

Embryonic diapause in the elasmobranchs

Daniela Waltrick · Cynthia Awruch ·
Colin Simpfendorfer

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Abstract Embryonic diapause is a temporary suspension of development at any stage of embryogenesis, which prolongs the gestation period, allowing parturition to occur in conditions that are more suitable for newborns. This reproductive trait is widespread among all vertebrates, including elasmobranchs. Although it has only been confirmed in two elasmobranchs (*Rhizoprionodon taylori* and *Dasyatis sayi*), evidence indicates that at least 14 species of rays and two sharks undergo diapause, suggesting that this form of reproduction exists within a wide range of elasmobranch reproductive modes, including lecithotrophs and matrotrophs. Where it has been studied, embryogenesis is arrested at the blastodisc stage and preserved in the uterus for periods from four to 10 months. There are still many questions that remain unanswered concerning the knowledge on the biology of most diapausing species but it is clear that species benefit differently from this reproductive trait. As in other vertebrates, it is likely that environmental cues and hormones (especially progesterone and prolactin) are involved in the control of diapause in

elasmobranchs, however rigorous testing of current hypothesis remains to be carried out.

Keywords Arrested development · Discontinuous development · Reproductive hormones · Reproductive trait · Pregnancy

Introduction

Elasmobranchs are a successful group of fishes that have persisted in the world's oceans for hundreds of millions of years (Grogan and Lund 2004), proving resilient to waves of extinction that saw many other groups vanished (Carroll 1988). One reason suggested for the resilience of this group over this long time period is the diversity of their reproductive modes (Carrier et al. 2004). Within the approximately 1,100 extant species in the group there are two forms of egg-laying (oviparity) and six forms of live-bearing (viviparity) (Carrier et al. 2004; Hamlett and Koob 1999; Musick and Ellis 2005), which are estimated to have evolved on six independent occasions from oviparity (Musick and Ellis 2005). This diversity of reproductive modes and the large number of occasions on which some have arisen through evolutionary time suggests that elasmobranch reproductive system is highly adaptable and that novel reproductive specializations may still await discovery within this taxa.

D. Waltrick (✉) · C. Awruch · C. Simpfendorfer
Centre for Sustainable Tropical Fisheries and Aquaculture
and School of Earth and Environmental Sciences, James
Cook University, Townsville, QLD 4811, Australia
e-mail: daniela.waltrick@my.jcu.edu.au

C. Awruch
School of Zoology, University of Tasmania, Hobart,
TAS 7001, Australia

One reproductive specialization that has been observed in a small number of viviparous elasmobranchs is embryonic diapause (Simpfendorfer 1992; Wyffels 2009), the temporary ceasing or retardation of development during any stage of embryogenesis, also known as discontinuous development or embryonic quiescence (Mead 1993a; Renfree and Shaw 2000). Within the elasmobranchs it was first hypothesized to occur in the Brazilian shovelnose shark *Rhinobatos horkelli* (Lessa 1982), and first conclusively demonstrated to occur in the Australian sharpnose shark *Rhizoprionodon taylori* (Simpfendorfer 1992). However, despite the knowledge of this phenomenon over several decades, it remains poorly identified and studied. The purpose of this review was to synthesize information available on the occurrence of embryonic diapause in elasmobranchs, examine the implications of diapause for life histories, construct a hypothesis of how it is controlled, and identify future areas where research is needed to improve the base of knowledge.

Embryonic diapause in vertebrates

Diapause has been reported in all vertebrate classes in a number of species within unrelated taxa, e.g. mammalia (Desmarais et al. 2004), reptilia (Ewert 2004; Jones and Guillette 1982), osteichthyes (Podrabsky and Hand 1999) and chondrichthyes (Wyffels 2009; Simpfendorfer 1992). This wide distribution amongst disparate taxa implies that embryonic diapause originated independently within each group during evolution (Lopes et al. 2004; Mead 1993a) and suggests it is an advantageous strategy across a wide range of species and life histories, and that the broader vertebrate reproductive system must be amenable to allow this adaptation to readily evolve.

Embryonic diapause has been best studied in mammals, and much of the information about diapause comes from this taxa. Within mammals, delayed implantation occurs when embryonic development is arrested prior to implantation of the embryo into the uterine wall (Mead 1993a) and has been classified in two separate types. Firstly, facultative diapause which is dependent on seasonal changes in the environment (e.g. food availability) and external stimuli (e.g. stress of lactation, deprivation of food and/or water) that may cause the onset of diapause, and thus results in a diapause period of variable length. In mammals, this

trait is known to occur in rodents, insectivores and marsupials (Lopes et al. 2004; Mead 1993a). The second form is obligate diapause, which occurs regularly at a specific stage of development and for a set period in every generation of a given species in spite of environmental conditions. This type of diapause is observed in species from a number of mammalian groups including mustelids, bears, pinnipeds, marsupials and some bats (Bleier 1971; Lopes et al. 2004; Mead 1993a).

Reptiles are the only egg layers within the higher vertebrates (mammals, reptiles and birds) to display embryonic diapause. Reptilian diapause occurs in several viviparous lizards (Chamaeleonidae and Gekkonidae) and freshwater turtles in which development is arrested at gastrula stage (Ewert 2004). Diapause may occur prior to oviposition (Shanbhag et al. 2003), subsequent to oviposition (Kennett et al. 1993; Andrews 2005) or even remain in diapause from pre-oviposition until after eggs have been laid (Booth 2002). In addition, some viviparous lizards prolong gestation after the completion of embryonic development, possibly awaiting better environmental conditions to guarantee the survival of the young (Atkins et al. 2007; Cree and Guillette 1995; Girling et al. 2002). Within this group, external stimuli, especially temperature and rainfall, play an essential role in the onset, maintenance and termination of diapause (Andrews 2005).

Embryonic diapause also occurs in some bony fishes with annual life cycles inhabiting temporary aquatic habitats, such as numerous species of killifish (Cypripodiformes) (Wourms 1972; Podrabsky et al. 2010). Seasonal drying of these habitats kills all adult and juvenile forms and, until the next rainy season, the population exists only in the egg stage, which undergoes diapause while embedded in the sediment (Hand and Podrabsky 2000; Wourms 1972). The hatching of the eggs occurs several months later, on the return of the rainy season, when embryos are released from diapause and the life cycle proceeds (Hand and Podrabsky 2000; Mead 1993a; Wourms 1972). The type of arrest may be facultative or obligate, depending on the fish genera and stage of development (Wourms 1972). The mechanisms controlling diapause are understudied in this group but may involve several environmental cues in addition to the presence of water, including photoperiod (Podrabsky and Hand 1999) and temperature (Matias and Markofsky 1978; Podrabsky and Hand 1999).

Embryonic diapause in elasmobranchs

Rhinobatos horkelli was the first elasmobranch species described with embryonic diapause as a possible reproductive strategy (Lessa 1982). Studying the embryonic development of this species, the author divided the gestation cycle in two distinct stages: a period of lethargy which extends over 9 months after fertilization of the eggs, where no macroscopic signs were observed for development of the uterine eggs (the embryonic diapause period); and a second period of 3 months of normal embryonic development during the summer. The author hypothesized that, although it was the first report of embryonic diapause in an elasmobranch, this phenomenon could not be exclusive to *R. horkelli* amongst this group. This conclusion was corroborated by subsequent studies by Simpfendorfer (1992) and Morris (1999) in which diapause has been positively identified in *Rhizoprionodon taylori* and *Dasyatis say* respectively.

Embryonic diapause in the elasmobranchs has been identified by the occurrence of fertilized eggs without visible embryos during extended periods (months) within populations with synchronous seasonal reproductive cycles (Wyffels 2009). Techniques such as histology and scanning electron microscopy have been employed to demonstrate the existence of diapausing elasmobranch embryos and the stage of their arrest (Simpfendorfer 1992; Morris 1999; Wyffels 2009). For species where these techniques have not been employed the presence of fertilized eggs in the uteri for extended time periods (Fig. 1) has been used to indicate the likely existence of diapause. This

phenomena, however, has not yet been found in asynchronous species, and would presumably be more difficult to determine due to the inconsistent embryonic developmental stages among specimens at each given time of the year, which could potentially obscure long periods of arrested development. The assessment of diapause in these species would be possible through serial assessment of individuals throughout pregnancy, perhaps using a non-destructive method such as ultrasonography (Daly et al. 2007; Carrier et al. 2003). Nevertheless, the likelihood of an asynchronous species having diapause is presumably low given that diapause would take away any seasonal advantages that asynchronous reproduction may provide to the species.

Obligate embryonic diapause has only been confirmed in two species of elasmobranch, but there is evidence for its occurrence in as many as 16 species: 14 batoids from two orders and five families, and two selachians from two orders and two families (Table 1). There is no evidence for facultative embryonic diapause in elasmobranchs. Simpfendorfer (1992) and Morris (1999) used histology to confirm diapause in *Rhizoprionodon taylori* and *Dasyatis say*, respectively. In both species, development was arrested at the blastodisc stage (Fig. 2) for a period of approximately nine (*D. say*) and seven (*R. taylori*) months before a short period of active development. Wyffels (2009) also confirmed diapause in *D. say* using scanning electron microscopy.

Diapause is spread throughout elasmobranch taxa and can exist in a wide variety of reproductive modes. All elasmobranchs with embryonic diapause (confirmed

Fig. 1 Relationship between embryo length and gestation time of Australian sharpnose shark *Rhizoprionodon taylori*. The stages of embryonic development are indicated as: stage I—diapausing fecundated oocytes; stage II—macroscopically visible embryo; and free embryos within the mother’s uterus (adapted from Simpfendorfer, 1992)

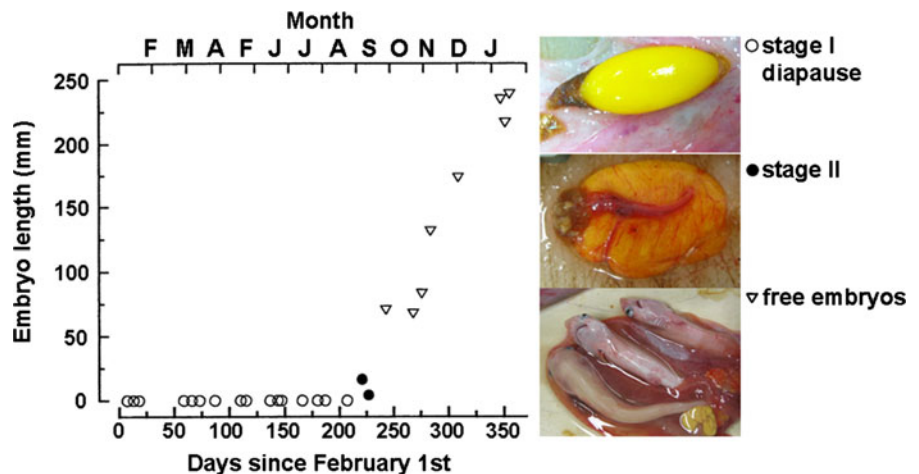


Table 1 Elasmobranch species in which embryonic diapause is classified as: confirmed (entire reproductive cycle have been studied, yolky ova have been observed for extended periods of time and histology was performed to confirm its developmental

stage) or probable (although yolky ova have been observed during extended periods of time no confirmation technique was performed)

Taxon	Species	Diapause Duration (months)	Active development (months)	Status	Reference
Order Myliobatiformes					
Dasyatidae	<i>Dasyatis say</i>	9–10	~2	Confirmed	Snelson et al. (1989); Morris (1999)
	<i>Dasyatis brevis</i>	9, 5–10	2–2, 5	Probable	Melendez (1997)
Myliobatidae	<i>Aetobatus flagellum</i>	9	~3	Probable	Yamaguchi (2006)
Urolophidae	<i>Trygonoptera personata</i>	5	5	Probable	White et al. (2002)
	<i>Trygonoptera imitata</i>	5–8	4–6	Probable	Trinnie et al. (2009)
Order Rhinobatiformes					
Rhinobatidae	<i>Rhinobatos cemiculus</i>	~4	~8	Probable	Seck et al. (2004)
	<i>Rhinobatos horkelli</i>	~9	3	Probable	Lessa (1982)
	<i>Rhinobatos hynnicephalus</i>	9–10	2–3	Probable	Kume et al. (2009); Wenbin and Shuyuan (1993)
	<i>Rhinobatos percellens</i>	4	8	Probable	Grijalba-Bendeck et al. (2008)
	<i>Rhinobatos productus</i>	~8, 5	3–4	Probable	Hoffmann (2007); Márquez-Farías (2007)
	<i>Rhinobatos rhinobatos</i>	8–9	3–4	Probable	Enajjar et al. (2008); Abdel-Aziz et al. (1993)
	<i>Zapteryx exasperata</i>	6	5	Probable	Blanco-Parra et al. (2009)
	<i>Trygonorrhina dumerilii</i>	7–8	4–5	Probable	Marshall et al. (2007)
Platyrrhinidae	<i>Platyrrhinidae sinensis</i>	?	?	Probable	Yamaguchi and Kume (2009)
Order Carcharhiniformes					
Carcharhinidae	<i>Rhizoprionodon taylori</i>	7	~5	Confirmed	Simpfendorfer (1992)
Order Pristiophoriformes					
Pristiophoridae	<i>Pristiophorus nudipinnis</i>	7–10	12–15	Probable	Walker and Hudson (1999)

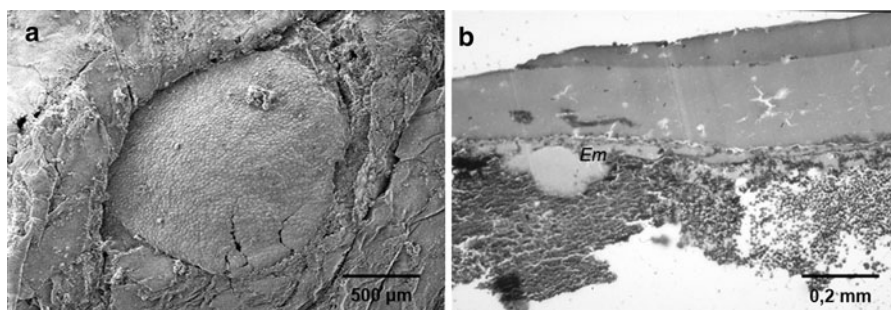


Fig. 2 Sections through the diapausing blastodiscs of *Dasyatis say* (a) and *Rhizoprionodon taylori* (b). Unpublished photos by Wyffels (a) and Simpfendorfer (b)

or with strong evidence of its occurrence) are lecithotrophic (e.g. *Rhinobatos horkelli*, *Trygonorrhina dumerilii*) or matrotrophic aplacental species (e.g. *Dasyatis*

say, *Trygonoptera imitata*). The only exception is *R. taylori*, which is matrotrophic placental. The reproductive cycle within all diapausing species lasts

approximately 12 months, except for *Pristiophorus nudipinnis* which has a 2 year cycle (Walker and Hudson 1999).

Since embryonic diapause is not a rule among all members of the same taxa, the reproductive trait has likely evolved independently in each species. There are at least two possible exceptions to this. Firstly, embryonic diapause occurs in at least six species of the genus *Rhinobatos* (Table 1), suggesting that it may have been an ancestral condition within the genus. However, it does not occur in all species in this genus, which may be due to loss of diapause in some branches. However, the genus is undergoing taxonomic revision, so the phylogeny of the species currently in this genus is uncertain. Specifically, embryonic diapause has not been reported in species from the genus *Glaucostegus* that now contains some of the species that were formally part of *Rhinobatos* (Last and Stevens 2009). If embryonic diapause has evolved separately within each of the rhinobatids then this genus would appear to have a pre-disposition to easily evolving this trait. The second possible exception is within the two species of *Dasyatis*. Both *D. brevis* (Melendez 1997) and *D. say* (Morris 1999) have been reported to employ embryonic diapause. These are sister species that are believed to have separated after the formation of the Isthmus of Panama 3 million years ago (Rosenberger 2001), suggesting that embryonic diapause was an ancestral trait that has existed more than 3 million years ago.

Ovulation and fertilization in elasmobranch species often take place immediately after mating (Callard et al. 2005). It is well documented in viviparous species that, as the oocytes pass through the oviducal gland and into the uterus, the eggs are fertilized and then enclosed in a membranous egg case (Carrier et al. 2004; Wourms 1977). Where it has been examined in diapausing elasmobranchs, embryogenesis is arrested at the blastodisc stage and preserved in the uterus for periods from four to 10 months (Table 1). The ovulated oocytes are encased in a gelatinous olive-green (Abdel-Aziz et al. 1993), delicate brown membranous (Marshall et al. 2007; Trinnie et al. 2009; White et al. 2002; Kume et al. 2009) or keratinized case (Marshall et al. 2007) assumed to be impervious to sperm (White et al. 2002) due to its thick, multilayered nature and the absence of pores and channels (Morris 1999), indicating that delayed fertilization is not a possible explanation for the observed state of the uterine eggs.

Generally speaking, embryonic diapause in elasmobranchs lasts for longer periods than the active development of the embryos. Within the species examined, embryonic diapause lasts up to five times longer than active development in at least 10 species, however the opposite has been observed in three species where diapause is up to two times shorter than active development (Table 1). Embryonic diapause in elasmobranchs has independently evolved as an obligate state in a number of species with a range of reproductive strategies, suggesting that its control may occur via a number of different mechanisms.

Possible control mechanisms in elasmobranchs

The arrest of embryonic development within distinct groups of animals occurs in three phases: (1) entry into diapause and the arrest of cell division (2) maintenance and (3) reactivation of development after the diapausing period (Renfree and Shaw 2000). Embryonic diapause starts when environmental conditions are optimal and would provide normal metabolism and development; in general, it precedes the commencement of an environmental change such as winter or the dry season (Hand and Podrabsky 2000). Environmental cues provide stimuli to arrest and restart the embryonic development in diapausing species, however, these factors are species-specific and vary widely (Morris 1999).

While the control mechanisms of embryonic diapause within elasmobranchs remain uninvestigated, other vertebrate taxa in which diapause has been further studied provide clues to understand the process in this group. Chang (1968) provided evidence that the uterine milieu, and not the embryo genetic programming, is the key to maintain mammalian diapause. In his experiments, reciprocal egg transfer between ferrets (non-diapausing) and minks (diapausing) resulted in the delayed implantation of the ferrets but not the minks. Similarly, dormant blastocysts of rodents become active when transferred into an active uterus (Dickmann and De Feo 1967).

Although the control of embryonic diapause in mammals is under maternal control (Lopes et al. 2004), the endocrine mechanisms vary widely among species. The main hormones associated with the termination of diapause in several species are prolactin and progesterone. Pituitary secretions of prolactin

terminate diapause and induce implantation in the mink (Henningsen et al. 2008; Fasano et al. 1989), however a single injection of cabergoline, a synthetic dopamine agonist that suppresses prolactin secretion, is sufficient to induce the termination of diapause and implantation in tammars (Hearn et al. 1998). Progesterone, on the other hand, is required for successful implantation in ferrets (Manire et al. 2004), mink (McMillan 2007), and the Australian sea lion (Podrabsky et al. 2010).

Secretions of prolactin and progesterone are closely related. Prolactin secretions act to restrain the growth and secretions of the corpora lutea (Sorbera and Callard 1995; Fasano et al. 1989), a temporary endocrine gland source of steroid hormones, mainly progesterone (Martin and Ferreira 2009; Mead 1993a; Koob and Callard 1999). Although the presence of prolactin is known in elasmobranchs (Claes and Mallefet 2009, 2010; Henningsen 1998), its roles remain unknown within this group.

The elasmobranch ovary (Gelsleichter 2004) and corpora lutea (Tsang and Callard 1987) have been described as a source of progesterone. Surges of this steroid in viviparous female elasmobranchs have been associated with the inhibition of follicular development (Koob and Callard 1999; Gelsleichter 2004; Mull et al. 2010) and the sexual maturation process

(Rasmussen and Gruber 1993). In pregnant animals it appears to be important for implantation (Sorbera and Callard 1995; Manire et al. 1995), inhibition of myometrial contractions—maintaining a quiescent uterus in early pregnancy—(Sorbera and Callard 1995) and parturition events (Snelson et al. 1997). Although levels of progesterone and other steroids have not been studied throughout the reproductive cycle of any diapausing elasmobranch, the presence of corpora lutea during the early stages of pregnancy suggests that progesterone affects the control of this reproductive trait (Dodd 1972; Tsang and Callard 1987).

Assuming that hormonal control maintains elasmobranch embryos in diapause, Simpfendorfer (1993) reported that *Rhizoprionodon taylori* possessed large and active corpora lutea in ovaries during the diapause period. However, the presence of corpora lutea have not been reported for other diapausing elasmobranchs such as *Dasyatis say* (Morris 1999; Snelson et al. 1989), suggesting the potential for the existence of multiple control mechanisms among different elasmobranchs or simply that they were present but not observed.

With the knowledge of observed reproductive structures in *Rhizoprionodon taylori* and the presumption that corpora lutea and progesterone are directly

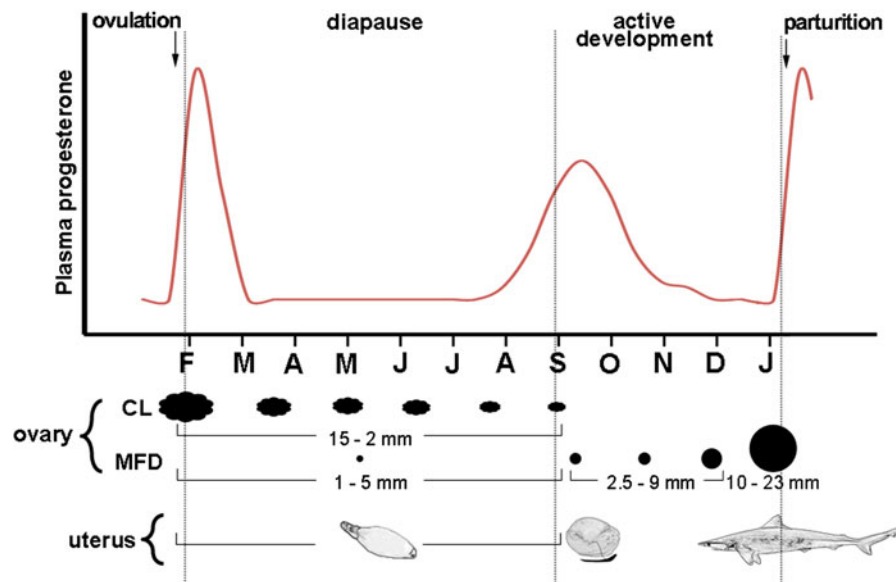


Fig. 3 Proposed circulating levels of progesterone throughout the reproductive cycle of a female *Rhizoprionodon taylori*. Corpora lutea (CL) and the maximum follicular diameter (MFD)

in the ovary and the embryonic stages of development are represented as observed by Simpfendorfer (1992) and Waltrick (unpublished data)

involved in the control of embryonic diapause, we propose a hypothesis for the control mechanisms in this species (Fig. 3). The presence of large and active corpora lutea during the early stages of pregnancy suggests that progesterone is required to arrest embryonic development. The size of this temporary gland is substantially reduced during the first month of diapause and gradually degenerates until the end of this stage, which is possibly associated with a decline in progesterone. However, a second peak in progesterone levels is expected towards the end of diapause in order to induce the active development of the young and induce implantation. At this stage, it is likely that the uterus becomes the main source of this steroid, since the corpora lutea is degenerating and its size very reduced or absent.

External stimuli such as photoperiod and temperature play an important role in the onset and termination of diapause in mammals, reptiles and bony fishes (Renfree and Shaw 2000; Wourms 1972; Hand and Podrabsky 2000; Lopes et al. 2004); changes in key environmental components may trigger endocrine reactions in the mother that will control the embryonic development (Wyffels 2009; Lopes et al. 2004). Amongst the diapausing sharks and rays, embryogenesis is usually arrested during late summer or autumn and terminated in the following spring or summer (e.g. Melendez 1997; Yamaguchi 2006; Kume et al. 2009; Simpfendorfer 1992), thus displaying a fast active development when temperatures are higher. As in other taxa, it is likely that environmental changes, such as day length (Renfree and Shaw 2000), play a role in the timing of diapause events acting as a trigger to the mothers endocrine system that will control embryonic diapause in elasmobranchs.

Benefits of diapause for elasmobranchs

Embryonic diapause allows the time between fertilization and parturition to be prolonged, possibly providing newborns with higher quality environmental conditions at the start of life (Mead 1993b; Renfree and Shaw 2000). It was suggested by Simpfendorfer (1992) that diapause allows *Rhizoprionodon taylori* to be born when sea temperature is at the highest so higher growth rates can be achieved, reducing the risk of predation (Branstetter 1990). Conversely, parturition in *Trygonoptera personata* (White et al. 2002) and

Trygonorrhina dumerilii (Marshall et al. 2007) occurs when sea temperature is declining towards its minimum, when the neonates' main food items are abundant and there might be less competition for food or space, as well as lower risk of predation (Marshall et al. 2007). Independent of the season of the year it may be that embryonic diapause has evolved as a mechanism that guarantees that parturition will occur when newborns are more likely to succeed through the early stages of life and reach maturity. While these authors have speculated on various reasons for diapause in elasmobranchs, there has been no rigorous testing of these hypotheses.

Embryonic diapause in *Rhizoprionodon taylori* has possibly evolved along with a reduction in the size at birth and a relative increase in litter size (Simpfendorfer 1992). In essence, a trade off between the size at birth and the litter size—probably imposed by the restricted space within the mother during internal development—could have allowed a reduction in the developmental time and thus allowing for a period of embryonic diapause. Simpfendorfer (1992) found evidence of other possible advantages of diapause by looking at trends in litter size and birth size of carcharhinid sharks (Fig. 4). *R. taylori* appeared to be an outlier among the family; young were proportionally smaller, and litter size was proportionally higher than average. Embryonic diapause may therefore relax some of the constraints of the elasmobranch reproductive system and allow species to pursue alternative strategies. However, this pattern does not match that observed in *T. personata* (White et al. 2002), as this species gives birth to a single and relatively large young. Therefore, it is possible that this species has evolved a larger young, as opposed to large litter size, in order to reduce predation.

Hypotheses in the literature have looked at embryonic diapause from the aspect of how the timing of birth will benefit the young (e.g. more food and less predators; Marshall et al. 2007) and sometimes in terms of life history traits (e.g. increased litter size in the *R. taylori*; Simpfendorfer 1992). However, the evolution of a period of embryonic diapause in elasmobranchs from the perspective of mothers' physiology has not yet been considered. It is important for females to have the breeding cycle at a favorable time of the year (Sandell 1990); a delay in the embryonic development could possibly allow females to restore/meet their energy requirements after events

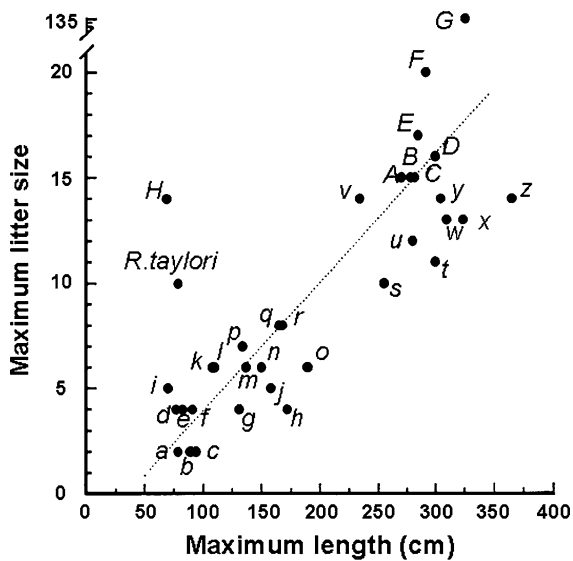


Fig. 4 Relationship between maximum length and maximum litter size for species in the family Carcharhinidae. Data for *Rhizoprionodon taylori* are from Simpfendorfer (1992), all other data are from Compagno (1984). Dotted line is from Compagno's equation: litter size = $-2.2 + (0.061 \times \text{maximum length})$. (a) *Rhizoprionodon taylori* (Compagno's estimate), (b) *Carcharhinus macroti*, (c) *C. sealei*, (d) *R. landan*, (e) *C. dussumieri*, (f) *Loxodon macrorhinus*, (g) *C. melanopterus*, (h) *C. wheeleri*, (i) *R. oligolinx*, (j) *Triaenodon obesus*, (k) *R. porosus*, (l) *R. terraenovae*, (m) *C. acronotus*, (n) *C. sorrah*, (o) *C. amblyrhynchus* and *C. isodon*, (p) *C. porosus*, (q) *R. acutus*, (r) *Lamiopsis temmincki*, (s) *C. limbatus*, (t) *C. albimarginatus*, (u) *C. signatus*, (v) *C. plumbeus*, (w) *Negaprion acutidens*, (x) *C. leucas*, (y) *C. falctformis*, (z) *C. obscurus*, (A) *C. longimanus*, (B) *C. brevipinna*, (C) *C. altimus*, (D) *C. galapagensis*, (E) *N. brevirostris*, (F) *C. brachyurus*, (G) *Prionace glauca*, (H) *Scoliodon laticaudus*. (adapted from Simpfendorfer 1992)

of birth, ovulation and mating. Sandell (1990) hypothesizes that a delay in seasonally breeding mammals has evolved to maximize male competition or female choice. In this hypothesis, mating season would coincide with a seasonal gathering of otherwise vagrant females and at a time with high quality resources easily available. In certain situations, these conditions are met by mating early and a delay in development would increase female fitness (Sandell 1990).

Simpfendorfer (1992) proposed that other alternate strategies adopted by viviparous elasmobranchs are functionally similar to embryonic diapause (i.e. they provide a shorter development period in a annual reproductive cycle). Delayed fertilization (e.g. *Chiloscyllium plagiosum*; Guillette et al. 1991) and

reduced gestation period (e.g. *Sphyrna tiburo*; Chen and Liu 2006) respectively, separate mating from the beginning of embryogenesis and parturition from mating. The reasons why embryonic diapause has evolved as opposed to other alternate modes is unknown. It is possible that diapause is involved with the timing of these events (embryogenesis, mating and parturition) and provides some behavioral or physiological advantages for individuals, especially females. In some species, aggregation of males and females only occurs during short periods of mating events and embryonic diapause could have evolved to extend gestation allowing parturition and mating to be synchronized (Kyne and Bennett 2002). However, results reported by Kume et al. (2009) do not provide any evidence of sex segregation in the population of *Rhinobatos hinnycephalus* in Japan. Although many hypotheses have been raised regarding the benefits a temporary arrest of embryonic development might confer to the species, none of them has been tested. Moreover, limited information makes it difficult to evaluate how this trait actually benefits the species in which it occurs.

Future research directions

Rigorous testing of current hypothesis on why embryonic diapause has evolved as a reproductive trait and what determines the optimal timing for reproduction are needed, but an understanding of the life-history parameters also need to be determined. Since the advantages of diapause are difficult to pinpoint, and likely to be species specific, there is also the need to better understand the basic biology of these animals. A number of sharks and rays have been described with this reproductive trait, however further studies are needed to confirm the absence of embryonic development during extended diapause periods. Very little is known about the control mechanisms of diapausing species. The correlation of the levels of circulating hormones and reproductive structure throughout the reproductive cycle will provide a better understanding of this trait among elasmobranchs.

A complete understanding of reproductive events is crucial to assist in the formulation of management strategies, therefore such knowledge will be particularly important for species taken in fisheries (e.g. *Pristiophorus nudipinnis* and *Trygonoptera fasciata*,

Bensley et al. 2009; *Rhinobatos horkelii*, IBAMA 2008; *Rhizoprionodon taylori*, Harry et al. 2011). Moreover, understanding the benefits and uses of each reproductive trait is an important step towards a more realistic evaluation of elasmobranch populations.

Conclusion

Embryonic diapause is a reproductive strategy widespread among vertebrate taxa and adopted by at least two species of elasmobranchs, and likely in at least a fourteen others. The reproductive cycles and the mechanisms involved in the control of the reproductive trait are poorly understood in elasmobranchs. However, as in other vertebrates, it appears that by delaying development and extending the gestation period, diapause allows the young to be born in the most favourable conditions for survival or enhances reproductive output. It is also possible that a period of embryonic diapause will benefit species by allowing reproductive events to be synchronized (parturition and mating) and/or prolonged (fertilization and parturition). There are still many questions that remain unanswered concerning the knowledge on the biology of most diapausing species but it is clear that species benefit differently from this reproductive trait. As in other vertebrates, it is likely that environmental cues and hormones (especially progesterone and prolactin) are involved in the control of diapause in elasmobranchs, however rigorous testing of current hypothesis remains to be carried out.

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