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Using Elasticity, Perturbation Analysis, Demographics and Elasmobranch Species Phylogenic Relationships as Indicators of Vulnerability to Exploitation

(Elasmobranch Fisheries – Oral)

by

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Abstract

Using exiting data from the literature for elasmobranch species we: (1) used stage-based population models and elasticity analyses to determine how the vital rates of mortality (M) and fertility (f) influence population growth rate (r), (2) determined the response of elasticity to changes in the levels of exploitation, (3) used model inputs and species vital rates, such as size maturity (L_{mat}), and total length (L_{max}), and phylogenic associations, as indicators of potential acceptability to over exploitation, and (4) estimated the effects on elasticity of perturbing model vital rates. We found a negative association between species size and elasticity of inter-stage transitions and a positive relationship between species total length and elasticity for adult and juvenile stages of the models. We found that there were no clear associations between trends in elasticity and phylogenic groupings. However, when reproductive modes and vital rates were added weak associations were found between species phylogenies and population dynamics.

Introduction

Several species of elasmobranchs have been shown to be susceptible to population declines and even extirpation when exploited (Frisk *et al*., 2002; Frisk *et al*., 2001; Dulvy *et al*., 2000; Simpfendorfer, 2000; Stevens, 2000; Casey and Myers, 1998; Walker and Hislop, 1998; Brander, 1981). The degree of susceptibility of different species has been linked to their life history. Research has shown that large elasmobranchs, with slow growth and delayed and or large size of maturation, display increased vulnerability to population declines when exploited (Frisk *et al*., 2001; Dulvy *et al*., 2000; Stevens, 2000; Walker and Hislop, 1998). If such species are indeed more susceptible to exploitation, can a similar exploration of life history patterns suggest approaches to management that may enhance their future sustainability?

Matrix models provide a convenient method for calculating growth rates, reproductive values, performing sensitivity and elasticity analyses (Caswell, 2001). Matrix projection models are attractive as they permit estimation of both the intrinsic rate of increase, r, and how populations may be expected to respond to external factors such as exploitation. Several authors have used age-based or stage-based models in order to observe and understand the population dynamics of elasmobranch species and determine population growth rates (Frisk *et al*., 2002; Mollet and Caillet, 2002; Brewster-Geisz and Miller, 2000; Heppell *et al*., 1999; Cortes, 1999; Walker and Hislop, 1998). When applied to elasmobranch populations, estimates of r are frequently based on limited data derived from exploited populations (Miller *et al*., submitted). The results of such endeavors thus provide an estimate of the r that currently characterizes the population but not necessarily that representative of the performance of virgin populations (Jennings, 1998). To evaluate the population dynamics of species for which only limited data are available, Jennings (1998) provided a method to access a population's potential productivity (r' = ln (fecundity)/(age of maturation)) independent of the intrinsic rate of increase.

The pattern and extent of responses to external factors exhibited by an individual species will be constrained by its phylogeny. Pagel and Harvey (1988) clearly demonstrated the importance of including phylogenetic relationships in comparative analyses of life history traits. Population dynamic consequences of elasmobranch life histories have not been examined within a phylogenetic framework. While there is some debate regarding the phylogenic relationships of elasmobranchs (for a general reference see Moyle and Cech, 2000; and for detailed discussions see Shirai, 1996; Carvalho, 1996; McEachran *et al*., 1996), for our purposes we will follow the classification system presented in Moyle and Cech (op.cit.). Elasmobranchs are generally thought to have two separate evolutionary lines: the sharks and rays (Moyle and Cech, (op.cit)). The families Carcharhinidae (requiem sharks), Triakidae (houndsharks) and Rajidae (skates and rays), fall into two superorders: Galea and Squalea. Galea is represented mostly by large predatory species and contains the families Carcharhinidae and Lamnidae, while the superorder Squala contains related species ranging from rays to many species of sharks, and contains Rajidae, the skates. Our analyses will be performed on the superorder and the family level.

Elasmobranch families, including those used in this study, exhibit considerably life history variation in important traits, such as modes of reproduction. Particularly evident is the difference between the skates and the two families of sharks. Live-bearing is the most common form of parity, found in 60% of elasmobranch species, while egg-laying is found in 25% (Dulvy, 1997). Dulvy (op. cit.) found that elasmobranch species show 9-10 separate evolutionary transitions from egg-laying to live-bearing in the class. These findings agree with earlier investigations that concluded that egg-laying is the ancestral form in sharks, rays, and ratfish (Wourms, 1977; Wourms & Lombardi, 1992). In Rajidae, it appears that egg-laying is also an ancestral form; however, skates transitioned to live-bearing and then back to egg-laying (Dulvy, op.cit). The transition from egg-laying to live-bearing possibly reflects a trade-off occurring when the benefits of increased offspring survival exceeds the cost of reduced fecundity (Goodwin *et al*., 2002). Such contrasting life strategies might also be reflected in differences in elasticity patterns between the reproductive modes? Do systematic relationships determine the pattern of the relative contribution of individual vital rates to growth rates (elasticity)?

Here, we developed stage-based matrix projection models for 45 species of the families Rajidae (9), Carcharhinidae (21), Triakidae (9) and 6 additional rajaforms from the families Dasyatidae, Urolophidae, Myliobatidae, and Rhinobatidae for which we were able to find information from the literature for age of maturation (T_{mat}), longevity (T_{max}), and fecundity (F). From these data we will: (1) use elasticity analyses to determine how the vital rates of mortality and fertility influence population growth rate, (2) determine the dynamics of elasticity with varying levels of exploitation, (3) use model outputs and species vital rates, such as size/age maturity, life-span, growth rate, and phylogenic associations, as indicators of potential susceptibility to over-exploitation. The results are not intended to estimate fishing limits, but rather observe how the species and phylogenic groups of species are potentially influenced by exploitation. However, model results may provide insight into which vital rates are important in potential conservation scenarios. We hope to add to the discussion of where potential compensatory responses may occur under exploitative or environmental changes and how they differ across species groupings. Our primary goal is to link life history theory, phylogeny, and conservation.

Methods

The Data

Species of the families Rajidae (9), Carcharhinidae (21), Lamnidae (9), Dasyatidae (1), Urolophidae (3), Myliobatidae (1) and Rhinobatidae for which adequate data could be gleaned from the literature were included in the analyses. Generally, estimates of age of maturity (t_{mat}), length of maturity (L_{mat}), maximum length (L_{max}) and longevity (t_{max}) were point estimates. However, if a range was given, the mid-point was used. Estimates of fecundity were either the average egg production per year, as for many skates, or the mean number of neonates born per year, as for many sharks. For live-bearing species, fecundity estimates were based on the size and frequency of litters. Natural mortality estimates were estimated using Hoenig's (1983) method, which used an empirical approach to determine total mortality (Z) using species maximum age (t_{max}) as a predictor. Since estimates are based on the oldest individual aged or extrapolations of the von Bertalanffy equation, we assume Hoenig's method reflects natural mortality (M). Because we are interested in elasticity and not calculating exact growth rate if estimates of M are closer to total mortality (Z), our analysis will not be hindered.

The Models

Several species had adequate estimates of vital rates to justify using age-based projection (Leslie) matrix models. This was not true of all species. In order to standardize methodologies among species, we chose stage-based models for all species. Models identified elasmobranch life history as consisting of three stages: egg stage/neonate, juvenile, and adult. The juvenile and adult stages may last several years. The egg or neonate stage last for a duration of one time step. All models were programmed in MATHCAD (v9. Mathsoft Corp. Cambridge, MA).

In stage-based models, individuals have three possible fates: they may survive and stay in the same stage, they can survive and grow into the next stage or they can die. The projection matrix took the form:

(1)
$$A = \begin{bmatrix} P_1 & 0 & f \\ G_1 & P_2 & 0 \\ 0 & G_2 & P_3 \end{bmatrix}$$

where P is the probability of surviving and remaining in the same stage, G is the probability of surviving and growing to the next stage and *f* is fertility.

We assumed a post-breeding census for all species. A post-breeding census assumes that individuals immediately before being censured, thus fecundity has to be weighted by the probability of adult survival (Caswell, 2001). Thus, fertilities were calculated with the following function:

(2)
$$f = P_t \bullet F_{(t+1)}$$

where F is annual fecundity.

G and P values were calculated using estimates of the probability that an individual survives (σ) and the probability that an individual grows to the next stage (γ_i) (Casswell, 2001). To determine the P's and G's to be used in the models we assumed individuals within a stage have the same probability of survival, regardless of age. This approach has been successfully used for the sandbar shark *Carcharhinus plumbeus* shark (Brewster-Geizs and Miller, 2000) and little skate *Leucoraja erinacea* winter skate *Leucoraja ocellata* and barndoor skate *Dipturus laevis* (Frisk, *et al*., 2002).

Following Caswell (2001) we iterated values of λ_{init} in the equation:

(3)
$$g_i = \frac{\left(\frac{s_i}{l_{\text{int}}}\right)^{T_i} - \left(\frac{s_i}{l_{\text{int}}}\right)^{T_i - 1}}{\left(\frac{s_i}{l_{\text{int}}}\right)^{T_i} - 1}$$

until λ_{int} equaled the value for growth rate (λ) in the eigen analysis of the projection matrix. The resulting value of γ was used to estimate appropriate values of P and G.

Egg/neonate mortality was calculated by assuming that every female must, on average, have one female offspring survive to successfully reproduce. This condition is empirically estimated by calculating the level of first year mortality (M_1) necessary to sustain a positive growth rate given values of lifetime fecundity and mortality rates (Fogarty *et al*., 1987). This is calculated by the constraint that:

(4)
$$1 = \sum_{i=1}^{t_{mat}} f \prod_{j=1}^{i=1} \exp^{-M_j}$$

where M is a vector of stage-specific mortalities and all other inputs are as defined above. In several species, the vital rates of fecundity, age of maturation and longevity did not allow for any mortality in the egg/neonate stage. This may be the result of low estimates of longevity or fecundity. In these cases, we used a value of $M_1 = 0.0$. Our approach to estimating M_1 yields estimates of population growth (λ) that are correlated with estimates of neonate/egg stage mortality. In this study, we are interested in the relationship between vital rates and their influence on growth rate and not estimates of growth rates per se.

Population growth rate (λ) was determined from the dominant eigen value of matrix **A**. The intrinsic rate (r) of population increase could be estimated by the natural logarithm of the population growth rate λ. The distribution of abundances of each stage in a population will converge so that each stage has a constant proportion of individuals.

Elasticity analyses

The following equation was used to calculate elasticity for all species:

(5)
$$e_{i,j} = \left(\frac{a_{i,j}}{l}\right)\left(\frac{\partial l}{\partial a_{i,j}}\right)$$

where $a_{i,j}$ is the ith, jth element of the projection matrix and λ is the population growth rate.

We correlated model inputs, vital rates and elasticity values with model base runs in order to elucidate underlying associations within the data in an effort to identify key aspects of the species life histories.

We performed multivariate statistical analyses to determine if elasticities and other life history traits follow similar patterns to species phylogenetic relationships. We used a median hierarchical cluster analysis assuming mean of 0 and a standard deviation of 1 (SAS: Proc Cluster Corporation, Cary, NC).

Perturbation analysis

Vital rates in populations change over the long-term as a result of evolution and over the short-term as a result of environmental fluctuations. Sensitivity of elasticity determines the magnitude and direction of the effect of changes in individual elasticity elements to the matrix element $e_{i,j}$. Sensitivities of $e_{i,j}$ provide an understanding of how life histories have shaped elasticity patterns (Caswell, 1996). For example, a positive sensitivity of e_{33}, (adult stage) would indicate that increasing the probability of remaining in adult stage would increase e_{33}, while increasing the probability of death (i.e., decreasing a_{33}) would have an negative effect on e_{33}. If values of sensitivity of elasticities with respect to e_{33} were negative, then reducing them would increase e_{33} and *vice versa*.

Sensitivity was calculated by taking the second derivative with respect to the element ($e_{i,j}$) in the elasticity matrix which had the greatest contribution to growth rate (Caswell, 1996; 2001).

(6)
$$\frac{\partial e_{i,j}}{\partial a_{k,l}} = \frac{a_{i,j}}{l}\frac{\partial^2 l}{\partial a_{i,j}\partial a_{k,l}} - \frac{a_{i,j}}{l^2}\frac{\partial l}{\partial a_{i,j}}\frac{\partial l}{\partial a_{k,l}} + \frac{d_{i,k}d_{j,l}}{l}\frac{\partial l}{\partial a_{i,j}}$$

where $\delta_{i,k}$ $\delta_{j,l}$ are the Kronecker delta functions.

Exploitation can change average vital rates in the short-term as a result of gear selectivity and possibly over the long-term if fishing is applied at a constant level. In order to understand the dynamics of elasticity for varying fishing levels, we ran models with no exploitation and increased mortality until M = 3.0 (a very high fishing mortality). To be concise, we selected representative species from each family to model.

Results

Model inputs and elasticity

Positive relationships were found between longevity (t_{max}) and elasticity of juvenile and adult survival for all elasmobranchs combined (Fig. 1 and 2). Significant relationships were also found between age of maturation (t_{mat}) and elasticity of juvenile and adult survival (Fig. 3 and 4). While, the relationship between elasticity of adult survival and age of maturation is significant, it explains only 27% of the variance. The data suggest that elasticity may be invariant to the age at maturity. Together, these four associations suggest that growth rates (λ) of short-lived and early maturing species are less sensitive to changes in survival during juvenile and adult stages than longer-lived stages. However, many short-lived species have elasticities for juvenile and adult survival as great as 0.2. Longer-lived and late maturing species tend to have higher elasticities of juvenile and adult survival; although, the rate of increase in elasticity decreases as longevity increases beyond 25 years.

Due to the structure of the matrices used, the estimated elasticity in all inter-stage transitions, including fertility, were equal. Inter-stage transition decreased logarithmically with increases in longevity and age of maturation (Fig. 5 and 6). These relationships indicate that longer-lived species have higher juvenile and adult elasticities and lower elasticity of fecundity and the transition between stages, while short-lived and early maturing species have higher elasticity values for fecundity and the transition between stages. A possible trade-off is apparent with these relationships: long-lived species may be investing more energy for survival, while selection pressure in short-lived species emphasize the desire to advance through the stages and reproduce.

Species vital rates and elasticity

Significant relationships were found between length of maturation and elasticity of juvenile and adult stages, and fecundity and the stages transitions (Table 1). All relationships for requiem sharks were significant at $p = 0.05$. For skates (Rajidae) and the Houndsharks (Triakidae), similar patterns were found with long-lived species having increased elasticity of survival and shorter-lived species exhibiting higher elasticity of fecundity. However, even though the same patterns were observed, not all relationships were significant (Table 1). Overall, longevity, age of maturation, total length, and length of maturation were all positively related to elasticity of juvenile and adult survival, while fecundity and the transitions between stages were negatively associated with elasticity.

Phylogenic analyses

We show hierarchical cluster tree dendrogram in Fig. 7 based on the individual elasticities for all species. We did not find definitive patterns on a superorder or family level; although, 7 of the 9 skates were grouped together and many of the requiem sharks were grouped together. Groupings on the superorder level and by reproductive modes indicate clearer clusters in Fig. 8 than family level associations. However, broad separation among families is shown for skates and requiem sharks. All dendrograms showed that patterns in elasticity are fairly similar in elasmobranchs and clusters did not have large distances between them.

Exploitation and stability of elasticity

Elasticity varied little as mortality rates increased from low to moderate levels. We illustrate the general pattern by showing details for little skate, common skate, dusky shark and the Atlantic Sharpnose (Table 2). When considering reasonable fishing mortality for little skate (0-0.5), elasticity changed 2 % or less. Similar results can be seen for the short-lived Atlantic Sharpnose shark and the long-lived common skate and dusky shark. In probable management scenarios with fishing mortality ranging from 0-0.5 elasticity stays relatively constant.

Perturbation Analysis

In 17 of 21 species of Carcharhinidae, elasticity of the adult stage displayed the greatest contribution to growth rate, while 3 showed larger values for the juvenile stage, and 1 for the fecundity and transition stages. Of the 9 Lamnidae species, 6 showed the greatest elasticity in the adult stage and 3 for the juvenile stage. Of the 9 Rajidae species, 7 showed the greatest elasticity for the adult stage, and 2 for the juvenile stage. In total for species in the superorder Galea, 24 had the greatest elasticity values for adult survival, 5 for juvenile survival, and 1 for fecundity and the transition stages. For the species in the *Squalea superorder*, 12 had the greatest elasticity for the adult stage and 3 for the juvenile stage.

The sensitivity of the elasticity with respect to the element that had the greatest contribution to λ was calculated. Sensitivity of elasticity was calculated for the adult stage (e_{33}) of species from the superorder Galea. Increases in survival would have the greatest positive effect of e_{33} (Fig. 9). Increases in the probability of transition from juvenile to the adult stage or juvenile survival would have large negative effects on e_{33}. In some cases, increases in the probability of transition to the juvenile stage had large negative effects on e_{33}. In addition, changes to fecundity would have little effect.

Sensitivities of e_{33} for species from the superorder Squalea do not differ from those found for Galea, with increases in the adult stage having large positive impacts and changes in the juvenile stage and the transitional stages and fecundity element having negative effects (Fig. 10). The sensitivity of elasticity for the juvenile stage (e_{22}) was positive indicating that increased survival would have a positive effect on e_{22} (Fig. 11). Any changes in the transition to adulthood would have large negative effects on e_{22}. Smaller negative effects would result from perturbations of fecundity, transition to juveniles, and the adult stage.

Discussion

Elasticity provides insight into what aspects of an individual's life history will play important roles in understanding population level changes in response to both short-term changes in harvest policies and to longer term evolutionary pressures (de Kroon *et al.*, 2000). We showed that there is evidence for a trade-off between survival and reproductive investment. Generally, short-lived species have higher elasticities of inter-stage transitions (selection pressure on age of maturation and fecundity), while long-lived species tend to have higher elasticties of adult and juvenile survival. These are relative differences, and it should be noted that elasticity of inter-stage transitions is usually less than survival for short- and long-lived species.

Previous studies have found that many of the vital rates used in this analysis are correlated with model inputs and with vital rates not explicitly used in our model. For example, in elasmobranchs, maximum size (L_{max}) and longevity are significantly related (Frisk *et al.*, 2001). Thus, it would be expected that if there were relationships between longevity and elasticity, there would also be relationships between elasticity and maximum size and other characteristics of species life histories. The nature of these relationships can provide useful insight into management alternatives and help identify key aspects of a species life history.

Relationships were generally stronger on a family level for non-model vital rates. For requiem sharks (Carcharhinidae), elasticity of juvenile and adult survival increased with species maximum size, while the opposite result was found for elasticity of inter-stage transitions. There are differences in how skates and requiem sharks as a group partition elasticity. However, more apparent relationships can be seen in the size of species and how a species partitions elasticity across the model's classes or stages. For example, the response of population growth rate to changes in inter-stage transitions is much greater in small skates and requiem sharks than for larger species. Changes in adult and juvenile survival would yield the greatest change in population growth rate for skates and requiem sharks, respectively. These differences may represent trade-offs that constrain the evolution of life history traits of these species. It should be noted that the life history traits used in this analysis represent just a few of the possible explanatory variables that could be used. Other explanatory variables include gestation period or even class variables such as reproductive mode.

The evolutionary history of elasmobranchs, particularly their reproductive modes, provides for the possibility that elasticity patterns may reflect phylogenic groups. However, we found little evidence of clustering of superoders or families with species elasticity. When reproductive modes and vital rates were included in the clustering analysis some evidence indicating separation of superorder and family groups was indicated. Although distinct clusters were not evident, 80% of skates and 85% of requiem sharks were found in groups.

Trade-offs involved in the development of each species life history reflect its evolved fitness strategy. The possibility that elasticity patterns should reflect the evolutionary development of reproductive modes and other life history traits is logical. The clustering of reproductive modes and life history traits indicate that the potential exists for defining patterns between life history characteristics, elasticity, phylogenic groups and even conservation needs. Although, we have observed weak associations, further analyses with other model structures and new data may elucidate underlying patterns and allow further applications.

The present analyses indicate that elasticity is robust for probable exploitation levels and using a "snapshot approach" with initial estimates of mortality should suffice in most management schemes unless, extreme changes in survival are expected to be occurring in the species' populations. Common skate, dusky shark and Atlantic sharpnose shark all show increasing elasticity of adult and juvenile stages with a decrease in inter-stage transitions. Little skate, on the other hand, showed a decrease in juvenile and adult survival and an increase in elasticity of inter-stage transitions. While there are differences in the response to exploitation, elasticity between species all showed less than a 2 % change in values with exploitation levels of F <1.0.

While elasticity provides a "snapshot" view the sensitivity of elasticity allows for a more flexible view of varying vital rates. We have calculated the sensitivity of elasticity for the stage that had the greatest elasticity in order to observe how that stage's elasticity is effected by perturbation of other stages. We showed both negative effects and positive effects of perturbing vital rates. However, the magnitudes of perturbation not the direction, are of importance. For all species the transition from the juvenile to the adult stage was high, indicating the importance of attaining maturity in elasmobranchs. In many species, the juvenile stage was important, and to a lesser extend, fecundity and the transition to the juvenile stage, was important.

Contribution of fecundity to the stage with the greatest elasticity was low for all species. Long-lived species often have low elasticity of fecundity, and the perturbation analyses further indicate that the dynamics of elasmobranchs are not strongly influenced by egg/neonate production. This is often contrary to what might be expected, and other authors have claimed that matrix models provide unreasonable elasticity values for fecundity (Mollet and Cailliet, 2002). However, Frisk *et al*. (2002) showed that fecundity levels for three western Atlantic skates were at the point where increases in egg production would have diminishing returns. Body cavity limitation and energetic constraints may lead to the relative fixation of fecundity in elasmobranchs (Brander, 1981). Thus, compensatory responses will not likely occur in changes in fecundity. However, indirectly compensatory responses decreasing the age of maturity may increase the lifetime rate of egg production. It appears that elasmobranch population dynamics is strongly influenced by juvenile and adult survival and the age of maturation and not fertility (Frisk *et al*., 2002; Brewter-Geisz and Miller, 2000; Heppel *et al*., 1999; Musick, 1999; Walker and Hislop, 1998).

We choose to use elasticity to observe how elasmobranchs partition elasticity over the stages of our model. Elasticity provides a convenient measure of trade-offs as it is proportional (adds to 1.0). Thus, trade-offs between vital rates (for example, reproduction vs survival) may be reflected in the portioning of elasticity. Elasticity also provides a measure of the intensity of selection pressure in each stage of our model (Caswell, 2001). However, models are abstractions of dynamic behavior of both individuals and the environment. No single model structure is comprehensive, and each model provides answers to different questions.

We assumed that all species in this analysis can be modeled with our three-stage model, which will, to some extent, produce similar elasticity patterns. Caswell (2001) points out that the assumption of one model structure representing all species is not true, and caution is advised. A similar approach to ours was successfully used for analyzing elasticity trends and trade-offs in plant species (Silvertown *et al*., 1993; Silvertown *et al*., 1994; but see Shae *et al*., 1994). The central issue revolves around annualizing trade-offs among related species using elasticity from a single model structure. We feel that trade-offs can be expressed in our analyses.

In addition we had to use indirect approaches to estimating key vital rates. There are numerous elasmobranchs species with a paucity of estimates of vital rates. Although ageing methods have now been validated for the porbeagle shark *Lamna nasus* (Campana *et al*., 2002), ageing elasmobranch continues to be problematical. In addition, juvenile mortality is poorly known for many elasmobranch species (but see Heupel and Simpendorfer, 2002). The lack of empirical estimates of many demographic characteristics has lead to the development of indirect methods to estimate vital rates. For example, Smith *et al*. (1998) used values of 2M for juvenile mortality for sharks, where M is the expected lifetime rate of natural mortality. Frisk *et al*. (2002) used estimated rates of survival for egg-cases and adult mortality rates to approximate egg stage mortality for three western Atlantic skates. Here we calculated the level of first year mortality necessary to maintain an equilibrium population where a female is replaced with one successfully reproducing female. These indirect methods lead to potential bias, and estimates of r may be correlated to the models characteristics, the data's limitations, and the state of the population during sampling (thus r values can be negative).

Several recent papers have shown that large elasmobranchs species are susceptible to over-exploitation (Frisk *et al*., 2002; Walker and Hislop, 1998; Dulvy *et al*., 2000; Stevens, 2000). The life history of larger, longer-lived species with late/large age/size of maturity and species with low productivity levels have been link to venerability to exploitation (Frisk *et al*., 2001, Stevens, 1999). As exploitation of elasmobranchs increases, the necessity to understand elasmobranch life histories and resilience to exploitation increases (Bonfil, 1994).

Elasticity analysis can provide a method of prioritizing stages of a species life history that will respond to management options. However, once a stage is identified as having the largest elasticity, consideration of how elasticity of that stage changes with perturbation of other stages is important for successful management (Doak *et al*., 1994). This goes beyond the simple observation of elasticity and instead views the consequences of the dynamics of vital rates.

Our results indicate that partiontioning of elasticity varies across species life histories. A conservation plan for the short-lived little skate may be completely different from the long-lived barndoor skate. Thought, elasmobranch life histories are relatively invariant (cluster analysis) patterns of the response to perturbation and elasticity varies greatly between species. Elasticity and life history analyses can aid in the identification of vulnerable species and provide advice for conservation strategies targeting vital rates and stages.

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Table 1. Relationships of vital rates of elasmobranchs species with elasticity of model parameters. Where (juv) = juvenile stage; (adult) = adult stage and (fec.tr1,tr2) = inter-stage transitions. * indicates that the relationship was not significant.

Species groups	Equation	r^2	df	F	p
Elasmobranchs	e(juv) = 0.16•Ln(T_{max}) - 0.21	0.60	43	63.55	0.000
Elasmobranchs	e(adult) = 0.09•Ln(T_{max}) + 0.07	0.61	43	68.75	0.000
Elasmobranchs	e(f,tr1,tr2) = - 0.08•Ln(T_{max}) + 0.38	0.82	43	196.61	0.000
Elasmobranchs	e(juv) = 0.17•Ln(T_{mat}) - 0.05	0.94	43	735.42	0.000
Elasmobranchs	e(adult) = 0.05•Ln(T_{mat}) + 0.23	0.27	43	16.29	0.000
Elasmobranchs	e(f,tr1,tr2) = - 0.07•Ln(T_{mat}) + 0.27	0.90	43	390.07	0.000
Elasmobranchs	e(juv) = 0.07•Ln(L_{max}) + 0.13	0.10	42	4.69	0.036
Elasmobranchs	e(adult) = 0.05•Ln(L_{max}) + 0.08	0.13	42	6.54	0.014
Elasmobranchs	e(f,tr1,tr2) = - 0.04•Ln(L_{max}) + 0.35	0.15	42	7.47	0.009
Elasmobranchs	e(juv) = 0.11•Ln(L_{mat}) - 0.26	0.25	39	12.68	0.001
Elasmobranchs	e(adult) = 0.16•Ln(L_{mat}) + 0.03	0.09	39	4.08	0.050
Elasmobranchs	e(f,tr1,tr2) = - 0.05•Ln(L_{mat}) + 0.37	0.25	39	12.87	0.001
Requiem sharks	e(juv) = 0.19•Ln(T_{max}) – 0.27	0.71	19	47.30	0.000
Requiem sharks	e(adult) = 0.10•Ln(T_{max}) + 0.05	0.65	19	35.16	0.000
Requiem sharks	e(f,tr1,tr2) = - 0.09•Ln(T_{max}) + 0.40	0.88	19	135.24	0.000
Requiem sharks	e(juv) = 0.17•Ln(T_{mat}) – 0.05	0.93	19	258.46	0.000
Requiem sharks	e(adult) = 0.06•Ln(T_{mat}) + 0.22	0.39	19	12.42	0.002
Requiem sharks	e(f,tr1,tr2) = - 0.08•Ln(T_{mat}) + 0.28	0.91	19	201.02	0.000
Requiem sharks	e(juv) = 0.20•Ln(L_{max}) – 0.80	0.51	19	19.54	0.000
Requiem sharks	e(adult) = 0.08•Ln(L_{max}) - 0.12	0.31	19	8.73	0.008
Requiem sharks	e(f,tr1,tr2) = - 0.09•Ln(L_{max}) + 0.64	0.55	19	23.48	0.000
Requiem sharks	e(juv) = 0.18•Ln(L_{mat}) - 0.59	0.61	18	28.24	0.000
Requiem sharks	e(adult) = 0.06•Ln(L_{mat}) + 0.06	0.21	18	4.83	0.041
Requiem sharks	e(f,tr1,tr2) = - 0.08•Ln(L_{mat}) + 0.51	0.57	18	23.74	0.000
Houndsharks	e(juv) = 0.21Ln(T_{max}) - 0.38	0.62	7	11.49	0.012
Houndsharks	e(adult) = 0.09•Ln(T_{max}) + 0.06	0.50	7	6.94	0.034
Houndsharks	e(f,tr1,tr2) = - 0.10•Ln(T_{max}) + 0.44	0.84	7	36.82	0.001
Houndsharks	e(juv) = 0.16Ln(T_{mat}) - 0.06	0.95	7	138.64	0.000
Houndsharks	e(adult) = 0.04•Ln(T_{mat}) + 0.25	0.22	7	2.02	0.198*
Houndsharks	e(f,tr1,tr2) = - 0.07•Ln(T_{mat}) + 0.27	0.95	7	130.02	0.001
Houndsharks	e(juv) = 0.10•Ln(L_{max}) - 0.30	0.03	7	0.21	0.66*
Houndsharks	e(adult) = 0.15•Ln(L_{max}) - 0.45	0.29	7	2.82	0.14*
Houndsharks	e(f,tr1,tr2) = - 0.08•Ln(L_{max}) + 0.58	0.12	7	1.00	0.35*
Houndsharks	e(juv) = 0.31•Ln(L_{mat}) – 1.16	0.31	7	3.18	0.118*
Houndsharks	e(adult) = - 0.02•Ln(L_{mat}) + 0.41	0.00	7	0.00	0.82*
Houndsharks	e(f,tr1,tr2) = - 0.09•Ln(L_{mat}) + 0.58	0.17	7	1.44	0.27*
Skates	e(juv) = 0.21•Ln(T_{max}) + 0.38	0.43	7	5.31	0.050
Skates	e(adult) = 0.09•Ln(T_{max}) + 0.06	0.87	7	48.32	0.000
Skates	e(f,tr1,tr2) = - 0.05•Ln(T_{max}) - 0.28	0.91	7	68.65	0.000
Skates	e(juv) = 0.14•Ln(T_{mat}) - 0.004	0.98	7	512.831	0.000
Skates	e(juv) = 0.08•Ln(T_{mat}) + 0.16	0.24	7	2.18	0.18*
Skates	e(adult) = 0.18Ln(T_{mat}) + 0.03	0.03	7	0.20	0.67*
Skates	e(f,tr1,tr2) = - 0.07Ln(T_{mat}) + 0.28	0.74	7	19.50	0.003
Skates	e(juv) = 0.09•Ln(L_{max}) - 0.11	0.52	7	7.59	0.028
Skates	e(adult) = 0.07Ln(L_{max}) + 0.005	0.25	7	2.32	0.17*
Skates	e(f,tr1,tr2) = - 0.05Ln(L_{max}) + 0.37	0.51	7	7.44	0.029
Skates	e(juv) = 0.08•Ln(L_{mat}) - 0.014	0.47	6	5.37	0.06*
Skates	e(adult) = 0.07Ln(L_{mat}) + 0.06	0.23	6	1.75	0.23*
Skates	e(f,tr1,tr2) = - 0.05Ln(L_{mat}) + 0.32	0.51	6	6.12	0.048

Table 2. The results of varying exploitation levels and elasticity patterns for shark and skates species, where (juv) = juvenile stage; (adult) = adult stage and (fec,tr1,tr2) = inter-stage transitions.

	Little skate			Common skate			Dusky shark			Atlantic Sharpnose shark		
F	**e(juv)**	**e(adult)**	**e(f,tr1,tr2)**	**e(juv)**	**e(adult)**	**e(f,tr1,tr2)**	**e(juv)**	**e(adult)**	**e(f,tr1,tr2)**	**e(juv)**	**e(adult)**	**e(f,tr1,tr2)**
0	0.19	0.24	0.19	0.47	0.45	0.02	0.42	0.42	0.05	0.47	0.45	0.02
0.2	0.19	0.23	0.19	0.47	0.45	0.02	0.42	0.42	0.05	0.47	0.45	0.02
0.4	0.19	0.22	0.20	0.47	0.45	0.02	0.42	0.42	0.05	0.47	0.45	0.02
0.6	0.18	0.22	0.20	0.47	0.45	0.02	0.41	0.41	0.06	0.47	0.45	0.02
0.8	0.18	0.21	0.20	0.47	0.46	0.02	0.42	0.42	0.05	0.47	0.46	0.02
1	0.17	0.20	0.21	0.47	0.46	0.02	0.42	0.41	0.06	0.47	0.46	0.02
1.2	0.17	0.20	0.21	0.47	0.46	0.02	0.43	0.42	0.05	0.47	0.46	0.02
1.4	0.17	0.19	0.21	0.48	0.47	0.02	0.43	0.43	0.05	0.48	0.47	0.02
1.6	0.17	0.19	0.22	0.48	0.47	0.02	0.44	0.44	0.04	0.48	0.47	0.02
1.8	0.16	0.18	0.22	0.48	0.48	0.01	0.45	0.45	0.03	0.48	0.48	0.01
2	0.16	0.18	0.22	0.49	0.48	0.01	0.45	0.45	0.03	0.50	0.48	0.01
2.2	0.16	0.17	0.22	0.49	0.49	0.01	0.46	0.46	0.02	0.50	0.49	0.01
2.4	0.15	0.17	0.23	0.50	0.49	0.01	0.48	0.48	0.02	0.50	0.49	0.00
2.6	0.15	0.16	0.23	0.50	0.49	0.00	0.48	0.48	0.01	0.50	0.49	0.00
2.8	0.15	0.16	0.23	0.50	0.50	0.00	0.50	0.49	0.01	0.50	0.50	0.00
3	0.15	0.16	0.23	0.50	0.50	0.00	0.50	0.50	0.00	0.50	0.50	0.00

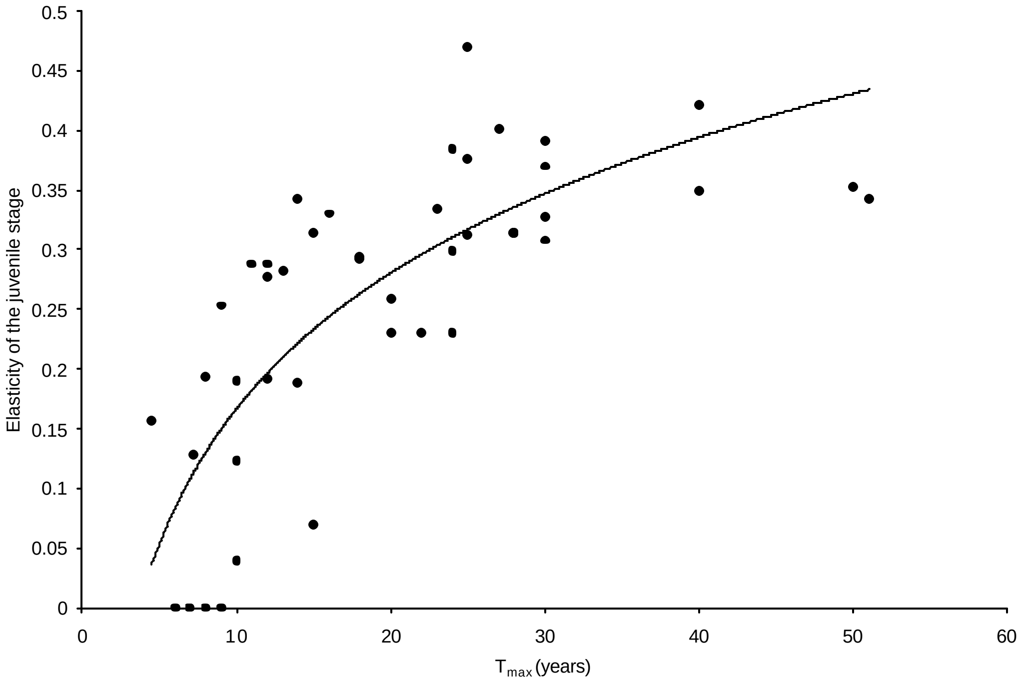

Fig.1. The relationship between elasticity of the juvenile stage and longevity (T_{max}). The least-squares relationship is given by e(juvenile) = 0.16•Ln(T_{max}) - 0.21 (n = 43, r^2 = 0.60, p = 0.00).

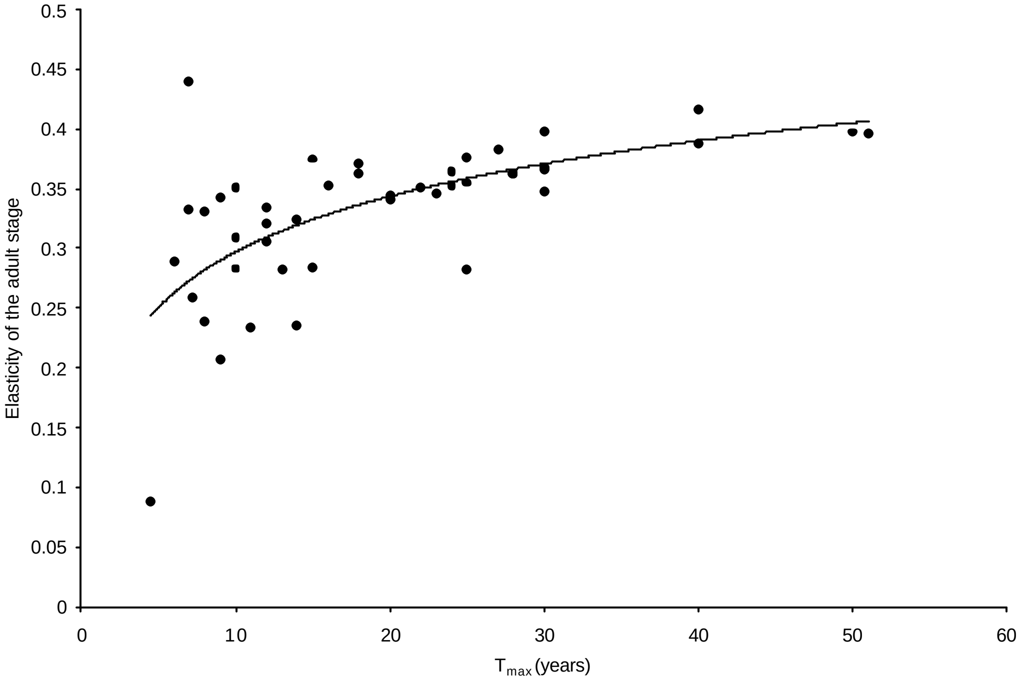

Fig. 2. The relationship between elasticity of the adult stage and longevity (T_{max}). The least-squares relationship is given by e(adult) = 0.09•Ln(T_{max}) + 0.07 (n = 43, $r^2 = 0.61$, p = 0.00).

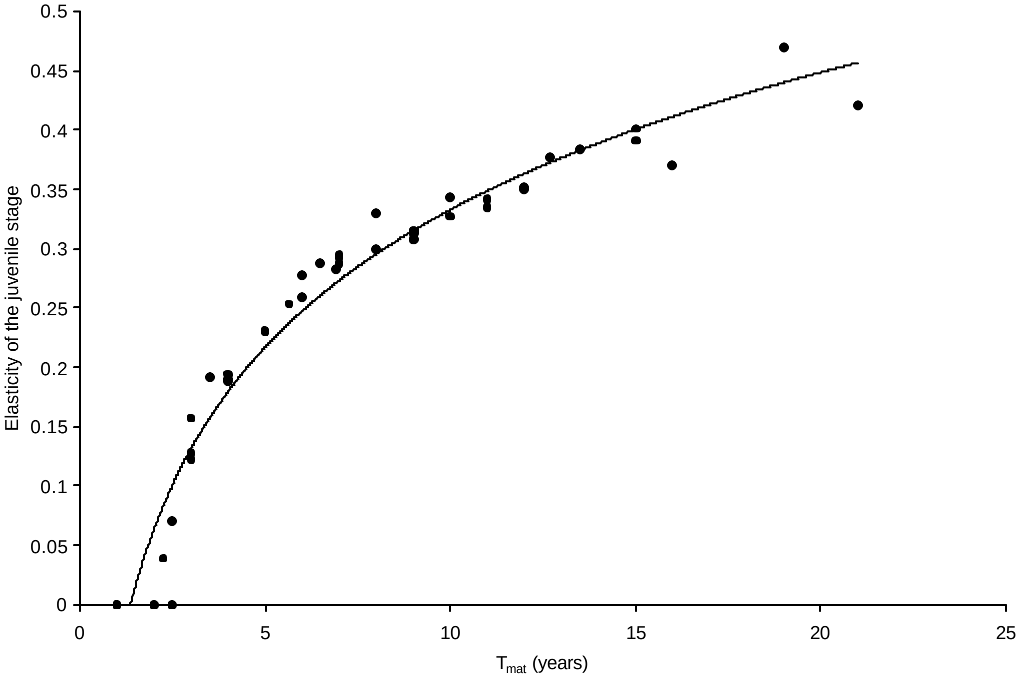

Fig. 3. The relationship between elasticity of the juvenile stage and age of maturation (T_{mat}). The least-squares relationship is given by e(juvenile) = 0.17•Ln(T_{mat}) - 0.05 (n = 43, $r^2 = 0.94$, p = 0.00).

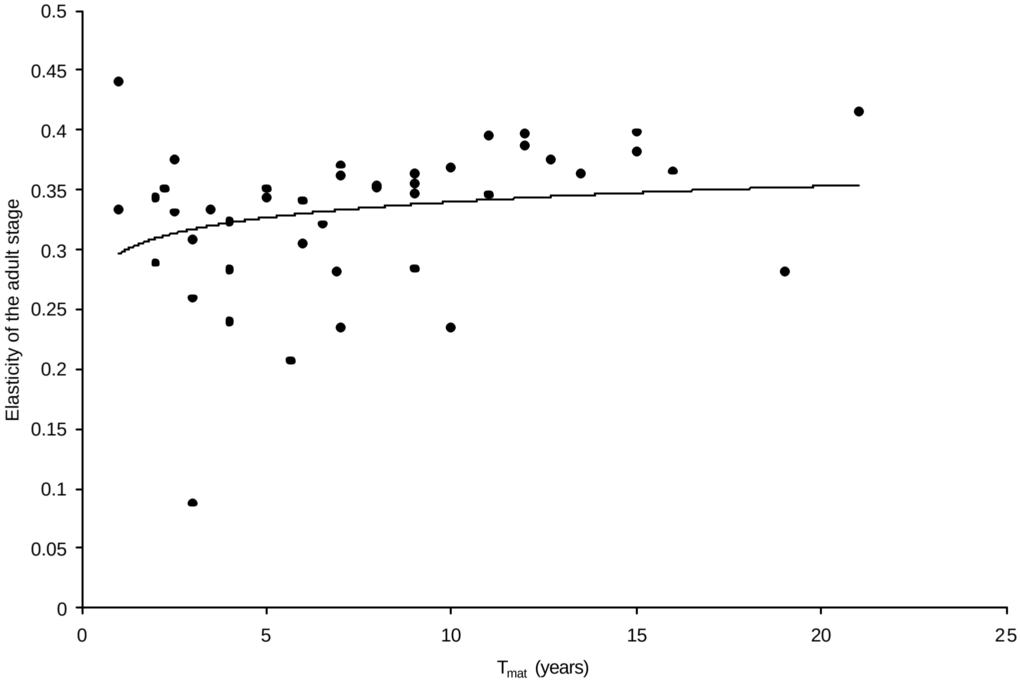

Fig. 4. The relationship between elasticity of the adult stage and age of maturation (T_{mat}). The least-squares relationship is given by e(adult) = 0.05•Ln(T_{mat}) + 0.23 (n = 43, r^2 = 0.27, p = 0.00).

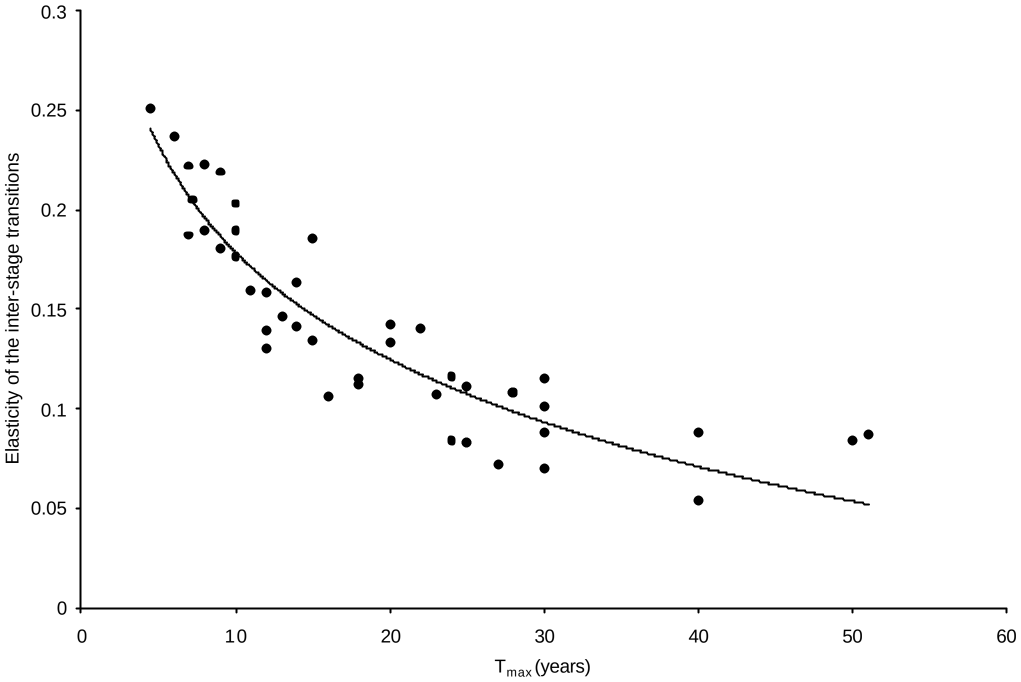

Fig. 5. The relationship between elasticity of the fecundity and the transition between stages and longevity (T_{max}). Note: in a three-stage model the elasticity of both transitional stages and fecundity will be the same. The least-squares relationship is given by e(inter-stage transitions) = - 0.08•Ln(T_{max}) + 0.38 (n = 43, r^2 = 0.82, p = 0.00).

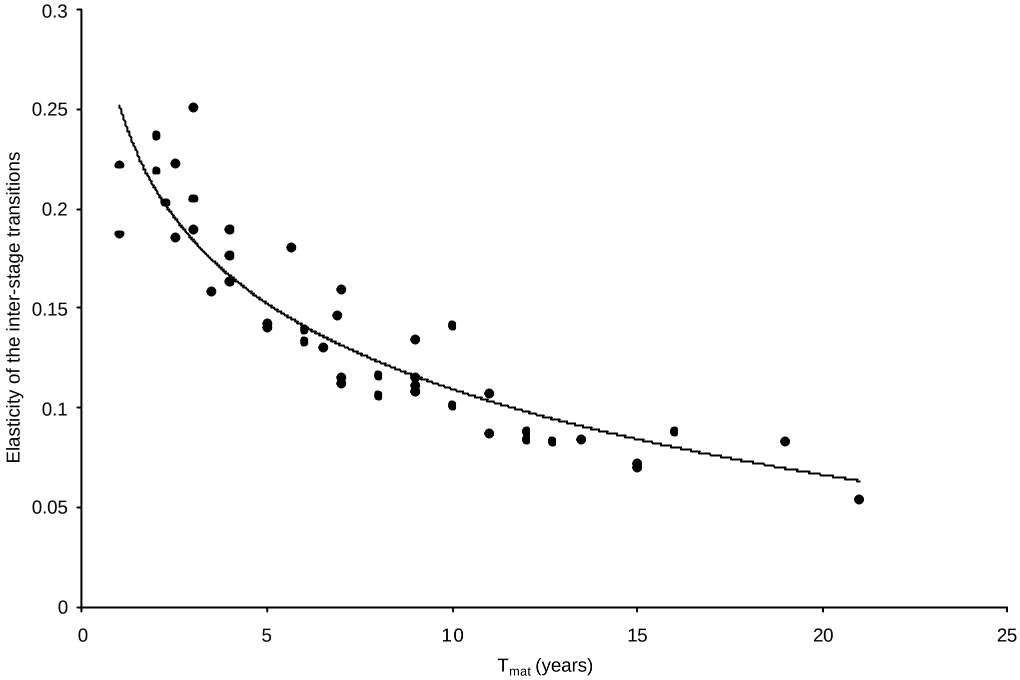

Fig. 6. The relationship between elasticity of the fecundity and the transition between stages and age of maturation (T_{max}). The least-squares relationship is given by e(inter-stage transitions) = - 0.07•Ln(T_{mat}) + 0.27 (n = 43, $r^2 = 0.90$, p = 0.00).

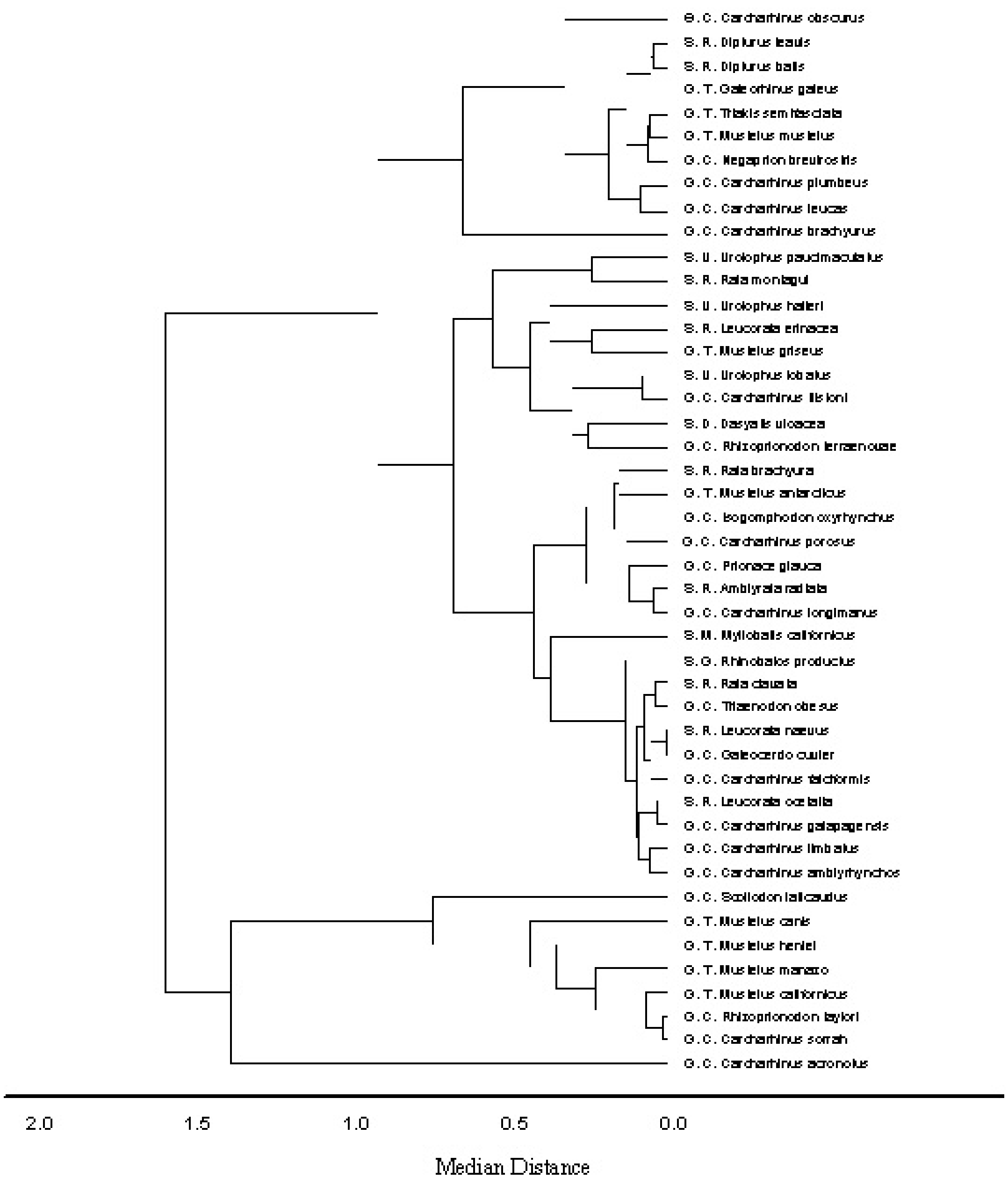

Fig. 7. A dendrogram shows clustering of elasticity patterns for elasmobranch species. Clusters were formed based on values of the elasticity of the juvenile stage, adult stage, and the fecundity and transitional stages. G = Galea, S = Squalea, C = Carcharhinidae, T = Tria kidae, R = Rajidae, U = Urolophidae, M = Myliobatidae, RR = Rhinobatidae.

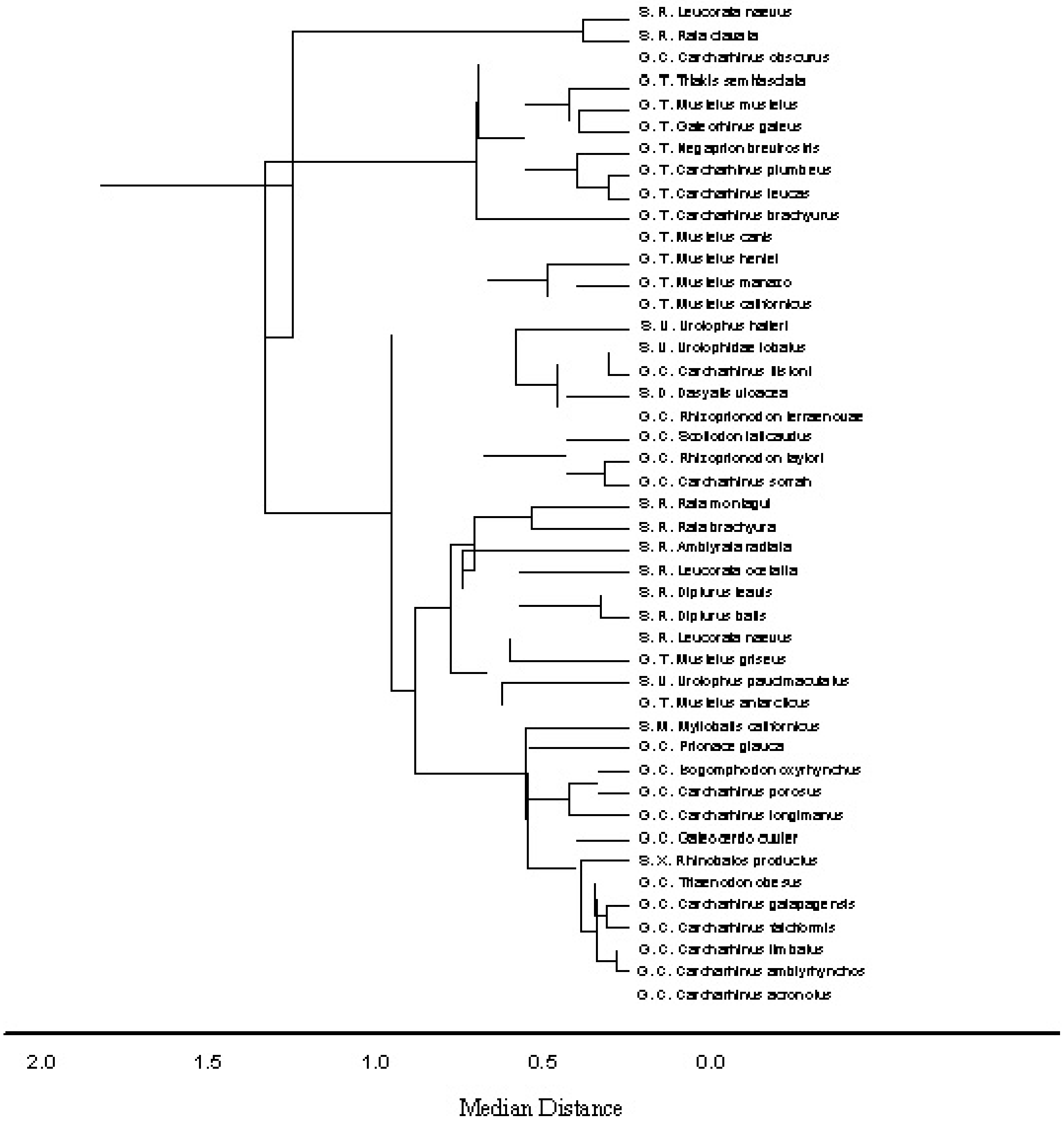

Fig. 8. A dendrogram shows clustering of elasticity patterns and reproductive characteristics of elasmobranch species. Clusters were formed based on values of the elasticity of the juvenile stage, adult stage, and the fecundity and transitional stages and age of maturation (T_{mat}), fecundity and reproductive mode. G = Galea, S = Squalea, C = Carcharhinidae, T = Triakidae, R = Rajidae, U = Urolophidae, M = Myliobatidae, RR = Rhinobatidae.

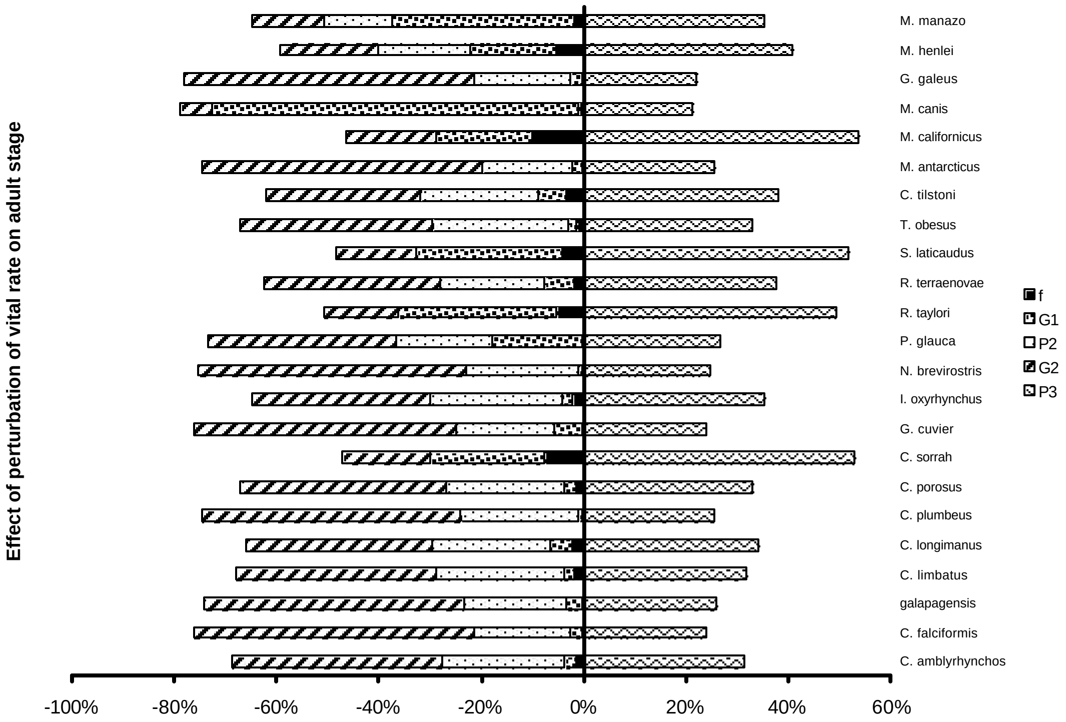

Fig. 9. The sensitivities of elasticity of the adult stage are shown for species in the superorder Galea for each stage of the matrix. The sensitivities to elasticity are shown as a percentage.

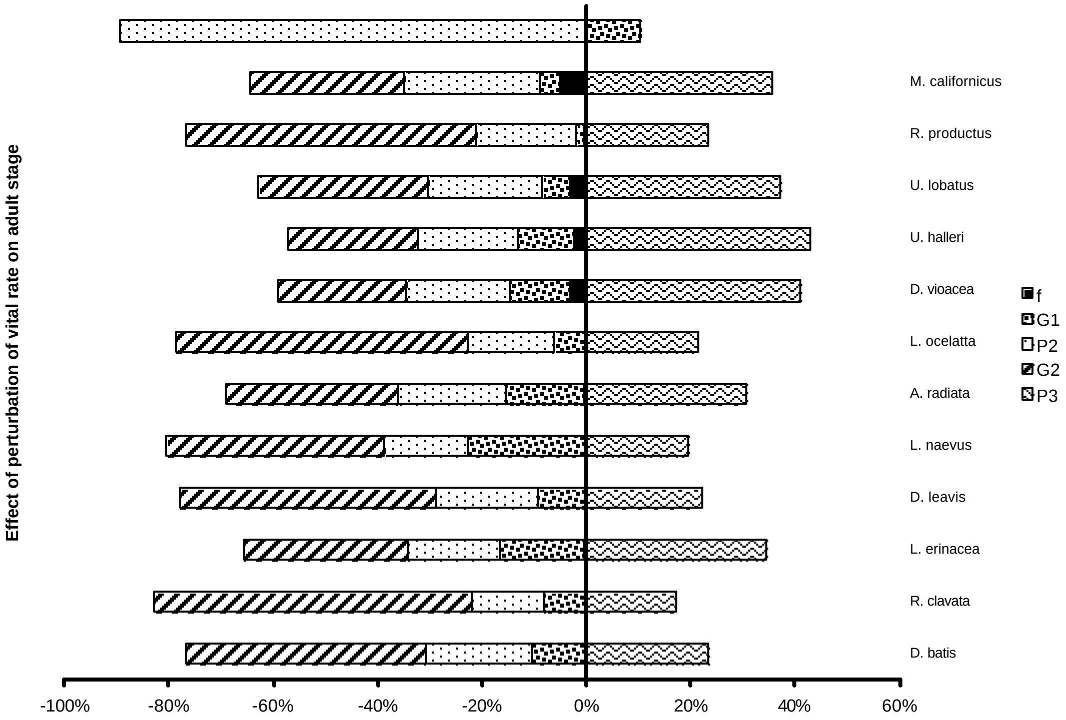

Fig. 10. The sensitivities of elasticity of the adult stage are shown for species in the superorder Squalea for each stage of the matrix. The sensitivities to elasticity are shown as a percentage.

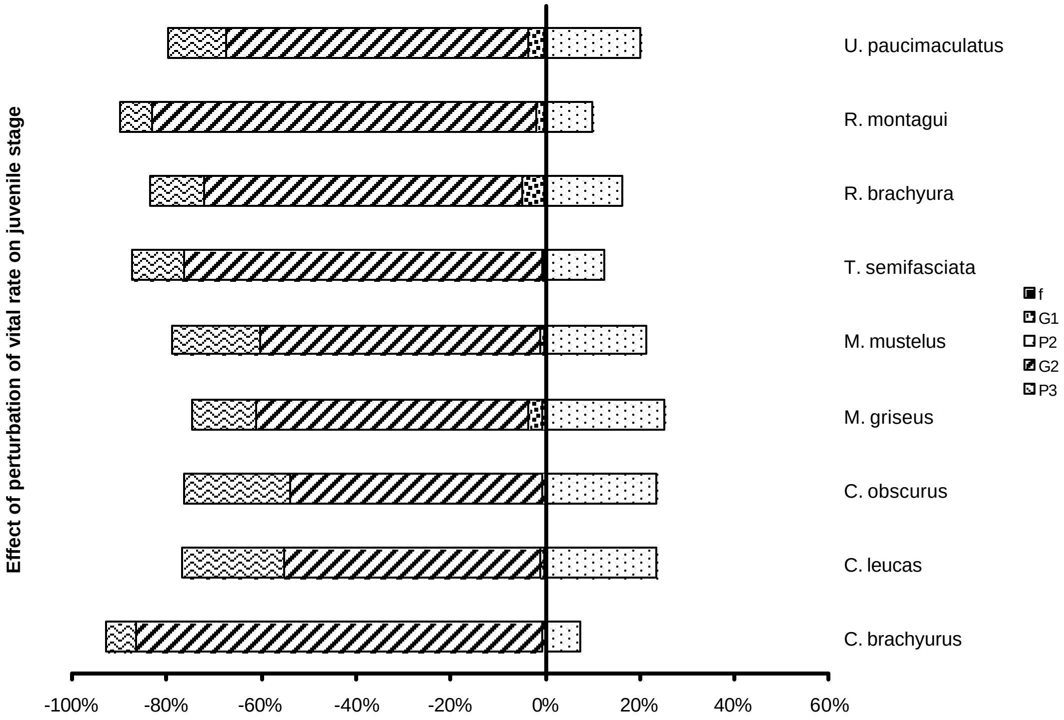

Fig. 11. The sensitivities of elasticity of the juvenile stage are shown for species of the superorders Squalea and Galea for each stage of the matrix. The sensitivities to elasticity are shown as a percentage.