

Egg cases of the genus *Apristurus* (Chondrichthyes: Scyliorhinidae): Phylogenetic and ecological implications

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Abstract

The genus *Apristurus* has been divided formerly into three species subgroups based on morphological and molecular phylogenies. Previous studies have agreed on the separation into distinct species groups, the largest two of which have been described as the *brunneus* and *spongiceps* groups. An examination of the egg cases produced by these oviparous catsharks corroborates the distinction in species groups: egg cases of the *brunneus* group have long fibrous and curly tendrils at either end, whereas egg cases of the *spongiceps* group lack tendrils. The egg cases of *A. kampae*, *A. manis*, *A. spongiceps* and *Apristurus* sp. D are described for the first time, and the egg cases of *A. brunneus* and *A. riveri* are re-described to include comparable morphological characteristics. The ecological implications of egg case morphology on oviposition and ventilation are also discussed.

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Introduction

The genus *Apristurus* is the largest within the family Scyliorhinidae, with approximately 32 valid and at least 7 undescribed species, and has been divided into several subgroups based on meristic and morphological as well as molecular phylogenies (Compagno, 1988; Nakaya and Sato, 1999; Sato, 2000; Compagno et al., 2005; Iglésias et al., 2005). Of the recognized *Apristurus* species, the egg cases of only 12 have been described previously (Table 1). Eight of these are known to have long fibrous tendrils: *A. brunneus*, *A. exsanguis*, *A. laurussoni*, *A. longicephalus*, *A. macrorhynchus*,

A. melanoasper and *A. saldanha*. All of these species, except *A. longicephalus*, are described as being “*brunneus*-like” by Nakaya and Sato (1999), who distinguished this *brunneus* group based on high spiral valve count, long upper labial furrow length, and discontinuous supraorbital sensory canals. In addition, free-swimming individuals of these species are generally elongate and slender, have small teeth, and are often found shallower than 1000 m depth. In contrast, the *spongiceps* group of *Apristurus* consists of *A. aphyodes*, *A. fedorovi*, *A. kampae*, *A. manis*, *A. microps*, *A. pinguis*, *A. profundorum*, *A. riveri*, *A. spongiceps*, and *A. stenseni*, and is characterized by lower spiral valve counts, upper labial furrows that are equal or shorter than the lower labial furrows, and continuous supraorbital canals (Nakaya and Sato, 1999). These species also tend to be robust, heavy-bodied sharks, with large teeth, large rough dermal denticles and placoid scales, and are

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Table 1. Egg cases of the genus *Apristurus*. *Apristurus* grouping as per Nakaya and Sato (1999)

<i>Apristurus</i> group	Species	Depth (m)	Tendrils	Egg case description
<i>brunneus</i>	<i>A. brunneus</i>	300–800	Yes	DeLacy and Chapman (1935), Cox (1963), present study
	<i>A. exsanguis</i>	Unknown	Yes	Sato et al. (1999)
	<i>A. gibbosus</i>	Unknown	Unknown	Unknown
	<i>A. indicus</i>	1289	Unknown	Unknown
	<i>A. internatus</i>	Unknown	Unknown	Unknown
	<i>A. investigatoris</i>	1040	Unknown	Unknown
	<i>A. japonicus</i>	820–915	Unknown	Unknown
	<i>A. laurussoni</i>	100–1250	Yes	Nakaya and Sato (1998), Iglésias et al. (2002)
	<i>A. macrorhynchus</i>	220–1140	Yes	Nakaya (1975)
	<i>A. macrostomus</i>	Unknown	Unknown	Unknown
	<i>A. micropterygeus</i>	Unknown	Unknown	Unknown
	<i>A. melanoasper</i>	512–1520	Yes	Iglésias et al. (2004)
	<i>A. nasutus</i>	400	Unknown	Unknown
	<i>A. parvipimis</i>	1115	Unknown	Unknown
	<i>A. platyrhynchus</i>	Unknown	No	Nakaya (1975), Springer (1979), Nakaya and Sato (2000)
	<i>A. saldanha</i>	914	Yes	Ebert et al. (2006)
	<i>A. sibogae</i>	655	Unknown	Unknown
<i>A. sinensis</i>	Unknown	Unknown	Unknown	
<i>longicephalus</i>	<i>A. herklotsi</i>	520–910	Half	Ivanov (1987), Nakaya (1991), posterior end only
	<i>A. longicephalus</i>	600–1140	Half	Ivanov (1987), posterior end only
<i>spongiceps</i>	<i>A. albisoma</i>	935–1564	Unknown	Unknown
	<i>A. aphyodes</i>	> 1000	No	Iglésias et al. (2002)
	<i>A. fedorovi</i>	810–1430	Unknown	Unknown
	<i>A. kampae</i>	> 1000	No	Illustration in Ebert (2003); present study
	<i>A. manis</i>	> 1000	No	Present study
	<i>A. microps</i>	> 1000	No	Ebert et al. (2006)
	<i>A. pinguis</i>	Unknown	Unknown	Unknown
	<i>A. profundorum</i>	> 1000	Unknown	Unknown
	<i>A. riveri</i>	> 1000	No	Springer (1966, 1979), present study
	<i>A. spongiceps</i>	> 1000	No	Present study
	<i>A. stenseni</i>	Unknown	Unknown	Unknown
<i>Apisturus</i> sp. D	> 1000	No	Present study	

typically found below 1000 m depth. Other morphological characteristics, such as egg case structures, have species-specific morphologic variability that may be useful in determining phylogenetic and taxonomic relationships (Gomes and de Carvalho, 1995). Egg cases of only 12 species of *Apristurus* have been described previously. Herein, the egg cases of *A. kampae*, *A. manis*, *A. spongiceps* and *Apristurus* sp. D are described for the first time, and the egg cases of *A. brunneus* and *A. riveri* are re-described to include comparable morphological characteristics. The ecological implications of egg case morphology are also discussed.

Materials and methods

Egg case descriptions

Egg cases were fully formed in utero and removed directly from gravid females to ensure proper species

identification. All animals were handled ethically in accordance with Institutional Animal Care and Use Committee standards under San Jose State University (SJSU) protocols 801 and 838. Institutional abbreviations are as listed in Leviton et al. (1985). Uncatalogued field specimens are denoted by the species prefix (AB) for *Apristurus brunneus* or (AK) for *A. kampae* and a numeric code. The number of egg cases present, total length (TL) of gravid female, and depth, location, and date of capture are also noted.

Measurements of egg cases (Fig. 1) were made following Gomes and de Carvalho (1995) and Ebert et al. (2006). Terminology for egg case measurements is as follows: anterior border width (ABW) of the flat anterior-most edge of the egg case; maximum anterior case width (ACW), the widest part of the case between the anterior border and the waist; anterior fissure length (AFL), the respiratory fissure on the anterior right of the case, alongside the keel; egg case total length (ECL), the anteroposterior length of the entire egg case to which all

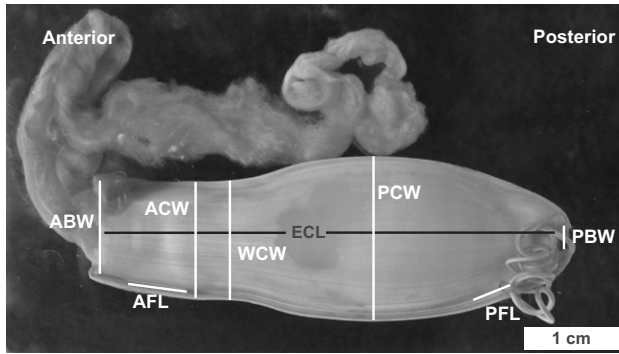


Fig. 1. Egg case of *Apristurus brunneus* (MLML uncatalogued AB113, 63.9 mm ECL) with egg case terminology and measurements as follows: anterior border width (ABW), maximum anterior case width (ACW), anterior fissure length (AFL), egg case total length (ECL) to which all other measurements are standardized, posterior border width (PBW), maximum posterior case width (PCW), posterior fissure length (PFL), and minimum waist width (WCW).

other measurements are standardized proportionally; posterior border width (PBW), the posterior-most edge of the case between the posterior horns; maximum posterior case width (PCW), the widest part of the case between the waist and the posterior border; posterior fissure length (PFL), the respiratory fissure on the posterior right of the case alongside the keel; and minimum waist width (WCW), the narrowest section of the case.

Morphometric analysis

Principal components analysis was performed using SYSTAT 10 software (SPSS Inc., 2000), to determine if the morphological variables measured separated the species into distinct groups. A cluster analysis of egg case morphometrics, standardized as a proportion of ECL, was performed also using SYSTAT 10 software, in order to quantify an estimate of how much the egg cases of each species differed. This was done to determine the Euclidean distance or root of square differences among egg cases, because continuous variables were available and other grouping methods would have biased the data set by arbitrary designation into discrete morphological variables by which to classify the egg cases.

Results

Egg case descriptions

Apristurus brunneus (Gilbert, 1892)

The egg case of *A. brunneus* was approximately 52–72 mm in length with long tendrils projecting from

either end (Fig. 1; $n = 20$). The tendrils on the anterior end were threadlike fibers, whereas the posterior tendrils were thicker and tightly coiled, tapering at the ends. The mean maximum ACW was $17.7 \pm 0.3\%$ (proportion of mean \pm standard error) of the egg case length (ECL), whereas the mean maximum PCW was $40.3 \pm 5.0\%$. The mean waist width (WCW) was $29.2 \pm 3.8\%$. Thus, the body of the case exhibited the characteristic vase-like shape of scyliorhinid egg cases. The mean AFL and mean PFL were $15.7 \pm 0.5\%$ and $11.2 \pm 1.8\%$, respectively. The mean ABW was $18.1 \pm 3.2\%$ and no anterior horns were present, as the lateral ridges of the keel (the lateral flange) did not continue distal to the anterior edge. The lateral ridges of the keel continued just slightly past the posterior edge and tapered sharply medially, in close proximity with one another, such that the mean PBW was only $4.6 \pm 1.7\%$. Approximately 6–8 small hair-like filaments, 2–4 mm in length, protruded from the posterior edge. The lateral keels were squarely shaped with rounded edges in cross-section and traversed the length of the egg case. The surface of the egg case appeared smooth. The case was a golden-yellow color when removed from the female. It maintained this color although becoming slightly more opaque through fixation in 10% formalin and preservation in 70% ethanol. Cases left in seawater turned a dark brown color after approximately 1 month.

Materials examined: MLML uncatalogued (AB013), 2 egg cases 67 and 69 mm ECL, female 556 mm TL, 640 m, $37^{\circ}07'09''N$, $122^{\circ}55'16''W$, 18 May 2002; MLML uncatalogued (AB046), 2 egg cases 61 and 62 mm ECL, female 567 mm TL, 777–823 m depth, $36^{\circ}53'26''N$, $122^{\circ}17'53''W$, 14 June 2002; MLML uncatalogued (AB075), 1 egg case 63 mm ECL, female 558 mm TL, 543–585 m, $36^{\circ}52'18''N$, $122^{\circ}14'57''W$, 15 June 2002; MLML uncatalogued (AB229), 1 egg case 62.5 mm ECL, female 599 mm TL, 170–186 m, $36^{\circ}54'41''N$, $122^{\circ}16'29''W$, 16 June 2002; MLML uncatalogued (AB230), 1 egg case 58.5 mm ECL, female 581 mm TL, 170–186 m, $36^{\circ}54'41''N$, $122^{\circ}16'29''W$, 16 June 2002; MLML uncatalogued (AB084), 2 egg cases 69 and 72 mm ECL, female 634 mm TL, 402–466 m, $36^{\circ}52'13''N$, $122^{\circ}12'52''W$, 9 August 2002; MLML uncatalogued (AB101), 2 egg cases 59 and 60 mm ECL, female 589 mm TL, 411 m, $36^{\circ}54'17''N$, $122^{\circ}18'35''W$, 14 October 2002; MLML uncatalogued (AB113), 2 egg cases 63.9 and 65.0 mm ECL, female 557 mm TL, 457 m, $36^{\circ}54'22''N$, $122^{\circ}18'02''W$, 30 November 2002; MLML uncatalogued (AB114), 2 egg cases 61 and 63 mm ECL, female 605 mm TL, 302–366 m, $36^{\circ}47'31''N$, $121^{\circ}52'26''W$, 10 December 2002; MLML uncatalogued (AB154), 2 egg cases 61 and 62 mm ECL, female 571 mm TL, 428–503 m, $36^{\circ}54'26''N$, $122^{\circ}17'37''W$, 03 March 2003; MLML uncatalogued (AB165), 1 egg case 56.2 mm ECL, female 570 mm TL, 373–406 m, $36^{\circ}54'47''N$, $122^{\circ}21'49''W$, 10

March 2003; MLML uncatalogued (AB166), 2 egg cases 63 and 65 mm ECL, female 598 mm TL, 373–406 m, 36°54'47"N, 122°21'49"W, 10 March 2003.

Apristurus kampae Taylor, 1972

The egg case of *A. kampae* was approximately 61–69 mm in length and did not have tendrils on either the anterior or posterior ends (Fig. 2; $n = 17$). The mean ACW and PCW were $29.4 \pm 1.7\%$ and $36.3 \pm 1.5\%$ of ECL, respectively. It had a rounded vase-like shape, the mean WCW narrowing to $28.3 \pm 1.8\%$ at about 25% of the length from the anterior end. The mean AFL was $16.8 \pm 0.019\%$ of ECL, whereas the mean PFL was $11.2 \pm 0.6\%$. The mean ABW was $21.1 \pm 2.4\%$ and there was a very thin filamentous sheet along the anterior border, extending not more than 2–3 mm, which was often found torn. No anterior horns were present, as the lateral ridges of the keel did not continue distal to the anterior edge. The lateral ridges of the keel continued just slightly past the posterior edge and tapered sharply medially as posterior horns, in close proximity with one another. Between these horns, the mean PBW was $11.2 \pm 0.6\%$. There were no fibrous tendrils on the anterior or posterior ends of the egg case. Approximately 8–10 small hair-like filaments, each 2–3 mm in length, protruded from the posterior edge and filled in the area between the posterior keel ends. A similar thin filament of 4–6 mm in length also protruded off each of the posterior keel ends. The lateral keels were gently sloped in cross-section and ran the length of the egg case. The surface was smooth and lustrous in appearance. The egg case was honey-yellow *in utero* and turned light olive-brown after fixation in 10% formalin and preservation in 70% ethanol.

Materials examined: CAS 58482, 1986-vi:4, 2 egg cases 65.4 and 64.2 mm ECL, female 543 mm TL, 1381–1408 m, 36°15'18"N, 122°22'54"W, 8 December 1985; CAS 58771, 1986-vii:28, 2 egg cases 62.8 and 60.9 mm ECL, female 559 mm TL, 1008–1171 m, 35°44'36"N, 122°03'48"W, 7 December 1985; UW045629, 2 egg cases 67 and 68 mm ECL, female 590 mm TL, 1042 m, 37°15'1.5"N, 123°08'25.89"W, 31

October 1997; UW045634, 2 egg cases 60 and 62 mm ECL, female 528 mm TL, 1253 m, 37°13'22.3"N, 123°10'30.3"W, 24 September 1997; UW045634, 2 egg cases 59 and 60 mm ECL, female 550 mm TL, 1253 m, 37°13'22.3"N, 123°10'30.3"W, 24 September 1997; UW046041, 2 egg cases 63 and 64 mm ECL, female 539 mm TL, 1132 m, 34°31'31.4"N, 121°14'54.9"W, 7 November 2001; MLML uncatalogued (AK015) 2 egg cases 66.8 and 68.8 mm ECL, female 555 mm TL, 1005–1010 m, 34°41'52"N, 121°29'59"W, 26 July 2002; MLML uncatalogued (AK016) 1 egg case 69.0 mm ECL, female 589 mm TL, 1110–1155 m, 36°14'53"N, 122°17'13"W, 15 September 2002; MLML uncatalogued (AK018) 2 egg cases 61.7 and 61.5 mm ECL, female 548 mm TL, 1044–1054 m, 37°15'13"N, 123°07'32"W, 14 September 2002.

Apristurus manis Springer, 1979

The egg cases of *A. manis* all lacked both anterior and posterior tendrils (Fig. 3; $n = 7$). They had a nearly columnar shape, ranging from 63 to 71 mm in length with mean ACW $32.4 \pm 2.0\%$ of ECL and mean PCW $36.7 \pm 3.1\%$, and a slight constriction (mean WCW $30.5 \pm 2.0\%$) about a third of the length from the anterior end. Short anterior horns were present (approximately 2 mm long), and there was no filamentous sheet along the anterior edge of the egg case. The mean AFL and PFL were $14.8 \pm 2.0\%$ and $11.2 \pm 1.1\%$, respectively. The mean ABW was $22.1 \pm 1.8\%$. The anterior edge was straight, but the anterior portion of the case before the waist was rotated approximately 30 degrees off center. The lateral ridges of the keel continued just slightly past the posterior edge and tapered sharply medially, in close proximity with one another. The mean PBW was $3.0 \pm 1.9\%$. Approximately 8–10 small hair-like filaments, 2–4 mm in length, protruded from the posterior edge and filled in the area between the posterior keel ends. The surface was smooth and lustrous in appearance; minute longitudinal ridges were visible running the length of the egg case but did not become enhanced if the egg case dried. The egg case was an olive to honey-brown color after fixation in 10% formalin and preservation in 70% ethanol.

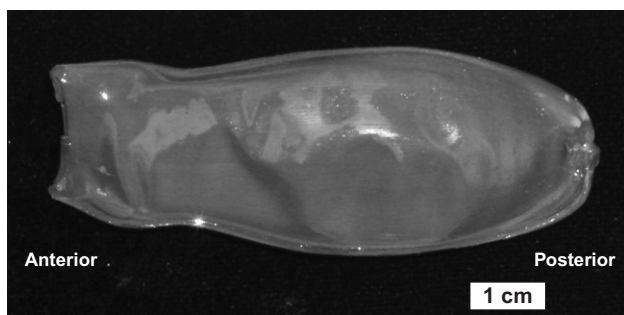


Fig. 2. Egg case of *Apristurus kampae* (MLML uncatalogued (AK018), 61.5 mm ECL).

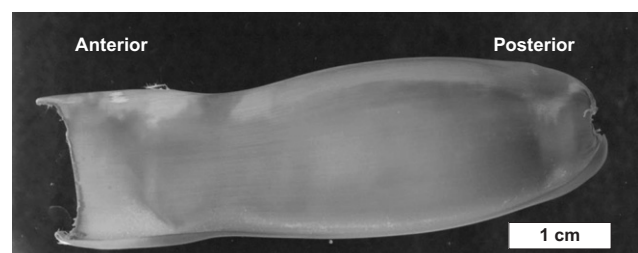


Fig. 3. Egg case of *Apristurus manis* (MCZ 158704, 71.0 mm ECL).

Materials examined: MCZ 158704, 1 egg case 71.0 mm ECL, 2140–2453 m, 39°57'4"N, 67°30'29"W, 03 December 2000; MCZ 158717, 1 egg case 67.0 mm ECL, 1128–1804 m, 39°55'7"N, 67°25'45"W, 06 December 2000; MCZ 158777, 3 egg cases (1 loose) 70.0, 69.0, and 63.0 mm ECL, 1120–1290 m, 39°55'27"N, 67°25'32"W, 04 December 2000; MCZ 164087, 2 egg cases 67.4 and 66.2 mm ECL, 1000–1186 m, 39°54'N, 67°27'W, 28 July 2002.

Apristurus riveri Bigelow and Schroeder, 1944

The *A. riveri* egg cases were 58 and 62 mm TL (Fig. 4; $n = 2$) and did not have tendrils. A small piece of egg case-like material was found with the specimen (pictured near the posterior end of the case in Fig. 4), but does not appear to be part of a tendril. A brief description by Springer (1966) also states that this species does not have “single tendrils at either corner”. The case shape was long and slender and the mean ACW and WCW were approximately equal at $16.3 \pm 0.4\%$ and $16.1 \pm 0.7\%$ of ECL, respectively. The mean PCW was $23.9 \pm 1.0\%$. The mean AFL was $9.1 \pm 2.6\%$, and twice the length of the mean PFL ($4.8 \pm 0.1\%$). The anterior edge of the egg case body was thin and extended farther medially than the lateral keels, giving an outwardly rounded appearance. The mean ABW was $9.4 \pm 0.3\%$. The posterior end of the egg case tapered sharply medially and the body of the egg case protruded farther than the lateral keels, with several filaments 2–3 mm in length attached to the end of the case. The mean PBW was $1.4 \pm 0.4\%$. The egg case was described as “green, striated” by Springer (1979), but appears light brown and smooth after preservation in ethanol.

Materials examined: USNM 201760, 2 cases 61.6 and 58.1 mm TL, 09°20'N, 81°24'W, 860–915 m, 25 May 1962.

Apristurus spongeiceps (Gilbert, 1905)

The holotype of *A. spongeiceps*, 495 mm TL, is the only known female example of this species and was found to have 2 completely formed egg cases, one in each uterus (Fig. 5). The egg cases lack both anterior and posterior tendrils but some fibrous material is attached long-



Fig. 4. Egg case of *Apristurus riveri* (USNM 201760, 58.1 mm TL).

itudinally along the exterior of the case. Egg cases from this specimen were 66 and 68 mm in length and the mean ACW and PCW were $29.9 \pm 1.4\%$ and $37.4 \pm 1.3\%$ of ECL, respectively. The mean WCW was $29.4 \pm 0.3\%$, thus the shape of the cases is not as vase-like as that of many other species. The mean AFL ($10.9 \pm 1.2\%$) was twice as long as the mean PFL ($5.3 \pm 0.2\%$). The lateral ridges of the keel do not continue distal to the anterior edge; therefore no anterior horns are present. The ABW was $23.4 \pm 0.6\%$. The posterior horns are approximately 4 mm in length and are contiguous with the lateral ridges of the keel, which continue just slightly past the posterior edge of the egg case and taper medially and anteriorly. The PBW was $6.4 \pm 0.1\%$. The egg case is olive-green in color after fixation in 10% formalin and preservation in 70% ethanol.

Materials examined: USNM 51590, 2 egg cases 64.2 and 62.0 mm TL, female 514 mm TL, 572–1462 m, Albatross station 4151 (no coordinates available), off Bird Island near Laysan Atoll in the NW Hawaiian Islands, 05 August 1902.

Apristurus sp. D Last and Stevens, 1994

Egg cases of *Apristurus* sp. D were 68 and 70 mm TL (Fig. 6; $n = 2$) and lacked tendrils. The mean ACW and WCW were approximately equal, measuring $31.6 \pm 2.8\%$ and $31.8 \pm 1.8\%$ of ECL, respectively. The mean PCW was $39.1 \pm 0.8\%$, giving the egg case a vase-like shape. The mean AFL was $12.1 \pm 0.9\%$, whereas the mean PFL was $7.8 \pm 2.1\%$. At the anterior end of the case, the keels did not project past the anterior border. The mean ABW was $22.4 \pm 2.3\%$. The lateral ridges of the keel tapered sharply medially on the posterior end of the case; the mean PBW was $2.5 \pm 1.2\%$. The surface of

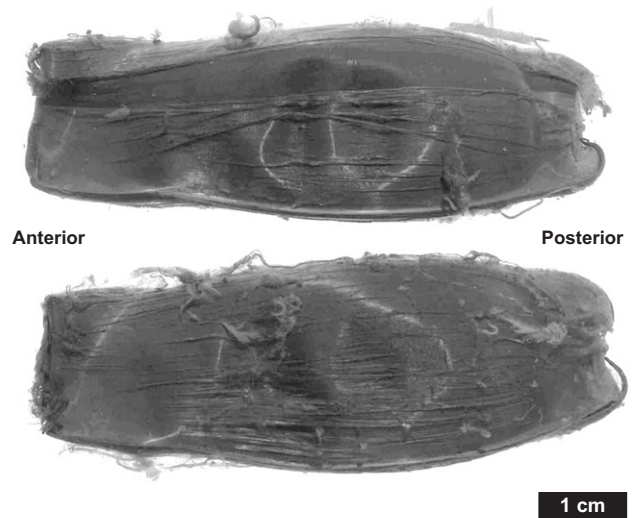


Fig. 5. Egg case of *Apristurus spongeiceps* (USNM 51590, 64.2 and 62.0 mm TL).

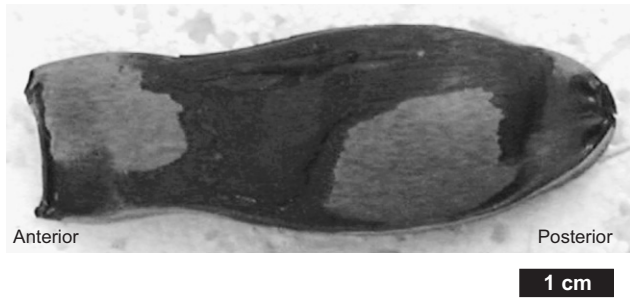


Fig. 6. Egg case of *Apristurus* sp. D (CSIROH 5220-01, 68.8 mm ECL).

the egg case appeared smooth and light brown in color following preservation in ethanol.

Materials examined: CSIROH 5220-01, 1 case 68.8 mm ECL, 47°09'S, 148°43E, 1100 m, 19 February 1999; CSIROH 5220-02, 1 case 70.2 mm TL, in area of South Tasman Rise, 1100 m, 09 March 1999.

Morphometric analysis

Principle components analysis of egg case morphometrics (Fig. 7a) identified two factors that together described 81.23% of the variance in the egg cases. Factor 1 pertained to the shape of the egg case. Along this axis, *Apristurus riveri* (*Ar*, square symbol in Fig. 7a), which has a long slender egg case shape, was distinctly different from the other curvy vase-shaped *Apristurus* egg cases. Factor 2 accounted for the presence or absence of tendrils, separating *A. brunneus* (*Ab*, triangle symbol in Fig. 7a), from the *spongiceps* group catshark egg cases (circle symbols in Fig. 7a).

A cluster analysis of the morphometrics of egg cases studied here (Fig. 7b) also supports differentiation within the genus *Apristurus*. The morphometric characteristics of the *spongiceps*-group egg cases (*A. kampae*, *A. manis*, *A. spongiceps*, and *Apristurus* sp. D) clustered closely together, whereas the *A. brunneus* and *A. riveri* egg cases were determined to be markedly different, by Euclidean distances of 0.05 and 0.095, respectively.

Discussion

The egg case morphology of scyliorhinids has received little attention as compared to adult scyliorhinid morphology. However, it is now apparent that egg cases themselves are as morphologically distinct as the free-swimming catsharks that hatch from them, and should be regarded as a valuable taxonomic tool. The egg cases of *A. aphyodes*, *A. kampae*, *A. manis*, *A. microps*, *A. riveri*, *A. spongiceps*, and *Apristurus* sp. D, which fits the adult *spongiceps* group morphotype, all lack fibrous tendrils. Although the remaining egg cases

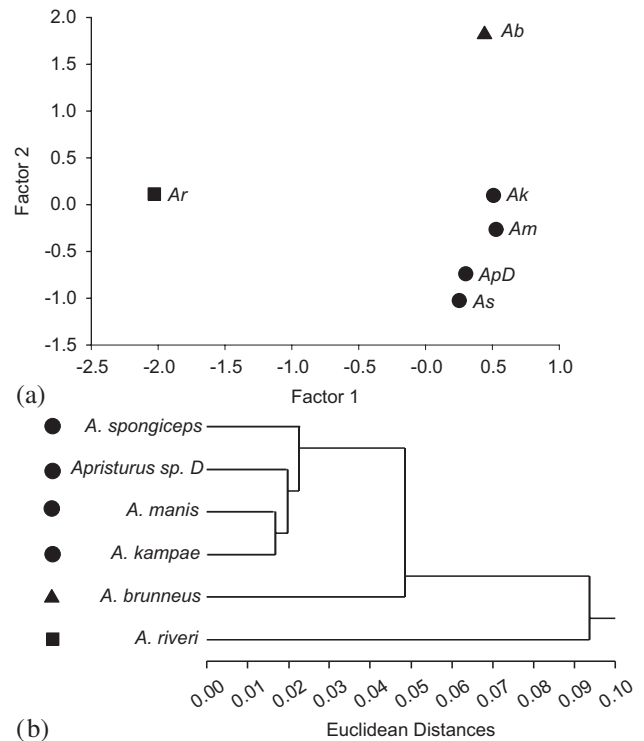


Fig. 7. (a) Principal component analysis (PCA) of egg case morphometric measurements of *Ab*, *Apristurus brunneus*; *Ak*, *A. kampae*; *Am*, *A. manis*; *Ar*, *A. riveri*; *As*, *A. spongiceps*; and *Ap D*, *Apristurus* sp. D. Circles, triangles, and squares denote different morphological groups of egg cases as determined by PCA. (b) Cluster analysis of morphological characteristics of egg cases based on Euclidean distances of morphometric means.

in this genus are unknown, the coincidence of the presence or lack of egg case tendrils with previously studied adult morphology and phylogeny of these species suggests that egg cases may be a valuable taxonomic character. Different egg case morphologies among the species groups of the genus *Apristurus* suggest that these catsharks might differ phylogenetically, in life histories, or in habitat utilization.

Cladistic analysis based on meristics and morphometrics of adults (Compagno, 1988; Nakaya and Sato, 1999; Sato, 2000) and molecular phylogenies (Iglésias et al., 2005) have shown that the genus *Apristurus* is comprised of at least three distinct species groups, the *brunneus* group, *longicephalus* group, and *spongiceps* group. Comparison of egg case morphologies, both those described in this paper and those described previously, indicate that the egg cases of *Apristurus* are also subject to these same species groupings. The lack of egg case tendrils and the deeper habitat of the *spongiceps* group catsharks suggest an evolutionary divergence from the *brunneus* group. This is corroborated by molecular work done by Iglésias et al. (2005), which determined the *brunneus* group species to be

basal to the *spongiceps* group and *longicephalus* sister group. A similar divergence in morphology may be evident in a reproductively isolated population of swell sharks (*Cephaloscyllium ventriosum*) off Santa Catalina Island in southern California which produces an egg case without tendrils, while all other populations of this species produce egg cases with long tendrils (Grover, 1972).

Variable egg case morphologies also have biological and ecological effects on oviposition. This is especially a concern for *spongiceps* group catsharks, the egg cases of which lack tendrils that might facilitate anchorage. Many scyliorhinids exhibit some form of long tendril or fibrous filament extending from the anterior or posterior ends, and it has long been thought that these tendrils may help to secure the egg case to some form of substrate (Springer, 1979; Castro et al., 1988; Able and Flescher, 1991; Ellis and Shackley, 1997; Hamlett and Koob, 1999). In remotely operated vehicle (ROV) video footage acquired from the Monterey Bay Aquarium Research Institute (MBARI; Fig. 8), egg case tendrils were securely wrapped around erect sessile invertebrates, thereby anchoring the case. Egg case tendrils were soft and pliable immediately following oviposition, and became hardened after exposure to seawater (Flammang, 2005). Tendrils hardened around the substrate on which they were entangled, which made them difficult to remove from their attachment site. Through examination of ROV video footage, it was determined that two species of deep-sea catsharks in the eastern North Pacific, *A. brunneus* and *Parmaturus xaniurus*, deposit egg cases specifically by entangling egg case tendrils on sessile invertebrates attached to rocky outcroppings at 300–400 m depth, in waters of about 6 °C (Flammang, 2005).

Egg-laying by a scyliorhinid, the onset of which can be marked by protrusion of the posterior tendrils through the cloaca (Castro et al., 1988) has also been observed in aquaria. The female circles a vertical structure allowing the anterior tendrils of the egg case to become entangled on the structure. Anchorage of the egg case allows the female to pull against the resistant structure, which may facilitate parturition of the egg case (Springer, 1979; Castro et al., 1988). This is an opportunity not afforded to those species of the *spongiceps* group whose egg cases lack tendrils. Springer (1966, 1979) described a ring of firm white tissue surrounding the cloaca in gravid female *A. riveri* and *A. parvipinnis*, and postulated that this flat ring was useful in rubbing against the substrate to help dislodge the egg case from the cloaca. This ring of firm tissue was not observed in *A. kampa* specimens, and no *spongiceps* group catshark has been observed depositing egg cases in aquaria or by ROV.

Placement of an egg case onto the seafloor due to the lack of tendrils and inability to hang an egg case in the

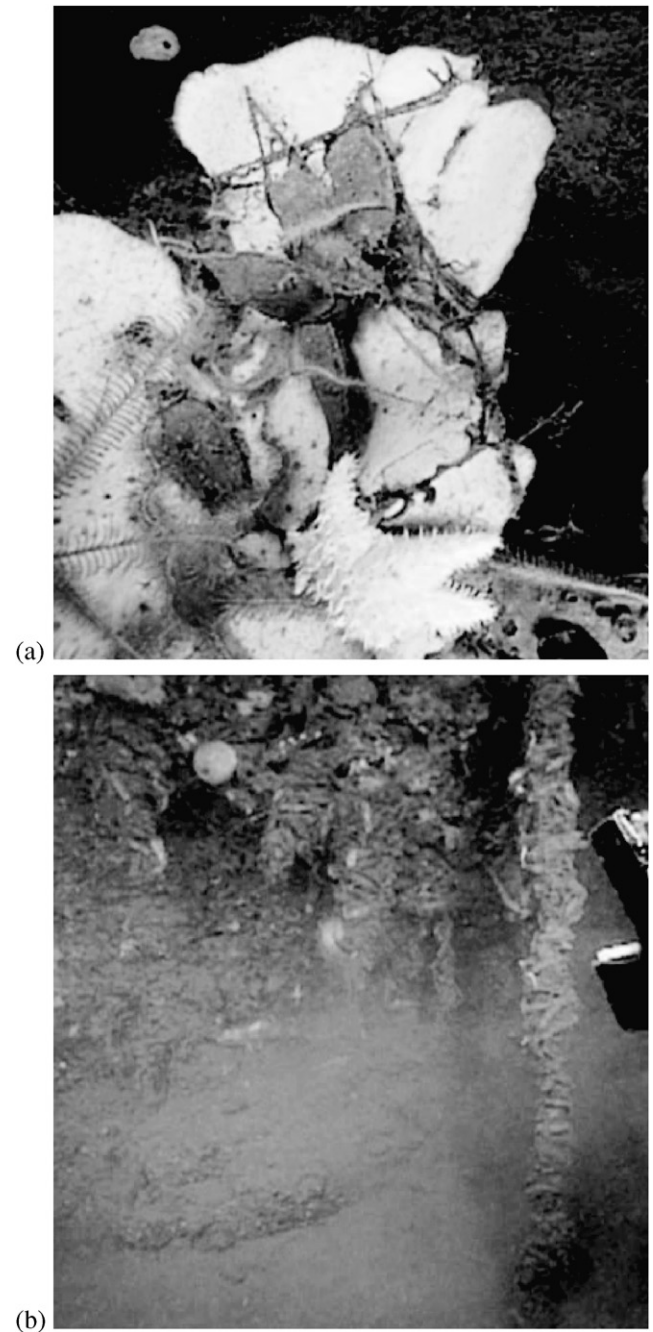


Fig. 8. (a) Catshark egg cases, approximately 60 mm ECL, attached to a deep sea coral by their tendrils. (b) Long bunches of egg cases attached to each other, the bundle on the far right is 2 m long.

water column may have tremendous ecological implications on ventilation of the egg case. In early stages of embryonic development, the anterior and posterior fissures of the egg case are plugged with albumen, which recedes to open the apertures approximately 3 months into the 2 years of development, in the cases of *Apristurus brunneus* and another scyliorhinid maintained in aquaria, *Parmaturus xaniurus*. As the embryo

develops, flow through these apertures is essential to provide adequately oxygenated water and remove metabolic wastes from the egg case; some water passes through the egg case via osmotic diffusion, but the exchange of wastes occurs at only 5% the rate of osmotic diffusion (Hornsey, 1978; Koob and Cox, 1993; Thomason et al., 1996; Leonard et al., 1999; Tullis and Peterson, 2000). Some embryonic sharks and skates actively ventilate their egg cases by waving their tails near the fissures (Diez and Davenport, 1987; Ballard et al., 1993; Thomason et al., 1996; Meehan et al., 1997; Tullis and Peterson, 2000). However, *A. brunneus* and *P. xaniurus*, the egg cases of which have long tendrils and were observed suspended off rocky outcroppings in ROV video, did not exhibit any active pumping during observations in aquaria. In fact, embryos of these species rarely moved at all during development. If passive ventilation provides adequate oxygenation and waste removal, then these catsharks may not have to endure the high metabolic cost of active ventilation (Diez and Davenport, 1987; Thomason et al., 1996; Meehan et al., 1997; Leonard et al., 1999).

Passive ventilation of the egg case is most likely due to one or more of the following mechanisms: pressure differences across the egg case arising from flow separation on the downstream side, a Pitot-tube effect resulting from differences between static internal and dynamic external pressures, and a Venturi effect that may occur due to the location of the upstream and downstream fissures (Vogel, 1994, 2003). The ventilation fissures of the egg case are positioned asymmetrically in cross-section (Fig. 9a) and allow for passive flow to ventilate a case free-hanging in the water column. In this perspective the egg case's long axis is perpendicular to the flow, as is the condition when the egg case is suspended by tendrils. Given this orientation, the egg case had an estimated Reynolds number (Re) of approximately 3000, based on in situ flow determined from ROV video; this Re is in the range in which flow separation will occur. In order to have passive ventilation of the egg case, the high dynamic pressure on the outside of the egg case must overcome the static pressure inside the egg case. Because fluids will passively flow from areas of high to low pressure, water would be pushed through the fissures from the upstream leading edge, and out of the downstream fissure (Fig. 9b, (p), dashed line). This is not a novel system in nature, and is known to occur in caddisfly (*Macronema*) aquatic egg masses and ascidians (Vogel, 1994, 2003). In addition, Koob and Summers (1996) found that, dependent upon orientation of the egg case, fluid would occasionally escape through the upstream fissure, suggesting the possibility of a Venturi effect (Fig. 9b, (v), dotted line). Future experimental research must be completed to test this hypothesis and better understand the complex hydrodynamics of this system.

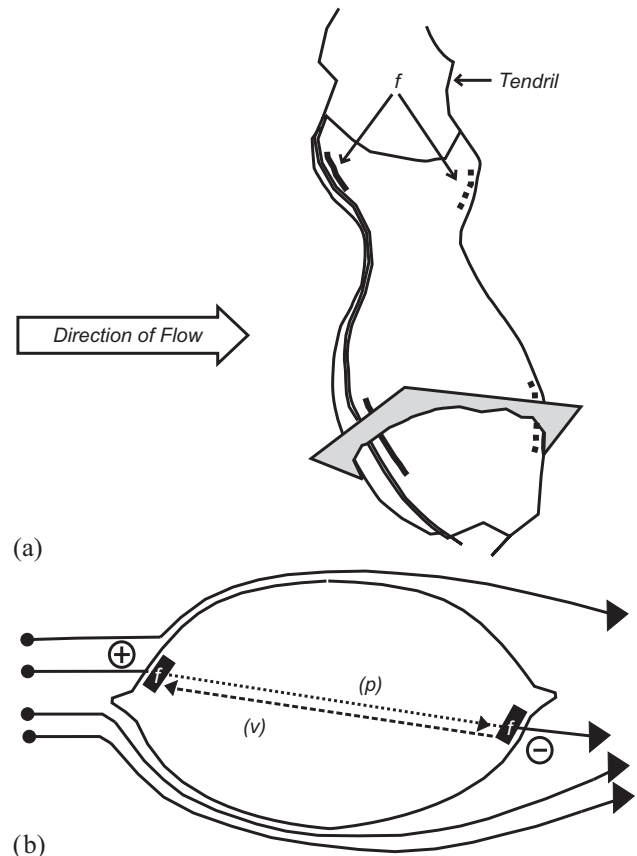


Fig. 9. (a) Illustration of egg case suspended by its tendrils in flow, the direction of which is described by the arrow. The dark and dashed bars designate the locations of the apertures, or fissures (f), above and below the egg case, respectively. The gray plate denotes the location of the cross-section for the flow diagram in (b). (b) Highly schematic theoretical diagram of passive ventilation of an egg case. Direction of flow is from left to right, the dark bars, f, denote the location of the fissures or apertures in cross-section. The plus and minus signs indicate areas of relative higher and lower pressure. The streamlines indicate predicted flow through and around the egg case as hypothesized from fluid dynamic theory; dotted (p) and dashed (v) lines are used within the egg case because we cannot predict at this time what flow patterns may be present internally; however, previous experiments on skate egg cases suggest that a combination of flow patterns may be present dependent upon orientation of the egg case (Karamcheti, 1966; Vogel, 1994, 2003; Koob and Summers, 1996).

Apristurus of the *brunneus* group, which are suspended by their tendrils in areas of flow, are most likely able to efficiently utilize passive ventilation of the egg case. Passive flow is an extremely efficient method of ventilation, functional in current speeds as low as 11 cm s^{-1} , and some shark egg cases have been determined to clear 10–50 egg case volumes/h using this method (Koob and Summers, 1996; Meehan et al., 1997). Skate egg case passive ventilation occurred through the downstream apertures when the egg case

was parallel to flow and through one downstream aperture and one upstream aperture (diagonal to the effected downstream aperture) when the egg case was perpendicular to flow (Koob and Summers, 1996). However, these high flow rates were measured for an egg case hanging in the water column, not lying on the substrate.

Apristurus of the *spongiceps* group must employ a different oviposition strategy to overcome the ecological implications of lacking egg case tendrils. With no tendrils by which to hang, it is presumable that the egg case is deposited directly onto the substrate, and is potentially in danger of the ventilation fissures becoming covered with sediment. Passive flow might be limited because the side of the egg case lying on the ground would be blocked from oncoming flow. Active ventilation would be necessary under these conditions to keep the fissures clear and allow ventilation, although this has a high metabolic cost for the embryo (Diez and Davenport, 1987; Thomason et al., 1996; Leonard et al., 1999). Additionally, an unrestrained egg case lying on the substrate, such as one without tendrils, is subject to lift and may be rolled over into a perpetual tumble in the presence of flow (Vogel, 1994; Denny and Blanchette, 2000). These *spongiceps* group catsharks may employ a strategy similar to that of the horn shark, *Heterodontus francisci*, and the Port Jackson shark, *H. portusjacksoni*, which have been observed placing their egg cases into rocky crevices with their mouths (McLaughlin and O’Gower, 1971) in order to restrict motion of the egg case and avoid silting over; however, it is unknown whether or not any scyliorhinids exhibit this same behavior.

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