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**A comparative study of the habitats, growth and reproduction  
of eight species of tropical anchovy from Cleveland and  
Bowling Green Bays, North Queensland.**

**Thesis submitted by  
Frank Edward Hoedt BSc (Hons) (JCU)  
in September 1994**

**for the degree of Doctor of Philosophy in  
the Department of Marine Biology  
James Cook University of North Queensland**

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## ABSTRACT

In this thesis the habitat preferences, growth and reproductive biology were examined for eight species of tropical anchovies from Townsville, North Queensland. The species examined were: *Encrasicholina devisi*; *Stolephorus insularis*; *Stolephorus carpentariae*; *Stolephorus nelsoni*; *Stolephorus commersonii*; *Thryssa aestuaria*; *Thryssa setirostris* and *Thryssa hamiltoni*. The study species grew to a wide range of maximum sizes (encompassing most of the size-range found amongst tropical clupeoid species), and therefore provided an opportunity to undertake a detailed comparative study of biological parameters and life-histories.

Samples were collected at three nearshore tropical habitats; mangroves, beaches and subtidal waters at 3-12m depth. Beach seines and gill nets were used to sample the first two habitats and an otter trawl at the subtidal habitat. The age-specific habitat preferences of each species were qualitatively investigated by comparing the catches of juveniles and adults in each habitat. In the subtidal waters of Cleveland Bay, anchovy were most common at depths of less than 7m. Juveniles of all species were common in shallow waters along beaches and the juveniles of some species were also common in mangrove estuaries. Age-related habitat differences were found to occur in *Stolephorus commersonii*, *Thryssa aestuaria*, *Thryssa setirostris* and *Thryssa hamiltoni*. In these species juveniles predominantly occurred in shallow nearshore habitats (beaches and mangroves) and adults occurred in the subtidal habitat at depths to 12m. *S. nelsoni*, *E. devisi* and *S. insularis* occurred in shallow water off beaches and in shallow subtidal waters throughout their life-cycle. *S. carpentariae* was almost exclusively caught along beaches and in mangroves (depths less than 3m) at all life stages.

Seasonal changes in habitat were exhibited by species in the present study. Adult *E. devisi* and *S. insularis* occurred in shallow waters off beaches in the autumn and winter months but were rare in summer. This suggests that these species move to deeper water in summer. Catches of all species in subtidal trawl samples in summer

were also lower, suggesting that a change in distribution occurs at this time, possibly movement to deeper water.

Growth was estimated in the study species using three methods: counting primary increments in the sagittal otolith; analysing length-frequency data; and in *Thryssa spp.* from counts of seasonal growth rings in the sagittal otolith. Prior to using primary otolith increments to age the study species, experiments were conducted to determine the periodicity of growth increment formation. The study species proved extremely sensitive to handling. However, evidence of daily periodicity of growth increment formation was obtained for four species: *E. devisi*; *S. carpentariae*; *S. nelsoni* and *T. aestuaria*. Evidence was also given that the seasonal growth rings in sagitta from *Thryssa spp.* were deposited annually.

Growth curves (length versus. age) were constructed for each species from primary otolith increment counts. Length versus age plots were linear in *E. devisi* and *S. insularis* while von Bertalanffy growth curves were fitted to this data for the remaining species. These findings suggest that growth in very small stolephorid anchovies may not conform to the conventional von Bertalanffy growth curve. Consequently, some standard techniques for analysing length-frequency data which are based on von Bertalanffy growth parameters should be employed with caution on small tropical anchovies. This study of primary otolith increments indicated that the longevities of the stolephorid anchovies ranged from several months to just over one year. These structures also indicate a 1-2 year lifespan for *Thryssa aestuaria*. The larger species of *Thryssa* could not be aged beyond a certain size with confidence using these structures.

Length versus age plots from primary otolith increment counts were linear for juvenile-sized fish in all of the study species. A comparison of the linear growth rates in the study species showed that growth rate was directly related to the maximum size attained by a species. This indicates that larger species of tropical anchovy have faster

growth rates than small species. Primary otolith increment age data was also used to compare the patterns of growth in weight (plots of weight versus age) between the study species. These were found to exhibit one of two patterns of exponential growth in weight. The larger species, *S. commersonii*, *T. setirostris* and *T. hamiltoni* had a common faster rate of weight-growth than *S. insularis*, *S. carpentariae*, *S. nelsoni* and *T. aestuaria*. The weight-age data in these smaller species followed a similar exponential pattern with a slower rate of increase. The similarity in weight-growth for groups of species show that growth can be conservative at an inter-species level in tropical anchovies. Furthermore, the difference in weight-growth between small and large species suggests that weight-growth may be another distinguishing feature of the life-history strategies of small and large tropical clupeoids (Lewis 1990).

An important outcome of the analyses of primary otolith increments and seasonal growth rings in this study was that the von Bertalanffy growth curve suitably described the length-age relationship for the three species of *Thryssa*. Growth in length in larger tropical anchovies therefore follows a pattern which is common to most other marine fishes. In the stolephorid anchovies, length-age plots did not exhibit a marked asymptote and consequently, a modified form of the equation had to be used. This finding indicates that length-frequency analysis methods that are based on the von Bertalanffy growth function may be more suited to large rather than small species of tropical anchovy. Growth parameters obtained from otoliths compared favourably with those from length-frequency analyses in the genus *Thryssa*, further confirming this view.

Counts of seasonal growth rings in otoliths gave estimates of longevity for the genus *Thryssa*. The oldest *T. hamiltoni* individual was 4 years of age, and the oldest individuals of *T. setirostris* and *T. aestuaria* were 2 and 1 years respectively. For *T. hamiltoni*, von Bertalanffy growth curves fitted to plots of length against age from seasonal growth rings indicated growth differences between male and female fish; females grew faster and larger than males.

Length-frequency data were analysed for all of the study species. Two methods of analysis were employed these being the estimation of growth rates in juveniles from modal progressions, and the estimation of growth parameters using the ELEFAN computer software. Length-frequency histograms indicated that growth differed between males and females in all *Thryssa spp.*, supporting the findings of otolith-ageing. Growth rates estimated visually for juvenile fish from modal progressions were consistent with those calculated from primary otolith increments for several species. This indicates that modal progressions can provide meaningful growth estimates in tropical anchovies. However, this analysis indicated that the residency-time for cohorts (or modes in length-frequency histograms) in populations of small species is short highlighting the importance of obtaining frequent and representative samples to allow analysis of modal progressions.

Von Bertalanffy growth parameters calculated from otoliths and ELEFAN analyses compared favourably in *S. nelsoni* and the three species of *Thryssa* indicating that these techniques give meaningful age estimates for larger clupeoids. Values of K computed from otolith-derived length-age data were generally higher than those computed by ELEFAN for the remaining stolephorid anchovies and this supports recent literature in the view that ELEFAN may yield biased growth estimates for small tropical clupeoids.

The following reproductive parameters were estimated for the study species: spawning season; length and age-at-maturity; fecundity and spawning frequency. Two types of spawning seasonality were observed. *E. devisi* and *S. insularis* spawned over most of the year while the remaining species spawned during the warmer part of the year between September and January. Length-at-maturity occurred at around 70% of maximum length in all species suggesting that this ratio may be conservative in tropical anchovies. Ages-at-maturity varied from several months in small species to around one year in larger species. Fecundity for all species combined was related to

both length (exponential curve) and weight (linear regression), indicating that the relationship between these parameters is conservative at an inter-species level in this group. Spawning frequency was estimated as three days for *S. nelsoni* and between 2 and 5 days in *T. hamiltoni*. The pattern of oocyte-diameter frequencies differed between stolephorid anchovies and *Thryssa spp.* indicating possible differences in spawning biology.

In the present study it was shown that fecundity and growth rate were related to maximum species-size at an inter-species level. Furthermore, longevity was shown to be directly related to maximum species-size for a wide range of tropical clupeoids. These findings indicate that it may be possible to estimate certain biological parameters based on maximum species size for tropical clupeoid species. Another finding of this study was that growth and reproductive parameters in large tropical clupeoids were comparable to those in some short-lived temperate species. Beverton's (1963) ratio of  $1/KT_{\max}$  was also similar in some large tropical clupeoids to that in temperate anchovies. Following Beverton's (1963) reasoning, the similarity in this ratio in these two groups suggests that these may exhibit similar population and fishery dynamics.



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## **STATEMENT OF SOURCES**

### **DECLARATION**

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from published or unpublished work of others has been acknowledged in the text and a list of references is given.

F. Hoedt

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## CHAPTER 1 GENERAL INTRODUCTION

### 1.1 Life-histories and population dynamics of clupeoids

Anchovies belong to the suborder Clupeoidei which is comprised of four families. Two of these families, the anchovies (*F. engraulidae*) and the herrings (*F. clupeidae*) are of particular importance to the ecosystems and fisheries along many of the world's coastlines. In the tropics there are 62 species of anchovy many of which are targeted by artisanal and commercial fisheries (Whitehead *et al.* 1988). Although this thesis specifically examines the biology and habitat of tropical anchovies, it will be useful to begin with a consideration of the general biological and population characteristics of the clupeoids. Species within this group exhibit broad similarities in biological and population characteristics and throughout this thesis comparisons are made with other species of engraulids and members of the family clupeidae.

Clupeoids are found along most of the world's coastlines and populations attain large biomasses in productive cool-water areas, examples being the Benguela, California and Peruvian upwelling systems. In the eastern boundary currents clupeoids support large fisheries and their economic importance has prompted numerous studies of their biology, ecology and population dynamics. Clupeoid populations are noted for exhibiting large fluctuations in abundance and spatial distribution which can occur independently of fishing pressure (Murphy 1977, Blaxter and Hunter 1982, Longhurst and Pauly 1987, Le Clus 1990, Lluch-Belda *et al.* 1992). Inter-year changes in population abundance have been related to variations in environmental conditions which have in turn can effect spawning and recruitment (Longhurst and Pauly 1987, Lluch-Belda *et al.* 1989). Reproductive success in most clupeoid fishes with high larval mortality rates appears to be greatly dependent on the influence of the environment (Bloomer *et al.* 1994). Heavy fishing pressure in combination with unfavourable environmental conditions are



thought to have caused major declines in several temperate clupeoid stocks (Murphy 1977, Longhurst and Pauly 1987). Concern over the management of these unpredictable fisheries continues to give impetus to scientific study on this group.

The clupeoids as a group exhibit a range of biological parameters and life-history characteristics. Compared to other marine teleosts, most clupeoids are small, mature early, have short lifespans, and have relatively low fecundities (Kawasaki 1980). Spawning seasons in clupeoids are usually protracted and individuals often spawn repeatedly during a season. Temperate clupeoids have longevities of 2-23 years and mature at 1-6 years of age (Beverton 1963). In contrast most tropical clupeoids have longevities of less than three years and all species mature within one year (Lewis 1990).

Particular biological parameters vary amongst tropical and temperate clupeoid species and this results in inter-species differences in life-history strategy and fishery and population dynamics (Beverton 1963, Lewis 1990). Variation in life-history strategy amongst clupeoid fishes are thought to have evolved as adaptations to different environmental conditions, particularly levels of environmental variability (Murphy 1968, Kawasaki 1980). Kawasaki (1980) suggested that temperate clupeoid species with high age-at-maturity, long lifespan and high batch fecundity are adapted to live in conditions where long-term environmental variations occur. Thus, in a series of favourable years, these populations can 'build up' numbers through high recruitment levels and 'store' these as large age-classes which are capable of producing increasing numbers of eggs in successive years. A single good year class can remain in a clupeoid population for a number of years, boosting abundance to greater than normal levels (Murphy 1977). The existence of several age-classes also serves as a buffer for years when recruitment is poor.

In contrast, all tropical clupeoids undergo early maturity and have a short lifespan.

Population-turnover rates in small tropical clupeoids are high (Lewis 1990) and this strategy suits conditions of short-term change in environmental conditions (Kawasaki 1980, Milton *et al.* 1993). Lewis (1990) distinguished two 'types' of life-history strategy amongst tropical baitfish (mostly clupeoids). He defined these by size, namely small (<10cm) and large (10-24cm) species; each group exhibiting different ranges of the biological parameters longevity (and therefore mortality), spawning season and relative fecundity. The affect of these differences in life-history strategy (and associated biological parameters) on the population and fishery dynamics of tropical clupeoids have not been studied in detail.

Another feature of clupeoid fishes is their pelagic existence which may allow a high degree of mobility. Different life-stages within species may occupy different habitats (Tiews *et al.* 1970, Tham 1972, De Silva 1973; Nicholson 1978, Luther 1979), and adults may also undergo substantial migrations (Dalzell and Wankowski 1980, Vouglitois *et al.* 1987, Longhurst and Wooster 1990). In light of this feature, it is evident that the dynamics of clupeoid populations must be studied from the point of view of age-specific events.

## 1.2 Conservatism of biological parameters

A feature of clupeoid fishes is the conservatism of biological parameters within the group (Beverton 1963, Murphy 1977, Blaxter and Hunter 1982, Milton *et al.* 1993). Examples of this include the common inter-species relationship between fecundity and weight (Blaxter and Hunter 1982), and the similarity of the ratio of length-at-maturity to maximum length across a wide range of tropical and temperate clupeoids (Beverton 1963, Milton *et al.* 1993, Milton *et al.* 1994). There is considerable scope for further studies of the relationships between biological parameters in clupeoid fishes, particularly for tropical clupeoids for which there has been little work in this area.

Beverton (1963) examined the relationships between biological parameters namely, mortality, growth (K-a von Bertalanffy growth parameter), longevity ( $T_{max}$ ) and length-at-maturity, across a wide range of temperate clupeoid fishes. He showed that a ratio incorporating the first three of these parameters ( $1/KT_{max}$ ) had the same value for groups of species within the order. Thus, the ratio had a similar value for the anchovies he examined and certain other clupeoid subgroups each had a different and unique range of values. This is a further example of inter-species conservatism of biological parameters in this group. Beverton (1963) showed that species with a similar value of this ratio should exhibit a similar response to fishing pressure. A parallel study, examining Beverton's (1963) ratio amongst tropical clupeoids has not been undertaken. The estimation of Beverton's (1963) ratio across a range of tropical clupeoids may be one method of comparing the biological parameters and fishery dynamics of tropical and temperate species. This may in turn allow a preliminary assessment of the applicability of information on the fishery and population dynamics of temperate clupeoid fishes for the management of tropical anchovy stocks.

At first sight there appear to be some fundamental differences in the biology of tropical clupeoids and their temperate counterparts which would suggest that these two groups may exhibit very different population dynamics. However, some large tropical clupeoids live for 1 to several years and have a short spawning season (Lewis 1990), and therefore have similar biological parameters to some short-lived temperate species with similar characteristics. Given that clupeoids exhibit conservatism in biological parameters and fishery dynamics it is possible that there may be broad similarities between the responses to fishing by certain tropical and temperate species.

### 1.3 Growth and reproduction in tropical anchovies

While growth and reproductive parameters are well documented for most temperate

clupeoids, there are still gaps in our knowledge of these basic parameters for the diverse tropical clupeoids. A prerequisite to a comparative biological study of tropical and temperate clupeoids is the availability of accurate estimates of these parameters across a range of tropical clupeoids.

Most of our present knowledge of growth in tropical anchovies and indeed tropical clupeoids as a group, has been obtained from length-frequency analysis (eg. Venkataraman 1956, Tham 1966, Tiews *et al.* 1970, Burhanuddin and Hutomo 1975, Muller 1977, Luther 1990, Tiroba *et al.* 1990, Milton and Blaber 1995, Wise and Potter 1995). However, several authors point out that the analysis and interpretation of length-frequency data from tropical fish populations can be prone to a number of biases (Qasim 1973b, Casselman 1977, Brothers 1979, Wise and Potter 1995). Biases can be a major problem in small, short-lived species such as tropical clupeoids (Brothers 1979, Wise and Potter 1995). The life-history traits of continuous reproduction and short lifespan in small tropical clupeoids can mask length modes in samples leading to erroneous growth estimates (Wise and Potter 1995). The problems of using length-frequency analysis alone to estimate age and growth in tropical clupeoids has lead to some inconsistencies in growth estimates for particular species (eg. Dayaratne and Gjøsaeter 1986, Milton *et al.* 1990b). Castro and Erzini (1988) recommended that more than one method of age estimation be used for species with these characteristics.

The relatively recent introduction of the otolith-based ageing methodology for estimating growth in tropical clupeoids has provided new insights into the growth and longevity of these species (Struhsaker and Uchiyama 1976, Gjøsaeter *et al.* 1984, Dayaratne and Gjøsaeter 1986, Thorrold 1988, Wright *et al.* 1990, Milton *et al.* 1990b, Milton *et al.* 1991, Milton *et al.* 1993, Milton and Blaber 1995). While primary otolith increments have the potential to provide more precise growth estimates than length-frequency analysis, there have been difficulties with the

interpretation of these structures in some tropical anchovies (Dalzell and Wankowski 1980, Gjøsaeter *et al.* 1984, Wright *et al.* 1990). Another obstacle to otolith-based growth studies on tropical anchovies is the problem of the sensitivity to handling of these fish (Luther *et al.* 1984, Milton *et al.* 1993); this feature makes it difficult to validate otolith increment periodicity by mark-recapture or aquarium studies (Milton *et al.* 1990b). Struhsaker and Uchiyama (1976) have been the only authors to validate the daily periodicity of primary otolith increments in a tropical anchovy. The problems associated with the interpretation and validation of primary otolith increments for tropical anchovies need to be addressed before accurate growth estimates can be made for individual species.

Another aspect of research into the growth of tropical anchovies and other clupeoid fishes that requires attention, is the possible presence and potential use for ageing of seasonal growth rings in otoliths and scales. While a few studies have found growth rings of probable annual periodicity in tropical clupeids (Nair 1949, Heald and Griffiths 1967, Okera 1970), there are no reports where these structures have been used to age tropical anchovies. Given the problems associated with the use of the ageing methods mentioned so far, it is important that the use of seasonal growth rings in scales or otoliths be investigated. Seasonal growth rings should be useful for ageing larger species of anchovy which live for several years and will provide estimates of longevity which have previously been difficult to obtain in tropical fish from length-frequency data (Qasim 1973b). Annuli have recently been validated in a number of tropical fish species, highlighting the potential of these structures for age and growth studies in the tropics (eg. Longhurst and Pauly 1987, Ferreira and Russ 1992, Fowler and Doherty 1992).

The reproductive biology of tropical anchovies and other clupeoids has received considerable attention (eg. Pelakar and Karandikar 1952, Shamsul Hoda 1983, Clarke 1987, Dalzell 1987a, Clarke 1987, Fernandez and Devaraj 1989, Milton *et*

*al.* 1990a, Wright 1990, Milton and Blaber 1991, Wright 1992, Milton and Blaber 1995). However, there have been few comparative studies of reproductive parameters across tropical clupeoid species (see Conand 1985), and once again given the conservatism of reproductive parameters in clupeoid fishes (Blaxter and Hunter 1982) this line of research may reveal useful inter-specific patterns.

One aspect of the reproductive biology of tropical clupeoids that is poorly understood is the spawning frequencies of different species (see Clarke 1987, Wright 1992). Spawning frequency estimates are an essential component of a routinely used method (Daily Egg Production Method) for population biomass estimation in temperate and tropical anchovies. This technique provides estimates of parental biomass in pelagic fishes from surveys of planktonic eggs (Lasker 1985, Hunter and Macewicz 1985, Sommerton 1990), and is an area of research with proven applicability in fisheries management. Further estimates of spawning frequency are needed across a wider range of species to better understand the reproductive dynamics of tropical clupeoids.

Most of the existing information on reproduction in tropical anchovies concerns species from latitudes close to the equator. In these regions spawning seasons are extended or may occur throughout the year and reproductive cycles are often linked to monsoonal seasons (Tiews *et al.* 1970, Dalzell and Wankowski 1980, Dalzell and Ganaden 1987, Longhurst and Pauly 1987, Milton *et al.* 1990a). At present there is little information available on the reproductive biology and spawning seasons of tropical anchovies from northern Australia (see Hoedt 1984). Tropical Australia includes coastlines that lie at the southernmost tropical latitudes and the seasonal weather pattern in these areas differs from the typical monsoonal pattern in equatorial countries. In these sub-tropical latitudes, the annual variation in water temperature is greater resulting in distinct warm and cool seasons. More information on the reproductive biology and spawning season of anchovies from

northern Australia is needed and the influence of the annual temperature cycle on reproductive life-histories requires investigation.

#### 1.4 Ecological and fishery considerations

Information on the biology and population dynamics of tropical clupeoids is important because of the economic and commercial importance of this group. Tropical anchovies along with other clupeoids make a significant contribution to the commercial and artisanal catches of many tropical countries (Luther 1979, Chullasorn and Martosubroto 1986, Whitehead *et al.* 1988, Lewis 1990, Luther 1990). They are also key components in coastal marine food chains (Longhurst 1971, Luther 1979, Longhurst and Pauly 1987). Most species feed on zooplankton and therefore occupy a low trophic level. The small size and high local abundances typical of anchovies also make these important prey species for a variety of predatory fishes and seabirds (Peterson 1956, Tham 1972, Major 1978, Luther 1979, Blaxter and Hunter 1982, Blaber *et al.* 1990, Smith 1993). Pelagic fish species which prey on anchovies in the tropics include carangids, scombrids and thunnids which are themselves of importance to tropical fisheries.

In northern Australia there are no fisheries for anchovies and as a result little attention has been paid to the biology, distribution and habitat preferences of the species inhabiting coastal waters. However, there is some evidence that anchovies do occur in considerable numbers in parts of tropical Australia. Okera *et al.* (1981) reported large catches of stolephorid anchovies (700 kg/half hour trawling) during trawl surveys in the Arafura Sea off northern Australia, indicating that there may be sizeable anchovy stocks in the region. In addition, studies have shown that anchovy larvae and juveniles comprise a significant component of the ichthyoplankton in light trap and plankton samples collected across the Great Barrier Reef lagoon off tropical eastern Australia, indicating that this family is common in shelf waters of north-eastern Australia (Milward and Hartwick 1986, Leis and Goldman 1987,

Moltschaniwskyj pers. comm., Doherty pers. comm). Robertson and Duke (1987) also showed that several species of anchovy were amongst the most abundant fish in tropical mangrove estuaries in northern Australia. The ecological importance of these fish and the comparatively small amount of biological information for this group in Australia indicates a need for more study.

### 1.5 Aims of the study

The primary aim of the present study is to investigate the habitat, growth and reproduction in eight species of tropical anchovy from the inshore waters of Townsville, North Queensland. The study was undertaken in conjunction with research on the habitat and biology of the closely related family Clupeidae in Bowling Green and Cleveland Bays by the Australian Institute of Marine Science.

The sampling strategy employed in this study consisted of several methods which allowed sampling in three important inshore habitats: mangroves; beaches and nearshore waters to 12m depth. Comparisons of catches between habitats are made to determine the age-specific habitat preferences of the study species.

A major component of this study is the estimation of the growth parameters for the study species. Three ageing methods: length-frequency analysis; counting primary otolith increments and counting seasonal growth rings in otoliths; are employed to age the study species. This presents the opportunity to compare different methods and review the applicability of commonly used ageing methods for tropical clupeoids. A prerequisite to conducting detailed growth analyses for each species is the validation of the periodicity of primary and seasonal growth increments in otoliths. Aquarium experiments and other methods are employed in this study to solve this problem.

The reproductive biology of the study species will also be examined and compared.



Spawning season, length and age-at-maturity, fecundity and spawning frequency will be estimated. Again, inter-species comparisons of these parameters will be made and related to life-history strategies for this group.

A further aim of this investigation is to examine the quantitative relationships between biological parameters and compare them at an inter-species level. In particular, the relationships between species-size (length and weight) and particular biological parameters is investigated. Size (maximum size of a species)-related patterns of growth and reproductive parameters will also be related to current information on the life-history strategies of different sized tropical clupeoids (Lewis 1990). Further, the possibility that similarities in the relationships between biological parameters between species found here, may be also be true for a wider range of tropical clupeoids and therefore useful for obtaining preliminary estimates of certain parameters in species for which little biological information is available, will be discussed.

Finally the information collected in this study will be used as a basis to undertake a preliminary comparison of the life-histories and fishery dynamics of tropical and temperate clupeoids. One aspect of this will be to calculate the ratio of biological parameters used by Beverton (1963) in his comparative study of temperate clupeoid fishes. Similarities between the tropical and temperate species may imply similarities in fishery and population dynamics.

## CHAPTER 2 GENERAL METHODS

### 2.1 Sampling locations, gears and treatment of samples.

Samples of anchovy were collected between August 1987 and May 1991 at sites in Cleveland and Bowling Green Bays, Townsville (Fig. 2.1). The sampling locations were chosen to include three major habitats: mangrove estuaries; beaches and the subtidal habitat to 12m. Mangrove estuary samples were collected adjacent to the shore in the main channel or a tributary channel within a mangrove tree-lined creek or river. All beach sites were coastal areas of sandy substrate with no mangrove vegetation or rocky substrates. The subtidal habitat sampled was within Cleveland Bay which is predominantly a muddy substrate of terrigenous origin.

In Cleveland Bay, seine nets were deployed at each site on a monthly basis (Fig. 2.1). The collection sites were: Pallarenda (beach); the Strand (beach) and Ross River (mangrove estuary) (Fig. 2.1). During most collecting trips two seine nets were used (net1: 15m long; 1.5m drop; 12mm mesh; 2m cod-end and net2: 10m long; 2m drop; 5mm knotless mesh). The finer mesh net retained smaller fish and was also used to collect live fish. In Cleveland Bay, samples were collected from the subtidal habitat at 3-12m water depth using otter trawls deployed from 'R.V. James Kirby' (Fig. 2.1). These cruises were run by other research projects therefore the sampling locations and gear (mesh size) were not specifically designed to sample anchovy (see Chapter 4 for discussion of sampling biases). Trawl samples were collected each month between January 1988 and December 1989 at fixed stations (Fig. 2.1). An additional trawl collection was made in April 1990. At each station, the twin otter trawls (38 mm mesh) were towed along the sea floor for 20 minutes.

Samples were also collected each month at four sites in Bowling Green Bay between August 1987 and August 1989 using one seine net and three gill nets (Fig. 2.1). The seine deployed in Bowling Green Bay was 150m in length with two mesh sizes decreasing from 30mm in the wings to 13mm at the cod-end. The three gill nets each comprised 3X10m

panels of the following mesh sizes: 19mm; 32mm and 45mm. The collection sites in Bowling Green Bay were: Cape Bowling Green Spit (abbrev.:CBGS); Houghton River (HR); Chunda Flats (CF) and the AIMS Wharf (AW). The seine net was used at CBGS, HR and CF. The gill nets were used at CBGS, HR, CF and AW.

Larger anchovies collected in trawl samples and in seine and gill net samples were preserved in a 10% formalin solution or frozen. Most of the smaller anchovy collected in seine net samples were preserved in absolute alcohol. All length measurements referred to in this thesis are total lengths (nearest mm), unless otherwise specified.

## 2.2 Species names and terminology used in this thesis

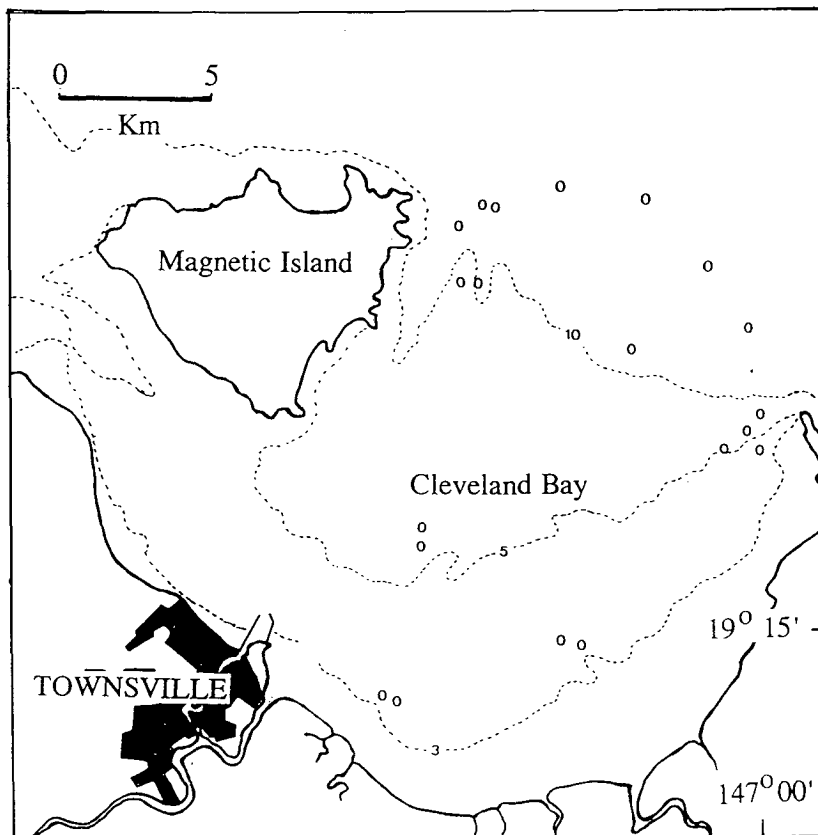
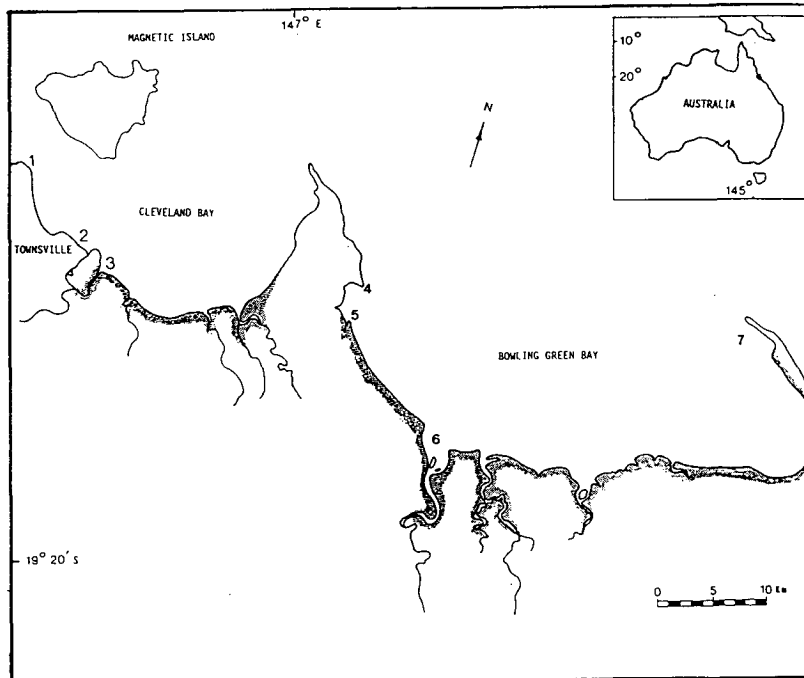
Species identifications were based on descriptions provided in the most recent taxonomic revision of the family Engraulidae (Whitehead *et al.* 1988). Individuals of each of the study species were also sent to Dr. Thosoporn Wongratana (Chulalongkorn University, Bangkok), who confirmed identifications.

Two of the species collected during the present study, *Encrasicholina devisi* and *E. heteroloba* were until recently classified as *Stolephorus* species. In this thesis they are referred to as '*Encrasicholina*' throughout. The collective term 'stolephorids' in this thesis refers to species from both of these genera.

In some chapters the distinction is made between juvenile and adult life stages of anchovies. 'Juveniles' in this study refers to fish which were smaller than the mature-length for the particular species. Maturity was estimated to occur at approximately 68% of maximum length. This value was obtained from the mean of published lengths-at-maturity for nine species of tropical anchovies (Palekar and Karandikar 1952, Venkataraman 1956, Masurekar and Rege 1960, Marichamy 1970, Leary *et al.* 1975, Dalzell and Wankowski 1980, Milton and Blaber 1991). Reproductive studies confirmed that this was a reasonable estimate for the species studied.

The map of the study locality and sampling sites (1-7)

Figure 2.1 A map of the study locality and sampling sites. (a) Cleveland and Bowling Green Bays showing nearshore seine and gill netting sites (numbered). Key: 1-Pallarenda; 2-Strand; 3-Ross River; 4-AIMS Wharf; 5-Chunda Flats; 6-Houghton River; 7-Cape Bowling Green Spit. (b) Cleveland Bay showing the monthly otter trawl sites (circles). Depth contours in metres are shown.



## CHAPTER 3 SPECIES COLLECTED AND THEIR DISTRIBUTION AND FISHERIES IN THE INDO-PACIFIC

### 3.1 Introduction

The anchovy fauna of the tropical Indo-West Pacific region is characterised by its rich species diversity (Longhurst 1971). The majority of tropical anchovy species are found in the Indian and Western Pacific Oceans where there are around 62 marine species (Whitehead *et al.* 1988). A third of the 62 species have been recorded on the northern Australian coast. Of these, six species have only been recorded in Australian waters and a further five species have only been recorded in Australia and Papua New Guinea (Whitehead *et al.* 1988).

The inshore waters of most countries in the Indo-West Pacific region support a multi-species clupeoid fauna. In some regions, one or more anchovy species are present in sufficient abundance to support large artisanal fisheries (Tiews *et al.* 1970, Luther 1979, Chullasorn and Martosubroto 1986). The most important tropical anchovies in this regard are the stolephorid anchovies and members of the genus *Thryssa* (Longhurst and Pauly 1987, Whitehead *et al.* 1988). Large artisanal fisheries for tropical anchovies occur in India (Luther 1979, Luther 1990), the Philippines (Tiews *et al.* 1970, Tham 1972, Dalzell and Ganaden 1987), Singapore (Tham 1966, Whitehead *et al.* 1988), Thailand (Chullasorn and Martosubroto 1986, Whitehead *et al.* 1988), Indonesia (Wright *et al.* 1990) and the Arabian Gulf (Hussain and Ali 1987). Stolephorid anchovies also make a significant contribution to the live-bait fisheries for pole and line tuna fishing operations in the Indo-Pacific region (Lewis 1990). Although tropical anchovies are not caught commercially in Australia, a number of species found here are of economic or commercial importance in other countries.

In the following chapter, the species of anchovy collected in Cleveland and Bowling Green Bays are listed and the geographic distribution and fishery significance in the Indo-Pacific

region of the eight most common species are given. Published scientific studies on each of the study species are also referred to.

## 3.2 Results and discussion

### 3.2.1 Species collected.

Eleven species of anchovy were collected in Cleveland and Bowling Green Bays during the present study. Only eight of these species were caught on a regular basis and these were the focus of the present study (Table 3.1). The remaining species collected were 77 individuals of *Stolephorus sp. A* (Whitehead *et al.*, 1988); 24 individuals of *Stolephorus indicus* (van Hasselt, 1823); and 1 individual of *Thryssa baelama* (Forsskål, 1775). In addition, 42 individuals of *Encrasicholina heteroloba* (Rüppell, 1837) were identified by the author from samples collected by other workers from coralline habitats adjacent to Townsville (Lizard Island and Magnetic Island) during the period of the study.

### 3.2.2 Distribution and fisheries

#### 3.2.2.1 *Encrasicholina devisi*

This species is widely distributed in inshore waters along coasts of the northern Indian and Western Pacific Oceans (Table 3.1). In some regions, *E. devisi* is one of the dominant species in the anchovy fauna (Dalzell and Wankowski 1980, Dalzell and Lewis 1989), and therefore probably makes a significant contribution to world '*Stolephorus*' catches (Whitehead *et al.* 1988). *E. devisi* is suitable as a 'live bait' species for pole and line tuna fisheries and has been utilised as such in Palau, Fiji, Papua New Guinea and Solomon Islands (Luther *et al.* 1984, Dalzell and Lewis 1989, Lewis 1990).

The biology of *E. devisi* in South East Asia and the South Pacific Region has been dealt with in some detail. Aspects that have been studied include growth (Tiews *et al.* 1970 - referred to as '*Stolephorus species A*', Dalzell and Wankowski 1980, Syda Rao 1988a, Luther 1990); reproduction (Tiews *et al.* 1970, Dalzell and Wankowski 1980, Conand 1985, Syda Rao 1988a, Luther 1990, Milton and Blaber 1991) and habitat preference (Dalzell

1986). Diet and length-frequency information for *E. devisi* from the Townsville region are analysed in Hoedt (1984).

At present, little is known concerning the growth and reproduction of *E. devisi* from Australia. Growth in the local *E. devisi* population is of particular interest because this species appears to be smaller in Australia than in other countries (see Dalzell and Wankowski 1980, Luther 1990). The existing information on growth in *E. devisi* has been derived from the analyses of length-frequency data. The periodicity of primary otolith increments are yet to be determined for this species and age and growth has not been estimated from primary otolith increments.

#### 3.2.2.2 *Stolephorus insularis* (Hardenberg's anchovy)

*Stolephorus insularis* is widespread along coasts of the northern Indian Ocean and north west Pacific Ocean (Table 3.1). This species has not previously been recorded in Australia (Whitehead *et al.* 1988). It is fairly common throughout its range and it is therefore probably an important component of '*Stolephorus*' catches in this region (Whitehead *et al.* 1988). This species also contributes to the pole and line tuna bait-fishery in the South Pacific region (Whitehead *et al.* 1988).

*S. insularis* has probably been wrongly identified in a number of past studies (confused with *S. baganensis*), making it difficult to rely on the results of these studies (Whitehead *et al.* 1988). If identifications are correct, then growth and feeding in *S. insularis* has been studied by Burhanuddin and Hutomo (1975) in Indonesia, and growth has been examined for the population in Singapore Straits by Tham (1966). A preliminary study of some aspects of the biology of *S. insularis* from the Townsville region can be found in Hoedt (1984-referred to as '*Stolephorus species 2*').

The possibility of misidentification of *S. insularis* in past studies is one reason for re-examining the biology of this species. As is the case with *E. devisi*, past growth studies on *S.*



*insularis* are based on length-frequency information and these studies estimate longevities of around 1 year. A preliminary study of growth based on presumed daily growth increments in otoliths by Hoedt (1984), suggests that this species has a shorter lifespan. More information on growth using primary otolith increments is required for this species.

#### 3.2.2.3 *Stolephorus carpentariae* (Gulf of Carpentaria anchovy)

*S. carpentariae* has a limited distribution, occurring on the southern coast of Papua New Guinea, the Gulf of Carpentaria and the coast of Queensland (Table 3.1). The only record of *S. carpentariae* on the East Queensland coast is from Moreton Bay, near Brisbane (Whitehead *et al.* 1988) however, this may be a reflection of the scarcity of samples available from the Queensland coast. The occurrence of this species in Townsville suggests that it may have a wider distribution along the Queensland coast than is shown in Whitehead *et al.* (1988).

A preliminary account of aspects of the biology of *S. carpentariae* in the Townsville region are given in Hoedt (1984). Robertson and Duke (1990) report the seasonal occurrence of *S. carpentariae* in a mangrove estuary near Townsville and also briefly discuss growth in this species based on length-frequency data. Due to the limited geographical distribution and lack of fisheries for this species there appears to be no further information regarding its biology. Further data on the habitat, growth and reproduction in *S. carpentariae* are required.

#### 3.2.2.4 *Stolephorus nelsoni* (Nelson's anchovy)

*S. nelsoni* was only recently described from specimens collected near Townsville, North Queensland (Wongratana 1987). Specimens are known only from two localities in the coastal waters of the northern Australia (Table 3.1), although *S. nelsoni* was common in catches in the present study.

At present, information on the biology of this species is limited. A preliminary account of aspects of growth, reproduction and diet can be found in Hoedt (1984-referred to as '*Stolephorus species 1*'). Robertson and Duke (1990) note the temporal patterns of occurrence of this species in a mangrove estuary near Townsville.

*S. nelsoni* appears to be one of the more common species in the nearshore waters off Townsville and is therefore an important component of the local clupeoid fauna. It is also one of the larger, more robust stolephorids. More data on the distribution, growth, longevity and reproduction in this species should provide interesting comparisons with other tropical anchovies.

#### 3.2.2.5 *Stolephorus commersonii* (Commerson's anchovy)

This species is widespread along the coastal waters of the Indian and Western Pacific Oceans (Table 3.1), and it probably contributes to artisanal catches in parts of this range (Whitehead *et al.* 1988). *S. commersonii* has not been recorded in Australian waters (Whitehead *et al.* 1988). *S. commersonii* appears to inhabit deeper waters further from shore and is sometimes caught in small numbers, suggesting that it may be a solitary species (Tham 1972). These habits restrict the availability of *S. commersonii* to coastal fisheries.

The fishery for *S. commersonii* in India is briefly described by Luther (1979). Reproduction in *S. commersonii* in the Philippines and India are discussed in Tiews *et al.* (1970) and Dharmamba (1959) respectively. The habitat of *S. commersonii* in the coastal waters of the Philippines and the South China Sea are reported in Tiews *et al.* (1970) and Tham (1972) respectively. Blaber (1979) collected small numbers of this species in Lake St. Lucia, Zululand and briefly describes the feeding and reproduction of these. The biology of *S. commersonii* is of particular interest as it is one of the largest of the stolephorid anchovies, growing to 160 mm in the study area (similar in size to *S. indicus*). At present there is no information on the growth of *S. commersonii*. Tham (1966) found that another large stolephorid, *S. indicus* was longer-lived and grew faster than two smaller species. More

information on the growth and longevity of the larger stolephorids using otoliths will make a useful contribution to our understanding of the patterns of life-history in tropical anchovies.

#### 3.2.2.6 *Thryssa aestuaria* (estuarine thryssa)

*Thryssa aestuaria* is known only from the northern coasts of Australia (Table 3.1). At present the only biological data relating to this species come from two studies. Hoedt (1984) described the post-larvae (referred to as '*Thrissina nasuta*'), and Robertson and Duke (1990) noted that juvenile *T. aestuaria* (referred to as '*T. brevicauda*'), were occasionally common in a mangrove estuary near Townsville. Further details on all aspects of the biology and habitat of this species are required.

#### 3.2.2.7 *Thryssa setirostris* (long-jaw Thryssa)

This is a widely distributed species occurring along coasts throughout the Indian and Western Pacific Oceans (Table 3.1). While there are no special fisheries for this species, it probably contributes to mixed anchovy catches taken by artisanal fisheries (Whitehead *et al.* 1988).

Aspects of the biology of *T. setirostris* are discussed in Hoedt (1984). The occurrence of juveniles in the inshore waters of Madras, India has also been reported (Basheerudin and Nayar 1962). At present little is known about the growth and longevity of this species. More information on the biology of *T. setirostris* is needed.


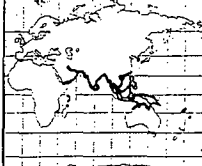

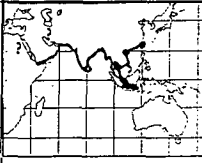



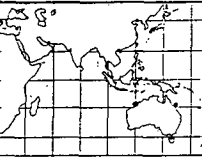

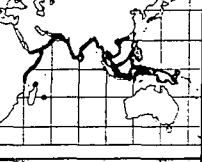
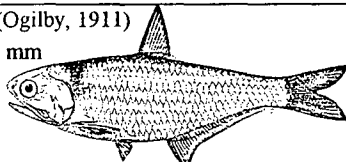
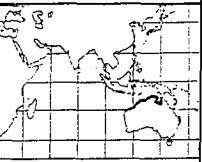
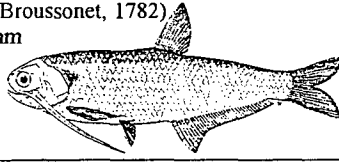
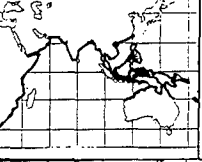
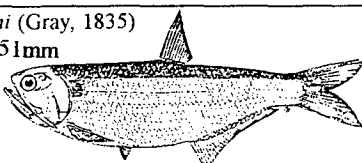
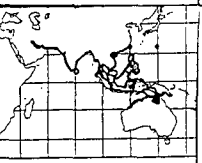
#### 3.2.2.8 *Thryssa hamiltoni* (Hamilton's thryssa)

This species is both geographically widespread (Table 3.1), and relatively abundant in the Indo-Pacific region (Whitehead *et al.* 1988). It is probable that this species makes a significant contribution to artisanal fisheries in a number of countries (Hussain and Ali 1987, Whitehead *et al.* 1988).

There have been several of studies on the biology of *T. hamiltoni*. These include: Mookerjee and Mookerjee (1950-general biology); Bapat and Bal (1950-diet); Masurekar and Rege (1960-reproduction); Hussain and Ali (1987-reproduction). In Australia, Hoedt (1984) gave a preliminary account of the growth, reproduction and diet of this species in the Townsville region. Robertson and Duke (1990) analysed length-frequency data for juvenile *T. hamiltoni* in a mangrove estuary in North Queensland.

*T. hamiltoni* is one of the larger tropical clupeoid species, growing to 270 mm in the Arabian Sea (Hussain and Ali 1987) and 250 mm at Townsville (Hoedt 1984). At present, information on the growth and longevity of this species is only of a preliminary nature (Hoedt 1984, Robertson and Duke 1990). More data is needed, and will be of particular interest due to the large size of this species. The majority of studies of growth in large tropical clupeoids are based on length-frequency information and few of these provide accurate longevity estimates. Information on the longevity of this large species will help our understanding of the maximum lifespans that can be achieved by large tropical clupeoids. The possible difference in growth of male and female *T. hamiltoni* suggested by Hoedt (1984) is also worthy of further investigation.

Table 3.1 The species of anchovy examined in the present study with geographical distribution (after Whitehead et al 1988), reported fishing countries, and the number of individuals collected during the present study. \* - tuna live bait fishery

Species	Geographical Distribution	Reported fishing centres	Number caught in this study
<i>Encrasicholina devisi</i> (Whitley, 1940) Max. length = 62mm 		India <sup>1</sup> Philippines <sup>2</sup> Indonesia <sup>3</sup> PNG <sup>4*</sup> New Caledonia Solomons <sup>6*</sup>	2880
<i>Stolephorus insularis</i> (Hardenberg, 1933) Max. length = 64mm 		Singapore <sup>7</sup> Indonesia <sup>3</sup>	2,620
<i>Stolephorus carpentariae</i> (de Vis, 1883) Max. length = 71mm 		None <sup>8</sup>	2,241
<i>Stolephorus nelsoni</i> (Wongratana, 1987) Max. length = 103mm 		None <sup>8</sup>	3,242
<i>Stolephorus commersonii</i> (Lacepede, 1803) Max. length = 158mm 		India <sup>1</sup> Philippines <sup>2</sup>	416
<i>Thryssa aestuaria</i> (Ogilby, 1911) Max. length = 142 mm 		Little <sup>8</sup>	1,350
<i>Thryssa setirostris</i> (Broussonet, 1782) Max length = 220mm 		General clupeoid catches <sup>8</sup>	585
<i>Thryssa hamiltoni</i> (Gray, 1835) Max. length = 251mm 		Arabian Gulf <sup>9</sup> India <sup>10</sup>	1,459

1- Luther (1979)

2- Tiews et al. (1970)

3- Burahannudin and Hutomo (1975)

4- Dalzell (1987)

5- Conand (1985)

6- Lewis (1990)

7- Tham (1966)

8- Whitehead et al. (1988)

9- Hussain and Ali (1987)

10- Masurekar and Rege (1960)

## **CHAPTER 4. Age-specific distributions of anchovies in Cleveland and Bowling Green Bays.**

### **4.1 Introduction**

Clupeoid fishes are highly mobile and characteristically undertake seasonal migrations of varying distances (Blaxter and Hunter 1982, Hampton 1992). Many species exhibit seasonal movements to depths or regions that are favourable for spawning or feeding (Longhurst 1971, Longhurst and Pauly 1987, Longhurst and Wooster 1990, Hampton 1992). Knowledge of the seasonal movements of clupeoid stocks can be an important aspect of fishing operations and fishery management (Luther 1979, Blaxter and Hunter 1982, Longhurst and Wooster 1990). For example, the coastal fishery for the oil sardine (*Sardinella longiceps*) along the Indian coast is dependant on the seasonal shoreward migration of breeding adult fish (Longhurst 1971, Longhurst and Pauly 1987).

Another aspect of the distribution of clupeoid fishes is the phenomenon of age-specific habitat preferences. Nicholson (1978) showed that Atlantic menhaden stratify by age and size along the coast from Maine to Florida. Tham (1970 in Tham 1972) found that the eggs and different life stages of *Stolephorus pseudoheterolobus* (= *Encrasicholina heteroloba*) had distinct distributions within the Singapore Straits. Ramirez *et al.* (1989) also noted age-specific habitat partitioning in anchovies in the Gulf of Nicoya, Costa Rica; adults spawned in nearshore waters and larger larvae migrated into estuaries where they remained as juveniles. Similarly, Luther (1979) noted that the juveniles of some stolephorid anchovies along the Indian coast were found closer to shore than adults. These and other studies (eg. Blackburn 1950a, De Silva 1973), indicate that the juveniles of clupeoid stocks may have a different distribution to the adult stock, therefore the recognition and management of the habitat of juveniles may be an important component of the management of these stocks. Information on the ecology of

juvenile stages of clupeoid fishes is of importance as the abundance of future parent stocks is thought to be related to the size of the juvenile stocks (Peterman *et al.* 1988).

Many tropical countries have a diverse clupeoid fauna in nearshore waters and the habitat preferences of adults in different species of anchovy at a given locality may differ (Tham 1972, Luther 1979, Dalzell 1986, Whitehead *et al.* 1988). Dalzell (1986) divided the preferred habitats of different species of anchovy in Papua New Guinea into three broad categories: estuarine; inshore coralline and oceanic. Tham (1972) and Dalzell (1986) concluded that the distribution of anchovy species in coastal habitats is determined by a combination of physical and chemical environmental conditions, particularly salinity and the availability of different types of food. These studies suggest that inter-specific differences in habitat preference are probably a factor which enables diverse species assemblages to co-exist in tropical coastlines.

One aspect of tropical clupeoid distributions that has received little attention is the interaction of shallow coastal habitats such as beaches and mangrove estuaries, with the adjacent subtidal waters as habitats for different life-stages. Several studies have examined the fish communities of nearshore habitats in tropical Queensland (Blaber 1980, Robertson and Duke 1987, Robertson and Duke 1990). Robertson and Duke (1990) found that five species of anchovy (mostly juveniles), were amongst the 20 most abundant species in a mangrove creek system in tropical northern Australia. This suggests that anchovies may comprise an important component of tropical mangrove fish communities. There have been several trawl surveys examining the distribution of tropical fish assemblages in shelf waters of tropical Australia (eg. Rainer 1984, Ramm *et al.* 1990), and these give some information on anchovy distribution on the shelf. However, there is little information on the distribution of anchovies in both shallow and subtidal habitats at one locality. Data of this nature

will enable the assessment of the importance of different coastal habitats to tropical anchovy stocks.

In this chapter, the distribution of juveniles and adults of eight species of anchovy in Cleveland and Bowling Green Bays, Townsville are examined. Information on the age-specific distributions for each species is interpreted from an analysis of the composition of catches from three nearshore habitat types : mangrove estuaries; beaches; and nearshore bay waters at depths of 3-12 metres.

## 4.2 Materials and methods

The age-specific habitat preferences of the anchovy species studied were assessed by comparing the abundances of juvenile and adult fish collected in different habitats. To achieve this, each sampling site was classified as one of three habitat types: subtidal or trawl; beach; or mangrove. Total numbers of juvenile and adult fish collected from each habitat type from the entire study period were pooled by month into a single twelve month data set. The resulting data allowed a qualitative analysis of seasonal patterns in the age-specific distribution of the study species.

## 4.3 Results

### 4.3.1 Sampling biases

#### 4.3.1.1 Gear selectivity

A variety of sampling devices were used in the present study. Two nets with different mesh-sizes (5 and 12mm) were used during inshore seine netting in Cleveland Bay, this enabling the collection of juvenile through to adult-sized fish. The main limitation of these seine nets was their relatively small length (10 and 15 m), which decreased the depth and area sampled. Given that only small numbers of adult *Thryssa spp.* were caught in these nets, the possibility of net avoidance by larger anchovies must be considered. However, adults of the larger *Thryssa spp.* were also infrequently caught in the 150m beach seine used in Bowling Green Bay,



suggesting that they were not common in shallow waters. When adults were caught in this net (*T. aestuaria* and *T. hamiltoni* were occasionally caught), these were often young adult fish (0+) suggesting that older fish preferred deeper water. Gill nets set at night at the AIMS wharf and at Cape Bowling Green Spit occasionally caught larger *T. hamiltoni* and *T. setirostris* indicating that individuals may move close to shore at night. The small number of adult *Thryssa spp.* caught in shallow habitats in the present study suggests that these fish prefer subtidal habitats.

Another source of sampling bias that requires consideration is the escapement of small anchovies from the otter trawl nets due to the large mesh size (38 mm stretched). Field observations indicate a wide size-range of the deep bodied *Thryssa spp.* including juveniles as small as 100 mm (T.L.) were retained in the trawl net. Trawl samples were therefore considered suitable for examining the distribution of both adult and larger juvenile *Thryssa spp.* Field observations also indicate that adults of the larger robust stolephorids such as *S. nelsoni* and *S. commersonii* were also retained by the trawl net mesh. However, sampling bias was thought to have occurred for small species of *Stolephorus* and juveniles of all *Stolephorus spp.* due to their small body-size. Retention of very small anchovies appeared to be greater when large catches of fish were made because the weight of the catch tended to reduce mesh width (the meshes stretched and closed), and the presence of other fish in the net tended to trap small anchovies.

An indication of the degree of mesh selectivity that was occurring for small stolephorid species was obtained during an experiment when a fine mesh bag (3mm) was placed over the normal trawl mesh in April 1990. In a sample collected at one of the shallow stations, only 42 out of a total catch of 1451 *E. devisi* individuals were retained in the normal trawl mesh indicating a 3% retention rate. In the same sample, 71 out of a total catch of 638 (or 11%) of juvenile *S. nelsoni* were retained in the normal trawl mesh. These data indicate that the losses of small

stolephorid anchovies are high but not complete. Therefore the trawl sampling could at best only give an indication of the presence or absence of small anchovies when large catches were made. The regular presence of post-larval through to adult *E. devisi* (one of the smallest species), in normal trawl samples indicates that trawl samples provided limited information on the distribution of this species in the subtidal zone.

#### 4.3.1.2 Sampling effort in habitats

A summary of the numbers of samples collected at mangrove and beach sites each month in Cleveland Bay is given in Table 4.1. Mangrove and beach sites were sampled in most months between 1988 and 1989 and in 1991. In 1990, due to time restrictions, few samples were collected at mangrove sites (Table 4.1). Examination of the total numbers of samples taken in the different months of the year summed for the period of the study reveals that there were approximately half as many samples taken at the mangrove estuary site as were collected at beach sites (Table 4.1). The lower effort in mangroves must be taken into account when comparing the numbers of fish caught in each habitat.

Samples were collected from four sites in Bowling Green Bay. Only the Houghton River site was classified as a mangrove estuary while the remaining sites were included in the 'beach' category. Thus sampling effort in mangrove estuaries was considerably less than for the 'beach' sites in Bowling Green Bay also. There were no trawl samples taken in Bowling Green Bay and therefore no 'subtidal' samples.

In light of this information it is evident that quantitative comparisons between numbers of fish caught in each habitat cannot be made. However, the catch data was considered suitable for detecting major differences in the preferred habitats of juveniles and adults of each species.

#### 4.3.2 Age-specific distributions

##### 4.3.2.1 *Stolephorus insularis*

Seine catches of *S. insularis* (juvenile and adult) were predominantly taken from sandy beaches; very few fish were collected in mangrove estuaries (Fig. 4.1a&b). A small number of trawl samples in the shallow subtidal waters (<5m) contained this species. The catch data therefore suggests that *S. insularis* is predominantly a shallow water species and is not common in mangrove estuaries.

##### 4.3.2.2 *Encrasicholina devisi*

Most juvenile and adult *E. devisi* individuals were collected during seine netting operations from beaches (Fig. 4.1c&d). However, the regular catches of this species (including larvae) in trawl shots indicates that the species also frequents the subtidal habitat in Cleveland Bay (Fig. 4.1c&d). A large number were caught at 5-7m in April 1990 when a fine mesh liner was placed over the trawl nets which suggests that *E. devisi* may be abundant in shallow subtidal waters. *E. devisi* was less frequently caught in mangrove estuaries than beaches however, sizeable catches were taken in some months indicating that the species periodically enters this environment (Fig. 4.1c&d). The catch information suggests that this species inhabits both shallow inshore beach and subtidal habitats in Cleveland Bay. Juvenile and adult distributions appear to overlap (Fig. 4.1c&d).

##### 4.3.2.3 *Stolephorus carpentariae*

Juveniles and adults of *S. carpentariae* were mostly collected from sandy beach habitats, and occasionally in mangrove estuaries (Fig. 4.1e&f). This species was extremely rare in trawl net samples taken in the subtidal habitat (only 1 individual caught), suggesting that it is predominantly found close to shore in waters less than 3m depth (Fig. 4.1e&f).

##### 4.3.2.4 *Stolephorus nelsoni*

Juveniles and adults of *S. nelsoni* were collected in all three habitats (fig. 4.1g&h). Juveniles were common in both mangrove estuary and beach samples (Fig. 4.1g). Juvenile *S. nelsoni* were also present in otter trawl samples but were generally only caught at shallow stations (depths less than 5m). Large numbers of adult *S. nelsoni* were collected in otter trawls in the subtidal habitat (3-7m), and if losses of smaller individuals due to net selectivity are considered then it is probable that this species was very common at these depths. Adult *S. nelsoni* were seasonally common in seine net samples collected off beaches but were comparatively rare in mangrove estuaries (Fig. 4.1h). The catch data indicates that juvenile *S. nelsoni* are found in mangroves, beaches and shallow subtidal waters and adults are mostly found off beaches and in subtidal waters to 7m but are uncommon in mangroves.

#### 4.3.2.5 *Stolephorus commersonii*

Juvenile and adult *S. commersonii* appeared to have distinct depth distributions within Cleveland Bay. Juveniles were mostly caught in the mangrove and beach sites and adults were almost exclusively caught in trawl samples in the subtidal habitat at depths of 3-12m (Fig. 4.2a&b). Some adult *S. commersonii* were taken in the 150m seine net but these were generally smaller than individuals taken in trawl samples suggesting that larger individuals prefer deeper water.

Given that there was a lower sampling effort in mangrove estuaries than on beaches it is evident from the relatively large number of juvenile *S. commersonii* caught in mangroves that this habitat may be an important nursery site for this species (Fig. 4.2.a).

#### 4.3.2.6 *Thryssa aestuaria*

Juvenile *T. aestuaria* were common in samples collected at the beach sites and in the mangrove estuaries (Fig. 4.2c&d). Few juveniles were taken in trawl samples and when present these were large juveniles. This suggests that juvenile *T.*

*aestuaria* prefer nearshore shallow habitats (Fig. 4.2c). Adult *T. aestuaria* were mostly caught in the subtidal bay habitat (depths of 3-7m), and were only occasionally present in samples from the beach sites (Fig. 4.2d). Most adult *T. aestuaria* collected off beaches were caught in the 150m seine net but these were smaller than adults caught in trawl samples. No adult *T. aestuaria* were collected at the mangrove sites (Fig. 4.2d). These data suggest that juvenile and adult *T. aestuaria* have different depth preferences with juveniles inhabiting shallow intertidal habitats and adults, subtidal habitats.

#### 4.3.2.7 *Thryssa setirostris*

Small juvenile *T. setirostris* were regularly caught from beach sites (in small numbers) but not in mangrove estuaries (Fig. 4.2e). Larger juveniles were only rarely collected in seine nets suggesting a movement offshore with age. Adult *T. setirostris* were almost exclusively collected in trawl samples at depths of 3-12m (Fig. 4.2e&f). The catch data indicates that adult *T. setirostris* are mostly found in the subtidal habitat and juveniles probably frequent shallower water.

#### 4.3.2.8 *Thryssa hamiltoni*

Juvenile *T. hamiltoni* were common in samples from both the mangrove and beach sites (Fig. 4.3g). A small number of juvenile *T. hamiltoni* were also caught in otter trawls however, these were mostly collected in the shallow trawl sites at around 3-5m depth. Adult *T. hamiltoni* were rare in the mangrove sites but were occasionally caught using gill nets at beach sites in Bowling Green Bay, indicating that adults sometimes move close to shore (Fig. 4.3h). Adult *T. hamiltoni* were the most common component of anchovy catches made using trawl nets in the subtidal habitat (3-12m), indicating a preference for the subtidal habitat. The catch data for *T. hamiltoni* therefore suggests that juveniles and adults have different depth preferences (with some overlap), with juveniles largely occurring in shallow nearshore habitats and adults in subtidal waters.

#### 4.3.3 Seasonal changes in catch

There was considerable seasonal variation in the catches of all of the study species. Juveniles of all species exhibited strong seasonality in catches. Juvenile anchovy were more common in seine net catches between October and June than between July and September (Figs 4.1 and 4.2), however this could reflect growth to adult sizes in the latter months. Catches of juveniles of most species in seine nets were high in October/November but decreased between December and January (the warmest months). As these months are still within the recruitment period of most species the absence of juveniles suggests movement away from very shallow water

Catches of adults of most species also varied seasonally. Catches in the seine nets were highest between February and September and lower in the warmest months of October to January. Peak catches in a number of species occurred in April/May (Figs 4.1 and 4.2). The monthly catches of *S. insularis* adults in the seine nets suggested a strong seasonal pattern with higher catches in winter. Catches of *E. devisi* in the seine nets were highest between February and August. It is interesting that most *E. devisi* individuals caught between September and December were taken in trawl samples, this being evidence of a movement to deeper water in the spring and summer (Fig. 4.1). Numbers of *Thryssa spp.* in trawl catches were lower in the spring and early summer than autumn and winter, suggesting a movement away from the trawling area at this time (Figs. 4.1 and 4.2).

The highest catches of anchovy in the subtidal habitat occurred at depths of 3-7m. However, on 17-10-88 large catches of anchovy (mainly *Thryssa spp.*), were taken at 10-12m this being consistent with previous evidence that some species may move to deeper water in the spring and summer.

#### 4.3.4 A summary of the age-specific distributions

Based on the number of juveniles and adults of each anchovy species collected in different habitats during the present study, three broad types of age-specific depth distribution were identified. The first type included those species where juveniles and adults had different depth preferences, with juveniles predominantly occurring in nearshore shallow habitats (<3m), and adults mostly occurring further from shore in the subtidal bay habitat (3-12m). This type of distribution was identified in the larger anchovy species, *T. hamiltoni*, *T. aestuaria*, *S. commersonii* and *T. setirostris*.

The second type of distribution included those species where juveniles and adults had overlapping distributions frequenting both the shallow intertidal and shallow subtidal (3-7m) habitats. Adults in these species periodically moved close to shore and were accessible to seine nets. *S. nelsoni* and *E. devisi* were placed in this grouping. *S. insularis* probably also belongs to this category but adults were less frequently caught in subtidal samples than other species.

A third type of distribution was that observed in *S. carpentariae*. In this species both the juvenile and adult life-stages appear to prefer very shallow waters (0-3m).

#### 4.4 Discussion

Tropical anchovies generally inhabit continental shelf waters, with most species preferring shallow nearshore waters (Dalzell 1986, Whitehead *et al.* 1988). Within this zone different anchovy species can have distinct habitat preferences (Tham 1972, Dalzell 1986), and this may be a factor which facilitates the diversity of species along tropical coastlines. There is some scientific information on the habitat preferences of anchovies in the coastal waters of Indo-Pacific countries (Tham 1972, Dalzell 1986, Conand *et al.* 1985). However, at present there is little detailed information on the age-specific habitat preferences of tropical anchovies, particularly the interaction of shallow nearshore habitats such as beaches and mangroves with adjacent subtidal habitats.

During the present study, anchovy were collected from two types of coastal intertidal habitat (0-2m), and from the adjacent subtidal habitat to 12m in Cleveland Bay. In the trawl samples, there was a marked decrease in catches of anchovy at depths greater than 7m indicating that the anchovy fauna of Cleveland Bay exhibits a preference for relatively shallow waters. Rainer (1984) found a similar depth range for anchovies during an extensive trawl survey at depths of 5-30m in the Gulf of Carpentaria. He showed that the four species of anchovy (*Stolephorus tri*, *Thryssa kammalensis*, *T. setirostris* and *T. hamiltoni*), mostly occurred at depths less than 10m. Studies in other parts of Australia and the Indo-Pacific indicate that anchovies can occur at greater depths than found in the present study. Ramm *et al.* (1990) collected some individuals of *Thryssa setirostris* and *T. hamiltoni* as deep as of 30-50m in the Gulf of Carpentaria and Arufura sea. Shamsul Hoda (1983) found that the best catches of *Thryssa mystax* occurred at 50-60m along the coast of Pakistan. Fishing for anchovy on the coast of India occurs at depths down to 40m (Luther 1979). Chullasorn and Martosubroto (1986) listed the depth ranges of several species of *Stolephorus* as being 5-45m.

Comparisons of the catches from nearshore shallow habitats and subtidal habitats during this study indicated that some degree of age-specific habitat partitioning was occurring in the larger species of anchovy. Juveniles of these species were common in shallow habitats (beaches, mangrove estuaries or both), and adults were mostly caught in adjacent deeper waters with trawl nets. Species with this distribution were, *S. commersonii*, *T. aestuaria*, *T. setirostris* and *T. hamiltoni*. In other species, juvenile and adult distributions overlapped with both occurring in relatively shallow water. Peterson (1956) also found age-specific depth differences in *Anchoa macrolepidota* in the gulf of Nicoya. Juveniles up to 70mm (TL) were caught in seine nets along beaches after which they moved to deeper water and were caught in trawl samples. Ramirez *et al.* (1989) showed that anchovies in the Gulf of



Nicoya spawned in shallow coastal waters and the larvae and juveniles moved into estuaries. These findings emphasise the importance of shallow nearshore habitats as nursery grounds for juvenile tropical anchovies.

Blaber and Blaber (1980) caught two of the anchovy species examined in the present study during a study of the fish communities in different habitats in Moreton Bay (sub-tropical Queensland). These authors collected adult *T. hamiltoni* at only one out of four of their sites, Deception Bay. This habitat is tidal (3m depth), fringed with mangroves and has a muddy substrate, and is therefore similar to Cleveland Bay. Adults were not caught in a nearby estuary, this being consistent with the apparent absence of adult fish in estuaries during the present study. Another species, *S. carpentariae* occurred both within the estuary site and in Deception Bay indicating a preference for shallow water as found in the present study (Blaber and Blaber 1980). The absence of anchovy at other habitats sampled in Moreton Bay (areas of sandy substrate, seagrass beds and oyster banks), indicates that these species prefer muddy substrates. Blaber and Blaber (1980) also studied the factors which influenced the distribution of juvenile fish in several nearshore habitats in Moreton Bay. Variation in turbidity was most strongly correlated with juvenile and adult distribution in this area. These authors suggested that turbid waters may be richer in plankton and therefore attractive to planktivorous fish. Substrate type and depth are most closely linked to turbidity. In addition, the calm water of inshore habitats and the reduced number of predators may also be important factors (Blaber and Blaber 1980).

Juveniles of several species examined in the present study were common in mangrove estuaries (*S. nelsoni*, *S. commersonii*, *T. aestuaria*, *T. hamiltoni*). Larger numbers of *Stolephorus commersonii* juveniles than those of other species were collected in mangroves compared to beaches early in the recruitment season, and this suggests that mangroves may be important nursery areas for very young *S.*

*commersonii*. Several studies have shown that juvenile anchovies and clupeids are amongst the dominant species in mangrove estuaries in the tropical Pacific region (Robertson and Duke 1987, Robertson and Duke 1990, Tzeng and Wang 1992). Robertson and Duke (1987 and 1990) found that juveniles of *Stolephorus nelsoni*, *Thryssa brevicauda* (= *T. aestuaria*), and *T. hamiltoni* were common in Alligator Creek, a mangrove estuary near Townsville. Juveniles of *T. hamiltoni* were present for 11 months of the year in Alligator Creek indicating that these may spend a considerable time period in mangrove nursery systems (Robertson and Duke 1990).

In the present study, the only species for which adults were caught in large numbers in mangroves were *E. devisi* and *S. carpentariae* and this only occurred in May 1989, suggesting that their movement into estuaries is irregular. Robertson and Duke (1987 & 1990) also recorded adult *E. devisi* and *S. carpentariae* in the Alligator Creek estuary at a similar time (peak in April), and suggested that these species periodically enter estuaries from nearby shallow water habitats. Blaber (1980) caught adult *T. hamiltoni* in trinity Inlet (a tropical estuary at Cairns, North Queensland), indicating that adults of this species may also occur in estuaries. However, the overall low incidence of adult anchovies of most species collected in mangroves during the present study suggests that these habitats are generally avoided by adult anchovy in preference for beach or subtidal habitats.

There were marked seasonal variations in the catches of most species in the present study. The low catches of anchovy in seine nets and trawl shots in the warm months of December and January, may be related to water temperature. Rainer (1984), during an extensive trawl study in the Gulf of Carpentaria, found that a number of inshore fish species moved further offshore during the warmest months. In the present study *Thryssa spp.* were collected at 10-12m in October 1988 (catches in autumn/winter were mostly shallower than 7m), supporting the possibility of a seasonal movement to deeper water. Blaber and Blaber (1980) found that catches of

*T. hamiltoni* in shallow water in Moreton Bay were also strongly seasonal with most fish caught in Autumn. Tiews *et al.* (1970) and Muller (1977) also found evidence of limited offshore migrations for spawning in several stolephorid anchovies.

Salinity has been noted as an important factor affecting the distribution of tropical anchovies (Tham 1972, Dalzell and Ganaden 1987). Lowered salinities due to rainfall have been implicated with the offshore movement of tropical stolephorid anchovies (Tham 1972). The larger catches of *S. insularis* and *E. devisi* in nearshore habitats (mangroves and beaches) in the dry season may reflect a preference by these species for higher salinities. Several authors have suggested that *E. devisi* is not tolerant of low salinity water (Tham 1972, Dalzell 1986). *E. devisi* was regularly caught in subtidal trawl samples during the present study and was also the commonest species caught during several sampling trips at Horseshoe Bay, Magnetic Island (a coralline environment). These results are consistent with previous observations that *E. devisi* prefers higher salinities and coralline environments (Dalzell 1986). Turbidity may also be important for influencing the depth distribution of *E. devisi* and *S. insularis*. Blaber and Blaber (1980) identified 'turbid' and 'clear water' species in Moreton Bay, and showed that clear water species move into shallow habitats in winter when turbidities are lower.

Another factor that is thought to regulate anchovy distributions are the feeding habits of individual species (Tham 1972, Dalzell and Ganaden 1987). Data on the feeding preferences of anchovies in the Townsville region is available (Hoedt 1984). Hoedt (1984) showed that the sergestid shrimp (*Acetes sibogae australis*) is an important food item for several species of anchovies in nearshore habitats. These include *S. nelsoni*, juvenile *S. commersonii* and juvenile *T. hamiltoni*. *S. carpentariae* and juvenile *T. aestuaria* also periodically feed on *A. sibogae* (Hoedt Unpublished data). *A. sibogae* is a shallow water shrimp and is most abundant in

mangroves and shallow coastal waters (Xiao and Greenwood 1992). Robertson and Duke (1987) and Jackson (1991) both found that *A. sibogae* undergoes large seasonal fluctuations in abundance in estuarine habitats. Jackson (1991) presented evidence that peak abundances of *A. sibogae* occur in the cooler months from April to September in estuaries at Townsville. The high abundance of *A. sibogae* in nearshore waters at this time may partly explain the higher catches of anchovy in the seine nets in the autumn and winter months.

Table 4.1. A summary of the number of sample trips each month at the two shallow habitat types in Cleveland Bay.

		1988	1989	1990	1991	Total
Mangrove	J	4	1	0	2	7
	F	2	2	0	1	5
	M	3	2	0	1	6
	A	2	2	0	1	5
	M	3	3	0	1	7
	J	0	2	0	0	2
	J	2	0	0	1	3
	A	1	1	0	1	3
	S	0	0	0	0	0
	O	1	0	0	0	1
	N	0	1	0	0	1
	D	1	0	2	0	3
<b>Totals</b>		<b>19</b>	<b>14</b>	<b>2</b>	<b>8</b>	<b>43</b>
Beach	J	1	1	0	3	5
	F	5	1	1	3	10
	M	1	2	4	2	9
	A	3	2	1	1	7
	M	2	3	1	1	7
	J	1	9	1	0	11
	J	2	5	0	1	8
	A	2	9	3	0	14
	S	0	3	5	0	8
	O	1	3	0	0	4
	N	3	1	4	0	8
	D	2	1	2	0	5
<b>Totals</b>		<b>23</b>	<b>40</b>	<b>22</b>	<b>11</b>	<b>96</b>

Figure 4.1. Total numbers of juveniles and adults of four anchovy species caught each month at three habitat types (mangrove estuary, beach and subtidal or trawl). Data for each month are pooled for the period 1988-1991. (a) *Stolephorus insularis* juveniles; (b) *S. insularis* adults; (c) *Encrasicholina devisi* juveniles; (d) *E. devisi* adults; (e) *Stolephorus carpentariae* juveniles; (f) *S. carpentariae* adults; (g) *Stolephorus nelsoni* juveniles; (h) *S. nelsoni* adults.

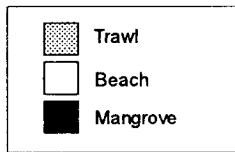
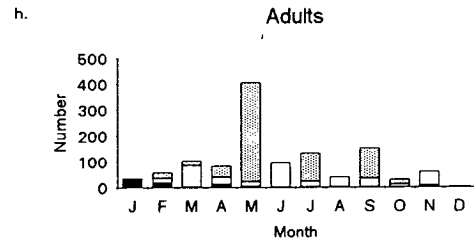
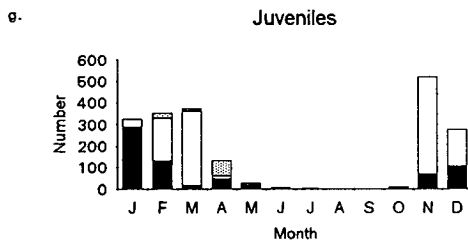
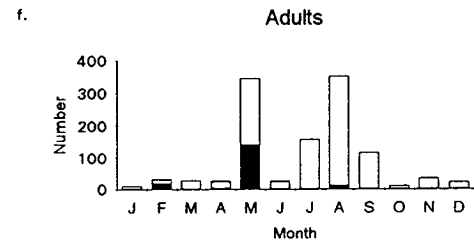
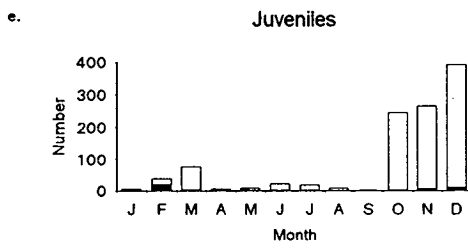
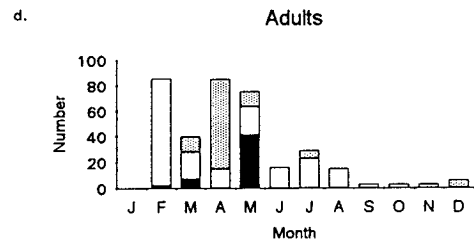
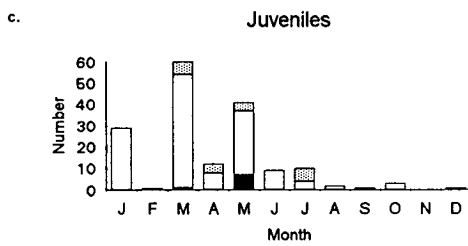
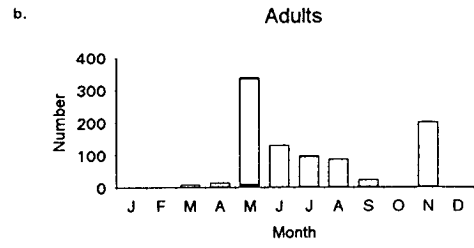
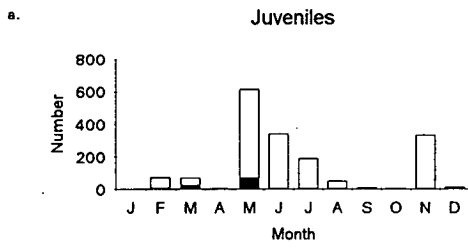
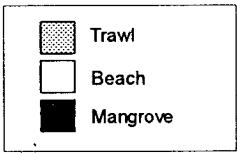
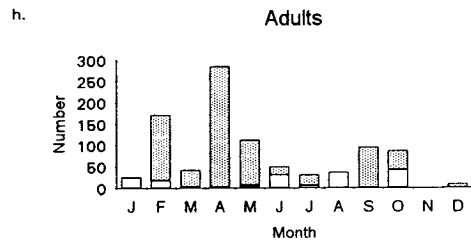
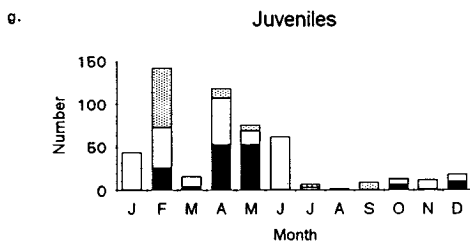
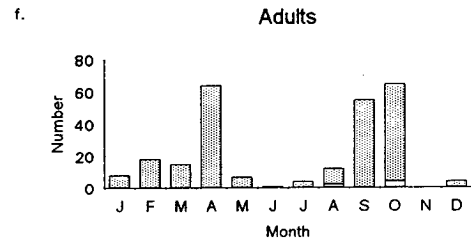
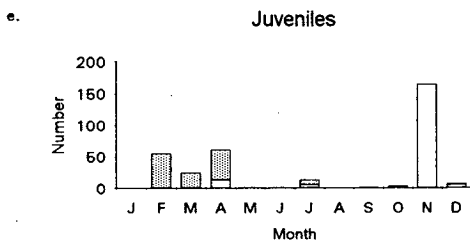
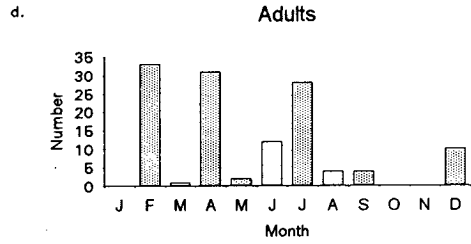
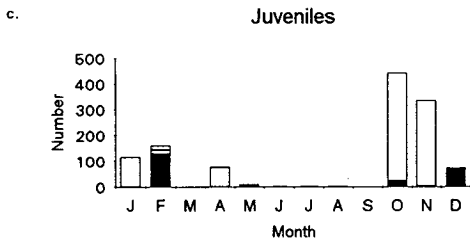
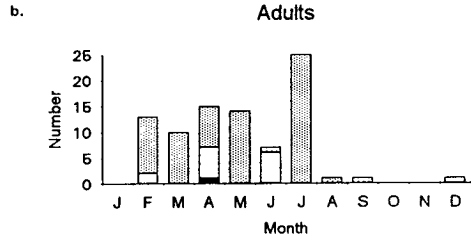
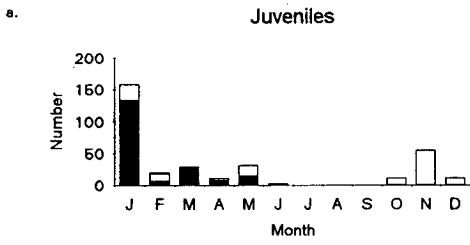


Figure 4.2 Total numbers of juveniles and adults of four anchovy species caught each month at three habitat types (mangrove estuaries, beaches and subtidal or trawl). Data for each month pooled for the period 1988-1991. (a) *Stolephorus commersonii* juveniles; (b) *S. commersonii* adults; (c) *Thryssa aestuaria* juveniles; (d) *T. aestuaria* adults; (e) *Thryssa setirostris* juveniles; (f) *T. setirostris* adults; (g) *Thryssa hamiltoni* juveniles; (h) *T. hamiltoni* adults.





## CHAPTER 5. PRIMARY GROWTH INCREMENTS IN OTOLITHS

### 5.1 Introduction

The Indo-West Pacific region contains a diverse anchovy fauna. Length-frequency information has been used to estimate growth in most economically important species but otolith-based ageing methods have only been applied to a small number of stolephorid anchovies. A number of possible biases can occur when length-frequency analysis is applied to small tropical fish with extended spawning seasons (Dayaratne and Gjøsaeter 1986, Brothers 1979, Milton *et al.* 1990b, Wise and Potter 1995). These largely result from the absence of clear modal progressions which in turn is due to the short lifespan and continuous reproduction of these species (Brothers 1979). Primary otolith increments have been used to obtain accurate age estimates for larval and juvenile fish (see Campana and Neilson 1985) and these structures should enable both age and longevity to be estimated in short-lived species. However, the periodicity of growth increment formation needs to be established prior to using these structures.

Otolith microstructure has been used in age and growth studies on larval and juvenile temperate anchovies (eg. Brothers *et al.* 1976, Methot and Kramer 1979, Methot 1983, Leak and Houde 1987, Mitani 1988, Zastrow *et al.* 1991), and for some species of tropical stolephorid anchovies (Struhsaker and Uchiyama 1976, Gjøsaeter *et al.* 1984, Milton *et al.* 1990b, Wright *et al.* 1990). Struhsaker and Uchiyama (1976) were able to validate the daily periodicity of primary otolith increments for the small tropical anchovy, *Stolephorus purpureus* and were able to age this species over its entire length-range. Subsequent to Struhsaker and Uchiyama's (1976) work there have been no conclusive validations of primary otolith increments in tropical anchovies. Milton *et al.* (1990b) attempted to validate primary otolith increments in stolephorid anchovies from the Solomon Islands but their results were inconclusive due to the high aquarium mortality of these delicate fish. Gjøsaeter *et al.* (1984) and Wright *et al.* (1990) both reported difficulties in

the interpretation of primary otolith increments in stolephorid anchovies. Gjøsaeter *et al.* (1984) observed large growth increments interspaced by smaller ones and had difficulty distinguishing which were likely to represent daily growth increments described for other marine fish species. These problems need to be addressed if further progress is to be made in the use of otolith microstructure for this group of fishes.

In the present study, growth increments analogous to the 'daily growth increments' reported in otoliths from other marine fish species are examined in juvenile through to adult stages of eight species of anchovy. Experiments are conducted to determine the periodicity of these growth increments. Counts of primary otolith increments are then used to analyse growth in length and weight for each of the study species. Inter-species comparisons of growth are made for the study species.

## 5.2 Materials and methods

### 5.2.1 Preparation and reading of otoliths

In anchovies less than 30-40mm TL, sagittal otoliths were whole-mounted in crystal bond thermoplastic cement and counted at 400X magnification. Sagittae from larger fish required grinding and polishing to allow counting of primary otolith increments. Otoliths from juvenile and adult *Encrasicholina* and *Stolephorus* species and juvenile *Thryssa* species were attached to a microscope slide with thermoplastic cement and hand-ground on the proximal and distal faces (terminology follows Pannella 1980), using wet carborundum paper of grades 800 to 1200. A section of approximately 0.05-0.2mm including the nucleus was suitable for counting growth increments. Both surfaces were polished with 0.05µm grade wet alumina powder prior to counting. Primary otolith increments in this type of section were counted from the nucleus to the anti-rostrum.

Otoliths from large juvenile and adult *Thryssa spp.* were sectioned transversely as this method improved the clarity of the narrow growth increments in older fish. To produce a transverse section, the distal face of the otolith was glued against a microscope slide with the rostrum protruding past the end of the slide. The otolith was then orientated so that the edge of the slide was in line with the nucleus and the tip of the anti-rostrum. The anterior end of the otolith (the rostrum) was then ground away while holding the slide vertically until the grinding plane approached the nucleus. The otolith was then re-glued with the ground anterior face against the slide so that the otolith stood at 90° to the slide with the posterior end upwards. The posterior end was ground until a transverse section of desired thickness which included the nucleus remained. Unless otherwise specified all growth increment counts in sectioned sagittae were made at 400x magnification.

## 5.2.2 Determination of primary otolith increment periodicity

### 5.2.2.1 Aquarium studies

Live fish were collected from beach seine samples by carefully bucketing fish from the 5mm knotless mesh seine net while it was still in the water. This method reduced direct contact between the fish and the net, reducing mortality due to the loss of scales and stress. Live fish were then transported in 20 litre buckets (with portable aerators) to the laboratory. At the laboratory, the container was floated in a 300 or 1000 litre seawater aquarium to equalise temperatures prior to release in the main aquarium. Samples of live fish were either released immediately into the aquarium or were first kept in a solution of tetracycline hydrochloride. All fish were maintained in the aquaria until they died naturally. The aquarium was inspected twice daily and any dead fish removed. Aquarium-held anchovy were fed twice per day on live shrimp (*Acetes sibogae australis*) and finely chopped prawn flesh.

Fish to be marked with tetracycline were placed in a 250mg/litre solution of tetracycline hydrochloride for 4-12hr. prior to release into the aquarium. The

otoliths were dissected from these fish when they died and these were prepared for growth increment examination. Tetracycline was incorporated into the otoliths of fish held in the solution, being visible as a fluorescent ring in the otolith when viewed using a high power ultra-violet light microscope. In all of the fish that were treated with tetracycline the fluorescent ring was accompanied by a distinct microstructural growth check which could be seen using normal light microscopy. The periodicity of increment formation of aquarium-held fish was determined by comparing the number of growth increments formed after the tetracycline band or growth check with the number of days that the fish survived following tetracycline immersion.

Survivorship rates were low during tetracycline treatments due to the sensitivity of anchovies to stress. Therefore an alternative method of validating primary otolith increment deposition rates was attempted for fish that had not been subjected to tetracycline treatment. Here the presence of a 'capture stress mark' and/or a change in increment structure in the otolith which would serve as a temporal marker corresponding to the day of capture and the time period in the aquarium was used. This was considered possible because in tetracycline-treated fish, a check mark and narrower primary increments were associated with the day of capture and aquarium holding respectively. Primary increments in otoliths from these fish were counted and measured (widths) from the otolith margin inwards. Each increment was assigned a date of formation with the assumption that each represented one day's growth. Increment width was then plotted against estimated date of formation for all fish in a sample. If clear changes in otolith microstructure were associated with primary otolith increments corresponding to events occurring on known dates this would suggest that growth increments were being deposited on a daily basis in the aquarium.

#### 5.2.2.2 Evidence from field samples

Following the reasoning of Dayaratne and Gjøsaeter (1986), the periodicity of growth increments in otoliths was determined by comparing growth increment counts in samples of fish assumed to belong to a cohort, collected on successive dates. This was done for juvenile *Thryssa aestuaria* collected between October 1990 and January 1991. The assumption that these fish belonged to a single cohort was based on several lines of evidence. Firstly, fish in each sample were of similar sizes and the mean size of individuals increased in successive samples. Secondly, length-frequency data for *T. aestuaria* collected during the three year period of the study indicates that this species has a short recruitment period as samples of recruits generally comprised a narrow size-range in a given month. These observations support the assumption that these fish were born within a short time-interval.

Growth increments were counted in the left sagitta from 20 fish randomly selected from each of the three samples. The mean increment count for pairs of successive samples were subtracted and this value was compared to the known time interval that elapsed between these collection dates. Close agreement between the difference in the mean increment count in two samples and the time elapsed between these samples would suggest that growth increments were formed at a daily rate at sea.

A statistical analysis of this data was also applied. The otolith increment count for each of the 60 fish (20 from each of the three sample dates) was plotted against the number of days elapsed between the date of capture of each individual and an arbitrarily chosen date (1-9-90). If the assumption that the fish from these three samples were from the same cohort (ie. born at approximately the same time) was true and growth increments in these otoliths were deposited daily, then the slope of this plot should equal one. A t-test (Zar 1984), was used to determine if it differed significantly from one. A slope not significantly different from one would be

interpreted as suggesting a growth increment deposition rate of one per day for this cohort of fish in the field. The statistical power of the regression to detect deviations of the slope from one was tested following the method of Rice (1987).

### 5.2.3 Fitting growth curves

Length was plotted against age from primary otolith increment counts for each of the study species. As length-age plots were linear over at least the smaller size-range for each species, a comparative study of the linear growth phase was undertaken for the study species. To determine the appropriate size-range to use in this comparison straight lines were fitted to length-age plots for each species and data points for larger fish were removed until the  $r^2$  value reached a maximum value. Length-age plots were linear over all sizes in *E. devisi* and *S. insularis* (the two smallest species). Growth rate comparisons in juveniles were only made using age estimates for fish collected in the warm months of the year (October-April) to reduce variability in growth associated with seasonal differences in water temperature.

Growth curves were also fitted to length-age plots from otolith increments for each species over the full size-range aged. Linear regressions and von Bertalanffy growth curves (VBGC) were fitted to the data for each species. Linear regressions were fitted using the least squares method and iterative least squares non-linear curve fitting was used to fit VBGC's. The growth curve (linear or VBGC) with the lowest sum of squares was chosen to describe the length-age relationship for each species.

The VBGC used in this study was a reparameterised form of the equation (Francis 1988). This form of the equation allows curve fitting within specified size and age-range and therefore avoids extrapolation beyond the data (Milton *et al.* 1991). For small tropical baitfish this form of the VBGC produces biologically meaningful

estimates of  $L_{\infty}$ ,  $K$  and  $t_0$ , enabling inter-species comparisons to be made (Milton *et al.* 1991, Milton *et al.* 1993). Francis (1988) modified the equation of Schnute and Fournier (1986) as follows:

$$L_t = L_1 + (L_3 - L_1) * (1 - r^{2(t-\phi)/(\omega-\phi)}) / (1 - r^2) \quad (5.1).$$

Here,  $r = (L_3 - L_2) / (L_2 - L_1)$ ,  $L_t$  is the mean length of a fish at age  $t$  and  $L_1$ ,  $L_2$  and  $L_3$  are the length at the lower, middle and upper limits of two arbitrary ages  $\phi$  and  $\omega$ . The three lengths were chosen within the size-range aged for a species, this avoiding extrapolations beyond the data. The two ages  $\phi$  and  $\omega$  put in the equation, were selected from within the range of ages estimated from otolith increment counts for each species. The parameters of equation 5.1 were estimated using a computerised iterative least squares method for fitting non-linear regressions. The VBGC parameters  $L_{\infty}$ ,  $K$  and  $t_0$  were calculated from the final parameters of equation 5.1 using the conversions provided by Francis (1988).

#### 5.2.4 Statistics

Linear regressions were compared using a t-test to detect differences in slopes and elevations (Zar 1984). Exponential curves were compared by first log-transforming the data, fitting a linear regression to the data and performing a t-test as above.

### 5.3 Results

#### 5.3.1 Validation of growth increment periodicity

##### 5.3.1.1. Aquarium experiments

Anchovies collected on 13 occasions between April 1989 and April 1991 survived transportation to the aquarium (Table 5.1). A total of 138 individuals belonging to six species were placed in the aquarium. These were: *E. devisi*; *S. insularis*; *S. carpentariae*; *S. nelsoni*; *T. aestuaria*; *T. hamiltoni* and *T. baelama*. Of these only 62 individuals of the following species: *E. devisi*; *S. carpentariae*; *S. nelsoni*; *T. aestuaria* and *T. baelama* survived for longer than 24 hours (Table 5.1).



A total of 96 fish were placed in 250 mg/litre tetracycline hydrochloride in seawater prior to release into the aquarium. Mortality rates were high with only 9 individuals surviving the treatment (Table 5.1). Initially anchovies were kept in the tetracycline solution for 10-12 hours. However, this was reduced to 4-7 hours for some samples in an attempt to improve the survival rates amongst tetracycline-treated fish.

The first fish to survive after immersion in tetracycline were three *S. nelsoni* individuals caught on 26-4-90. Two of these survived for four days and the remaining fish survived for five days following the treatment (Table 5.2). The otoliths from these fish had 4-5 growth increments after the tetracycline mark, this being close to the number of days the fish spent in the aquarium following immersion (Table 5.2). On 15-8-90, four *S. carpentariae* individuals were immersed for eight hours in tetracycline. These fish died in the aquarium 24-32 hours after removal from the tetracycline solution. Otoliths from these fish all contained a fluorescent ring when viewed with ultra-violet light microscopy and a single growth increment was formed after this ring. Therefore one growth increment was formed in the 24-32 hour period after tetracycline treatment.

On 28-11-90, two *T. aestuaria* individuals were immersed for four hours in a tetracycline solution and then transferred to a holding tank. Both individuals were immersed a second time in tetracycline solution 20 days later (18-12-90), this time for seven hours. One of the fish died within 24 hours of the second exposure and the other survived for a further 37 days (until 24-1-91). The sagittae from the first fish which lived for 20 days following the first tetracycline treatment were examined with a high power ultra-violet light microscope. Both sagittae contained a narrow fluorescent ring some distance in from the otolith margin and a microstructural growth check was associated with this fluorescent ring (Fig. 5.1a&b). Growth increment counts from the growth check to the margin in the

sagitta ranged from 19-20 (Fig. 5.1a&b). This was in close agreement with the number of days the fish survived in the aquarium since the treatment (Table 5.2). The sagitta and asteriscus from the second specimen (this fish survived 57 days after the first treatment), were examined using ultra-violet light microscopy. Both otoliths contained two parallel fluorescent bands, each of which coincided with a microstructural growth check (Fig. 5.1c). Growth increment counts between the two growth checks and from the second check to the margin ranged from 19-20 and 36-38 respectively (Table 5.2). These primary otolith increment counts were close to the known time interval in days between the two marking experiments and from the second marking to the fish's death respectively (20 and 37 days-Table 5.2). Therefore the tetracycline marking experiments indicate that primary otolith increments were deposited with a daily periodicity for these fish in the aquarium.

Survivorships were higher for anchovy that were not treated with tetracycline prior to release into the aquarium (90% compared to 9% in tetracycline treated fish). Several species of anchovy that were not treated with tetracycline survived for periods of several weeks (Table 5.1). However, most of these were mature-sized individuals and growth increments near the otolith margin were too narrow to examine for changes in increment width. The otoliths from a mixed sample of juvenile *E. devisi* (n=14) and *S. carpentariae* (n=2) collected on 11-4-90 and held in the aquarium for between 9 and 24 days were suitable for an analysis of growth increments at the otolith margin. Primary increments in these otoliths were wide and easily discernible suggesting that growth was fast prior to capture. The structure of the marginal primary otolith increments strongly suggested that capture and aquarium holding had altered the otolith microstructure in all individuals. Firstly, in most otoliths from these fish there was a microstructural growth check on or close to the increment that corresponded to the date of capture. Additionally, primary otolith increments back-calculated to have formed subsequent to the date of capture were narrower than increments estimated to have been deposited at sea

prior to capture in all fish (Fig. 5.2, Table 5.3). Narrow primary otolith increments were back-dated to have commenced forming between 10-4-90 and 13-4-90 with most at 12-4-90, the day after capture (Table 5.3). The mean widths of the three primary otolith increments before and after the transition in structure was 8.5 and 3.3  $\mu\text{m}$  respectively and the mean change in width was 5  $\mu\text{m}$  (Table 5.3).

#### 5.3.1.2 Growth increment deposition in a cohort of juvenile *Thryssa aestuaria*.

Three beach seine samples collected between October 1990 and January 1991 contained large numbers of *T. aestuaria* juveniles. The first sample taken on 17-10-90 was comprised of 125 fish with a modal length of 25mm. Subsequent samples on 6-12-90 (n=63) and on 4-1-91 (n=125) had modal lengths of 47mm and 65mm (Fig. 5.3). The mean number of growth increments in otoliths from fish in each of these samples are given in Table 5.4. The variation between increment counts in fish in a particular sample was small suggesting that fish in each sample were of a similar age (Table 5.4). The difference in the mean otolith increment count for fish from the first two samples (17-10-90 and 6-12-90) was 49.9 increments and the difference in fish collected on 6-12-90 and 4-1-91 was 31.7 increments. These differences were close to the elapsed time interval between each of the pairs of successive samples (51 days for samples 1 and 2 and 29 days for samples 2 and 3). The close agreement between the number of days between samples and the increase in mean growth increment number suggests that if the fish from these samples belonged to a single cohort, then growth increments in the sagitta were formed on a daily basis (Dayaratne and Gjøsaeter 1986, Campana and Neilson 1985).

The slope of a plot of growth increment counts in fish from these three samples versus the number of days between the date of capture of each fish and an arbitrarily fixed date (1-9-90) was 1.041 (Fig. 5.4). The slope was found to not differ significantly from one (t-test  $0.01 < P < 0.05$ ), suggesting that growth increments were deposited at a rate of one per day. Using the method of Rice

(1987), the probability of detecting a difference of 0.1 from the expected slope of one was calculated as being 0.99. This high probability indicates a high confidence level for these results.

#### 5.3.1.3 Summary of growth increment periodicity validation

Tetracycline labelling experiments demonstrated daily deposition of primary otolith increments in *Thryssa aestuaria* and *S. nelsoni* over the time periods held captive. The single increment formed in 24-32 hours in the 4 *S. carpentariae* individuals also suggests daily periodicity but longer periods of captivity are necessary for proper validation. Changes in mean number of primary growth increments in successive samples of a probable cohort of *T. aestuaria* in the wild further confirmed the daily periodicity of increment formation in this species. *E. devisi* and *S. carpentariae* individuals held in the aquarium exhibited clear changes in growth increment structure and counts of these altered growth increments suggested they were formed on a daily basis.

Evidence of the daily periodicity of primary otolith increments was demonstrated for four species in this study and given the similarities in otolith microstructure amongst the study species, counts of primary otolith increments were assumed to be indicative of age in days in the remaining chapters.

#### 5.3.2 A description of the primary otolith increments

The growth increments observed in the otoliths from anchovies examined in this study agreed with the descriptions of these structures in other tropical fish species (eg. Pannella 1971, Pannella 1980, Gjsaeter *et al.* 1984, Dayaratne and Gjsaeter 1986, Longhurst and Pauly 1987). Each growth increment consisted of one translucent and opaque zone when viewed with transmitted light (Figs. 5.5&5.6).

Otolith growth increments were sometimes difficult to interpret in a restricted region of the otolith in all of the species studied. The first 30-40 growth increments were narrow and easily counted. However, primary otolith increments numbering approximately 40 to 80-100 were wider (6-12 $\mu$ m), and each contained 2-5 zones which could be confused as being primary increments (Fig. 5.5b). A similar type of increment structure has been described for other stolephorid anchovies (Gjøsaeter *et al.* 1984, Wright *et al.* 1990) and tropical clupeids of the genus *Sardinella* (Dayaratne and Gjøsaeter 1986). Primary increments validated as daily using tetracycline in *T. aestuaria* were closely examined and it was noted that subdaily increments were present within each daily growth increment. These are probably the same as those previously confused as primary (daily) increments (eg. Gjøsaeter *et al.* 1984, Wright *et al.* 1990). If the structure of successive otolith increments was examined from the nucleus outwards it was evident that the wider increments were equivalent structures to other primary otolith increments in the otolith. The wider growth increments in this region retained the contrast of previous narrow increments and could be seen when the microscope focus was changed. In contrast, the subdaily zones could only be seen within a narrow focussing depth range.

Growth increments corresponding to growth in older fish were narrower (2-5 $\mu$ m), and fainter than the 'early juvenile' increments, but were still discernible when viewed with a high-power light microscope (Fig. 5.5 c&d). The narrow growth increments in older fish were easier to read in transversely sectioned otoliths than in surface ground sections (Fig. 5.6). The pattern of increment widths in otoliths from four specimens of *T. aestuaria* is shown (Fig. 5.7). This pattern was characteristic of all anchovy species examined.

### 5.3.3 Growth in juveniles

Length was plotted against the number of primary otolith increments counted in otoliths for the size-range over which linear growth occurred for each species.

Linear regressions were fitted to these length-age plots; the slopes and intercepts of these are given in Table 5.5. Growth rates obtained from the slopes of length versus age plots for juveniles were higher in larger species (Table 5.5). Growth rate was plotted against maximum recorded size for each species to determine if there was a relationship between these variables (Fig. 5.8). A significant linear regression ( $G.R.=0.001847TL + 0.2816$ ,  $r^2=0.63$ ,  $p<0.05$ ), described the relationship between these variables. The fit of this linear regression was improved by removing data for species smaller than 100mm ( $GR.=0.00259TL + 0.136$ ,  $r^2=0.862$ ,  $p<0.05$ ).

Linear regressions suitably described growth over the full size-range in *E. devisi* and *S. insularis* (the two smallest stolephorids in the study area) (Fig. 5.9). In *E. devisi*, significantly different growth was occurring between warmer and cooler months. The slopes of the linear regressions for each of the two periods were significantly different (t-test,  $p<0.05$ ), with growth being faster in the warmer months (Table 5.5).

#### 5.3.4 Growth over all sizes

Growth increments were counted for 44 to 146 individuals of each of eight species belonging to the genera *Encrasicholina*, *Stolephorus* and *Thryssa* (Table 5.6). Total length was plotted against the number of primary otolith increments counted in the sagitta for each of the study species (Figures 5.9 & 5.10). Von Bertalanffy growth curves could not be fitted to length/age data for *E. devisi* collected in the cool months or *S. insularis* due to the absence of an asymptote; linear regressions were consequently chosen to describe growth in this species (Table 5.5, Fig. 5.9). A von Bertalanffy curve was fitted to the length/age data for *E. devisi* collected in the warm months but the fit was not as good as a linear regression; however, the growth parameters for this equation are noted (Table 5.7) for later comparison to length-frequency analyses. Von Bertalanffy growth curves provided the best fit for all remaining species (Table 5.7, Figs. 5.9 and 5.10). Realistic estimates of  $L_{\infty}$  (close

to known maximum size) were obtained for all species except *S. commersonii* (Table 5.7). The high  $L_{\infty}$  estimate may have resulted from the lack of asymptotic curvature in the length-age plot and the paucity of large fish in the samples. Values of K ranged from 0.77 in *S. commersonii* to 7.09 in *S. carpentariae* (Table 5.7).

### 5.3.5 Longevity estimates from primary increment counts

Longevities were estimated for stolephorid anchovies based on the maximum ages obtained from primary otolith increment counts. The oldest individual of *E. devisi* was a 51mm fish caught in winter aged at 95 days. Fish up to the maximum recorded size for this species in Townsville (62mm) were aged in the warmer months but were not older than the oldest specimen aged in the cool months. It is therefore likely that this species has a longevity of 3-4 months.

The largest and oldest *S. insularis* individual aged from primary otolith increments was 62mm long and 126 days old. Based on this information it was concluded that this species is also relatively short-lived, probably not exceeding 4-6 months of age.

For *S. carpentariae*, the oldest individual aged from primary otolith increments was a 67mm individual aged at 158 days. This would suggest a maximum longevity of around 5-6 months for this species. It is thought that large individuals collected in September/October which must have been born late in the previous spawning period and grew to maturity during the winter months, could be older than six months due to the probable slower growth rate in winter. However, adults collected at the end of winter were not aged in the present study.

The oldest *S. nelsoni* individual from the warmer months (November-April) was a 90mm fish aged at 169 days. However, a 70mm individual caught in October (which would have been recruited at the tail-end of the previous spawning season), was aged at 247 days. This individual must have lived through the winter period,

growing slower than individuals which grew to maturity in the warm season. The growth increments in this individual were extremely narrow, reflecting the slow rate of growth in length (Campana and Neilson 1985). Given that *S. nelsoni* can grow to 100mm it is likely that this species lives for six months to one year.

The oldest *S. commersonii* individual aged from primary otolith increments was a 139mm fish aged at 236 days. This species can grow to 160mm in the study area but few individuals of this length were collected. It is therefore likely that *S. commersonii* individuals can survive at least to 1 year of age. The form of growth in length (Fig. 5.10a) suggests that *S. commersonii* completes most of its growth in length in 1 year and probably does not attain 2 years of age.

Primary increments were too compressed in large individuals of *T. setirostris* and *T. hamiltoni* to count, therefore it is considered inappropriate to estimate longevity from these structures. The largest and oldest *T. aestuaria* individual was 120mm and had 348 primary increments in the sagitta which suggests that this species attains at least one year of age. *T. aestuaria* grows to at 142 mm in the study area and therefore probably lives for between 1 and 2 years.

#### 5.3.6 Inter-species comparisons of growth in weight

The relationship between fish weight and age (from primary otolith increment counts), was examined for the study species. Weight was plotted against age on one graph for all species (Fig. 5.11 a). The data points for each species were clustered into one of two distinct groups. Exponential curves were fitted to the weight-age data for each of the two species groupings. The first group ('group 1') with the fastest rate of weight-growth included *E. devisi*, *S. commersonii*, *T. setirostris* and *T. hamiltoni*. The second group ('group 2') with slower weight-growth included *S. carpentariae*, *S. insularis*, *S. nelsoni* and *T. aestuaria*. The equations for the two exponential curves are given below:



Group 1 :  $WEIGHT=5.345 \times 10^{-6} AGE^{2.839}$ ,  $n=207$ ,  $r^2=0.913$

Group 2 :  $WEIGHT=3.29 \times 10^{-5} AGE^{2.319}$ ,  $n=212$ ,  $r^2=0.906$

To test if these curves were significantly different, the data for each of the two groups were transformed to logarithmic values. The log-transformed values were plotted for each group (Fig. 5.11 b), and linear regressions fitted to each. T-tests showed that the slopes were significantly different ( $p < 0.001$ ) but the elevations were not ( $0.2 < p < 0.1$ ). Therefore growth in weight was significantly different between these two species-groups.

#### 5.4 Discussion

The daily periodicity of primary otolith increments has been validated for a range of tropical and temperate clupeoid species. In the tropics most studies have focussed on the family Clupeidae and validated species include *Brevoortia patronus* and *B. tyrannus* (Deegan and Thompson 1987), *Spratelloides delicatulus* (Schmitt 1984), *S. gracilis* (Milton *et al.* 1991), *Herklotsichthys quadrimaculatus* (Williams and Clarke 1983) and *H. castelnaui* (Thorrold 1988). Primary otolith increments have been shown to be daily in the tropical anchovy, *Encrasicholina purpurea* from Hawaii (Struhsaker and Uchiyama 1976), and a few temperate anchovy species including *Engraulis mordax* (Brothers *et al.* 1976) and *Anchoa mitchelli* (Luo and Musick 1991). Given the diversity and economic importance of anchovies in the tropics it is clear that primary otolith increments need to be validated and growth estimated for more species.

In the present study, aquarium experiments and other means of testing the periodicity of primary otolith increment deposition gave evidence that these were daily in *Encrasicholina devisi*, *Stolephorus carpentariae*, *S. nelsoni* and *Thryssa*

*aestuaria*. The daily periodicity of otolith growth increments was most convincingly demonstrated in two individuals of *T. aestuaria* which were shown to deposit daily growth increments over a 20 and 57 day period respectively. These results are consistent with Struhsaker and Uchiyama's (1976) validation of daily growth increment formation in the otoliths of *Encrasicholina purpurea* from Hawaii.

Changes in increment width and structure resulting from capture stress and aquarium holding were used as an alternative method to determine the periodicity of primary increment formation in *E. devisi* and *S. carpentariae* juveniles in this study. The findings of the present study suggest that capture stress resulted in the formation of a check mark within a short time period in juvenile anchovy. Although this method is not as conclusive as tetracycline marking experiments, it may be a useful alternative method for species which are difficult to maintain in aquaria. Check marks have been shown to be induced by stress in the salmon, *Oncorhynchus kisutch* (Campana 1983) and Adams *et al.* (1992) found that primary otolith increments in Arctic charr (*Salvelinus alpinus*) were significantly disrupted when fish were transferred between holding facilities. However, caution must be applied when relating otolith microstructure to temporal events as there may be a time lag between application and appearance on the otolith (Campana and Neilson 1985).

A problem facing workers using otolith increments in age and growth studies on tropical anchovies is the sensitivity of these species to handling, this making aquarium-validation experiments difficult (Luther *et al.* 1984, Milton *et al.* 1990b). Milton *et al.* (1990b) encountered difficulties during attempts to validate increment deposition rates in *Encrasicholina devisi* and *E. heteroloba* from the Solomon Islands. They were only able to keep four out of several hundred fish that were placed in sea cages and aquaria alive. In the present study, two species, *E. devisi*

and *T. aestuaria* were noticeably hardier than others and had high survival rates. *E. devisi* is widely used for live-bait in pole and line fisheries in south Pacific countries (Dalzell and Wankowski 1980, Dalzell and Lewis 1989) and would therefore be expected to tolerate handling stress.

The experimental validation of daily periodicity in growth increments for species in present study helped resolve the problem of defining what constitutes a 'primary otolith increment' in tropical anchovies. In the region of the otolith following the early 'larval' increments (Dayaratne and Gjøsaeter 1986), growth increments increased in width and contained subdaily growth zones which were probably previously confused as daily (Gjøsaeter *et al.* 1984, Wright *et al.* 1990). Gjøsaeter *et al.* (1984) counted both types of increment and suggested that the wider increments in stolephorid anchovies gave growth estimates that were consistent with other studies. In contrast, Wright *et al.* (1990) estimated growth in *Stolephorus heterolobus* by counting the smallest growth increments in the otoliths. These authors were not able to perform validation experiments on captive fish to justify their interpretation. Similar growth increment patterns (wide increments comprised of several narrower zones) have been described in tropical clupeids of the genus *Sardinella* (Dayaratne and Gjøsaeter 1986), and in other unrelated marine fishes (D'Amours and Landry 1990, Prince *et al.* 1991). D'Amours and Landry (1990) conducted validation experiments to determine the period of increment formation in Atlantic mackerel (*Scomber scombrus*) and concluded that the widest growth increments in this species were daily. Dayaratne and Gjøsaeter (1986) also concluded that the wider otolith increments in *Sardinella spp* were equivalent to daily increments described in other marine fishes.

The pattern of length-growth in two of the smallest stolephorid anchovies in the present study was linear. In larger species there was some asymptotic curvature and von Bertalanffy growth functions were fitted to length-age data. Struhsaker and

Uchiyama (1976) found that length-age plots in *Encrasicholina purpurea*, a small anchovy from Hawaii, were linear, this being consistent with the pattern in *S. insularis* and *E. devisi* in this study. In other small tropical clupeoids, length-age plots vary in form (Milton *et al.* 1990b, Milton *et al.* 1991); growth patterns varied with location in small clupeids of the genus *Spratelloides* from the Solomon Islands (Milton *et al.* 1990b). These findings suggest that the growth pattern of small clupeoids is influenced by environment.

A linear growth phase was evident from length-age plots for all of the species studied. This is consistent with growth patterns derived for other species of anchovy aged from primary otolith increments (Brothers *et al.* 1976, Mitani 1988, Wright *et al.* 1990). Growth rates (length in mm/day) during this phase were found to range from 0.34-0.78 mm/day in the study species. These compare favourably with the reported growth rates of other tropical and temperate clupeoids aged from primary otolith increments. Struhsaker and Uchiyama's (1976) study of growth in *Stolephorus purpureus* indicate a growth rate of around 0.33 mm/day for this species. Mean daily growth rates for *Brevoortia patronus* and *B. tyrannus* from the Gulf of Mexico were estimated as ranging from 0.33 to 0.62 mm/day (Deegan and Thompson 1987). Similar growth rates (0.44-0.5mm/day) were also estimated in the temperate Bay Anchovy, *Anchoa mitchelli* (Zastrow *et al.* 1991).

The von Bertalanffy growth parameters 'L<sub>∞</sub>' and 'K', has been calculated for many tropical clupeoids, most frequently using length-frequency analyses. The ability of length-frequency analysis to give meaningful estimates of growth parameters for small tropical clupeoids has been questioned because of biases that arise from their life-history traits of continuous reproduction and short lifespan (Milton *et al.* 1990, Milton *et al.* 1991, Milton and Blaber 1991, Wise and Potter 1995). Thus otoliths may provide better estimates of growth in these species. Values of K estimated in this study from primary otolith increments ranged from 0.77 to 7.1 with a mean of

3.0 in the seven species for which von Bertalanffy growth functions could be fitted.

The highest value (7.1) was for the smallest species, *S. carpentariae*; *E. devisi* in this study also had a high K value at 4.45. Milton *et al.* (1993) also estimated high K values for the small clupeid *Spratelloides delicatulus* from various locations in the tropics (range of 2.7-14).

Growth in length and weight were both faster in large than small species examined in the present study. The only exception to the pattern was weight-growth in *E. devisi* which appeared faster than the other small anchovy species. However, the individuals of this species that were aged were from a narrow size-range, therefore this result should be viewed with caution. The finding that groups of species exhibited very similar patterns of growth in weight suggests that weight-growth patterns may be conservative at an inter-species level in tropical anchovies.

Weight-age relationships are not routinely examined for marine fishes. Milton *et al.* (1993) examined the weight-age relationships in three species of clupeids from Kiribati. These authors found that growth in weight varied between sites in *Herklotsichthys quadrimaculatus*, suggesting that environment may influence growth in weight. The largest species examined by these authors, *Amblygaster sirm*, exhibited two phases of weight-growth with a marked increase in the rate of weight-gain after 150 days of age. *A. sirm* ( $L_{\max}=230$ ) grew more rapidly in weight than a smaller species *H. quadrimaculatus* ( $L_{\max}=110\text{mm}$ ) during this phase. This is consistent with the finding of different rates of weight growth in different-sized species in the present study.

Primary otolith increment counts were suitable for estimating longevity in the smaller species aged during the present study. The three smallest species had longevities ranging from three to six months which is consistent with other otolith-based studies on similar-sized tropical clupeoids (Struhsaker and Uchiyama 1976,

Milton *et al.* 1991, Milton *et al.* 1993). Otolith-derived ages indicate that the larger stolephorid species, *S. nelsoni* and *S. commersonii* can live to approximately one year of age and *T. aestuaria* lives for 1-2 years. These results confirm previous suggestions that most small to medium-sized tropical anchovies complete their life-cycle within one year (Conand 1985, Lewis 1990).

Table 5.1. Details of the aquarium experiments for determining the periodicity of primary otolith increment formation. The table is divided into three sections: (1)-tetracycline treated fish which lived for 24 hours or more after treatment; (2) non-tetracycline treated fish that also lived for 24 hours or more; and (3) fish from both treatments which died within 24 hours and were therefore not used for validation studies. (n)- number of fish; (imm.)-tetracycline immersion time; (n.s.)-the number of fish surviving after 24 hours; (l.s.f.)- longest surviving fish from the sample.

1. Tetracycline-treated fish

Date	species	n.	imm. (hrs.)	n.s.	l.s.f. (days)
26-4-90	<i>S. nelsoni</i>	5	12	3	5
15-8-90	<i>S. carpentariae</i>	4	8	4	1
28-11-90	<i>T. aestuaria</i>	3	4	2	57

2. Not tetracycline-treated (survivors)

Date	Species	n	n.s.	l.s.f. (days)
17-4-89	<i>T. aestuaria</i>	15	15	17
11-4-90	<i>S. carpentariae</i>	2	2	22
11-4-90	<i>E. devisi</i>	19	16	24
11-4-90	<i>S. nelsoni</i>	4	3	1
24-4-91	<i>T. baelama</i>	1	1	174

3. Fish from both treatments that did not survive

Date	Species	n.	tetracycline	imm. (hrs.)
5-2-90	<i>S. insularis</i>	20	yes	-
1-3-90	<i>S. carpentariae</i>	6	yes	8
9-3-90	<i>T. aestuaria</i>	1	yes	12
14-8-90	<i>S. carpentariae</i>	46	yes	12
14-8-90	<i>S. insularis</i>	2	yes	12
14-8-90	<i>E. devisi</i>	1	yes	12
15-8-90	<i>S. nelsoni</i>	1	yes	8
4-1-90	<i>T. aestuaria</i>	7	yes	6
24-4-91	<i>T. hamiltoni</i>	1	no	-

Table 5.2. Comparisons between the number of primary otolith increments and time elapsed after tetracycline marking in individual fish. Growth increments were counted from a tetracycline band to the next region of an otolith of known time of formation (the otolith margin or a subsequent tetracycline band). The data for four *S. carpentariae* individuals which only lived for 24 hours after marking is not shown.

Species	Date	Survival time (days)	Increments
<i>S. nelsoni</i>	26-4-90	4	5
<i>S. nelsoni</i>	26-4-90	4	4
<i>S. nelsoni</i>	26-4-90	5	4
<i>T. aestuaria</i> (spec. 1)	28-11-90	20	19-20
<i>T. aestuaria</i> (spec. 2)	28-11-90	20	19-20
<i>T. aestuaria</i> (spec. 2)*	18-12-90	37	36-38

\* second marking



Table 5.3. Back-calculated dates when narrow increments commenced in the sagitta of fourteen *E. devisi* and two *S. carpentariae* (Nos. 1&2) individuals caught and held in an aquarium from 11-4-90. The mean width (all widths in  $\mu\text{m}$ ) of the three increments prior to the first narrow increment and of the first three narrow increments are given (width1 and width 2).

Spec. No.	Date of narrow incs.	Width 1	Width 2	Width change
1	11-4-90	3.9	1.53	2.37
2.	13-4-90	6.2	3.5	2.8
3	12-4-90	7.1	4.4	2.8
4	12-4-90	6.6	3.1	3.6
5	12-4-90	6.1	4.3	1.8
6	12-4-90	4.8	1.8	3.1
7	10-4-90	3.6	1.3	2.3
8	12-4-90	4.8	1.8	3
9	10-4-90	12	4.1	7.9
10	11-4-90	8.4	2.8	5.6
11	12-4-90	10.2	6.6	3.6
12	13-4-90	10.2	5.4	4.8
13	11-4-90	10.2	2.55	7.7
14	12-4-90	10.2	2.8	7.4
15	12-4-90	12	2.8	9.2
16	12-4-90	16.1	4.3	11.8
<b>Averages</b>		<b>8.3</b>	<b>3.3</b>	<b>5</b>

Table 5.4. Mean growth increment counts in otoliths from three samples of *Thryssa aestuaria*. Increments were counted in sagittae from subsamples of 20 fish from each of three sampling dates.

Sample number	1	2	3
Date	17-10-90	6-12-90	4-1-90
Mean count	43.6	93.5	125.2
Standard deviation	3.2	5.8	5.8

Table 5.5 Slopes and intercepts of the linear regressions describing the relationship between length (L) and number of primary otolith increments (I) in *E. devisi* and *S. insularis* (all sizes), and in juveniles of the remaining study species. (w)-warm months; (c)-cool months.

Species	Sizes (mm)	Equation	r <sup>2</sup>	n
<i>E. devisi</i> (w)	all	$L=14.95 + 0.55*I$	0.73	32
<i>E. devisi</i> (c)	all	$L=32.27 + 0.23*I$	0.49	26
<i>S. insularis</i>	all	$L=20.44 + 0.28*I$	0.67	76
<i>S. carpentariae</i>	29-50	$L=12.1 + 0.5*I$	0.81	40
<i>S. nelsoni</i>	17-81	$L=10.7 + 0.39*I$	0.91	37
<i>S. commersonii</i>	32-139	$L=4.87 + 0.65*I$	0.90	64
<i>T. aestuaria</i>	23-65	$L=7.84 + 0.44*I$	0.91	110
<i>T. setirostris</i>	26-157	$L=10.95 + 0.688*I$	0.94	29
<i>T. hamiltoni</i>	25-174	$L=-2.82 + 0.78*I$	0.92	83

Table 5.6. The number and size-range of fish aged using primary otolith increments in each species. Also shown are the maximum lengths recorded for each species in the study area.

Species	No. aged	Size range	Max T.L.
<i>S. commersonii</i>	89	32-137	158
<i>S. nelsoni</i>	44	17-90	103
<i>S. carpentariae</i>	63	26-67	71
<i>S. insularis</i>	74	31-62	64
<i>E. devisi</i>	59	26-62	62
<i>T. aestuaria</i>	111	23-120	142
<i>T. setirostris</i>	46	25-199	220
<i>T. hamiltoni</i>	146	25-235	251

Table 5.7. Parameters of von Bertalanffy growth equations describing the fish length versus growth increment count relationship in anchovies over all sizes aged. Linear equations for *E. devisi* and *S. insularis* are given in Table 5.5.

Species	$L_{\infty}$ (mm)	K (yr <sup>-1</sup> )	$t_0$ (yr)
<i>E. devisi</i> (warm)	94.2	4.45	-0.0013
<i>S. commersonii</i>	381	0.77	0.0066
<i>S. nelsoni</i>	99.8	2.87	0.0093
<i>S. carpentariae</i>	70.55	7.089	0.027
<i>T. aestuaria</i>	147	1.56	-0.007
<i>T. setirostris</i>	186	2.77	0.0402
<i>T. hamiltoni</i>	216	1.85	0.039

Figure 5.1 A photomicrograph of otoliths from two tetracycline-treated *Thryssa aestuaria* individuals. (a) Transverse section of sagitta showing the tetracycline induced growth check (T). This fish was marked once and died 20 days later. (b) Magnified view of the same otolith section showing the tetracycline-induced check (T) and 18 growth increments (white dots) to the otolith edge (E); (c) The asteriscus from the *T. aestuaria* individual that was marked on twice. The two tetracycline induced growth checks are shown (T<sub>1</sub> and T<sub>2</sub>). Scale bars equal 0.1 mm in (a) and (b) and 0.05mm in (c).

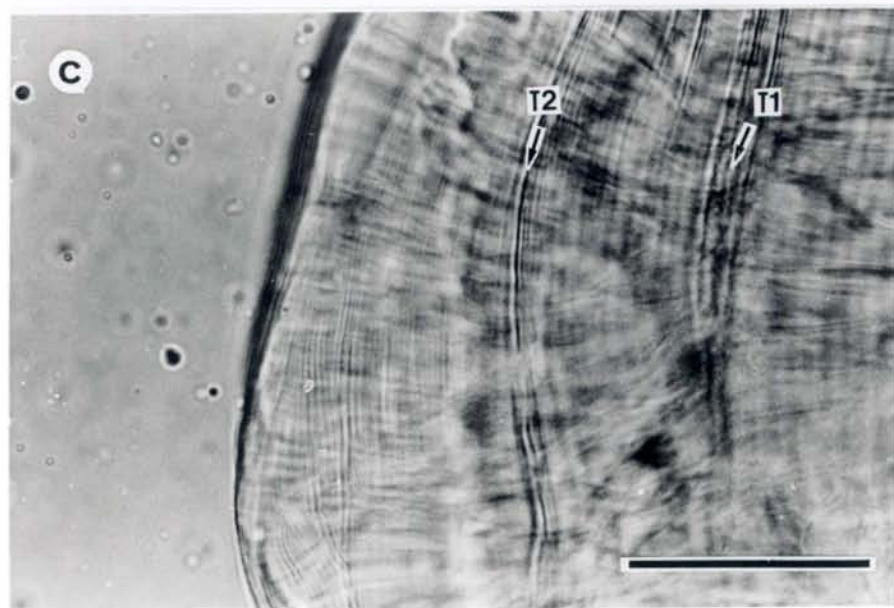
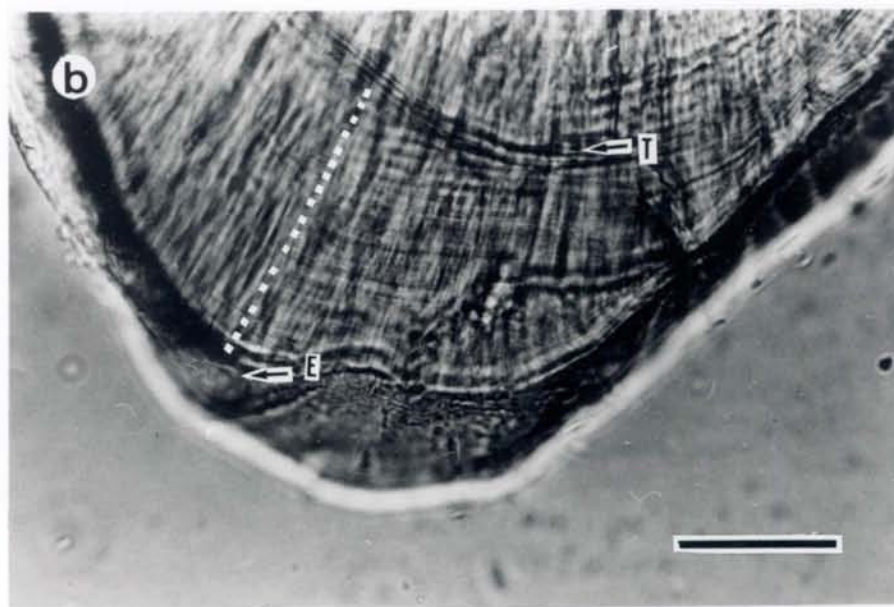
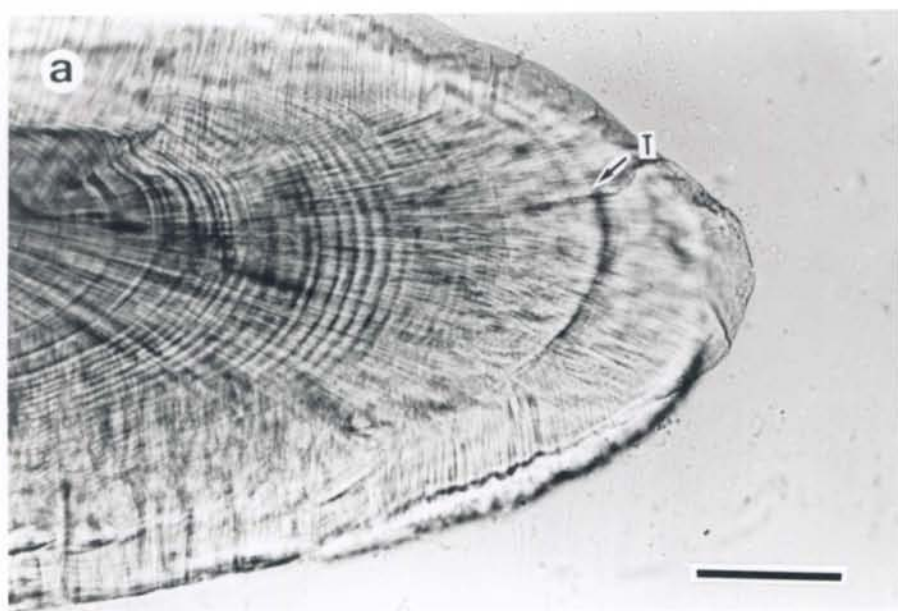


Figure 5.2 Widths of primary otolith increments plotted against the back-calculated date of formation in aquarium-held *Encrasicholina devisi* (n=14) and *S. carpentariae* (n=2). Date of capture (11-4-90) is denoted with an arrow. 1 eye-piece unit measure (e.p.u.)=2.55  $\mu\text{m}$ .



Figure 5.3. Length-frequency histograms for *Thryssa aestuaria* juveniles collected between October 1990 and January 1991.



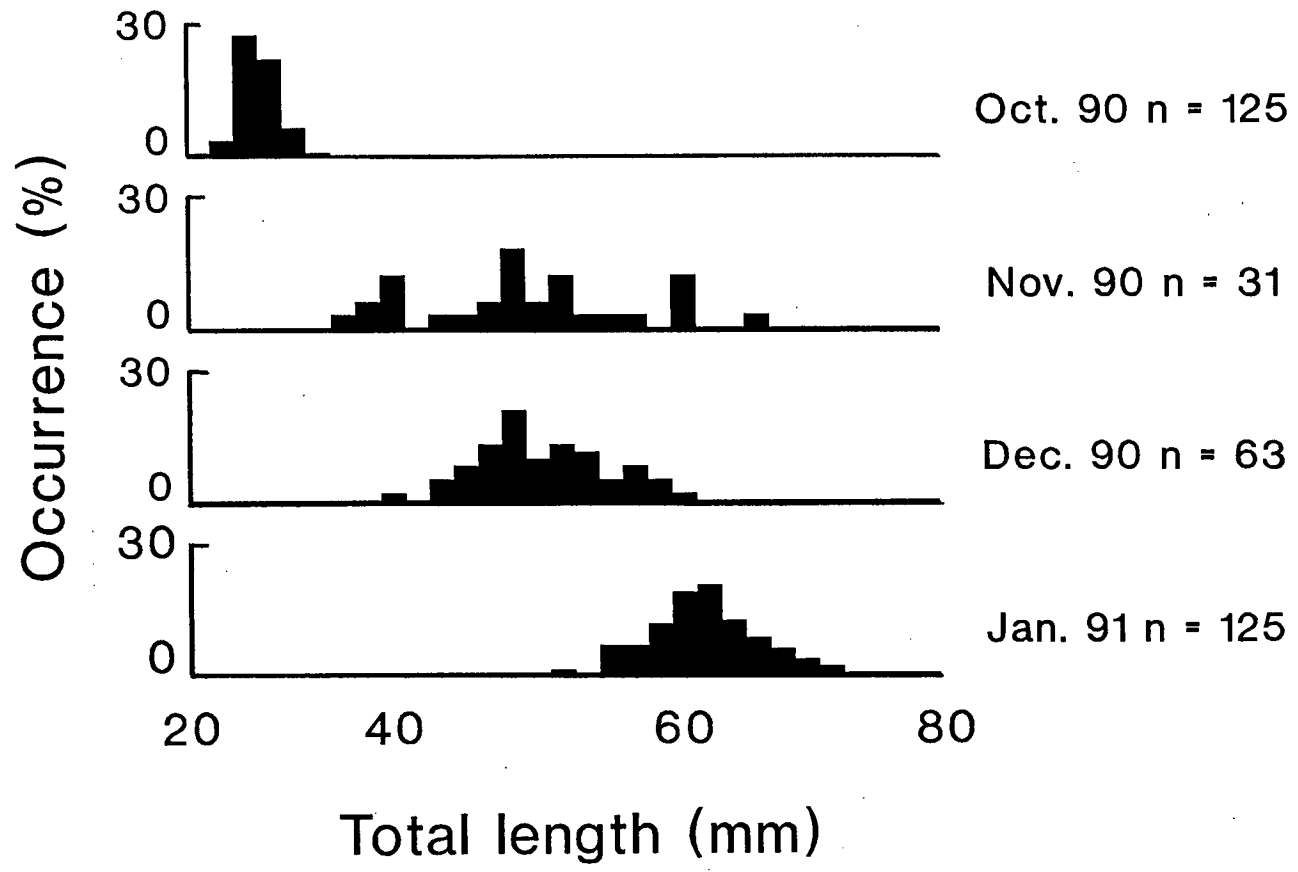


Figure 5.4. Regression of primary otolith increment counts against time for *Thryssa aestuaria* juveniles from three field samples. Increment counts from 60 juveniles (20 fish from each of three samples) are plotted against time in days (calculated by subtracting the date of capture of the individual from an arbitrarily chosen fixed date, 1-9-90). A regression line is fitted to the data and intercepts the x-axis at the estimated 'birth-date' of the cohort (6-9-90).

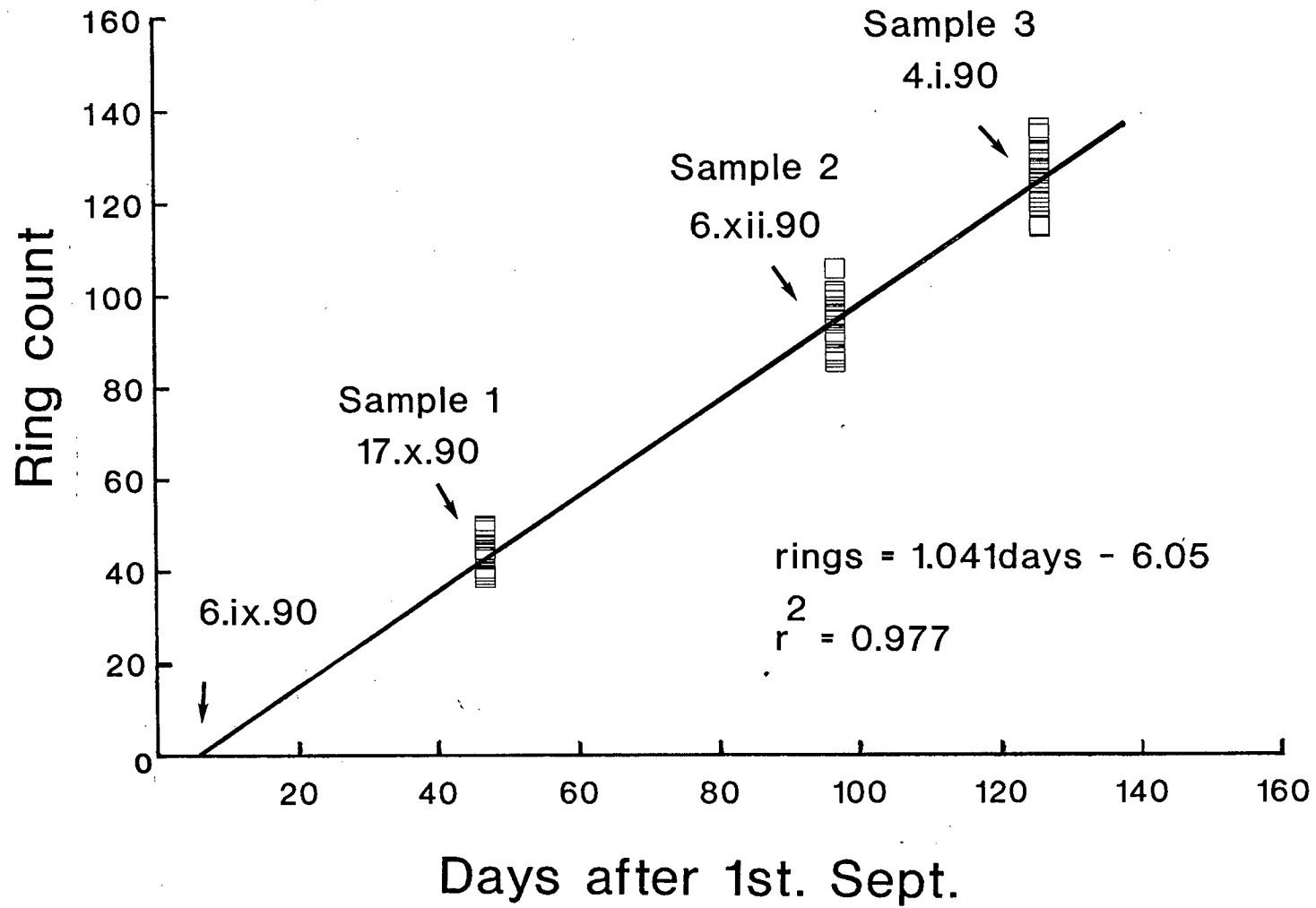


Figure 5.5. Photomicrographs of primary otolith increments in surface-ground sagittae. (a) *Stolephorus carpentariae* (T.L.=33mm), showing nucleus and concentric 'larval growth rings'; (b) *Thryssa hamiltoni* (T.L.=62mm), showing wide growth rings (large arrows) and smaller subdaily growth increments (small arrows); (c) *Stolephorus commersonii* (TL.=110mm), showing narrow growth increments characteristic of the adult growth phase; (d) The same otolith showing a magnified detail of the growth increments. Scale bars=0.05mm.

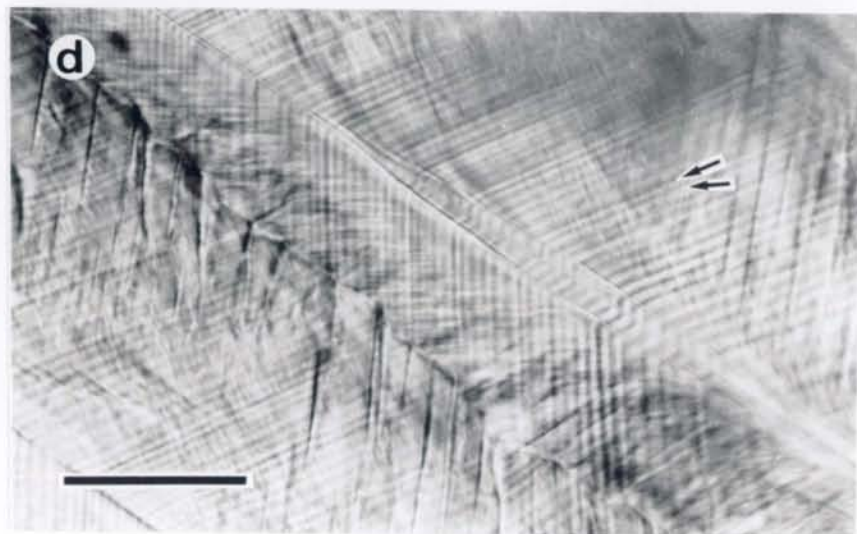
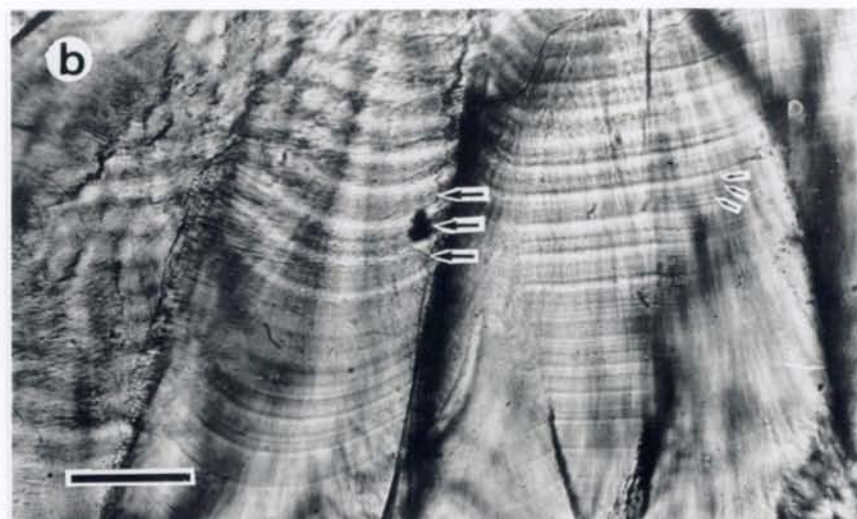
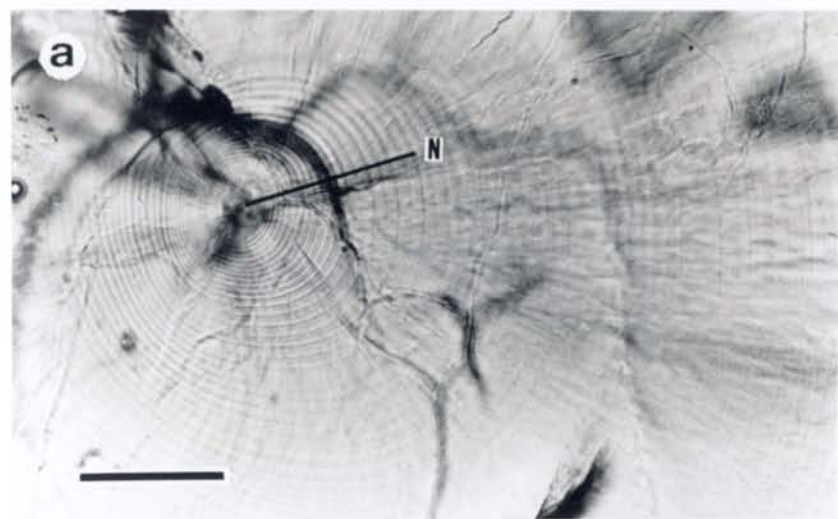
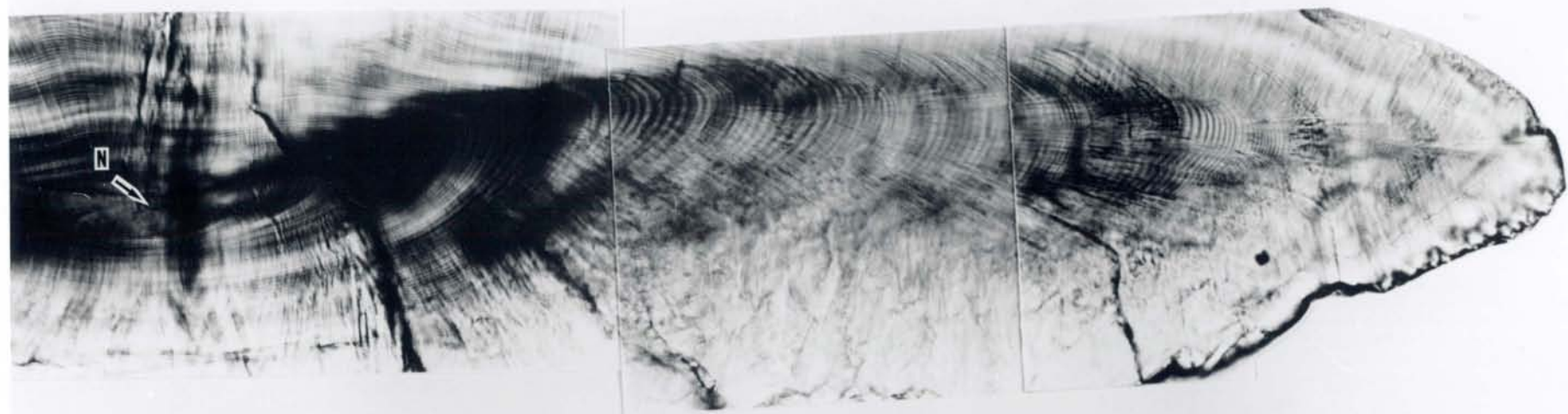


Figure 5.6. A composite photomicrograph of a transverse section of a sagitta from a 100mm *Thryssa hamiltoni* individual. N-nucleus.



0.5 mm

Figure 5.7. The mean widths of groups of ten consecutive growth increments plotted against increment number in four *T. aestuaria* individuals.



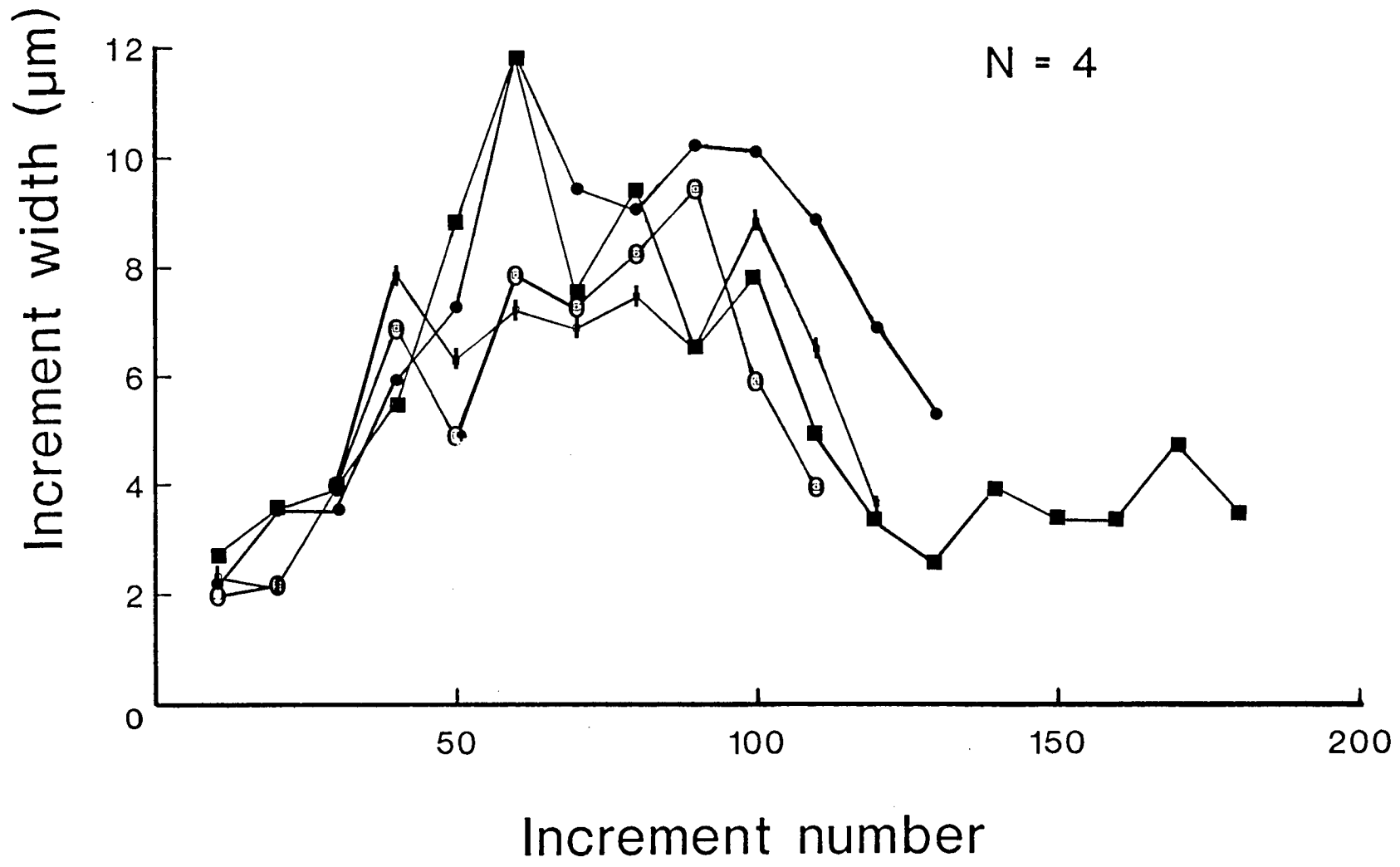


Figure 5.8. Growth rate (from the slopes of plots of length against number of primary otolith increments) plotted against species-specific maximum length in eight species of anchovy. A regression line fitted to data is shown.

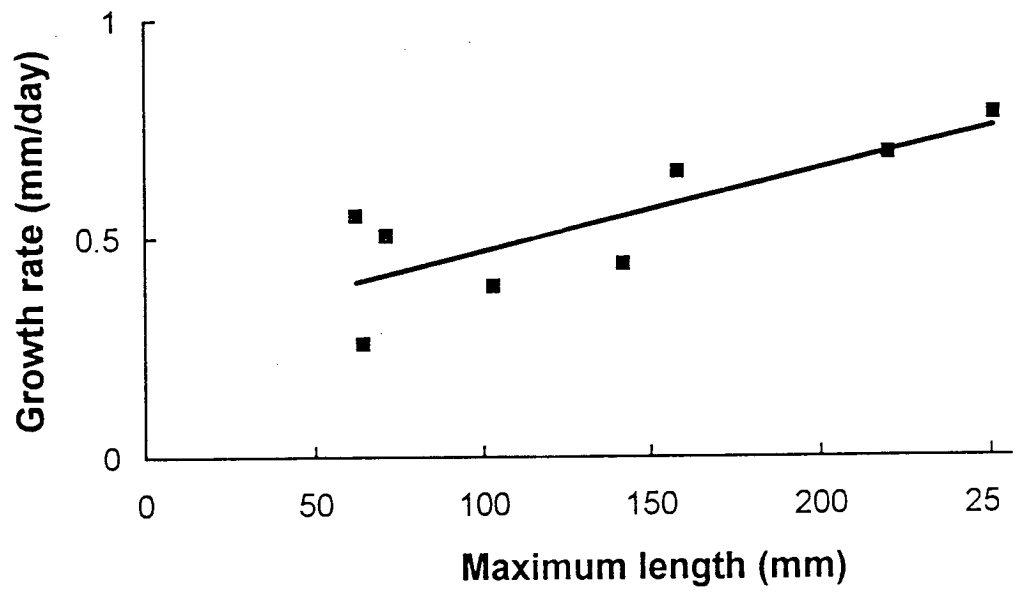


Figure 5.9. Total length plotted against number of sagittal growth increments in stolephorid anchovies. Growth curves fitted to the data are shown. (a) *Encrasicholina devisi* (linear regressions are fitted to data for individuals collected in the warm and cool seasons separately); (b) *Stolephorus insularis*; (c) *S. carpentariae*; (d) *S. nelsoni*.

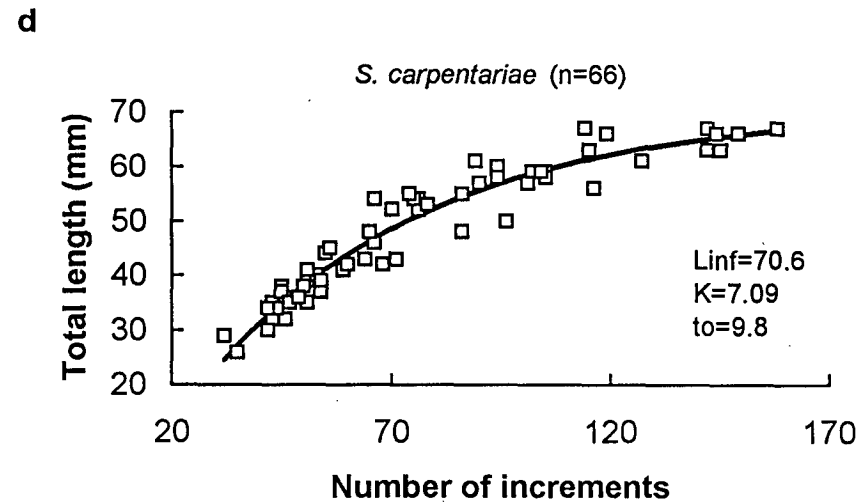
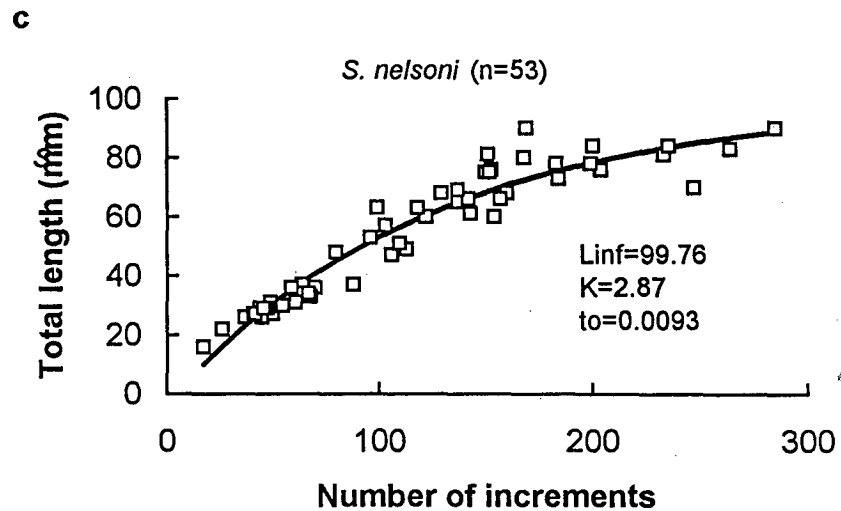
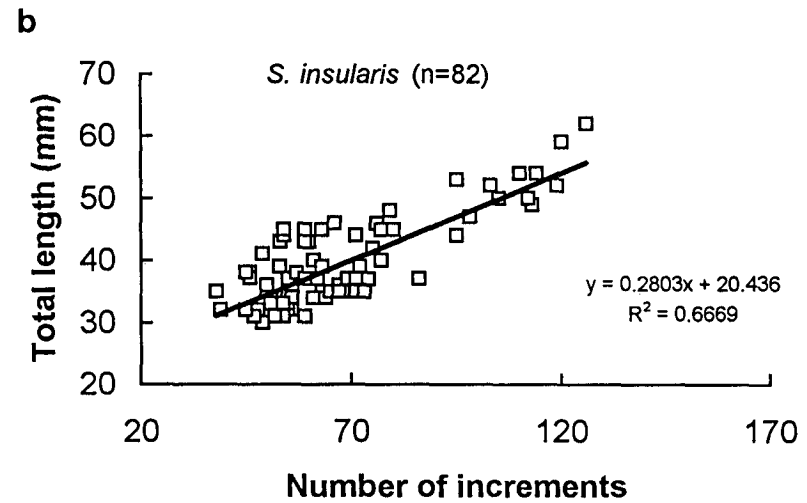
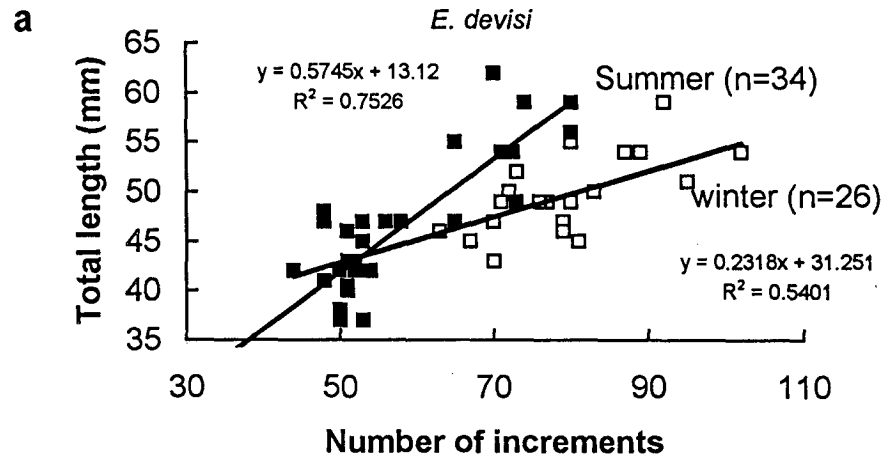
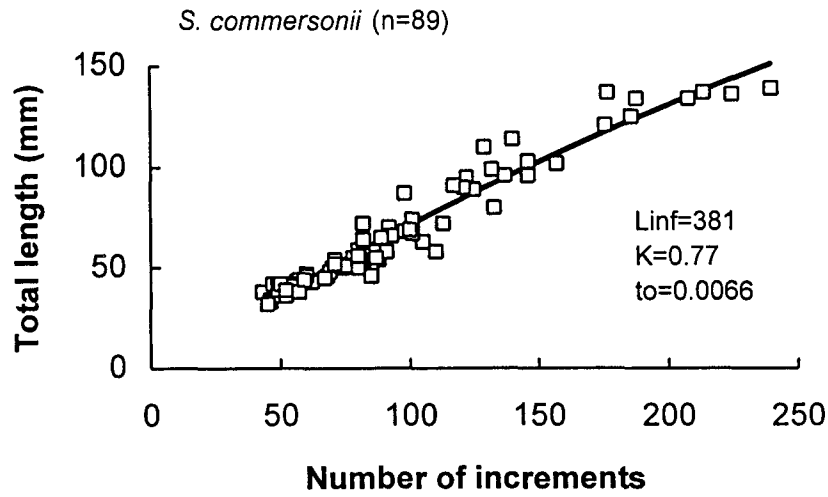
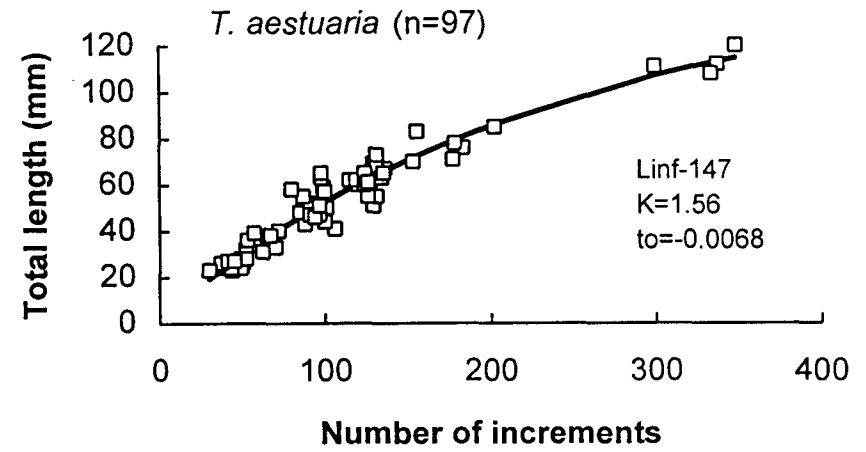


Figure 5.10. Total length plotted against number of primary otolith increments for anchovy. Fitted growth curves are shown. (a) *Stolephorus commersonii*; (b) *Thryssa aestuaria*; (c) *Thryssa setirostris*; (d) *Thryssa hamiltoni*.

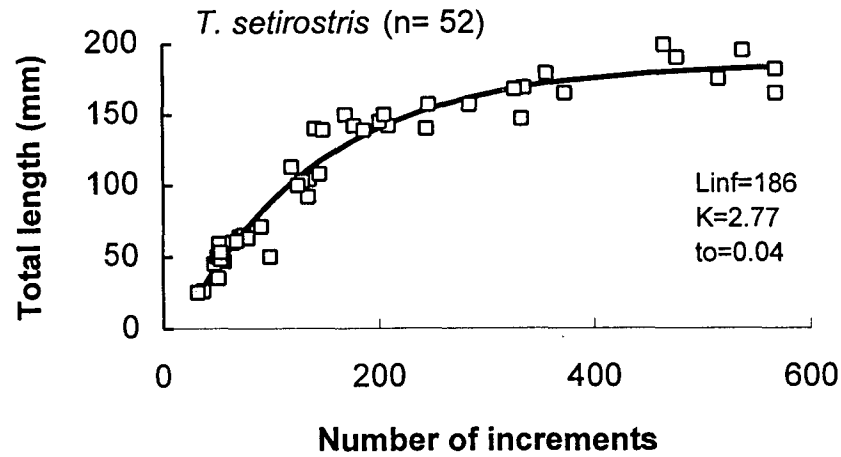
a



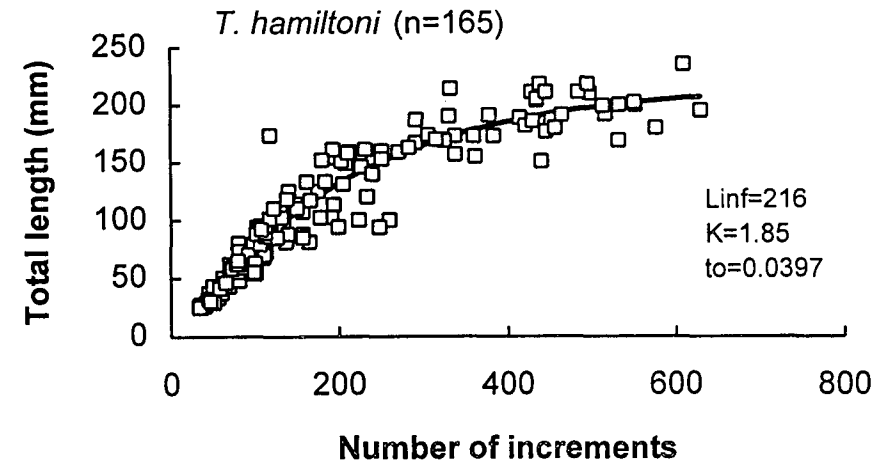
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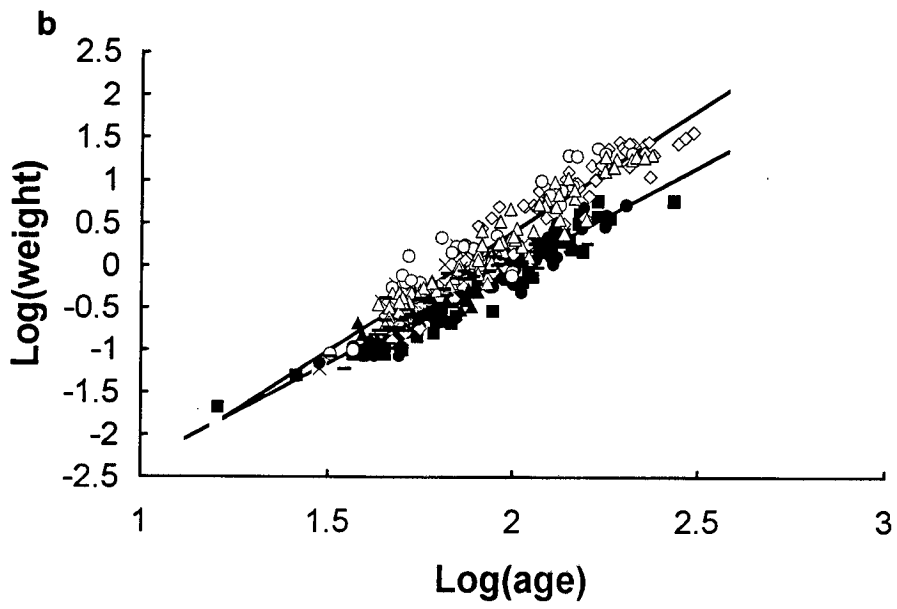
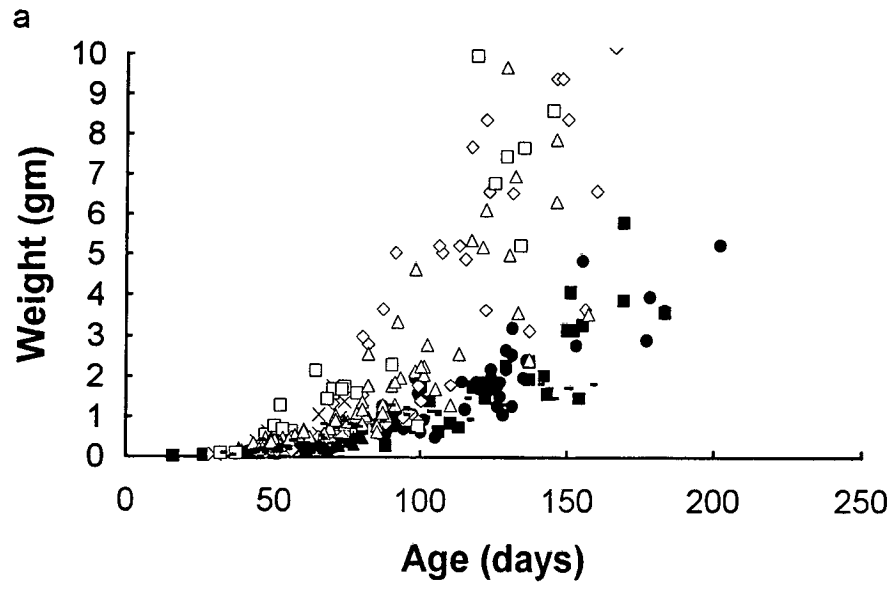


d



5.11 (a) Body weight plotted against age (from counts of primary otolith increments) for eight species of anchovy. (b) Log-weight plotted against log-age with fitted linear regressions for the two species groupings. Key: X -*E. devisi*;  $\Delta$  -*S. commersonii*;  $\circ$  -*T. setirostris*;  $\diamond$  -*T. hamiltoni* (upper curve);  $\blacktriangle$  -*S. insularis*, -- -*S. carpentariae*,  $\blacksquare$  -*S. nelsoni*;  $\bullet$  -*T. aestuaria* (lower curve).





## CHAPTER 6 SEASONAL GROWTH RINGS IN THE SAGITTA OF *THRYSSA HAMILTONI*.

### 6.1 Introduction

Seasonal growth rings in scales and otoliths have been increasingly used for age and growth determinations on tropical fish in recent years (Fagade 1974, Longhurst and Pauly 1987, Ferreira and Russ 1992, Fowler and Doherty 1992). Annual growth rings have been validated and widely used to age temperate fish species but there have been far fewer reports of seasonal or annual growth rings in tropical fish species. Recent studies show that seasonal environmental variations and changes in reproductive activity in longer-lived tropical fish may be of sufficient intensity to induce the formation of recognisable periodic growth marks in skeletal structures (Brothers 1979, Casselman 1987, Longhurst and Pauly 1987, Ferreira and Russ 1992, Fowler and Doherty 1992).

Although tropical clupeoids are generally regarded as being short-lived (Lewis 1990), length-frequency studies show that some of the larger species can have longevities of one to several years (eg. Venkataraman 1956, Pillay 1958, Dayaratne and Gjøsaeter 1986, Conand 1991). At present there is little information on seasonal growth rings in skeletal structures of large tropical clupeoids and most growth studies on these fish have used length-frequency analyses or primary otolith increments. However, a few authors have reported growth rings of probable annual periodicity in scales or otoliths from large tropical herrings (F. Clupeidae). Examples of these are *Sardinella longiceps* (Nair 1949), *Sardinella anchovia* (Heald and Griffiths 1967) and *Sardinella gibbosa* (Okera 1970). These studies indicate that growth rings suitable for ageing may be present in the calcareous structures of members of this family.

Given the potential biases that can occur when using length-frequency data to estimate growth in short-lived tropical fish with extended spawning seasons (Qasim

1973b, Brothers 1979), it is important to investigate alternative methods of ageing such as seasonal growth rings in scales or otoliths. One advantage of this method over length-frequency analysis is the potential for more accurate estimates of age in older individuals (modes of older fish overlap and are difficult to detect in length-frequency data-Brothers 1979). Therefore, seasonal growth rings of known periodicity have the potential to improve longevity estimates for large tropical clupeoids.

The genus *Thryssa* is comprised of 21 species. These species are among the larger tropical clupeoids attaining lengths between 10 and 37 cm. *Thryssa scratchleyi* (Ramsey and Ogilby) at 37 cm is the largest anchovy known (Whitehead *et al.* 1988). The large size and probable greater longevity of *Thryssa* species compared to other smaller anchovies such as *Stolephorus* made these fish suitable for an investigation into the possibility of determining age and growth from seasonal growth rings in otoliths. In this chapter, growth marks of probable seasonal periodicity are described from the otoliths from three species of *Thryssa*. The seasonal growth rings in otoliths from *Thryssa hamiltoni* are studied in detail. The temporal periodicity of growth ring formation is investigated for *T. hamiltoni* and age and growth are estimated based on counts of these growth rings.

## 6.2 Materials and methods

Otoliths were removed from fish stored frozen or in 70% alcohol and examined for evidence of seasonal growth rings. Initially a sample of otoliths was examined whole using transmitted and reflected light at 4X magnification. Although there was evidence of alternating opaque and translucent growth zones these were difficult to distinguish in whole otoliths. A number of otoliths were then sectioned transversely (using the method outlined in Chapter 5), and examined with transmitted light at 4X magnification. Alternating translucent and opaque zones could be counted in otolith sections from all three species. This technique was used to prepare all otoliths. The pattern of growth rings and their optical properties were

compatible with descriptions of seasonal and annual growth rings in otoliths from other fish species (Casselman 1987, Longhurst and Pauly 1987, Fowler and Doherty 1992).

The periodicity of growth ring formation was determined by analysing changes in the appearance of otolith margins in samples collected in different months of the year (Blackburn 1950a, Baird 1970, Casselman 1987). Months in which a high proportion of otoliths had a newly formed opaque growth ring on the margin were considered to approximate the time of growth ring formation for the species. If the period of growth ring formation occurred in a single, restricted time period each year then this would suggest an annual periodicity of growth ring deposition (Casselman 1987). A second method was also used to verify the periodicity of growth ring formation. This involved counting presumed daily growth increments prior to the first seasonal growth ring in a sample of otoliths. A t-test (Zar 1984) was used to test if the mean growth increment count differed significantly from 365 days or one year.

Von Bertalanffy growth curves were fitted to length-at-age data from counts of seasonal growth rings. The growth parameters  $L_{\infty}$ ,  $K$  and  $t_0$  were estimated using the iterative least squares method within the "FISHPARM" computer software. Standard errors were calculated for each parameter.

Lengths-at-age were also estimated in *T. hamiltoni* using Lee's back-calculation formula (Carlander 1981). Lengths-at-age were calculated from measurements of the distances of seasonal growth rings from the nucleus in each otolith using the following equation:

$$L_i = a + \frac{L_{\infty} - a}{NM} * NA_i$$

where: NM = distance from the nucleus to the otolith margin measured on a transversely sectioned otolith (Fig. 6.1)

NA<sub>i</sub> = distance from the nucleus to the i<sup>th</sup> seasonal growth ring in a T.S. (Fig. 6.1)

L<sub>c</sub> = length of the fish at capture

a = intercept of the fish-length versus otolith radius (NM) regression

A prerequisite of this method is that there exists a direct relationship between fish length and otolith length (Carlander 1981). This was tested by plotting fish length against otolith radius ('OR' in Fig. 6.1) measured on whole otoliths from juvenile and adult fish of both sexes. The parameter 'a' in equation 1 was estimated from the intercept of a plot of fish length versus 'NM' (distance between the nucleus and otolith margin in transversely sectioned otoliths).

## 6.3 Results

### 6.3.1 Description of seasonal growth rings

Sagittae from 80 adult *T. hamiltoni* (47 males and 33 females), were sectioned transversely and examined for seasonal growth rings. Otolith sections from 16 adult *T. setirostris* and 3 adult *T. aestuaria* were also examined to see if similar structures were present. The sagitta in all species were found to contain discernible growth rings consistent with descriptions of seasonal and annual growth rings in other fish species (Casselman 1987, Longhurst and Pauly 1987, Fowler 1990). Growth rings in transverse otolith sections were regularly spaced 'dark' or 'opaque' rings that alternated with wider translucent zones in the otolith (Fig. 6.2). These growth rings appeared to be narrower than analogous structures reported in temperate fish.

The opacity of seasonal growth rings appeared to result from a combination of a change in otolith chemical composition and a narrowing of primary otolith increments in the region of the seasonal growth ring. The latter suggests that growth was slower at the time of growth ring formation. The first seasonal growth ring in a

few otoliths was subdivided into 2-3 rings however, the close proximity of these sub-divisions left no doubt that they comprised a single growth ring. Otolith sections from most fish also contained a lesser growth mark approximately half-way between the nucleus and the first seasonal growth ring and minor growth rings between seasonal rings (Fig. 6.2). These were considered 'false rings' for two reasons. Firstly, the false ring before the first seasonal growth ring had a different appearance to what were considered as 'seasonal growth rings'; the former were visible due to differences in primary increment structure compared to adjacent ones (increments there were narrower, erratic and minor growth checks occurred in the region). In contrast the seasonal growth rings consistently had a strong opaque colour which appeared to be unrelated to primary increment structure. Secondly, false rings were variable in their location and counts of primary increments showed that these formed early in life at 3 to 6 months of age and were therefore not representative of one year's growth. The first seasonal growth ring was formed at around 1 year of age as will be shown later and these were usually located at a consistent distance from the nucleus. The estimated time of formation of false rings corresponded to the onset of cool months and the smaller primary increments in the region of these marks suggests that they result from changes in growth at this time. Minor rings observed between seasonal growth rings again differed in appearance and were irregularly located compared to seasonal growth rings.

### 6.3.2 The periodicity of growth ring formation in *T. hamiltoni*

The season of formation of new growth rings at the otolith margin was studied. Otoliths with an opaque ring on the otolith margin (ie. a newly formed ring) were only found in fish caught in the months of August to December (spring/summer). Marginal growth rings were found in 2 out of the 7 individuals from August, 4 out of 9 individuals from October and 10 out of 11 individuals examined from December (Fig. 6.3). No evidence of new growth ring formation was found in otoliths from fish caught in the months of February to July (n=58). This suggests

that seasonal growth rings in *T. hamiltoni* were formed in the spring/summer months and that these structures were formed annually.

Further evidence of the temporal significance of seasonal growth rings in *T. hamiltoni* was obtained from counts of presumed daily otolith growth increments prior to the first seasonal growth ring (Morales-Nin 1989). Primary otolith increments to the first seasonal growth ring were counted in otoliths from 21 adult *T. hamiltoni*. A t-test showed that the mean growth increment count (354±23.9) was not significantly different from 365 days or one year. This suggests that the first growth ring is formed after approximately 1 year.

Adult *T. hamiltoni* with one growth ring in the otolith were frequent in samples collected between February and April. The presence of only a single growth ring in these individuals (which according to length-frequency data were 1+-aged individuals), suggests that only one growth ring forms during the spring/summer period.

### 6.3.3 Growth estimates for *T. hamiltoni*

Seasonal growth rings were counted in 80 *T. hamiltoni* individuals by two readers. Agreement between counts occurred in 76% of otoliths, differences of 1 year occurred in 20% of otoliths and 4% differed by 2 years. The maximum age for *T. hamiltoni* from counts of seasonal growth rings was 4 years for males and females.

Ages-at-length in *T. hamiltoni* were estimated from seasonal growth rings using Lee's back-calculation method (Carlander 1981). A significant linear relationship was found when fish length was plotted against otolith radius (Fig. 6.4). A significant linear regression (FL = 76.1NM + 16.83,  $r^2 = 0.68$ ,  $p < 0.05$ ), also described the relationship between fish length (FL) and nucleus to margin distance on the sagitta (NM) in otolith sections and from this the parameter 'a' in equation 1 was obtained. Von Bertalanffy growth curves were fitted to the back-calculated

length/age data for each sex (Table 6.1, Figs. 6.5a & b). Mean lengths-at-age were also calculated for male and female *T. hamiltoni*; this data demonstrated the larger sizes-at-age attained by females (Table 6.2). Age-length data was also obtained from direct counts of growth rings in the sagitta from each fish. Von Bertalanffy growth curves were fitted to the resulting length-at-age data for each sex (Table 6.1, Fig. 6.5c&d). The von Bertalanffy growth parameter 'K' estimated by both methods for *T. hamiltoni* ranged from 0.64 to 1.12, and the mean value for males and females were 0.89 and 0.74 respectively (Table 6.1, Fig. 6.5).

#### 6.3.4 Seasonal growth rings in other *Thryssa* species

Sagittae from 16 adult *T. setirostris* individuals were transversely sectioned and examined for seasonal growth rings. Of these, 13 fish had otoliths with a single growth ring and three individuals had two growth rings (Table 6.3). One of the fish with two seasonal growth rings was a female caught in December with a newly formed growth ring on the otolith margin. The formation of a new growth ring in December was consistent with the timing of growth ring formation in *T. hamiltoni*. A growth curve was not fitted to the length-at-age data in *T. setirostris* because the sample-size and age-range were considered too small (Table 6.3).

Otoliths from three adult *T. aestuaria* caught in December were sectioned. In all fish there was a single, newly formed growth ring at the otolith margin, again indicating that growth rings are formed at a similar time as observed in *T. hamiltoni*.

#### 6.4 Discussion

Studies of annual growth rings in scales and otoliths have been the favoured method for ageing temperate clupeoid fishes (eg. Blackburn 1950a, Beverton 1963, Collins and Spratt 1969, Baird 1970). At present, there are few reports of analogous structures in tropical clupeoids and these are not routinely used for age-analysis. An important prerequisite for the routine use of seasonal growth rings in hard parts to



estimate age is validation of the periodicity of growth ring formation (Beamish and McFarland 1983). In the present study, seasonal growth rings were identified in transversely sectioned otoliths from three species of *Thryssa*. Although based on relatively small sample sizes of otoliths, the evidence suggests that the period of ring formation in *T. hamiltoni* is annual. A more comprehensive study is required to show that these structures are reliable for routine age and growth estimates.

This study gives the first record of annually formed growth rings in the calcareous structures of a tropical anchovy. Counts of these structures provided useful estimates of longevity in these species. The maximum number of seasonal growth rings found in each species were one in *T. aestuaria*, two in *T. setirostris* and four in *T. hamiltoni*. These longevity estimates are within the range of estimates based on presumed annual growth rings in scales and otoliths from some tropical clupeids. Nair (1949) counted up to three presumed annual growth rings in otoliths from the clupeid, *Sardinella longiceps* from India. Heald and Griffiths (1967) aged *Sardinella anchovia* from Venezuela to 5 years from growth rings in scales, and Okera (1970) found up to two annual growth rings in the scales of *Sardinella gibbosa* from East Africa.

Counts of seasonal growth rings indicate that the largest species, *T. hamiltoni* can live to four years. Three and four year-old fish were uncommon in collected in this study and most of the population is probably comprised of fish up to 2 years of age. Length-frequency studies on other large tropical clupeoids generally suggest longevities of two years (Venkataraman 1956, Lazarus 1987, Lewis 1990, Conand 1991). Palekar and Karandikar (1952) presented length-frequency data for a large species of *Thryssa*, *T. purava* ( $L_{\max}=270\text{mm}$ ). The combined length-frequency histogram had distinct modes at 185mm, 205mm, 235mm and 270mm which could indicate that several year classes were present in their samples. Pillay (1958) examined growth in the large clupeid, *Hilsha ilisha* ( $L_{\max}=500\text{mm}$ ) from length-frequency data and concluded that this species lives for at least four years. The

available information suggests that large clupeoids have maximum longevitys of 3-4 years.

Seasonal growth rings in *T. hamiltoni* were evident near the margin of otoliths between August and December. Fowler (1990) obtained a similar result with regard to the formation of annual growth rings in the small tropical reef fish *Pomacentrus mollucensis* collected at similar latitudes to *T. hamiltoni* in the present study. Growth ring formation for *P. mollucensis* was initiated between September and October. Ferreira and Russ (1992) also found that annual growth rings were deposited in late winter and spring months in the coral trout, *Plectropomus maculatus* collected near Townsville. These studies suggest that a common factor related to season may influence the deposition of growth rings in fish in this region.

The time of formation of the opaque growth rings in *T. hamiltoni* and other species correlates with the seasonal rise in water temperatures off Townsville (Walker 1981, Fowler and Doherty 1992). However, other factors such as the onset of maturation or changes in food abundance which may occur concurrently with the rise in water temperature may be important. Reproductive maturation has been associated with annual growth ring formation in a number of tropical fishes (Longhurst and Pauly 1987). Morales-Nin and Ralston (1990) related annulus formation to reproductive periods in *Lutjanus kasmira* from Hawaii. Heald and Griffiths (1967) found that annual growth rings formed in the scales of *Sardinella anchovia* from Venezuela at a time corresponding to low water temperature, upwelling and spawning. Growth ring formation in *T. hamiltoni* in the present study also occurs at the time of gonad maturation and spawning which commences in September (Hoedt 1984). The observed narrowing of primary otolith increments in the region of the seasonal rings in otolith sections from *T. hamiltoni* suggests that growth slows at the time of growth ring formation (Campana and Neilson 1985). This is contrary to the expected increase in growth rate (and corresponding increase in increment width), that would occur if the growth rings were laid down as a

response to increased sea temperature or food availability. A likely cause of growth retardation during this time is gonad maturation and spawning, and therefore this may be a factor inducing the formation of growth rings in this species. Recent studies of spawning in engraulid fishes have shown that members of this family may be multiple spawners (Hunter and Goldberg 1980, Clarke 1987, Zastrow *et al.* 1991). The observed subdivisions within the first seasonal ring in some individuals of *T. hamiltoni* may reflect more than one spawning episode during the period of growth ring formation.

Age-at-length data from an analysis of seasonal growth rings show that female *T. hamiltoni* grow faster and attain larger sizes than males. This life-history strategy has the effect of increasing the fecundity and therefore reproductive output of female fish during their lifetime (Kawasaki 1980). Sexual growth differences have been noted for several other tropical and temperate clupeoid species (Pillay 1958, Baird 1970, Beverton 1963, Williams and Clarke 1983, Lazarus 1987). In all of these examples female fish grew larger than males. Sexual growth differences are also a feature of other fish groups. McPherson (1992) showed that female Spanish Mackerel, *Scomberomorus commerson* grow larger than males.

The finding of growth rings of annual periodicity in the otoliths from three large tropical clupeoids from Townsville is relevant to future age and growth studies on other large tropical clupeoid fishes. This result raises the possibility that these structures may be found in other large tropical clupeoids. Further studies are required to detect and validate these structures in clupeoid species from different latitudes. The study locality is located at 19°S and therefore is subject to subtropical weather patterns different from those in equatorial regions. The annual temperature fluctuation in Townsville is large compared to equatorial regions where monsoonal seasons are the major seasonal variable. Furthermore, some tropical anchovies exhibit two spawning peaks near the equator (eg. Palekar and Karandikar 1952) and the effect of this on growth ring formation requires investigation. The

application of the transverse sectioning methods used on otoliths in this study may elucidate growth rings that were previously not detected in tropical clupeoids.

Table 6.1. Von Bertalanffy growth parameters calculated for *Thryssa hamiltoni* from analyses of seasonal growth rings. Growth parameters calculated from length-at-age data from otolith growth ring counts and also from lengths-at-ages obtained using Lee's back-calculation equation and standard errors are shown.

	Growth ring counts		Back-calculation	
	Females	Males	Females	Males
$L_{\infty}$	259 +/-16.6	214+/-8.46	238+/-12.1	218+/-14.9
K	0.66+/-0.35	0.85+/-0.47	1.12+/-0.56	0.64+/-0.32
$t_0$	-1.43+/-0.95	-1.2+/-0.99	-0.2+/-0.49	-1.2+/-0.8

Table 6.2. Mean lengths-at-ages in *Thryssa hamiltoni* derived from length-at-age data estimated using Lee's back-calculation method. Standard deviations about the mean lengths-at-age (s) and the numbers of lengths estimated in each age-class (n) are given.

Males

Age (years)	1	2	3	4
Length	167.4	189.9	202.6	210.1
s	16.5	9.9	5.7	3.4
n	43	24	10	4

Females

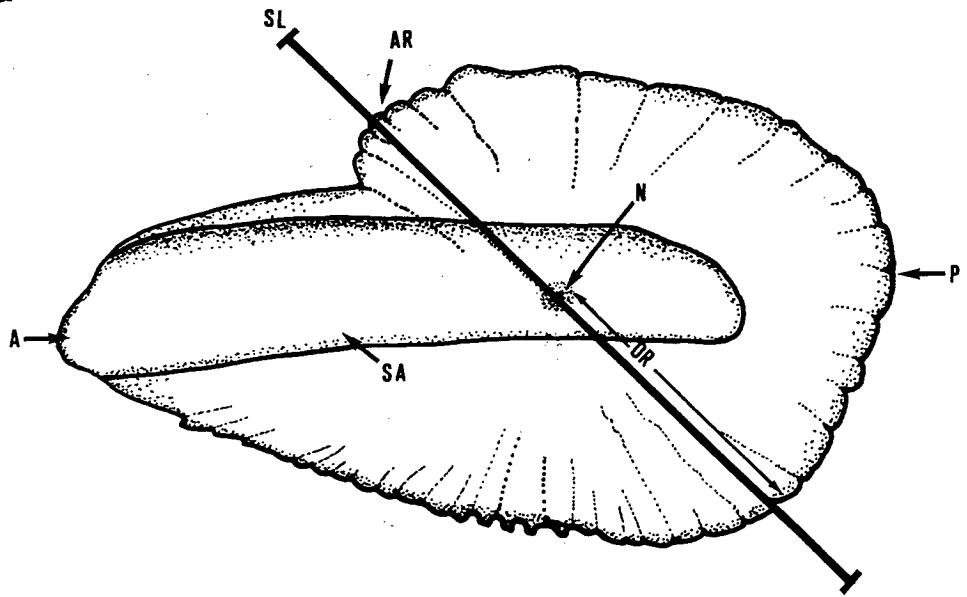
Age (years)	1	2	3	4
Length	179.1	224.3	236.4	245.5
s	18.4	11.3	6.1	1.5
n	37	15	3	2

Table 6.3. Lengths-at-age estimated from seasonal growth ring counts in *Thryssa setirostris*. Mean length for each age class and standard deviation are given.

Length (mm)	No. in age group	
	I	II
150	1	-
155	-	-
160	1	-
165	3	-
170	1	-
175	1	-
180	1	-
185	-	-
190	2	1
195	2	1
200	-	3
Mean length	175	197
SD	14.9	4.5
N	12	5

Figure 6.1 The sagittal otolith of *Thryssa hamiltoni*. (a) Proximal face showing the line of sectioning (SL) and the otolith radius measured on whole otoliths (OR); (b) Transverse section showing the distance of the first seasonal growth ring from the nucleus ( $NA_1$ ), and the distance from the nucleus to the otolith margin (NM). A-anterior margin; AD-anterodorsal margin; AR-antirostrum; N-nucleus; P-posterior edge; PR-proximal surface; SA-sulcus acusticus; VP-ventro-posterior margin (terminology follows Pannella 1980).

a



b

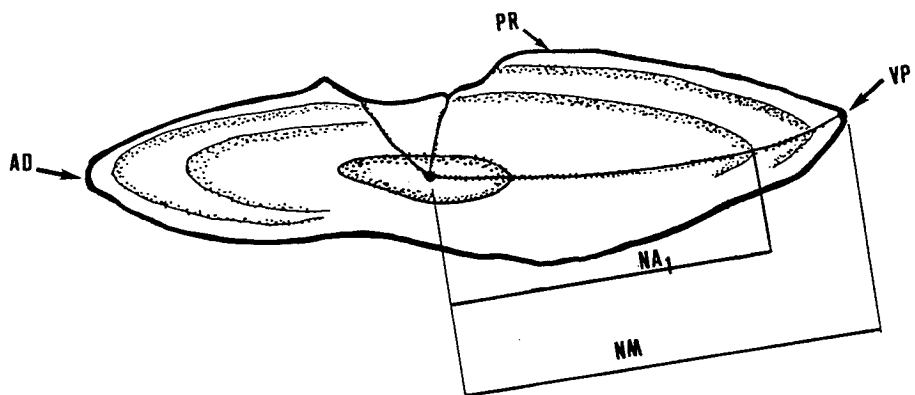




Figure 6.2. Photographs showing seasonal growth rings in transverse sections of sagittae from *Thryssa hamiltoni*. (a) 1+ female, 202 mm; (b) 2+ female, 246 mm; (c) 3+ female, 248 mm; (d) 2+ male, 194 mm e); 4+ male, 216 mm. Growth rings are denoted by arrows; F= false growth ring. Scale bars = 1mm.

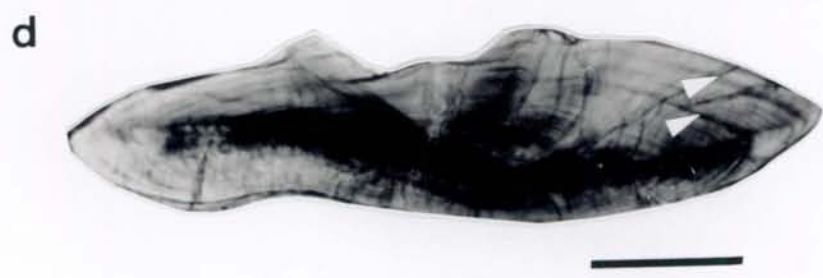


Figure 6.3. Frequencies of otolith margins with opaque (new growth ring forming) or hyaline margins for different months of the year. Based on examination of 80 *Thryssa hamiltoni* otoliths.

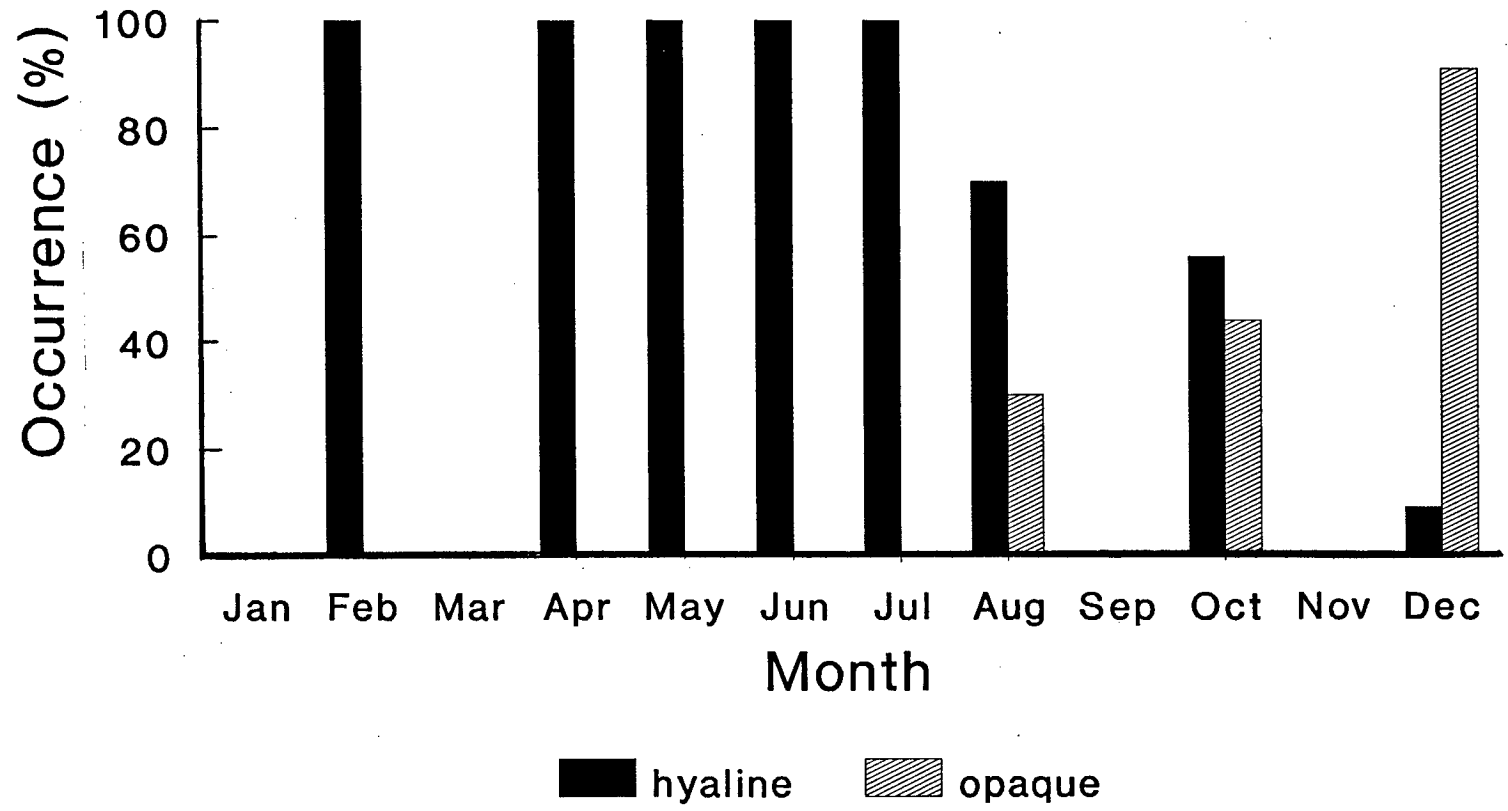
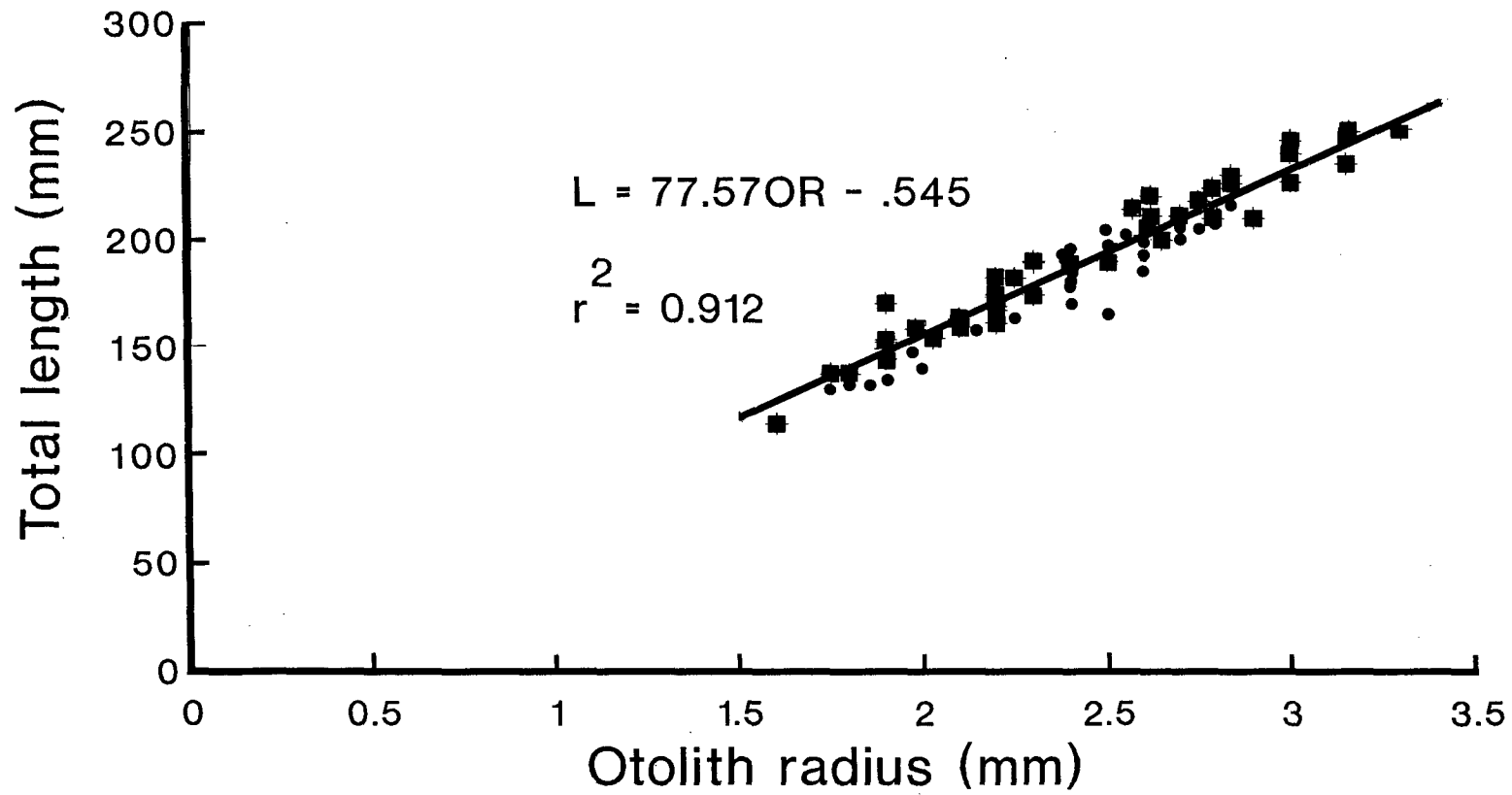
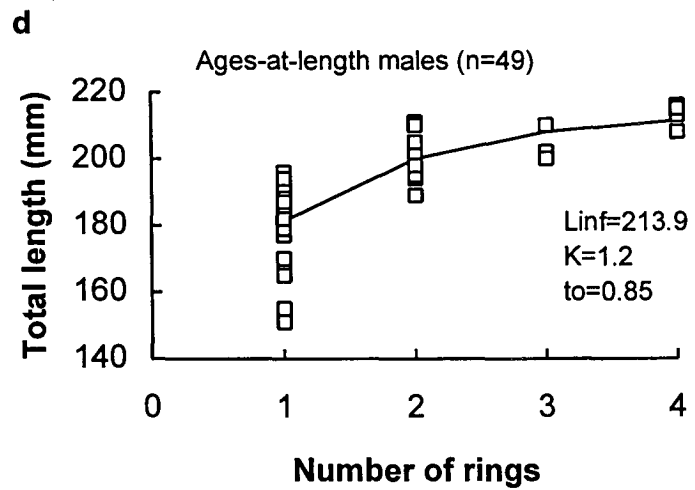
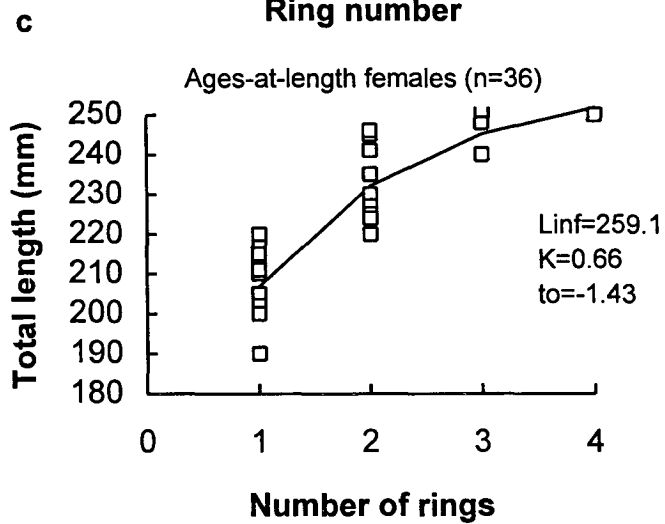
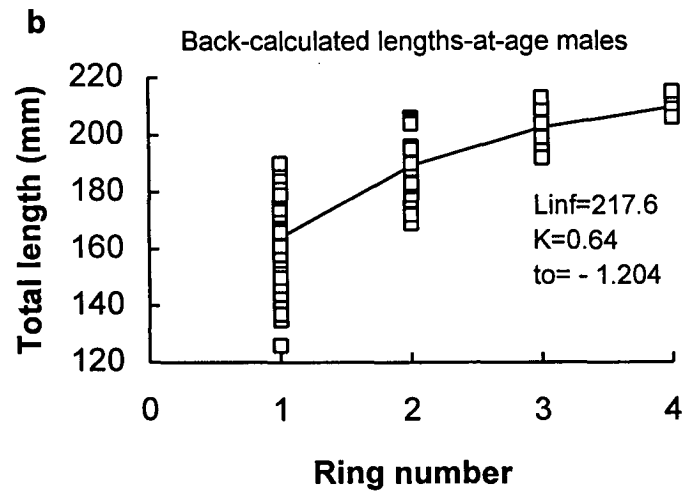
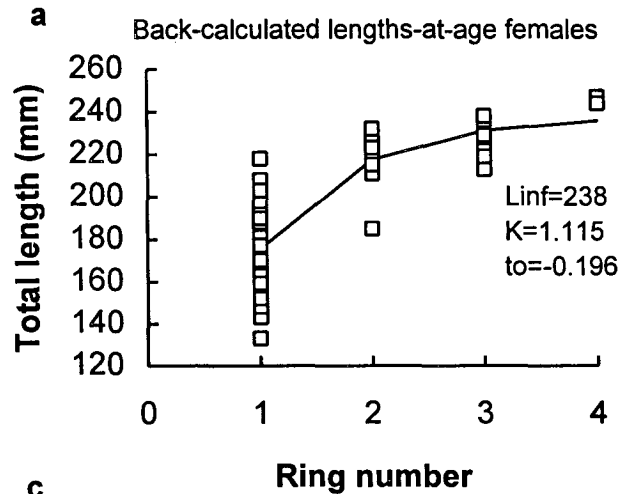


Figure 6.4. Fish length plotted against otolith radius in *Thryssa hamiltoni*. The regression line fitted to the data is shown.



• males n = 44      ■ females n = 45

Figure 6.5. Age plotted against length with fitted von Bertalanffy growth curves for *Thryssa hamiltoni*. a) Age plotted against back-calculated length (Lee's method) for females. b) Age plotted against back-calculated length (Lee's method) for males. c) Age (from direct counts of seasonal growth rings in otoliths) plotted against length for females. d) Age (from direct counts of seasonal growth rings in otoliths) plotted against length for males.





## CHAPTER 7 ANALYSIS OF LENGTH-FREQUENCY INFORMATION

### 7.1 Introduction

The majority of studies of growth in tropical clupeoids have been based on length-frequency analyses (eg. Venkataraman 1956, Barrett and Howard 1961, Tham 1966, Tiews *et al.* 1970, Burhanuddin and Hutomo 1975, Conand 1985, Muller 1977, Luther 1990, Tiroba *et al.* 1990). The analysis of length-frequency information is useful for estimating growth and other population parameters in tropical fisheries because the data are easily collected during routine fishing operations. Another advantage of this method is that analysis does not require complex methodology or equipment. The more commonly used methods for analysing length-frequency data in tropical clupeoids have been the 'modal progression method' (eg. Tham 1966, Burhanuddin and Hutomo 1975, Luther 1990), and more recently the ELEFAN computer software has been used (eg. Rawlinson 1989, Tiroba *et al.* 1990).

Despite the widespread use of length-frequency analysis, tropical clupeoids, particularly the small stolephorid anchovies, exhibit life-history characteristics which do not lend themselves to such analysis. Firstly these fish typically have prolonged or continuous breeding seasons and this can make the identification of modal groupings difficult in length-frequency histograms (Brothers 1979). Secondly, they are short-lived and relatively fast-growing which results in a short residency-time for cohorts in the population, and as a result modal growth may be difficult to detect without frequent sampling. A third factor which can be a problem in any species is the difficulty of obtaining representative samples of the size-composition within the population. Clupeoids are pelagic in habit and may exhibit seasonal and age-related movements at various scales (Tham 1972, Luther 1979), and these factors increase the difficulty of obtaining representative samples.

In light of these problems it is not surprising that different growth studies on tropical clupeoids have produced some conflicting results. For the commercially and

economically important tropical anchovy genera *Encrasicholina* and *Stolephorus*, most studies have estimated that the von Bertalanffy growth constant  $K$  to be around 2.0-2.6. In contrast, several authors have estimated higher  $K$  values (3.7-5.2) for stolephorid anchovies and small clupeids of the genus *Spratelloides* (Dalzell *et al.* 1987, Milton *et al.* 1990b). Milton *et al.* (1990b) aged *E. heteroloba* from primary otolith increments and their results indicated that growth was considerably faster than estimated by the ELEFAN computer software. This example and other reports of conflicting growth estimates for tropical clupeoids (eg. Dayaratne and Gjøsaeter 1986), suggest that the suitability of conventional length-frequency analyses for tropical clupeoids needs to be assessed.

In this chapter, length-frequency information collected between 1988 and 1991 for eight species of tropical anchovy are analysed. Two methods are used, these being the computation of growth parameters using the ELEFAN computer software and the visual analysis of the progression of modes in length-frequency histograms. One aim of this study is to determine the extent to which modal progressions in length-frequency data provide accurate growth estimates for different anchovy species. To achieve this, growth estimates from modal progressions are compared to growth rates determined for each species from primary otolith increments. Also, von Bertalanffy growth parameters derived from ELEFAN are compared to those estimated from otolith ageing. Recruitment seasons in the different anchovy species are also interpreted from length-frequency information.

## 7.2 Materials and methods

### 7.2.1 Modal progression analysis

The monthly length measurements for each species were pooled into length-classes and plotted as length-frequency histograms. The length data for *S. insularis*, *S. carpentariae*, and *E. devisi* were pooled into 2mm length-classes and 5mm length-classes were used for the remaining larger species. Growth rates were calculated by linking pairs of modes in successive monthly length-frequency histograms and average

daily growth rates were calculated by subtracting the two modal lengths and dividing this value by the time elapsed between samples. Modes used to estimate growth were only chosen when the monthly data containing the connected modes was comprised 50 or more fish; two modes were only connected if the samples were collected in the same bay. Estimates of modal growth rate were only applied to fish in their first year of life in *Thryssa spp.* because growth rates slow considerably in fish older than one year.

For the stolephorid anchovies, each new mode that was connected to a subsequent mode in length-frequency histograms was denoted by a letter of the alphabet. A new letter (a,b,c etc.) was assigned each new chain of modes that were connected. In *Thryssa spp.* modes of adult fish (older than 1 year) were labelled according to the proposed age and sex of fish dominating the mode (if this was known) as follows: M1- 1+ year old males; M2- 2+ year-old males; F1- 1+ year-old females; F2- 2+ year-old females; F3- 3+ year-old females. Alternatively, some modes of adult fish were simply designated 1+, 2+ etc. when distinction of sex was not made.

Modes of adult *Thryssa spp* were assigned ages using December as the approximate 'birthdate' for year classes because spawning in *T. hamiltoni* occurs between September and February. Using this system of age assignments, modes of first year (0+) fish were not categorised as '1+' until after December in the recruitment season subsequent to that in which they were born.

#### 7.2.2 ELEFAN computer software analysis

The monthly length-frequency data for each species was pooled into 2, 5 or 10mm size classes for analysis using the ELEFAN computer software (Pauly and David 1981). The ELEFAN software only accepts a limited number of length-classes (40), so in larger species lengths were pooled into larger length-intervals than small species.

Length-data for each species were analysed in several ways: data for individual years; data over several or all years and as monthly length-frequency data pooled from all

years into a single 12 month data set. The latter was only used for the longer-lived species with annual life cycles when sample sizes in individual years were small. In these species, the temporal distribution of modal patterns was similar in consecutive years.

The ELEFAN computer software fits a modified form of the von Bertalanffy growth function to length-frequency data by choosing the best combination of growth parameters. The best growth curve is one that passes through the most peaks or modes in the length-frequency data. Details of the operation of ELEFAN are given by several authors (Pauly and David 1981, Longhurst and Pauly 1987, Morales-Nin 1989). When a clear pattern of modal growth was evident it was possible to initially fit a growth curve using the 'curve fitting by eye routine'. This allowed the estimation of an initial set of growth parameters which could be used as a starting point for the 'automatic search routine', a subprogram which automatically improved the fit of the growth curve by testing different combinations of growth parameters until the best 'rn' value (a measure of goodness of fit), was achieved. When an suitable curve could not be fitted by eye, the automatic search routine was used with several different sets of starting parameters which encompassed the expected range of possibilities.

### 7.3 Results

#### 7.3.1 Modal progressions

Length-frequency data for the eight species of anchovy collected in the present study were illustrated as monthly length-frequency histograms (Figs. 7.1-7.7, Fig. 7.9, Fig. 7.11, and Figs. 7.14-7.17). Average daily growth rates estimated for each species from the progression of linked modes in these length-frequency histograms are given in Table 7.1. The sample sizes for *S. commersonii* were considered too small to estimate growth rates.

There were two special cases where modes linked for growth rate estimations were not clearly illustrated in the length-frequency histograms. The first instance involved a

sample of 65 *S. insularis* collected in Cleveland Bay in May 1989. These had a modal length of 44 mm (labelled "b" in Fig. 7.2b) but the position of this mode was masked by a larger sample collected in the same month at Bowling Green Bay (modal length = 46mm). The Cleveland Bay mode was connected to the mode in June also from Cleveland Bay (Fig. 7.2b). The second case involved two samples of *S. nelsoni* individuals collected on the 9th and 31st of May 1989 at Pallarenda Beach. These samples were pooled for May 1989 in Figure 7.6. The sample from 9.5.89 was comprised of 223 fish with a modal length of 60mm, and the 31.5.89 sample was comprised of 142 fish with a modal length of 70mm. The calculated average daily growth rate over the 22 day interval was therefore 0.45 mm/day (Table 7.1).

### 7.3.2 Recruitment and age-composition analysis

#### 7.3.2.1 *Encrasicholina devisi*

*E. devisi* were collected between March 1988 and October 1990 (Figs. 7.1a&b). These samples were mostly comprised of individuals between 40 and 60mm in length. Smaller fish were rarely caught in seine samples suggesting that this life-stage was not common in the areas sampled. A sample of post-larval recruits was collected at Horseshoe Bay, Magnetic Island (a coralline habitat) in January 1989 (Fig. 7.1a). This site was only sampled twice in the course of the study. Some small juvenile *E. devisi* (<40mm) were also caught in May and July 1988 and in March 1990. These fish were between 30 and 40mm and would be 27 to 46 days old (from the age-length regression in Chapter 5). This indicates that recruitment occurs in summer, autumn and early winter. The low numbers of larval and juvenile fish in samples limited the conclusions that could be drawn concerning the recruitment period in *E. devisi*.

Length-frequency histograms for March, May, June and July, 1989 and March 1990 contained two modal length-groups, suggesting that temporally distinct recruitment episodes were producing cohorts in the population (Fig. 7.1a&b). The only evidence of modal growth in length-frequency histograms for this species was for two samples

in March and April 1990 (Fig. 7.1b). Small sample sizes prevented the detection of other growth trends.

#### 7.3.2.2 *Stolephorus insularis*

*S. insularis* were collected between February 1988 and April 1990 (Fig. 7.2). Small juveniles less than 40mm were caught in February, March, June and November 1988 and between February and November 1989. This suggests that *S. insularis* recruits throughout the year. In larger samples, two or three distinct modes were evident in monthly length-frequency histograms (February, March, November 1988, May-August 1989 and April 1990-Fig. 7.2). This suggests recruitment into the population may occur in pulses. Cohort growth was evident in the autumn and winter months when the largest samples were collected.

The progression of modal groups in successive months suggests that there may be a succession of cohorts growing in the population during each year. Therefore it is suggested that *S. insularis* has a lifespan of less than one year.

#### 7.3.2.3 *Stolephorus carpentariae*

Samples of *S. carpentariae* were collected between December 1987 and April 1991 (Figs. 7.3, Fig. 7.4). Small juveniles (20-40mm) were common between October and December but were also present in smaller numbers between January and June (Fig. 7.3, Fig. 7.4). This suggests that recruitment in *S. carpentariae* mostly occurs in the spring/summer but some recruitment also occurs to early winter.

Modal shifts in the length-frequency histograms for *S. carpentariae* indicate a general trend of length increase in the population during the course of the year (Fig. 7.3, Fig. 7.4). This trend is evident between December 1987 and July 1988 (in spite of small sample sizes) and between November 1988 and May 1989 (Fig. 7.3, Fig. 7.4). During the period, November 1988 to September 1989, three modal groups or cohorts were present in samples (Fig. 7.3). The first cohort in 1989 had grown to a mature size by

May (Fig. 7.3) and cohorts of adult fish from that year disappeared after December. This indicates that *S. carpentariae* attains mature sizes within one year and this species has a longevity of less than one year (Fig. 7.3, Fig. 7.4).

#### 7.3.2.4 *Stolephorus nelsoni*

*S. nelsoni* were collected between January 1988 and April 1991 (Figs. 7.5b, Fig. 7.6). Length-frequency data collected in 1984 (Hoedt 1984) was also analysed (Fig. 7.5a). Most post-larval and small juvenile fish were caught between the months of November and December, suggesting that this is the period of peak recruitment (Figs. 7.5b, Fig. 7.6). Some small juveniles were also caught in April 1989 indicating that some recruitment occurs in Autumn also (Fig. 7.5b).

The trend of modal movement in length-frequency histograms indicates an annual growth cycle in the population. Fish from the spring/summer recruitment attain lengths up to 60-80mm by April/May the following year (approximately 6-7 months). Modes of adults from the previous year's recruitment persisted up to September/November and even as late as January in the next year. The loss of the mode of adult fish at the end of the year indicates that *S. nelsoni* has a longevity of 1 year or less (Figs. 7.5b, Fig. 7.6).

#### 7.3.2.5 *Stolephorus commersonii*

*S. commersonii* were sampled between January 1988 and April 1991 (Fig. 7.7). Small juvenile recruits (30-50 mm) were most common in samples between October and January but were also present in April and May (Fig. 7.7). This suggests that the recruitment period occurs over an extended period in this species but peaks during the spring/summer months (Fig 7.7).

The progression of modes of juvenile fish between January and May in 1988, indicates that recruits from the spring/summer period can grow rapidly attaining lengths of up to 110-130mm by May (Fig. 7.7). Changes in modal patterns indicate that juvenile fish

grow to around 90mm in February and probably reach 120-140mm between May and July (Fig. 7.7). Length-frequency data for *S. commersonii* therefore suggests that this species grows rapidly with a life-cycle of approximately one year.

#### 7.3.2.6 *Thryssa aestuaria*

*T. aestuaria* were collected between February 1988 and April 1991 (Fig. 7.9). Small juvenile *T. aestuaria* were caught in spring (Fig. 7.8). Only a single mode of similar-sized juveniles were collected in months subsequent to the spawning period suggesting that the recruitment season in this species may be of short duration (Fig. 7.8). The progression of modes in length-frequency histograms indicate that *T. aestuaria* attains lengths of around 100-115mm within one year (Fig. 7.8). The presence of modes of adult fish (1+) in addition to the growing juvenile cohort in February 1988 and April 1989/90, indicates that some individuals survive into their second year (Fig. 7.8).

Combined length-frequency data for male and female adult *T. aestuaria* were separately plotted as length-frequency histograms (Fig. 7.9). This figure indicates that females grow larger than males. The length-distributions of adults in monthly length-frequency histograms were sometimes divided into two modes (Fig. 7.8). When information on the sexual composition of samples was available (eg. February and July 1988) it was apparent that the smaller mode (mode 'M1') was comprised of male fish and the larger mode was females (mode 'F1'). Therefore the modes 'M1' and 'F1' probably represent 1+ males and females respectively. Length-frequency information therefore indicates that *T. aestuaria* has a longevity of between 1 and 2 years.

#### 7.3.2.7 *Thryssa setirostris*

Length-frequency data for *T. setirostris* was collected between February 1988 and April 1991 (Fig. 7.10a&b). Monthly sample sizes were often small, so to better illustrate population growth trends, the monthly length data from all years (including 1984-Hoedt 1984) were pooled to give a twelve month length-frequency data set (Fig.



7.11). For analysis of this figure, it was assumed that growth and recruitment were similar each year. Length-frequency data for adult male and female fish were each pooled as two length-frequency histograms to compare sizes between sexes (Fig. 7.12).

Juvenile *T. setirostris* were uncommon in samples but most small juveniles (30-60mm) were collected between October and December indicating a spring-summer recruitment period (Figs. 7.10a&b, Fig. 7.11). The growth of juvenile fish during their first year could be inferred from modal progressions in length-frequency data (Figs. 7.10, Fig. 7.11). The 0+ modes in November 1988, November 1989 and October 1990 were small juveniles recruited in spring in those years (Fig. 7.10a&b). The main mode of 0+ recruits was 100mm in February 1988 and March 1989. In April 1991 the modal size of recruits was 145mm (Fig. 7.10a&b). These growth trends indicate that first year *T. setirostris* are approaching mature sizes by the autumn/winter following hatching, therefore this species probably attains mature sizes within 1 year.

The combined length-frequency histograms for fish longer than 100mm for each sex indicated that male and female fish grow to different sizes (Fig. 7.12). The length-frequency histograms for each sex were each comprised of two modes; modes in female fish occurred at 195 and 205mm, and in males at 180 and 195mm (Fig. 7.12). This suggests that female *T. setirostris* attain larger sizes than males.

Adult fish in the monthly length-frequency histograms comprised 2-3 modes in larger samples (Fig. 7.10, Fig. 7.11). These modes were labelled according to the known sex and proposed age of fish comprising them. Some of the largest samples of adult *T. setirostris* were caught trawling in September and October 1988 and all adults in these samples were sexed (Fig. 7.10a). In September and October most fish were males. In both of these months the mode labelled '0+(m)' at 175-185 mm was comprised of male fish and these were thought to be males born at the end of 1987 (Fig. 7.10a). Therefore these fish were approaching 1 year of age. Male fish also dominated the second mode

('M1') at 195mm in these months, and these were thought to be 1+ males hatched in late 1986 or early 1987 and approaching 2 years of age (Fig. 7.10a). The October 1988 sample contained some female fish and two modal sizes were distinguished amongst these. The first mode was at 195 mm (obscured by 'M1') and the second at 215mm (mode 'F1'). The first mode was thought to be comprised of females close to 1 year of age and the second mode was thought to be females almost 2 years of age. The 'M1' and 'F1' modes were also present in 1989. In summery, the length-frequency data indicates that *T. setirostris* grows to a maximum of 175-195mm in one year; small sample sizes prevented a confident estimation of longevity but at this stage it appears as though individuals live for one to two years.

#### 7.3.2.8 *Thryssa hamiltoni*

Length-frequency data for *T. hamiltoni* collected in 1984 (Hoedt 1984), and between February 1988 and April 1991 were analysed (Figs. 7.13-7.16). Length-frequency data for each month from all years were pooled to better illustrate recruitment and modal patterns (Fig. 7.17). The monthly length-frequency histograms from all years indicate that new recruits appear in catches between October and December, however, small juveniles (< 50mm) were caught as late as April in 1990 indicating that the recruitment season can protract into late summer/autumn (Fig 7.17). An initial large pulse of recruits followed by several smaller pulses was evident in all years (Figs. 7.13-7.16). This suggests that recruitment in *T. hamiltoni* may occur in pulses (Figs. 7.13-7.16). The pooled monthly length-frequency histograms (Fig. 7.17) revealed that two major pulses of recruits dominated catches in most years; the first pulse can be seen in February with a modal size of 115mm (this mode was present in February in 1984, 1988 and 1989), and the modal size of this cohort appeared to increase to 175mm in August and 185mm in September (Fig. 7.17). The second, smaller can be seen in the pooled length-frequency histograms to progress from 105mm in March to 150mm in September (Fig. 7.17).

Measurements of 426 male and 203 female *T. hamiltoni* were each combined and plotted as length-frequency histograms to compare the size composition of adult fish of each sex (Fig. 7.18). The positions of modes in these graphs indicate that females grow larger than males (maximum length was 253mm in females and 225mm in males). In light of the sexual growth differences for adults of this species and the small sample sizes of adult fish in many months it was deemed necessary to separately analyse the monthly length-frequency data for male and female fish before interpreting the length-frequency histograms for individual years. Length data for fish of each sex (using samples where sexes were determined) from all years were pooled into single 12 month data sets (Fig. 7.19a&b). For male fish, the largest samples of sexed fish were in February (Fig. 7.19a). The February length-frequency histogram was comprised of three distinct modes at 170, 195 and 210mm respectively (Fig. 7.19a). It is thought that these modes represented male fish aged 1+, 2+ and 3+ years respectively. The progression of the first two modes could be followed in consecutive months, supporting the proposal that these modes represent year classes (Fig. 7.19a). In September, the 1+ mode appeared to have progressed to 190 mm and the 2+ mode to 210mm (Fig. 7.19a). The combined monthly length-frequency histograms for female fish for all years also appeared to contain three modes of adult fish. However, the position of these modes was less consistent in successive months due to the smaller numbers of female fish in most catches (Fig. 7.19b). At the beginning of the year, 1+ and 2+ females appeared to have lengths of 185-215mm and 235mm respectively, and these grew to around 220 and 245mm respectively by September/October (Fig. 7.19b). Females assigned the age 3+ were 250-255mm in length but these individuals were rare in trawl samples (Fig. 7.19b). For both males and females, 1+ and 2+ adults appeared to comprise the bulk of the adult population in Cleveland Bay.

The modes identified in Figure 7.19 could also be identified in the monthly length-frequency histograms (combined sexes), for the years 1984, and 1988 to 1991 (Figs 7.13-7.16). The identification of modes was assisted by the fact that in many trawl samples, similar-sized fish were often dominated by one sex. Modes were labelled

according to the dominant sex of individuals comprising them (when this was known), and the probable age of the individuals that dominated the mode.

Adult male fish were numerically dominant in samples throughout the study and generally comprised two distinct modes in length-frequency histograms labelled 'M1' and 'M2' (Figs. 7.13-7.16). Mode 'M1' probably represents 1+ males and the 'M2' mode, 2+ males (Figs. 7.13-7.16). Mode 'M1' was situated at lengths of 170-175mm in February each year (Figs. 7.13-7.16), and increased in length to 185-190mm by September (Figs. 7.13, Fig. 7.15). The 'M2' mode was consistently located at 195mm at the beginning of each year and appeared to grow to 210mm by September (Figs. 7.13-7.16). Modes of female fish were generally distinguishable from the male modes due to size-differences. The mode 'F1' was comprised of female fish of lengths 205 to 225mm and this was thought to represent 1+ females (Figs. 7.13-7.15). Mode 'F2' at 225 to 245mm was thought to represent 2+ female fish, and mode 'F3' at 250mm probably represents 3 + females (Figs. 7.13-7.16).

The dominant modes of adult fish could also be traced in the pooled length-frequency histograms for all years, indicating that their position was consistent between years (Fig. 7.17).

### 7.3.3 ELEFAN analyses

The monthly length-frequency data for each species of anchovy was analysed using the ELEFAN computer software. Von Bertalanffy growth parameters were calculated for each species in individual years and also for combined years (Table 7.2). Values of the growth parameters  $K$  and  $L_{\infty}$  were consistent for most of the study species when different data sets were analysed (Table 7.2).  $K$  and  $L_{\infty}$  values differed in male and female *T. hamiltoni*.

Values of 'K' from Table 7.2 were plotted against corresponding  $L_{\infty}$  values (Fig. 7.20). A linear regression was fitted to this data; the relationship between these parameters was:  $K = -0.007637L_{\infty} + 3.0694$  ( $r^2 = 0.65$ ).

#### 7.3.4 Comparisons with otolith-derived growth estimates

##### 7.3.4.1 Modal progressions and primary otolith increments

The accuracy of growth rate estimates obtained from the modal progressions was tested by comparing these with growth rates during the 'linear growth phase' calculated from primary otolith increments (Table 7.3). There was good agreement between the two methods for *E. devisi*, *S. nelsoni*, *T. aestuaria*, *T. setirostris* and *T. hamiltoni*, which suggests that modal progressions in length-frequency histograms can sometimes provide reasonable estimates of growth for these species (Table 7.3). Growth rate estimates from length-frequency data were considerably lower than those from primary otolith increments in *S. carpentariae* and *S. insularis* (Table 7.3).

##### 7.3.4.2 ELEFAN and otolith-derived growth estimate

Table 7.4 summarises the von Bertalanffy growth parameters estimated from otolith ageing methods and those calculated by the 'ELEFAN' software in those species where the data was available. Values of  $L_{\infty}$  calculated by otoliths and ELEFAN were generally similar and close to the expected maximum size attained by each species (Table 7.4). Values of K showed close agreement or were within 25% of each other for *S. nelsoni*, *S. commersonii*, *T. aestuaria* and *T. hamiltoni* (Table 7.4). This finding indicates that there is reasonable agreement between otolith and length-frequency based methods for growth estimations in these species. In contrast, K values from otoliths were considerably higher than ELEFAN derived estimates in the smaller stolephorids, *E. devisi* and *S. carpentariae*. A higher K value from primary otolith increments than from ELEFAN was also obtained for *T. setirostris*, however small sample sizes in both analyses make these results open to question (Table 7.4).

##### 7.3.4.3 Length-frequency data and seasonal growth rings

The ages assigned to modes in length-frequency histograms for *T. hamiltoni* were consistent with lengths-at-age estimated from counts of seasonal growth rings in otoliths (Table 7.5). However, the otolith ageing method indicated that a few individuals of age 4+ years were present in the population, this being older than the maximum age of 3+ found from length-frequency information (Table 7.5).

Seasonal growth ring counts gave the oldest individuals of *T. aestuaria* and *T. setirostris* as being 1 and 2 years respectively, this being consistent with the results of length-frequency analyses. The good agreement between otolith-based ageing methods and length-frequency analysis for *Thryssa spp.*, supports the validity of each these methods for ageing these species.

#### 7.4 Discussion

While there have been a large number of studies of growth in tropical clupeoid fishes based on the analysis of length-frequency information, there have only been a small number where the results are compared with those obtained using other ageing methods (eg. Milton *et al.* 1990b, Wise and Potter 1995). The study of age and growth in tropical clupeoid fishes has improved with increasing understanding and use of otolith-based ageing methods (eg. Struhsaker and Uchiyama 1976, Dayaratne and Gjøsæter 1986, Milton *et al.* 1990b, Milton *et al.* 1991). In the present study, age and growth information was available from both primary and seasonal otolith increments enabling comparisons with the results of length-frequency based methods for the species studied.

In the present study, the two methods (otolith and ELEFAN) gave consistent estimates of von Bertalanffy growth parameters for five of the larger species of anchovy. This indicates that ELEFAN is suitable for estimating growth in tropical anchovies of various sizes. However, there was poor agreement between parameter estimates for two small species with otoliths giving higher K values. In recent years the ELEFAN computer software has seen increasing use for estimating growth in tropical fishes.

However, this computer software, like any form of length-frequency analysis, has an increased potential for producing biased estimates in short-lived tropical fish with protracted recruitment (Brothers 1979). Small tropical clupeoids exhibit biological characteristics which increase the possibility of obtaining biased growth estimates from length-frequency information (Wise and Potter 1995). Thus it is important to test the applicability of ELEFAN for such species.

Values of the von Bertalanffy growth parameter  $K$  obtained using ELEFAN for stolephorid anchovies in the present study ranged from 2.2 to 2.8. Estimates using data sets from differing time periods were also reasonably consistent, and were very close in *S. carpentariae* and *S. nelsoni*. The values calculated in the present study are consistent with most published estimates for Indo-Pacific stolephorid anchovies (Table 7.6). Otoliths gave higher  $K$  values than length-frequency analysis for *E. devisi* and *S. carpentariae* in the present study, these values being similar to the high length-frequency derived 'K' values calculated for *E. devisi* in Papua New Guinea and *E. heteroloba* in New Caledonia (Table 7.6). Recent studies using otoliths indicate that  $K$  values in small tropical clupeoids are probably higher than previous length-frequency derived estimates, this reflecting the short lifespan of these species (Milton *et al.* 1991, Milton *et al.* 1993, Milton and Blaber 1995). Wise and Potter (1995) showed that ELEFAN tends to give biased estimates of  $K$  for small tropical baitfish.

While it is apparent that continuous recruitment in these species can mask modal shifts in length-frequency histograms giving biased growth estimates, in some instances, length-frequency information appears to provide useful growth information in small tropical clupeoids. Milton *et al.* (1990b) found that ELEFAN and otolith-derived growth estimates were in agreement for the small tropical clupeid, *Spratelloides delicatulus*. The growth parameter  $K$  for *S. delicatulus* in their study was relatively high, ranging from 4.35-4.5, and was similar to values estimated for this species in other Indo-Pacific countries (eg. Dalzell *et al.* 1987).

With the exception of the otolith-derived value of K for *T. setirostris*, values of K estimated from otoliths and length-frequency data for *Thryssa* species in this study ranged from 0.64-1.85. This value is consistent with the K value of 1.3-1.7 calculated for another large tropical anchovy, *Cetengraulis mysticetus* from length-frequency data (Barrett and Howard 1961). Estimates of K in *Amblygaster sirm* using length-frequency information from New Caledonia ranged from 1.1-1.58 (Conand 1991). These values are again consistent with the results of the present study.

When larger samples of the smallest stolephorid anchovies (*E. devisi* and *S. insularis*) were collected, 2-3 modal size-groups were present in monthly length-frequency histograms. This suggests that recruitment occurred in pulses giving rise to cohorts of similar-sized fish. The presence of such cohorts in well sampled populations of small clupeoids with prolonged breeding should allow some interpretation of growth. In the present study, comparisons were made between growth estimates derived from the progression of individual modes in length-frequency histograms and linear growth rates from primary otolith increment counts. With the exception of *S. carpentariae* and *S. insularis* there was reasonable consistency between the two methods. This suggests that modal progressions can sometimes provide meaningful growth estimates in different-sized tropical anchovies. Analyses of length-frequency histograms for small tropical anchovies in the present study indicates that modal progressions are usually only traceable over short time periods (1-3 months), emphasising the need to obtain frequent and representative samples for these species.

Average growth rates obtained from modal progressions for species in the present study ranged from 0.12-0.67 mm/day. These growth rates are within the range of those reported in other length-frequency studies on tropical clupeoids (Table 7.7). Robertson and Duke (1990) estimated that juvenile *T. hamiltoni* (near Townsville), grew from 26 to 95 mm in 258 days (0.26 mm/day). However, their length-frequency data suggests modes corresponding to smaller fish (26-75 mm), grew faster than 0.26 mm/day, which would bring their estimate closer to value estimated for *T. hamiltoni* in the



present study (Table 7.7). The growth rate of 0.15-0.19 mm/day estimated for *S. carpentariae* by Robertson and Duke (1990) was close to the average growth rate of 0.12 mm/day estimated for this species from length-frequency data in the present study (Table 7.7). The high growth rates of juvenile *Sardinella sirm* (a large Indian clupeid) estimated by Lazarus (1987) are close to the growth rates estimated for *Thryssa spp.* in the present study (Table 7.7).

In the present study, sexual growth differences were evident from the length-frequency histograms in the three species of the genus *Thryssa*. In all species of *Thryssa*, females appeared to be larger and grow faster than males. This finding is consistent with the growth curves obtained using seasonal growth rings in otoliths (see Chapter 6). For *T. hamiltoni*, the sizes-at-age for each sex deduced from the location of modes in length-frequency histograms were in agreement with those estimated from seasonal growth rings in otoliths. This finding emphasises the importance of analysing length-frequency data separately for each sex in large tropical clupeoids. There are no reports of sexual growth differences in *Thryssa spp.* in the literature however, females have been reported to grow larger than males in some tropical clupeids (Williams and Clarke 1983, Conand 1991).

Table 7.1. Growth rates estimated from modal progressions in seven species of anchovy. Dates and lengths ( $L_1$  and  $L_2$ ) of linked modes used for growth rate estimates.

Species	Year	Mode	Months	$L_1$	$L_2$	GR (mm/day)	Figure
<i>E. devisi</i>	1990	a	Mar.-Apr.	42	50	0.27	7.1b
<i>S. insularis</i>	1988	a	Aug.-Nov.	42	48	0.2	7.2
	1989	b	May-Jun.	44	50	0.2	7.2
	1989	c	Jun.-Jul.	36	38	0.07	7.2
	1989	c	Jul.-Aug.	38	46	0.26	7.2
	1989	d	Jul.-Aug.	48	52	0.13	7.2
<i>S. carpentariae</i>	1988	a	Nov.-Feb.	36	48	0.13	7.3
	1988	a	Feb.-May	48	60	0.13	7.3
	1988	a	May-Aug.	60	64	0.04	7.3
	1988	b	Nov.-Feb.	45	54	0.14	7.3
	1989	c	Jul.-Aug.	48	54	0.2	7.3
	1989	d	Jul.-Aug.	58	60	0.07	7.3
	1989	d	Aug.-Sep.	60	64	0.13	7.3
	1989	e	Oct.-Nov.	36	40	0.13	7.3
1990	f	Mar.-Aug.	44	62	0.12	7.4	
<i>S. nelsoni</i>	1984	a	Mar.-Apr.	60	74	0.47	7.5
	1988	b	Feb.-Mar.	65	80	0.5	7.5
	1988	c	Apr.-May	80	85	0.17	7.5
	1988	c	May-Sep.	85	93	0.06	7.5
	1988	d	Nov.-Dec.	35	40	0.17	7.5
	1988	e	Nov.-Dec.	55	65	0.33	7.5
	1989	f	Feb.-Mar.	50	60	0.33	7.6
	1989	f	Mar.-May	60	85	0.42	7.6
	1989	*	9/5-31/5	60	70	0.45	7.6
	1989	g	Jun.-Jul.	80	88	0.25	7.6
	1990	h	Dec.-Jan.	35	55	0.67	7.6
<i>T. aestuaria</i>	1990	a	Oct.-Dec.	25	47.5	0.38	7.9
	1990	a	Dec.-Jan.	47.5	65	0.58	7.9
<i>T. setirostris</i>	1988	a	Feb.-Sep.	100	180	0.38	7.11
	Comb.	a	Feb.-Apr.	100	145	0.75	7.12
<i>T. hamiltoni</i>	1984	a	Feb.-May	100	175	0.83	7.14
	1988	a	Feb.-Apr.	115	150	0.58	7.15
	1989	a	Feb.-Apr.	114	150	0.6	7.16
	1989	b	Mar.-May	105	140	0.58	7.16
	1989	c	Apr.-May	85	105	0.67	7.16

Table 7.2. von Bertalanffy growth parameters calculated using the ELEFAN computer software. Growth parameters were calculated for in each species individual years and/or combined years. In *T. hamiltoni* growth parameters were also separately estimated for each sex.

	Year	$L_{\infty}$ (mm)	K (yr <sup>-1</sup> )	m	
<i>E. devisi</i>	1989	60	2.8	0.31	
	1989/90	56	2.4	0.15	
<i>S. insularis</i>	1988	58	2.8	0.23	
	1989	55	2.2	0.27	
<i>S. carpentariae</i>	1988/89	70	2.3	0.17	
	1990/91	62	2.4	0.25	
<i>S. nelsoni</i>	1988	95	2.4	0.37	
	1989	98	2.4	0.19	
	1990/91	98	2.7	0.35	
<i>S. commersonii</i>	1988/89	150	2.2	0.16	
	1988/91	155	2.6	0.16	
	Combined*	160	2.8	0.14	
<i>T. aestuaria</i>	1988/91	118	1.6	0.22	
<i>T. setirostris</i>	1988-89	197	1.4	0.17	
	1988-91	200	1.6	0.2	
	Combined*	200	1.4	0.15	
<i>T. hamiltoni</i>	1988	200	1.4	0.27	
	1989	240	0.95	0.18	
	1990/91	220	1.4	0.18	
	females	1988/89	235	1.34	0.22
	males	1988/91	215	0.9	0.26

\*-monthly length-data from all years combined into a single twelve month set of length-frequency histograms.

Table 7.3. A comparison of growth rates (in mm/day) estimated from modal progressions and primary otolith increment counts. The estimated growth rates in *Thryssa spp.* were for the juvenile growth phase only. n-number of modal pairs used to obtain a mean growth rate.

Species	Length-frequency			Primary increments
	n	range	mean	
<i>E. devisi</i>	1	0.27	0.27	0.23-0.55
<i>S. insularis</i>	5	0.07-0.26	0.17	0.26-0.34
<i>S. carpentariae</i>	9	0.04-0.14	0.12	0.5
<i>S. nelsoni</i>	11	0.06-0.67	0.35	0.39
<i>T. aestuaria</i>	2	0.38-0.58	0.48	0.44
<i>T. setirostris</i>	2	0.38-0.75	0.57	0.69
<i>T. hamiltoni</i>	5	0.58-0.83	0.65	0.78

Table 7.4. Von Bertalanffy growth parameters calculated for anchovies using primary and seasonal otolith increment counts and from length-frequency analysis using ELEFAN computer software.

Species	Parameter	Primaries	Seasonals	ELEFAN
<i>E. devisi</i>	L <sub>∞</sub> (mm)	94	-	56-64
	K	4.45	-	2.4-2.8
<i>S. carpentariae</i>	L <sub>∞</sub> (mm)	70.6	-	62-70
	K	7.09	-	2.3-2.4
<i>S. nelsoni</i>	L <sub>∞</sub> (mm)	99.8	-	95-98
	K	2.87	-	2.4-2.7
<i>S. commersonii</i>	L <sub>∞</sub> (mm)	381	-	150-160
	K	2.87	-	2.2-2.8
<i>T. aestuaria</i>	L <sub>∞</sub> (mm)	147.6	-	118
	K	1.56	-	1.6
<i>T. setirostris</i>	L <sub>∞</sub> (mm)	186	-	197-200
	K	2.77	-	1.4-1.6
<i>T. hamiltoni</i>	L <sub>∞</sub> (mm)	216	-	223
	K	1.85	-	1.26
<i>T. hamiltoni</i> (males)	L <sub>∞</sub> (mm)	-	214-218	215
	K	-	0.64-0.85	0.9
<i>T. hamiltoni</i> (females)	L <sub>∞</sub> (mm)	-	238-259	235
	K	-	0.66-1.12	1.34

Table 7.5. The range of lengths-at-age estimated for *Thryssa hamiltoni* from seasonal growth ring counts and from modes identified in length-frequency histograms.

Age	Seasonal rings		Length-frequency	
	Male	Female	Male	Female
1 year	151-196	190-220	170-190	195-225
2 year	189-213	220-246	190-210	235-250
3 year	200-210	240-248	210-225	250-255
4 year	208-216	250-251		

Table 7.6. Values of the growth parameters  $L_{\infty}$  and K estimated from length-frequency information for Indo-Pacific stolephorid anchovies.

Species	$L_{\infty}$ (mm)	K	Author
<i>E. heteroloba</i>	89	2.08	Tham (1966)
<i>S. insularis</i>	99	2.05	Tham (1966)
<i>E. heteroloba</i>	79-87	2.4-2.6	Rawlinson (1989)
<i>E. heteroloba</i>	91	2.11	Muller (1977)
<i>E. heteroloba</i>	96	4.09	Dalzell & Wankowski (1980)
<i>E. heteroloba</i>	-	3.7-4.8	Conand (1988)
<i>E. devisi</i>	82	5.037	Dalzell & Wankowski (1980)
<i>E. devisi</i>	102.5	2.8	Luther (1990)
<i>E. devisi</i>	113	2.04	Syda Rao (1988a)
<i>S. waitei</i>	134.6	1.54	Luther (1990)
<i>S. bataviensis</i>	116	1.97	Syda Rao (1988b)

Table 7.7 Growth rates in tropical clupeoids estimated from modal progressions in length-frequency data.

Species	Locn/Author	Length range(mm)	Interval (months)	Growth (mm/day)
<i>Thryssa hamiltoni</i>	Aust. (1)	26-95	8.5	0.26
<i>Thryssa mystax</i>	India (2)	30-90	5.5	0.36
<i>Stolephorus carpentariae</i>	Aust. (1)	32-50	4	0.15
<i>S. carpentariae</i>	Aust. (1)	0-57	10	0.19
<i>Sardinella sirm</i>	India (3)	55-110	-	0.67-1.0
<i>S. sirm</i>	India (3)	75-175	6	0.55

1-Robertson and Duke (1990); 2-Venkataraman (1956); 3-Lazarus (1987)

Figure 7.1. Monthly length-frequency histograms for *Encrasicholina devisi*.(a) 1988 and 1989; (b) 1990.



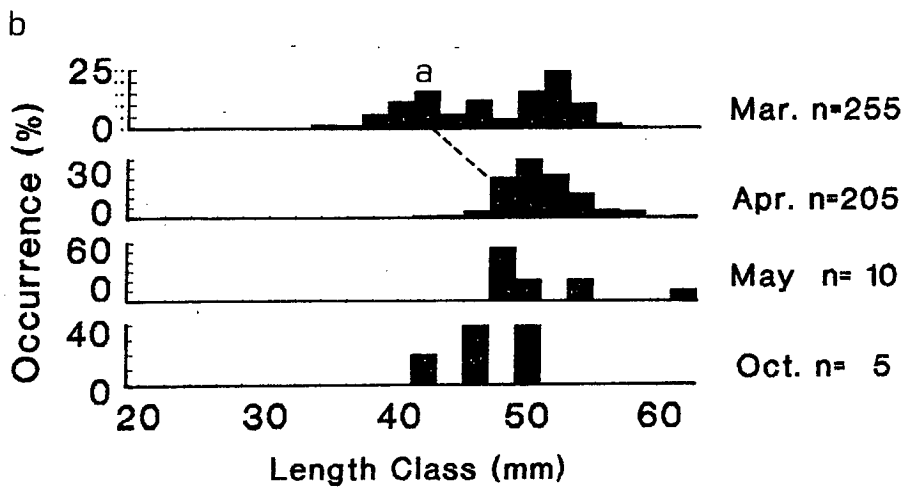
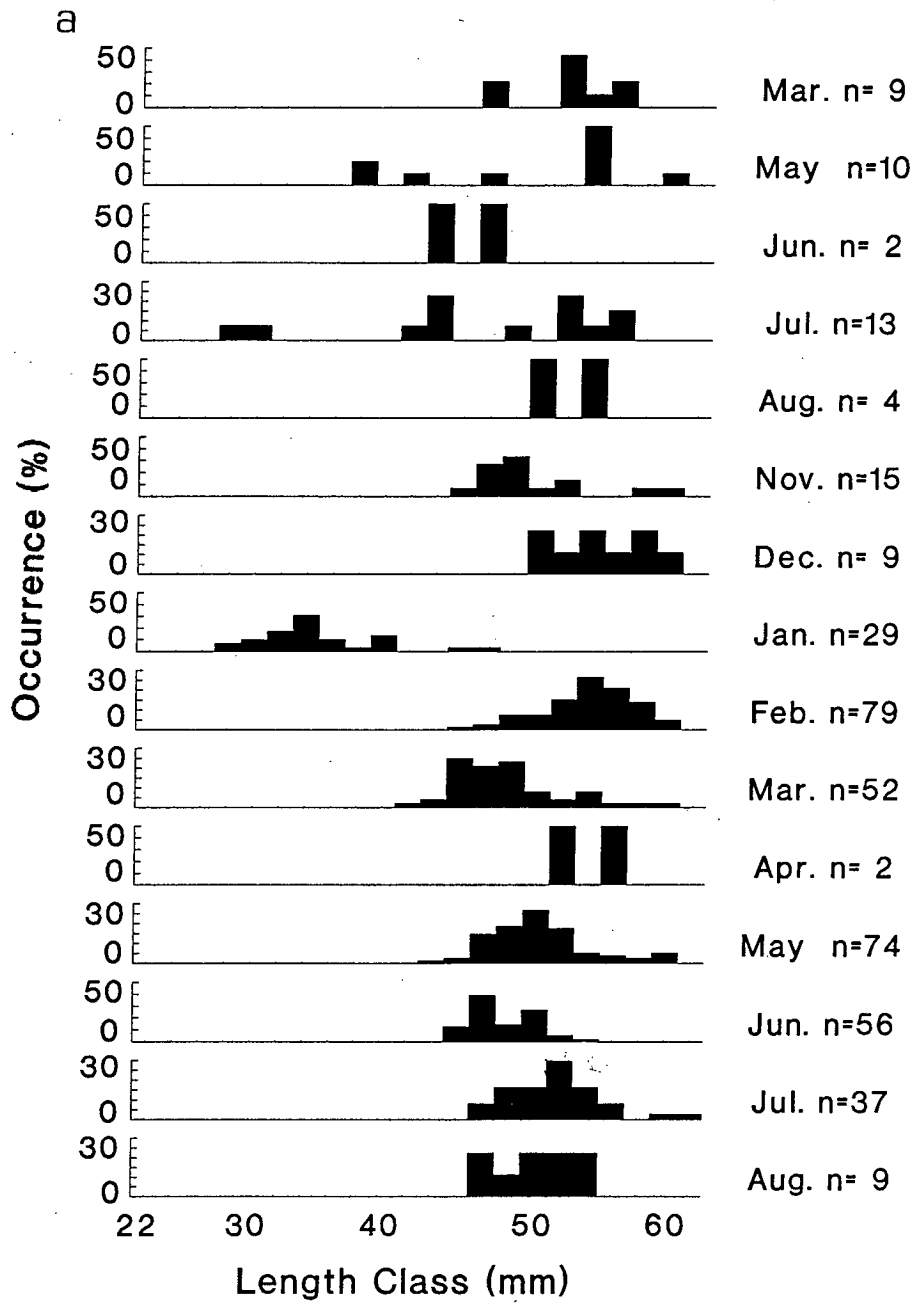


Figure 7.2. Monthly length-frequency histograms for *Stolephorus insularis* for February 1988 to April 1990.

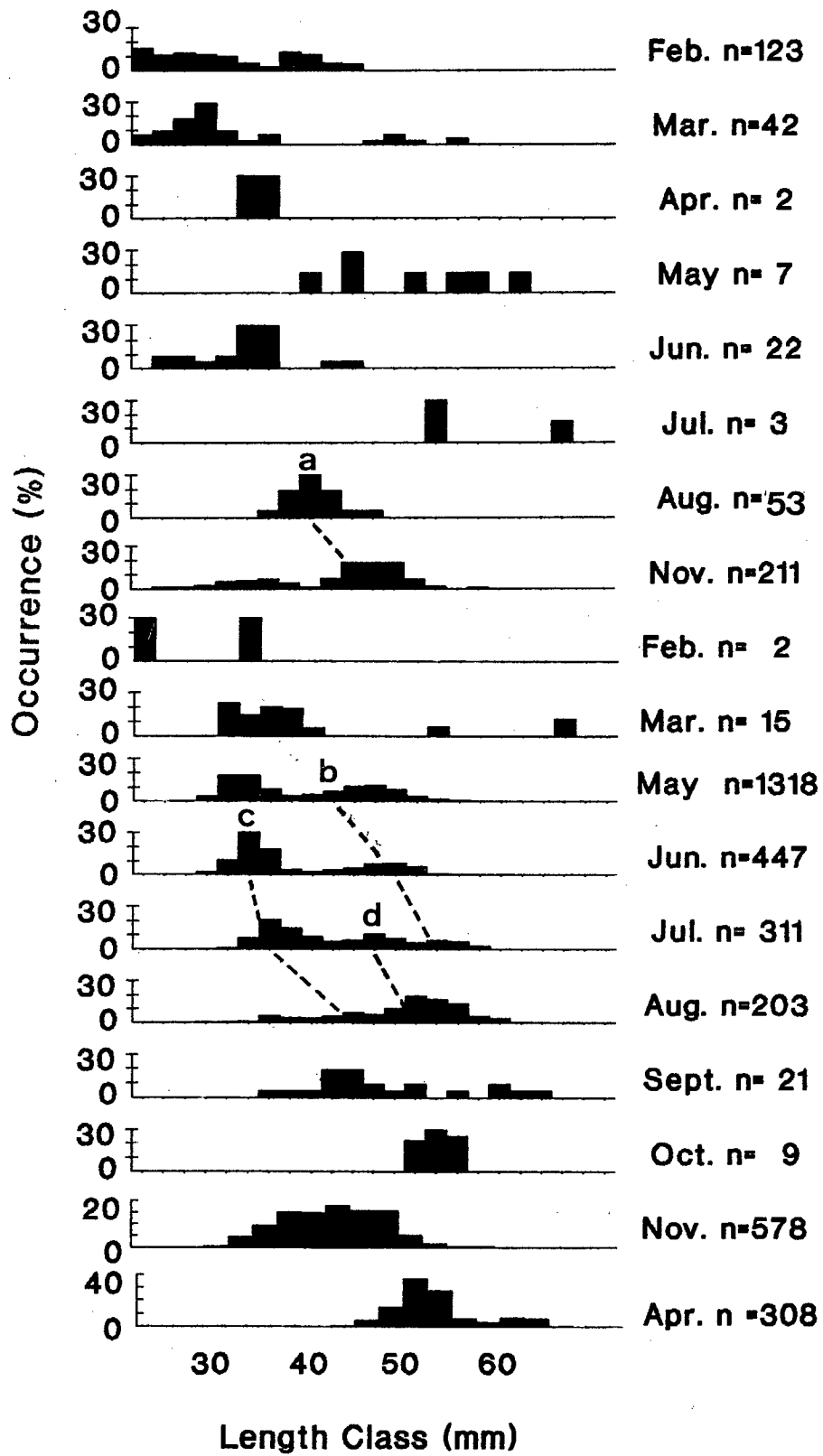


Figure 7.3. Monthly length-frequency histograms for *Stolephorus carpentariae* for December 1987 to December 1989.

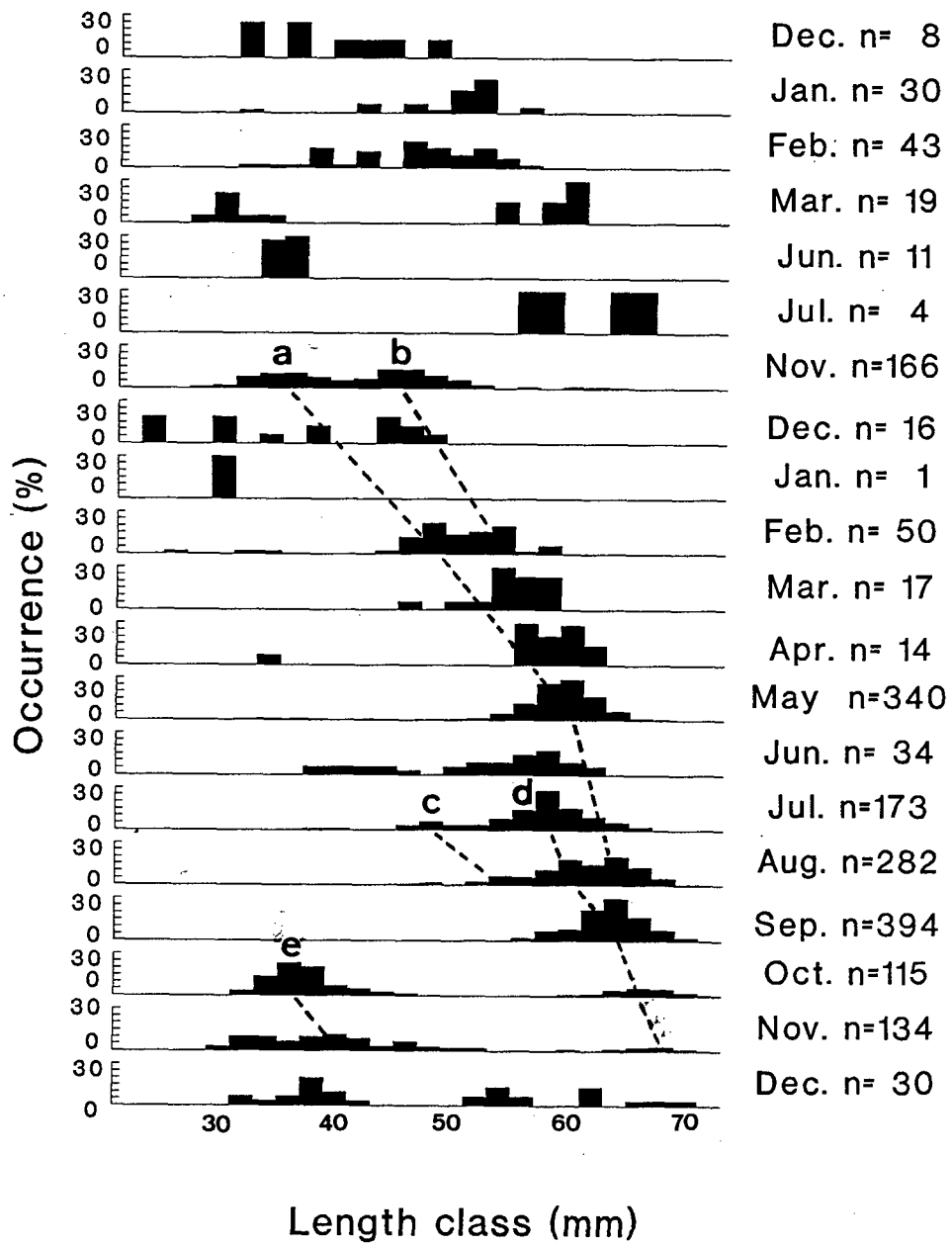


Figure 7.4 Monthly length-frequency histograms for *Stolephorus carpentariae* for March 1990 to April 1991.

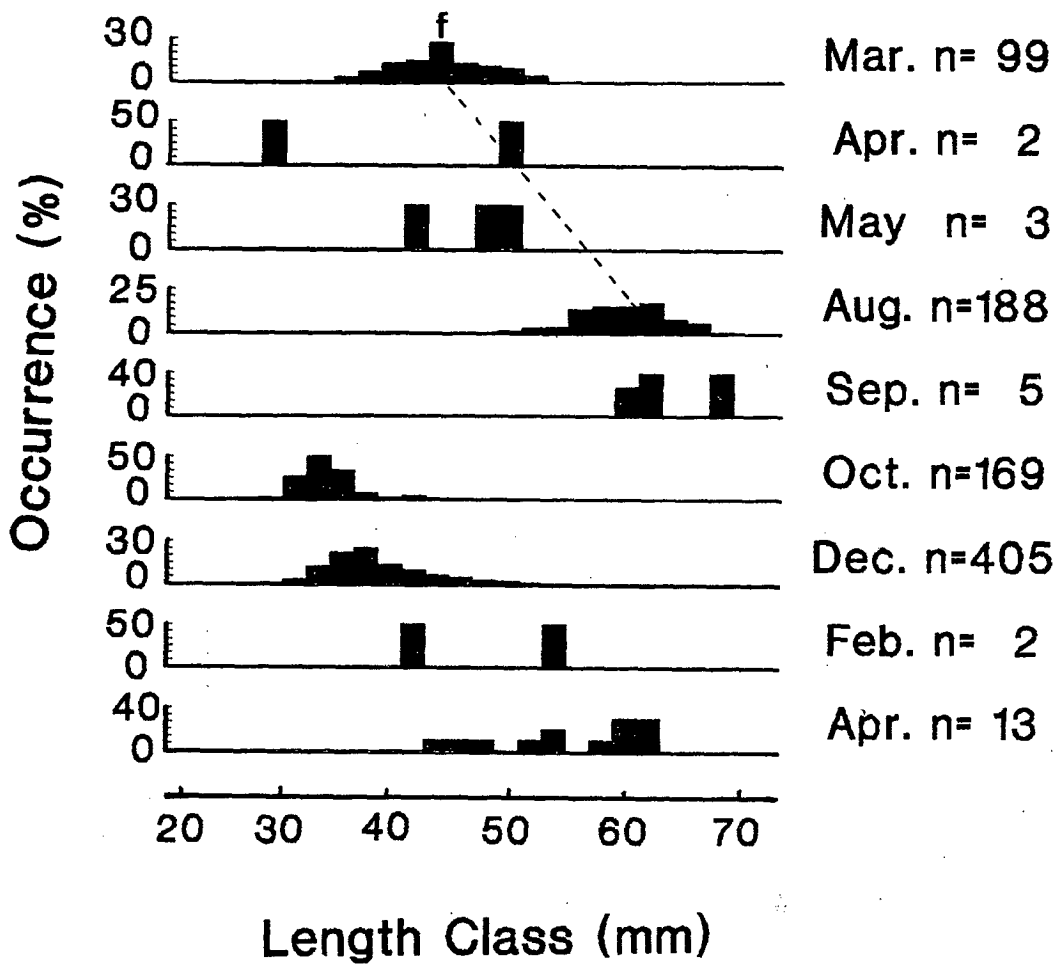


Figure 7.5. Monthly length-frequency histograms for *Stolephorus nelsoni*. (a) 1984 (from Hoedt 1984); (b) 1988.



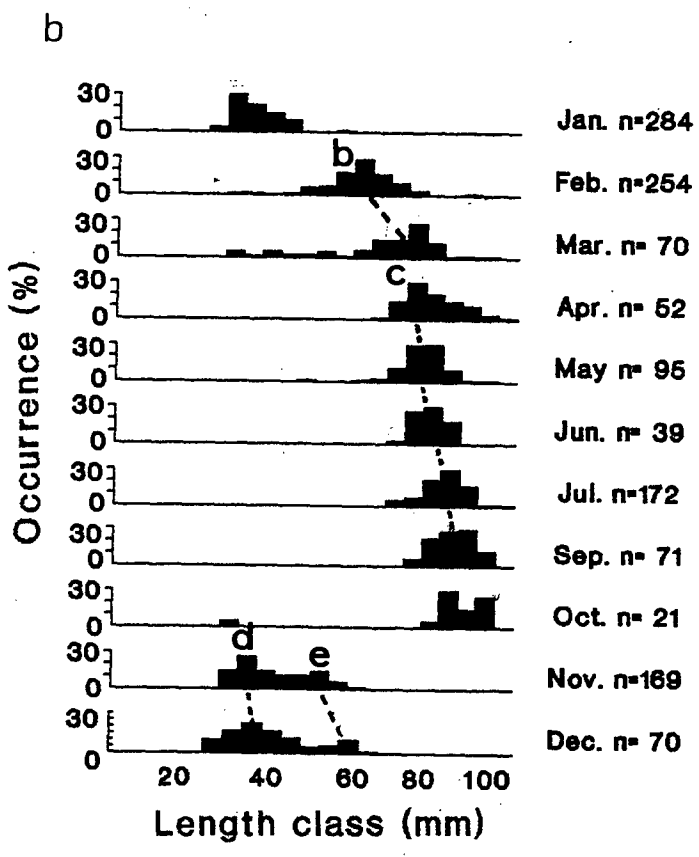
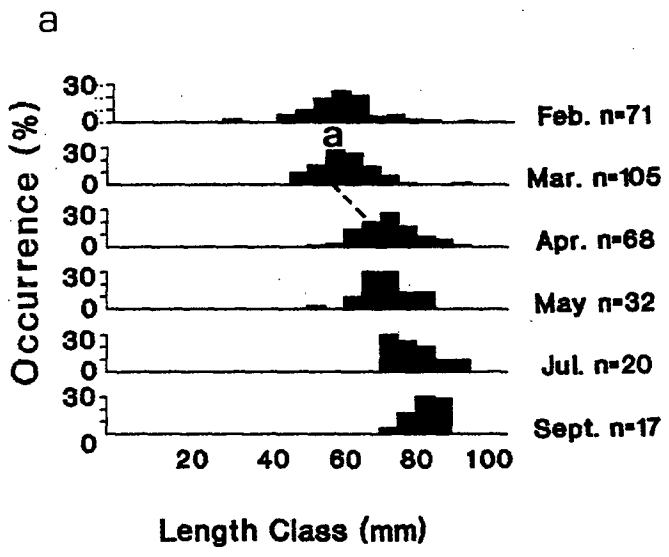


Figure 7.6. Monthly length-frequency histograms for *Stolephorus nelsoni* for 1989 to 1991.

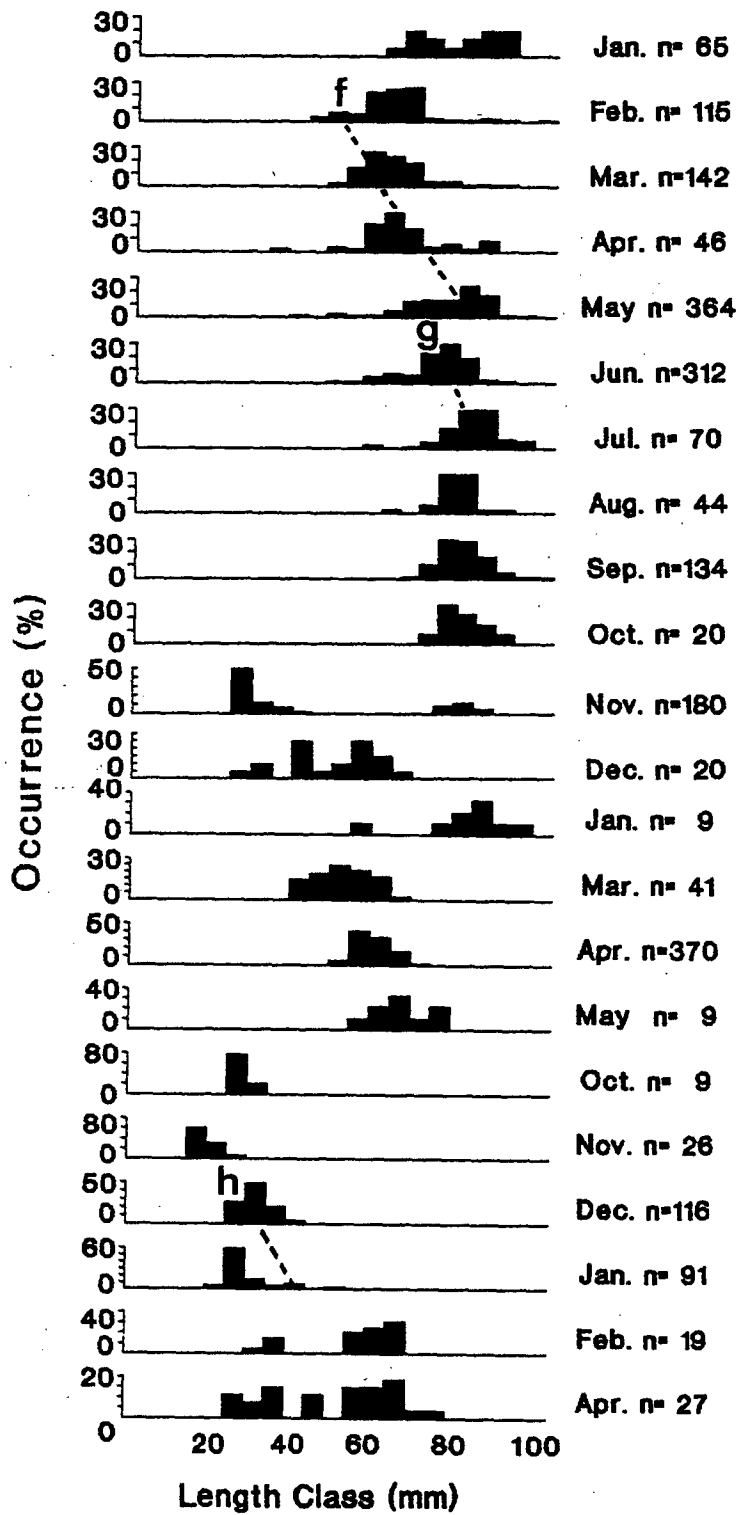


Figure 7.7. Monthly length-frequency histograms for *Stolephorus commersonii* from January 1988 to April 1991.

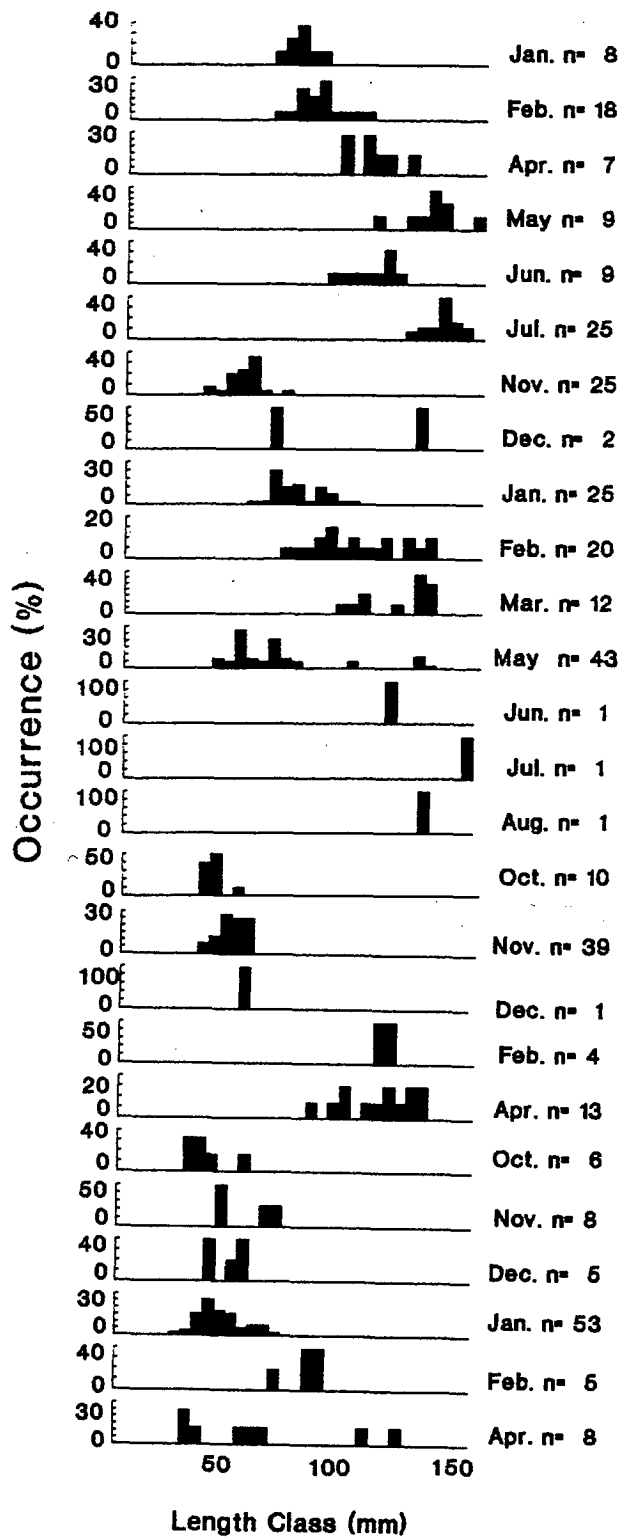


Figure 7.8. Monthly length-frequency histograms for *Thryssa aestuaria* from February 1988 to April 1991. M1-1+ males; F1-1+females.

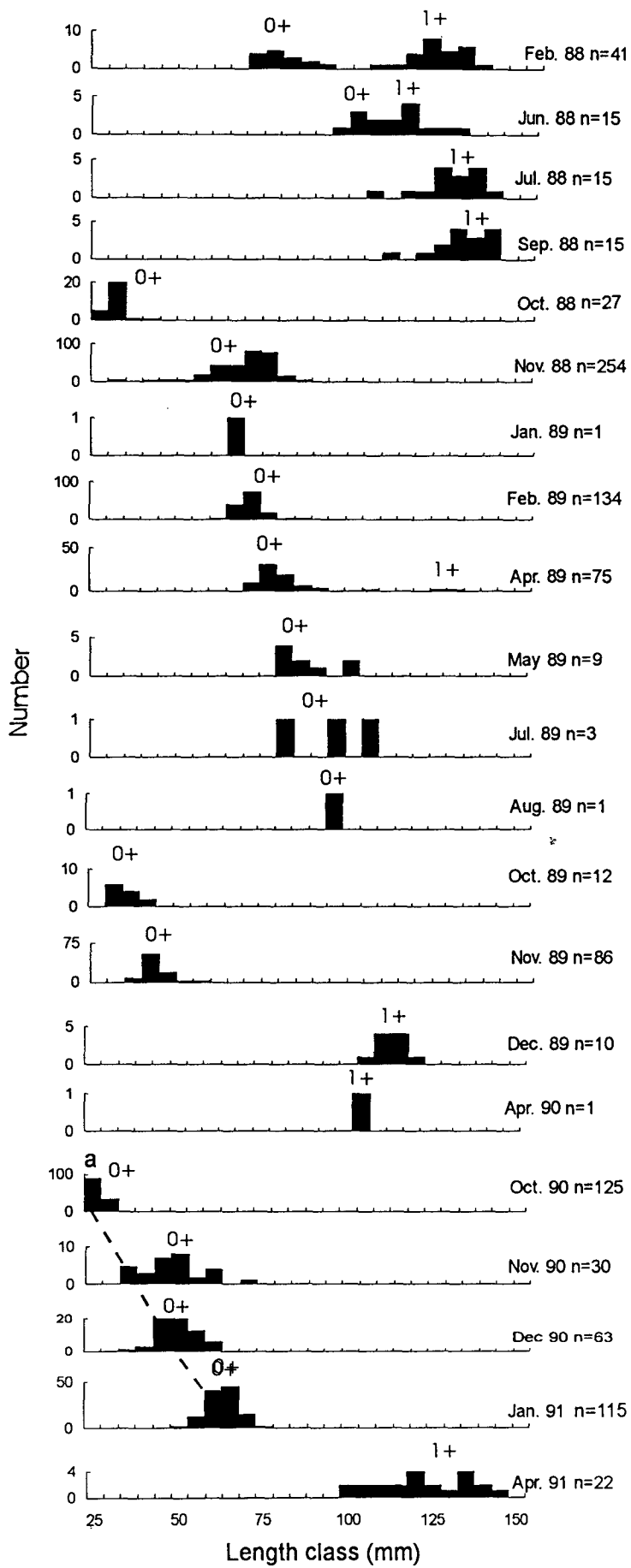


Figure 7.9. Combined length-frequency histograms for adult male and female *Thryssa aestuaria* larger than 100mm.



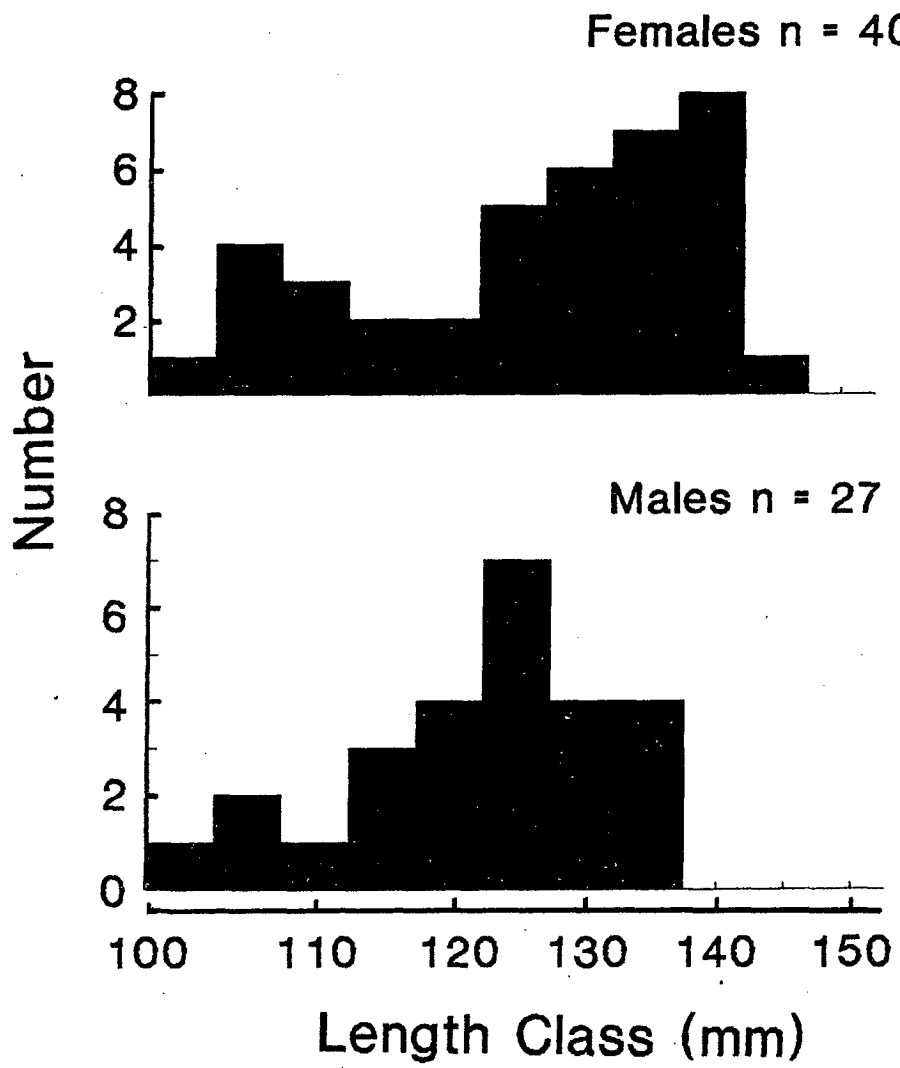


Figure 7.10. Monthly length-frequency histograms for *Thryssa setirostris*. (a) 1988/89; (b) 1990/91. M1-1+males; F1-1+females.

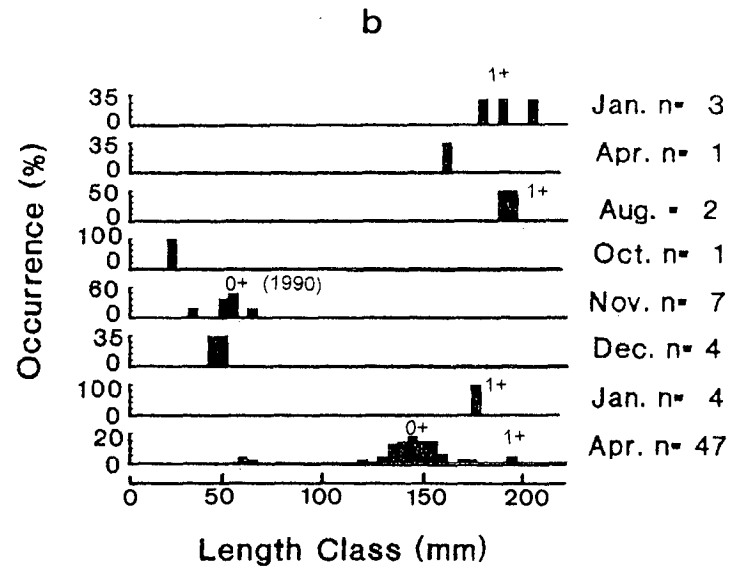
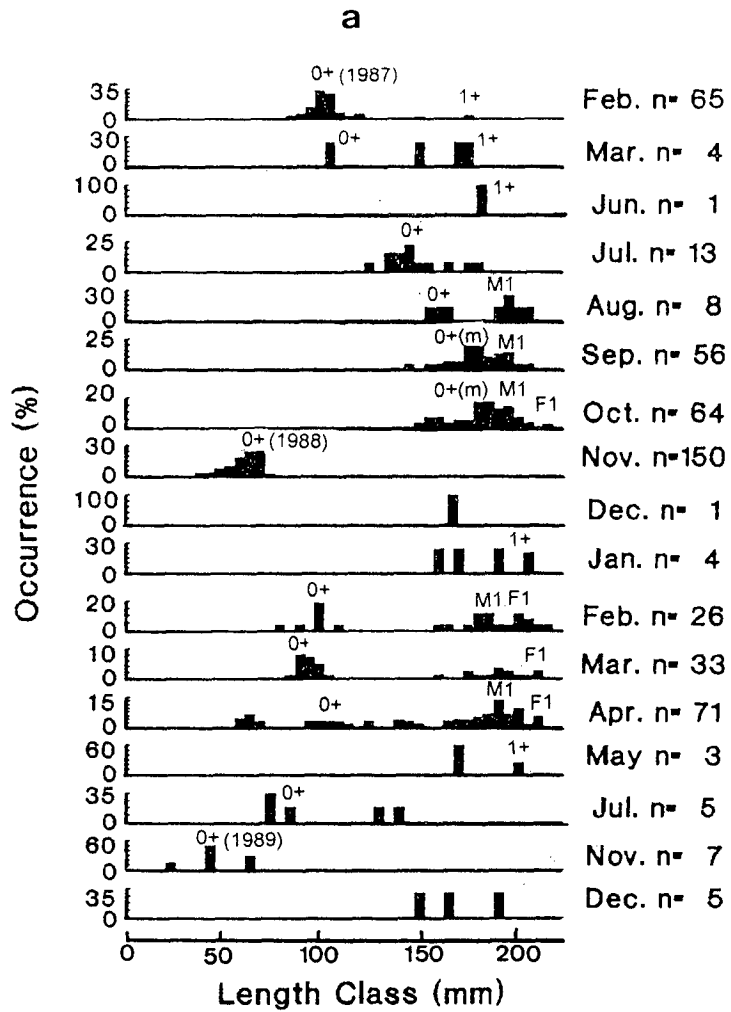


Figure 7.11. Monthly length-frequency histograms for *Thryssa setirostris* using data from all years pooled into twelve monthly length-frequency histograms. M1-1+ males; F1-1+ females

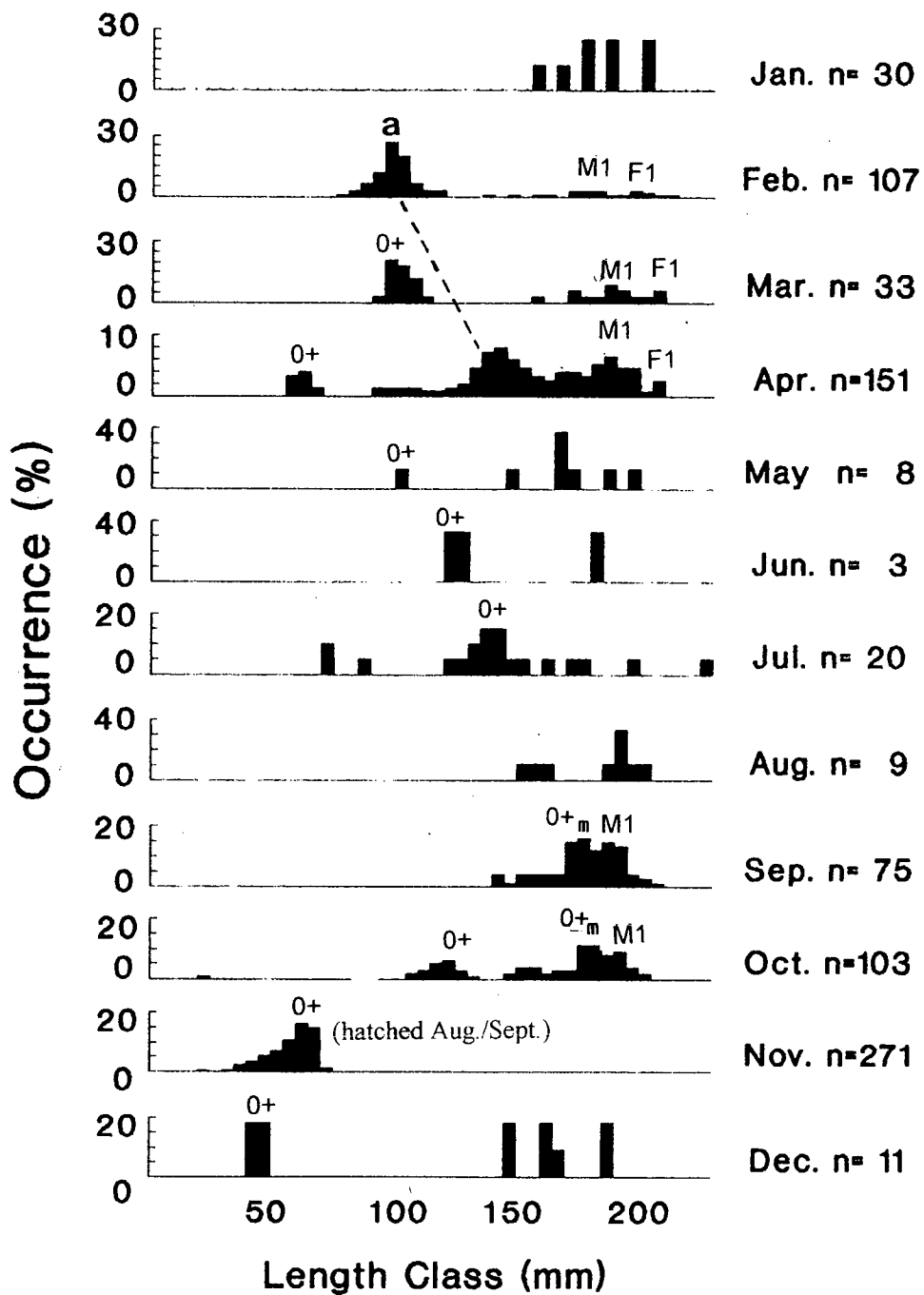


Figure 7.12. Combined length-frequency histograms for adult male and female *Thryssa setirostris* larger than 140mm.

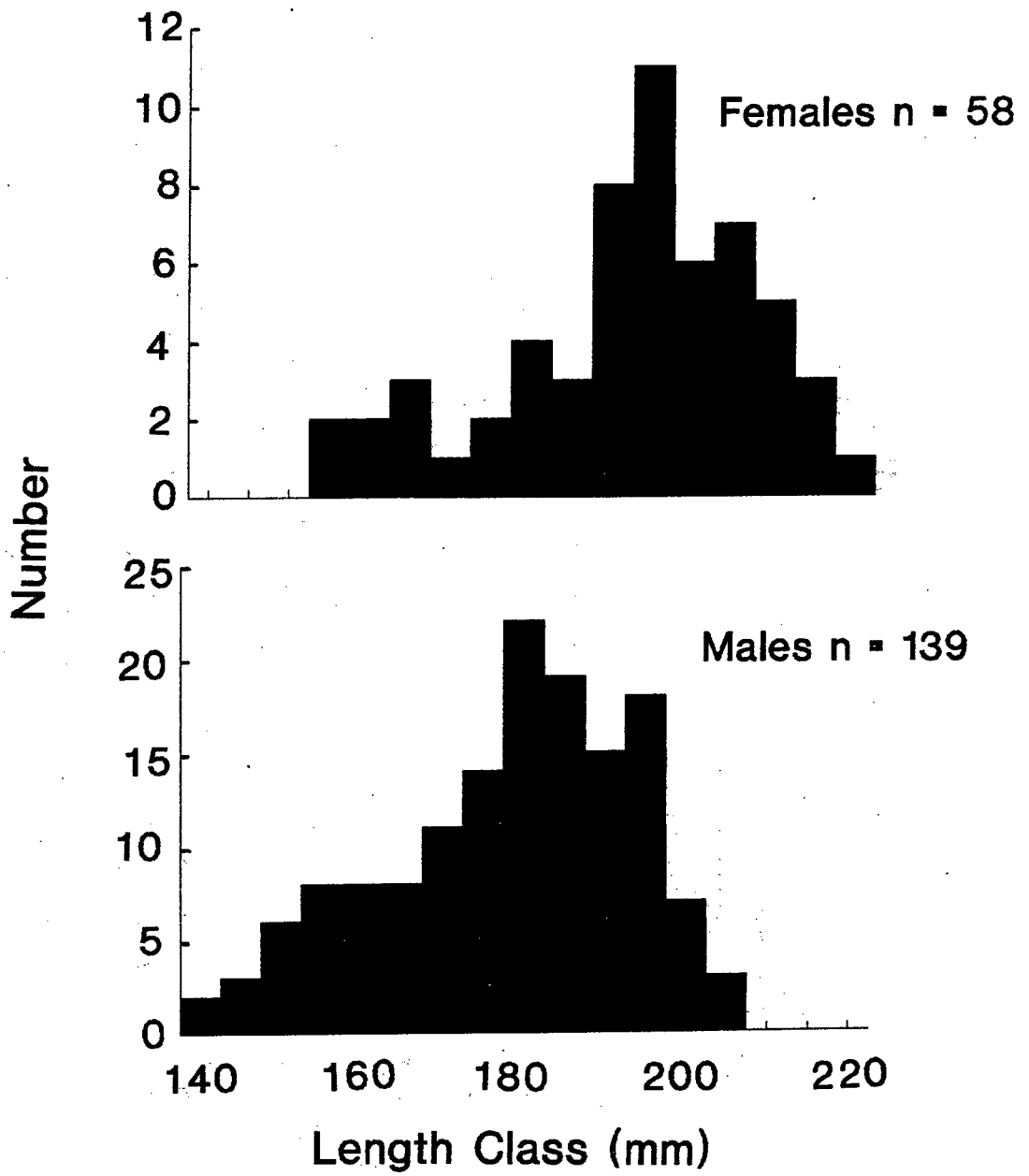


Figure 7.13. Monthly length-frequency histograms for *Thryssa hamiltoni* in 1984. M1- 1+ males; M2- 2+ males; F1-1+ females; F2- 2+ females; F3- 3+ females.



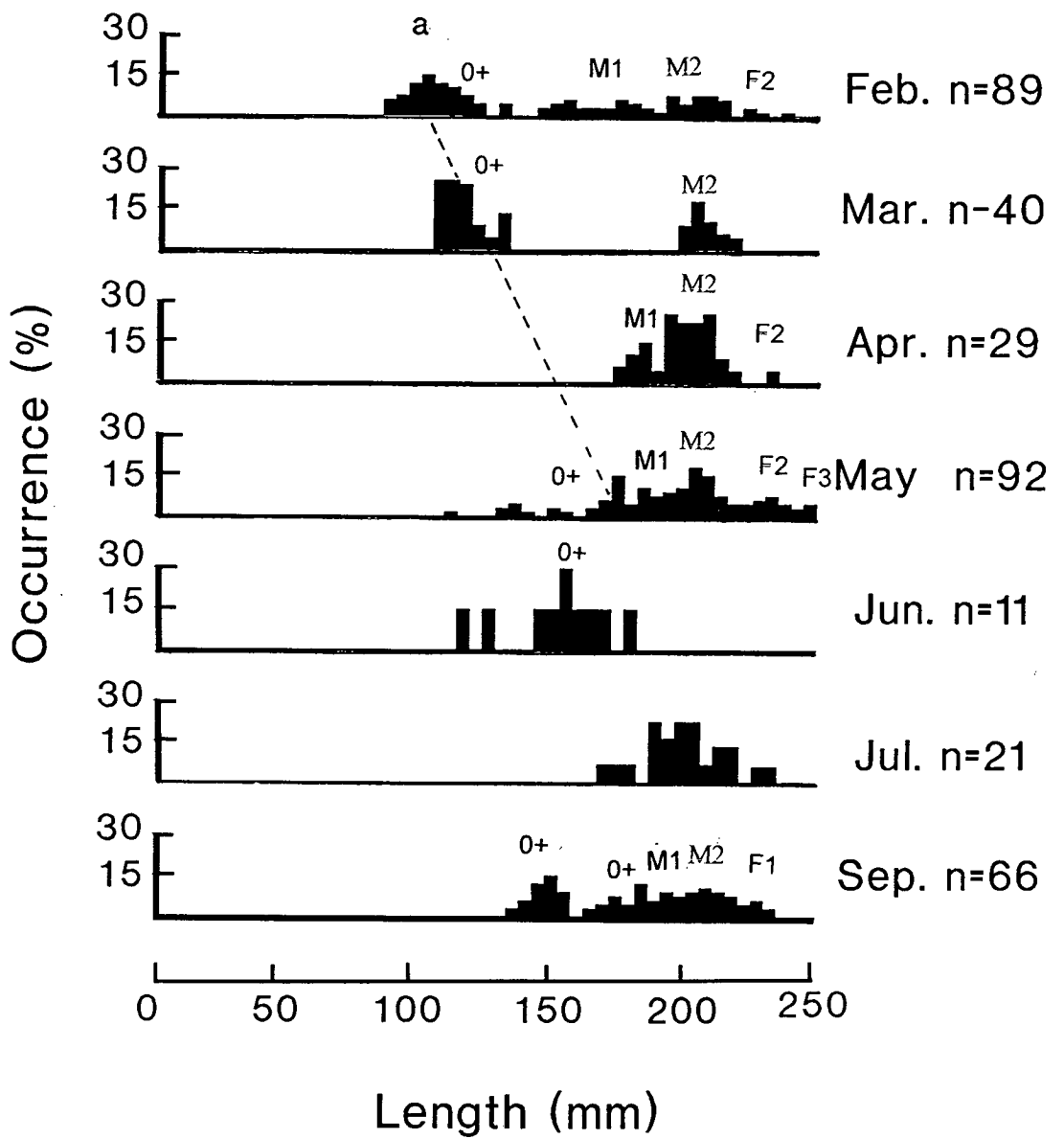


Figure 7.14. Monthly length-frequency histograms for *Thryssa hamiltoni* in 1988. M1- 1+ males; M2- 2+ males; F1-1+ females; F2- 2+ females; F3- 3+ females.

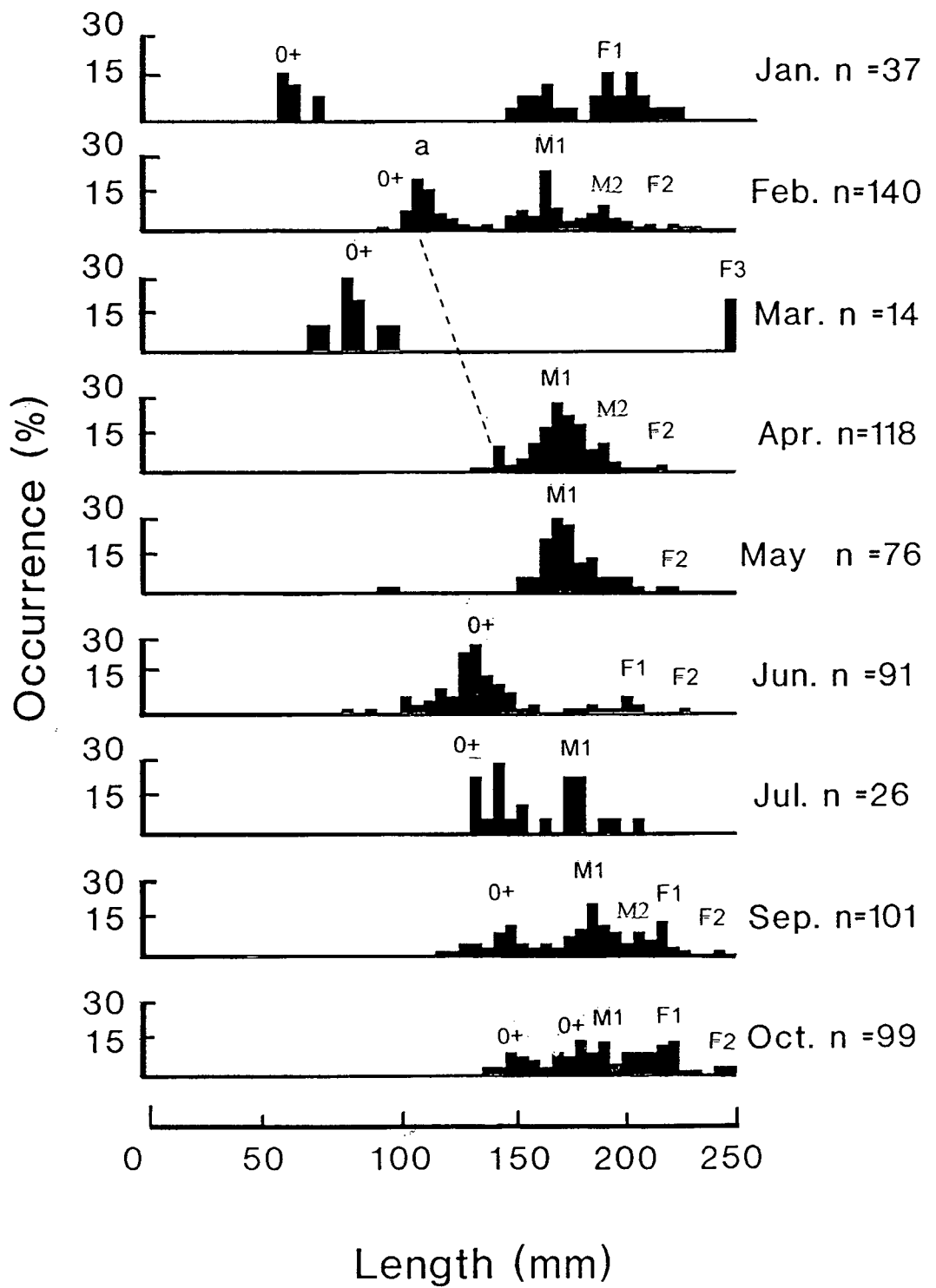


Figure 7.15. Monthly length-frequency histograms for *Thryssa hamiltoni* in 1989.  
M1-1+ males; M2- 2+ males; F1-1+ females; F2- 2+ females; F3- 3+ females.

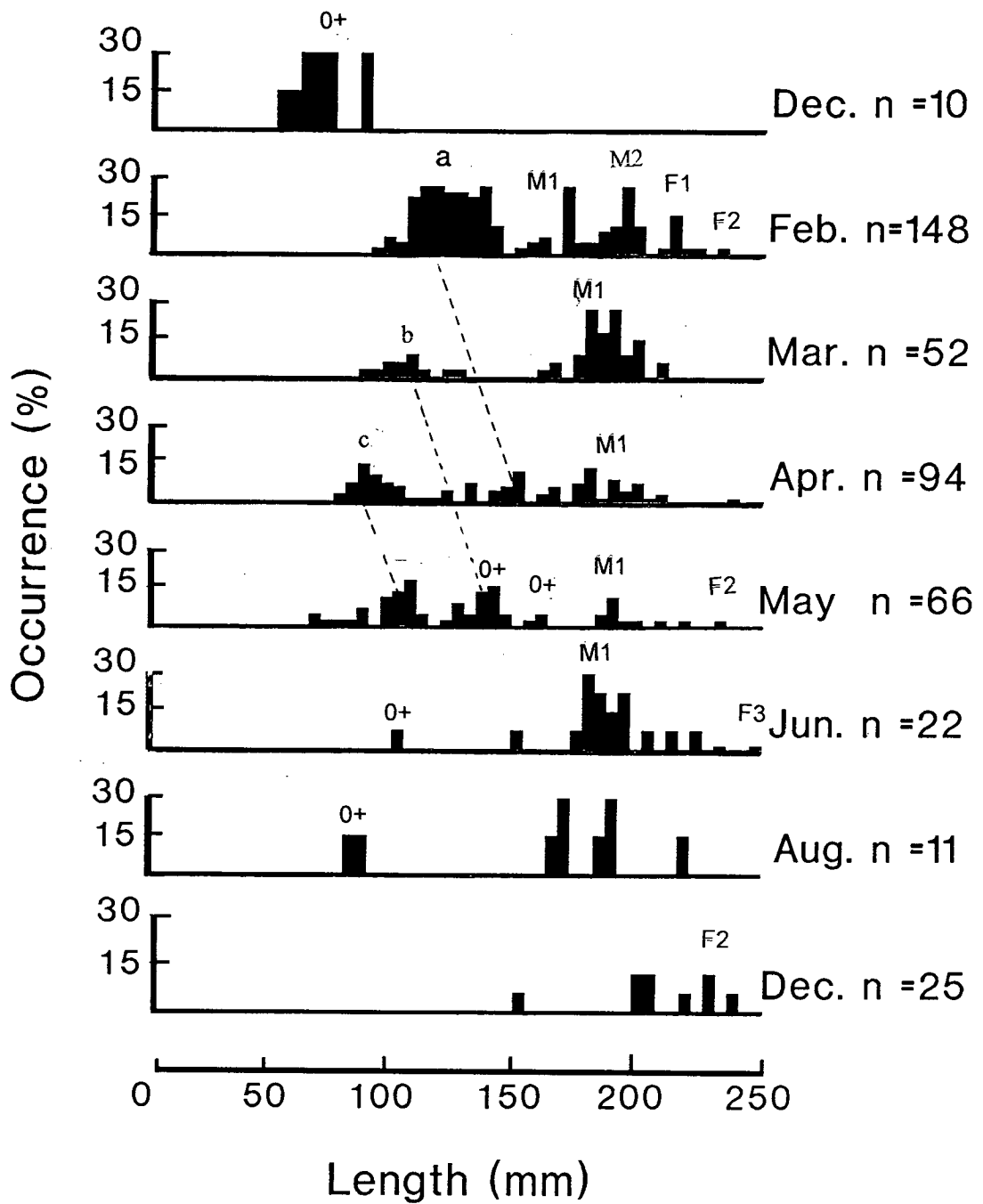


Figure 7.16. Monthly length-frequency histograms for *Thryssa hamiltoni* in 1990 and 1991. M1-1+ males; M2- 2+ males; F1-1+ females; F2- 2+ females; F3- 3+ females.

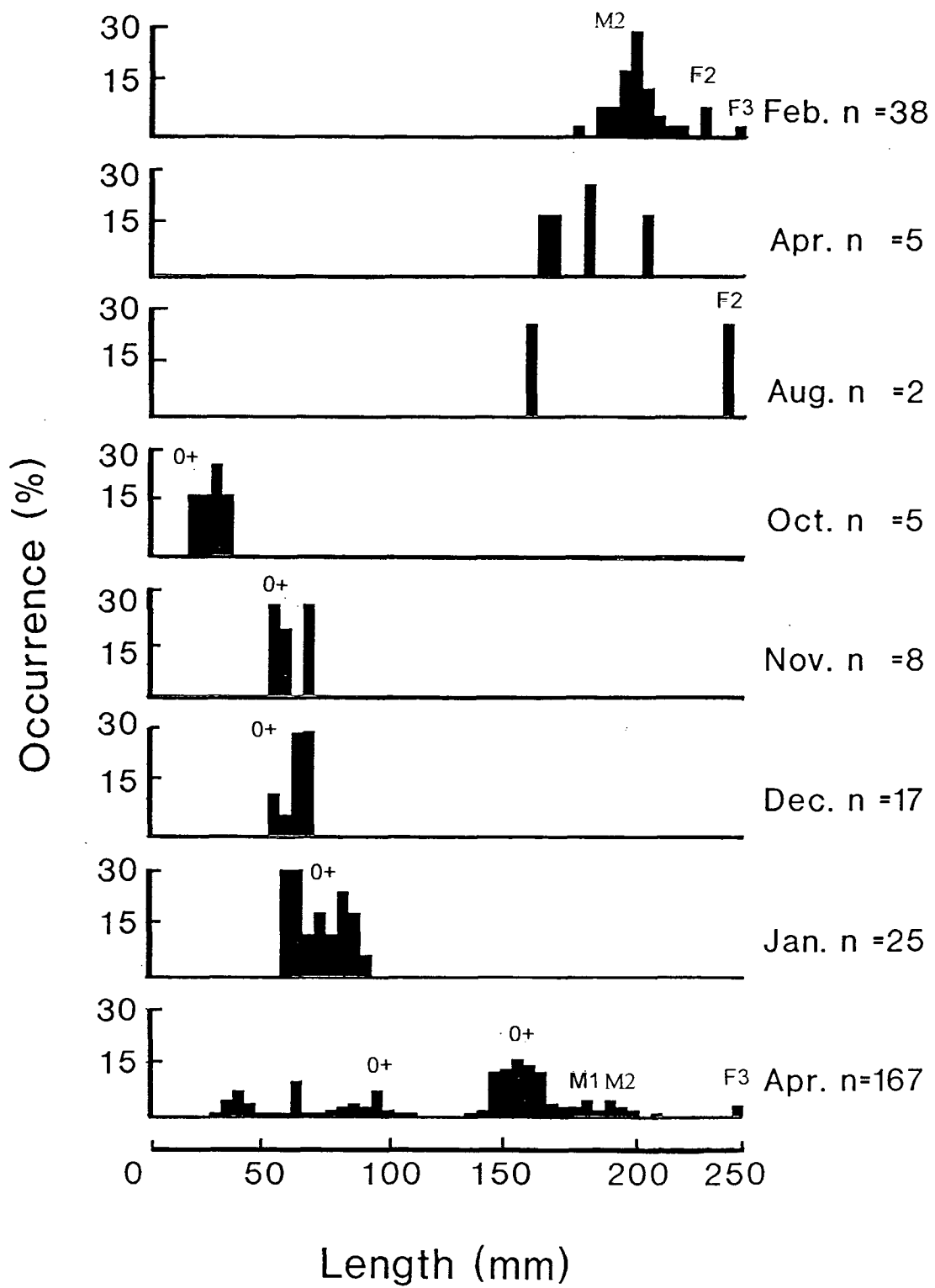


Figure 7.17. Monthly length-frequency histograms for *Thryssa hamiltoni* using data pooled for all years twelve monthly length-frequency histograms. M1-1+ males; M2-2+ males; F1-1+ females; F2- 2+ females; F3- 3+ females.



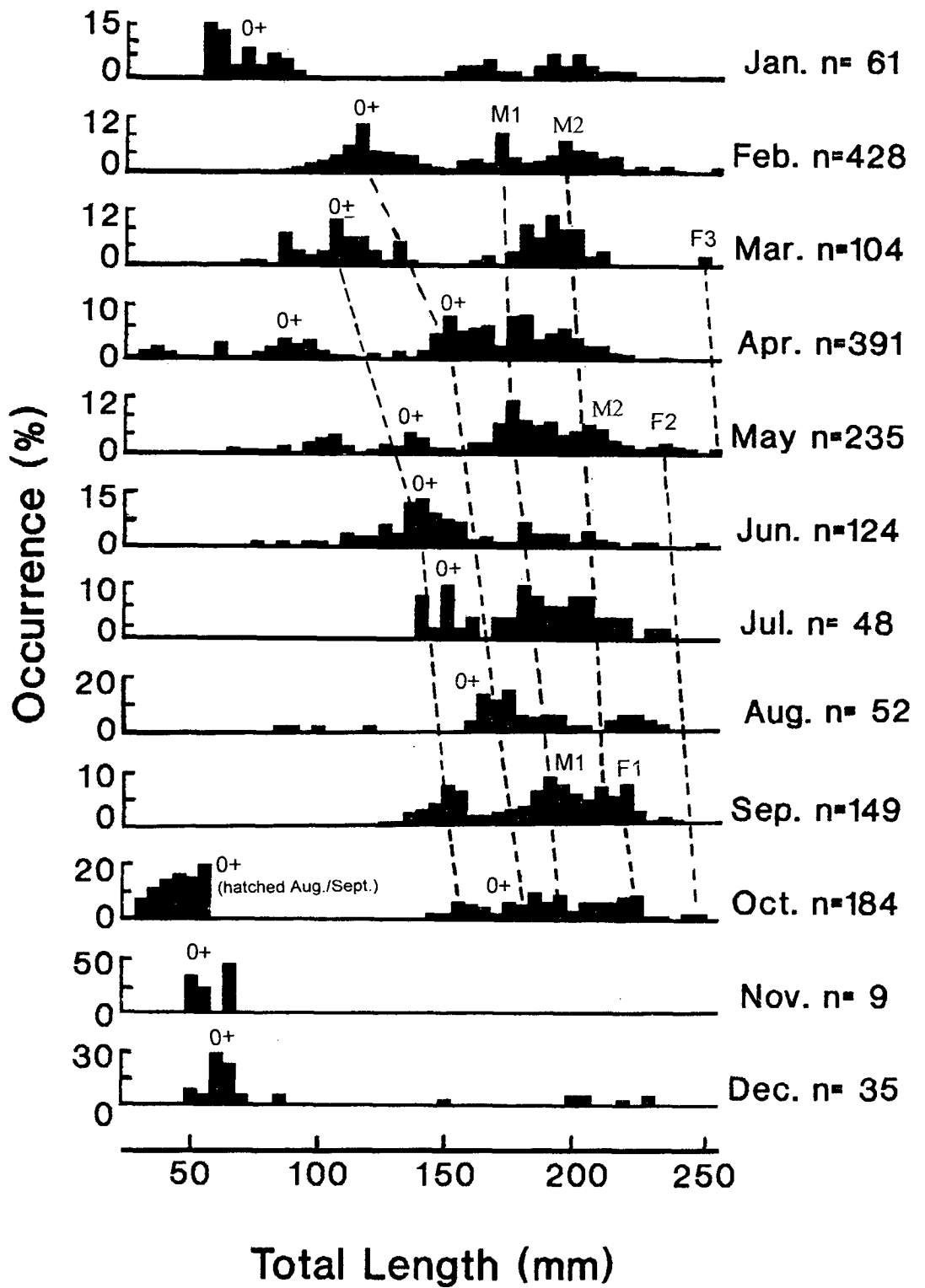


Figure 7.18. Combined length-frequency histograms for male and female *Thryssa hamiltoni* larger than 150mm.

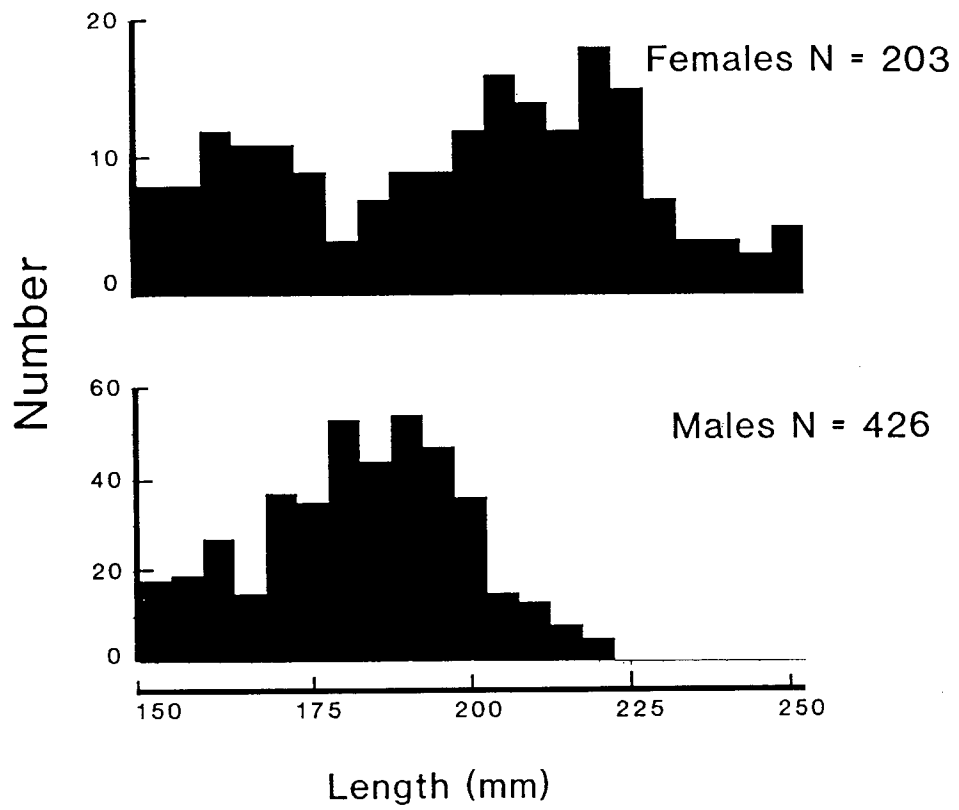


Figure 7.19. Monthly length-frequency histograms for sexed *T. hamiltoni*. (a) Male *Thryssa hamiltoni*; (b) Female *Thryssa hamiltoni*. Length data for each month was pooled from all years.

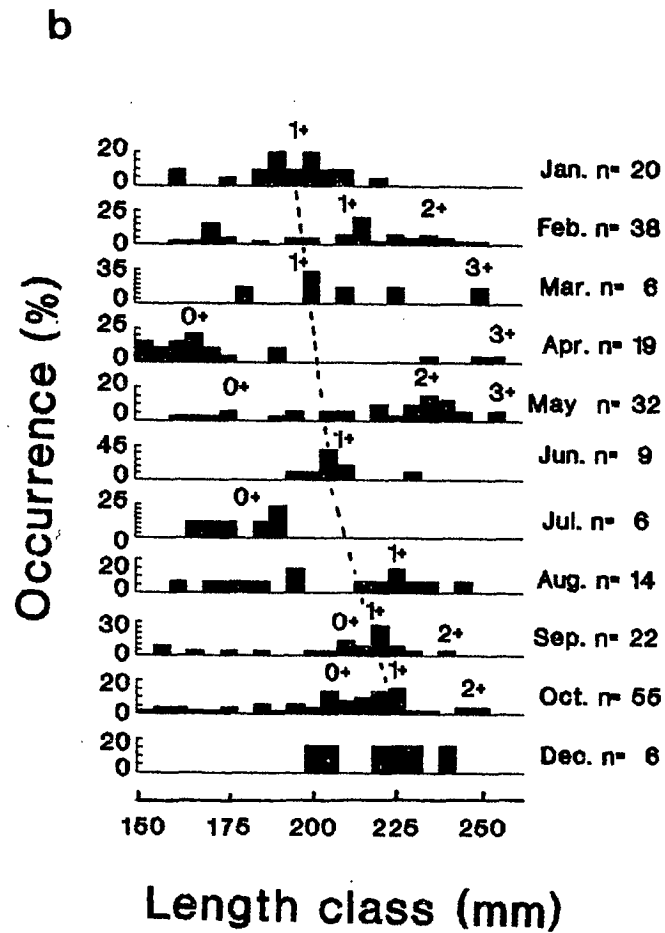
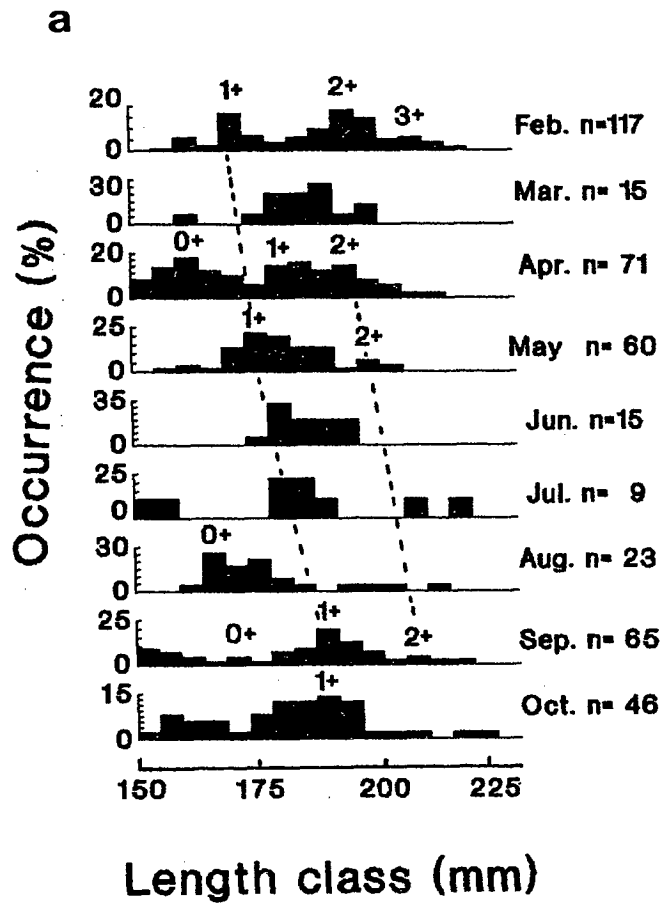
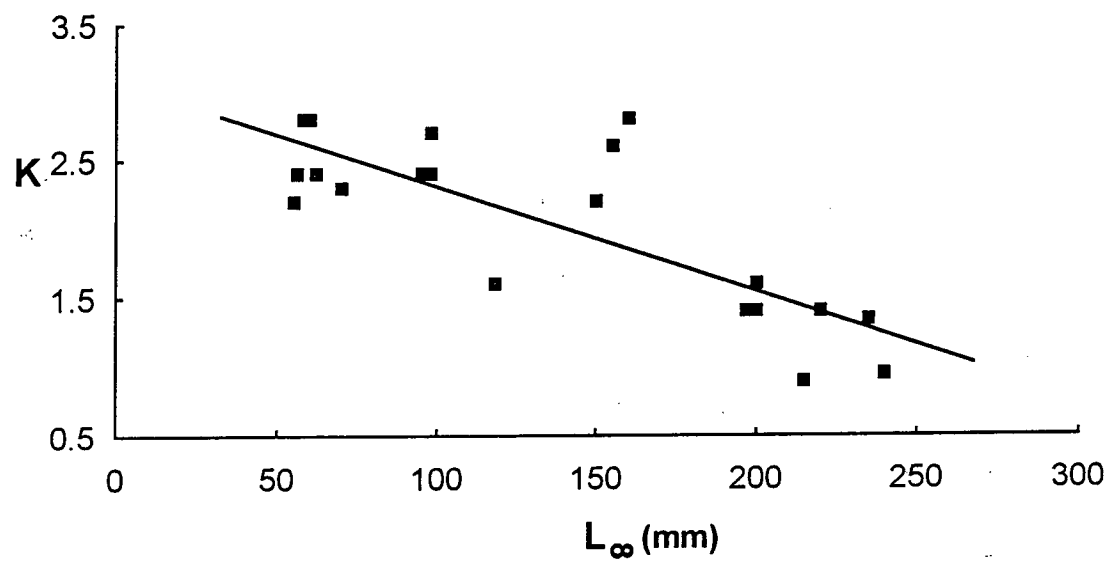


Figure 7.20. A plot of the von Bertalanffy growth parameter  $K$  against  $L_{\infty}$  for eight species of anchovies. Growth parameters were obtained from ELEFAN computations on length-frequency data.



## CHAPTER 8. REPRODUCTIVE LIFE-HISTORIES

### 8.1 Introduction

The reproductive biology of tropical anchovies has several characteristic features. Like most clupeoids they have relatively low batch fecundities and females spawn successive batches of eggs during the reproductive season (Tiews *et al.* 1970, Clarke 1987, Milton *et al.* 1990a, Wright 1992). Tropical anchovies also exhibit protracted or year-round spawning seasons (Tiews *et al.* 1970, Milton and Blaber 1991). All species of tropical anchovy appear to mature within one year (Lewis 1990). These reproductive traits result in high population turnover rates which is thought to lead to relatively stable populations (Milton *et al.* 1993). However, certain reproductive parameters exhibit considerable inter-species variation within tropical clupeoids (Lewis 1990), and these differences may influence their fishery and population dynamics.

Reproductive parameters have been examined in a range of tropical anchovy species (eg. Tiews *et al.* 1970, Dalzell and Wankowski 1980, Conand 1985, Shamsul Hoda 1976, Clarke 1987, Dalzell 1987a, Fernandez and Devaraj 1989, Wright 1990, Milton and Blaber 1991, Wright 1992). Most of these studies have focussed on spawning season, fecundity and length-at-maturity in particular species. Recent studies indicate that basic reproductive parameters such as length-at-maturity and relative fecundity in stolephorid anchovy species can vary on local and regional scales (Milton *et al.* 1990a, Wright 1992). This finding emphasises the need to examine the reproductive parameters of individual species in different parts of their range. Spawning frequency is another important reproductive parameter in clupeoid fishes but this has only been estimated in a small number of tropical anchovies (Clarke 1987, Wright 1992, Somerton *et al.* 1993). Estimates for more species are needed.

Most of the available information on reproduction in tropical anchovies concerns economically important species from countries close to the equator. There is less



information on the reproductive biology of anchovies at higher tropical latitudes. A preliminary study of reproduction in anchovies at Townsville suggests that spawning seasons are linked to the annual temperature cycle (Hoedt 1984). Conand (1985) found a similar relationship for clupeoids at New Caledonia which is at a similar latitude to Townsville. This contrasts with the spawning seasons of equatorial species which are usually linked to monsoonal seasons (Tiews *et al.* 1970, Johannes 1978, Dalzell and Wankowski 1980). The influence of sub-tropical weather patterns on reproductive seasons in different species of anchovy requires further investigation.

In this chapter, the length-at-sexual-maturity, batch fecundity, oocyte diameter frequencies and spawning season are analysed for eight anchovy species. Relative fecundity, the ratio of length-at-maturity to maximum length and the relationship between fecundity and length and weight are compared amongst the study species. Further, age information (from primary otolith increments) is incorporated into length-at-maturity estimates to obtain ages-at-maturity for different-sized species. In addition, a preliminary analysis of spawning frequency is undertaken based on the proportions of females with hydrated oocytes. Recruitment patterns in juvenile anchovies are also investigated from otolith-derived, back-calculated birthdates.

## 8.2 Materials and methods

### 8.2.1 Gonado-somatic indices

The spawning cycle of anchovies was studied by weighing gonads dissected from monthly subsamples of formalin preserved fish. Each month a minimum of 20 gonads of each sex (when available), were dissected from each of the study species and the gonado-somatic index (g.s.i.) was calculated. The g.s.i. is an index of gonad weight relative to body weight which increases as fish mature. G.s.i. values were calculated using the formula:  $\text{g.s.i.} = (\text{gw}/\text{bw}) \times 100$ ; where gw = gonad weight (grams) and bw = body weight including viscera (grams). Mean g.s.i. values were calculated monthly for both sexes in each species.

### 8.2.2 Histological and visual staging of maturity

To quantify the maturity composition of anchovy schools during reproductive periods, gonads from a subsample or all fish in each sample were staged visually. Subsamples of formalin preserved gonads were also processed for histological examination mainly for the purpose of confirming the adopted maturity stages but also to obtain some preliminary information on the frequency of certain histological features.

The procedure for processing gonads for histology involved embedding tissue in paraplast, cutting 6µm serial sections and staining the sections in Harris' haematoxylin followed by eosin counter stain (Hunter and Macewicz 1985). In most samples that were collected between September and February (these were the main spawning months for all species), a subsample of gonads (usually 5 of each sex per month) were randomly chosen for histological processing. Only when larger samples of females were obtained were more gonads processed (a large subsample or the whole sample were processed), to quantify the occurrence of ovaries with post ovulatory follicles (p.o.f.s), hydrated oocytes or atretic oocytes. Gonads from *T. hamiltoni*, *S. nelsoni*, and *S. carpentariae* were specifically targeted for histological preparation as these species were caught more regularly during the months of spawning. A small number of gonads from *Thryssa setirostris*, *T. aestuaria*, *E. devisi* and *Stolephorus insularis* were also processed for comparison.

External morphological criteria (the criteria used to assign stages to ovaries and testis based upon external appearances are given in Appendix 1.) were used to assign one of four maturity stages to all anchovy gonads upon dissection. To assess the accuracy of maturity classifications based on external morphological criteria, initially assigned maturity classes for individual gonads were compared to the maturity stage assigned later from an examination of a histological preparation of the same gonad.

Anchovy eggs ripen rapidly (hydrate) prior to being spawned over a short time period at night (Clarke 1987, Wright 1992), and the presence of ripe or hydrated oocytes indicates imminent spawning in an individual female (Hunter and Macewicz 1985). Thus, the number of hydrated ovaries can be used to estimate the proportion of spawning females in a sample. From this value the mean interval between spawning in individual fish or 'spawning frequency' can be calculated. The proportion of females with hydrated oocytes collected during the day were used in this study to estimate mean spawning interval (Clarke 1987, Wright 1992). Early stage post-ovulatory follicles (p.o.f.'s) in histological preparations of ovaries are an indicator of recent spawning (usually the previous night as these structures degenerate within 1-2 days in tropical anchovies-Clarke (1987)). These structures encase hydrated oocytes and collapse following spawning, appearing as distinctive convoluted structures. They then degenerate and are absorbed within a few days. The ratio of fish with p.o.f.s was also used to quantify the proportion of spawning individuals in anchovy schools when this information was available (see Hunter and Goldberg 1980). Ovaries with significant numbers of atretic oocytes indicate that a fish is approaching the end of its spawning activity for the season (Hunter and Macewicz 1985).

### 8.2.3 Fecundity analyses

Fecundity was estimated in female fish with mature or ripe gonads (stage III or IV), in different species. Fecundity in this study referred to batch fecundity which is the number of eggs in the most mature batch of oocytes (Hunter *et al.* 1985, Clarke 1987). Ovaries used for estimating fecundity were weighed to the nearest 0.1 gm. For ovaries from *Thryssa spp.*, a subsample of ovarian tissue (usually 1/2-1/8) was weighed and all of the oocytes in the most mature batch were counted. The total fecundity was then calculated by dividing the whole ovary weight by the weight of the ovary subsample and multiplying this number by the oocyte count from the subsample. In stolephorid anchovies, all of the oocytes in one weighed ovary were counted and the total egg number was estimated from the total ovary weight as described above. When possible fecundity was estimated for a range of sizes in each species to examine the

relationship between fecundity and fish length and weight. Relative fecundity (eggs/gram body weight) was also calculated for each fish.

#### 8.2.4 Length and age-at maturity

The length at which onset of maturity occurs was determined for each species by plotting gonado-somatic index against length for specimens collected during periods of spawning activity (Dalzell and Wankowski 1980, Milton and Blaber 1995). A preliminary analysis of the relationship between gonado-somatic index and maturity stage indicated that mature or later stage gonads had a g.s.i. value greater than 2. The exception was male *Thryssa spp.* which had relatively small gonads. Mature testes in males had a minimum g.s.i. value of between 0.5 and 1. The length at which gonado-somatic index increased to a value above the minimum for maturity was therefore used to approximate the length at onset of sexual maturity in a species. Age-at-maturity was calculated from the otolith-derived age at the estimated length-at-maturity for each species (see length-age regressions in Chapter 5).

#### 8.2.5 Ova-diameter measurements

The diameters of oocytes in formalin preserved stage III and stage IV ovaries were measured for several fish of each species at 50X magnification. A subsample of 500-1000 oocytes were measured as they were encountered using an ocular micrometer. Ova-diameter frequency polygons were drawn for each ovary with the aim of inferring spawning patterns from the temporal pattern of distribution of modes of oocyte diameters (Qasim 1973a, West 1990).

#### 8.2.6 Back-calculated birthdates in juveniles

Between October and March each year, juvenile anchovies were common in seine net samples. Occasionally large numbers of similar-sized fish were collected in a sample. A study into the recruitment patterns of the more common species was undertaken by back-calculating the birthdates of juvenile anchovies from primary otolith increment counts (Dayaratne and Gjøsaeter 1986, Thorrold 1988). The distributions of birthdates

were compared to stages of the moon to determine if spawning is related to lunar periodicity as has been observed in some other tropical clupeoids (Thorrold 1988, Milton and Blaber 1991).

### 8.3 Results

#### 8.3.1 Gonado-somatic indices

Mean monthly gonado-somatic indices (g.s.i.) for male and female *T. hamiltoni* indicate that this species exhibits a seasonal reproductive cycle (Fig.8.1 a&b). Low g.s.i values were found between March and July. Gonads in fish from these months were all immature or inactive, indicating that there was no reproduction during this period. Fish were observed to build up fat reserves around the viscera during this period. High g.s.i. values occurred in the months of August to October and although few adult *T. hamiltoni* were caught in November and December, those that were caught were mature or hydrated. Only a small proportion of fish collected in January and February were mature or hydrated indicating a substantial reduction in reproductive activity at this time (Fig.8.1a&b). Therefore the spawning season for *T. hamiltoni* extends between August and February and peak spawning probably occurs between September and October-December.

A similar seasonal pattern of reproductive activity was observed in *T. setirostris*. Mean g.s.i. values increased sharply in September and October and were uniformly low in all other months (Fig. 8.1 c&d).

Adult *T. aestuaria* were less numerous in samples than other species of *Thryssa*, however monthly g.s.i. values suggest that the spawning season is similar to other species in the genus. High g.s.i. values were calculated for individuals collected in July and September and low values were calculated in the months of February to June (Fig. 8.2a&b). These limited observations indicate that *T. aestuaria* spawns seasonally with reproductively active individuals occurring in late winter and early spring. No fish were collected in summer therefore reproductive activity may have extended into this

period also. The presence of mature fish in July 1988 indicates an earlier start to spawning than other species of *Thryssa* in that year (Fig. 8.2a&b).

Mean monthly g.s.i. values in *S. nelsoni* again suggest that a seasonal pattern of reproductive activity is characteristic for this species (Fig. 8.2c&d). High g.s.i. values were measured in fish collected in the months of August to December while fish collected between February and July had low g.s.i. values (Fig. 8.2c&d). A small number of ripe fish were also collected in January however, no mature fish were encountered between February and July. Therefore the spawning season for *S. nelsoni* is from August to January.

Numbers of adult *S. commersonii* were comparatively low in samples. However, the few mature individuals observed were collected between July and November indicating that some reproductive activity takes place in the late winter and spring months (Fig. 8.3a&b). In July 1988, fish were maturing (stage II-III), and mature fish were collected in December 1988, August 1989 and September 1989. G.s.i. measurements were uniformly low in the months of March to June (Fig. 8.3a&b).

Mean monthly g.s.i. values calculated for *S. carpentariae* show that this species has a seasonal pattern of reproduction (Fig. 8.3c&d). The highest g.s.i. values occurred from August through to November (Fig. 8.3c&d). Few adults were collected in December, but some adult fish collected in January 1988 were immature. However, some mature individuals were collected in February 1989 and several ripe fish were caught in a trawl sample in May 1988, suggesting that there may be some residual spawning in late summer and autumn. The majority of specimens collected between March and July were immature and this is reflected in the low g.s.i. values in these months (Fig. 8.3c&d). The g.s.i. data suggest that the reproductive period for *S. carpentariae* is predominantly during the spring/summer months.

The mean monthly g.s.i. values in *S. insularis* indicate that spawning occurs during the greater part of the year (Fig. 8.4a&b). Although samples were not collected in all months, high g.s.i. values were calculated in May, July and November 1988 and in July, August and November 1989 and again in April 1990 (Fig. 8.4a&b). The presence of maturing and mature fish in the months of April, May and July, indicates that *S. insularis*, unlike most other species, is reproductively active in the autumn and winter months. However in 1989, low g.s.i. values were calculated for individuals collected in May and June suggesting that the timing of reproduction in this species may be variable. Few adults were caught in the spring and summer months however, those collected in November 1989 were in reproductive condition indicating that spawning occurs in spring.

Mean monthly g.s.i. values in *E. devisi* indicate that this species also spawns over a large part of the year (Fig. 8.4c&d). In most months that adult *E. devisi* were caught, some individuals were maturing or mature. High g.s.i. values reflecting large proportions of mature and ripe fish occurred in May, November and December 1988, and February and June 1989 (Figs. 8.4c&d). Small numbers of mature fish were also present in samples in July through to August in 1989, indicating some spawning activity in winter. Samples of this species were irregular but the reproductive status of fish collected indicate that *E. devisi* is reproductively active in the summer, autumn and winter.

### 8.3.2 Histological and visual staging of maturity

Gonads from 296 individuals in four of the study species (*T. hamiltoni*, *T. setirostris*, *S. nelsoni*, *S. carpentariae*), collected between August and February were processed for histological examination (Table 8.1). Small numbers of gonads from the remaining study species were also examined.

Four stages of maturity were distinguished in histological preparations of male and female gonads in the study species (Figs. 8.5, 8.6 and 8.7). In ovaries, the following

stages were recognised based on histological criteria: (I) immature; (II) maturing; (III) mature; and (IV) ripe or hydrated. These maturity stages correspond to immature, mature, prespawning and imminent spawning ovaries described for northern anchovy, *Engraulis mordax* (Hunter and Macewicz 1985). In addition, two other reproductive categories of ovaries were recognised, these being ovaries containing post-ovulatory follicles (p.o.f.s), and resting ovaries with atretic oocytes (Fig. 8.6). Four stages of maturity were also recognised in histological preparations of testes from male fish (Fig. 8.7). These maturity stages were equivalent to the stages I-IV described from histological sections of testis from the red sea bream, *Pagrus major* (Matsuura *et al.* 1987).

Histological staging is considered to be the most accurate method for the assessment of the reproductive state of individual gonads (West 1990). The accuracy of maturity stage assessments based on a visual examination of whole, preserved gonads upon dissection (the main method used in this study), was determined by comparing these to the assigned maturity stage after examining a histological preparation of the same gonad. In female anchovies, 80% of ovaries in *Stolephorus spp.* (n=59), and 86% of the ovaries of *T. hamiltoni* (n=95), were found to have been correctly classed into stages I to IV based on external morphological criteria. Almost all ripe/hydrated ovaries for both genera had been correctly staged using external characteristics of the whole ovary, suggesting that this stage is easily identifiable without histological preparation. These results suggest that ovaries could be classed into four maturity stages based on external morphological features with a reasonable degree of accuracy.

Maturity stage assessments on whole, preserved testis were less accurate than those for ovaries. Agreement between the initially assigned maturity stage and that determined from histological characteristics on individual gonads was 53% for *Stolephorus* (n=66) and 56% (n=57) for *T. hamiltoni*. Given the problems associated with visually staging whole male gonads, the maturity composition of anchovy schools was assessed from the stages assigned to ovaries (Table 8.2).



Mature and ripe *T. hamiltoni* were present in samples collected between August and February but the proportions of these stages were lower in January and February indicating that spawning activity is lower after December (Table 8.2). Mature and ripe *T. setirostris* were collected from September to January and these stages were observed in *T. aestuaria* individuals caught in July and September (Table 8.2). Mature and ripe *S. nelsoni* were collected between August and January and these maturity stages occurred in *S. commersonii* collected in September and December (Table 8.2). Mature and ripe *S. carpentariae* were collected between August and March (Table 8.2). Mature and ripe *E. devisi* were caught in summer, autumn and winter samples and for *S. insularis* these stages were present in fish from all seasons of the year (Table 8.2).

Most ripe *T. hamiltoni* were collected in a trawl sample on 2-9-88. Of the 27 females caught on this 2-9-88, 44% were ripe. This proportion of hydrated ovaries indicates a spawning interval of approximately 2 days. Histological sections of ten male testis from this sample showed that seven of these were also ripe. This indicates that spawning was occurring at the depths where the sample was collected (4-12m). In the sample collected by gill net close to shore on 12-10-88, 4 of 19 fish (or 21%) had p.o.f.s. indicating that these had spawned recently. There were no ripe fish in this sample. This sample gave an estimated spawning interval of approximately 5 days. Post ovulatory follicles were only found in significant numbers in this sample of *T. hamiltoni* (12-10-88) and so were not used to estimate spawning interval for any other species.

Sex ratios in trawl samples of *T. hamiltoni* in September and October 1988 were strongly in favour of male fish (71% males (n=93) and 75% males (n=59) respectively). In contrast, two inshore gill net samples taken in summer (1-1-88 and 12-10-88), were almost exclusively comprised of female fish and none of these were ripe.

*Thryssa setirostris* exhibited similar sex ratios and reproductive condition to *T. hamiltoni* in trawl samples on 2-9-88 and 17-10-88. Sex ratios were 84% (n=55) and 90% (n=62) males respectively in these two samples and most males and females collected on 2-9-88 were also ripe (80% ripe females, n=9) indicating a high spawning frequency.

Most samples of stolephorid anchovies caught between August and January were taken close to shore using seine nets. The proportion of ripe female *S. carpentariae* in samples between September and November was lower (11%) compared to *S. nelsoni* (28%) for the period from September to January (Table 8.2). The proportions of hydrated ovaries indicate that *S. nelsoni* has a spawning frequency of approximately three days and *S. carpentariae* spawns at least every ten days. However, an examination of Table 8.1 shows that four out of the six samples of *S. carpentariae* were collected in the morning while all samples of *S. nelsoni* were from afternoon collections (Table 8.1). Given that the proportions of ripe female stolephorid anchovies is highest in the afternoon and early evening (Clarke 1987), it is likely that the spawning frequency estimate for *S. carpentariae* is an underestimate.

Gonads from all fish in a sample of *E. devisi* (n= 80), caught under a light suspended from the AIMS jetty at night on 13-2-89 were staged into maturity classes. A large proportion of ovaries from fish in this sample were classed as ripe (90%-Table 8.2) indicating a spawning interval close to one day. The stages assigned to these gonads were confirmed when a subsample of gonads (n=10) were processed for histological examination.

Atretic oocytes in ovaries were observed in some histological sections. These were uncommon in samples collected between September and November indicating high levels of spawning activity. The exception was on one occasion in a sample of *S. nelsoni* collected on 20-9-89 where there was a high incidence of atretic oocytes in mature and ripe ovaries in these fish. Fecundities were also low in this sample

suggesting that spawning output may have been suboptimal in these females. Atretic oocytes were observed in a small number of *S. carpentariae* females from October and November and some female *S. nelsoni* collected on 18-1-89. A significant proportion of female *T. hamiltoni* collected in January and February had atretic oocytes suggesting that spawning activity was nearing an end in these months.

### 8.3.3 Fecundity analyses

Batch fecundities were estimated for eight species of anchovy. Means and ranges of fecundity estimates for each species are given in Table 8.3. Fecundity was plotted against length for *E. devisi* (Fig. 8.8a). Fecundity was found to increase with length and the relationship between these two variables was described using a linear regression (Fecundity=47.53\*Length-2113.8,  $r^2=0.55$ ).

Fecundity was plotted against length using combined data for the four species of stolephorid anchovies (Fig. 8.8b). A linear regression (Fecundity=21.9\*Length-827.4,  $r^2=0.5$ ), was fitted to this data. Fecundity was also plotted against length using the combined data for the five largest species of anchovy (Fig. 8.9a). An exponential curve (Fecundity= $125.9 \times 10^{0.0099 \text{Length}}$ ,  $r^2=0.88$ ), was fitted this data. Fecundity was plotted against weight for the combined data in seven of the study species (Fig. 8.9b). A linear regression ( $F = 248.9W - 808.5$ ,  $r^2 = 0.913$ ), was fitted to this data.

Relative fecundities were calculated for the eight study species (Table 8.4). Mean relative fecundities ranged from 137 (*T. aestuaria*) to 439 (*E. devisi*) (Table 8.4).

### 8.3.4 Length and age-at-maturity

Length-at-maturity was estimated for those species for which a sufficient size-range of individuals were caught during reproductive periods. G.s.i. values were plotted against length for male and female *T. hamiltoni* (Figs. 8.10a&b). In females, the first g.s.i. value above 2 was a female at 160mm, and after 180mm mature fish became common. (Fig. 8.10b). In male *T. hamiltoni*, g.s.i. values increased to between 0.5 and

1 at 155mm (Fig. 8.10a). Histological sections confirmed that males below 155mm were immature. Therefore length-at-maturity for female and male *T. hamiltoni* were estimated as 160 and 155mm respectively.

G.s.i. was plotted against length for individuals of *T. setirostris* collected during the reproductive period (Fig. 8.10c). In females, g.s.i. values increased sharply between 158 and 163mm, therefore length-at-maturity in females was estimated as 160mm. The scarcity of small males in samples collected in the spawning season made it difficult to estimate minimum length-at-maturity. Histological sections revealed that individuals of lengths 140-158mm were immature and the smallest mature specimen was 155mm. G.s.i. values approaching 1 were indicative of maturity and the first occurrence was at 155mm (Fig. 8.10c). All individuals longer than 165mm were mature (Fig. 8.10c). The length-at-maturity for male *T. setirostris* was taken as the length of the smallest mature individual, this being 155mm.

In *S. carpentariae*, g.s.i. was plotted against length for fish collected on 18-11-88 (Fig. 8.11a). Gonad weights sharply increased to greater than 2 in fish longer than 50mm, and this value was used as an estimate of length-at-maturity for this species.

A plot of g.s.i. against length for *S. nelsoni* individuals collected during reproductive months indicated that almost all of these fish were mature (Fig. 8.11b). The smallest female (63mm) was immature while all females longer than 68mm were mature (fig. 8.11b). Males larger than 73mm were all mature. An approximate estimate of length-at-maturity was obtained by taking a value in between the first maturity sizes of each sex, this being 70mm.

For *E. devisi*, g.s.i. values were plotted against length for 47 fish from a sample collected on 13-2-89. G.s.i. values increased markedly in fish longer than 47mm (Fig. 8.12a). Fish smaller than this length had immature gonads. Therefore, 47mm was the estimated length-at-maturity for *E. devisi*.

G.s.i was plotted against length for *S. insularis* individuals collected on 18-11-88 (Fig. 8.12b). The first mature fish was at 42.5mm and gonad weights increased markedly in most fish at a length of 45mm (Fig. 8.12b). Therefore, length-at-onset of maturity in *S. insularis* was 42.5mm but maturity in most fish appears to occur at 45mm.

Too few adults of *T. aestuaria* and *S. commersonii* were caught during the reproductive season to estimate length-at-maturity.

The ratios of length-at-maturity to maximum length were calculated for six of the study species (Table 8.5). Age-at-maturity was also calculated for these species (Table 8.5).

#### 8.3.5 Ova-diameter measurements

Ova-diameter frequency polygons were constructed for stage III and IV ovaries for all species. Two distinct patterns of ova-diameter frequencies occurred in the stolephorid anchovies and *Thryssa spp.*. Examples of the two types are illustrated by the ova-diameter frequency polygons for *S. nelsoni* (Fig. 8.13a&b) and *T. hamiltoni* (Fig. 8.14a&b). The pattern of oocyte development seen in the ovary of *S. nelsoni* was common to other species of stolephorid anchovy. In stage (III) and stage (IV) ovaries in *S. nelsoni*, the batch of most mature oocytes was clearly distinguishable from the stock of immature and maturing oocytes (Fig. 8.13a&b). However, the stock of maturing oocytes was comprised of a continuum of oocyte-sizes and these were not clearly separated from the immature stock of oocytes (Fig. 8.13a&b). The close proximity of maturing oocyte batches suggests that these may be spawned successively over short time intervals.

The ovaries of *Thryssa* species showed a different pattern of oocyte maturation (Fig. 8.14a&b). In addition to the mode of mature or ripe eggs, a single distinct mode of smaller maturing oocytes was clearly distinguishable from the immature oocyte stock

(Fig. 8.14a&b). There were only two clearly separated batches of maturing oocytes at any time in ovaries from these species. This suggests that the time interval between spawning may be longer in this genus (Dharmamba 1959).

The differences in ovarian development between stolephorid anchovies and *Thryssa spp.* are consistent with the egg maturity stages observed in histological sections of ovaries. Histological preparations of mature ovaries of stolephorid anchovies contained at least three distinct egg developmental stages, while mature ovaries from *Thryssa spp.* contained only two egg stages, the immature batch and the maturing batch.

#### 8.3.6 Back-calculated birth-dates in juveniles

On 17-10-90 a large sample of juvenile *S. carpentariae*, *S. commersonii* and *T. aestuaria* were collected in the seine net. Individuals within each of these species were of a similar size suggesting that they were born at approximately the same time period. Otolith increments were counted in randomly chosen subsamples of 14 *S. carpentariae* juveniles and 20 *S. commersonii* juveniles from this sample. Plots of the birth-date frequencies in these species showed an aggregation of births around two dates corresponding to new and full moon phases (Fig. 8.15 a&b).

Birthdates were also estimated for a subsample of 20 individuals from a large sample of similar-sized juvenile *T. aestuaria* collected on 3-10-91. Back-calculated birthdates ranged from 17-8-91 to 28-8-91 (Fig. 8.15c). There was a suggestion of a peak in hatching at 18-8-91; this date was close to a new moon (Fig. 8.15c).

The birthdate of three samples of a presumed cohort of *T. aestuaria* juveniles was estimated from the x-intercept of a linear regression fitted to a plot of otolith-derived ages for each fish against the time between date of capture and a fixed date of 1-9-90 (see Chapter 5, Fig. 5.4). The regression intercepted the x-axis at 6-9-90 and a full moon occurred on this date (Fig. 5.4).

The birthdates of juvenile *T. hamiltoni* from samples collected between October 1990 and April 1991 were back-calculated from otolith-derived ages (Fig. 8.16). Although sample-sizes were small, the data suggests that birthdates were not random, with larger numbers of fish having birthdates close to, or shortly after, the full moons at the start of each month (Fig. 8.16).

A sample of *E. devisi* (n=11), collected on 1-3-90, was comprised of individuals ranging in length from 37-48 mm. During routine age estimates it was noted that all individuals had very similar ages in spite of the variation in length. Age estimates for these 11 fish ranged from 48 to 54 days (mean=50 days) and the birthdate estimated from the mean age was 11-1-90 which was a full moon.

These findings suggests that spawning in several species of anchovy may be associated with lunar events, particularly new and full moon periods.

#### 8.4 Discussion

In spite of the wide range of maximum-sizes in the anchovy species studied, comparisons of reproductive parameters revealed some inter-species patterns. Firstly, relative fecundity values were similar and relatively low in all species (137-436 eggs/gram-Table 8.6). Also, a linear regression described the relationship between fecundity and weight at an inter-species level. Ratios of length-at-maturity to maximum length in the study species were also similar, being close to 70% in all species (Table 8.6). These findings suggest that certain reproductive parameters exhibited conservatism in the anchovies studied. This finding is consistent with other studies that have shown reproductive parameters to be conservative in temperate and tropical clupeoids (Beverton 1963, Blaxter and Hunter 1982, Milton and Blaber 1991).

Spawning seasons in the anchovies studied differed. The two smallest species, *E. devisi* and *S. insularis* appeared to spawn throughout the year with short periods of little or no reproductive activity. In contrast, the remaining larger species exhibited a distinct seasonal pattern of spawning commencing in August/September and finishing in early summer (Table 8.6). These different spawning strategies are probably related to size and longevity. Species which spawned seasonally had longevities greater than six months which enables the population to survive a prolonged period of little or no reproductive activity. *E. devisi* and *S. insularis* which live for less than five months need to spawn over a greater part of the year to maintain the population. These strategies parallel the two life-history strategies of tropical baitfish proposed by Lewis (1990). He distinguished small (<10cm) species with year-round spawning from large (10-24cm) species with a annual spawning period of several months.

The reproductive seasons found in the present study are consistent with the temporal patterns of larval anchovy abundance off Townsville (Milward and Hartwick 1986). These authors found that anchovy larvae were amongst the more abundant families in their samples and they recorded two peaks in the abundance, one between August and November and another between February and June. The August to November peak is consistent with the spring/summer spawning found in the larger anchovy species in this study. The February-June peak probably reflects the autumn spawning in *E. devisi* and *S. insularis*.

The onset of reproduction in most anchovy species in Townsville occurred in the spring and summer months and this coincides with rising water temperatures following winter. In Townsville there is a considerable seasonal variation in seawater temperature with a minimum of around 22° in June and a maximum of around 30° in December (Walker 1981). Water temperature has been correlated to reproductive activity in other clupeoid fishes (Baker 1972, Jenkins 1986) however, associated factors such as increased food supply may also be important for spawning in clupeoid fishes (Tiews *et al.* 1970, Sitthichokpan 1972, Blaxter and Hunter 1982, Dalzell



1987a, Wright 1990, Wright 1992).. The relationship between clupeoid spawning seasons and environment at Townsville contrasts with equatorial countries where temperature shows little annual variation and spawning in clupeoid fishes is usually correlated with monsoonal seasons, particularly periods of calm wind (Marichamy 1970, Tiews *et al.* 1970, Qasim 1973a, Johannes 1978, Dalzell and Wankowski 1980, Milton and Blaber 1991). Furthermore, the reproductive strategy of the stolephorid anchovies from Townsville differs from that exhibited by this group in countries closer to the equator where these species generally spawn throughout the year (Tiews *et al.* 1970, Milton *et al.* 1990a, Wright 1990, Milton and Blaber 1991). The reproductive life-history strategies of stolephorid anchovies at sub-tropical latitudes may therefore be modified from the pattern typically exhibited by species near the equator.

Milward and Hartwick (1986) found a correlation between the temporal pattern of larval fish abundance and water temperature in a wide range of families in the waters adjacent to Townsville. These authors showed that spawning in a number of families occurs shortly after the onset of warmer water temperatures in spring, this being consistent with the results of the present study. During one year of their study, an earlier elevation in water temperature in August led to the earlier appearance of larvae in some families. Conand (1985) also found that several clupeoid fishes from New Caledonia (at a similar latitude to Townsville), commenced spawning with the onset of increased water temperatures following winter. Spawning in anchovies in the present study did not correlate with rainfall which is generally highest between December and April in Townsville but varies markedly from year to year (Milward and Hartwick 1986).

Estimates of age-at-maturity for species in the present study indicate that this parameter can vary considerably amongst different-sized tropical anchovies (Table 8.6). In the three smallest species, *E. devisi*, *S. insularis* and *S. carpentariae* maturity was attained quickly, ranging from 2-2.5 months. Conand (1985) estimated similar ages-at-maturity (2-4 months) for the small anchovies *E. devisi* and *E. heteroloba* in

New Caledonia. In the larger anchovy species from Townsville, ages-at-maturity ranged from 5-13 months (Table 8.6) and this would result in spawning readiness towards the end of one year. These ages-at-maturity are consistent with the proposal that tropical clupeoids mature within their first year (Lewis 1990).

Several authors have suggested that small stolephorid anchovies and clupeids do not live for long after attaining maturity (Struhsaker and Uchiyama 1976, Dalzell and Wankowski 1980, Williams and Clarke 1983, Dalzell 1987b). Otolith-derived growth estimates are consistent with this proposal, as they indicate that the smaller stolephorid anchovies in the present study only survive for 1-3 months after attaining maturity. The ratio of age-at-maturity to maximum-age provides quantitative information on the proportion of life prior to and after maturity. Primary otolith increment derived ages indicate that this ratio is similar amongst the stolephorid anchovies in this study (0.47-0.67), but is lower in *Thryssa spp.* (0.18-0.38), reflecting the greater longevity and 'spawning life' of this genus (Table 8.6). Milton *et al.* (1994) estimated that maturity occurred at around 50% of longevity in three species of clupeids from Kiribati, this value being similar to that estimated for stolephorid anchovies in the present study.

Recent studies using the frequency of females with hydrated oocytes and/or females with p.o.f.'s to estimate spawning frequency, have shown that temperate and tropical clupeoids spawn more frequently than previously thought (Hunter and Goldberg 1980, Clarke 1987, Wright 1992). At present the only estimates of spawning frequency available for tropical clupeoids are for anchovies of the genus *Encrasicholina* (Clarke 1987, Wright 1992), and several species of clupeids (Isaac-Nahum *et al.* 1988, Milton *et al.* 1994). Unfortunately, in the present study only small numbers of mature females of all of the study species were collected in samples from November to January (sex ratios in *T. hamiltoni* and *T. setirostris* were strongly in favour of male fish), this limiting the information on female spawning biology. Based on this limited information, a mean spawning interval of three days was estimated for *S. nelsoni*. One sample of *T. hamiltoni* had 44% ripe ovaries and another 21% p.o.f.s. These suggest

spawning frequencies of approximately 2 and 5 days respectively for this species. A sample of *E. devisi* collected at night during this study contained 90% ripe females, indicating a spawning interval close to one day. Although these results should be taken with caution, the estimated spawning intervals are within the range of estimates for other tropical anchovies (Clarke 1987: 2 days in *E. purpurea*, Wright 1992: 2-16.5 days in *E. heteroloba*). Daily spawning by females has been estimated for some tropical clupeids from Kiribati (Milton *et al.* 1994).

There are presently no published estimates of spawning frequency for *Thryssa spp.*. The difference in the pattern of ova-diameter frequency polygons between stolephorid anchovies and *Thryssa spp.* found in the present study suggests that the spawning biology of these two groups may differ. There were only two distinct oocyte batches in ova-diameter frequency polygons for *Thryssa spp.* (Stolephorids had a continuum of oocyte stages), and this could be interpreted that this genus spawns less frequently than the genera *Encrasicholina* and *Stolephorus*. However, the two preliminary spawning frequency estimates were 2 and 5 days for *Thryssa* which was close to 3 days for *S. nelsoni*. More data on spawning frequency is needed to understand the significance of this difference in maturation. The two types of ova-diameter frequency polygons observed for species in the present study are consistent with other published ova-diameter frequency polygons for individual species within these genera (Prabhu 1956, Dharmamba 1959, Masurekar and Rege 1960, Shamsul Hoda 1976, Dalzell 1987a).

In the present study, there was evidence that the sex ratio of *T. hamiltoni* differed in samples collected close to shore and from trawling grounds in spring-summer. Samples in the trawl (2-9-88) were dominated by males and a high proportion of the females present were ripe. In contrast, two inshore samples dominated by females and none were ripe. Trawled samples of *T. setirostris* in September and October were also dominated by male fish. Spatial segregation of spawning and non-spawning fish has been observed in some anchovy and clupeid species (eg. Williams and Clarke 1983, Alheit *et al.* 1984, Clarke 1987). In two species of anchovy, *Encrasicholina purpurea*

and *Engraulis mordax*, hydrated (spawning) females separate either by depth or area from the non-spawners taking with them a high percentage of males and forming 'spawning schools' dominated by males (Alheit *et al.* 1984, Clarke 1987). The difference in sex ratio in shallow and deeper water observed for *Thryssa spp.* may therefore indicate similar reproductive schooling behaviour.

The relative fecundity estimates for the stolephorid anchovies in the present study were lower than those reported for stolephorids in other parts of the Indo-Pacific. Some reported values of relative fecundity in stolephorid anchovies are; *E. purpurea*: 432-4098 eggs/gram (Clarke 1987); *E. heteroloba*: 382-776 eggs/gram; and *E. devisi*: 811-1308 eggs/gram (Dalzell 1987). Lewis (1990) gave a range of 500-1500 eggs/gram as typical batch fecundities in small tropical baitfish (including stolephorid anchovies). The stolephorids in the present study had relative fecundities of 169-436 eggs/gram which is at the lower end of the range of relative fecundities found in other stolephorid anchovies. Fecundity in tropical clupeoids can vary in different localities (Milton and Blaber 1991), and some authors have suggested that fecundity is related to food supply (Clarke 1987, Wright 1990). Sommerton (1990) also showed that temporal variations in fecundity in *Encrasicholina purpurea* were positively related to prey density. The low relative fecundities observed for stolephorid anchovies at Townsville may therefore reflect low plankton abundances in the region. The relatively low abundances of anchovy in nearshore waters near Townsville compared to other Indo-Pacific countries supports the possibility that food abundance may be low at this locality.

Lunar periodicity in spawning and recruitment is being reported in an increasing number of tropical fishes (eg. Johannes 1978, Walsh 1987, Thorrold 1988). This phenomena has been reported for two tropical herrings (F. clupeidae), *Herklotsichthys punctatus* (Johannes 1978) and *H. castelnaui* (Thorrold 1988). Increased spawning on full moons was also inferred from planktonic egg collections by Milton and Blaber (1991) for *Encrasicholina heteroloba* at Solomon Islands. Back-calculated birthdates

for several species in this study also suggest peaks of births around new and full moons. Some possible advantages of this behaviour have been suggested by different authors. Associated with new and full moon periods are increased tidal ranges and these may result in increased flushing and dispersal of eggs. The greater tidal height may also increase the distance between eggs and benthic predators (Johannes 1978). In addition, the stronger illumination associated with a full moon may enhance visibility for spawning behaviour as anchovies spawn at night (Blaxter and Hunter 1982, Clarke 1987).

Table 8.1. Samples of anchovies collected during the reproductive season (August-January) used for gonad maturity analyses. Dates, methods and times of collection are given. (T)-trawl; (G)-inshore gill net; (S)-inshore seine net; (L)- light attraction device; +-morning sample; \*-afternoon or evening sample; ?-time not recorded. M and F are the total number of male and female fish in the sample (numbers processed for histological examination are shown in brackets).

Date/Method	Species	M	F
1-1-88 (G*)	<i>T. hamiltoni</i>	0	16 (7)
2-9-88 (T)	<i>T. hamiltoni</i>	66 (10)	27 (22)
	<i>T. setirostris</i>	46 (9)	9 (3)
	<i>S. nelsoni</i>	14 (6)	12 (8)
12-10-88 (G*)	<i>T. hamiltoni</i>	3 (3)	42 (19)
17-10-88 (T)	<i>T. hamiltoni</i>	44 (17)	15 (9)
	<i>T. setirostris</i>	56 (4)	6 (2)
	<i>S. nelsoni</i>	6 (6)	10 (10)
19-12-88 (T)	<i>T. hamiltoni</i>	2 -	6 -
6-1-89 (S?)	<i>S. nelsoni</i>	2 (2)	2 (2)
18-1-89 (S?)	<i>S. nelsoni</i>	1 (1)	5 (5)
13-2-89 (L*)	<i>E. devisi</i>	45 (8)	31 (7)
31-8-89 (S*)	<i>S. nelsoni</i>	8 (2)	13 (6)
	(S*) <i>S. carpentariae</i>	5 (2)	6
20-9-89 (S*)	<i>S. nelsoni</i>	18 (18)	17 (17)
	(S+) <i>S. carpentariae</i>	25 (16)	9 (7)
26-9-89 (S+)	<i>S. carpentariae</i>	1 (1)	4 (4)
5-10-89 (S*)	<i>S. nelsoni</i>	7 (5)	2
	(S*) <i>S. carpentariae</i>	2 (2)	4 (4)
25-10-89 (S+)	<i>S. carpentariae</i>	1 (1)	2 (2)

Table 8.1 Continued...

Date/Method	Species	M	F
6-11-89 (S*)	<i>S. nelsoni</i>	12 (3)	8 (5)
	(S*) <i>S. carpentariae</i>	10 (7)	4 (4)
10-11-89 (S+)	<i>S. carpentariae</i>	9 (8)	4 (4)

Table 8.2. The maturity composition of samples collected between August and January for individual species and the maturity composition of samples containing mature or ripe fish in other months of the year. Maturity was determined from histological sectioning and visual staging of whole ovaries.

I. *T. hamiltoni*

Stage	I	II	III	IV
Date				
1-1-88	2	5	9	-
25-2-88	3	7	1	-
2-9-88	-	3	12	12
12-10-88	2	4	15	-
17-10-88	-	6	8	1
9-12-89-	-	-	5	-
26-2-89	-	4	4	-
14-8-90	-	-	1	-
15-8-90	-	-	1	-
15-2-90	3	2	1	-

II. *T. setirostris*

Stage	I	II	III	IV
Date				
11-8-88	-	5	-	-
2-9-88	-	-	2	7
17-10-88	-	-	5	1
9-12-89	-	-	1	-
24-1-89	-	1	-	-
30-8-90	-	-	2	-
11-1-91	-	-	-	1

III. *T. aestuaria*

Stage	I	II	III	IV
Date				
12-7-88	-	-	7	-
2-9-88	-	-	4	4

IV. *S. commersonii*

Stage	I	II	III	IV
Date				
5-12-88	-	-	-	1
5-9-89	-	-	1	-



Table 8.2 Continued...

*V. S. nelsoni*

Stage	I	II	III	IV
Date				
2-9-88	-	2	10	-
17-10-88	-	1	8	1
6-1-89	1	-	1	-
18-1-89	-	-	2	3
31-8-89	-	3	3	7
20-9-89	-	6	5	6
5-10-89	-	-	-	2
6-11-89	-	-	8	-
15-11-90	-	1	-	1

*VI. S. carpentariae*

Stage	I	II	III	IV
Date				
11-3-88	1	2	2	-
18-11-88	-	-	4	-
9-2-89	-	1	2	-
15-8-89	-	1	1	-
25-8-89	-	-	1	-
31-8-89	-	4	6	-
20-9-89	-	-	9	-
26-9-89	-	-	4	-
5-10-89	-	-	2	2
25-10-89	-	1	1	-
10-11-89	-	2	1	1

*VII. E. devisi*

Stage	I	II	III	IV
Date				
19-5-88	-	-	1	1
12-12-88	-	-	5	-
13-2-89	-	-	3	28
31-3-89	1	4	2	-
14-4-89	-	-	2	-
18-5-89	-	1	2	-
22-5-89	-	3	1	-
30-5-89	1	2	2	-
7-7-89	-	2	1	-
31-8-89	-	-	1	-

Table 8.2. Continued...

VIII. *S. insularis*

Stage

Date	I	II	III	IV
23-2-88	-	1	1	-
19-5-88	-	-	2	-
12-7-88	-	-	-	1
18-11-88	-	7	7	-
22-5-89	-	-	1	-
6-6-89	-	-	1	-
31-8-89	-	5	12	-
10-4-90	-	10	8	-

Table 8.3. Range and mean of batch fecundity estimates for eight species of anchovies. n - number of gonads examined, s-standard deviation.

Species	n	range	mean	s
<i>S. insularis</i>	6	50-350	205	114
<i>E. devisi</i>	24	94-824	381	221
<i>S. carpentariae</i>	7	215-825	515	253
<i>S. nelsoni</i>	18	213-2526	1055	714
<i>S. commersonii</i>	2	1392-6000	3696	3260
<i>T. aestuaria</i>	11	1678-5273	3043	1077
<i>T. setirostris</i>	10	7902-20923	12920	3801
<i>T. hamiltoni</i>	14	8615-27583	18200	7820

Table 8.4. Relative fecundities (eggs/gram body weight) for eight species of anchovy. The range and mean of the relative fecundity estimates for each species are given. s-standard deviation, n-number.

Species	n	Range	Mean	s
<i>E. devisi</i>	23	128-781	436	192
<i>S. insularis</i>	6	69-360	221	127
<i>S. carpentariae</i>	7	240-551	349	117
<i>S. nelsoni</i>	19	67-384	169	100
<i>S. commersonii</i>	2	51-358	204	217
<i>T. aestuaria</i>	10	65-265	137	59
<i>T. setirostris</i>	10	204-350	252	52
<i>T. hamiltoni</i>	13	155-342	239	63

Table 8.5. A summary of the lengths and ages-at-maturity ( $L_m$  and  $A_m$ ), and the ratios of length-at-maturity to maximum length ( $L_m/L_{max}$ ) for six anchovy species. Age-at-maturity was calculated from the primary otolith increment length-age regressions.

Species	$L_m$ (mm)	$L_{max}$ (mm)	$L_m/L_{max}$	$A_m$ (days)
<i>E. devisi</i>	47	62	0.76	59-68
<i>S. insularis</i>	42.5	64	0.66	79
<i>S. carpentariae</i>	50	71	0.7	74
<i>S. nelsoni</i>	70	103	0.68	158
<i>T. setirostris</i> (males)	155	217	0.71	251
<i>T. setirostris</i> (females)	160	220	0.63	274
<i>T. hamiltoni</i> (males)	155	221	0.7	265
<i>T. hamiltoni</i> (females)	160	251	0.64	281

Table 8.6. A summary of the reproductive life-histories and reproductive parameters in the 8 species of anchovy studied.

Species	Spawning season	L-maturity (L <sub>m</sub> )	Max. length (L <sub>max</sub> )	L <sub>m</sub> /L <sub>max</sub>	Age maturity (A <sub>m</sub> -days)	Max age (A <sub>max</sub> -days)	A <sub>m</sub> /A <sub>max</sub>	Mean batch fecundity	Relative fecundity
<i>E. devisi</i>	year round	47	62	0.76	59-68	95	0.67	381	436
<i>S. insularis</i>	year round	42.5	64	0.66	79	126	0.63	205	221
<i>S. carpentariae</i>	spring/sum. (Sep.-Jan.)	50	71	0.7	74	158	0.47	515	349
<i>S. nelsoni</i>	spring/sum. (Sep.-Jan.)	70	103	0.68	158	247	0.64	1055	169
<i>S. commersonii</i>	spring/sum. (Sep.-)	-	158	-	-	240	-	3696	204
<i>T. aestuaria</i>	spring/sum. (Jul/Sep.-)	-	142	-	-	-	-	3043	137
<i>T. setirostris</i> m f	spring/sum. (Sep.-Jan.)	155 160	220	0.71 0.73	251 274	730	0.34 0.38	12920	252
<i>T. hamiltoni</i> m f	spring/sum. (Sep.-Jan.)	155 160	220 251	0.7 0.63	265 281	1460	0.18 0.19	18200	239

Figure 8.1. Mean monthly gonado-somatic indices plotted against month. (a) Male *Thryssa hamiltoni*; (b) Female *T. hamiltoni*; (c) Male *Thryssa setirostris*; (d) Female *T. setirostris*. Standard deviations about the mean monthly values are given.

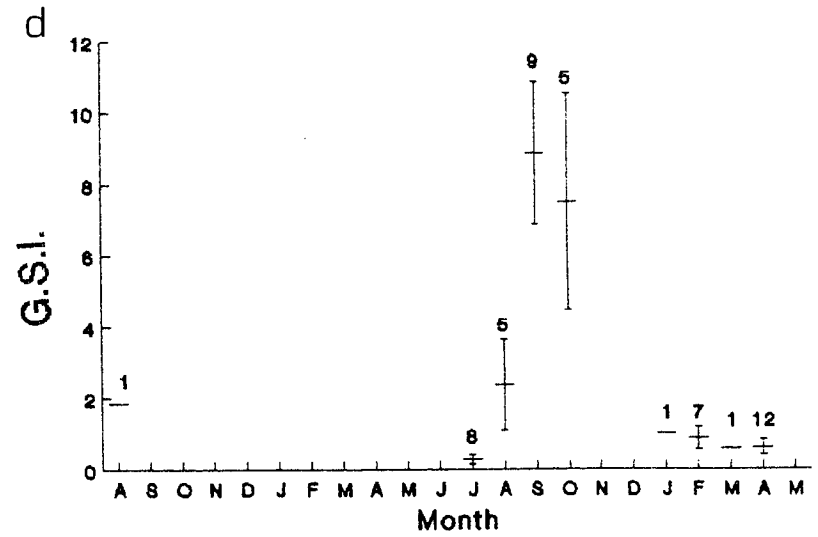
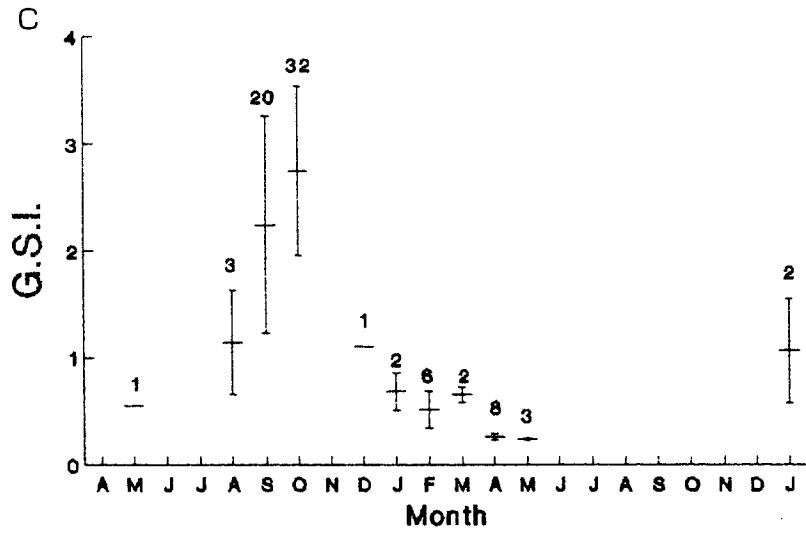
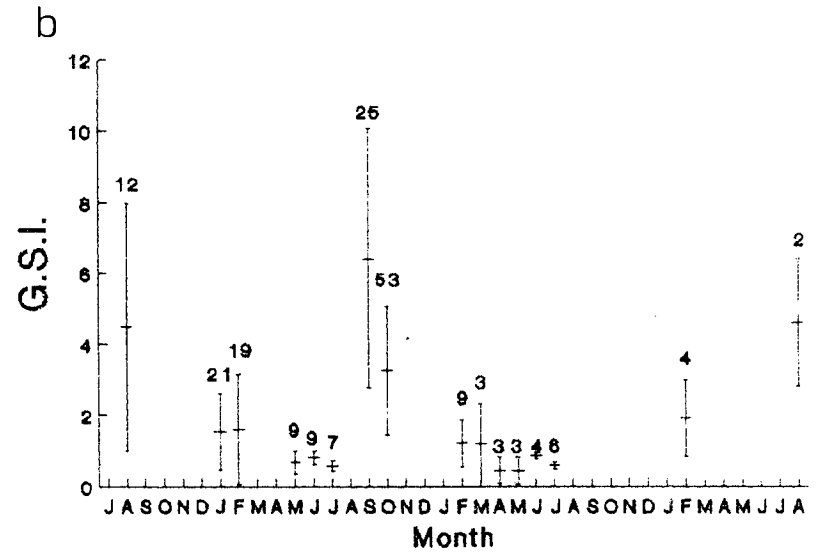
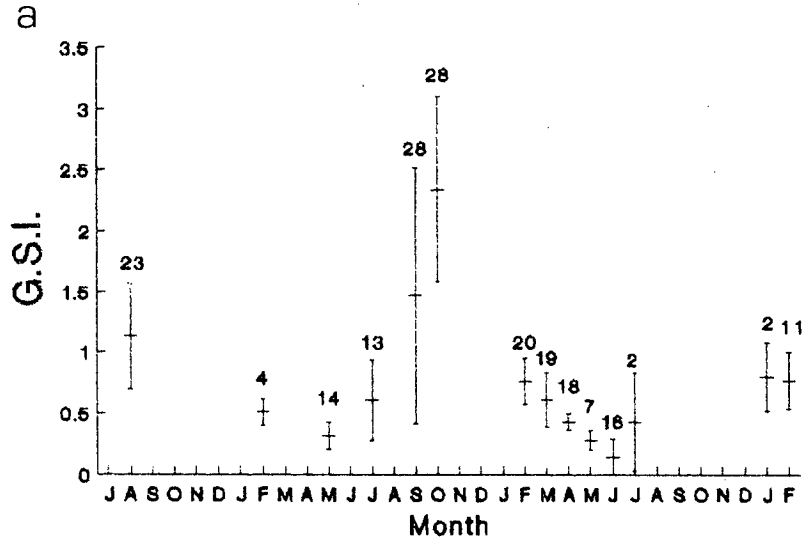


Figure 8.2. Mean monthly gonado-somatic indices plotted against month. (a) Male *Thryssa aestuaria*; (b) Female *T. aestuaria*; (c) Male *Stolephorus nelsoni*; (d) Female *S. nelsoni*. Standard deviations about the mean monthly values are given.



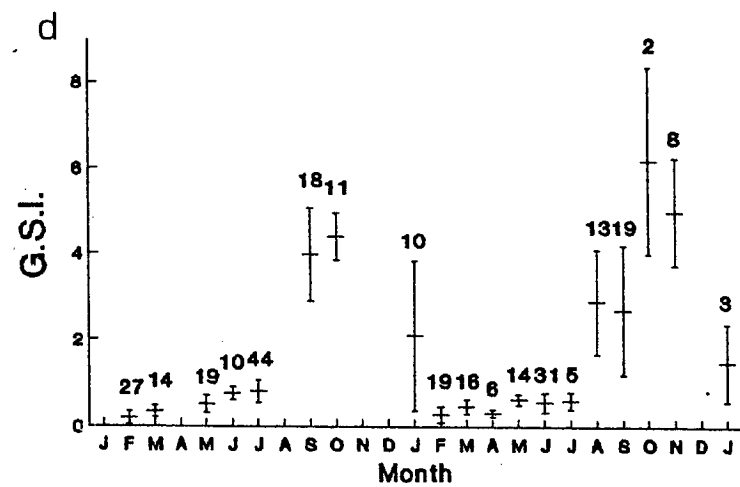
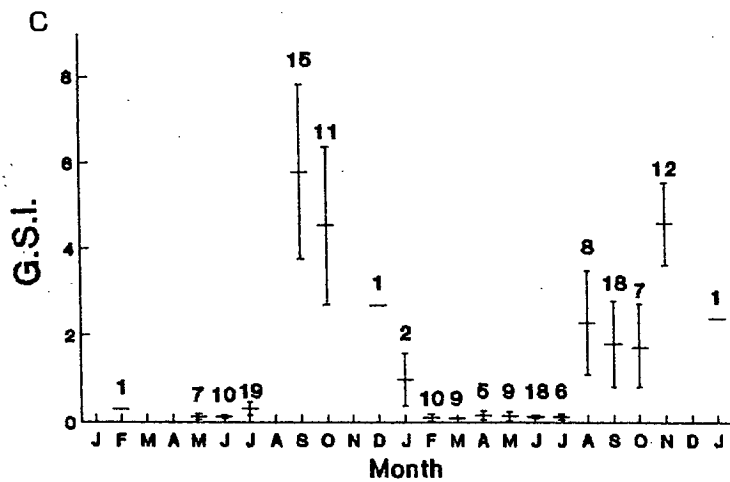
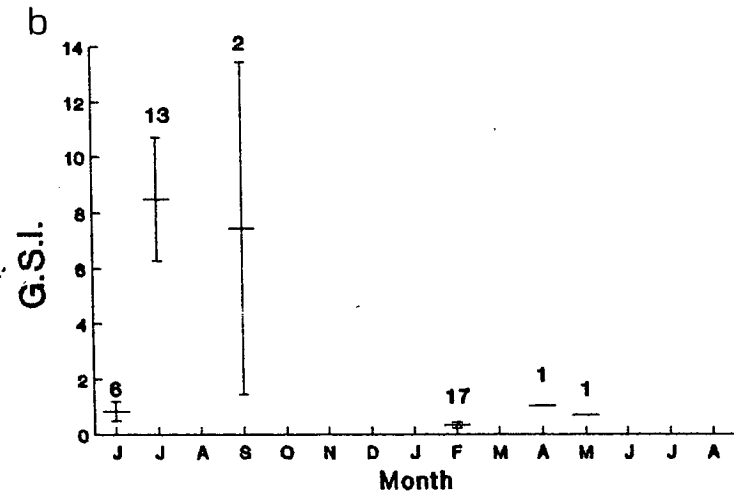
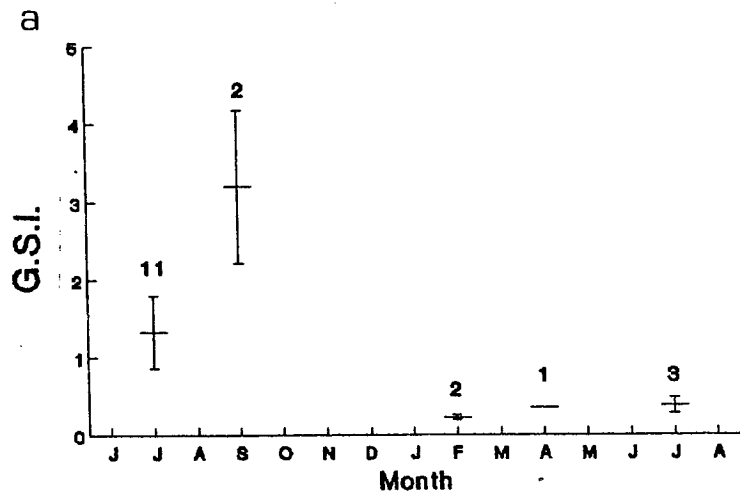


Figure 8.3. Mean monthly gonado-somatic indices plotted against month. (a) Male *Stolephorus commersonii*; (b) Female *S. commersonii*; (c) Male *Stolephorus carpentariae*; (d) Female *S. carpentariae*. Standard deviations about the mean monthly values are given.

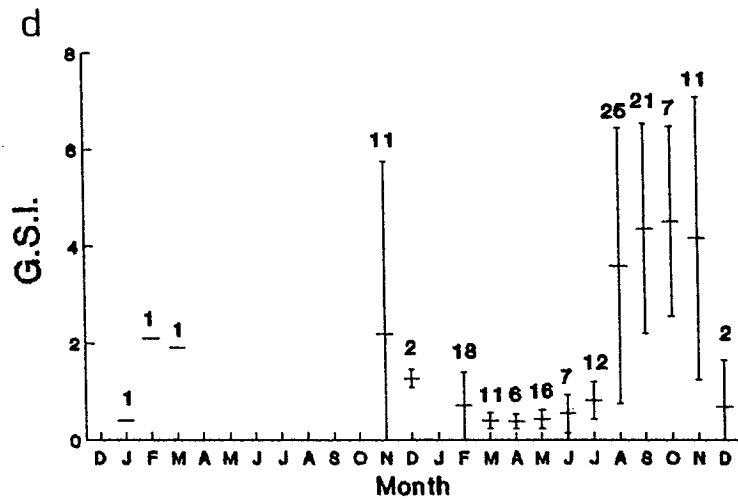
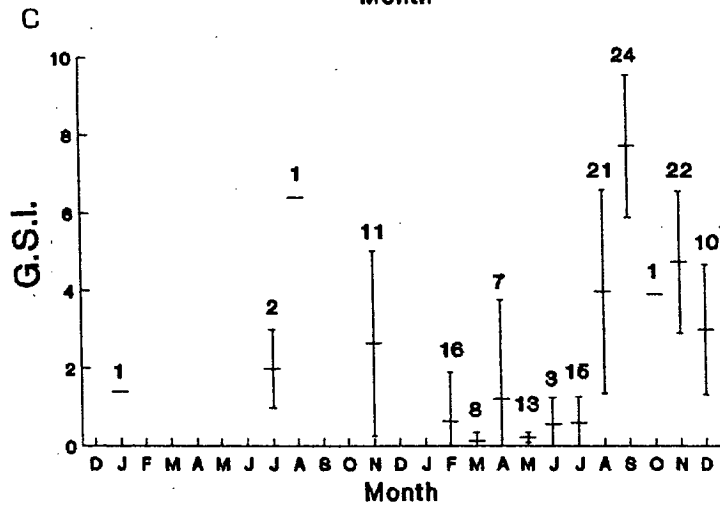
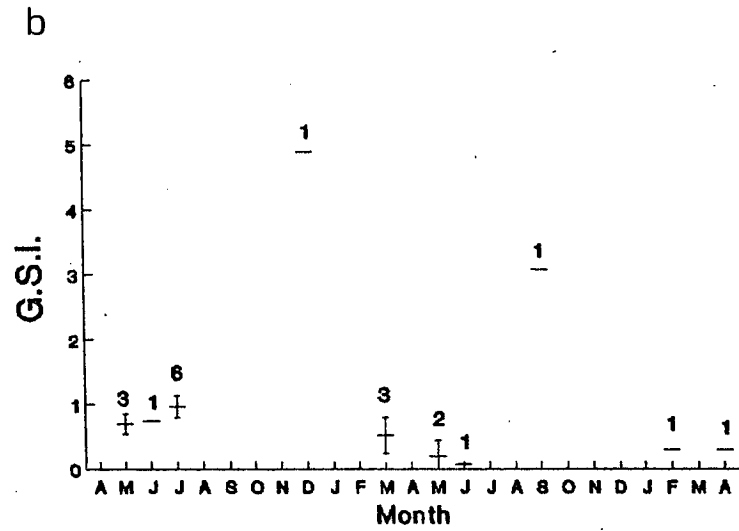
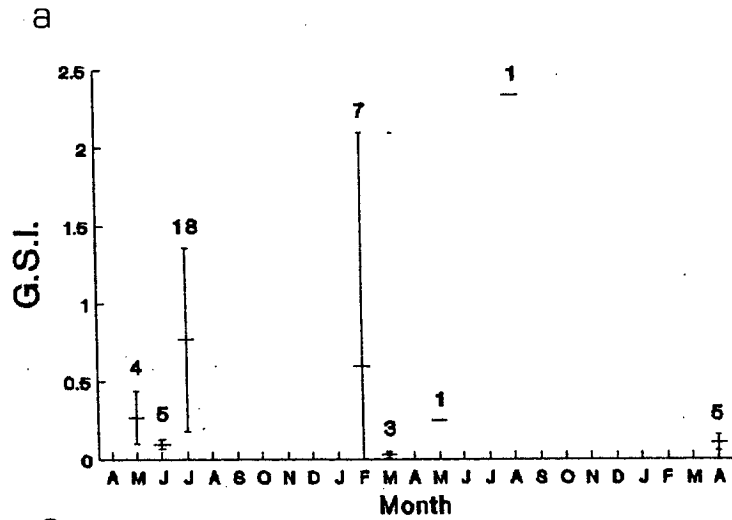


Figure 8.4. Mean monthly gonado-somatic indices plotted against month. (a) Male *Stolephorus insularis*; (b) Female *S. insularis*; (c) Male *Encrasicholina devisi*; (d) Female *E. devisi*. Standard deviations about the mean monthly values are given.

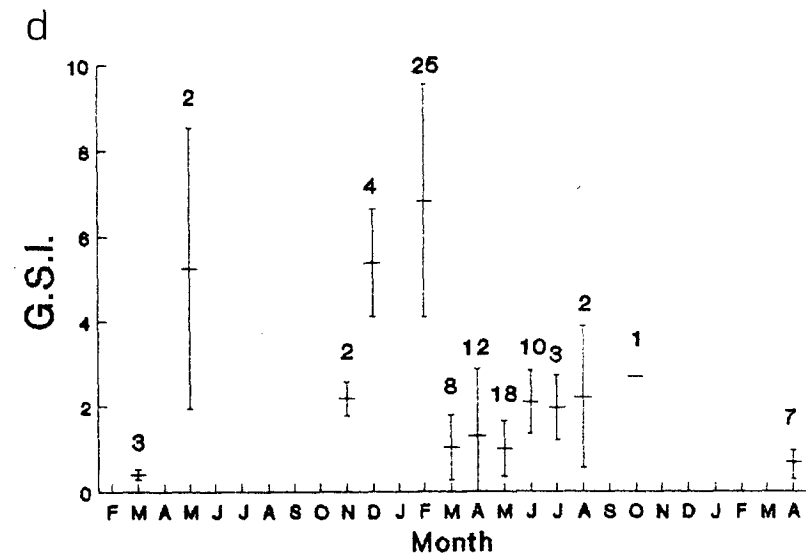
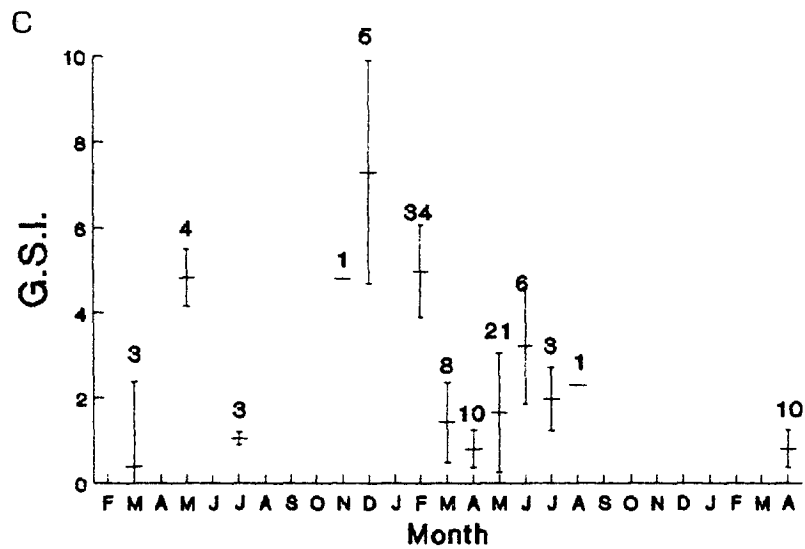
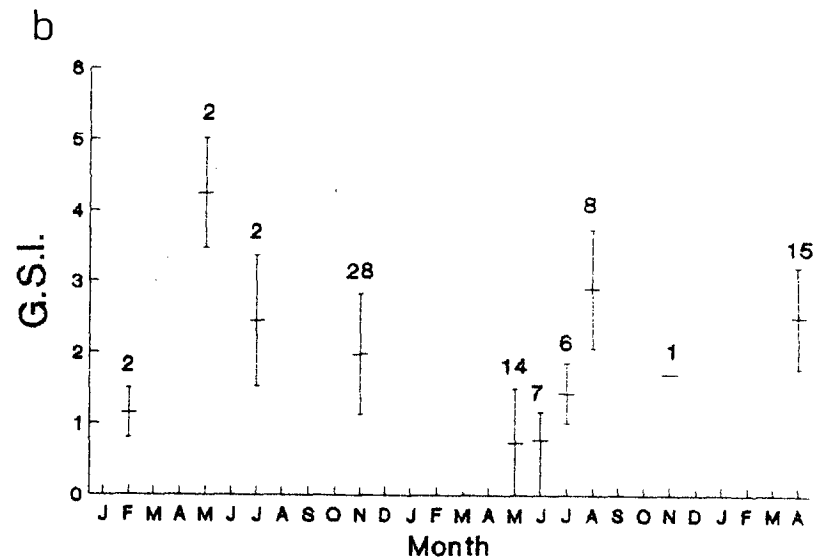
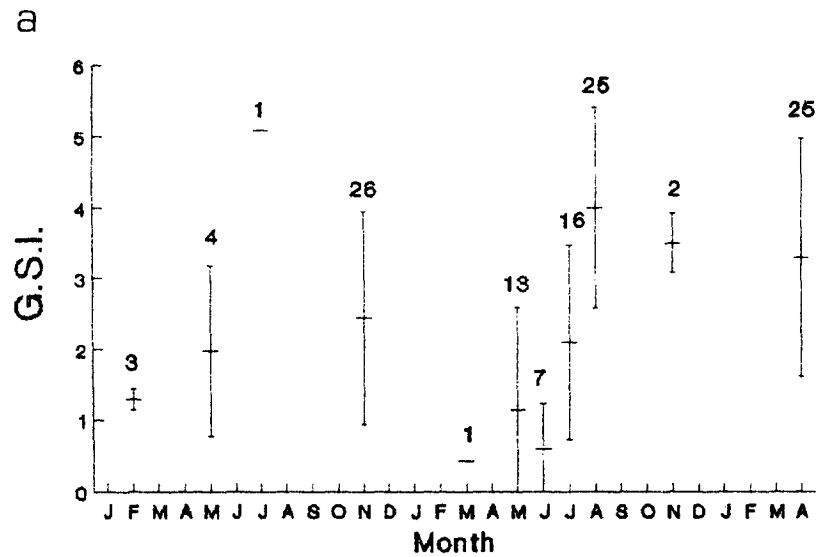


Figure 8.5. Photomicrographs of four maturity stages in histological preparations of anchovy ovaries. (a) Immature or stage I ovary (just commencing oocyte development) in *Stolephorus nelsoni*; (b) Maturing or stage II ovary in *S. nelsoni*; (c) Mature or stage III ovary from *Thryssa hamiltoni*; (d) Ripe or stage IV ovary in *Encrasicholina devisi*. U-unyolked oocyte; VS- vesicle stage oocyte; PY-primary yolked oocyte; SY-secondary yolked oocyte; ZR-zona radiata; FC-follicle cells; N-nucleus; YP-yolk plates; MN-migratory nucleus. Scale bar=0.5mm in (a),(b) and (d). Scale bar=0.25mm in (c).

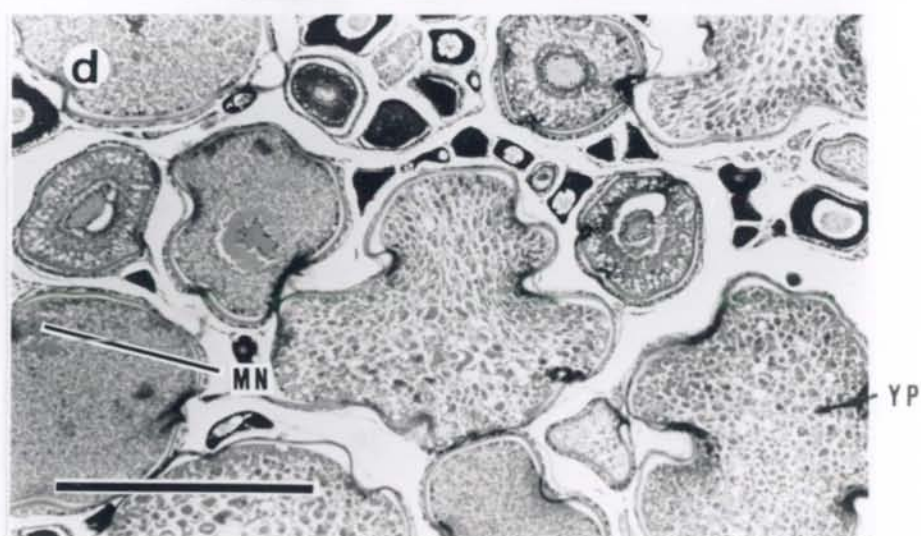
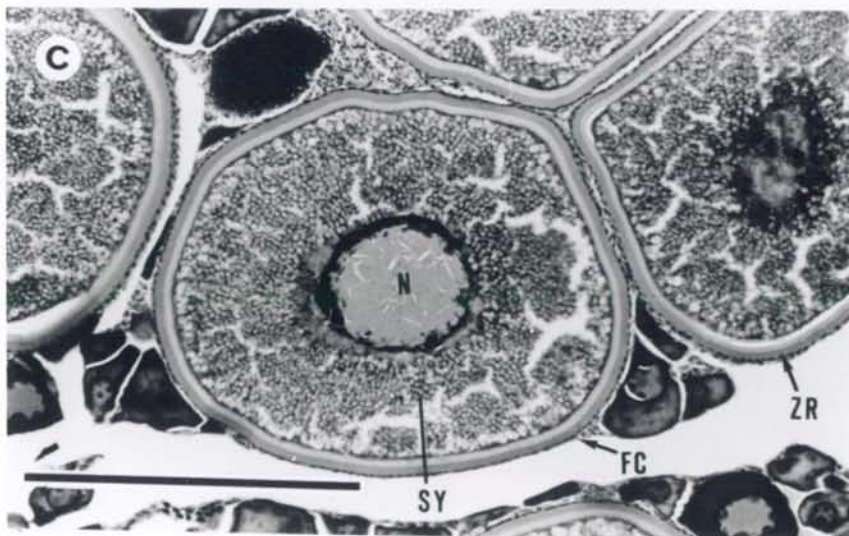
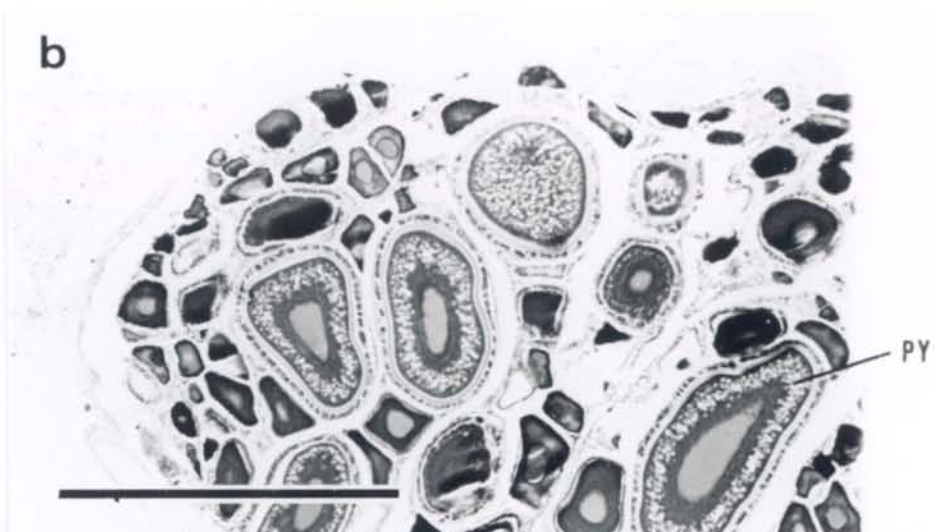
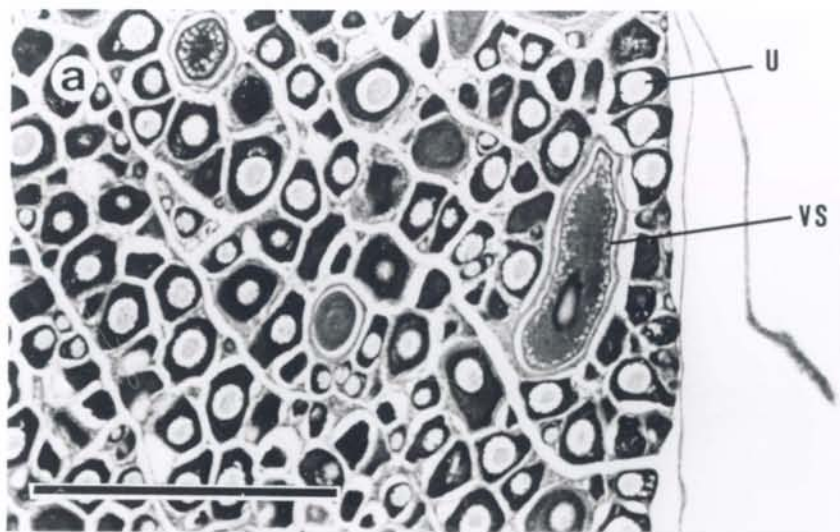


Figure 8.6. Photomicrographs of ovarian post-ovulatory follicles and atretic oocytes in histological preparations of anchovy ovaries. (a) Post-ovulatory follicles in a *Thryssa hamiltoni* ovary; (b) Atretic stage II oocyte in an ovary from *Stolephorus nelsoni*; (c) An atretic secondary yolked oocyte in a stage III *S. nelsoni* ovary; (d) A degenerated atretic oocyte in a stage III *S. nelsoni* ovary. L-lumen; T-thecal connective layer; G-granulosa epithelial cell layer; POF-post-ovulatory follicle; A-atretic oocyte; S-spawning scar (old follicle cell); Y-yolked oocyte. Scale bars=0.1mm.



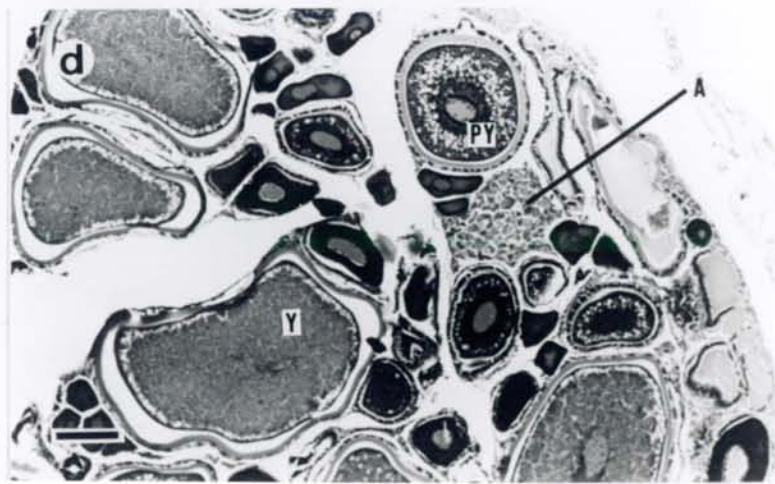
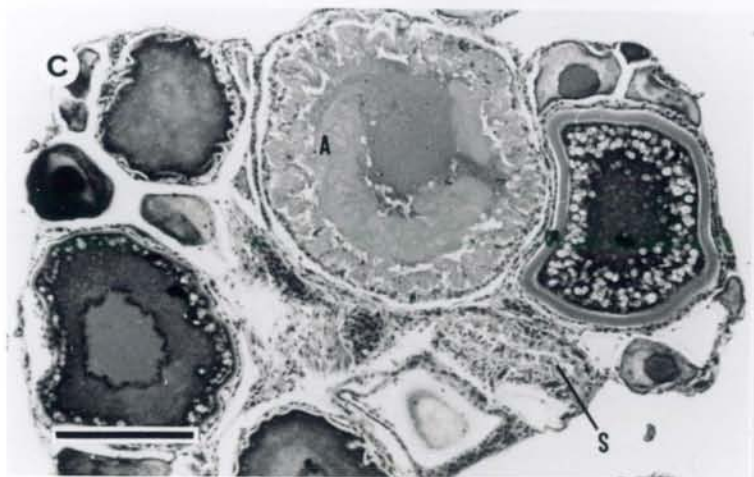
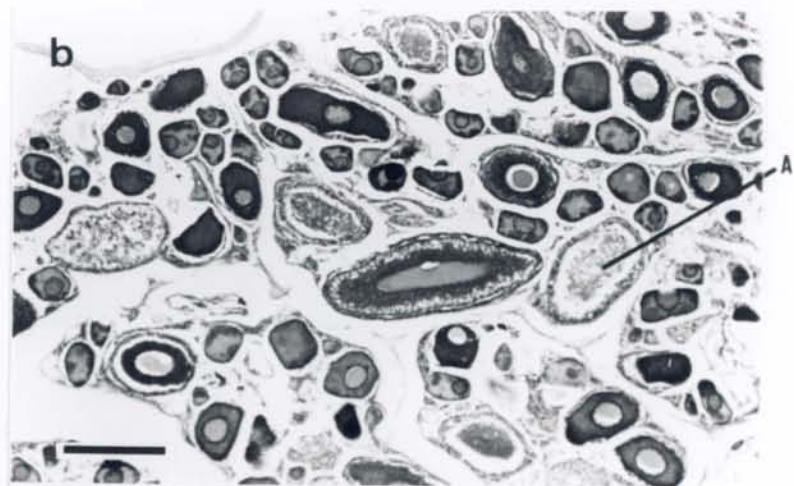
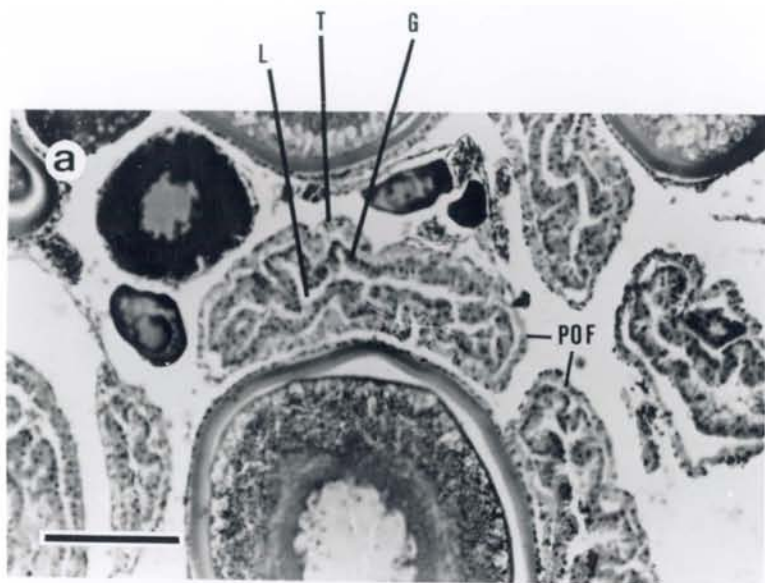


Figure 8.7. Photomicrographs of histological preparations of the stages of maturity in anchovy testis. (a) Immature or stage I testis in *Stolephorus nelsoni*; (b) Maturing or stage II testis in *Stolephorus carpentariae*; (c) Mature or stage III testis in *Thryssa setirostris*; (d) Ripe or stage IV testis showing spermatozoa in tubules in *T. setirostris*. SG-spermatogonia; SC-spermatocytes; ST-spermatids; SZ-spermatozoa; ER-erythrocytes; PS-primary spermatocytes; SS-secondary spermatocytes. Scale bar=0.1mm in all plates.

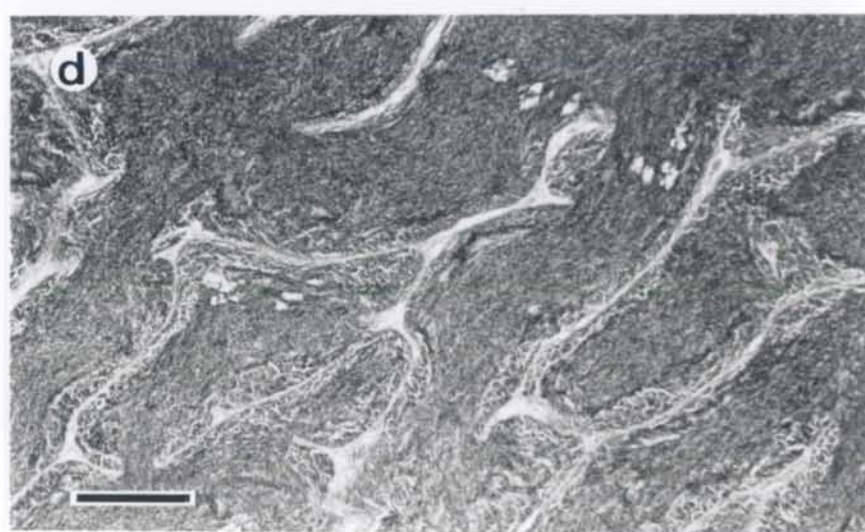
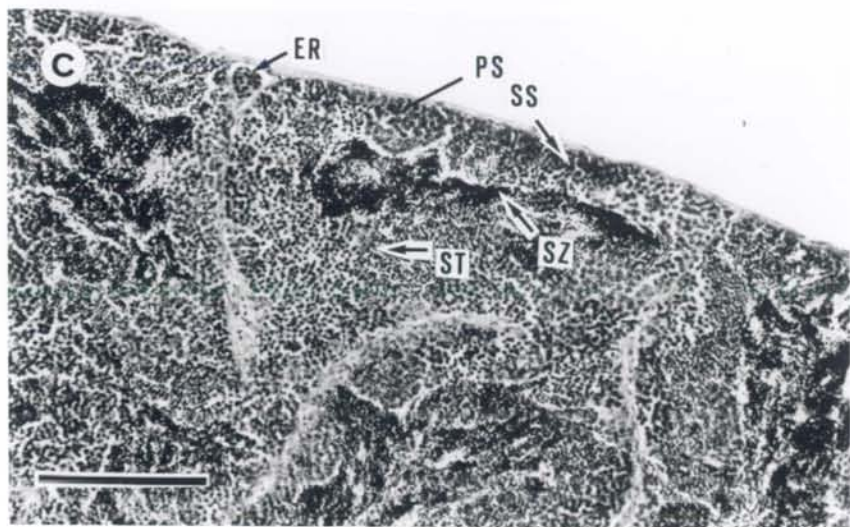
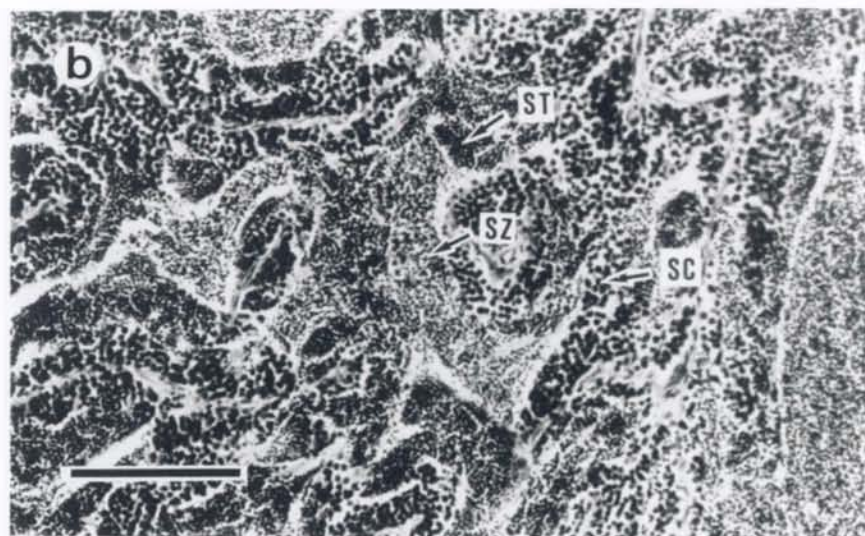
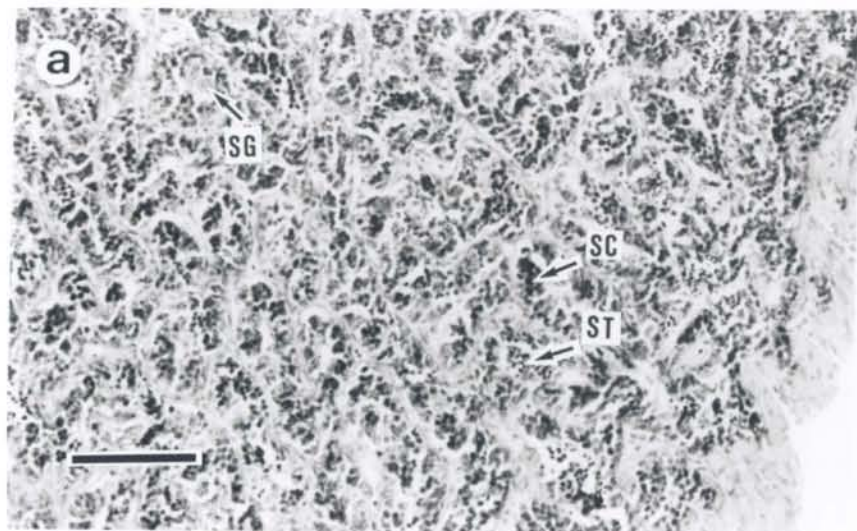
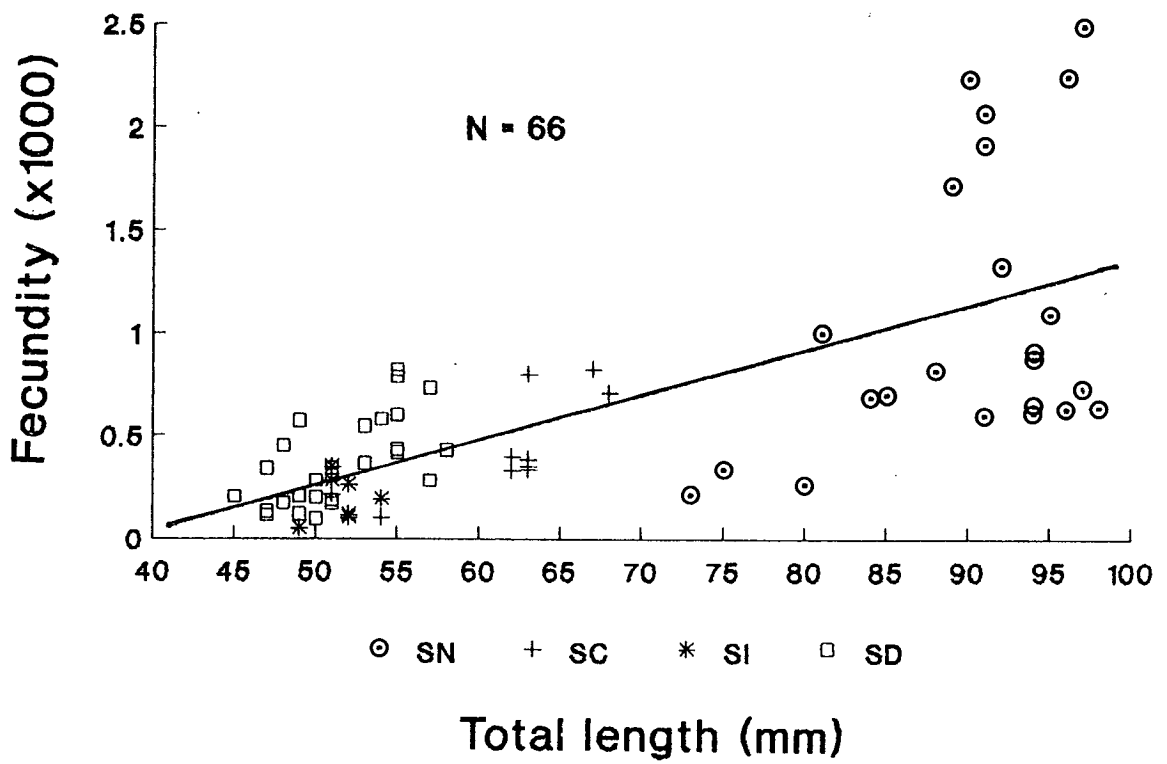
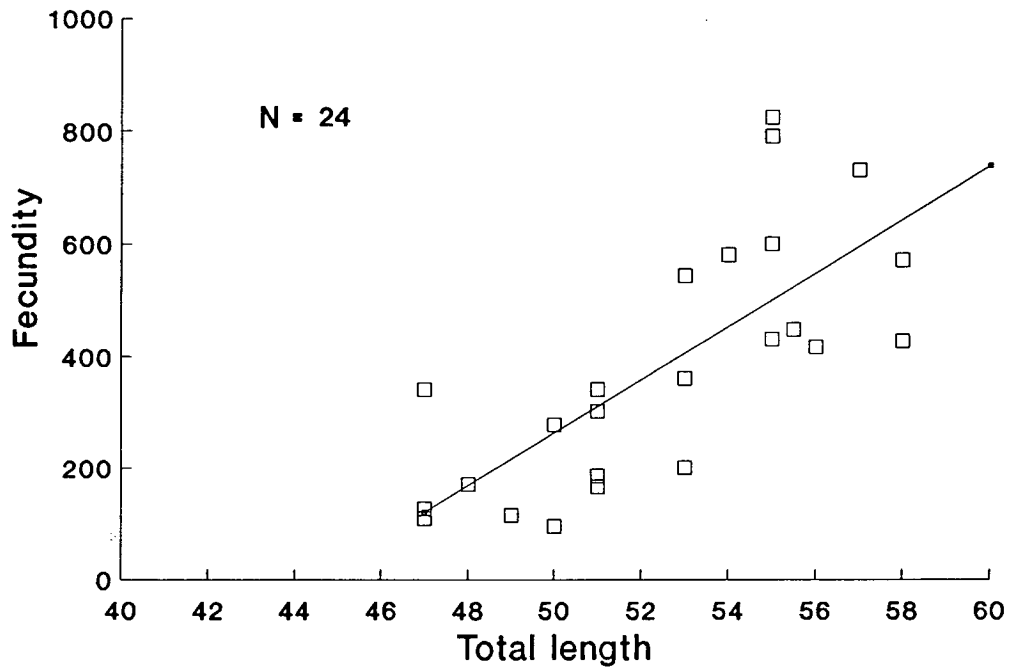


Figure 8.8. Fecundity plotted against length for anchovy species. (a) *Encrasicholina devisi* individuals caught on 13-2-89; (b) Combined data from four stolephorid species. Key : □- *Encrasicholina devisi* (SD), \*- *Stolephorus insularis* (SI), +- *Stolephorus carpentariae* (SC) and o- *Stolephorus nelsoni* (SN). A fitted linear regression is shown.



8.9 Fecundity plotted against length using combined data for more than one anchovy species. (a) Fecundity plotted against length for *Stolephorus nelsoni* (◊); *Thryssa aestuaria* (●); *Thryssa setirostris* (Δ) and *Thryssa hamiltoni* (■). An fitted exponential curve fitted to the combined data is shown. (b) Fecundity plotted against weight for *Stolephorus nelsoni*, *Stolephorus commersonii* (X), *Thryssa aestuaria*, *Thryssa setirostris* and *Thryssa hamiltoni*. A linear regression is fitted to the combined data for all species.

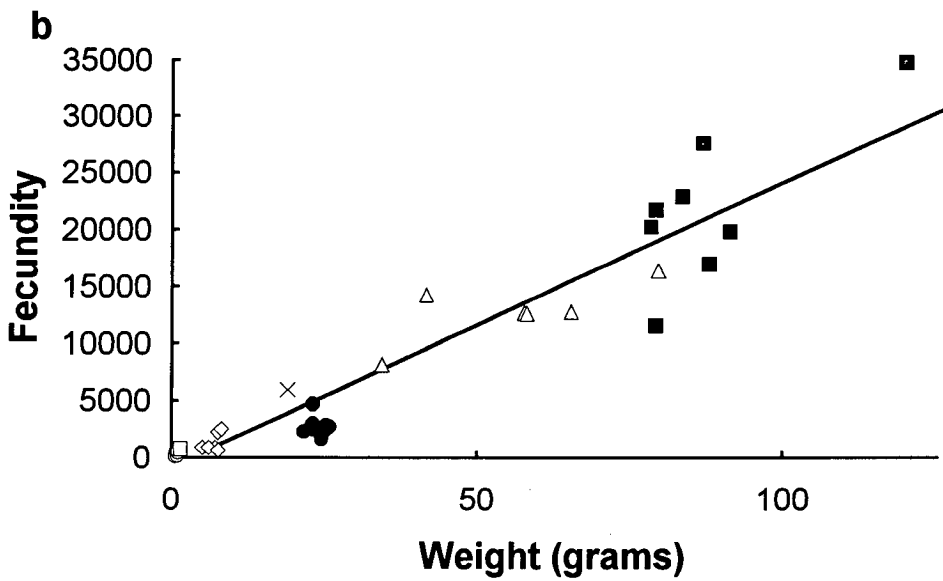
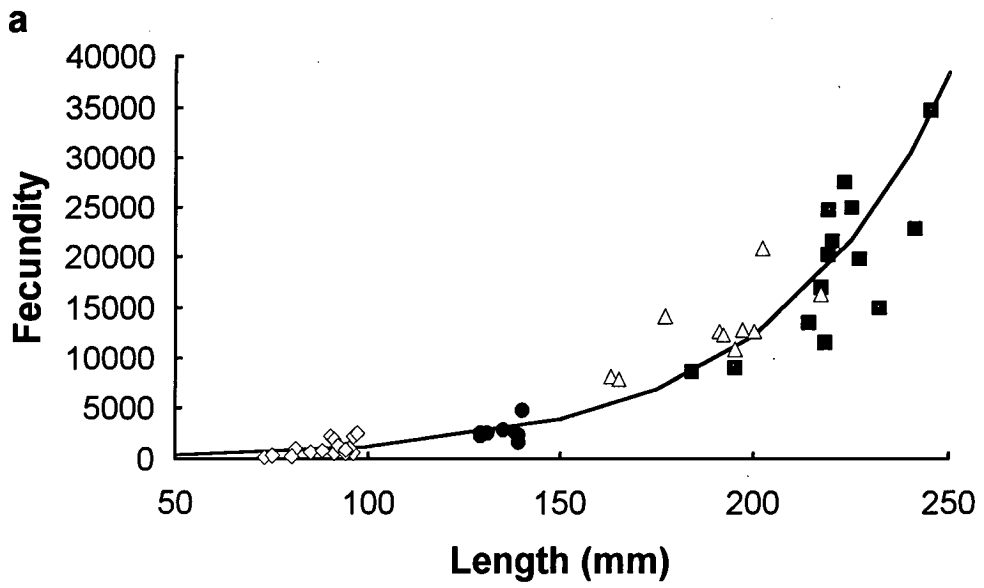
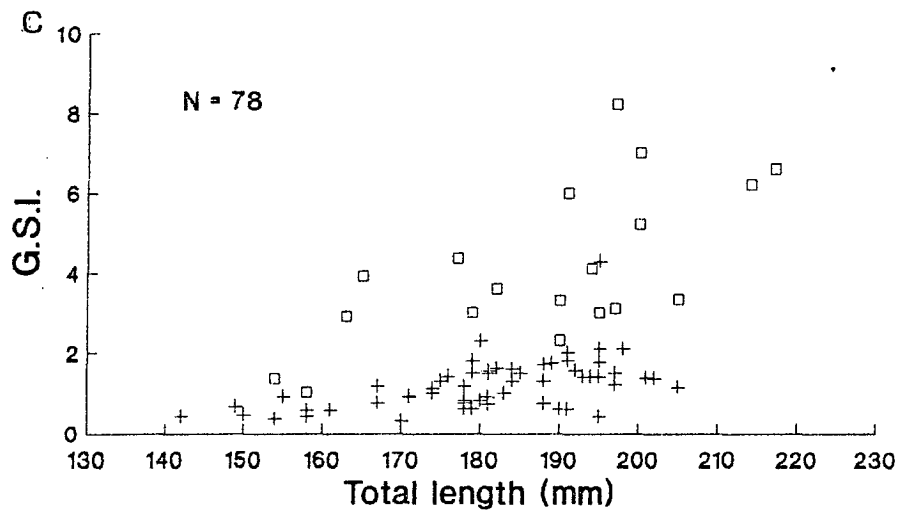
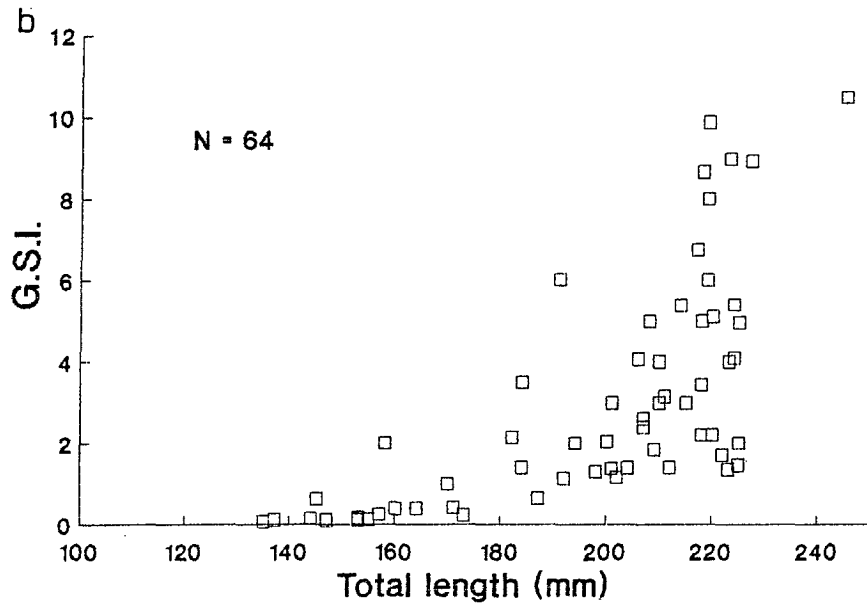
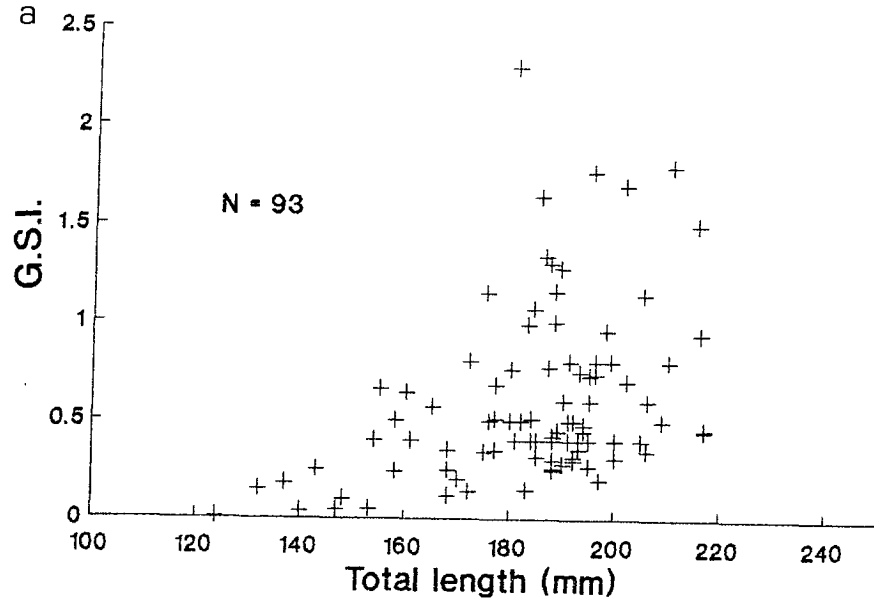


Figure 8.10 Gonado-somatic index plotted against length. (a) Male *Thryssa hamiltoni*, (b) Female *T. hamiltoni*; (c) Male and female *Thryssa setirostris*.

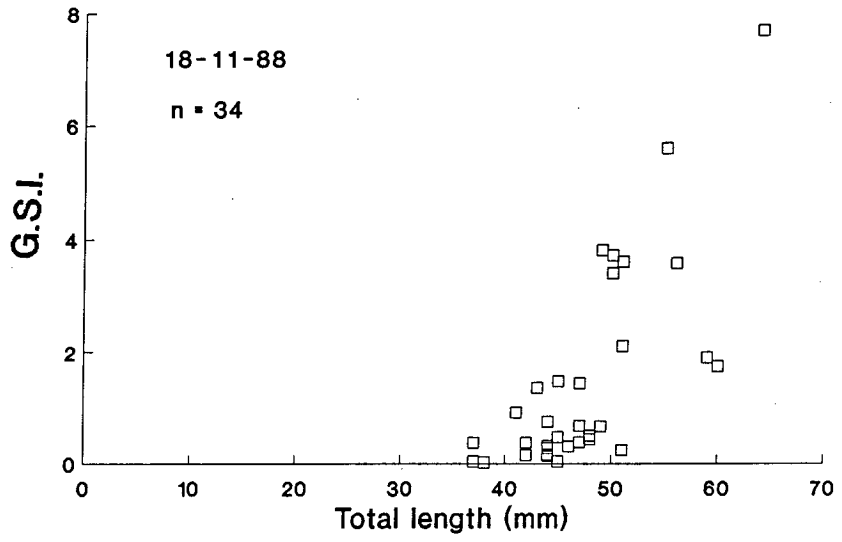




+ Males    □ Females

Figure 8.11. Gonado-somatic index plotted against length. (a) *Stolephorus carpentariae* individuals caught on 18-11-88; (b) *Stolephorus nelsoni* individuals collected during spawning months.

**a**



**b**

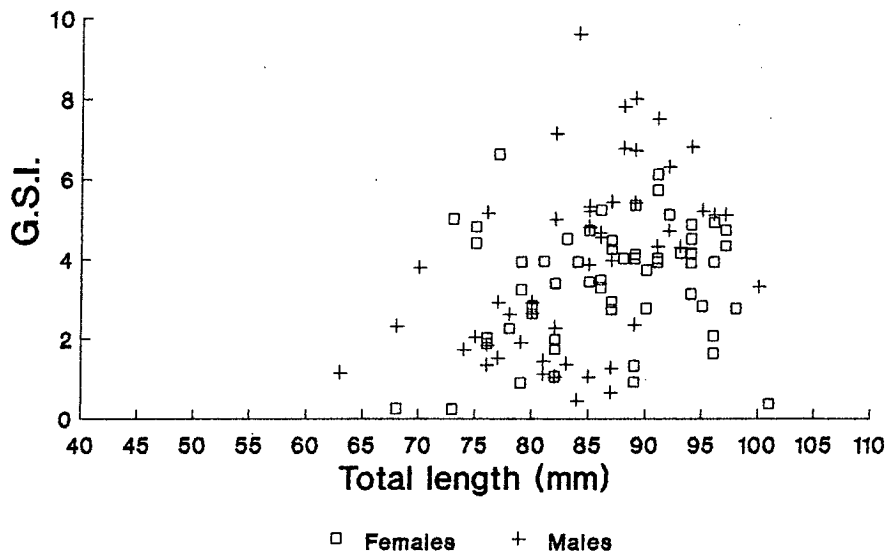
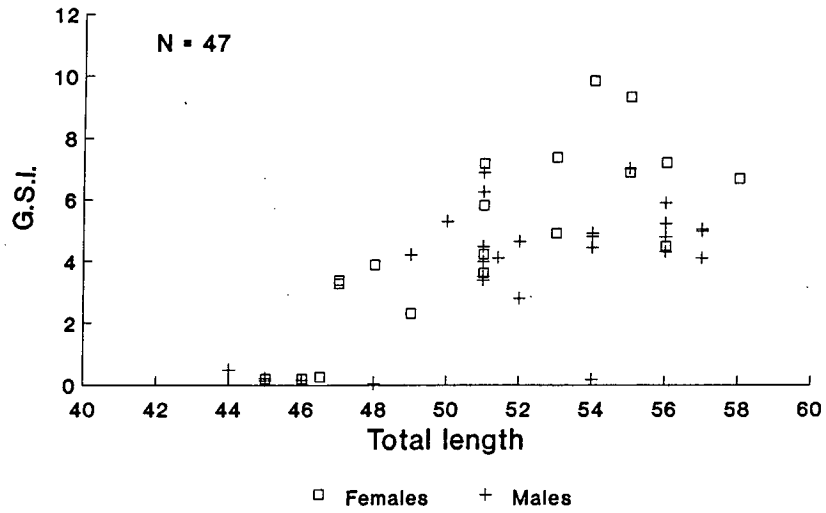


Figure 8.12. Gonado-somatic index plotted against length. (a) *Encrasicholina devisi* individuals collected on 13-2-89; (b) *Stolephorus insularis* individuals collected on 18-11-88.

**a**



**b**

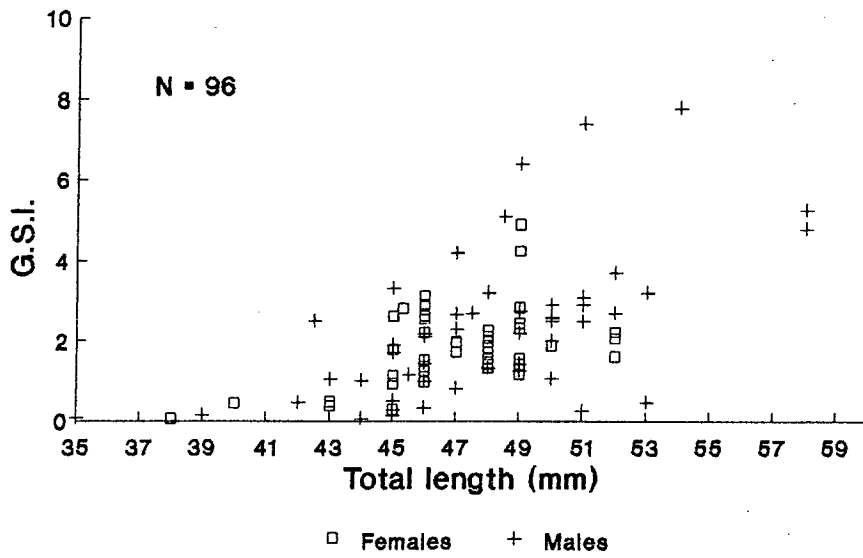


Figure 8.13. Ova-diameter frequency polygons characteristic of stolephorid anchovies.  
(a) A stage III ovary from *Stolephorus nelsoni*; (b) A stage IV ovary in *S. nelsoni*.

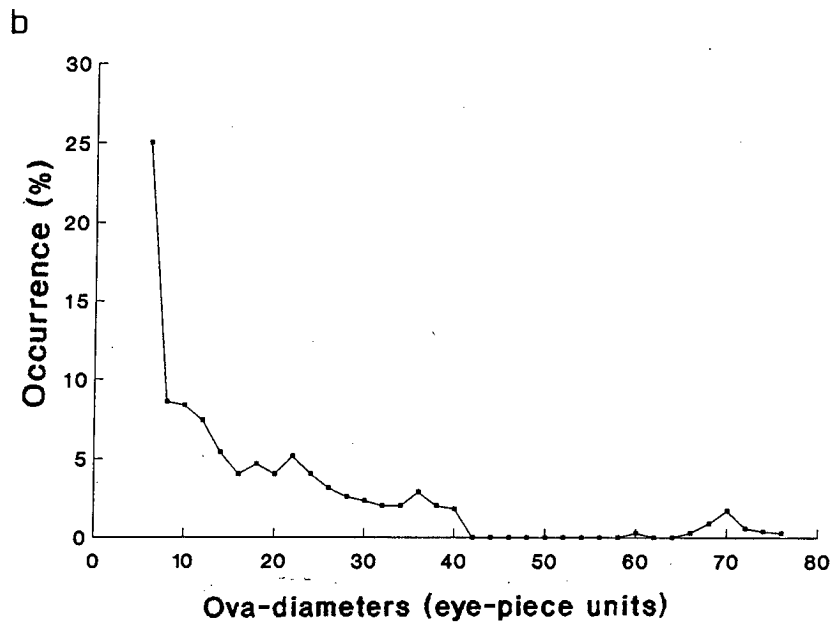
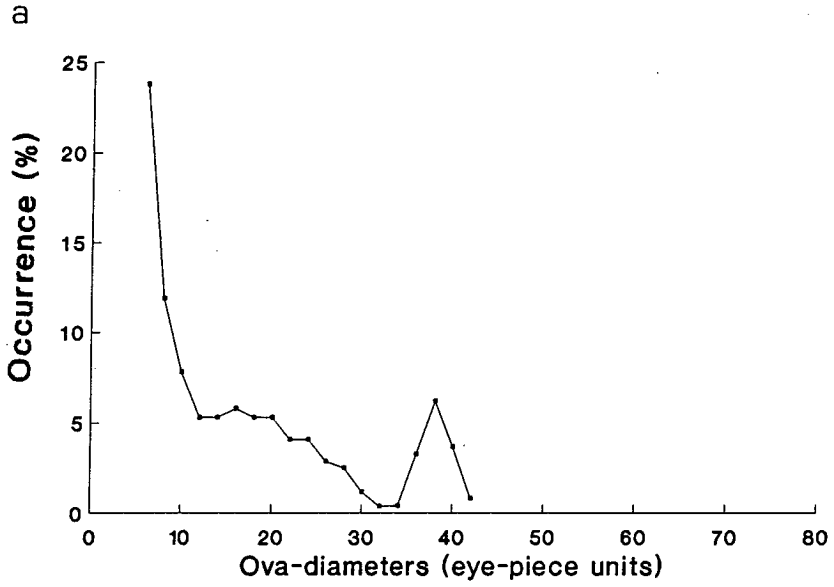
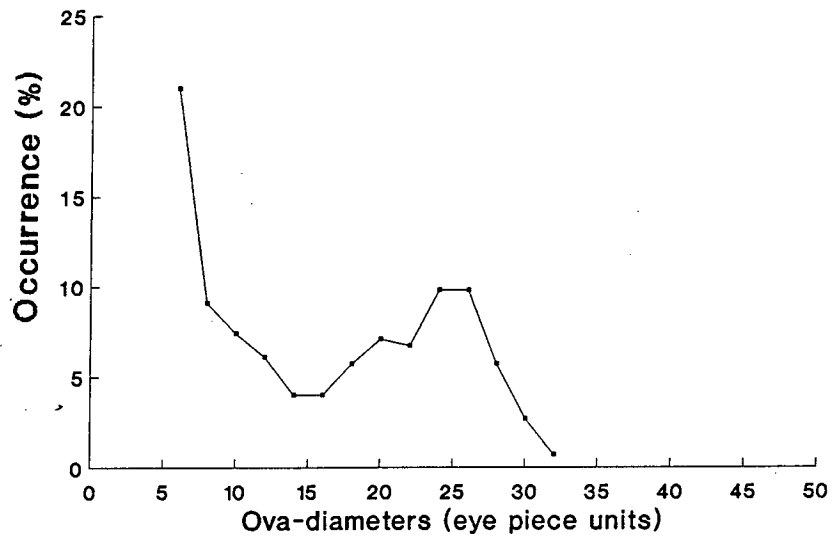


Figure 8.14. Ova-diameter frequency polygons characteristic of *Thryssa* spp. (a) A stage III ovary from *Thryssa hamiltoni*; (b) A stage IV ovary from *T. hamiltoni*.



a



b

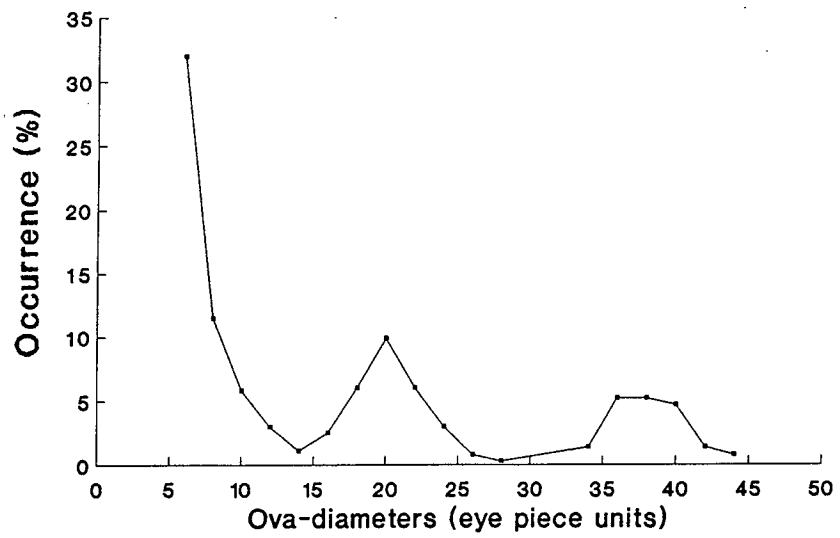


Figure 8.15. Back-calculated birth-dates for juvenile anchovies. (a) *Stolephorus carpentariae* collected on 17-10-90; (b) *Stolephorus commersonii* collected on 17-10-90; (c) *Thryssa aestuaria* collected on 3-10-91. Key: ●- new moons; ○- full moons.

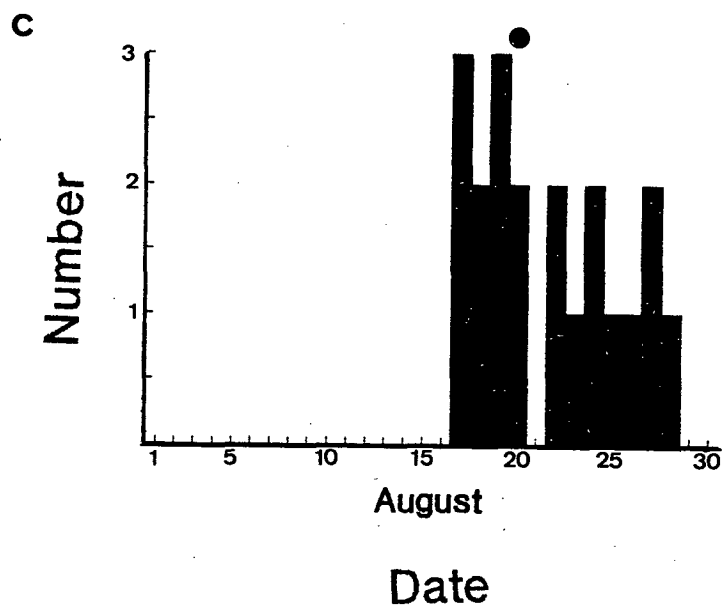
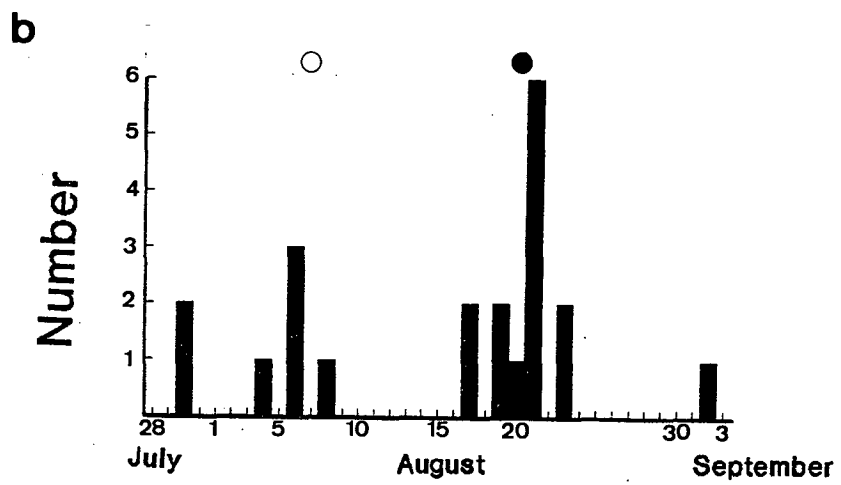
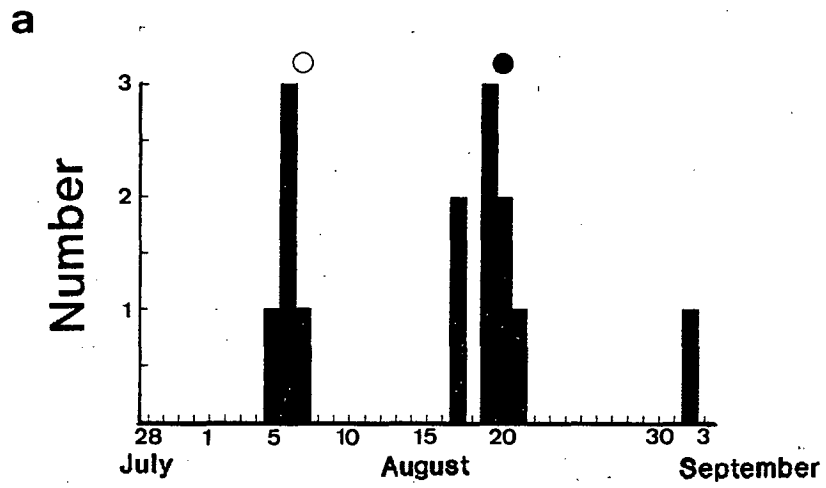
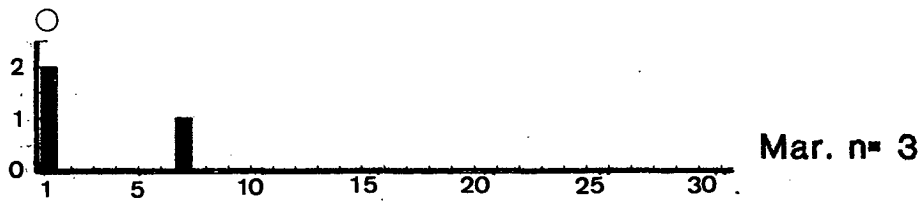
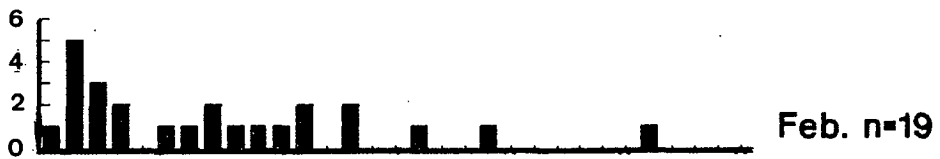
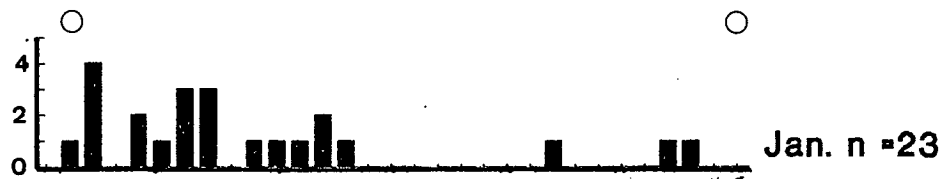
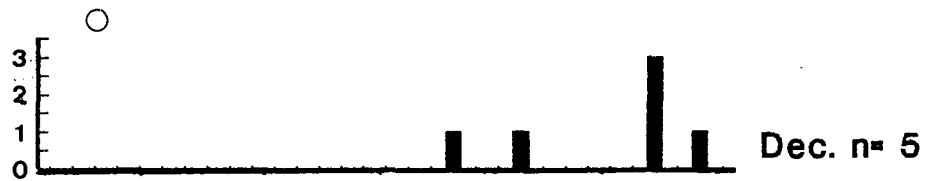
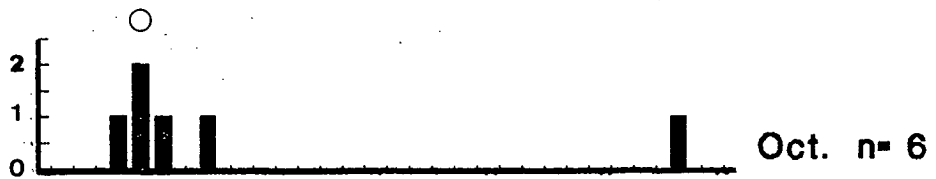
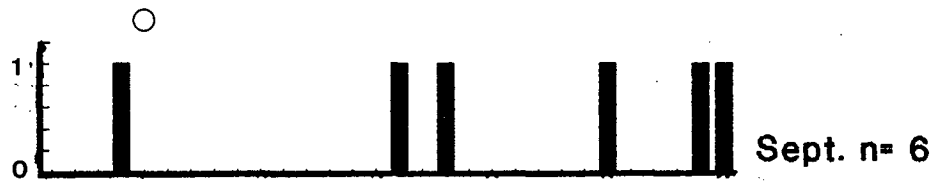


Figure 8.16. Back-calculated birthdates for *Thryssa hamiltoni* juveniles collected between October 1990 and April 1991. Key: ●- new moons; ○-full moons.

Number of births



Date

## CHAPTER 9 GENERAL DISCUSSION

### 9.1 Biological parameters and life-histories of tropical clupeoids

Winemiller and Rose (1992) identified three gradients of life-history strategies for a wide range of North American fish species. The extremes of these gradients were the opportunistic, periodic and equilibrium strategies. The opportunistic strategy is characterised by early maturity, frequent reproduction over an extended spawning season and rapid larval growth and consequently high population turnover rates. The periodic strategy is characterised by delayed maturation, large body and clutch-size and decreased number of spawnings, and the equilibrium strategy is characterised by a high degree of parental care, small clutches and few, large eggs. According to this classification of life-history types, tropical clupeoid fishes exhibit the 'opportunistic' strategy. Small tropical clupeoids probably represent an extreme form of this strategy.

Kawasaki (1980) recognised that temperate clupeoid species exhibit a range of body-size, ages-at-maturity, longevities and batch fecundities and this results in a spectrum of life-history types in this group. He suggested that these represented adaptations to different environmental conditions. These key biological parameters also vary in tropical clupeoids and it has been suggested that the life-history strategies of tropical baitfish can be qualitatively categorised into two types (Conand 1985, Lewis 1990). Lewis (1990) distinguished the life-histories exhibited by small tropical baitfish ('Type 1' species) such as *Stolephorus spp.* and *Spratelloides spp.*, from those in large species ('Type 2' species) such as *Amblygaster spp.* and *Thryssa spp.*. Type 1 species were characterised by small-size (<10cm), longevity of less than one year and continuous spawning. The 'Type 2' species are larger (10-24cm), live for 1-2 years, matured at the end of one year and spawned during a restricted period of several months each year.

The maximum lengths of the species of anchovy examined in the present study encompassed most of the range of adult-size in tropical clupeoids and therefore these species are likely to exhibit both of the life-history types recognised by Lewis (1990). The smallest species *E. devisi*, grows to 62mm, lives for three to four months and matures at two months (Table 9.1). In contrast, the largest species *T. hamiltoni* grows to 250mm, is capable of living for four years and matures at approximately one year of age (Table 9.1). Access to this range of species at one locality provided a unique opportunity to undertake a comparative study of biological parameters and relate these to life-history strategies.

The proposal that two size-related life-history strategies are exhibited by tropical clupeoids can be examined from the frequencies of maximum-sizes for species in this group. These were compared amongst tropical Indo-Pacific anchovy and herring (F. clupeidae) using maximum lengths reported in Whitehead *et al.* (1988) (Fig. 9.1). The Engraulidae exhibited some bimodality in the frequency of maximum-sizes (4-12cm and 14+cm groupings), supporting Lewis's (1990) proposal (Fig. 9.1a). While all species in the genus *Stolephorus* were small species, the genus *Thryssa* was comprised of two size-groups, small species (10-12cm) and larger species (16+cm). This suggests that the genus *Thryssa* may include species with different life-history strategies. The clupeids as a group did not exhibit marked bimodality in size but particular genera were comprised of species with a narrow size-range which suggested similarity in life-history strategy (Fig. 9.1b). The genera *Spratelloides* and *Herklotsichthys* were comprised of small species while the genus *Amblygaster* only included large species. In contrast, the genus *Sardinella* included a wide range of species' sizes, again suggesting that more than one life-history strategy may be exhibited by species in this genus (Fig. 9.1b).

Growth parameters were estimated and compared for the species examined in the present study. An important prerequisite to this comparative study was the

availability of growth estimates based on validated ageing methods. Previously, most of the available age and growth information for tropical clupeoids was based on length-frequency analyses. However, the use of validated daily and annual growth increments in otoliths offered certain advantages over the length-frequency method. These techniques can potentially provide greater accuracy in age estimates and consequently growth pattern and longevity estimates.

One of the growth parameters estimated for the species in the present study was longevity. Primary otolith increments were used to estimate longevity in the smaller anchovy species as growth increments could be counted in fish of all sizes. For large species, seasonal growth rings in otoliths appeared to provide reasonable estimates of longevity. Longevities estimated for the anchovies in the present study ranged from four months to four years with longevity increasing in larger species (Table 9.1). These are summarised in Table 9.2 in addition to published longevity estimates for 25 other species of tropical clupeoids. To examine the quantitative relationship between longevity and species-specific maximum-size, maximum-size was plotted against longevity for these species (Fig. 9.2). A power curve ( $\text{Length}=96.6(\text{Longevity})^{0.6073}$ ,  $r^2=0.88$ ), described the relationship between maximum length and longevity. This suggests that longevity in tropical clupeoids can be predicted with some degree of confidence from the maximum length of a species. Further, this indicates that longevity may be a phylogenetically conservative growth parameter in tropical clupeoids.

The finding that longevity is a function of maximum length of a species implies that the large stolephorid anchovy, *S. commersonii* ( $L_{\text{max}}=158\text{mm}$ ) and the smallest species of *Thryssa*, *T. aestuaria* ( $L_{\text{max}}=145\text{mm}$ ) from the present study should have similar longevities as they are of similar size. This is confirmed by otolith and length-frequency derived age estimates which indicate that both species probably live for between one and two years. It is also evident from Figure



9.2 that few species of tropical clupeoids should exceed 3-4 years of age (given that most species are smaller than 30cm).

Inter-species comparisons of growth in weight made in the present study revealed patterns which support the proposed distinction of two life-history types for tropical clupeoids. The study species exhibited one of two distinct exponential growth patterns, and with the possible exception of *E. devisi*, smaller species exhibited slower growth in weight than large species. On the basis of this graph (Fig. 5.13a), the study species could be classified as slow-growing (*S. insularis*, *S. carpentariae*, *S. nelsoni*, *T. aestuaria*), and fast-growing (*S. commersonii*, *T. setirostris*, *T. hamiltoni*) (Table 9.1). This again suggests that the type of life-history exhibited by a species is not dependent on taxonomic grouping as there were members of the genera *Stolephorus* and *Thryssa* in each group.

There has been little research into the patterns of growth in weight amongst tropical clupeoids. Milton *et al.* (1993) examined weight-growth in two species of tropical clupeids from Kiribati. Their finding that a large clupeid, *Amblygaster sirm* ( $l_{\max}=230\text{mm}$ ), had a faster rate of weight gain than the smaller *Herklotsichthys castelnaui* ( $L_{\max}=110\text{mm}$ ), was consistent with the inter-species trend observed in the present study. The results of comparisons of weight-growth in the present study suggest that this relationship may be a useful tool for comparative growth studies in tropical clupeoids.

Primary otolith increment analyses enabled growth rate to be estimated for juveniles of each of the study species. Growth rates during the juvenile life-phase in species from the present study ranged from 0.23 to 0.78mm/day. Growth rate was quantitatively related to maximum-size for these species. Larger species had higher growth rates than small species, this being consistent with the faster growth in weight estimated in large species. Comparisons of these values with growth rates derived from otolith studies for other tropical clupeoids indicate that growth

rates are relatively conservative in this group (Table 9.3). Growth rate estimates in 18 other tropical clupeoids ranged from 0.29 to 1.07 with a mean of 0.47 (Table 9.3).

Juvenile marine fishes achieve a wide range of growth rates and these can be considerably higher than those of tropical clupeoids. Growth is three to four times as fast in juvenile Atlantic mackerel (*Scombrus scombrus*) which grow at 2.79mm/day between 30 and 40 days of age (D'Amours and Landry 1992), and the Atlantic blue marlin (*Makaira nigricans*) grows at a very fast 1.66cm/day at an age of 50 days (Prince *et al.* 1991). The narrow range and relatively low values of growth rates in tropical clupeoids may indicate that there is a limitation on the rate of growth that can be achieved by species in this group. A possible reason is that growth is constrained by the planktivorous diet characteristic of most clupeoids.

There is some evidence that diet may influence growth rate in the species of anchovy examined in this study. Larger species in the present study which were shown to have higher growth rates than small species also have different diets. Small species (*E. devisi*, *S. insularis*, *S. carpentariae*) predominantly feed on copepods and small zooplankton but *T. hamiltoni* preys on larger crustacea (sergestid shrimps, penaeid prawns, mysids) and fish, and *T. setirostris* also takes mysids, sergestids and chaetognaths (Hoedt 1984). *S. commersonii* individuals dissected during the present study were also found to prey on fish and larger planktonic crustaceans. Blaber (1979) also showed that *Thryssa vitirostris* mostly preyed on fish. The selection of larger prey by large species may contribute to faster growth in length and weight.

Several studies examining growth in more than one species of tropical clupeoid have also found faster growth rates in larger species. Milton *et al.* (1993) showed that after four months of age, *Amblygaster sirm* grew faster than *Herklotsichthys quadrimaculatus* in Kiribati. Tham (1966) and Tiews *et al.* (1970) also found

evidence that larger species of stolephorid anchovy had faster growth rates than smaller species, supporting the findings of the present study. The faster rates of growth exhibited in large species of anchovy is consistent with the expected growth strategy associated with the evolution of increased body-size. According to Murphy (1968) larger body size has certain adaptive advantages, particularly increased clutch-size (batch fecundity). Large size is also thought to reduce predation and may assist individuals to survive in periods of sub-optimal conditions (eg. winter). Murphy (1968) reasoned that it would be advantageous for large species to minimise the time taken to attain a large size. Inter-species comparisons of growth made in this study suggest that this strategy has evolved large species of anchovy.

The growth rates in small anchovy species from the present study (mean=0.43mm/day for species<110mm) are similar to otolith-derived estimates of growth in other small tropical clupeoids (Table 9.3). Species smaller than 10cm in length in Table 9.3 had growth rates ranging from 0.29 to 0.52 with a mean of 0.39mm/day. The growth pattern of tropical anchovy in the present study determined from primary otolith increments was compared to that in some small tropical clupeoids from Kiribati and Fiji (Fig. 9.3). This comparison shows that growth in the latter areas is faster than for species from Townsville. *Spratelloides delicatulus* from Townsville also grew relatively quickly (Fig. 9.3). However, growth in *S. carpentariae* from Townsville was similar to that in *E. devisi* from Fiji (Fig. 9.3).

The results of inter-species comparisons of reproductive parameters made in the present study again supported the existence of two types of life-history strategy. Spawning season differed between small and large species and differences in the pattern of oocyte diameters indicated possible differences in spawning characteristics. In the present study, the smallest species (*E. devisi*, *S. insularis*) spawned throughout the year with short periods of little or no spawning activity in

contrast to larger species which spawned in the spring and summer months only (Table 9.1). An interesting finding was that the larger stolephorid anchovies, *S. nelsoni* and *S. commersonii* had a similar seasonal spawning cycle to *Thryssa spp.* (Sept.-Jan.). Stolephorid anchovies at equatorial latitudes generally exhibit year-round reproduction (Tiews *et al.* 1970, Clarke 1987, Milton and Blaber 1991, Wright 1992), but the findings of this study suggest that the spawning strategy of this genus is modified to suit the seasonal environmental cycle at sub-tropical latitudes.

The strategy of seasonal spawning exhibited by stolephorid anchovies in southern tropical latitudes could influence growth patterns in these species. One outcome of this strategy is that during the period of non-spawning (February to July), recruits can grow past the length-of-maturity in the late summer and autumn without the energetic drain of gonad-maturity and spawning activity. This contrasts with the life-cycle of small equatorial clupeoids such as *Spratelloides spp.* which spawn all year and consequently most individuals spawn at or close to mature sizes. Milton *et al.* (1991) showed that growth slows in *Spratelloides spp.* after maturity is reached which indicates that sexual maturity can influence growth rate. However, growth comparisons between small tropical clupeoids from Fiji and Kiribati and Townsville show that in the former two countries, early growth is more rapid than for species from Townsville. This would decrease the time taken to attain sexually mature sizes and may be an adaptation to compensate for the constraints imposed by early maturity and continuous breeding.

Another consequence of the 4-6 month period of no spawning seen in larger stolephorid anchovies in the present study is the cessation or reduction of recruitment during that period. For this strategy to be successful, these species must have sufficient longevities and survival rates to maintain population levels until spring when spawning commences. The preference for shallow water exhibited by small anchovy species in autumn and winter observed in the present

study (highest seine net catches were during these months) may reduce predation and therefore mortality levels during the non-spawning period.

Lewis (1990) did not consider spawning frequency when he defined the biological characteristics exhibited by species in each life-history type; at that time there was little information available. Differences in ova-diameter frequency polygons between genera found in this study suggested that spawning frequency in the stolephorid anchovies could be higher than in *Thryssa spp.*, this being consistent with Lewis's (1990) division of these two genera into different life-history types. However, the small amount of information on spawning frequency collected in the present study did not give evidence of such differences. Presently available information shows that spawning frequency in tropical clupeoids can vary; Clarke (1987) showed that *E. purpurea* (Hawaii) spawns every second day, but Wright (1992) found that the spawning interval was variable in *E. heteroloba* from Java, ranging from 2-16 days. Milton *et al.* (1994) estimated spawning frequency in three clupeids from Kiribati and found that the largest species, *Amblygaster sirm* ( $L_{\max}=230\text{mm}$ ) spawned less frequently than two smaller species. Thorrold (1988) presented evidence of a low spawning frequency in a large tropical clupeid from Townsville; hatching dates of larval *Herklotsichthys castelnaui* back-calculated from primary otolith increments suggested that larvae were spawned in pulses of fortnightly periodicity. However, this may be a reflection larval survival, not spawning frequency. The significance of differences in the pattern of oocyte diameter frequency polygons between the stolephorid anchovies and *Thryssa spp.* in relation to spawning frequency is unclear and requires further investigation.

Another biological parameter that has an important influence on life-history strategies in marine fishes is fecundity. Blaxter and Hunter (1982) showed that fecundity was directly related to weight at an inter-species level across a wide range of tropical and temperate clupeoid species. A similar relationship was demonstrated for the species in the present study. The relative fecundities of small

anchovies in the present study (mean of 276 eggs/gram) were similar to those of the two largest species (mean of 246 eggs/gram in *T. setirostris* and *T. hamiltoni*). This contrasts with Lewis's (1990) statement that 'Type 1' baitfish have higher relative fecundities (500-1500 eggs/gram) than 'Type 2' species (300-500 eggs/gram). Published estimates of relative fecundity in small tropical clupeoids (Table 9.4) confirm that some species (particularly *Spratelloides spp.*) have higher relative fecundities than found in the present study. A further 16 estimates of relative fecundity for *Spratelloides spp.* given in Milton *et al.* (1994) had a mean of 874 eggs/gram again suggesting relatively high reproductive investment. This suggests that small tropical clupeoids exhibit relatively high levels of reproductive investment.

Several authors have shown that relative fecundity in small tropical clupeoids varies with locality (Milton *et al.* 1990a, Wright 1992, Milton *et al.* 1994) and season (Clarke 1987, Sommerton 1990). Some published regressions of fecundity against weight were compared for a range of small tropical clupeoid species (Fig. 9.4). Fecundity-at-weight varied widely in different species with the fecundity at 5 grams in six populations of *Encrasicholina spp.* ranging from 748 eggs to 4877 eggs. An example of the regional variability of relative fecundity in small clupeoids is given by Wright (1992) who found that two populations of *Encrasicholina heteroloba* in Java had mean fecundities of 490 and 2159 eggs at 3gm. In the tropical clupeids, *Herklotsichthys quadrimaculatus* had low fecundity-at-weight values but *Spratelloides gracilis* from Papua New Guinea had the highest value of any species (1689 eggs/gram-Table 9.4). In the present study fecundity in *S. nelsoni* also varied widely with relative fecundity in individuals ranging from 74 to 384 eggs/gram. Food availability and time within the spawning season are thought to influence relative fecundity in small tropical clupeoids (Wright 1992).

There are few reports of relative fecundity in large tropical clupeoids and those available indicate that relative fecundities are lower in these species than in small tropical clupeoids. Milton *et al.* (1994) reported relative fecundities of 187-300 eggs/gram for three populations of *Amblygaster sirm* in the tropical Indo-Pacific, this being close to the value obtained for large anchovy species in the present study. The mean of several relative fecundity estimates for *T. hamiltoni* in Bombay was again close to that in other large clupeoids (285 eggs/gram-Masurekar and Rege 1960). Inter-species comparisons of the relationship between fecundity and weight were made for some large tropical clupeoids (Fig. 9.5). Fecundity-weight plots reported in the literature were very similar in several species (*T. dussumieri*, *T. mystax*, *C. dussumieri*, *A. sirm*), indicating that there may be some conservatism in this relationship in large species. However, the regression lines for the combined data for three *Thryssa spp.* from the present study, *T. gutamiensis* and *T. baelama* indicated lower fecundities-at-weights than other species (Fig.9.5). Milton *et al.* (1994) showed that relative fecundity varied with site for *Spratelloides delicatulus* but not for two larger species of clupeids at Kiribati, suggesting that fecundity may be less variable in large tropical clupeoids than in small species.

Fecundity is a function of body-size in marine fishes and one advantage of large body-size is increased batch fecundity. However, species which grow large decrease the value of the rate of intrinsic increase ( $r$ ) due to higher age-at-maturity (Kawasaki 1980). One strategy to lessen the decrease in ' $r$ ' to compensate for higher ages-at-maturity is to produce smaller eggs. Another is to increase the size and g.s.i. of females while having small males with low g.s.i. values (Kawasaki 1980). Larger females with higher g.s.i. values than males were a feature of all species of *Thryssa* in the present study. In contrast, g.s.i. and maximum size in male and female stolephorid anchovies did not differ. Large size in females has been reported for other tropical clupeoids including *Herklotsichthys*

*quadrifasciatus* in Hawaii (Williams and Clarke 1983) and *Amblygaster sirm* in New Caledonia (Conand 1991).

Several studies have found that length-at-maturity varies with location for some tropical clupeoids (Milton *et al.* 1990a, Milton *et al.* 1994). However, the ratio of length-at-maturity ( $L_m$ ) to maximum length ( $L_{max}$ ) appears to be conservative at around 0.7 in clupeoid fishes (Beverton 1963, Milton and Blaber 1991, Milton *et al.* 1994), suggesting that variation in  $L_m$  may reflect variable  $L_{max}$  values. Maximum-size in *Spratelloides delicatulus* populations from Solomon Islands varies with location ranging from 60-90mm (Milton *et al.* 1991) and Dalzell (1987b) also found considerable differences in the estimated maximum length of *Spratelloides lewisi* populations between sites in Papua New Guinea. Values of the ratio  $L_m/L_{max}$  were calculated for 18 tropical clupeoid species based on values of  $L_m$  and  $L_{max}$  reported in the literature (Table 9.5). The mean of this ratio for all species was 0.65 which is slightly lower than the value 0.7 obtained in the present study. This data therefore suggests that the ratio of  $L_m/L_{max}$  is conservative amongst tropical clupeoid fishes.

In summary, comparisons of biological parameters amongst tropical anchovies and other tropical clupeoids indicate that a number of these are strongly dependent on the maximum size attained by a species. The existence of quantitative relationships between certain parameters and the maximum size of a species indicates that biological parameters are conservative in this group. Furthermore, these findings suggest that some key biological parameters can be roughly estimated for clupeoid species when information on maximum size is available. The inter-species comparisons of biological parameters confirm the existence of biological differences between small and large tropical clupeoids which result in different life-history strategies.

## 9.2 Comparisons with temperate species



A major difference in the life-histories of tropical and temperate clupeoids is longevity. Most tropical clupeoids live for less than 4 years (Lewis 1990), but many temperate clupeoids live for 5-15 years and a few species for 20-30 years (Beverton 1963). However, there are a number of short-lived temperate clupeoids which have similar biological parameters and life-history traits to large tropical clupeoids. Table 9.6 lists some key biological parameters for several of these temperate clupeoids. Further, these species exhibit similar reproductive season lengths and spawning frequencies to tropical species and age-at-maturity is also close to that in large tropical clupeoids occurring at 1-2 years (Table 9.6).

The relationship between maximum-size and longevity was compared for large tropical and temperate clupeoids to explore possible similarities between these groups (Fig. 9.6). The data used in Figure 9.6 are from Tables 9.2 (tropical species 1.5 years and older) and 9.7 (temperate species). Figure 9.6 indicates that some species of temperate anchovy exhibit similar combinations of maximum-size and longevity to large tropical clupeoids. These were mostly temperate anchovy species with short longevities in relation to size compared to other temperate clupeoids (Fig. 9.6). The similarities in biology between large tropical clupeoids and temperate anchovies are further highlighted by examining von Bertalanffy growth parameters reported for some of these species. The growth parameters estimated for *Thryssa spp.* in this study (from length-frequency analysis and seasonal growth rings  $L_{\infty}$ =118-240 mm and  $K$ =0.64-1.6), are similar to those of *Engraulis japonicus* ( $L_{\infty}$  =15cm,  $K$ =1.6-Beverton 1963), *E. encrasicolus* ( $L_{\infty}$  =16.5cm,  $K$ =1.4-1.8-Beverton 1963) and *E. ringens* ( $L_{\infty}$ =16cm,  $K$ =1.4-1.7-Beverton 1963).

A useful comparative tool for temperate clupeoid fishes is Beverton's (1963) ratio,  $1/KT_{max}$ . Beverton (1963) undertook a comparative study of maturation, growth and mortality in a number of temperate clupeoid fishes. He concluded that the relationships between these parameters in certain groups of species had properties

in common which would result in a similar response to fishing pressure. He showed that the essential biological characteristics which determine the response of a stock to fishing (in terms of catch per recruit) are contained in the ratios of  $M/K$  and  $L_m/L_{max}$  where:  $M$ =natural mortality;  $K$ =von Bertalanffy growth constant;  $L_m$ =maturation length and  $L_{max}$ =asymptotic length. He used  $1/T_{max}$  as an index of mortality rate, therefore the ratio of  $1/KT_{max}$  could be used instead of  $M/K$ . Beverton (1963) found that all of the temperate engraulids he examined and two species of clupeids had similar  $1/KT_{max}$  values (mean= 0.26). It is not known if the conservatism of this ratio seen in temperate clupeoids extends to tropical species. This is of interest as it would suggest that there may be similarities in the response to fishing pressure by tropical clupeoid stocks.

The ratio of  $1/KT_{max}$  was calculated for anchovies from the present study and also for several large tropical clupeids for which  $K$  and longevity estimates were considered reliable (Table 9.8). In these species, values of the ratio  $1/KT_{max}$  ranged from 0.19-1.1 with a mean of 0.49 (Table 9.8). This ratio increased with decreasing body-size in the clupeoids examined. The values of  $1/KT_{max}$  in Table 9.8 suggest that those of *Thryssa spp.* and the larger clupeids are reasonably close to Beverton's (1963) value for temperate anchovy species (the mean for clupeoids that live for 1.5 years or longer ( $n=7$ ) was 0.28-Table 9.8). This suggests that the value of this ratio in large tropical clupeoids is similar to that in temperate anchovy species therefore following Beverton's (1963) reasoning, these could be expected to exhibit similar responses to fishing pressure. This finding again supports the proposed similarities between large tropical clupeoids and some temperate clupeoids.

It is interesting that the  $1/KT_{max}$  value for *T. aestuaria* was larger than in *T. setirostris* and *T. hamiltoni* (Table 9.8). This species also had a lower relative fecundity value (Table 9.1), and slower growth in weight to the other species of

*Thryssa* (Fig. 5.13a, Table 9.1). The differences in the biology and ratio of  $1/KT_{\max}$  in *T. aestuaria* suggest that the fishery characteristics of this species may differ from other large *Thryssa spp.*

The growth parameters of temperate and tropical clupeoids were also compared by examining the relationship between the growth parameter  $K$  and maximum length in species from these two groups. Reported values of  $K$  were plotted against the corresponding  $L_{\infty}$  values for a range of tropical and temperate clupeoid species (Fig. 9.7). In both groups  $K$  decreased with increasing  $L_{\infty}$  values. For temperate species the relationship between these parameters was illustrated using a time-rate curve ( $K=1/(-0.5927 + 0.01346(L_{\infty}))$ ,  $r^2=0.613$ ). The data points in the  $K$  versus maximum length plot for tropical clupeoids exhibited greater vertical scatter than for temperate clupeoids (Fig. 9.7). An exponential decay curve ( $K=4.39e^{-0.006059(L_{\infty})}$ ,  $r^2=0.295$ ) served to illustrate the general trend of this data.  $K$  values in temperate species were generally lower at a particular length than in tropical species (Fig. 9.7). This figure shows that in larger species from both regions,  $K$  values-at-length become more similar; this may indicate biological similarities between larger species within tropical and temperate regions (Fig. 9.7). The greater spread of  $K$  values in similar-sized tropical clupeoids, particularly smaller species may be partly due to biases in growth parameter estimates obtained from length-frequency information (Dayaratne and Gjøsaeter 1986, Milton *et al.* 1990b).

The study of Milton *et al.* (1993) is one of the few to compare the biological parameters of tropical clupeoids with temperate species. These authors found that 'relative growth performance' (from plots of  $\ln K$  against  $\ln W_{\infty}$ ) was similar in tropical and temperate species. Although temperate species live longer and become heavier than tropical species their  $K$  values are correspondingly lower.

This finding further supports the conservatism of biological parameters across the temperate-tropical boundary in clupeoids.

Published relative fecundities of small tropical clupeoids are similar to those reported in temperate species (compare tables 9.4 and 9.5). This suggests that relative fecundity in these two regions is conservative, the exception apparently being large tropical clupeoids which have low values compared to most clupeoids. This may indicate that decreased relative fecundity is associated with larger body-size in tropical clupeoids and this may be a factor limiting the size attainable by tropical clupeoids. More estimates of relative fecundity in large tropical clupeoids are needed to verify this.

In summary, there appear to be similarities in the life-histories of larger tropical clupeoids and some short-lived temperate clupeoids. The similar values of certain biological parameters and the conservatism of the ratio  $1/KT_{\max}$ , further suggest that these two groups may exhibit similar responses to fishing. These comparative studies indicate that small tropical clupeoids differ from temperate clupeoids both in life-history strategy and fishery dynamics.

### 9.3 Fisheries implications

The behaviour of populations in terms of natural and fishery induced fluctuations in abundance are highly relevant to fishing operations. Temperate clupeoids are notorious for exhibiting large inter-annual fluctuations in year-class strength arising from inter-year variations in recruitment (Murphy 1977, Blaxter and Hunter 1982, Longhurst and Pauly 1987). There is less information on the long-term population dynamics of tropical clupeoids than for temperate species as long-term catch records for the former group are few. This section discusses the possible influences of differences in life-history on fishery and population dynamics in tropical clupeoids.

The evidence presented so far suggests that small tropical clupeoids differ in a number of key life-history parameters from large species. The difference in the ratio of  $1/KT_{\max}$  between small and large tropical clupeoids by Beverton's (1963) reasoning is evidence that the fishery and population dynamics of these two groups may differ. Therefore, fisheries on species in each of these two groups may require different management methods.

The life-history traits typical of small tropical clupeoids namely, early maturity, year-round spawning, high spawning frequency and high relative fecundity all result in high population turn-over rates. Milton *et al.* (1994) suggested that the reproductive traits of small tropical clupeoids evolve to cope with intense predation. These traits also equip these species to recover rapidly following population declines resulting from fishing pressure. The resilience of these species to fishing has been demonstrated for some heavily exploited populations in the Indo-Pacific. Annual bait catches of *Spratelloides gracilis* have exceeded 60.5 tonne in Male atoll in the Maldives without detectable effects on stocks (Milton *et al.* 1991). Another example is the small stolephorid, *Encrasicholina purpurea* that is heavily exploited as a tuna baitfish in Hawaii (Sommerton 1990). The population biomass of *E. purpurea* was estimated on a weekly basis using the egg production method (Somerton 1990). Stock-size was found to fluctuate in direct response to fishing effort indicating the very high fishing pressure on this species. Stocks appeared to recover quickly when fishing effort was decreased (Sommerton 1990).

Several authors have discussed the management of fisheries on small tropical clupeoids that support tuna baitfisheries (Dalzell and Wankowski 1980, Dalzell 1990, Lewis 1990, Rawlinson and Nichols 1990). Modelling the fishery dynamics of small tropical clupeoids has been difficult due to the biological characteristics of these fish and the nature of the fisheries which target them (Rawlinson and Nichols 1990). However, given the biological characteristics and resulting fast

population turn-over rates of these fish, depleted stocks of small tropical clupeoids have the potential to recover in relatively short time periods. Rawlinson and Nichols (1990) showed that baitfish stocks in intensely fished lagoons in Solomon Islands subsequently declined. At Solomon Islands there are around 87 baitfishing areas and Rawlinson and Nichols (1990) suggested that the presence of alternative fishing sites allowed boats to fish elsewhere when stocks declined in an area thus preventing a population collapse in the region. The closure of over-fished baitfishing localities appears to be a practical management strategy in baitfisheries that utilise small tropical clupeoids.

Characteristics of large tropical clupeoids that could result in different fishery and population dynamics compared to small species are their higher ages-at-maturity (around 1 year), shorter spawning season and greater longevity compared to small species. These life-history traits tend towards the 'periodic strategy' of Winemiller and Rose (1992) explained earlier. The reproductive strategy results in recruitment occurring over a restricted period, presumably during favourable conditions. This type of strategy would be expected increase the chance of inter-annual variability in recruitment success, particularly if environmental conditions vary between years. The higher age-at-maturity in large tropical clupeoids will also make these species slower to recover from population declines due to environmental factors or fishing. However, the existence of more than one year-class in longer-lived species could help 'stabilise' the effects of inter-annual recruitment variability.

The biological parameters and life history strategy of large tropical clupeoids should be taken into account for the management of fisheries which target these species. Given that these stocks may be slower to recover from over-fishing than stocks of small species, one management option could be to selectively fish for particular size or age-groups. This could be done spatially if there are age-related habitat differences for the species in question (see Chapter 4), or through the use of selective fishing gear. Given that tropical clupeoids mature in their first year,

the protection of at least the first year class will assist maintenance of the spawning stock.

Another aspect of population dynamics in tropical clupeoids that requires consideration are natural population fluctuations. One of the few fisheries for a tropical clupeoid where reliable long-term catch statistics are available is the Indian oil sardine (*Sardinella longiceps*) fishery in India. The oil sardine is a relatively large species with a seasonal spawning period. The life-cycle of this species is closely tied to periodic phytoplankton blooms off the coast of India. Reproduction and consequently recruitment levels appear to be related to the intensity of this bloom (Longhurst and Pauly 1987). The oil sardine population appears to periodically undergo significant natural fluctuations in abundance on a decadal scale. These fluctuations appear to be related to the adverse effect of ENSO events on the strength of the phytoplankton bloom and hence recruitment (Longhurst and Pauly 1987, Longhurst and Wooster 1990). The population fluctuations of *S. longiceps* demonstrate that the long-term behaviour of a large tropical clupeoid population that is dependant on a rich but variable food source is very similar to that exhibited by temperate clupeoids in seasonally productive regions (see Murphy 1977). This example further supports the proposal of similarities in life-history and fishery/population dynamics between large tropical and some temperate clupeoids.

Seasonal and inter-annual fluctuations in abundance are also exhibited by tropical clupeoids in lower nutrient environments such as coral reefs. Catches of the sardine, *Amblygaster sirm* by the tuna baitfishery in Kiribati varies considerably on seasonal and annual levels. At the same locality catches of a smaller species, *Spratelloides delicatulus* were less variable (Milton *et al.* 1994) and this could reflect the greater population stability achieved by the life-history strategy of small tropical clupeoids. However, it is unclear to what extent catch fluctuations in these fisheries reflect migrations from the fishing area (Milton *et al.* 1994). Sommerton

(1990) showed that the population biomass of *Encrasicholina purpurea* varied seasonally with lower numbers occurring at cooler water temperatures and times of lower productivity. Relative fecundity also decreased during these periods. This example highlights the short-term responsiveness of small tropical clupeoid stocks to environmental change.

Variable environmental conditions are believed to influence the population size of temperate clupeoids largely through the effect on reproduction and recruitment (Blaxter and Hunter 1982). However, Murphy (1977) points out that adult clupeoids mostly feed on plankton with high turnover rates. Thus in stable environments clupeoids may be less density dependent (due to resource limitation) than benthic feeding fish which eat organisms with much slower turnover rates and consumption of these can have a significant and lasting effect on resource levels (Murphy 1977). However, limited food supply and consequently density-dependence may affect the size of populations of large tropical clupeoids such as *Thryssa hamiltoni*. These fish feed chiefly on penaeid prawns and fish as adults (Hoedt 1984). Penaeids and fish are larger and longer-lived than the copepod prey of stolephorid anchovies and therefore may be susceptible to overgrazing. Moreover, the biomass of penaeids in tropical waters is linked to rainfall (rainfall causes juveniles in estuaries to move seaward). The shrimp *Acetes australis* is also considerably larger than copepods and is an important food item for several species of anchovy in Townsville. Fluctuations in abundance of this food source (Jackson 1991, Robertson and Duke 1987), may influence population size in some clupeoids.

The finding that two distinct weight-growth patterns were exhibited by species in the present study is relevant to the fishery dynamics of tropical anchovies. The significance to fisheries is that those species which have higher rates of weight-gain would also have higher biomass production rates assuming equal recruitment rates. This factor may result in significant yield differences in heavily fished



populations of fast-growing species. The different patterns of weight-gain would also influence reproductive output. Fecundity is proportional to weight, therefore fast-growing species would have higher egg production during their life-spans.

#### 9.4 Recommendations for future research

The findings of the present study indicate that there are several lines of research that have practical implications towards the management of tropical clupeoid resources. There is a need to improve our knowledge of spawning frequencies in different species of tropical clupeoids. At present there are no estimates of spawning frequency in large tropical anchovies and few for tropical clupeids. Estimates of spawning frequency in serial spawning fishes have become an important component of stock assessment (Lasker 1985, Sommerton 1990).

Further, it would be useful to investigate the influence of environmental conditions and species-size on spawning frequency in tropical clupeoids. Wright (1990) stated that spawning frequency varied in different populations of *E. heteroloba* in Java and spawning interval was inversely proportional to prey abundance. More information comparing the spawning frequencies of small and large tropical clupeoids will determine if this parameter consistently differs between these groups, adding to our understanding of the comparative life-histories of tropical clupeoids. The relationships (if any) between spawning frequency, temperature, food and species-size should be examined and quantified. If such relationships can be quantified this will have the application of enabling estimates of spawning frequency for species where biological information is unavailable.

The present study indicates that seasonal growth rings in the sagittal otolith can provide useful growth and longevity estimates for large tropical anchovies. However, the periodicity of these structures needs to be validated for species from equatorial regions where seasonal environmental cycles and reproductive periods

differ from those at sub-tropical latitudes. If seasonal growth rings of known periodicity are present in the otoliths of other tropical clupeoids these will facilitate future age and growth estimates for this group.

The relationship between early growth rate of tropical clupeoids and the maximum size of a species could be investigated for a wide range of tropical clupeoids to determine if there is a general relationship for this group. Further, the growth rates for species in different trophic categories (eg. zooplankton feeders, benthic feeders) could be compared to examine the influence of diet on growth. The latter study could also involve laboratory experiments to test the effects of diet and ration levels on growth rate.

An important finding from this study is that there may be similarities in the biological parameters and therefore population and fishery dynamics of large tropical anchovies and some temperate clupeoids. More detailed comparisons need to be made in order to determine to what extent the rich resource of information on temperate clupeoid fisheries can be useful for the management of tropical clupeoid stocks.

The population dynamics of tropical clupeoid fishes (particularly large tropical clupeoids), are poorly understood. For larger anchovy species, the effect of fluctuations in the abundance of key food species (eg. *Acetes* sp. and penaeid prawns) on population-size may also be a useful line of research.

Table 9.1 A summary of the habitats, spawning season and biological parameters of the 8 species of anchovy studied. m-male. f-female

Species	Maximum length (mm)	Distribution		Maximum age	Linear growth L-length (mm) d-days (age) w-warm months c-cool months	Growth parameters				Spawning season	Length-at-maturity (mm)	Age-at-maturity (days)	Relative fecundity (eggs/grm)	Mean batch fecundity	
		Juv.	Adult			ELEFAN		Otoliths (* -primary incs.)							
						Year	Linf (mm)	K (yr <sup>-1</sup> )	Linf (mm)	K (yr <sup>-1</sup> )					
<i>E. devisi</i>	62	Beach/ Bay	All	3-4 mo.	(w) L=15+0.55d (c) L=32+0.23d	1989 1989/90	62 56	2.8 2.4	56-94	4.5*	All year	47	59-68	436	381
<i>S. insularis</i>	64	Beach	Beach Shallow Bay	4-6 mo	L=20+0.28d	1988 1989	58 58	2.8 2.2	----	----	All year	42.5	79	221	205
<i>S. carpentariae</i>	71	Beach	Beach/ mangrove	6 mo.	L=8.8+0.56d (<55mm)	1988/89 1990/91	70 62	2.3 2.4	70.6	7.1 *	Spring/ summer	50	74	349	515
<i>S. nelsoni</i>	103	Widespread	Beach/ Bay	6-12 mo.	L=9.7+0.41d	1988 1989 1990/91	95 98 98	2.4 2.4 2.7	99.8	2.9 *	Spring/ summer	70	158	169	1055
<i>S. commersonii</i>	158	Beach/ mangrove	Bay	1-2 yr.	L=6.6+0.63d	1988/89 1988/91 1988/91	150 155 155	2.2 2.6 2.8	381	0.77*	Spring/ summer	-	-	204	3936
<i>T. aestuaria</i>	142	Beach/ mangrove	Bay	1-2 yr.	L=9.6+0.41d	1988/91	118	1.6	148	1.56*	Spring/ summer	-	-	137	3043
<i>T. setirostris</i>	220	Beach	Bay	2 yr	L=10.9+0.69d	1984/91 1988/89	191 210	1.4 1.6	186	2.77*	Spring/ summer	m:155 f:160	m:251 f:274	252	12920
<i>T. hamiltoni</i>	251	Beach/ mangrove	Bay	4 yr.	L=8.3+0.78d	1988 1989 1990/91 1988/89 1988/91	200 240 220 235 215	1.4 0.9 1.4 1.3 0.9	216 f 259 f 238 m 214 m218	1.85* 0.66 1.12 .85 0.64	Spring/ summer	m:155 f:160	m:265 f:281	239	18200

Table 9.2. Longevities (in years) for clupeoids from tropical regions. Maximum lengths (S.L.) are given. Longevities were rounded to the nearest 0.5 year.

Species	L <sub>max</sub>	Long.	Author/Location
<i>Encrasicholina devisi</i>	51	0.5	Present study N. Qld
<i>Stolephorus insularis</i>	54	0.5	Present study N. Qld.
<i>Spratelloides lewisi</i>	57	0.5	Dalzell (1987b) P.N.G.
<i>Stolephorus carpentariae</i>	58	0.5	Present study N. Qld.
<i>Encrasicholina purpurea</i>	63	0.5	Struhsaker & Uchiyama (1976) Hawaii
<i>Spratelloides delicatulus</i>	64	0.5	Milton <i>et al.</i> (1990b) Solomons
<i>S. gracilis</i>	64	0.5	Dalzell & Wankowski (1980) P.N.G.
<i>S. delicatulus</i>	65	0.5	Dalzell <i>et al.</i> (1987) Fiji
<i>Encrasicholina heteroloba</i>	69	0.5	Milton <i>et al.</i> (1990b) Solomons
<i>E. heteroloba</i>	74	1.0	Wright <i>et al.</i> (1990) Indonesia
<i>E. devisi</i>	75	0.5	Dalzell and Wankowski (1980) P.N.G.
<i>E. devisi</i>	82	1.0	Luther (1990) India
<i>Stolephorus nelsoni</i>	85	1.0	Present study N. Qld.
<i>S. heterolobus</i>	89	1.0	Tham (1966) Singapore
<i>Encrasicholina devisi</i>	93	1.0	Syda Rao (1988a) India
<i>Stolephorus waitei</i>	110	1.5	Luther (1990) India
<i>Sardinella albella</i>	112	1.5	Dayaratne & Gjøsaeter (1986) India
<i>S. gibbosa</i>	113	1.0	Dayaratne & Gjøsaeter (1986) India
<i>Herklotsichthys quadrimaculatus</i>	121	1.0	Williams and Clarke (1983) Hawaii
<i>Sardinella gibbosa</i>	132	2.0	Okera (1970) E. Africa
<i>Thryssa aestuaria</i>	120	1.5	Present study N. Qld.
<i>Stolephorus commersonii</i>	128	1.0	Present study N. Qld.
<i>Thryssa mystax</i>	164	3.0	Venkataraman (1956) India
<i>Cetengraulis mysticetus</i>	175	2.5	Barrett & Howard (1961) Trop. Pac.
<i>C. mysticetus</i>	180	3.0	Barrett & Howard (1961) Trop. Pac.
<i>Thryssa setirostris</i>	180	2.0	Present study N. Qld.
<i>Amblygaster sirm</i>	184	1.5	Dayaratne & Gjøsaeter (1986) India
<i>A. sirm</i>	184	2.0	Lazarus (1987) India
<i>A. sirm</i>	192	2.0	Conand (1991) New Caledonia
<i>Thryssa hamiltoni</i>	204	4.0	Present study N. Qld.
<i>Sardinella longiceps</i>	208	5.0	Beverton (1963) India
<i>Brevoortia patronus</i>	214	3.0	Nicholson & Schaaf (1978) Gulf Mexico
<i>Sardinella anchovia</i>	230	5.0	Heald & Griffiths (1967) Venezuela

Table 9.3 Growth rates during the juvenile life-phase for tropical clupeoids obtained using primary otolith increments. M.L.-maximum length (\*-standard lengths).

Species	G.R. (mm/day)	M.L. (mm)	Locn./author
Small species			
<i>Encrasicholina devisi</i>	0.48	90	PNG <sup>1</sup>
<i>E. purpurea</i>	0.33	60	Hawaii <sup>2</sup>
<i>Spratelloides delicatulus</i>	0.34	57*	Kiribati <sup>3</sup>
	0.43	64*	Kiribati <sup>3</sup>
	0.43	56*	Kiribati <sup>3</sup>
	0.52	63*	Kiribati <sup>3</sup>
	0.29	61*	Kiribati <sup>3</sup>
	0.38	56*	Kiribati <sup>3</sup>
	0.44	56*	Kiribati <sup>3</sup>
	0.21	44*	Kiribati <sup>3</sup>
	0.47	66*	Kiribati <sup>3</sup>
	0.37	59*	Kiribati <sup>3</sup>
Large species			
<i>Amblygaster sirm</i>	0.56	221*	Kiribati <sup>4</sup>
	0.55	205*	Kiribati <sup>4</sup>
	0.37	196*	Kiribati <sup>4</sup>
	1.07	230*	Sri Lanka <sup>5</sup>
<i>Sardinella albella</i>	0.53	140*	Sri Lanka <sup>5</sup>
<i>S. gibbosa</i>	0.67	170*	Sri Lanka <sup>5</sup>

1. Dalzell & Wankowski (1980); 2-Struhsaker and Uchiyama (1976); 3-Milton *et al.* (1991); 4-Milton *et al.* (1993); 5-Dayaratne & Gjøsæter (1986).

Table 9.4 Relative fecundity estimates for small tropical clupeoids from the Indo-Pacific region.

Species	Rel. Fec.	Locn./Author
<i>Spratelloides gracilis</i>	1689	PNG-Dalzell (1987b)
<i>Herklotsichthys quadrimaculatus</i>	160-311	Hawaii-Williams & Clarke (1983)
<i>Stolephorus bataviensis</i>	314	India-Syda Rao (1988b)
<i>S. waitei</i>	224	India-Dalzell (1987a)
<i>Encrasicholina devisi</i>	1039	PNG-Dalzell (1987a)
<i>E. devisi</i>	523	India-Syda Rao (1988a)
<i>E. heteroloba</i>	592	PNG-Dalzell (1987a)
<i>E. heteroloba</i>	450	Palau-Muller (1977)
<i>E. heteroloba</i>	694	Singapore-Dalzell (1987a)
<i>E. purpurea</i>	538	Hawaii-Leary <i>et al.</i> (1975)
<i>E. purpurea</i>	432-4098	Hawaii-Clarke (1987)
<i>E. punctifer</i>	875	PNG-Dalzell (1987a)

Table 9.5 Ratios of length-at-maturity ( $L_m$ ) on maximum length ( $L_{max}$ ) for a range of tropical clupeoids.

Species	$L_m/L_{max}$	Location/Author
<i>Thryssa hamiltoni</i>	0.75	India-Masurekar and Rege (1960)
<i>T. hamiltoni</i>	0.56	Arabia-Hussain and Ali (1987)
<i>T. purava</i>	0.63	India-Pelakar and Karandikar (1956)
<i>T. gutamiensis</i>	0.62	India-Babu Rao (1977)
<i>T. mystax</i>	0.71	Arabia-Shamsul Hoda (1983)
<i>Encrasicholina devisi</i>	0.59	India-Syda Rao (1988a)
<i>E. devisi</i>	0.7	Solomons-Milton and Blaber (1991)
<i>E. devisi</i>	0.59	PNG-Dalzell and Wankowski (1980)
<i>E. heteroloba</i>	0.7	Solomons-Milton and Blaber (1991)
<i>Stolephorus macrops</i>	0.87	India-Luther (1979)
<i>S. commersonii</i>	0.75	India-Luther (1979)
<i>S. anhadriensis</i>	0.69	" "
<i>S. indicus</i>	0.75	" "
<i>S. buccaneeri</i>	0.47	" "
<i>S. indicus</i>	0.62	Philipp.-Tiews <i>et al.</i> (1970)
<i>S. commersonii</i>	0.62	" "
<i>S. heteroloba</i>	0.61	" "
<i>S. sp.A</i>	0.61	" "
<i>Coilia dussumieri</i>	0.42	India-Fernandez and Devarej (1989)
<i>Herklotsichthys quadrimaculatus</i>	0.67	Hawaii-Williams and Clarke (1983)
<i>Spratelloides gracilis</i>	0.65	PNG-Dalzell (1987b)

Table 9.6 Some biological parameters in temperate clupeoid fishes with relatively short lifespans.  $T_{max}$ -maximum age;  $A_m$ -age-at-maturity; R.F.-relative fecundity (eggs/gram body weight); season-spawning season.

Species	$T_{max}$	$A_m$	R.F.	Season	Author
<i>Anchoa mitchelli</i>	2	2-10mo.	687	3-5 mo.	1
<i>Engraulis australis</i>	5	1 yr.	-	5 mo.	2
<i>Engraulis mordax</i>	7	2 yr.	389-720	5 mo.	3,4,5
<i>Engraulis ringens</i>	2	1	502-637	-	6
<i>Sprattus sprattus</i>	-	-	187-413	-	7
<i>Sardinops neopilchardus</i>	6	1-2	-	5 mo. -	8

1-Zastrow *et al.* 1991; 2-Blackburn (1950a); 3-Blaxter and Hunter (1982); 4-Hunter & Goldberg (1980); 5-Laroche & Richardson (1980); 6-Sanz & Uriarte (1989); 7-Alheit (1988); 8-Blackburn (1950b)

Table 9.7 Reported values of maximum size and longevity for temperate clupeoids used in Figure 9.6.

Species	Size (cm)	Longevity (years)	Author
<i>Clupea palleli</i>	30	14	1
<i>C. palleli</i>	34	13	1
<i>Sardinops caerulea</i>	29	13	1
<i>Clupea palleli</i>	27	12	1
<i>C. harengus</i>	29.5	12	1
<i>C. palleli</i>	25	11	1
<i>C. palleli</i>	23	9	1
<i>Sardinops melanosticta</i>	27	9	1
<i>Sardina pilchardus</i>	23.5	9	1
<i>Sardinops ocellata</i>	30	8	1
<i>Clupea palleli</i>	21.5	7	1
<i>Sprattus sprattus</i>	16	7	1
<i>Engraulis mordax</i>	21	7	1
<i>Sprattus sprattus</i>	16.2	6	1
<i>S. sprattus</i>	15.3	6	1
<i>Sardinella aurita</i>	28	6	1
<i>Sardinops neopilchardus</i>	16	6	2
<i>Sprattus sprattus</i>	14	5	1
<i>Engraulis australis</i>	16	4	3
<i>S. sprattus</i>	12.5	4	1

Table 9.7 Continued...

Species	Size (cm)	Longevity (years)	Author
<i>Engraulis encrasicolus</i>	20	3	1
<i>S. sprattus</i>	15.5	3	1
<i>Engraulis encrasicolus</i>	15	3	1
<i>E. japonicus</i>	15	2.5	1
<i>E. encrasicolus</i>	16	2	1
<i>E. ringens</i>	20	2	4

1-Beverton (1963); 2-Blackburn (1950b); 3-Blackburn (1950a); 4-Longhurst & Pauly (1987)

Table 9.8. Values of the ratio  $1/KT_{max}$  for the species of anchovy from the present study and several other tropical clupeids.

Species	K	$T_{max}$ (yrs)	$1/KT_{max}$	Author
<i>Encrasicolina devisi</i>	3.5	0.26	1.1	1
<i>Stolephorus carpentariae</i>	2.35	0.5	0.85	1
<i>S. insularis</i>	4.0	0.35	0.73	1
<i>Spratelloides lewisi</i>	5.0	0.27	0.68	2
<i>Stolephorus nelsoni</i>	2.5	0.7	0.57	1
<i>Spratelloides gracilis</i>	4.3	0.47	0.47	2
<i>Thryssa aestuaria</i>	1.6	1.5	0.42	1
<i>Amblygaster sirm</i>	1.58	2.0	0.32	3
<i>Thryssa setirostris</i>	1.65	2.0	0.32	1
<i>T. hamiltoni</i> (males)	0.7	4.0	0.32	1
<i>Stolephorus commersonii</i>	3.1	1.5	0.22	1
<i>T. hamiltoni</i> (females)	1.31	4.0	0.19	1
<i>T. hamiltoni</i> (combined)	1.26	4.0	0.2	1

1-Present study; 2-Dalzell (1987b); 3-Conand (1991)



Figure 9.1 Size-frequencies of maximum lengths of species (SL) of tropical Indo-Pacific clupeoids. (a) Engraulidae; (b) Clupeidae. Data from Whitehead *et al.* (1988).

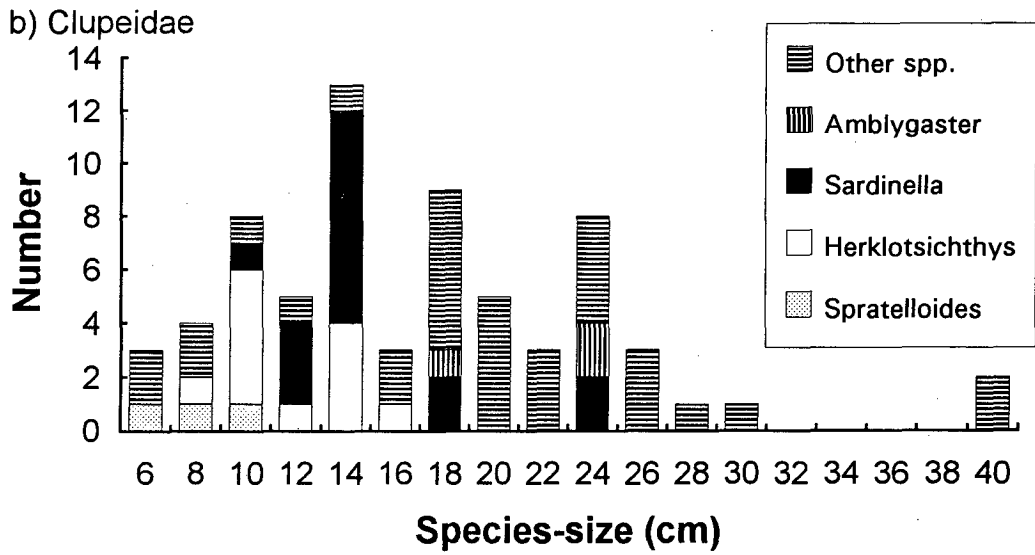
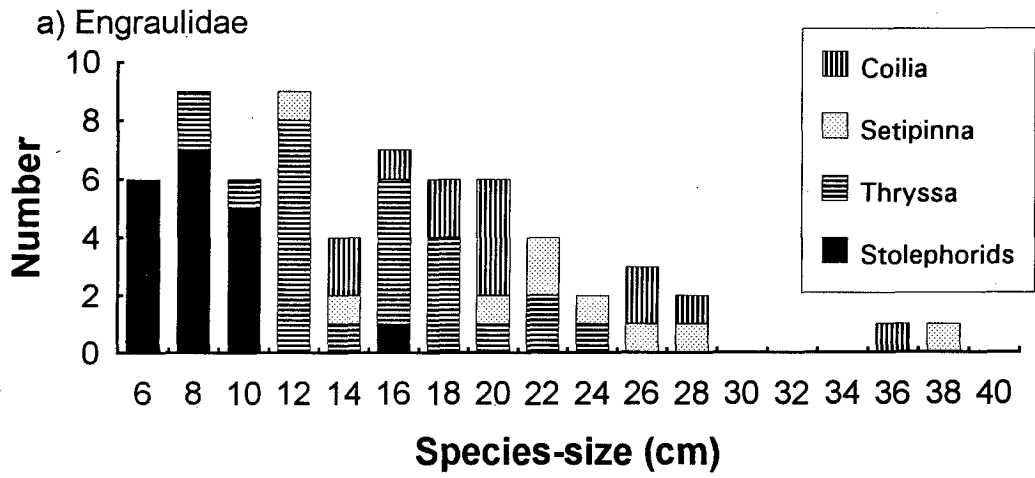


Figure 9.2 Maximum-length plotted against longevity for 26 species of tropical clupeoids (based on data in Table 9.2).

Figure 9.3. Length versus age plots based on primary otolith increment counts for small tropical clupeoid species. Growth curves for species in the present study and from Milton *et al.* (1993) and Milton and Blaber (1995) are compared.

Figure 9.4 Fecundity plotted against weight for small tropical clupeoids. Key-  $\Delta$  - *Spratelloides gracilis* (Dalzell 1987b);  $\diamond$  - *Encrasicholina devisi* (Dalzell (1987a);  $\square$  -*E. devisi* (present study); \* -*E. heteroloba* (Dalzell 1987a);  $\blacksquare$  -*E. heteroloba* (Wright 1992);  $\circ$  -*E. devisi* (Syda Rao 1988a);  $\bullet$  -*Herklotsichthys quadrimaculatus* (Williams and Clarke 1983);  $\blacklozenge$  -*E. heteroloba* (Wright 1992).

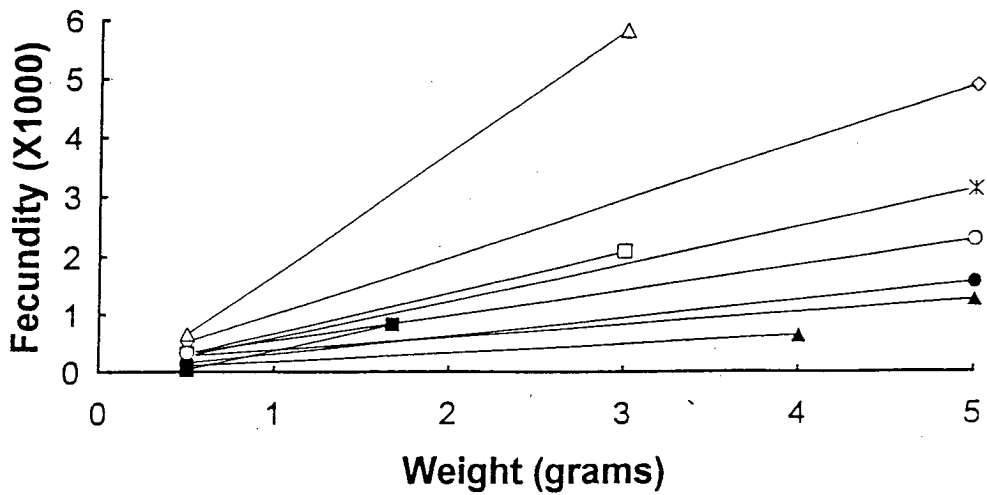
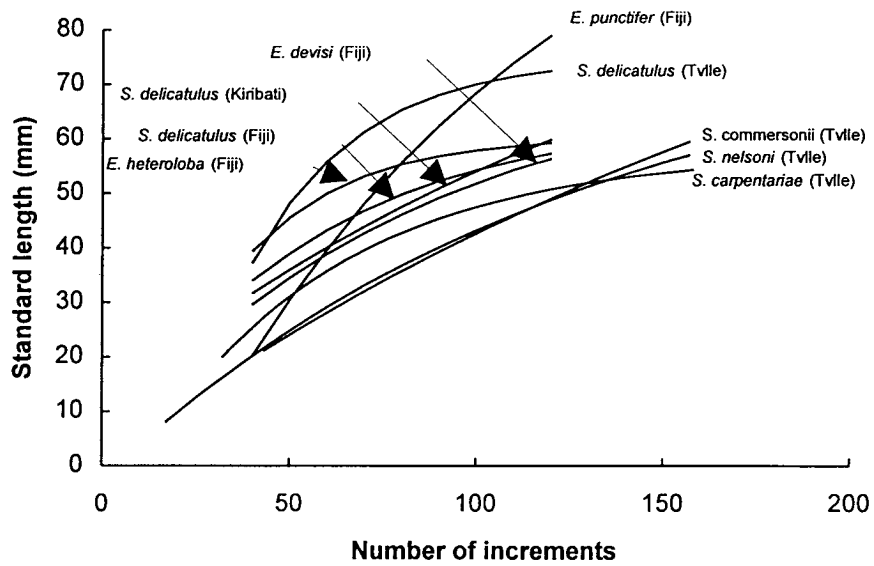
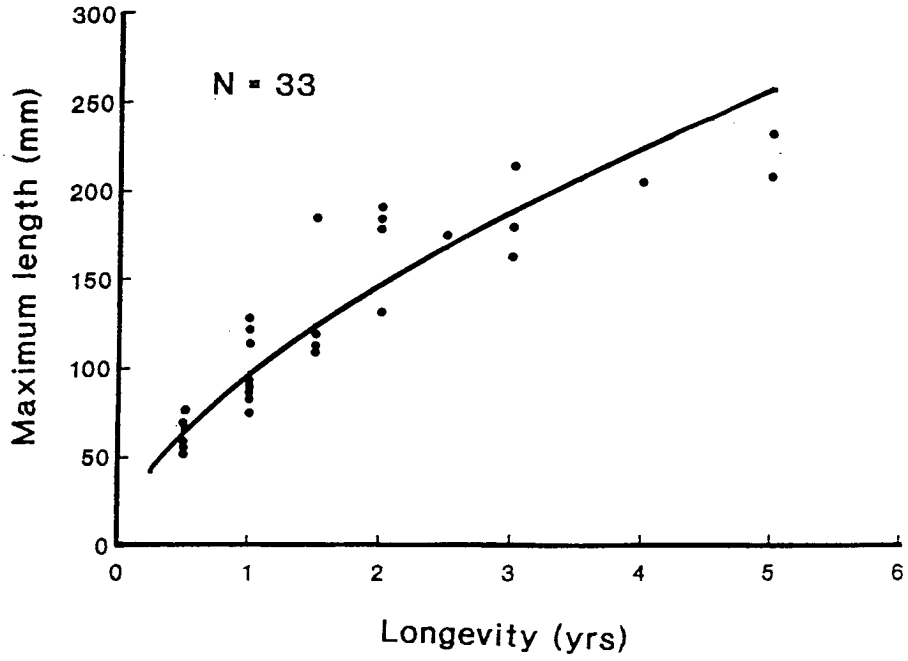
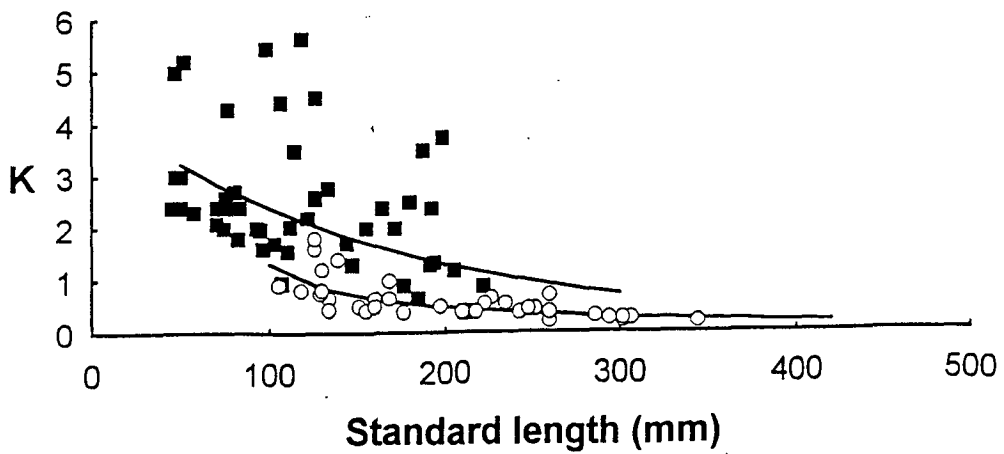
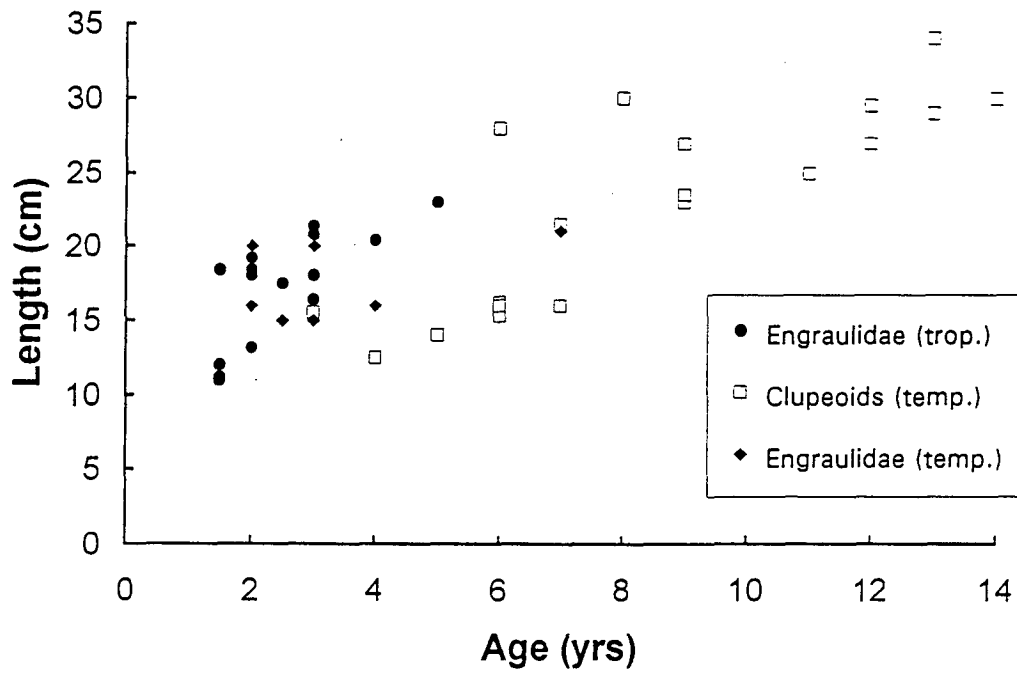
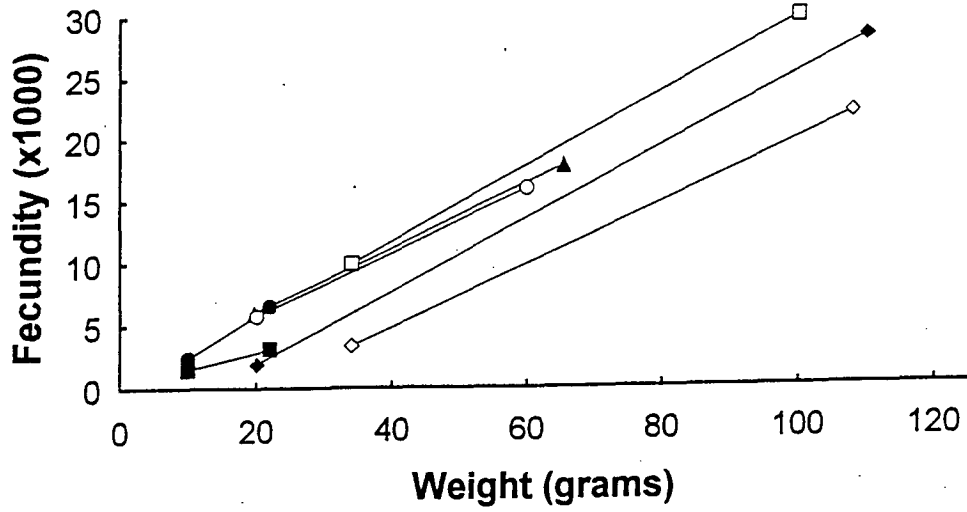


Figure 9.5. Fecundity plotted against weight for large tropical clupeoids. Key- □ - *Amblygaster sirm* (Conand 1991); ◆ - *Thryssa spp.* (regression for three species, present study); ◇ - *Thryssa gutamiensis* (Babu Rao 1977); ▲ - *Thryssa mystax* (Shamsul Hoda 1983); O - *Coilia dussumieri* (Fernandez and Devaraj 1989); ■ - *Thryssa baelama* (Marichamy 1970); ● - *Thryssa dussumieri* (Shamsul Hoda 1986).

Figure 9.6. Maximum length of species plotted against longevity for some large tropical clupeoids and some temperate clupeoids. Data from Tables 9.2 and 9.7.

Figure 9.7 A plot of K versus  $L_{\infty}$  or maximum length (SL) for tropical and temperate clupeoids. Key -■-tropical species; O-temperate species.



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## APPENDICES

### APPENDIX 1

Description of the morphological characteristics used to visually assign stages to whole ovaries.

#### Stage I (Immature)

Ovary thin and strap-like, translucent only occupying a small volume of body cavity. Eggs not visible to naked eye but seen through a microscope are uniformly small. Nucleus visible. In Stolephorid anchovies eggs are not yet elongated.

#### Stage II (Maturing)

Ovary larger, and shape becoming deeper dorso-ventrally but still thin laterally. Occupying less than a quarter of the body cavity. Colour pale yellow. When viewed through a microscope a batch of larger eggs just distinguishable from the small immature eggs. Nucleus visible in eggs. In stolephorid anchovies these eggs are beginning to elongate.

#### Stage III (Mature)

Ovary becoming large and lobate (deeper posteriorly), occupying half to three quarter of body cavity. Ovary firm and eggs remain attached during dissection. Eggs visible to naked eye but less than 1mm in diameter. Nucleus visible in eggs when viewed under a microscope. Colour: yellow/orange when fresh.

#### Stage IV (Ripe)

Ovary very large usually occupying all available space in body cavity. Colour pale orange. Ovary flaccid and eggs loose, falling out upon dissection. Eggs are large (>1mm) and thin walled with only a small oil droplet visible internally. No nucleus visible in eggs.