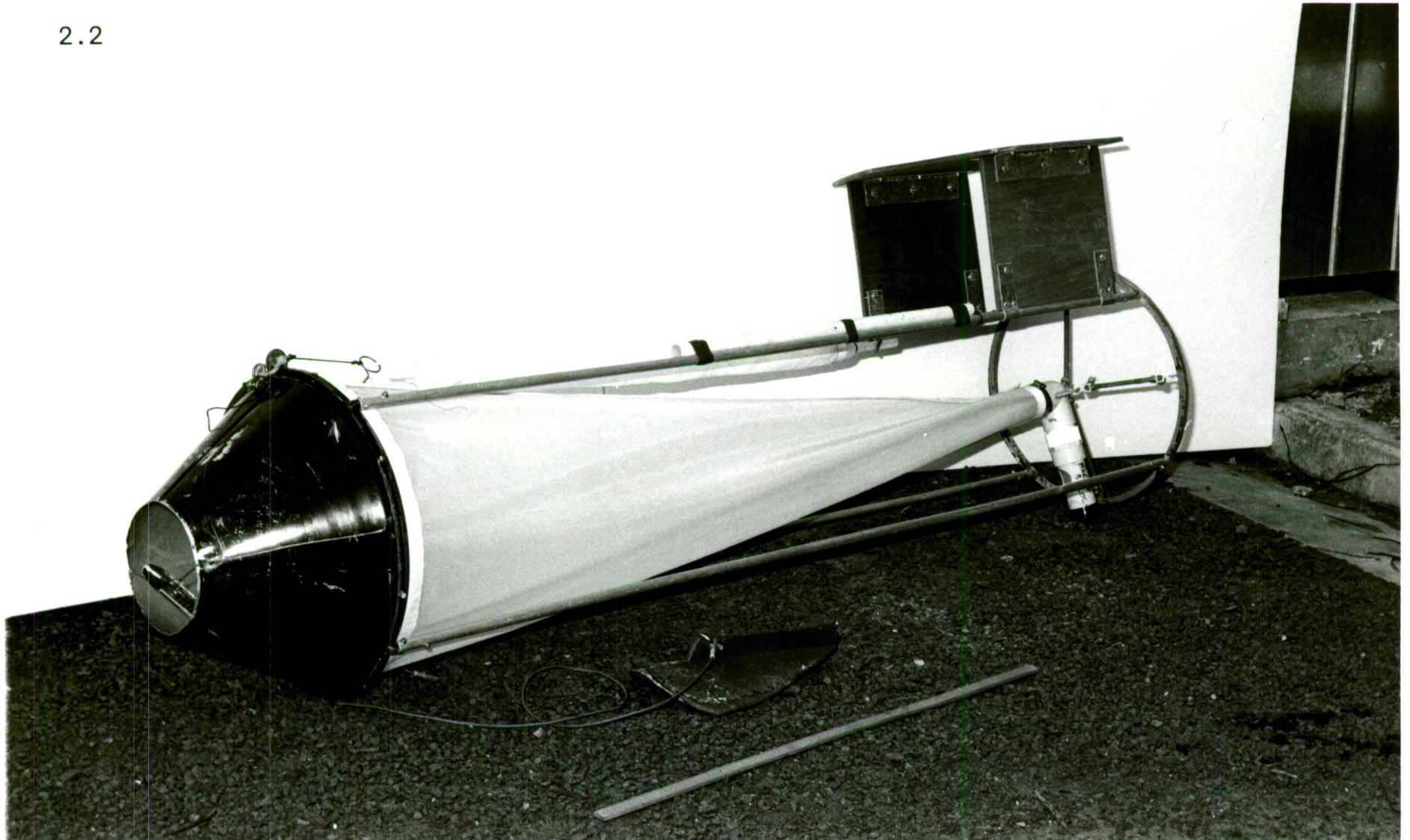
The sampling technique selected was a stepped horizontal tow. This was preferred to an oblique, vertical or horizontal haul to ensure that sufficient water from the entire column was sampled. At each station the sampler was lowered to within 10 m of the bottom, or closer in the shallow stations SB7 and 9, while travelling at 3 ms^{-1} (6 knots). After hauling for 1 or 2 minutes, enough warp was retrieved to lift the net 5 to 10 m vertically, as determined by wire angle. Hauling then proceeded for a further 1 or 2 minutes. This procedure was repeated until the sampler reached the surface. Occasionally this sequence was reversed so that the surface was sampled first. Sampling in this way, together with the recording of hydrological data, a station could be completed within 30 minutes. The catch was fixed immediately in 5% formalin in seawater, for later analysis.

In order to capture individuals that may have been located close to the bottom, a characteristic of this species noted by Blackburn (1980) and Sheard (1953), an epibenthic sampler (EBS) with 500 μm mesh was used (Fig. 2.3). A paravane was fitted on top of the EBS, at an angle of 20° to keep the net on the bottom and the whole unit was mounted on skis. The bottom of the mouth of the net cleared the seabed by 40 cm to prevent fouling by sediment. The aperture of the net was 0.196 m^{2} in area and was fitted with a General Oceanic, Inc. flowmeter. Some contamination with material from the water was expected as the mouth of the net was permanently open. This was minimized by lowering and retrieving the net vertically. It proved to be impracticable to carry both bulky samplers on the available vessels and this hindered the use of the EBS on a regular basis.

At each station, salinity and temperature measurements were taken, using a Hamon Salinity-Temperature meter (Autolab Model 602). This was calibrated regularly and is capable of an accuracy of $\pm$ 0.03 S$^{\circ}$/oo and $\pm$ 0.1°C.

FIGURE <u>2.3</u>   Epibenthic sampler (EBS). Size is indicated by the 1 m

rule in the foreground. Note: the skis are not attached.

2.3
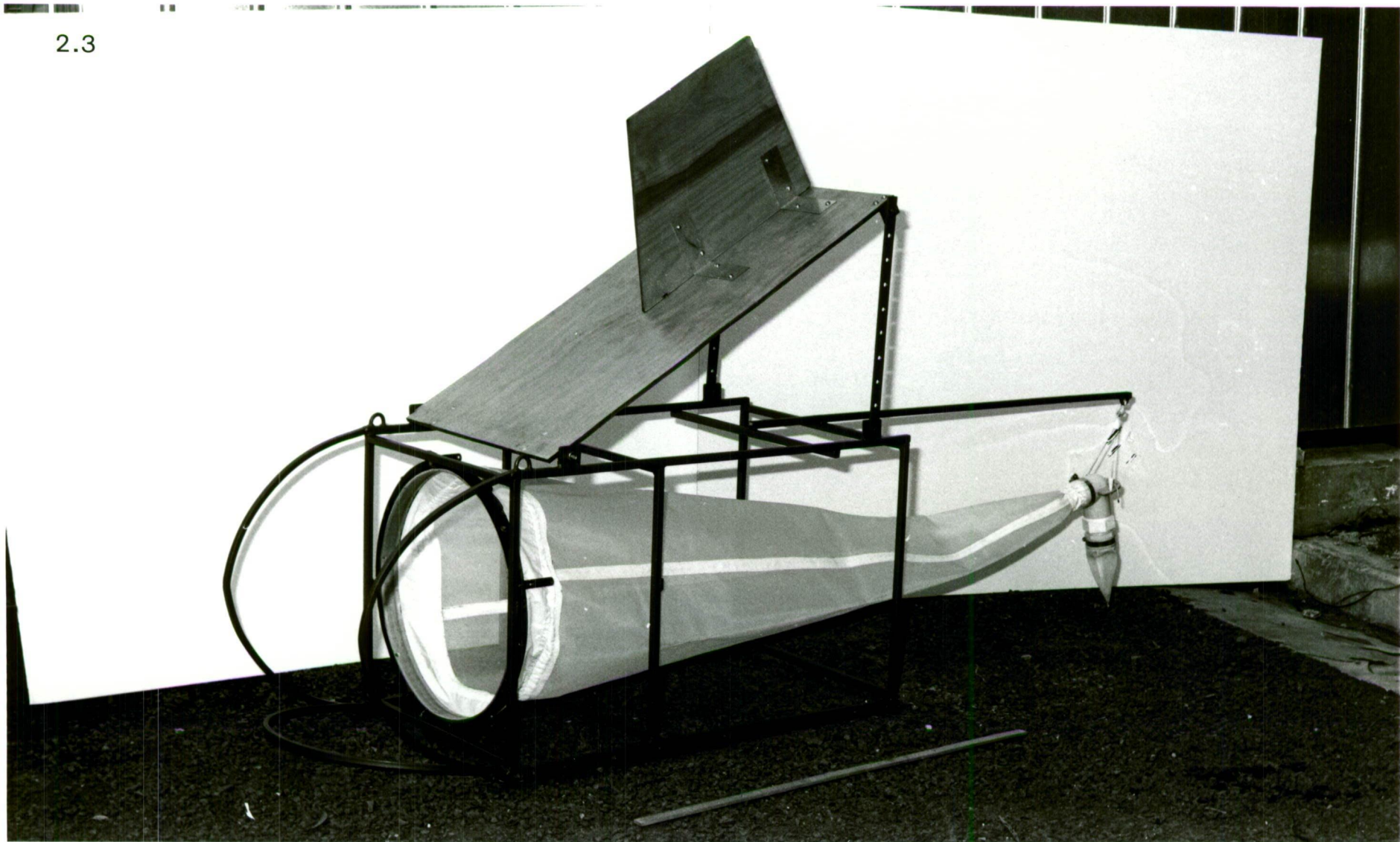
2.2.2 Laboratory Techniques

Large samples were sub-sampled for counting using a whirling sub-sampler (Kott, 1953). At least 500 individuals were counted in each sub-sample. Before sub-sampling, macroplankters, such as salps and jellyfish were removed and washed. Small larvae of N. australis were often trapped in the mucus of these animals. Adult and larval stages of N. australis were sorted and classified to their respective stages according to Sheard (1953), i.e. Calyptopis I, II, III; Furcilia I, II, III; postlarval, adolescent and adults. Total length from the tip of the rostrum to the tip of the telson spines was measured using an ocular micrometer. For ease in data handling the larvae and adults were grouped into 1 mm size-classes, rather than instars which exhibit considerable variation in size (Sheard, 1953).

To obtain a length-weight relationship, 40 specimens varying in size between 3.7 and 16.2 mm were rinsed briefly in distilled water and dried at $60^{\circ}C$ overnight. They were then weighed to the nearest μg. Although preserved specimens were used for this purpose, they had been fixed only a few days prior to drying.

The percentage composition of N. australis in the zooplankton biomass was determined for each month by drying one tenth of the total zooplankton in each sample at $60^{\circ}C$ overnight. The results were compared with the N. australis biomass of each sample calculated by multiplying the mean dry weight of the stages by their respective abundances.

2.3 Results

2.3.1 Hydrology

The complete salinity and temperature data for all stations sampled each month are presented in Appendix 1. However, data are presented graphically for two stations SB4 and SB9 (Figs. 2.4 and 2.5), for which a full data set is available. Station SB9 reflects the influence of

FIGURE 2.4   Salinity data for stations SB4 and SB9,
              at 0 and 20 m.
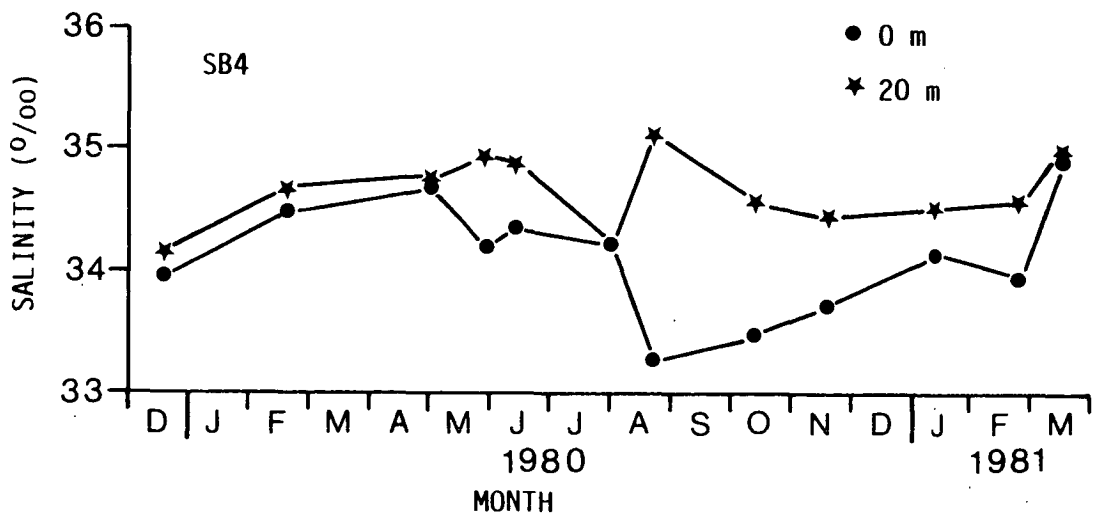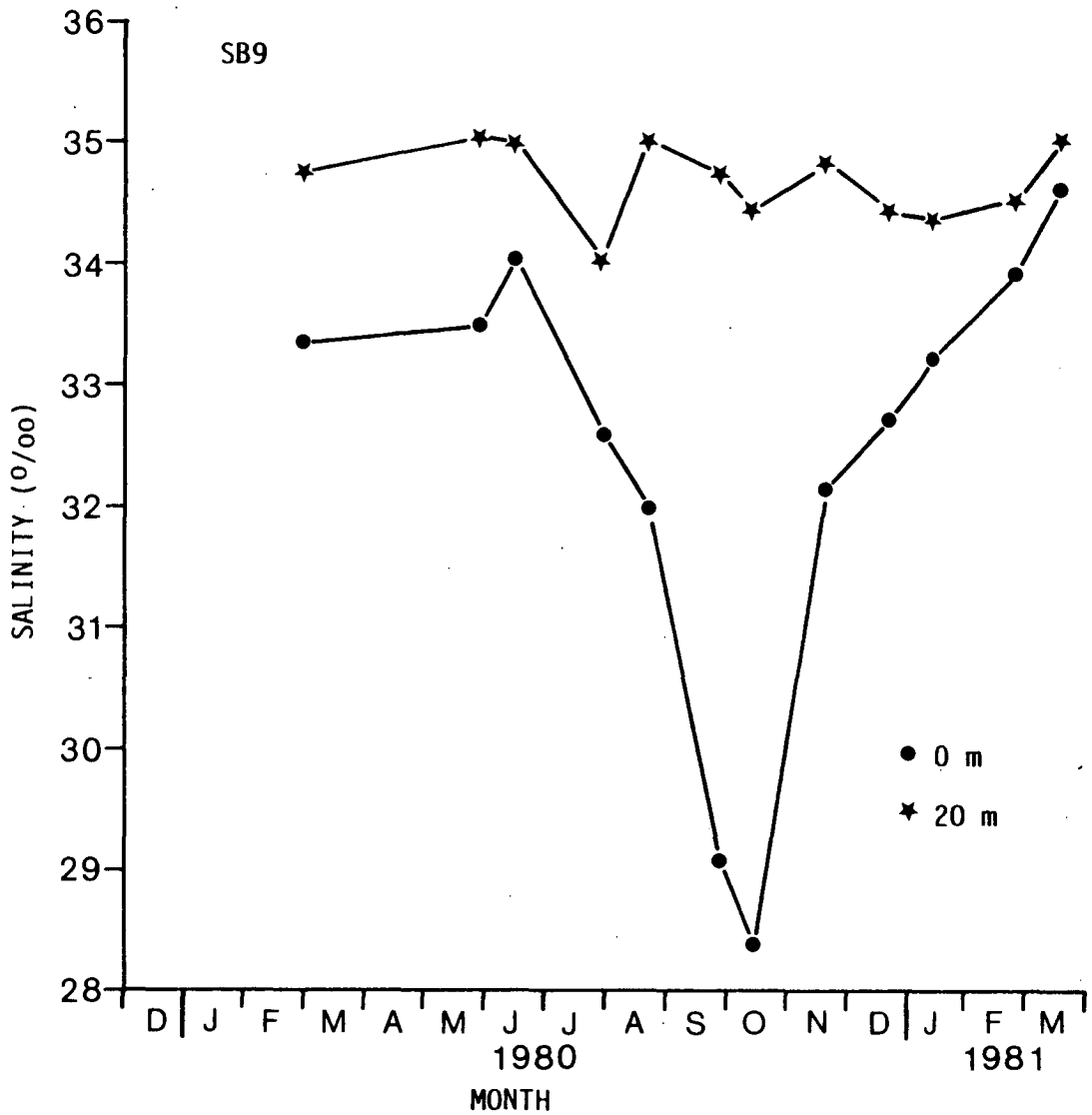
FIGURE 2.5 Temperature data for stations SB4 and SB9, at 0 and 20 m.
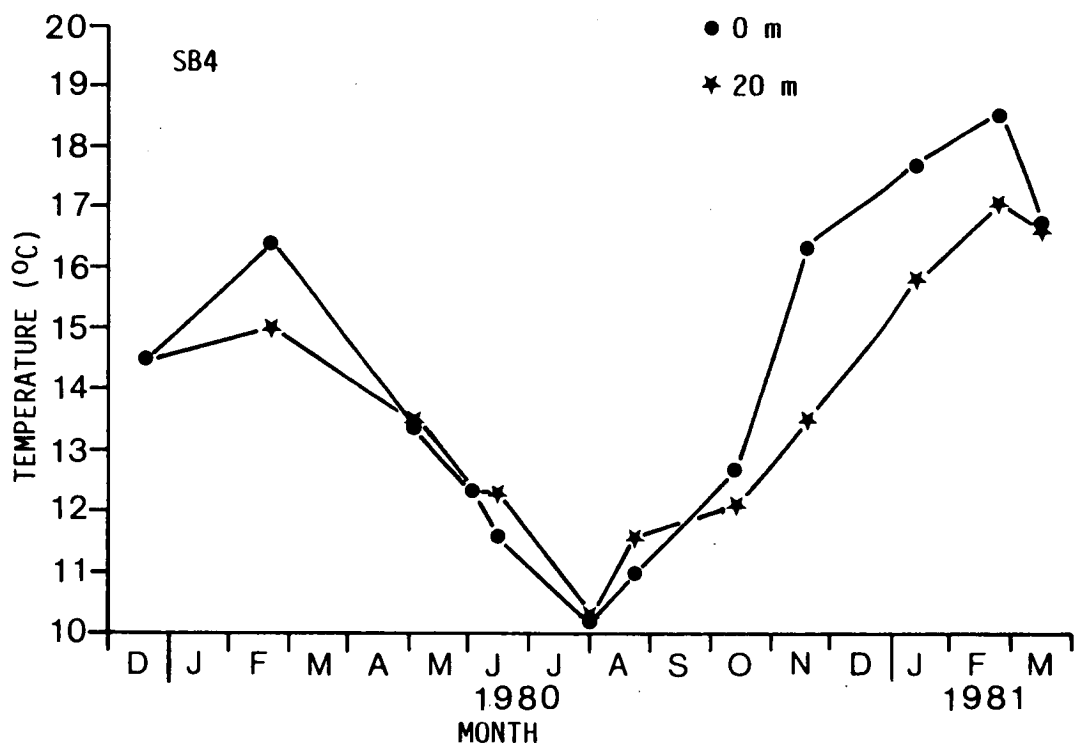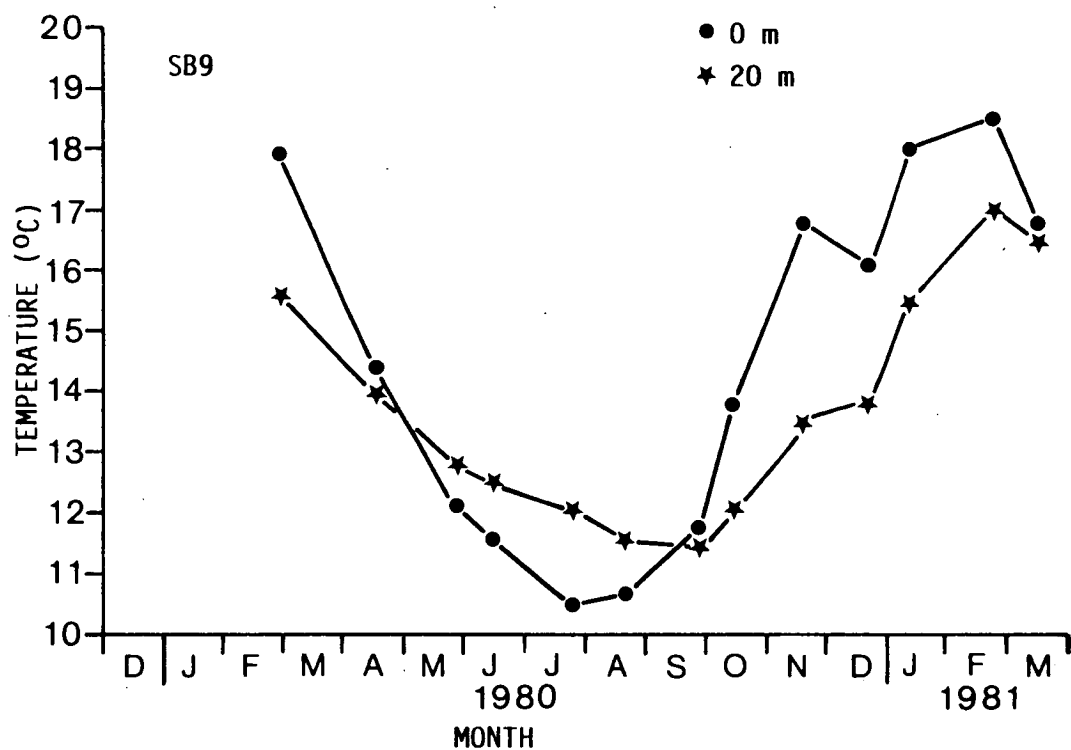
FIGURE 2.6 Fluctuations in mean sea temperature of Storm Bay, integrated for all stations.
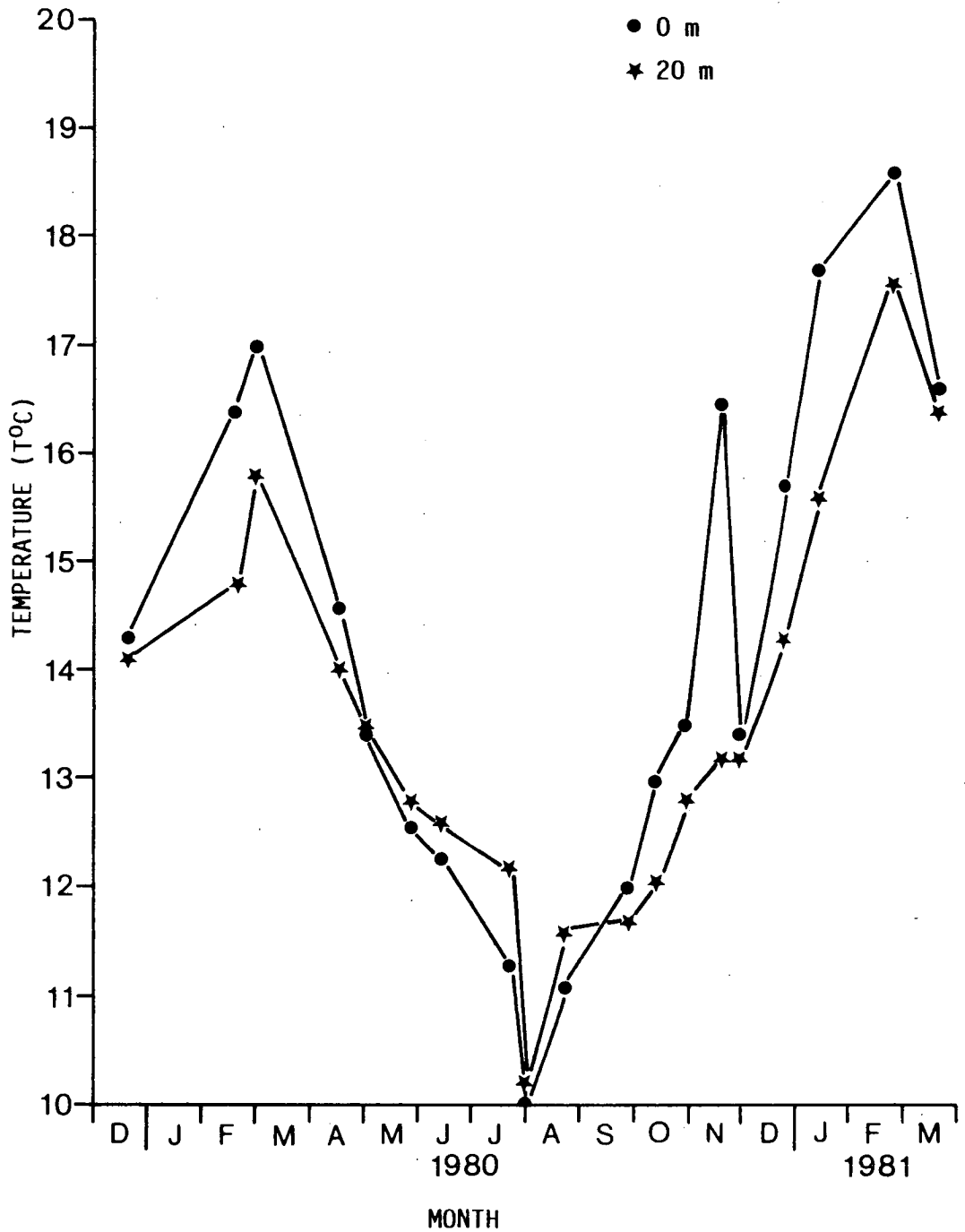
the winter freshwater run-off from the Derwent River into Storm Bay, with extremely low surface salinities in September and October 1980 (Fig. 2.4). Station SB4 was also subject to freshwater influence but to a much lesser extent (Fig. 2.4). At both stations salinities at 20m fluctuated little compared to surface salinities, with no apparent regular seasonal pattern.

Wide seasonal temperature fluctuations were observed in Storm Bay during the sampling period, ranging from approximately $10^{o}C$ in July 1980 to $19^{o}C$ in February 1981. Similar temperature patterns were observed at both SB4 and SB9 (Fig. 2.5) and also throughout Storm Bay (Fig. 2.6). In general slightly wider temperature ranges were observed at the surface than at 20 m.

Larvae were taken throughout the full salinity range observed in Storm Bay, while adults were taken in salinities varying between 33.04 and 35.09 S^{o}/oo. N. australis therefore occurs in water less saline than that previously recorded for the species (Bary, 1956; Sheard, 1965). The temperatures observed in this study are within the ranges reported by Sheard (1965).

2.3.2 Abundance and size distribution

The monthly samples show that the mean density of N. australis underwent considerable variation from 0.29 m^{-3} in July 1980 to 191.20 m^{-3} in March 1981 for all stages. In general, high densities occurred throughout the year except in winter, i.e. May to July (Fig. 2.7). The maximum density recorded was 692.24 m^{-3} at Station SB6 in March 1981. The high densities were due mainly to extremely large numbers of calyptopis larvae (1 to 2 mm). Since adults ($\geqslant$ 11 mm in total length) occurred in relatively low numbers compared to the larvae, the transformation to $\log_{10}$ densities has been used to emphasise the relative contribution of the larger sizes. Densities of individual size-classes for each month are shown in Appendix 11.

FIGURE 2.7   Size-frequency distributions for N. australis
sampled monthly from December 1979 to March
1980.   Note;   that the ordinate is a $\log_{10}$ scale.

DENSITY (m^{-3})

LENGTH (mm)
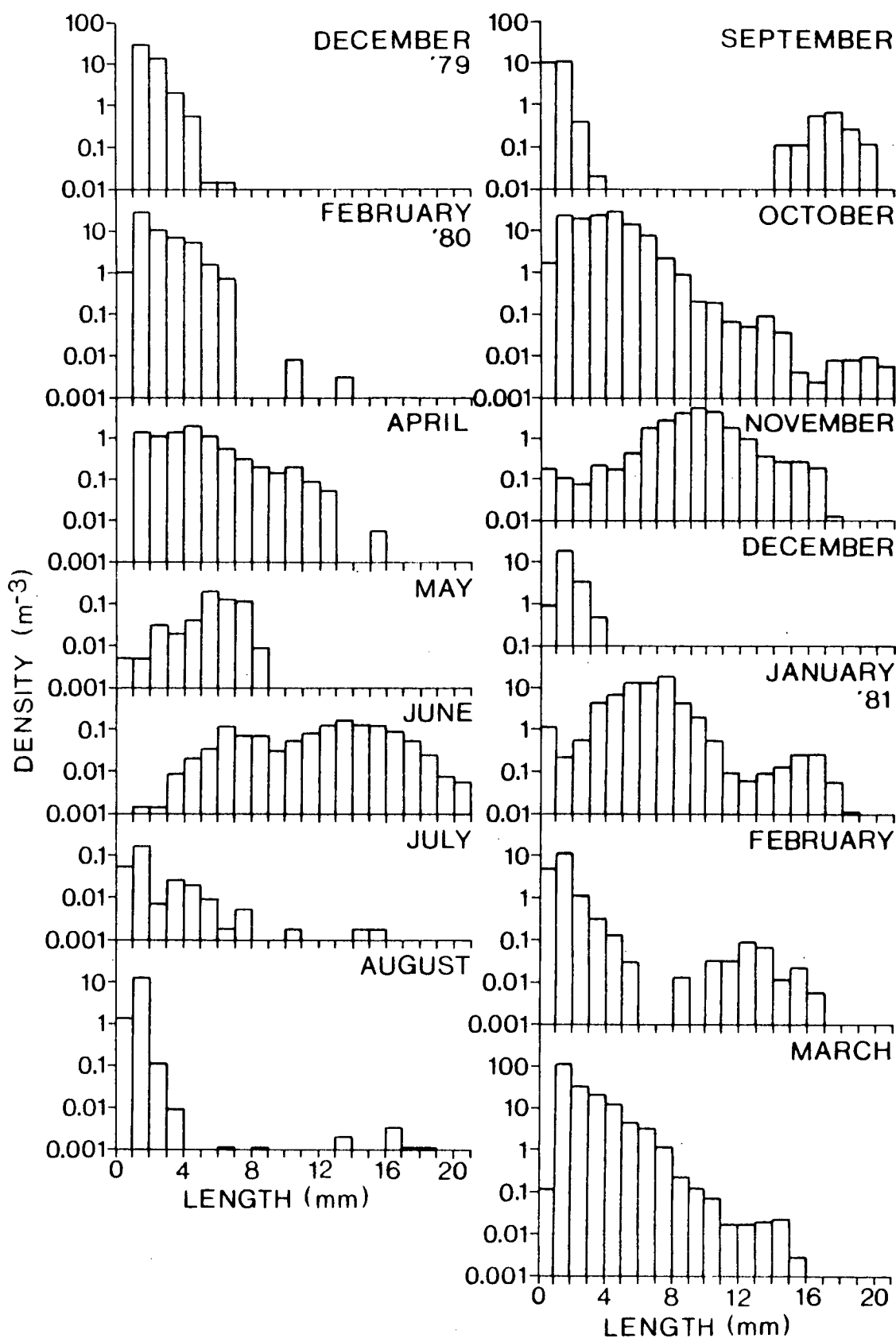
Metanauplii, which occupy the 0.00 - 0.99 mm size-class, were never recovered in large numbers, suggesting either that the stage is passed very rapidly (Sheard, 1953; Wang, 1965), or that there was some passive escapement through the mesh.

In the June, August, September and October samples adults of between 17.00 - 20.99 mm were taken. These adults are notably larger than the largest previously recorded by Sheard (1953) and Palmer (1978), i.e. 14.3 mm and 17.4 mm respectively. The largest adult recorded in the present study was a female of 20.75 mm total length taken in October 1980.

Out of a total of 6 EBS hauls made during June, August 1980 and July 1981, only 1 sample taken halfway between SB4 and SB8 in June 1980 returned specimens of N. australis. These were larvae and adolescents in the size range 4.00 - 10.99 mm, with a combined density of 138.37 m^{-3}. This was much greater than the mean value of 0.43 m^{-3}, for the same size distribution, in the June 1980 plankton samples (Fig. 2.8). Although animals smaller than 4 mm may have been lost through the 500 μm mesh, Blackburn (1980) noted that only animals 5 mm and larger migrated to the bottom in winter. Adults may have avoided the net, which was towed at a speed of only 0.5 ms^{-1}.

The percentage dry weight of N. australis in the plankton varied considerably from month to month and the ranges within months were extreme, e.g. from 0.15 to 100% in June 1980 (Fig. 2.9). On the whole higher percentages of N. australis occurred during the warmer months, at times far exceeding the copepod biomass. Monthly biomasses of N. australis and total zooplankton are shown in Fig. 2.10. The biomass of N. australis ranged from 0.05 mg m^{-3} in August 1980 to a maximum of 30.54 mg m^{-3} in November 1980, while the total zooplankton biomass, including non-crustacean zooplankton, varied between 0.91 mg m^{-3} in August 1980 to 58.90 mg m^{-3} in November 1980.

FIGURE 2.8 Comparison of the size-frequency distributions
of the June 1980 EBS sample and the June 1980
plankton sample (shaded) (from Fig. 2.7).
Note; larvae smaller than 4.00 mm may have been
lost from the EBS, while adults may have avoided
capture.
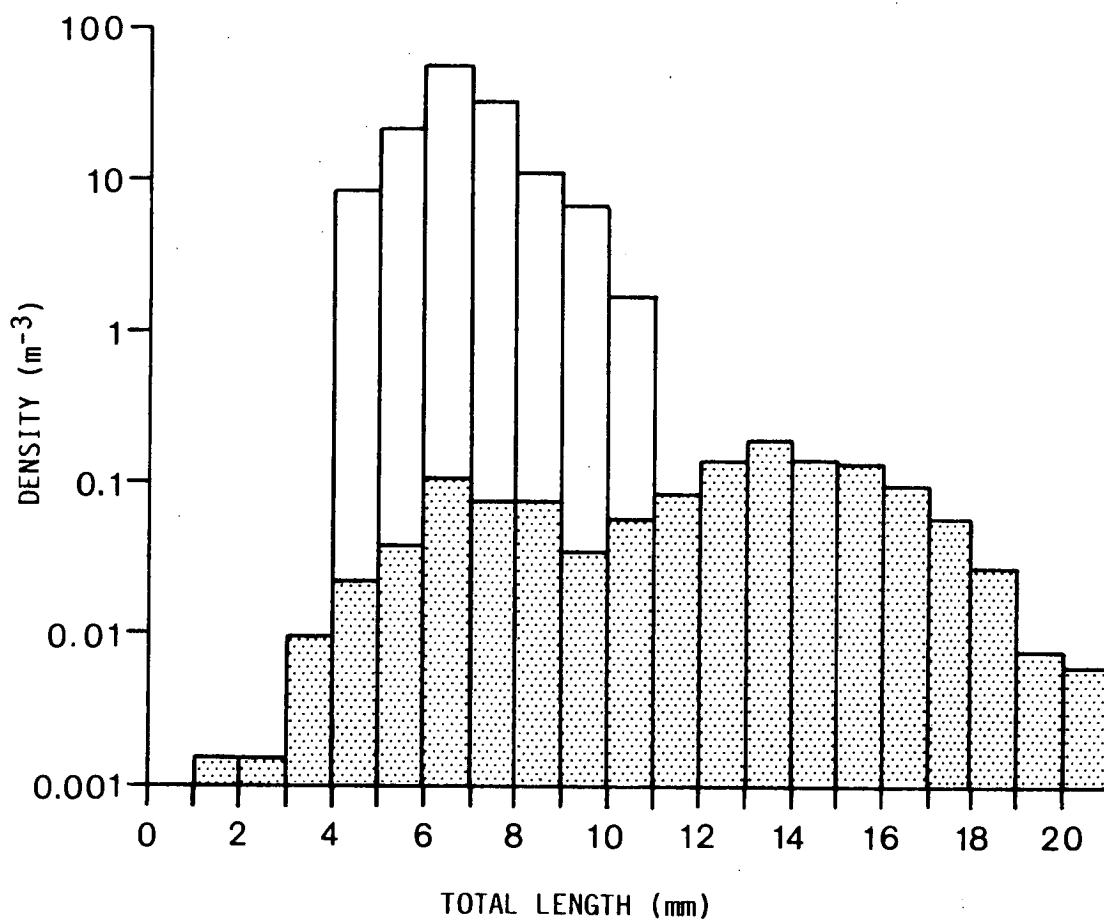
FIGURE 2.9 Mean monthly percentage content of N. australis
by dry weight in total zooplankton biomass for
all stations. Bars represent ranges.
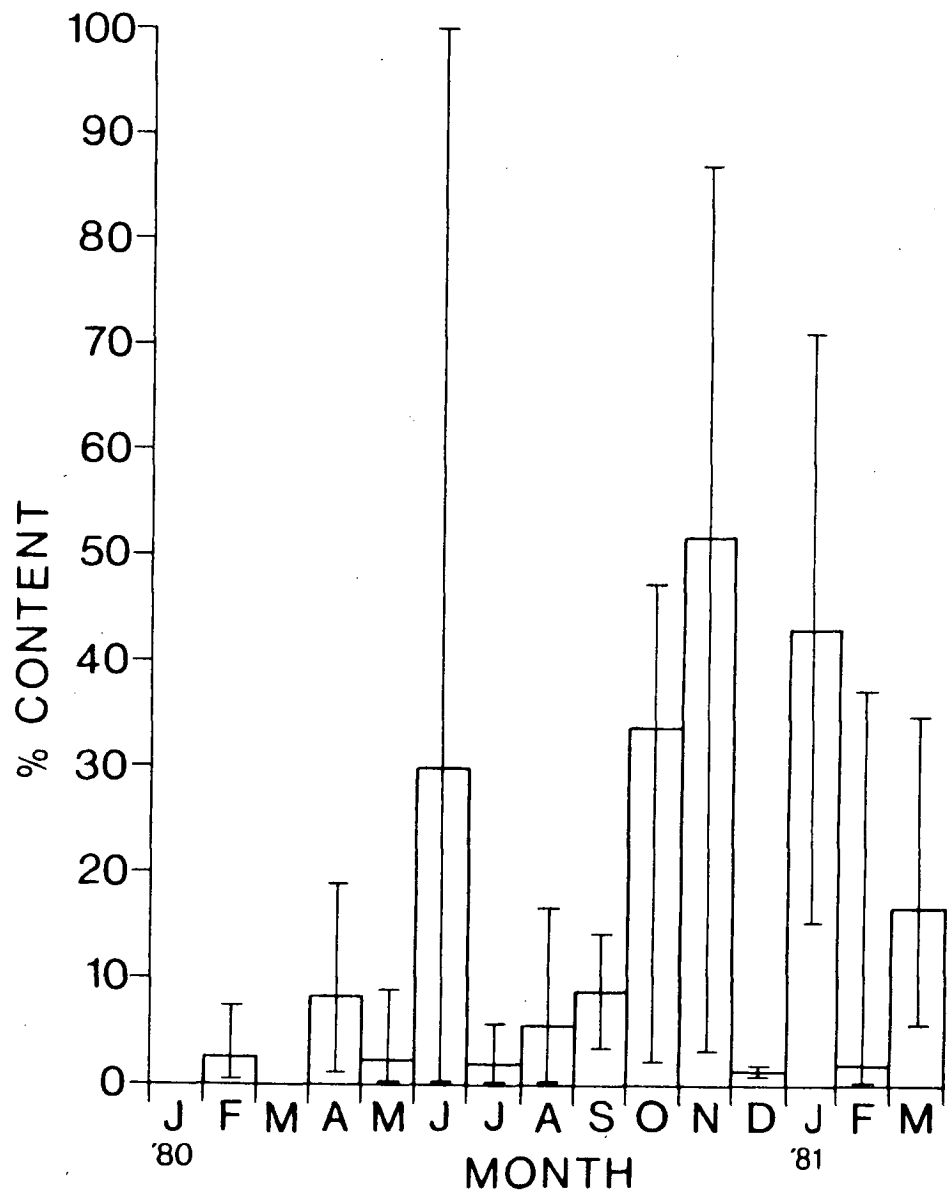
FIGURE 2.10   Monthly dry weight biomasses of N. australis

(shaded) and total zooplankton.
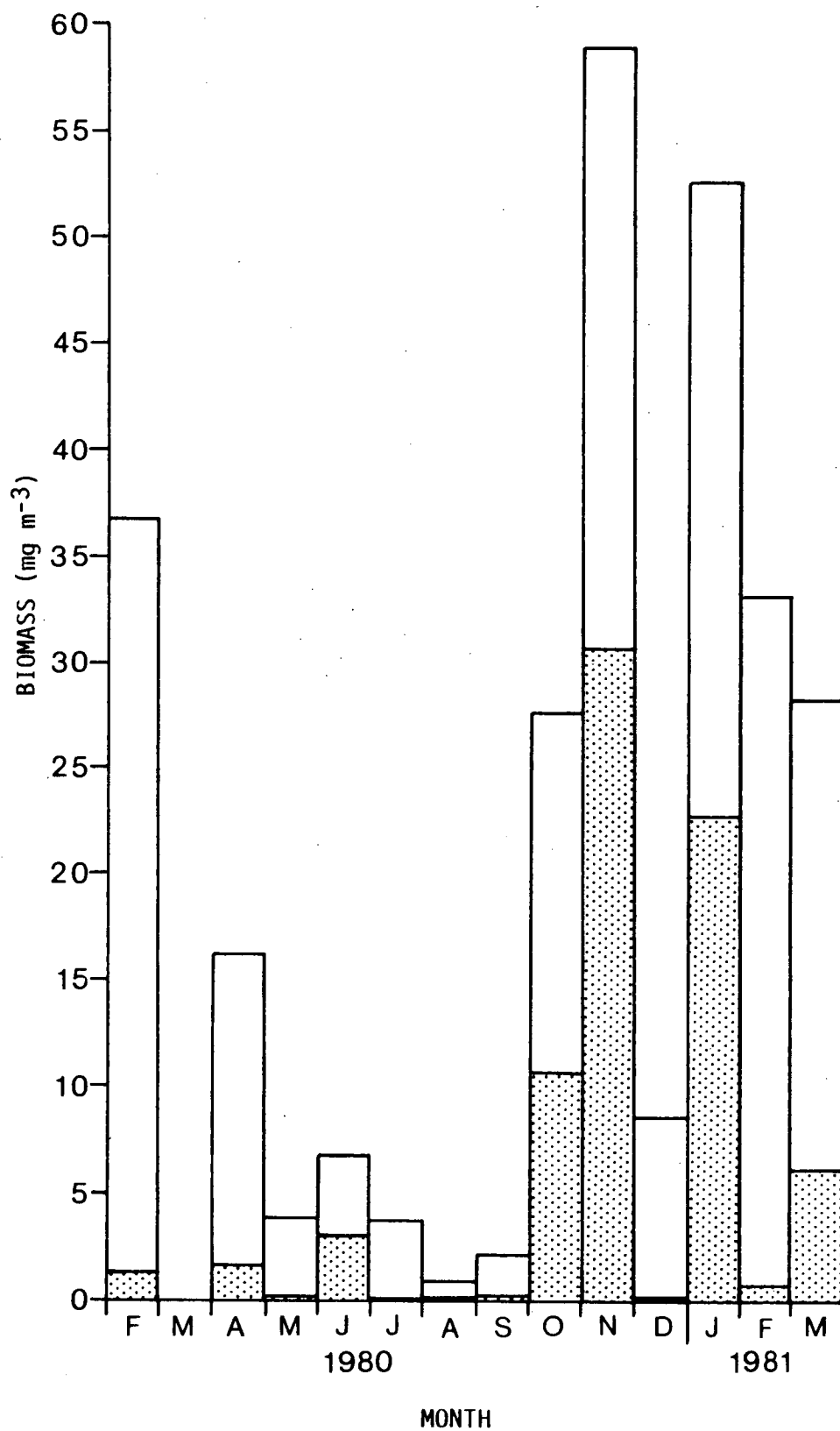
Figure 2.11   Relationship between total length and dry body weight.
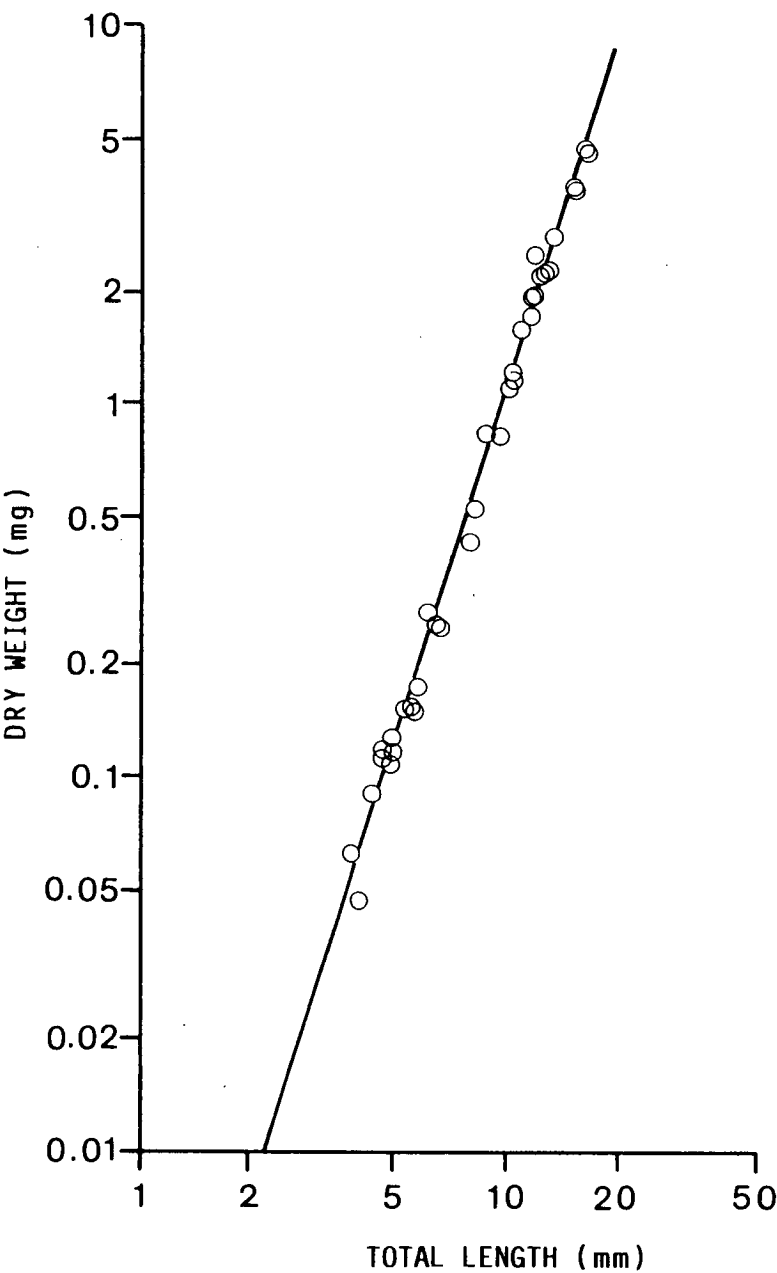
2.3.3 Length-Weight Relationship

The relationship between total length and dry weight is given by the regression equations :-

$$W = 0.000965L^{3.0449} \quad , \qquad (2.1)$$

where L is the total length in mm and W is the dry weight in mg (Fig. 2.11). This length-weight relationship is comparable with those determined for other euphausiids (Mauchline, 1967a, 1980; Mauchline and Fisher, 1969). Mauchline (1967a) noted that length-weight relationships of euphausiids vary little between species.

2.4 Methods B : Growth and Moulting

The size-frequency histogram (Fig. 2.7) shows that there was continuous recruitment of N. australis larvae, of the 1.00 - 1.99 mm size-class, into the population, throughout the sampling period. Distinct cohorts were therefore, not readily discernible. However, it was possible to determine a growth curve for N. australis by following the development of the December 1979 release of larvae through time. The cohort could be identified each month using the probability paper method described by Harding (1949) and Cassie (1954).

Live animals were taken from Storm Bay using a standard plankton net of 250 μm and 0.25 m^2 aperture, towed at 1 ms^{-1} (2 knots) from the Zoology Department vessel "Wobbegong". Although many of the adults probably escaped capture at this speed, those that were taken were generally free from damage. Capture at higher speeds tended to damage the thoracic legs. Specimens of N. australis were separated from the rest of the catch while on board the boat and about 20 individuals were placed in large plastic bags in approximately 2 litres of sea water. The bags were then placed in a portable ice box, which prevented injurious increases in water temperature. With this treatment mortality was reduced and animals arrived back in the laboratory in the best possible condition.

Individuals were measured using an ocular micrometer and then placed into separate containers within two light-proof growth cabinets. It has been found that individuals will live longer if kept in the dark (Komaki, 1966; Lasker, 1964; Macdonald, 1927b; Mackintosh, 1967). One cabinet was kept in a $10^{o}C$ constant temperature room, the other at $15^{o}C$. These temperatures are within the range observed in Storm Bay (Fig. 2.6). Each cabinet comprised a closed system of 20 litres capacity, with 20 individual containers. The containers were lined on the bottom with 250 μm mesh and suspended over a jet of water which was continually recirculating by means of a magnetically coupled centrifugal pump (Fig. 2.12). This system allowed individual specimens to be monitored separately so that their exuviae could be recovered.

Individuals were checked twice daily as near as possible to 0830 and 2030 hours, in order to determine the intermoult period to the nearest half day. Each container was, in turn, lifted out of the water trapping both the animal and exuviae on the mesh. The exuviae was carefully washed with a **stream** of distilled water **while** still on the mesh, which offerred support, thus minimizing damage. The stream of distilled water was kept away from the animal. The moult was then retrieved with fine forceps, placed on aluminium foil, and the animal was quickly returned to the water. Each examination took no more than 15 seconds. After the examination the indiyiuals were fed "Mikropan", a commercial food prepared for fish fry. Studies on the dietary requirement of N. australis have suggested that this species is an omnivore/detritivore (Chapter 4). The "Mikropan" was expected to reflect that particular diet. Ikeda and Dixon (1982) used an artificial pet food for Euphausia superba, a known herbivore. Based on the results of Fenton (1981), which suggested that early stages of N. australis fed more on phytoplankton than later stages, larvae in the present experiments were presented a cocktail of 5 species of the genera Chaetoceros, Chlamydomonas, Dunaliella, Pavlova and Thalassiothrix.

FIGURE 2.12 Growth cabinet.

a: Individual containers lined on the bottom with 250 µm

b: Perspex support for containers

c: Outflow

d: Water jet

e: Inflow

f: Pump

g: Supporting blocks

2.12

SIDE PROJECTION

20 cm

TOP PROJECTION

FIGURE 2.13 Recirculating culture chamber.

20 cm
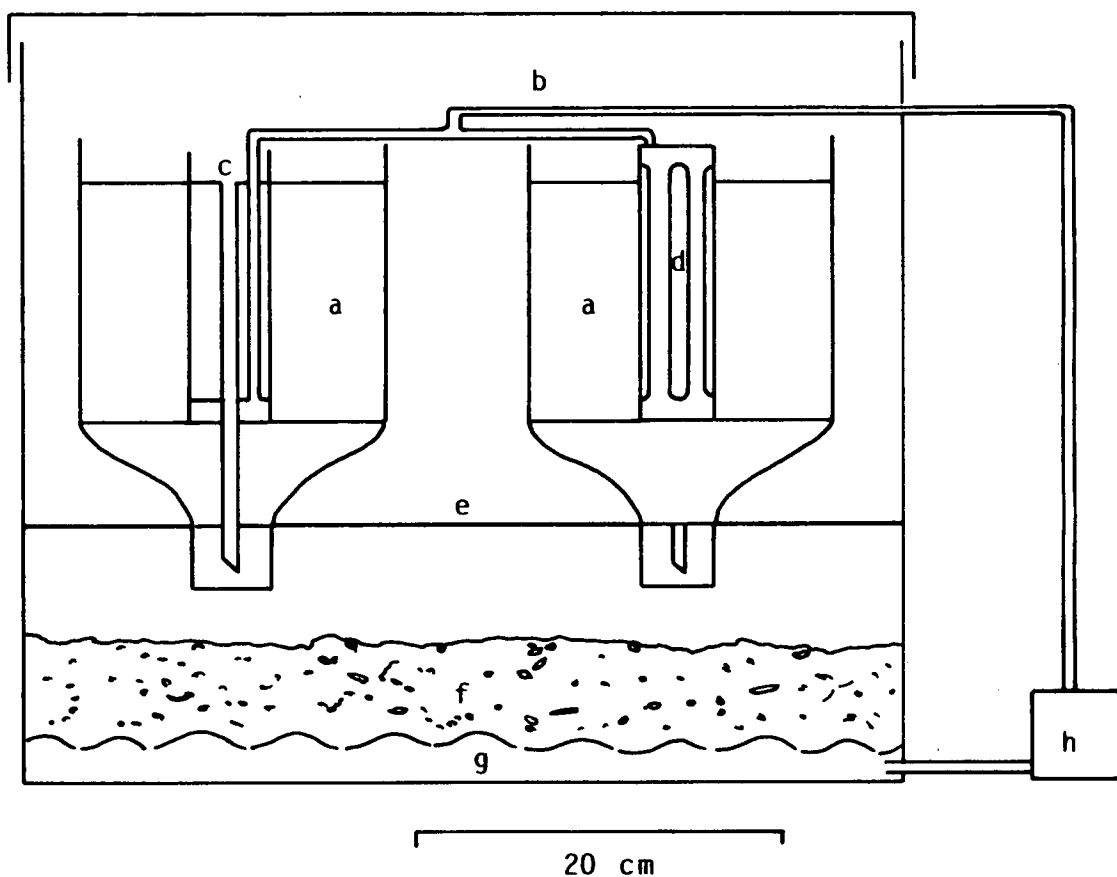
a: Water filled culture vessels made from flagons

b: Inflow

c: Overflow pipe

d: Mesh filter around inflow & outflow pipes

e: Perspex support

f: Gravel filter innoculated with denitrifying bacteria

g: Water collected below corrugated fibreglass

h: Water returned to system by pump

Cells were separated from the culture medium and resuspended in sea water before being added to the culture vessels. The algal cultures were obtained from the Bicheno Oyster Hatchery, East Coast Tasmania.

At the end of the experiments, or when the individuals had died, specimens were again measured to note growth. Experiments usually ceased after 20 days, at a time when most animals appeared to be dying. Most larvae, however, died before day 10. It has been noted in other studies that larvae are particularly difficult to keep, with handling probably contributing to mortality (Gopalakrishnan, 1973; Ross, 1981). Individuals that died during the experiments were replaced from a reserve stock of N. australis kept in a 40 litre recirculating culture chamber (Fig. 2.13). In this system animals were kept alive and apparently healthy for several weeks, though individuals could not be monitored.

Retrieved exuviae were dried over night at 60°C, then stored in a desiccator until weighed to the nearest μg on a microbalance.

2.5 Results

The growth curve determined from the December 1979 cohort is shown in Fig. 2.14. The initial growth rate of 0.095 mm d^{-1} for early larvae, followed by a lower rate of 0.045 mm d^{-1}, decreasing again to 0.026 mm d^{-1} in adults is comparable with growth rates determined for other euphausiids (Table 2.2), in particular Euphausia pacifica (Smiles and Pearcy, 1971), Meganyctiphanes norvegica (Fowler et al., 1971a) and an East Coast Tasmania population of Nyctiphanes australis (Fenton, 1981). The largest adult so far collected, a female of 20.75 mm, is estimated, using the calculated growth curve, to be approximately 360 days old. It appears unlikely that N. australis lives longer than one year. Other cohorts' could be traced for brief periods between October 1980 to March 1981 (Fig. 2.15). Added together these yield the growth curve given in Fig. 2.15. As can be seen the growth rates of larval stages were much faster, 0.16 - 0.119 mm d^{-1}, than in the December 1979 cohort, but as in

FIGURE 2.14   Growth curve derived from data calculated for December

1979 cohort.   Dashed portion of line is an extrapolation

back to hatching stage ie., Time 0, 1 mm.   Bar represents

$\pm$ SD.   Growth rate in mm d^{-1} is indicated.
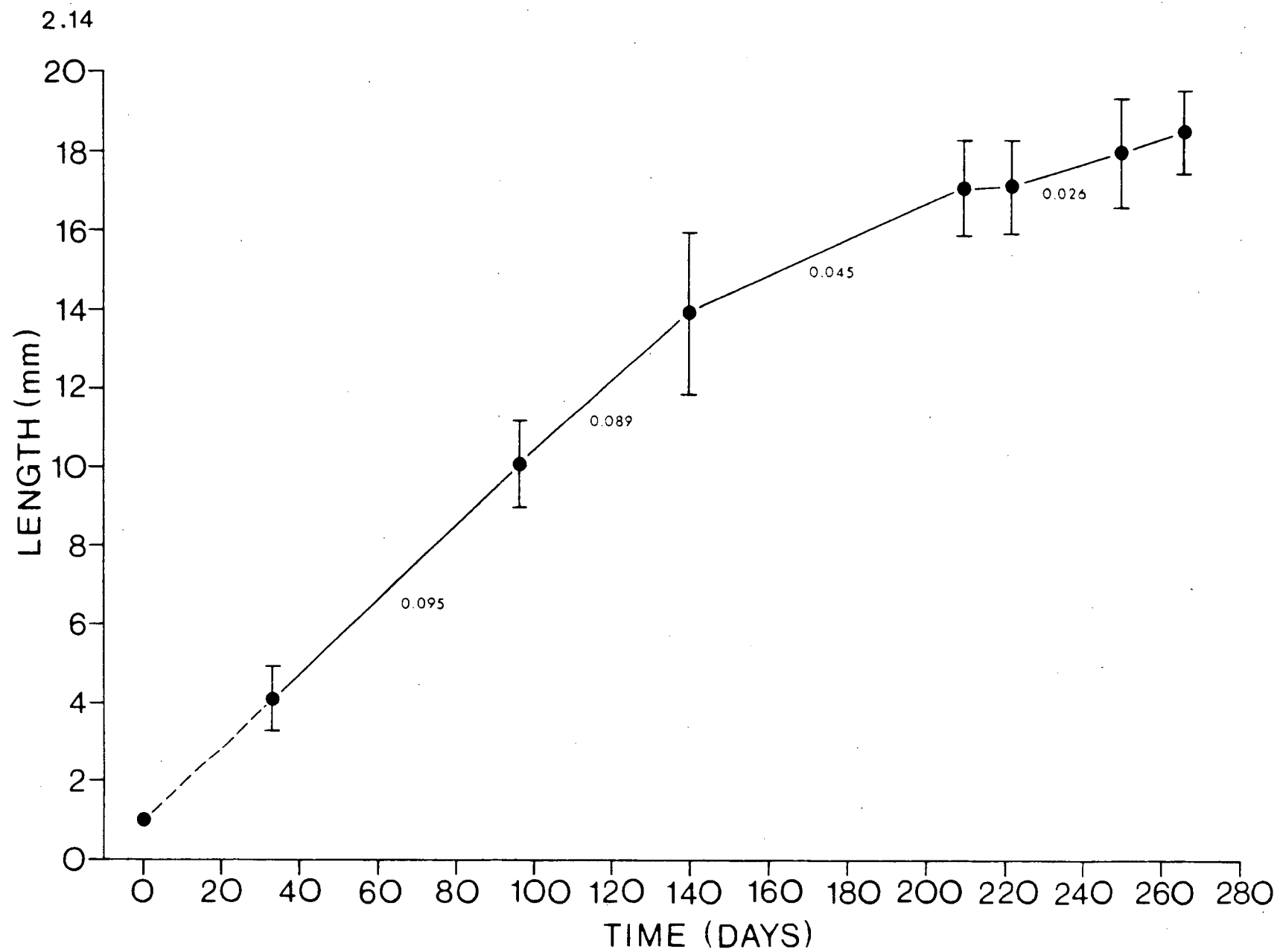
FIGURE 2.15   Growth curves for cohorts observed between October 1980

and March 1981.   Bar represents $\pm$ SD.   Growth rate in

mm d^{-1} is indicated.

2.15
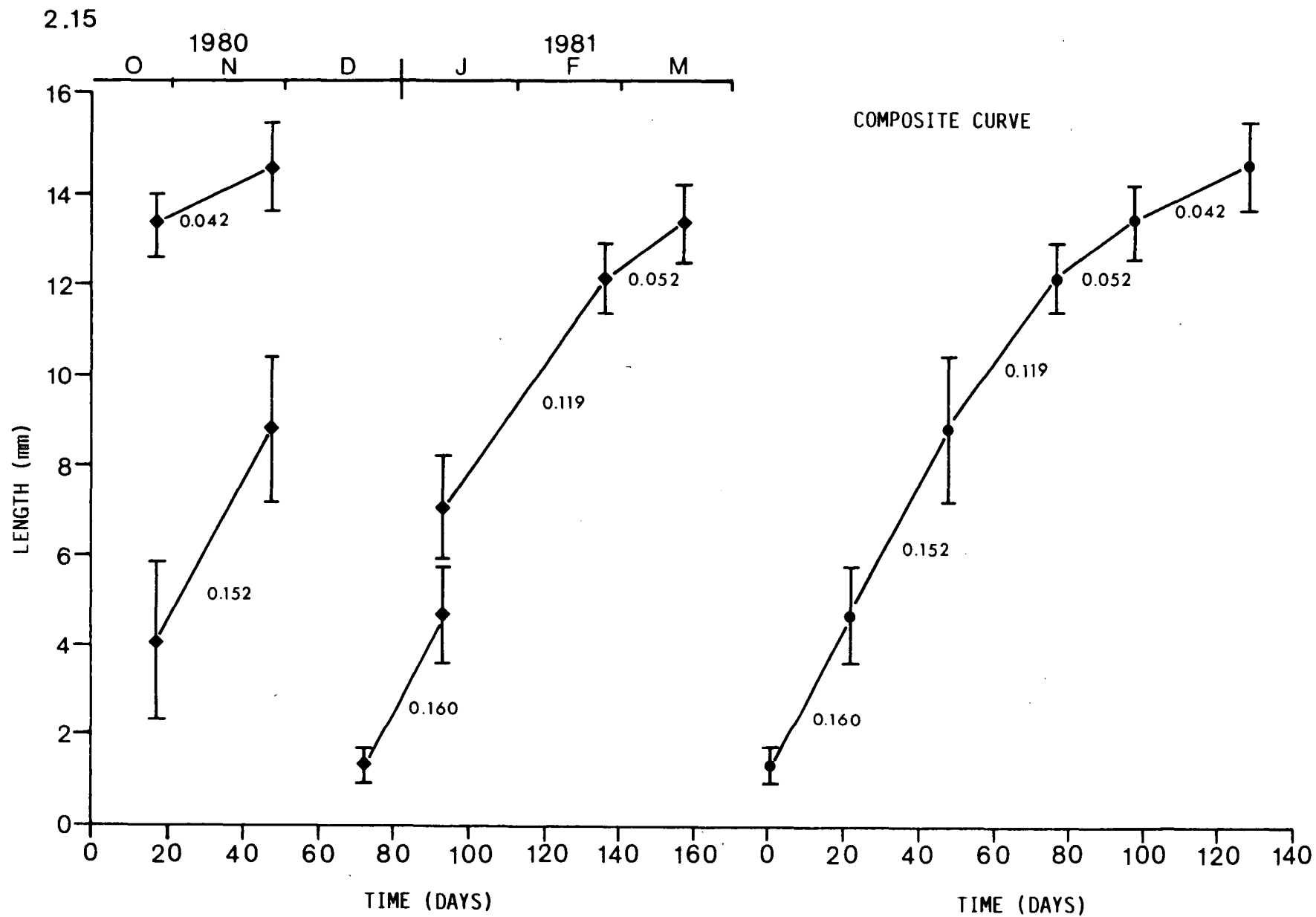
TABLE 2.2 Growth rates for various euphausiid species.

Juveniles refers to postlarvae and adolescents.

T, indicates tropical species.

Species	Growth rate mm d^{-1}	Source
Thysanoessa raschi larvae	0.043-0.071	Berkes(1976)
Meganyctiphanes norvegica larvae to adult	0.085-0.032	Fowler et al.(1971a)
Nematoscelis difficilis larvae to juveniles	0.150-0.040	Gopalakrishnan(1973)
Euphausia pacifica larvae	0.034-0.048	Lasker (1966)
E. pacifica mean (larvae to adult) larvae	0.065 0.095	Smiles and Pearcy (1971)
E. diomedae	0.033	Roger(1974)
Bentheuphausia amblyops T	0.033	Roger(1974)
Nematobrachion boopis T	0.047	Roger(1974)
Nematoscelis tenella T	0.053	Roger(1974)
Thysanopoda aequealis T	0.040	Roger(1974)
T. monacantha T	0.067	Roger(1974)
T. triscuspidata T	0.067	Roger(1974)
Nyctiphanes couchi larvae	0.130	Le Roux(1973)
N. australis larvae and juveniles	0.089	Fenton(1981)

Fig. 2.14 the rate still declined as animals approached maturity.

The laboratory experiments on growth failed to confirm the growth curve calculated from the size-frequency data. In fact, as can be seen from Tables 2.3 and 2.4, 30 out of the total of 40 adults used exhibited negative growth. A further 5 animals showed no increase, with only 4 growing positively. One adult, a female carrying external eggs (Specimen No. 8, 10°C), failed to moult during the experiments, therefore no measurement of growth could be taken. Most animals which showed negative growth, had "shrunk" by a considerable amount, in particular, specimen No. 4, 15°C. Therefore, it is unlikely that the negative growth rates observed, are a result of error in measurements. There were no data for larvae since they did not live long enough for an accurate measure of growth to be obtained.

Despite the failure of the laboratory growth experiments, considerable information on moulting was obtained. On average, adults at both 10° and 15°C moulted seven times in 20 days. Larvae moulted at least twice between 6 to 10 days to provide an estimate of intermoult period. A logarithmic relationship was observed between size and intermoult period, with a better correlation existing between dry body weight than with length (Figs. 2.16 and 2.17) The calculated relationships between size and intermoult period are :-

at 10°C $\qquad \log_{e} (IP) = 1.2640 + 0.0335(L)$ $\qquad (r = 0.851, P < 0.01), (2.2)$

$\qquad \log_{e} (IP) = 1.4267 + 0.0912(W)$ $\qquad (r = 0.875, P < 0.01), (2.3)$

at 15°C $\qquad \log_{e} (IP) = 0.7314 + 0.0388(L)$ $\qquad (r = 0.874, P < 0.01), (2.4)$

$\qquad \log_{e} (IP) = 0.9173 + 0.1037(W)$ $\qquad (r = 0.952, P < 0.001), (2.5)$

where IP is the intermoult period in days, L is total length in mm, and W is dry body weight in mg. The intermoult period at 15°C ranged from 2·5 days for larvae of 3-4 mm to 4-5 days for large adults. Intermoult period at 10°C was almost double that for the same sized animal at 15°C.

TABLE 2.3 Experimental growth rates of N. australis individuals held
          at 10°C.

Specimen	Length at Start mm	Length at End mm	Duration days	Growth rate mm d^{-1}
1	13.78	12.68	17	-0.0647
2	16.13	14.50	20.5	-0.0795
3	15.25	14.63	18.5	-0.0335
4	15.13	14.63	23	-0.0217
5	11.80	11.80	9	0
6	14.28	14.38	21	+0.0048
7	14.18	14.18	17	0
8		Animal failed to moult		
9	14.75	13.45	20.5	-0.0634
10	11.00	10.70	16.5	-0.0182
11	16.18	15.38	10	-0.0800
12	15.40	14.88	16	-0.0325
13	15.08	14.88	19.5	-0.0103
14	14.38	13.25	17.5	-0.0646
15	11.93	10.50	22	-0.0650
16	14.05	13.25	16	-0.0500
17	12.75	11.63	15	-0.0747
18	13.00	11.75	21	-0.0595
19	11.83	11.63	21.5	-0.0093
20	17.03	15.30	23	-0.0752

TABLE 2.4   Experimental growth rates of N. australis individuals held
            at 15°C.

Specimen	Length at Start mm	Length at End mm	Duration days	Growth rate mm d^{-1}
1	12.25	12.38	9	+0.0144
2	14.50	14.38	9.5	-0.0126
3	17.63	17.63	20	0
4	16.58	13.38	23	-0.1391
5	13.80	11.25	15	-0.1700
6	10.05	9.63	20.5	-0.0205
7	12.45	12.05	6	-0.0667
8	12.50	9.50	15.5	-0.1935
9	11.58	11.43	3	-0.0500
10	12.00	12.13	6	+0.0217
11	12.98	11.63	20.5	-0.0659
12	14.50	13.55	6	-0.1583
13	13.00	12.25	17	-0.0441
14	12.68	13.13	5.5	+0.0818
15	14.75	14.00	6.5	-0.1154
16	12.25	12.25	18.5	0
17	12.88	12.88	19	0
18	16.25	15.63	13	-0.0477
19	14.05	14.00	9	-0.0056
20	14.40	13.63	9.5	-0.0811

FIGURE 2.16 Relationship between mean intermoult period and mean dry body weight for 1 mm size-classes, at $10^{O}C$ (r = 0.875, P < 0.01) and $15^{O}C$ (r = 0.952, P < 0.001).
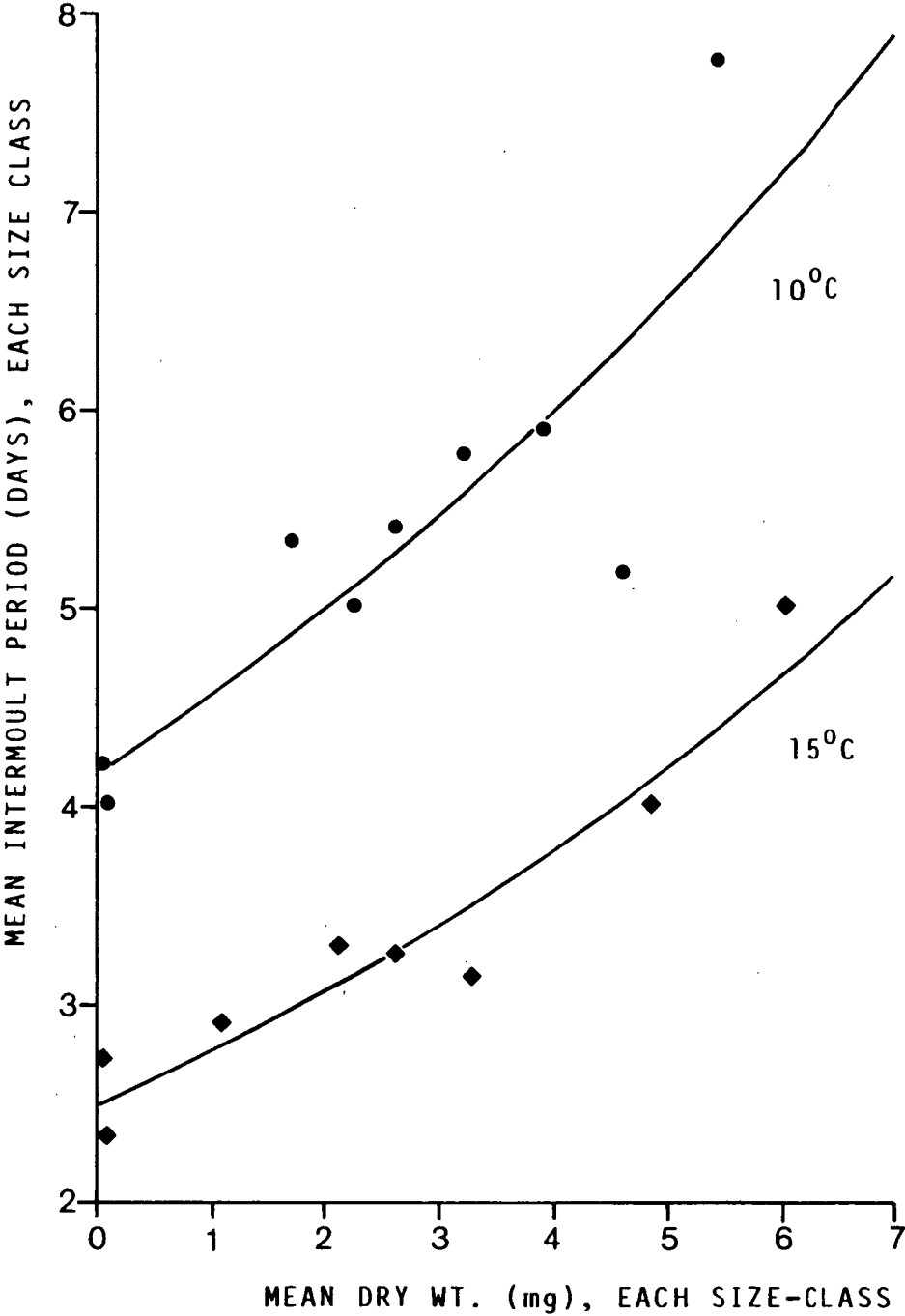
FIGURE 2.17   Relationship between mean intermoult period
and mean length for 1 mm size-classes, at 10°C
$(r = 0.851, P < 0.01)$ and 15°C $(r = 0.874, P < 0.01)$.
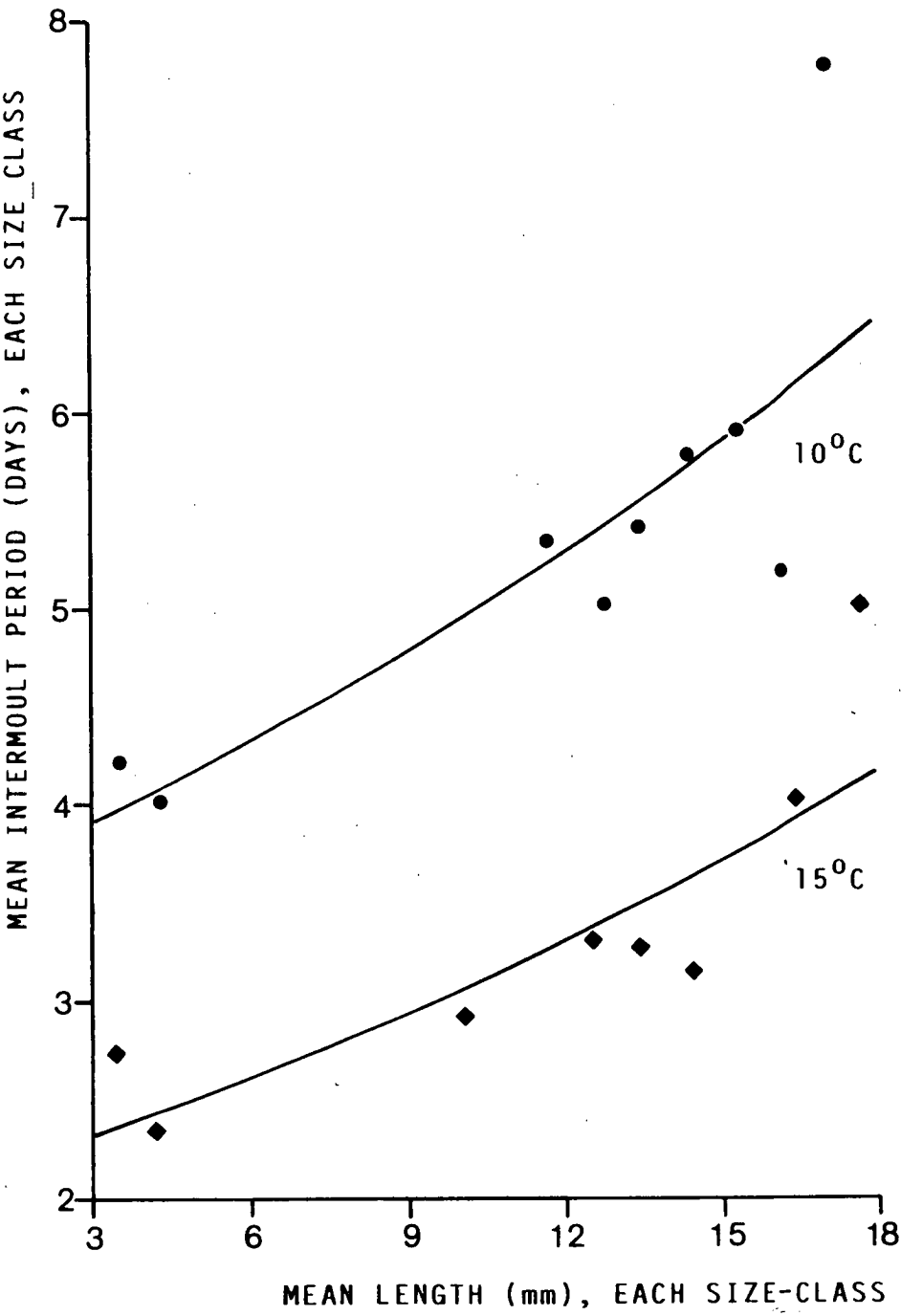
TABLE 2.5 Percentage moult weights and intermoult periods (IP) for various

euphausiid species.

Species		IP days	% moult wt.	Source
Euphausia eximia		4-6	6.4	Jerde and Lasker 1966
E. gibboides			7.7	Jerde and Lasker 1966
E. pacifica	15°C	4		Fowler et al. 1972
	8°C	10		
	5°C	12		
E. pacifica		5-6	10.9	Jerde and Lasker 1966
E. pacifica		5	10	Lasker 1964
E. pacifica		4-6	9.39	Paranjape 1967
E. recurva			10.1	Jerde and Lasker 1966
E. superba		13-14	3	Clarke 1976
E. superba	fed	26.4-27.1	3.23-4.35	Ikeda and Dixon 1982
	starved	29.6	2.63	
E. superba		25-36		Ikeda et al.1980
E. superba		16-26		Murano et al. 1979
Meganyctiphanes norvegica	larvae	4-7		Mauchline 1977b
	juveniles	5-8		
M. norvegica			6.2	Sameoto 1976b
Thysanoessa inermis			5.7	Sameoto 1976b
T. raschi		6	5.92	Paranjape 1967
T. raschi			5	Sameoto 1976b
T. spinifera		5-6	11.7	Jerde and Lasker 1966
T. spinifera		5	8.82	Paranjape 1967
Thysanopoda aequalis			5.3	Jerde and Lasker 1966
Nyctiphanes couchi		5-9		Fowler et al.1971b
N. couchi	larvae	2.9-3.3		Le roux 1973
N. simplex		5-7	12.8	Jerde and Lasker 1966

Mauchline (1977b) also noted logarithmic relationships between size and intermoult period.

It is interesting to note a tendency for the intermoult period to be extended by half to a full day in cases where an animal died in or soon after the moult. The majority of individuals died during moulting, either at stages referred to by Dexter (1981) as premoult, where apolysis is visible, or at post moult.

During the laboratory experiments a total of 123 exuviae were recovered, dried and weighed. The ratio between exuviae weight and dry body weight (% moult weight) ranged between 2.12 and 15.44% with a mean for both 10° and 15°C experiments combined of 5.75% (s = 2.65). Percentage moult weights and IP estimates previously recorded for other euphausiids are shown in Table 2.5. At 10°C, 54.2% of the moults recovered occurred during the night while at 15°C the figure was 68.4%.

2.6 Discussion

Nyctiphanes australis occurred in high densities in Storm Bay during most of the sampling period, at times exceeding the biomass contribution from copepods. Moreover, at times, the densities observed in this study might have been underestimated, because of some of the behavioural aspects of this species. The June 1980 EBS haul indicated that the bulk of the population may have migrated to the sea-bottom in winter, as suggested by Blackburn (1980), and therefore would not have been adequately sampled by the high speed plankton net. The fact that swarms and mass strandings of N. australis were observed at several localities around Hobart in July 1980 (Appendix III) illustrates clearly that while the water column in Storm Bay was almost devoid of N. australis in winter, adults still occurred in extremely high numbers within the general area. The swarming behaviour can also result in vast areas of low densities or no individuals at all, with effective sampling becoming a matter of

chance, a strike or miss situation (Mackintosh, 1966, 1968).

The growth rates of 0.095 mm d^{-1} for larvae and adolescents of
N. australis, with an overall mean growth rate of 0.067 mm d^{-1}, are
almost identical to those determined for an Oregon population of
Euphausia pacifica by Smiles and Pearcy (1971), viz. 0.095 and 0.065
mm d^{-1} respectively. The growth curve of that population of E. pacifica,
determined by Mauchline (1977b) from the data of Smiles and Pearcy
closely approximates the curve for N. australis (Fig. 2.18). Smiles and
Pearcy noted that the year round growth rate of the Oregon population
was faster compared to that obtained by Lasker (1966) for the same species
off the Californian coast. The faster growth rate was attributed to the
higher productivity of the region and the absence of severe winter
temperatures which normally typify the rest of the north-eastern Pacific
Ocean. Lasker (1966) had previously reported a growth rate of 0.034 to
0.048 mm d^{-1} for laboratory reared E. pacifica and noted that these
estimates were more than double values reported previously for larvae in
the field. There are no data on primary production for Storm Bay, though
enrichment from the Derwent estuary is to be expected. However, the sea
temperatures experienced by N. australis in Storm Bay apparently did not
markedly curtail growth in winter. Thus N. australis as expected has a
growth curve more of the von Bertalanffy form than the sigmoid curves
typical of the temperate species (Mauchline, 1977b; Mauchline and Fisher,
1969). The minimum sea temperature of 10°C recorded in July 1980 for
Storm Bay is considerably milder than the winter temperatures of higher
latitudes, which are often associated with lack of growth in cold temperate
and polar euphausiids (Bamstedt, 1976; Clarke, 1976; Fowler et al., 1971b;
Jorgensen and Matthews, 1975; Kulka and Corey, 1978; Mauchline, 1966, 1977b;
Mauchline and Fisher, 1969). The development of N. australis is more
akin to that of tropical species (Roger, 1974) in that the life span
occupies only 12 months with maturity attained in 3 to 4 months. Possibly
this could be shorter, when the faster growth rate of 0.16 mm d^{-1}

FIGURE 2.18   Comparison of growth curves for Euphausia
pacifica (Mauchline, 1977b) and Nyctiphanes
australis.
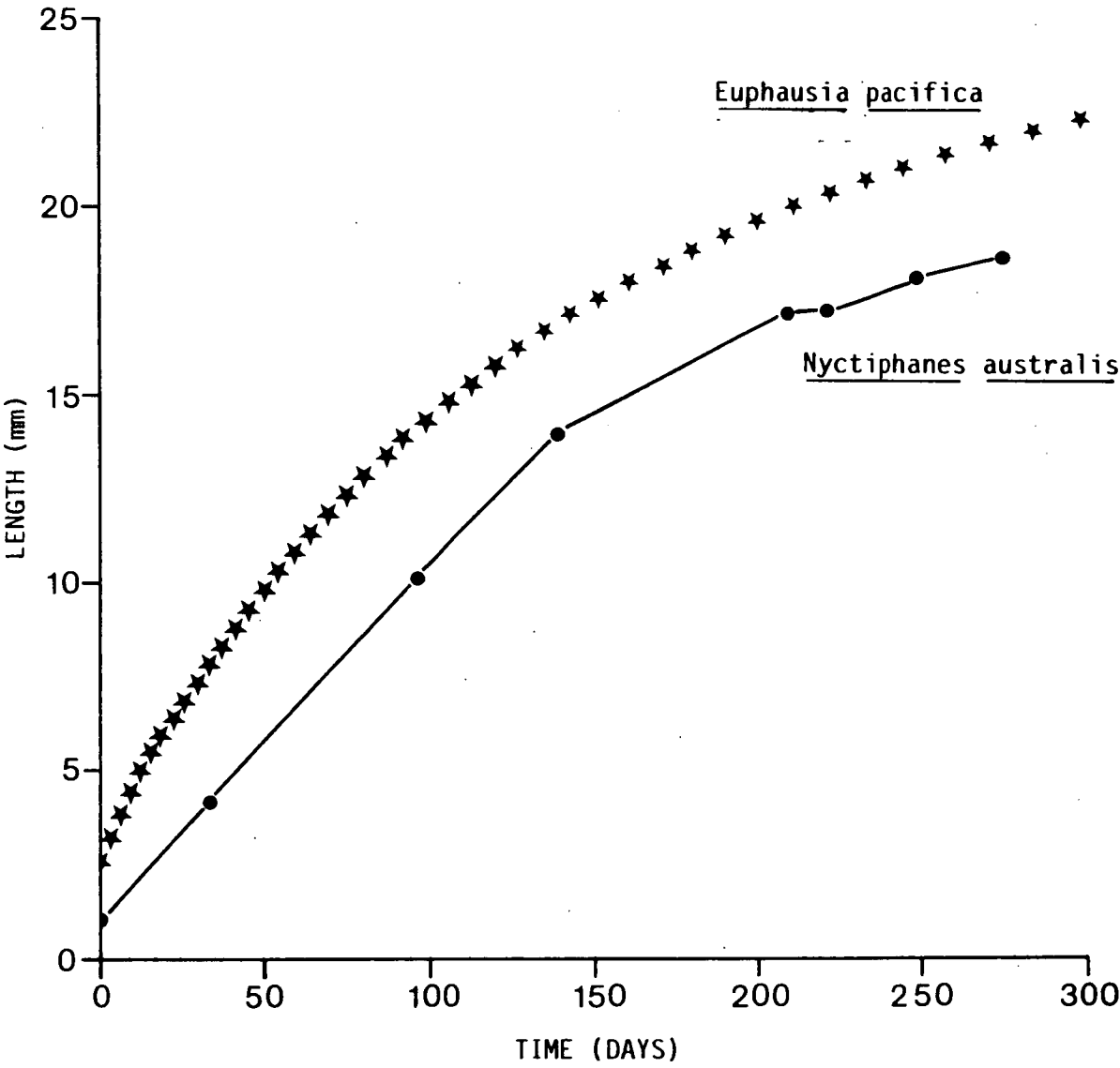
recorded for December 1980 to January 1981 is taken into account.

It is unfortunate that the laboratory experiments failed to confirm the growth estimates obtained from the field data. However, the negative growth recorded by N. australis is not unique. Lasker (1966) had previously noted that some E. pacifica larvae shrank during his laboratory growth studies, while negative growth rates were obtained for Euphausia superba kept in captivity for 7 weeks (Mackintosh, 1967). Bamstedt (1976) attributed the negative growth of a population of Meganyctiphanes norvegica in the field to poor food supply. Le Roux (1973, 1974) had also noted that the quality and quantity of food available affected growth in M. norvegica and Nyctiphanes couchi. Although the stomachs of N. australis were full of food, as seen through the carapace, apparently the artificial food was deficient in some respect. The quality of food used in the experiments is also likely to have had some affect on moulting in N. australis. Inadequate food has been held responsible for the increasing intermoult period seen in M. norvegica (Le Roux , 1974). In E. superba the type of food consumed affected the weight of the exuviae (Ikeda and Dixon, 1982). In this species starvation caused a decrease in exuviae weight by nearly half, with an associated slight lengthening of the intermoult period (Table 2.5). Thus, the % moult weight obtained in the present study may be too low compared to that in the field, with the true intermoult period being slightly shorter. Fowler et al. (1971b), however, found that starved individuals of E. pacifica and M. norvegica moulted at the same frequency as healthy feeding specimens. They reported a trend for the final intermoult period to be prolonged by about 1 day prior to death. Indications of a similar trend were noticed in N. australis.

Despite likely effects on moulting due probably to food, N. australis still displayed a clear trend for the intermoult period to increase as the size of the individual increased in the same exponential fashion as previously reported by Kurata (1962) and Mauchline (1977a,b). The inverse relationship between intermoult period and temperature is similar

to relationships reported for other euphausiids (Fowler et al., 1971b; Ikeda and Dixon, 1982; Kurata, 1962; Lasker, 1966; Le Roux , 1974).

It is particularly interesting to note that while N. australis failed to grow it still moulted regularly. This phenomenon was also observed by Fowler et al. (1971b) and Lasker (1966) for N. couchi and E. pacifica, respectively. Both sources concluded that moulting was a metabolic necessity and continued at the expense of the organic reserves of the animal until death, which in laboratory held euphausiids is most likely to occur during moulting (Clarke, 1976; Fowler et al., 1971b; Mackintosh, 1967; Paranjape, 1967).

The trend for moulting to occur at night has been demonstrated for several euphausiid species (Clarke, 1976; Komaki, 1966; Lasker, 1966; Mackintosh, 1967; Mauchline, 1977b). This was not clearly evident in N. australis, particularly at 10^0C where the percentage moulting at night was only 54%.

CHAPTER 3

BREEDING SEASON AND FECUNDITY

3.1 Introduction

The breeding season of euphausiids can be determined in a number of
ways, viz. by noting the presence of a spermatophore on the female
copulatory organ, the thelycum, changes in the sex ratio, the appearance
of eggs and larvae in the plankton, by the size of larvae, or by the
state of maturation of the ovaries (Falk-Petersen and Hopkins, 1981;
Makarov, 1979; Mauchline, 1980; Mauchline and Fisher, 1969). The
spermatophore method is noted for its accuracy as the length of time
that females are found with attached spermatozoa is usually closely
parallelled by the duration of the breeding season (Mauchline and
Fisher, 1969). Nevertheless in some species, e.g. Euphausia superba,
deposition of the spermatophore on the thelycum may precede egg laying
by months (Mauchline, 1980). However, this particular method cannot
always be employed, as many species lack a thelycum, in particular
Nyctiphanes australis (Sheard, 1953).

One of the most accurate methods would seem to be the direct monitor-
ing of eggs and/or larvae in the water and possibly also, noting the
presence of eggs in external ovisacs in those species that protect their
eggs. Makarov (1979) successfully defined the breeding season of
Thysanoessa macrura by the presence of large numbers of nauplii and
metanauplii in the water during the summer months.

In general, most temperate euphausiids tend to have short, distinct
breeding seasons either post-winter or in summer (Berkes, 1976; Boden,
1951; Mauchline, 1980; Mauchline and Fisher, 1969), while the season
in tropical euphausiids is usually all year round (Roger, 1974).

Following oviposition in euphausiids, the eggs are either shed
directly into the water or retained attached to the last 2 pairs of

thoracic legs. The hatching stage in the latter case, is usually a pseudometanauplius as opposed to a nauplius in direct release (Mauchline and Fisher, 1969). Out of the total of 85 species of euphausiids, 57 have direct egg release. Fecundity in these species has been estimated by counting the eggs in the mature ovary (Bargmann, 1937; Naumov, 1962; Ponomareva, 1959; Roger, 1978; Zelikman, 1958). Fecundity has been defined as the total number of eggs released by a female in any one breeding season (Mauchline, 1968). Bargmann (1937) counted all ova within the ovary, regardless of the developmental stage, while the other authors counted Stage IV (mature) eggs only.

Mauchline (1968) criticized the ova counting techniques, claiming overestimates of fecundity result, as not all Stage IV eggs within the ovary are necessarily released. He developed another method based on the assumption that the volume of the spent ovary is approximately half that of a mature ovary. Thus fecundity could be calculated as the number of eggs whose volume equals the difference in volume between the mature and spent ovary. However, he criticized his own method, noting that there was a tendency to underestimate fecundity and a multiplication factor of 2.5 was often necessary. The method was also questioned by Roger (1976), who claimed that it can be difficult at times to recognise spent ovaries, particularly in tropical species.

Fecundity can be estimated by keeping females in captivity, although individuals apparently lay only a few eggs and numbers tend to bear little relation to the number of eggs released in the sea (Mauchline and Fisher, 1969).

The ova counting and volume methods for determining fecundity are applicable to species which carry their eggs, i.e. those belonging to the genera Nematobrachion, Nematoscelis, Nyctiphanes, Pseudeuphausia, Stylocheiron and Tessarabrachion. However, a simpler method exists, i.e. by counting the number of external eggs in the ovisacs. Care must be taken when counting, as the number of eggs in each of the

paired egg sacs can differ (Boden, 1951). In particular Gros and Cochard (1978) found more eggs in the left ovisacs of Nyctiphanes couchi than in the right. Ovisacs can often be ruptured, resulting in partial or complete loss of eggs, as observed in N. capensis (Talbot, 1974). Although counting of external eggs gives an accurate account of a single egg release, it does not give a total measure of fecundity. It is still necessary to examine the maturation of the ovary to determine the number of batches produced.

Estimates of fecundity in euphausiids have ranged from as low as 3.5 (mean value) for Stylocheiron elongatum in the tropics (Roger, 1978) to 33,300 for Euphausia superba in the antarctic (Naumov, 1962). Roger (1974) has commented that fecundity in the tropics is in general lower than in cold and temperate species, however, this is counterbalanced by a more rapid cycle and earlier maturity.

Sheard (1953) claimed that N. australis exhibits continuous release of larvae in south-eastern Australia coastal waters, as CI larvae were found in all months, though actual figures were not provided, nor any figures for fecundity. Jillett (1971) however, presented evidence of several peaks of larval release in a population of N. australis in New Zealand.

In the present study, the life history of N. australis was studied in detail to ascertain accurately the extent of the breeding season and the main peaks of larval release. Fecundity was also examined particularly in relation to size of the female. It has been demonstrated in other euphausiids that egg production increases with body size (Gros and Cochard, 1978; Komaki, 1967; Nemoto et al., 1972; Wang, 1965). In addition, the degree of maturation of ovaries was monitored throughout the year to establish if N. australis females are capable of multiple releases of eggs.

3.2 Methods

The female Nyctiphanes australis lacks a thelycum (Sheard, 1953),

therefore the breeding season could not be determined by the presence

of spermatophores. Instead the presence of CI larvae (second instar

after hatching) in the water, was monitored for each month. Although

the hatching stage, the pseudometanauplius, would normally be observed,

the sampling technique described in Chapter 2 resulted in a failure to

capture this instar in large numbers. The sex ratio of adults and the

presence of external eggs on females was also noted for each month, to

provide further information towards defining the breeding season.

Fecundity was determined by counting external eggs on 31 females.

Another 27 females carrying developing nauplii were also examined. To

observe seasonal development, ovaries were removed from a total of 40

females (36 adults and 4 adolescents) captured in Storm Bay over a period

spanning 11 sampling months. These were compared with ovaries from 4

other females taken near Mewstone Is., South Tasmania, taken in April

1980 and 4 more females from Pt. Phillip, Victoria, August, 1978.

All animals were fixed in 5% formalin in seawater. The ovaries were

teased out on microscope slides and wet mounts were prepared. The

developmental stage of ova were classified according to the nomenclature

used by Kulka and Corey (1978) for Thysanoessa inermis and for

Meganyctiphanes norvegica and T. raschi by Mauchline (1968) (Table 3.1).

A total of 200 eggs and 200 developing nauplii, that had been preserved

for 12 months in 70% alcohol, were dried overnight at 60°C and weighed

so that counts of these stages could be converted to dry weight.

3.3 Results

It can be seen from Fig. 2.7 that larvae of the size-class 1.00-1.99 mm

were present throughout the entire sampling period, though in very low

numbers in winter months May-June 1980, indicating that breeding occurs

TABLE 3.1 Description of ova stages for Thysanoessa inermis (Kulka and Corey, 1978), and T. raschi and

Meganyctiphanes norvegica (Mauchline, 1968).

	SIZE (mm)			
Stage	T. inermis	T. raschi	M. norvegica	DESCRIPTION
I	0-0.10	0.011	0-0.12	Nucleus very large relative to total size, granular cytoplasm.
II	0.10-0.20	0.11-0.19	0.12-0.18	Nucleus and egg grow at roughly the same rate, but at end of Stage II cytoplasmic space increases faster in size. Very granular cytoplasm.
III	0.20-0.27	0.19-0.27	0.18-0.23	Growth rate of nucleus appears to accelerate a little, Yolk globules distinct.
IV	0.27-0.36	0.27-0.37	0.23-0.37	Transparent yolk globules. Nucleus rarely visible.

virtually all year round. The actual breeding season can be more

clearly defined by plotting the number of CI larvae for each month

(Fig. 3.1), which shows that the main period of larval release was

continuous from August 1980 to March 1981, except for breaks in November

1980 and January 1981. Sampling ceased in March 1981, thus it is quite

possible that the main peak may have extended beyond this period.

Certainly females carrying eggs were observed in April 1980. The period

during which females carrying eggs were observed, in fact, corresponded

with the main release of larvae, i.e. females with external eggs were not

found in winter months (Fig. 3.2). Only very low densities of CI larvae

were observed in the colder months April–June 1980, therefore it is not

surprising that females with external eggs were not taken. The percentage

fluctuated markedly from as low as 1.14% in November 1980, to 44.44% in

March 1981. The overall mean was 20.03% during the main period of larval

release. The fact that not all females were carrying external eggs at the

same time, shows that there is no synchronised release of larvae.

Synchronisation is usually seen in temperate and polar species of euphausiids

which have short but distinct peaks of egg release (Mauchline, 1980;

Mauchline and Fisher, 1969).

The sex ratio also varied from month to month around a mean of 65.74%

♀, with values ranging from 49.62% in November 1980 to 86.32% in April

1980 (Fig. 3.2). However, there was no apparent pattern in the fluctuations.

The low values of 49.62% for females and 1.14% for females carrying eggs

in November, coincided with the disappearance of large adults which have

carried through from the preceding 1979/80 summer. These adults, identified

earlier in Chapter 2 as the December 1979, cohort were last observed in

October 1980 (Fig. 2.7).

A clear trend exists between the production of eggs and increase in

body weight of the female (Fig. 3.3). The relationship can be expressed

as:-

$$y = 23.99 + 17.38x \quad , \quad (3.1)$$

FIGURE 3.1 Monthly densities of Calyptopis I larvae.
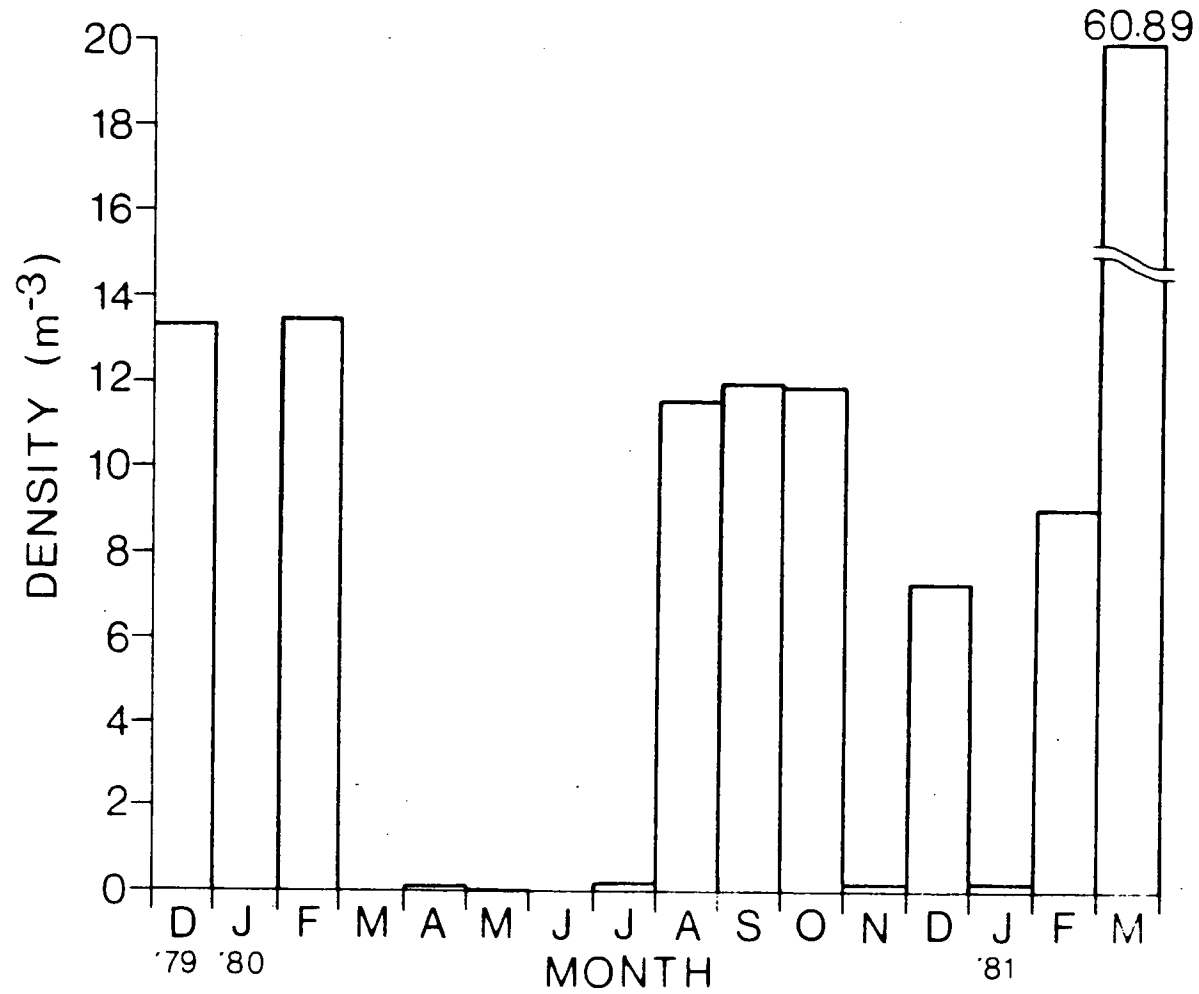
FIGURE 3.2   Percentage of females in adult population and
percentage of females bearing external eggs (shaded).
The total number of adults captured per month is indicated.
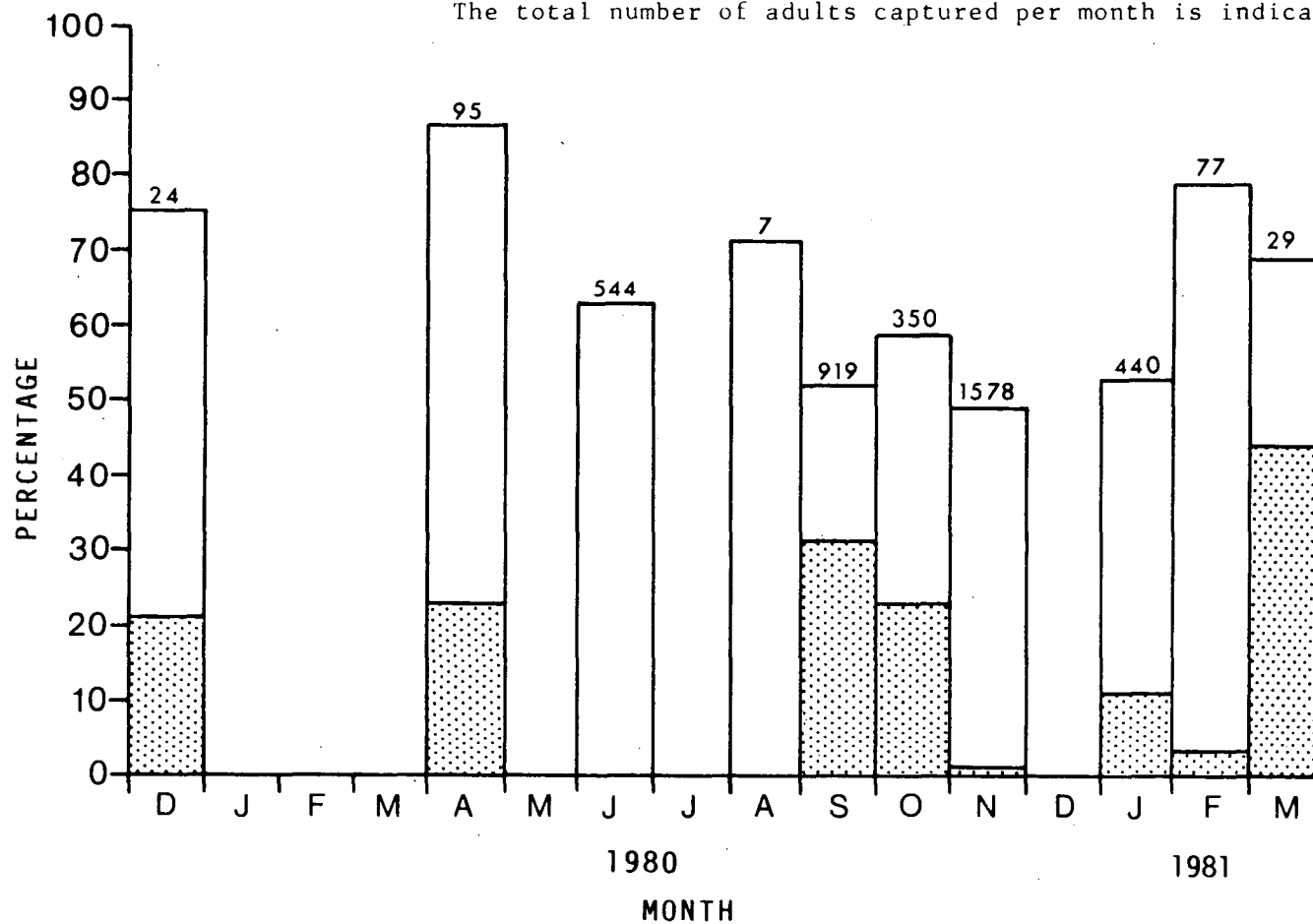
FIGURE 3.3   Relationship between the number of eggs in the external ovisacs and weight of female. ($r = 0.734$, $P < 0.001$)
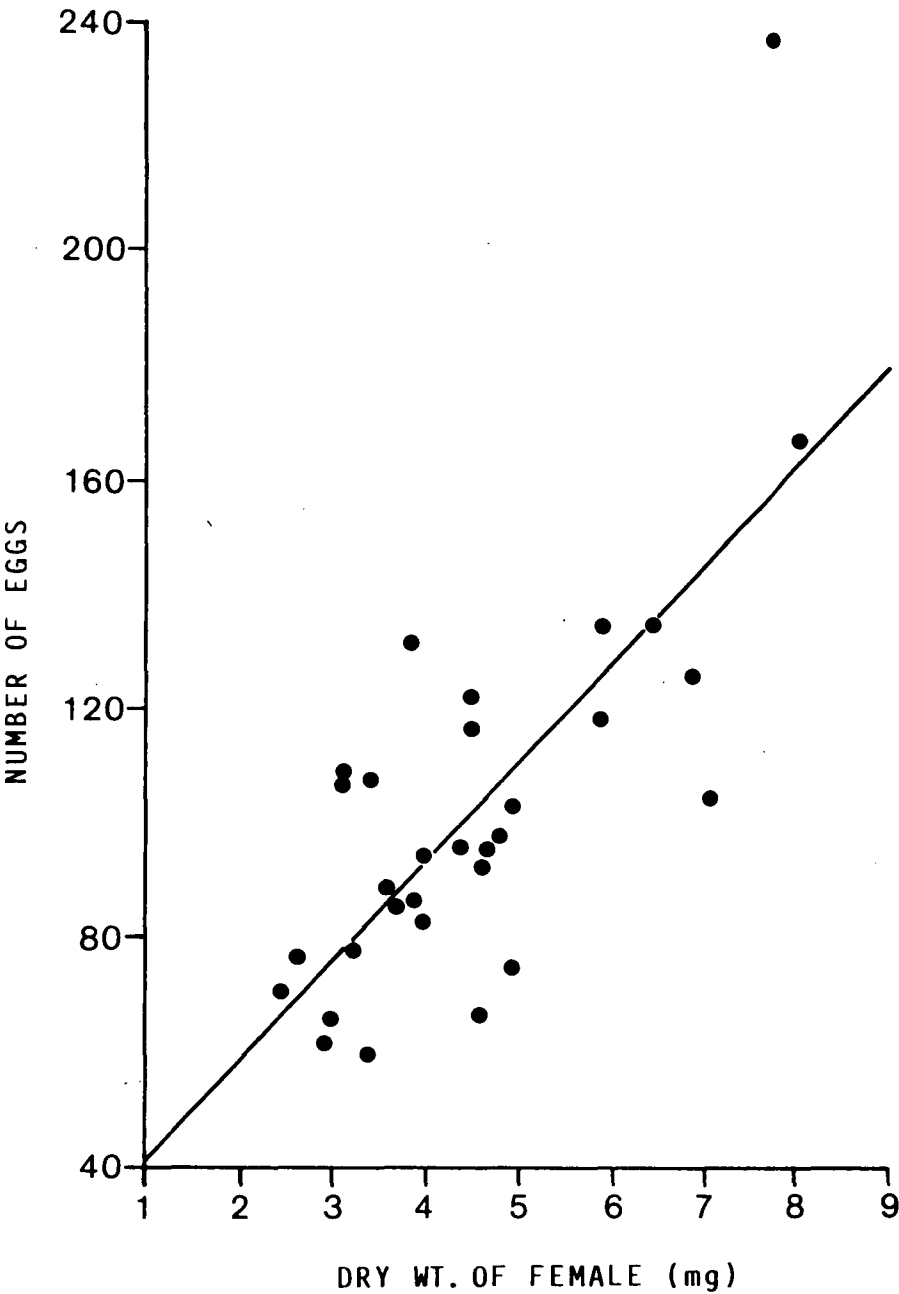
FIGURE 3.4   Number of nauplii in the ovisacs per
              weight of female. (No significant
              relationship)
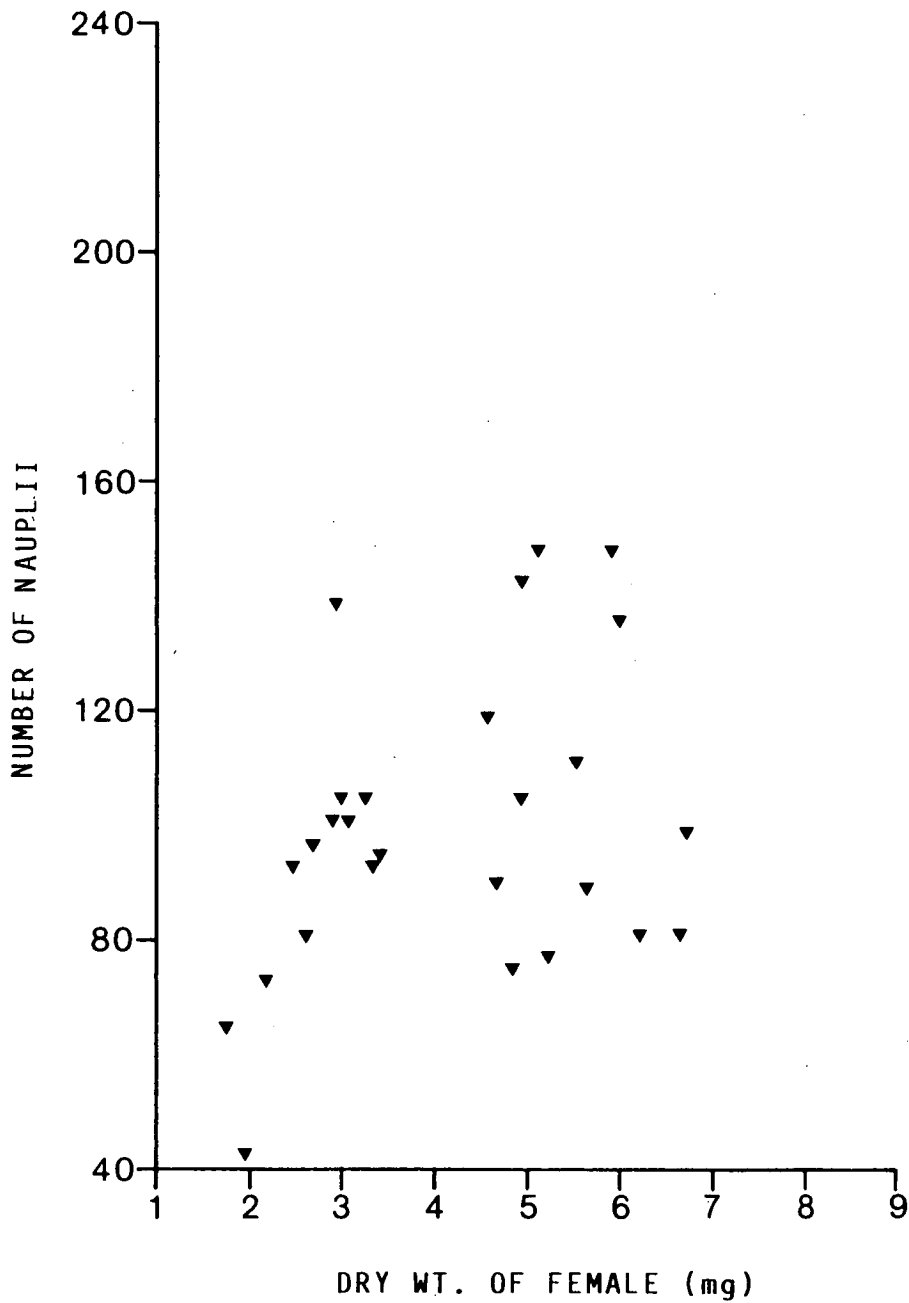
where y is number of eggs and x is the dry weight in mg of the female
(r = 0.734, P<0.001). No relationship was found between size and the
number of nauplii retained in the ovisacs (Fig. 3.4). Since all care
was taken to count females with intact egg sacs, the results imply that
some eggs are lost during external development.

The average dry weights of the egg and developing nauplius for
N. australis were 0.0086 and 0.0081 mg respectively. The egg weight
is similar to that recorded by Nemoto et al. (1972) for Euphausia
pacifica.

Female N. australis are capable of producing more than one batch of
eggs (or multiple generations) as evident in Table 3.2., i.e. ova are
developing within the ovary while external eggs are present, In many
cases more than one stage (batch) of ova are developing within the
ovary (Table 3.2, Fig. 3.5). For example, specimen 13 (14.00 mm) had
75 eggs in the ovisacs with approximately 100 Stage III ova (181 μm mean)
and yet more Stage I ova (.88 μm mean) developing in the ovaries. Only
3 undeveloped ovaries were found, two of these being in adolescents
while the third was in a small female of 11.8 mm, taken at the end of
the main period of larval release. The values in Table 3.2 are the mean
size of ova of that particular stage found in the ovary. The size ranges
of the various egg stages are similar to those given by Kulka and Corey
(1978) and Mauchline (1980) (Tables 3.1 and 3.3).

If the growth curve for egg development in Meganyctiphanes norvegica
(Mauchline, 1968) is applied to the developing eggs of N. australis, then
the development time can be calculated as follows, using the ova of
specimen 13 (Table 3.2) as an example:-

	Development time (days)
Primary oocyte – 88 μm (Stage I)	12.6
88 um – 181 μm (Stage III)	13.3
181 um – 398 μm (external egg)	31.0
Total	56.9

TABLE 3.2 Size of ova in the ovaries and ovisacs of N. australis.
Gonad condition refers to whether the ovary was either undeveloped (u)
or spent (s). n = nauplii in ovisacs, + = very few ova of that stage
and were not measured.

Location Month, Year	Specimen	Size of female mm	Gonad condition	Size of ova at each stage (µm)				External eggs on ovisacs
				I	II	III	IV	
Storm Bay								
February 1980	1	13.9		88.1	–	–	293.6	–
April 1980	2	11.5		77.4	–	–	–	–
	3	12.5	s	65.6	–	–	–	393
	4	11.5		88.1	–	–	–	–
	5	11.8	u	–	–	–	–	–
June 1980	6	15.4		63.6	–	–	–	–
	7	16.7		55.1	165.2	–	–	–
	8	17.9		85.9	–	–	–	–
	9	13.9		61.3	–	–	–	–
July 1980	10	14.0		75.2	–	–	–	–
August 1980	11	18.0		87.4	–	–	267.3	–
	12	15.8		93.2	–	–	261.3	–
September 1980	13	14.0		88.1	–	181.2	–	398
	14	17.6		103.4	–	210.1	–	n
	15	18.0		57.8	127.7	195.7	–	385
	16	16.6		86.3	–	–	337.9	n
October 1980	17	14.3		87.6	–	–	338.4	–
	18	12.6		51.4	129.2	–	–	370
	19	13.5		55.1	163.3	–	243.4	405
	20	13.1	s	+	+	–	–	395
November 1980	21	13.7		77.1	–	198.2	–	–
	22	15.3		73.4	143.7	–	–	375
	23	13.4		56.9	–	193.6	–	–
	24	12.6		106.7	–	–	–	–
January 1981	25	15.3		81.8	123.3	229.1	–	–
	26	14.7		67.5	137.6	–	–	–
	27	14.4		70.8	140.9	–	–	n
	28	15.8		98.0	–	209.5	–	n
February 1981	29	13.8		48.9	112.7	–	352.3	–
	30	12.4		91.8	–	–	320.8	–
	31	14.1		97.3	–	–	280.5	–
	32	15.8		97.3	–	219.3	–	–
March 1981	33	11.9		63.8	117.0	–	248.6	n
	34	12.5		88.1	–	189.0	–	384
	35	13.4		80.7	143.4	–	–	378
	36	11.4		100.9	166.4	–	–	–
February 1981	37	10.2		40.4	–	–	–	–
	38	10.8	u	–	–	–	–	–
(Adolescents)	39	10.0	u	–	–	–	–	–
	40	9.2		40.4	–	–	–	–
Mewstone Island,	41	14.2		62.4	–	–	–	–
S. Tasmania,	42	15.4		74.7	121.1	–	–	–
April 1890	43	14.7		56.3	–	–	–	–
	44	14.6		61.9	–	–	–	–
Port Phillip Bay	45	14.7		83.9	140.7	–	–	–
Victoria	46	15.1		85.6	151.4	–	–	–
August 1978	47	15.1		99.1	–	192.9	–	–
	48	14.6		98.7	145.7	225.7	–	–

FIGURE 3.5   Ovary of <u>N. australis</u> with two stages of developing ova.

N: nucleus, ST I: Stage I ova, ST III: Stage III ova.

Scale bar = 100 μm.

3.5
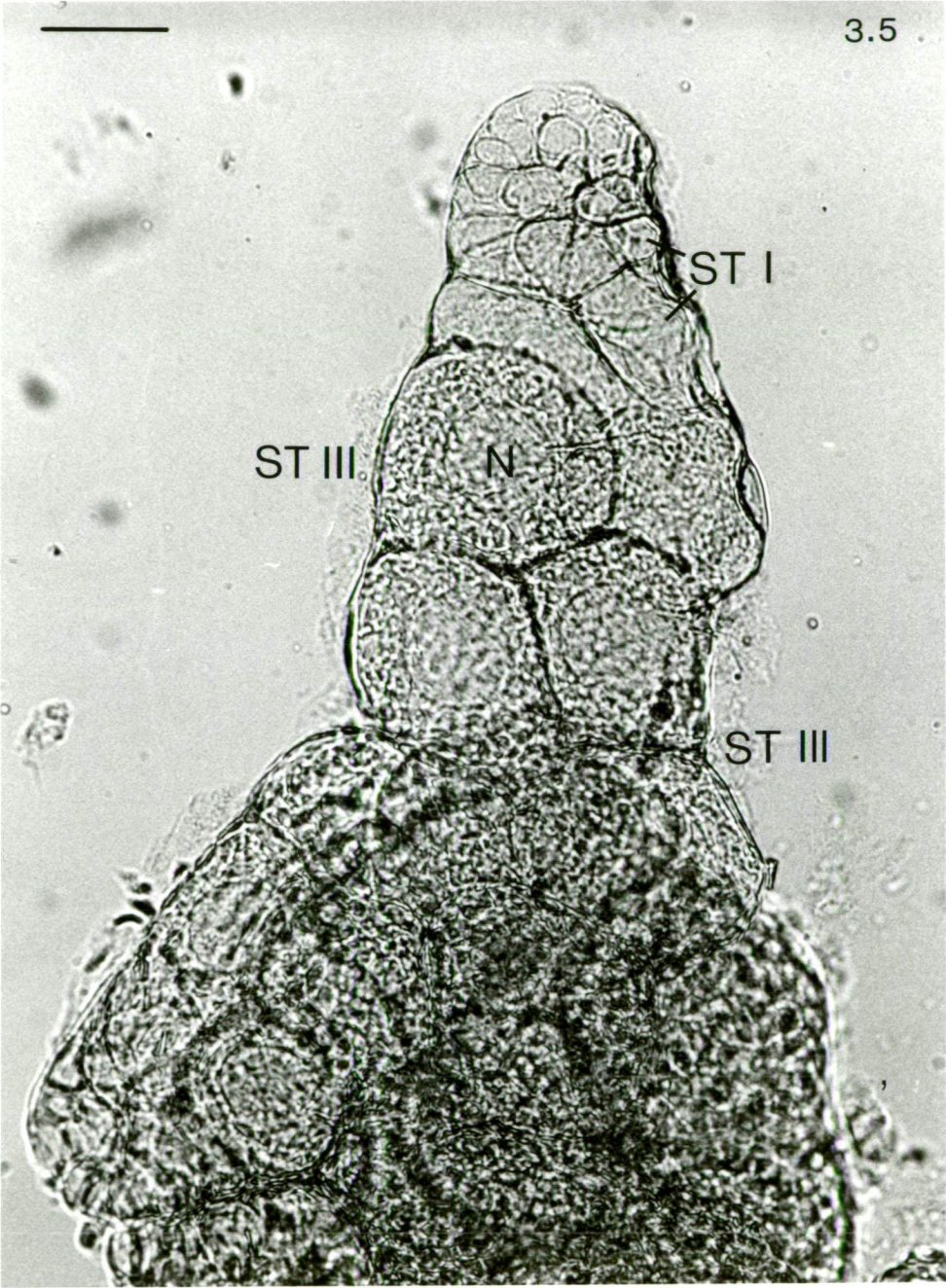
TABLE 3.3 Size ranges of developing ova in N. australis.

Stage	Size Range mm
I	0 – 0.11
II	0.11 – 0.17
III	0.17 – 0.24
IV	0.24 – 0.35

TABLE 3.4 Estimated total development time for external eggs and time between successive ovipositions for N. australis.

Specimen	External egg size µm	Total development days	Time between oviposition days
13	398	56.9	31.0
15	385	55.0	27.0
18	370	52.9	34.4
19	405	57.9	23.1
22	375	53.6	33.0
34	384	54.9	27.9
35	378	54.0	33.5
		Mean 55	Mean 30

TABLE 3.5   Fecundity. Estimated total egg production during the
lifetime of a female N. australis. Length was
determined from the growth curve (Fig. 2.14) every 30
days. The number of eggs was determined using equation 3.1.

Time days	Length of female mm	Dry body wt. mg	Number of eggs
0	11.00	1.4300	49
30	13.67	2.7714	72
60	15.10	3.7520	89
90	16.45	4.8697	109
120	17.47	5.8487	126
150	18.26	6.6918	140
180	19.05	7.6129	156
210	19.84	8.6156	174
240	20.03	9.7025	193

Total   1108

This technique was applied to another 6 females which were carrying
eggs, mainly to establish the interval between oviposition, of one batch
and the next (Table 3.4). The interval between ovipositions was calculated
to be 30 days, with total development time of the egg approximately 55
days. These values may, in fact, be considerably shorter, since
M. norvegica experiences much lower temperatures than does N. australis.
To the best of my knowledge, the development curve of M. norvegica
offered the fastest growth rate of ova. Previous estimates of egg
maturation have ranged from 60 days in M. norvegica (Mauchline, 1968),
90 days in Thysanoessa inermis (Kulka and Corey, 1978), and as long as
120 days in Euphausia superba (Mauchline, 1968).

The smallest recorded female bearing external eggs was 11.00 mm, while
the largest female taken in this study was 20.75 mm. If the smaller size
is taken as the start of egg release and the larger size as the size
limit of N. australis, then the total number of eggs produced by a female
in a lifetime can be calculated as 1100 (Table 3.5). This is assuming
that a female produces a batch of eggs every 30 days over a season of
approximately 240 days. The value of 1100 can also be taken as a measure
of fecundity, since the total expected spawning time of a female is
shorter in length than the duration of the main peak of larval release.

3.4 Discussion

Repeated maturation has been observed in several species of Euphausia
and Thysanoessa (Makarov, 1975). Makarov noted that the ovaries were
capable of producing more than one batch of eggs, with the ovaries
usually regressing to a distinct spent stage between each release.
Roger (1974) reported that reproduction in tropical euphausiids was
nearly a continuous process. Later, Roger (1976) observed that the ovaries
of many tropical species contained large Stage IV, as well as very small
eggs. However, he claimed that this was no indication of continuous

maturation, as other stages were not present between the two sizes. It could be argued that, in fact, maturation was continuous because of the presence of the smaller ova, i.e. there was no regression to a spent stage.

The results of the present study show clearly that in the Storm Bay population of N. australis, maturation of the ovaries was continuous, as evidenced by the presence of more than one stage of developing ova in the majority of ovaries examined (Table 3.2, Fig. 3.5). The fact that 2 adults with spent ovaries were observed out of a total of 44 examined would suggest that while maturation was continuous for prolonged periods, the ovaries do occasionally regress to a resting stage. The estimated fecundity of 1100 eggs, should, therefore, be taken as an absolute maximum, since periods of regression to spent stages would naturally reduce this figure. The results indicate that the population from Port Philip Bay also exhibited continuous maturation. However, the extent of continuous maturation in other populations can only be determined by more extensive sampling over the entire range of N. australis.

Linear relationships between the number of eggs in the ovisacs and body size has already been demonstrated for a number of egg-carrying euphausiids (Gros and Cochard, 1978; Komaki, 1967; Nemoto et al., 1972; Wang, 1965). Thus, it is not surprising that N. australis shows a similar relationship. Komaki (1967) generalised, that in Nematoscelis difficilis the number of eggs produced doubled as the weight of the female doubled. A similar trend occurred in N. australis. More importantly the number of eggs produced by N. australis related closely to that of other species of Nyctiphanes. Gros and Cochard (1978) noted that a female N. couchi of 4.48 mm carapace length, approximately 10.50 mm total length, carried a mean number of 41.5 eggs. Boden (1951) observed as many as sixty eggs in N. simplex, while 100 eggs were approximated for N. capensis (Talbot, 1974). All values are within the observed range for N. australis.

The lack of a relationship between size and number of nauplii in the

ovisacs, despite the proportionality between eggs and body size
already demonstrated for N. australis, is somewhat puzzling. Viability
of the eggs and natural mortality during development may be contributing
factors. Certainly there was a tendency for large females to release
fewer nauplii than eggs produced. However, this did not occur in
smaller females, if anything there tended to be a higher number of
nauplii in relation to size. Mortality of eggs should affect all brood
sizes with some sort of relationship between nauplii and size of female
expected. A seasonal effect on viability may be responsible, since
females were sampled from more than one month. As yet a clear explanation
cannot be provided, thus further sampling is required. In this study
only a small number of females with intact ovisacs were obtained, since
ovisacs are easily ruptured during sampling (Talbot, 1974).

The continuous breeding of N. australis over most of the year, with
a prolonged post-winter peak extending over the summer, is similar to the
pattern reported for N. couchi (Frost, 1932; Gros and Cochard, 1978).
Sheard (1953) had previously claimed that CI larvae of N. australis
occurred throughout the year. While actual figures were not given, he
noted that the breeding was most intense in the warmer months from
October to January. Examination of CI densities (Fig. 3.1) and the
presence of females carrying eggs (Fig. 3.2), has indicated that the main
peak of larval release in the Storm Bay population was August to March,
possibly extending to April. The duration of the main breeding period
is, however, likely to vary seasonally. Mauchline and Fisher (1969)
noted that the breeding season of Meganyctiphanes norvegica in the Clyde
River, Scotland, varied from year to year. In the present study, the
lack of females with eggs in August 1980, at a time of high densities
of CI larvae may have resulted from the fact that a low number of adults
were captured (7).

N. australis larvae growing at the rate of 0.095 mm d^{-1} (Fig. 2.14)
would reach sexual maturity in approximately 3.5 to 4 months, or 2.5

months at the rate of 0.160 mm d^{-1} (Fig. 2.15). Thus, at least 3 generations could be produced during the main breeding period August to March. A batch of larvae released by an overwintering female in August would itself produce a generation in November-December, which in turn would produce a third generation in February-March. This interpretation corresponds with observations of Jillett (1971). That is, populations of N. australis in Hauraki Gulf, New Zealand, exhibit three breeding periods per year, which indicates the production of multiple generations. The only other euphausiid known to have multiple generations is Thysanoessa longicaudata, which produces two discrete generations in some regions of the eastern North Atlantic (Lindley, 1978).

A definite break in the main breeding season occurred in November, 1980, as shown by both the lack of CI larvae and females bearing external eggs. Thus, the breeding season was divided into two main peaks. A similar break, of apparent regularity, also split the breeding season of N. couchi into two periods (Gros and Cochard, 1978). In the present study, the November break coincided with the disappearance of the December 1979 cohort. Apparently the sudden removal of reproductive females, which have carried over from the previous breeding season 1979/80, resulted in the decline in egg production. Breaks of this nature are likely to be regular events and should be taken into account when calculating fecundity. Therefore the estimate given in Table 3.5 should be reduced to approximately 1,000. Although a decrease in the number of CI larvae was also observed in January 1981, it is doubtful that it is a true break in the breeding season, as females carrying eggs were prominent in that month.

Changes in the sex ratio are often associated with the breeding season (Falk-Petersen and Hopkins, 1978; Mauchline, 1980; Mauchline and Fisher, 1969). Other changes can be attributed to the male portion of the population dying off, as the cohort progresses through time. Gros and Cochard (1978) reported a change from 1:1 to 0:1 for female N. couchi.

Although there was considerable variation in the sex ratio of N. australis, there was no apparent pattern, particularly in relation to the breeding season. Thus examination of the sex ratio was an ineffective tool for establishing the breeding season for N. australis.

PART TWO

CHAPTER 4

FOOD AND FEEDING

4.1 <u>Introduction</u>

The importance of euphausiids at intermediate trophic levels in the sea is well recognized (Kulka <u>et</u> <u>al</u>., 1982). However, in order to define the exact position of a particular species within a food web, detailed knowledge of the species' dietary requirements is necessary (Mauchline, 1977a). Efforts in the past to define the diets of euphausiids have mainly centred around the structure and function of the feeding appendages, particularly setation, and direct stomach content examination supplemented with feeding experiments. Previous investigations have been reviewed by Mauchline (1967b, 1980), Mauchline and Fisher (1969) and Nemoto (1972).

Mauchline (1967b) considered the principal feeding appendages to be the labrum, and the paired mandibles, labia, maxillules and maxillae, together with the first and second thoracic legs. Mauchline suggested that the rest of the thoracic legs are of less importance, particularly in relation to filter feeding, as they are generally less setose than the first two pairs. Instead, these limbs are used mainly for detrital feeding and for snatching prey by rapid lateral movements of all the thoracic limbs, which results in a suction effect. Nonetheless, Berkes (1975) claimed that active predation in euphausiids is still to be demonstrated. The thoracic legs are often referred to collectively as the "food basket" (Mauchline, 1967b; Mauchline and Fisher, 1969).

In small larvae the main filtering appendages are the maxillae and maxillipeds (Gopalakrishnan, 1973). The maxilliped of the larvae later differentiates into the first thoracic leg. Other thoracic legs develop progressively, a pair at a time, with each instar during the furcilial stages. Previously differentiated legs increase in complexity as others develop, with the first thoracic leg being one of the last legs to fully

differentiate. Development of thoracic limbs is generally complete
by the postlarval stage. The development and functioning of the
thoracic legs, and other feeding appendages, has been described for a
number of species. A remarkable similarity in development is exhibited
(Boden, 1951; Gopalakrishan, 1973; Knight, 1975, 1976, 1978).

Examination of the setation on feeding appendages is one aspect of
structural analysis that can define the likely diet of a species
(Berkes, 1976; Mauchline and Fisher, 1969; Nemoto, 1967). In particular,
the structure and spacing of setules on the setae i.e. the filtering
mesh, is indicative of the relative importance of filter feeding and the
minimum particle size that can be filtered (Nemoto, 1967). Typical
filter-feeding euphausiids have well developed setae and close spacing
between setules on the maxillae and the ischium and merus of the thoracic
legs. These euphausiids tend to occupy surface waters where phytoplankton
is abundant. In Euphausia superba, a species with a high content of
phytoplankton in its diet, the spacing between setules on the thoracic
leg ischium is 5-7 µm, the finest mesh so far recorded on thoracic legs
(Nemoto, 1967). The carnivorous Thysanopoda egregia lacks setae on the
ischium and merus of its thoracic legs (Nemoto, 1977). Nemoto (1967)
also claimed that in filter feeding euphausiids, the ischium of the
thoracic leg is long in relation to the merus, with a shortening of the
ischium occurring in tropical and sub-tropical species which are
considered more carnivorous.

Recently two methods have been devised, that can be used to indicate
the feeding mode of a euphausiid, i.e. predatory, omnivorous or filter
feeding. The first method is by analysis of the structure of the mandible.
Itoh (1970), working on copepods, developed the "edge index", a measure
of the dentition of the pars incisiva or cutting surface. Animals with
an "edge index" less than 500 were considered herbivorous, those with a
value greater than 900 were considered carnivorous, while others with an
index in between 500 and 900 were omnivorous. This method was applied

to _Meganyctiphanes norvegica_ and _Euphausia krohni_ by Artiges _et al_. (1978),
who obtained values of 895 and 700 respectively, thus defining these two
species as omnivores. However, Mauchline (1980) considered that the
"edge index", when applied to euphausiids, was too cumbersome compared
to the method devised by Nemoto (1977). It had been noted previously
that filter feeding euphausiids tended to have a large _pars molaris_, the
grinding surface of the mandible (Mauchline and Fisher,1969; Ponomareva,
1976). Nemoto (1977) simply compared the length of the _pars molaris_ (pm)
to that of the _pars incisiva_ (pi) and produced a pm/pi ratio index.
Filter feeding euphausiids have a large pm/pi ratio, e.g. _E. superba_
with 1.09 (Nemoto, 1977), while predatory species have a low ratio, an
example of which is _Stylocheiron abbreviatum_ with a ratio of 0.27
(Mauchline, 1980).

The stomach of euphausiids is relatively small, representing only about
1% of the body weight when full (Roger, 1978). Thus analysis of stomach
contents has usually been restricted to providing a qualitative list of
items only (Roger, 1974). Roger (1973a, 1974) noted that one major
drawback of this type of investigation, is that only a few dietary items
are recognisable, with a bias towards structures that are resistant to
digestion and maceration. The relative contribution of crustacean zoo-
plankton can often be underestimated because the exoskeleton may not
necessarily be ingested (Ponomareva, 1954). Nevertheless, stomach content
analysis is still important when defining the diet of a species (Berkes,
1976, 1977b; Fisher and Goldie, 1959; Mauchline, 1959, 1960, 1966; Ruud,
1936; Sameoto, 1976a, 1980; Talbot, 1974). On the basis of stomach contents,
contents, Mauchline and Fisher (1969) divided the diet of euphausiids
into three classes; (1) material filtered from the water, e.g. diatoms,
dinoflagellates, and tintinnids; (2) zooplankton taken by predation;
and (3) bottom detrital matter. Recently, Nemoto (1977) provided
evidence that the large euphausiid _T. egregia_ may predate on fish.

Some aspects of feeding in N. australis have already been documented. Mauchline (1967b) noted that the maxillae and thoracic legs of N. australis are heavily setose, as are those of the other species in the genus, and thus concluded that N. australis was potentially a very effective filter feeder. However, a measure of the filter mesh size, i.e. the distance between the setules, was not provided. In preliminary studies the diet of N. australis adults has been described as being primarily detrital, with diatoms and crustaceans occasionally being taken (Palmer, 1978; Sheard, 1953). An analysis of the larval diet was not included. The diet of Nyctiphanes couchi has also been described as detrital (Mauchline, 1967b; Ruud, 1936).

Fenton (1981) recently attempted to establish the diet of N. australis by fluorometric analysis of chlorophyll pigments in the gut and also by stable isotope analysis. The fluorometric analysis indicated that larvae fed on phytoplankton while larger larvae fed more on detrital matter. Stable isotope analysis, which provides a dietary history of the animal rather than an analysis of the previous meal, suggested that larvae were more predatory while adults consumed phytoplankton. This work was supplemented with particle size selection experiments using inert plastic beads of varying sizes. Preference was exhibited towards large particles by N. australis when the plastic beads were used, with the largest beads ingested in the 50 - 60 μm range. The results obtained by Fenton (1981) are somewhat contradictory and confusing, particularly between the fluorometric and stable isotopes analyses, however, the author stressed the preliminary nature of the study. Fenton acknowledged the difficulty in interpreting results from several methods yet still stressed the value of using as many techniques as possible when defining the diet of a species. Previous studies typically dealt with only one method.

In order to expand upon the previously acquired knowledge on feeding in N. australis detailed analysis of stomach contents for all stages, from

CI to adult, was conducted. Likely seasonal changes in diet were also noted. A complete description of the feeding appendages of larvae and adult N. australis, together with their development, has already been given by Bary (1956) and Sars (1885) and therefore will not be described in this study. However, the setation of the maxillae, maxilliped and thoracic legs was studied in more detail, particularly in relation to the filtering mesh size. Data on the pm/pi ratios of larval and adult mandibles will also be presented.

4.2 Methods

For the analysis of feeding appendages, only specimens with intact limbs, particularly the thoracic ones, were used. The specimens were taken from the formalin-fixed monthly samples. After dehydration through a series of graded alcohols to absolute, specimens were cleared in clove oil. This particular clearing agent works quickly, even with large adults, and renders the appendages firm but brittle, allowing easy dissection (Pantin, 1969). All stages of N. australis were prepared in the same way. Appendages were permanently mounted in Euparal. This medium has a high refractive index, thus rendering the unstained setae and setules more clearly visible (Pantin, 1969). The distance between setae and setules was measured to the nearest μm using an ocular micrometer, as were the pars incisiva and pars molaris of the mandible.

Qualitative analysis of stomach contents was made for all stages of N. australis present in each month sampled between December 1979 and March 1981. Where possible, at least 5 individuals of each stage from 2 station samples per month were used. In some months many of the stages were poorly represented, particularly adults, or few specimens had stomach contents. Thus, only 1 or 2 individuals of a particular stage may have been examined. Stomach contents of N. australis post larvae and adolescents taken in the June 1980 EBS haul were also examined.

Presumably these individuals were feeding on bottom detritus (Blackburn, 1980; Sheard, 1953) though the sampler could have been contaminated with organisms in the water column as it was hauled up (see Chapter 2).

After dehydrating and clearing the entire stomach was removed and mounted in Euparal. The clove oil rendered the stomach wall clear, resulting in the contents being clearly visible. Therefore, it was unnecessary to open the stomach and risk dispersion of the contents throughout the mounting medium.

Caution is required when interpreting the diet of a species by qualitative listing of stomach contents, because of the limitations of this method. Although the relative frequency of each item can be estimated, the method gives no indication of the respective total biomass of individual components.

4.3 Results

4.3.1 Examination of feeding appendages.

The thoracic limbs of the "food basket", the maxillules, maxillae and mandibles of the adult N. australis, as well as the larval maxilliped, are shown in Fig. 4.1 to clarify the terminology.

There is a clear trend for the distance between setules, i.e. the size of the filtering mesh, on the thoracic legs of the adult to decrease, passing from the anterior to posterior limbs and also from distal to proximal segments on the same limb (Table 4.1). The trend is also apparent in adolescents, postlarvae and to a lesser extent in FIII larvae (Tables 4.2 to 4.5). Earlier larval stages lack developed thoracic legs, while the first thoracic leg is still in the form of a maxilliped. A similar trend for a decrease in distance between setae is also apparent in adults, adolescents and postlarvae and again less obvious in FIII larvae (Tables 4.6 to 4.10). Both the distance between setules and setae on the thoracic limb decrease from adult to postlarvae, particularly

FIGURE 4.1   Feeding appendages of <u>N. australis</u>. Setules are depicted

only in the enlarged diagram of the third thoracic leg.

Mxpd: maxilliped of F II larva, Md A: adult mandible-

left anterior, Md V: adult mandible- left ventral, Mx1:

adult maxillule, Mx2: adult maxilla, ThL 1,3 & 7: adult

thoracic legs 1,3, and 7.

b: basis, c: coxa, ca: carpus, d: dactyl, en: endopod,

ex: exopod, i: ischium, m: merus, p: propodus, pi:

<u>pars</u> <u>incisiva</u>, pm: <u>pars</u> <u>molaris</u>, ps ex: pseudoexopod,

sl: setules, st: setae.

4.1
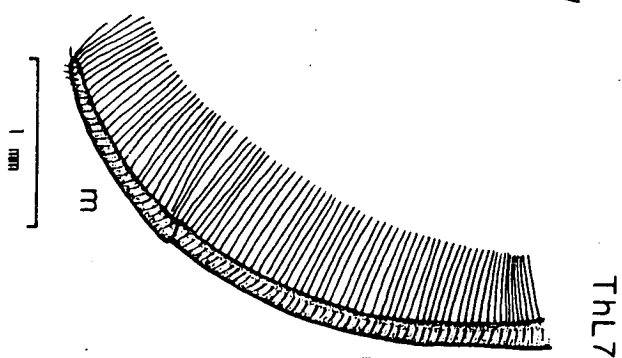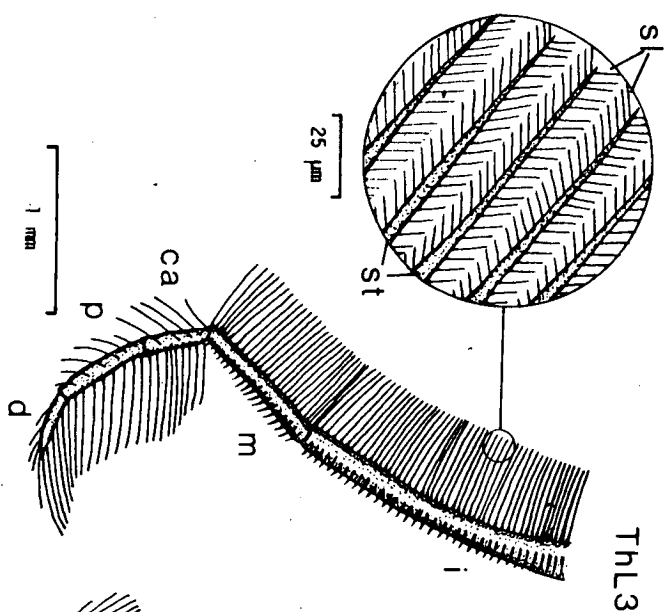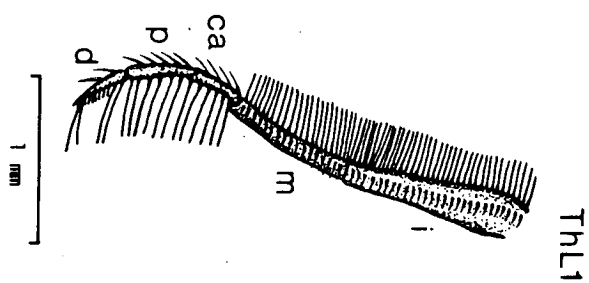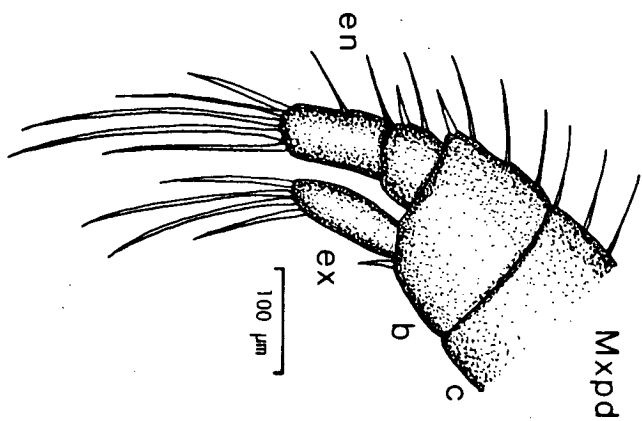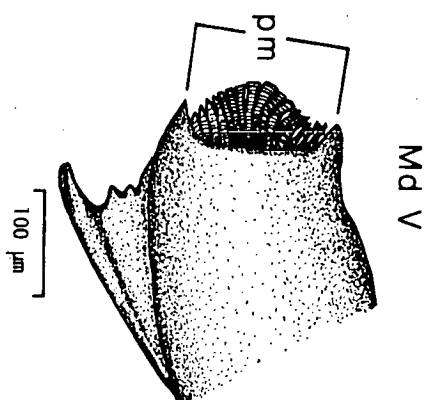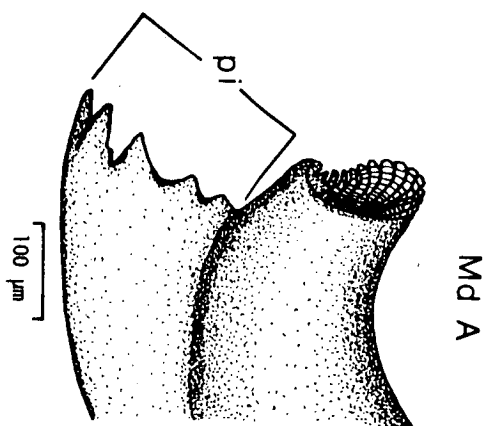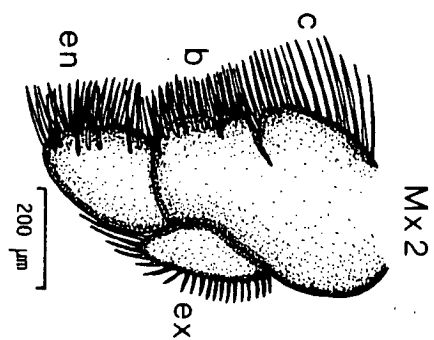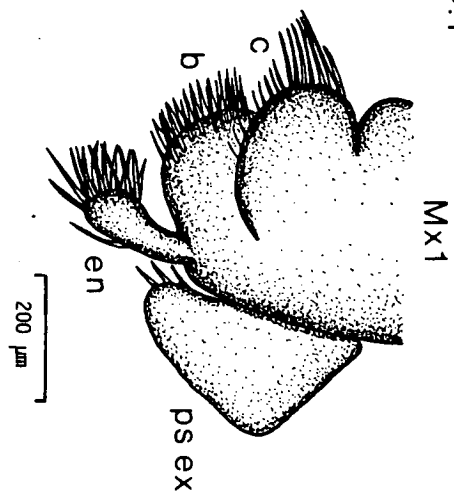
TABLE 4.1   Adult.   Distance between setules (mesh size) on

thoracic legs (μm).

Segment	Thoracic leg						
	1	2	3	4	5	6	7
ischium	2.5	2.5	2.5	3	2.5	2.5	2.5
merus	8	5	5	5	4	4	——
carpus	9.5	8.75	7.5	6.25	4	4	3.75
propodus	10.5	10.5	10.5	9.75	6.25	4	
dactyl	13.75	13.75	13	10.5	7.5	5	——

TABLE 4.2   Adolescent 10.4 mm.   Distance between setules (mesh size)

on thoracic legs (μm).

Segment	Thoracic leg						
	1	2	3	4	5	6	7
ischium	2.7	1.8	1.7	1.9	2	2.2	2.7
merus	3.5	4	3.7	3.9	3.6	3.6	——
carpus	6.7	5.9	5.4	4.7	4	4.2	3.3
propodus	7.6	7.7	6	5.3	4.1	4.7	
dactyl	11.5	9.8	7.9	6.9	5.9	6.9	——

TABLE 4.3   Post larvae 6.5 mm.   Distance between setules (mesh size) on thoracic legs (µm).

Segment	Thoracic leg						
	1	2	3	4	5	6	7
ischium	3	2.2	2.2	2.2	2.2	2.2	3
merus	5.1	3.4	3	3	3.1	2.8	
carpus	5.2	5.2	4.4	4.1	3.8	4.4	2.8
propodus	8	6.3	5.3	4.1	4.1	3.7	
dactyl	9.8	10	8.1	7.9	5.6	5.2	

TABLE 4.4   FIII (last instar, 5S1sp3PL) 4.7 mm.   Distance between setules (mesh size) on thoracic legs (µm).   Thoracic leg 7 is not developed.

Segment	Thoracic leg						
	1	2	3	4	5	6	7
ischium	4.4	3	2.8	2.7	3.6	5.6	
merus	5.8-10.7	2.5	4.9	4	4.1		
carpus	11.1	5.9	6.7	6.2	6.7	11.8	
propodus	12.4	8.9	7.6	6.3	5.9		
dactyl	2.8-14.2	11.5	12.1	7	14.1		

5S1sp3PL = 5 setose pleopods, 1 telsal spine, 3 posterior lateral spines (Sheard, 1953).

TABLE 4.5   FIII (second instar, 5S6sp) 3.4 mm.   Distance between

setules (mesh size) on thoracic legs (µm).   Thoracic

legs 5, 6 and 7 are not developed.   Mxpd = maxilliped.

Segment	Thoracic leg						
	Mxpd	2	3	4	5	6	7
ischium	7.1	8.9	10.2	13.2			
merus	7.5	13.1	13.3	-			
carpus	5.3-17.8	11.3	10.7	-			
propodus	8.4	18.3	12.2	-			
dactyl	_____	17.3	15.5	15.5			

5S6sp = 5 setose pleopods, 6 telsal spines (Sheard, 1953).

TABLE 4.6   Adult.   Distance between setae on thoracic legs (µm).

Segment	Thoracic leg						
	1	2	3	4	5	6	7
ischium	30	22.5	17.5	22.5	20	20	25
merus	42.5	52.5	45	40	35	32.5	
carpus	45	45	45	40	35	37.5	32.5
propodus	52.5	55	55	52.5	40	37.5	
dactyl	107.5	75	97.5	95	82.5	90	

TABLE 4.7   Adolescent 10.4 mm.   Distance between setae on thoracic legs (µm).

Segment	Thoracic leg						
	1	2	3	4	5	6	7
ischium	24.4	17.8	13.3	13.3	13.3	13.3	13.3
merus	32	37.7	31.1	24.4	31.1	24.4	
carpus	42.2	35.5	35.5	37.7	33.3	31.1	26.6
propodus	53.3	55.5	53.3	46.6	40	33.3	
dactyl	80	71	62.2	62.2	62.2	46.6	

TABLE 4.8   Post larvae 6.5 mm.   Distance between setae on thoracic legs (µm).

Segment	Thoracic leg						
	1	2	3	4	5	6	7
ischium	15.5	11.1	15.5	15.5	15.5	13.3	17.8
merus	33.3	26.6	22.2	22.2	20	21.9	
carpus	35.5	33.3	33.3	31.1	26.6	26.6	22.2
propodus	44.4	44.4	40	37.7	31.1	31.1	
dactyl	48.8	46.6	57.8	48.8	40	–	

TABLE 4.9 FIII (last instar, 5S1sp3PL) 4.7 mm. Distance between setae on thoracic legs (µm). Thoracic leg 7 is not developed.

Segment	Thoracic leg						
	1	2	3	4	5	6	7
ischium	22.2	17.8	13.3	17.8	22.2	48.8	
merus	33.3	31.1	20	31.1	24.4		
carpus	44.4	26.6	24.4	31.1	26.6	53.3	
propodus	40	40	40	35.5	31.1		
dactyl	46.6	40	40	40	–		

5S1sp3PL = 5 setose pleopods, 1 telsal spine, 3 posterior lateral spines (Sheard, 1953).

TABLE 4.10 FIII (second instar, 5S6sp) 3.4 mm. Distance between setae on thoracic legs (µm). Thoracic legs 5, 6 and 7 are not developed. Note, only one seta per segment on maxilliped (Mxpd).

Segment	Thoracic leg						
	Mxpd	2	3	4	5	6	7
ischium	–	35.5	37.7	–			
merus	–	40.0	48.8	–			
carpus	–	–	–	–			
propodus	–	40	–	–			
dactyl	–	–	–	–			

5S6sp = 5 setose pleopods, 6 telsal spines (Sheard, 1953).

TABLE 4.11   Comparison of distance between setules of the

ischium of the thoracic leg from various euphausiids

(Nemoto, 1967) and N. australis.

Species	Mesh size µm
Bentheuphausia amblyops	60 – 65
Thysanopoda tricuspidata	30 – 60
T. monacantha	25 – 50
Euphausia similis	20 – 30
E. diomedae	20 – 30
E. hemigibba	20 – 30
E. pacifica	7 – 12
E. mucronata	5 – 7
E. superba	5 – 7
Thysanoessa raschi	8 – 11
T. longipes	9 – 15
T. gregaria	15 – 20
N. australis	2 – 3

TABLE 4.12   Maxilla.   Distance between setules for all stages (μm).   PL = postlarva, J = adolescent, A = adult

Segment	CI	CII	CIII	FI	FII	FIII	PL	J	A
coxa	2.8–4.1	2.5–8.9	2.2–11.5	2–9.8	2.2–5.9	3–5.9	1.5–4.4	1.6–4.4	1.2–4.4
basis	3.3–8.9	3.2–6.7	3.3–7.3	4.4–8.9	2.9–9.8	3.9–11.1	1.5–5.8	2.7	3.8
endopod	5.6–13.3	7.8–16.9	7.4–14.7	8.9–10.2	6.5–16.9	4.4–12.2	4.4–8	4.5–8	5.6–8

TABLE 4.13 Maxillule. Distance between setules for all stages (µm). PL = postlarva, J = adolescent, A = adult.

Segment	CI	CII	CIII	FI	FII	FIII	PL	J	A
coxa	−	−	−	4−4.1	4.4	4−5.3	3.6−5.6	3.1−5.6	4.9−11.1
basis	−	−	−	−	−	4.1	4.4	4	4
endopod	6.2−9.8	4−11.1	4.1−12.9	4.3−15	5.3−12.4	4.4−13	3.8−5.1	4.4−6.7	5.6

TABLE 4.14 Maxilliped. Distance between setules for calyptopis and furcilia larvae (μm). 5S6sp = second instar of FIII stage, 5s1spPL = last instar of FIII stage.

Segment	CI	CII	CIII	FI	FII	FIII 5S6sp	FIII 5S1sp3PL
coxa	2.2-4.4	2.4-4.4	2.1-7.5	3.6	2.7	4.9-7.1	
basis	3.8	3.9	3.9	4.4	9.3	7.6	
ischium	7	6.7	6.2	6.7	6.2	7.1	4.4
merus						7.4	5.8-10.7
carpus	5.8	5.6	6.1	8.3	6.4	5.3-17.8	11.1
propodus						8.4	12.4
dactyl							2.8-14.2
exopod	3	3	3	3.3	3.2	3.6	

FIGURE 4.2   Mean pm/pi ratios for all stages of N. australis.

PL: postlarva, ADOL.: adolescent. Bar represents ± SD.
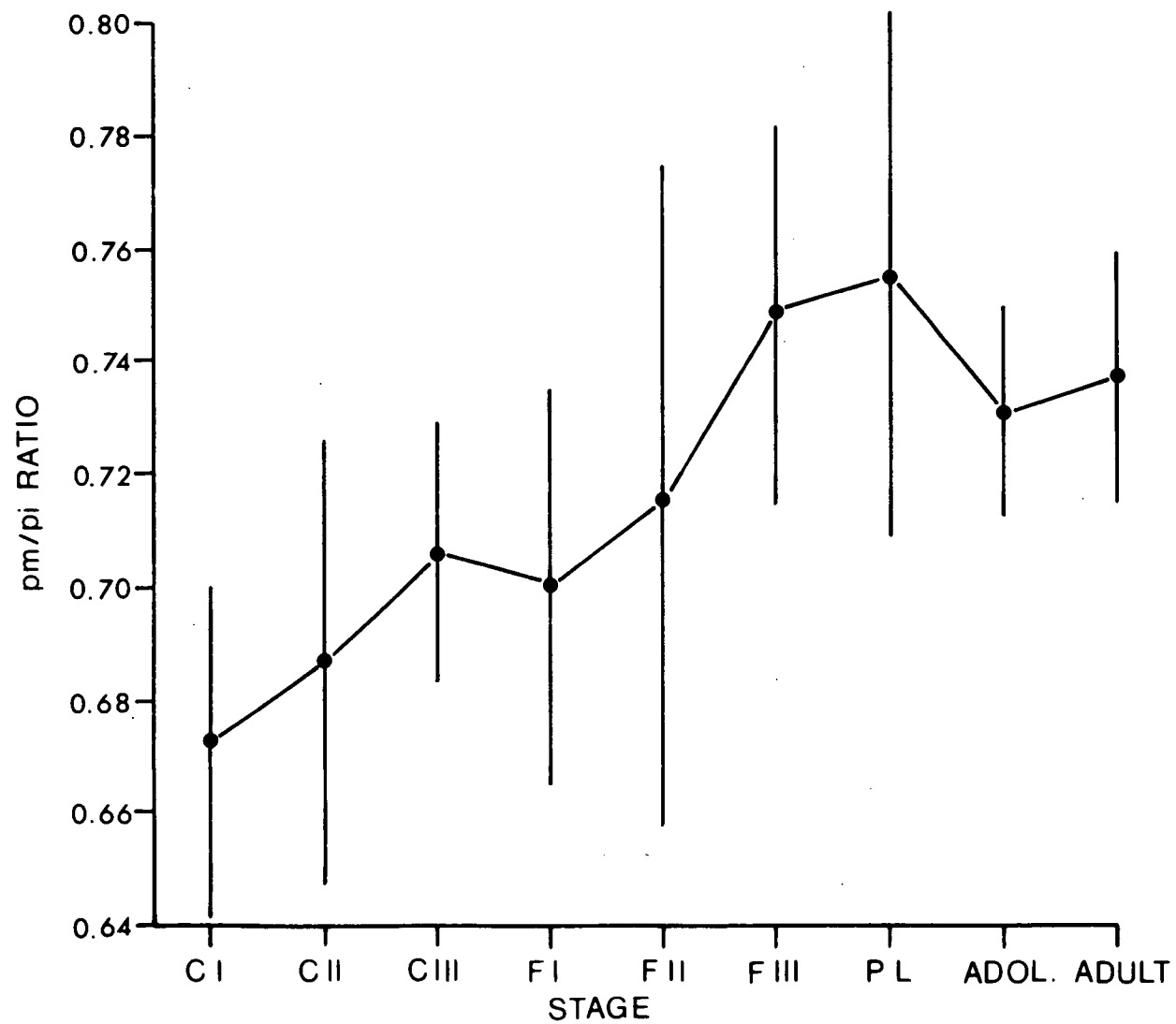
TABLE 4.15 Comparison of pm/pi ratios of the mandible of various

euphausiid species.

F = filter feeder, O = omnivore, P = predator.

Species	pm/pi	Feeding mode	Source
Bentheuphausia amblyops	0.71	O – F	Nemoto (1977)
Thysanopoda acutifrons	0.64	–	Nemoto (1977)
T. tricuspidata	0.78	O – F	Nemoto (1977)
T. cristata	0.49	P – O	Nemoto (1977)
T. cornuta	0.51	P	Nemoto (1977)
T. egregia	0.34	P	Nemoto (1977)
T. spinicaudata	0.41	P	Nemoto (1977)
Meganyctiphanes norvegica	0.74	P – O	Mauchline (1980)
Euphausia krohni	0.70	F – O	Mauchline (1980)
E. superba	1.09	F – O	Nemoto (1977)
Thysanoessa raschi	0.97	F – O	Mauchline (1980)
T. longicaudata	0.85	O	Mauchline (1980)
Nematoscelis megalops	0.69	O – P	Mauchline (1980)
Nematobrachion boöpis	0.29	P	Mauchline (1980)
Stylocheiron longicorne	0.31	P	Mauchline (1980)
S. elongatum	0.45	–	Mauchline (1980)
S. abbreviatum	0.27	P	Mauchline (1980)
S. maximum	0.42	P	Mauchline (1980)
N. australis adult	0.74		Present study
CI larvae	0.67		Present study

in relation to distal segments (Tables 4.1 to 4.3 and 4.6 to 4.8).
The larger spacing between setules and setae in FIII larvae, as well as
the lack of clear trends between segments and limbs described above,
can be attributed to the incomplete development of the newly formed
thoracic legs (Tables 4.4, 4.5, 4.9, 4.10). Overall the filtering mesh
size on the ischium of the thoracic leg of N. australis, is much finer
than those previously recorded for other euphausiids (Table 4.11).

There appears to be little change in the distance between setules on
the maxillae with development. However, the mesh size on postlarval,
adolescent and adult maxillae tends to be slightly finer (Tables 4.12,
4.13). No setules are present on the setae of calyptope maxillules,
which are more robust compared to later stages. There was no apparent
change observed in the spacing of setules on the maxilliped in all larvae
(Table 4.14), except in FIII instars where the maxilliped differentiates
into the first thoracic leg. The mesh sizes recorded for larval maxillae
and maxillipeds are notably as fine as those of the adult thoracic legs,
with the same trend of decreasing spacing between setules from distal·
to proximal segments.

Figure 4.1 depicts the way in which measurements of the pm/pi ratio
were obtained. The pm/pi ratio increased towards unity as the larvae of
N. australis developed, reaching an apparent plateau after the FIII stage
(Fig. 4.2). The apparent slight decrease in the ratio in adolescents
and adults may be a result of error in measuring. These results suggest
that the mandibles of the larvae, particularly calyptopes, are more
suited to predation than those of larger stages, which in turn are
comparable with pm/pi ratios of euphausiid species with omnivorous modes
of feeding (Table 4.15).

4.3.2 Stomach content analysis

The results of the stomach content analysis for all N. australis stages
are shown in Fig. 4.3, expressed as percentage frequency of occurrence.
N. australis consumes a wide variety of dietary components, with the

FIGURE 4.3   Percentage frequency of occurrence of

dietary components for each stage.
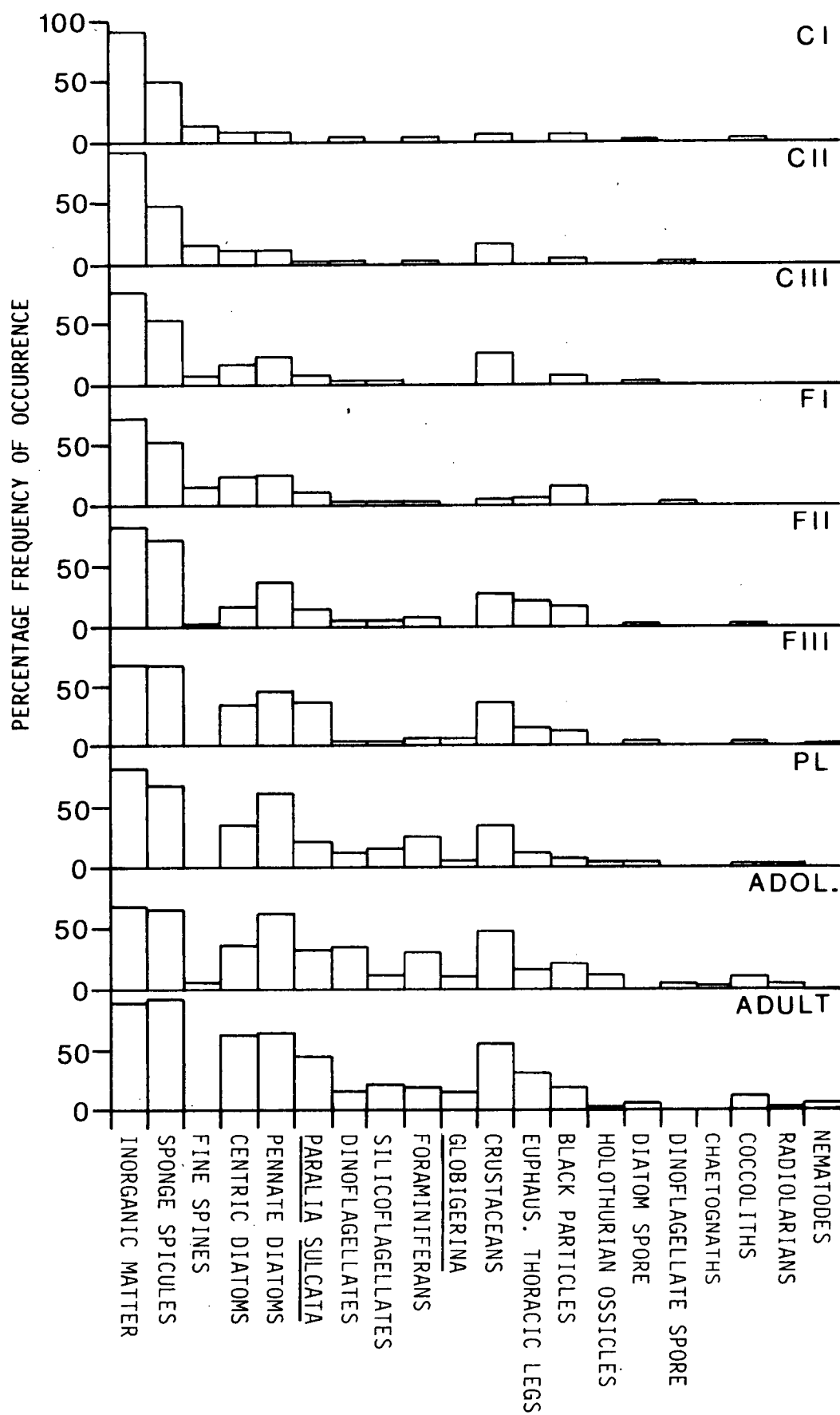
FIGURE 4.4   Percentage frequency of occurrence of dietary

components integrated for all stages.
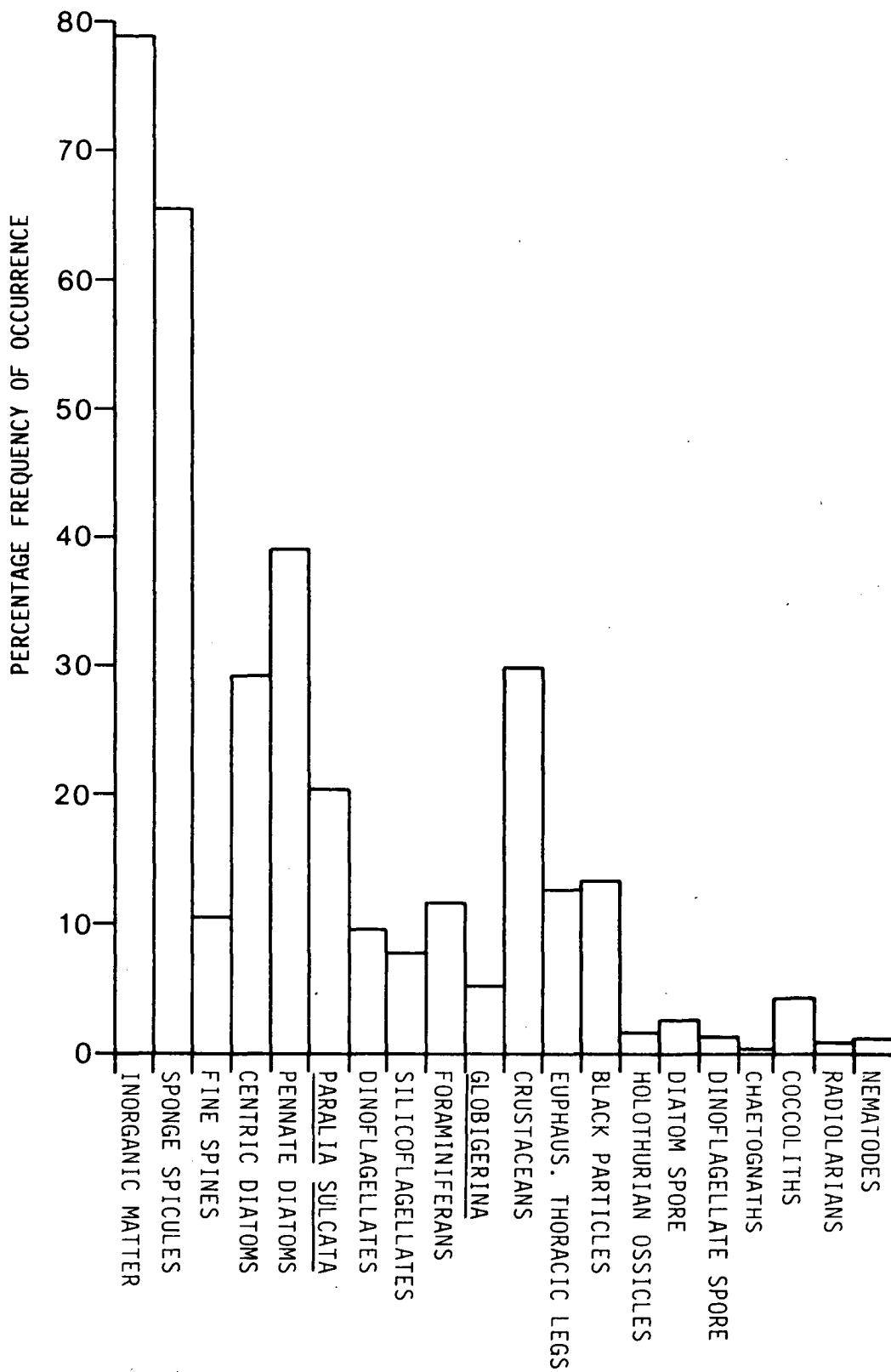
FIGURE 4.5   Percentage frequency of occurrence of dietary components for postlarvae and adolescents from the June 1980 EBS sample.
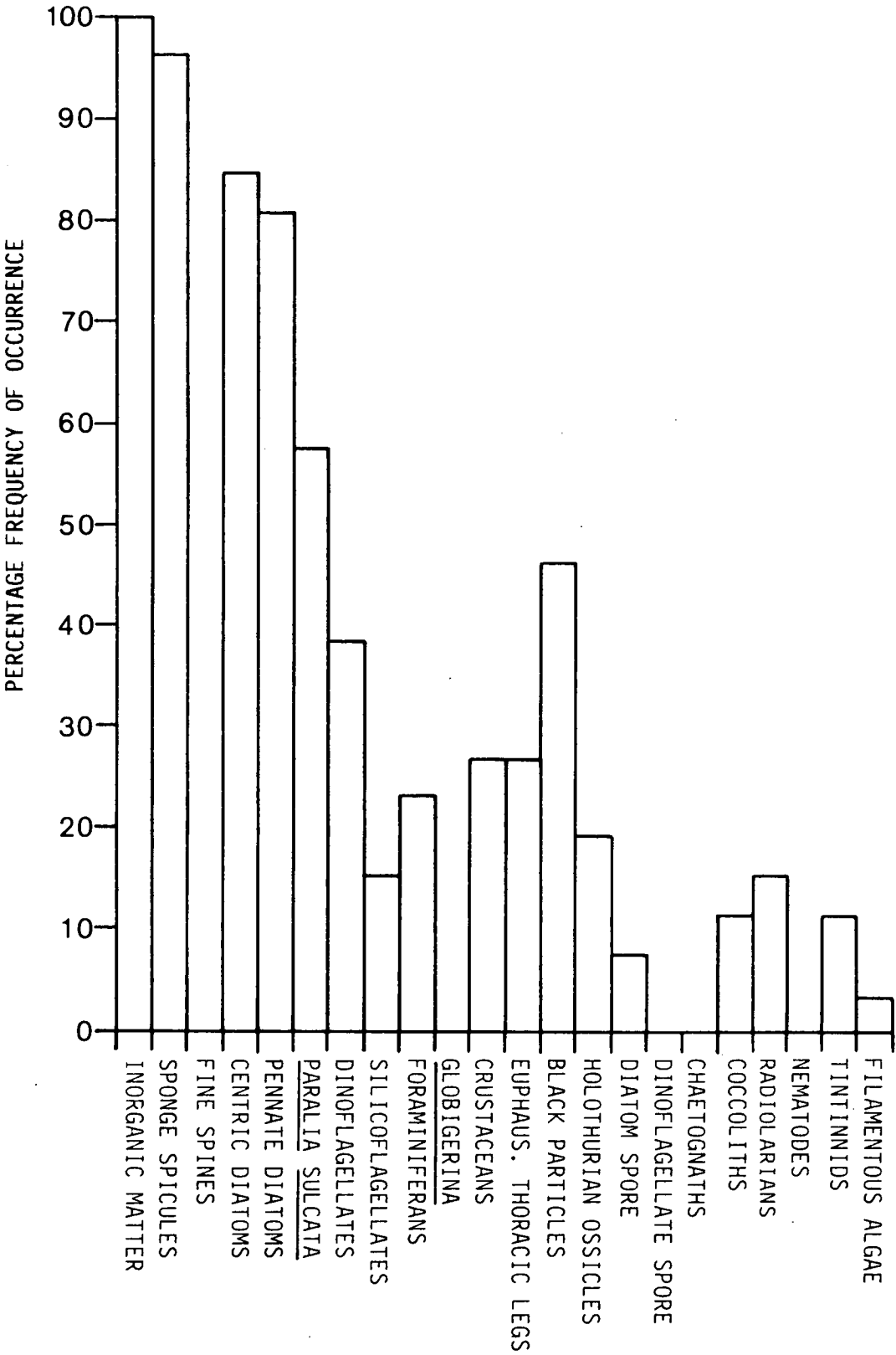
FIGURE 4.6   Seasonal changes in stomach contents   for all stages.
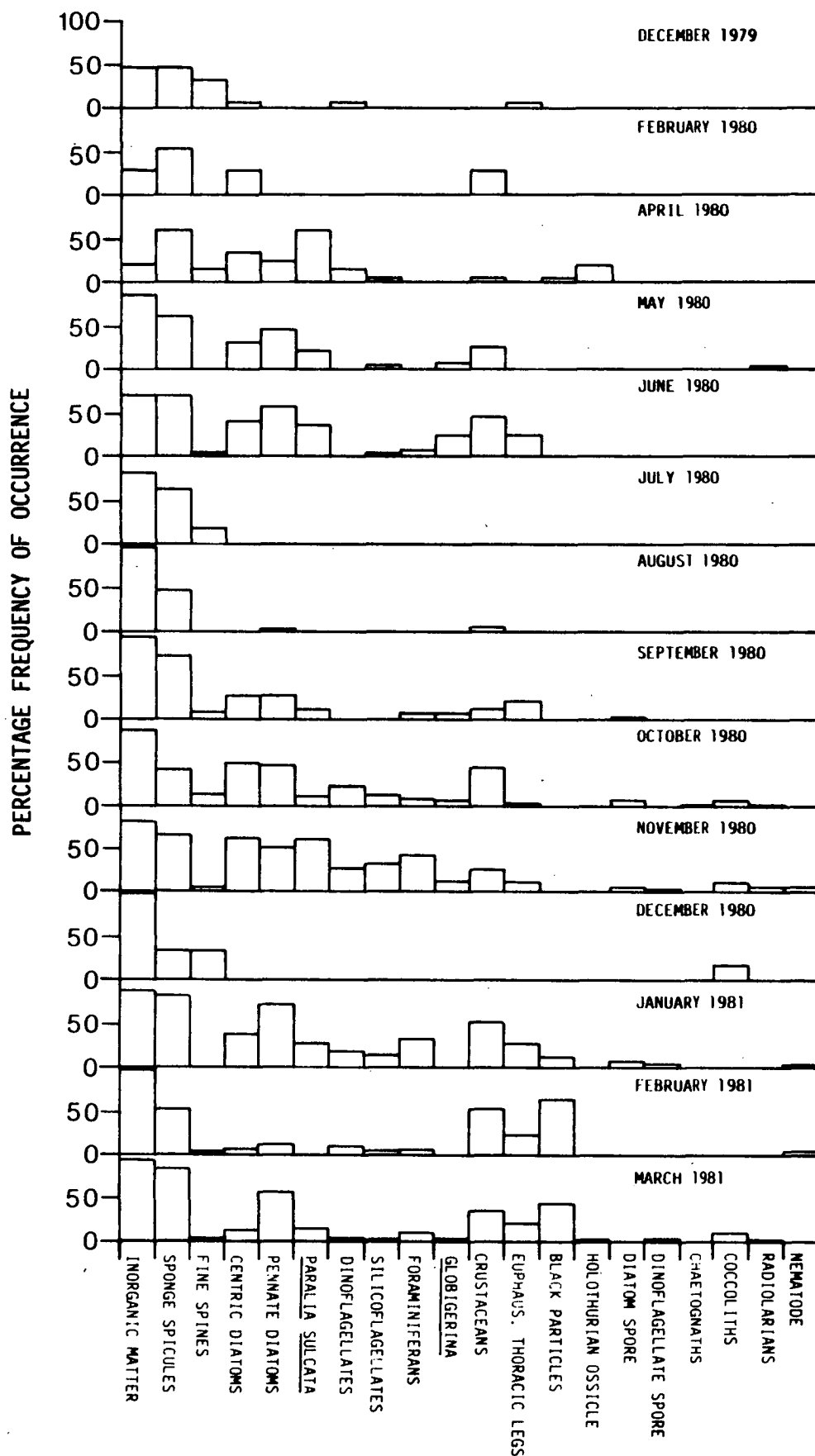
number of items apparently increasing with size of the individual.
The frequency of all food items ingested, integrated for all stages ·is
shown in Fig. 4.4. Although food items are grouped into broad taxa,
specific items were listed separately if particularly common, e.g. the
diatom <u>Paralia</u> <u>sulcata</u> and foraminiferan <u>Globigerina</u>.

The two most common items ingested throughout the life of <u>N. australis</u>
were inorganic matter and sponge spicules, either broken or whole.
Other major components were pennate and centric diatoms, especially
<u>P. sulcata</u>, dinoflagellates, silicoflagellates, foraminiferans and
crustaceans (Fig. 4.7 to 4.10). All these items increased in frequency
with increase in the size of <u>N. australis</u>. Diatoms were often ingested
whole, but more usually were fragmented. The remains of crustaceans
were common particularly in the larger <u>N. australis</u> stages. It could
not be determined if the crustaceans were taken live or only the
exuviae were ingested. There was also a high frequency of euphausiid
thoracic legs in the stomachs, which were presumably the remains of
ingested <u>N. australis</u> moults.

The clumped black particles which were progressively more frequent in
larger individuals, are most likely zooplankton faecal pellets
(MacWilliam, 1977; Sheard, 1953). Sheard noted that faecal pellets may
be important food items in euphausiids. In all stomachs examined there
was a large volume of amorphous matter which ranged in colour from green
to brown. Macdonald (1927a) from studies of other euphausiids had
originally described the matter as "flocculent detritus".

Analysis of stomach contents of postlarvae and adolescents from the
June 1980 EBS haul, showed dietary components similar to those of
individuals from the plankton samples, though there was a markedly
higher frequency of inorganic matter, sponge spicules, phytoplankton
and the clumped black particles (Fig. 4.5). Notably most of the matter
was fragmented, particularly <u>P. sulcata</u> and the inorganic particles were
larger. The benthic diatom <u>Pleurosigma</u> was occasionally observed in the

FIGURE 4.7   Stomach contents of FIII larva. CD: centric diatom,

FS: fine spine, IM: inorganic matter, Ps: Paralia

sulcata. Scale bar = 50 µm.

FIGURE 4.8   Stomach contents of postlarva. Ps: Paralia sulcata,

S: silicoflagellate. Scale bar = 25 µm.

4.7

IM

FS

CD

Ps

4.8

S

Ps

S

Ps
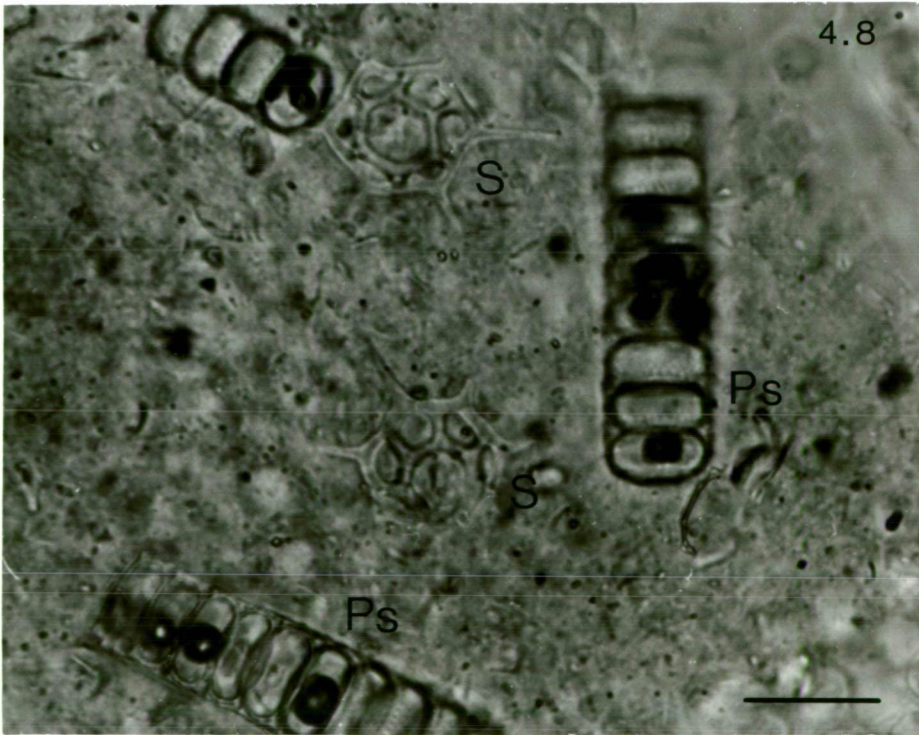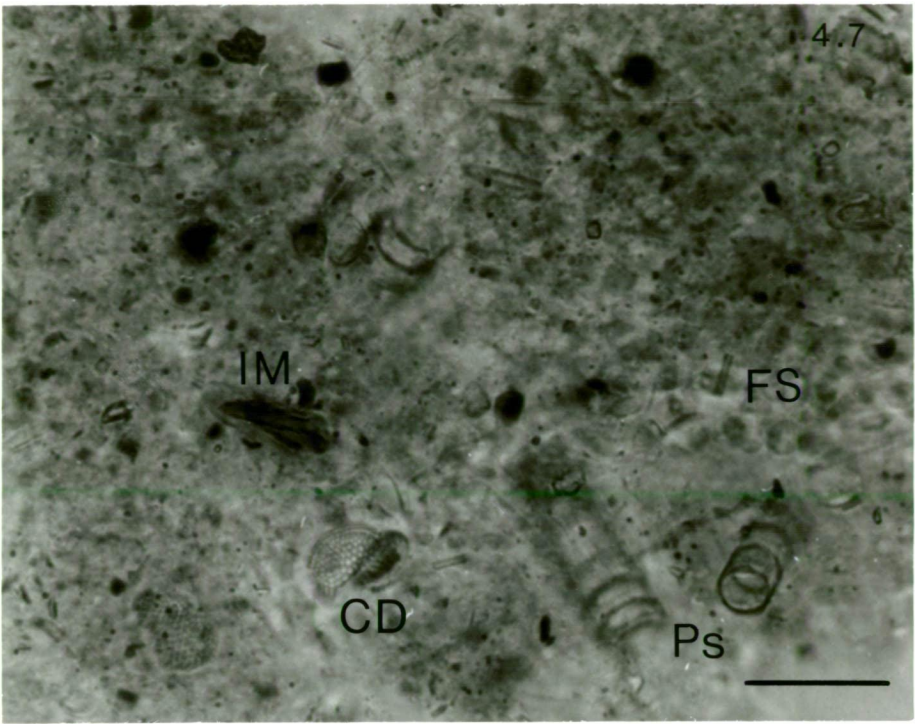
FIGURE <u>4.9</u>   Stomach contents of FIII larva. IM: inorganic matter,

SS: sponge spicule. Scale bar = 20 μm.

FIGURE <u>4.10</u>   Ornate sponge spicule in the stomach of an adolescent.

Scale bar = 20 μm.

4.9

4.10
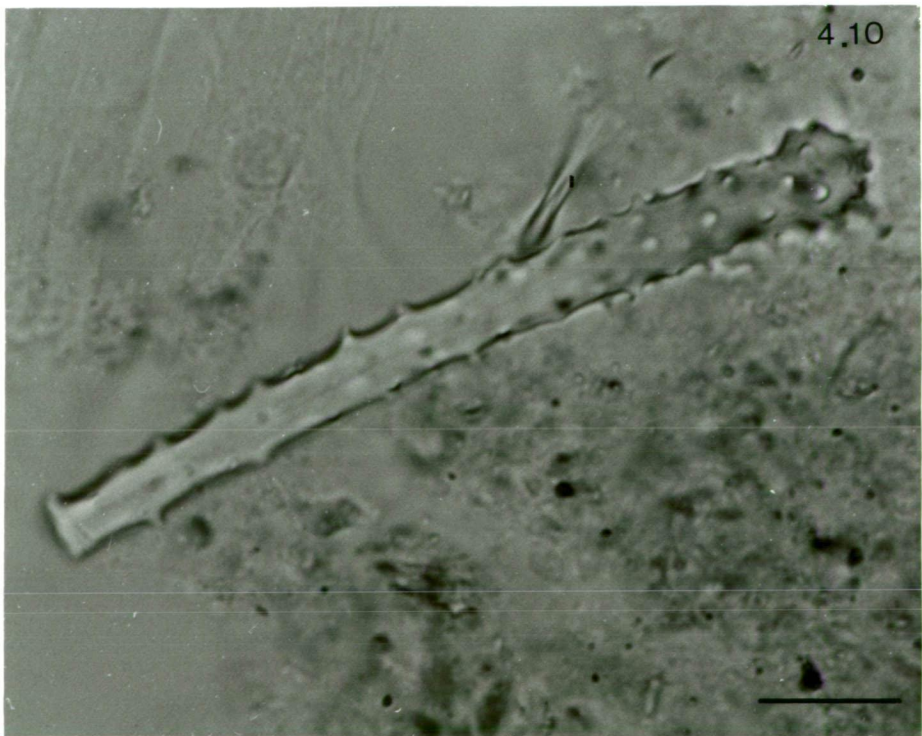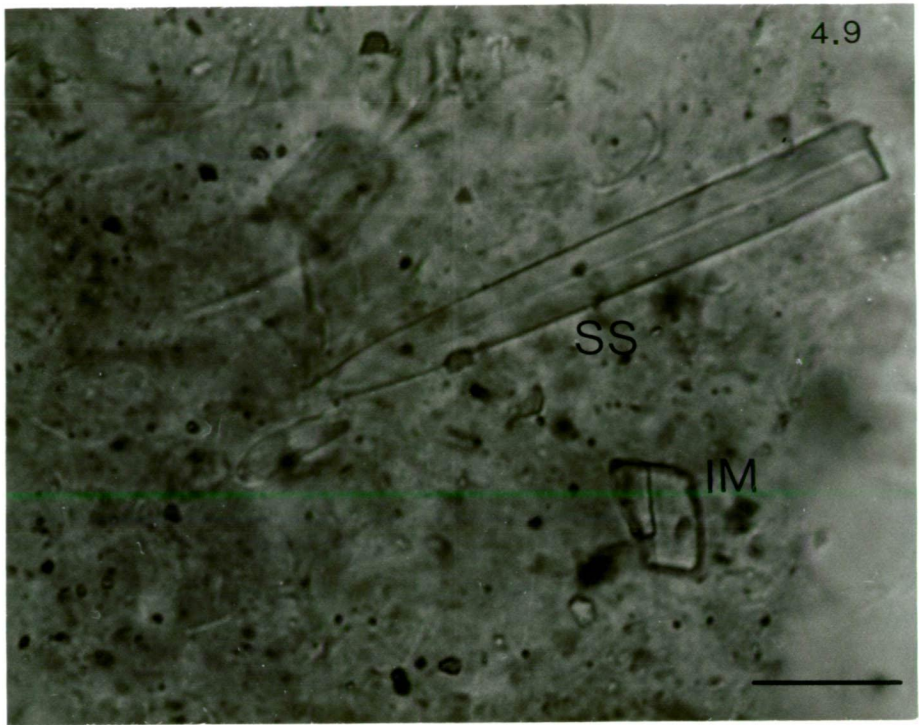
stomachs. Euphausiid thoracic legs, when present, were in high numbers often packed into a tight bolus.

It is particularly interesting to note that an adolescent in the benthic sample had ingested a triradiate sponge spicule, with a radius of 156 μm, completely undamaged. Also a postlarva observed in a May 1980 plankton sample had consumed an intact chain of P. sulcata, measuring 290 μm in length.

Some seasonal changes in stomach contents were apparent (Fig. 4.6). Minor components such as diatom resting spores, chaetognaths, coccoliths and radiolarians were more prevalent during the warmer months September 1980 to March 1981. Only a few items were recorded in the winter months of July and August 1980. The black particles, possibly faecal pellets, were most common in January, February and March 1981, which may be associated with a high zooplankton biomass for that period (Fig. 2.10). Both the inorganic matter and sponge spicules remained the two main items ingested throughout the year.

4.4 Discussion

The structural arrangement of the setae and setules on the thoracic limbs, suggests that water is filtered first by the distal segments of the most anterior legs, exiting towards the bases of legs, particularly the posterior limbs. This agrees with observation by Fenton (1981) on the feeding currents of N. australis, using high speed cinematography. This pattern of filtration was also observed in Euphausia superba (Pavlov, 1971). It appears that all the thoracic limbs of N. australis are involved in the filtration of water, rather than just the first 2 pairs of legs as claimed by Mauchline (1967b).

The "food basket" of N. australis would be expected to be a most efficient filtering apparatus, because of both the large surface area of the "basket" in relation to body size and the small sizes it is capable of retaining, i.e. a minimum of 2 μm. The means by which filtered matter is transported from the "food basket" to the mouth is still to be

determined. Possibly the maxillae waft the food forward, or the exopodites of the thoracic legs create a reverse current, thus moving the food towards the mouth.

Fenton (1981) noted that N. australis could snatch large particles, presumably too big to filter, by the combined lateral movements of the thoracic legs. Mauchline (1967b) associated this style of feeding with the capture of motile prey.

Slight differences in setation of the maxillae along with the differences in the morphology of the mandibles, would suggest that larvae may utilize a different food source to that of the adults. The linear decrease of the pm/pi ratio with decrease in size, suggests that the calyptope larvae are more suited to predation than are the adults. Kulka and Corey (1978) observed the same phenomenon in Thysanoessa inermis and drew the same conclusion. This agrees with the stable isotope study of Fenton (1981) that N. australis larvae possibly feed by predation while adults feed on phytoplankton. Le Roux (1973) had noted that Nyctiphanes couchi was capable of capturing prey from the calyptopis phase onwards. However, the differences in the pm/pi ratio between N. australis CI larvae and larger stages are relatively small compared to differences between the wholly predatory Stylocheiron abbreviatium, with a ratio of 0.27 and the filter feeding E. superba with 1.09 (Table 4.15). The linear trend in pm/pi ratios observed in this study, may be due to incomplete differentiation of the pars molaris in early larval stages. Differences in the setation of maxillae may also be related to development. However, the slight change to finer setation of the maxillae of larger stages, does coincide with the differentiation of the thoracic legs into the "food basket". This suggests that the larger stages may be capable of filtering smaller particles than are the larvae, though the maxillae and maxilliped of the larvae are still heavily setose.

Any suggestion of differences in diet between larvae and larger stages, tends to be dispelled by the stomach content analysis. There is little

change in the main dietary components between all stages. There was an
increase in frequency of some of the major dietary components with
increasing size, similar to that seen in other euphausiids (Fisher and
Goldie, 1959; Mauchline, 1966). There was, however, no associated
decrease in other components with size similar to that show by Mauchline
(1960) in Meganyctiphanes norvegica. Mauchline noted an increase in the
frequency of crustaceans ingested with increase in body size, while the
frequency of dinoflagellates decreased correspondingly, indicating a
change in diet between adults and larvae. The general increase in %
frequency of dietary items with size observed in N. australis is most
likely a function of the filtering area increasing with body size,
particularly with the development of the "food basket" in larger stages,
resulting in more items being filtered at a time. This would also explain
the overall increase in the total number of individual items consumed
with corresponding increase in body size.

Ponomareva (1954) had noted that euphausiids can feed on copepods by
sucking out the softer tissue and then discarding the exoskeleton. If
larvae of N. australis predate on crustaceans, as suggested by mandible
morphology and stable isotope analysis (Fenton, 1981), then the relative
importance of crustacean zooplankton in the diet of the larvae may have
been underestimated in the stomach content analysis. Roger (1974) had
noted that analyses of stomach contents are biased towards item with
resistant structures, e.g. diatoms.

The number of midwater individuals with inorganic matter in their
stomachs, was markedly high compared to other euphausiid species that are
known to feed on bottom detritus (Berkes, 1977b; Fisher and Goldie, 1959;
Mauchline, 1960, 1966). Presumably the relatively shallow turbulent
nature of Storm Bay results in inorganic particles, together with detrital
matter and sponge spicules, being kept suspended in the water column.
Berkes (1976) noted that this phenomenon occurred in the shallow regions
of the Gulf of St. Lawrence. The reason why N. australis ingests such
matter as inorganic particles and sponge spicules, which would seemingly

be unpalatable is unknown. Possibly these aid in the maceration of
the food within the stomach, or the euphausiids utilizes bacteria
which most likely cover the surface of the material. Alternatively,
the matter is just taken in passively, since Fenton (1981) showed
that inert plastic beads are ingested by N. australis if the right
size.

The most interesting component of the stomach contents was the
amorphous matter, which was observed in large amount in all individuals
examined. The matter, often described as "mush" has been observed in
several euphausiid species, but not with the 100% frequency observed in
this study (Berkes, 1977b; Fisher and Goldie, 1959; Mauchline, 1959, 1966;
Sameoto, 1980). Talbot (1974) presumed the matter was algal in origin,
while Roger (1974) concluded it was either phyto- or zooplankton,
depending on whether the colour of the matter was green or brown,
respectively. This material has also been described as "flocculent
detritus".(Macdonald, 1927a). The amorphous matter observed in N. australis
may be any one of these in origin or a combination of all. Alternatively,
the "mush" may be derived from nannoplankton. During the winter months,
nannoplankton can comprise 80 to 90% of the total phytoplankton biomass
in the coastal waters adjacent to Hobart (Dr. D.P. Thomas, pers. comm.).
Nyctiphanes australis with its mesh size of 2 μm on the thoracic leg
ischium, would be suitably designed for exploiting nannoplankton as a
food source, particularly during winter months when other food items may
be lacking in the water column. This may explain why the mesh size of
the ischium is finer in N. australis compared to other euphausiids (Table 4.11).
More detailed analysis of fresh stomach contents using scanning electron
microscopy, would be required to confirm this hypothesis.

It can be concluded from the present study that N. australis is not
just a detritivore as previously claimed by Sheard (1953). The feeding
appendages of all N. australis stages are heavily setose, with an
extremely fine filtering mesh, indicating that N. australis can operate
as an efficient filter feeder. The pm/pi ratio of the mandibles is

comparable with ratios of other euphausiids with combined predatory, omnivorous and filter feeding modes (Mauchline, 1980), while the stomach content analysis showed that N. australis ingests a broad spectrum of dietary items. Fenton's (1981) results also indicated the presence of non-detrital dietary items in N. australis, as well as the existence of a predatory mode of feeding involving the thoracic legs. It would be more appropriate to classify N. australis as an opportunistic omnivore/ detritivore. That is, the species exploits whatever food source of an appropriate size is available at the time. Any seasonal differences in the diet of N. australis observed in this study are most likely a reflection of the food items available in the water column at the time of sampling.

CHAPTER 5

PRODUCTION

5.1 Introduction

Several techniques have been devised for the purposes of calculating

production in aquatic animals from life history data and have been

reviewed by Edmondson and Winberg (1971) and Winberg (1971). Basically

the methods fall into two main categories according to Mann (1969). In

the first category, production is calculated by integrating the product

of the number of individuals and their mean biomass lost from the

population, usually by predation, at various specified time periods.

An example of this category is expressed by the equation developed by

Mann (1969), which was used by Berkes (1977a) for a population of

Thysanoessa raschi in the Gulf of St. Lawrence. The second category

includes methods where production is estimated by multiplying the weight

increment of surviving members of a population by their respective number,

after specified time intervals. The Allen curve, a graphical method for

estimating production, is an example of the second category, that has

been successfully applied to several euphausiid species (Lindley, 1978,

1980, 1982). Regardless of which category, all methods for estimating

production should produce the same answer when applied over the total

life span of a species (Mann, 1969).

Calculation of production using Allen curves and the Mann equation,

in common with many other methods that have been applied to aquatic

species (Mann, 1969), depends on being able to trace discrete identifiable

cohorts through time. However, this is often difficult, particularly

with species that have prolonged breeding seasons accompanied with short

life spans, as is the case with tropical euphausiids (Roger, 1974).

Most previous studies on the production of euphausiids have been restricted

to temperate and Antarctic species which have short synchronised breeding

seasons, with resulting traceable cohorts (Allen, 1971; Berkes, 1977a; Lasker, 1966; Lindley, 1978, 1980, 1982; Mauchline, 1977a). Methods are available for estimating production of aquatic animals that have continuous release of larvae (Winberg, 1971).

By relating the biomass of a population to its daily production (B : P'), the "turnover time" of the population can be estimated, i.e. the time interval in days for the biomass to be replaced by fresh production (Tranter, 1976). The reverse relationship, often expressed as annual production to mean annual biomass (P : B), represents the rate of turnover of the population and is a useful concept for comparing production between different species and different localities (Mann, 1969; Mauchline, 1980; Tranter, 1976). The usefulness of the P : B ratio concept, in relation to euphausiids, has been discussed by Mauchline (1977a).

Previous estimates of P : B ratios for euphausiids have ranged from as low as 1.8 for the Antarctic species Euphausia superba (Allen, 1971), to 8.7 for a population of E. pacifica off the Oregon Coast (Mauchline, 1977a). In general, euphausiids in high latitudes have large standing stocks but low production rates, which can be attributed to their long life spans, as well as the fact that they produce only one generation per year (Mauchline, 1980).

Fowler et al. (1972) and Lasker (1966) suggested that euphausiids may be significant contributors to the pool of detritus because of their regular frequent moulting which continues throughout their life. Lasker further proposed that in one year, the total dry weight of euphausiid exuviae may be as much as seven times the mean annual biomass. However, to date, little consideration has been given to production of exuviae in euphausiids, with only a few estimates available (Ikeda and Dixon, 1982; Jerde and Lasker, 1966; Sameoto, 1976b).

Production in N. australis, in terms of flesh and exuviae, was calculated using the data detailed in the Life-History Section and then compared to biomass estimates to obtain a rate of turnover of the Storm

Bay population. An estimate of egg production has also been given in
this study. The relative contribution of eggs has not to the author's
knowledge been included in previous estimates of euphausiid production.

5.2 Methods

5.2.1 Production

It was demonstrated in Chapter 3 that the larval release in
N. australis is continuous for nearly the entire year, with discrete
cohorts difficult to trace. For this reason it is appropriate to
calculate production by applying a model suited to animals with continuous
recruitment (Winberg, 1971). The equation developed by Petrovich et al.
(1964) was selected and results using this method were then compared
to those obtained by means of a graphical method devised by Winberg (1971)
(first variant). Both techniques are summarized below.

5.2.1.1 Petrovich equation

Using the Petrovich method, production is estimated by summing the
growth rate for each size-class multiplied by their relative abundance.
The equation, initially designed for copepods, originally appeared as
follows :-

$$P = \left(\frac{q'}{D_e} \cdot N_i XF + \frac{n'-q'}{D_q} \cdot N_n + \frac{i'-k'}{D_k} \cdot N_k \right) , \qquad (5.1)$$

where q', n', k' and i' are the mean weights of eggs, nauplii, copepodid
and adult stages respectively; N_q, N_n, N_k and N_i are their respective
abundances; D_q, D_n, and D_k are the developmental time in days of the
eggs, nauplii and copepodids; D_e is the time interval in days between
ovipositions; X is the ratio of females to the number of sexually mature
individuals expressed as a percentage; and F is the number of eggs per
oviposition.

Winberg (1971) considered that this method overestimated the growth
rate, since mean weights were used. Instead he suggested that the
difference between initial and final weights of any particular stage

should be used, with the final weight also being the initial weight of the next stage. The equation was thus modified :-

$$P = \left(\frac{q}{D_e} \cdot N_i XF + \frac{n-q}{D_q} \cdot N_q + \frac{k-n}{D_n} \cdot N_n + \frac{i-k}{D_k} \cdot N_k \right) \quad , \quad (5.2)$$

where q, n, k and i are the initial weights of each stage.

In <u>N. australis</u>, however, there are more size classes present than in the original copepods, therefore the equation was further modified for present purposes and expressed thus :-

$$P = \sum_{i=1}^{s} \left(\frac{W_{i+1} - W_i}{D_i} \cdot \bar{N}_i \right) \quad , \quad (5.3)$$

where P is the daily production; W_i is the weight at the beginning of a size interval; W_{i+1} is the weight at the end of the interval (initial weight of the next size-class); D_i is the development time in days (calculated from the growth curve Fig. 2.14); $\bar{N}_i$ is the mean daily density m^{-3} over the entire sampling period; and s is the total number of size-classes.

5.2.1.2 Graphical method - 1st variant (Winberg, 1971).

In this method, production is calculated by summing the absolute growth increments of all the individuals within the population. Using empirical data, five graphs are constructed, from which both production and biomass are determined.

<u>Graph 1.</u> Growth of one individual in terms of weight against time. This was obtained by converting the original growth curve (Fig. 2.14) using the length-weight relationship (equation 2.1).

<u>Graph 2.</u> Daily absolute growth increments against age (time). The mean growth increment for a set period of observation can be calculated from the formula :-

$$\Delta w / \Delta t = (w_2 - w_1) (t_2 - t_1)^{-1} \quad , \quad (5.4)$$

with $\Delta w / \Delta t$ plotted at the midpoint of the relevant time interval, i.e. $t_1 + \frac{1}{2} (t_2 - t_1)$.

Graph 3. Age frequency curve - the number of different age-classes
          in the population.

This graph is based on the premise that a particular developmental

stage which lasts several days will consist of individuals of different

ages. For example,the N. australis size-class 1.00 - 1.99 mm lasts 10.5

days, as determined from the growth curve (Fig. 2.14) and thus will

comprise individuals between 1 and 10.5 days old. The mean number of

a particular size-class per day of development can be determined by

dividing the total number of individuals of that stage by the respective

development time. This value is plotted against the mid-point of the

size-class' development.

Graph 4. Production curve for all size classes.

          Production is calculated by multiplying the growth increments,

obtained from Graph 2, by the respective numbers of an age-group from

Graph 3. The resulting values of daily production for each size-class

are plotted as a production curve. The area under this curve, provides

the mean daily production for all size-classes within the population

that are growing.

Graph 5. Biomass curve for all size-classes.

    Biomass is calculated by multiplying the respective values from the

age-frequency curve (Graph 3) and from the individual growth curve

(Graph 1), for each age-group. These data are plotted, with the area

under the curve providing a measure of the mean annual biomass.

    Production and biomass estimates were obtained by weighing the cut-out

curve from Graphs 4 and 5 on a Sartorius balance to four decimal places.

5.2.2 Production of eggs.

    Production of eggs for N. australis was determined for each size-class

of adult ($\geq$11.00 mm total length) by applying a modification of part of

the Petrovich equation 5.1 :-

$$Po = \sum_{i=1}^{n} \left(\frac{q}{D_e} \; \bar{N}_i \; X \; F_i \right) \quad , \tag{5.5}$$

where Po is the production of ova (eggs) in mg $m^{-3} d^{-1}$; q is the

weight of the egg; D_e is the development time in days of the egg;

$\bar{N}_i$ is the mean daily density m^{-3} for each size-class of adult; X is the

ratio of females to sexually mature adults; F_i is the number of eggs

per female, per ovipositiom, for each size-class; and n is the number

of size-classes examined. The number of eggs F_i, was determined

using the number of eggs per weight of female relationship (equation 3.1).

5.2.3 Production of exuviae.

Production from exuviation was calculated for each size-class using

the formula devised by Sameoto (1976b) :-

$$Pe = \sum_{i=1}^{s} \left(\frac{\bar{W}_i \; x \; \bar{N}_i \; x \; \% \; moult \; wt.}{D_i} \right) \quad , \tag{5.6}$$

where Pe is production of exuviae in mg $m^{-3} d^{-1}$; $\bar{W}_i$ is the mean weight

of a size-class; $\bar{N}_i$ is the mean daily density m^{-3} over the entire sampling

period; % moult wt. is the mean dry weight of the moult expressed as a

percentage of body dry weight, which is calculated as 5.75% for N. australis

(Chapter 2); D_i is the intermoult period in days; and s is the total

number of size-classes. The intermoult period D_i, was determined using

the IP – weight equations 2.3 and 2.5 in which the correlation coefficients

exceeded those of the IP – length relationships.

5.2.4 Mean annual biomass.

Mean annual biomass was calculated using the method of Mauchline (1977a)

for the purpose of estimating the P : B ratio using the Petrovich

equation. The dry weight biomass for each month sampled was multiplied

by the time in days between that sample and the next monthly sample.

The resulting values were summed and then divided by the total number

of days, i.e. the sum of the periods.

5.3 Results

Using the Petrovich equation, daily production for the whole of Storm Bay was calculated for each size-class from 1 mm onwards (Table 5.1) and summed, giving a total production of 0.215 mg m^{-3} d^{-1} or 78.293 mg m^{-3} yr^{-1}. The size-class 0.00 - 0.99 mm was omitted from Table 5.1, since it was considered that this size group was not adequately sampled (Chapter 2). The mean annual biomass calculated using the method of Mauchline (1977a) was 5.389 mg m^{-3} (Table 5.2).

The five graphs required for determining production and biomass by the graphical method (Winberg, 1971), are depicted in Figs. 5.1 to 5.5. Table 5.3 shows the conversion of length increments (Fig. 2.14) to dry weight (Fig. 5.1). Table 5.4 shows the computation of the mean daily growth increment for various age groups required for Fig. 5.2, as determined from the growth curve (Fig. 5.1). The required data for producing the age-frequency graph (Fig. 5.3), i.e. $\bar{N}_i/D_i$, are depicted in Table 5.5. The production and biomass values calculated for different age-groups from Figs. 5.1, 5.2, 5.3, are shown in Table 5.6.

The production value calculated, using the graphical method, was 0.232 mg m^{-3} d^{-1} or 84.790 mg m^{-3} yr^{-1}. Results obtained using the Petrovich and graphical methods are thus in close agreement. The calculated mean annual biomass obtained by the graphical method was 6.322 mg m^{-3}. This gives P : B ratios of 14.5 and 13.3 respectively for the Petrovich and graphical methods. These values are higher than any previously reported P : B ratios for euphausiids (Table 5.7).

Using the estimates determined in Chapter 3 for sex raio, egg weight and egg development time, i.e. 65.74% female, 0.0081 mg and 55 days respectively, production of eggs was estimated as 3.858 μg m^{-3} d^{-1} (Table 5.8). The equation of Petrovich et al. (1964) used for this calculation, however, does not take continuous maturation of ova into account. Owing to the fact that as many as three separate batches of eggs can be developing in the ovaries of N. australis at the same time

TABLE 5.1 Production of N. australis in Storm Bay. Daily production per 1 mm size-class is given. D_i = development time (obtained from Fig. 2.14), W_i = weight at start of the size-class, $\bar{N}_i$ = mean daily density over entire sampling period, P_i = production for that size class.

Size-class mm	D_i days	W_i mg	$\bar{N}_i$ m^{-3}	P_i mg m^{-3} d^{-1}
1.00–1.99	10.5	0.0010	19.6668	0.0131
2.00–2.99	10.5	0.0080	7.2050	0.0133
3.00–3.99	10.5	0.0274	4.6432	0.0169
4.00–4.99	10.5	0.0657	4.0208	0.0245
5.00–5.99	10.5	0.1296	2.6835	0.0246
6.00–6.99	10.5	0.2258	2.1378	0.0275
7.00–7.99	10.5	0.3611	2.0513	0.0354
8.00–8.99	10.5	0.5423	0.6556	0.0146
9.00–9.99	10.5	0.7762	0.5243	0.0147
10.00–10.99	11.2	1.0698	0.3154	0.0101
11.00–11.99	11.2	1.4300	0.1209	0.0047
12.00–12.99	11.2	1.8638	0.0811	0.0037
13.00–13.99	13	2.3782	0.0541	0.0025
14.00–14.99	22.2	2.9802	0.0507	0.0016
15.00–15.99	22.2	3.6769	0.0584	0.0021
16.00–16.99	22.2	4.4753	0.0729	0.0030
17.00–17.99	38	5.3826	0.0477	0.0013
18.00–18.99	38	6.4059	0.0184	0.0006
19.00–19.99	38	7.5523	0.0077	0.0003
20.00–20.99	38	8.8289	0.0010	0.00004
21.00	0	10.2430	0.0000	0.0000

Total   0.2145

TABLE 5.2 Estimation of mean annual biomass of N. australis

using the method of Mauchline (1977a).

No sampling occurred after March 1981. The estimated

duration of 30 days is based on the average length of

a month.

Month	Biomass mg m^{-3} B	Time between monthly samples days D	B x D
December 1979	0.2144	72	15.4368
February 1980	1.4108	63	88.8804
April 1980	1.5918	28	44.5704
May 1980	0.2137	15	1.8555
June 1980	3.0251	48	145.2048
July 1980	0.0202	22	0.4444
August 1980	0.0530	40	2.1200
September 1980	10.0816	26	262.1216
October 1980	10.6052	31	328.7612
November 1980	23.1831	25	579.9775
December 1980	0.1160	21	2.4360
January 1981	22.6695	43	974.7885
February 1981	0.6774	21	14.2254
March 1981	5.1152	30	153.4560

Total 485   Total 2,613.8785

Mean Annual Biomass (B) = 5.3894 mg m^{-3}.

TABLE 5.3 Conversion of length increments

(from Fig. 2.14) to dry weight.

Length mm	Time days	Weight mg
1.00	0	0.0010
4.10	33	0.0708
10.06	96	1.0895
13.87	139	2.8967
17.04	209	5.4213
17.96	249	6.3626
18.50	275	6.9632

FIGURE 5.1   Growth curve calculated from the December

1979 cohort data.
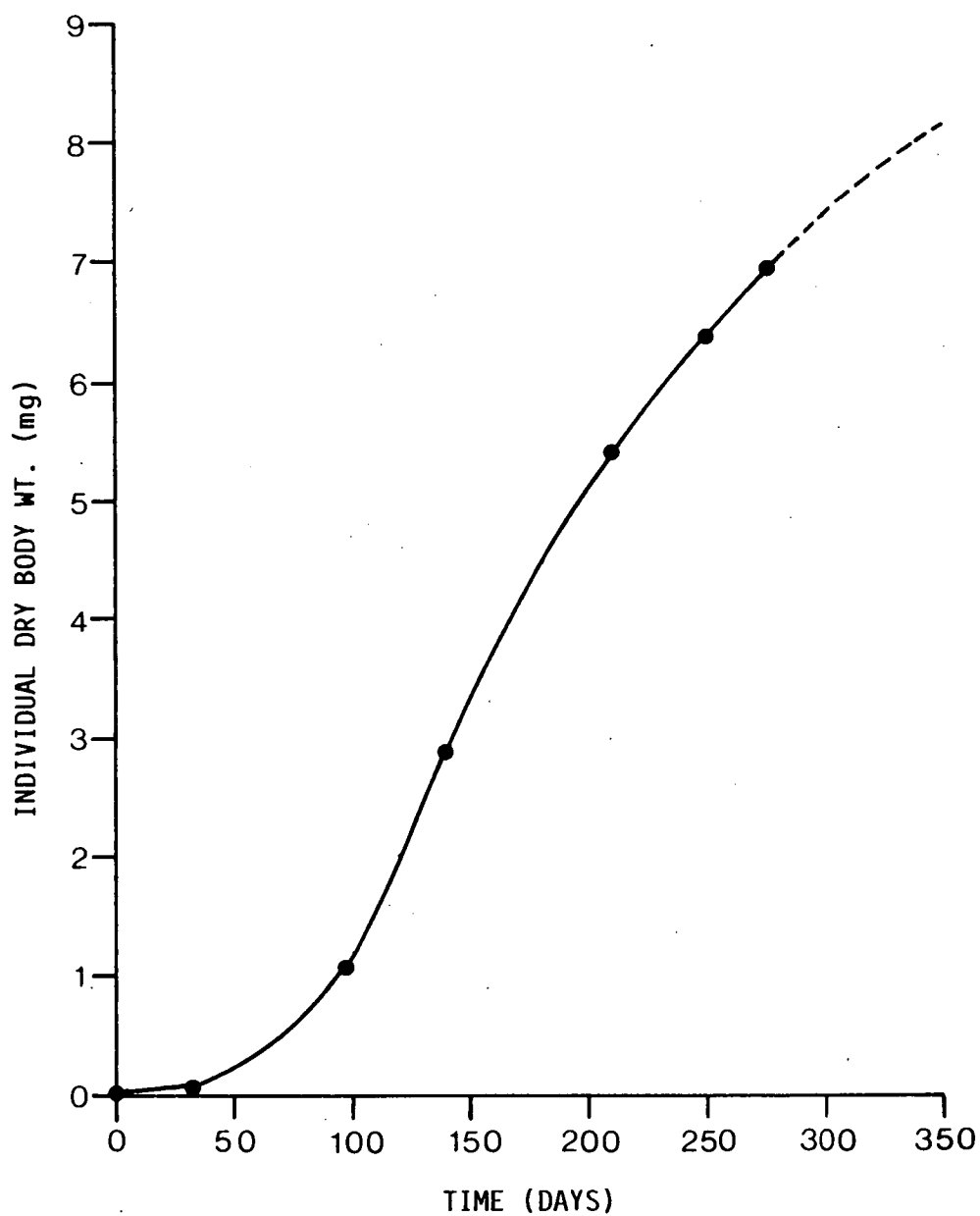
TABLE 5.4 Production of <u>N. australis</u> – graphical method (1st variant) (Winberg, 1971). Computation of the mean daily growth increment ($\Delta w / \Delta t$) of different age-classes (obtained from Fig. 5.1).

W_o = weight at start of interval, W_i = weight at end of interval, Δt = change in time, Δw = change in weight, T = midpoint of time interval.

Time interval days	W_o mg	W_i mg	Δt days	Δw mg	$\Delta w / \Delta t$ mg d^{-1}	T days
0–32	0.001	0.070	32	0.690	0.0022	16
32–50	0.070	0.230	18	0.160	0.0089	41
50–60	0.230	0.360	10	0.130	0.0130	55
60–80	0.360	0.720	20	0.360	0.0180	70
80–90	0.720	1.090	16	0.370	0.0231	88
96–108	1.090	1.480	12	0.390	0.0325	102
108–120	1.480	2.000	12	0.520	0.0433	114
120–140	2.000	2.920	20	0.920	0.0460	130
140–160	2.920	3.790	20	0.870	0.0435	150
160–170	3.790	4.170	10	0.380	0.0380	165
170–180	4.170	4.510	10	0.340	0.0340	175
180–200	4.510	5.120	20	0.610	0.0305	190
200–220	5.120	5.700	20	0.580	0.0290	210
220–240	5.700	6.200	20	0.500	0.0225	230
240–260	6.200	6.640	20	0.440	0.0220	250
260–280	6.640	7.030	20	0.390	0.0195	270
280–300	7.030	7.390	20	0.360	0.0180	290
300–320	7.390	7.700	20	0.310	0.0155	310
320–340	7.700	8.000	20	0.300	0.0150	330
340–360	8.000	8.270	20	0.270	0.0135	350

FIGURE 5.2   Individual daily growth increments.
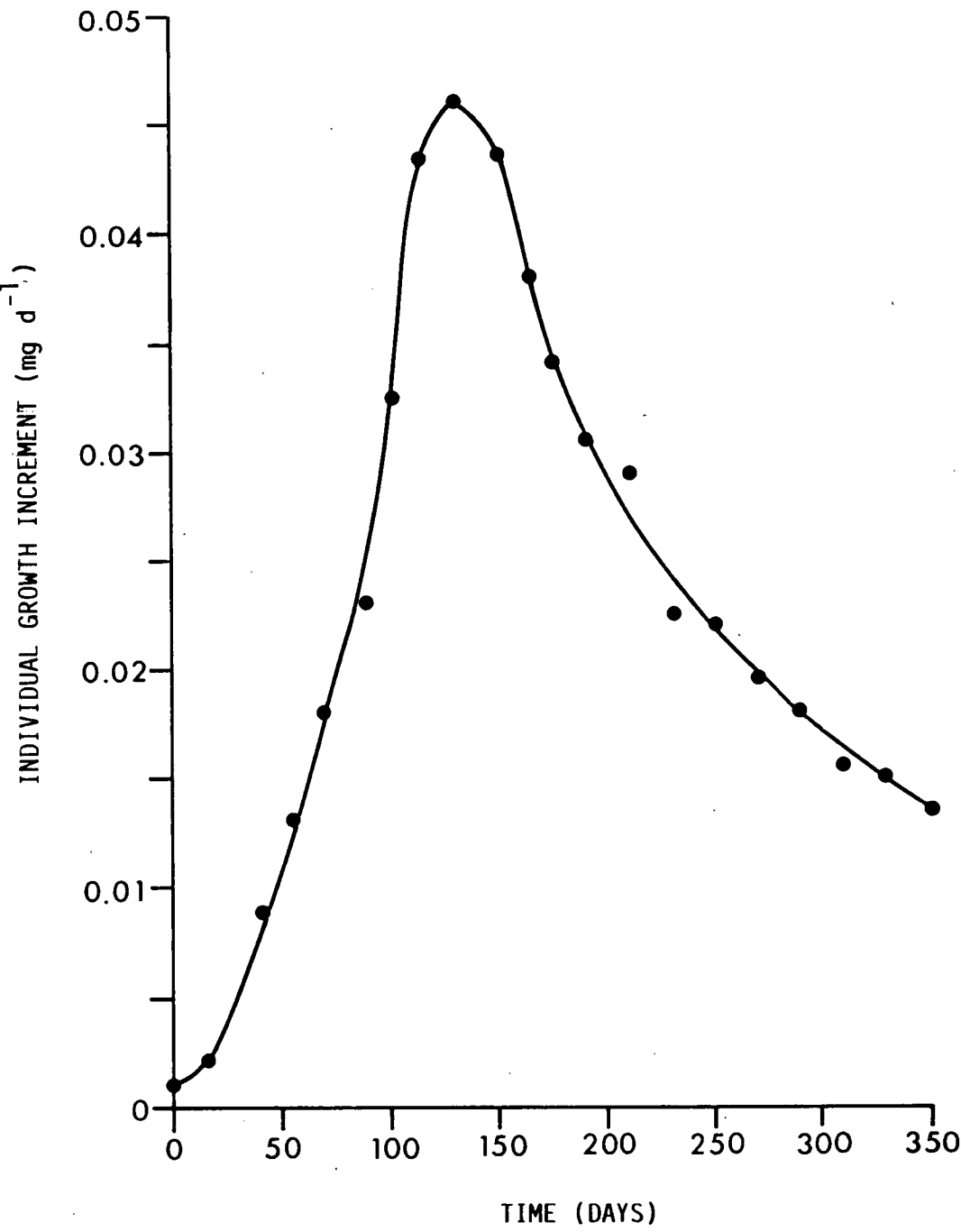
TABLE 5.5 Production of <u>N. australis</u> – graphical method (1st variant) (Winberg, 1971). Age frequency – the number of different age-classes in the population ($\bar{N}_i/D_i$).

D_i = development time (obtained from Fig. 2.14),

$\bar{N}_i$ = mean daily density over entire sampling period,

T = midpoint of time interval.

Size-class mm	D_i days	$\bar{N}_i$ m^{-3}	$\bar{N}_i/D_i$	T days
1.00–1.99	10.5	19.6668	1.8730	5.25
2.00–2.99	10.5	7.2050	0.6862	15.75
3.00–3.99	10.5	4.6432	0.4422	26.25
4.00–4.99	10.5	4.0208	0.3819	36.75
5.00–5.99	10.5	2.6835	0.2556	47.25
6.00–6.99	10.5	2.1378	0.2036	57.75
7.00–7.99	10.5	2.0513	0.1954	68.25
8.00–8.99	10.5	0.6556	0.0624	78.75
9.00–9.99	10.5	0.5243	0.0499	89.25
10.00–10.99	11.2	0.3154	0.0282	100.1
11.00–11.99	11.2	0.1209	0.0108	111.3
12.00–12.99	11.2	0.0811	0.0072	122.5
13.00–13.99	13.0	0.0541	0.0042	134.6
14.00–14.99	22.2	0.0507	0.0023	152.2
15.00–15.99	22.2	0.0584	0.0026	174.4
16.00–16.99	22.2	0.0729	0.0033	196.6
17.00–17.99	38.0	0.0477	0.0013	226.7
18.00–18.99	38.0	0.0184	0.0005	264.7
19.00–19.99	38.0	0.0077	0.0002	302.7
20.00–20.99	38.0	0.0010	0.00003	340.7

FIGURE 5.3   The number of different age-classes in the N. australis population. Note: the ordinate is $\log_{10}$ scale.
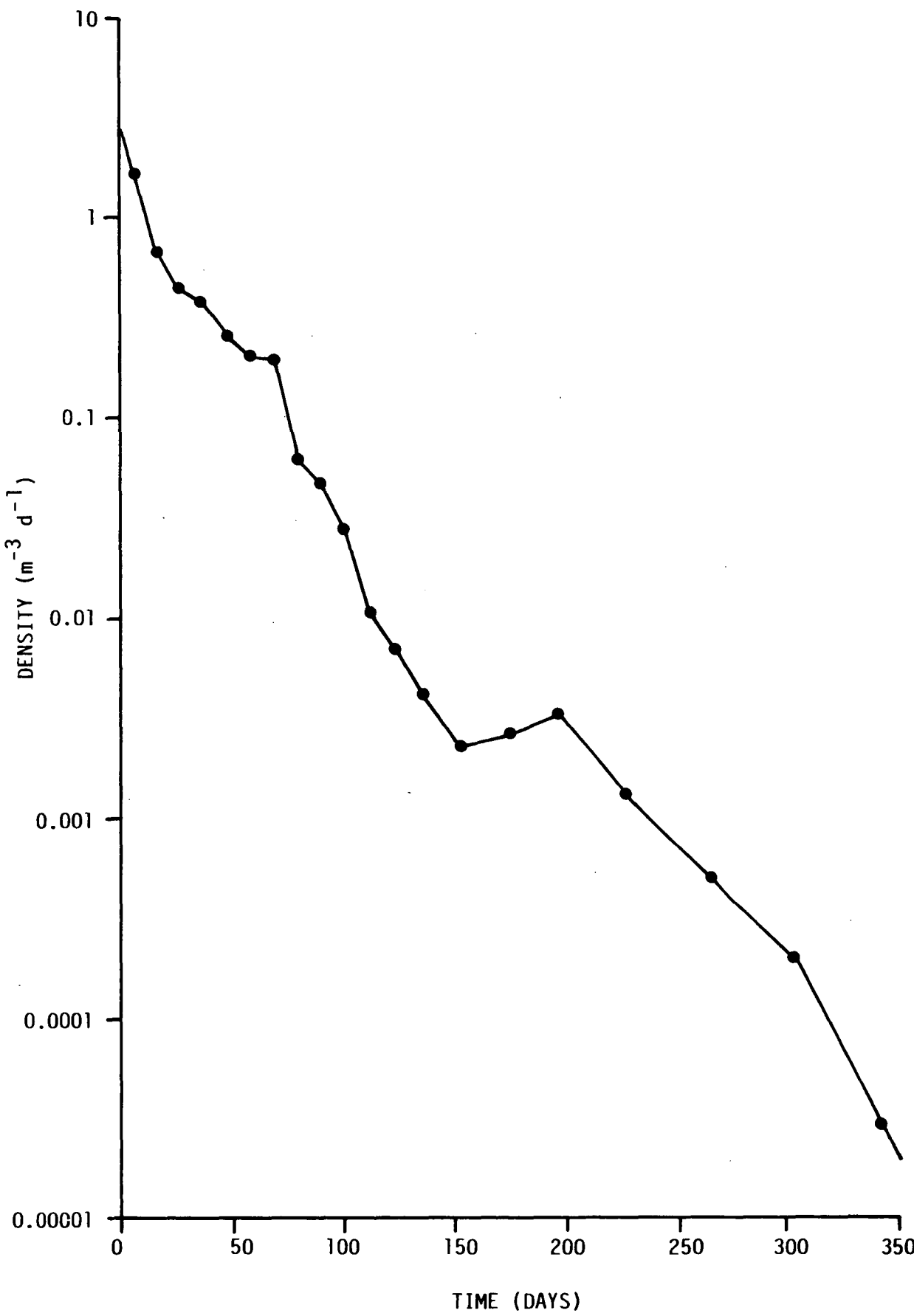
TABLE 5.6 Estimation of production and biomass of N. australis by
the graphical method (1st variant) (Winberg, 1971).
G = production as daily growth increments for each
age-group (obtained from Fig. 5.2),
N = density of age-group (obtained from Fig. 5.3).

Age days	G mg d^{-1}	N m^{-3}	Weight mg	Production μg m^{-3} d^{-1}	Biomass μg m^{-3}
0	0	2.41	0.001	0	2.410
5.25	0.0005	1.873	0.003	0.9365	5.619
15.75	0.0020	0.6862	0.020	1.3724	13.724
20	0.0028	0.5900	0.030	1.6520	17.700
30	0.0048	0.4400	0.060	2.1120	26.400
40	0.0076	0.3300	0.120	2.5080	39.600
50	0.0110	0.2530	0.230	2.7830	58.190
60	0.0147	00.1910	0.360	2.8077	68.760
70	0.0182	0.1350	0.520	2.4570	70.200
80	0.0222	0.0870	0.710	1.9314	61.770
90	0.0267	0.0530	0.930	1.4151	49.290
100	0.0313	0.0320	1.210	1.0016	38.720
110	0.0402	0.0180	1.550	0.7236	27.900
120	0.0448	0.0100	2.000	0.4480	20.000
130	0.0460	0.0060	2.460	0.2760	14.760
135	0.0457	0.0042	2.700	0.1919	11.340
152.2	0.0426	0.0023	3.470	0.0980	7.981
174.4	0.0347	0.0026	4.320	0.0902	11.232
196.6	0.0297	0.0033	5.030	0.0980	16.599
226.7	0.0250	0.0013	5.850	0.0325	7.605
264.7	0.0203	0.0005	6.740	0.0102	3.370
302.7	0.0168	0.0002	7.430	0.0034	1.486
340.7	0.0141	0.00003	8.010	0.0004	0.2403

FIGURE 5.4   Daily production of all age-classes of

N. australis. P = 0.2323 mg m^{-3} d^{-1}.

AGE (DAYS)
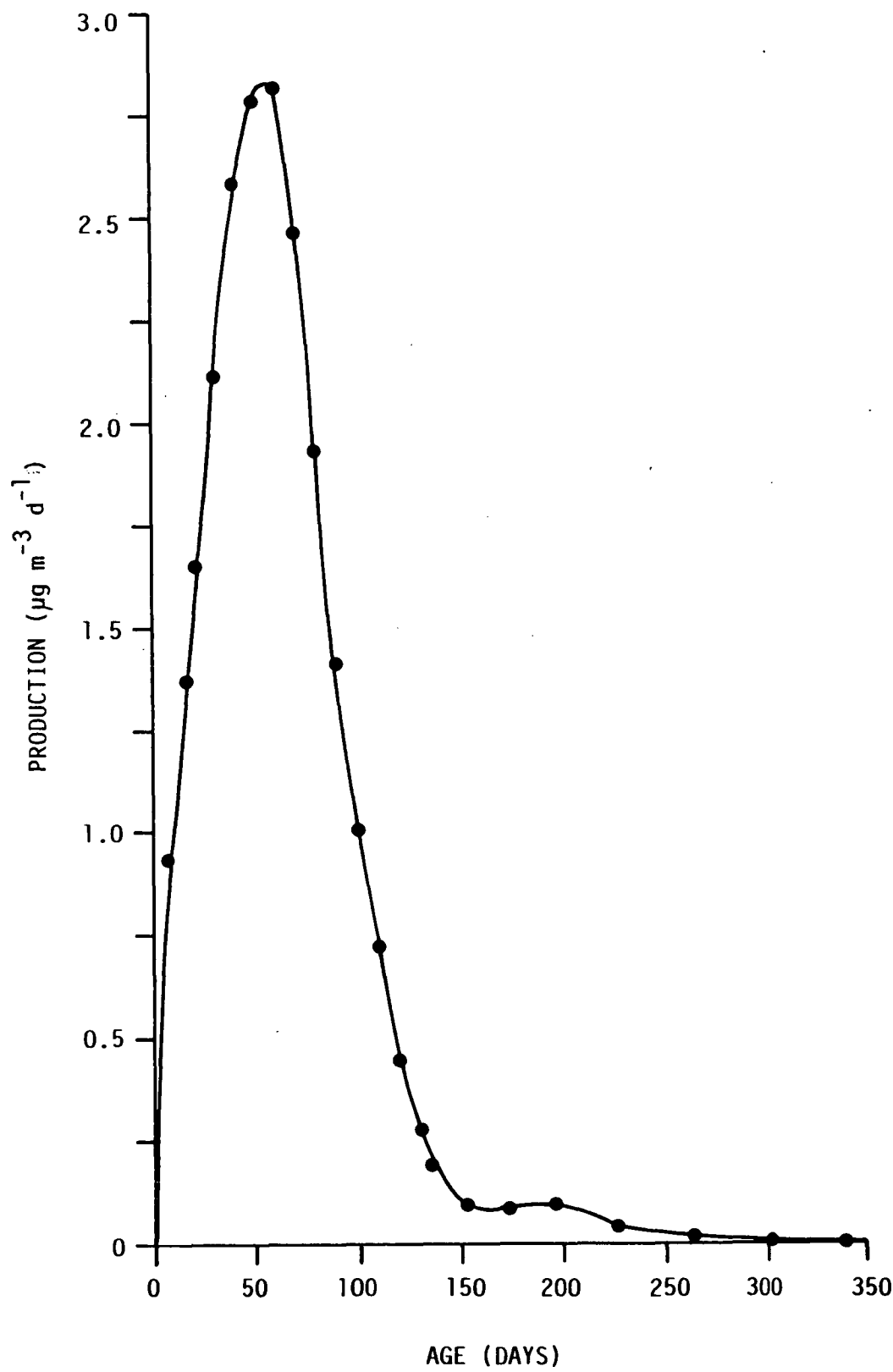
FIGURE 5.5   Biomass of all age-classes of N. australis.

B = 6.3881 mg m^{-3}.
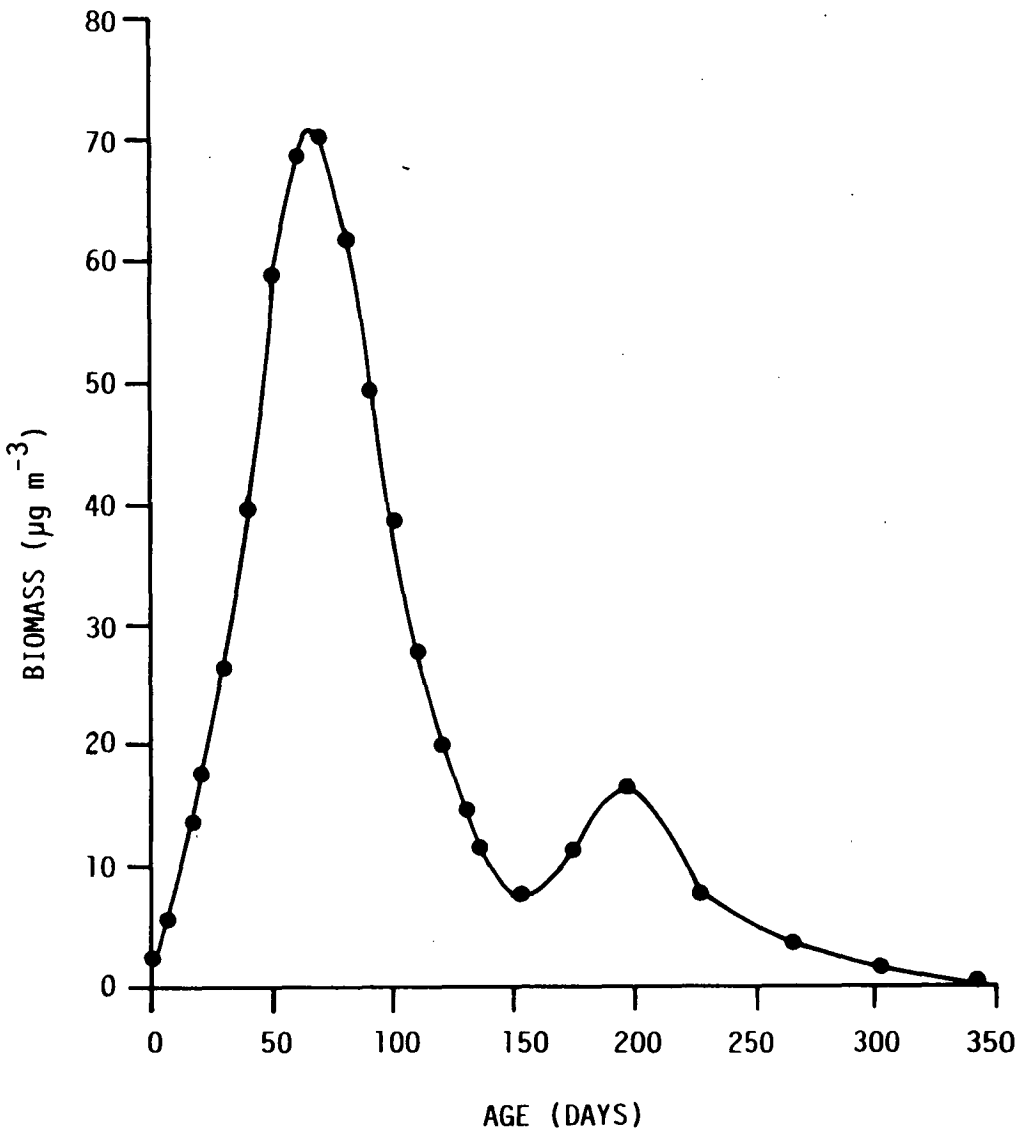
TABLE 5.7 Comparison of euphausiid P : B ratios. ★ = usual range of values, ▲ = usual range of values

combined for both species, ● = maximum recorded value.

Species	P : B	Locality	Source
Euphausia superba	1.8-2.3	Antarctica	Allen (1971)
E. pacifica	3.0	West Coast U.S.A.	Lasker (1966)
E. pacifica	8.7	Oregon Coast U.S.A.	Mauchline (1977) (using data from Smiles and Pearcy, 1971).
Thysanoessa raschi	4	Gulf of St. Lawrence	Berkes (1977)
T. longicaudata	2-8★, 11.6●	North Atlantic	Lindley (1978)
T. inermis	1.3-4.2▲	East Coast U.S.A.	Lindley (1980)
T. raschi	10.4●	North Sea	
Meganyctiphanes norvegica	2.3	Loch Fyne	Mauchline (1977)
M. norvegica	1.3-6.3	North Sea and Atlantic Ocean	Lindley (1982)
Nyctiphanes couchi	4.0-5.5	North Sea and Atlantic Ocean	Lindley (1982)
N. australis	21.4	East Coast Tasmania	Fenton (1981)
N. australis	13.3-14.5	Storm Bay Tasmania	Present Study.

TABLE 5.8 Estimation of egg production in N. australis.

Production per 1 mm size-class of adult is given.

W_i = weight of female, $\bar{N}_i$ = mean density of adults

over entire sampling period, F_i = number of eggs

per female, per oviposition, for each size-class

(calculated using equation 2.1),

P_i = production of ova within each size-class.

Size-class mm	W_i mg	$\bar{N}_i$ m^{-3}	F_i	P_i $\mu g\ m^{-3}\ d^{-1}$
11.00–11.99	1.4300	0.1209	49	0.5736
12.00–12.99	1.8638	0.0811	56	0.4397
13.00–13.99	2.3782	0.0541	65	0.3405
14.00–14.99	2.9802	0.0507	76	0.3731
15.00–15.99	3.6769	0.0584	88	0.4976
16.00–16.99	4.4753	0.0729	102	0.7199
17.00–17.99	5.3826	0.0477	117	0.5403
18.00–18.99	6.4059	0.0184	135	0.2405
19.00–19.99	7.5523	0.0077	155	0.1156
20.00–20.99	8.8289	0.0010	177	0.0171

Total   3.8579

TABLE 5.9 Estimation of exuviae production at 10°C and 15°C per

1 mm size-class. $\bar{W}_i$ = mean weight of size-class,

$\bar{N}_i$ = mean daily density over entire sampling period,

IP = intermoult period (calculated using equations

2.3 and 2.5), P_i = production for each size-class.

Size-class mm	$\bar{W}_i$ mg	$\bar{N}_i$ m^{-3}	IP days 10°C	15°C	P_i mg m^{-3} d^{-1} 10°C	15°C
1.00-1.99	0.0033	19.6668	4.17	2.50	0.0009	0.0015
2.00-2.99	0.0157	7.2050	4.17	2.51	0.0016	0.0026
3.00-3.99	0.0438	4.6432	4.18	2.51	0.0028	0.0047
4.00-4.99	0.0941	4.0208	4.20	2.53	0.0052	0.0086
5.00-5.99	0.1733	2.6835	4.23	2.55	0.0063	0.0105
6.00-6.99	0.2882	2.1378	4.28	2.58	0.0083	0.0137
7.00-7.99	0.4455	2.0513	4.34	2.62	0.0121	0.0201
8.00-8.99	0.6522	0.6556	4.42	2.68	0.0056	0.0092
9.00-9.99	0.9151	0.5243	4.53	2.75	0.0061	0.0100
10.00-10.99	1.2411	0.3154	4.66	2.85	0.0048	0.0079
11.00-11.99	1.6373	0.1209	4.84	2.97	0.0024	0.0038
12.00-12.99	2.1105	0.0811	5.05	3.11	0.0019	0.0032
13.00-13.99	2.6678	0.0541	5.31	3.30	0.0016	0.0025
14.00-14.99	3.3163	0.0507	5.64	3.53	0.0017	0.0027
15.00-15.99	4.0629	0.0584	6.03	3.81	0.0023	0.0036
16.00-16.99	4.9149	0.0729	6.52	4.17	0.0032	0.0049
17.00-17.99	5.8793	0.0477	7.12	4.60	0.0023	0.0035
18.00-18.99	6.9632	0.0184	7.86	5.15	0.0009	0.0014
19.00-19.00	8.1738	0.0077	8.78	5.84	0.0004	0.0006
20.00-20.99	9.5183	0.0010	9.92	6.72	0.0001	0.0001

Total   0.0705   0.1151

(Table 3.2), actual production may reach as high as 11.574 μg m^{-3} d^{-1} or 4.224 mg m^{-3} yr^{-1}.

Total production of exuviae from all size-classes, using the IP - weight relationship at 15 $^{\circ}$C (equation 2.5), was calculated as 0.115 mg m^{-3} d^{-1} or 42.012 mg m^{-3} yr^{-1}. When the IP - weight relationship (equation 2.3) at 10°C was substituted, a value of 0.071 mg m^{-3} d^{-1} of 25.733 mg m^{-3} yr^{-1} was obtained (Table 5.9). Previously recorded estimates of exuviae production are 0.45 g dry wt. m^{-2} yr^{-1} for Euphausia superba (Ikeda and Dixon, 1982) and 1.5 g dry wt. m^{-2} yr^{-1} for E. pacifica for its entire distributional range (Jerde and Lasker, 1966). The latter value is very close to the present Pe (15°C) estimate of 1.54 g dry wt. m^{-2} yr^{-1} for N. australis.

5.4 Discussion

As can be seen in Table 5.1, the bulk of the production of the Storm Bay population occurred in the non-adult stages, particularly between size-classes 4.00 - 7.99 mm which covers the FIII and post-larvae. The adults contribute little to the production, but do contribute a portion of the biomass (compare Figs. 5.4 and 5.5).

The two methods for estimating production, and the two estimates of mean biomass, produced very similar results. However, for ease of computation the methods of Petrovich et al.(1964) and Mauchline (1977a) are recommended.

The higher P : B ratio of N. australis compared to those reported for other euphausiids (Table 5.7), can probably be partially accounted for by the lack of a severe winter in south-eastern Tasmania. While N. australis is a sub-tropical species (Sheard, 1953), the euphausiids listed in Table 5.7 range in habitat from temperate waters of the eastern North Pacific, North Atlantic and North Sea to the much colder realms of Antarctica. In these areas little or no growth occurs in winter, the breeding season in shorter, and the euphausiids can apparently

live for 2-3 years (Lasker, 1966; Berkes, 1976, 1977a; Lindley, 1978, 1980, 1982; Mauchline, 1966, 1977b, 1980; Mauchline and Fisher, 1969). In particular _Euphausia superba_ in the Weddell Sea can take up to 3 years to mature (Fevolden, 1979). However, Smiles and Pearcy (1971) noted that for _E. pacifica_ off the Oregon Coast, the growth rate was comparatively rapid, the breeding season longer than for other geographical areas inhabited by the species and the lifespan was only 1 year instead of 3. This was attributed to the high productivity of the area and also to the lack of wide seasonal fluctuations of water temperature. The P : B ratio of this population was 8.7 (Table 5.7), the closest value to that obtained for _N. australis_. Similarly, in _N. australis_, the combined effect of a prolonged breeding season, accompanied by a short life-span and warmer water temperatures allowing growth throughout the year, has resulted in a higher rate of turnover compared to the other euphausiids in Table 5.7 and therefore a higher P : B ratio. There are no data on primary production for Storm Bay, though enrichment from the Derwent estuary is to be expected.

Lindley (1978, 1980) did record P : B values of 11.6 and 10.4 for _Thysanoessa longicaudata_ and _T. raschi_ respectively, from the North Atlantic. These values are higher than those listed in Table 5.7 for the same species and are more comparable to the P : B ratio of _N. australis_. However, the high turnover rates of the two _Thysanoessa_ species may have been an artifact caused by the low sampling frequency.

Low sampling frequency may also be responsible for the much higher P : B ratio recorded for the East coast population of _N. australis_ (Fenton, 1981). There was almost a complete absence of summer sampling and in particular adults were captured in very low numbers according to Fenton (1981). While adults would contribute little to the production estimates, their biomass would reduce the P : B ratio.

As far as I am aware, no other values of egg production with which

to compare the present estimate, are available. Previous estimates of production have generally neglected eggs and nauplii (Berkes, 1977a; Lasker, 1966; Mauchline, 1977a). Lindley (1978, 1980, 1982), in particular did not include data for eggs, nauplii and calyptopis larvae in his production estimates, as they were too small to be sampled quantitatively using a continuous plankton recorder. The maximum estimate of 11.573 μg m^{-3} d^{-1} or 0.012 mg m^{-3} d^{-1} for <u>N. australis</u> is, however, comparable with production estimates for the smaller size-classes (Table 5.1).

Production of exuviae calculated for 10°C was markedly lower than the value for 15°C. In turn, production of exuviae is expected to be much greater than 0.115 mg m^{-3} d^{-1} when water temperatures in Storm Bay exceed 15°C. The mean water temperature in Storm Bay between 0 and 20 m was approximately 14°C (Fig. 2.6). Thus, the estimates of exuviae production calculated for 15°C can be taken as a close approximation of the mean daily production throughout the year in Storm Bay.

The figures given in Table 5.7 do not include the production of exuviae. This is surprising since Lasker (1966) stated that the total dry weight of exuviae could contribute as much as 7 times the euphausiid biomass to detrital food webs. For <u>N. australis</u> the total dry weight of moults was calculated to be 7.8 times the mean biomass, or an annual production for the whole of Storm Bay of 779 tonnes. Thus, moulting alone forms a significant contribution to the environment. Total production, therefore, in terms of flesh, eggs and exuviae (P + Po + Pe) is approximately 124 gm m^{-3} yr^{-1} or 2,307 tonnes dry wt. yr^{-1} for the whole of Storm Bay. This represents a (P + Po + Pe) : B ratio of 23.1.

The distribution of N. australis extends along the east coast of Australia from 31° – 44°S, and as far west as 132°E (Blackburn, 1980). Storm Bay represents only a small portion of this distribution and is also close to the southern limit. Thus, estimates of production for Storm Bay could well be conservative when compared to values for lower latitudes.

CONCLUSIONS

Nyctiphanes australis exists in high densities in Storm Bay throughout

most of the year and contributes a large proportion to the total zooplankton

biomass. In Storm Bay, as well as on the east coast of Tasmania (Fenton,

1981), _N. australis_ exhibits a high rate of turnover, much higher than

previously reported for other euphausiid species from temperate and

polar regions. This high turnover rate is primarily due to the rapid

growth rate and maturation of _N. australis_ which extends throughout

the year, coupled with a prolonged breeding season, during which the

production of multiple generations is possible.

It is yet to be established clearly whether the diets of the larvae

and adult of _N. australis_ differ. However, _N. australis_ does feed on a

broad spectrum of dietary items and as an opportunistic omnivore/detritivore

forms an important link between its predators and several parts of the

food web. Sheard (1953), in particular, emphasized the role of detrital

feeding euphausiids, such as _N. australis_, in recycling back to carnivores

nutrient material that would normally bypass them. In turn, a good portion

of the detritus in Storm Bay is a consequence of _N. australis_ exuviating.

Overall, _N. australis_ must be considered as one of the most important

marine zooplankters in south-eastern Tasmanian coastal waters. The adult

N. australis is already recognised as an important dietary component of

several species of commercially exploited fish, as well as various sea

birds (Blackburn, 1957; Malcolm, 1959; Morgan, 1981; Morgan and Ritz, 1982;

Webb, 1976). Undoubtedly, this euphausiid, directly or indirectly, must

also represent an attractive food source for a number of other carnivores,

particularly the non-adult stages which form the bulk of the standing

stock and contribute most to the production of this species.

The importance of euphausiids in the marine ecosystem has only in

recent years been fully appreciated. Much emphasis, for example, is now

being placed in determining the complexity of the _Euphausia superba_ food web

and the exploitability of this species as a fishery. It is believed that
the present study has not only contributed to the understanding of the
biology and trophic status of N. australis, but also to that of the
euphausiids as a whole.

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APPENDIX I

SALINITY AND TEMPERATURE DATA FOR STORM BAY

December 1979

	Depth m.	T°C	S°/oo		Depth m	T°C	S°/oo
SB1	0	14.4	34.02	SB5			
18/12	5	14.4	34.07				
	10	14.2	34.16				
	15	14.2	34.16				
	20	14.2	34.16				
	30	14.0	34.22				
	40	13.8	34.32				
	50	13.7	34.34				
SB2	0	14.5	33.62	SB6			
18/12	5	14.5	33.67				
	10	14.4	33.82				
	14	14.0	33.82				
	16	13.8	34.32				
	27	13.8	34.34				
	36	13.5	34.44				
	45	13.1	34.52				
				SB7			
SB3	0	13.8	34.43				
18/12	5	13.7	34.43				
	10	13.7	34.47				
	15	13.7	34.47				
	20	13.7	34.47				
	35	13.6	34.47				
				SB8			
SB4	0	14.5	33.98				
18/12	4	14.5	33.98				
	8	14.5	33.98				
	12	14.5	34.02				
	16	14.6	34.07				
	25	14.5	34.14				
	32	13.2	34.53	SB9			

Appendix 1 continued:

February 1980

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1	0	16.2	34.58	SB5	0	16.2	34.62
	5	15.9	34.62		5	16.2	34.70
19/2	10	15.2	34.64	28/2	9	16.0	34.72
	20	14.5	34.72		18	15.7	34.80
	30	14.4	34.72		26	15.3	34.89
	40	14.0	34.76		35	14.4	34.95
	50	14.1	34.69		43	14.5	34.92
SB2	0	16.2	34.51	SB6	0	16.4	34.45
	5	16.0	34.56		5	16.2	34.52
19/2	10	15.8	34.60	19/2	10	15.5	34.62
	20	14.6	34.67		20	14.8	34.74
	30	14.3	34.72		30	14.3	34.74
	40	14.1	34.72				
	50	14.0	34.72				
				SB7	0	16.6	34.62
SB3	0	15.9	34.72		4	16.5	34.62
	5	15.3	34.72	19/2	7	15.9	34.52
19/2	10	15.0	34.72		16	15.6	34.52
	20	14.5	34.72		19	15.2	34.62
	30	14.3	34.75				
	40	14.2	34.75				
				SB8	0	16.8	34.17
					4	16.6	34.22
SB4	0	16.4	34.50	19/2	7	16.3	34.22
	5	16.2	34.54		16	16.2	34.34
19/2	10	15.7	34.62		19	15.3	34.52
	20	15.0	34.67				
	30	14.3	34.67				
				SB9	0	17.9	33.35
					5	16.2	34.41
				28/2	10	16.1	34.50
					20	15.6	34.75

Appendix 1 continued:

April 1980

	Depth m	T°C	S°/oo		Depth m.	T°C	S°/oo
SB1	0	13.5	34.61	SB5	0	13.4	34.69
	5	13.5	34.62		5	13.4	34.71
1/5	10	13.5	34.62	1/5	10	13.4	34.71
	20	13.5	34.64		20	13.4	34.71
	30	13.4	34.75		30	13.4	34.72
	40	13.4	34.80		40	13.4	34.72

SB2

SB6

				SB7	0	14.5	–
SB3				16/4	3	14.5	–
					6.5	14.5	–
					9.5	14.0	–
					13	14.0	–
					18	14.0	–

				SB8	0	14.7	–
				16/4	3	14.5	–
SB4	0	13.4	34.67		8	14.2	–
	5	13.4	34.67		13	14.2	–
1/5	10	13.4	34.67		18	14.0	–
	20	13.5	34.69		20	14.0	–
	30	13.5	34.75				

				SB9	0	14.4	–
				16/4	3.5	14.4	–
					6.5	14.4	–
					9.5	14.2	–
					16	14.0	–
					19	14.0	–

Appendix 1 continued:

May 1980

	Depth m	T°C	S°/oo			Depth m	T°C	S°/oo
SB1	0	13.2	34.96		SB5	0	12.3	34.20
	4	13.2	34.97			4	12.9	35.05
29/5	7	12.5	34.75		26/5	7	13.0	35.11
	14	13.3	35.02			14	12.9	35.11
	21	13.5	35.10			21	13.0	35.11
	28	13.5	35.18			28	12.9	35.13
	35	13.6	35.06			35	12.9	35.12
SB2					SB6	0	13.1	35.00
						4	13.0	35.08
					26/5	7	13.0	35.10
						14	13.0	35.12
						21	13.0	35.10
						28	13.0	35.10
						35	13.0	35.10
SB3					SB7	0	12.4	34.69
						4	12.4	34.87
					29/5	7	12.2	34.90
						14	12.1	35.08
						21	12.1	35.00
					SB8	0	12.0	32.90
						4	12.0	33.11
SB4	0	12.4	34.20		26/5	7	12.2	33.81
	4	12.4	34.40			14	12.5	34.60
29/5	7	12.5	34.75			21	12.4	35.03
	14	12.4	34.82					
	21	12.4	34.95					
	28	12.3	35.07		SB9	0	12.1	33.50
						4	12.3	34.33
					26/5	7	12.8	34.88
						14	12.8	35.05

Appendix 1 continued:

June 1980

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1	0	12.6	34.93	SB5			
	4	12.6	34.94				
12/6	7	12.6	34.98				
	14	12.7	35.03				
	21	12.8	35.11				
	28	12.8	35.11				
	35	12.9	35.11				
SB2	0	13.3	35.26	SB6	0	12.4	34.92
	4	13.3	35.26		5	12.4	34.92
12/6	7	13.3	35.26	12/6	10	12.4	34.94
	14	13.3	35.25		20	12.5	34.99
	21	13.2	35.25		30	12.5	35.03
	28	13.3	35.26				
	35	13.3	35.24				
SB3	0	12.6	35.01	SB7			
	4	12.6	34.99				
12/6	7	12.6	35.02				
	14	12.6	35.07				
	21	12.7	35.07				
	28	12.6	35.08				
	35	12.7	35.10				
				SB8	0	11.2	33.75
SB4	0	11.6	34.37		4	11.6	33.92
	4	11.7	34.49	13/6	7	11.8	34.36
13/6	7	12.1	34.79		14	11.8	34.42
	14	12.3	34.88		21	12.5	34.98
	21	12.3	34.88				
	28	12.5	34.96				
	35	12.6	35.06	SB9	0	11.6	34.04
					4	12.0	34.57
				13/6	7	12.3	34.88
					14	12.4	34.92
					20	12.5	35.00

Appendix 1 continued:

July 1980

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1				SB5			
SB2	0	12.5	34.42	SB6	0	9.9	32.60
23/7	4	12.5	34.42	23/7	4	10.9	33.09
	7	12.4	34.42		7	11.7	33.83
	14	12.5	34.42		14	12.3	34.50
	21	12.3	34.40		21	12.2	34.03
	28	12.2	34.32		28	12.1	34.00
	35	12.5	34.32				
				SB7	0	9.5	34.15
SB3	0	12.2	34.22	31/7	4	9.5	34.15
23/7	4	12.2	34.22		7	9.5	34.15
	7	12.2	34.22		14	9.7	34.26
	14	12.2	34.22		21	9.8	34.46
	21	12.2	34.22				
	28	12.2	34.22				
	35	12.3	34.21	SB8	0	10.2	34.24
				31/7	4	10.2	34.24
SB4	0	10.2	34.21		7	10.2	34.24
31/7	4	10.3	34.23		14	10.2	34.26
	7	10.3	34.23		21	10.5	34.41
	14	10.3	34.23				
	21	10.3	34.20				
	28	10.3	34.20	SB9	0	10.5	32.60
	35	10.3	34.15	23/7	4	10.5	32.85
					7	11.5	33.04
					14	12.1	34.16
					20	12.1	34.10

Appendix 1 continued:

August 1980

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1	0	10.9	33.10	SB5	0	11.2	31.90
20/8	4	11.2	33.95	22/8	4	10.8	33.66
	7	11.9	34.94		7	10.7	33.90
	14	11.9	35.00		14	11.2	34.78
	21	12.0	35.15		21	11.8	35.12
	28	12.0	35.19		28	11.8	35.12
	35	12.0	35.22		35	11.8	35.12
SB2	0	11.8	34.92	SB6	0	11.4	34.59
20/8	4	11.9	35.01	20/8	5	11.5	35.06
	7	12.0	35.17		9	11.5	35.09
	14	12.1	35.25		17	11.5	35.18
	21	12.0	35.25		26	11.5	35.19
	28	12.0	35.22		35	11.5	35.18
	35	12.0	35.22				
				SB7	0	10.3	32.88
SB3	0	11.8	35.19	22/8	4	9.9	33.95
20/8	4	11.8	35.20		7	10.0	34.06
	7	11.8	35.18		14	10.1	34.12
	14	11.8	35.20		21	10.5	34.56
	21	11.8	35.20				
	28	11.8	35.20				
	35	11.8	35.20	SB8	0	10.6	31.70
				22/8	4	10.7	33.60
SB4	0	11.0	33.29		7	10.5	34.04
22/8	4	10.9	33.40		14	10.5	34.69
	7	10.8	33.60		21	11.5	34.96
	14	10.8	34.02				
	21	11.6	35.13				
	28	11.8	35.25	SB9	0	10.7	32.00
	35	11.8	35.25	20/8	5	11.0	34.54
					9	11.4	34.87
					17	11.6	35.02

Appendix 1 continued:

September 1980

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1				SB5			
SB2				SB6 25/9	0	11.7	34.68
					4	11.7	34.67
					7	11.7	34.64
					14	11.7	34.70
					21	11.7	34.70
					28	11.7	34.77
					35	11.6	34.77
				SB7			
SB3 25/9	0	11.9	34.62				
	4	11.9	34.62				
	7	11.8	34.59				
	14	11.8	34.69				
	21	11.8	34.69				
	28	11.6	34.69				
	35	11.6	34.69	SB8 1/10	0	12.2	30.98
					5	11.9	31.91
SB4					10	11.8	32.87
					20	11.7	34.69
				SB9 25/9	0	11.8	29.09
					4	11.4	34.48
					7	11.6	34.67
					14	11.6	34.76
					20	11.6	34.76

Appendix 1 continued:

October 1980

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1	0	13.9	33.29	SB5	0	13.7	33.19
	4	13.7	33.37		4	13.5	33.19
27/10	7	13.5	33.54	27/10	9	13.2	33.69
	14	13.5	33.58		17	13.0	33.83
	21	13.0	34.39		26	12.6	34.57
	28	12.7	34.58		35	12.4	34.46
	35	12.7	34.59		43	12.5	34.53
SB2	0	13.3	34.21	SB6	0	13.2	34.22
	5	13.3	34.33		5	13.1	34.27
27/10	10	13.2	34.47	27/10	10	12.9	34.31
	20	12.9	34.49		20	12.6	34.42
	30	12.9	34.49		30	12.6	34.51
	40	12.7	34.58				
	50	12.6	34.51				
				SB7	0	12.8	33.19
SB3	0	13.5	34.52		4	12.7	33.24
	5	13.3	34.52	12/10	7	12.7	33.24
27/10	10	13.1	34.44		14	12.0	34.47
	20	12.7	34.53		21	12.0	34.47
	30	12.7	34.60				
	40	12.7	34.60				
				SB8	0	12.5	33.67
					4	12.4	33.71
SB4	0	12.7	33.46	12/10	7	12.4	33.80
	4	12.6	33.46		14	12.2	34.14
12/10	7	12.6	33.46		21	12.0	34.39
	14	12.1	34.28				
	21	12.1	34.58				
	28	12.1	34.58	SB9	0	13.8	28.39
	35	12.1	34.58		4	12.2	34.18
				12/10	7	12.2	34.46
					14	12.1	34.46
					20	12.1	34.46

Appendix 1 continued:

November 1980

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1				SB5			
SB2	0	13.4	34.79	SB6	0	13.5	34.54
	5	13.4	34.79		4	13.4	34.55
27/11	8	13.4	34.79	27/11	7	13.4	34.55
	15	13.4	34.79		14	13.4	34.68
	23	13.2	34.74		21	13.2	34.68
	40	12.9	34.74		28	13.2	34.68
	50	12.9	34.74		35	13.4	34.72
				SB7	0	16.3	33.71
SB3	0	13.4	34.71	18/11	4	16.0	33.41
	5	13.4	34.71		7	15.3	33.64
27/11	9	13.3	34.71		14	14.0	34.18
	17	13.4	34.71		21	13.0	34.59
	26	13.2	34.76				
	35	13.1	34.69				
	43	13.1	34.69	SB8	0	16.5	31.59
				18/11	4	15.5	33.44
SB4	0	16.3	33.71		7	14.8	33.79
	4	14.9	33.98		14	13.0	34.59
18/11	7	14.6	34.04		21	12.8	34.59
	14	14.3	34.09				
	21	13.5	34.45				
	28	13.0	34.67				
	35	13.0	34.57	SB9	0	16.8	32.17
					5	14.3	33.84
				18/11	10	13.8	34.77
					20	13.5	34.85

Appendix 1 continued:

December 1980

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1				SB5			
SB2				SB6			
SB3				SB7 22/12	0 5 10 20	15.6 15.5 15.4 14.9	33.89 33.90 33.89 33.99
SB4				SB8 22/12	0 5 10 20	15.4 15.2 15.1 14.2	33.98 33.98 33.81 34.44
				SB9 22/12	0 5 10 20	16.1 15.2 14.0 13.8	32.72 33.82 34.28 34.47

Appendix 1 continued:

January 1981

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1				SB5	0	17.7	33.90
					5	17.0	34.11
				12/1	9	16.4	34.41
					17	15.7	34.60
					26	15.6	34.65
					35	14.8	34.65
					43	14.6	34.58
SB2				SB6	0	17.3	34.11
					4	16.1	34.49
				12/1	7	15.9	34.50
					14	15.9	34.58
					21	15.8	34.15
					28	15.6	34.51
					35	15.4	34.15
SB3				SB7	0	18.0	34.20
					5	17.5	34.20
				12/1	10	17.2	34.22
					20	15.6	34.28
				SB8	0	17.5	33.70
					5	17.5	34.00
SB4	0	17.7	34.13	12/1	10	17.3	34.15
	4	17.6	34.18		20	14.9	34.50
12/1	7	17.4	34.19				
	14	17.2	34.19				
	21	15.8	34.50				
	28	14.4	34.50				
	35	14.3	34.45	SB9	0	18.0	33.22
					5	17.0	33.90
				12/1	10	15.9	34.40
					20	15.5	34.40

Appendix 1 continued:

February 1981

	Depth m	T°C	S°/oo		Depth m	T°C	S°/oo
SB1	0	18.3	34.70	SB5	0	18.0	34.51
	5	17.5	34.60		5	18.0	34.51
24/2	10	17.5	34.60	24/2	10	17.8	34.51
	20	17.3	34.60		20	17.8	34.51
	30	16.7	34.64		30	17.4	34.61
	40	16.7	34.62		40	16.5	34.61
	50	16.7	34.50				
SB2				SB6	0	19.1	34.49
					5	18.1	34.49
				24/2	10	17.9	34.51
					20	17.7	34.62
					30	17.3	34.62
SB3				SB7	0	19.5	34.50
					5	18.3	34.50
				24/2	10	18.3	34.50
					20	18.2	34.50
SB4	0	18.6	34.62	SB8	0	18.2	34.43
	5	17.7	34.50		5	18.2	34.43
24/2	10	17.7	34.57	24/2	10	18.2	34.51
	20	17.6	34.60		20	17.5	34.51
	30	16.6	34.60				
				SB9	0	18.5	33.93
					5	17.8	34.43
				24/2	10	17.7	34.55
					20	17.0	34.57

Appendix 1 continued:

March 1981

	Depth m	T°C	S⁰/oo		Depth m	T°C	S⁰/oo
SB1 16/3	0	16.5	34.99	SB5 17/3	0	16.6	35.03
	5	16.5	34.99		4	16.5	35.02
	10	16.5	34.99		7	16.4	35.02
	20	16.3	34.99		14	16.4	35.02
	30	16.3	34.99		21	16.4	35.02
	40	16.5	34.99		28	16.4	35.02
					35	16.2	35.02
SB2 17/3	0	16.1	35.09	SB6 16/3	0	16.6	34.98
	5	16.1	35.09		5	16.5	34.98
	10	16.0	35.09		9	16.5	34.99
	20	15.9	35.09		17	16.4	34.99
	30	15.7	35.09		26	16.2	34.99
	40	15.6	35.09		35	15.8	34.99
	50	15.6	35.05				
SB3 17/3	0	16.0	35.05	SB7 17/3	0	17.2	35.02
	5	16.0	35.05		5	17.2	35.02
	10	15.9	35.05		10	17.0	35.02
	20	15.8	35.01		20	17.0	35.02
	30	15.7	35.01				
	40	15.6	35.01				
SB4 16/3	0	16.7	34.90	SB8 16/3	0	16.6	34.66
	5	16.6	34.90		5	16.6	34.77
	10	16.6	34.95		10	16.6	34.80
	20	16.6	34.98		20	16.6	34.80
	30	16.5	35.00				
				SB9 16/3	0	16.8	34.66
					5	16.8	34.74
					10	16.7	34.90
					20	16.5	35.02

APPENDIX II

MONTHLY LENGTH-FREQUENCY DATA INTEGRATED FOR ALL STATIONS

December 1979

Size-class mm	Number	Density m^{-3}	Cumulative $^o/o$ frequency
0.00-0.99			
1.00-1.99	9666	29.6085	64.694
2.00-2.99	4446	13.6188	94.452
3.00-3.99	631	1.9329	98.675
4.00-4.99	188	0.5759	99.933
5.00-5.99	5	0.0153	99.967
6.00-6.99	5	0.0153	100.000
7.00-7.99			
8.00-8.99			
9.00-9.99			
10.00-10.99			
11.00-11.99			
12.00-12.99			
13.00-13.99			
14.00-14.99			
15.00-15.99			
16.00-16.99			
17.00-17.99			
18.00-18.99			
19.00-19.99			
20.00-20.99			
Total	14941	45.7667	

Appendix II continued:

February 1980

Size-class mm	Number	Density m^{-3}	Cumulative % frequency
0.00-0.99	668	1.0052	1.854
1.00-1.99	18475	27.8003	53.143
2.00-2.99	7229	10.8779	73.211
3.00-3.99	4576	6.8858	85.914
4.00-4.99	3560	5.3569	95.797
5.00-5.99	1032	1.5529	98.662
6.00-6.99	475	0.7148	99.981
7.00-7.99			
8.00-8.99			
9.00-9.99			
10.00-10.99	5	0.0075	99.994
11.00-11.99			
12.00-12.99			
13.00-13.99	2	0.0030	100.000
14.00-14.99			
15.00-15.99			
16.00-16.99			
17.00-17.99			
18.00-18.99			
19.00-19.99			
20.00-20.99			
Total	36022	54.2043	

Appendix 11 continued:

April 1980

Size-class mm	Number	Density m^{-3}	Cumulative °/o frequency
0.00-0.99			
1.00-1.99	1302	1.6653	16.538
2.00-2.99	1034	1.3225	29.671
3.00-3.99	1326	1.6960	46.513
4.00-4.99	1758	2.2485	68.843
5.00-5.99	1049	1.3417	82.167
6.00-6.99	501	0.6408	88.530
7.00-7.99	284	0.3632	92.138
8.00-8.99	181	0.2315	94.437
9.00-9.99	133	0.1701	96.126
10.00-10.99	179	0.2289	98.400
11.00-11.99	76	0.0972	99.365
12.00-12.99	45	0.0576	99.936
13.00-13.99			
14.00-14.99			
15.00-15.99	5	0.0064	100.000
16.00-16.99			
17.00-17.99			
18.00-18.99			
19.00-19.99			
20.00-20.99			
Total	7873	10.0697	

Appendix 11 continued:

May 1980

Size-class mm	Number	Density m^{-3}	Cumulative ^{o}/o frequency
0.00–0.99	3	0.0052	0.958
1.00–1.99	3	0.0052	1.917
2.00–2.99	19	0.0332	7.987
3.00–3.99	11	0.0192	11.502
4.00–4.99	23	0.0402	18.850
5.00–5.99	110	0.1922	53.994
6.00–6.99	73	0.1275	77.316
7.00–7.99	66	0.1153	98.403
8.00–8.99	5	0.0087	100.000
9.00–9.99			
10.00–10.99			
11.00–11.99			
12.00–12.99			
13.00–13.99			
14.00–14.99			
15.00–15.99			
16.00–16.99			
17.00–17.99			
18.00–18.99			
19.00–19.99			
20.00–20.99			
Total	313	0.5469	

June 1980

Size-class mm	Number	Density m^{-3}	Cumulative $^o/o$ frequency
0.00-0.99			
1.00-1.99	1	0.0016	0.120
2.00-2.99	1	0.0016	0.240
3.00-3.99	6	0.0094	0.960
4.00-4.99	14	0.0219	2.641
5.00-5.99	25	0.0391	5.642
6.00-6.99	81	0.1268	15.366
7.00-7.99	49	0.0767	21.248
8.00-8.99	49	0.0767	27.131
9.00-9.99	22	0.0344	29.772
10.00-10.99	36	0.0563	34.094
11.00-11.99	51	0.0798	40.216
12.00-12.99	87	0.1362	50.660
13.00-13.99	108	0.1690	63.625
14.00-14.99	91	0.1424	74.550
15.00-15.99	87	0.1362	84.994
16.00-16.99	62	0.0970	92.437
17.00-17.99	37	0.0579	96.879
18.00-18.99	17	0.0266	98.920
19.00-19.99	5	0.0078	99.520
20.00-20.99	4	0.0063	100.00
Total	833	1.3037	

Appendix 11 continued:

July 1980

Size-class mm	Number	Density m^{-3}	Cumulative $^o/o$ frequency
0.00-0.99	31	0.0529	18.129
1.00-1.99	97	0.1654	74.854
2.00-2.99	4	0.0068	77.193
3.00-3.99	15	0.0256	85.965
4.00-4.99	12	0.0205	92.982
5.00-5.99	5	0.0085	95.906
6.00-6.99	1	0.0017	96.491
7.00-7.99	3	0.0051	98.246
8.00-8.99			
9.00-9.99			
10.00-10.99	1	0.0017	98.830
11.00-11.99			
12.00-12.99			
13.00-13.99			
14.00-14.99	1	0.0017	99.415
15.00-15.99	1	0.0017	100.000
16.00-16.99			
17.00-17.99			
18.00-18.99			
19.00-19.99			
20.00-20.99			
Total	171	0.2916	

Appendix 11 continued:

August 1980

Size-class mm	Number	Density m^{-3}	Cumulative $^o/o$ frequency
0.00-0.99	1299	1.3935	10.698
1.00-1.99	10724	11.5038	99.020
2.00-2.99	102	0.1094	99.860
3.00-3.99	8	0.0086	99.926
4.00-4.99			
5.00-5.99			
6.00-6.99	1	0.0011	99.934
7.00-7.99			
8.00-8.99	1	0.0011	99.942
9.00-9.99			
10.00-10.99			
11.00-11.99			
12.00-12.99			
13.00-13.99	2	0.0021	99.959
14.00-14.99			
15.00-15.99			
16.00-16.99	3	0.0032	99.984
17.00-17.99	1	0.0011	99.992
18.00-18.99	1	0.0011	100.000
19.00-19.99			
20.00-20.99			
Total	12142	13.0250	

Appendix II continued:

September 1980

Size-class mm	Number	Density m^{-3}	Cumulative ^{o}/o frequency
0.00-0.99	5323	10.6661	43.760
1.00-1.99	5712	11.4455	90.719
2.00-2.99	200	0.4008	92.363
3.00-3.99	10	0.0200	92.445
4.00-4.99			
5.00-5.99			
6.00-6.99			
7.00-7.99			
8.00-8.99			
9.00-9.99			
10.00-10.99			
11.00-11.99			
12.00-12.99			
13.00-13.99			
14.00-14.99	58	0.1162	92.922
15.00-15.99	58	0.1162	93.399
16.00-16.99	277	0.5550	95.676
17.00-17.99	335	0.6713	98.430
18.00-18.99	132	0.2645	99.515
19.00-19.99	59	0.1182	100.000
20.00-20.99			
Total	12164	24.3738	

Appendix 11 continued:

October 1980

Size-class mm	Number	Density m^{-3}	Cumulative o/o frequency
0.00-0.99	2093	1.6881	1.355
1.00-1.99	29767	24.0085	20.632
2.00-2.99	25568	20.6218	37.190
3.00-3.99	31068	25.0579	57.309
4.00-4.99	33684	27.1678	79.123
5.00-5.99	18368	14.8147	91.018
6.00-6.99	9193	7.4146	96.971
7.00-7.99	2783	2.2446	98.773
8.00-8.99	1100	0.8872	99.486
9.00-9.99	238	0.1920	99.640
10.00-10.99	206	0.1661	99.773
11.00-11.99	79	0.0637	99.825
12.00-12.99	63	0.0508	99.865
13.00-13.99	114	0.0919	99.939
14.00-14.99	48	0.0387	99.970
15.00-15.99	5	0.0040	99.973
16.00-16.99	3	0.0024	99.975
17.00-17.99	9	0.0073	99.981
18.00-18.99	10	0.0081	99.988
19.00-19.99	12	0.0097	99.995
20.00-20.99	7	0.0056	100.000
Total	154418	124.5457	

Appendix 11 continued:

November 1980

Size-class mm	Number	Density m^{-3}	Cumulative $^o/o$ frequency
0.00-0.99	97	0.1732	0.720
1.00-1.99	60	0.1072	1.165
2.00-2.99	40	0.0714	1.462
3.00-3.99	130	0.2322	2.427
4.00-4.99	96	0.1714	3.140
5.00-5.99	238	0.4250	4.906
6.00-6.99	1012	1.8073	12.418
7.00-7.99	1537	2.7448	23.827
8.00-8.99	2239	3.9985	40.447
9.00-9.99	3328	5.9433	65.150
10.00-10.99	2506	4.4753	83.751
11.00-11.99	1011	1.8055	91.256
12.00-12.99	549	0.9804	95.331
13.00-13.99	208	0.3715	96.875
14.00-14.99	153	0.2732	98.011
15.00-15.99	156	0.2786	99.169
16.00-16.99	105	0.1875	99.948
17.00-17.99	7	0.0125	100.000
18.00-18.99			
19.00-19.99			
20.00-20.99			
Total	13472	24.0588	

December 1980

Size-class mm	Number	Density m^{-3}	Cumulative $^o/o$ frequency
0.00–0.99	179	0.9662	3.953
1.00–1.99	3592	19.3890	83.282
2.00–2.99	672	3.6273	98.123
3.00–3.99	85	0.4588	100.000
4.00–4.99			
5.00–5.99			
6.00–6.99			
7.00–7.99			
8.00–8.99			
9.00–9.99			
10.00–10.99			
11.00–11.99			
12.00–12.99			
13.00–13.99			
14.00–14.99			
15.00–15.99			
16.00–16.99			
17.00–17.99			
18.00–18.99			
19.00–19.99			
20.00–20.99			
Total	4528	24.4413	

Appendix 11 continued:

January 1981

Size-class mm	Number	Density m⁻³	Cumulative °/o frequency
0.00–0.99	536	1.1612	1.758
1.00–1.99	104	0.2253	2.099
2.00–2.99	271	0.5871	2.987
3.00–3.99	1940	4.2028	9.349
4.00–4.99	3161	6.8479	19.715
5.00–5.99	6008	13.0156	39.416
6.00–6.99	6309	13.6677	60.105
7.00–7.99	8658	18.7565	88.496
8.00–8.99	1853	4.0143	94.573
9.00–9.99	962	2.0841	97.727
10.00–10.99	253	0.5481	98.557
11.00–11.99	41	0.0888	98.692
12.00–12.99	29	0.0628	98.787
13.00–13.99	41	0.0888	98.921
14.00–14.99	61	0.1321	99.121
15.00–15.99	117	0.2535	99.505
16.00–16.99	121	0.2621	99.902
17.00–17.99	25	0.0542	99.984
18.00–18.99	5	0.0108	100.000
19.00–19.99			
20.00–20.99			
Total	30495	66.0637	

Appendix 11 continued:

February 1981

Size-class mm	Number	Density m^{-3}	Cumulative °/o frequency
0.00-0.99	1685	4.9680	26.205
1.00-1.99	4107	12.1090	90.078
2.00-2.99	383	1.1292	96.034
3.00-3.99	109	0.3214	97.729
4.00-4.99	42	0.1238	98.383
5.00-5.99	10	0.0295	98.538
6.00-6.99			
7.00-7.99			
8.00-8.99	5	0.0147	98.616
9.00-9.99			
10.00-10.99	11	0.0324	98.787
11.00-11.99	11	0.0324	98.958
12.00-12.99	31	0.0914	99.440
13.00-13.99	22	0.0649	99.782
14.00-14.99	4	0.0118	99.844
15.00-15.99	8	0.0236	99.969
16.00-16.99	2	0.0059	100.000
17.00-17.99			
18.00-18.99			
19.00-19.99			
20.00-20.99			
Total	6430	18.9580	

Appendix II continued:

March 1981

Size-class mm	Number	Density m^{-3}	Cumulative $^o/o$ frequency
0.00-0.99	45	0.1194	0.062
1.00-1.99	43083	114.2967	59.840
2.00-2.99	12688	33.6605	77.445
3.00-3.99	8162	21.6533	88.770
4.00-4.99	4555	12.0842	95.090
5.00-5.99	1632	4.3296	97.354
6.00-6.99	1281	3.3984	99.131
7.00-7.99	433	1.1487	99.732
8.00-8.99	91	0.2414	99.858
9.00-9.99	47	0.1247	99.924
10.00-10.99	26	0.0690	99.960
11.00-11.99	6	0.0159	99.968
12.00-12.99	6	0.0159	99.976
13.00-13.99	7	0.0186	99.986
14.00-14.99	9	0.0239	99.999
15.00-15.99	1	0.0027	100.000
16.00-16.99			
17.00-17.99			
18.00-18.99			
19.00-19.99			
20.00-20.99			
Total	72072	191.2028	

APPENDIX III

SWARMS AND STRANDINGS

During the present study, 2 surface swarms of adult N. australis

were encountered, 1 in February 1981 at SB6, the other earlier in

July 1980 in the D'Entrecasteaux Channel near the mouth of the Derwent

Estuary (Fig. 2.1). The size of the swarm at SB6 could not be

determined, but the density was 5.65 m^{-3}. An extremely large flock

of mutton birds, Puffinus tenuirostris, was seen and the birds were

apparently feeding on the euphausiids at the time. The second swarm

was approximately 200m in diameter and remained in the area for at

least 3 days. Although samples of this swarm were collected, using

a ¼ m^2 net of 250 μm mesh, a flowmeter was not fitted, therefore an

accurate measure of density cannot be given. However, the adults

could easily be seen at the surface and high densities extended down

about 3 to 5m into the water column. Individuals were positioned

approximately 10cm apart, representing a density of about 1,000 m^{-3}.

The mean size of the adults was 16.48 mm. The biomass of the swarm

could be conservatively estimated as 0.5 t dry wt. Within the swarm,

however, there were several smaller denser aggregations of individuals,

approximately 5 to 20 m^3 in volume. Individuals were spaced approximately

1 cm apart, giving as estimated biomass of 5 kg m^{-3} dry wt. The total

biomass of the swarm could well have exceeded these estimates. The

swarming behaviour of N. australis may not be confined to adults.

Recently, Thomas (1980) observed a swarm of Nyctiphanes capensis larvae

off the coast of South West Africa, which had an estimated density of

81 x 10^6 m^{-3}.

Three mass strandings of N. australis adults were observed during this

study. Two occurred within the Derwent Estuary at Nutgrove, a metropolitan

Hobart beach, in July 1980 and June 1982, while the third stranding was

at Nebraska Beach in D'Entrecasteaux Channel in July 1980 shortly after

the plankton swarm was sighted. Although difficult to actually estimate, the biomass of individuals stranded was extremely large, particularly the Nutgrove July 1980 stranding which would have been in the order of tonnes. Similar strandings have been recorded previously at Nutgrove and in the D'Entrecasteaux Channel in July 1965 and July 1979 respectively.

REFERENCE

THOMAS, R.M. (1980) A note on swarms of Nyctiphanes capensis (Hansen) larvae off South West Africa. Fish. Bull. S. Afr. 13, 21-23.