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A continuum of life histories in deep-sea demersal fishes

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ABSTRACT

It is generally perceived that all deep-sea fishes have great longevity, slow growth, and low reproductive output in comparison to shelf dwelling species. However, such a dichotomy is too simplistic because some fishes living on continental slopes are relatively fecund and fast growing, important considerations in respect to the management of expanding deep-sea fisheries. We tested two hypotheses that might explain variation in life history attributes of commercially exploited demersal fishes: (1) phylogeny best explains the differences because deep-sea species are often in different families from shelf dwelling ones and, alternatively, (2) environmental factors affecting individual life history attributes that change with depth account for the observed variation. Our analysis was based on 40 species from 9 orders, including all major commercially exploited deep-sea fishes and several phylogenetically related shelf species. Depth of occurrence correlated significantly with age at 50% maturity increasing linearly with depth (r^2=0.46), while the von Bertalanffy growth coefficient, maximum fecundity and potential rate of population increase declined significantly and exponentially with depth (r^2=0.41, 0.25 and 0.53, respectively). These trends were still significant when phylogenetically independent contrasts were applied. The trends were also consistent with similar slopes amongst members of the order Gadiformes and the order Scorpaeniformes. Reduced temperatures, predation pressure, food availability, or metabolic rates may all contribute to such changes with depth. Regardless of the mechanisms, by analyzing a suite of fishes from the shelves to the slope the present analysis has shown that rather than a simple dichotomy between deep-sea fishes and shelf fishes there is a continuum of life history attributes in fishes which correlate strongly with depth of occurrence.

1. Introduction

Marine fisheries are classified almost exclusively according to their geography i.e. coastal, shelf, high latitude, high seas, and so on. Over the last 50–60 years fishers have increasingly exploited fish stocks in deeper and deeper water (Morato et al., 2006b) and the term "deep-sea fishery" for those conducted mainly below 200 is now commonplace. Some deep-sea species have extreme life history characteristics that make them particularly vulnerable to fishing. Great longevity, slow growth and low fecundity are often considered typical features of deep-sea fish species and many papers often make categorizations of species as either deep or shallow (e.g. Garcıa et al., 2008; Koslow et al., 2000; Morato et al., 2006a). This has led some to the conclusion that all deep-sea fish stocks have low productivity. If we were to consider any species living on the continental slope as a deep-sea species then this supposition can quickly be proven false. Species such as hoki and blue ling are captured to depths of 700 and 1200 m respectively, yet they grow relatively fast and are highly fecund (Schofield and Livingston, 1998; Thomas, 1987). This situation clearly illustrates the problems with using broad classifications and begs the question as to why some deep-sea fishes appear to be productive and capable of supporting fisheries while others do not.

Phylogenetic classification to reflect the evolutionary history of the harvested species could provide some insights for management. Some families or orders of fishes are found principally in the deep-sea where they have apparently evolved and diversified for instance the Stomiiformes and Myctophiformes. These groups are relatively small pelagic fish and therefore of little commercial interest. In the North Atlantic, the orders Gadiformes is a particularly important demersal group with species of commercial interest (Merrett and Haedrich, 1997). Some families within the order are principally found on the continental shelf and others on the slope or even the abyss. For instance, Grenadiers (family Macrouridae) are the gadiform family most widely exploited in deepwaters globally. Cods (family Gadidae) are the gadiform family most exploited on the shelf including such species as Atlantic cod. Differences in the life history attributes of each

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family are apparent. Grenadiers are typically late maturing with slow growth and metabolism whereas cods have much greater growth and metabolic rates (Drazen, 2008). It is possible that evolutionary lineage explains variation in the productivity and life histories of deep-sea fishes.

Another view considers the environmental continuum and ecological forces acting on individual species' biology. Features such as metabolism decline exponentially with depth of occurrence (Drazen and Seibel, 2007; Seibel and Drazen, 2007). With increasing depth many environmental variables change rapidly including light levels, food availability, temperature, pressure, and in some areas oxygen concentration. Thus there is an alternative hypothesis: not all deep-sea species are equal with regards to life history and productivity because they occupy different depth levels within a gradient of environmental change.

Phylogenetic and depth-related hypotheses are not mutually exclusive but are a challenge to separate. Different families of fishes are predominant on the continental shelves and upper slopes and still others dominate lower slope and abyssal habitats. Our goal was to explain variation in the life histories and productivities of deep-sea fishes that are commercially exploited. We have taken a meta-analysis approach, assembling data on all of the major commercially exploited deep-sea fishes along with several phylogenetically related shelf dwelling species. These data were evaluated using depth as a continuous variable while taking into account phylogenetic relationships. We have not included data for elasmobranchs because a recent review of their life histories has already been completed (Garcıa et al., 2008).

2. Methods

Data on the productivity and life history of deep-sea fishes were extracted from the peer-reviewed literature and from the online database www.fishbase.org (Froese and Pauly, 2008). Data were also compiled for eight shelf dwelling species phylogenetically related to at least one commercially exploited species living on the continental slope for a total of 40 species of fishes in 9 orders (Table 1). For some species data were available from multiple populations or studies (i.e. Atlantic cod). We used mean values because we wanted to evenly weight species in our statistical analysis.

The biological variables used were related to longevity, growth and reproduction. Maximum longevity ($A_{\max}$) is related to the rate of natural mortality, i.e. the mortality rate observed in an unexploited population. Age at 50% maturity (A_{50}) is related to growth rate and generation time. Most fisheries scientists use the von Bertalanffy equation to parameterize growth so its K coefficient or rate constant, which describes the rate of growth to the asymptotic size (Cailliet et al., 2006), was also used. This value is for both sexes combined except for a few cases when only data for separate sexes were available, in which case data for females were used. Age and growth data are derived from studies of otoliths. Early studies were concerned with interpretation of the otolith rings as annuli but deep-sea habitats do exhibit seasonal variations in food supply (Smith et al., 2006, 2001) and a growing body of studies validate the periodicity of the rings using isotope and other techniques (Morales-Nin and Panfili, 2005). Radiometric validation has occurred for orange roughy, oreos, Pacific and giant grenadier, rockfishes, and Patagonian toothfish (see references cited in Table 1). Annual fecundity is one metric of annual reproductive effort for which data are available across many species. Egg sizes vary inversely with fecundity and deeper living species often have larger egg diameters (Koslow et al., 2000) but all the species evaluated are broadcast spawners and none have very large eggs such as those found in demersal egg layers (Sargent et al., 1987). Maximum fecundity data ($F_{\max}$) were compiled as the fecundity of the largest females but most individuals do not reach this size. Therefore, we also used the fecundity at the size of 50% maturity (F_{50}). Some life history variables co-vary with species size so we also tabulated the maximum size ($L_{\max}$) and size at 50% maturity (L_{50}) using length measurements. Other variables such as natural mortality could have been used but are often derived from and directly related to other variables in the table such as longevity. We did calculate the potential rate of population increase ($r^1 = \ln(F_{50})/A_{50}$) which incorporates both basic metrics of productivity (Jennings et al., 1998). This metric has been used for deep-sea fishes before but with a very limited number of species (Clarke, 2003).

To evaluate the environmental influence on life history parameters, the biological variables were regressed on depth of occurrence. Linear regressions but also exponential regressions were applied because many environmental variables such as food supply and temperature have exponential functions to depth. Depth ranges of adult fishes were tabulated to include the common depths of occurrence (minimum, maximum, and median), rather than occasional captures at extremes. In some instances depth ranges were difficult to ascertain. Some species undergo ontogenetic vertical migration the affects of which we have attempted to minimize by using data on adults. Some species exhibit polar emergence. For instance the giant grenadier is found no shallower than about 700 m off California (Lauth, 2000; Miller and Lea, 1972) but at 300 m in the Bering sea (Clausen, 2008). In such cases we have used a depth range for the population at roughly the midpoint of its latitudinal range.

To evaluate whether the trends held in spite of phylogenetic covariance we applied the method of phylogenetically independent contrasts (Felsenstein, 1985). The basic phylogenetic relationships between the species was used following (Nelson, 2006) by constructing a rooted tree in the program Mesquite. The contrasts were applied using the "ape" package in the R programming environment (Paradis, 2006; Paradis et al., 2004). This approach reruns the regression model after removing the expected degree of covariance (i.e., expected family resemblance) from the data (Felsenstein, 1985).

3. Results

Regressions between minimum, maximum and median depths of main occurrence and the life history attributes yielded several significant relationships (Table 2). A_{50}, K, $F_{\max}$ and r^1 were significantly correlated to all three metrics of depth (in all cases $p < 0.001$). In each case minimum depth of occurrence explained the most variability, although for K, the differences in fit to each depth metric were slight. Depth explained the greatest amount of variability in the potential rate of population increase ($r^2 = 0.53$), a decline with depth best represented by a negative exponential function indicating greater change in productivity at shallower depths than deeper (Fig. 1). K also showed a negative exponential relationship with depth whereas A_{50} showed a positive linear increase with depth. $A_{\max}$ was only weakly correlated ($r^2 = 0.12$, $p < 0.05$; Table 2) to minimum depth. $F_{\max}$ declined exponentially with each metric of depth. So did F_{50} but these relationships were not significant. It is well known that size strongly affects fecundity and we found a weak correlation between $L_{\max}$ and $F_{\max}$ in our data. However, there is no significant relationship between $L_{\max}$ and depth (Table 2). There was a significant increase in L_{50} with depth but only when regressed on maximum depth. If only size were affecting the pattern in fecundity then such a trend should lead to increased fecundity with depth.