

The final publication of this paper is available at www.publish.csiro.au/paper/MF10315.htm

Morton JK and Gladstone W (2011) Spatial, temporal and ontogenetic variation in the association of fishes (family Labridae) with rocky-reef habitats. *Marine and Freshwater Research* 62: 870-884. DOI: 1323-1650/11/070870

Spatial, temporal and ontogenetic variation in the association of fishes (family Labridae) with rocky reef habitats.

Authors

Jason K. Morton^{1,2*} and William Gladstone^{1,3}

Addresses

¹School of Environmental and Life Sciences, University of Newcastle (Ourimbah Campus), PO Box 127, Ourimbah NSW 2258, Australia

²Current address: School of Science and Mathematics, Avondale College, PO Box 19, Cooranbong NSW 2265, Australia

³Current address: School of the Environment, University of Technology, Sydney, PO Box 123, Broadway NSW 2007, Australia

*Corresponding author: School of Science and Mathematics, Avondale College, PO Box 19, Cooranbong NSW 2265, Australia; Email: Jason.Morton@avondale.edu.au; 0249 802 220 (wk), 0249 802 219 (fax)

Keywords: fish distribution, ontogeny, labrid, habitat partitioning

Running title: Association of wrasses with rocky reef habitats

Abstract

Habitat variability is an important factor structuring fish assemblages of rocky reefs in temperate Australia. Accepting the generality of this model requires that habitat-related variation is consistent through time, across multiple spatial scales, and applies to all life history stages. We used repeated underwater visual surveys at multiple spatial scales over a 22-month period to test whether three distinct rocky reef habitats had different wrasse assemblages and whether these assemblages were subject to spatial, temporal and ontogenetic variability. Overall, the strongest and most consistent habitat association was with sponge gardens, which had the most distinct assemblage, and the greatest species richness and density of individuals. Habitat associations in fringe and barrens were less consistent. A substantial increase in the abundance of small individuals coinciding with warmer sea temperatures contributed to temporal fluctuations in the density of wrasses. Overall, habitats were not strongly partitioned among larger individuals of the most abundant species, suggesting that adults are largely habitat generalists but small, recruiting individuals showed greater habitat specialisation. The present study emphasises the importance of incorporating spatial, temporal and ontogenetic variability into surveys of fish assemblages to understand more fully the dynamics of temperate rocky-reef systems.

Introduction

Habitat, defined using physical (e.g. substrate type, depth, wave exposure) and biological (e.g. algal type and cover) attributes, influences the spatial distribution of temperate rocky reef fish assemblages (Anderson and Millar 2004; García-Charton *et al.* 2004; Consoli *et al.* 2008). For example, in south-western Australia, Harman *et al.* (2003) found differences in the presence and abundance of fish species between limestone reefs which were highly fissured and granite reefs that consisted of large boulders and bedrock, with few crevices. Assemblages also differed between high- and low-relief limestone reefs and this pattern was attributed to differences in algal assemblages and structural complexity. In northern New Zealand, reefs dominated by high densities of laminarian and furoid algae support large numbers of small fishes and few large benthic-feeding fish species, whereas coralline reef flats dominated by echinoids support a different fish assemblage, with more large benthic-feeding species (Choat and Ayling 1987). Associations such as these are beneficial for marine conservation planning as habitat may be used as a surrogate for biodiversity for rapid and cost-effective selection of marine reserves (Ward *et al.* 1999).

Attempts to describe habitat-related patterns in the distribution and abundance of fish assemblages need to recognise variability in these patterns because fish assemblages exhibit significant spatial (Anderson and Millar 2004; García-Charton *et al.* 2004; La Mesa *et al.* 2011) and temporal (Letourner 1996; Thompson and Mapstone 2002; Malcolm *et al.* 2007) variability over various scales. Whilst many studies explore the interaction of these variables

on habitat associations among temperate fishes (e.g. Pihl and Wennhage 2002; Pérez-Matus *et al.* 2007), these are usually conducted for whole fish assemblages without sufficient resolution to determine the importance of habitat for particular species, families or functional groups.

The family Labridae (wrasses, labrids) is one of the most species-rich and abundant families in tropical (Bellwood *et al.* 2002; Floeter *et al.* 2007) and temperate fish assemblages (García-Charton and Pérez-Ruzafa 1999; Pihl and Wennhage 2002; Kleczkowski *et al.* 2008). In temperate systems, wrasses are almost exclusively associated with rocky reefs and/or algal habitats (Treasurer 1994; García-Rubies and Macpherson 1995; Pihl and Wennhage 2002) where they prey on a variety of benthic invertebrates including molluscs, echinoderms, crustaceans, polychaetes, sipunculans and ascidians (Shepherd and Clarkson 2001; Morton *et al.* 2008b; Platell *et al.* 2010). The foraging behaviour of wrasses, in association with their high abundance and diversity, makes it likely they play a significant role in reducing prey abundances, altering prey behaviour and modifying subtidal assemblages (Choat 1982; Rilov and Schiel 2006; Morton *et al.* 2008b).

An understanding of the distribution of wrasses is essential for determining the extent of this family's ecological importance in temperate reef systems, so the distribution of this family (Fulton *et al.* 2001; Denny 2005; Tuya *et al.* 2009), or single species within this family (Jones 1984b; Gillanders and Kingsford 1998; Kingsford and Carlson 2010), has been the focus of several studies. In many instances, wrasses have demonstrated strong associations with different rocky reef habitats. For example, 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). On the central coast of New South Wales, Australia, Curley *et al.* (2002) found highest abundances of *Austrolabrus maculatus*, *Eupetrichthys angustipes* and *Ophthalmolepis lineolatus* in sponge gardens, whereas *Pictilabrus laticlavius* were more abundant in *Ecklonia* forests than urchin-grazed barrens. These habitat associations are influenced, at least in part, by the benthic invertebrate assemblages represented within each habitat (Underwood *et al.* 1991). For example, the association of *P. laticlavius* with *Ecklonia* forests is likely to be in response to the abundance in algal habitats of amphipods and small molluscs (Jones 1999; Edgar 2001; Shepherd 2006), which collectively contribute over 60% to the dietary volume of this species (Morton *et al.* 2008b).

Habitat associations may also be influenced by the structure and availability of refuges. Refuge requirements of wrasses have not been well addressed; however, these fishes are known to shelter beneath algal canopies (Jones 1984a; Choat and Ayling 1987; Curley *et al.* 2002), in holes, crevices and caves within, beneath and between rocks (Sayer *et al.* 1993;

Gillanders and Kingsford 1998), and beneath soft sediments and coral fragments (Tribble 1982; Nanami and Nishihira 1999; Takayanagi *et al.* 2003). Refuges are important for providing places of retreat from predators, protection from wave surge, as areas for concentrated foraging activity, as nocturnal retreats and as nesting sites (Nanami and Nishihira 1999; Takayanagi *et al.* 2003; Russell *et al.* 2008). The association of wrasses with certain habitats may also be based on morphology, notably the relationship between pectoral fin morphology, swimming speed and their resulting tolerance to wave exposure (Bellwood *et al.* 2002; Wainwright *et al.* 2002; Floeter *et al.* 2007). In assessing the influence of pectoral fin morphology on temperate wrasse assemblages, Fulton and Bellwood (2004) found differences in fin shape and swimming speed corresponded to predicted patterns of distribution. In this study, low fin aspect ratios and slow relative swimming speeds in *A. maculatus*, *E. angustipes* and *P. laticlavius* are thought to have restricted these species to sheltered habitats with limited water movement.

Contributing to changes in habitat associations among wrasses are increases in species richness and the density of individuals that coincide with late summer and autumn in temperate systems (Sayer *et al.* 1993; Magill and Sayer 2002; Pihl and Wennhage 2002). These dynamics are due primarily to periodic recruitment of juveniles of tropical origin expanding their distribution in response to seasonally warm sea temperatures at higher latitudes and recruitment of temperate fish stocks after a dispersive planktonic larval stage, which may last up to 50 days (Caselle and Warner 1996; Masterson *et al.* 1997; Fontes *et al.* 2011). As juveniles, wrasses have reduced mouth size, gape and crushing strength of the pharyngeal jaws (Wainwright 1988; Helfman *et al.* 1997; Clifton and Motta 1998), so their diet is restricted principally to amphipods and small molluscs (Denny and Schiel 2001; Shepherd and Clarkson 2001; Morton *et al.* 2008b), which are abundant in shallow algal habitats (Jones 1999; Edgar 2001). Therefore, the association of recruits and juveniles with algal habitats, including those in temperate Australia (Gillanders and Kingsford 1998; Curley *et al.* 2002; Shepherd and Brook 2003) and New Zealand (Jones 1984a; Choat and Ayling 1987; Pérez-Matus and Shima 2010), is likely to be due to their preferred prey being more available in these habitats. Algal habitats may also provide an opportunity to forage in a habitat with reduced competition from larger wrasses and other benthic carnivores that are known to avoid feeding in algal cover (Choat and Ayling 1987). Reduced risk of predation is also likely to be offered to individuals that use refuges created by canopy forming algae.

Despite the likely ecological importance of wrasses in temperate rocky reef systems, there is still insufficient understanding of habitat-related patterns in their distribution and abundance, and spatial and temporal consistency of these patterns. Furthermore, despite differences in the habitat preferences of juveniles and adults of many species (Jones 1984a; Gillanders 1997b; Curley *et al.* 2002), many studies do not factor ontogenetic shifts in habitat use in their sampling design and, as such, the dynamics of wrasse associations with rocky reef habitats are not well described. The present study tested the hypothesis that distinct rocky reef

habitats are occupied by different wrasse assemblages and that these habitat associations vary temporally but not spatially. This study also investigated ontogenetic variation in the association of wrasses with rocky reef habitats by testing the hypothesis that there is a difference in the mean size of individuals among habitats and among sampling periods. It was predicted that the structure of wrasse assemblages would be distinct in each habitat as species exhibit differences in their resource requirements and locomotor abilities. It was also predicted that these associations would not experience large spatial variability; however, temporal and ontogenetic variability in the representation of wrasses was expected due to seasonal recruitment of small individuals of resident and tropical species, particularly into algal habitats.

Methods

Study location

The present study was undertaken on the Central Coast of New South Wales (NSW), Australia, between August 2003 and May 2005, at two locations separated by approx. 30 km, namely Terrigal (33°27' S, 151°27' E) and Bull Reef (33°17' S, 151°35' E) (Fig. 1a). Three clearly differentiated rocky-reef habitats occurred in each location: fringe, barrens and sponge gardens. Fringe (3-7 m depth) consisted of several patchy, non-dominant algal species, including various crustose, filamentous and turfing algae. Patches of the canopy-forming, laminarian algae *Ecklonia radiata* were scattered throughout the fringe habitat. Barrens (8-15 m) contained minimal algal coverage due to high densities of the herbivorous echinoid *Centrostephanus rodgersii*, which typically remove all but crustose coralline algae. Sponge gardens (15-22 m) consisted of distinct assemblages of erect and branched sessile fauna, including large sponges, gorgonians and bryozoans not found in shallower depths. Sponge garden habitat is termed 'deep reef' by Underwood *et al.* (1991). These habitats are more fully described by Underwood *et al.* (1991) and Andrew (1999).

Data collection

Wrasse assemblages were surveyed using a mixed-model hierarchical sampling design. Within each location, two sites separated by 250-800 m were sampled (Fig. 1b, c). Each of the three rocky-reef habitats were surveyed at each site. In each habitat, fish assemblages were recorded within each of six replicate transects located at least 10 m away from transitional zones between habitats. Surveys were conducted on 5 occasions, termed 'periods', separated by approx. 4 months, over 22 months.

Visual surveys of wrasse assemblages were completed by a single observer to ensure recording techniques were consistent, using SCUBA, between 1000 and 1600 h when visibility exceeded 8 m. Mobile non-cryptic species were surveyed in 5 x 25-m transects and

smaller cryptic species were surveyed in 1 x 25-m transects, with transects laid along a depth contour (Lincoln Smith 1988). Replicate transects within each site were separated by 10 m. Transects were laid whilst performing fish counts, termed the ‘simultaneous’ census technique (Fowler 1987), because many fishes would otherwise retreat from the presence of divers resulting in reduced richness and abundance estimates. Furthermore, inquisitive fish species, such as *Ophthalmolepis lineolatus*, are attracted to divers from beyond the transect boundary and may follow divers so overestimates of the abundance of these species and questions about the independence of transects arise when tape deployment and fish counts occur using the otherwise ‘sequential’ technique. All wrasses observed were counted and assigned to 50-mm total length (TL) size classes (e.g. 50-99, 100-149 mm etc.). Species were identified and distributions determined using Kuitert (1993, 1996).

Data analyses

The null hypotheses of no difference in wrasse species richness, total density of wrasses, and densities of the six most abundant wrasses (*Ophthalmolepis lineolatus*, *Notolabrus gymnogenis*, *Achoerodus viridis*, *Pictilabrus laticlavus*, *Austrolabrus maculatus*, *Eupetrichthys angustipes*) among habitats, locations, sites within locations and periods were each tested with a four-factor mixed-model analysis of variance (ANOVA). Habitat was analysed as an orthogonal factor with 3 levels (fringe, barrens, sponge) and period as an orthogonal factor with 5 levels (the 5 survey periods). Both habitat and period were treated as fixed factors as they were deliberately chosen to represent distinct habitat types and times of the year. Location was analysed as an orthogonal factor with 2 levels (Bull Reef, Terrigal) and site was analysed with 2 levels nested in each location. Locations and sites represented several potential survey areas so were treated as random factors. Analyses were performed with GMAV5 software (Institute of Marine Ecology, University of Sydney). Assumptions of homogeneity of variance were tested using Cochran’s C test and, when necessary, data were transformed when variances were heterogeneous (Underwood 1981). Significant main effects and interactions were examined using *post-hoc* Student-Newman-Keuls (SNK) multiple comparisons of means tests (Underwood 1981).

The null hypothesis of no differences in wrasse assemblages among habitats, locations, sites within locations and periods was tested by a four-factor permutational multivariate analysis of variance using PERMANOVA+ (Anderson *et al.* 2008) in PRIMERV6 (Clarke and Gorley 2006). Densities of cryptic wrasses were standardized to number per 125 m² and combined with the data for larger mobile species. PERMANOVA was performed on the Bray-Curtis similarity matrix after square-root transformation of raw data. Monte Carlo *P*-values were obtained from 999 permutations of residuals. Variation in wrasse assemblages was visualised using non-metric multidimensional scaling (nMDS) ordination plots. The similarity percentages (SIMPER) routine in PRIMERV6 was used to determine the species that typified

the wrasse assemblages of each habitat and those used to distinguish between habitats (Clarke 1993).

For each of the abundant species *O. lineolatus* (size range 50-399 mm), *N. gymnogenis* (50-399 mm), *A. viridis* (150-849 mm) and *P. laticlavus* (50-299 mm), a one-way ANOVA was used in SPSS 14.0 for Windows (2005) (SPSS Inc., Chicago, IL, USA) to test the null hypotheses of no differences in the mean size of individuals among habitats within each sampling period and no differences among sampling periods for each habitat. Size estimates at all sites were pooled to provide a mean size of individuals in each habitat across both locations. The assumptions of homogeneity of variance were tested using Levene's test. When necessary, data were transformed to stabilise variances (Underwood 1981); however, heterogeneity could not always be removed. In such cases, a more conservative critical value of $P < 0.01$ was adopted to reduce the chance of a Type I error (Underwood 1981) 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 SNK test (Underwood 1981). Differences in the mean size of individuals among habitats was not tested for *A. maculatus* and *E. angustipes* (both 50-199 mm) as these species were typically represented only in sponge gardens.

Results

Overall wrasse assemblage

Nineteen species and 3084 individuals of wrasses were recorded. The most abundant wrasses were *Ophthalmolepis lineolatus* (38% of all individuals), *Notolabrus gymnogenis* (20%), *Austrolabrus maculatus* (16%), *Achoerodus viridis* (10%), *Eupetrichthys angustipes* (6%) and *Pictilabrus laticlavus* (5%) (Table 1). These wrasses, in addition to *Coris picta* and *Pseudolabrus guentheri*, were recorded in all sampling periods. Seven species were endemic to the southern and/or eastern coastline of Australia, three had distributions extending from the south-eastern region of Australia to New Zealand, and six were distributed throughout the Indo-West Pacific.

Wrasse richness and density

The total number of wrasse species observed in fringe, barrens and sponge gardens was 5, 11 and 10 species at Terrigal and 10, 13 and 11 species at Bull Reef, respectively. The mean species richness of wrasses at each location ranged from 1.3 to 4.6 species per 125 m², and the mean density of wrasses ranged from 2.7 to 20.8 individuals per 125 m² (Fig. 2). Significant differences in species richness among habitats did not occur at each location but significant differences did occur in wrasse densities (Table 2) with *post hoc* tests revealing significantly higher densities in sponge gardens than fringe and barrens which themselves did

not differ. Differences in species richness and densities among habitats were not consistent across sites (Table 2). Species richness and densities differed among sampling periods (Table 2) with *post hoc* tests revealing both to be significantly higher in Dec 2003/Jan 2004, Apr/May 2004 and Apr/May 2005.

Multivariate analyses of wrasse assemblages

MDS ordinations showed assemblages in sponge gardens formed a discrete group at the bottom right of the plot in each sampling period (Fig. 3). Wrasse assemblages in fringe and barrens were broadly scattered across the plot and exhibited considerable overlap. Differences in wrasse assemblages among habitats were not consistent across locations and sites (Table 2) but *post hoc* tests revealed assemblages in sponge gardens remained significantly different to other habitats at both spatial scales, with sponge gardens having overall higher densities of *O. lineolatus*, *A. maculatus* and *E. angustipes* (Tables 1 and 3). *Post hoc* tests also revealed that significant differences in wrasse assemblages did not occur between fringe and barrens at either location but at each site these assemblages remained significantly distinct. Overall, the wrasse assemblages associated with fringe were distinguished from both barrens and sponge gardens by higher densities of *N. gymnogenis*, and from barrens by higher densities of *A. viridis* and *P. laticlavus* (Tables 1 and 3). Wrasse assemblages differed significantly among sampling periods with *post hoc* tests revealing Aug/Sept 2003 assemblages differing to Apr/May 2004 and Apr/May 2005, and the latter also differing to Dec 2003/Jan 2004.

Patterns in the abundance of selected labrids

Mean densities of *O. lineolatus*, *N. gymnogenis* and *A. viridis* in all habitats ranged between 0.3 and 15.5 individuals per 125 m² at each location in all sampling periods (Fig. 4a-c). Lower mean densities of *P. laticlavus* (0.0-2.4 individuals per 125 m²) and highly variable mean densities of *A. maculatus* and *E. angustipes* (0.0-54.5 and 0.0-20.5 individuals per 125 m², respectively) were observed (Fig. 4d-f). Differences among habitats in the densities of *O. lineolatus*, *N. gymnogenis*, *A. viridis* and *A. maculatus* were inconsistent with significant and complex interactions between the effect of habitat at different sites and locations, and in different sampling periods (Table 4). A significant difference among habitats in the density of *A. maculatus* occurred at each location (Table 4) with *post hoc* tests revealing significantly higher densities in sponge gardens compared to fringe and barrens where this species was often absent (Fig. 4e). Similarly, despite a significant three-way interaction between habitat, site and period (Table 4), *post hoc* tests revealed a significantly higher density of *A. maculatus* in sponge gardens at each site in most sampling periods. The effect of habitat on the density of *E. angustipes* varied between locations (Table 4); however, *post hoc* tests revealed significantly higher densities at both locations in sponge gardens compared to other habitats.

Size-related patterns for selected wrasses

O. lineolatus of sizes 100-349 mm, *N. gymnogenis* of sizes 150-249 mm and *A. viridis* of sizes 450-749 mm were recorded in all habitats in each sampling period and represented 85.5%, 33.9% and 77.4% of all individuals, respectively. Small individuals (i.e. <200 mm) of *O. lineolatus* were typically found at higher abundances in sponge gardens (56.7% of all individuals of this size) compared with barrens (24.3%) and fringe (19%), whilst the majority of small individuals (i.e. <250 mm) of *N. gymnogenis* and *A. viridis* were recorded in fringe habitat (61.1% and 92.9%, respectively). A peak in the number of individuals belonging to the smallest size class (i.e. 50-99 mm) and an associated reduction in the mean size of individuals occurred for *O. lineolatus* in sponge gardens and *N. gymnogenis* in all habitats in Apr/May 2004 and Apr/May 2005 (Fig. 5a-b). In both species, significant differences in the mean size of individuals occurred among habitats in all sampling periods and across sampling periods for each habitat (all $P < 0.01$). An increase in the number of small individuals (i.e. <250 mm) and a reduction in the mean size of individuals occurred for *A. viridis* in Apr/May 2004 (Fig. 5c), contributing to a significant difference in the mean size of individuals among habitats in this sampling period only ($P = 0.001$) and a significant difference across sampling periods in sponge gardens ($P = 0.003$).

Individuals of *P. laticlavus* of sizes 100-199 mm were observed most commonly in fringe and sponge gardens (i.e. 51.7 and 39.7% of all individuals, respectively) with the smallest size class (i.e. 50-99 mm) representing 51.9% of all individuals. A peak in the number of these smallest individuals and an associated reduction in the mean size of individuals occurred in the fringe and sponge gardens in Aug/Sept 2003 and in the fringe and barrens in Apr/May 2004 (Fig. 5d). Differences among habitats in the mean size of individuals occurred in these months and Sept/Dec 2004, and across sampling periods for each habitat (all $P < 0.05$). The smallest size class of *A. maculatus* and *E. angustipes* (i.e. 50-99 mm) represented 85.6% and 61.7% of all individuals, respectively. The majority of these individuals (i.e. >90%) were recorded in sponge gardens. A peak in the number of small *A. maculatus* individuals occurred in Apr/May 2004 and a relatively high representation of small *E. angustipes* individuals occurred in fringe in Dec 2003/Jan 2004.

Discussion

Wrasses of the central coast region of NSW

Wrasses were visually conspicuous on the rocky reefs of the central coast of NSW with 19 species recorded in the present study. This number is similar to the 24 species previously reported in the region by Gladstone (2007) and the 19 species reported by Malcolm *et al.* (2007), but is substantially lower than the 83 species reported by Hoese *et al.* (2007) and the 74 species reported by Parker (1999) in coastal waters of NSW. Contributing to the higher

representation of wrasse species in the two latter studies are the larger number of habitats sampled and their inclusion of coastal waters in northern NSW. The northern region of NSW lies in the east Australian warm temperate-subtropical overlap zone and is strongly influenced by the south-flowing East Australian Current, which maintains sea temperatures warm enough for a high number of tropical wrasse species to survive. Although tropical wrasses may contribute up to 57 species to wrasse assemblages in coastal waters of northern NSW (Parker 1999), these tropical vagrants contributed only six species and less than 1.5% to the total abundance of wrasses in the present study, and so are not considered numerically important in the study region.

Habitat associations among wrasse assemblages

Prior to this study, it was predicted that the structure of wrasse assemblages would be distinct in each habitat. Overall, wrasse assemblages in sponge gardens remained the most distinct of all habitats. Sponge gardens supported the greatest species richness and densities of individuals including higher densities of *Austrolabrus maculatus* and *Eupetrichthys angustipes* which, given their infrequent occurrences in other habitats, suggests these species are habitat specialists. As sponge gardens occur at greater depths, they are protected from the high wave energy experienced in fringe and barrens. Fulton and Bellwood (2004) found slow swimming speeds associated with the low fin aspect ratios of *A. maculatus* and *E. angustipes* is likely to restrict these species to sheltered habitats with limited water movement, and may have restricted these species largely to sponge gardens in the present study. Furthermore, these wrasses infrequently use shelter (J. Morton, personal observation), so they are susceptible to wave-induced displacement from shallower habitats.

Whilst depth may have an influence on the association of wrasses with different habitats, it is likely that other habitat characteristics also contribute to these associations (Anderson and Millar 2004). For example, cobbles and sediment are removed from fringe and barrens by high wave energy but these smaller substrates accumulate in deeper sponge gardens. Cobble regions and sand flats adjacent to sponge gardens may be used by *A. maculatus* and *E. angustipes* for foraging and/or for shelter and, thus, their distributions may be limited to sponge gardens due to ecological requirements rather than morphological constraints. The actual resources sponge gardens represent requires further examination; however, this habitat contains distinct assemblages of erect and branched sessile fauna, including sponges, gorgonians and bryozoans, which are not found in other habitats (Underwood *et al.* 1991; Andrew 1999); therefore, associated wrasses are likely to have a diet unique to those in other habitats. Future studies are required to determine the foraging behaviour, activity patterns and use of resources of these species as well as studies to determine the representation of invertebrate prey in the different habitats.

The association of wrasses with fringe and barrens were subject to the effect of spatial scale with differences occurring between habitats within each site but not at each location, suggesting that at the scale of hundreds of metres these habitats do not differ. Contributing to the similarity of habitats is the strong association that three of the four most abundant species (i.e. *Notolabrus gymnogenis*, *Ophthalmolepis lineolatus*, *Achoerodus viridis*) have with each habitat. These habitat generalists attain relatively large sizes and, having larger mouths and greater crushing power of their pharyngeal teeth (Wainwright 1988; Clifton and Motta 1998), are able to incorporate a broad range of hard-shelled prey into their diet (Gillanders 1995b; Morton *et al.* 2008b). Larger size also provides these species with improved locomotion abilities allowing movements over large reef areas and into various habitats, including those that are wave-affected on exposed coasts (Fulton and Bellwood 2004). For example, *N. gymnogenis* and *O. lineolatus* feed in various microhabitats (Morton *et al.* 2008b) within broad reef areas in excess of 600 m² and 2500m², respectively (Morton 2007; Kingsford and Carlson 2010). Similarly, *A. viridis* feed in various habitats (Gillanders 1995b) and range over large reef areas, which in the similar species *Achoerodus gouldii* may be up to 15000 m² (Shepherd and Brook 2005). Habitat associations are therefore less meaningful for these species at larger spatial scales.

Substantial spatial variability in fish assemblages is well documented (Fowler 1990, Meekan and Choat 1997; Floeter *et al.* 2001), 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 wrasses in the present study could be due to several factors, including the observability of individuals and spatial variation in food and refuge availability, recruitment and microhabitat representation. The identification and experimentation of these factors was beyond the scope of this study but observations of wrasse behaviour and investigations into the dietary composition of wrasses provides substantial insight into the probable observability of individuals and habitat components most important to these fishes. For example, many *N. gymnogenis* and *Pictilabrus laticlavius* may not have been observed due to their frequent use of shelter (Morton 2007). 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.

The higher overall abundances of *N. gymnogenis* and *A. viridis* in fringe and of *O. lineolatus* in sponge gardens suggests that these species exhibit habitat associations, although these associations were primarily due to high seasonal representation of 50-99 mm individuals. Habitats were not partitioned among larger individuals of these species. To allow larger individuals of these species to co-occur, inter-specific competition is likely to be minimised by using available resources differently. For example, larger individuals of *O. lineolatus* forage opportunistically in a variety of microhabitats over broad areas of reef while *N. gymnogenis* forage increasingly on decapods in bare hard-structure microhabitats within relatively small reef areas (Morton *et al.* 2008b). Reliance on similar prey among smaller

individuals is likely to result in considerable inter-specific competition were it not for the high abundance of their crustacean prey, and recruitment of wrasses at different times of the year (Morton *et al.* 2008a) and into different habitats. There was no evidence of smaller individuals occupying habitats exclusive to that of larger individuals, suggesting that highest levels of recruitment occur where favourable resources exist rather than onto areas of reef where adult densities are lowest. Intra-specific competition among these co-occurring individuals is minimised by size-related shifts in diet (Morton *et al.* 2008b) and behaviour (Morton 2007), which assist in the partitioning of rocky reef resources.

Temporal variation and recruitment in wrasse assemblages

Wrasse assemblages experienced significant temporal variation owing to higher wrasse richness and densities in the autumn months of April and May (mean sea temperature = 21-22°C: Manly Hydraulics Laboratory) and lower richness and densities in the late winter and early spring months of August to December (mean sea temperature = 18-19°C). This suggests that sea temperature is important in influencing the dynamics of wrasse assemblages in this study. For some temperate-zone wrasses, 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.

Prior to the present study, it was predicted that seasonal recruitment of juvenile wrasses of tropical origin would occur and this would contribute to temporal fluctuations in the representation of wrasses. Holbrook *et al.* (1994) have recognised *Thalassoma lunare*, *Halichoeres nebulosus* and *Stethojulis interrupta* as wrasses likely to recruit into the study region, with these fishes indeed contributing to wrasse assemblages in the present study. In addition, this study also found the tropical wrasses *Labroides dimidiatus* and *Anampses caeruleopunctatus* present only in periods of warmest sea temperatures. However, these wrasses were recorded infrequently and in very low densities, and therefore contributed little to the observed increase in overall species richness and the density of individuals in late summer and autumn.

Contributing most to temporal fluctuations in wrasse density was a substantial increase in the abundance of resident wrasses, particularly *O. lineolatus* and *N. gymnogenis*, of the size class 50-99 mm. These individuals, which belonged to the smallest size class of each species, have been tentatively 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 gardens. Relatively high recruitment of *N. gymnogenis* occurred into fringe habitat from September to May (i.e. spring to late autumn), with recruitment peaking in April and May. In these months, relatively high levels

of recruitment also occurred into barrens and sponge gardens. Similarly, all recruits of *A. viridis* of the size class 50-149 mm were observed in April and May and only in the fringe habitat. For *A. maculatus* and *E. angustipes*, an increase in the density of small individuals (50-99 mm) in sponge gardens also typically occurred in April and May. The recruitment of wrasses during the period of warmest annual sea temperatures experienced in late summer and autumn coincides with the settlement of large numbers of crustaceans, including amphipods and copepods, which are important prey items for juvenile wrasses (Shepherd and Clarkson 2001; Shepherd 2006; Morton *et al.* 2008b). In contrast to the other species, the densities of *P. laticlavus* recruits were not observed to peak seasonally into their recruiting fringe habitat.

Peaks in wrasse recruitment often occur soon after their known period of reproduction. For example, gonadosomatic indices of *A. viridis* peak in winter (Gillanders 1995a) and recruitment peaks in spring (Gillanders 1997b). Peak recruitment of *N. gymnogenis* is also likely to occur in spring if the planktonic larval stage for this species is of similar duration, given the gonadosomatic indices for this species also peaks in winter (Morton *et al.* 2008a); however, in the present study, recruitment for both species peaked in autumn. Asynchrony in the period of reproductive activity and the sighting of recruits may be due to the size, behaviour and habitat selection of recruits in the study region. For example, both *N. gymnogenis* and *A. viridis* recruited 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 larger and less reliant on algal canopies as frequent sightings of *N. gymnogenis* individuals of sizes 0-49 mm occur on sheltered reefs in early summer (J. Morton, unpublished data), suggesting that these individuals are recruiting earlier than was recorded in the present study. In the case of *A. viridis*, individuals may have exhibited post-settlement migrations from juvenile nurseries in other habitats (Gillanders 1997a), thus lengthening the time between reproduction and recruitment onto coastal rocky reefs.

Reproductive activity of *P. laticlavus* peaks in late spring/early summer (Barrett 1995; Morton *et al.* 2008a), yet this period did not always coincide with recruitment events. Periodic recruitment in *P. laticlavus* was less evident than in other wrasses owing to one of 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 (Morton *et al.* 2008a). Therefore, the 50-99-mm size class used to define 'recruits' in *O. lineolatus* and *N. gymnogenis* included mature fishes in *P. laticlavus* 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. laticlavus* are likely to be overlooked due to their relatively small size and cryptic behaviour (Morton 2007), which proves problematic for visual surveys.

The preferential use of shallow algal habitat by small individuals of *N. gymnogenis*, *A. viridis* and *P. laticlavus* has also been observed for wrasses from other rocky reefs in temperate Australia (Gillanders and Kingsford 1998; Curley *et al.* 2002; Shepherd and Brook 2003) and New Zealand (Jones 1984a; Choat and Ayling 1987). Algal habitat provides smaller individuals with opportunities to feed on amphipods and small molluscs (Denny and Schiel 2001; Shepherd and Clarkson 2001; Morton *et al.* 2008b), which are abundant in this habitat (Jones 1999; Edgar 2001). However, in these shallow habitats small wrasses are susceptible to the influence of wave surge on their swimming performance and their ability to undertake daily activities (Fulton and Bellwood 2004). It is likely, that overhead algal canopies offer sufficient protection to allow these individuals to occupy reef areas from which wave surge would otherwise displace them.

In contrast to other wrasses, highest gonadosomatic indices of *O. lineolatus* occur in late summer which precedes their observed peak in recruitment by little more than two months. Sightings of *O. lineolatus* recruits 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 (Morton 2007) and recruitment mostly into sponge gardens which is largely devoid of algal canopies. Like other wrasses, amphipods and small molluscs are similarly important for recruits and juveniles of *O. lineolatus* (Morton *et al.* 2008b), 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. laticlavus* (Morton 2007), making *O. lineolatus* individuals far more susceptible to displacement by wave surge in the relatively shallow fringe habitat. Furthermore, association of *O. lineolatus* with interfaces between rocky reef and sand flats, as occurs in sponge gardens in the study region, may be in response to a need for sandy habitat to bury within for nocturnal refuge (e.g. Breder 1951; Tribble 1982; Takayanagi *et al.* 2003).

In conclusion, this paper has shown that wrasses demonstrate rocky reef habitat associations, with several species strongly associated with sponge gardens. The frequent representation of other wrasses in this habitat suggests that sponge gardens are biodiverse areas that require special consideration in the conservation of rocky reef fishes (Gladstone 2007). Juveniles of several species were strongly associated with fringe suggesting a significant conservation value as a nursery habitat. Variation in habitat associations at different spatial scales and over time highlights the importance of incorporating spatial and temporal replication into studies that describe patterns of fish distribution, and size-related shifts in habitat associations emphasises the need for recognising ontogeny in such studies. As this study did not include large spatial scales, further studies are needed to determine latitudinal variation in the association of wrasses with each habitat as these may vary in response to differences in ocean climate, delivery of larval fishes and the level of fishing pressure (Tuya *et al.* 2008). Finally, this paper has emphasised the need for future studies on the resource needs and habitat use of

wrasse species to understand more fully the mechanisms driving habitat associations and their role in the ecology of temperate rocky reefs.

Acknowledgements

We thank all divers for assisting with fish surveys, in particular D. Powter, R. Ramos, B. Neuschulz, S. Mors, S. Lindfield, M. R. Shokri, V. Owen, M. Kennedy, S. Gray, G. Campbell, L. Greive, J. Alvarez and G. Courtney. Thanks also to I. Potter, S. Shepherd, A. Boulton, F. Tuya and an anonymous reviewer for their constructive comments on an earlier version of the manuscript. This research was supported by an Australian Postgraduate Award (APA) scholarship and additional funding provided by Avondale College and the University of Newcastle.

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Table 1. Wrasse species including the proportion of individuals recorded in each habitat and total abundances.

Sampling periods are those in which the species was observed (1=Aug/Sept 2003, 2=Dec 2003/Jan 2004; 3=Apr/May 2004, 4=Sept/Dec 2004, and 5=Apr/May 2005). Distributions are those reported in Kuitert (1993, 1996).

Species of wrasse	Proportion of individuals			Total	Sampling period/s	Distribution
	Fringe	Barrens	Sponge			
<i>Ophthalmolepis lineolatus</i>	0.22	0.31	0.47	1179	All	Southern Aust.
<i>Notolabrus gymnogenis</i>	0.46	0.25	0.29	625	All	Eastern Aust.
<i>Austrolabrus maculatus</i>	0.01	0.04	0.95	506	All	Southern Aust.
<i>Achoerodus viridis</i>	0.43	0.32	0.25	319	All	South-eastern Aust.
<i>Eupetrichthys angustipes</i>	0.08	0.08	0.84	196	All	Southern Aust.
<i>Pictilabrus laticlavus</i>	0.60	0.07	0.33	156	All	Southern Aust.
<i>Coris picta</i>	0.00	0.47	0.53	38	All	Eastern Aust. to NZ
<i>Pseudolabrus guentheri</i>	0.08	0.15	0.77	13	All	Eastern Aust.
<i>Thalassoma lunare</i>	0.00	0.92	0.08	13	2, 3, 4, 5	Indo-West Pacific
<i>Coris dorsomaculata</i>	0.00	0.00	1.00	11	4, 5	Indo-West Pacific
<i>Labroides dimidiatus</i>	0.14	0.00	0.86	7	2, 5	Indo-Pacific
<i>Stethojulis interrupta</i>	0.17	0.83	0.00	6	5	Indo-West Pacific
<i>Halichoeres nebulosus</i>	0.00	1.00	0.00	5	5	Indo-West Pacific
<i>Coris sandageri</i>	0.00	1.00	0.00	4	2, 3, 4	South-eastern Aust. to NZ
<i>Pseudolabrus luculentus</i>	0.00	0.50	0.50	2	1, 3	South-eastern Aust. to north-eastern NZ
<i>Anampses caeruleopunctatus</i>	1.00	0.00	0.00	1	2	Indo-Pacific
Unidentifiable 1	1.00	0.00	0.00	1	1	Unknown
Unidentifiable 2	0.00	1.00	0.00	1	2	Unknown
Unidentifiable 3	0.00	1.00	0.00	1	4	Unknown

Table 2. Summary of ANOVA and PERMANOVA results testing for differences in wrasse species richness, wrasse density and wrasse assemblages among habitats, locations, sites (within locations), and sampling periods.

¹data square-root (x+1) transformed, ²data square-root transformed. Significant results are in bold.

Source of variation	Wrasse species richness		Wrasse density ¹		Wrasse assemblages ²	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Habitat (H)	18.76	0.051	44.57	0.022	4.13	0.019
Location (L)	5.12	0.152	2.72	0.241	5.31	0.017
Site (Location) = S(L)	2.20	0.113	6.50	0.002	4.91	0.001
Period (P)	34.63	0.002	25.39	0.004	3.65	0.008
H x L	0.27	0.777	0.23	0.805	2.57	0.043
H x S(L)	9.85	<0.001	6.84	<0.001	2.58	0.001
H x P	2.84	0.080	2.46	0.112	1.36	0.212
L x P	0.23	0.914	0.48	0.753	0.63	0.849
S(L) x P	0.81	0.949	1.19	0.306	1.27	0.122
H x L x P	0.61	0.755	0.86	0.569	1.08	0.372
H x S(L) x P	1.44	0.120	1.39	0.146	1.27	0.056

Table 3. Species contributing most to typifying the wrasse assemblage within fringe, barrens and sponge gardens (shaded), and the species distinguishing between habitats (non-shaded) 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 gardens
Fringe	<i>Notolabrus gymnogenis</i> <i>Ophthalmolepis lineolatus</i> <i>Achoerodus viridis</i>		
Barrens	<i>Notolabrus gymnogenis</i> * <i>Achoerodus viridis</i> * <i>Pictilabrus laticlavus</i> * <i>Ophthalmolepis lineolatus</i>	<i>Ophthalmolepis lineolatus</i> <i>Notolabrus gymnogenis</i> <i>Achoerodus viridis</i>	
Sponge gardens	<i>Notolabrus gymnogenis</i> * <i>Austrolabrus maculatus</i> <i>Ophthalmolepis lineolatus</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>

Table 4. ANOVA results for the densities of six wrasse species.All data $\ln(x+1)$ transformed (Cochran's C test, $P>0.05$). Significant results are in bold.

Source of variation	<i>Ophthalmolepis lineolatus</i>		<i>Notolabrus gymnogenis</i>		<i>Achoerodus viridis</i>		<i>Pictilabrus laticlavus</i>		<i>Austrolabrus maculatus</i>		<i>Eupetrichthys angustipes</i>	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
	Habitat (H)	5.62	0.151	1.41	0.415	0.96	0.510	3.02	0.249	244.23	0.004	4.75
Location (L)	13.18	0.068	3.74	0.193	5.85	0.137	0.37	0.605	3.60	0.198	2.07	0.287
Site (Location) = S(L)	7.85	0.001	4.67	0.010	1.57	0.210	23.38	<0.001	0.80	0.448	2.46	0.087
Period (P)	6.86	0.044	8.30	0.032	11.06	0.020	15.23	0.011	8.77	0.029	1.91	0.273
H x L	5.48	0.071	0.80	0.509	1.63	0.303	0.45	0.669	1.14	0.405	59.06	0.001
H x S(L)	1.61	0.172	4.11	0.003	3.40	0.010	13.39	<0.001	0.47	0.755	0.16	0.959
H x P	0.66	0.717	0.68	0.703	0.61	0.752	2.77	0.086	22.85	<0.001	2.89	0.077
L x P	0.40	0.804	0.66	0.639	0.36	0.829	0.17	0.947	0.43	0.781	0.28	0.885
S(L) x P	1.55	0.140	1.10	0.363	1.12	0.349	2.30	0.021	2.20	0.023	1.32	0.232
H x L x P	1.32	0.300	0.85	0.575	3.97	0.009	0.50	0.839	0.18	0.990	0.67	0.713
H x S(L) x P	1.85	0.025	2.07	0.010	0.53	0.932	3.29	<0.001	1.85	0.024	1.40	0.139

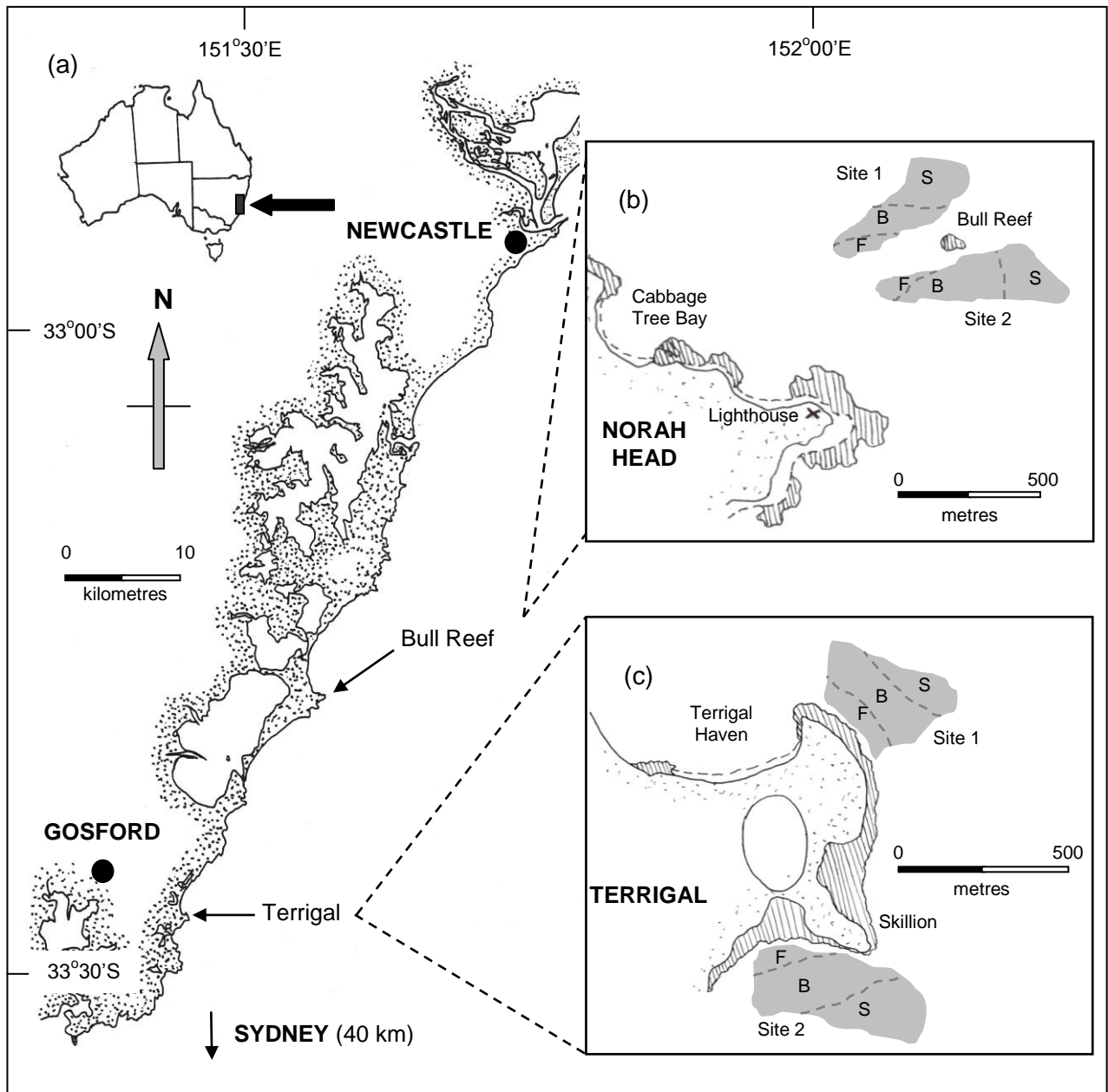


Fig. 1. Map of the central coast region of New South Wales (Australia) showing the two locations used for sampling wrasse assemblages (a). The position of the two sites within each location is indicated by grey shading on the expanded location maps of Bull Reef (b) and Terrigal (c). The general area used to sample subtidal fringe (F), barrens (B) and sponge gardens (S) is shown at each site. Exposed reef is shown in cross-hatched shading.

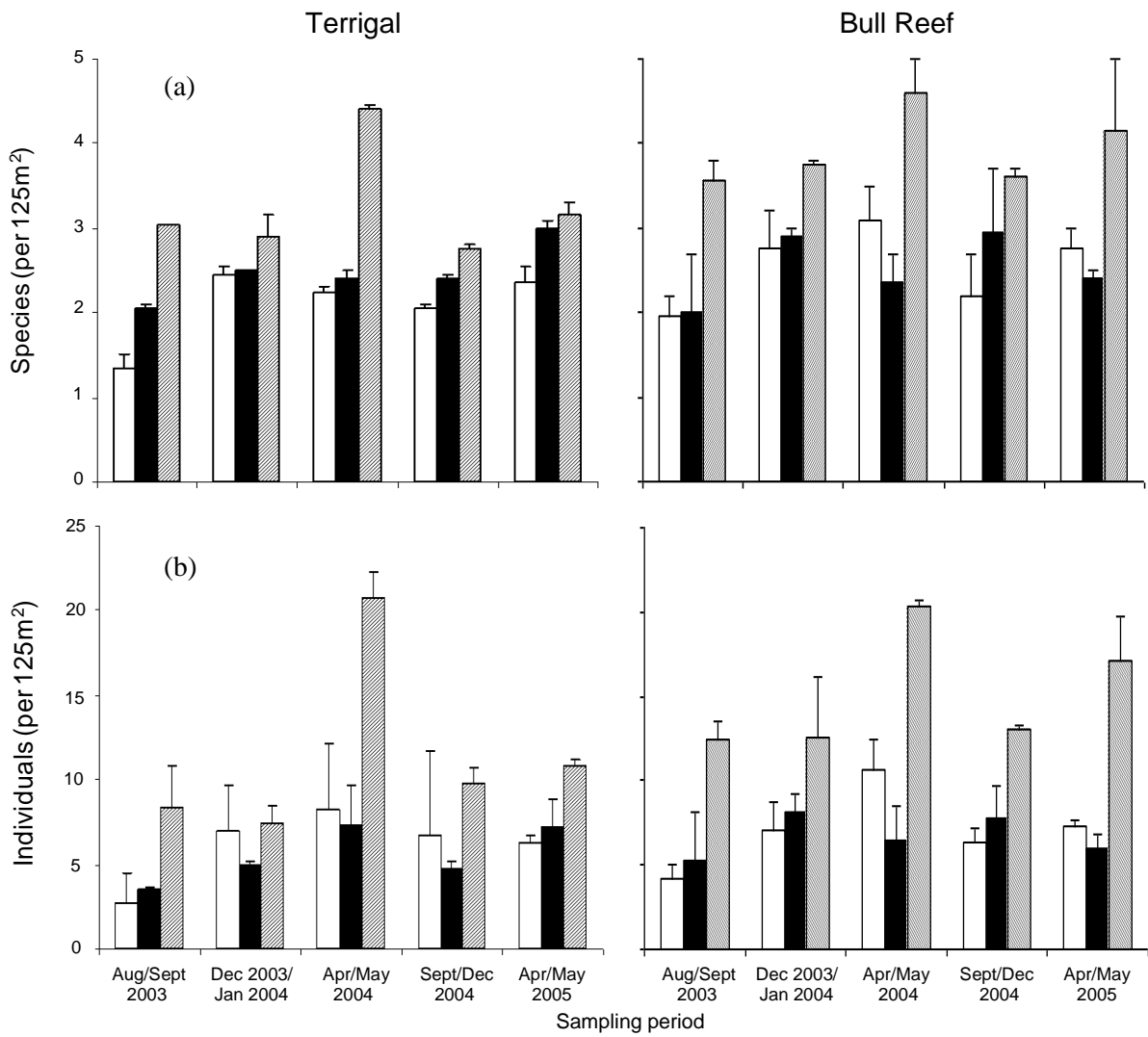


Fig. 2. Species richness (a) and density (b) of wrasses in fringe (□), barrens (■) and sponge gardens (▨) at Terrigal and Bull Reef in each combination of Habitat x Period (n=2 sites with each site representing the average across 6 transects). Values are mean and s.e.

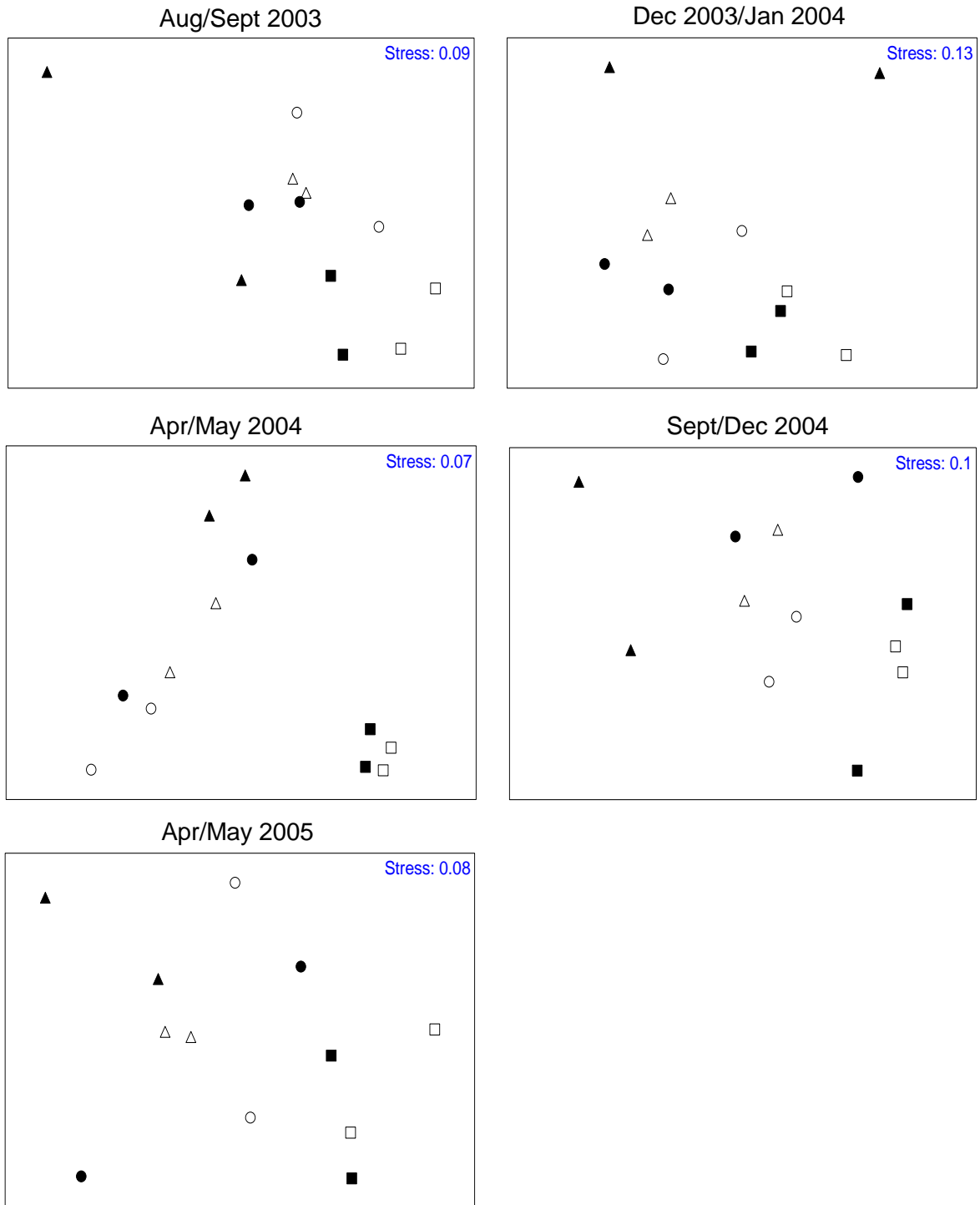


Fig. 3. Non-metric multidimensional scaling ordinations comparing wrasse assemblages across sites (within locations) and habitats over five sampling periods. Habitats are fringe (▲), barrens (●) and sponge gardens (■) at Terrigal (shaded) and Bull Reef (non-shaded) sites.

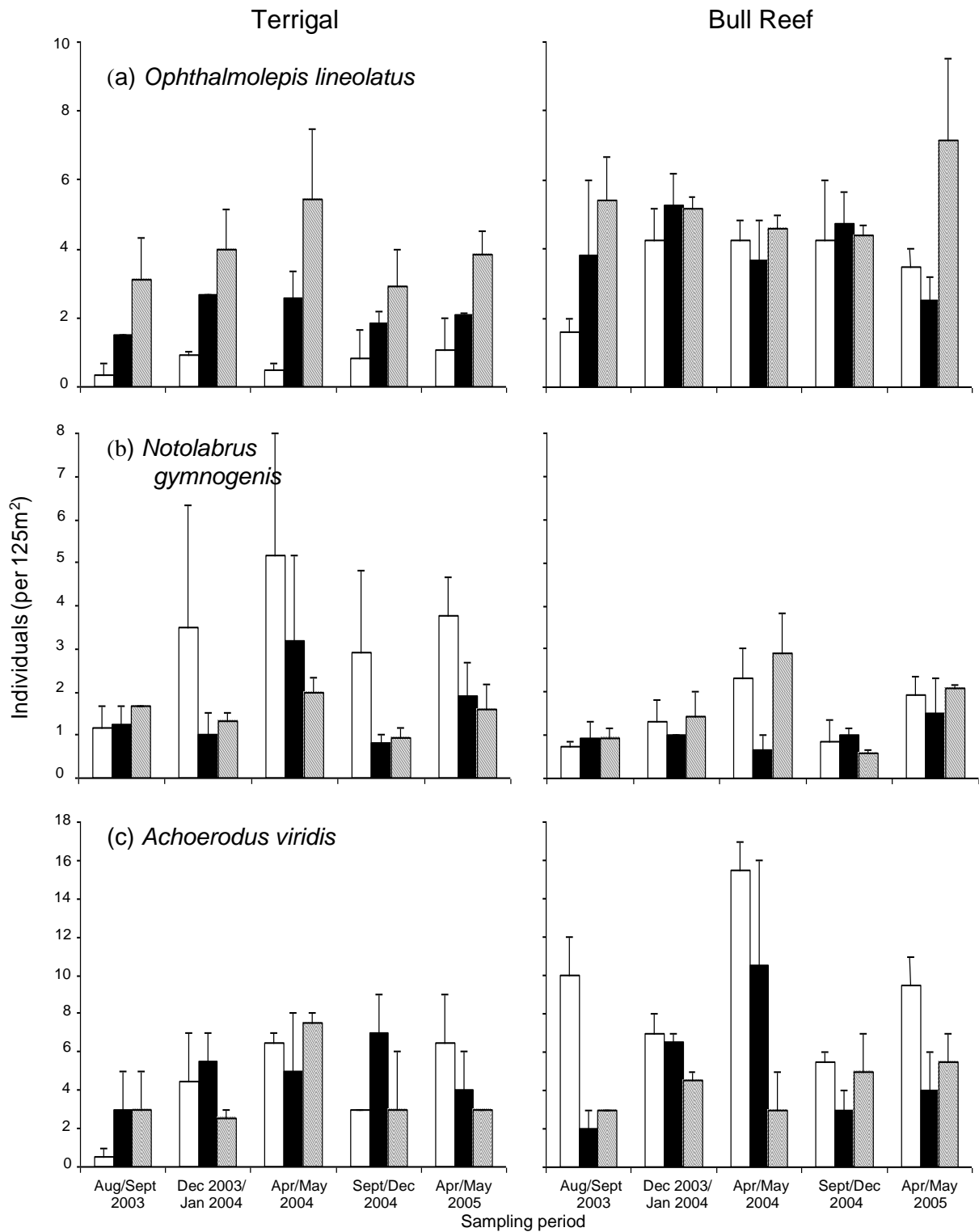


Fig. 4. Density of six wrasse species in fringe (□), barrens (■) and sponge gardens (▨) at Terrigal and Bull Reef in each combination of Habitat x Period (n=2 sites with each site representing the average across 6 transects). Values are mean and s.e.

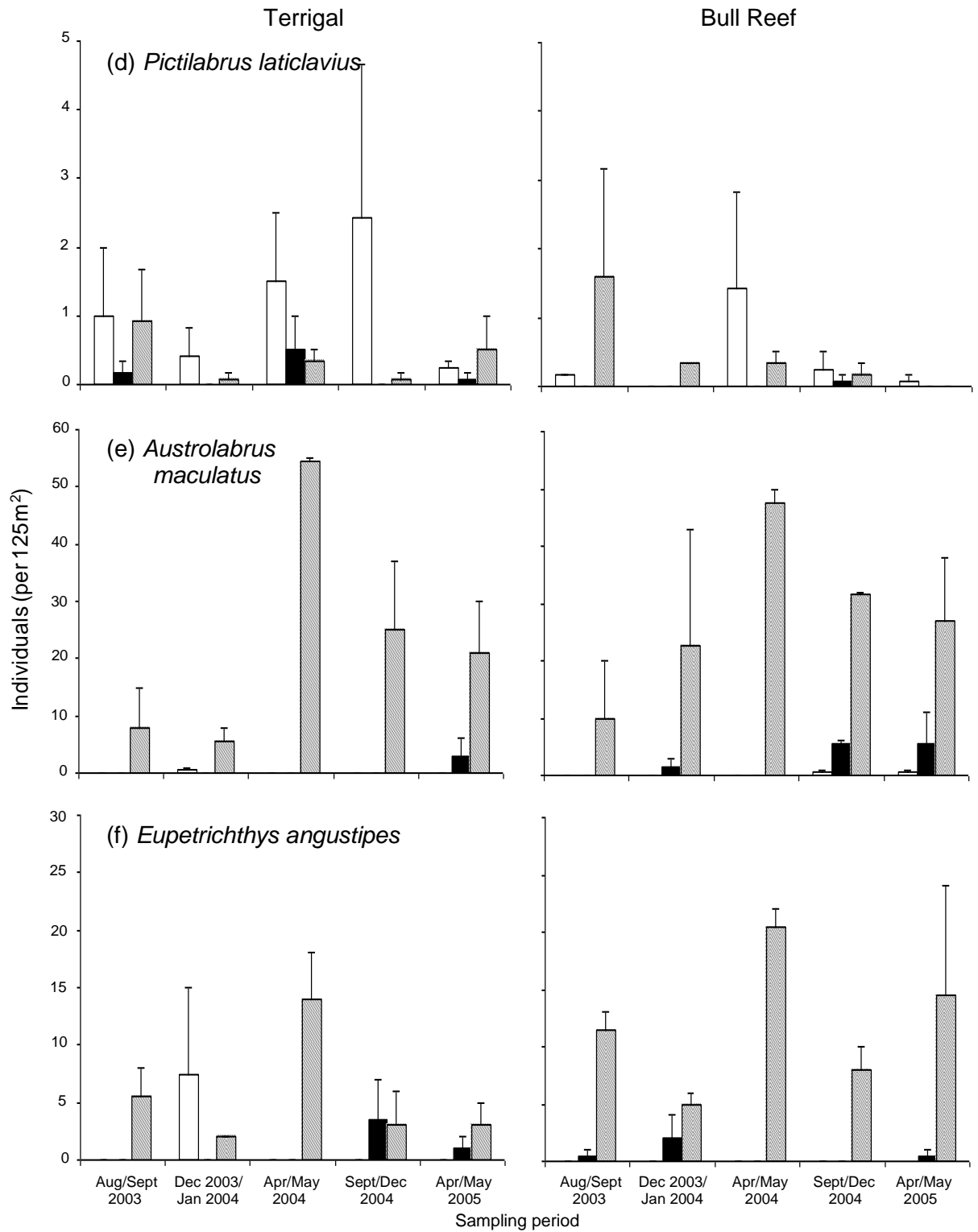


Figure 4 continued...

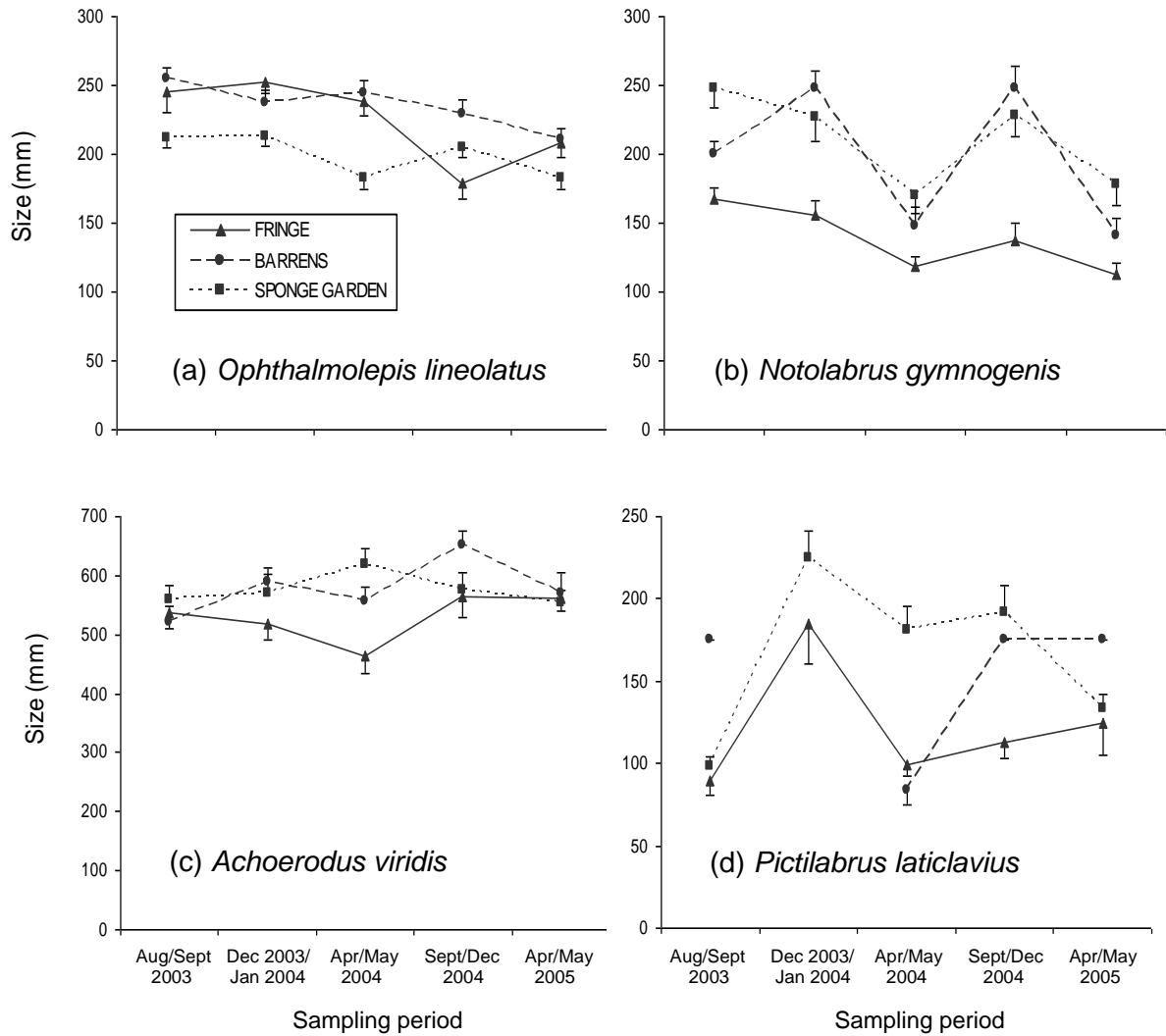


Fig. 5. Size of individuals of four wrasse species in fringe, barrens and sponge gardens in each sampling period (locations have been combined). Values are mean and s.e.