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## Deep-Sea Research II

journal homepage: [www.elsevier.com/locate/dsr2](http://www.elsevier.com/locate/dsr2)

## Patterns in life history traits of deep-water chondrichthyans



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## ARTICLE INFO

Available online 11 September 2013

## Keywords:

Chondrichthyes  
 Deep water  
 Life history traits  
 Age  
 Growth  
 Longevity  
 Body size  
 Habitat  
 Productivity

## ABSTRACT

Life history traits are important indicators of the productivity of species, and their ability to tolerate fishing pressure. Using a variety of life history traits (maximum size, size and age at maturity, longevity, growth rate, litter and birth size) we demonstrated differences in chondrichthyan life histories between shelf, pelagic and deep-water habitats and within the deep habitat down the continental slope and across geographic regions. Deep-water species had lower growth rates, later age at maturity, and higher longevity than both shelf and pelagic species. In the deep habitat, with increasing depth, species matured later, lived longer, had smaller litters and bred less frequently; regional differences in traits were also apparent. Deep-water species also had a smaller body size and the invariants of relative size and age at maturity were higher in deep water. The visual interaction hypothesis offers a potential explanation for these findings and it is apparent habitat influences the trade-offs in allocation of energy for survival and reproduction. Body size is not appropriate as a predictor of vulnerability in deep-water chondrichthyans and regional trait differences are possibly due to a fishing pressure response. Deep-water chondrichthyans are more vulnerable to exploitation than shelf and pelagic species and this vulnerability markedly increases with increasing depth. The life history traits of deep-water chondrichthyans are unique and reflect adaptations driven by both mortality and resource limitations of their habitat.

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## 1. Introduction

Chondrichthyans have a suite of life history traits that, in comparison to teleosts, lower their productivity and ability to tolerate fishing pressure (Simpfendorfer et al., 2011). They are generally slow growing, late maturing, have low fecundity, long gestation periods and long life spans that results in low reproductive output (Hoenig and Gruber, 1990). This is a successful strategy for their environment where the main natural predator is larger sharks and they only need to produce a few young capable of reaching maturity to maintain population levels (Cailliet et al., 1990; Cortés, 2000). Yet this is also a strategy that reduces their capacity to recover from exploitation and thereby increases their vulnerability to human disturbances (Stevens et al., 2000; Devine et al., 2006; Field et al., 2009). There is a wide range of chondrichthyan life histories, and species studied to date vary in their degree of vulnerability (Smith et al., 1998; Cortés, 2002; Dulvy and Forrest, 2010), though this is mostly based on shelf and pelagic species with less knowledge of deep-water chondrichthyans. Life history traits are useful indicators of productivity (Simpfendorfer and Kyne, 2009) and the increase in deep-water

life history studies in recent years has provided an opportunity to more closely examine patterns in the traits of this group.

Evolution of life history traits is a selective and adaptive response to a complex interaction of density dependence, resource availability, environmental conditions and extrinsic mortality (Reznick et al., 2002), with on-going debate about the relative importance of these factors (Ricklefs, 2000; Dulvy and Forrest, 2010). Variations in resource availability, mortality and environmental conditions between marine habitats are hypothesised to play a major role in patterns of life history traits (García et al., 2008). Differences are apparent in both fish and chondrichthyan traits among three distinctive marine habitats: continental shelf, pelagic open ocean and deep sea (Koslow et al., 2000; Cailliet et al., 2001; Clarke et al., 2003; García et al., 2008; Norse et al., 2012). The continental shelf is the most productive and diverse habitat encompassing waters from the intertidal to 200 m depth and contains the majority of the world's chondrichthyan species (Compagno, 1990). The pelagic open ocean, a far less diverse habitat, extends beyond the edge of the shelf and into the ocean basins with generally low productivity, except in some areas of near-surface waters where the abundant light contributes to primary productivity (Robison, 2004). Pelagic chondrichthyans are highly mobile species that primarily inhabit the open ocean waters and account for ~2% of the global chondrichthyan diversity (Stevens, 2010).

The deep sea reaches from the 200 m edge of the shelf to the maximum depths of the ocean and is a relatively stable habitat of

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low productivity, low temperatures, high pressures, dim to absent light and limited food (Angel, 1997; Gartner et al., 1997; Gibbs, 1997). However it is not a completely uniform habitat as these parameters vary, particularly on the upper to mid continental slope where a thermocline from 200 m down to 1000 m drops the temperature rapidly to just above freezing and varies with circulation patterns of the ocean, latitude and season (Marshall, 1979). Light levels diminish down this slope to the limit of visible light at 1000 m, beyond which it is permanently dark (Angel, 1997). Food availability declines rapidly down the slope and beyond as it sinks to the seafloor, yet this appears to vary not just with depth but also with season and region as it likely reflects seasonal surface productivity that varies among oceanic regions (Robison, 2004; Drazen and Haedrich, 2012; Norse et al., 2012).

Deep-water chondrichthyans rarely occur below 3000 m (Priede et al., 2006) and the currently 530 known species (Kyne and Simpfendorfer, 2010) account for almost half of the world's estimated 1200 species of chondrichthyans. They are a diverse group dominated by dogfish (Squaliformes), skates (Rajidae, Arynchobatidae and Anacanthobatidae) and the highly speciose catsharks (Scyliorhinidae), with the majority of species geographically and bathymetrically restricted and high levels of endemism among the lantern sharks (Etmopteridae), catsharks and skates (Kyne and Simpfendorfer, 2010). While life history data is lacking for most deep-water species, adequate data on dogfish, skates and some other taxa was previously available for analysis. This indicated that deep-water chondrichthyans have a set of life history traits common to the deep habitat and beyond phylogenetic relationships: they grow more slowly, mature later and live longer than their relatives in the shelf and pelagic habitats (García et al., 2008). They are considered to have even lower productivity and hence greater vulnerability to exploitation than the chondrichthyans in these shallower habitats (García et al., 2008; Simpfendorfer and Kyne, 2009). Consequently, their extinction risk from fishing pressure is also higher. García et al., 2008 estimated that the fishing mortality that would drive deep-water species to extinction was 58% of shelf species and just 38% of pelagic species. There is also evidence that within the deep-water habitat this vulnerability to fishing increases with increasing depth and that viviparous species in the deep habitat are more vulnerable than oviparous species (Simpfendorfer and Kyne, 2009).

The association of life history traits with habitat and the lower productivity of deep-water chondrichthyans have been variously attributed to environmental conditions (temperature), resource availability (food) and mortality (predator–prey interactions) (García et al., 2008; Simpfendorfer and Kyne, 2009). Low temperatures and limited food logically may result in slow growth rates that lead to late maturity and these factors along with possible effects of pressure and lower oxygen levels have also been offered as the cause of similar traits and reduced metabolism with depth in deep-water fish (Vetter and Lynn, 1997; Cailliet et al., 2001; Gordon, 2001; Drazen and Haedrich, 2012). However, the observed decreases in metabolic rates and growth rates often cannot be entirely accounted for by such parameters as low temperatures, limited food, increased pressure and lower oxygen (Robison, 2004; Seibel and Drazen, 2007). An alternative hypothesis suggested by Childress et al. (1980) was that declining light levels with depth reduce the reactive distances between predator and prey which relaxes the selective pressure on rapid locomotory capacity providing an opportunity for reduced energy expenditure and a decline in metabolic rates. Conversely, in the pelagic habitat with reasonable light levels and no refuges from predators, there is a need for strong locomotory capacity and much higher metabolic rates (Childress, 1995). Shelf waters tend to be more turbid, providing more opportunities for refuge from predators and reducing the distance over which predators and prey interact and thus lessening the need for metabolic rates to be as high as

those in pelagic habitats (Childress and Somero, 1990; García et al., 2008). This visual interactions hypothesis is supported by differences in metabolic rates and other physiological characteristics with depth for visual and non-visual taxa. The metabolic rates of visual fauna such as fishes, cephalopods and active crustaceans decline rapidly in the first 500 m and then level off below around 1000 m where light is absent. In contrast, no such depth related declines in metabolic rates are evident in non-visual animals such as echinoderms, cnidarians and worms (Childress, 1995; Seibel et al., 2000).

This hypothesis may not provide the only explanation for the observed patterns in traits. While it deduces that the decrease in metabolic and growth rates is not due to food availability, in the deep habitat where food is limited and creates a resource or energy poor environment it may be a relevant factor to the selection pressure on other life history traits. Life history theory is based on the concept that the finite energy available in the environment imposes constraints or trade-offs in the allocation of this energy among life history traits (Dulvy and Forrest, 2010). Beverton and Holt (1959) identified that these trade-offs were expressed in relationships between growth, age and size at maturity and adult mortality rate (and hence longevity) that are relatively consistent among a wide range of taxa. These relationships are referred to as life history invariants, or 'rules of life', and provide insight into patterns in life history traits. Invariants have been published for some groups of sharks, elasmobranchs and skates (Cortés, 2000; Frisk et al., 2001; Frisk, 2010), but never for chondrichthyans as a whole.

We aimed to examine the association of habitat and life history traits among the three broad marine habitats and also within the deep habitat. To separate habitat from phylogenetic effects we used an analytical approach that controlled for the correlation among species due to their common evolutionary history (García et al., 2008; Chamberlain et al., 2012). Specifically we (1) reassessed the association of chondrichthyans traits between shelf, pelagic and deep habitats with a larger and more diverse range of species than previously considered, (2) investigated the relation of traits within the deep habitat to depth and geographic region, (3) compared invariants and other relationships between traits among shelf, pelagic and deep habitats, (4) assessed whether body size varied among the three marine habitats and with increasing depth within the deep habitat, and (4) examined associations of reproductive mode, body size and habitat.

## 2. Methods

### 2.1. Data

Life history trait data were obtained from 226 populations (144 species) of chondrichthyans: 56 deep, 29 pelagic and 141 shelf populations. The maximum body size ( $S_{max}$ ), size at maturity ( $S_m$ ), age at maturity ( $T_m$ ), longevity ( $T_{max}$ ) (both observed  $^oT_{max}$  and theoretical  $^tT_{max}$ ) and von Bertalanffy growth constant ( $k$ ) (von Bertalanffy, 1938) were collated for females (F) and males (M) separately. Size at birth ( $S_{birth}$ ), litter size ( $l$ ), interbirth interval ( $I_i$ ) (the interval in years between births) and reproductive mode ( $R_m$ ) were collated by populations, though not all populations had available data for  $l$  or  $S_{birth}$  (Table A.1 in the electronic supplementary material). The data were organised at population level where available so as not to exclude the variability in life history traits exhibited by some species (Cortés, 2000; Cope, 2006). The area of occurrence of the species or population's life history data was described using the FAO Fishing Areas (the Food and Agriculture Organisation of the United Nation's Major Fishing Areas for Statistical Purposes) with the taxonomic classification and species names

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