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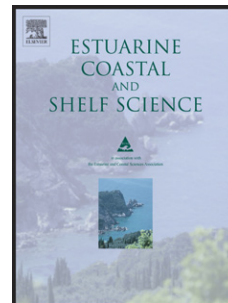
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# Accepted Manuscript

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Ben French, Margaret E. Platell, K. Robert Clarke, Ian C. Potter



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**Ranking of length-class, seasonal and regional effects on dietary compositions  
of the co-occurring *Pagrus auratus* (Sparidae) and  
*Pseudocaranx georgianus* (Carangidae)**

Ben French, Margaret E. Platell, K. Robert Clarke<sup>∞</sup>, Ian C. Potter\*

Centre for Fish and Fisheries Research  
Murdoch University, South Street, Murdoch,  
Western Australia, 6150

<sup>∞</sup> Plymouth Marine Laboratory, Prospect Place, West Hoe,  
Plymouth PL1 3DH, United Kingdom.

\*Corresponding author I.Potter@murdoch.edu.au

Tel: 61 (08) 9239 8801  
Fax: 61 (08) 9239 8808

**ABSTRACT.** Using an effective combination of multivariate testing and ordination analyses, this study compares the extents to which the diets of two co-occurring fish species (*Pagrus auratus* and *Pseudocaranx georgianus*) are related to body size (length class), season and region and the rank order importance of those effects. Thus, volumetric dietary compositions were determined for these species on the lower west coast of Australia, where both are abundant, and for *P. auratus* from the mid west coast and *P. georgianus* from the south coast. The diet of *P. auratus* on the lower west coast was strongly related to body size and slightly less to season. With increasing body size, its diet shifted from predominantly ophiuroids to larger prey, such as brachyuran crabs, teleosts, echinoids and ultimately asteroids, probably reflecting a shift from foraging over soft sediments to areas over and around reefs. Seasonal changes on the lower west coast were restricted mainly to small *P. auratus*, while larger fish underwent seasonal changes further north. Analyses using a common size range of medium to larger *P. auratus* demonstrated that dietary composition differed more between regions than seasons. The relationships between diet and length class of *P. georgianus* on both the lower west and south coasts were less pronounced than for *P. auratus* and seasonal changes were restricted to the south coast, where amphipod consumption increased markedly in summer. The diet of *P. georgianus* was related far more to region than length class and season, with more small teleosts, small crabs, carideans and littorinids and less amphipods, isopods and small bivalves being ingested on the lower west than south coasts. Although crabs and teleosts were important typifying prey of *P. auratus* and *P. georgianus*, when co-occurring, the former predator tended to ingest greater volumes of larger and often less mobile prey. This reflects differences in dentition, jaw morphology and feeding behaviour and reduces the potential for competition for food resources. The results imply that *P. auratus* and *P. georgianus* are opportunistic feeders and that the effects of length class, season and region on dietary composition and their rank orders can vary markedly between species and for length class and season between regions for the same species.

**Keywords:** Diet, body size, season, region, feeding mechanism, resource partitioning, Western Australia

## 1. Introduction

The successful co-occurrence of abundant fish species is regarded as depending, at least to some extent, on the partitioning of resources among those fish species and thus to a beneficial reduction in the potential for interspecific competition for those resources (Connell, 1980; Ross, 1986; Platell and Potter, 2001). Ross (1986) considered resources to be partitioned along three axes, i.e. habitat, food and time, of which food is the most important. The partitioning of food resources among fish species of similar size in the same habitat should not be taken, however, as implying that the prey species ingested by each of those species need to be completely discrete. Rather, it is far more likely to involve differences in the compositions of the prey (i.e. variations in the relative abundances of the prey) at a level which allows the effects of predation to be spread among those species (Platell et al., 2010; Lek et al., 2011). Furthermore, any comparison between the dietary compositions of co-occurring medium to large-sized fish species should take into account the fact that the food ingested by such species typically changes with body size (Werner and Gilliam, 1984; Platell et al., 1998, 2010; Cocheret de la Morinière et al., 2003; Sommerville et al., 2011) and generally with season and often with region/habitat (Packer et al., 1994; Platell et al., 1998, 2010; Mariani et al., 2002; Chuwen et al., 2007; Fanelli et al., 2011; Schückel et al., 2011). There have, however, been no attempts to quantify in rank order the effects of body size (length class), season and region on the dietary composition of any species.

The snapper *Pagrus auratus* (Bloch & Schneider, 1801) is an important commercial and/or recreational fish species in marine waters throughout the southern part of the Indo-Pacific region, occurring northwards to as far as 18°S in Australia (Paulin, 1990; McGlennon et al., 2000; Willis et al., 2003; Wakefield et al., 2011; Saunders et al., 2012a). The numbers of this and other iconic fish species on the lower west coast of Australia have declined so markedly through intense fishing, however, that strict regulations, including selected seasonal and area closures to fishing, have been introduced for those species (Wise et al., 2007; Fletcher and Santoro, 2008, 2010).

The silver trevally *Pseudocaranx georgianus* (Cuvier, 1833) is found throughout the coastal waters of southern Australia and around New Zealand (Smith-Vaniz and Jelks, 2006; Gomon et al., 2008). In many regions, this species, sometimes previously referred to as *Pseudocaranx dentex* (see Smith-Vaniz and Jelks, 2006), or its congeners make a substantial contribution to recreational and/or commercial fisheries (Ralston and Polovina, 1982; Rowling and Raines, 2000; Walker et al.,

2005; Sumner et al., 2008). The category listed by the Department of Fisheries, Western Australia as Trevally, which comprises predominantly *P. georgianus*, constitutes the third and fifth most abundant components in the catches of shore and boat-based recreational anglers on the lower west coast of Australia, respectively (Sumner et al., 2008). *Pseudocaranx georgianus* co-occurs with *P. auratus* over reefs and in immediately surrounding areas of sandy substrate along the lower west coast of Australia, where they are both abundant (Denny and Babcock, 2004; B. French, pers. observ.), recognising however, that the 0+ age class of particularly *P. auratus* are especially abundant over soft substrata as they are in South Australian waters (Saunders et al., 2012b).

An understanding of the role played by a fish species within an ecosystem and how prey might be partitioned between that and other potentially competing species requires sound volumetric or gravimetric data on the dietary compositions of those species to elucidate whether those compositions change with body size and time of year and, if so, how. In view of the ecological and fishery importance of *P. auratus* and *P. georgianus*, it is surprising that no such comprehensive data are available for either of these carnivorous species in marine waters, especially as this type of data has been recorded for a range of species in south-western Australia, including the iconic *Glaucosoma hebraicum*, *Epinephelides armatus* and *Bodianus frenchii* (Platell et al., 2010). From studies in a gulf and estuary in New Zealand, the diet of *P. auratus* in those waters, which did not include the larger individuals of this species, changes with increasing body size from smaller prey, such as small crustaceans, to larger prey, such as crabs and teleosts (Colman, 1972; Usmar, 2012). Any exploration of the dietary composition of *P. auratus* should bear in mind, however, that this species belongs to the Sparidae and that the dietary composition of at least some of the species within this family varies greatly among habitats, presumably reflecting the ability of such species to feed opportunistically on the main and most accessible prey in the environment (Sarre et al., 2000; Mariani et al., 2002; Tancioni et al., 2003; Chuwen et al., 2007; Platell et al., 2007). The limited dietary data for *Pseudocaranx* species demonstrate that these species feed extensively on small benthic invertebrates, zooplankton and, when larger, on small benthic-pelagic fish (Rainer and Unsworth, 1991; Platell et al., 1997; Sazima, 1998; Hindell et al., 2000; Bulman et al., 2001; Hindell, 2006).

The possession by sparids, such as *P. auratus*, of medium-sized strong canines and rounded molars and oral jaws capable of exerting a strong crushing force enable this species to capture and

masticate their prey (Stoner and Livingston, 1984; Wainwright and Richard, 1995; Hernandez and Motta, 1997; Gomon et al., 2008). In contrast, carangids, including those of *Pseudocaranx* species, have far weaker oral jaws and irregular rows of small teeth, and possess pharyngeal jaws (Grubich, 2003; Gomon et al., 2008). Furthermore, *Pseudocaranx* species can use ram feeding to obtain their prey (Sanderson et al., 1996; Sazima, 1998). The above differences would presumably be accompanied by marked differences in the composition of the prey of *P. auratus* and *P. georgianus*, even when these species co-occur.

Volumetric dietary compositions have been determined for a wide size range of both *P. auratus* and *P. georgianus* collected seasonally on the lower west coast of Australia, where they are both abundant and co-occur. Dietary data have also been collected for *P. auratus* from waters much further north and for *P. georgianus* from the western south coast of Australia where, respectively, those species are also both numerous. Employing contemporary multivariate statistical analyses, the resultant data were used to explore the relative extents to which the dietary composition of each species is related to body size (length class) and season, and whether the same trends are exhibited by such variables for each species in both of the regions in which it was sampled. They were also employed to confirm that the compositions of the diets of *P. auratus* and *P. georgianus* differ when these species co-occur and to test whether such interspecific differences are stronger than those related to length class and season and how they reflect interspecific differences in feeding morphology and behaviour. Finally, the results of the present and other relevant studies are discussed to ascertain whether *P. auratus* and *P. georgianus* are likely to be at least moderately opportunistic in their feeding behaviour and thus be able to adapt to any modifications in prey composition that might result from anthropogenic effects, including climate change.

## **2. Materials and methods**

### *2.1. Sampling localities and regimes*

*Pagrus auratus* and *Pseudocaranx georgianus* were collected from over soft substrata when small and from over and around reefs and in the immediately surrounding areas of soft substrate in marine waters on the lower west coast of Australia between ca 31°00'S and 32°30'S (Fig. 1). The former and latter species were also obtained respectively from over and immediately around reefs in

marine waters further north between ca 27°30'S and 28°15'S on the mid west coast and from between ca 34°30'S, 119°E and 34°S, 123°E on the south coast (Fig. 1). The reefs on the west coast comprise limestone outcrops that are encrusted with the macroalga *Ecklonia radiata* and surrounded by areas of sand, which are sometimes colonised by seagrass, consisting mainly of *Amphibolis antarctica*, *Amphibolis griffithii*, *Posidonia australis* and *Posidonia sinuosa*, whereas reefs on the south coast consist predominantly of granite boulders that are sparsely covered by macroalgae, represented by *Sargassum* spp (Kendrick, 1999; Sanderson et al., 2000; Wernberg et al., 2003; Tuya et al., 2009). The samples of both species on the lower west coast were collected monthly between January 2009 and February 2011, while those of *P. auratus* from the mid west coast were obtained at least seasonally during the same period and those of *P. georgianus* from the south coast at least bimonthly between July 2009 and February 2011.

The small individuals of both species, i.e. with a total length (TL) <200 mm, were sampled by otter trawling using a net with a cod end comprising a stretched mesh of 45 mm. The medium-sized (200-400 mm) and larger (>400 mm) individuals of *P. auratus* were caught mainly using fish traps (consisting of 50 mm square steel mesh) and rod and line fishing, respectively, whereas all *P. georgianus* >200 mm were caught using rod and line and spear fishing. The clupeid *Sardinops sagax* was used as bait for both fish traps and rod and line fishing, with the traps being set for 3h. Note that, because of legal fishing restrictions, *P. auratus* <400 mm TL, the minimum legal length (MLL) for retention, were unable to be obtained from the mid west coast.

## 2.2. Preparation of jaws and analyses of diets

After immersion in 100°C water for 15 min, the oral jaws of *P. auratus* and *P. georgianus* and the pharyngeal jaws of the latter species were removed from small and large individuals of both species, using a scalpel and fine tweezers. The jaws were prepared for examination by carefully removing the attached flesh with fine tweezers and brushes and then drying at 60°C for 6h.

Each fish was measured to the nearest 1 mm TL and its gut (stomach and intestine) dissected out and stored at -18°C. Each gut was subsequently defrosted and, when containing food, was placed in 100% ethanol for at least a week prior to further examination. The fullness of each gut was recorded, with values ranging from 1-10, i.e. 10 to 100% full. In the case of *P. auratus*, the fullness of the intestine, as well as of its stomach, was recorded because food was frequently found



only in the intestine. The fullness of just the stomach of *P. georgianus* was recorded, however, as the stomach always contained food when food was present in the gut.

The dietary items in the stomach and intestine of each *P. auratus*, and in the stomach of each *P. georgianus* in which there was food, were examined under a dissecting microscope and identified to the lowest taxonomic level possible, usually family or order, by employing one or more of the following taxonomic references; Shepherd and Thomas (1982ab), Hutchins and Swainston (1986), Coleman (1994), Lamprell and Healy (1998), Norman and Reid (2000), Wells and Bryce (2000), Jones and Morgan (2002), Wilson (2002), Poore (2004) and Edgar (2008). Cephalopods were identified to order using the descriptions of their beaks (Lu and Ickeringill, 2002). A combination of the morphology of the remnants of fish prey and of otoliths extracted from individual prey remnants enabled ca 6 and 60% of the fish prey of *P. auratus* and *P. georgianus*, respectively, to be identified to family. The far less successful identification rate with *P. auratus* is due to the majority of the gut contents used for the former species being located in the intestine and thus having undergone greater digestion than those of the latter species, which came exclusively from the stomach (see above). The use of otoliths to identify prey to the family level was undertaken employing the descriptions given by Rivaton and Bourett (1999) and Furlani et al. (2007) for the otoliths of different taxa and the substantial reference collection of otoliths for a range of fish species that was developed by E. Lek of Murdoch University in Western Australia.

*Sardinops sagax*, which was employed as bait, was distinguishable from the natural prey in the gut contents of the two species as its remnants could still clearly be seen to have been cut into pieces. Bait could thus readily be excluded from the dietary samples. As a preliminary analysis, using Analysis of Similarities (ANOSIM – Clarke, 1993), demonstrated that the dietary compositions of the stomachs and intestines of *P. auratus* were not significantly different ( $P > 5\%$ ), the data for the contents of those two gut regions were pooled when both contained food.

The percentage frequencies with which each dietary item was found in the stomachs and/or intestines of *P. auratus* and of the stomachs of *P. georgianus* (%F) were recorded. The percentage volumetric contribution of each dietary item to the total volume of the stomach and/or intestinal contents (%V) was estimated visually with the aid of a grid-marked Petri dish (Hynes, 1950; Hyslop, 1980). Unidentifiable material, which on average contributed <15% of the overall dietary volume, was excluded from analyses. Each of the 96 dietary items identified in the gut contents of

both species collectively was allocated to one of 33 broader taxonomic groups, subsequently referred to as dietary categories, the volumetric data for which were then used for multivariate analyses of the dietary compositions of the two species.

The mean percentage volumetric contributions of the various dietary categories to the diets of fish in each length class of both species, in each of the two regions in which they were sampled, were calculated and plotted as stacked bar graphs to examine visually the trends exhibited by the dietary compositions of each species as it increased with body size. Length class widths were set at 150 mm for *P. auratus* and 75 mm for *P. georgianus*, but with the smallest and largest individuals being grouped as <150 and >750 mm, respectively, for *P. auratus* and as <150 and >450 mm, respectively, for *P. georgianus*.

### 2.3. Multivariate analyses

The following general approach and specific procedures follow those described in detail by Lek et al. (2011). Individuals in each length class of *P. auratus* on the lower west and mid west coasts and of *P. georgianus* on the lower west and south coasts in each season were randomly sorted into groups of three to five, depending on the number of fish sampled. The percentage volumetric contributions of the different dietary categories in the guts of the resultant groups were then averaged and square root transformed prior to multivariate analyses.

The averaged and square root transformed volumetric dietary data were used to construct three Bray-Curtis similarity matrices, namely for each season and length class of (i) *P. auratus* on the lower west and mid west coasts, (ii) *P. georgianus* on the lower west and south coasts and (iii) both species on the lower west coast. These matrices were subjected to a series of a two-way and three-way crossed Permutational Analysis of Variance tests (PERMANOVA - Anderson et al., 2008) to assess, where appropriate, whether there were significant interactions in dietary compositions between length class, season, region and species, and, if so, to determine the extent of those interactions relative to that of each of the main effects. Note that the tests involving both length class and season for *P. auratus* on the mid west coast were not undertaken because individuals representing the two size classes of smallest fish could not be obtained (see earlier) and the possibility that there was a seasonal effect in this case is explored in the comparisons between the dietary compositions of *P. auratus* on the lower west and mid west coasts (see later). While only

the values for  $P$  and pseudo- $F$  in the PERMANOVA tests are given in the text, the full results of those tests are provided in the Appendix. Note that type III sums of squares were used in all but one of the PERMANOVA analyses because the designs were generally unbalanced only at the replicate level. The one exception involved the comparison between the dietary compositions of *P. georgianus* on the lower west and south coasts, where, because the design was structurally less balanced due to the absence of data for several of the length class x season combinations in both regions, type I sums of squares were employed, and terms entered into the model in a specific order.

Separate two-way crossed Analyses of Similarities (ANOSIM - Clarke and Green, 1988; Clarke and Gorley, 2006) were used to determine the relative importance of length class, season and/or region effects on the dietary compositions of *P. auratus* and *P. georgianus* for the same three similarity matrices as used in the PERMANOVA tests (see above). The ANOSIM average  $R$  value ( $\bar{R}$ ) was computed for one factor (e.g. length class) removing the effect of the other factor (e.g. season) or the combined effects of two other factors (e.g. region and season). The magnitude of ANOSIM  $R$ -statistics typically range from 1, when the compositions of all samples within each group are more similar to each other than to any of the samples from other groups, down to ca 0, when the average similarity among and within groups do not differ (Clarke and Green, 1988; Clarke and Warwick, 2001). The resultant  $\bar{R}$ -statistics for region, length class, season and species (as appropriate) provide a robust, dimensionless and well-understood measure of the relative extents to which dietary composition is related to each of those factors.

The results of the statistical tests were visualised, as in classic univariate analyses, by 'means plots' of the effects of factors in different combinations. For multivariate analyses these are best defined as a non-metric multi-dimensional scaling (MDS) ordination on the resemblance matrix which determines 'distances among centroids' in the high-dimensional resemblance space (Anderson et al., 2008), though typically, as in this case, such an MDS plot will differ only marginally from an MDS plot based on the averages of the transformed data matrix for the relevant factor combinations. Here, centroid plots are used to display the mean changes in dietary composition over: (i) length classes for all seasons, (ii) length classes separately for pairs of seasons, (iii) seasons for pairs of regions averaged over length classes, (iv) length classes for pairs of regions averaged over season, (v) length classes for pairs of species averaged over season and (vi) seasons averaged over length classes for pairs of species.

In the case of the length class factor, note that ANOSIM (or PERMANOVA) analyses both test the null hypothesis of equality of all length classes in their effect on dietary composition against the unordered alternative that differing length classes have different effects, whereas the interpretation of the MDS plots makes much use of the ordering of length classes, often displaying a trajectory of increasing length. A supplementary test therefore becomes relevant when considering length class effects. The RELATE procedure in PRIMER (Clarke et al., 1993; Clarke and Gorley, 2006) tests the same null hypothesis as ANOSIM, but against the ordered alternative that dietary composition changes in a serial way through the increasing length classes. It is therefore an appropriate test in this case and, based on the same numbers of replicates, will be more powerful than ANOSIM for that ordered alternative (Somerfield et al., 2002). In the current context, given the presence also of a seasonal factor, the relevant test will be to use the same 'distances among centroids' matrix as exploited in the MDS plots, to carry out a RELATE test of the seriation (Clarke et al., 1993) of mean dietary composition with length class, in effect averaging over the seasonal data separately for each combination of species and region. As with the corresponding MDS plots, these tests have few points, either five or six length classes, and thus will only detect significant serial changes for which the RELATE  $\rho$  statistic is close to its upper limit of 1, representing a full serial change in dietary composition. They are, nonetheless, useful tests in this context, because they are the direct, and more accurate, counterpart to the visual information represented (sometimes imperfectly) in the MDS plots. For example, they result in a more realistic test of the length class differences in the case of *P. georgianus* on the south coast, where the effects are clearly seen in the corresponding ordination plots but are difficult to demonstrate when the natural ordering of length classes is ignored.

When the dietary composition was significantly related to a specific factor, two-way Similarity Percentages analysis (SIMPER – Clarke, 1993; Clarke and Gorley, 2006) was used to determine the dietary categories which typified and distinguished between the compositions of the fish diets, removing the (combined) effect of the other factors. In the few cases when, due to low levels of replication, the typifying and/or distinguishing dietary categories for an a priori group could not be determined using two-way SIMPER analyses, a one-way SIMPER analysis was employed.

### 3. Results

#### 3.1. Jaws and dentition

The anterior part of the upper and lower jaws of *Pagrus auratus* each contain four pairs of prominent, pointed and re-curved canine teeth (Fig. 2a-d). Immediately inside these canines are numerous and very small teeth that grade into two rows of rounded and stout molariform teeth which run along the wide margins of both jaws.

The jaws of *Pseudocaranx georgianus* are far more slender than those of *P. auratus* and contain a single row of very small, pointed teeth that do not extend along the full length of the jaw margins (Fig. 2e-h). Unlike *P. auratus*, *P. georgianus* possesses pharyngeal jaws, which contain numerous small rounded teeth that are largest along the central longitudinal axis.

#### 3.2. Overall dietary compositions

A large proportion of the guts of *P. auratus* and *P. georgianus* contained no food (Table 1), with the percentage of empty guts ranging from ca 70% for large *P. auratus* (i.e. >400 mm TL) on the mid west coast to ca 40% for *P. georgianus* on the south coast. The mean fullness of the guts with food ranged from 3.2 for *P. georgianus* on the lower west coast to 4.0 for large *P. auratus* on the same coast (Table 1).

Echinoderms, teleosts, crustaceans and molluscs made the greatest overall contributions to the diet of *P. auratus* on the basis of both their frequency of occurrence in the gut contents and their volumetric contributions to those contents (Table 1). Thus, for example, the most important of these major taxa (echinoderms) was ingested by as many as 78% of individuals <400 mm and contributed as much as 59% to the gut contents of those individuals.

While ophiuroids (belonging entirely to the family Ophiuridae) and echinoids were the two major echinoderm classes in the gut contents of *P. auratus*, the former was ingested far more frequently and made a far greater contribution to those of smaller fish (<400 mm) from the lower west coast than to those of large fish from both this region and the mid west coast (Table 1). The decapod component of the diet of *P. auratus* was always overwhelmingly dominated by crabs, which represented a number of different families, such as the Portunidae and the Majidae.

With the two most important dietary groups of molluscs consumed by *P. auratus* on the lower west coast, gastropods tended to be ingested slightly more frequently and in greater volumes

by larger fish (i.e. >400 mm), whereas the reverse was the case with bivalves (Table 1). While polyplacophorans and cephalopods made a small but appreciable contribution to the diets of larger *P. auratus* from the lower west coast, these two groups were either absent or present in only small volumes in the gut contents of both small *P. auratus* from the lower west coast and larger individuals from the mid west coast (Table 1).

In terms of both their frequency of ingestion and volumetric contribution to the guts, the most important contributors to the diets of *P. georgianus* on the lower west and south coasts were crustaceans, molluscs and then teleosts (Table 1). Among crustaceans, amphipods made a far greater volumetric contribution to the diets of fish on the south coast (28.1%) than lower west coast (6.7%), a trend paralleled by those for isopods and cumaceans. In contrast, the other main crustaceans in the diets of *P. georgianus*, i.e. carideans and crabs, contributed more to the dietary volume of fish on the lower west than south coasts, a trend followed, to varying degrees, by the main groups of mollusc (gastropods, bivalves and cephalopods) and echinoderms (echinoids) (Table 1).

### 3.3. Relationships between diets and body size

On the mid west coast, where smaller *P. auratus* could not be obtained, echinoids and teleosts were by far the most important contributors to the diets of this species and collectively contributed far more to those diets than to those of the corresponding size range of fish on the lower west coast (Fig. 3a). On the lower west coast, an increase in the body size of *P. auratus* was accompanied by a dramatic decline in the dietary contribution made by ophiuroids, from as high as ca 63% in the smallest fish, and an increase in that of teleosts, with asteroids becoming ingested by the larger individuals and contributing as much as 25% to the diets of the largest *P. auratus* (Fig. 3b). The dietary contributions of echinoids and gastropods tended initially to increase with body size and then decline in the larger individuals (Fig. 3b).

With *P. georgianus* from the lower west coast, the volumetric dietary contribution of teleosts and, to a lesser extent that of crabs, rose with increasing body size, whereas the reverse trend was exhibited by carideans (Fig. 3c). Cumaceans, isopods and bivalves were ingested by the smaller *P. georgianus* on this coast. On the south coast, amphipods were present in relatively greater volumes in the stomach contents of all length classes of *P. georgianus* than in those from the

lower west coast (Fig. 3c). As this species increased in body size on the south coast, the volumetric contributions of amphipods to the diet declined from their maxima of ca 25% in fish with lengths <300 mm to far lower levels in the largest fish (Fig. 3d). The dietary contributions of isopods also decreased with body size, while that of crabs increased and that of teleosts showed no conspicuous size-related trend. On the south coast, cumaceans were ingested only by those *P. georgianus* with lengths <300 mm (Fig. 3d).

#### 3.4. Analyses of dietary compositions of *Pagrus auratus* on the lower west and mid west coasts

PERMANOVA showed that, in relating dietary composition of *P. auratus* on the lower west coast to length class and season, there were significant main effects (pseudo- $F=3.3$  and  $3.7$  respectively, both  $P<0.01\%$ ) and a significant interaction between these two factors (pseudo- $F=2.2$ ,  $P=0.04\%$ ) (Appendix). Two-way crossed ANOSIM also showed that the dietary composition of *P. auratus* on this coast was significantly related to length class and season (both  $P=0.01\%$ ), with the global  $\bar{R}$  of  $0.63$  for length class (removing the effect of season) being greater than the global  $\bar{R}$  of  $0.55$  for season (removing the effect of length class). The interaction in PERMANOVA indicates, however, that these average values conceal some significant variations. Thus, one-way ANOSIM global  $R$  values for differences between seasons, computed separately for each length class, were significant for the first two length classes ( $R=0.85$  and  $0.65$ , both  $P<5\%$ ), but not for the other length classes ( $R=-0.05$  to  $0.15$ , all  $P>5\%$ ), thus accounting for the weighted average of  $0.55$  for the 2-way test.

On the ordination plot shown in Fig. 4a, most of the points representing the dietary samples for the length classes of *P. auratus* on the lower west coast in autumn and winter form a group in the centre of the plot, whereas those for spring and summer are more widely dispersed and located predominantly in the upper third of the plot. Because the trends exhibited by sequential length classes in each season cannot be readily visualised on Fig. 4a and the stress was relatively high, the data for autumn and winter and for spring and summer were plotted separately (Figs 4b,c). The points for the dietary samples of the sequential size classes represented in autumn and winter can then be seen to progress essentially from top to bottom on the ordination plot, but not in precisely the same manner (Fig. 4b). In contrast, the points for spring and summer each form more of a semi-circular pattern (Fig. 4c). This difference in the trends exhibited by sequential length classes in



particularly autumn and winter vs spring and summer helps explain the interaction between length class and season, though the primary effect here is clearly the progressive trend in dietary composition across sequential length classes and, secondarily, the different average compositions of the diets between autumn/winter and spring/summer.

The results of SIMPER emphasise that the typifying and distinguishing prey of the diets of sequential length classes of *P. auratus* on the lower west coast progressed from ophiuroids and small crabs to teleosts and larger crabs, with asteroids becoming prevalent in the diet of the largest individuals (Table 2). While ophiuroids were an important typifying prey category of *P. auratus* on the lower west coast in each season, they were consumed in greater volumes in summer and autumn than in winter and spring (Table 3). The diets in summer were distinguished from those in autumn and spring by consistently greater volumes of crabs, while consistently greater volumes of the echinoid *Echinocardium cordatum* distinguished the diet in spring from that in each of the other seasons and the volumetric contributions of teleosts to the diets in autumn and winter were consistently greater than those in spring and summer (Table 3).

In comparisons between the dietary compositions of *P. auratus* on the lower west and mid west coasts, which were involved the three length classes that were represented in samples from both regions (see earlier), there were significant interactions between season and both length class (pseudo- $F=2.0$ ,  $P=0.4\%$ ) and region (pseudo- $F=2.6$ ,  $P=0.5\%$ ), but not between length class and region (pseudo- $F=1.1$ ,  $P=38.7\%$ ), and neither was the 3-way interaction significant (pseudo- $F=0.6$ ,  $P=66.8\%$ ) (Appendix). The main effect of length class was not significant. A two-way crossed ANOSIM test, employing season vs region (with length being ignored as the size range of fish was incomplete; see earlier) demonstrated that the dietary composition of *P. auratus* changed with season ( $\bar{R}=0.50$ ,  $P=0.1\%$ ) and region ( $\bar{R}=0.30$ ,  $P=0.4\%$ ). The PERMANOVA interaction suggests that the average  $R$  of 0.50 for season may conceal some variability in the seasonal effects for the two regions, which is consistent with the fact that 1-way ANOSIMs carried out separately for each region yielded  $R$  values for the seasonal effect of 0.57 ( $P=0.1\%$ ) for the mid west coast and 0.39 ( $P=1.4\%$ ) for the lower west coast.

One-way SIMPER analysis showed that the diets of *P. auratus* on the mid west coast were typified by the consistent presence of substantial volumes of teleosts and other echinoids in autumn, winter and spring and of crabs in the latter two seasons. The diets during autumn were distinguished



from those in winter and spring by consistently greater contributions of *E. cordatum* and consistently lower contributions of other echinoids and crabs, whereas those in winter were distinguished from those in spring by a greater consumption of teleosts and crabs and smaller contributions by other echinoids and amphipods.

On the nMDS ordination plot shown in Fig. 5a, the dietary samples for *P. auratus* in each season on the lower west coast lie to the left of those for each season on the mid west coast. The points for the dietary samples arguably follow a better defined cyclic progression for fish on the lower west than mid west coasts, but primarily the change is of a smaller scale and in a different direction, which accounts for the season x region interaction. Turning to the nMDS ordination employing the three length classes in each of the four seasons (Fig. 5b), the dominant feature is the much smaller change in diet over the length classes in autumn and winter than in summer and spring, which explains the interaction seen between season and length class in the PERMANOVA analysis.

The Teleostei was the most important typifying dietary category for *P. auratus* on both the mid west and lower west coasts. The diets of *P. auratus* from the mid west coast were distinguished from those on the lower west coast by consistently greater contributions of *E. cordatum* and other echinoids and a more reduced range of prey, whereas the reverse trend applied to asteroids, trochids and ophiuroids.

### 3.5. Analyses of dietary compositions of *Pseudocaranx georgianus* on the lower west and south coasts

PERMANOVA showed that, in the case of the dietary compositions of *P. georgianus* on the lower west coast, there was no significant interaction between length class and season (pseudo- $F=1.2$ ,  $P=12.1\%$ ) (Appendix). Two-way crossed ANOSIM showed that the dietary composition of *P. georgianus* on this coast was significantly related to length class ( $\bar{R}=0.20$ ,  $P=1.7\%$ ) but not season ( $\bar{R}=0.05$ ,  $P=23.9\%$ ). SIMPER emphasised that the size-related change in diet reflected a sequential progressive shift from the ingestion of substantial volumes of bivalves to crabs and littorinid gastropods and also teleosts by the larger fish (Table 4).

There was also little evidence of an interaction between length class and season with the dietary composition of *P. georgianus* on the south coast (pseudo- $F=1.6$ ,  $P=6.2\%$ ) (Appendix).

Here, however, two-way crossed ANOSIM demonstrated that dietary composition was related to season ( $\bar{R}=0.49$ ,  $P=0.2\%$ ) but not length class ( $\bar{R}=0.13$ ,  $P=14.1\%$ ). Nonetheless, pulling together the length class information from the two regions, the nMDS ordination (Fig. 6) shows an essentially similar picture for the dietary samples of sequential length classes of *P. georgianus*, with both progressing from left to right across the plot, but with the pattern being weaker for the south coast region (non-significant in the ANOSIM test though marginally significant at the  $P=3.5\%$  level for the RELATE seriation test corresponding to the MDS ordination plot in Fig. 6). Amphipods were one of the two most important typifying dietary categories ingested by *P. georgianus* in summer, autumn and winter on the south coast. Consistently greater volumes of bivalves characterised the diets in spring from those in all other seasons and the same was true for amphipods in summer vs all other seasons and for teleosts in winter vs summer, autumn and spring on that coast.

In comparisons that employed the dietary data for *P. georgianus* from both the lower west and south coasts, there were significant interactions between length class and both region and season, though weak in the latter case (pseudo- $F=2.1$ ,  $P=0.4\%$  and pseudo- $F=1.4$ ,  $P=2.9\%$ , respectively) (Appendix). Two-way crossed ANOSIMs showed that the dietary composition of *P. georgianus* was most strongly related to region ( $\bar{R}=0.43$ ,  $P=0.1\%$ ), with much weaker relationships to length class ( $\bar{R}=0.18$ ,  $P=1.1\%$ ) and season ( $\bar{R}=0.16$ ,  $P=0.5\%$ ).

Although the points for the dietary samples of sequential length classes of *P. georgianus* from both regions progressed from left to right on the ordination plot shown in Fig. 6, the lines connecting the sequential points for the two regions transect and tend to pass downwards on the lower west coast and upwards on the south coast, thereby accounting for the stronger of the two interactions, i.e. that between length class and region.

As the multiplicity of points on Fig. 7a made it difficult to identify the trends exhibited by the various length classes in the four seasons, the data for autumn and winter were analysed and plotted separately from those for spring and summer (Figs 7b,c), thereby substantially reducing the stress to lower levels in both representations. While the points for the dietary samples for sequential length classes from autumn and winter progress together across the ordination plot shown in Fig. 7b, those from spring and summer (Fig. 7c) tend to work in opposite directions, reflecting the weak interaction between length class and season.

While crabs and amphipods were important typifying dietary categories for *P. georgianus* on both coasts, relatively greater volumes of crabs (and also of teleosts) were particularly important in distinguishing the diets of fish from the lower west and south coasts, and the reverse was true for amphipods.

### 3.6. Comparisons between the diets of *Pagrus auratus* and *Pseudocaranx georgianus* on the lower west coast

In the case of comparisons based on the dietary data for co-occurring *P. auratus* and *P. georgianus* on the lower west coast, PERMANOVA showed that each two way interaction and the three way interaction involving all three factors, i.e. length class, species and season, were significant, though that 3-way interaction was weak (pseudo- $F=1.5$ ,  $P=3.7\%$ ); other terms were significant at least at the 0.5% level, with the species effect having easily the largest pseudo- $F$  value, i.e. 6.6 ( $P<0.01\%$ ) (Appendix). Two-way crossed ANOSIM, employing, in turn, the dietary data for each of the above effects vs the other two combined, yielded global  $\bar{R}$  values of 0.51 for species, 0.35 for length class and 0.19 for season (all significant at least at the  $P<0.2\%$  level).

The lines connecting the dietary samples for sequential length classes of *P. auratus* and *P. georgianus* on the ordination plot shown in Fig. 8a both progress essentially from left to right and do not transect each other, illustrating the large difference in the dietary compositions of those two species. However, the two sets of lines do not follow precisely the same parallel trends, which account for the interaction between length class and species (pseudo- $F=2.2$ ,  $P=0.02\%$ ) (Appendix). The RELATE procedure, computed from the distances among centroids matrix underlying the ordination plots in Figs 6 and 8a, showed that the dietary composition is significantly related, in a serial manner, to length class in the case of both *P. auratus* ( $\rho=0.79$ ,  $P=0.3\%$ ) and *P. georgianus* ( $\rho=0.75$ ,  $P=0.8\%$ ) on the lower west coast. The corresponding seriation test to the ordination for *P. georgianus* on the south coast (Fig. 6) gave a similar  $\rho$  value of 0.76 ( $P=3.5\%$ ).

The large interspecific differences, seen with length class on Fig. 8a, are also apparent in the MDS ordination plot showing the seasonal patterns exhibited by the dietary compositions of the two species (Fig. 8b). However, they progress in somewhat different directions and on clearly different scales of change, illustrating the significant interaction between species and season (pseudo- $F=2.6$ ,  $P=0.02\%$ ) (Appendix).

Consistently large contributions by crabs and teleosts were very important in typifying the diets of both *P. auratus* and *P. georgianus* on the lower west coast of Australia. The diets of *P. auratus* were distinguished, however, from those of *P. georgianus*, by consistently greater contributions of ophiuroids (particularly by smaller individuals, see also Table 1), asteroids and *E. cordatum*, and consistently lower contributions of littorinids, other echinoids, amphipods and carideans.

#### 4. Discussion

##### 4.1. Influence of body size and season on the dietary composition of *Pagrus auratus*

The  $\bar{F}$ -statistic values in a two-way crossed ANOSIM test, using data for the wide size range of *P. auratus* collected from the lower west coast of Australia, demonstrate that the dietary composition of this sparid was strongly related to both body size (length class) and season in this region, with the former factor having a slightly greater influence. These size-related changes were largely driven by a very pronounced and progressive shift in the size and type of prey from small ophiuroid echinoderms (brittle stars) by the smallest individuals to substantial consumptions of brachyuran crabs, teleosts and echinoid echinoderms (sea urchins) and ultimately also asteroid echinoderms (starfish) by the largest individuals. The ingestion of very large amounts of small and slow-moving ophiuroids by small *P. auratus* contrasts with the situation elsewhere, with these echinoderms never being found in the gut contents of such *P. auratus* in a gulf in South Australia (Saunders et al., 2012b) and only occasionally in a gulf and estuary in New Zealand (Colman, 1972; Usmar, 2012). However, this shift from the consumption of such large volumes of ophiuroid echinoderms by the smallest fish to other prey by larger and older fish almost certainly reflects, in part, a change from foraging over soft sediments to areas over and around reefs. The view that small snapper feed over soft substrata is entirely consistent with the results of studies of the 0+ of this species in a large marine embayment in South Australia (Saunders et al., 2012b).

The above comparisons imply that, on the lower west coast of Australia, ophiuroids are either especially abundant and/or there is a shortage of alternative prey for the size class of the smallest *P. auratus*. Elsewhere, the dominant prey taxa of small *P. auratus* were polychaetes and, to a lesser extent, small teleosts and various crustaceans (particularly brachyuran crabs) in the above south Australian gulf (Saunders et al., 2012b), polychaetes, mysids and amphipods in a New

Zealand gulf (Colman, 1972) and carideans, mysids and crabs in a New Zealand estuary (Usmar, 2012). These comparisons strongly suggest that small *P. auratus* are readily able to target the most available prey in their environment, a form of “opportunism” characteristic of the Sparidae (Mariani et al., 2002; Chuwen et al., 2007).

Ophiuroids are abundant in Cockburn Sound (Marsh, 1978), where the majority of the small *P. auratus* were caught, and also over soft substrata in the waters of eastern Tasmania, where they likewise make a large contribution to the diet of two of the fish species studied in that environment (Blaber and Bulman, 1987; Blaber et al., 1987). Although brittle stars have a relatively low calorific value (Blaber et al., 1987), their high abundance over sand and hard structures in some waters (Shepherd and Thomas, 1982a) implies that they still potentially provide a substantial food source for fish species in those waters (Blaber et al., 1987; Packer et al., 1994). Furthermore, as their arms possess contrasting bands of colour (Edgar, 2008) and are “upraised and moving” when feeding, they would be particularly visible and accessible to fish predators (Blaber et al., 1987). As potential alternative prey for small *P. auratus*, e.g. polychaetes and amphipods, are relatively abundant in Cockburn Sound (Oceanica, 2007), it is proposed that brittle stars are targeted by small snapper in Cockburn Sound, because those echinoderms would be particularly visible in the turbid waters of this embayment.

Although, on the lower west coast of Australia, the increased ingestion of teleosts and crabs by *P. auratus*, as this predator increases in size, parallels that recorded for this sparid in a gulf and estuary in New Zealand, the other major prey of the larger fish in these regions differ conspicuously in some respects (Colman, 1972; Usmar, 2012). Thus, whereas the stomach contents of medium-sized *P. auratus*, i.e. 300-599 mm TL, on the lower west coast of Australia contained substantial volumes of sea urchins, these echinoderms were either rarely or never ingested by *P. auratus* of that size in those New Zealand waters (Colman, 1972; Usmar, 2012). As large starfish, such as *Astropecten preissei*, were only ingested by the larger fish on the lower western Australian coast, i.e. >600 mm TL (which exceeded the length of *P. auratus* in the two New Zealand water bodies), these echinoderms represent the culmination of the size-related changes in diets in those waters. While a pronounced and progressive size-related shift towards the consumption of larger and/or more robust prey is characteristic of a wide range of other sparids in different environments throughout the world (e.g. Tancioni et al., 2003; Platell et al., 2007; Santic et al., 2010, 2011), the

ingestion of substantial volumes of both starfish and sea urchins by *P. auratus* on the lower west coast of Australia is atypical for a sparid.

Although the overall dietary composition of *P. auratus* on the lower west coast changed with season, these changes were largely attributable to those exhibited by smaller fish and due, in particular, to the consumption of relatively greater volumes of ophiuroids in summer and autumn than in winter and spring. These seasonal changes are consistent with the fact that, elsewhere, the abundance of ophiuroids alters markedly with season, due to their recruitment varying as a result of spawning peaking at a particular time of the year and/or to migratory movements (Packer et al., 1994; Hinz et al., 2004). In contrast to the situation on the lower west coast, the diets of medium and large *P. auratus* on the mid west coast underwent conspicuous seasonal changes. The relatively greater consumption of brachyuran crabs by these *P. auratus* in winter and spring than in summer and autumn may be due to the 0+ age class *Portunus armatus* (Brachyura) in Western Australia having reached a sufficiently large size by the former seasons to provide a suitable food source (Potter et al., 1983). Seasonal differences in the diets of the co-occurring *Pagellus erythrinus* and *Pagellus acarne* and of another sparid *Lithognathus mormyrus* in the Mediterranean were also considered to be related, at least in part, to seasonal changes in prey abundance (Kallianiotis et al., 2005; Fanelli et al., 2011).

#### 4.2. Influence of body size and season on the dietary composition of *Pseudocaranx georgianus*

Two-way crossed ANOSIM tests demonstrated that, while the diet of *P. georgianus* was influenced significantly by length class ( $\bar{R}=0.20$ ) and not season ( $\bar{R}=0.05$ ) on the lower west coast, the reverse was true for the south coast, with the  $\bar{R}$ -statistic for length class being only 0.13, whereas that for season was 0.49. The largely progressive shift in the points for the dietary compositions of successive length classes of *P. georgianus* on the ordination plots for the lower west coast (Figs 6, 8) and the results of the RELATE procedure ( $\rho=0.75$ ,  $P=0.8\%$ ) demonstrate that the diet of this carangid changes in a mainly sequential manner with increasing body size. This represents a shift from the consumption of small benthic prey, such as isopods, carideans and small bivalve molluscs, to larger prey such as small crabs and small teleosts, a trend that largely follows that exhibited by another carangid, *Caranx bucculentus* (Brewer et al., 1989). The consumption of those particularly small benthic prey by the smallest *P. georgianus* is consistent with these small

carangids having been trawled over soft sediments and thus implying that, as with snapper, the silver trevally often forages over sand, at least early in life.

Although the trends exhibited by the points on the ordination plot in Fig. 6 indicated that the dietary composition of *P. georgianus* on the south coast also changed progressively with increasing body size, the dietary categories responsible for that trend differed markedly from those on the lower west coast. Thus, on the south coast, it reflected in particular, a decline in the importance of isopods, amphipods and cephalopods and an increase in the importance of crabs rather than teleosts. This regional difference presumably reflects a combination of differences in the relative abundances of the potential prey of this species on the two coasts and the ability of *P. georgianus* to feed opportunistically. The corresponding  $\bar{R}^2$ -statistic value for length class for the south coast was even lower (0.13) than for the lower west coast, suggesting that such opportunistic behaviour may be even more pronounced on this coast.

The small *P. georgianus*, i.e. <220 mm TL, correspond to the length range of the morphologically very similar but far smaller *Pseudocaranx wrighti*, with which it co-occurs on the lower west coast of Australia (Hyndes et al., 1999). The consumption by the smaller *P. wrighti*, i.e. <160 mm, of substantial volumes of mysids, copepods and zoeae/megalopae (Platell et al., 1997), imply that these *P. wrighti* feed within the water column and thus, in this respect, differ from those of *P. georgianus*, which, when of that size, feed predominantly on prey associated with the substrate. As it increases to its maximum size, *P. wrighti* ingests substantial amounts of polychaetes and echinoderms (Platell et al., 1997), dietary categories that were not ingested by *P. georgianus* of comparable size. There is thus a very conspicuous partitioning of food resources among these co-occurring and abundant congeners.

The marked seasonal changes in the dietary composition of *P. georgianus* on the south coast were due largely to a marked increase in the ingestion of amphipods during summer, which implies that the abundance of these invertebrates increases greatly in that season. Such a conclusion is consistent with the flatfish *Buglossidium luteum* feeding to a greater extent on amphipods in summer, and thus at the time when the numbers of this prey increased in the benthos (Schückel et al., 2011). The lack of a seasonal change in the diet of *P. georgianus* on the lower west coast presumably reflects a less pronounced increase in the relative abundances of amphipods and/or less marked seasonal differences between the abundances of other prey sources.



#### 4.3. Regional comparisons of dietary compositions of the two fish species

The main dietary categories consumed by the medium and large sized *P. auratus* on the lower west and mid west coasts were shown to be the same, and the Teleostei was the main typifying dietary category for this sparid on both coasts. However, the  $\bar{R}$ -statistic value of 0.30 for region in the ANOSIM comparisons between region and season demonstrates that the dietary compositions of this species in these two regions were conspicuously different, although this difference was not as pronounced as the overall seasonal effect, for which the  $\bar{R}$ -statistic was 0.50. The regional difference was due, in particular, to relatively greater dietary contributions by both *E. cordatum* and other echinoids and a narrower range of prey on the mid west than lower west coast, presumably reflecting differences in the compositions of the potential prey in the two regions.

The above conspicuous regional differences in the diet of *P. auratus*, together with the seasonal changes in particularly the diet of the smaller individuals on the lower west coast, imply that this species is able to respond effectively to changes that arise through spatial and temporal differences in potential prey. Indeed, Saunders et al. (2012b) concluded from comparisons of the diets of 0+ *P. auratus* in different areas of a South Australian embayment that prey availability is a driver of habitat selection by the young individuals of this species. Moreover, certain sparid species in the Mediterranean can exhibit a generalist feeding behaviour in one locality and yet focus on a small suite of prey in another locality where the range of prey is presumably far more restricted (Mariani et al., 2002). Furthermore, other sparids can even consume large amounts of macrophytes, and their associated epiphytes, when such plant material is abundant, and yet in some cases are carnivorous in other localities (cf Blaber, 1974; Whitfield, 1980; Sarre et al., 2000; Chuwen et al., 2007; Sheppard et al., 2012).

The marked regional differences between the major dietary taxa of *P. georgianus* on the lower west coast (mainly teleosts, crabs, carideans and small gastropods) and south coast (mainly isopods, amphipods, bivalves and cumaceans) contrasts markedly with the lack of any such regional difference with the labrid *B. frenchii* (Platell et al., 2010). This implies that the type of prey ingested by *P. georgianus* varies to a greater degree in response to variations in the abundances of potential prey, and is thus more opportunistic in its feeding behaviour than *B. frenchii*.



#### 4.4. Comparisons between the dietary compositions of co-occurring *Pagrus auratus* and *Pseudocaranx georgianus* on the lower west coast

The global  $\bar{R}$ -statistic of 0.51 for the comparison between the dietary compositions of *P. auratus* and *P. georgianus* on the lower west coast of Australia is substantially greater than the corresponding overall value of 0.35 for length class and even more particularly the 0.19 for season. This emphasises that, when those species co-occur on that coast, their diets differ markedly, a feature due, overall, to a relatively greater or exclusive ingestion of ophiuroids (brittle stars), asteroids (starfish) and *E. cordatum* (heart urchins) by *P. auratus* and the reverse trend for littorinids (small gastropods), other echinoids (other sea urchins), amphipods and carideans (shrimps). There is, however, a marked overlap in the suite of dietary categories ingested by both of these carnivorous predators, a feature emphasised by the fact that crabs and teleosts were among the most important typifying dietary categories in the stomach contents of both species.

From the above, it is evident that the prey of *P. auratus* comprises a number of taxa that possess either hard and/or protective shells/exoskeletons, e.g. large crabs and sea urchins, or are structurally robust, e.g. starfish. However, as these prey are represented in the gut contents by clearly identifiable small or large fragments, they are initially broken into smaller components which thereby helps them to be ingested. This process is facilitated by the possession of prominent canines for seizing the prey and two rows of strong, rounded molariform teeth on both the upper and lower jaws (Fig. 2a-d) to crush the prey through employing a jaw-lever mechanism, which maximises the biting force applied to the jaw (Wainwright and Richard, 1995).

In contrast to *P. auratus*, the diet of *P. georgianus* comprises a greater volume of smaller prey, e.g. amphipods, cumaceans, ostracods, small gastropods and small crabs, which is reflected in the presence of far smaller teeth and weaker oral jaws (Fig. 2e-h). The weakness of the oral jaws is partly compensated for, however, by the possession of robust and rounded teeth on its pharyngeal jaws, which enables small hard-shelled organisms to be crushed. Thus, *P. auratus* belongs to the feeding category designated by Wainwright and Richard (1995) as biters, whereas *P. georgianus* is essentially a suction feeder.

In summary, the combined use of ANOSIM, MDS ordination and the RELATE procedure demonstrates that the dietary compositions of *P. auratus* and *P. georgianus* were invariably influenced significantly by body size (length class) and region and, with the exception of

*P. georgianus* on the lower west coast, also by season. However, the extents and rank orders of those influences differ between those two carnivorous species, while the seasonal effect can be restricted to fish of a certain size range. Furthermore the dietary compositions of these two species differed conspicuously between regions and markedly so in the case of *P. georgianus*. The results imply that *P. auratus* and *P. georgianus* are, to a certain extent, opportunistic feeders, which would account for the success of these species in different regions and, in turn, imply that they would be able to accommodate at least any moderate changes that might occur in prey composition as a result of anthropogenic effects, including climate change. Furthermore, although some prey are common to both *P. auratus* and *P. georgianus*, their dietary compositions are demonstrably distinct when these species co-occur and are abundant, thereby reducing the potential for competition for food resources. The results and comparisons emphasise the need for caution when attempting to extrapolate regarding the extent of the influence of the above factors on dietary compositions on fish species in general.

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## List of Figures

**Figure 1** Map showing the sampling regions in western Australia for *Pagrus auratus* on its mid west and lower west coasts and for *Pseudocaranx georgianus* on its lower west and south coasts. Inset shows the location of the sampling regions in Australia.

**Figure 2** Plan and profile view of the upper (a,b) and lower (c,d) jaws of *Pagrus auratus*, respectively, and plan and profile view of the upper jaw and pharyngeal plate (e,f) and lower jaw and pharyngeal plate (g,h) of *Pseudocaranx georgianus*, respectively. Bar, 10 mm.

**Figure 3** Stacked bar graphs showing mean percentage volumetric contributions (%V) of the dietary categories (see key) in the gut contents of the length classes of *Pagrus auratus* on the mid west and lower west coasts and of *Pseudocaranx georgianus* on the lower west and south coasts. Sample sizes are given above the stacked bar graphs for each length class. N.B. For visual clarity, a few dietary categories for closely-related taxa with small volumetric contributions have been pooled.

**Figure 4** Centroid nMDS ordination plots, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of sequential total length classes of *Pagrus auratus* caught seasonally on the lower west coast. Plot (a) is derived from data for all seasons and length classes, while (b) is derived from data for autumn and winter and (c) is derived from data for spring and summer. 1=<150 mm, 2=150-299 mm, 3=300-449 mm, 4=450-599 mm, 5=600-749 mm, 6= $\geq$ 750 mm. In this and Figs 5,7 and 8, Su, summer, A, autumn; W, winter; Sp, spring.

**Figure 5** Centroid nMDS ordination plots, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of *Pagrus auratus* caught seasonally on the lower west and mid west coasts, separated firstly by (a) season and region and then (b) season and length class. Comparisons were restricted to the length classes of fish represented in both regions, i.e. 3=300-449, 4=450-599 and 5=600-749 mm.

**Figure 6** Centroid nMDS ordination plot, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of sequential total length classes of *Pseudocaranx*

*georgianus* caught seasonally from the lower west and south coasts. 1= $<150$  mm; 2=150-224 mm; 3=225-299 mm; 4=300-374 mm; 5=375-449 mm; 6= $\geq 450$  mm.

**Figure 7** Centroid nMDS ordination plots, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of sequential total length classes of *Pseudocaranx georgianus* caught seasonally on the lower west and south coasts. Plot (a) is derived from data for all seasons and length classes, while (b) is derived from data for autumn and winter and (c) from spring and summer. 1= $<150$  mm; 2=150-224 mm; 3=225-299 mm; 4=300-374 mm; 5=375-449 mm; 6= $\geq 450$  mm.

**Figure 8** Centroid nMDS ordination plots, derived from a distance among centroid matrix constructed from a Bray-Curtis similarity matrix that employed the volumetric contributions of the various dietary categories to the gut contents of sequential total length classes of co-occurring *Pagrus auratus* and *Pseudocaranx georgianus* on the lower west coast, separated firstly by (a) species and length class and then (b) species and season. Length classes are as follows; for *P. auratus* 1= $<149$  mm; 2=150-299 mm; 3=300-449 mm; 4=450-599 mm; 5=600-749 mm; 6= $\geq 750$  mm; for *P. georgianus* 1= $<150$  mm; 2=150-224 mm; 3=225-299 mm; 4=300-374 mm; 5=375-449 mm; 6= $\geq 450$  mm.

**Table 1** Frequencies of occurrence (%F) and mean percentage contributions by volume (%V) of the major taxa (bold), dietary categories (\*) and dietary items in the gut contents of different-sized *Pagrus auratus* in waters on the mid and lower west coasts of Australia and of *Pseudocaranx georgianus* in waters on the lower west and south coasts. Unid., unidentifiable.

Major taxa, dietary categories and dietary items	<i>P. auratus</i>		<i>P. auratus</i>		<i>P. auratus</i>		<i>P. georgianus</i>		<i>P. georgianus</i>	
	Mid west		Lower west		Lower west		Lower west		South	
	>400 mm		<400 mm		>400 mm					
	%F	%V	%F	%V	%F	%V	%F	%V	%F	%V
<b>Porifera*</b>	<b>3.8</b>	<b>1.9</b>	-	-	-	-	-	-	-	-
<b>Cnidaria*</b>	-	-	-	-	<b>1.7</b>	<b>0.2</b>	-	-	-	-
Actiniaria	-	-	-	-	1.7	0.2	-	-	-	-
Gorgonacea	-	-	-	-	-	-	-	-	-	-
<b>Sipuncula*</b>	<b>1.3</b>	<b>0.2</b>	-	-	<b>3.3</b>	<b>0.5</b>	-	-	-	-
<b>Polychaeta</b>	<b>3.8</b>	<b>0.5</b>	<b>14.5</b>	<b>3.3</b>	<b>8.2</b>	<b>1.5</b>	<b>4.5</b>	<b>2.0</b>	<b>9.1</b>	<b>5.1</b>
Aphroditidae*	-	-	-	-	1.6	1.2	-	-	1.3	0.3
Pectinariidae*	3.8	0.5	14.5	3.3	6.6	0.3	3.2	1.6	3.9	1.7
Other Polychaeta*	-	-	-	-	-	-	1.3	0.4	5.2	3.1
<b>Mollusca</b>	<b>27.6</b>	<b>8.8</b>	<b>25.6</b>	<b>9.0</b>	<b>40.0</b>	<b>14.4</b>	<b>53.9</b>	<b>32.2</b>	<b>23.4</b>	<b>13.2</b>
<b>Polyplacophora*</b>	-	-	<b>1.2</b>	<b>0.3</b>	<b>6.6</b>	<b>2.6</b>	<b>0.6</b>	<b>0.4</b>	<b>1.3</b>	<b>0.1</b>
<b>Gastropoda</b>	<b>13.2</b>	<b>2.6</b>	<b>13.4</b>	<b>3.1</b>	<b>16.7</b>	<b>3.8</b>	<b>39.6</b>	<b>19.1</b>	<b>11.7</b>	<b>4.9</b>
Olividae*	5.1	1.5	1.2	-	1.6	-	-	-	1.3	0.3
Trochidae*	2.5	0.8	4.8	2.4	8.2	1.4	14.9	5.4	5.2	2.0
Littorinidae*	1.3	0.1	8.4	0.7	-	-	20.8	13.0	5.2	1.3
Other Gastropoda*	-	-	1.2	<0.1	8.3	1.6	1.3	0.1	2.6	0.8
Columbellidae	-	-	-	-	-	-	0.6	<0.1	1.3	0.7
Cypraeidae	-	-	-	-	1.6	0.1	-	-	-	-
Haliotidae	-	-	-	-	1.6	0.4	-	-	-	-
Naticidae	-	-	-	-	1.6	0.9	-	-	-	-
Turritellidae	-	-	1.2	<0.1	3.3	0.2	0.6	<0.1	1.3	0.1

Unid. Gastropoda	5.3	0.2	-	-	8.2	0.8	4.5	0.7	1.3	0.5
<b>Bivalvia*</b>	<b>11.8</b>	<b>4.2</b>	<b>14.4</b>	<b>5.6</b>	<b>10.0</b>	<b>4.3</b>	<b>15.6</b>	<b>7.1</b>	<b>9.1</b>	<b>5.8</b>
Mytilidae	-	-	-	-	-	-	1.9	1.9	-	-
Pectinidae	-	-	-	-	4.9	2.5	-	-	1.3	1.7
Pinnidae	3.8	1.5	-	-	-	-	0.6	-	-	-
Veneroidea	2.5	0.1	2.4	0.5	1.6	0.2	-	-	-	-
Unid. Bivalvia	5.1	2.6	12.0	5.1	4.9	1.6	13.0	5.2	7.8	4.1
<b>Cephalopoda</b>	<b>9.2</b>	<b>2.0</b>	-	-	<b>16.4</b>	<b>3.7</b>	<b>5.2</b>	<b>5.6</b>	<b>2.6</b>	<b>2.4</b>
Octopoda*	1.3	0.2	-	-	6.6	1.4	0.3	0.4	2.6	2.4
Sepiida*	7.6	1.8	-	-	8.2	1.8	1.0	2.8	-	-
Teuthida*	-	-	-	-	1.6	0.5	1.3	2.4	-	-
<b>Crustacea</b>	<b>23.7</b>	<b>11.7</b>	<b>32.9</b>	<b>18.7</b>	<b>33.3</b>	<b>19.1</b>	<b>53.9</b>	<b>37.8</b>	<b>76.6</b>	<b>61.5</b>
Ostracoda*	-	-	-	-	-	-	6.5	1.5	10.4	1.7
Cumacea*	-	-	3.6	0.8	-	-	1.9	0.9	15.6	5.7
Isopoda*	2.5	0.4	1.2	0.4	3.3	2.5	7.1	1.9	24.7	10.1
Amphipoda*	1.3	0.9	2.4	2.2	-	-	20.8	6.7	45.5	28.1

*P. auratus**P. auratus**P. auratus**P. georgianus**P. georgianus***Table 1 (cont.)**

Major taxa, dietary categories and dietary items

	<i>P. auratus</i> Mid west		<i>P. auratus</i> Lower west		<i>P. auratus</i> Lower west		<i>P. georgianus</i> Lower west		<i>P. georgianus</i> South	
	>400 mm %F	>400 mm %V	<400 mm %F	<400 mm %V	>400 mm %F	>400 mm %V	%F	%V	%F	%V
<b>Decapoda</b>	<b>22.4</b>	<b>10.4</b>	<b>28.0</b>	<b>14.2</b>	<b>31.7</b>	<b>16.6</b>	<b>28.6</b>	<b>26.8</b>	<b>29.9</b>	<b>15.9</b>
Caridea*	-	-	2.4	2.2	1.6	0.8	17.5	10.1	13.0	4.9
Crabs	22.4	10.4	24.4	11.9	28.3	15.5	28.6	16.3	6.5	11.0
Larvae*	-	-	-	-	-	-	0.6	0.1	1.3	-
Adults*	22.4	10.4	24.4	11.9	28.3	15.5	28.6	16.2	19.5	11.0
Atelecyclidae	-	-	1.2	0.5	3.3	1.0	1.3	0.3	-	-
Majidae	2.5	0.7	7.2	3.6	1.6	-	2.6	0.8	1.3	0.1
Paguridae	5.1	0.9	2.4	0.4	8.2	3.5	1.3	0.1	5.2	2.0



Portunidae	7.6	4.0	2.4	1.7	11.5	7.1	2.6	2.0	10.4	8.2
Unid. crabs	11.4	4.8	12.0	5.7	11.5	3.9	22.7	13.0	5.2	0.7
Lobsters	-	-	1.2	0.1	3.3	0.3	-	-	-	-
Galatheoidea*	-	-	1.2	0.1	1.6	0.1	-	-	-	-
Achelata*	-	-	-	-	1.6	0.2	-	-	-	-
Unid. Decapoda	-	-	-	-	-	-	1.9	0.4	-	-
Unid. Crustacea	-	-	2.4	1.3	-	-	-	-	-	-
<b>Echinodermata</b>	<b>53.9</b>	<b>39.4</b>	<b>78.0</b>	<b>59.2</b>	<b>46.7</b>	<b>30.9</b>	<b>16.2</b>	<b>8.1</b>	<b>6.5</b>	<b>1.7</b>
<b>Asteroidea*</b>	<b>9.2</b>	<b>3.8</b>	<b>4.8</b>	<b>2.0</b>	<b>20.0</b>	<b>11.8</b>	-	-	-	-
<i>Astropecten preissei</i>	-	-	-	-	6.6	4.6	-	-	-	-
<i>Luidia australiae</i>	2.5	1.2	-	-	1.6	0.9	-	-	-	-
<i>Stellaster inspinus</i>	3.8	1.4	-	-	-	-	-	-	-	-
Goniasteridae	-	-	-	-	1.6	0.3	-	-	-	-
Unid. Asteroidea	5.1	1.2	4.8	2.0	11.5	6.0	-	-	-	-
<b>Ophiuroidea*</b>	<b>6.3</b>	<b>3.8</b>	<b>63.9</b>	<b>43.8</b>	<b>9.8</b>	<b>3.0</b>	<b>5.8</b>	<b>2.2</b>	<b>6.5</b>	<b>1.7</b>
<b>Echinoidea</b>	<b>46.1</b>	<b>31.8</b>	<b>19.2</b>	<b>13.4</b>	<b>25.0</b>	<b>14.1</b>	<b>10.4</b>	<b>6.0</b>	-	-
Clypeasteroidea*	-	-	-	-	1.6	1.8	-	-	-	-
<i>Echinocardium cordatum*</i>	29.1	18.4	10.8	8.6	6.6	3.8	0.6	0.7	-	-
<i>Heliocidaris erythrogramma*</i>	6.3	2.4	-	-	-	-	-	-	-	-
Other Echinoidea*	22.8	11.0	8.4	4.8	18.0	8.5	9.7	5.3	-	-
<b>Holothuroidea*</b>	-	-	-	-	<b>3.3</b>	<b>2.0</b>	-	-	-	-
<b>Teleostei*</b>	<b>53.9</b>	<b>38.4</b>	<b>18.3</b>	<b>9.8</b>	<b>50.0</b>	<b>29.3</b>	<b>19.5</b>	<b>19.9</b>	<b>16.9</b>	<b>18.3</b>
Atherinidae	-	-	-	-	-	-	8.4	10.7	7.8	10.5
Clinidae	-	-	-	-	-	-	2.6	1.7	-	-
Diodontidae	-	-	-	-	1.6	0.8	-	-	1.3	0.3
Gobiidae	-	-	-	-	-	-	-	-	1.3	0.2
Scorpaenidae	-	-	-	-	1.6	0.7	-	-	-	-
Syngnathidae	1.3	0.1	-	-	1.6	0.2	1.9	1.4	-	-
Tripterygiidae	1.3	0.1	-	-	-	-	0.6	0.3	-	-

Unid. Teleostei	53.2	38.1	18.1	9.8	47.5	27.6	6.5	5.8	6.5	7.3
Plant material*	-	-	-	-	9.8	4.1	-	-	-	-
Guts ( <i>n</i> )	252		159		119		367		130	
Guts with food ( <i>n</i> )	76		82		60		166		77	
Mean (SE) gut fullness	3.7 (0.2)		3.9 (0.2)		4.0 (0.2)		3.2 (0.2)		3.3 (0.2)	

**Table 2** Dietary categories that typify (shaded) the dietary compositions of sequential length classes of *Pagrus auratus* on the lower west coast of Australia and those which distinguish between the dietary compositions of those length classes (unshaded). In this table and Table 4, \* denotes that the relative contribution of that dietary category is greater for the length class represented in the vertical column than in the horizontal row. Note that, because of limited replication, the typifying dietary categories for the 300-449 mm length class are derived using a one-way rather than two-way SIMPER analysis.

Length class (TL, mm)	<150	150-299	300-449	450-599	600-749	≥750
<150	Ophiuroidea Bivalvia					
150-299	Ophiuroidea* Crabs Teleostei Polychaeta Other Echinoidea Trochidae <i>E. cordatum</i>	Ophiuroidea Teleostei Crabs Polychaeta				
300-449	Ophiuroidea* Other Echinoidea Teleostei Crabs * Trochidae Asteroidea	Ophiuroidea* Crabs* Trochidae Other Echinoidea Asteroidea <i>E. cordatum</i> *	Trochidae Polychaeta*			
450-599	Ophiuroidea* Teleostei Other Echinoidea Bivalvia* Other Gastropoda Crabs Trochidae	Ophiuroidea* Crabs* Other Echinoidea Polychaeta* Trochidae Other Gastropoda Bivalvia Asteroidea*	Sepiida Other Echinoidea Other Gastropoda Crabs Trochidae* Plant material Isopoda Asteroidea*	Teleostei Other Echinoidea Crabs		
600-749	Teleostei Ophiuroidea* Crabs Asteroidea Isopoda	Ophiuroidea* Asteroidea Crabs <i>E. cordatum</i> * Plant material Polychaeta* Other Echinoidea* Holothuroidea	Trochidae* Teleostei Asteroidea Plant material Polyplacophora Polychaeta* Crabs	Asteroidea Crabs Ophiuroidea* Other Echinoidea* Octopoda Bivalvia Polychaeta <i>E. cordatum</i> Teleostei*	Teleostei Crabs	

$\geq 750$	Ophiuroidea* Teleostei Crabs Asteroidea Bivalvia* <i>E. cordatum</i> Holothuroidea	Ophiuroidea* Asteroidea Crabs <i>E. cordatum</i> * Plant material Polychaeta Other Echinoidea Holothuroidea	Crabs Asteroidea Other Echinoidea* Trochidae* <i>E. cordatum</i> Clypeasteroidea Plant material	Other Echinoidea* Asteroidea Crabs <i>E. cordatum</i> Holothuroidea Ophiuroidea * Bivalvia Teleostei*	Asteroidea Crabs Polyplacophora* Teleostei* Octopoda* Polychaeta* Clypeasteroidea	Teleostei Asteroidea Bivalvia
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**Table 3** Dietary categories that typify (shaded) the dietary compositions of *Pagrus auratus* in sequential seasons on the lower west coast of Australia and those which distinguish between the dietary compositions in each pair of seasons (unshaded). \* Denotes that the relative contribution of that dietary category is greater for the season represented in the vertical column than in the horizontal row.

Season	Summer	Autumn	Winter	Spring
Summer	Ophiuroidea Crabs			
Autumn	Crabs* Teleostei Ophiuroidea Bivalvia Amphipoda <i>E. cordatum</i>	Ophiuroidea Teleostei Bivalvia Crabs Other Echinoidea		
Winter	Clypeasteroidea* Teleostei Asteroidea Bivalvia Crabs Isopoda* Polyplacophora Ophiuroidea*	Crabs Teleostei* <i>E. cordatum</i> Asteroidea Bivalvia Ophiuroidea* Sepiida Other Echinoidea Plant material	Teleostei Crabs Asteroidea Ophiuroidea Bivalvia Sepiida	
Spring	Crabs* Littorinidae <i>E. cordatum</i> Asteroidea Plant material Caridea Amphipoda*	Teleostei* Ophiuroidea* Crabs* <i>E. cordatum</i> Littorinidae Bivalvia*	Plant material Polyplacophora Teleostei* Crabs* Bivalvia* Asteroidea* <i>E. cordatum</i>	Ophiuroidea <i>E. cordatum</i>

**Table 4** Dietary categories that typify (shaded) the dietary compositions of sequential length classes of *Pseudocaranx georgianus* on the lower west coast of Australia and those which distinguish between the dietary compositions of those length classes (unshaded). Note that, because of limited replication, the typifying dietary categories for the diets of fish comprising the >150 and  $\geq 450$  mm length classes and the comparison between the diets of those two length classes, are based on the results of a one-way rather than two-way SIMPER analysis.

Length class (mm, TL)	<150	150-224	225-299	300-374	375-449	$\geq 450$
<150	Trochidae					
150-224	Trochidae* Cumacea* Ostracoda* Amphipoda Isopoda* Caridea* Other Echinoidea*	Bivalvia				
225-299	Crabs Isopoda* Trochidae* Caridea Amphipoda Teleostei Bivalvia	Bivalvia* Caridea Amphipoda Crabs Other Echinoidea Ostracoda Cumacea	Crabs Caridea Amphipoda Bivalvia Littorinidae			
300-374	Teleostei Cumacea* Crabs Ostracoda* Other Echinoidea Isopoda* Caridea* Amphipoda Trochidae*	Bivalvia* Trochidae* Teleostei Amphipoda* Crabs Cumacea Littorinidae Caridea	Teleostei Crabs* Caridea Littorinidae Other Echinoidea Amphipoda* Trochidae Bivalvia	Teleostei Littorinidae Crabs Caridea Amphipoda Trochidae		
375-449	Crabs Cumacea* Teleostei Littorinidae Trochidae* Ostracoda* Other Echinoidea*	Crabs Teleostei Bivalvia* Trochidae* Cumacea* Littorinidae Amphipoda* Ostracoda*	Teleostei Littorinidae Amphipoda Crabs Caridea* Other Echinoidea Bivalvia	Teleostei Littorinidae Crabs Caridea* Bivalvia Sepiida	Crabs Teleostei Littorinidae	
$\geq 450$	Teleostei Crabs Cumacea* Isopoda* Caridea* Trochidae* Ostracoda* Other Echinoidea	Teleostei Bivalvia* Polychaeta Isopoda Other Echinoidea	Teleostei Caridea* Other Echinoidea Amphipoda Isopoda Crabs	Littorinidae* Teleostei Crabs Caridea* Other Echinoidea Polychaeta Amphipoda*	Teleostei Caridea Littorinidae* Polychaeta Bivalvia	Teleostei Crabs

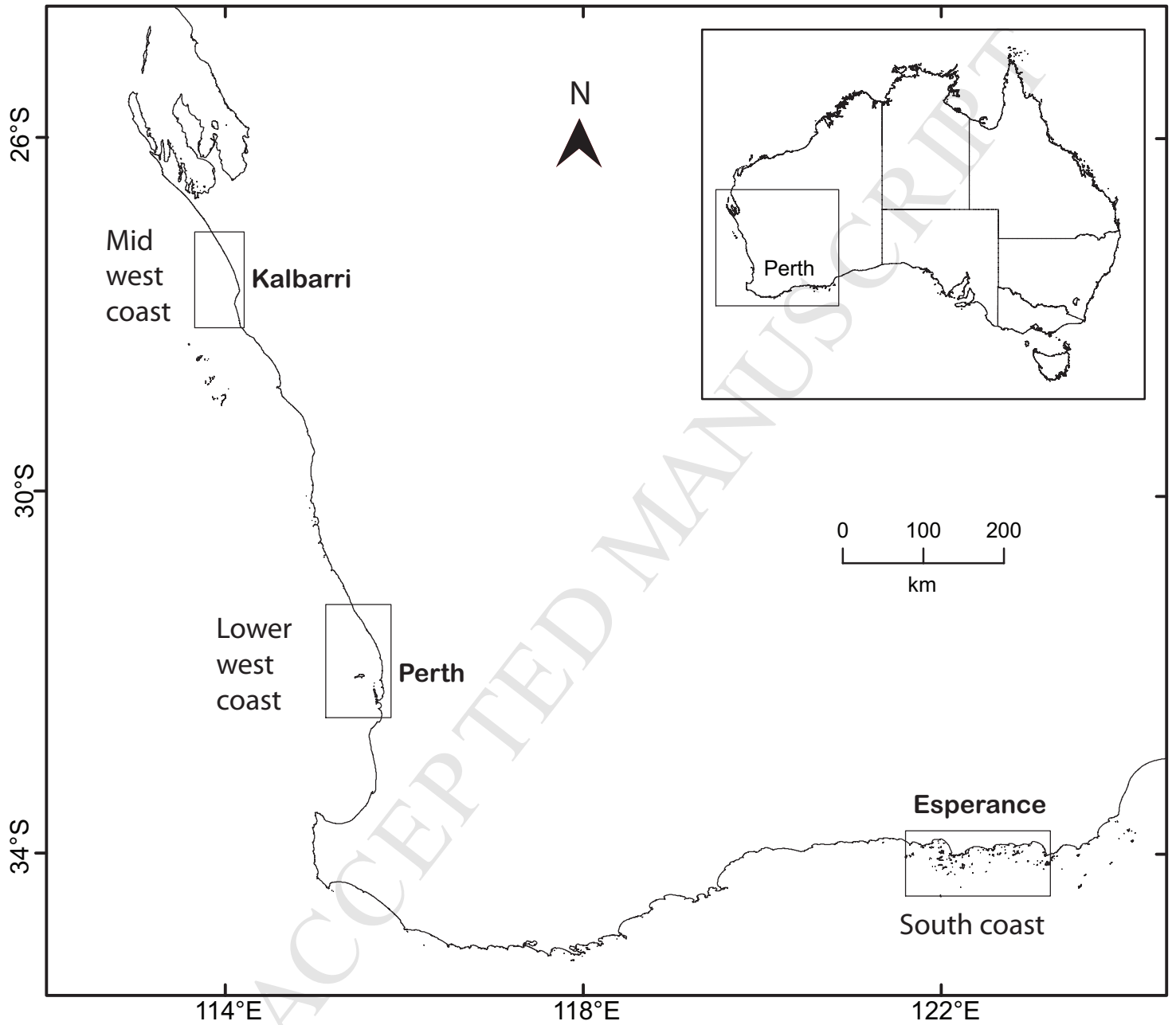
## Appendix

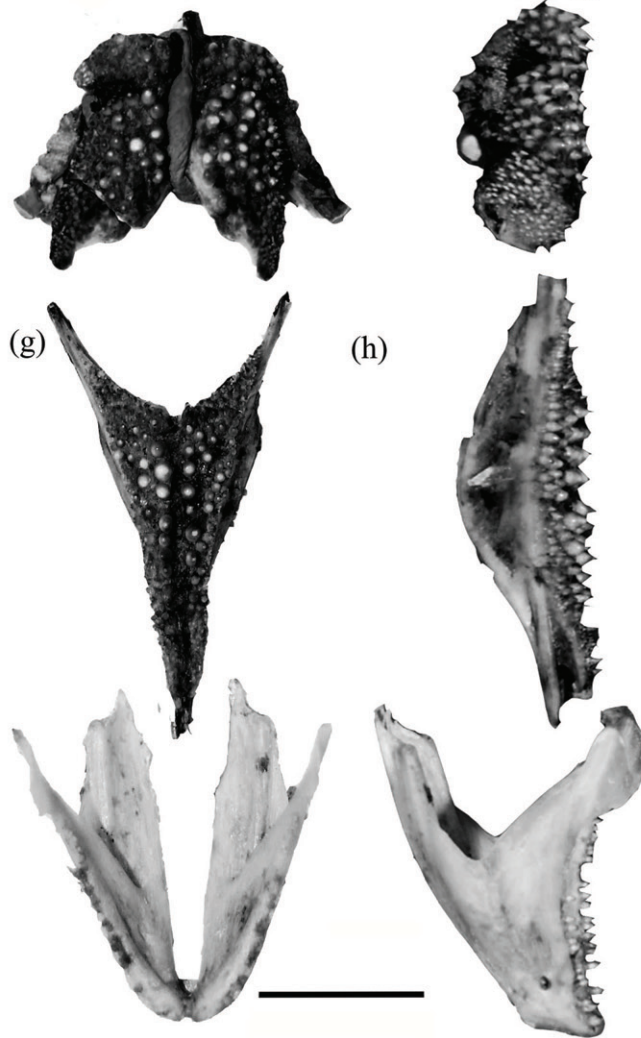
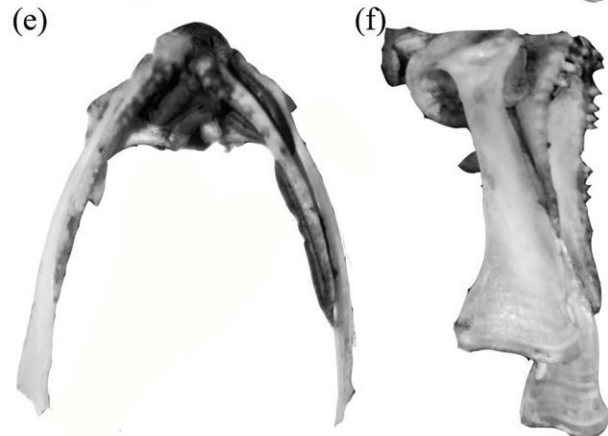
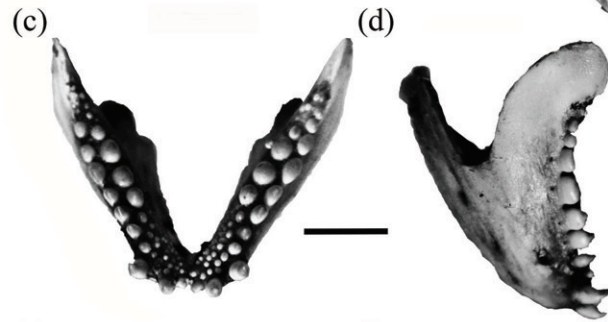
Mean squares (MS), pseudo-*F* ratios, significance levels (*P*,%) and components of variation (COV) for a series of PERMANOVA tests, employing Bray-Curtis similarity matrices derived from the mean percentage volumetric contributions of the various dietary categories to the gut contents of the fish species as designated.

<i>P. auratus</i> on the lower west coast	Df	MS	Pseudo- <i>F</i>	<i>P</i> (%)	COV
Main effects					
Length class	5	4333	3.3	0.01	25.6
Season	3	4805	3.7	0.01	23.6
Interaction					
Length class x season	10	2865	2.2	0.04	31.1
Residual	19	1303			36.1
<i>P. auratus</i> on the lower west and mid west coasts	Df	MS	Pseudo- <i>F</i>	<i>P</i> (%)	COV
Main effects					
Length class	2	2565	1.8	6.6	17.7
Season	3	2826	2.0	2.4	16.8
Region	1	6384	4.5	0.1	31.9
Interactions					
Length class x season	6	2873	2.0	0.4	28.8
Length class x region	2	1256	1.1	38.7	6.2
Season x region	3	3723	2.6	0.5	33.8
Length class x season x region	1	857	0.6	66.8	17.0
Residual	16	1416			37.6
<i>P. georgianus</i> on the lower west coast	Df	MS	Pseudo- <i>F</i>	<i>P</i> (%)	COV
Main effects					
Length class	5	4607	2.1	0.05	19.7
Season	3	3551	1.6	4.5	13.1
Interaction					
Length class x season	10	2679	1.2	12.1	14.5
Residual	35	2157			46.1
<i>P. georgianus</i> on the south coast	Df	MS	Pseudo- <i>F</i>	<i>P</i> (%)	COV
Main effects					
Length class	4	1857	1.1	37.1	6.5
Season	3	9877	5.9	0.01	34.8
Interaction					
Length class x season	4	2715	1.6	6.2	23.7
Residual	17	1676			40.9
<i>P. georgianus</i> on the lower west and south coasts	Df	MS	Pseudo- <i>F</i>	<i>P</i> (%)	COV
Main effects					
Length class	5	4922	2.5	0.02	16.0
Season	3	9265	4.6	0.01	18.9
Region	1	16879	8.4	0.01	19.8
Interactions					
Length class x season	11	2785	1.4	2.9	15.6
Length class x region	4	4124	2.1	0.4	19.7
Season x region	3	2636	1.3	18.2	12.4
Length class x season x region	3	3048	1.5	8.8	24.7
Residual	52	2000			44.7

**Appendix (cont.)**

<i>P. auratus</i> and <i>P. georgianus</i> on the lower west coast	Df	MS	Pseudo- <i>F</i>	<i>P</i> (%)	COV
Main effects					
Species	1	12426	6.6	0.01	21.2
Length class	5	3943	2.1	0.06	16.6
Season	3	4107	2.2	0.4	12.9
Interactions					
Species x length class	5	4156	2.2	0.02	23.8
Species x season	3	4951	2.6	0.02	24.1
Length class x season	13	2910	1.6	0.3	18.8
Species x length class x season	7	2722	1.5	3.7	22.6
Residual	56	1878			43.3

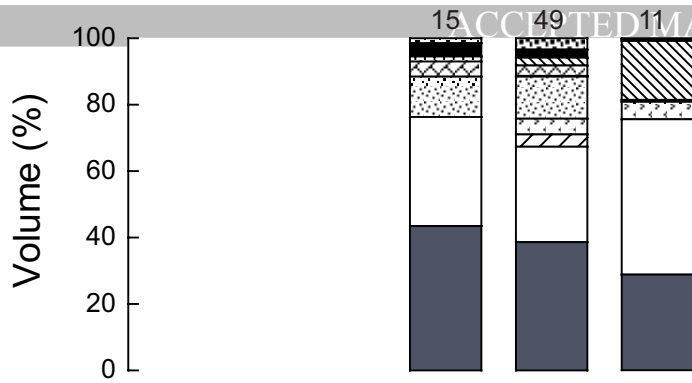




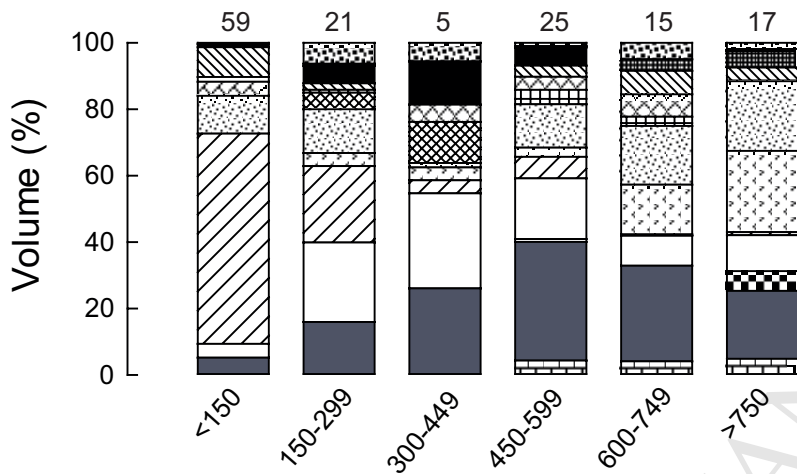
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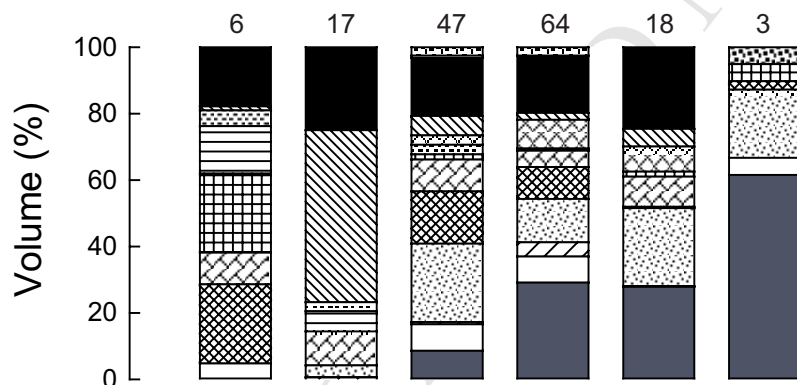


b) Lower west coast

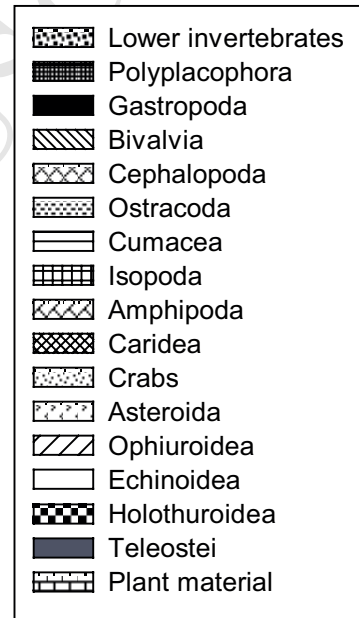
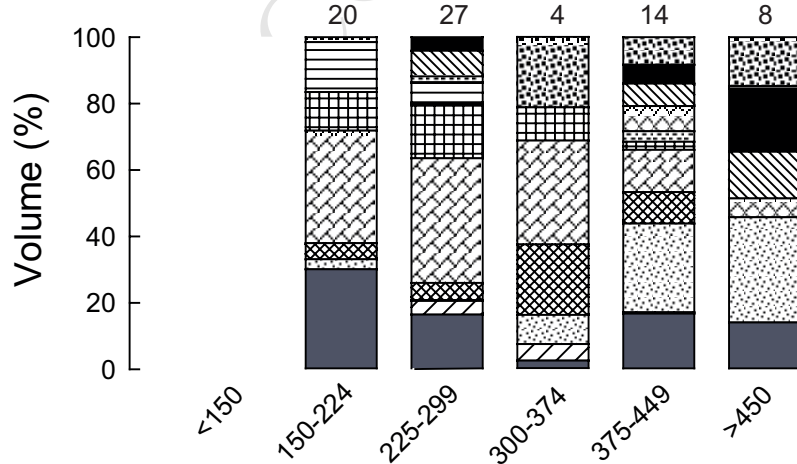


*Pseudocaranx georgianus*

c) Lower west coast



d) South coast



Length class (mm)

