

Variation in the population biology of protogynous coral reef fishes over tens of kilometres

Nick Gust

Abstract: This study describes changes in the timing of maturation and sex reversal and shifts in the sexual composition of unfished local populations of protogynous reef fishes across the continental shelf of the Great Barrier Reef. On outer shelf reef crests, both *Chlorurus sordidus* and *Scarus frenatus* matured as females and underwent protogynous sex reversal at reduced sizes and ages relative to fish from equivalent mid-shelf habitats 20 km away. Earlier maturation at smaller body sizes on the outer shelf is likely to be an adaptive response to the higher mortality rates in these habitats compared with the mid-shelf. Furthermore, reduced size and age at sex reversal on the outer shelf is consistent with the reduced growth and increased mortality regimes in these locations. The sexual composition of local populations changed markedly across the shelf for *C. sordidus* but not for *S. frenatus*. High densities of *C. sordidus* on the outer shelf were characterized by threefold higher proportions of both terminal-phase and primary males than on mid-shelf reefs. Differences between local populations separated by tens of kilometres highlight the danger of assuming homogeneous sexual compositions and life histories when managing exploited reef fishes over larger spatial scales.

Résumé : On trouvera ici une description des changements observés, à travers le plateau continental sur les récifs de la Grande Barrière, dans la phénologie de la maturation et de l'inversion sexuelle, ainsi que dans la composition sexuelle des populations locales de poissons protogynes non soumises à la pêche. Sur les crêtes des récifs externes du plateau, *Chlorurus sordidus* et *Scarus frenatus* atteignent, tous deux, la maturité comme femelles et subissent un changement de sexe protogyne à des tailles et des âges inférieurs à ceux des poissons dans des habitats semblables au milieu du plateau à 20 km de distance. La maturation précoce à une taille inférieure vers l'extérieur du plateau est sans doute une réaction adaptative aux taux de mortalité plus élevés dans ces habitats par comparaison à ceux du milieu du plateau. De plus, la taille et l'âge réduits au moment de l'inversion sexuelle sur le plateau extérieur correspondent à une croissance ralentie et un régime de mortalité accrue. La structure sexuelle des populations locales change de façon marquée chez *C. sordidus* à travers le plateau, mais non chez *S. frenatus*. Les fortes densités de *C. sordidus* sur les récifs externes du plateau se caractérisent par des proportions trois fois plus grandes de mâles en phase terminale et de mâles primaires que sur les récifs du milieu du plateau. Ces différences entre des populations locales séparées par des dizaines de kilomètres mettent en évidence le danger qu'il y a à présumer de l'existence de structures sexuelles et de cycles biologiques homogènes dans la gestion à des échelles spatiales plus grandes des poissons de récifs exploités.

[Traduit par la Rédaction]

Introduction

Marine organisms with dispersive larval propagules are predicted to benefit from plasticity in the timing of major life history events in response to variable and unpredictable physical and social environments encountered after settlement (Warner 1991; Scheiner 1993). Coral reef fishes with dispersive larvae typically become site-attached as adults in spatially heterogeneous habitats and can develop striking differences in social and mating systems between localities (Shapiro 1991). If the local density, mortality, and growth regimes experienced by particular taxa vary through space, then the life history characteristics of individuals and demography of

local populations should reflect these changes over similar spatial scales.

To date, most studies of spatial variability in coral reef fish demography and population biology have concentrated on small-bodied fish such as labrids and pomacentrids (e.g., Warner and Hoffmann 1980a, 1980b; Doherty and Fowler 1994) that occupy home ranges of metres to hundreds of metres and can be studied at these small scales. Because ecologically important patterns and processes occur at differing, but explicit, scales, the spatial scale at which a system is explored will determine which patterns are detected and which are missed (Sale 1998). As principles of reef fish ecology, established largely through work on small-bodied taxa, are explored for larger and more mobile taxa, the minimum spatial

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scales must increase (Kritzer 2002). Studies that examine a variety of aspects of population biology are rare for large reef fish but are needed to identify which traits exhibit variation and the spatial scales on which they vary (Kritzer 2002).

Natural variation in the demography and life histories of fishes on reefs separated by tens of kilometres may confound spatially based fisheries management practices operating over larger scales. Coral reef fisheries typically target large, mobile species (Jennings and Lock 1996), and management practices often consider species to be relatively homogeneous in demography and to consist of individuals with similar life history characteristics over large spatial scales extending to hundreds of kilometres. If differences in population parameters exist over tens of kilometres, many variables such as abundance, body size, age structure, age at maturation, and sexual composition of populations used to infer the effects of fishing between locations (Russ 1991) may be unreliable indicators of impact.

This study investigates spatial variability in the reproductive biology and sexual composition of two species of unharvested scarid fishes known to differ in size across the continental shelf of the northern Great Barrier Reef (GBR) (Gust et al. 2001). Fork lengths of scarid fishes on outer shelf reef crests were 30% smaller on average than for conspecifics on mid-shelf reef crests only 20 km away. Smaller body sizes on the outer shelf were documented in eight species including *Chlorurus sordidus* and *Scarus frenatus* (Gust et al. 2001). These body size differences reflect significant changes in the shape of growth curves and reduced asymptotic sizes on the outer shelf (Gust et al. 2002). Furthermore, these species experienced higher mortality rates and reduced longevity on outer shelf reefs than on mid-shelf reefs (Gust et al. 2002). Such differences in growth and mortality could have profound life history consequences (Stearns 1992) and may alter timing in the key life history events of maturation and sex reversal for both species between shelf positions.

Life history theory enables qualitative predictions of the relative timing of maturation and sex reversal between local populations of sequentially hermaphroditic species. The key assumption in these predictions is that the timing of both events should be flexible and respond to local conditions to maximize an individual's reproductive success. Age at maturity should respond to differences in mortality schedules, which can greatly influence the reproductive fitness of individuals (Stearns 1992). Both Reznick et al. (1990) and Kozlowski (1992) suggested that reduced adult survival should promote earlier maturation and increased reproductive effort in fishes. As such, both *C. sordidus* and *S. frenatus* should mature at younger ages on outer shelf reefs than on mid-shelf reefs. Maturation in many organisms is also accompanied by a decrease in or cessation of growth (Bernado 1993), and Sadovy (1996) suggested that sexual maturity in fishes tends to coincide with growth approaching an asymptote. Since growth curves approach an asymptote at smaller sizes for both species on the outer shelf (Gust et al. 2002), maturation should occur at smaller sizes as well as younger ages for both species on the outer shelf.

Differences in growth and mortality rates between locations are also predicted to influence the timing of sex reversal in hermaphroditic fishes (Sadovy and Shapiro 1987). In protogynous reef fishes (where some females undergo sex reversal to males), environmentally mediated sex change appears to be

the rule rather than the exception (Warner 1988). It is widely accepted that male reproductive success and the timing of sex reversal in hermaphroditic fish depend on the prevailing social system (e.g., Shapiro 1991), the number of females available for mating, and the number of males with whom those matings must be shared (Warner 1988). In turn, social systems and the composition of populations can be strongly influenced by local density (Warner and Hoffmann 1980a, 1980b).

The most broadly accepted hypothesis about sex change in fishes is termed the size advantage model and suggests that if the expected number of offspring produced differs between the sexes with size or age, then an individual that changes sex can take advantage of these differences and have more offspring than an individual that remains exclusively male or female (Warner 1988). Warner (1975) used simulations based on the size advantage model to show that the age of sex reversal in hermaphroditic fishes should decrease as mortality rates increase. As such, individuals of both *C. sordidus* and *S. frenatus* on outer shelf reef crests are predicted to undergo sex reversal at younger ages than conspecifics on exposed reef crests of the mid-shelf.

Accordingly, the major aim of this study was to investigate the effects of differing growth and mortality regimes on timing of maturation and sex change in local populations of two protogynous reef fishes. The study also aimed to describe spatial differences in the sexual composition of local populations of both *C. sordidus* and *S. frenatus* across the continental shelf of the northern GBR. Underwater visual censusing (UVC) was used to quantify local abundances of these fish and to estimate proportions of initial- and terminal-phase coloration. Otolith ageing combined with histological examination of gonads was used to investigate demographic patterns and shifts in the timing of maturation and sex reversal for both taxa between mid- and outer continental shelf reefs.

Materials and methods

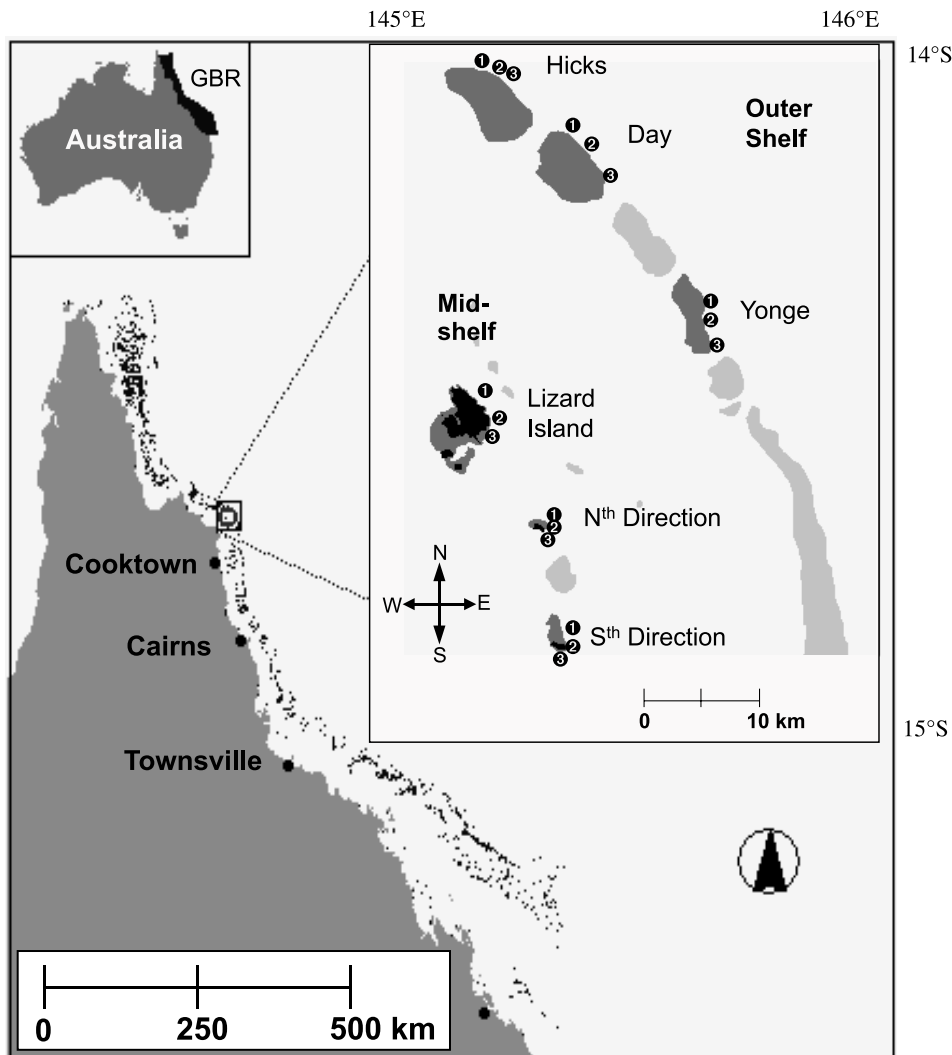
Study species

This study examines two common and widely distributed scarids: *C. sordidus* and *S. frenatus*, since previous research indicated that they differ significantly in body sizes, growth, and mortality rates between mid- and outer continental shelf positions (Gust et al. 2001, 2002). Both taxa are readily identified in the field and the annual nature of otolith markings has been validated for both species on the northern GBR (Choat et al. 1996). Validated annual otolith increments facilitate rigorous comparison of age-specific sexual development between shelf positions. Scarids are typically protogynous hermaphrodites and males and females display different colour phases (Choat and Robertson 1975). As a result, UVC techniques can provide estimates of sexual composition in local populations. Furthermore, scarids are moderately site-attached and unlikely to move between reefs or across the continental shelf, so patterns of sexual composition and life history characteristics should reflect local conditions rather than different ontogenetic stages of dispersing adults.

Study sites

Research was conducted over 18 exposed reef crest sites on the windward (eastern) sides of three mid- and three outer shelf reefs on the northern GBR (Fig. 1). Three sites

Fig. 1. The six reefs surveyed and sampled on mid- and outer continental shelf positions on the northern Great Barrier Reef (GBR), Australia. Replicate sample sites on each reef are indicated.



were surveyed on each of the mid-shelf reefs Lizard Island and North and South Direction islands and the outer shelf reefs Yonge, Hicks, and Day. Reefs and sites were chosen randomly from available locations subject to the constraints of travelling time from Lizard Island and suitable anchorages. This design ensured large sample sizes for comparison of equivalent habitat zones on the mid- and outer shelf and provides demographic information broadly representative of local populations on exposed reef crests. Because existing evidence strongly indicated that major differences in the demographic characteristics of both species exist only between shelf positions and not among replicate reefs within shelf positions (Gust et al. 2001, 2002), UVC and reproductive data were pooled at the shelf level for both species.

Underwater visual surveys

The author conducted all UVC surveys on SCUBA in 2–6 m of water at each site. Species abundance data from parrotfishes encountered on six replicate 45 m by 6 m transect swims at each site were recorded on waterproof data sheets. Individuals were identified to species and classified by colour phase along with an estimate of their fork length. Length estimates were made to the nearest 4-cm size class,

and individuals were only included in the census if greater than 10 cm in total length. The choice of 10 cm as the smallest size class to be surveyed reflected a conservative approach that aimed to avoid difficulties in identifying small, typically cryptic juvenile scarids that often school together and share common colour patterns (Bellwood and Choat 1989). Each day before visual censusing, the total lengths of 20 wooden parrotfish models were estimated underwater and compared with their known lengths. This procedure aided accurate estimation of sizes, typically to within ± 2 cm of true lengths, so no conversion factor was required to convert estimates to actual sizes (Gust et al. 2001). Operational sex ratios (i.e., numbers of mature female to mature males) were determined from UVC ratios of initial-phase (IP) to terminal-phase (TP) fish corrected by the proportions of IP fish that were mature females and primary males in each shelf position. These proportions were determined by histological investigation of over 300 individuals of each species.

Sampling procedures

After visual surveys were complete on each reef, hand spears were used to collect *C. sordidus* and *S. frenatus* from nine windward reef crest sites in both mid- and outer shelf

Table 1. Sample sizes for *C. sordidus* and *S. frenatus* collected from the northern Great Barrier Reef pooled over the austral summers of 1996 and 1997.

Species	Shelf position	November	December	February	March
<i>C. sordidus</i>	Mid-	48	226	46	0
	Outer	44	44	141	104
<i>S. frenatus</i>	Mid-	46	275	59	0
	Outer	47	9	7	18

positions (Fig. 1). A total of 661 *C. sordidus* and 525 *S. frenatus* were collected between November and March in 1996 and 1997 (Table 1). Differences existed in the peak timing of collections between shelf positions; however, observations of spawning behaviour throughout this period suggests that multiple batch spawning occurred and that reproductive data are broadly comparable between habitats. To broadly characterize populations from exposed reef crest habitats in each shelf position, sites were separated by hundreds to thousands of metres on each reef. Fish were stored on ice and returned to the Lizard Island research station for processing the same day. Each individual's fork length was measured to the nearest millimetre and whole-body weight was recorded to the nearest gram. Sagittal otoliths were removed, cleaned, washed in ethanol, and stored dry before ageing. Gonads were removed, weighed to the nearest gram, and stored whole in FAACC fixative (4% formaldehyde, 5% acetic acid, 1.3% calcium chloride dihydrate) before histological investigation of reproductive status. Gonadosomatic indices (GSIs) were calculated for each individual as the gonad's percent contribution to total body weight.

Reproductive and age analysis

In protogynous species, males may develop directly from the larval stage or may develop from adult females by sex reversal. The former are called primary and the latter secondary males. Species with one development pathway, i.e., where all males arise from sex change, are monandric, whereas species with both male development pathways are labelled diandric (Sadovy and Shapiro 1987). From collections on the southern GBR, Choat and Robertson (1975) classified *C. sordidus* as a diandric species and noted that *S. frenatus* was weakly diandric with very rare primary males present in the population.

Histological techniques were used to identify immature and mature females, transitional sex changing individuals (here after referred to as transitionals), and primary and secondary males. To avoid bias, gonads were processed and staged in random order without knowledge of the collection site or the species, size, age, or colour phase of the fish. Initially, gonads from 40 individuals of both species were subsampled in anterior, mid-, and posterior locations to determine whether consistent differences in reproductive status result from the sectioning location along the length of the gonad. No evidence existed for variation in development status along the length of gonads in either species, and subsequent histological staging was based on the central section of each gonad. Gonad lobes were cut transversely into 3-mm tissue blocks, placed into cassettes, and stored in 70% ethanol.

Standard histological techniques for teleost gonads were adopted, with gonad sections being infiltrated and embedded

in paraffin, sectioned at 5 μm thickness, placed onto slides, and stained with Mayers haematoxylin and Young's eosin-erythrosin. Females were classified histologically as immature (stage 1 and 2 oocytes, i.e., chromatin nucleolar and perinucleolar stages), maturing (stage 3 oocytes, i.e., cortical alveoli stage), or mature (stage 4 and 5 oocytes, i.e., vitellogenic and ripe stages) on the basis of the most advanced oocytes present (West 1990). Transitionals were classified according to Sadovy and Shapiro (1987), and primary and secondary males were classified on the basis of criteria presented in Shapiro and Rasotto (1993). Individuals were classified as males rather than transitional if there was evidence of vas deferens formation and mature spermatozoa even if ovarian regression was not yet completed and oocytes persisted within the gonad (Hastings 1981). Primary male gonads were readily identified macroscopically, as they are large and white in comparison with the pink gonads of other IP female *C. sordidus*. Percent frequencies were calculated for each sexual category, and age and size at first maturity were defined as when >50% of the histologically examined females were mature. Similarly, mean age at sex reversal was estimated for both species when >50% of the final proportion of TP males were present within the local population. Individuals were aged based on annuli counts from sectioned sagittal otoliths following Choat et al. (1996). Each otolith was read twice and removed from further analysis if there was a discrepancy of two or more years that could not be resolved by a third reader. Approximately 5% of all otoliths were eliminated following this procedure.

Data analyses

The following analyses were conducted for both species. One-way analysis of variance (ANOVA) was used to determine cross-shelf differences in mean abundance. The model tested the effects of shelf position (a fixed effect) using mean abundances of each species at the site level as replicates. Age at 50% maturation was determined in both shelf positions from frequency distributions of histological stage in each year class. Similarly, size at 50% maturation was determined from frequency distributions of histological stage in 20-mm fork length size classes. Before all ANOVA calculations, the assumption of homogeneity of variances was inspected via box plots of residuals, and $\log_{10}(X + 1)$ transformations were used to remove heterogeneity of variances as required. Ratios of IP to TP fish, operational sex ratios, and the proportions of primary males in *C. sordidus* populations were compared across the shelf by two-way contingency tables and chi square statistics using raw frequencies.

Results

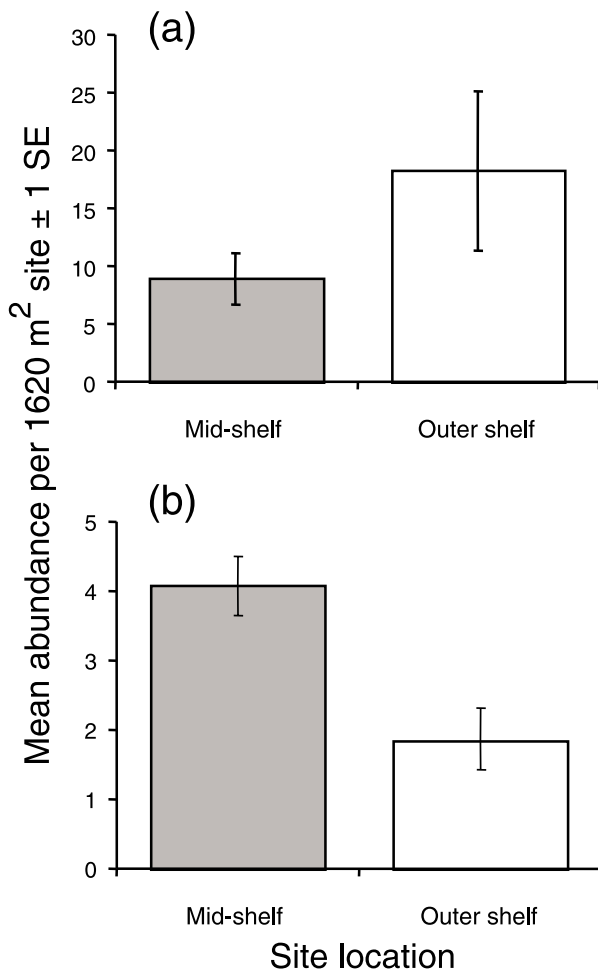
Chlorurus sordidus and *S. frenatus* were collected across the continental shelf in the summer months of 1996 and

Table 2. Summary of previous research findings for *C. sordidus* and *S. frenatus* populations on mid- and outer continental shelf positions on the northern Great Barrier Reef from Gust et al. (2002).

Species	Shelf position	Growth parameter (± 1 SE)	Mortality rate	Mean age (years) (± 1 SE)
<i>C. sordidus</i>	Mid-	$K = 1.10 \pm 0.50$ $L_{\infty} = 192 \pm 4$ mm	Low, $M = 0.31$	2.73 ± 0.15
	Outer	$K = 1.10 \pm 0.30$ $L_{\infty} = 158 \pm 4$ mm	High, $M = 0.49$	1.85 ± 0.10
<i>S. frenatus</i>	Mid-	$K = 0.80 \pm 0.20$ $L_{\infty} = 255 \pm 5$ mm	Low, $M = 0.24$	4.87 ± 0.21
	Outer	$K = 1.10 \pm 0.40$ $L_{\infty} = 196 \pm 4$ mm	High, $M = 0.40$	2.92 ± 0.17

Note: Growth parameters are derived from von Bertalanffy growth equations. K is the growth coefficient that describes the rate at which the asymptotic size L_{∞} is approached. L_{∞} is the mean asymptotic length of fish if they were to grow indefinitely. Natural mortality rate (M) is derived from the slope of a regression line plotted from the natural logarithm of the number of fish sampled in each age class.

Fig. 2. Mean abundance of (a) *C. sordidus* and (b) *S. frenatus* from exposed reef crest sites on the mid- and outer shelves.



1997, and sample sizes differed between months (Table 1). Previous research findings for these species across the shelf on the northern GBR are summarized from Gust et al. (2002) and provide information for interpreting shifts in maturation and sex change characteristics and population structures (Table 2). Differences in von Bertalanffy growth parameters, mortality regimes, and average age existed for both taxa between mid- and outer continental shelf positions. On the

Table 3. Comparison of mean abundances for *C. sordidus* and *S. frenatus* between sites on the mid- and outer continental shelves.

Species	Source of variation	df error	MS error	F	p
<i>C. sordidus</i>	Shelf position	1	395.1	4.7	0.046*
	Residual	16	84.3		
<i>S. frenatus</i>	Shelf position	1	22.6	12.1	0.003**
	Residual	16	1.9		

Note: *, $p < 0.05$; **, $p < 0.01$.

mid-shelf, both *C. sordidus* and *S. frenatus* achieved larger L_{∞} values (mean asymptotic length of fish if they were to grow indefinitely) and asymptotic body sizes, lower rates of natural mortality, and higher average ages than on the outer shelf (Table 2).

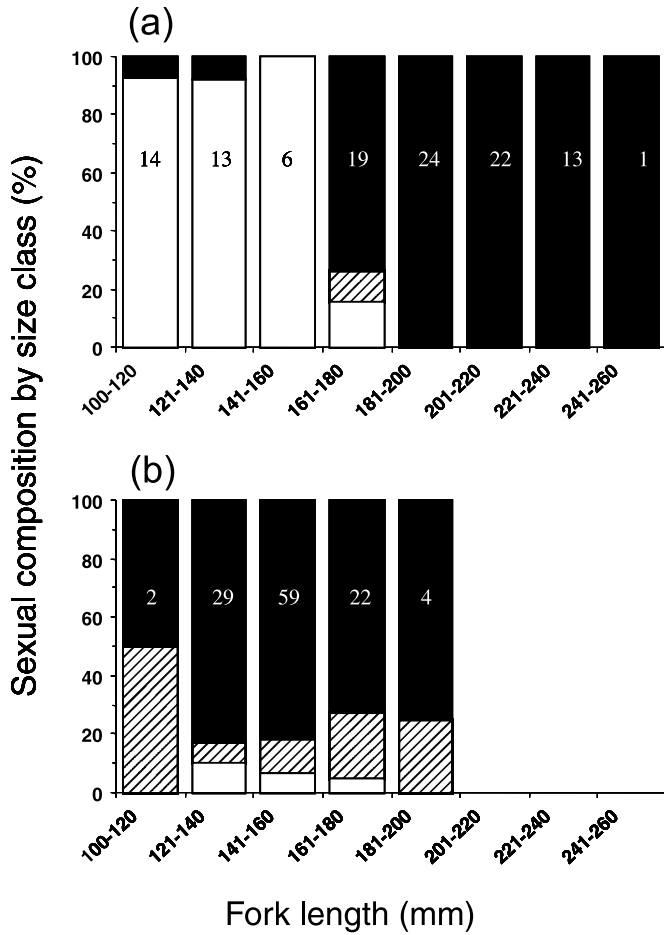
Distribution and abundance

UVC surveys revealed differences in the relative and absolute abundance of both species across the shelf. *Chlorurus sordidus* mean abundances at the site level were between 2- and 10-fold higher than those of *S. frenatus*, and the abundance of both species varied significantly across the shelf (Fig. 2). *Chlorurus sordidus* was more abundant on the outer shelf than on the mid-shelf (Fig. 2; Table 3), whereas *S. frenatus* was more abundant on the mid-shelf than on the outer shelf (Fig. 2; Table 3).

Maturation

Maturation in *C. sordidus* occurred at smaller sizes and younger ages on outer barrier reefs than on mid-shelf reefs. Fifty percent maturation levels were achieved once individuals reached the 161–180 mm fork length size class on the mid-shelf but occurred in the 100–120 mm size class on the outer shelf (Fig. 3). Fifty percent maturation was achieved in the 1-year age class on the mid-shelf and in the 0-year age class on the outer shelf (Fig. 4). Mean female gonadosomatic indices in the 0-year age class fish were significantly higher on the outer shelf than on the mid-shelf (ANOVA, $F_{[1,96]} = 10.3$, $p = 0.0018$), which also suggests earlier sexual maturation on the outer shelf. Thus, *C. sordidus* typically matured in the 0-year age class at fork lengths above 100 mm on

Fig. 3. Female *C. sordidus* frequency distribution of maturational stages on (a) the mid-shelf and (b) the outer shelf. Open bars, immature females; hatched bars, maturing females; solid bars, mature females. Sample sizes are indicated for each class.



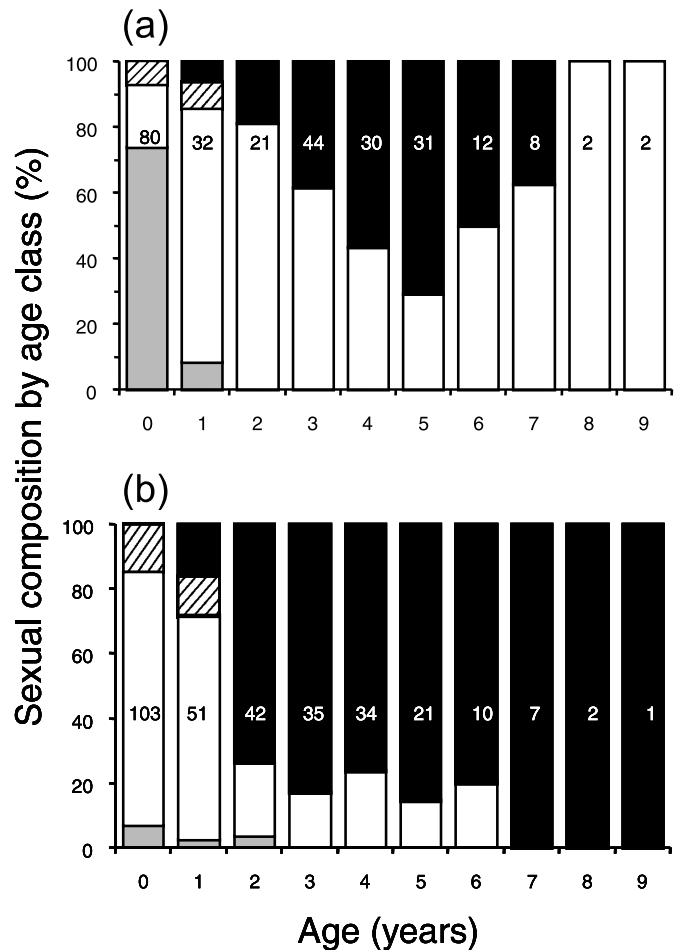
outer shelf reefs but did not mature until reaching the 1-year age class and fork lengths above 161 mm on the mid-shelf.

Maturation in *S. frenatus* on the outer shelf also occurred at smaller sizes and younger ages than on the mid-shelf. Fifty percent maturation occurred in the 221–240 mm fork length size class on the mid-shelf and in the 181–200 mm size class on the outer shelf (Fig. 5). Fifty percent maturation was achieved in the 2-year age class on the mid-shelf and in the 1-year age class on the outer shelf (Fig. 6). Thus, *S. frenatus* maturation typically occurred above 181 mm fork length as 1-year-olds on outer shelf reefs but was delayed until individuals reached 2 years of age and fork lengths exceeded 221 mm on the mid-shelf.

Protogynous sex change

Protogynous sex reversal was confirmed from the presence of sex-changing individuals in both species. Individuals captured in transitional colour phases were functional males in both species, indicating that functional sex change precedes colour changes in these scarids. The number of individuals detected with transitional gonads was low (<1% of individuals), especially for *S. frenatus*, such that statistical comparison of their characteristics was precluded. The low numbers of transitional individuals sampled for both species

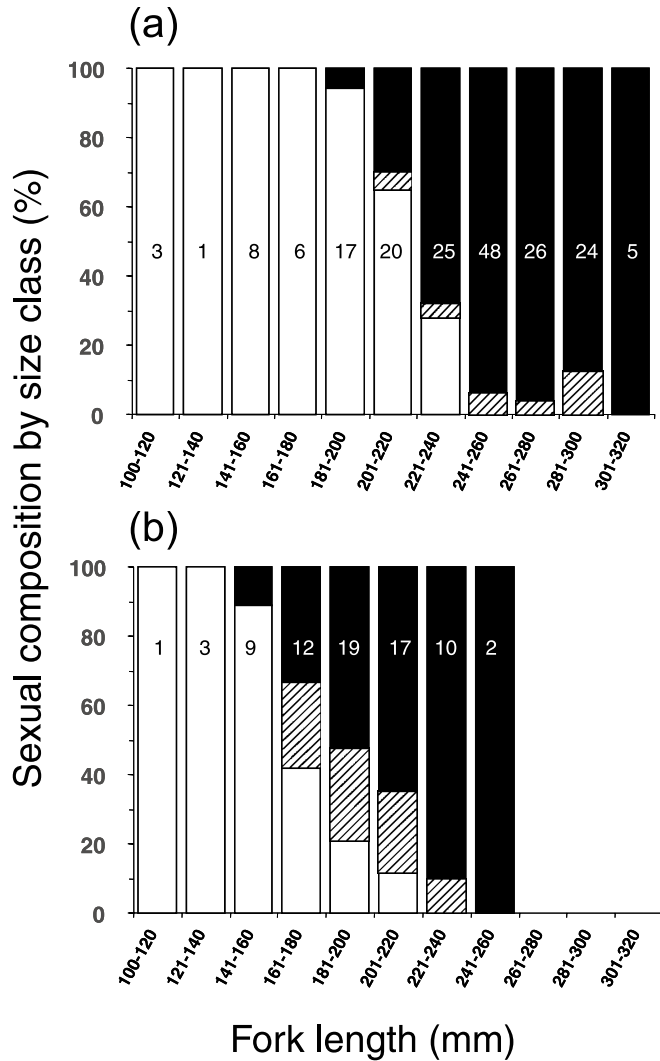
Fig. 4. *Chlorurus sordidus* age-based sexual frequencies on (a) the mid-shelf and (b) the outer shelf. Shaded bars, immature females; open bars, mature females; hatched bars, primary males; solid bars, terminal males. Sample sizes are indicated for each class.



precluded precise definition of the ages at sex reversal, which were inferred instead from age-specific sexual patterns. Sex reversal occurred over a wide range of sizes and ages for both taxa, although estimates of mean age at sex reversal in both species were reduced on the outer shelf relative to the mid-shelf. The mean age of sex reversal for *C. sordidus* was approximately 2.5 years on the mid-shelf and 1.5 years on the outer shelf (Fig. 4). The mean age of sex reversal for *S. frenatus* was approximately 3.5 years on the mid-shelf and 2.5 years on the outer shelf (Fig. 6).

TP males of both species on the outer shelf were significantly smaller and younger than conspecifics on the mid-shelf (Fig. 7; Table 4). On the outer shelf, *C. sordidus* TP males were on average 47 mm shorter in fork length than those on the mid-shelf (Fig. 7a; Table 4). On the outer shelf, *C. sordidus* TP males were on average 0.6 year younger than those on the mid-shelf (Fig. 7b; Table 4). The mean fork length of *S. frenatus* TP males on the outer shelf was 77 mm smaller than on the mid-shelf (Fig. 7c; Table 4). The mean age of *S. frenatus* TP males on the outer shelf was significantly younger, by 2.0 years, than on the mid-shelf (Fig. 7d; Table 4).

Fig. 5. Female *S. frenatus* frequency distribution of maturational stages on (a) the mid-shelf and (b) the outer shelf. Open bars, immature females; hatched bars, maturing females; solid bars, mature females. Sample sizes are indicated for each class.

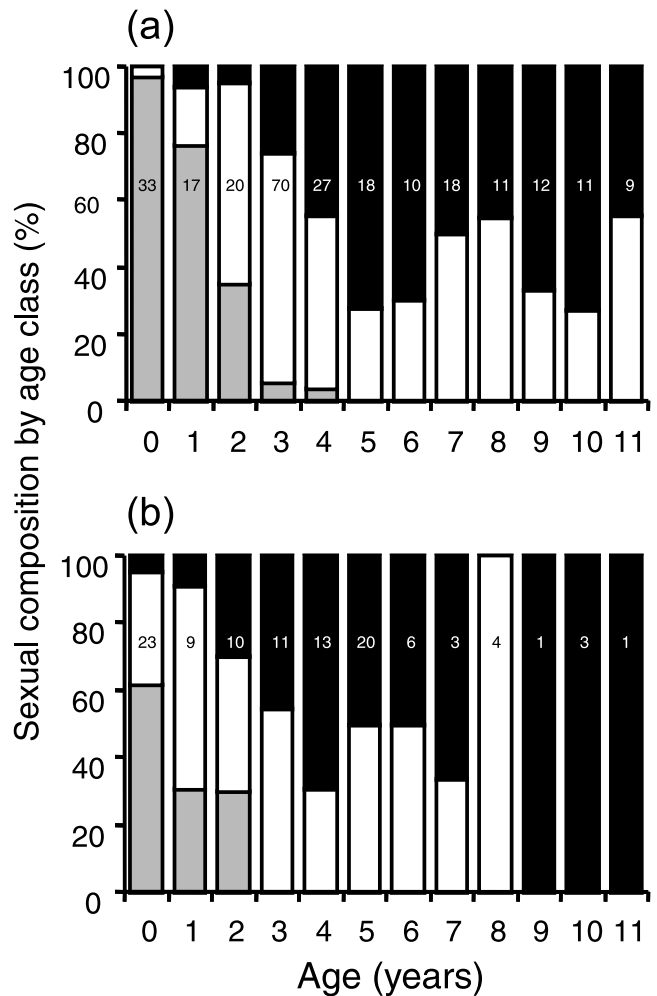


Population structures and sex ratios

Age-based population structures differed markedly between shelf positions for *C. sordidus* (Fig. 4). On the mid-shelf, females persisted through all age classes, and the proportion of TP males increased to age 5 and then declined (Fig. 4a). On the outer shelf, no females persisted beyond age 6 and TP males represented more than 70% of each age class older than 1 (Fig. 4b). Age-based population structures differed slightly between shelf positions for *S. frenatus*, although small sample sizes in the oldest age classes on the outer shelf make comparisons difficult (Fig. 6). Females persist to age 11 on the mid-shelf but only to age 8 on the outer shelf, although approximately 50% of fish from ages 8 to 11 are females in each shelf position (Fig. 6).

Plots of GSI versus fork length for different sexual categories revealed cross-shelf differences in both species. For *C. sordidus*, the proportion of primary males increased significantly ($\chi^2 = 47.7$, $df = 1$, $p < 0.001$) from the mid-shelf

Fig. 6. *Scarus frenatus* age-based sexual frequencies on (a) the mid-shelf and (b) the outer shelf. Solid bars, terminal-phase males; open bars, mature females; shaded bars, immature females. Sample sizes are indicated for each age class.



to the outer shelf (Fig. 8). Histology confirmed that 4.0% of IP fish on the mid-shelf were primary males as opposed to 12.9% on the outer shelf. Mid-shelf primary males displayed low GSI values (mean 0.1) that were equivalent to values for secondary males (Fig. 8a). However, outer shelf primary males displayed 20 times higher GSI values (mean 2.0) that were similar to values for mature females (Fig. 8b). Plots of GSI versus fork length for *S. frenatus* indicated that 10% of TP males on the mid-shelf possessed large gonads (GSI > 0.5) that were of similar proportions to mature female gonads (Fig. 9a). However, on the outer shelf, all TP males had small GSI values, with an average of 0.1 (Fig. 9b).

UVC surveys indicated marked differences in *C. sordidus* size distributions between shelf positions, where the largest size classes for both colour phases on the mid-shelf were missing for outer shelf positions (Figs. 10a and 10c). There were significant changes in IP to TP ratios between mid- and outer shelf populations ($\chi^2 = 60.6$, $df = 1$, $p < 0.001$), with TP fish being three times more common on the outer shelf (Figs. 10a and 10c). Operational sex ratios for *C. sordidus* on the mid-shelf were significantly more female biased than

Fig. 7. Mean terminal-phase male size (fork length) for (a) *C. sordidus* and (c) *S. frenatus* between shelf positions. Mean terminal-phase male age (years \pm 1 SE) for (b) *C. sordidus* and (d) *S. frenatus* between shelf positions.

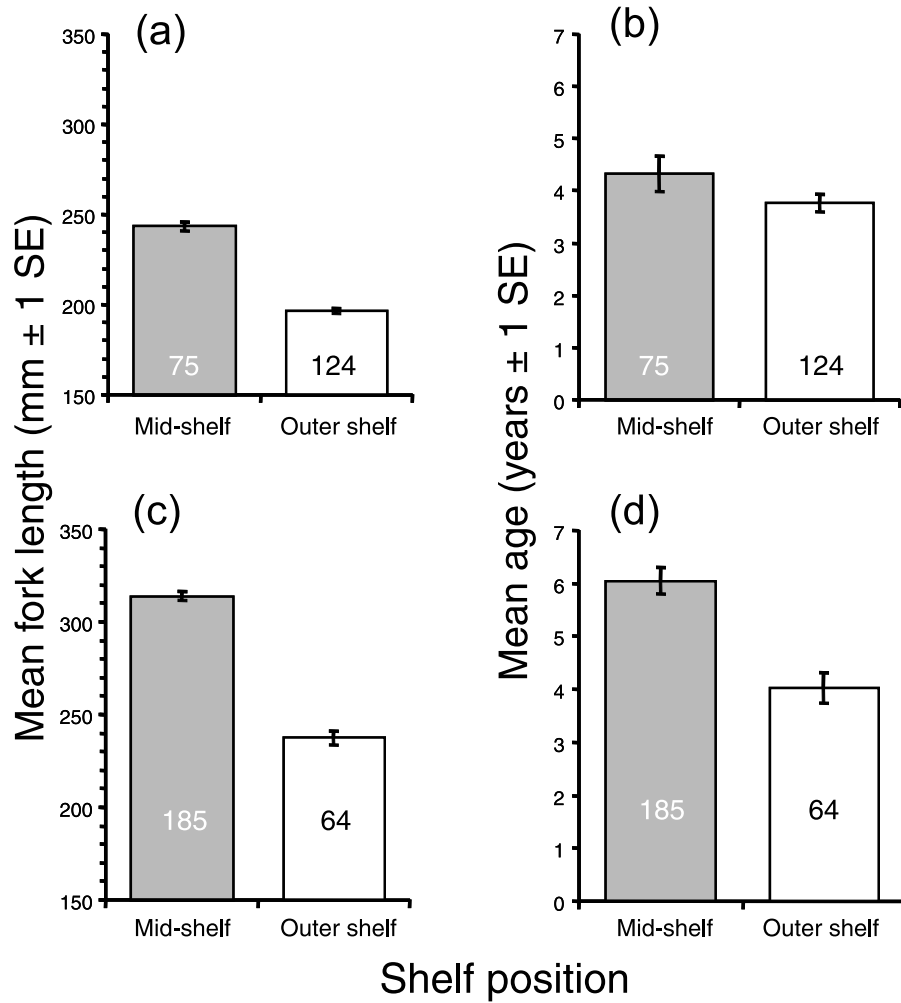


Table 4. Comparison of terminal-phase male body sizes and ages for *C. sordidus* and *S. frenatus* between mid- and outer continental shelf positions.

Species	Dependent variable	Source of variation	df	MS	F	p																										
<i>C. sordidus</i>	Size (fork length)	Shelf position	1	102 476	282.1	<0.0001***																										
		Residual	199	363.30			<i>C. sordidus</i>	Age (years)	Shelf position	1	13.10	5.4	0.0217*	Residual	199	2.40	<i>S. frenatus</i>	Size (fork length)	Shelf position	1	261 321	285.1	<0.0001***	Residual	249	916.40	<i>S. frenatus</i>	Age (years)	Shelf position	1	222.1	22.0
<i>C. sordidus</i>	Age (years)	Shelf position	1	13.10	5.4	0.0217*																										
		Residual	199	2.40			<i>S. frenatus</i>	Size (fork length)	Shelf position	1	261 321	285.1	<0.0001***	Residual	249	916.40	<i>S. frenatus</i>	Age (years)	Shelf position	1	222.1	22.0	<0.0001***	Residual	249	10.10						
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<i>S. frenatus</i>	Age (years)	Shelf position	1	222.1	22.0	<0.0001***																										
		Residual	249	10.10																												

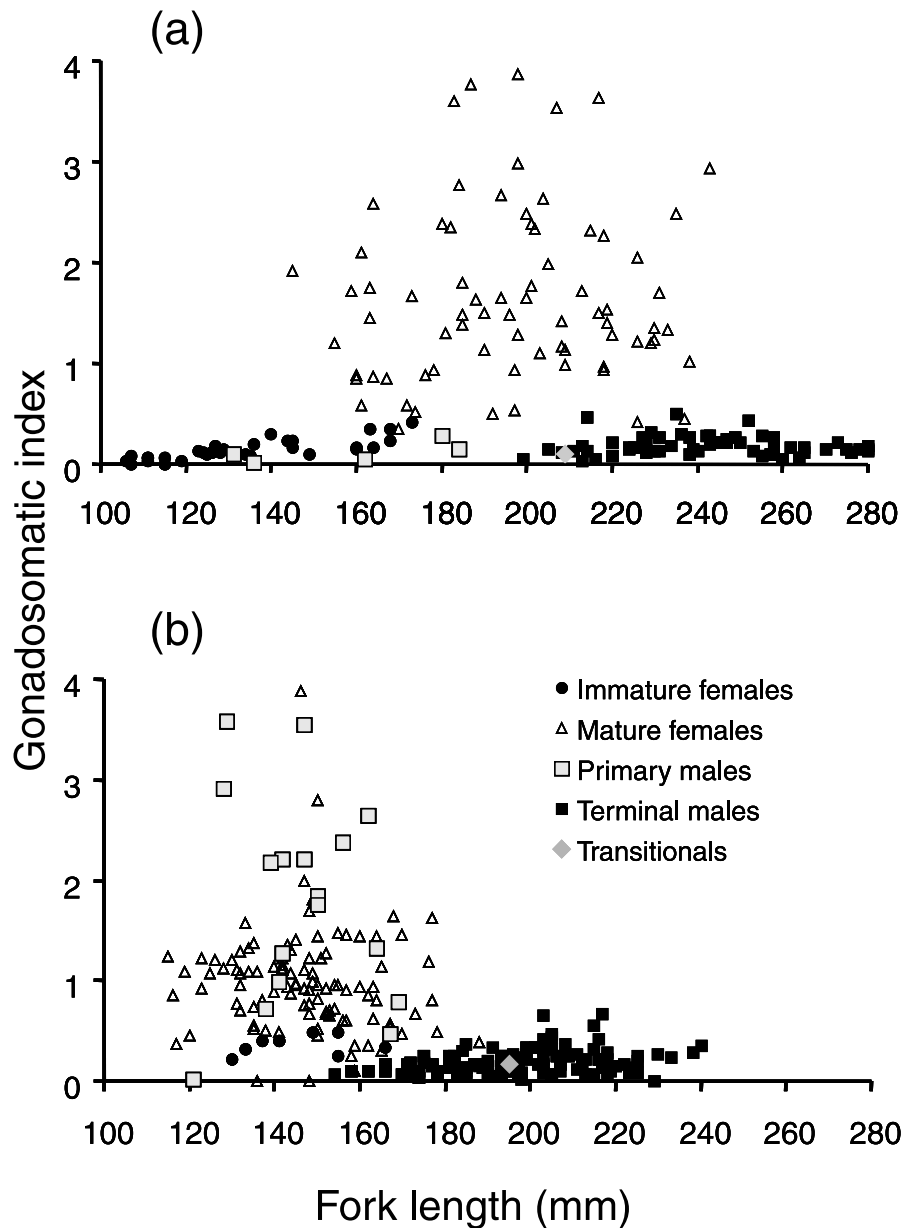
Note: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.0001$.

on the outer shelf ($\chi^2 = 8.39$, $df = 1$, $p = 0.0037$). Operational sex ratios changed by a factor of 3 from the mid-shelf (4.75:1) to the outer shelf (1.48:1).

UVC surveys indicated marked differences in *S. frenatus* size distributions between shelf positions, where the largest three size-classes on the mid-shelf were missing on the outer shelf (Figs. 10b and 10d). On the mid-shelf, IP to TP ratios (2.12:1) were 32% more female biased than on the outer

shelf (1.60:1), but chi square tests indicated no significant differences across the shelf ($\chi^2 = 1.43$, $df = 1$, $p = 0.231$). Since no primary-phase males were identified among the 558 *S. frenatus* sampled, the species appears monandric on the northern GBR. Operational sex ratios on the mid-shelf (1.49:1) were 40% more female biased than the outer shelf (1.07:1), although chi square tests indicated no significant difference across the shelf ($\chi^2 = 0.29$, $df = 1$, $p = 0.591$).

Fig. 8. *Chlorurus sordidus* gonadosomatic indices versus fork lengths on (a) the mid-shelf and (b) the outer shelf. Sexual categories were identified by histology.



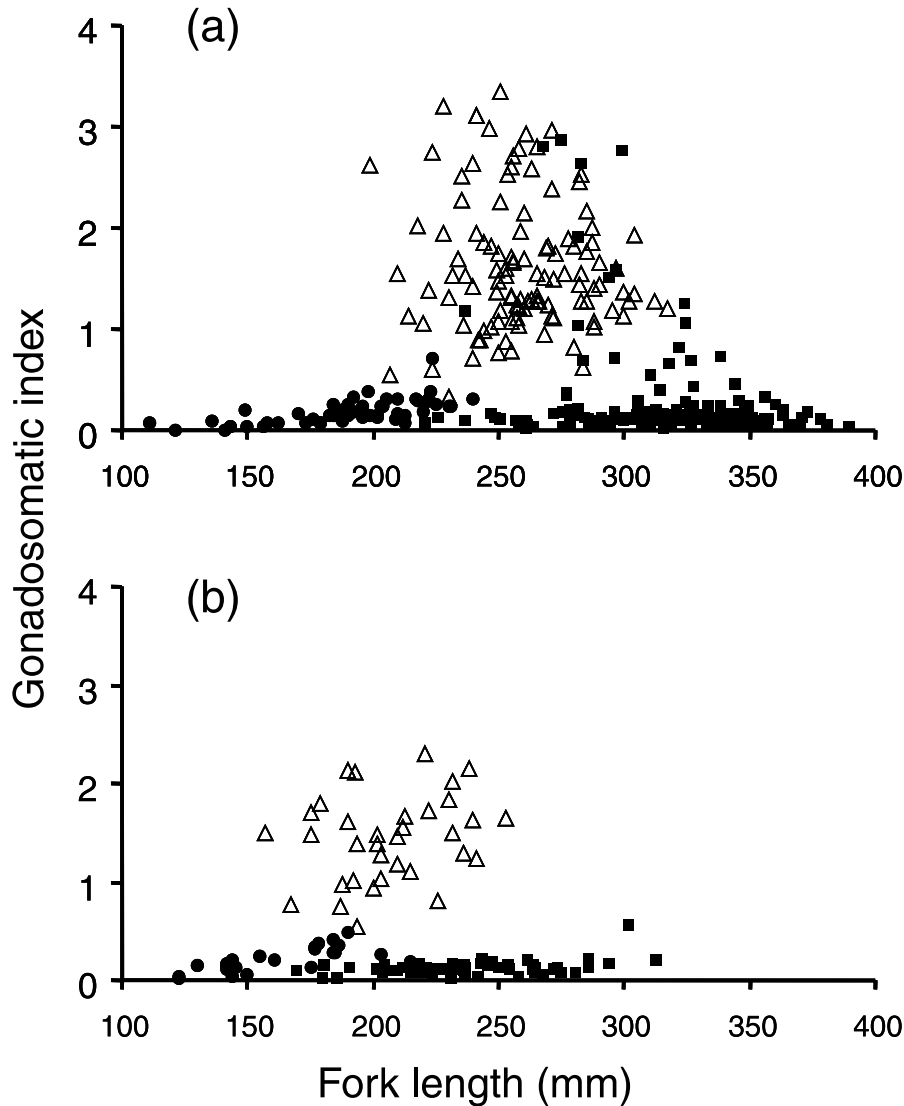
Discussion

This study revealed considerable differences in the size and age at maturity and sex change in the protogynous reef fishes *C. sordidus* and *S. frenatus* across a distance of only 20 km. Both species displayed changes in size structure across this spatial scale, and *C. sordidus* demography also changed markedly, with operational sex ratios altering by a factor of 3 between mid- and outer shelf positions. Since these species are not harvested on the GBR and are not subject to any known direct anthropogenic disturbances, observed changes in the timing of major life history events and demography over tens of kilometres are likely to reflect natural variability and responses to local environmental and social conditions. *Chlorurus sordidus* mean abundance per site doubled from the mid- to the outer shelf, whereas *S. frenatus* mean

abundance halved. Despite this opposite pattern in relative abundance between locations, both species matured and changed sex at reduced mean sizes and ages on the outer shelf. This suggests that conspecific density alone is not responsible for cross-shelf changes in the timing of maturation and sex reversal in both species. Rather, consistent differences in growth and mortality regimes for both species between shelf positions (Gust et al. 2002) are implicated.

Large changes in population biology over tens of kilometres may compromise fisheries management efforts over larger spatial scales. Research on predators commonly targeted in coral reef fisheries typically reports population parameters averaged across many locations or at best makes spatial comparisons on very broad scales (hundreds of kilometres or more; Newman et al. 1996). This study indicates that generalized population parameters produced over large-scale studies

Fig. 9. *Scarus frenatus* gonadosomatic indices versus fork lengths on (a) the mid-shelf and (b) the outer shelf. Sexual categories were identified by histology. Circles, immature females; triangles, mature females; squares, terminal-phase males.



may poorly represent fishery resources, since population parameters can change markedly over tens of kilometres. Without knowledge of the spatial scales at which population parameters differ and the magnitude of this natural variation, changes between locations in population size or age structures, sex ratios, or the size and age at which individuals mature and change sex may all be unreliable indicators of anthropogenic impacts such as fishing.

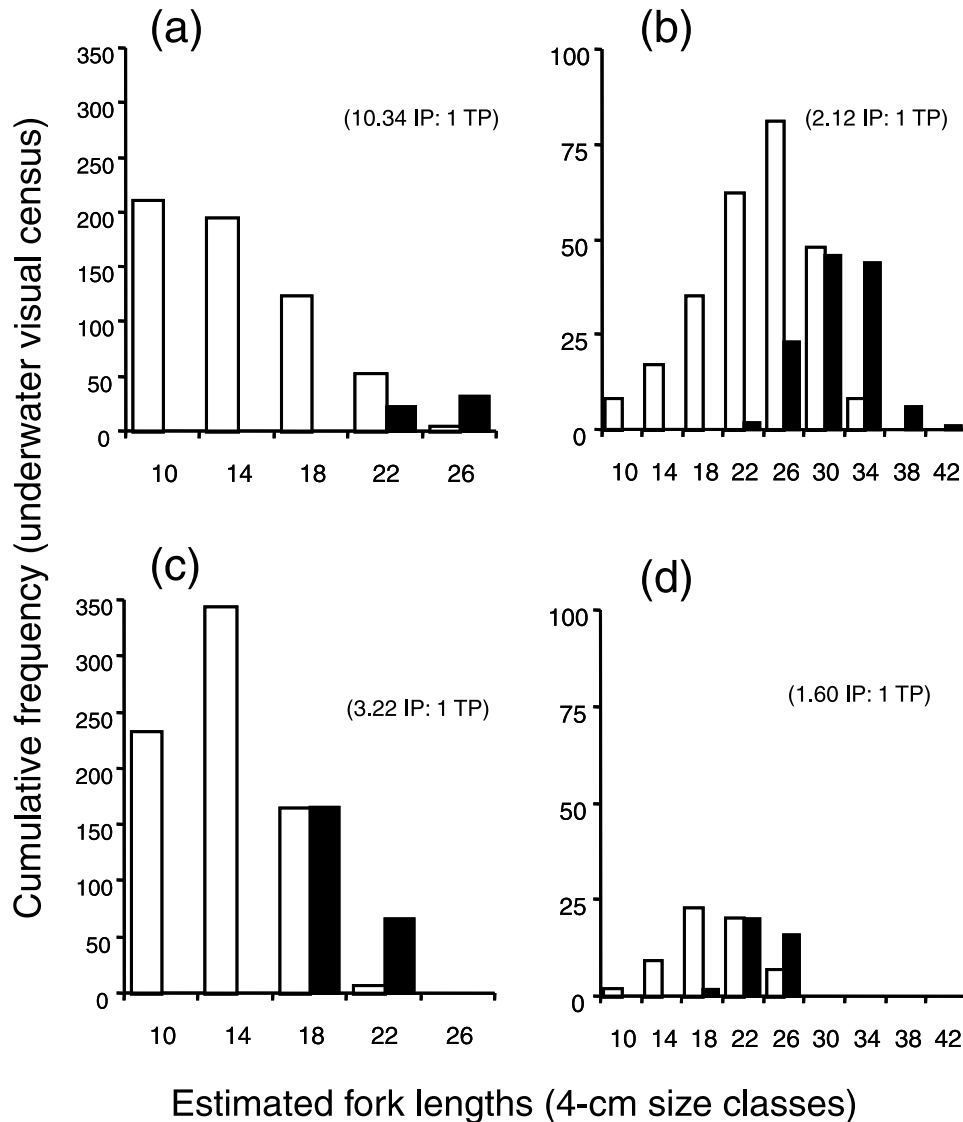
Maturation

Age at maturity is one of the most important traits in the life history of an organism (Belk 1998) and has a strong effect on lifetime reproductive success and the intrinsic rate of population growth, two common measures of fitness (Reznick 1990). Although flexibility in the timing of maturation within species has previously been widely documented in fishes (Stearns 1992; Berrigan and Koella 1994), Bernado (1993) provided some rare accounts of invariant age or size at maturation within species. For instance, Jones and Thompson

(1980) concluded that maturation and sex reversal in the temperate protogynous reef fish *Pseudolabrus celidotus* were more closely related to size than to age and found that maturation only occurred once a threshold body size was exceeded.

This study described flexibility in both the size and age at maturation in both *C. sordidus* and *S. frenatus*. Plasticity in the timing of maturation is generally considered to be a response to prevailing conditions, and empirical studies in teleosts using otolith ageing techniques have commonly shown a significant correlation between the age at first reproduction and both mortality and growth rates in local populations (Roff 1984). Roff (1984) proposed that the timing of maturation represented a trade-off between the demands of reproduction, growth, and survival in response to local conditions. A number of theoretical ecologists subsequently developed the concept of "optimal" ages or sizes at which maturation should occur to maximize an individual's fitness and reproductive output (Stearns and Koella 1986; Kozłowski 1992; Stearns 1992). The majority of their modelling approaches are sensitive to

Fig. 10. Size frequency distributions estimated from underwater visual censuses across nine sites in each shelf position: (a) *C. sordidus*, mid-shelf, (c) *C. sordidus*, outer shelf, (b) *S. frenatus*, mid-shelf, and (d) *S. frenatus*, outer shelf. Open bars, initial phase (IP); solid bars, terminal phase (TP). Ratios of IP to TP fish are indicated.



varying growth and mortality regimes and attempt to predict when animals should mature to obtain the optimal balance between costs and benefits of early and late maturation.

Theoretical models typically predict that maturation should occur earlier as adult mortality rates increase or as growth increases (e.g., Roff 1984; Stearns and Koella 1986). The findings of the present study are consistent with the first but not the second prediction. Both scarid taxa were found to become sexually mature at smaller sizes and younger ages on the outer shelf where prevailing mortality rates are higher and growth is reduced in comparison with the mid-shelf (Gust et al. 2002). Thus, although the most common pattern for variation in age and size at maturity involves animals maturing later at a smaller size when growth is reduced (Stearns and Koella 1986), the reduced size and age at maturity for both species on the outer shelf is more likely to represent a response to higher natural mortality rates on the outer shelf than prevailing growth differences across the shelf. The simplest way to improve survival to maturity is to mature earlier (Bell

1980), and it appears that on outer shelf reef crests, both species respond in this way. A similar pattern of reduced growth and earlier maturation in reef fish experiencing high mortality rates has been reported by Cowen (1990) and was suggested to reflect a reallocation of energy towards earlier or more intensive reproduction at the expense of somatic growth. Sadovy (1996) suggested that sexual maturity in fishes tends to coincide with growth approaching an asymptote. Thus, reduced asymptotic sizes for both species on the outer shelf may reflect the effects of earlier maturation and allocation of energy towards reproductive development at the expense of somatic growth.

Genetic mechanisms for maturation shifts in response to higher mortality regimes and the presence of predators have been noted in teleosts. For instance, Reznick et al. (1990) experimentally demonstrated that changes in the relative mortality of different age and size classes over several generations can result in selection of fish with genetically based differences in age and size at maturity. Genetic explanations

appear unlikely in this case, however, since both study species possess dispersive larval propagules, which are assumed to be freely exchanged between reefs in mid- and outer shelf positions. Analysis of mitochondrial DNA from *C. sordidus* and *S. frenatus* sampled during this study indicated high rates of gene flow for both species within and among shelf positions and provided no evidence of barriers to gene flow across the continental shelf (Dudgeon et al. 2000). Changes in the timing of maturation across the shelf could also reflect differences in water temperature and its effect of modifying metabolism (Jobling 1981). However, this seems unlikely in the present study, since the water body spanning mid- and outer shelf positions on the northern GBR is well mixed and has a similar temperature (Wolanski 1986).

Protogynous sex change

On the outer shelf, reduced size and age at sex reversal in both *C. sordidus* and *S. frenatus* is consistent with predictions of the size advantage model and reduced growth regimes for both species. Simulations based on the size advantage model by Warner (1975) predicted delayed sex change (and since size is loosely correlated with age, a larger size at sex change) where the rate of female increase in fecundity with age is improved. Since female fecundity in fishes is typically a function of body size, larger size achieved at a given age suggests a more rapid increase in fecundity. Since body size asymptotes at smaller sizes for both species on the outer shelf (Gust et al. 2002), female reproductive potential may be constrained in these habitats and male reproductive success may increase more rapidly with age than on the mid-shelf. As such, protogynous sex change at younger ages and smaller sizes is both predicted and observed in both species on the outer shelf.

The change in mean age at sex reversal in both species between shelf positions is also consistent with predictions of the size advantage model regarding the effects of prevailing mortality regimes. On the outer shelf, both scarids are subject to higher mortality rates than on the mid-shelf (Gust et al. 2002). Higher mortality and reduced survivorship should reduce the size and age at sex reversal in hermaphroditic species (Warner 1975; Cowen 1990). Thus, it is difficult to determine whether changes in growth or mortality regimes across the shelf have independent or additive effects on the timing of sex change in these species, since cross-shelf differences in both processes are consistent with the observed pattern. Both Jones and Thompson (1980) and Cowen (1990) have reported similar confounding of the effects of concurrent changes in mortality and growth between locations on the timing of sex reversal in protogynous fishes, such that the relative importance of each factor could not be determined.

Population structures and social systems

Studies of social and mating systems in teleost fishes have been biased towards small, easily observed and manipulated reef fishes (e.g., Cole and Robertson 1988; Warner 1988; Cole and Shapiro 1992). Detailed descriptions of these systems in many mobile, larger bodied fishes such as *C. sordidus* and *S. frenatus* are not currently available, which limits interpretation of observed changes in population structure between locations. However, we know from collections on the southern GBR that *C. sordidus* is diandric, whereas *S. frenatus* was described

as weakly diandric (Choat and Robertson 1975). On the northern GBR, the present study confirmed diandric male development in *C. sordidus* but found that *S. frenatus* was monandric with no primary males in this section of its geographic range. Preliminary observations on the northern GBR suggest that *C. sordidus* displays loose groupings of IP fish in feeding schools attended by TP males that often interact aggressively, presumably in competition over females or spawning site resources. In contrast, *S. frenatus* maintains small, well-defined harems consisting of a single TP male and one to four IP females (N. Gust, personal observation).

Marked changes in population structure of *C. sordidus* between mid- and outer shelf positions suggest shifts in social and mating systems, which may represent responses to local population density. *Chlorurus sordidus* mean abundance doubled from nine individuals to 18 individuals per 1620-m² site between mid- and outer shelf positions. High-density local populations on the outer shelf were characterized by three-fold higher proportions of both TP and primary males than on the mid-shelf, and operational sex ratios differed across the shelf from 4.7:1 to 1.5:1 (females to males). Although threefold shifts in sex ratio over 20 km appear large, sex ratios can be highly variable over even moderate spatial scales in protogynous reef fish and similar shifts have previously been documented between reefs in the goby *Corphopterus glaucofraenum* (Cole and Shapiro 1992) and the scarid *Sparisoma viride* (van Rooij et al. 1996).

In *C. sordidus*, increased proportions of primary males on the outer shelf and their large GSI values suggest that they may be involved in group spawning mating strategies in this location. Cole and Shapiro (1992) suggested that primary males might arise from an immature ovariform stage by social regulation, may be genetically determined, may be triggered by some aspect of the physical environment, or may arise from a combination of these factors. Previous studies have implicated local population density as an important factor influencing the frequency (and presumably success) of the primary male strategy in reef fishes. For instance, Warner and Hoffman (1980a, 1980b) also reported higher proportions of primary males in high-density local populations of diandric reef fish and found that this pattern arose from differences in the economic defendability of resources by larger TP males. They showed that although TP males can prevent primary males from obtaining spawning success in low-density populations, this ability diminished as population density increased. Population density has regularly been implicated in changes in the social and mating systems of coral reef fishes between localities (Shapiro 1991). This author emphasized the importance of spatially patchy recruitment in altering local population densities and influencing the development of both social systems and local population structures. Higher recruitment of *C. sordidus* to outer shelf reef crests than to equivalent mid-shelf habitats could explain higher population densities despite higher rates of natural mortality and may provide suitable reproductive opportunities for high proportions of primary males to persist in local populations.

Scarus frenatus displayed a similar age-based demographic structure in both mid- and outer shelf positions. Interestingly, some small TP *S. frenatus* on the mid-shelf displayed high GSI values equivalent to those of mature females, which suggests that they may be participating in group spawns or

other sperm-competitive forms of mating in this location where mean densities are twice as high as on the outer shelf. Alternatively, large GSI values for these small males may indicate that they are recently sex-changed individuals where functional sex reversal is complete but gonads have not yet regressed in size. Direct observational studies to determine the prevailing social and mating systems for both species are required to interpret the differences in population structure described in this study over scales of tens of kilometres.

In conclusion, this study has revealed considerable differences in the timing of maturation and sex reversal in local populations of two unharvested protogynous reef fishes separated by only 20 km. The sexual composition and operational sex ratios for one of these species also differed markedly over this spatial scale. If equivalent levels of variability exist over such fine spatial scales for commonly harvested protogynous reef fishes such as serranids, extensive sampling will be required to assess the impacts of fishing and separate anthropogenic impacts from natural spatial variability.

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