

Feeding habits of the apron ray, *Discopyge tschudii* (Elasmobranchii: Narcinidae), from off Uruguay and northern Argentina

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The feeding habits of the apron ray, Discopyge tschudii, were investigated, off Uruguay and northern Argentina, and we tested the hypothesis that the diet changes with increasing body size, between sexes and seasons using a multiple-hypothesis modelling approach. Discopyge tschudii preys mainly on polychaetes (88.77% index of relative importance (IRI)) followed by siphons of the clam Amiantis purpurata (8.13% IRI) and amphipods (3.08% IRI). Ontogenetic, sexual and seasonal changes were found. Larger individuals of D. tschudii consumed buried polychaetes more often. The consumption of errant polychaetes was higher in males and in the cold season. Also, amphipods were preyed on more heavily by females and the number of siphons of A. purpurata consumed was higher in the cold season.

Keywords: Argentina, diet variation, predation, Narcinidae, Uruguay

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INTRODUCTION

Elasmobranch predation plays an important role in marine community structure (Heithaus *et al.*, 2010). Large sharks are top predators in many marine ecosystems affecting the abundance of species at lower trophic levels (Heithaus *et al.*, 2008). Some mesopredatory batoids affect the species turnover of benthic communities by disrupting the structure of the bottom while feeding on benthic invertebrates (Thrush *et al.*, 1994). Therefore, declines in the abundance of elasmobranchs have broader ecological consequences on community structure (Heithaus *et al.*, 2010). Further study of the feeding habits of the elasmobranch populations should help to elucidate the ecological role of these fishes in the marine ecosystem.

The apron ray, *Discopyge tschudii* (Narcinidae) is an elasmobranch endemic to South America that occurs in two broadly separated geographical areas (Atlantic and Pacific coasts of the continent) (Cousseau *et al.*, 2007). In the south-west Atlantic it inhabits waters from Rio Grande do Sul, Brazil, to Patagonia, Argentina (Menni & Stehmann, 2000; Cousseau *et al.*, 2007). In northern Argentina, the area with the highest catch of elasmobranchs (Lucifora *et al.*, 2012), *D. tschudii* has been subjected to heavy fishing pressure as by-catch of bottom trawl fisheries (Massa *et al.*, 2004a). Therefore, this species has declined heavily in its population abundance and the International Union for Conservation of Nature (IUCN) categorized *D. tschudii* as near threatened (Massa *et al.*, 2004b). Studies about the feeding habits of this species are scarce and limited to the description of diet composition:

D. tschudii feeds mainly on polychaetes, amphipods and siphons of clams (García, 1984; Arrighetti *et al.*, 2005).

For understanding how elasmobranch predation impacts on prey populations and the whole community, studies on how the diet composition might vary with ontogeny, space and time are essential for the implementation of ecosystem-level management and a conservation programme. The aim of this study was to investigate the feeding habits of *D. tschudii*, from off Uruguay and north Argentina. The specific objectives were to: (1) quantify the diet composition; and (2) assess the effects of sex, maturity stage, body size and season on the diet.

MATERIALS AND METHODS

Study area and sampling

The study area, between 34°S and 38°S, consists of a stratified coastal system influenced by the discharge of continental waters of the Río de la Plata (Guerrero & Piola, 1997; Lucas *et al.*, 2005). This system is characterized by strong vertical stratification: freshwater flows seaward on the surface while denser shelf water intrudes along the bottom, taking the shape of a salt wedge (Acha *et al.*, 2004). Wind fields force seasonal patterns of surface salinity, while bottom salinity is controlled by the bathymetry (Guerrero *et al.*, 1997).

Individuals of *Discopyge tschudii* were collected from scientific trawl surveys (N = 176) conducted by the Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP, Argentina; Figure 1). Research cruises were conducted in November (2005 and 2008) and September (2010). For each individual captured, total length (TL, mm), sex and maturity stage were recorded. Maturity stage (juvenile or adult) was

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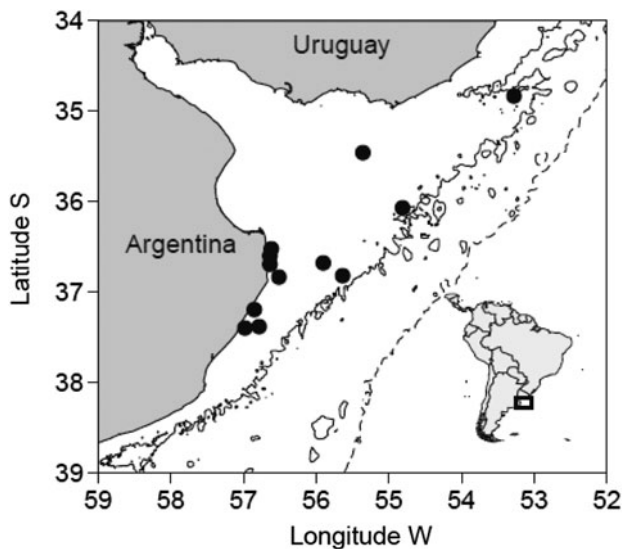


Fig. 1. Map of study area showing positions of trawl station where individuals of *Discopyge tschudii* were collected off North Argentina and Uruguay. The 50 m and 200 m isobaths are shown as solid and dashed lines, respectively. The rectangle in the inset shows the location of the study area in South America.

determined according to the degree of calcification of the claspers and the development of testes and reproductive ducts in males, and observation of the uteri, oviductal glands and ovarian follicles in females (Colonello, 2009). The stomachs were excised and frozen at -20°C for subsequent analyses in the laboratory.

Diet composition and analysis

Stomach contents were sorted and identified to the lowest possible taxonomic level, using reference collections preserved at the Laboratorio de Ictiología, Universidad Nacional de Mar del Plata (Argentina). Preys were counted and their wet weights recorded (± 0.01 g). To evaluate the importance of each prey and allow for comparisons with other studies the composition of diet was presented as percentage by number (%N), percentage by mass (%M), percentage frequency of occurrence (%FO) and index of relative importance (IRI) (Pinkas *et al.*, 1971). IRI was expressed in percentage (%IRI: Cortés, 1997).

To determine whether a sufficient number of *D. tschudii* was sampled, the stomachs sampled were randomized 100 times and the sample size was plotted against the mean cumulative Shannon–Wiener diversity index (Magurran, 2004). Sample size was considered sufficient to describe diet and to conduct statistical analyses if the curve reached an asymptote.

For identifying changes in the diet with sex, ontogeny and season, preys were grouped into four categories: errant polychaetes; buried polychaetes; siphons of clams; and amphipods. The majority of polychaetes live in close association with the substrate. The errant polychaetes are active worms that live on the substrate (Hesselberg, 2006). On the other hand, buried polychaetes are sedentary and live in tubes buried in the substrate (Hesselberg, 2006). Siphons of clams are an anatomical structure which is part of the body of molluscs bivalves and are used for feeding, respiration and reproduction (Hadley *et al.*, 2005; Grabarkiewicz & Davis, 2008).

Dietary variability of *D. tschudii* with sex, maturity stage (juvenile and adult), TL and season (warm = October–March; cold = April–September) were evaluated using generalized linear models (GLM: Venables & Ripley, 2002). For each prey category, models were built where the response variable was the number of prey consumed and the independent variables were sex, maturity stage, TL and season. Models with combinations between sex + season, maturity stage + season and TL + season as independent variables, were also fitted. We also fitted a model without any of the independent variables (i.e. null model) to test the hypothesis that none of the variables tested had an effect on the consumption of a prey category (Lucifora *et al.*, 2009). Models have a negative binomial error distribution because there were too many zeros and the variance was often much greater than the mean, and a log link (Crawley, 2005).

We used a multiple-hypothesis model approach to identify the best model explaining the consumption of a given prey (Anderson *et al.*, 2000; Franklin *et al.*, 2001; Johnson & Omland, 2004). For each competing model, we calculated the Akaike information criterion (AIC) and the model with the lowest AIC was selected as the best model (Crawley, 2005). To obtain the likelihood of each competing model given the data, Akaike's weight (w) was calculated (Franklin *et al.*, 2001; Johnson & Omland, 2004). If w did not provide strong support for any model fitted, we used model averaging to measure the effects of the variable explaining most of the variation (Johnson & Omland, 2004; Symonds & Moussalli, 2011).

RESULTS

Overall diet

A total of 176 stomachs of *D. tschudii* were examined (100% contained food). Of all specimens sampled, 59 were female (144–378 mm TL) and 117 were male (210–459 mm TL). Overall, 1777 preys with a total weight of 254.26 g were found in the stomachs. The cumulative curves of prey diversity reached an asymptote for all groups, indicating that sample size were sufficient to describe their diet (Figure 2).

Polychaetes were the most important prey in terms of %N, %M, %FO and %IRI in the diet composition of *D. tschudii*. Less important were siphons of the purple clam, *Amiantis purpurata*, and amphipods (Table 1). The consumption of the crab *Ermita brasiliensis* was considered occasional (%IRI < 0.01). Species belonging to 17 families of polychaetes were identified: seven families of errant polychaetes and 10 families of buried polychaetes. Among the errant polychaetes, Glyceridae was the main family consumed followed by Lumbrineridae and Onuphiidae. Among the buried polychaetes, Orbiniidae was the most important followed by Opheliidae.

Relationship between diet and sex, body size and season

Several patterns were found in the relationships between number of prey consumed with sex, TL and season (Table 2). As the *D. tschudii* size increased, the consumption of buried polychaetes increased in number (Figure 3). The consumption of errant polychaetes was higher in males than

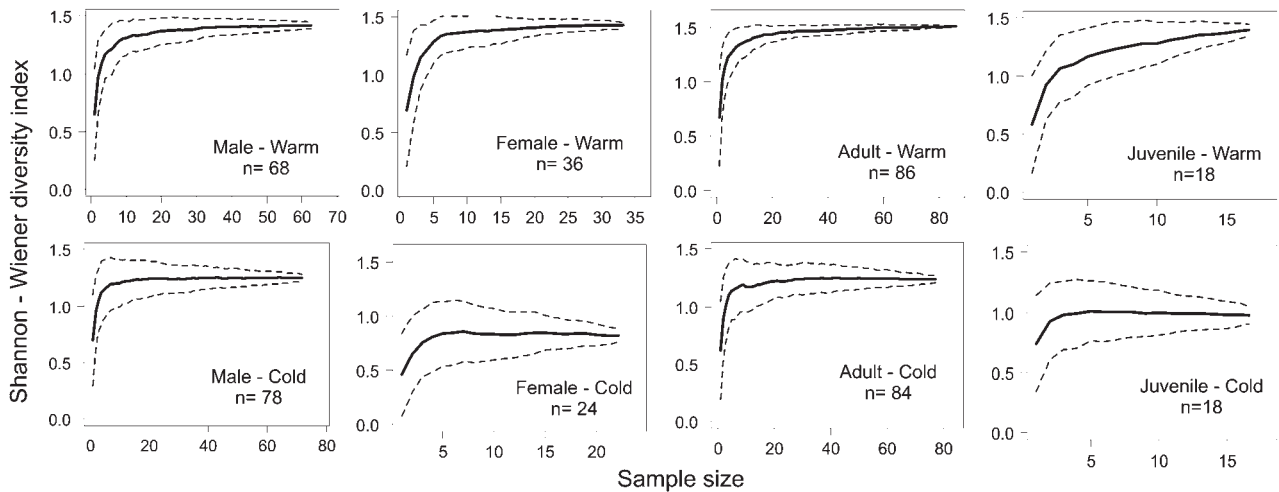


Fig. 2. Cumulative mean Shannon–Wiener diversity index (continuous lines) and standard deviation (dashed lines) as a function of sample size for *Discopyge tschudii*.

females, and that consumption was higher in the cold season than in the warm season (Figure 4). On the other hand, more amphipods were preyed by females than by males (estimated number of amphipods by GLM: females = 2.08 and males = 0.80). The number of siphons of *A. purpurata* consumed was higher in the cold season than in the warm season (estimated number of siphons by GLM: cold = 7.85 and warm = 0.47). The consumption of all prey categories was independent of the maturity stage.

The models for siphons of clams and amphipods had a low *w*, therefore model averaging was computed. For siphons, the

model averaging slope for the cold season was 0.462 (standard error (SE) = 0.54) with a combined *w* of 0.6348. The estimated averaged coefficient for amphipods was -0.714 (SE = 0.42) for males with a combined *w* of 0.999.

DISCUSSION

The feeding habits of *D. tschudii* are exclusively benthic because they feed mainly on polychaetes, followed by siphons of *A. purpurata* and amphipods. *Discopyge tschudii*

Table 1. Diet composition of *Discopyge tschudii*. %N, percentage by number; %M, percentage by mass; %FO, percentage of frequency of occurrence; IRI, the index of relative importance; %IRI, percentage of IRI. Bold indicates major taxonomic group.

Prey	%N	%M	%FO	IRI	%IRI	%IRI
POLYCHAETA	53.12	90.73	63.84	13260.80	88.77	
Unidentified remains	7.65	22.44	24.54	1341.34		19.26
ERRANT POLYCHAETES	26.45	36.67	28.47	2608.14		37.46
Lumbrineridae	7.82	8.30	10.28	271.76		
Goniadidae	0.90	0.94	1.62	5.64		
Glyceridae	10.63	17.98	13.17	550.77		
Nereidae	0.11	0.27	0.36	0.27		
Aphroditidae	0.11	0.27	0.36	0.27		
Onuphiidae	6.47	7.14	7.58	160.65		
Nephtyidae	0.39	1.75	0.90	2.75		
BURIED POLYCHAETES	19.02	31.61	19.13	1335.05		19.18
Orbiniidae	6.13	6.20	7.76	156.02		
Capitellidae	0.90	1.71	1.98	9.12		
Opheliidae	7.03	12.94	5.96	87.01		
Trochochaetidae	0.50	1.61	1.44	5.15		
Maldanidae	1.01	3.48	2.16	14.44		
Arenicolidae	0.05	0.29	0.18	0.096		
Polynoidae	0.11	0.33	0.36	0.28		
Questidae	0.11	0.06	0.18	0.06		
Flabelligeridae	0.11	0.87	0.36	0.48		
Sabellidae	2.87	3.99	3.25	32.86		
Tube of polychaetes	0.17	0.09	0.54	0.433		
MOLLUSCA						
Siphons of <i>Amiantis purpurata</i>	34.55	6.20	20	1215.09	8.13	17.46
CRUSTACEA						
Amphipods	12.21	2.32	15.38	460.31	3.08	6.62
<i>Ermita brasiliensis</i>	0.11	0.74	0.77	1.25	0.008	0.017

Table 2. Best models explaining the consumption of prey category in number of *Discopyge tschudii*. The intercept and coefficient for the variables are given. TL, total length (mm); AIC, Akaike information criterion; *w*, Akaike's weights; standard errors in parentheses.

Prey categories	Intercept	Coefficients	AIC	<i>w</i>
Buried polychaetes	-2.087 (0.69)	0.0076 (0.0019) TL	618.03	0.683
Errant polychaetes	0.0484 (0.23)	0.85194 (0.247)Male + 0.631 (0.224)Cold	736.45	0.978
Siphons of <i>Amiantis purpurata</i>	-0.752 (0.377)	2.8127 (0.562)Cold	508.59	0.461
Amphipods	0.734 (0.466)	-0.9535 (0.579)Male	386.9	0.331

showed changes in the diet composition between sexes, with increasing body size and also between seasons.

García (1984) described the diet of *D. tschudii* from individuals captured in Argentine waters and observed that the most important prey were polychaetes, followed by amphipods and cephalochordates. In agreement with García (1984), our results showed that the most important prey were polychaetes. In contrast with our results and García's (1984), Arrighetti *et al.* (2005) found that the diet of *D. tschudii* from Mar del Plata (38°S) was dominated by siphons of *A. purpurata*. These differences in the most important prey may be due to two reasons: the very restricted extent of the study area and a low sample size ($N = 67$) in Arrighetti *et al.* (2005).

Along its distribution range, *D. tschudii* coexist with other electric ray species such, as *Narcine brasiliensis*, *Torpedo puelcha* (Cousseau *et al.*, 2007) and *D. castelloi* (Menni *et al.*, 2008), but the ecology of these species is poorly known, including its feeding habits. Bornatowski *et al.* (2006) off São Francisco do Sul (Brazil), with a sample size of 15 individuals, found that *N. brasiliensis* feeds mainly on decapod crustaceans and polychaetes. In Argentinean waters, the stomach contents of *T. puelcha* contained fish species as prey (Cousseau & Bastida, 1982; Belleggia *et al.*, 2008). The diets of other species of Narcinidae are similar to that of *D. tschudii*. For example, off Colima (Mexico), *N. entemedor* consumed primarily polychaetes (Valadez *et al.*, 2000; Valadez-Gonzalez, 2007) and *N. vermiculatus* has a high incidence of polychaetes and presence of stomatopods, decapods and fishes in its diet (Valadez-Gonzalez, 2007). This and other studies confirm that Narcinidae are a group of electric rays highly specialized in their feeding

habits. On the other hand, the species of the genus *Torpedo* feeds mainly on active preys such teleost fishes (Bigelow & Schroeder, 1948; Abdel-Aziz, 1994; Capapé *et al.*, 2007; Belleggia *et al.*, 2008). These differences between Narcinidae and Torpedinidae may be related to the difference sizes that reach both families.

Electric rays are benthic suction feeders with a highly protrusible and versatile jaw apparatus, capable of adjustment of the mandibular apparatus in position to capture benthic invertebrates (Rudloe, 1989; Rudloe & Rudloe, 1993), obtaining their food by projecting their jaws and generating a negative pressure in the oral cavity to suck the food (Dean & Motta, 2004). Excavation of benthic prey by jaw protrusion can be performed only by an extremely protractile jaw and that is most likely unique to the Narcinoidea and Batoidea (Dean & Motta, 2004). As the numbers of *D. tschudii* increase their body size could increase the pressure in the oral cavity (i.e. increase the suction power), which allows them to hunt prey buried in the bottom. This could explain the increase in the consumption of buried polychaetes with increasing body size. Furthermore, the feeding behaviour of digging in the bottom (e.g. bioturbation) in search of prey could cause disturbances on the surface of the substratum. This physical disturbance to soft-bottom can play an important role in determining benthic community structure by removing prey species, providing secondary predators with access to normally unavailable prey and creating new opportunities for colonization (VanBlaricom, 1982; Thrush *et al.*, 1991; O'Shea *et al.*, 2012). From this way, some elasmobranchs of low trophic level, mainly mesopredatory batoids like *D. tschudii*, could be considered a key influence on marine ecosystems.

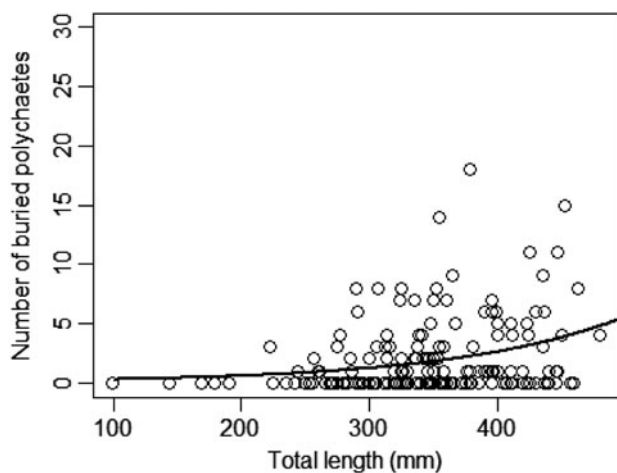


Fig. 3. Changes in consumption of buried polychaetes (in number) with body size of *Discopyge tschudii* estimated by generalized linear models. The models had a log link and a negative binomial error distribution.

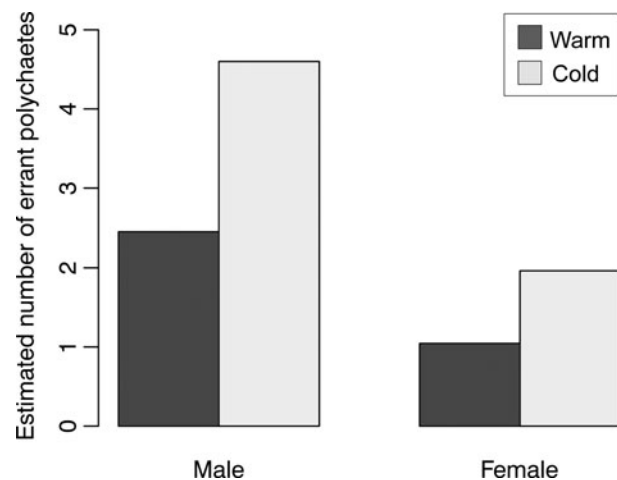


Fig. 4. Changes in consumption of errant polychaetes (in number) with sex and season of *Discopyge tschudii* estimated by generalized linear models. The models had a log link and a negative binomial error distribution.

Diet of predators may differ between sexes due to sexual size dimorphism (Begg *et al.*, 2003), differences on predatory capability of males and females (Floeter & Temming, 2003) and/or due to differences in the spatio-temporal foraging activity of males and females (Braccini *et al.*, 2005). In *D. tschudii* amphipods were most consumed by females than males and errant polychaetes were most consumed by males than females. The reasons for diet shifts between females and males could be the result, in part, of possible shift in habitat use between sexes. There are previous reports of sexual segregation in elasmobranchs (e.g. *Sphyrna lewini*, Klimley, 1987; *Scyliorhinus canicula*, Sims *et al.*, 2001; *Dasyatis longa*, Bohórquez-Herrera, 2006) and this pattern was previously proposed for *D. tschudii* (Menni *et al.*, 1981; Cousseau *et al.*, 2007). However, this hypothesis needs to be corroborated with dedicated studies at shifts in habitat use between sexes of *D. tschudii*. Also, females reach smaller sizes than males (Cousseau *et al.*, 2007). The fact that females consume greater amounts of amphipods than males may be related to the different sizes shown between them. This sexual dimorphism in body size may have an effect on the feeding habits of *D. tschudii*.

The diet composition of *D. tschudii* showed seasonal variation. This seasonal pattern is characterized by a higher consumption of siphons of *A. purpurata* and errant polychaetes in the cold season than in the warm season. These seasonal differences in the use of some trophic resources may be related to migration patterns of the predator and/or to a seasonal peak in abundance of different prey (Muto *et al.*, 2001). *Amiantis purpurata* inhabits shallow waters and the relative abundance of this species is constant throughout the year (Morsán E., personal communication). However, the consumption of this prey species changed between seasons. In the south-west Atlantic, Cortés *et al.* (2011) found onshore-offshore movements of *D. tschudii* with water temperature and salinity being the environmental factors with the highest effect on spatial distribution. In the winter, cool and high salinity waters cover a greater area of this region allowing the intrusion of *D. tschudii* into shallower waters (Cortés *et al.*, 2011). These onshore-offshore movements could explain the seasonal pattern observed in the diet composition.

The sublethal predation on siphons of bivalves might be interpreted as an important role in increasing secondary production, since that predation pressure stimulated the continuous regeneration of the lost siphons by clams (Tomiya *et al.*, 2004; Cledón & Nuñez, 2010). Thus, this prey constitutes a renewable source of food for predators (Penchaszadeh *et al.*, 2008).

Fishing affects marine populations both directly through removal of the individuals and indirectly through loss of habitat and modification of the trophic structure. Coastal areas off Uruguay and north Argentina are exposed to a high intensity of bottom trawling (Cousseau & Perrota, 2000). This activity alters the physical structure of the habitat, affecting the diversity of the benthic community (Kaiser, 1998), and generating potential indirect effects on the fish community (Brazeiro *et al.*, 2003). Our results show that the diet of *D. tschudii* was composed exclusively of benthic prey (i.e. polychaetes, amphipods and siphons of bivalves). Thereby, the loss of habitat caused by bottom trawling may alter the abundance and availability of prey for *D. tschudii* and of other benthic predators, with ecological consequences in the marine community.

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