Comparisons between the biological characteristics of three co-occurring and reef-dwelling labrid species at two different latitudes

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I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any tertiary education institution.

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ABSTRACT

The first aim of this PhD thesis was to obtain sound quantitative biological data for three abundant and co-occurring reef-dwelling labrid species, *i.e.* the Western King Wrasse *Coris auricularis*, the Brown-spotted Wrasse *Notolabrus parilus* and the Southern Maori Wrasse *Ophthalmolepis lineolatus*, in the Jurien Bay Marine Park (JBMP) and in the waters off Perth, 250 km to the south. These data were acquired to undertake the following. 1. Determine whether the maximum body size and age and the instantaneous growth rate of each of these species are consistent with the Metabolic Theory of Ecology (MTE). 2. Test the hypothesis that each species is a protogynous hermaphrodite and that the size and age at maturity and sex change of each species have a similar relationship to its maximum size and age. 3. Test the hypothesis that the food resources in temperate Western Australia are partitioned among each of the three species at both of the above locations and that the species compositions of the prey of each labrid species differs between locations as a result of the differences that are likely to be present in the relative abundances of prey at these two different latitudes. The specific aims associated with the different aspects of the biology and, where appropriate, hypotheses concerning those aspects, are given in the respective chapters.

The implications of the Metabolic Theory of Ecology (MTE) that certain variables for a species follow predictable trends with latitude, *i.e.* with temperature, was explored using data for three reef-dwelling species of labrid. The maximum length, mass and age of *C. auricularis*, *N. parilus* and *O. lineolatus*, when expressed as the average of the top 10 % of the values for those variables, were significantly greater (P generally < 0.001) in the waters off Perth at *c.* 32°S than in those of the Jurien Bay Marine Park at *c.* 30°S. While these latitudinal trends conform to the predictions of the MTE, the instantaneous growth rates of each species during the earlier part of life were similar at both latitudes. The greater rate of growth of each species throughout the

remaining and majority of life at the higher latitude suggests either that less energy is required for basal metabolism and/or physical activity in the cooler environment, or that these species are enzymatically better adapted to the lower temperature. In terms of interspecific comparisons, the rank order of maximum length, mass and growth (in terms of both length and mass at age) of these species is the same at both latitudes, but the precise order does vary slightly among these variables. This indicates that the three species respond to the differences between the temperature and other environmental variables at the two latitudes in a similar relative manner. The growth of *O. lineolatus* was least in both latitudes, irrespective of whether size was expressed in terms of length or mass. The growth of *C. auricularis* was greater, however, than *N. parilus* when using length, but either less or the same when employing mass, reflecting a greater body mass at length of the latter species. This difference is relevant as it would appear more appropriate to use mass as the indicator variable when considering predictions based on metabolic rate as this is related to temperature in ectotherms. Growth curves fitted to both the lengths and masses at age for the males of each species lay above and largely parallel to those for their females at all ages, indicating that sex change is size dependent. The rate of instantaneous growth at a given mass for each species, which began to diverge as mass increased, was consistently greater for the cooler than warmer environment (latitude), a trend that does not conform to the predictions of the MTE.

Examination of the histological characteristics of the gonads of a wide size and age range of *C. auricularis*, *N. parilus* and *O. lineolatus* from both the JBMP and waters off Perth, combined with the pattern of distribution of the lengths and ages of each sex, demonstrated that each of these three labrid species are protogynous hermaphrodites. The presence of two and young small *C. auricularis* with gonads consisting of both immature ovarian and testicular components suggests that this species, at least, may exhibit an early juvenile bisexual stage. All individuals of *C. auricularis*, *N. parilus* and

O. lineolatus with lengths less than 186, 162 and 223 mm, respectively, and ages less than 3.1, 3.0 and 4.7 years, respectively, were females, whereas the largest and oldest individuals of each species were males. The lengths and ages of the other bisexual individuals of *C. auricularis* and those of *N. parilus* and *O. lineolatus* all fell within the respective length and age ranges at which both females and males of those species were found. The oocytes of these bisexuals were all at the previtellogenic stage, whereas the testicular component always contained spermatocytes and sometimes advanced spermatids. These characteristics suggest that these individuals are changing from female to male.

While the spawning periods of each of *C. auricularis*, *N. parilus* and *O. lineolatus* in the two locations were similar, they differed markedly among those three species. This would reduce the potential for competition for food and space resources by the larvae and juveniles of these species. In the case of each species, a greater amount of energy was invested in gonadal development in the waters off Perth than in the JBMP, thereby parallelling the greater investment of energy in somatic growth in those waters. Thus, in the context of gonadal and somatic growth, each species is apparently better adapted to exploiting the environmental conditions found in the cooler temperatures at the higher latitude, *i.e.* waters off Perth, than to the warmer temperatures found at the lower latitude. *Coris auricularis* and *O. lineolatus* matured at a smaller length and younger age in the cooler waters off Perth than in the warmer environment of the JBMP, which is the converse of the pattern typically exhibited by ectothermic species. While *N. parilus* also matured at a younger age in the waters off Perth than in the JBMP, the difference was small and, in contrast to the other two species, maturation occurred at a greater length in the cooler environment.

This study confirmed that the dietary compositions of *C. auricularis*, *N. parilus* and *O. lineolatus* differed significantly with latitude (*i.e.* between JBMP at *c.* 30°S and *c.* 32°S off Perth), changed with increasing body size and almost invariably differed among those species in the more offshore reefs in each location in which they co-occurred. Latitudinal differences in the dietary compositions of each species in exposed reefs typically reflected greater contributions by large crustaceans, bivalve molluscs, echinoids and annelids to the diets in the waters off Perth than in the JBMP, whereas the reverse was true for gastropods and small crustaceans. The diet of each species exhibited similar, but not identical, quantitative changes with increasing body size, with the contributions of small crustaceans declining and those of large crustaceans and echinoids increasing, while that of gastropods underwent little change. Within the JBMP, the dietary compositions of both *C. auricularis* and *N. parilus* were similar in exposed and sheltered reefs and the same was true for *N. parilus* in the sheltered reefs and interspersed areas of seagrass. The latter similarity demonstrated that, in both of those divergent habitat types, *N. parilus* feeds on prey associated with either the sand or the macrophytes that cover and lie between the reefs. Although the main dietary components of each species were the same, *i.e.* gastropods, small crustaceans (mainly amphipods and isopods), large crustaceans (particularly penaeids and brachyuran crabs) and echinoids, their contributions varied among those species, which accounts for the significant interspecific differences in diet. *Coris auricularis* had the most distinct diet, due mainly to ingesting greater volumes of small crustaceans, *e.g.* amphipods and isopods, and lesser volumes of large crustaceans, *e.g.* brachyuran crabs, which was associated with a relatively narrower mouth and smaller teeth and the absence of prominent canines at the rear of the jaw. The above intra and interspecific differences in dietary composition would reduce, on the south-west coast of Australia, the potential for competition for food among and within these three abundant labrids, each of which belongs to different genera within the Julidine clade.

Publication resulting from this study

Chapter 5 of this thesis has been peer reviewed and published:

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Context of thesis

The establishment in 2005 of a management plan for the recently gazetted Jurien Bay Marine Park (JBMP) on the west coast of Australia (see below) was accompanied by the commencement of an extensive series of studies (e.g. Fairclough et al., 2011) aimed at providing data on the characteristics of the biota in this park. It was envisaged that these data could be used, in the future, as a baseline for detecting any changes that occur as a result from the spatial management regime developed for this marine park, which includes, for example, areas that are open and closed to fishing. The funding for this study provided the opportunity to elucidate the biological characteristics of three abundant labrid species in these waters and, together with comparisons of their biology in similar habitats further south, *i.e.* waters off Perth, constitute the basis for this PhD. It should be recognised, however, that as the new management plan for the park was only implemented in 2005, and thus at the same time as this study commenced, it was far too early to use the data obtained from this thesis to determine whether changes were occurring in the biota of the park. Emphasis has thus focused on using the biological data obtained for the three labrid species to explore, *inter alia*, some fundamental questions regarding the applicability of the Metabolic Theory of Ecology, factors associated with hermaphroditism and the extent to which food resources are partitioned among three relatively closely-related species in different habitats and regions.

1.2 Background

Many stocks of wild fish populations throughout the world have been subjected to heavy fishing pressure over the last few decades and this has frequently led to a significant reduction in the spawning biomass and thus the productivity of those stocks (Hilborn *et al.*, 2003; Myers & Worm, 2003; Pauly *et al.*, 2005; Hutchings *et al.*, 2010). The resultant decline in the abundance of higher trophic level species, and particularly of long-lived piscivores, has often been accompanied by a trophic cascade, *i.e.* leading to changes in the relative abundance of species belonging to lower trophic levels, such as pelagic planktivores, *e.g.* anchovies and sardines, and smaller invertebrates, all of which have shorter life cycles (Daskalov *et al.*, 2007; Casini *et al.*, 2008; Andersen & Pedersen, 2010). The reduction in top order predators in marine waters has also often led, however, to fishers moving their effort towards species at lower trophic levels, a phenomenon that has been termed “fishing down the marine food web” (Pauly *et al.*, 1998; Pauly & Palomares, 2005; Essington *et al.*, 2006; Smith *et al.*, 2011).

The above changes have the potential to influence the abundances of medium and small-sized species, such as those of many labrids that are particularly numerous over many reef habitats (Westneat, 1999; Parenti & Randall, 2000) and thus also to those of their invertebrate prey in those habitats (*e.g.* Morton *et al.*, 2008a). The latter group of teleosts incorporates the three species of labrids, (*i.e.* the Western King Wrasse *Coris auricularis*, the Brown-spotted Wrasse *Notolabrus parilus* and the Southern Maori Wrasse *Ophthalmolepis lineolatus*) that are abundant over reefs in south-western Australia and whose biology is the focus of the studies undertaken for this PhD.

Several large demersal fish species have been subjected to overfishing on the lower west coast of Western Australia (Wise *et al*., 2007; Fairclough *et al*., 2010). As a result, the Department of Fisheries in this State has recently imposed a number of regulations, which, by limiting the amount of fishing effort and thus the catches of recreational and commercial fishers, aim to reduce the extent to which the demersal fish species on this coast are exploited (Department of Fisheries, 2010). These species included the West Australian Dhufish (*Glaucosoma hebraicum*), Snapper (*Pagrus* *auratus*), Baldchin Groper (*Choerodon rubescens*) and Breaksea cod (*Epinephelides armatus*). The regulations involve, *inter alia*, the closure to commercial line and gillnet fishing along part of the coast and, in the case of recreational fishers, the introduction of licences for fishing from boats, seasonal closures for demersal fishing and reductions in the bag limits for high risk species (Department of Fisheries, 2011a).

It is logical to hypothesise that the reduction in the abundance of the above iconic species would lead to recreational fishers increasing their targeting of smaller fish species, such as the various species of medium and smaller wrasses (Labridae), which are abundant over reefs on the lower west coast of Australia (Hutchins, 2001; Delacy, 2008; Tuya *et al*., 2009). However, a shore-based creel survey of recreational anglers at Rottnest Island, a popular tourist resort a short distance from the mainland where Perth, the capital city of Western Australia is located, found that, while these small labrids are caught by these anglers, they are generally not yet retained in appreciable numbers (see Smallwood *et al*., 2006; Sumner *et al*., 2008; Appendix 2 in Fletcher & Santoro, 2010). Yet, it seems inevitable that, with the rapid increase in the number of recreational fishers in the State as a result of population expansion and the good eating qualities of labrids (Hutchins & Swainston, 1999), the low retention of these species is unlikely to continue.

Although the tightening of fishing regulations represents one way of overcoming the problem of overfishing, the introduction of marine protected areas (MPAs), in which fishing is restricted or banned, represents another complementary way of tackling this issue (Bohnsack & Ault, 1996; Russ & Alcala, 1996; Apostolaki *et al*., 2002; Lester *et al*., 2009). MPAs, which are defined as "areas of the ocean designated to enhance conservation of marine resources" (Lubchenco *et al*., 2003), include, in Western Australia, marine parks, such as the recently-established Jurien Bay Marine Park (Department of Conservation and Land Management, 2005). While the level of protection afforded to fish stocks within MPAs varies, such areas can yield multiple benefits, including the protection of habitat, conservation of biodiversity and the recovery of depleted stocks of exploited species, and provide sites for scientific investigation, baseline information, education and recreation (Allison *et al.*, 1998; Lester *et al.*, 2009). The establishment of protected areas may be of little benefit, however, to highly mobile species that move considerable distances and neither occupy a home range nor revisit specific sites repeatedly, *e.g.* spawning aggregation sites (Kenchington, 1990). Furthermore, while any benefits of a MPA may appear within three years and increase for many years (Gell & Roberts, 2003; Halpern, 2003; Watson *et al.*, 2007), the response to that establishment can be species specific, slow and vary with the boundary configuration of the MPA and may thus not become apparent for a far longer period of time (Russ *et al.*, 2005; Barrett *et al.*, 2007).

1.3 The Jurien Bay Marine Park

The Jurien Bay Marine Park (JBMP), within which the first location studied during this thesis is situated, was formally gazetted in August 2003. It is located *c.* 250 km north of Perth on the central west coast of Australia, extends *c.* 90 km along the coast from Green Head at 30° 4.18’ S southwards to Wedge Island at 30° 49.88’ S and covers an area of *c.* 824 km^2 (Department of Conservation and Land Management, 2005; see Fig. 2.1 in Chapter 2). This park encompasses waters that extend outwards from the coastline for *c.* 5.6 km (Department of Conservation and Land Management, 2005). The main objectives of the JBMP are to maintain ecosystem structure and function within that unique area of the western coast of Australia, by facilitating and managing its recreational and commercial activities within an equitable and ecologically-sustainable framework and promoting education, nature appreciation and scientific research (MPRSWG, 1994; Department of Conservation and Land Management, 2005).

The establishment of the JBMP in 2003 led to the Government of Western Australia funding comprehensive research of its environment and biota to produce benchmark data for the future and thus, *inter alia*, detailed information on the biology of the labrids *C. auricularis*, *N. parilus* and *O. lineolatus*, which are abundant in that park (Fairclough *et al.*, 2011). This initiative provided the stimulus to obtain directly comparable biological data for the same three species in the readily accessible marine waters at *c.* 32°S off the Western Australian capital city of Perth, and thereby at different latitudes (and thus also temperatures), but well within the geographical limits of the distributions of these species (see section 1.6).

The JBMP is dominated by intertidal and subtidal reef platforms, seagrass meadows and sparsely or unvegetated subtidal and intertidal sand habitats (Department of Conservation and Land Management, 2005). The extensive limestone reef system in the JBMP is representative of that found along the central west coast of Australia and represents a major marine ecosystem within the West Coast Bioregion (Searle & Semenuik, 1985; IMCRA, 1998). This bioregion includes the waters off Perth, which are located further south and represent the second location in which the biology of three labrid species were studied for this thesis and thus facilitate comparisons between the biological characteristics of those species at different latitudes.

1.4 Latitudinal trends in biological characteristics

Bergmann's rule (1847) draws attention to the tendency for endotherms to increase in body size with increasing latitude and thus with decreasing ambient temperature (Angilletta *et al.*, 2004a, b). According to this rule, the individuals of a particular mammal or bird species tend to have a greater body mass in colder than warmer areas. Subsequent studies indicated that, in general, this rule applied not only to endotherms, but also to ectotherms, such as fish, turtles and amphibians (Atkinson, 1994; Huey *et al.*, 2000; Ashton, 2002, 2004; Ashton & Feldman, 2003), although it did not apply to most species of lizards and snakes (Ashton & Feldman, 2003). In a collation of the results of 61 studies of aquatic ectotherms, Atkinson (1995) found that increased rearing temperature, which was apparently not stressful for growth and development, led to a reduction in organism size at a given developmental stage.

Compilations of data collected in the field for ectotherms, such as fishes, demonstrate that several biological variables, other than body size, often vary with latitude and thus temperature. Thus, a greater body size of ectotherms at higher latitudes is typically parallelled by a greater life span, size and age at maturity and reproductive output, and a slower growth rate early in life (Ray, 1960; Atkinson, 1994; Berrigan & Charnov, 1994; Walters & Hassall, 2006; Munch & Salinas, 2009). The positive relationship between the metabolism of a species of ectotherm and temperature led to the development of a number of ecological theories, including the Metabolic Theory of Ecology (MTE) (Angilletta *et al.*, 2004a; Brown *et al.*, 2004a; Charnov & Gillooly, 2004). The MTE attempts to provide a universal and integrated framework for predicting, on the basis of the relationship between metabolism and temperature, the latitudinal trends that would be expected in the above biological variables.

Some of the above latitudinal trends are occasionally not followed by a species in a particular geographical region, including Western Australia. For example, while the maximum length and age of the Foxfish *Bodianus frenchii* were greater at the higher latitude (south coast of Western Australia) than the lower and thus warmer latitude (lower west coast of Australia), and thus followed the trends predicted by the MTE, this species grew more rapidly and matured earlier at the former latitude and therefore exhibited the opposite trend to that predicted by the MTE (Cossington *et al.*, 2010).

Furthermore, despite marked differences in temperature, the growth of the sparid *Rhabdosargus sarba* in subtropical waters and temperate coastal marine waters on the west coast of Australia were essentially the same (Hesp *et al*., 2004). As the growth of this species in an estuary in the temperate region was greater than in the adjacent and less productive marine waters, the influence of habitat can apparently override that of temperature.

The exceptions to the trends predicted by the MTE have led certain authors to question the universal applicability of this theory. For example, it has been suggested that organisms contain a range of evolutionary modifications that render reaction rate relatively independent of the temperature at which an organism is adapted to live (Hochachka & Somero, 2002; Clarke, 2004; Clarke & Fraser, 2004).

1.5 Hermaphroditism

Hermaphroditism has been defined as the expression of both male and female function in a single individual, thereby distinguishing it from gonochorism when all individuals of a species or population reproduce exclusively as either a male or female during their lives, and irrespective of their gonadal morphology (Sadovy de Mitcheson & Liu, 2008). In their comprehensive review of hermaphroditism in teleosts, those authors have documented in detail the development of our knowledge of hermaphroditism in these bony fishes since the pioneering studies of Reinboth (1962) and Atz (1964). They have also emphasised the need to distinguish between functional hermaphroditism and other forms of hermaphroditism. A species or population is thus considered to exhibit functional hermaphroditism when a proportion of its individuals function as both sexes at some time during their lives. Functional hermaphrodites can then be subdivided into either simultaneous or sequential hermaphrodites (Sadovy & Shapiro, 1987; Hesp & Potter, 2003). In the former category, individuals can reproduce both as female and male at the same time, or within a short period of time, whereas, in the latter category, individuals change from the functional form of one sex to the functional form of another sex.

Sequential hermaphrodites are either protogynous, which involves a change from a functional female to a functional male, or protandrous, in which a functional male changes to a functional female (Sadovy de Mitcheson & Liu, 2008). Among sequential protogynous hermaphrodites, a species may exhibit monandry or diandry. In monandry, the males are derived exclusively from adult females and are thus termed secondary males (Sadovy & Shapiro, 1987). In contrast, in diandry, the males can be derived from small juveniles that contain an undifferentiated gonad and are therefore referred to as primary males, as well as from adult females (Sadovy & Shapiro, 1987; Sadovy de Mitcheson & Liu, 2008). Similar trends are found among protandrous species, with those in which all males become females belonging to the monogyny category and those where some males become females representing the digyny category. Sadovy de Mitcheson & Liu (2008) have emphasised the importance of satisfying certain criteria before concluding that a species represents a particular category of functional hermaphrodite. Such diagnostic criteria include, for example, the need to examine gonads histologically during key stages in development and obtaining data for a wide length and age range.

It has been proposed that sex change in hermaphroditic species is favoured when the reproductive success of one sex increases more rapidly than that of the other sex as size or age increases (Ghiselin, 1969; Warner, 1975, 1988; Charnov, 1993; Munday *et al.*, 2006). This size-advantage hypothesis predicts that sex change will occur at a younger age in populations with faster growth rates and/or higher mortality rates (Warner, 1988). Various social factors can influence the timing of sex change. For example, the loss of the large dominant male in harem social groups that consist of one large male and a few mature females can result in the largest female changing to a male (Robertson, 1972).

As fishers usually retain the largest fish, the largest and most fecund females of protogynous species as well as the large males are removed. This, in turn, can lead to a modification of aspects of the life histories and other characteristics of such species (Bannerot *et al.*, 1987; Ross, 1990; Alonzo & Mangel, 2005), *e.g.* reduction in the maximum length and age and the length and age at sex change, such as has occurred with another labrid, the Venus tuskfish *Choerodon venustus*, in eastern Australia (Platten *et al.*, 2002; see also Heppell *et al.*, 2006).

1.6 Competition for food resources

The coexistence of abundant fish species is often considered to be achieved by the partitioning of resources along one or more of three axes, *i.e.* food, space and time, with the first regarded as the most important (Ross, 1986). The partitioning of food and/or spatial resources among those closely-related, and thus morphologically similar species that co-occur, can be facilitated through those species feeding on different prey, occupying different habitats and/or by utilising either of these resources at different stages in their life cycle (Ross, 1986; Platell & Potter, 2001; Shepherd, 2005; Fairclough *et al.*, 2008; Morton *et al.*, 2008a, b; Morton & Gladstone, 2011).

Marked differences in the types of food that are ingested by the various teleost species are usually related to differences in mouth morphology and feeding behaviour (Wainwright, 1991; Motta & Kotrschal, 1992; Boyle & Horn, 2006; Platell *et al.*, 2010). Thus, planktivorous pelagic species, such as clupeids, which feed on zooplanktonic copepods, possess small terminal or subterminal mouths with numerous, fine and elongate gill rakers (*e.g.* Tanaka *et al.*, 2006). In contrast, piscivorous fish species, *e.g.* serranids, tend to have large mouths and sharp canines that enable them to grasp or seize and engulf whole prey (St John, 1999; Platell *et al.*, 2010). Furthermore, fish species, including those belonging to the Labridae, which feed on hard-bodied prey, *e.g.* gastropods and molluscs, typically have robust jaws and dentition which enable them to both extract and crush those prey (*e.g.* Gillanders, 1995a; Denny & Schiel, 2001; Platell *et al.*, 2010). However, quite subtle differences in dentition, mouth morphology and/or feeding behaviour can represent adaptations to ingesting the same suites of prey but in differing proportions (Hyndes *et al.*, 1997; Labropoulou & Markakis, 1998; Platell *et al.*, 1998; Mabragaña & Giberto, 2008; Morote *et al.*, 2010).

Many of the early comparisons between the diets of different species of fishes were largely descriptive, with such comparisons being based, for example, only on an account of the frequency of occurrence of dietary items in the stomachs of those species or on the percentage volumetric contributions of the dietary items to the total amount of food ingested by those fish species (Hynes, 1950; Hyslop, 1980; Lindquist *et al.*, 1994; Deady & Fives, 1995; Marshall & Elliott, 1997). During recent years, however, the ability to compare the diets of *a priori* groups has benefited greatly from the use of multivariate statistical analyses of the types that were developed for comparing the species compositions of faunal communities (Gillanders, 1995a; Platell & Potter, 2001; Clarke & Gorley, 2006; Connell *et al.*, 2010). These methods of analyses have enabled biologists to use Analysis of Similarities (ANOSIM) tests (Clarke, 1993) to determine statistically whether there are significant differences between the dietary compositions of *a priori* groups, such as species or their size groups, or of those of individual fish species that were caught, for example, in different seasons and/or regions. The values for the *R*-statistic in this test (Clarke, 1993) can then be employed to elucidate the extent of differences between the dietary compositions of different groups.

The above statistical tests thus detect differences between the diets of different *a priori* groups, even when the same suite of prey are present in the guts of those groups, but in different relative proportions (*e.g.* Platell *et al.*, 1998). These tests can then be complemented by the use of Similarity Percentages (SIMPER) analyses (Clarke, 1993) to tease out which dietary categories typify the diet of an *a priori* group and which distinguish between the diets of *a priori* groups. More recently, the development of Permutational Analysis of Variance (PERMANOVA- Anderson, 2001; Anderson *et al.*, 2008) has enabled biologists to test simultaneously whether there are interactions between each of the various factors that might influence the interpretations of the influence of those factors on the dietary compositions of *a priori* groups. Such factors could include, *inter alia,* species, size class, season, location and/or habitat type. This ability to investigate simultaneously the extent of any interactions between these factors brings these multivariate tests into line with univariate tests such as Analysis of Variance (ANOVA). The advent of the use of these statistical tests for dietary analyses therefore represented a crucial advance in the ability to determine whether there are genuine differences in the dietary compositions of *a priori* groups and to use the results to provide the basis for a more rigorous approach to elucidating whether food resources are partitioned among species. These tests are thus particularly useful for examining whether there are differences in the dietary compositions of morphologically similar species that are abundant and co-occur in the same habitat, such as was achieved with three labrid species over reefs in eastern Australia (Morton *et al.*, 2008a) and with five such species in seagrass in Western Australia (MacArthur & Hyndes, 2007).

1.7 The Labridae

1.7.1 Diversity, distribution and body size

The Labridae (wrasses), which is now considered to include the scarids and odacids, is represented by 82 genera and at least 600 species (Westneat & Alfaro, 2005; Kazancioğlu *et al.*, 2009). This family, the members of which are found in continental shelf waters of tropical and temperate oceans in many regions of the world (Westneat & Alfaro, 2005; Allen *et al.*, 2006), is one of the most morphologically and ecologically diverse of the numerous fish families that are found on coral and rocky reefs (Westneat *et al.*, 2005). Some labrid species do undergo, however, a habitat shift with increasing body size (*e.g.* Green, 1996; Fulton & Bellwood, 2004; Shepherd & Brook, 2007). Among labrids, the most common reproductive strategy is protogynous hermaphroditism (*e.g.* Robertson & Warner, 1978; Jones, 1980; Gillanders, 1995b; Cardinale *et al.*, 1998; Candi *et al*., 2004; McBride & Johnson, 2007; Sadovy de Mitcheson & Liu, 2008; Shepherd *et al.*, 2010).

Although labrid species range in maximum total length from the 40 mm recorded for the Minute Wrasse *Minilabrus striatus*, to as high as 2300 mm for the Humphead Maori Wrasse *Cheilinus undulatus*, the majority are small, with maximum total lengths less than 200 mm (Parenti & Randall, 2000; Westneat & Alfaro, 2005; Allen *et al*., 2006). Most of the species with maximum lengths less than 400 mm typically live for less than ten to fifteen years (*e.g.* Shepherd & Hobbs, 1985; Sayer *et al.*, 1996; Choat & Robertson, 2002; Choat *et al.*, 2003; Delacy, 2008; Morton *et al.*, 2008b), while a few medium-sized and larger species in temperate waters, such as the Foxfish *B. frenchii* and the Western Blue Groper *Achoerodus gouldii*, can live for up to at least 70 years (Coulson *et al.*, 2009; Cossington *et al.*, 2010).

Labrids, such as the Californian Sheephead *Semicossyphus pulcher*, the Tautog *Tautoga onitis* and *C. undulatus*, make an important contribution to recreational and/or commercial fisheries in various regions throughout the wide distribution of this family (Sadovy *et al.*, 2003; White *et al.*, 2003; Topping *et al*., 2005; Sadovy de Mitcheson *et al.*, 2010). Indeed, *C. undulatus* is listed as "endangered" on the IUCN red list, having been heavily fished for the trade in live reef fish (Russell, 2004). As pointed out earlier, the Baldchin Groper *C. rubescens* (Labridae) is one of the species that has been heavily fished in Western Australia to the point where it was considered necessary to introduce legislation to reduce fishing effort. In Tasmania and Victoria, the live fish trade for the smaller Purple Wrasse *Notolabrus fucicola* and Bluethroat Wrasse *Notolabrus tetricus* had expanded rapidly by the early 1990s, which led to legislation to reduce the fishing effort for these species (Lyle & Hodgson, 2001; Smith *et al.*, 2003). Poor management of this type of fishery can have deleterious effects on the stocks of target species, as has occurred in south-east Asia with *C. undulatus* (Sadovy *et al.*, 2003).

1.7.2 The three most abundant labrid species in coastal marine waters of south-western Australia

The Western King Wrasse *Coris auricularis*, the Brown-spotted Wrasse *Notolabrus parilus* and the Southern Maori Wrasse *Ophthalmolepis lineolatus* were among the five species of this family most frequently observed during a visual census of reefs along 800 km of the south-western Australian coast (Tuya *et al.*, 2009). They were also abundant over the numerous reefs studied by Hutchins (2001) and Delacy (2008) in south-western Australia. Each of the above three species, which all belong to the diverse Julidine clade (Kazancioğlu *et al.*, 2009), are of similar size, with *C. auricularis*, *N. parilus* and *O. lineolatus* attaining maximum total lengths (L_T) of 400, 490 and 400 mm, respectively (Edgar, 2008; Hutchins & Swainston, 1999; Gomon *et al.*, 2008). At present, the recreational fishing regulations for the West Coast Bioregion do not contain a minimum legal length for the retention of any of these three species (Department of Fisheries, 2011a). Although this Department considers these species to be at low risk to the effects of fishing, its regulations do restrict the combined catch of these species by each angler to 30 fish per day (Department of Fisheries, 2011a).

The Western King Wrasse *Coris auricularis* (Valenciennes 1839)

Coris auricularis, which is endemic to Western Australia, is found in coastal marine waters from the Recherche Archipelago, at 34ºS 112ºE on the south coast of Western Australia, westwards and northwards along the west coast of Australia to Coral Bay at 23ºS 114ºE (Hutchins & Swainston, 1999). This species, which belongs to a genus whose members are known as rainbow wrasses, is most abundant over reefs and nearby sandy areas which are found in water depths up to 45 m (Hutchins & Swainston, 1999; Gomon *et al.*, 2008). *Coris auricularis* undergoes dramatic changes in colour during its life cycle. The small juveniles are blackish, with a narrow white band mid-dorsally from snout to tail and a broader white band mid-laterally (Gomon *et al.*, 2008). The females are pale greenish white, with a reddish brown band tapering from the snout, through the eye and along each side of the body just above the lateral line (Fig. 1.1; Gomon *et al.*, 2008). The males are salmon pink, with a whitish chin and throat, a blue spot on the edge of the operculum and a broad white vertical band towards the posterior end of the abdomen (Fig. 1.1). The juveniles and small females act as 'cleaner fishes' by removing skin parasites from other fishes (Edgar, 2008; Gomon *et al.*, 2008; *pers. obs.*). The maximum age of this species is estimated to be nine years (Delacy, 2008).

The Brown-spotted Wrasse *Notolabrus parilus* (Richardson 1850)

Notolabrus parilus, which occurs in coastal marine waters from Victor Harbour in South Australia at 35ºS 139ºE westwards and northwards to Shark Bay in Western Australia at 26ºS 113ºE, is most abundant in shallow, algae-covered rocky reefs and in waters up to 20 m deep (Hutchins & Swainston, 1999; Gomon *et al.*, 2008). This species is also abundant in seagrass meadows along the lower west coast of Australia (MacArthur & Hyndes, 2007). The juveniles and females are pale brown or green, with

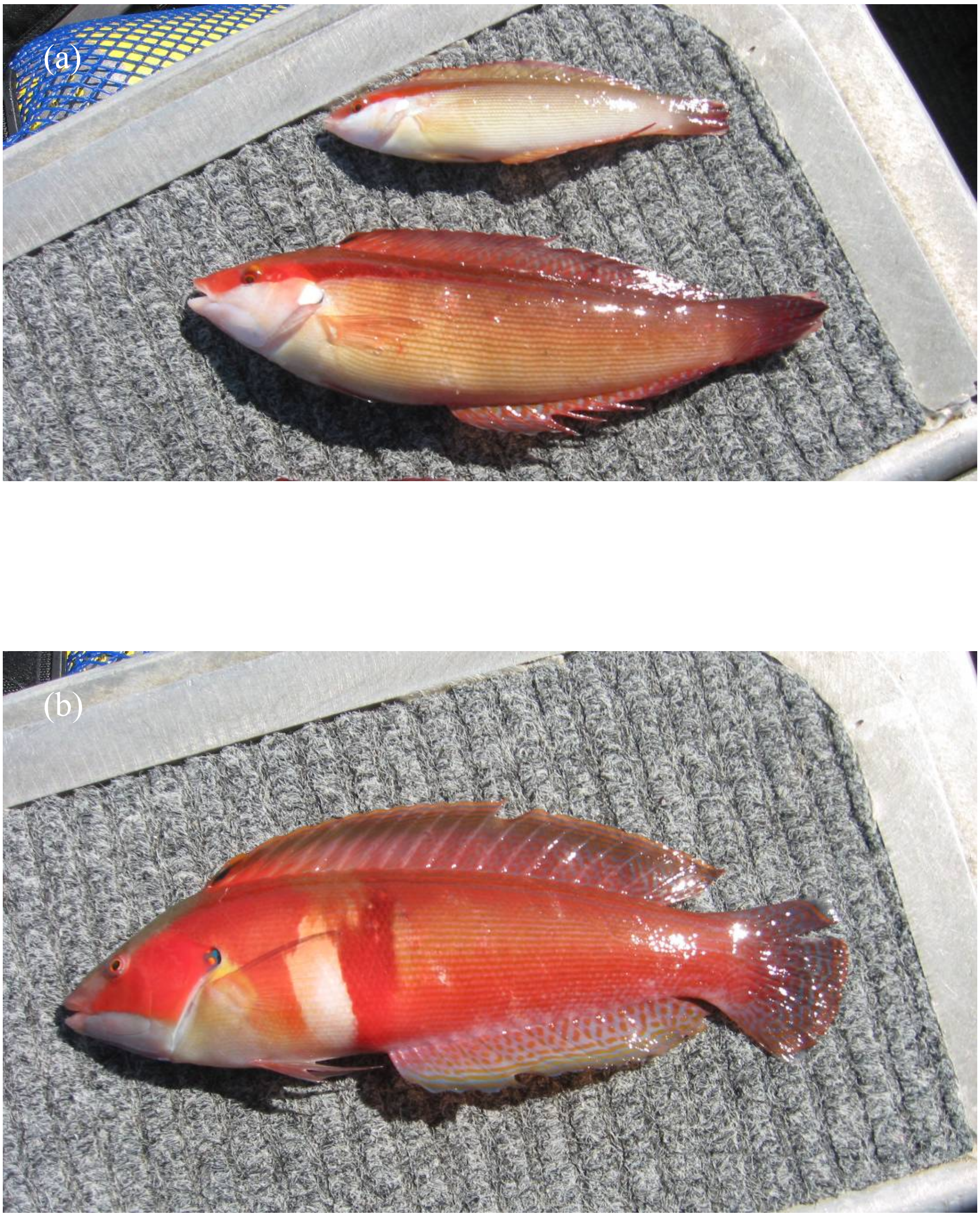


Figure 1.1. Photographs of (a) two females (*c.* 120 mm and 170 mm) and (b) a male (*c.* 320 mm) of *Coris auricularis*.

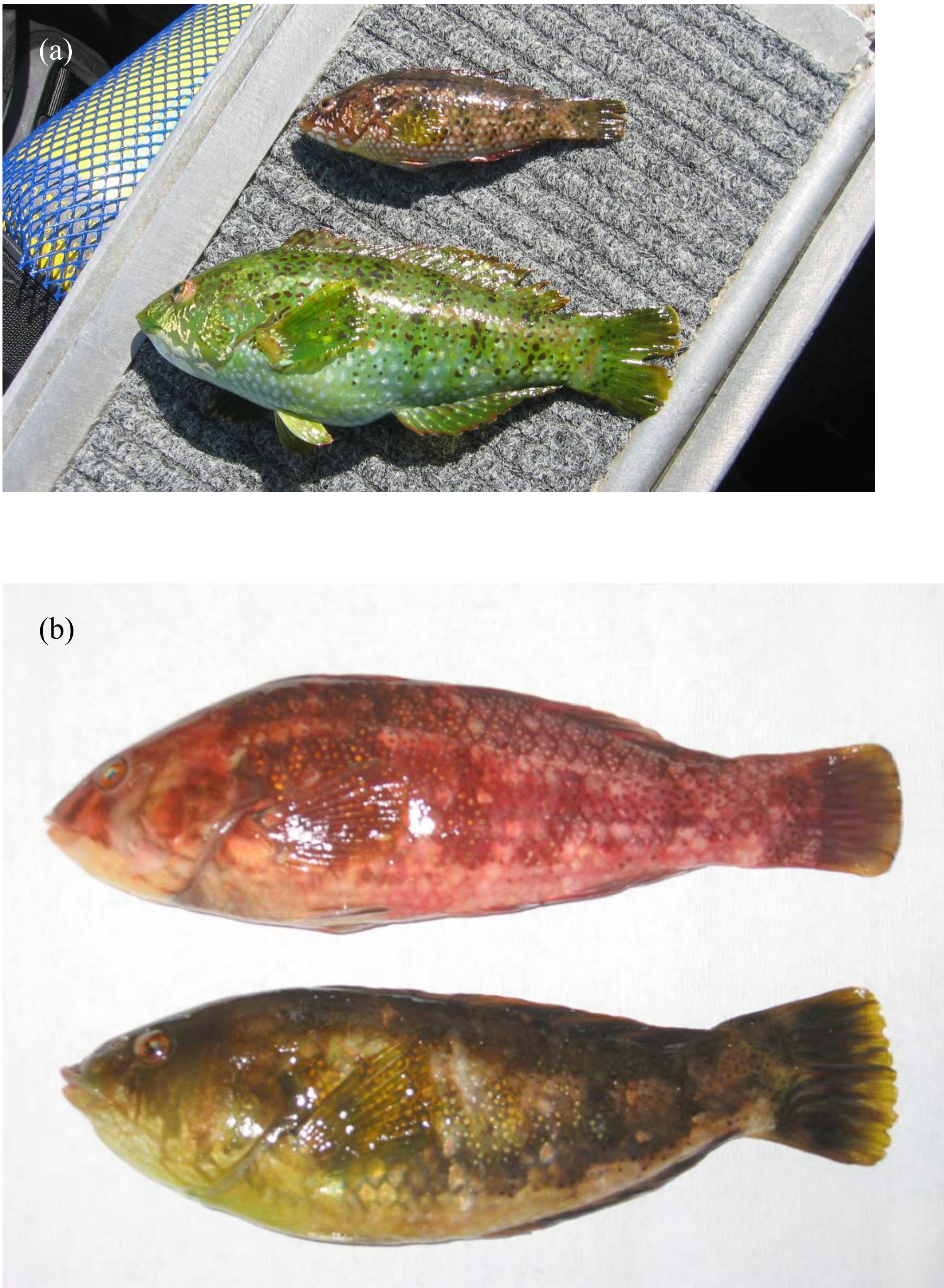


Figure 1.2. Photographs of (a) two females (*c.* 100 mm and *c.* 220 mm) and (b) two males (*c.* 340 mm) of *Notolabrus parilus*.

their heads and bodies containing dark markings (Fig. 1.2a; Gomon *et al*., 2008). The males are dark reddish brown to chocolate brown, with a broken horizontal white band under the lateral line and their scales have gold, dark brown or whitish centres, giving the body a marbled or spotted appearance (Fig. 1.2b). The maximum recorded age of *N. parilus* is nine years (Delacy, 2008).

The Southern Maori Wrasse *Ophthalmolepis lineolatus* (Valenciennes 1839)

Ophthalmolepis lineolatus is found in the coastal marine waters from Gladstone *c.* 25ºS 151ºE on the east coast southwards, including Tasmania, eastwards throughout southern Australia and northwards to the Houtman Abrolhos in Western Australia at 28ºS 114ºE, (Allen *et al.*, 2006; Kuiter, 2006; Gomon *et al.*, 2008). This species is common on the coastal reefs of south-eastern and south-western Australia, particularly in waters less than 30 m in depth (Hutchins & Swainston, 1999; Gomon *et al.*, 2008) and preferring reef habitats deeper than 6 m in south-eastern Australia (Kingsford & Carlson, 2010). The common name comes from the resemblance between the blue markings on the head and those of the tattoos of New Zealand Maoris (Fig. 1.3; Gomon *et al.*, 2008). The juveniles and females possess a reddish orange band on the upper and lower thirds of the body, with white colouration mid laterally and ventrally (Gomon *et al.*, 2008). The males are reddish brown dorsally and yellowish brown ventrally, with a distinctive black lateral band along both sides of the body, on either side of which is a band of blue spots (Fig. 1.3; Gomon *et al.*, 2008). The maximum estimated age for this species is eight years on the west coast of Australia (Delacy, 2008) and fourteen years in eastern Australia (Morton *et al.*, 2008b).

Figure 1.3. Photograph of *Ophthalmolepis lineolatus* showing the juvenile (*c.* 150 mm), female (*c.* 230 mm) and male (*c.* 290 mm) colour phases.

1.8 Aims

The overall aim of this PhD thesis was to obtain sound quantitative data for major biological characteristics of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* in the JBMP and in the waters off Perth *c.* 250 km further south, where water temperatures are lower, in order to address the following broad objectives. 1. Determine whether any differences between the maximum body size and age and the instantaneous growth rate of each of these species at the above two locations are consistent with the Metabolic Theory of Ecology (MTE) and/or other related ecological theories. 2. Determine the characteristics of the reproductive biology of each species and thus whether it is hermaphroditic and, if so, the type of hermaphroditism. 3. Test the hypothesis that the food resources in temperate Western Australia are partitioned among each of the three species at both of the above locations and that the relative abundances of species compositions of their prey is likely to differ among the two widely-spaced sampling localities. 5. Provide sound data of the type that would be valuable for fisheries and environmental managers when developing plans for managing the fisheries and other resources of reefs on the west coast of Australia. In the case of fisheries management, such data will be particularly valuable if the above three labrid species become increasingly targeted. It should be noted that, as the JBMP was only established in 2003, the data produced in this thesis were obtained specifically for comparing fundamental aspects of the biology of the three species and could not be used to explore the influence of such an introduction on the fish fauna of this park.

The specific aims associated with the studies on the different aspects of the biology and, where appropriate, the hypotheses concerning those aspects, are provided in Chapters 3, 4 and 5.

CHAPTER 2

GENERAL MATERIALS AND METHODS

2.1 Sampling localities

Jurien Bay Marine Park

The Jurien Bay Marine Park (JBMP) is located on the central west coast of Western Australia, *c.* 250 km north of Perth (Fig. 2.1), and was formally declared in August 2003 (Department of Conservation and Land Management, 2005). This marine park, whose mid-point is located at 30º 25’S, 115º 00’E, extends from the waters of Dynamite Bay at Green Head (30º 4.18’ S) to Wedge Island (30º 49.88’ S) *c.* 90 km further south along the shore and from the low water mark westwards to *c.* 5.6 km from the territorial baseline and covers an area of *c.* 824 km^2 (Department of Conservation and Land Management, 2005). The outer limestone reefs, which run parallel to the shore at a distance of 5 - 7 km, are located in water depths of 10 - 25 m and are exposed to substantial wave action. These reefs, and the islands with which they are associated, protect inshore reefs located 0.5 - 4 km from the shore and typically in water depths < 10 m. The series of limestone outcrops, which comprise both the outer exposed and inner sheltered reefs, are separated by sandy areas, with sand also being deposited on substantial areas of these reefs (Fig. 2.2). Macrophytes, such as the macroalgae *Ecklonia radiata* and *Sargassum* spp., are frequently found on the reefs and the seagrass species *Amphibolis griffithii* and *A. antarctica* often form thick canopies on the upper surface of reefs (Howard, 1989; Womersley & King, 1990; Huisman, 2000).

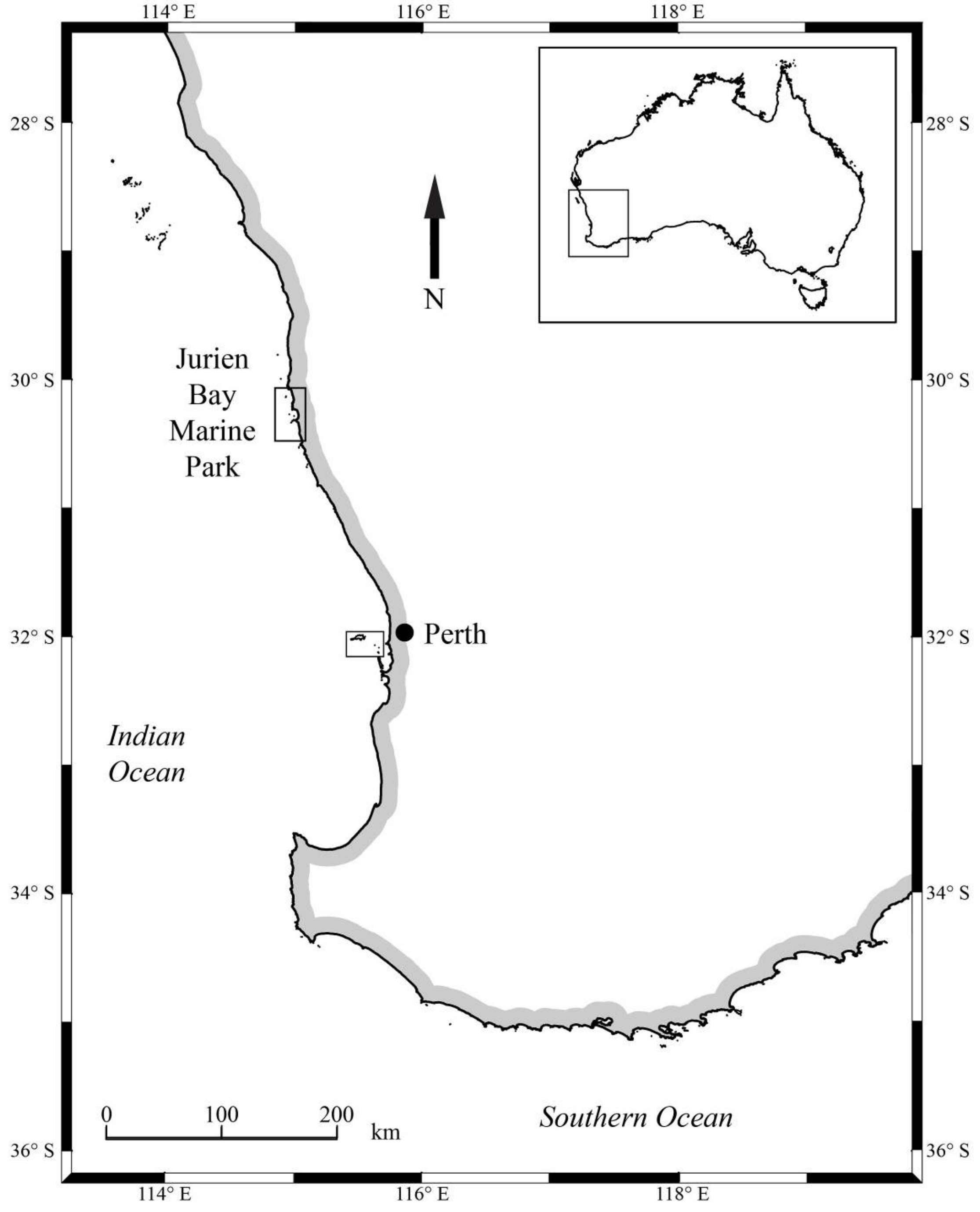


Figure 2.1. Map of Western Australia showing the location of the Jurien Bay Marine Park (JBMP) and the Perth metropolitan waters in which fish were sampled.

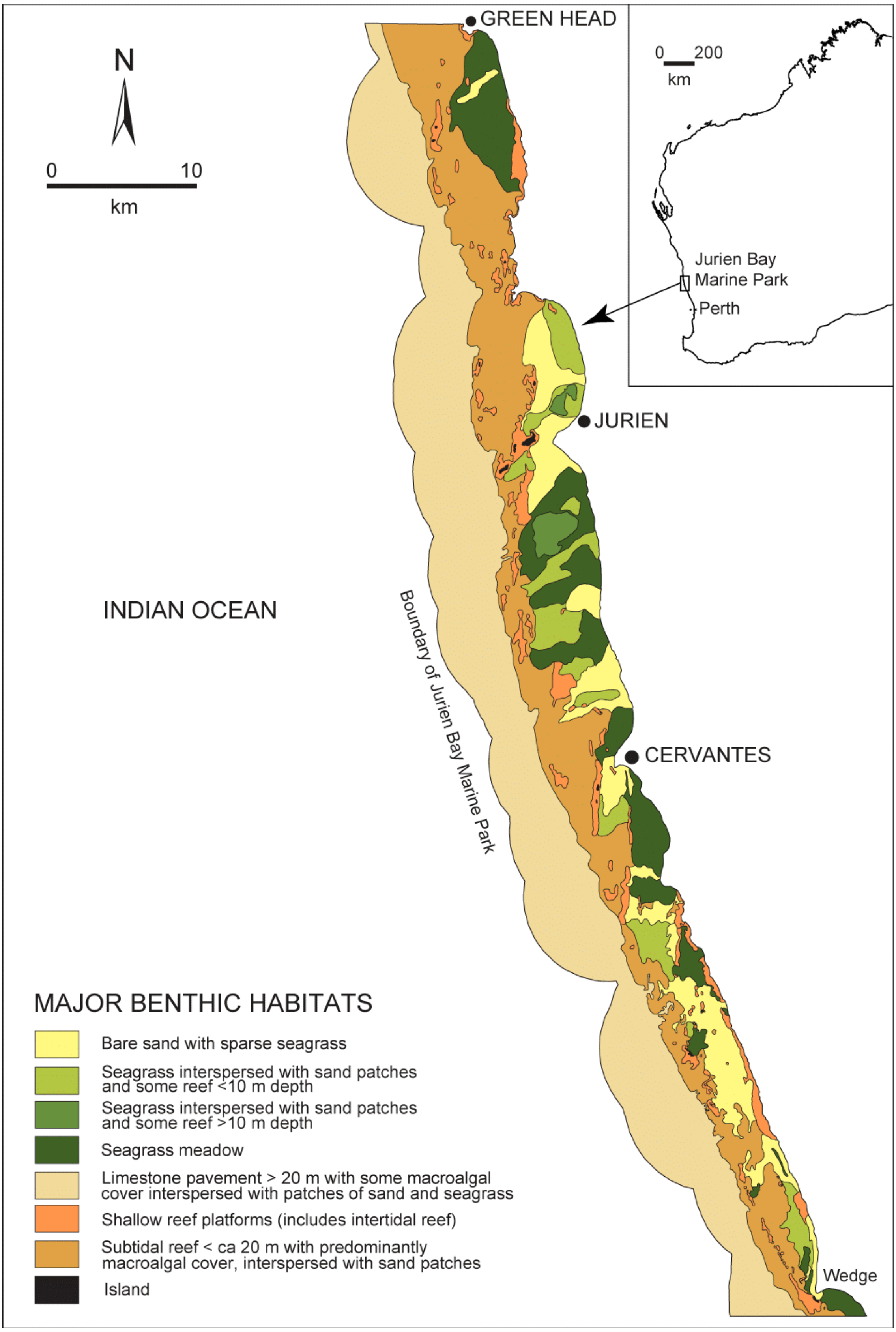


Figure 2.2 The main benthic habitats represented within the Jurien Bay Marine Park (JBMP). Derived from the Jurien Bay Marine Park Management Plan 2005 – 2015 (Department of Conservation and Land Management, 2005).

Rottnest Island, Perth metropolitan waters

Rottnest Island is located on the central west coast of Western Australia *c.* 17 km from Perth and at 32º00'S and 115º30'E (Fig. 2.1). It lies close to the outer edge of the continental shelf and is at the extreme eastern end of a series of rocky limestone ridges, which may be emergent or submarine (Wells & Walker, 1993). These reefs, which lie *c.* 9 km offshore from the mainland just to the south of Perth, are exposed to oceanic swell and are typically situated in water depths of 7 – 20 m. There are no well-developed inshore, sheltered reefs off Perth comparable with those in the JBMP. Rottnest Island lies in warm temperate waters and in an area of marine biogeographical overlap, with the marine fauna dominated by warm temperate southern Australian species (Wells & Walker, 1993).

2.2 Sampling regime

Coris auricularis, *Notolabrus parilus* and *Ophthalmolepis lineolatus* were sampled by line and spear fishing and trapping at numerous sites over reefs in the JBMP and in the waters off Perth in each season between the summers of 2005 and 2008. Note, however, that the number of days of sampling in the JBMP in each calendar month was *c.* six times greater in the JBMP than in the waters off Perth. This reflected the fact that a wide range of sites and habitats throughout the JBMP were required to be sampled as part of the overall study of the biota of this park. As the three labrid species were very abundant in the JBMP, this sampling programme resulted in the collection of large numbers of each of these species, which then became available for the range of analyses undertaken during this thesis. The sampling sites were distributed along distances of *c.* 40 km in the JBMP, south of Green Head and North of Cervantes (Fig. 2.2) and *c.* 20 km in the waters off Perth around Rottnest in water depths of between *c.* 5 – 35 m (Fig. 2.1).

Most individuals of each of the above three species (*c.* 70 %) were caught by line fishing, employed a small long-shank hook with coral prawns (*Metapenaeopsis* spp.) used as bait, yielded good samples of all but the smaller individuals of those species. The smaller fish were caught in fish traps, measuring 400 x 240 x 240 mm, which were covered with nylon (mesh size 1.5 mm) and contained a 50 mm diameter circular entrance at each end using the Australian Pilchard *Sardinops sargax* as bait. Spear fishing, using a small five-pronged gidgie tip, was employed to supplement the numbers of small fish. Sampling by all methods was undertaken between dawn and dusk. All fish were euthanased immediately using an ice slurry in accordance with permits W1069/04 and W1101/04 issued by the Murdoch University Animal Ethics Committee.

Mean monthly offshore sea surface temperatures for the JBMP and waters off Perth in 1995-2008 were derived using a combination of data from National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer (AVHRR) satellite imagery and from sea surface temperatures recorded by shipping and drifting buoys (see Reynolds & Smith (1994) for methods).

2.3 Laboratory procedures

The total length (L_T) and wet body mass (M_T) of each fish were recorded to the nearest 1 mm and 0.1 g, respectively. The two sagittal otoliths of each fish were removed, cleaned, dried and stored in paper envelopes. The gonads of the majority of fish could be macroscopically distinguished as either ovaries or testes, thereby enabling those individuals to be sexed. These gonads were removed, weighed to the nearest 0.01 g and their stage of development recorded, following modified schemes from Laevastu (1965) and Rhodes and Sadovy (2002) (see Tables 4.1, 4.2 in Chapter 4). The gonads of fish that could not clearly be identified as either ovaries or testes, together with those of a wide size range of a substantial subsample of each species from different times of the year were preserved in Bouin’s fixative for *c.* 24 h and sectioned for histology (for full details, see Chapter 4).

The details relating specifically to the topics covered in each chapter are given in the relevant chapter, *e.g.* details of treating and analysing of gut contents are given in Chapter 5.

CHAPTER 3

AGE AND GROWTH

3.1 Introduction

The five most abundant labrid species observed by Tuya *et al.* (2009) during a visual census of reefs along 800 km of the south-western Australian coast included *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus*. In Western Australia, the distributions of these three Australian endemics, which all belong to the diverse Julidine clade (Kazancioğlu *et al.*, 2009), extend from along the temperate south coast northwards to Coral Bay at *c.* 23^{o}S in the case of *C. auricularis*, to Shark Bay at *c.* 26^{o}S with *N. parilus* and to the Abrolhos Islands at *c.* 29^{o}S with *O. lineolatus* (Hutchins & Swainston, 1999; Allen *et al.*, 2006; Gomon *et al.*, 2008). Although *C. auricularis*, *N. parilus* and *O. lineolatus* all reach similar lengths, attaining a maximum L_T of 400, 490 and 400 mm, respectively, the body of *N. parilus* is far deeper than those of *C. auricularis* and *O. lineolatus* (Edgar, 2008; Hutchins & Swainston, 1999; Gomon *et al.*, 2008), which results in the body mass at any given length being substantially greater for the first species than either of the other two species (see Results). This could thus lead to differences in the ranking of growth rates among those species according to whether length or mass is used as the dependent variable.

Coris auricularis, *N. parilus* and *O. lineolatus* are not long lived, with their maximum recorded ages being only eight or nine years along the extensive coastline of south-western Australia (Delacy, 2008) and 14 years in the case of *O. lineolatus* in eastern Australia (Morton *et al.*, 2008b). These species are all shown in Chapter 4 to be protogynous hermaphrodites (see also Morton *et al.*, 2008b), as are numerous other labrids in temperate southern Australia, including *N. tetricus*, which is of similar size to its congener *N. parilus* and likewise lives to only a moderate age in South Australia and

Tasmania (Shepherd & Hobbs, 1985; Barrett, 1995), and another larger and longer-lived labrid, *Achoerodus gouldii*, in south-western Australia (Coulson *et al*., 2009) and *Achoerodus viridis* in south-western Australia (Gillanders, 1995b). Although the von Bertalanffy growth curve provided a good fit to the lengths at age of the females and males of *A. gouldii* collectively, the construction of separate curves for the two sexes emphasised that the lengths of the males and females increasingly diverged after 15 years, when some females have already changed sex (Coulson *et al*., 2009). An even more dramatic divergence of the growth curves for the males and females of a protogynous hermaphrodite is provided by *Cheilinus undulatus* (Choat *et al.*, 2006).

Comparisons of the biological characteristics of a diverse range of ectotherms at different latitudes, and thus covering a range of temperatures, demonstrate that these species frequently attain a larger body size, live longer and increase in size more slowly at higher (cooler) latitudes than at lower (warmer) latitudes (see Lindsey, 1966; Pauly, 1980; Atkinson, 1994; Angilletta & Dunham, 2003; Angilletta *et al.*, 2004a; Ashton, 2004; Kozlowski *et al*., 2004). If a species thus grows more slowly but reaches a greater maximum size at a higher than lower latitude, its growth rate in the cooler waters must be less early in life but greater later in life. The above trends, together with the known effects of temperature on the metabolism of ectotherms, led to the development of a number of theories, including the Metabolic Theory of Ecology (MTE) (Angilletta *et al.*, 2004b; Brown *et al.*, 2004a; Charnov & Gillooly, 2004; Kingsolver & Huey, 2008). The above latitudinal trends for size and growth are, however, sometimes not followed (*e.g.* Conover & Present, 1990; Parra *et al.*, 2009; Cossington *et al.*, 2010). Indeed, the broad applicability of the universal temperature dependence (UTD) term in the metabolic rate equation proposed by Gillooly *et al.* (2001), which relates metabolic rate to temperature and serves as the basis for the MTE, has been questioned (Clarke, 2004; Clarke & Fraser, 2004; Dell *et al.*, 2011; Huey & Kingsolver, 2011). Furthermore, although analyses of such latitudinal trends have often used length as the measure of body size in the case of groups such as fishes, the involvement of metabolism in these theories suggests that it would be more appropriate to use body mass.

During this study, sound quantitative biological data were obtained for *C. auricularis*, *N. parilus* and *O. lineolatus* over reefs in the JBMP and in waters off Perth *c.* 250 km further to the south. These data were acquired to test whether they support the validity of the following three hypotheses regarding latitudinal differences that would conform with the MTE and, if not, provide an alternative explanation. 1. The above three species each attain a greater length and mass and have a longer life span at the higher latitude, cooler waters off Perth. 2. The size of each species at a given age at the lower latitude changes from being greater early in life to less later in life than at the higher latitude. Attention was also focused on determining whether the use of mass rather than length influences the ranking of the sizes at each age among the three species at each location, in view of the fact that, at any given length, the mass of *N. parilus* is substantially greater than those of *C. auricularis* and *O. lineolatus*. 3. Instantaneous growth rate shifts from greater early in life at the lower latitude than at the higher latitude to the converse trend later in life. 4. If temperature has a similar influence on the metabolic rate of the three species, the directions of change and thus the rank orders of the maximum lengths, masses and ages and the growth rates of each species are the same for any one of those given variables in the waters of the JBMP and in the waters off Perth. Attention was also focussed on testing the hypothesis that the curves relating length and mass at age for males lie above those of females of these protogynous species, reflecting a greater tendency for the larger females at any age to become males.

3.2 Materials and Methods

3.2.1 Sampling regime and water temperatures

The sampling locations and regimes used in the JBMP and the waters off Perth are described in Chapter 2 Materials and Methods. In brief, *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* were collected by line and spear fishing and trapping over reefs in the waters of the JBMP and off Perth. Sampling was undertaken in every second or third month between January 2005 and February 2008, thereby enabling samples were obtained for each calendar month.

The total length (L_T) and wet body mass (M_T) of each fish were recorded to the nearest 1 mm and 0.1 g, respectively. The sex of the vast majority of the individuals of each species could be determined on the basis of the morphological characteristics of their gonads, a procedure that was validated by an examination of the histological characteristics of the gonads in a substantial subsample of those individuals (see Chapter 4). The small numbers of gonads that could not be clearly identified as ovaries or testes were subjected to histology, which revealed that 18 of the 37 *C. auricularis* and four of the eight *O. lineolatus* that were thus examined contained ovarian and testicular tissues (see Chapter 4). All of these fish, apart from two of the smallest *C. auricularis*, measuring 89 and 90 mm, fell within the length and age ranges within which both females and males are found and thus sex change is believed to occur (see Chapter 4). No such individuals of the 21 *N. parilus* subjected to histology were found.

3.2.2 Age determination

The otoliths of each *C. auricularis*, *N. parilus* and *O. lineolatus* were removed and stored. The otoliths of all fish, except those < 110 mm L_T in which the otoliths could clearly be seen to contain either no opaque zone or a single opaque zone, were subsequently sectioned for ageing purposes.

The left otolith of each fish was mounted in clear epoxy resin and, using an Isomet low-speed diamond saw (Buehler), cut into sections through its primordium and along its dorso-ventral axis. The *c.* 300 μm thick sections were polished using fine wet and dry carborundum paper (Grade 1200), cleaned and mounted on slides using DePX mounting medium. Each slide was placed on a black background and examined using a Leica Mz7.5 dissecting microscope and reflected light. A Leica DC300 camera and the computer imaging package Leica IM 1000 (Leica Microsystems; www.leica-microsystems.com) were then used to count the opaque zones and to make the following measurements; 1, the marginal increment, *r1*, the distance between the outer edge of the single or outermost opaque zone and the outer edge of that otolith and 2, the distance between the primordium and the outer edge of the single opaque zone, when one such zone was present, or to the outer edges of the two outermost opaque zones when two or more such zones were present, *r2*. All measurements, which were recorded to the nearest 0.01 mm, were made along the same axis to the left of the sulcus and perpendicular to the opaque zones and without prior knowledge of the date of capture of the fish. Marginal increment values were expressed as *r1*/*r2*.

The trends exhibited by the mean monthly marginal increments were used to ascertain whether the opaque zones in the otoliths of *C. auricularis* and *N. parilus* were formed annually, noting that such validation has already been undertaken for *O. lineolatus* (Morton *et al.*, 2008b).

The opaque zones could be clearly detected in the otoliths of all but a few individuals of the three species. The opaque zones in the sectioned left otolith from 1471 *C. auricularis*, 1361 *N. parilus* and 818 *O. lineolatus* were counted on two occasions without knowledge of the date of capture or size of that fish and noting whether the otolith margin was opaque or translucent and, if the latter, whether it was narrow or wide. The two counts for an otolith of each of those species differed only in

8.7, 5.2 and 6.1 % of cases, respectively. When there was a difference in the counts for an otolith, the opaque zones on that otolith were counted a third time and, in all cases, this third count was the same as one of the two previous counts, and thus the one recorded for that otolith. An experienced reader of labrid otoliths (either D.V. Fairclough or P. G. Coulson) counted the opaque zones in a random subsample of the otoliths of at least 400 individuals of each of *C. auricularis*, *N. parilus* and *O. lineolatus*, which covered the full size ranges of those species. The counts for the three species agreed with those recorded by the senior author in 97.1, 99.2 and 96.2 % of cases and, where there were discrepancies, the counts never differed by more than one.

3.2.3 Mass-length relationships

As ANCOVA demonstrated that the slopes and intercepts for the natural logarithmic relationships between mass and length differed among the three species in each location, a resampling analysis was undertaken to determine whether the mass predicted by their mass-length relationships differed significantly among species at all lengths within the range of the data for those species. For this analysis, the mass-length data were resampled, with replacement, to generate 200 sets of new mass-length data, each with the same number of observations as in the original data set for the corresponding species. A bisection algorithm was employed to determine the length at which the difference between the natural logarithms of the masses predicted by the curves for the two species was least. The predicted values for the mass of each species at that length were then back-transformed and corrected for bias using the equation of Beauchamp & Olson (1973). The corrected estimate, Est_{corr}, is thus determined as $Est_{corr} = Est_{uncorr} e^{(ms/2)}$, where Est_{uncorr} is the uncorrected value, e is Euler's number and ms is the mean of the squared residuals. The ratio between the back-transformed masses predicted by the equations for the two species being compared was then determined for each of the 200 data sets. If the ratio of the predicted value for equation 1 exceeded 1.05 times that for equation 2 on more than 95 % of occasions, the mass at any length predicted by the former equation were considered significantly greater than those for the latter equation ($P < 0.05$). The above form of analysis was next used to test whether the predicted masses at length of *C. auricularis*, *N. parilus* and *O. lineolatus* in the JBMP and waters off Perth were significantly different.

3.2.4 Length and age frequency compositions and growth

On the basis of the trends exhibited by a combination of the mean monthly gonad weights (standardised for L_T) and the prevalences of sequential ovarian maturity stages in each month (see Chapter 4), the approximate mid-points of the spawning periods of *C. auricularis*, *N. parilus* and *O. lineolatus* were 1 June, 1 September and 1 November, respectively, and thus considered to correspond to the "birth dates" of those species. The age of each individual of each species was then estimated using the birth date for that species, together with the date of capture of the fish, the number of opaque zones in its left otolith and the time of year when opaque zones (annuli) become delineated in the otoliths of that species.

The hypothesis that the maximum length of a given species was significantly greater in the waters off Perth than in the JBMP was assessed using a randomisation test. Samples of the same sizes as the original samples were thus randomly drawn, with replacement, from the pooled set of lengths. As the distribution of the maximum lengths in these random samples reflected discrete rather than continuous values and were thus irregular, the average length of the largest 10 % of the fish in each sample was adopted as the measure of the maximum length attained on average by the individuals of the species, a method adopted by Trip *et al.* (2008). This average maximum length off Perth minus that in the JBMP was calculated and stored, a process repeated for 10 000 samples to form a frequency distribution for the differences. The proportion of these 10 000 differences that were ≥ the difference between the average maximum lengths recorded for the original samples off Perth and in the JBMP was then calculated. If this proportion was ≤ 0.05, it was concluded that the average maximum length was significantly greater in the waters off Perth than in the JBMP. The hypotheses that the maximum mass (*i.e.* the average mass of the heaviest 10 % of fish in the sample) and maximum age (*i.e.* the average age of the oldest 10 % of fish in the sample) of a given species were significantly greater in the waters off Perth than in the JBMP were tested using the same approach as that just described for average maximum length. Note that, for convenience, the above average values for the top 10 % of L_T, M_T and A are subsequently referred to as the "maximum" L_T, "maximum" M_T and "maximum" A.

As *C. auricularis*, *N. parilus* and *O. lineolatus* are protogynous hermaphrodites (see Chapter 4), a single von Bertalanffy growth curve was initially fitted to the lengths at age of all of the individuals of each species at each location. The von Bertalanffy equation is $L_T = L_\infty\left(1 - e^{(-k(t-t_0))}\right)$, where L_T = the total length (mm) at age t (years), L_∞ = the asymptotic L_T (mm), k = the growth coefficient (year^{-1}) and t_0 = the hypothetical age (years) at which fish would have zero length. The von Bertalanffy growth equations for *C. auricularis*, *N. parilus* and *O. lineolatus* in the two localities, *i.e.* JBMP *vs* Perth, were compared using likelihood-ratio tests (Cerrato, 1990). The null hypothesis that the data for a species in the two localities could be described better by a common growth curve was considered against the alternative hypothesis that the data for each location would be better described by separate growth curves (Cerrato, 1990). The test statistic was calculated as twice the difference between the log-likelihood obtained by fitting a common growth curve to the data for both localities and by fitting separate growth curves to the data for each location. The null hypothesis was rejected at the $\alpha = 0.05$

level of significance if the test statistic exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the common curve and the separate curves (Cerrato, 1990).

The above model was re-parameterised for each species, employing the parameters, L_∞, $g = kL_\infty$ and t_0 for the growth curve in the JBMP and L_∞, $kL_\infty + D$ and t_0 for that in waters off Perth, where the value of the theoretical growth rate when fish have zero length, $g = kL_\infty$, is equal to that at the JBMP, and D is the difference between the growth rates at zero length in the two localities, to test the hypothesis that, when the expected length is zero, the growth rate was less off Perth than in the JBMP. The re-parameterised model may be written as

$$L_T = L_\infty \left\{ 1 - e^{\left[-\frac{g}{L_\infty}(t - t_0) \right]} \right\}$$

This model was then re-fitted and the likelihood profile over a range of values for D was constructed. From this, a reference value was determined such that, under the null hypothesis that the growth rate in the waters off Perth was the same as in the JBMP, the probability that D was ≤ this value was equal to the significance level, α. The observed value of the difference D was compared with the critical value to assess whether the growth rate was significantly less off Perth than in the JBMP. A likelihood-ratio test was also used to determine whether, for each species in each location, von Bertalanffy growth curves fitted to the lengths at ages of females and males were significantly different, with the curves for males lying above those for females. The same procedure was then applied to the mass-at-age data, but using a generalised von Bertalanffy growth curve (as described below).

In the case of mass, growth was assumed to be represented by the generalised von Bertalanffy growth equation $M_T = M_{T\infty}\left(1 - e^{(-k(t-t_0))}\right)^b$, where M_T = the total mass (g) at age t (years), $M_{T\infty}$ = the asymptotic total weight (g), k = the growth coefficient (year^{-1}) , t_0 = the hypothetical age (years) at which fish would have zero weight and b is a parameter that describes the shape of the curve (Schnute, 1981). Preliminary analysis demonstrated that, particularly for males, the information content of the data was insufficient to produce reliable estimates of the parameter b. The data were thus randomly allocated (with a probability of 0.5) to one or other of two subsets, to which a coupled pair of models, subsequently termed the "growth-in-mass model", was fitted simultaneously. This model took the following form.

$$\log_e M_{\mathrm{T}} = \begin{cases} \log_e \left[a L_{\mathrm{T}}^{b} \right] & \text{for data from first subset} \\ \log_e \left[M_{\mathrm{T}\infty} \left(1 - e^{(-k(t-t_0))} \right)^{b} \right] & \text{for data from second subset} \end{cases}$$

For each species and using the same subsets, the above model was fitted to the mass-at-age data for (1) each sex in each location, (2) for both sexes pooled in each location, (3) for each sex pooled across both localities and (4) pooled for both sexes and both localities. This was achieved by maximising the summed likelihoods of the deviations of the natural log of the recorded mass from the natural log of the predicted mass, assuming that these deviations were normally distributed, with a mean of zero and, for each subset of data, a constant variance. Likelihood-ratio tests were used to test whether the growth-in-mass model for each species differed between localities and between the sexes of each species at each location.

Recognising that the above approach might be sensitive to the random allocation of mass-at-age data between the two subsets, random samples of the data for each sex and location were drawn, with replacement, to produce samples with the same sizes as in the original data sets. The growth-in-mass model was then fitted to the resulting randomly-selected samples and the results subjected to likelihood-ratio tests. The process was repeated for 110 randomly drawn samples. The number of these 110 trials in which the likelihood-ratio test indicated that the models for the different sexes or localities were significantly different was then counted. Assuming that the result of each of these random trials represents the outcome from a binomial trial with a probability of "success", *i.e.* a significant outcome, equal to 0.05, the probability of observing a number of successes ≥ the observed number in a sample of 110 binomial trials was calculated. If this probability exceeded 1-α, it was concluded that the growth-in-mass models differed significantly. Median values and the 2.5 and 97.5 percentiles of the 110 parameter estimates and associated predictions of mass at age and rate of change of mass at mass (derived from the generalised von Bertalanffy growth curve component of the growth-in-mass model) were then adopted as the point estimates and lower and upper 95 % confidence limits, respectively.

Estimates of the rate of change of mass at specified values of mass over a range of masses were calculated by first estimating the age at which the expected mass predicted by the generalised von Bertalanffy growth curve, and employing the values of the parameters estimated when the curve was fitted, would be equal to the specified value, *i.e.*

$$t = t_0 - \frac{1}{k}\log_e\left[1 - \left(\frac{M_{\mathrm{T}}}{M_{\mathrm{T}\infty}}\right)^{-b}\right]$$

The resulting value of age was then inserted into the following equation to produce the required estimate of the expected rate of change of mass, $\frac{dM_{\mathrm{T}}}{dt}$, at different values of M_{T}.

$$\frac{dM_{\mathrm{T}}}{dt} = bkM_{\mathrm{T}\infty}e^{[-k(t-t_0)]}\left\{1 - e^{[-k(t-t_0)]}\right\}^{b-1}$$

3.3 Results

3.3.1 Water temperatures

The mean monthly sea surface temperature (SST) in the JBMP and the waters off Perth between 2005 and 2008 followed the same consistent seasonal trends, reaching their maxima in March and April and declining to their minima in September and October (Fig. 3.1). The maximum and minimum mean monthly temperatures were 23.3 and 19.6°C in the JBMP and 22.5 and 18.8°C in the waters off Perth. In each month, the mean temperature off Perth was between 0.6 and 0.9°C less than that in the JBMP.

3.3.2 Validation of ageing procedure

Irrespective of the number of opaque zones on the otoliths of *Coris auricularis*, the mean monthly marginal increments (MIs) on these otoliths declined from their maxima in mid to late spring to their minima in mid summer to early autumn and then increased (Fig 3.2). The single distinct decline and rise in the mean monthly MIs of the otoliths of *C. auricularis* during a calendar year demonstrates that, throughout life, a single opaque zone is laid down annually in the otoliths of *C. auricularis.* The trends shown by the mean monthly marginal increments on the otoliths of *Notolabrus parilus* were the same as those just described for *C. auricularis* (data not shown). The validation that an opaque zone is laid down annually in the otoliths of *C. auricularis* and *N. parilus*, and also in those of *Ophthalmolepis lineolatus* (Morton *et al.*, 2008b), confirms that the number of such zones in otoliths can be used to facilitate the ageing of each species.

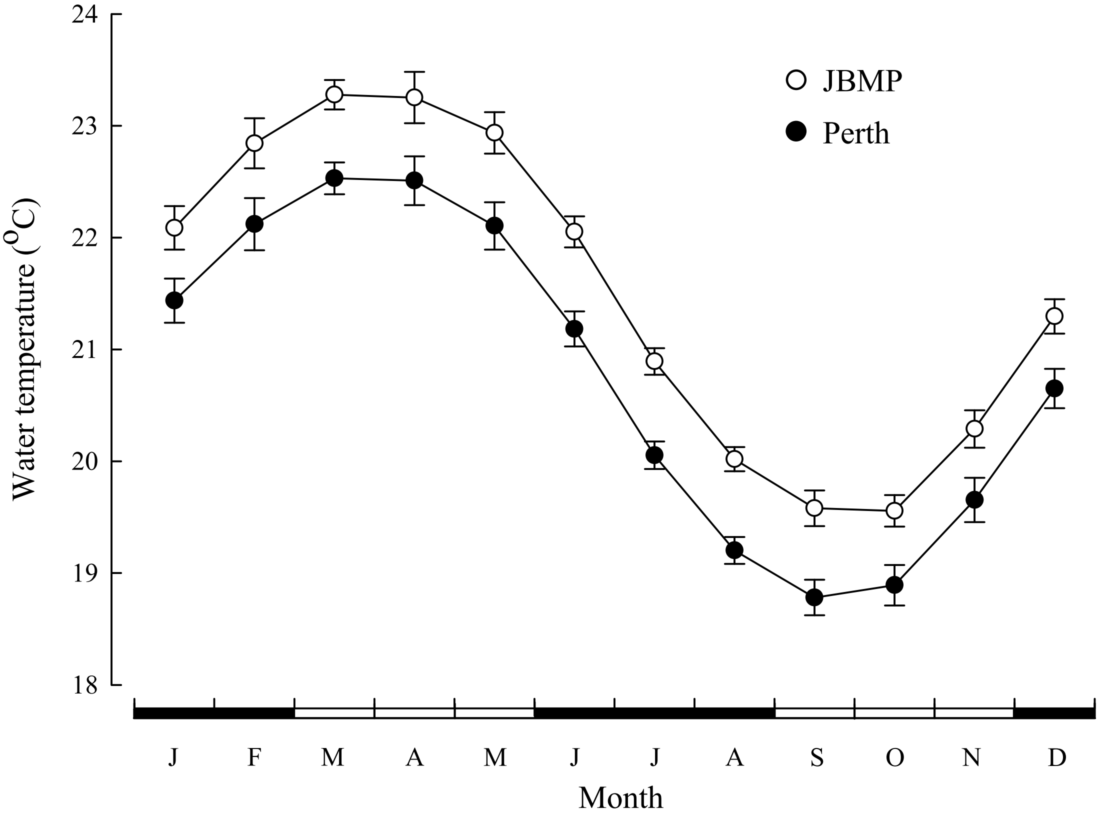


Figure 3.1. Mean monthly sea surface water temperatures ± 1 SE for the Jurien Bay Marine Park (open circles) and the waters off Perth (closed circles) between 1995 and 2008 and thus encompassing the period during which the year classes of the three labrid species were represented in samples. Data were derived from a combination of satellite imagery and sea surface temperatures recorded by shipping and drifting buoys (see Reynolds & Smith (1994) for the methods). On the x-axis, the black rectangles represent summer and winter months and the white rectangles the autumn and spring months.

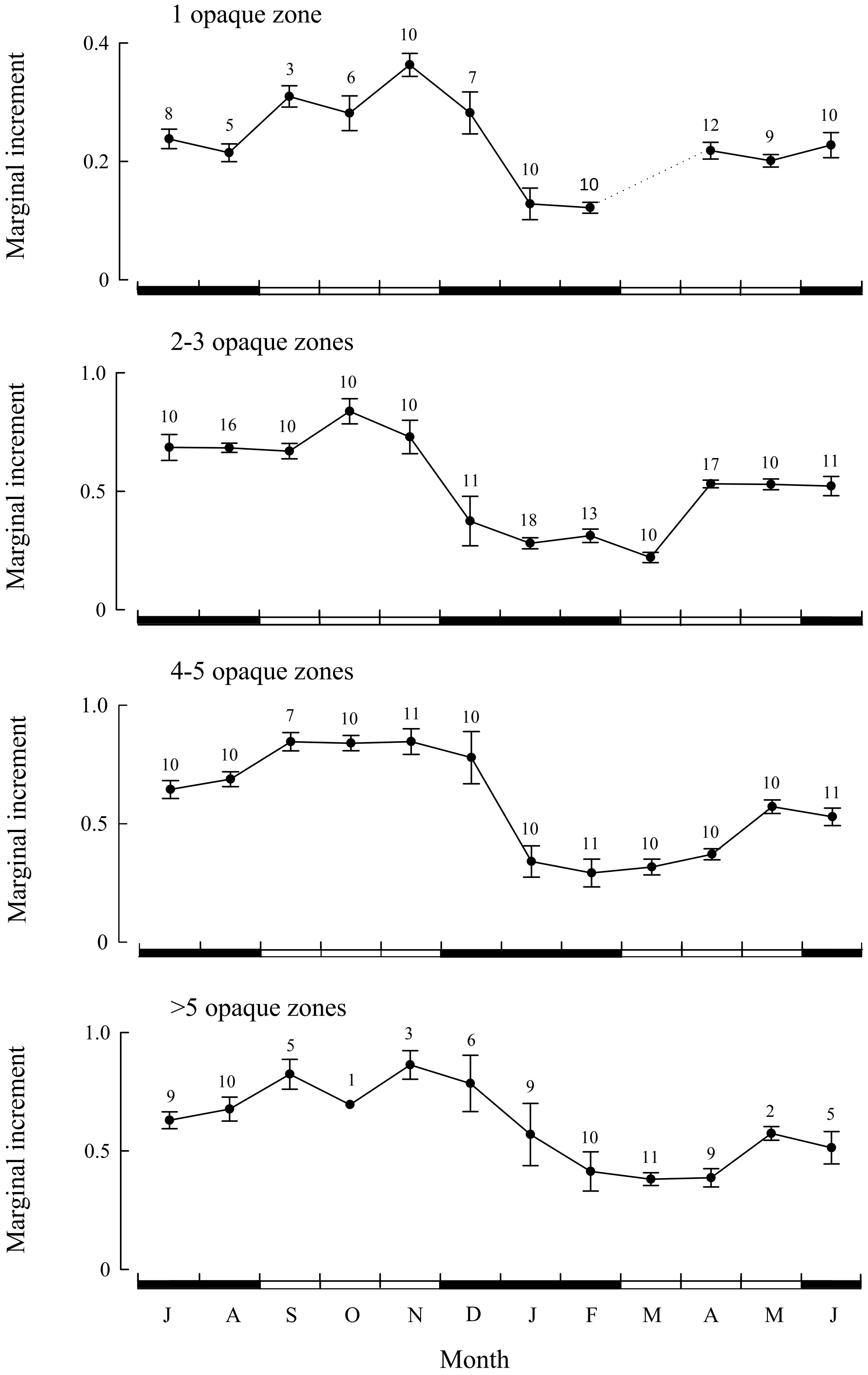


Figure 3.2. Mean monthly marginal increments ±1 SE for subsamples of *Coris auricularis* caught over reefs between January 2005 and June 2007. On the x-axis, the black rectangles represent winter and summer months and the white rectangles spring and autumn months. Numbers of otoliths examined in each month are given above each mean.

3.3.3 Mass-length relationships and length and age compositions

The relationships between the logarithms for M_T and L_T, which are shown in Fig. 3.3, are described by the following equations:

Coris auricularis

JBMP $\ln(M_T) = 3.056 \ln(L_T) - 11.731$ ($r^2 = 0.996$, $P < 0.001$, $n = 1097$)

Perth $\ln(M_T) = 3.071 \ln(L_T) - 11.813$ ($r^2 = 0.996$, $P < 0.001$, $n = 440$)

Notolabrus parilus

JBMP $\ln(M_T) = 2.993 \ln(L_T) - 10.955$ ($r^2 = 0.989$, $P < 0.001$, $n = 925$)

Perth $\ln(M_T) = 2.998 \ln(L_T) - 10.966$ ($r^2 = 0.990$, $P < 0.001$, $n = 521$)

Ophthalmolepis lineolatus

JBMP $\ln(M_T) = 3.333 \ln(L_T) - 13.291$ ($r^2 = 0.991$, $P < 0.001$, $n = 433$)

Perth $\ln(M_T) = 3.307 \ln(L_T) - 13.147$ ($r^2 = 0.993$, $P < 0.001$, $n = 462$)

In the mass-length data for the three species in both the JBMP and waters off Perth, the regression line for *N. parilus* lies well above those for *C. auricularis* and *O. lineolatus* throughout the length ranges of those species, while those of the latter two species are close at the lower end and converge towards the upper end of the length ranges of those species (Fig. 3.3). Resampling analyses demonstrated that, across the full length ranges of the species, the masses predicted were always significantly greater ($P < 0.001$) for *N. parilus* than for *C. auricularis* and *O. lineolatus*, whereas there were no such differences between the latter two species ($P > 0.05$). The same type of analysis failed to detect a significant difference between the mass-length relationships of each species at the two localities ($P > 0.05$).

The length and age-frequency distributions demonstrate that the smaller individuals of *C. auricularis*, *N. parilus* and *O. lineolatus* over reefs were typically

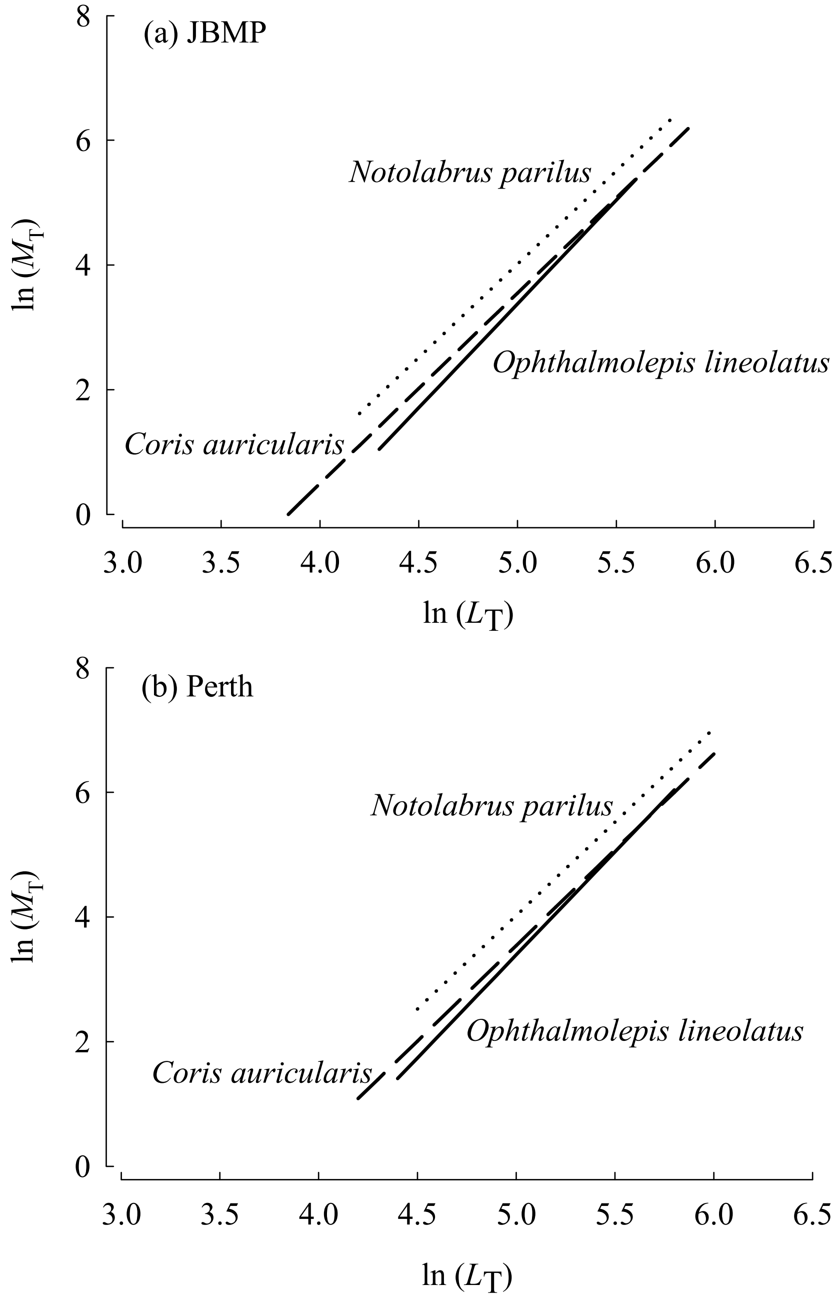


Figure 3.3. Relationships between the logarithms of the mass (M_T in g) and total length (L_T in mm) for *Notolabrus parilus*, *Coris auricularis* and *Ophthalmolepis lineolatus* in (a) the Jurien Bay Marine Park (JBMP) and (b) the waters off Perth.

females, while the larger ones were typically males (Fig. 3.4). Thus, for example, in the case of *C. auricularis* in the JBMP, 66.2 and 63.5 % of fish < 240 mm L_T and ≤ 4 years of age were females, respectively, whereas 86.2 and 76.2 % of fish > 260 mm L_T and ≥ 5 years of age were males. The trend for females to dominate the size classes of smaller fish and age classes of younger fish and the males to be far more prevalent among the larger and older fish was also the case with *C. auricularis* in the waters off Perth and with *N. parilus* and *O. lineolatus* in both localities (Fig. 3.4).

Although trapping over reefs yielded substantial numbers of smaller (< 200 mm) and younger (< 4+ age class) *C. auricularis* in the JBMP and the waters off Perth, this sampling method yielded very few *N. parilus* and *O. lineolatus* in either of those locations (Fig. 3.4). While this is clearly due to a greater propensity for *C. auricularis* to target bait in traps, it also reflects a far greater tendency for the smaller individuals of this species to form schools when feeding (*pers. obs.*). The greater prevalence of small *O. lineolatus* in the samples collected by spear fishing is due to these fish having been targeted to supplement the relatively few small individuals caught by line fishing. The marked contrast between the dominance of females among smaller and younger fish and the dominance of males among larger and older fish reflect the fact that all three labrid species are protogynous hermaphrodites (Chapter 4), as is also the case with *O. lineolatus* in eastern Australia (Morton *et al.*, 2008b).

The maximum recorded lengths of *C. auricularis*, *N. parilus* and *O. lineolatus* in the waters off Perth exceeded those of the corresponding species over reefs in the JBMP by 8.8, 11.3 and 3.8 %, respectively (Table 3.1). The average L_T of the longest 10 % of the individuals of each species was significantly greater in the waters off Perth than in those of the JBMP (all $P < 0.001$). The individual maximum masses of *C. auricularis*, *N. parilus* and *O. lineolatus* off Perth greatly exceeded those in the JBMP, *i.e.* by 40, 44.5 and 33 %, respectively. The average mass of the heaviest 10 % of individuals of

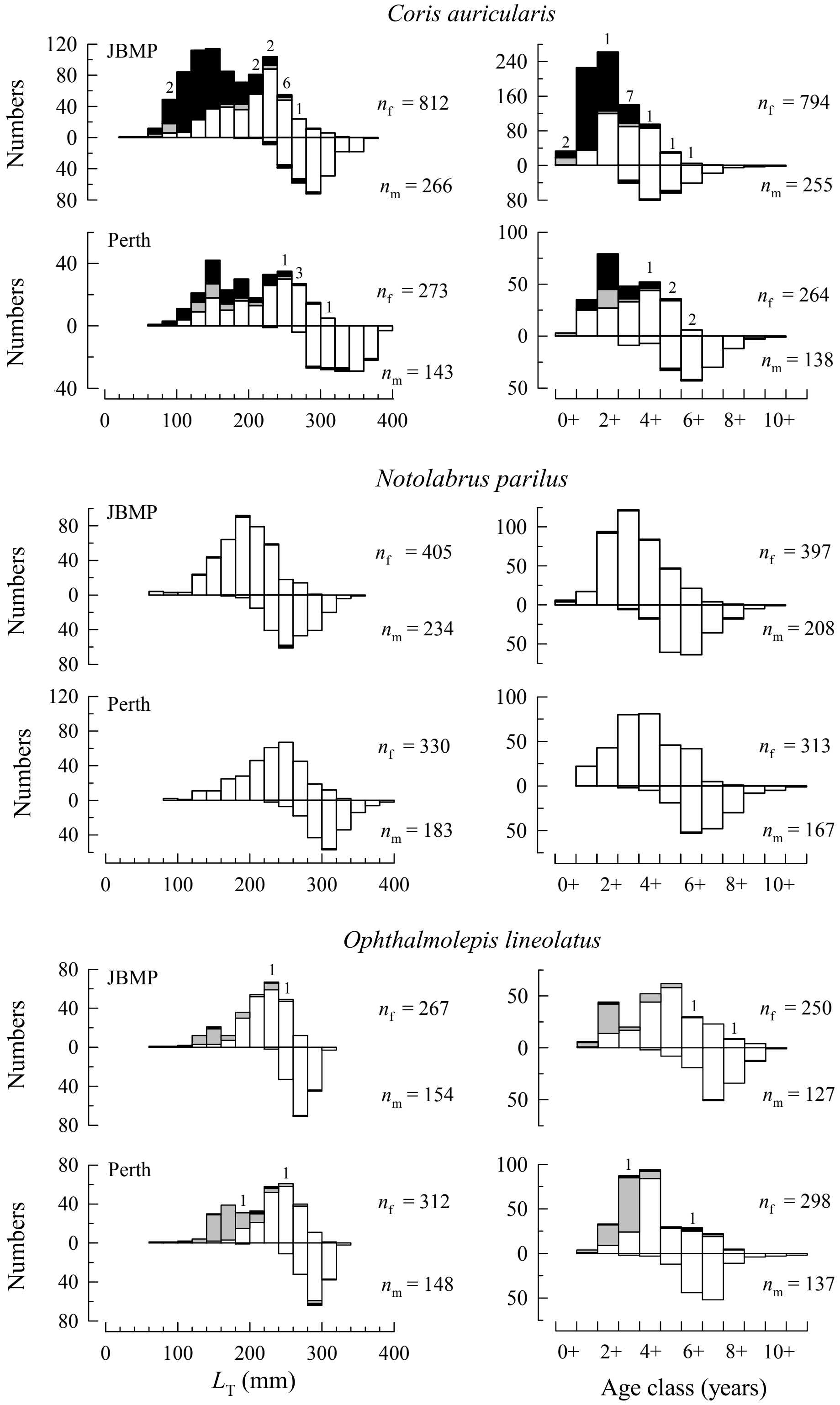


Figure 3.4. Length and age-frequency distributions for females (above horizontal line) and males (below horizontal line) of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* caught over reefs in the Jurien Bay Marine Park (JBMP) and in the waters off Perth by trap fishing (black histograms), rod and line fishing (white histograms) and spear fishing (light grey histograms). n_f, number of females; n_m, number of males. Number of bisexuals is given above histograms for the few length and age classes in which they are represented.

Table 3.1. Maximum lengths (L_{Tmax}), mass (M_{Tmax}) and ages (A_{max}) and von Bertalanffy growth curve parameters, L_∞, k and $t_0 \pm$ 95 % CLs (in parentheses), derived from the lengths at age of all individuals and of the females and males of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* that were caught over reefs in the Jurien Bay Marine Park (JBMP) and in the waters off Perth. The sample size for the overall growth curves for each species include, when present, a small number of bisexual fish.

				von Bertalanffy parameters				
	L_{Tmax} (mm)	**M_{Tmax} (g)**	**A_{max} (years)**	**L_∞ (mm)**	**k (year^{-1})**	**t_0 (years)**	**r^2**	**n**
C. auricularis								
JBMP	**365**	**558**	**10.5**	**378** (364, 394)	**0.25** (0.23, 0.28)	**0.10** (0.03, 0.18)	**0.96**	**1060**
Female	**329**	**396**	**7.6**	**333** (312, 355)	**0.29** (0.25, 0.33)	**0.05** (-0.06, 0.15)	**0.88**	**794**
Male	**365**	**558**	**10.5**	**399** (283, 514)	**0.14** (-0.01, 0.30)	**-3.76** (-8.33, 0.81)	**0.46**	**255**
Perth	**397**	**780**	**10.2**	**484** (445, 554)	**0.16** (0.13, 0.19)	**-0.21** (-0.44, -0.01)	**0.88**	**411**
Female	**312**	**376**	**6.6**	**361** (327, 420)	**0.24** (0.18, 0.31)	**-0.11** (-0.39, 0.14)	**0.83**	**264**
Male	**397**	**780**	**10.2**	**473** (225, 721)	**0.11** (-0.08, 0.30)	**-4.27** (-11.52, 2.97)	**0.49**	**138**
N. parilus								
JBMP	**346**	**729**	**10.4**	**335** (314, 368)	**0.20** (0.16, 0.24)	**-0.84** (-1.22, -0.58)	**0.78**	**605**
Female	**290**	**404**	**8.3**	**268** (253, 288)	**0.32** (0.26, 0.38)	**-0.43** (-0.64, -0.25)	**0.75**	**397**
Male	**346**	**729**	**10.4**	**385** (121, 649)	**0.10** (-0.11, 0.32)	**-4.50** (-13.47, 4.48)	**0.31**	**208**
Perth	**385**	**1054**	**11.8**	**410** (380, 456)	**0.15** (0.12, 0.19)	**-1.35** (-1.89, -0.93)	**0.84**	**495**
Female	**333**	**686**	**8.1**	**357** (324, 423)	**0.20** (0.13, 0.26)	**-1.05** (-1.69, -0.63)	**0.81**	**313**
Male	**385**	**1054**	**11.8**	**552** (-330, 1435)	**0.05** (-0.13, 0.23)	**-8.98** (-27.17, 9.22)	**0.39**	**167**
O. lineolatus								
JBMP	**310**	**308**	**10.4**	**296** (284, 313)	**0.27** (0.22, 0.32)	**-0.35** (-0.75, -0.02)	**0.79**	**380**
Female	**275**	**226**	**9.7**	**252** (245, 262)	**0.43** (0.35, 0.51)	**0.17** (-0.19, 0.41)	**0.79**	**250**
Male	**310**	**308**	**10.4**	**710** (-3735, 3877)	**0.01** (-0.76, 0.78)	**-46.68** (-1009.8, 916.5)	**0.08**	**128**
Perth	**322**	**409**	**11.8**	**328** (318, 340)	**0.28** (0.24, 0.31)	**0.19** (-0.08, 0.41)	**0.83**	**439**
Female	**305**	**336**	**8.7**	**299** (288, 314)	**0.33** (0.28, 0.38)	**0.22** (-0.09, 0.47)	**0.76**	**298**
Male	**322**	**409**	**11.8**	**303** (294, 312)	**0.53** (0.33, 0.73)	**1.20** (0.13, 2.26)	**0.42**	**139**

r^2, coefficient of determination; n, number of fish.

each of the three species off Perth was significantly greater than that of the corresponding species in the JBMP (all $P < 0.001$). While the individual maximum ages of *N. parilus* and *O. lineolatus* in the waters off Perth likewise exceeded those of these species in the JBMP, *i.e.* by 14.6 and 12.7 %, respectively, those of *C. auricularis* over reefs in those two locations were similar (Table 3.1). However, the average age of the oldest 10 % of fish was significantly greater in the waters off Perth than in those of the JBMP in the case of *C. auricularis* as well as *N. parilus* (both $P < 0.001$). While the average age of the oldest 10 % of *O. lineolatus* in the waters of Perth was not significantly greater than that in the JBMP ($P > 0.05$), it is noteworthy that the ages of the two oldest fish (11.8 and 11.5 years) in the former location were greater than that of the oldest fish (10.4 years) in the latter location and, an additional test demonstrated that the average maximum age of this species in the JBMP did not differ significantly from that in the waters off Perth ($P > 0.05$).

3.3.4 Intraspecific comparisons of growth in the two localities

The von Bertalanffy growth curve provided a good fit to the lengths at age and masses at age of *C. auricularis*, *N. parilus* and *O. lineolatus* from the JBMP and in the waters off Perth (Table 3.1, Fig. 3.5). This point is emphasised by the trends exhibited by residual plots (data not shown).

The growth curves fitted to the lengths at age (Fig. 3.6a, c, e) and to the masses at age (Fig. 3.6b, d, f) for each species in the JBMP differed significantly ($P < 0.001$) from those of the corresponding species in the waters off Perth. The asymptotic length (L_∞) for each of *C. auricularis*, *N. parilus* and *O. lineolatus* in the JBMP was always less than that for the corresponding species in the waters off Perth (Table 3.1, Fig. 3.6a, c, e), with the intraspecific differences in lengths being as high as 22, 18 and 10 %, respectively. While the converse trend was exhibited by the growth coefficient (k) for

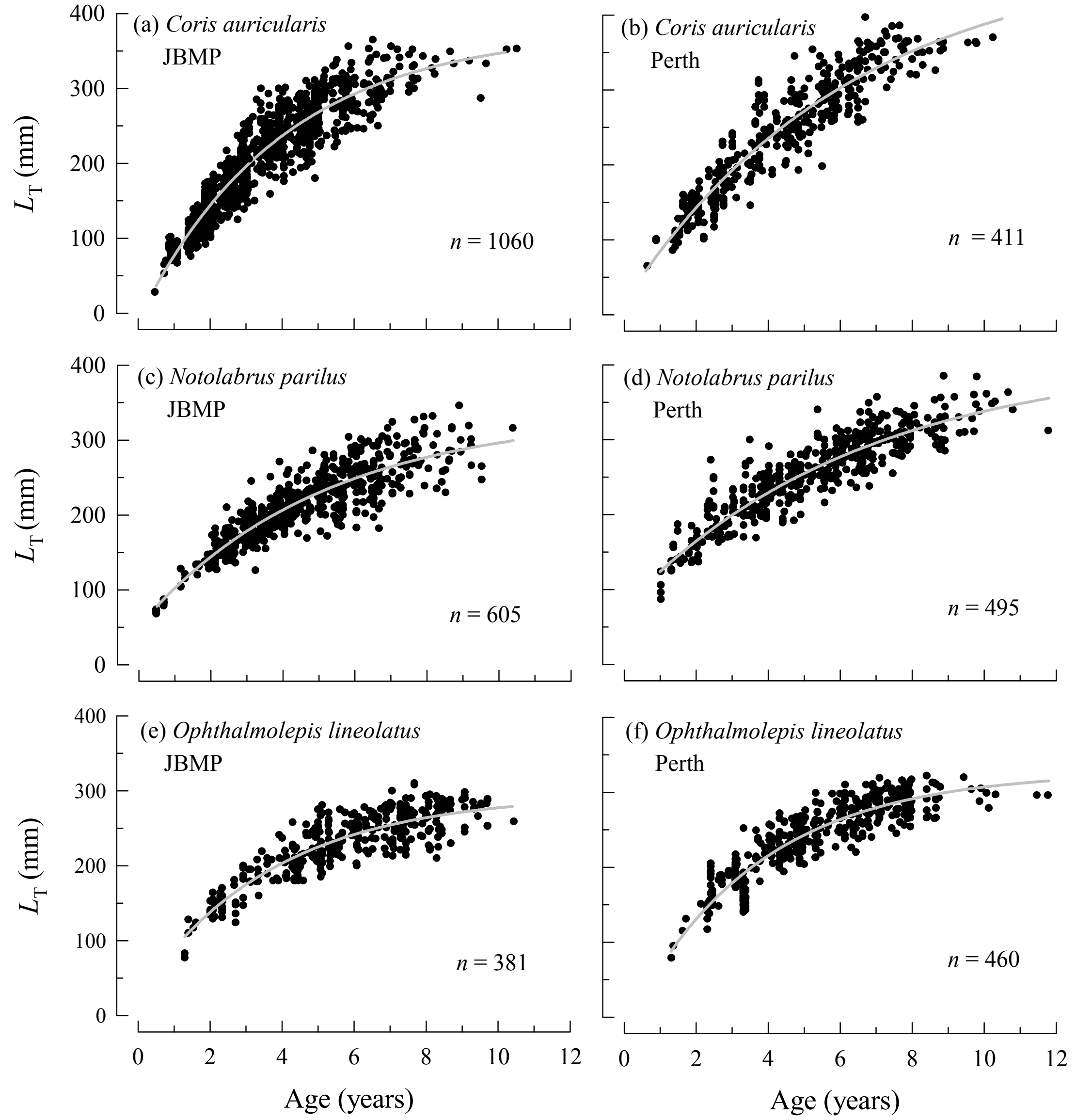


Figure 3.5. von Bertalanffy growth curves fitted to the total lengths at age of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* caught over reefs in the Jurien Bay Marine Park (JBMP) and in the waters off Perth. *n*, number of fish.

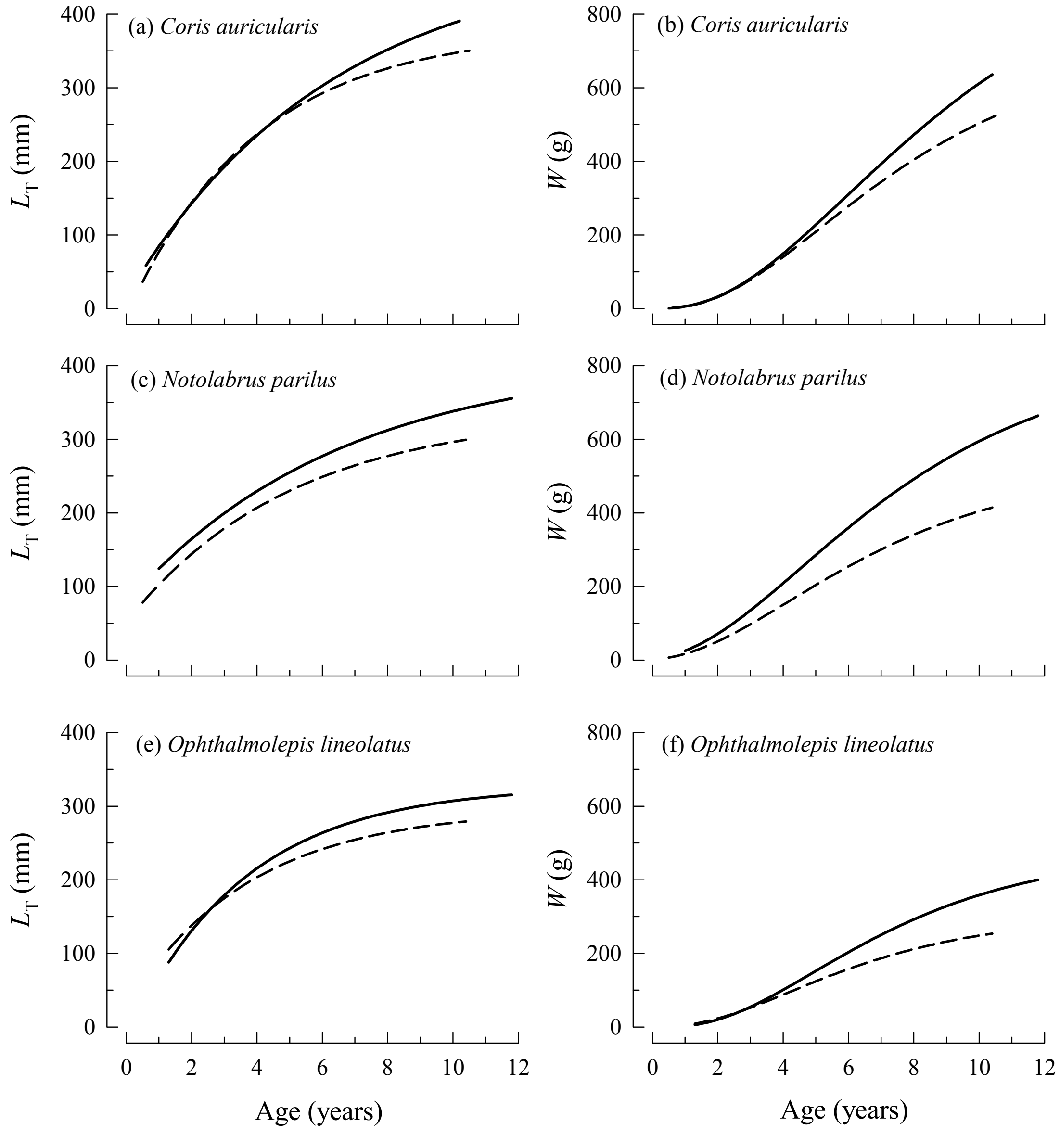


Figure 3.6. von Bertalanffy growth curves fitted to the lengths at age (a, c, e) and to the masses at age (b, d, f) of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* caught in the Jurien Bay Marine Park (JBMP) and in the waters off Perth. Dashed line, JBMP; solid line, Perth.

C. auricularis and *N. parilus*, the values for *k* for *O. lineolatus* in the JBMP and the waters off Perth were similar (Table 3.1). In the case of mass, L_∞ was far greater and *k* was less for each species in waters off Perth than in the JBMP (Table 3.2). On the basis of the growth curves, the length at age and mass at age of each species in the waters off Perth were greater than in the corresponding species in the JBMP over most of the age range of those species (Fig. 3.6a-f).

In terms of mass, the instantaneous rate of growth in each species in the JBMP and in the waters off Perth started to diverge at a relatively small body mass, particularly with *N. parilus* and *O. lineolatus* (*i.e.* < 20 g), and also reached a greater level and peaked at a larger body mass at the higher latitude (Fig. 3.7). The growth rate in each location peaked at a smaller mass in *O. lineolatus* than in *N. parilus*, which, in turn, occurred earlier than with *C. auricularis*. The peak instantaneous growth rate in both localities was least for *O. lineolatus* and greatest for *C. auricularis*.

3.3.5 Interspecific comparisons

In both the JBMP and off Perth, the rank orders of the average of the greatest 10 % of the lengths of the three species were the same, and those of the greatest 10 % of the masses were also the same (Table 3.3). However, in both localities, *C. auricularis* ranked first and *N. parilus* second in terms of length, whereas the reverse was the case with mass, with *O. lineolatus* ranking last for both of these measures of body size. While, at both latitudes, *C. auricularis* ranked last in terms of the corresponding values for age, *O. lineolatus* ranked first in the JBMP and second in the waters off Perth, while the opposite was true for *N. parilus* (Table 3.3).

The von Bertalanffy growth curves fitted to the lengths at age of *C. auricularis*, *N. parilus* and *O. lineolatus* were significantly different from each other in both the JBMP and in the waters off Perth ($P < 0.001$) (Fig. 3.8 a, b) and the same was true for

Table 3.2. Growth curve parameters, $M_{T\infty}$, *k* and t_0 ± 95 % CLs (in parentheses), derived from the masses at age of all individuals and of the females and males of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* that were caught over reefs in the Jurien Bay Marine Park (JBMP) and in the waters off Perth. The sample size for the overall growth curves for each species include, when present, a small number of bisexual fish.

	Growth parameters					
	$M_{T\infty}$ (g)	***k* (year $^{-1}$)**	**t_0 (years)**	**a**	**b**	***n***
Coris auricularis						
JBMP	**723**	**0.22**	**-0.02**	**-11.73**	**3.06**	**1049**
	(621, 930)	(0.19, 0.23)	(-0.11, 0.04)	(-11.82, -11.63)	(3.04, 3.07)	
Female	**478**	**0.26**	**-0.07**	**-11.82**	**3.07**	**794**
	(368, 726)	(0.20, 0.29)	(0.22, 0.03)	(-11.97, -11.67)	(3.05, 3.10)	
Male	**376**	**0.37**	**-0.64**	**-11.39**	**2.99**	**255**
	(325, 517)	(0.25, 0.44)	(-1.48, -0.01)	(-11.96, -10.84)	(2.90, 3.09)	
Perth	**1015**	**0.19**	**-0.12**	**-11.81**	**3.07**	**397**
	(841, 1509)	(0.14, 0.21)	(-0.33, 0.04)	(-11.95, -11.71)	(3.05, 3.10)	
Female	**621**	**0.22**	**-0.28**	**-11.82**	**3.07**	**264**
	(339, 1435)	(0.13, 0.33)	(-0.70, 0.17)	(-12.01, -11.64)	(3.04, 3.11)	
Male	**545**	**0.31**	**-0.94**	**-11.18**	**2.96**	**133**
	(463, 780)	(0.18, 0.39)	(-2.55, 0.00)	(-12.12, -10.06)	(2.77, 3.12)	
Notolabrus parilus						
JBMP	**532**	**0.23**	**-0.66**	**-10.90**	**2.98**	**594**
	(333, 821)	(0.16, 0.33)	(-1.10, -0.32)	(-11.10, -10.67)	(2.94, 3.02)	
Female	**337**	**0.30**	**-0.48**	**-10.80**	**2.96**	**397**
	(238, 536)	(0.21, 0.43)	(-0.75, -0.17)	(-11.06, -10.42)	(2.89, 3.01)	
Male	**462**	**0.29**	**-0.54**	**-11.08**	**3.02**	**207**
	(359, 658)	(0.18, 0.38)	(-1.95, 0.47)	(-11.95, -10.38)	(2.89, 3.17)	
Perth	**835**	**0.21**	**-0.80**	**-10.90**	**2.99**	**479**
	(581, 1425)	(0.13, 0.29)	(-1.55, -0.37)	(-11.23, -10.72)	(2.95, 3.04)	
Female	**681**	**0.22**	**-0.84**	**-10.95**	**3.00**	**312**
	(401, 1170)	(0.15, 0.38)	(-1.56, -0.22)	(-11.50, -10.65)	(2.94, 3.09)	
Male	**628**	**0.31**	**-0.83**	**-10.89**	**2.98**	**167**
	(551, 822)	(0.20, 0.40)	(-2.88, 0.00)	(-11.71, -10.03)	(2.83, 3.13)	
Ophthalmolepis lineolatus						
JBMP	**305**	**0.27**	**-0.26**	**-13.34**	**3.34**	**378**
	(253, 409)	(0.20, 0.33)	(-0.71, 0.16)	(-13.58, -13.08)	(3.29, 3.39)	
Female	**173**	**0.41**	**0.13**	**-13.17**	**3.31**	**249**
	(147, 217)	(0.30, 0.53)	(-0.38, 0.49)	(-13.53, -12.87)	(3.25, 3.38)	
Male	**239**	**0.39**	**-0.93**	**-11.13**	**2.95**	**128**
	(221, 302)	(0.28, 0.71)	(-3.83, 0.00)	(-12.59, -9.19)	(2.60, 3.21)	
Perth	**482**	**0.25**	**0.04**	**-13.17**	**3.31**	**439**
	(408, 567)	(0.22, 0.30)	(-0.14, 0.34)	(-13.41, -12.95)	(3.27, 3.36)	
Female	**348**	**0.27**	**-0.01**	**-12.90**	**3.26**	**298**
	(288, 576)	(0.18, 0.35)	(-0.71, 0.25)	(-13.26, -12.60)	(3.20, 3.33)	
Male	**336**	**0.43**	**0.51**	**-12.90**	**3.27**	**139**
	(299, 434)	(0.30, 0.85)	(-0.57, 2.44)	(-13.72, -11.16)	(2.96, 3.41)	

r^2, coefficient of determination; *n*, number of fish.

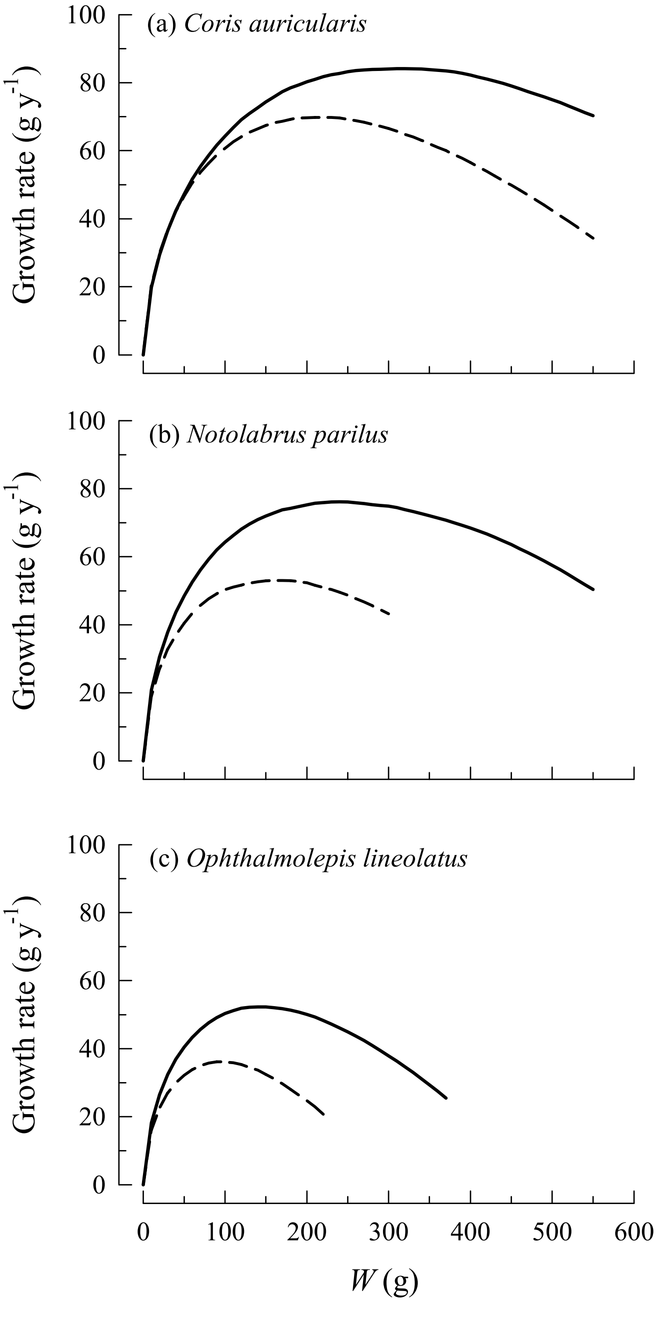


Figure 3.7. Instantaneous rate of growth for (a) *Coris auricularis*, (b) *Notolabrus parilus* and (c) *Ophthalmolepis lineolatus* in the JBMP (dashed line) and in the waters off Perth (solid line).

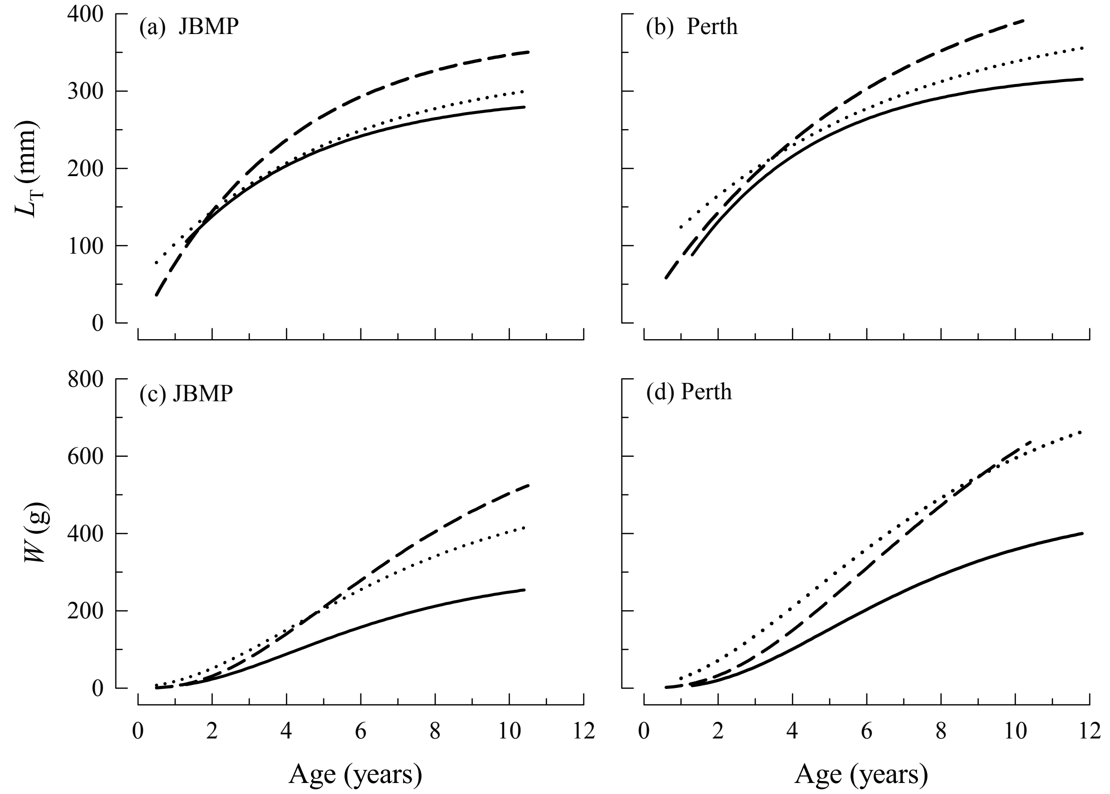


Figure 3.8. Growth curves fitted to the total lengths (a, b) and masses (c, d) at age of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* caught over reefs in the Jurien Bay Marine Park (JBMP) and in the waters off Perth. Dashed line, *C. auricularis*; dotted line, *N. parilus* and solid line, *O. lineolatus*.

Table 3.3. The average of the greatest 10 % of the values for L_T, M_T and A for *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* in the Jurien Bay Marine Park (JBMP) and in the waters off Perth, together with the 2.5th and 97.5th percentiles for those values. The rank order for each variable among each location are shown in brackets.

	L_T (mm)		**M_T (g)**		**A (years)**	
	JBMP	**Perth**	**JBMP**	**Perth**	**JBMP**	**Perth**
C. auricularis	**317 (1)**	**362 (1)**	**355 (2)**	**526 (2)**	**6.7 (3)**	**8.0 (3)**
	311, 322	356, 366	336, 372	497, 550	6.5, 7.0	7.6, 8.3
N. parilus	**298 (2)**	**341 (2)**	**460 (1)**	**690 (1)**	**8.0 (2)**	**9.0 (1)**
	292, 303	334, 347	432, 489	648, 728	7.7, 8.3	8.6, 9.3
O. lineolatus	**289 (3)**	**307 (3)**	**271 (3)**	**338 (3)**	**9.0 (1)**	**8.7 (2)**
	286, 292	304, 310	262, 280	324, 348	8.7, 9.2	8.3, 9.0

the curves fitted to the masses at age of each species in the two localities ($P < 0.001$) (Fig. 3.8c, d). At both localities and for all but the youngest age classes (*i.e.* < 2-4 years old), the estimated length at age of *C. auricularis* was the greatest of the three species and that of *O. lineolatus* was the least (Fig. 3.8a, b). The growth curve describing mass at age of *C. auricularis* remained similar to that of *N. parilus* in the JBMP up to *c.* age 6 and then diverged to lie above that latter curve (Fig. 3.8c). In contrast, the masses at age of *C. auricularis* were similar to those of *N. parilus* throughout the age ranges of the vast majority of individuals of those two species off Perth (Fig. 3.8d). von Bertalanffy growth curves fitted to the length at age and mass at age of the males of *C. auricularis*, *N. parilus* and *O. lineolatus* always lay above those derived for the females of the corresponding species in both the JBMP and in the waters off Perth (Figs 3.9, 3.10; Tables 3.1, 3.2).

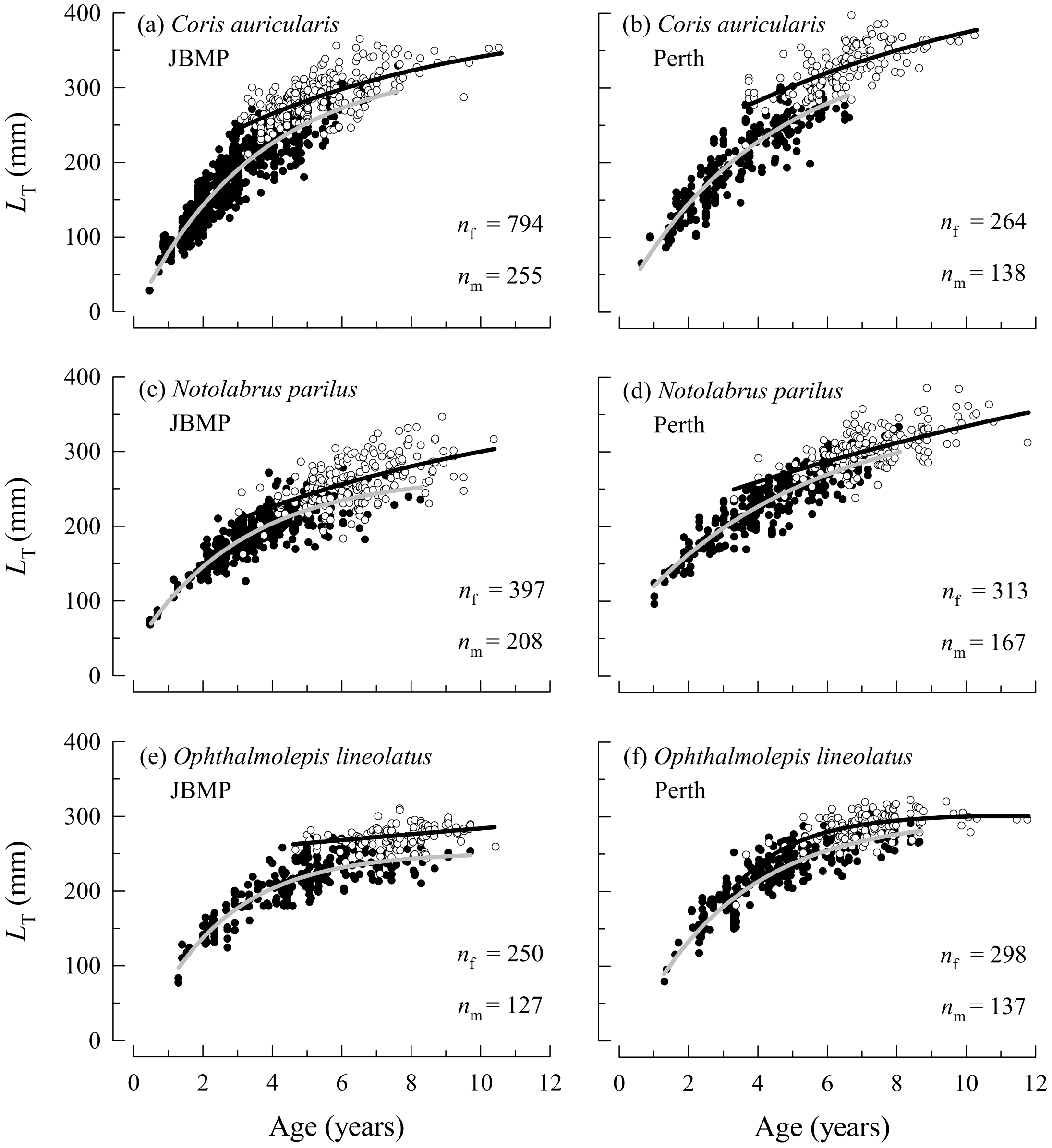


Figure 3.9. von Bertalanffy growth curves fitted separately to the lengths at age of the females (black circles) and males (white circles) of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* caught over reefs in the Jurien Bay Marine Park (JBMP) and in the waters off Perth. n_f, number of females; n_m, number of males.

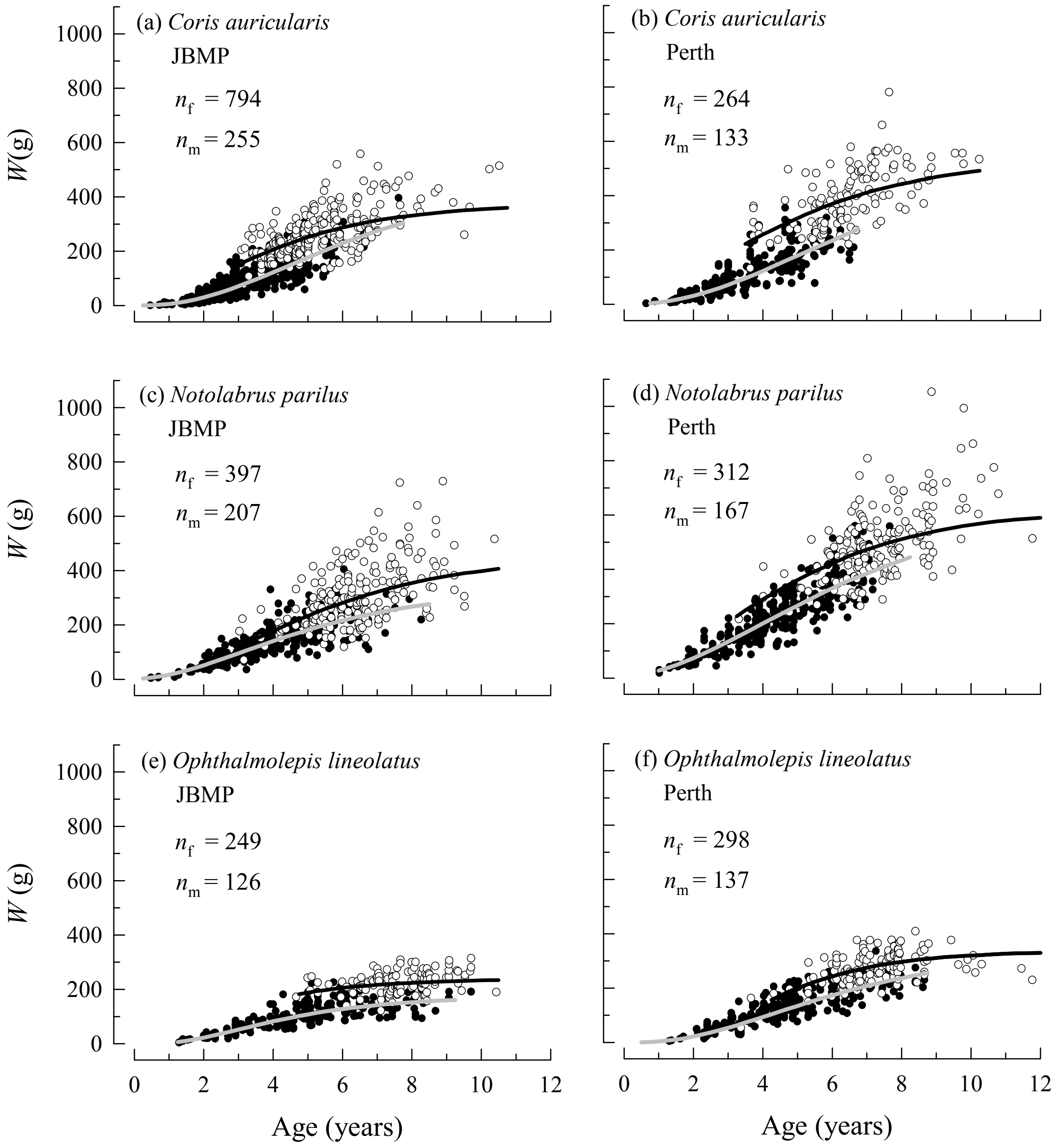


Figure 3.10. Growth curves fitted separately to the mass at age of the females (black circles) and males (white circles) of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* caught over reefs in the Jurien Bay Marine Park (JBMP) and in the waters off Perth. n_f, number of females; n_m, number of males.

3.4 Discussion

3.4.1 Maximum sizes and ages at different latitudes

The Metabolic Theory of Ecology (MTE) predicts that the individuals of a given species reach a greater body size, live longer and grow more slowly at a higher (cooler) latitude than at a lower (warmer) latitude (*e.g.* Berrigan & Charnov, 1994; Angilletta *et al.*, 2004b; Brown *et al.*, 2004a; Charnov & Gillooly, 2004). While latitudinal comparisons between both the maximum size and growth of a fish species are often based on length, it is appropriate that, as the role of metabolism is invoked in the MTE, such comparisons, and also those relating to patterns of growth, also employ body mass as the indicator variable. Thus, in the present study, the maximum size and growth rate of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* at the two latitudes have been compared in terms of mass as well as length and the same approach was adopted when comparing those variables among the three species at the same latitude.

When comparing the maximum size or age of a species in samples from one latitude with that in those of the same species from another latitude, such a single value for the population at a latitude might be atypical, *i.e.* lie outside the normal range of the distribution for that variable at that latitude and would thus not be representative of the population at that latitude as a whole (see Trip *et al.*, 2008). A single value for such variables is thus an imprecise measure of the characteristic under examination and is highly dependent on sample size (*e.g.* Hoenig, 1983). Furthermore, it is not possible to compare statistically the individual maxima recorded for a variable in single samples from different latitudes. During the present study, a randomisation test was used to test whether the average of the greatest 10 % of the values for a given variable in each re-sampled dataset for a species from the two localities were different. It was assumed that the resultant respective values for that top 10 % for L_T, M_T and A for a species in two localities reflected the relative differences in the true maxima for those variables. Comparisons between the values for these three variables for the populations of each species at the two different latitudes benefited from the substantial sample sizes obtained from both localities.

The results of the randomisation tests demonstrated that, in all cases except for age with *O. lineolatus*, the maximum L_T, M_T and A of *C. auricularis*, *N. parilus* and *O. lineolatus* for the populations in the waters off Perth (expressed as the average of the top 10 % of the values for each of those variables) were significantly greater than the corresponding values for those same species in the JBMP, in which average monthly water temperatures were greater by between 0.6 and 0.9ºC. Furthermore, the average ages of the oldest 10 % of *O. lineolatus* in the two localities were not significantly different and thus did not directly run counter to the predictions of the MTE. It is thus concluded that the trends exhibited by the L_T, M_T and A at two different latitudes/temperatures are consistent with those predicted by the MTE and that, through using a statistically sound approach, such conclusions can be regarded with confidence. The view that these differences in temperature could help account for the above differences between the body size and age characteristics of the three species at the two different latitudes is consistent with the fact that, on the basis of its relationship with temperature (Brown *et al.*, 2004a), the metabolic rate of the three species would be expected to differ by 6 to 8 % between the waters of the JBMP and Perth.

3.4.2 Growth rates at different latitudes

Our data demonstrated that the lengths at age and masses at age of *C. auricularis*, *N. parilus* and *O. lineolatus* are similar early in life at the two latitudes and then become greater at the cooler and higher latitude in the waters off Perth throughout the remainder of life. These trends were paralleled by those of the instantaneous rates of growth in mass of these species, with those rates being similar for fish with the smallest observed masses (*i.e.* < 50 g for the first species and < 20 g for the last two species) and then, at larger masses, becoming increasingly greater for fish in the waters off Perth. The fact that the lengths and masses at age and instantaneous growth rates of the younger individuals of each species at the cooler, higher latitude and warmer, lower latitude were similar did not parallel the implications of the MTE that "growth" would be greater early in life at the lower latitude (*e.g.* Brown *et al.*, 2004a; Gillooly *et al.*, 2001; Charnov & Gillooly, 2004). There is thus a marked contrast between the close agreement between the body size and age characteristics of the three species at the two latitudes and the MTE and the converse finding for the growth rates of those species.

The presence of very substantial densities of each of the three labrid species over reefs in the JBMP and in waters off Perth, as in this type of habitat throughout south-western Australia (Delacy, 2008; Tuya *et al.*, 2009), implies that environmental conditions are highly conducive to sustaining the populations of these three species in those localities and that, in particular, the requisite food resources for each of these species are abundant in the respective habitats. Furthermore, the densities of each species in the JBMP and around Rottnest Island, *i.e.* essentially off Perth, were not found to be significantly different by Delacy (2008). In this context, it is pertinent that foregut fullness of none of the three species differed significantly between the two localities and that, although the dietary composition of each species differed between localities, this was due to differences in the contributions by the individual prey species rather than differences in the actual prey taxa (see Chapter 5). It is also relevant that, as the locations of the waters of the JBMP and Perth lie well within the geographic ranges of the three species, none of those species would be expected to be subjected to any pronounced "edge of range" effects, *i.e.* those associated with environmental conditions which are likely to be less than optimal for the species. It thus seems likely that differences in water temperature, rather than the abundance of food resources, represent the most important difference between the environment of the JBMP and waters off Perth that would influence growth.

From the above, it follows that, as the growth of each species is less in the JBMP than in the waters off Perth, the proportion of ATP derived from catabolism of ingested prey that is directed towards anabolic processes, *e.g.* somatic growth, is greater in the location where water temperature is lower. Furthermore, the greater investment of energy into somatic growth in the cooler waters is accompanied by a larger allocation of energy into gonadal development in those waters (see Chapter 4). Thus, the enzymes responsible for converting energy into somatic and gonadal growth may operate more efficiently at the lower temperature, which would be consistent with these species having an essentially temperate distribution. Such a proposal is consistent with the proposal of Hochachka & Somero (2002) that evolutionary modifications have rendered reaction rates which are relatively independent of the temperature at which an organism is adapted (see also Clarke, 2004). It is also possible that the demand for energy for basal metabolism and physical activity is less in the cooler environment and thus a greater proportion of energy is available for anabolic processes. The conclusion that the conversion of ingested food into biomass by the three labrid species is more effective in the higher than lower latitudes would parallel the situation recorded for certain life cycle stages of some other taxa, *e.g.* the juveniles of turbot (Imsland *et al.*, 2000) and the tadpoles of *Rana temporaria* (Lindgren & Laurila, 2010). In the context of the MTE, it is noteworthy that several authors have concluded that, at least in certain circumstances, the MTE is overly simplistic and fails to take into account the possibility that certain species have become adapted such that their growth rates are not directly related to environmental temperature (Clarke, 2004; Clarke & Fraser, 2004; Dell *et al.*, 2011; Huey & Kingsolver, 2011).

Until now, comparisons between the growth curves of each species at the two localities have been based on a common curve fitted for the two sexes at each location. Our data show, however, that for each species, length and mass-at-age curves constructed separately for males lie above those for females, which implies that sex change is size-dependent. However, the distributions of the sizes at age for the two sexes of a species (Figs 3.9, 3.10) within the common curve for that species (Figs 3.5, 3.6) provided no clear indications that the growth of individuals changed when they became males. This implies that it was appropriate to have used a common growth curve for the two sexes when exploring the implications of differences in growth between the populations of our species at two latitudes. This situation thus contrasts markedly with that recorded for *Achoerodus gouldii* by Coulson *et al.* (2009) and even more particularly *Cheilinus undulatus* by Choat *et al.* (2006) in which the length at age for males increasingly diverged from that of females with increasing age.

The von Bertalanffy growth curves for *O. lineolatus* in the JBMP and waters off Perth are compared in Fig. 3.11 with that for this species in eastern Australia (Morton *et al.*, 2008) and thus at latitudes whose mid points are *c.* 30°25'S, *c.* 32°00'S and *c.* 33°15'S, respectively. These comparisons demonstrate that, at all ages above 1 year, the length at age was greatest for this species at the greatest latitude and that, at all ages above 3 years, it was least for this species at the lowest latitude.

3.4.3 Interspecific comparisons

The fact that the rank order of each of the "maximum" L_T and "maximum" M_T for each species is the same in the JBMP and off Perth is consistent with the hypothesis that, at each location, temperature has a similar relative effect on the metabolism of each

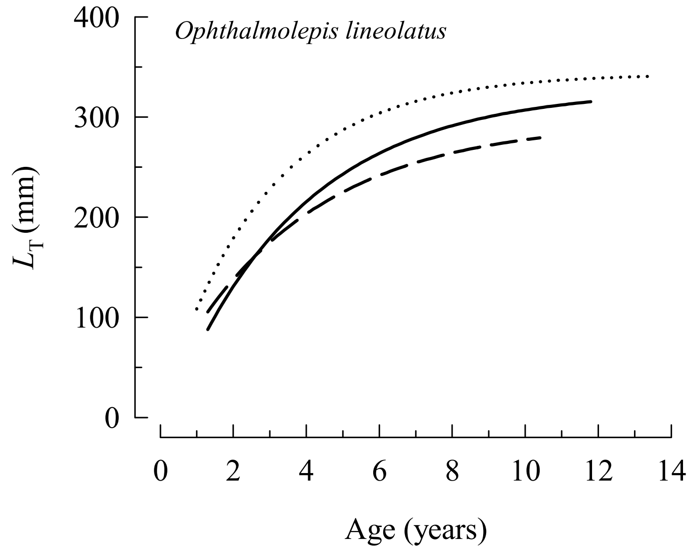


Figure 3.11. Comparisons between the von Bertalanffy growth curves for *Ophthalmolepis lineolatus* in waters of the Jurien Bay Marine Park (dashed line) and off Perth (solid line) and that recorded by Morton *et al.*, (2008) for eastern Australia (dotted line).

species, both of which lie well within their distribution ranges. Although the "maximum" A for the three species in the JBMP and off Perth differed in rank order, it was still least for *C. auricularis* in both of these localities. The rank order did vary however, among the three variables, with the "maximum" L_T being greatest for *C. auricularis* while that for "maximum" M_T was greatest for *N. parilus*. This reflects, in part, the masses at all lengths being far greater for the second than first species.

It was evident that the growth of *O. lineolatus* was least in both the JBMP and in the waters off Perth, irrespective of whether size was expressed in terms of length or mass. However, whereas the growth of *C. auricularis* was clearly greater than that of *N. parilus* over most of the common age range of those species, when expressed in terms of length at age, the differences, when based on mass at age, only became pronounced after six years of life in the JBMP and were never conspicuous at any stage throughout life in the waters off Perth. The tendency for the growth of *C. auricularis* to be more similar to that of *N. parilus* when employing mass rather than length as the independent variable is due, in part, to the latter species having a substantially greater mass at any given length (Fig. 3.3). This demonstrates the need to recognise that, as comparisons between the growth of fish species typically employ length as the dependent variable, the results of such inter-specific comparisons may differ when using biomass for species that have substantially different body shapes and thus also mass-length relationships.

CHAPTER 4

REPRODUCTION

4.1 Introduction

Hermaphroditism is widespread among teleost fishes. It has become increasingly evident, however, that it is crucial to obtain sound data on several aspects of the biology of a species before that species can be termed a functional hermaphrodite, *i.e.* one in which at least a proportion of its individuals can reproduce as both male and female at some stage during life (Sadovy & Shapiro, 1987; Sadovy de Mitcheson & Liu, 2008). When a species has been shown to be a functional hermaphrodite, such data can then be used to ascertain whether it is a simultaneous or sequential hermaphrodite and, if the latter, whether it involves a change from female to male (protogyny) or from male to female (protandry). With protogynous species, the next step involves attempting to determine whether it is monandric, *i.e.* all males are derived exclusively from functional females, or diandric, *i.e.* some males also develop from females that never became sexually mature. The analogous approach can be adopted for protandrous species.

Sadovy & Shapiro (1987) have pointed out that the presence, in size and age frequency distributions, of one mode that corresponds to males and another to females, or of sex ratios that differ from unity, do not constitute, on their own, reliable indicators that a species is hermaphroditic. Such size and age bimodality and differences in sex ratios can occur, for example, through differences in growth and/or segregation of the sexes among locations according to size or age. It thus follows that it is crucial to ensure that representative samples of a species are used to determine whether that species is a functional hermaphrodite and, if so, its type of sexual pattern. The above authors also emphasise the importance of examining histological sections of gonads from wide size and age ranges of a species to determine whether the gonads of that species possess the characteristics that typify hermaphrodites, *e.g.* the retention of the central ovarian lumen by the testes of protogynous hermaphrodites (Sadovy & Shapiro, 1987, Sadovy de Mitcheson & Liu, 2008).

As the Labridae is such a large and diverse family, it is not surprising that a wide range of sexual patterns is found among its species (Sadovy de Mitcheson & Liu, 2008). While protogyny is widespread in this family, having been confirmed for species from at least 21 of its genera, some of its species exhibit bi-directional sex change, *i.e.* reversal to the initial sex (Kuwamura *et al.*, 2002; Ohta *et al.*, 2003), and others are gonochoristic, *i.e.* all of their individuals reproduce exclusively as either a female or male (Hoffman, 1980; Denny & Schiel, 2002). Furthermore, both protogynous and gonochoristic species are found in three genera of labrids and many of the latter have a temperate distribution (Sadovy de Mitcheson & Liu, 2008).

This component of the thesis focuses on determining the characteristics of the reproductive biology of the populations of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* on reefs at two different latitudes on the lower west coast of Australia and whose size and age compositions and growth were described in the previous chapter. The only previous study of the reproductive biology of any of the above three species is that of Morton *et al.* (2008b), who demonstrated that, in eastern Australian waters, *O. lineolatus* is a protogynous hermaphrodite. Morton *et al.* (2008b) also concluded that the Crimsonband Wrasse *Notolabrus gymnogenis*, a congener of *N. parilus* was a protogynous hermaphrodite and suggested that it may also be monandrous. The Bluethroat Wrasse *Notolabrus tetricus* and the Spotty *Notolabrus celidotus* are also considered to be protogynous hermaphrodites (Jones, 1980; Barrett, 1995). In contrast, the Purple Wrasse *Notolabrus fucicola*, a congeneric of *N. parilus*, is a gonochorist (Denny & Schiel, 2002) and the Mediterranean Rainbow Wrasse *Coris* *julis*, a congener of *C. auricularis*, is a diandric protogynous hermaphrodite (Reinboth, 1967; 1970; Bruslé, 1987).

The results presented in the previous chapter demonstrated that differences between certain characteristics of each of the above three labrid species in the JBMP at *c.* 30ºS and in the waters off Perth at *c.* 32ºS conformed to the predictions of the Metabolic Theory of Ecology (MTE) regarding anticipated latitudinal trends. Thus, as expected, the maximum values for length, mass and age of each species were less at the lower latitude and thus higher temperature than at the higher latitude and thus lower temperature (Chapter 3). In contrast, however, to the predictions of the MTE, as well as empirical data for many ectothermic species, the growth rate of none of the three species was slower early in life at the higher latitude, although, as expected, it was faster later in life. Empirical data for ectotherms show that a reduction in temperature is also often accompanied by maturity being delayed and it occurring at a larger body size (Charnov & Berrigan, 1990).

Empirical data for a range of fish species have also demonstrated that the length and age at maturity are related to maximum length and age, respectively (Beverton & Holt, 1959; Charnov & Berrigan, 1990; Froese & Binohlan, 2000). Moreover, on the basis of data for 52 sequentially hermaphroditic fish species, it was concluded that, irrespective of body size, such species typically change sex when they have reached *c.* 80 % of their maximum body size and are *c.* 2.5 times their age at maturity (Allsop & West, 2003).

The collection of a wide size and age range of *C. auricularis*, *N. parilus* and *O. lineolatus* were used to obtain data which facilitated comparisons between the reproductive biology of each species at two different latitudes and also between those three labrid species, which each attain a similar maximum size and age (Chapter 3). The first aim of this chapter was to determine whether, as in eastern Australia, *O. lineolatus* is a protogynous hermaphrodite, and to elucidate whether *C. auricularis* and *N. parilus* are likewise protogynous hermaphrodites or, like *N. fucicola*, are gonochorists. The data were then used to test the following hypotheses. 1. Paralleling the situation with somatic growth (Chapter 3), the investment of energy into ovarian development by each species is greater at the colder, higher latitude location (Perth) than at the warmer, lower latitude location (JBMP). 2. The spawning periods of the three species differ conspicuously and thereby reduce the potential for competition for spatial and food resources by their larvae and young juveniles. The following points were also explored. 1. As *C. auricularis*, *N. parilus* and *O. lineolatus* do not follow the expected trend of exhibiting more rapid growth early in life at the warmer, lower latitude, do they still mature later in the cooler environment, as is the case with many ectotherms (*e.g.* Angilletta *et al.*, 2004a). 2. If each species is confirmed as a protogynous hermaphrodite, do they each change sex at both latitudes at a length equivalent to *c.* 80 % of their maximum length and at an age equivalent to 2.5 times the age at which they attain maturity, even though the growth, maximum length and age of each species varies with latitude. 3. Does each species undergo sex change when it has reached a similar proportion of its maximum age and irrespective of latitude.

4.2 Materials and methods

4.2.1 Sampling regime and laboratory processing

The sampling regimes used in the Jurien Bay Marine Park (JBMP) and waters off Perth are described in Chapter 2. In brief, *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* were collected by line and spear fishing and trapping at numerous sites over reefs in waters of the JBMP and off Perth. Sampling was undertaken in every second or third month between January 2005 and February 2008, thereby ensuring samples were obtained for each calendar month.

The total length (L_T) and wet body mass (M_T) of each fish were recorded to the nearest 1 mm and 0.1 g, respectively. On the basis of the macroscopic appearance of their gonads, the individuals of each species were categorised as either female or male and, in a few cases, as sex could not be determined. On the basis of the scheme of Laevastu (1965), each ovary was allocated to one of the following stages in development, *i.e.* I, virgin; II, immature/resting; III, developing; IV, maturing; V, pre-spawning; VI, spawning; VII, spent and VIII, recovering spent (see Table 4.1 in Results). The scheme of Rhodes and Sadovy (2002) was modified slightly to allocate each testes to one of the following developmental stages, *i.e.* I, inactive; II, mature, active; III mature, ripe and IV, post-spawning (see Table 4.2 in Results). The gonads of each definitive female and male fish were weighed to the nearest 0.01 g (M_G).

A minimum of 10 ovaries and 10 testes from a wide length range of each species from each calendar month, together with any gonads, which on the basis of macroscopic examination, did not clearly contain only ovarian or testicular material, were preserved in Bouin's fixative for *c.* 24 h. The latter group of gonads comprised those of a few of the smallest fish and those of a small number of larger fish, whose lengths lay within the size range at which both females and males were recorded. The gonads were subsequently dehydrated in a series of increasing concentrations of ethanol. The mid-region of each gonad was embedded in paraffin wax and cut into 6 μm thick transverse sections. Each section was then stained either with Mallory's trichrome or Ehlrich's haematoxylin and eosin, mounted on a microscope slide using DePeX mounting media and examined under a compound microscope. The histological sections were used to confirm the accuracy of the macroscopic staging of the gonads and to ascertain whether those gonads, which could not be categorised definitively as either ovaries or testes, contained one or both of those tissues. It should be noted that transverse sections of the anterior, middle and posterior regions of a subsample of gonads throughout the size range of fish representing each species confirmed that structure and development were consistent along the length of the gonad.

4.2.2 Analyses

The gonad weights of females of *C. auricularis*, *N. parilus* and *O. lineolatus* in the JBMP and waters off Perth were standardised for L_T using ANCOVA, employing month and location as fixed factors, ln L_T as the covariate and ln M_G as the dependent variable. For each location, this standardisation procedure employed females whose lengths were ≥ the L_T at which 50 % of that sex reached maturity (L_{T50}) in that location, the values for which are given in the Results.

For the females of each species in both the JBMP and waters off Perth, the monthly mean M_G and frequencies of occurrence of the different gonadal development stages (likewise determined for females ≥ L_{T50} at maturity) were plotted to describe the pattern of change in the development of ovaries throughout the year.

The L_T at which 50 and 95 % of females of each of the three labrid species in each location (JBMP and Perth) attained sexual maturity, *i.e.* L_{T50} and L_{T95}, respectively, were estimated using data for those months when ≥ 50 % of the ovaries of the females of each species were at stages III to VIII, *i.e.* were either developing, about to spawn, spawning or had recently spawned. These fish were thus considered to be sexually mature or about to become sexually mature (Fairclough, 2005; Moore *et al.*, 2007). The values for the L_{T50} and L_{T95} and their 95 % confidence limits were determined using logistic regression analysis. For this analysis, logistic curves were fitted to the probability that, during the above months for each species in each location, a female fish at a specific length would possess gonads at stages III to VIII. The equation used for this analysis is $P = \left\{1 + e^{\left[-\ln(19)(L_T - L_{T50})(L_{T95} - L_{T50})^{-1}\right]}\right\}^{-1}$, where P = the estimated proportion of mature females at a particular L_T and L_{T50} and L_{T95} = the L_T at which 50 and 95 % of fish would be expected to be sexually mature, respectively. The logistic curves were fitted using maximum likelihood estimation with SOLVER in Microsoft Excel. The length and maturity data were randomly resampled and analysed to create 1000 sets of bootstrap estimates of the parameters of the logistic equation and of the probabilities of maturity for a range of specified L_T. The 95 % confidence limits (CLs) of the probability of maturity at each specific length were taken as the 2.5 and 97.5 percentiles of the corresponding predicted values resulting from this resampling analysis. The medians of the bootstrap estimates were used as the point estimates of each parameter and of the probability of maturity at each specified length. A logistic regression analysis, of the form described above, was also used to determine the age (A) at which 50 % (A_{50}) and 95 % (A_{95}) of females of each species in each location reached sexual maturity, together with their 95 % CLs.

Logistic regression analyses were likewise used to determine the lengths and ages at which 50 % (L_{T50c}, A_{50c}) and 95 % (L_{T95c}, A_{95c}) of the individuals of each species in each location were male, *i.e.* had changed sex, together with their 95 % CLs. Likelihood-ratio tests were employed to determine whether the values for the L_{T50}, A_{50}, L_{T50c} and A_{50c} for *C. auricularis*, *N. parilus* and *O. lineolatus* in the JBMP were significantly different from those of the corresponding species in the waters off Perth. The null hypothesis that the data for a species in the two localities could be described by a curve with a common L_{T50}, A_{50}, L_{T50c} and A_{50c} was compared with the alternative hypothesis that the data for each location would be better described by curves with separate L_{T50}, A_{50}, L_{T50c} and A_{50c} (Cerrato, 1990). The test statistic was calculated as twice the difference between the log-likelihood obtained by fitting a common curve to the data for both localities and that obtained by fitting separate curves to the data for each location. The null hypothesis was rejected at the $\alpha = 0.05$ level of significance if the test statistic exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the common curve and the separate curves (Cerrato, 1990).

4.3 Results

4.3.1 Identification of type and stages in development of the gonads

On the basis of their macroscopic appearances, the gonads of all *C. auricularis* with lengths <186 mm L_T (the minimum length of any fish that were designated macroscopically as male) were recorded either as ovaries (n = 598) or as unsexable (n = 37). The lengths of the fish in the former and latter categories ranged from 72 to 184 mm and from 53 to 122 mm, respectively. Histological examination of 27 of the gonads designated as ovaries demonstrated that these gonads contained only ovarian tissue and that the same was true for all of the 37 unsexable gonads, apart from those of the two of the smallest individuals, which contained both ovarian and testicular tissue (Fig 4.1a) and were thus termed bisexuals. The two exceptions were found in fish with lengths of 89 and 90 mm and were thus among the very smallest representatives of this species that were examined histologically (see Fig. 3.4 in Chapter 3).

The gonads of all of the 224 *N. parilus* and 136 *O. lineolatus* with lengths < 162 and < 181 mm L_T, respectively (the respective minimum lengths of individuals of those species that were designated macroscopically as males) were recorded as ovaries on the basis of their macroscopic appearance. Histological examination of 42 and 38 of the above gonads of *N. parilus* and *O. lineolatus*, respectively, confirmed that these gonads comprised solely of ovarian tissue. A further 21 *N. parilus* and 8 *O. lineolatus*, with lengths ranging from 94 to 114 mm and from 77 to 117 mm, respectively, possessed unsexable gonads. All of these gonads were examined histologically and likewise shown to contain solely ovarian tissue. Thus, no bisexual fish were found among the small individuals of *N. parilus* and *O. lineolatus*.

Apart from the gonads of the two small bisexual *C. auricularis*, those of all *C. auricularis*, *N. parilus* and *O. lineolatus* with lengths <140 mm L_T that were examined histologically were shown to contain undifferentiated germ cells (protogonia *sensu* McPherson, 1977), oocytes in various stages of meiosis, chromatin nucleolar oocytes and occasionally also perinucleolar oocytes. Thus, as designated on the basis of their macroscopic appearance (Table 4.1), the gonads of these small fish belonged to females and were at stage I (virgin) in ovarian development. The characteristics of these gonads are similar to those of stage II (resting) ovaries of larger females (Fig. 4.1b).

While the gonads of the two small bisexual *C. auricularis* likewise possessed ovarian tissue with the same characteristics as those of stage I ovaries, they also possessed small areas of testicular tissue, that contained late stage spermatocytes and/or small areas of spermatids (Fig. 4.1a).

Macroscopically, the ovaries at stage IV were distinguished from those at stage III on the basis of their "tighter" structure and a greater prevalence of visible cream-coloured oocytes (Table 4.1). These differences were reflected microscopically in the presence of a greater number of cortical alveolar oocytes. Ovaries identified macroscopically as stages V (prespawning) and VI (spawning) were much larger than those of earlier stages and the latter possessed hydrated oocytes, which were clearly visible through their walls. Histological sections showed that stage V and VI ovaries contained numerous yolk granule oocytes (Fig. 4.1d). The combination of yolk granule oocytes, migratory nucleus oocytes, hydrated oocytes and post-ovulatory follicles in stage VI ovaries of each species demonstrates that these species are multiple spawners. Spent ovaries (stage VII) and recovering ovaries (stage VIII) comprised varying amounts of degenerating yolk granule and cortical alveolar oocytes, together with scar tissue. When examined histologically, none of the gonads identified macroscopically as ovaries at stages V-VIII were found to contain degenerating vitellogenic oocytes in

Table 4.1. Macroscopic characteristics of the stages in the development of the ovaries of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus*. Scheme adapted from Laevastu (1965). Terminology used for characteristics of oocyte development from Wallace & Selman (1981).

Stage	Macroscopic characteristics	Histological characteristics
I - *Virgin*	Ovarian lobes extend 1/4 of body cavity length. Strand-like, transparent and colourless.	Well organised lamellae with protogonia cells, oogonia, and chromatin nucleolar oocytes present.
II - *Immature/resting*	Ovaries occupy up to 1/4 of body cavity length. Translucent, pale yellow to pink. Ovarian lobe rounded. Small oocytes can be seen through ovary wall with magnifying glass.	Well organised ovarian lamellae, with oogonia and chromatin nucleolar and perinucleolar oocytes present. Note: these oocyte stages present in all subsequent ovarian stages.
III - *Developing*	Ovaries occupy approximately 1/3 of body cavity length. Few to many small white granular oocytes visible through ovarian wall.	Highly organised lamellae with few to many predominantly small yolk vesicle and early cortical alveolar oocytes.
IV - *Maturing*	Ovaries occupy approximately 1/3 of body cavity length. Ovarian lobes becoming enlarged, with few to many cream-coloured oocytes visible through ovarian wall.	Oogonia, chromatin nucleolar and perinucleolar oocytes present. Many small to large cortical alveolar oocytes.
V – *Pre-spawning*	Ovaries occupy 1/2 to 2/3 of body cavity length. Ovaries packed with many large cream-coloured oocytes, visible through ovarian wall.	Cortical alveolar and yolk granule oocytes abundant and at different stages of development.
VI - *Spawning*	Ovaries occupy about 2/3 length of body cavity and are swollen and packed with many large cream-coloured oocytes. Clear hydrated oocytes visible through the ovary wall.	Cortical alveolar oocytes and yolk granule oocytes abundant along with a combination of hydrated oocytes, migratory nucleus oocytes and/or post-ovulatory follicles.
VII - *Spent*	Ovaries occupy up to 2/3 of body cavity length. A few large cream-coloured oocytes visible through ovarian wall. Large spaces among oocytes. Flaccid and reddish in colour.	Ovarian lamellae disorganised and contain spaces. Cortical alveolar and yolk granule oocytes present, but > 50 % of those oocytes atretic.
VIII - *Recovering spent*	Ovaries occupy approximately 1/3 of body cavity length. Ovaries flaccid and red to brown.	Ovary disorganised, consisting of previtellogenic oocytes and connective tissue. Few remnants of atretic cortical alveolar and yolk granule oocytes may be present.

Table 4.2. Macroscopic characteristics of the stages in the development of the testes of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus*. Scheme adapted from Rhodes and Sadovy (2002).

Stage	Macroscopic characteristics	Histological characteristics
I - *Inactive*	Testes occupy 1/3 of body cavity length. Essentially flat and string like. Translucent and pinkish.	Some early proliferation of spermatocytes. Remnant ovarian lumen present.
II – *Mature, active*	Testes 1/3 to 1/2 of body cavity length. Flat to partially enlarged, tapering in diameter towards anterior end. Partially translucent with some cream coloured areas, to opaque and cream in colour in more developed testes.	Spermatocytes abundant. Spermatids present in crypts and represent < 50 % of the gonad volume.
III – *Mature, ripe*	Testes 2/3 of body cavity length. Swollen, almost triangular in shape at posterior end and tapering towards anterior end. Opaque and cream to white in colour. May have brown tinges at anterior ends.	Spermatids abundant in crypts representing > 50 % of the gonad volume. Sperm sinuses present and filled with spermatozoa.
IV – *Post-spawning*	Testes 1/3 to 2/3 of body cavity length. Flaccid, reddish brown in colour.	Sperm sinuses largely empty with little or no spermatozoa. Scar tissue abundant and gonad empty with early stages of spermatogenic tissue.

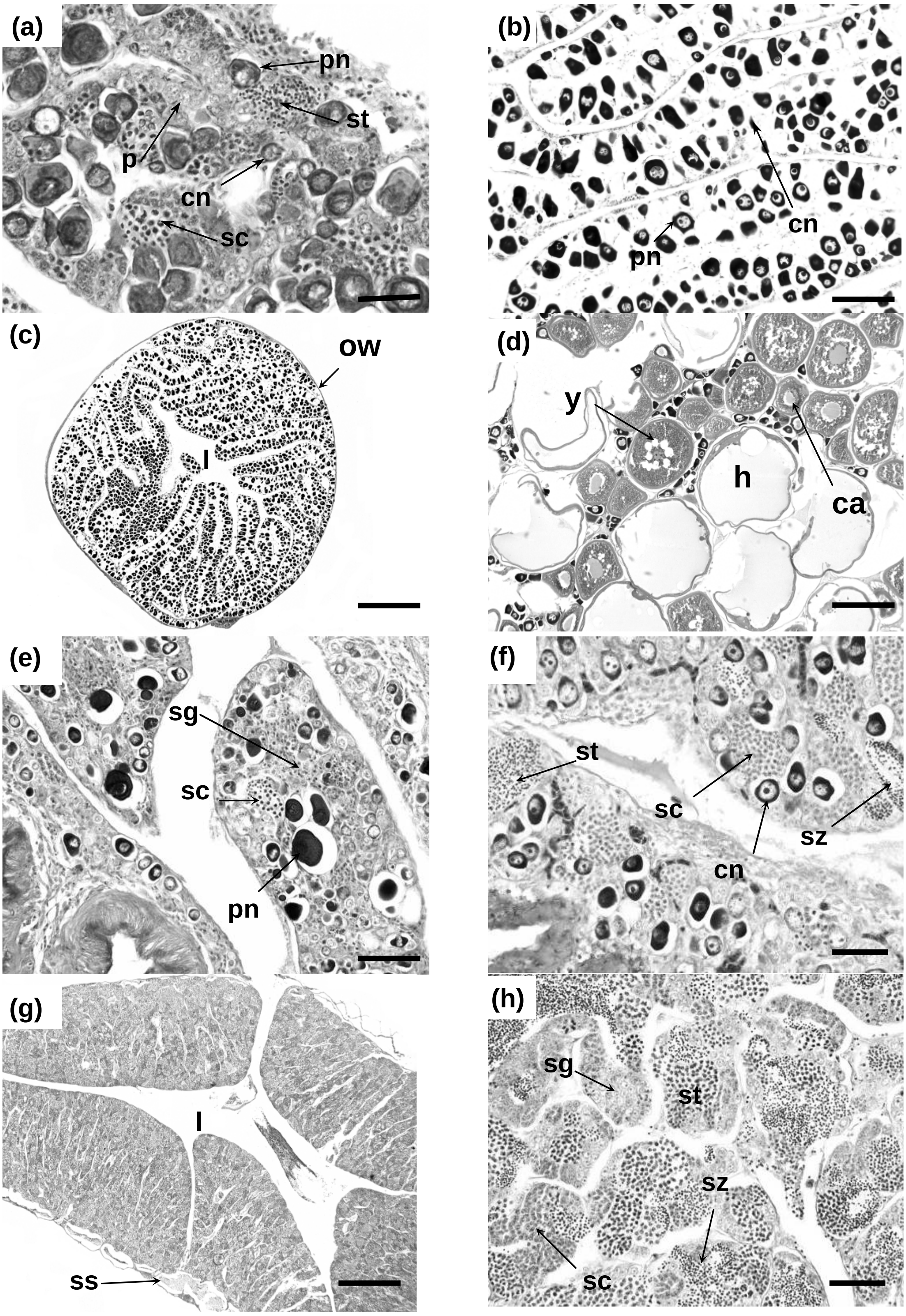


Figure 4.1. Photomicrographs of histological sections of gonads of (a) a small bisexual *Coris auricularis* (89 mm), (b) resting female ovary, (c) resting ovary showing ovarian wall, lumen and lamellae, (d) spawning ovary showing batches of different stage oocytes, (e) bisexual gonad showing immature ovarian and testicular tissue, (f) functional male gonad showing immature ovarian tissue and mature testicular tissue, (g) insert 'stage' male testis showing lumen and sperm sinuses and a (h) insert 'stage' male testis showing different stages of spermatogenesis. Scale bar: (a, b, e, f, h) 100 µm; (c, g) 1 mm; (d) 200 µm. ca, cortical alveolar oocyte; cn, chromatin nucleolar oocyte; g, gonia; h, hydrated oocyte; l, lumen; o, ovarian wall; p, protogonia; pn, perinucleolar oocyte; sc, spermatocytes; sg, spermatogonia; ss, sperm sinuses; st, spermatids; sz, spermatozoa; y, yolk granule oocyte.

conjunction with testicular tissue.

Most of the gonads of those *C. auricularis*, *N. parilus* and *O. lineolatus* whose L_T ranged from 186 to 329, 162 to 333 and 181 to 305 mm, respectively, were identifiable macroscopically as either ovaries or testes, with the proportion of fish with testes increasing with increasing body size (see later in Results). However, 16 *C. auricularis* with a L_T between 202 and 300 mm and six *O. lineolatus* with a L_T between 185 and 252 mm contained gonads that were reddish to brown in colour, flaccid and occupied one half to two thirds of the length of the body cavity and could not be definitively categorised macroscopically as either ovaries or testes (see Fig. 3.4). Histological sections demonstrated that, among the above exceptions, the gonads of all but two *O. lineolatus* comprised gonial cells and a combination of previtellogenic oocytes, *i.e.* chromatin nucleolar and perinucleolar oocytes, and immature testicular tissue comprising predominantly spermatogonia and varying amounts of spermatocytes (Fig. 4.1e). Among the above exceptions, 13 of the *C. auricularis* and four of the *O. lineolatus* were caught during the spawning periods of those species. The gonads of the other two *O. lineolatus*, however, also contained spermatids and spermatozoa in the sperm sinuses (Fig. 4.1f), and are thus considered to belong to functional males.

The testes of all males of *C. auricularis*, *N. parilus* and *O. lineolatus* contained a lamellar structure, a membrane-lined lumen and an external wall (Fig. 4.1g). Those testes that were identified macroscopically as inactive, *i.e.* stage I (Table 4.2), comprised predominantly undifferentiated protogonia and also spermatogonia and some spermatocytes, which are both located in small crypts. The crypts in mature, active testes (stage II) contained mainly spermatocytes and spermatids, while those of mature, ripe testes (stage III) contained predominantly late stage spermatids (Fig. 4.1g, h). In the latter gonads, spermatozoa were often found in the sperm sinuses, which are located in the outer wall of the testes (Fig. 4.1g). Spermatozoa were never observed in the lumen of stage III testes. The crypts of spent testes, *i.e.* stage IV, contained protogonia and spermatogonia on the inner sides of their lining and, while their central regions were usually empty, they occasionally contained a few remnant spermatids or spermatozoa. Spermatozoa were only rarely detected in the sperm sinuses of these testes.

4.3.2 Trends exhibited by gonad weights and prevalence of sequential gonadal stages

The mean monthly ovarian weights of female *C. auricularis* $\geq L_{T50}$ at maturity in the JBMP and waters off Perth and standardised for a L_T of 239 mm followed the same trends throughout the year [Fig. 4.2(a), (b)]. They thus rose from low levels between January and March to reach their maxima in May and June in the JBMP and in April and May in the waters off Perth and then declined to low levels in July and the ensuing months. The mean monthly ovarian weights for *C. auricularis* were much higher, however, in the waters off Perth in April and May (*c.* 1.3 g) than in the JBMP in May and June (0.5 – 0.8 g) [Fig. 4.2(a), (b)]. The prevalence of sequential stages in gonadal development of *C. auricularis* in the JBMP and waters off Perth followed similar trends throughout the year. Thus, in both localities, the ovaries of all fish between July and February were at stages I/II and individuals with spawning gonads were caught only from April to June and spent individuals were found predominantly or only in July (Fig. 4.2a, b).

Although the monthly mean ovarian weights and prevalences of sequential stages in the ovarian development of female *N. parilus* and *O. lineolatus* also underwent pronounced seasonal changes in both the JBMP and the waters off Perth, the times when those two variables “peaked” differed among the three species. Thus, the mean monthly ovarian weights for *N. parilus* in the two localities peaked later between July and October, and thus later than *C. auricularis*, the vast majority of fish with spawning stage ovaries were found in those months (Fig. 4.2c, d). The above two biotic variables in *O. lineolatus* peaked even later, with the mean monthly ovarian weights and the prevalence of females with spawning ovaries being greatest in October to December (Fig. 4.2e, f). As with *C. auricularis*, the two or three maximum mean monthly ovarian weights for both *N. parilus* and *O. lineolatus* in the waters off Perth were greater than the mean monthly maxima in the JBMP.

On the basis of months in which stage V and VI ovaries were present (Fig. 4.2), the spawning periods in both the JBMP and waters off Perth were the same for *C. auricularis*, *i.e.* April to June, and similar for *N. parilus*, *i.e.* July to October and August to November, respectively, and for *O. lineolatus*, *i.e.* September to February and October to February, respectively. However, those data also show that the spawning period in both localities lasts for the least time in the case of *C. auricularis*, *i.e.* three months, and was the longest with *O. lineolatus*, *i.e.* five or six months. Furthermore, in each location, the maximum mean monthly ovarian weights were far less for *C. auricularis* than for *O. lineolatus*, which was similar to those of *N. parilus* (Fig. 4.2).

The trends exhibited by the mean monthly weights of the testes of *C. auricularis*, *N. parilus* and *O. lineolatus* were essentially the same as those of their females (data not shown). The mean weights for the stage III testes (mature, ripe) of *C. auricularis*, *N. parilus* and *O. lineolatus* in both localities ranged from 17 to 31 % of the mean weights of stage V/VI (prespawning/spawning) ovaries of those species.

The prevalence of ovaries containing hydrated oocytes (stage VI) among all stage V and VI ovaries in the JBMP and waters off Perth was far lower for *C. auricularis* (30 and 48 %, respectively) and *N. parilus* (48 and 40 %, respectively) than for *O. lineolatus* (89 and 71 %, respectively). As these fish were sampled in mid morning to mid afternoon, they were collected during the hours, prior to the late afternoon when most temperate labrid species spawn, and thus when oocyte hydration occurs (Warner & Robertson, 1978, Hoffman, 1980; Sakai & Kohda, 2001; Cossington

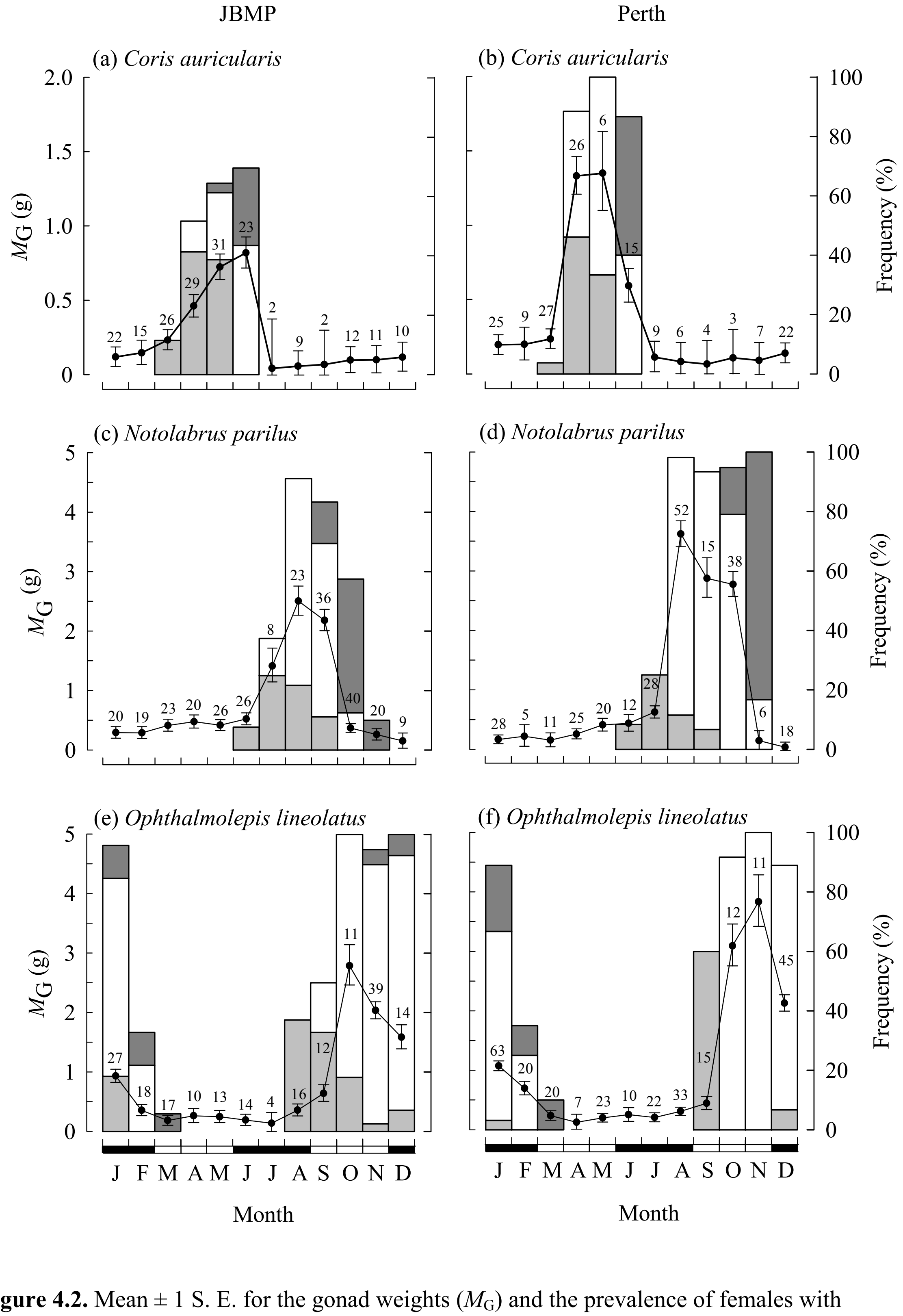


Figure 4.2. Mean ± 1 S. E. for the gonad weights (M_G) and the prevalence of females with ovarian stages III to IV (grey), V and VI (white) and VII and VIII (dark grey) in each month for (a, b) *Coris auricularis*, (c, d) *Notolabrus parilus* and (e, f) *Ophthalmolepis lineolatus* in the Jurien Bay Marine Park (JBMP) and waters off Perth. The M_G of *C. auricularis*, *N. parilus* and *O. lineolatus* were standardised for females with a L_T of those species ≥ L_T at maturity, *i.e.* 239, 227, 224 mm, respectively. Sample sizes for each month are shown.

et al., 2010). On the basis of the above prevalences of stage VI ovaries in each species, *C. auricularis* thus spawns approximately once every 3.2 and 2.1 days in the JBMP and off Perth, respectively, compared with every 2.1 and 2.5 days for *N. parilus* and once every 1.1 and 1.4 days for *O. lineolatus*. As a chi square test demonstrated that the prevalences of stage VI ovaries among the stage V and VI ovaries of each species did not differ significantly between the JBMP and in the waters off Perth (all $P > 0.05$), the spawning frequencies of each species in the two localities are likewise considered not to be significantly different.

4.3.3 Lengths and ages at maturity

The months during which ≥ 50 % of the ovaries of female *C. auricularis*, *N. parilus* and *O. lineolatus* were at stages III – VIII, *i.e.* considered to be mature, and for which the data were thus used to determine the lengths and ages at sexual maturity were as follows; April to June for *C. auricularis* and September to February for *O. lineolatus* in both the JBMP and waters off Perth, while, for *N. parilus*, they were from August to October in the JBMP and August to November in the waters off Perth (see Fig. 4.2).

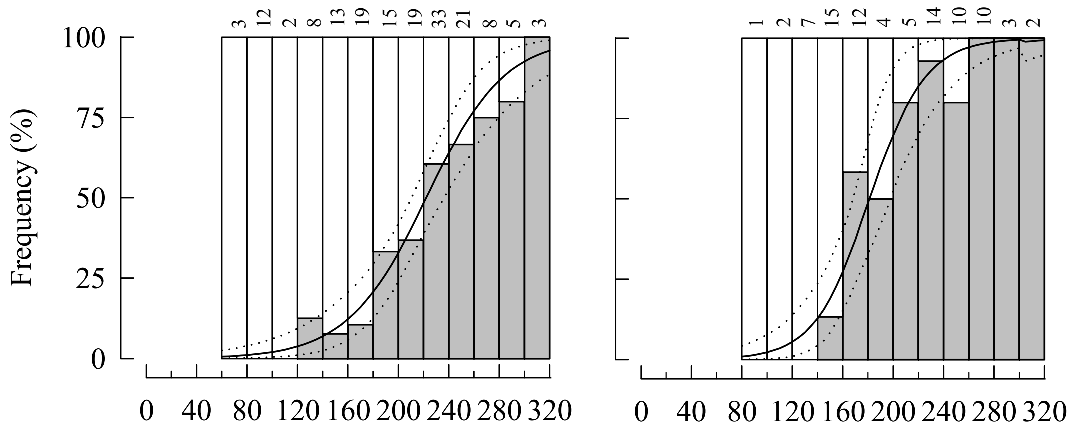
The minimum L_Ts at which sexually mature female *C. auricularis*, *N. parilus* and *O. lineolatus* were recorded were 139, 132 and 155 mm, respectively, in the JBMP and 155, 193 and 140 mm, respectively, in the waters off Perth (Fig. 4.3a, c, e). The prevalences of females with mature ovaries increased with increasing body size, with the result that in the 200-219 mm length class, ≥ 75 % of the females of *N. parilus* and *O. lineolatus* in the JBMP and waters off Perth and of *C. auricularis* in the latter waters were mature. A comparable prevalence of maturity was not achieved by *C. auricularis* in the JBMP until this species had reached lengths of 260-279 mm (Fig. 4.3b, d, f).

JBMP

Perth

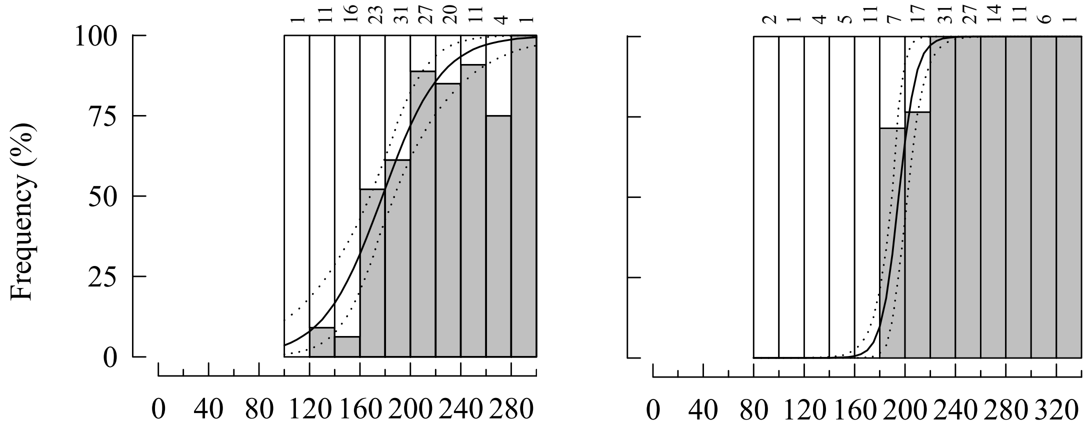
(a) *Coris auricularis*

(b) *Coris auricularis*



(c) *Notolabrus parilus*

(d) *Notolabrus parilus*



(e) *Ophthalmolepis lineolatus*

(f) *Ophthalmolepis lineolatus*

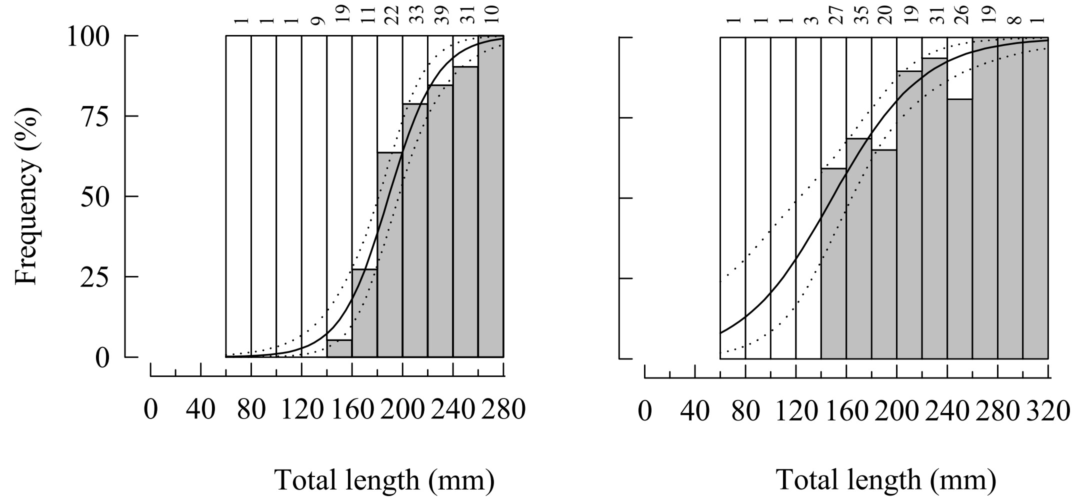


Figure 4.3. Percentage frequencies of occurrence of immature (white bars) and sexually mature (grey bars) females in sequential 20 mm length classes during the spawning periods of (a, b) *Coris auricularis*, (c, d) *Notolabrus parilus* and (e, f) *Ophthalmolepis lineolatus* in the Jurien Bay Marine Park (JBMP) and waters off Perth. The logistic curves (solid lines) and their 95 % confidence limits (dotted lines) were derived from logistic regression analysis that described the relationship between total length and the probability that an individual possessed mature gonads. Sample sizes for each length class are shown.

The L_{T50} for the females of *C. auricularis*, *N. parilus* and *O. lineolatus* at maturity in the JBMP was significantly different from that of the corresponding species in the waters off Perth ($P < 0.001$ for *C. auricularis* and *O. lineolatus*; $P < 0.01$ for *N. parilus*). However, whereas the L_{T50} for *C. auricularis* (222 mm) and *O. lineolatus* (189 mm) in the JBMP was greater than that for these species in the waters off Perth, *i.e.* 181 and 149 mm, the reverse was true for *N. parilus* with the L_{T50} in the JBMP being 178 mm compared with 195 mm for the waters off Perth (Table 4.3).

No individuals of any of the three species became mature at the end of their first year of life and only a few reached maturity one year later (Fig. 4.4a-f). The prevalence of mature females increased markedly with age, with *c.* 50 % or more of each species in each location becoming mature by the end of the third year of life (Fig. 4b-f), except in the case of *C. auricularis* in the JBMP in which this level was not achieved until one year later (Fig. 4.4a). The A_{50} for both *C. auricularis* and *O. lineolatus* in the JBMP was significantly greater than in the waters off Perth ($P < 0.001$), while that for *N. parilus* did not differ significantly between the two locations ($P > 0.05$).

Table 4.3. Estimates of the total length (L_{T50}, L_{T95}) and age (A_{50}, A_{95}) at maturity ± 95 % CLs for female *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* in the Jurien Bay Marine Park (JBMP) and in the waters off Perth.

	L_T (mm)					**Age (years)**				
	n	**L_{T50}**	**95 %**	**L_{T95}**	**95 %**	***n***	**A_{50}**	**95 %**	**A_{95}**	**95 %**
Coris auricularis										
JBMP	161	222	211, 236	314	283, 361	151	3.8	3.4, 4.3	6.7	5.6, 8.5
Perth	85	181	168, 198	247	209, 284	82	2.8	2.4, 3.2	4.7	3.6, 5.9
Notolabrus parilus										
JBMP	145	178	168, 188	247	224, 283	140	3.1	2.9, 3.4	4.8	4.1, 5.7
Perth	137	195	190, 202	215	202, 224	133	2.9	2.7, 3.1	3.9	3.7, 4.1
Ophthalmolepis lineolatus										
JBMP	177	189	181, 197	247	231, 265	167	3.8	3.5, 4.2	6.5	5.7, 7.4
Perth	192	149	122, 164	256	227, 297	182	2.6	2.0, 2.9	5.1	4.3, 6.5

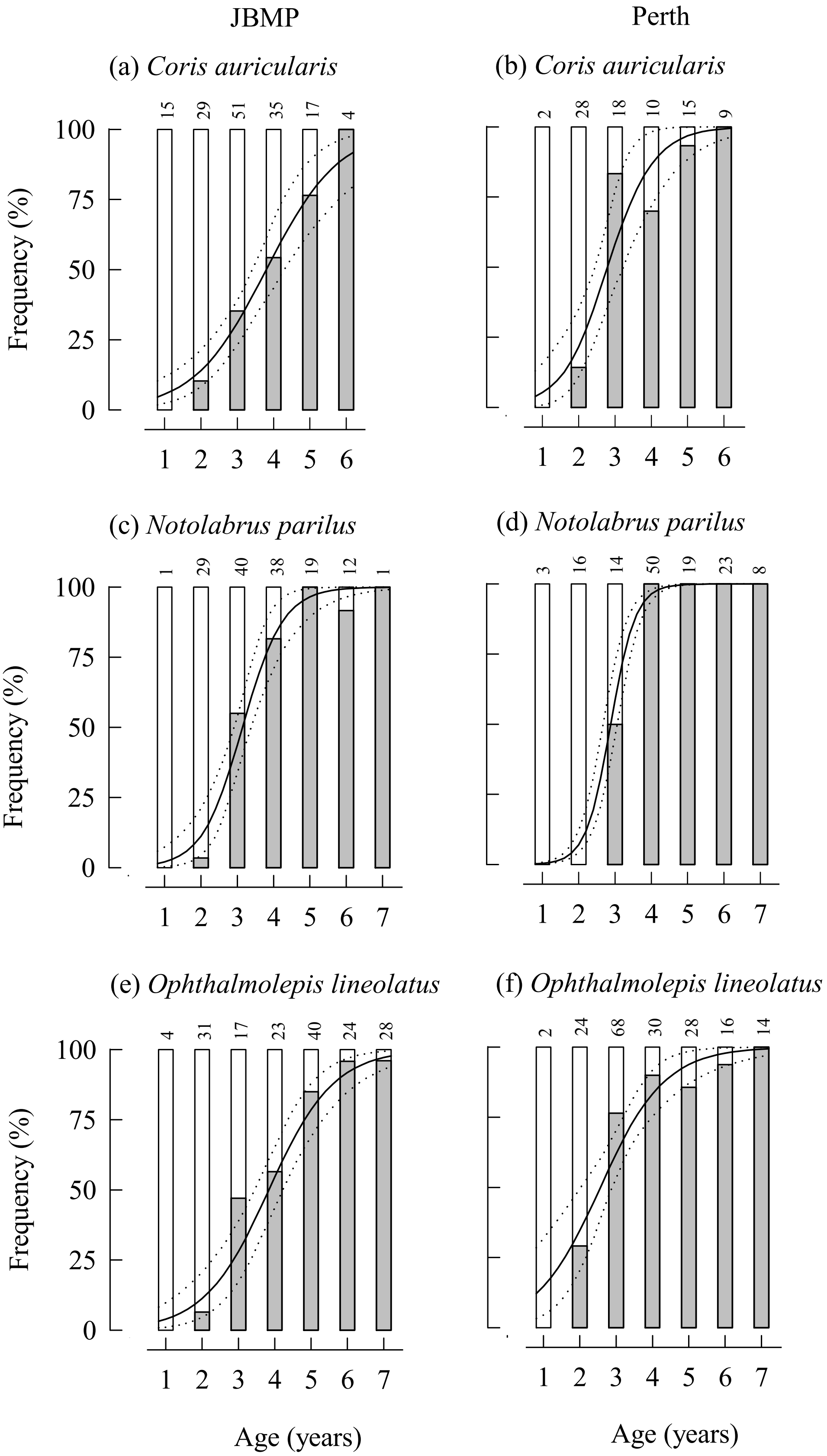


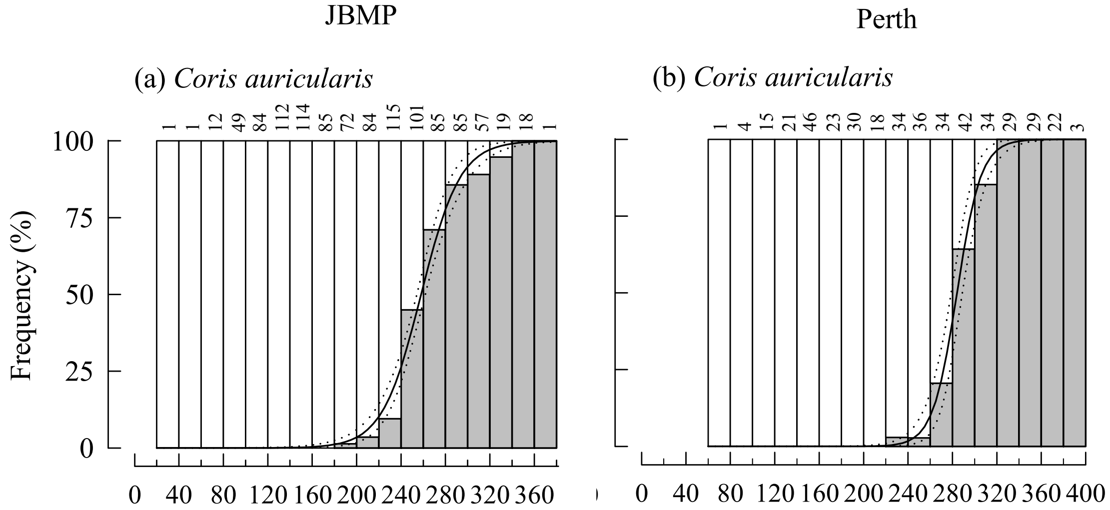
Figure 4.4. Percentage frequencies of occurrence of immature (white bars) and sexually mature (grey bars) females in sequential age classes during the spawning periods of (a, b) *Coris auricularis*, (c, d) *Notolabrus parilus* and (e, f) *Ophthalmolepis lineolatus* in the Jurien Bay Marine Park (JBMP) and waters off Perth. The logistic curves (solid lines) and their 95 % confidence limits (dotted lines) were derived from logistic regression analysis that described the relationship between age and the probability that an individual possessed mature gonads. Sample sizes for each age class are shown.

4.3.4 *Lengths and ages at sex change*

The smallest males of *C. auricularis*, *N. parilus* and *O. lineolatus* were 186, 162 and 223 mm, respectively, in the JBMP and 233, 236 and 181 mm, respectively, in the waters off Perth (Fig. 4.5a, c, e). While the prevalence of males of each species increased consistently with body size, there was a tendency for individuals of each species to become males at a slightly greater length in the waters off Perth. Thus, the length class at which 75 % of individuals had become males in those waters compared with the JBMP were 280-299 *v.* 300-319 mm for *C. auricularis*, 240-259 *v.* 300-319 mm for *N. parilus* and 260-279 *v.* 280-299 mm for *O. lineolatus* (Fig. 4.5). These trends are reflected in greater values for the L_{T50c} at sex change in the waters off Perth, *i.e.* 282 *v.* 258 mm for *C. auricularis*, 282 *v.* 236 for *N. parilus* and 270 *v.* 254 mm for *O. lineolatus* (Table 4.4), with each of these inter-location values being significantly different ($P < 0.001$).

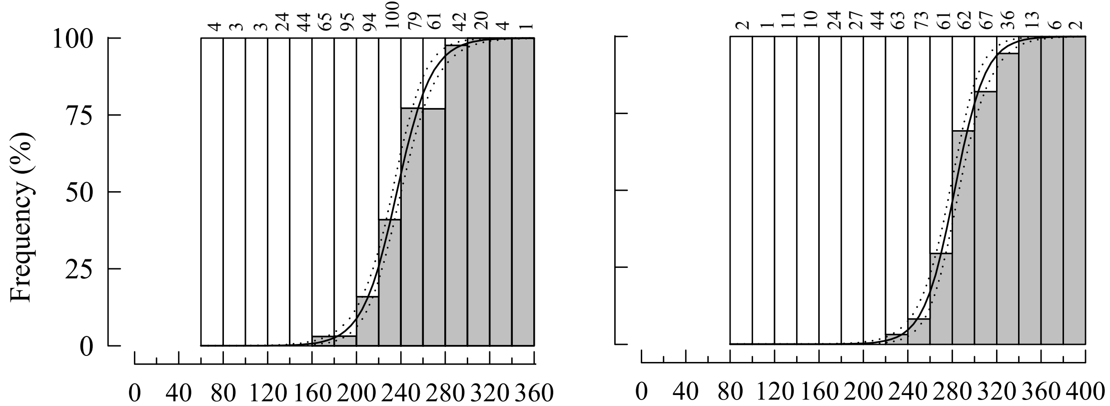
Table 4.4. Estimates of the total lengths (L_{T50c}, L_{T95c}) and ages (A_{50c}, A_{95c}) at sex change ± 95 % CLs for *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* in the Jurien Bay Marine Park (JBMP) and in the waters off Perth.

	L_T (mm)					**Age (years)**				
	n	**L_{T50c}**	**95 %**	**L_{T95c}**	**95 %**	***n***	**A_{50c}**	**95 %**	**A_{95c}**	**95 %**
Coris auricularis										
JBMP	1097	258	254, 262	310	299, 321	1066	4.7	4.6, 4.9	6.9	6.5, 7.3
Perth	421	282	279, 298	316	307, 325	411	5.4	5.2, 5.6	7.3	6.9, 7.7
Notolabrus parilus										
JBMP	639	236	232, 240	238	274, 315	605	5.5	5.3, 5.7	7.7	7.2, 8.1
Perth	502	282	278, 286	323	315, 332	480	6.3	6.1, 6.5	8.1	7.8, 8.6
Ophthalmolepis lineolatus										
JBMP	423	254	251, 257	277	272, 283	380	7.0	6.8, 7.3	9.4	8.8, 10.2
Perth	462	270	267, 274	306	297, 317	439	6.5	6.3, 6.7	9.0	8.4, 9.7



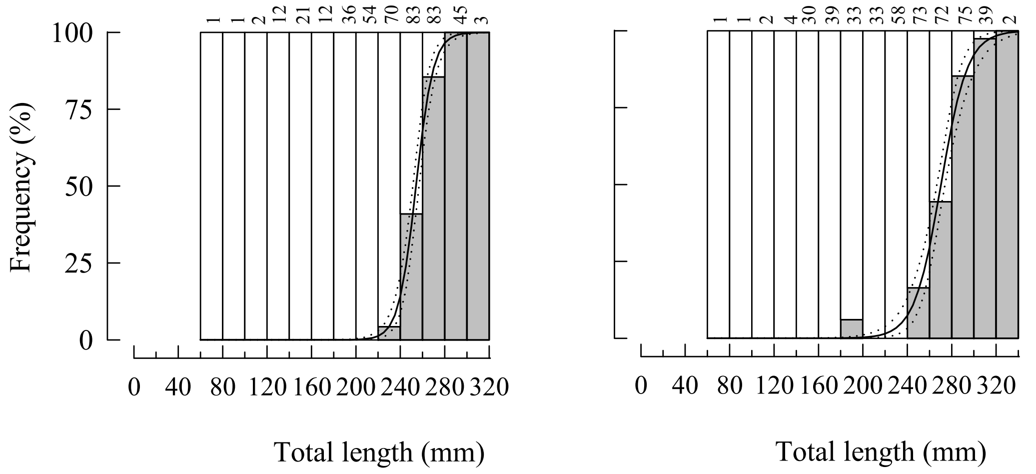
(a) *Coris auricularis*

(b) *Coris auricularis*



(c) *Notolabrus parilus*

(d) *Notolabrus parilus*



(e) *Ophthalmolepis lineolatus*

(f) *Ophthalmolepis lineolatus*

Figure 4.5. Percentage frequencies of occurrence of female (white bars) and male individuals (grey bars) in sequential 20mm length classes of (a, b) *Coris auricularis*, (c, d) *Notolabrus parilus* and (e, f) *Ophthalmolepis lineolatus* in the Jurien Bay Marine Park (JBMP) and waters off Perth. The logistic curve (solid line) and their 95 % confidence limits (dotted lines) were derived from logistic regression analysis that described the relationship between total length and the probability that an individual was male. Sample sizes for each length class are shown.

The youngest males of *C. auricularis*, *N. parilus* and *O. lineolatus* were 3.1, 3.0 and 4.7 years old in the JBMP, respectively and 3.6, 3.3 and 3.4 years old in the waters off Perth, respectively (Fig. 4.6). The prevalence of males rose with increasing age, with the result that generally ≥ 75 % of 6+ *C. auricularis* in both localities and of *N. parilus* in the JBMP, of 7+ *N. parilus* in the waters off Perth and of 7 or 8+ of *O. lineolatus* in the two localities were male (Fig. 4.6). The A_{50c} for *C. auricularis*, *N. parilus* and *O. lineolatus* at sex change in the JBMP were 4.7, 5.5 and 7.0 years, respectively, and 5.4, 6.3 and 6.5 years, respectively, that were estimated for those species in the waters off Perth (Table 4.4). The A_{50c} for each species differed significantly between the two localities ($P < 0.001$ for *C. auricularis* and *N. parilus* and $P < 0.01$ for *O. lineolatus*).

Apart from the two very small bisexual *C. auricularis* referred to earlier, the length and age of all of the other sixteen individuals of this species and the four *O. lineolatus* whose gonads contained both ovarian and testicular tissues fell in the length and age ranges within which both females and males were found (see Fig. 3.4).

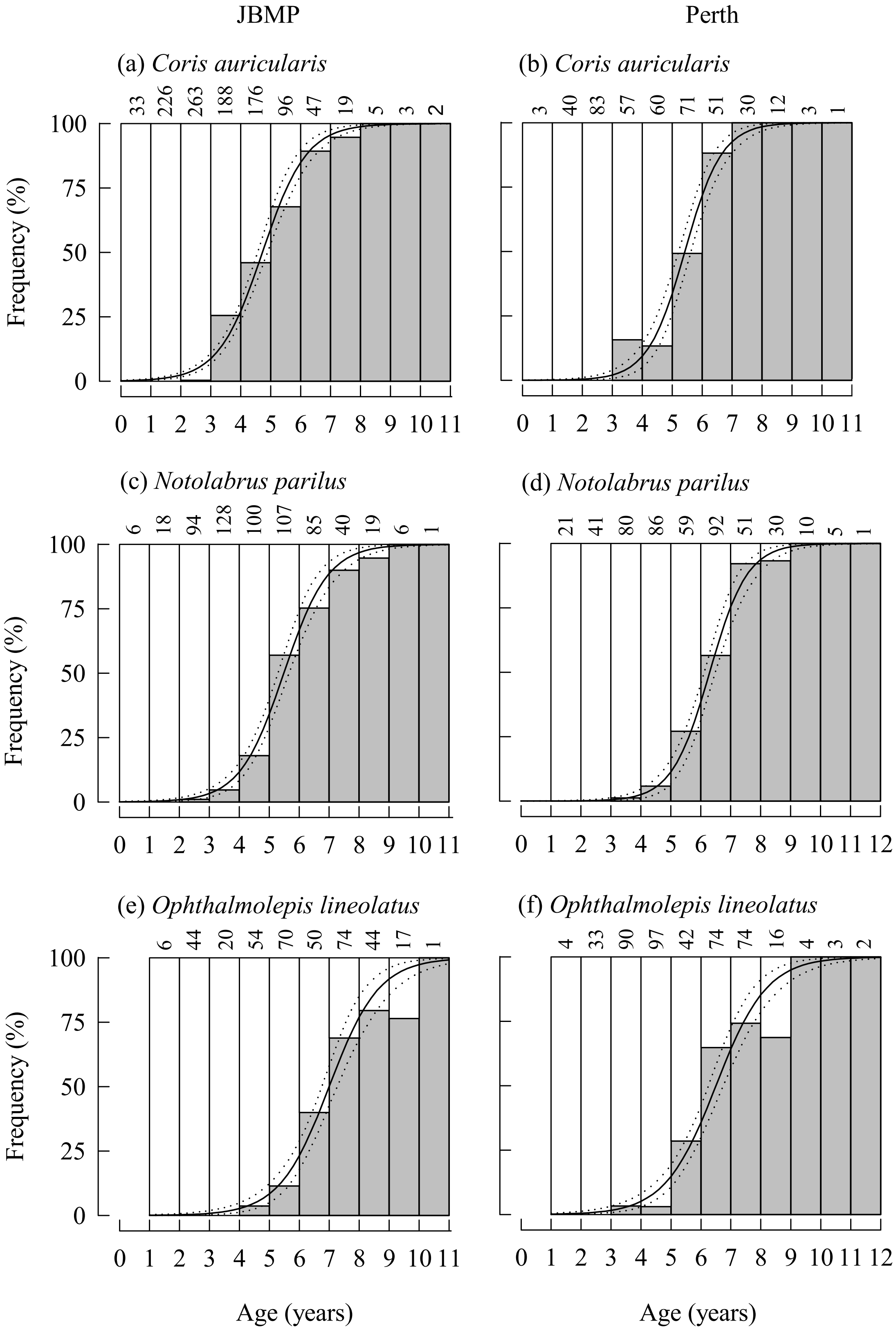


Figure 4.6. Percentage frequencies of occurrence of female (white bars) and male individuals (grey bars) in sequential age classes of (a, b) *Coris auricularis*, (c, d) *Notolabrus parilus* and (e, f) *Ophthalmolepis lineolatus* in the Jurien Bay Marine Park (JBMP) and waters off Perth. The logistic curve (solid line) and their 95 % confidence limits (dotted lines) were derived using logistic regression analysis that described the relationship between the age and the probability that an individual was male. Sample sizes for each age class are shown.

4.3.5 Length and age at maturity and sex change as a function of maximum length and age

When the L_{T50} at maturity was expressed as a percentage of the maximum length (L_{Tmax}), the values of 61 % for both *C. auricularis* and *O. lineolatus* in the JBMP were appreciably greater than the corresponding value of 46 % for both species in the waters off Perth (Table 4.5). In contrast, the corresponding value of 51 % for *N. parilus* in the JBMP was appreciably lower than those of the other two species in that location, but was the same as in the waters off Perth. The values for the A_{50} at maturity/maximum age (A_{max}) all lay within the range of 30-37 % for *C. auricularis*, *N. parilus* and *O. lineolatus* in the JBMP and were thus all greater than the corresponding values of 22-27 % for the waters off Perth (Table 4.5).

Table 4.5. Relationships between the L_{T50} and A_{50} at both maturity and sex change and the maximum L_T for *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* in the JBMP and waters off Perth.

	JBMP	Perth	JBMP	Perth
Maturity	L_{T50}/L_{Tmax} (%)		A_{50}/A_{max} (%)	
Coris auricularis	61	46	36	27
Notolabrus parilus	52	51	30	25
Ophthalmolepis lineolatus	61	46	37	22
Sex change	L_{T50c}/L_{Tmax} (%)		A_{50c}/A_{max} (%)	
Coris auricularis	71	71	45	53
Notolabrus parilus	68	73	53	53
Ophthalmolepis lineolatus	82	84	67	55

The values for L_{T50c} at sex change /L_{Tmax} for *C. auricularis*, *N. parilus* and *O. lineolatus* in the JBMP were the same or similar to those of the corresponding species in the waters off Perth (Table 4.5). However, the values for *C. auricularis* and *N. parilus*, which ranged from 68-73 % in the two localities, were far lower than the 82 and 84 % recorded for *O. lineolatus* in the JBMP and waters off Perth, respectively (Table 4.5). While the value for the age at sex change (A_{50c})/A_{max} for each species ranged only from 53 to 55 % in the waters off Perth, they ranged widely from 45 to 67 % in the JBMP (Table 4.5). There was no tendency for the values for the three species to be greater in one location.

The ratios of the A_{50c} to A_{50} for *C. auricularis*, *N. parilus* and *O. lineolatus* all lay within the range of 1.2-1.8 in the JBMP and were thus lower than those of the three species in the waters off Perth, which ranged from 1.9-2.5, recognising that, for each species, the differences between the two localities were pronounced (Table 4.6).

Table 4.6. Ratio of the age at sex change (A_{50c}) to the age at maturity (A_{50}) for *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* in the JBMP and waters off Perth.

	JBMP	Perth
	A_{50c}/A_{50}	
Coris auricularis	1.2	1.9
Notolabrus parilus	1.8	2.2
Ophthalmolepis lineolatus	1.8	2.5

4.4 Discussion

4.4.1 Pattern of sexual development

The sampling regime employed in this study, which involved the use of three methods, yielded very substantial numbers of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* from over the limestone reefs that contain the habitats typically occupied by these species. Furthermore, it enabled the full size and age ranges of each of these species, apart from their smallest and youngest individuals, to be obtained from two widely-spaced localities on the lower west coast of Australia in each calendar month. The samples are thus considered representative of the vast majority of the size and age ranges of these species on that coast and thereby fulfilled certain of the criteria required to demonstrate that a species is a functional hermaphrodite (Sadovy & Shapiro, 1987; Sadovy de Mitcheson & Liu, 2008).

An examination of histological sections of the gonads of a wide size and age range of each species demonstrated that the gonads, which had been categorised as either ovaries or testes on the basis of macroscopic examination, had been appropriately identified and assigned to the correct stage in development and that the pattern of gonadal development in each species was essentially the same. Such histological examination also enabled the small number of individuals, which contained gonads with both ovarian and testicular tissue, to be clearly identified and to elucidate the stages in development of their ovarian and testicular components. The appropriate use of the above histological studies, in conjunction with the macroscopic examination of the full suite of gonad stages, thus fulfilled further requirements for determining whether a species is a functional hermaphrodite.

The following trends in gonadal development during the life cycle of *C. auricularis*, *N. parilus* and *O. lineolatus* provide conclusive evidence that these species are protogynous hermaphrodites.

1. The gonads of all but two of the large number of individuals of all three species <160 mm in length and <3 years in age were exclusively ovaries and the vast majority of the largest and oldest individuals of each species were males. Furthermore, the above two exceptions, in which the gonads contained both ovarian and testicular components, belonged to individuals at the extreme lower end of the size and age ranges in the samples of *C. auricularis* and were thus far smaller than the smallest males and the minimum size and age at maturity. They are therefore assumed to represent an early and transient bisexual phase, as has been recorded for the diandric protogynous hermaphroditic labrid *Thalassoma bifasciatum* (Shapiro & Rasotto, 1993) and the serranid *Epinephelus coioides* (Liu & Sadovy de Mitcheson, 2009). Although only two bisexual fish were found among the small individuals of *C. auricularis*, such fish may have been more common among the very small juveniles of that species, which were not sampled during the present study.

2. Apart from the above two small bisexual individuals, all other individuals with gonads containing both ovarian and testicular tissues were restricted to the length and age ranges of each species within which both females and males were found. They are thus assumed to belong to individuals changing from female to male. This view is supported by the fact that the oocytes in the ovarian component of these gonads always comprised only previtellogenic stages, regardless of the time of year at which they are caught, whereas the testicular components of the gonads of individuals collected during the spawning period contained spermatocytes and sometimes even spermatids and which, in these cases, occupied much of the gonad. However, as with studies on other protogynous hermaphrodites in Western Australia (Fairclough, 2005; Coulson *et al.*, 2009; Cossington *et al.*, 2010), no vitellogenic or later stage oocytes were identified in these ovaries, that are presumed to be changing to testes, let alone undergoing the

degeneration described for such oocytes by Sadovy & Shapiro (1987) and Sadovy de Mitcheson & Liu (2008).

3. The testes of the males possessed characteristics that are consistent with their having functioned previously as ovaries, *i.e.* the central ovarian lumen, which is not used for sperm transport, has been retained, as also has the lamellar form of the ovary (Sadovy & Shapiro, 1987). The retention of the central ovarian lumen accounts for the sperm sinuses developing towards the periphery of the testes. It is recognised, however, that the above characteristics of the testes of all males of our three species do not necessarily provide conclusive evidence that all testes had been derived from a functional ovary rather than an ovary that never became mature.

During the spawning period, the length of the smallest male of each species generally only overlapped the lengths of the largest and thus mature females by 7 %. This small amount of overlap in lengths, combined with the fact that males were absent from the smaller size classes and younger age classes of fish clearly indicates that the vast majority of males are derived from mature females.

4.4.2 Spawning periods and investments in ovarian development

The data on the prevalences in each month of females with stage V and VI ovaries demonstrate that the timing and duration of the spawning periods of *C. auricularis*, *N. parilus* and *O. lineolatus* in the JBMP are similar to those of the corresponding species off Perth, but that they differ markedly among these three species. Thus, *C. auricularis* spawns in mid autumn to early winter and therefore earlier than *N. parilus* where it occurs in mid winter to mid or late spring, which, in turn, is earlier than the early or mid spring to late summer spawning period of *O. lineolatus.* This partitioning by time of the recruitment of the larval and early juvenile stages in each location would reduce the potential for competition for food and space resources by the early life cycle stages of those species. While the above spawning period for *O. lineolatus* in western Australian coastal waters overlaps that for this species in eastern Australian waters, it commences and finishes later in those latter waters, which are located at a slightly higher latitude (Morton *et al.*, 2008b).

The data shown in Fig. 4.2 demonstrate that the maximum mean ovarian weights of each species during their spawning periods were greater in the population at the higher latitude, *i.e.* in the waters off Perth. As the spawning periods of each species did not differ conspicuously with latitude, and assuming that there was likewise no marked difference in the spawning frequency of each species at the two latitudes, there was a greater investment of energy in gonadal development in the cooler waters. This thus parallels the greater investment of energy in somatic growth at those cooler temperatures (Chapter 3) and thereby provides further evidence that each species performs better in the more temperate conditions of the higher latitude. Such a finding would be consistent with the fact that each of these species have an essentially temperate distribution and thus likely to be better adapted to cooler conditions.

4.4.3 Size and age at maturity and sex change

The demonstration that *C. auricularis* and *O. lineolatus* mature at a smaller length and younger age in the cooler waters off Perth than in the warmer environment of the JBMP is the converse of the pattern typically exhibited by ectothermic species (Ray, 1960; Atkinson, 1994; see also Berrigan & Charnov, 1994). This difference in age is probably related to the fact that, both in terms of length and mass, the growth of these two species early in life in the cooler environment is not exceeded by that in the warmer environment and, as is typical of ectothermic species, subsequently becomes greater than in the warmer environment (see Figs 3.6, 3.7 in Chapter 3). The maturation of *C. auricularis* and *O. lineolatus* at a smaller length off Perth may be related to the fact that this species is able to invest a greater amount of energy into gonadal development in the cooler waters (see earlier) and thus the critical length for attaining maturity is less.

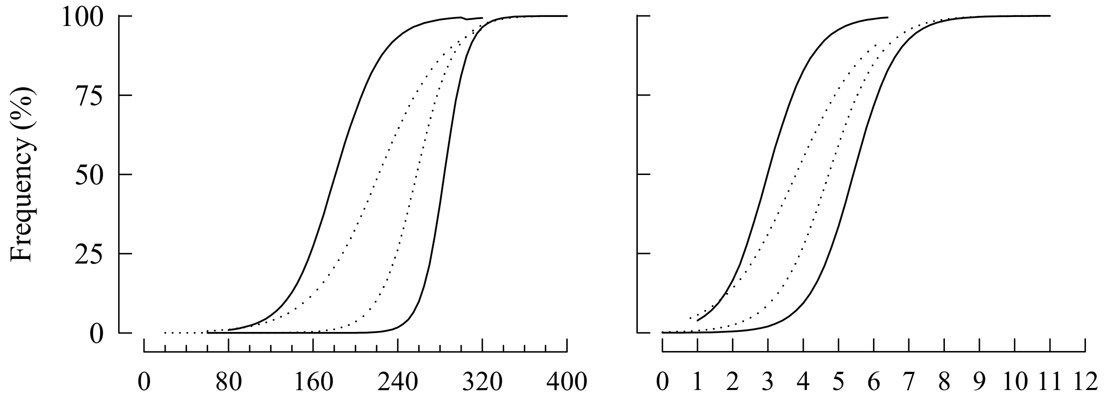
The attainment of maturity by *C. auricularis* and *O. lineolatus* at a younger age in the cooler environment parallels the situation with another labrid, *Bodianus frenchii*, in the same temperate region (Cossington *et al.*, 2010). In *N. parilus*, however, the length at maturity is greater and the age at maturity is the same in the cooler waters off Perth, which implies that the relative influences of the factors that govern the attainment of maturity in this species differ from those in *C. auricularis* and *O. lineolatus*.

Although each species grew more rapidly and reached a larger size at the higher latitude (Chapter 3), the size at sex change of each of *C. auricularis*, *N. parilus* and *O. lineolatus* relative to its maximum size was the same or similar at each latitude. In this respect, it contrasts with the trends exhibited by length at maturity relative to maximum length in *C. auricularis* and *O. lineolatus*, for which the values were greater for the populations in the JBMP. As sex change in each species occurs at a similar percentage of its maximum length, irrespective of any differences associated with latitude, such as maximum length, age and growth rate, that aspect of sex change is apparently “fixed” for the three labrid species. However, the actual percentage values for that measure did vary among the three species, ranging from 68 to 73 % for *C. auricularis* and *N. parilus* across both localities, to 82 % in the JBMP and 84 % in the waters off Perth for *O. lineolatus*. The above percentage values span the 80 and 72 % derived by Allsop & West (2003) and Gardner *et al.* (2005), respectively, from data for size at sex change *vs* maximum body size for 52 fish species and 77 species of sex changing animals across a range of broad taxa, respectively. However, as pointed out by Buston *et al.* (2004), the data used by Allsop & West (2003) showed that the size at sex change relative to maximum size varies greatly among species. Furthermore, there continues to be disagreement as to which is the most appropriate method for elucidating whether the relationship between the size at sex change and maximum size is invariant across species (*e.g.* de Jong, 2005; Nee *et al.*, 2005; Munday *et al.*, 2006; Molloy *et al.*, 2011).

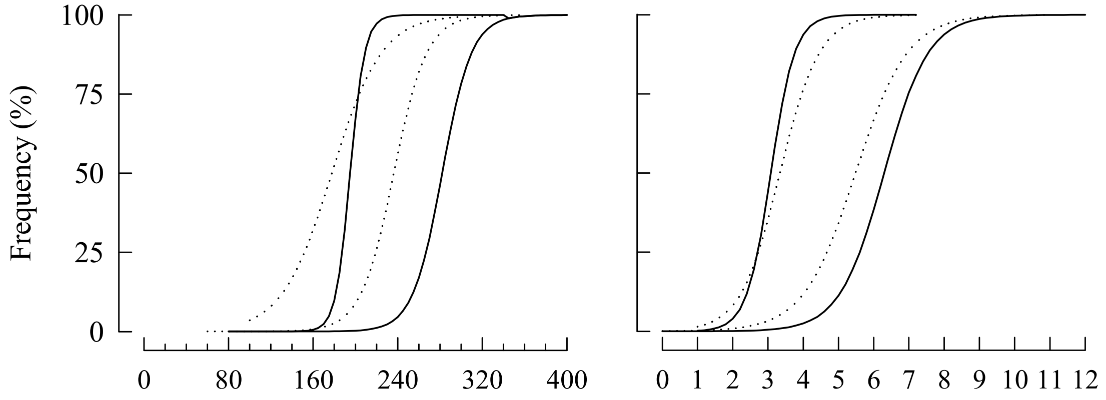
The results of the study demonstrated that the age at sex change relative to the age at maturity varied considerably among the three wrasse species, *i.e.* sex change occurred at between 1.2 and 2.5 times the age at maturity. Although Allsop & West (2003) concluded that hermaphroditic species typically change sex at 2.5 times the age at maturity, the data employed was highly variable, *i.e.* the values for this statistic ranged between 1.4 to 5.2, and limited, *i.e.* only 15 species.

Comparisons of the logistic curves, derived from the data on length and age at maturity and sex change for *C. auricularis*, *N. parilus* and *O. lineolatus* in both localities, emphasize that each of these species spend proportionately less time in their lives as mature females in the JBMP than in the waters off Perth (Fig. 4.7). For *C. auricularis* and *O. lineolatus*, this reflects the fact that, whereas their size at sex change relative to maximum size did not vary among the two localities, their sizes at maturity relative to their maximum size were each substantially lower at Perth (both 46 %) than in the JBMP (both 61 %). Thus, size at maturity and size at sex change in *C. auricularis* and *O. lineolatus* appear to be influenced by very different factors. Whereas the differences in size at maturity between the two localities may be related to differences in the performance of individuals in their environment (with those off Perth investing more energy into growth and gonadal development), size at sex change is directly related to maximum body size.

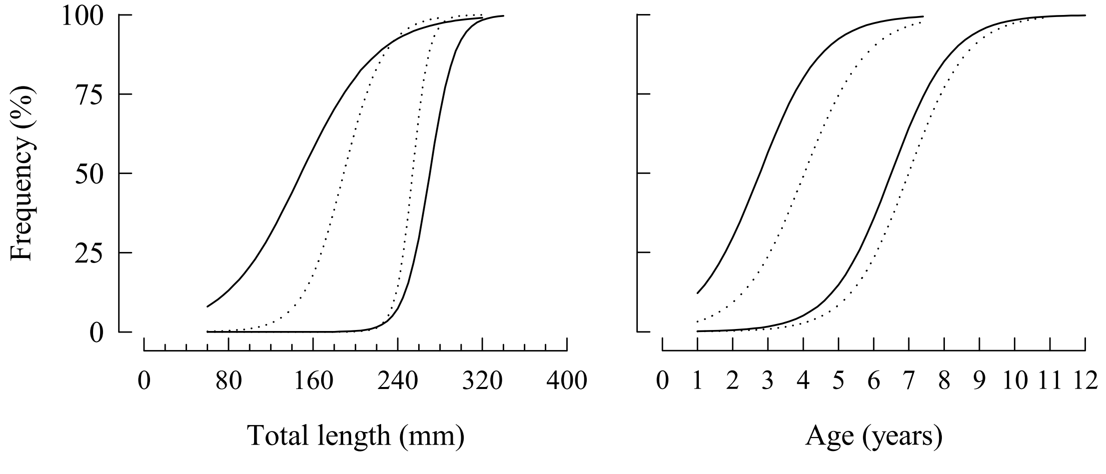
As *C. auricularis* is the most numerous of the three abundant labrid species in the two localities (Tuya *et al.*, 2009), the “spawning strategy” of this species must be particularly successful. It is thus noteworthy that, in comparison with *N. parilus* and



(a) *Coris auricularis* (b) *Coris auricularis*



(c) *Notolabrus parilus* (d) *Notolabrus parilus*



(e) *Ophthalmolepis lineolatus* (f) *Ophthalmolepis lineolatus*

Figure 4.7. The logistic curves for (a, c, e) lengths and (b, d, f) ages at maturity and sex change for *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* in the JBMP and the waters off Perth. The solid curves refer to data for the waters off Perth and the dotted curves to those for the JBMP. In the case of each species, the two curves on the left for a location are for maturity and on the right are for sex change.

O. lineolatus, individuals of *C. auricularis* spend less time as mature females and invest far less energy into ovarian development. Moreover, although *N. parilus* and *O. lineolatus* mainly spawn during spring and/or summer, as also does *B. frenchii*, another labrid species in the same waters (Cossington *et al.*, 2010). When labrid larvae are most abundant in coastal waters between Perth and the JBMP (Muhling *et al.*, 2007), *C. auricularis* spawns in autumn, when water temperatures are starting to fall. This implies that, for some reason(s), *e.g.* larval retention rate, level of competition for food resources or predation rate, environmental conditions in autumn are particularly favourable for the survival of the eggs and larvae of *C. auricularis*.

CHAPTER 5

DIETARY COMPOSITIONS

5.1 Introduction

The Labridae (wrasses) family is one of the most morphologically and ecologically diverse of the numerous fish families that are found on coral and rocky reefs (Westneat *et al.*, 2005) and its species feed on a wide range of food sources, including gastropod and bivalve molluscs, crustaceans, fishes, coral mucus, zooplankton, ectoparasites, detritus and algae, belonging to virtually all of the feeding guilds found on reefs and thus play a critical role in reef ecology (Wainwright & Bellwood, 2002).

Most studies of labrid diets have focused on either single species (Gillanders, 1995a; Denny & Schiel, 2001; Shepherd & Clarkson, 2001; Figueiredo *et al.*, 2005; Castriota *et al.*, 2005, 2010) or a group of species in the same habitat (Kabasakal, 2001; MacArthur & Hyndes, 2007; Morton *et al.*, 2008a). Certain studies have shown that the relative abundance of the prey taxa ingested by labrids tends to reflect the relative abundance of those prey in the environment (Deady & Fives, 1995; Shepherd & Clarkson, 2001). This would account for the new recruits of *Achoerodus viridis* feeding predominantly on tanaids in seagrass, but on harpacticoid copepods when on reefs (Gillanders, 1995a). When occupying seagrass on the lower west coast of Australia, *N. parilus* feeds mainly on brachyuran crabs, isopods and gastropod and bivalve molluscs (MacArthur & Hyndes, 2007), whereas *O. lineolatus* ingests mainly amphipods, decapods and gastropod molluscs when living over rocky reefs at a similar latitude on the east coast of Australia (Morton *et al.*, 2008a). Although *C. auricularis*, *N. parilus* and *O. lineolatus* all have small, pointed mouths, the rear of the upper jaws of

C. auricularis lack canines and *N. parilus* has a wider mouth than the other two species (Gomon *et al.*, 2008; Fig. 5.1 in Results).

The coexistence of abundant fish species is often considered to be facilitated by the partitioning of resources along one or more of three axes, *i.e.* food, space and time, with the first regarded as the most important (Ross, 1986). Moreover, the changes that frequently occur in dietary composition, and sometimes also habitat, as the individuals of a species increase in size, results in the food resources being partitioned among those individuals (Gillanders, 1995a; Castriota *et al.*, 2005; Platell *et al.*, 2007; Duffy *et al.*, 2010). The dietary composition of many fish species, including those of labrids, has been shown to change during the year (*e.g.* Jones, 1988; Gillanders, 1995a). This trend is conspicuous among those that feed on small prey, which have short life cycles and whose abundance thus peaks during a particular period of the year (*e.g.* Denny & Schiel, 2001; Castriota *et al.*, 2010). Analyses of diets must also take into account the possibility that dietary composition can vary markedly among the various populations of a species, presumably in response to variations in the spatial availability of the different types of prey in the environment (Sarre *et al.*, 2000; Chuwen *et al.*, 2007; Duffy *et al.*, 2010). In the case of labrids, few attempts have been made to compare statistically and in an integrated manner the extents to which the diets of various labrid species differ when they occur together and/or in different habitats, while, at the same time, taking into account any changes that occur with increasing body size and/or throughout the year.

Although the JBMP is located *c.* 250 km north of Perth, the composition of the invertebrate reef fauna in the JBMP differs, however, from that found offshore from Perth (IMCRA, 1998). For example, among the broad potential prey for labrids, gastropods are relatively far more abundant in the JBMP, whereas the reverse is true for crustaceans (Murphy *et al.*, 2006). Furthermore, the composition of the invertebrate faunas in macrophytes and reefs on the lower west coast of Australia varies along the coast (see Borowitzka *et al*., 1990; Murphy *et al*., 2006). Such variations are likely to be reflected in differences between the dietary compositions of a species when it occurs in the same habitat type but in different regions and/or in different habitat types in the same region.

Seagrass meadows within the JBMP comprise mainly *Posidonia sinuosa*, *Amphibolis griffithii* and *A. antarctica* and are found in some sandy areas between the limestone outcrops that comprise the inshore, sheltered reefs (Larkum & den Hartog, 1989). These meadows cover an area of *c.* 215 km^2, which represents 25 % of the total area of the JBMP (Department of Conservation and Land Management, 2005).

During the present study, wide size ranges of *C. auricularis*, *N. parilus* and *O. lineolatus* were collected seasonally from exposed reefs of both the JBMP and waters off Perth and, in the case of the first two species, also from sheltered reefs in the JBMP. Samples of *N. parilus* were also collected in the seagrass meadows that were interspersed among the latter reefs in the JBMP. Multivariate analyses were employed to test the following hypotheses. 1. The dietary compositions of each labrid species in exposed reefs of the JBMP differ from those of the corresponding species in coastal waters much further south and, in the case of *C. auricularis* and *N. parilus*, also from those in the rather different environment provided by inshore, sheltered reefs in the JBMP. 2. The dietary compositions of *N. parilus* over inshore, sheltered reefs and interspersed seagrass meadows also differ, the only species to occur in the latter habitat type. 3. The dietary compositions of each species vary with body size and season in each habitat in which that species is found. 4. The dietary compositions of the three labrid species differ, to a certain extent, when they co-occur over the same reefs, reflecting *inter alia* the presence of small differences in dentition and mouth morphology.

5.2 Materials and methods

5.2.1 Laboratory procedures

The sampling locations and regimes used in the JBMP and the waters off Perth are described in Chapter 2. In brief, samples of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* were collected by line and spear fishing and trapping over reefs in the waters of the JBMP and off Perth. Sampling was undertaken in every second or third month between January 2005 and February 2008, thereby ensuring samples were obtained for each calendar month. In addition, samples of *N. parilus* were also collected in the seagrass meadows in the JBMP in each season in 2005 and 2006. As sampling was undertaken during the day (see Chapter 2), it was conducted when labrids are known to feed (Kuiter, 2006; Allen *et al.*, 2006; *pers.obs*).

Twenty-four replicate trawls were carried out during the day using a small otter trawl. The net was 5 m long and 0.5 m high, had a 2.6 m effective fishing width and stretched meshes of 51 and 25 mm in the wings and bunt, respectively. The warp and bridle were 50 and 13 m long, respectively (Travers & Potter, 2002). Each replicate trawl covered a distance of *c.* 150 m, the precise distance being determined using a Garmin 178c GPS, and towed at a boat speed of *c.* 4 km h^{-1}. All fish were euthanased immediately using an ice slurry. The whole gut was removed from at least 20 randomly selected individuals in each of four sequential length classes, *i.e.* < 150, 150 - 199, 200 - 249 and ≥ 250 mm, of each species collected from each habitat and season in which that species was caught and preserved in 70 % ethanol for at least five days prior to examining its contents.

As labrids do not possess a distinct stomach, the contents of the first third of the gut (foregut), in which the dietary items were masticated but still relatively undigested, were examined. The foreguts of all fish examined contained food. The fullness of each foregut was recorded on a scale of 0 (empty) to 10 (fully distended). Each dietary item in each foregut was identified to the lowest possible taxonomic level using a dissecting microscope and taxonomic descriptions (*e.g.* Hutchins & Swainston, 1999; Norman & Reid, 2000; Wells & Bryce, 2000; Wilson, 2002; Jones & Morgan, 2002; Edgar, 2008). The frequency with which each dietary item was found in the foreguts of the individuals of each species (%F) was determined. The contribution of each dietary item to the total volume of the dietary components (%V) was then estimated visually (Hynes, 1950; Hyslop, 1980). Sand was not included in statistical analyses as it was presumably indigestible and, in any case, almost invariably contributed ≤ 6 % in volume to the foregut contents of each species. Unidentifiable material (which constituted < 7 % of the overall dietary volume of each species in the various habitats in all cases except for *C. auricularis* in the exposed reefs of the JBMP) was also excluded from analyses. Note that the coral prawns (*Metapenaeopsis* spp.) used as bait for line fishing and the Australian Pilchard *Sardinops sagax* employed as bait for traps could easily be distinguished from the prey and other food components in the gut contents of each labrid species and thus readily disregarded when determining diets.

Each of the 315 dietary items was allocated to one of 23 functional groups, subsequently referred to as dietary categories (Platell *et al.*, 2010), which were then used for multivariate analyses. Two of these categories, *i.e.* small crustaceans and large crustaceans, were relatively broad, owing to the large volumes of crustaceans that could not be reliably identified at a lower taxomomic level. For graphical purposes, the data for the dietary categories of foraminiferans, bryozoans, poriferans, cnidarians, sipunculids and nemerteans were combined as "lower invertebrates" and those for asteroids, echinoids, crinoids, ophiuroids and holothuroids were combined under "Echinodermata”. This pooling enabled the changes made by the resultant 13 main contributors to the diets of each species as it increased in size to be readily displayed in histograms. N.B. The contributions of one dietary category (scaphopods) were so negligible that they could not be clearly represented in the histograms.

The flesh on the upper and lower jaws of individuals of *C. auricularis*, *N. parilus* and *O. lineolatus* was removed by immersion in hot water and then by the use of forceps. The exposed jaws were then photographed to elucidate the extent to which, in particular, the dentition varies among the three species and related to the diet of each species (Fig. 5.1).

5.2.2 Multivariate analyses

The hypotheses outlined in the Introduction were tested using the routines in the PRIMER v6 multivariate statistics package (Clarke & Gorley, 2006) and the PERMANOVA+ add-on module (Anderson *et al*., 2008).

Because the contents of individual foreguts contained only a few of the 23 dietary categories and can therefore differ markedly in their compositions, the similarity coefficients calculated between the dietary compositions of individual fish can prevent effective multivariate analyses. For this reason, the foreguts of the samples for each length class of each species in each season, and in each habitat in which they were represented, were randomly sorted into groups of three to five, depending on the total number of fish in the samples (Platell & Potter, 2001; Sommerville *et al*., 2011). The percentage volumetric compositions of the different dietary categories in the groups comprising the various length classes, seasons and habitats of each species were then averaged. The resultant data, which were considered to represent replicates, were square-root transformed to avoid any tendency for the main dietary components to be excessively dominant. These data were then employed to construct separate Bray-Curtis similarity matrices for use in multivariate analyses (see below). This approach overcomes any potential bias that may result from pooling dietary data obtained from greatly unequal numbers of guts (the "species accumulation effect"). Although the resulting numbers of replicates may be unequal across the various habitats, length classes and seasons, such unbalanced designs can be analysed effectively with contemporary software, such as Permutational Multivariate Analysis of Variance (PERMANOVA) (Anderson, 2001; Anderson *et al*., 2008).

5.2.3 Intraspecific comparisons of dietary compositions

The following steps, which were carried out separately for *C. auricularis*, *N. parilus* and *O. lineolatus*, were aimed at testing firstly whether the volumetric dietary compositions of each of these species differed among the reef habitats in which they occur and between length classes and seasons within each of those habitats. The data for *C. auricularis* and *N. parilus* were each considered to represent a 3-way fully-crossed design of reef habitat (3 levels, *i.e.* exposed reefs in Perth and exposed and sheltered reefs in the JBMP) x length class (4 levels) x season (4 levels), with each factor being fixed. Although the same design was used for *O. lineolatus*, this species only occurred in exposed reefs in the JBMP and off Perth and thus there were two, rather than three levels for the reef habitat factor. Furthermore, as the largest of the four length classes of *N. parilus* did not occur in seagrass in the JBMP, the comparisons between the dietary composition of this species in this habitat type and adjacent inshore, sheltered reefs of the JBMP employed a separate 3-way crossed PERMANOVA design of habitat type (2 levels) x length class (3 levels) x season (4 levels). This was achieved by excluding from this particular analysis the data for the largest length class in the inshore, sheltered reefs.

The separate Bray-Curtis similarity matrices, that were constructed for each species from replicate data, were subjected to PERMANOVA to test whether there were interactions between the above factors and, if so, to determine the extent of those interactions relative to each other and to those of the main effects. If interactions were not significant, or relatively small in relation to the main effects, the matrix was subjected to a series of 2-way Analysis of Similarities (ANOSIM) tests for each factor *v.* each of the other two factors combined. This was achieved by flattening the values for the two removed factors in each case to a single factor representing all combinations of their levels. ANOSIM was preferred at this stage of the analysis because, unlike PERMANOVA, this test is fully non-parametric and thus more robust and because the ANOSIM *R*-statistic provides a universal measure of group separation.

In this and all subsequent ANOSIM tests, both *R*-statistics and their associated *P* values are always quoted, with small percentage values of *P*, typically 5 % or less, being interpreted as casting doubt on the null hypothesis of no significant difference in dietary composition. However, where 'significant' differences are found, and *R* values are less than about 0.1, these differences are considered negligible. The magnitude of the *R*-statistic typically ranges from 1, when all samples within each group are more similar to each other than to any of the samples from other groups, down to ~ 0, when the average similarity among and within groups do not differ (Clarke & Gorley, 2006). The *P* value from any test (ANOSIM or PERMANOVA) based on a finite selection of random permutations is never precisely known: thus for $n = 999$ permutations a *P* value of 5 % is only determined to an accuracy of about +/- 1.5 %, and for n = 9 999 to an accuracy of +/- 0.5 %, both $n = 999$ and $n = 9\,999$ being used in this chapter, depending on the complexity of the computational requirements for a particular test. On these grounds alone, therefore, it makes no sense to draw a distinction between 'borderline significant' *P* values of 4.5 and 5.5 %, and no fixed *P* value is therefore used to determine significance. More importantly, as in many studies, large numbers of statistical tests were carried out in the present study using both PERMANOVA and ANOSIM (a total of at least 100 in the study), and no attempt is made to adjust overall significance levels for such multiple testing. A Bonferroni correction, rigorously applied, would therefore suggest that a null hypothesis would be rejected unless the significance percentage attained smaller values than 0.05 %. Instead, more pragmatically and appropriately, *P* values ≤ 5 % are referred to as 'significant' but only *P* values ≤ 0.1 % (*i.e.* an observed *R* or pseudo-*F* statistic that is larger than that obtained from any of 999 permutations) are interpreted as near-irrefutable evidence for rejecting the null hypothesis, with values between those limits being considered more borderline evidence. Note that, for consistency, all *P* values are given as percentage values, *i.e.* significance at the 5, 1, 0.1 or 0.01 % level, since these figures are considered to be more easily understood and differentiated than the equivalent proportions of 0.05, 0.01, 0.001 and 0.0001, respectively.

In those cases where ANOSIM detected a significant difference, pairwise ANOSIM comparisons were then used to determine which levels of that factor showed the greatest differences. Where a difference had been established, this was followed by 2-way crossed Similarity Percentages analyses (SIMPER, Clarke & Gorley, 2006) to identify the dietary categories that typified the dietary composition of each *a priori* group and those which were responsible for distinguishing between the dietary compositions in each pair of those groups.

Non-Metric Multidimensional Scaling (nMDS) ordination plots were used to visualise the differences and similarities between factors and the basis for any interactions between those factors that were identified by PERMANOVA. These ordination plots were constructed by outputting the 'distances among centroids' matrix from the PERMANOVA+ package, which creates averages in the 'Bray-Curtis space' calculated from the replicate samples (Anderson *et al.*, 2008). The plots, which thus display low-dimensional approximations to the pattern of group centroids in the full-dimensional space, are subsequently referred to as 'centroid nMDS ordination plots'.

5.2.4 Interspecific comparisons of dietary composition

The hypothesis that the dietary compositions of *C. auricularis*, *N. parilus* and *O. lineolatus* over exposed reefs differed both in the JBMP and off Perth was tested using the Bray-Curtis similarity matrices constructed from the groups of replicates that had been generated for each of these three species in each reef habitat, length class and season (see earlier). However, as small *C. auricularis* and *O. lineolatus* were not represented in the samples from over exposed reefs at those two locations in all seasons, the comparisons between the dietary compositions of the three species in exposed reefs at both of those locations were restricted to dietary data for the 150 - 199, 200 - 249 and ≥ 250 mm length classes. Thus, the data for the three species in exposed reefs both in the JBMP and off Perth were considered to represent a 3-way crossed design of species (3 levels) x length class (3 levels) x season (4 levels), with each factor being fixed. The corresponding matrix and same 3-way crossed design were employed for comparing the dietary compositions of *C. auricularis* and *N. parilus* in sheltered reefs of the JBMP, except that species was now represented by two levels and length class by four levels, as all four length classes of each of these two species were represented in each season in sheltered reefs of the JBMP.

For the above interspecific analyses in a reef habitat, the dietary data were subjected to a 3-factor PERMANOVA, a series of 2-way crossed ANOSIM tests, 2-way crossed SIMPER and centroid nMDS ordination in the same manner as described earlier for intraspecific comparisons.

5.3 Results

5.3.1 Jaws and dentition

The mouth of *Coris auricularis* is relatively narrow and contains a single row of small, fine teeth on the upper jaw but no canines at the rear of that jaw (Fig. 5.1). In comparison, the mouths of *Notolabrus parilus* and *Ophthalmolepis lineolatus* are relatively wider and contain stouter teeth along their upper jaws and the rear of those jaws also possess prominent canines. However, *N. parilus* has a wider mouth, longer and more robust teeth on the upper jaw than *O. lineolatus* and also a double, rather than single, pair of canines at the rear of that jaw (Fig. 5.1).

5.3.2 Overall dietary compositions

The number of foreguts of each species in each of the three reef habitats and seagrass in which each species occurred is given in Table 5.1. Their foreguts always contained food, with their mean fullness ranging from 3.8 to 6.4 (Table 5.1). On the basis of both their frequency of occurrence in foreguts and volumetric contribution to diets, crustaceans and molluscs were the most important major dietary taxa for *C. auricularis*, *N. parilus* and *O. lineolatus* in each of the reef habitats in which they were found and of *N. parilus* in seagrass.

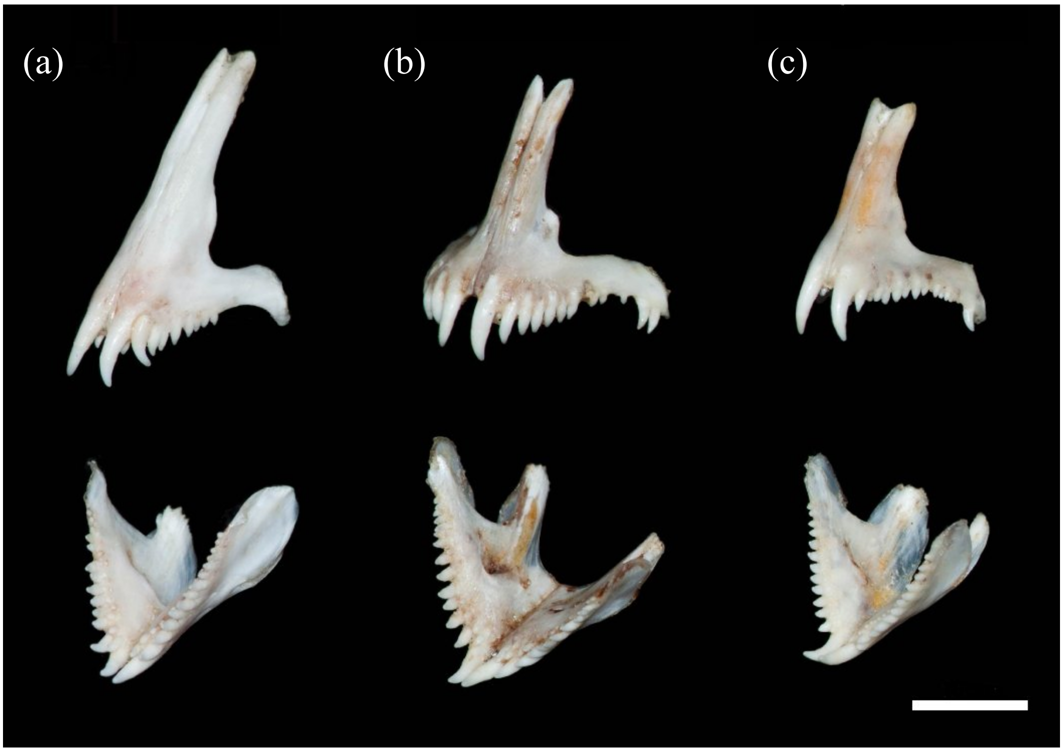


Figure 5.1. Photographs of the upper and lower jaws of (a) *Coris auricularis*, (b) *Notolabrus parilus* and (c) *Ophthalmolepis lineolatus*. Scale bar denotes 10 mm.

Table 5.1. Percentage frequencies of occurrence (%F) and mean percentage volumetric contributions (%V) of the major taxa (boldface) and dietary categories (*) to the diets of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* in different habitats on the lower west coast of Australia, *i.e.* exposed reefs off Perth and in the Jurien Bay Marine Park (JBMP) and in sheltered reefs and adjacent seagrass in the JBMP.

Dietary taxa	*Coris auricularis*						*Notolabrus parilus*								*Ophthalmolepis lineolatus*			
	Perth exposed		JBMP exposed		JBMP sheltered		Perth exposed		JBMP exposed		JBMP sheltered		JBMP seagrass		Perth exposed		JBMP exposed	
	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
Foraminifera*	**0.5**	**<0.1**	**2.5**	**0.1**	**19.6**	**1.0**	-	-	-	-	**1.4**	**0.1**	**3.1**	**0.2**	-	-	-	-
Bryozoa*	-	-	**3.4**	**0.4**	**1.3**	**<0.1**	-	-	-	-	-	-	-	-	-	-	-	-
Porifera*	-	-	**8.4**	**0.5**	**13.9**	**1.0**	-	-	-	-	**2.0**	**0.1**	**0.8**	**<0.1**	**0.6**	**0.6**	**0.8**	**0.8**
Cnidaria*	-	-	**0.8**	**<0.1**	**0.6**	**0.1**	-	-	-	-	-	-	-	-	-	-	-	-
Sipunculida*	**0.5**	**0.2**	**0.8**	**0.1**	**5.7**	**0.7**	**1.0**	**0.4**	-	-	**2.0**	**0.6**	**1.6**	**0.4**	**1.1**	**0.4**	**0.8**	**0.1**
Nemertea*	**2.4**	**0.4**	-	-	**1.9**	**0.2**	**0.5**	**0.5**	-	-	-	-	**0.8**	**<0.1**	**1.1**	**0.7**	**1.6**	**1.4**
Annelida*	**31.2**	**8.1**	**31.9**	**5.4**	**47.5**	**7.2**	**14.6**	**3.5**	**14.3**	**3.0**	**19.7**	**3.2**	**10.9**	**2.8**	**22.7**	**9.7**	**9.8**	**3.9**
Polychaeta	**31.2**	**8.1**	**31.9**	**5.4**	**47.5**	**7.1**	**14.6**	**3.5**	**14.3**	**3.0**	**19.7**	**3.2**	**10.9**	**2.8**	**21.6**	**8.9**	**9.8**	**3.9**
Oligochaeta	-	-	-	-	**0.6**	**0.1**	-	-	-	-	-	-	-	-	**1.1**	**0.8**	-	-
Mollusca	**69.3**	**18.4**	**76.5**	**20.5**	**86.7**	**24.8**	**88.4**	**37.9**	**87.8**	**38.5**	**85.0**	**39.9**	**80.6**	**41.8**	**62.5**	**23.9**	**63.1**	**30.2**
Polyplacophora*	**2.0**	**0.4**	**3.4**	**0.6**	**4.4**	**0.4**	**7.6**	**3.4**	**8.8**	**4.6**	**4.8**	**1.8**	**17.1**	**6.5**	**13.1**	**6.6**	**6.6**	**5.1**
Bivalvia*	**15.6**	**3.0**	**10.1**	**1.3**	**17.1**	**2.1**	**38.9**	**12.3**	**15.6**	**3.8**	**19.0**	**5.1**	**19.4**	**5.0**	**16.5**	**5.5**	**9.0**	**2.9**
Gastropoda*	**60.5**	**14.9**	**76.5**	**17.9**	**84.2**	**22.2**	**80.3**	**22.3**	**84.4**	**29.4**	**82.3**	**32.3**	**67.4**	**30.1**	**48.3**	**11.8**	**54.1**	**22.3**
Fissurellidae	1.0	0.2	1.7	0.3	0.6	0.1	6.6	1.5	0.7	1.2	1.4	1.4	-	-	1.7	0.6	2.5	0.6
Haliotidae	-	-	-	-	-	-	1.0	0.7	2.1	0.3	0.7	<0.1	-	-	-	-	0.8	0.3
Mitridae	-	-	1.7	0.3	0.6	0.1	-	-	10.9	1.8	8.8	1.8	-	-	1.1	<0.1	-	-
Naticidae	-	-	0.8	<0.1	3.2	0.3	-	-	-	-	2.0	0.3	1.6	0.7	0.6	0.1	-	-
Columbellidae	11.7	1.7	2.5	0.2	10.8	0.9	25.8	4.2	23.8	4.1	27.2	7.6	0.8	0.1	13.1	2.5	11.5	2.5
Cypraeidae	-	-	-	-	1.3	<0.1	-	-	-	-	-	-	-	-	-	-	-	-
Turbinidae	19.5	2.4	19.3	2.0	27.8	3.5	33.8	6.5	23.1	6.1	30.6	6.2	33.3	12.0	14.8	3.8	12.3	3.5
Trochidae	11.7	2.3	16.0	1.6	24.7	3.4	36.4	6.4	36.1	9.1	39.5	8.0	40.3	14.4	5.7	0.7	6.6	1.8
Buccinidae	-	-	7.6	0.9	9.5	0.6	-	-	2.7	1.0	2.0	0.1	-	-	-	-	6.6	1.6
Terebridae	-	-	-	-	-	-	-	-	-	-	0.7	<0.1	0.8	0.1	-	-	-	-
Unid gastropods	42.0	8.4	65.5	12.6	73.6	13.3	19.2	3.1	38.1	5.7	41.5	6.9	21.7	2.9	19.3	4.1	32.0	11.9
Cephalopoda*	-	-	**1.7**	**0.8**	**0.6**	**0.1**	-	-	**2.0**	**0.7**	**1.4**	**0.7**	-	-	-	-	-	-
Scaphopoda*	-	-	-	-	-	-	-	-	-	-	-	-	**3.9**	**0.2**	-	-	-	-
Arthropoda	**90.2**	**55.9**	**87.4**	**39.3**	**92.4**	**39.0**	**83.3**	**41.6**	**83.0**	**41.0**	**80.3**	**32.7**	**75.2**	**37.3**	**56.8**	**33.4**	**68.0**	**41.8**
Pycnogonida *	**0.5**	**0.1**	**0.8**	**<0.1**	**4.4**	**0.5**	**0.5**	**0.1**	**0.7**	**0.1**	-	-	**0.8**	**<0.1**	-	-	**0.8**	**0.7**
Crustacea	**90.2**	**55.8**	**87.4**	**39.2**	**91.8**	**38.5**	**83.3**	**41.5**	**83.0**	**40.9**	**80.3**	**32.7**	**75.2**	**37.2**	**56.8**	**33.4**	**67.2**	**41.1**

Dietary taxa	*Coris auricularis*						*Notolabrus parilus*								*Ophthalmolepis lineolatus*			
	Perth exposed		JBMP exposed		JBMP sheltered		Perth exposed		JBMP exposed		JBMP sheltered		JBMP seagrass		Perth exposed		JBMP exposed	
	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
Small crustaceans*	75.2	36.2	85.7	30.0	90.5	34.2	35.9	12.2	53.7	16.6	49.0	13.1	42.6	19.5	22.2	12.1	33.6	17.2
Nebaliidae	-	-	-	-	3.2	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Cumacea	-	-	1.7	0.1	2.5	0.1	-	-	-	-	-	-	-	-	-	-	-	-
Copepoda	-	-	0.8	0.3	2.5	0.4	-	-	-	-	-	-	-	-	-	-	-	-
Ostracoda	1.5	0.1	7.6	0.3	14.6	0.9	-	-	-	-	0.7	0.1	0.8	0.2	-	-	-	-
Amphipoda	60.0	19.7	74.8	17.1	77.8	18.1	29.3	9.1	37.7	8.0	38.8	8.0	10.1	1.0	8.2	3.4	10.8	3.6
Isopoda	9.3	2.2	21.0	2.8	31.0	3.1	0.5	<0.1	11.6	2.0	1.4	0.2	3.9	2.0	3.4	0.5	5.7	1.9
Tanaidacea	-	-	26.9	1.9	34.8	2.7	1.5	0.3	-	-	4.1	0.3	-	-	-	-	-	-
Mysidacea	-	-	4.2	0.8	3.2	0.3	-	-	0.7	<0.1	0.7	<0.1	-	-	-	-	-	-
Unid. small crustaceans	34.1	14.3	41.2	6.6	39.2	8.4	8.1	2.8	17.7	6.5	21.8	4.6	16.4	16.2	14.2	8.2	26.2	11.7
Large crustaceans*	38.8	19.6	34.5	9.2	29.7	4.4	68.2	29.3	61.9	24.3	60.5	19.6	41.9	17.9	36.0	21.3	36.1	23.9
Penaeidae	0.5	0.4	12.6	1.2	5.1	0.4	2.5	0.5	12.2	1.7	14.3	2.2	2.3	0.7	-	-	-	-
Stomatopoda	-	-	-	-	1.3	0.2	-	-	2.0	0.8	0.7	0.3	-	-	-	-	1.6	0.8
Alpheidae	0.5	0.2	-	-	-	-	-	-	0.7	0.1	-	-	1.6	0.8	0.6	0.3	-	-
Palinuridae	-	-	-	-	-	-	0.5	0.3	0.7	0.5	-	-	-	-	0.6	<0.1	0.8	0.5
Paguroidea	2.0	0.2	4.2	0.4	5.7	0.4	11.1	1.4	29.3	5.7	24.5	4.6	11.6	2.1	4.0	1.1	0.8	0.7
Brachuyra: Portunidae	-	-	-	-	-	-	-	-	-	-	-	-	0.8	0.8	-	-	4.1	0.8
Brachyura: Majidae	0.5	0.1	5.0	2.6	5.1	1.1	4.0	2.4	16.3	7.3	4.8	2.9	2.3	1.1	1.1	0.5	1.6	1.6
Brachyura: Hymenosomatidae	-	-	1.7	0.2	3.2	0.3	-	-	-	-	2.7	0.7	-	-	-	-	-	-
Brachyura: Leucosiidae	-	-	-	-	-	-	-	-	0.7	0.1	-	-	1.6	0.7	-	-	-	-
Unid. brachyurans	37.1	18.6	21.8	4.7	13.9	1.9	58.6	24.8	23.1	8.1	25.9	8.8	25.6	11.7	34.7	19.4	30.3	19.5
Echinodermata	**29.8**	**7.3**	**22.7**	**4.4**	**38.6**	**6.9**	**33.3**	**13.1**	**33.3**	**9.0**	**25.9**	**9.6**	**23.3**	**6.3**	**38.6**	**20.2**	**18.9**	**6.6**
Asteroidea*	**1.0**	**0.2**	**0.8**	**0.1**	**0.6**	**0.1**	**-**	**-**	**-**	**-**	**0.7**	**0.3**	**-**	**-**	**1.1**	**0.8**	**-**	**-**
Echinoidea*	**14.6**	**3.5**	**9.2**	**1.4**	**13.3**	**2.8**	**27.8**	**10.5**	**32.7**	**8.9**	**23.1**	**8.2**	**18.6**	**5.0**	**27.8**	**14.9**	**16.4**	**6.2**
Crinoidea*	**-**	**-**	**2.5**	**1.2**	**4.4**	**1.1**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**
Ophiuroidea*	**16.1**	**3.5**	**11.8**	**1.7**	**26.6**	**2.7**	**7.6**	**2.7**	**0.7**	**<0.1**	**2.7**	**0.8**	**5.4**	**1.2**	**10.8**	**3.3**	**2.5**	**0.4**
Holothuroidea*	**0.5**	**0.1**	**-**	**-**	**0.6**	**0.1**	**-**	**-**	**0.7**	**0.2**	**0.7**	**0.3**	**-**	**-**	**1.1**	**1.1**	**-**	**-**
Chordata	**8.3**	**5.3**	**8.4**	**4.3**	**5.1**	**2.3**	**4.5**	**2.7**	**8.2**	**4.6**	**16.3**	**8.8**	**9.3**	**5.6**	**12.5**	**7.9**	**11.5**	**7.0**
Ascidiacea *	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**-**	**2.5**	**1.6**
Teleostei*	**8.3**	**5.3**	**8.4**	**4.3**	**5.1**	**2.3**	**4.5**	**2.7**	**8.2**	**4.6**	**16.3**	**8.8**	**9.3**	**5.6**	**12.5**	**7.9**	**9.0**	**5.3**
Macrophyta*	**9.8**	**1.5**	**29.3**	**4.2**	**48.7**	**5.0**	**1.0**	**0.2**	**14.3**	**1.7**	**21.1**	**3.1**	**35.7**	**4.3**	**1.7**	**1.0**	**7.4**	**2.8**
Other Material	**11.7**	**3.0**	**55.5**	**20.9**	**50.6**	**11.8**	**0.5**	**<0.1**	**6.1**	**2.1**	**6.8**	**2.0**	**3.9**	**1.2**	**6.3**	**2.3**	**11.5**	**5.5**
Sand	11.7	3.0	31.1	5.7	34.2	4.5	0.5	<0.1	0.7	<0.1	-	-	2.3	0.5	6.3	2.3	3.3	0.8
Unidentified material	-	-	28.6	15.2	23.4	7.3	-	-	5.4	2.1	6.8	2.0	1.6	0.7	-	-	9.8	4.7
Number of foreguts examined (n)	213		119		158		199		147		146		129		189		133	
Foregut fullness (mean ± S.E.)	3.8 ± 1.8		6.1 ± 2.3		6.5 ± 1.9		5.0 ± 1.9		6.2 ± 2.3		6.1 ± 2.3		4.8 ± 2.1		4.4 ± 2.2		4.3 ± 2.6	

The volumetric contributions of crustaceans to the diets of the various species in the different habitats ranged from 33 to 42 %, except in the case of *C. auricularis* in the exposed reefs off Perth, where this major taxon contributed as much as 56 % (Table 5.1). Small crustaceans contributed far more to the diets of *C. auricularis* (30 – 36 %) than to those of both *N. parilus* and *O. lineolatus* (12 – 20 %). Among the substantial number of small crustaceans that could be identified at a finer taxonomic level, amphipods contributed most to the volume of the diet of each species (Table 5.1). In the different habitats, amphipods contributed more to the diets of *C. auricularis* (17 – 20 %) than to those of *N. parilus* (1 – 9 %), which, except in the case of this last species in seagrass, were greater than those of *O. lineolatus*, *i.e.* 3 – 4 % (Table 5.1). Large crustaceans contributed between 18 and 30 % to the diets of each of the three species in the different habitats in which they were found, except in the case of *C. auricularis* in the exposed and sheltered reef habitats in the JBMP, where they contributed only 9 and 4 %, respectively.

Molluscs contributed more to the diets of *N. parilus* (38 – 42 %) in the different habitats than to those of either *C. auricularis* (18 – 25 %) or *O. lineolatus* (24 and 30 %) (Table 5.1). Among molluscs, gastropods made by far the greatest volumetric contribution to the diet of each species in each habitat and, within a habitat, were consistently greatest for *N. parilus*. Although the most abundant gastropods in the diets of all three labrid species were trochids, turbinids and columbellids, their contributions to diets varied among those species, with, for example, trochids contributing more to those of *N. parilus* (6 – 14 %) than *C. auricularis* (< 3.5 %) and *O. lineolatus* (< 2 %) (Table 5.1).

The Echinodermata, comprising mainly echinoids and ophiuroids, was the third most important major taxon in the diets of the three species, but, in each habitat, typically contributed more to the diets of *N. parilus* (6 – 13 %) than *C. auricularis* (4 –

7 %) (Table 5.1). The greatest contribution of this major taxon to the diets was the 20 % recorded for *O. lineolatus* in exposed reefs off Perth. Teleosts contributed between 2 and 9 % to the dietary volume of each species in the different habitats (Table 5.1).

5.3.3 Intraspecific dietary relationships in reef habitats

Coris auricularis

PERMANOVA showed that the dietary composition of *C. auricularis* was significantly related to reef habitat (comprising exposed and sheltered reefs in the JBMP and exposed reefs off Perth), length class (both $P = 0.1$ %) and season ($P = 3.2$ %) (Table 5.2). There was a small and significant interaction between reef habitat and seasons ($P = 2.1$ %). The COV for reef habitat and length class were both approximately ten times that for season. Two-way crossed ANOSIM, employing dietary data for reef habitat *v.* season and length class combined (thus removing any confounding influence of the last two factors) gave a Global R of 0.29 ($P = 0.01$ %). The Global R in the corresponding test for length class, after removing the combined effects of reef habitat and season, was 0.25 ($P = 0.01$ %) and for season, after removing the combined effects of reef habitat and length class, was 0.16 ($P = 0.07$ %).

Pairwise ANOSIM comparisons showed that the dietary composition of *C. auricularis* in exposed reefs off Perth differed significantly from that in both the exposed reefs ($R = 0.28$, $P = 0.07$ %) and sheltered reefs ($R = 0.39$, $P = 0.01$ %) in the JBMP, but not between those in the exposed *v.* sheltered reefs in the JBMP ($P = 7.50$ %). SIMPER emphasised that small crustaceans and gastropods were important contributors to the overall diet of *C. auricularis* in each of the three reef habitats. Greater volumes of gastropods and small crustaceans were recorded in the diets of this species in exposed reefs in the JBMP than in those off Perth, while the reverse was true for large crustaceans (mainly penaeids, paguroids and brachyuran crabs).

Pairwise comparisons also demonstrated that the dietary compositions of each *C. auricularis* length class differed significantly from that of each of its other length classes (*R* = 0.23 - 0.43, *P* = 0.01 - 0.1 %), except in the cases of the 150 - 199 *v.* <150 and 200 - 249 mm fish, with the difference being greatest for the diet of fish < 150 *v.* ≥ 250 mm. SIMPER emphasised that small crustaceans and gastropods were present in relatively greater volumes in the guts of smaller than larger fish, whereas the opposite trend was exhibited by large crustaceans and annelids.

The dietary composition of *C. auricularis* in summer differed significantly from that in each of the other three seasons (*R* = 0.11 to 0.39, *P* = 0.02 to 4.1 %) and it also differed between autumn and winter (*R* = 0.14, *P* = 2.6 %). SIMPER demonstrated that the diet contained greater volumes of large crustaceans and smaller volumes of annelids in summer than in the other three seasons. The diet in autumn was distinguished from that in winter by greater volumes of large crustaceans and lesser volumes of annelids.

Notolabrus parilus

In the case of *N. parilus*, PERMANOVA showed that its dietary composition was significantly related to reef habitat, length class and season and that there was a significant interaction between reef habitat and length class (Table 5.2). The COV was far greater for length class and reef habitat than for season and the interaction between reef habitat and length class (Table 5.2). The results of 2-way crossed ANOSIM tests, using data for one factor *v.* the other two factors combined, were largely consistent with those of PERMANOVA in that they demonstrated that the dietary composition of *N. parilus* was significantly related to reef habitat (*R* = 0.16, *P* = 0.05 %) and length class (*R* = 0.21, *P* = 0.01 %), noting, however, that this analysis did not detect a significant relationship with season, with the *R*-statistic of 0.03 being negligible.

Table 5.2. Mean squares (MS), pseudo-*F* ratios, components of variation (COV) and significance levels (*P %*) for reef habitat x length class x season PERMANOVAs for the Bray-Curtis matrices of the volumetric data for the various dietary categories of replicates of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* from exposed reefs off Perth and exposed and sheltered reefs in the JBMP. df = degrees of freedom. Note that *O. lineolatus* was not found over sheltered reefs in the Jurien Bay Marine Park (JBMP).

	Coris auricularis					*Notolabrus parilus*					*Ophthalmolepis lineolatus*				
	df	MS	Pseudo-*F*	COV	*P %*	df	MS	Pseudo-*F*	COV	*P %*	df	MS	Pseudo-*F*	COV	*P %*
Main Effects															
Reef habitat	2	7645	10.63	147.5	0.1	2	6194	8.15	109.4	0.1	1	9385	5.44	170.5	0.1
Length class	3	5899	8.20	145.4	0.1	3	7377	9.70	183.2	0.1	3	8885	5.15	347.2	0.1
Season	3	1253	1.74	14.9	3.2	3	1508	1.98	20.1	1.6	3	1938	1.12	9.5	33.6
Interactions															
Reef habitat x Length class	6	1017	1.41	26.7	6.2	6	1312	1.73	47.1	1.2	3	1680	0.97	-4.4	49.5
Reef habitat x Season	6	865	1.20	12.9	2.1	6	977	1.29	17.9	15.5	3	2080	1.21	33.3	27.9
Length class x Season	9	864	1.20	17.2	17.2	9	946	1.24	21.4	14.7	9	1660	0.96	-14.0	54.3
Reef habitat x Length class x Season	17	891	1.24	63.4	8.1	17	679	0.89	-27.5	71.9	6	1982	1.15	87.5	28.1
Residual	100	719		719.4		104	760		760.4		63	1724		1723.8	

On the basis of pairwise ANOSIM comparisons, the dietary composition of *N. parilus* in the exposed reefs off Perth differed significantly from those in exposed reefs (*R* = 0.17, *P* = 1.0 %) and sheltered reefs (*R* = 0.22, *P* = 0.10 %) in the JBMP, whereas the dietary compositions of this species in exposed and sheltered reefs in the JBMP were not significantly different (*R* = 0.04, *P* = 29.0 %). SIMPER showed that gastropods and large crustaceans typified the diet of *N. parilus* in each of the three reef habitats, together with bivalves and echinoids in the exposed reefs off Perth. The diet of *N. parilus* in exposed reefs off Perth was distinguished from that in the exposed reefs in the JBMP by relatively greater volumes of large crustaceans, bivalves and echinoids and smaller volumes of small crustaceans and gastropods.

The dietary composition of each *N. parilus* length class differed significantly from that of each of the other length classes (*R* = 0.18 - 0.59, *P* = 0.01 - 2.20 %), except in the case of the 150 - 199 *v.* 200 - 249 mm fish, with the difference being greatest for fish < 150 *v.* ≥ 250 mm. SIMPER emphasised that small crustaceans were relatively far more important in the diets of smaller (<150 mm) than larger *N. parilus*, whereas the reverse was true for gastropods and echinoids.

Ophthalmolepis lineolatus

PERMANOVA detected a significant relationship between the dietary composition of *O. lineolatus* and both reef habitat and length class (*P* = 0.1 %), with the COV for the second factor being twice that of the first (Table 5.2). There was no significant seasonal effect and no significant 2-way or 3-way interactions. Two-way crossed ANOSIM tests, removing the effects of the other two factors when testing the third, also demonstrated that the dietary composition of *O. lineolatus* was significantly related to reef habitat (*R* = 0.16, *P* = 1.5 %) and length class (*R* = 0.15, *P* = 1.1 %), but not season (*R* = 0.05, *P* = 19.3 %).

The diets of *O. lineolatus* in the two reef habitats from which it was collected, *i.e.* exposed reefs off Perth and in the JBMP, were significantly different (*R* = 0.14, *P* = 0.3 %). SIMPER demonstrated that large crustaceans, gastropods, small crustaceans and echinoids were the four most important typifying dietary categories of *O. lineolatus* in the exposed reefs of both the JBMP and off Perth. However, their order of importance varied among those two reef habitats, with the diet of this species in the exposed reefs of the JBMP containing greater volumes of gastropods and large crustaceans and lesser volumes of echinoids and annelids, whereas the reverse was true for exposed reefs off Perth.

The diets of the smallest *O. lineolatus* (< 150 mm) differed significantly from those of the two length classes of largest fish (200 - 249 and ≥ 250 mm), with the highest *R*-statistic of 0.77 being recorded for the length classes of smallest *v.* largest fish. SIMPER showed that the diets of small fish were distinguished from those of large fish by containing far greater volumes of small crustaceans and lesser volumes of large crustaceans, gastropods and echinoids.

5.3.4 Comparisons of intraspecific trends exhibited by the three species

On the centroid nMDS ordination plots, derived from matrices constructed from the dietary compositions of the four length classes of *C. auricularis*, *N. parilus* and *O. lineolatus* in each reef habitat in which they occur, the samples of each successive length class progress sequentially from left to right (Fig. 5.2a, c, e). In the case of each species, the samples from exposed reefs in the JBMP lie above those for exposed reefs off Perth. The interaction between reef habitat and length class for *N. parilus* is reflected, on the ordination plot in Fig. 5.2c, by differences in the distances between samples for the various length classes of the species in the three habitats.

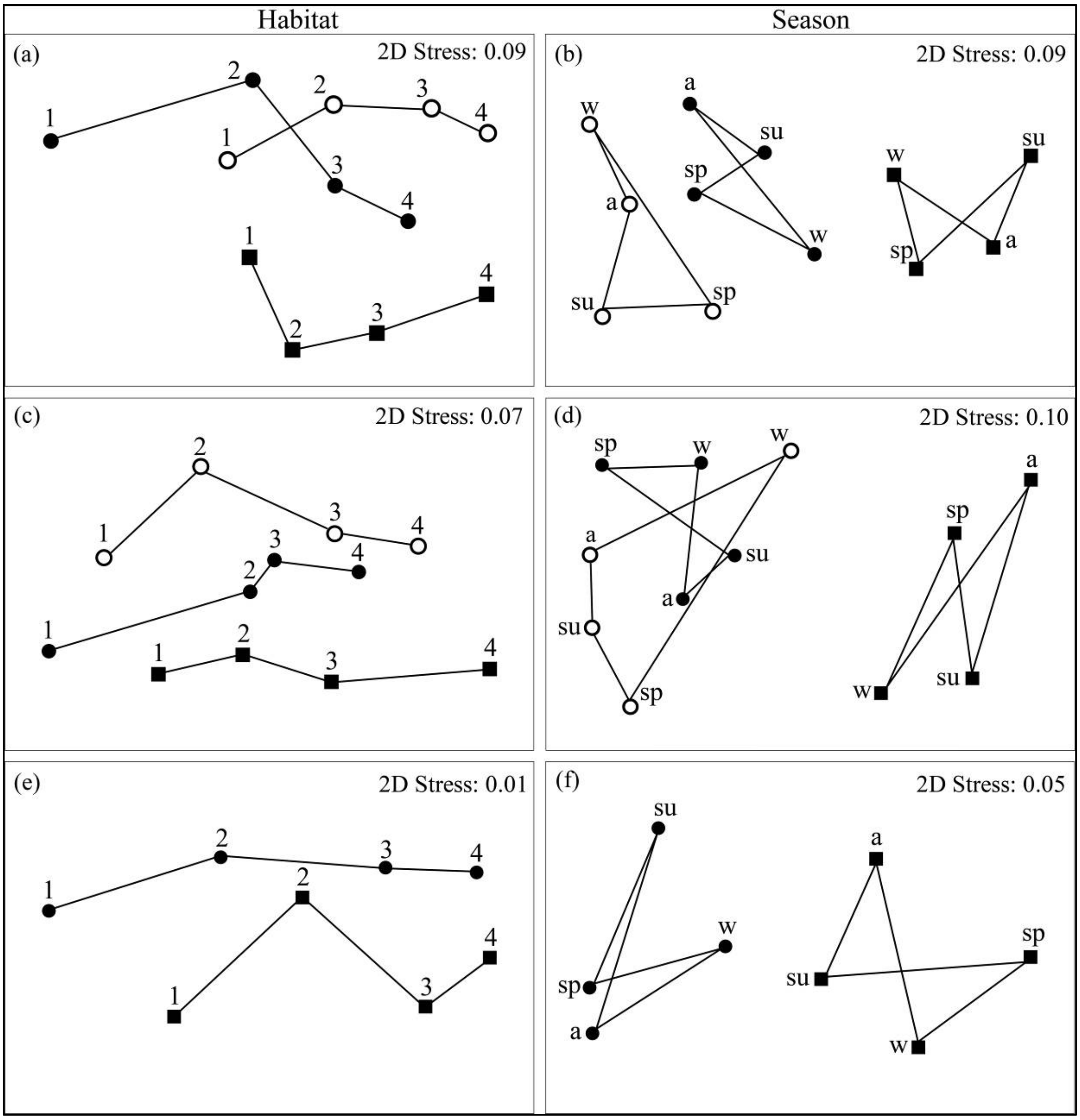


Figure 5.2. Centroid nMDS ordination plots, derived from distance among centroid matrices constructed from Bray-Curtis matrices of the volumetric contributions of the various dietary categories to replicates of the diets of sequential length classes (1: <150 mm, 2: 150-199 mm; 3: 200-249 mm; 4: ≥ 250 mm) in each (a), (c), (e) [●, exposed reefs in the Jurien Bay Marine Park (JBMP); ○, sheltered reefs in the JBMP; ■, exposed reefs off Perth] reef habitat and (b), (d), (f) season of (a), (b) *Coris auricularis*, (c), (d) *Notolabrus parilus* and (e), (f) *Ophthalmolepis lineolatus*.

On the centroid nMDS plots, derived from the matrices constructed from the dietary data for each species in each season in each reef habitat, the lines connecting the points for successive seasons of *C. auricularis*, *N. parilus* and *O. lineolatus* in offshore Perth waters lie in the right of the plot and do not overlap those for the first two species in either exposed or sheltered reefs in the JBMP or for the third species in exposed reefs in that marine park (Fig. 5.2b, d, f).

5.3.5 Notolabrus parilus in sheltered reefs and seagrass

PERMANOVA demonstrated that the dietary compositions of *N. parilus* from inshore, sheltered reefs and inshore seagrass in the JBMP were significantly related to habitat type, season and length class (Table 5.3). The COV was greatest for length class, followed by season and habitat type, with the last of these being almost a sixth of that for length class and about one quarter of that for season. There were also 2-way interactions for habitat type x length class (*P* = 0.3 %) and season x length class (*P* = 1.9 %).

Table 5.3. Mean squares (MS), pseudo-*F* ratios, components of variation (COV) and significance levels (*P %*) for habitat type x length class x season PERMANOVAs for the Bray-Curtis matrix of the volumetric data for the various dietary categories of replicates of *Notolabrus parilus* from sheltered reefs and seagrass meadows in the Jurien Bay Marine Park (JBMP). df = degrees of freedom.

	Notolabrus parilus in JBMP sheltered reefs and seagrass				
	df	MS	Pseudo-*F*	COV	*P %*
Main Effects					
Habitat type	1	2443	3.32	49.7	0.9
Length class	2	6994	9.50	281.4	0.1
Season	3	4241	5.76	204.7	0.1
Interactions					
Habitat type x Length class	2	2104	2.86	128.7	0.3
Habitat type x Season	3	1004	1.36	32.1	18.3
Length class x Season	6	1249	1.70	95.0	1.9
Habitat type x Length class x Season	6	361	0.49	-149.9	97.3
Residual	45	736		735.8	

On the basis of data for *N. parilus* in sheltered reefs and seagrass in the JBMP, habitat type was not significant in 2-way crossed ANOSIM tests for habitat type *v.* season and length class combined (R = 0.08, P = 19.7 %). In contrast, length class (R = 0.38, P = 0.01 %) and season (R = 0.24, P = 0.03 %) were significant in tests using the same approach of one factor *v.* the other two combined.

The points for successive length classes of *N. parilus* progress from left to right on the centroid nMDS ordination plot, which was derived from the matrix constructed from the dietary composition of each length class of this species in sheltered reefs and seagrass (Fig. 5.3a). The interaction between length class and habitat type, as demonstrated by PERMANOVA, is reflected in the very large differences for the distances between the points for the second and third length classes in the two habitat types.

On the centroid nMDS plot, derived from the matrix constructed from the dietary composition of *N. parilus* in each season in sheltered reefs and seagrass, the trends exhibited by the points for successive seasons were strikingly similar (Fig. 5.3b). This accounts for the negligible interaction term for these two factors in PERMANOVA (Table 5.3). The interspersion of the points for the sheltered reef and seagrass habitats (Fig. 5.3b) helps account for the absence of a strong habitat type effect (Table 5.3).

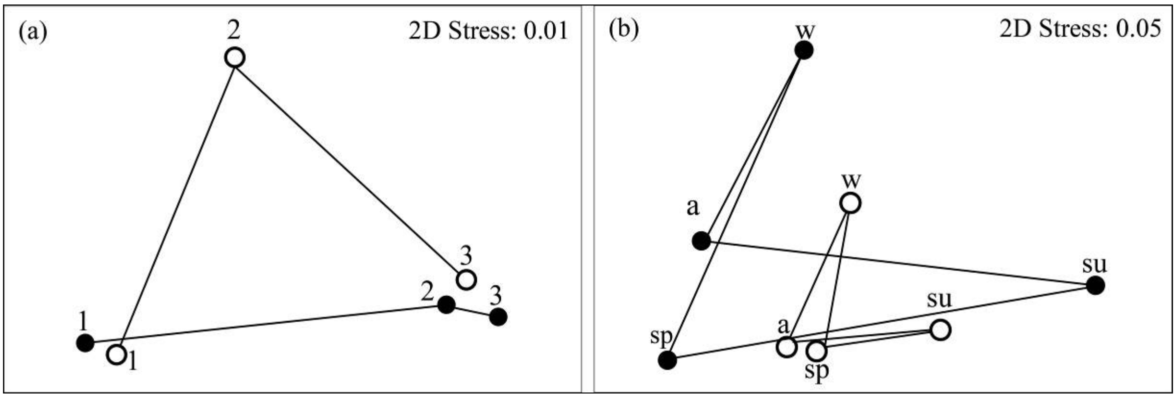


Figure 5.3. Centroid nMDS ordination plots, derived from distance among centroid matrices constructed form Bray-Curtis matrices of the volumetric contributions of the various dietary categories to replicates of (a) sequential total length classes (see Fig. 5.2) and (b) seasons of *Notolabrus parilus* over sheltered reefs (○) and in seagrass (●) in the Jurien Bay Marine Park (JBMP).

5.3.5 Size-related changes in dietary compositions

As shown previously, the diet of each of the three labrid species was always related to habitat and length class, and, while this was also true for season for *C. auricularis* and *N. parilus*, the COV and *R*-statistic values for this variable were always far smaller, and the difference was not even significant for two of the three species in ANOSIM tests. Thus, for all three species, the volumetric contributions of the main dietary components of each length class in each habitat were kept separate, but pooled for season (Fig. 5.4a-i).

In the case of *C. auricularis* in exposed reefs off Perth and exposed and sheltered reefs in the JBMP, the contribution of small crustaceans to the diet decreased progressively with increasing body size, whereas the reverse trend was exhibited by large crustaceans and particularly echinoderms and that of gastropods tended neither to increase nor decrease with body size (Fig. 5.4a, d, g). However, the contributions of large crustaceans to the diet of all length classes of *C. auricularis* were greater in the exposed reefs off Perth than in both the exposed and sheltered reefs in the JBMP, whereas the opposite was true for gastropods (Fig. 5.4a, d, g).

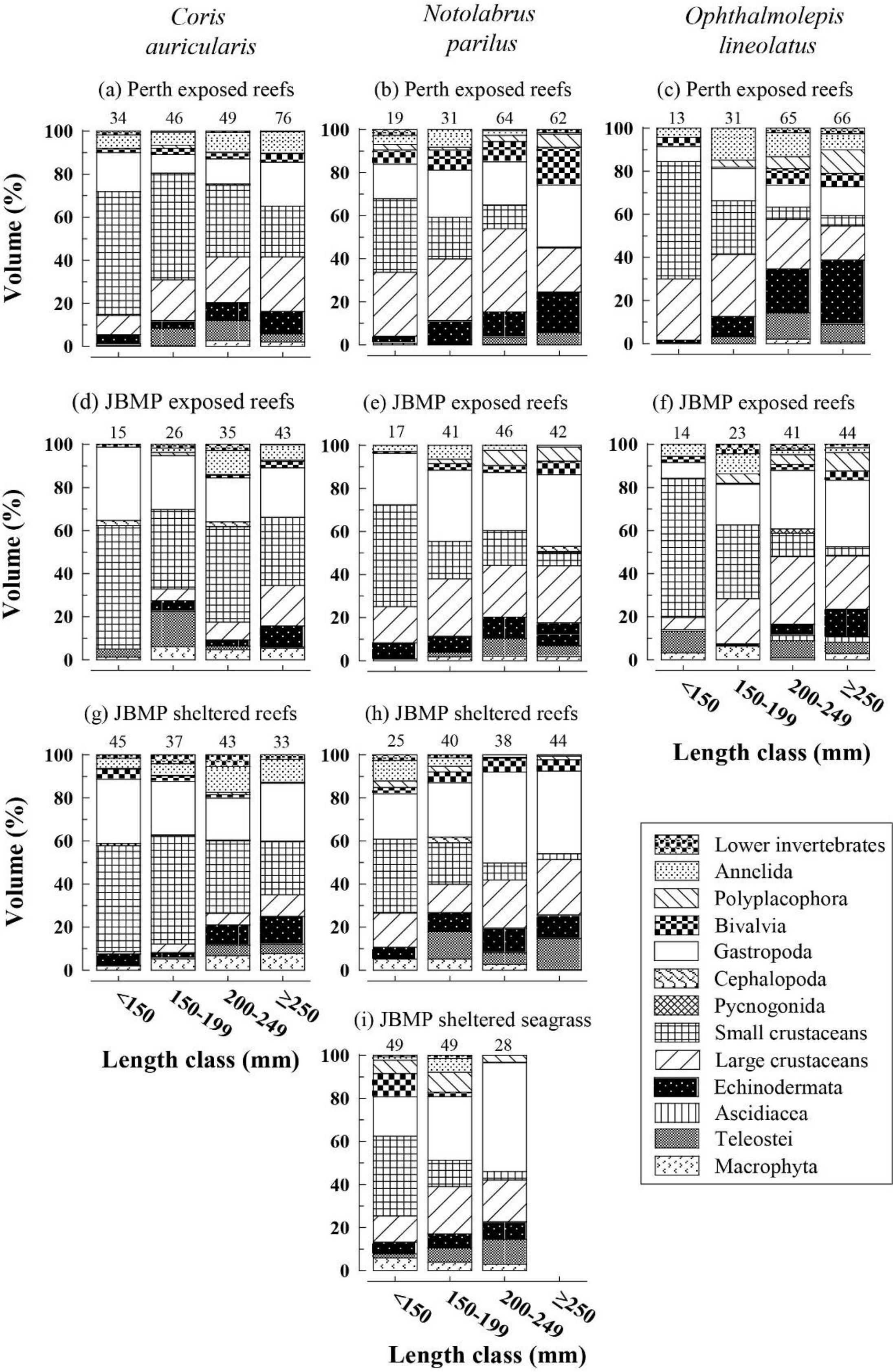


Figure 5.4 Mean percentage volumetric contributions of the various dietary categories to the diets of sequential length classes of (a), (d), (g) *Coris auricularis*, (b), (e), (h), (i) *Notolabrus parilus* and (c), (f) *Ophthalmolepis lineolatus* in the habitats of (a), (b), (c) Perth exposed reefs, (d), (e), (f) Jurien Bay Marine Park (JBMP) exposed reefs, (g), (h) JBMP sheltered reefs and (i) JBMP sheltered seagrass in which they occurred. Sample sizes are given above each histogram.

The trend towards a decrease in the volumetric contribution of small crustaceans with increasing body size was even more pronounced with *N. parilus* (Fig. 5.4b, e, h, i) and *O. lineolatus* (Fig. 5.4c, f) in each of the habitats in which those species occurred. Conversely, an increase in body size of these two species was typically accompanied by a rise in the contributions of gastropods (Fig. 5.5b, c, e, f, h, i) and, in the case of the exposed reefs off Perth, particularly of echinoderms (Fig. 5.4b, c).

5.3.6 Interspecific dietary relationships

On the basis of the results of PERMANOVA, the dietary compositions differed among labrid species, length classes and seasons in the exposed reefs of the JBMP and among species and length classes in both the exposed reefs off Perth and the sheltered reefs in the JBMP (Table 5.4). There were significant 2-way interactions between species and length class for the diets in the exposed and sheltered reefs in the JBMP and for species and season in the latter of those reef habitats and there was also a significant 3-way interaction for the diets in the exposed reefs off Perth. The COV in each reef habitat was always far greater for species than for length class, season or any of the interactions (Table 5.4).

A 2-way crossed ANOSIM for species *v.* the other two main factors combined showed that the dietary compositions of the three labrid species in the exposed reefs off Perth were significantly different ($R = 0.36$, $P = 0.01$ %). Pairwise comparisons revealed significant differences in the dietary compositions of *C. auricularis v. N. parilus* ($R = 0.47$, $P = 0.01$ %) and *O. lineolatus* ($R = 0.38$, $P = 0.01$ %) and of *N. parilus v. O. lineolatus* ($R = 0.23$, $P = 0.01$ %). SIMPER demonstrated that, although large crustaceans and gastropods were among the two most important typifying dietary categories for each of the three labrid species, small crustaceans, bivalves and echinoids

Table 5.4. Mean squares (MS), pseudo-*F* ratios, components of variation (COV) and significance levels (*P %*) for species x length class x season PERMANOVAs for the Bray-Curtis matrices of the volumetric data for the various dietary categories of replicates of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* from exposed reefs off Perth and exposed and sheltered reefs in the Jurien Bay Marine Park (JBMP). df = degrees of freedom.

	Perth exposed reefs					JBMP exposed reefs					JBMP sheltered reefs				
	df	MS	Pseudo-*F*	COV	*P %*	df	MS	Pseudo-*F*	COV	*P %*	df	MS	Pseudo-*F*	COV	*P %*
Main Effects															
Species	2	11567	10.79	280.2	0.1	2	8964	8.48	227.4	0.1	1	20953	30.30	455.4	0.1
Length class	2	5348	4.99	114.8	0.1	2	3142	2.97	60.6	0.1	3	3155	4.56	111.9	0.1
Season	3	1465	1.37	13.1	17.5	3	2553	2.41	57.8	0.1	3	636	0.92	-2.5	55.0
Interactions															
Species x Length class	4	1728	1.61	48.2	5.4	4	1783	1.69	64.4	3.4	3	3108	4.50	224.4	0.1
Species x Season	6	1241	1.15	15.6	27.5	6	843	0.80	-25.3	77.3	3	1651	2.39	87.2	0.3
Length class x Season	6	1472	1.37	37.0	11.5	6	951	0.90	-12.8	63.4	9	691	1.00	-0.1	48.7
Species x Length class x Season	11	1489	1.39	103.6	4.9	12	919	0.87	-51.4	73.8	9	593	0.86	-37.5	72.2
Residual	127	1073		1072.5		69	1058		1057.5		57	691.5		691.5	

also ranked amongst the three most important typifying species for the diets of *C. auricularis*, *N. parilus* and *O. lineolatus*, respectively (Table 5.5a). The diet of *C. auricularis* was distinguished from that of both *N. parilus* and *O. lineolatus* by greater volumes of small crustaceans and lesser volumes of echinoids, whereas the distinction between the diets of *N. parilus* and *O. lineolatus*, which was more marginal, was related to greater contributions of large crustaceans, gastropods and bivalves and smaller contributions of echinoids to the diet of the former than latter species (Table 5.5a).

When the corresponding ANOSIM tests were applied to the diets of the three species in the exposed reefs of the JBMP, the dietary compositions of those species likewise differed significantly ($R = 0.29$, $P = 0.01$ %). While the dietary composition of *C. auricularis* differed significantly from that of both *N. parilus* ($R = 0.48$, $P = 0.01$ %) and *O. lineolatus* ($R = 0.32$, $P = 0.04$ %), no such difference was found between those of the latter two species ($R = 0.09$, $P = 12$ %). The three main typifying dietary categories were the same for each species, *i.e.* small crustaceans, gastropods and large crustaceans, but their order of importance varied (Table 5.5b). The dietary composition of *C. auricularis* was distinguished from that of both *N. parilus* and *O. lineolatus* by, in particular, greater volumes of small crustaceans and lesser volumes of large crustaceans (Table 5.5b).

In the case of sheltered reefs in the JBMP, where only *C. auricularis* and *N. parilus* were found, a 2-way crossed ANOSIM for species *v.* the other two main factors combined showed that the dietary compositions of those two species were significantly different ($P = 0.01$ %), with a particularly high *R*-statistic value of 0.66. While gastropods and small crustaceans typified the diets of both species, small crustaceans and annelids contributed more to the diet of *C. auricularis*, while large crustaceans contributed more to that of *N. parilus* (Table 5.5c).

Table 5.5. Dietary categories that typify (shaded) and distinguish (non-shaded), listed in order of importance between the diets of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* from exposed reefs off Perth (a) and exposed (b) and sheltered reefs (c) in the Jurien Bay Marine Park (JBMP). Dietary categories are listed in order of importance. ns denotes the dietary compositions of the pair of species is not significantly different. * denotes that a dietary category makes a greater contribution to the diet of the species at the top of the column.

(a) Perth exposed	*C. auricularis*	*N. parilus*	*O. lineolatus*
Coris auricularis	Small crustaceans Large crustaceans Gastropods		
Notolabrus parilus	Small crustaceans* Large crustaceans Bivalves Annelids* Echinoids	Large crustaceans Gastropods Bivalves Echinoids	
Ophthalmolepis lineolatus	Small crustaceans* Large crustaceans* Echinoids Annelids	Large crustaceans* Echinoids Gastropods* Bivalves*	Echinoids Large crustaceans Gastropods Small crustaceans

(b) JBMP exposed	*C. auricularis*	*N. parilus*	*O. lineolatus*
Coris auricularis	Small crustaceans Gastropods Large crustaceans		
Notolabrus parilus	Small crustaceans* Large crustaceans Echinoids	Gastropods Large crustaceans Small crustaceans	
Ophthalmolepis lineolatus	Small crustaceans* Large crustaceans Gastropods*	ns	Large crustaceans Gastropods Small crustaceans

(c) JBMP sheltered	*C. auricularis*	*N. parilus*
Coris auricularis	Small crustaceans Gastropods Annelids*	
Notolabrus parilus	Small crustaceans* Large crustaceans Annelids*	Gastropods Large crustaceans Small crustaceans

On the centroid nMDS ordination plots, derived from the dietary data for exposed reefs off Perth, the points for both the length classes and seasons for the three species are discrete (Fig. 5.5a, b). While the points for *C. auricularis* are also discrete from those of the other two species on the corresponding ordination plots for the length classes and seasons in the exposed reefs in the JBMP, those for *N. parilus* and *O. lineolatus* lie close together on the plot (Fig. 5.5c, d). The points for the dietary compositions of *C. auricularis* and *N. parilus* in the sheltered reefs of the JBMP are discrete in the case of both length classes and seasons (Fig. 5.5e, f). The interactions revealed by PERMANOVA (Table 5.4) are reflected in the different patterns of progression exhibited by the length classes for the three species in Fig. 5.5c and for *C. auricularis* and *N. parilus* in Fig. 5.5e. The trends exhibited by the points for the four seasons for *C. auricularis* and *N. parilus* in Fig. 5.5f show that the compositions of the seasonal samples for these two species change in a cyclical manner. However, the cyclic patterns of the two species are in almost complete opposition, which explains both the significant interaction between species and season for sheltered reefs at JBMP (Table 5.4) and the lack of any overall seasonal main effect.

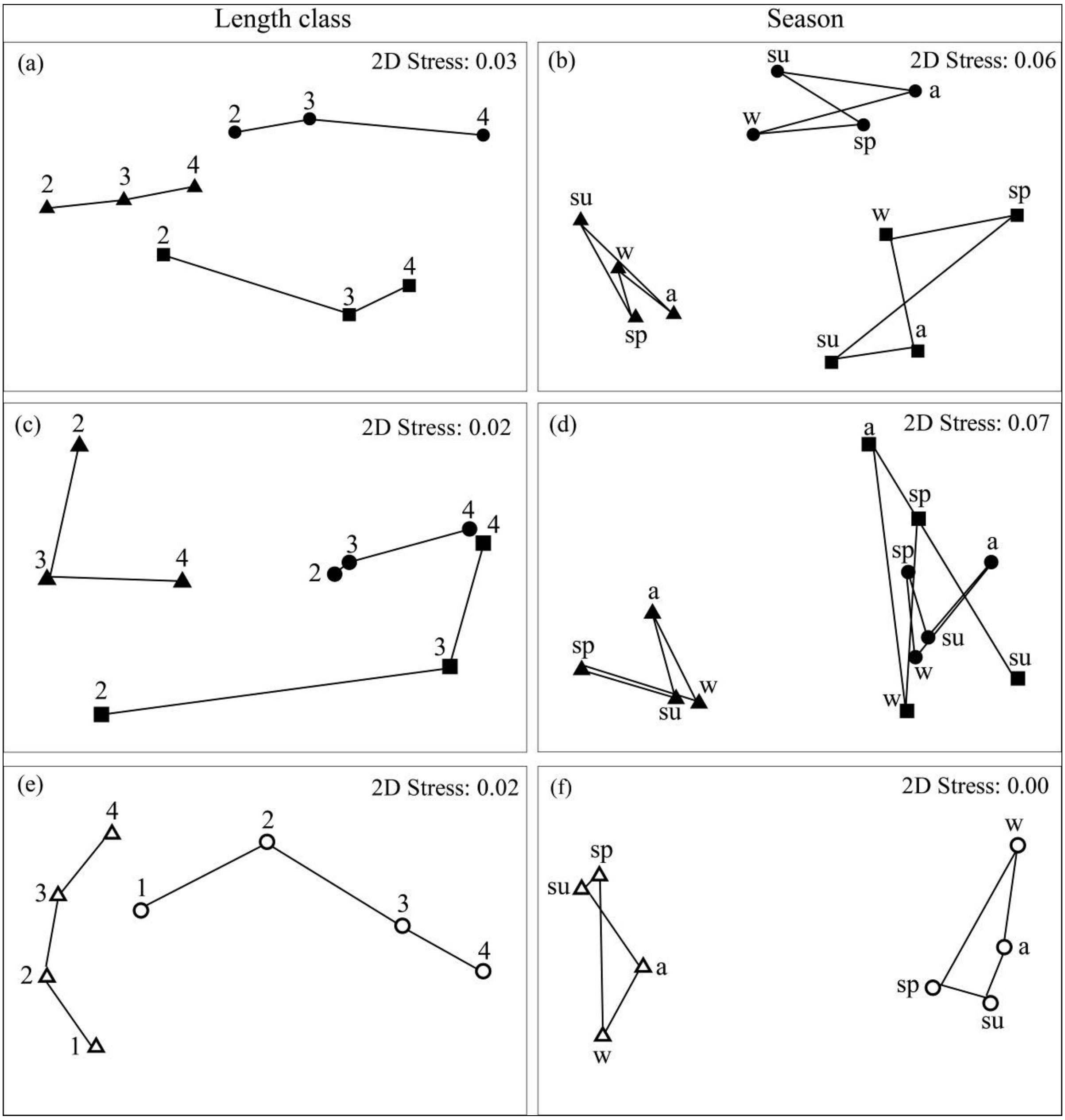


Figure 5.5. Centroid nMDS ordination plots, derived from distance among centroid matrices constructed from Bray-Curtis matrices of the volumetric contributions of the various dietary categories to replicates of sequential (a, c, e) length classes (see Fig. 5.2) and (b, d, f) seasons in each reef habitat for (a), (b) exposed reefs off Perth, (c), (d) exposed reefs in the JBMP and (e, f) and sheltered reefs in JBMP (e, f). ▲ = *Coris auricularis*, ● = *Notolabrus parilus* and ■ = *Ophthalmolepis lineolatus*. Closed symbols represent exposed reefs, open symbols represent sheltered reefs.

5.4 Discussion

5.4.1 Broad overall dietary compositions

The sampling regime developed for this study enabled a wide size range of the labrid species *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus* to be caught seasonally from exposed reefs in two locations (waters off Perth and in the JBMP), which were separated latitudinally by a distance of *c*. 250 km. It also facilitated comparable seasonal sampling of the first two species in sheltered reefs further inshore in the JBMP and of *N. parilus* in the seagrass meadows that were interspersed among the latter sheltered reefs. The resultant very substantial dietary data were therefore able to be used with confidence to explore statistically, and within a single integrated study, the extents to which the dietary compositions of each labrid species were related to latitude, exposure to wave action, body size, season and, where applicable, habitat type, *i.e.* reef *v.* seagrass. Those data also facilitated an examination of the degrees to which the diets of different species differed when those species co-occurred, taking into account any influence of one or more of the above factors on dietary composition.

This study demonstrated that, on the west coast of Australia and irrespective of habitat, *C. auricularis*, *N. parilus* and *O. lineolatus* ingest a wide range of benthic invertebrate prey, as is typical of other labrid species on the same coast (MacArthur & Hyndes, 2007; Platell *et al.*, 2010) and in other temperate regions of Australasia (Gillanders, 1995a; Denny & Schiel, 2001; Shepherd, 2005; Morton *et al.*, 2008a). However, in terms of volume, three dietary categories, namely gastropod molluscs and small and large crustaceans, dominated the diets of each of the above three species of labrid. Furthermore, the greatest volumetric dietary contributions were made by turbinids, trochids and columbellids among gastropods, by amphipods and isopods among small crustaceans and by brachyuran crabs among large crustaceans.

The large volumes of gastropods and small and large crustaceans ingested by *C. auricularis*, *N. parilus* and *O. lineolatus* over reefs on the west coast of Australia parallel the situation recorded for other labrid species over reefs in temperate Australia, such as *Notolabrus tetricus* on the central south coast (Shepherd & Clarkson, 2001) and *O. lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* on the east coast (Morton *et al.*, 2008a). Although gastropods and small and large crustaceans made very important volumetric contributions to the diets of all three species in each habitat in which they occurred, substantial volumes of echinoderms, and particularly of echinoids, were also consumed by each species in those habitats. Echinoderms also made a substantial contribution to the diets of *N. tetricus* and *A. viridis* over reefs further east in Australia (Gillanders, 1995a; Shepherd & Clarkson, 2001), but not to those of species such as *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* in that broad region (Morton *et al.*, 2008a).

Although bivalves were ingested by all three labrid species, their dietary contributions only exceeded 5.5 % in the case of *N. parilus* in exposed reefs off Perth, which contrasts with the situation found with labrids elsewhere, for which such molluscs were one of the three major contributors to the diets. These species included *P. laticlavius*, *N. gymnogenis* and particularly *O. lineolatus* in eastern Australia (Morton *et al.*, 2008a) and *Notolabrus fucicola* in New Zealand (Denny & Schiel, 2001). The implication from these dietary comparisons that bivalve molluscs are not prevalent over reefs on the lower west coast of Australia is consistent with the very small contributions that they make to both the invertebrate assemblages over reefs on that coast (Murphy *et al.*, 2006) and to the diets of several other demersal fish species that feed predominantly on invertebrates (Platell & Potter, 2001; Platell *et al.*, 2010).

5.4.2 Intraspecific latitudinal comparisons

The statistical tests employed in this study emphasised that the dietary composition of *C. auricularis*, *N. parilus* and *O. lineolatus* over exposed reefs in the JBMP each differed significantly from that of the same species in exposed reefs off Perth, *i.e.* at a higher latitude. It is thus particularly noteworthy that the Echinoidea was the most important of the dietary categories for distinguishing between the diets of both *N. parilus* and *O. lineolatus* in exposed reefs off Perth from those in the corresponding reefs in the JBMP. Furthermore, this taxon, together with another echinoderm class (Ophiuroidea), also contributed more to the dietary composition of *C. auricularis* in the former than latter habitat. In addition, consistently greater volumes of annelids (mainly polychaetes) were also important in distinguishing the diet of *O. lineolatus* in exposed reefs off Perth from that of this species in the JBMP, and they also made slightly greater contributions to the diets of *N. parilus* and *C. auricularis* in the former than latter reef habitat. As the relative abundance of prey taxa in the diets of labrids tends to reflect that in their environment (Gillanders, 1995a; Shepherd & Clarkson, 2001), echinoderms and polychaetes are presumably more abundant in the exposed reefs off Perth than in those reefs in the JBMP.

In contrast to the above trends, consistently greater volumes of gastropods and small crustaceans were recorded in the foreguts of *C. auricularis* and *N. parilus* in the exposed reefs of the JBMP than in the waters off Perth and the same was true for gastropods with *O. lineolatus*. These comparisons imply that gastropods and small crustaceans are relatively more available as prey in the exposed reefs in the JBMP than in those off Perth, which, at least in the case of gastropods, is consistent with the trends exhibited by the relative abundance data for these taxa among reef invertebrates in general in those waters (Murphy *et al*., 2006).

The very consistent latitudinal differences between the compositions of the diets of *C. auricularis*, *N. parilus* and *O. lineolatus* contrasts with the lack of a significant difference between those of assemblages of another labrid *Bodianus frenchii* at different latitudes and in two water bodies (Indian and Southern Oceans) in south-western Australia, when using the same level of taxonomic resolution (Platell *et al.*, 2010). Furthermore, the distinction was still negligible (R = 0.06) for *B. frenchii* when analyses were repeated at a finer level of taxonomic resolution (Platell *et al.*, 2010). This implies that *B. frenchii* focuses on particular prey, irrespective of the environment in which it is found.

In contrast to the differences found between the dietary compositions of each of the three species in exposed reefs in the JBMP and waters off Perth, the diets of neither *C. auricularis* nor *N. parilus* over exposed reefs in the JBMP differed significantly from those of these species over the sheltered reefs found further inshore, in which these species, but not *O. lineolatus*, were abundant. This strongly suggests that, while the dietary compositions of *C. auricularis* and *N. parilus* are likely to be influenced by differences in the composition of prey found at different latitudes, they are not influenced, in a given area, such as the JBMP, by factors associated with the extent of exposure to wave action, recognising that the exposed reefs in the JBMP were located in deeper waters and further from the shore than the sheltered reefs.

PERMANOVA and 2-way crossed ANOSIM tests both demonstrated that, overall, the dietary compositions of *C. auricularis*, *N. parilus* and *O. lineolatus* in reef habitats were each related, to a similar manner to both the particular reef habitat and length class. The at best marginal seasonal change in the diets of any of the three labrid species is consistent with the fact that the composition of the invertebrate fauna on the lower west coast does not change seasonally (Murphy *et al.*, 2006).

5.4.3 Comparisons between Notolabrus parilus *in sheltered reefs and adjacent seagrass*

There is strong statistical evidence that, as with the diets of *N. parilus* in exposed *v.* sheltered reefs in the JBMP, those of this species in sheltered reefs and nearby seagrass areas were similar, thereby negating the second hypothesis in the Introduction. This lack of a conspicuous difference between diets in different habitat types contrasts with the observation that new recruits of another labrid (*A. viridis*) fed predominantly on harpacticoids over rocky reefs and on tanaids in seagrass (Gillanders, 1995a) and is at variance with the observation that the relative abundances of prey taxa in the diets of labrids tend to reflect those in their environment (Shepherd & Clarkson, 2001). The similarities between the diets of *N. parilus* over sheltered reefs and in seagrass thus suggest that the individuals of this species forage in a similar niche in both habitat types and/or regularly move between habitat types. The tendency for *N. parilus* to occur over both reefs and seagrass has been recorded in other studies on the lower west coast of Australia, albeit that the densities were greater over reefs than in seagrass (Howard, 1989; Vanderklift *et al*., 2007).

Irrespective of the habitat type occupied at a given time and the extent of movement between those habitat types, *N. parilus* consumes large volumes of the prey that are typically associated with the sand found either on and around reefs, or which provides the substrate for seagrass. Such a view is consistent with the fact that many of the abundant prey of *N. parilus* caught over reefs and in seagrass typically live in or over sand, *e.g.* small crustaceans (amphipods and isopods), brachyuran crabs, polychaetes and bivalves other than mytilids. The diets of *N. parilus* collected from over reefs and in seagrass also contained, however, appreciable amounts of the turbinids *Phasianella australis* and *Phasianella ventricosa*, which typically live on plants (Edgar, 2008). Thus, *N. parilus* also forages on the fauna occupying the abundant macrophyte growths on reefs in the JBMP, as well as those on the macrophytes which constitute the seagrass meadows (Tuya *et al.*, 2010). This broadly parallels the feeding behaviour of the labrid *Achoerodus gouldii*, which feeds on epifauna associated with algal mats (Shepherd, 2005; Shepherd & Brook, 2005). As the dietary composition of *N. parilus* in seagrass meadows in the JBMP was similar to that of this species in *A. griffithii* meadows in the waters off Perth (MacArthur & Hyndes, 2007), this labrid presumably forages in similar microhabitats in seagrass in that more southern location.

5.4.4 Size-related changes in dietary composition

The dietary composition of *C. auricularis*, *N. parilus* and *O. lineolatus* each underwent similar size-related shifts in each habitat in which those species were abundant. Thus, as body size increased, the volumetric contributions to the diet of small crustaceans declined, while those of large crustaceans and echinoderms rose. The trend for an increasing contribution of echinoderms was particularly pronounced with *N. parilus* and *O. lineolatus* in the exposed reefs off Perth, where this dietary category made their largest overall contribution to the diets of the three species in any habitat. The above trends, which are due to the ingestion of progressively larger and more hard-bodied prey with increasing body size, largely parallel those recorded for other labrid species (*e.g.* Shepherd, 2005; Morton *et al.*, 2008a), and reflect an increase in mouth size and jaw strength (Wainwright, 1988; Sanderson, 1990).

5.4.5 Interspecific differences in diets within reef habitats

The appreciable *R*-statistic values in the ANOSIM tests for interspecific comparisons emphasised that, in both the exposed reefs of the JBMP and off Perth, the dietary compositions of *C. auricularis* differed conspicuously from those of both *N. parilus* and *O. lineolatus*. Furthermore, within the sheltered reefs of the JBMP, the diet of *C. auricularis* differed markedly from that of *N. parilus*, noting that *O. lineolatus* was not found in this habitat. The main overall distinctions between the diet of *C. auricularis* and those of the other two species reside in the ingestion by the former species of far greater volumes of smaller prey (*e.g.* amphipods and isopods) and lesser volumes of larger and harder-bodied prey (*e.g.* crustaceans and echinoids). Furthermore, *C. auricularis* tended far more to continue to ingest small crustaceans, the smallest of the dietary categories, as it increased in size than was the case with either of the other two species. The ingestion of small crustaceans by all length classes of *C. auricularis* is related to their possession of a relatively narrow mouth and a single row of small, fine teeth, noting that canines are absent at the rear of the upper jaw (Fig. 5.1). Moreover, underwater observations demonstrated that, when feeding, *C. auricularis* darts towards the substrate from which it removes small prey and "spits out" the sand ingested at the same time. In contrast, *N. parilus* and *O. lineolatus* have relatively wider mouths, stouter teeth in their upper jaws and prominent canines at the rear of those upper jaws (Fig. 5.1), which makes them better adapted for capturing and retaining larger, hard-bodied prey. Although the distinction between the diets of *N. parilus* and *O. lineolatus* is less marked, the former species did consume greater volumes of large crustaceans, gastropods and bivalves. It is thus relevant that these prey are hard-bodied and typically of a larger size and that, in comparison with *O. lineolatus*, *N. parilus* has a wider mouth, longer and more robust teeth on the upper jaw and a double, rather than single pair of canines at the rear of that upper jaw (Fig. 5.1). Furthermore, our observations show that the behaviour of *O. lineolatus* and *N. parilus* are conspicuously different, which is consistent with the detailed descriptions given for the former species and *N. gymnogenis*, a congener of *N. parilus* (Morton, 2007; Morton *et al.*, 2008a, b). Thus, *O. lineolatus* spends much time in the water column, venturing downwards at regular intervals to ingest its prey, whereas *N. parilus* tends to lie motionless on the substrate for periods and then "ambushes" its prey.

In summary, this chapter has emphasised that, when comparing the dietary compositions within and between species, it is appropriate to use firstly PERMANOVA to identify whether interactions are present between various selected factors and then to employ fully non-parametric ANOSIM tests to elucidate the extent of the difference between the levels of those factors. Analyses of foregut contents demonstrate that, on the lower west coast of Australia, *C. auricularis*, *N. parilus* and *O. lineolatus* feed on essentially the same broad suite of benthic invertebrate prey over reefs and on which those three labrid species are abundant. However, the dietary composition of *C. auricularis*, *N. parilus* and *O. lineolatus* over exposed reefs in the JBMP each differed significantly from that of the same species in a comparable habitat *c.* 250 km further south in the waters off Perth. As these differences were largely consistent across species, they are assumed to reflect latitudinal differences in the availability of the various potential prey species. Furthermore, within the JBMP, the dietary composition of neither *C. auricularis* nor *N. parilus* differed between the exposed reefs and inshore, sheltered reefs, and nor did that of *N. parilus* over sheltered reefs and in adjacent seagrass meadows. This implies that, when these two species occur in the same region, they occupy the same feeding niche. Thus, in the JBMP and irrespective of habitat type, *N. parilus* feeds on prey associated with either the sand and/or macrophytes that cover and lie between the reefs. PERMANOVA and ANOSIM tests showed that the volumetric contributions of the different dietary categories did differ, however, among species, and particularly between *C. auricularis* and the other two labrid species, reflecting small differences in mouth and jaw morphology and dentitional characteristics and to differences in feeding behaviour. These interspecific dietary differences and size-related changes in diet would reduce the potential for competition for food resources among and within the above three abundant reef-dwelling labrids.

CHAPTER 6

GENERAL CONCLUSIONS

6.1 Study implications for the Metabolic Theory of Ecology

The proposal of the Metabolic Theory of Ecology (MTE) that energy use by organisms can be understood from first principles of physics, chemistry and biology (*i.e.* effects of temperature on metabolism) (Brown *et al.*, 2004a) and that many biological attributes of organisms (*e.g.* growth rate, maximum body size and size and age at maturity) are explained by this theory (Allen & Gillooly, 2007), has been heralded by some as one of the greatest advances in ecology (Whitfield, 2004). However, for a variety of reasons, many others have criticised this theory (see O'Conner *et al.*, 2007; del Rio, 2008). For example, it has been suggested that the MTE is overly simplistic and fails to take into account the possibility that certain species have become adapted such that their growth rates are not directly related to environmental temperature (Clarke, 2004; Clarke & Fraser, 2004; Dell *et al*., 2011; Huey & Kingsolver, 2011). The results of this study, which are based on sound data and analyses, show that certain attributes of the biology of each of *Coris auricularis*, *Notolabrus parilus* and *Ophthalmolepis lineolatus*, *e.g.* growth rate, were not consistent with the predictions of the MTE. Thus, as has been suggested for other taxa, *e.g.* cold water fishes (Clarke, 2004; Clarke & Fraser, 2004), it may be the case that the three labrid species are enzymatically adapted to lower (than higher) temperatures.

The fact that the latitudinal patterns of differences in growth of the three labrid species were consistent and did not conform to the MTE raises several questions that warrant further investigation. For example, it would be informative to sample each of the three labrid species over a broader latitudinal range to determine the patterns of change in biological characteristics, such as growth rate, throughout their full distributional ranges. An understanding of such patterns would enable elucidation of whether the growth rates of these species are at a maximum towards the centre of their distributional range, as has been shown to occur, for example, with the Snapper *Pagrus auratus* (Wakefield, 2006), or whether growth follows a unidirectional trend throughout the majority of their distribution, as would be predicted if enzymatic rates were largely dependent on temperature. Extension of the types of analyses undertaken in this study to other species (and particularly to taxa other than the Labridae) would enable investigation of whether the types of differences found for the three labrid species represent a generality for fish and other species in this region of the world. The results presented in this thesis provide the basis for assessing the impacts of climate change on the biological characteristics of the three labrid species.

The focus on whether growth in the three labrid species conformed to the predictions of the MTE highlighted a level of ambiguity in the literature regarding the use of the word "growth". For example, several papers suggest that "fish in colder environments grow slower but attain a larger body size" (Berrigan & Charnov, 1994; Kozłowski *et al.*, 2004). However, for an individual to attain a larger body size (in a colder environment) than another (in a warmer environment), at some point during life, that individual in the colder environment must have grown faster than the one in the warmer environment. Thus, for the above statement to be true, in this study, it was interpreted that the MTE predicts that fish in colder environments grow slower than those in warmer environments early in life, but attain a larger body size. The fact that such clarification was unable to be found in the literature suggests that discussions relating to the MTE require a standardised use of certain terminology. Moreover, although theories related to predicted effects of temperature on metabolism have been developed within a mathematical framework (*e.g.* Charnov & Gillooly, 2004), such a framework for describing predictions regarding growth rate and trends among other variables with temperature (latitude) were not apparent from the literature. This is thus obviously an area of research that warrants further investigation.

The findings in this study relating to latitudinal patterns of differences in biological attributes of fish populations, such as growth, mortality and timing of maturity, have important implications for understanding the potential impacts of climate change on the productivity and distributions of fish stocks. There is little doubt that "long-term environmental change" will have an impact on such biological aspects of fish stocks and assessment strategies and management plans need to be developed to accommodate such changes (Pauly, 1980; Mangel, 2003; Griffths & Harrod, 2007; Thresher *et al.*, 2007; Hobday *et al.*, 2008). Moreover, the results highlight the point that although growth and maturity relationships are often assumed in fisheries stock assessments to remain constant, those relationships may be strongly influenced by factors such as environmental temperature. There is an increasing recognition that stock assessments and management plans will need to accommodate the changes to fish population dynamics brought about by climate change (Hall & Wise, 2011).

6.2 Study implications for ecosystem modelling and research

The data produced in this study for *C. auricularis*, *N. parilus* and *O. lineolatus* will be very valuable for studies aimed at understanding ecosystem function and applying to ecosystem-based fisheries management (EBFM) in Western Australia. There is an important need in this State, as with many regions of the world, to better understand the impacts of fishing, *i.e.* removing larger predatory fish species, and other impacts, *e.g.* climate change, on ecosystem function. The dietary data produced during this study are being used, in combination with those for numerous other species (in an existing database called "Guts", see Platell & Hall, 2005), to develop a detailed food-web for the demersal coastal marine environment in temperate Western Australia. These dietary data for the three labrid species are also highly relevant to Ecopath and Ecosim ecosystem models recently developed for the Jurien Bay Marine Park in Western Australia (Lozano-Montes *et al.*, 2011). Dietary data for Western Australian fishes have been used to “link” species at different trophic levels in a minimum realistic model (MRM), employed to explore the effectiveness of alternative management options for various multi-species fisheries (Hall & Wise, 2011). In this latter research, lack of dietary data for key fished species such as Snapper (*Pagrus auratus*) was considered a major contributing factor in the uncertainty of model predictions. The importance of acquiring high quality dietary data has been recognised by the State’s fisheries governing agency through supporting a research study to obtain such data for this and several other species.

6.3 Study implications for managing fish resources in Western Australia

For the purposes of monitoring, assessment and management of fish resources in Western Australia, the Department of Fisheries has divided the State into four bioregions, based on broad environmental characteristics (Fletcher *et al.*, 2010). This study of the biology of three labrids, *C. auricularis*, *N. parilus* and *O. lineolatus*, was conducted on the lower west coast, which falls within the West Coast Bioregion (WCB), *i.e.* from just north of Kalbarri to just east of Augusta. Within each bioregion, each fish species is categorised into one of five suites, based broadly on the environments that it inhabits. The suites include species that inhabit estuarine, nearshore (coastal waters < 20 m deep), inshore demersal (20-250 m deep), offshore demersal (> 250 m deep) and pelagic environments and species within a suite are considered to have similar biological characteristics and thus vulnerability to the effects of fishing (Department of Fisheries, 2011b). Although the three labrids that were the subject of this study occupy reefs, which are demersal habitats, they are most abundant in shallow reef environments (< *c.* 20 m) and were thus included by the Department of Fisheries in the nearshore suite rather than inshore demersal suite of species (Gomon *et al.*, 2008; Tuya *et al.*, 2009; Department of Fisheries, 2011b).

The different methods employed in fisheries that operate on each suite of species may catch one, several or many species. For example, the commercial line fishery that targets the inshore demersal suite can land over 70 species in a year (Fairclough *et al.*, 2010). However, it is not possible to monitor the status of stocks of every species, not only because of limited resources to do so, but because in many cases it would not be possible to obtain sufficient fishery-dependent samples for assessments (Craine *et al.*, 2009). Thus, as is the case with fisheries in some other parts of the world (Zacharias & Roff, 2001; Shertzer & Williams, 2008), in Western Australia, for each suite of species, certain "indicator" species are monitored and used to infer the state of the entire suite. In the case of the nearshore suite, species that are important in either commercial or recreational fisheries include the Australian Herring *Arripis georgianus* and Tailor *Pomatomus saltatrix*, which are both used as indicator species for this suite in the WCB (Department of Fisheries, 2011b). However, although these two species have similar longevity to *C. auricularis*, *N. parilus* and *O. lineolatus*, *i.e.* 10-12 years, they both occupy coastal nekton waters and are gonochorists (Fairclough *et al.*, 2000a, b; Salerno *et al.*, 2001; Robillard *et al.*, 2008, 2009), which contrasts with the habitats occupied by the three labrids and the fact that they are each protogynous hermaphrodites. In addition, *A. georgianus* is listed as a low risk species, as are the three labrid species of this study in the WCB, while *P. saltatrix* is listed as a medium risk species. Thus, the question arises as to whether the status of stocks of *A. georgianus* and *P. saltatrix* are sufficiently representative of the three labrid species and other inshore species with similar life cycle characteristics. The same types of questions have been raised by Shertzer & Williams (2008) for a multi-species fishery in the United States.

The extent to which monitoring of fishes is required is dependent on the risks to the sustainability of a species, which are related to the inherent vulnerability of a species to exploitation and the size and importance of fisheries that exploit such a species. These factors, in turn, will influence the level of monitoring and assessment required for indicator species and thus suites of species and can vary from monitoring of catch to full integrated stock-assessment models (Department of Fisheries, 2011b). When last assessed, the level of exploitation of *C. auricularis*, *N. parilus* and *O. lineolatus* in Western Australia was low in both commercial and recreational fisheries (Sumner *et al.*, 2008; Fletcher & Santoro, 2010). However, substantial numbers of these species are released by recreational fishers and a number of labrid species have been shown to be susceptible to barotrauma (Nardi *et al.*, 2006; Sumner *et al.*, 2008; Fairclough *et al.*, 2010). Thus, these and any other indirect impacts to the stocks of the three labrid species may not be detected by assessments of the indicator species (*e.g. A. georgianus* and *P. saltatrix*) for the nearshore suite of fish species considered by the Department of Fisheries. Age-based assessments of rates of fishing mortality are often used to assess the status of stocks of such indicators, but often a truncated age distribution is enough to reveal that overfishing may have been occurring in stocks of species. Although rates of mortality were not estimated during this study, the age distributions of *C. auricularis*, *N. parilus* and *O. lineolatus* did not indicate any negative impacts of fishing at either the Jurien Bay Marine Park or off Perth.

Substantial changes were made recently to the management of large demersal species in the WCB, because of evidence of overfishing of their stocks. Such changes restrict heavily the amount of fishing effort for such demersal species in the WCB. Thus, it might be expected that recreational fishers, in particular, will begin to target alternative species, such as *C. auricularis*, *N. parilus* and *O. lineolatus*, which are all edible. In this regard, it is relevant that in south-eastern Australia, a rapid increase in commercial catches of a medium-sized labrid, *Notolabrus tetricus*, occurred in the 1990s, as a result of demand for a live reef-fish trade. Within a few years, concerns in that part of Australia that catch rates had declined and the average size of fish had decreased triggered management action (Smith *et al.*, 2003). As the population of Western Australia is predicted to increase substantially over the next 30 years, recreational fishing effort is likely to increase accordingly and labrid species such as *C. auricularis*, *N. parilus* and *O. lineolatus* will become increasingly targeted. As the data acquired in this study on the key biological attributes of these three species are representative of their populations in a largely unexploited state, they provide an excellent benchmark for future assessments.

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