Application of life history strategies in managing sharks, rays and skates

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Abstract

Sharks, rays and skates belong to subclass Elasmobranchii in Class Chondrichthyes. They have diversified reproductive life history strategies: oviparous, ovoviviparous, and viviparous. The objective in this study is to explore if they have distinct strategies to adapt for different reproductive modes so as to management them by reproductive patterns. In this study, up to eight life history traits (***LHT***) were extracted for each species. They are asymptotic total length ($\mathbf{L_X}$), body length at maturity ($\mathbf{L_m}$), offspring size ($\mathbf{L_b}$), longevity ($\mathbf{A_X}$), age at maturity ($\mathbf{A_m}$), von Bertalanffy growth coefficient (**k**), instantaneous natural mortality (**M**), and fecundity (**f**). These ***LHT*** were analyzed individually, correlatively, and collectively. There were 448 Elasmobranchii species for reproduction analyses. The new 3 factors, namely time, size and k&M factors, in principal component analysis from selected 6 ***LHT*** can explain 98.6% of the total variance. Discriminate analysis was then utilized to verify reproductive modes. There were 71 to 95% correct classification were obtained in Elasmobranchii and Rajiformes among oviparous, ovoviviparous, and viviparous. These statistically significant reproductive life history patterns in shark, skate and ray can serve as basis for multi-species fisheries management and also may make up for rare and unknown species for conservation measures.

Key words: shark, ray, skate, life history, oviparous, ovoviviparous, and viviparous

Introduction

Background

Life cycle in fishes is from birth to death, including growth and reproduction (Stearns, 1992). Species have the unique life history strategies in the ecosystem and all evolutions depend on “survival of the fittest”. Cartilaginous fishes are possibly one of the most successful of all fishes in waters. The earliest evidence of Chondrichthyes in the fossil record is from the Devonian**,** from 350 to 400 million years ago, cartilaginous fishes have evolved continually to adapt a variant environment; they play the important part of vertebrate life history evolution (Compagno, 1990).

The cartilaginous fishes constitute Class Chondrichthyes and classified into two subclasses, the Elasmobranchii and the Holocephali. The Elasmobranchii are further divided into selachians and batoids, and the Holocephali are named chimaeras or ratfishes (Springer and Gold, 1989). There are approximate 1000 species in cartilaginous fishes (Last, 2007). Their taxonomy was not fully understood and there are some disagreements among taxonomists as to their phylogeny (Last and Stevens, 1994). Their classification is depended upon external and internal structure. Compagno (1990) defined the chondrichthyans in adopted alternative life history styles so as to exploit their environment. Selachians are the modern sharks, and batoids consist of two dominant groups as rays and skates. Hence batoids are highly modified and diversified (Compagno, 2002). The term “sharks, rays and skates” has been used broadly in many texts. The body shapes are quite uniquely different as shark, skate and ray (Last and Stevens, 1994).

In order to rival the advanced tetrapods, there are three main reproductive patterns of embryonic development in chondrichthyans, such as oviparity, ovoviviparity and viviparity. The earlier suggestion was that egg-laying was ancestral in shark, rays and ratfishes (Wourms, 1977). Dulvy and Reynolds (1997) evidenced for one to two reversals from live bearing to egg laying. The evolution of live bearing in elasmobranchs was correlated with predicted increases in offspring size and adult size (Dulvy and Reynolds, 1997). The young are also born at relatively larger size, reducing the number of potential predators and competitors while increasing the number of potential prey, thus enhancing their chances of survival (Castro, 1983). Actuality, life history strategies from reproductive modes in cartilaginous fishes are more diversified than that of bony fishes. Therefore, these distinctive reproductive modes can likely be classified into significant life history patterns that may be detected from the life history traits such as vital statistics in growth and reproduction.

General descriptions of the cartilaginous fishes

The cartilaginous fishes comprise almost 1170 extant species are known (Last, 2007). There have eight orders belong to Selachians (Froses, 2004) (Fig.1). The major order was the Hexanchiformes (frilled sharks) – they are world-wide species with ovoviviparous reproduction of two families; Squaliformes (dogfish sharks) – they have varied sizes and all are ovoviviparous reproduction; Pristiophoriformes (saw sharks) – they have two sensory barbells attached on the underside of the rostrum, and ovoviviparous reproduction; Squatiniformes (angel sharks) – they are raylike sharks having flattened bodies and ovoviviparous reproduction; Heterodontiformes (bullhead sharks) – they are characterized by big heads with heavy ridges over the eyes and oviparous reproduction; Lamniformes (mackerel sharks) – they include the maximum size sharks and ovoviviparous reproduction; Orectolobiformes (carpet sharks), – they include the world's biggest living fish the whale shark (*Rhincodon typus*) in ovoviviparous and oviparous reproduction; and the final Carcharhiniformes (ground sharks) – they have a large number of species having three reproductive modes: oviparous, ovoviviparous and viviparous.

The classification of batoids was diversified in literatures among researchers. This study follows FishBase in dividing batoids into three orders: Pristiformes (sawfishes) – they lack the barbells and have ovoviviparous reproduction; Torpediniformes (torpedo, electric ray) –they are all capable of delivering electric shocks and have ovoviviparous reproduction; and last Rajiformes (true rays) – they have diversified classifications for a long time, including ten families with ovoviviparous and oviparous reproductive modes (Compagno, 1999; Walker, 2005). The number of Batoid species has outnumbered all other cartilaginous fishes (Compagno, 2002).

Cartilaginous fishes have clear characteristic to discriminate from bony fishes, like five to seven pairs of gill slits for respiration, placoid scales for protection, no swimming bladder with large liver to maintain buoyancy, renewable teeth for feeding, internal fertilization to protect the young, etc. The body form of sharks, rays and skates mostly reflects their way of life, there are many variations in their body form (Last and Stevens, 1994).

The reproductive modes in cartilaginous fishes are more diversified than that of bony fishes. Furthermore, cartilaginous fishes have three basic methods of reproduction: oviparous, ovoviviparous and viviparous. Oviparous species lay the thick eggs that attach to rocks by tendrils. In ovoviviparous species, the embryo develops on the egg's yolk sac for sustenance in an egg within the female's body. In viviparous species, fetus get nourish in uterus via a placenta and females give birth to live young (Springer and Gold, 1989).

Objectives and significances of this research

Many sharks are rare or have a limited habitat and geographic distribution. They are often caught as by catch. Consequently, they are largely ignored by fisheries managers and may be under considerable risk of extinction from human factors (Compagno, 2000). To synthesize all the interrelated factors and develop life history patterns of elasmobranches is necessary; we can then manage and conserve the shark resources effectively.

In this study, we collect worldwide the biological traits for all available elasmobranch species so as to explore the possible life history patterns among reproductive strategies.

According to life history strategies, we can reliably estimate the missing data, or rare species data from statistically significant patterns. Furthermore, life history strategies can help to set up fisheries management and conservation policy based upon patterns instead of single species.

Materials and Methods

Data collecting

The life history traits from this study were collected from the FishBase website (Froese and Pauly, 2004) and others were collected from journal papers and/or book publications. In other words, life history traits published from conference proceedings and research documents are not included except they are later published from peer reviewed journals and books. In some reports, the values were presented by a range, so the midpoints of the ranges were taken. If multiple values from different literatures were collected for the same species, we then take an average value.

Life history traits (*LHT*)

In this study, up to 8 ***LHT*** were extracted for each species. $\mathbf{L_X}$ (cm) is the asymptotic total length from the von Bertalanffy growth equation (VBGE) (Beverton and Holt 1957); $\mathbf{L_m}$ (cm) is the body (total) length at mature; $\mathbf{L_b}$ (cm) is the offspring size, (i.e. the body length at birth); $\mathbf{A_X}$ (yr) is the approximate maximum age or the longevity that species would reach; $\mathbf{A_m}$ (yr) is the average length at which species mature for the first time; **k** is the von Bertalanffy growth coefficient, expressing the rate at the asymptotic length is approached; **M** is the instantaneous rate of natural mortality; **f** is fecundity, the average number of litter size per once reproduction.

Correlation analysis

A correlation analysis framework was used to find the correlation relationship between two variables and interrelated intensity. The Pearson correlation coefficient (r) was used to analyze correlations between pairs of life history parameters (Cortés, 2000). We are checking the correlation between six ***LHT***: the asymptotic length ($\mathbf{L_X}$), offspring size ($\mathbf{L_b}$), litter size (**f**), longevity ($\mathbf{A_X}$), growth coefficient (**k**), and natural mortality (**M**). The group variables are either reproductive modes (oviparous, ovoviviparous, or viviparous) or phylogenetic taxa. The statistical analyses are using STATISTICA (7) programs (StatSoft, 2004).

Principal component analysis (PCA)

Principal component analysis (PCA) is used to analyze similarities among species. The advantage of this analysis can simplify various traits into less number of factors by extracting major independent factors base on high correlation loadings. This statistical analysis is based on SYSTA (9) programs (SYSTAT, 2002).

Before analysis, the length traits such as $\mathbf{L_X}$, $\mathbf{L_m}$, and $\mathbf{L_b}$ were transformed by logarithm to stabilize and linearize the response of the traits for their normal distribution.

Discriminate analysis

LHT can be utilized to get the new principal factors from PCA so as to display the types of reproduction patterns. The outliers of each group are then picked out by discriminate analysis. The potential patterns are classified correctly by the jackknifed classification matrix. Discriminate analysis is repeatedly tested in different combinations of traits. It is applied to confirm the predict reproductive patterns in Elasmobranchii. This analysis is using SYSTA (9) programs (SYSTAT, 2002).

Results

Individual life history traits

There were 990 Elasmobranchii fishes collected in this study with 435 species in sharks and 555 species in Batoids. The sample size, mean values and 95% confidence interval for all 8 ***LHT*** in each order were displayed in Table 2.

In summary, sharks had **L_X** with a mean value of 139.4 cm (n=396 species); **L_m** 64.4 cm (396); **L_b** 35.5 cm (281); **A_X** 19.1 yrs (283); **A_m** 3.9 yrs (283); **f** 9.6 (281); **k** 0.2 (392); **M** 0.3 (391). Moreover, batoids had **L_X** with a mean value of 101.9 cm (295); **L_m** 51.1 cm (295); **L_b** 20.8 cm (42); **A_X** 19.3 yrs (266); **A_m** 4.2 yrs (266); **f** 3.6 (178); **k** 0.2 (266); **M** 0.4 (266).

The offspring sizes (**L_b**) and the litter sizes (**f**) were difficult to find, particularly for oviparous species due to limited reporting about the **L_b** in egg cases (Table 2). After calculating with 8 ***LHT*** in various combinations for reproductive modes in **PCA** analysis, we decided to compromise using only 6 ***LHT*** (**L_X**, **L_m**, **A_X**, **A_m**, **k** and **M)** for having larger sample sizes. We then verified the reproductive life history patterns with by correctness from the jackknifed classification matrix. All results were presented in Table 3; interestingly the total variance explained of 6 major ***LHT*** can be up to 95%.

Life history correlations

In ovoviviparous, they had significant correlations between **L_X** and other five ***LHT***. There are significant correlations either between **L_X** and **f** ($r=0.54$, $p<0.001$, $n=130$) or between **A_X** and **f**($r=0.26$, $p<0.001$, $n=92$), however, no correlations between **f** and either **L_b, k, M** ($r=0.09$, $p=0.38$, $n=100$; $r= -0.13$, $p=0.22$, $n=92$ and $r=-0.23$, $p=0.11$, $n = 126$). Unlike the other elasmobranches, the whale shark (*Rhincodon typs*) and Pacific sleeper shark (*Somniosus pacificus*) had very large fecundity that was over 300.

In oviparous, they had significant correlations between **L_X** and other ***LHT***, except with **f** ($r=-0.14$, $p=0.86$, $n = 241$). Almost all oviparous fishes had mainly two egg cases or just one egg case per reproduction, regardless the body size for females.

There were high significant correlations between **L_X** and other traits. They had no correlations between **L_b**, **k** and **f** ($r=0.16$, $p=0.19$, $n=66$ and $r=-0.21$, $p=0.09$, $n=63$). Elasmobranchii fishes had slow growth, low mortality, and long longevity. There was a highly significant negative correlation between **A_X** and either **k**, **M** for all three reproductive modes.

L_b had significant correlation with **L_X** for all species, and therefore, further analyses in different reproductive patterns were performed in detail. Although the sample size (40 species out of 347 species) for oviparous was much less, it still had significant correlation ($r=0.65$, $p<0.001$, $n=40$). The **L_b** was longer in viviparous than in oviparous, because the females sharks transfer nourishment to the embryos that develop as fetus inside the females. The range of **L_b** was wide in ovoviviparous.

Fecundity **(f)** also had diversified correlations with **L_X** in different reproductive patterns. Significant correlations were found in ovoviviparous ($r=0.72$, $p<0.001$, $n=120$) and oviparous ($r=0.75$, $p<0.001$, $n=69$) patterns but not oviparous.

Insignificant correlations were found in ovoviviparous ($r=0.09$), $p=0.38$, $n=100$), in oviparous ($r=0.03$, $p=0.86$, $n=37$); and in viviparous ($r=0.16$, $p= 0.19$, $n=66$). Range of **f** in ovoviviparous pattern was wide and had the largest fecundity in whale shark and Pacific sleeper shark. They both had 300 litter sizes; however, their range of body sizes was quite a large difference since whale shark could grow over than 1400 cm body length whereas Pacific sleeper shark had only half of whale shark. Body sizes were likely to correlate with the size at length. Interestingly, the cartilaginous fishes seem reproduced large eggs or embryos, but still had low fecundity (Compagno, 1990).

Reproductive patterns among oviparous, ovoviviparous, and viviparous

Cartilaginous fishes had 3 reproductive modes. With 6 ***LHT***, PCA analysis for 448 Elasmobranchii species could explain a total of 98.62% variance (Table 3) by 3 independent factors, namely time (33.38%), size (34.59%) and k&M (30.66%) factors (Table 4). It had 71% correctness in jackknifed classification matrix, where ovoviviparous range covered both oviparous and viviparous (Fig. 2). PCA analysis for 240 shark species could get 95.79% of the total variance from the same 6 ***LHT*** with 3 independent factors, time (33.53%), size (34.21%) and k&M (31.72%) factors. There was 69% correctness in jackknifed classification matrix derived among reproductive patterns. Oviparous and viviparous had now been separated clearly (Fig. 3).

Furthermore, only order Carchariniformes had 3 reproductive modes, and therefore, it resulted in 99.4% of the total variance in 3 (time, 33.46%; size, 33.48% and k&M, 32.41%) factors from 181 species. This had 71% correctness in Jackknifed classification matrix that oviparous patterns could be separated from viviparous more obviously whereas the ovoviviparous pattern was scattered covering other two patterns (Fig. 4).

Batoids had two kind of reproductive strategies, ovoviviparous and oviparous strategies, and the most diversified group was the order Rajiformes. They had the same 3 size, time and k&M factors that could explain 97.7% of the total variance in 209 species. They had a very high 91% correctness in Jackknifed classification matrix in batoids (Fig. 5). Again, analysis was then conducted in order Rajiformes. It could explain 97% of the total variance in 187 species and had 95% correctness in jackknifed classification matrix. Because only the skates were ovoviviparous, and therefore, they could easily be separated into two reproductive patterns (Fig. 6).

Discussion

Significant life history strategies from life history traits

A life history strategy was defined as a complex pattern of co-evolved life history traits designed for a particular environment (Rochet, 2000). The Chondrichthyes underwent extreme and often bizarre evolutionary experimentation with a variety of body-types, old mating structures, and feeding specializations (Gruber, 2000). Wu et al. (2004) suggested that biodiversity covers every aspect of ecology and evolution, particularly finding patterns to interpret biodiversity. This was because life history strategy can display phylogeny (evolution), ecology, and ethology effects.

In this study, we had tried to use 6 life history traits (***LHT***) in studying 508 elasmobranch species and surprisingly explored 95% variance coverage. Additionally, life history traits could be reduced into 3 factors, namely size, time, and k&M factors. These morphological and reproductive patterns were then verified with jackknifed classification matrix.

Significant reproductive strategies among oviparous, viviparous and ovoviviparous

The reproductive strategies of elasmobranchs were much diversified than bony fishes. Bony fishes are mainly oviparous with external fertilization; they usually produce a great number of small eggs. This r- strategy would produce lots of unprotected eggs and later as larvae. The larvae have very high mortality due to predation but some of them may survive from predators if environment after incubating is favorable. In contrast, cartilaginous fishes produce fewer, larger eggs or young, and fertilized internally (Last and Stevens, 1994). Males have modified pelvic claspers, a specialized organ used in mating, used for transferring sperm into females.

Using 6 ***LHT,*** 448 elasmobranch species could be explained with 98% variation from principal component analysis. These 3 reproductive strategies on oviparous, viviparous and ovoviviparous could then be classified statistically with 71% correct classification.

Only order Carcharhiniformes have viviparous reproductive strategy. Goodwin et al. (2002) suggested that the transition from oviparous to viviparous possibly reflects a trade-off occurring when the benefits of increased offspring survival exceed the cost of reduced fecundity.

No significant correlation between length at birth and fecundity in three reproductive strategies

Correlations between body size, offspring length and fecundity are not consistent in elasmobranchs (Goodwin et al., 2002). From our result, $\mathbf{L_X}$ had significant correlation between $\mathbf{L_b}$ in three reproductive modes. The observed patterns of increasing litter and offspring size with increasing body size are influenced by the various reproductive modes present in sharks (Cortés, 2000). Unlike the other elasmobranches, the whale shark (*Rhincodon typs*) and Pacific sleeper shark (*Somniosus pacificus*) have a very large fecundity that is over 300 per reproduction. Our study also indicating that there were no significant correlation between $\mathbf{L_b}$ and **f** in three reproductive strategies. Body sizes are larger in viviparous species than in oviparous species, it may have facilitated the evolution of viviparity by reducing the vulnerability of the female during prolonged uterine retention of embryos (Shine, 1989). The trade-off between egg size and number, their model predict the evolution of an optimal egg size that maximizes maternal fitness (Einum and Fleming, 2000). As reported by Cortés (2000) that correlations were found for several reproductive life history traits vary with body size, there are significant correlation between variables except length at birth ($\mathbf{L_b}$) and fecundity (**f**) that having either low or insignificant correlations in any reproductive modes. Shifts in fecundity are apparently a minor factor in the evolution of reproductive styles in Chondrichthyans (Compagno, 1990).

Fisheries management and Conservation measures

Fishery managements are mainly targeted at r-strategy teleost fishes and usually assessed by single species. To management with K-strategy elasmobranchs should probably focus on reproductive capability (Smith et al. 1998) and strategies rather than maximized sustainable yield that based upon growth and death rate since elasmobranchs has very low growth (k) and death rate (M). Understanding their biology and knowing how to recognize these species is fundamental to their conservation (Last, 2007).

Shark populations around the world are harvested by industrial, artisanal, traditional, and recreational fishes (Walker, 1998). Assessing and managing resources according to life history strategies is probably a better approach in developing ecosystem approaches (King and McFarlane, 2003).

Our knowledge of life history traits of most species is still limited and beginning to gain insight into life history patterns shared by some species and the relationships among life history traits (Compagno, 1990; Cortés, 2000; Frisk et al. 2001; Cortés, 2004). Life history traits exhibit remarkable diversity, and, as in other taxa, this variation is more obvious at the interspecific level but can also be observed intraspecifically (Cortés, 2000). Then we can expect to understand and soundly mange chondrichthyans faunas (Last, 2007).

It's hard to define life history patterns for every species, because knowledge and understanding of biological traits in elasmobranchs are limited (Cortés, 2000). We found the two life history strategies from morphology and reproductive that can be utilized for rare elasmobranch species those who do not have reliable vital statistics for fisheries management. Furthermore, it needs also considering spatial elements like distribution, migration, or behavioral effects. Estimating the Elasmobranchii fishery assessment by life history strategies can possible make up for rare or unknown species, and then to project them.

Summary

(1) Using 6 life history traits (**L_X, L_m, A_X, A_m, k** and **M)** in principal component analysis, we could explain a total of 98% variation for 990 shark, skate and ray species.
(2) Life history traits could be classified into 3 factors as size, time, and k&M (growth & death rate) factors that distinguished significantly into reproductive strategies.
(3) Elasmobranchii fishes got 71% correct classification into oviparous, viviparous and ovoviviparous strategies. Body sizes were larger in viviparous species, for breeding inside the females, than in oviparous species.
(4) Fecundity of elasmobranch fishes had not much variation in three reproductive modes. The total length at birth has significant correlation with asymptotic body size. However, females played the K-strategy that had trade-off in large offspring size instead of large number in fecundity.
(5) Unique life history reproductive (low fecundity) strategies would affect the resources from high fishing pressure. Our study could estimate the vital statistics for possible life history model of rare or unknown species and would provide basis for fisheries management and conservation policy.

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Table 1. The collected life history traits data, record by orders.
N: all sampled species; n: species number in each order; $\bar{X}$: mean value; SE: standard error.

	Order	**All**	**L_X**			**L_m**			**L_b**			**f**		
		N	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE
Shark	Carcharhiniformes	241	220	117.2	13.72	220	59.07	6.02	120	34.5	3.48	185	5.75	0.98
	Heterodontiformes	9	9	111.9	29.99	9	57.44	13.97	8	17.41	2.53	6	2	0
	Hexanchiformes	5	5	242.5	170.3	5	118.8	66.97	5	46.4	18.91	5	36.6	42.57
	Lamniformes	16	16	441.9	111.5	16	196.7	44.17	12	97.24	23.64	11	6.09	3.81
	Orectolobiformes	33	33	155.8	85.93	33	73.95	34.16	16	23.3	7.56	29	15.8	21.02
	Pristiophoriformes	5	5	132.1	40.81	5	66.9	18.72	4	30.63	6.79	3	10.17	8.99
	Squaliformes	109	92	93.18	19.89	92	47.63	8.62	32	27.4	4.02	36	21.82	17.55
	Squatiniformes	17	15	138.3	26.01	15	69.49	11.98	6	27.13	2.57	7	12.63	5.35
Batoid	Rajiformes	488	249	96.72	9.36	249	49.08	4.22	31	22.99	5.57	167	2.84	0.382
	Torpediniformes	60	39	57.75	12.56	39	31.23	6.01	10	10.1	3.9	8	16.25	15.49
	Pristiformes	7	7	530.2	194.5	7	231.8	78.83	1	61	0	3	13	13.44

Table 1. (Continue)

	Order	**All**	**A_X**			**A_m**			**k**			**M**		
		N	n	$\overline{X}$	SE	n	$\overline{X}$	SE	n	$\overline{X}$	SE	n	$\overline{X}$	SE
Shark	Carcharhiniformes	241	216	15.3	1.69	216	3.18	0.29	216	0.27	0.02	219	0.39	0.03
	Heterodontiformes	9	2	58.05	0.64	2	11.8	1.27	2	0.05	0	8	0.3	0.16
	Hexanchiformes	5	1	11.6	0	1	2.3	0	1	0.25	0	5	0.16	0.11
	Lamniformes	16	13	29.74	7.16	13	5.16	1.15	13	0.11	0.02	16	0.14	0.03
	Orectolobiformes	33	4	24.7	37.87	4	4.08	5.44	4	0.28	0.49	32	0.41	0.07
	Pristiophoriformes	5	1	15.2	0	1	3.1	0	1	0.19	0	5	0.22	0.06
	Squaliformes	109	27	39.22	5.14	27	8.23	0.98	27	0.09	0.01	91	0.29	0.04
	Squatiniformes	17	16	20.87	4.03	16	4.27	0.72	16	0.17	0.04	15	0.24	0.06
Batoid	Rajiformes	488	237	16.99	1.23	237	3.77	0.25	237	0.22	0.02	237	0.34	0.02
	Torpediniformes	60	22	46.41	11.79	22	10.39	2.51	22	0.08	0.03	38	0.5	0.12
	Pristiformes	7	7	38.33	14.48	7	6.54	2.26	7	0.1	0.07	7	0.15	0.11

Table 2. The collected life history traits data record by reproductive modes.
N: all simple sizes; n: simple size of each reproductive modes; $\overline{X}$: mean value; SE: standard error.

Reproductive	**All**	**L_X**			**L_M**			**L_b**			**f**		
	864	n	$\overline{X}$	SE	n	$\overline{X}$	SE	n	$\overline{X}$	SE	n	$\overline{X}$	SE
Ovoviviparous	398	265	159.2	10.4	266	76.55	4.33	120	35.08	2.51	130	16.71	3.4
Oviparous	347	250	79.2	3.13	250	41.36	1.42	40	14.55	0.76	241	2.08	0.05
Viviparous	81	78	183.2	13.01	78	89.5	5.58	69	43.86	1.96	69	7.9	0.83

Reproductive	**All**	**A_X**			**A_M**			**k**			**M**		
	864	n	$\overline{X}$	SE	n	$\overline{X}$	SE	n	$\overline{X}$	SE	n	$\overline{X}$	SE
Ovoviviparous	398	174	25.18	1.21	174	5.11	0.24	174	0.16	0.01	260	0.28	0.01
Oviparous	347	220	15.12	0.71	220	3.4	0.15	220	0.26	0.01	238	0.39	0.01
Viviparous	81	70	20.86	1.96	70	4.06	0.34	70	0.22	0.02	77	0.33	0.03

Table 3. Total variance explained from 6 life history traits for each category with jackknifed correct classifications. Both batoids and Rajiformes had high correct classifications in reproduction patterns.

With 6 Life history traits	Variance Explained	Jackknifed Classification (%) Reproductive modes
Elasmobranchii	98.617	71 (n=448)
Shark	95.791	69 (n=240)
Carcharhiniformes	99.351	71 (n=181)
Batoid	97.749	91 (n=209)
Rajiformes	97.155	95 (n=187)

Table 4. Principal component analysis of 6 life history traits in Elasmobranchii. A total of 98.6% variance can be explained by 3 time, size and k&M factors.

Life history trait	Time Factor 1	Size Factor 2	k&M Factor 3
Log L_X	0.257	**0.912**	0.308
Log L_M	0.241	**0.92**	0.297
A_X	**0.881**	0.335	0.314
A_M	**0.915**	0.192	0.338
k	-0.373	-0.31	**-0.862**
M	-0.354	-0.388	**-0.837**
% of Variance Explained	33.38	34.59	30.66

Table 5. F-matrix by discriminate analysis from 3 factors in reproductive patterns in Elasmobranchii. There are 71% correctness in jackknifed classification matrix is observed. (**OVI**: oviparous, **OVO:** ovoviviparous, and **VIV:** viviparous).

	OVI	OVO	VIV
OVI	0		
OVO	38.46	0	
VIV	50.71	15.07	0

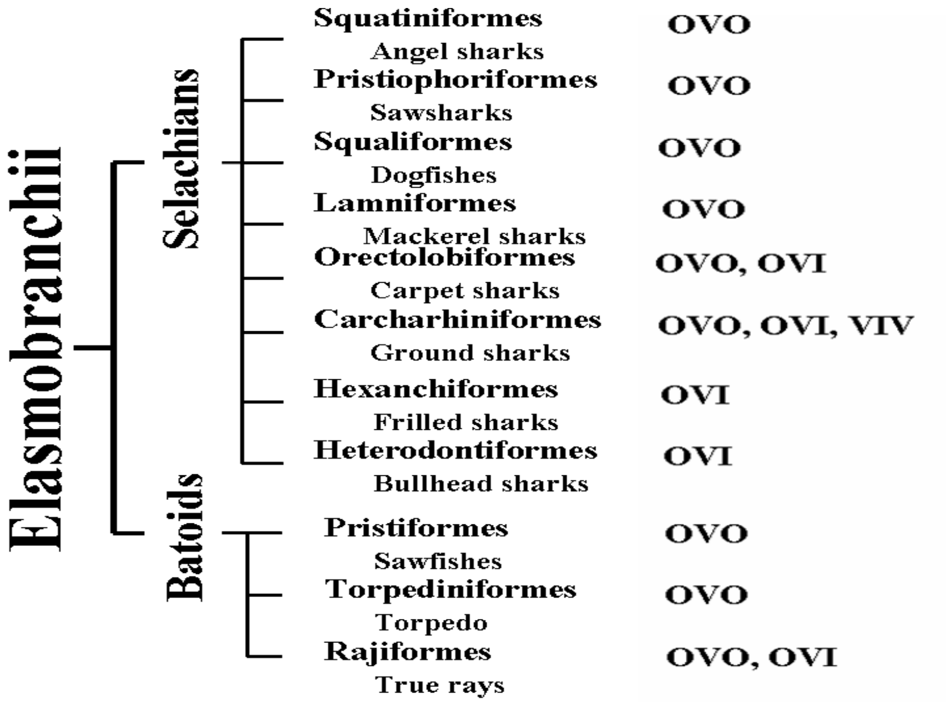

Fig. 1. Classification of Elasmobranchii fishes. Selachians have 8 orders and batoids have 3 orders (classification by following FishBase). (**OVI**: oviparous, **OVO:** ovoviviparous, and **VIV:** viviparous).

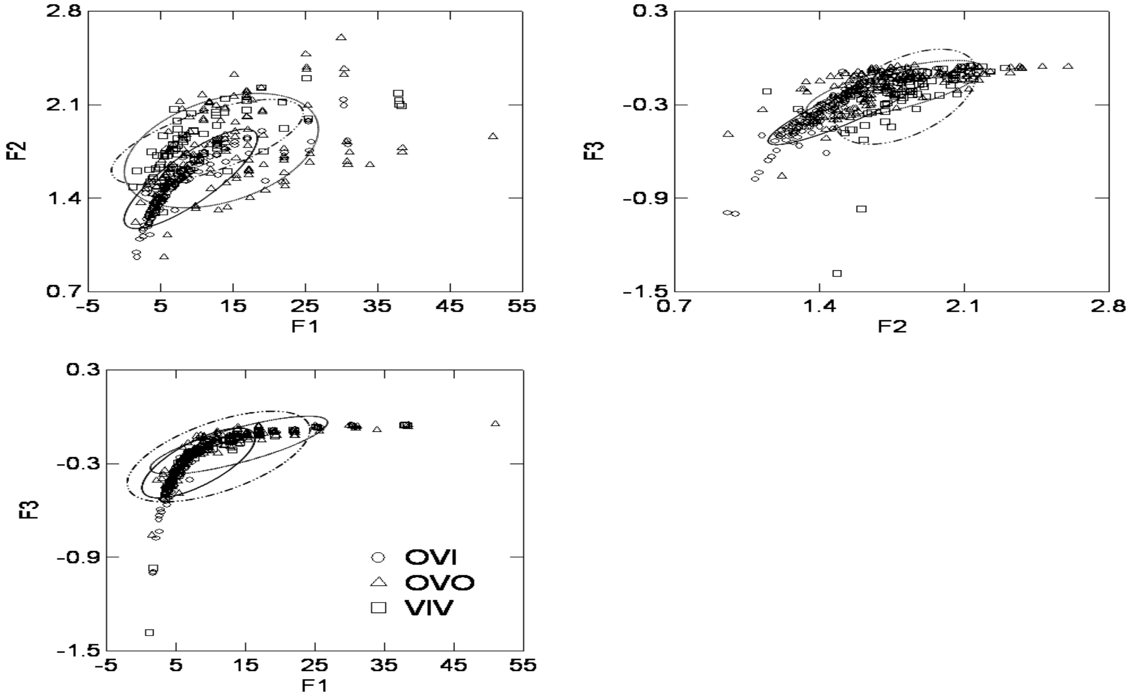

Fig. 2. Scatterplot of time factor 1 (F1: $\mathbf{A_X}$ and $\mathbf{A_m}$), size factor 2 (F2: $\mathbf{L_X}$ and $\mathbf{L_m}$) and **k&M** factor 3 (F3) in reproductive strategy in Elasmobranchii (N=448). The analysis result is high observed. (**OVI**: oviparous, **OVO:** ovoviviparous, and **VIV:** viviparous).

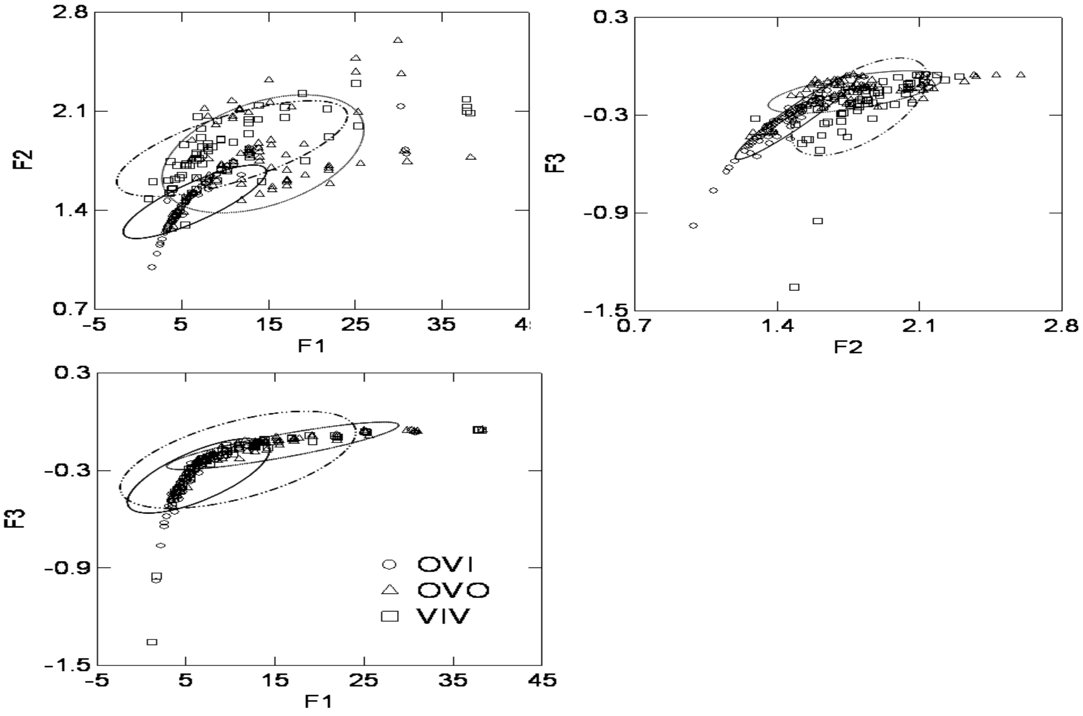

Fig. 3. Scatterplot of time factor 1 (F1: $\mathbf{A_X}$ and $\mathbf{A_m}$), size factor 2 (F2: $\mathbf{L_X}$ and $\mathbf{L_m}$) and **k&M** factor 3 (F3) in morphology strategy in sharks (N=240). (**OVI**: oviparous, **OVO:** ovoviviparous, and **VIV:** viviparous).

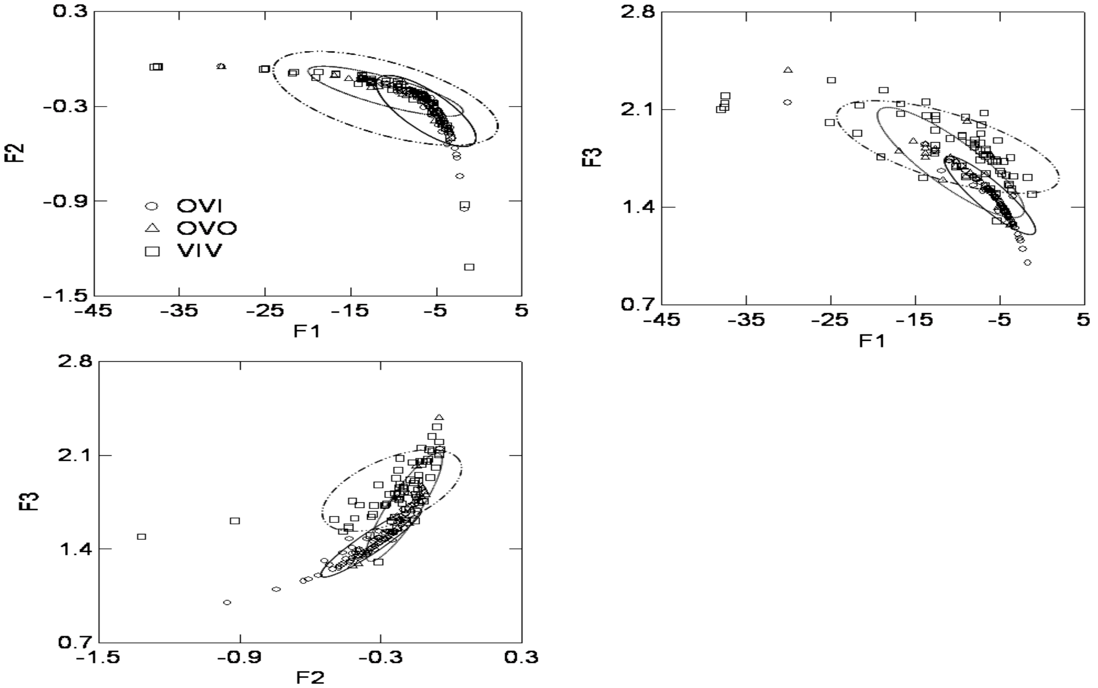

Fig. 4. Scatterplot of time factor 1 (F1: $\mathbf{A_X}$ and $\mathbf{A_m}$), size factor 2 (F2: $\mathbf{L_X}$ and $\mathbf{L_m}$) and **k&M** factor 3 (F3) in reproductive strategy in order Carcharhiniformes (N=181). (**OVI**: oviparous, **OVO:** ovoviviparous, and **VIV:** viviparous).

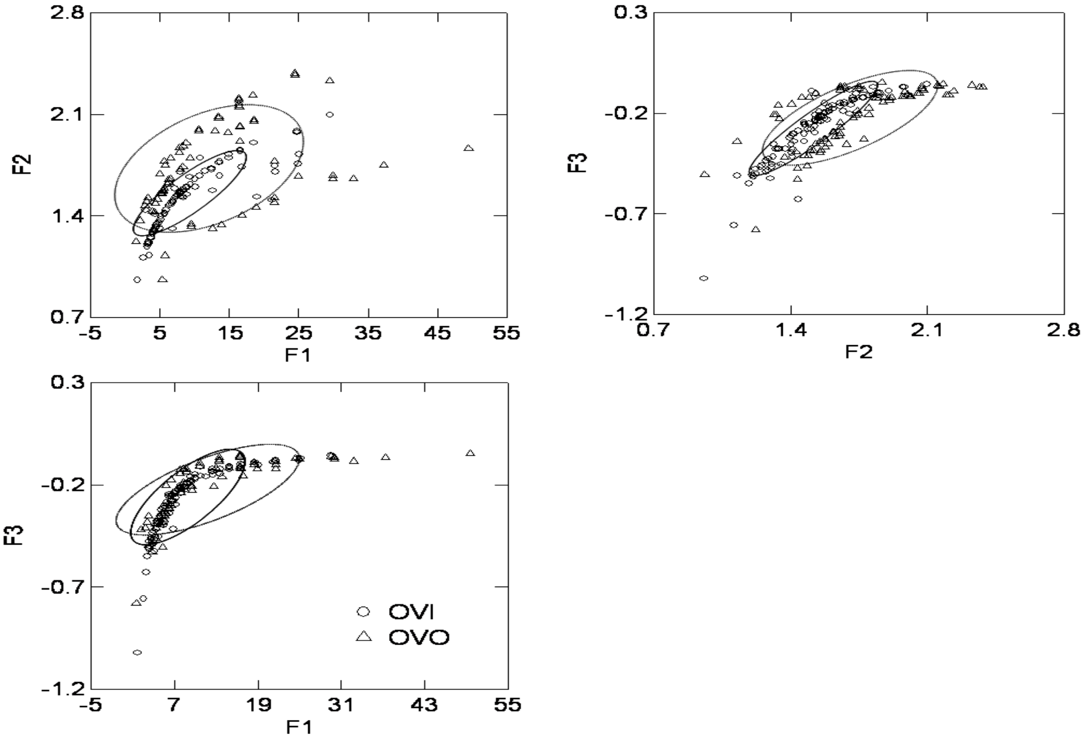

Fig. 5. Scatterplot of size factor 1 (F1: $\mathbf{L_X}$ and $\mathbf{L_m}$), time factor 2 (F2: $\mathbf{A_X}$ and $\mathbf{A_m}$) and **k&M** factor 3 (F3) in reproductive strategy in Batoids (N=209). (**OVI**: oviparous and **OVO:** ovoviviparous).

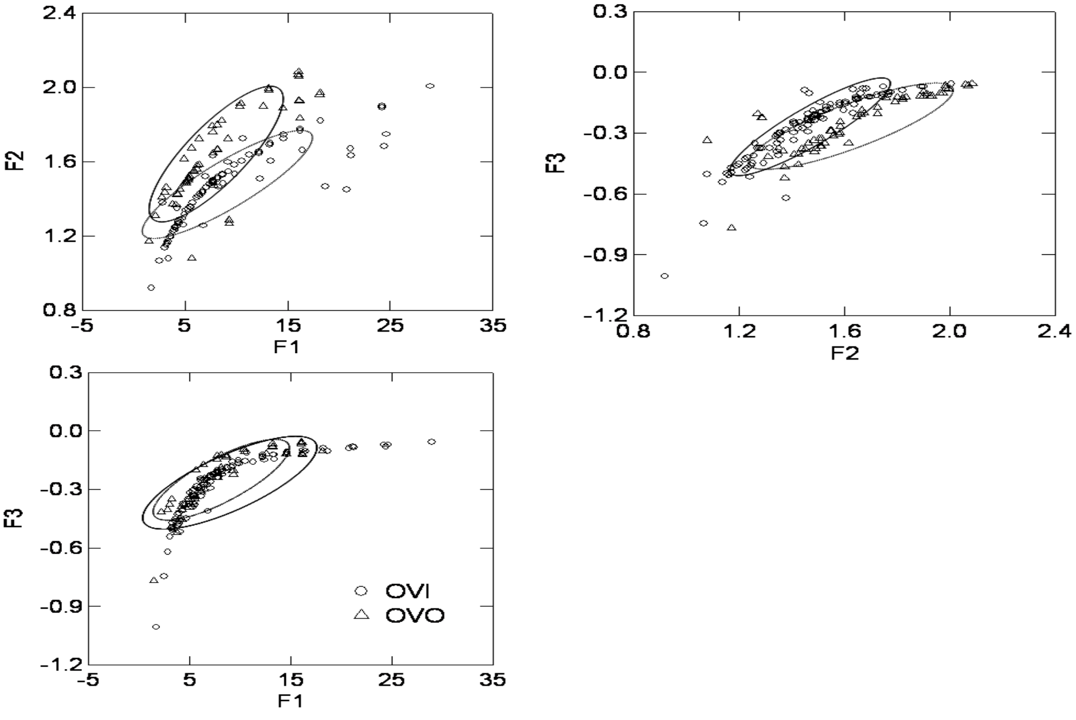

Fig. 6. Scatterplot of size factor 1 (F1: $\mathbf{A_X}$ and $\mathbf{A_m}$), time factor 2 (F2: $\mathbf{L_X}$ and $\mathbf{L_m}$) and **k&M** factor 3 (F3) in morphology strategy in order Rajiformes (N=187). (**OVI**: oviparous and **OVO:** ovoviviparous).