THE POPULATION AND REPRODUCTIVE BIOLOGY OF *PSEUDOCHROMIS QUEENSLANDICA* AT ONE TREE ISLAND, GREAT BARRIER REEF.

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ABSTRACT

This study reports on the reproductive biology and general demography of the coral reef fish, *Pseudochromis queenslandica*. *P. queenslandica* was found to be sexually colour-dimorphic, with a third, intermediate colour phase seen in between 5-10% of the population at any given time. *P. queenslandica* was found to be capable of changing sex from male to female and there was also a suggestion of female to male sex change. Sex change was found to occur at a wide range of sizes and ages. There was no evidence of the sex ratio being significantly different from 1:1.

Annual-forming increments were found in the otoliths of *P. queenslandica* and these were validated two different ways; by the thickness of the increment margin at different times of year, and also by marking otoliths with tetracycline. Annual increments could be seen in both whole otoliths and thin-sections of otoliths but counts from whole otoliths missed increments in older fish. Growth in thickness of the otolith was found to be allometric with the growth in length of the fish, causing difficulties for back-calculation. This growth in thickness of the otolith was found to be regular from year to year, and allowed age determinations to be made by simply weighing the otolith.

P. queenslandica in this study had longevities exceeding 10 years and survivorship was estimated from both mark-recapture studies and from age distributions. Average life expectancy ranged from 1.5 to 8.3 years in these estimates. *P. queenslandica* reached 90% maximum size by three years of age and growth of adult fish was variable and not associated with size or age.

This thesis is my own original work, except where specifically acknowledged.

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AKNOWLEDGEMENTS

CHAPTER FOUR

GROWTH AND SURVIVORSHIP OF *P. QUEENSLANDICA*

CHAPTER FIVE

CHAPTER ONE

GENERAL INTRODUCTION

Ecological research on coral reef fishes has primarily been directed at species assemblages and their structure (reviewed in Sale, 1980). Questions of interest related to the diversity and species composition of the communities studied and how they might be regulated. Disparate views developed about the degree to which communities could be structured by competitive partitioning of finite resources (Smith and Tyler, 1972; 1973; Smith, 1978; Gladfelter et al., 1980; Anderson et al., 1981; Ogden and Ebersole, 1981) or by chance events (Sale 1974; 1977; 1978). Despite the large number of community studies using coral reef fish as subjects, very little information on the population biology of individual species is available (Sale, 1980).

Coral reef fish continue to be used in studies of community structure but recent work on recruitment patterns has also focused interest, and started to address the shortage of information on population dynamics of individual species (Williams, 1980; Doherty, 1982; 1983a, b; Victor, 1983; 1986). Williams, Doherty and Victor have all pointed out the potential importance to populations of reef fish of fluctuations in recruitment from the plankton. Large variations in recruitment from year to year and at many spatial scales (Williams, 1980; Eckert, 1984; Sale et al., 1984; Victor, 1984) have been documented and suggested as a limiting factor in some populations (Williams, 1980; Doherty, 1982; 1983a; b; Victor, 1983; 1986). With few exceptions (eg. Victor 1986), these recruitment studies have drawn their conclusions in the absence of estimates of longevity of the species involved, yet life-span must be taken into account when assessing the potential effects of annual fluctuations in recruitment (Cushing, 1977). Recent work has demonstrated the potential of some small coral reef species to have longevities exceeding 10 years (Aldenhoven, 1986; Eckert, 1987), potentially dampening the effects of variable recruitment on local populations (Eckert ,1987).

Jones (1987) has recently emphasized that processes likely to be density dependent, such as competitive interactions over limited resources, and density independent processes, such as most recruitment variation, are not mutually exclusive and that both may be important in forming population structure. Jones (1987) and Eckert (1987) both make the point that the

relevance of factors such as variable recruitment and competitive interactions to the distribution and abundance of reef fish may depend on the time scale over which the questions are asked.

People seeking to manage temperate fisheries have long sought accurate age determination as this provides the most important demographic information (Ricker, 1975). Annual ageing studies of tropical reef fish have been sparse and only rarely successful (eg. Moe, 1969). Annual ageing studies on tropical reef fish have generally been thought to be difficult to achieve (Pannella ,1980; Brothers, 1980) and have not been emphasized by ecologists. Conversely, daily ageing using growth increments in otoliths has been successful for back-calculation of recruitment patterns and larval life-history of tropical species (Brothers and Mac Farland, 1981; Brothers et al, 1983; Victor, 1983; 1986).

Age determination can provide the key to most important demographic parameters but is not always possible. In its place, there are well established methods of analysing growth and mortality with mark-recapture techniques to provide predictions of size at age or mortality (Ricker, 1975). In some circumstances, direct measurements of parameters such as growth or mortality are necessary because interactions among such parameters (eg. mortality that changes with size) can make simply looking at size or age structures misleading (Ricker, 1969; 1975).

Demographic parameters are often very different between the sexes, and Ricker (1975) has pointed out that sex-specific demographic information is crucial in understanding the overall biology of a species. Sex-related demographic differences often are a consequence of different types of mating systems, especially hermaphroditic ones (reviewed in Charnov, 1982). Sequentially hermaphroditic fish commonly show large differences between the sexes in age and size structures and abundances that are important to the mating system (Warner and Downs, 1977; Warner and Hoffman, 1980; Hoffman, 1985; Warner and Lejeune, 1985). Warner and Downs (1977) have demonstrated differential growth and survival between males using different reproductive modes.

The overall aim of this study was to provide basic information on the population biology of the small coral reef fish *Pseudochromis queenslandica*. Age determination is probably the most powerful tool in life-history studies and so a primary aim of this study was to establish

whether *P. queenslandica* could be accurately aged. A further aim of this study is to determine the mode of reproduction and describe its influence on demographic parameters such as the growth and longevity of *P. queenslandica* .

MATERIALS AND METHODS

The Study Site

All the work reported here was done in the lagoon of One Tree Island Reef latitude 23°31 S and longitude 152°06 E. One Tree Reef is classified as a lagoonal platform reef (Maxwell, 1968), and has shallow margins with fully enclosed lagoons averaging approximately 5 m in depth. One Tree Reef has three lagoons but only the largest of those was used in this study. The lagoon floor is covered with continuous reef and patch reefs of varying sizes, all surrounded by sand. All patch and continuous reef used in this study was within 300 m of the shallow sandy margin of the reef and in from three to five metres of water (low tide). Patch reefs were of irregular shapes and ranged in area from 40 to 120 m² and were always surrounded by at least five metres of open sand on all sides. All patch reefs used in this study were first selected from aerial photographs or maps of One Tree lagoon. Area measurements of patch reefs were made underwater with a nylon tape measure and areas of irregularly shaped reefs were estimated by breaking them into a series of small, regular shapes whose areas could be easily measured. Where patch reefs were to be treated differently, treatments were allocated randomly.

The Species

Pseudochromis queenslandica (Saville-Kent 1893) is distributed from the Capricorn-Bunker group in the south to Torres Strait in the north, and occurs in both coastal waters and on the Great Barrier Reef (A.C. Gill, Pers. com.). Species identification was kindly provided by Anthony C. Gill (Armidale University, N.S.W.). The genus Pseudochromis has been allied to the Serranidae and is now in the family Pseudochromoidae (Springer, et al., 1976). *P. queenslandica* grows to a maximum length of 95 mm SL and occurs throughout all lagoonal reef substrates and is also found in rubble areas outside One Tree Lagoon (pers obs.). *P. queenslandica* is very secretive and rarely seen out in the open; more usually associated with small caves, cracks and holes in rubble and dead coral substratum.

Taking a Census

The secretive nature of *P. queenslandica* prevented any sort of normal visual census technique. The solution was to trap all the fish in a given area, usually a patch reef, and mark them so that it was clear to see that a particular fish had been included in the count. The census area was baited and trapped out until no unmarked fish had been seen for a 2-3 hour period. The amount of time was varied in proportion to the estimated size of the reef or area being censused.

capture

P. queenslandica is apparently a carnivore and was easily attracted to baits of several kinds. Fresh and frozen fish as well as crab meat, bacon and various tinned meats were all tried as attractants. While no quantitative estimates were made, it was clear that both fresh fish and fresh crab were very useful as baits. When a *P. queenslandica* was in sight, it could often be lured near simply by showing it a dismembered crab or fish. *P. queenslandica* were also attracted by fresh blood from both fish and crabs and the standard procedure for enticing *P. queenslandica* from surrounding reef was to wring out a dead fish. Once attracted to a bait, the fish were lured into a trap. All the traps used were of two basic designs. The first design was a remotely operated guillotine trap with a clear body, to allow the fish to see the bait. Once the fish was inside the trap, the rubber-band driven door was released, capturing the fish. The second, and more successful type of trap, was simply a clear plastic bag of approximately 30 × 50 cm. The bag was expanded with water and weighted with rocks from nearby, and a bait put inside the bag. When a fish had entered, the mouth of the bag was gently closed, trapping the fish inside.

marking

All fish were marked with fin clips. The pelvic fins, when trimmed as close to the body as possible, did not usually grow back in the largest fish. In smaller fish, the fins often grew back, but growth was distorted or twisted and easily distinguished. A clip of the right or left pelvic fin was used in combination with partial removal of either the dorsal or anal fins. Three positions on the dorsal fin were distinguished, as well as two on the anal fin, giving a total of ten combinations to use on each reef. When the fish were broken into size categories, the number of marks that could be assigned to a reef was sufficient to prevent confusion in identifying individuals. All fish were marked *in situ* and returned to the point of capture within five to 10 minutes. Fish showed no obvious reaction, apart

from anger (?!), to being marked and were often back, chasing the bait within a few minutes of release.

Literature surveyed in this report: caveat.

Every attempt was made to make the literature surveyed in this thesis comprehensive on the the topics examined. However, I suspect that some work was omitted, particularly with regard to ageing and growth of tropical reef fish. A primary source surveyed for references on ageing and growth was *Aquatic Sciences and Fisheries Abstracts*. Most of the material abstracted there was readily available and was obtained. However, a substantial body of fisheries research is only ever published within the organization that supplied the funding and not all of this research is even abstracted. These puplications are dfficult to find and obtain and as a consequence, it is possible that some important references were not actively sought. For the most part these publications were not in refereed journals and/or were written in foreign languages. The effort of obtaining and translating these references was not considered worthwhile.

CHAPTER TWO

AGE DETERMINATION IN *P. QUEENSLANDICA*

INTRODUCTION

The use of periodic markings in bony structures of fish for age determination has a long history (Bagenal, 1974). Scales, vertebrae, spines, and otoliths have all demonstrated annual markings for use in ageing. Scales were probably the first commonly used structure for ageing; primarily due to their easy access and simple preparation. More recently, otoliths have become the predominant structure used in ageing studies, because they give more accurate estimates than scales (Beamish and Chilton, 1982; Libby, 1985). The external surface of the otolith can show detail of the annual markings but several authors have shown that more information can be gained from older fish if the otolith is viewed in cross section (Beamish, 1979a; Campana, 1984a) Most annual ageing techniques work quite well on the young or rapidly growing fish but where growth is relatively slow as the fish becomes older, ages as estimated by some techniques can seriously underestimate the true age of a fish. Therefore, the need to validate the ageing technique over all ages has been stressed (Beamish and McFarlane, 1983).

The demonstration of daily markings in otoliths (Pannella, 1971) has inspired an enormous amount of work in the field of otolith microstructure (reviewed in Campana and Neilson, 1985; Gjøsaeter et al., 1984; Jones, 1986). The daily ageing technique has proven successful for fish from both temperate and tropical climates. The bulk of the work on ageing from daily increments has concentrated on young fish, when growth and clarity of daily increments are greatest. Some workers have, however, succeeded in ageing adult fish using daily increments (Ralston and Miyamoto, 1983; Radtke et al, 1985).

Widely used techniques for ageing temperate species from annual markings have not been applied as commonly in the tropics. Periodic markings have been found in tropical fish but their usefulness in ageing has been questioned (Pannella, 1974). Where apparent annual markings have been found in tropical fish (Moe, 1969; Goeden, 1978) they have not been subject to the same rigorous validation as those in many temperate species. The lesser variation in temperature and day length in the tropics

is generally held to be the reason for the lack of seasonal markings in bony structures of tropical fishes (Pannella, 1974).

Radtke et al. (1985) and Boehlert (1985) have both suggested that otolith weights might be useful in ageing fish. Both studies used otolith weight in combination with other variables to generate multiple regression models predicting fish age. These authors stressed the potential usefulness of an ageing technique that did not require the otoliths to be processed to yield an age determination. While not discussing otolith weight directly, several other authors (Beamish, 1979a; 1979b; Campana, 1984a) have shown that the otoliths of some fish continue to thicken with age, apparently out of expected proportion with fish growth.

When a time-based increment is laid down in a structure and the growth of that structure can be related to the growth of the animal, then the growth increments on the structure have been used to view the growth history of that animal (Bruyzgin, 1963; Ricker, 1969). While authors have stressed the need for validation of the ageing technique over all ages for accurate age determination, the fit of the body-otolith (or body-scale) relationship for use in back-calculation over the range of sizes encountered has not been equally emphasized. Many authors do not plot the data used to derive the curve and some do not even indicate the fit of the relationship.

The main aim of this study was to provide validation of an annual ageing technique for the tropical reef fish *Pseudochromis queenslandica* . Ages derived from whole otoliths, from cross sections of otoliths and from otolith weights were compared. The relationship of growth of the otoliths of *P. queenslandica* to the fishes' body size was also investigated. The relationship between otolith growth and fish growth and its effects on back-calculations of size-at-age derived from these otoliths is also discussed.

MATERIALS AND METHODS

Preparation of otoliths

Fish used in this study were captured by the methods outlined in Chapter 1. Otoliths were dissected from the fish by removing the lower jaw and musculature associated with the buccal cavity to expose the base of the skull. The lower portion of the skull was removed in one piece, exposing the otoliths. The otoliths were cleaned under a dissecting microscope, using fine forceps to remove any remaining tissue and then were rinsed in

ethanol and then stored dry until further use. Due to their larger size, the sagittal pair of otoliths were used in preference to either of the other pairs of otoliths and hereafter the term otolith will refer to sagittae only. Figure 2.1 is a schematic representation of an otolith from *Pseudochromis queenslandica* . The terms centrum, length, width, and thickness of otoliths will refer to those indicated in Figure 2.1.

Otoliths were embedded in Spurr's histological resin which allowed a clear view of the centrum of the otolith. Under a dissecting microscope, a fine line corresponding to the desired plane of section was drawn in the top of the resin block. This line was used for fine alignment when grinding. The block was ground down to the aligning line with 500 and 1000 grit emery paper and finally polished with Imperial lapping film (3M company) in a series of 16, 9.0, 3.0, 1.0 and 0.3 µm abrasive paper. The block was attached, polished side down, to a microscope slide with more resin and the other half of the otolith ground to a thin section of 50 µm which was then ready for viewing.

Counting and validation of annual increments

The accuracy of two methods of counting annuli on otoliths, reading the otolith surface, and cross sections were compared for 24 fish. The light and dark zones seen in the otolith are called opaque and hyaline respectively, and can be seen in the photos of Figure 2.2. The number of increments seen increased with the size of the fish and their appearance was similar to those in other species which have been demonstrated to form annually (eg: Beamish, 1979a). For viewing increments, both thin sections and whole otoliths were illuminated with reflected light against a black background. Markings on thin sections were counted and measured at magnifications of either 40X or 100X using a compound microscope. All counting and measuring of increments on otoliths was done with the aid of a high resolution video system. A Four-A video position analyzer (Four-A Company Ltd., Tokyo, Japan) superimposed an X-Y axis and a cursor on the video image transmitted from the microscope and measurements were output directly to a personal computer for compilation. Increments in thin sections were measured and counted from the centrum to the interior, ventral surface, just below the sulcus (see Figure 2.1).

The precision of counts of increments was also assessed by making two counts of each of 68 otolith thin sections. After the first count the sections were mixed and re-labeled to prevent knowledge of the previous count

Figure 2.1. Drawing of Sagittal otolith showing orientation in the fish, and the plane of section used in this study. C=centrum of the otolith, line A-B = length, line D-E = width, line C-F = thickness of the otolith, and S = sulcus. A is at the anterior end of the otolith, D is on the dorsal side, and the sulcus (S) faces the interior of the fish (ie. as drawn, this is an otolith from the right side.
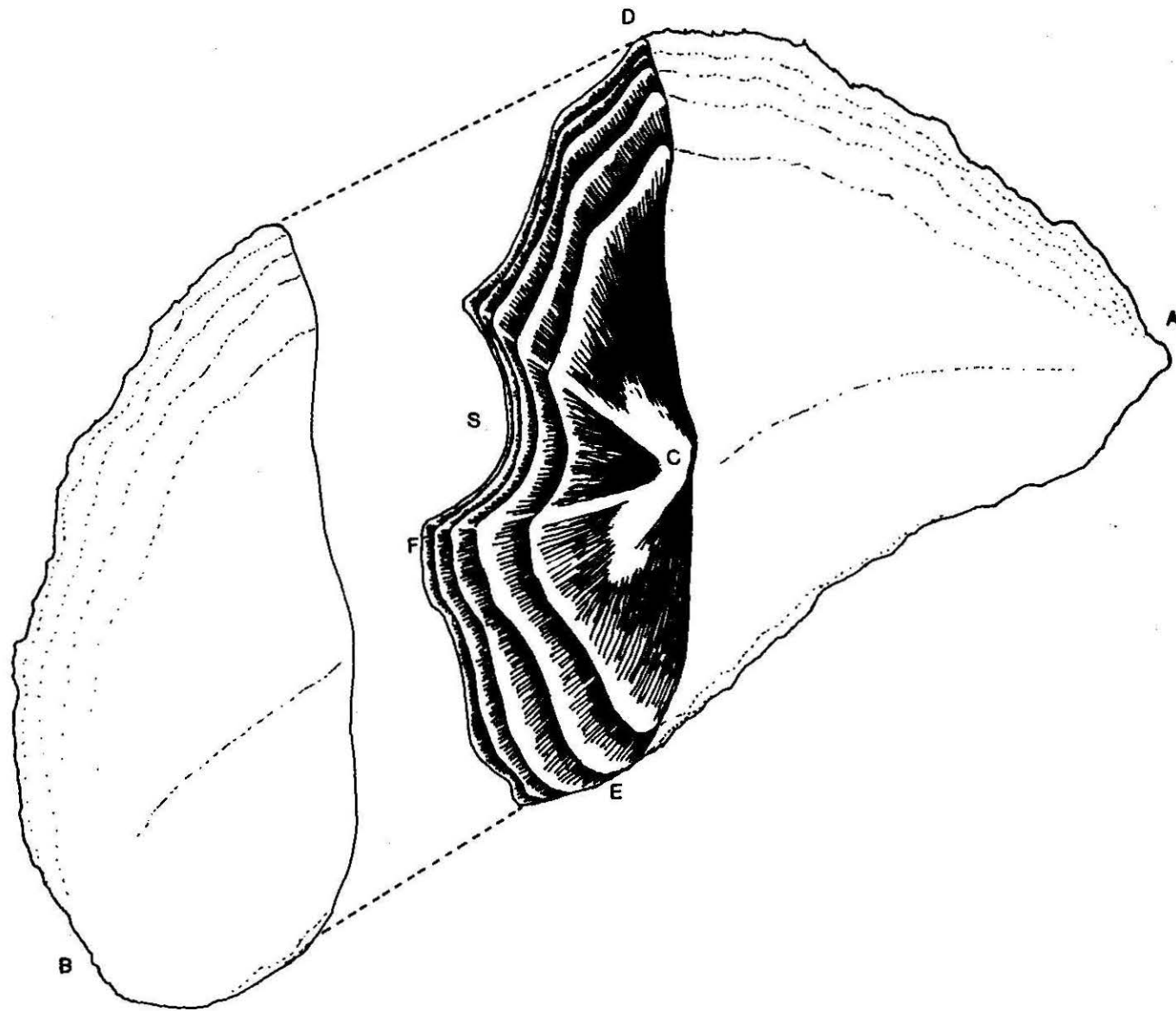
Figure 2.2. Photos of otoliths taken against a black background illuminated with reflected light. Figure 2.2a. (above) a whole otolith, and Figure 2.2b (below) a cross section of an otolith, both and showing detail of opaque (o) and hyaline (h) banding. Scale bar is 1.00 mm.
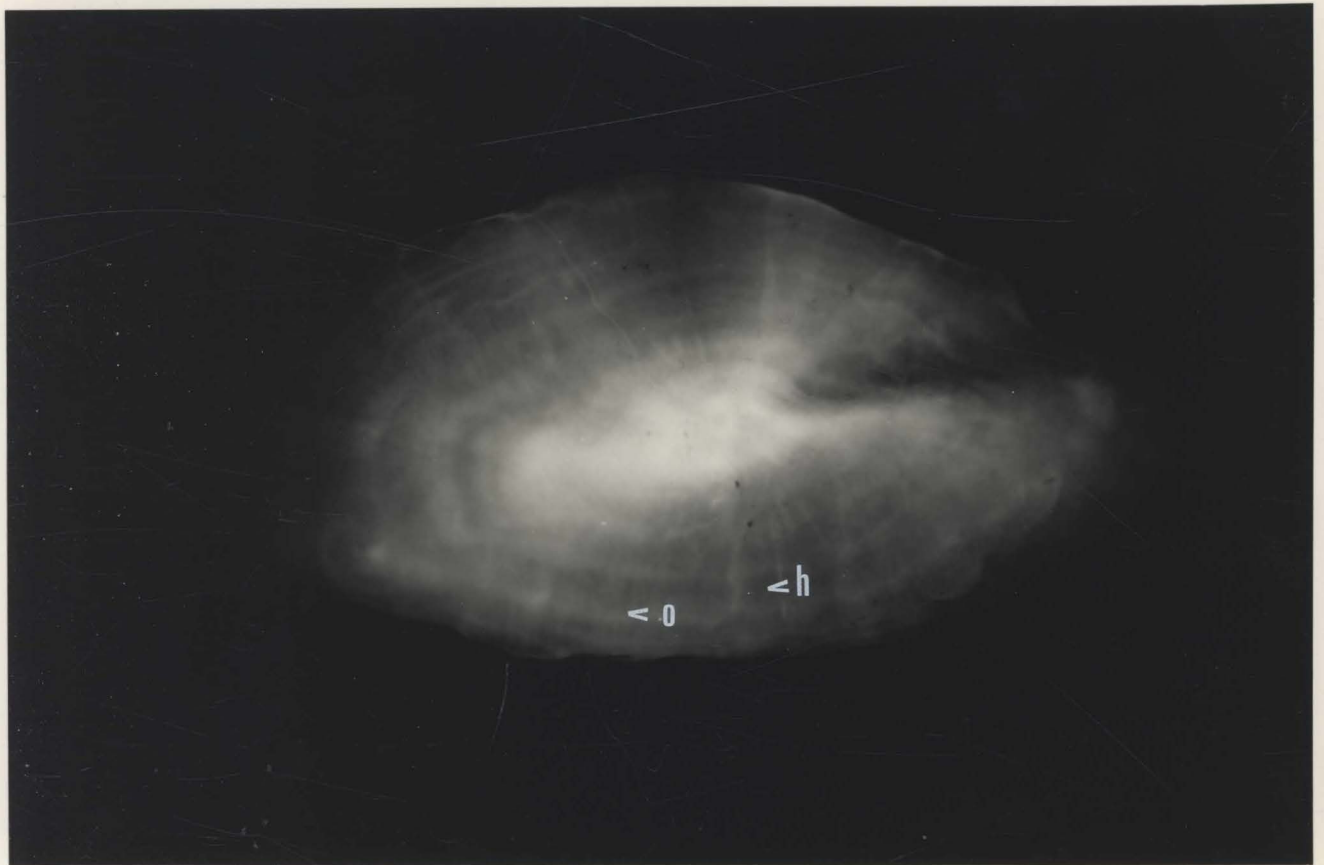
affecting the second count. The two counts were done one week apart. Of the 68 replicate counts, five did not agree. Of the five, four differed by only one increment and the fifth by two. All five of the fish had counts of over six increments on their otoliths. Two of the 68 preparations were considered unreadable and the same two were selected at both readings. Given this level of precision, subsequent increment counts were made only once.

Two methods of validating the periodicity of increment formation were used in this study. The first method, called the marginal increment method, relies on annual increment being laid down at the same time each year. The distance between the edge of the otolith and the closest increment should then be different at different times of the year (Thomas, 1983a). The second method of validation used the antibiotic tetracycline to put a mark on the otolith . Tetracycline is incorporated into growing bony structures (Campana and Neilson, 1982), leaving a mark that fluoresces under ultra-violet light. The position of the mark shows where the otolith was growing at the time of exposure to the drug.

Tetracycline marking was done in the last week of September, 1983, and 33 fish on six isolated patch reefs were marked. Fish were captured and fin-clipped in the usual way (Chapter 1) and then lightly anaesthetized with quinaldine, and given an intraperitoneal injection of tetracycline HCl at the dose rate of 50mg of the drug per kg. of fish (Wild and Foreman, 1980). Fish weight was estimated from displacement in a graduated cylinder. Sterile saline was used as the dilution medium to achieve an injection volume ranging from 0.1 to 0.3 ml, depending on the size of the fish. The fish were allowed to recover from the anaesthetic and were returned to the location where they were captured within 20 minutes.

Microstructure

Micro-increments seen in thin sections of otoliths, such as those in Figure 2.3 were viewed at magnifications of 250X to 1000X with a compound microscope using transmitted light. Counting and measuring of these increments was aided with the video system previously described. To allow comparison, all counts and measurements of micro-increments were done along the axis from the core toward the ventral tip of the otolith. Counts were stopped at the point where individual increments could no longer be clearly resolved.

Figure 2.3. Light microscope photos of otolith microstructure. Figure 2.3a (above) shows the transition from the broad, heavy microincrements to the finer, lighter increments that may denote settlement (sm). Figure 2.3b (below) shows an area of the otolith where the microincrements become too indistinct to be counted (va). Scale bar is 50 µm.

sm

va
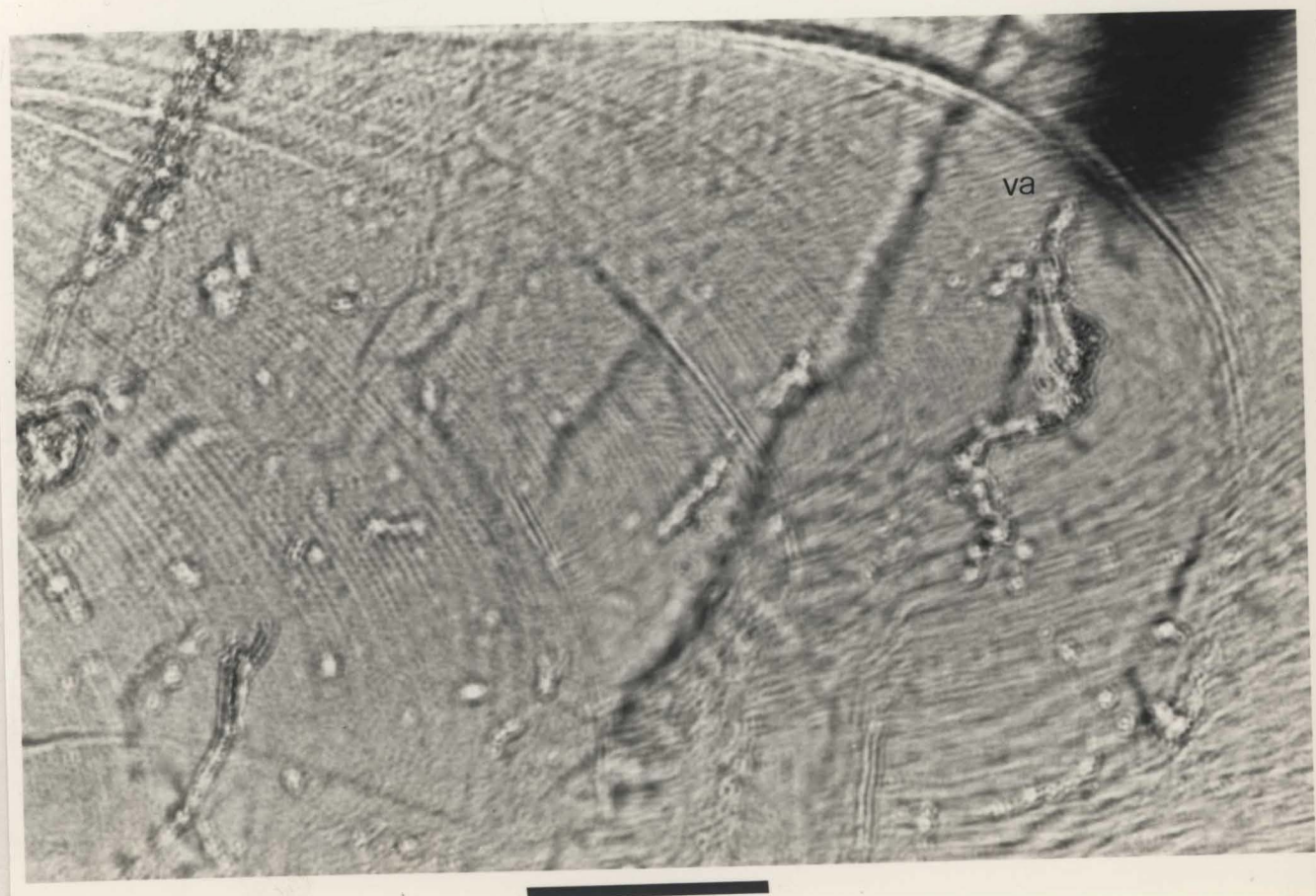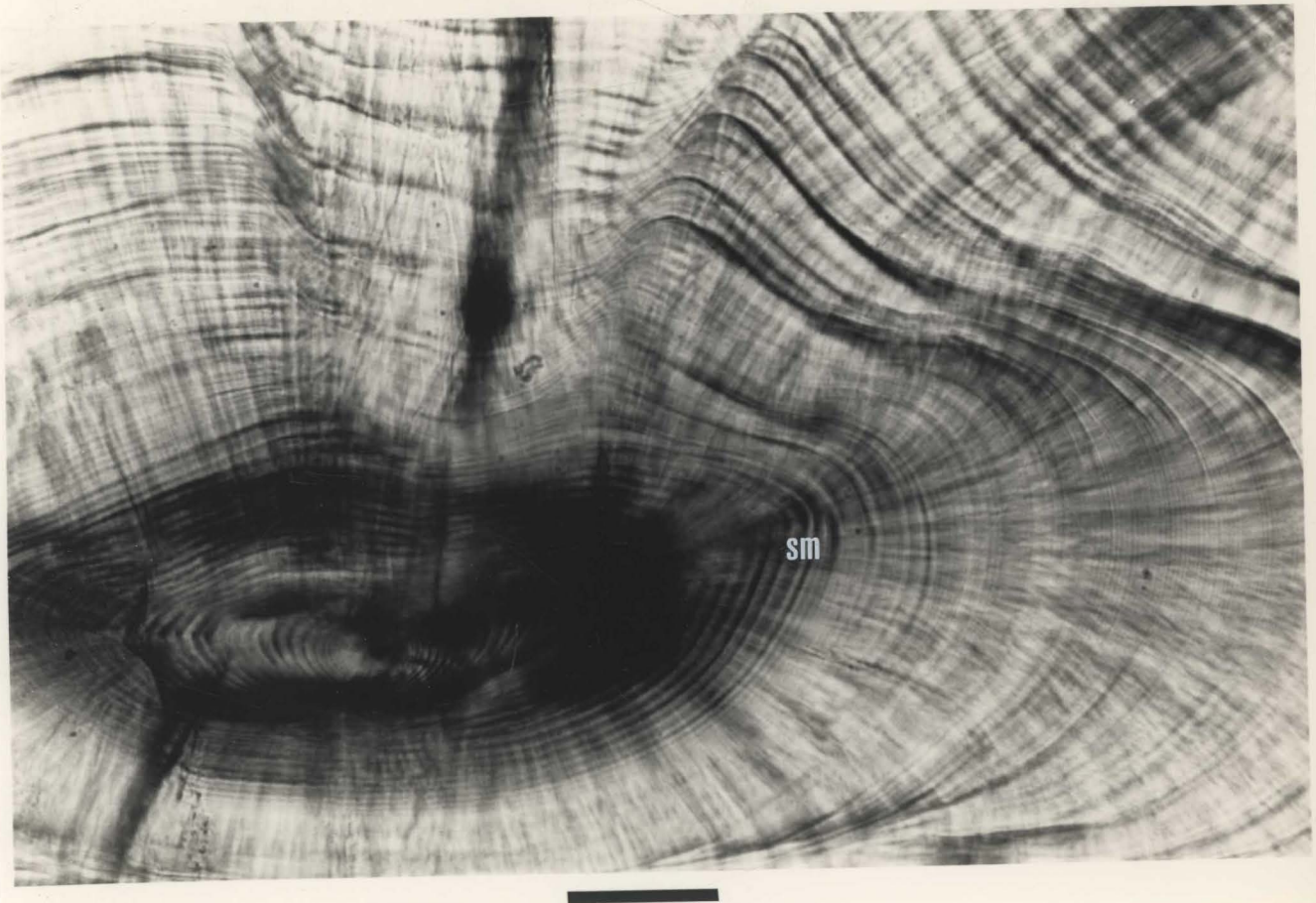
Scanning electron micrographs were made with a Jeol 023D SEM. Six otoliths in Spurr's resin were polished on one side and etched and coated with gold prior to viewing. Etching varied from two to five minutes in 0.1 M ethylenediaminetetraacetic acid (EDTA), a calcium chelating agent.

RESULTS

Validation of annual increments

Opaque and hyaline banding can clearly be seen in the photos of Figure 2.2. The agreement between the two veiwing methods (whole otoliths an otolith cross sections) was good at early ages but the whole otolith method missed some increments on older fish (Figure 2.4). All counts subsequent to this were done on cross sections of otoliths only.

Measurements from the centre of the otolith to the first annual increment and the distances between subsequent increments were taken from the otoliths of 152 fish (Table 1). The distance between successive increments declined in a regular way, with low variability among fish for any particular increment thickness.

Table 1. Thickness of increments seen in otolith cross section.

Increment	0 to 1	1 to 2	2 to 3	3 to 4	4 to 5	5 to 6	6 to 7	7 to 8	8 to 9
Mean increment thickness (μm)	332	89	64	52	45	41	38	37	32
S.E.	5.9	1.2	0.9	1.0	1.0	0.9	1.4	1.3	1.3
n	152	117	89	72	47	42	32	22	15

Otoliths from fish captured at different times of year show different thickness of the margin from the outer-most increment to the edge of the otolith (Figure 2.5). This relationship holds for fish with one, two and three increments, but no pattern was evident for fish with four or more increments. Finding the thickest margins in otoliths from fish sampled in November and the thinnest margins from February samples suggests that increments are formed sometime in between. The predicted thickness of the new increments being formed (ie. approximate marginal thickness in December) agrees with the measurements in Table 1.

Nine of the fish injected with tetracycline were recaptured in mid-December 1983 after approximately 11 weeks, and eight others were recaptured in the last week of February, 1984 after about 21 weeks. The

Figure 2.4. Comparison of two methods of counting opaque rings: Externally, from intact otoliths (Y), and from thin sections of otoliths (X).
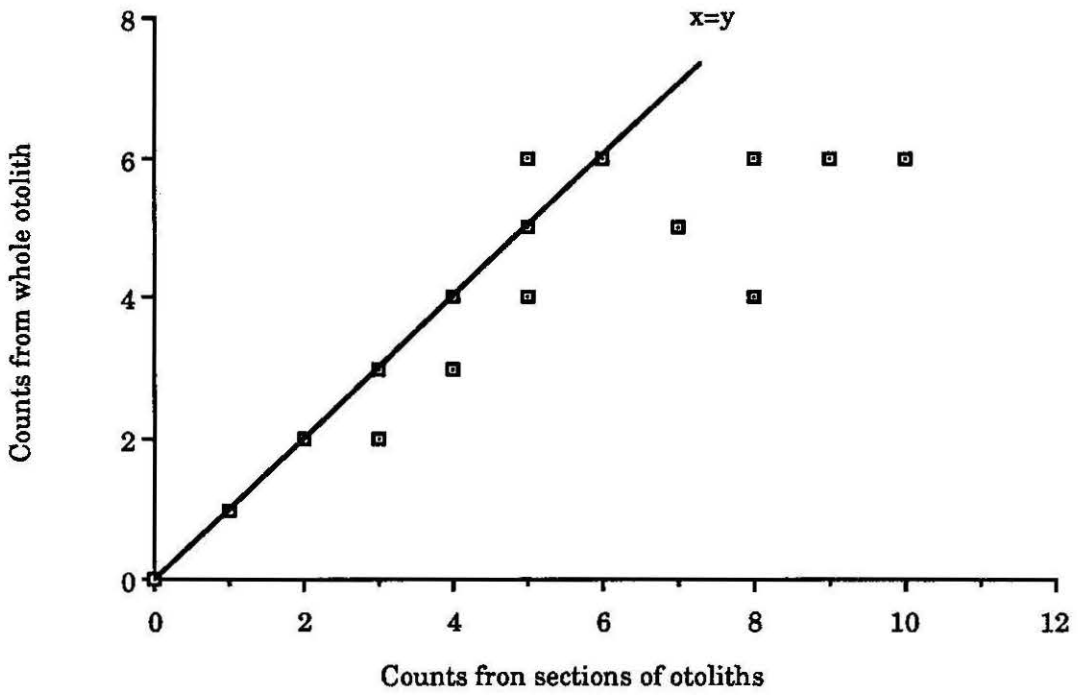
Figure 2.5. Regression of distance from outermost opaque ring to edge of otolith against the month when the fish was sampled for fish showing 1, 2 and 3 increments. Significance of regressions and numbers of fish given in box.

# increments	F value	df	r²	p
one	52.5	1,19	.73	<.01
two	16.0	1,22	.42	<.01
three	14.7	1,11	.57	<.01
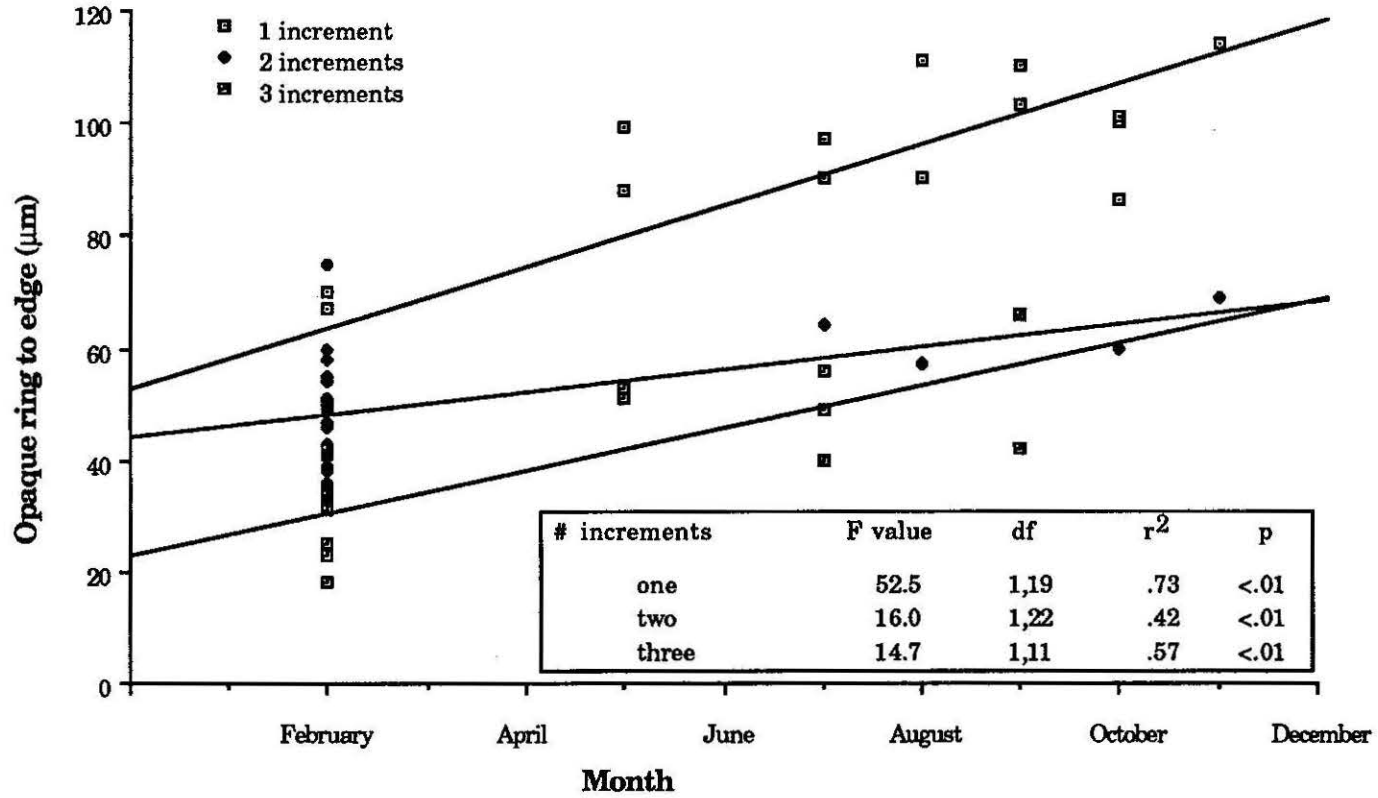
tetracycline injections produced a clear, fluorescent mark on the otoliths (Figure 2.6). The distance from the tetracycline mark to the edge of the otolith clearly differs between the two groups of fish (Figure 2.7) and indicates that the otoliths continued to grow in the extra 10 weeks that the fish captured in February were at large. Both groups of fish showed declining growth in thickness of the otolith with increasing number of increments seen in the cross section. As with the marginal increment data (Figure 2.5), the growth increments are comparable with those given in Table 1.

The proximity of the last visible annulus to the tetracycline mark on each otolith (Figure 2.8) gives a good indication of the timing of the annulus formation. Most of the annuli formed very near the tetracycline mark. The fish were treated in late September and the annuli had formed in some cases by December.

Microstructural information

When viewed in cross-section, the centre region of otoliths show concentric micro-increments. The core area of all otoliths examined had a zone of pronounced, widely spaced bands of approximately 20 μm in width. These abruptly changed to a zone of finer bands, that were 6-10 μm in width (Figure 2.3). Similar markings in other species of reef fish have been linked with the settlement of the planktonic larvae to a demersal existence (Brothers et al., 1983). Similarly, this abrupt transition in the increment width was assumed to represent settlement in this species and hereafter is called the settlement mark. The micro-increments were never resolved over the entire distance from the centre to the edge of the otolith and became obscure at varying distances from the centre. The appearance of the increments as they become visually indistinct and the location at which counting was stopped is shown in Figure 2.3b. The distance away from the centre of the otolith that micro-increments could be resolved varied, as did the count of increments in that distance. Figure 2.9 shows that the thickness of the increments generally decreased with increasing distance from the centre. The smallest increment widths were 1.6 μm, averaged over 10 increments, and the last 10 increments of all 10 fish from Figure 2.9 averaged 2.1 μm, ranging from 1.6 μm to 3.0 μm.

The view of micro-increments using SEM on polished and etched cross sections of otoliths did not appear to be any different from that achieved using light microscopy (Figure 2.10). The transitional area around the

Figure 2.6 a (above),b (below). Photographs, taken using ultraviolet light, showing the fluorescing tetracycline marker (1). The brightness around the edge of the otolith is autofluorescence of tissue and dirt on the edges of the otolith. Looking in a microscope, the two types of fluorescence were clearly distinguished because of colour differences. Scale bar is 1.00 mm.
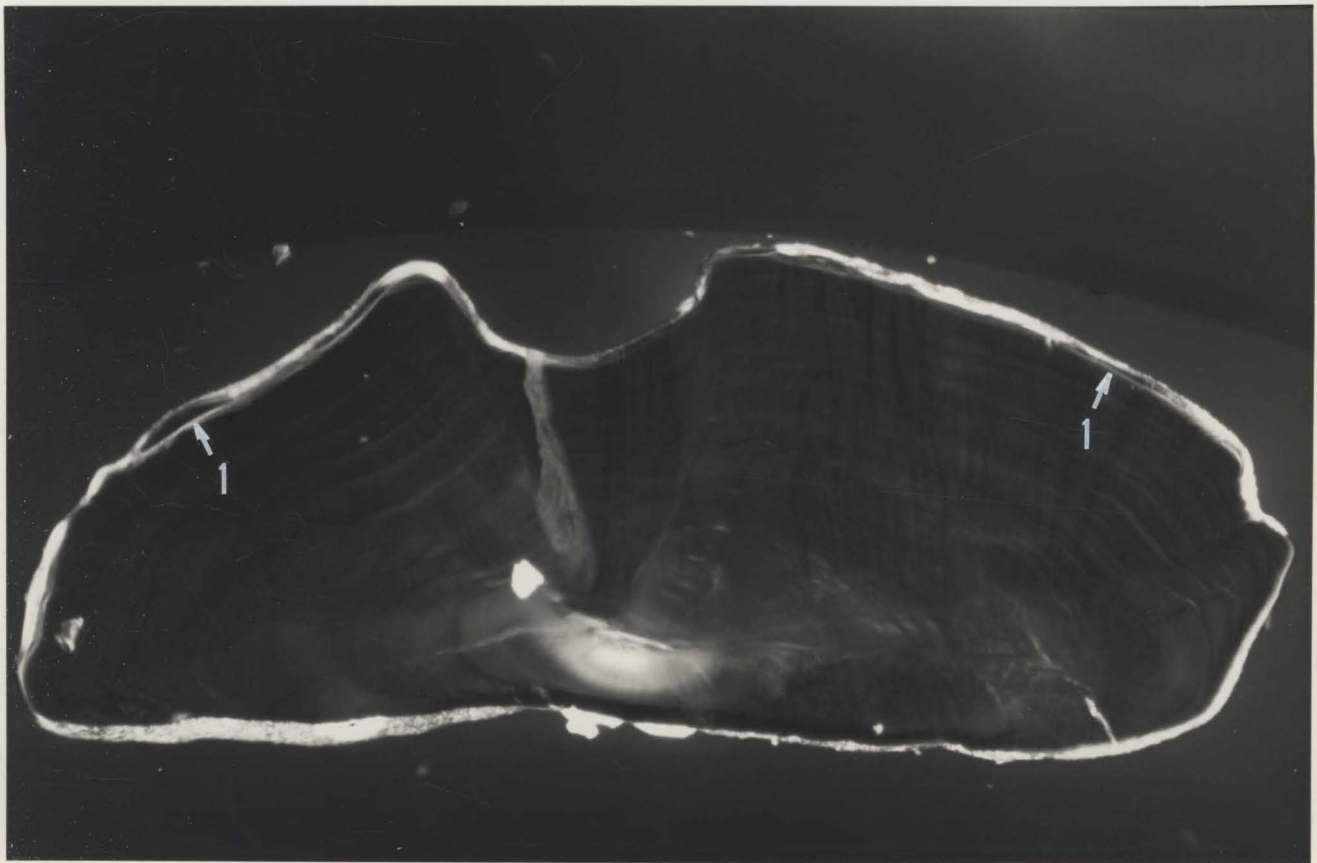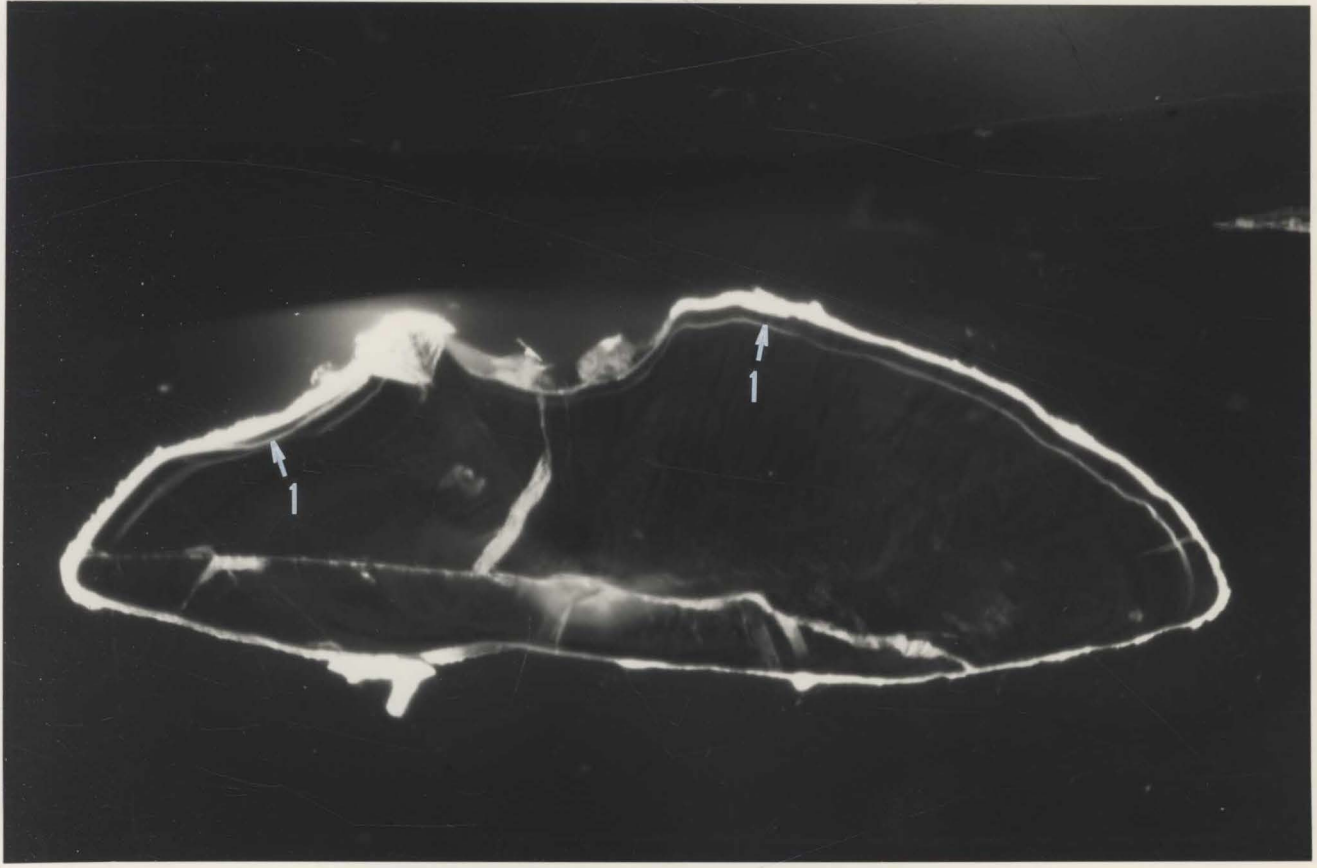
Figure 2.7. Distance, in microns, from the tetracycline marker to the edge of the otolith plotted against the number of increments seen in the otolith section.

Figure 2.8. Distance from tetracycline marker to the edge of the otolith plotted against the distance from the outermost opaque ring to the edge of the otolith.
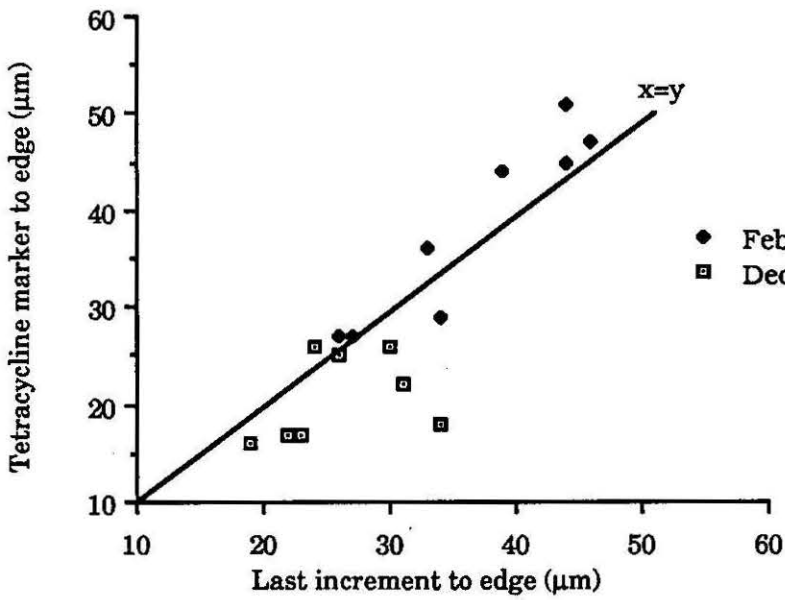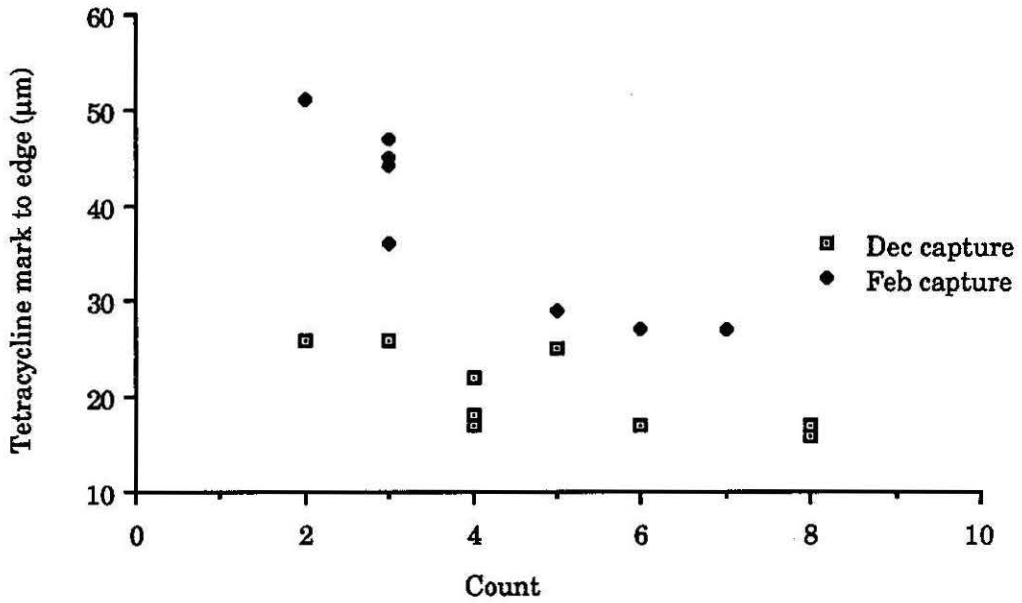
Figure 2.9. For ten otoliths, the settlement mark, the location of every 25th increment, and the position of the first annual ring, all on the dorsal-ventral axis, are plotted against the distance to the centrum.

FISH:

MICRONS FROM CENTRE OF OTOLITH
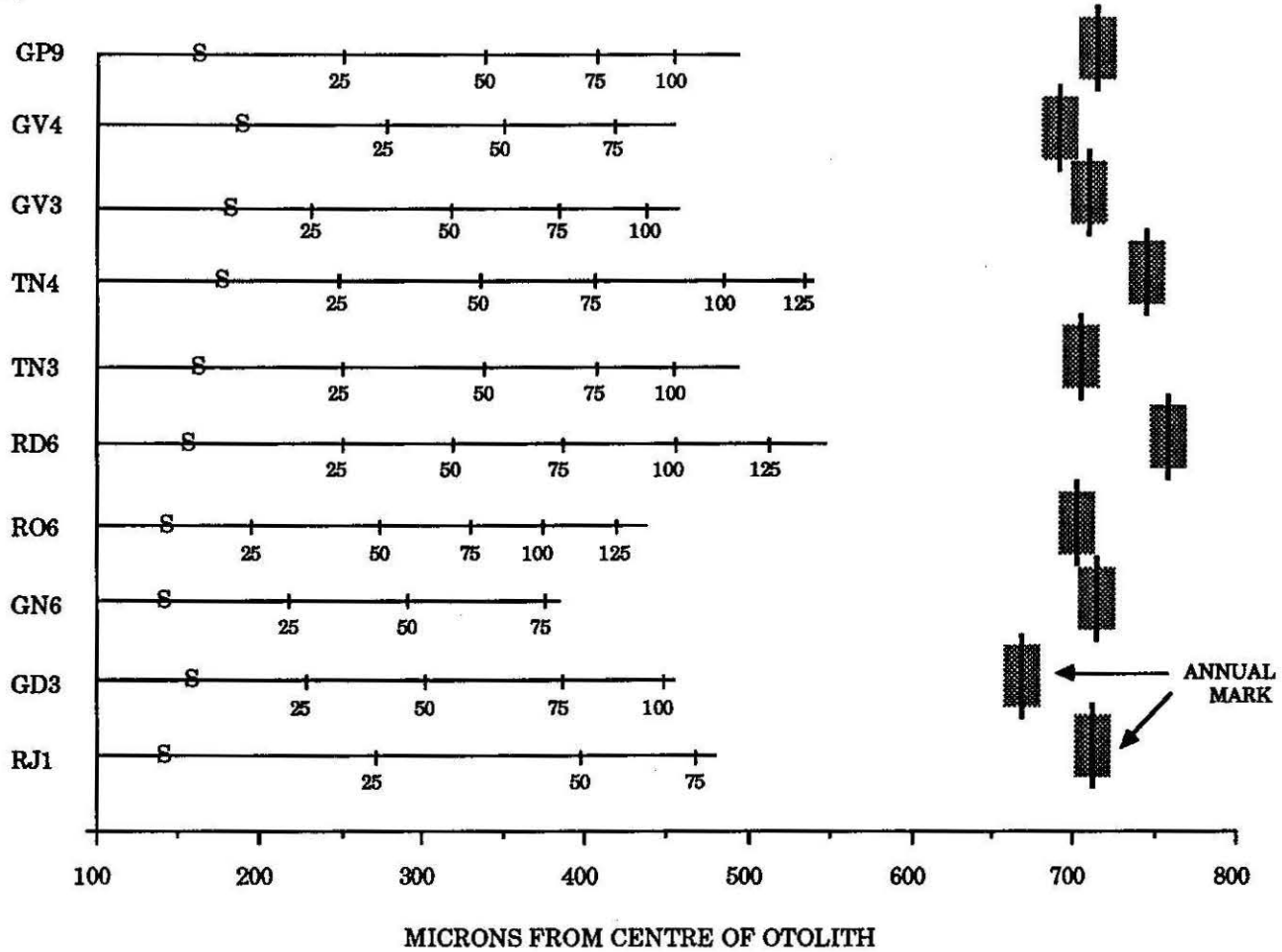
Figure 2.10 a (above), b (below). Scanning electron micrographs showing general detail (2.10 a) and finest increments seen (2.10 b). Scale bar = 1.0 µm.
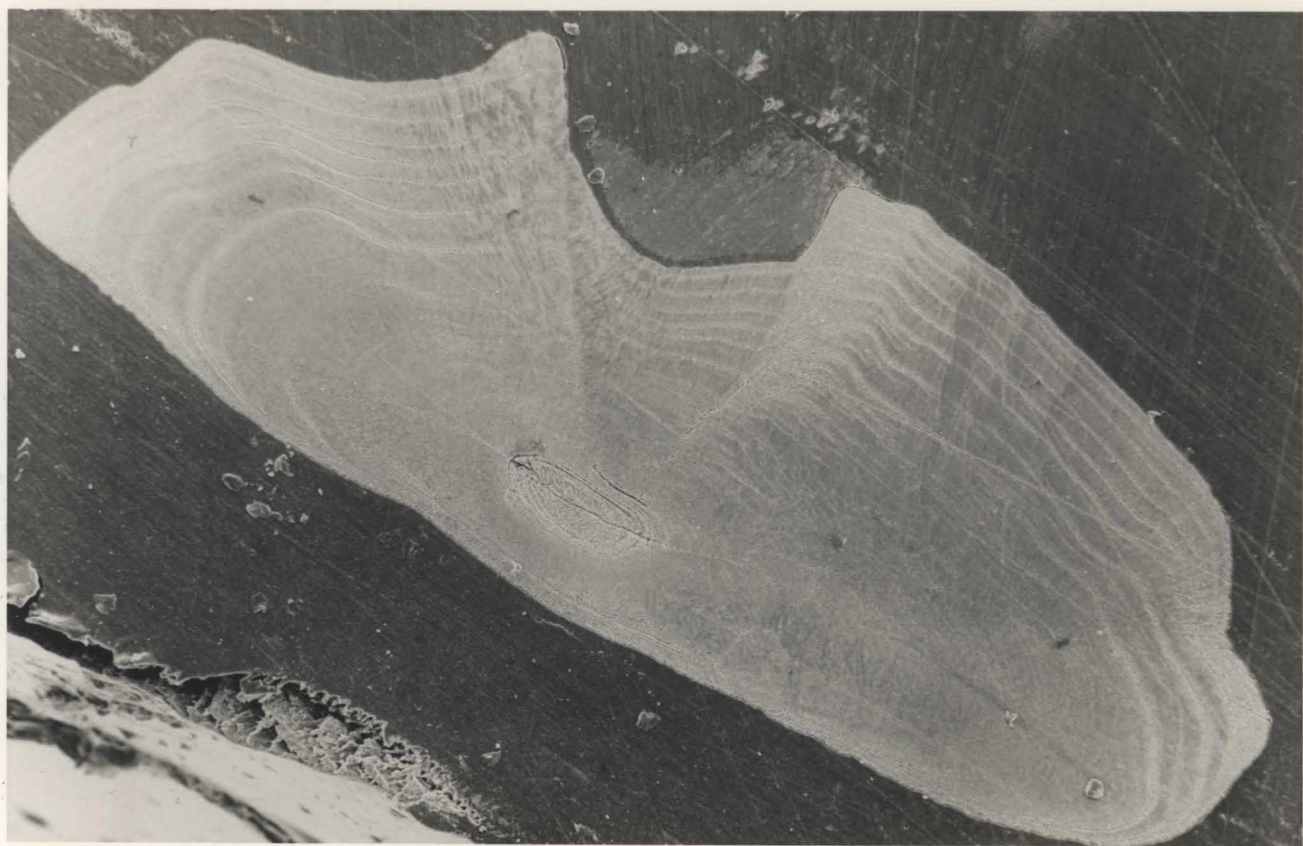
tetracycline was very even along the dorsal, interior, and ventral surfaces
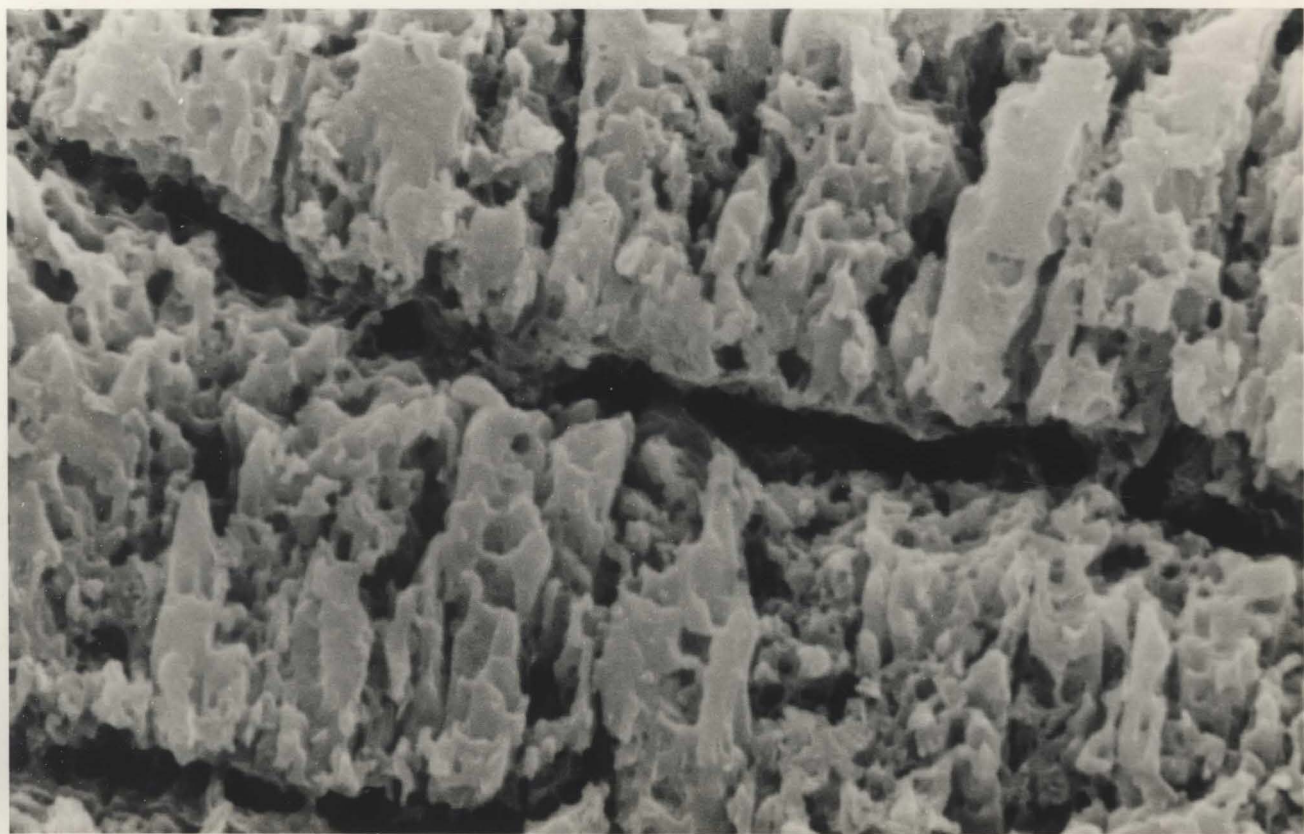
core and the banding leading away from it were readily apparent (Figure 2.10a). The finest increments seen were 1.4 μm and while exact measurements were not made, the increments appeared to fade from view at about the same place as seen in the light microscope.

Relationships between fish size and otolith size

The relationship between otolith growth and fish growth is crucial for any estimation of size-at-age using the growth increments of the otolith. Figure 2.11 plots fish size against the external length and width of the otolith and Figure 2.12 shows the thickness of fishes' otoliths plotted fish their size. The most obvious difference between these figures is that the plots of fish length against otolith width and length (Figure 2.11) are both linear, whereas the plot of fish length against otolith thickness (Figure 2.12) flattens with increasing otolith thickness. This implies that changes in otolith growth may be allometric with changes in fish growth, depending on which dimension of otolith growth is used.

A similar demonstration of how the otolith of P. *queenslandica* grows is shown in Figure 2.6. The growth of the otolith after the injection of tetracycline was very even along the dorsal, interior, and ventral surfaces of smaller otoliths (Figure 2.6a). On the large otolith shown in Figure 2.6b, the growth was only on the interior surface and did not thicken the dorsal and ventral surface. In other words, that particular otolith only grew in thickness and not in width.

Relationship of otolith size and weight to age of the fish

The appearance of the tetracycline mark evenly over the interior surface of the otolith, even in the largest fish, suggests regular growth in otolith thickness. The relationship between the increment count and the otolith thickness (Figure 2.13) is linear and a good fit at all counts whereas otolith width and length appear asymptotic with increasing count. If otolith thickness is a good predictor of age (ie increases in thickness are regular), then the weight of the otolith may also be a good indicator of age. Of the fish that had age determined from otolith cross sections, 72 had the remaining otolith undamaged and thus suitable for weighing. The linear relationship between the age of the fish and the weight of the otolith (Figure 2.14) implies that the growth in weight of the otolith is constant from year to year.

Figure 2.11. Standard length of fish plotted against otolith length and width.

Figure 2.12. Standard length of fish plotted against otolith thickness.

otolith width
$y = 5.5949 + 38.8608x \quad r^2 = .860$

otolith length
$y = -9.7236 + 23.2614x \quad r^2 = .90$

Fish length (mm SL)

Otolith dimension (mm)

Fish length (mm SL)

Otolith thickness (mm)
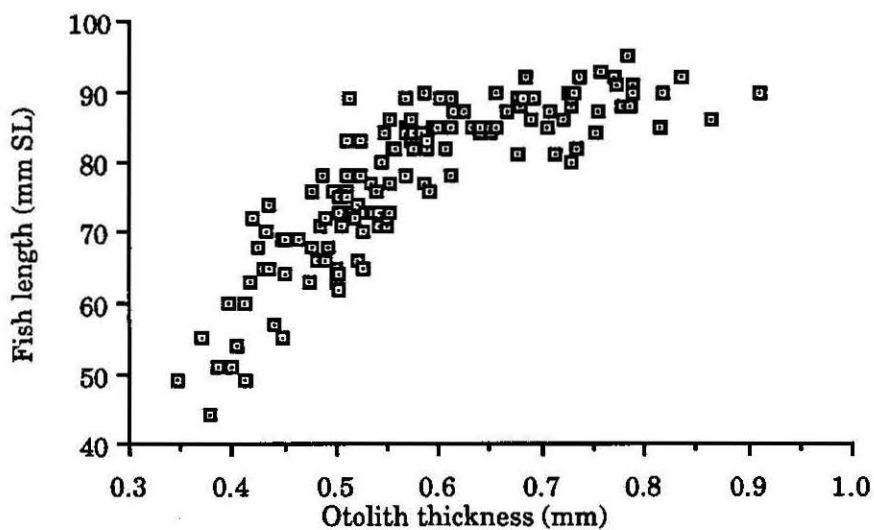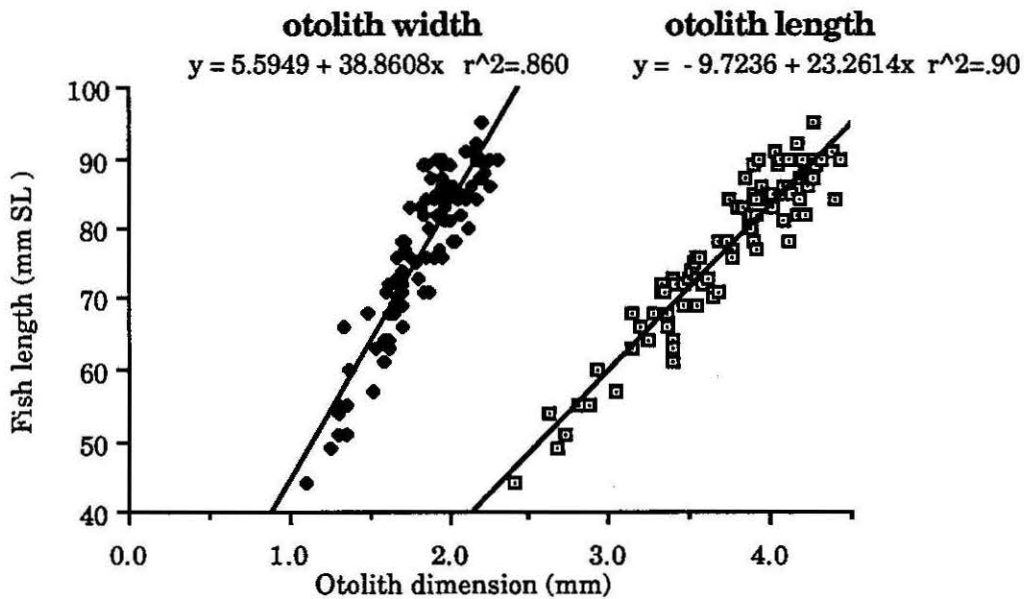
Figure 2.13. Count of opaque banding (annuli) plotted against otolith thickness.

Figure 2.14 Count of opaque banding (annuli) plotted against otolith weight.

$y = -8.9716 + 0.0225x \quad r^2 = 0.94$

Count

otolith thickness (µm)

$y = -2.4844 + 0.1018x \quad r^2 = .96$

Count

Otolith weight (mg*10)
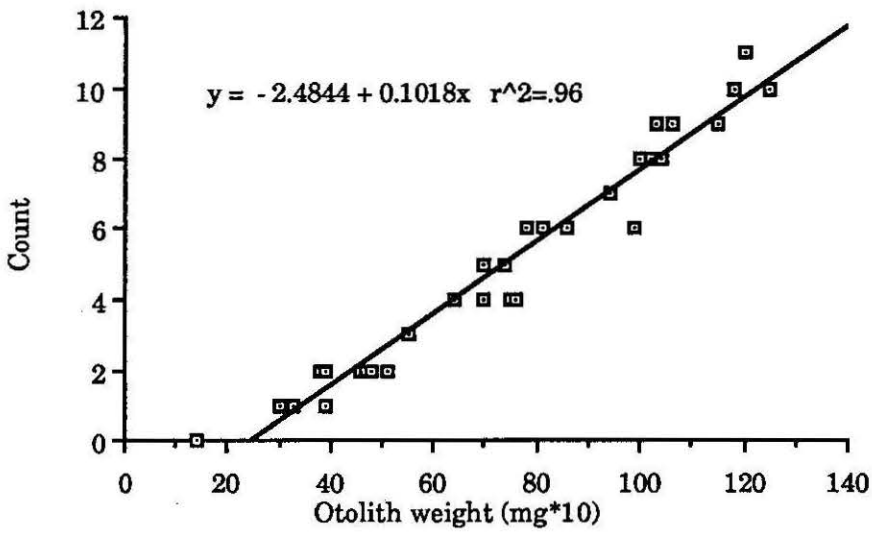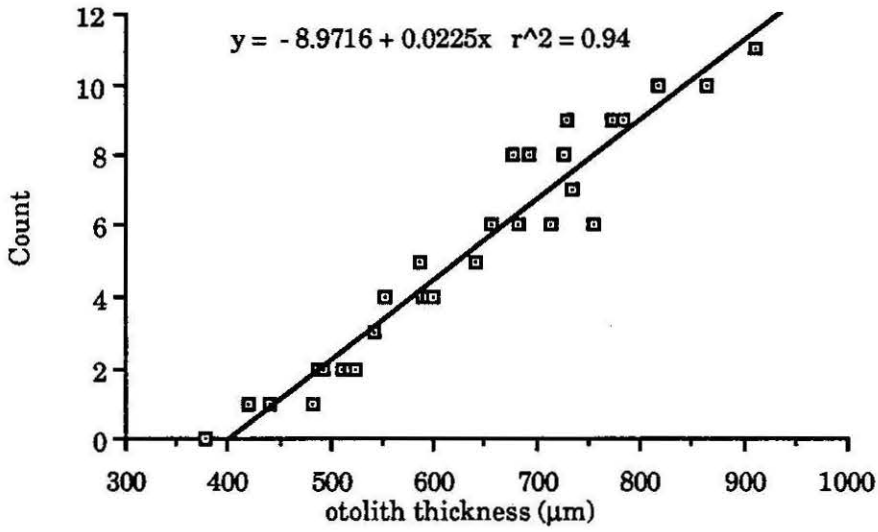
DISCUSSION

Annual Increments

The marginal increment method is an old and often-used method of validating the periodicity of increment formation (Bagenal and Tesch, 1978). Beamish and MacFarlane (1983) have pointed out that the method is often difficult to use on the older members of a population. This was the case with *Pseudochromis queenslandica*. The technique worked well for the first three age classes but older fish showed no trend in increment formation with time of year. The breakdown of the relationship for fish of four years and older is probably due to a combination of factors. The outer increments in old fish are thinner and more narrowly spaced than the earlier ones. If the outermost increment is newly formed, the distance to the prior increment is small, and/or the section is too thick, the last increment may be overlooked. Also, the numbers of fish in successive age classes decreased with increased age, making it difficult to obtain a sample of a older fish at all times of the year.

The mark placed on the otolith with tetracycline helps to substantiate the conclusions of the marginal increment study and also provides additional information. All fish injected with tetracycline that were recaptured in February had the tetracycline mark closely associated with the most recent annulus. However, the tetracycline mark in some fish from the December sample was much closer to the edge of the otolith than the outermost visible increment. That increment could have been missed for the reasons suggested above or because some fish may form the increment at different times, or not at all. This ambiguity probably could have been avoided by allowing the experiment to run for several years (Beamish and MacFarlane, 1983).

Both the marginal increment measurements and the tetracycline study show the formation of the opaque zone in the otolith to be in summer. This coincides with the period of peak growth of *P. queenslandica* (Chapter 4). Spring and summer formation of the opaque zone has been demonstrated in many other species (Bagenal and Tesch, 1978; Libby, 1985). The presence of a validated annual marker in *P. queenslandica* is something of a novelty because both Pannella (1974) and Brothers (1980) state that tropical fish may not have annual rings. Other authors working in the tropics have not found annual marks (Aldenhoven, 1986) or have assumed annual periodicity in increments based only on similarity in appearance to

annulae in temperate species (Moe, 1969; Goeden, 1978). There are apparently no other tropical studies where an annual ageing technique has been validated by marking the otoliths directly.

Microstructural information

The micro-increments seen in cross-section under transmitted light, as shown in Figure 2.3, look very much like those from any number of other species previously demonstrated to be daily (reviewed in Gjøsaeter et al., 1984). The placement of the transitional zone, thought to indicate settlement, occurs at a consistent place in the otolith. *Pseudochromis queenslandica* spawns in September and October (See Chapter 3) and could be expected to have a larval life of 20-40 days (Brothers et al., 1983). New settlers would then be expected any time from October to January but would not form an increment counted as an annulus in that summer (0^+ fish caught in February average 40 mm SL whereas 1^+ fish from the same time average 63 mm SL, see Chapter 4). The reason for not forming an annulus in the first summer of life is unknown but may be related to growth rate. The first annulus is more diffuse than subsequent ones and this may be due to more rapid growth in the first years than in later life. If this is the case, growth may be too rapid in the months after settlement for an annual mark to be visible. An approximate date for annulus formation would be December 1 (see above), leaving the latest settler at least 300 daily increments to fit in the space between settlement mark and annulus. The increments on different otoliths could be counted out different distances from the centre but none could be counted as far as the first annulus. The gaps between the annulus and the last increment, where counting could not take place, ranged from 225 to 300 μm. Using the minimum expected count from settlement to the annulus of 300 increments and the counts already in place, the predicted average increment width in those gaps ranges from 1.1 to 1.7 μm.

The number of missing bands, and therefore their width, is highly speculative. The transition in the micro-banding pattern has not been proven to indicate settlement and could be there for any number of reasons. The formation of a settlement mark is thought to be unreliable in some species (Brothers et al., 1983) and is known not to form in some others (Kingsford and Milisitch, 1987). Some authors have found that the daily increments are not formed year-round (Taubert and Tranquilli, 1982) and the rings may not be formed daily (Campana, 1984b). Therefore, length of

larval life, time of spawning, and time of formation of the annulus are only rough estimates.

If, however, all the above assumptions are sound, there may be technical reasons for not seeing further increments. The theoretical limit of resolution using a light microscope is 0.2 µm but in practice, the limit is much higher, and Campana and Neilson (1985) suggest a practical limit of 1.0 µm for light microscopy. However, some authors continue to claim greater precision (eg; Victor, 1986a). The averages of "missing" increments suggested (1.1-1.7 µm) are conservative (maximum) estimates. The increments may have been much thinner and beyond the resolution of the microscope used in this study. Campana and Neilson's (1985) 1.0 µm limit for resolving otolith microstructure with light microscopy seems to have a empirical basis, with very few studies surpassing that limit. These authors have also suggested that where micro-increments have not been found where expected, the cause may be difficulties in resolution and not the absence of increments.

One possible solution to this lack of resolution, pointed out by Campana and Neilson (1985), is to use the greater resolution afforded by SEM. However, for the few fish in this study examined using SEM, the increased resolution did not reveal many previously unresolved, fine increments. The width of the finest increments seen with SEM was 1.4 µm contrasted with the 1.6 µm increments seen with the light microscope. It did not appear that the SEM images provided any extra information beyond what could easily be seen in the light microscope. This is in contrast to the emphasis others have recently put on the usefulness of SEM (Campana and Neilson 1985). However, there are a number of reasons why smaller rings may not have been seen here. Etching time for the material used varied, but differences in the results of the differing etching times seemed very slight beyond the short time needed to expose the centre of the otolith. The longest etching period (5 min) did not seem to add any extra information. This is in contrast to Radtke (1987), who found that to see the full compliment of rings, the otolith section needed to be re-etched and re-photographed several times and that no one etching time would expose all the increments in the otolith section. The etching agent EDTA seemed to attack cracks and irregularities in the surface of the preparations more vigorously than the smooth areas. The final polish of the otolith prior to viewing was with a compound graded at 0.3 µm but this grading is a nominal grading and the largest particles on the abrasive sheet are less

than 4.0 μm and less than 4% of the abrasive particles are over 2 μm (Pers. com.: S.T. Sawai, 3M Company, St. Paul, Minnesota). Gouges and grooves up to 2-3 μm can therefore be expected to be common and it is not clear whether etching would be likely to highlight or dampen these irregularities. It makes sense that surface irregularities that are near the size of the expected increments could make the increments difficult to discern.

Growth and Weight of the Otolith as an Indicator of Age

It that there are relative changes among the growth rates of the three otolith dimensions considered here. Growth of otolith length and otolith width are isometric with fish growth whereas otolith thickness varied greatly among the largest fish. Several studies have demonstrated allometric growth in otolith thickness with other dimensions, particularly fish length (Beamish, 1979a & 1979b; Campana, 1984a; and Wilson, 1985). In all of these previous studies (except Wilson, 1985), the fish were predicted to grow to maximum length within half or less than half of the maximum life span but the otoliths were demonstrated to continue growing throughout life. While not discussing otolith thickness directly, Beamish and Chilton (1982) showed that the otoliths of mark-recapture fish had grown enough to allow ageing even though the fish had not grown appreciably while at large. This led them to state that "the otolith is a sensitive recorder of annual growth patterns even in periods of poor growth." For *Pseudochromis queenslandica* , otolith thickness is a very good predictor of age of the fish, far better than it predicts fish size.

An important result of the regular growth in the otoliths thickness is the ability to age the fish by simply weighing the otolith. The usefulness of this has been pointed out by Boehlert (1985), who used multiple regression techniques including otolith weight, otolith length and width, fish length and sex as independent variables to predict age. Radtke et al. (1985) used similar techniques for age prediction but used an index factor that included otolith weight. The single common factor and the factor that best predicts age in the many regression models so far developed has been weight of the otolith. Boehlert (1985) stated that otolith weight alone in *Sebastes diploproa* was a relatively poor predictor of age due to fluctuations in weight of otoliths at old ages. Templeman and Squires (1956) showed otolith weights could be used in assessing growth rates and also in distinguishing stocks of fish. The otolith weights within a stock appeared to be a good indicator of age, however among different stocks, a single

weight could indicate a number of different ages. Evidence that different stocks have different relationships between fish size and otolith size is not new (eg Neilson et al., 1985). Species with dispersive larvae may not show distinctive genetic stocks (Shaklee, 1984) but might be expected to grow at different rates in different habitats. Boehlert's (1985) samples ranged over 10° of latitude and may have therefore included many different stocks and habitats. Had he been able to analyze stocks separately, his ability to predict age by otolith weight alone may have been greater.

Of the many workers demonstrating allometric growth in otolith thickness (Beamish, 1979a & 1979b; Campana, 1984a; and Wilson, 1985), none compared the age of the fish with the weight of the otolith although some clearly had the information available (Beamish 1979b). The apparent regular increase in thickness in the otoliths of these fish and the diversity of groups from which they came would make their otolith weight-age relationships worth investigating. Radtke (1987, Table 1, p. 22) presents data on weight and age of otoliths that supports the suggestion that the otolith weights might be used for age determination. The regression of age on otolith weight from Radtke (1987) was: [Age(days)=-157.4+4.71*otolith weight(mg), $F_{(1,9)}=8.06$, $p \le 0.01$, $r^2=0.91$].

Back-calculation

The methods for back-calculation of size-at-age have been well discussed (Ricker, 1969; Bagenal and Tesch, 1978; Carlander, 1981). The relationship between fish size and otolith size is used to calculate the size of the fish from the successive annuli on the otolith (or other bony structure). Details of the calculation vary, but one common procedure used is to employ a correction factor when an individual fish's otolith size and body size do not exactly fit the derived relationship for that population. An example of how back-calculations are normally made with linear data is given in Figure 2.15. For example, without correction, a fish with an otolith larger than "normal" (Fish A, Figure 2.15) could easily have a back-calculated size at the most recent annulus that is greater than the actual size at which the fish was captured. When adjusting the calculation for an individual fish, the correction is applied to all measurements taken off the otolith (line A1 defines the fish-otolith relationship for Fish A in Figure 2.15). This means that the proportion that the fish deviates from the population line is assumed to be the same over the fishes' life. This has the effect that fish with otoliths larger than that predicted by the population relationship have their calculated sizes adjusted downwards. Similarly, fish with otoliths

Figure 2.15. Graphical demonstration of two different methods of back-calculating size at age from otoliths. Length at age using method one is given by the following equation:

$$L_i = a + \frac{L_c - a}{O_c} O_i$$

where a is the intercept of fish size of the population regression, L_c is the fish length at capture, O_c is the otolith size at capture and O_i is the otolith size at increment i. Using this equation, length at age will be taken off the two lines marked 1 for Fish A and Fish B. the second common way of back-calculating size at age assumnes that the existing relationship $\frac{O_c}{L_c}$ has been ths same throughout the life of the fish. Therefore, the back-calculated measurements will come off a straight line from the origin to $\frac{O_c}{L_c}$ (marked 2 for Fish A and Fish B).

population regression

Fish B

Fish A

B1

A1

O_c

O_i

0

Otolith size

L_c

$L_i B$

$L_i A$

a

Fish size
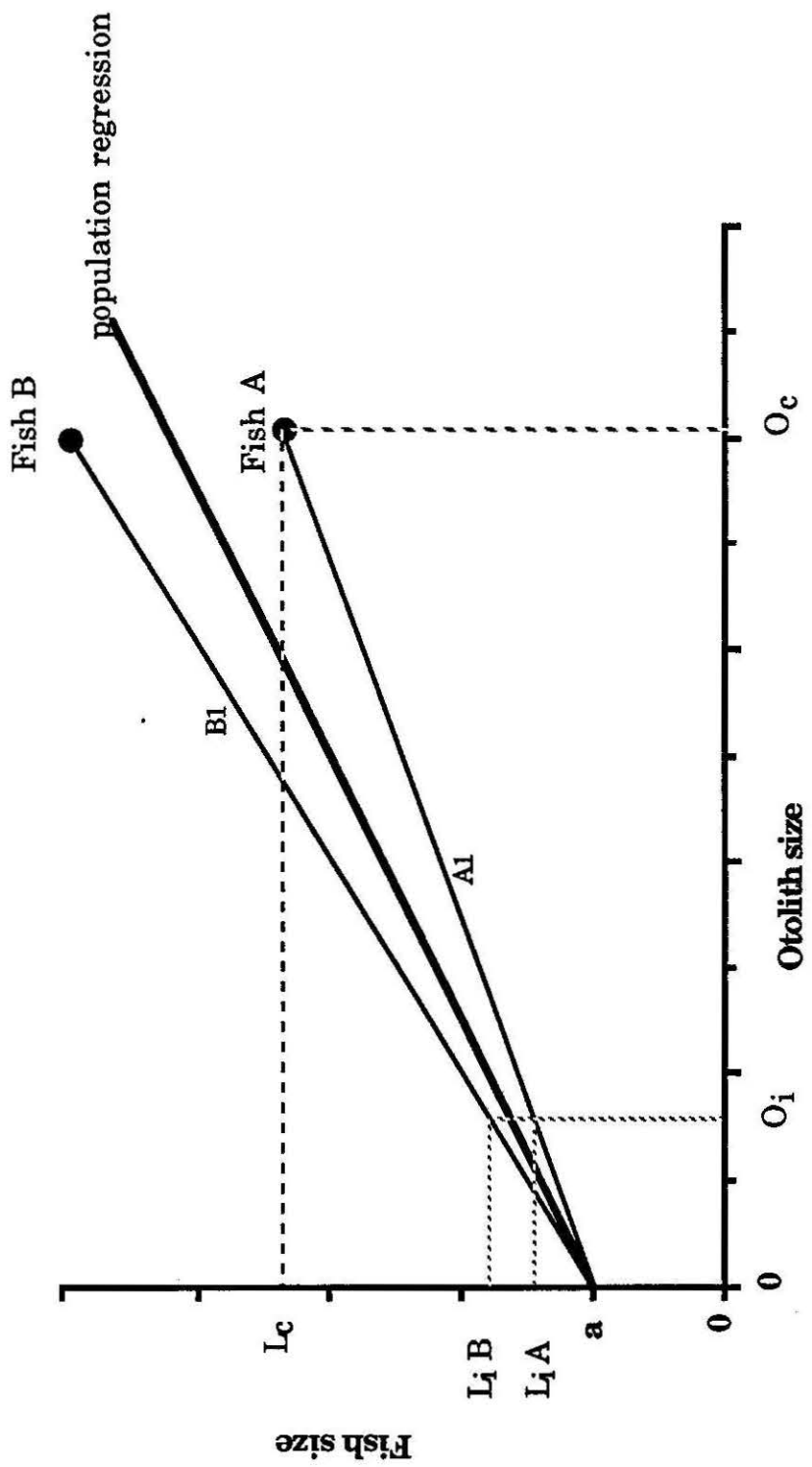
smaller than predicted would have their back-calculated sizes adjusted upwards [compare the back-calculated sizes at the same increment size (L_{iA} and L_{iB}) for Fish A and Fish B in Figure 2.15].

Lee's phenomenon, where the sizes back-calculated from older fish are smaller than the sizes calculated from younger fish, is well discussed and documented (Bruyzghin, 1963; Ricker, 1969 for examples and discussion). The usual explanation of Lee's phenomenon has been size-selective mortality. The survivors of each cohort subject to mortality that increases with the size of the animal will tend to be the smaller individuals. Over time, assuming growth rates maintain the size differences, the survivors will have been drawn from further and further down the original size distribution. However, biased sampling and improper back-calculation (Carlander, 1981) are also known to cause this phenomenon. For instance, a sample could miss some members of the youngest cohorts, and only capture the largest and most active of those cohorts. When those cohorts are sampled again, after full recruitment, the back-calculated size at the early ages should have gone down compared to the previous estimate (an example in Beacham, 1981).

It is apparent from the present study that there is another possible cause of Lee's phenomenon- allometric growth of the otolith in older fish. Fish length-otolith length regressions are commonly done using unequal numbers of fish from all size and age categories. It is also common for the variance in otolith size with respect to fish size to increase at large fish sizes (Ricker, 1969). If the data also depart from linearity at large body sizes and mainly in the direction of increased otolith dimension (in the direction of fish 1 as opposed to fish 2, in Figure 2.15) then a straight line could still give a good overall fit. The bulk of the data in most studies will be from smaller size classes and will provide a linear fit and minimize the effect of the deviation from linearity at large body sizes. Consider a fish such as *P. queenslandica*, with a strong correlation between the otolith dimension and the age of the fish. The fish that have deviated from the population regression at the large sizes will be some of the oldest fish. When back-calculation of size at age of these fish is done, the older fish (with thicker otoliths) will tend to have their back-calculated sizes reduced when corrected to the "normal" relationship. The ultimate effect of this will be Lee's phenomenon, the predominance of which will be dependent on the strength of the relationship between the age of the fish and the dimension of the otolith and also on the variance of the data around the

relationship used for back-calculation. The size of the otolith, whichever dimensions is used, will always be correlated with the age of the fish and if the variance around the regression line used for back-calculation changes shape in the way suggested, then the possibility for Lee's phenomenon exists.

The suitability of the model used in back-calculation could be assessed using residual analysis but this has rarely been done (Framstad et al, 1985). Even when the regression used is the most appropriate available, if the fish length-otolith length relationship is asymptotic and/or if r^2 is not large, then its value in predicting large fish sizes from otoliths is questionable.

Summary

The ability to detect annual markings in small, tropical reef fish such as *P. queenslandica* is important for several reasons. Annual ageing of tropical fish has long thought to be difficult or not possible (Pannella, 1974; Brothers, 1980) but this study has shown that such ageing is indeed possible. It may be that the pessimism of Pannella (op cit) and Brothers (op cit) has inhibited some inquiry for the techniques used here are standard in ageing studies in temperate fisheries and have long been available. Further, most ecological research on coral reef fish has been done using small, relatively sedentary species due to ease of collecting information (Sale, 1980) and annual ageing in such small reef fish has been difficult (Aldenhoven, 1986). Age determination in a small fish such as *P. queenslandica* suggests that the size of the fish may not be a problem when ageing reef fish, an area of ecological studies where information is much needed.

Allometric growth of otolith thickness relative to fish growth has appeared in a diverse group of fish, including the small coral reef fish in this study. This type of growth can cause difficulties when back-calculating size at age. Growth in otolith thickness appears to be very regular through time and it may be this fact that allows fish to be aged simply by weighing their otoliths. In studies where otolith weight has been examined as an indicator of fish age, it has been found to be a good predictor, suggesting that this technique could might be more widely applicable.

CHAPTER THREE

REPRODUCTIVE BIOLOGY OF *P. QUEENSLANDICA*

INTRODUCTION

Hermaphroditism is widely distributed throughout the animal kingdom (Ghiselin 1969, Hoagland, 1975, Policanski 1982). It appears in some form in most phyla but in the vertebrates is known only in fish. Theoretical treatments of the evolution of hermaphroditism have been fairly recent (Thomlinson 1966, Ghiselin 1969, Warner 1975a, Warner, Robertson and Leigh 1975a&b, Charnov 1979, Charnov 1982). All authors have made a clear distinction between two types of hermaphroditism- simultaneous and sequential. Simultaneous hermaphrodites function as both sexes at the same time, while sequential hermaphrodites mature first in one sex and then change sometime later to the other. Protandry is sequential hermaphroditism where individuals are first male and then become female and protogyny is the reverse.

Ghiselin (1969) outlined theories relating to both types of hermaphroditism. Simultaneous hermaphroditism ought to be advantageous (ie. selected for) when animals are in low density, allowing every conspecific encounter to be a potential mating. For sequential hermaphroditism, Ghiselin put forward the Size Advantage model. The idea behind the Size Advantage model is that if the changes in an animal's reproductive success with size are different between the sexes, then an animal that could spend its early reproductive life in the sex that suffers least from being small and then change to the sex that benefits most from being large, would be at a reproductive advantage over dioecious individuals.

The Size Advantage model has been expressed in a number of forms (Warner, 1975a&b; Warner, Robertson and Leigh, 1975a; Charnov, 1979; 1982). These workers and others have successfully applied the model to a wide variety of taxa including reef fish (Warner and Hoffman, 1980), prawns (Charnov, 1979) and an herbaceous plant (Policansky, 1981; Bierzychudek, 1984). Ghiselin's (1969) original treatment of the Size Advantage model refers only to size. However later elaborations of the model have made two important points: firstly, that age or experience could equally substitute for size in the model (Warner 1975a) and secondly,

that the model is best applied to discrete populations (Warner and Hoffman 1980) and that it is relative size within those populations rather than absolute size that is important (but see Shapiro and Lubbock (1980) for an alternate view).

Shapiro (1984) has argued that because there is ample evidence that sex change takes place at a wide variety of sizes within a species, size can not be the controlling factor, suggesting instead that local sex ratio is the controlling factor. However, Charnov (1982) argued that the wide range of sizes can make sense under the Size Advantage model if local population conditions are taken into account.

Coral reef fishes are particularly useful for examining the proximal mechanisms controlling sex and sex change and also for the study of the evolution of hermaphroditism in general. The various types of hermaphroditism are all common in fish, and the family Serranidae is interesting because all forms of hermaphroditism are exhibited within the family, making the group ideal for examining the different models proposed to account for hermaphroditism. This requires more work on little known groups such as the Pseudochromoids. The only work published on reproductive biology within the family was on *Anisochromis straussi* which was a protogynous hermaphrodite (Springer et al,1976).

This chapter describes the patterns of sexuality in *Pseudochromis queenslandica* and attempts to define the proximate mechanisms controlling the change of sex. In particular, I set out to examine the effects of local sex ratio on sex change patterns, specifically by:

1) describing the form of hermaphroditism in *P. queenslandica* .

2) examining colour dimorphism and the relationship between colour and sex, colour change and sex change.

3) determining the size and age specific patterns in the colour/sex ratios and the schedule of sex change.

4) using an experimental manipulation of sex/ colour ratios to examine potential effect of this on sex change.

MATERIALS AND METHODS

Sampling of *P. queenslandica*

Fish discussed in this section were all captured by trapping and/or spearing. To examine the gonadal state of *P. queenslandica* , five different destructive samples were taken. Histological preparations were examined from June and September 1984 (26 and 30 fish, respectively), July and October 1985 (36 and 19 fish) and February 1986 (37 fish). The samples from September 1984 and February 1986 were complete collections from isolated patch reefs, other destructive samples taken for histological analysis were haphazard collections of fish and may not be representative of all size classes. Only complete collections from isolated patch reefs were used for comparison of sex ratios and/or age and size structures.

Preparation and Classification of Histological Samples

Gonads for reproductive samples were dissected from the freshly killed fish and fixed in Bouin's solution. The fixed samples were transferred into 70% ethanol for storage. For thin sectioning, the samples were dehydrated and embedded in paraffin. Whenever possible, both lobes of the gonad were embedded side by side so that both were present on the same slide. Sections were made to approximately 10 μm and each gonad was sectioned serially in three separate locations within the gonad; proximal, medial and distal. Each slide contained approximately 20 serial sections of each lobe, and there were three slides per fish, giving a good range of coverage of the entire gonad. The slides were stained with haematoxylin and eosin and viewed with a compound microscope at magnifications from 100x to 400x.

The classification of histological specimens was based on the schemes used by Smith (1965) and Moe (1969). For my purposes an abbreviated number of categories was enough to describe the important differences in *Pseudochromis queenslandica*. As in Smith (1965), a gonad was classed as male if there were any signs of spermatogenesis seen in the serial sections. Animals showing signs of male tissue were further classified into active and inactive classes. Fish classed as active males had spermatids or tailed sperm visible in the sections (Figure 3.1a). Females were classed in three categories, the first two being non-reproductive (Moe, 1969). The classes used are based on oocyte development as outlined in Smith (1965) and Moe (1969). Class one indicates the presence of only stage I oocytes in the ovary (Figure 3.1c). In *P. queenslandica* stage I

Figure 3.1a. Histology of an active male. Note spermatids or tailed sperm (s) and stage I oocytes (o) around perimeter of testis.

Figure 3.1b. Histology of an inactive male. Spermatogenisis is taking place (s) but there are no spermatids or tailed sperm.

oocytes are no larger than 9 μm, stain very basophilically and have a reduced proportion of the cell devoted to the nucleus relative to other oocyte stages. Class two fish had both Stage I and Stage II oocytes present (Figure 3.1d). Stage II oocytes, often referred to as Resting Stage (Moe 1969), are about 15 μm in diameter with a much expanded nucleus relative to Stage I. Class three includes all further stages of development of the oocytes (Figure 3.1e). All these further stages involve yolk deposition in the oocytes and in *Pseudochromis queenslandica*, tended to occur simultaneously throughout the gonad. Only class three fish were considered to be capable of reproductive activity (Moe, 1969).

Analysis

All frequency distributions were compared using the Kolmogorov-Smirnov test (Siegel, 1956). The probabilities of sex ratios were derived using the binomial probability distribution and deviations from expected values within samples were tested using the chi-squared distribution. Chi-squared values were derived from the individual probabilities (p_i) using the formula:

$$X^2 = -2 \sum_{i=0}^{n_i} \log_e \text{ with 2n df.}$$

Growth information was compared using the method of McCuaig and Green (1983) where the slopes of Ford-Walford plots of length at recapture against starting length are compared using analysis of covariance.

Experimental manipulation of colour ratios.

In July 1985, 56 fish on four patch reefs were classified according to their colour, marked with fin clips and returned to the point where captured. On two other reefs all grey and transitional coloured fish were removed and 13 remaining red fish were marked and returned. Three more reefs had the reverse treatment- all red and transitional fish were removed leaving 14 marked grey fish behind. In February 1986 all fish on the reefs were captured and preserved for histological analysis of their gonads.

Figure 3.1 c. Histology of class one females. Note predominance of Stage I oocytes. Stage I oocytes are approximately 9 μm in diameter.

Figure 3.1 d. Histology of class two female. Stage I and II oocytes seen,but Stage II predominates. Stage II oocytes are approximately 15 μm in diameter.
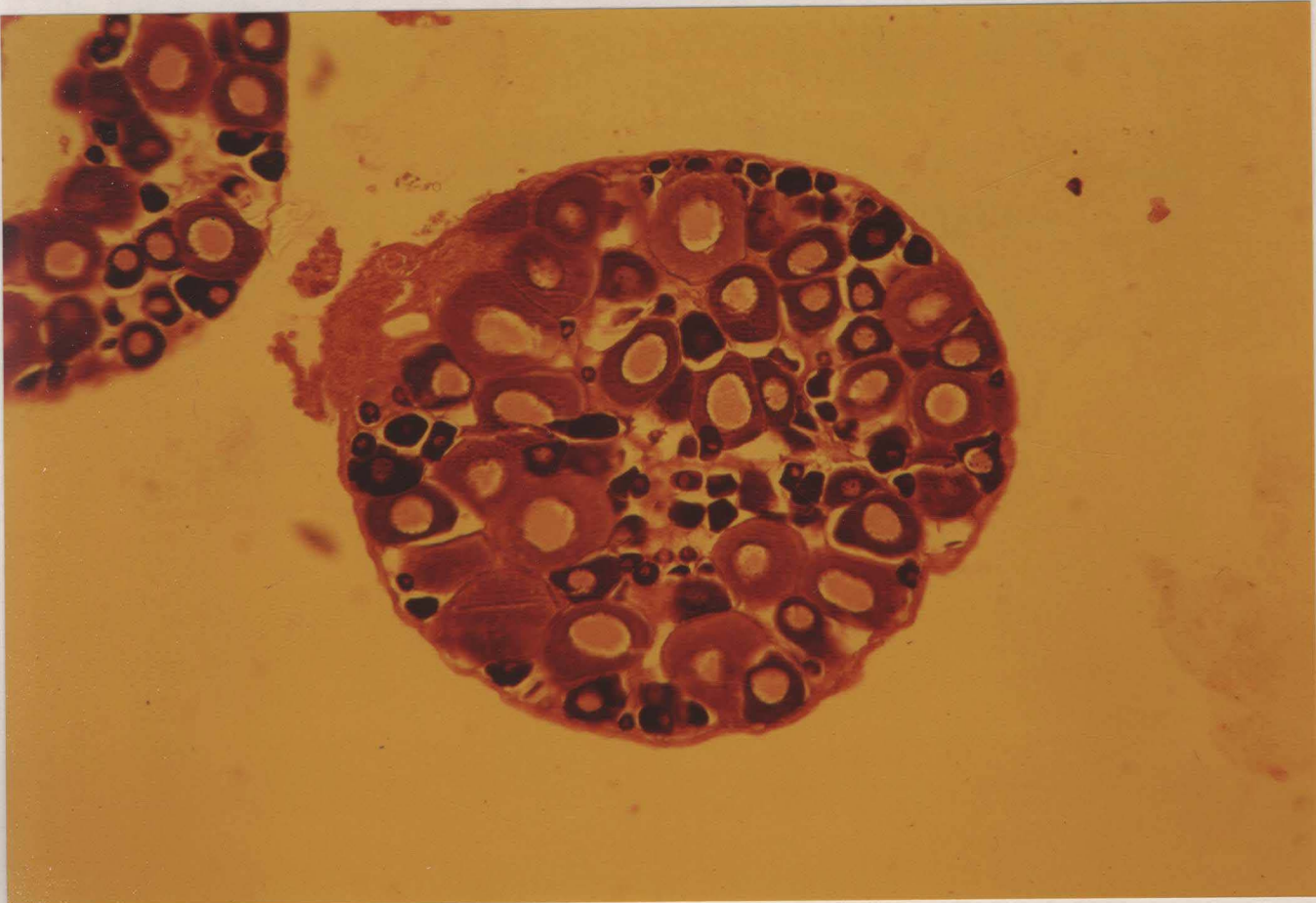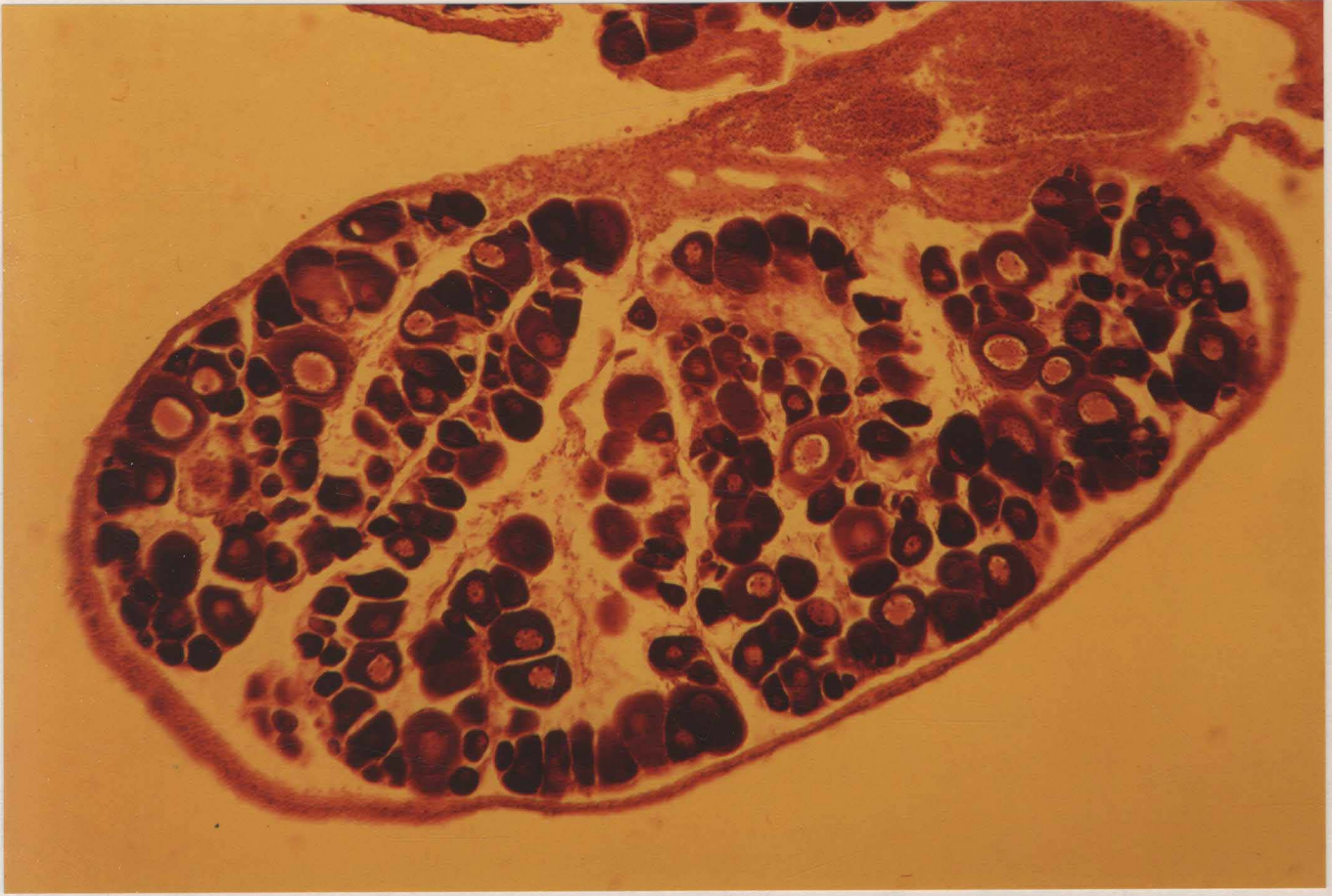
Figure 3.1 e. Histology of class three female. Note yolk build-up in many large oocytes (approximate diameter 40 μm).

RESULTS

Colour Dimorphism

Populations of *Pseudochromis queenslandica* shows distinct colour polymorphism at all times, with two patterns predominating and a third, intermediate pattern fairly common. The two main colour phases of *P. queenslandica* are virtually the reverse of each other from head to tail (Figures 3.2a and 3.2b). The fish I will refer to as red (Figure 3.2a) are red coloured about the head, a drab olive colour from about mid-body until the caudal fin, which is partially yellow. The anal fin on red fish is the drab olive colour but is edged with bright blue. The fish I will refer to as grey are a slightly darker olive grey colour about the head. This grey colour starts to change by mid body to become a fairly bright red posteriorly (Figure 3.2b). The posterior red colour may partially cover the anal fin, which, as in the red fish, is also lined with blue. The caudal fin in the grey fish is similar to that of the red fish with varying amounts of a bright yellow colour. The third colour pattern was found in all samples and is termed transitional because it is very much a dull combination of the two patterns described above. Transitional fish are a lighter shade of olive grey, with faint red colour showing all over the body and with the yellow on the caudal fin much reduced in intensity.

These colour patterns do not appear to change from day to day. The capture and marking of fish on a particular patch reef would often take several weeks, and, fish that were first captured were frequently seen when that reef was revisited, and individual fish became quite familiar. At no time during the trapping out of any patch reef were any fish seen to change colour over the several weeks trapping. The general amount of a colour change is also indicated in Table 1. After a seven to eight month period, between 11% and 23% of the fish had changed colour.

Table 1: Record of colour changes in three populations of free-ranging fish which were marked.

DATE MARKED	NO. FISH MARKED	MONTHS AT LARGE	NO. FISH RECAPTURED	COLOUR CHANGES
2/84	27	7	19	2
9/84	20	8	17	4
7/85	55	7	45	7

Figure 3.2. (a - above) Red fish in typical colouration. (b - below) Grey fish.

Figure 3.3. Proportion of females with class three histology (active) in five different samples. Details of numbers of fish are available in Appendix one (p.97).
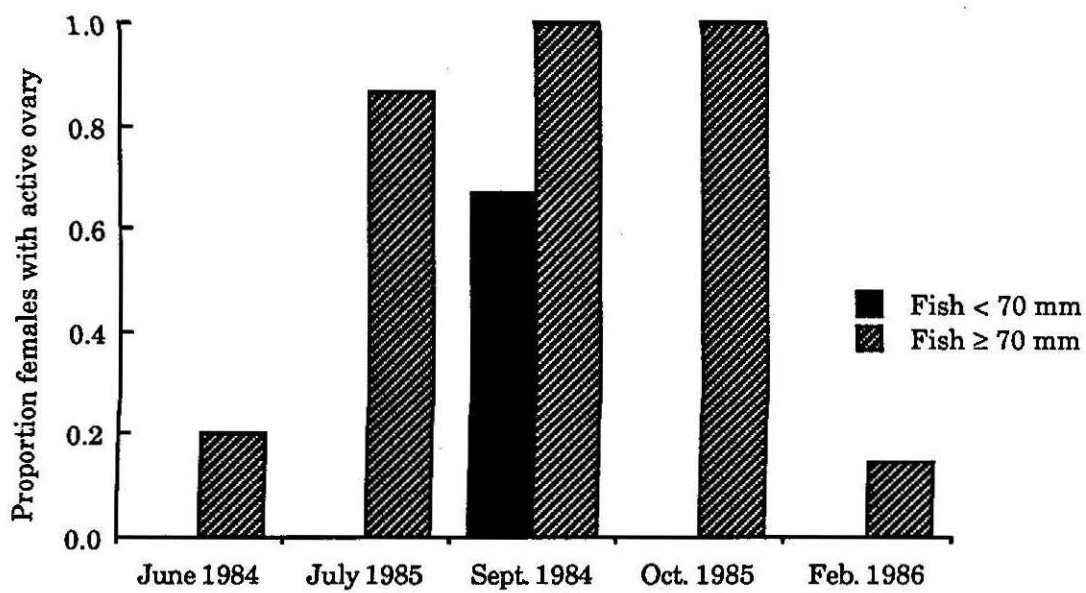
Individuals are obviously capable of changing colour. In the course of mark-recapture manipulations, some colour change in marked, but otherwise unmanipulated, fish was noted. As seen in Table 1, six fish changed colour in the mark-recapture manipulations between Feb. 1984 and May 1985 (the fish from July 1985 will be discussed later, in the context of the manipulation of which they were a part). Two transitional coloured fish (73 & 65 mm starting size) became grey, two red fish (65 & 58 mm) became grey and two grey fish (70 &73 mm) became red.

Relationship between Colour and Reproductive State

The colour of fish greater than 70 mm SL gave good indication of their sex (Table 2). Of the 45 red fish ≥ 70 mm SL histologically examined, only one showed no sign of male tissue. Similarly, of 52 grey fish ≥ 70 mm SL examined, only four showed some signs of male tissue. The sexual state of the smaller fish is less well defined by colour. Small red fish were 80% male but half of the small grey fish showed signs of male tissue. The numbers of transitionally coloured fish examined was small and there was no clear trend in their sexual state.

The state of development of oocytes in females showed a pronounced seasonal pattern (Figure 3.3). In samples from July, September and October, over 80% of the females ≥ 70 mm SL had yolked-up oocytes and half of the gonads of small females sampled in that period were similarly developed. Males did not show any detectable seasonal cycle in gonadal state and were apparently always capable of spawning. Two of nine transitional coloured fish classed as males were active and all others inactive. A complete breakdown of sexual state and colour for each of the five samples summarized above is available in Appendix 1.

Table 2: Relationships among size, colour and sex of *P. queenslandica*

Colour	Size(mm)	Female	Male
Grey	<70	8	8
	≥70	48	4
Trans	<70	1	5
	≥70	3	4
Red	<70	4	16
	≥70	1	44

Figure 3.4. Size distribution split by the colour of the fish from two samples taken in the reproductive season (July 1985 and Sept. 1984). The numbers in brackets above some size categories represent the number of transitional coloured fish in that size class. Please note the difference in scale between the two distributions.
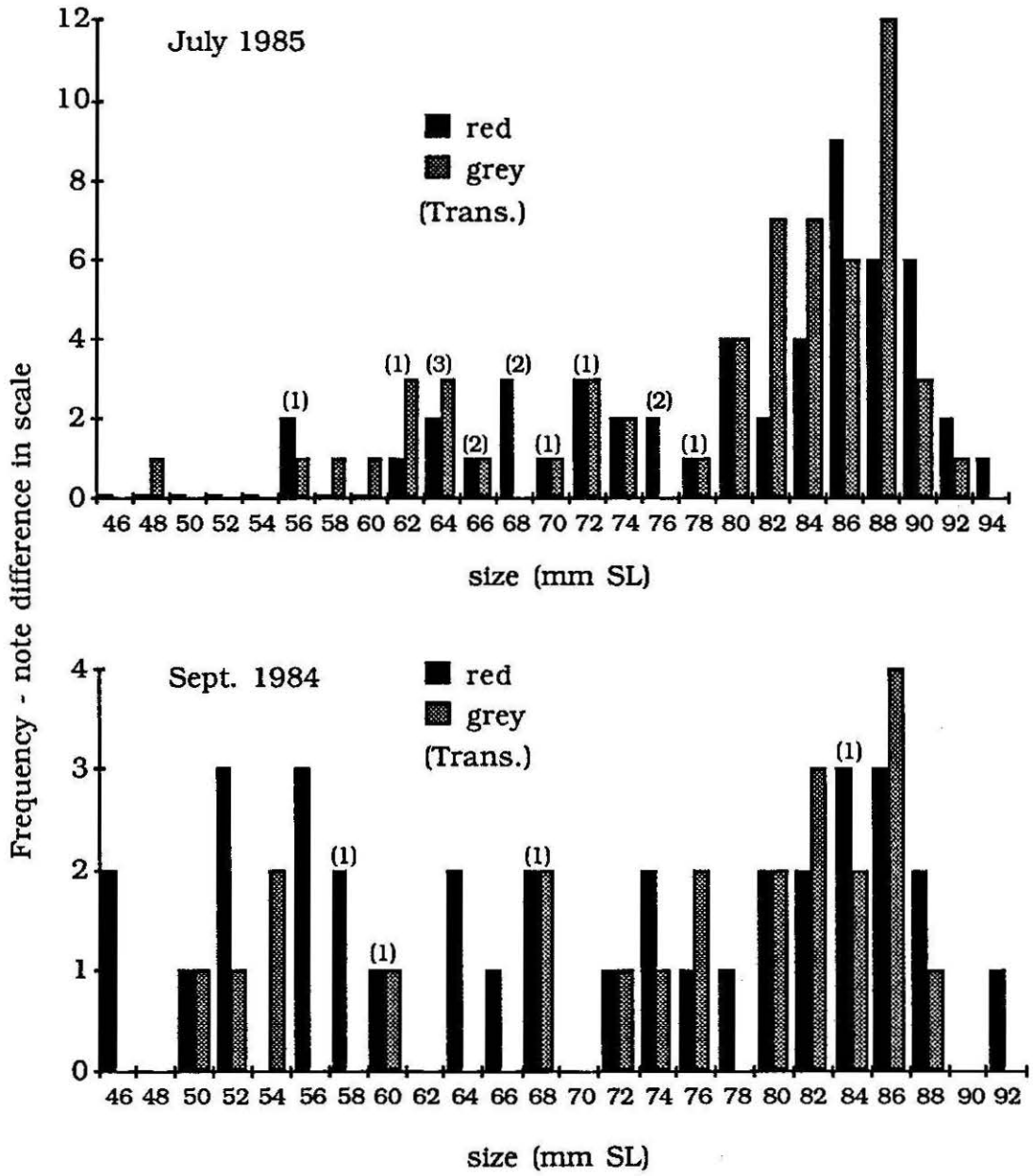
Gonad Structure

In general, the structural layout of the *Pseudochromis queenslandica* gonad (Figure 3.1a-e) is similar to that described for a generalized protogynous hermaphroditic serranid by Smith (1965). The gonad is a bi-lobed sac attached dorsally to the body cavity wall with a connecting mesentery. This dorsal mesentery is the location of the main vascular supply to the gonad. The wall of the body of the gonad is a thin layer of smooth muscle. Inside this muscular tunic lies the germinal epithelium, much folded, giving a lobed appearance. Spermatogenesis takes place in crypts of cells similar to those described in Smith (1965) and Moe (1969). (See Figure 3.1a-b). When the total amount of spermatogenic tissue is low, it is invariably clustered around the dorsal mesentery (Figure 3.1a-b) and as the amount of spermatogenic tissue in the section increases, it does so radially away from the dorsal area. In all animals where sperm was present (ie. active males), at least 15% of the gonad was devoted to spermatogenesis. In no fish where spermatogenesis was taking place, are oocytes beyond stage II seen, and even Stage II oocytes occurred in less than 5% of sections showing any male tissue. However,all cross sections, even those of the largest testis, showed oocyte remnants (Figure 3.1b). Atretic or yellow bodies, an often-used sign of degenerating oocytes, (references in Sadovy and Shapiro, 1987) are not seen in any section. The lumen of the gonad appeared to be involved in gamete transport in both sexes.

Sex/Colour ratios on Patch Reefs

Sex ratios of *P. queenslandica* on patch reefs, as determined by histological examination of gonads, were not significantly different from 1:1 (Table 3a). This sample was taken during the reproductive season (Figure 3.3) and is likely to be the best estimate of the potential sex ratio on those patch reefs. Other patch reef clearances in reproductive season could not be examined histologically but the ratio of red to grey fish, particularly those $\geq$ 70 mm SL, should mirror the sex ratio (see Table 2). Neither the three reefs cleared in September 1984 nor the five reefs cleared in July 1985 showed any significant differences from a 1:1 colour ratio (Table 3b,3c).

Table 3 Sex ratio based on patch reef clearances. X^2 tests: H_0=ratios differ from 1:1.

3a. Ratios based on histology and colour of fish cleared from seven reefs in September 1984 Numbers indicate total active males:total active females, and, in brackets, total red fish:total grey fish, from each reef.

Reef	All Fish male:female (red:grey)	≥ 70 mm male:female (red:grey)
N21	4:2 (4:3)	0:0 (0:0)
N19	2:1 (2:1)	1:1 (1:1)
N20	4:5 (6:5)	3:5 (3:5)
N25	1:0 (2:0)	1:0 (1:0)
N23	1:1 (2:1)	1:1 (1:1)
N22	1:1 (2:1)	1:1 (1:1)
N24	1:0 (1:1)	1:0 (1:0)
Total:	14:10 (19:12)	8:8 (8:8)
X^2=(sex)	6.82 n.s. 10 df, p>0.1	6.23 n.s. 8 df, p>0.1

3b. Number of fish (total red:total grey) cleared from three patch reefs in September 1984

Reef	All Fish red:grey	≥ 70 mm red:grey
N13	7:3	4:3
N14	3:2	2:2
N9	7:4	4:3
Total:	17:9	10:8
X^2=	6.54 n.s. 6 df, p>0.1	3.58 n.s. 6 df, p>0.1

3c. Number of fish (total red:total grey) cleared from five patch reefs in July, 1985.

Reef	All Fish red:grey	≥ 70 mm red:grey
S8	5:4	5:3
S7	5:7	3:5
S10	8:14	6:12
N31	5:5	5:4
N30	9:9	9:9
Total:	32:39	28:33
$X^2 =$	9.59 n.s.	11.13 n.s.
	10 df, p>0.1	10 df, p>0.1

Size Distribution and Colour

The distributions of fish sizes among the three colour phases of *P. queenslandica* during the reproductive season are shown in Figure 3.4. Both the September 1984 and the July 1985 size distributions were generated from complete clearances of patch reefs. The size distributions of red and grey fish in either sample do not differ from each other at the 0.25 probability level using the Kolmogorov-Smirnov test. The majority of transitional-coloured fish were in the lower 25% (less than 75 mm SL) of the size range but did occur all but the largest size classes, suggesting colour change may occur at a range of sizes.

Age structure

The age structures of the red and grey fish from the February 1986 sample were not significantly different (p> 0.25) using the Kolmogorov-Smirnov test (Figure 3.5). Transitional-coloured fish were found as young as one year old and as old as nine years, spanning most of the recorded life-span, suggesting that colour change can occur at most ages.

Growth

Growth of red fish was significantly greater than that of grey fish over the period from July 1985 to February 1986 [ANCOVA: $F_{1,31} = 4.44$, $p < 0.05$ (slopes)]. When the more variable growth from the transitional fish (those that were transitional-coloured at marking, or at recapture and also those that changed colour over the period) was included in the analysis, the result was non-significant [$F_{2,39} = 0.746$, ns. (slopes)].

Figure 3.5. Age structure of the red, grey and transitional coloured fish from the February 1986 sample.
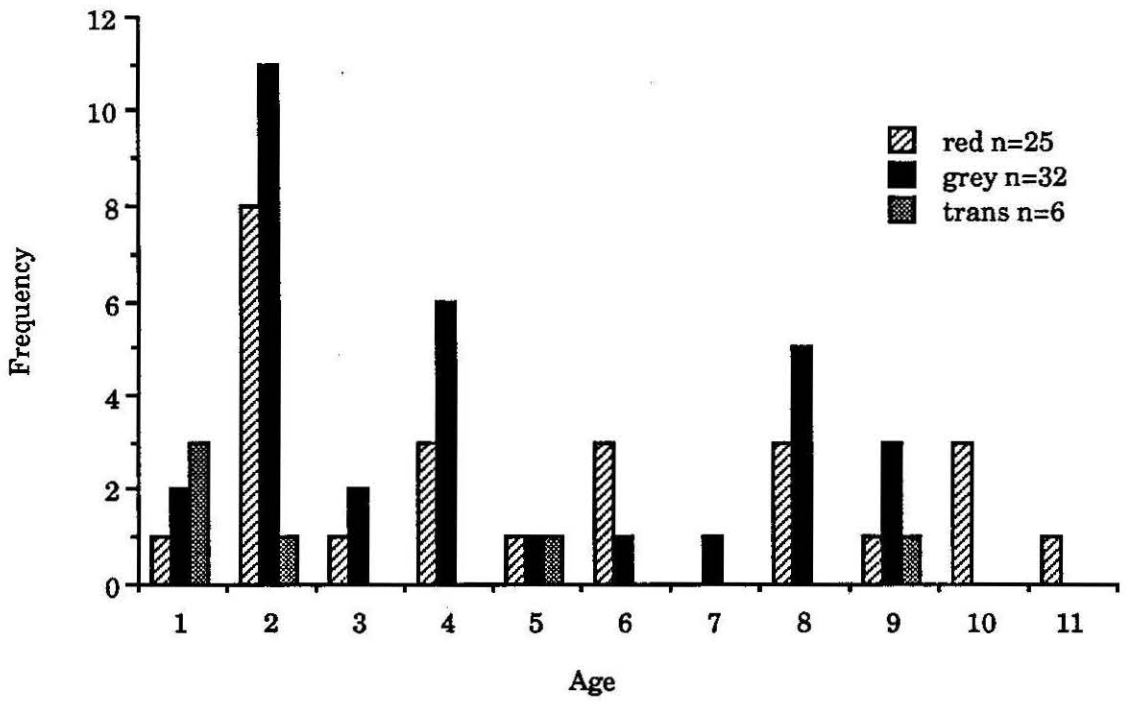
Behavioural Observations

Although the secretive nature of *Pseudochromis queenslandica* prevented detailed behavioural observations, many hours were spent catching and marking the fish and some information was collected in a haphazard way. Three reproductive seasons were covered in this study, with at least three weeks during each season spent in the field working on some aspect of the study. In that time only five nests of *P. queenslandica* were found. In all cases a red individual was guarding a small hole or cave in the reef rock. The defending *P. queenslandica* actively drove most species away from a distance of about 30 cm surrounding the opening to the nest site. Several hours were spent watching these five nests, and during this time the fish did not venture beyond this 30 cm area. The eggs could not be seen without some rearrangement of the nest site, but when this was done a globular egg mass of approximately 10 cm^3 was observed.

During September 1984, I found three pairs of fish engaged in active display and what would appear to have been courtship (cf. Thresher, 1983). These six fish were marked individuals on study reefs. After the initial sighting, each of the reefs where the fish lived were visited daily or every second day for between one and three weeks in each case. The fish that were originally seen together were always in close proximity and maintained their courtship on a sporadic basis. All other *P. queenslandica* were met with aggression or were ignored and courtship was only seen in the original pair. The grey fish in these associations were gravid (easily seen) but no evidence of spawning was seen and the females remained distended with eggs for the entire time. All six fish were over 80 mm SL and the greatest size difference within any pair was 3 mm. In two of the three pairs the red fish was the larger of the pair.

Colour Change Manipulation

P. queenslandica showed a proportionately higher number of colour changes on those reefs where one sex had been removed, compared with those fish living with unaltered ratios (Table 4). Three of the 18 red fish on control reefs changed colour over the course of the experiment compared with four of the eight red fish recaptured from reefs where grey and transitional fish had been removed. Grey fish showed fewer colour changes than red fish with none of the 18 grey fish from the control reefs, and only one of the seven grey fish from the experimental reefs changing

colour. All but one of the seven transitional-coloured fish from the control reefs changed colour, and all but one of these became grey.

Most of the colour changes seen in both the experimental and control treatments were fish becoming grey. One transitional-coloured fish became red and one of the grey fish where red fish had ben removed became red. Among the seven grey fish not recaptured from the reefs where red fish were removed, one 62 mm individual was seen in October to have changed colour to red, but could not be recaptured in February.

Table 4. The number of fish by colour, marked and recaptured from manipulations in which either all grey and transitional fish, or all red and transitional fish, were removed from patch reefs. Fish on control patch reefs were marked and returned only. Fish were marked in July 1985 and recaptured in February 1986.

MARKED FISH			RECAPTURED FISH			
			red	grey	trans	total
Controls						
	red	24	18	2	1	21
	grey	25	0	18	0	18
	trans	7	1	5	1	7
Grey and trans. removed						
	red	13	4	3	1	8
Red and trans. removed						
	grey	14	1	6	0	7

The *P. queenslandica* that changed colour ranged in age from one to four years and were from 55 to 84 mm SL when first captured in July 1985 (Table 5). Histologically, both of the fish that changed to become red were active males. All of the fish changing in the red-to-grey direction were reproductively inactive, but females are not expected to be active in February (Figure 3.3). Three of the colour-changed grey fish showed signs of male tissue, but none were active. There was no way to determine if any of the fish that changed to grey had spawned as females.

Table 5. Size and age of colour changers from Table 4. na.=not available.

Colour	Age	Size	Histology at Collection
	control		
R to G	2yr	66 mm	stage I female
"	4	81	inactive male
R to T	na.	72	inactive male
T to G	1	55	stage I female
"	na.	67	na.
"	2	69	stage I female
"	2	65	stage I female
"	2	67	inactive male
T to R	3	72	active male
	experimental		
R to G	2yr	73 mm	na.
"	3	84	stage II female
"	na.	83	stage II female
R to T	1	57	stage I female
G to R	2	73	active male

DISCUSSION

Sex and Colour

Pseudochromis queenslandica exhibits stable colour dimorphism on a time scale of months but individuals can clearly change from one colour morph to another. The two main colour phases are accompanied by a third, intermediate colour that mark-recapture manipulations indicate is a true transitional colour phase. In other words, fish found in the intermediate colour phase can be expected to adopt red or, more likely, grey coloration within a few months. Sadovy and Shapiro (1987) list colour change in sexually dichromatic fish as strong indirect evidence for sex change. The incidence of transitionally coloured fish of approximately 10% in both samples is somewhat higher than in other dichromatic fish where transitional phases have been reported. Choat and Robertson (1975) reported ranges of 2-6% in several species of scarid and Jones (1980a) found 2-3% transitional phase fish in populations of a temperate wrasse. One transitional-coloured fish remained that colour for the seven months that it was observed. A slow rate of sex change could explain a high incidence of fish with intermediate colour (Sadovy and Shapiro, 1987).

The colour of an individual *P. queenslandica* is a very good indicator of its sex. Red fish over 70 mm were nearly always active males (98%) and grey fish in that size class were predominantly active females in the reproductive season (87%). Outside the reproductive season, when all female gonads are inactive, it was impossible to histologically distinguish females of different sizes. Small fish at any time of the year were mostly inactive and 50% of the small grey fish showed signs of inactive male tissue. It is not uncommon in other species for juvenile or inactive fish to take on a general histology, often showing indefinite signs of both sexes (Zohar & Gordin, 1978; Moyer and Nakazono, 1978). Also, many fish show inactive tissue of the opposite sex that is functionally meaningless (Atz, 1964; Moyer and Nakazono, 1978).

Gonad Structure

In many instances the layout of the gonad and its gamete transport system changes when the animal changes sex (Smith, 1965; Moe, 1969; Warner, 1975b; Moore, 1979 and Jones, 1980a). However, the structure of the *P. queenslandica* gonad gave no indication of prior reproductive history. If some proportion of females had previously reproduced as males there was no sign of it in the histology of the gonad. This is not unusual as evidence of protandry in other species has been difficult to detect histologically (Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Sadovy and Shapiro, 1987). Sadovy and Shapiro (1987) suggest that gonad configuration is likely to be of less use in the diagnosis of protandrous as opposed to protogynous sex change (but see Moore 1979).

All males showed some sign of female tissue, predominantly around the periphery of the gonad. This is similar to the structure shown in the protandrous *Amphiprion* (Moyer and Nakazono, 1978). The sex of the undifferentiated germ cells in the periphery would be very difficult to determine without ultrastructural study (Brusle and Brusle, 1975)

Population Structure

Populations of sequential sex changers commonly exhibit a skewed sex ratio and sexual differences in size and age frequency distributions (Sadovy and Shapiro, 1987). These differences come about when some or all of the second or terminal sex is derived through sex change and must pass through the first sex.

Sexually based differences in size distributions are the most commonly reported feature of sex changing populations.(Warner and Robertson, 1978; Robertson and Warner, 1978; Choat and Robertson, 1975; Moyer and Nakazono, 1978 for examples). However, skewed size distributions can easily occur in gonochoristic species as a result of differential growth or mortality (Sadovy and Shapiro, 1987). Similarly, differential growth or mortality could hide expected differences in sex changing fish (Snelson, 1984). In *P. queenslandica* , male growth is significantly faster than female growth in the reproductive season. Even if all females were derived from males, these growth differences could disguise any expected difference in the size distributions.

Jones (1980 a&b) has shown clear differences in age structures of the two sexes in two unrelated species of protogynous hermaphroditic fish. Sadovy and Shapiro (1987) consider a bias in age-structure to be a better indicator of sequential sex change than differences in size distributions. There were no differences in age distributions of males and females of *P. queenslandica* . However, just as differential growth could change size structure, so could differential mortality alter ultimate age structures (or size structures). Size-specific mortality is common in fish (Warner and Downs, 1977; discussion and references in Ricker, 1969) and the potential for changes in the age distribution from selective mortality cannot be discounted. I have no direct data on mortality except loss from mark-recapture work which has shown no trend with sex (see Chapter 4). Another important point about age structure is that the ageing technique should have no bias between the sexes. This may well not be the case with *Pseudochromis queenslandica* as there is a possibility that slow growth at older ages may cause age to be underestimated (Chapter 2).

Sadovy and Shapiro (1987) also suggest that alternate developmental pathways can influence both age and size structure. The "typical" labroid system, where males may develop directly (primary males) or may be derived from females (secondary males) would be very much less clear if the two types of male could not be distinguished histologically (terminology from Warner and Robertson 1978). This idea will be discussed in more detail below.

Skewed sex ratios tend to be common in both protandry and protogyny. Shapiro (1984) put forward the hypothesis that sex ratio was the factor controlling sex change in *Anthias squamipinnis* and demonstrated through manipulations a tight control of local sex ratios by sex change.

Protogynous fish tend to show larger deviations in sex ratio than protandrous fish (Charnov, 1982) and Moyer and Nakazono (1978) found functional sex ratios of 1:1 in several protandrous species of *Amphiprion*. Charnov (1982) suggests that a breeding size of two (ie. 1:1 sex ratio) could select for protandry, the greatest reproductive output available when the largest fish is the female. The sex ratio of *Pseudochromis queenslandica* appears to be 1:1.

Sex change

The two large fish that changed from male to female coloration on the manipulated reefs both showed no sign of male tissue. The sizes of these two fish suggest that they would have been active males when marked in July 1985. These fish had oocyte development indistinguishable from other non-changed females of the same size suggesting female reproductive activity a few months earlier; however this is uncertain. The majority of fish seen to change colour or found in a transitional colour phase in this study were small fish, usually in the lower 25% (less than 75 mm SL) of the size distribution. As expected , these small fish are young-the two year old fish collected in February 1986 would have just passed through their second reproductive season. The predominant direction of change in these fish was from male to female coloration. The largest and oldest of the changed fish all took on female coloration. There were two colour changes in the female to male direction. In July 1985, both these fish were just over 70 mm in length, two years old, and when recaptured in February 1986, both showed gonad histology typical of any active male, including larger ones. The starting sex of these two males is less certain; one of the fish was in a transitional colour phase at the start, and both were of a size that makes the prior presence of male tissue a possibility.

MATING SYSTEM

The data given above that are probably most significant in determining the mating system of *Pseudochromis queenslandica* are as follows: that males can change sex to become females, that sex ratios and behavioural information strongly suggest pair mating, and that there are no detectable differences in the size or age structures between the sexes. These data do not immediately point to any commonly known mating system in fish. Here I can only speculate on what I believe to be among the three most creditable suggestions.

1) Labile Sex Determination

The high level of colour change at small size in *Pseudochromis queenslandica* may be a part of the sex determining process. Fish of small size show indeterminate gonad histology and may be able to delay sex determination until just prior to maturity. Labile sex determination is known in fish, although it usually occurs at an earlier age and has an environmental cause (Conover and Kynard, 1981; Harrington, 1975). Charnov and Bull (1977) state that "Labile sex determination is favoured by natural selection when an individual's fitness is strongly influenced by environmental conditions, and where the individual has little control over which environment it will experience." Conover and Kynard (1981) showed temperature based sex determination in a marine fish. The effect of this type of sex determination was that fish hatching early in the season, in low temperatures were females, and hatchlings from later in the year with warm temperatures were males. The supposed benefit in this annual species was that fish exposed to the longer growing season and attaining larger body size were likely to be better off being female than male.

All field based demonstrations of sex change in fish have shown sex change to be mediated at the level of the local population (Warner, 1984b). Sex changing fish have been found to be very sensitive to their social environment, changing their reproductive behaviour or sex in response to changed local conditions.(Fricke and Fricke, 1977; Jones, 1980a; Warner and Hoffman, 1980; Ross et. al., 1983; Shapiro, 1984). Adult local population structure in *P. queenslandica* would change from time to time on patch reefs with the combined effects of migration and mortality. For recruits coming into the breeding population,the benefits of deferring sex determination until just prior to maturation would depend on the mating system involved. In a pair mating system, as the data suggest, balancing of the local sex ratio by last minute sex determination will mean fewer non-reproductive individuals. Delayed sex determination in a system with pair mating would also cause population structures such as age and size distributions to be even between the sexes.

Little is known of the timing of sex determination in those sex changing fish with a dual life history (ie. 1° and 2° males). Warner and Hoffman (1980) have described differences in the distribution of 1° and 2° males between habitats where the two types of males would have different reproductive success. They have attributed these differences to

preferential settlement of different genotypes but labile sex determination and a single genotype would explain the data just as well.

2) Protandry

The population, histological and colour change data presented here can support the idea of *P. queenslandica* as a protandrous sex changer. The only unequivocal sex changes demonstrated in this study were from male to female. The Size Advantage model has successfully been applied to protandrous populations, including fish (Charnov, 1982). The Size Advantage model would predict that animals change sex in response to a supply of smaller males (Charnov, 1982) unless prevented from doing so by larger fish as in *Amphiprion* (Fricke and Fricke, 1977). In the case of pair mating animals, that supply of males could be a single fish. In other words, if there is no social inhibition of sex change, such as in *Amphiprion*, then fish would be able to pair and spawn from a small size. Harrington (1975) indicates that there may be some advantage in changing sex at a small size, minimizing physiological cost. Charnov (1982) believes that this sort of system would be evolutionarily unstable because of the great benefits to a male who 'cheated' ie. secured more than one partner. Male parental care, as noted in *P. queenslandica*, might limit this behaviour however. In the absence of better behavioural data on spawning and interactions, further interpretation is difficult.

3) Bi-directional sex change

Pseudochromis queenslandica may be able to change sex in either direction. A number of female-coloured fish were seen to change colour to the male coloration, and these fish were, or were likely to be functional males after the change. Bi-directional sex change has been suggested before in fish (Zohar et.al. 1978), but never demonstrated in a field population.

The original theory used to explain simultaneous hermaphroditism, outlined in Ghiselin (1969), was that in low densities any encounter could be a mating. Simultaneous hermaphroditism is really the ultimate in labile sex determination. In a pair mating system, there are reproductive benefits to be gained by having the largest fish in the pair female (Charnov 1982). Given the vagaries of recruitment (Doherty, 1982; Sale et al., 1984; Eckert, 1984a), migration (Chapter 4) and mortality (Aldenhoven, 1986), this may not always be possible with unidirectional sex change. With bi-directional sex change however, a pair of fish with the same starting sex could make the most economical sex change in terms of reproductive

output and cost of sex change. For example, with no cost of sex change, the largest of two males would become female and the smaller of a pair of two females would become male. The cost of sex change has been much discussed (Warner and Lejune, 1985; Hoffman et. al., 1985) but has proven very elusive to estimate.

Two attempts to make fish reverse sex in the "wrong " direction had results counter to what would have benefited the fish's reproductive success. Fricke and Fricke (1977) forced pairs of females of the protandrous fish *Amphiprion bicinctus* to live on the same anemone with the result that the subordinate fish was killed or severely injured. Ross et al (1983) put small terminal phase males in with large females (initial phase) of the protogynous wrasse *Thalassoma duperrey* and the females changed sex. Both these situations were likely to be fairly novel ones for the fish, especially for *Amphiprion*, who seldom move from their host anemone (Allen, 1972; Fricke and Fricke, 1977). In both situations the response resulted in the cessation of reproduction (although Ross said nothing of the histology of the small males at the end of the manipulation). One probable reason for the paucity of this type of manipulation, despite the abundance of work on sex change, would be the difficulty of changing size distributions upward in the field. It is fairly easy to remove the dominants in a group but quite a different matter to reconstitute a group with a size range of dominants from elsewhere.

Summary

The reproductive attributes outlined above can be seen to fit the data presented here for *Pseudochromis queenslandica.*, and the suggestions above are in no way exclusive of each other. Whatever the mating system of *Pseudochromis queenslandica*, at One Tree Reef, the species shows unusual population traits for a sex changer, and the distribution of sex and colour change throughout the population suggests extreme flexibility in sex determination.

CHAPTER FOUR

GROWTH AND SURVIVORSHIP OF *P. QUEENSLANDICA*

INTRODUCTION

Coral reef fish have been the focus of much ecological research (reviewed in Sale, 1980), and because of their prominence and their great diversity, have been well suited to study. Much of the ecological research has been directed toward communities, rather than toward populations, and consequently, measurements of life history parameters for coral reef fish are scarce. Topics of interest to ecologists such as the relative importance of recruitment to population structure (Doherty, 1982; 1983a&b; Victor, 1983; 1986; Eckert, 1984a; Sale et al, 1984) can be difficult to interpret without empirical demographic information (Eckert, 1987).

Recruitment, growth and survivorship rates will all greatly influence the composition of a population but direct measurements of the latter two of these parameters at least, can be difficult to get (Sale, 1980; Munro and Williams, 1984; Doherty and Sale, 1986). The need for this demographic information has led to the use of indirect methods and models to derive parameters such as mortality (Pauly, 1983) or population characteristics such as age structure (Ricker, 1975). Such indirect methods have been generalized across many species and their utility in any particular case cannot be assessed without further direct measurement of the parameter(s) in question.

The aim of this chapter is to present measurements of important life history parameters such as growth, mortality and age structure for *Pseudochromis queenslandica* . Where life history parameters can be derived both directly from sampling information and indirectly (eg. from other parameters, such as done by Pauly, 1980), a comparison among methods is given. The resulting life history framework for *P. queenslandica* is presented in the context of existing information on other coral reef species.

MATERIALS AND METHODS

Distribution and abundance

The secretive nature of *P. queenslandica* made it desirable to work with fish on isolated patch reefs to ensure that all fish in a given area had been accounted for. However the majority of the reef habitat in One Tree lagoon is continuous reef, so some assessment of the densities on both continuous and patch reef area was needed. In September 1983, three areas of continuous reef were staked out with boundaries defined by rope. Fish were captured and marked by clipping fins. The movements of most of the fish did not extend beyond the rope boundaries, but fish captured near the edges were included if they spent more than 50% of two ten minute observation periods within the roped area. These areas of continuous reef were compared with six patch reefs, all surrounded by at least 5 m of open sand. All fish on the patch reefs were marked and the reef completely searched until no unmarked fish remained. All work after September 1983 was done on patch reefs and there were three further censuses, each of six new patch reefs, carried out in February 1984, September 1984 and July 1985.

Census of recruitment

Juvenile fish were counted with the same technique used for adult fish except that searching was more intensive. Juvenile densities were estimated in February 1984, on six patch reefs which averaged 51.7 m^2. Censuses were considered complete after each reef had been searched for at least 3 hours on each of two sequential days without sighting any unmarked fish. Nearby adults often had to be captured and temporarily removed from reefs before juveniles could be captured because adults often chased juveniles away from the baited traps.

Age structure

Ages of *P. queenslandica* were estimated from either counts of annual marks in otolith cross sections or from otolith weights (Chapter 2). Samples of fish used for age structures were from complete clearances of patch reefs done in May 1985, July 1985 and February 1986. Ages for some fish from these samples were not available because otoliths broke during dissection or preparation.

Growth

Growth was monitored over several periods using mark-recapture methods described in Chapter 1. Length measurements from some recaptured fish were occasionally found to be less than their initial measurements. This occurred with five different fish and the second measurement was never more than 1 mm less than the original measurement. This was assumed to be measurement error in conjunction with very low or zero growth and not indicative of negative growth.

In February 1984, three patch reefs were thoroughly searched for juvenile and adult *P. queenslandica* and all fish on them captured and marked. These reefs were searched again in September 1984, but the search at this time was not as thorough as the previous one. In September 1984 some of the previously marked fish were captured and re-marked and some previously unmarked fish were captured and marked at that time. The final clearance of these reefs was in May 1985 and the three reefs received a second thorough search at that time. This census procedure resulted in three overlapping but distinct sets of growth data: from February 1984 to September 1984, from September 1984 to May 1985, and from February 1984 to May 1985. One further mark-recapture manipulation, using four patch reefs between July 1985 and February 1986 also provided growth increment data. As with previous mark-release programs, this was based on complete clearances of patch reefs.

Logistic, Gompertz and von Bertalanffy growth models were fitted to each set of growth increment data and compared using the methods of Kaufman (1980). The growth increment data could be represented by any of the three growth models so the von Bertalanffy model was chosen due to its more common usage (Ricker 1975). The von Bertalanffy growth model describes an exponential decay in rate of growth (Von Bertalanffy, 1957). The von Bertalanffy growth equation is commonly written as:

$$L_t = L_\infty * (1 - e^{-K(t-t_0)})$$

where L_t was the length of the animal at time t, L_∞ was the asymptotic length of the animal, K was the rate of decay of the growth rate, and t_0 was the (theoretical) point in time at which the size of the animal was zero. Growth increment data were fitted to the von Bertalanffy growth model using the method of Fabens (1965). Von Bertalanffy parameters were also

estimated from growth increment data for the July 1985-February 1986 period by another common method, using the Ford-Walford plot (Ricker, 1975). Both Fabens and the Walford plot methods estimate von Bertalanffy parameters K and L_∞ from growth increment data only, and some estimate of size at age is needed to derive t_0. The t_0 for each set of K and L_∞ was estimated iteratively to minimize least squares deviations from the size-at-age data in the February 1986 sample (Fabens, 1965; Pauly, 1984). Von Bertalanffy growth parameters were also estimated from the size-at-age data by the method given in Pauly (1984). In this method, the linear regression of y on x is calculated where $y=-\ln[1-(L_t/L_\infty)]$ and x=t (t=time in years). The slope of the regression line equals K, and t_0 equals -(intercept/slope). L_∞ is determined iteratively by maximizing r^2 of the regression.

Interference by adults prevented juveniles reaching the baits, suggesting that the adults might have some effect on juvenile growth. An experiment was done to assess growth of juveniles in the presence and absence of adults. In February 1984, all fish over 70 mm SL were removed from three randomly selected reefs and only fish between 35 and 70 mm SL were marked, measured and returned to the reefs. On three other reefs all fish, juveniles and adults, were marked and returned. The growth of fish that were initially less than 70 mm SL when the experiment started was compared between the two treatments using analysis of covariance.

Allometric growth of the otolith compared to the growth of the fish coupled with high variability in the fish length - otolith length relationship prevents back-calculation of individual growth (Chapter 2) However, the effect of different years on the growth of otoliths may be compared because one can attribute a particular increment to the calender year in which it was formed. The widths of increments were compared for 71 fish that were captured between February 1984 and February 1986. Growth of the otolith prior to the first annulus was considered likely to be influenced by time of settlement (early or late in the season), which could also vary among years, and would therefore be an unsuitable measurement for this test. Growth of the otolith in later years is less, making differences more difficult to detect. The growth of the otolith between the first and second annual increments was used as the dependent variable, and analysis of variance was used to compare the growth of the otolith among the years 1980 to 1985.

Survivorship

Estimates of survivorship were obtained from the losses of marked fish from patch reefs between successive censuses. Two sets of censuses were used for these estimates; from February 1984 to May 1985 and from July 1985 to February 1986. All unmarked fish that were greater than 75 mm SL when captured in February 1986 were assumed to be immigrants, and fish below that size were assumed to be recruits or to have been missed in the previous survey because of their small size.

Estimates of mortality were also obtained from samples of age distribution by regressing the natural log of the abundance in each age category against the age. The slope of this line gives an estimate of instantaneous mortality rate (Z) across year classes (Gulland 1983). Annual mortality (A) was calculated from the relationship $A = 1-e^{-Z}$. This was applied to three samples of 18, 20 and 77 fish from May 1985, July 1985, and February 1986, respectively. Mortality was estimated only from age classes 2+ and older to ensure that all age classes were equally well sampled (See Chapter 1).

Further estimates of mortality were obtained from the relationship derived by Pauly (1980), relating the natural mortality (M, which equals Z in unexploited populations) of a species to von Bertalanffy growth parameters K, L_{∞} and the average local water temperature ($\bar{T}$):

$$\log M = -0.0066 - 0.279 \log L_{\infty} + 0.6543 \log K + 0.463 \log \bar{T}$$

The water temperature average used in calculations in the above formula was 25°, taken from One Tree Island Field Station weather records.

RESULTS

Distribution and abundance

There was no significant difference in densities of *P. queenslandica* between areas of continuous reef and patch reef. The three areas of continuous reef censused had a mean size of 58.3 m² and supported a mean density of 17.3 *P. queenslandica* per 100 m² whereas the six patch reefs surveyed at the same time (mean size =51.7 m²) carried a density of 16.5 fish per 100 m² (t= .253, ns.). Further, an analysis of the September 1983 patch reef densities combined with three additional censuses, each of six different patch reefs, showed that there were no significant differences

($F_{3,20}$ =1.35, ns.) among the four censuses (Figure 4.1). The overall density on the 24 patch reefs was 15.7 fish per 100 m^2.

Recruitment

The secretive nature of juvenile *P. queenslandica* made enumerating fish less than 35 mm SL very difficult. The size distribution of fish near 40 mm SL from the sample of February 1984 showed a discrete peak (Figure 4.2). These fish were the young of the year and because of the difficulty counting them, this sample can be considered an underestimate of that summer's recruitment to the six reefs sampled. The density of that cohort was 3.2 fish per 100 m^2.

Age structure

Two of the three samples had individuals up to 11 years of age (Figure 4.3). Both samples from 1985 had relatively large numbers of one year old fish and the 1986 sample had a large number of two year olds, suggesting the possibility of a large cohort. However, neither 1985 sample had a peak of three year old fish that would correspond to the abundance of four year olds in the 1986 sample. The sizes of the 1985 samples limit any conclusions.

Growth

Von Bertalanffy parameters estimated from growth increments from the four sets of recaptures varied considerably (Table 1). The asymptotic size predicted by these curves differed by nearly 10 mm. The Fabens (1965) and Walford plot (Ricker, 1975) methods both predicted the same asymptotic size from the July 1985 to February 1986 growth increment data but the Ks predicted by the two methods differ. When those fish from February 1986 for which growth data were available were aged, their size-at-age relationship predicted a third, and different, set of von Bertalanffy parameters (Table 1, Figure 4.4). These estimates cannot be statistically compared because the models used to derive them are different (Kirkwood, 1983), however it is clear that the three methods predict substantially different sizes at some ages (Figure 4.4). None of the mark-recapture growth experiments span the same seasons so that any seasonal effects make comparisons among the growth increment data difficult. Small numbers of fish in some samples may also limit the value of the derived parameters.

Figure 4.1. The density of *P. queenslandica* from four censuses, each of 6 different patch reefs.
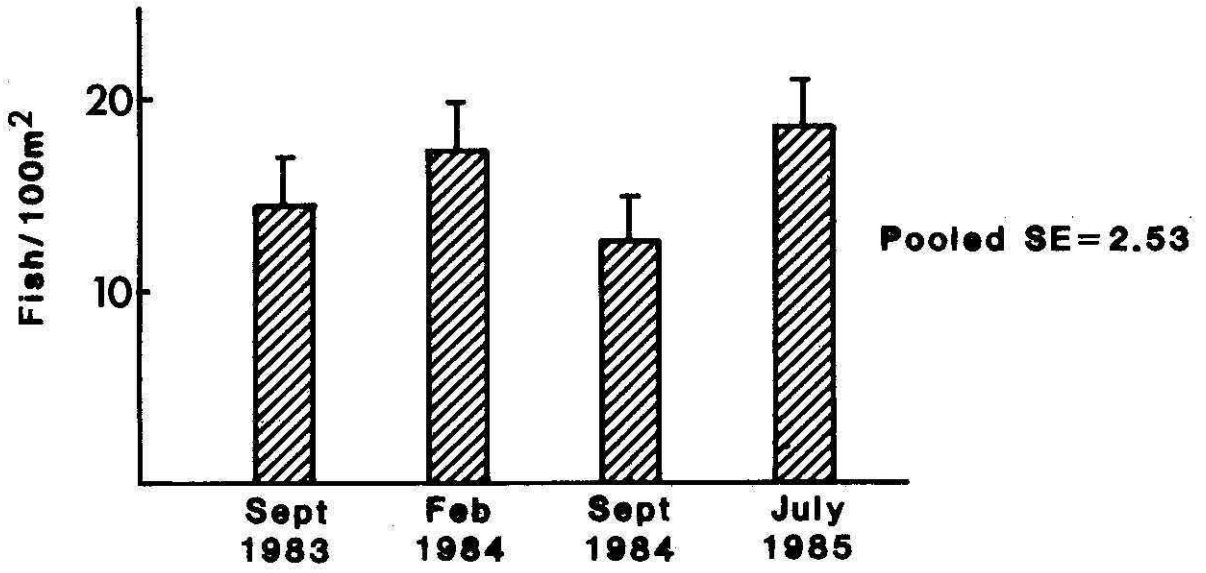
Figure 4.2. Size distribution of *P. queenslandica* from 6 completely cleared patch reefs in February 1984.
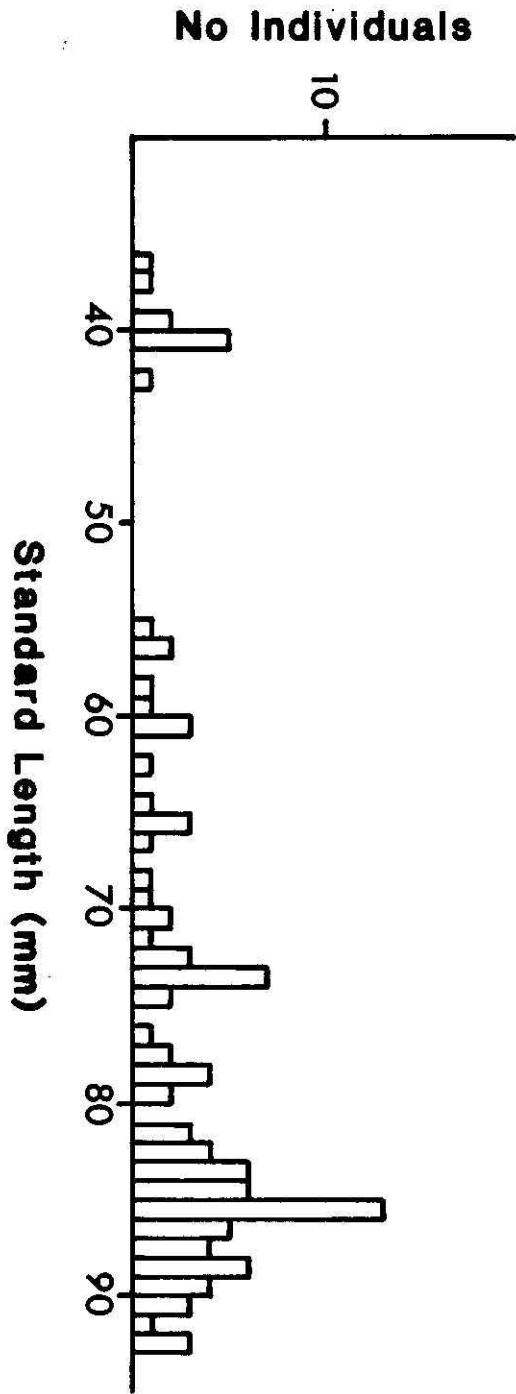
Figure 4.3. Age distribution of *P. queenslandica* in May 1985, July 1985 and February 1986.
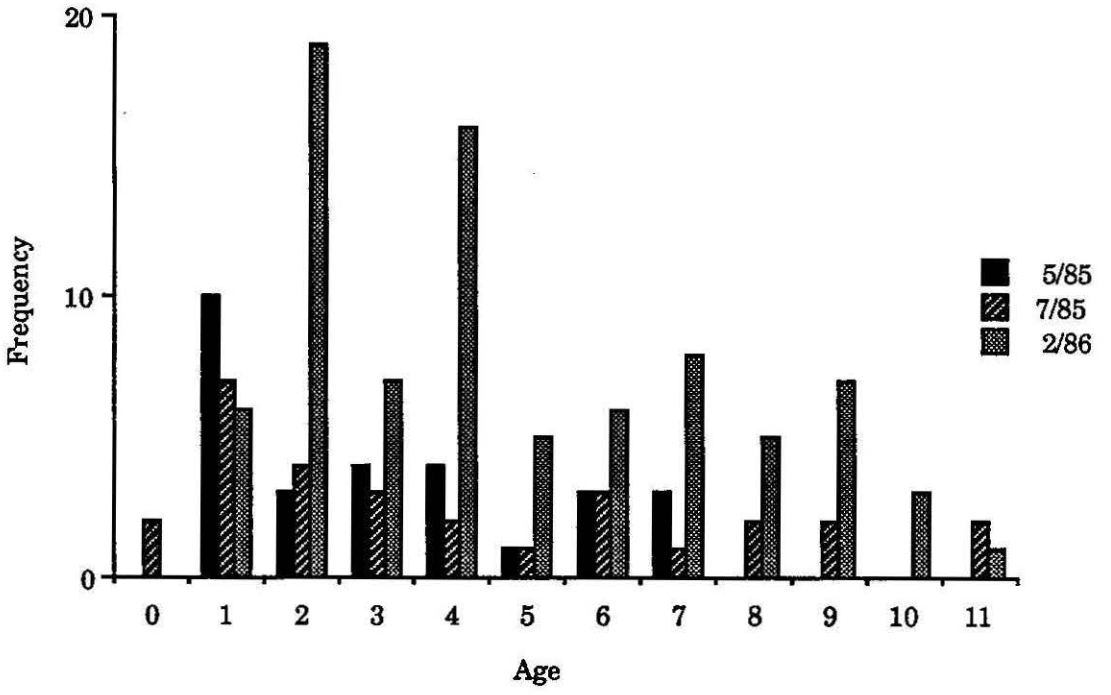
Figure 4.4. Two von Bertalanffy growth curves derived by the Ford-Walford plot and by the method of Fabens from the same set of growth increment data (from July 1985 to February 1986). The third von Bertalanffy plot given is derived from size-at-age data (shown) by the method of Pauly. The size at age data are only from those individuals whose growth increments made up the first two plots.
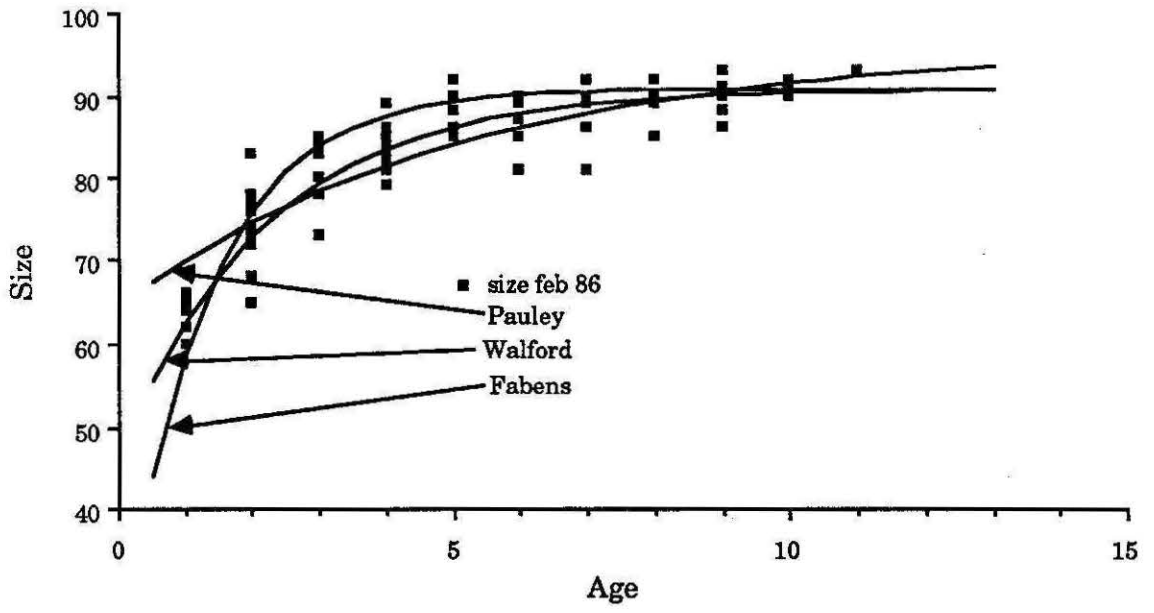
Table 1. Parameter estimation for von Bertalanffy growth curves.

Data type	Date(s)	Method	L∞ (mm)	K	n
increment	Feb '84-Sept '84	Fabens	94.3	.298	16
increment	Sept '84-May '85	Fabens	94.2	.617	13
increment	Feb '84-May '85	Fabens	100.0	.348	12
increment	July '85-Feb '86	Fabens	90.8	.770	45
increment	July '85-Feb '86	Walford plot.	90.8	.451	45
size at age	Feb '86	Pauly	96.1	.193	45

Effects of adults on juvenile growth

Of the 19 juvenile fish marked in February 1984 , six from each treatment were recaptured in September 1985. The growth of fish that were initially less than 70 mm SL was not significantly different in the presence or absence of adults [ANCOVA (slopes), $F_{1,9} = 2.358$, ns.], although there was a suggestion of increased growth of juveniles in the absence of adults (Figure 4.5).

Zero growth

It is worthwhile noting that in all but one of the mark-recapture manipulations, some fish showed no measurable growth (Figure 4.6). The size range of fish that showed no measurable growth was from 80 to 93 mm SL, which encompasses a considerable proportion of the population. Over the initial size range of 80-93 mm SL, fish growth between July 1985 and February 1986 was independent of size (Figure 4.7). Nor was growth in that same period correlated with age for fish four years of age and older (Figure 4.8). Although fish of different sexes grew at different rates in the period of July 1985 to Feb. 1986 (Chapter 3), when the range is restricted to ages ≥ four year and sizes ≥ 80 mm SL, there are no longer any significant differences between the sexes (ANCOVA $F_{1,30}=2.252$, ns.)

Back-calculation of otolith growth

Growth of the otolith between the first and second year of life of *P. queenslandica* was significantly different among the years 1979-1985 (Figure 4.9). The result of a Student-Newman-Kuels test on the ranked means showed that otolith growth in 1985 was greater than growth in 1979, 1980 and 1983 (Figure 4.9). The means were not ranked in the same order as the time sequence, precluding any suggestion of bias due to size-selective mortality. According to Ricker (1969) size-selective mortality

Figure 4.5. Growth of juvenile fish in the presence and absence of adults between February 1984 and September 1985.
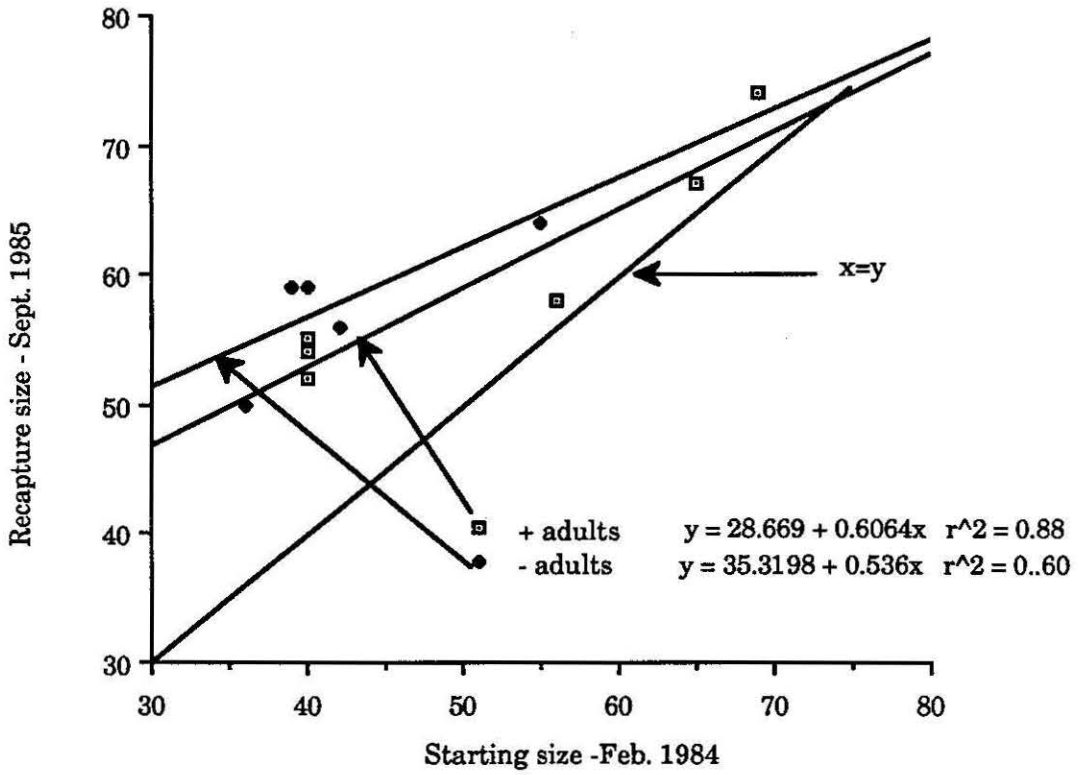
Figure 4.6. Walford plots of growth increments of
   P. queenslandica over four periods from mark-recapture.
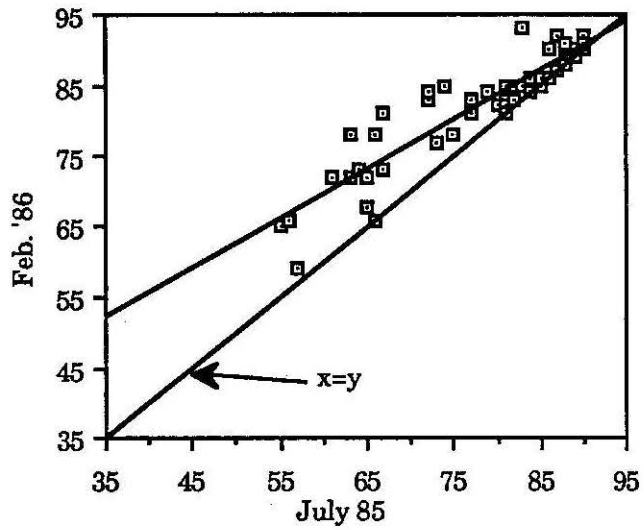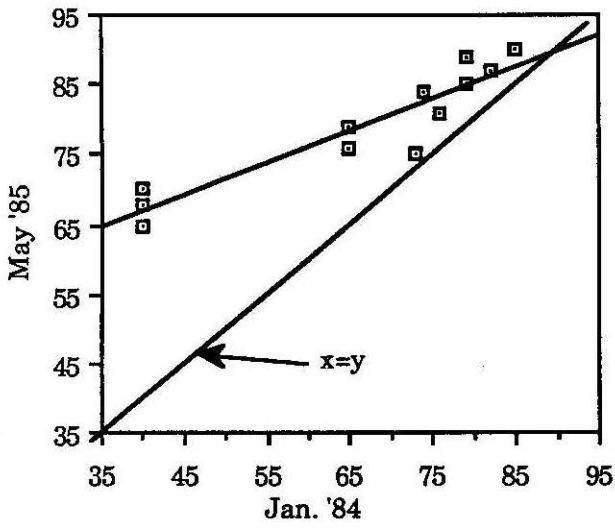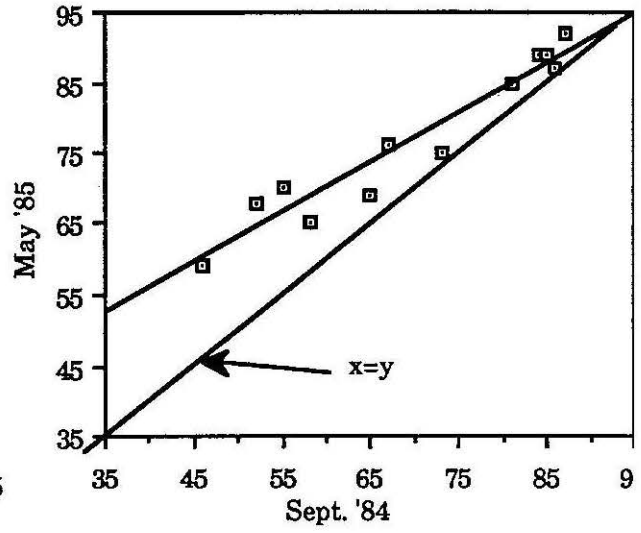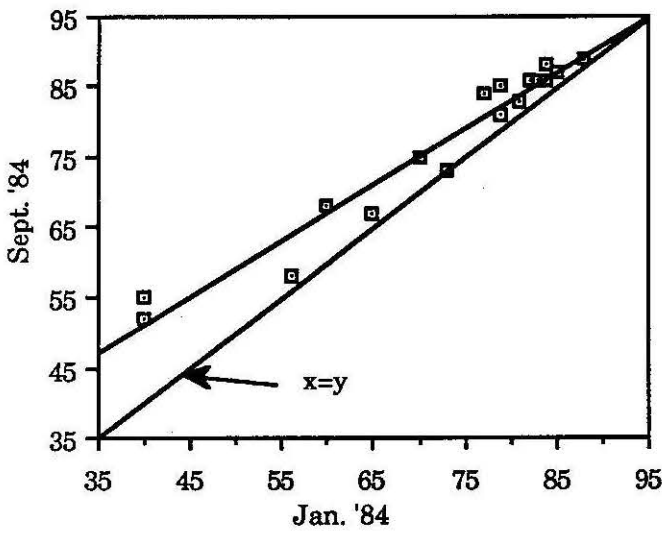
Figure 4.7. Size specific growth of *P. queenslandica* greater than 80 mm SL during the period July 1985 to February 1986.

Figure 4.8. Age specific growth of *P. queenslandica* greater than three years old during the period July 1985 to February 1986.
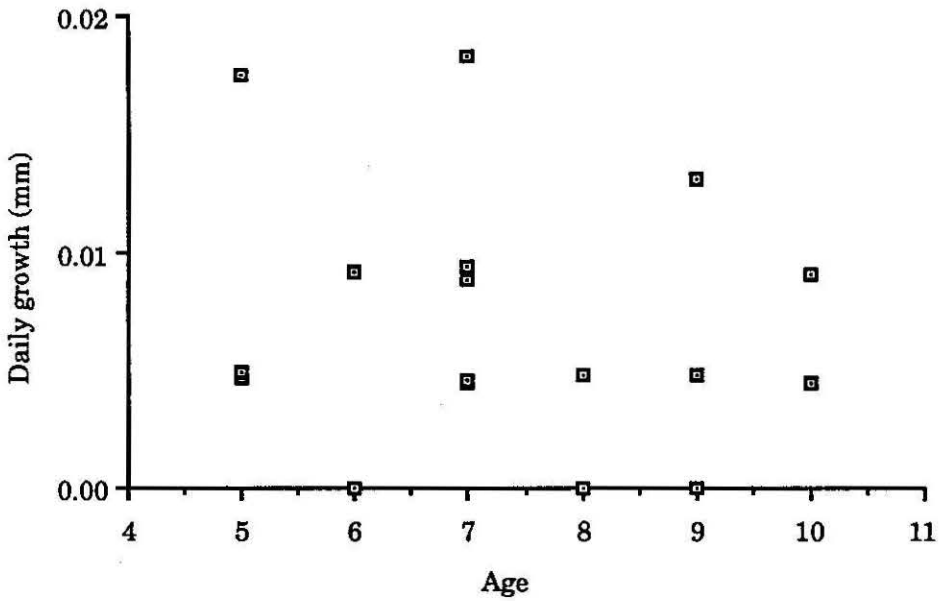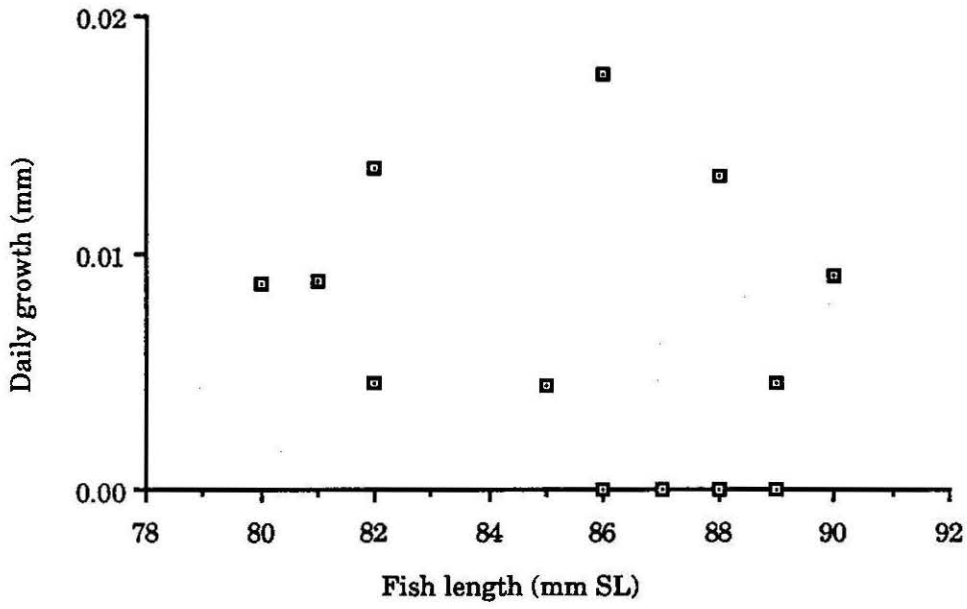
Figure 4.9. Growth of the otolith between the first and second
annual marks among seven years.
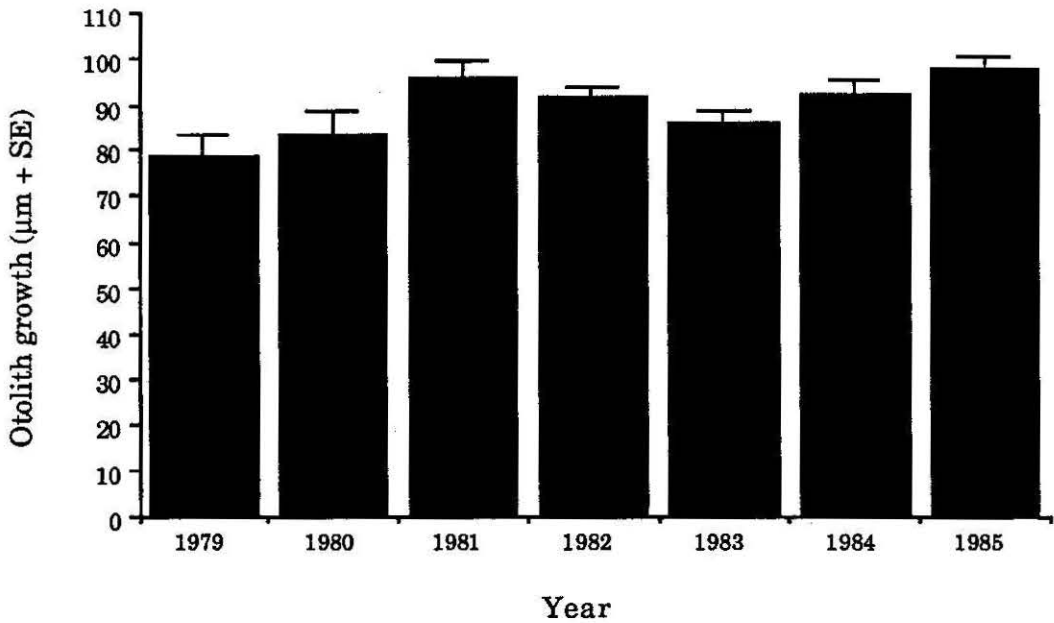
Analysis of Variance Table

Source:	DF:	Sum of squares:	Mean suare:	F:
among years	6	2174.36	362.39	3.50
within years	62	6421.84	103.58	p<.01
total	68	8596.20		

Ranked Means

Year	1979	1980	1983	1982	1984	1981	1985
Mean:	78.5	83.1	86.0	92.1	92.2	95.4	97.7

would cause faster (or slower) growing animals to be removed from the population over time. This could be seen when growth is back-calculated and younger animals show consistently faster growth than that back-calculated for older animals (this referred to as Lee's phenomena- see Chapter 2).

Survivorship

The mortality estimates generated from the two mark-recapture manipulations were similar (Table 2). The samples obtained at the final recapture for both censuses included some fish that did not have marks. These unmarked fish could be fish that had recruited since the first census, that had been missed in that census, fish that had lost their marks, or that had migrated onto the reefs between censuses. The sizes of the newly sighted fish compared with the sizes of the marked fish lost since the first census give some indication of the source of the unmarked fish. In both samples, the mean size of the missing fish was greater than the mean size of those fish not previously seen. Three of the six fish captured for the first time in May 1985 were over 80 mm SL and two of these were aged over four years old (the age for the third was unavailable- the fish was 81 mm SL), indicating that these fish were alive prior to the initial marking in February 1984 and probably migrants or fish that had lost their marks. The ages of all 12 other new fish in both these manipulations were two years or less. I believe it is unlikely that those young fish were migrants and suspect that they were missed in the July 1985 census.

These estimates of survivorship must be viewed in the light of the other capture information from these censuses. The few unmarked, older fish captured suggest that there was some migration or loss of marks over the study periods. Both migration and loss of marks would cause these estimates of survivorship to underestimate the true value.

Table 2. Survivorship of two cohorts of *Pseudochromis queenslandica* on patch reefs.

	Feb. '84 to May '85	July '85 to Feb '86
Time at large (months)	15	7
Fish marked	22	56
Fish not recovered	10	10
mean size (mm)	80.1	84.5
Unmarked fish recovered	6	9
mean size (mm)	74.0	70.3
Annual survivorship	.64	.69

Three samples were judged to be sufficiently large to estimate survivorship using age frequency data (Figure 4.3, Table 3). The survivorship estimates generated using the age structures do not include the 1+ age class where mortality might be expected to be high. The estimates generated from the patch reef surveys did include some small fish, however survivorship of fish less than 65 mm SL when marked was no lower than that of the group in total.

Table 3. Life expectancy of *P. queenslandica* based on age structures and mark-recapture manipulations. Life expectancy is calculated from instantaneous mortality rate (Z) using % remaining at time t = e^{Zt} (Gulland, 1983). For a given Z, and assuming constant mortality across all ages, the age to which 50% and 10% of the population should live is shown.

Based on:	Age structure			Mark-recapture	
Sample	7/85	5/85	2/86	May'85	Feb'86
Z	0.08	0.21	0.22	0.44	0.39
Annual survivorship	0.92	0.81	0.80	0.64	0.69
(±95% CI)	0.08	0.09	0.09		
Life expectancy (yrs)					
p=.5	8.3	3.3	3.1	1.5	1.7
p=.1	27.7	11.2	10.4	5.2	5.9

Annual survivorship estimates from the formula given by Pauly (1980) ranged from 35% to 65%, generally lower than estimates from other methods. The formula was most sensitive to the von Bertalanffy parameter K, and the samples with the extreme values of K from Table 1

gave the extreme estimates of annual survivorship by the Pauly method. In that formula, the higher the K, the lower the predicted mortality rate.

DISCUSSION

Growth

Munro and Williams (1984) concluded that comparison of growth among fish species was difficult even with the common denominator of von Bertalanffy growth parameters. They pointed out that there is little to be gained in drawing comparisons among different types of fish, given that estimates vary greatly within a family, genus, and among populations of the same species from different locations. This has been the case with *P. queenslandica* in so far as different mark-recapture episodes gave very different results. The differences among estimates of von Bertalanffy growth parameters in *P. queenslandica* may arise from generally small sample sizes coupled with seasonal differences in the collection of the data, real growth differences, or both. It was also clear, however, that the different methods of estimating von Bertalanffy parameters gave very different results from the same data.

The von Bertalanffy growth parameter K is generally expected to be higher in small fish relative to large fish (Ricker, 1975; Pauly, 1980). Where data are available for tropical fish, this has been the case (Pauly, 1980; Munro and Williams, 1984). By most standards, *P. queenslandica* is a small fish and yet the range in estimates in K given here are very much lower than those given for similar sized fish (Munro and Williams, 1984). It may be that previous studies of growth of small reef fish have been directed at much faster growing and shorter lived species.

The incidence of very low or zero growth in *P. queenslandica* over a wide range of size or age classes does not fit with the general idea of asymptotic growth. Instances of very low or zero growth are generally attributed to tagging and handling artifacts (eg. Gunn et al, 1979), and such effects on the growth of *P. queenslandica* , causing the low growth seen, cannot be ruled out. It is for this reason that instances of very low growth in mark-recapture experiments have sometimes been ignored [eg. see Pauly's (1984, p. 35) treatment of data from Randall (1962)]. Randall (1962) found low growth in a variety of species and considered that much of it "would not seem to be normal" (p. 210). While Randall believed tagging had some

effect on growth of the many species tagged, this could not be directly attributed to any particular cause (eg. type of tag, severity of tagging wound, or time at liberty). Very low growth over a range of sizes in the case of *P. queenslandica* may not be an artifact of handling but may simply indicate some other variable factor acting to slow growth in some fish (eg. reproduction, social interactions, etc.).

Von Bertalanffy's original derivation of the growth model was based on physiological properties of individual animals (von Bertalanffy, 1957). The fish in this study may be conforming perfectly to von Bertalanffy-type growth but operating on very different, individual parameters. The absence of any trend in growth rate of *P. queenslandica* with size or age of most fish suggests variabiltiy of individual growth rates may be high. Sainsbury (1980) discusses the effect of individual variability on von Bertalanffy parameter estimation and concludes that extrapolating from individual growth increments to generalize about population growth rates is risky at best.

If von Bertalanffy growth parameters can be so different when derived by different methods from the same data or from sample to sample, of what use are they in comparing fish growth generally? Certainly, the growth of many fish can be adequately modeled by the von Bertalanffy growth equation (Ricker, 1975) and for *P. queenslandica* there was no obviously superior model. Because von Bertalanffy parameters L_∞ and K are not estimated independently, using them in any sort of statistical test has proven difficult, though some have suggested methods (Kimura, 1979; Kirkwood, 1983). Other researchers have commented that the best way of testing hypotheses regarding growth remains through controlled statistical tests on growth measurements using analysis of variance or analysis of covariance (McCuiag and Green,1983; Sainsbury, pers. com.) and not through the use of growth models.

Effects of adults on juvenile growth

This study showed no effect on growth of juveniles of the presence or absence of adults, in contrast to two previous studies at One Tree Reef. However, both T. Jones (1983) and G. Jones (1987) showed significant depression of juvenile growth in the presence of adults in two different species of pomacentrid fish. The experiment done in this study to test the affects of adults on juvenile growth in this study may have been too weak,

given the variability in growth and the small numbers of fish, to detect any differences. Intraspecific effects on growth as demonstrated by Jones (1984) and Jones (1987) could be a contributing cause of variation in size distribution of different age classes.

Back-calculation of growth

Back-calculation of growth from bony structures is a common procedure (Ricker, 1969), most often applied using growth increments in mollusc shell, and has been shown to be of use in environmental monitoring (Jones, 1981; McCuiag and Green, 1983). Significant differences in otolith increment thickness among years, as demonstrated in *P. queenslandica* , require cautious interpretation. When differences in growth are found among years, based on back-calculation, there is often a trend detecting lower growth at a given age in the older fish (Ricker, 1969; Chapter 2). This is called Lee's phenomenon and is often attributed to size selective mortality. Another potential complicating factor occurs if there are slight differences from year to year in the time the annual mark is laid down. The back-calculation may only be detecting that shift, and not true differences in growth rate among years. If size selective mortality does not occur and the annual marks are deposited at the same time each year, then the growth of otoliths among different years may be of use in describing relative growth conditions for *P. queenslandica* otoliths in a particular year.

Survivorship

Very few direct estimates of survivorship of adult coral reef fish exist, but the information available has shown longevity in small fish to be quite variable. The ages seen in P. *queenslandica* in One Tree lagoon show clearly that some individuals can be expected to live for more than 10 years. Conversely, Thresher et al (1986) found a species of *Saurida* that lived less than one year and Warner et al (1975a) have found that *Thalassoma bifasciatum* had a mean life expectancy of one year and a maximum life expectancy of three years. Eckert (1987) found survivorship varied widely among several labrid species, with mean life expectancy ranging from 11.5 years in *Thalassoma lunare* down to 1.9 years in *Stethojulus strigiventer*. Aldenhoven (1986) described life expectancy in *Centropyge bicolor* that differed by more than an order of magnitude, from 1 to 13 years among different areas.

The survivorship estimates for *P. queenslandica* based on loss from the patch reef surveys were both lower than those estimates derived from age structures. However, I believe the mark-recapture-based estimates described here represent the lower limits of survivorship. This is because of the unknown numbers of emigrants and fish whose marks went undetected upon recapture. Both Aldenhoven (1986) and Eckert (1987) used a technique similar to the one described here, following individual adult fish through time. Neither Aldenhoven (op cit) nor Eckert (op cit) could account for migration in their estimates of survivorship and it may be that those estimates should also be considered lower limits, suggesting even higher estimates of life expectancy in those species.

The mortality figures derived from age structures of *P. queenslandica* have two inherent assumptions that must be emphasized. Firstly, deriving one survivorship figure for an entire age distribution assumes mortality to be constant across all ages. This may not be the case. Eckert (1987) found much higher survivorship in adults than in juveniles of several species of labrid at One Tree Reef. However, Aldenhoven (1986) did not show any significant differences in survivorship among size classes of *Centropyge bicolor* at Lizard Island. *P. queenslandica* did not show any trend in mortality with size but my inability to fully sample the small sized animals completely must also be taken into account. I believe that by limiting the mortality estimation to samples of fish aged 2 and older, any influence of size on the mortality estimate is reduced. The second assumption involved in estimating mortality from an age distribution is that the distribution be stable, ie. that recruitment be constant from year to year. This is almost certainly not the case for small samples of reef fish (Eckert, 1984a&b). However, even if recruitment varies from year to year, if the fish is long lived, the slope from the regression of (log) abundance against age should give a reasonable estimate of Z, the instantaneous mortality rate, because it has the effect of averaging recruitment over a number of years. Lastly, it is likely that the samples of 18 and 20 fish used for the age structures from May 1985 and from July 1985, respectively, were too small to provide reliable estimates of survivorship, given that they were distributed among nine age classes.

The survivorship estimates from the formula provided by Pauly (1980) would appear to be unrealistically low for *P. queenslandica* , given what is known of its age structure. Few of the species Pauly used to derive this

relationship had L_∞ less than 10 cm and none of these small fish had an annual survivorship greater than 30%. Pauly's relationship was derived from a wide variety of species, and represents a broad average among them, and can only be expected to yield first order estimates of survivorship.

A single estimate of recruitment for 1984 will be of little use if annual fluctuations in recruitment are similar to those shown in other coral reef fish (Williams, 1983; Eckert, 1984a). A rate of 3.2 recruit *P. queenslandica* per 100 m^2 is likely to be an underestimate, due to the difficulty of capturing fish of this small size (ca. 40 mm SL). *P. queenslandica* of that size are approximately three months old and may have completed the initial period of high mortality associated with settlement (Doherty and Sale, 1986). Note that a hypothetical population with a stable age distribution and 80% annual survivorship would require 4.1 recruits per 100 m^2 annually to maintain a density of 16 fish per 100 m^2.

General Comments

Parameters such as survivorship, growth rate, age structure estimated in this chapter can be affected by biased samples. In Chapter 1 I have outlined the problems with sampling *P. queenslandica* . For instance, I know that I cannot capture the smallest individuals and I suspect that catchability increases with increasing size. How does this affect the parameters estimated in this chapter?

Because samples of *P. queenslandica* will be biased toward larger fish, age structures generated from them will be biased toward older (larger) fish. If older fish are over-represented in the samples, the estimates of survivorship derived from these age structures will be too high. I have attempted to account for this by assuming that fish less than two years old are under-represented in my samples and omitting them from survivorship estimates. Also, estimates of growth rate must be considered in the light of this sampling bias. Very few fish between 40 and 70 mm SL were measured for growth rate so the von Bertalanffy curves extending into that part of the size range must be viewed with caution.

This study has confirmed the observations of Aldenhoven (1984) and Eckert (1987) that small coral reef fish can have longevity exceeding 10 years (cf. Thresher et al, 1986). This longevity highlights the point recently made by

Jones (1987) that studies of population dynamics of these species must span longer periods than have previously been thought adequate.

Individual variability in growth may cause different methods of obtaining von Bertalanffy growth parameters to give very different results. The incorporation of these von Bertalanffy growth parameters into models predicting other parameters, such as mortality (Pauly, 1980) or yield per recruit (Ricker, 1975) would be dubious for *P. queenslandica* and I suggest they must be treated with caution for other species.

CHAPTER FIVE

GENERAL DISCUSSION

Demographic information for small coral reef fishes is generally scarce (Sale 1980) and consequently has been left aside in much of the debate on coral reef fish ecology. Coral reef fish community structure has attracted considerable research interest, especially regarding the degree to which reef fish assemblages are structured by biotic (principally competitive) interactions (Smith and Tyler ,1972; 1973; Smith, 1978; Gladfelter et al., 1980; Anderson et al., 1981; Ogden and Ebersole, 1981) or chance events (Sale 1974; 1977; 1978). Arguments about community structure have mainly used evidence from fluctuations or stability in species composition to demonstrate particular points. However, the appearance of relative stability or instability in a species assemblage, as measured by changes in individual species' abundance through time, will surely depend in large part on the relative demographies of the species involved and the work to date has not considered this factor. Likewise, the more recent work discussing the potential importance to population structure of fluctuations in recruitment (Williams, 1980; Doherty, 1982; 1983a; b; Victor, 1983; 1986b) has largely lacked demographic information on the species studied and would benefit greatly from such information (but see Victor, 1986b).

This study has added to the information recently produced by Aldenhoven (1986) and Eckert (1987), demonstrating that small coral reef fish can have longevities exceeding 10 years. *Pseudochromis queenslandica* has also shown unexpected variability in all demographic parameters measured relative to age and size. Size of *P. queenslandica* was not a good predictor of age, which may follow from the fact that neither size nor age were good predictors of rates of growth. Similarly, *P. queenslandica* seemed to be capable of changing sex at a wide variety of sizes and ages.

Longevities of the extent demonstrated for *P. queenslandica* are an important consideration in both the debate about competitive structuring of coral reef fish communities (Smith and Tyler, 1972, Gladfelter et al., 1980; Anderson et al., 1981; Ogden and Ebersole, 1981; Sale, 1974; 1977; 1978) and the current discussion of the importance of variable recruitment to reef fish population dynamics (Doherty, 1982; 1983 a; b;

Victor, 1983; 1986b; Eckert, 1987; Jones, 1987). The local population of a long-lived fish such as *P. queenslandica* will be the sum of ten cohorts of recruitment. Recruitment may vary from year to year (Williams, 1980; Eckert, 1984a; Sale et al., 1984) but if survivorship is high, then the existing population is likely, on average, to be very much larger than the average recruitment. Gross year to year fluctuations in recruitment may still be small relative to the population reservoir. This dampening effect of high survivorship on recruitment fluctuations would cause populations to appear unchanging with time yet have nothing whatsoever to do with interspecific competitive interactions (Strong, 1983).

The presence of a high degree of individual variability in a study such as this presents a number of problems. Sainsbury (1980) has discussed the effects of variability in individual growth on von Bertalanffy growth models and analysis and has suggested that where individual growth is variable, age cannot be reliably predicted from growth increment data alone. This has been the case with *P. queenslandica* where there was no relationship between size or age and rate of growth in most of the population. Variability in growth will also make investigating the factors controlling growth rates more difficult. The experiment testing adult effects on rates of growth of juveniles was inconclusive on *P. queenslandica* where similar numbers of fish of another species (*Amphiprion akindydos*) were sufficient to show a clear result (Jones, 1983).

There could be many reasons for the variability in demographic parameters, but one potentially useful source of information that is missing from this study is information on social interactions. Other studies have shown social effects on feeding and reproductive behaviour that had direct effects on things like growth (Warner and Downs, 1977), age of maturation (Jones, 1987), and mortality (Warner, 1984b; Jones, 1987). Without knowledge of the scale at which interactions occur in *P. queenslandica* (within or among pairs, on patch reefs, or over many patch reefs), samples may well be a mix of different social groups or a subsample of one large one. Most fish marked in this study remained on the patch reefs where they were originally found, suggesting any social unit of importance is likely to operate at that scale or smaller. If social interactions are an important controlling factor of the demography of *P. queenslandica* , and if the social unit of importance is the mating pair,

as an even sex ratio might suggest, then a sample of an unknown number of pairs and surrounding strays from one patch reef could present a very disorganized picture.

If the individual variability shown in rates of growth of *P. queenslandica* extends to the growth of otoliths and/or the timing of the formation of the opaque band in the otolith, then the ageing technique must be reconsidered. The timing of increment formation was validated by the marginal increment method for only three age classes and the tetracycline validation for older fish may have been too short in duration and applied to too few fish to comment on the variance in timing of increment formation. The analysis applied to otolith growth among years would be invalid if individuals formed increments at slightly different times of year or at different times in different years. A superior validation of the timing of increment formation would have had more fish and allowed them to be at large for much longer, at least two years (Beamish and McFarlane, 1983). Given the variability in growth of *P. queenslandica* , the apparent consistency of otolith growth from year to year is somewhat surprising.

The methodological tools used in this study, such as those applied for marking and recapturing or ageing *P. queenslandica* , were not new or unusual, and the importance of the type of demographic data provided here has been stressed (Ehrlich, 1975; Sale, 1980). Given the research effort directed at coral reef fishes generally, why have there been so few studies providing demographic information?

The difficulty in capturing and marking small coral reef fish may have also influenced the type of work that has been done. The robust tags used in fisheries work can damage the fish (Randall, 1962), injection of dye or paint has proven useful but not permanent (Thresher and Gronell, 1978), and keeping track of individual markings is time consuming and requires meticulous records (Aldenhoven, 1986). Interest in fluctuations in recruitment has focused interest on population dynamics (because recruitment fluctuations are most interesting relative to existing populations), but those studies have not generally coincided with work on other demographic aspects of individual the species studied.

Data on survivorship or rates of growth are probably more difficult to gather than information on distribution and abundance. While those

studying coral reef fish have agreed that demographic information might be useful generally, the many studies of community ecology were not asking questions about individual species, but about species assemblages, and so had no direct use, for example, for survivorship information. Capturing, marking and measuring fish are all much more difficult and time consuming than simply counting them. *P. queenslandica* had to be captured and marked just to be censused so the amount of distribution and abundance data which came from this study was restricted relative to other studies but capturing and marking were not "extra" work.

Some of the difficulties in using mark-recapture studies to gather demographic information can be avoided if the fish studied can be accurately aged. The use of thin-sections of otoliths in ageing studies is common in large temperate fish (Beamish, 1979b; Campana, 1984a), and was successful on *P. queenslandica* , but had not been previously applied to small tropical fish. The paucity of annual ageing studies on small coral reef fish may be due to the pessimism about ageing tropical fish generally (Pannella, 1974; Brothers, 1980) and also due to the difficulty of working with the otoliths from small fish (pers obs.). Further, it is uncertain whether the otoliths from *P. queenslandica* from lower latitudes would continue to give accurate age determinations (cf. Moe, 1969; Thompson and Munro, 1978) and it may be that One Tree Reef is not a truly tropical location.

The relationship between fish age and otolith weight shown in *P. queenslandica* must be investigated further. The work of Boehlert (1985), Radtke et al. (1985) and Radtke (1987) suggests that other species may have a similar relationship. The relationship now only stands for *P. queenslandica* in One Tree Lagoon and should be validated in different habitats and locations. Should similarly useful relationships occur in other species, the time savings in age determination would allow the sort of questions asked by coral reef fish ecologists to be greatly expanded. Questions concerning the relative effects of inter- and intraspecific competition as well as fluctuating recruitment could be addressed toward age and size structures instead of simple abundances.

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APPENDIX ONE

The following five tables show the distribution of reproductive state among
P. queenslandica distinguished by colour and size at five different times.
Reproductive state was assessed from gonad histology as described in
Chapter 3.

Table 1: Reproductive state of fish in June 1984. n=26

Colour	Size(mm)	Ova Stage			Male Tissue		Total
		1	2	3	present	active	
Grey	<70	2	-	-	2	-	4
	≥70	4	1	1	-	-	6
Trans	<70	1	-	-	-	-	1
	≥70	-	-	-	-	-	-
Red	<70	2	-	-	3	2	7
	≥70	-	-	-	-	8	8

Table 2: Reproductive state of fish in July 1985. n=36

Colour	Size(mm)	Ova Stage			Male Tissue		Total
		1	2	3	present	active	
Grey	<70	1	-	-	3	-	4
	≥70	1	1	13	2	-	17
Trans	<70	-	-	-	3	-	3
	≥70	-	1	1	-	1	3
Red	<70	-	-	-	1	2	3
	≥70	-	-	-	-	6	6

Table 3: Reproductive state of fish in September 1984. n=30

Colour	Size(mm)	Ova Stage			Male Tissue		Total
		1	2	3	present	active	
Grey	<70	-	1	2	1	-	4
	≥70	-	-	8	-	-	8
Trans	<70	-	-	-	1	-	1
	≥70	1	-	-	-	-	1
Red	<70	1	-	-	1	6	8
	≥70	-	-	-	-	8	8

Table 4: Reproductive state of fish in October 1985 n=19

Colour	Size(mm)	Ova Stage			Male Tissue		Total
		1	2	3	present	active	
Grey	<70	-	-	-	1	-	1
	≥70	-	-	6	-	-	6
Trans	<70	-	-	-	1	-	1
	≥70	-	-	-	1	-	1
Red	<70	-	-	-	-	2	2
	≥70	-	-	-	-	8	8

Table 5: Reproductive state of fish in February 1986 n=37

Colour	Size(mm)	Ova Stage			Male Tissue		Total
		1	2	3	present	active	
Grey	<70	2	-	-	1	-	3
	≥70	5	7	2	2	-	16
Trans	<70	-	-	-	-	-	-
	≥70	-	-	-	1	1	2
Red	<70	1	-	-	-	-	1
	≥70	1	-	-	-	14	15