# Shark and skate egg-cases cast up on two South African beaches and their rates of hatching success, or causes of death

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Collections of chondrichthyan egg-cases cast ashore at two sites along the South African coastline were identified and examined for cause of mortality. A total of 574 egg-cases collected from False Bay could be attributed to five species of scyliorhinid shark, two skates and the elephantfish or chimaera, while the 538 egg-cases collected from Port Alfred belonged to four scyliorhinid sharks and two skate species. At both sites eggs of shy-sharks of the genus *Haploblepharus* made up more than 70% of the samples, followed by skates (5% in False Bay and 19% in Port Alfred) and then catsharks of the genus *Poroderma* (1 and 7% respectively). *Haploblepharus* egg-cases generally displayed relatively high rates of hatching success of over 60% and predation rates of 18–30%. *Haploblepharus fuscus* was the exception with a low hatching success of 37% and a predation rate of 40%. *Poroderma* egg-cases suffered predation losses of 43%, and had a hatching success of 47%. Skate egg-cases displayed non-predator induced egg mortalities of up to 35%, but predation rates of less than 14%. Hatching success was moderate at 57%. The holes found in egg-cases could be categorised into five types, of which four were clearly predator boreholes. The most abundant of these was shown to be caused by whelks of the genus *Burnupena*.

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Three modes of reproduction occur in cartilaginous fishes, namely ovipary (the laying of egg-cases which develop externally), ovovivipary (also refered to as aplacental or lecithotrophic vivipary) and vivipary (also known as matrotrophic or placental vivipary). In oviparous species the fertilized eggs are each encapsulated into a 'mermaid's purse', which is either attached by the mother to a suitable underwater substratum, or deposited unattached onto sand. In ovoviviparous species the egg-capsule is retained in the mother's uterus, until the embro is fully developed. Viviparous species retain free eggs in the uterus, where they are provided with nutrients from the mother, eventually developing into relatively large, well-developed, swimming young (Smith & Heemstra 1986; van der Elst 1993; Wourms & Demski 1993). Viviparity is considered to be the most advanced and most energetically expensive of these modes of reproduction, yet the majority of cartilaginous fishes have evolved this type of development (Wourms & Demski 1993).

The selection pressures responsible for this shift from oviparous to intra-uterine development are not clearly identified. Smith (1936) and Price & Daiber (1967) proposed that intra-uterine development has the advantage for the embryo of allowing more efficient osmoregulation, but Kormanik (1992, 1993) has shown that encapsulated embryos are in fact well capable of regulating urea and osmotic pressure. Read (1968) subsequently suggested that protection against predation and mechanical damage were more likely to be responsible for the evolution of viviparity, but provided no evidence to support this theory. The first quantitative assessment of predatory pressure on shark egg-cases was provided by Grover (1972), who examined a sample of 40 swell shark (*Cephaloscyllium ventriosum*) egg-cases collected from depths of 25–35 m at Santa Catalina Island, California. Only 20–27.5% of the sample hatched, while 72.5% were preyed upon and a maximum of 7.5% died owing to factors other than predation. In a simi-

lar study Cox & Koob (1993) collected approximately 100 *Raja* and 10 *C. ventriosum* egg-cases and found that 81% of the *Raja* and 70% of *C. ventriosum* material displayed predator bore-holes. Both studies thus tend to support Read's (1968) theory that predation may be a factor in the reproductive shift towards vivipary in chondrichthyans.

The primary aim of this study was to collect similar quantitative data to determine the egg mortality and hatching success rates of various species of oviparous sharks and skates from South African coastal waters, and hence to provide further evidence as to the importance of predation in this stage of their life histories. Subsidiary aims were to describe the egg-cases of the various species, to determine the species composition of chondrichthyan egg-cases cast ashore at selected beaches and to try to identify the predators of egg-cases.

## Methods

Samples of egg-cases washed ashore at Port Alfred (33°35'S; 26°36'E) and along the north and west coasts of False Bay (34°05'S; 18°29'E) were collected between April and December 1995. All egg-cases encountered during each search were collected and were subsequently pooled for each site. Since the majority of the egg-cases were dehydrated and rigid they were rehydrated in seawater and then analysed as follows.

Shark egg-cases were identified using the descriptions given by von Bonde (1945a, b), Bertolini (1993) and Branch, Griffiths, Branch & Beckley (1994). Note, however, that Von Bonde (1945a) inaccurately described the egg-cases of *Haploblepharus pictus* as belonging to *Haploblepharus edwardsii* (Bertolini, 1993). Skate egg-cases were identified by Dr Leonard Compagno of the South African Museum, Cape Town.

Egg mortality and hatching success were determined by examining the hatching slits of washed-up egg-cases, as well

as inspecting for signs of predation and mechanical damage. Each egg-case was categorized into one of the following groups:

— Hatched: displaying open hatching slit with no signs of predation.

— Depredated: with distinct boreholes, or other cut or chewed looking holes (hatching slit open or closed).

— Unknown: with closed hatching slit and no signs of predation. This could result from the embryo dying owing to factors other than predation; the decaying embryo would then be washed out of the egg-case through the respiratory slits (Grover 1972).

— Intact: containing a dead embryo — mortality probably being the result of suffocation, disease or dessication after being beach cast.

Egg-cases which were heavily eroded or disintegrating from long exposure to the elements, such that cause of death could not be ascertained, were discarded and are not included in the analysis. Holes in the egg-cases were enumerated and separated into recognizable types according to size and shape. Simple regressional analysis was used to test for correlation between borehole size and egg-case length.

Since Cox & Koob (1993) suspected that predatory gastropods were the principal predators of skate eggs we tested this by placing live eggs of *H. pictus* into separate tanks together with whelks of each of the following seven species — *Afrocominella elongata, Argobuccinum pustulosum, Burnupena lagenaria, B. papyracea, Fasciolaria lugubris lugubris, Fusinus ocelliferus* and *Nucella dubia*. Several specimens of each species of whelk were placed into each tank with 2–4 live egg-cases. No additional food source was provided and the tanks were monitored regularly and the egg-cases examined

for mechanical damage over the following eight weeks.

## Results

### Egg-case descriptions

Of the 1 012 egg-capsules collected, 574 were from False Bay and 538 from Port Alfred. These belonged to five different species of scyliorhinid sharks, namely, *Haploblepharus pictus, H. edwardsii, H. fuscus, Poroderma africanum,* and *P. pantherinum;* the elephantfish, *Callorhinchus capensis;* and four species of skate. The eggs of two skate species, *Raja alba* and *R. miraletus,* could be identified. The remaining two egg-cases could not be positively allocated to species, although one is likely to belong to the '*Raja* cf. *clavata*' of Lamberth, Bennett & Clark (1994), which is the skate most commonly caught by the commercial beach-seine fishery in False Bay (it is now thought that this species is in fact *R. strealeni* — S. Lamberth, pers. comm.). Morphologically the egg-cases fall into three groups. Of these, the egg-cases of scyliorhinid sharks (*Haploblepharus* and *Poroderma*) possess elongate tendrils at each corner, which are normally wrapped firmly around the stipes of large algae, or the branches of gorgonians during the process of egg-laying. The egg-cases of skates, on the other hand, possess short rigid horns, while those of the elephantfish are spindle-shaped structures that lack horns or tendrils (Figure 1). Both these types are laid unattached on sandy substrata.

The various egg-cases are shown to scale in Figure 1 and may be identified as follows:

Egg-cases of the catshark *P. africanum* are robust, dark brown and rectangular in shape with average dimensions of 95 × 45 mm. Eggs of *P. pantherinum* are similar in form, but
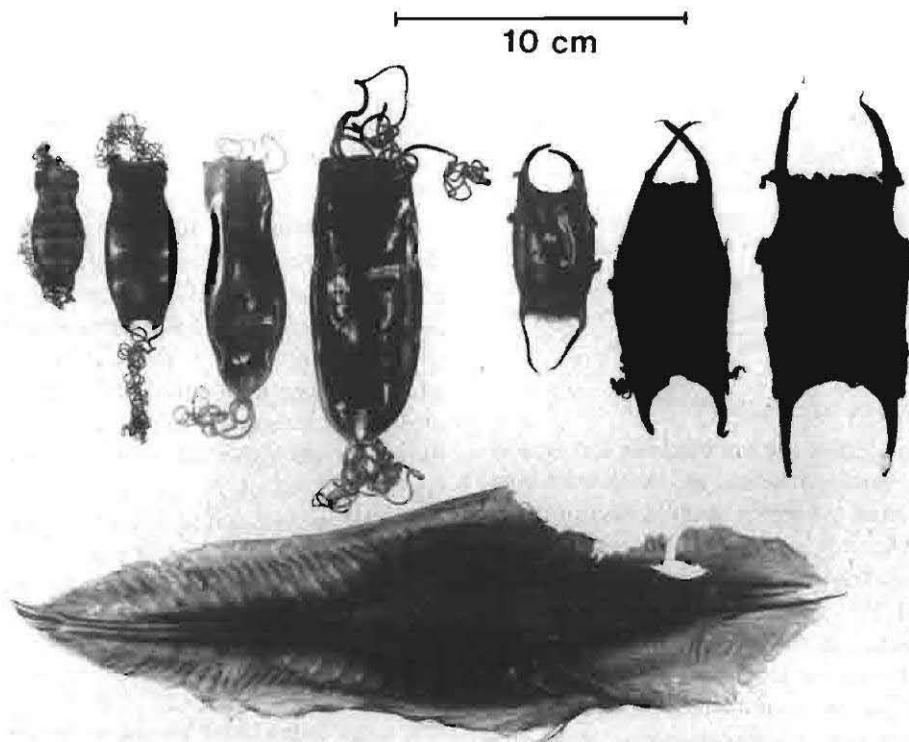


**Figure 1** Photograph showing some of the more common egg-cases encountered during this study. Top row, left to right, are: *Haploblepharus edwardsii, H. pictus (H. fuscus* look identical), *Poroderma pantherinum, P. africanum, Raja miraletus, Raja* sp.2 and *Raja* sp. 1; below is the egg-case of *Callorhinchus capensis.*

proportionally smaller at 70 × 30 mm. They range from light brown to greenish-brown in colour and have thinner tendrils and walls.

The closely related shysharks, *H. pictus* and *H. fuscus* (Branch *et al.* 1994), have identical purse-shaped egg-cases measuring 55 × 25 mm.Their colour varies from amber to dark brown and the walls and the tendrils are much thinner than those of the *Poroderma* species. The two egg-cases could only be distinguished on the basis of their distribution patterns — *H. pictus* being found from Luderitz to Cape Agulhas and *H. fuscus* from Cape Agulhas to southern Kwa-Zulu-Natal (Branch *et al.* 1994). *H. edwardsii* lays similar shaped eggs, but their dimensions are smaller (38 × 18 mm) and they can be recognised by their transverse, light coloured bands. Wall and tendril thickness are similar to those in *H. pictus.*

The elephantfish *C. capensis* deposits very unusual and unmistakable large, brown, spindle-shaped and 'hairy' egg-cases approximately 230 mm long. The egg-cases of *R. alba* are easily recognized by their extremely large size (over 100 mm length), robust appearance and 'lateral fins'. The surface is dark brown and bears longitudinal and transverse ridges, giving it a very characteristic net-like texture. *R. miraletus* lays small (42 × 27 mm), thin-walled, hairy, amber-coloured egg-cases which also possess 'lateral fins'. The two unidentified skate eggs are both hairy and possess 'lateral fins', but differ in colour and size. The egg-cases of the first species (termed *Raja* sp. 1) are dark brown, and average 52 × 37 mm, while those of the second skate species (*Raja* sp. 2) are golden brown and average 70 × 50 mm.

## Species composition by collection site

Species composition of samples collected in False Bay and Port Alfred differed considerably. The most abundant egg-cases washed up in False Bay were those of *H. pictus* and *H. edwardsii*, which made up 51.8% and 40% of the total, respectively (Figure 2). At Port Alfred the most abundant egg-cases were those of *H. edwardsii* (55.6% of the total), followed by *R. miraletus* (19.5%) and then *H. fuscus* (17.3%). In False Bay, *Haploblepharus* spp. thus had an overall abundance of 90%, followed by skates (7%) and *Poroderma* spp. (3%). In Port Alfred the ranking was the same, but *Haploblepharus* spp. has a lower relative abundance of 73%, followed by skates (19%) and *Poroderma* spp. at 8%.

## Hatching success versus egg mortality

Figure 3 illustrates comparative rates of hatching success and egg mortality for those species of sharks and skates from both False Bay and Port Alfred for which samples of at least 10 egg-cases were available.

The egg-cases of most *Haploblepharus* spp. displayed high hatching success of 60–75% and moderate depredation rates of 18–30%, but *H. fuscus* was the exception with a hatching success of only 37% and a depredation rate of 40%. Only one *Poroderma* species, *P. pantherinum* yielded sufficient material to estimate mortality rates. In this species egg-cases suffered from high depredation rates of 43% and a low hatching success of 47%. Proportions of egg-cases showing unknown egg mortality were below 20% in both *Haploblepharus* and *Poroderma* spp. By contrast, skate egg-cases displayed high
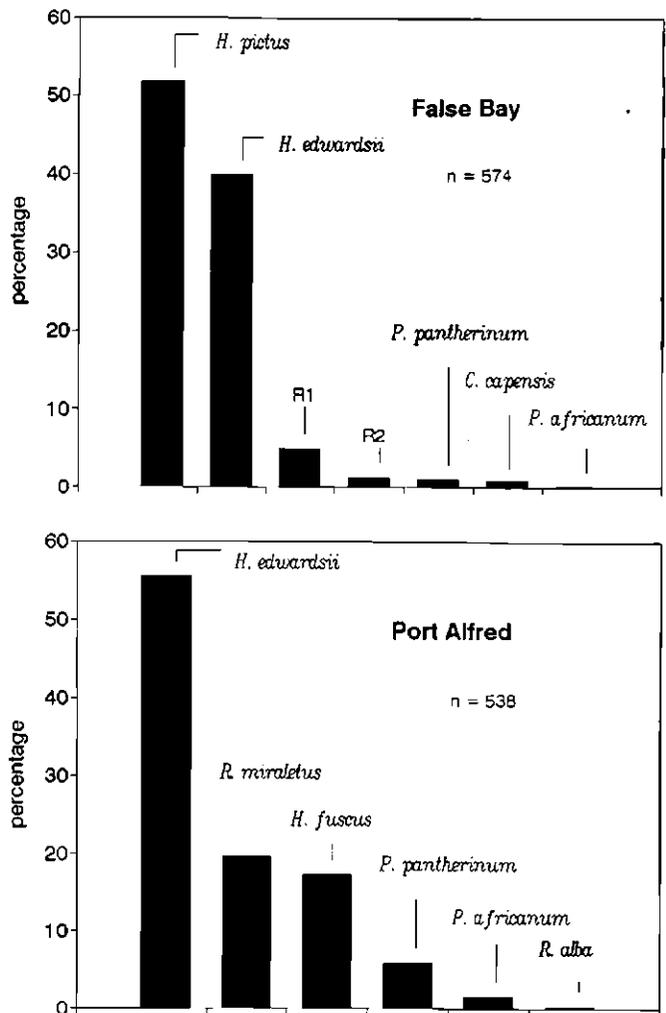


**Figure 2** Bar charts showing the species breakdown of egg-cases collected in False Bay, as compared to Port Alfred.

unknown egg mortalities of up to 35%, but depredation rates below 14%. Hatching success of skate eggs was moderate at 57%. Very few egg-cases of any type were washed ashore intact.

There were marked differences in hatching success for the same (*H. edwardsii*), or ecologically equivalent (*H. pictus* and *H. fuscus*), species in False Bay as compared to Port Alfred. *H. pictus* from False Bay had a high hatching success of 61.7% compared to *H. fuscus*, from Port Alfred, which had a hatching success of only 37.6%. This difference was attributed to lower depredation rates (20.8%) of *H. pictus* eggs in False Bay and higher depredation rates (40.0%) of *H. fuscus* eggs at Port Alfred. *H. edwardsii*, which occurs at both sites, displayed lower hatching success in False Bay (60.9%) than Port Alfred (74.6%). Lower hatching success in False Bay can be attributed to high depredation of 30.0%, compared to only 18.1% at Port Alfred.
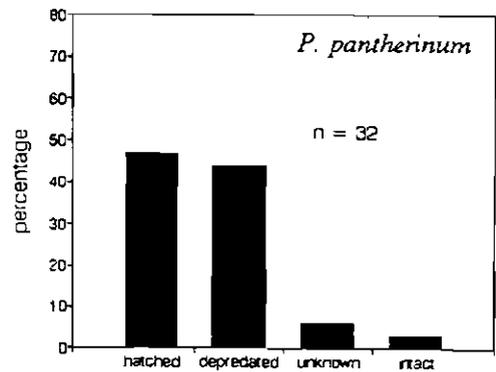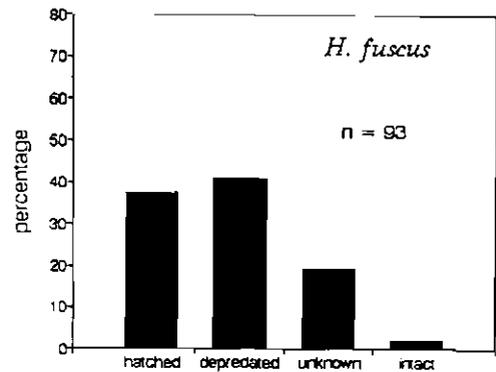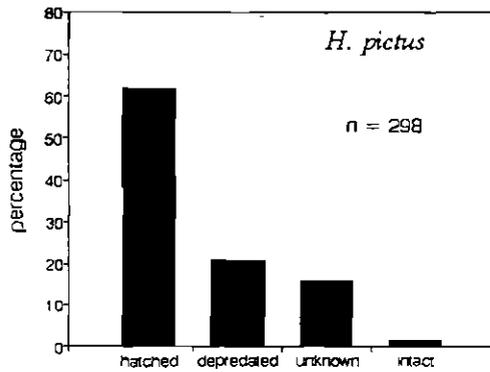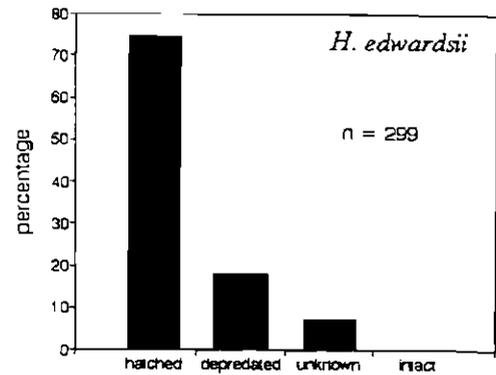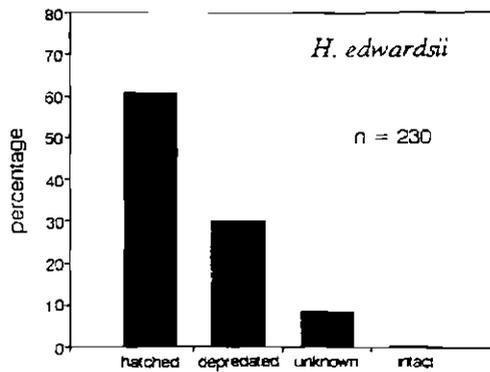
## Borehole analysis

The holes found in the egg-cases varied considerably in size and shape and could be classified into five types. Type 1 and 2 were parabolic-shaped boreholes with Type 1 being rounded and Type 2 arrow-shaped. These holes varied from 2–5 mm in length. Type 3 were circular boreholes, and

# False Bay

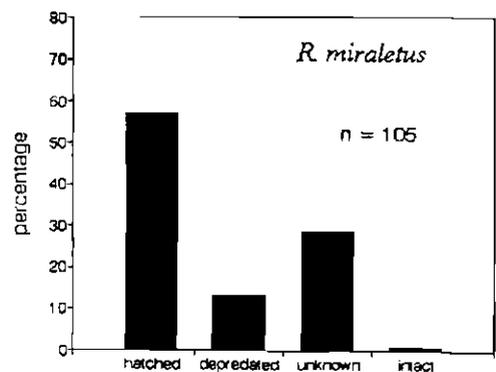# Port Alfred
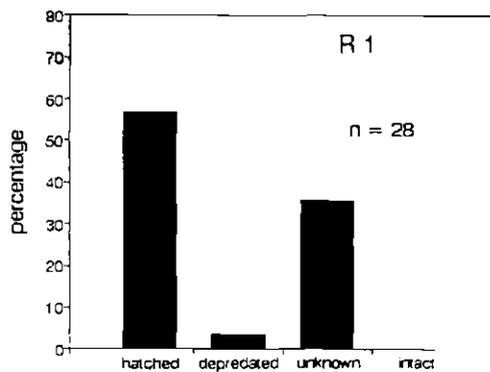
## Sharks



## Skates



**Figure 3** Fates of egg-cases belonging to each of the species in False Bay and Port Alfred. Only those species for which a sample of at least 10 egg-cases were collected are shown.
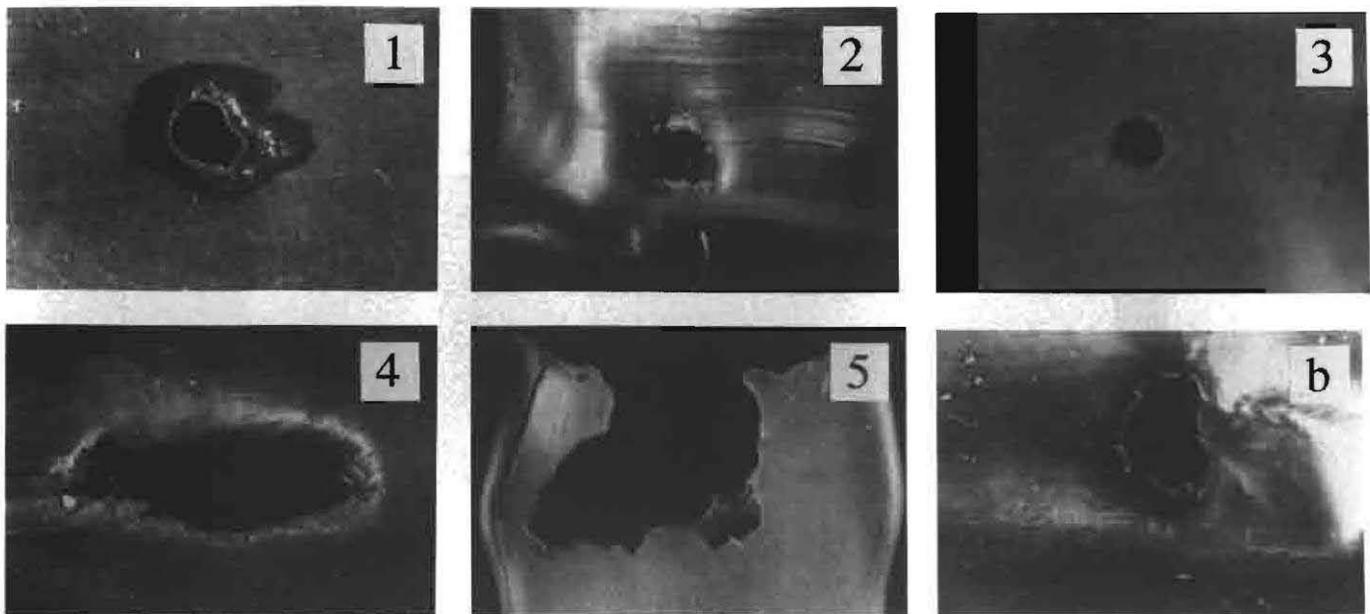
**Figure 4** The five categories of hole-type recognised in this study (see text for details), together with the borehole made by the predator whelk *Burnupena papyracea* under experimental conditions (b).

ranged from 1–2.5 mm in diameter. Type 4 were elongated holes which reached 40 mm in length. All holes which did not fit into any of the above categories were considered as another fifth type, which were generally irregular in shape. The most abundantly occurring hole type was Type 1, followed by Type 5 and Type 3. Of the egg-cases with distinct boreholes (Types 1–3) approximately 83.3% had single boreholes, 12.5% had two and 4.2% had three or more boreholes. Regressional analysis revealed that there was no correlation between borehole width and egg case length ($r = 0.017$, $p > 0.05$).

### Predation experiments

Of the whelks used in the feeding experiments only *B. papyracea* and *B. lagenaria* attacked *Haploblepharus* egg-cases, consuming three eggs in total during the eight week experiment. Both species created Type 1 boreholes (Figure 4).

## Discussion

### Species composition at beaches

There was strong variation of species composition between egg-cases found in False Bay and at Port Alfred (Figure 2). This is presumably the result of changes in temperature regime and hence of the species composition of the elasmobranch fauna (Bertolini 1993). It appears that *H. pictus*, *C. capensis*, and *Raja* sp. 1 and 2 prefer the cool temperate waters of the Western Cape, whereas *H. fuscus*, *H. edwardsii*, *Poroderma* species and *R. miraletus* prefer the warmer waters of the Eastern Cape.

The species composition of washed-up egg-cases at each site may also be influenced by the depth, or distance offshore, at which oviposition takes place in the various species. Haploblepharus spp. and *R. miraletus* are commonly found in shallow water (van der Elst 1993), where their egg-cases are thus most likely also deposited. As a result, these eggs might be more frequently washed ashore than those of deeper water

species, like *C. capensis* and most of the other skates (van der Elst 1993). Dredge samples from False Bay have recovered *C. capensis* eggs at depths exceeding 36 m (J.G. Field, UCT, pers. comm.). The few *Poroderma* egg-cases which washed ashore may indicate that these species are less common than the smaller *Haploblepharus* spp., or alternatively that *Poroderma* egg-cases are more firmly attached to the substratum and hence less frequently become detached and cast ashore.

### Hatching success versus egg mortality

Among the oviparous sharks and skates found in False Bay and at Port Alfred, *Haploblepharus* spp. appear to have the highest hatching success rate — a factor which may contribute to their abundance in the coastal waters of the region. One possible reason for this may be that the smaller egg-cases of *Haploblepharus* have a shorter gestation period (approximately 104 d) relative to those of the larger *Poroderma* spp., which have a gestation period of *ca* 164 d (von Bonde 1945a,b). *Pododerma* egg-cases are thus at risk to egg-case predators for approximately 50% longer (depending on species and incubation temperature at the time).

Skate eggs are deposited free on sand or gravel, whereas scyliorhinid shark eggs have tendrils to secure them to algae and rock. Skate eggs are therefore more likely to be cast ashore — an event considered here to be 'unknown egg mortality'. Hence, skates displayed higher unknown egg mortality in comparison to sharks. On the other hand, skate eggs displayed lower depredation rates than shark eggs. This can probably be attributed to the relative scarcity of predatory gastropods, such as *Burnupena* spp., on sandy bottoms as compared to rocky reefs.

### Borehole analysis and predation experiments

Of the four types of holes made in egg-cases (Figure 4), Types 1, 2 and 3 were clearly indicative of whelk activity. The origin of Type 4 and 5 holes is not known, but the proba-

ble cause would appear to be other as yet unidentified predators, such as octopus, fish, crabs or rock-lobsters. The predators responsible for Type 1 holes, the most abundant type, were found to be *B. papyracea* and *B. lagenaria.* Type 2 holes were small and probably made by juveniles of the above species, or other related gastropods.

There was no significant correlation between egg-case length and borehole width ($p > 0.05$). Hence, egg-case length does not influence the size of whelk which may prey on it. Wall thickness may, on the other hand, display a more significant correlation with borehole width. The latter remains to be tested.

In conclusion, predation on egg-cases by boring gastropods does appear to cause considerable mortality amongst oviparous sharks along the South African coastline. The rates reported here are, however, considerably lower than those found by earlier authors. This could be the result of geographical variations in predation pressure, characteristics of the egg-cases or egg-laying behaviour of the species studied, or simply a more accurate evaluation based on a sample ten times larger than those of earlier workers. Predation rates amongst skate egg-cases are lower than those of sharks, but amongst skates the risks of detached egg-cases being cast ashore appear to be greater. Both factors could be seen as selective pressures favouring a shift from oviparous to viviparous reproduction. However, some oviparous sharks, for example *Halaelurus lineatus,* show increased egg production and decreased incubation time (van der Elst 1993) and this may be seen as an alternative evolutionary response to predatory or other sources of mortality at the egg-case stage.

## Acknowledgements

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