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Egg capsules of the dusky catshark *Bythaelurus canescens* (Carcharhiniformes, Scyliorhinidae) from the south-eastern Pacific Ocean

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The external morphology of the egg capsule of *Bythaelurus canescens* and its fixation to the substratum are described. *Bythaelurus canescens* egg capsules are typically vase-shaped, dorso-ventrally flattened, pale yellow in colour when fresh and covered by 12–15 longitudinal ridges. The anterior border of the capsule is straight, whereas the posterior border is semicircular. Two horns bearing long, coiled tendrils arise from the anterior and posterior ends of the capsule. The presence of longitudinal ridges and long coiled tendrils at both anterior and posterior ends of the capsule readily distinguish these egg capsules from those of other chondrichthyans occurring in the south-east Pacific Ocean.

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Key words: egg capsule morphology; nidamental gland; reproductive biology; single oviparity; synchronic activity.

INTRODUCTION

Bythaelurus Compagno, formerly considered a subgenus of Halaelurus Gill (White et al., 2007; Last & Stevens, 2008), comprises eight species: Bythaelurus alcocki (Garman), Bythaelurus canescens (Günther), Bythaelurus clevai (Séret), Bythaelurus dawsoni (Springer), Bythaelurus hispidus (Alcock), Bythaelurus immaculatus (Chu & Meng), Bythaelurus incanus Last & Stevens and Bythaelurus lutarius (Springer & D'Aubrey). These small demersal species occur on the outer shelf and upper slope mainly between 250 and 1260 m depth throughout the Indo-Pacific (Compagno et al., 2005; Francis, 2006; Last & Stevens, 2008). The dusky catshark

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B. canescens is endemic to the south-east Pacific Ocean. It ranges from southern Peru to the Straits of Magellan (Compagno *et al.*, 2005) and is a common by-catch in demersal trawl and longline fisheries in central and southern Chile (Acuña & Villarroel, 2002; Lamilla *et al.*, 2005, 2008; Valenzuela *et al.*, 2008).

Oviparous chondrichthyans such as *B. canescens* and the overwhelming majority of the Scyliorhinidae (Compagno, 1990; Ebert *et al.*, 2006) deposit structurally complex egg capsules on the sea floor or attach them to epibiota; these then develop without further parental care (Ishiyama, 1958; Hamlett & Koob, 1999; Carrier *et al.*, 2004). Chondrichthyan egg capsules exhibit a range of genus- and species-specific morphological traits (*e.g.* presence or absence of tendrils, adhesion fibres and ridges, as well as general shape and size). Where known these are often useful taxonomic characters and egg capsule morphology has been included in several phylogenetic analyses of skates and oviparous sharks (Ishiyama, 1958; Hubbs & Ishiyama, 1968; Gomes & de Carvalho, 1995; Flammang *et al.*, 2007).

Scyliorhinid egg capsules are generally vase-shaped (Gomes & de Carvalho, 1995; Konstantinou $et\ al.$, 2000; Bor $et\ al.$, 2003; Hernández $et\ al.$, 2005; Ebert $et\ al.$, 2006; Flammang $et\ al.$, 2007, 2008). Distinguishing between the egg capsules of scyliorhinids requires detailed knowledge of their morphology. Springer (1979) provided a brief description of the egg capsules of $B.\ canescens$, including a photograph of an egg capsule collected from the oviduct of a 660 mm total length (L_T) female. Here, detailed data for 22 egg capsules collected from the Chilean continental slope, the first observation of female size at maturity and confirmation of the reproductive mode and spawning habitat of $B.\ canescens$, are provided

MATERIALS AND METHODS

Eighteen capsules were collected from nine gravid females and four were attached to two deep-sea corals (*Antipathes speciosa*). All females and corals were caught off southern Chile as by-catch of bottom longline fisheries targeting yellownose skate *Zearaja chilensis* Guichenot and Patagonian toothfish *Dissostichus eleginoides* Smitt. Capture data are presented in Table I. Egg capsules attached to corals and those from gravid females were deposited in the cnidarian (CNI) and marine fishes (PM) collections of the museum of Instituto de Zoología, Universidad Austral de Chile, Valdivia, respectively. Egg capsules were preserved in 80% ethanol.

Morphometric measurements of egg capsules follow Ebert *et al.* (2006). All measurements were taken point to point to the nearest 0·01 mm using digital callipers. These were anterior border width (ABW), anterior capsule width (ACW), waist width (WCW), posterior capsule width (PCW), posterior border width (PBW), anterior respiratory fissure length (AFL), egg capsule height (CHI), posterior respiratory fissure length (PFL) and egg capsule length (ECL) (Fig. 1). Respiratory fissures were only measured in capsules attached to corals as they were undeveloped in capsules collected *in utero*. Faces and sides of the egg capsules were determined according to their orientation *in utero* (Gomes & de Carvalho, 1995) (Fig. 2).

RESULTS

Gravid females ranged from 542 to 625 mm $L_{\rm T}$ and contained a single egg capsule in each uterus, both being at the same stage of development. Egg capsules collected *in utero* were pale yellow-brownish in colour when fresh, becoming darker after fixation (Figs 2 and 3). Each capsule contained a single egg. Capsules were

TABLE I. Collection data of the egg capsules of *Bythaelurus canescens* examined during this study

Collection code	Number of capsules	Capsule origin	Location	Coordinates	Date	Depth (m)
IZUA-PM 3981-89	8	Females uteri	Moraleda Channel	44° 18′ 30″ S; 73° 17′ 55″ W	04/11/2006	340
IZUA-PM- 4327-28	4	Females uteri	Valdivia	40° 11′ 57.6″ S; 74° 01′ 9.72″ W	27/05/2009	320
IZUA-PM- 4545, 4408-09	6	Females uteri	Valdivia	39° 56′ 0.6″ S; 73° 44′ 39.48″ W	01/06/2009	330
IZUA-CNI-003	2	Attached to Antipathes speciosa	Valdivia	40° 10′ 34·32″ S; 74° 09′ 57″ W	27/10/2000	600
IZUA-CNI-200	2	Attached to Antipathes speciosa	Valdivia	40° 10′ 52·38″ S; 73° 58′ 45·3″ W	05/06/2009	330

IZUA, Instituto de Zoología, Universidad Austral de Chile.

stout and vase-shaped, fusiform and dorso-ventrally flattened with an anterior-lateral constriction. The capsule is mildly translucent under transmitted and reflected light. Dorsal and ventral faces were convex and covered by 12–15 conspicuous longitudinal ridges of c. 1.5 mm height, with different thickness, giving the capsule a roughened appearance [Fig. 2(a), (c)]. Dorsal and ventral walls of the capsule are of the same thickness. No differences were observed between the ridges on each face of the capsule [Fig. 2(c)]. Anterior and posterior borders of the capsule were broadly concave. Lateral margins were thick, though the capsules lacked lateral keels [Fig. 2(c)]. Anterior and posterior aprons were absent. A thick flattened horn extended from each corner of the capsule. These were flexible when the capsules were found *in utero*. The anterior horns were more or less parallel, whereas the posterior horns were strongly curved inwards and crossed each other [Fig. 2(a)]. Each horn was produced into a long, coiled tendril up to 2.5 times the length of the capsule.

Egg capsules collected with deep-sea corals were strongly attached by their entangled anterior and posterior tendrils (Fig. 3). Respiratory fissures were located on each corner of egg capsules containing embryos at advanced developmental stages. Anterior and posterior respiratory fissures were dorsally situated on the left side of the egg capsule and ventrally situated on the right side. Summary statistics and range of measurements performed are given in Table II.

DISCUSSION

Compagno *et al.* (2005) reported mature female *B. canescens* between 590 and 660 mm $L_{\rm T}$. On the other hand, the present observation indicates females may be mature at 542 mm $L_{\rm T}$, which confirms Springer (1979) observations about the high variability of this species. Further research involving larger sample sizes from a

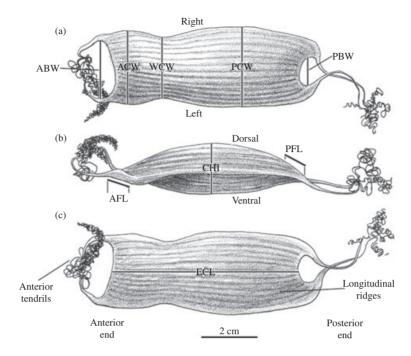


Fig. 1. Egg capsule terminology (ABW, anterior border width; ACW, anterior capsule width; WCW, waist width; PCW, posterior capsule width; AFL, anterior respiratory fissure length; CHI, egg capsule height; PFL, posterior respiratory fissure length; ECL, egg capsule length) and measurements: (a) dorsal, (b) left lateral and (c) ventral.

variety of locations is therefore required to determine size at 50% maturity and if this varies throughout the species range.

Springer (1979) reported that the single gravid female he examined contained a single egg capsule in each oviduct. Francis (2006) subsequently listed the reproductive mode of B. canscens as single oviparity but noted this required confirmation. The present observation confirms single oviparity in this species. The presence of egg capsules at the same developmental stage in each oviduct indicates synchronous nidamental gland synthetic activity. This also occurs in other schyliorhinids such as Scyliorhinus canicula (L.) (Feng & Knight, 1994) and Schroederichthys chilensis (Guichenot) (F. Concha, pers. obs.). Important morphological differences between the egg capsules of B. canescens and those of other scyliorhinids are more conspicuous corners and thicker walls than Apristurus spp. (Flammang et al., 2007) or S. chilensis (Hernández et al., 2005); the absence of adhesion fibres as found on the capsules of species such as Apristurus melanoasper Iglésias, Nakaya & Stehmann (Nakaya et al., 2008), Apristurus riveri Bigelow & Schroeder (Flammang et al., 2007), Parascyllium variolatum (Duméril) (Caruso & Bor, 2007) and S. chilensis (Hernández et al., 2005); the presence of conspicuous longitudinal ridges on the outer surface of the capsule. Iglésias et al. (2002) showed an uncatalogued egg capsule exhibiting longitudinal ridges and Ebert et al. (2006) describe similar structures on egg capsules possibly belonging to Apristurus saldanha (Barnard) from South Africa, otherwise they appear to be uncommon within the Scyliorhinidae, and rare in other oviparous chondrichthyans inhabiting the south-east Pacific.

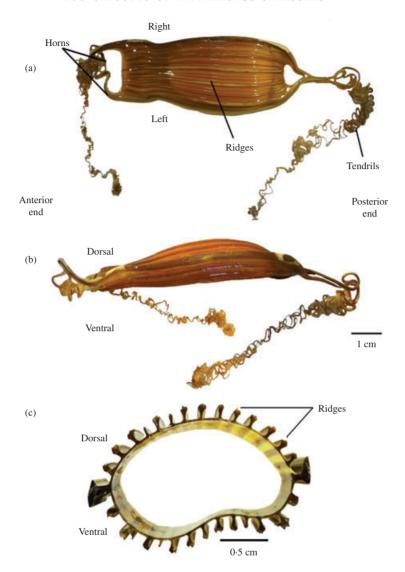


Fig. 2. Egg capsule of *Bythaelurus canescens* (IZUA-PM-4327): (a) dorsal view, (b) left lateral view and (c) cross-section.

Oviparity is a primitive reproductive strategy within elasmobranchs (Compagno, 1990; Dulvy & Reynolds, 1997), and the presence of long coiled tendrils on the egg capsules with single oviparity are considered basal traits among scyliorhinids (Iglesias *et al.*, 2002; Ebert *et al.*, 2006; Francis, 2006; Flammang *et al.*, 2007). Tendrils occur on the egg capsules of many scyliorhinids including some *Apristurus* spp., *Cephaloscyllium* spp., *Schroederichthyes* spp. and *Scyliorhinus* spp. (Graham, 1956; Compagno, 1984; Feng & Knight, 1994; Gomes & de Carvalho, 1995; Ebert, 2003; Hernández *et al.*, 2005; Ebert *et al.*, 2006; Last & White, 2008; Last *et al.*, 2008; Nakaya *et al.*, 2008). These tendrils are adherent and are used to attach the egg capsules to macroalgae, sessile epifauna such as hard corals and sea fans, and rocky

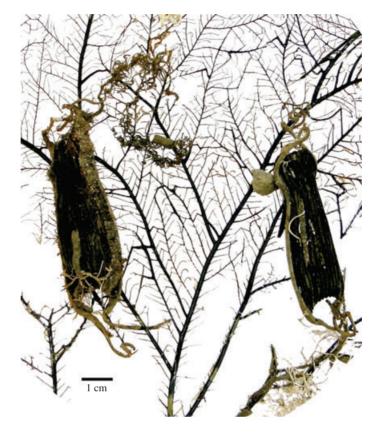


Fig. 3. Mode of attachment of egg capsules of Bythaelurus canescens to a deep-sea coral (Antipathes speciosa).

substrata (Wourms, 1977; Compagno, 1984; Ebert, 2003; Ebert *et al.*, 2006). The present observation of *B. canescens* egg capsules attached to *A. speciosa* confirms this species breeds at >300 m depth.

In situ observations of catshark egg capsules have been rarely documented. Lorenzen et al. (1979) pointed out that long tendrils in S. chilensis are tangled in coastal algae. Ellis & Shackley (1997) reported that S. canicula egg capsules can be found attached to different macroalgae, poriferans, bryozoans and hydroids. On the other hand, egg capsules of several Apristurus spp. and Scyliorhinus haeckeli (Miranda Ribeiro) are deposited on deep-sea corals (Compagno, 1984; Ebert, 2003; Ebert et al., 2006).

Although it has been suggested that structural differences between egg capsules may indicate differences in the habitats they are deposited (Ebert *et al.*, 2006) in species producing capsules with long tendrils deposit these in habitats as diverse as shallow coastal macroalgae (*e.g. S. chilensis* and *S. canicula*) and deep-sea corals, *e.g. Apristurus brunneus* (Gilbert), *B. canescens* and *Parmaturus xaniurus* (Gilbert) (Flammang, 2005; Flammang *et al.*, 2007, 2008). Dependence upon corals and other epifauna by egg laying deep-sea chondrichthyans is likely to increase their vulnerability to fishing activities, such as bottom trawling that damage these delicate habitats.

TABLE II. Mean values and ranges of measurements performed on the egg capsules of Bythaelurus canescens

Measurement (mm)	ECL	ABW	ACW	WCW	PCW	PBW	CHI	AFL	PFL
Mean ± s.b. Proportion FCI + s.p.	55.55 ± 1.10	$18.92 \pm 1.45 \\ 2.95 \pm 0.22$	$18.92 \pm 1.45 \ 20.70 \pm 0.94 \ 16.79 \pm 1.52 \ 23.27 \pm 1.03 \ 8.95 \pm 1.38 \ 14.83 \pm 0.71 \ 6.79 \pm 0.81 \ 5.97 \pm 0.74$ $2.95 \pm 0.22 \ 2.69 \pm 0.12 \ 3.33 \pm 0.25 \ 2.39 \pm 0.08 \ 6.34 \pm 0.95 \ 3.75 \pm 0.21 \ 8.27 \pm 0.89 \ 9.42 \pm 1.11$	16.79 ± 1.52 3.33 ± 0.25	16.79 ± 1.52 23.27 ± 1.03 8.95 ± 1.38 3.33 ± 0.25 2.39 ± 0.08 6.34 ± 0.95	8.95 ± 1.38 6.34 ± 0.95	$14.83 \pm 0.71 \\ 3.75 \pm 0.21$	$14.83 \pm 0.71 \ 6.79 \pm 0.81$ $3.75 \pm 0.21 \ 8.27 \pm 0.89$	5.97 ± 0.74 9.42 ± 1.11
Range	53.8-57.1	16.9–21.7	19.4–22.5 15.3–20.7		21.8–25.6 7.3–11	7.3–11	13.5–15.9 6.2–8.4	6.2-8.4	5.1-7.5

ABW, anterior border width; ACW, anterior capsule width; AFL, anterior respiratory fissure length; CHI, capsule height; ECL, egg capsule length; PBW, posterior border width; PCW, posterior capsule width; PFL, posterior respiratory fissure length; WCW, waist width. Authors wish to thank M. A. Alarcón for providing coral samples, coral identification and photographs of egg capsules attached to them; R. Johnson and V. Gudiño whose reviews helped improve this manuscript before submission and specially C. Duffy for his time, help and valuable advice. This contribution was supported by Fondo de Investigación Pesquera (FIP) N° 2008-60 and Programa de Conservación de Tiburones, Chile (Shark Conservation Program, Chile).

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