Comparative demography and assemblage structure of serranid fishes: implications for conservation and fisheries management

Thesis submitted by

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Abstract

This thesis examined the biology of some commercially exploited reef fishes with a view to better understanding their life histories and potential vulnerability to fishing or other threats. The focus of this research was comparative age-based demographics of tropical epinepheline serranids (or groupers) from two geographic areas: Australia's Great Barrier Reef (GBR) in the western Pacific; and the Seychelles Islands in the western Indian Ocean. The overall aim was to investigate age-based demographics and assemblage structure of tropical epinepheline serranids at multiple scales.

The epinepheline fauna in the study areas was partitioned for some analyses into three behavioural groupings based on foraging pattern, crypticity and body size. The behavioural groups are *cryptic serranids*, *roving serranids*, and *large mobile serranids* (Chapter 1). Less is known about cryptic and large mobile serranids than roving serranids in the study areas, so candidate species from those two groups were the focus of the detailed age-based demographic analyses.

A comprehensive account of epinepheline assemblages from the GBR and the Seychelles was presented (Chapter 3) using a modified visual survey technique tailored to epinepheline serranids (Chapter 2). I described and compared characteristics of epinepheline serranid faunas at a range of spatial scales from <1 to 1000's km along natural environmental and geographic gradients on the GBR and the Seychelles Islands, and provided abundance estimates for all three behavioural groups and for the almost 40 species they represent. The typical shallow-water, tropical epinepheline assemblages comprised a handful of abundant species from the cryptic or roving serranid behavioural groups, plus numerous species found only in low densities locally (i.e. rare species, less than 1 fish per 1000 m^2) from each behavioural group. All five characteristics used to describe assemblage structure (i.e. total density of epinepheline serranids; density of each behavioural group; species richness; size structure; and species distribution and abundance) varied at broad spatial scales (100's to 1000's km) and some at finer spatial scales (1 to 100 km). Three approaches were used to explore possible effects of fishing on densities: 1) incorporating the CRC Reef Research Centre's Effects of Line Fishing Experiment treatments, manipulating fishing level and Marine Park zone status for GBR reefs, into the GBR regional comparison; 2) comparing reefs open and closed to fishing for Lizard outer shelf reefs; and 3) exploring abundance patterns in relation to presumed gradients of historical fishing pressure. Each approach indicated some effects of fishing on epinepheline serranids, but patterns were complex.

Comparative demographic analyses were conducted for three species of cryptic serranids, *E. fasciatus* (blacktip grouper), *E. polyphekadion* (camouflage grouper) and *C. argus* (peacock grouper), from the GBR and the Seychelles based on age estimates derived from thin-sectioned otoliths (Chapter 4). I described size and age characteristics, longevity, and patterns of growth for each species, and explored broad-scale spatial patterns in demography and the nature of size-age-density relationships for each species in the GBR and the Seychelles. Comparative analyses revealed substantial spatial variation in demographics within and among species. Hence, our ability to generalise about the demography of the cryptic serranids appears to be limited. Linking information on abundance and demography revealed that different combinations of processes may influence local populations of the three species, with the possibility of broad-scale compensatory demographic trade-offs dependent on density noted for two of the three species. Further, lifespans tended to be shorter in the Seychelles than the GBR, suggesting higher recruitment levels and predictability of environmental conditions and resources in the Seychelles than the GBR.

I investigated age-specific demographic and reproductive characteristics of *E. fuscoguttatus* from the GBR and examined implications for resource management (Chapters 5 & 6). *Epinephelus fuscoguttatus* (brown-marbled grouper or flowery cod) is an example of a large mobile serranid that is widespread throughout the Indo-Pacific and features strongly in the live reef food fish trade and other reef fisheries. *E. fuscoguttatus* had an extended lifespan (42 yrs) and unusual reproductive ecology, such as large old females with a reproductive lifespan that may exceed 30 yrs and limited spawning in smaller, younger females until about 9 yrs and 566 mm FL. The spawning period of *E. fuscoguttatus* in the GBR was relatively narrow (November, December and January). Combined evidence from histological analyses and age-based demographics suggested monandric protogynous hermaphroditism, although confirmation awaits direct evidence of sex change, such as identification of transitional individuals.

The two biogeographic-scale studies (Chapters 3 & 4) provided support for the idea that there are fundamental differences in the ecology and population dynamics of reef fish assemblages over biogeographic scales. The contribution of fishing to the observed patterns could not, however, be resolved categorically. While the four aged serranids shared some characteristics associated with high vulnerability to fishing, e.g. relatively slow growth and moderate to long lifespans (20 – 40 yrs), differences among them in abundance, demography and body size, and perhaps in population dynamics, suggested vulnerabilities to fishing may vary. We still lack information on many Indo-Pacific species of epinepheline serranids, and this thesis indicates at least some of these, particularly larger bodied species, may be highly vulnerable to over-fishing or other threats.

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Statement of sources

Declaration

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

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Rachel J Pears Date

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Chapter 1. General introduction

1.1 Marine fish conservation

Marine conservation has become increasingly important as human population size surpasses seven billion people and negative human impacts on the world's oceans rise (Roberts & Hawkins 1999). There is increasing recognition that marine species are potentially vulnerable to extinction, with many species already severely depleted (Vincent & Hall 1996, Roberts & Hawkins 1999, Reynolds et al. 2002). A recent compilation of 133 known local, regional or global extinctions of marine populations found that exploitation is the most common cause (55%), followed closely by habitat loss (37%, Dulvy et al. 2003). Other threats include invasive species, pollution, coastal development, climate change and disease (e.g. Lessios 1988, Miller 1989, Kime 1995, Jones & Reynolds 1997, Spalding & Jarvis 2002, Vidthayanon & Premcharoen 2002, Clavero & Garcia-Berthon 2005). Examples of severe declines in marine fish populations include: Atlantic cod, *Gadus morhua*, in the north Atlantic (Myers et al. 1997a); orange roughy, *Hoplostethus atlanticus*, off New Zealand and southern Australia (Clark 1999); three skate species in the Irish Sea (common skate, *Dipturus batis*, long-nose skate, *D. oxyrhinchus*, white skate, *Rostroraja alba*, Brander 1981, Dulvy et al. 2000); humphead wrasse, *Cheilinus undulatus* in parts of southeast Asia (Donaldson & Sadovy 2001, Sadovy et al. 2003a); and many reef fish species in the Caribbean (e.g. Koslow et al. 1988, Sadovy 1994a, Sala et al. 2001). Furthermore, Myers and Worm (2005) have demonstrated a general decline in large predatory fish communities worldwide by at least 90% over the last 50 – 100 years.

A number of current efforts such as the World Conservation Union (IUCN) Red List assessments (IUCN 1996, Mace & Hudson 1996, www.redlist.org), national conservation assessments (e.g. in the USA and Australia, Musick et al. 2000, Pogonoski et al. 2002) and ecological assessments of specific fisheries (e.g. Andersen et al. 2005) are attempting to identify the species and habitats most at risk. The vulnerability of any species or population to threats will result from inherent biological characteristics (termed intrinsic factors), and external forces such as exploitation or habitat degradation (extrinsic factors), and some of these factors may interact or be highly correlated (IUCN 1996) (www.iucn.org/ssc). Intrinsic factors include: low population turnover; late maturity; sex change; aggregate spawning; restricted range or habitat; patchy distribution or reliance on threatened habitat; low natural abundance; and high trophic level (Roberts & Hawkins 1999). Research to improve our understanding of factors causing vulnerability and elucidate the extent to which we can generalise about them is important to help prevent further population declines and ensure the long-term viability of marine resources.

Additionally, the need to better understand general patterns and processes has been a major driver for the recent scaling-up of some marine ecological studies (e.g. Jennings et al. 1999a, Jackson et al. 2001, Hughes et al. 2002, Williams 2003). At the same time, there is an increased ecological focus in fisheries science, embracing a more general focus on ecosystem-based management (Russ & Zeller 2003, Pikitch et al. 2004). This approach not only includes greater interest in all of the species in fishery catches (Hall et al. 2000), but also strives to maintain biodiversity, support ecological processes and actively manage resilience (Holling 1973, Folke 2004, Hughes et al. 2005). For both marine ecology and fisheries science, it is important to understand the extent to which we can apply learning about one species or population to elsewhere. Furthermore, obtaining biological and fishery data is inherently difficult for large reef fishes such as the humphead wrasse, *Cheilinus undulatus,* and large epinepheline serranids (groupers) (Sadovy et al. 2003a). Thus, there are compelling reasons to take a more generic approach and examine life history attributes of multiple species and attempt to establish general patterns for exploited taxa (Beverton & Holt 1957, Hoenig 1983, Hoenig & Gruber 1990, Jennings et al. 1999a, Jennings et al. 1999b, Frisk et al. 2001, Dulvy & Reynolds 2002). The purpose of this thesis is to examine key intrinsic factors of some exploited reef fishes with a view to better understanding their life histories and potential vulnerability to depletion or extinction. The focus of my research is on comparative age-based demographics of tropical epinepheline serranids.

1.2 Tropical reef fisheries, ecology and population dynamics

Tropical reef fisheries typically involve multi-species harvests and are particularly difficult to manage because they involve multiple gear types, are spatially complex, target species with a diverse range of life histories, and many of the people dependent on fishery resources for income or protein lack alternative options (Russ 1991, Sale et al. 1994, Jennings & Lock 1996, Jennings & Kaiser 1998, Jennings et al. 1998). Healthy populations of reef fishes are important, however, for maintaining food supplies, incomes and ecological processes in diverse tropical marine communities (Russ 1991, McManus 1996, Bellwood et al. 2004). Intrinsic vulnerability of some reef fishes to over-fishing, increased fishing pressure on reef fish populations and concerns that many reef fisheries are now over-fished underpin the need for more effective management of coral reef fisheries (Russ & Alcala 1989, Russ 1991, Munro 1996, Sadovy 1997b, Jennings et al. 1999b, Sale 2002, Sadovy et al. 2003b). Understanding reef fish ecology, population dynamics and responses to fishing is fundamental to achieving that better management (Sale et al. 1994, Jennings & Lock 1996, Vincent & Sadovy 1998).

Considerable work has examined reef fish ecology over the last few decades, adding substantially to our knowledge of patterns and processes that shape reef fish communities (e.g. Sale 1991a, Sale 2002). Current understanding of reef fish communities generally regards them as open, dynamic, nonequilibrium, rather than static assemblages, and driven by patterns of recruitment and loss of individual fishes, with assemblage structure highly dynamic in space and through time (Mapstone & Fowler 1988, Sale 1991b, 2004). Ecological processes (competition, predation, etc) in conjunction with human impacts, through their effects on demographic processes (such as growth or mortality), produce patterns of abundance and structure in the post-recruitment phase of exploited reef fish populations (Jones 1991, Jennings & Lock 1996). Most reef fish research, however, has been on smaller, non-harvested reef fishes and, consequently, knowledge of dynamics of exploited reef fish populations is relatively limited (Sale 1991b, Roberts 1996, but see e.g. Sadovy et al. 2003a, Williams et al. 2003). Integrated studies of demographic processes that directly determine changes in the primary (abundance) and secondary (e.g. size and age structures) characteristics of exploited populations are relatively rarer (Jones 1991), but may allow insights into underlying reef fish population dynamics and vulnerability to over-fishing.

A multi-scale approach to reef fish studies is important for a thorough understanding of population dynamics (Jones 1991, Caley et al. 1996, Sale 1998). Previous studies have demonstrated that reef fish biology is variable at a range of scales, partly reflecting the spatially patchy and dynamic environments of coral reef ecosystems (Aldenhoven 1986a, 1986b, Shapiro 1991, Pitcher 1992, Connell 1996, Hart & Russ 1996, Munday et al. 1997, Connell & Kingsford 1998, Gust et al. 2001, Meekan et al. 2001, Williams et al. 2003, Gust 2004). Recent studies incorporating multiple spatial scales (e.g. Newman et al. 1997, Adams et al. 2000, Gust et al. 2001, Adams 2002, Gust et al. 2002, Kritzer 2002, Williams 2003, Williams et al. 2003, Mapstone et al. 2004) indicate that the relative importance of different biological characteristics varies at different spatial scales, and that the pattern of spatial variability of a particular characteristic appears to differ among species. Spatial variation in demographic and life history characteristics may give local populations varying resilience to disturbances including fishing, and consequently local populations may respond differently to fishing or other threats (Ricker 1975, Pella & Robertson 1979). Such spatial structure may also necessitate different management regimes over a species' range or a generally precautionary approach to avoid over-fishing of more vulnerable subcomponents of the population (Williams 2003). Thus, incorporating multiple spatial scales into sampling designs for studies of reef fish biology will help answer ecological questions related to the scales at which most variation in biological attributes occur, ensure results are widely applicable and provide useful data at scales applicable to fisheries and conservation management (Andrew & Mapstone 1987, Mapstone et al. 1997, Mapstone et al. 1998a, b, Sale 1998, 2004, Gust et al. 2001, Mapstone et al. 2004).

1.3 Epinepheline serranid biology

My thesis focuses on members of one of the five Subfamilies of the Serranidae, the Epinephelinae (or groupers), which includes species commonly known as groupers, rockcods, hinds, seabasses and coral trouts (Heemstra & Randall 1993, Randall et al. 1997). The Epinephelinae are an important component of the fauna on tropical reefs, both from ecological and fisheries perspectives (Randall & Heemstra 1991). As dominant predators, epinepheline serranids are likely to play a major ecological role in the population structure of the faunal communities in both tropical and temperate oceans (Hixon 1991a, Almany 2003, 2004, Almany & Webster 2004), and some species function as marine ecosystem engineers that modify, maintain and create habitats (Jones et al. 1994, Coleman & Williams 2002).

The Epinephelinae is a diverse taxon comprising about 159 species of marine fishes in 15 genera, with about 98 species in the genus *Epinephelus* (Heemstra & Randall 1993). Most epinepheline serranids are found in the vast Indo-West Pacific region where about 110 species have been identified, few of which occur in the eastern Pacific (Randall & Heemstra 1991). The geographic distribution of the taxon, however, extends throughout tropical and subtropical latitudes of all oceans (Heemstra & Randall 1993).

Many species of epinepheline serranids have widespread distributions, allowing large regional scale variation in their biology to be examined. Differing distributions and species diversity of epinepheline serranids between the Indo-Pacific and Atlantic Oceans may influence underlying demographic and life history attributes. Although latitudinal distributions often cover similar scales, the longitudinal distributions of some Indo-Pacific species extend over ocean basins with diverging evolutionary histories of marine species driven by historical sea level fluctuations (Montaggioni & Hoang 1988, Bay et al. 2004). Additionally, clear genetic structure separating populations from the Indian and Pacific Oceans has been demonstrated for several reef fishes (Bernardi et al. 2001, Bay et al. 2004) and multiple biogeographic barriers within the Indo-Pacific have led to subregions with different environmental conditions and geographic characteristics and relatively distinct faunas (Bellwood & Wainwright 2002). Consequently, significant variability in biological attributes of Indo-

Pacific species in particular is expected as a result of both latitudinal and longitudinal differences. An important issue is the magnitude and direction of variation at broad spatial scales because of the likely evolutionary significance of differences between communities that have probably been separated for many generations and the inferences that might be made about general patterns in the ecology and evolution of reef fish communities. Broader spatial scales are also of most practical significance to reef fisheries and conservation management.

Epinepheline serranids suffer from considerable taxonomic confusion and mis-identification, mainly because of difficulty differentiating species from their close relatives (Randall & Heemstra 1991, Craig et al. 2001). These identification problems have resulted in: 1) the recording of much biological and fisheries data for epinepheline serranids under erroneous species names and hence inaccuracies and unreliability of a number of previous studies (Randall & Heemstra 1991); and 2) a tendency for researchers to concentrate on a few of the better known species or to work at low taxonomic resolution (e.g. species-complexes, genus or subfamily). As a consequence, we know little about the biology of the vast majority of epinepheline serranids. Information on fisheries catch and effort is also limited, stemming from identification difficulties and lumping of species into non-specific groups in fisheries data collections, such as commercial landings and logbook records (Mapstone et al. 1996b, Williams et al. 2004).

The Epinephelinae includes a wide range of morphologies and sizes, ranging from the 18 cm leopard hind, *Cephalopholis leopardus,* to the Queensland grouper, *Epinephelus lanceolatus*, and goliath grouper, *E. itajara*, which can each attain total lengths of over 250 cm (Randall & Heemstra 1991). A practical approach to dealing with such a diverse and species-rich taxon is to partition the fauna into ecological groupings based on behaviours, termed "*behavioural groups*". This approach can help shed light on general patterns and processes, and has similarities to the functional group approach of Steneck and others (Steneck 2001), although we lack detailed resource-use information for most of these species, therefore preventing partition based on established knowledge of ecological roles.

The taxonomic diversity of the Epinephelinae, the issues with routine species identification and the aggregated nature of most available fisheries data, indicates that some form of aggregated analysis is inevitable for the family. It is important, however, to test the veracity of generalisations at lower taxonomic resolution or functional aggregations through detailed work on selected representative species. Accordingly, I take a dual approach throughout this thesis: I consider the characteristics of behavioural groups but I also analyse species-level patterns to ensure important species-level similarities and differences are not overlooked in the aggregate analyses. I partitioned the epinepheline fauna in the study areas into three behavioural groups (after Samoilys and Carlos 2000) based on foraging pattern, crypticity and body size inferred from published literature and in-water observations. The behavioural groups are "*cryptic serranids", "roving serranids",* and "*large mobile serranids"* (Table 1.1).

Table 1.1 Species groups of epinephelines from the study areas, termed behavioural groups, (modified from Samoilys and Carlos 2000), ecological characteristics and summary of previous GBR studies on aspects of demography or reproduction by species and behavioural group.

Behavioural Group	Species	Ecological characteristics	GBR studies on species demography and reproduction
Cryptic serranids	*Aethaloperca rogaa, Anyperodon leucogrammicus, Cephalopholis argus, C. boenak, C. cyanostigma, C. leopardus, C. microprion, C. miniata, C. sexmaculata, C. urodeta, Cromileptes altivelis, Epinephelus caeruleopunctatus, E. corallicola E. fasciatus, E. hexagonatus, E. howlandi, E. macrospilos, E. maculatus, E. merra, E. ongus, E. polyphekadion, E. quoyanus, E. spilotoceps, E. tauvina*	Small to medium sized rockcods. Highly sedentary predators, mostly well-camouflaged with cryptic behaviour.	*Cephalopholis cyanostigma*, *C. boenak* and *C. microprion* (Mackie 1993, Stewart 1998, Mosse 2002).
Roving serranids	*Gracila albomarginata, Plectropomus areolatus, P. laevis, P. leopardus, P. maculatus, P. punctatus, Variola louti*	Mainly species of *Plectropomus* and *Variola*. More visible and active predators that rove (or patrol) near the reef.	Extensive work on *Plectropomus leopardus* (including Goeden 1978, Ferreira & Russ 1994, Samoilys & Squire 1994, Ferreira 1995, Ferreira & Russ 1995, Russ et al. 1995, Adams 1996, Russ et al. 1996, Samoilys 1997, Russ et al. 1998, Zeller 1998, Adams et al. 2000, Samoilys 2000, Samoilys & Roelofs 2000, Zeller & Russ 2000). *P. maculatus, P. laevis,* (Ferreira & Russ 1992, Ferreira 1993, Adams 2002, 2003).
Large mobile serranids	*Dermatolepis striolata, Epinephelus coioides, E. cyanopodus, E. fuscoguttatus, E. lanceolatus, E. malabaricus, E. multinotatus, E. tukula*	Large-bodied groupers. Foraging activity and crypticity intermediate between other two groups.	Inshore study of *Epinephelus coioides* and *E. malabaricus* (Sheaves 1995).

Most of the biological research on epinepheline serranids has been on species from Caribbean and western Atlantic waters, even though the Indo-Pacific holds the majority of species within the taxon (Heemstra & Randall 1993). Our poor knowledge of Indo-Pacific members of the taxon can be illustrated by considering the Great Barrier Reef (GBR) in Australia, where the demography and reproduction of approximately 75% of the 48 species (Randall et al. 1997) are unstudied (Table 1.1). It is clear also that considerably more research has been done on roving serranids than on the other behavioural groups, particularly on the commercially valuable leopard coral grouper or common coral trout, *Plectropomus leopardus*. Consequently, it is important that further biological studies are on a broad spatial scale, and that more research effort is focused on Indo-Pacific representatives of the cryptic serranids and large mobile serranids in particular (Table 1.1).

Otolith-based age estimates were obtained for *Epinephelus morio* (red grouper) and *Mycteroperca microlepis* (gag) from sub-tropical waters in the 1960s (McErlean 1963, Moe 1969), and more recently for a number of topical species of epinephelines (e.g. *E. itajara*, Bullock 1992, *P. maculatus*, Ferreira & Russ 1992, *E. guttatus*, Sadovy et al. 1992, *P. leopardus*, Ferreira & Russ 1994, *E. labriformis*, Craig et al. 1999, *E. flavolimbatus* and *M. interstitialis*, Manickchand-Heileman & Phillip 2000, *E. niveatus*, Wyanski et al. 2000, *E. chlorostigma*, Grandcourt 2002). Although these studies have revealed that many epinepheline serranids may live for 20 years or more (Manooch 1987), there are still uncertainties regarding maximum ages within the taxon. Age estimates of over 40 years have been recorded (41 yrs *E. nigritus*, Manooch & Mason 1987, 41 yrs *M. interstitialis*, Manickchand-Heileman & Phillip 2000, 46 yrs *C. cyanostigma*, Mosse 2002), but may not reflect potential ages in the absence of fishing pressure (Huntsman et al. 1999). In a review of age-based studies of reef fishes, Choat and Robertson (2002) noted that many taxa may be long-lived, but large size may not correlate with great longevity and size may be decoupled from age in many taxa. They also noted that reef fish taxa tend to have highly distinctive patterns of growth and a strong phylogenetic structure may be evident in age-based demographic features. Their analysis was based on parrotfishes (Scaridae) and surgeonfishes (Acanthuridae), and it will be instructive to explore these predictions for the Epinephelinae.

Reproductive biology of epinepheline serranids is diverse and complex (Smith 1965, Shapiro 1987, Sadovy & Colin 1995). The sexual pattern of epinepheline serranids, for example, has previously been generalised as one of monandric protogyny in which juveniles mature and then function as adult females, before some change sex to males (secondary males) and all males are derived through this pathway (Smith 1965). Many epinepheline serranids appear to conform to this rule (Shapiro 1987), including *E. rivulatus* (Fennessy 2000, Mackie 2000), *E. tauvina* (Abu-Hakima 1987), *E. aeneus* and *E. guaza* (Brusle & Brusle 1975), *Mycteroperca microlepis* (McErlean & Smith 1964, Collins et al. 1987), *C. fulva* and *C. cruentata* (Smith 1965), *P. laevis* (Adams 2002) and *P. leopardus* (Adams 2002). A growing number of exceptions to this pattern are being discovered, however, including *E. andersoni* (Fennessy & Sadovy 2002), *C. boenak* (Chan & Sadovy 2002, Liu & Sadovy 2004a, b) and *P. maculatus* (Ferreira 1993, Adams 2003), which have all been found to be functionally diandric (two male pathways). Both males and females of the Nassau grouper, *E. striatus*, can develop directly from a bisexual juvenile phase and no evidence of mature female to male sex change has been found in the field. Hence, Sadovy and Colin (1995) classified the species as gonochoristic. Confirmation of sexual pattern has not yet been possible for a number of studied species, including *E. itajara* (Bullock 1992, Sadovy & Eklund 1999) and the camouflage grouper, *E. polyphekadion* (Rhodes & Sadovy 2002a). Hence, further research into epinepheline reproductive biology is required to understand generalised patterns and diversity of sexual patterns within the subfamily and predict responses to fishing (Shapiro 1987).

1.4 Fishing and vulnerability of epinephelines

Epinepheline serranids are valuable parts of fishing catches in countries where they occur and, since most species of epinephelines occur on shallow coral reefs, they are highly accessible to fishing through a variety of fishing methods (Heemstra & Randall 1993). Fishing of epinepheline serranids has a long history (e.g. Wing & Reitz 1982, Wing & Wing 2001) and they are still a major component of artisanal (Heemstra & Randall 1993), recreational and commercial fisheries in many countries (Pogonoski et al. 2002, Sadovy et al. 2003b). This fishing pressure includes the live reef fish trade, in which high profits are driving continued and rapid expansion of intensive commercial fisheries into new areas (Johannes & Riepen 1995, Bentley 1999, Sadovy & Vincent 2002). In many countries, exploitation occurs throughout the lifecycle of epinepheline serranids, increasing the risk of over-exploitation (Johannes 1997, Sadovy & Pet 1998, Sadovy 1999). Particularly problematic is targeted fishing of epinepheline spawning aggregations (Johannes & Riepen 1995, Johannes et al. 1999), which has led to the decline or disappearance of some aggregations (e.g. for *E. striatus*, Sadovy 1994a, Sala et al. 2001).

Many epinepheline serranids have biological characteristics associated with high vulnerability to fishing, such as low natural abundances, long lifespan, spawning aggregation behaviour and ease of capture (Sadovy 1994b, 1997a, Morris et al. 2000). In an assessment of 85 tropical epinephelines, Morris et al. (2000) classified 43.5% as *Threatened* according to 1996 IUCN Red List categories. The main threat for most epinepheline serranids is fishing pressure, which has increased in recent years and more species are now targeted (Bentley 1999, Sadovy et al. 2003b). Evidence of changes in demographic and life history characteristics and declines in abundance of heavily fished populations of epinephelines have been demonstrated (e.g. Koslow et al. 1988, Sadovy 1994b, a, Coleman et al. 1996, Koenig et al. 1996, Beets & Friedlander 1998, McGovern et al. 1998, Bentley 1999, Huntsman et al. 1999, Mamauag et al. 2000, Musick et al. 2000, Pogonoski et al. 2002, Gimenez-Hurtado et al. 2005). Epinephelines, especially the larger ones, are usually the first species lost from a reef fish population (e.g. Koslow et al. 1988). The ecological consequences of the loss of these species is not well understood but may be far-reaching (Jennings & Lock 1996, Hixon & Carr 1997, Huntsman et al. 1999, Carr et al. 2002).

Our understanding of marine species vulnerability to fishing and other threats is improving (Jennings et al. 1998, Russ & Alcala 1998, Jennings et al. 1999a, Jennings et al. 1999b, Dulvy et al. 2000, Hawkins et al. 2000, Reynolds et al. 2001), and some intrinsic factors, such as large body size (Jennings et al. 1998, Frisk et al. 2001) or transient spawning aggregation behaviour (Domeier & Colin 1997, Vincent & Sadovy 1998), may be biological correlates of vulnerability in exploited marine fishes (Reynolds et al. 2001, Dulvy et al. 2003). While vulnerability correlates may be useful for predictions of vulnerability in unresearched species (e.g. Jennings et al. 1999b), it is likely that the true picture will be complex and different combinations of factors may be important in each case. For example, no widespread agreement has been reached about which factors may explain evidence from several geographic areas of differing response to fishing pressure among species of epinephelines. Noted cases include the red grouper, *E. morio*, in the Gulf of Mexico, the southeast African endemic *E. andersoni*, and *P. leopardus* on the GBR, which are apparently more resilient to fishing than other groupers of those regions (e.g. *Mycteroperca microlepis, M. phenax, E. marginata, E. albomarginata, E. lanceolatus*) (Coleman et al. 1996, Coleman et al. 1999, Huntsman et al. 1999, Fennessy 2000, Samoilys 2000). However, a number of possible explanations have been advanced for these differences including: differences in spawning mode and mechanisms and timing of sex change (*E. morio*, Coleman et al. 1996); alternative male sex differentiation pathways (*E. andersoni*, Fennessy 2000, *P. leopardus*, Adams 2002, 2003); and flexibility in mating systems, increased spawning frequencies and high annual fecundities (*P. leopardus*, Samoilys 2000). Conversely, it also has been shown that fishing may have marked effects on these apparently more resilient species (Ferreira & Russ 1995, Ayling et al. 2000, Mamauag et al. 2000, Mapstone et al. 2004, Gimenez-Hurtado et al. 2005).

In conclusion, we need to strategically enhance our biological knowledge-base of reef fish species, particularly among groups such as the Epinephelinae which may be highly vulnerable to localised depletion or extinction (Pogonoski et al. 2002, Dulvy et al. 2003, Myers & Worm

2005). Linking reliable abundance and assemblage structure information to demographic and life history features of large, widely distributed epinephelines may enhance our knowledge of fundamental reef fish biology and provide a sound basis for management. Comparative multi-species analyses based on integrated spatially explicit datasets covering broad, biogeographically significant scales may help elucidate general patterns and processes in reef fish ecology. In making such large-scale comparisons, an approach using behavioural groups provides a basis for making appropriate multi-species analyses, and combining this with examinations of species-level patterns might extend the growing body of knowledge on relationships between intrinsic factors and vulnerability to over-fishing and other threats.

1.5 Objectives and thesis structure

The overall aim of my thesis is to investigate age-based demographics and assemblage structure of tropical epinepheline serranids at multiple scales. In doing this I provide information on the biology of some poorly known species of epinepheline serranids (focusing on members of the cryptic serranids and large mobile serranids, Table 1.1) and explore some general patterns for the taxon of interest to science and management. I am particularly interested in the magnitude and direction of differences in demographics and assemblage structure of epinepheline serranids at biogeographic scales (i.e. at a geographic area or regional level).

This work was carried out in two geographic areas: the Great Barrier Reef off north-eastern Australia in the western Pacific; and the Seychelles Islands to the north of Madagascar in the western Indian Ocean (Fig. 1.1). Incorporating two diverse study areas provided the opportunity to examine spatial patterns in biological characteristics of wide-ranging species of epinepheline serranids and to evaluate similarities and differences in assemblages over biogeographically significant scales.

Three integrated studies were designed to address the overall aim of the thesis.

Chapter 3: Assemblage structure of epinepheline serranids from the Great Barrier Reef and the Seychelles

Information on abundance and assemblage structure provides an ecological foundation for the study of demography and life histories by describing the biological setting within which candidate species occur. Abundance is also an important intrinsic factor related to vulnerability, and hence a required input into fisheries and conservation assessments.

The objectives of this study were to:

i. describe general characteristics of epinepheline serranid assemblages;
ii. explore broad-scale spatial patterns of abundance, distribution and size structure of epinepheline serranids in the GBR and the Seychelles; and
iii. explore regional and fine-scale spatial patterns of abundance, distribution and size structure of epinepheline serranids in the GBR.

It was necessary to develop a modified visual survey technique that gives improved abundance estimates for epinepheline serranids in order to complete this work, and a detailed account of that method is given in **Chapter 2**.

Chapter 4: Comparative demography of three species of cryptic serranids from the Great Barrier Reef and the Seychelles

This comparative study integrates demographic information with abundance profiles for three species of epinephelines, *Epinephelus fasciatus* (blacktip grouper)*, E. polyphekadion* (camouflage grouper) and *Cephalopholis argus* (peacock grouper), providing insight into spatial patterns in demography and potential evidence of density dependence in demographic characteristics. The study species are representatives of cryptic serranids (Table 1.1) covering a range of sizes, which are either target or bycatch species in regional fisheries. The objectives of this study were to:

i. describe size and age characteristics, longevity, and patterns of growth for each species; and
ii. explore broad-scale spatial patterns in demography and the nature of size-age-density relationships for each species in the GBR and the Seychelles.

Chapters 5 & 6: Demography and reproduction of a large mobile serranid, *Epinephelus fuscoguttatus*, from the Great Barrier Reef

Little information is available for many large Indo-Pacific species of epinepheline serranids, largely because of their natural rarity and difficulty in obtaining samples, yet they are subject to considerable fishing pressures. The focal species for this study was *Epinephelus fuscoguttatus* (brown marbled grouper)*,* a large mobile serranid (Table 1.1) not previously aged. The objectives of this in-depth study were to:

i. determine age-specific size, growth and maturity characteristics of *E. fuscoguttatus* and explore implications for harvest limits and size regulations (Chapter 5); and
ii. describe the reproductive biology, sexual pattern and temporal pattern of reproduction of *E. fuscoguttatus* (Chapter 6).

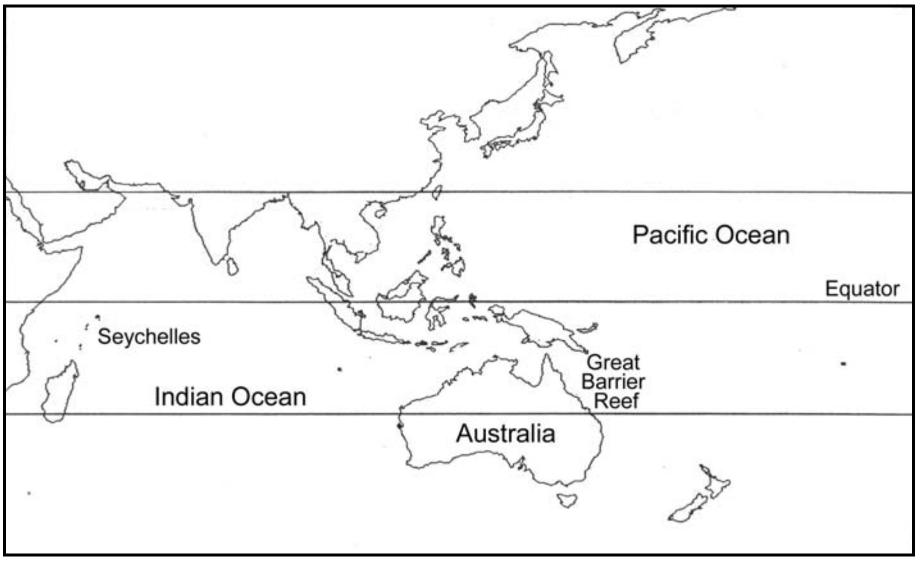


Figure 1.1 Map of the Indo-Pacific showing the two geographic areas where this research took place: the Great Barrier Reef and the Seychelles Islands.

1.6 Publications arising from this project

Pears RJ, Choat JH (Submitted) A rapid, quantitative visual survey method for groupers. Journal of Fish Biology. (Thesis Chapter 2).

Choat JH, Pears RJ (2003) A rapid, quantitative survey method for large, vulnerable reef fishes. In: Wilkinson C, Green A, Almany J, Dionne S (eds) Monitoring Coral Reef Marine Protected Areas: A practical guide on how monitoring can support effective management of MPAs. Version 1. Australian Institute of Marine Science, Townsville. (Includes simplified version of count protocol developed in Chapter 2).

Pears RJ (2005) Biology and management of the Flowery Cod and Camouflage Cod: how similar are they? In: Tobin R, Pears R, Marshall, N, Marriott, R, Busilacchi, S, Bergenius, M (eds) Fishing for more: a student-stakeholder workshop on the biology, ecology, sociology and economics of fisheries. CRC Reef Tech Rept 59, Townsville. (Based on Chapters 4 & 5).

Pears RJ, Choat JH, Mapstone BD, Begg GA (2006) Demography of a large grouper, *Epinephelus fuscoguttatus*, from the Great Barrier Reef: implications for fishery management. Marine Ecology Progress Series. 307: 259-272 (Chapter 5).

Pears RJ, Choat JH, Mapstone BD, Begg GA (Submitted) Reproductive biology of a large, aggregation-spawning serranid, *Epinephelus fuscoguttatus*: management implications. Journal of Fish Biology. (Chapter 6).

1.7 Study areas

1.7.1 The Great Barrier Reef

The Great Barrier Reef (GBR) is the largest system of coral reefs in the world, extending for over 2000 km along the east coast of Queensland (Fig. 1.1), with most of the GBR within both a Marine Park and World Heritage Area (347, 800 km^2, Wachenfeld et al. 1998). Connectivity among the nearly 3000 coral reefs and the numerous other habitats that make up the GBR is high (Cappo & Kelley 2001). The seasonal range of mean sea surface temperatures is about 23 to 28 ºC for offshore reefs and about 21 to 30 ºC for inshore reefs (Wachenfeld et al. 1998). Recent management changes include re-zoning of the multiple-use Great Barrier Reef Marine Park, with an increase in no-take zones to 33% of the Marine Park (Day 2002, GBRMPA 2004).

Shallow water epinepheline serranids are caught as part of the multi-species Coral Reef Fin Fish Fishery, hereafter termed *reef line fishery*, by commercial fishers (using hook and line) and recreational fishers (using hook and line or spear). While the two primary target species are *Plectropomus leopardus* (an epinepheline serranid) and *Lethrinus miniatus* (red throat emperor), at least 40 species of epinephelines occur in the catches. Species-level catch statistics are not available.

A lucrative export market for live reef food fish has been one of the major drivers for recent marked changes to the reef line fishery (Mapstone et al. 2001a). Changes have included a considerable increase in fishing effort since 1995, with fishing effort almost doubling to nearly 40,000 fishing days by over 700 operations taking 4,400 tonnes of reef fish from Queensland waters in 2001 (Mapstone et al. 2001a, Mapstone et al. 2001b, Mapstone et al. 2004). In response, the Queensland Fisheries Management Service introduced revised management arrangements for the fishery in 2003/2004, which included commercial catch quotas, seasonal closures, legal size regulations (includes all epinephelines, but size limits vary), no-take provisions (includes a few iconic epinephelines) and revised recreational bag limits (Anon 2003). Seasonal closure of reef line fishery is for nine day periods around the new moons in October to December, chosen mainly to encompass the spawning period of *P. leopardus* and some other reef fishes. The Great Barrier Reef Marine Park Authority Regulations include protection for two of the larger epinephelines (*Epinephelus lanceolatus,* the Queensland grouper and *E. tukula,* the potato cod), the iconic *Cromileptes altivelis* (barramundi cod) and *Cheilinus undulatus* (the humphead wrasse). The Regulations also protect all individuals of the genus *Epinephelus* over 1000 mm in length. Large groupers are of high value to the GBR tourism industry (D. Miller *Pers comm*).

1.7.2 The Seychelles

The waters of the Republic of Seychelles (Fig. 1.1) are extensive, with the Exclusive Economic Zone (EEZ) covering an area of 1,374,000 km^2 , but the landmass of the 42 granitic and 74 coralline islands comprises only 455 km^2 (Jennings et al. 2000). The inner granitic islands are remnants of the ancient continent, Gondwanaland, and now rise from the shallow (44 – 65 m) Seychelles Bank (Jennings et al. 2000). The remainder of the archipelago consists of outer coralline islands and atolls of the Amirantes Plateau, the Alphonse Group, the Providence and Farquhar Group and the Aldabra-Cosmoledo Group. There are three major reef types in the Seychelles: fringing reefs found around the coasts of the granitic islands; platform reefs; and atolls (Stoddart 1984). Sea surface temperatures range from 26 to 31°C.

Shallow water epinepheline serranids form part of the demersal reef fish catch of the Seychelles (Robinson & Shroff 2004), and are caught mainly by hook and line and some traps (MRAG 1995, Robinson & Shroff 2004). Similar to the GBR, species-level fisheries data are lacking. In the past, the fishery was largely confined to coastal areas near the main populated islands (Mahe, Praslin and La Digue) on the Seychelles Bank, but more recently has expanded southwards to the more distant regions such as the Amirantes group, partly because of the use of larger fishing vessels more suited to longer trips (MRAG 1995, Jennings et al. 2000, Robinson & Shroff 2004). A fishery for salted fish and subsistence now operates on Farquhar atoll, and epinepheline serranids including *Epinephelus fuscoguttatus* (brown marbled grouper or flowery cod) and *E. polyphekadion* (camouflage grouper or camouflage cod) are targeted (Robinson et al. 2004a). Epinepheline serranids were also targeted in the Farquhar group during trials for a live reef fish fishery in 1999, with approximately 26.4 tonnes exported (Bentley & Aumeeruddy 1999), although this activity was discontinued at the time of this study because of concerns regarding sustainability and high transport costs.

Fishing and tourism are the major sources of foreign revenue for the Seychelles economy (Jennings & Marshall 1995, Rosalie et al. 2002, Robinson & Shroff 2004). Six small (<1 to 11 km^2) Marine National Parks and two Special Reserves that include protection for marine habitats were established between 1968 and 1997 in the Inner Isles of the Seychelles (Jennings et al. 2000), but regulations have been difficult to enforce and the areas have received different levels of protection (Jennings 1996). No legal size regulations apply to epinepheline serranids in the Seychelles (MRAG 1995).

Chapter 2. A rapid, quantitative visual survey method for serranids

2.1 Synopsis

Established methods for counting coral reef fish have limitations for counting epinepheline serranids because of a tendency to underestimate their abundances, particularly for species that are rare, mobile or cryptic. This study developed a rapid, quantitative visual survey method for epinephelines that combines intense searches, timed-swim techniques and belt transects. A pilot study evaluated factors most likely to effect density estimates, i.e. observer swim-speed, transect dimensions, search efficiency and area estimation. The resulting method is called the long-swim transect, and covers a large area, more appropriate for counting larger mobile species, yet allows a narrower area to be searched carefully for the cryptic species. Trials were conducted in the northern Great Barrier Reef, and density estimates obtained were compared with published estimates using a variety of census methods from studies conducted in similar areas and habitats. The long-swim transect method was considered to offer an improvement in accuracy over established unbaited visual survey methods. The long-swim transect is a simple and effective method for providing species-level abundance estimates for the whole epinepheline fauna, with applications for science and management.

2.2 Introduction

Visual surveys are a widely used tool in ecological studies and status assessments of reef fishes, providing rapid, repeatable, non-destructive abundance estimates (Sale 1991b). Application of these techniques to small, cryptic or flighty species is problematic, however, because of a tendency to underestimate their abundances (Brock 1954, Brock 1982, Ackerman & Bellwood 2000, Willis 2001). Improved survey methods, tailored to the fishes of interest, are needed to better count these components of the reef fish community.

Counting of epinepheline serranids exemplifies these problems associated with established visual survey methods (e.g. small belt transects, point counts). The numbers of small, cryptic serranids (Chapter 1, Table 1.1) are seriously underestimated (by approximately 90%, Samoilys & Carlos 2000), and very few if any large mobile serranids (e.g. larger *Epinephelus*) are recorded by most previous methods (e.g. Samoilys & Carlos 2000, Stewart & Beukers 2000). In contrast, roving serranids (e.g. *Plectropomus spp.*) have been more reliably counted using well established and validated methods (e.g. Mapstone & Ayling 1993). Taxonomic complexity and difficulty in simple visual identifications have affected both the reliability and resolution of abundance estimates for the Epinephelinae (Randall & Heemstra 1991).

Consequently, some data are taxonomically inaccurate and of poor quality. The lack of reliable, comprehensive species-level abundance data means that questions relating to the assemblage of epinepheline serranids cannot be addressed adequately using most existing data.

Previous attempts to improve counts of small, cryptic or flighty species have included baited remote underwater video surveys (Willis & Babcock 2000), modified in-water visual surveys (e.g. using baiting, Stewart & Beukers 2000, or careful searching, Gilbert et al. 2005) and ichthyocides such as rotenone (Ackerman & Bellwood 2000, Willis 2001). Video surveys are expensive and the field of view covers relatively narrow areas that can be dominated by a few individuals and/or species and thus may not provide representative counts of whole assemblages. Ichthyocides are a destructive method with limited applicability, particularly in Marine Parks, and unsuitable for use over the large areas needed to characterise epinepheline faunas. Therefore, this study examined ways to further modify visual survey methods to improve counts of epinepheline serranids.

Considerations during a pilot study included the biological and behavioural attributes of the target species, accurate species identification, search intensity and the way each transect was surveyed, observer swim-speed, survey area, transect dimensions, area estimation, replication and feasible study designs with alternate methods. The method developed is known as the "long-swim transect" (a simplified version was presented in Choat & Pears 2003). It combines intense searches, timed-swim techniques and belt transects, and was based on experience from preliminary field work and other projects (Brock 1982, Williams 1982, Williams & Hatcher 1983, Russ 1984a, b, Lincoln Smith 1988, 1989, Samoilys 1992, Samoilys & Carlos 1992, Mapstone & Ayling 1993, Jennings et al. 1994, Cappo et al. 1996, Jennings 1996, Newman et al. 1997, Mapstone et al. 1998a, b, Samoilys & Carlos 2000). During the pilot study, I evaluated observer swim-speed, transect dimensions, search efficiency and area estimation because these are most likely to effect density estimates (Lincoln Smith 1988, Mapstone & Ayling 1993, Samoilys & Carlos 2000).

I tested the effects of observer swim-speed and transect length on relative accuracy of density estimates (the relative closeness of a density estimate to the true population mean). It was assumed that higher mean density estimates represented greater accuracy because observers will miss some fish in visual surveys but are unlikely to repeatedly count individuals of relatively sedentary or sparse species (Sale & Douglas 1981, Sale & Sharp 1983). Precision (the variability around an estimate) provides additional information on the usefulness of an estimate (Green 1979, Andrew & Mapstone 1987). Precision of density estimates was examined during trials in a variety of habitats in the Lizard region of the northern GBR (termed Lizard region). Potential for error exists in the visual estimation of survey area boundaries, and so I also attempted to minimise and quantify this source of error.

Observer swim-speed, search efficiency and transect dimensions (particularly width) are often closely related, and verification of appropriate methods for different studies is important (Lincoln Smith 1988, 1989, Mapstone & Ayling 1993, Cheal & Thompson 1997, Willis et al. 2000). The most appropriate observer swim-speed will optimise search efficiency and hence improve detection rates, minimise the presence of the diver, reduce risks of over-counting roving species and optimise costs. Slower swim-speeds provide for relatively higher search intensities and improve the detection of cryptic or evasive fishes such as many epinepheline serranids and hence are assumed to give more accurate abundance estimates (Lincoln Smith 1988, Mapstone & Ayling 1993, Samoilys & Carlos 2000). Variable biases or imprecisions arising from variable search efficiency can be controlled for, to some degree, by standardising swim-speed (Mapstone & Ayling 1993, Samoilys & Carlos 2000).

Transect width must optimise searchable-width and overall travel speed, without resulting in excessive diver-presence that could unduly affect sensitive fish in the vicinity or increase the risk of over-looking areas during long zigzag searches. Very narrow transects can yield artificially low densities of wary fish, whilst as transect width increases there will be a decline in the proportion of fish detected (Cappo et al. 1996, Cheal & Thompson 1997). As some of the larger, more mobile epinephelines (e.g. *Epinephelus fuscoguttatus*) typically do not allow close approach by a diver, a logical modification of previous methods is to search a narrow band for cryptic species and simultaneously record observations of large mobile species from a wider band. Increasing transect length should yield higher numbers for population assessment and lower variances for rarer species (Cappo et al. 1996, Newman et al. 1997), assuming search efficiency and detection rate are kept constant by using a fixed swim-speed per unit area. Logistical and safety considerations (e.g. operational distance between divers and boat) determine the upper limit (hundreds of metres) of transect length.

The aim of this Chapter was to devise a modified visual survey method specifically tailored for counting epinepheline serranids. The method was trialled and evaluated in the GBR.

2.3 Methods

2.3.1 Protocol development

All visual surveys of epinepheline serranids were conducted by the same observer (R.J.P.) at the species-level of resolution and only fish 6 cm fork length (FL) or greater were included in counts. This size was used to minimise the potential errors associated with counting small individuals when surveying large areas (Bellwood & Alcala 1988), while still allowing some preliminary observations of larger juveniles to be recorded. Each species was assigned to one of three "*behavioural groups*" based on foraging pattern, crypticity and body size after Samoilys and Carlos (2000) (see Chapter 1, Table 1.1). Behavioural groups were used in the development and comparison of the method.

The long-swim transect method consisted of intensely searched timed-swims along unmarked belt transects (see protocol below). In preliminary fieldwork, I found it was feasible to thoroughly search a 5 metre-width band without overlooking areas and within which contained the majority of sightings of small- and medium-sized cryptic serranids. More than half of the roving serranid sightings occurred within this 5 metre band, but large mobile serranids were generally very rare and tended to be wary and poorly represented by narrow transects. Therefore, to include species of large mobile serranids it was necessary to survey a wider band concurrently with the 5 metre search-band (Fig. 2.1). A band of 10 metres to either side of the diver was chosen since this was within the normal range of underwater visibility for the study sites and wide enough to include some wary and more mobile fish. All subsequent surveys covered an estimated 5 metre-width search band and also recorded species of large mobile serranids within an estimated 10 metres on either side of the central line of each swim (quantification of errors in width estimation is described below).

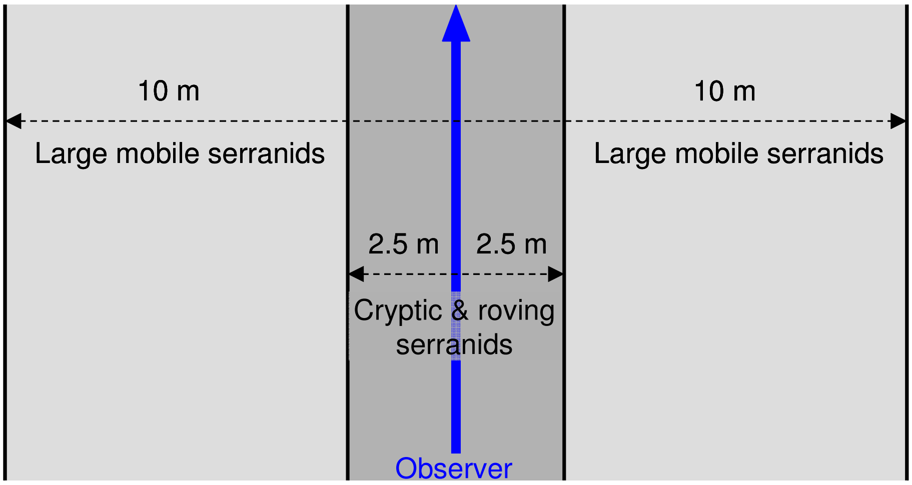


Figure 2.1 Diagram illustrating long-swim transect widths. The observer (= diver) searches the central 5 m width band for cryptic and roving serranids, and concurrently surveys a band 10 m to either side for large mobile serranids.

The effect of observer swim-speed on relative accuracy of abundance estimates was examined. An area of reef approximately 2.5 km long, between Watson's Bay and Mermaid Cove at Lizard Island (Fig. 2.2), known to have relatively high density and diversity of epinepheline serranids was used to minimise the occurrence of non-zero counts of target species in the pilot study dataset. I compared the densities for all epinepheline serranids combined and each behavioural group, and the total number of species from nine transects (each 48 m long) swum at each of three speeds (i.e. total 27 transects). The speeds were: medium (40 m^2 per minute), slow (30 m^2 per minute), and very slow (20 m^2 per minute), confirmed by checking linear progress along the measured transect (of width 5 m) at minute intervals. These swim-speed trial were conducted in a randomised order. One way analysis of variance (ANOVA) with *post-hoc* tests using Tukey's Honestly Significant Differences tests for multiple comparisons (Day & Quinn 1989) (hereafter termed *Tukey's tests*) were done to test the null hypotheses that there were no differences in estimates obtained using the three swimming and searching speeds.

The effect of transect length (giving different survey areas) on the mean total density and number of species and on density of each behavioural group was also examined. I compared long-swim transects of two different fixed times (20 min and 45 min duration) that were otherwise equivalent in terms of swim-speed (slow), transect width and the way each transect was surveyed. The 20 min transects were estimated to be approximately 120 m in length and the 45 min transects approximately 270 m in length from the known time and estimated swim-speed. Independent sample *t*-tests were used to compare the mean density of epinepheline serranids, the number of species, and the density of each behavioural group recorded for the 20 min and 45 min swim transects.

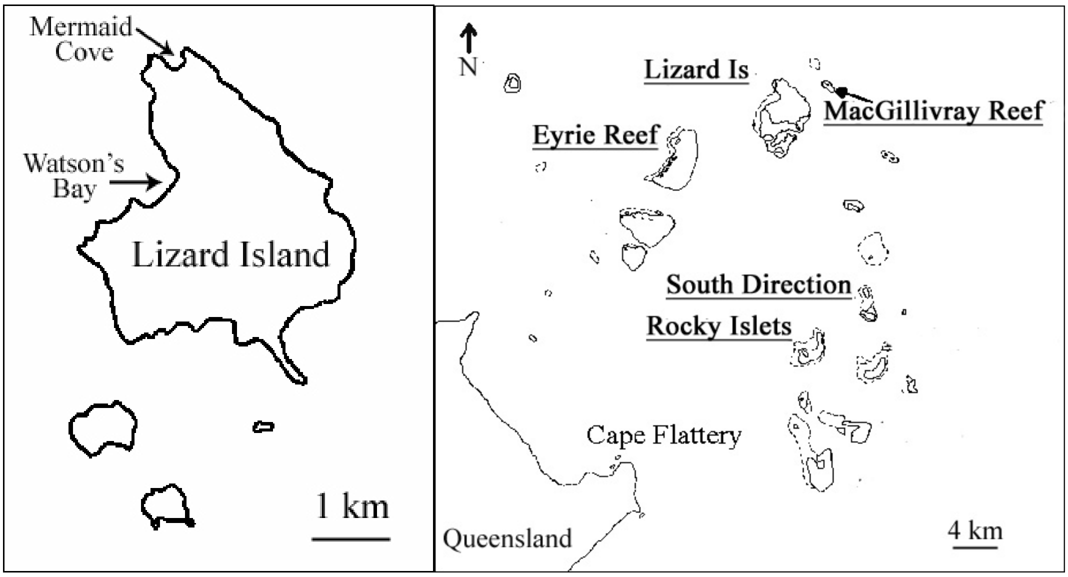


Figure 2.2 Map showing location of pilot study (left, between Watson's Bay and Mermaid Cove on northwest of Lizard Island, northern GBR) and reefs (underlined) where trials of the long-swim transect protocol took place (right) in the northern GBR (Lizard region).

The accuracy of underwater fish length estimation was evaluated following Bell et al. (1985) by estimating fork lengths of wooden fish models from a distance of 2 m and comparing them to measured lengths. This observation distance was chosen since it was generally possible to approach small to medium fish closely. Three trials were done using a random subset of 10 out of 25 models between 100 – 500 mm long. Incremental marks were drawn on the recording slates for reference to assist in estimating lengths during routine surveys.

The chosen protocol (see below) was then trialled in a variety of habitats (exposed reef fronts, sheltered back reef, lagoons) on mid and outer shelf reefs in the northern region of the GBR to examine precision of density estimates for each behavioural group using the formula:

precision = *standard error / mean* (Andrew & Mapstone 1987).

During this trial, I measured the percentage error in transect width estimation by comparing estimated widths to actual widths at the end of each transect (n = 42). Errors in transect length estimation were minimised by using a fixed average swim-speed and further checked by taking GPS readings from the surface of the start and end point of each long-swim transect.

2.3.2 Protocol evaluation

The long-swim transect protocol was subsequently used to derive species-level density estimates for epinepheline serranids (Chapter 3), and used for comparisons with density estimates for similar areas obtained by other methods in previous studies.

The first comparison was with data from surveys of epinepheline serranids by Samoilys and Carlos (1992) in March 1991 from exposed habitats on the north-east end of Arlington Reef, a mid-shelf reef off Cairns in the northern GBR, obtained by two methods: (1) surveys using visual point count surveys (n = 16); and (2) a calibration attempt using explosives (n = 6). I compared these estimates to data collected in 2000 – 2002 from exposed habitats of the northern GBR mid-shelf platform reefs (Eyrie, Rocky and MacGillivray Reefs, n = 9). Fish below 11 cm (the minimum size used by Samoilys and Carlos 1992) were excluded from my density estimates so that the comparisons covered the same size range. Assumptions underlying this comparison are that the abundance of species did not vary systematically: 1) over the approximately 200 km between Arlington Reef and Eyrie, Rocky and MacGillivray Reefs; or 2) between the years in which the different surveys were done. Samoilys and Carlos (1992) provided data on density of three species groups of epinepheline serranids (sedentary, roving, large) and these groups are directly comparable to the cryptic, roving and large mobile serranids behavioural groups, respectively, defined in Chapter 1, Table 1.1.

The second comparison was for *Plectropomus leopardus*, the most common roving serranid on GBR mid-shelf reefs, since species in this group are considered prone to over- as well as under-estimation due to their higher mobility and tendency to rove in and out of the survey area (Samoilys & Carlos 1992, Watson et al. 1995). Appropriate *P. leopardus* density estimates for comparison were obtained from unpublished data from the CRC Reef Effects of Line Fishing (ELF) Experiment: visual survey counts in Oct. 2000 and Oct. 2001 of *P. leopardus* of 6 cm or greater from two protected reefs, South Direction and MacGillivray Reefs, in the Lizard region. All ELF counts were made by A. Ayling using 30 belt-transects (50 m x 5 m) per reef (detailed in Mapstone et al. 2004). I compared these density estimates to those I obtained for the same reefs using long swim transects from Dec. 2000 and Dec. 2001 ($n = 10$).

The third comparison was with data on epinepheline serranids collected using a novel technique reported to give improved abundance estimates for cryptic species (Stewart & Beukers 2000). Stewart and Beukers (2000) used a technique to estimate species densities at Lizard Island that combined quadrat surveys for what they termed "mobile" serranid species (i.e. *Plectropomus leopardus, Epinephelus ongus*) and baited point counts for "cryptic" serranid species (all other species observed). They did not record any species of large mobile serranids as defined in Chapter 1, Table 1.1. I compared their mean density estimates from December 1994 and January 1995 for all epinepheline serranids in each of three habitats (exposed, sheltered and lagoonal, $n = 18$ each habitat type) and for all habitats combined ($n = 54$) to my total density estimates for the same habitats at Lizard Island obtained in 2000 – 2002 from long swim transects (exposed $n = 5$, sheltered $n = 6$, lagoonal $n = 4$). I randomly selected 4 long-swim transects from each habitat for the comparison of all habitats combined, to obtain a balanced sampling effort across habitat-types ($n = 12$).

2.4 Results

2.4.1 Pilot Study

Figure 2.3 shows mean total density of epinepheline serranids for each swim-speed. There was a significant effect of observer swim-speed on mean total density of epinepheline serranids ($F(2, 24) = 4.64$, $p < 0.05$). *Post-hoc* comparisons indicated that the mean total density of epinepheline serranids for medium speeds was significantly lower ($p < 0.05$) than estimates from both the slow and very slow speeds, which did not differ significantly (Fig. 2.3). There was also a significant effect of observer swim-speed on number of species of epinepheline serranids ($F(2, 24) = 4.35$, $p < 0.05$), with the mean number of species recorded from the medium speed (2.2 species per transect, S.D. = 1.6) significantly lower than for the slow speed (3.8 per transect, S.D. = 1.0), but neither of these differed significantly from the number of species recorded on the very slow swims (3.4 species per transect, S.D. = 0.7).

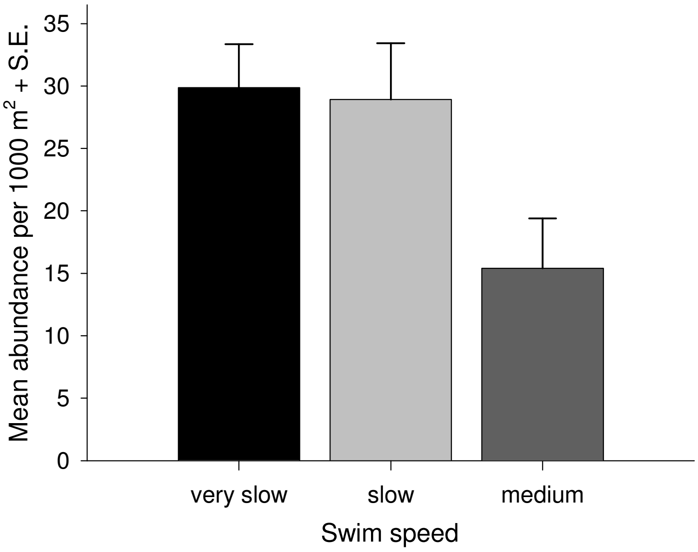


Figure 2.3 Swim-speed trial. Overall mean density of epinepheline serranids per 1000 m^2 estimated from transects (*n* = 27) swam at one of three different speeds. The speeds were: medium (40 m^2 per minute), slow (30 m^2 per minute), and very slow (20 m^2 per minute).

The ANOVAs for each behavioural group did not detect any significant differences in density between swim-speeds (cryptic serranids: $F(2, 24) = 2.89$, $p = 0.08$; roving serranids: $F(2, 24) = 1.30$, $p = 0.29$; large mobile: $F(2, 24) = 1.09$, $p = 0.35$). Densities from both slow and very slow speeds were consistently ranked above those for medium swim-speed, however, with no indication that counts from the former two speeds differed from each other (Fig. 2.4). Given these results, the slow swim-speed (30 m^2 per min) was selected as the most efficient means of recording the greatest species counts and estimated densities of epinepheline serranids.

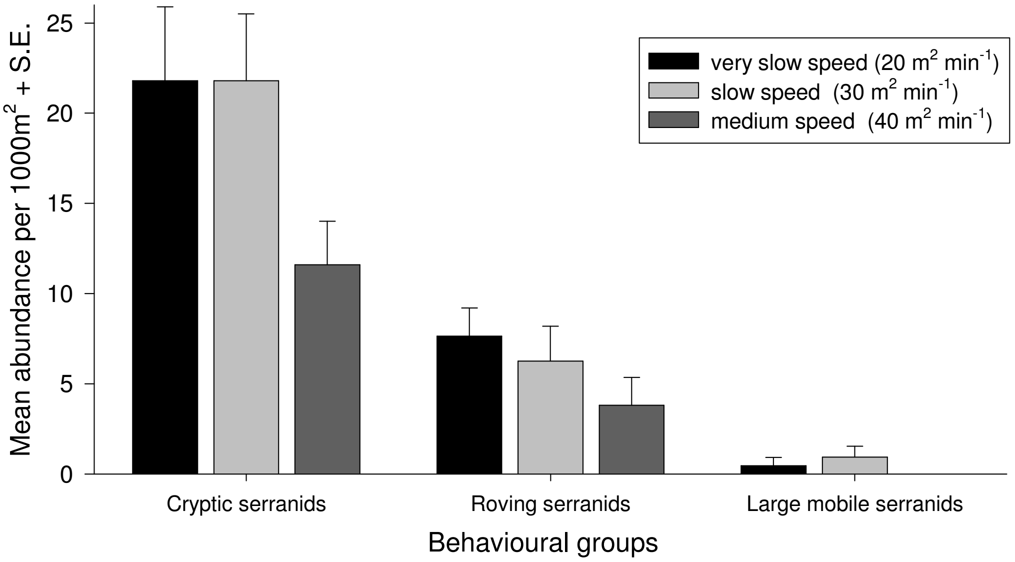


Figure 2.4 Swim-speed trial. Mean density per 1000 m^2 of each behavioural group of epinepheline serranids estimated from transects swam at one of three different speeds (*n* = 27).

There was no difference in mean density of epinepheline serranids from 20 min (mean = 18.9 per 1000 m^2, S.D. = 12.0) and 45 min swim transects (mean = 24.9 per 1000 m^2, S.D. = 10.8; $t(25) = 1.23$, $p > 0.05$). The number of species recorded, however, was significantly higher for the 45 min swim transects (mean = 5.9 , S.D. = 1.4) than for the 20 min swim transects (mean = 4.4, S.D. = 2.2; $t(22.4) = 2.18$, $p < 0.05$), indicating that 45 min swim transects were better for characterising serranid assemblages. The mean density of cryptic serranids was significantly higher from the 45 min transects (mean = 20.4, S.D. = 10.2; $t(25) = 2.15$, $p < 0.05$) than from the 20 min transects (mean = 12.6, S.D. = 8.6), but no significant differences between transect lengths were detected for the other behavioural groups (Fig. 2.5). Thus, slow, 45 min swim transects were chosen for the standard protocol for subsequent surveys.

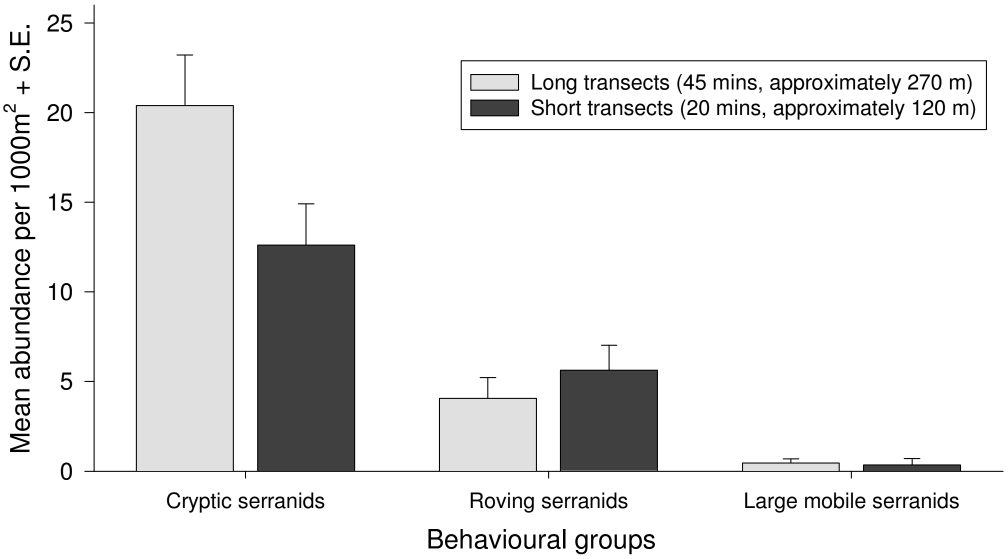


Figure 2.5 Transect length trial. Mean density of each behavioural group of epinepheline serranids per 1000 m^2 estimated from transects of two different lengths: short, 20 mins; long, 45 mins (*n* = 27). The 20 min transects were approximately 120 m in length and the 45 min transects approximately 270 m in length.

Trials of fish length estimation recorded absolute errors from –8 to +5 cm but 80% were within 2 cm of the actual (model fish) length. Estimated fish lengths were on average –0.84 cm or 3% less than actual lengths (± 1.5 S.E., *n* = 30). No corrections were made to subsequent length estimates. Trials of the long-swim transect indicated that precision was higher (< 0.1) for all epinephelines (0.06), cryptic serranids (0.08) and roving serranids (0.09), than for large mobile serranids (0.26).

Mean percentage errors (± S.E.) in the estimation of the two search widths (*n* = 42) covered on each transect (10 m, 2.5 m) were 3.3%, (± 0.37) and 3.8% (± 0.43), respectively (Fig. 2.6).

2.4.2 Long-swim transect protocol for serranid abundance data

The long-swim transect method resolved from this study consisted of surveys on SCUBA of transects with length set by swims of 45 min duration, with a fixed average search speed of 30 m^2 per min (slow) and detailed searches of substrata. A band with an estimated width of 5 m was searched for cryptic serranids and roving serranids (defined in Chapter 1, Table 1.1), and observations of large mobile serranids were made over an estimated 10 metre-width on either side of the central swim line. Each portion of each transect was viewed only once for each target species, and all epinepheline serranid individuals encountered of 6 cm FL or greater were identified to species-level and their fork-length estimated. All visual surveys were done by the same observer and the data were recorded onto prepared waterproof data sheets to ensure consistency. The transect length (estimated to be 270 m from the known time and estimated swim-speed) was checked regularly using GPS readings. Distance estimation and swim-speed was re-checked at the start of each field trip. One timed, uni-directional belt transect was swum in depths of 2 – 15 m of water at each site. Multiple sites surveyed within the same habitat-type on a reef were separated by hundreds of metres.

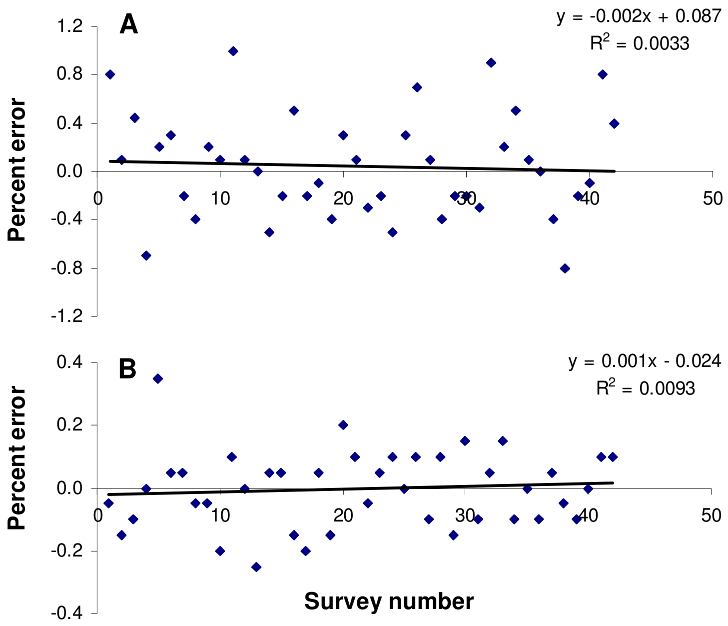


Figure 2.6 Percent errors in estimation of A) 10 metre width and B) 2.5 metre width transects from 42 trials. Errors due to width estimation were equi-distributed around zero (meaning the net effect on density estimates over several transects was approximately zero).

2.4.3 Comparisons with published data

Density estimates obtained using long-swim transects were compared with estimates obtained using a variety of methods from similar areas of the GBR (Samoilys & Carlos 1992, Stewart & Beukers 2000) (Tables 2.1 to 2.3). All estimates were converted to density per 1000 m^2 for comparisons. Considerably higher density estimates were obtained for cryptic serranids and roving serranids using the long-swim transect method compared to either point counts or explosives (Table 2.1). Density estimates obtained for *P. leopardus* at two protected reefs using the long-swim transect were similar to those obtained by Ayling / ELF Project using belt transects (Table 2.2). The long-swim transect produced lower density estimates than the combined survey method devised by Stewart and Beukers (2000) (Table 2.3).

Table 2.1 Comparison of mean density estimates per 1000 m^2 (± S.E.) for behavioural groups of epinepheline serranids from Samoilys and Carlos (1992) (using visual point count surveys and explosives) with results from this study (using long-swim transects). Definitions of behavioural groups given in Chapter 1, Table 1.1 and Samoilys and Carlos (1992, 2000).

Comparable estimates	**Density of epinepheline serranids per 1000 m^2 ± S.E.**		
Group	***Sedentary/Cryptic***	***Roving***	***Large/Large mobile***
Visual survey using point counts[a]	1.1 ± 0.5	0.5 ± 0.5	0
Explosives[b]	10.5 ± 1.2	0.7 ± 0.4	0
Long-swim transect[c]	22.3 ± 2.6	4.4 ± 0.6	0.2 ± 0.1

[a] Samoilys and Carlos 1992, [b] Estimated from Fig. C.6.3.2 in Samoilys and Carlos 1992. [c] This study.

Table 2.2 Comparison of mean density estimates per 1000 m^2 (± S.E.) for *P. leopardus* from unpublished visual survey data recorded by Ayling / ELF Project (using 50 m x 5 m belt transects, methods detailed in Mapstone et al. 2004, data provided by Mapstone) with this study (using long-swim transects). Data are from surveys at two protected mid-shelf reefs (South Direction and MacGillivray Reef) in the northern GBR.

Comparable estimates	**Density of P. leopardus per 1000 m^2 ± S.E.**
Belt transect by Ayling[a] (2000)	4.5 ± 0.5
Belt transect by Ayling[a] (2001)	3.7 ± 0.3
Long-swim transect[b] (2000 – 2001)	4.1 ± 0.6

[a]Data from Effects of Line Fishing Project, CRC Reef Research Centre, Townsville, [b] This study.

Table 2.3 Comparison of mean density estimates per 1000 m^2 (± S.E.) for epinephelines using a combined survey technique described by Stewart and Beukers (2000) with estimates from this study (using long-swim transects). Data are from surveys in three habitats at Lizard Island in the northern GBR. Stewart and Beukers (2000) used a baited point survey for all species of epinephelines except for *P. leopardus* and *E. ongus*, which they counted using quadrat surveys.

Comparable estimates	**Total density of epinepheline serranids per 1000 m^2 ± S.E.**			
Habitat	***Exposed***	***Sheltered***	***Lagoonal***	***All habitats***
Combined survey technique[a]	40 ± 5	85 ± 10	28 ± 5	55 ± 6
Long-swim transect[b]	26.4 ± 2.7	31.2 ± 2.9	14.0 ± 4.1	25.0 ± 3.2

[a]Estimated from Fig. 3 or 5, Stewart, 2000, [b] This study.

2.5 Discussion

The appropriateness of a fish count method will depend on the species and questions under investigation. My modified visual survey method using long-swim transects was tailored to provide species-level density estimates of all epinepheline serranids to characterise the assemblage. Advantages of long-swim transects for fishes such as epinephelines include: 1) coverage of large area in limited divetime compared to small transects, facilitating characterisation of the full assemblage and at least provisional estimation of abundances for the rarer species; 2) logistic simplicity; and 3) minimisation of disturbance or attraction of fish since no tape measures are used before counting. As for some other methods, the long-swim transects can be used to generate density estimates, not just coarse or qualitative estimates or abundance ranges (e.g. log scale records). For a given search intensity (time per unit area), however, the time and hence cost for each replicate will increase in proportion to survey area. There is a financial trade-off, therefore, between larger survey areas, requiring increased time per replicate, and the degree of replication.

Caution is needed when inferring relative accuracies of different methods if data on absolute density is not available. The long-swim transect method, by using a relatively intense and focused search, is likely to have reduced, but not eliminated, the tendency in visual surveys to underestimate population density of well-camouflaged, cryptic species of reef fish. An unknown proportion of fish are still likely to have been "missed" for two broad reasons: 1) some fish may not be visible to the observer; and 2) others may not be noticed by the observer (Thompson & Mapstone 1997). Overestimation is also possible in visual surveys, and may be of most concern for more mobile species of roving serranids (Andrew & Mapstone 1987, Watson et al. 1995). Approaches such as tagging all fish in an area to directly evaluate the accuracy of density estimates have rarely been attempted even for the most common and site-attached species of epinephelines (Stewart & Beukers 2000), and would be extremely difficult for the whole taxon. In the absence of practical tests of accuracy, this study compared density estimates to previous studies for similar species and locations to evaluate relative biases and the extent to which relative accuracies of the different methods can be inferred using auxiliary knowledge (Andrew & Mapstone 1987).

The long-swim transect method produced considerably higher estimates of mean density of total epinepheline serranids and both cryptic and roving serranids than those obtained by Samoilys and Carlos (1992) using visual surveys or explosives. There are several reasons why the explosives density estimate could be lower than that obtained by this study. Explosive counts are known to have two potential biases, both resulting in underestimation: failure to collect all killed individuals; and low kill efficiency. The first of these is most acute for small and/or cryptic individuals such as some serranids, and the second can occur if habitat relief provides cover from shock waves (Samoilys & Carlos 1992), which is possible within the coral reef matrix where many cryptic serranids occur. Another reason for the differences between my estimates and those of Samoilys and Carlos could be natural population differences between Arlington Reef and the reefs I surveyed around Lizard Island, approximately 200 km north of Arlington Reef, or temporal changes in abundance between 1991 when Samoilys and Carlos collected their data and 2000 – 2002 when my surveys were done. While Ayling et al. (2000) found no significant temporal differences in densities of *P. leopardus*, the main target species in the local reef fishery, between 1982 and 1999 for the Lizard region, time series data are lacking for other species and for Arlington Reef. It is also possible that I might have overestimated the number of fish, for example by counting the same individuals more than once or by errors in area estimation. Overestimation is considered unlikely, however, for several reasons: 1) the survey was limited to epinepheline serranids; 2) target fish were usually so sparse and relatively site-attached that it was relatively easy to keep track of individual fish to avoid over-counting; and 3) the errors due to area estimation were found to be reasonably low and equi-distributed around zero, meaning a net effect on density over several transects of approximately zero.

The comparison with results from Samoilys and Carlos (1992) suggests the long-swim method is an improvement on the point count visual survey method for epinepheline serranids in shallow reef habitats, since higher density estimates are assumed to be closer to the true population mean (Sale & Douglas 1981, Brock 1982, St John et al. 1990, Samoilys & Carlos 1992). Tailoring the count protocol specifically to epinepheline serranids may account for the apparent improvement in accuracy. In particular, benefits of the new method for improved accuracy may have arisen from low disturbance of fish, high search intensity and concentration on search-image of just one taxon throughout each transect. Attempts to simultaneously count other components of the reef fish fauna or the collection of additional data (such as benthic cover or substrate type) are likely to detrimentally affect the counts of the target group (epinephelines) because the observer may either over-look many of the more cryptic individuals, or particular components or species of the target group (Lincoln Smith 1989). Further, coverage of large areas enabled preliminary density estimates to be made of rarer species, including some large mobile serranids that are generally not recorded in visual surveys. The importance of information on rare species for providing insights into reef fish ecology and conservation biology and the difficulty in obtaining reliable abundance estimates has been recognised (Jones et al. 2002, Maxwell & Jennings 2005).

A possible concern of using the slower swim-speed of the long-swim transect is that roving serranids could be over-counted, but this appeared to be unfounded. The comparison with counts by Ayling / ELF Project from two protected northern GBR mid-shelf reefs suggested that density estimates for roving serranids such as the coral trout species *P. leopardus* by the new count protocol were consistent with those for the methods developed by Mapstone and Ayling (1993) and used widely in surveys on the GBR. Thus, there was no evidence that my revised method exacerbated any biases already present in the established method.

In contrast, this study produced lower density estimates than the combined survey method devised by Stewart and Beukers (2000). It is likely, however, that baiting might result in a degree of over-estimation of densities because fish are likely to be drawn from a large area to the single point of counting, around a bait. Tests of a baited point survey method during my preliminary field work indicated that several species of cryptic serranids and roving serranids were attracted from distances greater than 5 m (the diameter of baited surveys area used by Stewart & Beukers 2000), but such movements may easily be missed by observers since the fish tended to remain under cover unless moving very rapidly between shelters. If the effective diameter sampled by Stewart and Beukers (2000) during their baited point counts was greater than 5 m, species densities would have been over-estimated. For example, fish would only have to move in from just over 1 m outside the 5 m point count to effectively double the area covered and thus the density estimates provided by Stewart and Beukers. The authors acknowledged that at least the more mobile species did move into baited census areas, hence their choice of a combined technique using quadrat counts for the most mobile species (i.e. *P. leopardus, E. ongus*). However, there is lack of data for most species of epinephelines to verify that they do not move at least short distances (metres) into baited areas. Accordingly, comparison of baited and unbaited methods should be treated with caution. Other factors that might have caused different estimates include temporal or within habitat variation, but the available data were insufficient to examine these factors.

Overall, the long-swim transect method appears to offer an improvement in accuracy over established unbaited visual survey methods since densities are likely to be underestimated to a lesser degree. Technological advances may facilitate direct measurement of the length of long-swim transects in future studies, thereby reducing this source of error. Future research on correction factors to account for missed or hidden fishes during visual surveys (e.g. approaches based on mark-recapture methods, Gilbert et al. 2005), or development of methods to directly assess accuracy for the study species would be worthwhile. An important consideration for visual survey designs and interpretation of results is the influence of the relatively large imprecision in counts for rarer species, including most species of large mobile serranids, since it will reduce the power to detect pattern in survey data (Andrew & Mapstone 1987, Thompson & Mapstone 1997). As a result, conservation and management action for rare and vulnerable species, such as many epinepheline serranids, should not depend on detecting declines strictly according to conventional statistical criteria (e.g. $p < 0.05$)

(Maxwell & Jennings 2005). Nonetheless, the long-swim transect method is a useful tool for epinepheline serranids and can provide at least provisional species-level density estimates for the full species list of epinepheline serranids. Applications include characterisation of the epinepheline fauna (Chapter 3) and providing abundance information for fisheries and conservation assessments (e.g. Choat & Pears 2003).

Chapter 3. Multi-scale patterns of distribution, abundance and size structure of epinepheline serranids from the Great Barrier Reef and the Seychelles

3.1 Synopsis

Information on abundance and assemblage structure of epinepheline serranids provides an ecological foundation for the study of demography and life histories, and is important for sound management of these fishes. This study presents a comprehensive account of epinepheline assemblages from the Great Barrier Reef (GBR) and the Seychelles. I described and compared characteristics of epinepheline serranid faunas at a range of spatial scales from <1 to 1000's km along natural environmental and geographic gradients on the GBR and the Seychelles Islands, and provided abundance estimates for three behavioural groups (*cryptic serranids*, *roving serranids*, and *large mobile serranids*) and for the almost 40 species they represent. The typical shallow-water, tropical epinepheline assemblages comprised a handful of abundant species from the cryptic or roving serranid behavioural groups, plus numerous species found only in low densities locally (i.e. rare species, less than 1 fish per 1000 m^2) from each behavioural group. The various characteristics used to describe assemblage structure (i.e. total density of epinepheline serranids; density of each behavioural group; species richness; size structure; and species distribution and abundance) showed differing spatial patterns and magnitudes of variation among behavioural groups and species, with some strong differences, such as in local densities, likely to be biologically significant. Three approaches were used to explore possible effects of fishing on densities: 1) incorporating the CRC Reef Research Centre's Effects of Line Fishing Experiment treatments, manipulating fishing level and Marine Park zone status for GBR reefs, into the GBR regional comparison; 2) comparing reefs open and closed to fishing for Lizard outer shelf reefs; and 3) exploring abundance patterns in relation to presumed gradients of historical fishing pressure. Each approach indicated some effects of fishing on at least some species of epinepheline serranids.

3.2 Introduction

Reliable information on the distribution and abundance of epinepheline serranids is important for sound management of these fishes as well as to provide a foundation for understanding serranid demography and reef fish life history strategies (Pogonoski et al. 2002). Little information exists on patterns of abundance for the majority of Indo-Pacific epinepheline species (e.g. Pogonoski et al. 2002). The main exception is for *Plectropomus leopardus* on the GBR, as considerable information has been collected on patterns of abundance for this commercial species since 1980 (e.g. Ayling 1983, Mapstone et al. 1998a, Ayling et al. 2000, Mapstone et al. 2004).

It is now well established that reef fish abundance and distribution is variable at a range of scales (review Williams 1991, Newman et al. 1997, Gust et al. 2001). Further, given the multi-scale and heterogeneous nature of reef habitats, incorporating multiple scales into sampling designs is important to ensure results are widely applicable (Andrew & Mapstone 1987, Mapstone et al. 1998a, b, Sale 1998, Gust 2000, Gust et al. 2001). Few researchers have attempted to investigate multi-scale spatial variability in epinepheline serranid assemblages (see Newman et al. 1997, Stewart & Beukers 2000). In this study a sampling design was used that took into account spatial variability at multiple scales, spanning reefs to oceans. Detecting the pattern and magnitude of differences at broader biogeographic scales is of particular interest from the perspectives of reef fish ecology and evolution and practical management.

Combining the study of assemblage- and species-level characteristics of epinepheline serranids provides much needed abundance estimates for each species, and enables information on species abundance and distribution to be understood in the context of the whole taxon and their ecological function. Moreover, examination of assemblage-level characteristics over broad spatial scales allows comparative analyses of similarities and differences in epinepheline serranid faunas between localities with only partly overlapping species pools, but parallel behavioural groups of these important predators.

Estimates of body size of fish in visual surveys allows examination of patterns of fish size structure and biomass and the relationship between abundance and fish size. Size information is often not provided in assemblage-level studies of reef fishes (Robertson 1998), yet we might expect varying relationships between local density and fish size based on factors such as recruitment, local population dynamics, fishing effects or other disturbances, prevailing environmental conditions, movement or behavioural differences among places (Sale 1991a). Variations in size, as well as abundance, may have implications for individual fish, local population dynamics, population regulation and response to fishing or other disturbances (Kerr 1974, Peters 1983, Dickie et al. 1987, Miller 1996, Jennings et al. 1998, Robertson 1998, Jennings et al. 1999b, Dulvy et al. 2004, Sale 2004). Quantification of spatial patterns of abundance and size in this Chapter will provide the framework for the subsequent analysis of demographic and life history characteristics of a suite of species (Chapters 4 – 6).

Epinepheline serranids play important ecological roles as predators, competitors and or facilitators to other reef organisms, shaping local community structure (Hixon 1991b, Jones

1991, Hixon et al. 2002, Almany 2003). These interactions are likely to depend on the identities and sizes of individuals, since absolute and relative sizes of individuals can influence the intensity and outcome of predator-prey or competitive interactions in assemblages of reef fishes (Peters 1983, Munday & Jones 1998). Individuals and species of predatory reef fish are most likely to prey on smaller organisms, but compete with similar-sized organisms. Thus, the relative abundances and composition of ecological groupings or species in epinepheline assemblages may have important consequences for local population regulation of diverse species. Further, there may be cascading ecosystem effects of over-fishing predators, such as epinephelines, with regulatory roles in reef fish assemblages (Jennings & Lock 1996, Hixon & Carr 1997, Carr et al. 2002).

My aim in this study was to explore spatial patterns of abundance, distribution and size structure for epinepheline serranids in shallow reef habitats on the GBR and the Seychelles Islands, both as a context for subsequent life history research and to provide information on the whole epinepheline assemblage. I describe and compare characteristics of epinepheline serranid faunas at a range of spatial scales from <1 to 1000's km along natural environmental and geographic gradients on the GBR and the Seychelles Islands, and provide abundance estimates for three behavioural groups (cryptic, mobile and roving serranids, Chapter 1, Table 1.1) and for the almost 40 species they represent. The possible role of fishing in determining the abundance of these epinephelines was also considered.

3.3 Methods

3.3.1 Data collection

Visual surveys of epinepheline serranids were conducted by the same observer (R.J.P.) at the species-level of resolution, using the long-swim transect method detailed in Chapter 2. The accuracy of fish size and distance (transect width) estimation and consistency of swim-speed (Chapter 2) were maintained by practicing at the start of each field trip and then using the information obtained on any bias as a cue to improve the accuracy of estimation. The number of individuals and estimated fork length (FL) were recorded for all fish of 6 cm FL or greater. This size-range would certainly have included adults, as well as some sub-adults and juveniles, but no distinction has been made between life stages for analyses since the size at which such distinctions should be made remain unknown for many of the species counted. Behavioural groups of species (Chapter 1, Table 1.1) were used in some analyses to highlight similarities and differences in assemblage structure at various scales.

3.3.2 Sampling design

Four assemblage-level characteristics and species patterns of distribution and abundance were used to describe "assemblage structure" and compare epinepheline serranid faunas (detailed in Table 3.1).

Table 3.1 Characteristics used to describe and compare epinepheline serranid faunas and summary of analytical approaches.

Characteristic	Analyses
Assemblage-level	
1. Total density of epinepheline serranids	Analysis of variance
2. Density of each behavioural group	Analysis of variance
3. Species richness	Analysis of variance and bootstrap re-sampling
4. Size structure	Correspondence analysis and Kolmogorov-Smirnov two sample tests
Species-level	
5. Distribution and abundance	Species abundance plots, principal component analysis and hierarchical cluster analysis

Spatial scales

The following spatial scales were examined:

- **Area** – the GBR (Pacific Ocean) and the Seychelles Islands (Indian Ocean, see Fig. 3.1) – scale: 1000's km;
- **Broad Region** – four broad regions within each area covering similar spatial scales spread over 6° or 7° of latitude – scale: 100's to 1000's km;
- **Position** – two positions (mid shelf and outer shelf) across the continental shelf of the GBR – scale: 10's km,
- **Reef** – small to medium sized reefs (1 - 10 km maximum axis) or equivalent-scale sites within very large atolls (e.g. Farquhar Group) or large islands (e.g. Mahe) separated by up to several kilometres – scale: 1 to 10's km.
- **Habitat** – habitat type (exposed, sheltered, lagoonal) of GBR reefs distinguished by physical characteristics and orientation to prevailing wind and wave action – scale: <1 to 1 km.

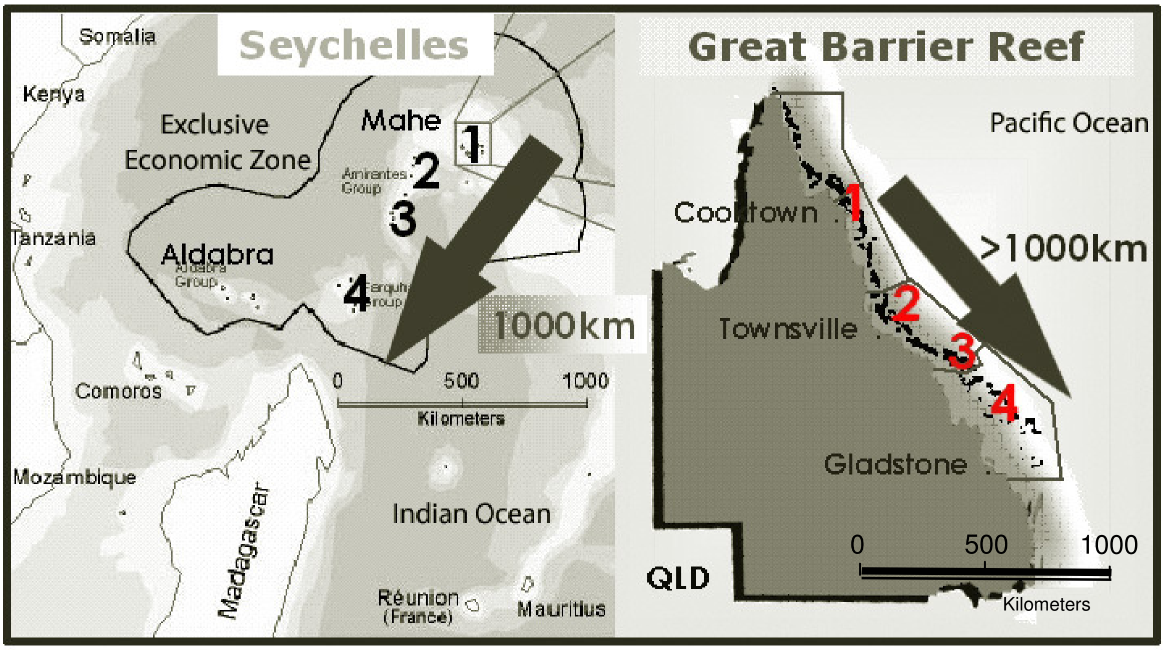


Figure 3.1 Map showing locations of visual surveys for epinepheline serranids used in this study. Four broad regions were surveyed in the Seychelles and the GBR. Key to broad regions – Seychelles: 1 = Inner Isles, 2 = Northern Amirante Isles, 3 = Southern Amirante Isles, 4 = Farquhar group. GBR: 1 = Lizard, 2 = Townsville, 3 = Mackay, 4 = Pompey.

Distinctions between habitats within a reef based on exposure as used for the GBR were not considered appropriate in the Seychelles given the more complex pattern of trade winds which affect different sides of each reef at different times of the year. Furthermore, since the type of reef naturally differs regionally in the Seychelles, with a mixture of mainly granitic boulder reefs and carbonate fringing reefs in the Inner Isles, carbonate platform reefs in the northern Amirante Isles and atolls in the southern Amirante Isles and Farquhar Group, similarities and differences between reef type or habitats in the Seychelles could not be examined consistently across all broad regions. Some comparison of reef type was possible, however, within the Inner Isles, the only Seychelles broad region where multiple reef types were surveyed, but habitat did not explain significant variations in abundances in that broad region (Appendix 1).

Surveys were conducted between December 2000 and December 2002 (Table 3.2). All surveys were done during the late austral spring and summer (October to February).

Table 3.2 Overall sampling design showing number of long-swim transects at each spatial scale. In total, 11,882 individual fishes were counted from all 221 transects in the GBR and Seychelles, consisting of 39 species from 9 of the 11 Indo-Pacific genera of epinephelines. Codes for areas and broad regions indicated in parentheses. Surveys took place during austral spring/summer from Dec 2000 to Dec 2002. Year indicates which spring/summer(s) a region was surveyed.

Area (codes)	Broad Region (codes)	Year	Number of long-swim transects
Great Barrier Reef,			
Pacific Ocean	Lizard outer shelf (LO)	2000-1, 2001-2, 2002-3	56
(GBR)	Lizard mid shelf (LM)	2000-1, 2001-2, 2002-3	53
	Townsville (TM)	2002-3	21
	Mackay (MM)	2001-2	20
	Pompey (PM)	2001-2	19
Great Barrier Reef total			169
Seychelles Islands,			
Indian Ocean	Inner Isles (II)	mostly 2001-2, 2002-3	18
(SEZ)	Amirante Isles, northern (AN)	2001-2	11
	Amirante Isles, southern (AS)	mostly 2001-2, 2002-3	13
	Farquhar Group (FG)	2002-3	10
Seychelles Islands total			52
Grand total			221

3.3.3 Data analyses

Replication

The effect of sample size (number of replicate swims) on the estimates of species richness (species count) was examined (Appendix 1) and indicated that a minimum replication of about 40 samples per area (Appendix 1: Fig. A1.1) or about 10 samples per broad region (Appendix 1: Fig. A1.2) were sufficient for species counts to estimate species richness at each scale. These plots also indicated that unequal sample sizes will tend to bias comparisons of species counts. Accordingly, estimates of the mean cumulative number of species for replication equal to the lowest sample size of any group being compared (Areas: n = 52; Broad Regions: n = 10), termed ‘bootstrap species counts’, are presented for comparisons with results from the full raw datasets (Table 3.2).

Spatial comparison of densities and species richness

Data were pooled across years for analyses in which sites surveyed in more than one year were being compared to other sites that were surveyed in only one year. This was considered reasonable since tests of interannual variation in the Lizard Island Region did not indicate significant temporal variation (Appendix 1) and it seemed unlikely that there would have been major changes in spatial factors (e.g. habitat or fishing mortality) potentially affecting adult epinepheline diversity or abundance during the study period, and any high recruitment events could be detected since fish size was recorded in the surveys.

All abundance estimates are expressed as mean density per 1000 m^2 ± 1 standard error (S.E.). Two measures of species richness were examined: 1) mean number of species per reef, and 2) total species count per broad region or area (estimated using two methods: raw counts of the number of species and a bootstrapping procedure detailed below). The following spatial comparisons were made using ANOVA to examine the first three assemblage characteristics (total density, densities of behavioural groups, and species richness; Table 3.1).

A. GBR and Seychelles regional comparison: Log density of all epinephelines and of each behavioural group were compared among Areas, Broad Regions and Reefs (Table 3.3) using 3 factor fully nested ANOVA with Reef nested in Broad Region (random factors) nested in Area (fixed factor). The number of species per Reef was compared among Broad Region nested in Area using a nested 2 factor ANOVA.

Table 3.3 Analysis of variance model A for GBR and Seychelles regional comparison. Random factors indicated by italics, df = degrees of freedom, error term = Mean Square term used as the denominator in calculating F-ratios.

Source of variation	df	Error term
Area	1	Broad-Region(Area)
Broad-Region(Area)	6	Reef(Broad-Region(Area))
*Reef(Broad-Region(*Area*))*	33	Error
Residual (error)	111	

B. Habitat and fishing effects among GBR regions: Density of all epinephelines and of each behavioural group were compared among Broad Regions (Lizard mid shelf, Townsville, Mackay, Pompey, random factor), Treatments (3 levels, detailed below), Reefs (random factor) and Habitats (sheltered or exposed only, fixed factor) using the 4 factor mixed model ANOVA detailed in Table 3.4. Reefs were nested in Broad Region and Treatment (two Reefs per Broad Region * Treatment). The number of species per Reef were compared among Broad Region (random factor) and Habitat (fixed factor) using a 2 factor mixed effects ANOVA.

C. Northern GBR cross-shelf comparison: Density estimates of all epinephelines and of each behavioural group were compared among Habitats (lagoonal, sheltered or exposed) and shelf Position (mid shelf reefs or outer shelf reefs) in the Lizard region using the 3 factor mixed model ANOVA detailed in Table 3.5. Reefs (random factor) were nested in Position. Reefs without lagoons (MacGillivray Reef and North Direction) were excluded from this analysis. The number of species per Reef were compared among Position and Habitat using a 2 factor fixed effects ANOVA.

Table 3.4 Analysis of variance model B comparing habitat and fishing effects among GBR regions. Random factors indicated by italics, df = degrees of freedom, error term = Mean Square term used as the denominator in calculating F-ratios.

Source of variation	**df**	**Error term**
Broad-Region	3	Reef(Broad-Region*Treatment)
Treatment	2	Broad-Region*Treatment
_Reef(Broad-Region*_Treatment)	12	Error
Habitat	1	Broad-Region*Habitat
_Broad-Region*_Treatment	6	Reef(Broad-Region*Treatment)
_Broad-Region*_Habitat	3	Reef(Broad-Region*Treatment)*Habitat
Treatment*Habitat	2	Broad-Region*Treatment*Habitat
_Broad-Region*_Treatment*Habitat	6	Reef(Broad-Region*Treatment)*Habitat
_Reef(Broad-Region*_Treatment)*Habitat	12	Error
Residual (error)	52	

Table 3.5 Analysis of variance model C for cross-shelf transect of the northern GBR. Random factors indicated by italics, df = degrees of freedom, error term = Mean Square term used as the denominator in calculating F-ratios.

Source of variation	**df**	**Error term**
Position	1	Reef(Position)
_Reef(_Position)	8	Error
Habitat	2	Reef(Position)*Habitat
Position*Habitat	2	Reef(Position)*Habitat
_Reef(_Position)*Habitat	16	Error
Residual (error)	68	

The datasets used for each comparison are detailed in Appendix 2: Tables A2.1-A2.3. Comparisons A and B excluded data from GBR outer shelf reefs and from lagoonal habitats since these were only surveyed in the Lizard region. The northern GBR cross-shelf (Position) comparison used the comprehensive dataset from the Lizard region, allowing examination of fine and medium scales. Multivariate analyses of variance (MANOVA) were done prior to separate univariate ANOVAs for each behavioural group to protect against inflated familywise Type I errors and to account for correlations between dependent variables (Field 2000). Pillais' Trace criterion was used to test for group differences in the MANOVAs since it is generally more robust than most alternatives to deviation from homogeneity of variances (Tabachnick & Fidell 1996). Type III Sums of Squares (Milliken & Johnson 1992) were used throughout to account for uneven sample numbers per cell in the tests. Normal probability plots and residual plots were used to examine the assumptions of normality and homogeneity of variances for all data prior to analysis. Log transformations were used to improve normality for the area comparison, but only minor improvements in homogeneity of variances were achieved. Data for large mobile serranids generally did not conform to the normality assumption after transformation attempts, with raw counts heavily skewed towards zero.

Analyses were still performed if normality and homogeneity of variances assumptions were not satisfied, since ANOVAs are relatively robust to departures from these assumptions (Underwood 1981, 1997), although interpretation of significant results was more circumspect for such analyses because heteroscedasticity is considered most likely to increase the prospects of Type I errors. Other data generally conformed to these assumptions and accordingly no transformations were necessary. Sources of significant differences indicated in ANOVAs were identified by Tukey's tests (Day & Quinn 1989). Estimates of the percent of variation attributable to each source in the ANOVA models were calculated (Searle et al. 1992). Plots of these percentages were made to provide a visual representation of the variation attributable to the various scales.

Effects of fishing

Fishing may have affected abundance and or size of epinepheline serranids in the study localities as there are local fisheries for these species in the GBR and the Seychelles (see Chapter 1: 1.7). Two analyses incorporated potential fishing effects. First, the effects of three experimental Treatment combinations of fishing level and Marine Park zone status on density estimates for all epinephelines and each behavioural group on the GBR were examined (as part of comparison B above). All but two of the reefs surveyed along the GBR are part of the ELF Experiment (Mapstone et al. 2004).

The principal aims of the ELF Experiment were to evaluate the resilience of harvested populations to fishing and the effectiveness of alternative strategies for effort management and area closure on the GBR (Mapstone et al. 2004). The experiment involves four clusters of six reefs (i.e. n = 24 reefs) located in four regions of the GBR spanning 7° of latitude (details in Mapstone et al. 2004). Four reefs in each cluster had been closed to fishing for 10 – 12 years prior to the start of the experiment in 1995 and two reefs had been open to fishing historically. Two of the closed reefs in each cluster remain closed to all fishing other than annual catch surveys (here termed "lightly fished"). The other two previously closed reefs in each cluster were subject to experimental manipulations that opened them to pulse fishing for one year periods (termed "moderately fished"). Increased fishing was also encouraged on the reefs open to fishing (termed "fully fished"). Closure of these latter reefs to fishing (in 1998 or 2000) happened shortly before the study reported here and thus only minimal rebuilding of biomass of relatively long-lived epinepheline serranids is expected. The factor Treatment (3 levels: high = fully fished, medium = moderately fished, low = lightly fished) was included into comparison B of GBR regions (Table 3.4). Of the 24 ELF reefs, 22 were surveyed in this study. Two alternative reefs (Lizard Island and North Direction) were surveyed in the Lizard region and allocated to the most similar treatment based on fishing history and Marine Park zoning.

Second, as a further rudimentary examination of the effect of fishing on density estimates for all epinephelines and each behavioural group, two-way fixed effects ANOVA were done using Fishing status (fixed factor: reefs open or closed to fishing) and Habitat (Fixed factor: lagoonal, sheltered or exposed) for the outer shelf reefs in the Lizard region. Counts were averaged over transects within reefs and habitats for these analyses. Only data from Lizard outer shelf reefs were used in these comparisons since that broad region was the only locality studied with both open (Day, Hicks and Yonge Reefs) and closed (Carter, No Name and Hilder) reefs that had not been subject to the ELF Experimental manipulations described above.

Finally, a presumed gradient in fishing intensity was defined for broad regions based on best available knowledge of past and current fishing pressure (Jennings et al. 1995, Jennings 1996). Reefs within broad regions were grouped according to the overall fishing pressure for the broad region and I did not separate out any small protected areas. In the Seychelles, the classifications were: Inner Isles – fully fished; northern Amirante Isles – moderately fished; southern Amirante Isles and Farquhar Group – lightly fished (MRAG 1995, Jennings et al. 2000). In the GBR, the Lizard region has generally experienced lower levels of fishing compared to the other regions studied (Ayling et al. 2000, Mapstone et al. 2004).

Species-level data

Species evenness (i.e. the relative abundance with which each species is represented in an area) and species patterns of distribution and abundance were examined graphically using relative abundance plots for each location (i.e. area, broad region, position, habitat or reef) within each spatial comparison. Based on local density, species with a mean abundance greater than or equal to 1 fish per 1000 m^2 were termed “abundant species” (above horizontal reference lines on mean abundance plots) and less abundant species were termed “rare species”. Unconstrained multivariate ordination using principal components analysis (PCA) was used to explore spatial patterns in the species abundance data from the GBR and the Seychelles. PCA aims to optimally display the relative positions of observations in an unstructured multivariate dataset in fewer dimensions and to help give insight into the way the observations vary. For the PCA, the correlation matrix of all 39 species variables was used in a variable selection process to exclude those that correlated with few or no other variables (Tabachnick & Fidell 1996), and a variety of alternative options were trialled (variable-sets, raw, square-root or log transformed data, correlation or covariance matrix) to investigate the consistency of spatial patterns in the data. Results were broadly similar across different methods and the PCA of square-root transformed data using 23 species and a covariance matrix is presented. The first two principal components (PCs) were used to display spatial patterns in community composition among the 221 samples on a Euclidean bi-plot, with species vectors indicated to help demonstrate the contribution of individual species to the observed multivariate patterns.

Following the PCA, hierarchical cluster analysis of the square-root transformed species abundance data was used to more clearly identify major groupings for comparison with those suggested by the PCA. A variety of clustering methods including group average linkage and Ward's method were trialled to investigate the consistency of assemblage clustering patterns. Results were broadly similar across clustering methods and the assemblage clustering patterns using Ward's method is presented in a dendrogram. Simulation tests have shown Ward's method to be one of the best hierarchical clustering methods at recovering natural clusters (Milligan 1981).

Size data

Size frequency plots for all epinepheline serranids were examined for each location (i.e. area, broad region, position or habitat). A Kolmogorov-Smirnov (K-S) two-sample test was used to compare size frequency distributions from the GBR and the Seychelles. For spatial comparisons A – C, size distributions (using 10 cm groups) of all epinepheline serranids were compared using correspondence analysis (row and column standardised), followed by *a posteriori* K-S two sample tests, with a Bonferonni correction factor for multiple tests (Field 2000, McCormick & Hoey 2004). Correspondence analysis is an exploratory technique to analyse and display similarity among frequency distributions (Greenacre 1984, McCormick & Hoey 2004). This technique is considered a special case of PCA and is analogous to doing a weighted PCA on frequencies, where distances are in chi-squared rather than Euclidean space. A bi-plot can be produced in which data points represent size frequencies from each location, and in which points closer to each other are similar with regard to the relative frequencies across the size groups, and vectors indicate the direction and strength of trends in each of the size groups used in the analysis. The vector(s) which project furthest relative to the other vectors in the same direction as a data point (i.e. size frequency) of interest indicate the size class(es) for which the size frequency deviates the most from others. Results of the K-S two-sample tests were superimposed on the correspondence analysis bi-plots, where locations in the same ellipse do not differ in size frequency distributions at a familywise error rate of 0.05.

3.4 Results

The key features to emerge from the analyses are summarised in Table 3.6 and described in detail thereafter. There are more differences than similarities at each spatial scale examined.

Table 3.6 Summary of spatial comparisons and examination of fishing effects.

Comparison	Similarities	Differences
1. Overall (GBR vs Seychelles, all transects).	➢ Few large mobile serranids. ➢ 50% species pool shared. ➢ 7 – 8 common species. ➢ Many rare species.	➢ Seychelles higher density of all epinephelines and cryptic serranids (due to two broad regions with high or very high densities). ➢ GBR higher density of roving serranids (due to two broad regions with high densities, see below). ➢ GBR greater overall species richness. ➢ Size frequencies differ with smaller mean size for Seychelles. ➢ Species composition, list of locally common species.
2. Broad Regions (4 broad regions in each of GBR and Seychelles)	➢ Broad region major source of variation in density for all epinephelines, cryptic serranids and roving serranids. ➢ Inner Isles low density of all behavioural groups. ➢ Species richness similar for several but not all broad regions.	➢ Densities of all epinephelines and each behavioural group varied with broad region: ➢ Southern Amirante Isles exceptionally high densities of cryptic serranids and hence all epinephelines. ➢ Farquhar Group high densities of cryptic serranids and relatively high density of large mobile serranids. ➢ Mackay and Pompey regions (southern GBR) high densities of roving serranids. ➢ Density of large mobile serranids varied most at level of replicates. ➢ Size distributions showed marked regional patterns. ➢ Based on species relative abundances, distinct epinepheline serranid assemblages were: southern Amirante Isles; Farquhar Group; Lizard mid shelf reefs, Mackay and Pompey; Lizard outer shelf and Townsville; Inner Isles; and northern Amirante Isles.
3. Habitat and fishing effects among GBR regions (clusters of reefs in four broad regions, two habitats, three fishing treatments)	➢ Complex patterns, but broad region (and its interaction) major source of variation in density for all epinephelines, cryptic serranids and roving serranids. ➢ Also fine-scale variation in density of all epinephelines and each behavioural group. ➢ Mean number of species per reef for different habitats. ➢ Size frequencies for sheltered and exposed habitats within broad regions, except for Lizard. ➢ For many species, densities were generally similar among reefs and habitats.	➢ Habitat effects on regional densities patterns were: ➢ Roving serranids (mainly *P. leopardus*) lower density in sheltered than exposed habitats in Pompey. ➢ Trend of higher densities of large mobile serranids in exposed than sheltered habitats in Lizard. ➢ Fishing effects detected, but differed regionally and/or at finer scales, and treatment effect not always in expected direction. ➢ As before, density of all epinephelines, cryptic serranids, and roving serranids varied with broad region: ➢ Mackay and Pompey high densities of roving serranids. ➢ Mackay high densities of all epinephelines & cryptic serranids. ➢ Townsville generally low densities for each group. ➢ Mean number of species per reef differed for broad regions (Lizard highest, Pompey lowest). ➢ Size frequencies for all epinepheline serranids generally differed between regions. ➢ Species relative abundances for Townsville differed to other regions. ➢ Species richness and size frequency of all epinephelines generally differ for broad regions.
4. Northern GBR cross-shelf comparison (mid shelf reefs or outer shelf reefs of Lizard region, three habitats)	➢ Species richness. ➢ Size frequency of all epinephelines generally similar within shelf position. ➢ *P. leopardus* common in each habitat and shelf position, although densities higher in sheltered and exposed habitats of mid shelf reefs.	➢ Densities of all epinephelines and each behavioural group varied at multiple scales. For example: ➢ Densities of all epinephelines and cryptic serranids higher on mid than outer shelf reefs, but not for lagoonal habitats. ➢ Densities of roving serranids on mid shelf reefs increased with increasing exposure, whereas on outer shelf reefs densities were higher for sheltered compared to other habitats. ➢ Densities of large mobile serranids tended to be higher for exposed than sheltered or lagoonal habitats. ➢ Species showed various distribution patterns, with some associated with particular exposure levels (combinations of habitat and position). ➢ Size frequencies for exposed habitats of Lizard mid shelf reefs differed from other mid shelf habitats but similar to exposed habitats of outer shelf reefs.
5. Fishing effects among GBR outershelf reefs (Lizard region, three habitats, reefs open or closed to fishing)	➢ No density differences detected for cryptic serranids or large mobile serranids in relation to fishing status.	➢ Densities of roving serranids on reefs closed to fishing were significantly higher than on reefs open to fishing, however this fishing effect only found for sheltered and lagoonal habitats. ➢ Density of all epinephelines higher on reefs closed to fishing, influenced by roving serranids .

3.4.1 GBR and Seychelles regional comparison

Assemblage patterns

GBR and Seychelles epinepheline serranid assemblages were characterised by seven or eight abundant species and many rarer species, but there were differences between areas in the locally abundant species and the species composition (Figs. 3.2 & 3.3). The combined contribution of all of the abundant species to the total epinepheline density in each area was very high (89% and 95% in the GBR and Seychelles, respectively), but roving serranids made up a much larger proportion of the total density in the GBR than the Seychelles (Figs. 3.3A & B). Further, over 50% of total abundance in each area was accounted for by just two species (GBR: *P. leopardus* and *C. cyanostigma*; Seychelles: *C. urodeta* and *E. fasciatus,* Figs. 3.3C & D).

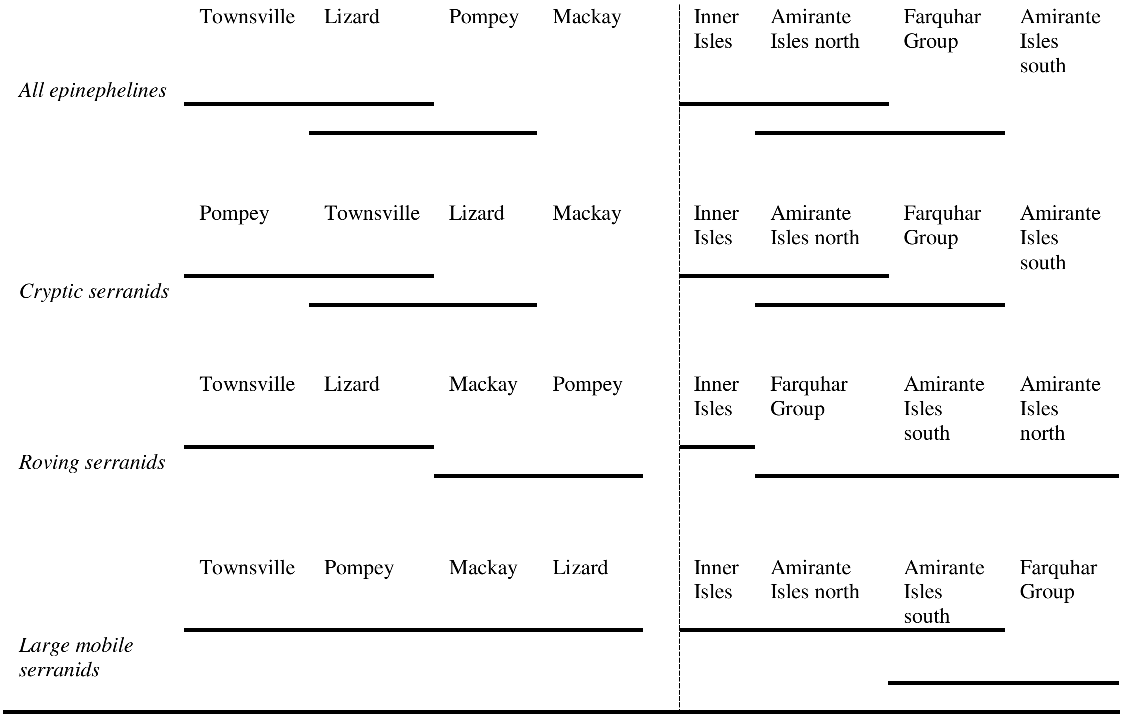
The effect of broad region nested in area was significant for all epinephelines, cryptic serranids, roving serranids and large mobile serranids (Table 3.7) indicating that density was different for broad regions within each area for all variables. Figure 3.4 shows that the density pattern for all epinepheline serranids (Fig. 3.4A) was largely driven by patterns in the abundance of cryptic serranids (Fig. 3.4B), which were the most abundant behavioural group in most regions. Cryptic serranids were more abundant in the Seychelles' southern Amirante Isles and Farquhar Group than in all other regions in either the Seychelles or the GBR (Fig. 3.4B). Whilst cryptic serranids were significantly more abundant in the Mackay region than other regions of the GBR, none of the GBR regions differed significantly from the Inner Islands or northern Amirante Isles regions in the Seychelles (Fig. 3.4B). A roughly analogous pattern was found for the large mobile serranids (but densities were much lower), though abundances of this group were significantly greater in the Farquhar Group than in the southern Amirante Isles (Fig. 3.4D).

Roving serranids were significantly most abundant overall in the Mackay and Pompey regions of the GBR, were about half as abundant in the northern Amirante Isles of the Seychelles and were at similarly lower abundances across the regions of Lizard and Townsville (GBR) and southern Amirante Isles and Farquhar Group (Seychelles) (Fig. 3.4C). Roving serranids were at very low abundance in the Inner Isles of the Seychelles (Fig. 3.4C). Indeed, the Inner Isles had much lower density of all serranids than any other broad region in either area, largely because of relatively few and low numbers of abundant species (Fig. 3.5E).

Table 3.7 Summary of analyses of variance using model A comparing density between broad regions of the GBR and Seychelles. Italics indicate random effects, F=F-ratio, p=probability of the data if no difference existed, bold indicates significant effects at p<0.05. Results of Tukey's tests for broad regions are also presented (lines join means that are not significantly different).

Source of variation	**Log All epinephelines**		**Log Behavioural groups**		**Log Cryptic serranids**		**Log Roving serranids**		**Log Large mobile serranids**	
	F	p	Pillai's Trace	p	F	p	F	p	F	p
Area	0.23	0.6451	2.12	0.2400	1.15	0.3242	2.34	0.1772	1.65	0.2457
*Broad-Region(*Area*)*	38.20	**<.0001**	8.24	**<.0001**	25.15	**<.0001**	28.62	**<.0001**	3.53	**0.0082**
*Reef(Broad-Region(*Area*))*	1.80	**0.0121**	1.47	**0.0062**	2.10	**0.0022**	1.10	0.3500	1.44	0.0836

Tukey's tests for differences among broad regions (ordered left to right by means from lowest to highest):



Thus, whilst abundances did not differ between areas overall for any group, it was clear that densities of all epinephelines, cryptic, and large mobile serranids were significantly greater in two regions of the Seychelles (southern Amirante Isles, Farquhar Group) than anywhere on the GBR and densities of roving serranids were greater in two regions of the GBR (Mackay, Pompey) than anywhere in the Seychelles.

There was a significant effect of reef nested in broad region and area on the density of all epinephelines and cryptic serranids (Table 3.7) indicating that density was variable at 10s km scales among reefs within broad regions for these groups.

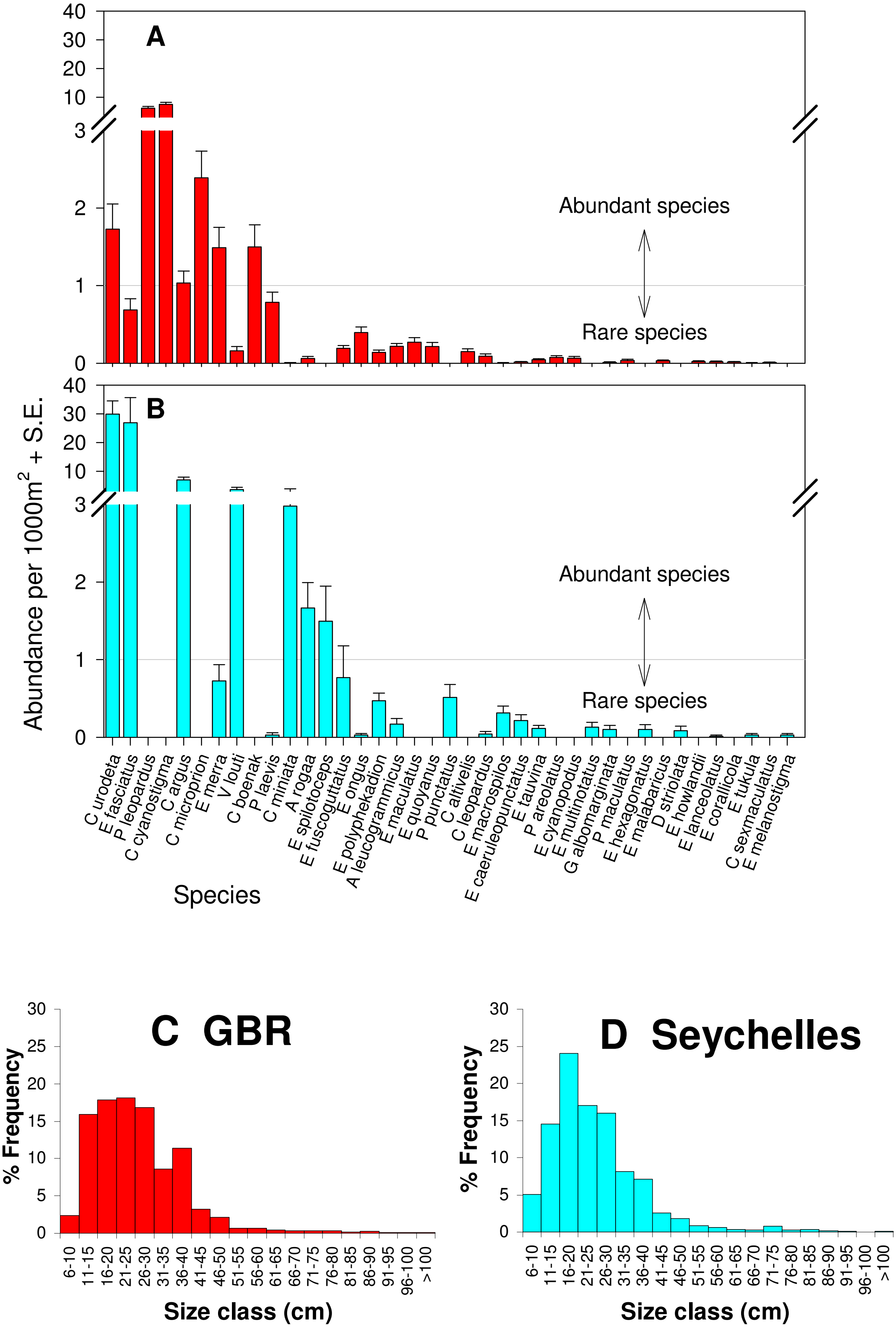


Figure 3.2 Comparison of the GBR and the Seychelles: density estimates for species of epinepheline serranids for (A) the GBR (n=169) and (B) the Seychelles Islands (n=52); (C) size frequency of all epinepheline serranids from the GBR and (D) size frequency of all epinepheline serranids from the Seychelles Islands. Error bars are standard errors.

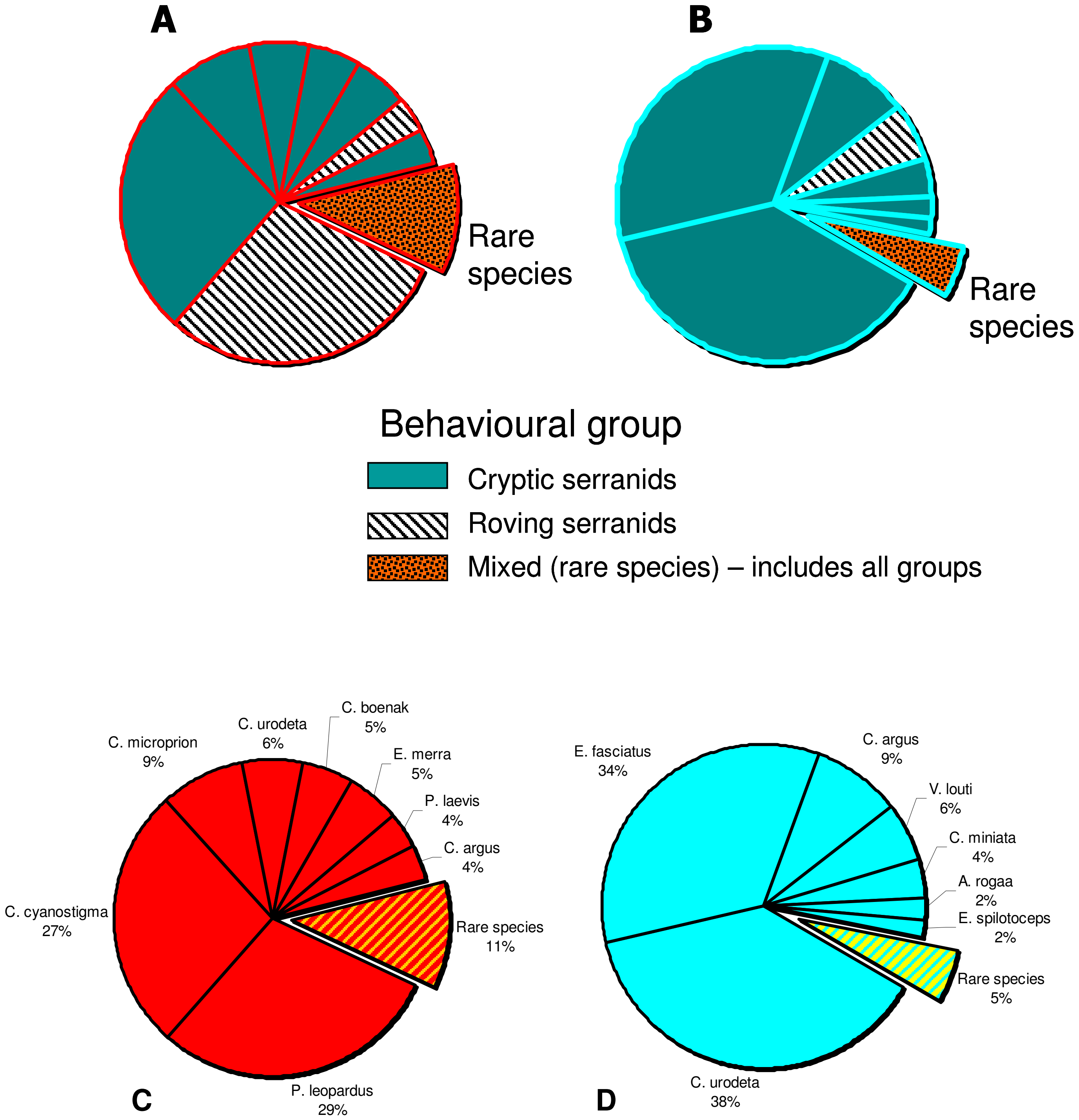


Figure 3.3 **Percent contribution of behavioural groups to overall epinepheline serranid abundance for (A) the GBR and (B) the Seychelles; and percent contribution of species to overall epinepheline serranid abundance in (C) the GBR and (D) the Seychelles Islands. Pooled contribution of rare species indicated by exploded segments.**

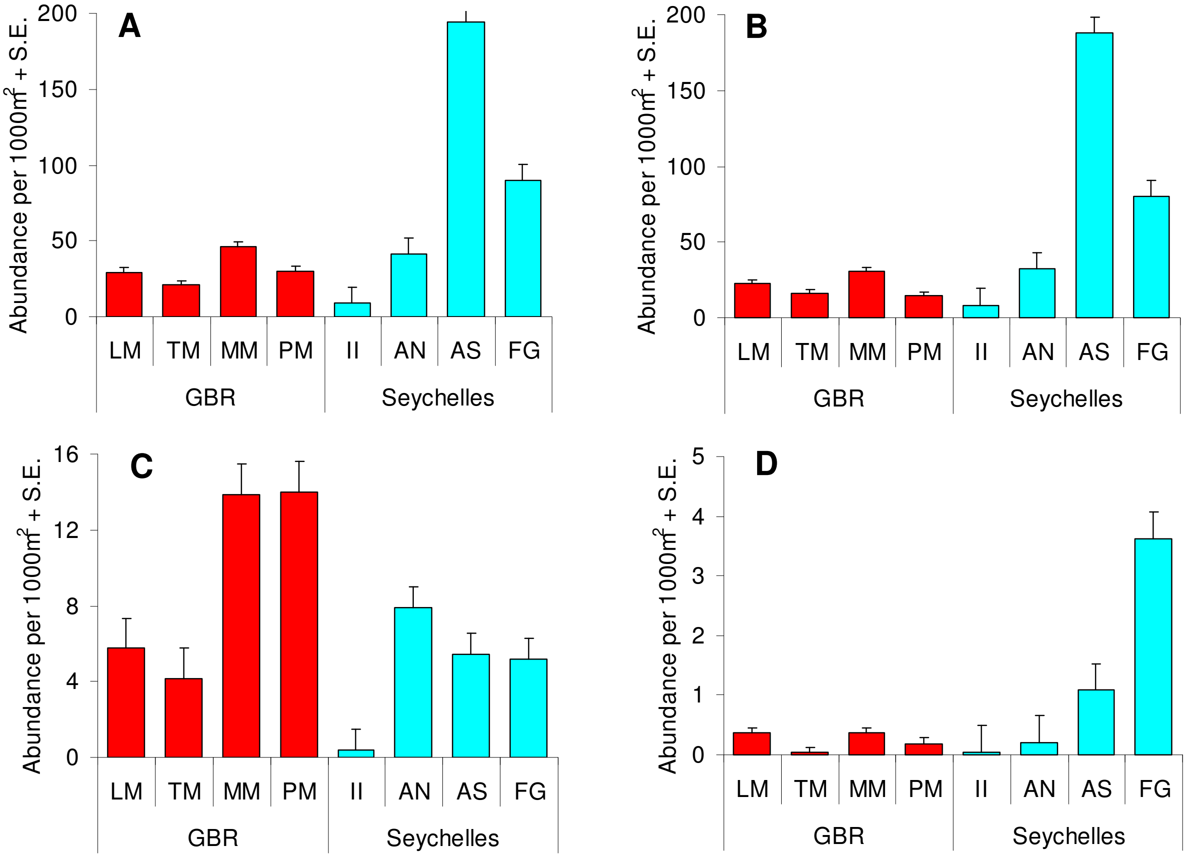


Figure 3.4 Comparison of density estimates from broad regions of the GBR (red bars) and the Seychelles (blue bars) for (A) all epinepheline serranids, (B) cryptic serranids, (C) roving serranids and (D) large mobile serranids. Note difference in vertical scales on the four plots. Broad regions: LM=Lizard mid shelf, TM=Townsville, MM=Mackay, PM=Pompey, II=Inner Isles, AN=northern Amirante Isles, AS=southern Amirante Isles, FG=Farquhar Group. Error bars are standard errors.

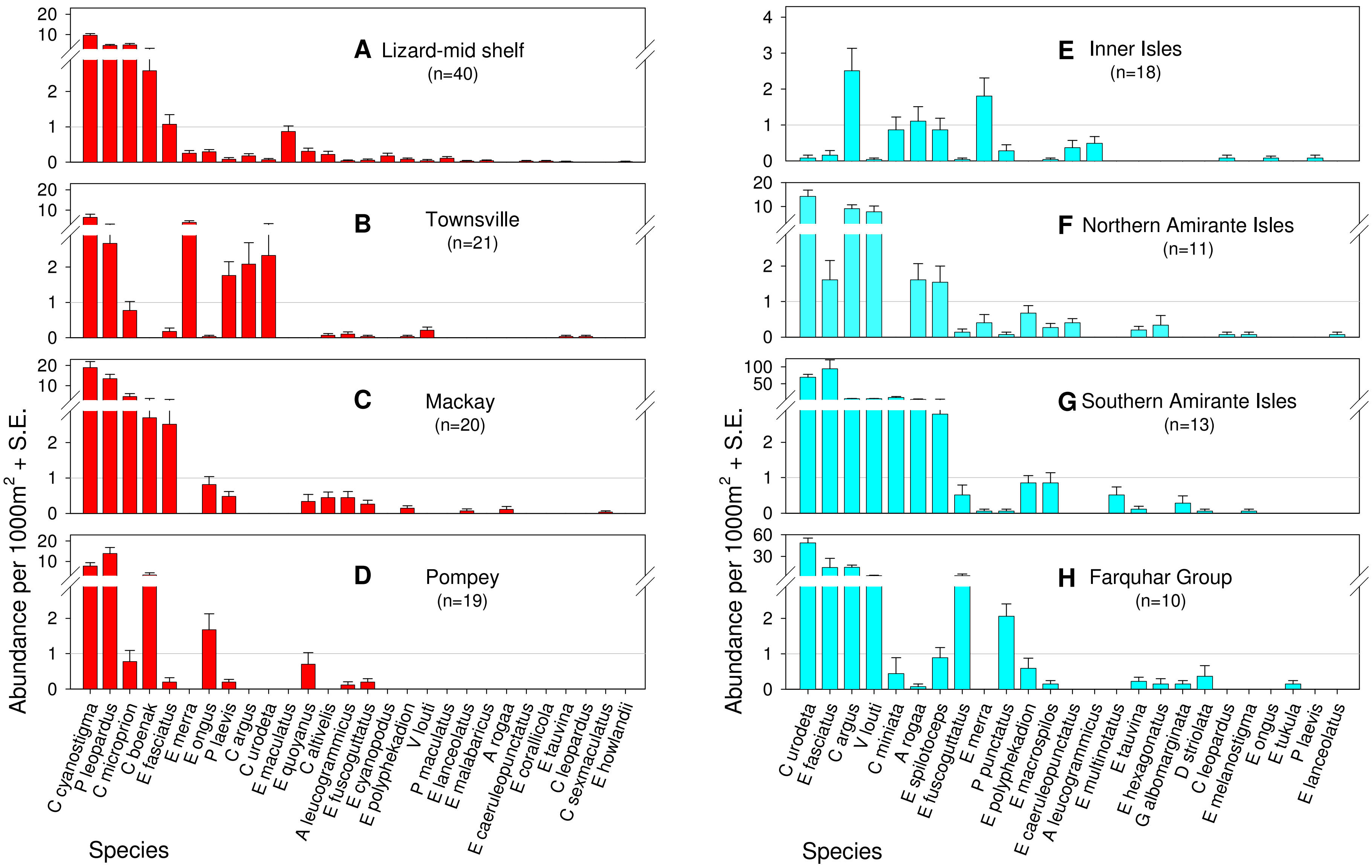


Figure 3.5 Regional comparison of species density estimates from GBR (left) and the Seychelles Islands (right). Sample numbers (n) indicated on plots. Note difference in vertical scales on plots. Error bars are standard errors.

The bootstrap species counts (Appendix 1: GBR = 27.3, Seychelles = 23.6) and the raw species counts (GBR = 33, Seychelles = 25) both suggested a higher species richness in the GBR than in the Seychelles, although the pattern was more complex at regional scales (Fig. 3.6). There was a significant effect of broad region nested in area on the mean number of species per reef ($F_{6,33}$ =10.462, p<0.0001) indicating that mean number of species differed among broad regions within each area (see Fig. 3.6A). Bootstrap species counts for broad regions are presented in Fig. 3.6B and show a similar pattern of regional variability *within* areas to that for mean number of species per reef. There are differences, however, in the relative magnitudes of regions *between* areas (Figs. 3.6A & B), but it is not clear how much this reflects differing species pools or sample sizes. The raw species counts (i.e. total number of species recorded per broad region) were highest for the Lizard region (mid shelf reefs only, 25 species) and lowest for the Pompey region (9 species), but otherwise similar among broad regions (15-18). Some caution should be applied to these results, however, because of the influence on species counts of different sample sizes in different regions.

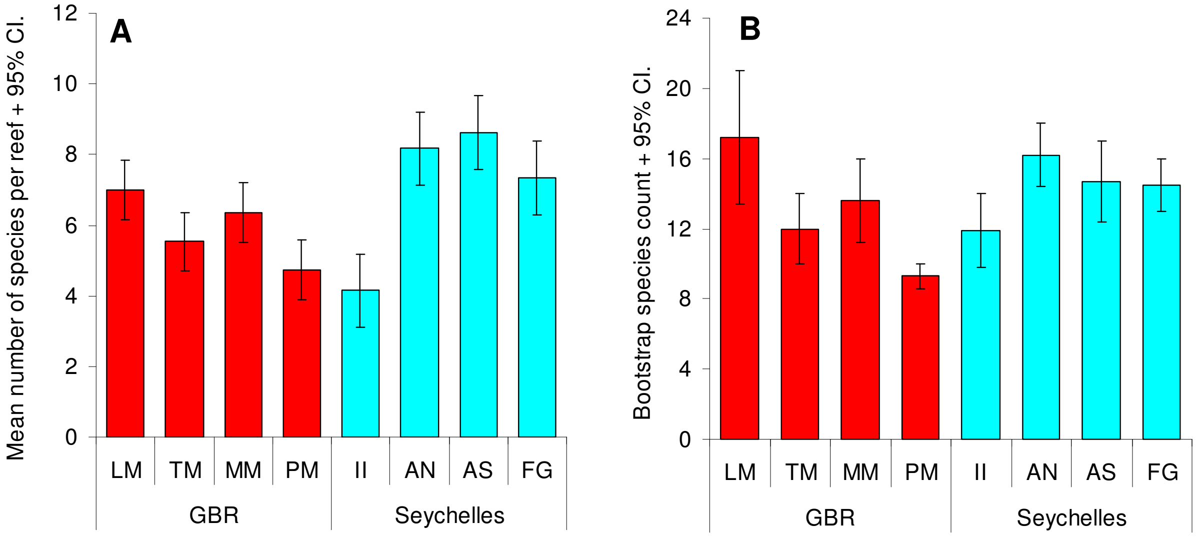


Figure 3.6 (A) Mean number of species per reef, and (B) bootstrapped species counts by broad region. Error bars are 95% confidence intervals.

Size frequencies for all epinepheline serranids were significantly different between the GBR and the Seychelles (K-S test: $p<0.001$). Figures 3.2C & D show that the mean sizes and the shape of the distributions differ, with more small individuals in the Seychelles. Closer examination showed that size frequencies for all epinepheline serranids showed marked regional patterns, and K-S tests indicated that size frequencies were significantly different for all but three pairs of regions (Figs. 3.7 & 3.8). Compared to other broad regions examined, small size groups were over-represented in the southern Amirante Isles, whilst large size groups were over-represented in Lizard outer shelf reefs and the Farquhar Group (Fig. 3.7).

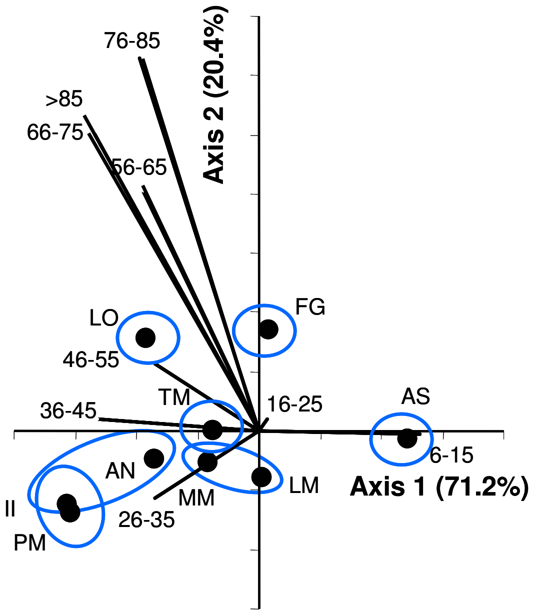


Figure 3.7 Correspondence analysis biplot of size frequencies of all epinephelines from broad regions. Broad regions: LO=Lizard outer shelf, LM=Lizard mid shelf, TM=Townsville, MM=Mackay, PM=Pompey, II=Inner Isles, AN=northern Amirante Isles, AS=southern Amirante Isles, FG=Farquhar Group. Vectors indicate size groups in cm. Ellipses indicate broad regions with no significant differences found using K-S tests.

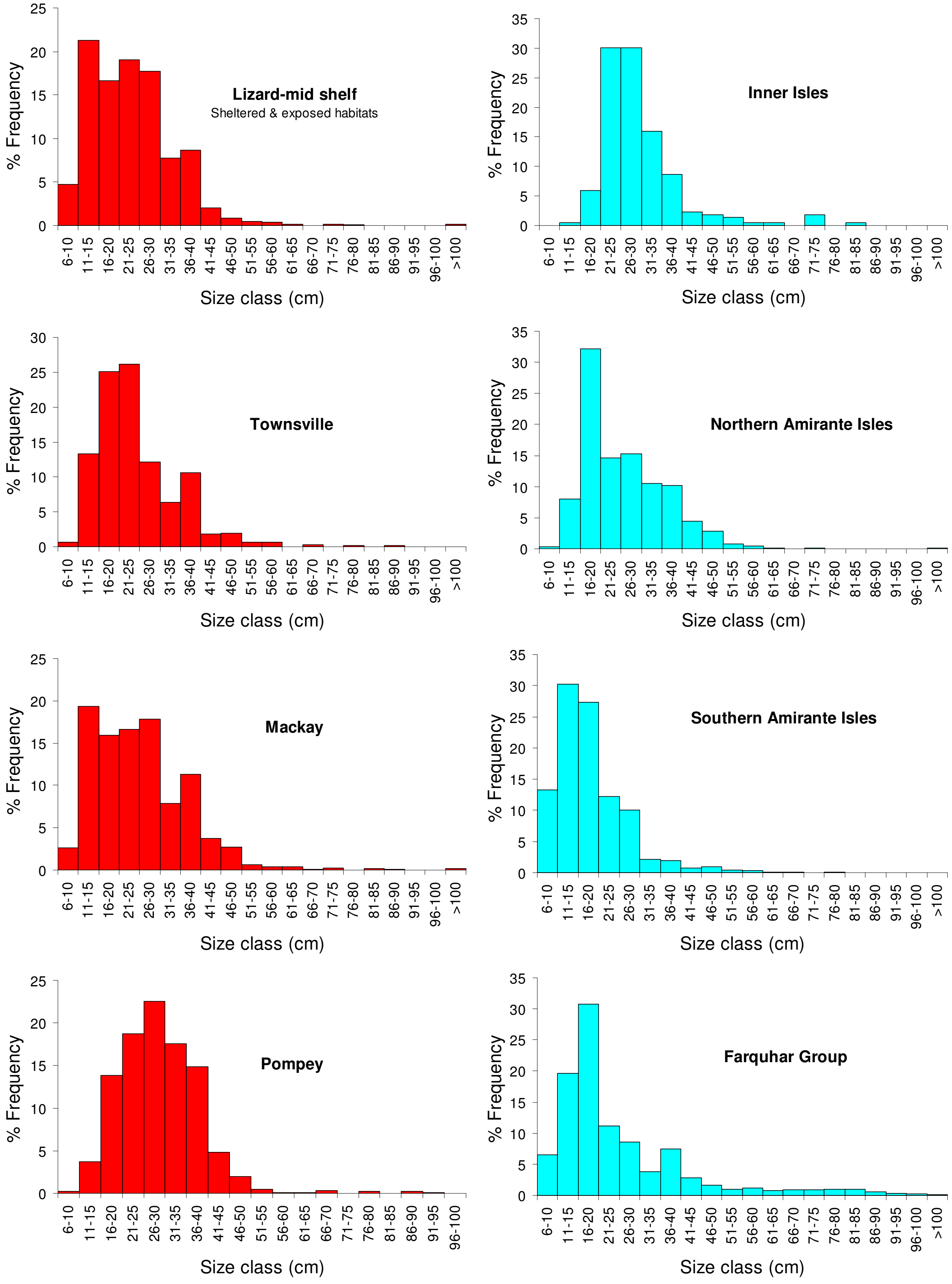


Figure 3.8 Regional comparison of size frequency histograms for all epinepheline serranids from GBR (left) and the Seychelles Islands (right).

Species patterns

The surveys provided good coverage of shallow water epinepheline serranid species documented previously from the areas (Randall & Heemstra 1991, Heemstra & Randall 1993). Half of the epinepheline species I recorded (19 out of 39) were widely-distributed (present in both areas, Figs. 3.2A & B), and of these about two-thirds were most abundant in one or more regions of the Seychelles. Of the remaining 20 species with restricted distributions, more were recorded in the GBR (14 species) than the Seychelles (6 species).

PCA identified marked spatial patterns in the data, with epinepheline assemblages differing between areas and broad regions within those areas (see Figs. 3.9A & B). The first two axes in the PCA explained a total of 67.5% of the variability in epinepheline serranid species abundance, while the third axis represented only an additional 7.5% and is not presented. The southern Amirante Isles, Farquhar Group and Lizard mid shelf reefs, Mackay and Pompey were distinct groupings in both the PCA (Fig. 3.9) and cluster analysis (Fig. 3.10). Cluster analysis also tended to group Lizard outer shelf reefs with Townsville reefs and distinguished these from the Inner Isles and northern Amirante Isles of the Seychelles. Varied clustering of reefs within these groupings suggested no pronounced differences of serranid assemblages within these groupings.

There were a variety of species patterns of abundance. Only *C. urodeta* and *C. argus* were abundant in both areas, but densities of these species were higher in the Seychelles than on the GBR (Fig. 3.3). The species of *Epinephelus* with overall highest densities was *E. fasciatus*. Many species were recorded only in low densities throughout (e.g. *E. polyphekadion* and many large mobile serranids).

In the GBR, southern regions (Mackay and Pompey) generally had higher densities of *C. cyanostigma* and *P. leopardus*, although these species were among those abundant in all regions of the GBR (Fig. 3.5). Townsville reefs stand out at the species-level (Fig. 3.5B), showing more similarities with Lizard outer shelf reefs than the mid shelf reefs from other regions, consistent with the results from the PCA and cluster analysis.

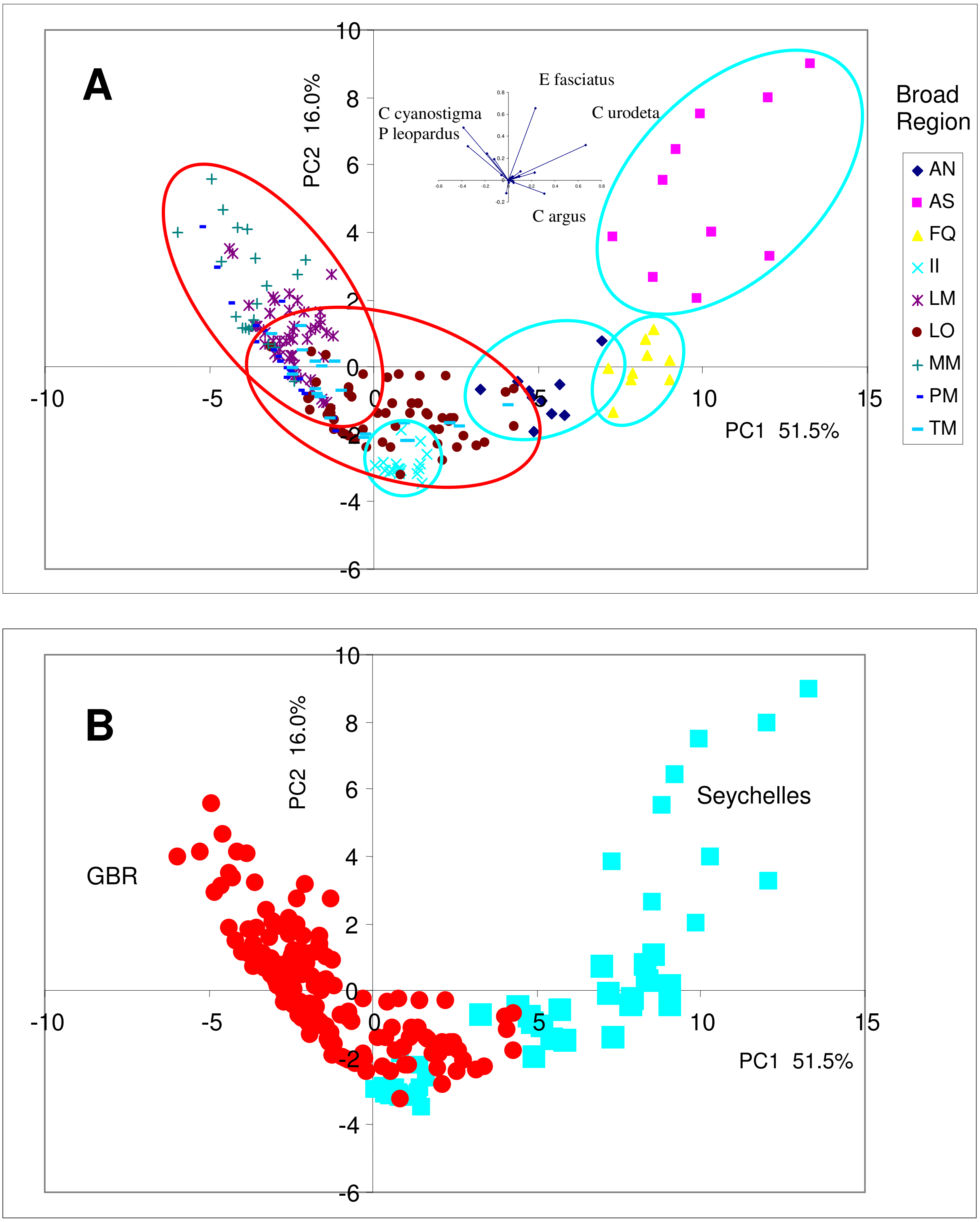


Figure 3.9 Euclidean biplot of species abundance data (square-root transformed) for the GBR and the Seychelles from Principal Components Analysis. Each data point represents a long-swim transect. For (A), symbols indicate Broad Regions as listed in legend: LO=Lizard outer shelf, LM=Lizard mid shelf, TM=Townsville, MM=Mackay, PM=Pompey, II=Inner Isles, AN=northern Amirante Isles, AS=southern Amirante Isles, FG=Farquhar Group. Insert in (A) shows species vectors. Ellipses indicate clusters from hierarchical cluster analysis, red=GBR, blue= Seychelles (Fig. 3.12). (B) Same datapoints recoded by Area: red circles=GBR and blue squares=Seychelles.

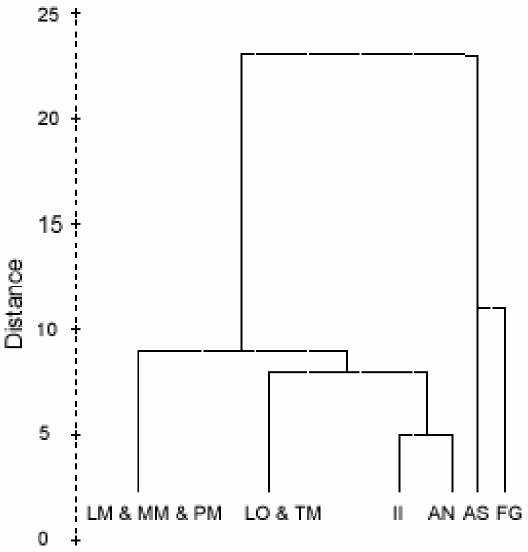


Figure 3.10 Dendrogram produced from a hierarchical cluster analysis using abundance of 23 species of epinepheline serranids from all localities surveyed. Broad regions: LO=Lizard outer shelf, LM=Lizard mid shelf, TM=Townsville, MM=Mackay, PM=Pompey, II=Inner Isles, AN=northern Amirante Isles, AS=southern Amirante Isles, FG=Farquhar Group.

The two most abundant species in the Seychelles, *C. urodeta* and *E. fasciatus*, were in exceptionally high densities in the southern Amirante Isles (means ± S.E.: 69.8 ± 8.0 and 95.0 ± 14.3, respectively), accounting for the majority of the high total density. *C. argus* was relatively abundant throughout the Seychelles, *C. urodeta* and *V. louti* relatively abundant everywhere but the Inner Isles, and *A. rogaa* and *E. spilotoceps* relatively abundant everywhere but the Farquhar Group (Fig. 3.5). The presence of large groupers was notable in the Farquhar Group as several large mobile serranids (*Dermatolepis striolata, E. fuscoguttatus* and *E. tukula*) and the large roving serranid, *Plectropomus punctatus* were all comparatively abundant (Fig. 3.5H). The small grouper *E. merra* was exceptional in that it was most abundant in the Inner Isles.

3.4.2 Habitat and fishing effects among GBR regions

Assemblage patterns

There was a significant effect of reef within broad region and treatment (Table 3.8) on the density of cryptic serranids and roving serranids, indicating that density was variable at the reef scale for these variables. The variation among reefs within broad region and treatment was also habitat dependent for roving serranids (significant Reef(Broad Region*Treatment)* Habitat interaction, Table 3.8).

Table 3.8 Summary of analyses of variance using model B comparing habitat and fishing effects among GBR regions. Italics indicate random effects, F=F-ratio, p=probability of the data if no difference existed, bold indicates significant effects at p<0.05. Results of Tukey's tests for broad regions are also presented.

Source of variation	**All epinephelines**		**Behavioural groups**		**Cryptic serranids**		**Roving serranids**		**Large mobile serranids**	
	F	P	Pillai's Trace	p	F	p	F	p	F	p
Broad-Region	12.71	**0.0005**	4.94	**0.0002**	4.09	**0.0326**	13.96	**0.0003**	2.96	0.0753
Treatment	0.09	0.9183	0.42	0.8517	0.47	0.6483	0.29	0.7610	0.86	0.4698
*Reef(Broad-Region**Treatment)	1.30	0.2450	1.70	**0.0146**	2.10	**0.0335**	3.08	**0.0024**	0.61	0.8199
Habitat	1.01	0.3895	0.52	0.7404	1.92	0.2599	0.61	0.4922	0.38	0.5800
*Broad-Region**Treatment	3.03	**0.0483**	1.17	0.3342	1.66	0.2131	1.08	0.4267	0.98	0.4815
*Broad-Region**Habitat	3.73	**0.0420**	1.86	0.0904	1.12	0.3785	3.81	**0.0397**	2.27	0.1324
Treatment*Habitat	1.07	0.4011	1.09	0.4294	1.09	0.3938	1.66	0.2666	0.23	0.8048
*Broad-Region**Treatment*Habitat	0.93	0.5055	0.90	0.5795	1.97	0.1496	0.16	0.9838	1.25	0.3491
*Reef(Broad-Region**Treatment)*Habitat	1.67	0.1004	1.41	0.0783	0.80	0.6530	4.24	**0.0001**	0.43	0.9431

Tukey's tests for differences among broad regions (ordered left to right by means from lowest to highest):

Lizard Townsville Pompey Mackay

Cryptic serranids

The interaction between broad region and habitat was significant for the density of all epinephelines and roving serranids (Table 3.8). This was because of a much lower density of roving serranids (and correspondingly all epinephelines) for sheltered than exposed habitats on Pompey reefs, whereas for other broad regions mean abundance was similar for each habitat (Figs. 3.11C & A). A similar, although non significant trend of lower densities on sheltered compared to exposed habitat in the Pompey region was also suggested for cryptic serranids (Fig. 3.11B). No significant effects or interactions were found for large mobile serranids, but exposed habitats of the Lizard region tended to have higher densities than sheltered habitats. Otherwise, sheltered and exposed habitats had similar densities of serranids in all regions (Fig. 3.11).

The interaction between broad region and treatment was also significant for the density of all epinephelines (Table 3.8), indicating that density was different for different treatments in broad regions. Figure 3.12A shows that the treatment effect was not always in the expected direction. For example, the density of all epinephelines was significantly higher on fully fished reefs than in other treatments in the Pompey region. Treatment effects were also evident in the Lizard and Mackay regions, but not in the Townsville region. Density of all epinephelines was significantly lower on fully fished reefs than on moderately fished reefs in the Lizard region, but no significant differences in densities were found between fully and lightly fished reefs (Fig. 3.12A). Densities of all epinephelines on fully fished reefs were significantly and markedly lower than on moderately or lightly fished reefs in the Mackay region, but otherwise similar (Fig. 3.12A). These findings indicate there was a fishing effect but it differed regionally. In addition, there was a significant main effect of broad region on the density of cryptic serranids (Table 3.6, see Fig. 3.4B). The density of cryptic serranids was significantly higher in Mackay than other broad regions.

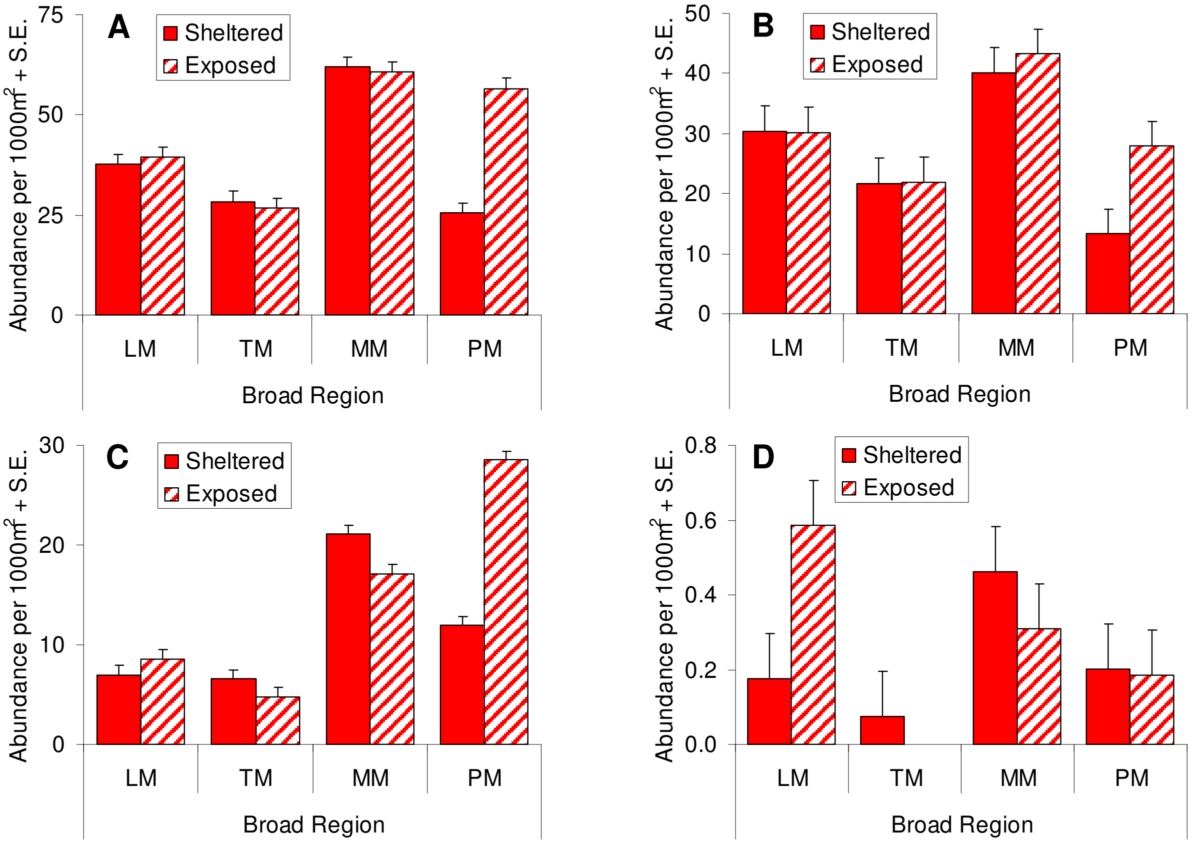


Figure 3.11 Comparison of density estimates from broad regions and habitats of GBR regions for (A) all epinepheline serranids, (B) cryptic serranids, (C) roving serranids and (D) large mobile serranids. Broad regions: LM=Lizard mid shelf, TM=Townsville, MM=Mackay, PM=Pompey. Error bars are standard errors.

The mean number of species per reef differed for broad region (significant main effect of broad region, $F_{3,40}=5.56$, $p<0.05$), but was similar for different habitats. The Lizard region had the highest mean number of species per reef (7.0 ± 0.4) and the Pompey region the least (4.9 ± 0.4). Likewise, correspondence analysis and K-S tests showed that size frequencies for all epinepheline serranids were similar for sheltered and exposed habitats within broad regions, except for Lizard, but generally differed between regions (Fig. 3.13).

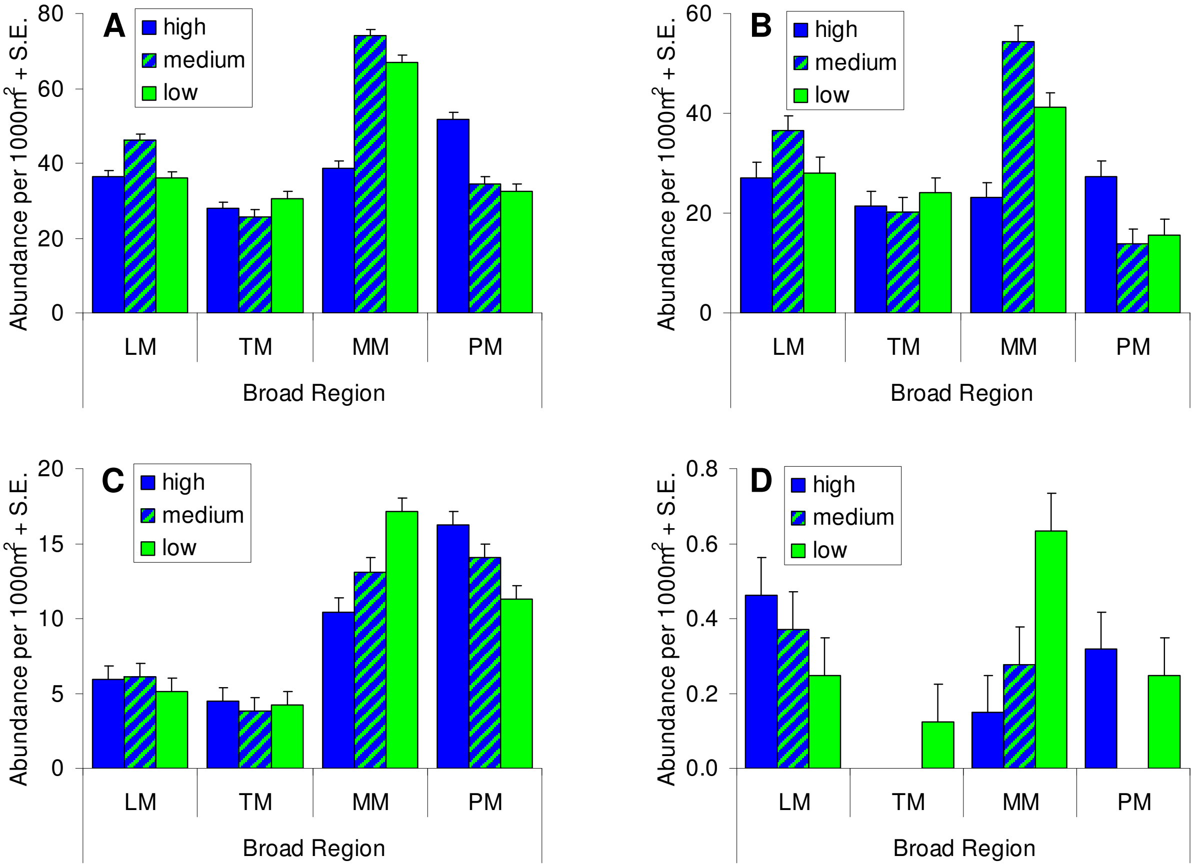


Figure 3.12 Comparison of density estimates from broad regions and treatments of GBR reefs for (A) all epinepheline serranids, (B) cryptic serranids, (C) roving serranids and (D) large mobile serranids. Broad regions: LM=Lizard mid shelf, TM=Townsville, MM=Mackay, PM=Pompey. Treatments: high=fully fished, medium=moderately fished, low=lightly fished. Error bars are standard errors.

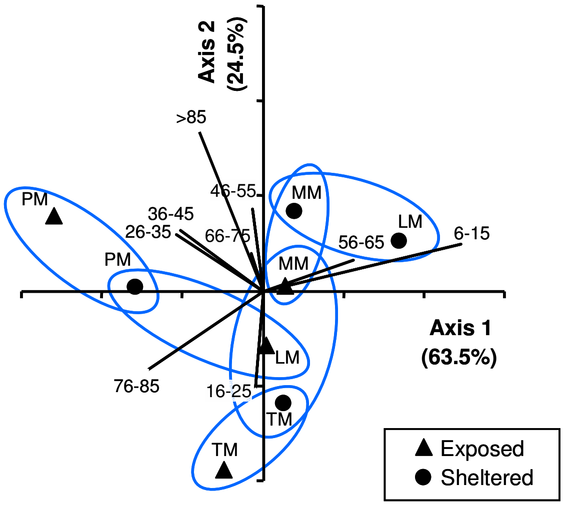


Figure 3.13 Correspondence analysis biplot of size frequencies of all epinephelines from habitats among GBR regions (see methods for description). Broad regions: LO=Lizard outer shelf, LM=Lizard mid shelf, TM=Townsville, MM=Mackay, PM=Pompey. Habitats indicated by symbols as per legends. Vectors indicate size groups in cm. Ellipses indicate locations no significant differences found using K-S tests.

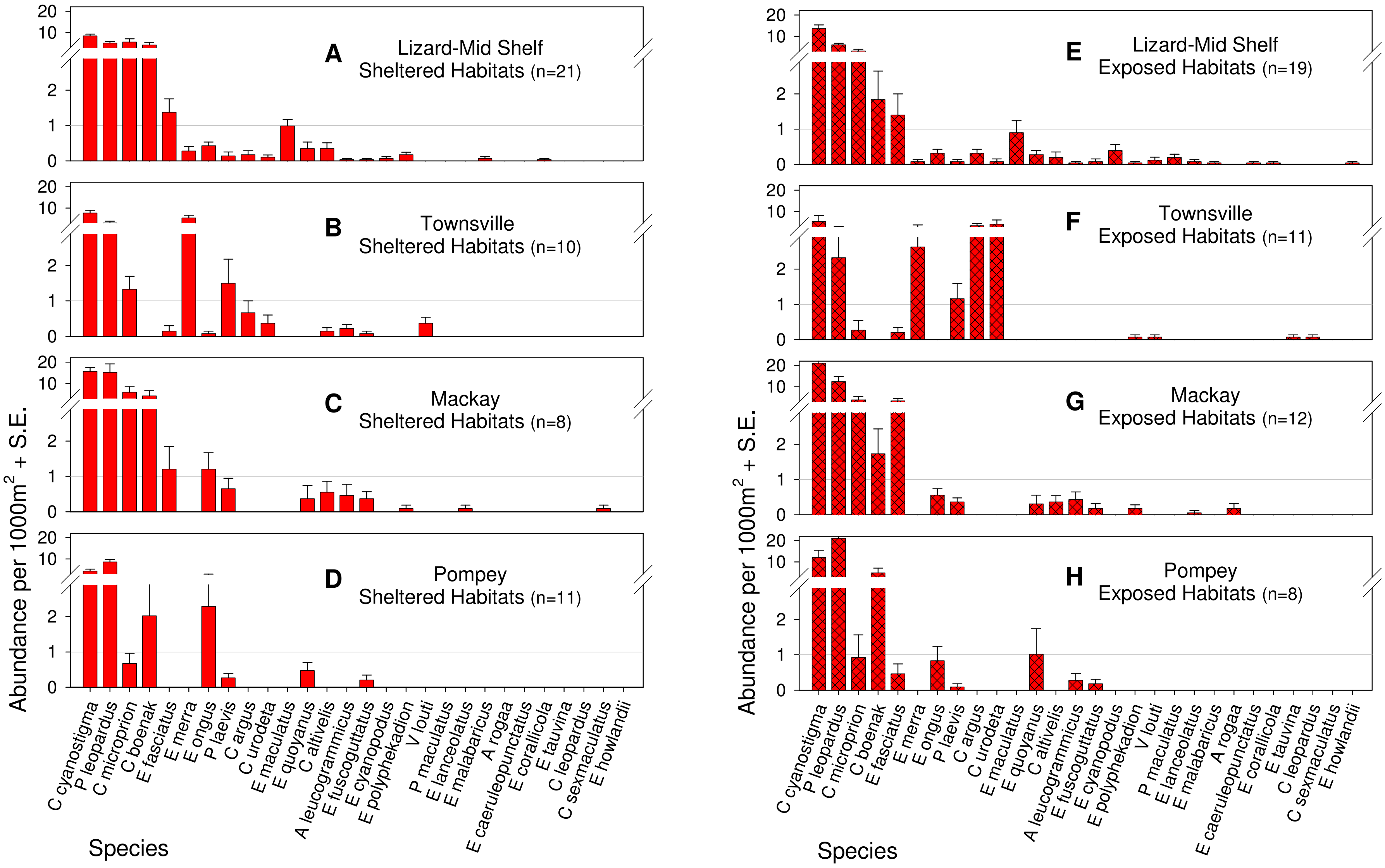


Figure 3.14 Comparison of species density estimates from broad regions of GBR from sheltered (left) and exposed (right) reefs. Sample numbers (n) indicated on plots. Error bars are standard errors.

Species patterns between habitats among GBR regions

Density of *P. leopardus* in sheltered habitats was less than half that in exposed habitats on Pompey reefs, largely accounting for the density patterns for roving serranids and contributing to the patterns for all epinepheline serranids already described (Figs. 3.14D & H). Densities of *P. leopardus* in other broad regions were similar between habitats. Additionally, densities of *C. cyanostigma* generally tended to be lower in sheltered than exposed habitats. Densities were generally similar among reefs and habitats for many other species, but as mentioned already, the species composition and relative abundances for Townsville reefs was distinct at the regional level.

3.4.3 Northern GBR cross-shelf comparison

Assemblage patterns

The pattern of total density of epinepheline serranids with shelf position, habitat and reef varied over several spatial scales on the northern GBR. Further, abundance varied among reefs within shelf position in habitat dependent ways (significant Reef(Position) * Habitat interaction, Table 3.9).

Table 3.9 Summary of analyses of variance using model C comparing density over a cross-shelf transect of the northern GBR. Italics indicate random effects, F=F-ratio, p=probability of the data if no difference existed, bold indicates significant effects at p<0.05. Results of Tukey's tests for habitats are also presented.

Source of variation	**All epinephelines**		**Behavioural groups**		**Cryptic serranids**		**Roving serranids**		**Large mobile serranids**	
	F	p	Pillai's Trace	p	F	p	F	p	F	p
Position	8.12	**0.0215**	4.69	0.0514	15.71	**0.0042**	0.60	0.4613	1.00	0.3464
Reef(Position)	2.29	**0.0309**	2.60	**0.0002**	1.93	0.0693	4.39	**0.0003**	2.03	0.0555
Habitat	1.62	0.2284	1.91	0.1111	0.62	0.5499	2.47	0.1159	3.89	**0.0421**
Position*Habitat	7.00	**0.0065**	2.19	0.0719	5.34	**0.0167**	4.56	**0.0271**	0.10	0.9083
Reef(Position)*Habitat	2.18	**0.0141**	1.55	**0.0192**	1.72	0.0626	1.64	0.0813	1.45	0.1475

Tukey's tests for differences among habitats (ordered left to right by means from lowest to highest):

Large mobile serranids Lagoonal Sheltered Exposed

There were significant interactions between habitat and shelf position influencing abundances of total epinepheline serranids, cryptic serranids and roving serranids (Table 3.9). Figure 3.15A indicates density of all epinepheline serranids for lagoonal habitats was greatest on outer shelf reefs, whereas for other habitat types density was highest on mid shelf reefs.

Density of cryptic serranids were significantly higher in sheltered and exposed habitats of mid shelf reefs compared to similar habitats of outer shelf reefs, but for lagoonal habitats densities were similar regardless of shelf position (Fig. 3.15B).

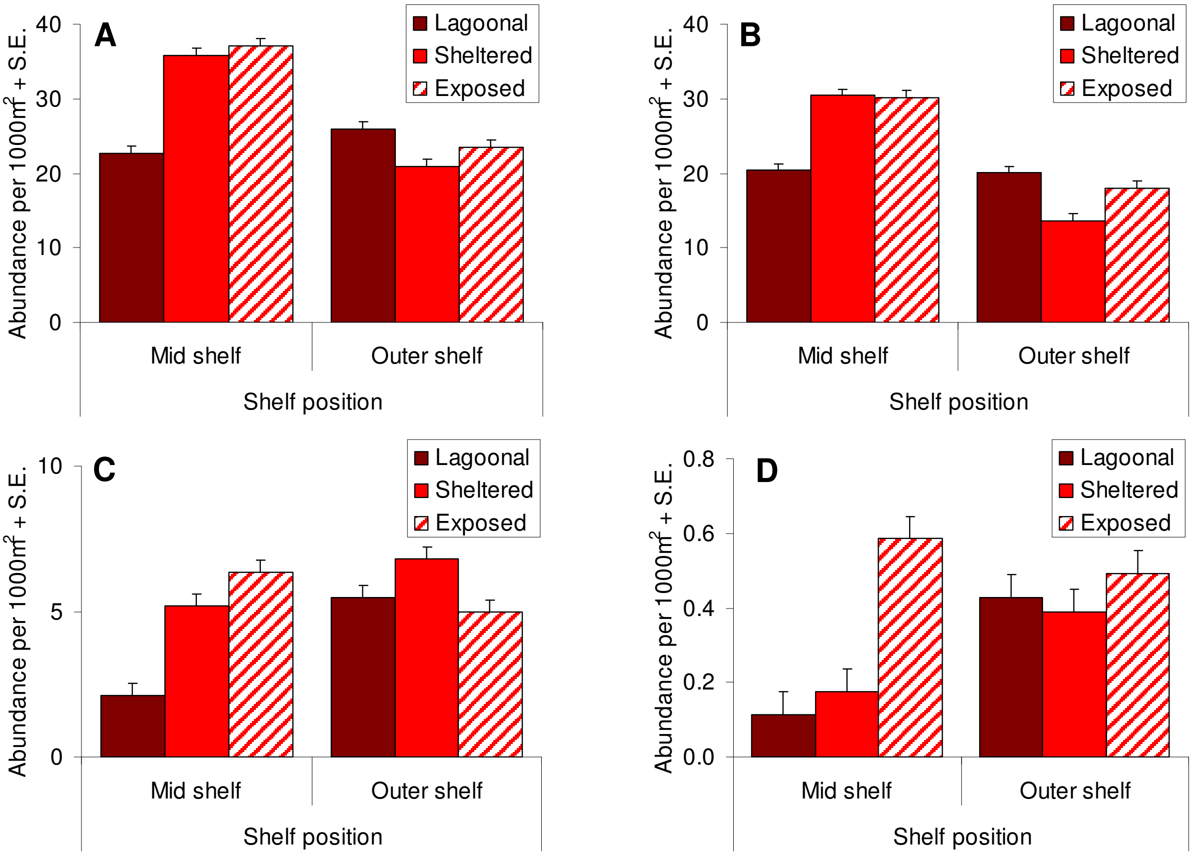


Figure 3.15 Comparison of density estimates from shelf positions and habitats of cross-shelf transect of the northern GBR for (A) all epinepheline serranids, (B) cryptic serranids, (C) roving serranids and (D) large mobile serranids.

Densities of roving serranids on mid shelf reefs increased with increasing exposure (lagoonal<sheltered<exposed), whereas on outer shelf reefs densities were higher for sheltered compared to other habitats. There was also a significant effect of reef nested in position on the density of all epinephelines and roving serranids (Table 3.9), indicating that density was variable at 10s km scales among reefs within shelf positions for these variables. Densities were similar among mid shelf reefs but varied among reefs on the outer shelf. This latter effect is investigated further taking into account habitat and potential fishing effects in the Section "Potential effects of fishing" below.

There was an unconfounded significant main effect of habitat on the density of large mobile serranids (Table 3.9), with exposed habitats tending to have higher densities than sheltered or lagoonal habitats, although *post hoc* tests could not resolve these effects unambiguously.

The null hypothesis of no significant difference in mean number of species per reef among habitats and shelf position was not rejected (Table 3.10).

Table 3.10 Analysis of variance comparing the mean number of species per reef among shelf positions (2 levels: mid, outer) and habitats (3 levels: lagoonal, sheltered, exposed) of the Lizard region. df=degrees of freedom, F=F-ratio, p=probability of the data if no difference existed.

Source of variation	df	F	p
Position	1	2.63	0.1140
Habitat	2	2.49	0.0978
Position*Habitat	2	2.18	0.1284
Error	35		

Size frequencies for all epinepheline serranids were similar for lagoonal, sheltered and exposed habitats of Lizard outer shelf reefs and for sheltered and exposed habitats of Lizard mid shelf reefs (Fig. 3.16). Size frequencies for exposed habitats of the mid shelf reefs, however, were similar to exposed habitats of outer shelf reefs rather than other mid shelf habitats (Fig. 3.16).

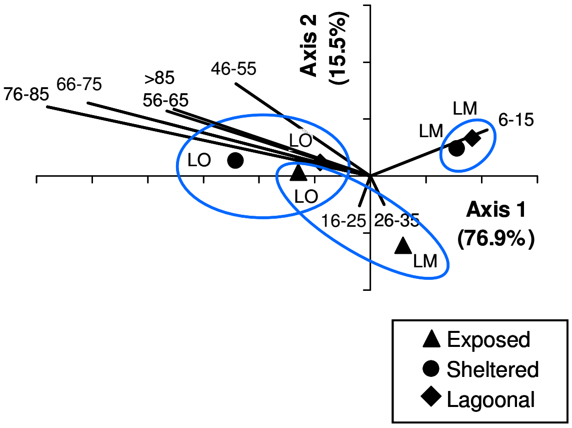


Figure 3.16 Correspondence analysis biplot of size frequencies of all epinephelines from cross-shelf comparison for northern GBR (see methods for description). Broad regions: LO=Lizard outer shelf, LM=Lizard mid shelf. Habitats indicated by symbols as per legends. Vectors indicate size groups in cm. Ellipses indicate locations no significant differences found using K-S tests.

Potential effects of fishing

The MANOVA comparing effects of fishing (reef zoning), habitat and reefs for outer shelf reefs in the Lizard region indicated a significant effect of fishing and the subsequent ANOVAs for each behavioural group also identified a significant interaction of fishing status with habitat for roving serranids on Lizard outer shelf reefs (Table 3.11). Densities of roving serranids in sheltered and lagoonal habitats on reefs closed to fishing were significantly higher than in the same habitats on reefs open to fishing, whereas densities in the exposed habitats were similar across reefs open and closed to fishing (Fig. 3.17). Densities of other behavioural groups were similar over habitats and different levels of fishing status (Fig. 3.17A). The density of all epinephelines was higher on reefs closed to fishing than on reefs open to fishing, most likely because of the pattern for roving serranids (Table 3.11, Fig. 3.17).

Table 3.11 Analysis of variance comparing density estimates for Lizard outer shelf reefs among habitats and Marine Park zone status (=fishing status).

Source of variation	**All epinephelines**		**Behavioural Groups**		**Cryptic serranids**		**Roving serranids**		**Large mobile serranids**	
	F	p	Pillai's Trace	P	F	p	F	p	F	p
Habitat	1.84	0.1699	1.52	0.1785	2.80	0.0706	1.30	0.2825	0.19	0.8294
Fishing status	5.58	**0.0221**	7.24	**<0.001**	0.00	0.9958	20.90	**<.0001**	0.01	0.9382
Habitat*Fishing status	2.63	0.0820	2.018	0.0525	0.49	0.6186	3.65	**0.0335**	2.04	0.1413

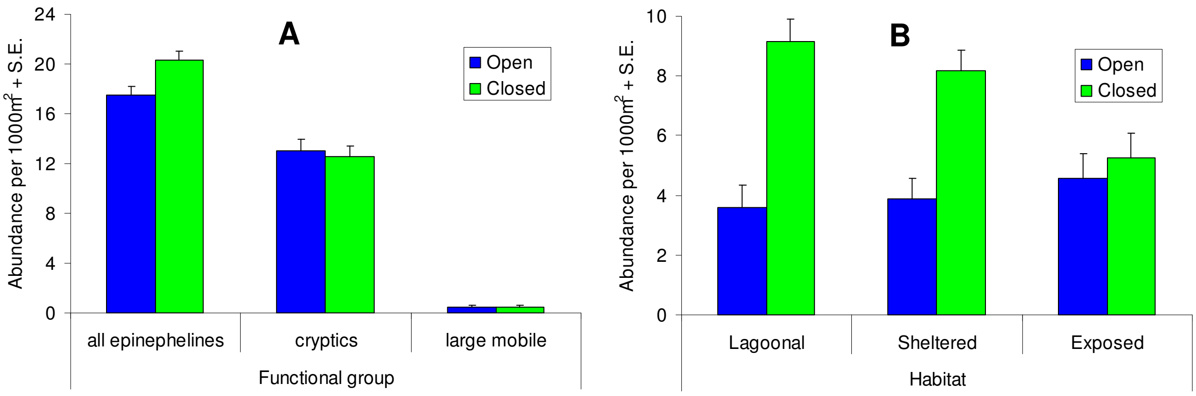


Figure 3.17 Mean density on Lizard outer shelf reefs by Marine Park zone status (i.e. whether closed or open to fishing, see legend) for (A) all epinephelines, cryptic serranids and large mobile serranids; and (B) roving serranids by habitat type. Error bars are standard errors.

Species patterns

Epinepheline serranid assemblages for mid-shelf and outer-shelf positions and for each habitat type of the northern GBR were characterised by a handful of abundant species and many rarer species, with just over one third of the species exhibiting a restricted distribution, being recorded in only one shelf position. Marked changes in the locally abundant species and the species pool are evident in Fig. 3.18. Abundant species characteristic of mid shelf reefs in order of decreasing density were *C. cyanostigma, P. leopardus, C. microprion, C. boenak*, and *E. fasciatus*, whereas for outer shelf reefs they were *P. leopardus, C. urodeta, E. merra, P. laevis, C. argus* and *C. cyanostigma* (Fig. 3.18).

A number of distinctive patterns were evident at the species-level in terms of both numerical abundance and distribution between habitats across the exposure gradient (Fig. 3.18). Some species were associated with more sheltered habitats on mid shelf reefs (e.g. *C. microprion* and *C. boenak*). In contrast, a number of species (e.g. *C. urodeta, C. argus* and *V. louti*) were in higher densities on outer shelf reefs, and tended to be associated with more exposed habitats but were either relatively rare, or absent, on mid shelf reefs. *P. leopardus* and *C. cyanostigma* showed a different pattern as densities of both species were higher on the mid shelf and their densities increased with increasing exposure within the mid shelf position. Densities of *P. leopardus* and to a lesser extent *C. cyanostigma* were still quite high on outer shelf reefs, but their densities were lower in exposed habitats of outer shelf reefs. *E. merra* again stood out as densities were higher in outer shelf lagoons than in any other habitat (Fig. 3.18D).

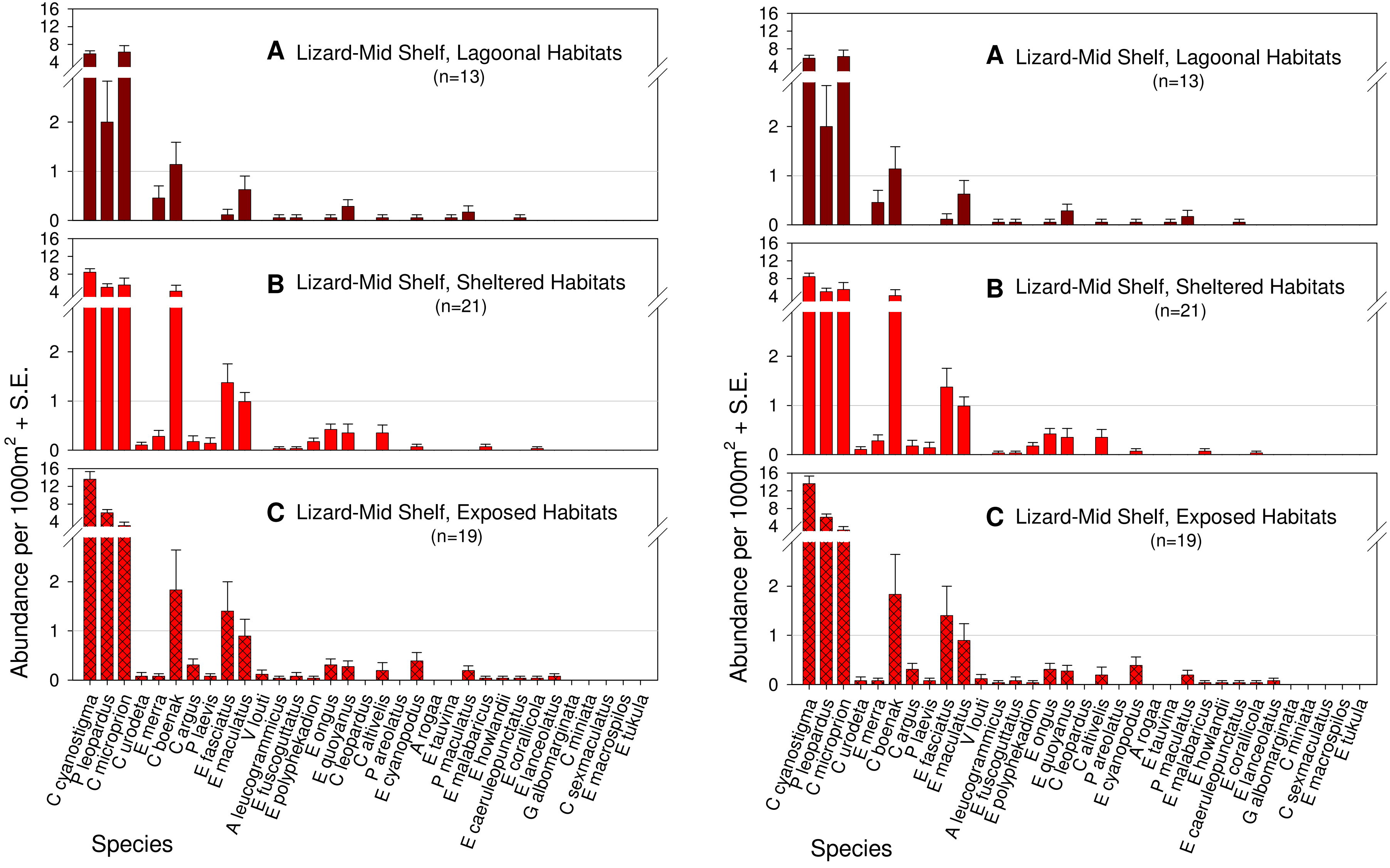


Figure 3.18 Northern GBR cross-shelf and among habitat comparison of species density estimates from Lizard mid shelf reefs (left) and Lizard outer shelf reefs (right). Sample numbers (n) indicated on plots. Error bars are standard errors.

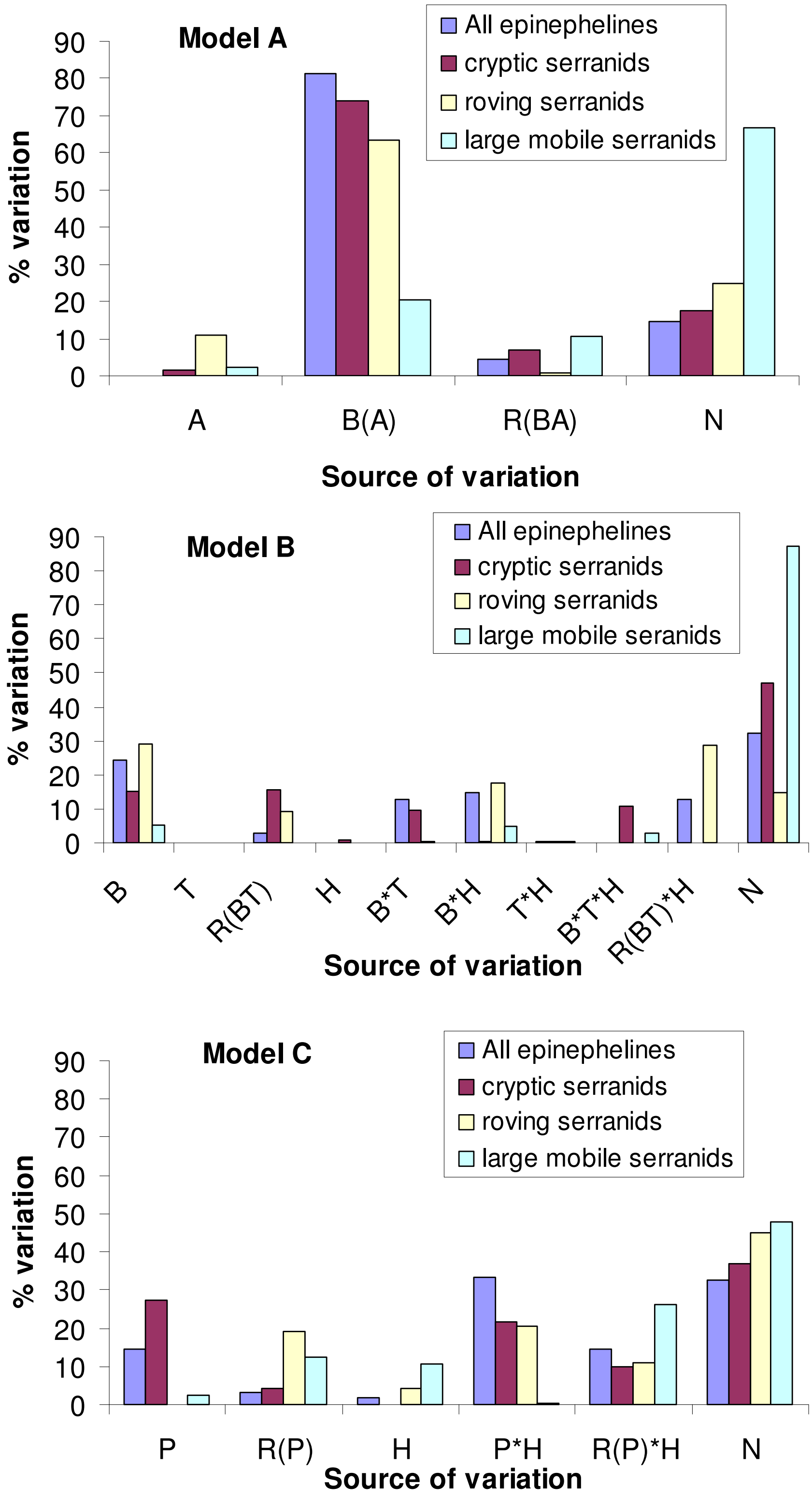


Figure 3.19 Variation attributable to different sources for three spatial comparisons. Key to sources of variation: A=Area, B=Broad-Region, R=Reef, N=replicates (transects), T=Treatment, H=Habitat, P=Position. Key to models: Model A = GBR and Seychelles regional comparison; Model B = Habitat and fishing effects among GBR regions; and Model C = Northern GBR cross-shelf comparison. Details of Models A-C given in Tables 3.3 - 3.5.

3.4.4 Major sources of variation

The plot (Fig. 3.19A) of percent variation attributable to each source in model A, the GBR and Seychelles regional comparison, shows that the broad region scale (100's to 1000's km) was the major source of variation in densities of all epinephelines, cryptic serranids and roving serranids. In contrast, variation among replicates (transects) was the major source for large mobile serranids. Combined with relatively low sample sizes and high frequency of zero counts, this feature indicates that the tests for spatial patterns in abundances of large mobile serranids would have had relatively low statistical power.

Figure 3.19B shows the percent variation attributable to each source in model B; the comparison of habitat and fishing effects among GBR regions. This plot shows that the spatial pattern of variation was complex, and low replication at the reef and transect levels made the estimates of variation attributable to each source fairly unstable. Nonetheless, broad region and its interactions with other factors accounted for a substantial amount of the variation in abundances of all epinephelines, cryptic serranids, and roving serranids.

The percent variation attributable to each source in model C, the northern GBR cross-shelf comparison, is shown in Fig. 3.19C. This plot indicates variation among replicates was high, but considerable variation due to the main effect or interactions with position (mid or outer shelf), the largest scale examined, was still apparent for all epinephelines, cryptic serranids, and roving serranids.

3.5 Discussion

Marked differences in composition of local assemblages were found, in terms of both behavioural groups and species, among regions of the GBR and the Seychelles. All five characteristics used to describe assemblage structure (i.e. total density of epinepheline serranids; density of each behavioural group; species richness; size structure; and species distribution and abundance) varied at a regional or area scale, and some at finer spatial scales. Differing assemblage structures of epinepheline serranids may affect local population regulation of reef faunal communities since the relative abundance and composition of epinephelines may alter predation pressure (or other biotic interactions) experienced by other species. The composition and biomass of local epinepheline assemblages also have repercussions for fishing, particularly the proportion and abundance of species of commercial or angling interest. It is difficult to determine how much fishing has shaped current epinepheline assemblages and species abundances because historical catch and effort data are lacking.

3.5.1 Broad-scale patterns

Broad-scale spatial structure in epinepheline serranid assemblages was evident, with distinct assemblages at scales of 100's to 1000's km. Density and size were more variable within geographic areas than species richness. Observed differences among broad regions and areas in the composition of epinepheline behavioural groups may have implications for local community structure, given that biotic interactions depend on the identities and sizes of the participant species (Hixon 1991a, Jones 1991).

Epinepheline serranids may contribute to the regulation of local community structure in several ways. Recent experimental work has shown that predation of reef fishes by established residents including epinepheline serranids may be significant during a narrow period immediately following settlement of recruits to the reef, with a strong effect on recruit persistence (e.g. Almany 2003, 2004). Loss or inhibition of colonization of older reef fishes due to the presence of dominant predators such as epinepheline serranids may also be important in shaping the composition of communities (e.g. Eggleston et al. 1997). Predators such as epinepheline serranids can also help shape local patterns of species richness (Hixon 1986, Ebeling & Hixon 1991, Hixon 1991a, Almany & Webster 2004). Habitat partitioning among sympatric *Cephalopholis* species in the Gulf of Aqaba (Red Sea) was attributed to interspecific competition and a size-related dominance hierarchy (Shpigel 1989), and Jones (1991) suggested interspecific competition may be more important in determining local scale habitat use than overall population abundances of species. Two *Cephalopholis* species at Lizard Island in the northern GBR appeared to be limited by the availability of prey, and Stewart (1998) suggested they were likely to be in competition for this resource. Some epinepheline serranids may also act as facilitators for other reef organisms (e.g. cleaner wrasse, Almany 2003). Hence, it might be expected that regulation of local reef fish populations by epinepheline serranid assemblages characterised by many small-bodied cryptic serranids is likely to differ from those dominated by roving or large mobile serranids.

The exceptionally high densities of cryptic serranids, particularly the small-bodied *C. urodeta* and *E. fasciatus*, in the southern Amirante Isles might be expected to result in high predation pressure on new reef fish recruits, other small juvenile or adult reef fish and invertebrates (mainly crustaceans). Randall and Brock (1960) found the diet of *C. urodeta* was 68% fishes and some crustaceans, and dietary observations by this study and Randall and Ben-Tuvia (1983) found *E. fasciatus* consumed mostly fishes and some crustaceans. Observations of very low numbers of excavating scarids in the southern Amirante Isles (J.H. Choat, *pers. comm.*) could be a manifestation of high predation pressure on young fish.

The very high estimate of total density of all epinepheline serranids for the southern Amirante Isles (194.7 ± 30.0 fish per 1000 m^2) was 4.2 – 9.4 times higher than the regions sampled on the GBR. Epinepheline serranid densities in the southern Amirante Isles reflect the very high local densities of cryptic serranids. Processes giving rise to high local species densities may include high recruitment rates, hydrodynamically driven concentration of recruits, attraction of conspecific recruits, high food availability, reduced interspecific competition or predation, increased survivorship, behavioural processes such as migration or spawning aggregation behaviour, and favourable disturbance regimes (e.g. Booth 1992, Jones & Syms 1998, Letourneur et al. 1998, Syms 1998, Zeller 1998, Chiappone et al. 2000, Stewart & Jones 2001). High densities of several species were observed on both sampling occasions in the southern Amirante Isles (January 2002 and November 2002). Investigating how persistent these patterns are over time and how the patterns arise may extend our understanding of processes structuring reef fish communities.

High population densities tend to intensify intraspecific competition and resource limitation, which can not only have a profound effect on the number of individuals in a population, but also on the individuals themselves by influencing rates of growth and development (Nicholson 1933, Munday & Jones 1998, Lorenzen & Enberg 2002). For example, density dependent effects are predicted to result in higher mortality regimes and recruitment rates or limit growth of individuals, resulting in a larger proportion of smaller fish at higher population densities. Regional variation in size structure of the epinepheline fauna was evident. Size differences among broad regions were partly because of differing relative abundances of each behavioural group (each with very different average sizes), but species-level variation in size structure among broad regions was also apparent and contributed to the overall size effects. For example, high population density for *E. fasciatus* was associated with smaller average size, as detailed in Chapter 4, Table 4.1. Integration of density information with size- and age-based demographic estimates may give insight into the processes structuring local populations, and is explored in Chapter 4.

Multivariate analyses of the species abundance data identified six distinct epinepheline serranid assemblages: southern Amirante Isles; Farquhar Group; the GBR broad regions of Lizard mid shelf, Mackay and Pompey; Lizard outer shelf and Townsville reefs; Inner Isles; and northern Amirante Isles. Epinepheline serranid assemblages of broad regions in the Seychelles were more discrete than in the GBR, which may reflect greater regional separation (e.g. hydrodynamically) in the Seychelles than on the GBR or different fishing histories, or both (Stoddart 1984, Jennings et al. 2000, Cappo & Kelley 2001, Wolanski 2001). Less broad-scale definition in epinepheline serranid assemblages within the GBR compared to the Seychelles may be because of the high biological connectivity within the system of reefs that make up the GBR (Cappo & Kelley 2001, Wolanski 2001). The similarity in epinepheline faunas between the reefs studied in the Townsville region and the outer shelf reefs of the Lizard region may reflect comparable physical conditions, and agrees with previous suggestions that at least some of these Townsville reefs are characteristic of the outer rather than mid shelf postion (e.g. Williams 2004).

The epinepheline serranid fauna of the Inner Isles was notably sparse, and lacked high densities of any species. The Inner Isles are an outlier in terms of reef structure, being predominantly fringing reefs around granitic islands (Jennings et al. 2000). This region also has the majority of the human population of the Seychelles and likely has been subjected to higher fishing levels than other Seychelles regions (MRAG 1995, Jennings et al. 2000). The structure of studied reefs in the GBR show more affinity to the carbonate reef structures of the Amirante Isles in the Seychelles (Stoddart 1984, Wolanski 2001). Differences in densities of cryptic serranids between reefs of the Amirante Isles and GBR reefs were particularly strong, due to remarkably high densities for this group in the southern Amirante Isles. The Farquhar Group is perhaps more similar environmentally to the outer shelf reefs of the GBR and/or oceanic reefs of the Coral Sea rather than the mid shelf reefs of the GBR (Stoddart 1984, Wolanski 2001). Preliminary observations indicate that species composition and size structure of the serranid assemblages at Farquhar Group and Osprey Reef (Latitude approx. 14°) in the Coral Sea show many similarities (pers. obs.).

3.5.2 Patterns within the GBR

Complex spatial patterns within the GBR in epinepheline serranid densities were evident from the examination of habitat and fishing effects among regions of the GBR and cross-shelf comparisons from the northern GBR. Again, these density patterns showed different spatial patterns for each behavioural group and among species. Little spatial variability in species richness or size structure was found within broad regions or shelf positions. Likewise, similar species richness has been found for scarids within the northern and central GBR (Russ 1984a, b, Gust 2000).

Densities were generally similar among reefs and habitats of the GBR, except for the two most abundant species, *C. cyanostigma* and *P. leopardus.* However, low replication at the level of transects and reefs combined with high variability may have affected the ability to detect density differences for less abundant species, so results should be treated with caution because the risk of Type II errors may be high (Zar 1999).

Much stronger species-level effects were detected in the detailed analyses of the northern GBR, with marked changes in the locally abundant species across the continental shelf and/or among habitats, reflecting pronounced species-level differences in relative abundance or distribution. A number of other studies have examined GBR reef fish distribution and abundance across the continental shelf over the last two decades, (Williams 1982, Williams & Hatcher 1983, Russ 1984a, b, Newman & Williams 1996, Mapstone et al. 1998a, Gust et al. 2001, Newman & Williams 2001), including a study that examined cross-shelf patterns in epinepheline serranids in the central GBR (Newman et al. 1997). Each of these studies demonstrated major cross-shelf differences in community structure, and many studies also revealed pronounced species-level patterns in abundance and distribution among shelf positions and/or habitats. The present study supports the view that there is far more complexity to the GBR 'cross-shelf' story than is generally inferred, a perspective shared by Mapstone et al. (1998a) who considered abundances of several other families of reef fishes on the Northern and Central GBR.

The observed spatial patterns within the GBR may reflect the differing nature and strength of environmental gradients underlying the two GBR comparisons. Strong cross-shelf environmental gradients on the GBR may result from changes in nutrient and water mass inputs and exposure to prevailing wind and waves with increasing distance from the coast (Wilkinson & Cheshire 1988, Wolanski 2001). Outer shelf reefs subject to full oceanic conditions will generally experience higher levels of exposure to wind and wave action and less terrestrial influences compared to mid shelf reefs. Within each shelf position, habitats also increased in exposure from lagoonal to sheltered to exposed, this gradient is likely to be strongest for outer shelf reefs. Many coral reef biota have been shown to co-vary with these abiotic conditions (e.g. Done 1982, Dinesen 1983, Mapstone et al. 1998a). In contrast, the environmental gradient (i.e. latitudinal) underlying the regional comparison of GBR reefs may be weaker since there is relatively little variation in water temperatures among the broad regions examined; monthly average sea surface temperatures differ by less than 2°C (Lough 1994). Differing fishing pressure may also have influenced observed patterns by this study, and is considered below.

3.5.3 General patterns

Visual surveys using a spatially explicit sampling design have allowed both the magnitude and direction of variations in abundance, distribution and size structure and the scales at which it is manifested to be examined. Large scale variation was important in structuring epinepheline serranid assemblages, although small scale variation also contributed considerably to overall variation in counts.

Some generalisations about epinepheline serranid assemblages are possible, despite the marked spatial variation at several scales. Epinepheline serranid assemblages were characterised by a handful of abundant species and many rare species at all of the spatial scales investigated. Only about half of the total species pool was shared between the GBR and the Seychelles, and large mobile serranids were few in number. Larger-bodied species were rare compared to their smaller counterparts, as found for other taxa (Damuth 1981, Peters 1983, Damuth 1991). Over 50% of abundance in each area was accounted for by just two species, although a different two in each area. While cryptic and roving serranids included both abundant and rare species, large mobile serranids were all rare. Understanding the fundamental demographic and reproductive features of large mobile serranids, therefore, is a priority for conservation biology because of the double jeopardy of rarity and large body size (Jennings et al. 1998, Jennings et al. 1999b, Jones et al. 2002, Dulvy et al. 2003). Detailed analyses of the demography of one of these species is considered further in Chapters 5 and 6.

3.5.4 Possible effects of fishing

An important difference between the GBR and the Seychelles from the perspective of resource use is the high density of a major commercial target species (*P. leopardus*) in the GBR but not in the Seychelles. This may account for the higher dominance of epinepheline serranids (principally *P. leopardus*) in shallow water reef fisheries of the GBR than the Seychelles (MRAG 1995, Mapstone et al. 1996b). Thus, it would be interesting to determine to what extent lower abundance of fishery target species in the Seychelles, particularly around the Inner Isles, is because of depletion due to fishing over an extended period or naturally different demographics compared with populations on the GBR.

Some degrees of fishing effects are likely for epinepheline serranids in both the GBR and the Seychelles due to a long history of fishing in both areas (Jennings & Marshall 1995, Jennings et al. 2000, Jackson et al. 2001). Distinguishing the effects of fishing from natural variation and quantifying the degrees of fishing effects are often difficult (Russ 1991, Jennings & Lock 1996). Ideally, replicated studies of areas with similar environmental profiles that are open and closed to fishing would be used to investigate these patterns (Mapstone et al. 1996a, Mapstone et al. 1997, Campbell et al. 2001, Russ 2002, Mapstone et al. 2004), but such areas were not available throughout the study areas. Instead, three approaches were used to explore possible effects of fishing on densities: 1) incorporating the ELF Experiment treatments (Mapstone et al. 2004), manipulating fishing level and Marine Park zone status for GBR reefs, into the GBR regional comparison; 2) comparing reefs open and closed to fishing for Lizard outer shelf reefs; and 3) exploring abundance patterns in relation to presumed gradients of historical fishing pressure (e.g. Jennings et al. 1995, Jennings 1996). Each approach indicated some effects of fishing on at least some species of epinepheline serranids.

Patterns in abundance related to exposure to fishing differed regionally or at finer scales on the GBR and were not always in the direction expected from direct effects of fishing. Fishing may have had indirect effects on the epinepheline fauna, however, such as elevated survival of juveniles, or direct impacts that were not measured by this study (e.g. reduced size or age). Further study is needed to unravel complex fishing effects from other sources of variation. As visual surveys included fish of 6 cm FL or greater, analyses of larger size groups caught by fishers may have shown clearer fishing effects or allowed discrimination of direct and indirect impacts of fishing. Most species of cryptic serranids in particular are small-bodied and hence only the upper size groups will be recruited to the fishery. Variation among or within reefs was apparent and may have masked fishing effects, or the parameter used (i.e. population density) may have been insensitive to fishing. Examination of a suite of parameters, including size, age and reproductive characteristics, may be more informative (e.g. Adams 2002, Begg et al. 2005). Variable recruitment and natural mortality or density-dependent movement among zones (closed or open to fishing) within regions could also influence densities and mask fishing effects.

Fishing effects were detected for roving serranids in lagoonal and sheltered habitats on outer shelf reefs on the northern GBR. This is consistent with expectations, since fishing pressure is likely to be significantly less in exposed habitats (i.e. reef fronts) of outer shelf reefs than other habitats due to weather and wave action limiting access for fishers and because of the very steep, deep reef fronts on those outer shelf reefs, which make it difficult for fishers to anchor and fish with the gear permitted for use in the Great Barrier Reef Marine Park. No fishing effect was detected for cryptic serranids, and some other density results (e.g. Fig. 3.15B) do not fit with presumed fishing pressures for habitats, indicating that fishing was unlikely to be the only important factor driving spatial patterns in density. The lack of fishing effect detected for large mobile serranids may reflect distributional problems with the data rather than no effect on this group (Underwood 1981).

Observed density patterns in the GBR generally did not fit with the prediction of reduced densities at higher fishing levels using a crude estimate of past regional fishing pressure, i.e. lower for mid shelf reefs of Lizard compared to Townsville, Mackay or Pompey regions (Mapstone et al. 1996a, Ayling et al. 2000), and lower for outer reefs than mid shelf reefs of Lizard region (Mapstone, pers. comm.). This may partly indicate that impacts of fishing on most epinepheline serranids on the GBR are relatively slight and or difficult to detect, but might also suggest that other processes may be important in driving abundance patterns for epinepheline serranids that outweigh any impacts of fishing. Historical declines may reduce the power of monitoring programs to detect changes in abundance (Maxwell & Jennings 2005). Other studies also have reported higher densities of epinepheline serranids (e.g. *P. leopardus,* Ayling et al. 2000) and other reef fishes (e.g. *L. miniatus*, Mapstone et al. 2004) in the southern GBR, but causal factors remain unclear. Generally, population abundance may be determined by some combination of larval supply, post-settlement processes, abiotic disturbances and human impacts (Doherty 1991, Jones 1991, Jennings & Lock 1996, Jennings & Kaiser 1998, Jones & Syms 1998). Exploration of the factors structuring epinepheline serranid faunas remains an important area for future research.

Low abundances in the Inner Isles of the Seychelles and very high abundances in the southern Amirante Isles and Farquhar Group are consistent with the presumed fishing gradient in the Seychelles (MRAG 1995, Jennings et al. 2000), but other confounding factors may also be important. As noted, the Inner Isles was the only region studied composed of predominantly granitic reefs but since that part of the Seychelles has likely experienced higher fishing pressures, it is not clear whether biological/ecological factors or fishing history or both are responsible for the observed low densities (Jennings et al. 2000). The possibility of indirect fishing effects explaining the exceptionally high densities of cryptic serranids in the southern Amirante Isles cannot be excluded, but seems unlikely given that fishing pressure is believed to be relatively low in this region and preferred target species such as large epinephelines were relatively abundant too. While inferences about fishing effects in the Seychelles should be treated with caution until more information is available on current and historic fishing pressure and the effects of fishing, these findings are consistent with other sources of information that have suggested depletions due to fishing in the more populated and heavily fished parts of the Seychelles (Jennings et al. 1995, MRAG 1995, Jennings 1996) and therefore are of concern.

3.5.5 Conclusions

Examination of the patterns of abundance, distribution and size structure of epinepheline serranids suggests significant regional variability, and differences in composition of local assemblages in terms of both behavioural groups and species among broad regions of the GBR and the Seychelles. Explicit finer scale comparisons in the GBR revealed variability in densities at scales of 1 to 100 km, but generally not in species richness or size structure. A variety of species patterns of distribution and abundance were found over the different spatial scales examined. The magnitude of the variation in some characteristics (e.g. density) are likely to be biologically meaningful, with consequences for individual fish, community structure, local population dynamics and responses to fishing or other disturbances.

Spatial structure in serranid assemblages at a range of scales was expected, given the heterogenous and multi-scalar nature of reef habitats (Williams 1991, Sale 1998), but has not previously been described for serranid assemblages in the majority of these locations, or at scales spanning reefs to oceans. The study has also provided valuable species-level information for almost 40 species of epinepheline serranids. Understanding the degree of regional- and fine-scale similarities and differences in epinepheline serranid assemblages contributes to our knowledge of the abundance patterns of the taxon, and the degree to which we can generalise about members of the taxon. Furthermore, spatial scales accounting for significant variation in abundance and size of epinepheline serranids may indicate the scales over which to expect variation in demographic and life history parameters and underlying population dynamics (Chapter 4). Directions for further research include investigation of fine-scale spatial patterns of abundance for the Seychelles, temporal stability of patterns, processes driving regional patterns and further analyses of fishing effects or response to protection from fishing.

Chapter 4. Comparative demography of *Epinephelus fasciatus, E. polyphekadion* and *Cephalopholis argus* from the Great Barrier Reef and the Seychelles

4.1 Synopsis

Comparative age-based demographic analyses were conducted for three species of cryptic serranids, *Epinephelus fasciatus* (blacktip grouper), *E. polyphekadion* (camouflage grouper) and *C. argus* (peacock grouper), from the Great Barrier Reef (GBR) and the Seychelles. I described size and age characteristics, longevity, and patterns of growth for each species, and explored broad, biogeographic-scale patterns in demography, and the nature of size-age-density relationships for each species in the GBR and the Seychelles. Comparative analyses revealed substantial spatial variation in demographics within and among species. Hence, our ability to generalise about the demography of the cryptic serranids appears to be limited. Linking information on abundance and demography revealed that different combinations of processes may influence local populations of the three species, with the possibility of broad-scale compensatory demographic trade-offs dependent on density noted for two of the three species. Further, lifespans tended to be shorter in the Seychelles than the GBR, suggesting higher recruitment levels and predictability of environmental conditions and resources in the Seychelles than the GBR.

4.2 Introduction

Information on life history characteristics of fish, such as size, age and growth, is essential for understanding population biology and managing exploited species (Gulland 1988, Choat & Robertson 2002). Spatial variation in these parameters has been found for many taxa including several species of epinepheline serranids (e.g. Manooch 1987, Craig et al. 1999, Manickchand-Heileman & Phillip 2000, Mapstone et al. 2004) and, therefore, it is important to consider within species variation when comparing characteristics of different species. Broad-scale comparative studies of reef fishes may help reveal general patterns and processes in marine ecology (Stearns & Koella 1986, Sale 1991b, Stearns 1992, Cury & Pauly 2000). Recent broad-scale work on demographics of other reef fishes, including Acanthurids and Scarids, has found a trend of shorter lifespans in the Indian than Pacific Ocean (Laman Trip 2004, Choat unpub. data), perhaps reflecting diverging evolutionary pathways (e.g. Bernardi et al. 2001, Bay et al. 2004). Variation in parameters such as size, age, growth or longevity seems likely over broad biogeographic scales, particularly where differences in histories, environmental conditions, recruitment, post-settlement processes or fishing impacts are pronounced (Sale 1991a, 2002). The pattern and magnitude of differences influences whether what we learn about one population or species can be applied to others.

Comparative studies of epinepheline serranids are important for determining characteristic life history attributes for the taxon that would form a basis for assessing relationships between intrinsic factors and vulnerability to fishing. In this study, I took a comparative approach to examine demographic characteristics of three species of Indo-Pacific epinepheline serranids between and within two diverse geographic areas: the GBR and the Seychelles Islands. The three study species, *Epinephelus fasciatus, E. polyphekadion,* and *Cephalopholis argus,* are diverse species chosen as representatives of the cryptic serranids behavioural group (Chapter 1, Table 1.1). Less is known about species of cryptic serranids or large mobile serranids (Chapters 5 & 6) compared to roving serranids in Australia. I chose candidate species that covered a range of body sizes and with widespread distributions across the Indo-Pacific, and for sampling reasons, with relatively high abundances. Because of their numerical and widespread fishery importance, I selected species from the common genera *Epinephelus* and *Cephalopholis* (Heemstra & Randall 1993). Abundance profiles and relationships between density and size differed for each species (Figs. 4.1 & 4.2, Table 4.1). I explored whether there were corresponding dynamic patterns in age-based demographics.

Integration of density information with size- and age-based parameter estimates may give insight into the processes shaping these populations (Jones 1991). For the two more abundant species (*E. fasciatus* and *C. argus*), the negative relationships between density and size (Table 4.1) suggest that either density dependent mortality and recruitment or density dependent growth, or both, may be influential in structuring populations. The first, or a combination of both, would affect age as well as size characteristics to give local populations dominated by a larger proportion of smaller, younger fish and shorter longevities at higher densities. The second alone would primarily affect size characteristics, giving smaller fish on average and lower size-at-age at high densities, but similar longevities regardless of density. Two contrasting scenarios may account for the observed larger average size at higher densities for *E. polyphekadion*. Reduced average size and abundance may result from heavy fishing pressure (Munro 1983, Koslow et al. 1988, Jennings & Lock 1996, Huntsman et al. 1999) with corresponding reductions in average age and longevity likely (e.g. *P. leopardus*, Ferreira & Russ 1995). Alternatively, a positive correlation between size and abundance may reflect favourability of prevailing environmental conditions, but would not be consistent with compensatory demographic trade-offs dependent on density.

The aim of this study was to examine life history characteristics of three species of cryptic serranids, *E. fasciatus, E. polyphekadion* and *C. argus,* from the GBR and the Seychelles. Specific objectives were to: 1) describe size- and age-based demographics and patterns of growth for the three species; and 2) explore spatial patterns in demographics and the nature of size-age-density relationships for each species.

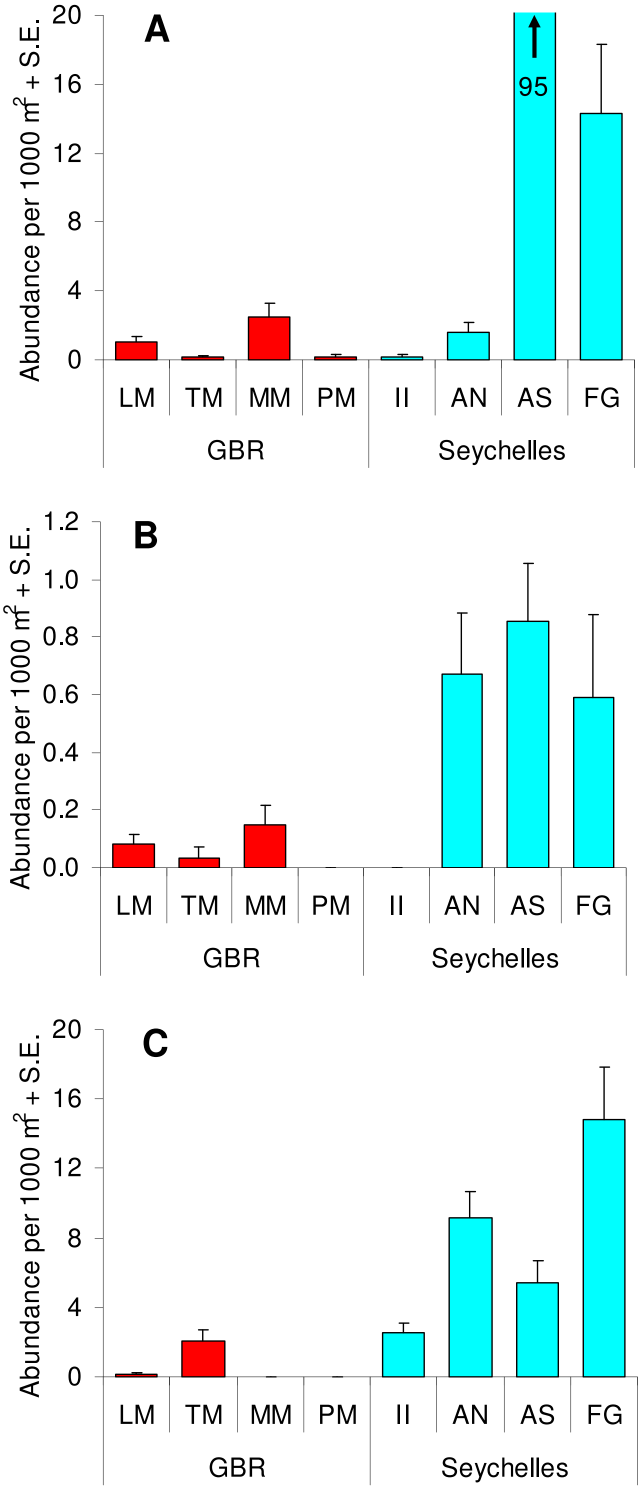


Figure 4.1 Comparison of density estimates from broad regions of the GBR and the Seychelles for (A) *E. fasciatus,* (B) *E. polyphekadion* and (C) *C. argus*. Note difference in vertical scales on plots. Broad regions: LM=Lizard mid shelf, TM=Townsville, MM=Mackay, PM=Pompey, II=Inner Isles, AN=northern Amirante Isles, AS=southern Amirante Isles, FG=Farquhar Group. Error bars are standard errors.

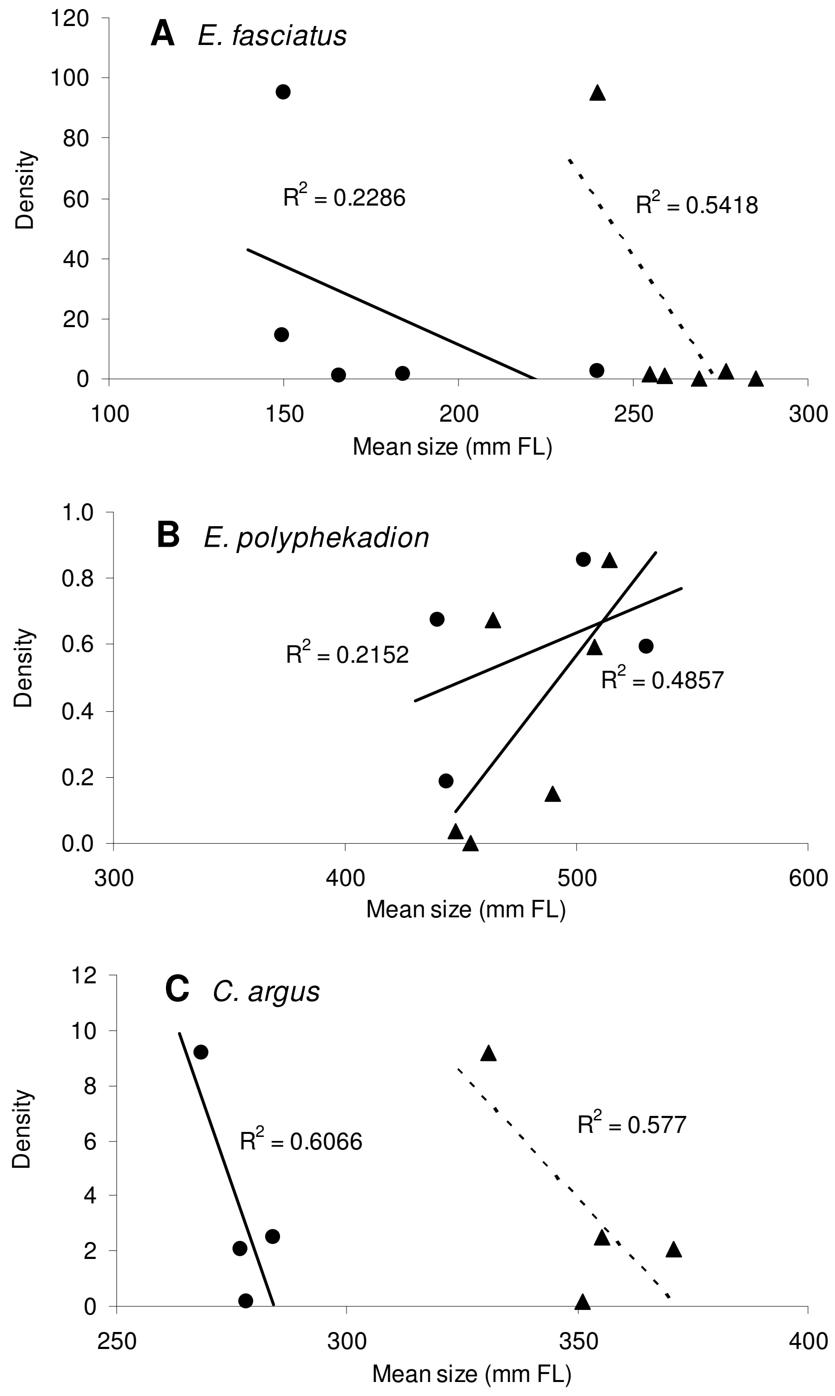


Figure 4.2 ***Epinephelus fasciatus, E. polyphekadion*** **and** ***C. argus*****. Relationships between mean size of fish and density for each species. Each data point represents a broad region (see Table 3.2 and Table 4.2 for sampling details). Negative correlations were found between mean size and density for (A)** ***E. fasciatus*** **and (C)** ***C. argus,*** **whereas a positive correlation was found for (B)** ***E. polyphekadion.*** **Density = abundance per 1000 m^2; Circles = mean size in visual surveys; triangles = mean size of specimens used for demographic analyses. Note that the shift to the right along the x-axis for the mean size estimates in A and C of the specimens compared to the visual surveys reflects the use of a minimum cut-off size for inclusion in demographic analyses (i.e. harvested components, shown by dashed lines) for these species – as detailed below in Section 4.3.2: Size ranges used for comparisons.**

Table 4.1 Summary table of spatial patterns in distribution and abundance of *E. fasciatus, E polyphekadion* and *C. argus* from the GBR and the Seychelles. Sources: 1 = Randall & Heemstra 1991; 2 = Sadovy et al. 2003; 3 = this study. Codes: GBR=Great Barrier Reef, SEZ= Seychelles Islands, LO=Lizard outer shelf, LM=Lizard mid shelf, TM=Townsville, MM=Mackay, PM=Pompey, II=Inner Isles, AN=Amirantes Isles northern, AS=Amirantes Isles southern, FG=Farquhar Group.

	E. fasciatus	**E. polyphekadion**	**C. argus**
General characteristics			
Maximum reported size worldwide (1)	At least 360 mm TL based on examination, possibly as high as 400 mm TL.	At least 750 mm TL based on examination.	Often reported to 500 mm TL, one report of 600 mm TL, but largest examined 440 mm TL.
Maximum observed size (3)	320 mm FL (equivalent to TL)	660 mm FL (equivalent to TL)	486 mm FL (equivalent to TL)
Remarks (1)	One of the two most common species of the genus and the most widespread. Occurs on coral reefs or rocky substrata over a wide range of depths, but common in shallows. Reported to depths of 150+ m.	Usually found in clear waters on coral reefs, and reported to be more common at atolls than high islands. Referred to by junior synonym, *E. microdon*, by some recent authors. Of considerable fisheries importance in the Indo-Pacific (3).	The most widespread Indo-Pacific epinepheline serranid. Common shallow-water species to depths of at least 40 m. Reported to be more common on exposed than protected reefs.
Spatial comparison of abundance (3)			
1. Overall comments	Two regions of SEZ (AS, FG) had very high densities (order of magnitude higher than elsewhere in either GBR or Seychelles).	SEZ generally higher densities than GBR.	SEZ generally higher densities than GBR.
2i. Broad Regions of the GBR	MM>LM>TM&PM.	Low densities everywhere except PM (none recorded).	Higher densities in more exposed or outer shelf localities (i.e. LO&TM). Very few or none recorded elsewhere. For LO, higher densities in more exposed habitats.
2ii. Broad Regions of the Seychelles	AS>>FG>AN>II.	Medium densities everywhere except II (none recorded).	Generally medium to high densities, with highest densities in FG.
Density-size relationships (3)			
Overall density-size patterns	Smaller mean sizes with higher densities.	Larger mean sizes with higher densities.	Smaller mean size with higher densities.

4.3 Methods

4.3.1 Study locations

Epinephelus fasciatus, E. polyphekadion and *C. argus,* are widespread in the Indian and Pacific Oceans (Table 4.1). The same four broad regions within each of two geographic areas, the GBR and the Seychelles Islands, as used for Chapter 3 were chosen for sampling (Fig. 4.3), so that demographics could be explored in the context of abundance information (Table 4.1). These locations allowed examination of demographics over spatial scales from 100’s to 1000’s km (Chapter 3).

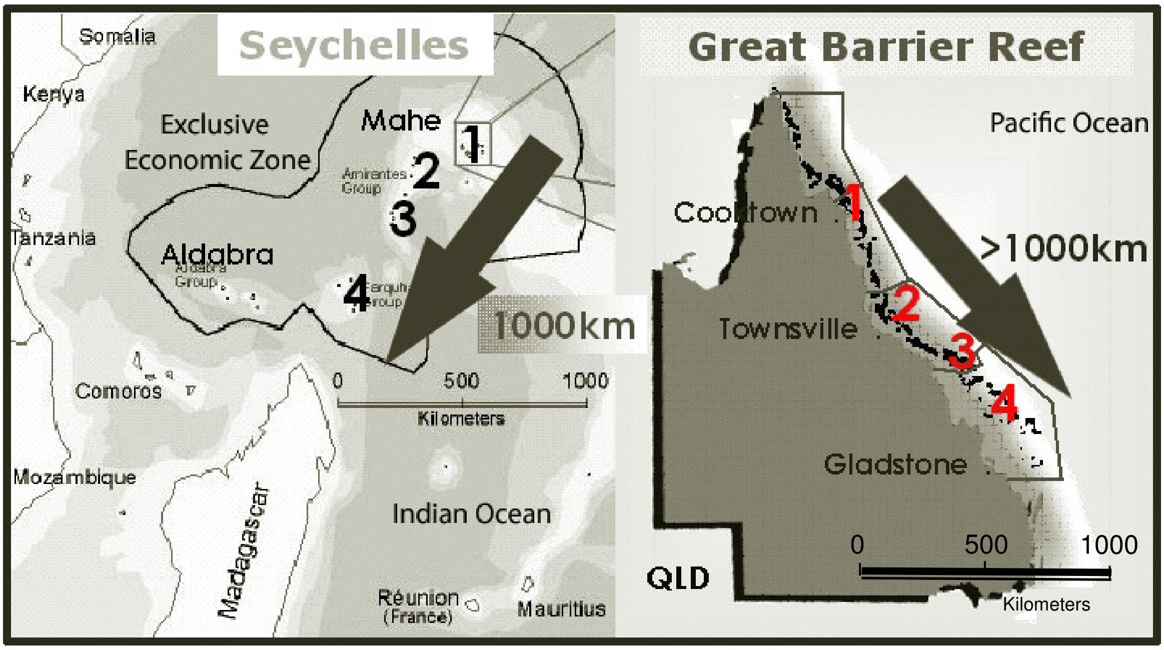


Figure 4.3 Map showing broad regions sampled from two geographic areas: the Seychelles and the GBR. Key to broad regions – Seychelles: 1 = Inner Isles, 2 = Northern Amirante Isles, 3 = Southern Amirante Isles, 4 = Farquhar group. GBR: 1 = Lizard, 2 = Townsville, 3 = Mackay, 4 = Pompey.

4.3.2 Sample collection

Relatively low natural abundances (Chapter 3) meant that collections were only possible in some of the broad regions for each species (Table 4.2). Samples of *E. fasciatus, E. polyphekadion* and *C. argus* were collected using a mixture of fishery independent and dependent methods (summarised in Table 4.2 and detailed below). Collection methods were: 1) research line fishing; 2) commercial line fishing; and 3) research spear fishing.

Details of sample collection by species, year, month and area are given in Appendix 3. Data collected on different dates within each broad region for each species were pooled to obtain adequate sample sizes for demographic analyses. The pooling of data across reefs and sampling dates within broad regions assumes that there were no systematic spatial or temporal patterns in demographic characteristics among reefs or over sampling dates respectively within broad regions. There were insufficient data to test these assumptions.

GBR sampling details

Most of the GBR samples for each species were obtained from line fishing sources. GBR research line fishing samples were collected from catch surveys for the ELF Experiment (Mapstone et al. 1996a, Campbell et al. 2001, Mapstone et al. 2004) during austral spring-summer (Oct – Dec) in 2000, 2001 and 2002 using a standardised structured fishing method

(Davies et al. 1998, Mapstone et al. 2004). It was necessary to pool samples over reefs within each broad region of the ELF Experiment due to low sample sizes (reflecting low natural abundances) per reef. GBR commercial line fishing samples were obtained from fishers operating out of Townsville, Bowen and Mackay on the east coast of Queensland between April 2001 and February 2003. Each specimen was assigned to one of the four broad regions (Lizard, Townsville, Mackay and Pompey) based on geographic proximity to the clusters of ELF reefs. Some additional adult samples were obtained by research spear fishing in spring-summer of 2000, 2001 or 2002 from the Lizard and Townsville regions (Table 4.2).

Table 4.2 Details of sample collection for demographic study of *E. fasciatus, E. polyphekadion* and *C. argus* from the GBR and the Seychelles. Collection methods: 1 = research line fishing, 2 = commercial line fishing, 3 = research spear fishing. Only harvested components were used in analyses (see main text "Size ranges used for comparisons").

Species	**Area**	**Broad Region**	**Sample size by collection method**			
			1	**2**	**3**	**Total**
E. fasciatus	GBR	Lizard	19	1	31	51
		Townsville	19	19		38
		Mackay	99	1		100
		Pompey	35	8		43
		GBR total	172	29	31	232
	Seychelles	Inner Isles				0
		Northern Amirante Isles	6	7	18	31
		Southern Amirante Isles	7		101	108
		Farquhar Group	2	4		6
		Seychelles total	15	11	119	145
		Total	187	40	150	377
E. polyphekadion	GBR	Lizard	8		3	11
		Townsville	21	95		116
		Mackay	26	16		42
		Pompey	17	20		37
		GBR total	72	131	3	206
	Seychelles	Inner Isles				0
		Northern Amirante Isles	25	15		40
		Southern Amirante Isles	11	6		17
		Farquhar Group	31	14	1	46
		Seychelles total	67	36		103
		Total	139	169	1	309
C. argus	GBR	Lizard	8	2	32	42
		Townsville	46	21	25	92
		Mackay	2	1		3
		Pompey				0
		GBR total	56	24	57	137
	Seychelles	Inner Isles	6	2	57	65
		Northern Amirante Isles	9	10	73	92
		Southern Amirante Isles	1	3		4
		Farquhar Group	1			1
		Seychelles total	17	15	130	162
		Total	73	39	187	299

Small, young fish were under-represented in samples collected by line fishing gear due at least in part to the selectivity characteristics of the gear, particularly due to the size of hook used. Attempts were made to supplement GBR samples of smaller fish for each species using research spear fishing, but only samples of small individuals of *E. fasciatus* were obtained and only from the Lizard region. Small individuals of the other species were not encountered.

Seychelles sampling details

The vast majority of Seychelles samples of *E. polyphekadion* were obtained from line fishing sources, whereas a combination of line sources and research spear fishing were used to sample *E. fasciatus* and *C. argus*. Seychelles research line fishing consisted of unstructured surveys conducted by the Seychelles Fishing Authority (SFA) periodically between December 1999 and November 2002 using similar hand held fishing gear to that used during the ELF catch surveys (Mapstone et al. 2004). Seychelles commercial line fishing samples were obtained by SFA from fishers operating in the Seychelles and assigned to the broad region from which they were collected. Seychelles collections of fish by research spear fishing followed the sampling protocol of Choat et al. (2003), providing an unbiased representative sample of each size class where possible. Again, small *E. polyphekadion* and *C. argus* were poorly represented in the research spear fishing samples since small individuals of these species were not encountered.

Size ranges used for comparisons

No legal fish size limits applied to the study species during any of the collections in either area. Different size-selectivity characteristics of line and spear fishing methods were apparent, with line gear failing to collect the smaller size groups of each species. A common minimum size was used as a lower cut-off for size, age and growth parameter estimates and spatial comparisons to remove the potential for confounding spatial comparisons in population parameters with the effects of collecting samples of smaller sized fish by spear fishing in some regions but not others. This cut-off size corresponded to the size at which each species recruited to the line fishing gear, which was the common method used successfully in all regions. These sizes were 200 mm FL for *E. fasciatus* and 290 mm FL for *C. argus*. The lack of speared *E. polyphekadion* meant no cut-off size was necessary for that species. The retained portions of the samples were termed “harvested components” since they would cover a similar size range to that sampled by fishers.

4.3.3 Data collection

Fork lengths of fish were measured to the nearest 1 mm at the time of collection or receipt from commercial fishers. Age estimates were obtained from thin-sectioned sagittal otoliths. The left or right otolith from each pair was selected at random, weighed to the nearest 0.1 mg, and individually embedded in West System™ 105 epoxy resin. A low-speed Buehler isomet saw was used to cut out a transverse section (200 – 300 µm), which was mounted on a labelled glass slide using Crystalbond™ mounting media. The section was then polished using 600 to 1200 grade abrasive paper until the optimum thickness for reading, as determined by frequent examination under a microscope, was obtained.

All otolith readings were conducted on an image analysis system using transmitted light at 25x magnification. Reference collections of sections for each species were produced to establish consensus of age estimates by experienced readers (Campana 2001). Alternating opaque and translucent bands were visible and it was assumed that one pair of opaque and translucent bands was laid down each year and represented one annulus. This assumption was examined using two methods (e.g. Choat & Axe 1996, Fowler & Short 1998, Cappo et al. 2000). Firstly, an oxytetracycline (OTC) experiment was conducted using captive individuals on the GBR as described by Pears et al. (Pears et al. 2006, see also Chapter 5) to establish timing and frequency of deposition of increments. Details are given in Appendix 4. Secondly, the correlation between otolith weight and number of increments (putative age) was examined, in which a strong correlation is expected if otoliths accrete calcium carbonate throughout the life of the fish (Choat & Axe 1996). Increments from the Seychelles were assumed to be annuli as they closely resembled annuli determined by OTC marking from the GBR. Counts of opaque bands were made along a consistent axis near the sulcus, where the bands were most visible (Choat & Axe 1996).

Species abundance estimates (fish per 1000 m^2) and estimates of fork length (FL) were obtained for each species in each broad region (Fig. 4.3) using the long-swim visual survey technique described in Chapter 2 and sampling design described in Chapter 3.

4.3.4 Data analyses

Ease and confidence of otolith interpretation

The readability of otolith sections can vary between fish taxa, individuals, sampling locations, preparation methods or some combination of these factors (Ackerman 2004). A method was developed to examine the ease and confidence of otolith increment interpretation. Each otolith section was given a subjective "readability" score on the basis of ease and consistency of interpretation of increments (rules detailed in Table 4.3). This readability index provided a measure of confidence in each age estimate, and only age estimates from otolith sections rated 1-3 (out of 5) were used for parameter estimates, spatial comparisons or fitting of growth models.

Table 4.3 ***E. fasciatus, E. polyphekadion*** **and** ***C. argus*****. Criteria used to evaluate readability of otolith sections for each species from 1 (easy to age, and high consistency of counts) to 5 (very difficult to age, very low consistency) as detailed in the table. Only age estimates from otoliths graded 1-3 were accepted as reliable and included in analyses.**

Readability Score	Description
1 (Very good)	Otolith section is easy to age, and consistent (±0) counts of presumed annuli are obtained.
2 (Good)	Consistency of counts fairly high (within ±1).
3 (Fair)	Consistency of counts relatively low (within ±2 if under 20 years or within ±3 if 20 years or over).
4 (Poor)	Otolith section is difficult to read and consistency of counts is low (not within ±2 if under 20 years or not within ±3 if 20 years or over).
5 (Very poor)	Unable to determine a reliable age since otolith section is very difficult to read and consistency of counts is extremely poor.

Spatial patterns of growth

The von Bertalanffy growth function (VBGF) provided the best fit to FL at age data for each species according to the parameter estimates from the Schnute (1981) growth function. Therefore, the patterns of growth for *E. fasciatus, E. polyphekadion* and *C. argus* were modelled by fitting the VBGF to species FL-at-age data for each broad region and area using non-linear least-squares regression. The form of the VBGF used was:

$$L_{t,r} = L_{\infty,r}(1 - e^{-K^{l}_{r}(t - t^{l}_{0,r})})$$

where

$L_{t,r}$ is the fork length at age t on broad region or area r;

$L_{\infty,r}$ is the mean asymptotic fork length on broad region or area r;

K^{l}_{r} is the rate at which L_{∞} is approached on broad region or area r;

$t^{l}_{0,r}$ is the age at which the sampled fish have theoretical length of zero on broad region or area r.

The intercept of the curves was constrained and standardised for all broad regions to the approximate size at settlement to facilitate comparisons among the species or regions since VBGF parameter estimates can be sensitive to the range of ages and sizes used (Ferreira & Russ 1994). Data from Leis (1987) was used for estimates of sizes at settlement (25 mm FL for *Epinephelus* and 18 mm FL for *Cephalopholis*, Leis 1987).

The VBGF's for each species were compared among broad regions within each area and between areas using Likelihood Ratio Tests (LRTs) (Kimura 1980), which is considered to be the most reliable procedure for such comparisons (Cerrato 1990). A common age range was used in each analysis (Haddon 2001) to ensure validity of comparisons and is detailed in the results for each comparison.

Parameter estimation

A suite of demographic parameters were examined using multivariate and univariate statistical analyses to explore the spatial patterns in demographics for each species (Begg et al. 2005). The demographic parameters examined and codes used are summarised in Table 4.4. These parameters were estimated from the harvested component of samples for each species in each broad region.

Table 4.4 *E. fasciatus, E. polyphekadion* and *C. argus*. Parameter estimates for harvested components used in analyses of species demographics. See depictions in Fig. 4.4.

Parameter	Code
Mean size	Mean size
Mean age	Mean age
Mean maximum size of largest 10% of individuals	Max size
10% longevity (mean age of oldest 10% of individuals)	Longevity
Size-at-mode-age	Growth
Length richness	N_L
Age richness	N_A
Density from visual surveys	Density

The size and age data were used to estimate mean size and age of the harvested components of *E. fasciatus, E. polyphekadion* and *C. argus* for broad regions and areas. The mean size of the largest 10% of individuals sampled (termed *mean maximum size*) was used as a measure of maximum fish size. Similarly, longevity estimates were based on the mean age of the oldest 10% of individuals sampled (termed *10% longevity*, Fig. 4.4A), rather than maximum observed age (T_{max}). This approach is considered preferable for small sample sizes since estimates do not rely on a single individual which may unduly influence results (Gust et al. 2002).

Length (N_L) and age (N_A) richness were used as proxies for size and age frequency distributions respectively (Begg et al. 2005 and Fig. 4.4B), and estimated as the number of length (20 mm) and age (years) groups for each broad region above the peaks of the overall size or age distributions for the harvested components of the species.

Size at a particular age is a directly observable proxy of growth that can be used to examine and compare growth rates among populations from different locations. Three ages were chosen for the examination of size-at-age (Fig. 4.4C): 1) the age group with the greatest number of samples (termed size-at-mode-age); 2) an age group corresponding to the initial steeper part of the growth trajectory with the least number of cell zeros across all levels of the factor broad region (size-at-initial-age); and similarly 3) an age group corresponding to the flatter part of the growth trajectory (size-at-later-age). The mean size-at-mode-age was used as the proxy of growth in the multivariate analysis since sample numbers per broad region were highest for this age group. The mean size-at-initial-age was also used as an alternative measure of growth since most variability was detected for these age groups, but resulting multivariate patterns were broadly similar to those for mean size-at-mode-age and are therefore not presented.

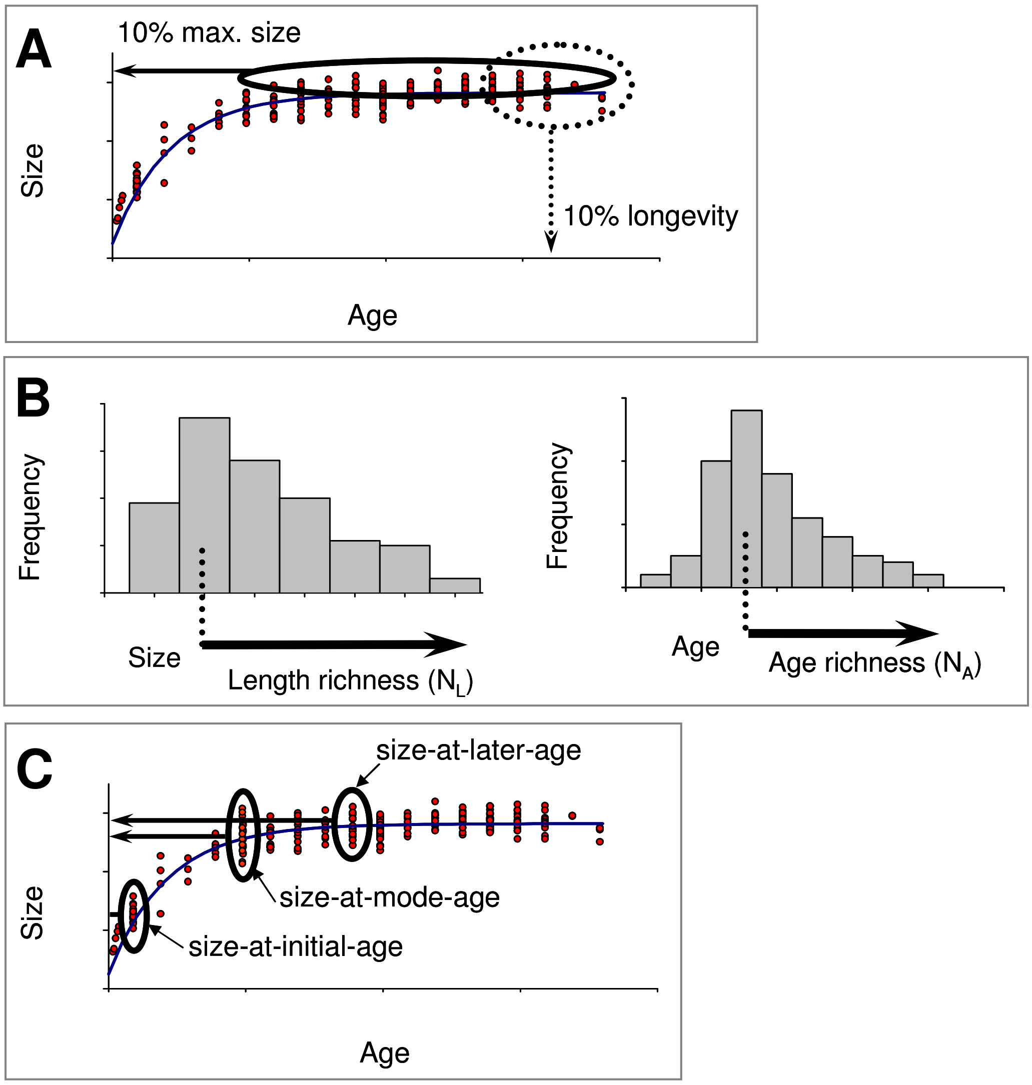


Figure 4.4 Diagram depicting demographic parameters: (A) 10% longevity and 10% maximum size, (B) measures used as proxies for size and age distributions, and (C) the three size-at-age measures used as proxies for growth.

Multivariate demographic indices

Unconstrained multivariate ordination using PCA was used to reduce the dimensionality of the demographic data and give insight into the spatial patterns in demographics. The correlation matrix was analysed, in which data have been standardised to z-scores (centred by their means and converted into standard deviation units) because of the different measurement scales of the various demographic parameters. The resulting principal components (PCs) can be interpreted as multivariate demographic indices (after Begg et al. 2005). The first two PCs (accounting for most of the total variation for each species) were used to display spatial patterns in demographics among the broad regions and areas on a Euclidean bi-plot, with vectors indicated to help demonstrate the contribution of individual demographic parameters to the observed multivariate patterns.

Spatial variation in demographic parameters

Following the PCA, ANOVA was used to explore spatial variation in size, age and growth parameters of each species among areas and broad regions using two factor ANOVAs with the factors Area (fixed) and Broad Region nested in Area (random). Parameters examined were: mean size, mean age, mean maximum size, 10% longevity, and the three measures of size-at-age. Type III Sums of Squares were used for all ANOVAs. Normal probability plots and residual plots were used to examine the assumptions of normality and homogeneity of variances for all data prior to analysis. The origins of significant patterns suggested by the ANOVAs were identified by Tukey's tests (Day & Quinn 1989). All significant differences are mentioned in the text, but not all non-significant tests are detailed.

4.4 Results

4.4.1 Age estimation from otoliths

Analysis of otoliths from the GBR satisfied the three criteria for estimating age from otolith microstructure (Beamish & McFarlane 1983, Fowler 1990, Fowler & Doherty 1992): 1) otoliths displayed an internal structure of increments that can be reliably interpreted; 2) otolith increments were predictably related to a regular (annual) period of formation; and 3) otoliths grew throughout the life of individual fish (Appendix 4).

The subjective readability scores ranged from 1 to 4 for *E. fasciatus* and *E. polyphekadion,* with 99.5% and 97.7% ≤3, respectively. The results indicated that otolith sections from these two species were generally easy to read and consistency of multiple reads was high. The otolith sections of *C. argus* were more difficult to read and consistency of interpretation was sometimes poor, with only 77.6% rated ≤3 on the readability scale (Table 4.3). Poorly estimated ages from *C. argus* (31.4% from the GBR and 14.8% from the Seychelles with readability 4 or 5) were included on plots of size-at-age (Fig. 4.5) and presumed age vs otolith weight (Appendix 4) using distinct symbols to explore any relationships between readability and size, age or location of the fish from which they came. No such relationships were apparent, rather the lower readability appeared to be characteristic of otoliths from *C. argus.*

4.4.2 Spatial patterns of growth

The overall shape of the growth curves (Fig. 4.5 – 4.8) were consistent for a given species, with the growth trajectory of each species flattening off and indicating that growth of these epinepheline serranids tended to be minimal in the latter 50% to 70% of the lifespan. Figures 4.6 – 4.9 also show, however, that there was some variation in the relationship between size and age among broad regions for *E. fasciatus, E. polyphekadion* and *C. argus,* and among areas for the latter two species. Figure 4.5 shows that there were generally fewer older fish in the Seychelles than the GBR for each species, and that *E. fasciatus* had a shorter lifespan than the other two species. There were notable shifts along the y-axis (and hence in L_∞) for *E. polyphekadion* among broad regions and areas (Fig. 4.5 & 4.7). Parameter estimates of the VBGF are given in Table 4.5 and the LRT results in Table 4.6, with significant differences found for most comparisons of growth curves. Parameters estimated from the smaller sample sizes (e.g. <50) should be considered provisional estimates only.

Table 4.5 Von Bertalanffy Growth Function parameters estimates for *E. fasciatus, E. polyphekadion* and *C. argus* from the full sample collection (not just harvested components).

Species	Area/Broad Region	L_∞	K	t_0	r^2	n
E. fasciatus	GBR	282.13	0.469	-0.198	0.898	230
	Lizard	267.65	0.536	-0.183	0.941	51
	Townsville	285.14	0.308	-0.298	0.521	36
	Mackay	284.68	0.443	-0.207	0.351	100
	Pompey	296.62	0.383	-0.230	0.488	43
	Seychelles	274.60	0.450	-0.212	0.821	145
	Northern Amirante	287.69	0.441	-0.206	0.803	31
	Southern Amirante	261.76	0.483	-0.208	0.834	108
E. polyphekadion	GBR	537.01	0.195	-0.245	0.542	201
	Townsville	526.02	0.186	-0.262	0.619	116
	Mackay	555.82	0.211	-0.218	0.550	38
	Pompey	597.48	0.169	-0.254	0.563	36
	Seychelles	582.37	0.206	-0.212	0.598	101
	Northern Amirante	587.76	0.191	-0.228	0.738	39
	Southern Amirante	560.42	0.323	-0.141	0.546	17
	Farquhar Group	596.65	0.227	-0.189	0.223	45
C. argus	GBR	399.01	0.271	-0.169	0.650	94
	Lizard	380.42	0.287	-0.169	0.664	28
	Townsville	398.52	0.294	-0.157	0.427	65
	Seychelles	371.19	0.339	-0.147	0.776	138
	Inner Isles	381.16	0.347	-0.139	0.722	61
	Northern Amirante	351.94	0.364	-0.144	0.807	73

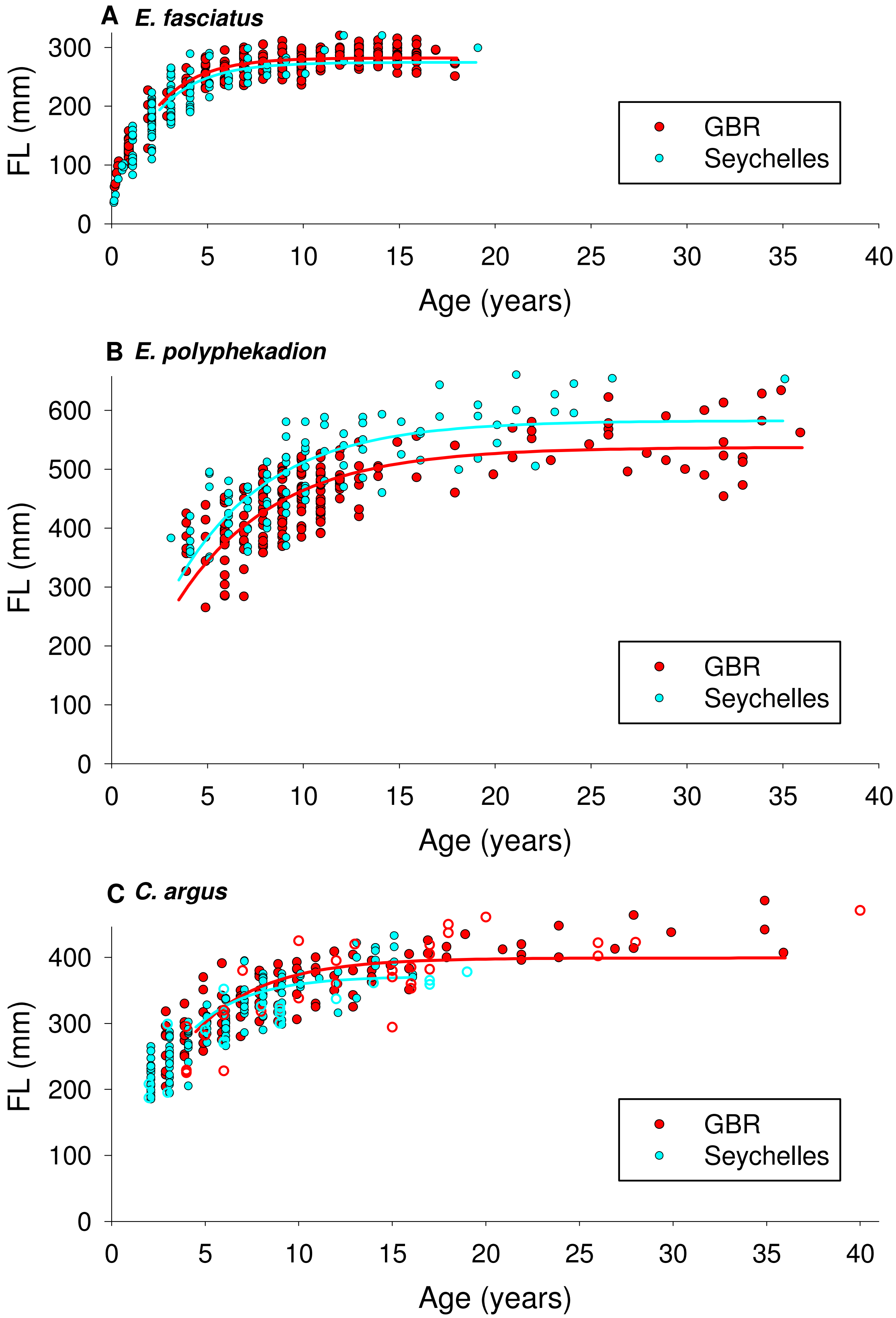


Figure 4.5 Size-at-age and fitted VBGF for (A) *E. fasciatus,* (B) *E. polyphekadion* and (C) *C. argus* from the GBR and the Seychelles. Open data points for *C. argus* indicate data not used in curve fitting due to poor readability score (4 or 5, Table 4.3).

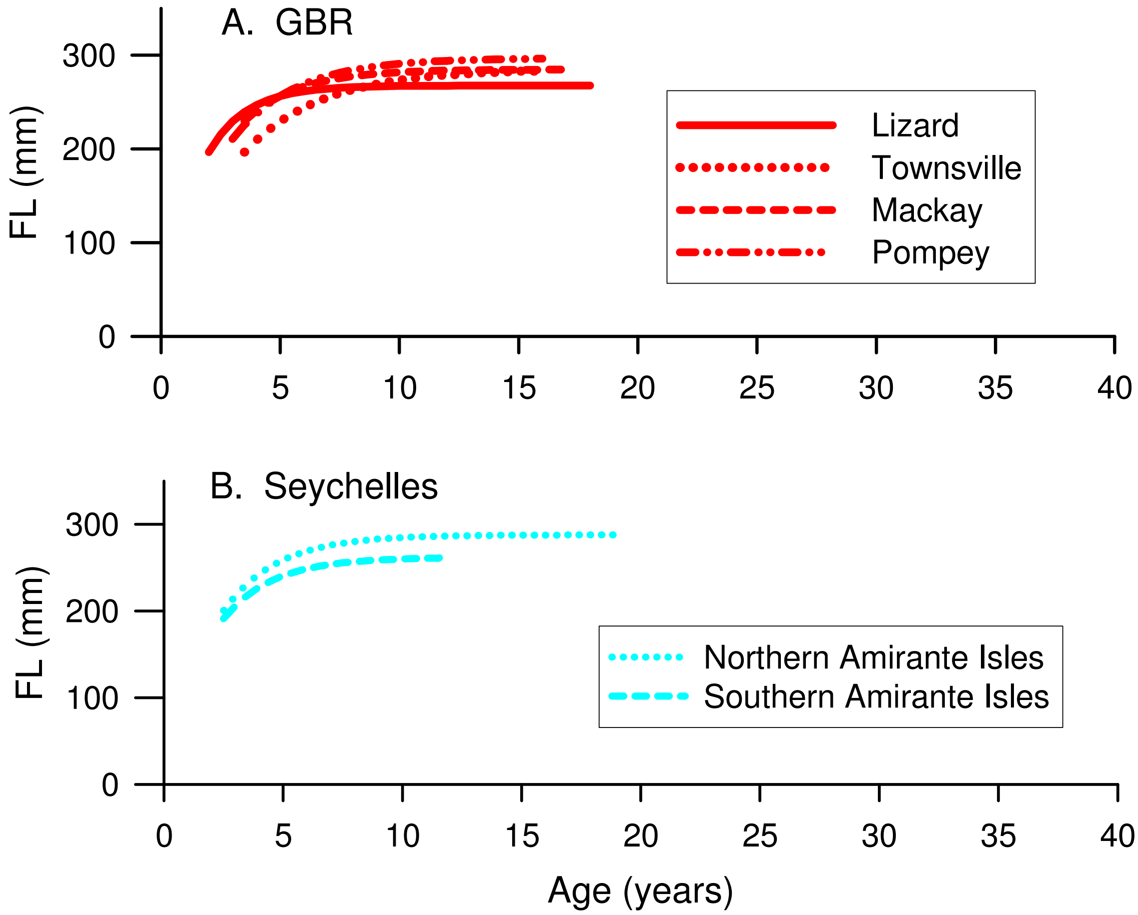


Figure 4.6 Regional comparisons of fitted VBGF for *E. fasciatus* from broad regions of (A) the GBR and (B) the Seychelles.

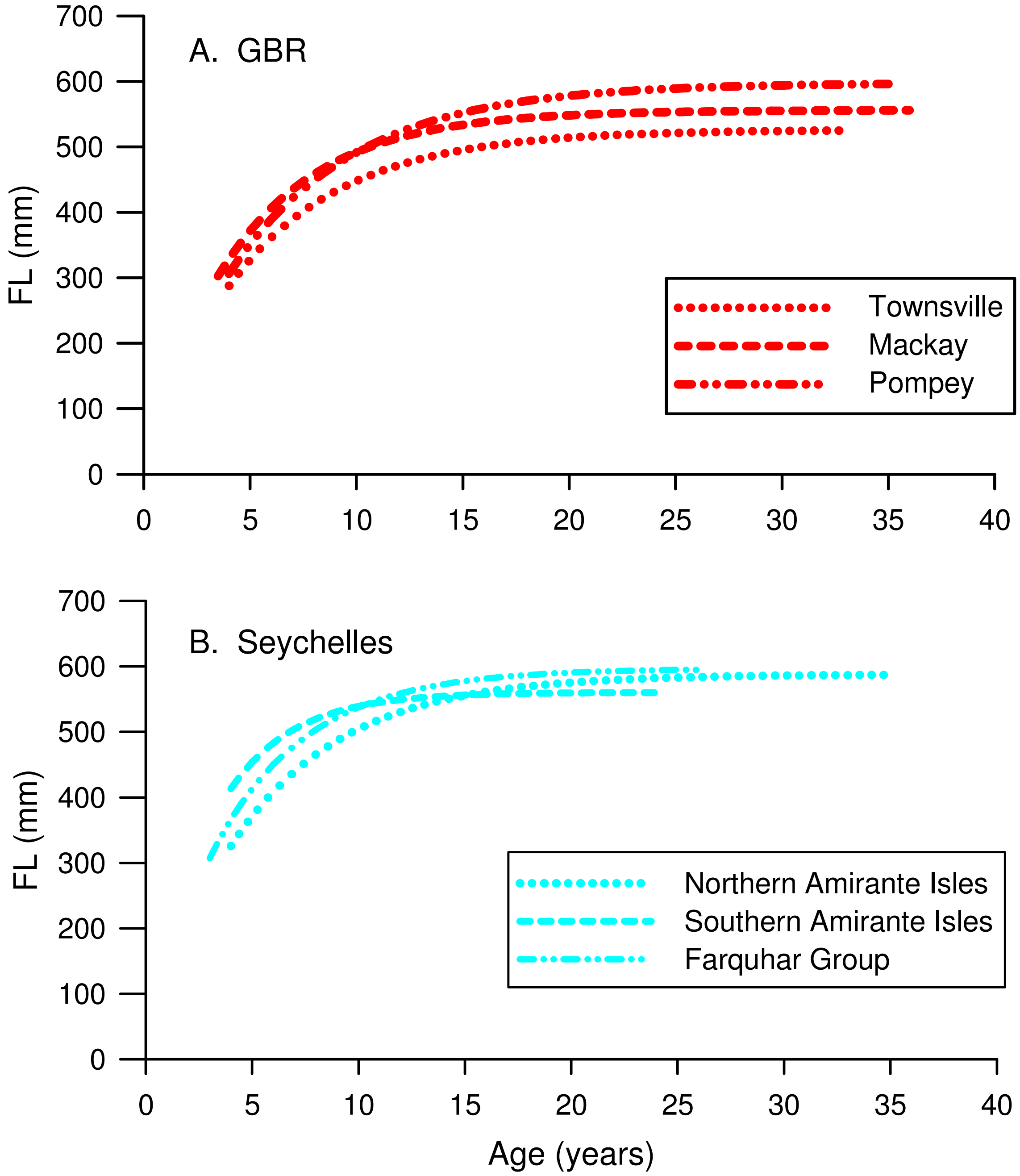


Figure 4.7 Regional comparisons of fitted VBGF for *E. polyphekadion* from broad regions of (A) the GBR and (B) the Seychelles.

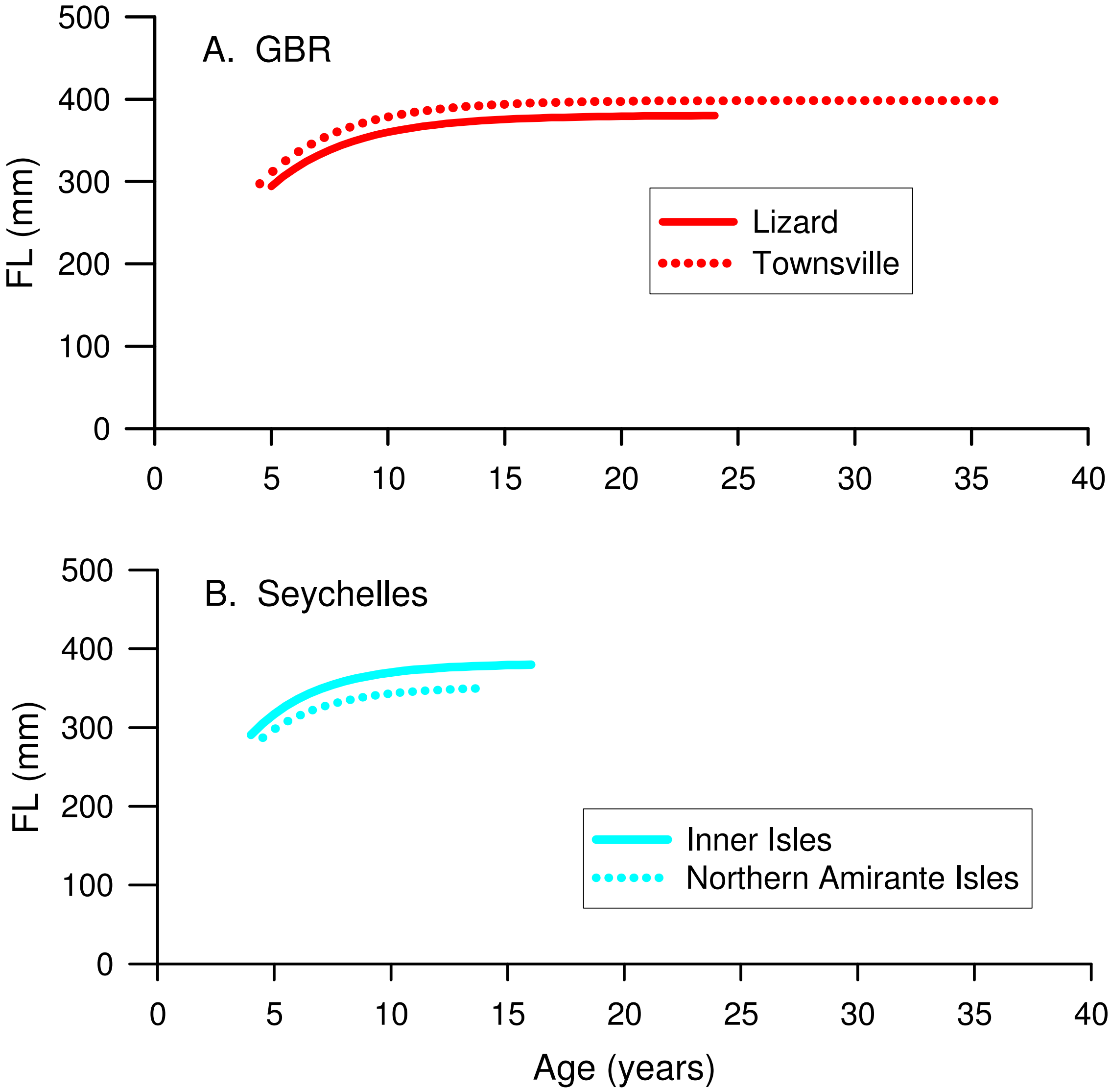


Figure 4.8 Regional comparisons of fitted VBGF for *C. argus* from broad regions of (A) the GBR and (B) the Seychelles.

Table 4.6 Results of likelihood ratio tests comparing estimates of von Bertalanffy Growth Function parameters for harvested components of *E. fasciatus, E. polyphekadion* and *C. argus* from broad regions within the GBR and the Seychelles. χ^2 = likelihood ratio Chi-squared statistic, p = probability of the data if no difference existed, df = degrees of freedom. "Age range" indicates the common age range used for comparisons.

Species	Area/Broad Region	Age range (yrs)	Comparison	df	χ^2	p
E. fasciatus	GBR	4 – 16	All broad regions (n=4)	9	50.11	**<0.001**
			Lizard vs Townsville	3	25.00	**<0.001**
			Lizard vs Mackay	3	15.58	**0.001**
			Lizard vs Pompey	3	24.42	**<0.001**
			Townsville vs Mackay	3	13.20	**0.004**
			Townsville vs Pompey	3	4.27	0.234
			Mackay vs Pompey	3	11.19	**0.011**
	Seychelles	3 – 12	All broad regions (n=2) i.e. N. Amirantes vs S. Amirantes	3	8.61	**0.035**
	GBR & SEZ	3 –18	GBR vs Seychelles	3	8.47	**0.037**
E. *polyphekadion*	GBR	4 – 33	All broad regions (n=3)	6	30.25	**<0.001**
			Townsville vs Mackay	3	26.39	**<0.001**
			Townsville vs Pompey	3	25.60	**<0.001**
			Mackay vs Pompey	3	2.75	0.432
	Seychelles	4 – 24	All broad regions (n=3)	6	15.52	**0.016**
			N. Amirantes vs S. Amirantes	3	21.04	**<0.001**
			N. Amirantes vs Farquhar	3	0.40	0.941
			S. Amirantes vs Farquhar	3	9.35	**0.025**
	GBR & SEZ	4 – 35	GBR vs Seychelles	3	56.63	**<0.001**
C. argus	GBR	3 – 24	All broad regions (n=2) i.e. Lizard vs Townsville	3	6.34	0.096
	Seychelles	3 – 14	All broad regions (n=2) i.e. Inner Isles vs N. Amirantes	3	13.77	**0.003**
	GBR & SEZ	3 – 16	GBR vs Seychelles	3	13.31	**0.004**

4.4.3 Multivariate demographic indices

The PCAs showed clear separation of the GBR and the Seychelles on PC1 for *E. fasciatus, E. polyphekadion* and *C. argus* (Fig. 4.9), indicating distinct demographic profiles for each species from the two areas. Broad regions were separated on each of the first two principal components for each species. PC1 and PC2 together accounted for 90.5%, 86.0% and 96.9% of the total variability for *E. fasciatus, E. polyphekadion* and *C. argus,* respectively, and were therefore considered to give a good representation of the data with relatively little loss of explanatory information.

The demographic parameters contributing most to PC1, and hence to the separation of areas, were density and the age-based parameters (mean age, age richness, longevity) for *E. fasciatus,* a combination of age- and size-based parameters for *C. argus* (mean age, age richness, longevity, mean size, size richness, max. size), and some non-age-based parameters for *E. polyphekadion* (mean size, size richness, max. size, density, growth, Fig. 4.9).

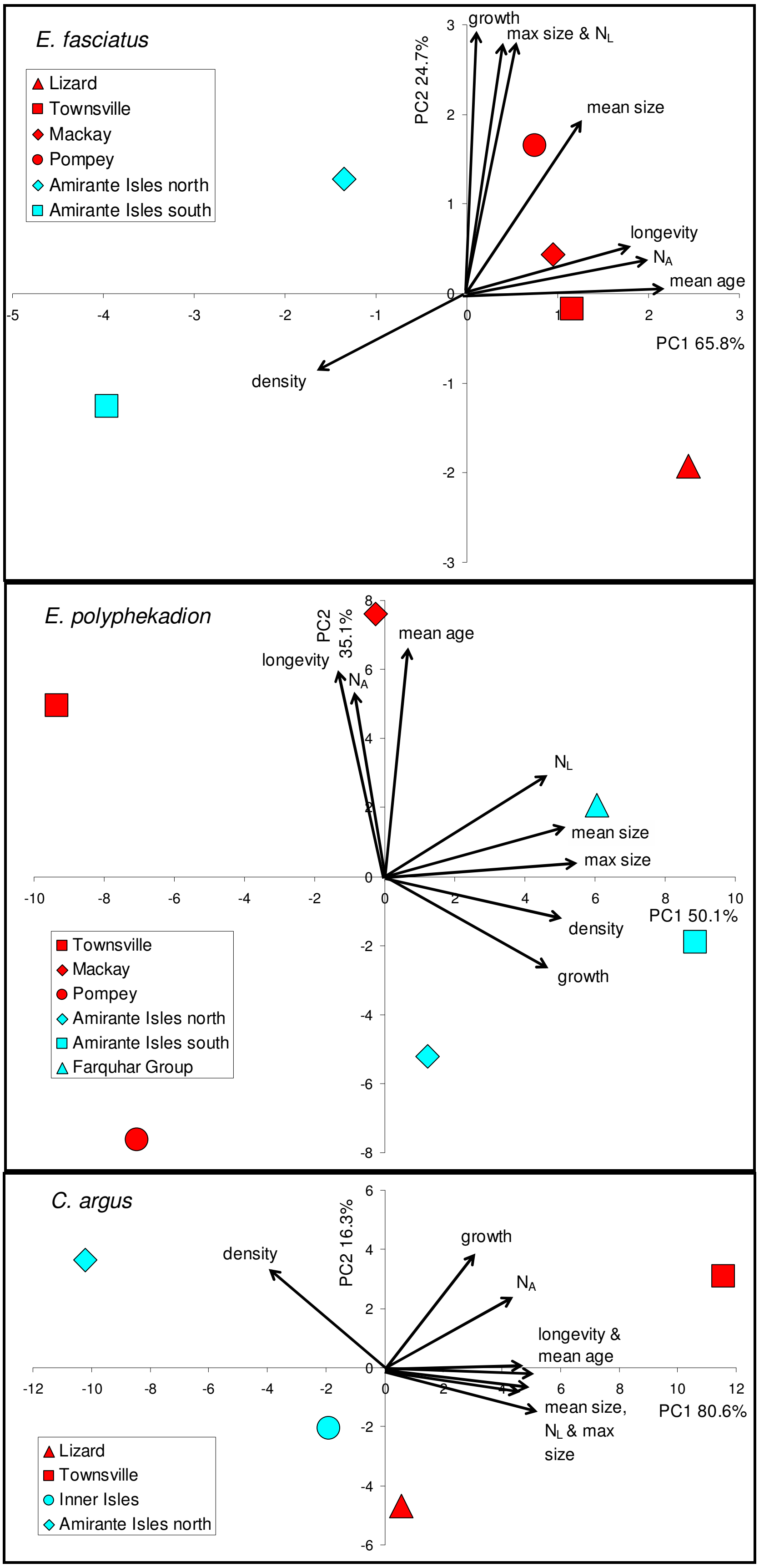


Figure 4.9 Multivariate demographic and abundance patterns for *E. fasciatus* (top), *E. polyphekadion* (middle) and *C. argus* (bottom) from the GBR and the Seychelles using PCA. Note the relative length and direction of vectors are informative but the absolute length is not, because of multiplication for ease of display.

Populations of *E. fasciatus* in the GBR tended to have older individuals, longer lifespans but lower densities than in the Seychelles. Populations of *C. argus* in the GBR tended to have older and larger individuals, greater maximum size and longer lifespans than in the Seychelles. Populations of *E. polyphekadion* in the GBR tended to have smaller individuals, lower maximum size, lower density and slower growth than in the Seychelles.

Regional-scale patterns in demographics were also marked and the patterns again differed among species, indicating complex spatial variability in demographics and that some regions within each area were as similar or more similar to regions in the other area than other regions in the same area. For example, *E fasciatus* in the northern Amirantes Isles region were demographically more similar to those in the Pompey, Mackay and Townsville regions than to *E. fasciatus* from the southern Amirantes Isles region (Fig. 4.9). Similarly, *C. argus* from the Inner Isles (Seychelles) and Lizard (GBR) regions were more similar to each other than to *C. argus* from either the northern Amirantes Isles (Seychelles) or Townsville (GBR) regions.

Similarities in the relationship between individual demographic parameters (i.e. angular patterns of vectors) were noted for *E. fasciatus* and *C. argus* (Figs. 4.10). High density was associated with low values of both size- and age- based parameters for both species and for *E. fasciatus* also slower growth. In contrast, relatively high density was associated with larger size and faster growth for *E. polyphekadion* (Fig. 4.9).

4.4.4 Mean size and age

ANOVA results for the comparisons of mean size and age are summarised in Table 4.7. For *E. fasciatus*, there was a significant effect of broad region nested in area on mean size due to differences between broad regions within the GBR (Table 4.8 Lizard < Mackay and Pompey; and Townsville < Pompey) but mean sizes (± S.E.) were not significantly different for the southern and northern Amirante Isles of the Seychelles (240 ± 3.2 and 255 ± 5.9 mm, respectively) although mean size in the southern Amirante Isles was the lowest recorded for any region. Both the mean size and age of *E. fasciatus* were lower in the Seychelles (247 ± 3.6 mm, 6.1 ± 0.6 yrs) than the GBR (272 ± 1.8, 10.7 ± 0.3 yrs) (significant main effects of area, Table 4.7).

Table 4.7 Analysis of variance comparing mean size and age of *E. fasciatus, E. polyphekadion* and *C. argus* among broad regions and areas. df = degrees of freedom, p = probability of the data if no difference existed. Areas and Broad Regions indicated on Fig. 4.3.

Species	Variable	Source of variation	df	Mean Square	F-ratio	p
E. fasciatus	Mean size	Area	1	21195.153	8.620	**0.036**
		Broad Region(Area)	4	3552.445	7.351	**<0.001**
		Residual	257	483.227		
E. fasciatus	Mean age	Area	1	700.424	28.225	**0.002**
		Broad Region(Area)	4	31.212	2.354	0.054
		Residual	257	13.261		
E. polyphekadion	Mean size	Area	1	52751.848	2.400	0.192
		Broad Region(Area)	4	25154.814	5.280	**<0.001**
		Residual	285	4764.292		
E. polyphekadion	Mean age	Area	1	54.826	0.473	0.525
		Broad Region(Area)	4	128.289	2.654	**0.033**
		Residual	285	48.341		
C. argus	Mean size	Area	1	8943.464	1.226	0.381
		Broad Region(Area)	2	7727.082	4.885	**0.009**
		Residual	148	1581.945		
C. argus	Mean age	Area	1	342.459	7.921	0.093
		Broad Region(Area)	2	43.845	1.249	0.290
		Residual	148	35.094		

Table 4.8 Results from Tukey's test for mean size of *E. fasciatus.* Mean lengths shown in mm (± S.E.).

lowest			*highest*
Lizard	Townsville	Mackay	Pompey
259 (±4.5)	269 (±3.7)	276 (±2.2)	285 (±3.4)

Table 4.9 Results from Tukey's test for mean size of *E. polyphekadion.* Mean lengths shown in mm (± S.E.).

lowest		*highest*	*lowest*		*Highest*
Townsville	Pompey	Mackay	Amirante Isles north	Farquhar	Amirante Isles south
448 (±6.4)	454 (±11.5)	490 (±11.2)	464 (±11.1)	508 (±10.3)	514 (±16.7)

Table 4.10 Results from Tukey's test for mean age of *E. polyphekadion.* Mean ages shown in yrs (± S.E.).

lowest		*highest*	*lowest*		*Highest*
Pompey	Townsville	Mackay	Amirante Isles north	Amirante Isles south	Farquhar
10 (±1.2)	12 (±0.6)	14 (±1.1)	10 (±1.1)	12 (±1.7)	12 (±1.0)

There was a significant effect of broad region nested in area on both mean size and age of *E. polyphekadion*, indicating broad-scale variability for these variables (Tables 4.9 & 4.10. Mean size: Townsville < Mackay; Amirante Isles north < Farquhar Group. Mean age: Pompey < Mackay).

Mean size also varied among broad regions for *C. argus*, (significant effect of broad region nested in area, Table 4.7), but mean age did not. The size results were due to smaller *C. argus* on average in the northern Amirante Isles (331 ± 6.0 mm) than the Inner Isles of the Seychelles (355 ± 5.1 mm), whereas *C. argus* from the Lizard and Townsville regions of the GBR did not differ significantly in mean size (351 ± 11.0 and 371 ± 5.0 mm, respectively).

Table 4.11 Analysis of variance comparing mean maximum size and 10% longevity of *E. fasciatus, E. polyphekadion* and *C. argus* among broad regions and areas. df = degrees of freedom, p = probability of the data if no difference existed.

Species	**Variable**	**Source of variation**	**df**	**Mean Square**	**F-ratio**	**p**
E. fasciatus	Mean maximum size	Area	1	2.792	0.004	0.951
		Broad Region(Area)	4	860.914	56.996	**<0.001**
		Residual	21	15.105		
E. fasciatus	10% longevity	Area	1	38.164	2.303	0.201
		Broad Region(Area)	4	21.166	14.066	**0.000**
		Residual	21	1.505		
E. polyphekadion	Mean maximum size	Area	1	17221.467	6.632	0.055
		Broad Region(Area)	4	2909.702	3.128	**0.032**
		Residual	25	930.140		
E. polyphekadion	10% longevity	Area	1	94.959	0.961	0.376
		Broad Region(Area)	4	110.171	2.894	**0.043**
		Residual	25	38.075		
C. argus	Mean maximum size	Area	1	3609.089	2.544	0.251
		Broad Region(Area)	2	1423.024	3.512	0.066
		Residual	11	405.242		
C. argus	10% longevity	Area	1	450.671	14.872	0.056
		Broad Region(Area)	2	33.149	4.395	**0.043**
		Residual	10	7.542		

4.4.5 Maximum size and longevity

The mean maximum size varied significantly at the regional scale for *E. fasciatus* and *E. polyphekadion* but no significant differences were detected for *C. argus* (Table 4.11). Table 4.12 shows that for *E. fasciatus,* mean maximum sizes in the GBR showed a north – south trend with means for Lizard, Townsville and Mackay lower than for Pompey; and the mean for Lizard was lower than for Mackay; and in the Seychelles mean maximum size was lower for the southern Amirante Isles (280 ± 1.7 mm) than for northern Amirante Isles (320 ± 2.7 mm). For *E. polyphekadion*, the regional effect was due to differences within the GBR where mean maximum size for Townsville was lower than for Mackay (Table 4.13).

Table 4.12 Results from Tukey's test for mean maximum size of *E. fasciatus* from the GBR. Mean maximum sizes shown in mm (± S.E.).

lowest			*highest*
Lizard	Townsville	Mackay	Pompey
290 (±2.7)	297 (±1.9)	302 (±1.2)	315 (±1.9)

Table 4.13 Results from Tukey's test for mean maximum size of *E. polyphekadion.* Mean maximum sizes shown in mm (± S.E.).

lowest		*highest*	*lowest*		*highest*
Townsville	Pompey	Mackay	Amirante Isles north	Amirante Isles south	Farquhar
552 (±8.8)	564 (±13.6)	606 (±15.2)	607 (±15.2)	636 (±21.6)	642 (±15.2)

The estimates of 10% longevity varied significantly at the regional scale for all three species (Table 4.11). The 10% longevity estimate for *E. fasciatus* at the Lizard region was significantly greater than other broad regions of the GBR (Table 4.14) and in the Seychelles the 10% longevity estimate for the southern Amirante Isles (10 ± 0.5 yrs) was lower than for the northern Amirante Isles (17 ± 0.9 yrs). The regional effect for *E. polyphekadion* was again due to the GBR, where 10% longevity in the Pompey region was lower than that in the Mackay region (Table 4.15). *C. argus* were shorter-lived at Lizard (23 ± 1.9 yrs) than Townsville (32 ± 1.1 yrs), but 10% longevities were similar for the Inner Isles and northern Amirante Isles of the Seychelles (15 ± 1.3 and 13 ± 1.5 yrs, respectively). Although no significant effect for area was found, the size-at-age data indicated that there tended to be fewer old fish caught in the Seychelles than the GBR (Fig. 4.5).

Table 4.14 Results from Tukey's test for 10% longevity of *E. fasciatus.* Mean 10% longevity estimates shown in yrs (± S.E.).

lowest			*highest*
Townsville	Mackay	Pompey	Lizard
15 (±0.6)	16 (±0.4)	16 (±0.4)	18 (±0.9)

Table 4.15 Results from Tukey's test for 10% longevity of *E. polyphekadion.* Mean 10% longevity estimates shown in yrs (± S.E.).

lowest		*highest*	*lowest*		*highest*
Pompey	Townsville	Mackay	Farquhar	Amirante Isles south	Amirante Isles north
20 (±2.8)	29 (±1.8)	34 (±3.1)	23 (±3.1)	24 (±4.4)	25 (±3.1)

4.4.6 Comparative growth estimates

ANOVA results for the comparisons of mean size at particular ages are summarised in Table 4.16. The mean size-at-initial-age varied significantly at the regional scale for all three species, whereas no significant differences were found among broad regions or areas in the proxies for growth at other ages. These results should be treated with caution, however, until larger sample sizes are available. Table 4.17 indicates for *E. fasciatus* that mean size-at-initial-age at Lizard was lower than for the Mackay and Pompey regions and the mean for the Townsville region was lower than for the Pompey region. Tukey's tests did not detect any significant differences among broad regions of either area for *E. polyphekadion.* Mean size-at-initial-age for *C. argus* from Lizard (245 ± 10.4 mm) was lower than for Townsville (307 ± 18.0 mm).

Table 4.16 Analysis of variance comparing mean size at particular ages of *E. fasciatus, E. polyphekadion* and *C. argus* among broad regions and areas. df = degrees of freedom, p = probability of the data if no difference existed. Depiction of size-at-ages parameters given in Fig. 4.4.

Species	Variable	Source of variation	df	Mean Square	F-ratio	p
E. fasciatus	Mean size-at-initial-age	Area	1	26.589	0.015	0.910
		Broad Region(Area)	3	1340.266	4.478	**0.015**
		Residual	19	299.284		
E. fasciatus	Mean size-at-mode-age	Area	1	75.884	0.263	0.617
		Broad Region	3	559.675	2.634	0.077
		Residual	21	212.511		
E. fasciatus	Mean size-at-later-age	Area	1	260.353	1.054	0.331
		Broad Region(Area)	4	344.784	2.058	0.155
		Residual	11	167.497		
E. polyphekadion	Mean size-at-initial-age	Area	1	13831.891	2.221	0.200
		Broad Region(Area)	4	7342.399	3.326	**0.024**
		Residual	27	2207.860		
E. polyphekadion	Mean size-at-mode-age	Area	1	11683.685	3.930	0.081
		Broad Region(Area)	4	3886.091	1.956	0.121
		Residual	39	1987.105		
E. polyphekadion	Mean size-at-later-age	Area	1	6114.220	3.406	0.104
		Broad Region(Area)	4	2244.692	1.880	0.134
		Residual	38	1194.292		
C. argus	Mean size-at-initial-age	Area	1	3573.046	0.883	0.439
		Broad Region(Area)	2	5314.278	8.182	**0.002**
		Residual	26	649.491		
C. argus	Mean size-at-mode-age	Area	1	193.395	0.246	0.650
		Broad Region(Area)	2	807.192	1.101	0.351
		Residual	21	733.442		
C. argus	Mean size-at-later-age	Area	1	1.481	0.003	0.962
		Broad Region(Area)	2	498.857	0.505	0.616
		Residual	12	987.833		

Table 4.17 Results from Tukey's test for mean size-at-initial-age of *E. fasciatus* from the GBR. Mean size-at-initial-age shown in mm (± S.E.).

lowest			*highest*
Lizard	Townsville	Mackay	Pompey
235 (±8.6)	244 (±10.0)	274 (±6.1)	282 (±7.7)

4.5 Discussion

Comparative analyses of three species of cryptic serranids, *E. fasciatus, E. polyphekadion* and *C. argus,* from several broad regions of the GBR and the Seychelles demonstrated biogeographic-scale spatial variation in demographics. Each species showed pronounced differences in multivariate demographic indices between the GBR and the Seychelles. Regional scale (100's to 1000's km) variation was also apparent for each species in both multivariate and univariate analyses. These strong patterns of variation may signify locally varying population dynamics and productivity, and should be considered in fisheries and conservation assessments. Furthermore, our ability to apply the demographic findings to other populations or species may be limited, even for closely related or ecologically similar species (e.g. among the cryptic serranids). Unravelling the influence of fishing on the observed patterns is difficult, however, and could only partly be resolved.

4.5.1 Size-age-density relationships

Relationships among parameters were not consistent among species, despite the marked separation of the GBR and the Seychelles in multivariate analyses for each species. Multivariate demographic indices separating areas differed in nature among species, as did size-age-density relationships. If persistent, this finding suggests underlying differences in the relative importance of processes structuring local populations of each species (Jones 1991). Proximate causal factors for differences in demography between populations may include some combination of intraspecific density, habitat, temperature or other environmental factors, diversity and density of local community and hence degree of predation and competition, recruitment, mortality, movement or other behavioural processes (Beverton & Holt 1957, Weatherley & Gill 1987, Conover & Present 1990, Doherty 1991, Hixon 1991a, Jones 1991, Williams 1991, Shapiro et al. 1994, Choat & Robertson 2002, Williams 2003, Ackerman 2004).

Size and age characteristics of the two high abundance species, *E. fasciatus* and *C. argus,* varied with density in patterns consistent with density dependence, but size and age characteristics of *E. polyphekadion* did not. Conversely, unless the effects of fishing differ to those normally expected, it seems unlikely that direct fishing effects would explain patterns for *E. fasciatus* or *C. argus* (Jennings & Lock 1996, Jennings & Kaiser 1998). The degree to which (if at all) high local densities reflect indirect effects of fishing (e.g. increased biomass of non-target species in response to the removal of their predators by fishing, Jennings & Kaiser 1998) is not clear since we lack information on the status of local predators from other families. However, densities of larger epinepheline serranids (which include smaller serranids in their diets) were relatively high in the same regions that high densities of cryptic serranids were found (Chapter 3), consistent with the presumed low fishing pressure. Hence, indirect effects of fishing seem unlikely. Observed size-age-density relationships suggest density dependent mortality and recruitment may contribute to the patterns for *E. fasciatus* and *C. argus*, since not just size but longevity and average age were reduced at high densities. For *E. fasciatus,* there was also slight evidence of reduced adult size-at-age, the proxy of growth, at higher densities, indicating density dependent growth may be influential for that species.

There is little information to assess the prevalence of density dependent mortality in adult reef fishes since most experiments have focused on juveniles (e.g. Doherty 1982, 1983, Hixon & Carr 1997, Connell 2000, Booth & Alquezar 2002). Density dependence in adult fishes is considered more likely to affect growth and development than mortality (Bystrom & Garcia-Berthon 1999, Lorenzen & Enberg 2002), but reduced growth and increased mortality of scarids at high densities on outer shelf compared to mid shelf reefs of the northern GBR were also suggested to be the result of density dependent processes (Gust et al. 2002, Gust 2004). Density dependent mortality and growth may be more common during the early part of fish life cycles (Cushing 1975, 1995, Shima 2001, Holbrook & Schmitt 2002). Even slight fitness advantages in early life history stages may enhance growth and survival, and so could be reflected in adult traits (Kerrigan 1996, McCormick 1998, Bergenius et al. 2002, Booth & Alquezar 2002, Wilson & Meekan 2002, McCormick & Hoey 2004).

The suggestion of differing relationships between density and demographics among species by this study is consistent with results from a series of small-scale field experiments (Forrester & Steele 2000), although the spatial scales considered are markedly different. The experiments done on patch reefs by Forrester and Steele (2000) identified variation in the presence and cause of density-dependent mortality in three closely-related species of reef fishes (gobies). Density dependence in *Lythrypnus dalli* resulted from mortality inflicted by predatory fishes, density dependence in *Coryphopterus glaucofraenum* was caused at least in part by an interaction other than predation, and survival of *C. nicholsii* was independent of density (Forrester & Steele 2000). For *E. fasciatus* and *C. argus,* an experimental approach is required to verify whether density dependence is important and determine the life stage(s) and scales over which it acts, if present.

Higher densities of *E. polyphekadion* (although still less than 1 per 1000 m^2) were associated with increased size and growth characteristics, suggesting conditions were more favourable in the broad regions where density was greatest (Farquhar Group and southern Amirante Isles, both atolls). It may be that more oceanic conditions provide a size or growth advantage for this species, and Randall and Heemstra (1991) noted this species was more common at atolls than high islands. The higher densities and size, however, also corresponded to presumed low fishing pressure within the Seychelles. Spawning aggregations of *E. polyphekadion* have occasionally been fished in at least one of the broad regions with relatively high densities and sizes (Robinson et al. 2004b), so the presumed fishing gradient (i.e. highest near the major human population centres on the Inner Isles (Mahe Plateau), and decreasing to the south, Chapter 3) may not represent actual fishing mortality. Unfortunately, no accurate species-specific fishery data for the study locations or data on the species biology in the certain absence of fishing are available. Thus, it cannot be resolved categorically whether greater size and density in the southern Seychelles regions are the result of presumed lower fishing activity or natural regional variability in environmental conditions, or both.

4.5.2 Demographic characteristics

Some demographic characteristics were similar for each of the three species of cryptic serranids across all spatial scales, despite differing abundance profiles and maximum body sizes. These species are relatively slow growing as it takes 5 to 10 years on average to reach adult sizes. A distinctive pattern of growth was shared by all species, with most growth occurring during approximately the first quarter of their lifespan. A corollary of this type of growth is that size is not a useful proxy for age in these fishes since size is relatively static over much of the adult lifetime. Comparable patterns of growth have previously been described for other species of cryptic serranids (e.g. *Cephalopholis cyanostigma*, Mosse 2002), suggesting that these genera might indeed have characteristic patterns of growth, as found for a number of other reef fish taxa (Choat & Robertson 2002).

A notable difference among the species was the shorter longevity of *E. fasciatus,* which was about half that of *E. polyphekadion* and *C. argus.* There was also a general trend for each species of fewer old fish, and hence reduced longevities, in the Seychelles compared to the GBR (Fig. 4.5), consistent with findings from a recent broad-scale study of a coral reef surgeonfish, *Ctenochaetus striatus,* across the Indo-Pacific (Laman Trip 2004). Although further research is required to confirm the generality and causes of these observations, reduced longevity despite larger-sized fish for *E. polyphekadion* in the Seychelles compared to the GBR suggests that fishing effects are unlikely to be the only or major driver of the observed demographic patterns. In addition to truncation of age structures by fishing (e.g. Ferreira & Russ 1995), shorter-lived populations of reef fishes may result from natural variation (e.g. Gust et al. 2002).

Varying longevities may have consequences for population turnover rates and hence productivity and fishery yield, with faster turnover, earlier maturation and higher potential rates of population increase for shorter lived species or populations (Gulland 1988, Hilborn & Walters 1992, Kirkwood et al. 1993). Hence, increased longevity is thought to be associated with increased vulnerability to over-harvesting (Jennings et al. 1998, Huntsman et al. 1999, Musick 1999b). Longevity may also influence reproduction, with increased reproductive lifespan but delayed maturity expected for longer lived species or populations (Crouse 1999, Musick 1999a). Because reproductive data were not available in this study of cryptic serranids, the relationships between longevity and reproduction could not be tested. It is also very difficult to meaningfully compare reproductive output between species because numerous factors could be involved. However, the findings of the in-depth study of *E. fuscoguttatus,* a large mobile serranid, in Chapters 5 and 6 are generally consistent with these expectations. Biogeographic-scale variation noted here in lifespans between and within the GBR and the Seychelles (if it is at least in part a natural effect) supports the view that there may be fundamental differences in reef fish population dynamics and processes at an area and or regional level (Sale 1991b).

4.5.3 Pattern and magnitude of variation

It seems likely that some observed differences in size and age characteristics will be of sufficient magnitude to have real influences on individuals and populations as demographic rates and reproductive output or success may be size/age dependent (Hislop 1988, Roff 1992, Stearns 1992, Gunderson 1997, Trippel et al. 1997, Caley 1998, Vincent & Sadovy 1998, Berkeley et al. 2004a). For example, population turnover is expected to be higher in areas or broad regions where longevity is shorter and there is a larger proportion of young fish. For *E. fasciatus,* the 10% longevity estimate in the southern Amirante Isles was 7 yrs lower than for the northern Amirante Isles, and 5 to 8 yrs lower than for any region in the GBR. Thus, relatively high turnover is expected for *E. fasciatus* in the southern Amirante Isles, which in turn may give higher regional productivity. Conversely, individual fecundity may be lower for *E. fasciatus* where fish reach smaller maximum sizes (i.e. southern Amirante Isles), as fecundity typically increases with body size (Roff 1992); the mean maximum size was 12% (40 mm) lower for the southern Amirante Isles than for northern Amirante Isles. However, total egg production will be influenced by the number of spawners, individual fecundity and spawning frequency, and so potential reproductive output and productivity may vary regionally in response to size and density. As a further example, the 10% larger average size and approximately two-fold density increase for *E. polyphekadion* in the Mackay region compared to the Townsville region may result in greater reproductive output from the Mackay region, as also suggested by a recent GBR study of the red throat emperor, *Lethrinus miniatus* (Williams 2003). Any patterns may be complex, however, as other reproductive characteristics such as the timing of maturation, the size of the effective spawning population, and quality of eggs and larvae may also vary regionally or with size and age and be potentially influenced by density dependent resource limitation at higher densities (Pollock

1984, Chambers & Leggett 1996, Kjesbu et al. 1996, Marteinsdottir & Steinarsson 1998, Trippel 1998, Crouse 1999).

Size- and age-based characteristics appeared to be more variable than growth. Limited differences in size-at-age, the proxy used for growth rates, may be a result of small sample sizes and substantial individual variation, as significant regional differences were apparent in growth of the average individual within the population (represented by the growth curves) over the lifespan. The extent to which any growth differences are biologically meaningful, however, could not be resolved. Comparisons of growth curves using the likelihood ratio test are highly sensitive to even small variations among samples (Kimura 1980).

4.5.4 Vulnerability to fishing

The three species of cryptic serranids, *E. fasciatus, E. polyphekadion* and *C. argus,* share some intrinsic factors associated with high vulnerability to fishing (relatively slow growth and moderate to long lifespans), but differences among them in abundance, longevity and body size, and perhaps in population dynamics, suggest vulnerabilities may vary. Based on this limited set of abundance and demographic parameters, *E. fasciatus* would appear the least vulnerable of the three, but is also of least importance commercially because of its small body size. The relatively low commercial value of small cryptic serranids such as *E. fasciatus* and, to a lesser extent, *C. argus* in fisheries such as the Queensland reef line fishery, however, means that discarding and post-release survival are likely to be significant issues for these species, particularly under regulation by commercial quotas and recreational bag limits. Relatively low natural abundances of *E. polyphekadion*, combined with its importance for commercial fishing (Sadovy et al. 2003b) and transient spawning aggregation behaviour, mean this species may be particularly vulnerable to depletion by aggregation fishing (Sadovy et al. 1994, Coleman et al. 1996, Rhodes & Sadovy 2002b, a). It is not yet clear to what extent, if at all, the two smaller study species also form transient spawning aggregations, but as larger (preferred target) species decline, these and other small bodied cryptic serranids may be subject to increased fishing pressures (e.g. as noted for the small bodied rockcod *Cephalopholis boenak* in Hong Kong, Chan & Sadovy 2002). In addition to fisheries issues, depleting these predatory fishes may have cascading ecological effects on coral reefs (Russ 1991, Jennings & Lock 1996, Carr et al. 2002, Bellwood et al. 2004, Myers & Worm 2005).

4.5.5 Future research directions

A limitation of broad-scale studies of demography is possible confounding in the comparisons of demographic parameters with unmeasured effects such as fishing mortality, recruitment rates or habitat variables (Choat & Robertson 2002). Further study of potential fishing effects on the demography of these species is warranted, given the inference of fishing effects in abundance patterns among similar locations (Chapter 3), but small sample sizes and lack of species-specific fishing data prevented more in-depth analyses. Recruitment, mortality or reproductive data are not yet available for these species from the GBR or the Seychelles, but region-specific information on recruitment rates, mortality rates, maturity, sexual pattern and egg production would be important for further exploration of population dynamics and productivity. Detailed recruitment surveys would provide the best estimates of the contribution of recruitment to pattens of abundance and demography (Williams et al. 1994, Robertson & Kaufmann 1998), though the difficulty experienced in finding small individuals of *C. argus* and *E. polyphekadion* in spear fishing suggests that these species may be recruiting to habitats different from those inhabited by adults. *E. fasciatus* as small as 36 mm FL were sampled on the surveyed reefs, and some juveniles and adults were observed in close proximity (<1 m) during visual surveys, suggesting that *E. fasciatus* recruits to adult habitats, and therefore may be a good candidate for further research on recruitment. Identification of critical habitats and associated life stages for epinepheline serranids and other reef fishes is a research priority. Examination of correlations between habitat variables and the observed patterns of abundance and demographics would allow quantification of the proportion of variation attributable to habitat, and is planned for future collaborative work. Sampling additional broad regions within these areas, and additional areas in the Indian and Pacific Oceans, would help determine the generality of observed patterns and allow examination of ocean-scale patterns. Since little is know about Indo-Pacific large mobile serranids, despite their interest to fisheries and conservation, study of the demography and reproduction of large mobile serranids (Chapters 5 & 6) is needed to give a more complete picture of tropical epinepheline serranids.

4.5.6 Conclusions

Our ability to generalise about demographic characteristics of the cryptic serranids behavioural group is likely to be limited because of the substantial variation found among species and populations. Provisional analysis above suggests *E. polyphekadion* may be the more vulnerable to fishing of the three species. Collective analysis of a suite of demographic parameters revealed distinct profiles between the GBR and the Seychelles for each species, despite strong regional variation within these areas and a lack of difference between areas once regional variation was accounted for in some demographic parameters when examined in isolation. This study also provided further indications that a range of processes, rather than a single dominant process, are important in governing the structure of reef fish communities (Jones 1991). The relative importance of these processes for local population regulation may differ among the three species, with possible broad-scale compensatory demographic trade-offs dependent on density noted for two of the three species.

Chapter 5. Demography of a large grouper, *Epinephelus fuscoguttatus*, from the Great Barrier Reef: implications for fisheries management

5.1 Synopsis

Epinephelus fuscoguttatus is an example of a large mobile serranid that is widespread throughout the Indo-Pacific and features strongly in the live reef food fish trade and other reef fisheries. I investigated age-specific demographic and reproductive characteristics of *E. fuscoguttatus* from the Great Barrier Reef, Australia and examined implications for resource management. Age, growth, longevity, and the relationships between size or age and female sexual maturity and the recruitment of males into the study population were examined. Age validation using both oxytetracycline marking and edge type analysis demonstrated that a single annulus formed each year. This grouper is long-lived (>40 yrs) and relatively slow growing. The size and age distributions of the sexes strongly suggested protogynous hermaphroditism. Histological data suggested infrequent spawning in small mature females. Females contribute very little to reproductive output until about 566 mm fork length and 9 yrs of age. Larger females make important reproductive contributions during their 30+ yr reproductive lifespan. Their relatively long lifespan, restriction of males to large size groups, and the disproportionate contribution of large females to reproduction have important implications for harvest of *E. fuscoguttatus*. For example, current Queensland size regulations are poorly matched to the species biology since they do not protect the reproductive elements of populations.

5.2 Introduction

Epinepheline serranids, primarily members of the genera *Epinephelus* and *Plectropomus,* bear the brunt of subsistence and commercial reef fisheries in the south-western Pacific (Heemstra & Randall 1993, Bentley 1999). Recent increases in catches are largely attributable to the live reef fish trade (Ayling et al. 2000, Sadovy et al. 2003b). Age-based demographic studies of *Plectropomus*, primarily *P. leopardus* and *P. maculatus* (coral trouts, Ferreira & Russ 1992, 1994, 1995, Russ et al. 1995) suggest relatively fast growth and moderate lifespans. While these features may provide some resilience in the face of increasing fishing pressure (but see Goeden 1982, Mamauag et al. 2000), the extent to which they are characteristic of other epinepheline serranids is unclear. For example, some smaller epinephelines, such as *Cephalopholis cyanostigma* (bluespotted hind), achieve far greater lifespans (46 yrs, Mosse 2002). The demographic characteristics of large mobile serranids (Chapter 1, Table 1.1), especially Pacific species, are poorly known (Manooch 1987).

Epinepheline serranids have complex patterns of sexual development. Most species are protogynous hermaphrodites, but schedules and patterns of female maturation and male recruitment (i.e. male developmental pathways) vary among species within the subfamily, especially in the diverse assemblages characteristic of coral reefs (Smith 1965, Shapiro 1987, Sadovy & Colin 1995, Adams 2003, Liu & Sadovy 2004a). In the absence of information on lifespans, growth rates and maturation it is difficult to predict the capacity of epinepheline serranids to tolerate fishing pressure.

Epinephelus fuscoguttatus (brown marbled grouper or flowery cod) is an example of a large mobile serranid that reaches approximately one metre in length and is widely distributed in the Indo-Pacific (Heemstra & Randall 1993). Although abundance estimates from the GBR indicate that *E. fuscoguttatus* is locally uncommon (<1 fish 1000 per m^2, Chapter 3), this species is a valuable component of regional fisheries, including the live reef fish trade (Lau & Parry-Jones 1999, Sadovy et al. 2003b), and a favourite of the dive industry because of its large size and iconic status (D. Miller pers com). This species also forms spawning aggregations that are reportedly targeted by fishers (Johannes 1981, Johannes et al. 1999, Robinson et al. 2004b).

In northeastern Australia, *Epinephelus fuscoguttatus* is caught as part of the reef line fishery by commercial and recreational fishers. Almost all (96% in 2003) of the commercial catch in this fishery is from the Great Barrier Reef Marine Park (Andersen et al. 2005). Total commercial catch of all reef fish species peaked in 2001 at just over 4800 tonnes, and since July 2004 has been subject to a total annual commercial quota of 3061 tonnes for all species. Although species-specific catch data are not available for *E. fuscoguttatus*, species composition of commercial line fishing operations was documented during an observer program by the ELF Project in 1996 – 1998 (Mapstone et al. 2001a). *E. fuscoguttatus* made up 1.2% of the total number of fish caught in fishing operations for processed reef fish. Estimates of the total recreational catch of all reef fish species were 2320 tonnes in 1997 and 2460 tonnes in 1999 (Williams 2002), an unknown, but relatively small proportion of which was believed to be *E. fuscoguttatus*.

There are two main reasons why I took an in-depth look at one species of large mobile serranid, *Epinephelus fuscoguttatus,* on the GBR in this study (which forms Chapters 5 and 6). Firstly, the rarity, large body size and research permitting restrictions on collections mean that it is difficult to obtain biological samples for large mobile serranids, and hence it was not possible to examine multiple species or locations. Secondly, there is a particular interest in members of the large mobile serranids from the perspectives of conservation biology and fisheries issues, not least because of their large size and potential vulnerability to depletion

(Sadovy 1997b, Sadovy 1997a, Huntsman et al. 1999, Jennings et al. 1999b, Pogonoski et al. 2002). Consequently, I also included a detailed reproductive component to determine critical information such as maturity patterns (this Chapter), sexual pattern and reproductive cycle (Chapter 6).

In this Chapter, I investigate the age-based demography of *Epinephelus fuscoguttatus* with a focus on longevity, pattern of growth, and size- and age-specific reproductive features. There are two aims in this Chapter. Firstly, to determine age-specific size, growth and maturity characteristics of *E. fuscoguttatus*, as an example of a large mobile serranid (and of the upper size range of the genus), and secondly, to obtain demographic information that is relevant to the management of a group of reef fishes subject to over-fishing (Koslow et al. 1988, Sadovy 1994a, Koenig et al. 1996, Bentley 1999, Huntsman et al. 1999, Musick et al. 2000, Wyanski et al. 2000, Pogonoski et al. 2002, Gimenez-Hurtado et al. 2005).

5.3 Materials and methods

5.3.1 Sample collection

Epinephelus fuscoguttatus were obtained from the GBR, with the majority collected from reefs between 18°20’S and 21°50’S (Fig. 5.1, Table 5.1). Pooling of these samples was necessary because of the low abundance of this species in the GBR (Chapter 3). Sampling was facilitated through commercial reef line fishers between April 2001 and January 2003, and supplemented by samples from research line fishing surveys conducted each austral spring/summer (October – December) from 2000 to 2002 by the ELF Project (Mapstone et al. 2004). Some specimens of *E. fuscoguttatus* were also obtained from the Australian National Spearfishing Association annual competition held between 24 – 28 November 2001 at Centipede, Grub and Broadhurst Reefs. These samples were included because the spear fishers targeted large individuals of each fish species, including the study species, and large individuals were considered under-represented by the ELF surveys because of selectivity characteristics of the fishing gear used. Fork length (FL) of all individuals and total weight of whole fish were recorded to the nearest 1 mm and 10 g, respectively. As the caudal fin of this species is rounded, fork length and total length are equivalent. A length-weight relationship was determined by least squares regression and used to predict total weight of some samples from which the fillets had been removed. Whole gonads were preserved in FAACC (formaldehyde 4%, acetic acid 5%, calcium chloride 1.3%, Samoilys & Roelofs 2000) or 10% formalin (ELF samples) for histological processing. Sagittal otoliths were removed, cleaned and stored dry.

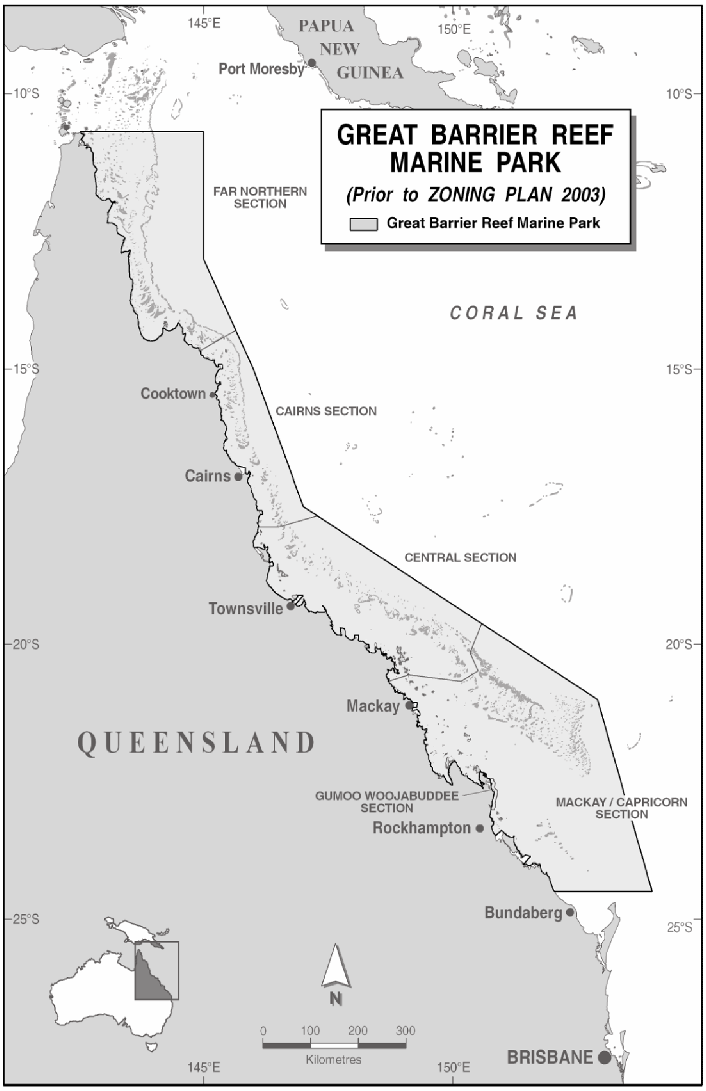


Figure 5.1 Map of northeastern Australia showing the GBR and regions sampled. Specimens of *Epinephelus fuscoguttatus* were obtained from the Cairns (n = 5), Central (n = 108) and Mackay / Capricorn (northern half, n = 129) Sections of the Great Barrier Reef Marine Park (see legend).

Table 5.1 Details of *Epinephelus fuscoguttatus* samples by collection method, month and year. Collection methods: 1=research line fishing, 2=commercial line fishing, 3=recreational spear fishing.

	Sample size by collection method and year							
	1	**1**	**2**	**3**	**1**	**2**	**2**	
Month	**2000**	**2001**	**2001**	**2001**	**2002**	**2002**	**2003**	**Total**
January						7	11	18
February						5		5
March						4		4
April			7			3		10
May			12			2		14
June						5		5
July			11					11
August			9					9
September			9					9
October	5	3	7			1		16
November	27	25	6	25	20	2		105
December		23	8		4	1		36
Total	32	51	69	25	24	27	14	242

5.3.2 Ageing protocol and validation

Age estimates were obtained from thin-sectioned sagittal otoliths (n = 242) because whole otoliths were unreadable (Fig. 5.2A), following methods modified from other otolith-based studies (e.g. Ferreira & Russ 1992, 1994, Choat & Axe 1996, Choat et al. 1996). One of each pair of otoliths was weighed to the nearest 0.1 mg, individually embedded in labelled resin blocks, sectioned through the nucleus using a low-speed diamond wafering saw and the section mounted on a glass slide. All otolith readings were conducted on an image analysis system using transmitted light at 25x magnification. A reference collection of sections (n = 20) covering the full size range of *Epinephelus fuscoguttatus* sampled was produced to establish consensus of age estimates by experienced readers (Campana 2001). Alternating opaque and translucent bands were visible (Fig. 5.2) so it was assumed that one pair of opaque and translucent bands was laid down each year and represented one annulus. Opaque bands were counted along a consistent axis near the sulcus, where the bands were most visible.

Three established validation methods were used to test the assumption that increments were annuli (e.g. Choat & Axe 1996, Fowler & Short 1998, Manickchand-Heileman & Phillip 2000). Firstly, oxytetracycline (OTC) injection was used to mark the otolith to determine the periodicity of increment formation. Because capture rates of *E. fuscoguttatus* are very low (0.17 fish fishing-day^{-1} by commercial line fishers on the GBR) and field tagging and release would have resulted in unacceptably low recapture probabilities, the OTC validation was done using captive individuals (Cappo et al. 2000). Two wild-caught adult *E. fuscoguttatus* were individually tagged, injected with 50 mg kg^{-1} total weight OTC in saline (McFarlane & Beamish 1987), and then maintained in an outdoor aquarium for a growth period of over 1 yr. They were fed a diet of discarded reef fish or commercial bait (fish and crustaceans) three times per week, and could prey on small reef fish in the aquarium. After the growth period, the fish's otoliths were removed and examined for the presence of an OTC mark using a Leica microscope with ultra violet illumination and an image capture facility. Each otolith was also examined at the same magnification using bright field (transmitted) light. The increments formed outside of the OTC mark were counted and measured. The following formula modified from Cappo et al. (2000) was used to determine the periodicity. The distance from the OTC mark to the edge of the otolith (x) is:

$$x = y * G * P,$$

where, y is the distance between increments (presumed annuli) in mm, G is the growth period (yrs), and P is the periodicity of increment formation (yr^{-1}), so that:

$$P = \frac{x}{y * G}$$

Secondly, edge type analysis (Manickchand-Heileman & Phillip 2000) was also used. In this analysis, the monthly frequency of occurrence of otoliths with an opaque or translucent edge was determined to provide further independent evidence of periodicity of increment formation. It was difficult to determine the edge-type for some otoliths because of their inherent variability. These otoliths were classified as uncertain edge-type. The proportion of uncertain edges increased with the putative age of fish and so fish over 12 yrs (n = 65) were excluded from the analysis. The percent of otoliths with opaque edge-types was plotted by month and the monthly frequency of occurrence of opaque edges compared to a uniform distribution by a chi-squared goodness-of-fit test for circular distributions (Zar 1999). Samples were pooled across years by month due to low sample sizes for some months. This assumes that temporal patterns in increment formation were broadly similar among years, as found for other reef fish taxa (e.g. Williams et al. 2005).

Thirdly, the relationship between otolith weight and number of increments was examined using correlation analysis. A strong correlation between otolith weight and putative age (number of increments) was expected if otoliths accreted calcium carbonate throughout the life of the fish (Choat & Axe 1996).

Counts of opaque bands for each section were made on three separate occasions by the author without prior knowledge of the fish's characteristics. Age estimates which coincided for at least two counts, or the median value if the range of age estimates did not differ by more than ± 5% of the median age estimate (e.g. not more than ± 1 yr for age 20 fish) were accepted and used to plot size-at-age. An index of average percent error (APE, Beamish & Fournier 1981) was calculated to assess reproducibility of the age estimates.

5.3.3 Demography

The size and age data were used to estimate mean size, age, and age of the oldest 10% of the sample (termed 10% longevity) (e.g. Gust et al. 2002). A von Bertalanffy growth function (VBGF) was fitted by nonlinear least-squares regression of FL on age data to estimate the growth characteristics of the species. As no fish under 2 yrs of age were collected, the intercept of the curve was constrained to the approximate size at settlement for *Epinephelus* (25 mm FL, Leis 1987) so that the von Bertalanffy parameter t_0 was –0.20 (Kritzer et al. 2001). Difference in size of the sexes in the overlapping age ranges was examined using analysis of covariance (ANCOVA) with age as the covariate and sex as a fixed factor. Hoenig's (1983) method, which estimates total instantaneous mortality from maximum observed age using data from 134 stocks, was used to predict mortality.

5.3.4 Reproductive features

Gonads were blotted dry and weighed to the nearest 0.1 g. All sex assignment and maturity staging was done from histological sections of gonads under a high power microscope using the criteria in Table 5.2; these include criteria used in combination to indicate female spawning history in inactive ovaries to distinguish between immature and mature individuals (Shapiro et al. 1993, Sadovy & Colin 1995, Samoilys & Roelofs 2000). Spawning history could not be determined for 13.1% of females, and those samples were excluded from the estimation of maturity since their actual and potential reproductive function is unknown. Males were considered mature if spermatozoa had proceeded to fill major sperm ducts or collapsed ducts were evident, indicating prior functioning as a male. Detailed histological descriptions of gonads are given in Chapter 6.

Table 5.2 Histological criteria used in classifying *Epinephelus fuscoguttatus* gonads into sex and maturity stages (modified from Smith 1965, Moe 1969, West 1990, Shapiro et al. 1993, Ferreira 1995, Samoilys & Roelofs 2000, Adams 2002).

Developmental stage	**Histological description**
Immature female	No evidence of prior spawning, ovary small and lamellae well-packed with gonia and pre-vitellogenic oocytes (chromatin nucleolar and perinucleolar stage).
Mature inactive female	Ovary dominated by pre-vitellogenic oocytes. Perinucleolar oocytes the most advanced healthy oocytes present. Prior spawning indicated by the presence of muscle bundles and/or occasional atretic vitellogenic oocytes. May have brown bodies. Ovary generally larger in diameter than those of immature females and may be vacuolated.
Undetermined inactive female	Ovary contains gonia and pre-vitellogenic oocytes but unable to determine if fish has spawned previously (mature) and is in a resting state or is an immature female.
Mature active female (i.e. ripening, ripe, near spawning & spent)	Ripening (yolk vesicle or cortical alveoli) or vitellogenic (yolk stage) oocytes present or indications of recent prior spawning (i.e. spent). May contain hydrated oocytes and/or post-ovulatory follicles (POFs) (i.e. near spawning ovaries). Early stages of oocytes may also be present in varying amounts. May contain signs of prior spawning. Ovaries of spent females generally disorganised and undergoing atresia, with muscle bundles and extensive vascularization.
Transitional	Proliferating testicular tissue in a gonad that has evidence of prior spawning as a female (degenerating vitellogenic oocytes and/or muscle bundles), where spermatozoa have not yet proceeded to fill the dorsal sperm sinuses. Spermatogenesis has progressed at least to the spermatid stage. Ovarian tissue dominates and perinucleolar stage the most advanced healthy female germ cells.
Mature male	Testes dominated by testicular tissue, which may contain crypts of gonia and germinal stages at various stages of development. Well-developed major sperm sinuses and peripheral ducts. Includes inactive and active males.

The size and age structures for females and males were obtained as were the mean size and age of the sexes. Ovary weight data were used as a proxy for female fecundity to identify potentially important female breeders and mapped onto the growth curve for mature active females. It was assumed that fecundity was positively correlated with ovary weight (Devlaming et al. 1982). Estimates of size and age at 50% sexual maturity were determined for females by two methods: (1) assessing the percent of all ovaries with signs of current or past spawning activity (i.e. mature active and mature inactive females, Table 5.2) by size or age groups; and (2) assessing the percent of females that were sexually active (i.e. mature active, Table 5.2) during the spawning season (November, December, January, see Chapter 6) by size or age group (termed *effective maturity*). *Effective maturity* recognises that despite being mature, only some females were sexually active. The relationships between gonad weight of inactive females with size and age were examined and were expected to show disproportionate increases during the size and age intervals of first maturity (Adams 2002). ELF research samples had highly accurate location and time data for each specimen (Mapstone et al. 2004), allowing me to calculate the percent coincidence of mature resting females being sampled from the same reef and day as ripe or near spawning females to determine if females that were inactive during spawning months were taken between spawning episodes. The pattern of male recruitment into the sampled population by size and age was also examined. The overlaps in the size and age frequencies of mature females and males were determined and the median values of these ranges calculated to give an indication of the size and age range over which sex change can occur (Shapiro 1987).

5.4 Results

5.4.1 Ageing protocol and validation

Otoliths of *E. fuscoguttatus* had visually distinct increments when examined microscopically (Figs. 5.2B, C) that enabled age to be estimated in 98.8% ($n = 239$) of the otoliths examined. Two age estimates were in agreement for 87.5% of otoliths and the index of average percent error was low (1.9%), thus indicating that reproducibility of the age estimations was high.

The OTC marking experiment and the edge-type analysis revealed an annual periodicity of increment formation (see Table 5.3 & Figs. 5.3 – 5.5). The number of full and partial increment cycles formed on the outside of the OTC mark indicated that a single opaque band and a single translucent band were formed each year (Fig. 5.4). This agreed with the calculated periodicity from measurements (1.02 – 1.04 yrs, Table 5.3). Inference from the coincidence of known dates (marking and end dates) with type of band (opaque or translucent) indicated that the opaque bands formed between September and November. *Epinephelus fuscoguttatus* showed a significant difference among monthly frequency of otoliths with opaque margins (Chi-square = 176.00, $P < 0.0005$), with elevated values (greater than 50%) occurring from August to November (Fig. 5.5). The findings from the edge-type analysis confirmed the results of the OTC marking experiment that increment periodicity is annual. Furthermore, both techniques were in close agreement on the seasonality (austral spring) of formation of opaque bands. The edge type of 28% of sections was uncertain for the age range examined. These uncertain edge types were present in months except March. There was a strong correlation ($r^2 = 0.94$) between otolith weight and fish age (Fig. 5.6).

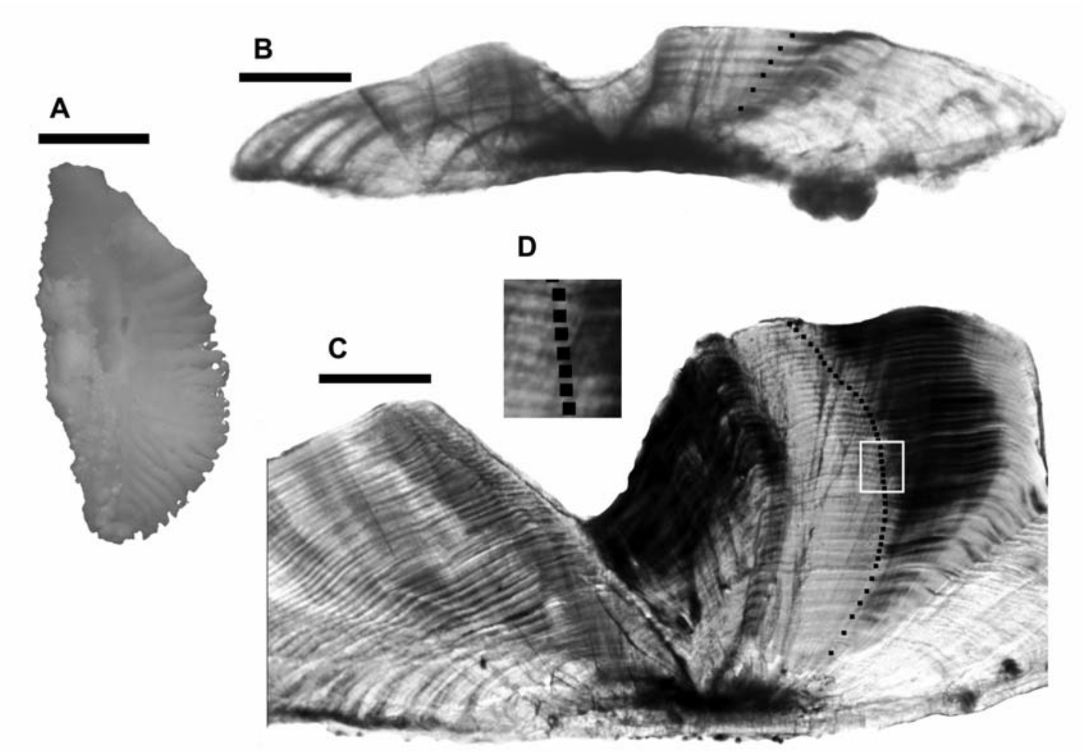


Figure 5.2 ***Epinephelus fuscoguttatus.*** **(A) Whole otolith (scale bar 5 mm). Sectioned otoliths with annuli indicated by dots: (B) 6+ year old female (FL = 468 mm, total weight = 1.89 kg) and (C) 42+ year old female (FL = 855 mm, total weight = 9.80 kg). Scale bars for (B) and (C) are 1 mm. (D) Detail from C.**

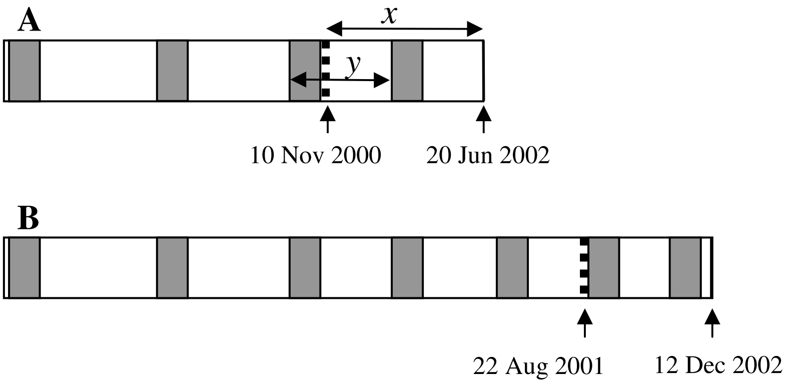


Figure 5.3 Diagram representing sections through *Epinephelus fuscoguttatus* otoliths from the first annulus (left) to outer edge of the otolith (right) from the oxytetracycline (OTC) marking experiment. OTC marks indicated by dashed lines, shaded areas represent opaque zones, clear areas represent translucent zones. The distance from the OTC mark to the outer edge (x), and from the start of the penultimate opaque band to the start of the last opaque band (y) are indicated on Fig. (A).

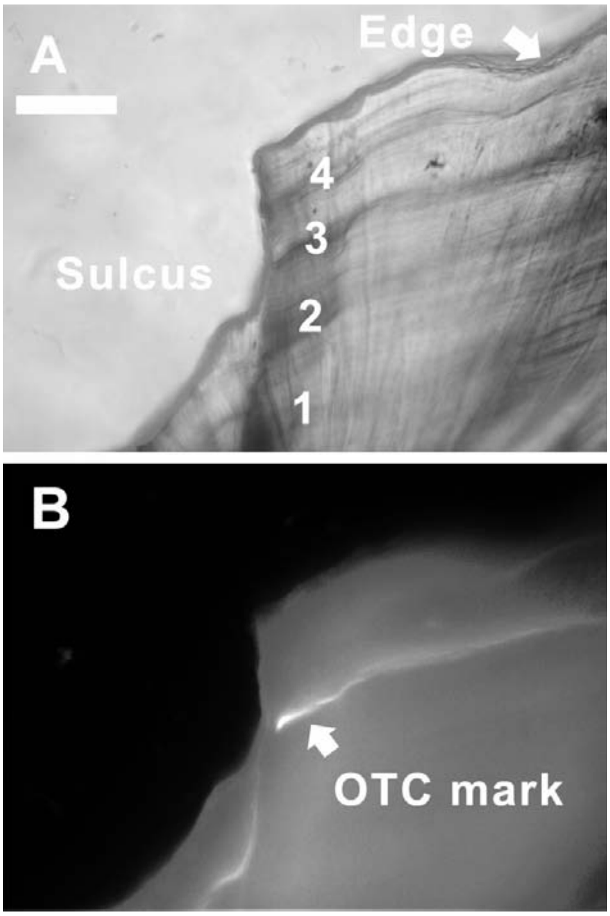


Figure 5.4 ***Epinephelus fuscoguttatus*. Details of oxytetracycline (OTC) marked otolith showing: (A) 4 annual bands and (B) OTC mark on same area under UV light. Scale bar 0.2 mm.**

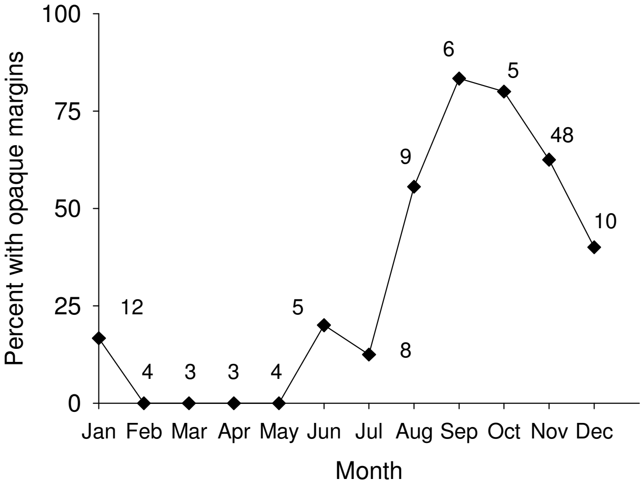


Figure 5.5 ***Epinephelus fuscoguttatus*. Edge type analysis for sectioned otoliths from the GBR showing percentage of otoliths with opaque margins. Numbers above data points indicate sample size.**

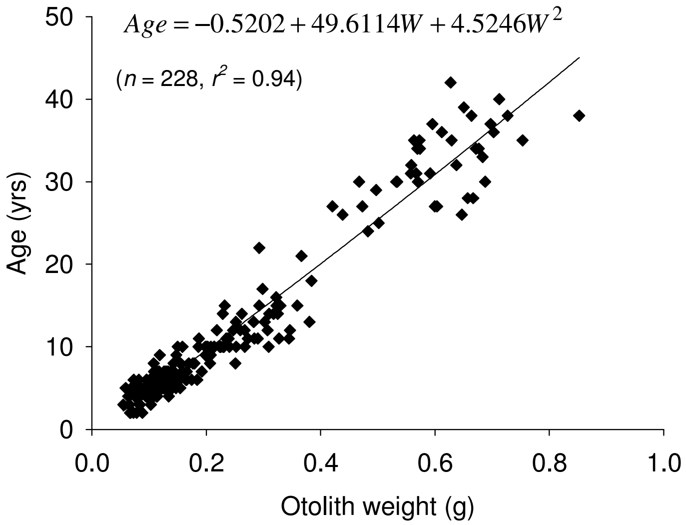


Figure 5.6 ***Epinephelus fuscoguttatus*****. Relationship between otolith weight (*****W*****) and presumed age.**

Table 5.3 ***Epinephelus fuscoguttatus*****. Details of age validation experiment of wild-caught adults marked with oxytetracycline (OTC).**

Specimen code	**RP150**	**RP786**
Sample location	Eyrie Reef	Centipede Reef
Date of OTC marking	10 Nov 2000	22 Aug 2001
End date	20 Jun 2002	12 Dec 2002
Growth period (days)	587	477
Growth period (yrs)	1.6	1.3
Fork length at start	343	420
Fork length at end	470	526
Growth in length (mm)	127	97
Growth in length per yr (mm yr^{-1})	79.4	81.5
Location of OTC mark	Start of T-zone	Near end of T-zone
Number of zones outside of OTC mark[a]	T + O + T	O + T + O
Margin type	Thick T-zone	Start of T-zone
Age at end (yrs)	4+	7+
Calculated periodicity of "annuli" formation (yrs)	1.02	1.04
Suggested timing of Opaque zone formation	September to October	September to November

[a] *T = translucent zone, O = opaque zone*

5.4.2 Size and age structures

The sampled *E. fuscoguttatus* ranged from 320 to 970 mm FL, 550 g to 17.75 kg total weight, and 2 to 42+ yrs of age. The mean (± S.E.) size, weight and age were 580 ± 9.6 mm FL, 5.76 ± 0.3 kg and 11.8 ± 0.7 yrs, respectively. Size distributions revealed that males had a larger mean size than females and the largest individuals were male (Fig 5.7A). Conversely, age-frequency distributions indicated that the oldest individual sampled was a female (Fig. 5.7B). Recruitment of *E. fuscoguttatus* to commercial line fishing gear begins at 2 yrs old and is complete by the modal age of 5-6 yrs.

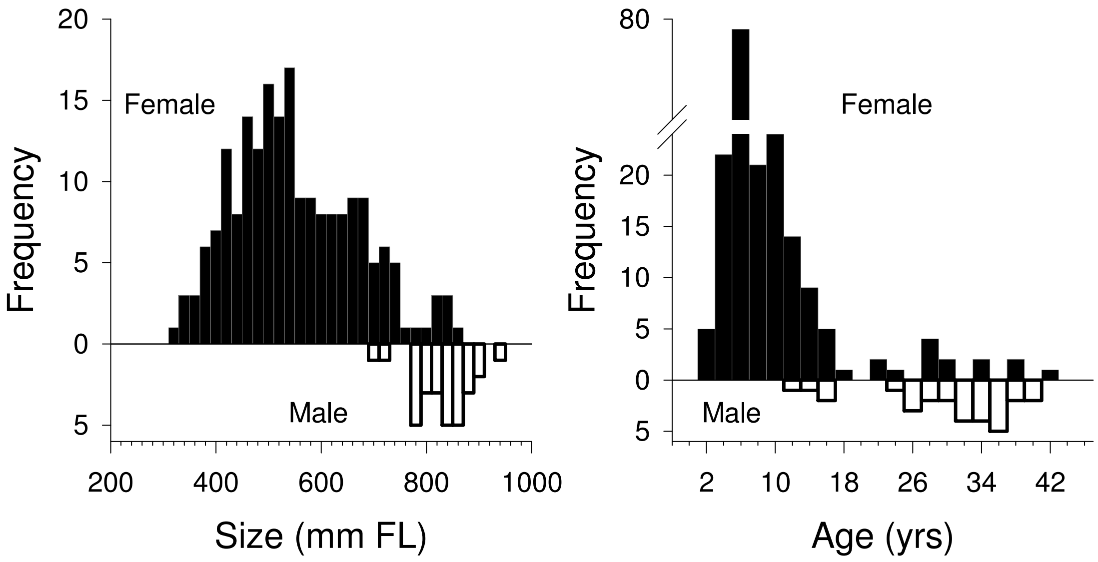


Figure 5.7 ***Epinephelus fuscoguttatus*****. (A) Size and (B) age frequency distributions for females (n = 203) and males (n = 29). Size groups are 20 mm fork length, age groups are 2 years. Note: the size and age graphs are from exactly the same fish.**

For 232 individuals from which gonads were examined histologically, 203 were females (87.5%) and 29 males (12.5%). Females ranged from 320 to 855 mm FL, 550 g to 11.40 kg total weight and 2 to 42 yrs (mean ± S.E.: 542 ± 8.3 mm FL, 3.46 ± 0.11 kg, 8.8 ± 0.5 yrs, respectively). Males ranged from 683 to 925 mm FL, 5.95 to 15.40 kg total weight and 11 to 40 yrs (mean ± S.E.: 820 ± 9.7 mm FL, 10.60 ± 0.47 kg, 29. 7 ± 1.5 yrs, respectively). Reproductive organs were not available for the largest fish (970 mm FL). The bimodal male and female size and age distributions (mode of females less than mode of males) are shown in Fig. 5.7. Females persisted in large size and age groups, suggesting that not all females change sex. Females were on average significantly smaller and younger than males (t-test$_{\mathrm{Size}}$: $t_{0.05(1),\ 78.5} = -21.72$, $P < 0.0001$. t-test$_{\mathrm{Age}}$: $t_{0.05(1),\ 221} = -14.95$, $P < 0.0001$). The slopes of the relationship between length and age for females and males were not significantly different ($F_{1,66} = 2.203$, $P = 0.143$), satisfying the assumption of homogeneity of slopes. Also, the ANCOVA indicated that males were significantly larger than females for the age range examined (11 to 40 yrs, $F_{1,67} = 15.281$, $P < 0.001$).

5.4.3 Longevity, growth and mortality

Epinephelus fuscoguttatus is a relatively long-lived reef fish: the oldest fish examined was 42 yrs old (female, 855 mm FL, 9.80 kg, Fig. 5.2C), and the 10% longevity estimate (± S.E.) was 36 ± 0.5 yrs. *Epinephelus fuscoguttatus* exhibited an asymptotic pattern of growth. Fitting the VBGF to observed length at age data (Fig. 5.8A) for both sexes combined gave a mean asymptotic fork length, L_∞, of 806.9 mm and a coefficient of growth, K, of 0.16 ($n = 239$, $r^2 = 0.84$). Most somatic growth occurred in the first 10 – 15 yrs: 80% of L_∞ is achieved by about

10 yrs on average. The predicted total mortality rate was 0.11 yr^{-1}. The length weight relationship was $Wt = 1.16 * 10^{-5} FL^{3.075}$ ($n = 127$, $r^2 = 0.98$).

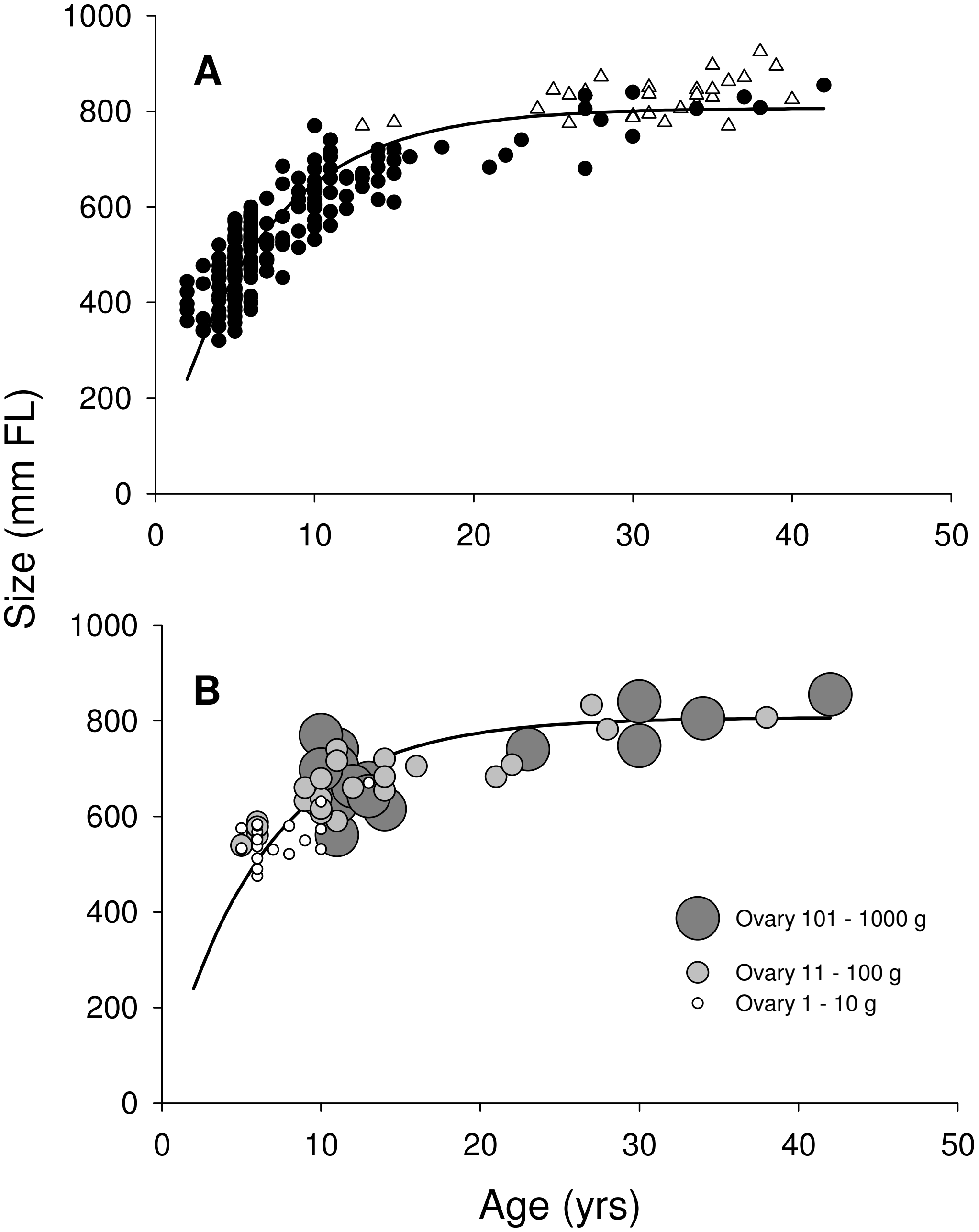


Figure 5.8 ***Epinephelus fuscoguttatus*****. (A) Growth curve. Von Bertalanffy growth function (VBGF) fitted to size-at-age data. Females indicated by circles; males indicated by triangles. The y-intercept of the VBGF is constrained to the approximate size at settlement for *Epinephelus* spp. (25 mm FL, Leis, 1987). (B) Ovary weights (as a proxy for fecundity) of mature active females mapped onto the growth curve. Mature active females indicated by circles, and their ovary weight indicated by the relative size of symbols.**

5.4.4 Reproductive activity

The sample comprised 6.9% immature females, 11.2% undetermined inactive females (of uncertain maturity status), 41.4% mature inactive females, 28.0% mature active females (includes ripening, ripe, near spawning and spent) and 12.5% mature males (definitions in Table 5.2). The plotting of ovary weight data (as a proxy for female fecundity) onto the growth curve indicated large old females (>600 mm FL and >10 yrs) were important breeders over a 30+ yr reproductive lifespan (Fig. 5.8B). Ovary weight increased by 2 to 3 orders of magnitude as size increased from approximately 400 to 700+ mm FL (from ~1 g up to 940 g, Fig. 5.9A). This increase of ovary weight was largely achieved by about 10 yrs of age, and then maintained for the remainder of the lifespan (Fig. 5.9B).

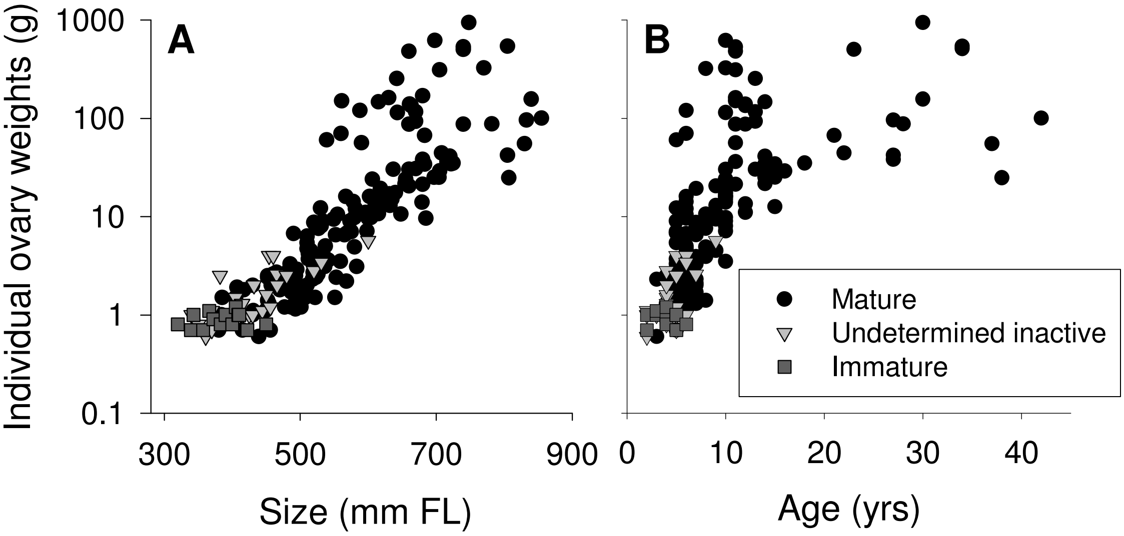


Figure 5.9 ***Epinephelus fuscoguttatus*. Ovary weights for females from the GBR using a $\log_{10}$ scale by (A) size and (B) age. Maturity indicated by symbols shown in the figure, where Mature = mature inactive and mature active females (definitions: Table 5.2).**

5.4.5 Female maturity and male recruitment

The size and age at 50% sexual maturity for females were estimated to be 408 mm FL and 3.7 yrs, respectively, using Method 1 (Figs. 5.10A, B). In contrast, Method 2 (*effective maturity*) gave higher estimates of 566 mm FL and 9.2 yrs, respectively (Figs. 5.10C, D). The plots of ovary weight of *inactive* females with size and age showed a disproportionate increase at about 550 mm FL and 9 – 10 yrs that supported the effective maturity estimates (Fig. 5.11). Analysis of ELF research samples found that during spawning months 72% of the mature inactive females were taken from the same reef and day as mature active females, 57% of which were taken from the same reef and day as females in near spawning condition (ovaries contained hydrating or hydrated oocytes). Mature inactive females were collected throughout the sampling range during the spawning months. Mature inactive females (mean ± S.E.: 498

± 54.2 mm FL and 6.2 ± 1.8 yrs) were on average smaller and younger than mature active females (645 ± 95.6 mm FL and 13.6 ± 9.2 yrs) during the reproductive season (t-test$_{\text{Size}}$: $t_{0.05(2),\,83.9} = -9.825$, $P < 0.0001$. t-test$_{\text{Age}}$: $t_{0.05(2),\,57.3} = -7.32$, $P < 0.0001$, Fig. 5.12).

Males did not occur in the samples until about 683 mm FL and 11 yrs of age, above the size and age of 100% female maturity, providing no evidence of primary males (Fig. 5.7). Males made up 50% or more of most cohorts over 760 mm FL and 24 yrs of age. From the overlap in size and age frequencies of mature females and males, sex change can occur from 683 to 855 mm FL and 11 to 40 yrs. The size and age at sex change was estimated to be 791 mm FL and 25.5 yrs (median values).

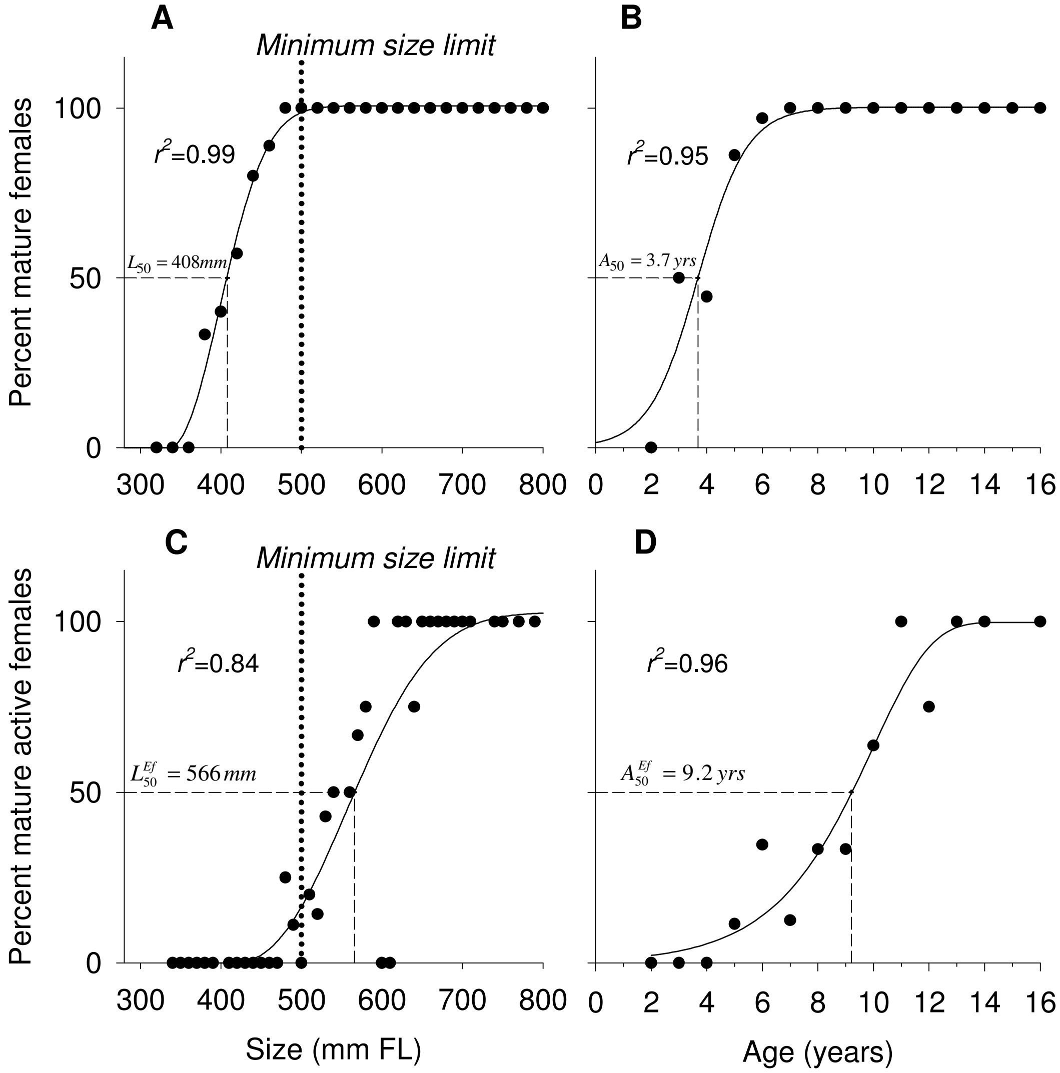


Figure 5.10 ***Epinephelus fuscoguttatus*****. Two estimates of female maturity based on (1) percentage of mature females by (A) size and (B) age; and (2) percentage of mature active females during the spawning months (Nov, Dec, Jan) by (C) size and (D) age. Dashed lines indicate 50% maturity estimates by size (L_{50}, L^{Ef}_{50}) and age (A_{50}, A^{Ef}_{50}). Sample sizes: n = 173 for (A) and (B); n= 141 for (C) and (D). The minimum size limit for this species on the east coast of Queensland, Australia is shown.**

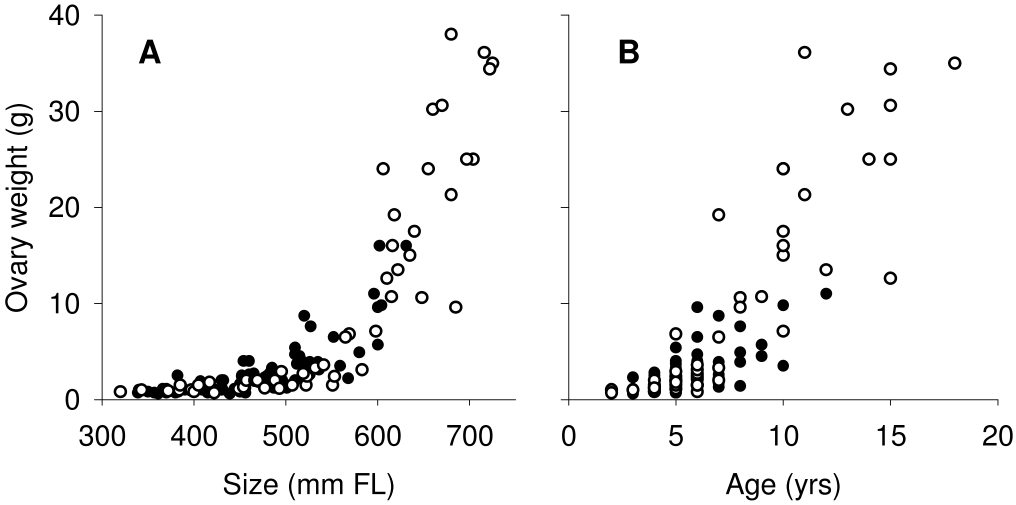


Figure 5.11 ***Epinephelus fuscoguttatus*****. Ovary weight of inactive females by (A) size and (B) age. The dark circles represent samples taken during the reproductive season, the open circles represent samples taken outside of the reproductive season.**

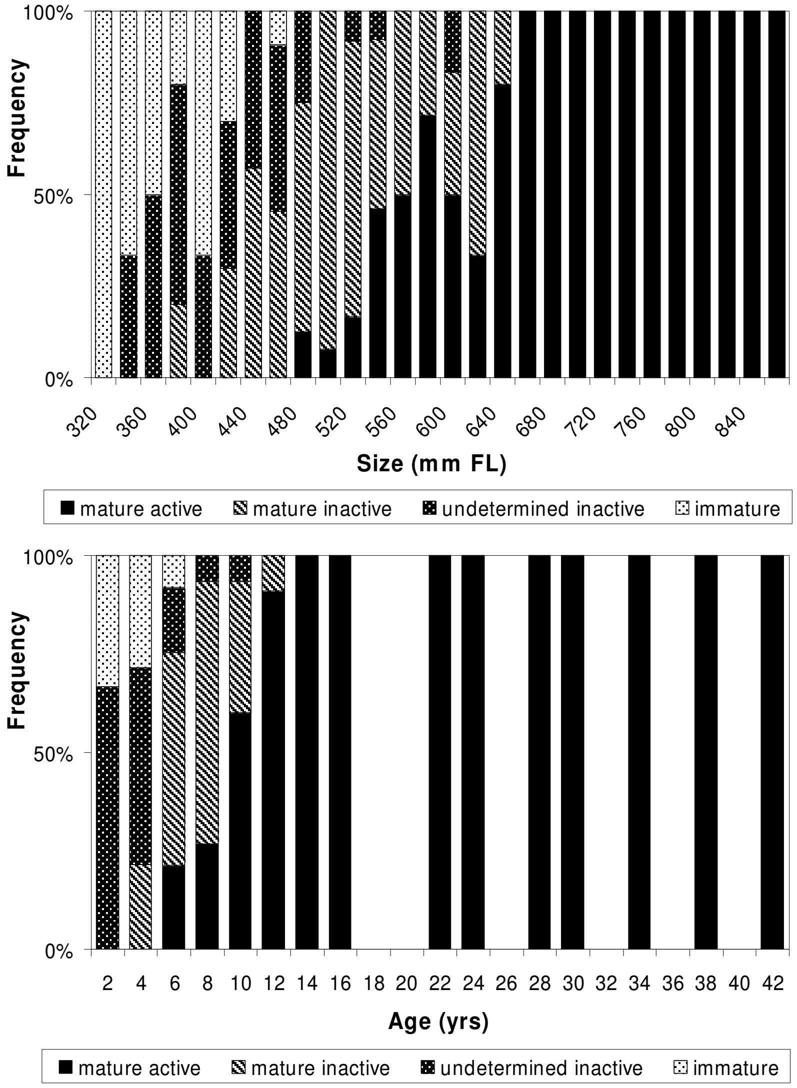


Figure 5.12 ***Epinephelus fuscoguttatus*****. Proportion of each reproductive category for ovaries collected during the spawning period (Nov, Dec & Jan) by (A) 20 mm size groups and (B) 2 yr age groups. Reproductive categories defined in Table 5.2.**

5.5 Discussion

Epinephelus fuscoguttatus from northeastern Australia are relatively long-lived, as the lifespan can exceed 40 yrs and is at the upper end of published records for this genus. Longevity can allow for greater cumulative reproductive success over time and may act as a buffer against occasional recruitment failure, however, it is also associated with greater vulnerability to fishing and lengthy recovery times after episodes of population depletion (Jennings et al. 1999b). Unusual reproductive ecology of this large mobile serranid included an extensive (>30 yr) reproductive lifespan, the likelihood that some females do not undergo sex change, late effective maturity, and the presence of inactive females with active females during the spawning period.

5.5.1 Demography and reproduction

Growth is asymptotic, with the majority of growth occurring within the first 30% of the lifespan. Thus, age and size are decoupled over much of the reproductive size range, agreeing with the predictions of Choat and Robertson (2002), and similar to the findings for cryptic serranids (Chapter 4). This decoupling means that a combination of size- and age-specific biological data are needed to understand the life history of this species and also to determine which components of the population are vulnerable to capture under various harvest regimes.

The ageing protocol using thin-sectioned sagittal otoliths from *E. fuscoguttatus* gave reliable results that satisfied the three criteria needed to validate the relationship between periodicity of increments in otoliths and fish age (Beamish & McFarlane 1983, Fowler 1990). Namely, *E. fuscoguttatus* otoliths showed a positive relationship between number of increments in otoliths (presumed age) and otolith weight indicating that otoliths grow throughout the life of individual fish, the increment pattern in sectioned otoliths can be reliably interpreted, and this pattern corresponds to an annual timescale. Although the analysis showed a strong unimodal pattern, larger monthly sample sizes and more individuals across a range of age groups would allow examination of individual variability within age groups. The annual timing of opaque band formation in austral spring agreed with findings for many other taxa (e.g. from the Great Barrier Reef see Fowler 1990, Choat & Axe 1996, Choat et al. 1996, Cappo et al. 2000).

The dataset is adequate to support the demographic and reproductive conclusions because the adult size ranges were well sampled and immature individuals were included. Individuals below 350 mm FL or 5 yrs of age were under-represented, however. This may be because of selectivity of the sampling gears or the absence of small fish-habitat at the sampling localities, or a combination of both. Visual surveys for this species on many of the same reefs also failed to find small individuals (below 300 mm FL, Chapter 3) suggesting that the habitat of juvenile and sub-adult *E. fuscoguttatus* may differ from those sampled in this thesis. Possible habitat of young *E. fuscoguttatus* may be seagrass (Sommer et al. 1996) or other inshore habitats. It is also possible that sampling did not include the largest, and hence oldest, individuals in the population, however there are no confirmed records of larger *E. fuscoguttatus* on the GBR than was observed in this study.

The observed distribution of the sexes by age and size strongly suggest that the sexual pattern of *E. fuscoguttatus* is monandric protogynous hermaphroditism, and individuals first function sexually as females and, later, at least some of these mature females change to males. Sex change may potentially occur over a wide range of sizes and ages, although the oldest members of the population included females indicating that not all individuals changed sex. Sex allocation theory indicates that individuals in hermaphroditic fishes should change sex whenever net future reproductive success would be higher for the opposite sex than the existing sex (Charnov 1982). However, it may not always be advantageous for the largest female to change sex in protogynous species because of the exponential relationship between fecundity and body size and individual variability in this relationship (Munoz & Warner 2003). Confirming the sexual pattern and schedule of sex change of *E. fuscoguttatus* are research priorities, and are considered further in Chapter 6.

5.5.2 Maturation and sexual activity

There was a discrepancy between female maturity estimates obtained using two different methods. Estimates of size and age at 50% maturity using the proportion of females that were sexually active during the peak spawning months (*effective maturity*) were significantly higher than those determined from the proportion of all ovaries with signs of current or past spawning activity. For the latter technique, difficulty in determining female spawning history from some inactive ovaries arises because the features used to indicate prior spawning (atretic oocytes, post-ovulatory follicles and muscle bundles) become harder to detect with increasing time since spawning and may eventually disappear (Shapiro et al. 1993, Sadovy & Colin 1995, Samoilys & Roelofs 2000, Adams 2002). A disproportionate increase in ovary weight at the corresponding size and age to the former maturity estimates, the lack of ripe females until large sizes, and the possibility that undetermined inactive females were immature all support the effective maturity estimate.

The considerable proportion of mature inactive females during the spawning season in each year suggests several different scenarios. These include that not all females spawn in all years, or spawn only infrequently during the spawning period or fish may not all spawn at the same times or locations. The presence of non-spawning mature females during the spawning season for two species of *Epinephelus* endemic to southern Africa were attributed to limited spawning near the edge of geographic ranges and/or because not all mature individuals spawn each year (Fennessy 2000, Fennessy & Sadovy 2002). Non-spawning in female gag, *Mycteroperca microlepis,* has been attributed to a shortage of males (Coleman et al. 1996). Insufficient energy reserves, stress or unsuitable environmental conditions may also mean females do not spawning in some years. For example, older females of an Australian sparid, *Acanthopargus australis*, had a low tendency to participate in seaward spawning migrations, possibly due to insufficient energy reserves to migrate and spawn (Pollock 1984).

This study found a strong pattern of female sexual activity with size and age. Despite histological signs indicating maturity, smaller and younger females were less sexually active than larger or older females. Non-spawning females should be regarded as effectively immature since they do not contribute to egg production in a given spawning event (Williams 2003). The apparent lack of reproductive activity and corresponding increase in the effective size and age of maturity may be a result of a trade-off between somatic growth and reproductive effort (e.g. Roff 1984). Support for this hypothesis is given by the size and ages of effective maturity corresponding to the change from relatively fast to slower growth. The limited sexual activity of small young females suggests a life history strategy for *E. fuscoguttatus* on the GBR in which energy is primarily invested in somatic growth for almost 10 yrs, after which growth slows and energy is invested in reproduction. Research to understand spawning details for *E. fuscoguttatus*, including behaviour of inactive and active females during spawning episodes would be worthwhile. A further priority is to investigate the temporal pattern of reproduction of *E. fuscoguttatus* (Chapter 6).

5.5.3 Conservation and fisheries management

The biological characteristics of *E. fuscoguttatus* (i.e. rarity, long lifespan, late effective maturity, protogynous sex change, spawning aggregation behaviour) and catchability indicate relatively low resilience to fishing pressure or other disturbances (Sadovy 1994b, 1997a, Jennings et al. 1999b, Pears 2005). Protogynous species, particularly if sex change is fixed (i.e. occurs at a specific size or age threshold), may be at risk of population collapse even at relatively low fishing mortality (Bannerot et al. 1987, Huntsman & Schaaf 1994, Alonzo & Mangel 2004). Large individuals are a rare but important part of the reproductive population, containing all of the males that are vital to maintain the sex ratio and prevent sperm limitation (Bannerot et al. 1987), and important female breeders that are highly fecund and contribute substantially to the reproductive output of the population for many years (Sadovy 1996). Recent studies indicate that reproductive success increases with maternal age and experience for some fish species (e.g. Hislop 1988, Trippel et al. 1997, Marteinsdottir & Steinarsson 1998, Trippel 1998, Berkeley et al. 2004a). Truncation of size and age structures by fisheries can, therefore, unduly reduce reproductive capacity (Berkeley et al. 2004a, Berkeley et al. 2004b, Palumbi 2004, Birkeland & Dayton 2005).

Fishing typically selects for larger fish on reefs, and such size-selective fishing can overfish large individuals with profound effects upon reproductive output (Jennings et al. 1999b, Alonzo & Mangel 2004). In addition, large *E. fuscoguttatus* may be particularly vulnerable to fishing as anecdotal reports indicate post-release mortality is higher for large groupers. Protected areas (or no-take zones) are considered a valuable management option for protecting intact size and age structures and breeding populations of reef fish (Russ & Alcala 1996, Berkeley et al. 2004b). Expansion of the no-take areas in the Great Barrier Reef Marine Park in 2004 (see www.gbrmpa.gov.au) is likely to provide some protection for *E. fuscoguttatus.*

Other recent changes to management regulations for the reef line fishery on Australia's GBR include slot size limits for *E. fuscoguttatus* (minimum 500 mm FL, maximum 1000 mm FL, Anon 2003). Setting practical legal size limits in a multi-species fishery such as the GBR reef line fishery is complicated, particularly for taxa such as epinepheline serranids for several reasons (Hancock 1990): at least 40 species are captured; species identification is difficult; maximum body sizes and life history traits vary widely; and biological knowledge is limited for most species. The effectiveness of size limits will depend on whether they protect a reasonable proportion of the intended component of the population, the level of compliance with the regulation, the survival of released illegal-sized fish (i.e. post-release survival), and keeping fishing mortality to a low level.

The fished component of the GBR population of *E. fuscoguttatus* still includes most of the active spawning stock and all of the males. Although 500 mm FL is above the size of first reproduction in *E. fuscoguttatus*, females below approximately 566 mm FL contribute very little to the total reproductive output of the population. Consequently, the current minimum size limit on the GBR is not protecting the population's breeding potential. A maximum size limit on the GBR is warranted given the importance of large old individuals for reproduction, however, the current maximum size limit is too high as few, if any, fish are afforded protection. Furthermore, large *E. fuscoguttatus* (>6 kg) can be difficult to sell because of concerns about potential ciguatera poisoning (Pears pers. obs.). To protect large female breeders, maintain the sex ratio, and prevent sperm limitation, the maximum size limit for this species should be revised based on the new biological data.

Chapter 6. Reproductive biology of a large, aggregation-spawning serranid, *Epinephelus fuscoguttatus*: management implications

6.1 Synopsis

The reproductive biology of a large long-lived grouper, *Epinephelus fuscoguttatus* (brown marbled grouper), from the Great Barrier Reef (GBR), Australia was investigated using histological analyses. Combined evidence of gonad morphology and age-based demographics suggest monandric protogynous hermaphroditism. Younger age groups contained only immature and mature females, and all males were above the size and age of 100% female maturity, consistent with secondary males derived from mature females by adult sex change, though confirmation awaits direct evidence of sex change (e.g. identification of transitional individuals). I provide the first information from the GBR on spawning seasonality and confirm from fishing data that spawning aggregations of this species (and the co-occurring *E. polyphekadion*) are sometimes targeted there. One relatively narrow annual spawning period (November to January) was identified for *E. fuscoguttatus*. The temporal pattern of reproductive activity within the spawning period, based on occurrence of near spawning ovaries (containing hydrated oocytes), indicated spawning events may occur throughout much of the lunar cycle and did not coincide with seasonal fishing closure periods on the GBR. Protection would be enhanced by a longer seasonal closure. Research and monitoring of spawning aggregations in the GBR (and other locations) is a priority.

6.2 Introduction

Large mobile serranids (Chapter 1, Table 1.1) are heavily fished for both the live and processed reef fish trades (Sadovy et al. 2003b). An understanding of the reproductive biology of these fishes is critical in order to evaluate management options for them. *Epinephelus fuscoguttatus* (brown marbled grouper or flowery cod), a large mobile serranid, widely distributed Indo-Pacific epinepheline targeted by the live reef fish trade (Sadovy et al. 2003b), achieves sizes of at least 95 cm (Heemstra & Randall 1993) and ages in excess of 40 yrs (Chapter 5, Pears et al. 2006). In the age-based demographic analysis in Chapter 5, I found that the reproductive lifespan of female *E. fuscoguttatus* could exceed 30 years, sexual activity of smaller and younger mature females was limited until about 9 yrs of age and 566 mm FL, and, on the basis of sex distributions by age and size, I postulated that monandric protogyny was the primary mode of sexual development but some females do not undergo sex change. These findings were considered in the context of new legal size limits governing recreational and commercial fisheries in Queensland, including the Great Barrier Reef, and it was concluded that the new minimum and maximum size limits (500 mm and 1000 mm) for *E. fuscoguttatus* would not protect the main reproductive elements of the population.

In this Chapter I used histological analysis of aged specimens to provide the first detailed description of *E. fuscoguttatus* reproductive biology and examine the temporal pattern of reproductive activity (i.e. reproductive cycle). Although the results from the demographic analyses (Chapter 5, Pears et al. 2006) were consistent with protogyny, confirmation of the sexual pattern requires histological analyses of gonad morphology (Sadovy & Shapiro 1987). Histological evidence of sexual transition in adults provides strong evidence of protogyny, and further evidence such as age data linked with histological analyses may be needed to determine sexual pattern (Sadovy & Shapiro 1987, Sadovy & Colin 1995, Rhodes & Sadovy 2002a). Age data are valuable in this context to resolve the sequence of sexual maturation and development for females and males in the population, and hence sexual pattern (e.g. Fennessy & Sadovy 2002), with bimodal age distributions suggesting hermaphroditism (Sadovy & Shapiro 1987). Size data are also important for reproductive studies, given that sex change is likely the result of social rather than genetic cues for many protogynous species and thus influenced by fish size (e.g. Ferreira 1995, Mackie 2003) and that reproductive traits such as fecundity also are likely to be size-dependent (Sadovy 1996). Bimodal size frequency distributions may be caused by many factors in addition to protogyny, however, and so have limited diagnostic value for hermaphroditism (Sadovy & Shapiro 1987). Information on sexual pattern is important for understanding fish life histories and predicting the response of a harvested population to fishing, particularly if the fishery is size-selective and/or governed by legal size limits (Bannerot et al. 1987, Koenig et al. 1996, Vincent & Sadovy 1998, Huntsman et al. 1999).

Large groupers typically restrict spawning to large aggregations at preferred sites during short periods of the year (transient spawning aggregations) (Sadovy et al. 1994, Domeier & Colin 1997). *E. fuscoguttatus* has been reported to aggregate in relatively large numbers to spawn, with over 350 individuals being counted at spawning aggregation sites in Palau (Johannes et al. 1999). Targeted fishing of reef fish spawning aggregations has been reported on the GBR (QFMA 1996, Mapstone et al. 2001a) and is a potential threat to *E. fuscoguttatus*, having been implicated in the decline or disappearance of some *E. fuscoguttatus* spawning aggregations in Palau (Johannes et al. 1999).

Details of the temporal pattern of reproductive activity in *E. fuscoguttatus* on the GBR would enable managers to determine if this species would benefit from recently introduced seasonal spawning closures (Anon 2003). Closure of the Queensland reef line fishery is for nine day periods around the new moons in October to December, chosen mainly to encompass the spawning period of the major target species *Plectropomus leopardus* and some other reef fishes.

In this Chapter, I describe the reproductive biology of *Epinephelus fuscoguttatus* on the GBR to determine the: (1) histological and morphological structure of gonads from fish of different sizes and ages and thus the pattern of sexual ontogeny; (2) the seasonal extent of the spawning period; and (3) the temporal pattern of reproductive activity within the spawning period, specifically in relation to the current seasonal closures to fishing on the GBR. I also examine catch records of a local fishery for evidence that spawning aggregations of this species sometimes may be being targeted.

6.3 Materials and methods

6.3.1 Samples used

I completed a detailed reproductive study of preserved gonads (n = 232 fish) from previously aged specimens of *Epinephelus fuscoguttatus* obtained from the GBR (detailed in Chapter 5). All but five samples came from reefs between 18°20'S and 21°50'S, and five from the Lizard region (ca. 14°40'S) (Chapter 5, Fig. 1). Pooling of these samples was necessary given the low abundance of this species on the GBR (Chapter 3) and the difficulty in obtaining specimens of large epinephelines (Sadovy et al. 2003a). Data available for each specimen included fork length (FL), total body weight, age, gonad weight, sampling location and date as detailed in Chapter 5. Samples came from three sources (detailed in Chapter 5, Table 1): (1) a fisheries collection program from the commercial reef line fishery between April 2001 and January 2003; (2) recreational spearfishers (Nov 2001); and (3) research line fishing surveys done each spring (Oct – Dec) from 2000 to 2002 as part of the ELF Project (Mapstone et al. 2004). Each fish from ELF was individually tagged and measured on landing and accurate collection location and date information recorded. Specimens were stored in iced sea water for up to 4 hrs before gonads were removed and fixed.

6.3.2 Reproductive biology

A transverse section of tissue for sectioning was taken from the central region of one lobe of each gonad and embedded in paraffin, sectioned at 5 µm, mounted on slides and stained with Mayer's Haematoxylin and Young's Eosin. Dorsal and ventral sub-samples of the central region were taken from large gonads. Twenty gonads were serially sectioned (anterior, mid, posterior and ductal regions), stained as above, staged as detailed below and examined for structural consistency to verify whether development was consistent throughout the gonad. This serial sectioning demonstrated that development was broadly consistent throughout the ovaries and testes, and there were no differences in assigned reproductive stage or sex among regions for any of the sub-sample. Hence, sampling of the central region was considered sufficient to reliably account for reproductive status of each gonad.

Sex assignment and reproductive staging was done from histological sections under a high power microscope, using the criteria in Table 1 (modified from Smith 1965, Moe 1969, Shapiro et al. 1993, Ferreira 1995, Samoilys & Roelofs 2000, Adams 2002, Fennessy & Sadovy 2002). Sections were read in random order without prior knowledge of the fish from which they originated or its place or time of capture. The stage of oocyte development was classified by the most advanced non-atretic oocyte present, as follows: Stage 1 – chromatin nucleolar stage; Stage 2 – perinucleolar stage; Stage 3 – yolk vesicle (cortical alveoli) formation; Stage 4 – vitellogenic (yolk) stage; and Stage 5 – hydrated stage (West 1990). Table 1 also outlines additional histological criteria and characteristics of gonad morphology used in combination to indicate female spawning history in inactive ovaries in order to distinguish between immature females and mature resting females and to identify spent females (Sadovy & Shapiro 1987, Sadovy & Colin 1995, Samoilys & Roelofs 2000). Only cells still recognisable as degenerating Stage 4-5 oocytes were included under the 'atretic vitellogenic oocyte' criterion because brown bodies are not reliable indicators of oocyte degeneration (Sadovy & Colin 1995). Males were classified by the presence/absence and relative proportions of germinal stages in conjunction with structural aspects of the gonad such as collapsed sperm ducts. Males were considered mature if spermatozoa had proceeded to fill major sperm sinuses or collapsed ducts were evident (indicating prior spawning as a male).

The size and age frequencies and mean sizes and ages for each sex and maturity category were derived from the available length and age data for the sample. Only mature females and males were used for calculating operational sex ratio. Spawning history could not be determined for 26 females (13.1%), and so these females were classified as 'undetermined inactive' and excluded from the estimation of sex ratio. Evidence for protogynous sex change was assessed using the criteria proposed by Sadovy and Shapiro (1987). Features strongly indicative of protogyny are transitional individuals, atretic bodies in stages 1, 2, or 3 of oocytic atresia present within testes, sperm sinuses in the gonadal wall, and experimental production of transitional or sex-reversed individuals through manipulation of the social system. The presence of membrane-lined central cavities in testes cannot be used on its own to determine the male developmental pathway because they are found in all epinepheline serranids (Sadovy & Colin 1995, Rhodes & Sadovy 2002a). Analyses of sexual pattern were considered with and without undetermined inactive females since their actual and potential function is unknown.

6.3.3 Reproductive seasonality and activity

The spawning period was determined based on the peak period of female reproductive activity. Reproductive activity was evaluated for each sex by examining seasonal variations in the gonadosomatic index (GSI = 100 x gonad weight/gonad-free total body weight) and in the relative proportion of individuals in each reproductive stage. Collection dates and locations for fish taken during ELF catch surveys were examined and the data for near spawning females (with ovaries containing hydrated oocytes and/or post-ovulatory follicles, indicating imminent or recent spawning activity) (Hunter & Macewicz 1983) were taken as a preliminary indication of the timing of spawning events in relation to the lunar cycle. Specimens from different years were pooled by month for these analyses because of low sample sizes.

Peaks in fishing catch and/or catch per unit of effort (CPUE) during the spawning period can result from fishing of spawning aggregations, although additional data are required for confirmation that fish were “spawning” (e.g. direct evidence that fish were in spawning condition such as hydrated oocytes) and that fishers were actively targeting aggregations as opposed to coincidentally experiencing higher catch rates because of increased catchability of fish during spawning periods (Fulton et al. 1999) (e.g. verification by fishers). The spawning periods for *Epinephelus fuscoguttatus* and the similar-looking, co-occurring, but smaller *E. polyphekadion (*camouflage grouper) are reported to be very similar in some locations, although there may be slight temporal (a few days) and spatial (10’s to 100’s m) segregation between the species’ aggregations (Johannes et al. 1999, Rhodes & Sadovy 2002b, Robinson pers com). Similarly for the GBR, fishers have reported large catches of both species in close proximity.

Detailed data of the combined catch of *E. fuscoguttatus* and *E. polyphekadion* from the central GBR were obtained from a commercial line fishing boat in the Queensland reef line fishery from December 1997 to 2001. Seasonal trends were examined in the total monthly catch and average catch per fishing day from the main vessel and its four tendered fishing dories combined. The boat reported fishing aggregations of these groupers in December and January, and the size and timing of these catches were examined. A sub-sample of specimens reported to be from a spawning aggregation in the central GBR on approximately 9 days after the full moon in December was obtained and examined histologically.

Table 6.1 Histological criteria used in classifying gonads of *Epinephelus fuscoguttatus* into reproductive stages (modified from Smith 1965, Moe 1969, Shapiro et al. 1993, Ferreira 1995, Samoilys & Roelofs 2000, Adams 2002, Fennessy & Sadovy 2002). Oocyte stages defined in text after West (1990).

Developmental stage	**Histological description**
Immature female	No evidence of prior spawning, ovary small and lamellae well-packed with gonia and pre-vitellogenic oocytes (chromatin nucleolar and perinucleolar stage).
Mature resting female	Ovary dominated by pre-vitellogenic oocytes. Prior spawning indicated by the presence of muscle bundles and/or occasional atretic vitellogenic oocytes. Ovary generally larger in diameter than those of immature females and may be vacuolated.
Undetermined inactive female	Ovary contains gonia and pre-vitellogenic oocytes but unable to determine if fish has spawned previously (mature) and is in a resting state or is an immature female.
Mature ripening female	Stage 3 oocytes the most advanced oocyte present. May contain signs of prior spawning.
Mature ripe female	Ovary in active vitellogenesis. Usually dominated by stages 3 and 4 oocytes although early stages of oocytes also present in varying amounts.
Mature near spawning female	Ovary in active vitellogenesis as ripe female but some oocytes have become hydrated (stage 5) indicating imminent spawning likely.
Mature spent female	Ovary generally disorganised and undergoing atresia, with muscle bundles and extensive vascularization. Many contain brown bodies. Stage 2 oocytes the most advanced healthy oocyte present.
Transitional	Proliferating testicular tissue in a gonad that has evidence of prior spawning as a female (degenerating vitellogenic oocytes and/or muscle bundles), where spermatozoa have not yet proceeded to fill the dorsal sperm sinuses. Spermatogenesis has progressed at least to the spermatid stage, and areas of testicular tissue with clusters of spermatocytes, spermatids or spermatozoa present within lamellae and/or associated with the gonad wall. Ovarian tissue dominates and the most advanced healthy female germ cells are stage 2. Atretic and fragmenting oocytes may be present.
Primary male	Proliferating testicular tissue in a gonad similar in appearance to an immature ovary, where spermatogenesis has progressed at least to the secondary spermatocyte stage. Ovarian tissue dominates the lamellae, which are not yet of the typical lobular form of the mature testes, and there are no signs of prior spawning as a female.
Mature resting male	Testes dominated by testicular tissue with which may contain crypts of gonia and spermatocytes. Later stages of spermatogenesis (spermatids and/or spermatozoa) rare or absent. Evidence of prior spawning as a male indicated by well-developed but collapsed major sperm ducts, which are now empty of sperm.
Mature ripening male	Testes contains proliferating testicular tissue including secondary spermatocytes, spermatids and spermatozoa, but major sperm ducts are not yet filled with sperm.
Mature ripe male	Testes dominated by crypts of spermatocytes, spermatids and spermatozoa. Crypts of spermatozoa ruptured and joined within the testicular lobules, forming central sperm sinuses, and major sperm sinuses and ducts filled with sperm.
Mature spent male	Testes disorganised and vacuolated with numerous brown bodies and well-developed stromal tissue. Some spermatozoa may still be present in lobules but major sperm sinuses and ducts empty or collapsed.

6.4 Results

6.4.1 Spawning period

The spawning period determined from histological assessment of ovaries (Fig. 6.1, near spawning females) was in agreement with that determined from GSI analysis for females (Fig. 6.2). *Epinephelus fuscoguttatus* had one peak annual spawning period between November to January, but because samples from different years were pooled by month for analysis the actual period may be narrower in any particular year. Males were functionally in spawning condition (ripe) between October and January. No ripe individuals of either sex were collected outside this four month period. For ripe females and males, there was a wide range in GSI values (up to 13.3 for females and 2.1 for males Figs. 6.2A, B).

6.4.2 Spawning events and interaction with fishery

The commercial line catch data examined showed increases of one to two orders of magnitude in catch of *E. fuscoguttatus* and *E. polyphekadion* during December and January, two of the three main spawning months. Total monthly catch and average catch per fishing day both showed one strong annual peak (Fig. 6.3) which occurred within the spawning periods for *E. fuscoguttatus* and *E. polyphekadion* (hydrated oocytes for *E. polyphekadion* also occur in Nov. – Jan. on the GBR, Pears, unpub. data). These peaks were the result of some large catches (>250 kg day^{-1}) during December and January. A particularly large catch (1500 kg) of these species was taken over two and a half days around the last quarter moon (5, 6 & 7 days after full moon) in December (Fig. 6.4). Histology revealed that 19 of the 20 specimens reported to be from a spawning aggregation were in spawning condition (six very ripe males with >90% of testes containing spermatozoa, 13 near spawning females and one ripe female). Although no estimate of the proportion of *E. fuscoguttatus* in the total catch is available, the combined catch and histological data are consistent with fishing of spawning aggregations.

A first approximation can be made of how large a catchment area (i.e. the geographic extent from which a particular aggregation site draws individuals, Sadovy & Domeier 2005) would be depleted to supply 1000 kg of *E. fuscoguttatus* from an aggregation site using mean weight (5.76 kg per individual, Chapter 5) and mean density estimates (0.19 fish per 1000 m^2, Chapter 3) for the GBR. From these estimates, an average of roughly 910,000 m^2, or almost 1 km^2, of catchment (i.e. suitable habitat) would be required for every 1000 kg of catch. This calculation assumes that 100% of *E. fuscoguttatus* (above the minimum observed ~300 mm FL) are taken from the catchment, whereas catch on spawning aggregation sites is generally reported to consist mainly of large individuals, meaning that the catch would be sourced from a much larger area.

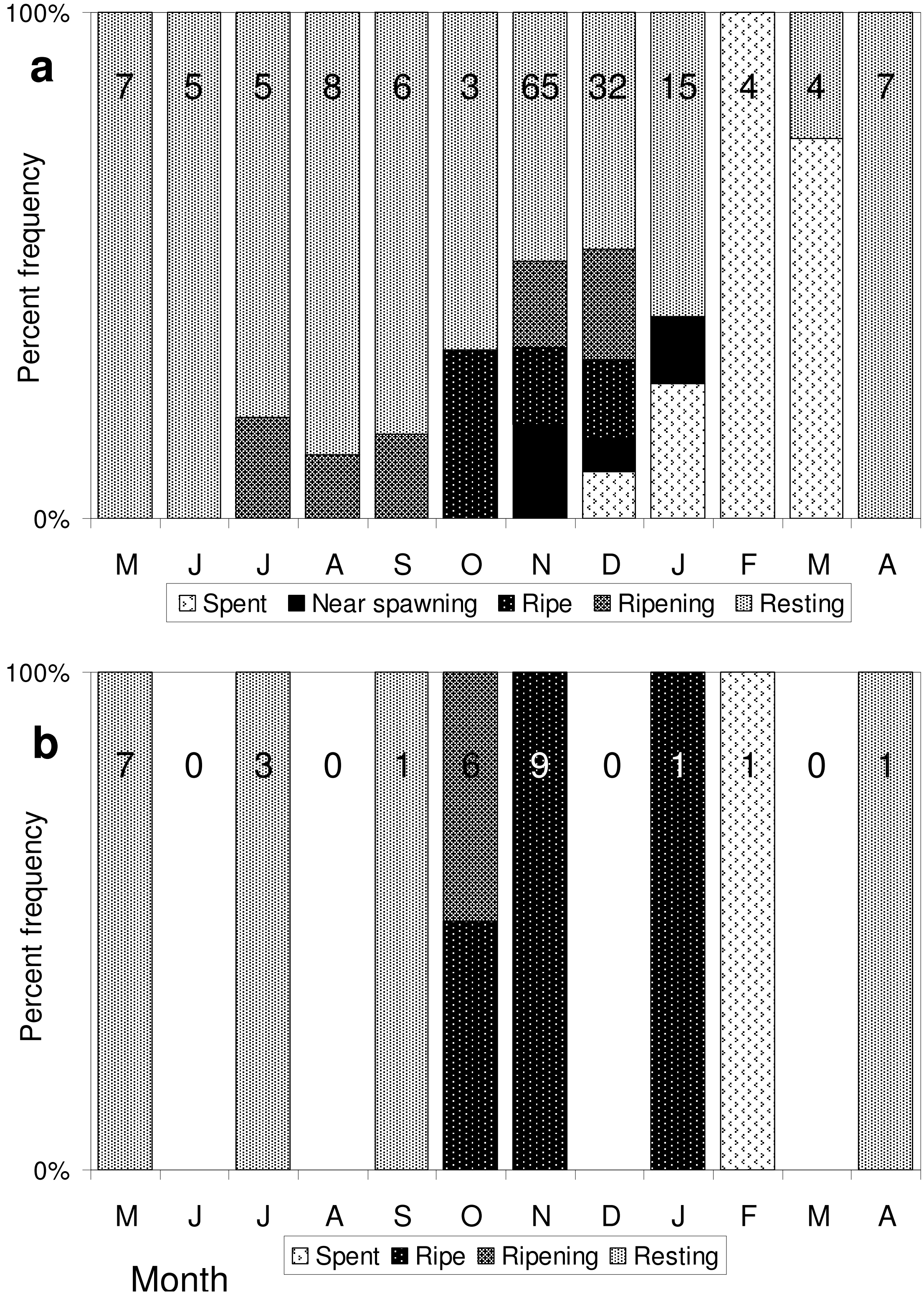


Figure 6.1 ***Epinephelus fuscoguttatus*****. Monthly percent frequencies of (A) mature females and (B) mature males according to sexual groups pooled over one year. Numbers on bars indicate sample numbers.**

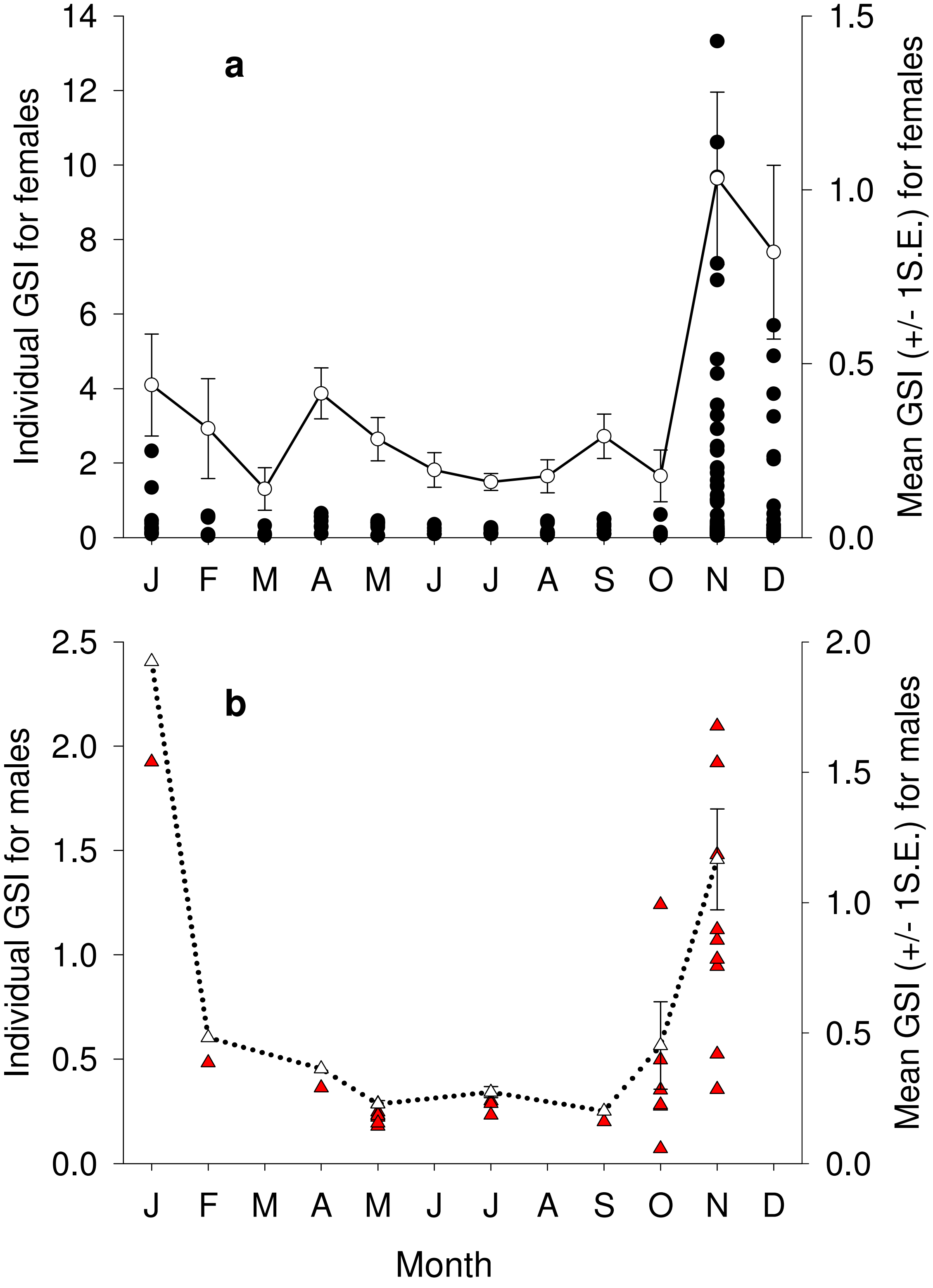


Figure 6.2 ***Epinephelus fuscoguttatus*. (A) Female and (B) male gonadosomatic index (GSI) for *Epinephelus fuscoguttatus* by pooled months. Closed symbols indicate individual GSI, open symbols joined by lines indicate mean GSI. Note different axes and scales for each data series.**

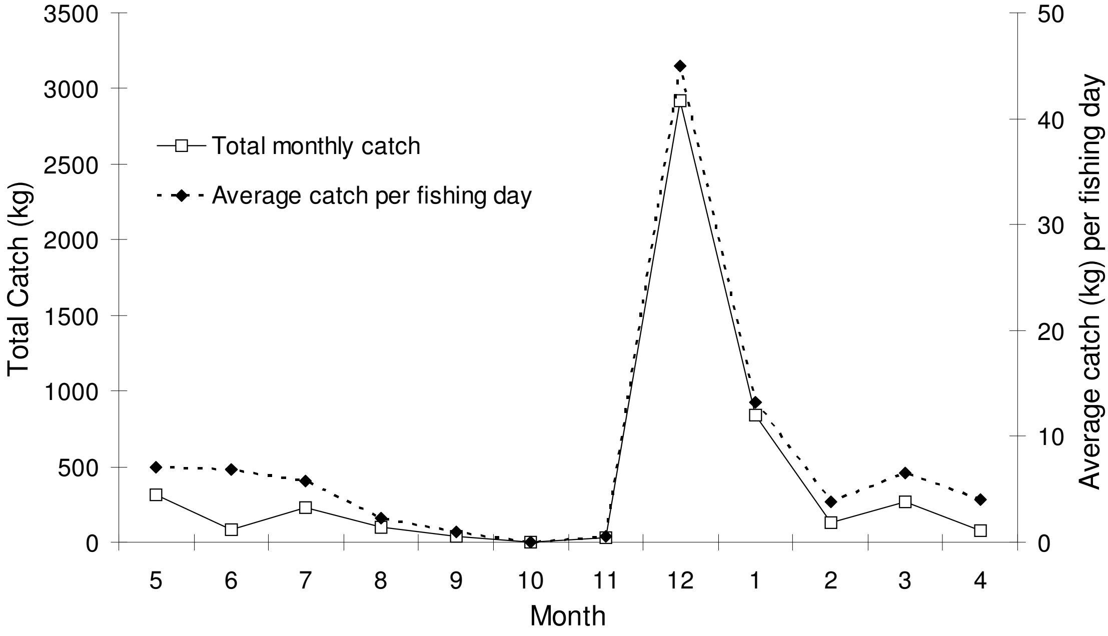


Figure 6.3 Total monthly catch and average catch per fishing day of *Epinephelus fuscoguttatus and E. polyphekadion* from the central Great Barrier Reef by a commercial line fishing boat. Data from 1997 to 2001 pooled by month.

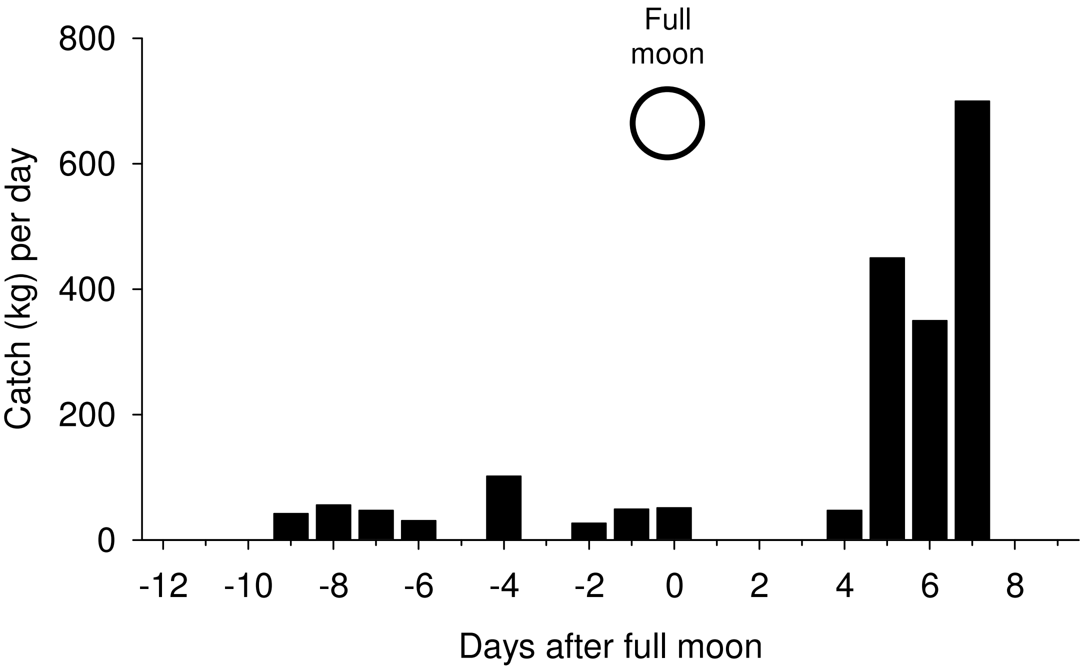


Figure 6.4 Detail of daily catch of *Epinephelus fuscoguttatus and E. polyphekadion* from the central Great Barrier Reef by a commercial line fishing boat during spawning period showing a large peak from day 19 to 21 of lunar month. Of the 15 fishing days that month, these species were caught on the 12 days shown. Total catch of these species for the month was 1952 kg, an average of 130.1 kg per fishing day.

The pooling of ELF sampling dates from November and December 2000-2002 by lunar day shows that ELF sampling occurred throughout 75% of the lunar month (from eight days before full moon to 13 days after full moon), and there was limited sampling effort around the new moon period (Fig. 6.5). The timing of the ELF sampling not dictated by the present project, but was to avoid sampling during peak *Plectropomus leopardus* spawning periods and so avoid confounding field sampling for the ELF Experiment with potential aggregating behaviour of their key species. Fig. 6.5 also shows the lunar pattern in occurrence of *E. fuscoguttatus* near spawning ovaries (containing hydrated oocytes) in ELF samples, which occurred throughout much of the lunar month. Because data were pooled over years, the timing of spawning events in any one month may be more restricted. Additionally, the peaks in commercial line catch are indicated on Fig. 6.5, which are likely to correspond to periods of spawning aggregations but not necessarily spawning events. In the main, near spawning ovaries and peaks in catch did not coincide with the new seasonal fishing closure periods in the Great Barrier Reef Marine Park (Anon 2003).

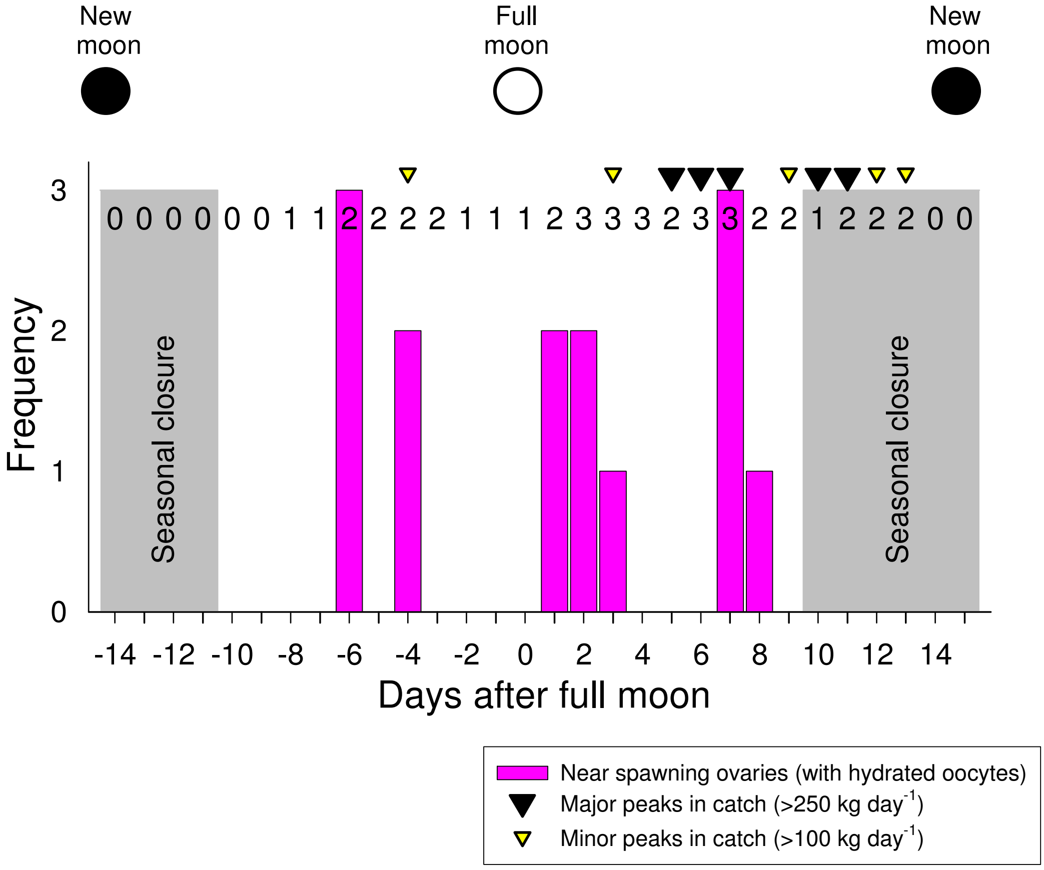


Figure 6.5 Lunar pattern of *Epinephelus fuscoguttatus* reproduction in relation to lunar cycle and GBR seasonal closure period. Bars indicate lunar day and frequency of occurrence of near spawning ovaries (containing hydrated oocytes) in ELF samples (research fishing) from November and December 2000–2002. Numbers above bars indicate the number of ELF sampling days (each day consisted of a full day of fishing by four commercial fishers) during the same time period. Peaks in commercial fishing catch of *E. fuscoguttatus* and *E. polyphekadion* indicated by triangles (catch data from December and January, 1997–2001). Note that only limited ELF sampling occurred around the new moon periods.

6.4.3 Reproductive biology

Plots of the size and age distributions of female reproductive categories (defined in Table 6.1) were generally overlapping and also indicated that mature females and males overlapped in size and age (Figs. 6.6, 6.7). Mature females significantly outnumbered males (sex ratio of 5.6:1, n = 186, Chi-square, $p < 0.01$). The female bias was greater (sex ratio of 13.8:1, n = 74, Chi-square, $p < 0.01$) if only samples obtained using the standardised line fishing gear of the ELF research surveys were included. The lower size and age groups were female biased, but above 760 mm FL and 28 yrs, males were more numerous. All males were larger and older than the size and age at 100% female sexual maturity (Figs. 6.6, 6.7), which is consistent with expectations for secondary males derived via adult sex change.

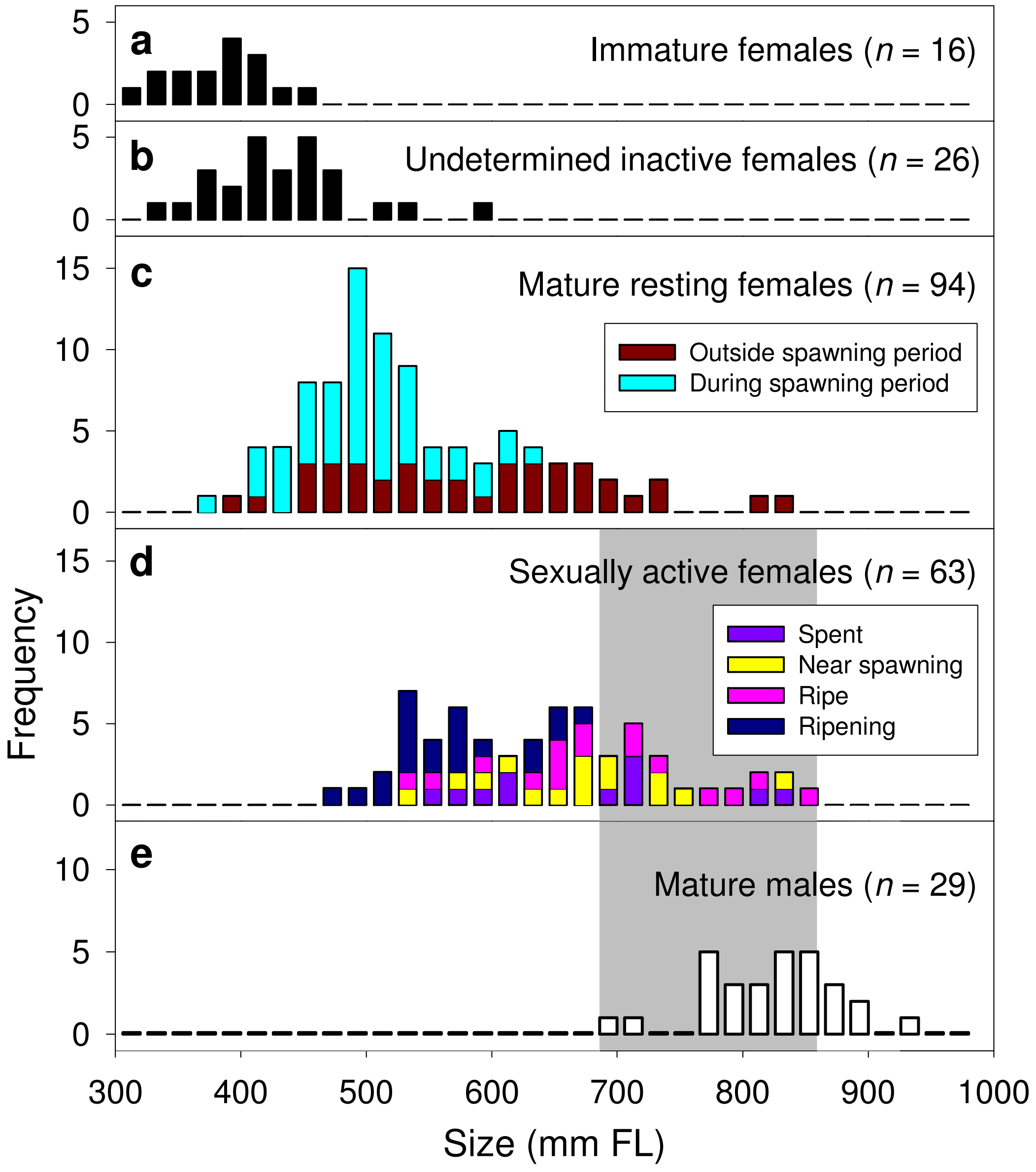


Figure 6.6 Size frequency of *Epinephelus fuscoguttatus* from the GBR: (A) immature females, (B) undetermined inactive females, (C) mature resting females, (D) sexually active females and (E) males. Shaded area (D & E) indicates overlap in female and male size distributions. Bar colours shown in C indicate collection time and in D indicate developmental stage.

Immature and undetermined inactive females

Histological assessment revealed the ovaries of immature females were very small (1.2 g or less), with short, neatly packed lamellae (Figs. 6.8A, B). Immature females (6.9% of sample) were aged 6 yrs or less and sampled both in and out of the spawning period. Undetermined inactive females (11.2% of sample) of uncertain maturity status occurred from 6 months onwards after the spawning period, and were intermediate in size and age between immature and mature females (Fig. 6.8H).

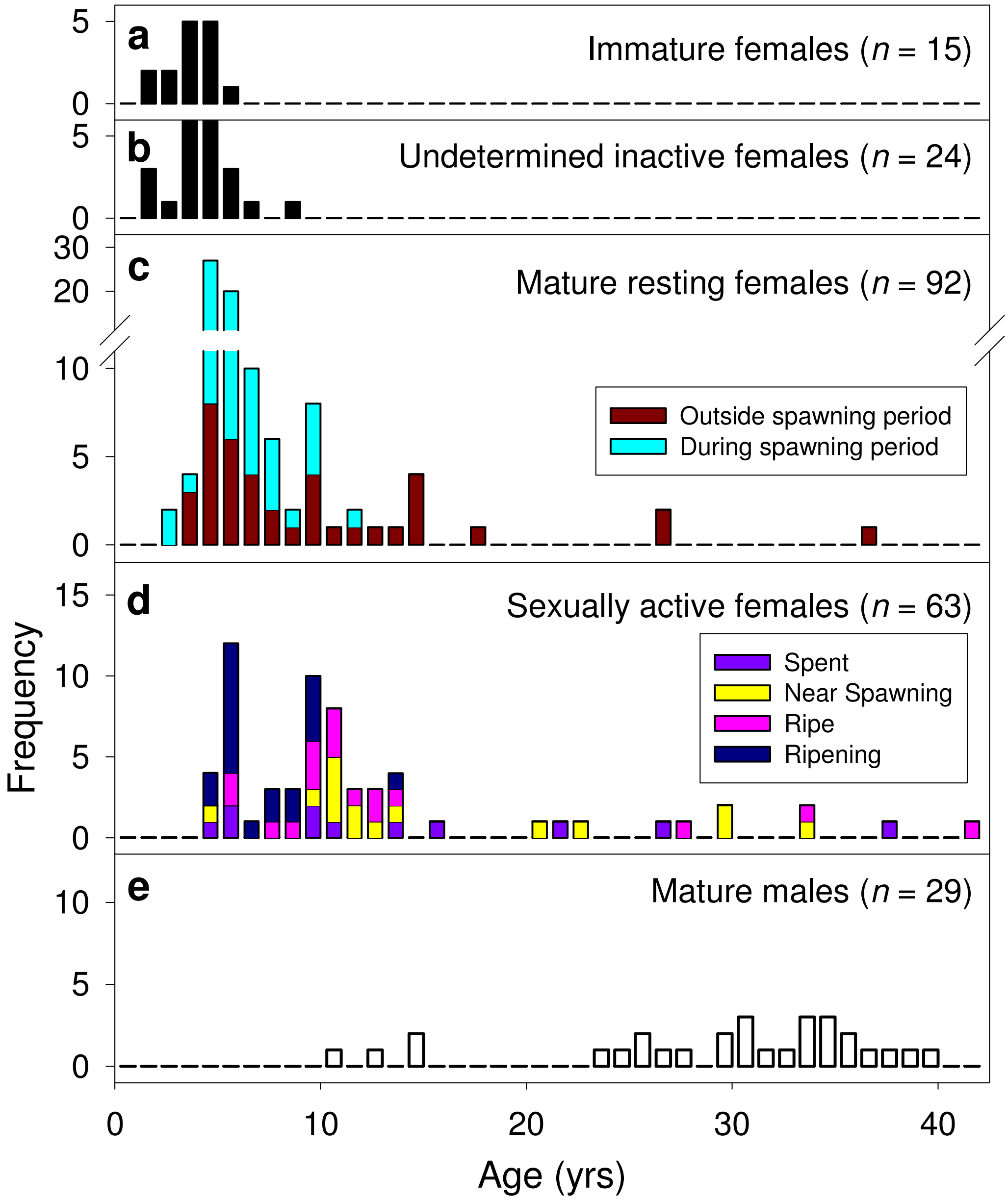


Figure 6.7 Age frequency of *Epinephelus fuscoguttatus* from the GBR: (A) immature females, (B) undetermined inactive females, (C) mature resting females, (D) sexually active females and (E) males. Bar colours shown in C indicate collection time and in D indicate developmental stage. Note the change of scale for C.

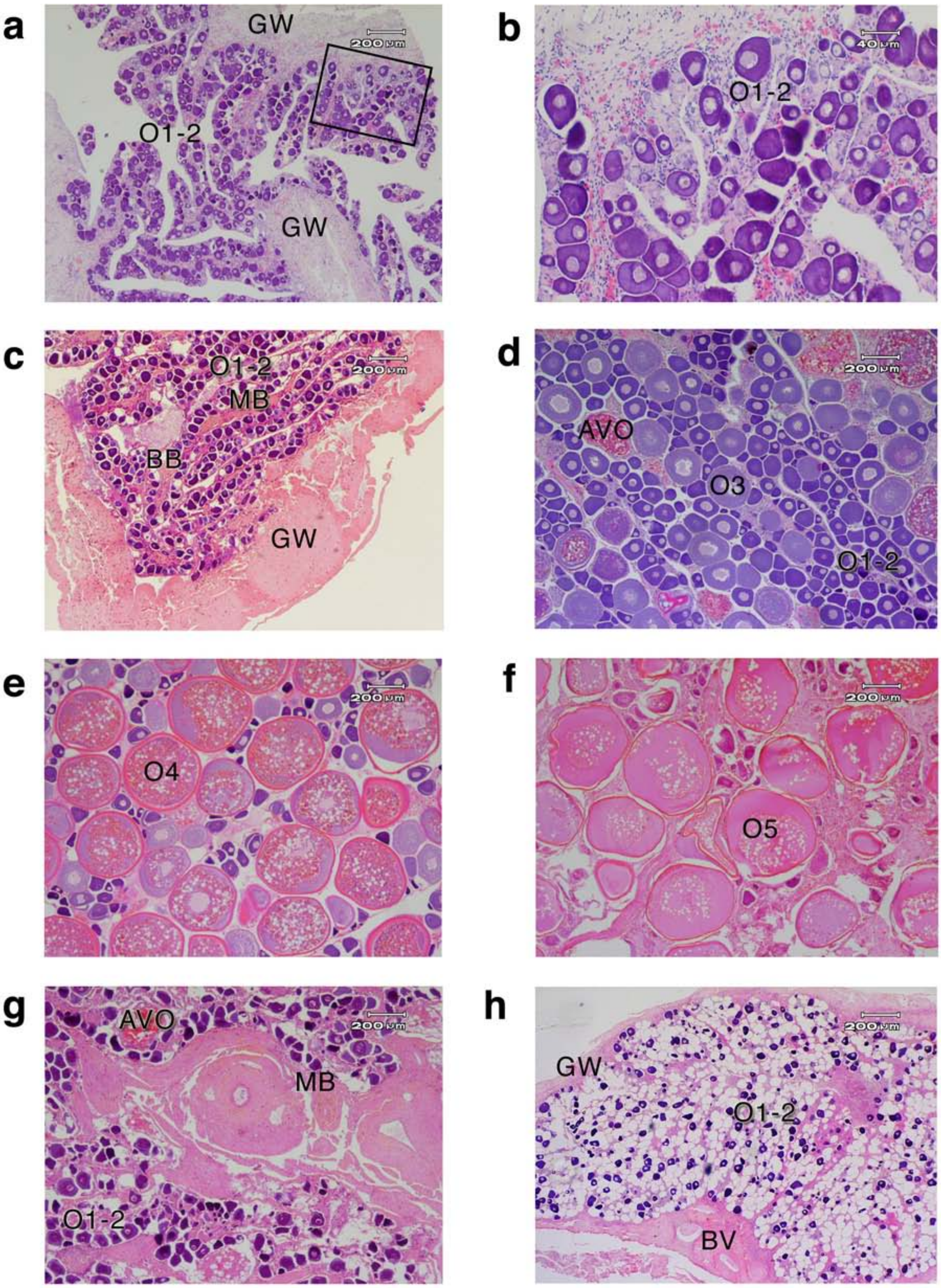


Figure 6.8 Histological sections of ovaries from *Epinephelus fuscoguttatus* depicting developmental stages: (A) immature, (B) detail from (A) at higher magnification, (C) mature resting, (D) mature ripening, (E) mature ripe, (F) near spawning, (G) mature spent and (H) undetermined inactive. Definitions in Table 6.1. Symbol key: GW, gonad wall; BV, blood vessel; O1-2, stage 1-2 oocytes; O3, stage 3 oocytes, O4, stage 4 oocytes; O5, stage 5 oocytes; MB, muscle and connective tissue bundle; AVO, atretic vitellogenic oocytes; P, parasite. Scale bar is 200 µm for A, C-H and 40 µm for B.

Mature or developing females

Mature or developing females comprised 69.4% of the sample. Mature resting females (Fig. 6.8C) were sampled in all months except February, and the smallest mature female was an inactive 3 yr old of 380 mm FL with signs of prior spawning. The smallest ripening, ripe and near spawning females, however, were 6 yr olds of 475 mm FL and 560 mm FL, and a 5 yr old of 539 mm FL, respectively. Ripening females (Fig. 6.8D) were taken from three months prior to the spawning period, and made up 18%, 22% and 0% during the spawning months of November, December and January, respectively. Ripe females (Fig. 6.8E) were sampled in October to December, and the relative proportion of vitellogenic and pre-vitellogenic oocytes in their gonads varied considerably. Development of oocytes was asynchronous which may indicate batch spawning. Atretic vitellogenic oocytes were observed in 68% of ripe ovaries and the occasional brown body was present. Near spawning females (Fig. 6.8F) occurred from November to January, and the number of hydrated oocytes per section varied from less than five to hydrated oocytes dominating (>50% of area). All near spawning ovaries contained some atretic vitellogenic oocytes and some of these ovaries had quite a few brown bodies and the occasional post-ovulatory follicle. Spent (post-spawning) females (Fig. 6.8G) were taken during the latter part of the spawning period (January) and in the following two months. Gonads of these individuals were disorganised and vacuolated, and all remaining vitellogenic oocytes were undergoing atresia. Prominent bundles of muscle and connective tissue surrounding blood vessels featured in ovaries for six months after the spawning period. A few crypts of precocious spermatocytes (Smith 1965) and/or small areas of possible precursory testicular tissue (Cole 1990) were found near the dorsal gonad wall in 9% of functional ovaries, but none had progressed to the transitional stage (Fig. 6.9).

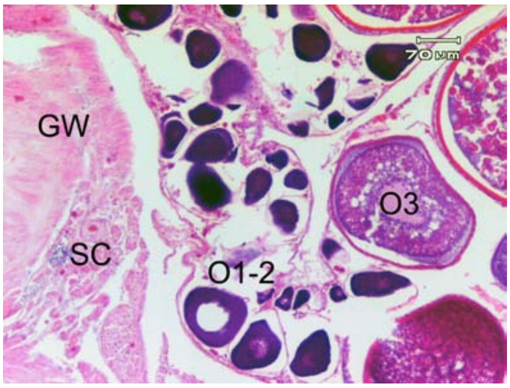


Figure 6.9 Histological sections of mature ripe ovary from *Epinephelus fuscoguttatus* showing spermatocytes near gonad wall. Symbol key: GW, gonad wall; O1-2, stage 1-2 oocytes; O3, stage 3 oocytes, SC, spermatocytes. Scale bar is 70 µm.

Males

All males (12.5% of sample) were mature and no primary males developing directly from the juvenile (immature female) phase were found (definitions: Table 6.1). Testicular tissue dominated (~100%) all male gonads. Only one testes contained a few remnant pre-vitellogenic oocytes and there were no signs of atretic oocytes in any males. Large and small brown bodies, scarring (Bean et al. 2003) and muscle bundles were common in all but the ripest males. Major sperm ducts developed around the periphery of the gonad (Fig. 6.10), with the largest ducts (up to 1.1+ mm in width) either side of the main dorsal blood vessel. Crypts of spermatozoa joined within the testicular lobules to form central sperm sinuses, which drained into the major sperm ducts. The ex-ovarian lumen was evident in many samples but apparently was not used in sperm transportation.

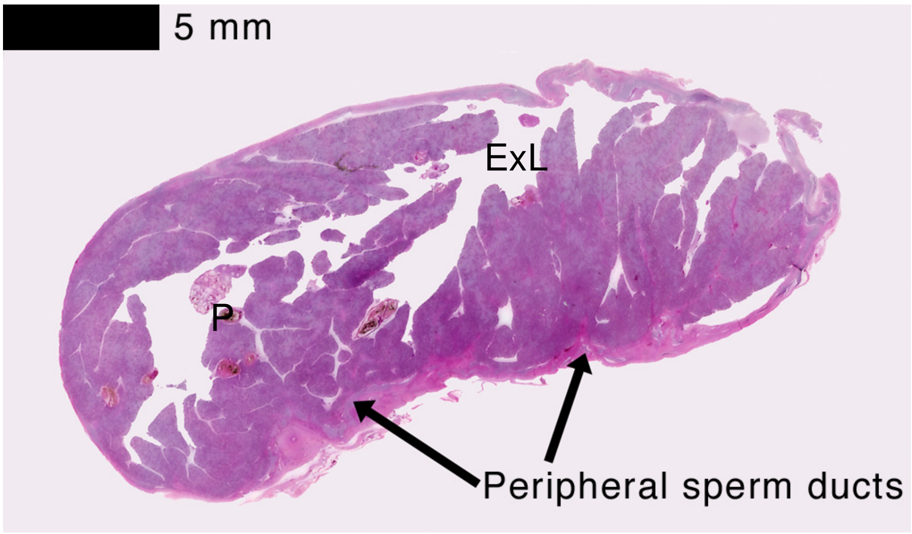


Figure 6.10 Transverse section of ripe gonad from a small male *Epinephelus fuscoguttatus* (683 mm fork length, 11 yrs) showing typical structure including peripheral sperm ducts and ex-ovarian lumen. Symbol key: ExL = ex-ovarian lumen; P = parasite.

Mature resting or inactive testes (16 to 35 g) were dominated by seminiferous tubules. In some testes the lobules had contracted leaving large empty spaces. Crypts of gonia and spermatocytes were rare or absent across the whole sections from 75% of inactive testes and no later stages of spermatogenesis (spermatids and/or spermatozoa) were observed (Figs. 6.11A, B). The other inactive testes contained a few scattered crypts of spermatozoa and one of these was dominated by gonia. All testes collected between March and September were from resting males, indicating that males had a prolonged period of inactivity. The ripening males were sampled in October, where they accounted for 50% of the males observed (Figs. 6.11C, D). Of 13 mature ripe males (Figs. 6.11E-G), two individuals from early in the spawning period had testes with less than 50% spermatids and spermatozoa and well formed but partly filled major sperm ducts (mean gonad weight 27 g). The remaining ripe testes had

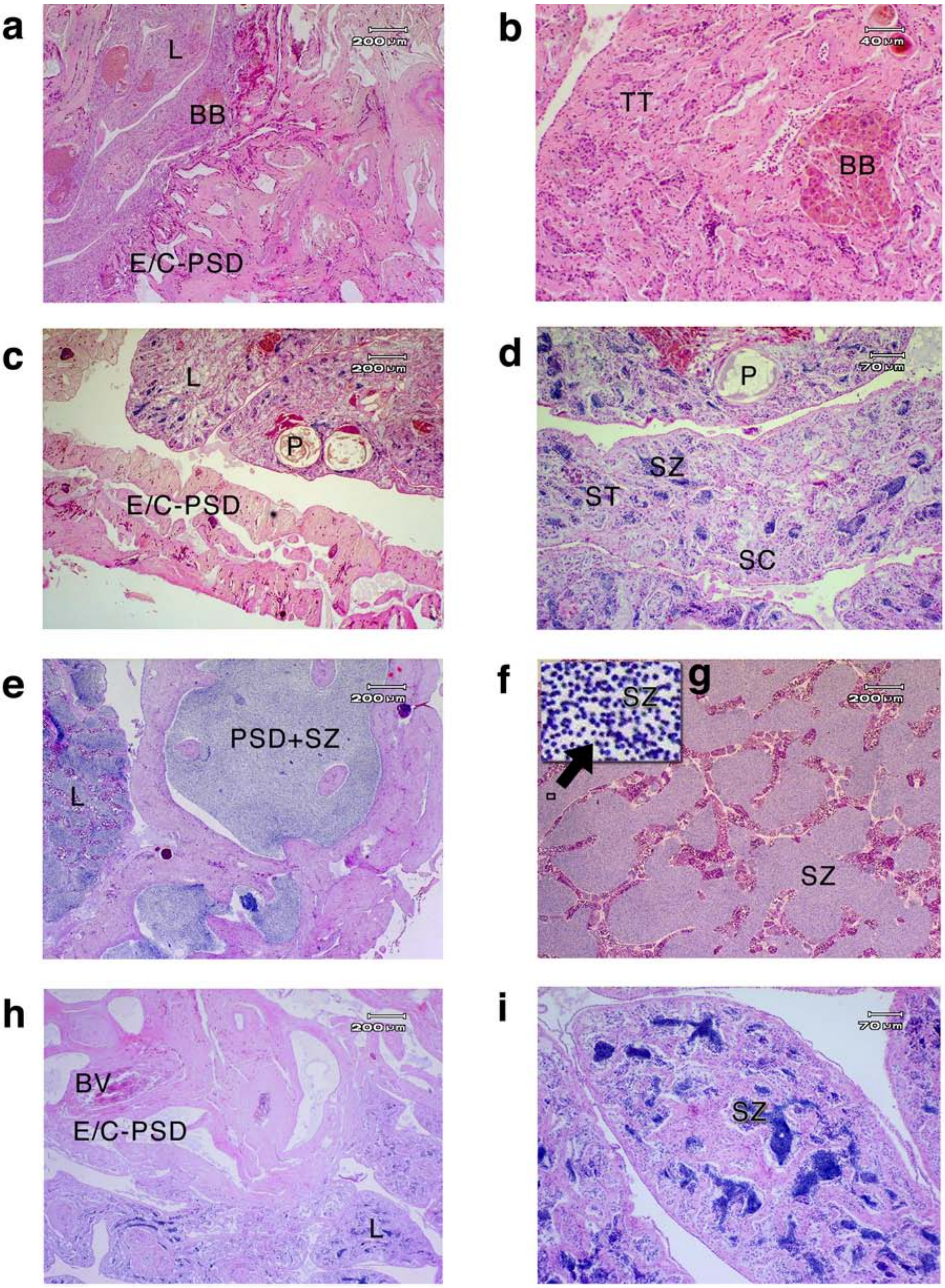


Figure 6.11 Histological sections of testes from *Epinephelus fuscoguttatus* depicting peripheral sperm ducts (left column) and typical detail of lobules (right column) of each developmental stages: (A), (B) mature resting, (C), (D) mature ripening, (E), (F) (G) mature ripe and (H), (I) mature spent. Definitions in Table 6.1. Symbol key: PSD+sz, peripheral sperm ducts full of sperm; E/C-PSD, empty or collapsed peripheral sperm ducts; GW, gonad wall; BV, blood vessel; BB, brown bodies; TT, testicular tissue; SC, spermatocytes; ST, spermatids; SZ spermatozoa; P, parasite. Scale bar is 200 µm for A, C, E, F, H, 40 µm for B, I, and 70 µm for D.

more than 50% spermatids and spermatozoa, with a few almost full of sperm, and all had ducts well formed and full of sperm (gonad weights 42 to 230 g, mean ± S.E.: 131 ± 18.0 g). All the above male types occurred throughout the full size and age range of males. Only one spent male was sampled in February (Figs. 6.11H, I). The tissue was disorganised, and even though spermatozoa were present in minor sinuses of some lobules, the major sinuses and ducts were empty, indicating that spawning had been completed for the season.

6.5 Discussion

The reproductive biology and reproductive cycle of *Epinephelus fuscoguttatus*, a large mobile serranid from the GBR, have been described for the first time. The findings are consistent with a monandric protogynous sexual pattern, and strongly suggest that all males are derived from mature females by adult sex change (i.e. secondary males), although confirmation of sex change (e.g. transitional gonads) is still required (Sadovy & Shapiro 1987). The presence of large old females in the population, however, suggest alternate female developmental pathways with only some females changing sex and others remaining female. The role of large, old females for aggregating reef fishes is not well understood, but may be important to social systems and reproduction. Younger, inexperienced fish may learn the way to traditional spawning sites by migrating with experienced fish (Warner 1988, Rose 1993, Coleman et al. 1996). It may also be that, in addition to having high fecundity (Sadovy 1996), larger, older and more experienced females produce offspring that are more viable with higher survivorship (e.g. Kjesbu et al. 1996, Kerrigan 1997, Trippel et al. 1997, Marteinsdottir & Steinarsson 1998, McCormick 1999, Berkeley et al. 2004a). It will be important to maintain the natural size and age structures (Berkeley et al. 2004b, Birkeland & Dayton 2005), and enough individuals of both sexes to ensure spawning aggregations continue to function (Coleman et al. 1996, Sadovy & Domeier 2005). A crude calculation suggested a large catchment area for *E. fuscoguttatus* on spawning aggregation sites, and refining this estimate will be important for understanding the scales of potential fishing effects and for designing appropriate management strategies to protect spawning individuals from over-exploitation (Sadovy & Domeier 2005).

6.5.1 Sexual pattern and reproductive analysis

The combination of gonad morphology and population structure strongly suggests a monandric protogynous sexual pattern for *E. fuscoguttatus* on the GBR, even though no transitional individuals have been reported to date for this species. Histological evidence consistent with protogyny includes the occurrence of crypts of precocious spermatocytes in some functional ovaries and the development of peripheral sperm ducts in the gonad walls which are used for the transport of sperm in mature males, rather than the distinct sperm duct typical of gonochores (separate sexes throughout life) (Sadovy & Shapiro 1987). The female-biased adult sex ratio, common but not exclusively in protogynous species, was within the expected range for a protogynous species (1 to 12 females per male, Sadovy & Colin 1995). The potential for monandry is supported by the size and age structures, with males dominating the larger and older groups and having a greater mean size and age than females (Sadovy & Shapiro 1987). Furthermore, the younger age groups contained only immature and mature females, and males were only observed above the size and age of 100% female maturity, consistent with a situation in which all males are secondary males. If sex change happens rarely and/or rapidly, larger sample sizes throughout the year will be required to sample individuals during sexual transition and confirm unequivocally the monandric protogynous sexual pattern. Future studies should also consider using an alternative criteria, experimental manipulation of adult females to induce male sex change to verify whether protogyny is likely (Sadovy & Shapiro 1987, Liu & Sadovy 2004a)

Reproductive analysis is problematic in epinepheline serranids with an extended period of reproductive inactivity (Samoilys & Roelofs 2000, Adams 2002). Distinguishing between mature resting and immature females is particularly problematic, as is sampling of transitional sex changing individuals. Inactive female *E. fuscoguttatus* for which the spawning history could not be determined (classified as undetermined inactive) occurred from six months onwards after the spawning period, which is consistent with previous findings that features used to indicate prior spawning may disappear within months of spawning. For example, Shapiro et al. (1993) noted that muscle bundles associated with contraction of the ovary after spawning could only be observed for five months following spawning in the red hind, *Epinephelus guttatus*. Undetermined inactive females were more prominent in younger and smaller groups. Two reasons may account for this. Firstly, signs of prior spawning may be easier to detect following numerous spawnings, making it easier to determine spawning history with age. Secondly, features used to indicate spawning history may have had longer to disappear if not all smaller and younger mature female *E. fuscoguttatus* spawn each year – a possible explanation of their low sexual activity noted in Chapter 5.

6.5.2 Reproductive cycle

The results identified one annual spawning period for *Epinephelus fuscoguttatus* on the GBR from about November to January, but the number of samples was insufficient to examine annual and spatial variation in the timing and duration of spawning. The prolonged period of male inactivity each year corroborates the finding of a relatively narrow spawning period for the species. The spawning period reported for *E. fuscoguttatus* in other areas is similarly restricted (Johannes 1981, Johannes et al. 1999, Robinson et al. 2004b). Transient aggregations related to spawning activity for this species in the Seychelles may form for over two weeks at a time and perhaps for two to three months per year (approximately November to January) (Robinson et al. 2004a). Inter-annual or spatial variation in spawning periods have been found for other reef fishes on the GBR (e.g. *P. leopardus*, Ferreira 1995, Turnbull & Samoilys 1997). More comprehensive study may reveal variability around the reported spawning period for *E. fuscoguttatus* on the GBR, possibly related to inter-annual variations in proximal environmental cues for spawning such as changes in water temperature (Samoilys 1997). In particular, spawning may be expected in October given the presence of active females and ripe males.

Females may spawn more than once during an aggregation period given the co-occurrence of post-ovulatory follicles and hydrated oocytes in a few ovaries from the GBR. The only published information on the frequency and lunar timing of spawning events within the season for *E. fuscoguttatus* comes from a detailed study in Palau (Johannes et al. 1999). Three or four significant spawning aggregations (peak diver counts were hundreds of *E. fuscoguttatus*) formed annually in Palau, with the peak between one and seven days before the new moon (i.e. eight to 14 days after full moon) and a duration of about five days (Johannes et al. 1999). However, sampling effort was largely confined to the 10 day period prior to new moons during their study because that period was considered to be the peak aggregation time locally. Thus, it is possible that spawning activity outside that period was missed. My results, based on occurrence of near spawning females, indicate spawning may occur at other times of the lunar month on the GBR. Although no information is available on the delay between oocyte hydration and ovulation (spawning) for *E. fuscoguttatus*, it is typically only a matter of hours for other reef fishes (e.g. <8 hrs, Ferreira 1995). The co-occurring species *E. polyphekadion* has also been reported to spawn on both the new (Johannes et al. 1999) and full moons (Rhodes & Sadovy 2002b) and the latter authors mention that reports show a wide variation in lunar periodicity and seasonal timing of spawning across the Indo-Pacific.

6.5.3 Implications for science and management

Uncertainty in the timing and duration of spawning aggregations means that future studies of spawning in *E. fuscoguttatus* should conduct sampling throughout the lunar cycle (and over several months) at least until the local pattern of spawning activity has been established. The recently introduced seasonal closures on the GBR for nine day periods around the new moons in October to December (based around the spawning period of *Plectropomus leopardus*) are likely to offer only limited protection to *E. fuscoguttatus* because aggregating behaviour is predicted to occur throughout much of the lunar cycle between November and January. A longer closure period would better protect *E. fuscoguttatus* (and any other reef fishes) that aggregate outside of the current closure periods. Some of their spawning aggregations may, however, be protected in no-take zones within the GBR network of marine protected areas (GBRMPA 2004).

Fishing information I present combined with histology revealing hydrated oocytes confirms that spawning aggregations of *Epinephelus spp.* are sometimes targeted on the GBR, and such targeted fishing can result in large catches. Occasional targeted fishing of aggregations of *E. fuscoguttatus* and *E. polyphekadion* on the GBR has been independently corroborated by other fishers (e.g. see discussion minutes in Pears 2005). Numerous fishers were reported fishing from the same aggregation on occasions (e.g. six mother boats carrying four dories). Such fishing practices have been implicated in the decline or disappearance of spawning aggregations of groupers in other parts of the world (Sadovy 1994a, Sadovy & Domeier 2005) and have been recognised as a potential concern in the Great Barrier Reef Marine Park (Turnbull & Samoilys 1997, Russell 2001). The vulnerability of *E. fuscoguttatus* spawning aggregations is apparent from the global spawning aggregation database compiled by the Society for the Conservation of Reef Fish Aggregations; out of 29 records for this species, 12 spawning aggregations (41%) are decreasing and one has gone (www.scrfa.org May 2005).

An important area for future work on the GBR (and elsewhere) is research and monitoring of spawning aggregations of potentially vulnerable reef fish such as *E. fuscoguttatus* and other large mobile serranids (Pears 2005). In particular, information is needed on fish spawning aggregation sites, the species using those sites, the timing and duration of aggregations, their catchment areas, dispersal dynamics and current status. There is also a lack of field behavioural observations for *E. fuscoguttatus* and the detailed spawning behaviour and mating system has yet to be described. It would be interesting to find out why reproductively inactive adult-sized fish are present at spawning sites, e.g. are they visiting an aggregation for population level information unavailable at other times? An important reproductive characteristic about which we know little for all but a few reef teleosts is the size and age specific annual reproductive output and success, yet such information would improve our understanding of and ability to model reef fish population dynamics and the effects of fishing.

By combining information on reproductive biology and reproductive cycle with a demographic study (Chapter 5) and abundance data (Chapter 3) I have provided an insight into the biology of *E. fuscoguttatus*, an example of a large mobile serranid. Groupers are very diverse on coral reefs, hence examining how well the reproductive and demographic characteristics of the studied population(s) of *E. fuscoguttatus* apply to other locations or other species of epinepheline serranids is a priority.

Chapter 7. General Discussion

7.1 Major findings and significance

Each of the three integrated studies presented in this thesis contribute to the primary aim of the thesis by extending our knowledge of tropical epinepheline serranid demography or assemblage structure, as well as adding to the growing knowledge of the complexity and variability of reef fish ecology and population dynamics. The comparative demographic study of cryptic serranids (Chapter 4) compared demographies for three species from several broad regions of the GBR and the Seychelles, revealing substantial spatial variation in demographics for each species. Hence, our ability to generalise about the demography of the cryptic serranids appears to be limited, notwithstanding that the prediction of a characteristic pattern of growth (Choat & Robertson 2002) may hold true for the behavioural group. By linking information on abundance and demography, it was also noted that different combinations of processes may influence local populations of the three species, with the possibility of broad-scale compensatory demographic trade-offs dependent on density noted for two of the three species.

The detailed study of a large mobile serranid, *E. fuscoguttatus* (Chapters 5 & 6) adds to our knowledge of reef fish ecology and intrinsic factors associated with vulnerability to fishing for a species of conservation concern, with findings that have direct relevance to management (harvest limits and size regulations, Pears et al. 2006, seasonal closures, Pears et al. Submitted). In particular, the extended lifespan (40+ yrs) and unusual reproductive ecology, such as the limited spawning in smaller, younger females, support the emerging view of epinepheline serranid biology as diverse and complex. The study of abundances of diverse epinepheline serranid assemblages over multiple scales on the GBR and in the Seychelles (Chapter 3) provided a comprehensive account of tropical epinepheline assemblages from which to consider potential spatial consistencies or differences in composition of these important predator assemblages. The various characteristics used to quantify “structure” in these assemblages showed differing spatial patterns and magnitudes of variation among behavioural groups and species, with some strong differences, such as in local densities, likely to be biologically significant. Some parameters (e.g. longevity) also showed significant variability within and among the four aged species. Thus, the research findings agree with the prediction of considerable variability in biological attributes of Indo-Pacific epinephelines.

The consistent picture obtained was that shallow-water epinepheline assemblages comprised a handful of abundant species from the cryptic or roving serranid behavioural groups, plus the numerous species found only in low densities locally (i.e. rare species) from each behavioural group but with different species abundant or rare in the GBR and Seychelles. While the ecological importance of rare species is not well understood, high biodiversity (i.e. the large number of species) and functional redundancy (i.e. overlap in functional roles among the group) is thought to be important to ecological resilience (Bellwood et al. 2002, Bellwood et al. 2004). Hence, rare species in epinepheline assemblages may be important for long term persistence and health of local reef fish assemblages . These rare species are difficult to study and often neglected in ecological studies, but there presence and diversity at all geographic scales I considered indicates a need to better understand the roles of this component of the fauna (Jones et al. 2002). Reef fisheries may severely deplete local populations of predatory reef fish (e.g. Koslow et al. 1988), including rare species, and an improved understanding is needed of the vulnerability of these assemblages to fishing to infer the consequences of their depletion or local extinction through fishing (Huntsman et al. 1999, Sadovy et al. 2003b). The results I present in this thesis contribute to that understanding.

Findings from the two biogeographic-scale studies (Chapters 3 & 4) have provided some support for the idea that there are fundamental differences in the ecology of reef fish assemblages over biogeographic scales (Sale 1991b) because several marked differences were found at an area or regional level. For example, assemblage structure was most variable at biogeographic scales where multivariate demographic indices (Chapter 4) showed clear separation of broad regions based on geographic area. If persistent, such differences suggest local population dynamics may also differ. Further, there was a trend of reduced longevities in the Seychelles than the GBR, which suggests higher recruitment levels and predictability of environmental conditions and resources in the Seychelles than the GBR. This follows from general theory that greater longevity in multiple spawners is an adaptive response to conditions of low and unpredictable recruitment that confers enhanced long-term population persistence (Warner & Chesson 1985, Longhurst 2002). Such differences may reflect diverging evolutionary histories of marine species from the two oceans, resulting from fluctuating sea levels and other biogeographic barriers (Bellwood & Wainwright 2002, Bay et al. 2004), although study of further geographic areas within the two oceans, including estimation of rates of recruitment, would be required to confirm this hypothesis. Consistency of my findings with other broad-scale demographic studies, such as on a surgeonfish, *Ctenochaetus striatus* (Laman Trip 2004), suggests that reduced longevities in the Indian Ocean compared to the Pacific Ocean may be a widespread phenomenon among coral reef fishes.

The extent to which we can generalise about species or behavioural groups of epinepheline serranids was a consistent theme throughout my thesis with clear scientific and applied relevance. The answer is multifaceted. For example, using behavioural groupings to examine assemblage-level patterns over multiple spatial scales demonstrated some shared characteristics in the studied epinepheline faunas (particularly rarity of large mobile serranids and similar characteristics of species diversity). Characteristics of abundance, distribution and size structure, however, varied in different ways for each behavioural group as well as for species within those groups. Extended longevities (> 35 yrs) are common but not universal in the Epinephelinae (Manooch 1987, Manooch & Mason 1987, Manickchand-Heileman & Phillip 2000, Mosse 2002, Pears et al. 2006). Three of the four aged species in this thesis were found to be relatively long-lived compared to some other epinepheline serranids (e.g. Ferreira & Russ 1992, 1994) and reef fish in general (Choat & Robertson 2002). Marked demographic variability was evident in the comparative study of cryptic serranids over broad spatial scales and among species. It was also emphasised that although *E. fasciatus, E. polyphekadion* and *C. argus* shared some characteristics associated with high vulnerability to fishing (relatively slow growth and moderate to long lifespans), differences among them in abundance, longevity and body size, and perhaps in population dynamics, suggest vulnerabilities may vary (Roberts & Hawkins 1999, Reynolds et al. 2001, Reynolds et al. 2002, Dulvy et al. 2003) and hence limit the applicability of generalisations across species or behavioural groups.

Comparisons of patterns of growth with published literature added some support for the hypothesis of Choat and Robertson (2002) that reef fish taxa tend to have highly distinctive, phylogenetically structured patterns of growth and age-based demographic features. Nevertheless, it is worth noting that for the Epinephelinae these patterns may not be shared by all genera, indicating considerable diversity with the family. For example, species of *Epinephelus* and *Cephalopholis* (e.g. this thesis, Grandcourt 2002, Mosse 2002) have more "flat-topped" patterns of growth than species of *Plectropomus* (e.g. *P. leopardus* and *P. maculatus*, Ferreira & Russ 1992, Ferreira & Russ 1994). The pattern of growth may affect opportunities for individual variation in growth, which largely occurs during the early years corresponding to the steeper part of the growth curve. The relationship between individual growth and sexual maturation and differentiation or reproductive allocation is not well understood, but may be important. For example, growth rates influenced patterns of maturation in five populations of *Thymallus thymallus* (the grayling, Haugen 2000), individual growth was thought to be important in juvenile sexual differentiation in *Cephalopholis boenak* (the chocolate hind, Liu & Sadovy 2004b), and in captive *Gadus morhua* (Atlantic cod) larger fish showed significantly longer spawning periods (Kjesbu et al. 1996). Thus, differing patterns of growth among genera of epinepheline serranids may be associated with substantial life history differences that would likely affect response to fishing and vulnerability to depletion or extinction. Differing responses to fishing among species of epinepheline serranids may reflect not only their age-based demographics, but also other intrinsic factors, most notably the detailed reproductive biology (e.g. Coleman et al. 1996, Samoilys 2000), and may occur even between closely related congenerics (e.g. Fennessy 2000).

This thesis has demonstrated that a multi-faceted approach can provide deeper insights into the biology of individual species and reef fish more generally. For example, examination of assemblage- or taxon-level patterns revealed not only differences but some similarities in epinepheline serranid faunas among locations. The results from Chapter 4, and from a recent study on the performance of no-take zones in the GBR (Begg et al. 2005), indicate that a holistic approach to the examination of demographic and life history characteristics can reveal patterns not detectable for individual parameters, leading to insights that would otherwise be unclear. Similarly, integrating datasets (abundance and size, Chapter 3; abundance and demography, Chapter 4; size, age and histology, Chapter 5 & 6) has allowed insights that would otherwise have been overlooked, such as possible differences among species in the presence and cause of broad-scale density-dependence or the occurrence of large old females with a reproductive lifespan that may exceed 30 years in *E. fuscoguttatus*. This also means that examination of only a narrow range of spatial scales or only a few species may lead to misleading conclusions regarding abundance patterns or generalisations for higher-level taxonomic groupings. Hence, there continues to be a need for integrated studies and comparative analyses of additional species of Indo-Pacific reef fishes to assess not only their vulnerability but also to evaluate alternative management options for those species subject to harvest.

7.2 Implications for conservation and fisheries management

There are growing conservation concerns regarding exploitation, potential vulnerability and current status of reef fishes such as epinepheline serranids (Russ 1991, Johannes & Riepen 1995, Russ et al. 1995, Koenig et al. 1996, Bentley 1999, Huntsman et al. 1999, Musick 1999b, Roberts & Hawkins 1999, Reynolds et al. 2002, Dulvy et al. 2003). This has prompted increasing efforts to better manage some reef fisheries (e.g. the reef line fishery in Queensland, Anon 2003). In this thesis I provide biological information on additional species of epinepheline serranids and explore some general patterns for the family which might further improve management planning.

Since I collected the data for this study, several management changes have taken place in the GBR, most notably the substantial increase in no-take zones within the Great Barrier Reef Marine Park (see GBRMPA 2004) and revision of management arrangements for the Queensland reef line fishery (Anon 2003). The latter included the introduction of new legal size limits for epinepheline serranids, which came into effect in December 2003. Measures were also implemented to reduce overall fishing effort in the reef line fishery, including a reduction in the number of licensed commercial operators under an individually transferable quota (ITQ) system and more stringent bag restrictions on charter and recreational catch. Amendments to the Great Barrier Reef Marine Park Authority's Regulations 1983 which came into force in July 2004 now list three species of epinepheline serranid (*Epinephelus lanceolatus, E. tukula, Cromileptes altivelis*) and all individuals of the genus *Epinephelus* greater than 1000 mm as Protected Species (no-take) within the Great Barrier Reef Marine Park. The dataset compiled for this thesis, therefore, represents an important record of biological parameters prior to major changes in management that will provide a valuable point of reference for future monitoring and evaluations of changes in response to the new measures (Vincent & Sadovy 1998). Such an evaluation would be complex, however, and there is some anecdotal evidence that fishing practices and targeting behaviour have also changed for the study species (Pears 2005) and we lack historical data prior to the onset of local fisheries (e.g. Jackson et al. 2001).

It is likely that *E. fuscoguttatus*, an example of both a large mobile serranid and a relatively rare epinepheline, may be rapidly depleted by fishing. Myers and Worm (2005) argued that management instruments for multi-species fisheries should be tailored to the most sensitive (or most vulnerable), rather than the more robust species, advocating reductions in fishing effort, reduction in bycatch mortality and protection of key areas to initiate recovery of severely depleted communities. *Epinephelus fuscoguttatus* may be one of the more vulnerable species in tropical reef fisheries. The detailed study of *E. fuscoguttatus* exposed biological characteristics associated with vulnerability to depletion or extinction (i.e. rarity, long lifespan, delayed effective maturity, protogynous sex change, spawning aggregation behaviour, Chapters 5 & 6) (Sadovy 1994b, 1997a, Morris et al. 2000). In particular, its natural rarity (<1 fish per 1000 m^2, Chapter 3) but probable susceptibility to rapid depletion through targeted fishing of its spawning aggregations (Johannes et al. 1999, Robinson et al. 2004b, Sadovy & Domeier 2005) indicate this species merits special management consideration (Pears 2005), as most likely other large mobile serranids.

We still know little of the biology of many species of large mobile serranids, but I would expect ongoing assessments (e.g. Red List assessments by the Grouper and Wrasse Specialist Group of IUCN's Species Survival Commission) to reveal additional species with relatively high vulnerability to over-fishing. *E. polyphekadion* is also known to aggregate to spawn but is otherwise found in low densities, and is therefore of some conservation concern (Rhodes & Sadovy 2002b). Depletions and extinctions at the population level are cause for concern because global extinctions are merely the end point of a series of local and regional extinctions (Pitcher 2001, Dulvy et al. 2003). Even when extinctions at global or regional spatial scales are considered unlikely, population depletions are of concern in themselves because depletions of predatory reef fishes can have indirect and cascading ecosystem effects, erode ecological resilience (the ability to cope and adapt), and limit future commercial, recreational or subsistence harvesting or tourism opportunities (Bohnsack 1996, Blaber et al. 2000, Carr et al. 2002, Hughes et al. 2005, Myers & Worm 2005).

The largest observed differences in abundance profiles were at the regional scale, and this scale also corresponded to significant variation in demographic characteristics. This suggests productivity varies regionally, and consequently local populations may respond differently to fishing or other threats. Such spatial structure raises the issue of spatially explicit management. For instance, differing size limits, catch quotas, effort levels or timing of closed seasons could be appropriate to match local variation in vital life history characteristics that influence productivity and reproductive output (e.g. growth, size at maturity, mortality schedules, abundance or reproductive seasons). Even though difficulties arise in seeking spatially variable fishery management arrangements within jurisdictions of single management agencies (e.g. in the GBR and the Seychelles), information on the levels of variation in biological characteristics is still important since such information can be explicitly incorporated into fishery assessments and managers can then select precautionary options that avoid over-harvesting the least productive/most vulnerable elements of a population (Williams 2003).

The issue of species-specific management arrangements in multi-species reef fisheries is also worth considering, given the results presented in this thesis. The large number of species of epinepheline serranids, difficulties in readily identifying many of them, and their diverse biological characteristics complicates their management and monitoring. Furthermore, where regulations have been introduced for the group, for example in Queensland, the same regulations are often applied across several similar-looking or similar-sized species even though biological attributes may differ (Pears 2005). From practical implementation and compliance perspectives, it is prudent to keep fisheries regulations such as size limits as simple as possible and to have the same limits apply to species that are easily mis-identified. Such an approach was adopted in the framing of the revised regulations for harvest of small (~ <50 cm) epinepheline serranids from the Queensland reef line fishery, based in part on the work presented in this thesis. New information on species biology and potential vulnerability to over-fishing, including this work, however, is valuable to enable evaluation and refinement of regulations to better protect size and age structures and spawning stock to ensure the future viability of the fishery.

Consider management of the very similar-looking larger epinephelines *E. fuscoguttatus* and *E. polyphekadion* in Queensland as an illustration. It seems likely that the new size limits (minimum 500 mm, maximum 1000 mm for both species) governing harvest of these species in Queensland will act differently on the two species because of differing body sizes, sexual patterns and demographic characteristics. *E. fuscoguttatus* reach about 1000 mm in length, and in Chapters 5 & 6 we saw that only limited protection was afforded to *E. fuscoguttatus* by the slot size limit. *E. polyphekadion* have been recorded up to about 700 mm (Chapter 4) and Rhodes and Sadovy (2002a) reported that *E. polyphekadion* in Pohnpei had substantially overlapping female and male size distributions and suggested two male sexual differentiation pathways (direct development from juveniles and probable adult sex change), based primarily on their histological analyses and work by Johannes et al. (1999). Both mature males and mature females were found at lengths less than 500 mm, suggesting that the current minimum legal size limit in Queensland will effectively protect the reproductive potential of *E. polyphekadion*. On the other hand, the fished component of the *E. fuscoguttatus* population will still include most of the female spawning stock and all of the males and the upper size limit is likely to have little, if any, effect. Hence, new knowledge of differences between these species in maximum body sizes, size distributions of breeding females and males, and patterns of male recruitment allow us to infer that the effectiveness of the size limits currently applied to both species is likely to differ between them (Pears 2005). Given the new information, a review of size limits for these species is advisable and I suggest lowering the maximum size limit for both species to protect some males and large breeding females of *E. fuscoguttatus*. *Epinephelus fuscoguttatus* and *E. polyphekadion* are also vulnerable to depletion by fishing of their spawning aggregations (Sadovy & Domeier 2005). Limited protection may be afforded to *E. fuscoguttatus* by current seasonal closures to fishing on the GBR (Chapter 6), but a longer closure period would be more precautionary. I suggest the situation may well be similar for *E. polyphekadion* on the GBR, given the reported similarities in timing of spawning aggregations (Johannes et al. 1999, Rhodes & Sadovy 2002b, Robinson et al. 2004a) and the occurrence of hydrated oocytes on the GBR in the same months as for *E. fuscoguttatus* (November, December, January, Pears *unpub. data*).

Any review of management arrangements for *E. fuscoguttatus* (and other large *Epinephelus*) should consider a combination of measures during aggregation and non-aggregation periods. Aggregation protection for *E. fuscoguttatus* on the GBR could be enhanced by a longer closure period of the reef line fishery, or the introduction of a longer closure period through special management arrangements only for particular species, such as *E. fuscoguttatus* and other epinepheline serranids that form relatively few, large, transient spawning aggregations. Although not popular with some fishers, effective seasonal closures reduce the risk of overfishing at a time when the species is particularly vulnerable, and a longer closure period for *E. fuscoguttatus* has been recommended by a Queensland fishing representative based on work presented here. The main protection measures during non-aggregation periods on the GBR focus on: 1) legal fish size limits; 2) protected areas (or no-take zones); and 3) keeping fishing mortality to an acceptably low level (through effort and catch restrictions). These measures are generally considered to be well-accepted, effective and enforceable for reef fishes on GBR (although no take areas are not popular with some fishery stakeholders). Improving the effectiveness of Queensland's size limits for *E. fuscoguttatus* is a priority.

In the Seychelles, ongoing research is focusing on spawning aggregations and reproductive biology of *E. fuscoguttatus* and *E. polyphekadion,* both valuable species in local fisheries, with a view to better protect their spawning aggregation sites (Robinson 2002, Robinson et al. 2004a, Robinson et al. 2004b). This understanding and protection is critical. It is not generally considered feasible at present to implement and enforce size regulations for reef fishes in the Seychelles. Nonetheless, given that this thesis provides further indications that some epinephelines are likely to be vulnerable to depletion at relatively low level of fishing pressure, it is important to protect natural size, age and sex ratios of epinephelines. This may be best achieved in the Seychelles through an enlarged network of no-take marine reserves (Jennings 1996, Murray et al. 1999, Russ 2002, Berkeley et al. 2004b, Begg et al. 2005), which can help counter shifting baselines by providing a window to the past (Pauly 1995, Bohnsack 2003).

7.3 Future directions

Continued efforts to identify those species or components of populations most vulnerable to fishing pressure and other threats, and the factors that make them so, will enable management efforts to be better directed and help prevent further serious depletions (Jennings et al. 1999b). Recent research has emphasised the important contribution of large, old females to reproductive output and success in a variety of fishes (Hislop 1988, Trippel et al. 1997, Marteinsdottir & Steinarsson 1998, Trippel 1998, Berkeley et al. 2004a). The results from Chapters 5 & 6 indicate that this effect might also apply to *E. fuscoguttatus,* a large bodied, long-lived reef fish of considerable interest to fisheries and conservation management. It will be necessary to evaluate the size and age specific annual reproductive output and reproductive success to quantitatively assess the relative contribution of different size or age groups of the population to the next generation, but such information is available for very few species. Experimental approaches previously confined to smaller reef fish species are becoming feasible for epinephelines with improved aquaculture techniques for completing the lifecycle of epinephenline serranids in captivity. Captive fish could be used to examine aspects of reproductive success such as quantifying maternal effects on eggs or larvae (e.g. Green & McCormick 2005).

Estimates of the degree to which various species of epinephelines effectively delay maturity will be important information for management because late maturity is associated with lower intrinsic rates of population increase and hence higher vulnerability to extinction (Myers et al. 1997b, Smith et al. 1998, Crouse 1999, Jennings 2000). Understanding factors causing a relatively high proportion of reproductively inactive fish above the size- and age-at-maturity for female *E. fuscoguttatus*, two other epinepheline serranids, *M. microlepis* and *E. andersoni,* (Koenig et al. 1996, Fennessy & Sadovy 2002) and some other reef fishes (e.g. Williams 2003) may enhance our ability to predict the effects of fishing and provide insights into possible life history trade-offs (e.g. between somatic growth and reproduction). Interestingly, the presence of mature-sized inactive females at spawning aggregation sites in Palau has been reported for two species, *P. areolatus* and *E. polyphekadion*, with close spawning association with *E. fuscoguttatus* (Johannes et al. 1999). A possible explanation could be that these non-reproductive fish could be visiting aggregations for population-level information unavailable at other times. It would be interesting to determine why such non-spawning females are present at spawning aggregation sites and such information would be useful for designing appropriate management strategies.

Investigating the underlying causes of observed spatial patterns in demographics and assemblage structure, including the degree of human and natural impacts, will be a rich area for future research. Epinepheline serranids have experienced varying levels of fishing pressure throughout the study areas, although only crude regional approximations of fishing pressure are available. Low densities of many epinepheline serranids tend to hinder the sampling required for comparisons of biological attributes from areas open and closed to fishing within a region. Historical depletions may have already occurred, but are difficult to detect. Alternative approaches for estimating the degree of fishing impacts may be worthwhile, such as retrospective analyses based on paleoecological, archaeological, and historical data (Jackson et al. 2001) and historical observations of distribution and abundance (Brander 1981).

Information is needed on extrinsic factors such as fishing mortality and habitat damage to complete robust fisheries or conservation assessments. Critical data gaps for epinepheline serranids in the GBR and the Seychelles include information on juvenile habitat affinities and species-level catch and effort data. While long-term collection of fisheries statistics at the species-level would provide the most valuable data, implementation would be difficult and a practical alternative is to use observer programs to record the species-composition of the catch (e.g. Mapstone et al. 2001a). Another important gap is robust indicators of the condition of, and pressures on, reef fish species, the ecosystem and dependent fisheries in the GBR and the Seychelles. Status reporting efforts, such as the Great Barrier Reef Marine Park Authority's State of the Reef Report (Wachenfeld et al. 1998), would benefit from careful identification of indicators of extrinsic influences on reef systems that might affect species vulnerabilities to over-fishing. An integrated multi-agency approach to data collection, monitoring and assessment would be required to achieve this goal.

Evaluation of the appropriateness of current harvest regulations, particularly size limits in the GBR, requires information on levels of post-release mortality, and on patterns of female maturation, reproductive output and male recruitment by size and age for each species (or population). With the introduction of quotas and no-take species and the use of legal size and bag limits, the issues of by-catch (including some epinephelines), high grading and post-release survival have become increasingly important in Queensland. Although some current research efforts on the GBR are investigating post-release survival for a number of reef fishes including *P. leopardus*, no species of *Epinephelus* or *Cephalopholis* have been included in the study. While a study found low levels of post-release mortality (5.1%) after capture with baited hooks from very shallow water (<2 m) for one small bodied species of *Epinephelus* (*E. quoyanus*, Diggles & Ernst 1997), capture depth, fish size, species identification, and de-hooking and handling practices are all likely to influence survival. Estimates of post-release survival for a wider range of species and situations are needed.

7.4 Conclusions

The findings reported here add to the emerging picture of epinepheline serranid biology as complex and diverse, and to a more holistic understanding of reef fish ecology. The thesis highlighted the importance of an integrated approach in the study of reef fish ecology and population dynamics, which can reveal patterns not detectable by more narrowly focused single-species studies. The dual approach of examining behavioural groups and selected species was more useful in the study of assemblage structure than demography. Variation within and among species was evident in some intrinsic factors, suggesting that vulnerabilities to fishing may vary at least on regional scales for a given species, as well as among closely related species. The importance of incorporating such variation into fisheries and conservation assessment was emphasised to avoid depletion of less resilient groups of individuals. Including this work, a substantial database is building on the abundance, age-based demographics and reproductive information on epinepheline serranids (e.g. Manooch 1987, Shapiro 1987, Coleman et al. 1996, Samoilys 1997, Sluka et al. 1998, Sadovy & Eklund 1999, Adams et al. 2000, Adams 2002, Fennessy & Sadovy 2002, Rhodes & Sadovy

2002a). Unlike this thesis, however, relatively few studies cover multiple spatial scales, whole assemblages and species-specific research in the one context. There are still many Indo-Pacific species of epinepheline serranids for which we know little of their biology, and this thesis indicates at least some of these, particularly larger bodied species, may turn out to be particularly vulnerable to over-fishing or other threats.

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Appendices

Appendix 1: Preliminary analyses for Chapter 3

This appendix provides details of three preliminary analyses for Chapter 3. The first examined the effect of sample size on the estimates of species richness, the second examined the effect of inter-annual temporal variation on count data, and the third examined the effect of reef type in the Seychelles on count data. The findings of these analyses were incorporated into the material presented in Chapter 3.

A1.1 Methods

Replication

The effect of sample size (number of replicate swims) on the estimates of species richness (species count) was examined by plotting the cumulative number of species as a function of the number of transects surveyed for each area or broad region using a bootstrapping technique (Efron & Tibshirani 1993). The dataset for each area or broad region was re-sampled 1000 times with replacement for every level of replication (1 to *n* long-swim transects, the total sample size) and for each set of 1000 re-samples the mean cumulative numbers of species was estimated (Haddon 2001). The number of replicates at which the rate of increase in number of species is sharply reduced can be used to determine the minimum acceptable level of replication (modified from Bros & Cowell 1987).

Temporal variation

Some sites were surveyed in more than one year and for these sites counts were compared among years to assess the importance of inter-annual variation in count data (Chapter 3, Table 3.2). Only data from the Lizard region were included in the analysis as very few sites elsewhere were surveyed on multiple occasions. The year 2001 – 2002 (Chapter 3, Table 3.2) was excluded from the analysis as insufficient data were available for calculations due to low numbers of transects conducted in that year. Counts were averaged over transects within reefs and habitats for these analyses. Accordingly, a three factor fixed effects analysis of variance (ANOVA) was used to compare density estimates for all epinephelines and each behavioural group among Position, Habitat and Year for data from the Lizard region. Sources of variation involving the factor Year (i.e. main effect of Year or interactions involving Year) were used to test the assumption that there was no difference in density between Years during the sampling period and that density was similar between Years for each shelf position and habitat.

Reef type in the Seychelles

In the Seychelles, comparison of reef type was only possible within the Inner Isles, the only Seychelles broad region where multiple reef types were surveyed. ANOVA was used to compare among reef-types (3 levels: granitic, mixed granitic boulder and carbonate, carbonate reef): (1) density estimates for all epinephelines; (2) each behavioural group; and (3) the number of species per transect.

A1.2 Results of preliminary analyses

The plots of mean cumulative number of species as a function of replication level for each area and broad region showed sharp decreases in the rates of increase of number of species within the available sample sizes (Figs. A1.1 & A1.2). The changes in slopes suggested that a minimum replication of about 40 samples per area (Fig. A1.1), or about 10 samples per broad region (Fig. A1.2), were sufficient for species counts to estimate species richness at each scale. These plots also indicated that unequal sample sizes will tend to bias comparisons of species counts. Accordingly, estimates of the mean cumulative number of species for replication equal to the lowest sample size of any group being compared (Areas: *n* = 52; Broad Regions: *n* = 10), termed 'bootstrap species counts', are presented for comparisons with results from the full raw datasets.

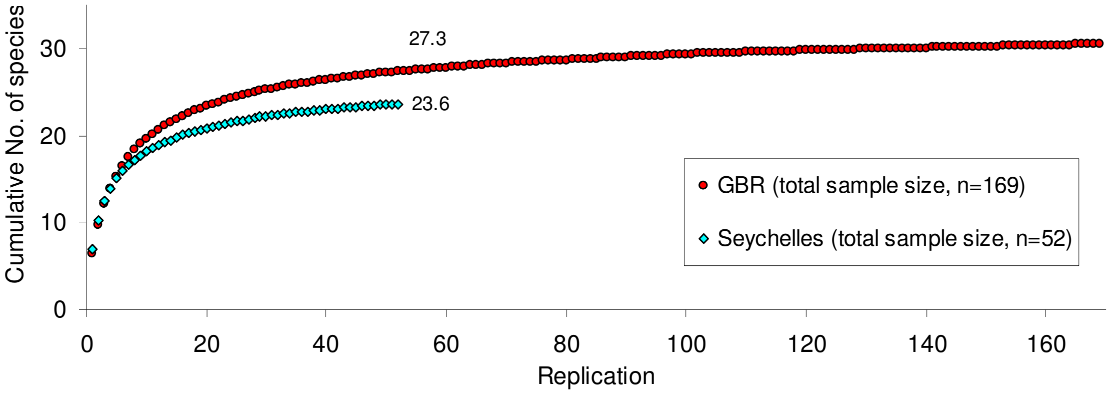


Figure A1.1 Change in cumulative number of species recorded with increasing replication level (i.e. number of long-swim transects) derived by bootstrapping for areas. Full dataset used. Data labels are y-values for replication = 52.

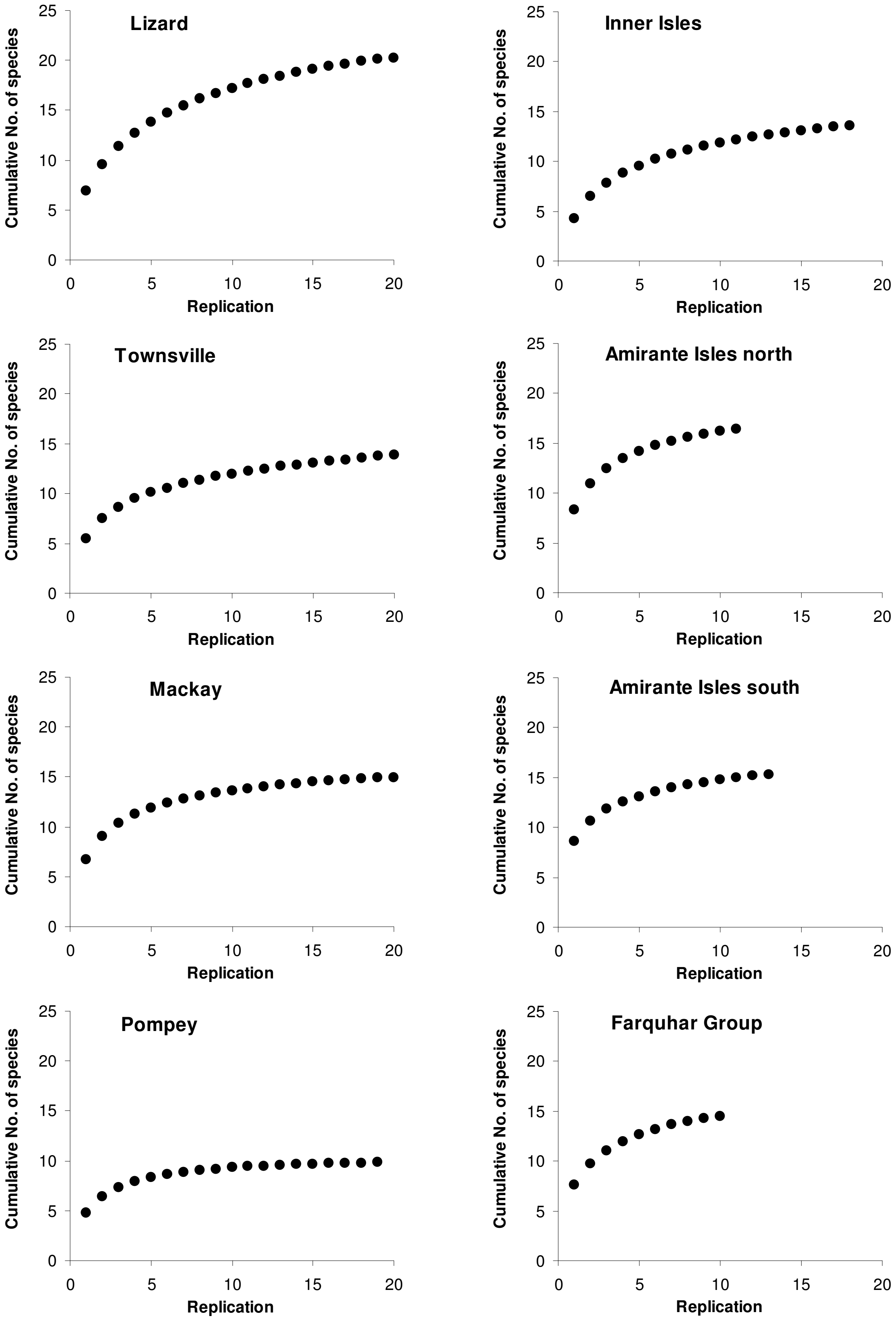


Figure A1.2 Change in cumulative number of species recorded with increasing replication (number of long-swim transects) derived by bootstrapping for broad regions. Data used as per Appendix 2: Table A2.1. Each plot presents the estimates for replication levels one to 20 or the total sample size if less than 20.

Analyses of inter-annual variation in density of all epinephelines and each behavioural group using data from the Lizard region did not detect any significant sources of variation involving Years (Table A1.1), meaning that density was similar between the years examined across the northern GBR (Lizard) region. Similarly for the Seychelles, one-way analysis of variance found no significant differences in 1) density of all epinephelines (Table A1.2); 2) density of each behavioural group (Table A1.2); or 3) number of species per transect ($F_{2,15}$=0.72, p=0.502) between reef types (fixed factor) in the Inner Isles. Accordingly, data were pooled across reef types within the Inner Isles for comparisons with other broad regions.

Table A1.1 Analysis of variance comparing density estimates for the Lizard region (GBR) among years (2 levels: summers of 2000-1, 2002-3) for all epinephelines and each behavioural group. Only results for sources of variation involving the factor Year (i.e. the main effect of Year or interactions involving Year) are shown as these were used to test for temporal variation. df=degrees of freedom, F=F-ratio, p=probability of the data if no difference existed.

Source of variation	**df**	**All epinephelines**		**Behavioural groups**		**Cryptic serranids**		**Roving serranids**		**Large mobile serranids**	
		F	p	Pillai's Trace	p	F	p	F	p	F	p
Year	1	1.04	0.3151	0.41	0.7492	1.01	0.3235	0.13	0.7247	0.13	0.7248
Position*Year	1	1.46	0.2357	0.50	0.6833	1.31	0.2617	0.39	0.5357	0.12	0.7367
Habitat*Year	2	0.28	0.7601	0.46	0.8381	0.30	0.7451	0.04	0.9600	0.73	0.4921
Position*Habitat*Year	2	0.20	0.8215	0.47	0.8298	0.47	0.6277	0.11	0.8964	0.73	0.4882
Residual (error)	30										

Table A1.2 Analysis of variance comparing density estimates for the Inner Isles (Seychelles) among reef-types (3 levels: granitic, mixed granitic boulder and carbonate, carbonate reef) for all epinephelines and each behavioural group. Degrees of freedom were 2, 15. F=F-ratio, p=probability of the data if no difference existed.

Source of variation	**All epinephelines**		**Behavioural groups**		**Cryptic serranids**		**Roving serranids**		**Large mobile serranids**	
	F	p	Pillai's Trace	p	F	p	F	p	F	p
Reef Type	0.72	0.5024	0.55	0.7677	0.38	0.6872	0.69	0.5148	0.60	0.5639

Appendix 2: Details of sampling design for Chapter 3

Table A2.1 Sampling design for GBR and Seychelles regional comparison.

Area	Broad Region	Reef code	Number of long-swim transects
Great Barrier Reef, Pacific Ocean	Lizard mid shelf	Eyrie	6
	(sheltered & exposed only)	Lizard	11
		Macs	6
		Northdir	5
		Rockyis	6
		Southdir	6
	subtotal		40
	Townsville	Dip	4
		Faraday	4
		Fork	3
		Glow	2
		Knife	4
		Yankee	4
	subtotal		21
	Mackay	20-136	3
		20-137	4
		20-142	3
		Bax	5
		Bolton	2
		Liff	3
	subtotal		20
	Pompey	21-124	4
		21-130	3
		21-131	3
		21-132	3
		21-133	3
		21-139	3
	subtotal		19
Great Barrier Reef total			100
Seychelles Islands, Indian Ocean	II	Harr&sec	5
		Isolated	1
		Mahe_ne	1
		Mahewest	3
		Silhouette	3
		StAnne	5
	subtotal		18
	AN	Poivre	6
		Remire	2
		StJoseph	3
	subtotal		11
	AS	Alphonse	6
		Bijoutier	7
	subtotal		13
	FQ	Far1	2
		Far2	1
		Far3	2
		Far4	1
		Far5	2
		Far6	2
	subtotal		10
Seychelles Islands total			52
Grand total			152

Table A2.2 Sampling design for examination of habitat and fishing effects among GBR regions. Treatments: high=fully fished, medium=moderately fished, low=lightly fished.

Broad Region	Habitat	Treatment	Reef code	Number of long-swim transects
Lizard mid shelf	Exposed	high	Lizard	5
			Northdir	2
		low	Macs	3
			Southdir	3
		medium	Eyrie	3
			Rockyis	3
	subtotal			19
	Sheltered	high	Lizard	6
			Northdir	3
		low	Macs	3
			Southdir	3
		medium	Eyrie	3
			Rockyis	3
	subtotal			21
Lizard mid shelf total				40
Townsville	Exposed	high	Fork	2
			Knife	2
		low	Dip	2
			Glow	1
		medium	Faraday	2
			Yankee	2
	subtotal			11
	Sheltered	high	Fork	1
			Knife	2
		low	Dip	2
			Glow	1
		medium	Faraday	2
			Yankee	2
	subtotal			10
Townsville total				21
Mackay	Exposed	high	Bolton	1
			Liff	2
		low	20-137	2
			20-142	2
		medium	20-136	2
			Bax	3
	subtotal			12
	Sheltered	high	Bolton	1
			Liff	1
		low	20-137	2
			20-142	1
		medium	20-136	1
			Bax	2
	subtotal			8
Mackay total				20
Pompey	Exposed	high	21-124	1
			21-139	2
		low	21-131	1
			21-132	1
		medium	21-130	1
			21-133	2
	subtotal			8
	Sheltered	high	21-124	3
			21-139	1
		low	21-131	2
			21-132	2
		medium	21-130	2
			21-133	1
	subtotal			11
Pompey total				19
				100

Table A2.3 Sampling design for Northern GBR cross-shelf comparison (Lizard region).

Region	Position	Habitat	Reef code	Number of long-swim transects
Lizard	Outer shelf	Exposed	Carter	7
			Day	1
			Hicks	3
			Hilder	3
			Noname	1
			Yonge	3
		subtotal		18
		Sheltered	Carter	5
			Day	2
			Hicks	3
			Hilder	4
			Noname	2
			Yonge	3
		subtotal		19
		Lagoonal	Carter	3
			Day	5
			Hicks	4
			Hilder	3
			Noname	1
			Yonge	3
		subtotal		19
	Outer shelf total			56
	Mid shelf	Exposed	Eyrie	3
			Lizard	5
			Macs	3
			Northdir	2
			Rockyis	3
			Southdir	3
		subtotal		19
		Sheltered	Eyrie	3
			Lizard	6
			Macs	3
			Northdir	3
			Rockyis	3
			Southdir	3
		subtotal		21
		Lagoonal	Eyrie	3
			Lizard	4
			Rockyis	3
			Southdir	3
		subtotal		13
	Mid shelf total			53
Lizard region grand total				109

Appendix 3: Details of sampling design for Chapter 4

Table A3.1 Sampling details by species, year, month and area used in Chapter 4 demographic study. A = *Epinephelus fasciatus,* B = *E. polyphekadion,* C = *Cephalopholis argus*.

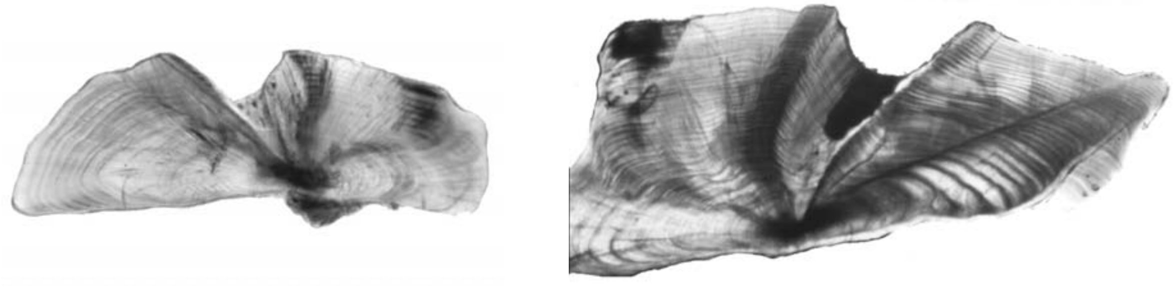
A. *Epinephelus fasciatus*		Area	
Year	Month	GBR	Seychelles
2000	10	17	
	11	65	13
	12	1	
2001	2	6	
	4	2	
	7	11	
	8	9	
	10	7	
	11	34	
	12	35	
2002	1		113
	11	36	19
	12	9	
Total		232	145

B. *E. polyphekadion*		Area	
Year	Month	GBR	Seychelles
1999	12		9
2000	7		14
	9		21
	10	12	
	11	19	24
2001	1	1	
	7	24	
	8	18	
	9	7	
	10	11	
	11	33	
	12	30	
2002	1	3	14
	2	4	
	3	7	
	4	3	
	5	4	
	6	7	
	11	6	21
	12	6	
2003	1	9	
	2	2	
Total		206	103

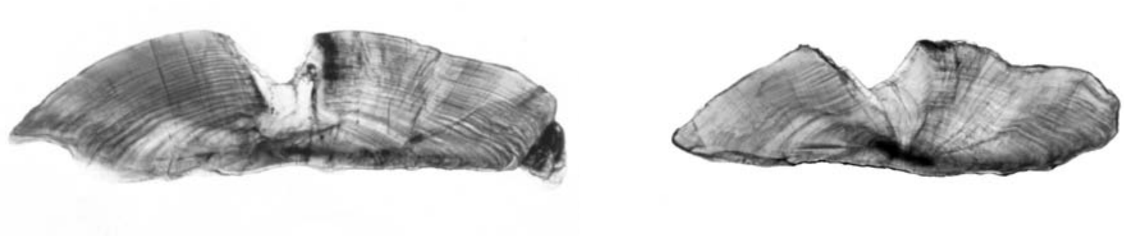
C. *C. argus*		Area	
Year	Month	GBR	Seychelles
1999	12		1
2000	9	1	
	10	24	
	11		8
	12	2	
2001	1	7	
	2	2	
	4	1	
	5	6	44
	7	6	
	8	5	
	9	5	
	10	1	
	11	41	
	12	20	
2002	1		104
	11	6	5
	12	5	
2003	1	5	
Total		137	162

Appendix 4: Summary of preliminary age validation for *E. fasciatus, E. polyphekadion* and *C. argus*.

Established age validation methods were used to test the assumption that increments were annuli for *E. fasciatus, E. polyphekadion* and *C. argus* from the GBR (e.g. Choat & Axe 1996, Fowler & Short 1998, Manickchand-Heileman & Phillip 2000). The approach taken follows the methods detailed in Chapter 5 and Pears et al. 2006. The otoliths of each species displayed an internal structure of increments (Fig. A4.1), although readability was relatively low for *C. argus* (Chapter 4). An oxytetracycline (OTC) marking experiment using three wild-caught individuals confirmed that otolith increments in *E. polyphekadion* were formed annually (Fig. A4.2, Table A4.1). The fish ranged in age from 7 to 15 years at end of experiment. It was assumed that validation of increment formation applied to other age classes, but data were insufficient to test this assumption. For *E. fasciatus* and *C. argus,* individuals marked with OTC (n = 1 and n = 4, respectively) survived for only 1 to 6 months. However, on examination of the otoliths, the width of marginal material deposited on the outer edge of the otolith since marking with OTC was generally consistent with an annual period of formation in each case. The relationship between otolith weight and number of increments was examined for each species from the GBR and the Seychelles using correlation analysis (Fig. A4.3). A strong correlation between otolith weight and putative age (number of increments) was found, indicating that otoliths accreted calcium carbonate throughout the life of the fish (Choat & Axe 1996).



E. fasciatus: 276 mm Fl, age 12 yrs *E. polyphekadion:* 546 mm Fl, age 32 yrs



C. argus: 404 mm FL, age 22 yrs, readability = 3 *C. argus:* 360 mm FL, age 16 yrs, readability = 4

Figure A4.1 ***Epinephelus fasciatus, E. polyphekadion*** **and** ***C. argus.*** **Sectioned otoliths showing internal structure of increments.**

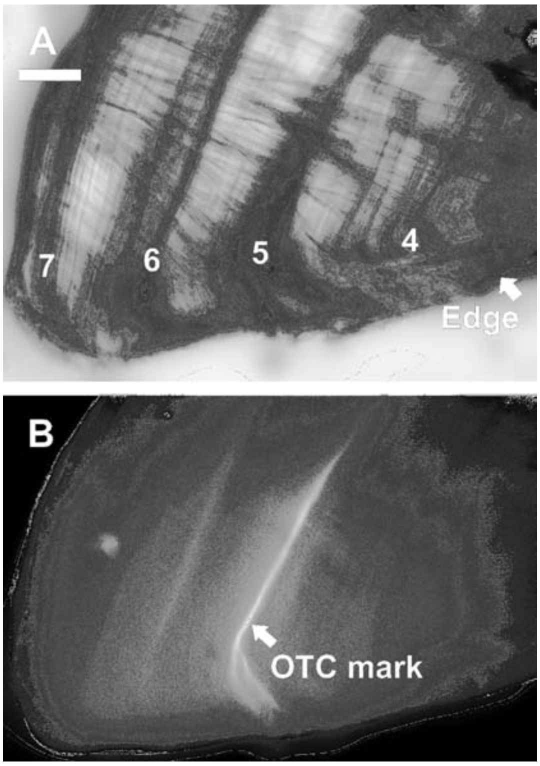


Figure A4.2 ***Epinephelus polyphekadion*****. Details of oxytetracycline (OTC) marked otolith showing: (A) annual bands (4th – 7th) and (B) OTC mark on same area under UV light. Scale bar 0.05 mm.**

Table A4.1 ***Epinephelus polyphekadion*****. Details of age validation experiment of wild-caught adults marked with oxytetracycline (OTC).**

Specimen code	**RP151**	**RP158**	**RP163**
Sample location	Eyrie Reef	MacGillivray Reef	MacGillivray Reef
Date of OTC marking	10 Nov 2000	10 Nov 2000	10 Nov 2000
End date	12 Dec 2002	12 Dec 2002	12 Dec 2002
Growth period (days)	762	762	762
Growth period (yrs)	2.1	2.1	2.1
Fork length at start	315	490	460
Fork length at end	404	546	532
Growth in length (mm)	89	56	72
Growth in length per yr (mm yr^{-1})	42.6	26.8	34.5
Location of OTC mark	Start of T-zone	Outer edge of O-zone	Start of T-zone
Number of zones outside of OTC mark[a]	T + O + T + O + T	T + O + T + O	T + O + T + O + T
Margin type	Thin T-zone	Outer edge of O-zone	Start of T-zone
Age at end (yrs)	7+	15	12
Calculated periodicity of "annuli" formation (yrs)	1.02	0.96	0.99
Suggested timing of opaque zone formation	Spring	Spring-early Summer	Spring

[a] *T = translucent zone, O = opaque zone*

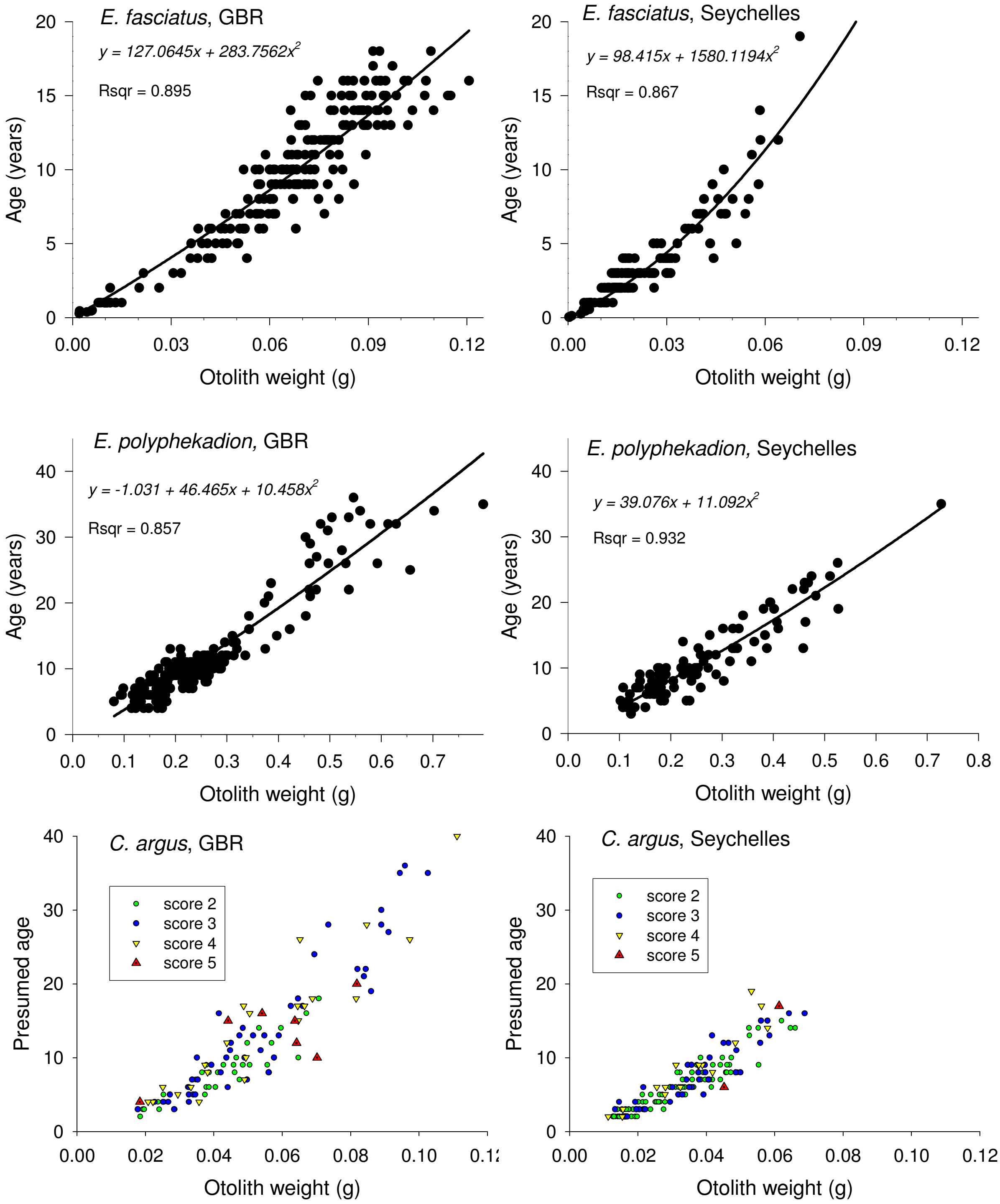


Figure A4.3 ***E. fasciatus, E. polyphekadion* and *C. argus*. Relationships between otolith weight and presumed age for the GBR (left) and the Seychelles (right). For *C. argus*, symbols indicate readability score (2 to 5, Chapter 4, Table 4.3) as shown in the legend.**