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Gastropod predation on egg cases of skates (Chondrichthyes, Rajidae) in the southwestern Atlantic: quantification and life history implications

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Abstract Mean predation rates (\pm SD) on egg cases of the skates *Bathyraja macloviana*, *B. albomaculata*, *Amblyraja doellojuradoi*, and *Psammobatis* spp. from the southwestern Atlantic were estimated to be 0.151 (\pm 0.230), 0.423 (\pm 0.344), 0.254 (\pm 0.390), and 0.150 (\pm 0.288), respectively. These estimates are within the ranges reported earlier (14–40%). Egg cases of *B. albomaculata* were preyed on in higher proportion than expected from their abundance and suffered a heavier predation rate where the snail *Trophon acanthodes* was present. Predation rates were not correlated with the thickness of the egg case wall, which indicates that other factors (ecological or chemical) could explain this pattern. Five types of boreholes were found in the egg cases: one was attributable to muricid gastropods, one to naticid gastropods, and a third type to an unknown gastropod (probably *Fusitriton magellanicus*); the remaining were of unknown origin. Cladistic analyses showed that skates are secondarily oviparous and have maximized adaptations for living in deep water. We suggest that oviparity in skates appeared as an adaptation to maximize fecundity (40–160 eggs per year, as compared to 2–18 pups annually or biannually in viviparous guitarfishes, the plesiomorphic sister clade of skates). If a predation rate of 24% (the mean of predation rates of all skate species studied to date) is applied to the range of fecundities reported for skates, the result is that 18–114 viable pups are produced annually per female skate. Even with a high mortality rate of 64% (the only direct estimate of natural mortality for any elasmobranch), each female skate produces 17–54 eggs annually. These values are higher

than most elasmobranch fecundities. This maximization of fecundity is possible mainly because the fecundity of oviparous species is not limited by body size, as in viviparity. The protracted egg-laying season (4–12 months) of most skates (as in many other deep-sea fishes) maximizes the number of eggs laid.

Introduction

Predation is the main source of mortality of eggs of marine fishes (Bunn et al. 2000). Eggs suffer predation because they are a nutritive food often locally or temporally abundant.

Skates are abundant oviparous fishes that lay eggs protected by a leathery capsule (Hamlett and Koob 1999). As they do not provide parental care, the leathery and tough capsule is the only mechanical protection from predators and also acts as a barrier from pathogens (Kormanik 1993). However, some predators (mostly gastropods) are able to feed on skate eggs by boring holes through the leathery capsule (Cox and Koob 1993). When boring predation was discovered it was thought to be of rare occurrence (Ansell 1961). However, predation rates of 22% on egg cases of the little skate *Leucoraja erinacea* from the northwest Atlantic (Cox and Koob 1993), 14–40% for egg cases of seven species of coastal elasmobranchs from South Africa (Smith and Griffiths 1997), and 18% for eggs of the thorny skate *Amblyraja radiata* off Denmark (Cox et al. 1999) have been estimated.

These high predation rates have been thought of as the selective pressure driving the shift from oviparity to viviparity in elasmobranchs (Grover 1972; Smith and Griffiths 1997). However, a survey of the phylogenetic relationships of skates shows that they are the sister group of viviparous taxa and that skate oviparity is derived (Dulvy and Reynolds 1997). For this shift from viviparity to oviparity to occur, egg laying should be at least as efficient (in terms of fitness

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maximization) as viviparity. When assessing this shift to oviparity one must bear in mind the new selective pressures faced by skates when passing from a shallow-water to a deep-water environment, where they radiate (McEachran and Dunn 1998). Oviparity should either maintain or increase the average individual fitness of skates. In this article we quantify predation rates on skate egg cases in the southwestern Atlantic, identify major patterns of gastropod predation on egg cases, and propose a hypothesis on why oviparity could have evolved in skates from a viviparous ancestor.

Materials and methods

Predation rates

Egg cases of southern thorny skate *Amblyraja doellojuradoi* ($n=60$), white-dotted skate *Bathyrāja albomaculata* ($n=167$), Patagonian skate *B. macloviana* ($n=194$), and sand skates *Psammobatis* spp. ($n=258$) were obtained from six research cruises carried out between December 1998 and July 1999. Samples were taken with a dredge between 39°09' and 43°19'S and 55°44' and 59°50'W (outer continental shelf off northern Argentina), at depths between 85 and 149 m. Egg cases were identified to species by comparing term embryos within egg cases with free-swimming individuals of known identity. Complementarily, egg cases were compared with egg cases found inside female skates of known identity. Egg cases of the genus *Psammobatis* were pooled because specific identification was not possible given the high similarity between egg cases of the two species of the genus that occur in the study area (i.e. *P. normani* and *P. rudis*).

Gastropod boreholes were identified following Smith and Griffiths (1997) and Carriker (1998). For each species, predation rates were calculated as the number of perforated egg cases divided by the total number of egg cases in a tow (sample). Minimum predation rate was also calculated as the number of bored egg cases that presented closed hatching seams divided by the total number of egg cases in a tow. The null hypothesis of no difference in mean predation rates among skate species was tested with the Kruskal–Wallis test (Zar 1984). Multiple comparisons were performed as indicated in Conover (1980).

To evaluate if egg cases were preyed on in the same proportion as found in the environment, we compared predation rates with the relative proportion of each skate species using the Mann–Whitney *U* test (Zar 1984). Alternatively, we calculated the Jacobs electivity index (Jacobs 1974) for each skate species, which varies from +1 for maximum preference to –1 for maximum avoidance.

The role of the snails *Trophon acanthodes* and *Fusitriton magellanicus* as potential predators of egg cases was assessed by comparing mean predation rates

in locations with and without *T. acanthodes* and *F. magellanicus* by using Student's *t* test (Zar 1984).

Borehole analysis

Length of boreholes was measured with the digital image analyzer program Otolis2 version 3.10 (Ratoc System Engineering Co. Ltd., Japan). The null hypothesis of no difference in borehole size among skate species was evaluated with analysis of variance (ANOVA) on log-transformed data.

The wall thickness of ten egg cases of each species was measured using Otolis2 version 3.10. The relationship of mean wall thickness of each egg case species with predation rate and borehole size was assessed through correlation analysis.

Results

Predation rates

Mean predation rates (\pm SD) of egg cases were 0.423 (± 0.344), 0.254 (± 0.390), 0.151 (± 0.230), and 0.150 (± 0.288), for *Bathyrāja albomaculata*, *Amblyraja doellojuradoi*, *B. macloviana*, and *Psammobatis* spp., respectively (Fig. 1). Predation rates were significantly different among skate species (Kruskal–Wallis, $H=19.4$, $df=3$, $P=0.002$). Egg cases of *B. albomaculata* were preyed on in higher proportion than those of *Psammobatis* spp. (Dunn's test, $Q=3.783$, $P<0.05$), *B. macloviana* (Dunn's test, $Q=3.712$, $P<0.05$), and *A. doellojuradoi* (Dunn's test, $Q=2.978$, $P<0.05$).

The number of egg cases with both closed hatching seams and boreholes gave a mean minimum estimate of predation rates of 0.141 (± 0.245 SD) for *B. albomaculata*, 0.037 (± 0.113 SD) for *B. macloviana*, 0.184

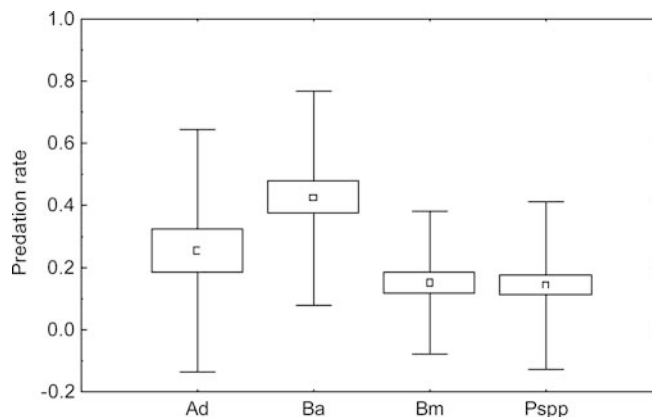


Fig. 1 Mean predation rates on egg cases of skates from the southwestern Atlantic. Boxes depict the standard error and whiskers show the standard deviation. Ad *Amblyraja doellojuradoi*, Ba *Bathyrāja albomaculata*, Bm *B. macloviana*, Pspp *Psammobatis* spp.

(± 0.354 SD) for *A. doellojuradoi*, and 0.060 (± 0.193 SD) for *Psammobatis* spp. These predation rates did not differ significantly among skate species (Kruskall–Wallis, $H = 7.65$, $df = 3$, $P = 0.054$).

The egg cases of *A. doellojuradoi* were preyed on in the same proportion as found in the environment (Mann–Whitney U test, $Z = 2.206$, $n_1 = 57$, $n_2 = 43$, $P = 0.052$). Mean predation rates of all other skates were not distributed as expected from the abundance of each egg case in the environment. Egg cases of *B. albomaculata* were consumed in higher proportion than expected from their abundance in the environment (Mann–Whitney U test, $Z = -2.179$, $n_1 = 57$, $n_2 = 43$, $P = 0.032$; Jacobs electivity index = 0.428). In contrast, egg cases of *B. macloviana* (Mann–Whitney U test, $Z = 2.549$, $n_1 = 57$, $n_2 = 43$, $P = 0.013$; Jacobs electivity index = -0.421) and *Psammobatis* spp. (Mann–Whitney U test, $Z = 2.223$, $n_1 = 57$, $n_2 = 43$, $P = 0.034$; Jacobs electivity index = -0.284) were preyed on in a lower proportion than expected from their abundance in the environment.

When predation rates in samples with and without *Trophon acanthodes* were compared, they differed significantly only for *B. albomaculata* (mean predation rate with *T. acanthodes* = 0.635, without *T. acanthodes* = 0.363; $t = 2.14$, $df = 29$, $P = 0.04$). Predation rates of egg cases in samples with and without *Fusitriton magellanicus* did not differ significantly for any skate species (*B. albomaculata*: t test, $t = 0.423$, $df = 26$, $P = 0.676$; *B. macloviana*: Mann–Whitney test, $Z = 124.5$, $n_1 = 8$, $n_2 = 20$, $P = 0.684$; *Psammobatis* spp.: Mann–Whitney test, $Z = 104.0$, $n_1 = 8$, $n_2 = 22$, $P = 0.359$).

Borehole analysis

The holes found in egg cases varied considerably in shape and size and could be classified into five types: elongate, muricid-like, naticid-like, scratched (Fig. 2), and other, those that could not be sorted into any of the other types. Elongate holes had a roughly circular outline, often resembling a wide open V (Fig. 2A); muricid-like holes were perfectly circular with walls perpendicular to the egg case wall, consistent with descriptions of holes made by muricid gastropods (Gordillo 1994; Carriker 1998; Fig. 2B); naticid-like holes were similar to muricid-like ones but the borehole walls were not perpendicular to the egg case walls, resulting in a cone-shaped hole with beveled edges (Carriker 1998; Fig. 2C); scratched holes had mostly a nearly circular outline with several long scratches departing from the center of the hole (Fig. 2D); and other boreholes had undefined shapes with irregular contours. These borehole types were not equally distributed, with elongate holes being the most abundant in all egg case species (Table 1). Muricid-like holes were especially abundant on egg cases of *B. albomaculata* (Table 1).

The mean maximum diameter (\pm SD) of boreholes was 3,130.967 μm ($\pm 1,442.069$) for *A. doellojuradoi*, 3,401.149 μm ($\pm 2,450.041$) for *B. albomaculata*, 3,907.104 μm ($\pm 2,615.085$) for *B. macloviana*, and 3,353.414 μm (± 422.101) for *Psammobatis* spp. The mean maximum diameter of boreholes did not show significant differences among skates (ANOVA of log-transformed data, $F = 0.480$, $df = 156$, $P = 0.697$). The

Fig. 2A–D Predatory boreholes observed on egg cases of skates from the southwestern Atlantic. **A** Elongate borehole, scale bar = 5,000 μm ; **B** muricid-like borehole, scale bar = 2,000 μm ; **C** naticid-like borehole, scale bar = 500 μm ; **D** scratched borehole, scale bar = 2,000 μm

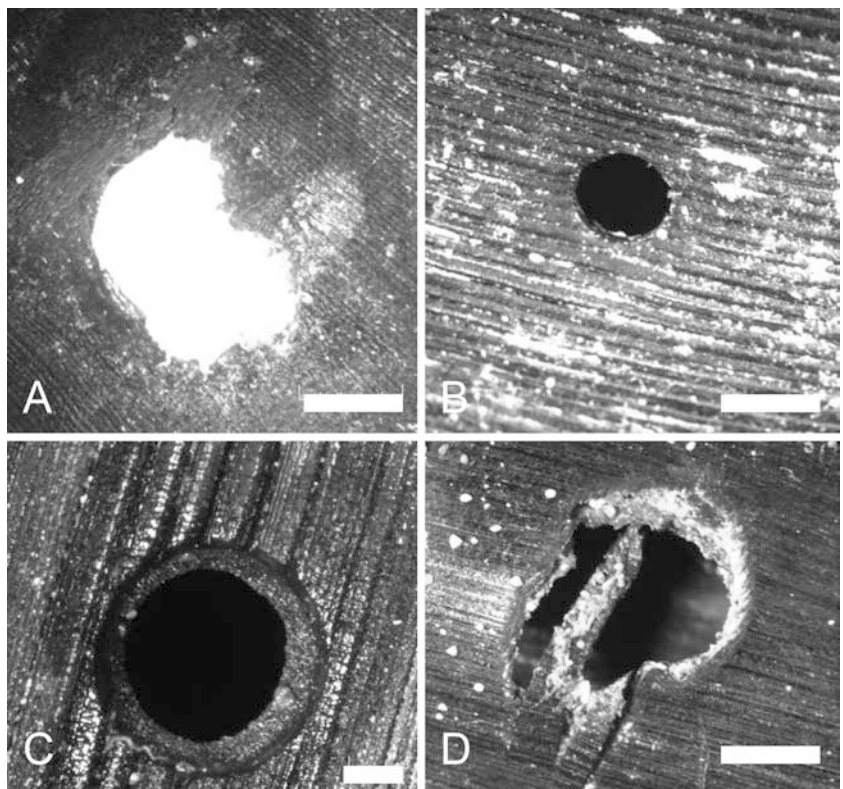


Table 1 Percent occurrence of borehole types on egg cases of the skates *Amblyraja doellojuradoi*, *Bathyrāja albomaculata*, *B. macloviana*, and *Psammobatis* spp. from the southwestern Atlantic

Species	Borehole type					Sample size
	Elongate	Muricid-like	Naticid-like	Scratched	Other	
<i>Amblyraja doellojuradoi</i>	70.83	0.00	0.00	12.50	16.67	24
<i>Bathyrāja albomaculata</i>	49.33	26.67	12.00	1.33	10.67	75
<i>B. macloviana</i>	65.22	17.39	0.00	4.35	13.04	23
<i>Psammobatis</i> spp.	64.10	10.26	0.00	10.26	15.38	39

frequency distribution of ventral versus dorsal boreholes did not deviate significantly from the 1:1 ratio in any species (*A. doellojuradoi*: $\chi^2=0.083$, $df=1$, $P=0.773$; *B. albomaculata*: $\chi^2=0.372$, $df=1$, $P=0.542$; *B. macloviana*: $\chi^2=1.389$, $df=1$, $P=0.541$; and *Psammobatis* spp: $\chi^2=1.531$, $df=1$, $P=0.216$). Mean diameter of boreholes was not different between dorsal and ventral walls of any species (*A. doellojuradoi*: $t=-0.103$, $df=9$, $P=0.920$; *B. albomaculata*: $t=-1.75$, $df=41$, $P=0.087$, paired t test on log-transformed data; *B. macloviana*: $t=-0.728$, $df=16$, $P=0.477$, paired t test; and *Psammobatis* spp: Mann–Whitney U test, $Z=188.0$, $P=0.711$). There was no correlation between mean egg case wall thickness and mean length of boreholes ($r=0.88$, $P=0.12$, $n=4$).

The egg case wall thickness was different among skate species (one-way ANOVA on log-transformed data, $F=62.4$, $df=38$, $P<0.0001$). The thickest egg case wall was that of *B. macloviana* (mean \pm SD = $1,013.77 \pm 226.67$ μm); followed by *B. albomaculata* (566.47 ± 77.52 μm), *A. doellojuradoi* (427.84 ± 110.55 μm), and *Psammobatis* spp. (291.71 ± 61.91 μm). All pairwise comparisons among skate species were significantly different (Student–Newman–Keuls test, $P<0.05$). There was no correlation between mean egg case wall thickness and mean predation rate ($r=-0.181$, $n=4$, $P=0.819$). Egg cases of *B. macloviana* were very rough due to a number of high parallel striations on the egg case surface (see Fig. 2B, C). All other egg cases were smooth because striations were not so high.

Discussion

Predation rates

We estimated two predation rates, a minimum rate as the proportion of egg cases with closed hatching slits and boreholes, and a maximum predation rate as the proportion of both open and closed egg cases with boreholes. However, we found egg cases with partially open hatching slits and no embryos. Also, some egg cases were stored with closed hatching seams but they had open hatching seams when reexamined. This is indicative of the opening of the egg case after the death of the embryo, and thus it suggests that an open egg case is not indicative of birth. Thus, the minimum predation rate might underestimate predation rates. In addition, Cox et al. (1999) found that the estimates of maximum predation rate (as calculated here) are consistent with

the experimental predation rate observed for egg cases of the little skate *Leucoraja erinacea* (22%, Cox and Koob 1993). For these reasons, we use maximum predation rates as estimators of predation rate.

Our estimates of predation rates are within the range of rates estimated for other oviparous elasmobranchs (see Introduction). It is noteworthy that predation rates differed among species. Also, all borehole types were not equally distributed among egg cases. These differences can be explained by variations in the behaviour and biology of both prey and predators, or a combination of both. Prey characteristics that can be of importance in explaining these differences are egg case wall thickness, egg case wall chemical composition, egg case microhabitat, egg development, and egg nutritive value. Predator characteristics that can explain the differences are predator microhabitat, predator preferences, and predator boring ability.

We found that egg case wall thickness is not correlated with predation pressure. Possibly egg cases are not a significant mechanical barrier to the boring organ and radula of gastropods, which are able to bore hard materials such as mollusk shells (Carriker 1981). Egg case surface could affect the predation process. We found that the egg case with the roughest surface (i.e. *Bathyrāja macloviana*) has a high predation rate. Further experimental studies on the effect of egg case surface on predator ability are needed to understand fully the interaction between these two variables.

The chemical composition of the egg case wall could produce a differential pattern of predation if it varies among species. None of the species studied here have been investigated with regard to egg case chemical composition. The chemical composition of egg cases of two unrelated chondrichthyans does not vary substantially (Hamlett and Koob 1999), which suggests common compositions of egg cases of distantly related species. This suggests that chemical composition could not explain the interspecific variation observed. However, more species need to be studied in order to have a good picture of variability in chemical composition of egg cases of oviparous chondrichthyans.

Although all samples were taken in the same habitat (scallop beds) there can be differences in microhabitat for each species that can make eggs differentially vulnerable to predators. These microhabitat differences could arise, for example, from selection of egg-laying sites by females (Hamlett and Koob 1999; Compagno 2002). This could explain, at least in part, the observed differences.

Egg development could affect predator preference and success. Recently laid eggs are softer than older eggs. This can affect predator success or preference because soft egg cases could be easier to bore than hard ones. In addition, a newly laid egg carries embryos in the first developmental stages and they are proportionally richer in yolk (hence more nutritive) than more advanced eggs. Thus, predators could prefer newly laid eggs over older eggs. The distinction of new and old eggs by a predator appears to be not difficult given the physical and chemical differences between new and old eggs (Koob 1991; Hamlett and Koob 1999).

Differences in predator microhabitat can enhance the encounter rate of a predator with a given egg and lower the encounter rate with eggs not occupying the same microhabitat. Also, boring ability is likely to vary among predators given differences in size and boring organs (Carriker 1981).

Our observations on borehole shape are in agreement with most descriptions of gastropod boreholes (Cox and Koob 1993; Smith and Griffiths 1997; Carriker 1998). The most common borehole was the elongate borehole type. These boreholes are similar to those produced by the gastropod *Burnupena papyracea* on elasmobranch egg cases off South Africa (Smith and Griffiths 1997). Muricid-like boreholes were much more common than naticid-like ones. This is in accordance with the gastropod fauna composition of the study area, in which muricid gastropods are more abundant than naticid ones (Bremec et al. 1998). The identity of predators could not be determined but some patterns informative on this subject are apparent. The most common borehole type can be made by some of the most common predatory gastropods: these are *Fusitriton magellanicus* and *Marginella warrenii* (Bremec et al. 1998). However, the size of the boreholes relative to snail size makes *F. magellanicus* the most likely predator boring elongate boreholes. Muricid-like boreholes may be the result of predation by, mainly, the snail *Trophon acanthodes*. This hypothesis is supported by the fact that the egg case with the highest incidence of muricid-like boreholes (i.e. *Bathyraja albo-maculata*) suffers, in addition, the highest predation rates where *T. acanthodes* was present. Further experimental work is needed to identify major boring predators and to correlate borehole types with identity of predators.

The proportion of boreholes was not different between dorsal and ventral surfaces of egg cases. This pattern was also found in egg cases of *Amblyraja radiata* (Cox et al. 1999). This pattern is expected if egg cases were laid on the bottom randomly on either dorsal or ventral surfaces.

Evolution of oviparity and life history implications

Guitarfishes (Rhinobatiformes) are the closest relatives of skates and they are considered to be plesiomorphic relative to skates (Nishida 1990; McEachran and Dunn 1998; Schwartz and Maddock 2002). They are inshore,

often large (50–300 cm total length, TL) batoids occurring in tropical and warm-temperate seas throughout the world (Compagno and Last 1999). Guitarfishes have low fecundities (2–18 pups per litter) and short reproductive seasons, and they depend on suitable inshore nursery areas for giving birth (Lessa et al. 1986; Villavicencio-Garayzar 1993, 1995; Wenbin and Shuyuan 1993; Capapé and Zaouali 1994; Hensley et al. 1998; Kyne and Bennett 2002). In addition, some species have reproductive cycles with a resting period of possibly a year (Kyne and Bennett 2002). In contrast, skates have annual fecundities of 40 to >160 eggs (Holden et al. 1971; Holden 1975, Capapé and Quignard 1975; Capapé 1977a, 1977b; Fuentealba and Leible 1990; Ellis and Shackley 1995) and protracted egg-laying seasons (Templeman 1982; Hamlett and Koob 1999; excepting some coastal temperate species, Mabragna et al. 2002).

Fecundity is positively correlated with body size in both guitarfishes (Lessa et al. 1986; Villavicencio-Garayzar 1993, 1995; Wenbin and Shuyuan 1993; Capapé and Zaouali 1994; Kyne and Bennett 2002) and skates (Capapé and Quignard 1975; Capapé 1977a, 1977b). Most skate species are in the range of 30–120 cm of maximum TL (Dulvy and Reynolds 2002), which is less than guitarfish size. This suggests that skates escaped from low fecundities imposed by a small body size by shifting to oviparity. In oviparous reproduction eggs develop outside the body and are produced (in general) over long periods, this implies that body size has little effect on the size of litters. However, having an external egg adds a life stage exposed to predation and other sources of mortality. Nevertheless, the application of a mean predation rate on egg cases of 24% (mean of predation on egg cases of all skate species studied to date) to the range of fecundities documented for skates leaves 36–114 non-predated eggs per female skate each year. Even the assumption of a natural mortality of 64% (direct estimate of neonate mortality for viviparous sharks, Manire and Gruber 1993) gives an estimated production of 17–54 pups per female per year. These figures are well above the fecundities of guitarfishes and most elasmobranchs.

The reproductive strategy of skates with protracted egg-laying seasons and benthic eggs is typical of many deep-water fishes (Gage and Tyler 1992) and agrees with the maximization of adaptations to deep-water environments observed in skates (McEachran and Dunn 1998).

Skates maximized their fitness by increasing their fecundity. These observations suggest that oviparity is an evolutionary adequate adaptation for the lifestyle of skates and that egg case predation levels estimated at present fit well in the general life history scheme of skates.

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