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Bathymetric gradients of fecundity and egg size in fishes: A Mediterranean case study

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ABSTRACT

There is a general hypothesis that species inhabiting deep-sea waters have lower fecundity and larger eggs than shallower species. However, there are few comparative studies which explore this trend because of the complexity of sampling in deep waters, especially in fishes. We present here the first analysis of fecundity and egg size with depth along an isothermal environment. We calculate the relative fecundity and egg size of 11 species of demersal deep-sea fish from the western Mediterranean and included in our analyses published data for an additional 14 species from the same geographic area. The results show that the relative fecundity (eggs per g of individual) of the analyzed fishes slightly decreased along the bathymetric gradient, whereas egg size increased with depth. When the analysis was conducted including only species from the order Gadiformes, the most speciose group in the region and with the widest depth range of distribution (50–2000 m), there was no relationship between relative fecundity and depth, while the deepest species had larger egg sizes than shallower ones. The finding of similar relative fecundities but larger egg sizes suggests that these deep-sea species are investing a higher amount of energy in the production of offspring than shallower water counterparts. The results are discussed in relation to the isothermal characteristics of the deep Mediterranean Sea and ecological adaptations for reproductive success.

1. Introduction

In recent decades, commercial fishing is occurring at increasing depths around the globe (Gordon et al., 2003; Swartz et al., 2010; Norse et al., 2012) and many important fish stocks have collapsed (Coll et al., 2008; Pontecorvo and Schrank, 2014). To understand population productivity and thus increase our predictive power for the management and conservation of marine ecosystems, it is crucial to have precise knowledge of life-history strategies (Jorgensen al., 2007; Clark et al., 2012; Hilário et al., 2015) and, in particular, the reproductive capacity of the species involved. Furthermore, the influence of environmental factors on fish fecundity and productivity is now relevant to improve our understanding of the effect of climate change in marine ecosystems (Kjesbu et al., 1998; Morgan et al., 2013). Despite its importance, the reproductive capacity of many fish species is still unknown (Hutchings and Baum, 2005). This is especially true for deep-sea species for which there is a scarcity of reproductive data because of the extreme difficulties and cost in exploration and sampling (Bergstad, 2013).

The assessment of fecundity and egg size is essential to understand the life-history evolution and adaptation of species to their environment (Roff, 1992; Stearns, 1992). Several authors have studied the latitudinal and bathymetric patterns of fecundity and egg sizes between phylogenetically-related species as well as between higher taxonomic groups (Thresher, 1988; Fleming and Gross, 1990; Johnston and Leggett, 2002; Vila-Gispert et al., 2002; Laptikhovsky, 2006; Finotto et al., 2015). Additionally, studies on timing of spawning and fecundity are fundamental topics in the biology and population dynamics of organisms (Lambert, 2008; Wright and Trippel, 2009; Lowerre-Barbieriet al., 2011).

Fecundity and egg size have been recognized as two of the main variables in the life-history strategies for invertebrates

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(Chambers, 1997; Ramirez-Llodra, 2002; Marshall and Keough, 2007) and fishes (Winemiller and Rose, 1992). Several processes, such as ovarian organization and development, are mostly phylogenetically constrained (Eckelbarger and Watling, 1995). However, the number and size of eggs is not a conservative character and can vary depending on female characteristics and environmental factors (Ramirez-Llodra, 2002). In fish, several studies have demonstrated a positive relationship between total fecundity and fish length (Merrettt, 1994; Rideout and Morgan, 2010) and mass (Johnston and Leggett, 2002; McBride et al., 2015) whereas the relationship between relative fecundity (i.e. fecundity standardized to the body mass) and size is not so clear and depends on the species. Both, total fecundity (standing stock of vitellogenic oocytes) and relative fecundity are modulated by environmental conditions, mainly by temperature and food availability. A decrease in food availability can cause a decrease in energy transfer to the gonads, resulting in a decrease either in yolk accumulation (e.g., smaller eggs) or the number of eggs produced (Kjesbu et al., 1991; Rideout et al., 2000; McBride et al., 2015). Higher fecundity has been related to physiological change during development caused by temperature (Kjesbu et al., 1998, 2010; Kraus et al., 2000; Pörtner et al., 2001; Marshall et al., 2010). Due to the usually low temperature and food scarcity in deep-sea ecosystems, Thorson (1950) predicted that benthic deep-sea invertebrates would show lower fecundity and larger egg sizes compared to shallow-water species. Indeed, this is the pattern most commonly observed in invertebrates, but it is not universal (Young, 2003; Ross et al., 2013). In fishes, the few intra- and inter-specific studies conducted to date also describe a negative correlation between maximum total fecundity and depth (Gibson, 2007; Drazen and Haedrich, 2012).

Because of the transitional nature of the continental slopes and their steep environmental and biological gradients, the study of bathyal species offers a good opportunity to understand the influence of a number of factors on the life histories of marine species (Company and Sarda, 1997; Levin and Dayton 2009). In addition, the Mediterranean Sea, offers a unique environmental setting for the study of ecological patterns along bathymetric gradients, where one of the most influential variables, temperature, remains constant at about 13 °C below the thermocline (Margalef, 1985; Sardà et al., 2004). Despite the low number of studied species in the deep Mediterranean, apparently similar bathymetric trends of fecundity are evident among invertebrate species (Company and Sarda, 1997; Sardà et al., 2009). For deep-sea Mediterranean fishes, only a few descriptive studies have analyzed fecundity (D'Onghia et al., 2008; Muñoz et al., 2010; Fernandez-Arcaya et al., 2012, 2013a) and evaluation of bathymetric patterns of fish fecundity and egg size at the community level is still lacking.

To address this knowledge gap, we compared the reproductive output of 25 fish species belonging to 9 orders in the western Mediterranean. We included also a specific analysis of the order Gadiformes, to evaluate phylogenetic effects, as this is the group with the widest depth range of distribution (50–2000 m). The objective of our study was to answer the following questions: (1) Does fish relative fecundity decrease and egg size increase along a bathymetric gradient in the Mediterranean Sea? and (2) What are the dominant forces driving the reproductive capacity of these species?

2. Materials and methods

2.1. Sampling

Data were obtained from 9 oceanographic cruises conducted in the western Mediterranean (41°34′N, 02°50′E–41°15′N, 02°48′E) based on a seasonal sampling over two annual cycles in 2008–2009 and 2012–2013. In total, 95 benthic trawls were conducted between depths of 400 and 2750 m, at 150 m intervals, to obtain a representative bathymetric dataset of demersal fish from the study area (Fig. 1). The sampling was conducted seasonally to cover the reproductive period of the different species, with cruises in March, May, September and October (2009); March, May, October (2012) and April (2013). All sampling was conducted on board the R/V *García del Cid* using the otter-trawl Marieta system (OTMS) fitted with a codend mesh of 40 mm (Sardà et al., 1998). The OTMs mouth opening was estimated at 12.7 ± 1.3 m horizontally and 1.4 m vertically. The OTMS was trawled at 2.6–2.8 knots with bottom haul times of approximately 40–60 min.

On board, all fish individuals were identified to species level, measured to the nearest 0.1 cm and weighed to the nearest 0.1 g. The standard length was considered in all species, except in macrourids and notocanthids, where pre-anal fin-length was measured. Depth was estimated as the depth at which the population of a given species exhibits the highest abundance within the species' depth range. For the 11 species for which fecundity was calculated, maximum abundances depth (MAD) was extracted from the Deep Med Research Group© database, hosted at the Institute of Marine Sciences (ICM-CSIC, Barcelona, Spain). The results of bathymetric distribution obtained were in accordance with previously published data (e.g. Stefanescu et al., 1992, 1993; Massutí et al.,1995; Tecchio et al., 2013). The MAD for the other 14 species was obtained from the literature (see Table 3 for details).

The reproductive developmental stage of the ovaries was classified macroscopically based on ovary color, ovary size and egg size. For the fecundity, only mature females corresponding to the two following categories were used: spawning capable (with ovaries of considerable volume, in which some oocytes appear translucent) and actively spawning stage (when gonads fully occupy the body cavity with many visible eggs) (Brown-Peterson et al., 2011).

2.2. Histological and image analysis

The ovarian developmental reproductive phases, oocyte development stages and the absence of postovulatory follicles, which indicate that the spawning has not already started, were confirmed by histological screening in all the subsamples used for the fecundity calculation. The samples were embedded in paraffin blocks, cut into 7 μm sections and stained with Harris' haematoxylin and eosin. Histological sections were also used to determine the size of each oocyte developmental stage by measuring the diameter of 100 oocytes with Sigma Scan Pro4, following the Brown-Peterson et al. (2011) maturation scale.

Fecundity was determined using the gravimetric method (reviewed in Murua et al. (2003)). The ovaries were wet-weighed and then a small subsample of approximately 0.1 g from each ovary was weighed to the nearest 0.001 g, stained with Rose Bengal and then filtered through a 125 μm sieve. The filtered subsamples were photographed using a Canon camera attached to a binocular microscope (Leica MZ12). These photographs were analyzed by Image J software (Thorsen and Kjesbu, 2001) to determine the ovarian organization and count the oocytes in the sample. The oocyte-size frequency distribution of a species provides information on the ovarian developmental organization (asynchronous, synchronous or group-synchronous ovary organization) and partial information about the type of fecundity, either determinate or indeterminate (reviewed in Murua and Saborido-Rey (2003)). The species with group-synchronous ovarian organization were considered to have determinate fecundity (Murua and Saborido-Rey, 2003). In the species with group-synchronous ovary organization,