

Predation and epibiosis on egg capsules of the Shorttail fanskate, *Sympterygia brevicaudata*

Depredación y epibiosis sobre cápsulas de la Raya de cola corta, *Sympterygia brevicaudata*

Mylene E. Seguel^{1*}, Sebastián Ramírez-Rivera², Francisco Concha^{3,4}, Mario Espinoza^{5,6,7} and Sebastián Hernández^{8,9}

¹Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile

²Laboratorio de Biología Molecular y Celular del Cáncer, Facultad de Medicina, Universidad Católica del Norte, Larrondo 1281, Coquimbo, Chile

³Laboratorio de Biología y Conservación de Condrictios, Facultad de Ciencias del Mar y de Recursos Naturales, Universidad de Valparaíso, Viña del Mar, Chile

⁴Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, United States of America

⁵Centro de Investigación en Ciencias del Mar y Limnología, Universidad de Costa Rica, San José, Costa Rica

⁶Escuela de Biología, Universidad de Costa Rica, San José, Costa Rica

⁷Museo de Zoología, Universidad de Costa Rica, San José, Costa Rica

⁸Laboratorio de Biología Molecular (BIOMOL), Centro de Programas Internacionales y Estudios de Sostenibilidad (CPIES), San José, Costa Rica

⁹Sala de Colecciones Biológicas, Facultad de Ciencias del Mar, Universidad Católica del Norte, Larrondo 1281, Casilla 117, Coquimbo, Chile

*Corresponding author: myleneseguel@gmail.com

Resumen. Después de su deposición, las cápsulas de condrictios se exponen con frecuencia a numerosas amenazas que afectan su supervivencia. Sin embargo, los factores ecológicos que afectan el desarrollo y la supervivencia de los embriones dentro de las cápsulas siguen sin estar claros. El objetivo de este estudio fue cuantificar y describir dos factores ecológicos que afectan a las cápsulas de la raya de cola corta *Sympterygia brevicaudata*: la depredación y la epibiosis. Se recolectaron 241 cápsulas varadas de la zona intermareal de la Bahía de Coquimbo en el norte de Chile (29°57'S; 71°18'O y 71°19'O). Luego se examinaron las marcas de depredación y epibiosis en los diferentes estados de desarrollo de las cápsulas. El 32,8% de las cápsulas presentaban evidencia de marcas de depredación, de las cuales el 48,1% aún no había eclosionado. La forma y el tamaño de las marcas de depredación fueron diferentes a las reportadas en la literatura. Por otro lado, el 78% de las cápsulas presentó epibiosis, de las cuales el 21% aún no había eclosionado. Las cápsulas no eclosionadas que se encontraban en un estado de desarrollo más avanzado (es decir, que poseían fisuras respiratorias abiertas) presentaron una mayor probabilidad de ser depredadas y presentar epibiosis que aquellas con un desarrollo más temprano (fisuras respiratorias cerradas). Las interacciones ecológicas, como la depredación y el asentamiento de epibiontes, pueden influir en aspectos demográficos como el éxito de la eclosión y la tasa de supervivencia, regulando el tamaño de la población de *S. brevicaudata* durante la fase embrionaria.

Palabras clave: Arhynchobatidae, rayas, marcas de depredación, desarrollo embrionario, epibiontes

Abstract. After deposition, chondrichthyan egg capsules are frequently exposed to numerous threats that affect their survival. However, the ecological factors affecting the development and survival of embryos inside egg capsules remain unclear. The aims of this study was to quantify and describe two ecological factors that affect of the Shorttail fanskate *Sympterygia brevicaudata* egg capsules: predation and epibiosis. The egg capsules were collected (241) stranded from Coquimbo Bay's intertidal zone in northern Chile (29°57'S; 71°18'W and 71°19'W), and examined predation marks and epibiosis of these egg capsules at different stages of development. About 32.8% of the egg capsules presented evidence of predation marks, of which 48.1% had not yet hatched. Based on our findings, the shape and size of predation marks were different from those reported in the literature. Additionally, 78% of the egg capsules presented epibiosis, of which 21% had not yet hatched. Non-hatched egg capsules with more advanced stages of development (i.e., possessing open respiratory fissures) showed a higher probability to be predated and present epibiosis than those with earlier development (closed respiratory fissures). Ecological interactions, such as predation and the settlement of epibionts, may influence demographic aspects such as hatching success and survival rate, regulating the population sizes of *S. brevicaudata* during the embryonic phase.

Key words: Arhynchobatidae, skates, predation marks, embryonic development, epibionts

INTRODUCTION

Cartilaginous fishes (Chondrichthyes) constitute a highly diverse group, with more than 1,250 nominal species reported around the world (Dulvy *et al.* 2014). About 25% have been estimated to be threatened and almost 50% are categorized as data deficient (DD) (Dulvy *et al.* 2014, Davidson *et al.* 2016), thus limiting the ability to reliably assess their conservation status and to update the actual

number of threatened species (Dulvy *et al.* 2014). Given most elasmobranchs have life-history traits which make them particularly vulnerable to overfishing (e.g., slow growth rates, late maturity, and late fecundity), understanding key demographic variables such as survival and mortality rates is crucial to evaluating the status of their populations and to effectively manage the impacts on fisheries (Gedamke *et al.* 2007).



Cartilaginous fishes have internal fecundation and display a variety of reproductive strategies, including different modes of embryonic nourishment ranging from lecithotrophic oviparity to placental viviparity (Hamlett *et al.* 2005). The former is the plesiomorphic condition, reported in approximately 40% of elasmobranchs (Hamlett & Koob 1999, Carrier *et al.* 2004). Fertilized eggs of oviparous elasmobranchs are protected by a leathery, structurally complex, and remarkably resistant egg capsule made of cross-linked proteins with anti-microbial and anti-fouling properties (Thomason *et al.* 1994, 1996; Hoff 2009). These egg capsules provide mechanical protection to embryos against biological and other environmental stressors such as bacteria, osmotic changes, desiccation, temperature shock and wave action (Kormanik 1993, Hamlett & Koob 1999, Lucifora & García 2004).

Developing embryos inside egg capsules are an important source of energy for predators and have been found in the stomachs of teleosts, elasmobranchs and marine mammals (Cox & Koob 1991, Bor & Santos 2003). However, predation on developing embryos is not limited to vertebrates. Macroinvertebrates such as echinoderms and gastropods have also been reported to cause large mortality rates (Cox & Koob 1991, Smith & Griffiths 1997, Cox *et al.* 1999, Lucifora & García 2004, Hoff 2009).

In addition, egg capsules of elasmobranchs are suitable surfaces for the adhesion of certain organisms (Sullivan & Regan 2011). Epibiosis is defined as the spatial association between a substrate organism (*i.e.*, basibiont) and a sessile organism (*i.e.*, epibiont) attached to the former's outer surface. Unlike parasites, an epibiont does not depend on its basibiont to fulfill its trophic needs (Wahl 1989, 2009). However, epibiosis is not always neutral to the basibiont and may have a direct impact on survival rates of developing

embryos by hampering the performance of the egg capsules during critical stages; for instance, by obstructing the normal ion and oxygen flow of permeable egg capsule walls (Evans 1981, Kormanik 1993, Lombardi & Files 1993, Leonard *et al.* 1999, Heiden *et al.* 2005). Egg capsules may also become heavier, less buoyant, more rigid and brittle due to epibiosis (Pretorius 2012).

Predation and epibiosis of the egg capsule may be of special interest for the Shorttail fanskate, *Sympterygia brevicaudata*, a species found in coastal waters from Ecuador to central Chile and currently this species was categorized by IUCN as "Near Threatened" (McEachran 1982, Lamilla & Sáez 2003, Last *et al.* 2016, Dulvy *et al.* 2020). Unlike other batoids, egg capsules of *Sympterygia* have extremely long posterior tendrils, which allow females to firmly entangle them in structures such as brown algae or other available substrata, unlike all other oviparous batoids which lay their egg capsules on the seabed (Leible 1988, Oddone & Vooren 2002, 2008; Hernández *et al.* 2005, Mabrugaña *et al.* 2011, Concha *et al.* 2013). The aim of this study is to quantify and describe both predation and epibiosis on egg capsules of *S. brevicaudata* to provide information on how they may affect survival of embryos during their first developmental stages.

MATERIALS AND METHODS

Egg capsules of *Sympterygia brevicaudata* were found stranded ashore, after a storm surge, at Peñuelas (29°57'S; 71°18'W) and Changa (29°57'S; 71°19'W) beaches, Coquimbo Bay, central Chile (Fig. 1). Specimens collected were preserved in ethanol (75%) and subsequently deposited at the Sala de Colecciones Biológicas, Universidad Católica del Norte, Coquimbo, Chile (Collection codes SCBUCN- 5000-5045, 5055-5221, 5152-5280).

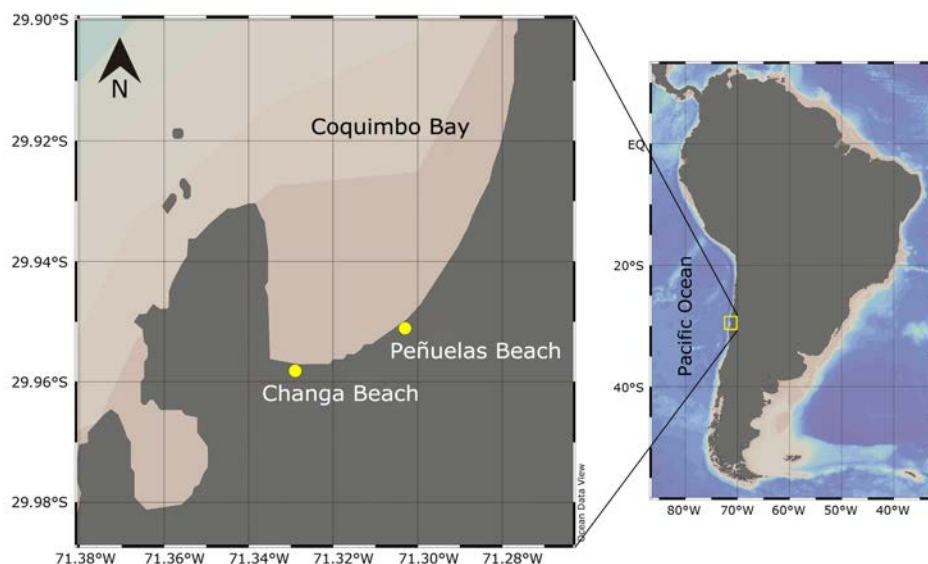


Figure 1. Map of the study area in Coquimbo Bay (Chile). Sampling sites, Changa and Peñuelas Beach, are represented by yellow circles / Mapa del área de estudio en la Bahía de Coquimbo (Chile). Los sitios de muestreos, playa Changa y Peñuelas, están representadas por círculos amarillos

Based on examination of the hatching slit (Fig. 2), egg capsules were classified as hatched (open hatching slit) and not-hatched (closed hatching slit). Additionally, each specimen was categorized according to the evidence of predation and epibiosis as indicated in Table 1. Marks on egg capsules attributed to predation were quantified and identified according to their shape (straight or zigzag) and orientation (longitudinal or transversal). To confirm that embryos were predated only the marks on non-hatched egg capsules were measured, using the software Image-pro Plus 6.0 (Media Cybernetics Corporation, USA). Straight cuts corresponded to lineal marks, whereas zigzag cuts corresponded to a serrated-like pattern of cut. Both types of predation marks were classified as transversal or longitudinal depending upon their orientation to the longitudinal striation of the egg capsule wall (Fig. 3).

Epibiosis was analyzed by identifying each epibiont found to the lowest possible taxonomic level. Subsequently, the frequency of occurrence of each epibiont taxon was expressed as the percentage of the total number of egg capsules examined with each epibiont item. The frequency of egg capsules with either obstructed hatching slit or obstructed respiratory fissures (ORF) was also recorded as the percentage of egg capsules with epibionts covering either the hatching slit or at least one of the four respiratory fissures (Fig. 2). ORFs were classified as open or closed, with a primary focus on non-hatched capsules.

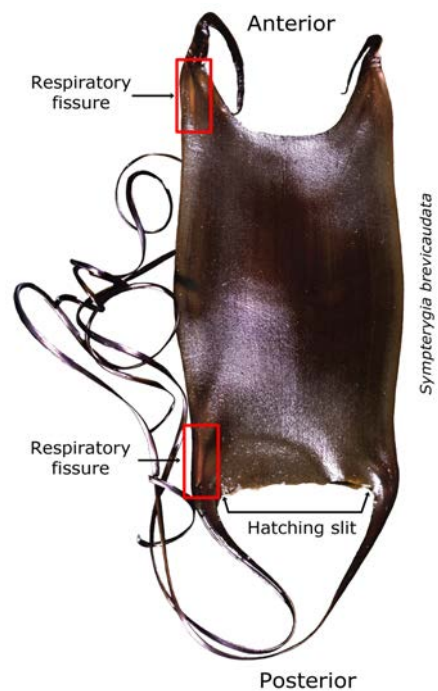


Figure 2. Egg capsules structures observed of the Shorttail fanskate *Sympterygia brevicaudata*. Respiratory fissures are the structures through which ion and oxygen interchange occurs during the last embryonic stages. Hatching slit is the zone where the neonates emerge / Estructura de las cápsulas de la raya de cola corta *Sympterygia brevicaudata*. Las fisuras respiratorias son las estructuras a través de las cuales se produce el intercambio de iones y oxígeno durante las últimas etapas embrionarias. La hendidura de eclosión es la zona por donde emergen los neonatos

Table 1. Classification of egg capsules according to the status of the hatching slit (hatched and non-hatched) and the evidence of predation and epibiosis / Clasificación de las cápsulas según el estado de la hendidura de eclosión (eclosionada y no eclosionada) y la evidencia de depredación y epibiosis

Egg capsule status	Definition
Hatched	Egg capsule whose hatching slit is clear and completely opened, allowing the embryo to hatch.
Non-hatched	Egg capsule whose hatching slit is either still sealed due to the time since egg laying or externally obstructed by the presence of epibionts. In both cases the embryo is not allowed to hatch.
Intact	Egg capsule lacking predation marks or epibionts on its surface.
Predated (P)	Egg capsule with cuts on its surface.
Epibiosis (E)	Egg capsule with epibionts on its surface.
P + E	Egg capsule showing both predation marks and epibionts.

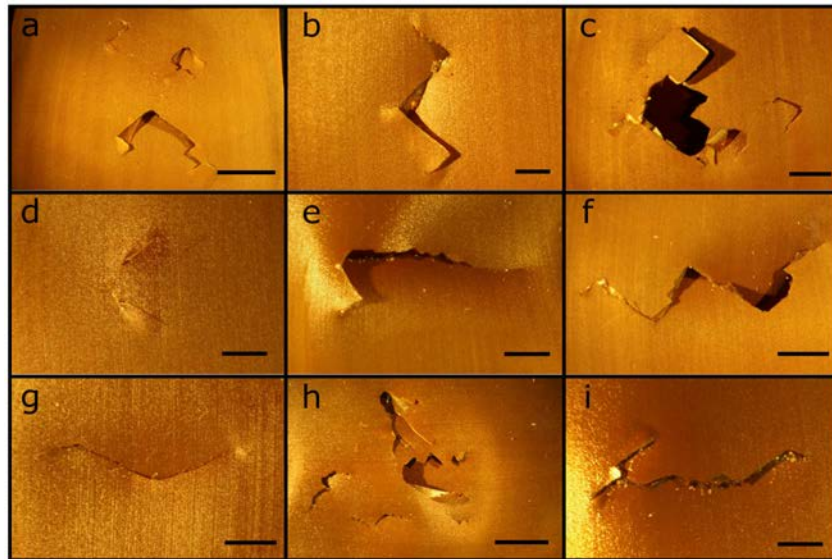


Figure 3. Predation marks in egg capsules from the Shorttail fanskate *Sympterygia brevicaudata* showing the orientation and zigzag shape of the cuts. Longitudinal (b, c, d, h) and transversals (a, e, f, g, i) cuttings. Scale bar: 10 mm / Marcas de depredación en cápsulas de la raya de cola corta *Sympterygia brevicaudata* que muestran la orientación y forma de zigzag de los cortes. Cortes longitudinales (b, c, d, h) y transversales (a, e, f, g, i). Barra de escala: 10 mm

Several independent generalized linear models (GLMs) with binomial distribution were used to determine: (1) the probability that predation marks (response variable: presence / absence of predation marks) were present on hatched vs. non-hatched egg capsules (categorical predictor), (2) the probability that epibionts (response variable: presence / absence of epibionts) were present on hatched vs. non-hatched egg capsules (categorical predictor), (3) the probability that predation marks (response variable: presence / absence of predation marks) were present on non-hatched egg capsules (categorical predictor: more developed / open respiratory fissures vs. early developed / closed respiratory fissures), and (4) the probability that epibionts (response variable: presence / absence of epibionts) were present on non-hatched egg capsules (categorical predictor: more developed / open respiratory fissures vs. early developed / closed respiratory fissures). The output of each independent model was examined to assess the effect of the predictor using maximum likelihood tests. Analysis of deviance tables and standard residuals GLM diagnostic plots were also used to evaluate the goodness of fit of the resulting models and to check that assumptions were not violated for each model. The libraries “pscl”, “MuMIn” and “lme4” were used to examine model outputs. GLMs were implemented using R version 3.0.2 (R Development Core Team 2014).

RESULTS

A total of 241 egg capsules were examined, 70.5% of which were hatched and the remaining 29.5% non-hatched. An 89.2% of egg capsules showed predation marks, epibionts and/or both. Evidence of predation marks was found in 32.8% (N=79) of the egg capsules and their frequency of occurrence was similar in hatched and non-hatched egg capsules, 51.9 and 48.1%, respectively. More information on the classification of egg capsules is summarized in Table 2. The probability of finding predation marks on hatched and non-hatched egg capsules was $P = 0.24$ (95% CI: 0.18-0.31) and $P = 0.54$ (95%CI: 0.42-0.65), respectively, these probabilities being significantly different (GLMs, $P < 0.0001$). This is consistent with the observed frequency of ORFs (see Table 3).

The shape and orientation of predation marks on egg capsules were mostly zigzag and transversal, 86.2 and 65.1%, respectively (Fig. 3). In total, predation marks were found on 38 non-hatched egg capsules; 21.1 and 78.9% for straight and zigzag cuts, respectively. Egg capsules with longitudinally and transversally oriented straight cuts corresponded to 21.1 and 0.0%, respectively, whereas egg capsules with longitudinally and transversally oriented zigzag cuts corresponded to 55.3 and 23.7%, respectively. The length of predation marks ranged from 4.92 to 50.95 mm (Mean= 22.33 ± 4.20 mm), whereas their perimeters ranged from 9.12 to 70.10 mm (Mean= 34.73 ± 5.51 mm). There were significant differences between the probability of finding predation marks in non-hatched capsules with open and closed respiratory fissures (GLMs, $P < 0.0001$), with probabilities of $P = 0.74$ (95% CI= 0.57-0.86) and $P = 0.33$ (95% CI= 0.20-0.50), respectively.

Table 2. Frequency of egg capsules (%) classified by the status of the hatching slit / Clasificación de las cápsulas según la frecuencia (%) del estado de la hendidura de eclosión

Egg capsule	Total n	Intact	Predated	Epibiosis	P + E
Hatched	170	6.47	7.06	69.41	17.06
Non-hatched	71	21.13	21.13	25.35	32.39

Table 3. Frequency of egg capsules (%) with epibiosis classified by the number of obstructed respiratory fissures (ORF) by epibionts, or by the obstruction of the hatching slit (HS) / Frecuencia de cápsulas (%) con epibiosis clasificadas de acuerdo al número de fisuras respiratorias obstruidas (ORF) por epibiontes o la obstrucción de la hendidura de eclosión (HS)

Egg capsule	Total n	0 ORF	1 ORF	2 ORF	3 ORF	4 ORF	HS
Hatched	147	25.2	11.6	17.0	16.3	29.9	45.6
Non-hatched	41	14.6	12.2	17.1	19.5	36.6	85.4

Epibionts were found in 78% (N= 188) of the egg capsules analyzed. More epibionts were observed in hatched than in non-hatched egg capsules (78.2 and 21.8%, respectively), with a probability of occurrence of epibiosis on hatched and non-

hatched egg capsules of $P = 0.86$ (95% CI: 0.80-0.90) and $P = 0.58$ (95% CI: 0.46-0.69), respectively. These probabilities were significantly different (GLMs, $P < 0.0001$). Bryozoans were the most common epibionts found on the surface of egg capsules, whereas the remaining epibionts corresponded to the tunicate *Pyura chilensis*, the barnacle *Balanus laevis*, and the polychaete *Polydora* sp. Some epibionts are shown in Figures 4 and 5, and their specific frequencies of occurrence are summarized in Table 4. Obstruction of the hatching slit or respiratory fissures was common among egg capsules with epibionts, with a total of 187. Epibionts obstructed at least one respiratory fissure on 145 egg capsules, of which 24.1% were non-hatched. The information on the egg capsules with obstructed respiratory fissures and/or hatching slit due to epibiosis is summarized in Table 3. The probability of occurrence of epibiosis on non-hatched egg capsules with open and closed respiratory fissures was $P = 0.80$ (95%CI: 0.64-0.90) and $P = 0.36$ (95% CI: 0.22-0.53), respectively (GLMs, $P < 0.001$), these probabilities being significantly different (GLMs, $P < 0.0001$). This is consistent with the observed frequency of ORF (see Table 3).

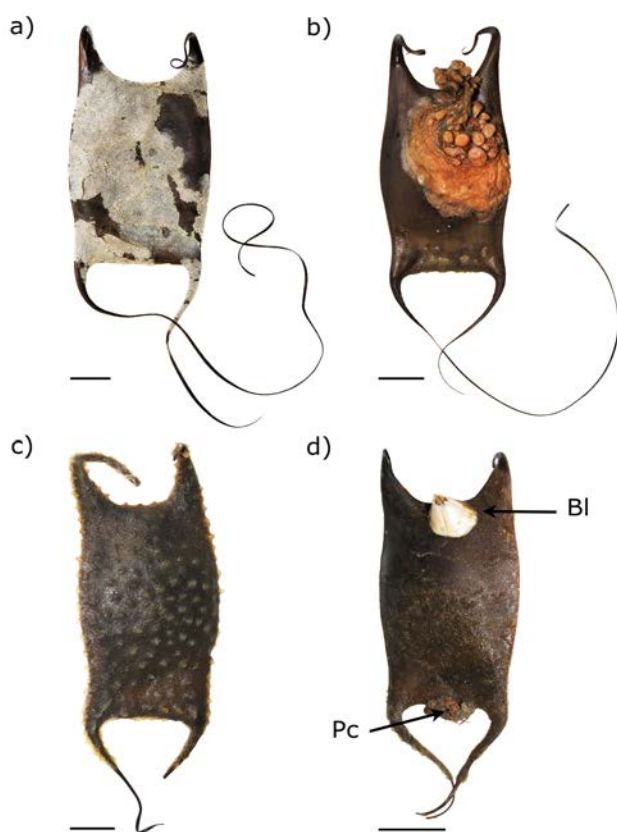


Figure 4. Epibionts on the egg capsules of the Shorttail fanskate *Sympterygia brevicaudata*. a) Bryozoan *Membranipora* sp. b) Colony of the tunicate *Pyura chilensis*. c) Unidentified ascidian and d) Barnacle *Balanus laevis* (BI) living in the anterior region of the egg capsule, and a colony of the tunicate *Pyura chilensis* (Pc) in the posterior region. Scale bar: 10 mm / Epibiontes sobre cápsulas de la raya de cola corta *Sympterygia brevicaudata*. a) Briozoo *Membranipora* sp. b) Colonia del tunicado *Pyura chilensis*. c) Ascidia no identificada y d) Cirripedio *Balanus laevis* (BI) posicionado en la región anterior de la cápsula, y una colonia de tunicado *Pyura chilensis* (Pc) posicionada en la región posterior. Barra de escala: 10 mm

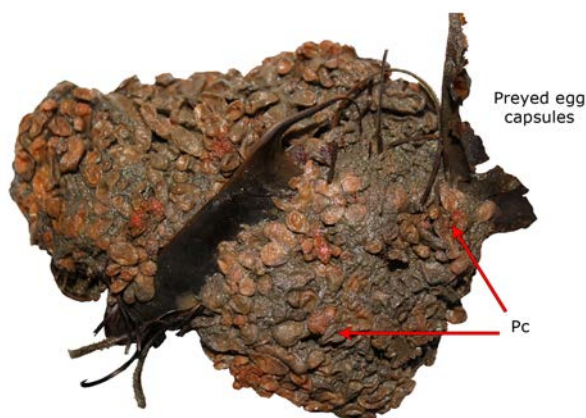


Figure 5. A large colony of the tunicate *Pyura chilensis* (Pc) covering an egg capsule of *Sympterygia brevicaudata* / Colonia grande de tunicado *Pyura chilensis* (Pc) cubriendo una cápsula de *Sympterygia brevicaudata*

Table 4. Frequency of epibionts (%) identified on egg capsules / Frecuencia de epibiontes (%) identificados sobre las cápsulas

Egg capsule	Total n	<i>Pyura chilensis</i>	<i>Balanus laevis</i>	Bryozoa	<i>Polydora</i> sp.
Hatched	147	6.1	4.1	82.4	7.4
Non-hatched	41	7.3	7.3	85.4	0.0

DISCUSSION

Egg capsules of the Shorttail fanskate *Sympterygia brevicaudata* are vulnerable to the effects of predation and epibiont growth on their surfaces. Ecological interactions such as these may influence hatching success and survival rates, thus regulating population sizes of *S. brevicaudata* during the embryonic development. Similar findings have been reported in other oviparous elasmobranch species with similar life-history strategies (Cox & Koob 1993, Smith & Griffiths 1997, Lucifora & García 2004). Therefore, the choice of a more secure area where females of *S. brevicaudata* lay their egg capsules may increase the chances of survival of the embryo relative to more exposed areas where predation risk is higher. Hatching success, however, can be counterbalanced by the high fecundity rates of some skates (*i.e.*, 40 to 160 eggs per year) (Fuentealba & Leible 1990, Ellis & Shackley 1995, Lucifora & García 2004, Jañez & Sueiro 2009).

Egg capsules of oviparous elasmobranchs provide mechanical protection to the embryo during development, as they have a longitudinal striation conformed of cross-linked proteins that are primarily composed by collagen (Thomason *et al.* 1994, 1996; Hamlett & Koob 1999). This structure makes the capsules more resistant to fractures that may be

caused by exposure to surge (Feng & Knight 1994). In case there is a fracture due to the surge, it is produced parallel to the striation (longitudinal cut), as the impact weakens the thinnest collagen structure. The fissure continues along with the pattern of striation lines, and only in very rare occasions these impacts do cross the striation (Feng & Knight 1994, Thomason *et al.* 1994). However, it is important to highlight that the cuts observed in the egg capsules examined in this study were transversely oriented to the longitudinal striation, which suggest they were made by a predator (Fig. 3).

Based on our observations, non-hatched egg capsules had a high probability of being preyed upon, and those with open respiratory fissures were more likely to be predated than those with closed respiratory fissures. This may be because capsules with open respiratory fissures have a longer embryonic development time and therefore a longer time exposed to possible predators. Additionally, during this time developing embryos have a highly nutritious yolk and transmit chemical signals that attract predators (Lucifora & García 2004). Egg capsules that have been recently laid are also softer and easier to break compared to older egg capsules including those already hatched (Lucifora & García 2004).

Based on our findings, the shape and size of predation marks in egg capsules from *S. brevicaudata* were different from the ones reported in the literature. Most studies have identified snails from the family Muricidae and Naticidae as the main predators of elasmobranch egg capsules (Cox *et al.* 1999, Lucifora & García 2004, Hoff 2009). These gastropod species perforate the surface of the capsule with the radula, introducing the proboscis into the orifice and devouring the embryo (Smith & Griffiths 1997, Cox *et al.* 1999, Lucifora & García 2004, Hoff 2009). For instance, in one study, five types of boreholes were identified in seven species of elasmobranch from the South African coastline. This study revealed that most perforations were attributed to the snail *Burnupena* sp. (Smith & Griffiths 1997). Lucifora & García (2004) also reported a snail (*Trophon acanthodes*) as the most common predator of four skate species from the Southwestern Atlantic, particularly on egg capsules from *B. albomaculata*. The rest of the boreholes were potentially caused by *Fusitriton magellanicus* and another unknown gastropod species (Lucifora & Garcia 2004). Hoff (2009) also identified the snail *Fusitriton oregonensis* as the main predator of egg capsules in three species of skates that utilize specific areas as nurseries in the North-Eastern Atlantic. However, Smith and Griffiths (1997), Lucifora & García (2004) and Hoff (2009) described circular perforations as a sign of predation events. Our results, by contrast, showed a zigzag pattern of cuts that are likely attributed to decapod crustaceans commonly found in the subtidal zone of Coquimbo Bay, such as *Rhynchocinetes typus*, *Synalpheus spinifrons*, *Talipeus dentatus*, *Homalaspis plana*, *Platyxanthus orbigny* or *Paraxanthus barbiger*

(Retamal 1981, Zuñiga 2002). Egg capsules of *S. brevicaudata* may also face attacks by the kelp gull *Larus dominicanus* when stranded on beaches (unpublished data). These gulls are commonly found along the tide line of sandy beaches, and their diet includes a wide range of food items such as invertebrates and wastes from fishing ports along with Coquimbo and Changa Beach (Bertellotti & Yorío 2000, Bertellotti *et al.* 2003, Ludynia *et al.* 2005). Further studies are needed to investigate other potential predators that may feed directly on egg capsules of *S. brevicaudata*. Also, long-term biological surveys along Coquimbo Bay shores could help in determining the number of stranded egg capsules, quantify natural mortality, and improve our understanding of how these causes and others, like predators, may shape these species' populations.

Egg capsules have anti-microbial and anti-encrusting properties, which help maintain their surfaces free of epiphytes and epibionts during the early stages of embryo development (Thomason *et al.* 1994, 1996; Hoff 2009). However, these characteristics were not apparent in some non-hatched egg capsules of *S. brevicaudata*; indeed, capsules of all developmental stages observed in our study showed the presence of epibionts. Interestingly, 10 egg capsules of *S. brevicaudata* were completely covered by a colony of the tunicate *Pyura chilensis* (Fig. 5). However, the poor condition of the egg capsules did not allow for assessment of their state (hatched or non-hatched). Growth rates of fouling organisms are known to be high in La Herradura and in some areas of Coquimbo Bay (*e.g.*, Changa Beach) with low current exchange, relatively cold, oxygen-poor, and high availability of nutrients in the environment, which may promote blooms of fouling organisms (Silva & Konow 1975, Viviani & DiSalvo 1980, Valle-Levinson *et al.* 2000, Thiel *et al.* 2007, Cifuentes *et al.* 2007, 2010). Newly available sources of space for the occupation of sessile organisms that colonize hard structures have been commonly described in *Pyura chilensis* (Viviani & DiSalvo 1980, Valdivia *et al.* 2005, Cifuentes *et al.* 2007, 2010). Bryozoans and polychaete families also represent one of the principal components of fouling communities (Tovar-Hernández *et al.* 2009, Abdelsalam 2016). However, several other species such as balanids and possibly other marine invertebrates can also settle on the surface of chondrichthyan egg capsules. As shown by the results, those capsules that have more developed embryos and open respiratory fissures are more vulnerable to epibionts due to their longer exposure time. Unfortunately, the degree of colonization of epibionts may also be a cause of mortality since the obstruction of respiratory fissures could cause suffocation and intoxication of the embryo due to the lack of circulation of water through the capsule, and thus both correct ventilation and excretion. Future research is needed to prove this hypothesis.

Through this study, it is suggested that the predation and adhesion of epibionts in high quantities to the capsules could contribute to mortality in the early stages of embryonic development of *S. brevicaudata*. This suggests that these factors can influence the abundance of the population of this species, which impacts in fluctuations and level of recruitment. These observations might help fill gaps in the general understanding of ecological and biological factors affecting the embryonic development of *S. brevicaudata*. The dynamic of some demographic variables in a particular population is crucial to address the current data deficiency surrounding oviparous elasmobranch species and is also important for the assessment of the status of their populations to contribute to effective management and conservation actions.

ACKNOWLEDGMENTS

We thank Courtney King, Victor Castelleto (Photographer) and instructors of the course entitled Management of Biological Collections of the curriculum of marine biology at the Facultad de Ciencias del Mar, held in the Sala de Colecciones Biológicas de la Universidad Católica del Norte (SCBUCN). The study was financed by FONDEF Project D10|1038.

LITERATURE CITED

- Abdelsalam KM. 2016.** Fouling bryozoan fauna from Hurghada, Red Sea, Egypt. II. Encrusting species. *The Egyptian Journal of Aquatic Research* 42(4): 427-436.
- Bertellotti M & P Yorío. 2000.** Age-related feeding behavior and foraging efficiency in kelp gulls *Larus dominicanus* attending coastal trawlers in Argentina. *Ardea* 88: 207-214.
- Bertellotti M, G Pagnoni & P Yorío. 2003.** Comportamiento de alimentación de la gaviota cocinera (*Larus dominicanus*) durante la temporada no reproductiva en las playas arenosas de península Valdés, Argentina. *Hornero* 18: 37-42.
- Bor P & M Santos. 2003.** Findings of elasmobranch eggs in the stomach of sperm whales and other marine organisms. *Journal of Marine Biological Association of the United Kingdom* 83: 1351-1353. <<https://doi.org/10.1017/S0025315403008804>>
- Carrier JC, JA Musick & M Heithaus. 2004.** Biology of sharks and their relatives, 585 pp. CRC Press, London.
- Cifuentes M, C Kamlah, M Thiel, M Lenz & M Wahl. 2007.** Effects of temporal variability of disturbance on the succession in marine fouling communities in northern-central Chile. *Journal of Experimental Marine Biology and Ecology* 352: 280-294. <<https://doi.org/10.1016/j.jembe.2007.08.004>>
- Cifuentes M, I Krueger, CP Dumont, M Lenz & M Thiel. 2010.** Does primary colonization or community structure determine the succession of fouling communities? *Journal of Experimental Marine Biology and Ecology* 395: 10-20. <<https://doi.org/10.1016/j.jembe.2010.08.019>>

- Concha F, N Morales & J Larraguibel. 2013.** Egg capsules of the filetail fanskate *Sympterygia lima* (Poeppig 1835) (Rajiformes, Arhynchobatidae) from the southeastern Pacific Ocean, with observations on captive egg-laying. *Ichthyological Research* 60: 203-208. <<https://doi.org/10.1007/s10228-012-0333-8>>
- Cox DL & TJ Koob. 1991.** Predation on eggs of the little skate (*Raja erinacea*) in the Gulf of Maine. *Bulletin of the Mount Desert Island Biological Laboratory* 30: 123-124.
- Cox DL & TJ Koob. 1993.** Predation on elasmobranch eggs. *Environmental Biology of Fishes* 38: 117-125.
- Cox DL, P Walker & TJ Koob. 1999.** Predation on eggs of the thorny skate. *Transactions of the American Fisheries Society* 128: 380-384.
- Davidson LNK, MA Krawchuk & NK Dulvy. 2016.** Why have global shark and ray landings declined: Improved management or overfishing? *Fish and Fisheries* 17: 438-458. <<https://doi.org/10.1111/faf.12119>>
- Dulvy NK, SL Fowler, JA Musick, RD Cavanagh, PM Kyne, LR Harrison, JK Carlson, LNK Davidson, SV Fordham, MP Francis, CM Pollock, CA Simpfendorfer, GH Burgess, KE Carpenter, LJV Compagno, DA Ebert, C Gibson, MR Heupel, SR Livingstone, JC Sanciangco, JD Stevens, S Valenti & WT White. 2014.** Extinction risk and conservation of the world's sharks and rays. *eLife* 3, e00590. <<https://doi.org/10.7554/eLife.00590>>
- Dulvy NK, E Acuña, C Bustamante, A Cevallos, F Concha, K Herman & X Velez-Zuazo. 2020.** *Sympterygia brevicaudata*. The IUCN Red List of Threatened Species 2020: e.T44596A124434224. <<https://doi.org/10.2305/IUCN.UK.2020-3.RLTS.T44596A124434224.en>>
- Ellis JR & SE Shackley. 1995.** Observations on egg-laying in the thornback ray. *Journal of Fish Biology* 46: 903-904.
- Evans D. 1981.** The egg capsule of the oviparous elasmobranch, *Raja erinacea*, does osmoregulate. *Journal of Experimental Biology* 92(1): 337-340.
- Feng D & P Knight. 1994.** Structure and formation of the egg capsule tendrils in the dogfish *Scyliorhinus canicula*. *Philosophical Transactions of the Royal Society B: Biological Sciences* 343(1305): 285-302.
- Fuentealba M & M Leible. 1990.** Perspectivas de la pesquería de la raya volantín *Raja (Dipturus) flavirostris*: estudio de edad, crecimiento y algunos aspectos reproductivos. In: Barbieri MA (ed) *Perspectivas de la actividad pesquera en Chile*, pp. 227-236. Escuela de Ciencias del Mar, Universidad Católica de Valparaíso, Valparaíso.
- Gedamke T, HM Hoening, JA Musick, WD DuPaul & HG Samuel. 2007.** Using demographic models to determine intrinsic rate of increase and sustainable fishing for Elasmobranchs: Pitfalls, advances, and applications. *North American Journal of Fisheries Management* 27(2): 605-618.
- Hamlett WC & TJ Koob. 1999.** Female reproductive system. In: Hamlett WC (ed). *Sharks, skates, and rays: the biology of elasmobranch fishes*, pp. 398-443. Johns Hopkins University Press, Baltimore.
- Hamlett WC, G Kormanik, M Storrie, B Stevens & TI Walker. 2005.** Chondrichthyan parity, lecithotrophy and matrotrophy. In: Hamlett WC (ed). *Reproductive biology and phylogeny of chondrichthyes: sharks, rays and chimaeras*, Vol. 3: 395-434. Science Publishers, Enfield.
- Heiden TCK, AN Haines, C Manire, J Lombardi & TJ Koob. 2005.** Structure and permeability of the egg capsule of the Bonnethead Shark, *Sphyrna tiburo*. *Revista de Zoología Experimental Parte A: Biología Experimental Comparativa* 303A(7): 577-589.
- Hernández S, J Lamilla, E Dupré & W Stotz. 2005.** Desarrollo embrionario de la Pintarroja común *Schroederichthys chilensis* (Guichenot, 1848) (Chondrichthyes: Scyliorhinidae). *Gayana* 69: 191-197.
- Hoff GR. 2009.** Embryo developmental events and the egg capsule of the Aleutian skate *Bathyraja aleutica* (Gilbert) and the Alaska skate *Bathyraja parmifera* (Bean). *Journal of Fish Biology* 74: 483-501.
- Jañez J & MC Sueiro. 2009.** Oviposition rate of the fanskate *Sympterygia bonapartii* (Elasmobranchii, Rajidae) (Müller and Henle, 1841) held in captivity. *Pan-American Journal of Aquatic Sciences* 4: 580-582.
- Kormanik GA. 1993.** Ionic and osmotic environment of developing elasmobranch embryos. *Environmental Biology of Fishes* 38: 223-240.
- Lamilla J & S Sáez. 2003.** Clave taxonómica para el reconocimiento de especies de rayas chilenas (Chondrichthyes, Batoidei). *Revista de Investigaciones Marinas* 31: 3-16.
- Last PR, WT White, MR Carvalho, B Séret, MFW Stehmann & GLP Naylor. 2016.** *Rays of the world*, 800 pp. CSIRO Publishing, Cleyton South.
- Leible M. 1988.** Revisión de métodos para estudios taxonómicos de rayas (Rajiformes, Rajidae). *Gayana, Zoología* 52(1-2): 15-93.
- Leonard J, A Summers & T Koob. 1999.** Metabolic rate of embryonic Little Skate, *Raja erinacea* (Chondrichthyes: Batoidea): the cost of active pumping. *Journal of Experimental Zoology*. 283: 13-18.
- Lombardi J & T Files. 1993.** Egg capsule structure and permeability in the viviparous shark *Mustelus canis*. *Journal of Experimental Zoology* 267: 76-85.
- Lucifora L & V García. 2004.** Gastropod predation on egg capsules of skates (Chondrichthyes, Rajidae) in the southwestern Atlantic: quantification and life history implications. *Marine Biology* 145: 917-922.
- Ludynia K, S Garthe & GJ Luna. 2005.** Seasonal and regional variation in the diet of the kelp gull in Northern Chile. *Waterbirds* 28: 359-365.
- Mabragaña E, D Figueroa, L Scenna, J Díaz de Astarloa, J Colonello & G Delpiani. 2011.** Chondrichthyan egg cases from the southwest Atlantic Ocean. *Journal of Fish Biology* 79: 1261-1290.
- McEachran J. 1982.** Revision of the South American Skate Genus *Sympterygia* (Elasmobranchii: Rajiformes). *Copeia* 1982: 867-891.
- Oddone MC & CM Vooren. 2002.** Egg-cases and size at hatching of *Sympterygia acuta* in the south-western Atlantic. *Journal of Fish Biology* 61(3): 858-861.
- Oddone MC & CM Vooren. 2008.** Comparative morphology and identification of egg capsules of skates species of the genera *Atlantoraja* (Menni 1972), *Rioraja* (Whitley 1939) and *Sympterygia* (Muller and Henle 1837). *Arquivos de Ciências do Mar, Fortaleza* 41: 5-13.

- Pretorius CA. 2012.** Factors influencing the development and mortality rate of shy and cat shark embryos in South African waters. Thesis Master of Science, University of Cape Town, Cape Town, 109 pp. <<https://open.uct.ac.za/handle/11427/10662>>
- R Development Core Team. 2014.** R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <<http://www.R-project.org>>
- Retamal M. 1981.** Catálogo ilustrativo de los Crustáceos de Chile. Gayana 44: 1-110.
- Silva N & D Konow. 1975.** Contribución al conocimiento de las masas de agua en el Pacífico Sudoriental, (Expedición Krill, Crucero 3-4, Julio-Agosto 1974). Revista de la Comisión Permanente del Pacífico Sur 3: 63-75.
- Smith C & C Griffiths. 1997.** Shark and skate egg-capsules cast up on two South African beaches and their rates of hatching success or causes of death. South African Journal of Zoology 32: 112-117.
- Sullivan T & F Regan. 2011.** The characterization, replication and testing of dermal denticles of *Scyliorhinus canicula* for physical mechanisms of biofouling prevention. Bioinspiration & Biomimetics 6: 1-11.
- Thiel M, EC Macaya, E Acuña, WE Arntz, H Bastias, K Brokordt, PA Camus, JC Castilla, LR Castro, M Cortés, CP Dumont, R Escribano, M Fernandez, JA Gajardo, CF Gaymer, I Gomez, AE González, HE González, PA Haye, JE Illanes, JL Iriarte, DA Lancellotti, G Luna-Jorquera, C Luxoro, PH Manriquez, V Marín, P Muñoz, SA Navarrete, E Perez, E Poulin, J Sellanes, HH Sepúlveda, W Stotz, F Tala, A Thomas, CA Vargas, JA Vasquez & JMA Vega. 2007.** The Humboldt Current System of northern and central Chile. Oceanographic processes, ecological interactions and socioeconomic feedback Oceanography and Marine Biology: An Annual Review 45: 195-344.
- Thomason J, J Davenport & A Rogerson. 1994.** Antifouling performance of the embryo and egg capsule of the dogfish *Scyliorhinus canicula*. Journal of the Marine Biological Association of the United Kingdom 74: 823-836.
- Thomason J, S Marrs & J Davenport. 1996.** Antibacterial and antisetlement activity of the dogfish (*Scyliorhinus canicula*) eggcase. Journal of the Marine Biological Association of the United Kingdom 12: 577-643.
- Tovar-Hernández MA, N Méndez & TF Villalobos-Guerrero. 2009.** Fouling polychaete worms from the southern Gulf of California: Sabellidae and Serpulidae. Systematics and Biodiversity 7(3): 319-336.
- Valdivia N, A Heidemann, M Thiel, M Molis & M Wahl. 2005.** Effects of disturbance on the diversity of hard bottom macrobenthic communities on the coast of Chile. Marine Ecology Progress Series 299: 45-54.
- Valle-Levinson A, J Moraga, J Olivares & JL Blanco. 2000.** Tidal and residual circulation in a semi-arid bay: Coquimbo Bay, Chile. Continental Shelf Research 20: 2009-2028.
- Viviani CA & LH DiSalvo. 1980.** Biofouling in a north central Chilean coastal bay. In: Fifth International Congress on Marine Corrosion and Fouling, Barcelona, pp. 69-74.
- Wahl M. 1989.** Marine epibiosis. I. Fouling and antifouling: some basic aspects. Marine Ecology Progress Series 58: 175-189.
- Wahl M. 2009.** Epibiosis: Ecology, effects and defences. In: Wahl M (ed). Marine hard bottom communities, Ecological Studies 206: 61-72.
- Zuñiga O. 2002.** Guía de biodiversidad N°2, Volumen 1 Macrofauna y algas marinas. Crustáceos, 76 pp. Centro Regional de Estudios y Educación Ambiental, Antofagasta.

Received September 3 2020
Accepted May 25 2021