

**The Ecology of Three Species of Wrasse (Pisces: Labridae) on
Temperate Rocky Reefs
of New South Wales, Australia**



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*I hereby certify that the work embodied in this thesis is the result of original research
and has not been submitted for a higher degree to any other University or Institution.*

Signed:

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Abstract

In temperate New South Wales, most fish species in the family Labridae have not previously been investigated with available knowledge restricted primarily to photographic identification guides providing brief notes on species distribution, habitat preferences and identification. This information is inadequate for assessing the impact of labrid harvesting on rocky reef systems and for making informed management decisions for the protection of these fishes. Therefore, this study aimed to fill some of the significant gaps in the understanding of labrid assemblages associated with rocky reefs of temperate eastern Australia. This was accomplished by concentrating primarily on three species - *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* - which are abundant and co-occur in shallow waters (<20 m) on the central coast of New South Wales. The methods used in this study included SCUBA surveys of labrid assemblages; *in situ* observations of labrid behaviour on SCUBA; and acquisition of labrid specimens for the extraction of intestines, gonads and otoliths, and for measurements of fish weight and length.

Labrids were found to be the most species rich family in the study region and were the most abundant of all non-planktivorous fishes. Overall, a higher number of labrid species and a higher number of labrid individuals occurred in sponge garden habitat (15-22 m depth) compared to fringe (3-7 m) and barrens (8-15 m), owing to greater densities of *O. lineolatus*, *Austrolabrus gymnogenis* and *Eupetrichthys angustipes*. The common labrids, *N. gymnogenis*, *Achoerodus viridis* and *P. laticlavius*, occurred at higher densities in fringe habitat due mostly to a higher representation of juveniles in this habitat. The effect of habitat on labrid assemblages was subject to small-scale variation between sites (separated by hundreds of metres) and experienced temporal changes due primarily to a substantial increase in the abundance of recruits coinciding with late summer and autumn (April-May).

Behavioural observations revealed that the three focal species differed substantially in their spatial structure. *O. lineolatus* were found to be temporary reef residents using home ranges in excess of 2500 m² for periods of up to 1 year before permanently emigrating outside these temporary home ranges. In contrast, *N. gymnogenis* exhibit strong site fidelity to reef patches of less than 600 m² in which they remain for periods

in excess of 2 years. Reef patches are shared by up to at least 10 juvenile and female individuals and a single, highly territorial male in a mating system suggestive of resource defence polygyny. An understanding of the spatial structure of *P. laticlavus* was constrained by its cryptic behaviour, but behavioural observations suggest this species is home ranging and establishes temporary territories for the purpose of feeding and/or reproduction. Intensive ethological observations allowed for the description and quantifying of several major behaviours in which all species typically engaged including encounters and interactions with other fishes, lying, use of shelter, side-swiping, bending, gaping, cleaning by clingfishes (Gobiesocidae) and colour change. The occurrence of these behaviours often demonstrated substantial differences among species (e.g. lying, shelter and bending) and/or experienced shifts with ontogeny (e.g. interactions and area usage). These trends generally remained consistent at different times of the day and periods of the year, and at both locations.

Dietary analyses revealed *O. lineolatus*, *N. gymnogenis* and *P. laticlavus* are generalist carnivores feeding on a variety of benthic invertebrates including polychaetes, amphipods, decapods, gastropods, bivalves, polyplacophorans, echinoderms and cirripedes. Differences in the volumetric contribution of prey items in the guts of each species showed that food resources are partitioned among species and observations of foraging behaviour demonstrated a partitioning of microhabitats used for feeding. Ontogenetic shifts in diet and feeding microhabitats demonstrate that food resources are further partitioned within a species. However, overall morphological and behavioural similarities within a species results in greater competition occurring among individuals of the same species than among individuals of different species. This was reflected in higher rates of intra-specific interactions compared with interactions between labrid individuals of different species. Observations of feeding episodes revealed the bite rates of all species were typically unaffected by the time of day and period of year in which sampling occurred, but a location effect occurred for *O. lineolatus* and *P. laticlavus*. A reduction in bite rate with ontogeny occurred for *N. gymnogenis*.

The population structure of the three species suggests each exhibits the typical labrid reproductive strategy of protogynous hermaphroditism. *O. lineolatus* and *N. gymnogenis* are both monandrous species, but the occurrence of some *P. laticlavus* males at small sizes and young ages suggests this species may be diandrous.

Similarities occurred between *O. lineolatus* and *N. gymnogenis* in the size/age at which individuals sexually matured (*c.a.* 180 mm, 2 years) and changed sex (*c.a.* 280 mm, 4.6 years), but these events occurred at substantially smaller sizes (95 and 138 mm, respectively) and younger ages (<0.9 and 1.9 years, respectively) in *P. laticlavus*. Sectioned otoliths were used to determine that the longevity of *O. lineolatus*, *N. gymnogenis* and *P. laticlavus* was at least 13.4, 9.6 and 4.8 years, respectively. Ages were validated using marginal increment analysis. Timing of reproduction in each species was asynchronous with peaks in the reproductive activity occurring in late summer to early autumn (February-March) for *O. lineolatus*, mid winter (July) for *N. gymnogenis* and mid spring to early summer (October-December) in *P. laticlavus*.

Information gained on the spatial structure, behaviour, diet, life history, growth and demographics of *O. lineolatus*, *N. gymnogenis* and *P. laticlavus* has revealed that, despite belonging to the same family, the ecological significance of each species is distinct, the susceptibility of each species to over-harvesting is different and that ‘blanket’ management strategies are inappropriate for this diverse family. It is recommended that this research acts a precursor for designing future studies aimed at these and other temperate labrids of Australia to more fully appreciate the ecology of these fishes, for predicting the foreseeable consequences of labrid exploitation and for making more informed decisions for the protection of these fishes.

Chapter 1:

Introduction

1.1 Research problem

Labrids, known commonly as wrasses, are frequently captured by recreational and commercial fishers, which are known to contribute to significant reductions in labrid densities and the mean size of individuals in some areas (Edgar and Barrett 1997, 1999; Jones 1999; Gladstone 2001; Platten *et al.* 2002). These fishers typically target larger, reproductive males that have undergone sex reversal from medium-sized reproductive females, thus potentially causing significant localised depletion in the density of reproductive males. Disruptions to labrid assemblages may result in flow-on effects to other components of rocky reef systems including prey, predators and competitors.

On temperate rocky reefs of eastern Australia the functional ecology, life history and demographics of most labrid species are yet to be investigated with available knowledge restricted mostly to photographic identification guides offering general notes on distribution, habitat preferences and basic identification. Such a limited scope of scientific research is surprising as, being predators of benthic invertebrates, the role of labrids in structuring benthic assemblages may be significant. With an increase in coastal fishing pressure occurring in temperate eastern Australia (Henry and Lyle 2003; Kennelly and McVea 2003) a greater understanding of the functional significance of labrids in rocky reef systems is needed. Therefore, the aim of this study is to provide information to fill some of the significant gaps in the current understanding of labrid assemblages associated with temperate rocky reefs of eastern Australia. This will be accomplished by focusing on three abundant and co-occurring species (i.e. *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*) in shallow waters of the central coast region of New South Wales (NSW). Information obtained in achieving this aim will be useful for making informed decisions about the ecological significance of labrids on temperate rocky reefs of eastern Australia, for predicting any foreseeable consequences of labrid overexploitation and for making informed management decisions for the protection of these fishes.

1.2 Thesis structure and overview

The following structure has been used to achieve the aim of this thesis. Chapter 1 outlines the general characteristics of labrids, their fisheries in south-eastern Australia and a description of each of the species focussed on in this thesis (i.e. *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*). Chapter 2 introduces the study region and describes the general methods and locations that were selected for achieving the thesis aim. As a component of the general methods, a brief overview of a pilot study is provided which was performed to determine the optimal sampling strategy for behavioural observations. In Chapter 3, SCUBA surveying techniques are used to quantify spatial and temporal patterns of labrid distribution and abundance, at two locations, for the purpose of determining the relative importance of labrids in fish assemblages within the study region. Special emphasis is given to the role of habitats in determining patterns of labrid distribution.

Having established that labrids are consistently abundant and diverse within the study region, the following three chapters investigate aspects of the functional ecology, life history and demographics of the three focal labrids. Chapter 4 explores the diurnal behavioural repertoires of each of these species using SCUBA and handheld, underwater, video techniques. Among other behaviours, special consideration is given to area usage, social spacing, interactions, shelter use and colour change. Chapter 5 explores the dietary compositions and foraging behaviour of the focal species using a combination of SCUBA observations and gut content examination. Chapter 6 outlines the reproductive strategies, growth and demographics of the focal species using SCUBA observations, gonad examination, age estimates derived from otoliths, and length and weight measures. Finally, Chapter 7 provides a summary of the contribution this research has made to better understanding the ecology of labrids on temperate rocky reefs of eastern Australia and for assisting in making informed management decisions to prevent the ecological consequences of their over-harvesting. Suggestions for future research are also provided in the concluding chapter.

1.3 Introduction to labrids

Australian marine and estuarine waters provide habitat for over 4200 fish species (Hoese *et al.* 2007), with temperate regions of Australia characteristically having high levels of fish endemism (approx. 80% of all fishes) (Pogonoski *et al.* 2002). Of all fishes inhabiting coastal Australia, fishes of the family Labridae (hereafter labrids) represent the second most speciose family after the family Gobiidae. Labrids are distributed worldwide within tropical, subtropical and temperate seas where they are represented by over 60 genera and in excess of 450 species (Parenti and Randall 2000). Of the 162 species in 41 genera currently reported in Australian waters (Pogonoski *et al.* 2002) more than 90 species have been recorded in temperate Australia (Jones 1999). On rocky reefs of temperate Australia, these fishes represent one of the most conspicuous, abundant and diverse groups, both morphologically and behaviourally. Worldwide, four labrid species are listed as ‘endangered’ or ‘vulnerable’ on the 2006 IUCN Red List of Threatened Species (IUCN 2006) with one, *Cheilinus undulatus*, occurring in waters of tropical Australia (Pogonoski *et al.* 2002). For several labrid species of south-eastern Australia (e.g. *Anampses elegans* and *Achoerodus viridis*), protection is offered in only part of their range (Pogonoski *et al.* 2002).

Labrids possess a pointed snout; terminal mouth usually with thick lips and protruding caniniform teeth; pharyngeal teeth and jaws used for crushing hard prey items; elongate bodies varying greatly in size, shape and colour; cycloid scales; a long dorsal fin extending the length of the back; and a square, or slightly rounded, caudal fin (Kuitert 1996; Moyle and Cech 2000). The majority of labrids do not exceed 400 mm in length but some may grow to sizes in excess of 1 m (e.g. *Achoerodus gouldii*, *Achoerodus viridis* and *Cheilinus undulatus*). Most labrids are diurnally active, benthic carnivores feeding on various soft-bodied and hard-shelled prey items on hard reef substratum; however, some such as *Labroides dimidiatus* feed exclusively by engaging in cleaning behaviour. The reproductive life history of labrids typically involves sex reversal in the form of protogynous hermaphroditism, whereby most individuals reproduce as egg-producing, initial phase (IP) females prior to changing sex to become sperm-producing, terminal phase (TP) males. Sex reversal is often associated with distinct colour changes. Variations on this reproductive strategy are outlined in Chapter 6.

1.4 Fisheries

Several species of labrid are keenly sought for consumption by both recreational and commercial fishers in south-eastern Australia. Commercial fishers involved in the use of trap and line fishing methods regularly catch labrids and provide these to fish markets as discrete species or as ‘mixed fish’. Commercial species include *Notolabrus fucicola*, *Notolabrus tetricus*, *Bodianus unimaculatus*, *Ophthalmolepis lineolatus* and, to a lesser extent, *Notolabrus gymnogenis* (Sydney Fish Market 2005). It is not possible to acquire accurate catch data for each species from commercial records but catches of 22180, 2914, 2156 and 165 kg for 2003 are reported for *N. tetricus*, *B. unimaculatus*, *O. lineolatus* and *N. gymnogenis*, respectively (Sydney Fish Market 2005). However, these catch statistics are likely to be vastly under-representative of the true landings of each species as the majority of labrids captured by NSW commercial fishers are reported as nondescript ‘mixed wrasses’ (NSW Fisheries Commercial Catch Database) or are provided to markets as ‘mixed fishes’.

Being colourful fishes, labrids have proven attractive for consumption in some cultures, particularly the growing Asian culture in Australia. This led to the expansion of the live fish trade in 1993 for *N. fucicola* and *N. tetricus* in coastal waters of Tasmania and Victoria (Murphy and Lyle 1999; Lyle and Hodgson 2001). These fishes are caught and sold live after being transported by refrigeration trucks in cooled seawater (Seafood Industry of Victoria 2005). Sydney restaurants and seafood outlets provide the major market for live fishes with a retail value up to \$30 per kilogram (Department of Primary Industries 2004). The rapid expansion of this fishery led to the introduction of management controls whereby minimum and maximum size limits were applied and limitations placed on the number of holders of live fish access licences (Murphy and Lyle 1999). Future expansion of the live fish trade to include *O. lineolatus* and *N. gymnogenis* is possible which prompts an immediate need for acquiring ecological and biological information on these species for their effective management.

Labrids are also commonly caught by recreational fishers using line and/or spear for use as bait, for consumption or, in the case of line fishers, as by-catch. Labrids taken by recreational fishers in temperate Australia include *Achoerodus viridis*, *O. lineolatus*, *N. gymnogenis*, *N. tetricus* and *Pictilabrus laticlavius* (Kingsford *et al.* 1991; Steffe *et al.*

1996; Henry and Lyle 2003; Kennelly and McVea 2003). Estimates of recreational captures of *O. lineolatus* and *N. gymnogenis* in NSW during 1993/94 are reported to be as high as 23970 and 6199 kg, respectively (Steffe *et al.* 1996), representing substantially higher harvest rates than the corresponding commercial harvesting rates of approximately 2500 and 150 kg in the same period (Sydney Fish Market 2005). More recent data on recreational landings of labrids in NSW is not available but personal observation and communication with recreational fishers suggests that, over the past decade, labrids are increasingly being retained for consumption. With approximately 17% of the NSW population (*c.a.* 100,000 fishers) participating in an estimated 30.4 million hours of fishing from mid-2000 to the end of 2001 (NSW Fisheries 2002), the impact of the recreational fishing sector on labrid populations is likely to be significant. Indeed, increases in labrid densities and the mean size of individuals are found in areas where recreational fishing is excluded (Edgar and Barrett 1997, 1999; Jones 1999; Gladstone 2001).

Whilst management initiatives have been employed for some labrids of NSW, such as *A. viridis* (bag limit of 2 fishes per day using hand line; no size limit), all other labrids (excluding the protected *Anampses elegans*) have a generous bag limit of 20 fish per day with no size restrictions (NSW Department of Primary Industries 2005b). As the population ecology and biology of most NSW temperate labrids is yet to be investigated (Table 1.1), it is not known whether these current management regulations are effective for sustaining labrid populations.

1.5 Labrids of temperate south-eastern Australia

The 83 labrid species found in NSW coastal waters (Hoese *et al.* 2007) are a mixture of both temperate and tropical species. In addition to resident temperate labrids, juvenile tropical labrids including *Thalassoma lunare*, *Halichoeres nebulosus* and *Stethojulis interrupta* may be found in temperate waters during late summer and autumn carried from tropical spawning sites by the East Australian Current (Holbrook *et al.* 1994; Parker 1999). Whilst tropical labrids have broad ranges extending throughout the Indo-Pacific, most temperate labrids of south-eastern Australia have distributions that are globally isolated and restricted (e.g. *Achoerodus viridis* and *Notolabrus gymnogenis*). Some labrids in this region do have extended distributions across southern Australia

(e.g. *Pictilabrus laticlavius* and *Ophthalmolepis lineolatus*) and to New Zealand (e.g. *Pseudolabrus luculentus* and *Notolabrus fucicola*) or as far east as Easter Island (e.g. *Notolabrus inscriptus*) (Jones 1999). On the NSW central coast, labrid assemblages consist predominantly of *N. gymnogenis*, *O. lineolatus*, *A. viridis* and *P. laticlavius*, in addition to lower densities of *Pseudolabrus guentheri*, *Coris picta*, *Austrolabrus maculatus* and *Eupictrichthys angustipes* (Curley *et al.* 2002; Kuiter 1993).

Despite labrids being conspicuous and well represented on rocky reefs of south-eastern Australia, there is a lack of information outlining their patterns of distribution and abundance, behaviour, feeding ecology, life history, demographics and ecological significance. Most research on temperate labrids has focused on species outside NSW or has focused on *A. viridis* (Table 1.1). This lack of information represents a significant gap in understanding the ecological role of temperate labrids, limits the capacity to predict the system-wide impact of human activities on rocky reef systems and places constraints on the effective management of fishing practices in the region. In response, three resident labrids of the central coast region of NSW have been selected for investigation as these species are locally abundant yet, to date, very little is known of their functional ecology, life history and demographics. The species *O. lineolatus* and *N. gymnogenis* represent fishes regularly caught by commercial and recreational fishers with the potential for an expanded market into the live fish trade. The labrid *P. laticlavius* has an ecological niche which preliminary investigations suggest is distinct from *O. lineolatus* and *N. gymnogenis*.

Table 1.1: Examples of research conducted on selected labrid species known to be part of rocky reef fish assemblages of temperate south-eastern Australia. Asterisks denote species investigated in the present study.

Common name/s	Scientific name	Theme	Study Region	Author/s
Eastern blue groper, Eastern blue wrasse	<i>Achoerodus viridis</i>	Distribution/size structure	NSW	Gillanders 1997b; Gillanders and Kingsford 1998; Curley <i>et al.</i> 2002
		Ecomorphology	NSW	Fulton and Bellwood 2004
		Reproductive biology	NSW	Gillanders 1995a
		Age/growth	NSW	Gillanders 1995a, 1997a
		Larval development	NSW	Leis and Hay 2004
		Feeding ecology	NSW	Gillanders 1995b
Western blue groper, Western blue wrasse	<i>Achoerodus gouldii</i>	Distribution/size structure	SA	Shepherd <i>et al.</i> 2002; Shepherd and Brook 2003
		Activity patterns	SA, WA	Shepherd 2006
		Feeding ecology	SA, WA	Shepherd and Brook 2005; Shepherd 2006
Blue-throated wrasse	<i>Notolabrus tetricus</i>	Movement patterns	Tas.	Barrett 1995a, b; Edgar <i>et al.</i> 2004
		Activity patterns	SA	Shepherd and Clarkson 2001
		Feeding ecology	SA	Shepherd and Clarkson 2001
		Otolith microstructure	Tas.	Welsford 2003
		Age/growth	Tas. Vic.	Barrett 1995a, 1999 Metcalf and Swearer 2005
		Reproductive biology	Tas.	Barrett 1995a
		Fisheries biology	Vic.	Smith <i>et al.</i> 2003
Purple wrasse, Saddled wrasse, Yellow-saddled wrasse, Banded wrasse	<i>Notolabrus fucicola</i>	Movement patterns	Tas.	Barrett 1995a, b; Edgar <i>et al.</i> 2004
		Otolith microstructure	Tas.	Welsford 2003
		Age/growth	Tas., NZ	Barrett 1995a, 1999; Taylor and Willis 1998; Ewing <i>et al.</i> 2003
		Feeding ecology	NZ	Denny and Schiel 2001
		Reproductive biology and population structure	NZ	Barrett 1995a; Denny and Schiel 2002
*Maori wrasse, Violet-line Maori wrasse	<i>Ophthalmolepis lineolatus</i>	Patterns of distribution	NSW	Curley <i>et al.</i> 2002
		Ecomorphology	NSW	Fulton and Bellwood 2004
*Crimson-banded wrasse	<i>Notolabrus gymnogenis</i>	Patterns of distribution	NSW	Curley <i>et al.</i> 2002
		Ecomorphology	NSW	Fulton and Bellwood 2004
		Germ cell development	NSW	McPherson 1977
*Senator wrasse	<i>Pictilabrus laticlavius</i>	Movement patterns	Tas.	Barrett 1995a, b; Edgar <i>et al.</i> 2004
		Patterns of distribution	NSW	Curley <i>et al.</i> 2002
		Ecomorphology	NSW	Fulton and Bellwood 2004
		Age/growth	Tas.	Barrett 1995a
		Reproductive biology	Tas.	Barrett 1995a
Other		Movement patterns	Tas.	Barrett 1995a, b
		Ecomorphology	NSW	Fulton and Bellwood 2004
		Age/growth	Tas.	Barrett 1995a

1.6. Focal species

1.6.1 Maori wrasse (*Ophthalmolepis lineolatus*) – [Valenciennes 1838]

Ophthalmolepis lineolatus, or Maori wrasse, derive their common name from the presence of numerous bright blue facial markings around the eyes (similar to facial tattoos in Maori culture). This species has recently received the common name of violet-line Maori wrasse (Sydney Fish Market 2005) to distinguish it from the tropical labrid *Cheilinus undulatus*, which is known commonly as Maori or humphead Maori wrasse. Individuals of *O. lineolatus* have a distinct body colouration with an orange-brown upper, white middle and yellow-orange lower bands extending horizontally along the length of the body (Figure 1.1a). Sexual dichromism exists between stages with TP males possessing a black band through the midsection (Figure 1.1b). Maximum attainable length is generally less than 450 mm TL (Kuiter 1996).

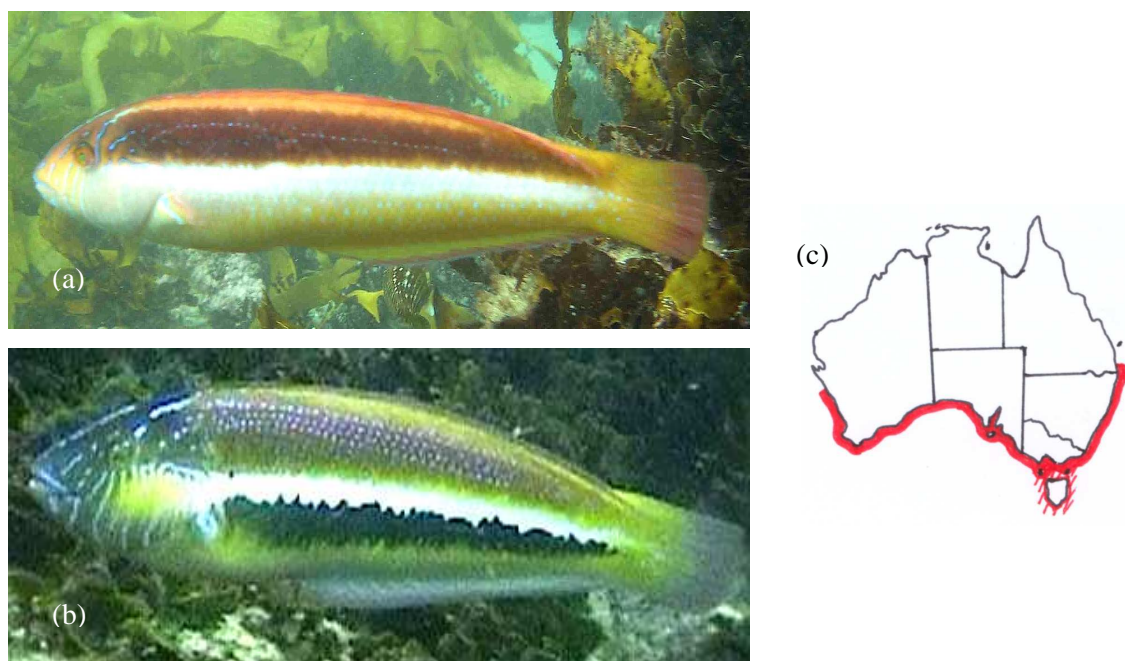


Figure 1.1: Morphology and distribution of *Ophthalmolepis lineolatus*. Shown are a 200 mm initial phase female (a) and a 330 mm terminal phase male (b). The distribution of *O. lineolatus* is highlighted in red (c). Cross-hatching around the coast of Tasmania indicates the distribution of this species is typically restricted to deeper waters. Photograph (a) provided by David Powder.

O. lineolatus are widespread throughout temperate Australia with a distribution extending from southern Queensland, throughout southern Australia (excluding shallow waters of Tasmania), to the Houtman Abrolhos (Western Australia) (Kuitert 1996) (Figure 1.1c). *O. lineolatus* are found in loose aggregations from depths of 3 m to at least 60 m, with highest densities on relatively deep coastal reefs at reef-sand interfaces (Kuitert 1993; Curley *et al.* 2002).

1.6.2 Crimson-banded wrasse (*Notolabrus gymnogenis*) – [Günther 1862]

Notolabrus gymnogenis are sexually dichromatic with TP males exhibiting a crimson transverse band through the midsection (not visible in Figure 1.2b); crimson dorsal and anal fins; white caudal peduncle; yellow caudal fin; and a head exhibiting a dark upper and light lower half (Figure 1.2b). Juvenile and IP individuals are light brown with numerous rows of white dots of various sizes covering the body (Figure 1.2a). TP males attain a maximum length of 400 mm TL (Kuitert 1993).

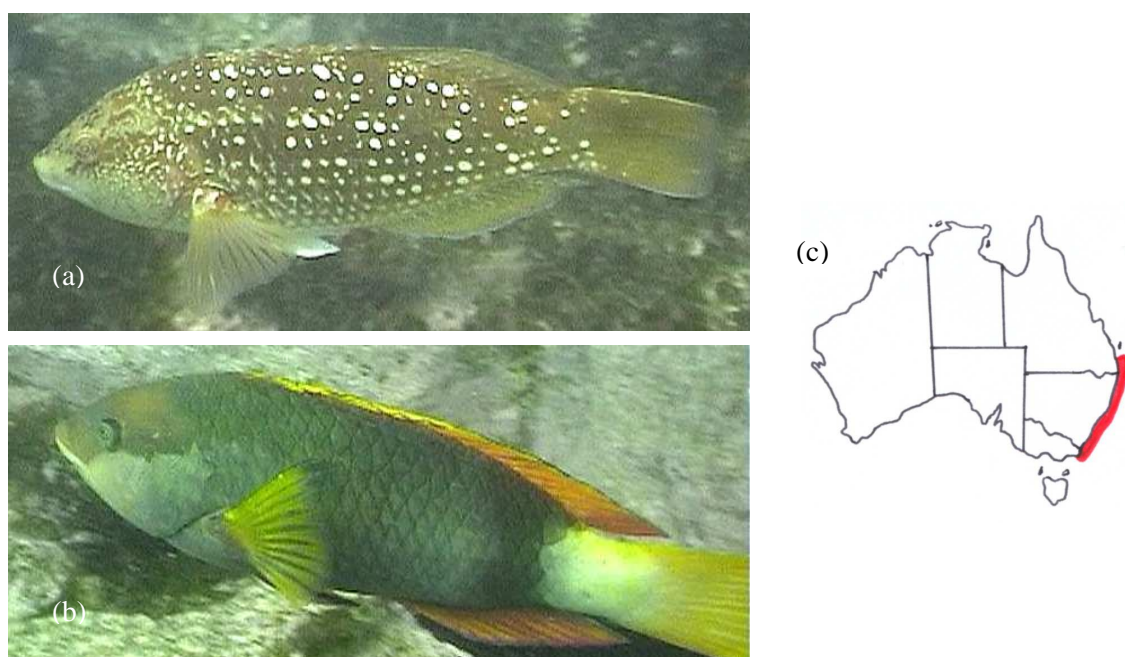


Figure 1.2: Morphology and distribution of *Notolabrus gymnogenis*. Shown are a 230 mm initial phase female (a) and a 320 mm terminal phase male (b). The distribution of *N. gymnogenis* is highlighted in red (c).

N. gymnogenis are found in high abundances from southern Queensland to Mallacoota (Victoria) (Figure 1.2c) on coastal rocky reefs in depths of 2 m to at least 40 m (Kuiter 1996). Juveniles are cryptic favouring reefs with high algal coverage, whilst IP and TP individuals are highly visual. Individual males and loose aggregations of females are distributed over most available hard substrate (Kuiter 1996; Curley *et al.* 2002).

1.6.3 Senator wrasse (*Pictilabrus laticlavius*) – [Richardson 1839]

Juvenile and IP *Pictilabrus laticlavius* are dull green to brown providing excellent cryptic colouration in their preferred algal habitat (Figure 1.3a). Juveniles also possess numerous small dots on the dorsal surface and a distinct black dot at the base of the dorsal fin (Kuiter 1996). *P. laticlavius* are sexually dichromatic with TP individuals lime green with 2 lateral, purple stripes extending from the opercula and merging into a single stripe through the caudal peduncle. An additional broad, perpendicular stripe extends from the lower stripe to the anal fin (Figure 1.3b).

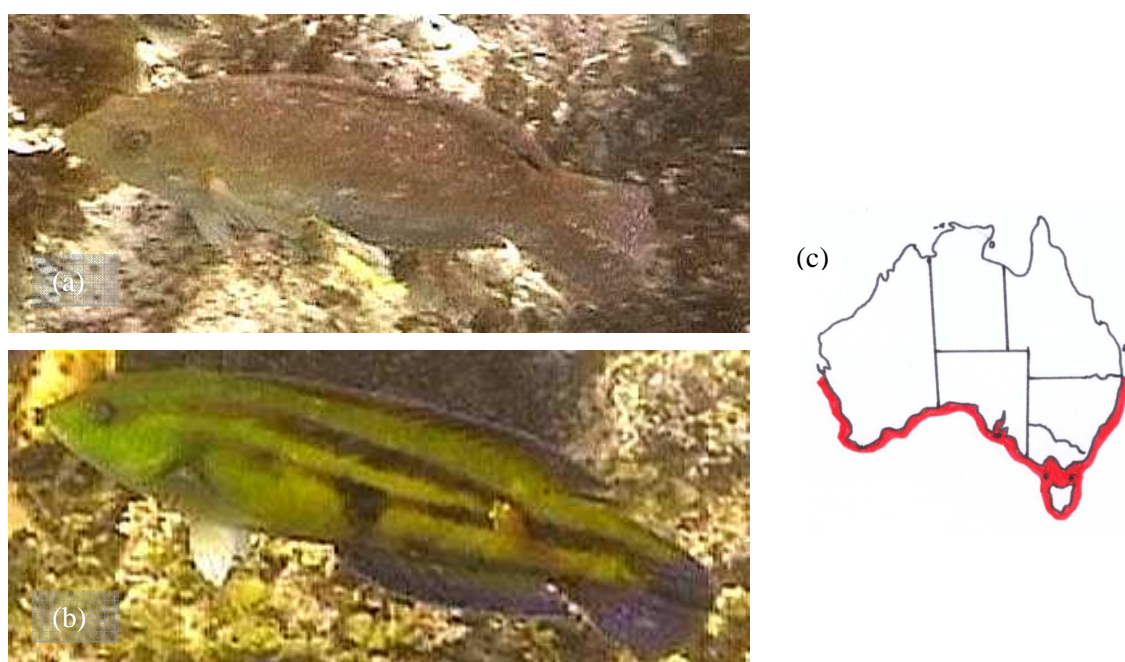


Figure 1.3: Morphology and distribution of *Pictilabrus laticlavius*. Shown are a 100 mm initial phase female (a) and a 190 mm terminal phase male (b). The distribution of *P. laticlavius* is highlighted in red (c).

P. laticlavius are widespread throughout temperate Australia with a distribution ranging from Byron Bay (NSW), throughout southern Australia, to the Houtman Abrolhos (Western Australia) in algal habitat from depths of 2 to 30 m (Kuiter 1996) (Figure 1.3c). Individuals typically do not exceed 250 mm TL (Kuiter 1996).

Chapter 2:

Study Region and General Methods

2.1 Study region

All data were collected between August 2003 and October 2006 from locations situated on the central coast of NSW, Australia, which is located within the Hawkesbury Shelf bioregion (Figure 2.1a). This bioregion extends approximately 210 km from Shellharbour (34°35' S, 150°53' E) to Stockton (32°54' S, 151°48' E) and is characterised as having a warm, temperate climate with warm to hot summers and no significant seasonal pattern of rainfall (IMCRA Technical Group 1998). Coastal oceanographic circulation is primarily influenced by the East Australian Current (EAC) flowing south from the tropics in summer, and cool water moving north from Bass Strait in winter (IMCRA Technical Group 1998; CSIRO 2000; NSW Fisheries 2001). Marine fauna is distinct with unique assemblages of reef fishes, asteroids, echinoderms, gastropods and bivalves (IMCRA Technical Group 1998).

2.2 Locations used for surveys of labrid assemblages

Labrid assemblages were investigated between August 2003 and May 2005 at two locations (Terrigal and Norah Head), which are separated by approximately 30 km (Figure 2.1a). These locations were selected based on their representation of fringe, urchin-grazed barrens and sponge garden habitat (see Table 3.1 for habitat descriptions) in a concentrated area. Locations representing all three habitats are locally rare as most local coastal rocky reefs are bordered by sand flats shallower than most sponge garden habitat (i.e. less than 15 m). Other locations containing sponge garden habitat are found on the central coast of NSW but these are either influenced by estuary outflow, fail to contain sufficient habitat area for adequate sampling, do not provide representative areas of all three habitat types and/or have access constraints.

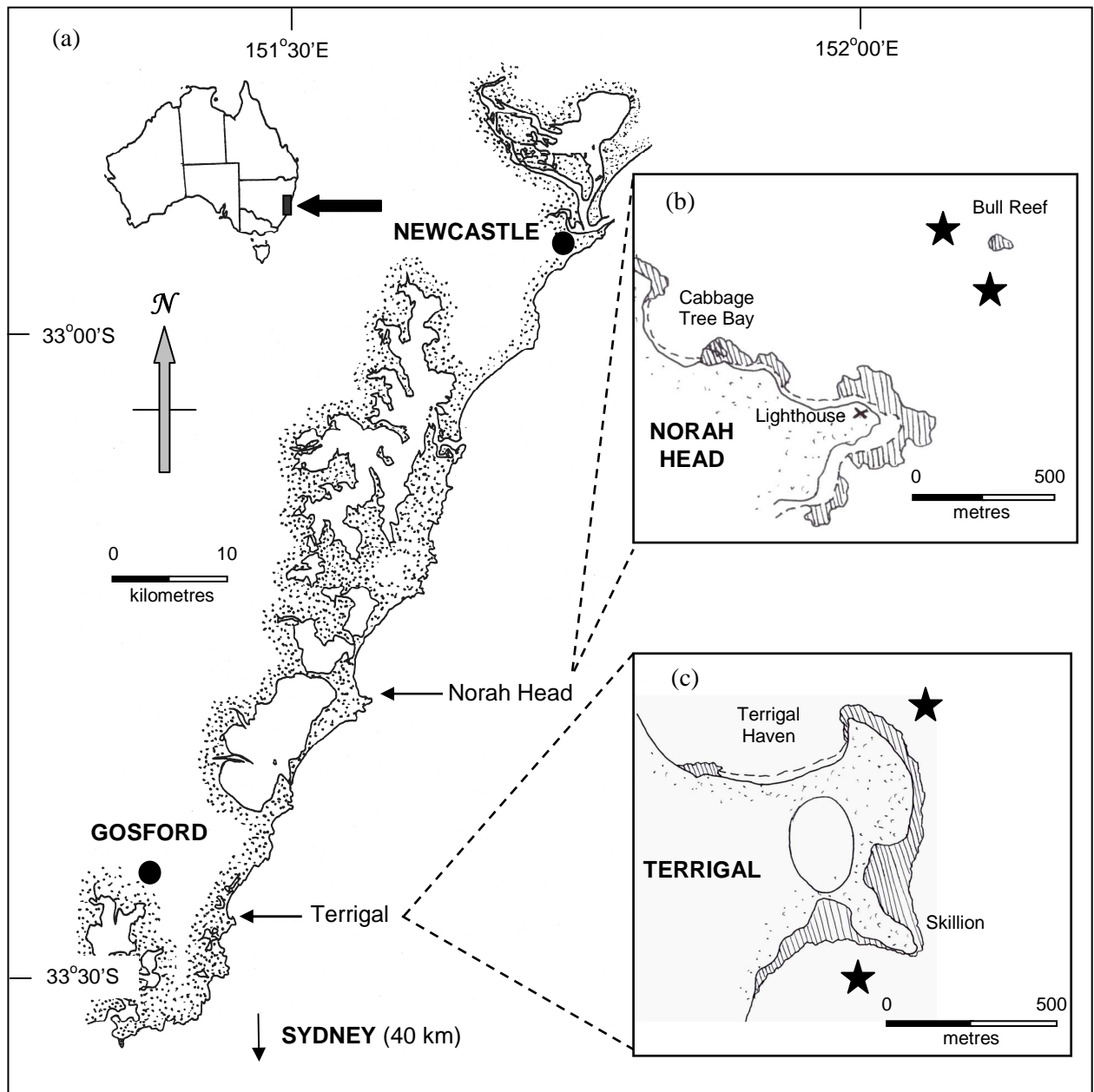


Figure 2.1: Map of the central coast region of New South Wales (Australia) showing the two locations used for sampling fish assemblages (a). The position of the two sites within each location is indicated by stars on the expanded location maps of Norah Head (b) and Terrigal (c). Each star is representative of the general area used to sample subtidal fringe, barrens and sponge garden habitat. Exposed reef is shown in cross-hatched shading.

Terrigal (33°27' S, 151°27' E) is represented by a cliff headland ('The Skillion') with an extensive intertidal rock platform at its base. These rocky platforms end abruptly at the littoral fringe with the subtidal reef stepping rapidly through fringe, barrens and sponge garden habitat at depths of 5-7, 8-15 and 15-21 m, respectively. The two sites selected

at Terrigal are located on the southern and the northern aspects of this headland. These survey sites were typically accessed from the adjacent rock platform, but boat access was available from Terrigal Haven when sea conditions were unfavourable for shore dives.

Bull Reef (33°17' S, 151°35' E) is an offshore rock pinnacle that is situated approximately 300 m north-east of the Norah Head lighthouse (Figure 2.1b). This reef is accessible only by boat, with a launching ramp available at Cabbage Tree Bay. The apex of the Bull Reef pinnacle is exposed at mid and low tides with a broad expanse of shallow (i.e. 5-7 m) fringe habitat, interspersed with large patches of *Ecklonia radiata*, extending toward the Norah Head lighthouse. On the north-western and south-eastern sides of this fringe habitat the barrens habitat starts in depths of 8 m and ends abruptly at sand interfaces in depths of approximately 15 m. Sponge garden habitat is located mostly on the northern side of Bull Reef in depths of 15 to 22 m. The two sites selected at the Bull Reef location roughly represent the western and the eastern side of this subtidal reef.

Details of the survey design, field techniques and data analyses relating to the surveys of fish assemblages are provided in Chapter 3.

2.3 Locations used for the investigation of labrid behaviour

Behavioural observations of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* were conducted at Catherine Hill Bay and Norah Head between August 2003 and January 2005 (Figure 2.2). Study locations were chosen for their high abundance of all three labrid species, protection from coastal swells, minimal constraints on accessibility and good representation of rocky reef habitat in depths of 3-9 m.

Catherine Hill Bay (33°10' S, 151°38' E) is a large, east-facing coastal embayment located approximately 85 km north of Sydney. The study site at Catherine Hill Bay is located at the southern end of this embayment and lies beneath, and to the south of, a jetty used until 2002 for loading coal from the Wallarah Colliery onto ships for transport to the Port of Newcastle (Figure 2.2b). Public access onto the 'Coal Loader'

structure is prohibited. All behavioural observations were made in rocky habitat found toward the seaward end of the Coal Loader in depths of 6-9 m. The rocky reef in the study area consists of barrens habitat in the form of rock piles and slabs, interspersed with steel refuse (e.g. ladders, chains, pipes etc.), and patches of kelp (*Ecklonia radiata*) and mixed species of algae. This 'mixed' habitat continues into shallow waters which extend from the beach and rocky shelf at the southern end of Catherine Hill Bay. Extensive sand flats are found on the north-western side of the Coal Loader and continue throughout the embayment of Catherine Hill Bay.

Norah Head (33°17' S, 151°34' E) is located approximately 75 km north of Sydney and consists of a large rocky headland with extensive rocky platforms and sandy beaches. The study site at Norah Head is located on the southern reef of Cabbage Tree Bay (Figure 2.2c). The seaward edge of this reef consists of a rock wall extending approximately 300 m in an easterly direction from Cabbage Tree Bay boat ramp. The base of this rock wall varies from depths of 3 m in the west to 9 m in the east. Shoreward of the rock wall is an extensive subtidal reef in depths of 2-4 m. The rocky reef at the Norah Head study site consists of urchin-grazed barrens, *Ecklonia radiata* forest and fringe habitat, and patches of mixed species of algae. Sand flats border the southern reef at Cabbage Tree Bay but vast areas of relatively shallow (i.e. <10 m) subtidal reef extend to the north of Norah Head.

Details of the study design, methods used in field observations, data collation and data analyses are provided in Chapter 4. The methods outlined in Chapter 4 for collecting and analysing behavioural data were also used for quantifying bite rate and use of feeding microhabitats (Chapter 5), and describing courting and spawning behaviour (Chapter 6).

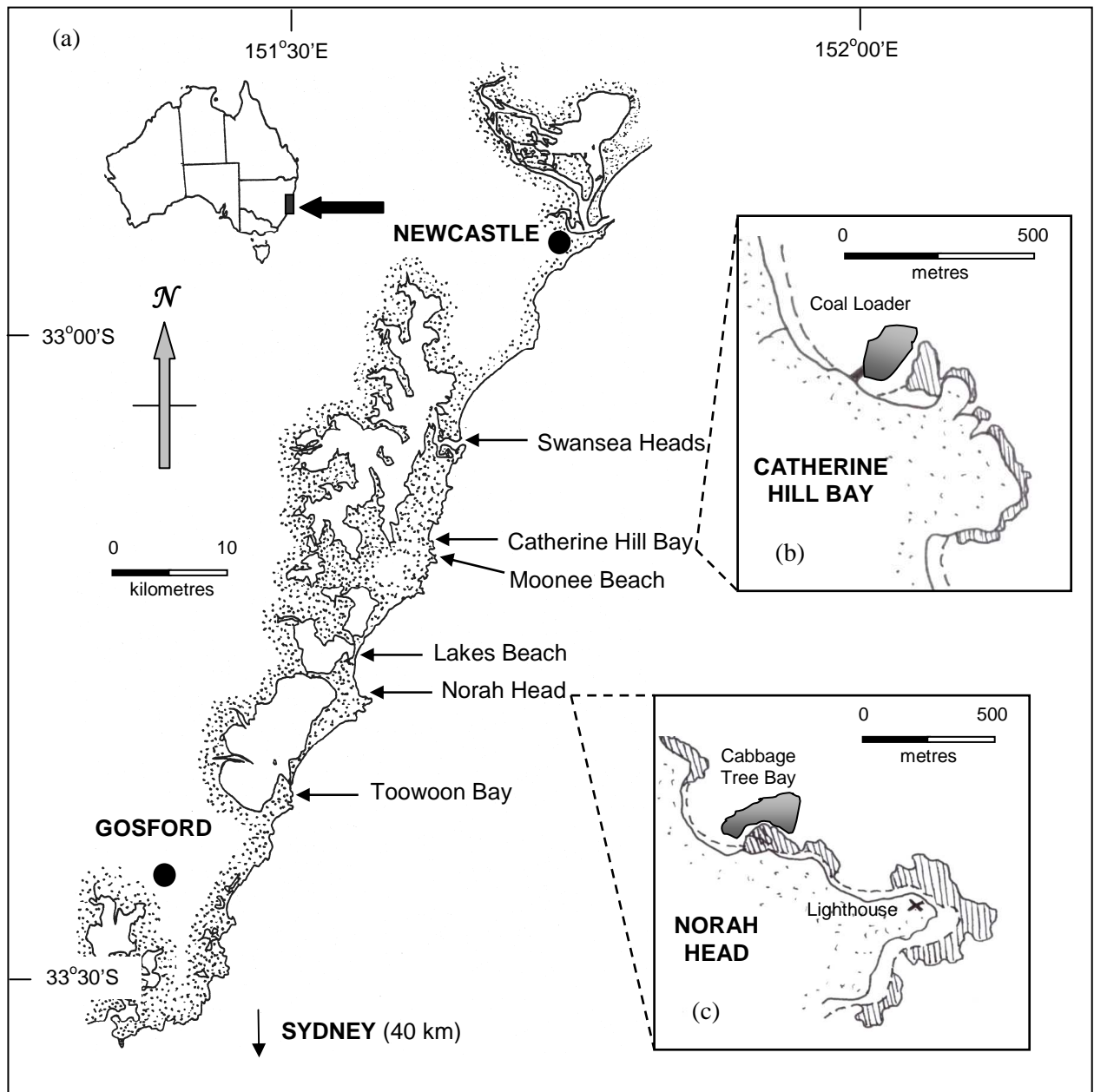


Figure 2.2: Map of the central coast region of New South Wales, Australia (a) showing the locations used for collecting fish specimens and behavioural data for *Ophthalamolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. Locations where individuals were obtained by spear are indicated by arrows. The position of the two areas where behavioural observations occurred within each location is shaded on the expanded location maps of Catherine Hill Bay (b) and Norah Head (c). Spearfishing of individuals did not occur within the shaded areas. Exposed reef is shown in cross-hatched shading.

2.4 Pilot study

Sampling strategies for documenting labrid behaviour include continuous recording of behaviours over a defined period of time (e.g. Jones and Thompson 1980; Jones 1981, 1983; Hoffman 1983; Sakai *et al.* 2001; Shepherd and Clarkson 2001; Bansemer *et al.* 2002; Fulton and Bellwood 2002b), over a non-defined period of time (e.g. Tribble 1982), or at 10 or 15 seconds intervals within a defined time period (e.g. Gillanders 1995a; Martha and Jones 2002).

The duration of time periods used to investigate labrid behaviour include 3 minutes (Hoffman 1983), 5 minutes (Hoffman 1983; Gillanders 1995b; Fulton and Bellwood 2002b), 10 minutes (Martha and Jones 2002; Shepherd and Brook 2005), 15 minutes (Jones and Thompson 1980; Jones 1981, 1983; Hoffman 1983; Shepherd and Clarkson 2001), 20 minutes (Sakai *et al.* 2001), 30 minutes (Jones and Thompson 1980; Jones 1981), 40 minutes (Moyer and Yogo 1982; Bansemer *et al.* 2002) and 60 minutes (Barrett 1995b). With few exceptions (e.g. Gillanders 1995b), most studies of fish behaviour proceed with trusting acceptance of traditional sampling methods without questioning issues of sampling efficiency and imprecision. However, the time period of choice for sampling fish behaviour is potentially influenced by factors such as the species of interest, the life history stage of an individual, the sampling location and the behaviour of choice. Therefore, preliminary sampling is required for optimising sampling effort to avoid wasted effort, failure to capture the full range of behaviours and/or high imprecision (Andrew and Mapstone 1987).

Lengthy time periods allow greater understanding of a single individual's behaviour over a longer period, but places constraints on replication. Conversely, shorter time periods allow larger sample sizes and sufficient power for statistical tests, but may inadequately represent the behaviour of the focal subject. A trade-off of cost-benefit therefore ensues. For this study, the period of time for observations of single individuals provided such a trade-off situation. Therefore, prior to the implementation of a sampling strategy for use in the major study (Chapters 4 and 5), a pilot study was undertaken for the purpose of determining the optimal sampling strategy for quantifying components of labrid behaviour.

The pilot study aimed to address two questions. Firstly, do behaviour rates and/or proportion of time engaged in behaviours differ for individuals followed for time periods of 10, 20 and 30 mins? Secondly, are conclusions consistent across species, life history stages and locations? At this stage of the research investigation *Pictilabrus laticlavius* was not a species of consideration for the major study so the pilot study was performed only for *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis*. For both species, three randomly selected individuals of each of three life history stages (i.e. juvenile, initial phase and terminal phase) were followed for separate periods of 10, 20 and 30 mins at Catherine Hill Bay and Norah Head (Table 2.1). All data were recorded from August to December 2003 between 0700 and 1130 hr at depths ranging from 4 to 9 m. Behavioural observations for the pilot study totalled 36 hours. Detailed descriptions of the methods involved with field observations and data collation are provided in Chapter 4.

A four-factor mixed model analysis of variance (ANOVA) using GMAV5 software (Institute of Marine Ecology: University of Sydney) was used to test for differences in the occurrence of behaviours in 10, 20 and 30 min observation times, and to determine whether differences, if any, were consistent for all life history stages of each species at two locations (Table 2.1). Behaviours chosen for analysis were area usage; total encounters with other fishes, dominant and subordinate interactions; percentage of time lying and within shelter; and episodes of side-swiping, bending, gaping and biting. All behaviours, excluding biting, are described in Chapter 4. Assumptions of homogeneity of variance were tested using Cochran's C test. Data were transformed when variances were heterogeneous (Underwood 1981).

Table 2.1: Four-factor mixed ANOVA model used to test for differences in the occurrence of behaviours in 10, 20 and 30 min observation times, and to determine whether differences, if any, are consistent for all life history stages of *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis* at two locations.

Factor	No. of Levels	Fixed (F) or Random (R)	Levels
Observation time	3	F	10 min, 20 min, 30 min
Species	2	F	<i>Ophthalmolepis lineolatus</i> , <i>Notolabrus gymnogenis</i>
Life stage	3	F	Juvenile, Initial phase, Terminal phase
Location	2	R	Catherine Hill Bay, Norah Head
(Replicates = 3)			
(Total observational units = 108)			

The pilot study revealed that all behaviours observed in 20 and 30 min periods were also observed in 10 min periods, and that area use, behaviour rates and/or proportion of time engaged in a behaviour did not differ among individuals followed for 10, 20 and 30 min time periods (see Appendix 1). These conclusions were consistent for each life history stage of each species at both Catherine Hill Bay and Norah Head. Therefore, it was concluded that the use of 10 min time periods for the following of focal individuals in the major study was most favourable as greater replication could be achieved.

2.5 Specimen collection

Up to 20 individuals of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* were collected monthly in 2005 from several locations on the central coast of NSW (Figure 2.2a). Further samples were also obtained opportunistically in 2003, 2004 and 2006. Most individuals were captured using hand-held spear or spear gun on snorkel-and-mask (Table 2.2). Additional specimens were provided by recreational anglers and commercial trap fishers. Whenever possible, specimens were collected to encompass the available size range of each species. Specimen collection occurred with permission from the University of Newcastle's Animal Care and Ethics Committee and the NSW Department of Primary Industries. Fish total length (TL) range and total fish numbers were: *O. lineolatus* (94-374 mm, n=225), *N. gymnogenis* (76-358 mm, n=195), and *P. laticlavius* (70-216 mm, n=93). Fewer *P. laticlavius* were obtained as this species is highly cryptic (i.e. remaining hidden within algal or rock shelter for extended periods of time), and specimens were not provided by recreational and commercial fishers.

The colour phase (i.e. initial phase or terminal phase), total length (± 1 mm) and weight (± 0.01 g) of each individual was recorded before the intestine, gonads and otoliths were extracted. Intestines were used for dietary analyses (Chapter 5), gonads were used to sex individuals and determine life history parameters (i.e. size at maturity and sex change, and reproductive season) (Chapter 6), and otoliths were used to determine the age of individuals (Chapter 6). Spearing of individuals occasionally caused significant damage to intestines, gonads and/or otoliths rendering these samples unusable. In such cases, the sample was omitted from the data set.

Details of sample preparation, data collection and data analyses are provided in Chapter 5 (for intestines) and Chapter 6 (for gonads and otoliths).

Table 2.2: Sample sizes, size ranges, collection method and collection locations for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* used for extraction of intestines, gonads and otoliths, and measurements of fish weight and total length. Total number of specimens for each species is provided in parenthesis.

Species	Sample size	Size range (mm TL)	Collection method	Locations
<i>Ophthalmolepis lineolatus</i> (n=225)	135	94 – 346	Spear	Norah Head, Catherine Hill Bay, Lakes Beach
	49	218 – 359	Line	Norah Head, Birdie Island
	41	316 – 374	Trap	Offshore (various)
<i>Notolabrus gymnogenis</i> (n=195)	176	76 – 354	Spear	Norah Head, Catherine Hill Bay, Lakes Beach, Moonee Beach, Toowoona Bay, Swansea Heads
	14	219 – 345	Line	Norah Head, Birdie Island
	5	282 – 358	Trap	Offshore (various)
<i>Pictilabrus laticlavus</i> (n=93)	93	70 – 216	Spear	Norah Head, Catherine Hill Bay, Toowoona Bay,

Chapter 3:

**Habitat-related Variation
in Labrid Assemblages**

3.1 Introduction

3.1.1 Problem statement and chapter aim

Before attempting to more fully understand the functional ecology of labrids on temperate rocky reefs, it is important to first determine whether these fishes are well represented on these reefs and to describe patterns in their distribution and abundance. Whilst general habitat associations are documented for some species of labrid (e.g. Gillanders and Kingsford 1998; Shepherd and Brook 2003), few studies have investigated the relationship between habitats and entire labrid assemblages including spatial, temporal and ontogenetic influences on these patterns. Therefore, the aim of this chapter is to determine the role of habitat as a source of variation in the distribution and composition of labrid assemblages. The effect of habitat is also explored for spatial, temporal and ontogenetic consistency. Another area of study which is lacking is the relationship between patterns of labrid distribution and the social organisation, behaviour, diet and life history of these fishes. So, findings from this chapter are used to complement data obtained in later chapters outlining the social organisation and behaviour (Chapter 4), feeding (Chapter 5), and reproductive life history (Chapter 6) of these fishes.

3.1.2 Patterns in assemblage structure

The description of spatial and temporal patterns in assemblages, and determination of the scales at which greatest variation exists, is an essential part of defining important ecological processes governing assemblage structure. Significant advances have been made in describing patterns of heterogeneity in temperate intertidal (Underwood and Chapman 1998a, b) and subtidal benthic assemblages (Choat and Schiel 1982; Underwood *et al.* 1991; O'Hara 2001; Schiel and Hickford 2001), but there has been limited progress in addressing assemblage patterns in highly mobile taxa such as fishes. Several studies have focused on fish assemblages in tropical systems (Williams 1986; Fowler 1990; Letourneur 1996a; Connell and Kingsford 1998; Ferreira *et al.* 2001), but most research on spatial and/or temporal variability of temperate rocky reef fishes is restricted to single species (e.g. Jones 1984a, b; Gillanders 1997a, b; Gillanders and Kingsford 1998; Shepherd *et al.* 2002; Shepherd and Brook 2003) or temperate assemblages in regions outside Australia (Choat and Ayling 1987; Holbrook *et al.* 1994;

Magill and Sayer 2002; Pihl and Wennhage 2002; Anderson and Millar 2004). This represents a significant gap in the understanding of fish assemblage dynamics on temperate rocky shores of eastern Australia and limits the capability to detect anthropogenic impacts, to develop appropriate management strategies and to understand the current status of fish species in the region.

3.1.3 Spatial variation in fish assemblages

Tropical and temperate reef fish assemblages exhibit considerable variability at a range of spatial scales. Differences in fish assemblages exist across latitudinal gradients (Floeter *et al.* 2001), across the continental shelf in the Great Barrier Reef (Williams 1986; Bellwood and Wainwright 2001), between mainland coasts and offshore islands (Meekan and Choat 1997; Floeter *et al.* 2001; Denny 2005), among locations separated by hundreds of kilometres (Anderson and Millar 2004) and between sites separated by several kilometres (Fowler 1990; Meekan and Choat 1997; Anderson and Millar 2004). However, the greatest variation often occurs at smaller scales. For example, Curley *et al.* (2002) found variation in the abundances of numerically dominant fishes on rocky reefs of NSW was higher at scales of metres (i.e. among transects) to hundreds of metres (i.e. between sites) than among locations separated by several kilometres. Similarly, reef fish assemblages in north-eastern New Zealand demonstrate greatest variability among replicate transects (separated by tens of metres) rather than among sites (separated by hundreds of metres) or locations (separated by hundreds of kilometres) (Anderson and Millar 2004).

Spatial variation in the representation of habitats contributes to spatial variation in fish assemblages. Habitats may be defined using physical or biological attributes, or a combination of both. Significant advances have been made on subtidal rocky shores describing relationships between benthic assemblages and habitat structure (Choat and Schiel 1982; Underwood *et al.* 1991; O'Hara 2001, Schiel and Hickford 2001) owing partly to the fact that benthic assemblages themselves may structure the habitat so therefore have a strong association with a particular habitat type (e.g. echinoids and barrens habitat: Andrew and Constable 1999). For more mobile assemblages, such as fishes, further work is needed in describing habitat-related patterns of distribution. Advances have been made in identifying relationships between the structure of fish

assemblages and substrate type (Harman *et al.* 2003), depth (Rooker *et al.* 1997; Lowry and Cappo 1999; Ferreira *et al.* 2001; Fulton *et al.* 2001; Bean *et al.* 2002; Fulton and Bellwood 2004; Denny 2005) and wave exposure (Bellwood and Wainwright 2001; Fulton *et al.* 2001; Bellwood *et al.* 2002; Shepherd and Brook 2003; Fulton and Bellwood 2004), but more information is needed on patterns of distribution before fish assemblages are fully understood.

In temperate systems of New Zealand and south-eastern Australia, trends in fish occurrence and abundance strongly coincide with habitats that have been identified using a combination of both dominant benthic assemblages (e.g. alga type and cover) and physical attributes of the reef (e.g. depth and exposure) (Gillanders and Kingsford 1998; Curley *et al.* 2002; Anderson and Millar 2004). However, there is currently an insufficient understanding of the processes underlying the observed patterns in fish distribution and abundance, the long-term temporal consistency in habitat-related patterns, and ontogenetic variation in habitat associations.

3.1.4 Labrid dominance in fish assemblages

Where hard substrata is available, labrids are a dominant component of tropical (Green 1996; Letourneur 1996a; Rooker *et al.* 1997; Mejia and Garzon-Ferreira 2000; Bellwood *et al.* 2002; Floeter *et al.* 2001) and temperate fish assemblages (Treasurer 1994; Garcia-Charton and Perez-Ruzafa 1999; Parker 1999; Ruitton *et al.* 2000; Magill and Sayer 2002; Pihl and Wennhage 2002) in terms of their species richness and abundance. The high contribution of labrids to total fish species is maintained across broad longitudinal and latitudinal gradients. For example, Bellwood and Hughes (2001) found approximately 12-38% of all coral reef fish species were labrids in sites across the Indian and Pacific Oceans. In sites with greater than 100 species, labrid contribution was constrained to approximately 13-28% of all fish species. Labrid assemblages in temperate regions have reduced species richness compared with tropical systems (Floeter *et al.* 2001), but it is not known whether this reduction is reflected in a reduced contribution of labrids to the entire fish assemblage.

3.1.5 Habitat associations in labrid assemblages

In temperate systems, labrids appear to be almost exclusively associated with rocky reefs and/or algal habitats (Treasurer 1994; Garcia-Rubies and Macpherson 1995; Pihl and Wennhage 2002) which potentially limits emigration between adjacent reefs that are separated by expanses of sandy sediment (Warner 1982; Barrett 1995b). Many species exhibit habitat-specific associations with kelp-forests, urchin-grazed barrens, deep sponge gardens and sandy areas adjacent to rocky reefs (Jones 1999). For example, Curley *et al.* (2002) found *Pictilabrus laticlavius* to be most abundant in *Ecklonia* forest compared to other rocky reef habitats in NSW, and *Ophthalamolepis lineolatus* and *Coris picta* most abundant in deep barrens and sponge habitat. Likewise, higher abundances of *Bodianus unimaculatus* and *Pseudolabrus miles* occur in kelp-forests compared to other rocky reef habitats in north-eastern New Zealand, and higher abundances of *Notolabrus celidotus*, *Notolabrus fucicola* and *Coris sandageri* are found in urchin-grazed barrens (Anderson and Millar 2004). Other labrids are known to be less restricted in habitat use. For example, *Achoerodus viridis* and *Notolabrus gymnogenis* occur in *Ecklonia* forests, urchin-grazed barrens and sponge habitat in similar abundances (Curley *et al.* 2002).

For many temperate labrids, significant size-related patterns of abundance occur across habitats that are reflective of ontogenetic shifts in habitat requirements. Whilst some labrids recruit directly into adult populations, many species exhibit post-recruitment migrations to adult habitat. For example, the typical juvenile habitats of *Achoerodus goudii* (Shepherd *et al.* 2002; Shepherd and Brook 2003) and *Achoerodus viridis* (Gillanders 1997a; Gillanders and Kingsford 1998; Gillanders 1999) are moderately sheltered, shallow (1-3 m) seagrass or kelp beds, whilst adult populations are associated with deeper (>5 m), exposed rocky reefs. The preferential use of shallow fringe and/or *Ecklonia* forest habitat by juveniles is well documented for other labrids on temperate rocky shores of south-eastern Australia (Curley *et al.* 2002) and New Zealand (Jones 1984a; Choat and Ayling 1987), but there is a substantial gap in the current understanding of spatial and temporal influences on these habitat associations.

As labrids exhibit associations with rocky reef habitats and demonstrate ontogenetic shifts in habitat use, it is evident that rocky reefs and the habitats they represent offer

ecological needs for these fishes which are not homogeneously available in subtidal systems. For example, the association of juvenile labrids with shallow algal habitats may be in response to the availability of manageable prey items, notably amphipods and small molluscs, which are abundant in this habitat (Jones 1999; Edgar 2001; Shepherd and Clarkson 2001). Habitat associations may also reflect refuge availability as bouts of diurnal activity are frequently interspersed with the seeking of shelter in many labrids. Refuge requirements of labrids have not been well addressed but these fishes are known to shelter beneath algal canopies, in rock crevices and within holes between or under rocks (Sayer *et al.* 1993; Barrett 1995b; Gillanders and Kingsford 1998; Shepherd and Clarkson 2001; Shepherd and Brook 2005). Furthermore, many diurnally active reef fishes, including labrids, require sleeping crevices to avoid nocturnal predation and/or avoid displacement caused by wave surge so may be restricted to habitats offering these nocturnal refuges.

Food and shelter requirements of labrids are explored more fully in Chapter 6 and Chapter 4, respectively, as are other processes likely to be important for describing patterns of labrid distribution and abundance (e.g. social organisation, resource partitioning etc.).

3.1.6 Temporal variation in labrid assemblages

Attempts to describe habitat-related patterns in the distribution and abundance of fish assemblages should be complemented with knowledge of how these patterns change over time. Yet, temporal influences on fish assemblages are not always explored. Temporal variability in fish assemblages occurs over scales of hours, days, seasons and years (Holbrook *et al.* 1994; Letourneur 1996b; Thompson and Mapstone 2002). Mechanisms driving variability include tidal cycles, lunar cycles, oceanographic events, ontogenetic habitat shifts, prey availability, competition, predation, migration and reproduction (Holbrook *et al.* 1994; Kingsford 1998b). Observed temporal changes in fish assemblages may be significant in temperate systems, but spatial variability is typically far greater (Jones 1984a, b; Choat *et al.* 1988; Barrett 1999; Anderson and Millar 2004).

Reef fish assemblages do not appear to exhibit large temporal variability in species richness; however substantial fluctuations in abundances of individual species do occur. Contributing to temporal fluctuations in abundance is periodic recruitment of juveniles (Holbrook *et al.* 1994; Letourneur 1996b; Rooker *et al.* 1997; Sponaugle and Cowen 1997; Green 1998). Most reef fishes, including labrids, possess a bipartite life cycle involving a dispersive, planktonic larval stage which may last for up to 50 days (Caselle and Warner 1996; Masterson *et al.* 1997; Jones 1999). Recruitment of juvenile labrids is typically associated with periods of warmest sea temperatures (i.e. summer and autumn) (Sayer *et al.* 1993; Garcia-Rubies and Macpherson 1995; Edgar and Barrett 1997; Masterson *et al.* 1997; Jones 1999; Magill and Sayer 2002; Pihl and Wennhage 2002). In temperate waters of eastern Australia, many of these recruits (e.g. *Thalassoma lunare*, *Halichoeres nebulosus* and *Stethojulis interrupta*) are of tropical origin having been transported to higher latitudes from tropical spawning sites by the East Australian Current (Holbrook *et al.* 1994; Parker 1999). Settlement of these ‘tropical’ fishes may contribute up to 20% to the species richness of fishes on temperate reefs. Juveniles of tropical origin generally do not survive into winter in response to cooling water temperatures (Holbrook *et al.* 1994).

Temporal patterns of recruitment for ‘local’ labrid species that are permanently associated with rocky reefs of temperate eastern Australia are largely unknown. An exception is *Achoerodus viridis* in which recruitment peaks in September to October after a reproductive season lasting from July to September (Gillanders 1995a; Gillanders 1997b). Labrids found on Tasmanian rocky reefs are known to have reproductive seasons extending from August to January (Barrett 1995a), but the timing and magnitude of recruitment in these and other labrids of south-eastern Australia is largely undetermined. It is likely that recruitment events coincide with the settlement of large numbers of small crustaceans which contribute substantially to the diet of juvenile labrids (Gillanders 1995b; Shepherd 1998, 2006; Jones 1999; Denny and Schiel 2001).

3.1.7 Overview and chapter objectives

Little is known about the structure, if any, of labrid assemblages in temperate waters of Australia and the role of habitat in contributing to this structure. Habitat associations are documented for selected labrid species, but these associations are often not explored

for spatial, temporal and ontogenetic consistency despite the likely significance of these factors in influencing patterns of distribution and abundance. The role of habitat in structuring labrid assemblages is explored in this chapter by determining habitat-related variation in labrid species richness and the contribution of labrids to total fish species, labrid density and the contribution of labrids to total fish density, species composition of labrid assemblages, and the density and size distributions of ‘common’ labrids (i.e. *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis*, *Achoerodus viridis*, *Pictilabrus laticlavius*, *Austrolabrus maculatus* and *Eupetrichthys angustipes*). Habitat-related patterns, if any, are also explored for spatial and temporal consistency.

3.2 Methods

3.2.1 Study area and locations

Surveys of fish assemblages were undertaken between August 2003 and May 2005 at Terrigal and Norah Head on the central coast of NSW. A detailed description of the study area and each location is provided in Chapter 2.

3.2.2 Survey design

Fish assemblages were surveyed using a mixed model hierarchical sampling design. Within each location, two sites separated by 250-800 m were sampled (Figure 2.1). At each site, three distinct habitats were surveyed (Table 3.1). Within each of these habitats, fish assemblages were recorded within each of six replicate transects. Surveys were conducted on 5 occasions, separated by approximately 4 months, over a 22 month period.

3.2.3 Field surveys

Visual surveys of fish assemblages were completed by a single observer (the author) to ensure recording techniques were consistent, using SCUBA, between 1000 and 1600 hr when visibility exceeded 8 m. After a desired habitat was located, a fibreglass tape was weighted to the substrate in preparation for the first transect. Whilst following a depth contour, the observer recorded all mobile non-cryptic fishes and their abundances in a 5 m wide band over a distance of 25 m (total area of 125 m²). For labrids, all individuals were placed into 50 mm total length (TL) size classes (i.e. 50-99, 100-149, 150-199 mm etc.) and colour phase (i.e. initial phase or terminal phase) was recorded for dichromatic species. All data was recorded *in situ* on survey sheets copied onto underwater paper. A dive buddy was used to deploy a fibreglass tape behind the observer and to alert the observer at the completion of each transect by pulling the observer's fin.

Table 3.1: Descriptions of fringe, barrens and sponge garden habitat used for conducting fish surveys. Descriptions are adapted from Underwood *et al.* 1991 and Andrew 1999.



Fringe:

Relatively shallow habitat (3-7 m) consisting of several patchy, non-dominant algal species including crustose coralline algae, filamentous algae and a high representation (>50% coverage) of turfing algae, particularly articulated *Amphiroa* and *Sargassum* spp. Patches of canopy-forming, laminarian algae *Ecklonia radiata* were scattered throughout the fringe habitat at all sites. Invertebrate herbivores are few, but turbinid gastropods are common.



Barrens:

Medium depth habitat (8-15 m) with minimal algal coverage due to high densities of the herbivorous echinoid *Centrostephanus rodgersii*. Coverage of crustose coralline algae may be very high (>70%), whilst filamentous algal coverage is generally less than 20% and turfing algae are absent. Well represented gastropods include *Patelloida alticostata*, *Cellana tramoserica* and *Astrarium tentoriformis*.



Sponge garden:

Sponge garden habitat (15-22 m) consists of distinct assemblages of erect and branched sessile fauna including large sponges, gorgonians and bryozoans not found in shallower depths. Densities of phaeophyte algae are particularly reduced as are abundances of invertebrate grazers. Sponge garden habitat is termed 'deep reef' by Underwood *et al.* (1991).

The laying of tape whilst performing the fish census, termed the 'simultaneous' census technique (Fowler 1987), was desirable as many fishes, especially pelagic fishes, would otherwise retreat from the presence of divers resulting in reduced richness and abundance estimates. Furthermore, inquisitive fishes such as *Ophthalmolepis lineolatus* are attracted to divers from beyond the transect boundary so may result in abundance overestimations when tape deployment and fish census occur using a 'sequential' technique.

At the completion of each 25 m transect, the tape was secured in preparation for the following replicate. A total of six replicate transects were laid out end-to-end along a depth contour and spaced a minimum of 5 m apart. At the completion of six 5 x 25 m transects, the recorder returned along the tapes identifying and counting cryptic fishes in a 1 m wide strip (i.e. 1 x 25 m, total area of 25 m²) to one side of the tape measure as the dive buddy wound in successive tapes. Cryptic fishes identified within the 1 m wide strip included juvenile and cryptic labrids (<100 mm), juvenile pomacentrids, juvenile monacanthids, gobiesocids, serranids, apogonids, and all individuals of the species *Lotella rhacina* and *Scorpaena cardinalis*. Abundances of cryptic fishes were multiplied by five to standardise the sampling area. The use of two census techniques for sampling different fish groups was important for maximising survey precision (Lincoln Smith 1988, 1989; De Girolamo and Mazzoldi 2001; Willis 2001).

3.2.4 Data analyses

3.2.4.1 Species accumulation curves

EstimateS 7 (Colwell 2005) was used to construct species accumulation curves for labrids to determine sampling adequacy. This procedure randomly selects samples without replacement, based on 400 randomisations of sample order, and computes richness estimators from pooled data until all samples have been selected (Colwell 2005). At both locations, species accumulation curves were constructed for each habitat using transect data obtained from both sites (i.e. a total of 12 transects) across 5 study periods (i.e. n=60 samples).

3.2.4.2 Univariate analyses

A four-factor mixed model analysis of variance (ANOVA) (Table 3.2) was employed using GMAV5 software (Institute of Marine Ecology: University of Sydney) to test for habitat-related differences at two spatial scales over time in labrid species richness; contribution (%) of labrids to total fish richness; overall labrid density; contribution (%) of labrids to total fish density; and the densities of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis*, *Achoerodus viridis*, *Pictilabrus laticlavius*, *Austrolabrus maculatus* and *Eupetrichthys angustipes*. The assumptions of homogeneity of variance were tested using Cochran's C test. When necessary, data were transformed to stabilise

variances (Underwood 1981). Where significant interactions or main effects were found, *post-hoc* tests were performed in GMAV5 using the Student-Newman-Keuls (SNK) multiple comparisons of means test (Underwood 1981).

Table 3.2: Four-factor mixed ANOVA model used to test for habitat-, spatial-, and temporal-related variation in labrid richness; labrid contribution (%) to total fish richness; overall labrid density; labrid contribution (%) to total fish density; and density of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis*, *Achoerodus viridis*, *Pictilabrus laticlavius*, *Austrolabrus maculatus* and *Eupetrichthys angustipes*. Asterisk denotes a nested factor.

Factor	No. of Levels	Fixed (F) or Random (R)	Levels
Habitat	3	F	Fringe, Barrens, Sponge garden
Location	2	R	Terrigal, Norah Head
Site (Lo)	2	R*	Site 1, Site 2
Period	5	F	Aug/Sept 03, Dec 03/Jan 04, Apr/May 04, Sept/Dec 04, Apr/May 05
(Transects = 6)			
(Total observational units = 360)			

Size distributions of *O. lineolatus*, *N. gymnogenis*, *A. viridis* and *P. laticlavius* were compared across habitats in each sampling period using ANOVA in SPSS 14.0 for Windows (2005). Observations at both locations were combined. For these analyses, size estimates for individuals were derived from the midpoint of the size class in which each individual was allocated. The assumptions of homogeneity of variance were tested using Levene's test. When necessary, data were transformed to stabilise variances (Underwood 1981), but heterogeneity could not always be removed. In such cases, a more conservative critical value of $P < 0.01$ was adopted (Kingsford 1998a) to reduce the chance of a Type I error and this critical value was also applied to corresponding *post hoc* comparisons. Where significant effects were found, *post-hoc* tests were performed in SPSS using the Student-Newman-Keuls (SNK) multiple comparisons of means test (Underwood 1981).

3.2.4.3 Multivariate analyses

Variation in labrid assemblage structure was visualised using non-metric multidimensional scaling (nMDS) procedures in PRIMER v5 (Clarke and Gorley 2001). Data were square-root transformed to reduce the influence of numerically dominant labrids and increase the importance of rare species, prior to the construction of

similarity matrices using Bray-Curtis dissimilarity coefficients. Stress values were used to indicate how faithfully the two dimensional plot represented multidimensional relationships. Stress values <0.2 provide a useful interpretation of the multivariate data set with little prospect of a misleading interpretation (Clarke and Warwick 1994).

The significance of each factor (Table 3.2) as a source of variation for labrid assemblages was tested with permutational multivariate analysis of variance (PERMANOVA 6) (Anderson 2005). PERMANOVA is a non-parametric test used to obtain P -values using permutations of dissimilarity distance in complex multivariate experimental designs (Anderson and Millar 2004). For each term in the analysis, P -values were obtained from 4999 permutations of the square-root transformed data using Bray-Curtis dissimilarity measures. Where results were significant, *a posteriori* comparisons were explored.

Habitat-related variation in labrid assemblages were complicated by a 3-way interaction with site (location) and period, but habitat contributed most to this interaction. Therefore, the similarity percentages (SIMPER) routine in PRIMER v5 was used to determine which species of labrid typify the labrid assemblages of each habitat and distinguish between habitats (Clarke 1993).

3.3 Results

3.3.1 General results

A total of 76,226 individuals representing 118 species were recorded across all sampling periods with labrids contributing 16.1% to total fish species. The most speciose families were Labridae (19 spp.), Monacanthidae (17 spp.), Pomacentridae (8 spp.), Serranidae (5 spp.) and Carangidae (5 spp.) (Appendix 2). Families contributing most to overall fish abundance were Plesiopidae (43% of all individuals), Microcanthidae (15%), Pomacentridae (13%), Monodactylidae (7%) and Carangidae (5%). Labrids contributed 4.1% to total fish abundance and 40.8% to the abundance of all non-planktivorous fishes. The most abundant labrids were *Ophthalmolepis lineolatus* (38% of all labrid individuals), *Notolabrus gymnogenis* (20%), *Austrolabrus maculatus* (16%), *Achoerodus viridis* (10%), *Eupetrichthys angustipes* (6%) and *Pictilabrus laticlavius* (5%) (Table 3.3). These labrids, in addition to *Coris picta* and *Pseudolabrus guentheri*, were represented in all sampling periods (Table 3.3). A total of 41 species, including 5 labrids, were sighted on only one occasion (Appendix 2). Of the 16 identified species of labrid, 7 had distributions restricted to the southern and/or eastern coastline of Australia, 3 had distributions extending from the south-eastern region of Australia to New Zealand, and 6 species were distributed throughout the Indo-West Pacific (Table 3.3).

Table 3.3: Labrid species observed in surveys of fish assemblages conducted from August 2003 to May 2005 at two locations on the central coast of New South Wales. Total abundance represents the total number of sighted individuals. Sampling periods are those in which the species was observed (1=Aug/Sept 03, 2=Dec 03/Jan 04; 3=Apr/May 04, 4=Sept/Dec 04, and 5=Apr/May 05). Distributions are those reported in Kuitert (1993, 1996).

Species of labrid	Total abundance	Sampling period/s	Distribution
<i>Ophthalmolepis lineolatus</i>	1179	All	Southern Aust.
<i>Notolabrus gymnogenis</i>	625	All	Eastern Aust.
<i>Austrolabrus maculatus</i>	506	All	Southern Aust.
<i>Achoerodus viridis</i>	319	All	South-eastern Aust.
<i>Eupetrichthys angustipes</i>	196	All	Southern Aust.
<i>Pictilabrus laticlavus</i>	156	All	Southern Aust.
<i>Coris picta</i>	38	All	Eastern Aust. to NZ
<i>Pseudolabrus guentheri</i>	13	All	Eastern Aust.
<i>Thalassoma lunare</i>	13	2, 3, 4, 5	Indo-West Pacific
<i>Coris dorsomaculata</i>	11	4, 5	Indo-West Pacific
<i>Labroides dimidiatus</i>	7	2, 5	Indo-Pacific
<i>Stethojulis interrupta</i>	6	5	Indo-West Pacific
<i>Halichoeres nebulosus</i>	5	5	Indo-West Pacific
<i>Coris sandageri</i>	4	2, 3, 4	South-eastern Aust. to NZ
<i>Pseudolabrus luculentus</i>	2	1, 3	South-eastern Aust. to north-eastern NZ
<i>Anampses caeruleopunctatus</i>	1	2	Indo-Pacific
Unidentifiable 1	1	1	Unknown
Unidentifiable 2	1	2	Unknown
Unidentifiable 3	1	4	Unknown

The number of labrid species observed in fringe, barrens and sponge garden habitat over all sampling periods was 10, 13 and 11 species at Norah Head, and 5, 11 and 10 species at Terrigal, respectively. Species accumulation curves varied among habitats, but showed little difference between locations in the barrens and sponge garden habitat (Figure 3.1b, c). Low levels of replication (i.e. <10) were insufficient in the fringe habitat at Norah Head, whereas at Terrigal this level of replication was sufficient to approach an asymptotic percentage of represented labrid species (i.e. 86% of species) (Figure 3.1a). In barrens habitat, species accumulation curves did not approach an asymptote until the last few replicates (i.e. >55 replicates). In sponge garden habitat, an asymptote was approached only at high levels of replication (i.e. >30 replicates).

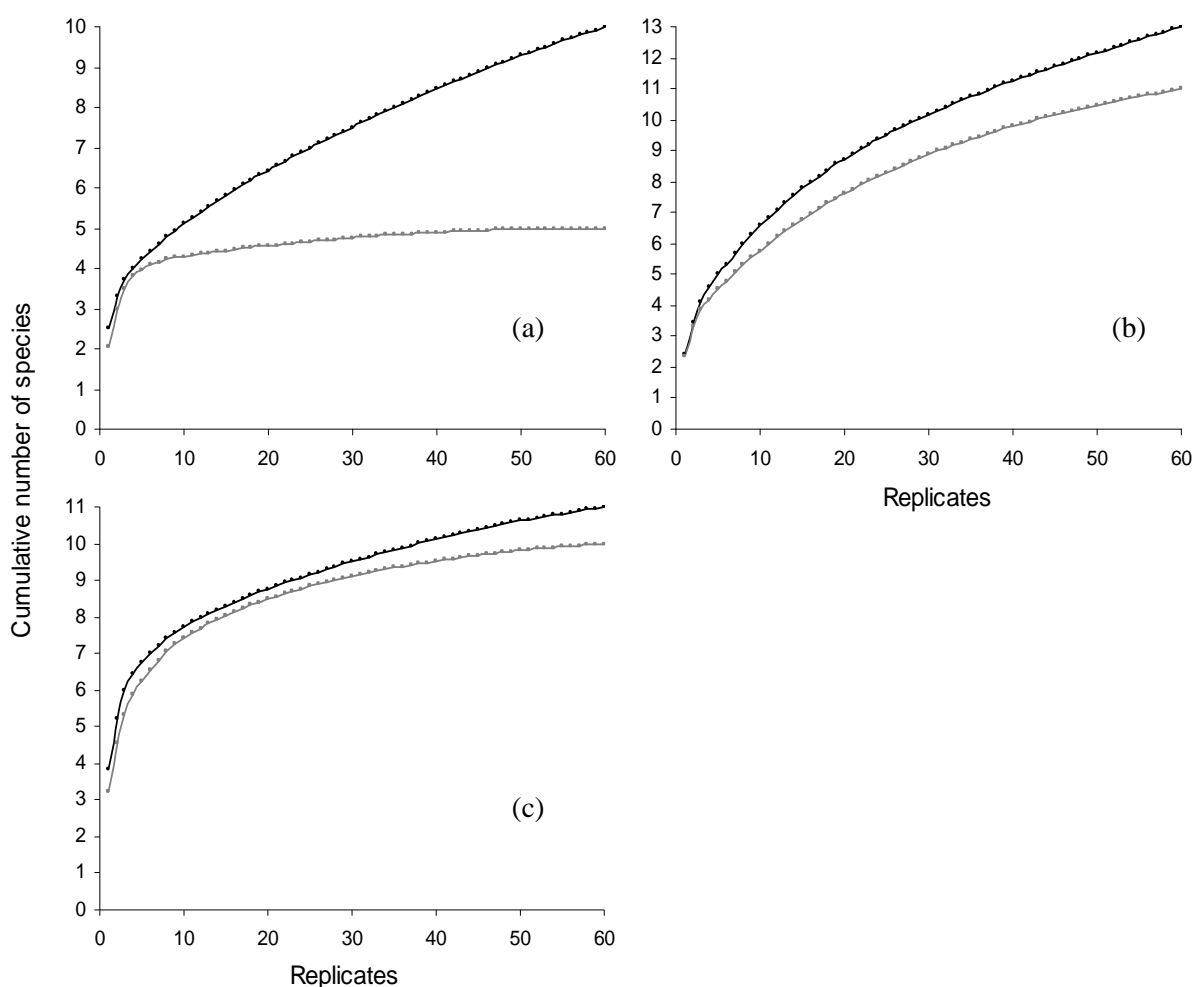


Figure 3.1: Species accumulation curves for labrids in fringe (a), barrens (b) and sponge garden (c) habitat at Terrigal (●) and Norah Head (●). Curves are based on average cumulative species derived from random transect selection from each of 2 sites over 5 sampling periods ($n=60$). Average cumulative species were calculated from 400 permutations.

3.3.2 Labrid richness and density

The mean species richness of labrids ranged between 1.3 ± 0.2 and 4.6 ± 0.4 species. 125 m^{-2} , representing between 18.7 ± 2.4 and $39.3 \pm 0.3\%$ of all fish species (Figure 3.2). A higher number of labrid species occurred in sponge garden habitat compared to both fringe and barrens, except at one site at Terrigal where there was no difference between sponge gardens and fringe (HxS(L) interaction, $P < 0.001$) (Table 3.4; Figure 3.2a). No differences occurred in the number of labrid species found in fringe and barrens habitat at Norah Head, but differences occurred at both Terrigal sites. However, the habitat with the higher number of species was not consistent at these sites at Terrigal. Compared to other sampling periods, significantly fewer labrid species were recorded in Aug/Sept 03 and Sept/Dec 04 (Table 3.4; Figure 3.2a). Labrid contribution to the total

number of fish species was lower in barrens habitat compared to both fringe and sponge gardens, which themselves were not different except at one site at Terrigal where fringe was significantly lower than both barrens and sponge gardens (HxS(L) interaction, $P < 0.001$) (Table 3.4; Figure 3.2b).

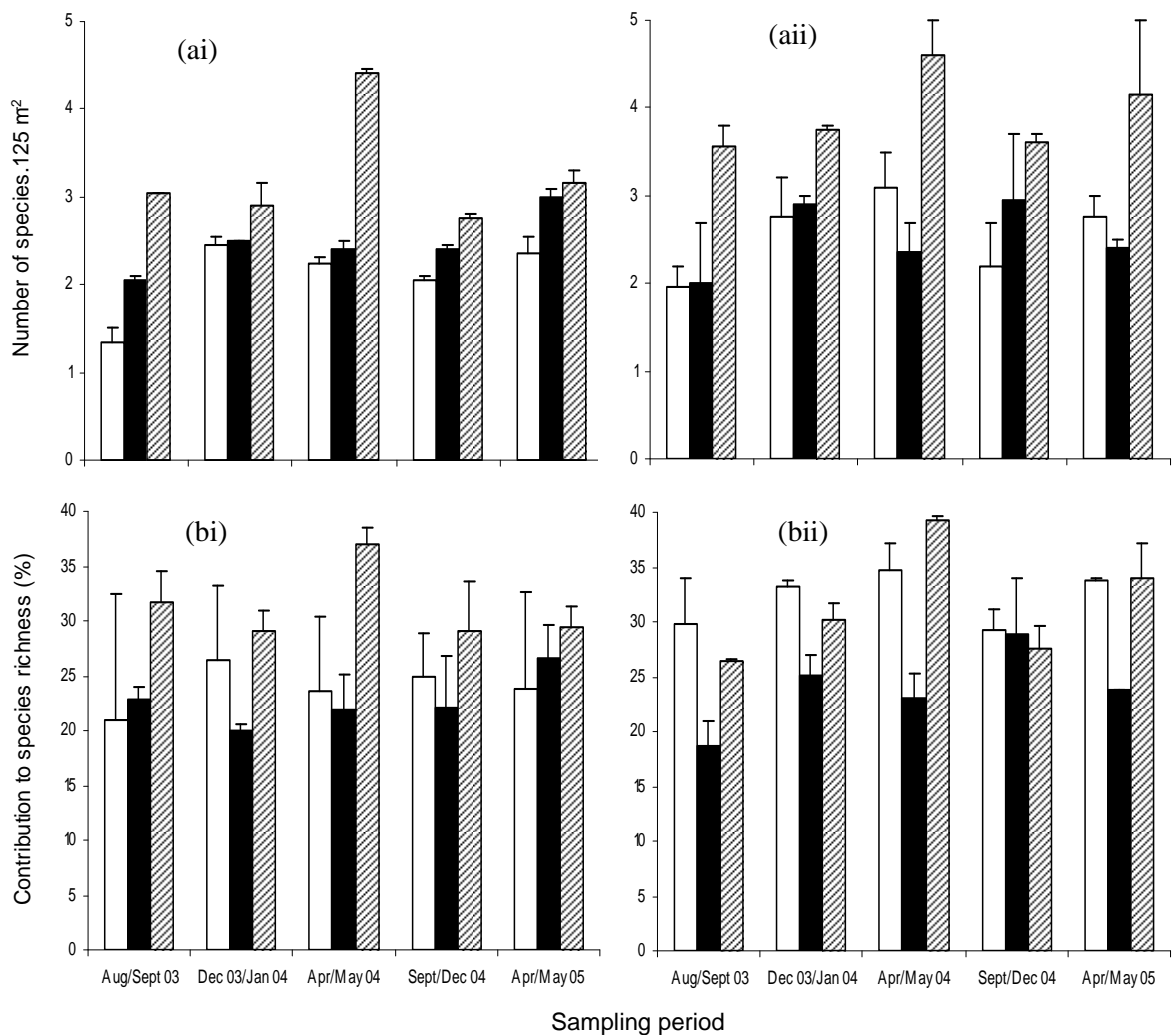


Figure 3.2: Mean (\pm SE) for species richness of labrids (a) and contribution of labrids to total fish species (b) in fringe (□), barrens (■) and sponge garden (▨) habitat at Terrigal (i) and Norah Head (ii) in each combination of HabitatxPeriod (n=2 sites with each site representing the average across 6 transects).

Table 3.4: ANOVA results of habitat-, spatial- and temporal-related variation in species richness of labrids and contribution of labrids to total fish richness. Data is untransformed (Cochran's C test, $P>0.05$). ** $P<0.01$, *** $P<0.001$

Source of variation	df	Species richness of labrids		Contribution of labrids to total richness	
		MS	F	MS	F
Habitat (H)	2	58.30	18.76	2910.17	4.72
Location (L)	1	13.23	5.12	1040.40	7.19
Site (Location) = S(L)	2	2.58	2.20	144.72	1.36
Period (P)	4	7.55	34.63**	312.59	3.94
H x L	2	3.11	0.27	616.13	0.77
H x S(L)	4	11.56	9.85***	798.96	7.53***
H x P	8	2.96	2.84	210.33	3.02
L x P	4	0.22	0.23	79.26	0.69
S(L) x P	8	0.95	0.81	114.63	1.08
H x L x P	8	1.04	0.61	55.94	1.25
H x S(L) x P	16	1.69	1.44	106.11	0.53
Residual	300	1.17			

Mean density of labrids ranged between 2.7 ± 1.8 and 20.8 ± 1.5 individuals. 125 m^{-2} , with labrids contributing between 2.0 ± 0.1 and $22.9 \pm 6.9\%$ to the density of all species (Figure 3.3). The effect of habitat on labrid density varied between sites (locations) as shown by the significant HxS(L) interaction (Table 3.5; Figure 3.3.a). Significantly higher labrid densities occurred in sponge gardens compared to other habitats at all sites. No difference in labrid density occurred between fringe and barrens habitat at either site at Norah Head, but differences occurred at both sites at Terrigal. However, the habitat with the higher labrid density was inconsistent across these sites at Terrigal. Significantly lower densities of labrids occurred in Aug/Sept 03 and Sept/Dec 04, and higher densities in Apr/May 04 (Table 3.5; Figure 3.3a). The effect of habitat on labrid contribution to total fish density was found to vary between sites (locations), and this variation was not consistent through time (HxS(L)xP interaction, $P<0.001$) (Table 3.5). Significant differences between habitats generally existed at each site and each period of sampling, but habitat differences were highly inconsistent. In only Apr/May 04 was one habitat (i.e. sponge gardens) found to represent a significantly higher labrid contribution to total fish density at all sites.

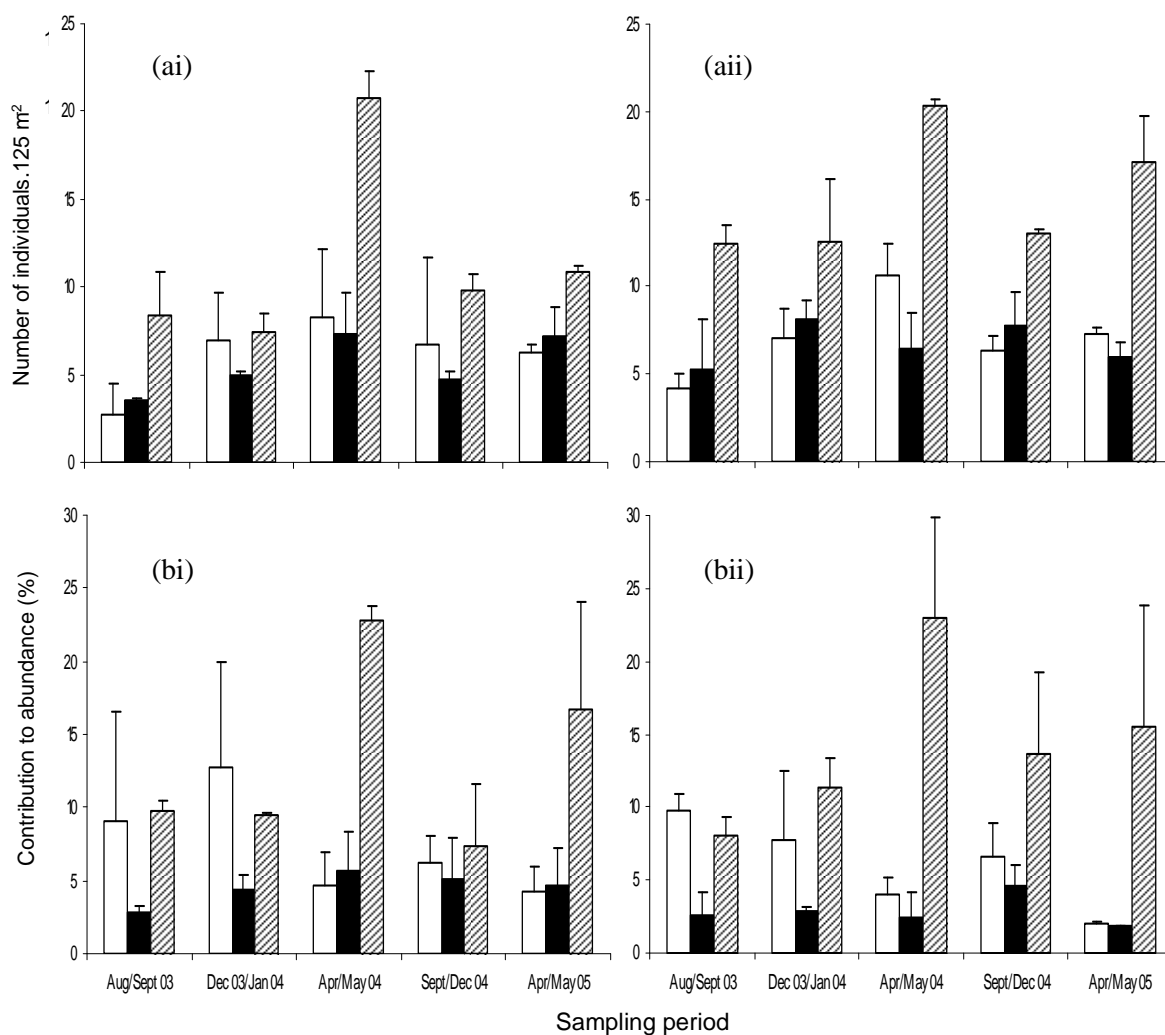


Figure 3.3: Mean (\pm SE) for density of labrids (a) and contribution of labrids to total fish density (b) in fringe (\square), barrens (\blacksquare) and sponge garden (\hatched) habitat at Terrigal (i) and Norah Head (ii) in each combination of Habitat \times Period (n=2 sites with each site representing the average across 6 transects).

Table 3.5: ANOVA results of habitat-, spatial- and temporal-related variation in labrid density and labrid contribution to total fish density. All data square-root (x+1) transformed (Cochran's C test, $P>0.05$). * $P<0.05$, ** $P<0.01$, *** $P<0.001$

Source of variation	df	Labrid density		Contribution of labrids to total fish density	
		MS	F	MS	F
Habitat (H)	2	42.35	44.57*	75.82	39.58*
Location (L)	1	10.71	2.72	2.54	1.03
Site (Location) = S(L)	2	3.93	6.50**	2.47	2.50
Period (P)	4	8.70	25.39**	2.54	2.30
H x L	2	0.95	0.23	1.92	0.19
H x S(L)	4	4.14	6.84***	9.99	10.11***
H x P	8	1.77	2.46	6.82	8.91**
L x P	4	0.34	0.48	1.11	0.45
S(L) x P	8	0.72	1.19	2.44	2.47*
H x L x P	8	0.72	0.86	0.77	0.27
H x S(L) x P	16	0.84	1.39	2.79	2.82***
Residual	300	0.61		0.99	

3.3.3 Multivariate analyses of labrid assemblages

MDS ordinations showed assemblages in sponge garden habitat formed a discrete group at the bottom right of the plot in each sampling period (Figure 3.4). Labrid assemblages in fringe and barrens habitat were broadly scattered and exhibited considerable overlap. PERMANOVA showed the effect of habitat on labrid assemblages varied between sites (locations), and this variation was not consistent through time (HxS(L)xP interaction, $P < 0.05$) (Table 3.6). Labrid assemblages associated with sponge gardens were found to differ significantly from those in fringe habitat in 14 of 20 comparisons of S(L)xP, including at all sites in Apr/May 04 and Apr/May 05, and all except one site at Norah Head in Sept/Dec 04. Sponge garden labrid assemblages differed from those in barrens habitat in 9 of 20 comparisons, including at all sites in Apr/May 04. Differences occurred between fringe and barrens habitat in only 6 of 20 comparisons. Three of these differences occurred at the one site at Terrigal in the sampling periods of Dec 03/Jan 04, Apr/May 04 and Sept/Dec 04.

Table 3.6: Non-parametric multivariate ANOVA of habitat-, spatial- and temporal-related variation in labrid assemblages based on Bray-Curtis dissimilarity measures. All data square-root transformed.

Source of variation	df	MS	<i>F</i>	<i>P</i> (Monte Carlo)
Habitat (H)	2	39060.14	4.06	0.032
Location (L)	1	36976.75	4.96	0.025
Site (Location) = S(L)	2	7455.34	5.37	0.000
Period (P)	4	4345.47	4.28	0.002
H x L	2	9610.60	2.36	0.060
H x S(L)	4	4077.40	2.94	0.000
H x P	8	2743.31	1.45	0.137
L x P	4	1015.78	0.57	0.891
S(L) x P	8	1776.59	1.28	0.132
H x L x P	8	1897.54	1.00	0.497
H x S(L) x P	16	1903.85	1.37	0.026
Residual	300	1388.81		

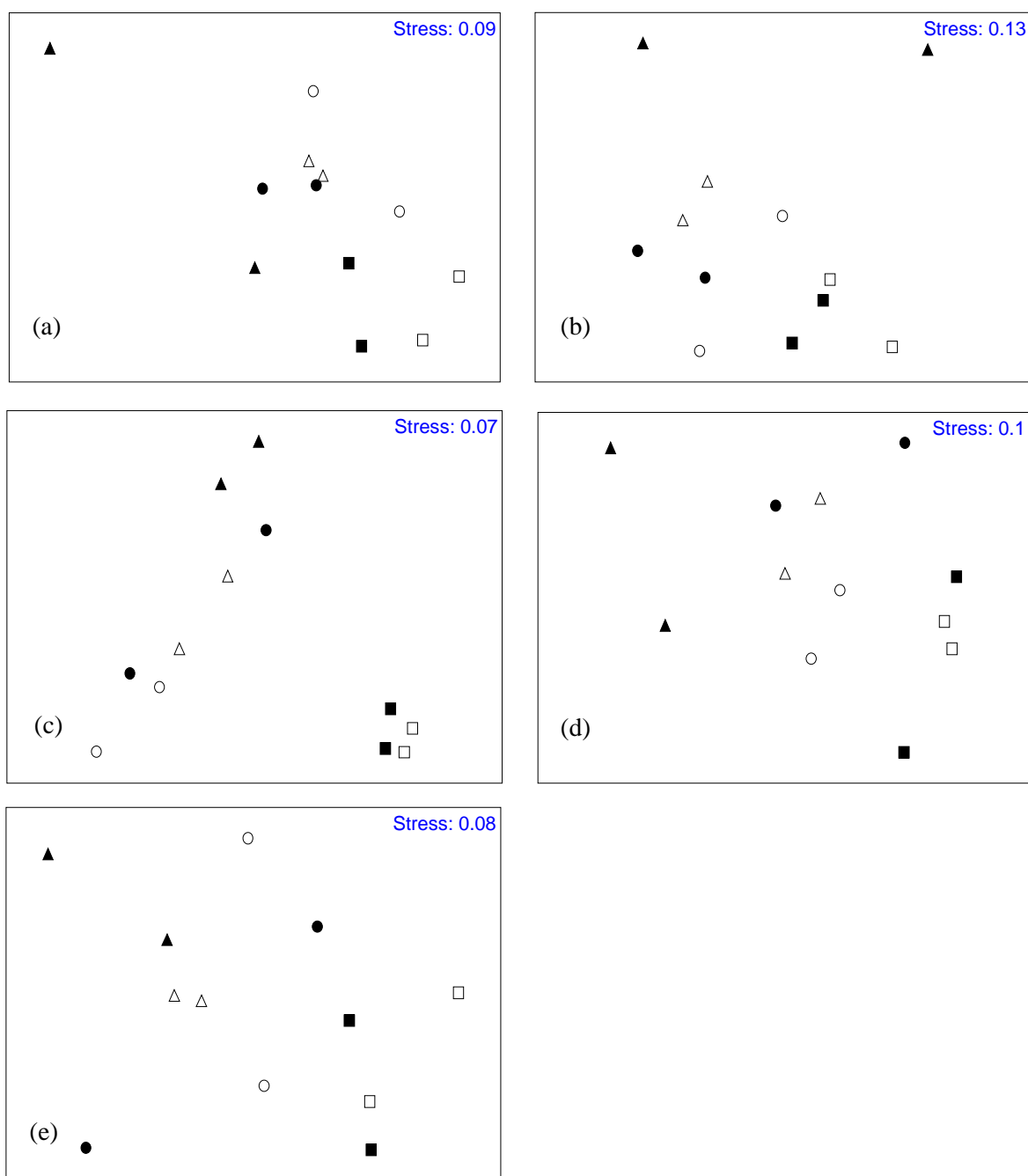


Figure 3.4: Non-metric multidimensional scaling ordinations comparing labrid assemblages across sites, locations and habitats for the sampling periods of Aug/Sept 03 (a), Dec 03/Jan 04 (b), Apr/May 04 (c), Sept/Dec 04 (d) and Apr/May 05 (e). Habitats are fringe (▲), barrens (●) and sponge garden (■), at Terrigal sites (shaded) and Norah Head sites (non-shaded).

Notolabrus gymnogenis and *Ophthalmolepis lineolatus* typified the labrid assemblage in all habitats. In addition, *Achoerodus viridis* typified the labrid assemblage of fringe and barrens, and *Austrolabrus maculatus* and *Eupetrichthys angustipes* typified the labrid assemblage of sponge garden habitat (Table 3.7). Labrid assemblages associated with fringe habitat were distinguished from both barrens and sponge garden habitat by higher densities of *N. gymnogenis*, and from barrens by higher densities of *A. viridis* and *Pictilabrus laticlavius* (Table 3.7; Figure 3.5). Labrid assemblages within sponge garden habitat had higher densities of *O. lineolatus*, *A. maculatus* and *E. angustipes* than other habitats. The less common labrids (e.g. *Coris dorsomaculata*, *Coris picta* and *Thalassoma lunare*) were restricted to habitats other than fringe (Figure 3.5; Appendix 2).

Table 3.7: Species contributing most to typifying (shaded) the labrid assemblage within fringe, barrens and sponge garden habitats, and the species distinguishing (non-shaded) between habitats as identified using SIMPER. Asterisks denote a higher density of individuals was recorded in the habitat at the top of the column. No asterisk signifies that a higher density of individuals occurred in the habitat at the left of the row.

Habitat	Fringe	Barrens	Sponge garden
Fringe	<i>Notolabrus gymnogenis</i> <i>Ophthalmolepis lineolatus</i> <i>Achoerodus viridis</i>		
Barrens	<i>Ophthalmolepis lineolatus</i> <i>Notolabrus gymnogenis</i> * <i>Achoerodus viridis</i> * <i>Pictilabrus laticlavius</i> *	<i>Ophthalmolepis lineolatus</i> <i>Notolabrus gymnogenis</i> <i>Achoerodus viridis</i>	
Sponge garden	<i>Austrolabrus maculatus</i> <i>Ophthalmolepis lineolatus</i> <i>Notolabrus gymnogenis</i> * <i>Eupetrichthys angustipes</i>	<i>Austrolabrus maculatus</i> <i>Ophthalmolepis lineolatus</i> <i>Eupetrichthys angustipes</i>	<i>Ophthalmolepis lineolatus</i> <i>Austrolabrus maculatus</i> <i>Notolabrus gymnogenis</i> <i>Eupetrichthys angustipes</i>

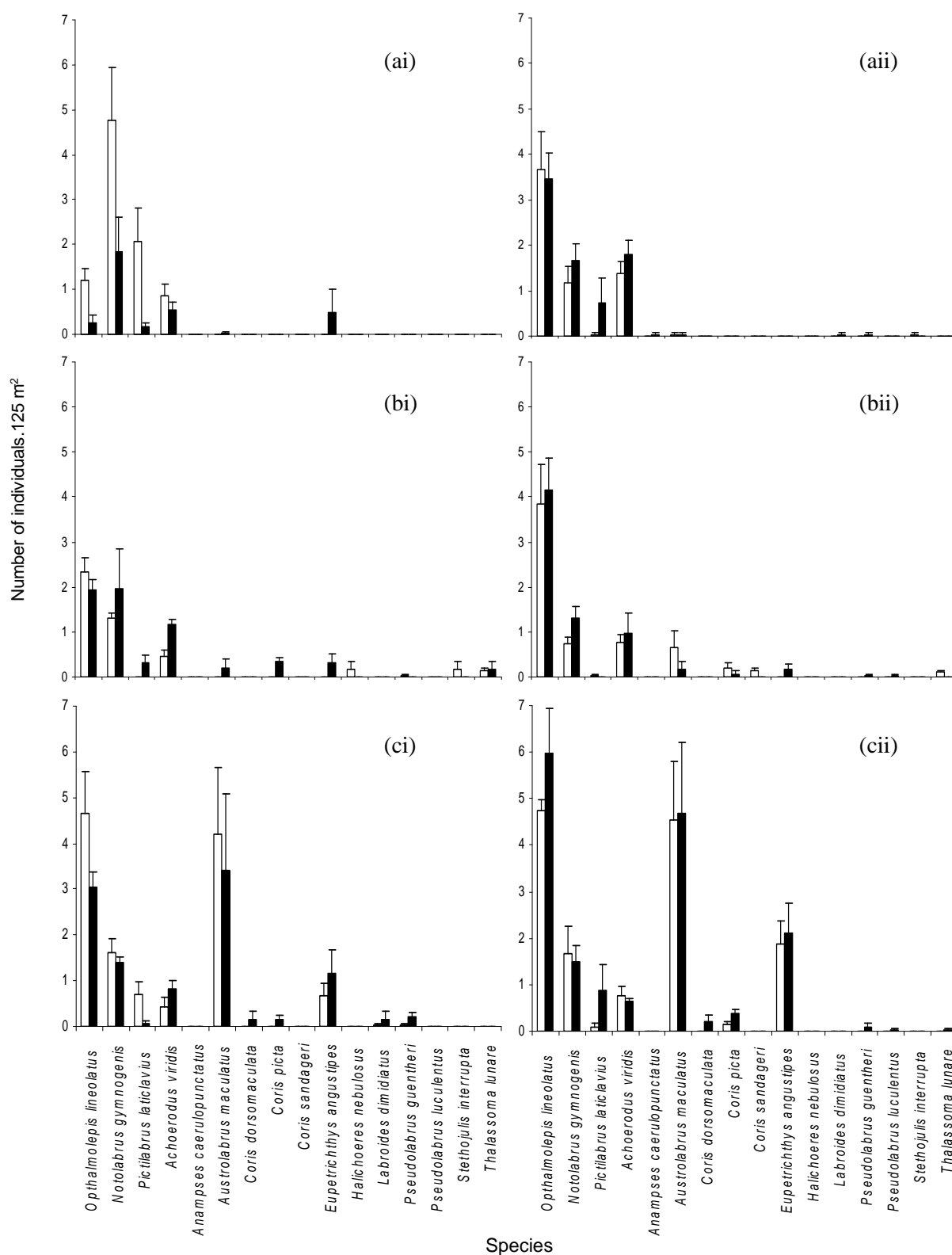


Figure 3.5: Mean (\pm SE) for density of labrids in fringe (a), barrens (b) and sponge garden (c) habitat at Terrigal (i) and Norah Head (ii). Values are average site densities over all sampling periods ($n=5$). Site 1 (non-shaded), site 2 (shaded).

3.3.4 Density and size distributions of selected labrids

3.3.4.1 *Ophthalamolepis lineolatus*

A total of 1,179 *Ophthalamolepis lineolatus* were observed with most individuals observed in sponge garden habitat (46.7%), followed by barrens (31.3%) and fringe (22.0%). Mean densities ranged between 0.3 ± 0.3 and 7.2 ± 2.3 individuals. 125 m^{-2} (Figure 3.6). The effect of habitat on the density of *O. lineolatus* varied between sites (locations), and the nature of this variation changed with the period of sampling (HxS(L)xP interaction, $P < 0.05$) (Table 3.8; Figure 3.6). Higher densities were observed in sponge gardens compared to fringe habitat in all sampling periods at one site at Terrigal, and for the first 3 sampling periods at the other site. Densities in sponge gardens were significantly higher than in barrens for half of these comparisons. Densities in fringe habitat were lower than barrens at one of the sites at Terrigal in each sampling period, but this was not always the same site. At Norah Head, densities in sponge garden habitat were greater than fringe at both sites in Aug/Sept 03, and at one site in Apr/May 05. Densities in sponge gardens were higher than in barrens for 2 of these comparisons. Densities of *O. lineolatus* in barrens were greater than fringe only at one site at Norah Head in Aug/Sept 03.

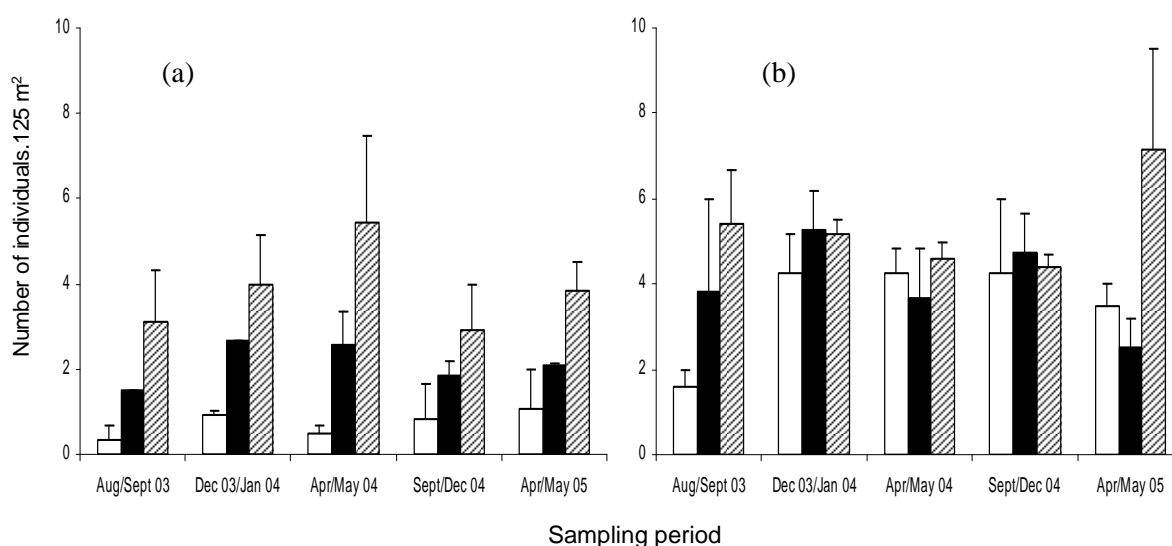


Figure 3.6: Mean (\pm SE) for density of *Ophthalamolepis lineolatus* in fringe (□), barrens (■) and sponge garden (▨) habitat at Terrigal (a) and Norah Head (b) in each combination of HabitatxPeriod (n=2 sites with each site representing the average across 6 transects).

Table 3.8: ANOVA results of habitat-, spatial- and temporal-related variation in the densities of *Ophthalamolepis lineolatus*, *Notolabrus gymnogenis* and *Achoerodus viridis*. All data $\ln(x+1)$ transformed (Cochran's C test, $P>0.05$). * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

Source of variation	df	<i>Ophthalamolepis lineolatus</i>		<i>Notolabrus gymnogenis</i>		<i>Achoerodus viridis</i>	
		MS	F	MS	F	MS	F
Habitat (H)	2	14.85	5.62	1.66	1.41	1.21	0.96
Location (L)	1	31.00	13.18	6.24	3.74	2.08	5.85
Site (Location) = S(L)	2	2.35	7.85***	1.67	4.67*	0.36	1.57
Period (P)	4	1.27	6.86*	2.14	8.30*	1.02	11.06*
H x L	2	2.64	5.48	1.18	0.80	1.26	1.63
H x S(L)	4	0.48	1.61	1.47	4.11**	0.77	3.40**
H x P	8	0.48	0.66	0.42	0.68	0.29	0.61
L x P	4	0.19	0.40	0.26	0.66	0.09	0.36
S(L) x P	8	0.46	1.55	0.39	1.10	0.25	1.12
H x L x P	8	0.73	1.32	0.63	0.85	0.47	3.97**
H x S(L) x P	16	0.55	1.85*	0.74	2.07**	0.12	0.53
Residual	300	0.30		0.36		0.23	

O. lineolatus of sizes 100-349 mm were recorded in all habitats in each sampling period, and represented 85.5% of all individuals (Figure 3.7a-e). Individuals of relatively small size (i.e. <200 mm) were typically found at higher abundances in sponge garden habitat. For example, 56.7% of individuals of this size were found in sponge garden habitat compared to 24.3% in barrens and 19.0% in fringe. A peak in the number of individuals belonging to the smallest size class (i.e. 50-99 mm) occurred in Apr/May 04 and Apr/May 05 in the sponge garden habitat (Figure 3.7c, e). A similar peak of smaller magnitude also occurred in the fringe habitat in Sept/Dec 04 (Figure 3.7d).

Differences among habitats in the mean size of *O. lineolatus* individuals occurred in all periods of sampling (all $P<0.01$), except for Apr/May 05 (Figure 3.7f). Mean size of individuals was lower in sponge garden habitat compared to fringe and barrens in Aug/Sept 03 and Apr/May 04, and lower than fringe only in Dec 03/Jan 04. In Sept/Dec 04 a lower mean size of individuals occurred in fringe compared to barrens habitat.

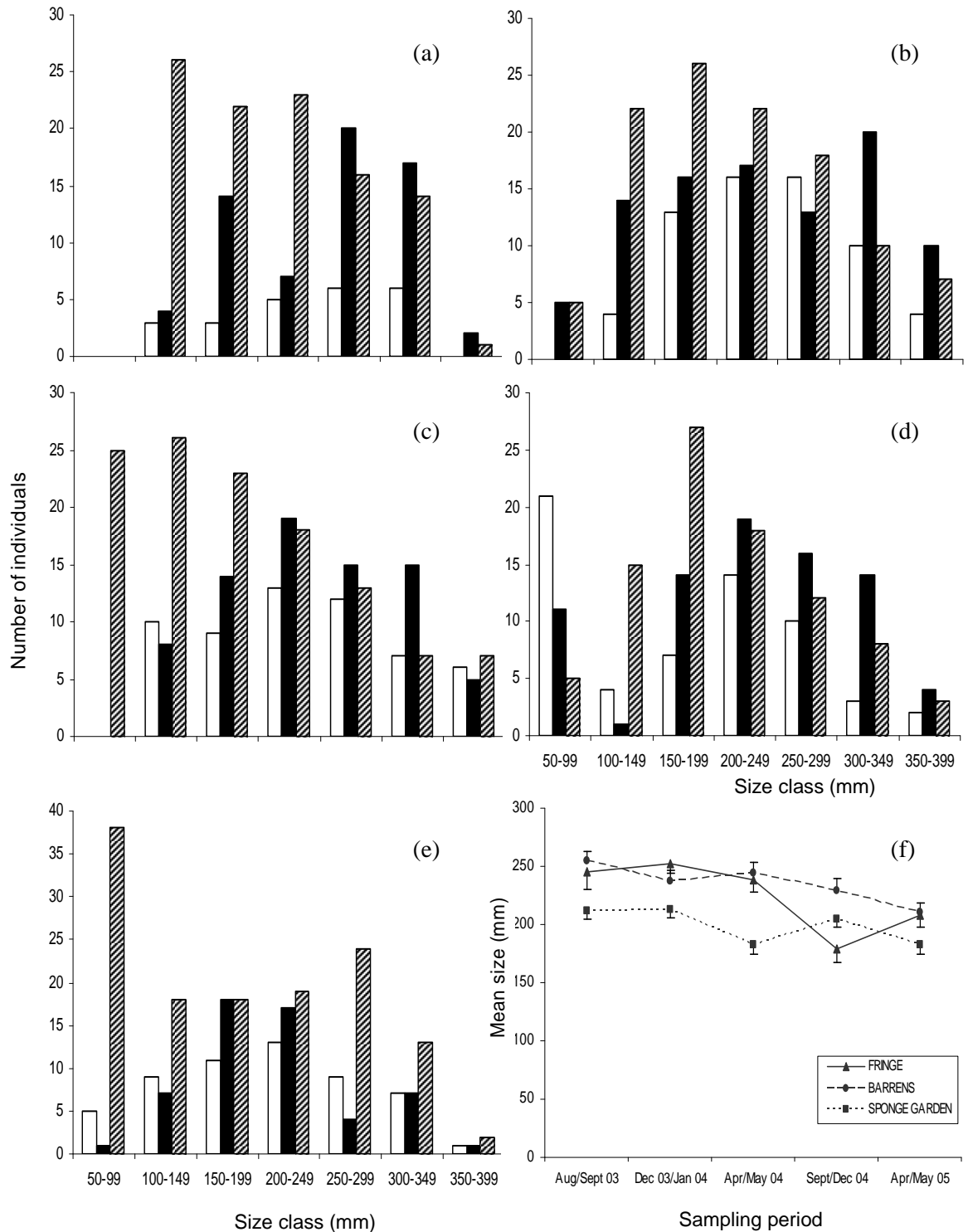


Figure 3.7: Size distributions of *Ophthalmolepis lineolatus* in fringe (□), barrens (■) and sponge garden (▨) habitat in the sampling periods of Aug/Sept 03 (a), Dec 03/Jan 04 (b), Apr/May 04 (c), Sept/Dec 04 (d), and Apr/May 05 (e). All individuals have been combined across locations so abundances reflect individuals recorded in 3000 m² of habitat. Note: figures use different scales of abundance. Figure (f) shows the mean size (\pm SE) of individuals of *O. lineolatus* across habitats in each sampling period (locations have been combined).

3.3.4.2 *Notolabrus gymnogenis*

A total of 625 *Notolabrus gymnogenis* were observed with most individuals observed in fringe habitat (45.6%), followed by sponge gardens (29.0%) and barrens (25.4%). Mean densities ranged between 0.6 ± 0.1 and 5.2 ± 2.8 individuals. 125 m^{-2} (Figure 3.8). The effect of habitat on the density of *N. gymnogenis* varied between sites (locations), and the nature of this variation changed with the period of sampling (HxS(L)xP interaction, $P < 0.01$) (Table 3.8; Figure 3.8). Generally, densities did not differ among habitats, with 13 of 20 habitat comparisons for the HxS(L)xP interaction being non-significant. However, significantly higher densities of *N. gymnogenis* occurred in fringe compared to at least one other habitat in 5 of the remaining 7 comparisons. Three of these were at the one site at Terrigal.

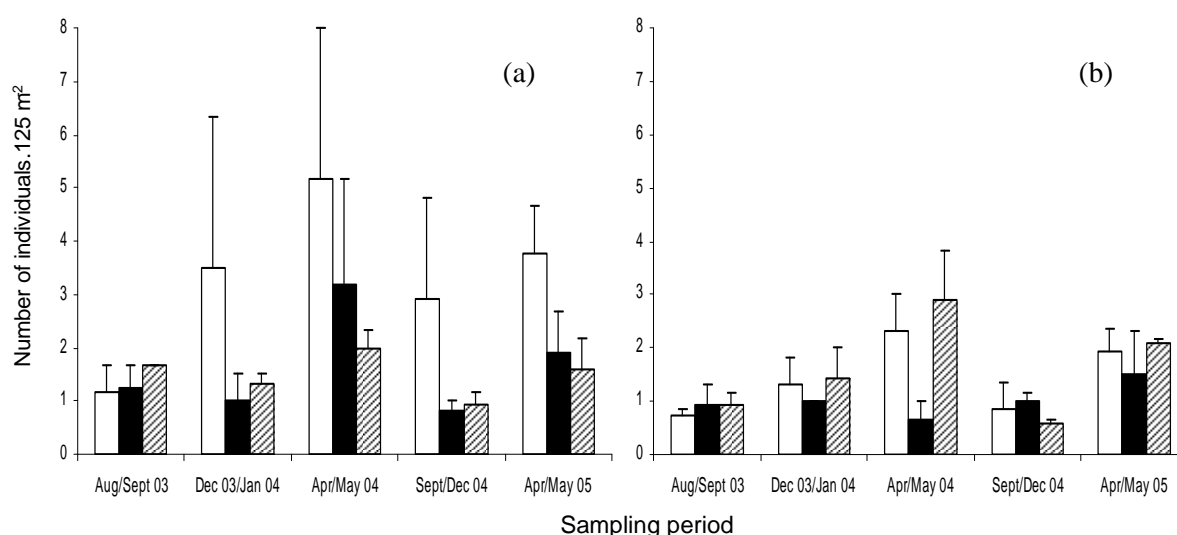


Figure 3.8: Mean (\pm SE) for density of *Notolabrus gymnogenis* in fringe (□), barrens (■) and sponge garden (▨) habitat at Terrigal (a) and Norah Head (b) in each combination of HabitatxPeriod (n=2 sites with each site representing the average across 6 transects).

N. gymnogenis of sizes 150-249 mm were recorded from all habitats in each sampling period, and represented 33.9% of all individuals (Figure 3.9a-e). Large individuals (i.e. >250 mm) were found predominantly in barrens and sponge gardens with these habitats representing 31.3 and 53.6% of all individuals of this size, respectively. In contrast, 61.1% of all small individuals (i.e. <150 mm) were recorded in fringe habitat compared with 19.9 and 18.9% in barrens and sponge gardens, respectively. Highest abundances of individuals belonging to the smallest size class (i.e. 50-99 mm) occurred in Apr/May

04 and Apr/May 05 (Figure 3.9c, d). Differences among habitats in the mean size of *N. gymnogenis* individuals occurred in all periods of sampling (all $P \leq 0.001$) with the mean size of individuals lower in fringe compared to sponge garden habitat in all periods, and also lower than barrens in Dec 03/Jan 04 and Sept/Dec 04 (Figure 3.9f).

3.3.4.3 *Achoerodus viridis*

A total of 319 *Achoerodus viridis* were observed with most individuals observed in fringe habitat (43.3%), followed by barrens (31.7%) and sponge gardens (25.1%). Mean densities ranged between 0.5 ± 0.5 and 15.5 ± 1.5 individuals. 125 m^{-2} (Figure 3.10). The effect of habitat on the density of *A. viridis* varied between locations, and the nature of this variation changed with the period of sampling (HxLxP interaction, $P < 0.001$) (Table 3.8; Figure 3.10). Higher densities were observed in barrens compared to fringe habitat at Terrigal in Sept/Dec 04. At Norah Head, higher densities were observed in fringe compared to other habitats in Aug/Sept 03 and Apr/May 04, and compared to barrens in Apr/May 05. Higher densities occurred in barrens compared to sponge garden habitat in Apr/May 04. Differences between habitats in the density of *A. viridis* also varied among sites (locations) (Table 3.8; Figure 3.10). Higher densities were observed in barrens compared to fringe habitat at one site at Terrigal. At both sites at Norah Head, fringe represented higher densities than either barrens or sponge garden habitats, which themselves were not different.

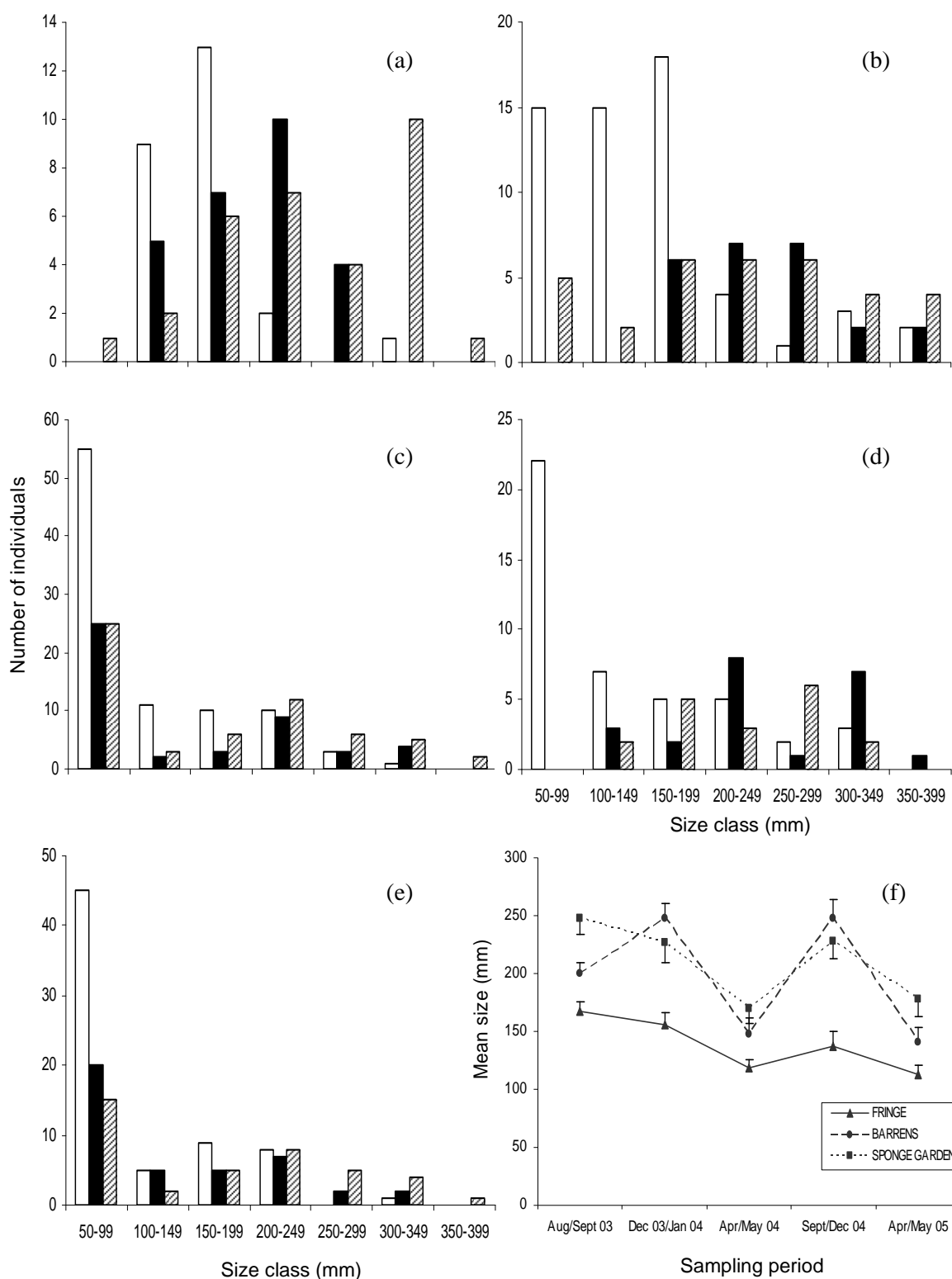


Figure 3.9: Size distributions of *Notolabrus gymnogenis* in fringe (□), barrens (■) and sponge garden (▨) habitat in the sampling periods of Aug/Sept 03 (a), Dec 03/Jan 04 (b), Apr/May 04 (c), Sept/Dec 04 (d), and Apr/May 05 (e). All individuals have been combined across locations so abundances reflect individuals recorded in 3000 m² of habitat. Note: figures use different scales of abundance. Figure (f) shows the mean size (\pm SE) of individuals of *N. gymnogenis* across habitats in each sampling period (locations have been combined).

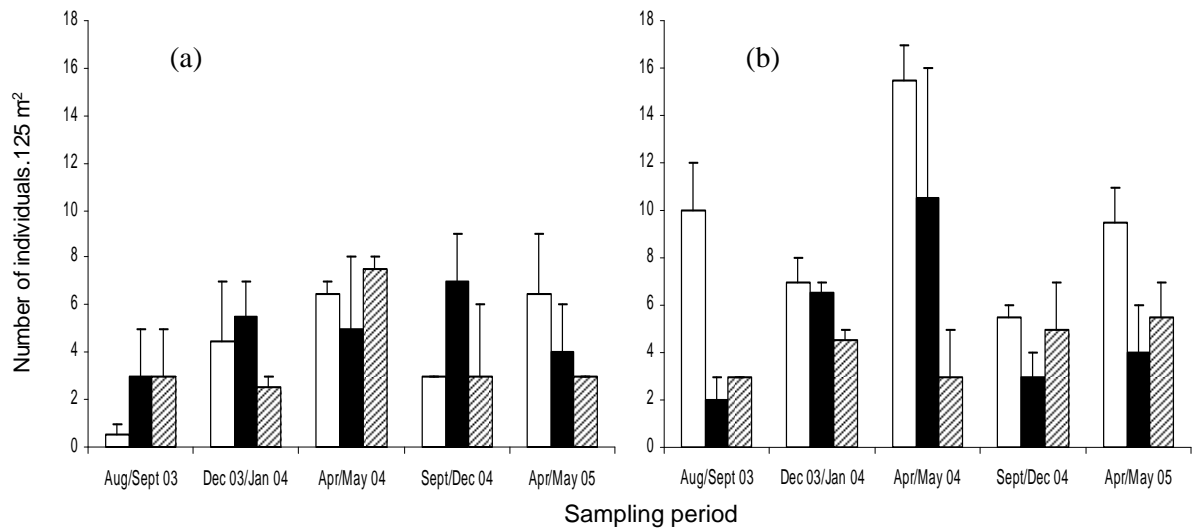


Figure 3.10: Mean (\pm SE) for density of *Achoerodus viridis* in fringe (□), barrens (■) and sponge garden (▨) habitat at Terrigal (a) and Norah Head (b) in each combination of HabitatxPeriod (n=2 sites with each site representing the average across 6 transects).

A. viridis of sizes 450-749 mm were represented in all habitats in each sampling period, and represented 77.4% of all individuals (Figure 3.11a-e). Half of all large individuals (i.e. 750-849 mm) were found in the barrens habitat. Of the small individuals (i.e. <250 mm), 92.9% were recorded in the fringe habitat. A peak in the number of these small individuals occurred in Apr/May 04 (Figure 3.11c).

Differences in the mean size of *A. viridis* individuals only occurred among habitats ($P=0.001$) (Figure 3.11f) in Apr/May 04. In this period, the mean size of individuals was lower in fringe compared to sponge garden habitat.

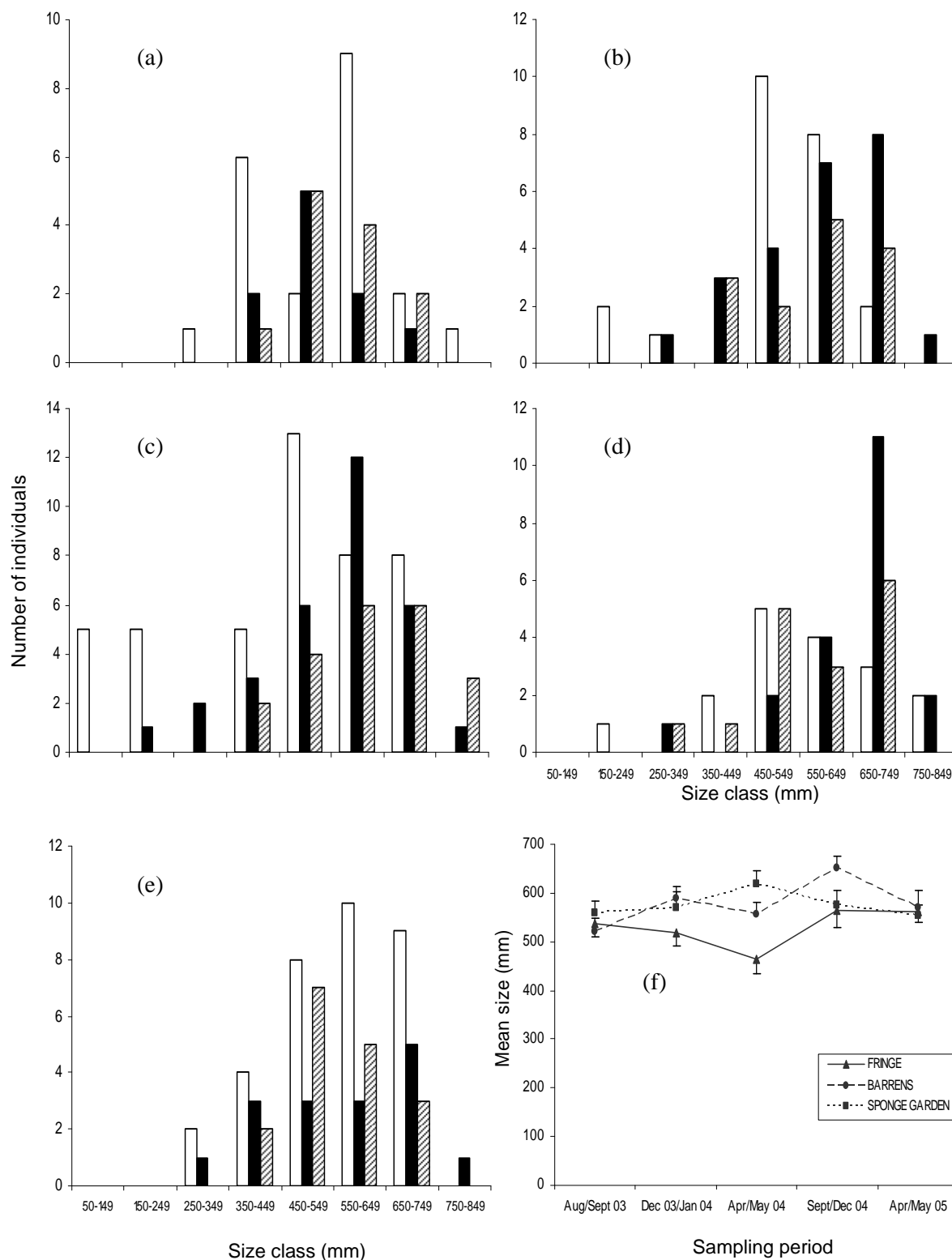


Figure 3.11: Size distributions of *Achoerodus viridis* in fringe (□), barrens (■) and sponge garden (▨) habitat in the sampling periods of Aug/Sept 03 (a), Dec 03/Jan 04 (b), Apr/May 04 (c), Sept/Dec 04 (d), and Apr/May 05 (e). All individuals have been combined across locations so abundances reflect individuals recorded in 3000 m² of habitat. Note: figures use different scales of abundance. Figure (f) shows the mean size (± SE) of individuals of *A. viridis* across habitats in each sampling period (locations have been combined).

3.3.4.4 *Pictilabrus laticlavius*

A total of 156 *Pictilabrus laticlavius* were observed with most individuals observed in the fringe habitat (60.3%), followed by sponge gardens (33.3%) and barrens (6.4%). Mean habitat densities ranged between 0 and 2.4 ± 2.2 individuals. 125 m^{-2} (Figure 3.12). The effect of habitat on the density of *P. laticlavius* varied between sites (locations), and the nature of this variation changed with the period of sampling (HxS(L)xP interaction, $P < 0.001$) (Table 3.9; Figure 3.12). Interpretation of *post hoc* comparisons was constrained by the infrequent occurrence of this species in replicate transects (i.e. many comparisons consisted of zero densities). However, higher densities of *P. laticlavius* occurred in fringe compared to at least one other habitat in all but the Apr/May 05 sampling period for one site at Terrigal. In each of these instances, densities within fringe were always significantly higher than in barrens. Higher densities in fringe habitat occurred only in Apr/May 04 at one site at Norah Head. In Aug/Dec 03, this site had significantly higher densities of *P. laticlavius* in sponge gardens compared to other habitats.

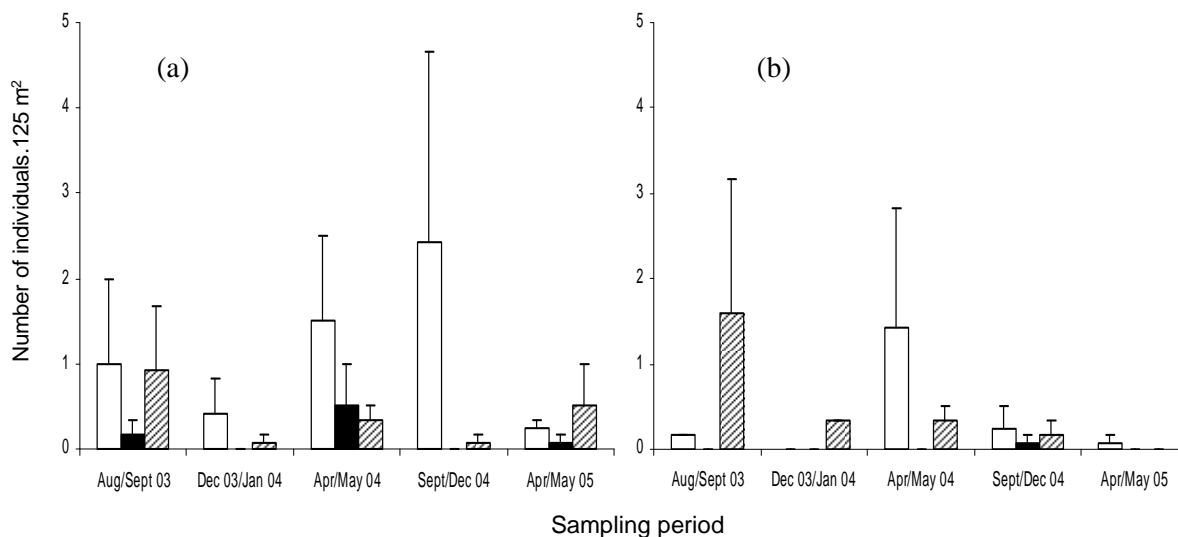


Figure 3.12: Mean (\pm SE) for density of *Pictilabrus laticlavius* in fringe (□), barrens (■) and sponge garden (▨) habitat at Terrigal (a) and Norah Head (b) in each combination of HabitatxPeriod (n=2 sites with each site representing the average across 6 transects).

Table 3.9: ANOVA results of habitat-, spatial- and temporal-related variation in the densities of *Pictilabrus laticlavius*, *Austrolabrus maculatus* and *Eupetrichthys angustipes*. All data $\ln(x+1)$ transformed (Cochran's C test, $P < 0.01$). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source of variation	df	<i>Pictilabrus laticlavius</i>		<i>Austrolabrus maculatus</i>		<i>Eupetrichthys angustipes</i>	
		MS	F	MS	F	MS	F
Habitat (H)	2	2.28	3.02	44.47	244.23***	9.50	4.75
Location (L)	1	1.10	0.37	0.97	3.60	1.08	2.07
Site (Location) = S(L)	2	2.96	23.38***	0.27	0.08	0.52	2.46
Period (P)	4	0.76	15.23*	2.81	8.77*	0.15	1.91
H x L	2	0.75	0.45	0.18	1.14	2.00	59.06**
H x S(L)	4	1.69	13.39***	0.16	0.47	0.03	0.16
H x P	8	0.58	2.77	2.60	22.85***	0.57	2.89
L x P	4	0.05	0.17	0.32	0.43	0.08	0.28
S(L) x P	8	0.29	2.30*	0.74	2.20*	0.28	1.32
H x L x P	8	0.21	0.50	0.11	0.18	0.20	0.67
H x S(L) x P	16	0.42	3.29***	0.62	1.85*	0.30	1.40
Residual	300	0.13		0.34		0.21	

Individuals of *P. laticlavius* of sizes 100-199 mm were observed most commonly in fringe and sponge garden habitats (i.e. 51.7 and 39.7% of all individuals of this size, respectively) (Figure 3.13a-e). No large individuals (i.e. >200 mm) were recorded in the barrens habitat. The smallest size class (i.e. 50-99 mm) represented 51.9% of all individuals. A peak in the number of these smallest individuals occurred in the fringe and sponge garden habitats in Aug/Sept 03, and in the fringe in Apr/May 04 and Sept/Dec 04.

The mean size of *P. laticlavius* within each of the three habitats differed only in Aug/Sept 03 and Apr/May 04 (Figure 3.13f). In Aug/Sept 03, the mean size of individuals was higher in barrens than any other habitat, but in the latter period sponge garden habitat was represented by a higher mean size of individuals compared to either fringe or barrens.

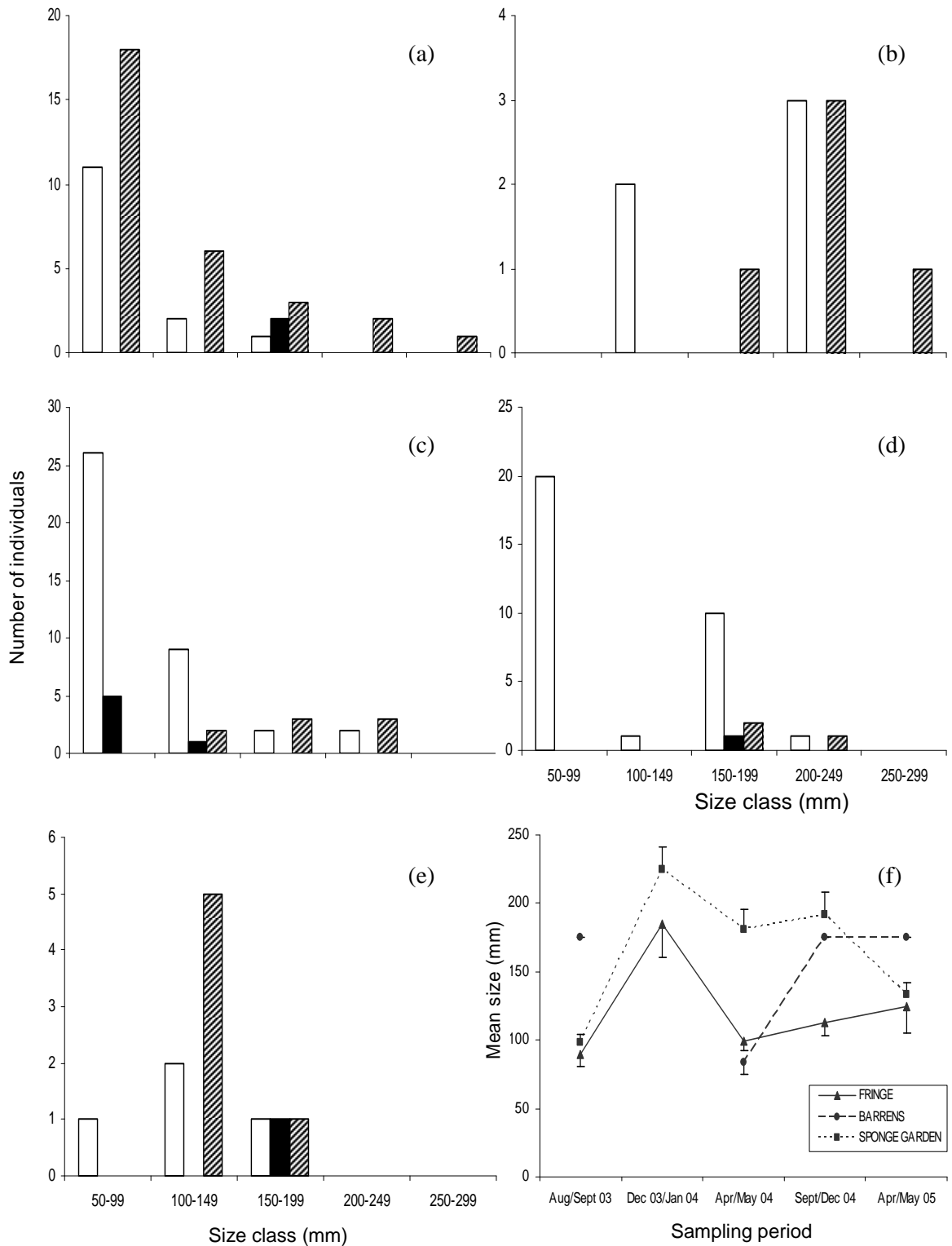


Figure 3.13: Size distributions of *Pictilabrus laticlavius* in fringe (□), barrens (■) and sponge garden (▨) habitat in the sampling periods of Aug/Sept 03 (a), Dec 03/Jan 04 (b), Apr/May 04 (c), Sept/Dec 04 (d), and Apr/May 05 (e). All individuals have been combined across locations so abundances reflect individuals recorded in 3000 m² of habitat. Note: figures use different scales of abundance. Figure (f) shows the mean size (\pm SE) of individuals of *P. laticlavius* across habitats in each sampling period (locations have been combined).

3.3.4.5 *Austrolabrus maculatus*

A total of 506 *Austrolabrus maculatus* were observed with most individuals observed in the sponge garden habitat (94.9%), followed by the barrens (4.2%) and fringe (1.0%). Mean habitat densities ranged between 0 and 54.5 ± 0.5 individuals. 125 m^{-2} (Figure 3.14). The effect of habitat on the density of *A. maculatus* varied between sites (locations), and the nature of this variation changed with the period of sampling (HxS(L)xP interaction, $P < 0.05$) (Table 3.9; Figure 3.14). Higher densities were observed in the sponge garden habitat compared to both fringe and barrens at one site at Terrigal and at both Norah Head sites in 4 of the 5 sampling periods. Higher densities in sponge garden habitat occurred at all sites in Apr/May 04 and Apr/May 05. No differences in the density of *A. maculatus* occurred between fringe and barrens habitat at any site in any sampling period.

The smallest size class of *A. maculatus* (i.e. 50-99 mm) represented 85.6% of all individuals. Individuals of this size were observed in all sampling periods with the highest number of these smallest individuals observed in Apr/May 04.

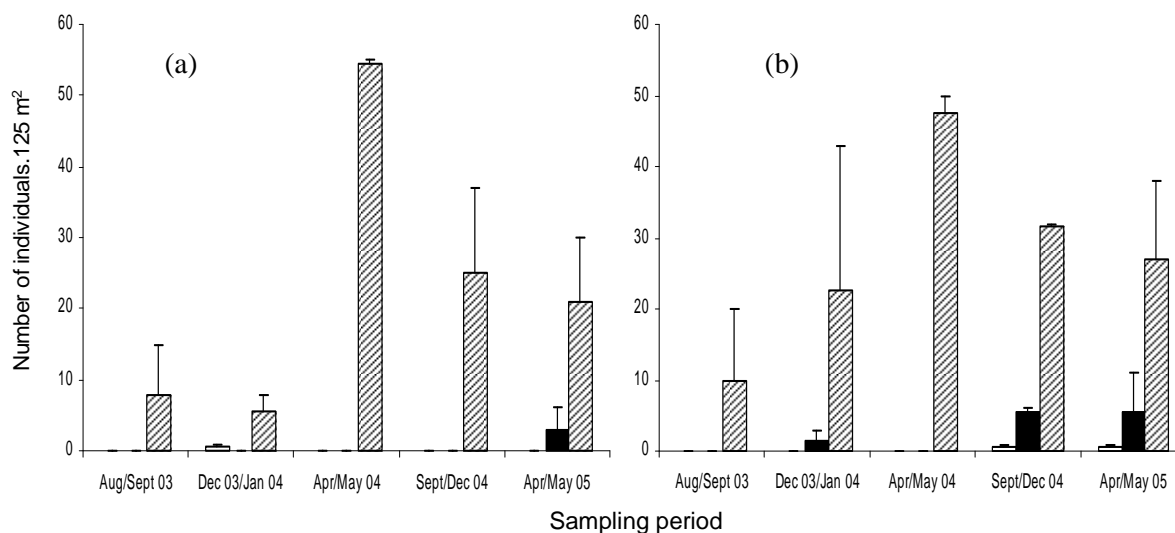


Figure 3.14: Mean (\pm SE) for density of *Austrolabrus maculatus* in fringe (□), barrens (■) and sponge garden (▨) habitat at Terrigal (a) and Norah Head (b) in each combination of HabitatxPeriod (n=2 sites with each site representing the average across 6 transects).

3.3.4.6 *Eupetrichthys angustipes*

A total of 196 *Eupetrichthys angustipes* were observed with most individuals observed in sponge garden habitat (84.6%), followed by barrens and fringe (both 7.7%). Mean habitat densities ranged between 0 and 20.5 ± 1.5 individuals. 125 m^{-2} (Figure 3.15). The effect of habitat on the density of *E. angustipes* varied between locations (Table 3.9; Figure 3.15). However, at each location higher densities were found in the sponge gardens compared with other habitats (Figure 3.15). No differences in density were observed between fringe and barrens habitat at either location.

Most individuals of *E. angustipes* (i.e. 61.7%) belonged to the 50-99 mm size class. The majority of these individuals were recorded in sponge garden habitat, except in Dec 03/Jan 04 when most individuals were observed in fringe habitat.

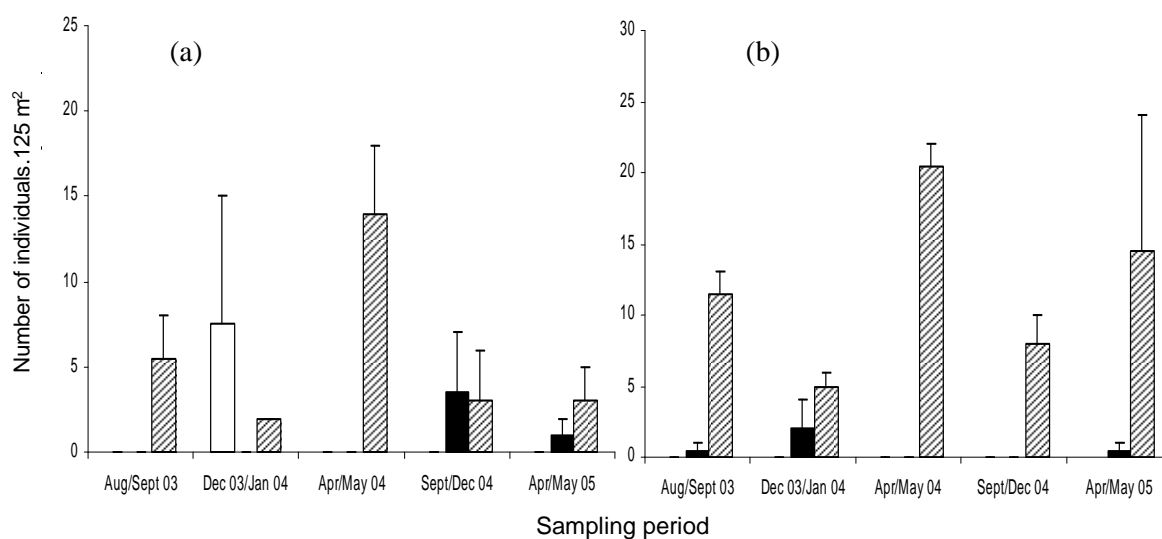


Figure 3.15: Mean (\pm SE) for density of *Eupetrichthys angustipes* in fringe (□), barrens (■) and sponge garden (▨) habitat at Terrigal (a) and Norah Head (b) in each combination of HabitatxPeriod (n=2 sites with each site representing the average across 6 transects).

3.4 Discussion

3.4.1 Labrids of the central coast region of New South Wales

Labrids were found to be visually conspicuous on rocky reefs in the study region, with this family represented by more species than any other family. A total of 19 labrid species were identified, contributing *c.a.* 16% to overall fish richness. Labrid assemblages consisted predominantly of species endemic to temperate waters of Australia, with less frequent occurrences of temperate species with distributions extending to New Zealand and infrequent tropical vagrants with distributions throughout the Indo-West Pacific. Common labrids included *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis*, *Pictilabrus laticlavius*, *Achoerodus viridis*, *Austrolabrus maculatus* and *Eupetrichthys angustipes*. Each of these species was relatively abundant and a permanent member of labrid assemblages within the study region (i.e. found at each location in all sampling periods). Less common labrids included *Coris picta*, *Coris dorsomacula*, *Pseudolabrus guentheri* and *Thalassoma lunare*. These labrids were present in at least 4 of the 5 sampling periods but in relatively low abundance. Rare species included *Anampses caeruleopunctatus*, *Coris sandageri*, *Halichoeres nebulosus*, *Labroides dimidiatus*, *Pseudolabrus luculentus*, *Stethojulis interrupta* and 3 unidentifiable labrids. Each rare species was found only in 3 or less of the 5 sampling periods and at very low abundances. Species accumulation curves revealed that rare species often continued to be found after high levels of sampling intensity suggesting that substantial effort is required to completely sample the full complement of labrid species found on rocky reefs of coastal NSW.

The contribution of labrids to overall fish species was generally between 20 and 35% in all habitats across all sampling periods. This relatively high representation of labrids in fish assemblages concurs with other temperate regions including the Mediterranean (Garcia-Charton and Perez-Ruzafa 1999), New Zealand (Choat *et al.* 1988; Schiel and Hickford 2001), Scotland (Magill and Sayer 2002) and Sweden (Pihl and Wennhage 2002), and is within the range of 12-38% described by Bellwood and Hughes (2001) for coral reef fish assemblages found across the Indian and Pacific Oceans.

Labrid species richness is second only to the gobiids (family Gobiidae) in coastal waters of Australia (Hoese *et al.* 2007) so it is unsurprising that labrids were found to be the most species rich family in the study area. Co-occurrence of the high number of labrid species is testament to the behavioural, dietary and morphological diversity found in this family (see Chapter 4 and Chapter 5). This diversity may promote co-occurrence by the partitioning of resources to reduce the overall competition among species (Helfman *et al.* 1997).

Despite being well represented within fish assemblages with regard to species richness, labrids typically contributed only 2 to 12% to overall fish abundance in all habitats in all sampling periods. This was due to the regular presence of highly abundant schooling species belonging to the families Carangidae, Monodactylidae, Pempheridae, Plesiopidae, Pomacentridae and Scorpididae. Each of these families are predominantly plankton feeders (Kuitert 1993) suggesting limitations on the availability of benthic invertebrate prey may constrain the density of labrid individuals that a rocky reef is able to support. Other families of benthic feeding carnivores were found in the study area, including Serranidae, Monocanthidae and Cheilodactylidae, but these families contribute only 2.2, 0.4 and 0.3% to overall fish abundance.

Across broader areas in temperate eastern Australia, labrids are known to maintain high species richness and high abundance. For example, Gladstone (2007) found labrids to be the most species rich family in sponge garden assemblages on a 140 km stretch of coastline on the central coast of NSW. In this instance, labrids contributed 23% to total fish species and 8.8% to total fish abundance. All families represented by higher abundances of individuals were planktivores. Therefore, results from the present study and that of Gladstone (2007) suggest that labrids are the most successful family of non-planktivorous fish associated with rocky reefs of the central coast of NSW with respect to both species richness and the density of individuals. Further investigations are needed to determine whether the importance of labrids in the study region translates to that in other regions of temperate Australia.

3.4.2 Habitat associations among labrids

The effect of habitat in structuring labrid assemblages often varied between sites, and the nature of this variation often changed with the period of sampling. Overall, labrid assemblages associated with sponge gardens remained the most distinct of all three habitat types. Sponge garden habitat contained a higher species richness, a higher contribution of labrids to total fish species and higher densities of labrids compared to barrens at all sites in all sampling periods. This was also true for comparisons with fringe habitat at most sites in most sampling periods, except for labrid density which was always higher in sponge garden habitat. Contributing to the high richness and density in sponge garden habitat was higher densities of *Austrolabrus maculatus* at most sites in the majority of sampling periods and consistently higher densities of *Eupetrichthys angustipes*. Also, the labrid *Coris dorsomaculata* was recorded only in the sponge garden habitat. Higher overall occurrences of *Ophthalmolepis lineolatus* were recorded in sponge gardens compared to other habitats, but the effect of habitat on the density of individuals was inconsistent across sites and sampling periods. Generally, labrid species richness, density of individuals and assemblage composition did not differ between fringe and barrens habitat. Higher overall densities were recorded in fringe compared to other habitats for *Notolabrus gymnogenis*, *Achoerodus viridis* and *Pictilabrus laticlavius*, but densities of individuals were not consistently higher at all sites in all sampling periods.

These observed patterns of labrid distribution reflect those previously found on the central coast of NSW. For example, Curley *et al.* (2002) found highest overall abundances of *Austrolabrus maculatus*, *Eupetrichthys angustipes* and *Ophthalmolepis lineolatus* occurred in sponge garden habitat; lowest overall abundance of *Pictilabrus laticlavius* occurred in barrens habitat; *Coris picta* occurred only in habitats at depths greater than 13 m; and densities of *Notolabrus gymnogenis* and *Achoerodus viridis* were similar across habitats.

Whilst the habitats defined in the present study are useful for describing patterns of distribution in semi-mobile and sessile benthic organisms in the region (Underwood *et al.* 1991; Andrew 1999), they appear less useful for assemblages of highly mobile species such as fishes. Although labrids as a family represent some species with evident

associations with sponge garden habitat (e.g. *A. maculatus* and *E. angustipes*), this family as a whole is unlikely to be important for describing habitat-related structure in fish assemblages on shallow rocky reefs of NSW as habitat associations were meaningless for most labrid species. In contrast, labrids contribute substantially to distinguishing between fish assemblages associated with shallow reef habitats in New Zealand (Choat and Ayling 1987; Anderson and Millar 2004).

The association of labrids with rocky reefs is undoubtedly influenced, at least in part, by the abundance of invertebrate prey including molluscs, echinoderms, crustaceans and polychaetes (Gillanders 1995b; Denny and Schiel 2001; Shepherd and Clarkson 2001; Shepherd and Brook 2005). However, these taxa are similarly abundant in soft-sediment habitats and contribute substantially to the diet of other fishes (Platell and Potter 1999, 2001; Linke *et al.* 2001; Schafer *et al.* 2002). Therefore, it is likely that limited refuge availability in soft-sediment habitats restricts the distribution of labrids. On rocky reefs, the presence of algal canopies, rocky crevices, and holes beneath and among rocks provide habitat complexity for use as both diurnal and nocturnal refuges from predators, and for preventing displacement by surge during large seas (Sayer *et al.* 1993; Gillanders and Kingsford 1998; Shepherd and Clarkson 2001; see Chapter 4).

The effect of habitat on labrid assemblages was highly variable between sites separated by 250-800 m, but typically did not differ between locations separated by approximately 30 km. Substantial spatial variation in fish assemblages is well documented (Fowler 1990; Meekan and Choat 1997; Floeter *et al.* 2001; Denny 2005), as is the phenomenon of greatest variation occurring at small spatial scales (Curley *et al.* 2002; Anderson and Miller 2004). Spatial inconsistencies in the occurrence of labrids could be due to a number of factors including the observability of individuals and spatial variation in food availability, recruitment and microhabitat representation. The identification and experimentation of these factors is beyond the scope of this chapter but observations of labrid behaviour and investigations into the dietary composition of labrids provides substantial insight into the probable observability of individuals and habitat components most important to these fishes (see Chapter 4 and 5). For example, many *Notolabrus gymnogenis* and *Pictilabrus laticlavius* may not have been observed due to their frequent use of shelter. Refuge seeking behaviour of these and other fishes is an

important consideration for methodological decisions aimed at maximising confidence in the estimations of fish densities based on transect surveying techniques.

3.4.3 Temporal variation and recruitment in labrid assemblages

Evidence of higher labrid richness and densities in the months of April and May (mean sea temperature = 21-22°C: Manly Hydraulics Laboratory), and lowest richness and densities in the months of August to December (mean sea temperature = 18-19°C) suggest sea temperature is important in influencing the dynamics of labrid assemblages. For some temperate labrids, periods of cool water may significantly decrease activity levels (Sayer *et al.* 1993; Costello *et al.* 1997; Arendt *et al.* 2001), thus reducing encounter rates and apparent abundances in surveys. However, this is unlikely within the study region as seasonal temperature fluctuations are not substantial.

Increases in species richness and the density of individuals in late summer and autumn is well recognised in temperate systems owing predominantly to species of tropical origin expanding their distribution in response to seasonally warm sea temperatures at higher latitudes. Holbrook *et al.* (1994) have recognised *Thalassoma lunare*, *Halichoeres nebulosus* and *Stethojulis interrupta* as members of this fauna, with these species indeed contributing to labrid assemblages in the study region. In addition, the present study also found the tropical labrids *Labroides dimidiatus* and *Anampses caeruleopunctatus* present only in periods of warmest sea temperatures. However, these labrids were recorded infrequently and in very low densities so contributed little to the observed increase in species richness and density of individuals in April and May.

A substantial increase in the abundance of recruits of 'common' labrids, particularly *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis*, contributed most to temporal fluctuations in labrid density. The individuals belonging to the smallest size class of each species have only tentatively been termed 'recruits' as the actual size at recruitment for each species is not known. A dramatic rise in the density of *O. lineolatus* recruits occurred in April and May (i.e. Autumn), with most recruitment occurring into sponge garden habitat. Relatively high recruitment of *N. gymnogenis* occurred into fringe habitat from September to May with recruitment peaking in April and May. In these months, relatively high levels of recruitment also occurred into

barrens and sponge garden habitat. Similarly, all recruits of *Achoerodus viridis* were observed in April and May and only in the fringe habitat. In the case of *Austrolabrus maculatus* and *Eupetrichthys angustipes*, an increase in the density of small individuals in sponge garden habitat also typically occurred in April and May. In contrast, the densities of *Pictilabrus laticlavius* recruits were observed to peak at some times of the year, but these events were not seasonal. Most recruitment for this species occurred into fringe habitat.

Recruitment coinciding with warmest sea temperatures in late summer and autumn appears to be the life history strategy employed by many temperate labrids (Sayer *et al.* 1993; Garcia-Rubies and Macpherson 1995; Jones 1999; Magill and Sayer 2002; Pihl and Wennhage 2002). This period of annual recruitment coincides with the settlement of large numbers of crustaceans, including amphipods and copepods, which are important prey items for juvenile labrids (Gillanders 1995b; Jones 1999; Denny and Schiel 2001; Shepherd and Clarkson 2001; Shepherd 2006).

Peaks in the recruitment of the investigated labrids did not necessarily coincide with known peaks in reproductive activity. For example, gonadosomatic indices of *N. gymnogenis* and *A. viridis* peak in winter (Chapter 6; Gillanders 1995b). Recruitment of *A. viridis* is known to peak in September to October (Gillanders 1997b) and it is also likely that this is the period of recruitment for *N. gymnogenis* if the planktonic larval stage is of similar duration. Asynchrony in the period of reproductive activity and the sighting of recruits may be due to the size, behaviour and habitat selection of recruits. For example, both *N. gymnogenis* and *A. viridis* recruit mostly into fringe habitat which has considerable algal coverage that may interfere with sightings of small, recently recruited individuals. Sightings of these individuals may occur only after they become slightly larger and less reliant on algal canopies. Another alternative yet to be tested is that *N. gymnogenis*, like *A. viridis* (Gillanders 1997a), exhibit post-settlement migrations onto coastal rocky reefs from juvenile nurseries in other habitats.

Reproductive activity of *P. laticlavius* peaks in late spring/early summer (Chapter 6; Barrett 1995a), yet this period did not always coincide with recruitment events. Periodic recruitment in *P. laticlavius* was less evident than in other labrids owing to at least two possibilities. Firstly, this species is relatively small with sexual maturity

occurring at sizes of <95 mm and ages of <0.9 years (see Chapter 6). Therefore, the 50-99 mm size class used to define 'recruits' in *O. lineolatus* and *N. gymnogenis* included mature fishes in *P. laticlavius* which are not likely to have been recently recruited into adult populations (i.e. they may be up to 1 year old). Secondly, recruits of *P. laticlavius* are likely to be missed due to their very small size and cryptic behaviour, which proves problematic for visual surveys.

In contrast to other labrids, highest gonadosomatic indices of *O. lineolatus* occur in late summer which precedes the observed peak in recruitment by little more than two months. Sightings of recruits of *O. lineolatus* occur shortly after periods of reproductive activity as small individuals of this species are easily observed on rocky reefs due to their infrequent use of refuges and recruitment mostly into sponge garden habitat which is largely devoid of algal canopies.

The preferential use of shallow algal habitat by recruits of *N. gymnogenis*, *A. viridis* and *P. laticlavius* has also been observed for labrids from other rocky reefs in temperate Australia (Gillanders 1997b; Gillanders and Kingsford 1998; Curley *et al.* 2002; Shepherd and Brook 2003) and New Zealand (Jones 1984a; Choat and Ayling 1987). As juveniles, labrids have reduced mouth size, gape and crushing strength of the pharyngeal jaws (Wainwright 1988; Helfman *et al.* 1997; Shibuno *et al.* 1997; Clifton and Motta 1998), so have a diet restricted principally to amphipods and small molluscs (see Chapter 5) which are abundant in shallow algal habitats (Jones 1999; Edgar 2001; Shepherd and Brook 2005). Therefore, the association of recruits and juveniles with algal habitats is likely to be due to their preferred prey being more available here. Algal habitats may also provide an opportunity to forage in a habitat with reduced competition from larger labrids and other benthic carnivores which are known to avoid feeding in algal cover (Choat and Ayling 1987). Reduced risk of predation is also likely to be offered to species which use refuges created by canopy forming algae.

Algal habitat was less important for recruits of *O. lineolatus* as highest densities of recruits were found in sponge garden habitat. Amphipods and small molluscs are similarly important for recruits and juveniles of *O. lineolatus* (see Chapter 5) suggesting that diet may be less important in explaining size-related distributions for this species than elements of behaviour. For example, *O. lineolatus* utilise shelter substantially less

frequently than *N. gymnogenis* and *P. laticlavius* (see Chapter 4), making *O. lineolatus* individuals far more susceptible to displacement by wave surge in shallow habitats. Furthermore, association of *O. lineolatus* with interfaces between rocky reef and sand flats, as occurs in sponge garden habitat in the study region, may be in response to a need for sandy habitat to bury within for nocturnal refuge (Breder 1951; Tribble 1982; Nanami and Nishihira 1999; Takayanagi *et al.* 2003; see Chapter 4).

3.4.4 Conclusion

Labrids were found to be species rich and abundant on rocky reefs of the central coast region of NSW, and represented the most dominant of all fish families that feed on benthic invertebrates. Habitat associations for most ‘common’ labrids were highly variable, particularly across sites within a single location, but some labrids exhibited strong associations with sponge garden habitat. Increases in labrid density occurred during periods of warmest sea temperatures (i.e. April and May) owing primarily to the ‘recruitment’ of common species. Describing habitat-related patterns, or inconsistencies, in labrid distribution and abundance is meaningless without further explorations into the underlying causes of these observations. Therefore, the following three chapters focus on some of these driving factors by exploring the social organisation and behavioural repertoires (Chapter 4), diet and foraging behaviour (Chapter 5), and reproductive strategies (Chapter 6) of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus gymnogenis*.

Chapter 4:

**Social Organisation
and Behavioural Ecology**

4.1 Introduction

4.1.1 Problem statement and chapter aim

A greater understanding of the ecological role of labrids on temperate rocky reefs and their susceptibility to over-harvesting requires an exploration of their behaviour. Behavioural aspects important in the ecology of labrids include foraging, reproduction, habitat usage, intra-specific and inter-specific interactions, and spatial organisation. For example, information on spatial organisation (e.g. territoriality) aids in understanding the factors that set upper limits to population densities and provides insight into the likely social disruptions caused by the removal of individuals from rocky reef systems. Ethological studies begin with the cataloguing of behavioural routines which are then used to construct a portrait of an animal's behavioural repertoire (Lehner 1996). For most temperate labrids, intensive ethological studies are lacking. This is especially true for labrids of NSW as the behaviour of only *Achoerodus viridis* has been investigated in detail (see Table 1.1). Therefore, the aim of this chapter is to describe the social organisation and behavioural repertoires of three previously unstudied labrids (i.e. *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*). Another major gap in the current understanding of labrid behaviour is that sources of variation in the occurrence of behaviours are poorly understood. In response, special consideration is given to the effect of ontogeny on labrid behaviour and whether ontogenetic differences, if any, are temporally and spatially consistent.

The role of labrids as significant predators of benthic invertebrates in reef systems has seen considerable interest in their foraging behaviour (Hoffman 1983; Gillanders 1995b; Shepherd and Clarkson 2001; Ferry-Graham *et al.* 2002; Fulton and Bellwood 2002b; Martha and Jones 2002; Shepherd and Brook 2005). The interesting reproductive strategy of this family (i.e. protogynous hermaphroditism) has also seen the focus of many studies directed at the reproductive behaviour of labrids (Robertson and Hoffman 1977; Moyer and Yogo 1982; Tribble 1982; Martel and Green 1987; Warner 1987; Sakai and Kohda 2001; Sakai *et al.* 2002; Adreani *et al.* 2004). As foraging and reproductive behaviour are addressed in Chapter 5 and Chapter 6, respectively, it is the purpose of this chapter to outline other elements of behaviour which are part of labrid behavioural repertoires.

4.1.2 Social organisation

Juvenile and initial phase (IP) female labrids are typically home ranging but terminal phase (TP) males may be territorial, home ranging or wide-ranging. Even within a genus, variability among male labrids in their use of space may be considerable. For example, in the genus *Bodianus*, some species have males that defend all-purpose territories with a harem of females, other species have males defending temporary reproductive territories, yet in other species males are not territorial and spawn together in groups (Hoffman 1983). Similarly, the genus *Notolabrus* is known to have both territorial and non-territorial representatives (Barrett 1995b). Nevertheless, most temperate labrids are either territorial or home ranging reef residents that exhibit high site fidelity, often remaining within restricted reef areas for periods in excess of 1 year (Jones 1981; Barrett 1995b; Edgar *et al.* 2004).

The home ranges of juvenile and female labrids often extensively overlap those of conspecifics (Robertson 1981; Barrett 1995b; Shepherd and Clarkson 2001). These home ranges expand with fish size (Jones 1984c, 2005). For example, area usage of *Achoerodus gouldii* increases from 2000 m² in small individuals (180-250 mm), to 4200 m² in mid-sized individuals (300-450 mm) (Shepherd and Brook 2005). Similarly, the home range of *Notolabrus tetricus* rises from 45 m² as juveniles (80-140 mm), to 135 m² as mid-sized individuals (150-200 mm) and up to 2300 m² in large females (>200 mm) (Shepherd and Clarkson 2001). Bigger home ranges are required by larger individuals because of their preference for larger, less common prey that is located mostly by chance encounters (Shepherd and Clarkson 2001).

Males of territorial species typically establish contiguous territories which are aggressively defended year-round from encroachments by neighbouring males (Thresher 1979; Jones 1981; Tribble 1982; Warner 1987; Helfman *et al.* 1997). Estimates of male territory size in Tasmanian labrids include 400-775 m², 280-330 m² and 175 m² for *Notolabrus tetricus*, *Pseudolabrus psittaculus* and *Pictilabrus laticlavius*, respectively (Barrett 1995b). The territory of male labrids encapsulates the home ranges of up to several dozen IP females and may even be occupied by several subordinate, non-spawning males (Thresher 1979). Interactions between males at territory boundaries provide evidence that males defend territorial areas which are

smaller than their non-contiguous optimum (Grant 1997), as the disappearance of a territorial male is followed by territorial expansion by neighbouring males within a day (Tribble 1982).

Territoriality is typically restricted to TP male labrids (Thresher 1979; Jones 1981; Moyer and Yogo 1982; Barrett 1995b; Adreani *et al.* 2004), but IP females are known to defend feeding areas from conspecifics of equal size and, as a result, the feeding areas of IP individuals of equal size usually do not overlap (Robertson 1981). Intraspecific aggression may involve displays, threats, rushes, chases and fighting (Jones and Thompson 1980; Moyer and Yogo 1982; Tribble 1982; Barrett 1995b; Shepherd and Clarkson 2001). Encounters such as these are typically concentrated at territory boundaries (Helfman *et al.* 1997). These interactions may become more frequent if food is concentrated (Shepherd and Clarkson 2001) or during the spawning season (Jones and Thompson 1980; Warner and Hoffman 1980b; Jones 1981; Robertson 1981; Moyer and Yogo 1982; Tribble 1982; Warner 1987).

Labrids with home ranging males include *Notolabrus fucicola* (Barrett 1995b) and *Achoerodus gouldii* (Shepherd and Brook 2005). In both species, males travel over large expanses of reef in excess of 3000 m² in *N. fucicola* (Barrett 1995b; Edgar *et al.* 2004) and 15000 m² in *A. gouldii* (Shepherd and Brook 2005). Yet, these labrids typically remain as permanent reef residents. Another strategy is that of the wide-ranging *Tautoga onitis* which periodically move up to 10 km, often over featureless sandy substrate which acts as a deterrent to most other labrids (Arendt *et al.* 2001).

Cohorts of juvenile labrids typically associate with conspecifics in loose aggregations (Jones 1984c; Martha and Jones 2002; Shepherd *et al.* 2002). However, if densities are low and home ranges of juveniles restricted then individuals of small size may have low encounter rates (Shepherd and Clarkson 2001). As individuals increase in size, heightened competition for resources such as food, refuge, mates and spawning grounds results in an increase in aggressive encounters between cohort members (Jones 1984c). In response, individuals become increasingly solitary and independent when larger (Jones 1980; Robertson 1981; Tupper and Boutilier 1995; Gillanders 1999; Martha and Jones 2002; Shepherd *et al.* 2002).

Resource defence produces both dominance hierarchies and territoriality in fish assemblages (Helfman *et al.* 1997). Dominance hierarchies are commonly exhibited in labrids in which individuals are linearly organised according to size. Typically, the alpha (i.e. most dominant) individual is a large TP male with a harem of smaller IP females who exhibit a dominance hierarchy based on size (Hoffman 1985). In such cases, larger fish will displace individuals of smaller size from prey items and/or feeding areas (Tribble 1982). As females of a harem share a common range and, as foraging behaviour constitutes a major portion of labrid energy expenditure (Fulton and Bellwood 2002b), daily competition for food may result in frequent interactions occurring between these individuals (Shepherd and Clarkson 2001).

Dominance hierarchies are also important for regulating sex change in labrids. When a male is absent from exerting dominance over a harem, the largest female reverses sex and takes over the male role (Sakai *et al.* 2001). Females may make temporary incursions into neighbouring harems to assess social hierarchies and emigrate permanently to another harem if doing so is likely to increase their social rank and further their chances of becoming the alpha male (Sakai *et al.* 2001).

4.1.3 *Inter-specific interactions*

Labrid use of space and access to resources may be influenced by interactions with other species. For example, *Achoerodus viridis* are chased by territorial *Parma microlepis* (Gillanders 1995b, 1999), the crab *Plagusia chabrus* defends shelter sites from juvenile *Notolabrus tetricus* (Shepherd and Clarkson 2001), and agonistic interactions are directed toward labrids by pomacentrids (Martha and Jones 2002) and territorial blennies (Thompson and Jones 1983; Jones 1984c). In addition, interference competition for food has been reported in several labrids (Gillanders 1999; Shepherd and Clarkson 2001).

Commensalism is exhibited in some planktivorous fish by following feeding labrids to prey on disturbed fauna (Gillanders 1999) and/or by labrids benefiting from the feeding activities of other fishes (Helfman *et al.* 1997; Moyle and Cech 2000; Matsumoto and Kohda 2001). Planktivorous fish may also feed directly on labrid spawn (Jones 1981; Tribble 1982; Sakai and Kohda 2001) and at least two species (*Coris dorsomaculata*

and *Thalassoma noronhanum*) are preyed upon by other fishes (Tribble 1982; Francini *et al.* 2000). In tropical Australian waters, labrids represent a substantial portion of the diet of the predatory coral trout *Plectropomus leopardus* (St John 1999; St John *et al.* 2001), but the author is unaware of marine species involved in labrid predation on rocky reefs of temperate Australia. The above examples provide insight into the role labrids undertake in fish assemblages, but intensive studies aimed at exploring and quantifying these interactions are lacking, especially in temperate NSW.

4.1.4 Shelter

Use of shelter is an important component of labrid behaviour. Indeed, the structure of fish assemblages may be significantly influenced by the availability of shelter sites. Shelter is important for providing refuge from predators and wave surge, as areas for concentrated foraging activity, as nocturnal retreats or as nesting sites (Nanami and Nishihira 1999; Steele 1999; Shepherd and Clarkson 2001; Takayanagi *et al.* 2003). In many temperate labrids, dependence on shelter reduces with increasing size in response to dietary shifts from cryptic microcrustaceans associated with algal habitats (e.g. amphipods) to larger, hard-bodied prey items (Jones 1984c; Gillanders 1995b; Denny and Schiel 2001; Shepherd and Clarkson 2001; Shepherd 2006). For example, percentage of time emergent from shelter for *Achoerodus gouldii* increases from 46% in small individuals (180-250 mm), to 66% in mid-sized individuals (300-450 mm), to 100% in large adults (750-800 mm) (Shepherd and Brook 2005).

In temperate reef systems, shelter is provided by macroalgae (Jones 1984a; Choat and Ayling 1987; Curley *et al.* 2002), and holes, crevices and caves within, beneath and between rocks (Gillanders and Kingsford 1998). Soft sediments and coral fragments are important as refuges and/or nesting sites for other labrids (Breder 1951; Tribble 1982; Nanami and Nishihira 1999; Takayanagi *et al.* 2003). Individuals may spend the majority of their time within shelter (e.g. *Pictilabrus laticlavius*: Barrett 1995b) or periodically return to shelter between bouts of foraging (e.g. *Notolabrus tetricus*: Shepherd and Clarkson 2001).

The use of shelter as a place of refuge is particularly important for species that remain inactive or have reduced activity levels in periods of lowered water temperatures (Sayer

et al. 1993; Costello *et al.* 1997; Arendt *et al.* 2001). Due to reduced fluctuations in sea temperature in temperate Australia, labrids are active throughout the year (Barrett 1995b), but may become less active during periods of high wave energy (Shepherd and Clarkson 2001).

4.1.5 Other behaviours

Studies of labrid behaviour have generally focused solely on one component of the behavioural repertoire of a species (e.g. foraging, social interactions or reproductive behaviour). Few studies attempt to investigate the broad range of behaviours exhibited by a species in an attempt to construct more fully its complete behavioural repertoire. One of the few examples of such a study is that of Martha and Jones (2002) who categorised 19 behaviours in five *Halichoeres* and one *Thalassoma* species, including behaviours novel to literature including eye flickering, tail curling, body rubbing, bobbing and tail flicking. Another ‘novel’ behaviour is that of rapid colour change exhibited by TP individuals of *Halichoeres maculipinna* and *Halichoeres garnoti* when chasing IP fish or fighting with TP conspecifics (Robertson 1981).

These behaviours are rarely quantified or qualitatively examined to determine their importance for individuals and/or labrid populations. This represents a significant gap in current descriptions of labrid behavioural repertoires and places constraints on comparative behavioural studies among fishes. Whether these behaviours are deemed ecological ‘unimportant’ so are excluded from behavioural studies of most labrids or do not occur in other labrids is not known.

4.1.6 Temporal and spatial consistency of behaviours

One of the significant gaps in the current understanding of labrid behaviour is that sources of variation in the occurrence of behaviours are rarely identified. Yet, these sources of variation may be highly significant to marine researchers. For example, if labrids were to concentrate the majority of their activity to a particular time of the day then surveys of labrid assemblages may be ineffective if conducted outside these periods of activity. Most studies that have identified sources of variation in labrid behaviour are restricted to those focusing primarily on foraging (e.g. Gillanders 1995b;

Shepherd and Clarkson 2001; Shepherd and Brook 2005), are restricted to a single behaviour (e.g. Edgar *et al.* 2004), investigate only ontogenetic shifts in behaviour (e.g. Martha and Jones 2002), or deal only with spatial replication (e.g. Bansemer *et al.* 2002). Therefore, high importance has been placed in the methods of this chapter to test simultaneously the effect of several potential sources of variation on the behaviour of labrids.

4.1.7 Overview and chapter objectives

The social organisation and behaviour of most labrids of temperate Australia are not well understood despite being species-rich and abundant in the region. Some of the major gaps in the current understanding of labrid behaviour are that the behaviour of most common labrids has not been described, behavioural diversity of labrids is poorly understood, the ecological significance of behaviours are rarely explored and sources of variation in the occurrence of behaviours are not recognised.

Therefore, the social organisation and behavioural ecology of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* are explored to investigate the size and type (i.e. home range/territory) of area usage; estimate periods of residency; investigate social interactions; quantify various behavioural acts (i.e. lying, use of shelter, side-swiping, bending and gaping); and to test for differences among life history stages in the occurrence of behaviours and determine whether differences, if any, are spatially and temporally consistent. Qualitative descriptions of labrid behaviour are also provided including cleaning behaviour and colour change.

4.2 Methods

4.2.1 Study area and locations

The behaviour of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* was investigated between August 2003 and January 2005 at Catherine Hill Bay and Norah Head on the central coast of NSW. A detailed description of the study area and each location is provided in Chapter 2.

4.2.2 Sampling strategy

For each species, the behaviour of five individuals was recorded for each of three life history stages (Juv. = juvenile, IP = initial phase, TP = terminal phase), at three times of the day (morning 0700-0930 hr, midday 1130-1400 hr, afternoon 1530-1800 hr), in two sampling periods (Period 1 = February to April 2004, Period 2 = September 2004 to January 2005), and at two locations (Catherine Hill Bay, Norah Head) (Table 4.2). The behaviour of each individual (n=180 individuals/species) was recorded for 10 min periods as determined from the pilot study (Chapter 2). Behavioural observations, including those conducted for the pilot study, totalled 126 h.

Behaviours were recorded on SCUBA with a handheld, underwater, digital video camera (Sony™ digital handycam within an Amphibico™ housing). A focal-animal sampling approach was used (Lehner 1996) in which individuals were haphazardly selected and followed at a distance which did not initiate diver-related behaviour (e.g. cessation of feeding, avoidance or attraction). This distance was approximately 2 m. Observations were not made when water visibility was less than 5 m.

Individuals were classified to the appropriate life history stage by a combination of length and colouration. Juveniles of *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis* were <120 mm and IP females and TP males were 120-250 mm and >250 mm, respectively. Juveniles of *Pictilabrus laticlavius* were <80 mm, and IP females and TP males were 100-160 mm and 140-200 mm, respectively. Sexual dichromatism assisted in classifying individuals as either IP females or TP males (see Chapter 1).

Digital footage was transferred to VHS video cassette and analysed with the option to pause activities as the behaviours were documented. This method was preferred over the recording of behaviours *in situ* on waterproof paper as behavioural repertoires could be continuously documented. It also eliminated the problems of losing sight of an individual and failing to observe important behaviours as information was transcribed. Documented behaviours were total encounters with other fish; frequency of dominant and subordinate interactions; percentage of time lying; percentage of time within shelter and type of shelter used; side-swiping, bending and gaping rates; and qualitative notes of other behaviours (e.g. cleaning by clingfishes and colour change). Observations recorded during the pilot study were pooled with the main study for detailed descriptions of intra-specific and inter-specific encounters/interactions, as well as for all qualitative notes on cleaning and colour changing behaviour. A full description of observed behaviours is provided in Table 4.1 and photographs of several of these are supplied in Appendix 3.

The area of reef used by each focal individual was recorded *in situ* on prepared maps copied onto waterproof paper. Area usage (m^2) was determined by the minimum convex polygon method (Lehner 1996). For some life history stages of *O. lineolatus* and *N. gymnogenis*, several individuals were able to be re-identified using unique facial and/or body markings. The period of residency was calculated for these individuals by determining the number of days between the first and final sighting, and an estimation of home range/territory size was made by applying the minimum polygon method to repeated areas of reef used.

Table 4.1: Descriptions of behaviours performed by *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* in 126 hours of SCUBA observations. Behaviours denoted by an asterisk have accompanying photographs provided in Appendix 3.

Encounters/interactions	
Encounters	Episodes whereby other non-cryptic fish come within 2 m of the focal individual.
Dominant interactions	Another fish moves away from the focal individual.
Subordinate interactions	The focal individual moves away from another fish.
Passive interactions	Dominant or subordinate interaction not involving following, chasing, posturing threats or courting.
Active interactions	Dominant or subordinate interaction involving following, chasing, posturing threats or courting.
Lying*	Remaining motionless, or nearly motionless, resting on the abdomen or side whilst foraging, resting and/or being cleaned. Often accompanied by pectoral fin movements to maintain body position.
Shelter	Use of canopy algae (i.e. <i>Ecklonia radiata</i> , <i>Phyllospora comosa</i> and/or mixed species of algae), rock holes/crevices or disposed steel structures, or rock/algal complexes (shelter provided by both rocky substrate and its associated mixed species of algae).
Cleaning by clingfishes (Gobiesocidae)*	Cleaning services provided by clingfish (family Gobiesocidae). Clingfish move over the head, fins and body of the focal individual to remove parasites and dead tissue.
Side-swiping*	Focal individual swipes one side of its body, or head, on the surface of hard substrate (i.e. rock or steel structure), sandy sediment or algal fronds.
Bending*	Flexure of the body as a head twitch, 'C' body bend or 'S' body bend.
Gaping*	Focal individual widely opens the mouth to display its prominent caniform teeth.
Colour change	Use of chromatophores to rapidly alter colour patterns of the body.

4.2.3 Data analyses

A four-factor mixed model analysis of variance (ANOVA) using GMAV5 software (Institute of Marine Ecology: University of Sydney) was used to test for differences in rates of behaviour, or proportion of time engaged in a behaviour, among life history stages for each species and to determine whether differences, if any, were consistent at all times of the day, in each period of sampling and at both locations (Table 4.2). Assumptions of homogeneity of variance were tested using Cochran's C test. Data

were transformed when variances were heterogeneous (Underwood 1981). Where significant main effects and/or interactions were found, *post hoc* tests were performed in GMAV5 using the Student-Newman-Keuls (SNK) test (Underwood 1981).

Table 4.2: Four-factor mixed ANOVA model used to test the effect of life history stage, location, time of day and sampling period on selected behaviours of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*.

Factor	No. of Levels	Fixed (F) or Random (R)	Levels
Stage	3	F	Juvenile, Initial phase, Terminal phase
Location	2	R	Catherine Hill Bay, Norah Head
Time of day	3	F	Morning (0700-0930 hr), Midday (1130-1400 hr), Afternoon (1530-1800 hr)
Period	2	F	Period 1 (Feb-Apr 04), Period 2 (Sept 04 – Jan 05)
(Replicates = 5)			
(Total observational units = 180)			

4.3 Results

4.3.1 Area usage and residency

The area of reef used by individuals was highest in *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis*, and lowest in *Pictilabrus laticlavius* (Figure 4.1). In all species, area usage varied among life history stages with the area used by juveniles always significantly lower than that of terminal phase individuals (Table 4.3; Figure 4.1). For example, area usage 10 min^{-1} ($\pm \text{SE}$) of juvenile and TP individuals was 27.6 ± 4.4 and $267.8 \pm 39.7 \text{ m}^2$ for *O. lineolatus*, 20.0 ± 2.7 and $129.4 \pm 9.5 \text{ m}^2$ for *N. gymnogenis*, and 4.6 ± 0.7 and $39.4 \pm 6.1 \text{ m}^2$ for *P. laticlavius*, respectively. Area usage increased from juvenile to IP to TP individuals of *O. lineolatus*, except IP was not different to TP at midday at Norah Head and in the afternoon at Catherine Hill Bay (SxTxL interaction, $P < 0.05$). Similar ontogenetic shifts in area usage occurred for this species at both locations in both sampling periods except at Norah Head in period 1 where area use of IP was similar to juveniles and TP individuals (SxLxP interaction, $P < 0.001$). Area usage for *N. gymnogenis* increased from juvenile to IP to TP individuals and area usage of juvenile and IP juveniles of *P. laticlavius* was lower than that of TP individuals.

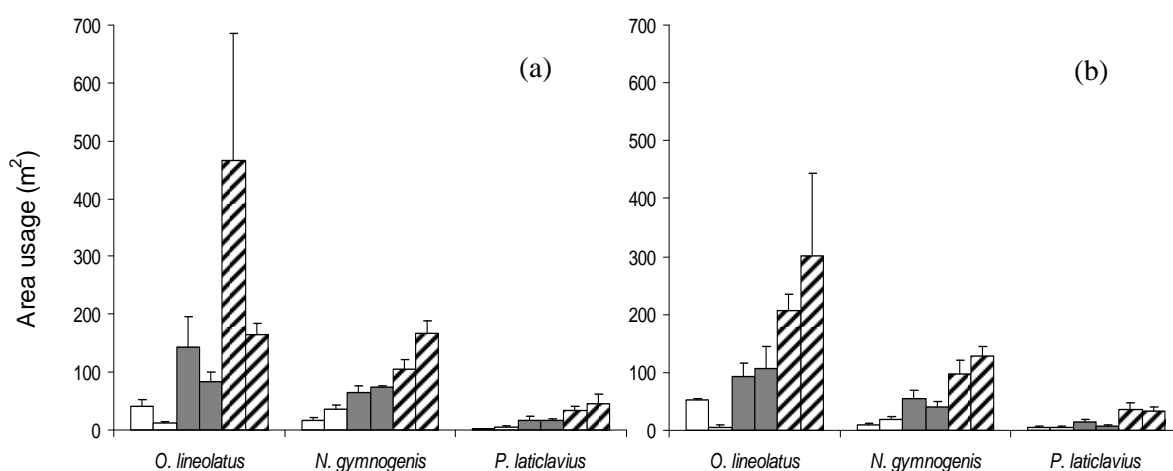


Figure 4.1: Mean area usage ($\pm \text{SE}$) in 10 minutes at Catherine Hill Bay (a) and Norah Head (b) for juvenile (\square), initial phase (\blacksquare) and terminal phase (\hatched) individuals of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* in two periods of sampling (replicated columns). All combinations of Stage \times Location \times Period are shown for each species ($n=3$ times of day with each time representing the average of five 10 minute replicates).

Table 4.3: Univariate ANOVA results for area usage ($\text{m}^2 \cdot 10 \text{ min}^{-1}$) for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. All data $\ln(x+1)$ transformed (Cochran's C test, $P > 0.05$). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source of variation	df	<i>O. lineolatus</i>		<i>N. gymnogenis</i>		<i>P. laticlavius</i>	
		MS	F	MS	F	MS	F
Stage (S)	2	105.90	293.59**	62.50	74.77*	48.13	37.34*
Time of day (T)	2	1.78	10.16	2.10	1.58	0.27	0.24
Location (L)	1	1.16	1.69	7.31	17.83***	1.43	1.93
Period (P)	1	23.50	27.55	5.94	3.65	0.01	0.00
S x T	4	0.47	0.22	0.54	3.44	0.20	0.15
S x L	2	0.36	0.53	0.84	2.04	1.29	1.74
S x P	2	11.82	1.90	0.74	3.70	1.45	2.10
T x L	2	0.18	0.26	1.33	3.24*	1.09	1.47
T x P	2	0.48	4.37	0.98	74.50*	0.07	0.27
L x P	1	0.85	1.25	1.63	3.96*	1.66	2.24
S x T x L	4	2.14	3.13*	0.16	0.38	1.31	1.77
S x T x P	4	1.07	2.42	0.23	0.61	1.02	2.18
S x L x P	2	6.23	9.09***	0.20	0.49	0.69	0.93
T x L x P	2	0.11	0.16	0.01	0.03	0.27	0.37
S x T x L x P	4	0.44	0.64	0.38	0.93	0.47	0.63
Residual	144	0.69		0.41		0.74	

A total of 21 *O. lineolatus* and 24 *N. gymnogenis* individuals were reliably re-identified using unique facial and/or body markings (Table 4.4). Juvenile *O. lineolatus* often associated with others of similar size on restricted reef patches, but became more independent and used larger areas of reef with an increase in size. This species was broad ranging and non-territorial with home ranges of at least 560 m^2 and 2500 m^2 in IP and TP individuals, respectively. However, home ranges are likely to be far greater as individuals would frequently move outside the study area. For example, one TP individual at Catherine Hill Bay travelled in a uniform direction for 90 m in 5 mins before being lost from sight. Likewise, a TP individual at Norah Head travelled along a rock wall for 170 m over a 9 minute interval without stopping. Up to 8 IP and 1 TP *O. lineolatus* moved independently over a common reef area and converged onto restricted reef patches only when feeding opportunities arose (e.g. substrate disturbance caused by the action of diver's fins). Residency for *O. lineolatus* typically lasted from several months to nearly one year (i.e. 350 days) with individuals regularly moving outside the study area for periods of hours to weeks. Populations remained stable by the immigration of IP and TP individuals from adjacent reefs.

In contrast, TP *N. gymnogenis* were highly territorial, defending reef areas of *ca.* $400\text{--}600 \text{ m}^2$ from rival TP males (Table 4.4; Figure 4.2). All chases between TP individuals occurred at territorial boundaries (Figure 4.2). Chases occurred only when territorial

boundaries were crossed. For example, TP males were found within 4 m of one another on several occasions but aggressive interactions did not transpire as the territorial boundary passed between the individuals. TP territories were held for up to at least 20 months (i.e. 593 days). IP individuals of *N. gymnogenis* used areas of up to 400 m² for at least 22 months (i.e. 665 days) with the majority of their activity contained within the territory of a single TP male (Table 4.4; Figure 4.3). Each IP *N. gymnogenis* shared a TP territory with approximately 8-10 other IP individuals of various sizes. Fights between similar sized IP *N. gymnogenis* generally occurred at the territorial boundaries of TP individuals. Of the 17 IP *N. gymnogenis* that could be re-identified on at least two successive occasions, 7 were always resighted within the territory of a single male, 6 concentrated the majority of their activity within the territory of a single male but had short excursions of up to 5 m into the territory of an adjacent male, and 4 had home ranges that considerably overlapped the territories of at least two males (Figure 4.3).

Table 4.4: Home range/territory sizes and residency times of known individuals of *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis*. Only those individuals observed on at least two occasions are shown. Home range/territory and residency times must be treated as minimums. Life history stages are initial phase (IP) and terminal phase (TP). Locations (Loc.) are Catherine Hill Bay (C) and Norah Head (N). Total number of times the individual was observed (obs.) is shown. Coloured asterisks denote individuals of *N. gymnogenis* represented in Figure 4.2 and Figure 4.3, respectively.

Species and Stage	Loc.	Area usage min-max (m ² .10 mins ⁻¹)	Home range/ territory (m ²)	Territorial?	Period of residency (days)	Obs.
<i>Ophthalmolepis lineolatus</i>						
IP	N	-	-	No	2	2
IP	N	120-376	560	No	48	2
IP	N	37-58	116	No	53	2
IP	N	-	-	No	97	2
IP	N	25-78	316	No	238	7
IP/TP	N	-	80	No	28	3
IP/TP	N	54-222	450	No	41	5
IP/TP	N	-	470	No	91	3
IP/TP	C	36-418	1256	No	110	4
IP/TP	N	41-112	310	No	152	3
IP/TP	N	18-356	1311	No	302	10
IP/TP	N	-	800	No	350	2
TP	C	101-177	628	No	1	4
TP	C	160-270	604	No	11	3
TP	C	-	50	No	12	3
TP	C	44-58	292	No	24	2
TP	N	-	196	No	63	2
TP	N	-	420	No	63	2
TP	N	33-628	844	No	67	4
TP	N	172-481	344	No	86	2
TP	C	71-542	2456	No	259	18
<i>Notolabrus gymnogenis</i>						
* IP	C	47-101	260	Yes	2	2
* IP	C	-	92	Yes	8	2
* IP	C	13-59	128	Yes	31	4
* IP	C	22-27	48	Yes	42	2
* IP	C	-	26	Yes	52	2
* IP	C	66	66	Yes	52	3
* IP	C	60-61	106	Yes	52	2
* IP	C	-	66	Yes	64	2
* IP	C	64-81	152	Yes	226	3
* IP	C	60	72	Yes	253	2
* IP	C	54-149	188	Yes	357	6
* IP	C	-	224	Yes	372	3
* IP	C	30	136	Yes	458	2
* IP	C	61-192	392	Yes	527	7
* IP	C	27-61	166	Yes	564	8
* IP	C	58-136	288	Yes	627	7
* IP	C	41-80	160	Yes	665	4
TP	C	74-378	380	Yes	20	2
TP	C	117-134	356	Yes	45	3
* TP	C	68-77	122	Yes	54	2
* TP	C	14-275	632	Yes	278	9
* TP	C	92-262	544	Yes	394	6
* TP	C	38-293	576	Yes	540	8
* TP	C	22-271	540	Yes	593	10

4.3.2 Interactions

4.3.2.1 Overall interactions

The mean overall encounter rate of *Ophthalmolepis lineolatus* with other fish was 24.4 ± 1.0 encounters.10 mins⁻¹, of which 18.2 and 13.3% of all encounters were classified as dominant and subordinate interactions, respectively. Dominant/subordinate interactions involved ‘passive’ movement of other fish/the focal individual and ‘active’ following, chasing and courting. Juveniles encountered other fish less frequently than IP individuals which themselves were lower than TP individuals in period 2 (SxP interaction, $P < 0.05$) and at Norah Head (SxL interaction, $P < 0.05$) (Table 4.5; Figure 4.4a). The number of dominant interactions.10 min⁻¹ increased from juvenile (1.2 ± 0.3) to IP (3.7 ± 0.4) to TP (8.8 ± 0.9) individuals (Table 4.5). Dominant interactions occurred more frequently at Catherine Hill Bay compared to Norah Head. Subordinate interactions.10 min⁻¹ were more frequent in IP individuals (4.2 ± 0.5) than TP individuals (1.9 ± 0.3) (Table 4.5).

The mean overall encounter rate of *Notolabrus gymnogenis* with other fish was 28.2 ± 1.4 encounters.10 mins⁻¹, of which 33.1 and 6.4% of all encounters were classified as dominant and subordinate interactions, respectively. Juveniles encountered other fish less frequently than TP individuals at all times of the day, and less frequently than IP at midday and in the afternoon (SxT interaction, $P < 0.05$) (Table 4.6; Figure 4.4b). Encounters and dominant interactions increased from juvenile to IP to TP individuals at Norah Head (both SxL interactions, $P < 0.05$). At Catherine Hill Bay, dominant interactions were less frequent in juvenile individuals compared to IP and TP (Table 4.6). Subordinate interactions were less frequent in TP compared to both juvenile and IP individuals at Norah Head in period 1 and Catherine Hill Bay in period 2, and to juveniles only at Catherine Hill Bay in period 1 (SxLxP interaction, $P < 0.01$) (Table 4.6).

The mean overall encounter rate of *Pictilabrus laticlavius* with other fish was 13.7 ± 0.9 encounters.10 mins⁻¹, of which 17.5 and 10.9% of all encounters were classified as dominant and subordinate interactions, respectively. The effect of life history stage on the rate of encounters with other fish differed between locations, and the nature of this

variation was inconsistent across sampling periods (SxLxP interaction, $P < 0.05$) and inconsistent across times of the day (SxTxL interaction, $P < 0.05$) (Table 4.7; Figure 4.4c). Dominant interaction rates were always higher for TP than either juvenile or IP individuals, with IP individuals higher than juveniles only at Catherine Hill Bay (SxL interaction, $P < 0.05$) (Table 4.7). Dominant interactions were more frequent in period 2. Subordinate interaction rates did not differ between life history stages, but subordinate interactions were more frequent at Catherine Hill Bay (Table 4.7).

Table 4.5: ANOVA results for *Ophthalmolepis lineolatus* for rates (10 min^{-1}) of encounters, dominant interactions and subordinate interactions with other fishes. All data square-root ($x+1$) transformed (Cochran's C test, $P > 0.05$). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source of variation	df	Encounters with other fish		Dominant interactions		Subordinate interactions	
		MS	F	MS	F	MS	F
Stage (S)	2	9.35	2.47	37.16	184.31**	4.45	20.15*
Time of day (T)	2	3.26	0.41	0.62	0.42	0.36	11.32
Location = (L)	1	20.00	19.30***	2.73	4.62*	2.88	6.71*
Period (P)	1	13.35	14.00	1.28	4.71	1.01	0.18
S x T	4	1.65	0.87	0.82	1.48	0.49	1.52
S x L	2	3.79	3.65*	0.20	0.34	0.22	0.51
S x P	2	12.29	36.52*	2.34	4.97	4.39	4.03
T x L	2	7.92	7.64***	1.50	2.53	0.03	0.07
T x P	2	3.57	1.55	0.08	0.76	0.65	2.29
L x P	1	0.95	0.92	0.27	0.46	5.71	13.28***
S x T x L	4	1.90	1.84	0.56	0.94	0.32	0.75
S x T x P	4	0.74	0.52	0.50	1.12	0.90	2.06
S x L x P	2	0.34	0.32	0.47	0.80	1.09	2.54
T x L x P	2	2.30	2.22	0.10	1.17	0.29	0.66
S x T x L x P	4	1.43	1.38	0.44	0.75	0.44	1.02
Residual	144	1.04		0.59		0.43	

Table 4.6: ANOVA results for *Notolabrus gymnogenis* for rates (10 min^{-1}) of encounters, dominant interactions and subordinate interactions with other fishes. ¹data square-root ($x+1$) transformed, ²data $\ln(x+1)$ transformed (Cochran's C test, $P > 0.05$). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Source of variation	df	Encounters with other fish ¹		Dominant interactions		Subordinate interactions ²	
		MS	F	MS	F	MS	F
Stage (S)	2	19.67	0.82	2186.5	11.55	7.69	4.19
Time of day (T)	2	5.92	1.68	266.1	3.34	0.33	0.27
Location (L)	1	2.51	1.28	172.1	2.98	3.21	9.88**
Period (P)	1	31.41	2.54	568.9	28.44	5.46	1.66
S x T	4	3.69	6.56*	199.8	5.11	0.62	3.76
S x L	2	23.96	12.20***	189.3	3.28*	1.84	5.65**
S x P	2	2.12	1.55	43.0	2.05	0.16	0.07
T x L	2	3.52	1.79	79.7	1.38	1.26	3.87*
T x P	2	1.16	0.22	23.2	0.54	0.22	0.16
L x P	1	12.39	6.31*	20.0	0.35	3.28	10.09**
S x T x L	4	0.56	0.29	39.1	0.68	0.16	0.51
S x T x P	4	4.91	4.57	49.9	1.19	0.16	0.48
S x L x P	2	1.37	0.70	21.0	0.36	2.10	6.46**
T x L x P	2	5.26	2.68	42.8	0.74	1.34	4.12*
S x T x L x P	4	1.07	0.55	41.8	0.72	0.33	1.03
Residual	144	1.96		57.7		0.33	

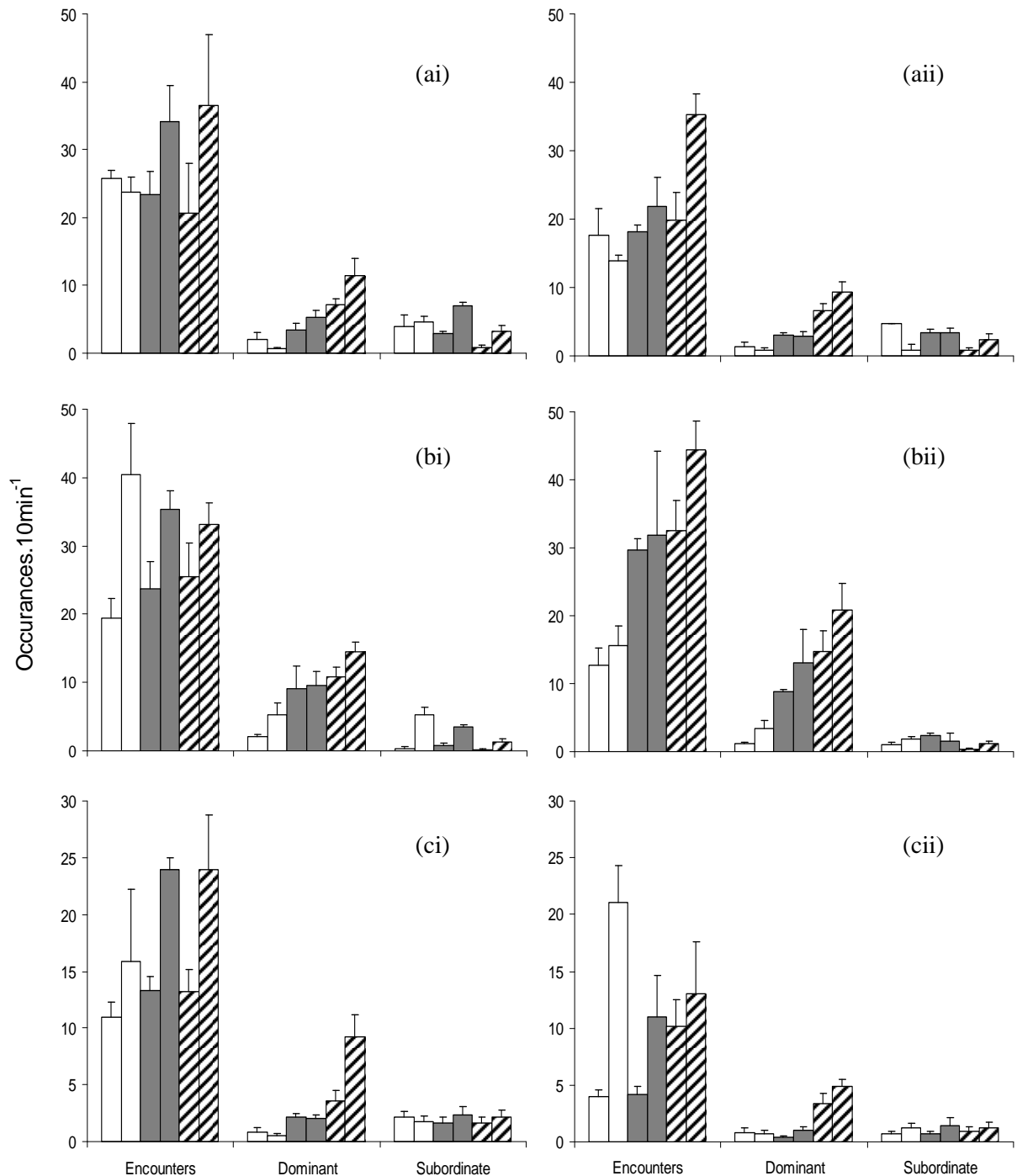


Figure 4.4: Mean rate (\pm SE) of encounters, dominant interactions and subordinate interactions with all other fish at Catherine Hill Bay (i) and Norah Head (ii) for juvenile (\square), initial phase (\blacksquare) and terminal phase (\hatched) individuals of *Ophthalmolepis lineolatus* (a), *Notolabrus gymnogenis* (b) and *Pictilabrus laticlavius* (c) in two periods of sampling (replicated columns). All combinations of Stage \times Location \times Period are shown for each species ($n=3$ times of day with each time representing the average of five 10 minute replicates).

Table 4.7: ANOVA results for *Pictilabrus laticlavius* for rate (10 min^{-1}) of encounters, dominant interactions and subordinate interactions with other fishes. ¹data square-root ($x+1$) transformed, ²data $\ln(x+1)$ transformed (Cochran's C test, $P>0.05$). * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

Source of variation	df	Encounters with other fish ¹		Dominant interactions ²		Subordinate interactions	
		MS	F	MS	F	MS	F
Stage (S)	2	2.04	0.32	16.42	9.47	0.11	19.00
Time of day (T)	2	4.52	52.05*	0.46	2.94	8.04	5.22
Location (L)	1	43.54	25.94***	4.96	10.37**	40.14	11.16**
Period (P)	1	50.65	35.47	1.10	676.01**	6.81	7.25
S x T	4	2.12	0.49	0.43	2.78	3.21	0.44
S x L	2	6.35	3.78*	1.73	3.63*	0.01	0.00
S x P	2	2.78	0.36	1.01	1.53	1.21	0.84
T x L	2	0.09	0.05	0.16	0.33	1.54	0.43
T x P	2	0.24	0.99	0.09	2.57	1.17	0.58
L x P	1	1.43	0.85	0.00	0.00	0.94	0.26
S x T x L	4	4.32	2.57*	0.16	0.33	7.23	2.01
S x T x P	4	1.01	0.26	0.20	0.46	2.80	0.65
S x L x P	2	7.70	4.59*	0.66	1.38	1.44	0.40
T x L x P	2	0.24	0.14	0.04	0.07	2.01	0.56
S x T x L x P	4	3.88	2.31	0.43	0.91	4.28	1.19
Residual	144	1.68		0.48		3.60	

4.3.2.2 Specific Interactions

Ophthalmolepis lineolatus, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* engaged more frequently in intra-specific than inter-specific encounters. Most intra-specific encounters involved juvenile and IP individuals (Figure 4.5-4.7). An intra-specific size-based dominance was evident in all species with a rise in dominant interactions and reduction in subordinate interactions with progressive life history stage. For example, IP *O. lineolatus* were dominant over juvenile *O. lineolatus* in 34% of encounters, but rarely were they subordinate to these individuals (1% of encounters) (Figure 4.5 middle). However, IP *O. lineolatus* were subordinate in 75% of encounters with TP *O. lineolatus* (Figure 4.5 middle). Courting behaviour (see Chapter 6) was regularly observed and contributed 67, 66 and 95% to all subordinate/dominant interactions between IP and TP individuals of *O. lineolatus* (n=126), *N. gymnogenis* (n=184) and *P. laticlavius* (n=167), respectively.

Dominant interactions with conspecifics of similar size (i.e. same stage) most often involved an active response in the form of rapid chases or adoption of visual posturing threats (involving flared dorsal fins and/or lateral arching) for *N. gymnogenis* and *P. laticlavius*. For *O. lineolatus*, non-courting active interactions were infrequent for all

stages and typically involved the larger individual following closely behind the smaller individual, rather than rapid chases or visual posturing.

Each species frequently encountered other labrids. *O. lineolatus* and *P. laticlavus* encountered substantially more *N. gymnogenis* than any other labrid (Figure 4.5 and 4.7). A size-based dominance hierarchy was evident among labrids. For example, interactions with the large labrid *Achoerodus viridis* involved this species taking on a dominant role over all stages of the three focal species, except for 1% of encounters with TP *O. lineolatus*. Similarly, *N. gymnogenis* were typically dominant over both *O. lineolatus* and *P. laticlavus* as this labrid is morphologically deep bodied and typically larger than either of the latter two species.

Dominant and subordinate encounters between *O. lineolatus* and other labrids were typically passive (i.e. did not involve chases, following or posturing); however, *O. lineolatus* individuals were chased on 5 occasions by *N. gymnogenis* (IP and TP) and *P. laticlavus* (TP only). A high proportion of active interactions occurred between juvenile and IP individuals of *N. gymnogenis* and the labrids *Pseudolabrus guentheri* and *P. laticlavus* (Figure 4.6). For IP individuals, all active interactions with these species involved *N. gymnogenis* assuming a dominant role. Most dominant and subordinate encounters between *P. laticlavus* and other labrids were passive, except for TP *P. laticlavus* which were chased in a high proportion of encounters with *N. gymnogenis* and *P. guentheri* (Figure 4.7).

Regular encounters occurred between the focal species and non-labrids (Figure 4.5-4.7). Non-labrid encounters included Acanthuridae, Aplodactylidae (*Crinodus lophodon*), Blennidae (*Plagiotremus tapeinosoma*), Cheilodactylidae (*Cheilodactylus fuscus*), Microcanthidae (*Atypichthys strigatus*), Mullidae (*Parupeneus signatus* and *Upeneichthys vlamingii*), Pempheridae (*Pempheris compressa*), Plesiopidae (*Trachinops taeniatus*), Pomacentridae (*Parma microlepis*, *Parma unifasciata* and *Chromis hypsilepis*) and Scorpionidae (*Scorpius lineolata*). These fishes would typically move away from an approaching labrid if the labrid was larger.

Active inter-specific dominant and subordinate interactions for *O. lineolatus* and *N. gymnogenis* occurred mostly with *Parma microlepis* (Pomacentridae) and less

frequently with *Plagiotremus tapeinosoma* (Blennidae). Chases by *P. microlepis* were prompted by its nest defence and occurred in 2 and 6% of all encounters with *N. gymnogenis* (n=1523) and *O. lineolatus* (n=620), respectively. Reciprocated chasing of *P. microlepis* was infrequent. Attacks from *P. tapeinosoma* involving a rapid strike in an attempt to remove scales or tissue were rare, but occurred in 26 and 50% of all encounters with TP *N. gymnogenis* (n=67) and TP *O. lineolatus* (n=6), respectively. Attacks on TP *N. gymnogenis* typically prompted retaliation in the form of a rapid counter-chase lasting up to 5 seconds. Active dominant and subordinate interactions between *P. laticlavus* and non-labrids were rare.

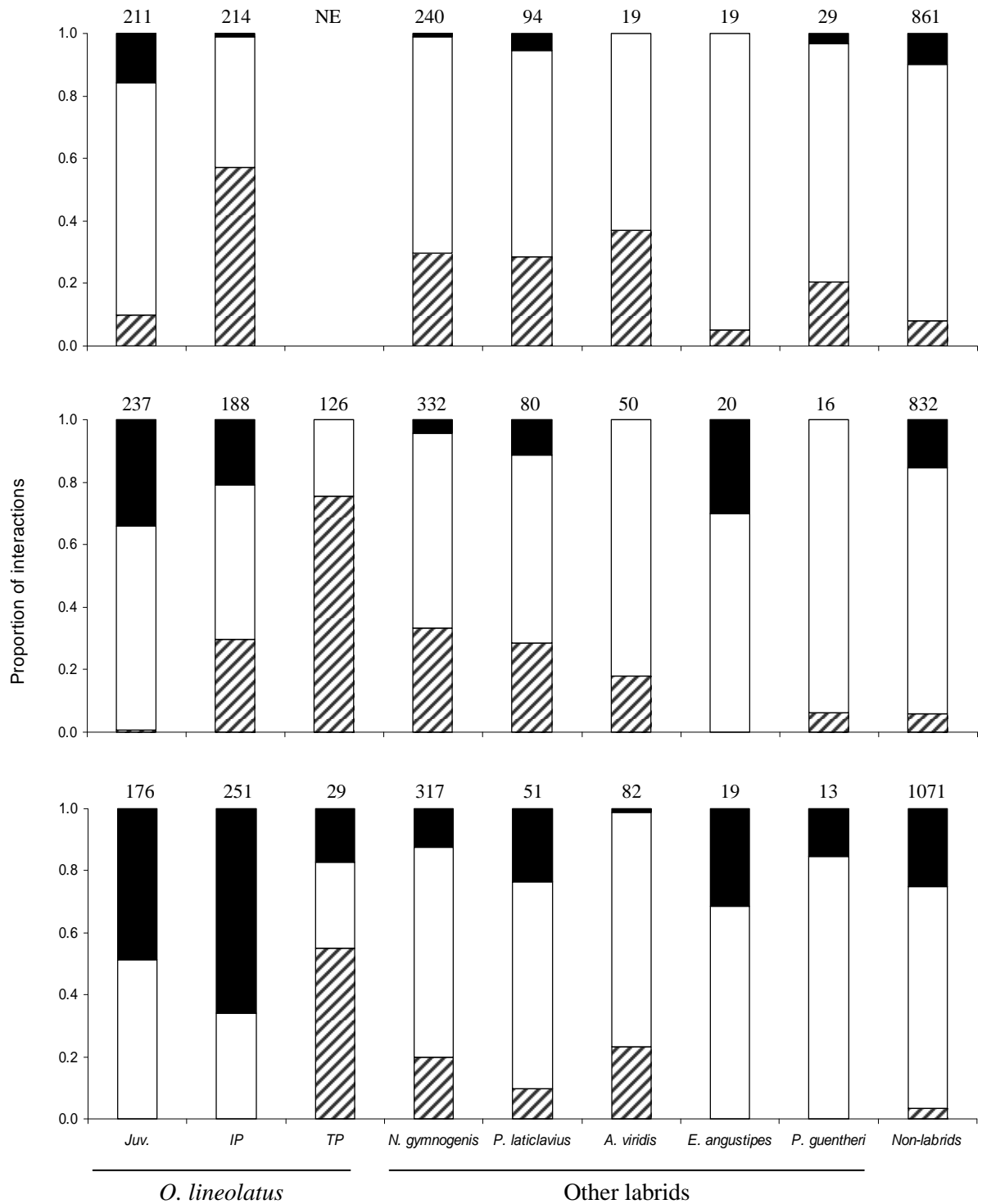


Figure 4.5: Summary of *Ophthalmolepis lineolatus* encounters with other fish for juvenile (top), initial phase (middle) and terminal phase (bottom) individuals. Proportion of encounters prompting no interaction (□), dominance (■) and subordination (▨) are shown. Interactions are the response of the focal individual from observations totalling *ca* 960 mins (i.e. 16 hours) for each life history stage. Encounters were defined as observed occurrences with other fishes within 2 m of the focal individual. Only species contributing to at least 20 encounters in one of the three life history stages were included. Total encounters are shown above each column (NE = no encounters observed).

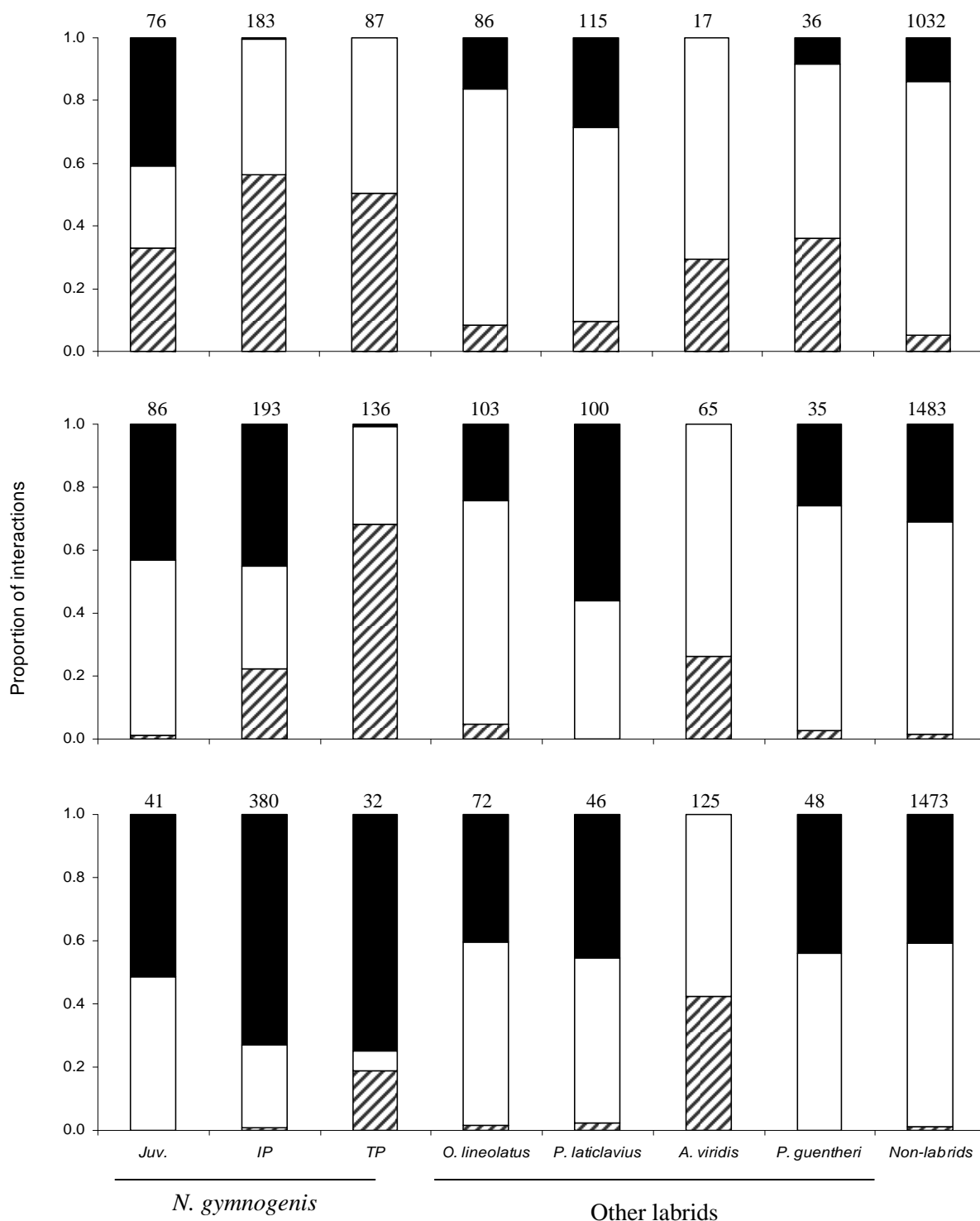


Figure 4.6: Summary of *Notolabrus gymnogenis* encounters with other fish for juvenile (top), initial phase (middle) and terminal phase (bottom) individuals. Proportion of encounters prompting no interaction (□), dominance (■) and subordination (▨) are shown. Interactions are the response of the focal individual from observations totalling *ca* 960 mins (i.e. 16 hours) for each life history stage. Encounters were defined as observed occurrences with other fishes within 2 m of the focal individual. Only species contributing to at least 20 encounters in one of the three life history stages were included. Total encounters are shown above each column.

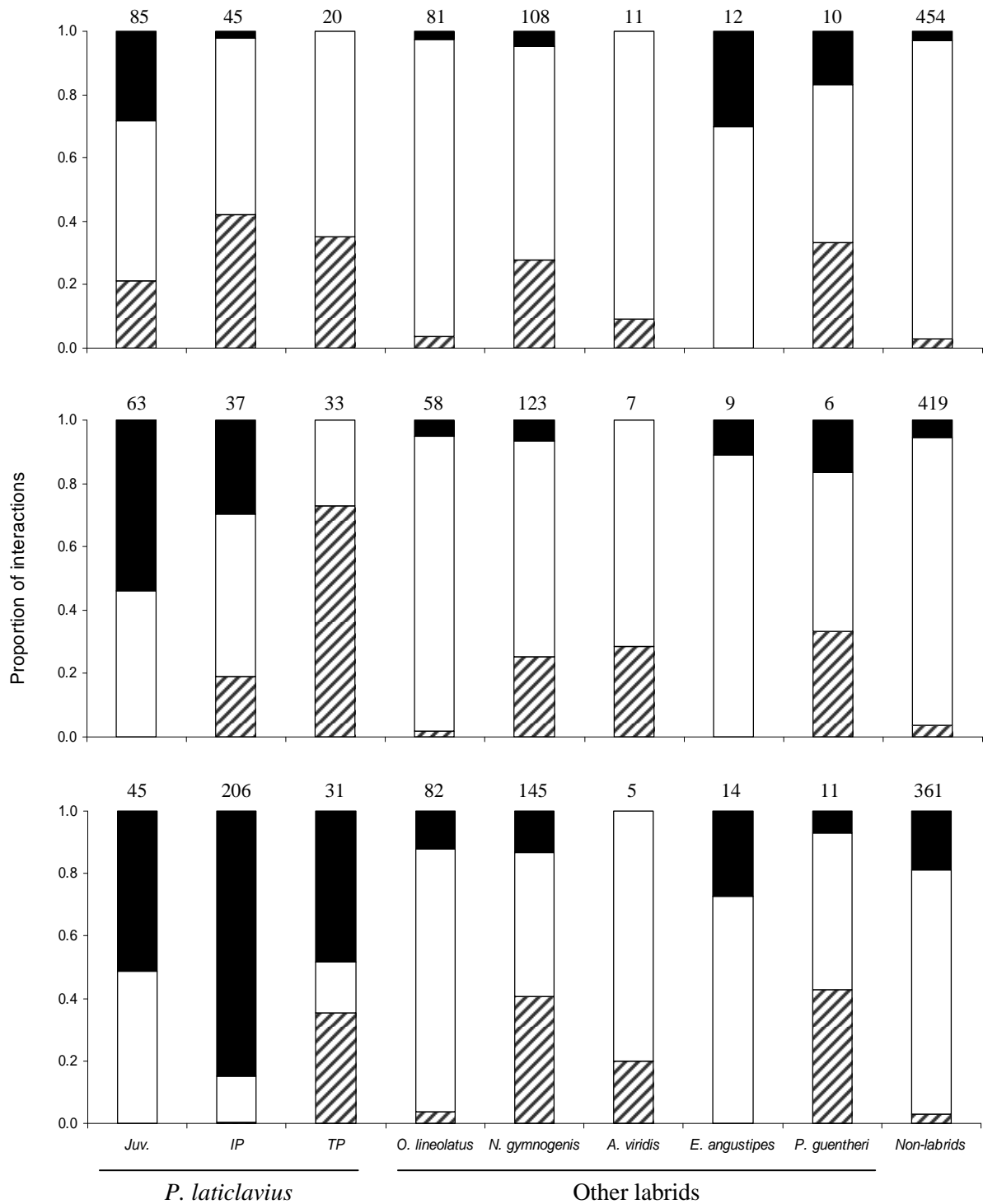


Figure 4.7: Summary of *Pictilabrus laticlavius* encounters with other fish for juvenile (top), initial phase (middle) and terminal phase (bottom) individuals. Proportion of encounters prompting no interaction (□), dominance (■) and subordination (▨) are shown. Interactions are the response of the focal individual from observations totalling *ca* 600 mins (i.e. 10 hours) for each life history stage. Encounters were defined as observed occurrences with other fishes within 2 m of the focal individual. Only species contributing to at least 20 encounters in one of the three life history stages were included. Total encounters are shown above each column.

4.3.2.3 Special Interactions – cleaning behaviour

Several interesting inter-specific relationships were observed. Interactions with fishes belonging to the family Mullidae and with *A. viridis* were typically mutual or commensal and related to feeding behaviour so are discussed in Chapter 5. Two species of clingfishes (*Cochleocephalus orientalis* and *Aspasmogaster costata*) were observed cleaning *Ophthalmolepis lineolatus*, *Notolabrus gymnotus* and *Pictilabrus laticlavius* on 206 occasions. Cleaning services were provided to all life history stages of each species, except juvenile *P. laticlavius* (Table 4.8).

Labrids initiated cleaning behaviour by lying, hovering or slowly swimming near a cleaning ‘station’ (e.g. rock overhang, bare rock surface, top of sponge or complex rock/algal habitat) which was followed by the clingfish attaching to the fish’s body. After attachment, the clingfish would rapidly move over the body. Post-cleaning, the clingfish would detach and promptly attach, or slowly drift, to nearby substrate.

Cleaning times were usually short (<10 seconds) but on 13 occasions lasted in excess of 1 minute, with one cleaning episode continuing for 4 min 18 sec (Table 4.8i). Single clingfish were usually involved in cleaning each fish (i.e. 92% of occurrences), but 2 and 3 clingfishes were observed simultaneously cleaning the same fish on 12 and 4 occasions, respectively (Table 4.8ii). Clingfishes regularly provided unwanted, or extended, cleaning services which prompted the focal labrid to twitch, side bend or side-swipe on substrate in an effort to cause dislodgement of the clingfish.

Table 4.8: Frequency of occurrence of cleaning periods provided by clingfishes (i) and number of clingfish simultaneously involved in each cleaning episode (ii) for juveniles (Juv.), initial phase (IP) and terminal phase (TP) individuals of *Ophthalmolepis lineolatus*, *Notolabrus gymnotus* and *Pictilabrus laticlavius*.

Species	Stage	(i) Cleaning period (sec)					Total time (min:sec)	(ii) No. of clingfish involved in each cleaning episode		
		0-10	10-30	30-60	60-180	180+		1	2	3
<i>O. lineolatus</i>	Juv.	4			2		3:28	6		
	IP	16	7	2			21:55	25		
	TP	39	12		2		15:02	53		
<i>N. gymnotus</i>	Juv.	5	4		1		3:05	9	1	
	IP	22	12	6	3	1	3:53	39	5	
	TP	38	11	5	3		8:57	47	6	4
<i>P. laticlavius</i>	Juv.						-			
	IP	2					0:18	2		
	TP	5	3		1		3:06	9		

4.3.3 Lying and shelter use

Episodes of fast movement (i.e. chasing, retreating, courting and spawning), slow swimming and hovering were sometimes interspersed with periods of lying. Lying behaviour was never observed in *Ophthalmolepis lineolatus*, but occurred often in *Notolabrus gymnogenis* ($16.1 \pm 1.2\%$ of time) and regularly in *Pictilabrus laticlavius* ($48.2 \pm 1.8\%$) (Figure 4.8). Juvenile *N. gymnogenis* spent more time lying than both IP and TP individuals at all times of the day and at both locations, except at midday at Catherine Hill Bay where no differences existed between life history stages (SxTxL interaction, $P < 0.01$) (Table 4.9; Figure 4.8). No differences between life history stages of *P. laticlavius* occurred for lying, but the time engaged in lying behaviour was significantly lower at Norah Head ($43.6 \pm 2.0\%$ of time) than Catherine Hill Bay ($52.9 \pm 1.6\%$).

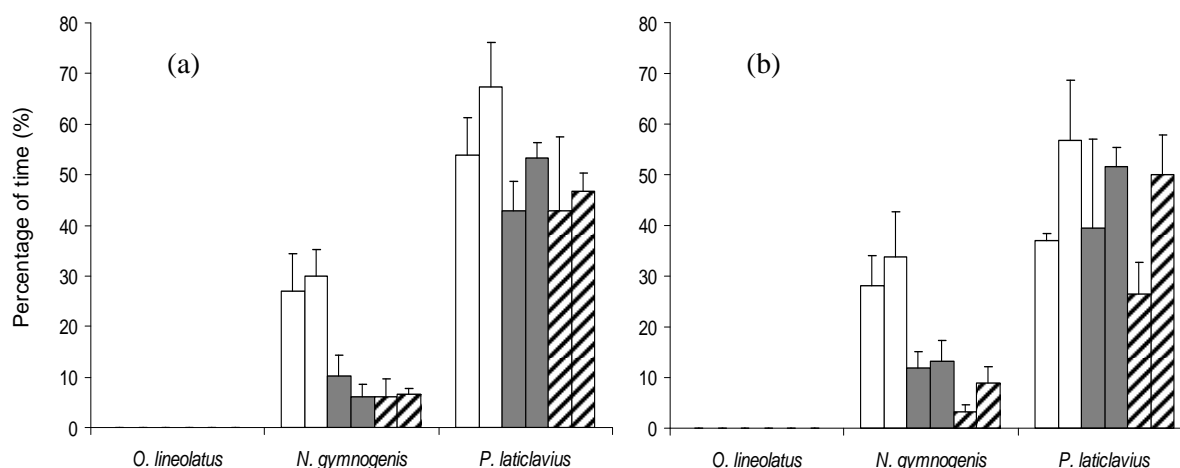


Figure 4.8: Mean percentage of time (\pm SE) engaged in lying behaviour at Catherine Hill Bay (a) and Norah Head (b) for juvenile (\square), initial phase (\blacksquare) and terminal phase (\hatched) individuals of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* in two periods of sampling (replicated columns). All combinations of Stage \times Location \times Period are shown for each species ($n=3$ times of day with each time representing the average of five 10 minute replicates).

Table 4.9: ANOVA results for percentage of time engaged in lying behaviour for *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. Lying behaviour did not occur in *Ophthalmolepis lineolatus*. ¹data arcsin(%) transformed (Cochran's C test, $P>0.05$). * $P<0.05$, ** $P<0.01$.

Source of variation	df	<i>N. gymnogenis</i> ¹		<i>P. laticlavius</i>	
		MS	F	MS	F
Stage (S)	2	6053.42	16.48	1537.00	2.96
Time of day (T)	2	167.41	0.95	3782.54	4.36
Location (L)	1	4.70	0.04	3859.57	8.24**
Period (P)	1	66.50	0.17	6819.12	3.81
S x T	4	27.24	0.05	619.21	0.62
S x L	2	367.36	32.99	518.91	1.11
S x P	2	47.18	0.44	251.39	0.28
T x L	2	175.83	1.43	867.24	1.85
T x P	2	43.99	0.09	769.36	0.90
L x P	1	387.33	3.16	1789.20	3.82
S x T x L	4	507.99	4.14**	997.62	2.13
S x T x P	4	293.85	3.13	371.26	0.57
S x L x P	2	108.24	0.88	883.86	1.89
T x L x P	2	474.45	3.86*	854.65	1.82
S x T x L x P	4	93.95	0.77	652.78	1.39
Residual	144	122.76		468.67	

Rock crevices, steel refuse (e.g. ladders, chains etc.) and algae (*Ecklonia radiata*, *Phyllospora comosa* and/or mixed species of algae) were used for shelter by each species (Figure 4.9). Sheltering occurred while searching for prey, being cleaned, lying and during travel. *O. lineolatus* exhibited the least use of shelter of all species ($11.5\pm0.9\%$ of time) (Figure 4.10). Juvenile *O. lineolatus* used mostly algae for shelter, IP individuals used more rocks (while still using mostly algae), and TP individuals used rock, algal and rock/algal complexes about equally (Figure 4.9a). Differences between life history stages of *O. lineolatus* occurred only in the morning at Catherine Hill Bay and the afternoon at Norah Head (SxTxL interaction, $P<0.05$) (Table 4.10; Figure 4.10).

Hard substrata (i.e. rock and steel refuse) were predominantly used for shelter by *N. gymnogenis*; however, use of algal and rock/algal complex was common for juveniles (Figure 4.9b). Shelter was used intermittently ($36.9\pm1.8\%$ of time) with regular short excursions into crevices to travel or to seek prey (Figure 4.10). Juvenile *N. gymnogenis* used shelter more frequently than TP individuals at both locations, and also IP at Catherine Hill Bay (SxL interaction, $P<0.05$) (Table 4.10; Figure 4.10). Shelter was used more frequently in period 1 than period 2 in this species.

P. laticlavius mostly used macroalgae (typically *Ecklonia radiata*) or rock/algal complexes for shelter (Figure 4.9c) and would remain lying or travel within the cover of

shelter for extended periods (i.e. $73.6 \pm 1.5\%$ of time) (Figure 4.10). Shelter was used more frequently by juvenile and IP individuals of *P. laticlavus* than TP individuals in the morning at Norah Head and midday at Catherine Hill Bay (SxTxL interaction, $P < 0.05$) (Table 4.10; Figure 4.10). In the morning at Catherine Hill Bay, juveniles used shelter more often than both IP and TP individuals.

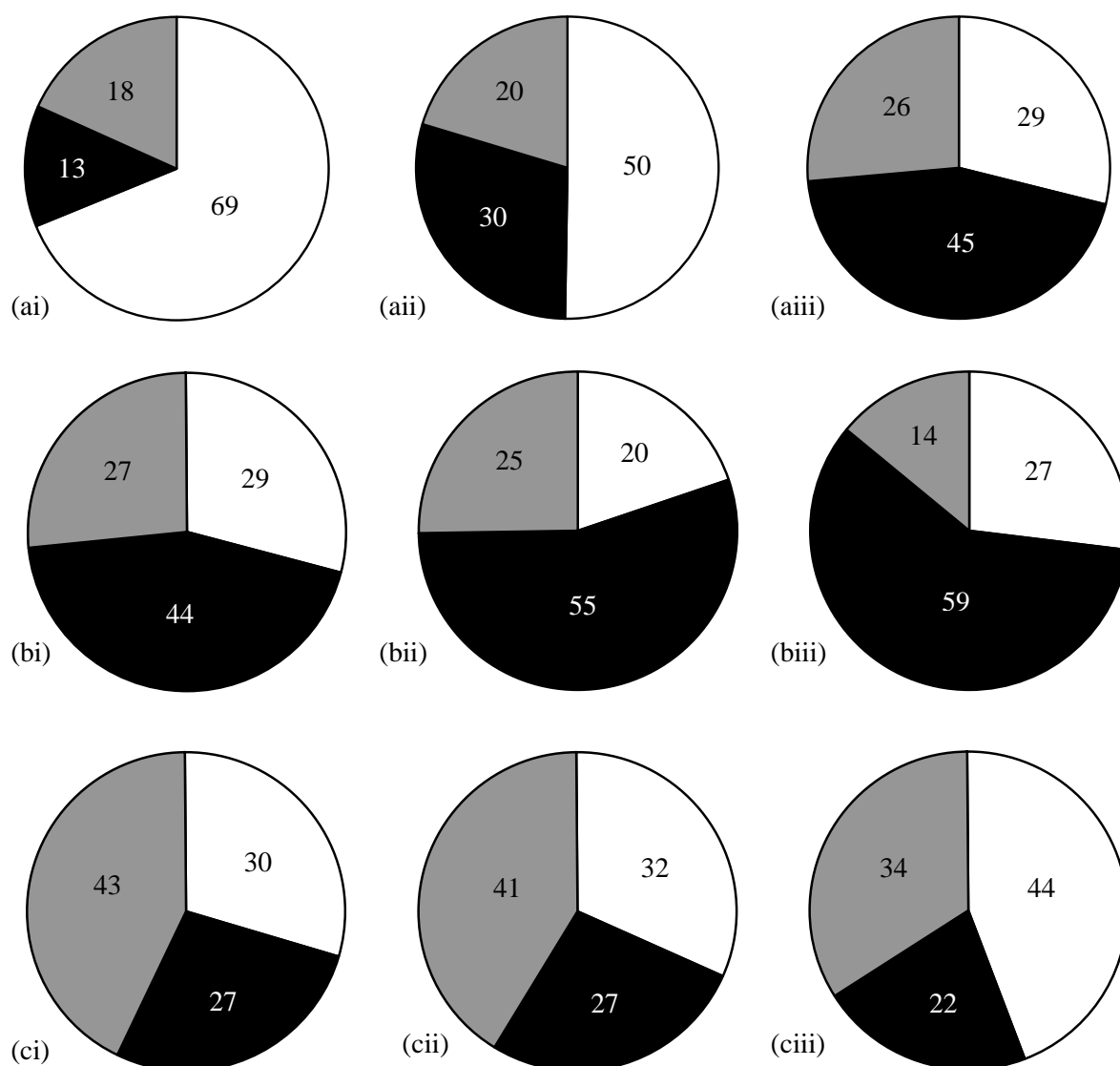


Figure 4.9: Percentage of time *Ophthalmolepis lineolatus* (a), *Notolabrus gymnogenis* (b) and *Pictilabrus laticlavus* (c) utilise algal (□), rock (■) and rock/algal complex (▒) for shelter. Stages are juvenile (i), initial phase (ii) and terminal phase (iii) individuals. Percentages (shown) are calculated from 600 mins of observations/stage/species.

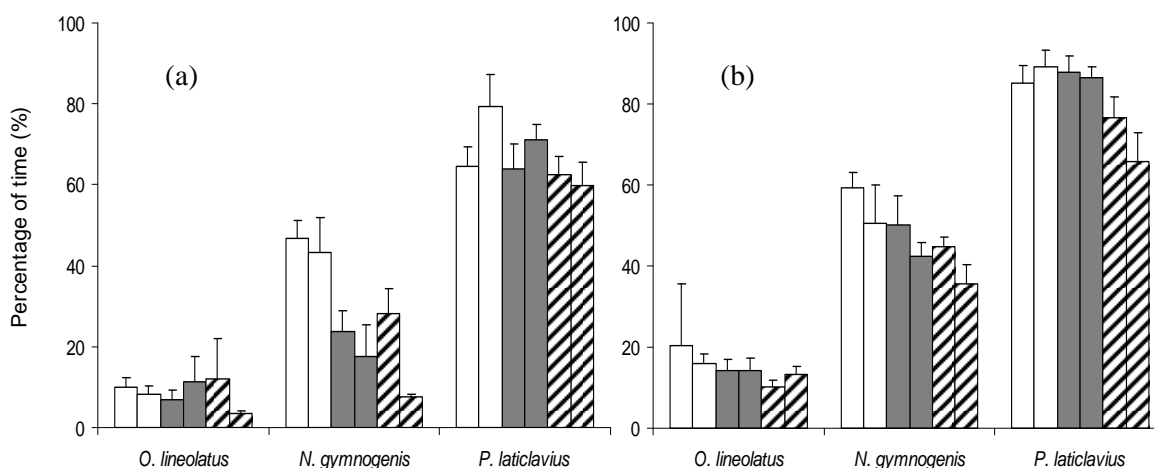


Figure 4.10: Mean percentage of time (\pm SE) utilising shelter at Catherine Hill Bay (a) and Norah Head (b) for juvenile (\square), initial phase (\blacksquare) and terminal phase (\hatched) individuals of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* in two periods of sampling (replicated columns). All combinations of Stage \times Location \times Period are shown for each species ($n=3$ times of day with each time representing the average of five 10 minute replicates).

Table 4.10: ANOVA results for percentage of time using shelter for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. ¹data arcsin(%) transformed (Cochran's C test, $P>0.05$). * $P<0.05$, *** $P<0.001$.

Source of variation	df	<i>O. lineolatus</i> ¹		<i>N. gymnogenis</i>		<i>P. laticlavius</i>	
		MS	F	MS	F	MS	F
Stage (S)	2	261.54	15.70	294.73	6.64	4256.10	34.13*
Time of day (T)	2	1022.16	2.60	840.80	6.87	214.42	44.03*
Location (L)	1	1790.30	17.61***	18894.85	53.08***	12139.31	45.07***
Period (P)	1	2.39	0.02	2894.42	292.56*	492.03	0.29
S \times T	4	31.29	0.10	357.45	5.97	388.50	0.54
S \times L	2	16.65	0.16	1250.00	3.51*	124.71	0.46
S \times P	2	7.17	0.13	113.57	1.30	551.25	8.06
T \times L	2	392.88	3.87*	122.46	0.34	4.87	0.02
T \times P	2	168.73	6.89	836.38	1.01	355.48	0.47
L \times P	1	111.00	1.09	9.89	0.03	1692.80	6.28*
S \times T \times L	4	308.06	3.03*	59.86	0.17	715.81	2.66*
S \times T \times P	4	355.72	1.96	490.54	0.81	377.18	1.12
S \times L \times P	2	56.33	0.55	87.43	0.25	68.43	0.25
T \times L \times P	2	24.47	0.24	826.04	2.32	750.99	2.79
S \times T \times L \times P	4	181.14	1.78	608.01	1.71	335.63	1.25
Residual	144	101.64		355.96		269.36	

4.3.4 Other Behaviours

4.3.4.1 Side-swiping and bending

Bends and side-swipes were observed regularly for *Ophthalmolepis lineolatus* (total of 830 and 351 occurrences, respectively), often for *Notolabrus gymnogenis* (222 and 142, respectively) and infrequently for *Pictilabrus laticlavius* (43 and 51, respectively). Side swiping and bending occurred as single isolated events, but episodes of up to 3 bends or

up to 8 side-swipes in rapid succession (i.e. <30 secs) were observed on several occasions. No differences occurred between life history stages of *N. gymnogenis* for rates of bending or side-swiping (Table 4.11, 4.12; Figure 4.11). In contrast, differences occurred between life history stages of *O. lineolatus* in some periods (for bends), at some times of the day at some locations (for bends), at some locations (for side-swipes) and at some times of the day in some periods (for side-swipes) (Table 4.11, 4.12). A four-way interaction occurred for rates of bending by *P. laticlavus*, but differences among life history stages occurred only in the morning at Catherine Hill Bay in period 2. Comparisons of side-swiping rates among life history stages of *P. laticlavus* in each sampling period (SxP interaction, $P<0.001$) was not possible due to the frequent zero occurrences of this behaviour. Side-swiping occurred more frequently at Catherine Hill Bay than Norah Head for this species.

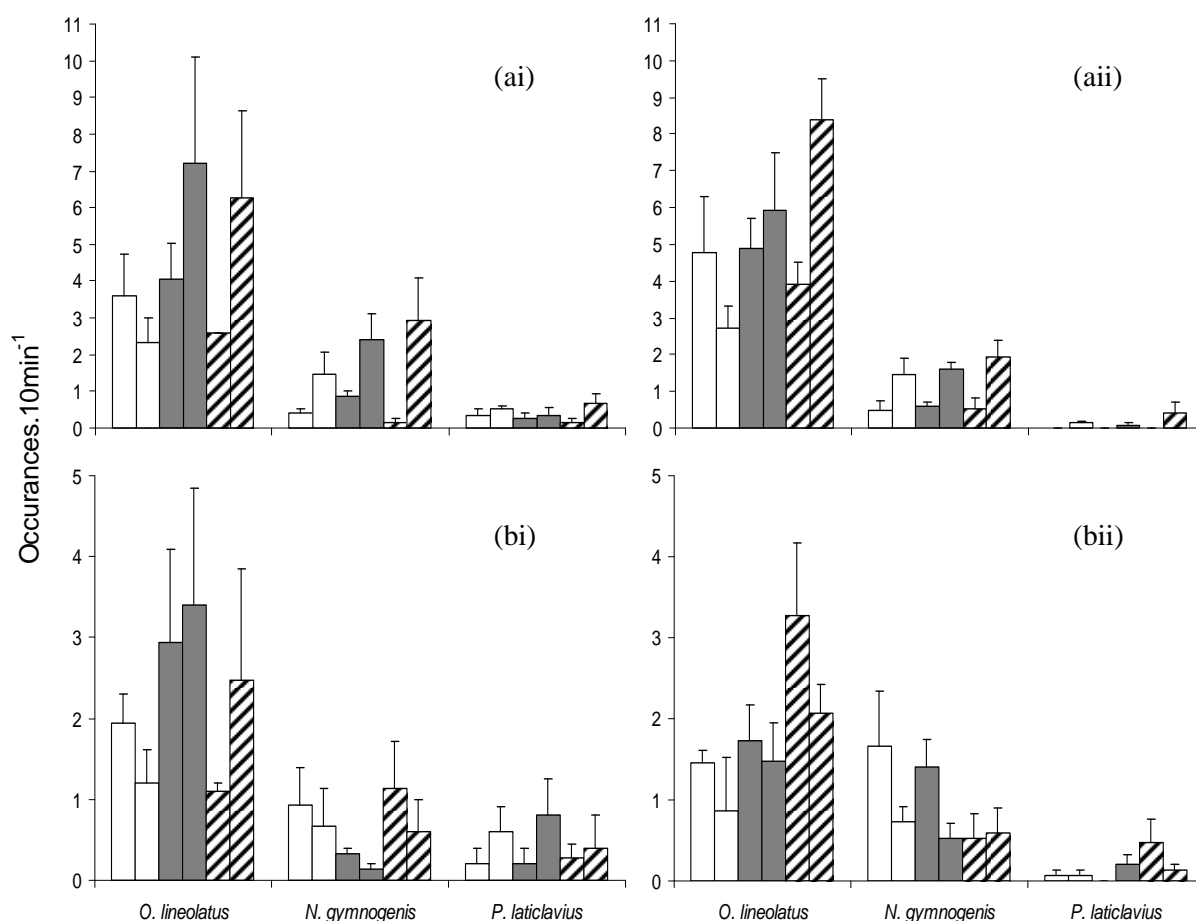


Figure 4.11: Mean rate (\pm SE) of bending (a) and side-swiping (b) at Catherine Hill Bay (a) and Norah Head (b) for juvenile (\square), initial phase (\blacksquare) and terminal phase (\hatched) individuals of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* in two periods of sampling (replicated columns). All combinations of Stage \times Location \times Period are shown for each species (n=3 times of day with each time representing the average of five 10 minute replicates).

Table 4.11: ANOVA results for rates of bending, 10 min^{-1} for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. ¹data square-root ($x+1$) transformed, ²data $\ln(x+1)$ transformed (Cochran's C test, $P>0.05$). * $P<0.05$, *** $P<0.001$.

Source of variation	df	<i>O. lineolatus</i> ¹		<i>N. gymnogenis</i> ²		<i>P. laticlavius</i> ²	
		MS	F	MS	F	MS	F
Stage (S)	2	3.36	5.34	0.49	1.48	0.03	10.88
Time of day (T)	2	2.85	5.62	1.03	1.51	0.14	2.08
Location (L)	1	2.16	4.72*	0.01	0.03	1.28	11.48***
Period (P)	1	3.61	25.11	11.98	111.47	0.58	86.66
S x T	4	0.81	0.51	0.06	0.72	0.04	0.82
S x L	2	0.63	1.37	0.34	0.95	0.00	0.03
S x P	2	5.10	30.95*	0.36	3.99	0.15	5.78
T x L	2	0.51	1.11	0.69	1.94	0.07	0.59
T x P	2	1.07	0.94	1.09	3.98	0.06	4.50
L x P	1	0.14	0.31	0.11	0.30	0.01	0.06
S x T x L	4	1.57	3.44*	0.09	0.24	0.05	0.48
S x T x P	4	0.33	1.74	0.11	0.55	0.15	0.53
S x L x P	2	0.16	0.36	0.09	0.26	0.03	0.23
T x L x P	2	1.14	2.49	0.27	0.78	0.01	0.13
S x T x L x P	4	0.19	0.41	0.21	0.58	0.29	2.57***
Residual	144	0.46		0.35		0.11	

Table 4.12: ANOVA results for rates of side-swiping, 10 min^{-1} for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. All data $\ln(x+1)$ transformed (Cochran's C test, $P>0.05$). * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

Source of variation	df	<i>O. lineolatus</i>		<i>N. gymnogenis</i>		<i>P. laticlavius</i>	
		MS	F	MS	F	MS	F
Stage (S)	2	1.87	1.34	0.33	0.45	0.08	0.69
Time of day (T)	2	1.16	1.17	1.16	3.10	0.94	2.83
Location = (L)	1	0.11	0.31	0.21	0.62	0.65	5.33*
Period (P)	1	0.67	0.42	1.26	38.10	0.29	0.94
S x T	4	0.52	0.80	0.05	0.28	0.10	0.45
S x L	2	1.40	3.91*	0.74	2.20	0.12	0.97
S x P	2	1.14	3.55	0.04	0.12	0.31	583.46***
T x L	2	0.99	2.78	0.37	1.11	0.33	2.75
T x P	2	0.36	0.50	0.24	1.02	0.08	0.26
L x P	1	1.59	4.45*	0.03	0.10	0.31	2.53
S x T x L	4	0.65	1.81	0.19	0.57	0.22	1.84
S x T x P	4	0.68	35.42**	0.36	3.45	0.24	5.93
S x L x P	2	0.32	0.90	0.32	0.96	0.00	0.00
T x L x P	2	0.73	2.04	0.24	0.70	0.31	2.53
S x T x L x P	4	0.02	0.05	0.10	0.31	0.04	0.33
Residual	144	0.36		0.34		0.12	

4.3.4.2 Gaping

Gaping occurred in all stages of each species with a total of 228, 154 and 109 gapes observed for *Notolabrus gymnogenis*, *Ophthalmolepis lineolatus* and *Pictilabrus laticlavius*, respectively. Gaping was most often associated with agonistic interactions in which a dominant fish would threaten another individual using a wide gape held for up to 3 sec or, in retreat, a subordinate fish would perform a rapid, shallow gape. No differences in gaping rates occurred among life history stages of *N. gymnogenis* and *P.*

laticlavus, but gaping was more frequent in TP than either juvenile or IP individuals of *O. lineolatus* at Norah Head in period 1 (SxLxP interaction, $P<0.05$) (Table 4.13; Figure 4.12). Gaping occurred more frequently in the morning for *N. gymnogenis* and at Catherine Hill Bay for *P. laticlavus*.

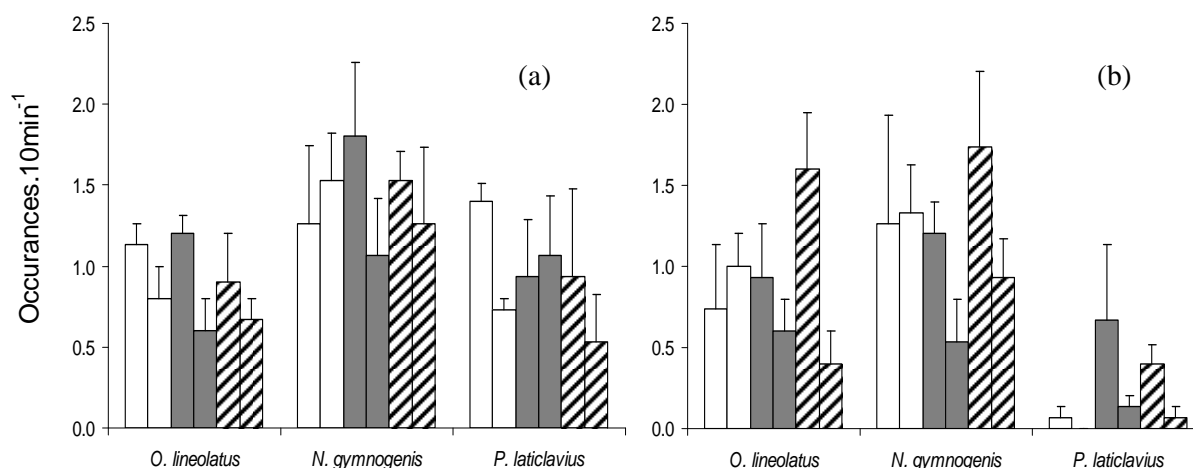


Figure 4.12: Mean rate (\pm SE) of gaping at Catherine Hill Bay (a) and Norah Head (b) for juvenile (\square), initial phase (\blacksquare) and terminal phase (\hatched) individuals of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* in two periods of sampling (replicated columns). All combinations of Stage \times Location \times Period are shown for each species (n=3 times of day with each time representing the average of five 10 minute replicates).

Table 4.13: ANOVA results for rates of gaping.10 min⁻¹ for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus*. ¹data square-root (x+1) transformed (Cochran's C test, $P>0.05$). * $P<0.05$, *** $P<0.001$.

Source of variation	df	<i>O. lineolatus</i>		<i>N. gymnogenis</i>		<i>P. laticlavus</i> ¹	
		MS	F	MS	F	MS	F
Stage (S)	2	0.12	0.23	0.65	0.40	0.06	0.64
Time of day (T)	2	5.60	9.00	14.72	67.92*	0.45	7.08
Location (L)	1	0.01	0.01	1.80	1.17	3.43	38.08***
Period (P)	1	7.61	369.00*	4.36	4.00	0.70	92.49
S x T	4	0.67	5.45	0.99	0.62	0.17	1.95
S x L	2	0.51	0.68	1.62	1.05	0.09	1.01
S x P	2	1.87	0.77	2.91	3.93	0.07	0.45
T x L	2	0.62	0.84	0.22	0.14	0.06	0.70
T x P	2	0.82	5.29	2.01	2.60	0.09	85.95*
L x P	1	0.01	0.01	1.09	0.71	0.01	0.08
S x T x L	4	0.12	0.16	1.61	1.04	0.09	0.96
S x T x P	4	0.09	0.15	1.58	1.58	0.01	0.17
S x L x P	2	2.44	3.29*	0.74	0.48	0.16	1.79
T x L x P	2	0.16	0.21	0.77	0.50	0.00	0.01
S x T x L x P	4	0.59	0.79	1.00	0.65	0.06	0.71
Residual	144	0.74		1.54		0.09	

4.3.4.3 Colour Change

Colour change was observed in all species. The most striking evidence of colour change occurred in terminal phase *Ophthalmolepis lineolatus* in which large individuals were observed altering the pigmentation of their black lateral band on 16 occasions (Figure 4.13). The black band changed from being displayed to hidden, or vice versa, at intervals of approximately 20 seconds.

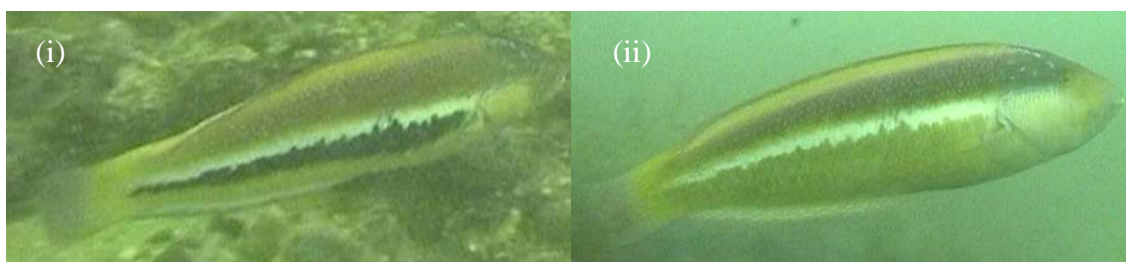


Figure 4.13: Socially-mediated colour change in a terminal phase *Ophthalmolepis lineolatus* (340 mm). Both photographs are of the same individual in display (i) and not in display (ii) of its lateral black band.

Expression of a lateral black band was typically a display of dominance among *O. lineolatus*. Due partly to the low density of TP individuals, two individuals displaying black bands were never seen together. On a single occasion, an individual displaying a black band promptly ceased its display and retreated upon encountering a larger individual.

Colour change was also used by all species for camouflage (Figure 4.14). In *O. lineolatus*, excursions over sand flats invoked a change in colour to a relatively uniform cream-yellow. On return to rocky or weedy habitat, distinct horizontal bands of brown and yellow returned. Variation in colour was observed in *Notolabrus gymnogenis* (juveniles and IP only) and *Pictilabrus laticlavius* (all stages), usually when lying, to match the substrate. Change in colouration involved altering the intensity of brown in *N. gymnogenis*, and subtle adjustments of vertical green/brown banding on the body and the addition of white spots in *P. laticlavius*.

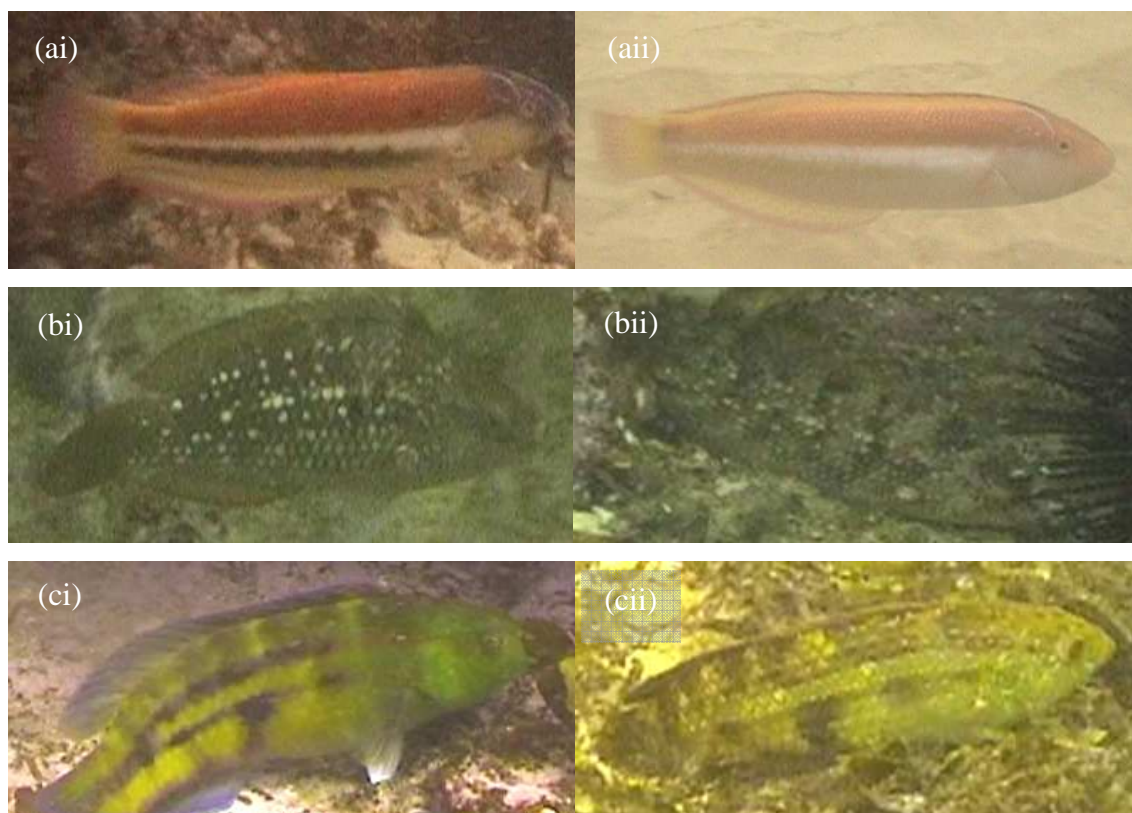


Figure 4.14: Camouflage-mediated colour change observed in *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. Figure (a) shows a single terminal phase *O. lineolatus* individual (310 mm) in distinct reef colouration (i) and in the pale colouration used for travel over sandy areas (ii). Figure (b) shows a single initial phase *N. gymnogenis* individual (180 mm) in typical (i) and cryptic (ii) colouration. Figure (c) shows two different terminal phase individuals of *P. laticlavius* (both 160 mm) in display of the typical non-banded colouration (i) used for travel among canopy forming algal fronds and its mottled, banded colouration (ii) used when lying among mixed species of algae.

4.4 Discussion

4.4.1 Spatial structure and residency

Ophthalmolepis lineolatus, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* differed substantially in their spatial structure and the area of reef used by individuals. Juvenile *O. lineolatus* often associated with others of similar size on restricted reef patches. Association of juveniles is a strategy employed by several labrids (Jones 1984c; Shepherd *et al.* 2002) and is likely to be important for avoiding predation (Martha and Jones 2002). Congregating with conspecifics of similar size is likely to be a particularly important survival strategy for *O. lineolatus* as, compared to other labrids, individuals of this species infrequently use refuges so are highly visual to predators.

With increased size, *O. lineolatus* become increasingly independent and use larger areas of reef, with home ranges of at least 560 m² and 2500 m² in IP and TP individuals, respectively. Known IP and TP individuals were reliably re-located within the study area, but frequent extensive searches revealed these fishes regularly moved outside these areas for periods of hours to weeks and continued to do so for up to 1 year before the individual permanently emigrated. Populations of *O. lineolatus* remained stable by the immigration of IP and TP individuals from adjacent reef areas. These movement patterns suggest *O. lineolatus* are temporary reef residents that utilise home ranges extending over large areas of rocky reef. Therefore, area usage of *O. lineolatus* is similar to that of the non-territorial labrids *Notolabrus fucicola*, *Achoerodus gouldii* and *Achoerodus viridis*. For example, *N. fucicola* range widely over available reef with home ranges up to at least 1700 m² (Barrett 1995b) and 3000 m² (Edgar *et al.* 2004). In *Achoerodus gouldii*, movement may be even greater with individuals moving over coastal areas as large as 15000 m² (Shepherd and Brook 2005).

The ecological benefits, or constraints, underlying the use of home ranges is not known for most fishes. When small, *O. lineolatus* feed primarily on high density prey (e.g. amphipods, small gastropods etc.), with their diet shifting in larger individuals to include prey which is less abundant (e.g. larger decapods, polyplacophores and echinoids) (see Chapter 5). These larger, less abundant prey items are located mostly by chance encounters within a large reef area. The type of shelter used by *O. lineolatus* is

also likely to be an important factor in determining why territoriality is not exhibited in this species. For example, *O. lineolatus* may bury within sandy sediment for nocturnal refuge (see Chapter 3), but move onto hard substrate for diurnal foraging. This forces individuals to have broader ranges than those species that remain in their foraging habitat within rocky crevices during nocturnal periods. The movements of juvenile *O. lineolatus* are likely to be reduced as they are able to make nocturnal use of shallow sand patches found dispersed throughout rock and algal habitat.

Observed colour change in *O. lineolatus* associated with short excursions over barren sand flats and the permanent emigration of individuals suggests this species may be capable of travelling between reefs over broad patches of sandy sediment. However, sand flats usually act as a barrier to the movements of labrids (Warner 1982; Barrett 1995b). Arendt *et al.* (2001) reported that *Tautoga onitis* travelled up to 10 kilometres over flat, featureless, bottom habitat but it is unknown whether *O. lineolatus* is capable of movement at such scales. Future tagging and acoustic studies are required to address this uncertainty. Determination of why *O. lineolatus* use temporary home ranges requires further investigation. The occurrence of emigration/immigration did not seem to coincide with storm events (suggestive of wave induced displacement) nor did they appear to be seasonal (suggestive of breeding migrations). More data is needed on the movement patterns of *O. lineolatus* before these hypotheses are tested.

Juvenile and IP *N. gymnogenis* demonstrated strong fidelity to a particular reef patch of *ca.* 150-400 m² in which they remained for up to 22 months (the duration of observations). Reef patches are shared with conspecifics of different size, but are defended from individuals of similar size by aggressive chases. Co-occurrence of different sized individuals is promoted by ontogenetic partitioning of food resources which is known to occur in this and other species of labrid (see Chapter 5; Jones 1984c, 1988; Gillanders 1995b; Denny and Schiel 2001; Shepherd and Clarkson 2001; Shepherd 2006). The evidence of heightened aggression between juveniles and between IP individuals of similar size is likely to be due to competition resulting from direct dietary overlap (see Chapter 5), but aggression may also be prompted by defence of social rank (see below).

In contrast, TP males of *N. gymnogenis* are highly territorial and actively defend contiguous reef patches of *ca.* 400-600 m² from rival males for periods of up to at least 20 months. These territories contain up to 8 IP females which typically restrict the majority of their activity to the territory of a single male. Therefore, the spatial arrangement of *N. gymnogenis* populations reflects that of other temperate, territorial labrids (Jones 1981; Barrett 1995b; Shepherd and Clarkson 2001), with residency time for this species similar to the 2 years reported in *Pseudolabrus celidotus* (Jones 1981), but considerably longer than the 1 year documented by Edgar *et al.* (2004) for labrids in Tasmanian waters. In territorial species, the occurrence of aggressive interactions between males is likely to force limitations on population densities and therefore present important considerations for their management (see Chapter 7).

As territoriality is exhibited only by males of the species and males do not actively confine females to their territory, there is strong support that male *N. gymnogenis* are involved in resource defence polygyny (Smith 1996). In this mating system males gain access to females by defending reef patches offering resources such as food and shelter that are required by females. Whether some territories represent resources of higher quality and are therefore more favourable to females is yet to be determined.

TP *N. gymnogenis* infrequently crossed territorial boundaries possibly for the purpose of determining territory occupancy and therefore assessing the potential for territory expansion. Grant (1997) proposed that interactions between males at territorial boundaries are indicative of males defending areas which are smaller than their non-contiguous maximum. That is, the territory size of individuals is restricted by interactions with other males. Indeed this appears the case for *N. gymnogenis* as opportunistic territory expansion occurred in some individuals, particularly those with territories adjacent to sand flats. These individuals took advantage of rocky substrate or macroalgae that was episodically present through the action of storm events that either removed sand or accumulated dislodged macroalgae at the reef edge.

Several TP *N. gymnogenis* disappeared over the study period and were replaced by a TP individual which continued the defence of the previous individual's territory. Causes of TP *N. gymnogenis* loss are not known but the former occupant was never resighted suggesting it was predated, despite behavioural observations providing no direct

evidence of predation of any of the investigated labrids. Other causes of male replacement include surge-induced displacement of territory holders during storm events; mortality due to capture by fishers; or fatalities through physical stress, including injury, caused by territory defence.

Whether the first male died or was displaced by the subsequent male is not known; however, each of the subsequent males did not previously hold one of the adjoining territories. Therefore, these TP males either came from outside the study area or represent a sex-changed individual from the IP harem which assumed the alpha male role after sex change lasting *c.a.* 2-3 weeks (Kuwamura *et al.* 2002). As TP individuals in transitional coloration were often seen to hold territories after the absence of the former TP occupant, it is assumed the latter hypothesis is most likely. This hypothesis also explains why IP *N. gymnogenis* typically constrain their activities to the territories of a single TP male and will defend these areas from females of similar size. By doing so, females become familiar with the territory of a TP male whilst excluding individuals of similar rank which would otherwise compete for their position in the dominance hierarchy and possibly affect their chances of becoming the alpha male (Sakai *et al.* 2001).

Interactions between TP individuals of *P. laticlavius* in the present study suggests several males utilised a common reef area within which small reef patches (i.e. 4-10 m²) are temporarily defended for the purpose of feeding, shelter and/or reproduction. For example, fights usually involved rushing toward another individual, side-to-side posturing (e.g. erecting and flickering of fins), then moving away from one another in random directions (i.e. not back into contiguous territories over which a boundary would have been contested). Such confrontations were also found in juvenile and IP individuals, but defended reef patches were substantially smaller (i.e. 1-3 m²).

Gaining an understanding of the spatial structure of *P. laticlavius* was, however, significantly constrained by its cryptic behaviour. Re-identification of individuals was also problematic so estimations of home range/territory size and reef residency were not made, but mean area usage (10 min⁻¹) was found to increase from 5 m², to 13 m², to 39 m² in juvenile, IP and TP individuals, respectively. Similarly, Barrett (1995b) found *P. laticlavius* a difficult species to study due to its cryptic coloration and frequent 'hiding'

behaviour beneath algal canopies. This species is reported to be relatively sedentary (Edgar *et al.* 2004) and, based on the behaviour of a single TP individual, proposed by Barrett (1995b) to actively defend territories of *c.a.* 175 m² from male intruders. Future studies are recommended to accurately describe the spatial structure of *P. laticlavus*.

4.4.2 Interactions

Ophthalmolepis lineolatus, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* regularly encounter other fishes, but intra-specific encounters occur more frequently than encounters with other species. A dominance hierarchy based on size was evident in all species. This form of social hierarchy is common to other labrids (Jones and Thompson 1980; Tribble 1982; Hoffman 1985; Sakai *et al.* 2001; Shepherd and Clarkson 2001). Dominance hierarchies were expressed by smaller individuals moving away from the approach of a larger individual, but also occurred as active chases, visual posturing threats (i.e. flaring of the dorsal fins and/or lateral flexion) and ‘tailing’ (i.e. following). In addition, threats in the form of gaping (i.e. the display of an individual’s caniform teeth) were often directed at other individuals.

In TP *O. lineolatus*, the largest and most dominant male advertises intra-specific dominance by episodically displaying a black lateral band. On only a single occasion were two TP male *O. lineolatus* in the same vicinity. This occurrence resulted in the smaller TP male fading the display of its black lateral band and moving away from the reef patch occupied by the larger individual. Whilst permanent colour transformations associated with sex change are well documented in labrids (Kuitert 1993; Gillanders 1999; Jones 1999) literature citing socially induced rapid colour changes are infrequent (e.g. Robertson 1981). Indeed, displays of colour change to advertise social dominance and for the purpose of camouflage as seen in the investigated labrids appear to be the only reports of rapid colour change in any of Australia’s temperate labrids.

A size-based dominance hierarchy was also evident among labrids of different species. For example, *Achoerodus viridis* (max. size = 1200 mm: Kuitert 1993) were dominant over all other labrid species, but *Eupetrichthys angustipes* (max. size = 150 mm: Kuitert 1993) were typically subordinate in interactions with *O. lineolatus*, *N. gymnogenis* and *P. laticlavus*. Whilst inter-specific dominance hierarchies were evident in labrid

assemblages, dominant interactions occurred more frequently between individuals of the same species. This is likely due to intra-specific similarities in mouth morphology, foraging behaviour and diet (see Chapter 5), which causes significant competition among individuals of the same species. Frequent aggressive interactions among individuals of the same species may even be used as a strategy by females to inhibit maturation of juveniles (Jones and Thompson 1980) and/or by males to inhibit sex change in females (Sakai *et al.* 2001; Perry and Grober 2003).

O. lineolatus, *N. gymnogenis* and *P. laticlavus* also regularly encountered and interacted with non-labrids. These non-labrids were typically schooling fishes and pomacentrids that moved away from an approaching labrid, but the pomacentrid *Parma microlepis* was observed to chase *O. lineolatus* and *N. gymnogenis* from nesting sites and the blennid *Plagiotremus tapeinosoma* was seen to rapidly strike these labrids in an attempt to remove scales or tissue. Agonistic interactions with pomacentrids, blennids and crabs have been documented in other labrid species (Thompson and Jones 1983; Jones 1984c; Gillanders 1995b, 1999; Shepherd and Clarkson 2001; Martha and Jones 2002). These interactions are typically infrequent, but aggressive attacks by the pomacentrid *P. microlepis* may affect the foraging rate and habitat use of *Achoerodus viridis* in sites where *P. microlepis* is abundant (Gillanders 1995b). However, neither nest defending pomacentrids nor territorial blennies were sufficiently abundant in the study area to substantially affect the behaviour routines of *O. lineolatus*, *N. gymnogenis* or *P. laticlavus*.

Cleaning by clingfishes (Gobiesocidae) occurred frequently and was initiated by labrids lying or slowly swimming near a cleaning 'station' to advertise their willingness to be cleaned. Single observations of *O. lineolatus* and *P. laticlavus* being cleaned by *Siphonognathus beddomei* (Odacidae) have been previously reported, as have observations of other labrids (e.g. *Notolabrus tetricus* and *Achoerodus viridis*) being cleaned by *Tilodon sexfasciatus* (Microcanthidae), *Cochleocephalus bicolor* (Gobiesocidae), *Austrolabrus maculatus* (Labridae) and *Enoplosus armatus* (Enoplosidae) (Shepherd *et al.* 2005). The importance of cleaning services provided by *Labroides dimidiatus* in tropical reef systems is well documented (Grutter *et al.* 2003), but the importance of cleaners in temperate systems is not known. *O. lineolatus*, *N. gymnogenis* and *P. laticlavus* evidently receive tactile stimulation from the cleaning activity of clingfish,

but removal of ectoparasites and dead tissue (Hutchins 1991) may be important in determining the health of these fishes and may influence their distribution.

4.4.3 Importance of lying behaviour and shelter availability for labrids

Each species typically spends the majority of their time actively swimming throughout their home range/territory, but the importance of lying behaviour was evident for *Pictilabrus laticlavius* and *Notolabrus gymnogenis*. *P. laticlavius* spent 48% of their time lying and juvenile *N. gymnogenis* spent 30% of their time lying. Lying was less frequent in IP and TP *N. gymnogenis* (9% of their time) and was never observed in *Ophthalmolepis lineolatus*. Lying was associated with resting and cleaning, but was used commonly for the purpose of prey ambush. In these instances, individuals would lie on their belly, or side, and orientate their mouth toward a prey source (e.g. fronds or bases of algae) (see Chapter 5). In this position, individuals would use their eyes to detect prey movement before rapidly consuming quarry using a combination of ram-and-suction (Ferry-Graham *et al.* 2002). Frequent use of lying behaviour by both *P. laticlavius* and juvenile *N. gymnogenis* to ambush prey results in considerable overlap in the diet (i.e. amphipods) and feeding microhabitats (i.e. algal fronds and algal bases) of these species (see Chapter 5). Lying behaviour was often associated with colour change for the purpose of concealment against the substrate background so as to be less readily identified by predators and/or prey.

It is apparent that lying behaviour is an important component of the behaviour repertoires of *N. gymnogenis* and *P. laticlavius*, especially for ambush feeding, but diurnal lying behaviour outside refuges is not reported in ethological studies of other labrids except for infrequent observations of labrids lying motionless when being cleaned (Shepherd *et al.* 2005). It is unlikely that the use by *N. gymnogenis* and *P. laticlavius* of lying behaviour for the purpose of ambush feeding are cases unique to the family Labridae, yet it is surprising that this behaviour has not been previously reported in the many studies of the feeding behaviour of other labrids (e.g. Gillanders 1995b; Shepherd and Clarkson 2001; Ferry-Graham *et al.* 2002; Fulton and Bellwood 2002; Shepherd and Brook 2005).

Shelter was used by each species, but the frequency of use differed substantially. Shelter was most important for *P. laticlavus* followed by *N. gymnogenis* and *O. lineolatus*, with these fishes on average using shelter 74, 37 and 11% of the time in their activities on the reef. In all species, shelter provided by both algal and rocky substrate were of great importance. The association of labrids with shelter offered by rocky reef and/or algal habitats is well documented (Treasurer 1994; Garcia-Rubies and Macpherson 1995; Gillanders and Kingsford 1998; Pihl and Wennhage 2002). Shelter is likely to provide refuge from predators, to prevent displacement by wave surge, to harbour prey items; and to provide nocturnal retreats (Steele 1999; Shepherd and Clarkson 2001; Takayanagi *et al.* 2003; Shepherd and Brook 2005). Frequent reliance on shelter by *N. gymnogenis* and *P. laticlavus* is likely to limit their passage across areas devoid of shelter (i.e. sand flats). However, after storm events, these species were found to opportunistically use shelter provided by the accumulation of displaced algae on sand flats. Expanses of drift algae between rocky reefs may, therefore, provide episodic opportunities for post-settled labrids to emigrate to otherwise inaccessible reefs.

4.4.4 Other behaviours

Many ethological studies fail to quantify or attempt to explain the significance of behaviours unconnected to reproduction, feeding or social spacing. Many of these behaviours may superficially appear unimportant, but further research may reveal that their proposed lack of importance to labrid ecology may be misjudged. Bending and side-swiping by *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* may be representative of such behaviours. Side-swiping and bending behaviours were associated with clingfish removal, but are also likely to provide relief from irritations on the body surface and possibly, in the case of strong bending, assist in passage of food items through the intestines. Support for evidence of body surface irritations was provided by several individuals engaging in scratching behaviour using the rays of a pectoral fin to relieve head irritations. As the frequency of side-swiping and bending was not high, it is unlikely that these behaviours significantly affect foraging or reproductive activity in these fishes. However, it is possible that the frequency of occurrence of these behaviours may be indirect measures of parasite load and overall fish health.

4.4.5 Spatial and temporal influences on behaviour

Observed ontogenetic shifts in behaviour were generally consistent at both locations, at all times of the day and in each period of sampling, especially for comparisons between juvenile and TP individuals. Therefore, these factors are not likely to be of great importance for incorporation into future sampling if the research aim is to test for ontogenetic trends in behaviour. Sampling at more than one location is recommended where quantifying the frequency of occurrence of behaviours is the primary aim. For example, dominant interactions in *Ophthalmolepis lineolatus* and subordinate interactions, lying, side-swiping and gaping in *Pictilabrus laticlavius* occurred more frequently at Catherine Hill Bay than at Norah Head. However, the magnitude of differences was not sufficiently great to suggest that the ecology of each species differed between the two locations. Both Catherine Hill Bay and Norah Head were selected for their relatively sheltered aspect from prevailing swell, yet each species is also found on highly exposed reefs (see Chapter 3). Whether the behaviour of *O. lineolatus*, *Notolabrus gymnogenis* and *P. laticlavius* differs between sheltered and exposed sites is a question of interest but is potentially constrained by logistics (e.g. diver safety, displacement of diver from focal individual by surge etc.).

Neither the time of the day nor period of the year in which observations occurred had much influence on the social organisation and behaviour of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*. Cool water temperatures are known to reduce activity levels of temperate labrids in regions outside Australia (Sayer *et al.* 1993; Costello *et al.* 1997; Arendt *et al.* 2001), but are unlikely to have influenced the behaviour of the investigated species due to a reduced seasonal fluctuation in sea temperatures in the study area (see Chapter 3). However, anecdotal observations suggest each species became less active (i.e. remained more often within refuges) during periods of strong wave surge, as is known to occur in other labrids (Shepherd and Clarkson 2001).

4.4.6 Conclusion

The present investigation of the behaviour of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* has provided substantial insight into the social organisation and behavioural repertoires of these species. The methodology employed

in this study (i.e. continuous recording of behavioural routines followed by later transcription of behaviours) was useful for quantitatively and qualitatively documenting a variety of behaviours simultaneously, and allowing their subsequent review. This ethological study has provided the opportunity to document the spatial structure of populations; residency periods of individuals; social interactions; lying behaviour; shelter use; and other behaviours such as side-swiping, bending, gaping and colour change. Whilst all species typically engaged in each of the investigated behaviours, the frequency of these behaviours often demonstrated substantial differences among species (e.g. lying, shelter, bending) and/or life history stages (e.g. interactions, area usage), but were usually spatially and temporally consistent. These behaviours are significant for complementing data on patterns of distribution, diet and foraging behaviour, and reproductive strategies of *O. lineolatus*, *N. gymnogenis* and *P. laticlavus* which are discussed in other chapters.

Chapter 5:

Feeding Ecology

5.1 Introduction

5.1.1 Problem statement and chapter aim

As dominant predators of benthic invertebrates, removal of labrids from coastal rocky reefs may cause trophic cascades. In determining the magnitude of the impact of these predators on subtidal assemblages, information gaps are needed to be filled with respect to prey items consumed (and in what proportion) and foraging behaviour (including its effect on subtidal assemblage structure). Acquisition of such data also provides insights into ecological questions pertaining to habitat selection, space utilisation, intra-specific competition, inter-specific interactions, resource partitioning, trophodynamics and life history of labrids.

Despite labrids being well represented on rocky shores of temperate Australia and potentially being important top-down predators within subtidal assemblages, the diet and/or foraging behaviour of only four species have been investigated (i.e. *Achoerodus gouldii*, *Achoerodus viridis*, *Notolabrus fucicola* and *Notolabrus tetricus*; see Table 1.1). These fishes represent the four largest labrids residing on temperate rocky reefs of Australia which limits the ability to make informed decisions on the ecological role of smaller members of this morphologically diverse family. Furthermore, no previous studies have been conducted which compare the diets of co-occurring labrids to determine whether food resources are partitioned among species. Therefore, the aim of this chapter is to investigate the feeding ecology of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* which are abundant, mid-sized and co-occurring labrid species, using both dietary and behavioural observations. This information will be used to define the trophic status of temperate labrids, to determine the extent of partitioning of food resources in labrid assemblages and to assist in describing the role of labrid foraging in rocky reef systems.

5.1.2 General labrid diet and food processing

Members of the family Labridae are predominantly opportunistic, benthic carnivores which employ powerful jaws and associated pharyngeal teeth to crush the hard exoskeletons and shells of their invertebrate prey (Bond 1996; Kuitert 1996). Some species will also consume small fishes (Randall *et al.* 1978; Connell 1998; Connell and

Kingsford 1998) and plankton (Warner and Hoffman 1980a, b; Warner 1987), whilst others are specialised coral feeders (McIlwain and Jones 1998; Fulton and Bellwood 2002b). Other labrids specialise or opportunistically feed on ectoparasites, mucus or scales of other fishes (Zander and Nieder 1997; Jones 1999; Bansemer *et al.* 2002; Bshary and Schäffer 2002; Shepherd *et al.* 2005).

The marginal teeth of labrids are relatively unspecialised cones with slight recurvature (Figure 5.1a), with these teeth playing a minor role in food processing beyond prey capture and immobilisation (*pers. obs.*). Most mechanical digestion of prey items is performed by upper and lower sets of robust, molariform, pharyngeal teeth (Figure 5.1b-c). Pharyngeal teeth assist in raking prey into the oesophagus, reorientating food items, immobilising prey and crushing the protective armoury of prey into sizes small enough to pass through the intestine (Helfman *et al.* 1997). For some labrids, small prey items may be sorted from indigestible sediment using gill rakers (e.g. *Achoerodus viridis* – *pers. obs.*); however, these structures are typically unspecialised in this family (i.e. short, blunt and few in number). The family Labridae is recognised as a family of fishes which lack a true stomach (Bond 1996) and have a relatively short intestine, which is typical of species with a carnivorous diet.

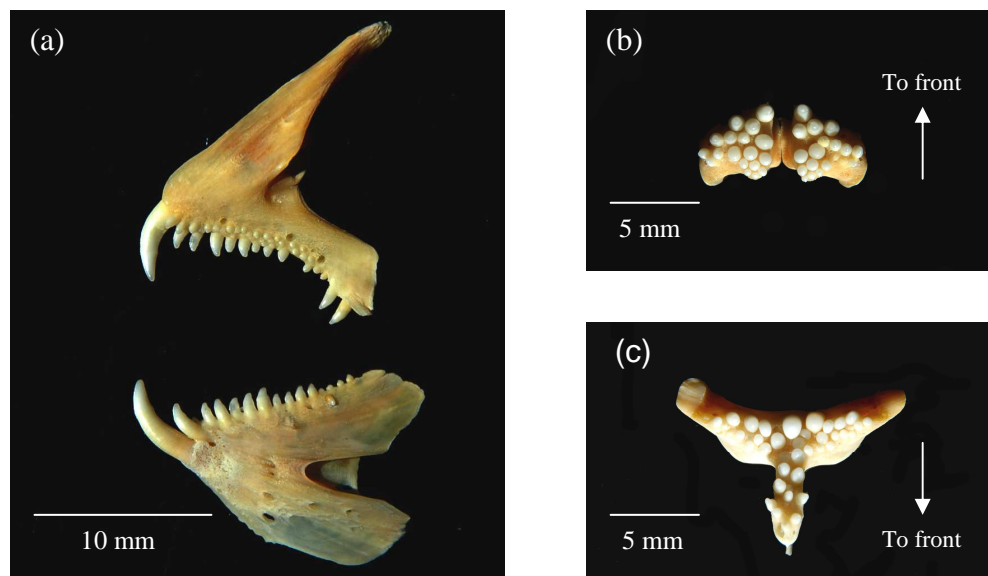


Figure 5.1: Morphology of labrid conical teeth borne on premaxillary (upper) and dentary (lower) jaw bones (a) used predominantly for prey capture, and the upper (b) and lower molariform pharyngeal teeth (c) used to crush the exoskeletons and shells of their invertebrate prey. Examples are from an individual of *Opthalmolepis lineolatus* (330 mm TL).

5.1.3 Diet of temperate labrids

Temperate labrids of Australia and New Zealand are known to be euryphagous (generalist) carnivores consuming prey items that include molluscs (bivalves, gastropods, chitons), crustaceans (amphipods, isopods, ostracods, barnacles, decapods), echinoderms (brittlestars, urchins, sea stars), ascidians, polychaetes, sipunculans, foraminiferans and algae (Russell 1983; Gillanders 1995b, 1999; Shepherd 1998, 2006; Denny and Schiel 2001; Shepherd and Clarkson 2001). These prey items are typically obtained using a combination of ram and suction aided by protrusible jaws to cause dislodgement from the rocky substrate (Ferry-Graham *et al.* 2002; Shepherd 2006).

The dietary intake of labrids shifts in response to morphological changes associated with ontogeny, spatial and temporal variation in the abundance of prey, and competition-induced resource partitioning. The diet of juvenile labrids consists predominantly of epifaunal crustaceans (such as amphipods and isopods) and small bivalve and gastropod molluscs, whilst larger individuals feed on harder bodied prey including bivalves, gastropods, crabs and urchins (Deady and Fives 1995; Gillanders 1995b; Jones 1999; Denny and Schiel 2001; Shepherd and Clarkson 2001, Shepherd 2006). However, substantial dietary overlap may exist between adjacent size classes (Shepherd and Clarkson 2001). Ontogenetic dietary changes may reflect an increased mouth size and gape, strengthened crushing power of the pharyngeal jaws and/or shifts in foraging habitat (Wainwright 1988; Gillanders 1995b; Shibuno *et al.* 1997; Clifton and Motta 1998; Helfman *et al.* 1997).

The diet of labrids varies spatially and temporally (Gillanders 1995b; Fjøsne and Gløsaeter 1996; Denny and Schiel 2001), reflecting variation in prey availability within habitats and sites, and seasonal recruitment of prey items (Gillanders 1995b; Jones 1999). The effects on labrid assemblages of spatial and temporal variation in the availability of prey items requires further investigation, but is likely to be significant in the underlying patterns of distribution, timing of recruitment and habitat selection of recruits (see Chapter 3).

The concept of dietary shifts in labrids in response to competition-induced resource partitioning has received little attention in the past. Dietary data is available for single

labrid species, but there are no known studies which have compared the diets of co-occurring species. Such comparisons are crucial to precisely elucidate the role/s of labrids on temperate reefs, since studies of fish species within the same family (e.g. Apogonidae, Mullidae, Pempherididae, Sillaginidae, Triglidae and Urolophidae) have typically shown that marked differences in diet and/or feeding behaviour can occur within the same family (McCormick 1995; Hyndes *et al.* 1997; Platell *et al.* 1998; Platell and Potter 1999, 2001; Linke *et al.* 2001; Schafer *et al.* 2002). This is an important area of labrid ecology which will be addressed in greater detail in the discussion.

5.1.4 Foraging behaviour

Dietary composition of fishes obtained from examination of guts provides direct evidence of fish trophodynamics; however, many aspects of the impact of foraging on subtidal assemblages remain a matter of conjecture without direct observation of feeding behaviour (e.g. social interactions and ontogenetic shifts in foraging behaviour). Foraging behaviour constitutes a significant portion of daily energy expenditure in fishes (Hoffman 1983; Fulton and Bellwood 2002) and should be a matter of importance for fish ecologists wishing to complement dietary data for the purpose of understanding the ecological significance of labrids. Whilst the feeding behaviour of the tropical cleaner fish *Labroides dimidiatus* is well described (e.g. Bansemer *et al.* 2002; Bshary and Schäffer 2002; Grutter *et al.* 2003), the feeding behaviour of most other labrids is poorly understood.

For many labrids, the time spent foraging reduces as fish length increases (Gillanders 1995b; Shepherd and Clarkson 2001; Martha and Jones 2002; Shepherd and Brook 2005). Males may also spend less time foraging during the breeding season when there is an increase in territorial and courtship activities (Hoffman 1983). Foraging rate may also vary diurnally. For example, the temperate labrid *Notolabrus tetricus* commences foraging soon after sunrise, reaching a peak during mid-morning, and declining in the afternoon until foraging ceases at dusk (Shepherd and Clarkson 2001). In contrast, most feeding in *Achoerodus gouldii* occurs in the morning and late afternoon (Shepherd and Brook 2005). In other labrids, diurnal foraging does not differ between morning,

midday and afternoon (Gillanders 1995b), but may be influenced by tidal cycle (Shepherd 2006).

Feeding microhabitats are defined as ‘physically, or biologically, distinguishable feeding substrata, which occur on a spatial scale such that individuals may encounter the entire range present at a site within their normal home range’ (Jones 1988, p455). Size-related shifts in feeding microhabitats have been demonstrated in labrids (e.g. Shepherd and Brook 2005), but whether ontogenetic shifts in microhabitat use occurs in the focal labrid species and/or whether feeding microhabitats are partitioned among co-occurring labrids is not known. Filling these information gaps will assist in determining the extent of resource partitioning in labrid assemblages and for determining whether linkages occur between the feeding behaviour and dietary composition of labrids.

5.1.5 Foraging interactions

Feeding activities of individual fish do not occur in isolation from the activities of other fishes. The most well documented example of interspecific interactions among fishes involves cleaning behaviour by *Labroides dimidiatus* (e.g. Bansemer *et al.* 2002; Bshary and Schäffer 2002; Grutter *et al.* 2003). However, feeding interactions involving other labrid species do occur and may be of considerable ecological importance on rocky reefs of temperate Australia. Inter-specific interactions among fishes are usually commensal whereby benefits are provided to only one member of the relationship, and usually for the benefit of improved feeding opportunities (Bond 1996). Many labrids are known to profit from the feeding habits of other organisms by intercepting invertebrates disturbed or flushed out from the substrate. Labrids are known to follow feeding individuals from the families Mullidae and Dasyatidae (Helfman *et al.* 1997), Muraenidae (Moyle and Cech 2000), Carangidae (Silvano 2001), and Cheilodactylidae (Matsumoto and Kohda 2001). Likewise, some planktivorous fish are known to follow feeding labrids to prey on disturbed fauna (Gillanders 1999). The prevalence and importance of feeding associations is not known for most labrids of temperate Australia and is a matter of consideration in the current investigation.

Inter-specific interference competition for food has been documented in several species of labrid. For example, *Achoerodus viridis* may chase or be chased by *Notolabrus*

gymnogenis (Labridae), *Atypichthys strigatus* (Scorpididae), Mullidae and Cheilodactylidae (Gillanders 1999). In addition, Shepherd and Clarkson (2001) have documented interactions between juvenile *Notolabrus tetricus* and *Pictilabrus laticlavius* in response to competition for food resources. Foraging time and feeding rates of labrids may also be reduced by aggressive interactions with nest-guarding pomacentrids (Gillanders 1995b, 1999), refuge defending crabs (Shepherd and Clarkson 2001) and territorial blennids (Thompson and Jones 1983). In other labrids, aggressive encounters with other fishes are infrequent despite sharing similar ecological profiles (Martha and Jones 2002; Shepherd 2006).

Many aspects of labrid non-feeding behaviour discussed in Chapter 4 (e.g. lying, shelter use and social interactions) relate to foraging and should be acknowledged as integral to the understanding of labrid feeding ecology. This is particularly evident when consideration is given to social interactions and social spacing arising from interference competition for food resources. For example, the establishment of size-related dominance hierarchies and territoriality is often an attempt to limit the access of prey items to conspecific competitors (Robertson 1981; Tribble 1982; Grant 1997; Wootton 1998), with interactions becoming more frequent if food is concentrated (Shepherd and Clarkson 2001).

Describing and quantifying components of foraging behaviour, including foraging rates and interactions, is of great significance for developing a greater understanding of the role of labrids in rocky reef trophodynamics. Other aspects of labrid feeding behaviour that have been investigated, or observed, include foraging paths (Fulton and Bellwood 2002; Shepherd 2006), methods of prey capture and manipulation (Gillanders 1999), and prey preference experiments (Shepherd and Clarkson 2001; Shepherd 2006). Despite these advancements, the feeding behaviour of labrids is an area of research requiring greater study, especially in NSW where few investigations have focused on the ecology of these fishes.

5.1.6 Foraging trophodynamics

As large, abundant, mobile predators of benthic invertebrates, labrids may have a significant role in reducing prey abundances and modifying subtidal assemblages in temperate rocky reef systems (Choat 1982; Sala 1997; Jones 1999). For example, in southern Australia, *Notolabrus tetricus* are considered to play an important role in controlling the recruitment of abalone (Shepherd 1998) and are major predators of limpets (Parry 1982). Labrids are also known to predate upon echinoids associated with temperate reefs (Sala 1997; Gillanders 1999; Shepherd and Clarkson 2001; Shepherd 2006). Since echinoids have been recorded as denuding the substrate of erect benthic macroalgae to create vast areas of relatively inedible crustose coralline algae (Underwood *et al.* 1991; Sala *et al.* 1998; Steinberg and Kendrick 1999; Edgar 2001), labrid predation of echinoids could have consequences for fishes and other organisms that are reliant on macroalgal habitat (Schiel 1994; Andrew and Constable 1999). Labrid feeding on small prey items, such as amphipods, may also have a considerable effect on algal assemblages (Duffy and Hay 2000; Edgar 2001). Whether labrids deserve 'keystone' status in controlling assemblage structure remains unknown (see Choat 1982); however, they are likely to have important ecological roles in temperate rocky reef systems of Australia nevertheless.

The predatory effects of labrids on invertebrate communities cannot be examined in isolation from other benthic carnivores such as rock lobsters, sea stars and whelks (Edgar 2001). In addition, labrids show considerable similarity in their ecological requirements to many non-labrid fish species. For example, the red morwong, *Cheilodactylus fuscus*, is a large, abundant, benthic carnivore that feeds on crustaceans (especially amphipods), polychaetes, echinoderms and molluscs on temperate reefs of eastern Australia (Lockett and Suthers 1998; Lowry and Cappel 1999). This species also exhibits similar ontogenetic dietary and habitat shifts to that of similar sized labrids. Similarly, many leatherjackets have a varied diet which includes shrimps, amphipods, polychaetes and ascidians (Hutchins 1999). With substantial niche overlap, ways that resources are partitioned and interactions between these species pose research questions of considerable interest that have yet to be investigated. However, it is likely the dominance of labrids on temperate reefs (see Chapter 3) makes them disproportionately important as top-down predators.

5.1.7 Overview and chapter objectives

Labrids are dominant fishes on rocky reefs of NSW, yet there is little information available on the foraging behaviour or dietary compositions of this family in the region. This is despite their potential importance in manipulating prey abundances and indirectly influencing the structure of rocky reef assemblages, and being important in influencing the spatial and temporal patterns of labrid distribution. To fill in some of the gaps in the current understanding of labrids, this chapter explores the feeding ecology of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* by investigating the dietary compositions of each species; determining the extent of any size-related changes in the diet of each species; determining whether the bite rates of each of the three species differ among life history stages and whether these differences, if any, are spatially and temporally consistent; establishing whether feeding microhabitats are partitioned among species or exhibit shifts with life history stage; and providing qualitative descriptions of foraging behaviour including prey consumed, prey manipulation strategies and feeding interactions.

5.2 Methods

5.2.1 Diet

5.2.1.1 Specimen collection

The dietary compositions of *Ophthalmolepis lineolatus* (n=193), *Notolabrus gymnogenis* (n=186) and *Pictilabrus laticlavius* (n=87) were investigated using specimens collected from coastal reefs on the central coast of NSW (Figure 2.2). Locations and methods used for collecting fish specimens, and a summary of the specimens collected, are provided in Chapter 2.

5.2.1.2 Dietary examination

The total length (± 1 mm) of each specimen was measured and individuals of each species were placed into 50 mm size classes (i.e. <100, 100-149, 150-199, 200-249 mm etc.). The entire intestinal tract (gut) of each specimen was removed and fixed in 5% formalin for at least 48 hours, then stored in 70% ethanol. The fullness of each gut was estimated using a scale ranging from 0 (empty) to 10 (fully distended). Gut contents were removed, spread on a petri dish and examined under a stereoscopic microscope using reflected light. For individuals obtained from anglers or commercial traps, bait found within the gut (typically pilchards or poultry intestines) was discarded and not included in estimates of gut fullness, nor were they recorded as dietary items.

Gut contents of each individual were identified to the lowest possible taxon and allocated into one of 49 dietary item categories (Table 5.1). The frequency of occurrence of each dietary item in the guts of each species (%F) and the percentage contribution of each dietary item to the total volume of gut contents of each fish (%V) were determined. Dietary items that were ingested by >5% of fish and/or made a percentage volumetric contribution to the overall diet of >1% for at least one of the three species were deemed to be sufficiently represented in the diet of labrids to be termed 'dietary categories'. This resulted in a total of 22 dietary categories which were used for subsequent analysis (Table 5.1). Unidentified organic material, which contributed 7.9, 2.7 and 1.2% to the overall diets of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*, respectively, was not included in

the analyses as this category may contain representatives of several dietary categories. Likewise, unidentifiable prosobranch gastropods, whose contribution to the diets of each species are shown in Table 5.1, was not included in further analyses.

5.2.1.3 Dietary analyses

To test whether volumetric dietary compositions differed among the three labrid species, multivariate statistical analyses (i.e. nMDS ordinations, MVDISP, ANOSIM and SIMPER) were undertaken using PRIMER v5 (Clarke and Gorley 2001). Gut contents were highly variable so group averages of 10-11 randomly selected individuals for each species were calculated for each of the 22 dietary categories. This resulted in 16, 17 and 8 replicate groups for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*, respectively. Dietary data for group averages were then square-root transformed to reduce the influence of numerically dominant taxa and similarity matrices were constructed using Bray-Curtis dissimilarity coefficients. The resultant similarity matrices were visualised with MDS ordinations and a one-way ANOSIM (Analysis of Similarities) was used to test for differences in dietary composition among the three species (Clarke 1993; Clarke and Gorley 2001).

As dietary compositions were found to differ among species, *post hoc* comparisons were investigated and the magnitude of the associated *R*-statistic value was used to offer an absolute measure of difference between paired groups. In general, if $R > 0.75$, groups are clearly distinguishable, if $R > 0.5$, groups overlap but are clearly different, and if $R < 0.25$, groups are typically indistinguishable (Clarke and Gorley 2001). Relative dispersion of samples representing each species was also calculated using multivariate dispersion indices (MVDISP), whereby higher values indicate greater dispersion (Somerfield and Clarke 1997). Similarity percentages (SIMPER) were used to determine the dietary categories that typify the diet of each species and distinguish between species (Clarke 1993).

Since the above analyses demonstrated that the dietary compositions differed overall among *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*, a second series of analysis was performed separately on each species to examine the dietary compositions of different size classes. For these analyses, group averages of 4-5 randomly selected individuals

from each 50 mm size class were calculated for each of the 22 dietary categories. Dietary data for group averages were then square-root transformed and subject to nMDS ordinations and ANOSIM as previously described.

5.2.2 Foraging behaviour

5.2.2.1 Study area and locations

The foraging behaviour of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* was investigated between August 2003 and January 2005 at Catherine Hill Bay and Norah Head on the central coast of NSW (Figure 2.2). A detailed description of the study area and each location is provided in Chapter 2.

5.2.2.2 Sampling strategy, field observations and data collation

Foraging behaviour was recorded simultaneously with other aspects of labrid behaviour using the sampling strategy and techniques for field observations outlined in Chapter 4. Each 10 min period of recorded video footage was reviewed to determine bite rate (number of bites.10 min⁻¹) and the total number of bites occurring in each of eight feeding microhabitats (i.e. sand/rubble, bare rock or steel, algal base, algal frond, floating particle, *Diopatra dentata* tubes, jetty piles, or 'other' which included prey fragments, rope fibres, surface of broken shells, wire etc.). Qualitative notes of other feeding behaviours including prey items consumed, prey manipulation and feeding interactions were also recorded opportunistically.

5.2.2.3 Data analyses

A four-factor mixed model analysis of variance (ANOVA) using GMAV5 software (Institute of Marine Ecology: University of Sydney) was used to test for differences in bite rates among life history stages for each species and determine whether differences, if any, were consistent at all times of the day, in each period of sampling and at both locations (see Table 4.1). Assumptions of homogeneity of variance were tested using Cochran's C test. Data were transformed when variances were heterogeneous (Underwood 1981). Where significant main effects and/or interactions were found, *post*

hoc tests were performed in GMAV5 using the Student-Newman-Keuls (SNK) test (Underwood 1981).

The percentage of bites recorded in each of the eight feeding microhabitats was visualised using non-metric multivariate scaling (nMDS) procedures in PRIMER v5 (Clarke and Gorley 2001). Data were first square-root transformed, as is appropriate for percentage data (Platell and Potter 2001), prior to the construction of similarity matrices using Bray-Curtis dissimilarity coefficients. MDS ordinations were used to compare microhabitat usage among species and to determine the extent of shifts in microhabitat use with progressive life history stage at each location. Stress values were used to indicate how faithfully the two dimensional plot represented multidimensional relationships. Stress values <0.2 provide a useful interpretation of the multivariate data set with little prospect of a misleading interpretation (Clarke and Warwick 1994).

5.3 Results

5.3.1 Diet of labrids

5.3.1.1 Overall dietary compositions

The guts of a total of 193 *Ophthalmolepis lineolatus*, 186 *Notolabrus gymnogenis* and 87 *Pictilabrus laticlavius* were examined with 86.5, 93.0 and 98.9% of guts containing food items, respectively. For those guts containing food items, mean fullness (\pm SE) was 3.2 ± 0.1 , 4.3 ± 0.2 and 5.1 ± 0.2 for *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*, respectively.

Arthropods were found in 72.5, 93.6 and 87.2% of the guts of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*, respectively, and comprised *ca.* 23% of the overall dietary volume of the former species and 45-48% of the dietary volume of the latter two species (Table 5.1). Amphipods and decapods, which were by far the most important of the ingested arthropods for all three species, each contributed between 10.3 and 28.6% to the overall dietary volume for all species.

Molluscs were also important in the diets of each species, being found in 88.0, 94.2 and 90.4% of the guts of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*, respectively (Table 5.1). This phylum contributed the most to the overall dietary volume of *O. lineolatus* (47.6%), followed by *P. laticlavius* (44.7%) and *N. gymnogenis* (38.5%). Although this taxon was similarly important in the diets of all three species, differences among dietary categories associated with this taxon occurred for each species. For example, polyplacophorans, trochid gastropods and bivalves contributed 7.4, 12.0 and 12.2%, respectively, to the overall dietary volume of *O. lineolatus*, with no other molluscan dietary category contributing more than 4% to the dietary volume of this species (Table 5.1). In the case of *N. gymnogenis*, trochid and columbellid gastropods and bivalves comprised 15.8, 3.6 and 9.0% of the overall diet, respectively, while trochid gastropods were by far the most important dietary category for *P. laticlavius* (%V=27.8) with only one other dietary category (i.e. bivalves) contributing more than 5% to the overall dietary volume (Table 5.1).

Polychaetes were found in *ca.* 33-39% of the guts of all species and ranged in their contribution to overall diet from 3.9% in the diets of *N. gymnogenis* to 7.9% in *O. lineolatus* (Table 5.1). Echinoderms, particularly echinoids, were found in 29.3% of all guts of *O. lineolatus* and made a moderate contribution of 6.9% to the overall dietary volume in this species. They were less important in the diets of *N. gymnogenis* and *P. laticlavus*, being found in 26.0% and 15.1% of all guts and contributing 3.4 and 1.2% to the overall dietary volume of each species, respectively.

5.3.1.2 Multivariate comparisons of diet among species

MDS ordination of the mean percentage contribution of the different dietary categories for each species showed that the points representing *Ophthalmolepis lineolatus* lay largely on the left of the plot while those for *Notolabrus gymnogenis* and *Pictilabrus laticlavus* formed discrete, tightly clustered groups on the lower right and upper right portions of the plot, respectively (Figure 5.2). Overall there was a significant difference in dietary compositions among species (Global $R=0.48$, $P=0.001$) as well as between each pair of species (all $R>0.43$, $P=0.001$). Clustering of points was relatively tight for *P. laticlavus* and *N. gymnogenis* (dispersion values of 0.601 and 0.672, respectively), whilst the points were more dispersed in the case of *O. lineolatus* (dispersion value = 1.465).

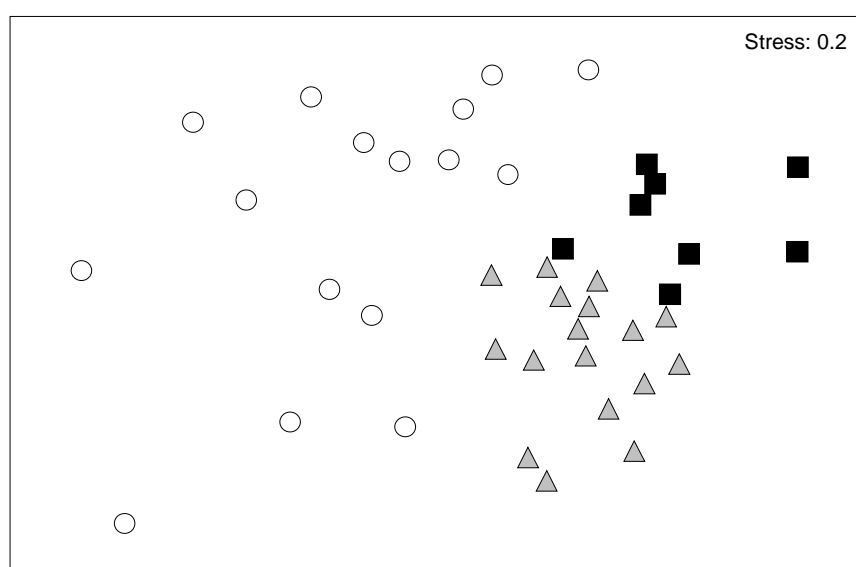


Figure 5.2: MDS ordination of dietary categories for *Ophthalmolepis lineolatus* (○), *Notolabrus gymnogenis* (△) and *Pictilabrus laticlavus* (■). Each point represents the mean of 10-11 randomly selected individuals.

Table 5.1: Frequency of occurrence (%F) and contribution by volume (%V) of dietary items and dietary categories to the overall diet of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. Asterisks and bold denote dietary categories used for dietary analyses. Only those prey items able to be identified within each taxa are listed. Bracketed values are those of major taxa represented by several dietary items.

Dietary items and dietary categories		<i>O. lineolatus</i>		<i>N. gymnogenis</i>		<i>P. laticlavius</i>	
Dietary items	Prey examples able to be identified	%F	%V	%F	%V	%F	%V
Foraminifera		1.8	<0.1	0.6	<0.1	1.2	<0.1
Algae*	Dictyotaceae, <i>Hormosira banksii</i> , <i>Ectocarpus</i> sp., <i>Cystophora</i> sp., <i>Amphiroa anceps</i>	15.0	1.0	32.4	2.2	18.6	1.1
Magnoliophyta				0.6	<0.1		
Cnidaria*	Hydrozoa, Actiniaria, Zoanthidea, Scleractinia, Alcyonacea	6.6	0.2	6.9	0.4	2.3	0.1
Platyhelminthes		1.2	0.4			1.2	<0.1
Nemertea		1.8	0.4	0.6	<0.1		
Nematoda		25.7	0.7	0.6	<0.1	1.2	<0.1
Polychaeta*	<i>Galeolaria caespitosa</i> , Spirorbidae	38.9	7.9	35.3	3.9	32.6	5.0
Sipuncula		1.2	0.1	2.9	0.3		
Echiuroidea		1.2	0.2	1.2	0.1		
Arthropoda		(72.5)	(23.3)	(93.6)	(48.1)	(87.2)	(45.5)
Pycnogonida		1.2	0.1	0.6	<0.1		
Insecta				0.6	<0.1	2.3	<0.1
Cirripedia*	<i>Austrobalanus imperator</i> , <i>Balanus</i> spp.	11.4	1.3	13.9	1.3		
Ostracoda		1.8	<0.1			4.7	0.2
Tanaidacea		0.6	<0.1			1.2	0.1
Isopoda*	Flabellifera, Valvifera	4.2	0.3	12.1	0.9	15.1	1.9
Amphipoda*	Gammaridea	32.3	11.4	54.3	17.3	68.6	25.7
Decapoda*	<i>Halimacarcinus ovatus</i>	43.7	10.3	79.2	28.6	57.0	17.5
Mollusca		(88.0)	(47.6)	(94.2)	(38.5)	(90.7)	(44.7)
Polyplacophora*	<i>Ischnochiton australis</i> , <i>Cryptoplax striata</i>	26.3	7.4	30.6	3.1	26.7	3.2
Gastropoda		(78.4)	(28.0)	(84.4)	(26.0)	(81.4)	(36.2)
Ammaeidae*	<i>Patelloida insignis</i> , <i>Patelloida latistrigata</i> , <i>Notoacmea</i> sp.	9.0	0.9	11.0	1.2	15.1	1.2
Cerithiidae	<i>Cerithium fasciatum</i>	1.8	0.1	0.6	<0.1		
Columbellidae*	<i>Mitrella</i> sp.	29.9	3.6	43.4	3.6	25.6	2.5
Epitonidae	<i>Epitonium</i> sp.	4.8	0.1	0.6	<0.1	3.5	0.1
Fasciariidae		0.6	<0.1	0.6	<0.1		
Fissurellidae*	<i>Amblychilepas nigrita</i> , <i>Tugali</i> sp.	6.6	0.7	24.9	1.6	31.4	3.5
Haliotidae*	<i>Haliotis</i> spp.			7.5	1.2		
Littorinidae	<i>Bembicium</i> sp.	0.6	<0.1	0.6	<0.1	1.2	<0.1
Marginellidae*	<i>Austroginella</i> sp.	19.2	3.0	5.2	0.2	7.0	0.5
Muricidae*	<i>Agnewia tritoniformis</i> , <i>Morula marginalba</i>	16.2	1.2	22.0	0.6	4.7	0.1
Nassariidae	<i>Nassarius glans</i>	1.8	0.1				
Naticidae*	<i>Notocochlis sagittate</i> , <i>Ectosinum zonale</i>	5.4	0.3	1.7	0.1		
Olividae	<i>Oliva</i> sp.			0.6	<0.1		
Patellidae	<i>Patella chapmani</i>	0.6	0.1	2.3	0.1		
Potamididae*		10.2	0.9	7.5	0.1	1.2	<0.1
Rissoiidae	<i>Rissoina</i> sp.	1.8	<0.1	2.3	<0.1		
Terebridae	<i>Hastula brazieri</i>	0.6	<0.1				
Trochidae*	<i>Stomatella impertusa</i> , <i>Euchelus asperses</i> , <i>Clanculus</i> sp., <i>Phasianotrochus</i> sp., <i>Calliostoma</i> sp.	55.7	12.0	64.7	15.8	73.0	27.8

Table 5.1 (continued):

Dietary items and dietary categories		<i>O. lineolatus</i>		<i>N. gymnogenis</i>		<i>P. laticlavus</i>	
Dietary items	Prey examples able to be identified	%F	%V	%F	%V	%F	%V
Gastropoda (continued)							
Turbinidae*	<i>Turbo</i> spp., <i>Phasianella</i> sp., <i>Subnirrella undulata</i>	6.0	0.6	4.6	0.1		
Turridae	<i>Euguraleus jacksonensis</i>	2.4	0.7				
Unidentifiable Prosobranchia		31.1	2.6	23.7	1.1	19.8	0.5
Opisthobranchia	<i>Bulla</i> sp.	3.0	0.8	1.2	0.4	2.3	0.1
Bivalvia*	Mytilidae, Arcidae, Limidae, Chamidae, Mactridae, Erycinidae, Tellinidae, Carditidae, Trigonidae	50.3	12.2	62.4	9.0	58.1	5.3
Cephalopoda	<i>Sepioteuthis australis</i>			1.2	0.3		
Bryozoa		0.6	<0.1				
Echinodermata		(29.3)	(6.9)	(26.0)	(3.4)	(15.1)	(1.2)
Ophiuroidea*		8.4	2.1	17.3	2.0	7.0	0.6
Echinoidea*		23.4	4.9	13.9	1.4	9.3	0.6
Chordata		(8.4)	(2.5)	(8.1)	(0.4)	(5.8)	(1.3)
Ascidiacea	<i>Pyura stononifera</i>	0.6	<0.1			3.5	0.7
Osteichthyes*	Gobiesocidae	7.8	2.5	8.1	0.4	2.3	0.5
Unidentifiable organic material		34.1	7.9	15.6	2.7	15.1	1.2
Sediment		1.8	0.7				
Total number of guts with prey items		167		173		86	
Gut fullness (mean±SE)		3.16±0.14		4.31±0.15		5.07±0.23	

Trochid gastropods and decapods typified the diets of each of the three species, bivalves also typified the diets of *O. lineolatus* and *N. gymnogenis*, and amphipods also typified the diets of *N. gymnogenis* and *P. laticlavus* (Table 5.2). The diet of *O. lineolatus* was distinguished from other species by the presence of greater volumes of echinoids and marginellid gastropods, and fewer decapods and amphipods (Table 5.2). Higher volumes of decapods and ophiuroids distinguished the diet of *N. gymnogenis* from *P. laticlavus*, whilst the reverse occurred for amphipods and trochid gastropods.

Table 5.2: Dietary categories contributing most to typifying (shaded) the dietary composition of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*, and dietary categories distinguishing (non-shaded) between the dietary composition of species as identified using SIMPER. Asterisks denote a greater volumetric contribution to the diet of the species at the top of the column. No asterisk signifies a greater volumetric contribution to the species at the left of the row.

Species	<i>O. lineolatus</i>	<i>N. gymnogenis</i>	<i>P. laticlavius</i>
<i>O. lineolatus</i>	Trochidae Bivalvia Decapoda		
<i>N. gymnogenis</i>	Decapoda Amphipoda Marginellidae* Echinoidea* Polyplacophora* Polychaeta*	Decapoda Amphipoda Trochidae Bivalvia	
<i>P. laticlavius</i>	Amphipoda Trochidae Echinoidea* Decapoda Bivalvia* Fissurellidae Marginellidae*	Trochidae Decapoda* Amphipoda Ophiuroidea*	Trochidae Amphipoda Decapoda

5.3.2.3 Size-related changes in dietary compositions

The diets of the smallest size class of *Ophthalmolepis lineolatus* (i.e. <150 mm) were dominated by amphipods (%V=33), whilst polychaetes, decapods, columbellid and trochid gastropods, and bivalves also made moderate contributions of between 7 and 11% to the diets of this size class (Figure 5.3a). With increasing body size, the contribution of amphipods in the diet declined to 6% in fish of 200-249 mm and were not ingested by fish belonging to the largest size class (i.e. ≥ 300 mm). In contrast, the dietary volume of decapods, polyplacophorans and echinoids was highest in the larger size classes (i.e. 250-299 and ≥ 300 mm) compared to the smallest size classes (i.e. <150 and 150-199 mm). Cirripedes, and muricid and turbinid gastropods, were present only in the two largest size classes of fish (Figure 5.3a).

Likewise, amphipods dominated the diets of the smallest size classes of *Notolabrus gymnogenis* and *Pictilabrus laticlavius* (i.e. %V=53 and 51, respectively), but they did so to a far greater extent than in *O. lineolatus* (Figure 5.3b-c). The contribution of this small crustacean also progressively declined with increased body size in both species.

For *N. gymnogenis*, the dietary contribution of decapods typically increased with body size, with this taxa contributing 16% to the diets of fish <150 mm and 42% to the diets of fish 250-299 mm (Figure 5.3b). Furthermore, taxa such as cirripedes; amaeid, haliotid and columbellid gastropods; echinoids; and fish were typically only recorded in the diets of *N. gymnogenis* ≥ 200 mm in size.

Along with a marked decline in the contribution of amphipods from the smallest *P. laticlavus* (i.e. <100 mm) to the diet of the largest fish (i.e. 200-299 mm) was a similar decline in the dietary volume of polychaetes (7 to 1%, respectively), decapods (18 to 9%), amaeid gastropods (5 to 1%) and bivalves (9 to 3%) (Figure 5.3c). Accompanying these reductions was a substantial increase in the volumetric contribution of trochid gastropods from 1 to 65% and polyplacophorans from 1 to 9% in the smallest and largest size classes, respectively. Furthermore, marginellid gastropods were only ever ingested by the largest size class of *P. laticlavus* and contributed 6% to the diet of these individuals.

MDS ordination of dietary categories for each size class of each species revealed a dietary progression from the bottom left of the plot in all species (Figure 5.4). However, the points for both *O. lineolatus* and *N. gymnogenis* moved upwards on the plot and those for *P. laticlavus* moved to the right. Thus, the points for the largest size class of both *O. lineolatus* and *N. gymnogenis* (i.e. ≥ 300 mm) were located in the upper centre of the plot, whilst that of *P. laticlavus* (i.e. 200-249 mm) lay in the bottom right corner of the plot.

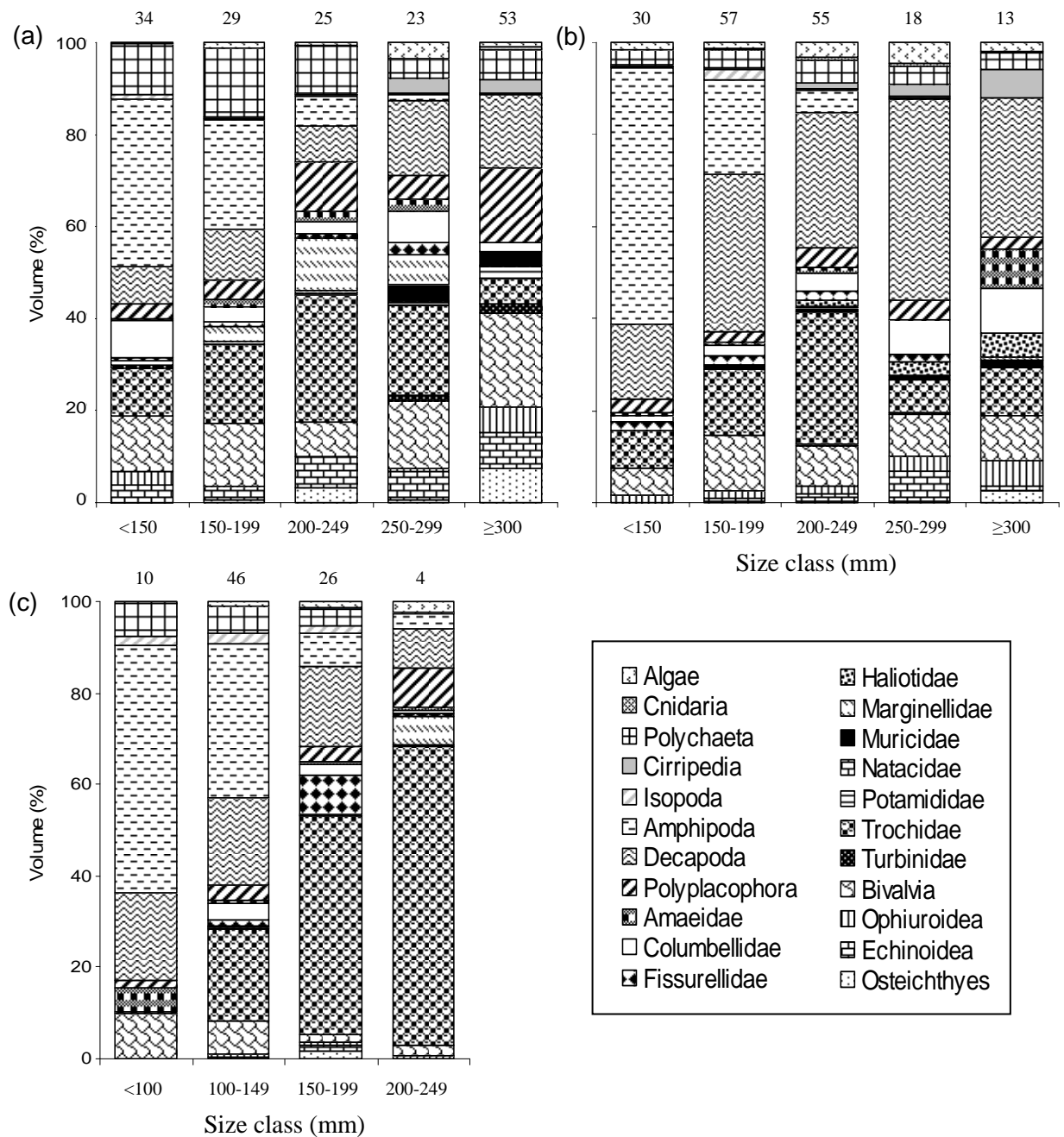


Figure 5.3: Percentage volumetric contribution of dietary categories to total gut contents for various size classes of *Ophthalmolepis lineolatus* (a), *Notolabrus gymnogenis* (b) and *Pictilabrus laticlavius* (c). Sample sizes are provided above each column.

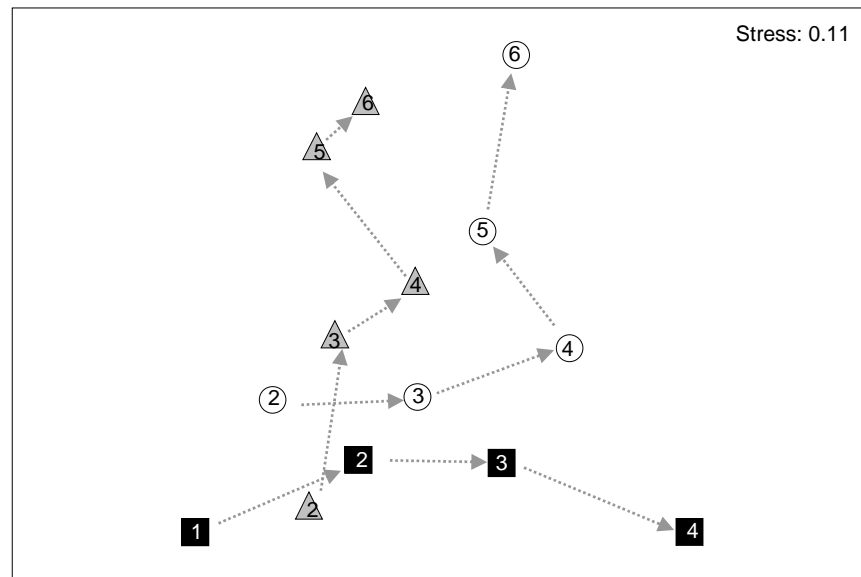


Figure 5.4: MDS ordination of dietary categories for *Ophthalmolepis lineolatus* (○) *Notolabrus gymnogenis* (Δ) and *Pictilabrus laticlavius* (■) at size classes of <100 (1), 100-149 (2), 150-199 (3), 200-249 (4), 250-299 (5) and ≥300 mm (6). Each point represents the mean of corresponding size classes (see Figure 5.3 for sample sizes). Arrows show progression through size classes for each species.

When each species was subjected to MDS ordinations separately there was a distinct shift from the left to the right of the plot with an increase in body size for all species (Figure 5.5). Whilst ordination points representing adjacent size classes overlapped, ANOSIM revealed a significant change in diet between non-adjacent size classes for all species (all $R > 0.329$, $P < 0.05$; Table 5.3). In addition, significant differences in diet occurred between the 200-249 and 250-299 mm size classes of *O. lineolatus*; all adjacent size classes of *N. gymnogenis* except 250-299 and ≥300 mm; and the 100-149 and 150-199 mm size classes of *P. laticlavius*. In all species, directional ontogenetic dietary change was reflected in the typical rise in R -values between progressively separated size classes (Table 5.3).

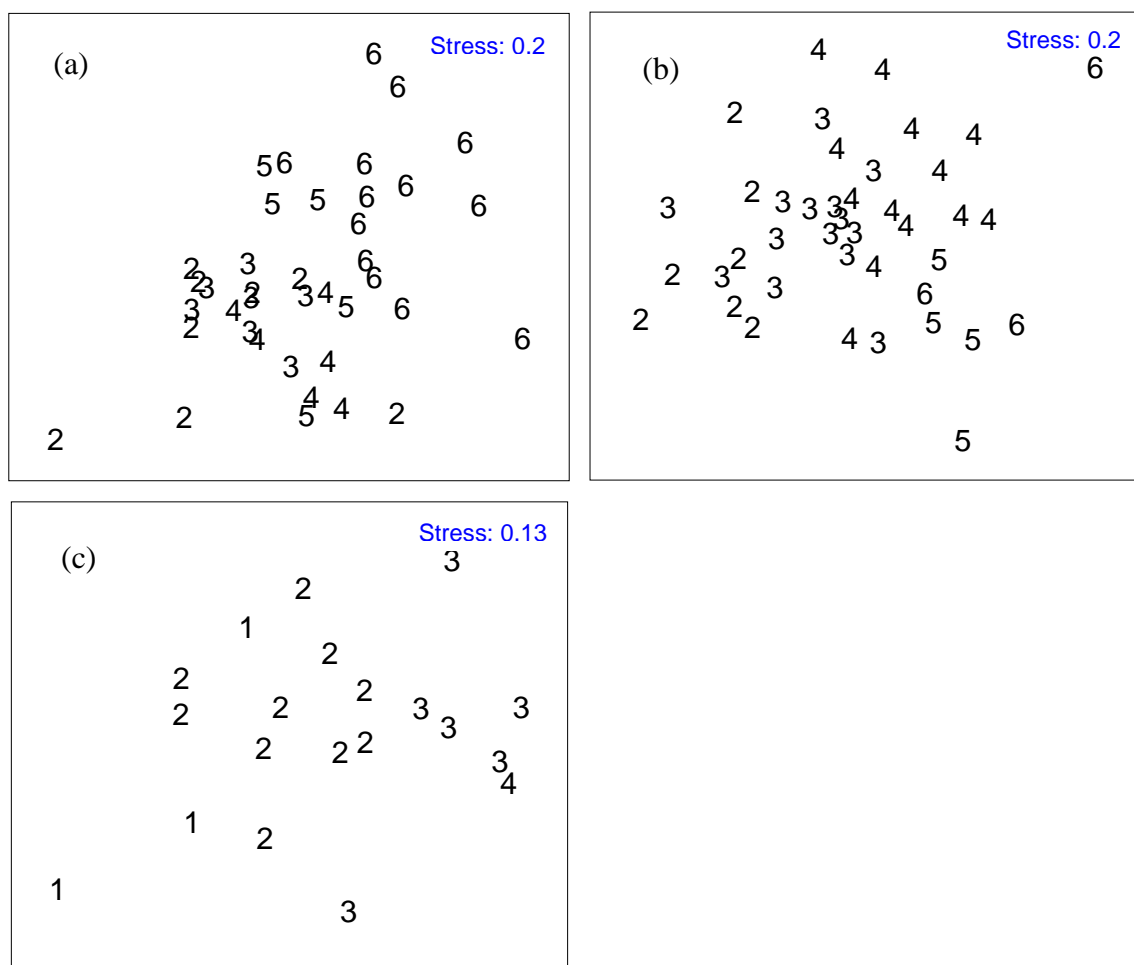


Figure 5.5: MDS ordinations of dietary categories for *Ophthalmolepis lineolatus* (a), *Notolabrus gymnogenis* (b) and *Pictilabrus laticlavius* (c) at size classes of <100 (1), 100-149 (2), 150-199 (3), 200-249 (4), 250-299 (5) and ≥ 300 mm (6). Each point represents the mean of 4-5 randomly selected individuals within corresponding size classes.

Table 5.3: *R* values obtained from ANOSIM for pair-wise comparisons of size classes for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. n/a denotes comparisons whereby too few possible permutations were available (i.e. <20) for significance testing at the $P=0.05$ level. ns = not significant (i.e. $P>0.05$), * $P<0.05$, ** $P<0.01$.

<i>Ophthalmolepis lineolatus</i> (Global $R=0.371$, $P=0.001$)				
Size class (mm)	150-199	200-249	250-299	≥ 300
<150	0.013 ns	0.329**	0.443**	0.636**
150-199		0.173 ns	0.593**	0.536**
200-249			0.267*	0.519**
250-299				0.246 ns
<i>Notolabrus gymnogenis</i> (Global $R=0.498$, $P=0.001$)				
Size class (mm)	150-199	200-249	250-299	≥ 300
<150	0.452**	0.743**	0.992**	0.905**
150-199		0.234**	0.675**	0.768**
200-249			0.305*	0.492*
250-299				0.204 ns
<i>Pictilabrus laticlavius</i> (Global $R=0.518$, $P=0.001$)				
Size class (mm)	100-149	150-199	200-249	
<100	0.268 ns	0.840**	1.000 n/a	
100-149		0.550**	1.000 n/a	
150-199			-0.111 n/a	

5.3.2 Foraging behaviour

5.3.2.1 Bite rates

Bites occurred most frequently in *Ophthalmolepis lineolatus* (768 bites, 84% of individuals) followed by *Notolabrus gymnogenis* (645 bites, 67% of individuals) and *Pictilabrus laticlavius* (504 bites, 62% of individuals). Ontogenetic differences in bite rates occurred only for *N. gymnogenis*. In this species, the bite rate of juveniles was higher than both IP and TP individuals in both periods of sampling, and the bite rate of IP individuals was higher than TP individuals in period 2 (SxP interaction, $P<0.05$) (Table 5.4; Figure 5.6). Despite the significant SxTxL interaction occurring for *P. laticlavius*, no differences among life history stages occurred at any time of the day at either of the locations (Table 5.4; Figure 5.6). The significant interaction was mostly due to typically higher bite rates occurring at Catherine Hill Bay. Bite rates (10 mins^{-1}) of *O. lineolatus* were consistently higher at Catherine Hill Bay (5.3 ± 0.5) than Norah Head (3.5 ± 0.3) (Table 5.4; Figure 5.6).

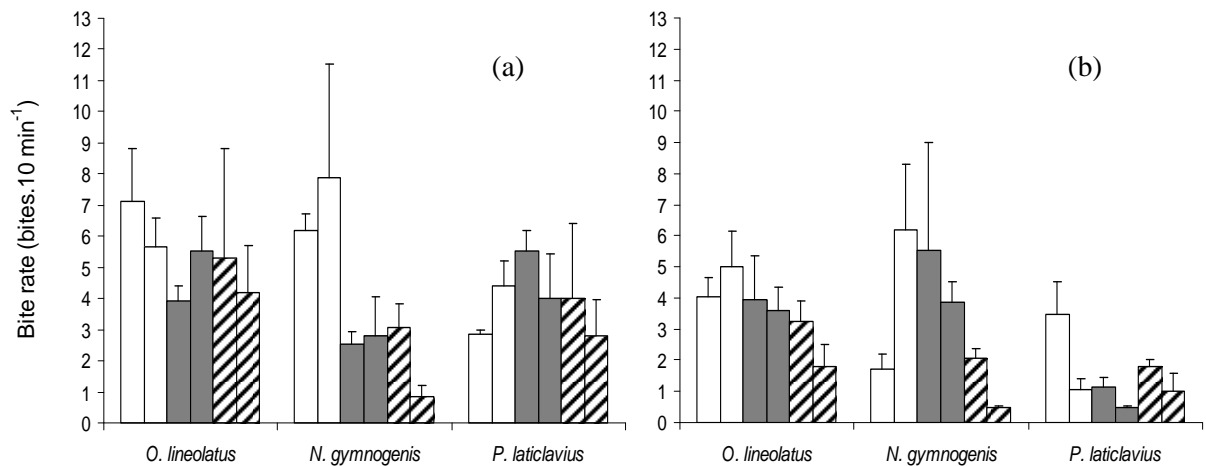


Figure 5.6: Mean bite rate (\pm SE) at Catherine Hill Bay (a) and Norah Head (b) for juvenile (\square), initial phase (\blacksquare) and terminal phase (\hatched) individuals of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* in two periods of sampling (replicated columns). All combinations of Stage \times Location \times Period are shown for each species ($n=3$ times of day with each time representing the average of five 10 minute replicates).

Table 5.4: Univariate ANOVA results for rates (10 mins^{-1}) of biting for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus*. ¹data $\ln(x+1)$ transformed, ²data square-root ($x+1$) transformed (Cochran's C test, $P>0.05$). * $P<0.05$, ** $P<0.01$, *** $P<0.001$.

Source of variation	df	<i>O. lineolatus</i>		<i>N. gymnogenis</i> ¹		<i>P. laticlavus</i> ²	
		MS	F	MS	F	MS	F
Stage (S)	2	55.57	8.36	10.34	12.93	0.51	0.54
Time of day (T)	2	71.24	16.50	2.75	8.17	1.08	2.32
Location = (L)	1	130.05	9.04**	1.91	2.47	19.11	32.40***
Period (P)	1	2.94	58.78	0.72	0.52	1.54	1.34
S \times T	4	11.62	1.24	0.61	3.64	0.25	0.16
S \times L	2	6.65	0.46	0.80	1.03	0.95	1.61
S \times P	2	11.71	0.65	3.90	90.35*	0.00	0.00
T \times L	2	4.32	0.30	0.34	0.43	0.47	0.79
T \times P	2	21.41	0.50	0.33	0.19	0.08	0.11
L \times P	1	0.05	0.00	1.39	1.80	1.14	1.94
S \times T \times L	4	9.37	0.65	0.17	0.22	1.53	2.59*
S \times T \times P	4	8.62	0.35	0.20	0.52	0.43	0.79
S \times L \times P	2	17.92	1.25	0.04	0.06	0.75	1.27
T \times L \times P	2	42.62	2.96	1.68	2.17	0.78	1.31
S \times T \times L \times P	4	24.73	1.72	0.37	0.48	0.55	0.93
Residual	144	14.38		0.77		0.59	

5.3.2.2 Feeding microhabitats

For each species, the majority of bites occurred in relatively complex microhabitat (e.g. algal bases, algal fronds and *Diopatra dentata* tubes), although some bites were also directed into less complex microhabitats (e.g. sand/rubble and bare rock or steel) (Figure 5.7). Juvenile *Ophthalmolepis lineolatus* fed in a variety of microhabitats including sand/rubble, algal bases, algal fronds and floating particles (Figure 5.7a, d).

Each of these microhabitats contributed 12-33% to all observed bites for juveniles at both locations. At Catherine Hill Bay, the percentage of bites recorded for TP individuals increased at algal bases (i.e. 58% of bites) with a concurrent reduction in the percentage of bites aimed at floating particles (Figure 5.7a). In contrast, the percentage of bites associated with algal bases, algal fronds and floating particles at Norah Head reduced to 5-11% in TP individuals and the percentage of bites recorded in sand/rubble microhabitat increased (i.e. 70% of bites) (Figure 5.7d).

Juvenile *Notolabrus gymnogenis* at Catherine Hill Bay directed bites into a variety of microhabitats with the highest percentage of bites occurring at algal bases, algal fronds and *Diopatra dentata* tubes (Figure 5.7b). The percent contribution of each of these microhabitats to total bites reduced from 18-26% in juveniles to 2-13% in TP individuals, whilst the contribution of bare rock or steel increased from 10 to 24%, respectively. For juvenile *N. gymnogenis* at Norah Head, algal base and algal frond microhabitats contributed 71 and 20% to total bites, respectively, with the contribution of these microhabitats reducing substantially in TP individuals (i.e. 6 and 0%, respectively) (Figure 5.7e). Associated with this decline was an increase in the contribution of bare rock or steel and *Diopatra dentata* tubes microhabitats from 2 and 0% in juveniles to 57 and 27% in terminal phase individuals, respectively.

Juveniles of *Pictilabrus laticlavius* at Catherine Hill Bay fed predominantly at sand/rubble, bare rock or steel, algal base and *Diopatra dentata* tubes microhabitats with each contributing 15-26% to all bites (Figure 5.7c). The contribution of these microhabitats declined to 7-11% in TP individuals, except for algal bases which rose to 52%. Juveniles of *P. laticlavius* at Norah Head fed predominantly in algal base and algal frond microhabitats (i.e. 61 and 25% of all bites, respectively), with a reduction in the percentage of bites in the algal frond microhabitat occurring for TP individuals (i.e. reduced to 5%) (Figure 5.7f). Associated with this decrease was a rise in the contribution of sand rubble and bare rock or steel microhabitats.

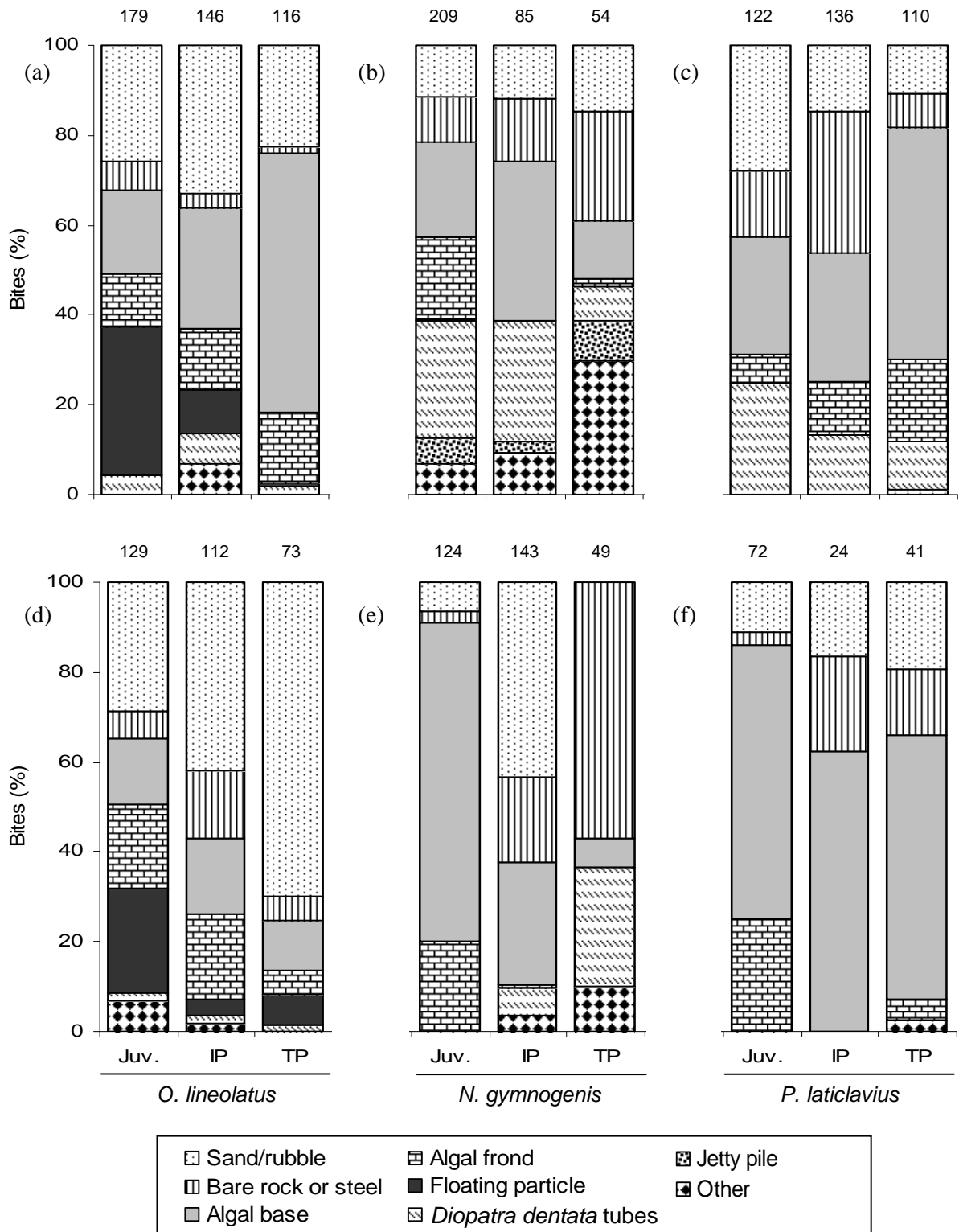


Figure 5.7: Percentage of total bites in various microhabitats at Catherine Hill Bay (a-c) and Norah Head (d-f) for three life history stages (Juv. = juvenile, IP = initial phase, TP = terminal phase) of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus*. Total observed bites in 300 minutes of behavioural observations for each stage of each species at each location are provided above each column. Microhabitats of 'other' bites included prey fragments, rope fibres, broken shells and wire.

When the percentages of total bites by each species in the various microhabitats were subjected to MDS ordination it was obvious that feeding microhabitats differed among species, microhabitat use changed with life history stage and that the pattern of change was different for the three species and different at the two locations (Figure 5.8). For example, at Catherine Hill Bay all points representing the life history stages of *O. lineolatus*, *N. gymnogenis* and *P. laticlavus* were located in the left, right and middle of the plot, respectively (Figure 5.8a). For both *O. lineolatus* and *P. laticlavus*, points representing successive life history stages generally progressed upward, whilst the points for *N. gymnogenis* progressed downward. At Norah Head, points representing *O. lineolatus* and *P. laticlavus* were distinct from one another and formed a tight group at the bottom left and upper left of the plot, respectively. Progressive shifts in microhabitat use with successive life history stage were not evident in either of these species at Norah Head. Microhabitat use by juvenile *N. gymnogenis* was similar to that of juvenile *P. laticlavus* at Norah Head, but progression in the points representing successive life history stages of *N. gymnogenis* occurred toward the lower right of the plot. These later life history stages remained discrete from other species.

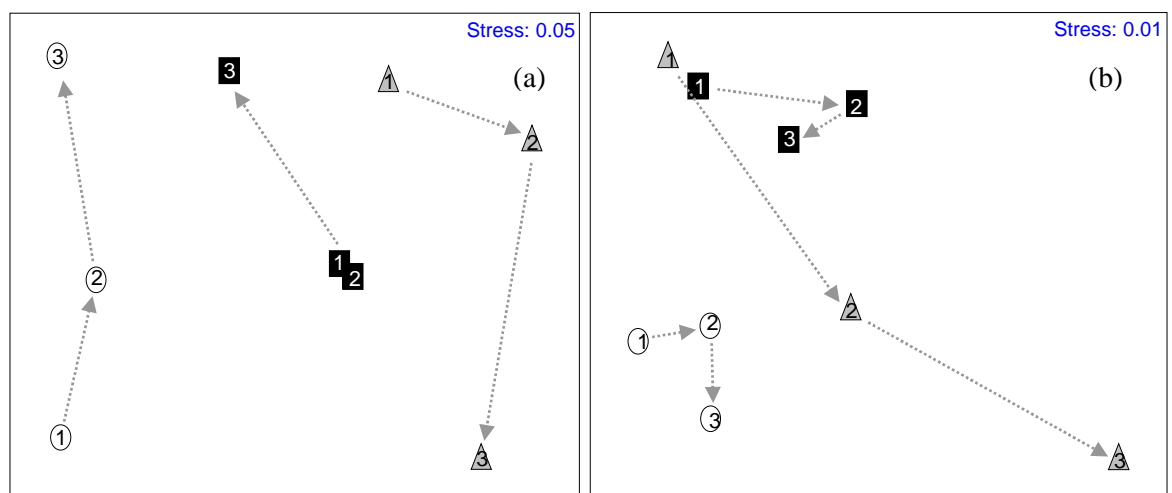


Figure 5.8: MDS ordination of the proportion of bites in various microhabitats at Catherine Hill Bay (a) and Norah Head (b) for *Ophthalamolepis lineolatus* (○), *Notolabrus gymnogenis* (△) and *Pictilabrus laticlavus* (■) at the life history stages of juvenile (1), initial phase (2) and terminal phase (3). Each point represents total bites for corresponding life history stages. Arrows show progression through life history stages for each species.

5.3.2.3 General feeding observations

Whilst many feeding episodes were observed, in most instances prey items were not able to be recorded as they were either too small, obtained too rapidly or were obscured from view. However, prey items were identified during some episodes of feeding by *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis*. Observed prey items included many of the major dietary items identified in Table 5.1 such as polychaetes, isopods, amphipods, cirri of barnacles, small decapods, polyplacophorans, gastropods, bivalves, ophiuroids, echinoid fragments and ascidian/poriferan fragments. On rare occasions, *O. lineolatus* also fed opportunistically on fish prey. In one feeding event, a TP individual was observed biting a discarded fish frame, whilst another large individual was observed swimming with the tail of an *Atypichthys strigatus* (Microcanthidae) protruding from its mouth. Active pursuit of fish prey was observed as isolated incidents with juvenile *O. lineolatus* chasing and/or biting *Enoplosus armatus* (Enoplosidae), Gobiesocidae and Gobiidae. Only a single prey item (limpet) was recorded for *Pictilabrus laticlavius* as this species is highly cryptic so the identification of prey items during field observations was problematic.

Small, highly mobile prey items such as amphipods and small decapods were swallowed directly from the substrate, often after lying-in-ambush. Ambush techniques were not employed by *O. lineolatus*, but *N. gymnogenis* and *P. laticlavius* regularly spent periods of up to several minutes lying on the substrate scanning for the movement of invertebrate prey at algal bases, on algal fronds or between *Diopatra dentata* tubes (see Chapter 4). Pectoral fin digging was regularly employed by *P. laticlavius* whilst lying in sandy microhabitats to expose prey items within sediment and to obtain access to prey beneath cobbles.

In all labrids, small-sized molluscs were crushed by the pharyngeal teeth before spitting shell fragments and swallowing the nutritious soft tissues. For large invertebrate items exceeding gape width (e.g. some polychaetes, gastropods, polyplacophorans and ophiuroids), a manipulation of prey was required before swallowing. On such occasions, prey was held in the mouth and bashed against rocky substrate with sideways head movements to fragment tissues or, in the case of limpets and chitons, to remove

the soft tissue from hard exoskeletons. Individuals would often retreat to shelter after swallowing these larger invertebrate items.

5.3.2.4 Feeding interactions

When occasions were presented, *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* opportunistically fed on retreating prey that was disturbed by the feeding activities of larger conspecifics, other Labridae (*Achoerodus viridis*), Mullidae (*Upeneichthys vlamingii*), Scorpaenidae (*Scorpaena cardinalis*), Plotosidae (*Cnidogobius macrocephala*), Muraenidae (*Gymnothorax prasinus*), Urolophidae (*Urolophus* sp.), Dasyatidae (*Dasyatis thetidis*), Myliobatidae (*Myliobatis australis*), Brachaeluridae (*Brachaelurus waddi*) and Octopodidae (*Octopus tetricus*). Of these, substrate disturbance caused by the feeding activity of *A. viridis* contributed most to attraction of the focal labrids. Winnowing of prey items through the gills of *A. viridis* also prompted following by *O. lineolatus* and *N. gymnogenis*. Reciprocated following behaviour by other fishes to the feeding activities of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* were not common, but larger individuals were followed by Serranidae (*Acanthistius ocellatus*), Cheilodactylidae (*Cheilodactylus fuscus*), Microcanthidae (*Atypichthys strigatus*), Pomacentridae (*Chromis hypsilepis*, *Parma microlepis* and *Parma unifasciata*) and other Labridae (*Pseudolabrus guentheri*).

Interactions between small *O. lineolatus* (<150 mm) and juvenile *Upeneichthys vlamingii* (Mullidae) provided an example of apparent mutualism. Encounters between these fishes involved *O. lineolatus* hovering <200 mm above *U. vlamingii* whilst attempting to intercept disturbed prey. Superficially this relationship appears exploitative; however, movement of *O. lineolatus* of up to several metres would typically result in *U. vlamingii* following beneath. Benefits for *U. vlamingii* would include the opportunity to feed in relative safety whilst *O. lineolatus* remained overhead. This association between species often lasted for periods of 3-9 mins.

5.4 Discussion

5.4.1 Dietary composition

Gut content analysis revealed *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* fed predominantly on polychaetes, gammarid amphipods, decapods (notably small crabs), gastropods (particularly trochids) and various bivalves. Polyplacophorans, echinoderms (ophiuroids and echinoids) and cirripedes were also frequently represented in the guts of these fishes. Whilst some labrids are known to primarily consume plankton (Warner and Hoffman 1980a, b; Warner 1987), coral (McIlwain and Jones 1998; Fulton and Bellwood 2002b), and ectoparasites, mucus or scales of other fishes (Zander and Nieder 1997; Jones 1999; Bansemer *et al.* 2002; Bshary and Schäffer 2002), the species investigated are unequivocally generalist carnivores feeding on an assortment of benthic invertebrates. The dietary breadth and importance of crustaceans, molluscs, polychaetes and echinoderms in the diets of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* are consistent with other temperate labrids of Australia and New Zealand (Russell 1983; Gillanders 1995b, 1999; Shepherd 1998, 2006; Jones 1999; Denny and Schiel 2001; Shepherd and Clarkson 2001).

Small fishes are rarely considered to be important dietary items for labrids, yet species within this family are known to engage in piscivory (Randall *et al.* 1978; Connell 1998; Connell and Kingsford 1998; Denny and Schiel 2001). Indeed guts of all focal species frequently contained the remains of small fishes and *O. lineolatus* were observed pursuing fish prey and feeding on fish frames. The ability of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* to feed on other fishes is likely to be constrained by gape width as fish prey are consumed in high volumes when presented as bait in the form of fragmented pilchards (Clupeidae).

5.4.2 Food partitioning among labrids

The occurrence of most prey items in the guts of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* revealed considerable reliance on a common food resource. However, substantial differences in the volumetric contribution of these prey items resulted in significant partitioning of food resources among species. For example, *O. lineolatus* fed on proportionately higher volumes of bivalves, polychaetes,

echinoids and marginellid gastropods (especially *Austroginella* sp.), whilst the diet of *N. gymnogenis* consisted of greater proportions of decapods (mostly unidentified), and *P. laticlavus* fed on greater proportions of amphipods and trochid gastropods. It is well established that when a resource is limited in a community these resources must be partitioned to reduce overall competition between consumers (Helfman *et al.* 1997). Resource partitioning allows co-existence with minimal competition and provides an important insight into the creation and maintenance of biodiversity (Helfman *et al.* 1997). In terrestrial systems, partitioning of habitat is most responsible for minimising competition between co-occurring species but for fish assemblages, especially in temperate waters, partitioning of food resources (i.e. trophic separation) is of greater importance (Ross 1986).

Partitioning of food resources among species within the same family has been demonstrated in soft sediment habitats (McCormick 1995; Hyndes *et al.* 1997; Platell *et al.* 1998; Platell and Potter 1999, 2001; Linke *et al.* 2001; Schafer *et al.* 2002), but this is the first known study to document trophic separation within a family of fish associated with rocky reef habitat. It is possible that the method of collection (and hence the habitat in which specimens were obtained) could have influenced the extent of dietary separation. For example, many more *O. lineolatus* were obtained using line and trap methods in deep waters (i.e. 20-70 m) than for other species. However, most specimens of each species were obtained using hand spear from common rocky reefs in shallow waters (<5 m). Therefore, causes of dietary separation are most likely due to differences in foraging strategy employed by each species (e.g. microhabitat use).

O. lineolatus, *N. gymnogenis* and *P. laticlavus* represent the three most abundant labrids on rocky reefs of the NSW central coast in depths of 2-10 m (*pers. obs.*) so competition for benthic invertebrate prey is likely to be great. Therefore, for these fishes, partitioning of food resources appears to be an important strategy for allowing co-occurrence. Whilst *N. gymnogenis* is restricted to temperate eastern Australia, *O. lineolatus* and *P. laticlavus* occur throughout much of southern Australia, including temperate Western Australia. In parts of their range, these species co-occur with *Notolabrus tetricus* and *Notolabrus fucicola* (Kuiter 1996) so partitioning of food resources among members of the family Labridae is likely to occur in southern Australia as occurs on the NSW central coast. As *N. gymnogenis* shares similar

characteristics with *N. tetricus* and *N. fucicola* (e.g. max size <500 mm; deep bodied) determining whether these species occupy similar dietary niches is of interest. In addition, how food resources are partitioned among these labrids and other benthic carnivorous fishes (e.g. Cheilodactylidae and Monacanthidae) poses ecological questions requiring further study. However, it is likely that co-occurring benthic carnivores from different families will demonstrate reduced competition compared to that within families due to family similarities with regard to body shape, mouth morphology, use of microhabitats and foraging behaviour (Linke *et al.* 2001; Wootton 1998; Platell and Potter 1999, 2001; Hyndes *et al.* 1997).

5.4.3 Ontogenetic dietary shifts

All species underwent significant ontogenetic dietary shifts owing mostly to changes in the proportional representation of prey items rather than to exclusive dietary preferences at different size classes. For small fishes, amphipods were the dominant prey item with small decapods (particularly *Halicarcinus ovatus*), small bivalves (most unidentifiable) and small trochids comprising the majority of the remaining prey. With increasing size, all species fed on greater volumes of hard-shelled molluscs with larger individuals of *Ophthalamolepis lineolatus* and *Notolabrus gymnogenis* feeding unselectively on a broad range of prey items, whilst larger individuals of *Pictilabrus laticlavius* focussed their feeding on trochid gastropods. Similar ontogenetic shifts in diet have been demonstrated in *Achoerodus viridis*, *Achoerodus gouldii*, *Pseudolabrus celidotus*, *Notolabrus fucicola* and *Notolabrus tetricus* (Jones 1984c, 1988; Gillanders 1995b; Denny and Schiel 2001; Shepherd and Clarkson 2001; Shepherd 2006). Small individuals of these species (i.e. 30-200 mm) fed predominantly on amphipods, isopods, polychaetes and small molluscs. Larger fish fed increasingly on hard-bodied prey such as larger molluscs, urchins and crabs. Contributing to ontogenetic dietary changes in labrids is an increase in mouth size and gape, greater crushing power of pharyngeal teeth, shifts in foraging habitat (see below), and improved locomotion and/or sensory abilities (Wainwright 1988; Gillanders 1995b; Shibuno *et al.* 1997; Clifton and Motta 1998; Wootton 1998; Helfman *et al.* 1997).

The importance of amphipods as a common food resource for small individuals (<150 mm) of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* resulted in considerable dietary

overlap among early life history stages of each species. Amphipods are also important for juveniles of other fish families including Cheilodactylidae (McCormick 1998; Lowry and Cappo 1999) and Monocanthidae (Hutchins 1999) suggesting that inter-specific competition is likely to be greatest among small individuals as dietary divergence occurs among larger fish in response to the utilising of a wider diversity of food resources (Helfman *et al.* 1997). Differential use of feeding microhabitats is likely to assist in reducing competition between juveniles of these species (see below).

The diet of recently recruited *O. lineolatus*, *N. gymnogenis* and *P. laticlavus* were not examined in the present study as individuals of very small sizes were generally not observed. However, the identification of prey items used by recruits and the availability of these food resources may be important in predicting the survival of recruits upon settlement onto a reef, and hence useful in describing patterns in the distribution and abundance of adults. Gillanders (1995b) found newly recruited *Achoerodus viridis* (17-26 mm) on coastal rocky reefs of eastern Australia fed almost exclusively on benthic crustaceans (primarily harpacticoid copepods), before shifting to a diet of mostly amphipods in small juveniles (50-150 mm). The smallest fishes examined in this study were 94, 76 and 70 mm for *O. lineolatus*, *N. gymnogenis* and *P. laticlavus*, respectively, corresponding to ages of 0.83, 0.5 and 0.83 years (Chapter 6). Guts of these fishes were found to contain 100% amphipods. For recently recruited fishes (i.e. <50 mm and <0.5 years), it is proposed that amphipods may be too large to manipulate into the mouth so, like *A. viridis*, other prey items (e.g. harpacticoid copepods) are likely to be of greater importance upon recruitment.

5.4.4 Microhabitat use

Complex microhabitat in the form of algal bases, algal fronds and *Diopatra dentata* tubes proved especially important to labrids for feeding, but less complex habitat in the form of bare rock or steel, and sand/rubble were also used regularly. At each location, most microhabitats were used for feeding by all stages of each species but, overall, substantial differences in microhabitat profiles occurred across locations due partly to the differential representation of habitats. For example, jetty piles were absent at Norah Head and densities of the erect tubes of the polychaete *Diopatra dentata* was considerably higher at Catherine Hill Bay. However, it was evident that the feeding

microhabitat profiles for each species was distinct within each location, except microhabitat use by juvenile *Notolabrus gymnogenis* was similar to that of *Pictilabrus laticlavius* at Norah Head. This is the first known example of the partitioning of feeding microhabitats among labrids which is potentially important for determining how this family remains so species-rich on subtidal reefs (see Chapter 3). For example, partitioning of microhabitats promotes the sharing of food resources among species (Helfman *et al.* 1997) and therefore reef areas are able to support a greater number of labrid species through minimising competition. Microhabitat use is likely to be influenced by the presence of favourable prey (Shepherd and Brook 2005), but this currently remains conjecture as prey associated with each of the identified microhabitats in the present study was not determined. Future studies are required to quantify microhabitat-prey associations and examine correlations between prey densities in frequently used microhabitats and the gut contents of each species.

Ontogenetic shifts in feeding microhabitats were evident in *Ophthalmolepis lineolatus*, *N. gymnogenis* and *P. laticlavius* at Catherine Hill Bay, but shifts occurred only for *N. gymnogenis* at Norah Head. Size-related shifts in feeding microhabitats have also been demonstrated in *Achoerodus gouldii* in temperate Australia (Shepherd and Brook 2005). In this species, smaller fish fed on individual prey using bites directed into foliose algae and algal canopies, whilst larger fish foraged increasingly on epifaunal aggregates associated with substratum, particularly algal mats. The progressive shifts in microhabitat use as described by Shepherd and Brook (2005) for *A. gouldii* were not clearly evident in the focal species of this study, nor was there a clear relationship between the profile of the feeding microhabitats for each species and their dietary composition. For example, progressive shifts in the dietary compositions of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* occurred with increased size, but these shifts were not consistently reflected in microhabitat use by each species at both locations. Future work is needed to determine relationships, if any, between diet and use of feeding microhabitats in these species.

5.4.5 Feeding behaviour

Bite rates of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* were unaffected by the time of day and period of the year in which

observations occurred suggesting that the feeding intensity, and the associated effects of these fishes on subtidal assemblages, is temporally consistent on rocky reefs. Consistent foraging rates throughout a diurnal period is reflective of the feeding behaviour of *Achoerodus viridis* (Gillanders 1995b), but in *Notolabrus tetricus* (Shepherd and Clarkson 2001) and *Achoerodus gouldii* (Shepherd and Brook 2005) diurnal variation in foraging rates occur. Causes of variation in feeding intensity within a diurnal period are not known, but tidal cycle may influence foraging rate (Shepherd and Brook 2005) and anecdotal evidence suggests that temporal consistency in foraging rates of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* is disrupted by periods of lower foraging intensity during periods of reduced water visibility and/or increased wave activity.

Feeding rate decreased with ontogeny in *N. gymnogenis* but remained consistent through progressive life history stages of *O. lineolatus* and *P. laticlavius*. This was surprising given studies of other labrids have shown the time engaged in foraging behaviour is highest in small individuals and reduces with an increase in size (Hoffman 1983; Gillanders 1995b; Shepherd and Clarkson 2001; Martha and Jones 2002; Shepherd and Brook 2005). Variation in feeding rates may be in response to dietary shifts from small, highly abundant prey in small-sized fishes to large, less abundant prey located by chance encounters in larger fishes (Jones 1999), or may reflect the cost of reproductive success (e.g. reduced feeding opportunities due to the patrolling of territory boundaries and harem defence: Gladstone 1988). As juvenile *P. laticlavius* were highly cryptic and often lost from sight beneath algal canopies it is possible that many bites were not observed which reduced the overall bite rate for small individuals of this species. By comparison, ontogenetic changes in *N. gymnogenis* were revealed as this species is less cryptic than *P. laticlavius* and most biting episodes are likely to have been observed giving an accurate representation of foraging rate. Why ontogenetic shifts did not occur in *O. lineolatus* is not known, but biting episodes directed at floating particles (a commonly used microhabitat by juveniles of this species) were often hard to detect and many may not have been recorded.

Feeding interactions occurred between the investigated labrids and other benthic carnivores in the form of following behaviour which provided the opportunity for the focal labrids to intercept prey that was disturbed by the feeding activities of other fishes.

O. lineolatus, *N. gymnogenis* and *P. laticlavus* are unlikely to be strongly reliant on these associations as encounters were opportunistic and occurred infrequently. Likewise, the feeding activities of labrids are unlikely to be of great importance to other fishes though significant substrate disturbance caused by large labrids, such as *Achoerodus viridis* (Gillanders 1999), may be important to the many species which congregated around these feeding sites.

The most evident of all feeding interactions was the displacement of small individuals from feeding sites by conspecific individuals of larger size, prompted by a size-based dominance hierarchy (see Chapter 4). Small individuals typically fed on prey items that could be rapidly manipulated and swallowed (e.g. amphipods). When larger prey items were obtained (e.g. crabs), small individuals would rapidly retreat into crevices to manipulate and fragment the prey in order to avoid confrontation with larger conspecifics which would otherwise attempt to steal the prey item. Therefore, it is proposed that the dietary composition of small individuals may be significantly influenced by their need to feed on prey items that are able to be rapidly swallowed before detection by larger conspecifics. This hypothesis requires future investigation.

5.4.6 Ecological role of labrids on temperate rocky reefs

Many studies have attempted to test whether the effect of feeding of selected fishes on subtidal assemblages is disproportionately greater than that of other species (i.e. 'keystone predators') (see reviews in Choat 1982 and Jones 1988). These proposals have not been directly tested on rocky shores of temperate Australia despite several species being reported as possibly important in influencing assemblage structure. For example, *Notolabrus tetricus* may control recruitment of abalone (Shepherd and Clarkson 2001), whilst *Achoerodus gouldii* may control the abundance of crabs (which feed on small abalone) and echinoids (which feed on macroalgae) (Shepherd *et al.* 2002). As generalist, benthic predators of small to mid-sized invertebrates, the foraging activities of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* are unlikely to influence habitat structure as much as larger labrids feeding on echinoids as these prey are known to modify the biotic structure of rocky reefs by the removal of erect macroalgae (Underwood *et al.* 1991; Sala *et al.* 1998; Steinberg and Kendrick 1999; Edgar 2001).

Prior to this study, the author hypothesised that the focal labrids may have a negative effect on adult echinoid densities by preying on smaller individuals that are unavailable to larger species of labrid. However, dietary analysis showed that echinoids contributed only a small volume to the overall diet of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* (i.e. %V<5 in all species). Whether the prey of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* significantly affect other biota is currently unknown; however, the role of these ‘mid-sized’ labrid species in reducing prey densities may be more important than those of larger size due to their higher relative abundance (see Chapter 3).

The potential impact of grazing by small to mid-sized invertebrates in temperate rocky reef systems and the effect of labrid foraging on these grazers is an area needing considerably more study. Such studies require experimental manipulations in the form of fish exclusion/inclusion experiments or modification of fish densities; however, implementation of these impact studies are not without their constraints (Choat 1982; Steele 1996; Connell 1997; Connell and Anderson 1999). A first step toward adequate design of such experiments is knowledge of prey preferences, feeding microhabitats and the biotic interactions between prey and potentially important predators. Whilst other benthic carnivores such as cryptobenthic fishes (Depczynski and Bellwood 2003), Cheilodactylidae (Lowry and Cappo 1999), Monacanthidae (Hutchins 1999), rock lobsters (Edgar 2001) and elasmobranch fishes (Choat 1982) also feed on benthic invertebrate prey, the high densities of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* on temperate reefs of eastern Australia makes them likely to be disproportionately important as moderators of prey abundances.

Whether predation by *O. lineolatus*, *N. gymnogenis* and/or *P. laticlavius* significantly alters population densities of prey and thereby indirectly affects other biota is presently unknown, but foraging strategies employed by these fishes almost certainly modifies prey behaviour. For example, prey may respond to high rates of diurnal predation by engaging in nocturnal foraging and retreating to crevices during daylight (Choat 1982; Shepherd and Clarkson 2001). Determining the effect of predation by labrids on prey behaviour is beyond the scope of this thesis, but is a matter of consideration for future studies.

5.4.7 Conclusion

This chapter has described the diet and feeding behaviour of different life history stages of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. These species are abundant and co-occur on rocky reefs of temperate eastern Australia, yet their comparative feeding ecology has not previously been investigated. Dietary analysis revealed these labrids were generalist carnivores feeding on an assortment of benthic invertebrates including polychaetes, various crustaceans, molluscs and echinoderms. Whilst *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* relied on similar prey, differences in the volumetric contribution of prey items resulted in significant partitioning of food resources among species. In addition, ontogenetic dietary shifts were significant suggesting food resources were further partitioned within species.

Feeding behaviour revealed differential use of feeding microhabitats among species and to some extent showed shifts with ontogeny. Bite rates of all species were typically unaffected by the time of day and period of year in which sampling occurred, but a location effect occurred for *O. lineolatus* and *P. laticlavius*, and a reduction in bite rate occurred with ontogeny for *N. gymnogenis*. Feeding interactions were also explored. Information presented in this chapter has provided foundational knowledge of the diet and foraging behaviour of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* for the purpose of describing how high biodiversity is maintained on rocky reefs through resource partitioning and for assisting in the design of future tests to determine the ecological significance of these and other labrids on rocky reefs of temperate Australia.

Chapter 6:

Reproduction, Growth and Demographics

6.1 Introduction

6.1.1 Problem statement and chapter aim

An understanding of life history and population demographics is an important initiative in effective management of fish stocks. Information important in the management of fisheries includes length, weight, age, growth and reproductive data. Specifically, this data may be used for establishing size and age compositions and biomass estimates for populations, assessing the status of populations, determining levels of mortality, establishing age/length at maturity for setting appropriate minimum or maximum legal lengths, determining bag limits, determining periods of spawning to impose temporary bans on captures, assessing and predicting the impact of fishing or habitat modification on fish populations, and for understanding the processes of population replenishment. Unfortunately, the importance of this information is usually overlooked until doubts occur about the sustainability of a currently operating fishery.

Lacking significant commercial value, *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* currently have little information available for their effective management despite the threat of increased levels of harvesting (Henry and Lyle 2003; Kennelly and McVea 2003) and the potential for the expansion of the live fish trade to include these species. Therefore, the aim of this chapter is to examine the reproduction, growth and demographics of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*. Reproduction, growth and the demographics of these species are discussed in this chapter, but the potential applications of the results are explored in the conclusion chapter of this thesis.

6.1.2 Labrid reproductive strategies

Labrids have received considerable attention from fish biologists due to their unusual reproductive strategy (i.e. protogynous hermaphroditism) whereby, in most species, fitness of individuals is maximised by first reproducing as an initial phase (IP) female when small, then changing sex to reproduce as a terminal phase (TP) male when sufficiently large to compete with other males for spawning opportunities (Sakai *et al.* 2001). In most species, only one morphological male type is present with these individuals having developed from adult females (termed monandry) (Gillanders 1995a;

Denny and Schiel 2002). Monandric labrids are generally sexually dichromatic with males typically found in TP colouration. The sizes of IP and TP coloured individuals may exhibit considerable overlap, but TP individuals are usually larger (Jones 1980; Gillanders 1995a). Whilst IP colouration is exhibited predominantly by females and TP colouration generally restricted to males, exceptions occur. For example, Gillanders (1995a, 1997b) found male *Achoerodus viridis* exhibiting IP colouration and large females possessing TP colouration. Jones (1980) has also found male *Pseudolabrus celidotus* to exhibit IP colouration. This may be due to the male being in transition into its TP colouration or, if small, acting as ‘sneaker’ males in their attempt to spawn with females (Jones 1980, 1981; Alonzo and Warner 1999). Whilst most labrids are sexually dichromatic, some such as *Notolabrus fucicola* and *Austrolabrus maculatus* are not (Barrett 1995a; Jones 1999).

Sequential hermaphroditism is an important reproductive strategy for labrids and at least 12 other families of fish (Wootton 1998), but other reproductive strategies, including gonochorism (i.e. genetic fixation of sex), have been found to occur in labrids (Barrett 1995a; Denny and Schiel 2002). Other labrids, termed diandric species, may have two morphological male types with males having developed from adult females (termed secondary males) or existing from the larval or juvenile state (termed primary males) (Warner and Robertson 1978). In some populations of *Thalassoma lucasanum*, primary males are the most common male type (Warner 1982).

Maturity, sex change and colour change of many labrids is size-related (Jones 1980; Gillanders 1995a). In addition, many aspects of development are socially controlled. For example, intrasexual aggression by females may inhibit maturation of small females (Jones and Thompson 1980), and dominant males may inhibit sex change in females (Sakai *et al.* 2001; Perry and Grober 2003). For harem species, individual rank position may therefore be very important in determining reproductive success. In response, individual females of *Labroides dimidiatus* move among harems to shift their rank position and increase the likelihood of sex change (Sakai *et al.* 2001). Preceding harem shifts, these females may do several assessment trips to neighbouring harems. Once initiated, sex change from female to male generally lasts 2-3 weeks (Kuwamura *et al.* 2002). Reverse sex change lasting 53-77 days has also been documented in *L. dimidiatus* if a male returns to a subordinate rank (Kuwamura *et al.* 2002).

Labrid sex ratios are strongly biased toward females in both temperate (Jones 1980, 1981) and tropical waters (Hoffman 1983). Gillanders (1995a) found the ratio of mature males to adult females in *Achoerodus viridis* may be as high as 1:62 at some sites and, when juvenile fish are also considered, ratios may be as high as 1:124. Evidence of uneven sex ratios and the bimodal size and age frequency distributions of males and females are often used as evidence for protogynous hermaphroditism (Gillanders 1995a).

6.1.3 Reproductive behaviour

Spawning behaviour has been observed in several labrids with spawning episodes typically between a single male and single female (i.e. pair spawning). Pair spawning involves both fish rapidly ascending up to 1.5 m above the substrate, usually with ventral surfaces in close proximity, and shedding gametes at the apex of the ascent (Jones 1981; Tribble 1982; Martel and Green 1987; Clavijo and Donaldson 1994; Sakai and Kohda 2001; Adreani *et al.* 2004). For territorial species, the majority of pair spawning activity is restricted to a small number of males (Jones 1980, 1981; Robertson 1981; Moyer and Yogo 1982; Hoffman 1983). Preceding pair spawning, males may engage in courting behaviour involving a series of fin flaring, passing displays directed toward the female (Jones 1981; Moyer and Yogo 1982; Barrett 1995a). For non-territorial males, spawning success is optimised by spawning in multi-male groups with single females (Warner 1984), in mating aggregations of up to several thousand fish (Warner 1995), or interfering with pair spawning events between a female and territorial male (Warner and Hoffman 1980a, b; Warner 1982; Martel and Green 1987).

Daily spawning activity may be restricted to short time periods at a specific time of the day (Moyer and Yogo 1982; Tribble 1982), and may be adjusted to coincide with outgoing tides (Tribble 1982). Spawning may also exhibit lunar periodicity (Masterson *et al.* 1997). Use of outgoing tides is an important strategy in reducing predation of eggs by other fishes as are spawning migrations to either deeper waters (Jones 1981) or reef edges (Warner and Hoffman 1980a; Tribble 1982). The migrations of *Thalassoma bifasciatum* are up to 1.5 km to find suitable reef edges (Warner 1995). Post spawning behaviour involving ‘pseudo-spawning’ episodes occurs in *Coris dorsomaculata*

(Tribble 1982) and *Tautogolabrus adspersus* (Martel and Green 1987) for the purpose of attracting additional females or advertising reproductive success.

Spawning behaviour is documented for many labrids, but in others spawning behaviour has yet to be observed despite regular observations of courting behaviour (Barrett 1995a; Adreani *et al.* 2004). Therefore, determination of reproductive activity is usually inferred from macroscopic or histological examination of fish gonads (e.g. Gillanders 1995a; Fairclough 2004; Nardi *et al.* 2006). In general, these strategies are useful for determining sexual maturity, sex identification, reproductive ripeness and sexual strategy (e.g. gonochoristic or sequential hermaphroditic). Studies involving observations of reproductive behaviour and/or gonad examination have revealed labrid reproductive seasons to be broad, often lasting up to 5 months (Jones 1980; Denny and Schiel 2002; Nardi *et al.* 2006); however, most spawning activity is usually concentrated into 2-3 months within a reproductive season (Jones and Thompson 1980; Gillanders 1995a; Fairclough 2004). For *Thalassoma lucasanum*, sexually active females are present year round (Warner 1982).

Suitability of the environment for larval offspring varies throughout the year so fish reproduction occurs at times of the year most favourable to the survival and growth of their offspring. In response, spawning usually coincides with an increase in water temperature so more food is available for their planktonic larvae (Jones 1980). For several labrids of southern Australia and New Zealand, reproductive activity precedes warming sea temperatures by up to several months with reproduction occurring in most species within the period of mid winter (July) to early summer (December) (Jones 1980; Barrett 1995a; Gillanders 1995a; Denny and Schiel 2002; Fairclough 2004; Nardi *et al.* 2006).

6.1.4 Age and growth

Fish growth is indeterminate (i.e. fish continue to grow throughout life), but growth rate reduces with increasing size (Wootton 1998). Other factors affecting the growth of fishes include food supply, water temperature, competition and spawning activity (Moyle and Cech 2000; Bond 1996; Wootton 1998). Differential growth rates are often recorded on hard, typically calcified structures within the body and may be used to

estimate fish age. Hard structures used for this purpose include fin rays, dorsal fin spines, opercula, vertebrae, scales and otoliths (Bond 1996; Kingsford 1998; Wootton 1998; Metcalf and Swearer 2005), with otoliths being the most favoured structures in aging studies of teleost fishes (Campana and Thorrold 2001; Begg *et al.* 2005; Choat *et al.* 2006; Nardi *et al.* 2006). Otoliths are composed of crystals of calcium carbonate deposited in a proteinaceous matrix within the inner ear (Wootton 1998), and are involved in hearing and equilibrium (Popper *et al.* 2005). Otoliths are unique structures as they are inert (i.e. material deposited within the otolith is not reabsorbed) (Campana and Thorrold 2001; Thorrold and Hare 2002), so provide a historical, permanent record of fish growth. The largest of the three paired otoliths is the sagittal otolith, or sagitta, and this otolith is usually favoured for aging studies.

Within each otolith are alternating, concentric bands of opaque and translucent material with opaque bands usually deposited in periods of rapid growth and translucent bands representing slow growth periods (Wootton 1998). Viewing these growth bands often requires the otolith to be sectioned, especially in larger fishes (e.g. Gillanders 1995a; Choat *et al.* 2006; Nardi *et al.* 2006). Typically, one opaque and one translucent band represent one year but validation in the form of capture-release-recapture, chemical tagging, holding captive individuals of known age, or marginal increment analysis is critical (Kingsford 1998). Yearly opaque bands, termed *annuli* (sing: *annulus*), form in response to seasonal variation in somatic growth, environmental factors (e.g. water temperature) and/or reproductive activity (Cailliet *et al.* 1996; Wootton 1998; Ewing *et al.* 2003). In temperate labrids of Australia and New Zealand annuli typically complete their formation in mid spring to early summer (i.e. October to November) (Jones 1980; Gillanders 1995a; Ewing *et al.* 2003). In general, labrids are long lived with adults of many species exceeding 10 years of age (Barrett 1995a; Fairclough 2004). In temperate Australia, individuals of *Notolabrus fucicola*, *Achoerodus viridis* and *Achoerodus gouldii* may reach ages of 20 years (Ewing *et al.* 2003), 35 years (Gillanders 1995a) and 50 years (Gillanders 1999), respectively.

6.1.5 Management needs for temperate labrids

As protogynous hermaphrodites, labrids are thought to be somewhat resilient to exploitation as males removed from the population may be replaced by sex-changing

females (Peterson and Warner 2002). However, high mortality of older, larger males may result in sex reversal occurring at younger ages and/or smaller sizes (Platten *et al.* 2002; Hawkins and Roberts 2003), reducing the overall spawning success of populations through decreased sperm output and social disruption. In temperate Australia, labrids have not historically been targeted by fishers; however, spearfishers caused rapid declines in populations of *Achoerodus viridis* in eastern Australia and *Achoerodus gouldii* in southern Australia before these fishes were offered protection in 1969 and 1980, respectively (Pogonoski *et al.* 2002).

As most labrids of temperate Australia are not targeted by fishers, biological information is limited as motivation to acquire such information is generally prompted by threats of over-harvesting by an operational fishery. For example, the rapid expansion of the live fish trade in Tasmania and Victoria in 1993 for *Notolabrus fucicola* and *Notolabrus tetricus* (Murphy and Lyle 1999; Lyle and Hodgeson 2001; Department of Primary Industries 2004) led to the assessment of this fishery for the purpose of introducing management controls including the application of minimum and maximum size limits and limitations on the number of holders of live fish access licences (Murphy and Lyle 1999). Effective management of fish stocks requires a detailed understanding of life-history information and population parameters to provide scientifically based management decisions. For *N. fucicola* and *N. tetricus*, this information is now being provided albeit many years after the rapid expansion of their fishery (e.g. Barrett 1995a; Denny and Schiel 2002; Smith *et al.* 2003; Ewing *et al.* 2003; Welsford 2003). Where possible, it is important to take a precautionary approach in acquiring biological information for fishes that have the potential for future exploitation. This is certainly a possibility for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* in eastern Australia if similar expansions of the live fish trade occur as occurred in Tasmania and Victoria, and if levels of recreational and commercial harvests increase.

6.1.6 Overview and chapter objectives

The reproduction, growth and demographics of several temperate labrids have been investigated in South Australia, Tasmania and New Zealand, but little work has been conducted on labrids associated with coastal New South Wales (see Table 1.1). To fill

some of the gaps in the current understanding of these labrids this chapter investigates the reproduction, growth and demographics of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* by describing relationships between length and weight, discovering size and age at maturity and sex change, determining spawning season, describing reproductive behaviour (i.e. courting and spawning), determining the suitability of otoliths for aging and validating the yearly formation of annuli, quantifying maximum annulus radii (AR_{max}) measures, and determining longevity and growth rates.

6.2 Methods

6.2.1 Study area and specimen collection

The reproduction, growth and demographics of *Ophthalmolepis lineolatus* (n=225), *Notolabrus gymnogenis* (n=195) and *Pictilabrus laticlavius* (n=93) were investigated using specimens collected from coastal reefs on the central coast of NSW (Figure 2.2). A description of the study area, the locations and methods used for collecting fish specimens, and a summary of the specimens collected is provided in Chapter 2.

6.2.2 Size distributions and length at sex change

The colour phase (initial phase (IP) or terminal phase (TP)), sex (male or female, see Table 6.1 for criteria), total length (± 1 mm) and weight (± 0.01 g) were recorded for each individual. For each species, individuals were placed into 10 mm size classes (i.e. <100, 100-109, 110-119, 120-129 mm etc.) and the proportion of individuals having changed sex (i.e. males) in each size class was graphed. To determine the size at which half of all individuals undergo sex change, termed L_{50c} , a logistic curve (Equation 6.1) was fitted to the relationship between the median of each size class and the proportional representation of male fish using the SOLVER add-in option in Microsoft Excel 2000. Constants derived from the fitted logistic equation were used to estimate the size at which 25, 50 and 75% of individuals undergo sex change (i.e. L_{25c} , L_{50c} and L_{75c} , respectively) using Equations 6.2 to 6.4.

$$P_L = \frac{\exp[a + b(L/10)]}{1 + \exp[a + b(L/10)]} \quad \begin{array}{l} P_L = \text{proportion of sex changed fish at length } L \text{ (mm).} \\ L = \text{total length (mm)} \\ a \text{ \& } b = \text{constants} \end{array} \quad (\text{Equation 6.1})$$

Estimations derived from Equation 6.1:

$$L_{25c} = \frac{[\ln(1/3) - a]}{b} \quad L_{50c} = -\frac{a}{b} \quad L_{75c} = \frac{[\ln(3) - a]}{b} \quad (\text{Equation 6.2 to 6.4})$$

6.2.3 Length/weight relationships

Relationships between total length (TL) and weight were investigated using least squares linear regression applied to natural log (ln) transformed data (Equation 6.5). A transposed form of this equation was used to predict the weight of a fish at a given length (Equation 6.6).

$$\ln(W) = b \cdot \ln(L) + a$$

W = weight (g)
 L = total length (mm)
 a & b = constants (Equation 6.5)

Transposed form of Equation 6.5:

$$W = \ln(a) \cdot L^b$$

(Equation 6.6)

6.2.4 Reproductive biology

Gonads were removed and fixed in 5% formalin for at least 48 hours and then stored in 70% ethanol. Gonad wet weight was recorded (± 0.0001 g) to calculate gonadosomatic indices (GSIs) (Equation 6.7).

$$GSI(\%) = 100 \times \left(\frac{w_g}{(W_f - w_g)} \right)$$

w_g = wet weight of gonad
 W_f = wet weight of whole fish
 $W_f - w_g$ = somatic weight. (Equation 6.7)

Sex, sexual maturity and reproductive ripeness were determined by macroscopic examination of gonads at x10 magnification and classified according the criteria outlined in Table 6.1.

Table 6.1: Macroscopic criteria used to classify gonads of *Ophthalamolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* (adapted from Fairclough 2004)

Gonad classification	Gonad criteria
Female	
(i) Immature/ non-ripe	Rounded in cross section; visible oocytes are present, but these are small and not substantially hydrated.
(ii) Ripened/spawning	Rounded in cross section; granular with large, tightly packed and hydrated oocytes; yellow to orange in colour.
Male	Flattened or triangular in cross section, but swollen when spawning; opaque to cream especially in the spawning season, but may be brownish outside these periods; margins often undulating; no visible oocytes present.

For months where hydrated oocytes were present in several individuals (i.e. months signifying gonadal reproductive activity), female fish were placed into 10 mm size classes (i.e. <100, 100-109, 110-119, 120-129 mm etc.) and the proportion of females with gonads classified as ripened/spawning for each size class was determined. To establish the size at which half of all females were sexually mature, termed L_{50m} , a modified version of Equation 6.1 was used to fit a curve to the relationship between the median of each size class and the proportional representation of female fish with hydrated oocytes. In this instance, P_L represented the proportion of mature females at length L . Constants derived from the fitted logistic equation were used to estimate the size at which 25, 50 and 75% of individuals sexually mature (i.e. L_{25m} , L_{50m} and L_{75m} , respectively) using modifications to Equations 6.2 to 6.4 whereby L_{25m} replaces the L_{25c} value, L_{50m} replaces L_{50c} etc. Reproductive season was recognized as the months where mean GSI values for mature females (i.e. $\geq L_{50m}$) were highest.

6.2.5 Reproductive behaviour

Behavioural observations (see Chapter 4) revealed ‘apparent’ courtship behaviour occurred regularly in all species with spawning events observed only for *Pictilabrus laticlavius*. The proportion of total interactions between TP males and IP females which represented reproductive activity (i.e. spawning and courting) were determined and compared to GSI calculations. Descriptions of courting and spawning behaviour were made from field observations.

6.2.6 Age and growth

Both sagittal otoliths were removed from each specimen, then cleaned and dried. In preparation for sectioning, the primordium of each otolith was marked with a lead pencil before embedding in Stuers epofix resin. Otoliths were transverse sectioned through the primordium at 400-500 μm using a mounted rotating diamond blade. Each section was further sanded to 200-300 μm with fine 600-1200 grade wet-and-dry carborundum paper. Sections were then mounted on glass slides using clear epoxy resin. Viewing of sectioned otoliths at x100 magnification revealed distinct concentric opaque and translucent bands. These ‘annuli’ were best observed in an aqueous medium on a black background using reflected light (Figure 6.1 and 6.2). Each otolith was photographed using a Nikon D70 digital camera mounted on an Olympus CH-2

microscope for later marginal increment ratio (MIR) analyses, maximum annulus radii (AR_{max}) measures and annuli counts.

MIR analysis was performed to resolve whether opaque ‘annuli’ zones were indeed formed yearly. When only one opaque band was present, MIRs were determined by expressing the distance between the edge of the otolith and the middle of the first opaque band (i.e. marginal increment, MI) as a percentage of the distance between the primordium and the middle of the first opaque band (i.e. previous increment, PI), using the formula, $MIR = MI/PI \times 100$ (Figure 6.1a). When more than one opaque band was located, the MI represented the distance between the edge of the otolith and the middle of the outermost opaque band, and the PI represented the distance between the two outermost opaque bands (Figure 6.1b). Measurements were made using the image analysis software package ImageTool (University of Texas Health Science Centre, San Antonio, TX, USA). If annuli are formed yearly, the MIRs will demonstrate a sinusoidal trend during the year with a single peak. All annuli counts and MIR measurements were made on otoliths selected randomly without prior knowledge of fish size or capture date.

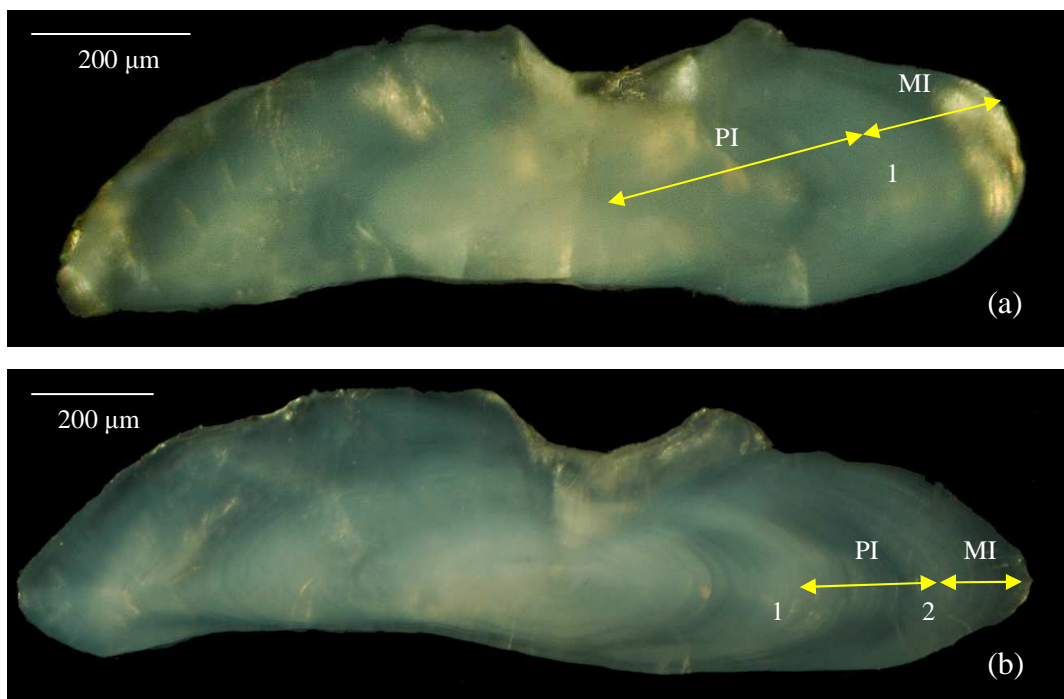


Figure 6.1: Measurements used for marginal increment ratio (MIR) calculations for fish with 1 opaque zone [119 mm, 1.25 years old *Pictilabrus laticlavius* shown] (a) and >1 opaque zone [180 mm, 2.33 years old *P. laticlavius* shown] (b). MIRs were calculated using the equation: $MIR = MI/PI \times 100$, where MI = marginal increment and PI = previous increment. Annulus counts are shown.

Measurements of maximum annulus radii, termed AR_{max} , were made for successive annuli counts to determine whether annuli were formed predictably in the same position on the otolith. Measurements of AR_{max} were defined as the maximum distance between the middle of an annulus band extending either side of the primordium (Figure 6.2a). In *Ophthalmolepis lineolatus*, annulus formation within an otolith cross section was typically symmetrical about the primordium; however, annulus formation was asymmetrical in many *Notolabrus gymnogenis* and *Pictilabrus laticlavius* (Figure 6.2b). A von Bertalanffy curve (see Equation 6.9) was fitted to the relationship between annulus count and mean AR_{max} using the SOLVER add-in option in Microsoft Excel 2000 to apply least squares regression. In this instance, annulus count (termed ‘a’) replaced fish age (t) and mean AR_{max} replaced fish length (L).

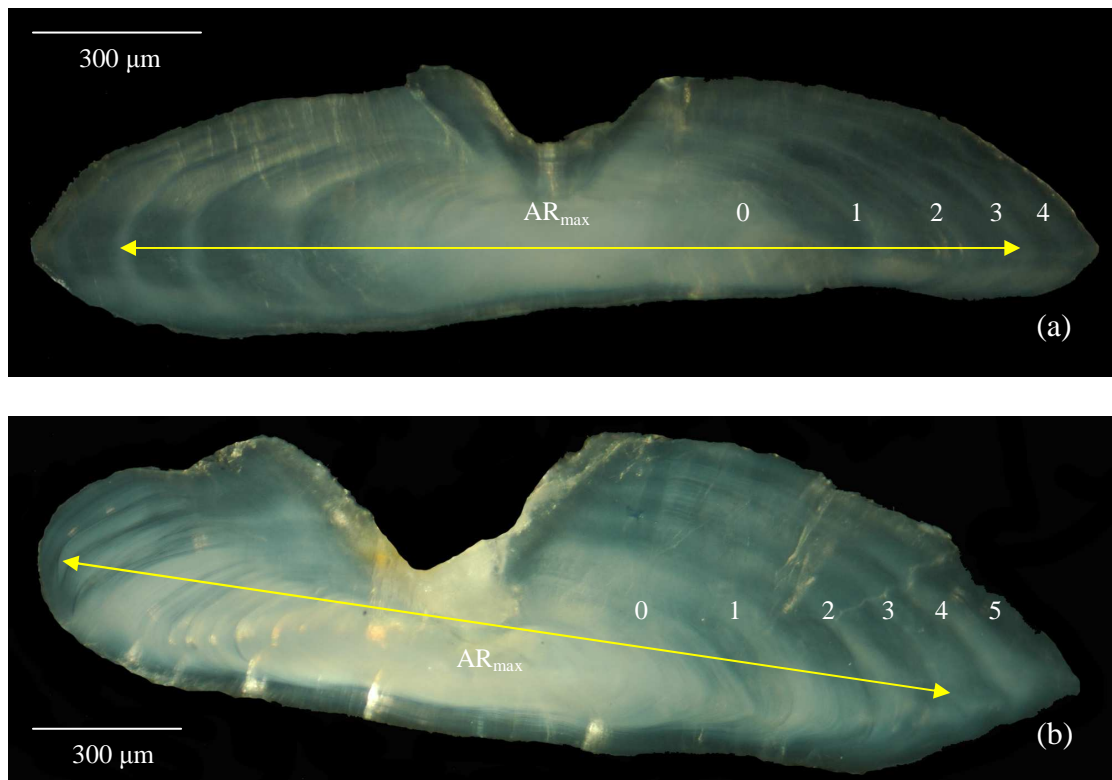


Figure 6.2: Location of measurements used to determine the maximum annulus radii (AR_{max}) of the 3rd annulus for symmetrical annuli [294 mm, 5.2 years old *Ophthalmolepis lineolatus* shown] (a) and asymmetrical annuli [316 mm, 5.6 years old *Notolabrus gymnogenis* shown] (b). Annulus counts are provided.

Once validated, counts of annuli were made on two successive occasions, in random order, by the same observer. Recounts were performed by a second, experienced observer. Between occasions and observers, counts were the same in 97.3% and 98.6%

of instances, respectively. If disagreements could not be rectified the otolith was not used. Fish age was estimated using annuli counts in association with known date of capture, date of birth (estimated from GSI values) and period of annuli formation (determined by MIR measurements) (Table 6.2).

Table 6.2: Age estimates (years) at annulus formation for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. Date of birth was estimated from the peak in GSI values for females $\geq L_{50m}$ (see Section 6.2.4). Annulus formation was determined from MIR measures (see earlier in this section).

Species	Date of Birth	Annulus formation	Annulus count						
			0	1	2	3	4	5	etc.
<i>Ophthalmolepis lineolatus</i>	01 Feb	01 Sept	0.6	1.6	2.6	3.6	4.6	5.6	etc.
<i>Notolabrus gymnogenis</i>	01 Jun	01 Sept	0.3	1.3	2.3	3.3	4.3	5.3	etc.
<i>Pictilabrus laticlavius</i>	01 Nov	01 Sept	-	0.8	1.8	2.8	3.8	4.8	etc.

Individuals of each species were placed into 1 year age classes (i.e. 0-0.9, 1.0-1.9, 2.0-2.9, 3.0-3.9 years etc.) and the proportion of individuals having changed sex (i.e. males) in each age class was graphed. To determine the age at which half of all individuals undergo sex change, termed A_{50c} , a logistic curve (Equation 6.8) was fitted to the relationship between the median of each age class and the proportional representation of male fish using the SOLVER add-in option in Microsoft Excel 2000. Constants derived from the fitted logistic equation were used to estimate the age at which 25, 50 and 75% of individuals undergo sex change (i.e. A_{25c} , A_{50c} and A_{75c} , respectively) using a modified version of Equations 6.2 to 6.4 whereby A_{25c} replaces the L_{25c} value, A_{50c} replaces L_{50c} etc. To determine fish growth, a von Bertalanffy equation (Equation 6.9) was fitted to the relationship between estimated fish age and fish total length using the SOLVER add-in option in Microsoft Excel 2000 to apply least squares regression.

$$P_A = \frac{\exp(a + bA)}{1 + \exp(a + bA)}$$

P_A = proportion of sex changed fish at age A (years)
 A = age (years)
 a & b = constants

(Equation 6.8)

$$L_t = L_{\infty}[1 - e^{-k(t-t_0)}]$$

L_t = total length (mm) at age t (years)
 L_{∞} = asymptotic length (mm)
 k = von Bertalanffy growth coefficient
 t = fish age (years)
 t_0 = hypothetical fish age (years) at 0 mm length

(Equation 6.9)

6.3 Results

6.3.1 Size distributions

The growth and reproductive biology of up to 225 *Ophthalmolepis lineolatus* (94-374 mm TL), 195 *Notolabrus gymnogenis* (76-358 mm TL) and 93 *Pictilabrus laticlavius* (70-216 mm TL) were examined (Table 2.2; Figure 6.3). In all species, females were generally restricted to smaller size classes with the largest size classes representing only males (Figure 6.3). All females of *O. lineolatus* were found to be ≤ 332 mm and males ≥ 278 mm, with $L_{50c} = 284$ mm (Figure 6.3a; Table 6.3). Sexual dichromatism could be used to accurately determine sex in 99% of female and 92% of male *O. lineolatus*. Female *N. gymnogenis* were found to be ≤ 294 mm and males ≥ 230 mm, with $L_{50c} = 273$ mm (Figure 6.3b; Table 6.3). Twelve *N. gymnogenis* of transitional colouration were collected with nine of these individuals being of sizes 260-295 mm, two individuals of sizes 230-239 mm and one at size 204 mm. Colour phase accurately predicted sex in all individuals of *N. gymnogenis*, with 58% of transitional colour being female. A considerable overlap in the sizes of each sex of *P. laticlavius* occurred with females ≤ 180 mm and males ≥ 98 mm, with $L_{50c} = 138$ mm (Figure 6.3c; Table 6.3). A total of six *P. laticlavius* of transitional colour were collected with four between the sizes of 129 to 144 mm and two individuals of size 161 mm. Colour phase accurately predicted sex in 96% of individuals, with 60% of those in transitional colour being female.

Table 6.3: Parameters for the fitted curve used to determine the length at which half of all individuals changed sex into males (i.e. L_{50c}) for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. Equation of the fitted curve is $P_L = \exp(a+b(L/10))/[1+\exp(a+b(L/10))]$, where P_L = proportion of fish that have undergone sex change at length L (mm).

	Parameters		Length estimates (mm)		
	a	b	L_{25c}	L_{50c}	L_{75c}
<i>Ophthalmolepis lineolatus</i>	-26.925	0.947	273	284	296
<i>Notolabrus gymnogenis</i>	-19.597	0.718	258	273	288
<i>Pictilabrus laticlavius</i>	-118.279	8.577	137	138	139

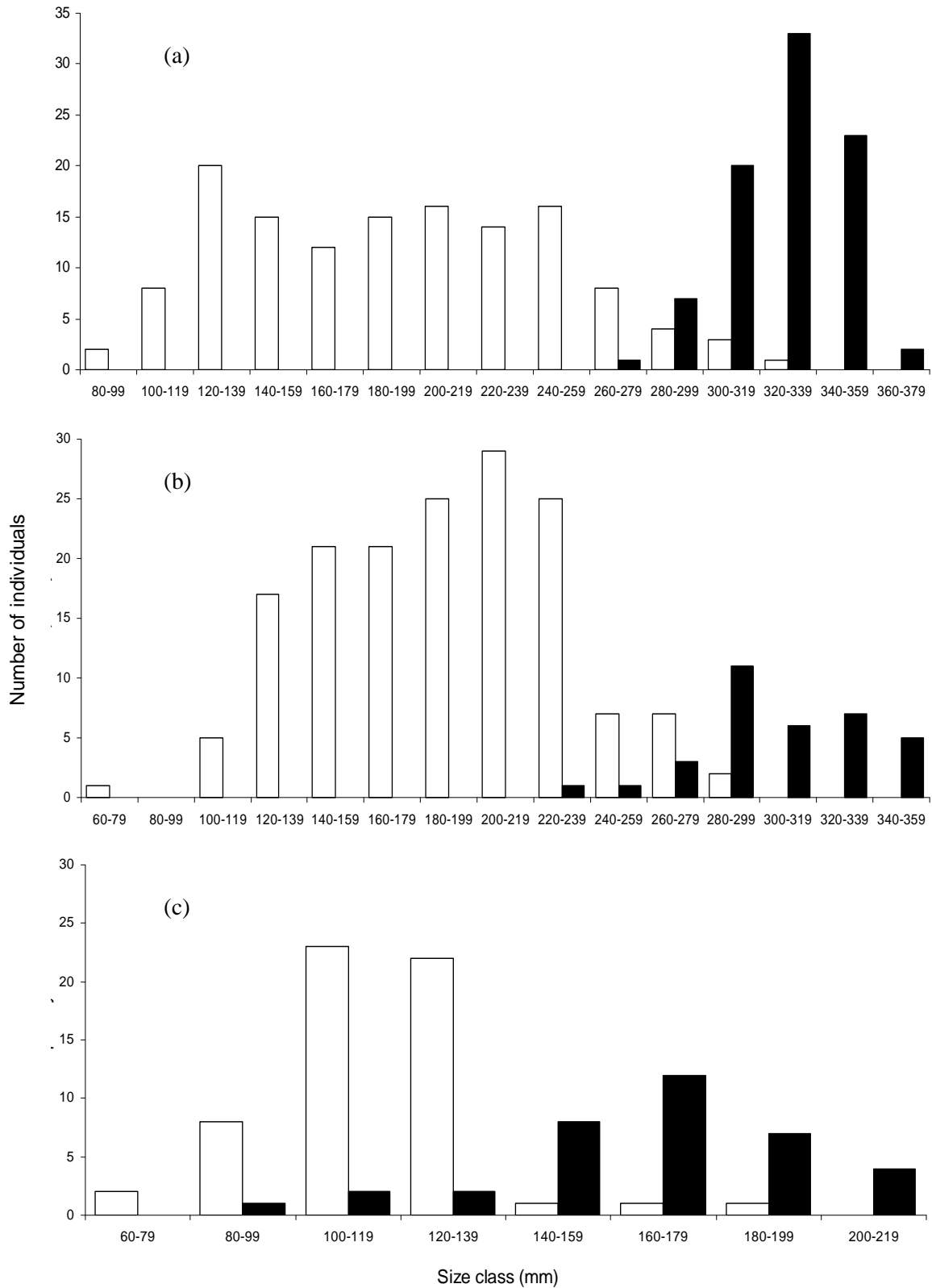


Figure 6.3: Size distribution of females (□) and males (■) of *Ophthalmolepis lineolatus* [n=220] (a), *Notolabrus gymnogenis* [n=194] (b) and *Pictilabrus laticlavius* [n=94] (c). Sexes were determined by the macroscopic examination of gonads.

6.3.2 Length/weight relationships

All species recorded an exponential rise in weight with increasing length (Figure 6.4ai-ci). Logarithmic transformation of data revealed a strong, significant, linear relationship between length (ln) and weight (ln) for all species (Figure 6.4aii-cii; Table 6.4). Fitted regression lines revealed the weight of *Ophthalamolepis lineolatus* rose from 8 g at 100 mm TL to 504 g at 350 mm, the weight of *Notolabrus gymnogenis* rose from 16 g at 100 mm TL to 713 g at 350 mm, and the weight of *Pictilabrus laticlavius* rose from 14 g at 100 mm TL to 249 g at 250 mm (Table 6.5).

Table 6.4: Linear regression of the relationship between length (L mm) and weight (W g) for *Ophthalamolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* (95% confidence intervals shown in parentheses). Parameters are for the fitted equation $\ln(W) = b \cdot \ln(L) + a$. *** $P < 0.001$

Species	Parameters		Mean of squared residuals	F	R ²	n
	a	b				
<i>O. lineolatus</i>	-13.195 (-13.382, -13.008)	3.315 (3.281, 3.349)	308.57	36371.1***	0.994	218
<i>N. gymnogenis</i>	-11.058 (-11.282, -10.834)	3.008 (2.966, 3.051)	133.21	19565.9***	0.991	185
<i>P. laticlavius</i>	-11.921 (-12.342, -11.499)	3.158 (3.072, 3.245)	53.06	5268.5***	0.983	93

Table 6.5: Estimated weights (g) of *Ophthalamolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* at several lengths (mm TL) as predicted by the regression equations in Figure 6.4 and Table 6.4. Estimated weights were calculated using Equation 6.6.

Species	Total length (mm)					
	100	150	200	250	300	350
<i>Ophthalamolepis lineolatus</i>	8	30	79	165	303	504
<i>Notolabrus gymnogenis</i>	16	55	132	257	445	708
<i>Pictilabrus laticlavius</i>	14	50	123	249	-	-

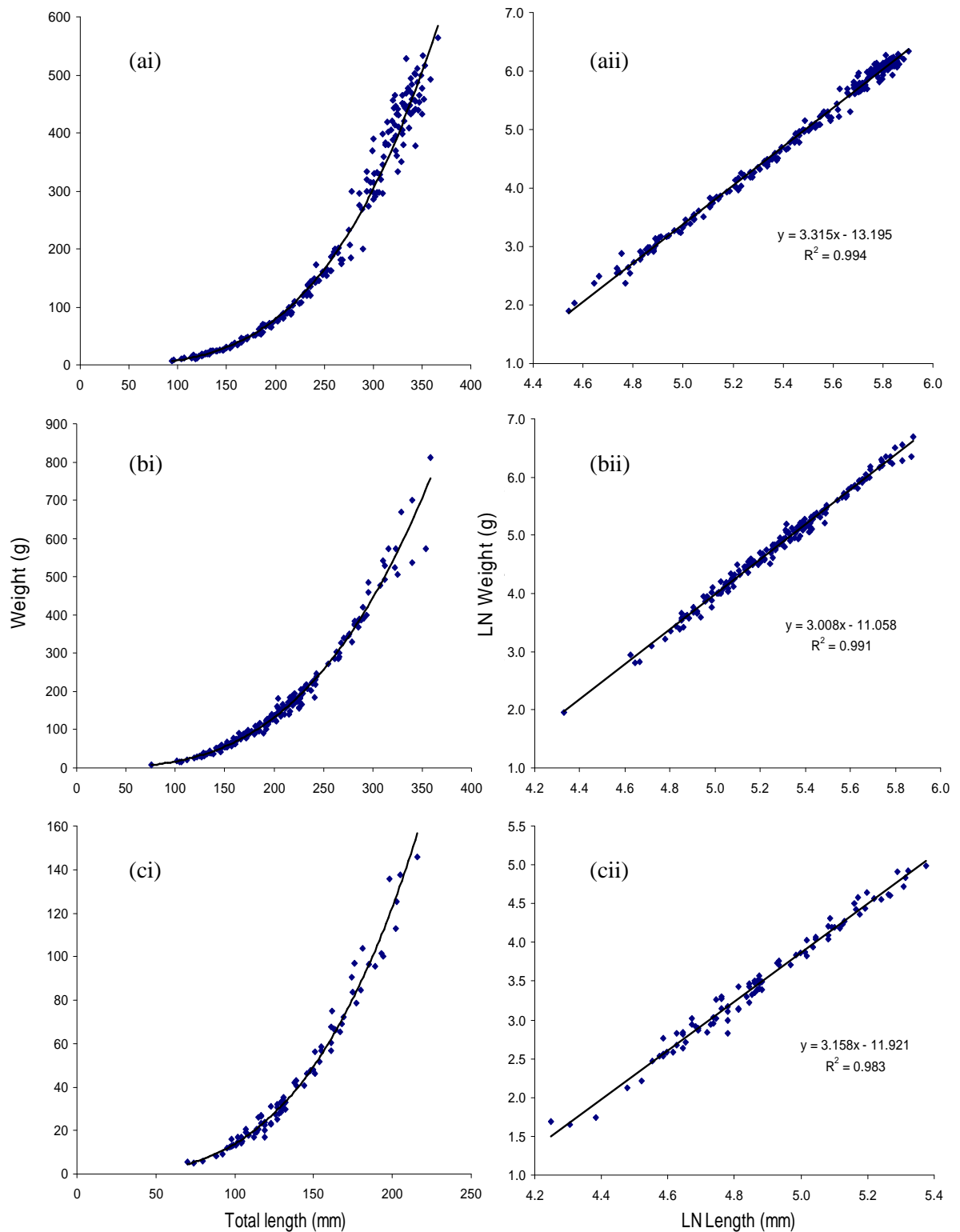


Figure 6.4: Relationship between length and weight (i) for *Ophthalmolepis lineolatus* [n=218] (a), *Notolabrus gymnogenis* [n=185] (b) and *Pictilabrus laticlavius* [n=93] (c). Logarithmic transformations (ln) have been applied to the axes of (ii) and linear regression performed. Statistics for this regression are provided in Table 6.4.

6.3.3 Reproductive biology

6.3.3.1 *Ophthalmolepis lineolatus*

a) Size at Maturity

Macroscopic examination of female *Ophthalmolepis lineolatus* gonads revealed hydrated oocytes were present from December to April. Pooled data for these months revealed all individuals <180 mm were sexually immature (Figure 6.5). Seventy-five percent of 180-189 mm individuals possessed ripened/spawning gonads. The L_{50m} for *O. lineolatus* was determined as 186 mm (Figure 6.5; Table 6.6). All females ≥ 200 mm possessed hydrated oocytes, except a single individual of 300 mm captured in early December.

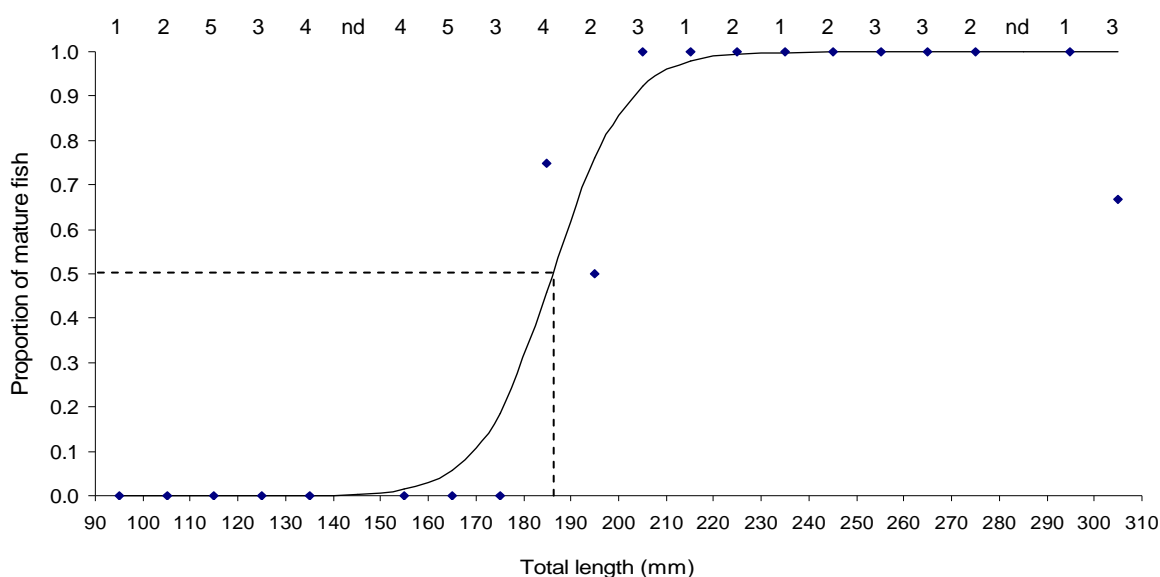


Figure 6.5: Proportion of female *Ophthalmolepis lineolatus* with ripened/spawning gonads at various sizes for individuals obtained in the months of December to April. Points represent size class midpoints. Sample sizes are provided above the graph. Fitted curve for estimation of L_{50m} is shown (see Table 6.6 for curve equation). Dashed line shows predicted L_{50m} .

Table 6.6: Parameters for the fitted curve used to determine the length (mm) at which half of all females reached sexual maturity (i.e. L_{50m}) for *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. Equation of the fitted curve is $P_L = \exp(a+b(L/10)) / [1 + \exp(a+b(L/10))]$, where P_L = proportion of mature fish at length L (mm).

	Parameters		Estimates		
	a	b	L_{25m}	L_{50m}	L_{75m}
<i>Ophthalmolepis lineolatus</i>	-24.573	1.319	178	186	195
<i>Notolabrus gymnogenis</i>	-14.333	0.810	163	177	191
<i>Pictilabrus laticlavius</i>	-	-	-	<95	-

b) Reproductive season

The GSIs of female *Ophthalmolepis lineolatus* $\geq L_{50m}$ (i.e. ≥ 186 mm), were lowest from May to October (0.21-0.38%) (Figure 6.6a). A rapid increase in GSIs occurred in December and January with values peaking in February (2.53%), followed by a rapid decline in April. Annual variation in GSIs coincided with changes in the representation of females $\geq L_{50m}$ with ripened/spawning gonads. Ripened/spawning gonads were absent in females $\geq L_{50m}$ from May to October; however, representation rose to 83% of individuals in December and 100% of individuals in January to March before declining to 67% in April (Figure 6.6b).

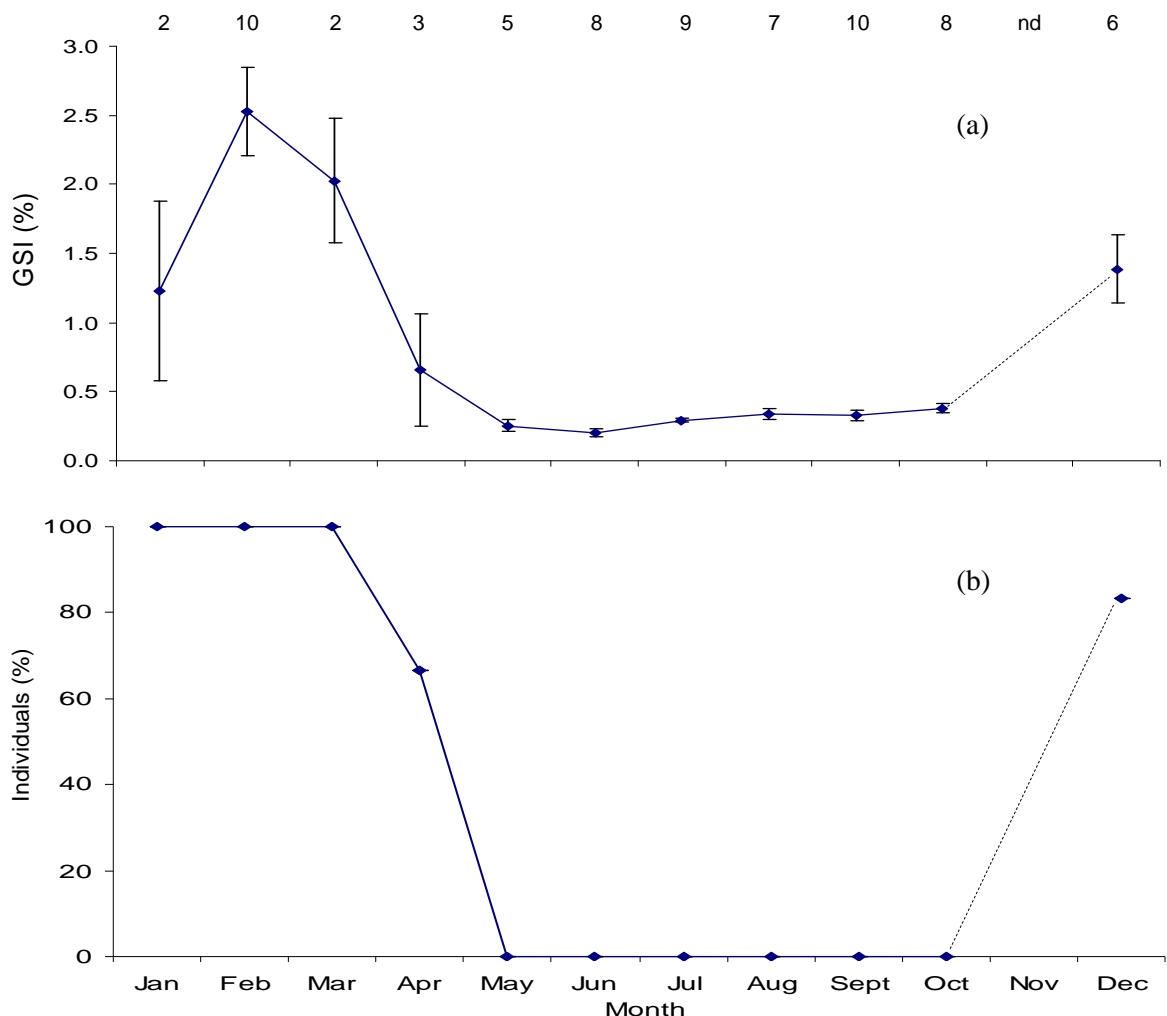


Figure 6.6: Monthly variation in mean gonadosomatic indices (GSIs) (a) and percentage of individuals with ripened/spawning gonads (b) for female *Ophthalmolepis lineolatus* $\geq L_{50m}$ (i.e. ≥ 186 mm). Sample sizes shown above the graph in (a) are common to both figures. Dashed line indicates no data (nd).

6.3.3.2 *Notolabrus gymnogenis*

a) Size at Maturity

Macroscopic examination of female *Notolabrus gymnogenis* gonads revealed hydrated oocytes were present in all sampled months; however, highest GSIs were found from April to October. Pooled data for April to October revealed all individuals <150 mm were sexually immature (Figure 6.7). Ripened/spawning gonads were found in 13 and 40% of individuals from size classes 150-159 and 160-169 mm, respectively. A sharp rise in the percentage of females with ripened/spawning gonads occurred at size classes ≥ 180 -189 mm with over half of all females (i.e. 56%) possessing ripened/spawning gonads in the size class 180-189 mm. The L_{50m} for *N. gymnogenis* was determined as 177 mm (Figure 6.7; Table 6.6).

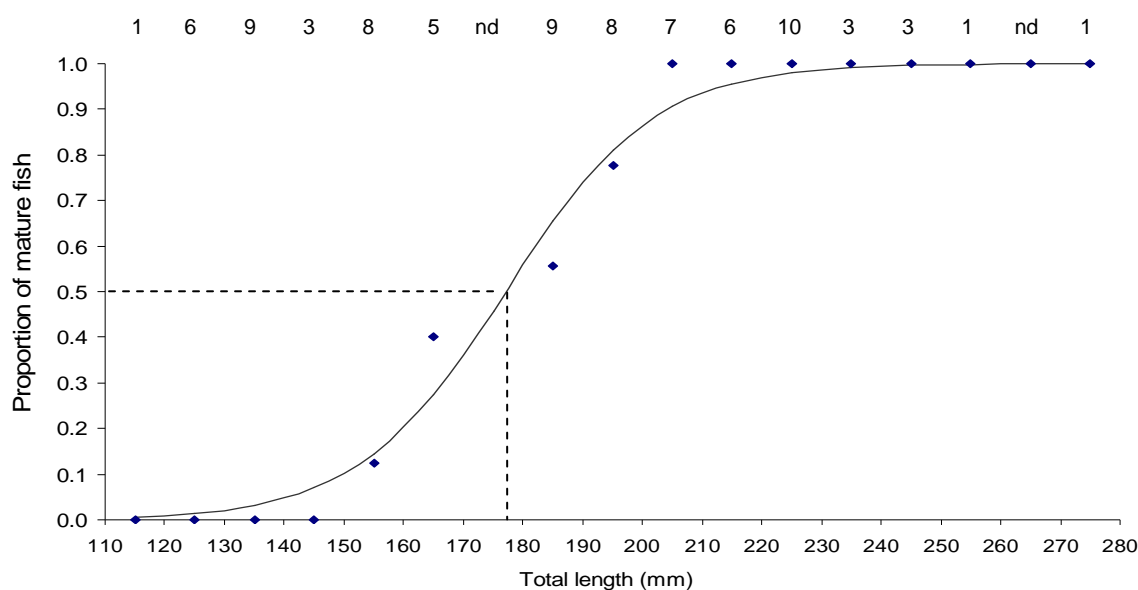


Figure 6.7: Proportion of female *Notolabrus gymnogenis* with ripened/spawning gonads at various size classes for individuals obtained in the months of April to October. Points represent size class midpoints. Sample sizes are provided above the graph. Fitted curve for estimation of L_{50m} is shown (see Table 6.6 for curve equation). Dashed line shows predicted L_{50m} . (nd: no data)

b) Reproductive season

GSI of female *Notolabrus gymnogenis* $\geq L_{50m}$ (i.e. ≥ 177 mm), were lowest from December to March (0.42-1.04%) (Figure 6.8a). GSIs rose in the months of April to June (1.46-2.45%), peaked in July (3.52%), then declined from August to December. Females L_{50m} with ripened/spawning gonads were present in all sampled months. Ripened/spawning gonads were found in >50% of mature females (i.e. $\geq L_{50m}$) in January and the months of March to October, but in only 10% of individuals in February and December (Figure 6.8b).

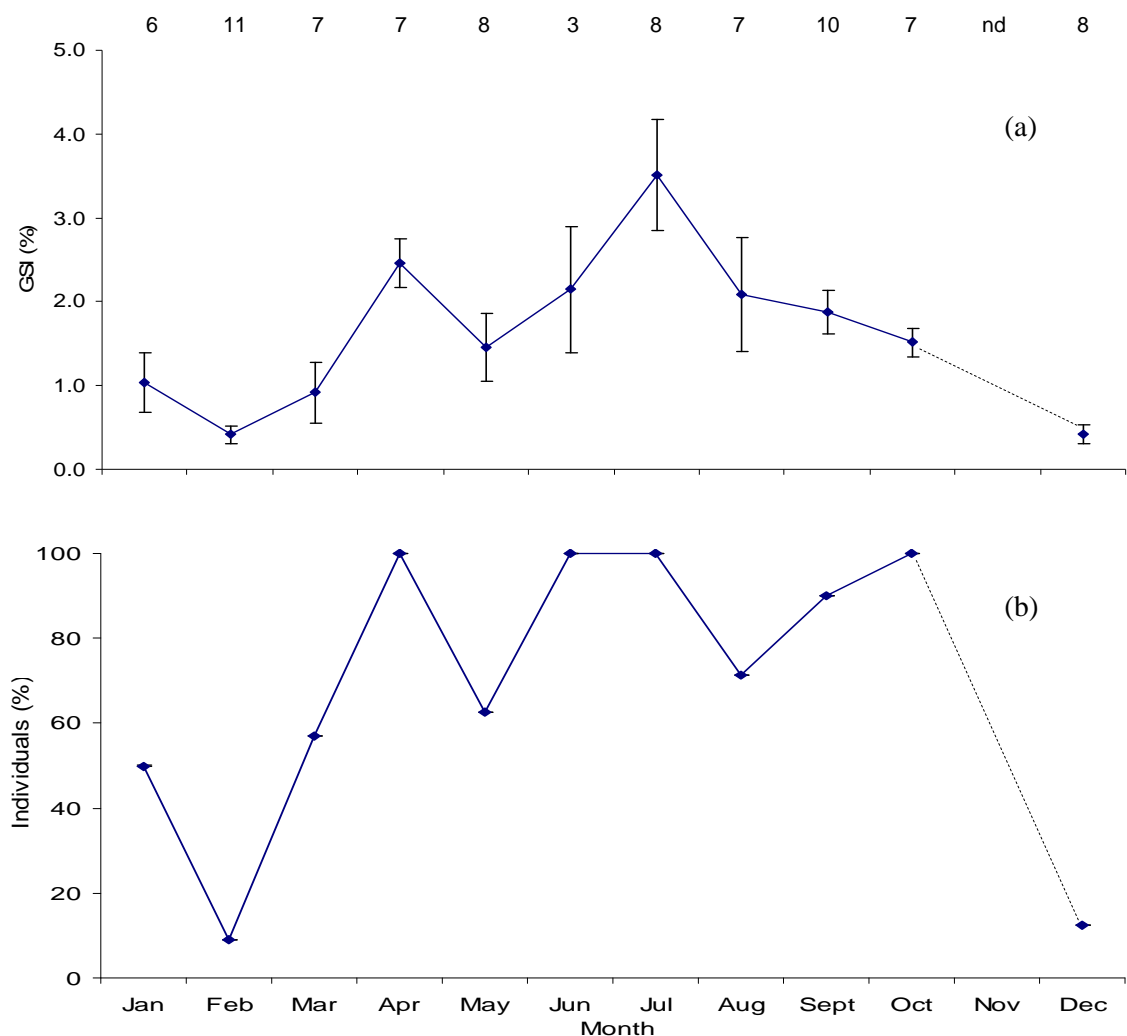


Figure 6.8: Monthly variation in mean gonadosomatic indices (GSIs) (a) and percentage of individuals with ripened/spawning gonads (b) for female *Notolabrus gymnogenis* $\geq L_{50m}$ (i.e. ≥ 177 mm). Sample sizes shown above the graph in (a) are common to both figures. Dashed line indicates no data (nd).

6.3.3.3 *Pictilabrus laticlavius*

a) Size at Maturity

Macroscopic examination of female *Pictilabrus laticlavius* gonads revealed hydrated oocytes were present from August to March. Pooled data for these months revealed >70% of individuals in all size classes possessed ripened/spawning gonads, except for the size class 160-169 mm which was represented by a single individual in transitional colouration (Figure 6.9). The L_{50m} for *P. laticlavius* was determined as 95 mm; however, as the data set was restricted to mostly mature individuals, L_{50m} is likely to be less than that predicted (Figure 6.9; Table 6.6).

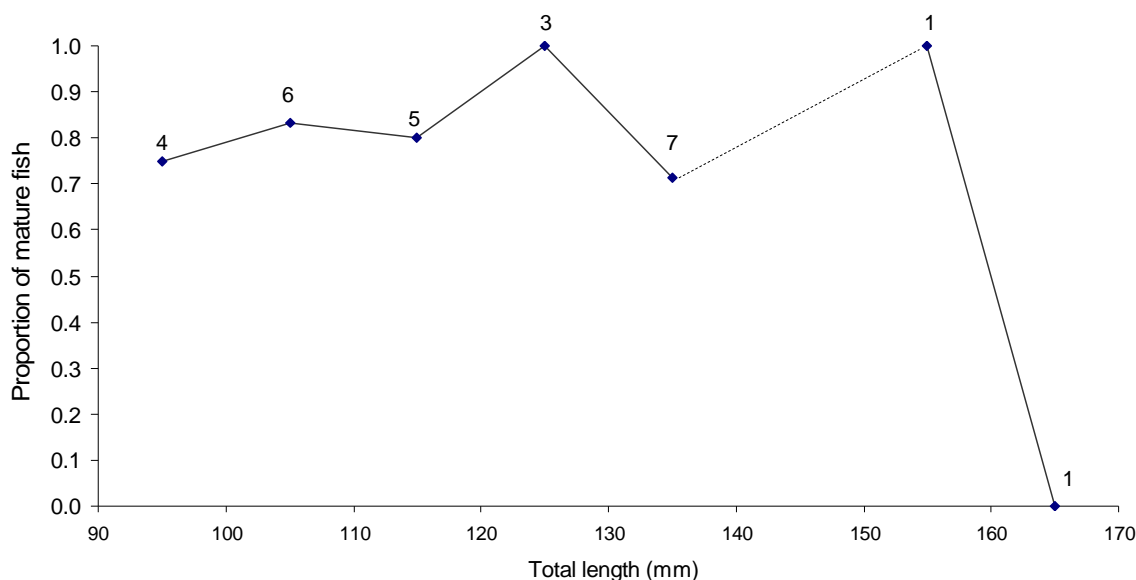


Figure 6.9: Proportion of female *Pictilabrus laticlavius* with ripened/spawning gonads at various sizes for individuals obtained in sampled months from August to March. Points represent size class midpoints. Sample sizes are provided above the graph. Dashed line indicates no data (nd).

b) Reproductive season

GSI of female *Pictilabrus laticlavius* $\geq L_{50m}$ (i.e. ≥ 95 mm) were lowest from April to May (0.06-0.08%) (Figure 6.10a). GSIs rose in August and peaked in October and December (2.60 and 2.54%, respectively), followed by a rapid decline from January to March. A close relationship occurred between the annual variation of GSIs and changes in the representation of females $\geq L_{50m}$ with ripened/spawning gonads (Figure 6.10b). Ripened/spawning gonads were absent in females $\geq L_{50m}$ from April to May, but their representation rose in August (50%). Gonads of all females $\geq L_{50m}$ contained hydrated oocytes in October and December before a decline occurred in January to March.

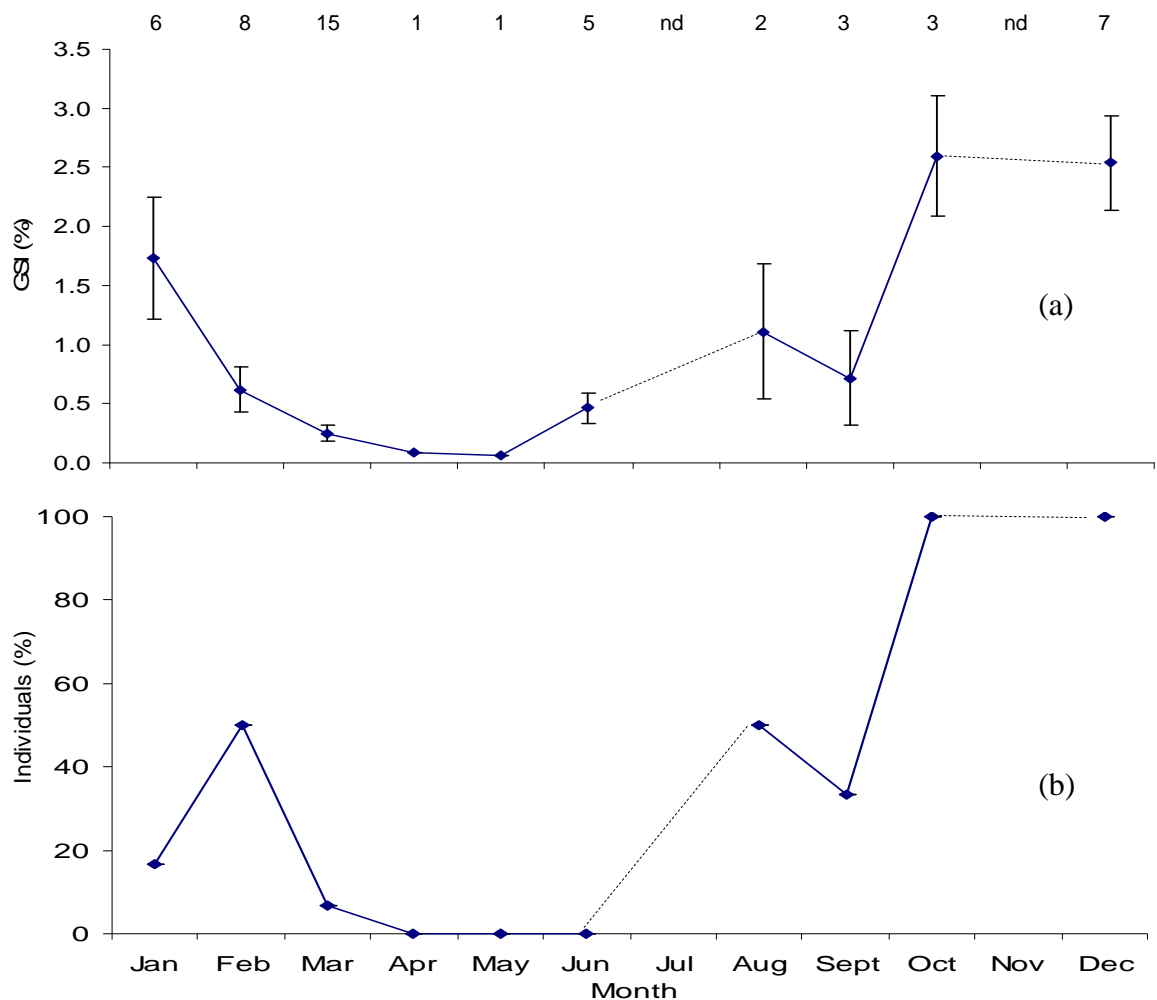


Figure 6.10: Monthly variation in mean gonadosomatic indices (GSIs) (a) and percentage of individuals with ripened/spawning gonads (b) for female *Pictilabrus laticlavius* $\geq L_{50m}$ (i.e. ≥ 95 mm). Sample sizes shown above the graph in (a) are common to both figures. Dashed line indicates no data (nd).

6.3.4 Reproductive behaviour – courting and spawning

Apparent ‘courting’ of females by males was observed in most months in all species (Figure 6.11). Courting involved flaring (i.e. erection) of dorsal and anal fins in association with repeated lateral body flexion whilst swimming alongside female individuals. In *Pictilabrus laticlavius*, lateral body flexions were far more rapid than those of *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis*. Females typically moved away from a courting male. In all species, the prevalence of courting behaviour did not necessarily coincide with their reproductive season. For example, the reproductive season of *O. lineolatus* peaks in February (Figure 6.6); however, no courting behaviour was observed in this month or the preceding month of January (Figure 6.11a). Similarly, no courting behaviour was observed for *N. gymnogenis*, in August (Figure 6.11b) despite it representing one of the months of high reproductive activity (see Figure 6.8). Courting behaviour constituted 59 to 91% of all interactions between male and female individuals of *P. laticlavius* from October to February (Figure 6.11c). A reduction in courting interactions occurred in the post-spawning months of March and April (i.e. 38 and 19% of interactions, respectively).

Spawning behaviour was observed only in *P. laticlavius* and only in October (i.e. the beginning of the spawning season for this species) (Figure 6.11c). All spawning acts (n=5) occurred at midday (i.e. 1130-1400 hr) and were not timed to a particular state of the tide. Pre-spawning behaviour involved the male performing repeated courting passes (up to 20) above the female which was resting within algal shelter. A rapid, vertical swim up to 100 cm above the substrate was initiated by the female and followed by the male. At the apex of the ascent, eggs and sperm were shed in a cloud of gametes.

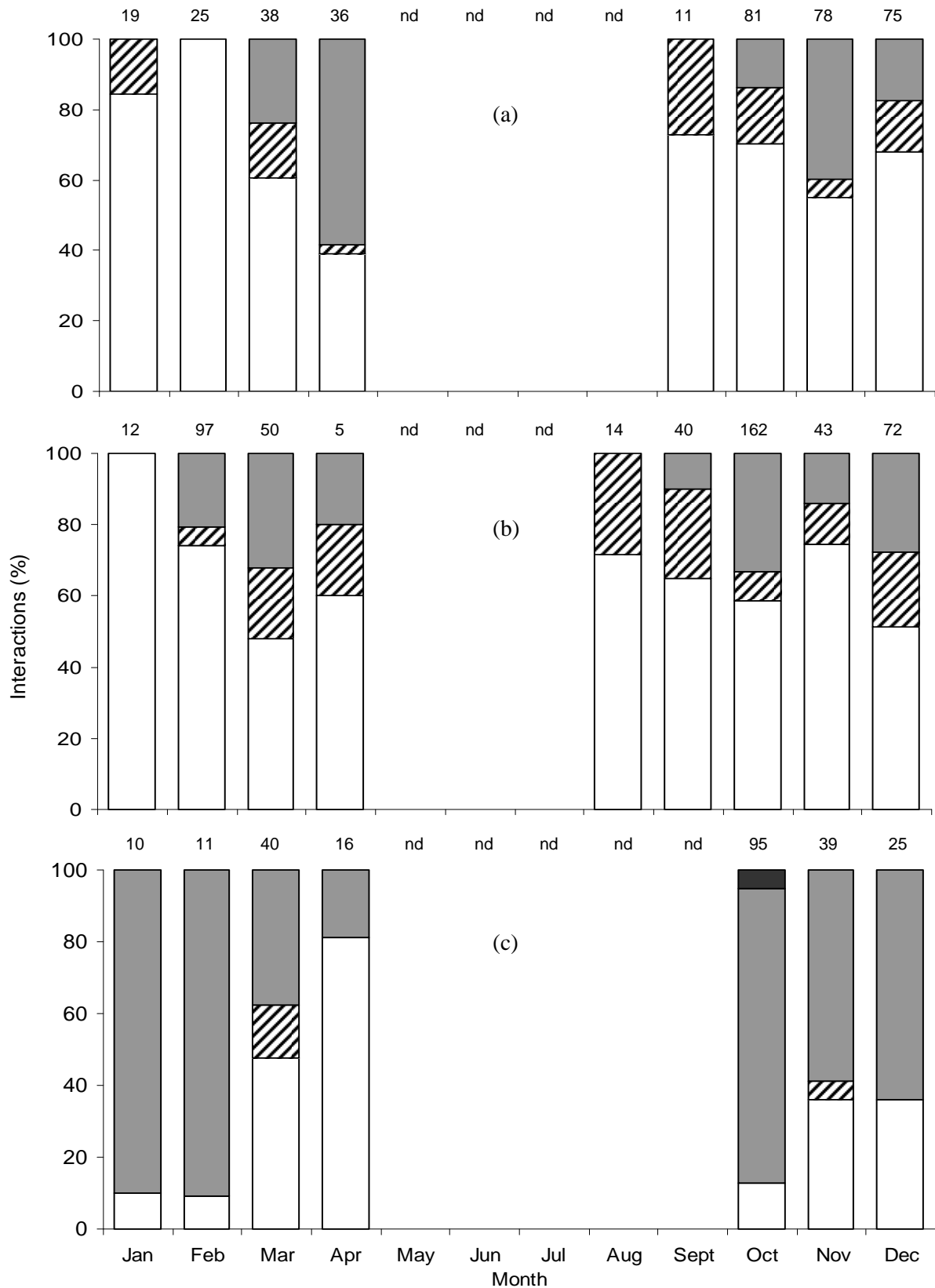


Figure 6.11: Percentage of interactions between terminal phase males and initial phase females involving spawning (■) courting (■), chasing (▨) or passive (□) behaviour for *Ophthalmolepis lineolatus* (1870 min of observations) (a), *Notolabrus gymnogenis* (1920 min) (b) and *Pictilabrus laticlavius* (1200 min) (c) over several months. Total number of interactions are provided above each column.

6.3.5 Age and growth

6.3.5.1 Validation of annulus formation

Sectioned otoliths revealed distinct translucent and opaque banding in all size classes of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. Marginal increment ratio (MIR) measures in all species showed a common trend. In *O. lineolatus* and *N. gymnogenis*, a rise in MIRs occurred from *ca.* 40% in January for both species to *ca.* 60-70% and *ca.* 55-60% in July-October for each species, respectively (Figure 6.12ai and bi). Associated with high MIRs was the formation of the outer annulus on the otolith growing edge. In *O. lineolatus*, the percentage of individuals with an annulus on the otolith growing edge rose from 0% in August to 14 and 38% in September and October, respectively (Figure 6.12aii). The percentage of *N. gymnogenis* otoliths with an annulus on the outer edge rose from 0% in July to 35, 44 and 54% in August, September and October, respectively (Figure 6.12bii). Growth of the otolith outer edge surpassed the centre of the annulus band by October resulting in a rapid decline in MIRs in December (i.e. *ca.* 30-35%) and a substantial rise in the percentage of otoliths with a formed annulus on the growing edge (i.e. 95 and 85% for *O. lineolatus* and *N. gymnogenis*, respectively).

Similarly, a general rise in MIRs occurred for *P. laticlavius* from January (*ca.* 65%) to September (*ca.* 90%) with the proportions of otoliths with an annulus on the growing edge increasing from 0% in July to 43 and 64% in August and September, respectively (Figure 6.12c). By October, growth of the otolith outer edge surpassed the centre of the annulus band (i.e. MIR = 34%) with the percentage of otoliths with a formed annulus on the growing edge peaking in this month (i.e. 75%)

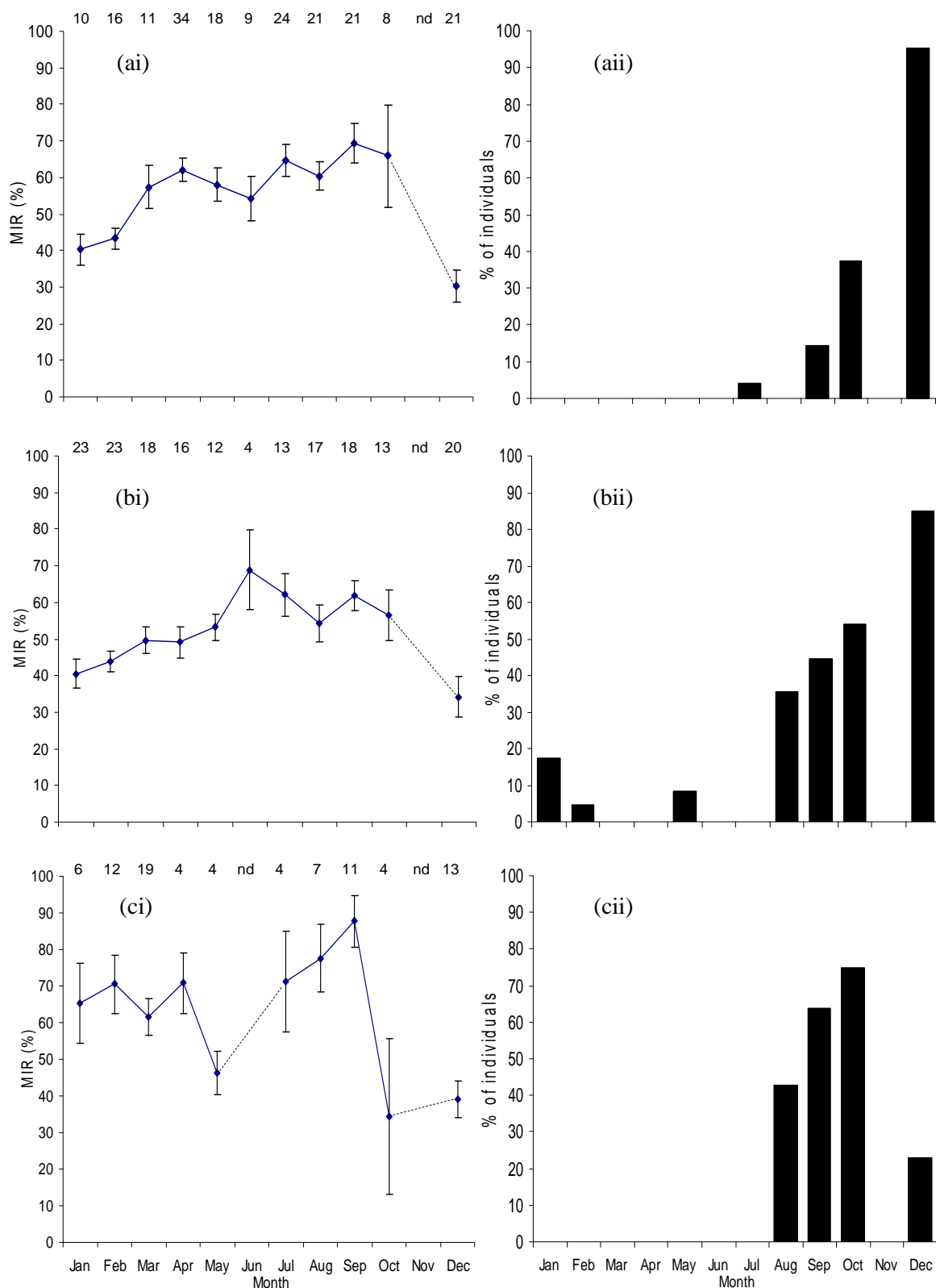


Figure 6.12: Monthly average marginal increment ratios (i) and percentage of individuals with an annulus on the growing edge (ii) for *Ophthalmolepis lineolatus* (a), *Notolabrus gymnogenis* (b) and *Pictilabrus laticlavius* (c). Standard error bars are shown. Sample sizes provided above the graph in (i) are common to both (i) and (ii). Dashed line indicates no data (nd).

6.3.5.2 *Annulus radii*

Maximum annulus radii (AR_{max}) measurements revealed otolith annuli were incremented consistently in individuals of each species with a reduction in annuli increments with increased annuli count (Figure 6.13). For example, AR_{max} incremental distance between the 1st and 2nd annuli was 0.323 mm in *Ophthalmolepis lineolatus*, whilst that between the 3rd and 4th, and 5th and 6th was 0.192 and 0.104 mm, respectively (Figure 6.13a). The mean AR_{max} ($\pm SE$) for the first annulus of *O. lineolatus* (n=145), *Notolabrus gymnogenis* (n=156) and *Pictilabrus laticlavius* (n=84) was 1.287 ± 0.007 , 1.440 ± 0.009 and 0.879 ± 0.010 mm, respectively (Figure 6.13a-c). Accurate location of the first and successive annuli using mean AR_{max} measurements allowed consistent interpretation of otolith growth and was used to identify false annuli.

6.3.5.3 *Age distribution*

Annulus counts were used to assign age ranges of 0.9 to 13.4, 0.5 to 9.6 and 0.8 to 4.8 years to collected individuals of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*, respectively (Figure 6.14). Over 68% of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* were <6.0, <3.0 and <2.0 years of age, respectively. In all species, females were generally restricted to younger age classes with the older age classes represented only by males. All females of *O. lineolatus* were ≤ 7.1 years old and males ≥ 3.4 years with A_{50c} determined as 4.7 years (Figure 6.14a; Table 6.7). Female *N. gymnogenis* were aged ≤ 4.8 years and males ≥ 2.8 years with A_{50c} determined as 4.5 years (Figure 6.14b; Table 6.7). Of the eleven *N. gymnogenis* in transitional colour, nine were 3.5 to 4.6 years of age with the remaining individuals of age 2.8 and 7.0 years. For *P. laticlavius*, a considerable overlap in the ages of each sex occurred with all females ≤ 2.3 years and males ≥ 0.8 years with A_{50c} determined as 2.4 years (Figure 6.14c; Table 6.7). Each of the six transitional coloured *P. laticlavius* were 1.2 to 2.3 years of age.

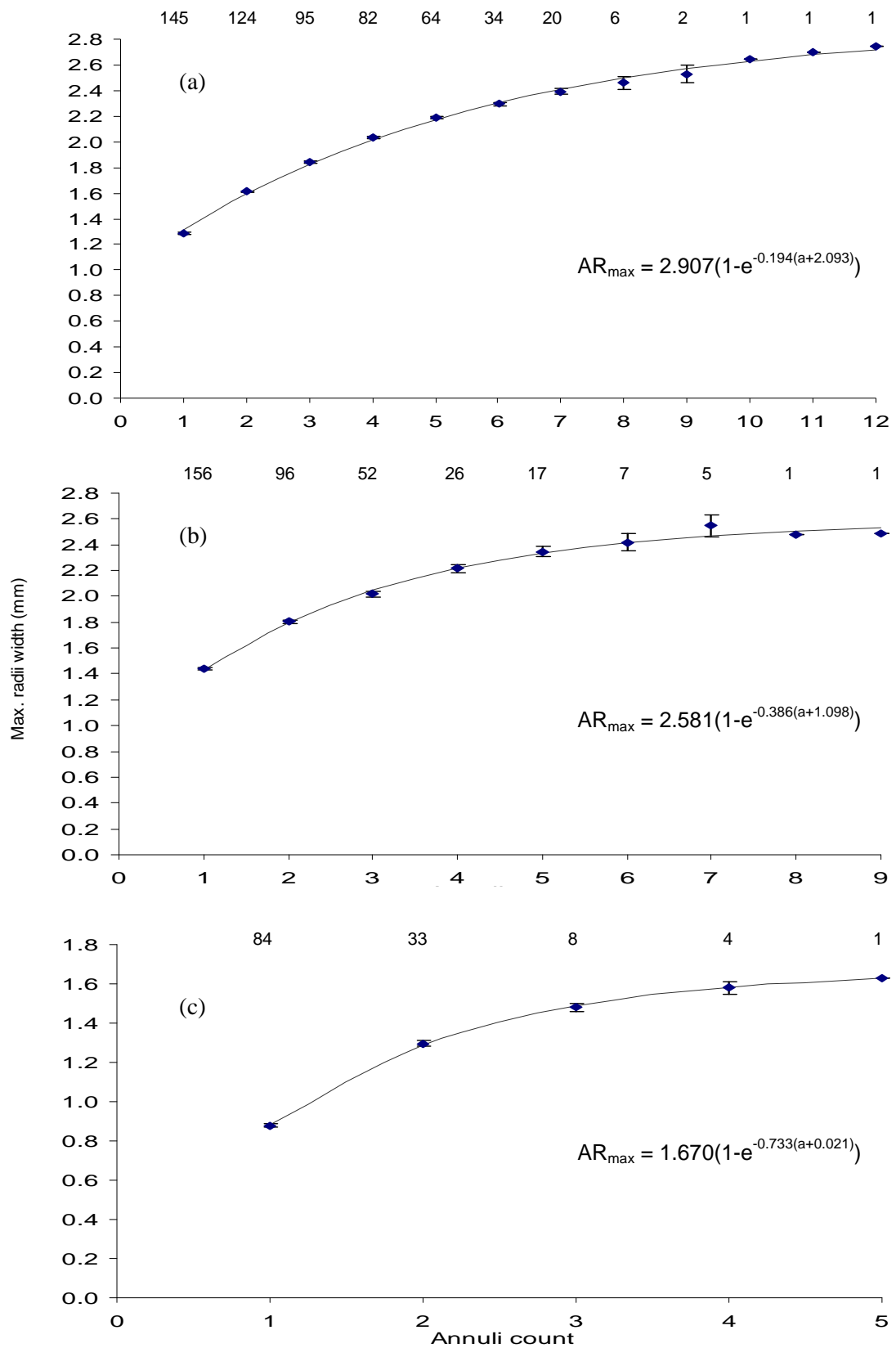


Figure 6.13: Maximum width of annulus radii (AR_{\max}) (mean \pm SE) for annuli counts of *Ophthalmolepis lineolatus* (a), *Notolabrus gymnogenis* (b) and *Pictilabrus laticlavus* (c). Fitted von Bertalanffy curves and equations are shown, where a is the annulus count. Sample sizes are provided above each graph.

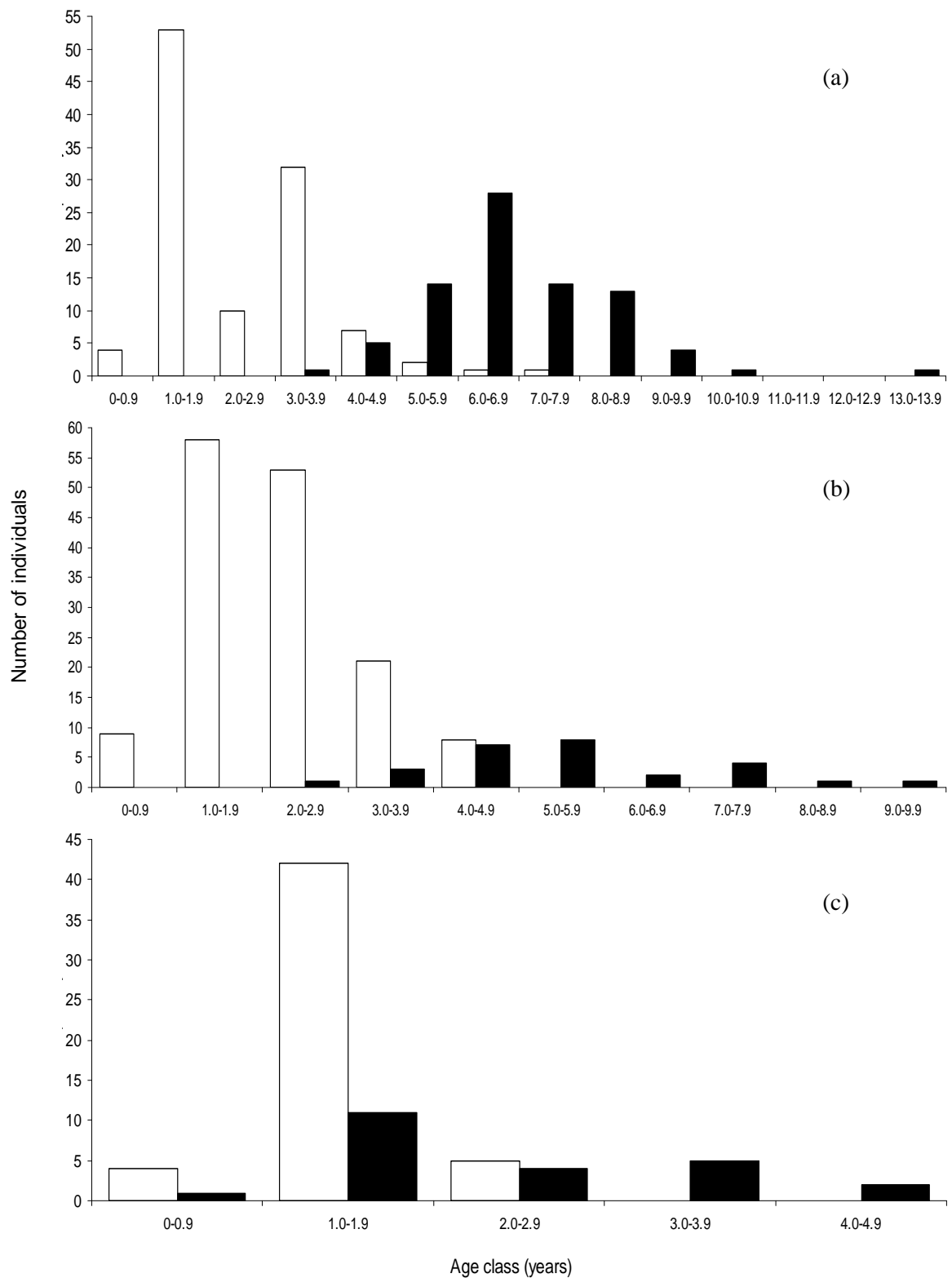


Figure 6.14: Age distributions of female (□) and male (■) individuals of *Ophthalmolepis lineolatus* [n=191] (a), *Notolabrus gymnogenis* [n=176] (b) and *Pictilabrus laticlavius* [n=74] (c).

Table 6.7: Parameters for the fitted curve used to determine the age at which half of all individuals changed sex into males (i.e. A_{50c}). Equation of the fitted curve is $P_A = \exp(a+bA) / [1 + \exp(a+bA)]$, where P_A = proportion of fish that have undergone sex change at age A (years).

	Parameters		Age estimates (years)		
	a	b	A_{25c}	A_{50c}	A_{75c}
<i>Ophthalmolepis lineolatus</i>	-11.204	2.405	4.20	4.65	5.11
<i>Notolabrus gymnogenis</i>	-12.203	2.709	4.09	4.50	4.91
<i>Pictilabrus laticlavius</i>	-4.094	1.713	1.74	2.39	3.03

6.3.5.4 Growth

Derived von Bertalanffy growth curves were found to provide a good representation of age-length relationships for all species (Figure 6.15; Table 6.8). Length (TL) estimates obtained from the von Bertalanffy equation for *Ophthalmolepis lineolatus* were 108, 177, 228, 265 and 293 mm at 1, 2, 3, 4 and 5 years, respectively. Growth rates for *Notolabrus gymnogenis* were similar with lengths of 130, 184, 226, 259 and 284 mm at 1, 2, 3, 4 and 5 years, respectively. For *Pictilabrus laticlavius*, growth was less rapid with estimated lengths of 100, 151, 180, 196 and 205 mm at 1, 2, 3, 4 and 5 years, respectively.

Table 6.8: Growth parameters for von Bertalanffy growth curves fitted to lengths at age for three labrids. The von Bertalanffy equation is: $L_t = L_{\infty}(1 - e^{-k(t-t_0)})$.

	von Bertalanffy parameters			R^2	n
	L_{∞} (mm)	k (year ⁻¹)	t_0 (years)		
<i>Ophthalmolepis lineolatus</i>	373.3	0.300	-0.150	0.954	193
<i>Notolabrus gymnogenis</i>	371.5	0.254	-0.705	0.878	176
<i>Pictilabrus laticlavius</i>	216.9	0.577	-0.076	0.744	84

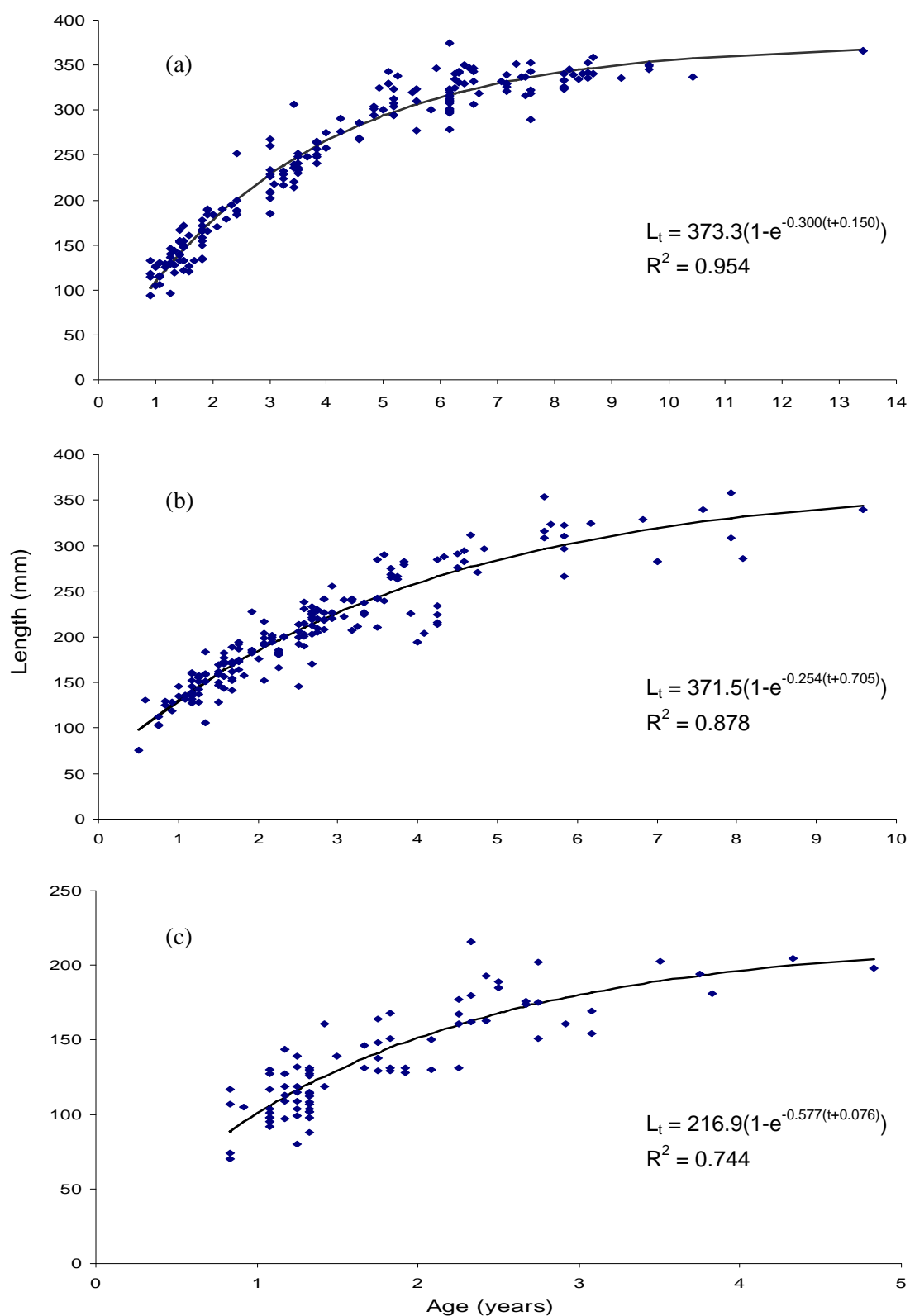


Figure 6.15: Relationship between age and total length for *Ophthalmolepis lineolatus* [n=193] (a), *Notolabrus gymnogenis* [n=176] (b) and *Pictilabrus laticlavius* [n=84] (c). Fitted von Bertalanffy curves and equations are shown where t is fish age (years).

6.4 Discussion

6.4.1 Evidence for protogynous hermaphroditism

Evidence of sex-related bimodal length and age distributions in fish populations is suggestive of protogynous hermaphroditism (Sadovy and Shapiro 1987). Protogynous hermaphroditism appears to be the reproductive strategy of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* as the length and age distributions of females and males were bimodal with smaller sizes and younger ages typically restricted to females, and males restricted mostly to larger sizes and older ages. For example, only female *O. lineolatus* were found at sizes below 278 mm and ages less than 3.4 years and only males were found above sizes of 332 mm and ages of 7.1 years. Similarly, size and age distributions for *N. gymnogenis* revealed only females were found at sizes below 230 mm and ages less than 2.7 years and only males above 294 mm and greater than 4.8 years. For female and male *P. laticlavius*, considerable overlap in size and age occurred with small size classes (i.e. 80-99 mm) and young of the year (i.e. 0-0.9 years) not restricted to females; however, only males were found at sizes greater than 180 mm and ages greater than 2.3 years. As protogynous hermaphrodites, *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*, follow the reproductive strategy common to the family Labridae (Jones 1980; Barrett 1995a; Gillanders 1995a; Andrew *et al.* 1996; Candi *et al.* 2004; Fairclough 2004; Nardi *et al.* 2006).

Evidence of biased adult sex ratios in favour of females provides further supporting evidence for sex-change (Sadovy and Shapiro 1987; Shapiro 1987). Estimates of adult male to adult female sex ratios for *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* were approximately 1:5-10 at locations used for behavioural observations. These ratios are similar to other temperate protogynous hermaphrodites with male to female ratios of 1:4-9 in *Notolabrus celidotus* (Jones 1980) and 1:7-40 in *Achoerodus viridis* (Gillanders 1995a). In contrast, sex ratios in gonochorist (i.e. non-sex changing) labrids are similar. For example, male to female sex ratios of 1:1.6 are found in the gonochorist labrid *Notolabrus fucicola* (Denny and Schiel 2002).

Whilst the population structure of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* strongly suggest protogynous hermaphroditism, proof of this sexual strategy requires an

examination of gonadal structure using histological techniques to provide evidence of remnant ovarian tissue in male gonads (e.g. Barrett 1995a; Gillanders 1995a; Denny and Schiel 2002; Fairclough 2004; Nardi *et al.* 2006). Previous histological examination of *N. gymnogenis* germ cells by McPherson (1977) found females with small cysts of primary spermatangia and males with remnants of degenerate mature oocytes, which supports this study's population-based conclusions of sex inversion in this species. Similarly, Barrett (1995a) concluded males of *P. laticlavus* underwent sex inversion as transitional gonads were identified as having both oocytes and developing spermatocytes, and gonads of mature males revealed residual ovarian structures. Unfortunately, Barrett (1995a) obtained few small individuals (<160 mm) resulting in all males being restricted to larger sizes (>170 mm). In the present study, the occurrence of males at small sizes (<100 mm) and young ages (<1 year) suggest that not all male *P. laticlavus* experience sex change after sexual maturity (i.e. not all are post-maturational secondary males), but rather some may function as males from the larval or juvenile state (Warner and Robertson 1978). Such males may be defined as either primary males (i.e. genetically fixed males) or pre-maturational secondary males (i.e. sex change occurs before the female ever sexually matures) (Warner and Robertson 1978). Future histological examination of testes from small *P. laticlavus* males is required to determine conclusively the sexual strategy of this species.

6.4.2 Colour phase as an indicator for sex recognition

Permanent sexual dichromatism was evident in all species and was used to predict sex with high accuracy. In *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* 99, 100 and 96% of females exhibited initial phase (IP) colouration and 92, 100 and 96% of males were terminal phase (TP), respectively. Misidentification of colour phase and sexual transition most probably contributed to colour-sex discrepancies.

As male *O. lineolatus* and *N. gymnogenis* were found almost exclusively in TP colouration and were restricted chiefly to larger, older individuals, these species may be described as monandric (i.e. only one morphological male type is present) (Warner and Robertson 1978). Monandry, involving only secondary males (i.e. all males are derived from mature females) is known to occur in many labrids (Jones 1980; Tribble 1982;

Gillanders 1995a; Andrew *et al.* 1996; Candi *et al.* 2004). Labrids with both primary/pre-maturational males and secondary males are termed diandrous (i.e. two male types are present) (Warner and Robertson 1978). Diandry appears to be the reproductive strategy of *P. laticlavius*; however, in most diandrous labrids only the larger, post-maturational secondary males exhibit TP colouration. For example, *Thalassoma bifasciatum* and *Thalassoma lucasanum* exhibit TP colouration only in larger males which are able to defend territories (Warner and Hoffman 1980a, b; Warner 1982). Smaller males are non-territorial and, like females, exhibit IP colouration. These IP males may represent nearly half of the IP population (Warner 1982).

Expression of IP colouration in male labrids is often due to the male being in transition into its TP colouration (Jones 1980, 1981) or, if small, used as a disguise to act as a 'sneaker' male in an attempt to spawn with females (Warner and Hoffman 1980a, b; Alonzo and Warner 1999). Uniquely, small males ($<L_{50c}$) of *P. laticlavius* possess TP colouration advertising their sexuality and therefore are unable to act unrecognised as sneaker males among larger TP males. Whether these small males are successful spawners is not known and is of particular interest for future studies. If this species is territorial, as is suggested by Barrett (1995a), then these small TP males are unlikely to be successful spawners as they are less able to defend territories, and the females contained within, from larger TP males. However, behavioural work (see Chapter 4) provides evidence that this species does not defend permanent territories which suggests that the ability to defend a resource is not of great importance in determining the reproductive success of males in this species.

6.4.3 Relationship between length and weight

A strong relationship was found between length and weight for all species. Estimated weights for *Ophthalmolepis lineolatus* were approximately 50-60% that of *Notolabrus gymnogenis* and *Pictilabrus laticlavius* for lengths up to 200 mm. At 350 mm, *O. lineolatus* weights were approximately 70% that of *N. gymnogenis*. Coefficients for length-weight equations revealed values of b (i.e. 3.008-3.315) were typical of the range calculated for other wrasses (i.e. 2.670-3.227) (Taylor and Willis 1998; Gordoa *et al.* 2000; Fairclough 2004). The magnitude of the coefficient b in *N. gymnogenis* and *P.*

laticlavius (3.007 and 3.158, respectively), being close to 3, revealed fish shape remained relatively constant with growth (Taylor and Willis 1998) compared with that of *O. lineolatus* ($a = 3.312$) which became deeper bodied at larger sizes.

6.4.4 Reproduction

6.4.4.1 Sexual maturity

Sexual maturation represents an important transition in the life of fish as resources previously required solely for growth and survival must now also be utilised for purposes of reproduction (Wootton 1998). Sexual maturity occurred typically within a narrow size and age range for each species. Size at sexual maturity (i.e. L_{50m}) was estimated to occur at lengths of 186 mm (all 183-190 mm), 177 mm (majority 165-194 mm) and <95 mm in *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*, corresponding to von Bertalanffy predicted ages of 2.1, 1.8 and <0.9 years, respectively. Identification of critical ages and sizes at sexual maturity has been demonstrated in other temperate labrids (Jones 1980; Gillanders 1995a) with most maturing at ages of $0^+ - 2^+$ years. However, it has been suggested that females of some labrids may socially inhibit sexual maturity in smaller females by intra-sexual aggression (Jones and Thompson 1980).

6.4.4.2 Sex change

Sex change in fishes is known to occur at critical sizes/ages (Warner 1975; Jones 1980; Charnov and Skuladottir 2000; Allsop and West 2003) or may be socially controlled by dominant males (Warner 1982; Shapiro 1987; Warner and Swearer 1991; Sakai *et al.* 2001; Kuwamura *et al.* 2002; Perry and Grober 2003). Sex change in *Ophthalmolepis lineolatus* was highly predictable, occurring at sizes of 278-332 mm ($L_{50c} = 282$ mm) and predicted von Bertalanffy ages of 4.4-7.2 years ($A_{50c} = 4.7$ years). Similarly, most females of *Notolabrus gymnogenis* experience sex change at the critical size of 266-294 mm ($L_{50c} = 277$ mm) and corresponding von Bertalanffy ages of 4.2-5.5 years ($A_{50c} = 4.5$ years). However, the presence of TP and transitional males of *N. gymnogenis* at sizes of 230-254 mm revealed early sex change can occur in this species and may be in response to the mortality of an older, larger male (Platten *et al.* 2002).

In the case of *Pictilabrus laticlavius*, sex change occurred at sizes of 138 mm (L_{50c}) and ages of 1.9 years (A_{50c}); however, several transitional coloured females up to 180 mm were found. Perhaps, for these individuals, sex change is being inhibited by the aggressive behaviour of larger males (Sakai *et al.* 2001; Perry and Grober 2003). As previously outlined, some probable primary or pre-maturational males $<L_{50c}$ and $<A_{50c}$ were also found in the *P. laticlavius* population. Results for *P. laticlavius* are in contrast to that of Barrett (1995a) who found sex change in this species to occur at sizes of 174-225 mm and 3⁺-5⁺ years reflecting either a difference in the population dynamics in Tasmania compared to that of New South Wales or is in response to the different size distributions sampled. In the present study, the age at sex change for each species was comparable to that predicted by Allsop and West (2003) whereby fish change sex at ages 2.5 times their age at maturity; however, the prediction that size at sex change was 79% of their maximum length substantially overestimated the actual L_{50c} in *P. laticlavius* (i.e. 138 mm compared with the predicted 174 mm).

Determination of whether sex inversion is predominantly biologically or socially induced in *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* requires future experiments involving the removal of dominant males to discern whether such manipulations within a social group prompt sex change in females $<L_{50c}$. Such experiments also allow the determination of time required for sex reversal for comparisons with the 2-3 weeks described in other labrids (Kuwamura *et al.* 2002).

6.4.4.3 Reproductive season

Reproductive seasons of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* extended over approximately 5-7 months, but GSI measures indicate spawning is mostly concentrated into a few months. The pattern of concentrating most spawning into a few months within a reproductive season lasting up to six months typifies the strategy employed by most temperate labrids (Jones 1980; Jones and Thompson 1980; Barrett 1995a; Gillanders 1995a; Sakai and Kohda 2001; Denny and Schiel 2002). Post-spawning, larval labrids are transported in the plankton for 15-50 days (Gillanders 1995a; Jones 1999), but may be as long as 120 days (Victor 1986), before metamorphosing into juveniles upon settlement onto a reef. Therefore, fish reproductive activity is timed to periods of the year most favourable to the survival

of their larval offspring, particularly to times offering an increase in the availability of appropriate food resources for planktonic larvae. For example, Jones (1980) suggested spawning in *Pseudolabrus celidotus* in mid winter (July) through to late spring (November) coincided with an increase in water temperature and greater availability of food for larvae.

As with many other labrids of southern Australia and New Zealand (e.g. Barrett 1995a; Gillanders 1995a; Denny and Schiel 2002; Fairclough 2004; Nardi *et al.* 2006), the reproductive period of mid winter to early summer is the life history strategy employed by *P. laticlavius*. In this species, the reproductive period extends from August to January with a peak in spawning occurring in mid spring (October) to early summer (December). However, this is not the reproductive strategy used by *O. lineolatus* or *N. gymnogenis*. Gonadal examination and GSI measures indicated that the reproductive season of *O. lineolatus* was December to April with a peak in spawning occurring in late summer (February) to early autumn (March), and that of *N. gymnogenis* was April to October with a peak in spawning occurring in mid winter (July). In these species, post-larval processes may be more important in determining spawning period than that of food availability for larvae prior to reef settlement. For example, asynchrony of spawning may ensure recruits settle onto reefs at different times of the year to reduce early competition for food resources among species. Alternatively, reproductive activity in *O. lineolatus* and *N. gymnogenis* is possibly determined by adult condition which may be susceptible to annual fluctuations due to seasonal availability of prey items to adults. Future studies are needed to determine the processes driving asynchronous breeding in the three investigated labrids.

6.4.4.4 Reproductive behaviour

Apparent ‘courting’ behaviour involving fin flaring and repeated lateral body flexions was not a reliable indicator of the reproductive season of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* or *Pictilabrus laticlavius*. Barrett (1995a) reported male *P. laticlavius* courting females from mid August to late January and suggested this period of courting coincided with the spawning season for this species. Indeed, the present study revealed these months to broadly represent the reproductive period for this species, but courting was also observed in months outside their known reproductive

period. Therefore, the effectiveness of courting behaviour as a predictor of spawning season must be questioned despite the accuracy of predictions made by Barrett (1995a) for *P. laticlavius* and *Notolabrus fucicola* (compare with the known reproductive period in this chapter and Denny and Schiel (2002), respectively). In non-reproductive periods, courting behaviour may act as a form of social dominance thus potentially inhibit females from undertaking sex inversion (Kuwamura *et al.* 2002). By enforcing subordination of females, males maximise egg production in the spawning season and minimise intra-sexual competition for fertilisation.

Spawning behaviour was observed only in *P. laticlavius* with all spawning acts (n=5) occurring at midday (i.e. 1130-1400 hr). Spawning occurred between a single male and single female at the apex of a rapid ascent after repeated acts of courting by the male. Therefore, the mode of spawning for *P. laticlavius* is similar to the pair spawning observed in many other labrids (Jones 1981; Tribble 1982; Martel and Green 1987; Clavijo and Donaldson 1994; Sakai and Kohda 2001; Adreani *et al.* 2004). No false spawning ascents by the male were observed in *P. laticlavius* prior to the spawning event as has been previously reported in this species (Barrett 1995a) and in other labrids (Jones 1981), nor was there evidence of the post-spawning behaviours (e.g. downward arcing around the female after gamete release) reported in some labrids (Martel and Green 1987).

Despite frequent observations of interactions between male and female *O. lineolatus* in the reproductive season of December to April, spawning was not observed. As behavioural observations were restricted to periods of daylight, it is possible *O. lineolatus* spawn around sunset (e.g. Adreani *et al.* 2004) and/or may engage in temporary migrations to deeper reef areas outside the study region for spawning purposes (e.g. Jones 1981; Warner 1995). For *N. gymnogenis*, behavioural observations were restricted to periods primarily outside the peak spawning months of April to August. Therefore, further behavioural observations are required in these months to determine the spawning strategy employed by this species.

6.4.5 Age, growth and annulus formation

6.4.5.1 Validation of annulus formation and annuli measures

Sectioning of whole sagittal otoliths revealed distinct translucent and opaque banding in all size classes of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*. Marginal increment analysis revealed that a single opaque band was formed once a year from late August to early December (i.e. spring) in each species and each may therefore be accurately termed an ‘annulus’. This period of annulus formation coincides with other fishes of southern Australia and New Zealand (e.g. Jones 1980; Ewing *et al.* 2003; Lowry 2003; Fairclough 2004). Annulus formation has been associated with periods of fast growth, spawning season and rapid increases in water temperature (Jones 1980; Cailliet *et al.* 1996; Wootton 1998; Ewing *et al.* 2003). Of these, the physiological response to a rapid increase in water temperature seems most likely to govern annulus formation in each of the investigated labrids as annuli form outside the spawning season of *O. lineolatus* (i.e. Dec-Apr) and is slightly out-of-phase with the spawning season of *N. gymnogenis* (i.e. Apr-Oct). Furthermore, juvenile individuals (i.e. <L_{50m}) who are yet to engage in spawning activity still predictably form annuli in spring.

Annuli of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* were found to be incremented consistently at a predictable location on the otolith. Measurements of maximum annulus radii (AR_{max}) quantified the position of yearly annuli for the purpose of consistent interpretation of otolith age by the accurate location of the first and successive annuli. Mean AR_{max} for the first annulus of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* was determined as 1.287, 1.440 and 0.879 mm, respectively, with successive annuli formed at mean AR_{max} measures predicted accurately by von Bertalanffy equations. It is recommended the established AR_{max} measures be used for future interpretation of otoliths in these species and the technique to be implemented for other species as a means of reducing reader error associated with poor otolith readability. An analogous technique utilising mean transverse radius measures was employed by Ewing *et al.* (2003) to confirm that the first opaque zone in sagittae of *Notolabrus fucicola* was formed before the first birthday. Similarly, the present study revealed the first opaque zone of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* was

formed before the first birthday (i.e. at ages of 0.6, 0.3 and 0.8 years, respectively). In *O. lineolatus* and *N. gymnogenis*, this first opaque zone was termed the '0' annulus (see Table 6.2). Determining the position of annuli, especially the first annulus, is of great importance for assurance that fish ages are not over- or under-estimated (Ewing *et al.* 2003; Campana 2001).

6.4.5.2 Growth and longevity

Age at length data revealed *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* are initially fast growing to the sizes (ages) of approximately 300 mm TL (6 years), 280 mm TL (5 years) and 180 mm TL (3 years), respectively. Thereafter, growth continues at a substantially slower rate such that little discernible difference in fish length occurs between fish of 6 to 13 years of age for *O. lineolatus*, 6 to 10 years for *N. gymnogenis*, and 2 to 5 years for *P. laticlavius*. Annuli counts were used to assign maximum ages of 13.4, 9.6 and 4.8 years to *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*, respectively. These ages were younger than some similar sized species of labrid in Tasmania (Barrett 1995a; Ewing *et al.* 2003), New Zealand (Jones 1980) and Europe (Treasurer 1994), but reflect that of *Notolabrus tetricus* in Tasmania (Barrett 1995a), *Choerodon* spp. in Shark Bay, Western Australia (Fairclough 2004), and *Symphodus tinca* and *Coris julis* in the north-western Mediterranean sea (Gordoa *et al.* 2000). The maximum age for *P. laticlavius* was substantially lower than the 11.5 years reported for this species by Barrett (1995a). Estimated maximum ages in the present study are likely to be underestimates of the true maximum ages for each species as specimens were collected from inshore waters which are known to be frequented by recreational fishers, thus potentially resulting in the harvesting of larger/older individuals from the population.

Derived von Bertalanffy growth curves provided a good representation of length-age relationships for each species with asymptotic lengths (L_{∞}) for *O. lineolatus* and *N. gymnogenis* of approximately 370 mm, reflecting the maximum reported sizes for these species (i.e. 400 mm: Kuiter 1993). In contrast, the asymptotic length of *P. laticlavius* of approximately 220 mm was lower than the asymptotic length (*ca* 250 mm) reported by Barrett (1995a) and considerably lower than the maximum size of 300 mm reported by Kuiter (1993). The von Bertalanffy growth coefficients (k) were comparable for

both *O. lineolatus* and *N. gymnogenis* (i.e. $k = 0.300$ and 0.254 , respectively) and were within the range of estimates made for other labrids (Treasurer 1994; Barrett 1995a; Gordoa *et al.* 2000; Ewing *et al.* 2003; Fairclough 2004) and other fishes (Taylor and Willis 1998; Lowry 2003). The growth coefficient is a measure of how rapidly the asymptotic length is approached (Taylor and Willis 1998). In *P. laticlavus*, the estimated k (i.e. 0.577) was substantially higher than otolith-based predictions for this species by Barrett (1995a) (i.e. 0.45). This reflects the absence of larger specimens (i.e. >220 mm) in the present study which resulted in a rapid approach to the lowered asymptotic length. For *P. laticlavus*, at ages less than 5 years, the fitted von Bertalanffy curves from the present study and that of Barrett (1995a) were comparable despite Barrett (1995a) constructing the von Bertalanffy curve for fish aged below 4 years using less than 10 specimens. For example, length estimates by Barrett (1995a) of *ca* 100, 150, 180, 200 and 210 mm at ages of 1^+ , 2^+ , 3^+ , 4^+ and 5^+ years were the same as those at ages of 1, 2, 3, 4 and 5 years in the present study.

6.4.6 Conclusion

The reproduction, growth and demographics of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* have been determined in this chapter. The population structure of each species suggests the typical labrid reproductive strategy of protogynous hermaphroditism is employed in all species. Size/age at sexual maturation and sex-change were similar in *O. lineolatus* and *N. gymnogenis*, but occurred at substantially smaller sizes and younger ages in *P. laticlavus*. Reproductive seasons and peak periods of spawning were asynchronous among species. Aging studies revealed these species to be relatively long-lived. Determining the reproductive strategy, growth and demographics of each species has provided important information for assessing the impact of fishing on labrid populations and for evaluating the current management strategy for these fishes in NSW. Implications of this chapter for the management of *O. lineolatus*, *N. gymnogenis* and *P. laticlavus* are discussed in Chapter 7.

Chapter 7:

Conclusion

7.1 Study initiative and general approach

The present study was motivated by observations of higher labrid densities and larger mean size of individuals on coastal reefs of NSW experiencing reduced fishing pressure. This led to questions regarding the effects of the fishing sector on labrid populations and the effect that labrid over-harvesting may have on rocky reef systems. These concerns were justified when consideration was given to the increase in fishing pressure occurring in coastal regions of eastern Australia (Henry and Lyle 2003; Kennelly and McVea 2003) and the potential for an expansion of the live fish trade to include additional labrid species. Secondly, the functional ecology, life history and demographics of most labrid species had yet to be investigated in NSW, with available knowledge restricted mainly to photographic identification guides providing brief notes on species distribution, habitat preferences and identification.

Therefore, it was evident that a significant gap existed between what was known about labrids and the information required to adequately understand their ecological significance, to predict the system-wide impact of labrid harvesting and to provide informed decisions for the effective management of these fishes. The present study has provided a substantial contribution to filling some of these previous gaps by primarily focusing on *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* which are abundant and co-occurring species associated with temperate rocky reefs of south-eastern Australia. The methods used to provide this information included SCUBA surveys of labrid assemblages; *in situ* observations of labrid behaviour; and acquisition of labrid specimens for the extraction of intestines, gonads and otoliths, and for measurements of fish weight and length.

This conclusion chapter provides a brief summary of the major findings of this study, suggests possible ecological implications of these findings, offers recommendations for the effective management of the focal labrids and provides suggestions for future research.

7.2 Patterns of distribution and abundance

Chapter 3 aimed to describe patterns of distribution and abundance in labrid assemblages with special emphasis given to the effect of habitat on these patterns. Labrids were found to be species-rich (total of 19 species) and abundant on rocky reefs of the central coast region of NSW, with assemblages consisting mostly of species endemic to temperate waters of Australia. Labrids represented the most speciose and abundant family of all non-planktivorous fishes. Overall, sponge garden habitat represented the habitat with highest species richness and diversity of individuals due to a greater representation of *Ophthalmolepis lineolatus*, *Austrolabrus maculatus* and *Eupetrichthyes angustipes*. Neither fringe or barrens habitat contained distinct labrid assemblages, but higher overall densities of *Notolabrus gymnogenis*, *Achoerodus viridis* and *Pictilabrus laticlavius* occurred in fringe habitat due mostly to the periodic recruitment of each species into this habitat. The effect of habitat on structuring labrid assemblages often varied between sites separated by 250-800 m, but was consistent between locations separated by approximately 30 km, which emphasises the importance of replication at various spatial scales when sampling labrid assemblages. Contributing to temporal fluctuations in labrid diversity was a substantial increase in the abundance of 'recruits' coinciding with the warm sea temperatures experienced in late summer and autumn (Apr-May). Recruitment events were most notable for *N. gymnogenis* (into fringe habitat), and *O. lineolatus*, *A. maculatus* and *E. angustipes* (into sponge garden habitat).

7.3 Spatial structure and behaviour

Chapter 4 aimed to describe the social organisation and behavioural repertoires of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* by employing an intensive ethological study. The need for this information was prompted by the fact that the social organisation and behaviour of most labrids are not described, the behavioural diversity of labrids is poorly understood and sources of variation in the occurrence of behaviours is generally not recognised. The three focal species differed substantially in the spatial structure of their populations and in the area of reef used by individuals. *O. lineolatus* were found to be temporary reef residents using home ranges in excess of 2500 m² for periods of up to 1 year before permanently emigrating to areas

outside these temporary home ranges. Few interactions occurred between individuals of this species but, like the other focal species, a size-based dominance hierarchy was evident. *N. gymnogenis* demonstrated strong fidelity to reef patches of less than 600 m² in which they remained for up to at least 2 years. Juvenile and IP individuals shared reef patches with up to at least 10 conspecifics of various sizes, but defended reef areas from individuals of similar size. In contrast, TP males were highly territorial and actively defended contiguous territories from rival males. Gaining an understanding of the spatial structure of *P. laticlavus* was constrained by its cryptic behaviour, but observations suggest that individuals of this species share a common reef area within which they temporarily defend small reef patches of up to 10 m² for the purpose of feeding, shelter and/or reproduction.

Other behaviours introduced in Chapter 4 were lying, use of shelter, rubbing, bending, gaping, cleaning by clingfishes and colour change. All species typically engaged in each of the reported behaviours, but the occurrence of these behaviours often demonstrated substantial differences among species (e.g. lying, shelter and bending) and/or exhibited shifts with ontogeny (e.g. interactions and area usage). These trends generally exhibited consistency at different times of the day and periods of the year, and at both locations, but the magnitude of occurrences were often different across locations.

7.4 Diet and feeding behaviour

Dietary and behavioural observations were used in Chapter 5 to investigate the feeding ecology of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus*. As no previous studies have been conducted which compare the diets of co-occurring labrids, special consideration was given to determining whether food resources were partitioned among species. All species were found to be generalist carnivores feeding on a variety of benthic invertebrates including polychaetes, amphipods, decapods, gastropods, bivalves, polyplacophorans, echinoderms and cirripedes. These prey items were obtained mostly from complex microhabitat in the form of algal bases and fronds, and *Diopatra dentata* tubes, but less complex habitat such as bare rock or steel, and sand/rubble were also used regularly for feeding. Substantial differences among species in the volumetric contribution of prey items and

differences in feeding microhabitat profiles revealed that the partitioning of food resources may be an important strategy for allowing the focal species to co-occur with minimal competition. In addition, ontogenetic dietary shifts were significant and, to some extent, changes in feeding microhabitat profiles occurred suggesting that food resources are further partitioned within species.

Observations of feeding episodes revealed the bite rates of *O. lineolatus*, *N. gymnogenis* and *P. laticlavus* were unaffected by the time of day and period of the year in which observations occurred; however, differences between locations and among life history stages did occur for some species. This suggests that future quantification of the feeding behaviour of the focal species needs to be less concerned with temporal than with spatial replication, and that sampling across all life history stages needs to be considered.

7.5 Reproduction, growth and demographics

The reproduction, growth and demographics of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavus* were investigated in Chapter 6 for the purpose of providing information for the effective management of these species. The occurrence of males only at larger sizes and older ages strongly suggests that *O. lineolatus* and *N. gymnogenis* are monandrous species (i.e. all males are secondary males having derived from females), but the occurrence of some *P. laticlavus* males at small sizes and young ages suggests this species is diandrous (i.e. some males are primary males having never functioned as females).

Juveniles reached sexual maturity (i.e. L_{50m} and A_{50m}) at 186 mm (2.1 years) in *O. lineolatus*, 177 mm (1.8 years) in *N. gymnogenis* and <95 mm (<0.9 years) in *P. laticlavus*. Individuals remained as a sexually active IP female until sex change occurred into a TP male (i.e. L_{50c} and A_{50c}) at 282 mm (4.7 years) in *O. lineolatus*, 277 mm (4.5 years) in *N. gymnogenis* and 138 mm (1.9 years) in *P. laticlavus*. However, variable sizes (ages) at sex change suggest social interactions may influence the timing of sex change. Timing of reproduction was asynchronous among species with reproductive activity peaking in late summer (February) to early autumn (March) in *O. lineolatus*, mid winter (July) in *N. gymnogenis* and mid spring (October) to early

summer (December) in *P. laticlavius*. *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* were fast growing to the sizes (ages) of approximately 300 mm (6 years), 280 mm (5 years) and 180 mm (3 years), respectively, with longevity up to at least 13.4, 9.6 and 4.8 years.

7.6 Implications for better understanding labrid ecology

The present study has contributed substantially to the development of a greater understanding of ecological processes important in the structuring and functioning of fish assemblages on temperate rocky reefs, as well as providing important information for determining the ecological significance of labrids for use in predicting any foreseeable consequences of labrid over-exploitation. Evidence of relatively few inter-specific interactions and evident differences among species in their food resources, feeding microhabitats, spatial structure, periods of reproduction and behaviour suggests that past ecological pressures have contributed to significant niche differentiation among species to reduce overall competition, allow co-occurrence and contribute to high species diversity in reef systems. In contrast, frequent intra-specific interactions in the form of size-based dominance hierarchies, competition for food resources and territoriality suggests that competition between individuals of the same species is of consideration when describing processes likely to influence the structure of labrid populations in rocky reef systems. Ontogenetic partitioning of resources (e.g. habitat and food) contributes to reducing overall competition within populations, but morphological and behavioural similarities within a species places constraints on the availability of resources, especially between individuals of similar size.

The availability of shelter and type of substrate used for nocturnal refuge were identified as potentially important sources of variation in the spatial structure of labrid assemblages. In the case of *Ophthalmolepis lineolatus*, the potential use of soft sediments for nocturnal refuge, but reliance on rocky substrate for foraging, may preclude territoriality in this species and may provide insight into why individuals are most abundant at sand-reef interfaces. Whether *O. lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* are considered 'keystone' predators in rocky reef systems was beyond the scope of this present study, but the role of these species in reducing prey densities and influencing prey behaviour is potentially significant. However,

future experimental manipulations in the form of exclusion/inclusion experiments and/or modification of fish densities are required to adequately assess the direct impact of labrid foraging on prey densities and to determine the indirect effects of predation on modifying habitat structure.

7.7 Applications for the management of labrids

Determining the spatial structure, behaviour, life history, growth and demographics of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius* has provided important information for evaluating the current management strategy for these fishes in NSW. Lacking significant commercial value, little was previously known about each of the focal species for their effective management. Currently, a bag limit of 20 fish per person per day with no size restrictions is applied to *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*. Findings from the present study suggest the bag limit for these species is too generous as larger, reproductive males are usually targeted potentially causing a depletion of males, and hence sperm output, within populations. Therefore, the author supports the initiative of the NSW Department of Primary Industries (2005a) to reduce the general bag limit for *O. lineolatus* and *P. laticlavius* to 10 fish per person per day to reduce the risk of their over-harvesting. Furthermore, if *O. lineolatus* and *P. laticlavius* were to be more frequently targeted by fishes it is recommended that minimum size limits of 310 mm (5.7 years) and 180 mm (2.9 years) be applied, respectively, to ensure the representation of males $\geq L_{50c}$ for at least one year beyond sex change to provide sperm input to populations before becoming susceptible to harvesting.

A limitation on the density of reproductive males of *N. gymnogenis* in response to territoriality presents an important consideration for their management. For this species, the current bag limit is highly ineffective for their sustainability as males may be easily eliminated from large reef areas by fishers. For example, the harvesting of 10 reproductive males from a common reef area results in the absence of males over an area of up to 6000 m². Replacement of *N. gymnogenis* males appears to be only from the female population due to sand flats deterring immigration of males from neighbouring reefs. This highlights an important consideration for the exploitation of males in areas where their rate of removal by fishers may be higher than the occurrence

of sex change in females. In such cases, populations of *N. gymnogenis* would be sustained by the recruitment of progeny from other reefs, but the population itself would not contribute to maintaining fish stocks. Therefore, the susceptibility of *N. gymnogenis* to over-harvesting prompts the need to reduce bag limits for this species to no more than 5 fish per person per day and to place minimum size limits of at least 300 mm (5.5 years) to ensure the representation of males $\geq L_{50c}$ for at least one year beyond sex change to provide sperm input to populations before becoming susceptible to harvesting.

It is also recommended that better strategies be developed to acquire accurate catch data for labrids from both commercial and recreational fishers. Currently, statistics are likely to be vastly under-representative of the true rates of harvesting of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius*. This places serious constraints on the ability to assess the impact fishers have on these species. Indeed, populations of *O. lineolatus*, *N. gymnogenis* and *P. laticlavius* may be very sensitive to harvesting by fishers due to low rates of ‘natural’ mortality. For example, the author is unaware of any species associated with temperate rocky reef systems that are involved in labrid predation and no evidence of labrid predation occurred in over 126 hours of behavioural observations.

7.8 Future research

This study has provided important insights into the spatial distribution, social structure, behaviour, feeding ecology, reproduction, growth and demographics of *Ophthalmolepis lineolatus*, *Notolabrus gymnogenis* and *Pictilabrus laticlavius*, but represents only the foundation of knowledge needed to fully understand the ecology of these fishes. It is therefore recommended that future studies be conducted to address some of the questions that have arisen throughout this thesis. For example, the spatial distribution of labrids needs further exploration to compare labrid assemblages associated with sheltered and exposed reefs, the importance of shelter availability on the distribution of labrids needs to be determined and patterns of recruitment need to be more fully understood. Of special consideration for future studies of labrid behaviour is exploring how these fishes use nocturnal refuges, tagging studies are required to more fully explore the spatial structure of populations and acoustic studies of *O. lineolatus* are recommended to determine patterns of movement in this species.

With regard to feeding ecology, further investigation is required to establish relationships between diet and the use of feeding microhabitats, the effects of labrid foraging on prey abundance and behaviour need to be determined, and hypotheses regarding the ecological role of these fishes need to be established and tested. Finally, future studies are recommended to explore the importance of asynchrony in the reproductive seasons of the focal species, the spawning behaviour of *O. lineolatus* and *N. gymnogenis* needs to be documented, and larval duration is to be determined. Histological examinations of gonads are also of importance to confirm protogynous hermaphroditism in *O. lineolatus* and *N. gymnogenis*, and to establish whether small males of *P. laticlavius* are indeed primary males. Variation in the reproductive strategy (e.g. age/size at maturity and sex change) of each species is also an area of future interest to determine whether uniform management strategies can be applied to each species throughout their range in temperate Australia.

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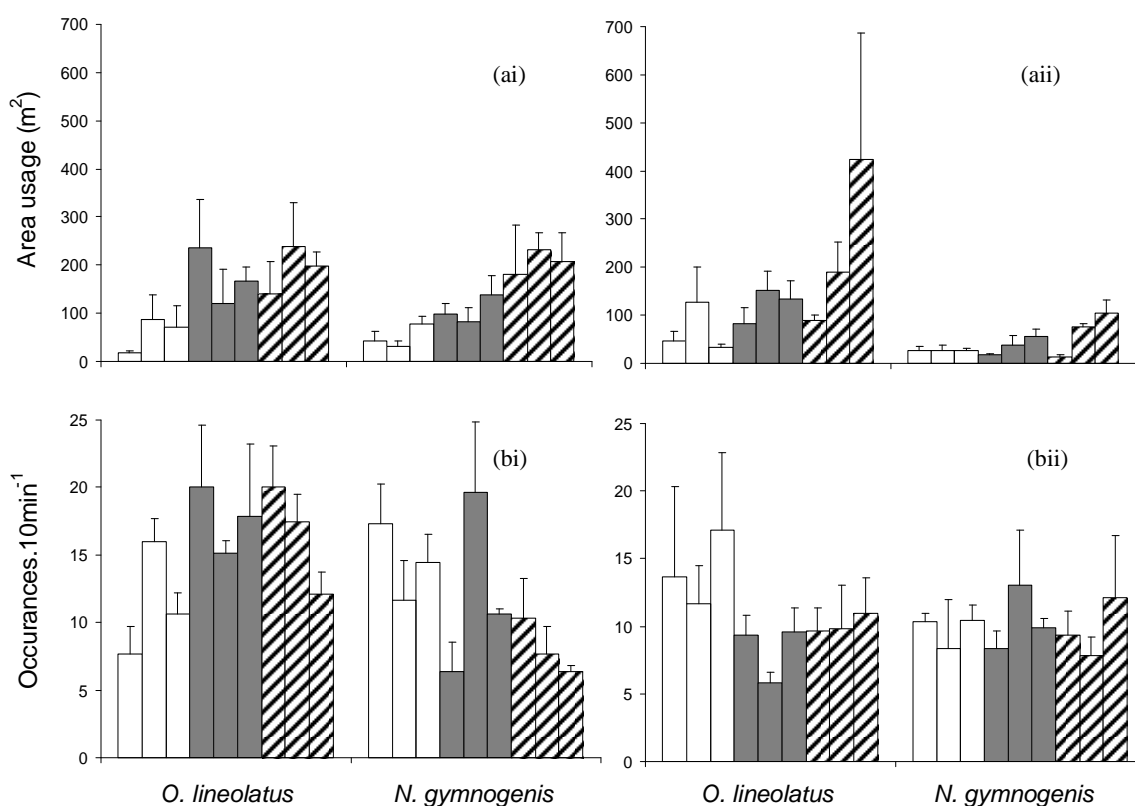
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Appendices

Appendix 1: Pilot study results used to determine the optimal sampling strategy (i.e. 10, 20 or 30 mins) for quantifying labrid behaviour, as discussed in the pilot study section of Chapter 2.



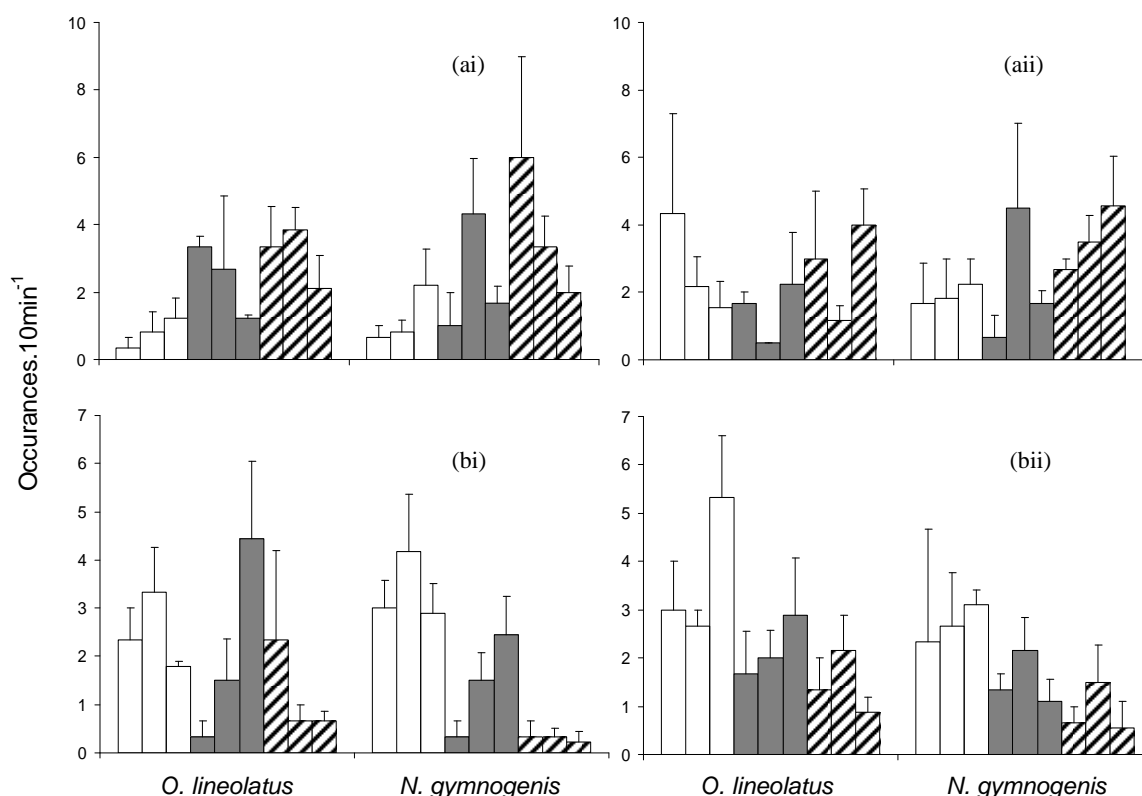
Source of variation	df	a) Area use ¹		b) Encounters with other fish ¹	
		MS	F	MS	F
Time (T)	2	3438.68	2.04	30.36	7.66
Species (Sp)	1	849.74	1.02	210.01	0.39
Stage (St)	2	4226.92	3.27	34.36	0.98
Location (L)	1	71378.83	53.13***	7109.46	65.26***
T x Sp	2	195.40	0.56	87.38	0.52
T x St	4	673.69	2.25	22.55	0.29
T x L	2	1682.21	1.25	3.96	0.04
Sp x St	2	501.38	0.54	108.09	0.37
Sp x L	1	830.02	0.62	537.47	4.93*
St x L	2	1294.42	0.96	35.22	0.32
T x Sp x St	4	335.86	1.05	222.24	2.33
T x Sp x L	2	348.72	0.26	168.86	1.55
T x St x L	4	300.05	0.22	76.70	0.70
Sp x St x L	2	927.40	0.69	292.67	2.69
T x Sp x St x L	4	320.90	0.24	95.34	0.88
Residual	72	1343.58		108.96	

¹data square-root (x+1) transformed (Cochran's C test, $P>0.05$)

* $P<0.05$, *** $P<0.001$

Graphs and ANOVA results used to compare area usage (a) and encounter rates with other fishes (b) in 10, 20 and 30 minute observation times (sequential replicated columns) for several life history stages of *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis* at Catherine Hill Bay (i) and Norah Head (ii). Life history stages are: Juv. = juvenile (□), IP = initial phase (■), TP = terminal phase (▨). Standard error bars are provided (n=3 replicates).

Appendix 1 (continued):

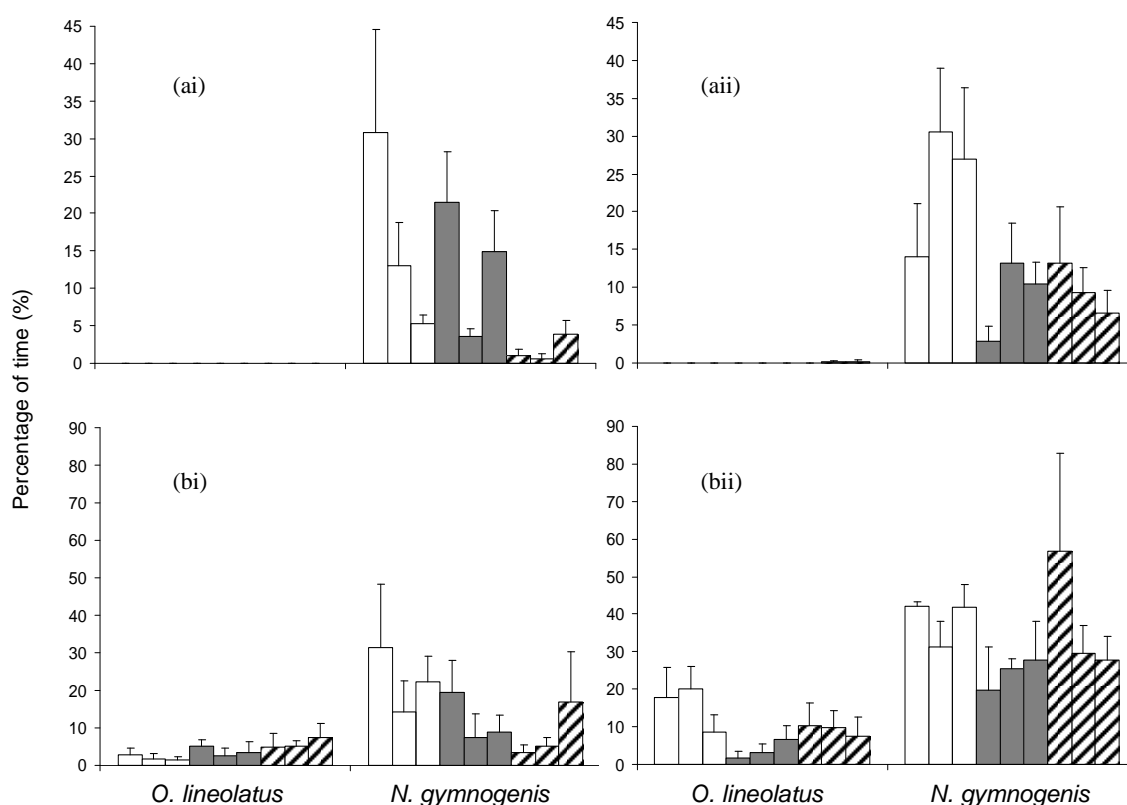


Source of variation	df	a) Dominant interactions ¹		b) Subordinate interactions ²	
		MS	F	MS	F
Time (T)	2	1.69	0.47	14.01	4.42
Species (Sp)	1	0.60	0.10	53.25	1.46
Stage (St)	2	2.22	0.40	105.01	5.38
Location (L)	1	1147.24	77.13***	266660.39	45.72***
T x Sp	2	2.78	1.38	4.05	2.16
T x St	4	2.89	1.10	8.26	0.65
T x L	2	3.62	0.24	3.17	0.00
Sp x St	2	5.33	2.73	21.42	0.38
Sp x L	1	6.22	0.42	36.56	0.01
St x L	2	5.50	0.37	19.51	0.00
T x Sp x St	4	2.53	0.88	2.87	0.95
T x Sp x L	2	2.02	0.14	1.88	0.00
T x St x L	4	2.63	0.18	12.77	0.00
Sp x St x L	2	1.95	0.13	56.54	0.01
T x Sp x St x L	4	2.88	0.19	3.01	0.00
Residual	72	14.87		5832.83	

¹data square-root (x+1) transformed, ²data ln(x+1) transformed (Cochran's C test, $P > 0.05$)
 *** $P < 0.001$

Graphs and ANOVA results used to compare rates of dominant (a) and subordinate (b) interactions in 10, 20 and 30 minute observation times (sequential replicated columns) for several life history stages of *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis* at Catherine Hill Bay (i) and Norah Head (ii). Life history stages are: Juv. = juvenile (□), IP = initial phase (■), TP = terminal phase (▨). Standard error bars are provided (n=3 replicates).

Appendix 1 (continued):



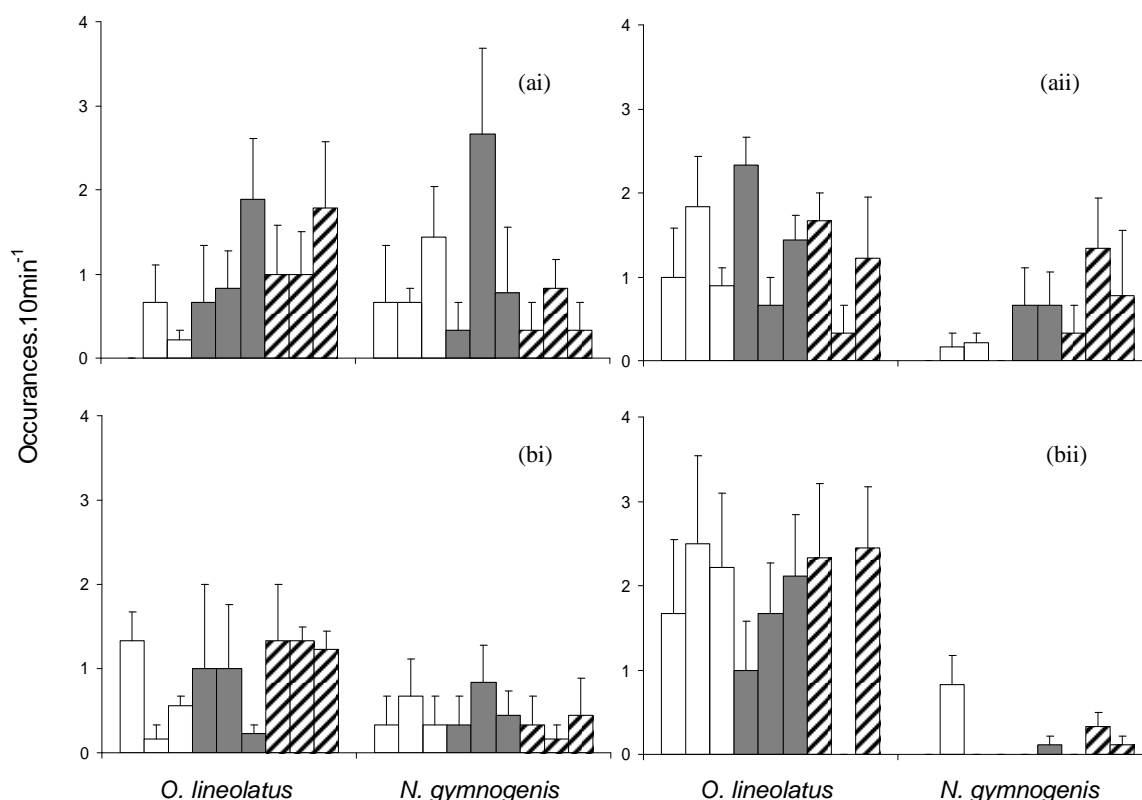
Source of variation	df	a) Lying ²		b) Shelter use ¹	
		MS	F	MS	F
Time (T)	2	0.10	0.15	81.55	1.15
Species (Sp)	1	10.09	312.86*	1084.04	7.30
Stage (St)	2	1.93	0.93	127.82	34.92*
Location (L)	1	113.98	35.91***	1502.37	11.56**
T x Sp	2	0.23	0.44	8.15	0.39
T x St	4	0.42	0.61	24.57	0.86
T x L	2	0.70	0.22	70.65	0.54
Sp x St	2	0.30	0.14	193.79	0.47
Sp x L	1	0.03	0.01	148.53	1.14
St x L	2	2.07	0.65	3.66	0.03
T x Sp x St	4	0.52	0.95	23.97	0.66
T x Sp x L	2	0.52	0.16	20.83	0.16
T x St x L	4	0.68	0.22	28.45	0.22
Sp x St x L	2	2.11	0.67	413.94	3.18*
T x Sp x St x L	4	0.55	0.17	36.33	0.28
Residual	72	3.17		129.98	

¹data square-root (x+1) transformed, ²data ln(x+1) transformed (Cochran's C test, $P > 0.05$)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Graphs and ANOVA results used to compare the percentage of time engaged in lying (a) and sheltering (b) in 10, 20 and 30 minute observation times (sequential replicated columns) for several life history stages of *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis* at Catherine Hill Bay (i) and Norah Head (ii). Life history stages are: Juv. = juvenile (□), IP = initial phase (■), TP = terminal phase (▨). Standard error bars are provided (n=3 replicates).

Appendix 1 (continued):

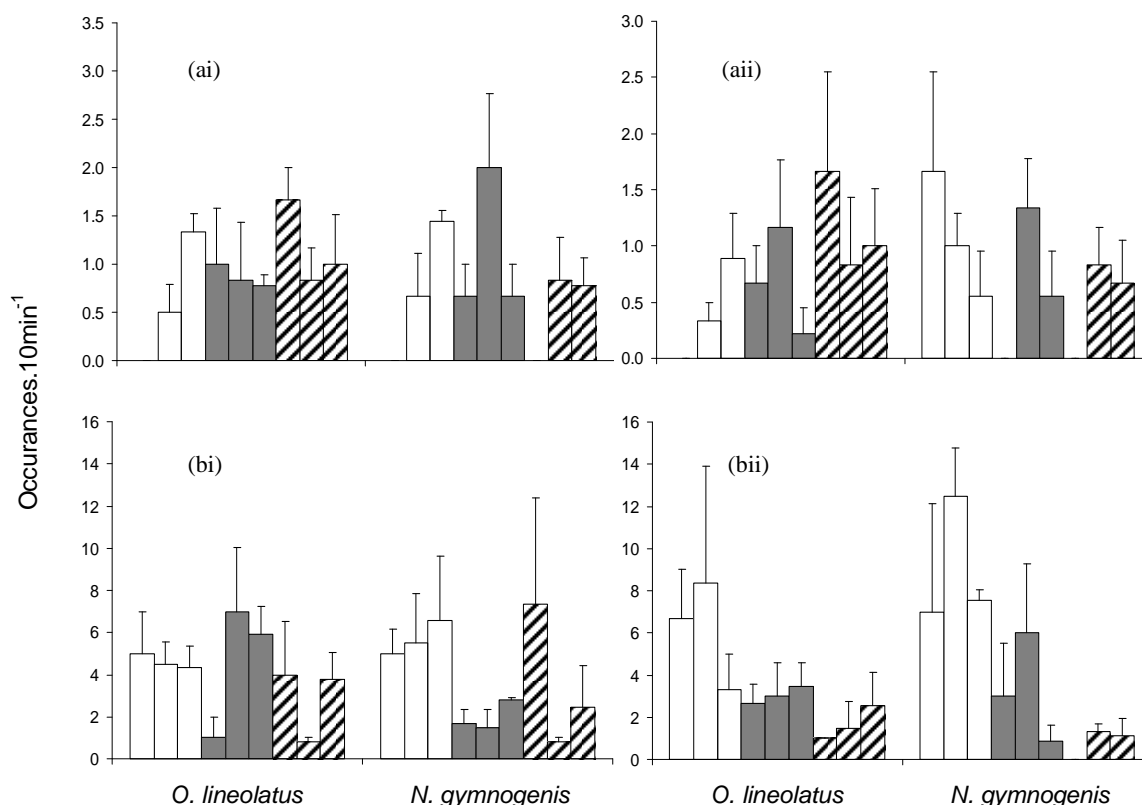


Source of variation	df	a) Side-swiping		b) Bending	
		MS	<i>F</i>	MS	<i>F</i>
Time (T)	2	8.58	4.88	1.64	0.40
Species (Sp)	1	52.78	1.00	92.93	1.81
Stage (St)	2	23.39	0.59	35.97	0.85
Location (L)	1	265566.35	45.51***	264280.61	45.49***
T x Sp	2	3.47	3.11	1.84	0.45
T x St	4	2.39	0.76	2.30	0.75
T x L	2	1.76	0.00	4.06	0.00
Sp x St	2	28.62	0.59	32.72	0.83
Sp x L	1	52.81	0.01	51.39	0.01
St x L	2	39.56	0.01	42.49	0.01
T x Sp x St	4	4.14	0.85	2.35	0.75
T x Sp x L	2	1.12	0.00	4.11	0.00
T x St x L	4	3.15	0.00	3.08	0.00
Sp x St x L	2	48.87	0.01	39.58	0.01
T x Sp x St x L	4	4.87	0.00	3.15	0.00
Residual	72	5835.84		5809.26	

*** $P < 0.001$

Graphs and ANOVA results used to compare rates of side-swiping (a) and bending (b) in 10, 20 and 30 minute observation times (sequential replicated columns) for several life history stages of *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis* at Catherine Hill Bay (i) and Norah Head (ii). Life history stages are: Juv. = juvenile (□), IP = initial phase (■), TP = terminal phase (▨). Standard error bars are provided (n=3 replicates).

Appendix 1 (continued):



Source of variation	df	a) Gaping		b) Bite rate ²	
		MS	F	MS	F
Time (T)	2	6.23	4.62	0.59	0.95
Species (Sp)	1	34.69	1.20	0.00	0.02
Stage (St)	2	26.92	0.72	2.95	1.10
Location (L)	1	265501.89	45.60***	117.29	44.44***
T x Sp	2	2.60	0.75	0.07	0.12
T x St	4	6.58	6.44*	0.39	0.78
T x L	2	1.35	0.00	0.62	0.24
Sp x St	2	26.21	0.87	0.11	0.13
Sp x L	1	28.86	0.00	0.23	0.09
St x L	2	37.47	0.01	2.68	1.01
T x Sp x St	4	6.23	1.47	0.04	0.10
T x Sp x L	2	3.48	0.00	0.60	0.23
T x St x L	4	1.02	0.00	0.50	0.19
Sp x St x L	2	30.21	0.01	0.84	0.32
T x Sp x St x L	4	4.25	0.00	0.37	0.14
Residual	72	5822.72		2.64	

²data $\ln(x+1)$ transformed (Cochran's C test, $P>0.05$)

* $P<0.05$, *** $P<0.001$

Graphs and ANOVA results used to compare rates of gaping (a) and biting (b) in 10, 20 and 30 minute observation times (sequential replicated columns) for several life history stages of *Ophthalmolepis lineolatus* and *Notolabrus gymnogenis* at Catherine Hill Bay (i) and Norah Head (ii). Life history stages are: Juv. = juvenile (\square), IP = initial phase (\blacksquare), TP = terminal phase (\hatched). Standard error bars are provided (n=3 replicates).

Appendix 2: Fish species recorded within fringe, barrens and sponge garden habitat at Terrigal and Norah Head over 5 sampling periods. Numbers correspond to the total number of individuals observed.

Species (118 species)	FRINGE		BARRENS		SPONGE GARDEN	
	Terrigal	Norah Head	Terrigal	Norah Head	Terrigal	Norah Head
Heterodontidae						
<i>Heterodontus galeatus</i>			1	2		
<i>Heterodontus portusjacksoni</i>		6	3	4	1	12
Orectolobidae						
<i>Orectolobus maculatus</i>			3		2	
<i>Orectolobus ornatus</i>			3	1		4
Carcharhinidae						
<i>Carcharhinus</i> sp.	1					
Urolophidae						
<i>Urolophus sufflavus</i>						1
Dasyatidae						
<i>Dasyatis thetidis</i>	2		1			5
Muraenidae						
<i>Gymnothorax prasinus</i>			1			
Plotosidae						
<i>Plotosus lineatus</i>			600			
Aulopidae						
<i>Aulopus purpurissatus</i>	3	7	14	2	5	9
Gobiesocidae						
<i>Cochleocephalus orientalis</i>	1					
Moridae						
<i>Lotella rhacina</i>		1		1	5	
Trachichthyidae						
<i>Trachichthys australis</i>			1		2	11
Syngnathidae						
<i>Phyllopteryx taeniolatus</i>					1	
Platycephalidae						
<i>Thysanophrys cirronasus</i>						5
Scorpaenidae						
<i>Scorpaena cardinalis</i>	10	5	20	45	7	16
<i>Scorpaenidae</i> sp.			1			
Serranidae						
<i>Acanthistius ocellatus</i>	1		5	9	2	
<i>Epinephelus corallicola</i>					1	
<i>Hypoplectrodes annulatus</i>						2
<i>Hypoplectrodes maccullochi</i>	15	5	192	107	715	635
<i>Serranidae</i> sp.		1				
Plesiopidae						
<i>Paraplesiops bleekeri</i>			1		3	2
<i>Trachinops taeniatus</i>	987	6446	5239	13325	3792	3348

Appendix 2 (continued):

	FRINGE		BARRENS		SPONGE GARDEN	
	Terrigal	Norah Head	Terrigal	Norah Head	Terrigal	Norah Head
Apogonidae						
<i>Apogon limenus</i>			6		15	12
Dinolestidae						
<i>Dinolestes lewini</i>	35	23	24	275	93	113
Pomatomidae						
<i>Pomatomus saltatrix</i>	1					
Carangidae						
<i>Pseudocaranx dentex</i>	1		8	1	70	
<i>Pseudocaranx wrighti</i>			5			4
<i>Seriola lalandi</i>				4		60
<i>Trachurus novaezelandiae</i>	1257	371	322	750	562	331
Trevally sp.		1				
Sparidae						
<i>Chrysophrys auratus</i>			1	2	1	1
<i>Rhabdosargus sarba</i>			1		40	
Mullidae						
<i>Parupeneus multifasciatus</i>					1	
<i>Parupeneus signatus</i>	8		30	7	8	4
<i>Upeneichthys vlamingii</i>	1		4		34	9
Pempheridae						
<i>Pempheris affinis</i>			263	171	81	158
<i>Pempheris compressa</i>	132	5	958	292	100	109
<i>Pempheris multiradiata</i>			2	20		48
Monodactylidae						
<i>Monodactylus argenteus</i>	126		39		70	
<i>Schuettea scalaripinnis</i>	596	528	130	2728		1124
Scorpididae						
<i>Scorpius lineolata</i>	582	174	194	180	209	754
Kyphosidae						
<i>Kyphosus sydneyanus</i>		2		26		
Girellidae						
<i>Girella tricuspidata</i>	37	3	13	13		
Girellidae sp.				1		
Microcanthidae						
<i>Atypichthys strigatus</i>	2518	6071	510	2001	56	340
<i>Microcanthus strigatus</i>	80		1	1		
Chaetodontidae						
<i>Chaetodon guentheri</i>						2
<i>Chelmonops truncatus</i>				1	1	2
Pomacentridae						
<i>Abudefduf vaigiensis</i>		20				
<i>Chromis hypsilepis</i>	130	327	1593	1831	342	1823
<i>Mecaenichthys immaculatus</i>	45	50	171	47	240	164
<i>Parma microlepis</i>	44	79	363	113	517	279

Appendix 2 (continued):

	FRINGE		BARRENS		SPONGE GARDEN	
	Terrigal	Norah Head	Terrigal	Norah Head	Terrigal	Norah Head
Pomacentridae (continued)						
<i>Parma unifasciata</i>	409	731	326	581	1	2
<i>Pomacentrus chrysurus</i>	1					
<i>Pomacentrus coelestis</i>			3	3		
<i>Pomacentridae</i> sp.				1		
Enoplosidae						
<i>Enoplosis armatus</i>			69	14	31	11
Chironemidae						
<i>Chironemidae</i> sp.	1					
Aplodactylidae						
<i>Crinodus lophodon</i>	231	38	28	7	3	3
Cheilodactylidae						
<i>Cheilodactylus fuscus</i>	25	13	58	40	45	32
<i>Nemadactylus douglasi</i>					3	1
Latrididae						
<i>Latridopsis forsteri</i>	2		1			
Labridae						
<i>Achoerodus viridis</i>	42	96	49	52	38	42
<i>Anampses caeruleopunctatus</i>		1				
<i>Austrolabrus maculatus</i>		2	7	25	215	257
<i>Coris dorsomacula</i>					5	6
<i>Coris picta</i>			10	8	5	15
<i>Coris sandageri</i>				4		
<i>Eupetrichthys angustipes</i>	15		9	6	55	111
<i>Halichoeres nebulosus</i>			5			
<i>Labroides dimidiatus</i>		1			6	
<i>Notolabrus gymnogenis</i>	197	85	98	64	90	91
<i>Ophthalmolepis lineolatus</i>	45	218	130	237	232	327
<i>Pictilabrus laticlavus</i>	69	24	9	1	23	30
<i>Pseudolabrus guentheri</i>		1	1	1	7	3
<i>Pseudolabrus luculentus</i>				1		1
<i>Stethojulis interrupta</i>		1	5			
<i>Thalassoma lunare</i>			9	3		1
<i>Labridae</i> sp. 1		1				
<i>Labridae</i> sp. 2				1		
<i>Labridae</i> sp. 3				1		
Odacidae						
<i>Odax acroptilus</i>	1					
<i>Odax cyanomelas</i>	137	73	4	2	4	6
Gobiesocidae						
<i>Heteroclinus whiteleggi</i>	5	5				
<i>Gobiesocidae</i> sp.	10					
Blennidae						
<i>Plagiotremus tapeinosoma</i>	1	2		1	2	2

Appendix 2 (continued):

	FRINGE		BARRENS		SPONGE GARDEN	
	Terrigal	Norah Head	Terrigal	Norah Head	Terrigal	Norah Head
Acanthuridae						
<i>Ctenochaetus binotatus</i>			1			
<i>Prionurus microlepidotus</i>						20
Zanclidae						
<i>Zanclus cornutus</i>				1		
Balistidae						
<i>Rhinecanthus rectangulus</i>	1	25				
<i>Sufflamen chrysopterus</i>	1	1				
Monacanthidae						
<i>Acanthaluteres vittiger</i>	1	2				
<i>Eubalichthys bucephalus</i>	4	3	19	16	47	59
<i>Meuschenia flavolineata</i>	6	11		1		13
<i>Meuschenia freycineti</i>	2	1	1	2	2	1
<i>Meuschenia scaber</i>				1		
<i>Meuschenia trachylepis</i>	1	2	2	4	1	23
<i>Sufflamen bursa</i>						1
Monacanthidae sp. 1					1	
Monacanthidae sp. 2					1	
Monacanthidae sp. 3	5					
Monacanthidae sp. 4	4	1			1	
Monacanthidae sp. 5		15				
Monacanthidae sp. 6				1		
Monacanthidae sp. 7		2				
Monacanthidae sp. 8	1					
Monacanthidae sp. 9		7				5
Monacanthidae sp. 10					5	
Aracanidae						
<i>Anoplocapros inermis</i>				1	2	
Tetraodontidae						
<i>Canthigaster callisterna</i>				3		
<i>Tetractenos hamiltoni</i>	1					
Diodontidae						
<i>Dicotylichthys punctulatus</i>	2			4	1	
Unknown Fishes						
Fish 1						1
Fish 2	7					
Fish 3						30
Fish 4					2	
Species Abundance	7840	15487	11567	23047	7804	10481
Wrasse Abundance	368	430	332	404	676	884
Total Species	53	47	58	60	57	58
Wrasse Species	5	10	11	13	10	11

Appendix 3: Descriptions and corresponding photographs of selected labrid behaviours.

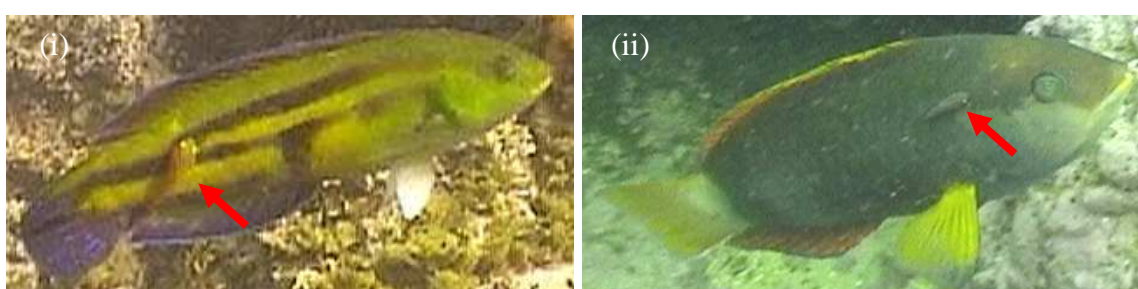
a) Lying:

Remaining motionless, or nearly motionless, resting on the abdomen or side. Lying behaviour is often accompanied by pectoral fin movements to maintain body position. Examples are of an IP *Notolabrus gymnogenis* (230 mm) resting on its abdomen (i) and a TP *N. gymnogenis* (310 mm) resting on its side (ii).



b) Cleaning by clingfishes (Gobiesocidae):

Clingfish (family Gobiesocidae) move over the head, fins and body of the focal individual removing parasites and dead tissue. Examples are of a TP *Pictilabrus laticlavius* (190 mm) being cleaned by *Cochleocephalus orientalis* (i) and a TP *Notolabrus gymnogenis* (320 mm) being cleaned by *Aspasmogaster costata* (ii).



Appendix 3 (continued):**c) Side-swiping:**

An individual swipes one side of its body, or head, on the surface of hard substrate (i.e. rock or steel structure), sandy sediment or algal fronds. The example is a side-swiping sequence of an IP *Ophthalmolepis lineolatus* (170 mm).

**d) Bending:**

Flexure of the body as a head twitch, 'C' body bend or 'S' body bend. The example is an IP *Ophthalmolepis lineolatus* (230 mm) performing a strong 'S' body bend.

**e) Gaping:**

Focal individual widely opens the mouth to display its prominent caniniform teeth. Gaping behaviour examples are of an IP *Notolabrus gymnogenis* (240 mm) (i) and TP *N. gymnogenis* (300 mm) (ii).

