



Comparative diets of sympatric batoid elasmobranchs in the Gulf of Oman

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ABSTRACT: Documenting the interactions and mechanisms of coexistence among predators is important for understanding their ecological roles in food webs. Here, we examined the diet and trophic relationships of 6 demersal batoids coexisting in the Gulf of Oman by analyzing stomach contents. There were significant differences in diets among the batoid species, suggesting differential preferences. Diets of *Gymnura poecilura* and *Torpedo sinuspersici* were similar and consisted mostly of teleost fishes. In contrast, *Brevitrygon walga* and *Rhinobatos punctifer* mostly ate crustaceans. The diets of *Maculabatis randalli* and *Pastinachus sephen* were diverse and included crustaceans, teleosts, polychaetes, bivalves and echinoderms. The differences in diet among these batoids may be related to morphological differences in feeding structures and to differences in behavior, which could explain their diversity and coexistence in the Gulf of Oman.

KEY WORDS: Elasmobranch · Foraging ecology · Diet · Gulf of Oman

INTRODUCTION

Knowledge about the diets of marine predators is pivotal to understanding the potential for intra- and inter-specific differences in habitat use (e.g. Papastamatiou et al. 2006, Barría et al. 2015, Navia et al. 2017). Among marine predators, some sharks and batoids can be important top predators (i.e. mesopredators) in marine ecosystems (Cortés 1999, Barría et al. 2015, Navia et al. 2017). Though there have been several studies on elasmobranchs in recent decades (Field et al. 2009, Navia et al. 2017), few have focused on interactions among sympatric species, an important element for understanding how species that appear to be ecologically similar might coexist (e.g. Albo-Puigserver et al. 2015, Barría et al. 2015, Navia et al. 2017). The principle of competitive exclusion predicts that predators that occupy similar niches will diverge ecologically or perhaps be dis-

placed (Pianka 2000). Nonetheless, closely related species do sometimes live together. Partitioning of food resources has been proposed as one of the main mechanisms explaining the coexistence of closely related elasmobranchs (e.g. Heithaus et al. 2013, Albo-Puigserver et al. 2015), owing to differences in prey or micro-habitats (e.g. Platell et al. 1998, Papastamatiou et al. 2006).

There has been relatively little research on elasmobranchs of the Gulf of Oman, in the northwestern Indian Ocean, despite the diversity of species there (e.g. Valinassab et al. 2006, Jabado et al. 2017, Rastgoo & Navarro 2017). Indeed, 82 species of sharks and more than 20 species of batoids have been described for the Gulf of Oman and nearby areas (Almojil et al. 2015), though several species appear to be declining, evidently from degradation and disappearance of habitats or the direct impacts of fishing (Valinassab et al. 2006, Jabado et al. 2017). An

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understanding of diet of the various species is important for determining whether differential vitality of elasmobranchs in the Gulf of Oman might be due to natural changes in ecosystems or is perhaps owing to human activities.

In this study, we analyzed the stomach contents of 6 demersal species of batoid elasmobranchs (*Gymnura poecilura*, *Brevitrygon walga*, *Maculabatis randalli*, *Pastinachus sephen*, *Rhinobatos punctifer*, *Torpedo sinuspersici*) that live in the Gulf of Oman to characterize their diets, which are poorly known, in an area of sympatry such as the Gulf of Oman. Our goal was to use data on comparative diets to begin to understand what might allow these species to coexist and, apparently, thrive.

MATERIALS AND METHODS

Study area and sampling procedure

We conducted the study in Iranian waters of the Gulf of Oman (Fig. 1), a marginal sea with an area of 94 000 km² that lies between the Arabian Sea and the Persian Gulf. It is a relatively deep body of water with a narrow continental shelf. About $\frac{3}{4}$ of the Gulf is deeper than 1000 m (Reynolds 1993). It is highly productive owing to the combined effects of monsoons, seasonal upwelling, and cold water intrusion from the Arabian Sea (Reynolds 1993). Although the demersal topography is flat and dominated by soft sediments, the northern coastline of the Gulf of Oman is

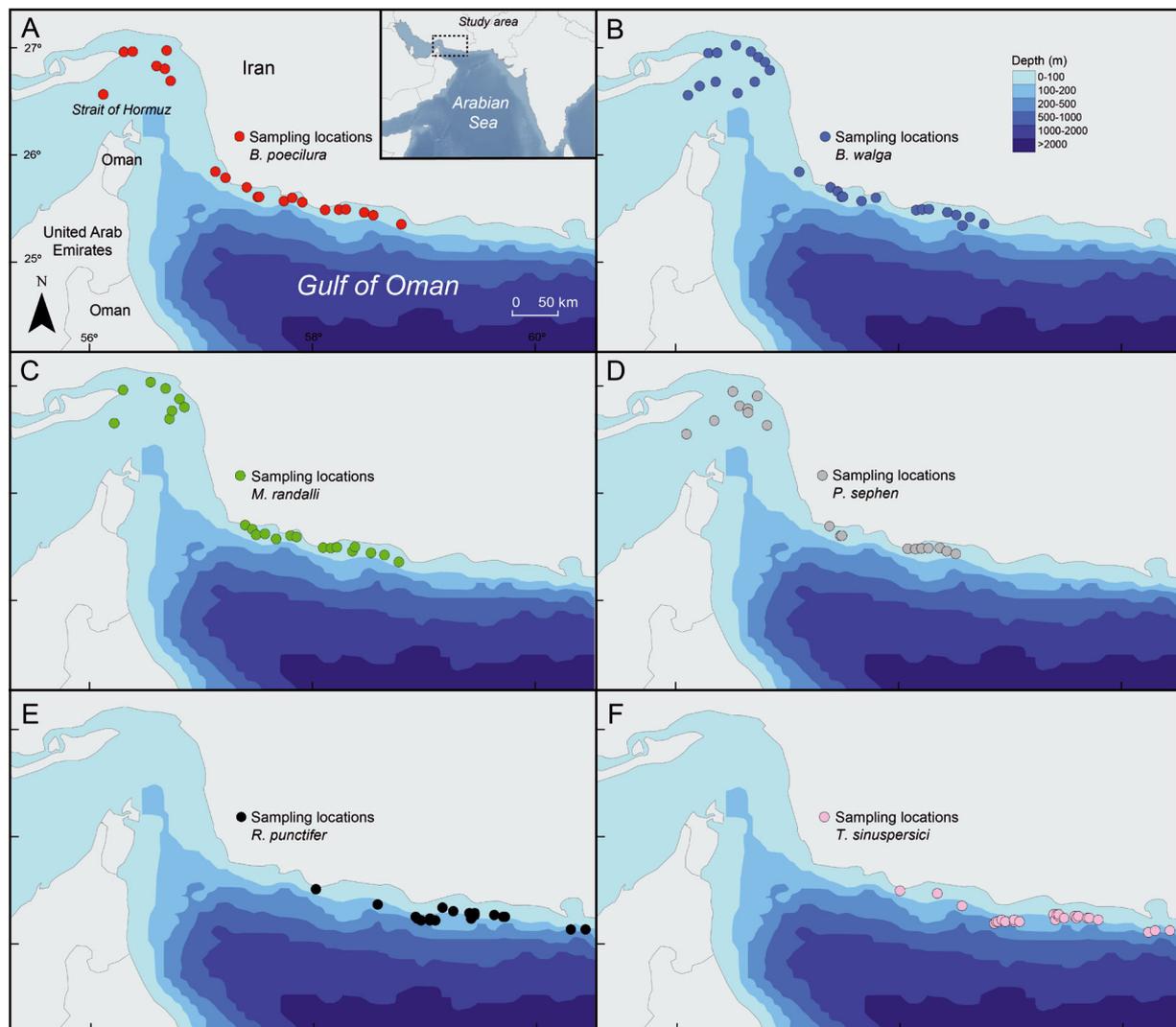


Fig. 1. Study area and sampling locations where (A) *Gymnura poecilura*, (B) *Brevitrygon walga*, (C) *Maculabatis randalli*, (D) *Pastinachus sephen*, (E) *Rhinobatos punctifer*, and (F) *Torpedo sinuspersici* were collected in the Gulf of Oman and Strait of Hormuz

highly irregular with diverse habitats, including rocky shores, estuaries, and mangroves.

We obtained specimens of the 6 species of batoid elasmobranchs (see Table 1) as bycatch from commercial bottom trawlers and during 2 bottom-trawling cruises (with the R/V 'Ferdows-1') from May through December 2014 (see Table S1 in the Supplement at www.int-res.com/articles/suppl/b027p035_supp.pdf for sampling days by species). The mesh size of the cod end net was 80 mm and the headline net mesh was 72 mm. Batoids were collected from bottom depths between 10 and 110 m during 256 hauls (Fig. 1). The duration of each haul varied from 60 to 90 min, depending on the sampling station. Specimens were identified onboard the ships, and the sex, body weight (nearest 10 g), disk width (for *Gymnura poecilura*, *Brevitrygon walga*, *Maculabatis randalli* and *Pastinachus sephen*) and the total body length (for *Rhinobatos punctifer* and *Torpedo sinuspersici*) were recorded.

Stomach content analyses

We weighed the stomachs and then recovered the stomach contents of the batoids during dissections in the laboratory. All prey parts recovered were separated, identified to the lowest possible taxon, counted, and weighed to the nearest 0.1 g. The number of individuals of each prey type was determined as the least number that these fragments could have originated from, to avoid overestimation of the occurrence of a particular prey item. We combined data from the stomach contents into 7 functional groups (teleosts, crustaceans, polychaetes, cephalopods, gastropods, bivalves, and echinoderms) and calculated the vacuity index for each batoid species as the percentage of empty stomachs (Hyslop 1980).

We used the combined index of relative importance (IRI; Pinkas et al. 1971) to estimate the relative importance of each prey group in the diet of each batoid species and to allow interspecific comparison as:

$$IRI_i = (N_i + W_i) \times FO_i \quad (1)$$

where FO_i is the frequency of occurrence of a particular functional prey group (i) in relation to the total number of stomachs, N_i is the contribution by number of a type of prey group i in relation to the whole content of the stomach, and W_i is the weight of a prey group i in relation to the entire contents of the stomach.

All calculations were based on the number of non-empty stomachs. IRI values were expressed as a percentage to allow comparisons between prey groups and species (Cortés 1997):

$$\%IRI_i = 100 \times IRI_i / \sum_{i=1}^n IRI_i \quad (2)$$

We also estimated the diet diversity for each batoid species using the Shannon-Wiener diversity index (H) (Ludwig & Reynolds 1988) as:

$$H = -\sum_{i=1}^n p_i \ln p_i \quad (3)$$

where p_i is the proportion of prey group i in the diet.

We graphically described the diets for each species by plotting the prey-specific quantity of the prey groups against %FO (Amundsen et al. 1996). Prey-specific abundance was estimated as the number of prey i divided by the total number of prey in the stomachs that included prey i , expressed as a percentage. The vertical axis suggests either specialization or generalization of the predator; points located in the upper part of the graph suggest specialization, whereas points in the lower part indicate that those prey were eaten less often.

We categorically estimated the trophic level (TL) that each batoid preyed upon using %W with TrophLab software (Pauly et al. 2000). TrophLab estimates TL considering the diet composition and the trophic level of the different prey present in the diet, according to %W (Pauly et al. 2000) as:

$$TL_j = 1 + \sum_i^G TL_i \times DC_{ij} \quad (4)$$

where TL_i is the fractional trophic level of prey i , DC_{ij} represents the fraction of i in the diet of consumer j and G is the number of prey categories. The trophic level of each prey category was extracted from the FishBase dataset (Froese & Pauly 2000).

In order to examine effect of sample size in estimating the diet of the batoid species, we constructed cumulative prey curves (Ferry & Caillet 1996) using the Shannon-Wiener method to evaluate if the number of sampled stomachs was enough to describe the diversity of the diet of each batoid species. We randomized the samples 50 times with the computer routine 'sample-based rarefaction' using EstimateS v.9.1 software (Colwell 2013). We considered sample size to be sufficient if the curves visually reached an asymptote (Magurran 2004).

Statistical analysis

We tested for differences among the 6 batoids in their stomach contents (based on %W) with the semi-

parametric permutation multivariate analyses of variance (PERMANOVA) tests on the Bray-Curtis distance matrix. PERMANOVA allows for the analysis of complex designs (multiple factors and their interaction) without the constraints of multivariate normality, homoscedasticity, and when there are a greater number of variables than in traditional ANOVA tests. The method calculates a pseudo- F statistic analogous to the traditional F -statistic for multifactorial univariate ANOVA models, using permutation procedures to obtain p-values for each term in the model. When results were significant, we conducted pairwise tests. We evaluated similarities in diets using the Bray-Curtis similarity coefficient and then applied non-metric multidimensional scaling (nMDS) analysis. All statistical tests were performed using PRIMER v.6 software (Clarke & Gorley 2006).

RESULTS

We examined 424 stomachs of batoids. About 68.9% of *Gymnura poecilura*, 12.5% of *Brevitrygon walga*, 16.2% of *Maculabatis randalli*, 23.9% of *Pastinachus sephen*, 13.1% of *Rhinobatos punctifer* and 53.7% of *Torpedo sinuspersici* were empty (Table 1 and Table S2 in the Supplement). The cumulative prey curves based on diversity of prey indicated that

sample sizes were adequate to suggest their trophic habits for all species but *G. poecilura* (Fig. 2).

We found 7 prey types (teleosts, crustaceans, cephalopods, bivalves, gastropods, and echinoderms) among the 6 batoids. A total of 10 lower taxa groups occurred in the teleost group, 5 in the crustacean group, and 2 in the echinoderm group (Tables 1 & S2). Based on the % W , diet differed among the 6 batoid species (PERMANOVA tests; pseudo- F = 45.67, $p < 0.0001$; Table 1). Although we found marginal overlaps among several species by nMDS analysis (Fig. 3), pairwise tests revealed that diet differed among all batoids species (Table 2). Specifically, we found that the diet of 2 batoids (*G. poecilura* and *T. sinuspersici*) consisted mostly of teleosts (Table 1, Figs. 3 & 4), showing low diet diversity and high TL values (Table 1). In contrast, the diets of *B. walga* and *R. punctifer* contained mostly crustaceans (Table 1, Figs. 3 & 4), also with a low diet diversity (Table 1). The diets of *Maculabatis randalli* and *P. sephen* were more diverse (Table 1). The diet of *P. sephen* included bivalves, followed by echinoderms and then polychaetes, whereas the diet of *M. randalli* included crustaceans, followed by polychaetes and teleosts (Table 1, Figs. 3 & 4).

Teleosts appeared to be important prey for *G. poecilura* and *T. sinuspersici*. In contrast, *B. walga* and *R. punctifer* mostly ate crustaceans (Fig. 4), whereas the diets of *M. randalli* and *P. sephen* were broader (Fig. 4).

Table 1. General information and diet composition (standardized index of relative importance, IRI) of 6 batoid species from the Gulf of Oman. N: sample size; V: vacuity index; H: Shannon-Wiener diversity in number. See Table S2 in the Supplement for more accurate diet description. Disc width is reported for *G. poecilura*, *B. walga*, *M. randalli*, and *P. sephen* and total body length for *R. punctifer* and *T. sinuspersici*

	<i>Gymnura poecilura</i>	<i>Brevitrygon walga</i>	<i>Maculabatis randalli</i>	<i>Pastinachus sephen</i>	<i>Rhinobatos punctifer</i>	<i>Torpedo sinuspersici</i>
N	58	72	80	39	69	108
Weight (g) mean \pm SD	3785.6 \pm 2859	401.9 \pm 122.4	3071.2 \pm 3228.3	3771.5 \pm 2332.4	884.4 \pm 496.0	1407.1 \pm 786.1
Weight (g) min. – max.	310–12370	140–750	110–16170	470–12080	160–1940	340–3820
Length (cm) mean \pm SD	68.6 \pm 19.7	22.0 \pm 2.2	40.6 \pm 15.1	45.1 \pm 9.8	60.1 \pm 11.0	40.4 \pm 6.8
Length (cm) min. – max	33.5–107.5	15.2–27.5	18–80	24–71	38–80	27.5–56.1
V (%)	68.9	12.5	16.2	23.9	13.1	53.7
Trophic level	4.5	3.5	3.7	3.2	3.6	4.5
H	0	0.28	0.93	1.54	0.25	0.1
Teleosts	100	0	7.16	6.94	0.43	99.96
Crustaceans	0	98.70	80.67	10.56	99.34	0
Cephalopods	0	0	0.01	0	0	0.04
Bivalves	0	0	1.69	31.55	0	0
Echinoderms	0	0	0.02	24.65	0	0
Gastropods	0	0.02	0.02	0.77	0	0
Polychaetes	0	1.28	10.42	25.52	0.23	0

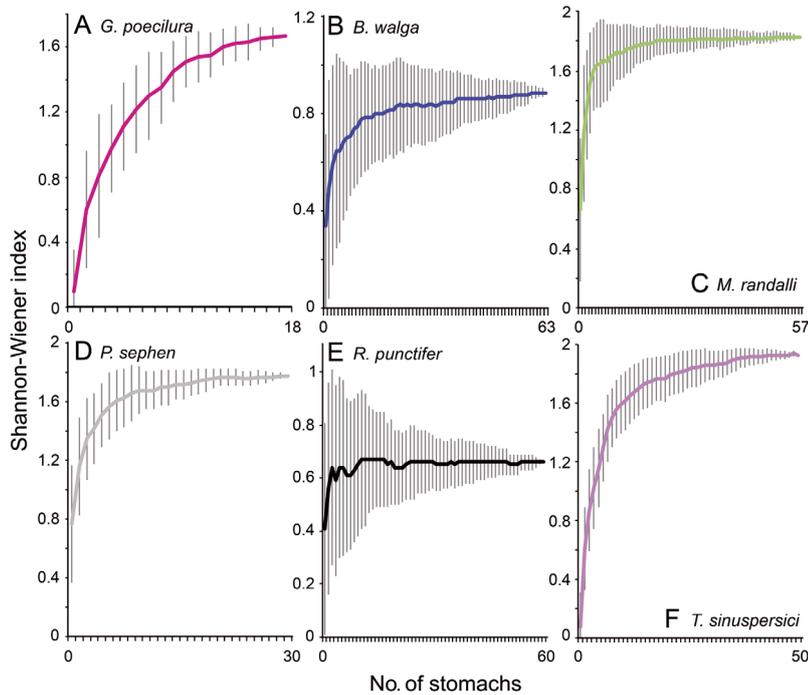


Fig. 2. Cumulative average (solid line) and standard deviation of Shannon-Wiener diversity index for samples of studied batoid species in the Gulf of Oman: (A) *Gymnura poecilura*, (B) *Brevitrygon walga*, (C) *Maculabatis randalli*, (D) *Pastinachus sephen*, (E) *Rhinobatos punctifer*, and (F) *Torpedo sinuspersici*

DISCUSSION

In this study, we presented new information on the seasonal diets of 6 demersal batoid species that co-occur in the northern Gulf of Oman. Though the use of stomach contents to describe diets is limited to indicating what individuals ate within a few days before

capture, we suggest that it can still provide general baseline information, particularly for species whose diets are not well known (Barría et al. 2015). We also maintain that the data we collected provide useful information about the main trophic levels at which all the batoids except *Gymnura poecilura* forage (Cortés 1999), and that this information enhances our knowledge about the foraging of batoids in the Gulf of Oman.

Our results reveal that there are differences among the 6 batoid species with respect to the habitats that they feed in. The stomach contents of *G. poecilura* included mostly teleosts, similar to other *Gymnura* spp. (Jacobsen et al. 2009, Yokota et al. 2013, Barría et al. 2015, Yemişken et al. 2018). Teleosts were also the most common prey in the diet of *Torpedo sinuspersici*, consistent with previous studies conducted on other *Torpedo* species conducted in other areas (Bray & Hixon 1978, Barría et al. 2015, Espinoza et al. 2015). On the other hand, the diet of *Rhinobatos punctifer* consisted mostly of crustaceans, especially shrimp species. Similar results have been reported in other guitarfish species (Harris et al. 1988, Blanco-Parra et al. 2012, Navarro-González et al. 2012, Espinoza et al. 2013, Lara-Mendoza et al. 2015). *Brevitrygon walga*, *Maculabatis randalli*, and *Pastinachus sephen* preyed on epibenthic organisms like crustaceans, polychaetes, bivalves, and echinoderms,

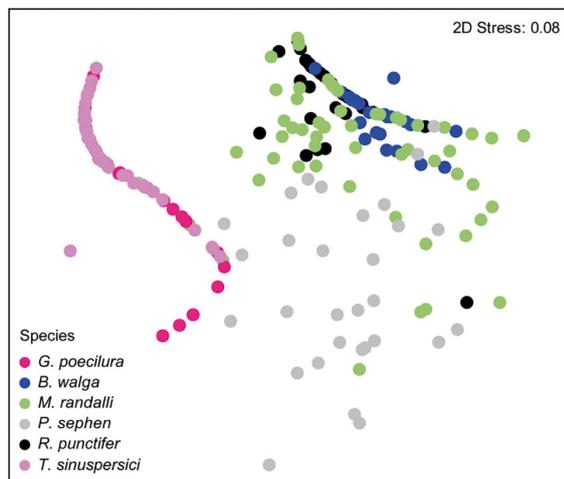


Fig. 3. Non-metric multidimensional scaling (nMDS) analysis of the stomach contents of 6 batoids (see Fig. 2 for full species names) sampled in the Gulf of Oman

Table 2. ANOSIM pairwise tests to compare the diet of 6 batoid species from the Gulf of Oman

Species × Species	R	p
<i>G. poecilura</i> × <i>B. walga</i>	0.995	0.001
<i>G. poecilura</i> × <i>M. randalli</i>	0.641	0.001
<i>G. poecilura</i> × <i>P. sephen</i>	0.661	0.001
<i>G. poecilura</i> × <i>R. punctifer</i>	0.869	0.001
<i>G. poecilura</i> × <i>T. sinuspersici</i>	0.391	0.001
<i>B. walga</i> × <i>M. randalli</i>	0.083	0.001
<i>B. walga</i> × <i>P. sephen</i>	0.671	0.001
<i>B. walga</i> × <i>R. punctifer</i>	0.192	0.001
<i>B. walga</i> × <i>T. sinuspersici</i>	0.970	0.001
<i>M. randalli</i> × <i>P. sephen</i>	0.400	0.001
<i>M. randalli</i> × <i>R. punctifer</i>	0.084	0.001
<i>M. randalli</i> × <i>T. sinuspersici</i>	0.765	0.001
<i>P. sephen</i> × <i>R. punctifer</i>	0.675	0.001
<i>P. sephen</i> × <i>T. sinuspersici</i>	0.884	0.001
<i>R. punctifer</i> × <i>T. sinuspersici</i>	0.927	0.001

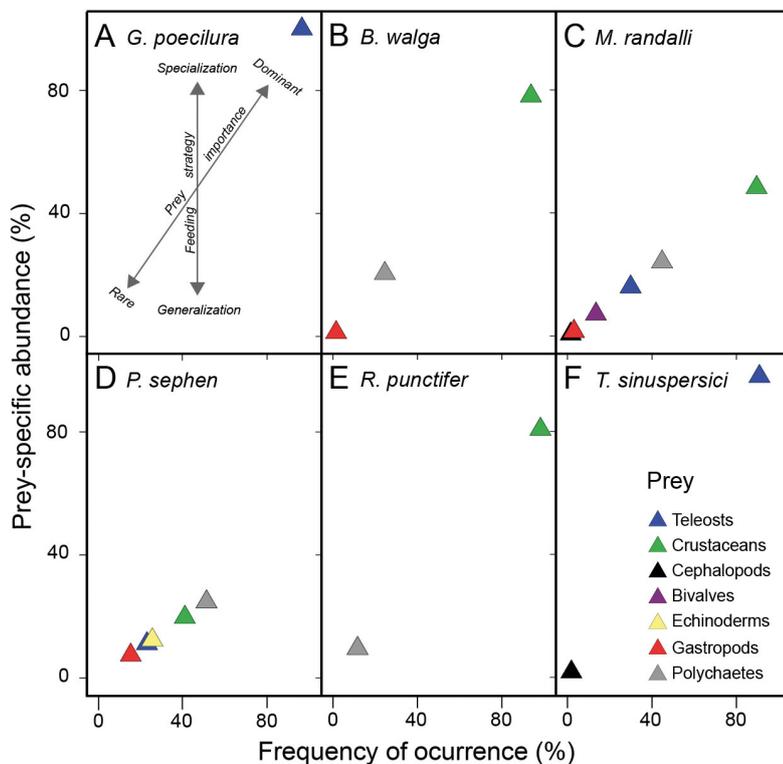


Fig. 4. Graphical representation of the feeding strategy of *Gymnura poecilura*, *Brevitrygon walga*, *Maculabatis randalli*, *Pastinachus sephen*, *Rhinobatos punctifer*, and *Torpedo sinuspersici* based on the method proposed by Amundsen et al. (1996). An explanatory diagram for interpretation of feeding strategy and prey importance from the proposed method appears in (A)

as previously reported for other dasyatids (Jacobsen & Bennett 2012, O'Shea et al. 2013), suggesting that those groups are the most important prey for this family.

Our results also showed that the stomachs of *G. poecilura* and *T. sinuspersici* were mostly empty when collected, which suggests that they had not eaten for one to several days (Vaudo & Heithaus 2011b). The stomachs of some marine predators, like elasmobranchs, are often found to be empty or contain highly digested prey remains that are difficult to identify (e.g. Jacobsen et al. 2009, Yokota et al. 2013).

In conclusion, we found that the diets of 6 batoid elasmobranchs in the Gulf of Oman differed during the sampling period. We cannot yet judge whether those differences were due to differences in the seasonal timing of capture or differences in the areas where they were captured. We recommend more intensive systematic sampling and observation of batoid elasmobranchs in the Gulf of Oman to address these questions and to help develop adequate conservation and management plans for the commercial fisheries that operate there.

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