

## Ecological singularity of temperate mesopredatory myliobatoid rays (Chondrichthyes: Myliobatiformes)

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**Abstract.** Many myliobatoid rays are important mesopredators, having significant effects on coastal benthic communities. In tropical and subtropical high-diversity oligotrophic ecosystems, they partition their trophic resources, which results in high ecological singularity. However, it is unknown whether this is true for temperate low-diversity eutrophic ecosystems. In the present study, we tested, for the first time, the hypothesis that myliobatoid mesopredators are ecologically redundant in a temperate low-diversity eutrophic ecosystem. We quantified diet and measured intra- and interspecific trophic overlap in the three species that regularly occur off Uruguay and northern Argentina, namely *Myliobatis goodei*, *Myliobatis ridens* and *Dasyatis hypostigma*. *M. ridens* had a typical durophagic diet composed of bivalves and gastropods, *M. goodei* fed primarily on polychaetes and decapods, diverging from the durophagic diet typical of its genus, and *D. hypostigma* preyed primarily on amphipods and decapods. There were ontogenetic and seasonal dietary differences in all three species. It is concluded that ecological singularity is present in this temperate myliobatoid assemblage, with each species having a different trophic niche. The practice of pooling together myliobatoid mesopredators in trophic models must be abandoned unless there is evidence of ecological redundancy.

**Additional keywords:** Dasyatidae, durophagy, ecological redundancy, Myliobatidae, niche partitioning, trophic ecology.

Received 23 December 2015, accepted 10 June 2016, published online 17 August 2016

### Introduction

Ecological (or functional) redundancy among species implies that several species play identical or similar roles in an ecosystem. Ecological redundancy is a fundamental characteristic of ecosystems, and it is a central concept to understanding the relationship between biodiversity and ecosystem functioning. Theoretically, ecosystems with a higher redundancy will be more resilient than ecosystems with low redundancy, because more species will play similar roles (Reich *et al.* 2012). The opposite to ecological redundancy is ecological singularity, in which different species play different roles in ecosystem functioning (Naeem 1998). Therefore, understanding how redundant or singular species are is key to estimating their importance in ecosystem functioning.

Most species in the order Myliobatiformes (eagle rays, stingrays and relatives) are benthic predators that may cause effects of great magnitude on the soft-bottom communities on which they feed. They can modify the benthic community either through consumption or because they modify the habitat when excavating, creating feeding pits (VanBlaricom 1982; Thrush *et al.* 1991, 1994; Ebert and Cowley 2003; O'Shea *et al.* 2012). Some myliobatoid rays are keystone species because they have a

strong effect on one or more characteristics of the ecosystem and their impact is disproportionately large relative to their abundance (Power *et al.* 1996). In fact, in some regions where myliobatoid species have been released from predation, large reductions in their benthic invertebrate prey have been observed (Myers *et al.* 2007).

Knowledge regarding the trophic ecology of myliobatoids is fragmentary. Despite the ecological importance of myliobatoid rays as benthic predators, their trophic ecology has received less attention than that of other batoids. Approximately 12% (59 species) of the species of Myliobatiformes have at least one study on their diet (Jacobsen and Bennett 2013); this figure is not different to that of better-known batoid groups, such as skates (Rajiformes; Ebert and Bizzarro 2007). However, the replication of studies within species is significantly lower among myliobatoids than among skates (Jacobsen and Bennett 2013). Furthermore, most analyses of the trophic ecology of myliobatoid rays are monospecific, which precludes trophic comparison among species of the same region (Jacobsen and Bennett 2013).

Resource partitioning is believed to be a major driver of elasmobranch diversity (White and Sommerville 2010). Most studies comparing the trophic niche of sympatric myliobatoid

mesopredators have found a marked pattern of interspecific resource partitioning (Platell *et al.* 1998; Marshall *et al.* 2008; Flores-Ortega *et al.* 2011; Jacobsen and Bennett 2012; Navarro-González *et al.* 2012; Pardo *et al.* 2015), which indicates high species singularity. Only one study found high trophic redundancy among four species of myliobatoid rays from coral reefs, hypothesising that these species partition their niches spatially or temporally rather than trophically (O'Shea *et al.* 2013). Most of these studies have been performed in ecosystems with very high myliobatoid species richness in tropical or subtropical waters. These observed high levels of species singularity could be related to the high myliobatoid species richness typical of tropical coastal ecosystems (Compagno 1990; White and Sommerville 2010), such as those of the northern half of Australia or the eastern central Pacific, because niche partitioning is a common process allowing species coexistence in high-diversity ecosystems (Luiselli 2006). So far, studies on trophic resource partitioning among myliobatoid mesopredators of low-diversity eutrophic temperate regions are under-represented compared with high-diversity oligotrophic tropical ecosystems. This precludes analysing latitudinal and geographic patterns of the ecological role of these mesopredators.

Highly productive temperate coastal ecosystems, with lower myliobatoid diversity than oligotrophic tropical ecosystems, could impose weaker selective pressures for niche differentiation. The temperate coastal ecosystem off northern Argentina and Uruguay is characterised by very high primary productivity. This is driven primarily by the considerable discharge of the Río de la Plata (i.e.  $22\,000\text{ m}^3\text{ s}^{-1}$ ), which brings very large amounts of organic matter and nutrients into the coastal ocean (Acha *et al.* 2004). This temperate eutrophic ecosystem contrasts markedly with oligotrophic coastal ecosystems in which myliobatoid resource partitioning has been studied before (see Sherman *et al.* 2007). Therefore, investigating trophic resource partitioning of myliobatoid rays off northern Argentina and Uruguay will allow for the first estimation of the degree of ecological singularity of these rays in a temperate ecosystem with very high primary productivity.

In the temperate coastal ecosystem off northern Argentina and Uruguay, up to nine species of myliobatoid rays have been reported, namely *Bathytoshia centroura* and *Dasyatis hypostigma* (Dasyatidae), *Gymnura altavela* (Gymnuridae), *Myliobatis freminvillei*, *Myliobatis goodei* and *Myliobatis ridens* (Myliobatidae), *Rhinoptera brasiliensis* (Rhinopteridae) and *Manta birostris* and *Mobula hypostoma* (Mobulidae; Menni and Lucifora 2007; Ruocco *et al.* 2012). Most of these species are present just occasionally and only three species are regularly found in this region, namely *D. hypostigma*, *M. goodei* and *M. ridens*, being common components of the inshore community (Cousseau *et al.* 2007). Cousseau *et al.* (2007) reported *D. hypostigma* as feeding on benthic invertebrates, such as cumaceans and lancelets, without any quantification. The available information on the species of *Myliobatis* is less reliable because, until recently, the two common species were grouped together under '*M. goodei*' (Ruocco *et al.* 2012). As such, these data have to be treated at the genus level. Refi (1975) and Cousseau *et al.* (2007) reported a diet comprising molluscs, crustaceans and polychaetes for *Myliobatis* spp. More recently, Molina and Lopez Cazorla (2015) reported a diet composed of bivalves, polychaetes and amphipods, in decreasing

order of importance, for *M. goodei*. However, these results should be interpreted with caution because Molina and Lopez Cazorla (2015) did not address species identification and their samples were taken in 2008, before the formal description of *M. ridens*. Functionally, these myliobatoid rays are mesopredators because they are regularly preyed upon by large sharks occurring in the study area (Lucifora *et al.* 2005, 2006, 2009a, 2009b).

Herein we provide, for the first time, a quantitative analysis of the trophic ecology of the three common species of Myliobatiformes present off Argentina and Uruguay. We took particular care in the species identification of each sample in order to provide reliable information for every species. The main objective of the study was to test the hypothesis that, given the low species richness and high biological productivity, ecological singularity is low among myliobatoid rays of the temperate eutrophic ecosystem off Uruguay and northern Argentina. If this hypothesis holds true (i.e. the three species are ecologically redundant), we predict a homogeneous diet composition for the three species; alternatively, if our hypothesis is false, the diet composition will differ significantly among species. Given the lack of quantitative information on the trophic ecology of these species, we also quantified the diet of each species and analysed seasonal and ontogenetic trends in diet composition.

## Materials and methods

Samples were collected during research cruises undertaken by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP; Argentina) in the south-west Atlantic between 34 and 42°S, aboard research vessels 'Capitán Oca Balda' and 'Doctor Eduardo Holmberg'. The sampling scheme was randomly stratified and designed for the assessment of hake (*Merluccius hubbsi*). A 59-m Engel-type bottom trawl net, with a stretched mesh size of 200 mm in the wings and 103 mm in the codend, a vertical height of 4 m and a horizontal opening of 15 m, was used in all research cruises. Haul duration was 30 min at a trawling speed of  $1.852\text{ m s}^{-1}$ . Samples (i.e. whole rays) were also taken by a fishery observer aboard a commercial vessel between 2001 and 2010 in the same area (Table 1).

For each individual, disc width (DW; measured to the nearest millimetre), sex and maturity stage were recorded. The stomachs were removed, frozen and subsequently analysed in the laboratory. Maturity was assessed by reproductive condition, according to macroscopic observation of the uteri, oviductal glands, ovarian follicles and embryos in females, and clasper calcification and the shape of efferent ducts in males.

Prey were identified to the lowest possible taxonomic level, counted and weighed (wet weight) to the nearest 0.01 g. To determine whether a sufficient number of stomachs had been collected, the order of stomachs sampled was randomly pooled (100 times) and a cumulative prey curve was constructed by plotting total number of prey items observed against the number of stomachs examined (Kyne and Bennett 2002). The number of examined stomachs was deemed sufficient to adequately describe the diet when the curve reached an asymptote (Ferry and Cailliet 1996). Frequency of occurrence (*F*; proportion of stomachs that contained a given prey), frequency by number (*n*; number of individuals of a particular prey divided by the total number of consumed prey) and frequency by mass (*M*; mass of individuals of

**Table 1. Research cruises undertaken by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP; Argentina) and commercial vessels in the south-west Atlantic between 34 and 42°S from 2001 to 2010**

| Species                    | Source                 | Dates               | Location        | Number of stomachs |
|----------------------------|------------------------|---------------------|-----------------|--------------------|
| <i>Myliobatis goodei</i>   | Scientific survey      | 13-Nov-05–20-Dec-05 | 33°5′–41°4′S    | 122                |
|                            | Scientific survey      | 17-Jun-06–4-Jul-06  | 34°04′–38°5′S   | 36                 |
|                            | Scientific survey      | 4-Nov-08–22-Nov-08  | 35°4′–41°4′S    | 50                 |
|                            | Commercial vessel      | 1-Aug-10–20-Aug-10  | 36°06′–37°05′S  | 2                  |
|                            | Fundación Mundo Marino | Dec-09–Jan-10       | Samborombón Bay | 2                  |
| <i>Myliobatis ridens</i>   | Scientific survey      | 13-Nov-05–20-Dec-05 | 33°5′–41°4′S    | 38                 |
|                            | Scientific survey      | 17-Jun-06–4-Jul-06  | 34°04′–38°5′S   | 22                 |
|                            | Scientific survey      | 4-Nov-08–22-Nov-08  | 35°4′–41°4′S    | 8                  |
|                            | Fundación Mundo Marino | Dec-09–Jan-10       | Samborombón Bay | 13                 |
| <i>Dasyatis hypostigma</i> | Scientific survey      | 13-Nov-05–20-Dec-05 | 33°5′–41°4′S    | 13                 |
|                            | Scientific survey      | 17-Jun-06–4-Jul-06  | 34°04′–38°5′S   | 10                 |
|                            | Scientific survey      | 4-Jul-01–17-Jul-01  | 34°09′–37°5′S   | 4                  |
|                            | Scientific survey      | 22-Mar-02–31-Mar-02 | 39°–41°3′S      | 2                  |
|                            | Scientific survey      | 28-Nov-03–21-Dec-03 | 34°08′–41°3′S   | 12                 |
|                            | Scientific survey      | 7-Jul-04–14-Aug-04  | 34°08′–41°3′S   | 1                  |
|                            | Scientific survey      | 17-May-09–1-Jun-09  | 35°05′–40°46′S  | 2                  |
|                            | Commercial vessel      | 22-Mar-08–27-Mar-08 | 36°06′–37°05′S  | 6                  |

a particular prey divided by the total mass of consumed prey) were calculated for each prey item and used to determine the index of relative importance (IRI; Pinkas *et al.* 1971; Hyslop 1980). To facilitate comparisons among prey items, the percentage IRI was calculated (Cortés 1997). Prey items were classified into six prey taxonomic categories: bivalves, amphipods, gastropods, decapods, polychaetes and others. These broader taxonomic groups were used in the analyses rather than finer-level classifications in order to better represent the general diet.

The number of each prey group consumed by each individual was modelled as a function of species, sex, disc width, maturity stage and season in order to test for differences between species while controlling for the effects of the other variables. For each prey, a generalised linear model (GLM) with a log link and a negative binomial error distribution was constructed (Venables and Ripley 2002). Afterwards, the best minimum model (BMM) was chosen by minimisation of the Akaike's information criterion (AIC).

We evaluated the hypotheses that the consumption of each prey group is determined by body size (DW), sex, maturity stage or season (spring or winter) using GLMs (Venables and Ripley 2002). For each species of *Myliobatis*, models were built in which the number of each prey category was used as the response variable and body size, sex, maturity stage or season were used as explanatory variables (Barbini and Lucifora 2012a, 2012b). Changes in the diet of *D. hypostigma* were evaluated using only models with one explanatory variable at a time, because the number of samples was insufficient to assess more complex models. Akaike's weights were computed for each model (Franklin *et al.* 2001). All statistical analyses were performed using the statistical software R, ver. 2.9.1 (R Foundation for Statistical Computing, Vienna, Austria).

Intraspecific differences in dietary composition were assessed between sexes and among size classes. Among species, dietary overlap was evaluated using the Horn and Schoener indices of overlap (Krebs 1989), in which values range from 0

(no overlap) to 1 (complete overlap) and values  $\geq 0.6$  are considered biologically significant (Wallace and Ramsey 1983).

To quantify interspecific differences in the consumption of different prey we used two different methods: classification trees and analysis of similitude (ANOSIM). For both analyses, prey categories were defined as amphipods, bivalves, decapods, gastropods, polychaetes, microcrustaceans (i.e. cumaceans, ostracods, isopods), cephalochordates, fish, echinoderms, cnidarians and cephalopods. Classification trees are a recursive method in which explanatory variables are evaluated one at a time. This procedure sets a threshold in the variable that explains the largest proportion of the deviance in each instance, and all cases are split above and below that threshold. The procedure is repeated until no further increase in the explained deviance occurs or the subgroups left are homogeneous or have low sample size (Venables and Ripley 2002). In our case, we set species identity as a response variable and prey consumption (in numbers) as explanatory variables. By conducting this analysis we evaluated whether myliobatoid species could be separated on the basis of their dietary composition.

ANOSIM is a multivariate method commonly used to evaluate dietary differences in elasmobranchs (Marshall *et al.* 2008; Jacobsen *et al.* 2009; Jacobsen and Bennett 2012; O'Shea *et al.* 2013). It evaluates differences among groups (i.e. species) by assessing whether differences in a distance matrix are greater among groups than within groups. ANOSIM was run using the Bray–Curtis distance on number of each prey group consumed and 999 permutations.

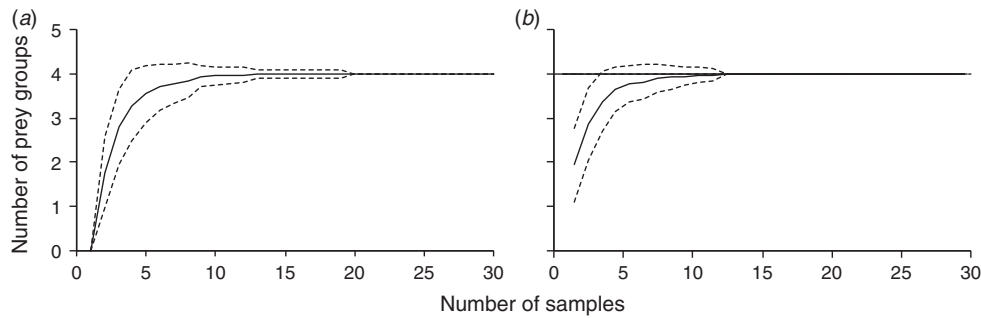
## Results

### Feeding ecology of *M. goodei*

Of a total of 290 stomachs examined, 212 (73%) contained food (105 females, 107 males). Twenty-seven prey taxa were identified (Table 2). Polychaetes were the most important (%IRI = 45.5), with *Travisia* spp. being the most common. Decapods were also abundant (%IRI = 40.3), with the family

**Table 2. Diet composition of *Myliobatis goodei*, off Uruguay and northern Argentina (sexes and sizes combined), expressed as percentage by number (%N), weight (%W), frequency of occurrence (%F) and index of relative importance (%IRI) for individual prey and prey groups**

| Prey                              | %F    | %N    | %P    | %IRI  | %IRI (prey group) |
|-----------------------------------|-------|-------|-------|-------|-------------------|
| Polychaeta                        |       |       |       |       | 45.5              |
| Onuphidae                         | 10.85 | 1.68  | 4.29  | 1.26  |                   |
| Opheliidae                        |       |       |       |       |                   |
| <i>Travisia</i> sp.               | 25.47 | 28.37 | 17.74 | 22.80 |                   |
| Nereidae                          | 3.77  | 0.25  | 5.03  | 0.39  |                   |
| Sabellidae                        | 8.49  | 0.50  | 0.97  | 0.24  |                   |
| Lumbrineridae                     | 1.42  | 0.09  | 0.65  | 0.02  |                   |
| Unidentified polychaetes          | 14.62 | 1.84  | 18.81 | 5.86  |                   |
| Crustaceans                       |       |       |       |       |                   |
| Cumacea                           | 7.55  | 1.70  | 0.27  | 0.29  | 0.17              |
| Isopoda                           |       |       |       |       | 0.16              |
| Cirolanidae                       |       |       |       |       |                   |
| <i>Cirolana</i> sp.               | 4.72  | 0.32  | 0.41  | 0.07  |                   |
| Serolidae                         |       |       |       |       |                   |
| <i>Serolis schythei</i>           | 0.47  | 0.09  | 0.18  | 0.002 |                   |
| Idoteidae                         | 2.36  | 0.20  | 0.05  | 0.01  |                   |
| Amphipoda                         |       |       |       |       | 12.46             |
| Gammaridea                        | 41.98 | 19.31 | 3.51  | 18.60 |                   |
| Caprellidea                       | 9.43  | 1.66  | 0.29  | 0.36  |                   |
| Stomatopoda                       |       |       |       |       |                   |
| Lysiosquillidae                   |       |       |       |       |                   |
| <i>Heterosquilla platensis</i>    | 2.36  | 0.52  | 4.55  | 0.23  | 0.13              |
| Ostracoda                         | 0.94  | 0.14  | 0.02  | 0.003 | 0.002             |
| Decapoda                          |       |       |       |       | 40.30             |
| Penaeoidea                        |       |       |       |       |                   |
| Solenoceridae                     |       |       |       |       |                   |
| <i>Pleoticus muelleri</i>         | 10.85 | 1.14  | 1.03  | 0.46  |                   |
| Anomura                           |       |       |       |       |                   |
| Paguridae                         |       |       |       |       |                   |
| <i>Sympagurus</i> spp.            | 42.92 | 40.98 | 17.14 | 48.44 |                   |
| Albuneida                         |       |       |       |       |                   |
| <i>Blepharipoda doelloi</i>       | 0.94  | 0.07  | 0.90  | 0.02  |                   |
| Brachyura                         |       |       |       |       |                   |
| Pinnotheridae                     |       |       |       |       |                   |
| <i>Austinixa patagoniensis</i>    | 4.72  | 0.48  | 0.45  | 0.08  |                   |
| Unidentified crustaceans          | 1.42  | 0.07  | 1.52  | 0.04  |                   |
| Mollusca                          |       |       |       |       |                   |
| Bivalvia                          |       |       |       |       | 0.02              |
| Unidentified bivalves             | 1.42  | 0.25  | 0.83  | 0.03  |                   |
| Cephalopoda                       |       |       |       |       | 0.003             |
| Octopodidae                       |       |       |       |       |                   |
| <i>Octopus tehuelchus</i>         | 0.47  | 0.02  | 0.46  | 0.004 |                   |
| Chordata                          |       |       |       |       |                   |
| Actinopterygii                    |       |       |       |       | 1.12              |
| Clupeiformes                      |       |       |       |       |                   |
| Engraulidae                       |       |       |       |       |                   |
| <i>Engraulis anchoita</i>         | 4.25  | 0.25  | 4.54  | 0.39  |                   |
| Perciformes                       |       |       |       |       |                   |
| Carangidae                        |       |       |       |       |                   |
| <i>Trachurus lathami</i>          | 0.47  | 0.02  | 2.15  | 0.02  |                   |
| Sciaenidae                        |       |       |       |       |                   |
| <i>Paralanchurus brasiliensis</i> | 0.47  | 0.02  | 13.32 | 0.12  |                   |
| Anthozoa                          |       |       |       |       | 0.10              |
| Unidentified anemones             | 0.94  | 0.14  | 10.03 | 0.19  |                   |
| Ophiuroidea                       |       |       |       |       | 0.04              |
| Unidentified ophiurans            | 4.25  | 0.36  | 0.41  | 0.06  |                   |
| Holothuroidea                     |       |       |       |       | 0.004             |
| Unidentified holothurians         | 0.47  | 0.02  | 0.86  | 0.01  |                   |



**Fig. 1.** Cumulative prey curves for stomachs from (a) male and (b) female *Myliobatis goodei* off Uruguay and northern Argentina, considering four prey groups (amphipods, decapods, polychaetes and others) used in the statistical analyses. Solid lines indicate the mean number of new prey; dashed lines indicate standard deviations, after 100 permutations.

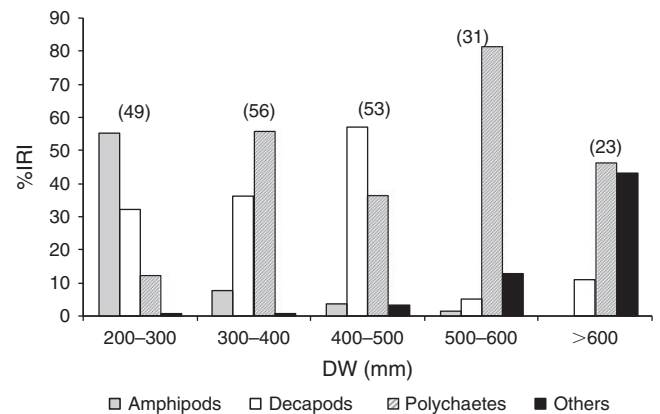
Paguridae the most represented. Gammarid amphipods were third in order of importance, with a %IRI of 18.6. The remaining groups had a %IRI <1.1 (Table 2). All polychaetes and crustaceans consumed by *M. goodei* were of small size and were ingested whole, without any crushing by the dental plates.

After identification to the lowest possible taxonomic level, prey were classified into four major taxonomic groups (i.e. amphipods, polychaetes, decapods and ‘others’) to perform statistical analyses. The ‘others’ category included cumaceans, ostracods, stomatopods, ophiuroids, holothuriids, unidentified invertebrates, fish, cephalopods and anemones. Results from the cumulative prey curve analysis indicated 18 stomachs in males and 14 in females were sufficient to represent the diet of *M. goodei* (Fig. 1).

Male *M. goodei* consumed more polychaetes (%IRI = 67) than females (%IRI = 29), whereas in the latter the highest values of %IRI corresponded to decapods (%IRI = 44.7). With regard to the type of food consumed by the different size classes, specimens with a DW <500 mm primarily consumed decapods and amphipods. The smallest individuals of *M. goodei* were the main consumers of amphipods of all size classes analysed (amphipod %IRI = 55.3 for *M. goodei* in the 200–300 mm DW class). In individuals >600 mm DW, the group ‘others’ presented the greatest value found (%IRI = 43.1), whereas polychaetes had maximum peaks in the 500–600 mm DW size class (%IRI = 80.9) and minimum peaks (%IRI = 11.8) in the 200–300 mm DW size class (Fig. 2).

According to the GLMs, the consumption of amphipods was dependent on the size of the predator and season. The smallest individuals consumed more amphipods than the largest individuals. Amphipods were consumed more heavily in winter than in spring. The consumption of decapods and polychaetes was dependent on maturity, and was independent of the size of the predator, sex or season. Immature individuals preyed more heavily on decapods and polychaetes than mature individuals. None of the variables evaluated explained the use of the item ‘others’ (Table 3).

Dietary overlap between males and females was high (i.e. overlap index values were >0.6). Female *M. goodei* showed no trophic overlap among the size classes analysed (Horn and Schoener = 0.51), whereas young and adult males significantly overlapped in diet (Horn and Schoener overlap index >0.6; Table 4).



**Fig. 2.** Relationship between the percentage index of relative importance (%IRI) of each prey item and the different size classes for both sexes of *Myliobatis goodei* combined off Uruguay and northern Argentina. Numbers in parentheses above columns indicate the number of stomachs analysed for each size class. DW, disc width.

**Table 3.** Best models explaining the consumption of the main prey groups of *Myliobatis goodei* off Uruguay and northern Argentina

Intercept and variable coefficients are given for each model (standard errors are given in parentheses). Coefficients of maturity stage and season are relative to immature stage and spring respectively. DW, disc width; AIC, Akaike information criterion; w, Akaike’s weights

| Prey        | Intercept    | Coefficients                              | AIC  | w    |
|-------------|--------------|---|------|------|
| Amphipods   | 7.34 (0.69)  | –0.014 (0.001) DW –<br>1.15 (0.38) spring | 847  | 0.94 |
| Decapods    | 0.07 (0.33)  | 2.26 (0.37) immature                      | 1064 | 0.69 |
| Polychaetes | 1.15 (0.33)  | 0.93 (0.37) immature                      | 978  | 0.33 |
| Others      | –0.17 (0.22) |   | 450  | 0.21 |

*Feeding ecology of M. ridens*

Of a total of 125 stomachs of *M. ridens* examined, 90 (72%) contained food (38 females, 52 males). Twelve different types of prey were identified. The species consumed were primarily bivalves (%IRI = 44.1), gastropods (%IRI = 40.6) and crustaceans (%IRI = 15.3), with the family Paguridae the most

**Table 4. Trophic niche overlap index of *Myliobatis goodei* off Uruguay and northern Argentina**

Values in bold indicate a biologically significant overlap

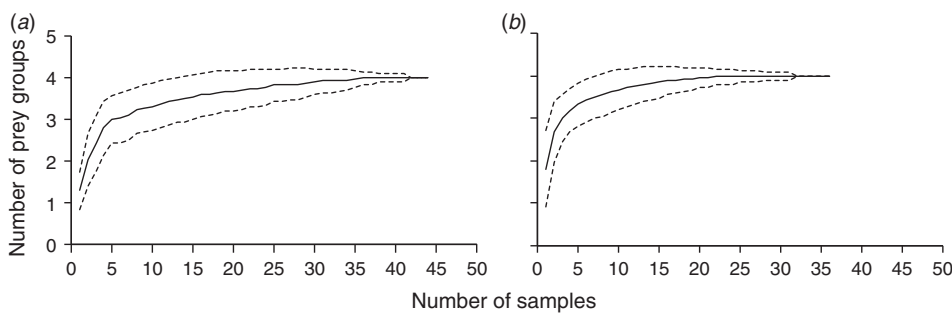
| Categories             | Schoener's index | Horn's index |
|------------------------|------------------|--------------|
| Males v. females       | <b>0.56</b>      | <b>0.68</b>  |
| Young v. adult females | 0.51             | 0.51         |
| Young v. adult males   | <b>0.78</b>      | <b>0.95</b>  |

represented; the remaining groups had a %IRI <1 (Table 5). *M. ridens* ate only the soft parts of the molluscs, expelling the shells. For this reason, the specific identification of gastropods and bivalves was difficult.

After identification, prey were categorised into four major taxonomic groups: polychaetes, bivalves, gastropods and crustaceans. Results from cumulative prey curves indicated 32 stomachs in females and 42 in males were sufficient to evaluate the diet of *M. ridens* (Fig. 3).

**Table 5. Diet composition of *Myliobatis ridens*, off Uruguay and northern Argentina (sexes and sizes combined), expressed as percentage by number (%N), weight (%W), frequency of occurrence (%F) and index of relative importance (%IRI) for individual prey and prey groups**

| Prey items                   | %F   | %N   | %P   | %IRI | %IRI (prey group) |
|------------------------------|------|------|------|------|-------------------|
| Unidentified polychaetes     | 3.3  | 1.5  | 0.5  |      | 0.08              |
| Crustaceans                  | 35.6 | 27   | 7.6  |      | 15.3              |
| Amphipoda                    |      |      |      |      |                   |
| Gammaridea                   | 2.2  | 0.3  | 0.01 | 0.01 |                   |
| Decapoda                     |      |      |      |      |                   |
| Penaeoidea                   |      |      |      |      |                   |
| Solenoceridae                |      |      |      |      |                   |
| <i>Pleoticus muelleri</i>    | 2.2  | 0.3  | 0.2  | 0.02 |                   |
| Anomura                      |      |      |      |      |                   |
| Paguridae                    |      |      |      |      |                   |
| <i>Sympagurus</i> spp.       | 32.2 | 25.7 | 7.0  | 20.2 |                   |
| Mollusca                     |      |      |      |      |                   |
| Bivalvia                     |      |      |      |      | 44.1              |
| Scrobicularidae              |      |      |      |      |                   |
| <i>Semele casali</i>         | 6.7  | 4.9  | 3.1  | 1.8  |                   |
| Merethricidae                | 1.1  | 2.5  | 6.1  | 0.3  |                   |
| Solenidae                    | 1.1  | 4.3  | 10.9 | 0.6  |                   |
| Lediidae                     |      |      |      |      |                   |
| <i>Leda patagonica</i>       | 2.2  | 1.3  | 0.7  | 0.1  |                   |
| Unidentified bivalves        | 33.3 | 26.3 | 33.9 | 38.5 |                   |
| Gastropoda                   |      |      |      |      | 40.6              |
| Volutidae                    | 2.2  | 1.1  | 20.8 | 1.6  |                   |
| <i>Adelomelon brasiliana</i> | 6.7  | 3.2  | 10.5 | 3.0  |                   |
| Unidentified gastropods      | 31.1 | 33.5 | 31.3 | 38.7 |                   |



**Fig. 3.** Cumulative prey curves for stomachs from (a) male and (b) female *Myliobatis ridens* off Uruguay and northern Argentina, considering four prey groups (polychaetes, crustaceans, bivalves and gastropods) used in the statistical analyses. Solid lines indicate the mean number of new prey; dashed lines indicate standard deviations, after 100 permutations.

Male *M. ridens* consumed more bivalves than females (%IRI = 73.7 and 7.9 respectively). In the latter, the highest values of %IRI corresponded to gastropods (%IRI = 51.3) and crustaceans (%IRI = 40.6); polychaetes were found in both sexes with %IRI values <0.1.

Specimens with a DW <450 mm primarily consumed crustaceans and gastropods. This latter prey had a %IRI of 71 for this size class, the largest value observed for that item in all size classes analysed. Polychaetes were much less important (%IRI <1). In individuals with a DW >450 mm, bivalves had the highest importance, with values of %IRI >50 (Fig. 4).

The consumption of crustaceans was dependent on maturity. Immature individuals of *M. ridens* preyed more heavily on crustaceans than mature individuals. The consumption of polychaetes depended on size (DW), with smaller individuals consuming more polychaetes than large size classes, in which this prey was absent. Consumption of bivalves was dependent on sex and season. In males, the consumption of this prey was higher than in females, and bivalves were consumed in larger proportion in spring than in winter. None of the variables evaluated explained the use of gastropod prey (Table 6).

There was no overlap of trophic niche between males and females (values <0.4). There was no significant overlap among size classes of female *M. ridens* (Horn and Schoener overlap indices = 0.31), whereas males showed high dietary overlap between young and adults (Horn and Schoener overlap index >0.6; Table 7).

Feeding ecology of *D. hypostigma*

A total of 56 stomachs of *D. hypostigma* were collected, of which the great majority (89%; n = 50) contained prey items. Twenty-one prey taxa were identified. Amphipods were the most important prey in terms of %IRI (88.7); the remaining prey represented less than 7% of %IRI (Table 8). Prey were grouped into four major taxonomic groups (amphipods, crustaceans, polychaetes and ‘others’) to perform comparisons. The category ‘others’ included bivalves, gastropods, fish and lancelets.

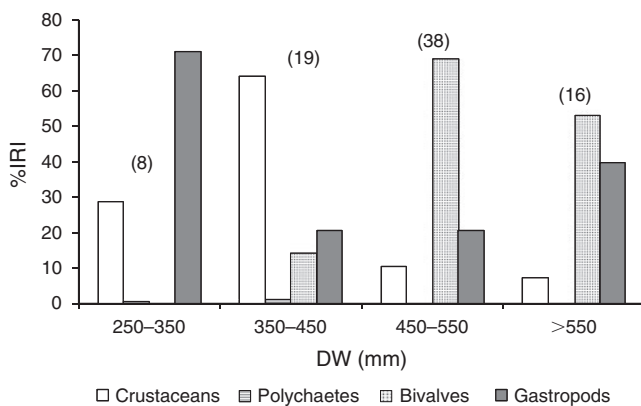


Fig. 4. Relationship between the percentage index of relative importance (%IRI) of each prey item and the different size classes for both sexes combined in *Myliobatis ridens* off Uruguay and northern Argentina. Numbers in parentheses above columns indicate the number of stomachs analysed for each size class. DW, disc width.

The minimum number of stomachs needed to have a sample representative of the population was performed with both sexes combined because of the low number of samples collected; the asymptote was reached in 29 stomachs (Fig. 5). Amphipods dominated the smallest size classes, whereas polychaetes dominated the largest ones. The smallest individuals of *D. hypostigma* primarily consumed amphipods (amphipod %IRI = 64.5 and 97.8 in the 150–250 and 250–350 mm DW classes respectively). Specimens in the 150–250 mm DW class primarily consumed amphipods, followed by crustaceans and polychaetes, in decreasing order of importance. Medium-sized specimens (DW 350–450) primarily consumed amphipods (%IRI = 43.2), however polychaetes and the group ‘others’ were also present in the diet, with %IRI <30. This latter prey group, had a %IRI of 28.7 for this size class, the largest value observed for that item in all size classes analysed. In large individuals (>450 mm DW) polychaetes were predominant (%IRI = 50.4), crustaceans were the second most important dietary category (%IRI = 42) and amphipods were much less important (%IRI <3) in the diet (Fig. 6).

The consumption of amphipods and polychaetes depended on maturity stage. Amphipods contributed substantially to the diet of immature individuals; conversely, polychaetes were common prey of mature specimens. The consumption of crustaceans and ‘others’ depended on season: crustaceans predominated in winter, whereas ‘others’ predominated in spring (Table 9).

At the intraspecific level, there was trophic niche overlap between males and females, with values of the overlap index >0.8. With regard to maturity level, there was no overlap among adult and immature individuals (Horn and Schoener indices <0.21; Table 10).

Table 6. Best models explaining the consumption of the main prey groups of *Myliobatis ridens* off Uruguay and northern Argentina

Intercept and variable coefficients are given for each model (standard errors are given in parentheses). Coefficients of sex, maturity stage and season are relative to males, immature stage and spring respectively. DW, disc width; AIC, Akaike information criterion; w, Akaike’s weights

| Prey        | Intercept    | Coefficients                             | AIC   | w    |
|-------------|--------------|--|-------|------|
| Crustaceans | -1.09 (0.47) | 2.38 (0.59) immature                     | 275   | 0.68 |
| Polychaetes | 18.4 (2.91)  | -0.05 (0.01) DW                          | 389   | 0.36 |
| Bivalves    | -0.81 (0.41) | 1.12 (0.36) Male +<br>1.26 (0.43) spring | 343.7 | 0.54 |
| Gastropods  | 1.08 (0.25)  |  | 330.2 | 0.34 |

Table 7. Trophic niche overlap index of *Myliobatis ridens* off Uruguay and northern Argentina

Values in bold indicate a biologically significant overlap

| Categories             | Schoener’s index | Horn’s index |
|------------------------|------------------|--------------|
| Males v. females       | 0.35             | 0.34         |
| Young v. adult females | 0.31             | 0.31         |
| Young v. adult males   | <b>0.56</b>      | <b>0.78</b>  |

**Table 8.** Diet composition of *Dasyatis hypostigma*, off Uruguay and northern Argentina (sexes and sizes combined), expressed as percentage by number (%N), weight (%W), frequency of occurrence (%F) and index of relative importance (%IRI) for individual prey and prey groups

| Prey items                       | %F   | %N   | %P   | %IRI  | %IRI (prey group) |
|----------------------------------|------|------|------|-------|-------------------|
| Polychaeta                       |      |      |      |       | 7                 |
| Onuphidae                        | 1.8  | 0.3  | 0.8  | 0.02  |                   |
| Opheliidae                       |      |      |      |       |                   |
| <i>Travisia</i> sp.              | 3.6  | 0.1  | 0.2  | 0.01  |                   |
| Aphroditidae                     | 1.8  | 0.4  | 6.7  | 0.1   |                   |
| Lumbrineridae                    | 10.7 | 0.4  | 4.2  | 0.4   |                   |
| Unidentified polychaetes         | 32.1 | 2.3  | 9.5  | 3.5   |                   |
| Crustacea                        |      |      |      |       | 3.2               |
| Stomatopoda                      |      |      |      |       |                   |
| Lysiosquillidae                  |      |      |      |       |                   |
| <i>Heterosquilla platensis</i>   | 1.8  | 0.1  | 0.0  | 0.001 |                   |
| Cumacea                          | 3.6  | 0.3  | 0.1  | 0.01  |                   |
| Isopoda                          |      |      |      |       |                   |
| Flabellifera                     |      |      |      |       |                   |
| Cirolanidae                      |      |      |      |       |                   |
| <i>Cirolana</i> sp.              | 8.9  | 0.5  | 2.8  | 0.3   |                   |
| Valvifera                        | 3.6  | 0.2  | 0.1  | 0.01  |                   |
| Tanaidacea                       | 3.6  | 0.2  | 1.0  | 0.04  |                   |
| Decapoda                         |      |      |      |       |                   |
| Penaeoidea                       |      |      |      |       |                   |
| Solenoceridae                    |      |      |      |       |                   |
| <i>Pleoticus muelleri</i>        | 21.4 | 2.8  | 1.3  | 0.8   |                   |
| Unidentified crustaceans         | 7.1  | 0.2  | 0.3  | 0.03  |                   |
| Amphipoda                        |      |      |      |       | 88.7              |
| Gammaridea                       | 66   | 85.1 | 69.7 | 94.4  |                   |
| Caprellidea                      | 5.4  | 1.4  | 0.2  | 0.08  |                   |
| Mollusca                         |      |      |      |       | 1.07              |
| Bivalvia                         |      |      |      |       |                   |
| Scrobicularidae                  |      |      |      |       |                   |
| <i>Semele casali</i>             | 1.8  | 0.1  | 0.2  | 0.01  |                   |
| Solenidae                        | 1.8  | 0.1  | 0.5  | 0.01  |                   |
| Lediidae                         |      |      |      |       |                   |
| <i>Leda patagonica</i>           | 1.8  | 0.06 | 0.01 | 0.001 |                   |
| Unidentified bivalves            | 1.8  | 0.2  | 0.2  | 0.01  |                   |
| Gastropoda                       |      |      |      |       |                   |
| Unidentified gastropods          | 1.8  | 0.1  | 0.1  | 0.002 |                   |
| Chordata                         |      |      |      |       |                   |
| Cephalochordata                  |      |      |      |       |                   |
| Branchiostomidae                 |      |      |      |       |                   |
| <i>Branchiostoma lanceolatus</i> | 3.6  | 5.1  | 1.6  | 0.2   |                   |
| Vertebrata                       |      |      |      |       |                   |
| Actinopterygii                   |      |      |      |       |                   |
| Unidentified actinopterygians    | 3.6  | 0.2  | 0.6  | 0.03  |                   |

### Interspecific comparisons

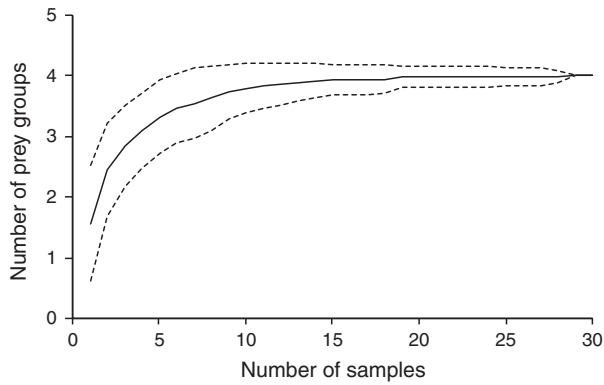
When the diets of the three species of Myliobatiformes were compared, they were found to differ. There was no overlap of the trophic niche among the three species (in all cases, Horn and Schoener indices <0.29; Table 11).

All three species could be separated on the basis of diet composition (Fig. 7). A very high consumption of hard-shelled molluscs (both gastropods and bivalves) was typical of *M. ridens*. High consumption of amphipods was typical of *D. hypostigma*. *M. goodei* was differentiated from the other two species by a high consumption of decapods and

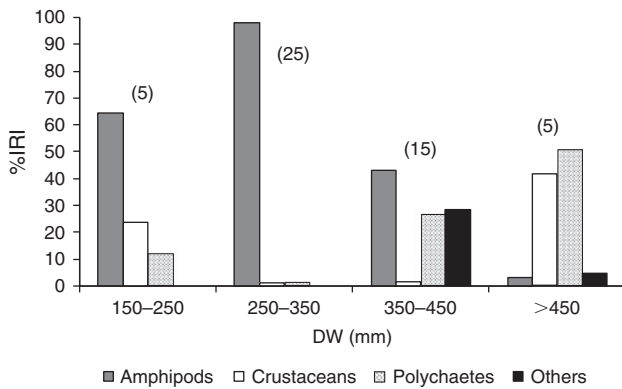
polychaetes. In all cases, grouping of samples on the basis of diet composition had a high probability of correct assignment, often higher than 0.88 and never lower than 0.62 (Fig. 7).

The diets of the three species were also significantly different when analysed using ANOSIM (ANOSIM  $R = 0.3423$ ;  $P = 0.001$ ). Differences were also significant when comparing each species pairs: *M. goodei* v. *D. hypostigma*, ANOSIM  $R = 0.08954$ ,  $P = 0.005$ ; *M. goodei* v. *M. ridens*, ANOSIM  $R = 0.4559$ ,  $P = 0.001$ ; and *M. ridens* v. *D. hypostigma*, ANOSIM  $R = 0.4788$ ,  $P = 0.001$ .





**Fig. 5.** Cumulative prey curve for *Dasyatis hypostigma* (males and females combined) off Uruguay and northern Argentina, considering four prey groups (amphipods, polychaetes, crustaceans, and ‘others’). The item ‘others’ includes bivalves, gastropods, fish and amphioxii. Solid lines indicate the mean number of new prey; dashed lines indicate standard deviations, after 100 permutations.



**Fig. 6.** Relationship between the percentage index of relative importance (%IRI) of each prey item and the different size classes for both sexes combined in *Dasyatis hypostigma* off Uruguay and northern Argentina. Numbers in parentheses above columns indicate the number of stomachs analysed for each size class. DW, disc width.

**Table 9. Best models explaining the consumption of the main prey groups of *Dasyatis hypostigma* off Uruguay and northern Argentina**

Intercept and variable coefficients are given for each model (standard errors are given in parentheses). Coefficients of maturity stage and season are relative to immature stage and spring respectively. DW, disc width; AIC, Akaike information criterion; w, Akaike’s weights

| Prey        | Intercept    | Coefficients          | AIC   | w    |
|-------------|--------------|-----------------------|-------|------|
| Amphipods   | 0.69 (0.39)  | 2.95 (0.45) immature  | 385.4 | 0.39 |
| Crustaceans | 0.86 (0.34)  | -1.68 (0.55) spring   | 149.6 | 0.9  |
| Polychaetes | 0.92 (0.33)  | -1.55 (0.42) immature | 134   | 0.35 |
| Others      | -1.42 (0.73) | 2.76 (1) spring       | 89.7  | 0.36 |

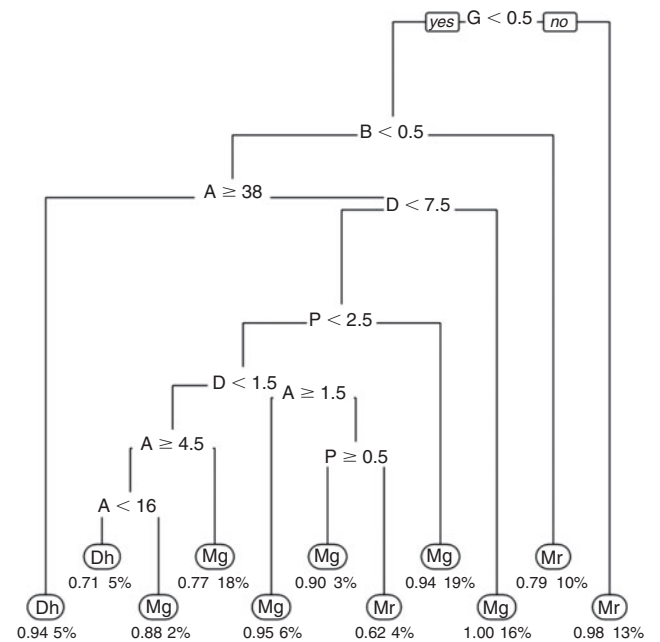
**Table 10. Trophic niche overlap index of *Dasyatis hypostigma* off Uruguay and northern Argentina**  
Values in bold indicate a biologically significant overlap

| Categories       | Schoener’s index | Horn’s index |
|------------------|------------------|--------------|
| Males v. females | <b>0.89</b>      | <b>0.98</b>  |
| Young v. adult   | 0.17             | 0.21         |

**Table 11. Interspecific niche overlap between species of Myliobatiformes occurring off Uruguay and northern Argentina**

Horn and Schoener indices of overlap with values  $\geq 0.6$  were considered biologically significant

| Interspecific niche overlap                            | Schoener’s index | Horn’s index |
|--|------------------|--------------|
| <i>Myliobatis goodei</i> v. <i>Myliobatis ridens</i>   | 0.29             | 0.25         |
| <i>Myliobatis goodei</i> v. <i>Dasyatis hypostigma</i> | 0.16             | 0.15         |
| <i>Dasyatis hypostigma</i> v. <i>Myliobatis ridens</i> | 0.04             | 0.02         |



**Fig. 7.** Classification tree of the diet composition of *Myliobatis goodei* (Mg), *Myliobatis ridens* (Mr) and *Dasyatis hypostigma* (Dh) from off Uruguay and northern Argentina. Prey were grouped into the following taxonomic groups: amphipods (A), bivalves (B), decapods (D), gastropods (G), and polychaetes (P). At each node, a decision rule is given about a threshold in mean consumption of a prey (in numbers of individual prey); samples positive for that decision rule (‘yes’) are split to the left, negative samples (‘no’) are split to the right. Leaves of the tree are labelled according to the species with the highest number of samples in that leaf. Below the species label, the proportion of cases in the leaf belonging to the species of the leaf label is shown. In addition, at each leaf, the percentage of the total sample allocated to that leaf is shown.

## Discussion

The present study provides the first quantification of intra- and interspecific variations in the diet of the most common myliobatoid rays of the south-west Atlantic. The results indicate that ecological singularity is high among mesopredatory myliobatoid rays in a temperate coastal ecosystem with high primary productivity, implying that ecological singularity in mesopredatory myliobatoids is not restricted to high-diversity oligotrophic ecosystems. High levels of deposition of suspended organic matter support a high biomass of benthic invertebrates of the coastal ecosystem off Uruguay and northern Argentina (Acha *et al.* 2004; Lercari *et al.* 2015). This suggests that resource partitioning among benthic myliobatoid predators would be low, as a result of high prey abundance. This would be exacerbated by the low species richness of myliobatoids (only three species with a regular presence) compared with subtropical and tropical ecosystems with higher species richness (e.g. O'Shea *et al.* 2013). However, this is not the case, and we found significant trophic differences among closely related myliobatoid mesopredators of the south-west Atlantic.

A bad taxonomic resolution can have serious negative consequences on the knowledge of a taxon's ecology and its conservation status (Bortolus 2008). Taxonomy is at the basis of all biological sciences because it provides the foundations on which biological knowledge is rooted and a platform for interspecific comparisons. Among elasmobranchs, recent taxonomic work has resulted in substantial changes in our knowledge of the ecology of several species groups, with applied consequences on the conservation and management of these species (White and Last 2012). South-west Atlantic species of *Myliobatis* are another example of how a bad taxonomy has hampered the recognition of important ecological differences between the two species involved. What was thought to be a single species with a wide trophic niche was actually a group composed of two species with highly divergent and more specialised diets. Detailed data on diet were previously available only for *M. goodei*, but they are not reliable because they suffered from the misidentification of *M. ridens* as *M. goodei*. After accurate species identification, a clear trophic segregation between *M. goodei* and *M. ridens* becomes clear. The diet of *M. goodei* is based primarily on polychaetes and crustaceans, with molluscs not a significant prey of this species. In contrast, the diet of *M. ridens* is characterised by gastropods and bivalves. Previously, bivalves and gastropods were said to be frequent in the diet of *M. goodei* (Refi 1975; Cousseau *et al.* 2007; Molina and Lopez Cazorla 2015). This is most likely a result of the inclusion of specimens of *M. ridens*, misidentified as *M. goodei*, in previous work.

The type of feeding of the genus *Myliobatis* is usually described as durophagy because they are hard-prey specialists capable of crushing the exoskeletons of crabs, snails and mussels (e.g. Gray *et al.* 1997; Jardas *et al.* 2004; Schluessel *et al.* 2010; Sommerville *et al.* 2011; Szczepanski and Bengtson 2014). The teeth of *Myliobatis* spp. are hexagonal interlocking units that form a band of teeth. These bands form a continuous dental plate specialised to compress and grind prey (Summers 2000). In the south-west Atlantic, *M. ridens*, a consumer of hard-shelled molluscs such as gastropods and bivalves, fits this

typical description. Conversely, *M. goodei* predominantly eats softer prey, such as polychaetes and decapods, diverging to some extent from the typical description of durophagy. This adds evidence indicating higher-than-expected diet variation in rays with a presumably specialist durophagous feeding mechanism, as observed in the genus *Rhinoptera* (e.g. Collins *et al.* 2007; Ajemian and Powers 2012, 2013; Navarro-González *et al.* 2012; Bornatowski *et al.* 2014).

The pattern of *M. goodei* and *M. ridens* feeding on different kinds of prey appears to be the same in different geographic locations. Preliminary data from off southern Brazil (28°36'S to 33°45'S) indicate that 95% of the diet of *M. ridens* is composed of bivalves, whereas in *M. goodei* 80% of the diet consists of polychaetes (Rezende *et al.* 2006). This suggests that, although sympatric, both species have different ecological roles regardless of the geographic location. These dietary differences between south-west Atlantic *Myliobatis* species are likely related to the differences in morphology between both species. *M. goodei* has a smaller mouth (Ruocco *et al.* 2012) and teeth (Rezende *et al.* 2006) than *M. ridens*. Because a large mouth and dental plates are beneficial to grind prey with hard exoskeletons, *M. goodei* may be unable to efficiently prey on hard-shelled molluscs. If morphology is the main determinant of the dietary differences between both species, trophic geographic variation, as observed in other myliobatoid mesopredators (Collins *et al.* 2007; Ajemian and Powers 2012, 2013), should not occur in *M. goodei* even in places where it is allopatric to *M. ridens*. At present, it is known that both species occur sympatrically between 28°36'S and 41°S (Ruocco *et al.* 2012), but the southern and northern limits of the distribution for each species remain unknown.

The coastal seas around the Americas are the only areas where different species of *Myliobatis* occur sympatrically. In the western Atlantic, *M. freminvillii* and *M. goodei* are sympatric throughout most of their range (McEachran and de Carvalho 2002a; Menni *et al.* 2010), and these two species overlap *M. ridens* off southern Brazil and, to a lesser extent, off Uruguay and northern Argentina (Ruocco *et al.* 2012). In the Pacific Ocean, *M. peruvianus* and *M. chilensis* co-occur off Peru and northern Chile (Romero Camarena and Bustamante Ruiz 2007; Bustamante *et al.* 2014), and *M. californicus* and *M. longirostris* in the Gulf of California (McEachran and Notarbartolo di Sciarra 1995). In other regions, species of *Myliobatis* occur only allopatrically, such as *M. tenuicaudatus*, *M. hamlyni* and *M. tobijei* in the western Pacific and eastern Indian Ocean (White *et al.* 2015) and *M. aquila* in the Mediterranean and eastern Atlantic (Compagno *et al.* 1989; Serena 2005; Ebert and Stehmann 2013). Closely related elasmobranchs should differ more in their ecological traits when in sympatry than in allopatry (Rezende *et al.* 2009), therefore this geographic pattern suggests that ecological differentiation among species of *Myliobatis* should be more common around the Americas than in other regions.

Trophic variation in elasmobranchs can be attributed to multiple sources (Braccini *et al.* 2005). In *M. goodei* and *D. hypostigma*, body size is the main variable explaining the consumption of amphipods; in *M. ridens*, this variable best explains the consumption of polychaetes. Many skates are known to consume fewer amphipods or polychaetes as they

grow (e.g. Orlov 1998; Belleggia *et al.* 2008; Ruocco *et al.* 2009; Barbini and Lucifora 2011, 2012b, 2016; Main and Collins 2011; Barbini *et al.* 2013; Šantić *et al.* 2013). Among myliobatoid rays, microcrustaceans (such as amphipods) or polychaetes are dominant prey of species in the families Urolophidae and Urotrygonidae (Platell *et al.* 1998; Marshall *et al.* 2008; Flores-Ortega *et al.* 2011; Navia *et al.* 2011; Yick *et al.* 2011; Navarro-González *et al.* 2012; Jacobsen and Bennett 2013), which are generally small (McEachran and de Carvalho 2002b; Last and Stevens 2009), and several dasyatid species consume fewer amphipods or polychaetes with increasing body size (e.g. Ebert and Cowley 2003; Dale *et al.* 2011; Jacobsen and Bennett 2012; López-García *et al.* 2012). This interspecific trend is in agreement with the intraspecific pattern of amphipod consumption observed in *M. goodei* and *D. hypostigma* and may indicate a preference for bigger prey as predators grow. This hypothesis may also explain the decreasing consumption of polychaetes with body size in *M. ridens*.

Season, sex and maturity stage are also important determinants of diet composition in the three species studied. Myliobatoid rays are highly mobile and seasonal differences in habitat use are apparent for *Myliobatis* spp. and *D. hypostigma* in the study area (Jaureguizar *et al.* 2004). These differences may produce variability in the predator–prey relationship through interseasonal differences in prey encounter rate or prey availability, as suggested by similar seasonal and habitat-specific differences in amphipod consumption in other myliobatoids with a durophagous anatomy (Sommerville *et al.* 2011; Ajemian and Powers 2012).

The role of myliobatoid mesopredators appears to vary geographically. Experimental work has shown that in some regions they have strong effects in structuring the benthic community (e.g. VanBlaricom 1982; Peterson *et al.* 2001), whereas in others their effect is less marked (Ajemian *et al.* 2012; Ajemian and Powers 2013). These differences may be the result of dietary differences among closely related but different species inhabiting different regions, intraspecific geographic variability in feeding habits and structural differences among different food webs. The low ecological redundancy and the observed intraspecific geographic variation in the feeding habits of many mesopredatory myliobatoids have implications for the ecosystem modelling of trophic pathways as well. Myliobatoid mesopredators are often pooled together in analyses of trophic webs, especially for regions with low diversity (e.g. Arreguín-Sánchez *et al.* 2002; Gasalla and Rossi-Wongtschowski 2004; Barausse *et al.* 2009; Lercari and Arreguín-Sánchez 2009; Ruiz and Wolff 2011). Unless there is evidence of ecological redundancy among myliobatoid mesopredators of a given region, as found by O'Shea *et al.* (2013), the results of the present study indicate that the practice of pooling together all myliobatoid mesopredators should be abandoned. As exemplified by Navia *et al.* (2010), a more objective approach would be to group myliobatoids according to trophic guilds.

Consumer-driven (i.e. top-down) trophic control is more prevalent in ecosystems of temperate than tropical continental shelves, which appears to be related to the higher ecological singularity of temperate compared with tropical ecosystems (Frank *et al.* 2007). This suggests that exploitation of apex predators should be especially monitored in temperate

species-poor ecosystems (Frank *et al.* 2007). In the coastal ecosystem off Uruguay and northern Argentina, there is evidence that apex predators have been overfished (e.g. Jaureguizar and Milessi 2008; Barbini *et al.* 2015). Monitoring of abundance trends of myliobatoid mesopredators is required to evaluate potential changes in the trophic web of the south-west Atlantic.

## Acknowledgements

The authors thank the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), especially 'Programa Pesquerías de Condrictios', for the specimens collected during research cruises. The authors are especially grateful to C. Lasta for putting us in contact with Fundación Mundo Marino, San Clemente del Tuyú, and the latter for collecting the material and lending facilities for eagle ray sampling. This work would not have been possible without the help of a fishery observer aboard a commercial vessel. This paper is part of N. Ruocco's Ph.D. dissertation, which was supported by a scholarship from CONICET (Argentina). This is INIDEP contribution number 1996.

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