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# Reproductive biology of bisexual and all-female populations of chaetodontid fishes from the southern Great Barrier Reef

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## Synopsis

The reproductive biology of three species of chaetodonts from One Tree Reef (southern GBR) is described by analysis of gonads and population structure. Reproductive biology is related to age by a capture-mark-recapture study of growth. For *Chaetodon rainfordi* there was a significant habitat effect. On the reef slope, females outnumbered males by 5.6 : 1 and both sexes became reproductively active by the age of 2 years. In the lagoon, no males were found and females were reproductively inactive. For *C. plebius*, males were essentially missing from all samples and no reproductively active females were found. For *Chelmon rostratus* (1 : 1 sex ratio) some males had mature testes but there was no evidence of female reproductive activity. This species is likely to be gonochoristic, but the reproductive mode of the other two species remains ambiguous.

## Introduction

Chaetodontid fishes are important members of the ichthyofauna of coral reefs around the world (Allen 1981) and are amongst the ten most abundant families, in terms of biomass and numbers, on the Great Barrier Reef (GBR) of Australia (Williams & Hatcher 1983). Furthermore, these fish are important as indicator species for assessing the healthiness of coral reefs (Reese 1981, Hourigan et al. 1988). Yet, despite this importance, their reproductive biology has only been superficially examined at the family level. To date, spawning behaviour has been described for a small percentage of species (Suzuki et al. 1980, Neudecker & Lobel 1982, Thresher 1984, Fricke 1986, Colin & Clavijo 1988, Colin 1989, Lobel 1989). Gonosomatic indices have been used to assess reproductive status for one Hawaiian species (Ralston 1981) and detailed histological analysis of gonad development has been reported for another Hawaiian species (Tricas & Hiramoto 1989). There has been no examination of the reproductive biology of any species from the Indo-West Pacific region (including the GBR), where the diversity of this family is highest (Allen 1981).

The aim of this study was to describe the reproductive biology of three species of the family Chaetodontidae, from the southern GBR of Australia. The emphasis was to determine the reproductive mode of each species, to relate reproductive activity to size and age of individuals, and to determine the seasonality of spawning. The three species are small reef fish which attain maximum sizes in the vicinity of 100 mm SL. The dominant reproductive mode for such small coral reef fish is hermaphroditism (Barlow 1981). Given the phylogenetic closeness of this reproductive mode to the Chaetodontidae in their closest relatives the Pomacanthidae (Moyer & Nakazono 1978, Hourigan & Kelley 1985, Aldenhoven 1986), it is necessary to screen for bisexuality in this family. This requires the application of comprehensive methods involving both the histological analysis of gonads and the determination of population parameters (Hourigan & Kelley 1985, Sadovy & Shapiro 1987). In this study the methods were a combination of micro and macroanalysis of gonads to search for primary and secondary features of sex change and to determine the stage of development of gonads, and the determination of various population parameters. These included sex-ratios, size frequency distributions of both sexes and the relationship between reproductive maturity and age.

Here, the reproductive biology of three species, *Chaetodon rainfordi, C. plebius* and *Chelmon rostratus,* common on the southern GBR (Fowler 1988, Williams 1990) is described. The first two species are obligate corallivores, which occur individually or in small groups and occupy overlapping home ranges which can be maintained for at least 3 years (Fowler 1988). *Chelmon rostratus* feeds on benthic invertebrates and occurs singly with individuals rarely maintaining the same home range for more than a few months (Fowler 1988). The study was done at One Tree Reef (23° 30′ S, 152° 06′ E), which is close to the southern limit of the distribution of each species. This reef has a continuous reef crest which isolates the shallow lagoon from the surrounding ocean for half the tidal cycle (Ludington 1979) so that the lagoon and reef slope present extremes in habitat type which support different densities of each of the three species (Fowler 1990). These habitat differences may also affect the social and reproductive biologies of these species.

The specific aims addressed in this study were:

(1) to diagnose each species as either gonochoristic or hermaphroditic by analysis of gonads and consideration of size structures and sex ratios;
(2) to identify the temporal pattern of sexual activity and the size and age at which fish become reproductively active;
(3) to compare reproductive biology between two habitats, i.e. the lagoon and the leeward slope, between which population characteristics differ considerably for each species (Fowler 1988).

## Materials and methods

Samples of fish were removed from the reef between August 1984 and April 1987 and the state of development of their gonads compared amongst sampling occasions. Concomitantly, a capture-mark-recapture study was done to describe growth of each species so that gonad maturation and reproductive activity could be related to age.

### *Capture-mark-recapture study of growth*

In a large study area, The Gutter, on the eastern side of the reef (Fig. 1), fish were captured and marked on eleven occasions (August and November 1984, January, March, August and November 1985, February, May, August and November 1986 and finally April 1987). The increments of growth between capture occasions, were used to develop a growth curve for each of the three species.

Fish were captured with the anaesthetic Quinaldine and small hand nets. For each fish the standard length (SL) was measured (to 1 mm) and it then may have been marked depending on its size. All fish $>40$ mm SL were marked by subcutaneous injection of acrylic paint (Thresher & Gronell 1978, Schwartz personal communication) or tattooing ink (Mapstone personal communication) and returned to the place of capture. Those $<40$ mm SL were too small to mark because of the risk of injury and were returned to their place of capture after measurement. Fish were marked with one colour at one or two of six possible positions on both their sides, forming a personal code that was maintained throughout the study. The pigment solution was injected from a 1.0 mm syringe using a 26 gauge hypodermic needle (0.45 × 13 mm), the smallest needle that did not clog with the pigment solutions. Marking apparently had little effect on the fish as they were usually seen swimming freely

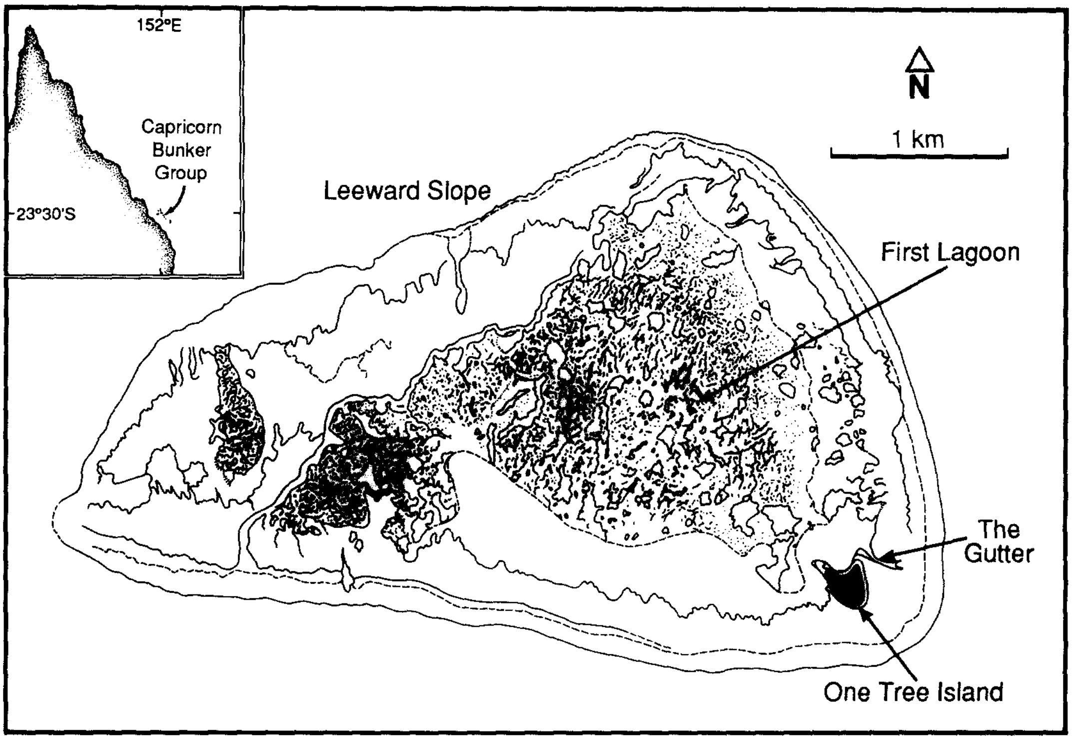

*Fig. 1.* Map of One Tree Reef showing First Lagoon, the leeward slope and The Gutter. Inset shows the general location of the Capricorn/Bunker groups of reefs.

and feeding soon after marking. The individual code and site of capture within the study area were used for the identification of individuals.

The Von Bertalanffy growth equation was applied to the mark-recapture data in the general form of $X = A[1 - Be^{(-KT)}]$, where X is length at time T. Only those increments of growth recorded over a period that spanned at least 10 months were used here to minimise the effect of seasonal variation of growth on the estimation of parameters (Fowler 1988). The parameters A, B and K were calculated using Fabens' (1965) method where the rate of proportional growth (K) and the asymptotic size (A) were calculated by an iterated least squares procedure. The parameter B was then calculated from an explicit formula which required the input of known sizes-at-age (Fabens 1965), for which post-settlement juvenile size and age from otolith counts were used (Fowler 1989). For both *Chaetodon rainfordi* and *C. plebius* fifteen estimates and for *Chelmon rostratus* 9 estimates of size-at-age were used. The parameter B was calculated from the equation: $B = 1/A[\sum p_i - (A - X_i)/\sum (p_i)^2]$, where $p_i = e^{(-KT)}$, $X_i$ = size at age $T_i$ and A = the asymptotic size.

### Analysis of gonads

Fish of a broad size range were collected for gonad analysis from First Lagoon and/or the leeward slope (Fig. 1), by spearing after which wet weight (to 0.01 g) and SL (to 1 mm) of each individual were recorded. During dissection, the presence/absence of visceral fat within the coelomic cavity and surrounding the gonads was noted. These gonads were cleaned of extraneous tissue and fat, fixed in Bouin's solution for a minimum of 36 hours and later transferred to 80% ethanol. Such collections were made in November 1984, April, August, November 1985, February, May, September and November 1986 and February 1987.

Treatment of gonads depended on when the fish were captured. Gonads from samples collected between November 1984 and May 1986 were prepared using standard histological techniques and examined microscopically. For all fish collected after November 1985, the wet weight was recorded and the gonosomatic indices calculated as GI = [Gonad Weight(g)/Body Weight(g)] × 100. Fish collected during and after September 1986, were sexed by macroscopic examination of gonads using a binocular microscope. Here, ovaries and testes were discriminated on the basis of colour, structure and to some extent shape, based upon the experience of the microscopic analysis of the earlier samples. Ovaries were yellow-orange and had a lamellar structure, testes were cream-white and their tissue was dense, smooth and lacked lamellar projections. There were no obvious differences in macroscopic features of the gonads among the three species. For those females with maturing ovaries captured in November 1986 and February 1987, an estimate of instantaneous fecundity (total number of eggs in the ovary) was obtained. This was done by taking ten small sub-samples, weighing and counting the number of eggs and then estimating the total number in the whole gonad.

Standard histological procedures were used to produce sections of gonads. They were washed and dehydrated in ethanol and cleared in cedar-wood oil, after which they were washed in benzene, embedded in wax and sectioned at 9–10 $\mu$ms. Three slides, each from a different position along the gonad, were stained with haemotoxylin and eosin. By microscopic examination, this tissue was sexed and classified according to the dominant stages of gametogenesis using the classification system developed by Moe (1969). The classes of development of ovaries and testes used in this study are defined in Table 1.

## Results

### *Chaetodon rainfordi*

There were 41 growth increments measured over a time period of >0.8 years, which were used to calculate the Von Bertalanffy parameters of K and A (Fabens 1965). The resulting equation ($X = 118.5[1 - 0.8227e^{-0.3118T})$ was used to estimate the growth curve of *C. rainfordi* for the first ten years (Fig. 2). This relationship suggests that fish reach 50% of their asymptotic size at 2 years and 95% at 9 years.

Gonads from 305 *Chaetodon rainfordi* individuals were analysed: 126 from the lagoon and 179 from the reef slope. Samples from the two habitats differed considerably in their gonad development and sex ratios and so are described separately below.

#### *Samples from the lagoon*

The 126 fish collected from the lagoon ranged in size from 44–111 mm SL (Table 2), thus incorporat-

*Table 1.* Classes of development of gonads of both sexes. Stages of oocyte development as defined by Moe (1969).

| Class | Female | Male |
|---|---|---|
| Class 1 | Immature – Oocytes exist only as oogonia and Stages 1 and 2, unless otherwise stated in the text. Atretic bodies do not exist. | Tissue consists of spermatogonia and primary spermatocytes. This tissue is dense and consistent without tubules or sinuses. |
| Class 2 | Mature Resting – Oocytes exist as oogonia and Stages 1 and 2. Atretic bodies located generally central to the lamellae. | Tissue predominantly comprised of primary and secondary spermatocytes, later stages are sparse if present at all. |
| Class 3 | Mature Active – Ovary is undergoing vitellogenesis and oocytes are predominantly at Stages 3 and 4. | Tissue consists predominantly of secondary spermatocytes, spermatids and spermatozoa. |
| Class 4 | Spent – The gonad structure is greatly disrupted, empty follicles are evident and the density of tissue in lamellae is sparse. | Tissue at least 50% spermatids and spermatozoa in large extensive sinuses. |

ing the likely age range of < 1–7 years. The gonads from all individuals were examined microscopically and all turned out to be ovaries which showed no sign of testicular development. All 126 ovaries were classified as Class 1, i.e. immature as all but one contained only pre-vitellogenic oocytes, and the ovary structure was as in Fig. 3a. The one exception here (103 mm SL, 5–6 years old) had ovaries with a sparse distribution of early vitellogenic Stage 3 oocytes, but their density was so low that this fish was still classified as immature. No ovaries contained any atretic bodies in the lamellae, suggesting that none had ever previously undergone vitellogenesis.

Gonosomatic indices were calculated for 49 fish from the three consecutive collections of November 1985, February and May 1986. Some seasonal variation was detected as the sample from February had significantly higher GSI's (anovar, df = 2, 47; f = 8.67; $p < 0.001$) than the other two samples. Yet, despite this, GSI's never exceeded 0.4%, indicating that gonads always constituted a minute percentage of the total body weight. Of 25 fish that did not contain visceral fat (Fig. 4), the majority were small and included all fish that were < 60 mm SL. Alternatively, > 90% of the fish that were > 60 mm SL did contain visceral fat, at all times of the year.

### *Samples from the leeward slope*

The 179 fish collected from the reef slope ranged in size from 40–105 mm SL (Table 2). Assuming the same growth rate, this collection represented approximately the same range of ages (< 1–7 years) as the lagoonal samples. However, unlike the exclusively female collections from the latter habitat some males were present, although they were outnumbered by females by 5.6 : 1 (Table 2). The size distributions of the two sexes (Fig. 5) were compared using a Kolmogorov-Smirnoff test on populations of equal sample sizes (n = 27, randomly selected from the larger number of females) without finding a significant difference (at p = 0.05, D = 0.33 < test statistic = 0.4).

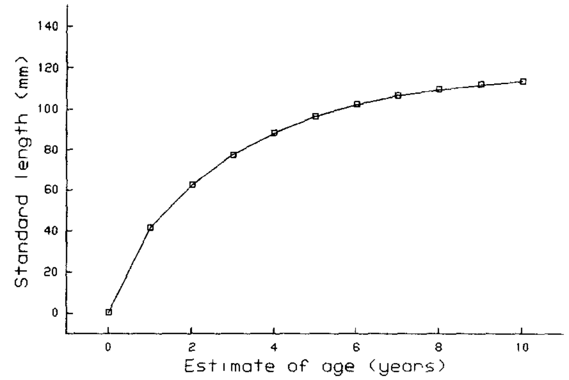

*Fig. 2. Chaetodon rainfordi.* Von Bertalanffy growth curve calculated from 41 increments of growth obtained from the capture-mark-recapture study.

Ovaries from 73 individuals were examined microscopically, most of which were classified as either Class 1 or 2 (Table 2). The eight ovaries in Class 3 or 4, all collected in the November samples of 1984 and 1985, were at an advanced stage of vitellogenesis and were dominated by Stage 4 oocytes, indicative of fish approaching spawning. There were 17 ovaries which were classified as Class 2, which were likely to have previously undergone vitellogenesis.

Gonosomatic indices were calculated for 127 fe-

*Table 2.* Summary of the analysis of gonads for each species collected from One Tree Reef between November 1984 and February 1987 (M = Male, F = Female, I = Indistinguishable).

| Species/habitat | n | SL range | M | F | I | Class of development of females | | | | Class of development of males | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| *C. rainfordi*/lagoon | 126 | 44–111 | 0 | 126 | 0 | 126 | 0 | 0 | 0 | – | – | – | – |
| *C. rainfordi*/leeward slope | 179 | 40–105 | 27 | 150 | 2 | 48 | 17 | 7 | 1 | 0 | 4 | 4 | 1 |
| *C. plebius* | 117 | 52–97 | 1 | 114 | 2 | 57 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| *C. rostratus* | 171 | 52–131 | 89 | 82 | 0 | 60 | 0 | 0 | 0 | 13 | 23 | 15 | 2 |

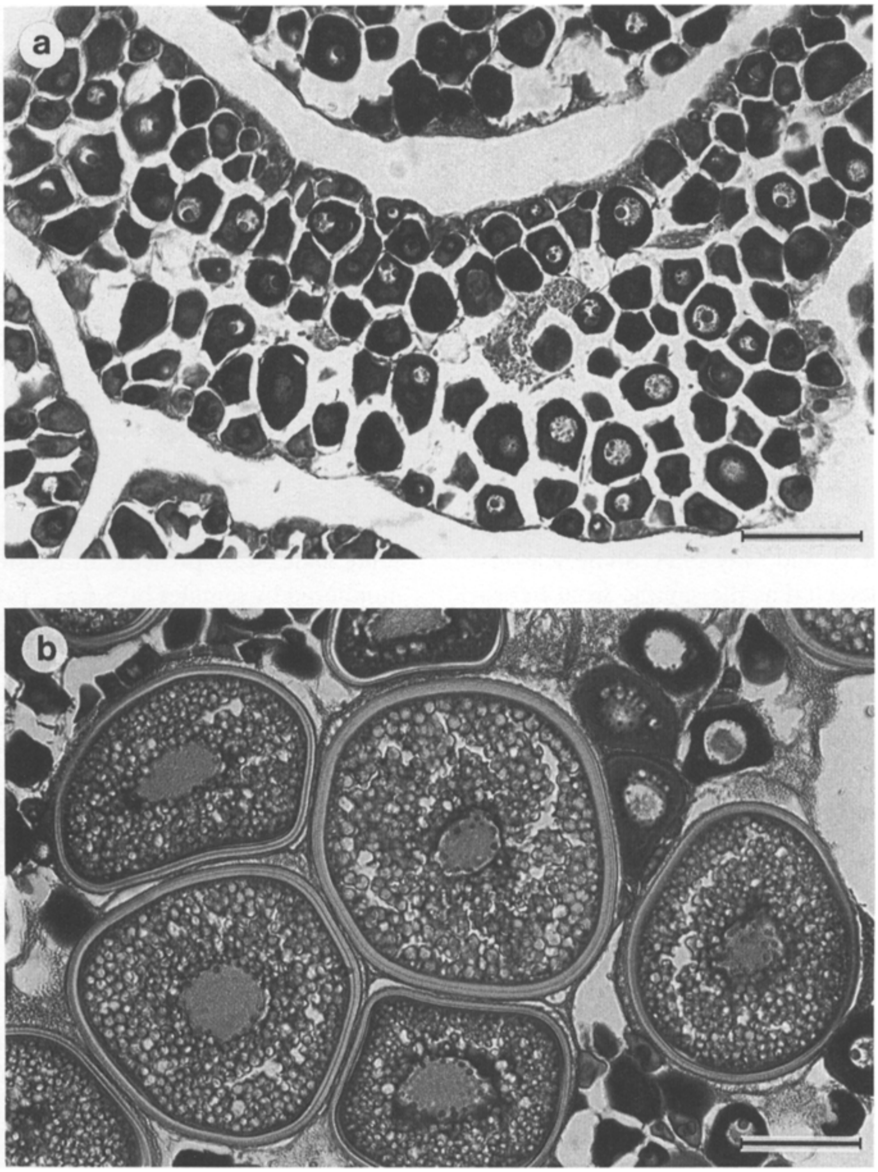

*Fig. 3. Chaetodon rainfordi.* a – Structure of an ovarian lamella from a typical Class 1 female (81 mm SL) collected from the lagoon of One Tree Reef, with no evidence of vitellogenesis. b – Stage 3 and 4 oocytes of a maturing female collected from the leeward slope (97 mm SL). (Both scale bars = 200 μms.)

males (Table 3). These included 40 that were collected in November 1985, from which ovaries were also examined microscopically thus allowing a comparison between gonosomatic index and class of development. The lowest indices (0–0.3%) were always associated with immature ovaries. Those between 0.4–0.5% were associated with early vitellogenesis or post-spawning states, while the largest (> 1.0%) were associated with Class 3 ovaries dominated by Stage 4 oocytes. These latter ovaries were always large, distended, easily ruptured and contained large, loose eggs. Therefore, of the fish captured in November 1985, November 1986 and February 1987, at least some females were approaching spawning as they had GSI's of > 1.0%. Alternatively, of those fish captured in May and

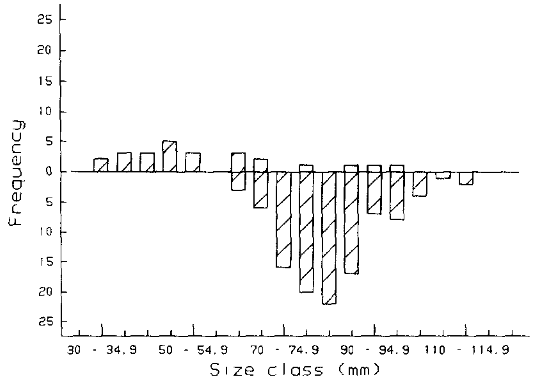

*Fig. 4. Chaetodon rainfordi.* Size distributions of specimens collected from the lagoon of One Tree Reef with no fat (upper graph) and with fat (lower graph) in the coelomic cavity. Size classes are in 5 mm intervals.

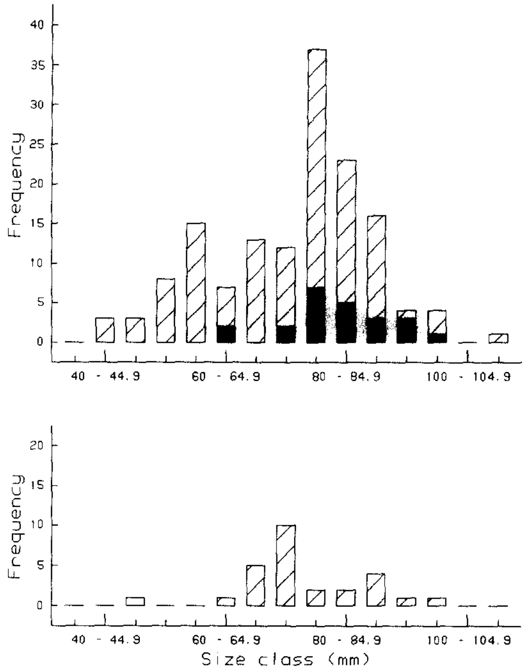

*Fig. 5. Chaetodon rainfordi.* Size frequency distributions of females (upper graph) and males (lower graph) from the leeward slope of One Tree Reef. Shaded areas show those females with mature gonads.

September 1986, none were at such an advanced state of gonad maturation (Table 3). Consequently, both the histological analyses from the earlier collections and the gonosomatic indices from the later ones indicate that ovary maturation was seasonal, ranging at least from November to February, but having finished by May.

Not all females were reproductively active at any one time. The smallest female with active ovaries was 62 mm SL (Fig. 5) and was likely to have been a 1 + fish. Of the 57 females of this size or greater collected in November 1985, November 1986 and February 1987, 22 had active ovaries at their time of capture. The remainder, including some large individuals, contained small, inactive gonads.

Estimates of instantaneous fecundity were obtained for a small sample of fish which ranged in size from 60–87 mm SL (Table 4). Estimates were in the tens of thousands of eggs per ovary, and varied considerably amongst the different individuals. Although the smaller fish tended to have lower instantaneous fecundity, the relationship between number of eggs and body size, measured in both SL and weight, was quite variable. Alternatively, the number of eggs per weight of ovary was more consistent amongst individuals (Table 4), suggesting that variability in fecundity amongst individuals was related to the size of the ovary at the time of capture.

The presence of visceral fat appeared to be inversely related to reproductive activity. Most of the larger females with active ovaries did not contain fat (Fig. 6), except for two which had small amounts at the tip of the gonad, that may have been in the process of being resorbed. Alternatively, most of the females containing large amounts of visceral fat did not have active gonads.

Twenty seven males were collected from the leeward slope, 9 of which were identified by microscopic examination and 18 by macroscopic examination. The former revealed testes in various stages of spermatogenesis (Table 2) including several with large quantities of spermatozoa. Gonosomatic indices were calculated for the 24 males (collected between November 1985 and February 1987), which were always very low, generally approximating $<0.1\%$ of the total body weight. However, they differed significantly amongst the five occasions (anovar, df = 4, 20; f = 3.3865; p = 0.03) with the highest indices obtained in November 1985 and November 1986. Although the sample sizes are low because of the bias in the population towards females, this suggests that the maturation of testes was seasonal and that the weight of the testes changed with maturation.

### *Chaetodon plebius*

Von Bertalanffy parameters for this species were calculated from 15 growth increments measured over time periods that exceeded 10 months. The growth equation ($X = 94.2[1 - 0.9733e^{-0.724T}]$ indicated that fish reached > 50% of their asymptotic size in the first year of growth and > 95% in < 4 years (Fig. 7).

Between November 1984 and September 1986, 38 fish were collected from the lagoon and 28 from the reef slope for gonad analysis. Because no differences were detected in the relevant characteristics between these samples, all subsequent collecting was done on the leeward slope, where spearing was easier. In total 117 fish were collected from both habitats (Table 2), which ranged in size from 52–97 mm SL and encompassed the likely age range of 1–7 years. These fish demonstrated an overwhelming bias towards females, with 114 females and only 1 male (Table 2). The gonads from two small individuals could not be sexed macroscopically.

Fifty seven ovaries were examined microscopically. All were immature (Table 2) regardless of their size, age and time of collection. All oocytes were pre-vitellogenic and no atretic bodies were ever detected. Gonosomatic indices ranged between 0.01–0.18% which are minute and varied only in relation to fish size, showing no evidence of consistent seasonal change. The single male fish was captured in the austral autumn (April 1985) on the leeward slope. The testis of this fish was minute relative to the weight of ovaries from similar sized fish, and was classified as Class 4 because it contained a high density of spermatozoa.

Although there was considerable overlap in the size distributions of fish with and without visceral fat, particularly in the size range of 60–75 mm SL, most small fish (< 70 mm SL), did not contain fat and most of the larger ones (i.e. > 70 mm SL) did (Fig. 8). The larger fish lacking fat were collected during Winter in August 1985.

### *Chelmon rostratus*

Von Bertalanffy parameters for this species were calculated from 13 growth increments measured over 10 months. The resulting growth curve (Fig. 9), calculated from the equation ($X = 122.8[1 - 0.8656e^{-0.502T}]$) indicates that fish attained almost 50% of their asymptotic size in the first year of growth and almost 95% after 5 years. The fish considered in the analysis of gonads ranged in size from 52–131 mm SL encompassing the likely age range of 1–10 years, although the majority were probably < 6 years of age.

Of 171 fish, only 5 were obtained from the leeward slope because of the low densities in this habitat (Fowler 1990) and after preliminary inspection these were pooled with the samples from the lagoon. The total yielded 89 males and 82 females giving a 1 : 1 sex ratio ($X^2_1 = 0.2865$, $p > 0.05$, ns) (Table 2). Size frequency distributions of both sexes overlapped (Fig. 10) and were not significantly

*Table 3.* Distribution amongst classes of gonosomatic indices of five samples of *Chaetodon rainfordi* collected from the leeward slope between November 1985 and February 1987. Data presented are the percentages of the total number in each sample (shown in parentheses), represented in each class of gonosomatic index.

| Gonosomatic index (%) | Occasion | | | | |
|---|---|---|---|---|---|
| | Nov '85 (40) | May '86 (14) | Sept '86 (12) | Nov '86 (37) | Feb '87 (24) |
| 0–0.1 | 20 | 7.1 | 8.3 | 21.6 | 54.2 |
| 0.1–0.2 | 52.5 | 64.3 | 41.7 | 43.2 | 16.7 |
| 0.2–0.3 | 12.5 | 21.4 | 25.0 | 5.4 | 8.3 |
| 0.3–0.4 | | 7.2 | 16.7 | | |
| 0.4–0.5 | 5.0 | | 8.3 | | |
| 0.5–0.6 | | | | | |
| 0.6–0.7 | | | | | |
| 0.7–0.8 | 2.5 | | | | |
| 0.8–0.9 | | | | | |
| 0.9–1.0 | | | | | |
| 1.0–2.0 | 2.5 | | | 2.7 | 8.3 |
| 2.0–3.0 | 2.5 | | | 2.7 | 8.3 |
| 3.0–4.0 | 2.5 | | | 5.4 | 4.2 |
| 4.0–5.0 | | | | 13.5 | |
| 5.0–6.0 | | | | 2.7 | |
| > 6.0 | | | | 2.7 | |

different, when tested by a Kolmogorov-Smirnoff test ($D = 0.0984 <$ test statistic $= 0.2082$).

The ovaries of fish captured between November 1984 and February 1986 contained only pre-vitellogenic oocytes, dominated by those at Class 2 (Table 2). No evidence of vitellogenesis was observed either in the form of Stage 3 oocytes or as atretic bodies in the ovarian lamellae. Gonosomatic indices calculated for 37 females captured between November 1985 and February 1987 ranged between 0.07–0.41% and showed no evidence of seasonal variation.

Fifty three testes were examined microscopically, some of which were classified into each of the four possible classes of development (Table 2). The frequencies of the four classes varied among the seasons ($X^2_{12} = 71.6136$, $p < 0.005$) with Class 1 and 2 prevalent during the austral winter/spring and Classes 3 and 4 more common amongst the summer/autumn samples of February and April. It is likely therefore that testis development and sperm production was seasonal. However, no consistent pattern was detected in the GSI's to support this observation, which may have been at least partly related to the difficulty of weighing these minute organs (maximum 0.05% of body weight).

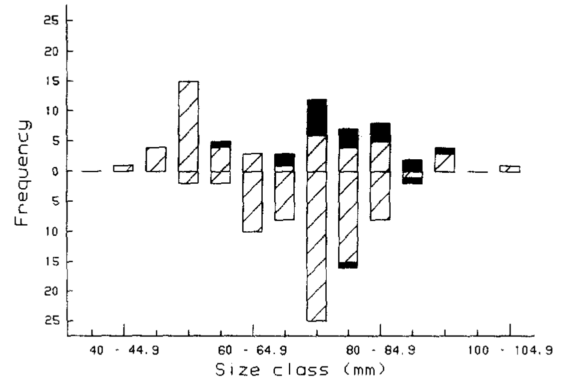

*Fig. 6. Chaetodon rainfordi.* Size distributions of females collected from the leeward slope with no fat (upper graph) and with fat (lower graph) in the coelomic cavities. Shaded areas show those females with mature ovaries.

## Discussion

The population structure and analysis of gonads differed amongst the three species. These results are summarised in Table 5 and are considered separately below.

### *Chaetodon rainfordi*

The best evidence for the reproductive mode of this species is provided by the samples from the reef

*Table 4.* Results from the calculations of instantaneous fecundity and their relationship with fish and ovary size for *Chaetodon rainfordi*. Fish no. 1–9 were collected in November 1986 and no. 10–14 were collected in February 1987.

| Fish no. | Instantaneous fecundity (± CL) | SL | Eggs per mm SL | Fish wet weight (g) | Eggs per fish wt | Ovary wt (g) | Eggs per g |
|---|---|---|---|---|---|---|---|
| 1 | 15658 ± 1479 | 60 | 261.0 | 16.3 | 960.6 | 0.726 | 21.6 |
| 2 | 7772 ± 863 | 62 | 125.4 | 15.4 | 504.7 | 0.328 | 23.7 |
| 3 | 26221 ± 3745 | 72 | 364.2 | 25.5 | 1028.3 | 1.188 | 22.1 |
| 4 | 41675 ± 2894 | 75 | 555.7 | 29.6 | 1407.9 | 3.94 | 10.6 |
| 5 | 29467 ± 4141 | 77 | 382.7 | 27.4 | 1075.4 | 1.337 | 22.0 |
| 6 | 33189 ± 4895 | 78 | 425.5 | 31.2 | 1063.8 | 1.759 | 18.9 |
| 7 | 38447 ± 2413 | 84 | 457.7 | 40.0 | 961.2 | 1.951 | 19.7 |
| 8 | 10621 ± 1727 | 85 | 125.0 | 41.0 | 259.1 | 0.759 | 13.4 |
| 9 | 27776 ± 1373 | 86 | 323.0 | 41.1 | 675.8 | 1.305 | 21.3 |
| 10 | 15390 ± 2110 | 75 | 205.2 | 25.4 | 605.9 | 0.61 | 25.2 |
| 11 | 22096 ± 2326 | 78 | 283.3 | 24.8 | 890.9 | 0.812 | 27.2 |
| 12 | 17657 ± 1378 | 80 | 220.7 | 28 | 630.6 | 0.717 | 24.6 |
| 13 | 8711 ± 644.9 | 84 | 103.7 | 34.5 | 252.5 | 0.484 | 18.0 |
| 14 | 10760 ± 1570 | 87 | 123.7 | 38.0 | 283.2 | 0.422 | 25.5 |

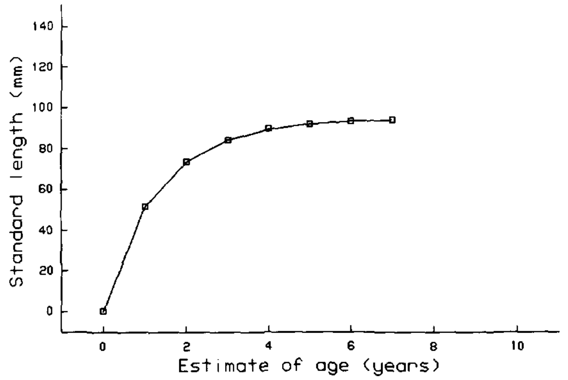

*Fig. 7. Chaetodon plebius.* Von Bertalanffy growth curve calculated from 15 increments of growth obtained from the capture-mark-recapture study.

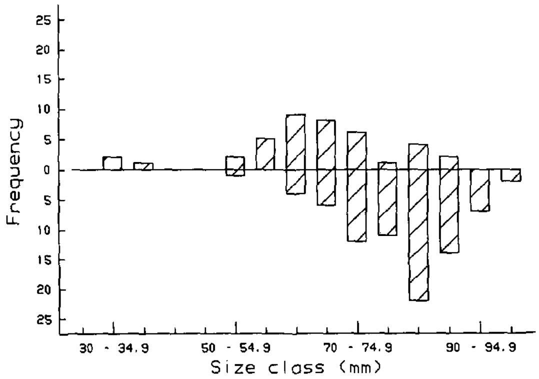

*Fig. 8. Chaetodon plebius.* Size distributions of specimens collected from One Tree Reef without fat (upper graph) and with fat (lower graph) in the coelomic cavities.

slope, where individuals of both sexes co-habited and underwent gonad maturation (Table 5). The uneven sex ratio of this species is a feature typical of protogynous hermaphroditism, which is generally associated with a bias in the size frequency distribution or a lack of small males (Warner 1975, Moyer & Nakazono 1978, Shapiro 1981, Sadovy & Shapiro 1987). However, hermaphroditism appears unlikely for this species for two reasons: the larger individuals were not always males; and the microstructure of both types of gonads was simple, showing either spermatogenic crypts or ovarian lamellae, but no characteristic of sex change.

The likely reproductive mode for *Chaetodon rainfordi* is gonochorism, although this is suggested cautiously. Overlapping size-frequency distributions, although suggestive of gonochorism, may arise for sex-changing species due for example to differential growth rates between the sexes (Sadovy & Shapiro 1987). Furthermore, the histological analysis of gonads remains indeterminate. Although in none of the testes examined microscopically was there a membrane-lined cavity, which could be the remnant of an ovarian lumen, such a cavity can close and not be evident after sex change is complete (Sadovy & Shapiro 1987). Therefore, it is necessary to examine a large number of testes before prior sex change from ovaries can be excluded. Here, only 9 testes were examined microscopically, a number which is probably too low to exclude the possibility of prior sex change.

Mature gonads were found between November and February, but spawning is likely to have continued past this time. Settlement occurred between December and late April, and since the mean pre-settlement duration is 28 days (Fowler 1989), settlement in late April suggests that spawning continued at least until late March. Spawning of butterflyfish has generally been correlated with water temperatures of 24–26° C (Ralston 1981, Neudecker & Lobel 1982, Fricke 1986, Colin 1989, Lobel 1989, Tricas & Hiramoto 1989). Although measurements of the water temperature are not available for the reef slope of One Tree Reef, the summer water temperatures from Heron Reef, located 20 km west of One Tree Reef, vary between 24–26° C (Potts & Swart 1984). Therefore, *C. rainfordi* supports the model of Colin (1989) that the seasonality of spawning of chaetodonts varies geographically in response to temperature regimes, and occurs locally when water temperatures are around 23–26° C.

The estimates of instantaneous fecundity provided here are similar to, if not slightly higher than those for similar-sized individuals of both *Chaetodon miliaris* (Ralston 1981) and *C. multicinctus* (Colin 1989) from Hawaii, although larger *C. miliaris* contained substantially more eggs. The estimates for *C. rainfordi* are of limited value in estimating total fecundity across a breeding season, because of the lack of knowledge of the number of spawnings per season. However, if these fish did spawn several times during the extensive breeding season then estimates of total fecundity of 100 000–

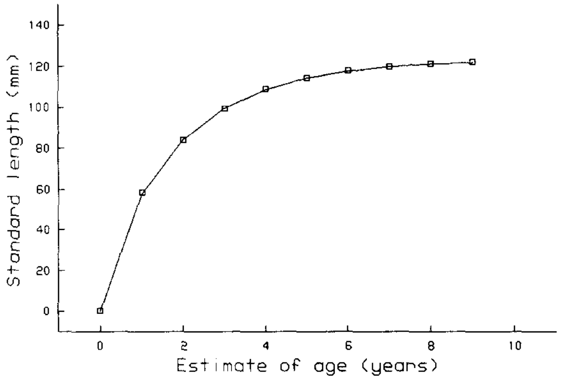

*Fig. 9. Chelmon rostratus.* Von Bertalanffy growth curve calculated from 13 increments of growth obtained from the capture-mark-recapture study.

300 000 eggs per year per individual, as estimated for small Bahaman and Hawaiian chaetodonts (Colin 1989), would appear reachable totals.

The between-habitat differences for *Chaetodon rainfordi* are most obvious in the lack of males in the lagoon. Explanations for this include both developmental and ecological scenarios. The former include both environmental sex determination and environmentally controlled sex change. Environmental sex determination, most common amongst reptiles (Bull 1980, Elgar & Crozier 1975), has been recorded for one gonochoristic species of fish (Conover & Kynard 1981). Here, water temperature caused variation in sex ratios over a large geographic scale. However, because of the physical structure and hydrodynamics of coral reefs, lagoons and reef slopes experience different temperature regimes (Potts & Swart 1984). Therefore, at One Tree Reef conditions for the development of testes may be suitable only on the reef slope. Alternatively, some other physical factor may be important. For example, for *Chaetodon miliaris* from Hawaii, fish from one habitat were reproductively inactive and smaller than reproductively active individuals from another (Ralston 1976). The author

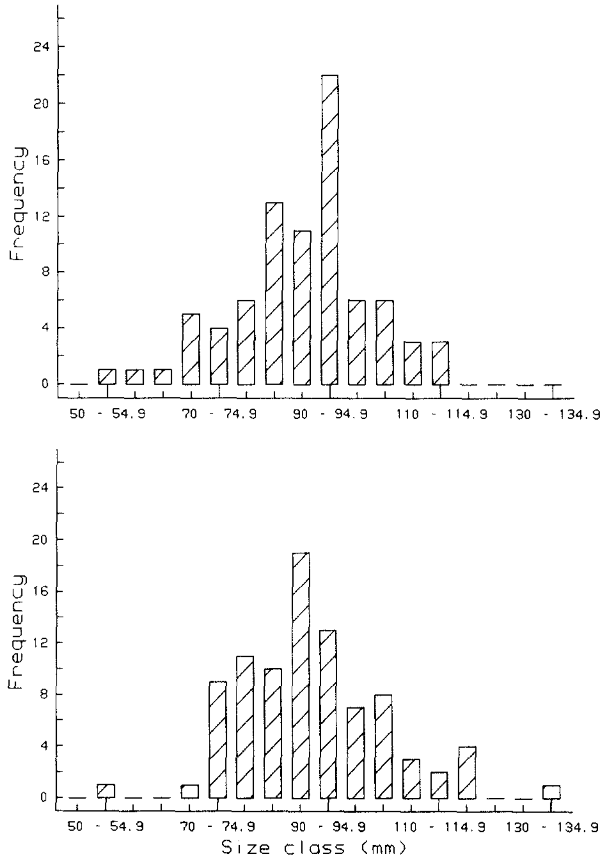

*Fig. 10. Chelmon rostratus.* Size frequency distributions of females (upper graph) and males (lower graph) from One Tree Reef.

*Table 5.* Summary table showing the presence/absence of both sexes (related to habitat when appropriate), whether gonads developed to maturity and whether fat levels were correlated with gonad development. The occurrence of *C. plebius* on the reef slope is based upon one individual.

| | *C. rainfordi* | | | | *C. plebius* | | | | *C. rostratus* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | lagoon | | reef slope | | lagoon | | reef slope | | lagoon | |
| | M | F | M | F | M | F | M | F | M | F |
| Occurrence | no | yes | yes | yes | no | yes | yes | yes | yes | yes |
| Gonad maturation | – | no | yes | yes | – | no | – | no | yes | no |
| Fat metabolism changes with reproduction | – | no | yes | yes | – | no | – | no | – | – |

suggested that this was related to a difference in the lipid components of the diets in the two habitats. For *C. rainfordi* at One Tree Reef the diets differed between the two habitats because of the coral faunas (Fowler 1988), and this may have resulted in a nutritional difference.

*Chaetodon rainfordi* may be a protogynous hermaphrodite where sex change relies on environmental conditions that are present on the reef slope but are absent in the lagoon. Since small males and females were found on the reef slope then sex change would have to occur when the fish were juveniles. Juvenile sex change was documented for *Chaetodon multicinctus*, where testis formation occurred within the ovarian lamellae of several differentiated but immature females (Tricas & Hiramoto 1989). However, this was observed in only a small number of individuals, and testicular development primarily resulted from undifferentiated tissue. Furthermore, other species of hermaphroditic reef fish have social groups composed entirely of females (Shapiro 1979, Coates 1982).

The two ecological scenarios to account for the lack of males from the lagoon involve habitat selection at settlement and post-settlement behaviour and survival of males. Males may be more selective than females at the time of settlement to the reef and actively discriminate against settlement in the lagoon. Alternatively, they may settle in the lagoon but emigrate or die within the first 12 months of settlement. Despite the apparent unlikelihood of both these scenarios they cannot be excluded at this stage in preference for either of the developmental scenarios.

### *Chaetodon plebius*

For *Chaetodon plebius* only one male was collected (April 1985). Since collections were never made during May–July the possibility that more males would have been collected during these months cannot be excluded. However, there was no evidence from a behavioural study for this species that fish would be likely to move into the collection areas from other parts of the reef (Fowler 1988). Therefore, males were essentially absent from extensive areas of the lagoon and reef slope. To account for this the developmental and ecological scenarios discussed for *C. rainfordi* also apply. The development of testes, either directly from undifferentiated tissue or from ovarian tissue, may normally be environmentally controlled, and the conditions at One Tree Reef may generally be unsuitable so that such development rarely proceeds. As *C. plebius* is predominantly a tropical species occurring in the Indo-West Pacific, particularly the South-East Asian Peninsula (Allen 1981), it may not be able to cope physiologically with the cooler sub-tropical waters of the southern Great Barrier Reef.

Ecological situations that might account for the all-female populations of *Chaetodon rainfordi* in the lagoon seem even less likely for the larger scale paucity of male *C. plebius*. These scenarios are that pre-settlement fish destined to become males either do not reach One Tree Reef; they find it unsuitable for settlement; or they die or emigrate within the first 12 months after settlement. Again, such scenarios cannot be excluded without further work.

### *Chelmon rostratus*

The population characteristics and the analysis of gonads suggest that *Chelmon rostratus* is a gonochoristic species. The gonads were simple in structure, distinguishable as testes and ovaries even in fish likely to be less than one year of age. There were no transitional gonads and no secondary features, such as atretic bodies or membrane-lined central cavities indicative of prior sex change. The sex ratios and size distributions did not differ between the sexes and there was no apparent dimorphism or dichromatism between the sexes.

The anomaly for *Chelmon rostratus* was that there was no observed ovary maturation, a phenomenon which must be environmentally determined. This could potentially operate on two spatial scales. It may be a local phenomenon whereby One Tree Reef is unsuitable for this species, due for example to poor quality or low abundance of food. No individuals of this species accumulated visceral fat, as did the non-reproductive members of the populations of the other two species. Alternatively, the phenomenon may have been related to a biogeographical trend, in which One Tree Reef approaching the southern limit of the distribution of this species, did not offer the appropriate conditions for gonad maturation. Since *Chelmon rostratus* is predominantly a tropical species (Allen 1981), the lower water temperature regime of the Capricorn/Bunker Group of the GBR may have been the reason for this.

### *Ecological considerations*

Over the period of this study of reproduction, recruitment of each species was also studied (Fowler 1988, Fowler 1990). Recruitment of *Chaetodon rainfordi* was seasonal, varied amongst years and varied between the leeward slope (5.2–12.3 recruits 150 $m^{-2}$ $yr^{-1}$) and the lagoon (1.7–3.6 recruits 150 $m^{-2}$ $yr^{-1}$). The timing of recruitment of *C. rostratus* was similar to *C. rainfordi*, but occurred in much lower densities, which also varied amongst years (0.13–0.6 recruits 150 $m^{-2}$ $yr^{-1}$). For *C. plebius*, recruits were rare although there was evidence of a non-seasonal pattern with recruits appearing broadly across the reef at different times of the year (Fowler 1988, Fowler 1990). These rates of recruitment were sufficient to maintain *C. rainfordi, C. plebius* and *C. rostratus* as the three most abundant out of the twenty three species of chaetodonts at One Tree Reef through the course of the study (Fowler 1990).

Consequently, populations of these species arose from reproductive activity elsewhere, perhaps from neighbouring reefs of Capricornia, tens of kilometres distant, or from further north on the GBR, hundreds of kilometres distant. Each of the three species has a pre-settlement duration in excess of 20 days (Fowler 1989), a period during which travel over considerable distances in the pelagic environment is possible (Williams et al. 1984, Victor 1987). The complex of reefs closest to the Capricorn Group (the Swains Group) is < 200 km away, a distance which appears insignificant compared to the estimates travelled by the planktonic stages of other reef fishes (Victor 1987). At present there is little information on the hydrodynamic processes which may transport plankton through and around Capricornia.

This study has revealed that the reproductive output of the inhabitants of the GBR can vary on at least two spatial scales. The difference in reproductive biology described for *Chaetodon rainfordi* between the lagoon and reef slope, indicates a small-scale, within-reef phenomenon. Here, one habitat was suitable for fish to develop to reproductive maturity, whilst the other was not. For the other two species the likely arrival of reproductive products from elsewhere establishes at least a between-reef and potentially a between-region qualitative difference in reproductive activity. Therefore, it is erroneous to consider that populations of fishes produce and release gametes at rates proportional to their abundance.

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