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Greenwell, C.N., Coulson, P.G., Tweedley, J.R. and Loneragan, N.R. (2018) Regional differences in the feeding of the ambush predator *Neosebastes pandus* and comparisons of diets in the Scorpaenidae, Triglidae and Platycephalidae. *Journal of Fish Biology*

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**Regional differences in the feeding of the ambush predator *Neosebastes pandus* and comparisons of diets in the Scorpaenidae, Triglidae and Platycephalidae**

RUNNING HEAD: DIETS OF SOME SCORPAENIFORMES

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This article has been accepted for publication in the *Journal of Fish Biology* and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/jfb.13677

This study provides a comprehensive assessment of the dietary composition of the ambush predator *Neosebastes pandus* and compares the diets of 49 species from 39 studies of three benthic predatory families in the Scorpaeniformes: Scorpaenidae (20 species), Triglidae (19 species) and Platycephalidae (10 species). A total of 275 *N. pandus* were collected from the west (Rottnest Island) and south coasts (Esperance) of south-western Australia and the percentage frequency and volumetric contribution of the stomach contents identified. Fish from the west coast consumed a greater mean number of broad taxonomic groups and were more diverse in their diet than fish from the south coast. Cephalopods, brachyurans and teleosts were the largest overall contributors to diet, with teleosts being more important to diets of west-coast fish and polychaetes for south-coast fish. This reflects differences in habitat between the two locations. Dietary composition also changed with increasing body size, reflecting morphological changes that allow bigger fish to capture and ingest larger, more mobile prey. Meta-analysis of the diets of 49 species of scorpaenid, triglid and platycephalid revealed that they feed predominantly on teleosts and large crustaceans. Significant differences in diet were detected among families, with platycephalids being the most distinct and feeding more on teleosts than scorpaenids and triglids.

**Key words:** gurnard perch; habitat structure; Scorpaenoidei; size-related changes; south-western Australia.

## INTRODUCTION

The Scorpaeniformes are a diverse order comprising six suborders, 41 families, 398 genera and 2092 species (Nelson *et al.*, 2016). Encompassing around 660 species, the Triglidae (searobins or gurnards), Platycephalidae (flatheads) and Scorpaenidae (scorpionfishes or rockfishes) make up 32% of the Scorpaeniformes with 125, 80 and 454 species, respectively (Nelson *et al.*, 2016). The Neosebastinae (gurnard perches) are a small subfamily of the Scorpaenidae (two genera, 18 species) typically found in the south-west Pacific (Nelson *et al.*, 2016). The bighead gurnard perch *Neosebastes pandus* (Richardson, 1842) is the largest of the 12 species of *Neosebastes* Guichenot 1867 species, reaching lengths of up to 500 mm. It is endemic to southern Australia (Houtman Abrolhos Islands, *c.* 29° S; 114° E, to the Gulf of St Vincent *c.* 5° S; 138° E), occurring on rocky reefs and macrophyte areas at depths ranging from 10 to 200 m (Hutchins & Swainston, 1986; Edgar, 2008; Gomon *et al.*, 2008).

Many scorpaenoids are well camouflaged and often characterized by a wide range of cryptic colouration, decorative cirri, spiny ridges and leaf-like appendages (Gomon *et al.*, 2008; Bray, 2016). To capture their prey, these fish rely largely on ambush predation (Platell & Potter 1998; Motomura *et al.*, 2006; Consoli *et al.*, 2010), a specialized form of feeding behaviour that relies on camouflage, cryptic behaviour and rapid, selective strikes to capture prey (Curio 1976; Keenleyside 1979; Gerking 1994). This feeding strategy uses little energy, yet is highly effective at catching prey with precision (Schultz & Kruschel, 2010; Coulson *et al.*, 2015; French *et al.*, 2017).

Owing to their ecological and economic importance, there is extensive dietary information for many members of the Scorpaenidae, Triglidae and Platycephalidae (Boudaya *et al.*, 2007; Consoli *et al.*, 2010; Horn *et al.*, 2012; Coulson *et al.*, 2015). While these studies

have shown that teleosts and crustaceans (*e.g.* euphausiids, mysids and decapods) contribute significantly to the diets of these fishes (Brodeur & Pearcy 1984; Chess *et al.*, 1988; Bulman *et al.*, 2001; Demirham & Can 2009), no comprehensive comparisons have been made to investigate how diet varies among families. Of the two studies of neosebastids, *Maxillicosta scabriceps* Whitley 1935 ate mainly large crustaceans, while 50% of the diet of *Neosebastes scorpaenoides* Guichenot 1867 comprised large crustaceans, with small crustaceans, gastropods and teleosts constituting the remaining portions (Bulman *et al.*, 2001; Platell & Potter, 2001). As some sebastid and scorpaenid species increase in size, their diets shift from mainly crustaceans to primarily fish (Harmelin-Viven & Bouchon, 1976; Murie, 1995; Neves *et al.*, 2011; Baeck *et al.*, 2013).

The west and south coasts of south-western Australia exhibit major differences in geomorphology and habitat, which significantly influence their fish communities (Howard, 1989; Ayvazian & Hyndes, 1995). Extensive limestone reefs covered with dense growths of the kelp *Ecklonia radiata* are a conspicuous feature of the west coast, while less extensive, impermeable, Proterozoic granite reef structures dominated by the macroalgae *Sargassum* spp, are found along the south coast (Ayvazian & Hyndes, 1995). In addition, waters along the west coast are located in the Indian Ocean and are thus appreciably warmer than those of the south coast (Coulson *et al.*, 2010). Differing habitat and environmental conditions may result in differences in dietary composition among conspecifics from different locations. For example, on the west coast of Australia, the diet of *Pseudocaranx georgianus* (Cuvier 1833) is dominated by molluscs, but, on the south coast, crustaceans are more prevalent (Platell *et al.*, 2010). The diet of the labrid *Bodianus frenchii* (Klunzinger 1879), does not however, differ between coasts (French *et al.*, 2012).

This study aimed firstly to quantify the volumetric dietary contributions of different prey to the diet of *Neosebastes pandus*, obtained from marine waters off the west and south

coasts of south-western Australia. Since this ambush predator was collected from two coasts and over a large size range, we tested the following hypotheses: first, the diet of *N. pandus* from the west coast will contain a more diverse range of prey types due to the greater complexity of habitats available and therefore the dietary compositions will differ; second, the dietary composition of *N. pandus* will undergo a size-related change shifting to larger and more mobile prey items with increasing size. Another main aim of this study was to investigate whether the diet of *N. pandus* in the marine waters of Western Australia is consistent with published dietary information on other species in the Scorpaenidae, Triglidae and Platycephalidae and if dietary composition differs among families. This study of dietary composition of *N. pandus* and the meta-analysis of species in the three families provides fundamental knowledge for identifying functional feeding groups and estimating trophic flows for trophodynamic modelling of the marine ecosystems of south-western Australia.

## MATERIALS AND METHODS

### COLLECTION OF *NEOSEBASTES PANDUS*

Samples of large ( $> 230$  mm total length,  $L_T$ ) *N. pandus*, caught by commercial scallop (*Amusium balloti*) trawlers in waters off Rottnest Island (west coast of Western Australia;  $32.0^\circ$  S;  $115.5^\circ$  E), were collected from fish processors or purchased from a market between July and September 2012 (Austral winter and early spring) and in January and May 2013 (Austral summer and autumn; Table I). Samples of *N. pandus* (148–427 mm  $L_T$ ) were also obtained from commercial scallop trawlers operating off Esperance (south coast of Western Australia;  $33.9^\circ$  S;  $121.9^\circ$  E), between May and September of 2013, 2014 and 2015. *N.B.* that very little, or no, commercial trawling occurs between October and January due to

the seasonal closure of the scallop fishery (Kangas *et al.*, 2011). On both coasts, commercial trawling mostly occurs at depths of 16 to 40 m, using a trawl net with a mesh size of 50 mm in the wings and 45 mm in the cod-end that is towed at a speed of *c.* 6.5 km h<sup>-1</sup> for 60 to 180 min (Jones *et al.*, 2010). Scallop trawlers operate mostly at night, since this is when greater numbers of scallops are caught (Laurenson *et al.*, 1993; Sporer *et al.*, 2012). Trawling occurs on bare substratum adjacent to reef and rocky habitats.

#### QUANTIFICATION OF *NEOSEBASTES PANDUS* DIETARY COMPOSITION

The  $L_T$  of each *N. pandus* was measured to the nearest mm and its stomach removed. Stomach fullness was estimated visually on a scale of 1 to 10, with 10 being the equivalent of 100% full and fully distended (Platell *et al.*, 1998; Lek *et al.*, 2011; Coulson *et al.*, 2015). The items in each stomach were identified to the lowest possible taxonomic level, often to species, using macroscopic and microscopic examinations and the descriptions in Wells & Bryce (1988), Hutchins & Swainston (1986), Norman & Reid (2000), Miskelly (2002), Poore (2004), Edgar (2008) and Gomon *et al.*, (2008). When teleost prey had undergone extensive digestion, a combination of the morphology of their remains and the characteristics of their otoliths were used to identify the prey to family using an extensive reference collection of otoliths from fish species in south-western Australia (M. Dowling, Department of Primary Industries and Regional Development, Western Australia, unpubl. data).

The occurrence of each of the 52 prey items found in the stomachs of *N. pandus* was recorded as percentage frequency (%*F*) and the volumes of the items were estimated visually and expressed as a percentage volume (%*V*) by order or family, subsequently termed dietary components (Table II). For graphical and analytical purposes, these 33 dietary components were combined to form 12 dietary categories (Table II). Note that seagrass (Posidoniaceae)

was not selected as it was probably ingested as an unintentional consequence of prey capture (Harmelin-Vivien *et al.*, 1989). Likewise, scallop roe, which was found in only two fish and is discarded by commercial fishers, was not included in the analyses, nor was unidentifiable material, which made up only 1% of the total dietary volume and was limited to the stomachs of four *N. pandus* from the south coast.

To determine dietary trends, the mean %V contributions of the dietary categories for fish in 50 mm length classes from the lower west and south coasts were calculated and plotted as histograms. *N.B.* that the contributions of Echinodermata and Batoidea were so small that they could not be clearly represented in the histograms and were therefore not presented.

#### STATISTICAL ANALYSES OF *NEOSEBASTES PANDUS* DIETARY COMPOSITION

Preliminary multivariate analyses were aimed at exploring the major sources of variation in the dietary composition of *N. pandus*. The %V data were square-root transformed to down-weight the contributions of dietary categories with consistently high values and to avoid any tendency for those dietary components to be excessively dominant. These transformed data were then used to construct a Bray-Curtis resemblance matrix and subjected to a three-way crossed permutational multivariate analysis of variance (PERMANOVA; Anderson *et al.*, 2008) to determine whether dietary composition differed significantly with the main effects of Location (2 levels; west and south coasts, Rottnest Island and Esperance, respectively), Length Class (5 levels; 150–199, 200–249, 250–299, 300–349 and 350–399 mm), Season (4 levels; spring, summer, autumn and winter) and their interaction terms. Note that samples from fish < 150 mm and > 400 mm  $L_T$  were not included in this analysis due to small sample sizes ( $n \leq 2$ ; Table I). This PERMANOVA test demonstrated that significant



differences ( $P < 0.001$ ) were detected for location and length class, but not for season or any of the two or three-way interaction terms ( $P > 0.05$ ). Thus, season was removed as a factor from further analyses.

## LOCATION AND SIZE RELATED DIFFERENCES IN DIET

As the stomachs of individual fish may contain only a small number of the dietary categories, two samples of the same species, collected at the same time from the same location, may differ markedly in their dietary composition, which can mask subtle but real trends in diet. To reduce this potential effect, stomachs of fish from each length class at each location were randomly sorted into groups of three to five, depending on the number of fish collected (Platell *et al.*, 2001). The %V contribution of the different dietary categories in each group of replicates was averaged and square-root transformed. As the number of individual fish differed among locations and length classes (Table I), this averaging approach overcomes any potential bias created by pooled dietary data obtained from unequal numbers of individual guts, *i.e.*, a species accumulation effect (Lek *et al.*, 2011). While, this approach did result in an unequal number of replicates (*i.e.* five to eight) across the various location  $\times$  length class combinations, such unbalanced statistical designs can be analysed effectively using analysis of similarity (ANOSIM) and PERMANOVA (Anderson *et al.*, 2008; Clarke and Gorley 2015).

The averaged data for all locations and length classes were used to create a Bray-Curtis resemblance matrix, which was used to construct a distance among centroids matrix using the Location  $\times$  Length Class factor (Anderson *et al.*, 2008; Lek *et al.*, 2011). This latter resemblance matrix was then used to create a centroid non-metric multidimensional scaling

(nMDS) ordination plot, which provided a visual representation of the similarity among samples.

As fish in the 250–299, 300–349 and 350–399 mm length classes were collected from both coasts, these samples (each representing a group of three to five replicate *N. pandus*) were used to construct a Bray-Curtis resemblance matrix and subjected to a two-way crossed PERMANOVA to determine whether there was a significant location  $\times$  length class interaction and, if so, to determine the extent of that interaction relative to the main effects. As no interaction was detected, the same resemblance matrix was analysed with a two-way crossed ANOSIM test. *N.B.* that the levels in the location factor were not ordered, whereas those in the length-class factor were. Thus, while the null hypothesis for both tests were the same, *i.e.* level *A* = level *B*, the alternative hypothesis for the test for location was west coast  $\neq$  south coast, *i.e.* they were different, but in an unspecified way and that for length class was 250–299 < 300–349 < 350–399 mm, *i.e.* that the smallest difference would be 250–299 *v.* 300–349 mm and the largest would be 250–299 *v.* 350–399 mm (Clarke *et al.*, 2014a). In those cases where ANOSIM detected a significant difference, pair-wise ANOSIM comparisons were used to determine which levels of that factor showed the greatest differences. Similarity percentages analysis (SIMPER; Clarke & Gorley, 2015) and shade plots (Clarke *et al.*, 2014b) were employed to identify those dietary categories that typified and distinguished the dietary composition of each *a priori* group (SIMPER) and those that contributed the greatest proportion by volume. Shade plots are a simple visualization data matrix where a white space for a dietary category demonstrates that a dietary category was not consumed, while the depth of shading from grey to black is linearly proportional to the percentage contribution of that dietary category to the total diet (Clarke *et al.*, 2014b; Valesini *et al.*, 2014). Note that the volumetric data for location and length class were averaged prior to constructing the shade plots.

As substantial numbers of *N. pandus* in the 150–199 and 200–249 mm length classes were only collected from the south coast, a second suite of analyses were conducted solely on individuals from Esperance to examine change in diet across a wider range of lengths *i.e.* 150–400 mm  $L_T$ . The differences in mean volumetric data for groups of replicates in the 150–199, 200–249, 250–299, 300–349 and 350–399 mm length classes were tested by one-way ANOSIM to determine whether dietary composition differed across a broader range of sizes. SIMPER and shade plots were then used to help interpret the results, as described above.

#### DIETARY COMPOSITION OF THE SCORPAENIFORMES

A meta-analysis of the diet of species within the Scorpaenoidei (families Platycephalidae, Scorpaenidae and Triglidae) was conducted to determine how similar the diet of *N. pandus* was to other species within this suborder globally. Dietary information was obtained from the literature for 48 species covering a large geographical area, from the Chatham Rise at 44° S, to the Irminger Sea at 60° N and including the Mediterranean Sea, Atlantic, Pacific and Indian Oceans. To ensure consistency of taxonomic resolution among the published studies, prey items were allocated to seven dietary categories: gastropods, polychaetes, cephalopods, teleosts, large crustaceans (*e.g.* brachyurans, penaeids and stomatopods), small crustaceans (*e.g.* amphipods, isopods, mysids and ostracods) and other prey. Dietary items were recorded as either percentage mass (%*M*) or volume (%*V*) or number (%*N*). Only those studies recording data as either %*M* or %*V* were included in the meta-analysis. Percentage frequency (%*F*) of occurrence data were not available for all studies and thus were not included in Table III or the subsequent statistical analyses.

For this meta-analysis, 10 species of platycephalid, including two populations of three species (six studies), 20 scorpaenids, including two or more populations of six species and *N.*

*pandus* in the present study (18 studies) and 19 triglids, including two, or more populations of nine species (18 studies), were included (a total of 49 species from 39 studies; Table III). The dietary studies for the platycephalids (predominantly *Platycephalus* Bloch 1795 species) were carried out in southern Australian waters; those for the Scorpaenidae came largely from the Pacific Ocean, Mediterranean Sea and the Atlantic Ocean; while the Triglidae came from the broadest range of regions (Mediterranean Sea, Pacific, Atlantic and Indian Oceans and the Gulf of Mexico; Table III).

The dietary compositions by  $V\%$  and  $\%M$  of the 49 species in 77 ‘samples’ (*i.e.* each a species–location combination; Table III) were compared statistically. While each sample comprised between 20 and 26 381 individual stomach samples and thus provided a sound representation of the diet of an individual species in a given location, samples were collected from a range of geographic areas and habitats (see Table III). To remove the potentially confounding effects of intra-family differences and spatial differences in dietary composition, samples were randomly sorted into groups of two (platycephalids) or four to five (scorpaenids and triglids) species. The percentage contribution of each major dietary category in each group of replicates (18 groups) was averaged, square-root transformed and used to construct a Bray-Curtis resemblance matrix. This matrix was subjected to one-way ANOSIM to determine whether dietary compositions differed among families (three levels; Scorpaenidae, Triglidae and Platycephalidae) and to construct an nMDS ordination plot. The transformed data were then subjected to SIMPER and averaged across the replicates within a family and used to construct a shade plot.

## RESULTS

### OVERALL DIETARY COMPOSITION

A total of 25 dietary components, excluding unidentifiable components, were found in the 106 stomachs with prey items on the west coast, compared with 19 components in 125 stomachs with items on the south coast (Table I). This difference was mainly due to differences in the diversity of teleosts ingested, with 15 identified on the west coast and only seven on the south coast (Table I).

The dietary components contributing to the highest percentage volume (%*V*) also had the highest percentage frequency of occurrence (%*F*; Table II). Crustaceans, molluscs (mainly octopuses) and teleosts combined comprised 93% and 79% of the dietary contents by volume of *N. pandus* off Rottneest Island and Esperance, respectively (Table II). Among these two groups, crustaceans were the most important, constituting 33 and 45% of the %*V* of west and south-coast fish, respectively. The larger volumetric contributions made by dendrobranchs (prawns), isopods and amphipods accounted for the overall contribution of crustaceans to the diet of *N. pandus* on the south coast being 12% greater than in fish on the west coast. The contribution of polychaetes in the diets differed markedly between coasts, constituting only 6% by %*V* (12.6% by %*F*) of the diet on the west coast compared to 18% by %*V* (32% by %*F*) on the south coast, largely due to the Aphroditidae being consumed only on the south coast. The frequency and volumetric contributions of teleosts to the diet of *N. pandus* in the two locations also differed markedly, representing 33%*V* of the diet (47.2%*F*) on the west coast, but only 6%*V* (8.8%*F*) on the south coast. Tetradontids, clupeids, ostraciids, monacanthids, sillaginids and gerreids all comprised > 1%*V* of the diet of west coast *N. pandus*. On the south coast, the gerreids were the only family to contribute to > 1%*V* of the diet of *N. pandus* (Table II).

As *N. pandus* increased in body size, the volumetric contributions of different dietary categories changed greatly in both locations (Fig. 1). On the west coast, the %*V* of cephalopods and polychaetes decreased with increasing body size, from 27 and 8.5%, respectively for the 250–299 mm length class, to 9 and 1% respectively for 350–399 mm fish [Fig. 1(a)]. In contrast, the relative contribution of teleosts doubled from 21% in 250–299 mm fish to 42% in 300–349 mm fish. Decapods made similar contributions to the %*V* across

the 250 to 399 mm size classes, contributing between 26–35% to the diet of these fish [Fig. 1(a)].

On the south coast, the contribution of isopods and decapods to %V declined with increasing body size of *N. pandus*: isopods declined from 25% in the 100–149 mm length class to 5% in the 150–199 and 200–249 mm length classes. Decapods declined from 49% in the 200–249 mm fish to 31 and 2.5% in the 250–299 and 350–399 mm length classes, respectively [Fig 1(b)]. While the volumetric contributions of polychaetes also decreased from 27 to < 1% in the 150–199 and 300–349 mm length classes, this group constituted 31% of the volumetric contributions of fish in the 350–399 mm length class [Fig. 1(b)]. In contrast to the trends on the west coast, the contributions of cephalopods to the diet of south coast *N. pandus* increased with body size, peaking at 300–349 mm (50% V) and then declined to 20% V [Fig. 1(b)]. Although the proportion of teleosts consumed by *N. pandus* on the south coast increased with body size, the largest %V was 18% in the 350–399 mm length class, compared with 42% for the same length class on the west coast (Fig. 1).

#### VARIATIONS IN DIET LOCATION AND SIZE RELATED DIFFERENCES

On the centroid nMDS ordination, the points representing samples from the west coast lie to the left of those from the south coast. Both groups however, progressed sequentially from the bottom (smallest length classes) to the top of the plot (300–349 mm), before the 350–399 mm length class progress horizontally to the left (west coast) and right (south coast; Fig. 2). Two-way PERMANOVA detected a significant difference in the dietary composition of *N. pandus* between Locations (west and south coast; pseudo- $F_{1,31} = 5.33$ ,  $P < 0.01$ ) and length classes (250–299, 300–349 and 350–399 mm; pseudo- $F_{2,31} = 2.94$ ,  $P < 0.01$ ), but the location  $\times$  length class interaction was not significant (pseudo- $F_{2,31} = 1.44$ ,  $P >$

0.05). In other words, the length class differences were consistent in both locations and *vice versa*. Two-way crossed ANOSIM demonstrated that location ( $\bar{R} = 0.31$ ) accounted for more of the variation in dietary composition than length class ( $\bar{R} = 0.20$ ). Teleosts and brachyurans were identified by SIMPER as typifying the diets of west coast *N. pandus*, while brachyurans and cephalopods typified the diet of south-coast fish, as shown on the shade plot where these categories made large volumetric contributions to the overall diet at each location (Fig. 3). The significant differences in diet between the two locations were mainly due to larger quantities of teleosts and brachyurans in west-coast fish, while cephalopods and polychaetes were consumed in greater proportions on the south coast (Fig. 3).

Dietary composition differed significantly among the three length classes common to both locations (one-way ANOSIM global  $R = 0.20$ ,  $P < 0.01$ ). The diet of *N. pandus* in the 350–399 mm length class differed significantly ( $R = 0.17$ ,  $P < 0.05$ ) from the two smaller size classes (250–299 mm,  $R = 0.17$ ,  $P < 0.05$ ; 300–349 mm,  $R = 0.21$ ,  $P < 0.01$ ) because the larger fish ate fewer brachyurans and octopuses and more teleosts (Fig. 4). Cephalopods and teleosts were identified by SIMPER as typifying the diet of each length class, along with brachyurans in the two smallest classes. The uniqueness of the 350–399 length class was due to the larger individuals containing lower contributions of brachyurans and cephalopods, but relatively greater proportions of teleosts (Fig. 4).

Significant differences in dietary composition with increasing length over a wider range of length classes (*i.e.* 150–399 mm total length) were detected on the south coast (global  $R = 0.48$ ,  $P < 0.001$ ). Typically, all pair-wise comparisons differed significantly except those between consecutive length classes. The largest differences were detected between the 150–199 mm and both the 300–349 and 350–399 mm length classes ( $R > 0.80$ ,  $P < 0.01$ ). This was due to smaller *N. pandus* eating more polychaetes and brachyurans than larger individuals (Fig. 5). In contrast, larger length classes contained greater proportions of

teleosts. Cephalopods, on the other hand, were eaten in similar proportions by all size classes except the smallest fish (150–199 mm; Figs 4 and 5).

#### DIETARY COMPOSITION OF SCORPAENIFORMES

Overall, the dietary composition of members of the Scorpaenidae, Triglidae and Platycephalidae comprised large proportions, by %V or %M, of teleosts and large crustaceans (Table III). Among the scorpaenids, the diet of *N. pandus* was most similar to the diets of *Helicolenus* spp., particularly *Helicolenus barathri* (Hector 1875), due to the relatively high contribution by cephalopods and polychaetes and low proportion of small crustaceans (Table III). The high volumes of large crustaceans and lower contribution of teleosts to the diet of *N. pandus* on the south coast is comparable to other *Neosebastes* and *Scorpaena* L. 1758 species. The lower contribution of teleosts and small crustaceans to the diet of *N. pandus* from both locations in south-western Australia differs however, from that of platycephalids and triglids (Table III).

The diets of fish in the Scorpaenidae, Triglidae and Platycephalidae differed significantly among families (one-way ANOSIM global  $R = 0.74$ ,  $P < 0.001$ ). From the pairwise comparison of diets between families, the greatest differences in dietary compositions were found between platycephalids and each of the other two families (scorpaenids  $R = 0.98$ ,  $P < 0.01$ ; triglids  $R = 0.98$ ,  $P < 0.01$ ). This is evident on the nMDS plot, with the points representing platycephalids forming a discrete group on the right-hand side, clearly separated from those of the other two families (Fig. 6). Although the dietary compositions of scorpaenids and triglids differed significantly ( $R = 0.29$ ,  $P < 0.05$ ), the extent of this difference was markedly less than those for comparisons involving platycephalids. This is demonstrated on the nMDS plot where the points representing the scorpaenids and triglids



form less discrete and overlapping groups than those for the platycephalids (Fig. 6). The dietary composition of platycephalids contained greater proportions of teleosts than both the scorpaenids and triglids and lower contributions of small crustaceans. The less marked differences in diet between the latter two families was due mainly to the greater contribution of cephalopods, teleosts and gastropods to their diets (Fig. 7). Despite the geographic spread of studies, the differences in diet between the families remained consistent across regions.

## DISCUSSION

This study of the dietary composition of *N. pandus* and the meta-analysis of diets of members of the Scorpaenidae, Triglidae and Platycephalidae found major differences in the diets of *N. pandus* on the west coast (Rottneest Island) and south coasts (Esperance) of southwestern Australia and among the three families, particularly between the Platycephalidae and the two other families.

### OVERALL CONTRIBUTIONS OF TAXA TO THE DIET OF *N. PANDUS*

Although the volumetric contributions of crustaceans and molluscs to the diet of *N. pandus* from the west and south coast were similar, conspicuous differences were found in the contributions of polychaetes and teleosts. Overall, the dietary analysis revealed that this species is a carnivore and feeds predominately on benthic prey, paralleling the findings of two other neosebastids in Australia (Platell & Potter, 1998; Bulman *et al.*, 2001). For example, all prey types ingested by *N. scorpaenoides* were benthic invertebrates, crustaceans and teleosts and the large majority of the crustacean prey of *M. scabriceps* was also benthic (Platell & Potter, 1998; Bulman *et al.*, 2001). The high volumetric contribution of

polychaetes to the diet of *N. pandus* on the south coast is unusual, with this prey contributing > 10% to the diets of only two other scorpaenids, *Scorpaena notata* Rafinesque, 1810 and *H. barathri* (Bulman *et al.*, 2001; Morte *et al.*, 2001, Table III).

Like other scorpaenoids, *N. pandus* feeds on a diverse range of prey (Harmelin-Viven & Bouchon, 1976; Harmelin-Vivien *et al.*, 1989; Platell & Potter, 1998; La Mesa *et al.*, 2007) including infauna, epifauna and nektonic prey, with the greatest volumetric contributions being made by cephalopods, brachyurans, demersal teleosts and to a lesser degree, polychaetes. Since *N. pandus* is a cryptic ambush predator with a relatively large mouth, they are probably able to capture and ingest relatively large prey, even from a small size (Harmelin-Viven & Bouchon, 1976; Gerking, 1994; Platell & Potter, 1998). This strategy reduces the frequency of feeding and thus energy expenditure (French *et al.*, 2017) and explains why the dietary components contributing to the highest %V also had the highest %F.

While the diet of *N. pandus* is similar to those of other scorpaenids and neosebastids, the contribution by various prey components is distinct from other species. For example, *Scorpaenopsis cirrosa* (Thunberg 1793), previously recognized as *Dendroscorpaena cirrosa*, feeds predominantly on fishes (78% by mass) and cephalopods (16%); *Pterois volitans* (L. 1758) consumes fishes and crustaceans in relatively equal amounts; *Scorpaenopsis gibbosa* (Bloch & Schneider 1801) is exclusively piscivorous; *Sebastapistes nuchalis* (Günther 1874) [current status *Sebastapistes strongia* (Cuvier 1829)] feeds predominantly on fishes and crustaceans; and *Scorpaenodes hirsutus* (Smith 1957) (formerly *Parascorpaenodes hirsutus* Smith 1957), consumes mainly polychaetes (Harmelin-Viven & Bouchon, 1976). The neosebastid *M. scabriceps* consumes mainly crustaceans (91%), particularly small taxa such as amphipods and mysids, which is probably related to their small body size and mouth gape compared to the other species (Platell & Potter, 1998).

Studies of these closely related scorpaenid fishes reveal that their prey typically

comprises decapods and to a lesser extent teleosts and polychaetes, irrespective of size or geographical zone where the species were studied (Harmelin-Viven & Bouchon, 1976; Harmelin-Vivien *et al.*, 1989; La Mesa *et al.*, 2007; Morris & Akins 2009). With the exception of *Helicolenus percooides* (Richardson & Solander 1842), the contribution of cephalopods to the diet of other scorpaenids (*e.g.* *Scorpaena notata* Rafinesque 1810 and *M. scabriceps*), is relatively small compared with those of *N. pandus* (Harmelin-Vivien *et al.*, 1989; Platell & Potter, 1998; Morte *et al.*, 2001).

#### COMPARISONS OF DIET BETWEEN LOCATIONS

A greater number of taxa, particularly teleosts, were found in the diets of *N. pandus* from the west than south coast, which may be explained by differences in reef complexity, the physical nature of the sea floor and sediment composition (Howard, 1989; Ayvazian & Hyndes, 1995; Hutchings, 1998). The fact that the limestone reef on the west coast is structurally more complex than the granite-based reefs on the south coast is likely to influence the abundance and diversity of teleosts (Friedlander & Parrish, 1998; Gratwicke & Speight, 2005; Lingo & Szedlmayer, 2006). Teleosts were a very significant component of the diet of west-coast *N. pandus* and much less on the south coast. Eight of the 11 families of teleost prey identified in the stomachs of fish from the west coast occupy sheltered sand, reef or seagrass habitats, while four of the five fish families found in the stomachs of south-coast fish are typically found in moderately exposed sandy bays and open seas (Hutchins & Swainston, 1986; Edgar, 2008). The west-coast limestone reefs offer numerous microhabitats and refugia for the many teleost species inhabiting these waters, while at the same time providing ideal cover for *N. pandus* and an opportunity for *in situ* foraging (Howard, 1989; Ayvazian & Hyndes, 1995).

Differences in microhabitat and sediment composition may also explain the locational disparity in contributions made by brachyurans, polychaetes and gastropods to the diet of *N. pandus*. On the west coast, sediments comprise a mix of moderately coarse carbonate sands and detrital quartz derived from limestone, while those on the south coast are typically composed of fine quartz sand, which has eroded from regional granite over time (Commander, 2003; Short *et al.*, 2009). Polychaetes and gastropods were more important in the diets of south-coast fish. If teleosts are less diverse and abundant on the south coast (Ayvazian & Hyndes, 1995), *N. pandus* may be feeding opportunistically on other abundant prey types, accounting for the greater contribution of polychaetes and gastropods to the diets of fish from this coast.

Nocturnal variation in feeding patterns may also be a factor contributing to differences in the dietary composition of *N. pandus*. For example, Harmelin-Viven & Bouchon (1976) documented diel variation in scorpaenid diets, with greater volumes of polychaetes, shrimps and teleosts being consumed at night than during the day. However, the reverse pattern was found for brachyurans, which were consumed in greater numbers during the day. As scorpaenids hide in reef holes during the day, they may feed opportunistically on the fauna that takes refuge within these environments (Harmelin-Viven & Bouchon, 1976), which may differ to the prey consumed at night. A number of the prey of *N. pandus*, such as the Aphroditidae, Octopoda and other species from the Mollusca (Polyplacophora and Volutidae) are active night-time feeders (Edgar, 2008).

#### SIZE-RELATED CHANGES IN DIETARY COMPOSITION

The dietary composition of *N. pandus* differed markedly with increasing body size on both coasts, shifting from small prey such as amphipods and isopods in smaller fish (< 249

mm in length), to larger prey such as large brachyuran crabs, cephalopods and teleosts in larger individuals ( $\geq 250$  mm). Similar size-related changes in diet have been documented in other scorpaenid species. For example, Harmelin-Vivien *et al.*, (1989) found that juveniles of *Scorpaena* species feed mainly on small crustaceans and amphipods, while the larger adult fish ingest teleosts and decapods, with other species in the Sebastidae and Platycephalidae also showing this pattern ( Blaber & Bulman, 1987; Platell & Potter, 1998; Baeck, *et al.*, 2013; Hashemi & Taghavi Motlagh, 2013). The shift to larger prey probably reflects morphological and maturational changes such as an increased mouth gape, as well as improved locomotory and sensory abilities, resulting in an increase in the ability of larger *N. pandus* to capture and ingest larger, more mobile prey (Keenleyside, 1979; Gerking, 1994; Wootton, 1998; Consoli *et al.*, 2010). Size related dietary changes suggest that the most significant transformations in feeding occur once fish reach a length of *c.* 300 mm.

#### DIETARY VARIATION WITHIN THE SCORPAENIFORMES

The meta-analysis of 49 species of scorpaeniformes demonstrated that the diet of the platycephalids differed strikingly from those of the scorpaenids and triglids, with more subtle differences occurring between these latter two families. These findings are consistent with Platell & Potter (2001), who showed that interspecific dietary variation is typically significant between families due to distinct differences in body shape, head and mouth morphology and feeding behaviour. Unlike the triglids and scorpaenids, platycephalids have a distinctly flattened head with large sub-terminal jaws that open downwards, a large gape and dorsally located eyes (Gosline, 1996; Platell & Potter, 2001; Gomon, *et al.*, 2008). They usually burrow just below the substratum and have a tendency to feed on large benthic prey such as teleosts and crabs (Platell & Potter, 1998; Barnes *et al.*, 2011, Coulson *et al.*, 2016). Their

capacity for ingesting large prey is accommodated by the ability to expand their stomach ventrally, due to a clear separation in the pelvic girdle; a feature not found in the scorpaenids and triglids (Douglas & Lanzing, 1981; Gosline, 1996).

Triglids, in contrast, have a small sub-terminal mouth that opens downwards, well-developed eyes (Platell & Potter, 2001; Gomon *et al.*, 2008) and modified pectoral fin rays equipped with tactile chemosensory receptors, which enable these bottom-dwelling species to detect, excavate and flush out epibenthic prey (Bardach & Case, 1965; Silver & Finger, 1984; Manderson *et al.*, 1999). Superficially, the scorpaenids are morphologically similar to the triglids (Poss & Eschmeyer, 2003), but have a more prominent head with a large terminal mouth that opens outwards (Platell & Potter, 2001; Gomon *et al.*, 2008). The tendency of scorpaenids to take refuge during the day within and around reef cavities, where they prey on cryptofauna (Harmelin-Viven & Bouchon, 1976), may explain their overlap of dietary categories with the triglids (Fig. 6). The greater contributions of cephalopods and teleosts to the diet of scorpaenids than triglids may however, be explained by their significantly larger gape (Gomon *et al.*, 2008), which allows them to capture and ingest a larger range of prey types.

Special thanks are due to M. Jackson (SELfish Fine Seafoods, Applecross), commercial fisherman B. McGovern and his crew and S. Flynn (All Seas Fish Supply, Esperance) for their very generous assistance in obtaining samples. Financial support was provided by Murdoch University.

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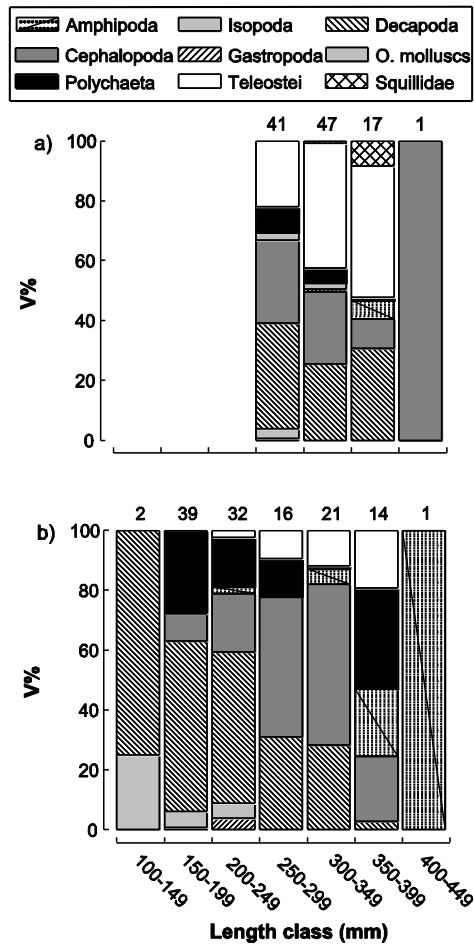
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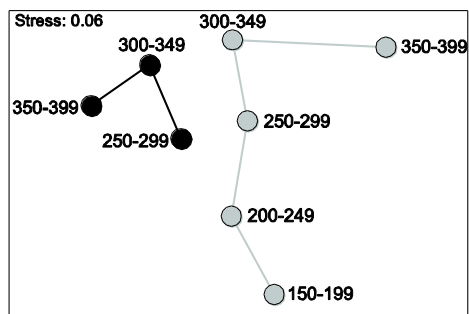


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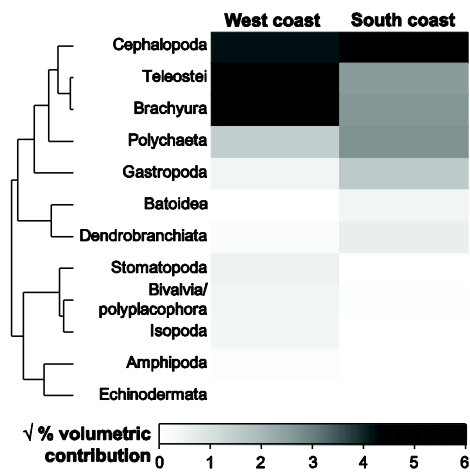
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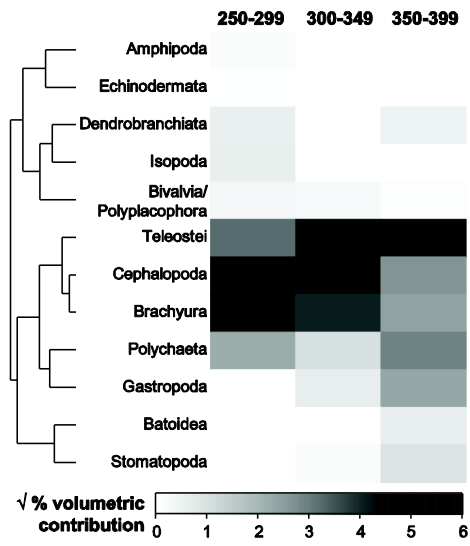
**Fig. 1.**



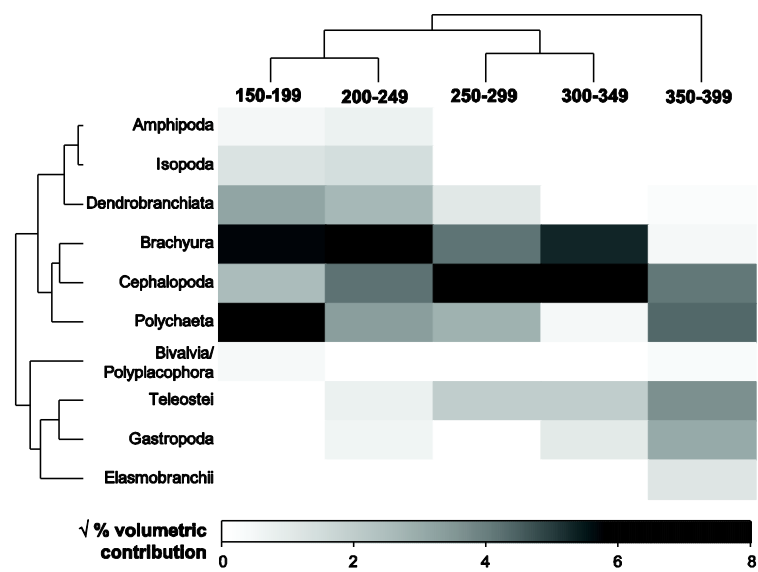
**Fig. 2.**



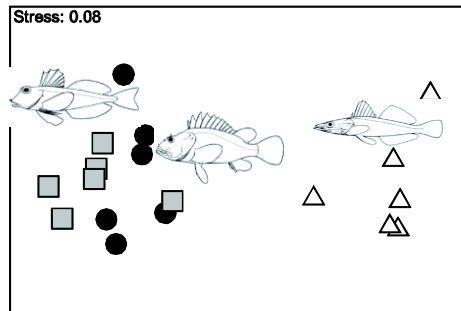
**Fig. 3.**



**Fig. 4.**

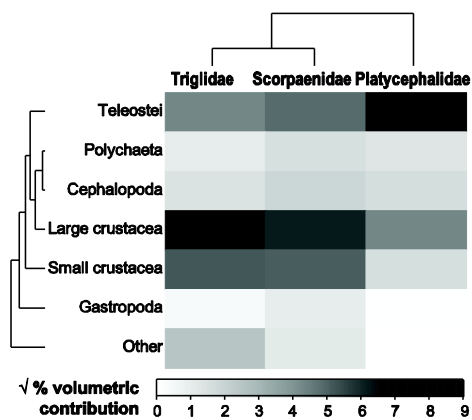


**Fig. 5.**



**Fig. 6.**





**Fig. 7.**

FIG. 1. Stacked bar graphs, showing the mean percentage volumetric (%V) contributions of dietary categories (◻, Amphipoda; ■, Isopoda; ◻, Decapoda; ■, Cephalopoda; ◻, Gastropoda; ■, other molluscs; ■, Polychaeta; □, Teleostei; ⊠ Squillidae) of prey to the stomachs of sequential 50 mm length classes of *Neosebastes pandus* from (a) the west coast (Rottneest Island) and (b) the south coast (Esperance) of south-western Australia. Sample sizes are given above the bar graphs for each total length ( $L_T$ ) class. Unidentified material has been removed and percentages adjusted to equal 100 in total. Amalgamated dietary categories as listed in Table II (●).

Typesetter

- 1 Change Length class to  $L_T$ .
- 2 X-axis: change - to –.
- 2 Change V% to %V.

FIG. 2. Non-metric multidimensional scaling (nMDS) ordination plot, derived from distance-among-centroid matrix constructed from Bray–Curtis similarity matrices that employed the volumetric contributions of the 12 main prey categories to the diets of sequential 50 mm length classes of *Neosebastes pandus* from the west coast (Rottneest Island; ●) and south coast (Esperance; ●) of south-western Australia.

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- 1 Change - to –.

FIG. 3. Shade plot showing the mean square-root transformed percentage volumetric contributions of 12 main dietary categories to the stomach contents of *Neosebastes pandus* from the west coast (Rottnest Island) and south coast (Esperance) of south-western Australia. White represents an absence of prey, and grey to black represents the increasing contribution of a dietary category to the total diet.

FIG. 4. Shade plot showing the mean square-root transformed percentage volumetric contributions of 12 main dietary categories to the stomach contents of *Neosebastes pandus* in the 250–299, 300–349 and 350–399 mm length classes from the west coast (Rottnest Island) and south coast (Esperance) of south-western Australia, combined. White represents an absence of prey, and grey to black represents the increasing contribution of a dietary category to the total diet.

Typesetter

1 Change - to –.

FIG. 5. Shade plot showing the mean square-root transformed percentage volumetric contributions of 12 main dietary categories to the stomach contents of *Neosebastes pandus* collected from the south coast (Esperance) of south-western Australia in the 150–199, 200–249, 250–299, 300–349 and 350–399 mm length classes. White represents an absence of prey, and grey to black represents the increasing contribution of a dietary category to the total diet. Note that within the category Bivalve and polyplacophora, bivalves were recorded only for south-coast fish.

1 Change - to –.

FIG. 6. Non-metric multidimensional scaling (nMDS) ordination plot, derived from distance-among-centroid matrix constructed from Bray–Curtis similarity matrices that employed the volumetric contributions of the seven main prey categories to the diets of scorpaenids (●), triglids (■) and platycephalids (△). A line drawing of a typical member of each family is provided to highlight the similarities and differences in their morphology. (Line drawings reproduced with permission from Nelson *et al.*, 2016).

FIG. 7. Shade plot showing the mean square-root transformed percentage volumetric contributions of seven main prey categories to the diets of scorpaenids (●), triglids (■) and platycephalids (△). White represents an absence of prey, and grey to black represents the increasing contribution of a dietary category to the total diet.

TABLE I. Total number of stomach samples of *Neosebastes pandus* that contained prey in each sequential 50 mm length class in each season from the west coast (Rottnest Island) and south coast (Esperance) of south-western Australia.

Total length (mm)	Location and Season								
	West Coast					South Coast			
	Su	Au	Wi	Sp	Total	Au	Wi	Sp	Total
100–149							2		2
150–199						12	26	1	39
200–249						10	18	4	32
250–299	12	16	11	2	41	2	6	8	16
300–349	12	16	17	2	47	5	5	11	21
350–399	2	7	6	2	17	4	3	7	14
400–449	1				1			1	1
Total	27	39	34	6	106	33	60	32	125

Au, autumn; Sp, spring; Su, summer; Wi, winter

TABLE II. Mean volumetric contribution (%*V*) and frequency of occurrence (%*F*) of the different dietary components, including the amalgamated dietary categories used for multivariate analysis (◆) and stacked histograms (●) of *Neosebastes pandus* from the west coast (Rottnest Island) and south coast (Esperance) of south-western Australia. Bold denotes total %*V* and %*F* contribution of 12 major groups, shading denotes dietary contributions > 15% for %*V* and > 20% for %*F*.

Dietary component/category		West coast			South coast		
		% <i>V</i>	± S.E.	% <i>F</i>	% <i>V</i>	± S.E.	% <i>F</i>
Crustacea (total)		<b>32.58</b>	–	<b>57.55</b>	<b>44.49</b>	–	<b>88.00</b>
Amphipoda	◆●	0.20	1.94	1.89	1.16	4.61	3.20
Isopoda	◆●	1.27	6.31	2.83	3.28	4.01	8.80
Stomatopoda	◆	1.65	–	2.83	–	–	–
Decapoda (total)	●	<b>29.46</b>	<b>5.94</b>	<b>50.00</b>	<b>40.05</b>	<b>5.37</b>	<b>76.00</b>
Brachyura	◆	26.76	6.14	44.34	25.28	4.30	40.00
Dendrobranchiata	◆	0.38	6.98	0.94	6.20	4.31	14.40
Unidentifiable		2.31	–	4.72	8.57	–	21.60
Crustacea							
Mollusca (total)		<b>26.82</b>	–	<b>33.96</b>	<b>29.12</b>	–	<b>35.20</b>
Gastropoda	◆●	1.27	10.26	1.89	4.52	8.31	4.80
Other molluscs (total)	◆●	<b>1.89</b>	–	1.89	<b>0.28</b>	–	1.60
Bivalvia		0.94	–	0.94	0.28	1.92	1.60
Polyplacophora		0.94	–	0.94	–	–	–
Cephalopods (total)	◆●	<b>23.66</b>	–	<b>30.19</b>	<b>24.32</b>	–	<b>28.80</b>
Octopoda		22.72	7.08	29.25	19.56	6.99	23.20
Teuthida		0.94	–	0.94	0.72	8.05	0.80
Unidentifiable		–	–	–	4.04	7.57	4.80
Cephalopoda							
Polychaeta (total)	◆●	<b>5.66</b>	–	<b>12.26</b>	<b>17.75</b>	–	<b>32.00</b>
Aphroditidae		–	–	–	9.63	5.19	19.20
Other polychaetes		5.66	5.67	12.26	8.12	6.08	12.80
Teleostei (total)	◆●	<b>33.47</b>	–	<b>47.17</b>	<b>5.64</b>	–	<b>8.80</b>
Tetraodontidae		1.32	4.51	2.83	–	–	0.00
Clupeidae		3.20	8.27	3.77	0.36	4.02	0.80
Ostraciidae		7.50	7.88	9.43	–	–	0.00
Pinguipedidae		0.19	1.94	0.94	–	–	0.00
Monacanthidae		1.89	9.67	1.89	–	–	0.00
Gerreidae		1.51	7.98	1.89	1.60	8.91	1.60
Sillaginidae		4.25	7.85	5.66	–	–	0.00
Carangidae		0.94	9.71	0.94	0.80	8.94	0.80
Pleuronectidae		–	–	–	0.32	3.58	0.80
Leptoscopidae		0.94	9.71	0.94	–	–	0.00
Syngnathidae		0.19	1.94	0.94	–	–	0.00
Callionmidae		–	–	0.00	0.80	8.94	0.80
Congridae		0.47	4.86	0.94	–	–	0.00
Unidentifiable		11.08	6.85	16.98	1.76	4.28	4.00
Teleostei							
Posidoniaceae		0.67	3.89	3.77	–	–	–
Echinodermata	◆	0.05	1.00	0.94	–	–	–

Elasmobranchii	♦	–	–	–	0.80	–	–
Scallop roe		0.75	–	0.94	0.80	8.94	0.80
Unidentified material		–	–	–	1.40	4.48	3.20
Stomachs examined ( <i>n</i> )		122			153		
Stomachs with prey ( <i>n</i> : %)		106: 87%			125: 82%		

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TABLE III. The mass (%M) and volume (%V) of the seven main prey groups, gastropods (G), polychaetes (P), cephalopods (C), teleosts (T), large crustaceans (LC), small crustaceans (SM) and other prey (O; <sup>a</sup>offal; <sup>b</sup>echinoderms; <sup>c</sup>ascidians; <sup>d</sup>tunicates; <sup>e</sup>unidentified material; <sup>f</sup>amphioxiforms), in the diets of the species within the Platycephalidae, Scorpaenidae and Triglidae for which published data were available

Species	Data	Main prey categories							<i>n</i>	Length range	Location	Habitat	Reference
		G	P	C	T	LC	SC	O					
Scorpaenidae													
<i>Scorpaena scrofa</i>	%M			17	70	12	5	64	~1–320	W Mediterranean	Soft sediment	Cabiddu <i>et al.</i> , 2010	
<i>Scorpaena scrofa</i>	%M			5	71	24		39	111–230 <sup>LS</sup>	CN Mediterranean	Seagrass	<sup>2</sup> Harmelin-vivien <i>et al.</i> , 1989	
<i>Scorpaena porcus</i>	%M		4	5	7	73	1	230	~ 110–150	NW Mediterranean	Soft sediment	Morte <i>et al.</i> , 2001	
<i>Scorpaena porcus</i>	%M				29	69	1	321	85–225	C Mediterranean	Rubble-seagrass	Arcuelo <i>et al.</i> , 1993	
<i>Scorpaena porcus</i>	%M				24	72	2	277	22–240 <sup>LS</sup>	CN Mediterranean	Seagrass	<sup>2</sup> Harmelin-vivien <i>et al.</i> , 1989	
<i>Scorpaena porcus</i>	%M	1	2		4	90	2	715	87–246	CS Mediterranean	Sand, mud, rock	Rafrafi-Nouira <i>et al.</i> , 2016	
<i>Scorpaena notata</i>	%M		11	12	3	65	6	576	~ 110–150	NW Mediterranean	Soft sediment	Morte <i>et al.</i> , 2001	
<i>Scorpaena notata</i>	%M	1	3		7	48	22	230	27–176 <sup>LS</sup>	CN Mediterranean	Seagrass	<sup>2</sup> Harmelin-vivien <i>et al.</i> , 1989	
<i>Scorpaena maderensis</i>	%M				16	65	10	245	49–135 <sup>LS</sup>	NE Atlantic	Rocky reefs	Machado <i>et al.</i> , 2014	
<i>Scorpaena maderensis</i>	%M				5	74	15	182	48–109	C Mediterranean	Rocky reefs	La Mesa <i>et al.</i> , 2007	
<i>Helicolenus dactylopterus dactylopterus</i>	%M			1	43	51	2	619	52–469	NE Atlantic	Soft sediment	Neves <i>et al.</i> , 2011	
<i>Helicolenus dactylopterus dactylopterus</i>	%M	1	1		11	69	7	455	33–249	C Mediterranean	Soft sediment	Consoli <i>et al.</i> , 2010	
<i>Helicolenus percoides</i>	%M	2	1	32	45	9	8	848	na	SW Pacific	Soft sediment	Bulman <i>et al.</i> , 2001	
<i>Helicolenus percoides</i>	%M			9	16	60	1	494	116–490	SW Pacific	Soft sediment	Horn <i>et al.</i> , 2012	
<i>Helicolenus barathri</i>	%M	8	12	5	29	9	21	74	na	SW Pacific	Soft sediment	Bulman <i>et al.</i> , 2001	
<i>Helicolenus hilgendorffii</i>	%M				54	43	3	93	35–135 <sup>LS</sup>	NW Pacific	Soft sediment	Baeck <i>et al.</i> , 2013	
<i>Sebastes flavidus</i>	%M			2	15	2	57	164	300–580 <sup>LF</sup>	NE Pacific	Soft sediment	Bodeur & Pearcy, 1984	
<i>Sebastes pinniger</i>	%M				8		92	368	370–600 <sup>LF</sup>	NE Pacific	Soft sediment	Bodeur & Pearcy, 1984	
<i>Sebastes alutus</i>	%M					4	95	73	365 ± 60 (s.d.)	NE Pacific	Soft sediment	Bodeur & Pearcy, 1984	
<i>Sebastes diploproa</i>	%M					8	90	62	265 ± 42 (s.d.)	NE Pacific	Soft sediment	Bodeur & Pearcy, 1984	
<i>Sebastes crameri</i>	%M				1	1	98	30	330 ± 77 (s.d.)	NE Pacific	Soft sediment	Bodeur & Pearcy, 1984	
<i>Sebastes jordani</i>	%V						89	977	99–272 <sup>LS</sup>	E Pacific	Soft sediment	Chess <i>et al.</i> , 1988	
<i>Sebastes caurinus</i>	%M				78	20	1	602	~ 110–350	NE Pacific	Rocky reefs	Murie, 1995	
<i>Sebastes maliger</i>	%M		1		68	19	11	285	~ 110–350	NE Pacific	Rocky reefs	Murie, 1995	
<i>Sebastes mentella</i>	%V			10	10	5	2	73 <sup>a</sup>	26,38 1	N Atlantic	Soft sediment	Gonzalez <i>et al.</i> , 2000	



<i>Neosebastes scorpaenoides</i>	%M	23			18	50	8	30	na	SW Pacific	Soft sediment	Bulman <i>et al.</i> , 2001
<i>Neosebastes pandus</i> (west coast)	%V	1	6	24	33	31	2	122	254–418	SE Indian	Sand–rubble	Present study
<i>Neosebastes pandus</i> (south coast)	%V	4	18	24	6	40	4	153	148–416	SE Indian	Sand–rubble	Present study
<i>Maxillicosta scabriceps</i>	%V		7					207	30–145	SE Indian	Soft sediment	Platell & Potter, 1998
Triglidae												
<i>Chelidonichthys capensis</i>	%V			3	34	62		1,416	na	SW Indian	Soft sediment	McPhail, 1998
<i>Chelidonichthys obscures</i>	%M				9	30	60	555	116–193 <sup>LS</sup>	CS Mediterranean	Soft sediment	Boudaya <i>et al.</i> , 2007
<i>Chelidonichthys obscures</i>	%V		1	3	1	53	39	1,092	225 ± 0.1 (S.E.)	NE Atlantic	Soft sediment	Lopez–Lopez <i>et al.</i> , 2011
<i>Trigloporus lastoviza</i>	%M			6		60	33	860	98–165 <sup>LS</sup>	CS Mediterranean	Soft sediment	Boudaya <i>et al.</i> , 2007
<i>Chelidonichthys lucerna</i>	%M					40	58	1,114	113–415	NE Mediterranean	Soft sediment	Lopez–Lopez <i>et al.</i> , 2011
<i>Chelidonichthys lucerna</i>	%V		2	1	23	73	1	1,073	295 ± 0.1 (S.E.)	NE Atlantic	Soft sediment	Lopez–Lopez <i>et al.</i> , 2011
<i>Chelidonichthys lucerna</i>	%M					40	58	1,096	63–415	NE Mediterranean	Soft sediment	Stagioni <i>et al.</i> , 2012
<i>Chelidonichthys kumu</i>	%M	3				90		25	na	SW Pacific	Soft sediment	Bulman <i>et al.</i> , 2001
<i>Chelidonichthys kumu</i>	%V		4	1	12	37	17	135	160–267	SW Pacific		Park <i>et al.</i> , 2017a
<i>Trigla lyra</i>	%V	2	2		1	44	15	807	203 ± 0.1 (S.E.)	NE Atlantic	Soft sediment	Caragitsou & Papaconstantinou, 1994
<i>Trigla lyra</i>	%M	5	1	2		44	48	246	65–295 <sup>LF</sup>	NE Mediterranean	Soft sediment	Caragitsou & Papaconstantinou, 1994
<i>Lepidotrigla cavillone</i>	%M					7	93	203	40–140	E Mediterranean	Soft sediment	Terrats <i>et al.</i> , 2000
<i>Lepidotrigla cavillone</i>	%M						56	694	64–176	NE Mediterranean	Soft sediment	Labropoulou & Machias 1998
<i>Lepidotrigla modesta</i>	%V		3	1		15	80	133	50–180	SE Indian	Soft sediment	Platell & Potter, 1999
<i>Lepidotrigla modesta</i>	%M		4		1	63	10	129	na	SW Pacific	Soft sediment	Bulman <i>et al.</i> , 2001
<i>Lepidotrigla modest</i>	%V		2	1		50	27	86	139–197	SW Pacific	Soft sediment	Park <i>et al.</i> , 2017a
<i>Lepidotrigla papilio</i>	%V		1	3		20	73	181	50–175	SE Indian	Soft sediment	Platell & Potter, 1999
<i>Lepidotrigla Vanessa</i>	%M					88	11	20	na	SW Pacific	Soft sediment	Bulman <i>et al.</i> , 2001
<i>Lepidotrigla mulhalli</i>	%M					4	68	170	105–218	SW Pacific	Soft sediment	Park <i>et al.</i> , 2017b
<i>Lepidotrigla mulhalli</i>	%V					1	12	106	103–207	SW Pacific		Park <i>et al.</i> , 2017a
<i>Lepidotrigla Vanessa</i>	%M					44	39	162	119–248	SW Pacific	Soft sediment	Park <i>et al.</i> , 2017b
<i>Trigloporus lastoviza</i> ( <i>Chelidonichthys</i> )	%M		1	14	1	59	24	203	50–250	E Mediterranean	Soft sediment	Terrats <i>et al.</i> , 2000
<i>Trigloporus lastoviza</i> ( <i>Chelidonichthys</i> )	%M						91	396	50–250	NE Mediterranean	Soft sediment	Labropoulou & Machias 1998
<i>Trigloporus lastoviza</i> ( <i>Chelidonichthys</i> )	%M		1	4	15	59	17	296	106–260	CS Mediterranean	Soft sediment	Ben Jrad <i>et al.</i> , 2010
<i>Chelidonichthys cuculus</i> ( <i>Aspitrigla</i> )	%M			6	20	36	39	209	50–300	E Mediterranean	Soft sediment	Terrats <i>et al.</i> , 2000
<i>Chelidonichthys cuculus</i> ( <i>Aspitrigla</i> )	%V			3	26	55	15	4,569	189 ± 0.1 (S.E.)	NE Atlantic	Soft sediment	Lopez–Lopez <i>et al.</i> , 2011
<i>Chelidonichthys cuculus</i> ( <i>Aspitrigla</i> )	%M		2	5	27	41	20	193	~ 85–235	NW Mediterranean	Soft sediment	Moreno–Amich, 1992
<i>Eutrigla gurnardus</i>	%M					25	50	449	60–255	NE Mediterranean	Soft sediment	Montanini <i>et al.</i> , 2010
<i>Eutrigla gurnardus</i>	%V			4	30	46	19	5,031	171 ± 0.1 (S.E.)	NE Atlantic	Soft sediment	Lopez–Lopez <i>et al.</i> , 2011
<i>Eutrigla gurnardus</i>	%M					18	33	589	~ 85–235	NW Mediterranean	Soft sediment	Moreno–Amich, 1994
<i>Prionotus roseus</i> ( <i>scitulus</i> )	%V		14	2	1	16	7	60 <sup>f</sup> 469	~ 21–140 <sup>LS</sup>	NE Gulf of Mexico	Soft sediment	Ross, 1978

<i>Prionotus nudigula</i>	%M	1		13	54	32 <sup>c</sup>	248	54–166	SW Atlantic	Soft sediment	de Sao Clemente <i>et al.</i> , 2014
<i>Prionotus punctatus</i>	%M		1	33	18	48 <sup>c</sup>	67	54–305	SW Atlantic	Soft sediment	de Sao Clemente <i>et al.</i> , 2014
<i>Pterygotrigla polyommata</i>	%M		77	23			22	na	SW Pacific	Soft sediment	Bulman <i>et al.</i> , 2001
<i>Bellator brachyichir</i>	%M		1	19	16	64 <sup>c</sup>	537	34–83	SW Atlantic	Soft sediment	de Sao Clemente <i>et al.</i> , 2014
Platycephalidae											
<i>Ratabulus diversidens</i>	%M		100				126	95–409	SW Pacific	Soft sediment	Coulson <i>et al.</i> , 2015
<i>Platycephalus richardsoni</i>	%M		96	2	1		350	na	SW Pacific	Soft sediment	Coulson <i>et al.</i> , 2015
<i>Platycephalus bassensis</i>	%M	1	6	91	1		42	na	SW Pacific	Soft sediment	Klumpp and Nichols, 1983
<i>Leviprora inops</i>	%V		1	92	7		140	138–631	SE Indian	Seagrass	Coulson <i>et al.</i> , 2015
<i>Platycephalus caeruleopunctatus</i>	%M	8	2	79	10	1	270	154–470	SW Pacific	Soft sediment	Barnes <i>et al.</i> , 2011
<i>Platycephalus richardsoni</i>	%M			83	13	4	83	83–197	SW Pacific	Soft sediment	Klumpp and Nichols, 1983
<i>Ambiserrula jugosa</i>	%M			78	19	3	74	83–197	SW Pacific	Soft sediment	Coulson <i>et al.</i> , 2015 ; Platell <i>et al.</i> , 2006
<i>Platycephalus westraliae</i>	%V	1	1	75	20	3	362	49–600	SE Indian	Sand	Barnes <i>et al.</i> , 2011
<i>Platycephalus grandispinis</i>	%M	20	10	51	15	1	406	41–275	SW Pacific	Soft sediment	Barnes <i>et al.</i> , 2011
<i>Platycephalus laevigatus</i>	%V		8	64	27	1	296	~ 280–510	SW Pacific	Seagrass	Bulman <i>et al.</i> , 2001
<i>Platycephalus laevigatus</i>	%V		5	63	32		415	171–545	SE Indian	Seagrass	Bulman <i>et al.</i> , 2001
<i>Platycephalus speculator</i>	%V	1	1	33	63	2	413	~ 200–500	SE Indian	Sand, seagrass	Barnes <i>et al.</i> , 2011
<i>Platycephalus grandispinis</i>	%M	4	4	29	37	26	304	103–380	SE Indian	Sand, soft sediment	Barnes <i>et al.</i> , 2011

*n*, sample size. Length range is provided as total length ( $L_T$ , mm), unless otherwise specified ( $L_S$ , standard length in mm;  $L_F$ , fork length, mm) and ~ is used to denote those studies in which length range was ascertained from length-frequency data. The mean length ( $\bar{x}$ ) and S.D. or S.E. is presented for those studies which only provided this information. Location refers to the broad geographic region in which the study was conducted and habitat refers to the benthos type over which samples in each study were collected. Table ordered to match the order defined by seriation in a shade plot (Fig. 7).