The Ecological Significance of Body Size
in Tropical Wrasses
(Pisces : Labridae)

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Abstract

Among terrestrial organisms, body size exhibits predictable relationships with many characteristics including growth rate, mortality rate, longevity, reproductive traits, abundance, species richness and habitat use. However, the majority of studies identifying such relationships have looked at a limited range of terrestrial taxa, in particular mammals, birds and beetles. These patterns have received much less attention among marine organisms and consequently their generality is questionable. Factors influencing growth of organisms in terrestrial and marine environments may be fundamentally different. This variation could result in considerable differences in growth processes among marine and terrestrial organisms and influence constraints on body size among species in these environments. The principal aim of this study was to identify whether numerous body size-related patterns observed in terrestrial taxa were repeated in a group of coral reef fishes, and assess reasons for differences when predicted relationships were not detected.

This study employed a multispecific comparative approach to examine life history and ecological correlates of body size in coral reef fishes of the wrasse family (Pisces: Labridae), a group in which species range in length from 4cm to over 2m. To account for the influence of evolutionary history of species on the patterns observed, a working hypothesis for a wrasse phylogeny was derived for the sampled species. This phylogeny was integrated into the analyses for Chapters 2 and 3 of this thesis.

The study comprised four main data chapters examining relationships between body size and a range of life history traits and other ecological characteristics. In Chapter 2, the relationships between maximum body size of species and growth rate, mortality rate and longevity were examined among ten species of wrasses which encompassed a ten-fold size range. Based on current theory it was predicted that there should be a positive relationship between maximum size of species and maximum age and a corresponding negative relationship between maximum species size and mortality rate. Both of these relationships were detected for the wrasses studied here. Conceptual models indicating ways in which differences among body sizes of fish species can arise were developed and tested. It was found that in some species larger size was simply attained by growing at the same rate as smaller species but for a longer period of time. In other species faster growth enabled the attainment of larger body size but at the cost of shortened life-span. There was limited evidence that by growing faster individuals became larger and less susceptible to predation sooner, resulting in larger body sizes and longer life spans. A further idea was that smaller species are smaller because they have determinate growth and stop growing sooner than larger species. Wrasse species studied here exhibited the range from indeterminate to determinate growth but there was no apparent relationship between maximum body size of species and growth strategy.

In Chapter 3 covariation between maximum size of species and reproductive characteristics was explored. It was predicted that smaller species should mature and change sex at a smaller proportion of maximum size and proportionally earlier in life than larger species. They were also expected to have greater reproductive effort than larger species. Despite this, none of these relationships between maximum species size and reproductive traits were evident. Relationships between maximum size and size at maturity and sex change were in fact opposite to those expected as smaller species matured and changed sex at a greater proportion of maximum size than larger species. Similarly, short-lived species matured and changed sex proportionally later in life than long-lived species. In general, body size appeared more important than age in determining when maturation and sex change occurred both among and within species. Energy invested per reproductive episode was not significantly related to species body size.

In Chapter 4, covariation among body size, growth rate, longevity, reproductive effort and size/age at maturity and size/age at sex change was examined in the wrasse *Halichoeres melanurus*. Individuals were sampled at four locations along a latitudinal cline. Consistent with patterns identified to date it was predicted that with an increase in latitude there should be a decrease in growth rate, and an increase in body size and longevity. Initial growth rate was slightly slower at the two higher latitude locations and the maximum body size and maximum age of individuals within populations did tend to increase with an increase in latitude. It was also considered that an increase in latitude should be associated with an increase in the proportion of adult size and age attained before maturation and sex change, and an increase in reproductive effort. However, there was no consistent relationship between the latitude at which individuals were sampled and the proportion of maximum size/age attained at maturity or sex change. In addition reproductive effort of individuals did not vary predictably as latitude increased. Individuals collected at the Palm Islands matured relatively earlier, exhibited greater

reproductive effort and changed sex proportionally earlier in life than those collected at Kimbe Bay, Lizard Island and Heron Island.

In Chapter 5, relationships between body size and ecological characteristics including local abundance, species richness, habitat use and depth range, were investigated among all wrasse species present at a range of locations. Based on patterns identified within both marine and terrestrial taxa it was predicted that the smallest species would not be the most abundant with abundances peaking in species of small to intermediate size. Very large species were expected to have low abundances. This relationship was expressed for the wrasse species examined here. In addition, the body size-species richness distribution of wrasses at a number of locations was log normal, with many species of small to intermediate size and low numbers of very small or very large species. Smaller reef fish species were expected to be associated with a smaller range of microhabitats than larger species, be more habitat specific and have smaller depth ranges than larger species. The small wrasse species examined here were found to use a small, intermediate or large diversity of available microhabitats, whereas the larger species consistently used a wide diversity of microhabitats. Depth ranges of small species lay on a continuum from very small to very large, whereas larger species consistently had large depth ranges.

Variation between some of the patterns observed in this study and those described in previous studies, demonstrates the need to replicate similar studies in a wide range of organisms inhabiting a wide range of habitats before their generality can be assessed. Repeating similar studies among species within a large range of reef fish families is crucial to determine the utility of species body size as a predictor of life history characteristics and other ecological variables in reef fishes.

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Chapter 6: General Discussion

CHAPTER 1: General Introduction

Body size is one of the most conspicuous biological characteristics of a species. The size range of organisms on earth encompasses at least 21 orders of magnitude from mycoplasma with a mass of less than 0.1 picograms, to the largest living organism, the blue whale reaching over 100,000 kilograms (Schmidt-Neilsen 1984, Ebenman & Persson 1988). Biological and ecological descriptions of species often begin with reference to their adult body size, although species are usually born at a characteristic size and grow at a characteristic rate before this size is reached. There are predictable relationships between variation in body size among species and a range of ecological variables. For example, in the majority of taxa examined to date, body size distributions of species are log-normally distributed, with very small and very large species being rare and small to intermediate-sized species predominating (Blackburn & Gaston 1994, Warwick & Clarke 1996, Loder 1997, Brown et al. 1993, Hodkinson & Casson 2000). What biological rules determine differences in adult sizes among species? How is adult body size related to other aspects of the biology and ecology of a species? An evaluation of the causes and consequences of body size is an issue that is central to nearly all branches of biology.

Growth and maximum size are recognised as fundamentally important attributes of organisms and have a direct bearing on patterns and processes at all levels of biological organisation (Peters 1983, Calder 1984, Schmidt-Neilsen 1984). At the physiological level for example, metabolic rate and physiological times such as time between heartbeats, scale predictably with body size (Peters 1983, Clarke & Johnston 1999). At the whole organism level, growth and body size often covary with other important life history traits, such as the size and age at maturity (Calder 1984, Promislow & Harvey 1990), reproductive output (Roff 1986, Barbraud et al. 1999) and life expectancy (Stearns 1983). An individual's access to and requirements for resources, such as food (Wainwright 1988, Clifton & Motta 1998), shelter (Hixon & Beets 1993, Caley & St John 1996) and living space (Gaston & Blackburn 1996), are closely linked to body size. The intensity and outcome of ecological interactions such as predation and competition can be predicted on the basis of size differences between interacting species (Ebenman & Persson 1988, Robertson 1998, Sih et al. 2000). For nearly all groups of organisms examined to date, key population and community parameters, including geographic distribution (Gaston 1990), local distribution and habitat use (Ziv 2000), population size and local density (Damuth 1981, Johnson 1999, Polishchuck & Tseitlin 1999) all appear to be related either directly or indirectly, to body size (Munday & Jones 1998).

When considering relationships between body size and biological variables of interest, emphasis is often placed on consistent patterns among taxa and/or the predictive power of quantitative relationships (Gaston & Lawton 1988, Nee et al. 1991, Loder 1997). If similar relationships are detected in a wide range of species in a wide range of habitats they may be of general importance (Lawton 1999). Many allometric relationships conform to the mathematical relationship $Y=aM^b$ (where Y is the biological characteristic to be predicted, M is body mass, and a and b are empirically derived constants), suggesting consistent functional relationships. As an example, metabolic rate scales to body size with an exponent b of 3/4 (Peters 1983). However, the underlying basis for these relationships requires much clarification (Peters 1983) and illustration of such relationships cannot differentiate between cause and effect (Charnov & Berrigan 1991, Harvey & Keymer 1991, Millar & Hickling 1991, Reznick et al. 1996). Nevertheless, an examination of the biological correlates and forms of relationships between body size and critical biological variables, across a range of species and habitats, is a necessary first step toward understanding the functional relationships between these variables (Millar & Hickling 1991).

Most studies supporting generalisations about relationships between size and important ecological parameters have been confined to terrestrial species, particularly beetles, birds and mammals (eg. LaBarbera 1989, Promsolow & Harvey 1990, Blackburn & Gaston 1994, Loder 1997; but see Munday & Jones 1998, Jones et al. 2002). Due to this taxonomic bias, current understanding of body size relationships may be unrepresentative of organisms in general, particularly aquatic species (Munday & Jones 1998, Jones et al. 2002). Fishes are one group of vertebrates for which the evolutionary and ecological causes and consequences of body size remain poorly understood. The ways in which biological characteristics of fishes scale with size may differ from their terrestrial counterparts for many reasons, some of which are associated with the denser aquatic medium and the three dimensional nature of the habitats fishes occupy (Juanes 1986).

Firstly, there may be fewer constraints on maximum body size and a reduced need for skeletal strength to support larger organisms in species inhabiting water (Schmidt-

Neilsen 1984). Secondly, there may be greater costs associated with movement through the denser medium. Thirdly, in contrast to most other vertebrates, many fishes exhibit indeterminate growth where individuals continue to grow until they die (Charnov & Berrigan 1991, Stearns 1992). In species with indeterminate growth, a trade-off between allocation of available energy to growth and reproduction continues throughout life (Bell 1980, Schwarzkopf & Shine 1992, Charnov 1993, Shine et al. 1996). Energy allocation strategies are likely to be much simpler in species with determinate growth. In these species energy is largely directed to somatic growth in the early stages, whereas following maturation energy is diverted mostly to reproduction causing a cessation of growth (Peters 1983, Charnov 1993).

The role of temperature variation in constraining growth and body size may also differ between aquatic and terrestrial environments. In terrestrial animals, individuals in warmer climates tend to be smaller than those in colder environments (Bergmann's rule - Bergmann 1847, Mayr 1956). One potential explanation for this pattern is that when ambient temperature is high, large organisms have problems dissipating heat, as they have a lower surface area: volume ratio than smaller animals. Consequently, the energetic cost of regulating temperature is greater in larger animals (Begon et al. 1996). In aquatic poikiliotherms such as fish, body temperature is determined by ambient water temperature, so trends in body size associated with average environmental temperatures cannot be explained in terms of energy devoted to temperature regulation (Atkinson 1994). Despite this, absolute temperature and patterns of temperature variation still have the potential to directly affect growth and body size via effects on physiological processes (LaBarbera 1989, Sibly & Atkinson 1994, McCormick & Molony 1995, Todd 1997). The environmental differences between marine and terrestrial habitats suggest that a wider range of studies on the significance of body size in aquatic species is required to assess the generality of current theory.

Studies that have focussed on the life history and ecological significance of body size in fishes have primarily been concerned with freshwater and commercially important species (eg. Alm 1959, Bromage et al. 1992, Lorenzen 1996, Sogard 1997) and the vast majority of these studies have been restricted to temperate environments (eg. Anderson et al. 1989, Litvak & Leggett 1992, Turner et al. 1996). Despite the fact that a large proportion of the world's marine fish species inhabit coral reefs, the importance of body size in reef fishes has only recently begun to be examined (Munday & Jones 1998, Jones et al. 2002). While this work has suggested that coral reef fishes conform to some terrestrial patterns (eg. larger species have larger geographic ranges), there have been no detailed comparative studies of species within any tropical reef fish family. Clearly, our understanding of relationships between body size and other biological and ecological variables will be incomplete without consideration of species living in warm, relatively aseasonal tropical reef environments. The implications of body size for highly diverse communities characterised by complex ecological interactions, such as those found on coral reefs, have not been fully examined.

1.1 Body size and reef fish life histories - Implications for growth, mortality and longevity

In this thesis, I have focussed on four general areas related to reef fish ecology. Within each section I examined a range of ecological correlates of body size, in order to contribute to our understanding of the biology and ecology of coral reef fishes and investigate the ecological significance of body size. The first area of focus concerns relationships between size and other life history parameters, in particular, patterns relating to growth, mortality and life-span. While recent work on tropical reef fishes indicates that they display a wide range of growth trajectories, mortality rates and longevities (eg. Russ & St John 1988, Choat et al. 1996, Choat & Axe 1996, Adams et al. 2000, Choat & Robertson 2002), there have been few attempts to examine how interactions between growth and mortality determine the maximum body size and age of a species. It could be that larger species simply grow at a similar rate to smaller species but become larger by growing for a longer period of time. Alternatively, energetic trade-offs may be operating. For example, small species have high mass-specific metabolic rates (Promislow & Harvey 1990) and tend to be associated with higher initial growth rates and an earlier age and smaller size at maturity (Lamb 1977, Blueweiss et al. 1978, Calder 1984, Stearns 1992). However, high early growth and early reproduction can exact a cost in terms of increased mortality (Schwarzkopf 1993). If such trade-offs commonly occur in reef fishes, small body size should be correlated with greater initial growth, increased mortality and consequently, shorter life-spans.

Currently it is not clear whether reef fishes conform to these patterns. Extrinsic factors (such as resource limitation, predation, climatic variation, physical disturbance and disease), determining inter- and intraspecific differences in growth and mortality may also interact to determine maximum body sizes and longevities (Jones &

McCormick 2002). All else being equal, faster growing species could be expected to reach greater body sizes and live longer if they escape high extrinsic mortality rates caused by size-selective predation (Olson 1996, Sogard 1997). Coral reef fish species with large adult size appear to be associated with reduced mortality rates (Munday & Jones 1998), but there is little evidence to date to indicate whether the size or age of individuals within species greatly influences mortality schedules (Caley 1998). It is usually assumed that at least within reef fish families, larger size equates to greater life-spans, but this is not known. Despite the widespread occurrence of indeterminate growth in species of reef fishes, determinate growth, in which adult size is attained relatively early in life has been identified in some groups (Choat & Axe 1996, Kingsford & Tzioumis 1999, Meekan et al. 2001). Families characterised by determinate growth also tend to have longer life-spans than expected for their size (Choat & Robertson 2002). With such mixed growth strategies, there may be little relationship between life-span and body size among these species. The diversity of relationships between body size and initial growth rate, growth trajectories, longevity and mortality rates has not been fully described.

1.2 Body size and reproduction in reef fishes – Inter-relationships among body size, maturation, reproductive effort and sex change

The onset of reproduction, the extent of gamete production, and reproductive success are all highly dependent upon body size in fishes (Blueweiss et al. 1978, Bell 1980, Roff 1981, Roff 1986, Bromage et al. 1992). Thus, growth trajectories and adult size are crucial covariates and potential determinants of life-time patterns of reproduction. It has been argued that in species with indeterminate growth, maturation occurs at a fixed proportion of maximum size or age (Charnov & Berrigan 1991). Mortality-risk theory, however, suggests individuals of species which suffer high levels of mortality should enter the reproductive population as soon as possible to increase chances of reproducing before dying. This is expected to entail faster growth and earlier attainment of maturity (Millar & Zammuto 1983, Sutherland et al. 1986, Promislow & Harvey 1990, Shine & Charnov 1993). As smaller species are expected to experience greater mortality than larger, it can be predicted that they should mature at a smaller proportion of adult size and proportionally earlier in life than larger species. Smaller species should also allocate more energy to reproduction than larger species. Interspecific covariation among adult body size, maturation and reproductive effort has not been examined for coral reef fishes, so the plausibility of these mechanisms has yet to be evaluated.

Sequential hermaphroditism is not expressed in terrestrial vertebrates, but is widespread among reef fish species (eg. Warner 1978, Warner 1984, Warner 1988, Sadovy & Shapiro 1987, Warner 1988). The evolution and occurrence of sex change has been closely linked with body size (Warner 1975). Sex change appears to arise in species in which the relationships between potential fecundity and body size differ markedly between males and females (the ‘size-advantage’ model of Ghiselin 1969, Warner 1975). For example, where small females have a potentially higher reproductive success than small males and large males have a disproportionate reproductive success relative to large females, sex change from female to male is expected to occur (protogynous hermaphroditism). Within some species, sex change transitions appear to be correlated more closely with body size than with age and occur at a critical size at which the social system permits a male to establish a territory and monopolize multiple females (e.g. Jones 1980, Warner & Hoffman 1980). The influence of maximum size or age on when sex change takes place among different species, has not yet received any theoretical attention. As has been suggested for maturation, it could be that sex change occurs at a similar proportion of maximum body size or age in different species. This would not be expected though, if predictable changes in sex-specific patterns of growth, fecundity and mortality rates occurred in relation to body size. If extrinsic factors such as predation pressure vary in relation to species size, they may also play a role in influencing when sex change occurs.

1.3 Relationships between body size, life history and latitude in a reef fish

General trends in body size and life history parameters have been linked to latitudinal gradients in a wide variety of organisms (eg. Stevens 1989, Iverson et al. 1993, Sand et al. 1995, Arnett & Gotelli 1999, van' t Land et al. 1999). Among fishes, most latitudinal relationships explored have been for temperate species over latitudes characterised by dramatic changes in average temperatures and a high degree of seasonal variation (eg. L' Abée-Lund et al. 1989, Fleming & Gross 1990, Conover et al. 1997). Within species, a trend towards slower growth, larger body size and increased longevity with increasing latitudes has been described in a range of taxa (Charnov 1982, Forsman & Shine 1995, Arendt 1997, Jackson & Moltschaniwskyj 2001). Covariation among these traits is consistent with life history theory (Berven and Gill 1983, Sinervo & Svensson 1998, Mangel & Stamps 2001). Selection for longer life and associated traits might be favoured in extreme temperate climates where the probability of offspring survivorship is unpredictable. Covariation of these traits is also consistent with models directly implicating the effects of temperature on physiological processes (LaBarbera 1989, Todd 1997). For example, increased temperature is associated with a faster potential growth rate. Therefore intrinsic energetic trade-offs related to faster growth of individuals at the equator could result in shorter life-spans and a smaller body size than those living in colder areas (Atkinson 1994). Changes in growth are also expected to be associated with changes in reproductive traits. Larger individuals with slower growth such as those at higher latitudes should mature later in life and have greater reproductive effort if fecundity is size specific.

Covariation of life history traits in coral reef fishes has only recently been examined and latitudinal trends have been described for very few species. Although the temperature changes across tropical latitudes are less extreme than across temperate environments, coral reef organisms appear to reach physiological limits that determine the latitudinal extent of their geographic ranges (Atkinson 1994, Jones et al. 2002). It is argued that warm water tolerant species in environments with minimal temperature fluctuations are likely to be extremely sensitive to changes in water temperature (McCormick & Molony 1995). Therefore, although temperature changes across tropical latitudinal clines are subtle, they could still have a considerable effect on life history strategies in coral reef fishes.

1.4 Body size and the ecology of reef fishes - Implications for distribution, abundance and habitat use

Body size is central to ecological theory relating to both large-scale (biogeographic) and local-scale patterns of diversity, distribution and abundance. Greater species richness and greater maximum abundances in species with small body size are thought to be general characteristics of all organisms (Gaston & Lawton 1988, Gaston & Blackburn 1996). There is some evidence that these patterns also apply to coral reef fishes (Munday & Jones 1998, Jones et al. 2002). However, geographic variation in body size, diversity and abundance relationships has not been extensively examined in this group, especially at low taxonomic scales such as within families.

Body size has also been implicated in patterns of habitat use (Hutchinson & MacArthur 1959, Price 1984, Pyron 1999), diet and resource specificity (Wainwright 1988, Clifton & Motta 1998), distribution among habitats (Ziv 2000) and the local coexistence of species (Hutchinson 1959, Maurer et al. 1992). There have been few analyses of the significance of body size though, for local scale ecological interactions among reef fishes. Small reef fish species are generally observed to be more closely associated with the reef matrix than larger species (Fishelson et al. 1974), this is potentially due to the greater susceptibility to predation of smaller species (Munday & Jones 1998). Smaller species may also be more habitat specific than larger ones, as larger species may need to forage over greater areas due to high energetic requirements, although there is little quantitative evidence for or against this prediction (Warburton 1989, Munday et al. 1997).

Very few studies have examined the structure of fish communities with respect to body sizes at different depths on coral reefs (but see Bean et al. 2002). Within species, recruitment of juveniles into shallow water is often followed by a migration of adults into deeper water where adults are more common (eg. Clarke 1977, Green 1996). Whether depth zonation of species is consistent among different assemblages of reef fishes, or is somehow related to species size requires further investigation. The implications of body size for interpreting local-scale ecological patterns have been largely overlooked by reef fish researchers.

1.5 Aims of the thesis

The overall aim of this thesis was to evaluate the significance of body size for the life history and ecology of tropical wrasses (Family: Labridae), a speciose family on coral reefs. Variation in body size, both among and within species, was exploited to identify key correlates of body size and to examine generalisations developed from comparative studies of terrestrial organisms. Wrasses were chosen, because out of all teleosts that are associated with coral reefs, they exhibit the greatest range of body sizes, from the small pseudocheilinid *Pseudocheiliops ataenia* reaching only 4 cm total length (TL) to the giant napoleon wrasse *Cheilinus undulatus* which can reach over two metres TL (Randall et al. 1997, Munday & Jones 1998). The rationale was that, if body size is of fundamental importance, correlates of size will be most obvious in this group.

Although wrasses exhibit an unusually large range of body sizes, the species richness–body size distribution of wrasses (Figure 1.1), is typical of other animals (Munday & Jones 1998, Maurer et al. 1992, Loder 1997). Most species are small to intermediate in size and large species and extremely small species are rare, resulting in a log-normal distribution. Wrasses exhibit many other desirable characteristics as a model group for examining relationships between body size, life history and other aspects of ecology. They are almost all protogynous hermaphrodites (changing sex from female to male) and exhibit a range of sex change strategies, making them suitable to test predictions regarding size and age at sex change (Warner & Robertson 1978). Species of wrasse tend to have large geographic ranges and the family is broadly distributed in tropical and temperate waters which facilitates comparisons associated with differences in latitude. Wrasses are an extremely abundant component of the reef fish fauna on coral reefs and are the second most diverse family of fishes on the Great Barrier Reef (Randall et al. 1997). Their high diversity, abundance and trophic importance as carnivorous fishes on coral reefs (Randall et al. 1997) enables comparisons between numerous ecological variables and body size.

Examination of correlates of body size among species requires the use of comparative methods. Both inter- and intraspecific variation in body size and associated variables were assessed. Surprisingly few such studies have been carried out on reef fishes (but see Munday & Jones 1998, Jones et al. 2002). Although wrasses have been well researched in tropical and temperate waters, no studies have integrated body size, life history and ecological relationships in this group.

A multi-species comparative approach was applied to ten species of wrasses drawn from two locations, which represent the typical size range of wrasse species in the tropical Australian region. These are, in order of maximum recorded size (Allen 1997, Randall et al. 1997): *Pseudocheilinops ataenia* (40mm), *Pseudocheilinus hexataenia* (75mm), *Pseudocheilinus evanidus* (80mm), *Halichoeres melanurus* (105mm), *Bodianus mesothorax* (200mm), *Bodianus axillaris* (200mm), *Choerodon fasciatus* (300mm), *Epibulus insidiator* (350mm), *Cheilinus fasciatus* (360mm), *Hemigymnus melapterus* (600mm), (Figure 1.2). A ubiquitous and abundant species, *H. melanurus*, was used as a focal species to examine intra-specific variation in body size and life history characteristics among four geographic locations. Relationships between body size, abundance, species diversity, microhabitat specificity and depth range, were examined for all common wrasse species present at widely separated geographic locations.

1.6 Structure of the thesis

Chapter 2: Body size variation in wrasses - Associations with growth, longevity and mortality

This chapter presents a multi-species comparative study of the potential relationships between body size, growth rates and trajectories, mortality and longevity in ten wrasse species from the Palm Islands, Great Barrier Reef. The aim was to evaluate whether there are predictable changes in life histories associated with interspecific differences in adult body size, and if so, whether these are likely to reflect trade-offs among life history traits (e.g. growth vs. mortality). Specifically, it tested the predictions that smaller species should be characterised by faster early growth, higher mortality and shorter life-spans compared to larger species. This information was then used to test a number of conceptual models suggesting why different species attain different body sizes. In addition, this chapter explored the correlations between different growth trajectories (i.e. determinate versus indeterminate growth) and other life history traits.

Chapter 3: Body size and its relationship to maturation, reproduction and sex change in coral reef fishes

This chapter analysed how differences in body size are related to patterns of reproduction in wrasses. Specifically, it investigated interspecific covariation between body size/longevity and two critical life history transitions which were the size and age at maturity and size and age at sex change. It assessed whether these events occur at a fixed proportion of maximum body size, or are likely to be associated with trade-offs between growth, reproduction and mortality. It also identified whether attainment of maturity and occurrence of sex change was more closely associated with body size than age. In addition, the relationship between maximum female size within species and reproductive effort was examined, to see if consistent patterns of growth and reproduction identified in terrestrial organisms are repeated in coral reef fishes.

Chapter 4: Geographic covariation in life history traits of the coral reef fish *Halichoeres melanurus* (Pisces: Labridae)

This chapter explored whether there are differences in the life history of the wrasse *Halichoeres melanurus* associated with differences in latitude among four widely separated geographic locations. I tested the prediction that within species, individuals at lower latitudes tend to have smaller adult size than at higher latitudes. Based on predicted covariation between changes in body size and other life history traits, maturation and sex change should occur relatively earlier and at a smaller proportion of adult size in individuals at lower latitudes. In addition the larger individuals expected at higher latitudes should be more fecund and have greater reproductive effort. Patterns of covariation in life history traits were used to assess whether geographic variation in *H. melanurus* is explained by intrinsic shifts in the allocation of energy among different life history functions or are more strongly influenced by environmental factors.

Chapter 5: Body size and the ecology of reefs fishes - Implications for species abundance, diversity and habitat use

In this chapter, the potential role of body size in influencing local abundance, species richness, distribution among habitats and microhabitat specificity was evaluated. I explored whether patterns between body size and ecological characteristics commonly observed in terrestrial organisms, hold in coral reef fishes. Firstly, I assessed interspecific relationships between body size, abundance and species richness based on visual sampling of wrasse communities at four widely separated geographic locations. I then inspected patterns of microhabitat use among all wrasse species present at three of the locations and examine how they relate to interspecific body size differences. Finally, I examined the depth distributions of species to identify whether body size is a good predictor of the depth ranges used by these species.

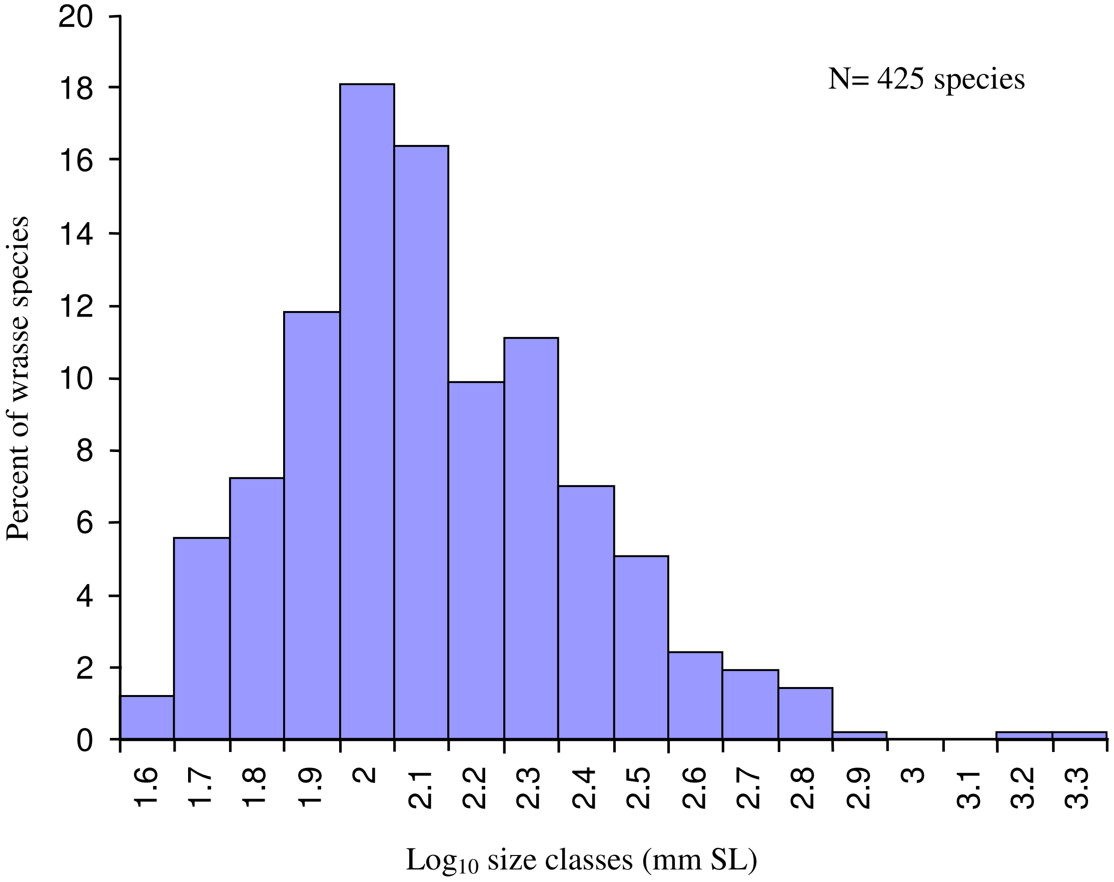

Figure 1.1: Log-transformed size frequency distribution of species within the wrasse family. Includes tropical and temperate species. Data collated from Froese & Pauly (2002).

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Figure 1.2: Wrasse species sampled in this study, in order from smallest to largest maximum size: a) *Pseudocheilinops ataenia*, b) *Pseudocheilinus hexataenia*, c) *Pseudocheilinus evanidus*, d) *Halichoeres melanurus*, e) *Bodianus mesothorax*, f) *Bodianus axillaris*, g) *Choerodon fasciatus*, h) *Epibulus insidiator*, i) *Cheilinus fasciatus* and j) *Hemigymnus melapterus*. Photograph a from Allen (1997), photographs d and j from Froese & Pauly (2002), remaining photographs from Randall et al. (1997).

CHAPTER 2: Body size variation in wrasses - Associations with growth, longevity and mortality

2.1 Introduction

The life history characteristics of organisms can influence all aspects of their ecology, from their interactions among individuals to their functional role in ecosystems (Calder 1984, Bruton 1989, Stearns 1992). The life history trait of greatest potential ecological significance is body size. Differences in body size can determine who is dominant and who is subordinate (Werner & Gilliam 1984, Jones 1987, Persson 1988), who is predator and who is prey (Wilbur 1988, Robertson 1998) and who can co-exist in ecological communities (eg. Schoener 1974, Ebenman & Persson 1988, Boyce 1988). Smaller species tend to live shorter lives, and their populations exhibit faster turnover rates, have greater fluctuations and reach greater numbers than larger species (Promislow & Harvey 1990, Harvey & Nee 1991, Munday & Jones 1998). Therefore, the population characteristics and functional role of a species can potentially be predicted from the complex interplay between body size of an organism and other aspects of its life history. Despite this, covariation among life history traits associated with variation in body size among species is still poorly understood.

The maximum body size reached by an organism is a function of interactions among life history traits that influence growth and longevity. For example, an individual can reach a larger size by growing faster or living longer if growth continues throughout life. A positive correlation between body size and maximum life-span has been repeatedly observed in terrestrial taxa (Rensch 1959, Lamb 1977, Blueweiss et al. 1978, Calder 1984, Stearns 1992). Body size also covaries with growth and survival rates among diverse groups of species (Alm 1959, Roff 1984, Charnov & Berrigan 1991, Harvey & Nee 1991, Olson 1996). Therefore, faster growth and increased life-span together should result in larger body size. However, both empirical data and life history theory suggest that this combination may not be possible. Maximum body size and age appear to result from trade-offs between the amount of energy allocated to growth and survival, more energy invested in one function resulting in less energy available for the other (Sinervo & Svensson 1998, Mangel & Stamps 2001).

Allocation of energy appears to obey the same rules among many different terrestrial taxa resulting in consistent relationships among life history parameters. In comparison to large species, smaller species usually have faster initial growth (Stearns 1983, Harvey & Keymer 1991, Arendt 1997, McCann & Shuter 1997). The faster growth is potentially related to higher mass specific metabolic rates in smaller species (Harvey et al. 1991, Clarke & Johnston 1999). Smaller species should also have greater mortality rates (Harvey et al. 1989, Promislow & Harvey 1990, Harvey & Nee 1991, Abrams & Rowe 1996). For example, smaller species are likely to be more susceptible to predation than larger ones. The faster initial growth of small species may also contribute to reduced survivorship due to increased allocation of energy into growth at the expense of survival (Mangel & Stamps 2001). Consequently, smaller species should also have shorter life-spans (Blueweiss et al. 1978, Harvey & Read 1989). While these appear to be general patterns, the relationships between maximum body size, age, growth and survival are not well known for marine species.

Fishes are one group in which relationships between body size and other life history characteristics may take a different form from terrestrial species. Maximum body size of terrestrial animals may be constrained, due to the greater investment required for structural support (Schmidt-Neilsen 1984). Aquatic organisms are mainly supported by water and therefore structural requirements do not impose the same constraints on body size. In addition, mammals exhibit determinate growth or an upper limit to body size, which is achieved by a shift in the allocation of energy from growth prior to maturation to reproduction once adult size is reached (Peters 1983, Charnov 1993). In contrast, poikilothermic organisms, including most fishes, tend to exhibit indeterminate growth (i.e. continue to grow throughout their life) and reach greater maximum body sizes by growing slowly and living longer. Therefore, in fishes, shifts in the balance of energy allocated to growth, reproduction and survival occur throughout life (Charnov & Berrigan 1991, Charnov 1993). Although indeterminate growth is predominant in fishes, some species are functionally determinate (Choat & Robertson 2002). In animal groups that exhibit a range of determinate and indeterminate growth patterns, there may be no simple relationships between body size, longevity, growth and mortality, and species exhibiting contrasting growth strategies (i.e. determinate and indeterminate growth) may obey different rules.

Life history theory predicts that growth and mortality rates and longevity are traits that have co-evolved under different environmental or ecological conditions (eg. Roff 1981, Promislow & Harvey 1990, Harvey & Keymer 1991, Millar & Hickling 1991, Stearns 1992, Arendt 1997). Therefore, this theory generally assumes that these traits are intrinsic properties of the species. However, growth and mortality are greatly influenced by extrinsic environmental and ecological factors (Charnov & Berrigan 1991, Ebenman & Persson 1988, Bertram & Leggett 1994, Olson 1996, Sogard 1997, Munday & Jones 1998). For example, small body size or slower growth is associated with a greater susceptibility to predators (Munday & Jones 1998) and extrinsic sources of mortality such as predation are likely to vary in space and time (Caley 1995). Patterns of mortality and longevity of species have been shown to vary in response to predator pressure (eg. Reznick et al. 1990, Rochet 1998). In addition, organisms with indeterminate growth characteristically exhibit considerable plasticity in growth, which is often influenced by local ecological conditions (Weatherley & Gill 1987, Jones 1984, Abrams et al. 1996, Arendt 1997). Hence, the relationship between life history theory, body size, growth and mortality schedules is likely to reflect complex interactions between evolved life history patterns and responses to local ecological conditions.

Coral reefs, compared to any other habitat, host the greatest diversity of the world's fishes (Sale 1991). Despite this, we are only beginning to document the wide range of life history characteristics of coral reef fishes (Munro & Williams 1985, Russ & St John 1988, Williams & Russ 1994, Munday & Jones 1998, Choat & Robertson 2002). Although the ecological implications of body size variation in coral reef fishes have received some attention (Munday & Jones 1998, Jones et al. 2002), covariation between body size and other life history traits in coral reef fishes remains poorly understood. Coral reef teleosts reach a wide range of body sizes, from gobies with a mean maximum body size among species of only 40 mm to large groupers and wrasses which can reach one to two metres in length (Randall et al. 1997, Munday & Jones 1998). Different reef fish taxa appear to exhibit a range of different growth strategies, with many groups such as wrasses and parrotfishes being characterized by indeterminate growth (Choat et al. 1996, Gillanders 1997, Gordoa et al. 2000) and others such as surgeonfishes and some damselfishes often exhibiting determinate growth trajectories (Choat & Axe 1996, Tzioumis & Kingsford 1999, Meekan et al. 2001). Determinate and indeterminate growth can be viewed as extremes of a continuum of growth strategies. The position of a species on this continuum is likely to have a profound impact on other life history traits such as growth rates and mortality. The potential relationships between growth strategies and trade-offs between growth and survival have not been examined previously in coral reef fishes.

The range of growth strategies observed in coral reefs fishes suggests that the relationships between maximum body size and longevity could be weak or non-existent in this group of species. For example, the average size of parrotfishes is greater than that of surgeonfishes and damselfishes, yet the life-spans of parrotfishes are considerably shorter (Choat & Axe 1996, Choat et al. 1996, Munday & Jones 1998, Choat & Robertson 2002). These broad taxonomic differences suggest that phylogenetic history has had a major influence on general patterns of body size and growth patterns in coral reef fishes (Warburton 1989, Munday & Jones 1998). In addition to the effects of phylogeny, there is ample evidence that patterns of growth and survival in coral reef fishes are highly sensitive to local environmental conditions (Jones 1991, Caley et al. 1996, Caley & St John 1996, Jones & McCormick 2002, Hixon & Webster 2002). Therefore, evolutionary history and ecological linkages between growth and mortality may contribute to body size-longevity patterns in this group of organisms.

One approach to examining the relationship between body size and life history traits is to use multi-species comparative methods. As species within a lineage are derived from a common ancestor, closely related species are more likely to express similarities in life history traits than two distantly related species. Consequently, for comparative purposes species cannot be considered statistically independent from one another. This lack of independence violates a basic assumption of most statistical techniques and can create problems when directly comparing trait values among species (Stearns 1983, Harvey & Pagel 1991). Hence, comparative methods must be used to control for evolutionary relationships among species.

A number of methods are now available to test comparative relationships which incorporate phylogenetic information to define statistically independent comparisons (Harvey & Pagel 1991). The importance of the consideration of evolutionary history in comparative studies is now widely accepted and phylogenetic comparative methods (PCMs) can be used to attain a clearer understanding of covariation in ecological traits. For this study I used both phylogenetic and non-phylogenetic comparative approaches and assessed variation in results using these techniques.

This chapter presents comparative analyses of the relationships between body size, longevity, growth and mortality among wrasse species (Pisces: Labridae) on coral reefs. The two primary goals were to establish whether body size-related patterns are more likely to be controlled by intrinsic or extrinsic factors and to evaluate whether differences in growth trajectories (ie. determinate vs. indeterminate growth) influence relationships among life history parameters in a reef fish family. Wrasses are an ideal group with which to examine body size-life history relationships because the family encompasses nearly the whole size range of fish species observed on coral reefs, from *Pseudocheilinops ataenia* (4 cm) to *Cheilinus undulatus* (>2 metres) which is a greater size range than observed in any other reef fish family. Wrasses are also a very important component of coral reef fish faunas and are widely distributed among temperate rocky reef habitats (eg. Treasurer 1994). Despite this, the implications of their large range in adult size for patterns of growth, survival and longevity expressed in these species have not been explored. In addition phylogenetic relationships are available for wrasse species examined here, facilitating the implementation of phylogenetic comparative methods.

By examining life history characteristics of ten tropical wrasse species, I tested predictions from life history theory. The results of these predictions were used to assess the importance of five conceptual models, indicating potential ways in which large body size can be achieved. For example, if there was evidence for the following set of predictions: life-span increases with an increase in body size of species, growth rate is similar among species and smaller species have greater mortality rates than larger, it provided support for model a) 'same growth rate, longer life-span', in which large body size is attained by growing at the same rate as smaller species but living longer (Figure 2.1a). If there was no relationship between size of species and their life-spans, larger species had faster growth than smaller species and mortality rates did not vary predictably with body size then model b) 'faster growth, same life-span', was supported. Under this model larger body size is attained by growing faster on average throughout life but life-span is similar among small and large species (Figure 2.1b). If life-span increased with an increase in size of the species and larger species had slower growth and lower mortality rates than smaller species, this indicated support for model c) 'slower growth, longer life-span'. In this case allocation of energy among growth and other processes, influences the maximum size attained and rapid initial growth is accompanied by an energetic cost resulting in reduced life-span and smaller adult body size (Figure 2.1c). If life-span increased with an increase in size of the species and larger species had faster growth and lower mortality rates than smaller species then model d) 'faster growth, longer life-span', was supported. Under this model extrinsic factors such as predation play a determining role, for example by growing faster, body size increases rapidly providing a refuge from predation which augments chances of survival and therefore increases longevity (Figure 2.1d). Among species exhibiting different growth strategies it was predicted that larger body size is associated with longer periods of indeterminate growth, smaller species have determinate growth and are smaller because asymptotic size is reached earlier in life than in larger species. This is expressed in model e) 'smaller size, more determinate growth' (Figure 2.1e). The main criterion to assess compatibility with this model was whether small species consistently express more determinate growth than larger ones. Variation in life-span and mortality rates among species was not a consideration of this particular model. Based on the results of this study, evidence for and against each conceptual model was assessed and the degree to which different growth trajectories (determinate vs. indeterminate growth) disrupt overall relationships was examined.

2.2 Materials and Methods

2.2.1 Study species and locations

Ten species were selected in order to encompass a wide range of genera and body sizes. These species in order of increasing body size were *Pseudocheilinops ataenia*, *Pseudocheilinus hexataenia, Pseudocheilinus evanidus, Halichoeres melanurus, Bodianus mesothorax, Bodianus axillaris, Choerodon fasciatus, Cheilinus fasciatus*, *Epibulus insidiator* and *Hemigymnus melapterus* (Table 2.1). Collections of wrasses with the exception of the pseudocheilinids were made in April 1999 and November 2000 at the Palm Islands, Great Barrier Reef (18°36'S, 146°29'E) with collections concentrated at Pelorus Island (Figure 2.2). As no extremely small wrasse species are found at the Palm Islands, the smallest species *P. ataenia*, *P. hexataenia* and *P. evanidus* were collected at Kimbe Bay, Papua New Guinea (5°33'S, 150°08'E) in April 1999, March 2000 and March 2001 (Figure 2.2). Although there is intraspecific geographic variation in maximum body size of wrasses (see Chapter 4 this thesis, Jones 1980), this variation even among widely distributed species was far smaller than interspecific variation given the 10-fold range in body sizes of species examined here. Consequently, comparisons among species are not compromised by sampling at different locations.

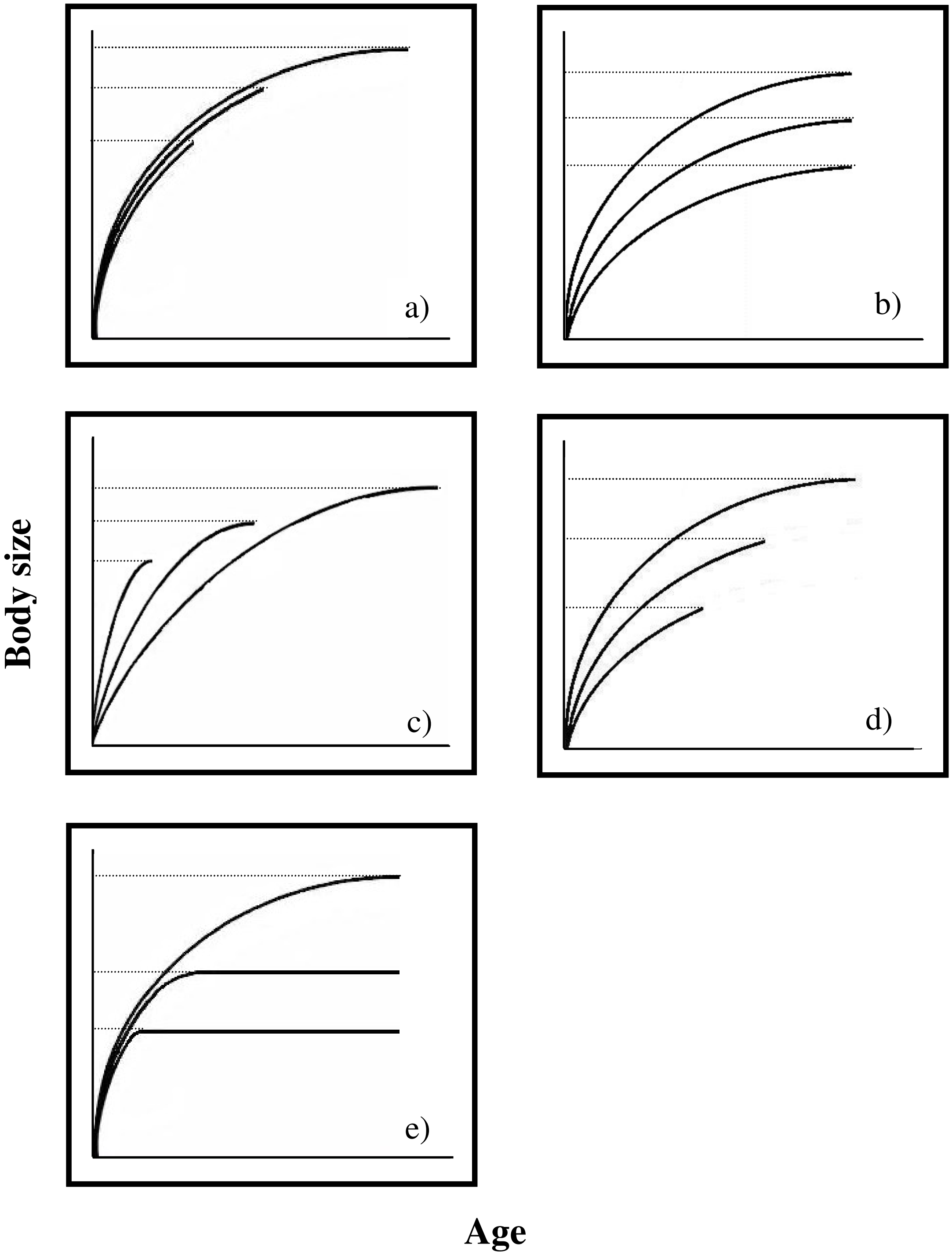

Figure 2.1: Five conceptual models indicating ways in which species can attain large body sizes. Relationship between size and age is illustrated based on potential combinations of growth and mortality schedules.

2.2.2 Measurement of body size

All wrasses at the Palm Islands were collected by spearing on SCUBA, whereas the smaller pseudocheilinids were collected by anaesthetising individuals using clove oil (1 part clove oil: 10 parts 70% ethanol). Once speared, fish were stored on ice and dissected as soon as possible. The standard length (mm), and mass of individual fish (mg) were recorded. The utility of standard length as a proxy for mass was assessed by examining length-weight relationships. Curves of the form $W=aL^b$ where W is weight in g, L is standard length in mm, a is a multiplicative factor and b an exponent, were fitted to length and weight data for all species. Ninety five percent confidence limits about b were calculated following the method outlined in King (1995).

Table 2.1: List of wrasse species sampled including size range of individuals sampled, maximum standard lengths of species observed during collections, number of individuals of each species collected (N) and sampled locations, PNG (Papua New Guinea), GBR (Great Barrier Reef, Australia).

Species	Sample size range (SL mm)	Maximum observed size (SL mm)	N	Location
Pseudocheilinops ataenia	5-35	35	149	Kimbe Bay, PNG
Pseudocheilinus hexataenia	11-47	47	138	Kimbe Bay, PNG
Pseudocheilinus evanidus	20-53	55	67	Kimbe Bay, PNG
Halichoeres melanurus	29-88	85	144	Palm Is., GBR, Australia
Bodianus mesothorax	89-127	160	51	Palm Is., GBR, Australia
Bodianus axillaris	90-132	158	46	Palm Is., GBR, Australia
Choerodon fasciatus	88-167	207	74	Palm Is., GBR, Australia
Cheilinus fasciatus	64-190	275	90	Palm Is., GBR, Australia
Epibulus insidiator	80-225	286	88	Palm Is., GBR, Australia
Hemigymnus melapterus	44-233	328	77	Palm Is., GBR, Australia

2.2.3 Age estimates

2.2.3.1 *Preparation of otoliths and increment counts*

Sagittal otoliths were removed, cleaned with distilled water and dried before storing in a culture dish. Otoliths were weighed to the nearest 0.01 mg. Each otolith was attached to a slide using a thermoplastic glue, Crystal bond^{TM} with the nucleus centred over the edge of the slide and the distal end protruding. Larger otoliths were then ground with abrasive paper (600, 800 and 1200 grit) and for smaller ones lapping film (0.3 to 12 μm grit size) was used. The otolith section was then mounted ground-side down on another slide and was ground again until a thin transverse section was obtained. Age was estimated by counting increments visible on these otoliths. These increments had a bipartite structure of a translucent band and narrower opaque band (incremental zone). Two types of increments were visible depending on the species, these were characteristic of daily and annual increments (Campana & Neilson 1985, Lou & Moltschaniwskyj 1992). Daily increments were counted for short-lived species and annual increments were counted for long-lived species. Daily increments were counted by eye using a high power microscope and transmitted light at a magnification of ×400 and ×1000 when required. Annual increments were counted using a dissecting microscope and transmitted light. The exception was for otoliths of *Choerodon fasciatus* for which it was most effective to examine sections using incident light and a black background. When increments were considered annual, three separate counts of increments were made for each otolith. Two counts only were made for otoliths with daily increments as estimating numbers of daily increments on an otolith was far more time intensive than counting annual increments. Average percentage error for these age estimates was calculated as an estimate of precision using Equation 2.1 (Beamish & Fournier 1981):

$$\text{Average percentage error} = \frac{1}{N}\sum_{j=1}^{N}\left[\frac{1}{R}\sum_{i=1}^{R}\frac{|Xij - Xj|}{Xj}\right]\times 100 \qquad \text{(Equation 2.1)}$$

Where N is the number of fish aged, R is the number of times the number of increments on each otolith was counted, Xij is ith age determination for the jth fish and Xj is the average age estimated for jth fish.

2.2.3.2 *Validation of age estimates*

Least-square linear regressions were calculated for sagittal weight versus age for all species. These were used to determine whether otoliths displayed linear or curvilinear growth during development and to identify variation in age estimates for a given sagittal weight.

The short life-spans of *P. ataenia*, *P. hexataenia*, *P. evanidus* and *H. melanurus* were estimated from counts of daily rings, doing so required the identification of pre-settlement and post-settlement daily increments and the validation of daily ring formation in a focal species. Validation of daily increments was carried out for

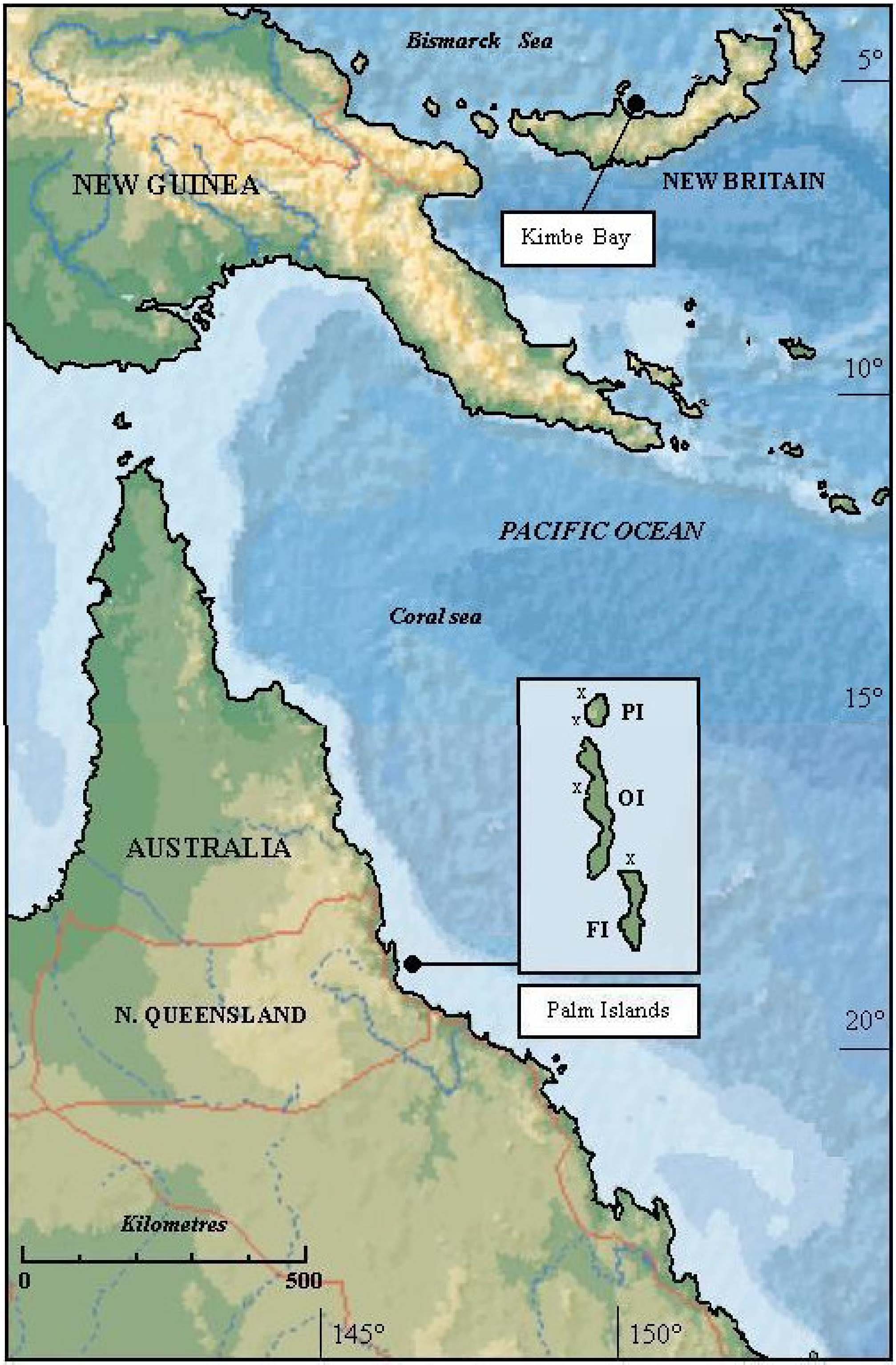

Figure 2.2: Map of study locations (PI = Pelorus Island, OI = Orpheus Island, FI=Fantome Island). Crosses indicate collection sites at each island.

H. melanurus only. Individuals were captured in the field by herding them into large plastic bags and transplanting them to outdoor aquarium facilities. Validation of the timing of deposition of rings is required to indicate that rings are actually laid down on a daily basis. Tetracycline hydrochloride can be used to mark the otoliths of a range of fish species by forming a fluorescent band (Campana & Neilson 1985, Lou & Moltschaniwskyj 1992, Hernaman et al. 2000), which forms within as little as 12-24hrs after injection (Campana & Neilson 1985, Lou & Moltschaniwskyj 1992). The count of the number of daily bands between a first and second tetracycline mark can be related to the known number of days between injections and the periodicity of band deposition determined. Individuals were injected with tetracycline in saline solution at a concentration of 50 mg kg^{-1} weight of fish (McFarlane & Beamish 1987). Fishes were first sprayed with a solution of clove oil and 70% ethanol to anaesthetise them and then tetracycline solution was injected into their coelomic cavities. Fishes were injected at various times and re-injected between two weeks and a month later. Following the second injection the fishes were not sacrificed immediately, as resolution of rings toward the edge of the otolith was often greatly decreased. In addition, autofluorescence at the otolith margin often blended with the tetracycline mark making it difficult to identify its position. Instead, fish were left to continue growth between four and twelve months in an attempt to maximise resolution of rings between injection marks.

2.2.4 Phylogenetic analysis

Using information from available phylogenies for the labrid tribes Hypsigenyini (Gomon 1997) and Cheilinini (Westneat 1993), a ‘supertree’ was constructed that postulates an evolutionary relationship between eight of the tropical wrasse species sampled for this study (*P. ataenia*, *P. hexataenia*, *P. evanidus*, *B. mesothorax*, *B. axillaris*, *Choerodon fasciatus*, *Cheilinus fasciatus* and *E. insidiator*) and two additional species for which maximum size versus maximum age relationships were available (*Choerodon schoenleinii*, *Cheilinus undulatus*). Phylogenetic relationships remain unresolved for the remaining two species *H. melanurus* and *H. melapterus* sampled in this study. It appears reasonable, however, to assume these species are derived from the Cheilines (Westneat M. pers. comm.). Therefore, a working phylogeny for twelve wrasse species was erected for the application of phylogenetic comparative methods (PCMs), (Figure 2.3).

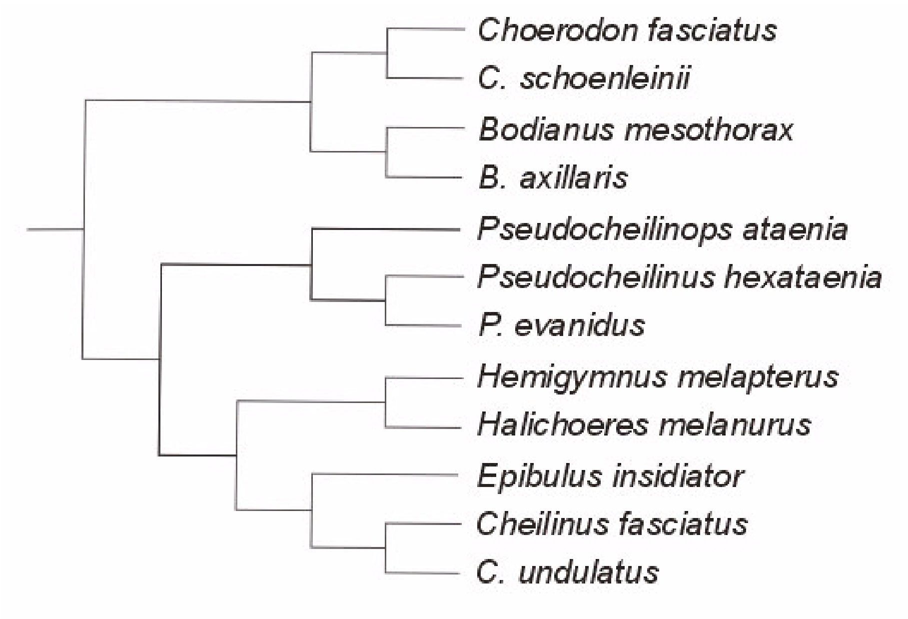

Figure 2.3: Working phylogeny for the wrasse species studied. Derived from trees for the wrasse tribes Hypsigenyini (Gomon 1997) and Cheilinini (Westneat 1993), and personal communication with Westneat M.

Felsenstein's independent contrasts method (FIC), (Felsenstein 1985) is commonly used to account for phylogenetic variation in comparative studies. Concern about its widespread use is increasing as FIC models the evolution of species as a Brownian motion (BM) process in which values for a given trait change randomly in either a positive or negative direction with each time step resembling a 'random walk' (Harvey & Pagel 1991). Therefore, FIC models evolution due to random genetic drift as opposed to natural selection and its performance is greatly dependent on how severely this assumption is violated (Martins et al. 2002). When life history traits are not expected to evolve randomly but change over time due to the effects of natural selection (Martins et al. 2002), a more appropriate technique to use is the phylogenetic generalised least-squares approach (PGLS) (Martins & Hansen 1997). Following the recommendation of Martins et al. (2002) data were analysed using a combination of three comparative methods: a) TIPS (a non-phylogenetic approach), b) FIC and c) PGLS, all of which were implemented in COMPARE (Martins 2001).

Branch lengths were not known for the phylogeny used here. Therefore, I estimated twenty possible trees for the described topology but with varied branch lengths generated using a standard Markovian branching process (Martins 1996).

The analyses were then run for all trees. The mean r^2 value for the correlation over the twenty trees and standard deviation of the mean was calculated for the FIC and PGLS results. When equal branch lengths were assumed for the tree, values of r^2 obtained rarely fell within the standard deviation of the mean calculated for the twenty trees with simulated branch lengths, therefore for comparative purposes the mean r^2 value derived from the twenty trees was used.

I examined the correlation coefficients returned by each of the three methods. The results of all three methods for all traits examined were consistent (eg. there were no reversals in the signs of correlations). Therefore, the results for the non-phylogenetic approach are presented in detail for ease of interpretation and r^2 values derived from the PCMs are provided for comparative purposes.

2.2.5 Interspecific relationships between body size, growth and mortality

2.2.5.1 *Maximum size vs. maximum age*

Log-transformed values of maximum size and maximum age of individuals for each species were plotted against each other. In many species the largest individual was not necessarily the eldest, therefore the point for the x-axis (maximum size of species sampled) and that for the y-axis (maximum age of species sampled) were often derived from different individuals. Data were plotted for the species sampled in this study, also included in this data plot is information for two larger species *Choerodon schoenleinii* (maximum size sampled 548mm) and *Cheilinus undulatus* (maximum size sampled 1050mm), (unpublished data provided by Ackerman J. and Choat J. H.). Data were collated from the literature for a further fourteen species of temperate wrasses (Table 2.2). Least-square regressions were performed on both data sets and regression slopes were compared using a student's t-test.

2.2.5.2 *Growth*

Description of growth is complex and both the absolute changes in size in relation to age, and the age-specific change in size relative to maximum size (growth trajectory) are relevent to life history theory. That is, two species may differ in their absolute increase in size relative to age, but exhibit exactly the same pattern of growth toward their maximum size. Early growth can be described most accurately by focussing on the

Table 2.2: Maximum size and age data collated for fourteen temperate wrasse species. Provided are the maximum size, maximum age, number of fish aged in study (N), location and literature source from which information was obtained. Sources: 1 - Gordoa et al. 2000, 2 - Treasurer 1994, 3 - Jones 1980, 4 - Gillanders 1997; 5 – Barrett N. pers. comm.; 6 – Nardi 1999)

Species	Max. size (mm SL)	Max. age (yrs)	N	Location	Source
Symphodus roissali	130	2.7	120	N. W. Mediterranean, Spain	1
Ctenolabrus exoletus	150	9	67	W. Scotland	2
Ctenolabrus rupestris	150	16	121	W. Scotland	2
Coris julis	180	8	228	N. W. Mediterranean, Spain	1
Crenilabrus melops	191	5	19	W. Scotland	2
Notolabrus celidotus	220	8	486	Leigh/Wellington, New Zealand	3
Labrus mixtus	243	11	12	W. Scotland	2
Symphodus tinca	340	8	292	N. W. Mediterranean, Spain	1
Achoerodus viridis	340	12	101	NSW, Australia	4
Labrus bergylta	370	15	26	W. Scotland	2
Notolabrus tetricus	400	10	94	Tasmania, Australia	5
Labrus merula	410	20	135	N. W. Mediterranean, Spain	1
Notolabrus fucicola	447	17	201	Tasmania, Australia	5
Choerodon rubescens	640	20	533	Abrolhos Islands, W. Australia	6

first part of the growth curve, rather than estimating a rate at which they approach their asymptotic size. Consequently, growth here is quantified in a number of different ways.

2.2.5.2.1 *Absolute changes in size in relation to age*

The von Bertalanffy growth function (VBGF) was used to describe growth in terms of absolute changes in size in relation to age:

$$L_t = L_\infty \left\{1 - e^{[-K(t-t_0)]}\right\} \qquad \text{(Equation 2.2)}$$

Where L_t is length at age t, L_∞ is asymptotic length, K is Brody growth coefficient defining growth towards L_∞, t is fish age and t_0 is age at length 0 as determined by the trajectory of the curve fitted to the equation.

The VBGF was fitted to size and age data of all individuals of each species in Microsoft Excel, variances of the calculated parameters L_∞, K and t_0 were minimised via multiple iterations using the Solver function. All growth curves were constrained to intercept the y-axis at a realistic estimate of size at age 0 (Kritzer et al. 2001). No data could be found for size at settlement of any of the wrasse species in this study with the exception of a newly settled individual of *E. insidiator* in French Polynesia which was measured at 5mm SL (Lo-Yat pers. comm.), *H. melanurus* at the Palm Islands (7mm SL, pers. obs.) and the pseudocheilinid species at Kimbe Bay, PNG (5mm SL, Jones G. P. pers. comm.). In other wrasse species, the average size at settlement appears to range between 8 and 12mm SL (Sponaugle & Cowen 1997). Based on this limited information 5mm SL was used as an estimate for minimum size at settlement for all species. Although this may be a slight under-estimate for some species, varying the settlement size to which curves were constrained (between 5-15mm SL), did not greatly influence the estimates for L_∞ and K obtained from the growth function for each species. Consequently t_0 values were constrained to the particular value at which size at age 0 indicated by the growth curve was equal to 5mm SL.

2.2.5.2.2 *Early growth (absolute)*

Absolute growth early in life was approximated by simply comparing standard length of the species at 0.5 and 1 yr of age estimated from the VBGF for each species. The relationship between early growth and maximum body size could then be examined.

2.2.5.2.3 *Estimating growth trajectories: indeterminate vs. determinate growth*

To examine these species on a continuum between indeterminate and determinate growth, the percentage of asymptotic length (L_∞) reached at a given percentage of maximum age (0-100% at 5% intervals) was plotted for each species. This produced a curve depicting the growth of each species relative to both adult size and maximum age. As growth in *H. melanurus* was best described as linear, asymptotic length estimated from the VBGF was unrealistic for this species and was almost twice as great as the maximum length attained by this species in the field. To obtain a curve for *H. melanurus* which was comparable with the other species, the percentage of the maximum length of individuals sampled instead of the percentage of asymptotic length (L_∞), was plotted against percentage of maximum age. Early growth was defined as the percent of adult size attained after 20% of life-span and this value was then compared among species.

2.2.5.3 *Mortality*

Estimates of natural mortality were calculated using two methods. The first method used was Hoenig's equation (Hoenig 1983):

$$\ln Z = a + b \ln (t_{max}) \qquad \text{(Equation 2.3)}$$

Where Z is instantaneous rate of total mortality, t_{max} is the maximum age in the sample. The values of a and b are 1.46 and -1.01, respectively and are estimated from the linear regression of log mortality rate per year and log maximum age of species for 175 fish stocks.

The other method used was Pauly's (1984) equation which utilises the parameters estimated from the VBGF:

$$\ln M = -0.0066 - 0.279 \ln L_{\infty} + 0.6543 \ln K + 0.4634 \ln T \qquad \text{(Equation 2.4)}$$

Where M is instantaneous rate of natural mortality, L_{∞} is asymptotic length in cm, K is the Brody growth coefficient and T is average annual seawater temperature (25.6°C at the Palm Islands for 1999, 29°C at Kimbe Bay 2000). Wrasse species collected are not subjected to fishing pressure at the locations sampled, therefore $Z = M$ (Pauly 1984) and estimates using the two methods should be directly comparable.

2.3 Results

2.3.1 Validation of techniques

2.3.1.1 *Standard length as a measure of body size*

The high r^2 values for all species indicated standard length was a good predictor of body mass. The exponent b was within the range 2.705 – 3.087 for all species (Table 2.3). Such values are typical of fishes.

2.3.1.2 *Validation of age estimates*

A significant positive linear relationship between sagittal otolith weight and age of individuals was evident for each species, but the strength of this relationship varied among species (Figure 2.4). Despite some variation in estimated age for an otolith of given weight, plots indicate that for most species otolith weight was a good estimator of age.

In *H. melanurus*, tetracycline marks corresponded to the number of days between injection dates indicating rings were daily (Figure 2.5). One problem encountered during estimation of daily rings in some otoliths of species with daily rings, especially for *H. melanurus*, was the lack of definition of rings towards the edge of the otolith, particularly in older individuals. Therefore, the age of some of the older individuals may have been slightly underestimated.

Sectioned sagittae of the six largest species sampled (ie. *B. mesothorax, B. axillaris*, *Choerodon fasciatus*, *Cheilinus fasciatus*, *E. insidiator* and *H. melapterus*) had distinctive incremental markings evident as dark, opaque zones separated by translucent, hyaline zones when observed under transmitted light (Figure 2.6). In *Choerodon fasciatus* these increments were less clear than in the other species and resolution of rings was often better with incident light and a black background (Figure 2.6, c2). Based on validation of daily rings in *H. melanurus* and the patterns of increment formation evident on sectioned sagittae of each species, increment marks were considered to be laid down daily in the smaller species (*P. ataenia, P. hexataenia, P. evanidus* and *H. melanurus*) and annually in the remaining species. For all species the percentage error for repeated counts of rings indicated that these counts were relatively precise (Table 2.4). The percentage error ranged from 3.6-13.5% and remained under 7.5% for all species with the exception of *Choerodon fasciatus*. The high percentage error for *Choerodon fasciatus* illustrates the difficulty in counting annual bands in this species.

2.3.2 Prediction 1: An increase in maximum size is associated with an increase in adult life-span

There was a significant increase in maximum age with an increase in maximum body size for both tropical ($F_{1,10}$=14.71, p=0.003) and temperate ($F_{1,11}$=8.47, p=0.014) wrasse species (Figure 2.7). The regression slopes for tropical and temperate species were significantly different (t_{21}=3.83, p<0.001), indicating tropical wrasses were slightly older for a given body size than temperate wrasses. Temperate wrasses did not encompass the size or age range (size range: 130-640mm, age range: 2.7-20 yrs) exhibited by tropical species (size range: 35-1050mm, age range: 1.2-30 yrs), particularly in terms of smaller and shorter lived species.

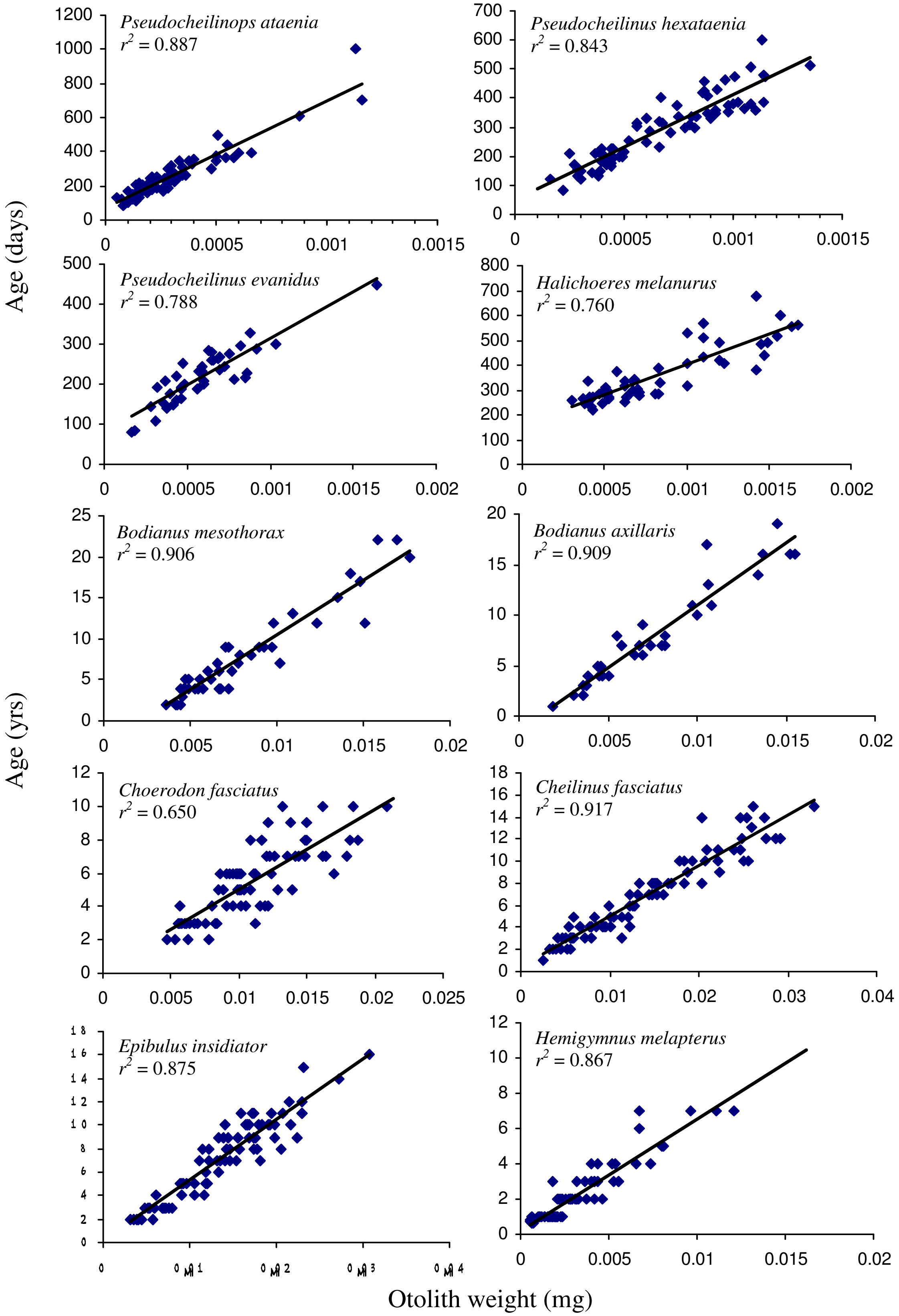

Figure 2.4: Least-squares regressions of otolith weight versus age. In order of increasing species size: *Pseudocheilinops ataenia*, y = 640991x + 70.292, N=82; *Pseudocheilinus hexataenia*, y = 359696x + 25.921, N=80; *Pseudocheilinus evanidus*, y = 220343x + 85.717, N=45; *Halichoeres melanurus*, y = 242984x + 157.93, N=80; *Bodianus mesothorax*, y = 1342.6x - 2.9694, N=50; *Bodianus axillaris*, y = 1239.4x - 1.3664, N=41; *Choerodon fasciatus*, y = 476.14x + 0.2957, N=72; *Cheilinus fasciatus*, y = 460.02x + 0.391, N=89; *Epibulus insidiator*, y = 518.49x + 0.1015, N=82 and *Hemigymnus melapterus*, y = 632.51x + 0.204, N=72.

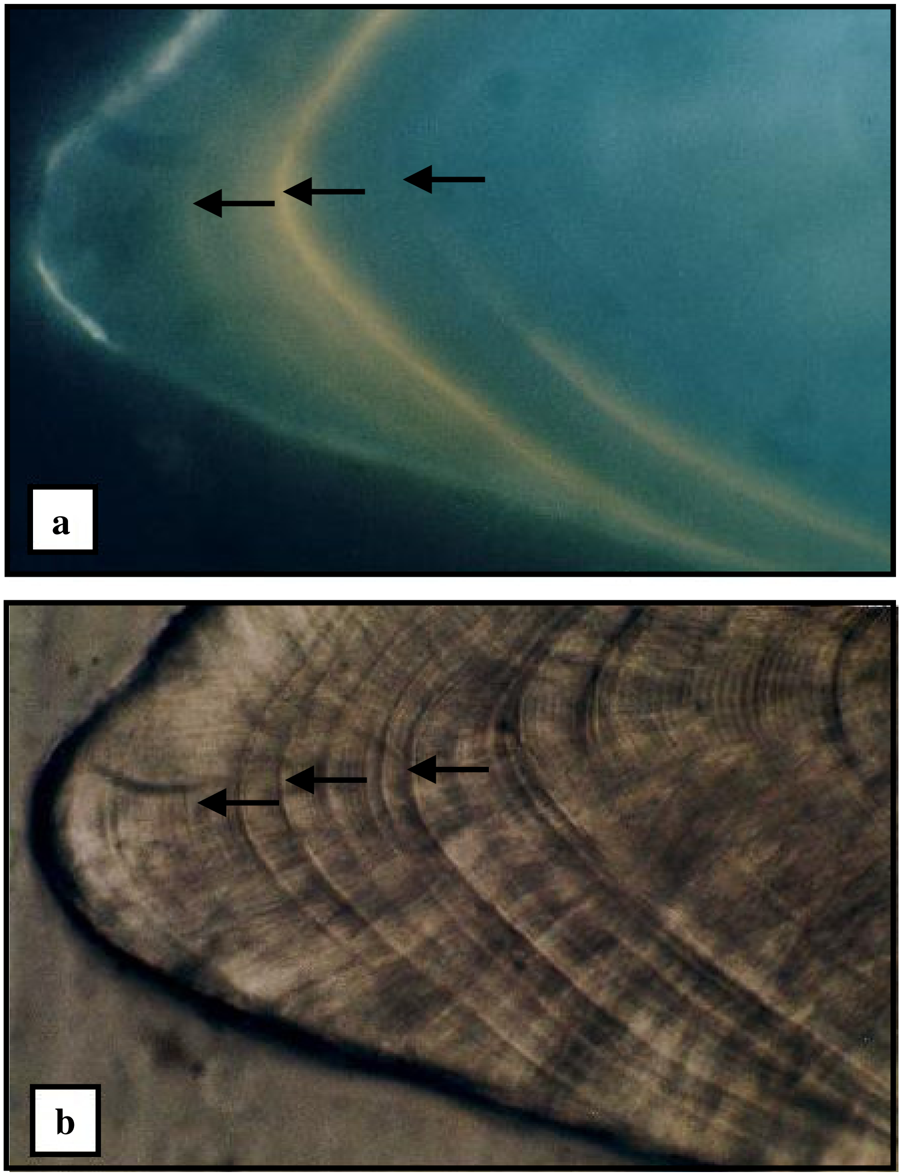

Figure 2.5: Validation of periodicity of increment deposition in otoliths of *Halichoeres melanurus*: a) Otolith indicating fluorescent tetracycline markings under ultra-violet light source, injections were made on 13/03/01, 09/04/01 and 01/05/01; b) Same otolith under transmitted light. 27 increments were counted between the first and second tetracycline mark (note that tetracycline marks were laid down 12-24 hrs after injection) and 22 were counted between the second and third tetracycline marks, therefore deposition of increments corresponded to a daily rate. Arrows indicate position of tetracycline markings under ultra-violet and transmitted light.

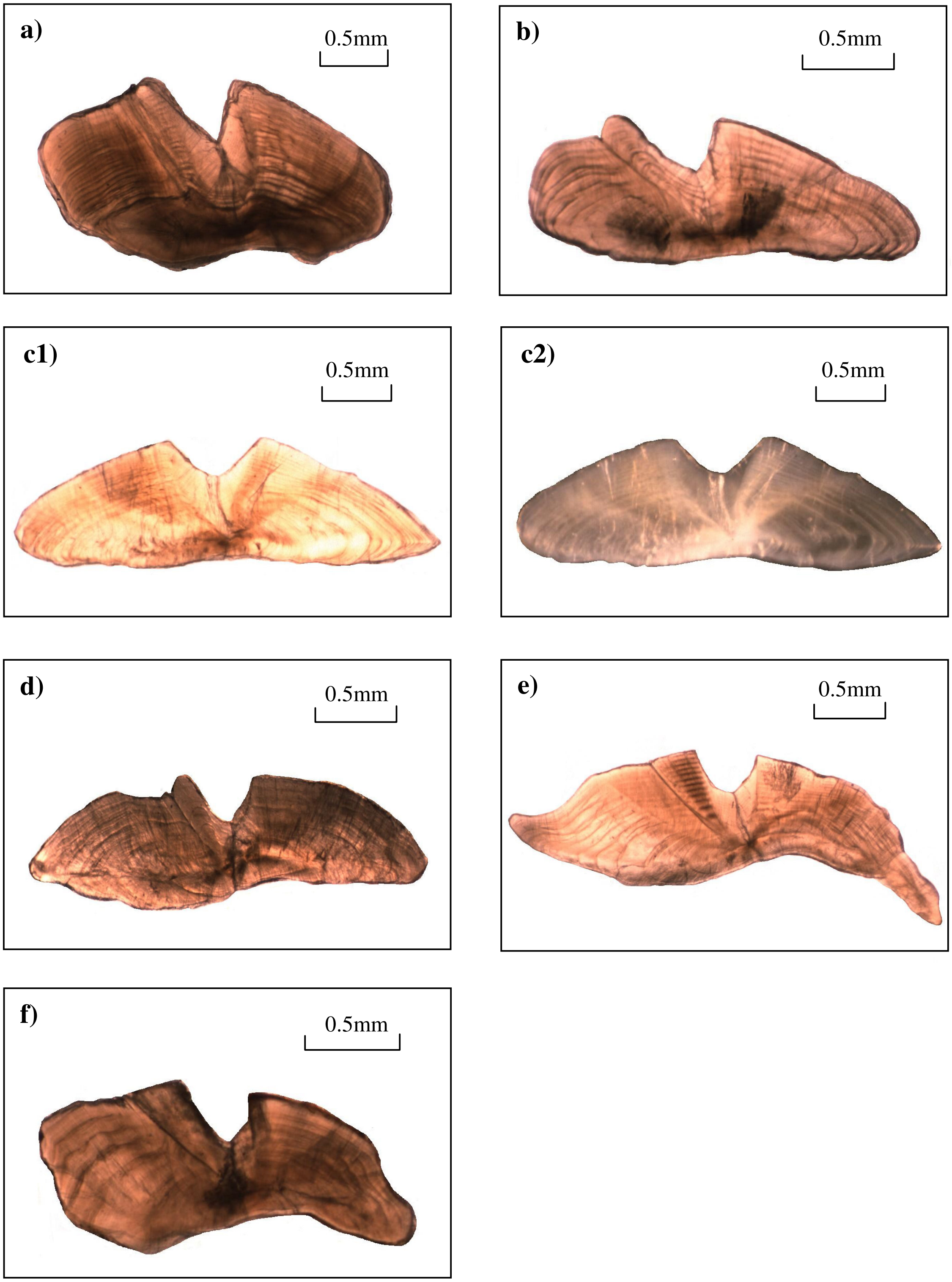

Figure 2.6: Sectioned otoliths of species with annual rings: a) *Bodianus mesothorax* (22 yrs), b) *Bodianus axillaris* (7 yrs), c1) *Choerodon fasciatus* (transmitted light) (5 yrs), c2) same otolith as c1 but with incident light and a black background, d) *Cheilinus fasciatus* (5 yrs), e) *Epibulus insidiator* (14 yrs), f) *Hemigymnus melapterus* (6 yrs).

Table 2.3: Relationships between length and mass for 10 species of tropical wrasses. The equation $W=aL^b$ was fitted to relationships for the sampled species, where W is mass (g) and L is standard length (mm). Provided are estimates of coefficients a and b, 95% confidence limits for b, coefficient of determination (r^2), and total number of individuals in sample (N).

Species	$a \times 10^{-5}$	b	95% confidence limits	r^2	N
Pseudocheilinops ataenia	7.474	2.84	2.78-2.90	0.930	149
Pseudocheilinus hexataenia	6.022	2.85	2.74-2.96	0.951	138
Pseudocheilinus evanidus	1.999	3.09	2.87-3.31	0.921	67
Halichoeres melanurus	5.888	2.80	2.73-2.87	0.977	144
Bodianus mesothorax	6.178	2.87	2.56-3.18	0.867	51
Bodianus axillaris	4.152	2.94	2.58-3.30	0.870	46
Choerodon fasciatus	17.417	2.71	2.53-2.89	0.935	74
Cheilinus fasciatus	7.011	2.90	2.82-2.98	0.983	90
Epibulus insidiator	5.118	2.96	2.87-3.07	0.971	88
Hemigymnus melapterus	13.264	2.75	2.68-2.82	0.989	77

Table 2.4: Percentage error for repeat counts of daily and annual rings. Number of aged individuals (N) is provided for each species. Estimates calculated using the method of Beamish & Fournier (1981), see text for further details.

Species	Percentage error	N
Pseudocheilinops ataenia	3.7	82
Pseudocheilinus hexataenia	6.0	80
Pseudocheilinus evanidus	5.9	45
Halichoeres melanurus	4.7	80
Bodianus mesothorax	6.3	51
Bodianus axillaris	5.3	41
Choerodon fasciatus	13.5	72
Cheilinus fasciatus	5.8	89
Epibulus insidiator	3.6	82
Hemigymnus melapterus	7.5	72

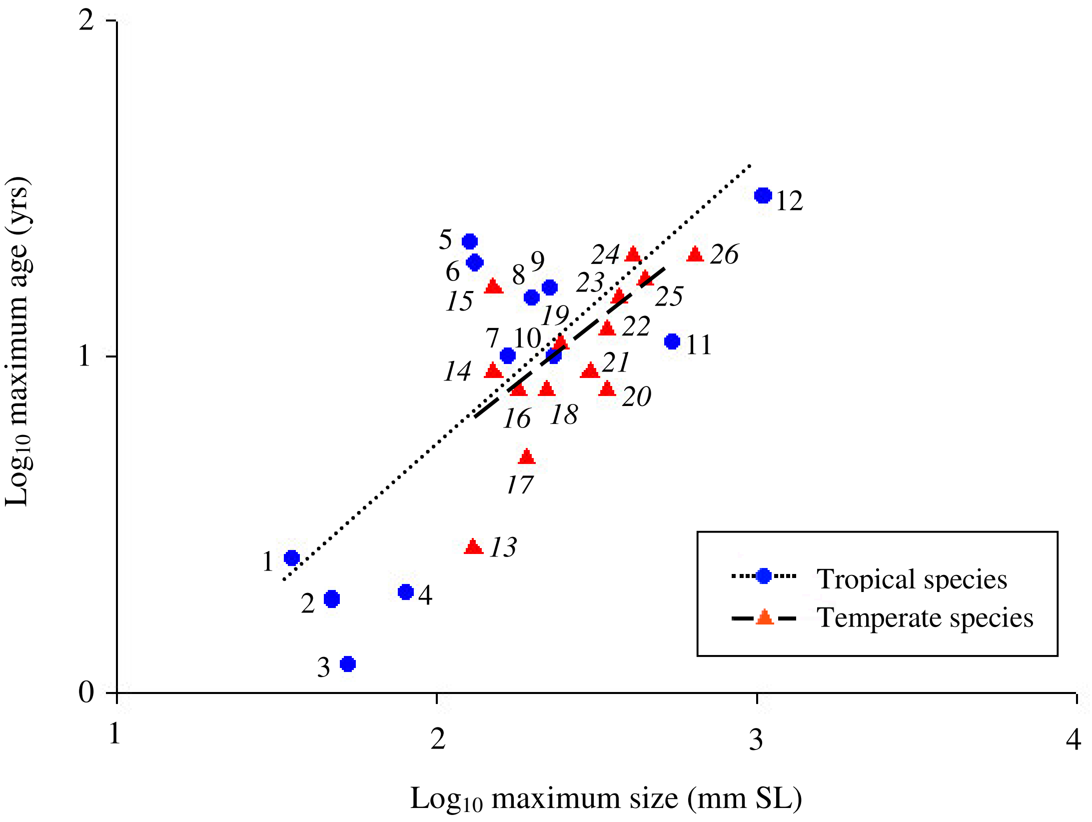

Figure 2.7: Log-transformed plot of maximum species size versus maximum age for tropical and temperate wrasses. Linear regression lines for tropical species: y=0.870x-1.007, r^2=0.595 and temperate species: y=0.786x-0.902, r^2=0.435. Species in order of maximum size are: Tropical species - 1. *Pseudocheilinops ataenia*, 2. *Pseudocheilinus hexataenia*, 3. *Pseudocheilinus evanidus*, 4. *Halichoeres melanurus*, 5. *Bodianus mesothorax*, 6. *Bodianus axillaris*, 7. *Choerodon fasciatus*, 8. *Cheilinus fasciatus*, 9. *Epibulus insidiator*, 10. *Hemigynus melapterus*, 11. *Choeredon schoenleinii*, 12. *Cheilinus undulatus*. Temperate species - *13. Symphodus roissali*, *14. Ctenolabrus exoletus*, *15. Ctenolabrus rupestris*, *16. Coris julis*, *17. Crenilabrus melops*, *18. Notolabrus celidotus*, *19. Labrus mixtus*, *20. Symphodus tinca*, *21. Achoerodus viridis, 22. Labrus bergylta*, *23. Notolabrus tetricus*, *24. Labrus merula*, *25. Notolabrus fucicola*, *26. Choerodon rubescens.* For 11 and 12, data were provided by Choat H. & Ackerman J.

Maximum size explained 44% of the variation in maximum age in the temperate wrasses and 60% in the tropical ones. The tropical species which deviated most from the regression line were *H. melanurus* and *P. evanidus*, which were shorter lived than expected for their respective body sizes and the two *Bodianus* species which had a far greater life-span than expected for their relatively small size. The positive relationship between size and age provided support for the following models explaining variation in adult size of species (Introduction 2.1, Figure 2.1): ‘Same growth, longer life-span’ (model a), ‘faster growth, shorter life-span’ (model c) and ‘faster growth, longer life-span’ (model d). On the basis of this relationship the model of ‘faster growth, same life-span’ (model b) could be rejected as small and large species did not have similar life-spans. The conceptual model e (‘smaller size, more determinate growth’), is mainly concerned with the expression of determinate or indeterminate growth and similarity in age is not necessarily a requirement, therefore no assessment of this model could be made from this result.

2.3.3 Prediction 2: An increase in maximum size is associated with faster early growth in larger species

To test whether large body size is associated with a faster absolute increase in body size at an early age, I examined the relationship between maximum body size and the absolute size reached at 0.5 and 1 year of age. No significant trend relating body size to size at either 0.5 years ($F_{1,8}$=0.563; p=0.475), or 1 year of age ($F_{1,8}$=3.393; p=0.103) was apparent in the plot of absolute growth (Figure 2.8). For example, after 0.5 years *P. evanidus* (maximum adult size of about 52mm SL) had grown more than many of the largest species sampled. It is worth noting though that the smallest species (*P. ataenia*) grew the least over the first six months and the largest species (*H. melapterus*) had the greatest absolute growth for this period. At 1 year of age the pattern was similar. As expected, growth in the larger species between 0.5 and 1 year was far greater than in the smaller pseudocheilinids, as these were much closer to their maximum size after 1 year. Overall, the lack of a systematic change in size attained after 0.5 and 1 year with an increase in body size of species, provides some support for the ‘same growth, longer life-span’ model (Figure 2.1, model a). Even though absolute growth after 1 year was similar in for example, *P. evanidus* and *E. insidiator*, the latter species can get considerably larger by living longer. However, to attain a clearer view of the processes operating it was necessary to examine growth beyond the first year of life.

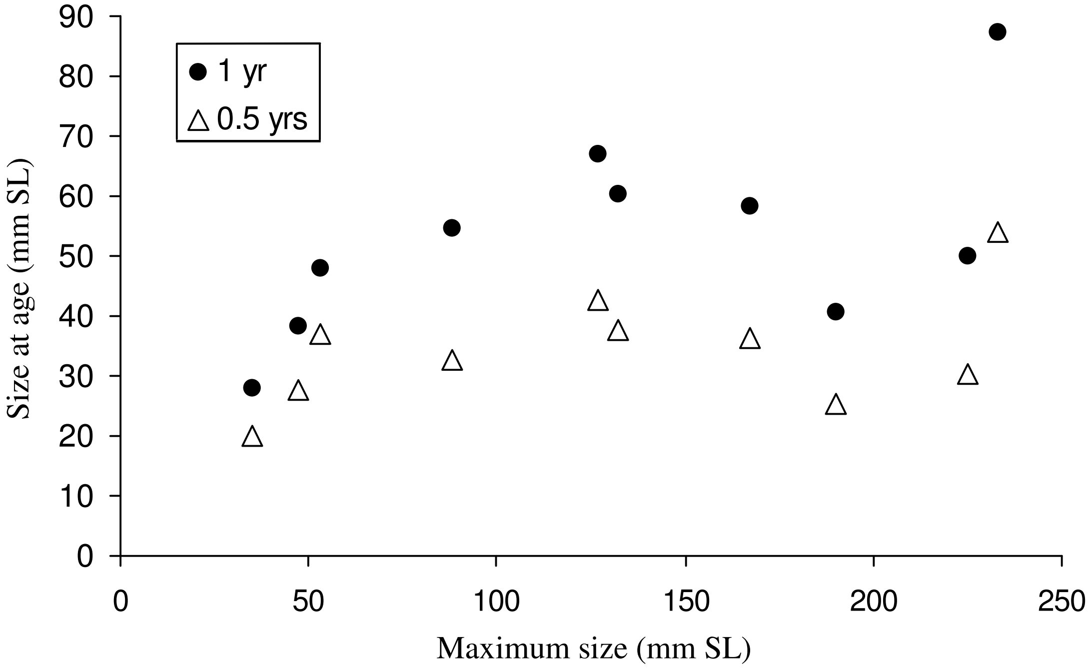

Figure 2.8: Size of species at 0.5 and 1 year of age estimated using the von Bertalanffy growth function. Species in order of increasing size are *Pseudocheilinops ataenia*, *Pseudocheilinus hexataenia*, *Pseudocheilinus evanidus*, *Halichoeres melanurus*, *Bodianus mesothorax*, *Bodianus axillaris*, *Choerodon fasciatus*, *Cheilinus fasciatus*, *Epibulus insidiator* and *Hemigymnus melapterus*.

2.3.4 Prediction 3: Increased growth exacts a cost in terms of smaller body size and decreased life-span

The ten wrasse species examined in this study exhibited a wide range of relationships between size and age. The von Bertalanffy growth function (VBGF) provided a good fit to size-at-age data plots for all species (Figure 2.9, Table 2.5). The low r^2 values for the fits for the two *Bodianus* species and *Choerodon fasciatus* reflect the fact that although few very small individuals were collected for these species, the curve was still constrained to intercept the y-axis at an estimated size at settlement (5mm SL).

When all the VBGFs were superimposed it was clear no single model explained the variation in adult size among species (Figure 2.10). There was some support for the 'faster growth, reduced life-span' model (Figure 2.1, model c). The observed relationship, however, was a variation on that proposed, as the faster growth was associated with reduced life-span but not necessarily smaller body size. This was evident within the pseudochelinid species. *P. evanidus* (the largest pseudocheilinid) had the fastest initial growth and the shortest life-span of the pseudocheilinids, *P. hexataenia* had slightly slower growth and a slightly longer life-span but reached a smaller body size. The smallest species sampled (*P. ataenia*) had slower growth than the other pseudocheilinids but attained the longest life-span despite its smaller size. This relationship was also apparent in *H. melapterus*. In the field, this species reached the largest body size of those sampled. It was found to grow very rapidly in comparison to the other large species and this was associated with a short life-span, the oldest individual sampled was only 7 years old.

2.3.5 Prediction 4: Increased growth provides a survival advantage resulting in larger body size and increased life-span

Growth curves (Figure 2.10) only supported the 'faster growth, longer life-span' model (Figure 2.1, model d) for species at extremes of the size ranges. For example, when comparing the slower growth of *P. ataenia* to the faster growth of *Cheilinus fasciatus* and *E. insidiator*. Nevertheless, support for this model was weak given the other two pseudocheilinid species grew as rapidly as *Cheilinus fasciatus* and *E. insidiator* over their entire lives (Figure 2.10), so the 'same growth, longer life-span' model was again supported among these species.

2.3.6 Prediction 5: Smaller species have more determinate growth

There was no relationship between maximum body size and growth trajectory (Figure 2.11). Therefore, the 'smaller species, more determinate growth' model (Figure 2.1, model e) could be rejected for these wrasses. There was also no relationship between early growth and maximum body size of individuals sampled within species (where early growth was defined as the proportion of adult size attained after 20% of maximum life-span). Early growth relative to size and age, appeared quite constant among most species (Figure 2.12). Only the two *Bodianus* species exhibited determinate growth. Both these species had very rapid early growth, *B. mesothorax* reaching asymptotic length after ~24% of its life-span and *B. axillaris* reaching it slightly later after ~31% of its life-span.

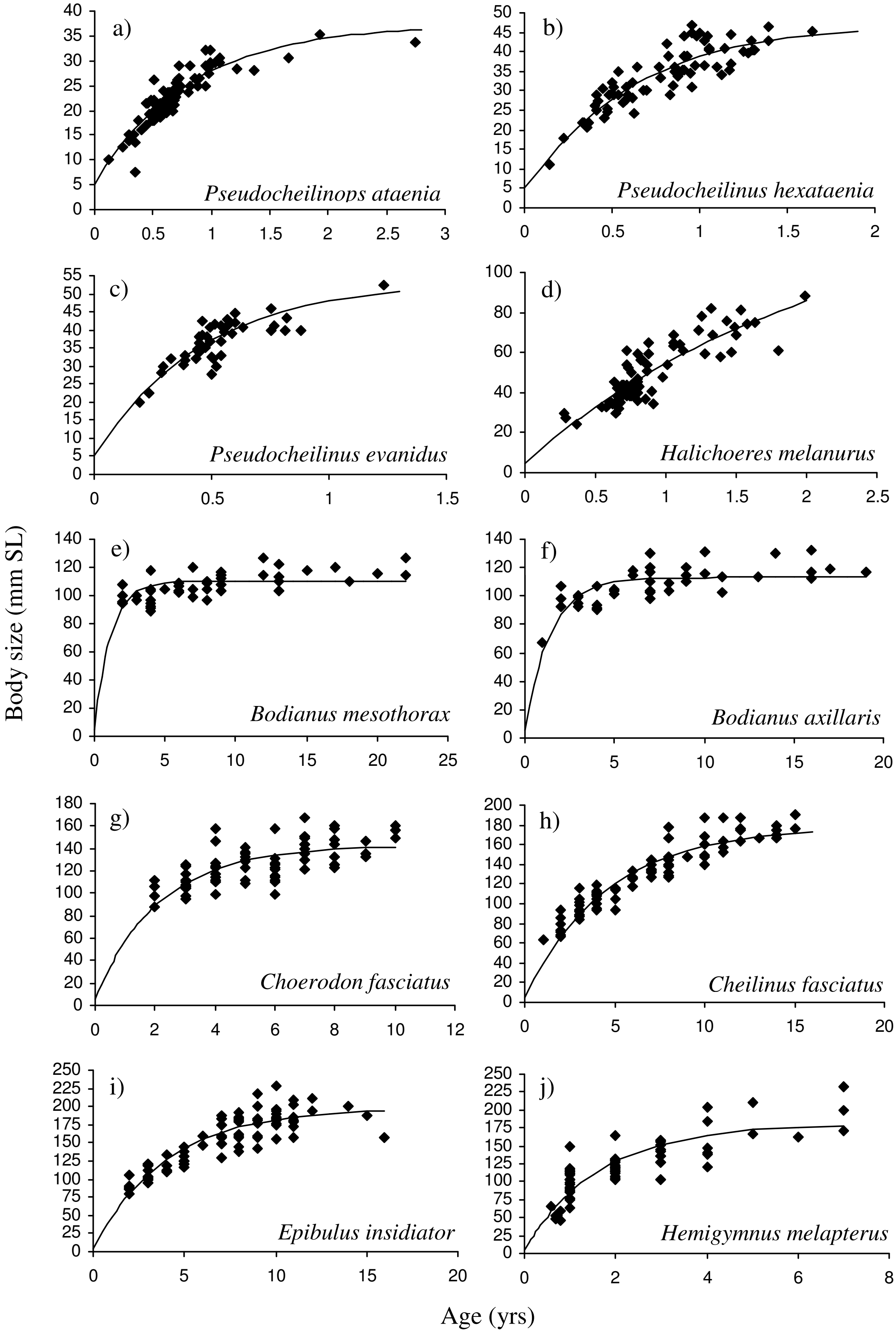

Figure 2.9: von Bertalanffy growth functions fitted to size-at-age data. Species are displayed in order from smallest to largest maximum sampled body size.

Table 2.5: Parameters estimated for von Bertalanffy growth functions fitted to size-at-age data for each species: Asymptotic length (L_∞), Brody growth coefficient (K), coefficient of determination (r^2) and age at size 0 (t_0) and sample sizes (N). * due to its approximately linear growth, this species was the only one for which the estimate of asymptotic length exceeded the size of individuals observed in the field.

Species	L_∞	K	r^2	t_0	N	Size range (mm SL)
Pseudocheilinops ataenia	37.36	1.23	0.834	-0.120	82	5-35
Pseudocheilinus hexataenia	46.78	1.62	0.764	-0.050	80	11-47
Pseudocheilinus evanidus	53.40	2.18	0.747	-0.045	45	20-53
Bodianus mesothorax	110.06	0.89	0.143	-0.052	50	89-127
Bodianus axillaris	113.07	0.72	0.452	-0.063	41	90-132
Choerodon fasciatus	142.59	0.46	0.450	-0.140	72	88-167
*Halichoeres melanurus**	138.08	0.47	0.750	-0.080	82	29-88
Cheilinus fasciatus	179.96	0.21	0.887	-0.220	89	64-190
Hemigymnus melapterus	184.70	0.61	0.683	-0.085	82	44-233
Epibulus insidiator	198.94	0.25	0.764	-0.172	72	80-225

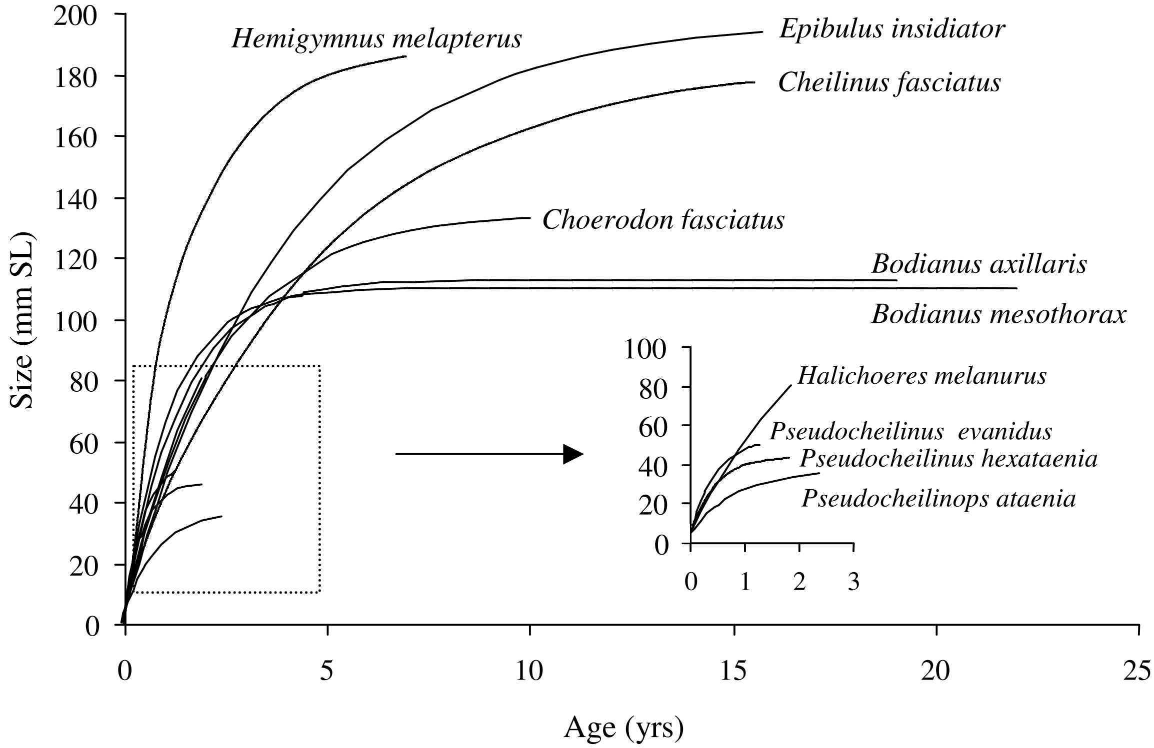

Figure 2.10: Superimposed von Bertalanffy growth functions for all sampled species.

H. melanurus lay at the other extreme of the continuum. In this species, there was an almost linear increase in size with age, where proportionally the same amount was added to its size throughout life (Figure 2.11).

Individuals belonging to the remaining species had non-linear growth trajectories and did not reach their asymptotic length until they were almost at the end of their life-spans. The majority of species including the smallest and largest examined displayed a similar indeterminate growth trajectory. This indicates that for a given proportion of life-span species reached a similar proportion of adult size, regardless of differences in the adult sizes attained among species. It is noteworthy that the two species with determinate growth were also the longest lived species.

2.3.7 Prediction 6: Smaller species have higher mortality rates than larger species

The prediction that larger body size is associated with reduced mortality rates was confirmed. There was a significant decrease in mortality rate with an increase in maximum body size of species using both Pauly's ($F_{1,8}$=16.91; p=0.003) and Hoenig's ($F_{1,8}$=11.70; p=0.009) techniques (Figure 2.13). Although the slopes of the regressions using Pauly's and Hoenig's techniques were not significantly different (t_{16}=0.768; p=0.2) there was a significant difference in elevation (t_{17}=8.621; p<0.001). Mortality estimates using Pauly's equation were generally higher with the exception of estimates for *H. melanurus* for which mortality was estimated to be lower. Pauly's method illustrated a more consistent trend of decreasing mortality rate with an increase in size. The high mortalities and reduced longevities of smaller species are compatible with three of the five models suggested: 'Same growth, longer life-span'; 'faster growth, shorter life-span' and 'faster growth, longer life-span' (Figure 2.1, models a, c and d).

2.3.8 Phylogenetic analyses

The non-phylogenetic approach in COMPARE (TIPS) plots the same relationships between actual trait values of species as those illustrated in these results. Therefore, r^2 values presented so far for relationships in this chapter are exactly the same as those derived from TIPS. Results of the non-phylogenetic approach are presented again here for comparison with the results using phylogenetic comparative methods (PCMs) (Table 2.6).

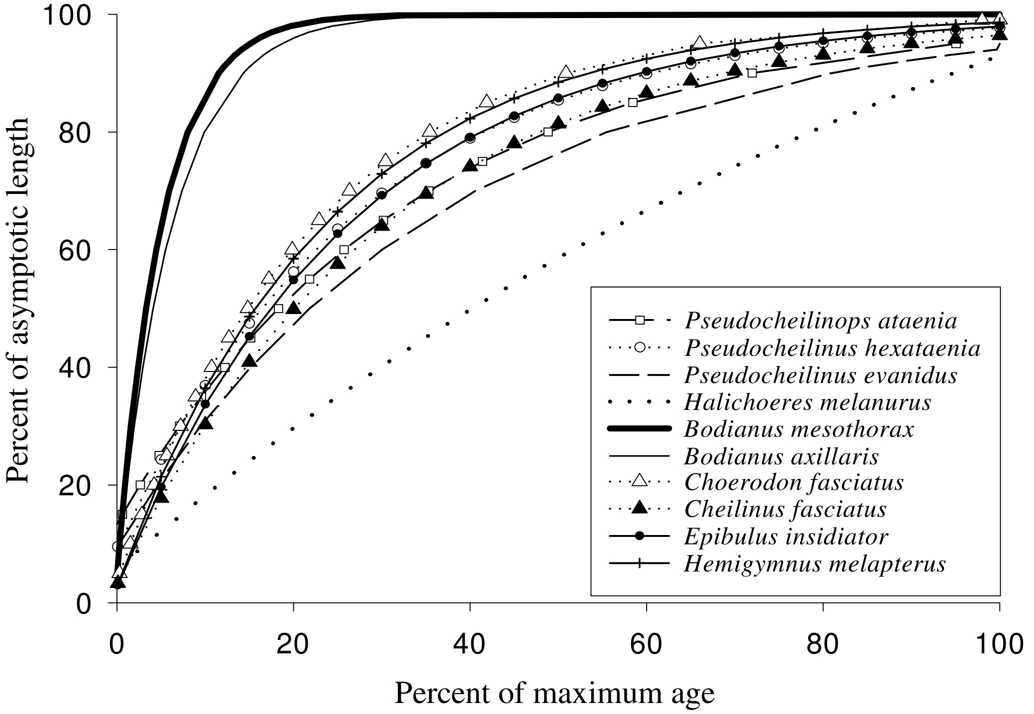

Figure 2.11: Growth of wrasse species relative to maximum age and asymptotic length (L_∞). As asymptotic length obtained from the von Bertalanffy growth function was unrealistic for *Halichoeres melanurus* the percent of maximum age is plotted against the percent of maximum size and not the percent of asymptotic length for this species (see section 2.2.5.2.3). Species listed in order of body size starting with smallest species.

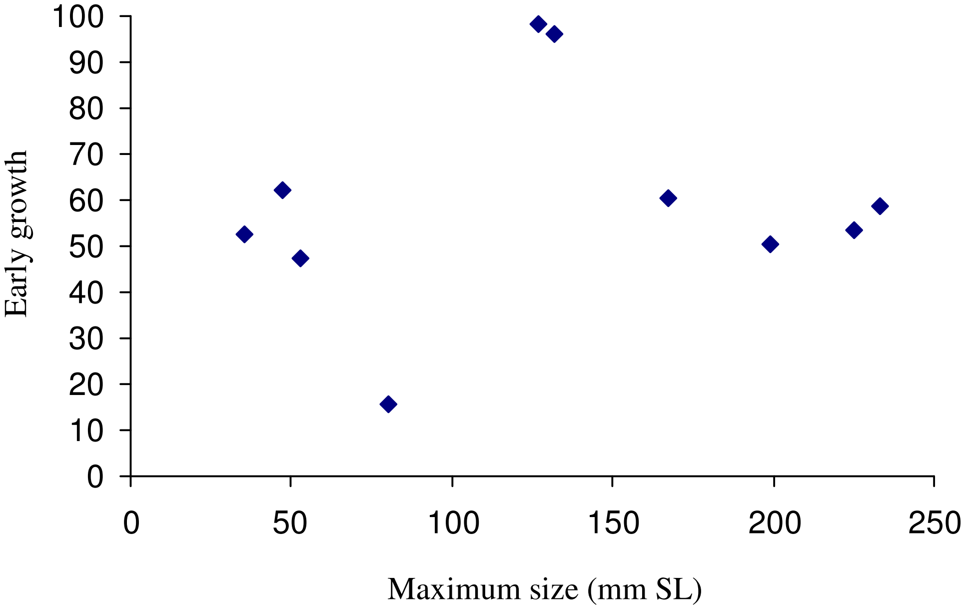

Figure 2.12: Relationship between maximum body size of species and early growth of wrasses (percentage of asymptotic length reached after 20% of maximum life-span). Species in order of increasing maximum size: *Pseudocheilinops ataenia, Pseudocheilinus hexataenia, Pseudocheilinus evanidus, Halichoeres melanurus*, *Bodianus mesothorax*, *Bodianus axillaris*, *Choerodon fasciatus*, *Cheilinus fasciatus*, *Epibulus insidiator, Hemigymnus melapterus.*

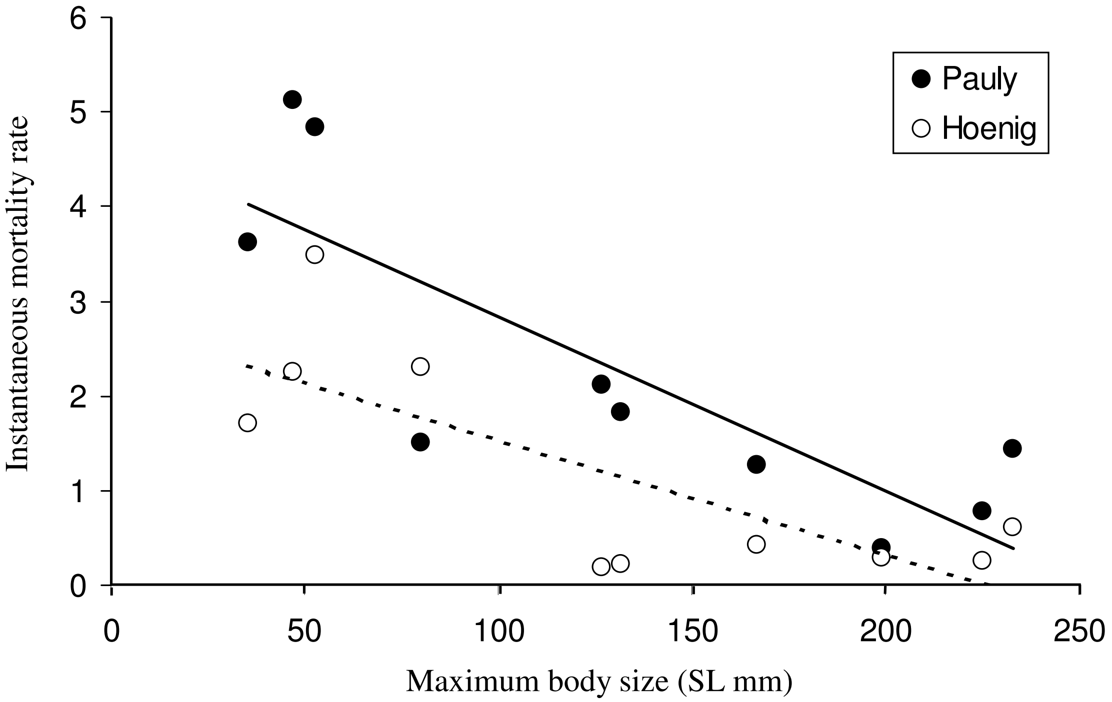

Figure 2.13: Relationship between maximum size of species and instantaneous mortality rate. Mortality rates calculated using the formulae of Pauly (1984) and Hoenig (1983). Least-squares regression for the plot using Pauly's method (solid line) is $y = -0.0178x + 4.5522$, $r^2=0.616$. Hoenig's method (dotted line), $y = -0.0122x + 2.7526$, $r^2 = 0.594$. Species in order of increasing maximum size: *Pseudocheilinops ataenia, Pseudocheilinus hexataenia, Pseudocheilinus evanidus, Halichoeres melanurus*, *Bodianus mesothorax*, *Bodianus axillaris*, *Choerodon fasciatus*, *Cheilinus fasciatus*, *Epibulus insidiator, Hemigymnus melapterus.*

The correlations between values derived from TIPS and PCMs are not the same. Those derived using TIPS are for comparisons of actual values for a given trait, whereas the correlations for PCMs are for contrasts between trait values for different species calculated in relation to where species lie in a phylogenetic tree. Despite the methods of calculating relationships among traits, coefficients of determination (r^2) indicating the strength of a relationship are directly comparable among techniques. It is evident here that there is variation among r^2 values using the different methods and the degree of variation depends on the traits of interest (Table 2.6).

For relationships examined the r^2 value using TIPS was often the highest (Table 2.6), indicating the strength of the relationship obtained was slightly greater when phylogeny was not considered. Of the two phylogenetic comparative methods, the phylogenetic generalised least-squares approach (PGLS), consistently produced estimates of r^2 close to those obtained using TIPS. Felsenstein's independent contrasts (FIC) consistently produced weaker correlations. This could be due to the unrealistic assumption of FIC that a Brownian motion model adequately describes evolutionary processes.

Table 2.6: Results of data analysis using a non-phylogenetic comparative method (TIPS) and two phylogenetic comparative methods; Phylogenetic Generalised Least-Squares approach (PGLS) and Felsenstein's Independent Contrasts method (FIC). Provided are the slope of the relationship, the mean values of r^2 obtained by each method after analysing data on twenty different phylogenetic trees of the same topology but varying branch lengths, the standard deviation of the mean (SD), and for comparative purposes, the value of r^2 when analyses were conducted on a tree assumed to have equal branch lengths.

Relationship examined:	**Method**	**Slope**	**r^2 (average of 20 trees)**	**SD**	**r^2 (equal branch lengths)**
Maximum body size vs. maximum age (both values log transformed): tropical species	PGLS	+ve	0.457	0.083	0.490
	FIC	+ve	0.289	0.074	0.427
	TIPS	+ve	0.595		
Maximum body size vs. size at 0.5 yrs	PGLS	+ve	0.131	0.025	0.123
	FIC	+ve	0.089	0.104	0.123
	TIPS	+ve	0.123		
Maximum body size vs. size at 1.0 yr	PGLS	+ve	0.311	0.045	0.313
	FIC	+ve	0.113	0.111	0.179
	TIPS	+ve	0.313		
Maximum body size vs. early growth (% of asymptotic length attained after 20% life-span)	PGLS	+ve	0.022	0.006	0.014
	FIC	+ve	0.157	0.177	0.023
	TIPS	+ve	0.020		
Maximum body size vs. mortality	PGLS	-ve	0.524	0.053	0.449
	FIC	-ve	0.262	0.178	0.194
	TIPS	-ve	0.616		

2.4 Discussion

This study highlights the complexities of growth and illustrates the expression of diverse growth strategies within a family of coral reef fishes. Overall, it is evident that no single conceptual model can account for the wide variation in body sizes observed among the reef fish species studied here. It was possible to reject the 'faster growth, same life-span' and 'smaller, more determinate growth' models (Figure 2.1, models b & e). Most support was provided for a combination of the 'faster growth, shorter life-span' model (which implies intrinsic trade-offs between energy allocated to growth and survival are important in some coral reef fish species) and the 'same growth, longer life-span' models (Figure 2.1, models a & c). There was also some evidence to support the 'faster growth, longer life-span' model (Figure 2.1, model d). Outcomes of the predictions and support for and against each model is discussed below.

2.4.1 Maximum size vs. maximum age

The wrasses examined here exhibited a positive interspecific relationship between maximum size and maximum age, consistent with the pattern observed in similar comparative studies of terrestrial mammals (eg. Rensch 1959, Blueweiss et al. 1978). Life history strategies to reach a larger body size may inevitably result in a positive relationship between size and age. It is not clear whether the age and size correlation indicates a causal relationship, or both are influenced by variation in other life history parameters.

This positive correlation between size and age was consistent with the 'same growth, longer life-span', 'faster growth, shorter life-span' and 'faster growth, longer life-span' models. It also provided evidence to reject the 'faster growth, same life-span' model. However, expression among species of the 'faster growth, shorter life-span' model varied significantly from that described in the original model. Although some species appeared to suffer a cost of faster growth in the form of reduced life-span, they were still able to attain a large body size. Such a process could result in a negative relationship between size and age, which was evident within the pseudocheilinids and when comparing *H. melapterus* with the other larger species. These relationships can weaken the strength of the overall positive relationship expected between size and age among species.

An increase in maximum age with maximum body size among species was evident in both tropical and temperate wrasses. In addition, the similarity of regression slopes indicates the growth pattern of increased age with size does not differ greatly among temperate and tropical wrasses although tropical fishes may be slightly older for a given size than temperate ones. This pattern supports the finding of Edwards (1984) that growth rates in tropical and temperate fish from equivalent ecological niches may be similar. It runs counter, however, to the common expectation of a higher growth rate in tropical species due to higher water temperature (Atkinson 1994). Edwards (1984) suggested reasons for retarded growth in the tropics, including the observation that food sources may be limiting in tropical habitats which are typically oligotrophic.

Life history traits in fishes can vary on a range of spatial scales (eg. Gillanders 1997, Barrett 1999, Meekan et al. 2001, Gust et al. 2001). In this study with the exception of the pseudocheilinids and the single individuals of *C. schoenleinii* and *C. undulatus*, tropical species were collected at the same location to minimise the effects of spatial variation on life histories of wrasses. It could be suggested that the fact that only the three smallest species (*P. ataenia, P. hexataenia* and *P. evanidus*) were collected at Kimbe Bay potentially confounds variation in traits with body size due to location effects. Latitudinal variation in life histories has been demonstrated in reef fishes (Chapter 4 this thesis, Bray 2001). As an example, the largest individual of *P. hexataenia* observed at Kimbe Bay had a fork length of 57mm and this species can reach 75mm on the southern GBR (Randall et al. 1997). This only represents a 1.3 fold change in maximum body size among locations while among species sampled there was a 10 fold increase in size from smallest to largest. Therefore, variation in growth and body size within species is not sufficient to confound relationships among species.

In addition, as the temperate wrasses were collected at a diverse range of locations, they are likely to differ considerably in terms of abundance, availability of resources, diet, habitat preferences, predation, mortality rates and other selective pressures (Begon et al. 1996). Despite this, the elevation and slope of the line of least-squares regression is similar to the tropical wrasses. This suggests that the interspecific relationship between maximum size and maximum age is robust to geographic variation in the above factors. Environmental and phylogenetic factors may still have some influence on the patterns observed and contribute to the observed variation in expected age for a given body size.

2.4.2 Absolute Growth

Large body size was not associated with faster absolute growth early in life. Very small species grew to a similar size as much larger species over the first year, providing support for the ‘same growth, longer life-span’ model. This implies reaching a larger size may not necessitate faster growth per unit time, but individuals may simply attain a large size by growing at a similar rate as smaller species for a longer period of time (Arendt 1997). *H. melapterus* appears to be an exception. It was the largest of the species and had the greatest absolute early growth. The short life-span of this species (7 years) relative to the other large species could be related to this faster growth.

2.4.3 Growth (Relative to Maximum Size and Age)

Due to a combination of greater mass-specific metabolic rates in smaller species and the possible need to attain maturation size more rapidly when mortality-risk is high (Reznick et al. 1990, Arendt 1997, McCann & Shuter 1997, Clarke & Johnston 1999), smaller species should be selected to reach a greater proportion of their maximum body size earlier in life than larger species. When growth was examined in relation to age and asymptotic size (L_∞), however, no relationship with body size was evident. Contrary to the expectations of life history theory, the growth of the small pseudocheilinids was not greater in the early part of life (0-20% of life-span) than the larger species and there was very little variation in early growth among species. These results suggest that there is no environmental pressure for small wrasse species to reach a greater proportion of adult size early in life than larger species. Within the wrasses, a diversity of growth trajectories were exhibited, from determinate (*Bodianus* spp.) to indeterminate (eg. *H. melanurus*) and early growth appeared to be more closely linked to the expression of indeterminate or determinate growth than the maximum body size of species.

2.4.4 Growth strategy (indeterminate vs. determinate)

There was no predictable relationship between growth trajectory and body size. Therefore, the ‘smaller species, more determinate growth’ model was rejected. The *Bodianus* species were unusual compared to other wrasses studied to date in that they display determinate growth. Determinate growth in fishes has only previously been described in a few families, in particular damselfishes (Meekan et al. 2001, Tzioumis & Kingsford 1999), butterflyfishes (Nangle P. unpublished data) and surgeonfishes (Choat

& Axe 1996), in which this growth strategy appears to be a relatively consistent characteristic of the whole family. Two species demonstrating determinate growth in this study and many other fish species in which it has been described (eg. Choat & Axe 1996, Meekan et al. 2001, Tzioumis & Kingsford 1999, Choat & Robertson 2002), have all had long life-spans. Hence, determinate growth appears to be closely linked with increased longevity.

Why determinate growth should be associated with increased life-span requires further investigation. The rapid attainment of adult body size in these species may confer a survival advantage. For example, if predation is the main cause of mortality of coral reef fishes (Caley 1993), then for some reason adults of these long-lived species have reduced susceptibility to attack. This could be due to cryptic behaviour or maybe adults of some of these species have chemical defences and are unpalatable. An alternative explanation, is that species with determinate growth dramatically shift energy reserves from growth to survival and reproduction once they reach maximum size and consequently have more energy with which to forage for food and avoid predators (van Rooij et al. 1995, Sinervo & Svensson 1998, Mangel & Stamps 2001). Expression of different growth strategies in coral reef fish species has important implications for the expected relationships between life history traits among species. For example, within families characterised by determinate growth the interspecific relationship between size and age can become decoupled (Newman et al. 1996, Choat & Robertson 2002).

H. melanurus exhibited almost linear growth. In the other small species studied here, growth curves indicated that at a particular size and age somatic growth slows down regardless of environmental influences, but in *H. melanurus* this was not the case. Ecologically, *H. melanurus* differs from the other species in that it is one of the most abundant wrasse species on the Great Barrier Reef (Green 1994, Manthachitra 1996). Indeterminate growth in this species can afford considerable flexibility in growth in relation to environmental conditions, which may contribute to its broad distribution and high local abundance (Abrams et al. 1996). Further work is needed to examine potential relationships between growth trajectories and abundance of species.

2.4.5 Mortality

The inverse relationship found here between mortality rates and body size is consistent with the finding of Munday & Jones (1998). While each of the methods used to estimate mortality had limitations (neither method accounts for interspecific behavioural differences in terms of wariness of predators and closeness of association to shelter, which influence mortality rates), they both established a similar pattern. The similarity in growth early in life among many of the species makes it difficult to assess the importance of intrinsic and extrinsic sources of mortality among these species. The 'faster growth, shorter life-span' and 'faster growth, longer life-span' models which integrated intrinsic and extrinsic sources of mortality, respectively, required differences in growth to be expressed among species to be tested effectively. It is known though, that extrinsic sources of mortality are important in coral reef fishes. For example, larger individuals have a reduced susceptibility to predation (Wootton 1990, Hixon 1991, Mittlelbach & Chesson 1992). Larger body sizes confers a refuge from predation and the mouth gape of many predatory fishes limits their prey options to smaller species (Olson 1996). It is suggested here that a combination of intrinsic and extrinisic factors may contribute to mortality of smaller species but as body size increases and there is reduced risk of predation, extrinsic factors may become less influential.

Based on plots of mortality against body size, wrasses appear to suffer lower mortality than species in other fish families (Munro & Williams 1985, Eckert 1987, Williams & Russ 1994, Munday & Jones 1998). Results from many of the species studied here also fall below the regression line for mortality estimates of fishes (Figure 2.14), although they do fall within the range of 'scatter' around the regression line of data points for species belonging to other reef fish families (see Munday & Jones 1998). Estimates of mortality for species sampled in this study should be directly comparable to those from Munro & Williams (1985) and Williams & Russ (1994) as they were also mostly derived using Pauly's equation (Pauly 1984). Eckert (1987), however, used empirical observations to calculate mortality (Figure 2.14). It is possible that wrasse mortality may on average be lower than that observed in the majority of reef fish but mortality estimates for a greater number of wrasse species are required before any generalisations can be made.

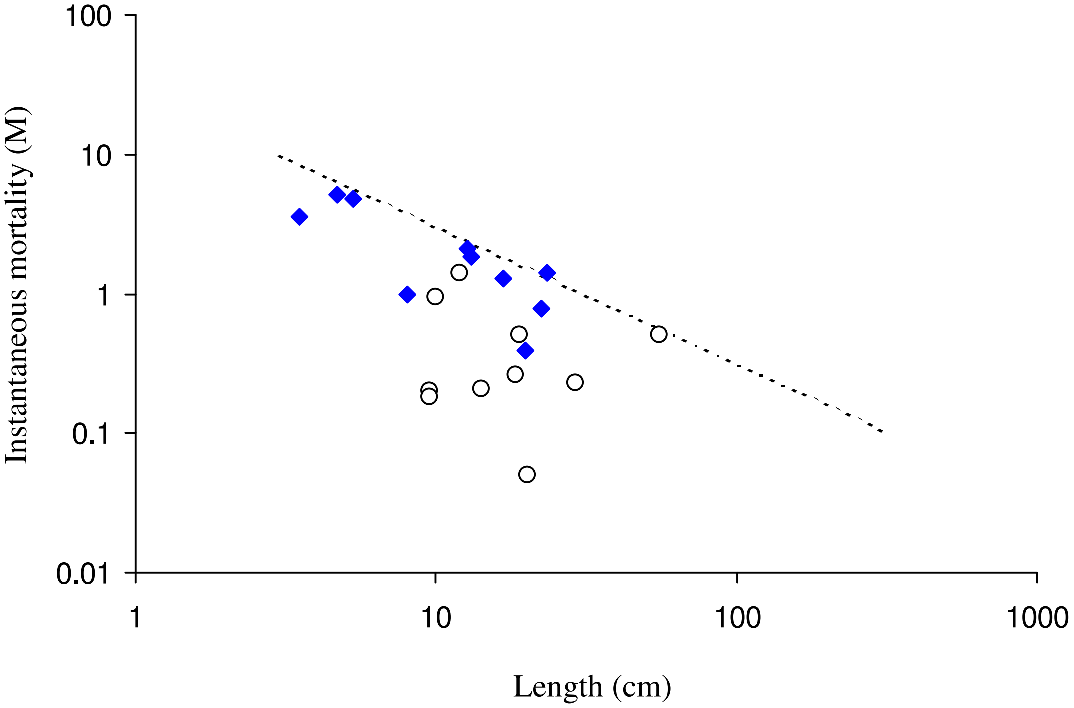

Figure 2.14: Comparison of the relationship between species size and instantaneous mortality rates for wrasses and that obtained for other coral reef fishes. Mortality rates calculated for wrasses in this study (solid diamonds) were estimated using the method of Pauly (1984). Mortality estimates for wrasses at One Tree Reef (open circles), were derived from empirical observations by Eckert (1987). The dotted line indicates mortality estimates reported for other coral-reef families by Munro and Williams (1985) and Williams and Russ (1994), (mortality=29.55*cm$^{-0.986}$, r^2=0.765)

2.4.6 Phylogeny

Although integration of phylogenetic information did not confound the overall trends identified here, it is evident that evolutionary history can play an important role in defining variation in life history traits among species. The three smallest species *P. ataenia*, *P. hexataenia,* and *P. evanidus* were closely related and had similar life history traits. The expression of determinate growth is also likely to be determined by evolutionary history. This is supported here by the expression of extremely similar determinate growth patterns in both *Bodianus* species and could be tested further by identifying if determinate growth is predominant among other *Bodianus* species over a wide geographic scale. Further evidence is provided by the consistent expression of determinate growth in some reef fish families (Choat & Robertson 2002). Although phylogenetic information for many reef fishes is lacking, it is clearly important to integrate phylogeny into comparative studies and consider its potential influences on patterns observed.

2.6.7 Future work

Although some consistent relationships have emerged from this study, only ten species were studied in detail. Extrapolation of the results to other species and families of reef fishes should be made with caution. Growth patterns and therefore body size–related relationships may vary considerably among families (Choat & Robertson 2002). Only by studying these relationships in a greater range of taxa, can their underlying importance and generality be evaluated. Within the wrasses it would be beneficial to examine growth patterns across a greater size range of species in order to examine patterns at both extremes of the size range, especially to identify how the largest wrasse species *C. undulatus* reaching over 2 metres in length, fits in with the relationships found in this study.

Greater sample sizes for each species would improve confidence in estimates of life history traits. Maximum ages of species are likely to be greater in the field than the oldest individual contained within a sample, which is an inherent problem when dealing with maximum longevities (Kritzer et al. 2001). For interspecific comparisons, however, mean age should only be used when a similar number of each age cohort or life phase is contained in the samples for each species. Despite the problems associated with the use of maximum longevities, they may be more useful than mean ages in describing adult longevities and a difference in estimation of maximum longevity of 10-30% should not confound any overall trends (Rose 1991).

Although daily rings were validated in *H. melanurus*, deposition of annual rings in species was not validated. Confidence in the assumption of such clear rings being annual should be high though as validation of annual rings using mark-recapture has been successful for parrotfish species (Choat et al. 1996), a family of fishes very closely related to wrasses. In addition marginal increment analysis has validated annual rings in temperate wrasses (Treasurer 1994, Gillanders 1997) and counts of daily rings were used to estimate the annual deposition of rings in juveniles of four temperate wrasse species (Gordoa et al. 2000). Fowler (1995) reviewed results of validation studies in coral reef fishes. Thirty-five studies attempted to validate annual deposition of increments and of these only two could not validate periodicity of ring deposition. Since that review twenty or so further studies have successfully validated annuli for a large number of reef fish species from a range of families (Choat & Robertson 2002). Future validation of the species involved in this study is encouraged.

2.4.7 Conclusions

Only some of the predictions put forward in the chapter, which were mainly based on studies of terrestrial organisms, were supported. The broad correlation between maximum size and age suggests that there is some underlying constraint on the time it takes for wrasses to reach large sizes. Variation in growth over the first year of life or growth trajectory relative to body size and longevity, had little effect on the absolute body size reached. In addition, trade-offs between rapid growth and mortality and the relative importance of intrinsic and extrinsic influences on size and longevity appear to be species specific. Achievement of large size is associated with reduced mortality rates with small species exhibiting dramatically higher losses.

Alternative hypotheses to assess variation in life history traits among species have arisen from this study and warrant further investigation. Variation in growth trajectories for example, is closely associated with longevity, species with determinate growth living longer than those with indeterminate growth. It is evident a complex interplay of a range of influences determine body sizes and longevities of reef fish species.

Relationships between body size and growth, longevity and mortality have been assessed in this chapter. A more complete picture of the processes which affect life history traits in reef fishes can be obtained by also examining reproductive parameters. Patterns of growth may be strongly influenced by reproductive parameters such as size and age at maturity, reproductive effort and in sequential hermaphrodites, size and age at sex change (Bell 1980, Warner & Lejeune 1985, van Rooij et al. 1995). When resource acquisition is limiting, the consequences of energetic trade-offs predicted for growth and mortality are also applicable to growth and reproduction. For example, life history theory predicts an increase in reproductive effort will result in slower somatic growth (Bell 1980, Reznick 1983, Reiss 1989). Variation in reproductive traits with species body size are examined in the following chapter.

CHAPTER 3: Body size and its relationship to maturation, reproduction and sex change in coral reef fishes

3.1 Introduction

Trade-offs in the allocation of resources between growth and reproduction are well-known and represent a central theme in the study of life histories (Bell 1990, Stearns 1992). Body size and reproductive characteristics are therefore intrinsically related and differences in size among species have the potential to directly influence reproductive effort and the timing of life history transitions such as maturation and sex change (Calder 1984, Roff 1992). The reproductive characteristics of species may also covary with body size in response to extrinsic factors. Social systems (Jones 1980, Garber & Leigh 1997), population density and structure (Ebenman & Persson 1988, Charnov 1993), predation pressure (Hixon & Beets 1993, Blackenhorn 2000, Chase et al. 2002), food availability (Jones 1986, Clifton 1995, Tenhumberg et al. 2000) and temperature (Atkinson 1994) can all directly influence both body size and reproductive traits. As growth characteristics and reproductive traits are influenced by each other and by similar extrinsic factors, there should be general rules governing their interaction. Although such generalisations are supported by numerous empirical studies, other research has found relationships between growth and reproductive characteristics that do not conform to general theory (Calder 1984, Millar & Hickling 1991, Stearns 1992, Day & Rowe 2002). More rigorous testing of the relationships between body size and key life history traits is necessary to evaluate whether established theory should be accepted, modified or abandoned.

Species use a diverse range of life history strategies, but some critical life history traits are common to the vast majority of animals (Bruton 1989). For example**,** age or size at maturity is a crucial determinant of an individual's fitness (Promislow & Harvey 1990, Roff 1992, Stearns 1992, Abrams et al. 1996). Following maturation, an individual is expected to allocate energy between reproduction and growth to optimise fitness. Consequent energetic trade-offs between growth and reproduction can have numerous implications for other fitness related traits such as adult size and longevity (Bell 1980, Stearns 1992, Madsen & Shine 1994). Species exhibiting sequential hermaphroditism also dramatically change how much energy is invested in female or male function during their life-span and are predicted to make allocation 'decisions' about when these changes should occur. Such allocation of energy among the sexes in hermaphroditic species may also be related to body size (Warner 1975, Charnov 1993, Rogers & Sargent 2001, Munday 2002). In the presence of these inter-relationships between growth and reproduction, body size should be a good predictor of reproductive characteristics among species.

Assuming that there is a trade-off between mortality-risk and size dependent fecundity, species should evolve proportionally earlier maturity when mortality is high and life-span is short (Harvey & Zammuto 1985, Sutherland et al. 1986, Promislow & Harvey 1990, Reznick et al. 1990, Stearns 1992). This pattern is evident for terrestrial species, as those with high levels of natural mortality also tend to mature proportionally earlier in life (Millar and Zammuto 1983, Sutherland et al. 1986, Promislow & Harvey 1990, Shine & Charnov 1993). Smaller species are expected to suffer greater mortality than larger species, therefore body size of species may indirectly influence attainment of maturation due to its close association with mortality rates (Promislow & Harvey 1990, Blackenhorn 2000). Maturing early in life does increase the probability of surviving to a reproductive age, but it can also be associated with a cost of reduced growth and lower fecundity (Roff 1992, Stearns 1992, Charlesworth 1994, Stamps et al. 1998, Day & Rowe 2002). Maximum body size itself could simply be an outcome of the trade-off between survival and reproduction, however, the potentially complex interactions between body size, mortality rate, longevity and maturation mean it is likely there are no simple cause-effect scenarios. Based on current theory and empirical research it can be predicted that smaller species mature at a proportionally earlier stage than larger species. In circumstances where there is a positive relationship between size and age within species, this should also correspond to attainment of a smaller proportion of adult size before maturation.

Following maturation, the amount of energy invested by an individual per reproductive episode is often related to its life-span. In longer-lived individuals, less energy is expected to be allocated to each bout, but the number of reproductive bouts an individual is likely to complete throughout life is greater (Bell 1990, Schwarzkopf 1993, Crespi & Teo 2002). Life-spans of species and their adult sizes are often positively related (Chapter 2 this thesis, Blueweiss et al. 1978, Stearns 1992), therefore reproductive effort should also be closely correlated with body size. Many terrestrial species conform to this pattern showing a decrease in reproductive effort with increasing body size (Peters 1983, Reiss 1989), where reproductive effort is defined as the proportion of available resources (time or energy, measured in seconds or calories) committed to reproduction, as opposed to other functions (Bell 1980). Body size can also indirectly influence reproductive effort through its association with mortality rates. For example, lower survivorship expected for smaller species is often associated with higher reproductive effort (eg. French et al. 1975, Boyce 1988, Gunderson 1997, Crespi & Teo 2002). Within species, increased reproductive effort can also have a survival cost in the form of increased mortality (Marshall 1988, Bell 1990, Schwarzkopf 1993, Caley et al. 2001), although it is not clear whether intraspecific relationships between body size and reproduction can explain differences in growth and reproductive characteristics at an interspecific level. Based on evidence available to date a decrease in reproductive effort of wrasse species with an increase in body size of species is predicted.

Within species, males often have a lower energetic investment into gametes than females (Reiss 1989), which can leave more energy available for growth (eg. Bruton 1989, Randriamahazo 2000, McNab & Armstrong 2001). The benefits of faster growth are considerable as larger males can monopolise mating and have a disproportionately high reproductive success relative to the effort expended (eg. Warner 1984, Warner 1988, Madsen & Shine 1994). When the expected reproductive success at a critical body size is consistently greater for males than females, protogynous hermaphroditism (sex change from female to male) is selectively advantageous (Ghiselin 1969, Warner 1975). Manipulation of populations has revealed that the social system of a species is important in determining when an individual changes sex (Robertson 1972, Shapiro 1987) and socially induced sex change of individuals is closely linked with body size. For example, if a dominant male in a group of females is removed, usually the largest female will become a male (eg. Robertson 1972, Warner 1975, Sakai et al. 2001).

As sequential hermaphroditism is absent in terrestrial vertebrates, occurrence of sex change has received far less attention than variation in other reproductive traits. In addition research to date has focussed mainly on the size and age at sex change within single species (Munday et al. 1998, Nakashima et al. 2000, Kuwamura & Nakashima 1998). No studies have specifically examined relationships between body size, longevity and the size or age at sex change among species. Sex change is likely to be closely linked to body size and to occur at a size or age which optimises fecundity throughout life (Warner 1975, Charnov 1993). It is expected that the selective pressures acting on size and age at maturity will also have comparable effects on size and age at sex change. Therefore, it is predicted that smaller species should change sex proportionally earlier in life and at a smaller proportion of maximum size than larger species.

Evidence to date, suggests that relationships which have been largely described for terrestrial organisms also apply in some marine and freshwater organisms (eg. Roff 1984, Charnov & Berrigan 1991, Roff 1992, Kozlowski 1996, Munday & Jones 1998). Intraspecific studies have indicated maturation occurs proportionally earlier in fish populations with higher mortality rates (eg. Blueweiss et al. 1978, Reznick et al. 1990, Rochet 1998, Bertschy & Fox 1999). Within and among some marine species reproductive effort has also been shown to increase as their chances of survival decrease (eg. Ebert 1975, Lardies & Wehrtmann 1997, Carlson & Ebersole 1995). However, relative to terrestrial species, little is known about the consistency of these relationships among aquatic taxa. Fundamental differences between poikilotherms (eg. fish) and homeotherms (eg. mammals) have the potential to modify relationships observed. For example, the increase of female fecundity with age is much more pronounced in poikilotherms than in homeotherms, and maturation is generally later in life in poikilotherms (Bell 1990).

In addition, the prevalence of indeterminate growth in fishes and other poikilotherms and determinate growth in many terrestrial homeotherms, could greatly influence patterns observed (Kozlowski 1996, Heino & Kaitala 1999). Growth following maturation slows down drastically or even ceases in species with determinate growth. In contrast there is an energetic trade-off between growth and reproduction throughout life in species with indeterminate growth (Charnov & Berrigan 1991). In species that grow continuously, reproductive effort should be even more closely linked with body size as the proportion of energy allocated to reproduction should be inversely related to that invested in growth (assuming energetic costs of maintenance remain constant). Research on sex change to date is based almost exclusively on studies of aquatic animals. Recent work in this area has demonstrated complex relationships between the determinants of sex change and variation in the sex change responses of hermaphroditic species to different situations (Kuwamura & Nakashima 1998, Munday et al. 1998). A great deal of work is required to clarify the factors which influence the timing of sex change given the extent of the variation within and among species.

Coral reef fishes provide an ideal opportunity to test predictions relating to inter-relationships between body size and reproductive strategies. Predation is known to be a very important structuring process within reef fish communities (eg. Caley 1993, Hixon

& Beets 1993, Caley & St John 1996, Caley 1998, Hixon & Webster 2002) and is likely to be a prime source of mortality for many reef fish species (Caley 1995). The importance of body size in determining susceptibility to predators is now well recognised in fishes with smaller species being more prone to predation than larger (eg. Ebenman 1988, Mittlelbach & Chesson 1992, Olson 1996, Munday & Jones 1998). As a consequence, mortality rates of smaller reef fish species are expected to be consistently greater than for larger species (eg. Chapter 2 this thesis, Munday & Jones 1998). Strong inter-relationships between body size, mortality and reproductive characteristics such as size and age at maturity and reproductive effort are expected across the size range of species observed in coral reef fishes. Sequential hermaphroditism is widespread in a number of fish families and is especially prevalent in coral reef fishes (Warner 1978, Warner 1988, Rogers & Sargent 2001, Munday 2002). Coral reef fishes should be integral to the examination of relationships between body size, size/age at sex change and other life history traits among different species. Such studies may reveal inter-relationships which have received little attention to date.

Wrasses (Pisces: Labridae) encompass the widest range of sizes of any reef fish family (Munday & Jones 1998). They are common on coral reefs and form an important component of reef ecosystems. Wrasses are protogynous hermaphrodites, enabling an assessment of the relationship between body size and longevity and size and age at sex change (eg. Warner & Robertson 1978). Phylogenetic information is available for wrasse species in this study which enabled the use of comparative phylogenetic techniques to remove the influence of evolutionary history on the patterns observed (Harvey & Pagel 1991).

The main aim of this study was to examine how strongly body size is correlated with the sexual characteristics of wrasses and whether the patterns observed conform to predictions based on current theory. Ten species of wrasse covering a ten-fold size range were used to examine interspecific relationships between body size and three reproductive characteristics: a) size/age at maturity, b) reproductive effort and c) size/age at sex change. The following three predictions were tested: 1) Smaller species mature at a smaller proportion of both adult size and life-span than larger species (Figure 3.1a), 2) Smaller species have greater reproductive effort than larger species (Figure 3.1b) and 3) Smaller species change sex at a smaller proportion of adult size and earlier in life than larger species (Figure 3.1c).

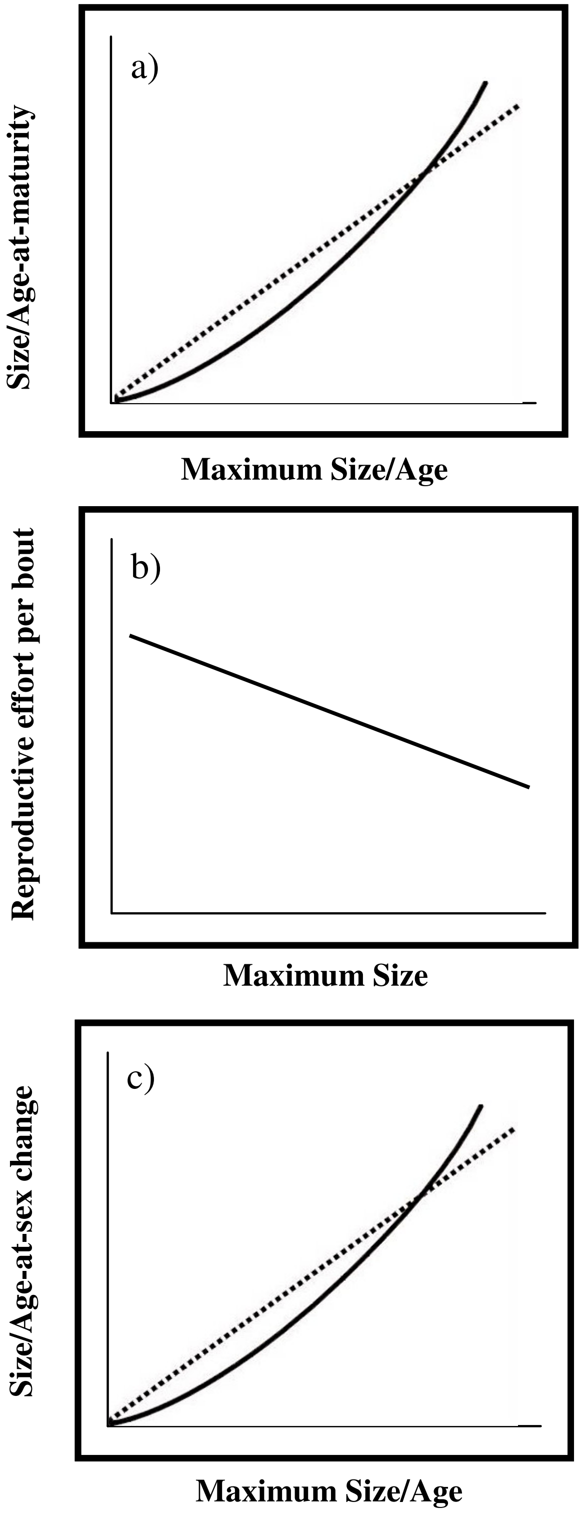

Figure 3.1: Conceptual models illustrating predicted covariation between body size of species and reproductive traits: a) Smaller, short-lived species mature at a smaller proportion of adult size and earlier in life than larger species (bold line). Dotted line indicates relationship if species of different body size/age mature at the same proportion of maximum size/age; b) Smaller, short-lived species have greater reproductive effort than larger and; c) Smaller, short-lived species change sex at a smaller proportion of adult size and earlier in life than larger species (bold line). Dotted line indicates relationship if species of different body size/age change sex at the same proportion of maximum size/age.

3.2 Materials and Methods

3.2.1 Sample species and location of sites

Ten species of wrasse were collected encompassing a size range of 35 – 233 mm SL (Table 3.1). All are protogynous hermaphrodites changing sex from a female to a male. Females and males of *Halichoeres melanurus* and *Epibulus insidiator* are easily identifiable based on colouration. Collections of wrasses with the exception of the pseudocheilinids were made at the Palm Islands, Great Barrier Reef (18°40'S, 146°33'E) with collections concentrated at Pelorus and Fantome Island. The three smallest species *Pseudocheilinops ataenia*, *Pseudocheilinus hexataenia* and *Pseudocheilinus evanidus* were not present at this site and were collected at Kimbe Bay, Papua New Guinea (Chapter 2, Figure 2.2).

Table 3.1: Wrasse species sampled. Including maximum standard lengths of sampled individuals, maximum size of observed individuals (defined as mean size of largest 10% individuals observed for each species, and as a consequence, for the four smallest species the maximum observed size is indicated as less than the maximum sampled size), maximum body weight of sampled individuals, sample sizes (N) and collection sites (GBR, Great Barrier Reef; PNG, Papua New Guinea). * indicates this species is sexually dichromatic and the initial phase females can be easily differentiated from terminal phase males based on colouration.

Species	Sampled			Observed		Location
	Max. SL (mm)	N	Max. body weight (g)	Max SL (mm)	N	
Pseudocheilinops ataenia	35	137	1.02	32	100	Kimbe Bay, PNG
Pseudocheilinus hexataenia	47	127	3.72	40	100	Kimbe Bay, PNG
Pseudocheilinus evanidus	53	62	4.62	51	100	Kimbe Bay, PNG
*Halichoeres melanurus**	88	140	12.33	76	100	Palm Is., GBR, Australia
Bodianus mesothorax	127	41	71.67	149	63	Palm Is., GBR, Australia
Bodianus axillaris	132	40	76.72	145	56	Palm Is., GBR, Australia
Choerodon fasciatus	167	72	173.6	213	100	Palm Is., GBR, Australia
Cheilinus fasciatus	190	82	301.15	245	100	Palm Is., GBR, Australia
*Epibulus insidiator**	225	86	461.83	267	100	Palm Is., GBR, Australia
Hemigymnus melapterus	233	76	449.36	273	100	Palm Is., GBR, Australia

All wrasses at the Palm Islands were collected by spearing on SCUBA, whereas the smaller pseudocheilinids were collected by anaesthetising individuals using clove oil (1 part clove oil: 10 parts 70% ethanol). Once speared, fish were stored on ice and dissected as soon as possible. The standard length (mm SL), fork length (mm FL) and weight of fishes (to nearest mg) were recorded (Table 3.1). Gonads were removed and stored in FAAC for a minimum of 48 hrs before being transferred to 70% ethanol. Sagittal otoliths were removed, cleaned with distilled water and dried before storing in a culture dish.

3.2.2 Phylogenetic analysis

For reasons explained in Chapter 2 (Section 2.1) and following the methodology outlined in Chapter 2 (Section 2.2.4), all relationships were examined using both non-phylogenetic and phylogenetic comparative methods (PCMs). For ease of interpretation, the results presented here graphically are for the non-phylogenetic approach. Following results for the non-phylogenetic approach, the slopes of the relationships using the PCMs and their coefficients of determination (r^2 values) are presented to enable comparisons of results when phylogenetic information is incorporated into the analyses.

3.2.3 Age determination

Ages of individual wrasses examined here were estimated by counting incremental markings on ground sagittae (Chapter 2, Section 2.2.3). *Pseudocheilinops ataenia*, *Pseudocheilinus hexataenia*, *Pseudocheilinus evanidus* and *Halichoeres melanurus* were aged by counting daily rings. *Bodianus mesothorax*, *Bodianus axillaris*, *Choerodon fasciatus*, *Cheilinus fasciatus, Epibulus insidiator* and *Hemigymnus melapterus* had longer life-spans and annual increments were used to estimate their ages.

3.2.4 Reproduction

Histological techniques were used to sex individuals and stage oocytes. Sections were embedded in paraffin, sectioned at a thickness of 5µm and stained with haematoxylin and eosin-erythrosin (Winsor 1984). Sections taken from the posterior, centre and anterior ends of the gonads of females of each species (*N*=10), were examined. No obvious variation in oocyte stage or gonad development was observed throughout the gonad of any individual. Therefore, only central sections were taken for all remaining individuals. Oocytes were staged from 1-5 indicating progressively greater degrees of maturity modified from (West 1990), (Table 3.2). Gonads were categorised according to the most advanced oocyte present (West 1990).

Table 3.2: Criteria used to stage oocytes of wrasse species and to identify developmental stage of individuals (adapted from West 1990).

Stage	Developmental stage	Description
1	Immature (Chromatin nucleolar stage)	Chromatin nucleolar stage of primary oocyte growth. Oocyte surrounded by a few squamous follicle cells and has a large nucleus surrounded by a thin layer of cytoplasm. Nucleus contains single large nucleolus
2	Immature (Perinucleolar stage)	Nucleolus increases in size and multiple nucleoli appear. This and stage 1 are sometimes known as the ' first growth phase'
3	Mature (Yolk vesicle formation stage)	Characterised by appearance of yolk vesicles in cytoplasm. Oil droplets (fat vesicles, vacuoles or globules, fatty or lipid droplets) may begin to accumulate in the cytoplasm of oocytes
4	Mature (Vitellogenic stage)	Characterised by appearance of yolk proteins in fluid-filled spheres (yolk spheres, granules or globules)
5	Mature (Ripe stage)	Oocytes hydrated. Nucleus absent as start of this stage is indicated by peripheral migration of the nucleus and the dissolution of its membrane.

3.2.4.1 *Size and age at maturity*

In species for which samples included both immature and mature females, the size range over which the transition from immature to mature individuals occurred was readily observed. Size at maturation was then estimated as the size at which 50% of individuals were mature (ie. at stage 3 or greater). However, this method could only be applied to five of the ten species (*P. ataenia*, *P. hexataenia*, *Cheilinus fasciatus*, *E. insidiator* and *H. melapterus*), as in the remaining five species (*P. evanidus*, *H. melanurus*, *B. mesothorax*, *B. axillaris*, *Choerodon fasciatus*) immature individuals were either rare or absent in the field and were not sampled. For these remaining species, with the exception of *H. melanurus*, size at maturity (L_m) was estimated using Equation 3.1 (Roff 1986).

$$L_m = L_\infty \left(\frac{3K}{3K + M} \right) \qquad \text{(Equation 3.1)}$$

Where L_∞ is asymptotic length, K is the Brody growth coefficient estimated by the von Bertalanffy growth function and M is mortality rate. Values for L_∞, K and M for these species were estimated previously (Chapter 2) and are provided here (Table 3.3). To assess how accurately this equation predicted size at maturity in the wrasses sampled, values of size at maturity for the five species for which immature individuals were sampled and size at maturity could be estimated directly, were plotted against estimates for size at maturity derived for these species using the equation of Roff (1986). A regression of this relationship had an r^2 value of 0.95 indicating that observed values and predicted values using the equation were closely correlated.

The predicted size at maturity was not used for *H. melanurus* as the equation of Roff (1986) involves the use of L_∞ to calculate size at maturity. In *H. melanurus*, due to its linear growth, the value of L_∞ obtained from the von Bertalanffy growth function is far greater than the maximum size of this species in the field and is unrealistic (Chapter 2, Table 2.5), therefore the estimate of size at maturity would also be inaccurate. For *H. melanurus* only an estimate of minimum size of mature individuals was available for comparisons, although there is evidence that *H. melanurus* is unlikely to mature at a significantly smaller size than indicated here (Chapter 4, Table 4.5).

Age at maturity was estimated as the age at which 50% of sampled individuals had attained maturity within a species. There was no method available to directly estimate age at maturity in the species for which no immature specimens were sampled (*P.evanidus*, *H. melanurus, B. mesothorax*, *B. axillaris* and *Choerodon fasciatus*). For these species age at maturity was estimated as the age which corresponded to the size at maturity estimated using the equation of Roff (1986) (Equation 3.1), which was determined from VBGFs for these species (Chapter 2, Figure 2.9).

It was important to use visual estimates of maximum size of species for comparisons (as opposed to maximum size of sampled individuals), when examining size at maturity in relation to maximum size. This is because for the larger species the largest individuals observed in the field, consistently had a slightly greater size than the largest individual sampled (Table 3.1). The size at maturity estimated for a species, however, is applicable to the largest individuals observed even though estimates of size and age at maturity are derived from sampled individuals. Therefore, when comparisons are made between maximum size of species and size at maturity, maximum size estimates were based on observed individuals (Chapter 5, Section 5.2.2). A conservative but robust estimate of maximum size was obtained by defining maximum size as the mean size of the 10% largest individuals observed for each species based on Choat & Robertson's (2002) derivation of maximum age.

Table 3.3: Information used to predict size at maturity using the equation of Roff (1986) for species in which no immature individuals were sampled and size at maturity could not be estimate directly. Provided are the von Bertalanffy growth function (VBGF) parameters, L_∞ (asymptotic length) and K (Brody's growth coefficient), and M (instantaneous mortality rate).

Species	**VBGF parameters**		**Mortality**
	L_∞	K	M
Pseudocheilinus evanidus	53.4	2.18	4.84
Bodianus mesothorax	110.06	0.89	2.11
Bodianus axillaris	113.07	0.72	1.82
Choerodon fasciatus	134.88	0.44	1.26

3.2.4.2 *Reproductive effort*

Gonadosomatic indices (GSIs) were calculated as a proxy for reproductive effort (DeVlaming et al. 1982). They provide a simple method with which to make an initial estimate of energy inputted by species per reproductive bout. Wet weight of gonads were recorded to the nearest 0.01 of a milligram and gonadosomatic indices were calculated using the following equation:

$$\mathrm{GSI} = \frac{\text{Gonad weight}}{\text{Fish weight}} \times 100 \qquad \text{(Equation 3.2)}$$

Gonad weight and fish weight were measured in milligrams. The rationale is that species with higher GSI values input more energy in to growth of reproductive tissue relative to somatic tissue than species with lower GSI values, therefore higher GSI values imply a greater reproductive effort. GSI comparisons among species included only mature females. Species collected at the Palm Islands (Table 3.1) were sampled in April and November. For these species average and maximum GSIs are only presented for individuals collected in November as these were in spawning condition unlike those collected in April. GSI values were derived directly from samples of females of each species and do not include male GSIs which are far smaller and a poor measure of reproductive effort. Consequently, when GSI values are plotted against maximum size, this is defined by the largest female sampled within each species.

3.2.4.3 *Size and age at sex change*

Histograms were used to explore size and age frequency distributions for females and males of each species. To obtain an estimate of mean size at sex change, the range over which sex change occurred within species was estimated. If sex change occurred over a very narrow range with no individuals falling outside this range, the lower limit to the range of sex change was defined as the size below which 100% of individuals were female, and the upper limit as the size above which 100% of individuals were male. For some species, one or two individuals changed sex at a far smaller or greater size than the majority. In this case, individuals were then ranked in order of size. If the number of individuals between the suspected outlier and the next individual of the same sex represented 10% or more of the total number sampled, the outlier was not included in the size range of sex change. This method reduced the influence of outliers on the final estimate of size at sex change. Size at sex change was then estimated as the mean size of all individuals within the range of sex change as defined above. The same process was used to derive an estimate for age at sex change. When size at sex change is plotted against maximum size of species, estimates of maximum size are derived from observations and it is defined as the mean size of the 10% largest individuals observed for each species (as for comparisons with size at maturity). Maximum age of species was estimated from the oldest individual sampled.

3.2.5 Data analysis

Evidence for the predictions that maturity and sex change occur at a smaller proportion of maximum size and relatively earlier in life in smaller species, was assessed as follows: Relationships were plotted between maximum size and size at maturity and maximum age and age at maturity. Linear and quadratic equations were then fitted to the data to see which of these models was the best descriptor of the relationship (Section 3.1, Figure 3.1a and c). For example, when considering size, if size at maturity was constant among species regardless of maximum size of species, a linear relationship (Equation 3.3) would be the best fit to the data, rejecting the prediction that smaller species tend to mature at a smaller proportion of size and age. If a quadratic equation (Equation 3.4), was the best fit to the data, there were still two possible types of relationship between maximum size and size at maturity depending on the trajectory of the curve of the quadratic fit.

Size at maturity = b(maximum size) + c (Equation 3.3)
Where c is a constant and b is a multiplicative factor.

Size at maturity =a(maximum size)^2 + b(maximum size) + c (Equation 3.4)
Where c is a constant and a and b are multiplicative factors.

If the curve was convex up (Figures 3.1a and c), it indicated smaller species mature at a smaller proportion of maximum size than larger species which supports the original prediction. If it curved in the opposite direction (concave down), then it indicated smaller species mature at a greater proportion of maximum size than larger species, which is opposite to the original prediction. Therefore, to fully examine the relationship between maximum size and size at maturity it firstly had to be determined whether the linear or quadratic model was the best fit to the data. If a quadratic model proved to be the best fit it had to be examined visually to identify the exact nature of the relationship.

Akaike's information criterion (AIC) value provides information for how well different models fit a set of data (Akaike 1973, Burnham & Anderson 1998). This method was used to examine how well the linear and quadratic models fitted relationships between maximum size/age and size/age at maturity and sex change. AIC in effect, describes how different each model is from the 'true' mechanism which generated the observed data. The AIC value is obtained from the following equation:

$$\mathrm{AIC} = -\,2\log(\mathrm{L}(\hat{\theta}/y)) + 2\mathrm{K} \qquad \text{(Equation 3.5)}$$

Where $-\log(\mathrm{L}(\hat{\theta}/y)) + \mathrm{K}$ is the estimated relative expected K-L distance between the fitted model and the unknown true mechanism. It is comprised of $(\mathrm{L}(\hat{\theta}/y))$ which is the likelihood function of the model parameters given the data represented by y, and K which is the number of parameters in the model (Burnham & Anderson 1998). The model with the smallest AIC value is the model which minimises the K-L distance and is the closest to the 'truth' of the models tested. It is therefore the best approximation of the data in question. Once AIC values have been obtained for each model, an Akaike weight (w_i) can be calculated for them (Equation 3.6).

$$w_i = \frac{\exp(-1/2\Delta\mathrm{AIC}\ )}{\sum_{r=1}^{R}\exp(-1/2\Delta\mathrm{AIC}\ )} \qquad \text{(Equation 3.6)}$$

The relative difference in AIC between a model and the unknown 'truth' (ΔAIC) is calculated as 'AIC_i – min AIC', where AIC_i is AIC of the model in question and min AIC is the minimum AIC value of the models tested. Once Akaike weights have been calculated for the two models, the weight of evidence in favour of each model is known, as is the ability of each model to describe the truth in relation to the other models (Burnham & Anderson 1998). For example if two models are tested and w_i for model 1 is 0.95 and for model 2 is 0.05 it can be said that there is 95% confidence that model 1 is the best fit to the data and it is 19 times (0.95/0.05 =19) more likely to describe the truth than model 2. In other words model 1 is a 19 times better descriptor of the data in question.

3.3 Results

3.3.1 Prediction 1: Small, short-lived species mature at a smaller proportion of maximum size and earlier in life than larger species

Body size and age frequency distributions of mature females for *P. ataenia*, *P. hexataenia*, *Cheilinus fasciatus*, *E. insidiator* and *H. melapterus* enabled a direct estimation of the size and age at which 50% of sampled individuals were mature. Larger species matured at a larger absolute size than smaller species (Figure 3.2). A similar result was obtained for age specific maturation (Figure 3.3).

The positive relationship between estimates of absolute size at maturity and maximum body size was significant ($F_{1,8}$=281.41; p<0.001) (Figure 3.4). Calculation of akaike weight values for the models fitted to the data revealed the non-linear regression model (AIC=60.65) was ~2600 times better than the linear model (AIC=76.18) at describing the relationship between maximum size of species and size at maturity. Therefore, small and large species did not mature at a similar proportion of maximum size (which would have been described by a linear model). However, the curve of best fit was the opposite to that predicted, with the smaller wrasse species tending to mature at a greater proportion of their maximum size than the larger species (Section 3.1,

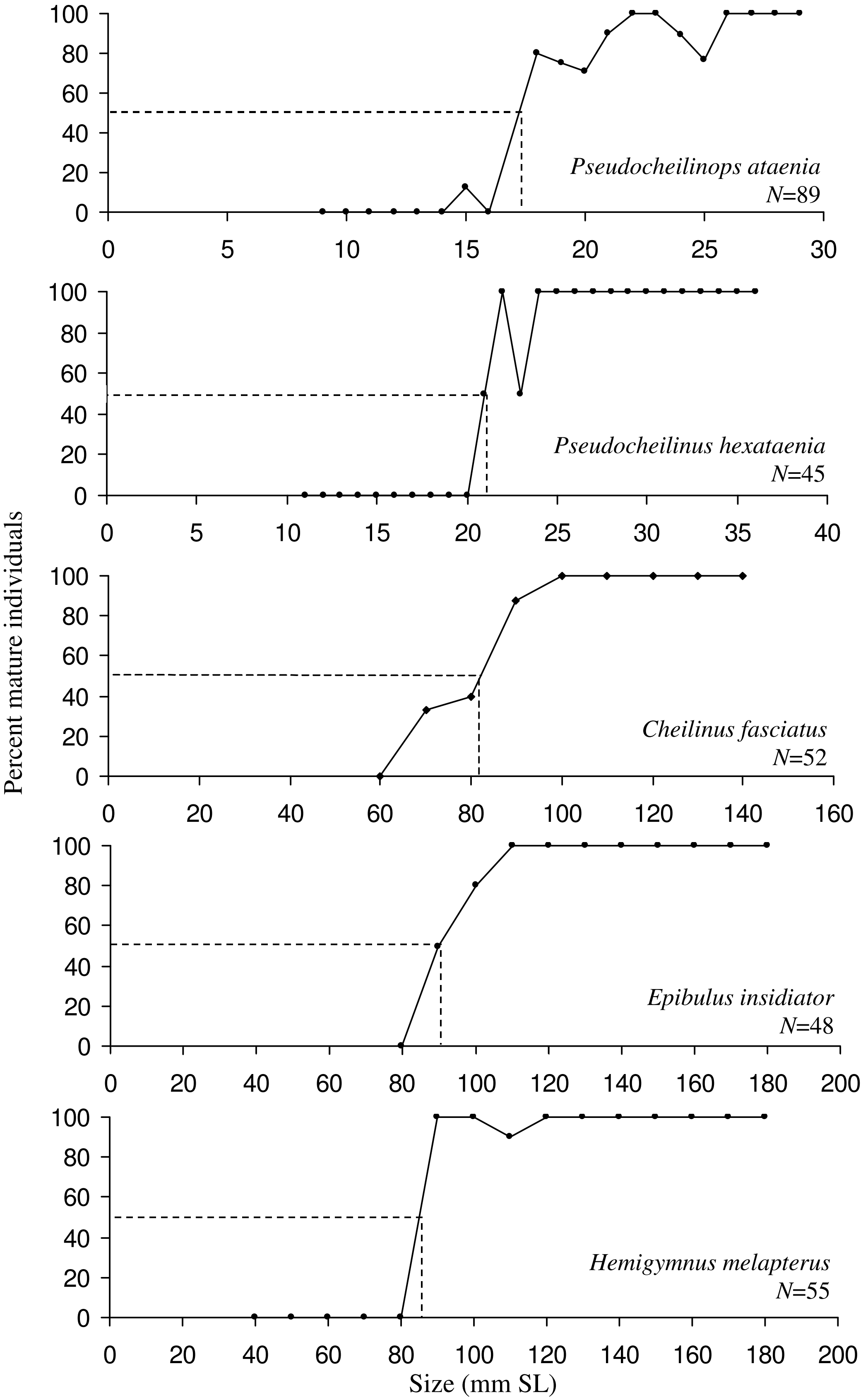

Figure 3.2: Body size-frequency distributions of mature females and estimated size at maturity of five wrasse species. For these species immature individuals were sampled and size at maturation could be estimated directly. Dotted line indicates body size at which 50% of the sampled individuals are mature.

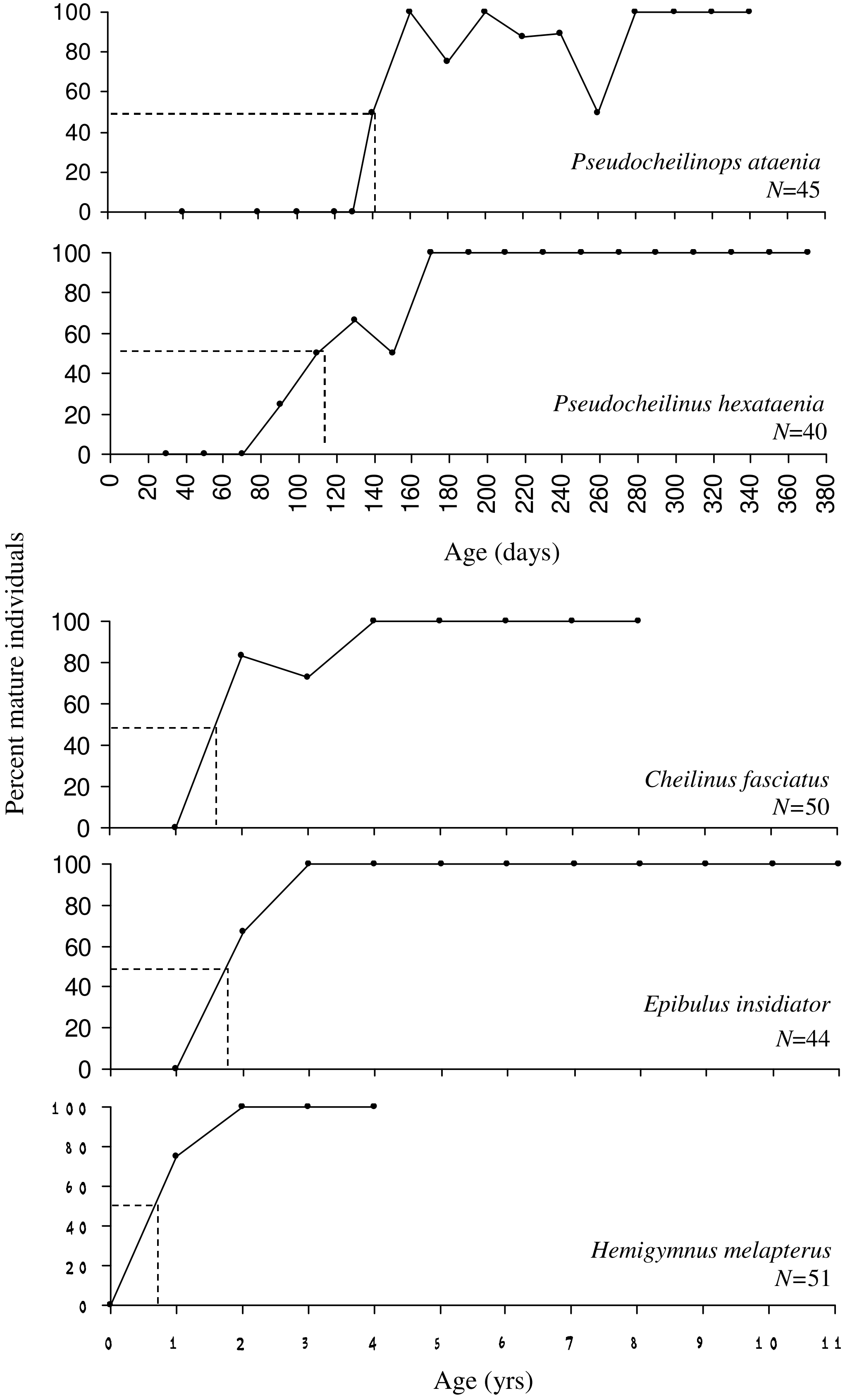

Figure 3.3: Age-frequency distributions of mature females and estimated age at maturity of five wrasse species. For these species immature individuals were sampled and age at maturity could be estimated directly. Dotted line indicates age at which 50% of the sampled individuals are mature.

Figure 3.1a). The smallest wrasse species matured between 50-55% of their maximum size and this value decreased significantly with an increase in species size, the largest species maturing at about 30% of their maximum size ($F_{1,8}$=35.78; p<0.001), (Figure 3.5). Even though only a maximum value for size at maturity could be estimated for *H. melanurus,* this species still appeared to mature at a smaller propotion of maximum size than expected for its body size.

There was also a significant positive relationship between absolute age at maturity and maximum age of species ($F_{1,8}$=42.88; p<0.001). The results obtained for age at maturity were similar to those for size at maturity. The non-linear model (AIC=-8.71) had a ~3380 times better fit than the linear model (AIC=7.55) as calculated using Akaike weights (Figure 3.6). Therefore, small and large wrasse species did not mature at a similar proportion of life-span. Again, the curve for the non-linear fit was concave down, opposite to that described in the original model (Section 3.1, Figure 3.1a). This indicated the smaller species tend to mature relatively later in life than the larger species. The relationship between maximum age of species and the proportion of maximum age at maturity was not as strong as that found for body size, although the relationship was statistically significant ($F_{1,8}$=8.25; p=0.021), (Figure 3.7). In the shorter lived species maturity was attained at 20-25% of maximum life-span but in the longer lived species this value was generally between 7 and 14%.

3.3.2 Prediction 2: Smaller species tend to have greater reproductive effort than larger species

Gonadosomatic indices (GSI) of females varied considerably among species. There was no significant relationship between mean ($F_{1,8}$=0.057; p=0.817) and maximum ($F_{1,8}$=0.174; p=0.688) GSI and species body size (Figure 3.8). The predicted decrease in reproductive effort (estimated by gonadosomatic index) with an increase in species size was not evident. *H. melapterus* and *E. insidiator*, the two largest species, had greater mean and maximum GSIs than the other species, with the exception of *H. melanurus*. The mean and maximum GSI of *H. melanurus* was far greater than for any of the other species. The remaining species had similar mean GSI values. Overall the mean GSI ranged from 0.73% for *Choerodon fasciatus* to 4.54% for *H. melanurus*, these species also had the lowest and highest maximum GSIs of 1.63 and 9.39 %, respectively.

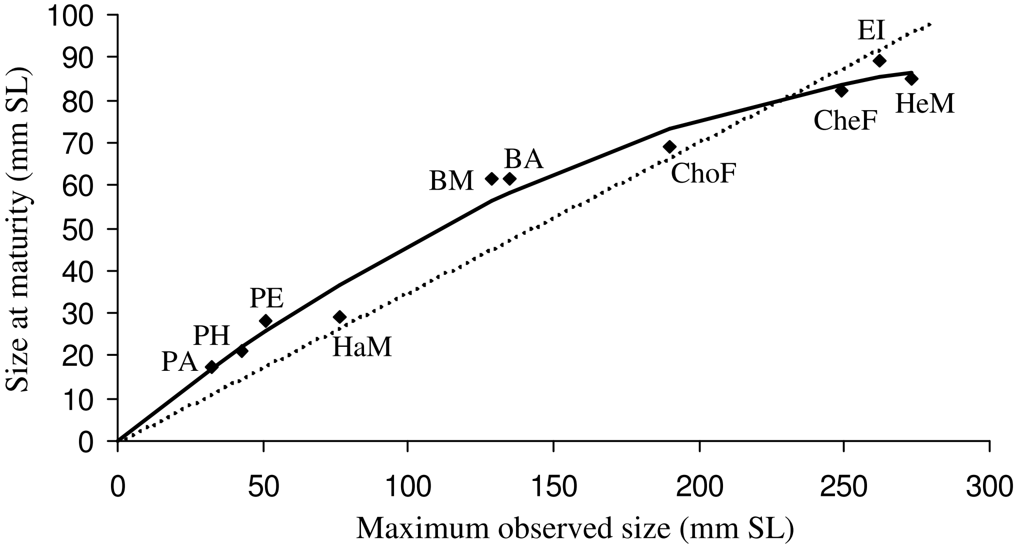

Figure 3.4: Relationship between maximum size of species and absolute size at maturity. Linear model (dotted line, AIC=76.18), y = 0.353x. Non-linear model (solid line, AIC=60.65), $y=0.547x-0.000846x^2$. Species in order of increasing maximum body size (where maximum size is mean of 10% largest individuals observed for each species) are: PA=*P. ataenia*, PH=*P. hexataenia*, PE=*P. evanidus*, HaM=*H. melanurus***, BA=*B. axillaris**, BM=*B. mesothorax**, ChoF=*Choerodon fasciatus**, CheF=*Cheilinus fasciatus*, EI=*E. insidiator* and HeM=*H. melapterus*. * size at maturity predicted using equation of Roff (1986), ** minimum size of mature individuals sampled.

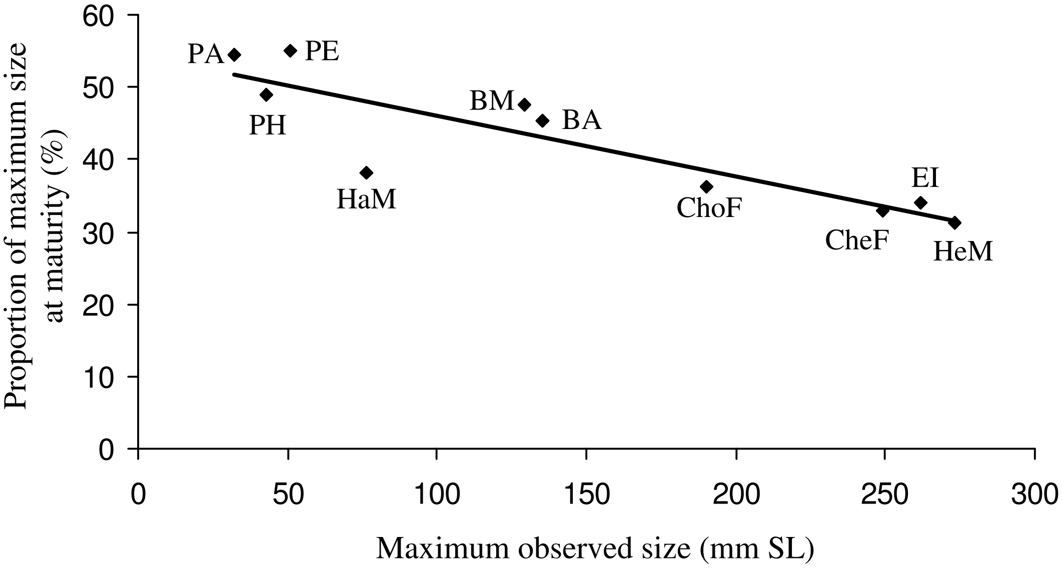

Figure 3.5: Relationship between maximum size of species and proportion of maximum size at which maturity is attained. Least-squares regression: y = -0.0839x + 54.47, r^2 = 0.775. Species in order of increasing maximum body size (where maximum size is mean of 10% largest individuals observed for each species); PA=*P. ataenia*, PH=*P. hexataenia*, PE=*P. evanidus*, HaM=*H. melanurus***, BA=*B. axillaris**, BM=*B. mesothorax**, ChoF=*Choerodon fasciatus**, CheF=*Cheilinus fasciatus*, EI=*E. insidiator* and HeM=*H. melapterus*. * Size at maturity predicted using equation of Roff (1986), ** minimum size of mature individuals sampled.

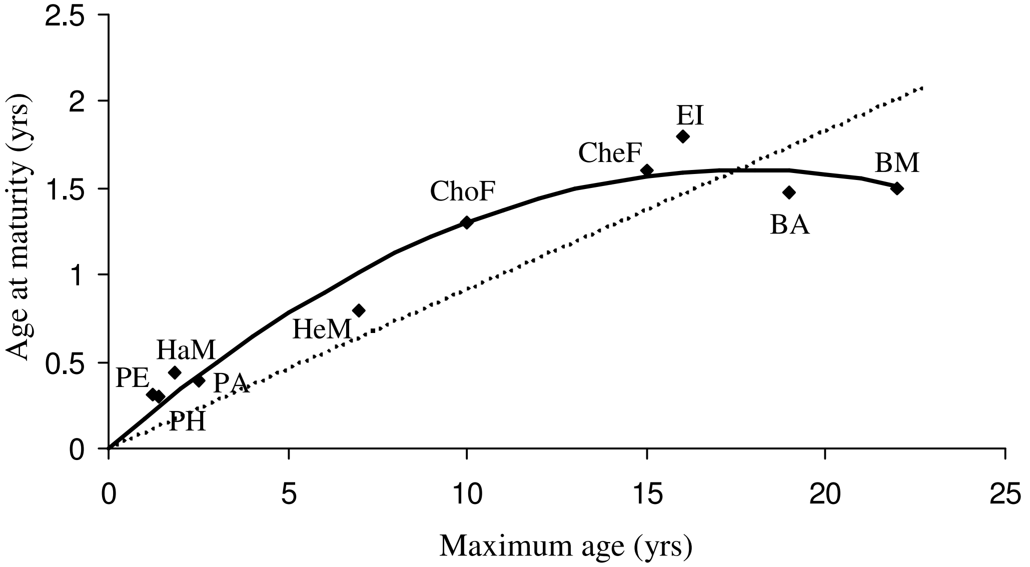

Figure 3.6: Relationship between maximum age of species and absolute age at maturity. Linear model (dotted line, AIC=7.55): y = 0.0908x. Non-linear model (solid line, AIC=-8.71): y=0.1814x-0.005x^2. Species in order of increasing maximum age are: PE=*P. evanidus**, PH=*P. hexataenia,* HaM=*H. melanurus***, PA=*P. ataenia*, HeM=*H. melapterus,* ChoF=*Choerodon fasciatus**, CheF=*Cheilinus fasciatus*, EI=*E. insidiator,* BA=*B. axillaris**, BM=*B. mesothorax**. * Age corresponding to size at maturity predicted using equation of Roff (1986), ** minimum age of mature individuals sampled.

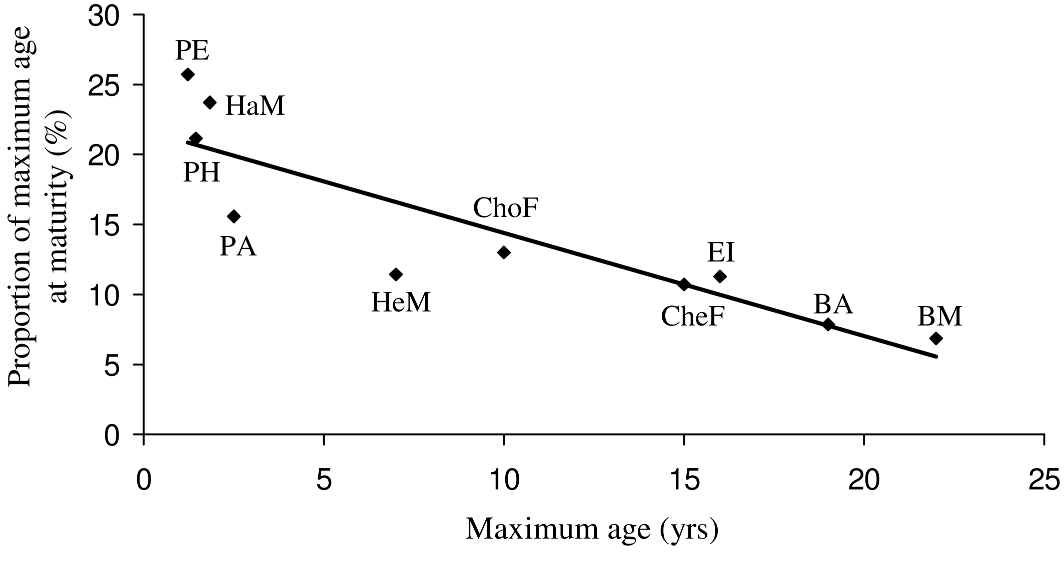

Figure 3.7: Relationship between maximum age of species and proportion of maximum age at which maturity is attained. Least-squares regression: y = -0.7404x + 21.815, r^2 = 0.785. Species in order of increasing maximum age are: PE=*P. evanidus**, PH=*P. hexataenia,* HaM=*H. melanurus***, PA=*P. ataenia*, HeM=*H. melapterus,* ChoF=*Choerodon fasciatus**, CheF=*Cheilinus fasciatus*, EI=*E. insidiator,* BA=*B. axillaris**, BM=*B. mesothorax**. * Age corresponding to size at maturity predicted using equation of Roff (1986), ** minimum age of mature individuals sampled.

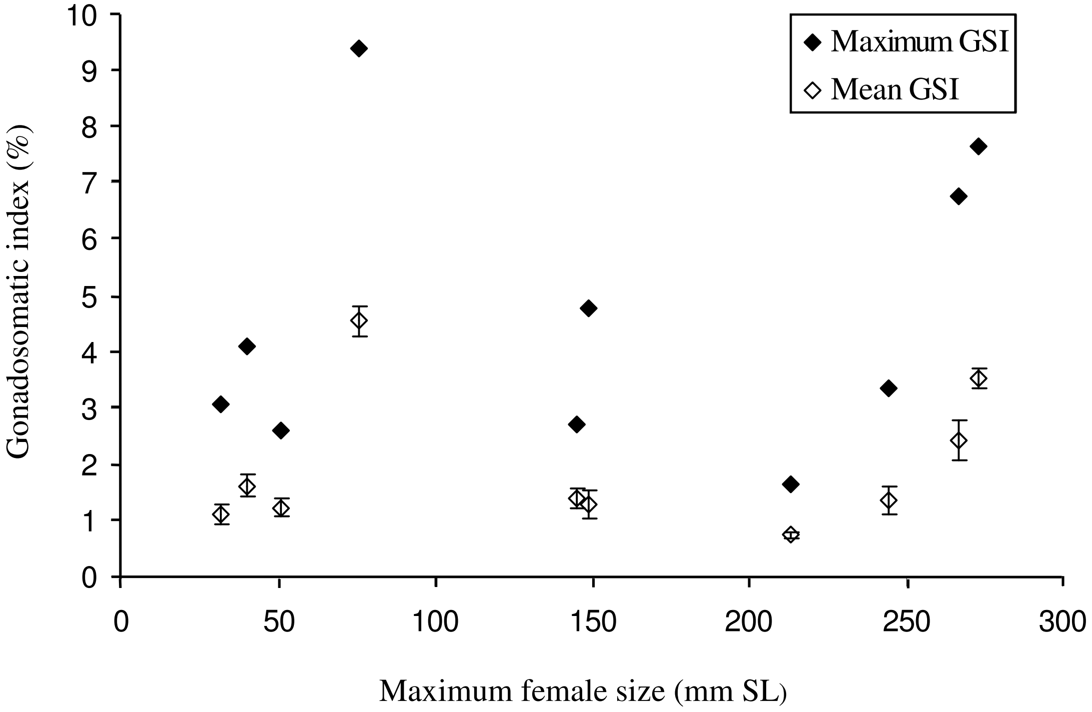

Figure 3.8: Maximum female body size versus estimates of mean and maximum gonadosomatic indices for sampled species. Species in order of increasing maximum female size are: *P. ataenia*, *P. hexataenia*, *P. evanidus*, *H. melanurus*, *B. mesothorax*, *B. axillaris*, *Choerodon fasciatus*, *Cheilinus fasciatus*, *E. insidiator* and *H. melapterus.* Standard error is indicated for mean gonadosomatic index values of ripe females for each species (for species collected at the Palm Islands, only mature specimens collected in November were used to derive estimates as they were in spawning condition).

3.3.3 Prediction 3: Small, short-lived species change sex at a smaller proportion of maximum size and earlier in life than larger species

The sex-specific size frequency distributions were characteristic of species with protogynous sex change, with males restricted to the larger size classes (Figure 3.9a & b). A corresponding pattern was observed for the age frequency distributions, with males dominating the older age groups in all species (Figure 3.10a & b).

The positive relationship between maximum size and size at sex change was significant ($F_{1,8}$=173,15; p=<0.001), (Figure 3.11). Akaike weights of AIC values indicated the non-linear model (AIC=73.45) had a ~500 times better fit to the data than the linear model (AIC=85.9). Therefore, it is evident the wrasse species sampled here did not change sex at a similar proportion of body size. The concave down trajectory of the curve fitted to the relationship indicated the opposite trend to that predicted

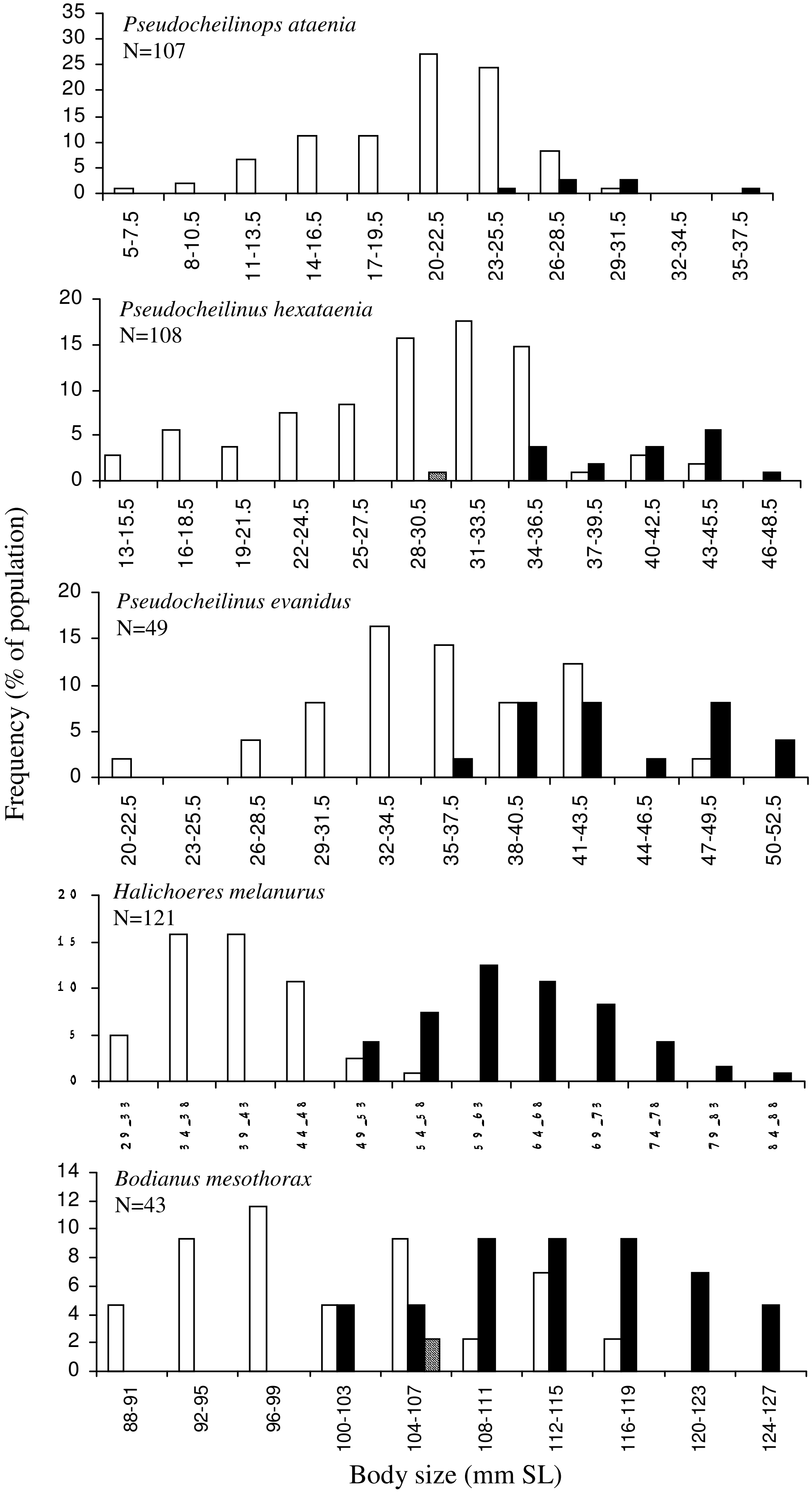

Figure 3.9a: Sex-specific size frequencies of *Pseudocheilinops ataenia*, *Pseudocheilinus hexataenia*, *Pseudocheilinus evanidus*, *Halichoeres melanurus* and *Bodianus mesothorax* (open bars, females; black bars, males; stripes, transitionals).

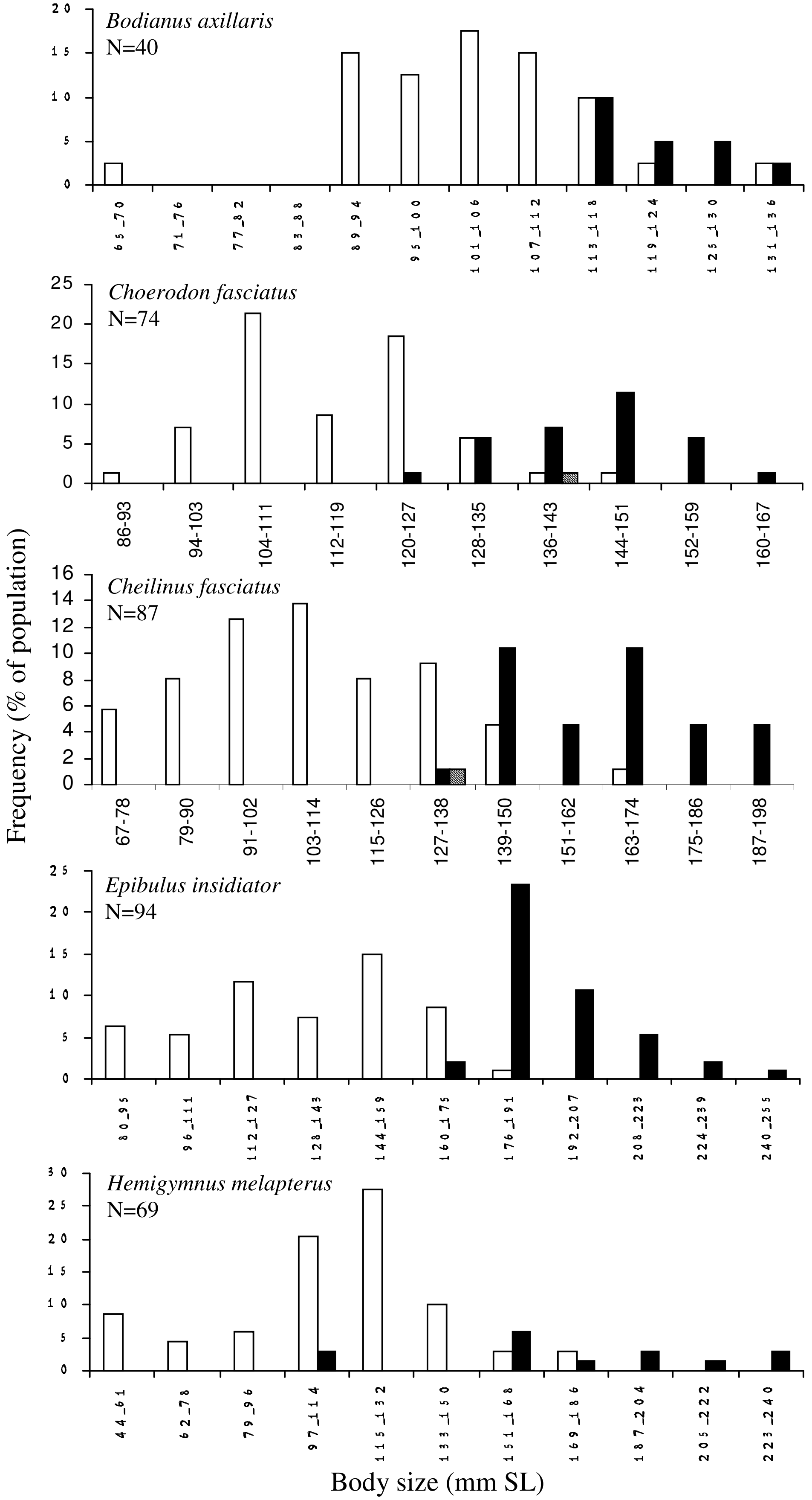

Figure 3.9b: Sex-specific size frequencies of *Bodianus axillaris*, *Choerodon fasciatus, Cheilinus fasciatus*, *Epibulus insidiator* and *Hemigymnus melapterus* (open bars, females; black bars, males; stripes, transitionals).

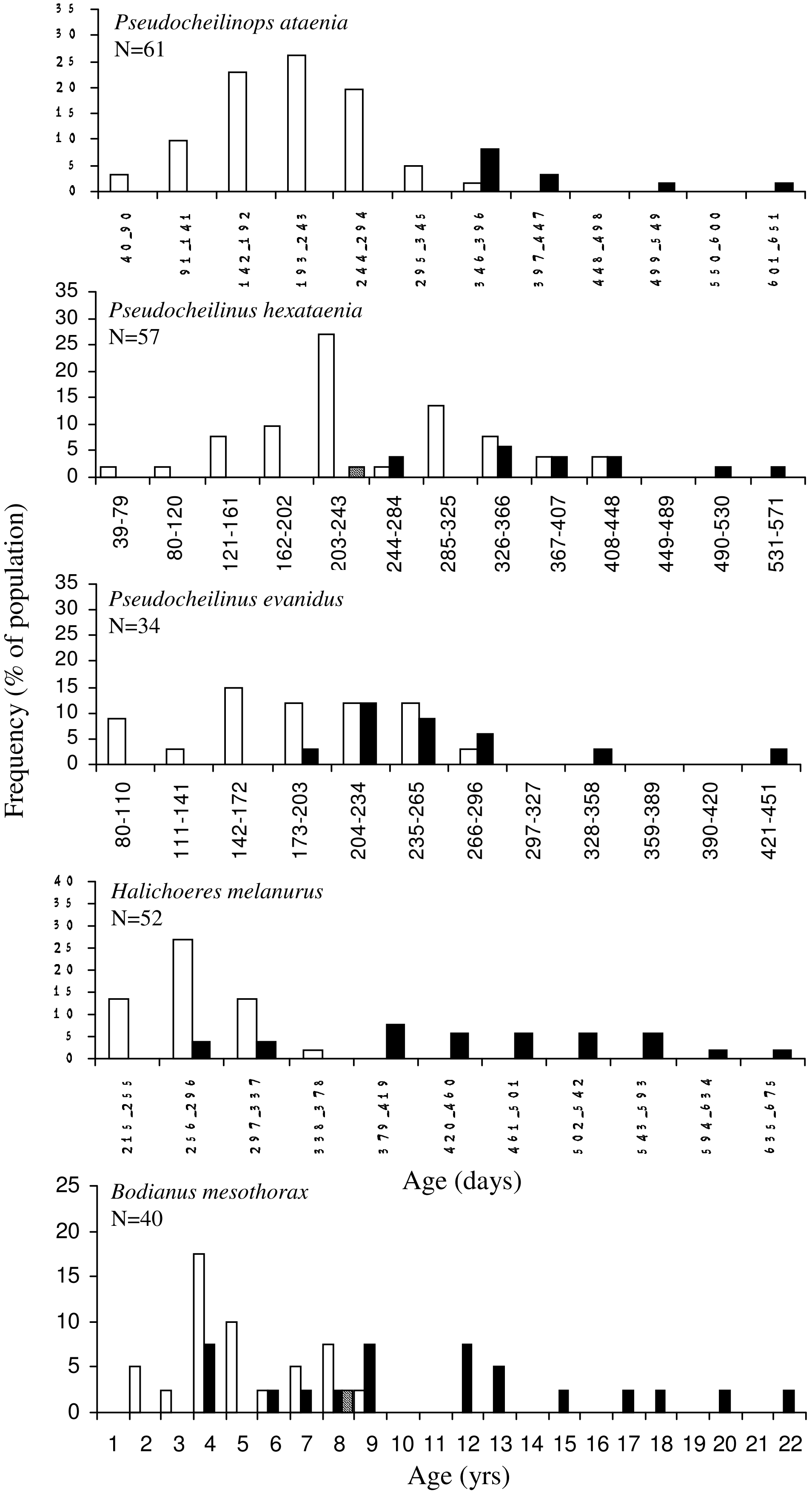

Figure 3.10a: Sex-specific age frequencies of *Pseudocheilinops ataenia*, *Pseudocheilinus hexataenia*, *Pseudocheilinus evanidus*, *Halichoeres melanurus* and *Bodianus mesothorax* (open bars, females; black bars, males; stripes, transitionals).

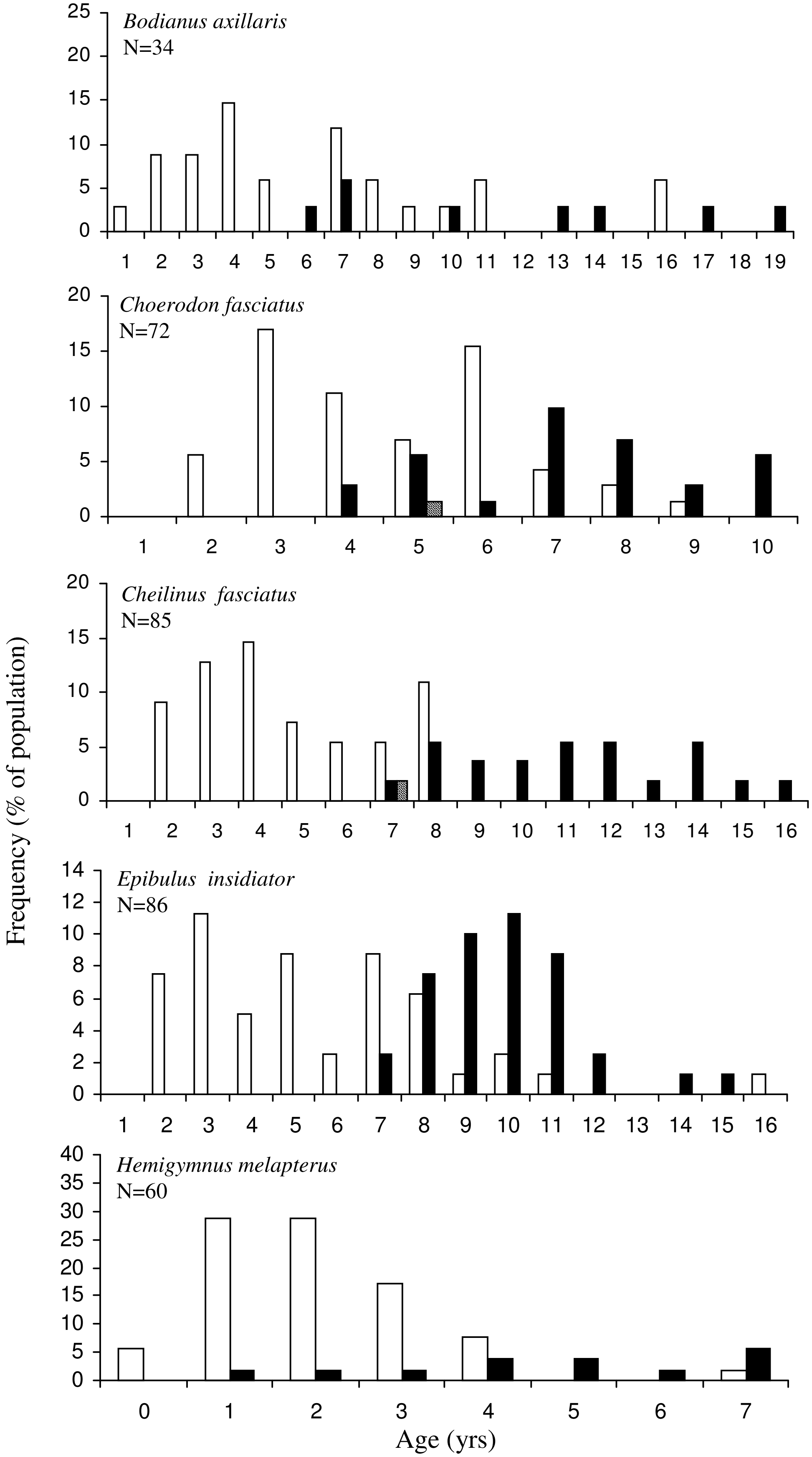

Figure 3.10b: Sex-specific age frequencies of *Bodianus axillaris*, *Choerodon fasciatus*, *Cheilinus fasciatus*, *Epibulus insidiator* and *Hemigymnus melapterus* (open bars, females; black bars, males; stripes, transitionals).

(Figure 3.1c). Smaller wrasse species changed sex at a greater proportion of maximum size than the larger species. The standard deviation of the mean size at sex change was generally small, indicating for each species there was a narrow range of sizes at which sex change tended to occur (Figure 3.11). In fact, the range of sizes over which the majority of sex change occurred lay between only 2 – 17mm for all species with the exception of *H. melapterus* which displayed slightly more variation with a range covering 28mm.

The negative relationship between proportion of maximum size at sex change and maximum size of species was quite strong (r^2=0.79) and significant ($F_{1,8}$=29.64; p=0.001), (Figure 3.12). The proportion of maximum size attained at sex change varied from 90.1% of maximum size in one of the smallest species *P. hexataenia*, to 57.5 % in one of the largest species *Cheilinus fasciatus*. The proportion of maximum size attained at sex change in the two *Bodianus* species was slightly higher than expected in relation to the other species. Comparing the proportion of maximum size attained at sex change (Figure 3.12) and the proportion of maximum size at maturity (Figure 3.5), indicated the proportion of body size representing the period between these two transitions is relatively constant among species. This value was quite high in *B. mesothorax* (40%) and *B. axillaris* (44%), but ranged from 26 – 38 % of maximum size across the remaining species. This revealed most of the species spend a similar proportion of their maximum size as reproductive females, regardless of body size.

When age at sex change was examined there was a significant positive correlation between maximum age of species and age at sex change ($F_{1,8}$=28.37; p=0.001), although the relationship was not as strong as observed for size at sex change (Figure 3.13). The non-linear model (AIC=27.19) was a ~1430 times better fit to the relationship than the linear model (AIC=41.8). Again, the direction of the curve was opposite to that predicted indicating smaller wrasses species tended to change sex proportionally later in life than larger species which is opposite to the expected relationship. The proportion of maximum life-span attained when sex change generally occurred, ranged considerably from 71.6% in *P. hexataenia* to 27.1% in *B. mesothorax* (Figure 3.14). Overall though, the relationship between life-span of species and the proportion of life-span attained at sex change was non-significant ($F_{1,8}$=1.81; p=0.215). In addition, standard deviations of the mean for the proportion of maximum size attained at sex change ranged from 1.2 to 4.3% of maximum size among species. Standard deviations of the mean for the proportion of maximum age attained at sex change, however,

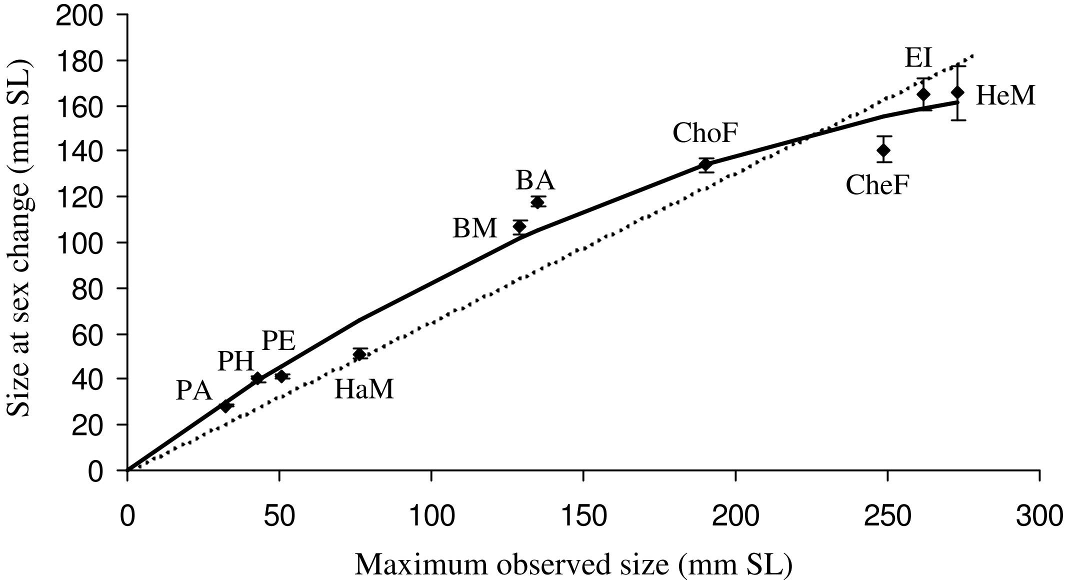

Figure 3.11: Relationship between maximum size of species and mean size at sex change. Linear model (dotted line, AIC=85.9), y = 0.6336 x. Non-linear model (solid line, AIC=73.10), y=0.9573x-0.00134x^2. Standard deviation of the mean is indicated. Species in order of increasing maximum body size (where maximum size is mean of 10% largest individuals observed for each species): PA=*P. ataenia*, PH=*P. hexataenia*, PE=*P. evanidus*, HaM=*H. melanurus*, BM=*B. mesothorax*, BA=*B. axillaris*, ChoF=*Choerodon fasciatus*, CheF=*Cheilinus fasciatus*, EI=*E. insidiator* and HeM=*H. melapterus*.

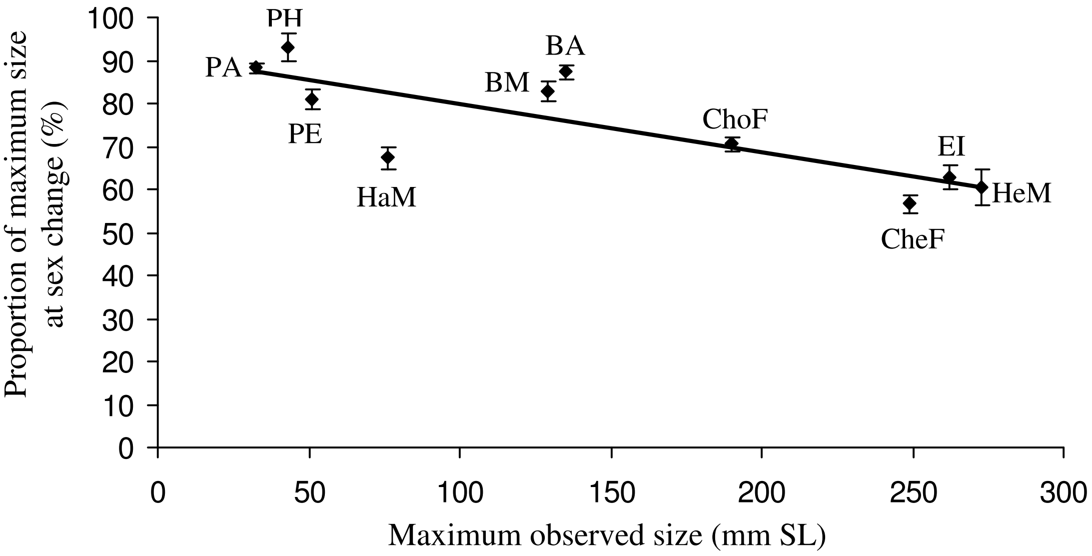

Figure 3.12: Relationship between maximum size of species and proportion of maximum size at which sex change occurs. Least-squares regression: y = -0.1124x + 91.19, r^2 = 0.665. Standard deviation of the mean is indicated. (where maximum size is mean of 10% largest individuals observed for each species); PA=*P. ataenia*, PH=*P. hexataenia*, PE=*P. evanidus*, HaM=*H. melanurus*, BA=*B. axillaris*, BM=*B. mesothorax*, ChoF=*Choerodon fasciatus*, CheF=*Cheilinus fasciatus*, EI=*E. insidiator* and HeM=*H. melapterus*.

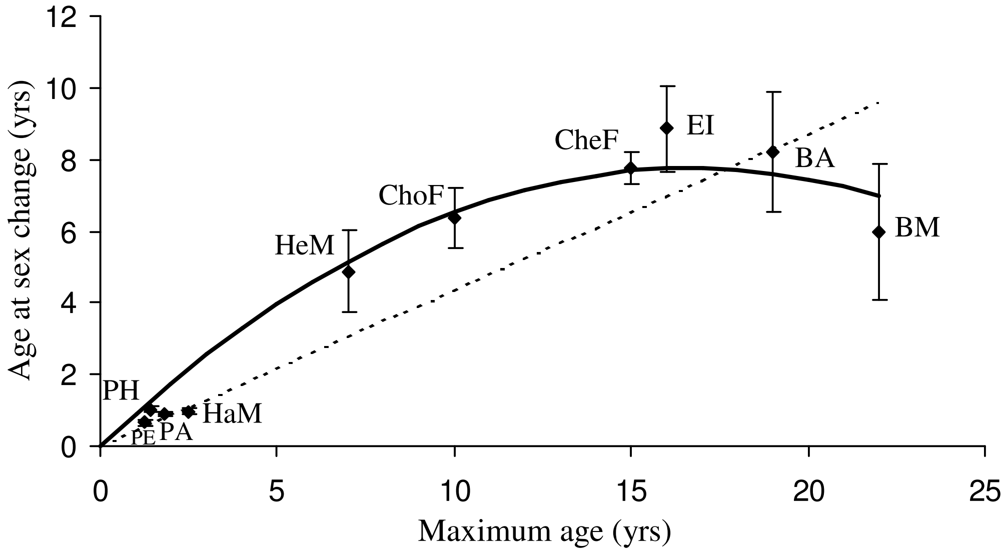

Figure 3.13: Relationship between maximum age of species and age at sex change. Linear model (dotted line, AIC=41.8): y = 0.4363x. Non-linear model (solid line, AIC=27.19): $y=0.9303x-0.0279x^2$. Standard deviation of the mean is indicated. Species in order of increasing maximum age: PE=*P. evanidus,* PH=*P. hexataenia,* HaM=*H. melanurus,* PA=*P. ataenia*, HeM=*H. melapterus,* ChoF=*Choerodon fasciatus*, CheF=*Cheilinus fasciatus*, EI=*E. insidiator,* BA=*B. axillaris,* BM=*B. mesothorax.*

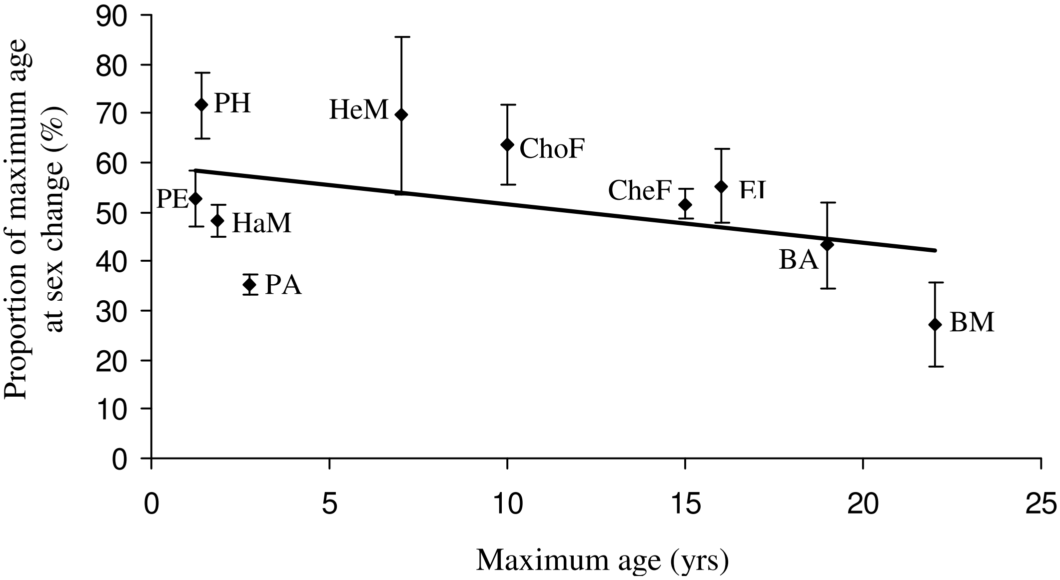

Figure 3.14: Relationship between maximum age of species and proportion of maximum age at which sex change occurs. Least-squares regression: y = -0.7751x + 59.318, r^2 = 0.185. Standard deviation of the mean is indicated. Species in order of increasing maximum age: PE=*P. evanidus,* PH=*P. hexataenia,* HaM=*H. melanurus,* PA=*P. ataenia*, HeM=*H. melapterus,* ChoF=*Choerodon fasciatus*, CheF=*Cheilinus fasciatus*, EI=*E. insidiator,* BA=*B. axillaris,* BM=*B. mesothorax.*

ranged from 2.1 to 16% of maximum age (Figures 3.12 & 3.14). This reveals there is far more variation within species in the age at sex change than the size at sex change, especially in the larger species (Figure 3.14).

3.3.4 Phylogenetic analyses

For all of the relationships examined in this study there was no significant variation in the results obtained when wrasse phylogeny was incorporated into the analyses (Table 3.4). The slopes of the relationships were the same using the non-phylogenetic approach (TIPS) and the two phylogenetic comparative methods (PCMs). The r^2 values obtained using TIPS and the phylogenetic generalised least-squares approach (PGLS) were consistently similar. The strength of relationships attained using Felsenstein's independent contrasts (FIC) were often slightly weaker than when using the PGLS and non-phylogenetic approaches.

The assumption of equal branch lengths in the phylogenetic tree did not greatly influence the results attained here. This assumption produced r^2 values very similar to the mean values of r^2 derived from analyses of traits on twenty different trees, each with the same topology but varying branch lengths. In general the standard deviation of the mean r^2 value for twenty different trees was greater using FIC than PGLS although it was generally quite small for both methods. Standard deviations of the mean r^2 values were very small using PGLS, especially for the significant relationships with high r^2 values.

3.4 Discussion

The predictions derived from the literature that smaller species would: 1) mature proportionally earlier in life, 2) allocate more energy to reproduction and 3) change sex proportionally earlier in life were not supported by this study. Size and age at key life history events (maturation and sex change) were positively correlated with maximum size and maximum age of species, respectively. However, the trends observed among these traits were *opposite* to those predicted. Smaller species matured and changed sex at a greater proportion of maximum size and proportionally later in life than larger species. Size appeared to be more closely correlated with these life history transitions than age, both within and among species. No consistent pattern was apparent between body size and the amount of reproductive effort invested per reproductive bout.

Table 3.4: Results of data analysis using a non-phylogenetic comparative method (TIPS) and two phylogenetic comparative methods, the Phylogenetic least-squares approach (PGLS) and Felsenstein's independent contrasts method (FIC). Provided are the slope of the relationship, the mean values of r^2 obtained by each method after analysing data on twenty different phylogenetic trees of the same topology but varying branch lengths, the standard deviation (SD)of the mean and for comparative purposes and the value of r^2 when analyses were conducted on a tree assumed to have equal branch lengths.

Relationship examined:	**Method**	**Slope**	**r^2 (average of 20 trees)**	**SD**	**r^2 (equal branch lengths)**
Maximum body size vs. size at maturity (absolute)	PGLS	+ve	0.947	0.007	0.972
	FIC	+ve	0.845	0.040	0.974
	TIPS	+ve	0.951		
Maximum age vs. age at maturity (absolute)	PGLS	+ve	0.830	0.009	0.843
	FIC	+ve	0.690	0.051	0.583
	TIPS	+ve	0.861		
Maximum size vs. proportion of maximum size at maturity	PGLS	-ve	0.712	0.091	0.806
	FIC	-ve	0.690	0.094	0.677
	TIPS	-ve	0.775		
Maximum age vs. proportion of maximum age at maturity	PGLS	-ve	0.732	0.048	0.596
	FIC	-ve	0.745	0.116	0.448
	TIPS	-ve	0.785		
Maximum female size vs. mean gonadosomatic index	PGLS	+ve	0.288	0.256	0.007
	FIC	+ve	0.386	0.259	0.039
	TIPS	+ve	0.014		
Maximum female size vs. maximum gonadosomatic index	PGLS	+ve	0.184	0.226	0.0014
	FIC	+ve	0.243	0.021	0.0264
	TIPS	+ve	0.021		
Maximum body size vs. size at sex change (absolute)	PGLS	+ve	0.942	0.008	0.970
	FIC	+ve	0.941	0.007	0.968
	TIPS	+ve	0.945		
Maximum age vs. age at sex change (absolute)	PGLS	+ve	0.720	0.011	0.888
	FIC	+ve	0.583	0.073	0.765
	TIPS	+ve	0.780		
Maximum size vs. proportion of maximum size at sex change	PGLS	-ve	0.634	0.039	0.756
	FIC	-ve	0.510	0.145	0.505
	TIPS	-ve	0.665		
Maximum age vs. proportion of maximum age at sex change	PGLS	-ve	0.113	0.044	0.139
	FIC	-ve	0.167	0.187	0.028
	TIPS	-ve	0.140		

3.4.1 Size and age at maturity

Over a wide range of organisms the size or age at which sexual maturity is reached has been shown to be positively related to body size or longevity (eg. Blueweiss et al. 1978, Stearns 1983, Promislow & Harvey 1990, Kozlowski 1992, Charnov 1993). As expected, the wrasses studied here conform to this relationship. When size and age at maturity were considered relative to maximum size or age of species though, the results were unexpected. Smaller species were found to mature at a greater proportion of maximum size and maximum age than larger species.

These results suggest that although there may be a strong selective pressure to attain maturity as quickly as possible when mortality is high (Harvey & Zammuto 1985, Sutherland et al. 1986, Millar & Hickling 1991, Tilley & Bernardo 1993, Abrams & Rowe 1996), this does not exceed the benefits of delayed maturity of smaller species. The delayed maturity of smaller species in relation to larger species has only been described previously in reptiles (Andrews 1982, Shine & Charnov 1992, Shine 1994) although underlying reasons for this were not well understood (Shine 1994).

A number of suggestions can be put forward to explain the delayed maturation in the smaller wrasse species. Egg size does not vary predictably with body size in coral reef fishes (Blueweiss et al. 1978, Munday & Jones 1998) and is relatively constant among wrasse species (Colin & Bell 1991). Therefore small wrasses cannot simply overcome physiological restrictions on fecundity by producing a greater number of smaller eggs (Poulin 1995, Munday & Jones 1998, Caley et al. 2001). The number of eggs that can be carried by females of one wrasse species relative to another, is dependent on size of the body cavity which restricts the potential fecundity of small species. This means smaller species may have a development threshold (Roff 1992, Day & Rowe 2002) and have to reach a greater proportion of their adult size (corresponding to a greater proportion of maximum age), before the body cavity is large enough to satisfy minimum fecundity requirements.

In smaller species, growing for a proportionally longer period of time relative to life-span (to reach a larger proportion of adult size) and delaying maturity, could provide a disproportionately large fecundity advantage (Bell 1980, Stearns & Crandall 1981, Schwarzkopf 1993). For example, consider a species with longevity of three years reaching an adult size of 5cm. If there is a considerable percentage increase in annual production of offspring between the first and second year or at a particular body size (eg. far more offspring produced at 4 than 3cm in size), and this advantage outweighs disadvantages in the form of decreased chances of surviving to the second year (or to 4cm), then maturity should be delayed to optimise life-time reproductive output (Harvey et al. 1989, Madsen & Shine 1994). Estimating age and size-specific mortality rates for the small pseudocheilinids and the other wrasse species studied, could elucidate the mechanisms involved in the delayed maturation of the smaller species. If fecundity benefits are driving the observed relationships here, why they should be expressed more strongly in smaller species requires further investigation.

There is some evidence that physicial constraints on fecundity are not operating for the pseudocheilinids. For example, the size of female gonads in relation to the body cavity in the psuedocheilinids was very small, so available space for gonads did not appear to be a limiting factor. This was not the case for other species such as *H. melanurus* in which gonad tissue was observed to entirely fill the body cavity in many of the more fecund females. A further possible explanation of the observed relationship is more closely related to the life-span of species than their body size. The pseudocheilinids collected at Kimbe Bay, Papua New Guinea are expected to spawn year–round (in common with most of the species at Kimbe Bay, Jones G. P. pers. comm.). This contrasts with the remaining species collected at the Palm Islands which are seasonal spawners (pers. obs.). If the species from the Palm Islands have a restricted period of time over which they can reproduce each year it could be beneficial to mature and start reproducing relatively earlier, increasing the number of potential reproductive bouts throughout life (Bell 1980). The small psuedocheilinids, despite experiencing high mortality, are able to delay maturity and still make a significant contribution to future generations as they spawn regularly throughout the year once maturity is attained.

The relationship observed here between maximum size and size at maturity is more significant and a lot stronger than that for maximum age and age at maturity. This provides evidence that on an interspecific level, size is more closely related to attainment of maturation, than age. Within species, size has also been shown to be more closely correlated with maturation than age in the wrasse, *Notolabrus celidotus* (Jones 1980). Traditionally, attainment of maturity is commonly expressed in terms of age (eg. Charnov 1989, Murphy & Rodhouse 1999, Arkhipkin et al. 2000, Ergon et al. 2001, Madsen & Shine 2001). However, the ability of age to describe maturation processes may vary considerably among taxa. Consideration of body size may be more effective for examining aspects of maturation in wrasses and potentially other reef fishes.

It has been demonstrated that maximum body size and age of wrasse species are closely and negatively correlated with the proportion of maximum size and age attained at maturity. Body size is a relatively easy life history characteristic to measure quantitatively and appears to be an effective predictor of maturation size for the wrasse species examined here at the Palm Islands. Size and age at maturity within species, however, can vary on a temporal (eg. Arkhipkin et al. 2000, Madsen & Shine 2001) and spatial scale (eg. Ergon et al. 2001). Other factors affecting maturation include social inhibition (Jones & Thompson 1980), microhabitat preference (Kuwamura et al. 1996), food availability (Tenhumberg et al. 2000) and climate (Promislow & Harvey 1990). Such complexities within species can contribute to variation in size and age at maturity among species. The robustness of the relationship observed here needs to be tested by identifying whether or not it holds for different species at a range of locations.

3.4.2 Reproductive effort

In terrestrial organisms reproductive effort generally declines with an increase in body size (Peters 1983, Begon & Mortimer 1986, Reiss 1989). In the wrasses examined in this study, there is no support for the prediction that smaller species have greater reproductive effort per bout than larger species. Comparisons of GSI values alone though, cannot account for some of the complexities related to measurement of reproductive effort. Reproductive effort is difficult to quantify accurately, as among other factors it requires knowledge of energetic resources available to an individual before energy allocation, the amount of energy invested in each reproductive bout and the number of bouts per unit of time (Calder 1984, Stearns 1992). In addition the effect of external factors eg. temperature, on reproductive effort, are poorly understood (Calder 1984).

GSI values have been used previously to reveal a negative correlation between body size and reproductive effort per bout in fishes (eg. Gunderson 1997). One reason for the lack of an apparent relationship between maximum size and reproductive effort found here could be because this method only indicates investment in reproduction at the time of sampling (West 1990). For example, the pseudocheilinids were the smallest species sampled and were collected at Kimbe Bay, Papua New Guinea. As mentioned earlier, they are likely to spawn year-round in contrast to the species sampled at the Palm Islands. Therefore, due to energetic trade-offs they may input less energy into each reproductive bout (indicated by low GSI values) but have many reproductive bouts over the course of the year (Bell 1980). In contrast the species collected at the Palm Islands have a specific breeding season from around October-November to January-February the following year. Reproductive effort is condensed into fewer reproductive bouts over this period so mean GSIs are likely to be higher. The seasonal variation in reproductive effort illustrates just one of the limitations of using GSIs as an estimate of reproductive effort (DeVlaming et al. 1982, West 1990). For example, the cumulative annual reproductive effort of the pseudocheilinids could be greater than for species in the Palm Islands despite the results attained here based on GSI values. Even though species at the Palm Islands are seasonal spawners, the frequency of reproductive bouts is likely to vary considerably both within and among species. Interspecific allocation of energy to reproduction should be examined further by comparing spawning frequencies of species throughout the year and combining this with GSI information for species. Estimates of energy inputted into each reproductive bout would also be required to calculate annual reproductive effort.

When only the seasonally spawning species collected at the Palm Islands are considered there is still no overall trend between size and GSI. The particularly high GSI value of *H. melanurus* suggests this species puts the greatest amount of energy into reproduction, which could partly explain why this species is the most abundant wrasse species at the Palm Islands (Manthachitra 1996). Overall it appears body size is not closely correlated with reproductive effort per bout among species. Reproductive effort per bout may be influenced to a greater degree by other factors such as seasonality of spawning, mating system (Robertson 1981, Colin & Bell 1991) and population density (Charnov 1986).

3.4.3 Size and age at sex change

The original prediction that smaller species should change sex at a smaller proportion of maximum size and proportionally earlier in life than larger species, was not supported. In fact, the *opposite* trend was apparent with smaller species delaying sex change. Comparison of variability in size and age at sex change within species and the non-significance of the relationship between maximum age and the proportion of maximum age at sex change, suggest size is more important that age in determining when sex change occurs in these wrasses, at both the intra- and interspecific level**.** Therefore, explanations for observed trends are discussed in the context of size variation only. So why do smaller species change sex at a proportionally larger size? One explanation is that it could be related to gradual changes in fecundity schedules of males and females with an increase in species size. Consider the hypothetical fecundity curve for male and females labelled ‘a’ representing individuals in a population where mating is non-random with females choosing males of an equal or larger size. These curves cross at the size at which male fecundity is greater than female fecundity, indicating the size at which sex change should occur (line 1, Figure 3.15). The optimum size at sex change could then vary in relation to differences in the fecundity schedules of females and males within a species. If size-specific male fecundity (relative to maximum fecundity) is similar among small and large species (male ‘a’) but size specific female fecundity systematically increases with size at a greater rate in smaller species size (female ‘b’) then later sex change would be expected (line 2). In contrast, if female fecundity schedules for females were similar in all species (female ‘a’) but the size specific fecundity of males was initially more depressed in smaller species and only began to rise after a greater proportion of maximum size had been attained (male ‘b’), later sex change would again be predicted (line 3).

Variation in female fecundity schedules among species in relation to size is unknown. Further study is required to elucidate whether or not female fecundity, relative to body size, does tend increase at a faster rate in smaller species. Plasticity in male fecundity schedules may be more likely and mechanisms can be suggested for variation in the male fecundity schedules among species. For example, the greater the reproductive benefits of increased male size within a species, the more the male fecundity curve will be pushed to the right (male ‘b’). This would be the case if females preferentially mated with larger males (Robertson 1981), or if males had to defend spawning territories and larger males were competitively superior (eg. Warner 1975, Robertson 1981). For this variation to lead to the observed trend, the proportion of maximum size at which males optimise the advantages of a larger size and have most reproductive success, would have to increase gradually with a decrease in species size.

Perhaps the most interesting result is that size at sex change tends to covary with size at maturity. Another explanation for the proportionally later sex change in smaller species may be that delayed sex change is a consequence of delayed maturity, or that both size at maturity and size at sex change are similarly influenced by selective pressures. This suggestion is supported by this study as results suggest a correlation

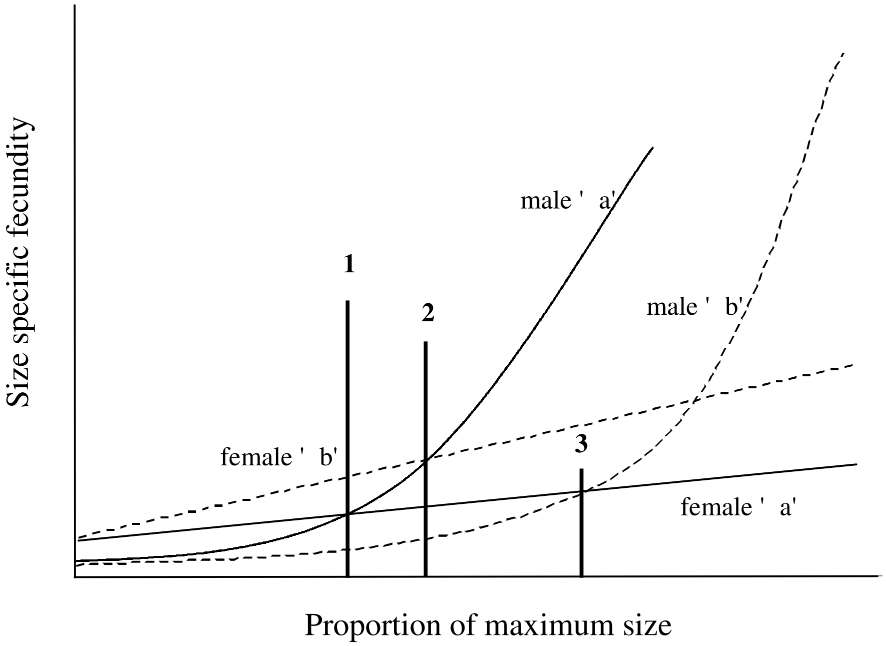

Figure 3.15: Size-specific fecundity curves indicating how variation in fecundity schedules of males and females can influence the proportion of maximum size at which sex change occurs among species. Female and male curves ‘a’ are adapted from Warner 1975. Mating is non-random with females selecting males of equal or larger size. Line 1 is the expected size at sex change, Line 2 is the size at sex change if the size-specific female fecundity increases at a greater rate than in female ‘a’ and size-specific male fecundity is unchanged, Line 3 represents size at sex change if size-specific fecundity of males is lower and increases at a slower rate up to the point of sex change than in male ‘a’ and size-specific female fecundity is unchanged.

between these reproductive traits. The proportion of maximum size spent between attainment of maturity and sex change (ie. period during which individual is a reproductive female), was similar among species. Such relationships have received sparse scientific attention to date and further research is required to attain an insight into the mechanisms which could potentially link maturation and sex change.

Growth strategy also has implications for when sex change occurs. It is important to note that the *Bodianus* species changed sex at a greater proportion of their body size than expected for their adult size. This is likely to be a consequence of the determinate growth within these species. As adult size of the *Bodianus* species is attained so rapidly and females and males have similar sizes, age as opposed to size is more likely to regulate when sex change occurs in these species (Chapter 2, Section 2.3.6).

Size and age at sex change are not thought to be genetically determined (Warner 1988, Shapiro 1989). Shapiro (1989) argued that in certain demographic situations, sex change can occur at virtually any size. Following removal of a male from a harem the largest female will change sex to replace it, even if this is below the expected size of sex change (eg. Robertson 1972, Sakai et al. 2001). Optimal size at sex change can also vary in relation to the degree of parental care (Warner & Lejeune 1985) and sex ratios (Shapiro 1987). Size at sex change within species can vary among patch reefs separated by several kilometres or less and even among neighbouring social groups separated by only tens of metres (Warner & Robertson 1978, Shapiro 1981, Aldenhoven 1986). Variation in recruitment and its effect on age-frequency distributions has also been suggested as one possible cause of spatial differences in size at sex change among populations (Warner 1988). Although numerous factors can stimulate plasticity of size at sex change within species, this study has indicated maximum body size of species is an important covariate of sex change on an interspecific level.

3.4.4 Phylogeny

Evolutionary history of the wrasses examined in this study was not found to influence the relationships observed here between body size and reproductive characteristics. Strength of relationships attained using Felsenstein's independent contrasts (FIC) were consistently weaker than using the non-phylogenetic approach and the phylogenetic generalised least-squares method (PGLS)**.** This may be related to the fact that FIC assumes evolution is mainly directed by random genetic drift and follows a Brownian motion process in which changes in life history characteristics of species over time are considered to be random. This is unlikely to be the case, as traits of species are subject to selective pressures and their variation is expected to be non-random when influenced by natural selection. Such non–random variation in traits is modelled more effectively by the phylogenetic generalised least-squares approach (Martins & Hansen 1997). Standard deviation of the mean for r^2 values derived from twenty different trees with varying branch lengths was generally very small when using PGLS. This indicates relationships observed here among wrasses are also robust to the degree of divergence among species.

3.4.5 Further study

The accuracy with which maximum size and age of individuals within sampled species reflects maximum size and age of species in the field is dependent on sample size (Kritzer 2001). In this study interspecific comparisons for size at maturity and sex change involved estimates of maximum size which were derived from observations of individuals in the field (Chapter 5). Therefore, estimates of maximum size are expected to be very close to the true values found in the field. For maximum age though, only estimates derived from sampled individuals of species could be used. Due to relatively small sample sizes for some of the species here, maximum age estimated is expected to be less than that attainable in the field. Greater sample sizes are required to attain more accurate estimates of maximum age of species which could modify the relationships observed here between longevity and age at maturity and sex change. For those species for which the equation of Roff (1986) was used to derive a prediction for size at maturity, sampling is required to collect juveniles of these species (juveniles of the *Bodianus* spp. and *Choerodon fasciatus* were rarely seen in the field during sampling). This would enable attainment of direct estimates of size at maturity and age at maturity for these species.

The gonadosomatic index (GSI) is a convenient measure which gives some indication of energy allocation to reproduction per reproductive bout. It does have limitations though, including a strong dependence on seasonality of spawning (DeVlaming et al. 1982, West 1990). Examination of the frequency of spawning of each species over the year and attaining GSI values for species at monthly intervals would provide a much more detailed picture of how much energy species input into reproduction and whether or not this is related to body size of species. Greater sample sizes of species could also provide more accurate estimates of size and age at sex change and provide a clearer indication of sex specific size and age frequencies among species.

Patterns such as those identified here need to be tested across a greater range of species encompassing a wider range of body sizes to see how robust these relationships are. Inclusion of reproductive information for the largest wrasse *Cheilinus undulatus* (reaching over 2m in length) would be particularly informative. Consideration of phylogenetic relationships among wrasses in this study had no effect on the relationships attained. Despite this, evolutionary history can influence patterns of growth and reproduction which may vary considerably from one family of reef fish to another (Stearns 1992, Choat et al. 1996, Choat & Axe 1996, Munday & Jones 1998). Therefore, comparisons examined here should be repeated within different families of reef fishes to identify how taxonomic variation modifies the patterns observed.

3.4.6 Conclusion

A number of relationships between size of species and their reproductive characteristics were identified. The main findings of this study were: a) smaller species matured at greater proportion of maximum size and age than larger species, b) reproductive effort per bout may be correlated more closely with factors other than body size, including frequency of spawning and c) Smaller species changed sex at a greater proportion of maximum size and longevity than larger species. In addition, there was covariation between size at maturity and size at sex change among species. Despite the numerous processes influencing aspects of growth and reproduction in wrasses and their complex interactions, body size appears to be a good predictor of life history transitions such as maturation and sex change. Further work is required to identify how widely the relationships illustrated here can be applied to other taxa, both marine and terrestrial.

CHAPTER 4: Latitudinal variation in life history traits of the coral reef fish *Halichoeres melanurus* (Pisces: Labridae)

4.1 Introduction

Life history traits are extremely variable both within and among species, and studies of covariation among them have played an important role in the development of life history theory (Roff 1986, Stearns 1992). Interspecific comparisons have been particularly powerful in identifying trade-offs between growth, reproduction and maintenance (Peters 1983, Calder 1984, Boyce 1988), which can determine how life history traits scale with body size (Harvey & Read 1989, Millar & Hickling 1991, Stamps et al. 1998). Although the interspecific approach has proven very valuable, non-independence of species due to shared phylogenetic histories can complicate evaluation of the determinants of life history variation (Harvey & Pagel 1991). Comparative studies of geographic variation within a single species have an advantage in that they provide a description of covariation in life history traits uncomplicated by evolutionary history (Harvey & Keymer 1991, Stearns 1992, Martins & Hansen 1997). Many species exhibit interspecific variation in life history traits among and within populations (eg. Berven & Gill 1983, Reznick 1983, Marshall 1988, Schwarzkopf 1993, Shine et al. 1998, Jonas & Geber 1999, Kuhlmann & Walker 1999). This variation can be exploited to detect trade-offs associated with life history strategies and identify the biotic and abiotic factors influencing their evolution.

Species distributed across a range of latitudes provide an opportunity to study intraspecific changes in life history in relation to gradual changes in environmental conditions (Jonas & Geber 1999, Cardillo 2002, Yamahira & Conover 2002). Variation in life history traits can demonstrate remarkably consistent trends along latitudinal clines. An example is Bergmann's rule (Bergmann 1847, Mayr 1956) which states that within species adult body size tends to increase with an increase in latitude (Sand et al. 1995, Blackburn & Gaston 1996, van' t Land et al. 1999, Arnett & Gotelli 1999). Bergmann's rule appears to be a general trend in mammals (Ashton et al. 2000), although its general applicability to other animal groups such as ectotherms remains unclear, an issue which has courted much debate (eg. Van Voorhies 1996, Mousseau 1997, Patridge & Coyne 1997, Van Voorhies 1997, Arnett & Gotelli 1999).

The ambient temperature of individuals and its variability is of key importance in determining consistent latitudinal trends in life histories within species (Berven et al. 1979, Johnston & Bennett 1996, Travis et al. 1999, Camp & Marshall 2000). In organisms from all environments there is a consistent positive correlation between ambient temperature and metabolic rate, which influences the growth and development of an organism (Robinson et al. 1983, Clarke & Johnston 1999). Ectotherms grow at a slower rate at lower temperatures and this is generally associated with longer life of individuals and attainment of larger adult sizes (Charnov 1989, reviewed in Atkinson 1994, Jackson & Moltschaniwskyj 2001). Mechanisms causing this relationship between temperature, growth rate and longevity are not well understood. One explanation invokes developmental processes which cause an increase in cell size at lower temperatures (Van Voorhies 1996), others consider variation in the rate of food intake and oxygen availability with temperature (Atkinson & Sibly 1997). Energetic trade-offs are likely to be particularly important as reduced allocation of energy to growth leaves more energy available for other requirements such as maintenance, defence and movement, all of which increase chances of survival (Arendt 1997, Sinervo & Svensson 1998, Mangel & Stamps 2001). As populations evolve locally to optimise growth rate (Levinton 1983) it has been suggested the effect of temperature on growth rate alone may be sufficient to determine variation in size and life-span of individuals (L' Abée-Lund et al. 1989, Abrams et al. 1996, Yamamoto et al. 1999).

Life history theory generates the expectation of Bergmann size clines in ecotherms which is supported in many cases (Atkinson 1994, Van Voorhies 1996 & 1997, Ashton 2002). Despite this, some recent studies including a comprehensive study of freshwater fishes (Belk & Houston 2002), have indicated the opposite trend in which adult body size within species decreases with an increase in latitude (Mousseau 1997). Clearly more taxa need to be examined to assess how general Bergmann's rule is among ecotherms.

Growth and reproductive activity are closely linked (Calder 1984, Stearns 1992). With consistent latitudinal patterns in growth characteristics, variation in reproductive traits can also be predicted. If life-spans of ectotherms increase with latitude then mortality rates must be higher at lower latitudes (Fernandezdelgado & Herrera 1995, Ebert 1975). In the presence of high mortality, earlier maturation is advantageous as by becoming reproductive earlier individuals increase their chances of reproducing successfully before dying (Reznick et al. 1990 & 1996, Abrams & Rowe 1996, Gasser et al. 2000). In addition, when fecundity is size-specific, lower mortality at higher latitudes increases the viability of delaying maturation so individuals can reach larger body sizes and have greater initial fecundity (Stearns & Crandall 1981, Stearns 1992, Bertschy & Fox 1999). Both cases lead to the prediction that maturation should occur earlier and at a smaller proportion of adult size at lower latitudes.

Greater reproductive effort per bout is characteristic of smaller, short lived individuals such as those expected to be found at lower latitudes (Sutherland et al. 1986, Harvey et al. 1989). In ectotherms a positive relationship between latitude and reproductive effort has been described in shrimp (Lardies & Wehrtmann 1997) and amphibians (Morrison & Hero 2003). However, the opposite trend is predicted here as fecundity in fishes is often size specific (Bromage et al. 1992). If maturation is delayed in the larger individuals at higher latitudes as expected, they should then have greater initial fecundity and increased reproductive effort per bout (Blueweiss et al. 1978, Roff 1981, Roff 1986, Marshall 1988). Reproductive effort per bout is also likely to vary considerably in relation to factors such as length of the reproductive season which tends to decrease with an increase in latitude (Bilenca et al. 1994, O'connor 2002, Morrison & Hero 2003) and the frequency of bouts during the season. Perhaps due to such complications few studies have examined variation in reproductive effort with increasing latitude.

A further critical reproductive characteristic within hermaphroditic species is the size and age at sex change. Within species, male and female fecundity schedules differ dramatically and sex change should occur at a size or age which optimises fecundity over the course of an individual's life (eg. Warner 1975, Warner 1988, Charnov & Bull 1989). If fecundity and mortality schedules vary predictably with latitude then so too should size and age at sex change. Environmental pressures selecting for earlier maturation such as high mortality should also result in earlier sex change in order to optimise lifetime fecundity before dying. Alternatively, size and age at maturity and sex change may be linked, with earlier maturation promoting earlier sex change. No studies to my knowledge have examined latitudinal variation in size and age at sex change within a species. Based on life history theory it can be predicted that sex change should occur earlier in life and at a smaller proportion of adult size in individuals at lower latitudes.

Most studies examining latitudinal life history patterns have been conducted in terrestrial species. The marine environment differs greatly from terrestrial habitats in terms of environmental variability and the selection pressures found along latitudinal gradients. Therefore, it should not be assumed that generalisations applicable on land will hold for marine organisms (Clarke & Crame 1997). Factors responsible for trends such as Bergmann's rule remain unclear. Explanations invoking the importance of thermoregulation and heat-conserving mechanisms have been disputed in terrestrial organisms (Begon et al. 1996, Ashton et al. 2000), but they are certainly inapplicable to marine poikilotherms as their body temperature is not physiologically controlled but fluctuates with ambient water temperature. Nevertheless, some terrestrial poikilotherms do exhibit the changes in body size with temperature expected for homeotherms (Iverson et al. 1997, Ashton 2002). This suggests that despite differences in terrestrial and marine environments, latitudinal variation in life history traits could be similar among marine and terrestrial environments even if different mechanism(s) are selecting for them. All general trends have exceptions and this can be expected when life histories in some species are influenced by specific environmental factors which vary unpredictably with latitude (Sand et al. 1995, Berkenbusch & Rowden 2000, Chown & Gaston 1999). Such complexities highlight the need to examine latitudinal relationships in many taxa and over large geographic ranges, in order to identify robust trends in life histories.

Our understanding of latitudinal trends in marine organisms has been restricted by an absence of studies focussing on the tropics. Most studies to date have examined species in temperate waters in which fluctuations in ambient temperature are often far greater than in tropical habitats (eg. L' Abée-Lund et al. 1989, Fleming & Gross 1990, Conover et al. 1997, Brown et al. 1998, Yamahira & Conover 2002, Belk & Houston 2002). In the tropics there are smaller absolute changes and fluctuations in temperature, than over an equivalent latitudinal range in the temperate zone. Therefore, tropical latitudinal patterns need to be examined to see if they conform to those detected for both terrestrial and marine organisms in temperate environments. Environmental variability in the tropics may be more subtle than in temperate habitat, but due to acclimation of individuals to a particular set of environmental conditions a small change in water temperature can have a disproportionate effect on the expression of life history traits (McCormick & Molony 1995).

In this chapter I examined intraspecific variation in life history traits exhibited by a small coral reef fish along a latitudinal gradient in the tropical Indo-Pacific. The species examined here is the protogynous hermaphrodite, *Halichoeres melanurus* (Bleeker, 1851). This is a small wrasse (~105 mm maximum FL), which has a large geographic range from the Western Pacific to Micronesia and Samoa in the east (Randall et al. 1997) and the Ryukyu Islands of Japan in the north to the southern Great Barrier Reef, they are found as far south as Coffs Harbour on the east coast of Australia (Fulton C. pers. comm.). This species is extremely abundant throughout its range indicating it successfully optimises reproductive output in a range of diverse locations and habitats.

The main aim of this chapter was to identify whether changes in life history along a latitudinal gradient in a tropical marine ecosystem conform to predictions based on life history theory, and examine covariation among growth and reproductive characteristics. Populations at four locations ranging from a latitude of 5ºS to 23ºS were compared to test the following predictions: 1) Growth rate decreases with an increase in latitude (Figure 4.1a), 2) Body size increases with an increase in latitude (Figure 4.1b), 3) Longevity increases with an increase in latitude (Figure 4.1c), 4) The proportion of adult size and age attained before maturation increases with an increase in latitude (Figure 4.1d), 5) Reproductive effort increases with an increase in latitude (Figure 4.1e) and 6) The proportion of adult size and age attained before sex change increases with an increase in latitude (Figure 4.1f).

4.2 Materials and Methods

4.2.1 Species and locations sampled

H. melanurus was sampled at four locations along a tropical latitudinal gradient encompassing 18° of latitude: 1) Kimbe Bay, Papua New Guinea (PNG) (5°33'S, 150°08'E); 2) Lizard Island, north Great Barrier Reef (GBR) (14°39'S, 145°27'E); 3) Palm Islands, mid GBR (18°36'S, 146°29'E) and 4) Heron Island, south GBR (23°26'S, 151°55'E) (Figure 4.2). Mean sea water temperature for the year 2000 gradually decreased with an increase in latitude from 29ºc at Kimbe Bay to 24ºc at Heron Island. The interannual variation in water temperature was considerable (6.1-7.2ºc) at each of the locations on the GBR and only encompassed about 3ºc at Kimbe Bay (Figure 4.3). Specimens were collected during March 2000 and February 2002 at Kimbe Bay, early October 2000 at Lizard Island, November 2000 at the Palm Islands and late October 2000 at Heron Island. *H. melanurus* was one of the most abundant wrasse species at each of these locations. It is sexually dichromatic with the terminal phase males and initial phase females exhibiting distinct colouration patterns (Figure 4.4).

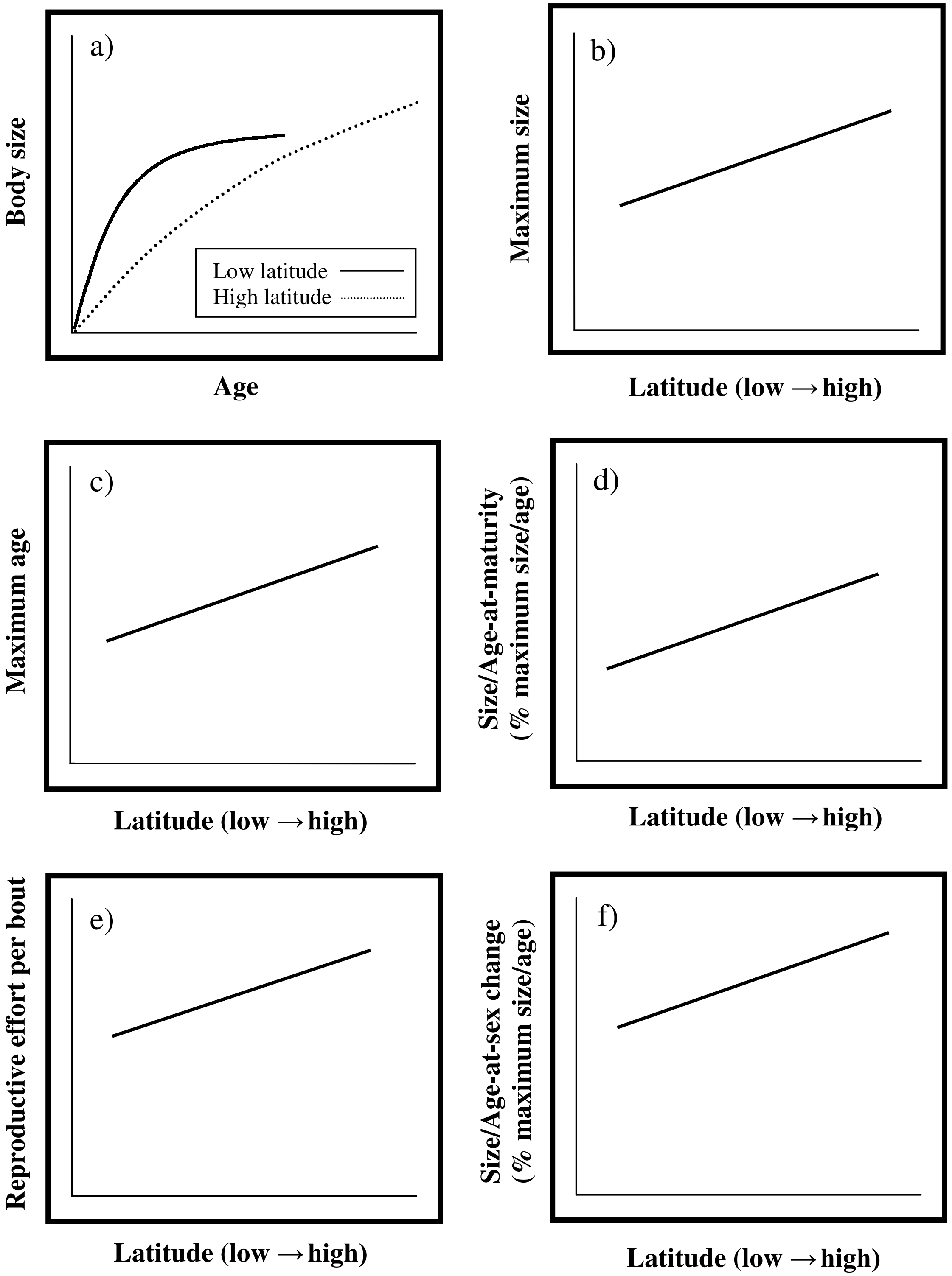

Figure 4.1: Conceptual models illustrating predicted variation in growth characteristics and reproductive traits along a latitudinal cline; a) Growth decreases with an increase in latitude, faster growth associated with decreased body size and life-span; b) Body size increases with an increase in latitude; c) Longevity increases with an increase in latitude; d) The proportion of adult size and age attained before maturation increases with an increase in latitude; e) Reproductive effort decreases with an increase in latitude; f) The proportion of adult size and age attained before sex change increases with an increase in latitude.

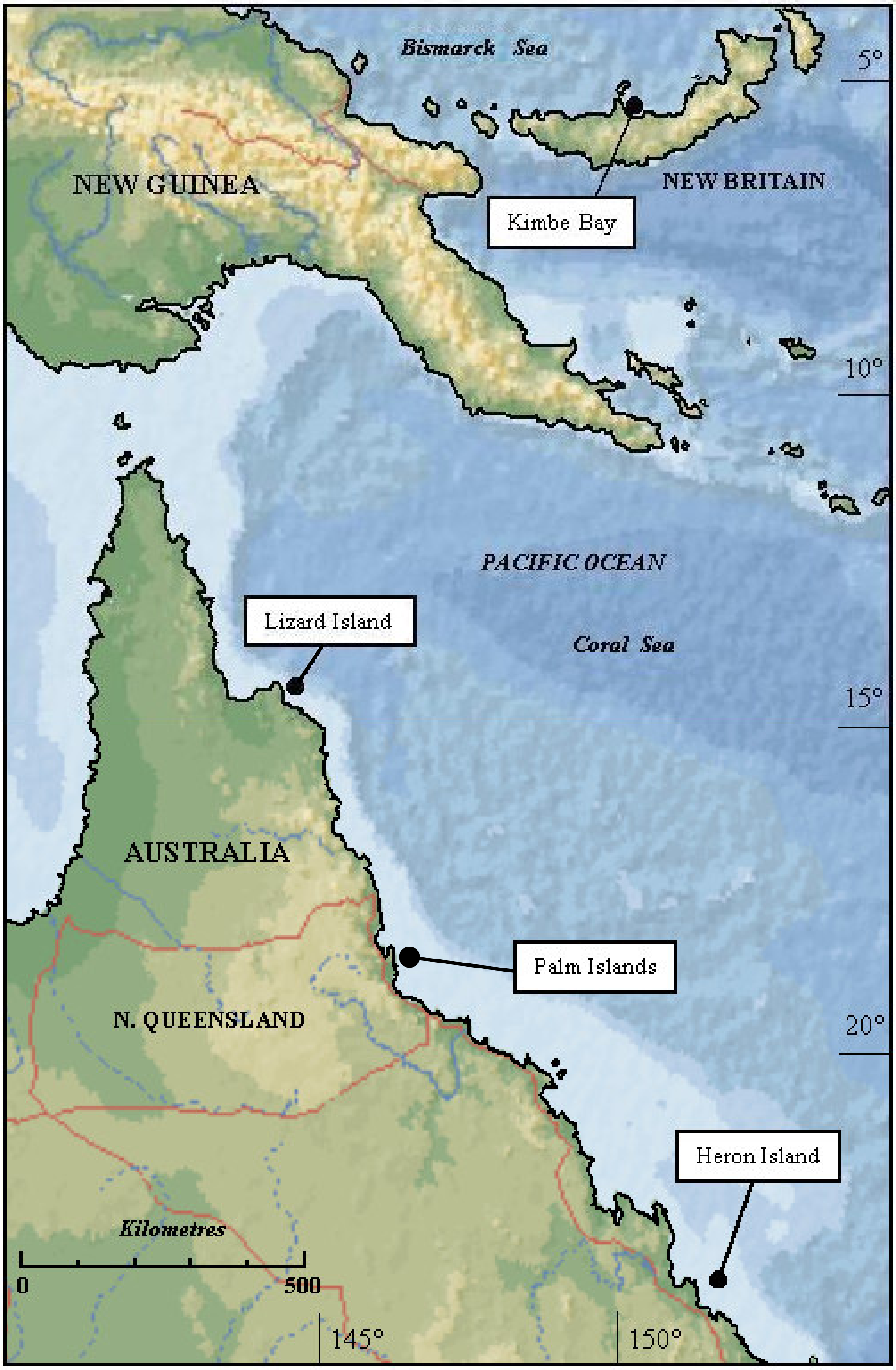

Figure 4.2: Locations at which *Halichoeres melanurus* individuals were sampled: Kimbe Bay, Papua New Guinea; Lizard Island, northern GBR; Palm Islands, mid GBR; Heron Island, southern GBR.

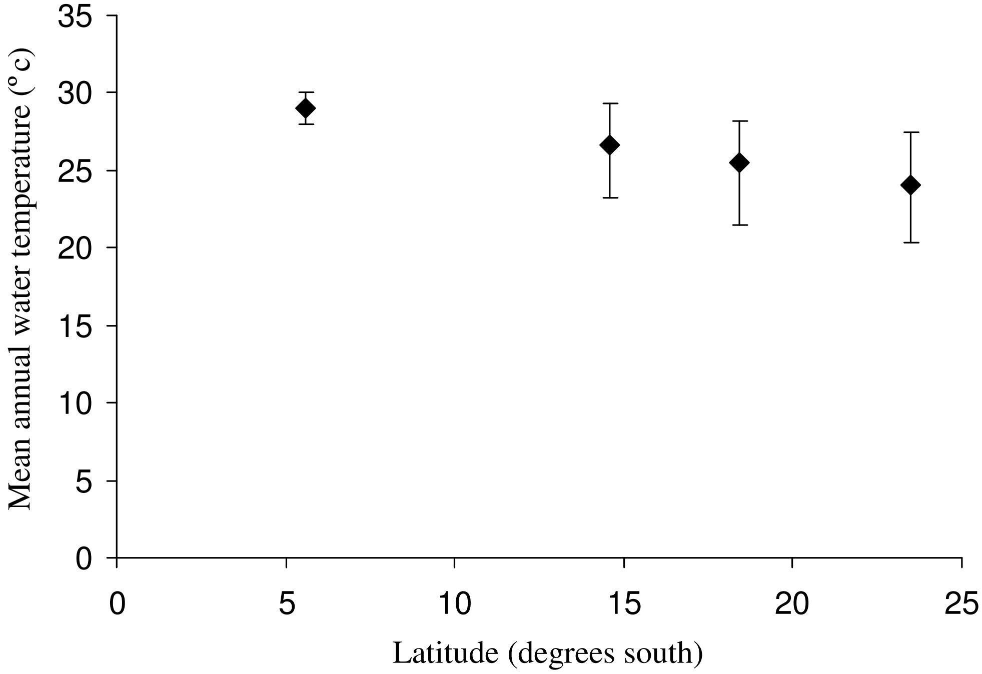

Figure 4.3: Relationship between mean annual seawater temperature and latitude of locations at which *Halichoeres melanurus* was sampled. Locations in order of increasing latitude are: Kimbe Bay, Papua New Guinea; Lizard Island, north Great Barrier Reef (GBR); Palm Islands, mid GBR; Heron Island, south GBR. Bars indicate the range of seawater temperatures during the year at each location. Data for Lizard Island, Palm Islands and Heron Island recorded daily by Australian Institute of Marine Science and provided by Berkelmanns R. (pers. comm.). Data for Kimbe Bay, Papua New Guinea provided by Jones G. P. (pers. comm.).

Individuals were collected using small hand spears or by spraying them with the anaesthetic clove oil. Specimens were stored on ice and dissected within a few hours. The standard length (mm), fork length (mm) and mass of each fish (to nearest mg) were measured. Gonads were removed from individuals and stored in FAAC for a minimum of 48 hrs before being transferred to 70% ethanol. Sagittal otoliths were removed, cleaned with distilled water and dried before being stored in a culture dish.

4.2.2 Age and longevity estimates

4.2.2.1 *Preparation of otoliths and increment counts*

Otoliths were prepared using the methods described in Chapter 2 (Section 2.2.3). Thin sections of sagittal otoliths were examined and incremental rings counted to age each individual, seventy to eighty individuals were aged for each location. Tetracycline

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Figure 4.4: Colour patterns of *Halichoeres melanurus* with (a) an initial phase female, and (b) terminal phase male. Photographs from Randall et al. (1997).

validation had previously indicated incremental marks in *H. melanurus* are laid down on a daily basis (Chapter 2: Section 2.3.1.2).

Two counts of increments were made for each otolith and the average age used as a final estimate. Percentage error between counts (Chapter 2, Section 2.2.3.1) revealed differences between counts of daily rings were acceptably low (Kimbe Bay 4.6%, Lizard Island 5.4%, Palm Islands 5.0%, Heron Island 7.1%).

4.2.3 Growth

4.2.3.1 *Relationships between size and age among locations*

Although growth appeared to be relatively linear at some of the locations, fitting regressions to size-at-age data indicated the quadratic term was significant when describing the relationship between size and age at all locations (Table 4.1). Therefore quadratic regressions ($\text{size} = c + B_1\text{age} + B_2\text{age}^2$), were fitted to size-at-age data in all cases. As the growth curves describe post-settlement growth, regressions for each location were constrained to intercept the y-axis at 10mm SL. Based on estimates derived by Sponaugle & Cowen (1997) for settlement size of six species of *Halichoeres* in the Caribbean and personal observations of newly settled *H. melanurus*, this was considered a biologically meaningful estimate for size at settlement for *H. melanurus*.

Table 4.1: Significance of linear and quadratic terms in describing the relationship between age and size among locations. Linear term (age), quadratic term (age x age). ***p<0.001 **p<0.01.

Location	**Term**	**n**	***MS***	**F**	**p**
Kimbe Bay, PNG	age	80	1295.2	49.02	0.000***
	age × age	80	119.4	4.519	0.000***
Lizard Island, north GBR	age	81	1397.8	22.54	0.000***
	age × age	81	701.3	11.31	0.000***
Palm Islands, mid GBR	age	80	1498.9	27.05	0.000***
	age × age	80	283.2	5.11	0.005**
Heron Island, south GBR	age	73	856.4	21.24	0.000***
	age × age	73	63.9	1.59	0.001***

An ANCOVA of data for all locations indicated age was a significant covariate of size. Therefore, differences in size among locations were examined with the effects of age removed. A scatter plot of this relationship indicated the interaction between age and size had a marked 2nd order polynomial trend. A regression of the form, size = c + B_1age + B_2age^2, gave a closer fit than a linear regression. Therefore, to remove the interaction between age and size, a quadratic regression was performed with log size as the dependent factor and age + age^2 as the independent factor and the residuals of this regression were used for further analysis (Stearns 1992). Size was log transformed to satisfy the assumption of homogeneity of variances for an ANOVA of the residuals. A post-hoc Tukey's test was performed to identify which locations differed significantly.

Similarly, differences in age among locations were examined following removal of the effects of size. Therefore, the process described above was repeated for age at each location. A linear regression with age as the dependent factor and log size as the independant factor removed the interaction between age and size. When an ANOVA was performed on the residuals of this regression homogeneity of variances could not be obtained despite trying a range of transformations prior to the regression. Therefore, to provide further support for the results of this ANOVA a non-parametric Kruskal Wallis ANOVA with a Monte Carlo simulation of 1000 samples and a 99% confidence interval was also performed on the residuals. This method does not assume homogeneity of variances.

To examine absolute growth among locations, I compared the body size attained after 200 days at each location. The age of 200 days was chosen because from 0-200 days the growth trajectories of *H. melanurus* at each location are relatively constant and differences in size attained among locations are most apparent. To examine relative growth, size and age relative to maximum size and maximum age were plotted against each other for the life-span of *H. melanurus* at each location. Early growth (defined as the percentage of maximum body size reached after 20 percent of the maximum life-span), was compared among locations (as in Chapter 2, Section 2.2.5.2.3). Maximum life-span was the age of the oldest individual in the sample from each location and therefore, all else being equal, this represented an age any individual in the population had the potential to attain.

4.2.4 Reproduction

4.2.4.1 Size and age at maturity

Gonad tissue was processed according to the procedure outlined in Chapter 3 (Section 3.2.4). Individuals were sexed and oocytes were staged (as stage 1-5) using the criteria of Ferreira (1995), (Chapter 3, Table 3.2). Gonads were classified by the highest staged oocyte present (Adams et al. 2000). Individuals containing oocytic stages of 1 or 2 only, were categorised as immature. An estimate could be derived for the size at which 50% of the population had matured at Kimbe Bay and Heron Island as both immature and mature individuals were present in the field at the time of collection. When sampling was undertaken at Lizard Island and the Palm Islands, however, individuals less than 28mm SL were not observed. Samples from these populations contained no immature individuals, therefore size at 50% maturation could not be estimated. By using the smallest size of mature individuals it was still possible to identify an upper boundary to the size at which maturation occurred. Both size and age at maturity were examined relative to maximum size and maximum age at each site.

4.2.4.2 ***Reproductive effort***

In order to assess how much energy individuals at each location were devoting to reproduction, gonadosomatic indices (GSIs) were determined. Wet weight of gonads was recorded to the nearest 0.01 of a milligram and GSIs were calculated using Equation 3.2 (Chapter 3, Section 3.2.4.2).

Gonad weight and fish weight were measured in milligrams. GSI was plotted against size for each female at each site. Although individuals with stage 5 oocytes were common at Kimbe Bay, Lizard Island and the Palm Islands there was only one stage 5 individual collected at Heron Island. Therefore, intraspecific comparisons of GSIs among locations included only mature females with ripe gonads which had been classified as stage 4 based on the highest oocytic stage present, as gonads at this stage were common at each of the study locations. The GSI is a simple expression of the amount of energy an individual invests in reproductive tissue compared to somatic tissue and has been used as a proxy for reproductive effort (West 1990). ANCOVA revealed size was not a significant covariate of GSI therefore the effects of size did not need to be removed. Mean GSIs of stage 4 individuals among locations were compared using ANOVA. GSI values were first square root-transformed to homogenise variances.

4.2.4.3 *Size and age at sex change*

Size and age at sex change were examined graphically. Histograms were plotted indicating the frequencies of size and age at each location. Sex change usually occurred within a specific size range. To remove the effect of outlying individuals which were not representative of the population as a whole, this range was defined as outlined in Chapter 3 (Section 3.2.4.3). Size at sex change was then estimated as the mean size of all individuals within this size range of sex change. The same method was used to determine an estimate of age at sex change. To standardise for any size differences among locations, these estimates were then expressed as a percentage of maximum body size and maximum age, respectively.

4.3 Results

4.3.3 Prediction 1: Early growth rate decreases with an increase in latitude

Plots of size at age data for each location revealed growth was described well by quadratic regressions (Figure 4.5). Variation in absolute growth did not support the prediction that there is a consistent decrease in early growth rate with increasing latitude. Individuals at Lizard Island had the greatest growth rate (Figure 4.6). Growth at Kimbe Bay (the location at the lowest latitude) was only slightly greater than at the Palm Islands for the first year of life. Individuals at Heron Island had the slowest absolute growth (Figure 4.6, Table 4.2). Growth at the two lower latitude sites (Kimbe

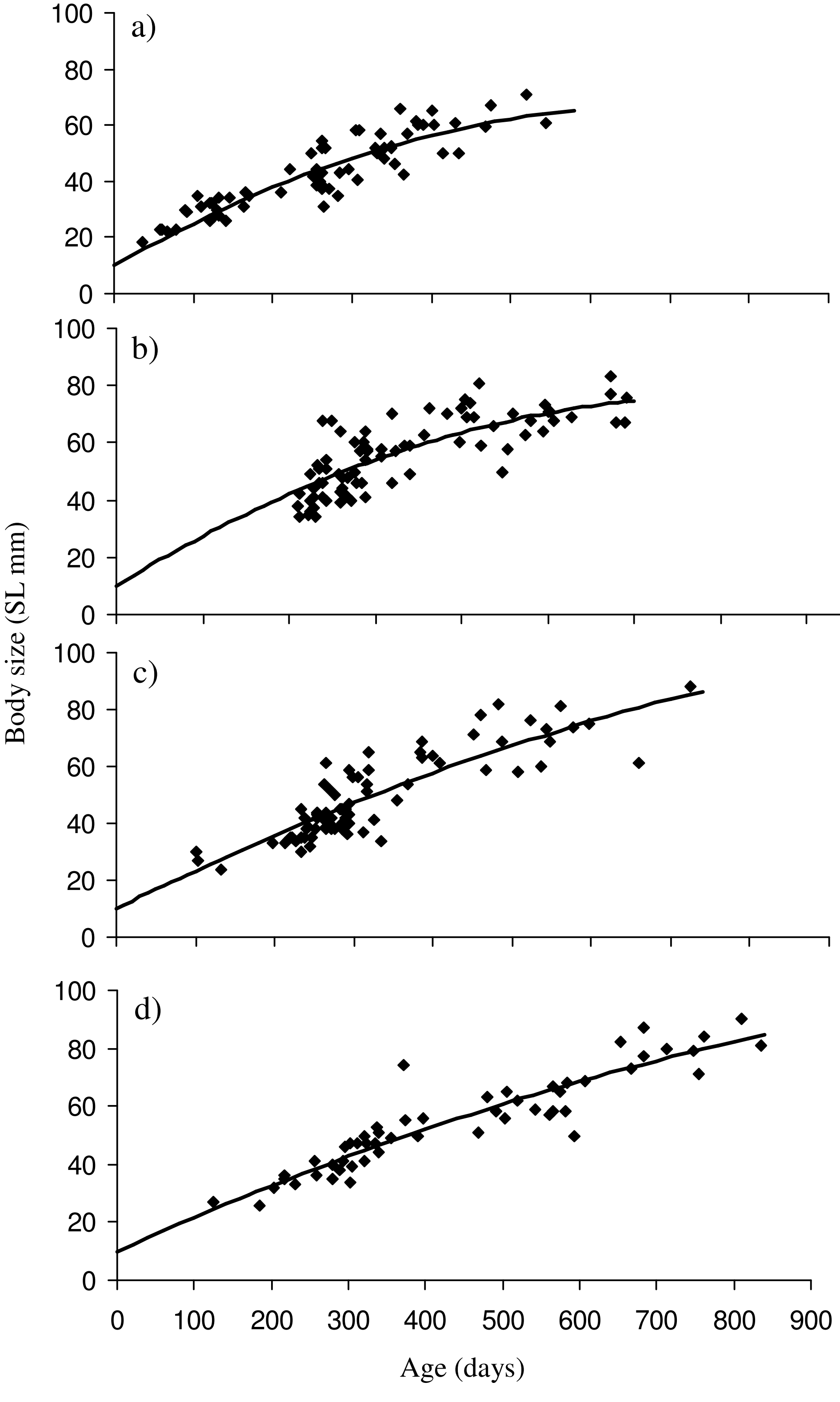

Figure 4.5: Quadratic regressions fitted to size-at-age data for *Halichoeres melanurus* individuals at four locations. a) Kimbe Bay, Papua New Guinea ($y=10+0.161x-0.000113x^2$, N=80), b) Lizard Island, northern Great Barrier Reef ($y=10+0.186x-0.000131x^2$, N=81), c) Palm Islands, mid GBR ($y=10+0.138x-0.0000470x^2$, N=80) and d) Heron Island, Capricorn Bunker Group, south GBR ($y=10+0.120x-0.0000375x^2$, N=73).

Bay and Lizard Island) was slightly less linear than at the two higher latitude sites (Palm Islands and Heron Island) (Figure 4.6).

Growth rate relative to maximum life-span and maximum body size provided stronger support for the prediction. Although differences in growth among locations were small, early growth (percentage of maximum body size reached after 20% of life-span) was highest at Kimbe Bay (37.1% of maximum size). It declined slightly to 36.7% in the Lizard population and was lower still in the two locations at higher latitudes (Palm Islands, 32.9% and Heron Island, 32.2%), (Table 4.2, Figure 4.7). The growth pattern of *H. melanurus* relative to maximum size and age was almost identical at the two lower latitude locations and at the two higher latitude locations.

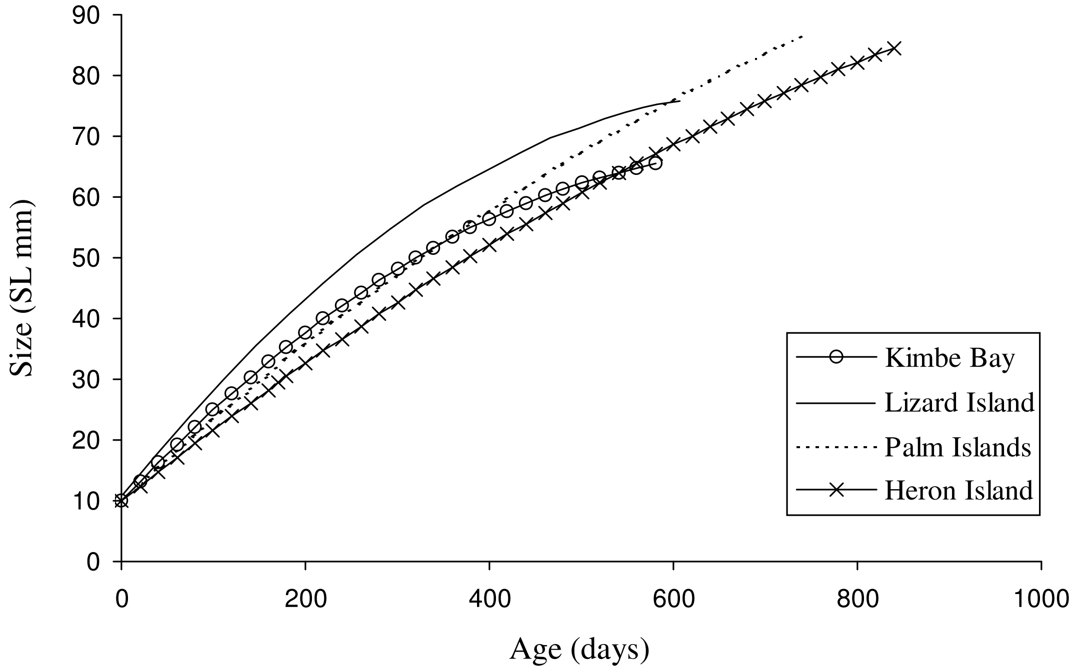

Figure 4.6: Superimposed growth curves for *Halichoeres melanurus* at each location sampled.

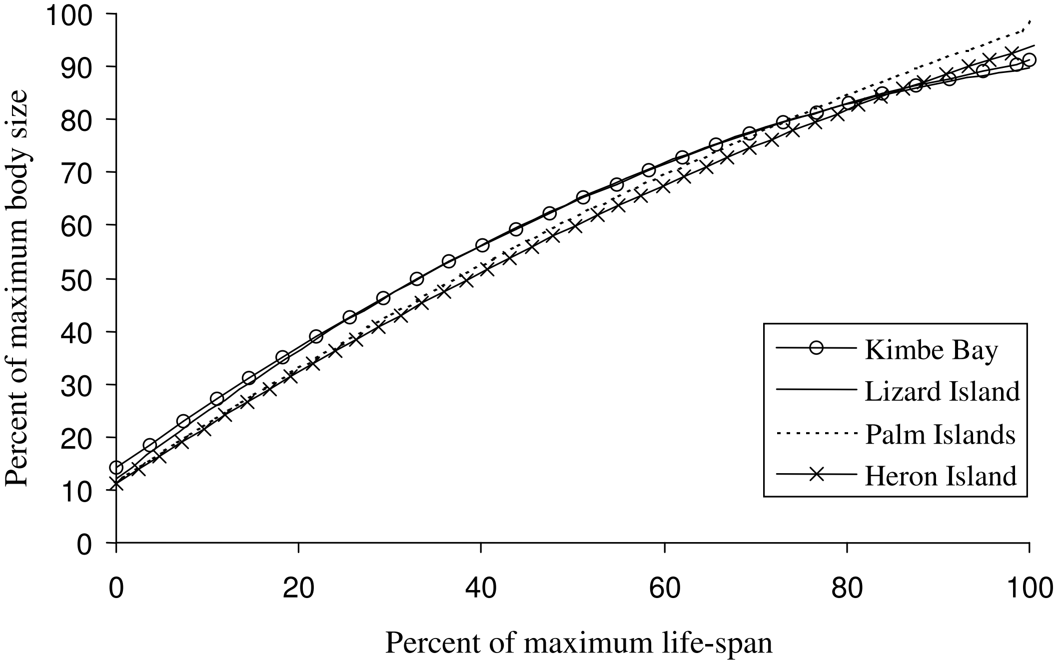

Figure 4.7: Growth of *Halichoeres melanurus* relative to both maximum life-span and maximum body size at Kimbe Bay (PNG), Lizard Island (north GBR), Palm Islands (mid GBR) and Heron Island (south GBR).

Table 4.2: Absolute and early growth at the four locations. Also provided are estimates of maximum longevity and body size and the values from which an estimate of early growth was calculated.

Location	Absolute growth (mm after 200 days)	Max life-span (days)	20% max. life-span (days)	Size at 20% max. life-span (SL mm)	Max. size (mm SL)	Early growth (% max. body size after 20% max. life-span)
Kimbe Bay, PNG	37.7	548	110	26.3	71	37.1
Lizard Island, GBR	42.0	590	118	30.5	83	36.7
Palm Islands, GBR	35.8	726	145	29.0	88	32.9
Heron Island, GBR	32.5	836	167	29.0	90	32.2

4.3.1 Prediction 2: Body size increases with an increase in latitude

There was a considerable increase in maximum body size with latitude, from 71mm SL at Kimbe Bay to 90mm SL at Heron Island (Figure 4.8). There was, however, considerable overlap in size distributions at the sites and no consistent relationship between median size and latitude was evident. An ANOVA indicated residual size (residuals derived from a regression of log size on age + age^2 to remove the interaction between size and age), varied significantly among locations (Table 4.3). A post-hoc Tukey's test identified a significant difference between all locations with the exception of the interaction between Kimbe Bay and the Palm Islands (Table 4.3). Examination of an error bar plot indicating 95% confidence limits for the means of residuals supported results of the Tukey's test.

4.3.2 Prediction 3: Longevity increases with an increase in latitude

The relationship observed between latitude and maximum age was similar to that between latitude and maximum body size (Figure 4.9). As predicted maximum age gradually increased with an increase in latitude, from 548 days at Kimbe Bay to 836 days at the most southerly site Heron Island. There was no apparent relationship between median age and latitude. The median age at Kimbe Bay, Lizard Island and the Palm Islands was similar among locations but was almost twice as great at Heron Island (Figure 4.9). ANOVA indicated there was a significant difference in residuals of age (derived from regression of age on log size) among sites (Table 4.4). A post-hoc Tukey's test revealed the only sites at which residuals of age did not differ significantly from one another were Kimbe Bay and the Palm Islands. The assumption of homogeneity of variances required for the One-Way ANOVA was not met. Therefore, a Kruskal Wallis test with Monte Carlo simulation which is not subjected to this assumption was performed, and produced the same result (Table 4.4). Examination of box plots of 95% confidence intervals around the means of residuals among locations, strongly supported results of the One-Way ANOVA and post-hoc test.

4.3.4 Prediction 4: Maturation occurs at a smaller proportion of maximum size and earlier in life at lower latitudes

Size and age at maturity could only be estimated for individuals at Kimbe Bay and Heron Island, the two extremes of the latitudinal gradient sampled (Materials & Methods 4.2.4.1). However, minimum size and minimum age of mature individuals are provided for Lizard Island and the Palm Islands (Figure 4.10, Table 4.5). Individuals at Kimbe Bay matured at about 29mm SL, 6mm less than at Heron Island. Relative to maximum size, maturation of individuals at Kimbe Bay occurred at a proportionally similar size (40.8 % of maximum size) to those at Heron Island (39.9 % of maximum size). Sizes of the smallest mature individuals collected at Lizard Island (30 mm SL,

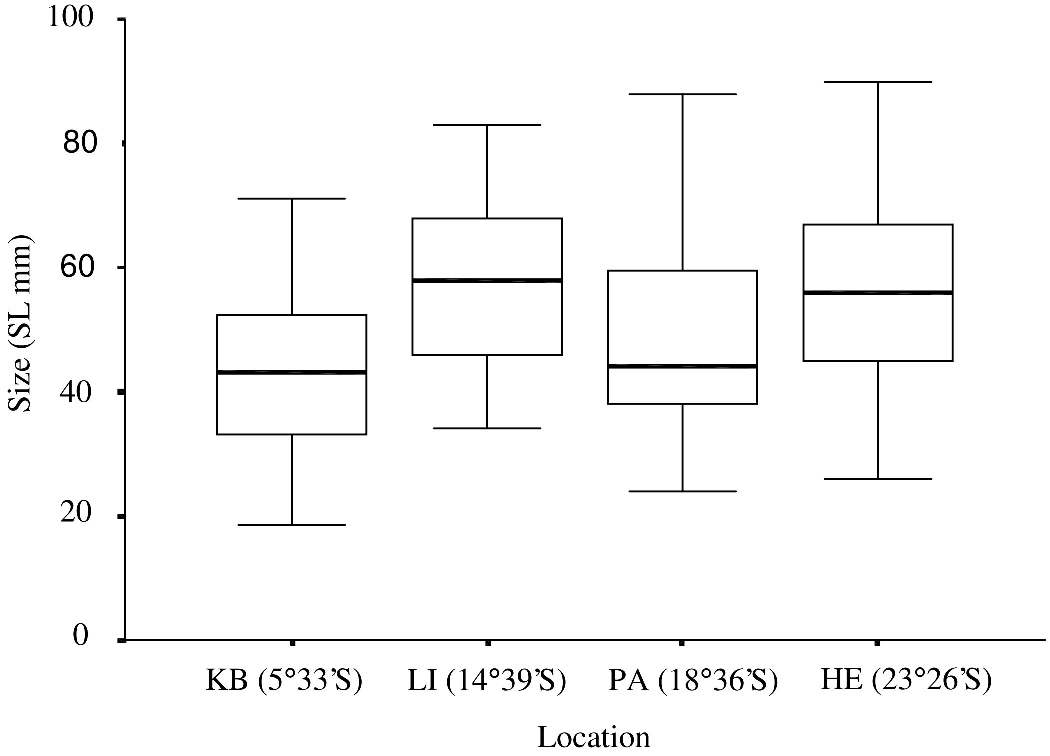

Figure 4.8: Box plot of size distributions of *Halichoeres melanurus*. Indicating median size (black bar within box), interquartile range, maximum and minimum size. Locations in order of increasing latitude are Kimbe Bay, PNG (KB); Lizard Island, GBR (LI); Palm Islands, GBR (PA) and Heron Island, GBR (HE).

Table 4.3: Summary of ANOVA and Tukey's post-hoc comparison for residual size (residuals from quadratic regression of log size on age + age^2) of *Halichoeres melanurus* among locations. Tukey's test results identify locations for which residuals of size significantly differed from each other: Kimbe Bay, PNG (KB); Lizard Island, GBR (LI); Palm Islands, GBR (PA) and Heron Island, GBR (HE). Means of residuals sharing common underline did not differ at p<0.05.

Analysis of variance

	df	MS	*F*	p
Between locations	3	0.0816	23.44	0.000
Within locations	313	0.0035		
Total	316			

Comparisons of means of residual size

Location	HE	PA	KB	LI
Mean of size (SL mm)	56.1	49.2	43.4	56.5
Mean of residuals	-0.035	-0.010	-0.0007	0.042

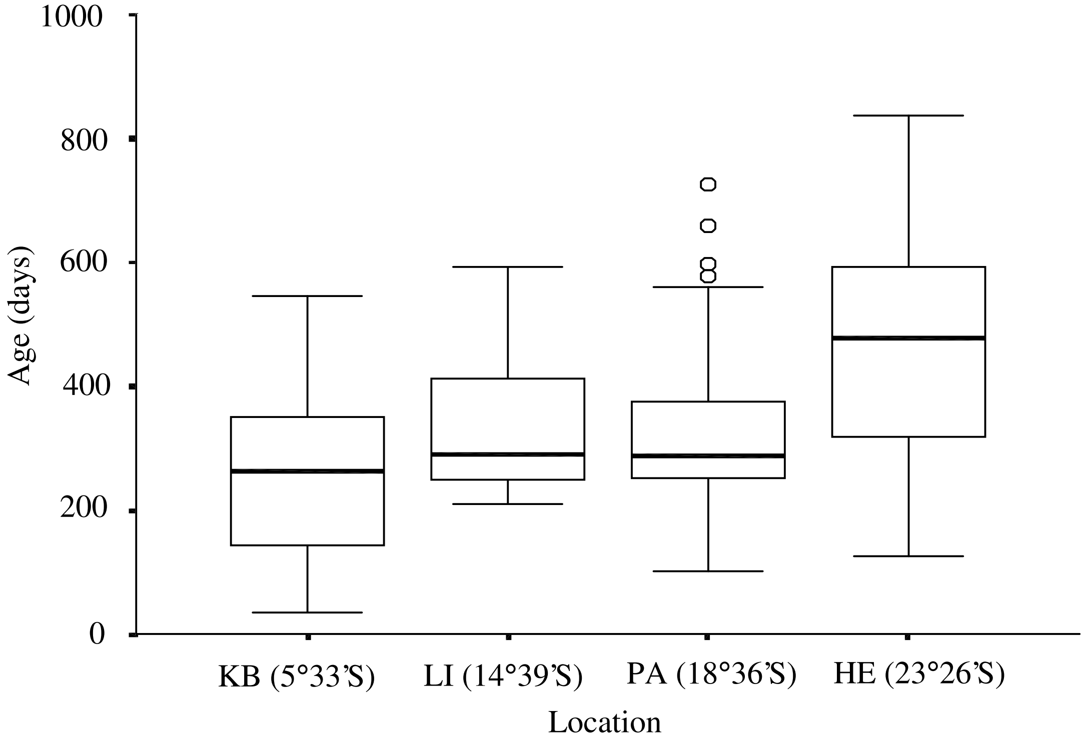

Figure 4.9: Box plot of age distributions of *Halichoeres melanurus*. Indicating median (horizontal line), interquartile range (box length), maximum and minimum age (ends of tails) and outliers (circles). Outliers are defined as cases with values between 1.5 and 3 box lengths from the upper edge of the box. Locations in order of increasing latitude are Kimbe Bay, PNG (KB); Lizard Island, GBR (LI); Palm Islands, GBR (PA) and Heron Island, GBR (HE).

Table 4.4: Summary of ANOVA, Tukey's post hoc comparison and Kruskal Wallis test for residual age (residuals from linear regression of age on log size) of *Halichoeres melanurus* among locations. Kruskal Wallis test used a Monte Carlo estimate based on 1000 sampled tables; Tukey's test results identify locations for which residuals of size significantly differed from each other; Kimbe Bay, PNG (KB); Lizard Island, GBR (LI); Palm Islands, GBR (PA) and Heron Island, GBR (HE). Means of residuals sharing common underline did not differ at $p<0.05$.

One-Way Analysis of variance

	df	**MS**	*F*	**p**
Between locations	3	248366	48.82	0.000***
Within locations	313	5086.5		
Total	316			

Kruskal-Wallis test

Chi-Square		90.55
df		3
p		0.000***
Monte Carlo		0.000***
99% conf.	**Lower**	0.000
Interval	**Upper**	0.005

Comparisons of means of residual age

Location	**LI**	**KB**	**PA**	**HE**
Mean of age (days)	338	259	326	465
Mean of residuals	-53.3	-17.8	-3.0	81.9

36.1% of maximum size) and the Palm Islands (29 mm SL, 32.9% of maximum size), indicate individuals in these populations are likely to mature at a smaller relative size than individuals in the Kimbe Bay or Heron Island populations. There was no overall trend relating proportion of life-span attained before maturation and latitude (Table 4.5). It is evident that maturation of individuals at the Palm Islands occurs considerably earlier than at each of the other locations (the youngest mature individual at the Palm Islands was 16.5% of maximum age) (Table 4.5).

4.3.5 Prediction 5: Reproductive effort decreases with an increase in latitude

Within locations, there was no apparent relationship between gonadosomatic index and body size of individuals (Figure 4.10). When considering both maximum and mean GSIs of females with stage 4 gonads (Materials & Methods 4.2.4.2), there was considerable variation in the estimated values of GSIs among locations although there was no apparent relationship between reproductive effort and latitude (Figure 4.11). Maximum reproductive effort was greatest at the Palm Islands with a maximum GSI of 6.92%, it was slightly lower at Lizard Island (6.23%) and considerably lower at Heron Island (3.46%) and Kimbe Bay (2.39%). Mean GSIs for each site followed a similar pattern with the greatest average reproductive effort at the Palm Islands (4.01%), followed by Lizard Island (2.44%), Heron Island (1.87%) and Kimbe Bay (1.10%), (Figure 4.11). A post-hoc Tukey test indicated a significant difference between gonadosomatic indices (square root transformed) of females at all sites with the exception of Lizard Island and Heron Island (Table 4.6).

4.3.6 Prediction 6: Sex change occurs at a smaller proportion of maximum size and earlier in life at lower latitudes

Age and size frequencies of males and females observed at all sites support the interpretation that this species is a protogynous hermaphrodite. Larger and older fish were males (Figures 4.12 & 4.13). In terms of absolute size there was a general increase in median size at sex change from 48 mm at Kimbe Bay to 66 mm at Heron Island (Figure 4.14a). At all sites sex change was concentrated in a range covering one or two size classes (ie. a size range of 6 – 12 mm). No consistent latitudinal pattern was apparent when size at sex change was examined relative to maximum size. Individuals at the Palm Islands changed sex at the smallest proportion of maximum size (Table 4.7).

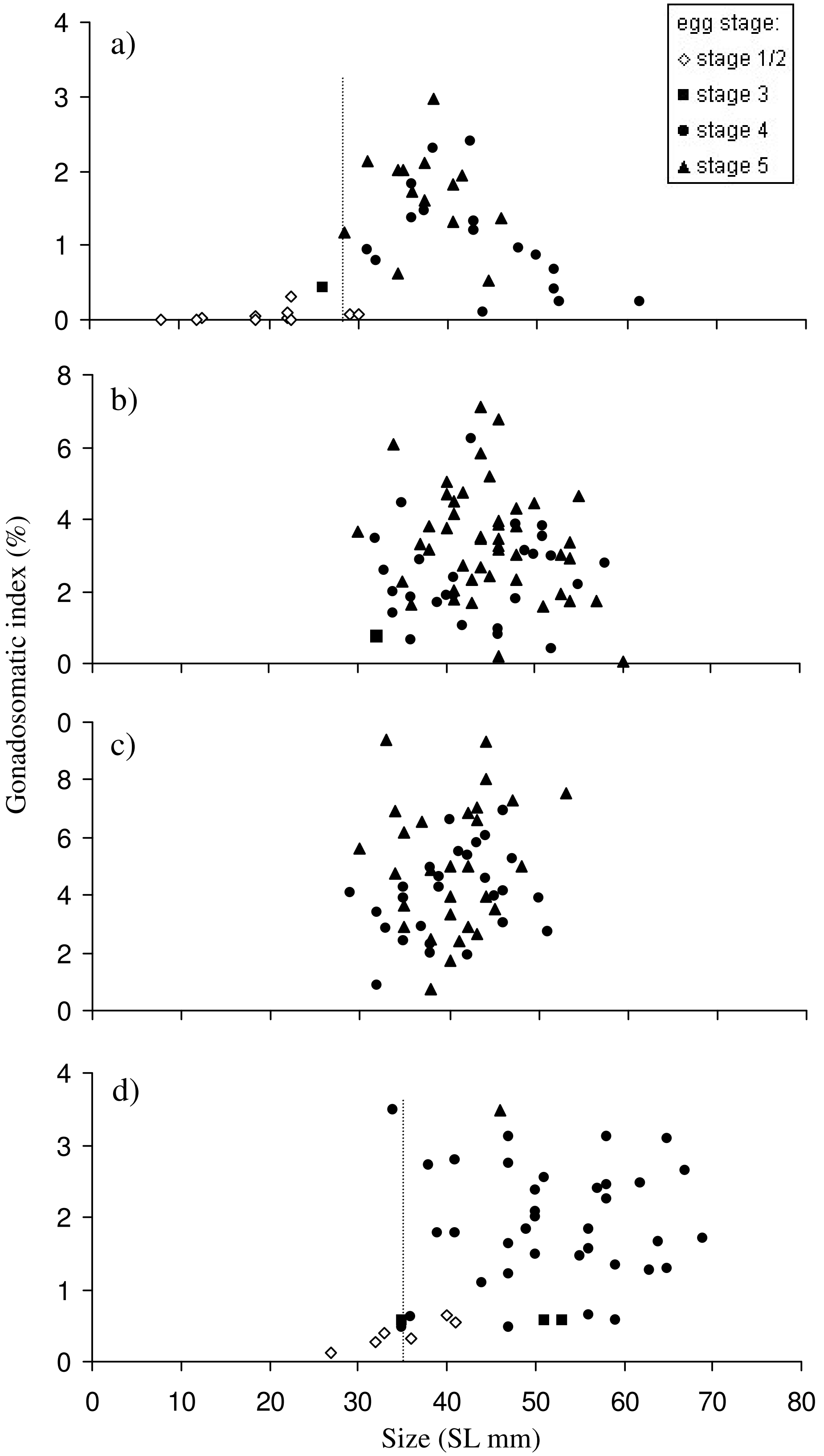

Figure 4.10: Gonadosomatic indices for females at different developmental stages for each location: a) Kimbe Bay, PNG; b) Lizard Island, GBR; c) Palm Islands, GBR and d) Heron Island, GBR. Dotted line indicates estimated size at maturity. Females with egg stages 1 and 2 are immature.

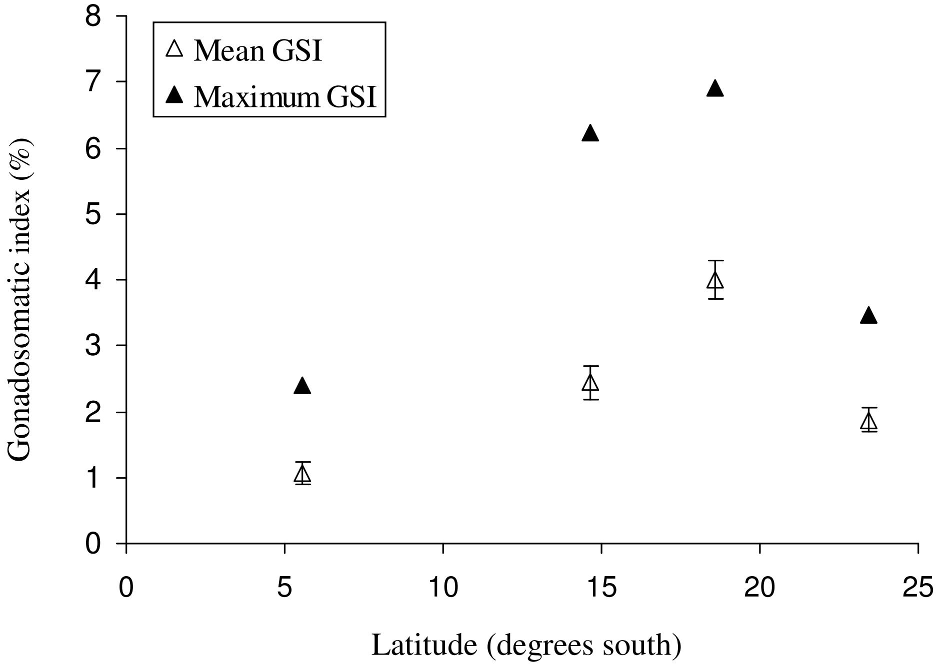

Figure 4.11: Maximum and mean gonadosomatic indices for *Halichoeres melanurus* females in which stage 4 represents the most developed oocyte (Ferriera 1995), at four locations along a latitudinal gradient. Standard errors of the means are indicated. Locations in order of increasing latitude are Kimbe Bay, PNG (N=16); Lizard Island (N=26), north GBR; Palm Islands, mid GBR (N=27) and Heron Island, south GBR (N=35).

Table 4.5: Estimates of size and age at maturity for each location. Provided are Maximum adult size, absolute and relative size-at-maturity, maximum age, absolute and relative age-at-maturity (where relative values are the proportion of maximum size and maximum age attained before maturation occurs).

	Kimbe Bay, PNG	**Lizard Island, GBR**	**Palm Islands, GBR**	**Heron Island, GBR**
Maximum size (SL mm)	71	83	88	90
Size at maturity (SL mm)	29	<30	<29	35
% maximum size	**40.8**	**<36.1**	**<32.9**	**39.9**
Maximum age (days)	548	590	726	836
Age at maturity (days)	110	<212	<120	240
% maximum age	**20.1**	**<36.9**	**<16.5**	**28.7**

Table 4.6: Summary of ANOVA and Tukey's post-hoc comparison for square root transformed GSIs of female *Halichoeres melanurus* (stage 4 gonads only) among locations. Tukey's test results identify locations for which GSIs significantly differed from each other. Locations are Kimbe Bay, PNG (KB); Lizard Island, GBR (LI); Palm Islands, GBR (PA) and Heron Island, GBR (HE). Means of square root transformed GSIs sharing common underline did not differ at $p<0.05$.

Analysis of variance

	df	**MS**	***F***	**p**
Between locations	3	1348.46	22.31	0.000
Within locations	101	60.44		
Total	104			

Comparisons of means

Location	**KB**	**HE**	**LI**	**PA**
Mean of GSI	1.07	1.87	2.44	4.01
Mean of square root transformed GSIs	1.59	4.21	7.61	18.32

Although sex change occurred at a smaller percentage of maximum size at Kimbe Bay than at Heron Island the difference was not considerable (5% of maximum size), in addition sex change occurred at a smaller size relative to maximum size at both Lizard Island and the Palm Islands than at the lowest latitude location, Kimbe Bay (Table 4.7).

Similarly, there was no obvious relationship between latitude and median age at sex change (Figure 4.14b). Median age at sex change was similar among Kimbe Bay, Lizard Island and the Palm Islands (277-302 days) but individuals changing sex at Heron Island were almost twice as old (574 days). Sex change occurred at a wide range of ages at each location. The time period over which sex change could occur decreased moving from Kimbe Bay (173 days) to higher latitudes and the age range of sex change was particularly small at Heron Island (46 days), (Figure 4.14b). Relative to maximum age, sex change occurred far earlier in life at the Palm Islands than at the other locations (Table 4.7).

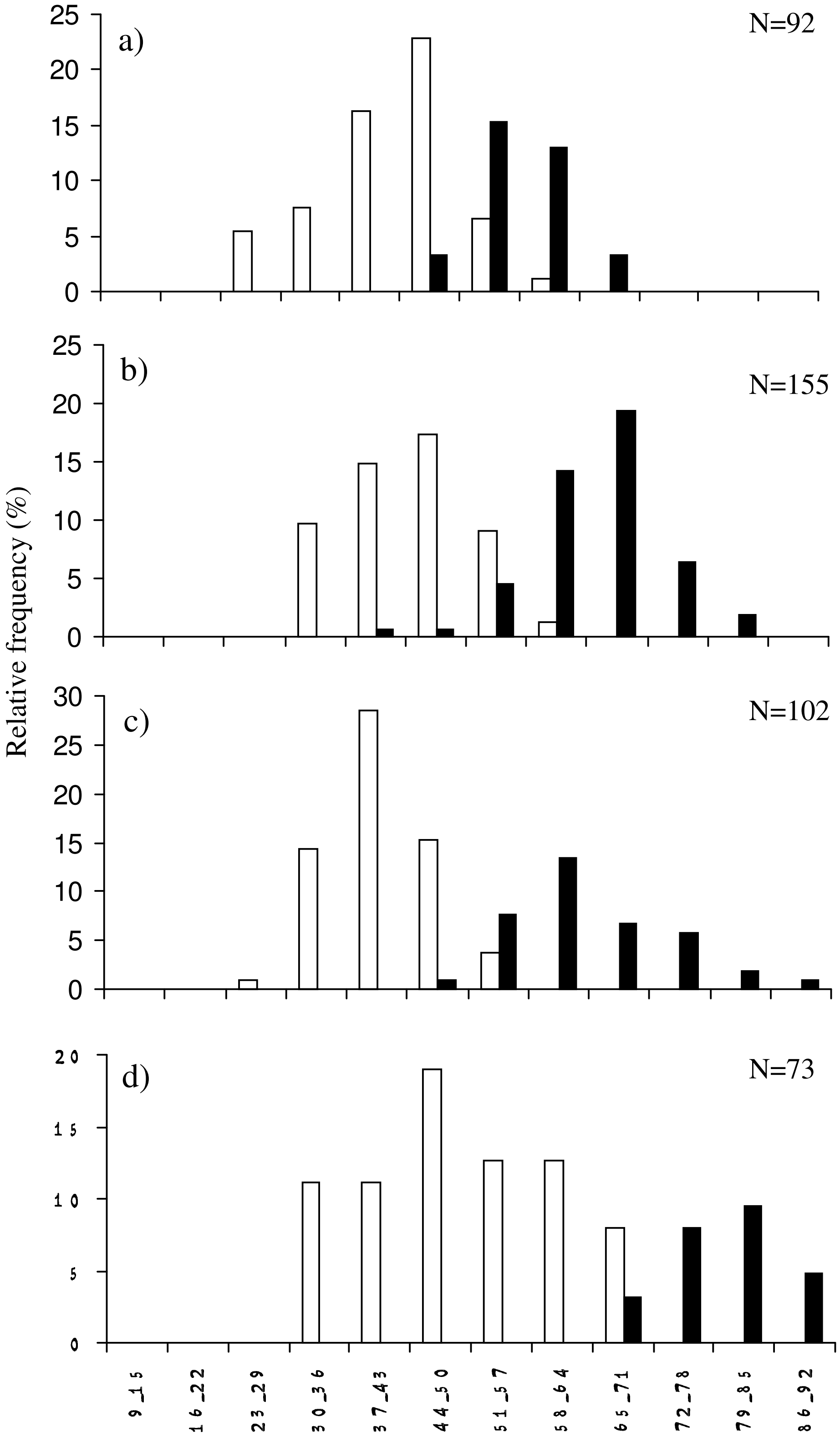

Figure 4.12: Size frequencies of males and females (open bars, females; solid bars, males) at a)Kimbe Bay, PNG; b)Lizard Island, GBR; c)Palm Islands, GBR; d)Heron Island, GBR.

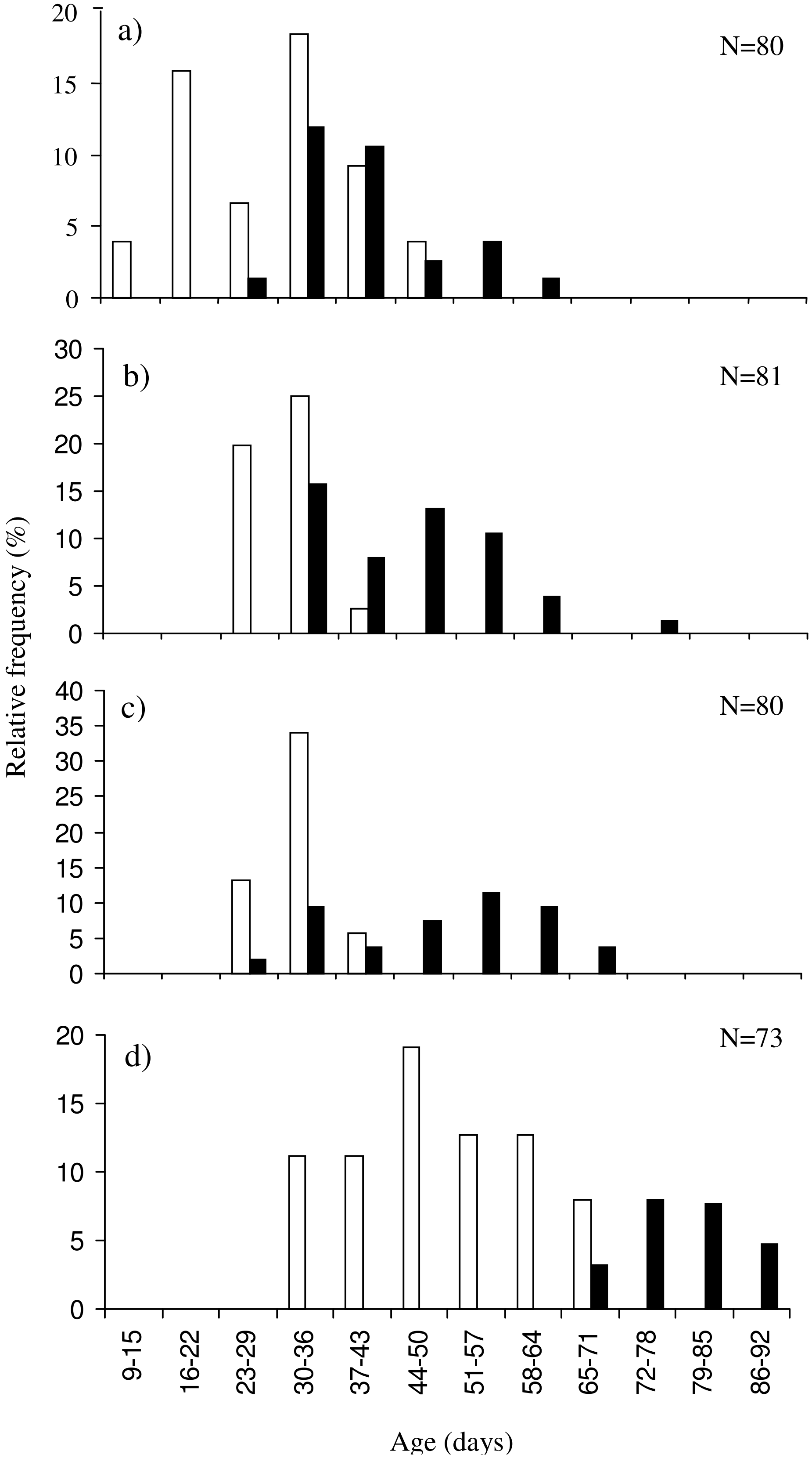

Figure 4.13: Age frequencies of males and females (open bars, females; solid bars, males) at a) Kimbe Bay, PNG; b) Lizard Island, GBR; c) Palm Islands, GBR; d) Heron Island, GBR.

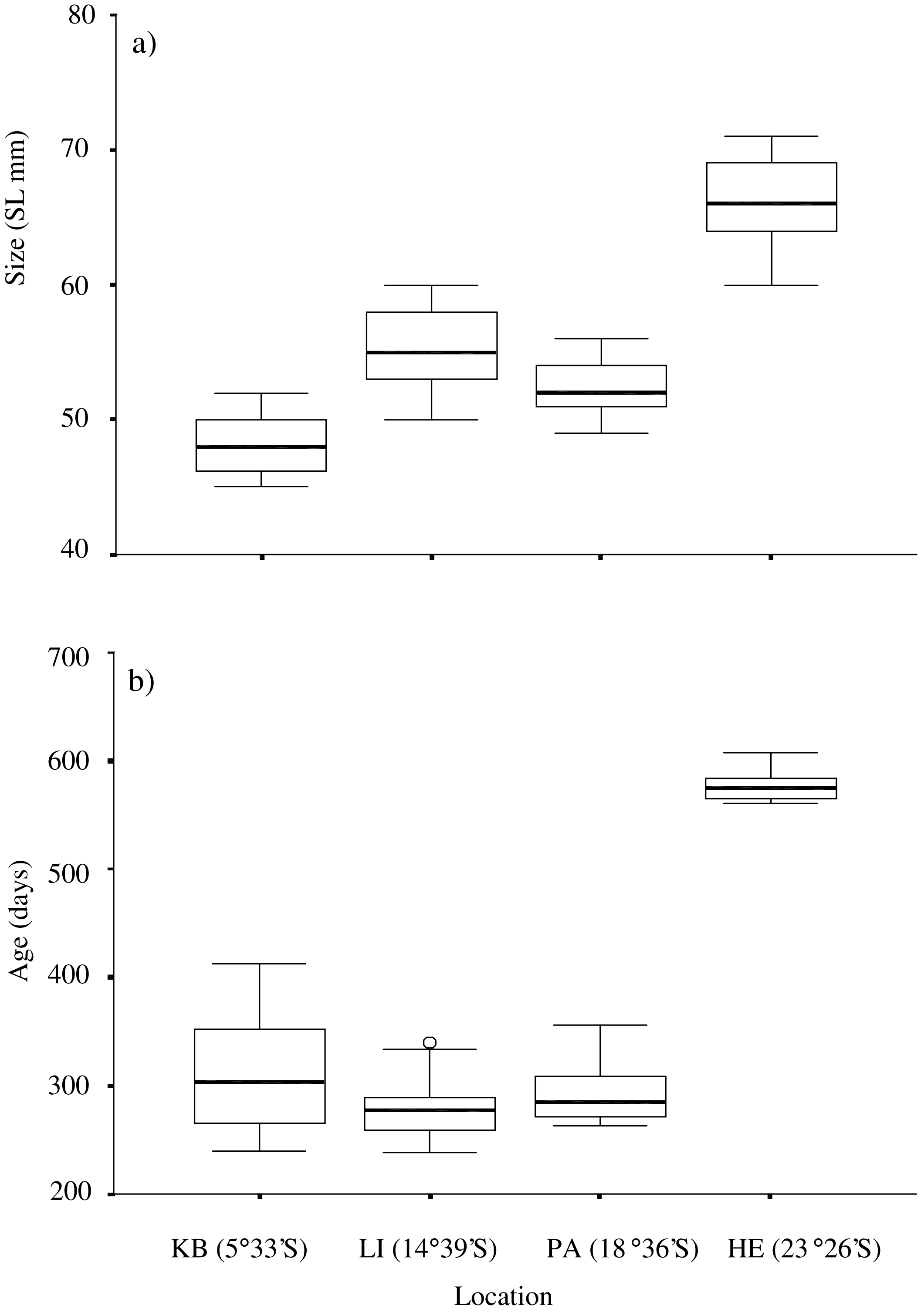

Figure 4.14 a & b: Size and age range at which sex change occurred at each location. Indicated is the median, interquartile range, maximum and minimum age and outliers (circles). Locations in order of increasing latitude are Kimbe Bay, PNG (KB); Lizard Island, GBR (LI); Palm Islands, GBR (PA) and Heron Island, GBR (HE).

Table 4.7: Size and age at sex change of *Halichoeres melanurus* at four locations. Provided are the total number of individuals in histograms for size and age at sex change, number of individuals within size and age range over which sex change occurred, mean size and age at sex change and standard errors of the mean, relative size and age at sex change (% of maximum body size and maximum age at which sex change occurs).

	Kimbe Bay, PNG	**Lizard Island, GBR**	**Palm Islands, GBR**	**Heron Island, GBR**
Total number of individuals (size)	92	156	102	73
Number of individuals within size range of sex change	23	34	13	18
Mean size at sex change	48.2	55.2	52.46	65.4
Standard error	0.48	0.52	0.54	0.78
% maximum size	**67.9**	**66.5**	**59.6**	**72.7**
Total number of individuals (age)	80	81	80	73
Number of individuals within age range of sex change	43	36	19	9
Mean age at sex change	311.29	278.81	291.18	512.88
Standard error	7.80	4.45	5.97	5.33
% maximum age	**56.9**	**47.3**	**40.1**	**61.3**

4.4 Discussion

This study is one of the first to assess covariation of life history traits along a latitudinal gradient in a coral reef fish species. All life history traits examined including body size, longevity, growth rate, size and age at maturity, reproductive effort and size and age at sex change varied among geographic locations. The life history traits associated with growth conformed more closely to predictions derived from life history theory, and exhibited more consistent trends in relation to latitude, than traits associated with reproduction.

4.4.1 Growth pattern

Terrestrial ectotherms raised at different temperatures usually exhibit predictable variation in growth. Individuals in warmer temperatures have more rapid growth early in life, which is often associated with a decrease in both body size and life-span of individuals (Atkinson 1994, Jackson & Moltschaniwskyj 2001). Support for the expectation of greater growth in warmer temperatures is unclear based on the results of this study. Growth of *H. melanurus* was most rapid at Lizard Island, and slowest at Heron Island. However, growth was not fastest at Kimbe Bay which has the highest mean seawater temperature, suggesting factors other than ambient temperature are influencing the patterns observed here.

Variation in growth rates can be caused by a range of factors other than temperature. Food availability is important, slower growth being associated with low resource levels (Jones 1986, Abrams & Rowe 1996, Arendt 1997). Kimbe Bay and the surrounding Bismarck sea, is an area of low productivity (Jones G. P. pers. comm.), which could result in reduced availability of resources and slower growth than at Lizard Island, despite the differences in temperature among locations. Therefore, the observed patterns of growth at each location potentially represent an optimisation of growth within the constraints of both environmental temperature and resource availability.

Although the cause of the variation in growth in unclear, there is evidence for an energetic trade-off between growth, size and longevity (Camp & Marshall 2000). Comparison of growth curves indicates the faster growth at Lizard Island is associated with smaller maximum size and shorter life-span of individuals than at the two higher latitude locations. However, overall differences in growth among locations were small. This is partly due to the small size and short life-span of the species, limiting the variation in size and longevity that can be observed among locations. A further reason may be the considerable interannual variation in water temperature (5-7°c) at each location sampled on the Great Barrier Reef (Berkelmanns R. pers. comm). Therefore, even though mean seawater temperature gradually decreases with an increase in latitude, the interannual variation almost encompasses the range of mean seawater temperature among locations. Examination of populations subjected to a greater range of water temperatures could reveal more significant differences in growth.

4.4.2 Body size

This study indicated that maximum body size of *H. melanurus* increased gradually with latitude, whereas no obvious trend was evident among locations for median body size. Although the number of studies examining changes in body size of coral reef fishes across different latitudes is limited, it is already evident that there is considerable variation in the overall patterns expressed in this group. For example, over the same latitudinal range as that examined here, there was no change in body size with an increase in latitude in the pomacentrid *Pomacentrus moluccensis* (Bray 2001). Between Kimbe Bay and the southern Great Barrier Reef, however, the wrasse *Thalassoma lunare* did exhibit an increase in size with an increase in latitude (Ackerman J. pers. comm.). In temperate freshwater habitats, brown trout (*Salmo trutta*) appear to be consistent with Bergmann's rule (L'Abée-Lund et al. 1989) although a study of eighteen species of freshwater fishes suggests that in general, they express the opposite trend to that observed here with a decrease in adult body size within species as latitude increases (Belk & Houston 2002). Slower growth in colder waters was suggested as a reason for this trend in freshwater fishes (Belk & Houston 2002). Over the course of an individual's life though, slower growth rate in ectotherms is expected to lead to the attainment of a greater age and larger body size (Atkinson & Sibly 1997). Despite slower growth at colder temperatures in both marine and freshwater fishes, latitudinal variation in resource availability, food intake, predation levels or other environmental factors yet to be determined, are likely to contribute to differences in patterns observed among different aquatic environments (Sibly & Atkinson 1997). Before comparisons can be effectively made, the generality of latitudinal trends in growth characteristics of coral reef fishes needs to be comprehensively assessed by examining latitudinal variation in numerous species from a range of families. Only then can we begin to understand the relative impact of enviromental stoichasticity and life history variation in determing patterns observed.

Sampling artefacts could have contributed in part to the lack of an obvious latitudinal relationship for median size. During the sampling period at Lizard Island very small individuals were absent in the field which caused estimated median size to be slightly higher than expected if more juveniles had been sampled. The median is a more robust measure than the mean though, which would have been strongly affected by concentration of individuals at extremes of the body size distribution. A further contributor to the higher median size in relation to maximum size at Lizard Island is the faster growth of *H. melanurus* at this location so for a given age individuals at Lizard Island were larger than at the other locations.

4.4.3 Longevity

In the presence of an expected positive correlation between size and age of individuals (Peters 1983, Calder 1984), an increase in body size with an increase in latitude should be closely associated with an increase in life-span of individuals. In marine ectotherms studies of squid and pandalid shrimp have indicated a trend towards increased life-span with an increase in latitude (Charnov 1989, Jackson & Moltschaniwskyj 2001). In this study of *H. melanurus* the positive correlation between maximum age and latitude also supports this expectation. When the median age was compared among locations though, a general latitudinal pattern was no longer clear. Median age at Heron Island was the greatest as predicted but Kimbe Bay, Lizard Island and the Palm Islands had very similar median ages. This contrasted with the results for median body size which indicated individuals at Lizard Island were on average over 10mm greater than at Kimbe Bay and the Palm Islands but can be explained by the faster growth of individuals at Lizard Island. If larger collections had been conducted older individuals at some sites may have been found, but as representatives of the largest individuals observed at each site were collected they are also likely to encompass some of the oldest individuals.

The median age of individuals collected at Heron Island was almost twice as great as for the other populations. One possible explanation is that there are fewer potential predators of *H. melanurus* at Heron Island than the other sites. The number of piscivores at Lizard Island is an order of magnitude greater than at One Tree Reef, which is within 20km of Heron Island in the Capricorn bunker group (Caley 1995). It is not known, however, how the density of potential predators varies among the other locations in this study and the influence of predation requires further examination.

4.4.4 Size and age at maturity

Under the assumption that populations at lower latitudes would have more rapid initial growth and reduced longevities, it was predicted that populations at lower latitudes should mature at a smaller proportion of body size and earlier in life than those at higher latitudes (Stearns & Koella 1986, Sinervo & Svensson 1998). Life-spans of individuals were found to be similar at Kimbe Bay, Lizard Island and the Palm Islands and considerably greater at Heron Island. This implies mortality rates at Heron Island are far lower than at the other locations. If mortality levels strongly influence when maturity is attained the individuals at Kimbe Bay, Lizard Island and the Palm Islands would be expected to mature at a similar proportion of maximum size and life-span but maturity should be attained far later at Heron Island (Reznick et al. 1990, Abrams & Rowe 1996, Rochet 1998). From the information available the above prediction is supported to an extent as the proportion of maximum life-span attained at maturity at Heron Island was 9% greater than at Kimbe Bay and at least 12% greater than at the Palm Islands. A lack of immature individuals present at Lizard Island mean comparisons with this location could not be made. Although individuals at Heron Island did mature latest in life relative to maximum life-span, this pattern was not the same when size was considered as individuals had attained a greater proportion of adult size at Kimbe Bay than at Heron Island before maturation. Minimum size of mature individuals at the Palm Islands revealed they matured at a smaller percentage of life-spand and maximum size than at each of the other locations.

4.4.5 Reproductive effort

Despite a steady increase in mean and maximum GSI for individuals between Kimbe Bay and the Palm Islands the low GSI value for those at Heron Island meant there was no evidence overall for an increase in reproductive effort with latitude. Mean gonadosomatic index (GSI) was greatest at the Palm Islands and lowest at Kimbe Bay, there was no significant difference between mean GSI at Lizard Island and Heron Island. New recruits of *H. melanurus* are present throughout the year at Kimbe Bay (Jones G. P. pers. comm.) implying they spawn year-round at this location. At the locations sampled on the Great Barrier Reef, however, spawning is seasonal (females generally spawn between October-December). Therefore, one reason for the low GSI values at Kimbe Bay relative to the other locations, could be that individuals at Kimbe Bay spawn more often throughout the year but invest less energy in each reproductive bout. Such seasonal variation is one problem associated with the use of GSIs to estimate reproductive effort (DeVlaming et al. 1982, West 1990). A more detailed study including information on frequency of spawning and the amount of energy invested in each spawning, is required to identify whether over the course of the year reproductive effort is actually greater at Kimbe Bay than at the other locations.

Numerous ripe females with gonads containing stage five oocytes were found at Kimbe Bay, Lizard Island and the Palm Islands. Only one of the individuals collected at Heron Island had reached this stage of development. This indicates females at this location may not have reached full reproductive potential by late October when collections were made. Although this was accounted for by only comparing GSIs of individuals with gonads in which stage four was the most developed oocyte, it is not known whether the mean GSI of stage four individuals sampled at Heron Island would have been slightly greater if collections were made when the population was fully reproductive. Mean gonadosomatic indices provided no evidence that reproductive effort varies predictably with either latitude of the sampled location, or with the growth characteristics of individuals. This suggests location specific factors are important in determining reproductive effort at each location. Reasons why the population of *H. melanurus* at the Palm Islands is so fecund in comparison with the other sites requires further investigation.

4.4.6 Size and age at sex change

Absolute size and age at sex change did tend to increase with latitude although trends were not entirely consistent. When these characteristics were examined relative to maximum size and age though, any potential latitudinal patterns disappeared. The results for relative size and age at sex change are consistent with those attained for relative size and age at maturity, in that both maturation and sex change occurred at a smaller proportion of adult size and earlier in life at the Palm Islands. Therefore, attainment of maturity and size and age at sex change may be closely correlated within *H. melanurus*. This is expected if individuals at the different locations spend a similar proportion of adult size and life-span as reproductive females. The combination of earliest maturity, greatest reproductive effort and earliest sex change of individuals at the Palm Islands compared to the other locations, could be selected by a common set of extrinsic factors. Such a combination of reproductive traits would be favourable if instantaneous mortality rates were higher at the Palm Islands than at the other locations (Skelly & Werner 1990, Abrams & Rowe 1996). This provides strong evidence that reproductive characteristics of *H. melanurus* are influenced more strongly by local effects, than predictable variation in sea water temperature and the associated changes in body size found along a latitudinal gradient.

4.4.7 Conclusion

The above predictions associated with growth characteristics were generally supported by the results of this study. Although it is commonly considered that reproductive traits should be closely correlated with aspects of growth (eg. Calder 1984, Stearns 1992, Schwarzkopf 1993, Arendt 1997), no covaration between growth and reproductive characteristics was evident in this study. Consequently, despite some support for predictions of latitudinal growth patterns based on life history theory, there was no support for reproductive trends with latitude. A number of different theories have attempted to explain the mechanisms causing covariation in aspects of growth and reproduction, emphasising the influence of selection on different traits (Schwarzkopf 1993, Stamps et al. 1998, Day & Rowe 2002). For example, considering age at maturity, it has been suggested: a) Changes in body size are subject to selection and this causes variation in age at maturity (Highton et al. 1989, Bruce 1996), b) age at maturity is selected by environmental factors and this causes variation in body size (eg. Tilley 1980, Bruce & Hairston 1990) and c) environmental influences on growth rates may determine adult body size and/or age at maturity (Berven et al. 1979, Camp & Marshall 2000). Indeed, body size and reproductive traits such as size and age at maturity may evolve independently but appear to covary because they are modified by the same selective forces (Millar & Hickling 1991, but see Winkler & Wallin 1987, Caley *et al.* 2001). Although the theories vary, they are based on an expectation of covariation between growth rate or body size and reproductive traits. The lack of such covariation in *H. melanurus* implies selection on reproductive traits in response to environmental factors is independent of selection on growth characteristics.

This study illustrates the considerable phenotypic plasticity of *H. melanurus*. However, species may respond to environmental gradients and local environmental influences in different ways. For example, a study of a pomacentrid, *Pomacentrus moluccensis* demonstrated a highly significant increase in longevity with increased latitude but no expected covariation with other traits including size and age at maturity, and reproductive effort. In addition temperature appeared to have no effect on growth rate (Bray 2001).

Local factors can play an important role in determining patterns of growth and reproduction within *H. melanurus* and can confound latitudinal trends. A range of potential influences on growth and reproduction have been documented in fishes, including density-dependent factors such as resource limitation (Jones 1986, Clifton 1995, Gust et al. 2002), social interactions (Robertson 1972, Jones 1987, Forrester 1990, Lutnesky 1994, Nakashima et al. 2000) and predation (Reznick et al. 1990, Olson 1996, Rochet 1998). Other environmental factors such as seasonality may also be influential (Clifton 1995, Arkhipkin et al. 2000, Jackson & Moltschaniwskyj 2001, Yamahira & Conover 2002).

The potential for variable responses among reef fish species and variation in environmental influences on a local scale, highlights the necessity to replicate similar studies in a greater range of species and geographic locations. Replication of sampling at a greater number of sites along a latitudinal cline will facilitate the use of regression techniques to identify the importance of latitude as a predictor of life history variation. Such studies will help elucidate whether a general latitudinal trend in life history tactics of coral reef fishes is prevalent and if certain responses to environmental gradients such those found along latitudinal clines are species specific. In addition they could clarify whether temperature is an influential factor in determining latitudinal clines in life histories of reef fishes, or if a range of other factors such as abundance of food and predation rates play an important, but as yet undetermined, role.

CHAPTER 5: Body size and the ecology of reef fishes - Implications for species abundance, diversity and habitat use

4.1 Introduction

Body size and associated life history strategies are of fundamental importance in explaining ecological patterns within and among species (Peters 1983, Calder 1984, Schmidt-Neilsen 1984). At the population level, the greater reproductive effort of individuals of smaller species promotes higher abundances (May 1978, Marzluff & Dial 1991). Species richness and body size also appear to be intrinsically related, with greatest species richness found in small to intermediate size classes (Griffiths 1986, Morse 1988, Barlow 1994, Brown 1995, Siemann et al. 1996). It has also been suggested that habitat versatility within species is governed by body size and smaller species tend to exhibit greater habitat specificity than larger species (Wasserman & Mitter 1978, Gaston & Lawton 1988, Ziv 2000). However, the relationships among body size, abundance, species richness and versatility may be complex, as abundance-diversity (Morse 1988, Siemann et al. 1996), abundance-habitat specificity (Griffiths 1986) and diversity-habitat specificity (Marzluff & Dial 1991, Ziv 2000) are intrinsically related to one another (Harvey & Lawton 1986). Most studies quantifying covariation between body size and ecological patterns have focussed on terrestrial taxa (Maurer et al. 1992). In marine communities the relationships between body size and these ecological characteristics have received little attention (but see Warwick & Clarke 1996, Munday & Jones 1998).

Covariation between abundance and body size was highlighted when Damuth (1981) illustrated a linear decline in abundance with an increase in body size among mammals. A relationship between body size and population abundance or density has now been described for a range of terrestrial organisms, especially birds and insects (eg. Griffiths 1986, Blackburn et al. 1990, Blackburn et al. 1993, Nee et al. 1991, Blackburn & Lawton 1994, Marquet et al. 1995, Hodkinson & Casson 2000). These studies indicate that species in the smallest size classes are generally not the most abundant. Species of small to intermediate size can be rare or common with maximum abundances peaking in these size classes. Large body size is always associated with reduced abundance. Therefore, the overall relationship tends to be triangular (Blackburn et al. 1992, Blackburn & Lawton 1994, Marquet et al. 1995). Factors including spatial scale and methodology of the study (Blackburn 1997) and phylogeny (Nee et al. 1991, Cotgreave & Harvey 1992, Cotgreave 1995, Marquet et al. 1995), have the potential to influence whether linear, triangular or no relationships are identified between body size and abundance. This illustrates the need to examine body size-abundance patterns in a wider range of organisms and on different spatial scales.

Species richness is predicted to be intrinsically related to body size and follow from body size-abundance relationships (Morse 1988, Blackburn et al. 1990, Siemann et al. 1996). About 1.5 million plant and animal species are currently classified globally, more than 70% of these are animal species (May 1988) and most of these are small (0.5-1cm), (May 1986, Fenchel 1993). In a diverse range of terrestrial taxa, species richness within different size classes typically exhibits a right log-skewed or log normal distribution. This indicates there are few very small species and the greatest species richness is in small to intermediate size classes, this is followed by a gradual decrease in species richness with an increase in body size (May 1986, Maurer et al. 1992, Finlay et al. 1996, Loder 1997, Hodkinson & Casson 2000). Local species richness is determined by a balance between local extinction and immigration of species to an area (Siemann et al. 1996). Small species have greater dispersal capabilities than larger and tend to have more cosmopolitan distributions, so immigration rates of small species to a locality may be higher (Gaston & Lawton 1988, Dial & Marzluff 1988, Brown 1995). As the smallest and largest species are expected to have low abundances, their chances of local extinction due to stochastic population fluctuations are higher, reducing local species richness in these size classes (Siemann et al. 1996, Dial & Marzluff 1988, Marzluff & Dial 1991). In addition, as species richness in small to intermediate size classes is expected to be greatest, there is an increase in the chances of dominating species appearing in these size classes and attaining high abundances (Blackburn et al. 1990, Finlay et al. 1996).

An alternative explanation for smaller species being more speciose than larger, is that smaller species tend to be more habitat specific and a range of habitats can support a greater number of small than large species (Hutchinson 1959, May 1978, Price 1984, Pyron 1999). Therefore, when competition for resources among individuals is high the scope for niche segregation among habitats is greater for smaller species, thus more small species can be accommodated in communities (Brown 1995). Although it is widely expected that larger species are more likely to utilise a greater range of habitats than smaller ones, very few studies have demonstrated this empirically. A recent model has provided theoretical support for the assumption (Ziv 2000). Ziv (2000) illustrated that habitat specificity scales negatively with body size in Eutherian mammals and suggested that smaller species should be habitat specialists persisting mainly in high quality habitats. In contrast, larger species should be habitat generalists being able to use high and low quality habitats (Hutchinson & MacArthur 1959, Ziv 2000). The opposite view, that larger species use a reduced range of habitats, has also been argued (Morse 1974). Clearly, more work on the relationship between body size and habitat speciailisation is necessary to evaluate these alternatives.

To clarify patterns of habitat use by species of different body size more taxa need to be examined encompassing species occupying a range of diverse habitats, including the marine environment. Studies of rocky intertidal communities and benthic marine species suggest relationships between body size, local abundance and species richness observed in terrestrial organisms may be repeated in marine communities (Marquet et al. 1990, Warwick & Clarke 1996). If processes governing habitat use are similar in terrestrial and marine organisms it can be predicted that habitat specificity also scales negatively with body size in marine taxa and smaller species utilise a reduced range of microhabitats. The relationships among body size, abundance, diversity and habitat versatility in marine assemblages are currently poorly understood.

The association between body size and abundance has recently been examined in reef fish communities at a number of locations (Munday & Jones 1998). The pattern found was similar to that in many terrestrial taxa, potential abundance peaking at a small-intermediate body size from which a decrease or increase in size was associated with reduced abundance. However, these patterns were described for whole reef assemblages. If taxonomic level can influence observed abundance-body size relationships (Nee et al. 1991, Cotgreave & Harvey 1992, Marquet et al. 1990), it is important to also examine them at lower taxonomic levels such as species within a single family to ascertain the consistency of overall relationships between size and abundance. Body size-species richness patterns found in coral reef fishes to date parallel size frequency distributions in terrestrial taxa (Munday & Jones 1998, Pauly 1998). Pauly (1998) indicated species richness of tropical fishes peaks at a body length of about 75-125mm which corresponds with the most speciose size range for tropical fishes associated specifically with coral reefs (Munday & Jones 1998). It can be expected though that species richness of fish communities on coral reefs is skewed to the right when plotted against body size, as two of the most diverse reef fish families are the Gobies (Gobiidae) and Blennies (Blennidae), both of which have a mean species body size of less than 50mm (Randall et al. 1997, Munday & Jones 1998). It has not been ascertained if similar patterns are evident on an intrafamilial level.

The complex topography and abiotic and biotic diversity of coral reefs provides numerous potential microhabitats for small and large species (Sale & Douglas 1984, Hixon & Beets 1993). Indeed it has been argued that the coexistence of reef fishes is promoted when there is a wide extent of size differences among species (Smith 1978). Variation in habitats in terms of provision of prey refuges or food resources are likely to be of considerable importance for the community dynamics of coral reef fishes (eg. Anderson et al. 1989, Caley & St John 1996, Clarke 1996, Jones & Syms 1998) as an increase in available microhabitats augments possibilites for habitat specialisation. If small reef fish species are more adaptable to this strategy than larger species, then the observation that larger species use a broader and more diverse range of microhabitats than smaller species should be repeated in coral reef fishes.

Inter-relationships among body size, microhabitat use and depth range of coral reef fishes have rarely been considered in the literature (but see Bean et al. 2002). Habitat types are not evenly distributed among reef zones. For example, the reef crest may be dominated by a few fast growing coral species and species diversity can increase with depth to about 20m (Huston 1994). The decrease in light availability and wave energy with depth results in considerable vertical gradients of productivity and disturbance (Huston 1994, Fulton 2001). Therefore, the type, abundance and quality of food resources such as macrobenthic organisms which are commonly consumed by reef fishes (McCormick 1995), can vary with depth. Utilisation of greater depth ranges increases the pool of resources available to an individual. It is therefore predicted here that larger species which are expected to have greater manoeuvrability over the reef and utilise a greater range of microhabitats, should have greater depth ranges than smaller species. In addition, as light becomes attenuated with an increase in depth, the structural diversity of corals gradually decreases changing from branching morphologies to more plate-like, lamellar and massive forms. Deeper environments with reduced topographic complexity may be avoided by some smaller species due to increased susceptibility to predation. Smaller species reliant on microhabitats with high topographic complexity (Warburton 1989), are therefore more likely to be restricted to shallower depths and have small depth ranges.

The main aim of this chapter was to determine relationships between body size and a) abundance, b) species richness, c) microhabitat use and d) depth range, in wrasses (Pisces: Labridae) on coral reefs. Wrasses encompass the largest range of body sizes of any reef fish family and the wrasse family is the second most speciose fish family on coral reefs. It is an ideal group in which to assess relationships between body size and species diversity at low taxonomic levels. Specific predictions are as follows: 1) Smallest species are not the most abundant, small to intermediate sized species are more likely to be common and very large species consistently have low abundance (Figure 5.1a); 2) Body size-species richness distributions are right skewed or normal on a logarithmic scale, with many species of small to intermediate size and low numbers of very small or very large species (Figure 5.1b); 3) Smaller species are associated with a smaller range of microhabitats than larger species and tend to be more habitat specific (Figure 5.1c); 4) Larger species have greater depth ranges than smaller (Figure 5.1d).

5.2 Materials and methods

5.2.1 Study locations

Relationships among body size, abundance and species richness were examined at four widely separated geographic locations: 1) Kimbe Bay, Papua New Guinea (PNG) (5°33'S, 150°08'); 2) Lizard Island, north Great Barrier Reef (GBR) (14°39'S, 145°27'E); 3) Orpheus and Pelorus Islands (18°33'S, 146°29'E) (these are neighbouring islands in the Palm Island group. Abundance was estimated for species at Orpheus Island and species richness was derived from the observation of species at Pelorus Island); and 4) One Tree Island, south GBR (23°29'S, 152°04'E), which lies less than 20km SE of Heron Island (see Figure 4.2, Chapter 4). To identify patterns among body size, habitat use and depth range, detailed observations of wrasses were conducted at each location with the exception of One Tree Island. Observational studies at Kimbe Bay, Lizard Island and Pelorus Island took place over three-week periods in April 2001, November 2000 and July 2000, respectively.

5.2.2 Abundance

Estimates were made of abundances of species at Kimbe Bay, PNG and Lizard Island, GBR. Abundances at Orpheus Island and One Tree Island were obtained from

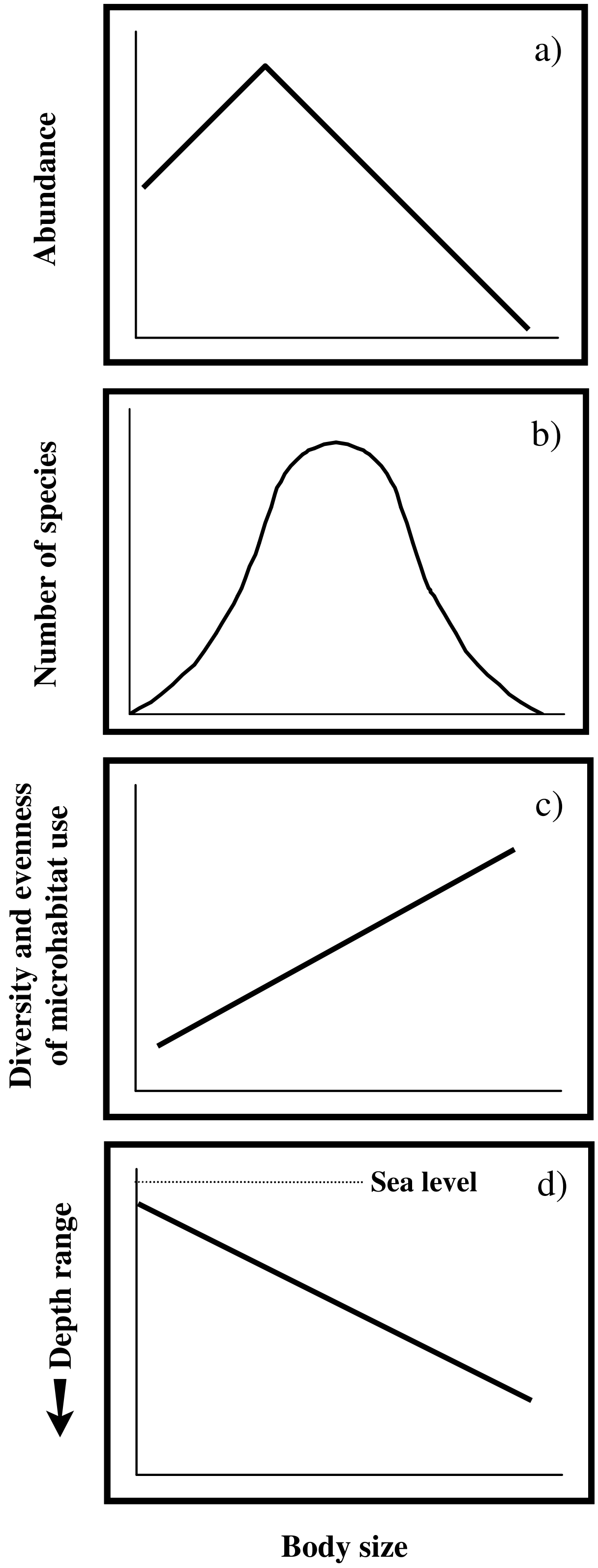

Figure 5.1: Conceptual models illustrating predicted relationships between body size and abundance, species richness, habitat use and depth range: a) Smallest species are not the most abundant, abundance peaks at intermediate body size and the largest species have low abundances; b) There are more small to intermediate sized species than very small or very large species; c) Number of microhabitats used and diversity and evenness of microhabitat use, increases with an increase in body size of species; d) Depth range increases with an increase in body size of species.

the literature (Eckert 1985, Manthachitra 1996). All abundance estimates were derived using visual transects and a range of transect sizes and methods were employed.

Wrasses were counted using the instantaneous visual census technique (Fowler 1987) which is very effective at quantifying abundances of wrasses including the more cryptic and smaller species (Ackerman & Bellwood 2002). At Kimbe Bay four replicate 50m × 4m transects were used for censusing. Eight separate reefs were surveyed with four replicate transects randomly laid out in each of four depth strata (Reef flat, 2m, 6m, 10m). At Lizard Island, species abundance was estimated using 30m × 3m transects. Eight separate locations were surveyed with ten replicate transects laid out in each of ten depth strata (1.5m to 28.5m depth at 3m depth intervals), (Syms 1998). Estimates of abundance of wrasses at Orpheus Island were obtained from Manthachitra (1996). Nine sites around Orpheus Island were sampled using a 30m × 5m line transect with six replicates per site, these were laid at random in the middle reef slope and reef edge. Species abundance was calculated from ten independent sampling times at 2-3 month intervals between December 1993 and December 1995. Two of the census sites were surveyed again in 2002 which verified that abundance estimates were similar over a large temporal scale. Abundance information for wrasses at One Tree Island was derived from Eckert (1985). Individuals were censused along five 50 m × 2m transects, laid at random within five sites covering a range of habitats available at One Tree Reef. In total six censuses took place, each at six monthly intervals over a 30 month period from November 1981 to April 1984.

Although variation in transect sizes influences absolute abundances of species recorded at each location, it does not affect the shape of the body size-abundance relationship which was the main aspect examined. To facilitate the comparison of abundances of species among locations, plots represent logarithmic values of the number of individuals of each species observed per $100m^2$.

Maximum sizes of species at each location were used to examine body size-abundance relationships and other body size-related relationships in this study. These were obtained from observations of wrasse species at each location. To assess accuracy of body size estimates, fish templates with 1cm intervals from 3-60 cm in length were suspended in the water prior to a dive and the diver estimated the size of ten random templates from a range of distances (Gust et al. 2001). The dive commenced once confident accurate size estimates were obtained. Comparison of estimated sizes with actual size of templates, revealed estimates were usually accurate to within ±10% of fish length and had low standard errors. This was considered acceptable to identify general patterns across the size range of species examined here.

The majority of studies examining relationships between body size and abundance express body size as mass and not length. Therefore, body length of wrasses was converted to body mass. A power curve with the form $W=aL^b$ (where W is mass, L is fork length, a is a multiplicative factor and b an exponent) was fitted to scatter plots of maximum fork length vs. body weight for six wrasse species covering a ten fold size range (Table 5.1). The average value for a and b among species for this relationship was then used to derive estimates of body weight from fork length for observed species. Although values of a and b were available for the *Bodianus* spp. and *Halichoeres melanurus*, these were not included as growth in these species is not characteristic of most wrasses (Chapter 2, Section 2.3.6).

Table 5.1: Mean parameter values derived from fitting the power curve $W=aL^b$ (W is mass, L is fork length, a is a multiplicative factor and b an exponent) to describe the relationship between fork length and mass of seven wrasse species. Mean values of a and b were used to estimate maximum mass of all species present at each location based on maximum body size estimates.

Species	***a***	***b***	**r^2**	**size range**
Pseudocheilinops ataenia	0.0000290	2.823	0.979	13-39
Pseudocheilinus hexataenia	0.0000300	2.914	0.993	14-57
Pseudochelinus evanidus	0.0000156	3.107	0.951	24-65
Choerodon fasciatus	0.0000127	3.097	0.974	115-224
Epibulus insidiator	0.0000202	3.016	0.985	99-278
Cheilinus fasciatus	0.0000200	2.960	0.979	85-285
Hemigymnus melapterus	0.0000240	2.951	0.986	61-293
Mean values	**0.0000216**	**2.982**		

In accordance with other studies examining body-size abundance relationships, ordinary least-squares regressions were fitted to the upper and lower bounds of the data set. The upper bound is the ordinary least-squares regression line fitted to data points indicating the decline in abundance with an increase in body size. The lower bound is the regression fitted to data points indicating a decrease in abundance with a decrease in body size. Data points to which regressions were fitted were selected by modifying the method of Blackburn et al. (1992). For a given body weight, the data point chosen to include in the regression was that which represented the highest abundance for species. Species which had a very low or high abundance for their weight, which would not accurately represent the lower or upper bound were omitted from the regression.

5.2.3 Species richness

All species recorded in observation surveys at Kimbe Bay, Lizard Island and Pelorus Island were categorised by their maximum observed body size and placed into a 50mm size interval. A histogram was produced for each location indicating the number of species (as a percent of the total number of wrasses species recorded at the location) occuring within each size interval, to indicate the size frequency distribution of species. Histograms were also produced indicating absolute values of different species in different size classes at each locality. Observational studies (Section 5.2.4) were not conducted at One Tree Island. Therefore, the community of wrasse species found at this location was obtained from Eckert (1985) and size information was obtained from Russell (1983).

5.2.4 Habitat use and depth range

Information for habitat use of species and depth zonation was attained visually by conducting observations of adults of all wrasse species encountered at Kimbe Bay, Lizard Island and Pelorus Island. Observation dives commenced at the base of the reef slope and continued in a systematic search up the reef slope. Some time was spent at the reef crest to ensure all species in this zone were recorded, then the dive continued along the reef flat and ended on the back reef. The following information was recorded for each wrasse individual observed: Species, size of individual, depth when first sighted and nearest microhabitat. This was repeated until as many individuals as possible were observed for each species. When 100 independent observations were recorded no more data were collected for that species. If it was suspected an individual had been previously recorded then it was not recorded again. On occasions where many individuals of one species were aggregated in one area, only observations of a few individuals for that aggregation were used so it did not bias overall observations for that species.

Microhabitats present at each site were divided into 32 categories representing abiotic and biotic microhabitats present on coral reefs (Table 5.2). Species were observed more commonly on some microhabitats than others. It should be noted that specialisation of a species in one or more habitats could not be confirmed without relating microhabitat use to microhabitat availability in the field. Specificity of habitat use could be compared among species though, as accessibility to different microhabitats was similar among different species.

Using information from observations, the prediction that smaller species are more habitat specific than larger species was tested. Firstly, the number of microhabitats occupied by species of different sizes was examined in relation to body size. Identification of the number of microhabitats used by a species, however, provided no evidence of how individuals were spread throughout these microhabitats and whether some microhabitats were commonly or rarely used. Therefore, the distribution of individuals of species throughout the microhabitats occupied was assessed. This was achieved by calculating the diversity and evenness of the microhabitats associated with different species using Simpson's diversity index (Equations 5.1, 5.2), (Begon et al. 1996). The diversity measure incorporates information for both the number of microhabitats used and how much each microhabitat was used (Equation 5.1, where P_i is the proportion of observed individuals associated with the ith habitat).

$$\text{Diversity } (D) = \frac{1}{\sum_{\mathrm{i=1}}^{\mathrm{S}} P_i^2} \qquad \text{(Equation 5.1)}$$

The maximum value for the diversity index is the same as the total number of microhabitats used by a species. The evenness with which different microhabitats were used was determined by expressing the diversity index as a proportion of the maximum possible value for diversity if individuals were evenly distributed among all microhabitats (Equation 5.2, where D is the diversity index and S is the number of different microhabitats used by the species.). Therefore, this value lies between 0 and 1 with species using microhabitats more evenly having an evenness value closer to 1 (Begon et al. 1996).

$$\text{Evenness } (E) = D \times \frac{1}{S} \qquad \text{(Equation 5.2)}$$

Table 5.2: The different categories into which microhabitats were divided

Substrate	Microhabitat type
Sand	Coarse sand
	Fine sand
Rubble	Gravel
	Gravel on bare rock
	Rubble
	Rubble/gravel with turf
	Sediment covered rubble
Rock	Bare rock
	Coralline rock
	Sand covered rock
	Turf rock
Algae	Macroalgae
Sponge	Sponge
Soft Coral	Soft coral
Hard Coral	Anacropora
	Bushy coral
	Columnar coral
	Corymbose coral
	Dead branching coral
	Encrusting coral
	Finger coral
	Foliose coral
	Massive coral (live and dead): not including massive form of Porites
	Montipora
	Plate coral
	Pocillopora
	Porites (massive and other forms)
	Staghorn
Other	Ascidian
	Gorgonian
	Halimeda
	Pavona

Depth estimates of all individuals were used to test the prediction that larger species have greater depth ranges than smaller species. Maximum depth of species was defined as the greatest depth at which an individual of that species was observed, minimum depth was obtained from the shallowest individual observed and depth range of species was estimated by subtracting minimum from maximum depth. Maximum body size of species was then plotted against the depth range to identify whether a consistent relationship was present among locations. Habitat use measurements and depth information is not presented for species with less than 30 independent observations. (Table 5.3).

Table 5.3: Number of individuals observed within species at each study location. Those species for which less than 30 individuals were observed were not included in analyses of information for microhabitat usage and depth range.

	Number of species at location:		
Number of individuals observed	**Kimbe Bay**	**Lizard Island**	**Pelorus Island**
0-9	3	14	11
10-19	5	3	1
20-29	0	4	1
30-39	1	5	4
40-49	1	2	2
50-59	0	3	3
60-69	0	0	1
70-79	2	0	1
80-89	0	2	0
90-100	29	21	10
Total number of species	41	54	34
Number of species included in analyses (ie. over 30 observations)	33	33	21

5.3 Results

5.3.1 Prediction 1: Intermediate sized species can reach greater local abundance than very small or large species

As predicted, logarithmic relationships between body weight and abundance approximated a triangular pattern with species of intermediate size usually reaching the greatest local abundance (Figure 5.2, a-d). The overall strength of the relationship varied among locations, but at each locality most species were encompassed within the upper and lower bounds of the triangle (Figure 5.2, a-d). Abundances peaked in species with a small-intermediate body size and at each location extremely small or large species seldom reached a high local abundance. The triangular relationship was approximated most strongly at Kimbe Bay and One Tree Reef. Abundance estimates were available for the greatest number of wrasse species at these two locations. Although the relationship was consistently triangular, the shape of the triangle created

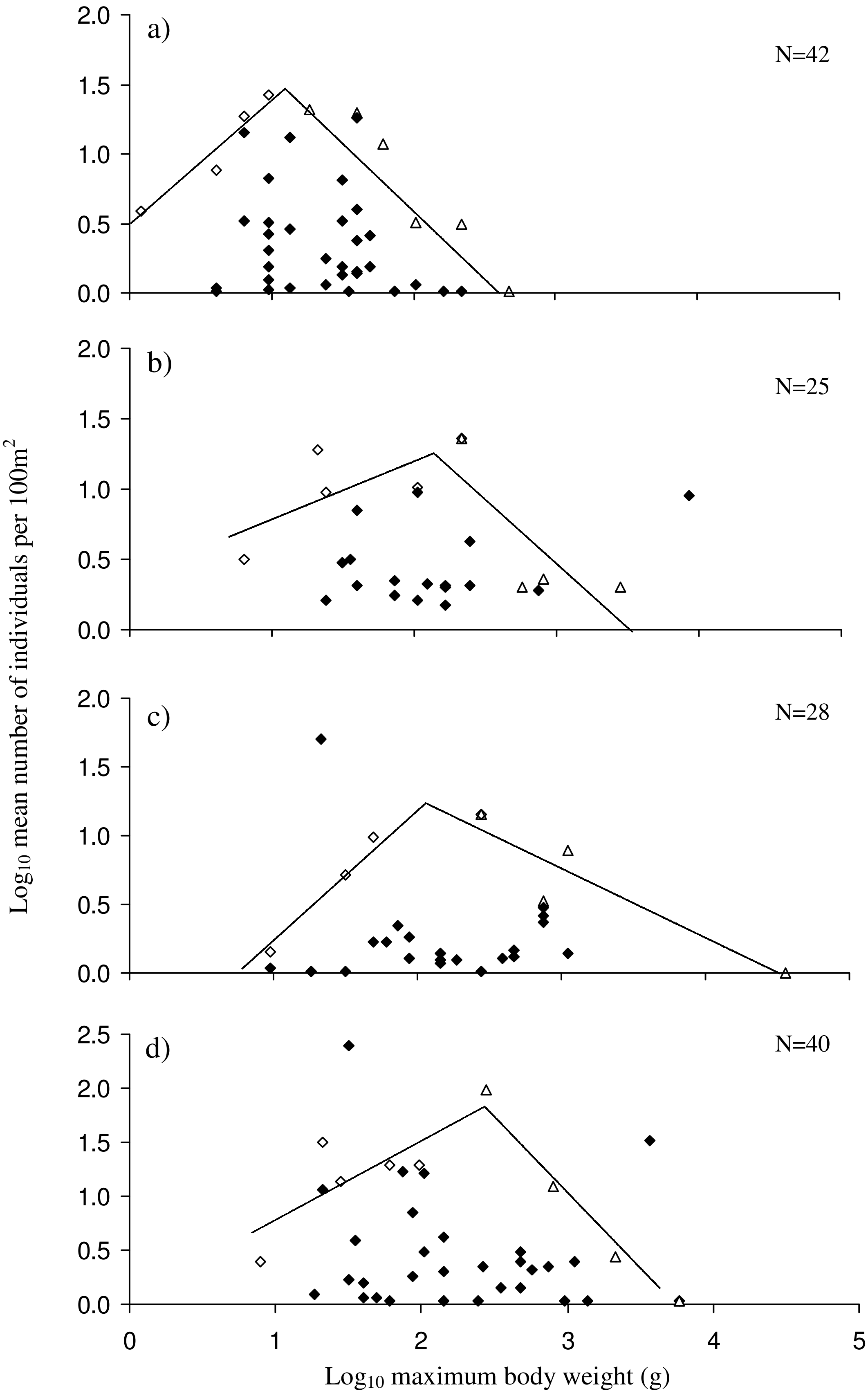

Figure 5.2: Log maximum body weight versus log abundance of wrasse species: a) Kimbe Bay, PNG; b) Lizard Island, north GBR; c) Orpheus Island, mid GBR; d) One Tree Island, south GBR. Data points used to fit regression to lower bound (open diamonds) and upper bound (open triangles) are indicated.

by joining regression lines of upper and lower bounds varied among locations (Figure 5.2 a-d). There was considerable difference among locations in the slopes of the regression lines which defined the upper and lower bounds. Positive slopes of the lower bound ranged from 0.41 to 0.95 and slopes of the negative upper bound varied between –0.49 and –1.48 (Table 5.4).

The triangular relationships appeared to shift to the right in locations supporting larger species. For example, at Kimbe Bay where average size of species was smaller than at the other locations, small species reached greater absolute abundances than equivalent sized species at the other locations. In contrast, the largest species at Kimbe Bay were less abundant than similarly sized species at the other localities. At three of the locations one or two species did not fit in with the overall relationship as their abundances were considerably higher than expected for their body size.

Peak abundances for wrasse species were similar among locations (ie. abundance corresponding to the point at which lower and upper bounds intersected). Peak abundance ranged from 18 individuals per 100m^2 at Lizard Island and Orpheus Island to 50 individuals per 100m^2 at One Tree Island (Figure 5.2 a-d), although one or two species at Orpheus Island and One Tree Island had abundances greater than those estimated using the intersection method. The species size corresponding with a peak in abundance was smallest at Kimbe Bay (88 mm FL) and was similar in the three localities supporting larger species (180-220 mm FL).

Table 5.4: Least squares regressions for lower bound slope (LBS) and upper bound slopes (UBS), describing the relationship between log body size and log abundance at four locations: Slopes and r^2 values for upper and lower bounds are provided.

Location	**LBS**	$r^2_{\mathrm{(LBS)}}$	**UBS**	$r^2_{\mathrm{(UBS)}}$
Kimbe Bay	0.95	0.938	-0.99	0.915
Lizard Island	0.41	0.538	-0.87	0.604
Orpheus Island	0.67	0.851	-0.49	0.827
One Tree Island	0.70	0.485	-1.48	0.978

5.3.2 Prediction 2: Species richness peaks in small to intermediate size classes and there are relatively few very small or very large species

The prediction that body size-species richness distributions would have a right-log skewed or log normal distribution was supported at all locations, with the latter being the best descriptor of relationships observed (Figure 5.3). Smaller size classes were usually more speciose than larger size classes except for the smallest size classes which contained few species. The number of species in smaller size classes was greater at Kimbe Bay than at the other locations.

The most speciose size class at Kimbe Bay contained slightly more species than at Lizard Island and considerably more species than at Pelorus Island or One Tree Island despite a similar total number of species among locations (Figure 5.4). The largest species observed at Kimbe Bay only attained a maximum length of 300mm and Kimbe Bay was the only site at which the species reaching a maximum size of less than 100mm were most diverse. At the remaining sites the size class representing most species was slightly larger (105-150mm).

5.3.5 Prediction 3: Larger species use a greater range of microhabitats than smaller species and are less likely to exhibit microhabitat specificity

Species varied considerably in the number of microhabitats used. There was support for the prediction that larger species tend to use a greater number of microhabitats than smaller species. This was provided by the significant positive slopes of lower bounds fitted to plots of the number of microhabitats used by species at Kimbe Bay ($F_{1,6}$ = 12.71; p=0.012), Lizard Island ($F_{1,9}$ = 95.52; p<0.001) and Pelorus Island ($F_{1,7}$ = 32.24; p=0.001), (Figure 5.5). There was similarity in the general pattern observed among locations, despite considerable variation in the range of body sizes at different localities. The overall relationship was triangular indicating that the larger species for a given location, consistently associated with numerous microhabitat types. Use of either a restricted range, a very wide range of microhabitats or a range between these two extremes was equally viable among smaller species and the range of microhabitats used varied greatly among them. For example, at Kimbe Bay, one species reaching 80mm FL associated with the greatest number of microhabitats at that location (24), while another species reaching this size used the lowest number (6). On average,

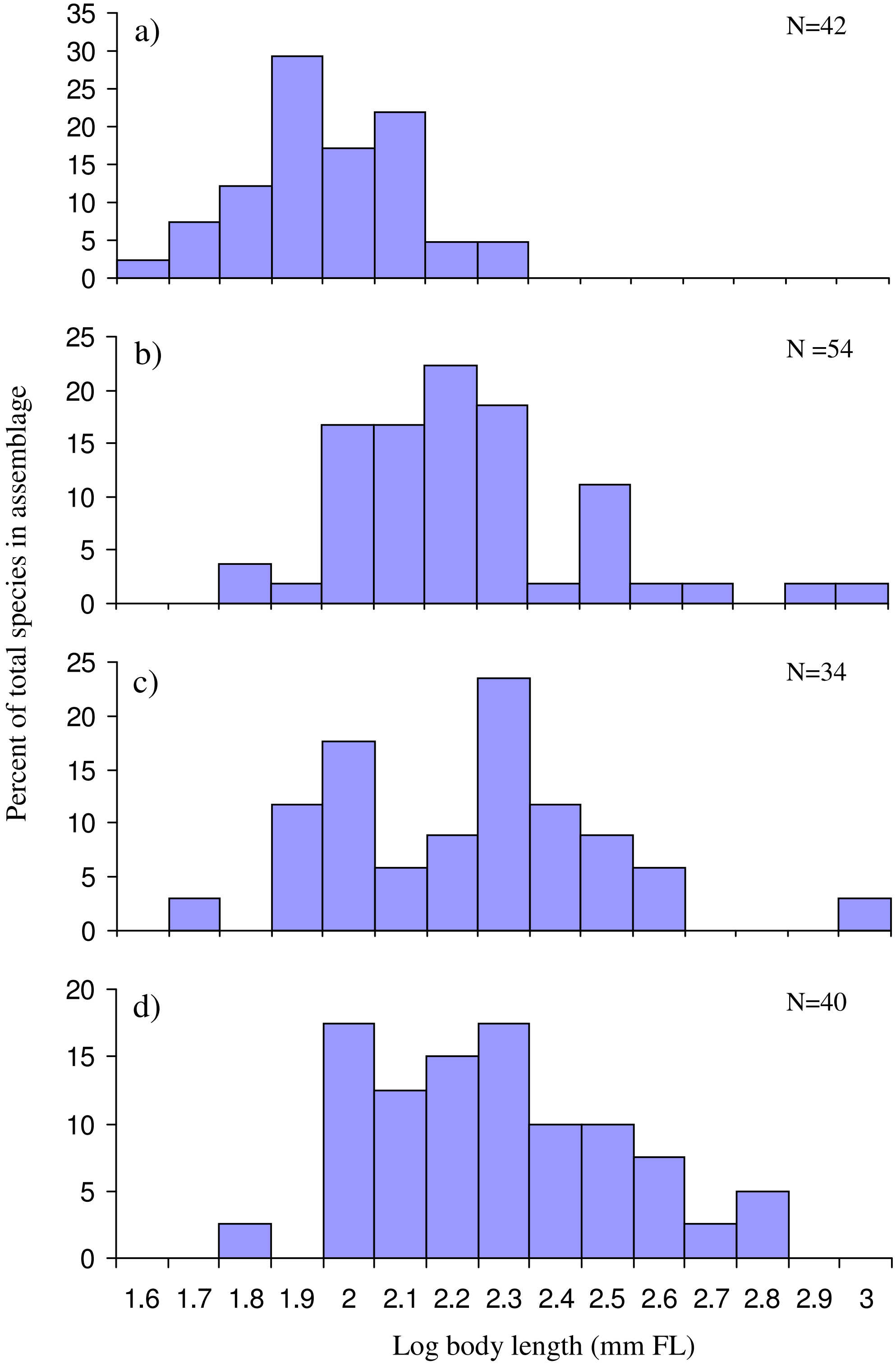

Figure 5.3: Histograms illustrating the percentage of wrasses species found in different size classes (log body length), at four locations: a) Kimbe Bay, PNG; b) Lizard Island, north GBR; c) Pelorus Island, mid GBR; d) One Tree Island, south GBR. N = number of species

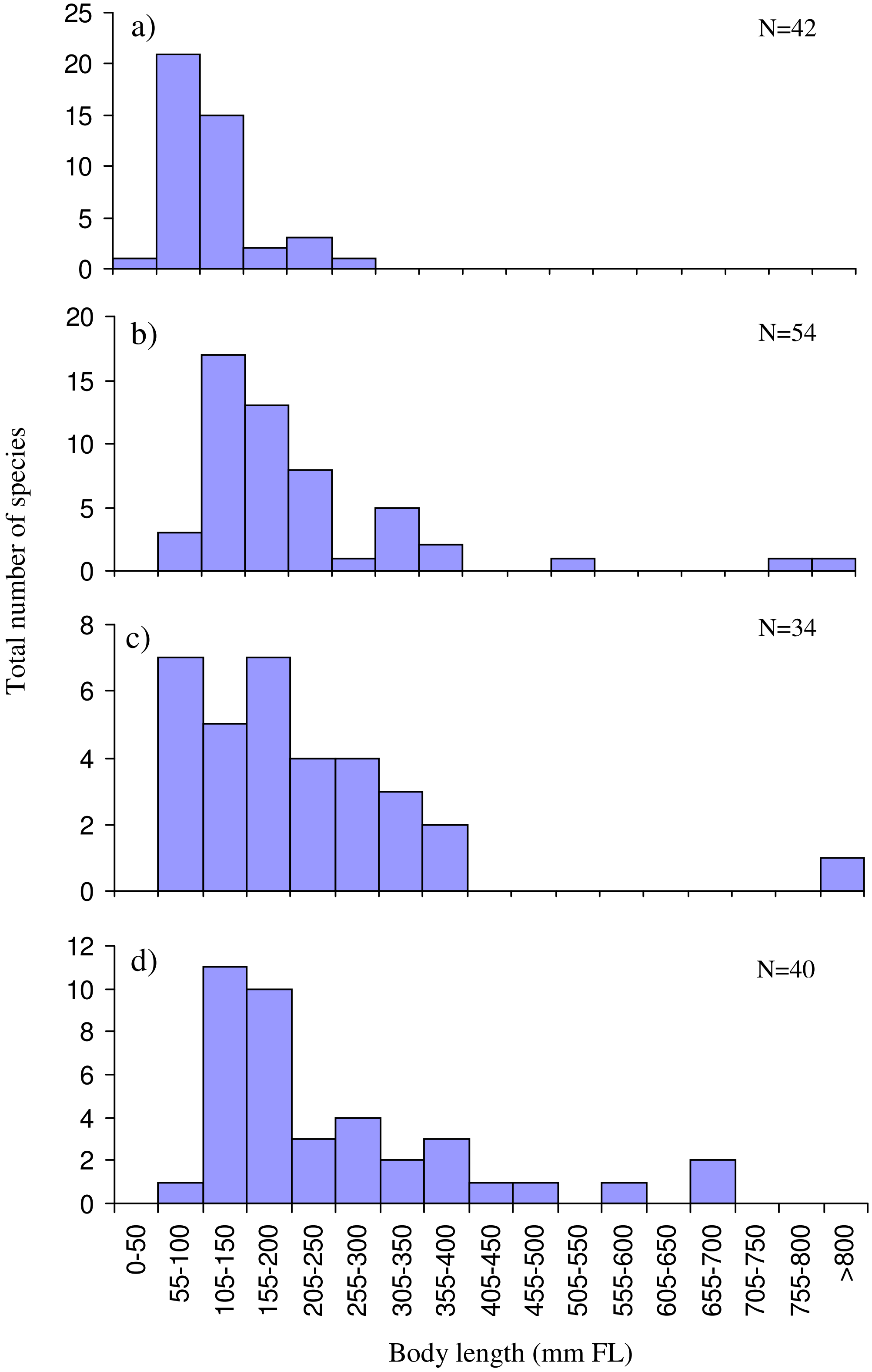

Figure 5.4: Histograms illustrating the total number of wrasse species found in different size classes (body length), at four locations: a) Kimbe Bay, PNG; b) Lizard Island, north GBR; c) Pelorus Island, mid GBR; d) One Tree Island, south GBR. N = number of species.

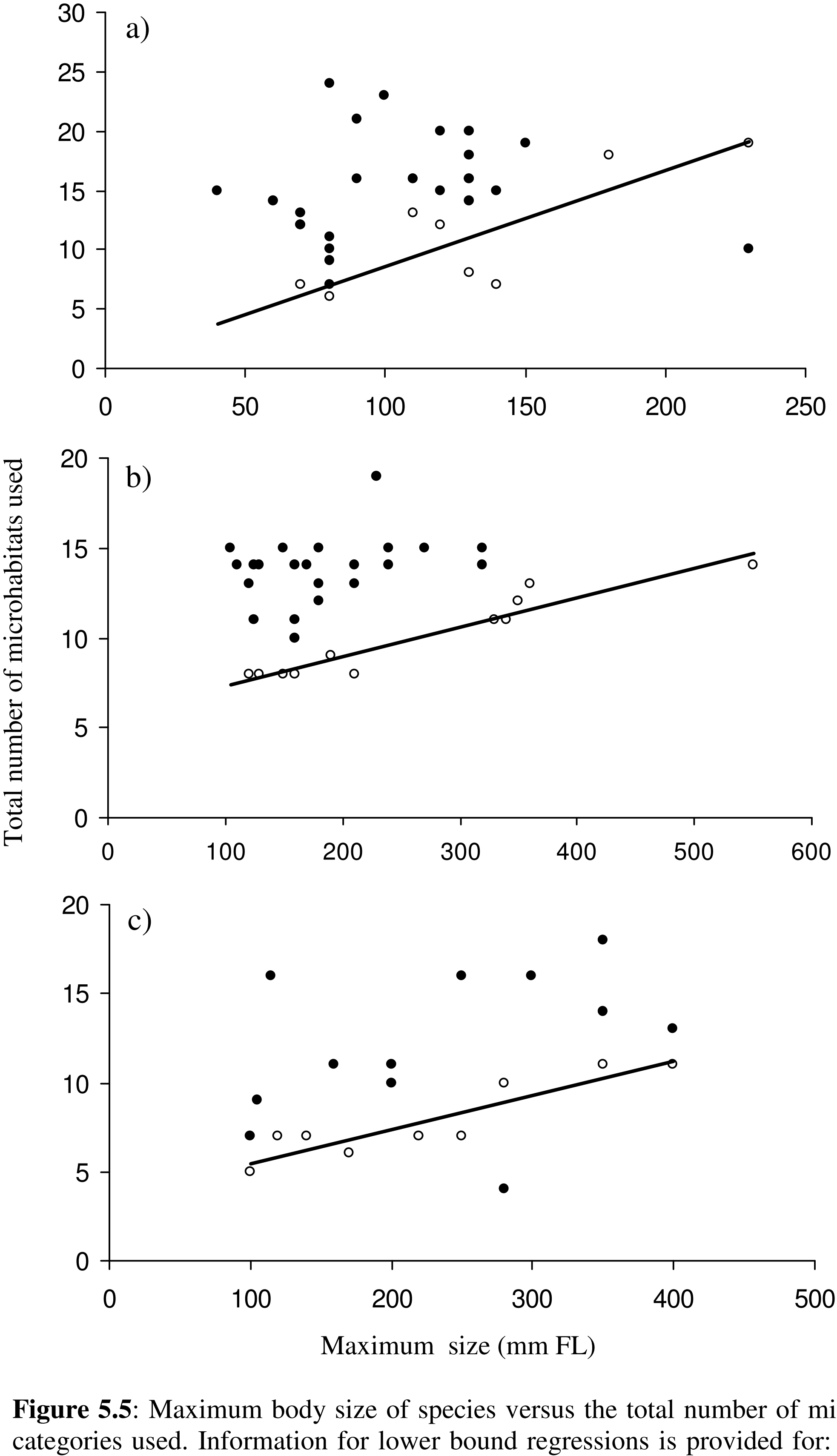

Figure 5.5: Maximum body size of species versus the total number of microhabitat categories used. Information for lower bound regressions is provided for: a) Kimbe Bay, PNG (y=0.081x + 0.560, r^2=0.679), b) Lizard Island, north GBR (y=0.0163x + 5.724, r^2=0.914), c) Pelorus Island, mid GBR (y=0.019x + 3.562, r^2=0.822). Open circles are data points to which lower bound was fitted. Plot only includes species for which over 30 individuals were observed.

species at Kimbe Bay appeared to use a greater range of microhabitats than at Lizard Island and Pelorus Island.

Calculation of diversity indices for species at each location implied larger species were generally associated with a greater diversity of microhabitats than smaller species. The pattern attained at each location was triangular, the lower bound of which was described by a significant regression with a positive slope at each location (Kimbe Bay: $F_{1,6}$=36.24; p=0.001, Lizard Island: $F_{1,11}$=57.31; p=<0.000, Pelorus Island: $F_{1,7}$=5.59; p=0.049), (Figure 5.6). The triangular relationship attained suggests that on average larger species tend to use a greater diversity of microhabitats than smaller species. The diversity of habitat use of smaller species varied greatly as they had either very low or very high diversity indices or values lying in between these extremes. In general, the diversity of microhabitats used by species was greatest at Kimbe Bay, slightly lower at Lizard Island and lower still at Pelorus Island. In addition, the overall relationship at Pelorus Island appeared to be a lot weaker than at Kimbe Bay or Lizard Island.

Relationships attained for evenness of microhabitat use in relation to size were very similar to those attained for diversity indices (Figure 5.7). At Kimbe Bay and Lizard Island the observed pattern was triangular and defined by significant positive lower bounds (Kimbe Bay: $F_{1,5}$=34.71; p=0.002, Lizard Island: $F_{1,9}$=30.01; p=<0.000). At these locations there was evidence that larger species tended to be spread more evenly among the microhabitats they used than the smaller species. The smaller species formed a continuum, from those which used microhabitats to similar extents, to those which exhibited specificity for certain microhabitats. The lower bound of the relationship at Pelorus Island was non-significant ($F_{1,4}$=0.895; p=0.398), there was no apparent relationship between evenness of microhabitat use and body size at this location.

Mean values of the total number of microhabitats used and the diversity and evenness of microhabitat use were compared among species belonging to different size classes at each location. Consistent variation in these values with an increase in size of species was found among locations (Figure 5.8). As size of species increased, the mean number of microhabitats used by species tended to increase. Although increases were consistent, they were quite small (on average an extra one to four microhabitats were used by the largest species in relation to the smallest species). A similar pattern was evident with diversity indices among size classes, there were small but consistent increases in the diversity of microhabitats used with an increase in species size. A relationship between species size and evenness of microhabitat use was less evident

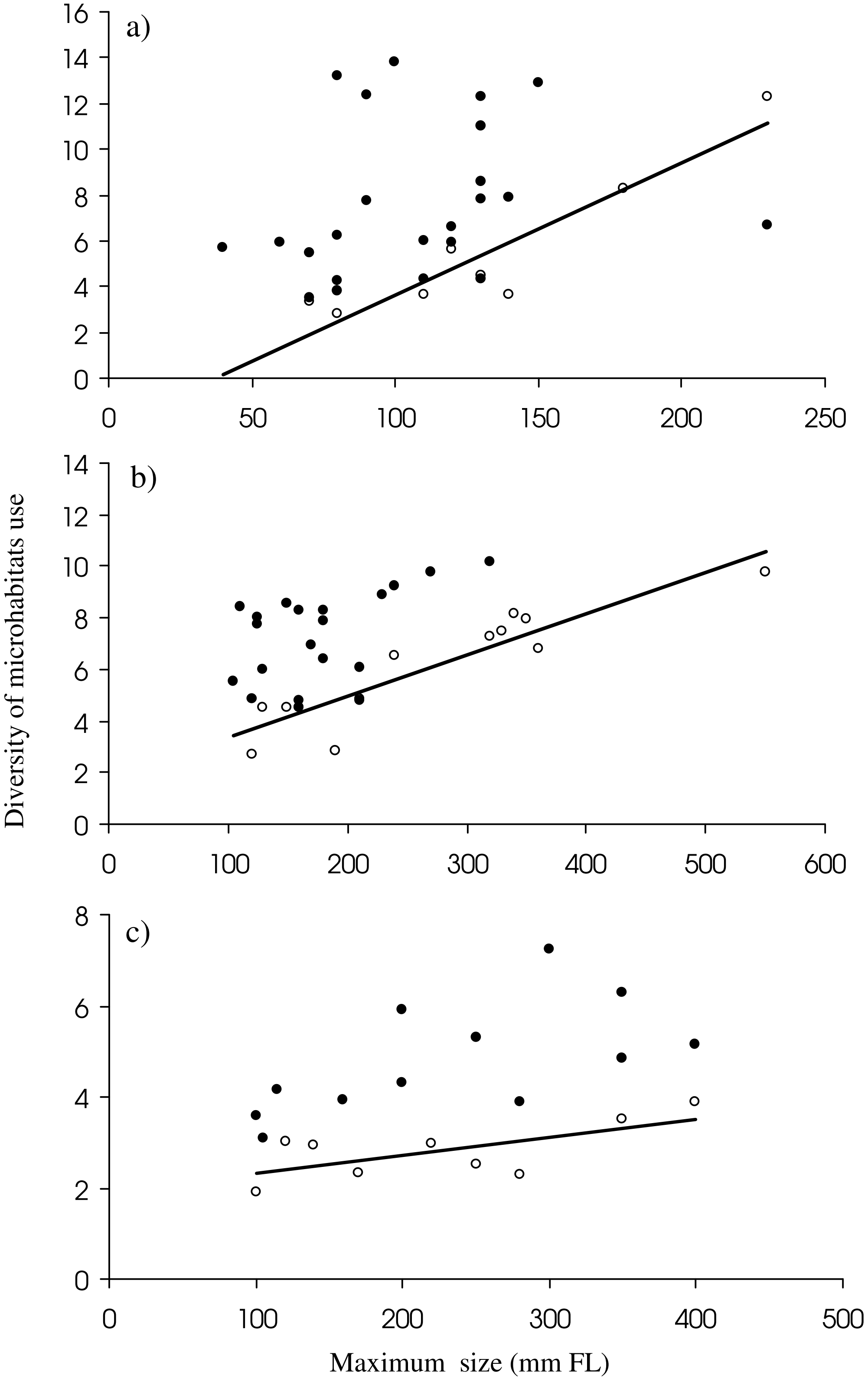

Figure 5.6: Maximum body size of species versus diversity of microhabitats used. Information for lower bound regressions is provided for: a) Kimbe Bay, PNG (y=0.058x – 2.125, r^2=0.858), b) Lizard Island, north GBR (y=0.016x + 1.710, r^2=0.839), c) Pelorus Island, mid GBR (y=0.004x + 1.910, r^2=0.441). Open circles are data points to which lower bound was fitted. Plot only includes species for which over 30 individuals were observed.

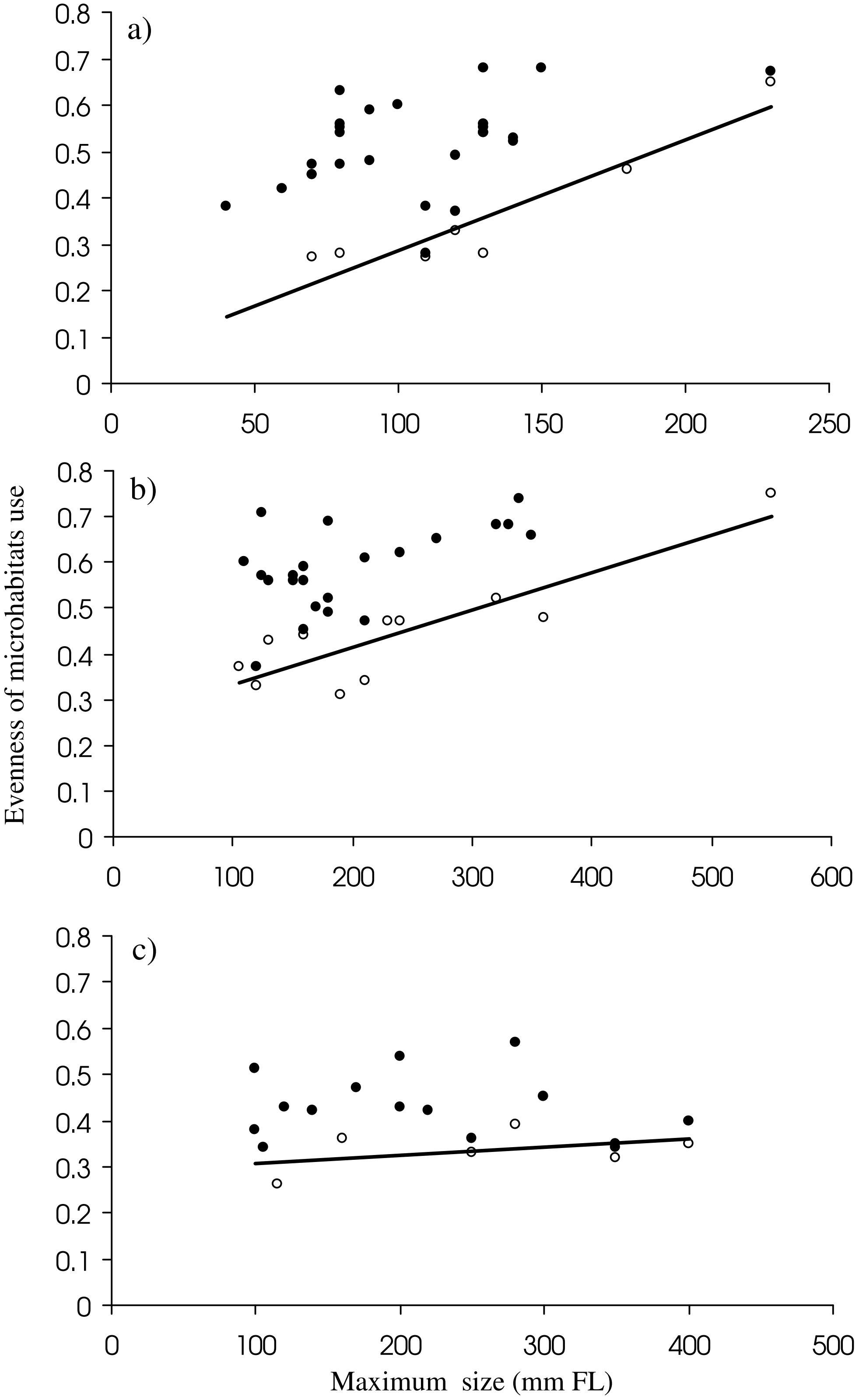

Figure 5.7: Maximum body size of species versus evenness of microhabitat use. . Information for lower bound regressions is provided: a) Kimbe Bay, PNG (y=0.002x + 0.0497, r^2=0.874), b) Lizard Island, north GBR (y=0.001x + 0.252, r^2=0.769), c) Pelorus Island, mid GBR (y=0.0002x + 0.290, r^2=0.183). Open circles are data points to which lower bound was fitted. Plot only includes species for which over 30 individuals were observed.

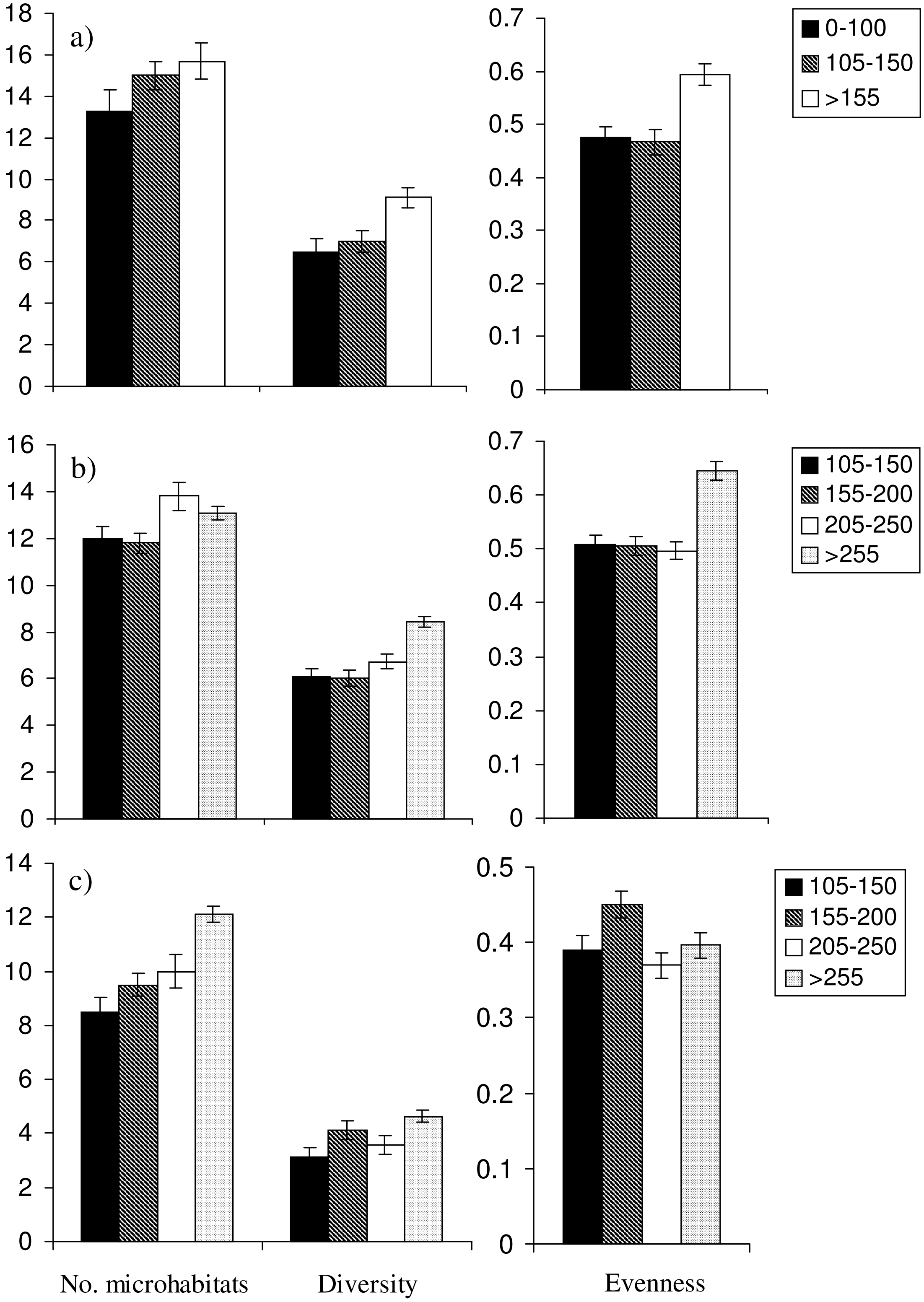

Figure 5.8: Mean of the total number of microhabitats used and mean diversity and evenness indices for species within different size classes (mm FL) at four locations: a) Kimbe Bay, PNG; b) Lizard Island, north GBR; c) Palm Islands, mid GBR. Provided are the mean number of microhabitats used; mean diversity index; mean evenness index (maximum possible value is 1). Standard errors of the mean are indicated.

when comparing mean values of evenness indices among locations. There was an increase in evenness of microhabitat use in the largest size class at Kimbe Bay and Lizard Island in relation to the other size classes. Species with small or intermediate body size were, on average, equally evenly spread among different microhabitats among these locations. There was no apparent trend for evenness of habitat use among species of different size at the Palm Islands, at this location intermediate sized species were the most evenly distributed among different microhabitats. Specific details of the number of habitats used, most commonly associated habitats and estimates of diversity and evenness for species at each location (for which at least thirty individuals were observed) are provided in Appendix I (parts 1 to 3). A full species list including locations at which they were observed, number of individuals observed and maximum size at each location can be found in Appendix II.

5.3.4 Prediction 4: Larger species have greater depth ranges than smaller species

Plots of body size of species against depth range support the prediction that larger species tend to exploit a greater range of depths on coral reefs than smaller species at both Kimbe Bay (upper bound: $F_{1,6}$=25.35; p=0.002) and Lizard Island (upper bound: $F_{1,10}$=32.69; p<0.000), (Figure 5.9). At these locations the relationship approximated a triangle with larger species being more likely to occupy a large depth range and smaller species being able to have either very small, very large depth ranges or ranges inbetween. One species at Kimbe Bay (*Choerodon anchorago*) had a far shallower depth range than expected for its body size, in relation to other species at this location. The upper bound for the relationship at Pelorus Island had a negative slope but was non-significant ($F_{1,4}$= 6.63; p=0.062), suggesting at this location there is little or no relationship between maximum species size and depth range. The depth range of species was greatest at Kimbe Bay (up to 45m), smaller at Lizard Island (up to 20m) and reduced further at Pelorus Island (up to 17m). This reflected variation in the maximum available depth at each location.

At each location there was a significant positive relationship between maximum depth at which species were observed and their depth range (Kimbe Bay: r^2=0.890, $F_{1,31}$=298.61, p<0.000; Lizard Island: r^2=0.930, $F_{1,31}$=481.42, p<0.000; Pelorus Island:

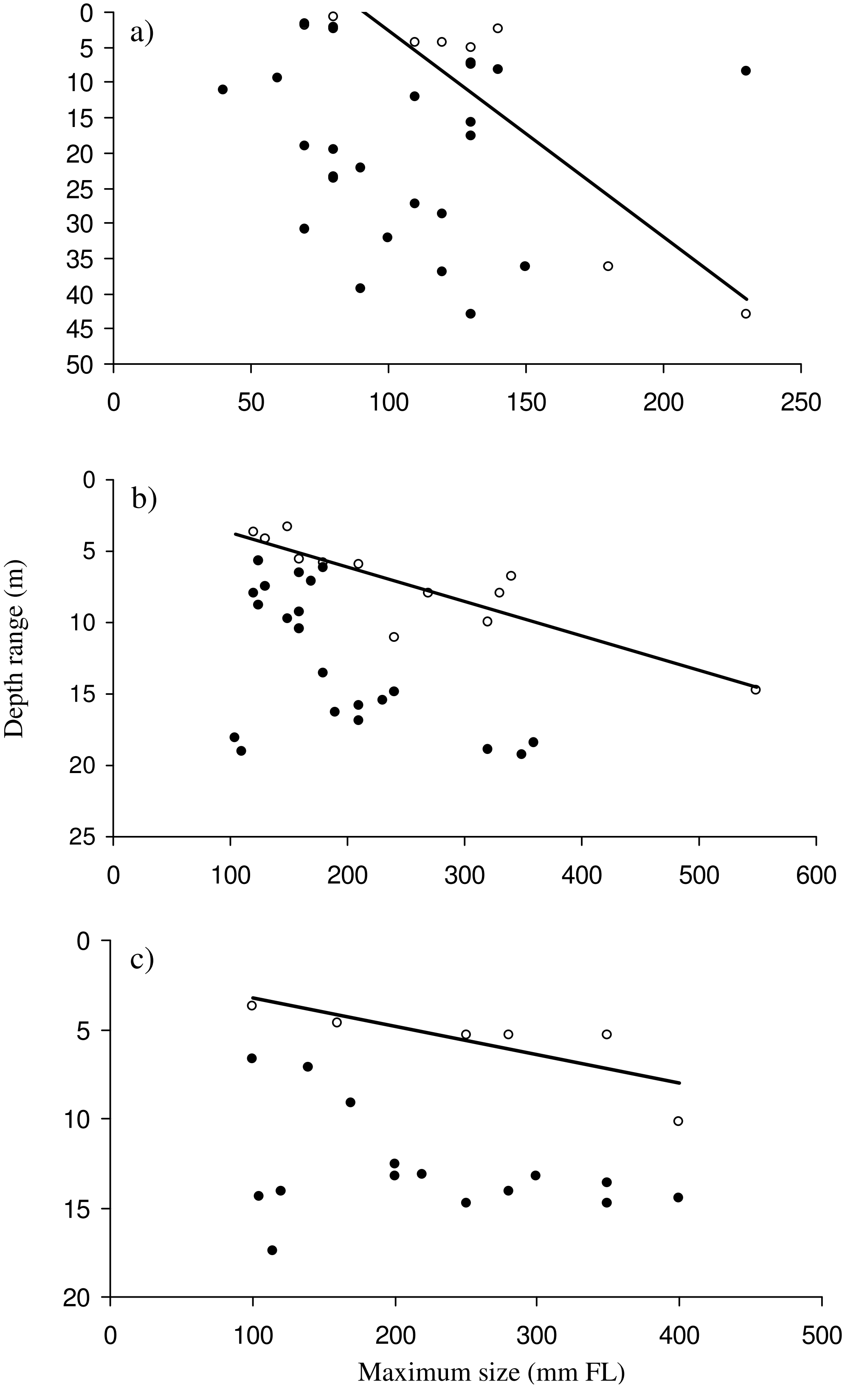

Figure 5.9: Relationship between maximum body size and depth range of species. Information for upper bounds is provided: a) Kimbe Bay (y = 0.293x – 27.419, r^2=0.808), b) Lizard Island (y = 0.0241x + 1.2348, r^2=0.766); c) Pelorus Island (y = 0.0159x + 1.6785, r^2= 0.624). Open circles indicate data points to which upper bound was fitted.

r^2=0.960, $F_{1,19}$=457.07, p<0.000). The depth range of most species was only defined by how deep it could be found as individuals of the vast majority of species were observed at shallow depths, about 1-3 metres in depth (although for some species individuals were more common at particular depths). Only a few species were never observed at shallow depths.

5.4 Discussion

Relationships between body size, abundance, species richness and microhabitat specificity in the wrasses examined are comparable to those obtained for a variety of terrestrial taxa (eg. Maurer et al. 1992, Blackburn 1997, Loder 1997, Hodkinson & Casson 2000, Ziv 2000). In addition to these ecological characteristics, body size was also found to be related to depth range. The polygonal structure of many of the relationships identified are similar to those predicted from theory and observed in other comparative studies. They indicate that being very small, of intermediate size or very large, has important implications for how coral reef fish species interact with their biotic and abiotic environment (Munday & Jones 1998, Jones et al. 2002). Results imply small or intermediate sized species exhibit greater flexibility than larger species in many aspects of life. For example, they can have high or low local abundances and exhibit high or low habitat specificity, whereas large species consistently have low abundances and are more likely to be habitat generalists.

Marine and terrestrial environments differ considerably in terms of environmental influences (May 1994). Despite this, the consistency of patterns among these two environments (eg. this chapter, Marquet et al. 1995, Warwick & Clarke 1996, Munday & Jones 1998) suggests they may be determined by similar processes acting on organisms in both environments. General explanations invoked to account for observed patterns should be applicable to both terrestrial and marine organisms although additional specific explanations may be relevant to different groups.

5.4.1 Local abundance

Recent studies have revealed a triangular relationship between body size and abundance in a wide range of organisms on land (eg. Griffiths 1986, Blackburn et al. 1990, Blackburn 1997, Hodkinson & Casson 2000). Coral reef fish assemblages encompassing many species from a range of families at different locations fit the triangular body size–abundance relationship (Munday & Jones 1998). In these assemblages, there is a distinctive decline in maximum potential abundance above or below a critical body size of about 100mm.

The present study indicates similar relationships are repeated on an intrafamilial level in the wrasses. Body sizes at which abundances peak in wrasses appear to be location specific, varying from 88mm SL to 220mm SL. This variation may reflect the size range of species present at a given locality. Relative to the size of other species present at a location it is the intermediate sized wrasse species which attain greater maximum local abundances than very small or very large species. This simple pattern is consistent for a large range of habitats and groups of organisms (eg Brown & Maurer 1987, Morse 1988, Blackburn & Gaston 1994, Warwick & Clarke 1996), implying that there are underlying processes acting on diverse communities of organisms preventing very small and very large species from attaining large population numbers.

Some explanations suggested for low population numbers of large terrestrial species are less applicable to coral reef fishes. For example, viviparity is common in terrestrial species and gestation lengths in large terrestrial mammals are often considerably longer than in smaller mammals (Calder 1984). Therefore, large terrestrial mammals generally adopt the strategy of giving birth to fewer offspring throughout their lifetime than smaller species, which is often accompanied by provision of parental care. This optimises the chances of offspring surviving to adulthood, although such a strategy is associated with low local abundance (Calder 1984, Reiss 1989). In contrast, most coral reef fishes spawn pelagic eggs and females of larger species have the capacity to produce and spawn more eggs than smaller species (Blueweiss et al. 1978, Andersson 1994). In fact, in oviparous reef fishes only demersal spawners tend to provide parental care and these are usually the smallest species (Munday & Jones 1998). Therefore, if the trade-off between investment of energy into reproduction and parental care does play a role in defining patterns observed, it should only influence the abundance of large species in terrestrial mammals and the abundance of some of the smallest species in coral reef fishes. The vast majority of wrasses, however, including those examined in this study, are pelagic spawning species. Therefore alternative explanations are required for the low population numbers within the smallest species.

Evidently, factors other than reproductive strategy suppress numbers of individuals within both large and small species of wrasses. Energetic explanations for low numbers of larger species are relevant to both terrestrial and marine taxa. Larger species are expected to consume a greater amount of food resources for growth and maintenance and usually have greater spatial requirements, therefore a given pool of resources in a local area can sustain less individuals of a large than small size (Brown & Maurer 1986, Harvey & Godfray 1987, Reiss 1989, Nee et al. 1991). Energetic requirements relative to available resources are likely to be a prime constraint on the abundance of large species (Marquet et al. 1995, Jones & McCormick 2002).

Explanations for low numbers within very small species are less apparent. Very small species may have increased susceptibility to predation (Wilbur 1988) and reduced energy available for movement, foraging for food and somatic maintenance (Peters 1983, Calder 1984), all of which could increase mortality rates and directly decrease numbers of individuals. Direct sources of mortality are only likely to be adequate to keep abundances at the very low levels observed for very small species when they are coupled with reproductive constraints. In terrestrial mammals very small species may be limited physiologically in the number of offspring they can carry, keeping offspring numbers low (Calder 1984, Stearns 1992). Although wrasses spawn pelagic eggs, they may still be subject to reproductive constraints. Across many wrasse species egg size is similar regardless of body size (Sponaugle & Cowen 1997), therefore smaller wrasse will produce fewer pelagic eggs than larger species because their ovary size is constrained by the size of the body cavity. This could decrease their fecundity and partly explain their decreased numbers. A further possibility is that greater habitat specificity of some smaller species could confine them to smaller areas and exacerbate competition among them, resulting in reduced densities. Little is known about the reasons for low population sizes of very small species. Further work is required to identify whether or not reproductive constraints are a principal factor depressing the potential abundance of the smallest species within communities.

5.4.2 Species richness

As predicted, body size distributions of wrasses at all locations approximated a log normal relationship with most species being of intermediate size relative to the size of other species at a given locality. Very small and very large wrasse species were rare. Few studies have examined body size-species richness relationships in marine organisms. Species richness-body size distributions found for wrasses in this study parallel patterns found in recent studies of marine macrobenthic communities and coral reef fishes and are equivalent to those found for a diverse range of terrestrial taxa (Warwick & Clarke 1996, Munday & Jones 1998, Pauly 1998). Collation of data by Pauly (1998) and Munday & Jones (1998), indicates species richness of tropical fishes peaks at a body length of about 75-125mm. This is similar to the size range of the most speciose size classes identified in this study. Therefore, body size-species richness relationships within widely separated wrasse communities are comparable to those at the community level when numerous reef fish families are included (Munday & Jones 1998). Evidently, factors constraining species richness in very small and large size classes are acting at a range of taxonomic levels in both marine and terrestrial habitats.

Within the wrasse communities examined there appears to be a correlation between the body size at which there was greatest species richness and the size at which local abundance peaked. The most speciose size class at Kimbe Bay was 55-100mm SL and abundance was estimated to peak at about 88mm SL. At the other locations larger size classes (105-150mm and 155-200mm) contained the largest number of species and abundances were estimated to peak within species of larger body size (180mm-220mm SL) at these locations. The greater diversity of smaller species at Kimbe Bay, may be an expression of Bergmann's rule, which states body size within and potentially among species tends to increase with an increase in latitude (eg. Sand et al. 1995,Arnett & Gotelli 1999, Ashton et al. 2000). Visual sampling of more locations is required to clarify this issue.

Body size, abundance and species richness have previously been shown to be interrelated in terrestrial taxa (Morse 1988, Blackburn et al. 1990**,** Rosenzweig 1995). The pattern observed for wrasses, in which the size class containing most species diversity tends to correspond to the size of species with the greatest local abundance of individuals, is the same as that observed in an insect community by Siemann et al. (1996). Siemann et al. (1996) formalised the relationship in insects as $S=I^{0.5}$, where S is species richness and I is abundance in a given size class.

Inter-relationships among body size, abundance and species richness imply a potential for variation in local abundance to influence patterns of local species diversity. For example, larger species generally have lower abundances than smaller species and are more patchily distributed in local populations (Dial & Marzluff 1988, Fenchel 1993). Small population numbers can be reduced further by unexpected environmental disturbances such as a population explosion of predators, increase in parasite occurrence or disease, or catastrophic damage of habitat (Marzluff & Dial 1991, Brown 1995). This renders larger species more susceptible to local extinction so they are less likely to be present at a specific locality (Maurer et al. 1992, Fenchel 1993, Siemann et al. 1996, Dulvy & Reynolds 2002).

Another explanation for low numbers of large species on a local scale, is that they generally have lower dispersal rates than smaller species leading to a less cosmopolitan distribution of larger species (Dial & Marzluff 1988, Marzluff & Dial 1991, Siemann et al. 1996). If large species have reduced geographic ranges in comparison to smaller species, this can influence the body size-species richness distribution on local scales, larger species having a lower chance of occurring at a given location. Consequently, the proportion of sites occupied by a species is a decreasing function of body size (Gaston & Lawton 1988). Although this explanation may hold for terrestrial species, it is not applicable to wrasses and other coral reef fishes as dispersal rate and geographic distribution of reef fishes are related to dispersal abilities of pelagic larvae as opposed to adult movement. There is some evidence that larger species may tend to have larger geographic ranges than smaller species, although this relationship does not appear to hold within reef fish families (Jones et al. 2002).

Explanation of low numbers of very small species has received less theoretical attention than the low abundances of large species (Loder 1997). In some taxa, dispersal efficiency may decrease below a certain size (Hodkinson & Casson 2000) and it may be harder to locate resources for survival. Very small species are also likely to be subjected to physiological constraints, the nature of which may vary among taxa. For example, a lower limit to body size in insects may be determined by minimum specifications for trachea channelling oxygen to the organism (Finlay et al. 1996). In terrestrial mammals body size is directly related to the number of live young that can carried in the body cavity (Peters 1983, Calder 1984, Shine & Charnov 1992) and very small size can limit the potential for population growth of a species. In other groups such as fish, physiological constraints and minimum fecundity requirements may also be of importance although the exact nature of these constraints requires elucidation. The consistency with which very small species are rare within different groups of organisms, implies disadvantages of very small body size are common to the majority of taxa.

5.4.3 Habitat use

Further ideas invoking variation in habitat use of species have been put forward to account for a local predominance of small to intermediate sized species and low numbers of large species. One explanation suggests this pattern could be related to differences in the way large and small organisms perceive the environment, habitat structure appearing more complex to smaller species (Hutchinson & MacArthur 1959, May 1978). An argument against this view is that as the environment has a fractal geometry, it should seem equally heterogeneous regardless of body size (Morse 1988, Fenchel 1993). The important concept though is that although perception of habitat diversity should not vary with body size, a greater range of microhabitats provides a greater range of potential niches for smaller individuals (May 1978, Brown 1995). Therefore, smaller species may avoid intraspecific competition by specialising in the use of certain microhabitats which are not used by many other species (May 1986, May 1988, Morse 1988, Fenchel 1993, Brown 1995). A consequence of this is the expectation of increased rates of speciation in smaller species and greater numbers of small species (Marzluff & Dial 1991). This expectation is supported by empirical and theoretical findings for terrestrial animals which found habitat specificity scales negatively with body size in Eutherian mammals Ziv (2000). These results suggest smaller species should be habitat specialists while larger species should be habitat generalists (Hutchinson & MacArthur 1959, Ziv 2000).

It has been suggested that species number may be more closely linked to structural diversity of habitat rather than species diversity of habitat (Pianka 1967). As coral reefs offer high diversity in terms of both coral species and structural complexity (Veron 1993), the range of potential niches on coral reefs is particularly large. Therefore, microhabitat selectivity of small species is likely to be of considerable importance in coral reef fishes. Wrasse species examined in this study do not express a simple linear relationship between body size of species and diversity and evenness of habitat use among locations. A polygonal relationship is evident which is expressed most strongly at Kimbe Bay and Lizard Island. At these locations it is apparent that smaller species of wrasses use either a small or wide number of available microhabitats and within these habitats they either exhibit high or low levels of habitat specificity. Larger wrasse species on the other hand, tend be generalists occupying a larger number of microhabitats and exhibiting greater evenness of microhabitat use than smaller species.

The reduced variation in microhabitat use in relation to body size at Pelorus Island could be associated with less diversity in the range of microhabitats available at this location. There are also fewer wrasse species present at Pelorus Islands than at the other locations increasing the difficulty of assessing overall patterns within the wrasse community.

There are two main reasons why a species associates with a particular microhabitat. Firstly, certain microhabitats harbour food resources required by a species. Individuals of smaller species have lower absolute energetic requirements than larger species. Smaller species may be able to exploit a narrower range of food resources (Brown & Maurer 1986, Harvey & Godfray 1987, Reiss 1989, Nee et al. 1991) and appear to have more restricted diets in terrestrial organisms than larger species (eg. Wasserman & Mitter 1978, Peters 1983). In wrasses, morphological constraints of smaller reef fish species can prevent consumption of hard bodied prey (Wainwright 1988, Clifton & Motta 1998) and constraint of diet could restrict the range of microhabitats in which preferred food items are found. Consequently, smaller species with a constrained diet may forage over a low diversity of microhabitats. Out of necessity, large species requiring a greater number of food items are likely to utilise a wider range of microhabitats when foraging.

Secondly, microhabitats can provide shelter and a refuge from predation. Predation is a particularly important structuring process on coral reefs and refuge space is of prime importance for small species (Caley 1993, Caley 1998, Hixon & Beets 1993, Caley & St John 1996, Hixon & Webster 2002). Some small species may remain associated with a particular microhabitat which confers a survival advantage and rarely stray from that microhabitat. For example, some gobies spend their entire lives in the branches of *Acropora* corals and different species may be associated with different species of *Acropora* (Munday et al. 1997). Larger species do not rely on coral cover as heavily for protection, increasing the range of microhabitats with which they can associate. Specifying in one or more habitats appears to be a strategy more suited to smaller species. However, evidence provided by this study suggests the use of a diverse range of microhabitats is also a viable tactic for small wrasse species. The small species which exhibit low habitat specificity may not be so reliant on a limited number of microhabitats with high structural complexity to evade predators, or they may consume prey items which are widely dispersed throughout available microhabitats.

5.4.4 Depth range

Relationships described in this study between body size and depth range at Kimbe Bay and Lizard Island approximate the polygonal relationship of those illustrated between body size and microhabitat use. For example, small wrasse species at these locations either have very large, intermediate or very small depth ranges and an increase in body size is associated with an increase in depth range. This would tend to support the notion that species exploiting a greater range of microhabitat types may also exploit a greater range of depths.

The implications of depth variation on the scale of tens of metres often found on coral reefs are rarely examined and are poorly understood. Depth zonation in coral reef fish species between shallow and deep zones has been documented (Clarke 1977, Eckert 1985, Eagle et al. 2001, Fulton 2001, Holbrook et al. 2002) and some species demonstrate ontogentic shifts in depth (Green 1996). On artificial reefs placed at 21m and 7m in Florida, more large fish were found at the deeper reefs (Sherman et al. 1999). The results of this study of the depth distribution of coral reef fishes within the wrasse family provides evidence that body size may be related to depth range of species. The idea of covariation between diversity of habitat use and depth range has received little empirical attention. Larger species may need to exploit most of the available resources found on coral reefs and forage over a greater number of microhabitats at different depths in order to attain energy required for growth, reproduction and maintenance. If smaller species exhibit varying degrees of habitat specialisation this could be reflected by variation in the depth ranges occupied by small species, as one way of encountering and utilising different microhabitats is by varying depth on the reef slope. Depth zonation can also be related to use of different reefal zones. For example, if the reef flat environment fulfils all of the requirements of a species it is likely to remain in this area and consequently have a very small depth range.

The idea of inter-relationships among body size, microhabitat use and depth range is one of a number of suggestions which could help explain depth zonation of coral reef fishes. For example, interspecific competitive interactions can potentially define the depth zone occupied by species, although very few species in this study exhibited upper depth limits to their distributions so such interactions, if operating, would have to define lower limits to depth ranges. Other suggestions can be projected which are largely independent of variation in body size. Spatial distribution of resources and feeding mode of species may be important, for example herbivorous fishes may be more dominant in shallow habitats than planktivores (Mejia & Garzon-Ferreira 2000). There is evidence that water movement energy is strongly associated with species depth distributions (Mcghee 1994, Mejia & Garzon-Ferreira 2000, Fulton 2001), species in shallower waters being better adapted to swimming in high wave energy habitats (Fulton 2001). Also, selective recruitment of species to microhabitats or reef zones can determine adult distributions, especially in small site attached species (eg. Gutierrez 1998). More research is required to clarify the relative contribution of these factors to use of the water column by different reef fish species. Our understanding of coral reef dynamics is not complete without an assessment of the distribution of coral reef fishes with depth. This is an important aspect of coral reef ecology requiring further scientific attention.

5.4.5 Conclusion

A number of ecological advantages are associated with an increase in body size within species. These include higher fecundity, greater mating and reproductive success, greater competitive abilities and reduced susceptibility to predation (Calder 1984, Boyce 1988, Ebenman & Persson 1988). There is little empirical information indicating the costs of being large, but despite this we are not surrounded by large organisms (reviewed in Blackenhorn 2000). Instead of focussing on the disadvantages of being large to explain this paradox it appears to be more appropriate to examine the advantages of small to intermediate body size in terms of ecological versatility. This study has provided evidence that small to intermediate sized wrasse species can occupy a continuum from low to high abundances, low to high diversity of microhabitat use and small to large depth ranges. In the presence of environmental stoichasticity, the ability to utilise different life-style strategies to optimise survival may confer an advantage which exceeds the disadvantages associated with small to intermediate body size. Amenability to both specialisation and generalisation could partly explain why species diversity is greatest in small to intermediate size classes.

CHAPTER 6: General Discussion

The main aim of this study was to identify whether generalisations concerning relationships among body size and other aspects of life history and ecology could be extended to coral reef fishes. Wrasses provided only mixed support for theory largely developed for organisms that live on land. Some body size relationships described for wrasses were similar to those described in terrestrial species, while others differed in some way from the predicted pattern. In some cases variation in traits appeared unrelated to body size. This suggests that while a number of generalisations hold, others may need to be refined or rejected and new theories developed to account for the diversity of life history strategies and ecological patterns of coral reef fishes.

As expected, mortality rate decreased and consequently longevity increased with an increase in size (Blueweiss et al. 1978, Calder 1984, Stearns 1992). However, the common expectation that smaller species have faster initial growth than larger species was not supported (Harvey & Keymer 1991, Arendt 1997, McCann & Shuter 1997). The approach of examining growth relative to both life-span and adult size indicated that growth among most of the species was similar at all stages of life and was independent of adult size. Initial growth was more closely related to growth strategy (indeterminate–determinate growth) than size, with determinately growing species having faster initial growth. The *Bodianus* species provided further evidence that the expression of determinate growth is consistently correlated with long life-spans (Choat & Robertson 2002). The relationship between growth strategy and longevity requires further investigation.

No *a priori* predictions relating body size to reproductive traits of species were supported. Body size was found to be a good predictor of the occurrence of life history transitions such as attainment of maturity and sex change. The relationship expressed between body size and proportion of maximum size and age at maturity, however, was opposite to that predicted. Maturation occurred later in life and at a greater proportion of maximum size in smaller species. Smaller species also changed sex at a greater proportion of maximum size than larger species, which is the first evidence for this relationship among sequential hermaphrodites. Although smaller species were expected to have greater reproductive effort (Peters 1983, Reiss 1989, Marzluff & Dial 1991), no consistent relationship was found between body size of species and reproductive effort per bout. These results should be interpreted cautiously though as the presence of year-round spawning in the pseudocheilinids and seasonal spawning in wrasses collected at the Palm Islands, complicated comparisons of reproductive effort among species.

Latitudinal trends predicted for body size and longevity were generally supported within *Halichoeres melanurus*, as there was an increase in maximum size and age as latitude increased (van' t Land et al. 1999, Arnett & Gotelli 1999, Atkinson 1994). Despite this, reproductive traits of individuals within geographically separated populations did not vary predictably with an increase in either latitude or maximum body size of individuals. *H. melanurus* individuals at the Palm Islands had earlier maturation and sex change and greater reproductive effort than at the other locations which was not associated with differences in growth among locations. Therefore, in this species reproductive traits may be more closely linked to environmental influences than to intrinsic energetic trade-offs between energy allocation to growth and reproduction.

Relationships between body size and ecological variables, such as local abundance and species richness, generally parallelled those observed in terrestrial organisms (eg. Morse 1988, Brown 1995, Siemann et al. 1996, Blackburn et al. 1990, Blackburn et al. 1993). Similar relationships have also been described for other marine organisms (Warwick & Clarke 1996, Marquet et al. 1995). This implies the effects of selective processes on community structure may be consistent among terrestrial and marine species. Relationships between size and microhabitat use agreed with predictions based on terrestrial studies, with larger species appearing to be less habitat specific than smaller species (Hutchinson & MacArthur 1959, May 1978, Price 1984, Pyron 1999, Ziv 2000). The idea that smaller species can occupy a continuum from low to high habitat specificity has received less theoretical attention and further research is required to examine the versatility of small species relative to larger species. In addition, small wrasse species were found to have either small or large depth ranges, whereas larger species consistently had greater depth ranges. There is currently little published information relating to depth zonation of reef fishes and our understanding of why fishes occupy particular depth ranges is limited. There is considerable scope for studies of depth range to increase our understanding of community dynamics of coral reef fishes.

Each of the chapters outlined above were designed to examine specific aspects of growth, reproduction and other ecological characteristics in relation to body size. While the results thus far have been discussed in relation to the specific hypotheses in each chapter there are broader implications concerning inter-relationships among growth pattern, reproductive traits and ecological characteristics (Calder 1984, Stearns 1992, Marzluff & Dial 1991). Clearly, the effect of natural selection on one or more aspects of life history has the potential to either directly or indirectly influence many others.

A number of inter-relationships commonly found among aspects of ecology and life history of species are illustrated in Figure 6.1. Many of these were not found to occur among the wrasses examined. This is most evident when examining associations between aspects of growth and reproduction. For example, early maturation is often correlated with faster initial growth (Abrams et al. 1996, Day & Rowe 2002). In the wrasse species studied, however, larger species were found to mature earlier than smaller. This was not related to initial growth which was relatively constant among species of different body sizes. In addition, reproductive effort and the proportion of maximum size and age attained at sex change varied considerably among species, but this variation appeared to be independent of interspecific differences in growth and mortality. These results imply that at least in some species, reproductive traits may be more closely linked to extrinsic influences such as predation rates, than to variation in the amount of energy invested in growth and reproduction (Promislow & Harvey 1990). Another common expectation is that growth should slow down following maturation due to the extra energy invested in reproduction (Charnov 1982). Although this was the case for most species, *H. melanurus* was an exception to the rule having almost linear growth throughout life.

The continuum between determinate or indeterminate growth has important implications for the expected life-span of species and requires greater theoretical attention. Therefore, different growth strategies also potentially influence reproductive characteristics of species (Figure 6.1). As the expression of both of these contrasting growth strategies has rarely been described at low taxonomic levels such as within a family, some new ideas can be put forward integrating growth strategy into predictions relating growth and reproduction of species. For example, it could be suggested species with determinate growth which cease growth after maturation should have more energy available for reproduction and therefore have greater reproductive effort per bout than closely related species with indeterminate growth (Roff 1992, Stearns 1992). Alternatively, excess energy available once growth has ceased, may actually be invested in maintenance and survival strategies as opposed to reproduction which could

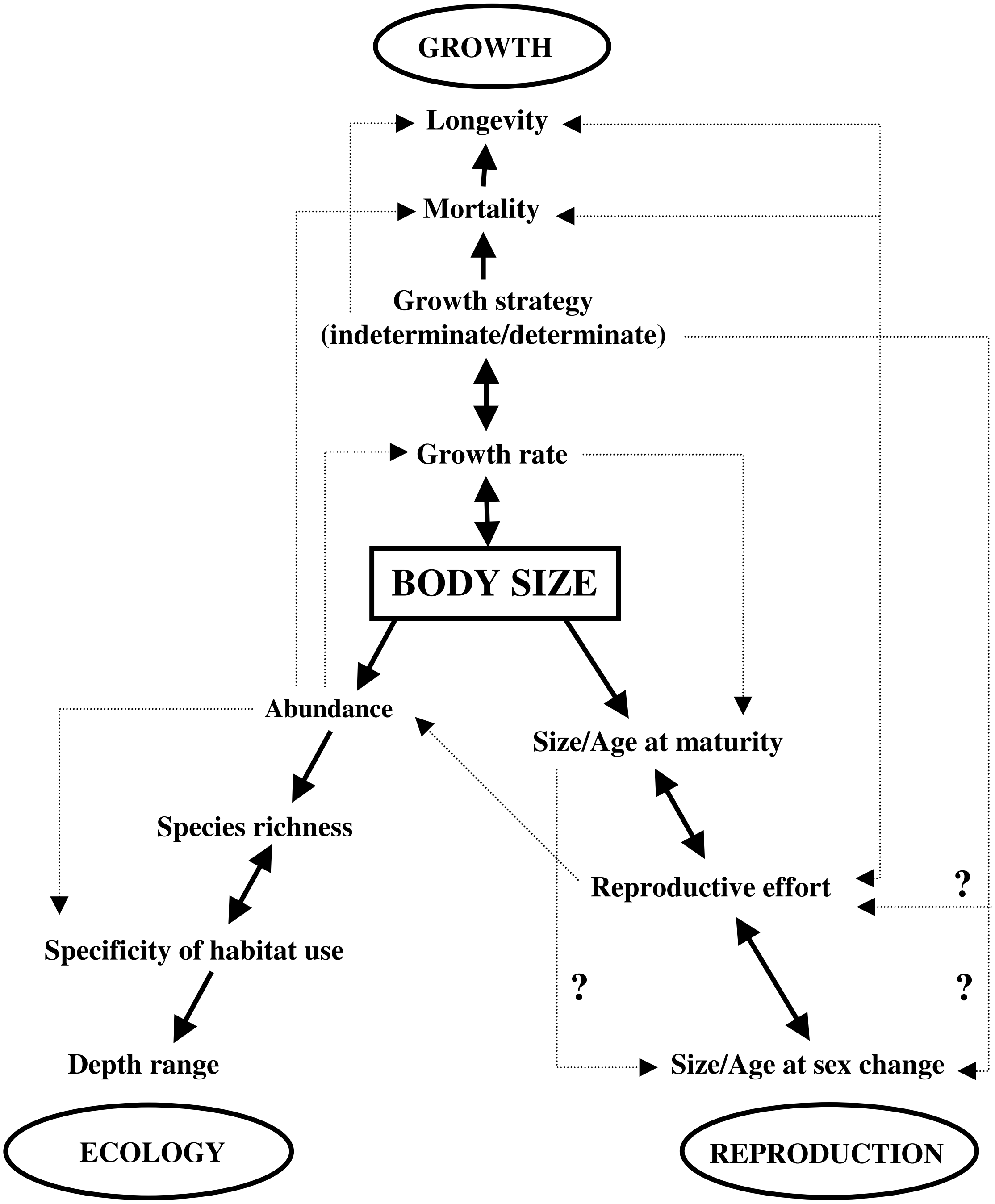

Figure 6.1: Inter-relationships among aspects of growth, reproduction and other ecological traits. An arrow from one life history characteristic to another indicates that changes in one characteristic can directly influence changes in the other. Many of these relationships, however, were not evident in the wrasses studied. ? = potential relationship requiring further exploration.

contribute to the attainment of long life-spans. Therefore, a contrasting idea is that as species with determinate growth tend to be long lived, reproductive effort should be spread over many bouts and the energy invested in each bout should be low (Bell 1980). Further evidence is required to assess these ideas. The relative importance of size and age at sex change can also vary in relation to growth strategy. Differences in body size have the potential to initiate sex change in species with indeterminate growth, which grow continuously throughout life. In species with determinate growth though, the body size of mature adults is similar, therefore only differences in age can determine when sex change occurs in these species.

Inter-relationships expected between growth and reproduction should also be repeated at an intraspecific level. Despite this, there appeared to be no relationship between growth characteristics and these reproductive traits in *H. melanurus*. This contrasts with many intraspecific studies in terrestrial species in which growth and reproduction appear closely linked (Marshall 1988, Schwarzkopf 1993, Forsman & Shine 1995, Stamps et al. 1998, Day and Rowe 2002). Lack of covariation among traits implies changes in growth and reproduction in *H. melanurus* occur independently of one another. Whether this is typical or atypical of coral reef fishes remains to be clarified as *H. melanurus* differs in a number of ways from the other wrasse species studied here. It was the only species to have linear growth throughout life and at the Palm Islands reproductive effort was far higher than in any other species. It demonstrates considerable plasticity in both growth and reproduction on a wide spatial scale. *H. melanurus* used one of the greatest ranges of microhabitats of the wrasses observed at Kimbe Bay and Lizard Island and occupied very large depth ranges at each location studied. At Okinawa Island, Japan this species has a far more diverse diet than any of the other wrasse species (Sano et al. 1984). This perhaps unique combination of life history and ecological characteristics may have helped this species to thrive over such as large geographic range and become one of the most abundant wrasse species on coral reefs.

Links between mortality, reproductive effort of a species and abundance, highlight relationships between reproductive traits of species at an individual level and ecological characteristics expressed at the community level (Figure 6.1). High mortality can promote increased reproductive effort, resulting in increased abundance (Marzluff & Dial 1991, Promislow & Harvey 1990). When a species has high local abundance, density dependent factors can also increase mortality rates. For example, intra- and interspecific competition for resources can reduce energy available for growth and maintenance (Ebenman 1988, Persson 1988, Jones 2002). Therefore, interactions among mortality, reproductive effort and density dependent factors determine local abundance of species which is, in turn, a critical factor in defining patterns of habitat use and species richness (Figure 6.1), (Abrams & Rowe 1996). Although not examined specifically there is some limited evidence that reproductive effort and abundance may be related in the wrasses examined. *H. melanurus* had the highest reproductive effort per bout (estimated from gonadosomatic index) and was the most abundant wrasse sampled at the Palm Islands, while *Hemigymnus melapterus* had the second highest reproductive effort per bout and was the second most abundant species of those sampled. An examination of a considerable number of species is required to assess the consistency of this relationship.

Clearly, a full understanding of the role of body size in the ecology and life history of animals in both terrestrial and marine habitats has yet to be achieved. This study confirms that within a single reef fish family, body size is central to many aspects of an organism's life. While addressing only a limited number of potential relationships between body size and characteristics of species, this study has provided both support for well-established theory and the basis for new hypotheses and has highlighted the scope for variation among different taxa. It is unclear how much the variation in body size-growth/reproduction patterns, or the similarities in body size-abundance/species richness patterns among terrestrial species and wrasses, can be attributed to different or consistent selective pressures within the marine and terrestrial environments. In order to identify the selective pressures operating in different environments and assess their influences on patterns observed, further studies are required in a greater range of reef fish families and other groups of marine organisms. Only by describing body size relationships for many diverse taxa in numerous environments, can the underlying reasons defining body size-related patterns be elucidated and the generality of these patterns be accurately assessed.

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Appendix I (Part 1):

Provided for wrasse species at Kimbe Bay with over 30 observations: Number of observations (N); maximum observed size (mm FL); the microhabitat with which individuals were most commonly associated; values of Simpson's diversity index (*D*) for each species and evenness (*E*). Species listed in order of size and separated into size classes.

Species	N	Max. size	No. habitats	Most commonly associated habitat	*D*	*E*
Pseudocheilinops ataenia	100	40	15	Anacropora	5.70	0.38
Pseudocheilinus hexataenia	100	60	14	Pocillopora	5.91	0.42
Halichoeres argus	100	70	13	Bare rock	3.46	0.27
Thalassoma amblycephalum	100	70	12	Turf rock	5.44	0.45
Paracheilinus filamentosus	100	70	12	Gravel	5.45	0.45
Cirrhilabrus walindi	100	70	7	Rubble w/sediment	3.32	0.47
Halichoeres melanurus	100	80	24	Turf rock	13.21	0.55
Halichoeres miniatus	100	80	10	Turf rock	2.78	0.28
Halichoeres nebulosus	100	80	6	Turf rock	3.79	0.63
Pseudocheilinus evanidus	78	80	9	Rubble w/turf	4.21	0.47
Stethojulis trilineata	100	80	11	Turf rock	6.19	0.56
Cirrhilabrus cyanopleura	100	80	7	Rubble	3.80	0.54
Diproctacanthus xanthurus	100	90	16	Porites (cylindrica)	7.74	0.48
Labroides dimidiatus	100	90	21	Porites (cylindrica)	12.38	0.59
Halichoeres purpurescens	100	100	23	Turf rock	13.77	0.60
Halichoeres marginatus	100	110	13	Turf rock	3.66	0.28
Halichoeres new	100	110	16	Sand covered rock	6.00	0.38
Halichoeres richmondi	95	110	16	Staghorn	4.35	0.27
Gomphosus varius	73	120	12	Corymbose coral	5.90	0.49
Halichoeres prosopeion	100	120	20	Encrusting coral	6.60	0.33
Labrichthys unilineatus	100	120	15	Porites (cylindrica)	5.58	0.37
Bodianus mesothorax	100	130	16	Encrusting coral	8.56	0.54
Cheilinus orientalis	91	130	18	Rubble	12.27	0.68
Halichoeres chloropterus	100	130	8	Coarse sand	4.29	0.54
Hemigymnus melapterus	40	130	14	Staghorn	7.84	0.56
Thalassoma hardwicke	100	130	16	Turf rock	4.51	0.28
Thalassoma lunare	100	130	20	Massive coral	10.99	0.55
Halichoeres hortulanus	99	140	15	Gravel	7.90	0.53
Halichoeres scapularis	100	140	7	Coarse sand	3.63	0.52
Cheilinus celebicus	100	150	19	Encrusting coral	12.90	0.68
Epibulus insidiator	97	180	18	Porites (cylindrica)	8.23	0.46
Cheilinus fasciatus	100	230	19	Rubble	12.32	0.65
Choerodon anchorago	39	230	10	Porites (cylindrica)	6.70	0.67

Appendix I (part 2):

Provided for wrasse species at Lizard Island with over 30 observations: number of observations (N); maximum observed size (mm FL); the microhabitat with which individuals were most commonly associated; values of Simpson's diversity index (*D*) for each species and evenness (*E*). Species listed in order of size and separated into size classes.

Species	N	Max. size	No. habitats	Most commonly associated habitat	*D*	*E*
Halichoeres melanurus	100	105	15	Dead branching coral	5.55	0.37
Labroides dimidiatus	100	110	14	Massive coral	8.43	0.60
Halichoeres nebulosus	100	120	13	Coarse sand with macroalgae	4.87	0.37
Stethojulis strigiventer	58	120	8	Dead branching coral	2.68	0.33
Halichoeres margaritaceus	100	125	11	Turf rock	7.76	0.71
Stethojulis bandanensis	100	125	14	Rubble w/sediment	8.04	0.57
Cirrhilabrus punctatus	94	130	8	Massive coral	4.49	0.56
Thalassoma amblycephalum	100	130	14	Soft coral	5.99	0.43
Coris batuensis	100	150	15	Coarse sand	8.53	0.57
Macropharyngodon meleagris	29	150	8	Staghorn	4.50	0.56
Anampses neoguinaicus	50	160	8	Dead branching coral	4.52	0.56
Halichoeres chloropterus	100	160	14	Rubble w/turf	8.29	0.59
Halichoeres prosopeion	35	160	10	Turf rock	4.49	0.45
Labrichthys unilineatus	100	160	11	Staghorn	4.80	0.44
Halichoeres marginatus	84	170	14	Dead branching coral	6.94	0.50
Bodianus mesothorax	47	180	12	Rubble w/turf	8.30	0.69
Thalassoma hardwicke	100	180	13	Corymbose coral	6.38	0.49
Thalassoma jansenii	100	180	15	Corymbose coral	7.86	0.52
Bodianus axillaris	30	190	9	Massive coral	2.83	0.31
Choerodon fasciatus	58	210	14	Massive coral	4.81	0.34
Hemigymnus fasciatus	100	210	13	Soft coral	6.05	0.47
Halichoeres trimaculatus	30	210	8	Coarse sand	4.86	0.61
Thalassoma lunare	100	230	19	Dead branching coral	8.91	0.47
Gomphosus varius	100	240	14	Corymbose coral	6.52	0.47
Oxycheilinus digrammus	86	240	15	Soft coral	9.25	0.62
Halichoeres hortulanus	99	270	15	Rubble w/turf	9.75	0.65
Cheilinus chlorourus	100	320	15	Coarse sand	10.17	0.68
Cheilinus trilobatus	100	320	14	Soft coral	7.24	0.52
Coris gaimard	47	330	11	Rubble w/turf & coarse sand	7.50	0.68
Novaculichthys taeniorus	38	340	11	Rubble w/turf	8.16	0.74
Epibulus insidiator	100	350	12	Massive coral	7.94	0.66
Cheilinus fasciatus	100	360	13	Coarse sand	6.78	0.48
Hemigymnus melapterus	100	550	14	Massive coral	9.78	0.75

Appendix I (part 3):

Provided for wrasse species at Pelorus Island with over 30 observations: Number of observations (N); maximum observed size (mm FL); the microhabitat with which individuals were most commonly associated; values of Simpson's diversity index (*D*) for each species and evenness (*E*). Species listed in order of size and separated into size classes.

Species	N	Max. size	No. habitats	Most commonly associated habitat	*D*	*E*
Cirrhilabrus punctatus	100	100	5	Porites (finger)	1.90	0.38
Halichoeres miniatus	100	100	7	Soft coral	3.59	0.51
Halichoeres melanurus	100	105	9	Soft coral	3.10	0.34
Labroides dimidiatus	100	115	16	Soft coral	4.17	0.26
Stethojulis strigiventer	40	120	7	Rubble w/turf	3.01	0.43
Coris batuensis	71	140	7	Soft coral	2.93	0.42
Halichoeres chloropterus	50	160	11	Soft coral	3.93	0.36
Labrichthys unilineatus	63	170	6	Pocillopora	2.34	0.47
Bodianus mesothorax	54	200	11	Soft coral	5.92	0.54
Bodianus axillaris	50	200	10	Soft coral	4.32	0.43
Cheilinus chlorourus	47	220	7	Soft coral	2.96	0.42
Choerodon cyanodus	35	250	7	Rubble w/turf	2.51	0.36
Thalassoma lunare	100	250	16	Soft coral	5.29	0.33
Cheilinus trilobatus	30	280	4	Rubble w/turf	2.29	0.57
Oxycheilinus digrammus	30	280	10	Soft coral	3.88	0.39
Choerodon fasciatus	100	300	16	Porites (massive)	7.24	0.45
Cheilinus fasciatus	100	350	18	Soft coral	6.28	0.35
Choerodon anchorago	100	350	11	Rubble w/turf	3.50	0.32
Epibulus insidiator	100	350	14	Soft coral	4.83	0.34
Hemigymnus fasciatus	33	400	13	Rubble w/turf	5.16	0.40
Hemigymnus melapterus	100	400	11	Soft coral	3.90	0.35

Appendix II:

Provided for each species: Number of individuals of each species observed at each location (N) and maximum size of species. A value for N is not indicated for One Tree Island as observations were not conducted at this location, however, maximum size data is provided based on information in Russell (1983). KB=Kimbe Bay, LI=Lizard Island, PS=Pelorus Island and OT=One Tree Island.

		KIMBE		**LIZARD**		**PELORUS**		**ONE TREE**	
Species	**Observed at:**	**N**	**max size (cm)**	**N**	**max size (cm)**	**N**	**max size (cm)**	**N**	**max size (cm)**
Anampses caruleopunctatus	LI			5	13			-	
Anampses geographicus	LI			2	11			-	24
Anampses meleagris	LI			2	14			-	
Anampses neoguinaicus	LI			50	16			-	17
Bodianus axillaris	LI			30	19	50	20	-	20
Bodianus diana	KI, LI, OT	18	9	2	15			-	
Bodianus mesothorax	KI, LI, PS	100	13	47	18	54	20	-	
Cheilinus celebicus	KI	101	15					-	
Cheilinus chlorourus	LI, PS			104	32	47	22	-	36
Cheilinus fasciatus	KI, LI, PS, OT	100	23	108	36	104	35	-	30
Cheilinus orientalis	KI	91	13					-	
Cheilinus trilobatus	LI, PS			111	32	30	28	-	
Cheilinus undulatus	LI, PS			5	120	1	130	-	
Cheilio inermis	LI			3	23			-	
Choerodon anchorago	KI, LI, PS	39	23	1	24	105	35	-	
Choerodon cyanodus	PS					35	25	-	70
Choerodon fasciatus	LI, PS, OT			58	21	108	30	-	30
Choerodon graphicus	LI, PS, OT			2	18	6	25	-	
Choerodon schoenleini	LI, PS			10	80	14	30	-	
Cirrhilabrus cyanopleura	KI	107	8					-	
Cirrhilabrus punctatus	LI, PS			94	13	100	10	-	13
Cirrhilabrus walindi	KI	100	7					-	12
Coris aygula	LI			9	40			-	70
Coris batuensis	LI, PS, OT			106	15	71	14	-	16
Coris dorsomaculata	OT							-	20
Coris gaimard	LI, OT			47	33			-	40
Diproctacanthus xanthurus	KI, OT	104	9					-	
Epibulus insidiator	KI, LI, PS	97	18	104	35	103	35	-	35
Gomphosus varius	KI, LI, PS, OT	73	12	103	24	1	20	-	32
Halichoeres argus	KI	115	7					-	
Halichoeres biocellatus	PS					1	80	-	12
Halichoeres chloropterus	KI, LI, PS, OT	101	13	110	16	50	16	-	
Halichoeres hortulanus	KI, LI	99	14	99	27			-	27
Halichoeres margaritaceus	LI, PS, OT			120	12.5	7	6	-	12.5
Halichoeres marginatus	KI, LI, OT	100	11	84	17			-	17
Halichoeres melanurus	KI, LI, PS, OT	171	8	200	10.5	100	10.5	-	10.5
Halichoeres miniatus	KI, LI, PS, OT	109	8	12	11	110	10	-	
Halichoeres nebulosus	KI, LI, PS	100	8	108	10	6	8	-	
Halichoeres new	KI	100	11					-	
Halichoeres ornatissimus	PS					4	10	-	
Halichoeres prosopeion	KI, LI, PS	113	12	35	16	8	13	-	13
Halichoeres purpurescens	KI, OT	113	10					-	
Halichoeres richmondi	KI	95	11					-	
Halichoeres scapularis	KI	100	14					-	
Halichoeres trimaculatus	LI			29	21			-	20
Halichoeres wisata	KI	8	7					-	
Hemigymnus fasciatus	LI, PS			101	21	33	40	-	50
Hemigymnus melapterus	KI, LI, PS, OT	40	13	106	55	105	40	-	60
Hologymnosus annulatus	LI			1	14			-	
Hologymnosus doliatus	LI, OT			12	21			-	38
Labrichhys unilineatus	KI, LI, PS, OT	120	12	101	16	63	17	-	17.5
Labroides bicolor	OT							-	14
Labroides dimidiatus	KI, LI, PS, OT	107	9	136	11	103	11.5	-	11.5
Labroides pectoralis	KI, OT	15	6					-	
Labropsis alleni	KI	17	8					-	
Labropsis australis	LI, PS			5	9	9	9	-	10.5
Labropsis manabei	KI, OT	11	16					-	
Macropharyngodon choati	LI, PS			4	7	5	8	-	10
Macropharyngodon meleagris	LI, OT			29	15			-	15
Novaculichthys taeniorus	LI, OT			38	34			-	
Oxycheilinus digrammus	LI, PS			86	24	30	28	-	30
PSracheilinus filamentosus	KI, OT	101	7					-	
Pseudocheilinops ataenia	KI	100	4					-	
Pseudocheilinus evanidus	KI	78	8					-	
Pseudocheilinus hexataenia	KI, LI	100	6	15	7			-	7.5
Pseudolabrus guentheri	OT							-	18
Stethojulis bandanensis	KI, LI, OT	9	8	111	12.5			-	
Stethojulis interrupta	KI	12	6					-	13
Stethojulis strigiventer	LI, PS, OT			58	12	40	12	-	15
Stethojulis trilineatus	KI, LI, OT	100	8	4	14			-	
Thalassoma amblycephalum	KI, LI	109	7	146	13			-	
Thalassoma hardwicke	KI, LI, PS	110	13	101	18	24	20	-	18
Thalassoma jansenii	KI, LI, PS, OT	4	8	103	18	2	17	-	20
Thalassoma lunare	KI, LI, PS, OT	123	13	130	23	108	25	-	25
Thalassoma lutescens	LI, OT			24	16			-	24.7
Thalassoma purpureum	OT							-	43
Thalassoma quinquivitatum	LI, OT			26	20			-	
Thalassoma trilobatum	LI			2	19			-	
Mean body size of species			10.63		22.5		25.3		25.11
Total number of species		41		54		34		40	