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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.

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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. Garcia 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 (Garcia 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.

Table 1
Life history attributes of 41 species of fishes. Maximum longevity (A_{max}), age at 50% maturity (A_{50}), von Bertalanffy growth coefficient (VB K), length at 50% maturity (L_{50}), maximum length (L_{max}), fecundity at L_{50} (F_{50}), maximum fecundity (F_{max}) and the potential rate of population increase ($r^1 = \ln(F_{50}/A_{50})$) are given.

Common name	Species	Family	min d	max d	Depth refs	A_{max}	A_{50}	VB K	L_{50}	L_{max}	F_{50}	F_{max}	r^1	References
Order Osmeriformes														
Greater Silver smelt	<i>Argentina silus</i>	Argentinidae	150	550	Hureau (1996)	35	7	0.16	35	70	4478	16,284	1.20	Clarke (2003), Froese and Pauly (2008)
Order Salmoniformes														
Baird's slickhead	<i>Alepocephalus bairdii</i>	Alepocephalidae	650	1700	Hureau (1996)	38	15	0.07	55	100	2000	7049	0.51	Allain (1999), Allain and Lorange (2000)
Order Gadiformes														
Giant grenadier	<i>Albatrossia pectoralis</i>	Macrouridae	500	1300	Clausen (2008), Miller and Lea (1972), Tuponogov et al. (2008)	58	23	0.02	82	201	35,000	231,000	0.45	Burton et al. (1999), Rodgveller et al. (2010)
Pacific grenadier	<i>Coryphaenoides acrolepis</i>	Macrouridae	700	2000	Miller and Lea (1972), Lauth (2000)	73	20	0.02	50	95	23,000	150,000	0.50	Andrews et al. (1999), Matsui et al. (1990), Stein and Pearcy (1982)
Popeye grenadier	<i>Coryphaenoides cinereus</i>	Macrouridae	500	1400	Tuponogov et al. (2008)	15	5	0.22	32	66	3500	17,000	1.63	Froese and Pauly (2008), Tuponogov et al. (2008)
Roundnose grenadier	<i>Coryphaenoides rupestris</i>	Macrouridae	400	1500	Hureau (1996)	72	14	0.03	52	133	3300	70,000	0.58	Allain (2001), Lorange et al. (2003)
Roughhead grenadier	<i>Macrourus berglax</i>	Macrouridae	300	1000	Hureau (1996)	25	15	0.09 ^a	74	123	19,000	80,000	0.66	Fossen et al. (2003), Murua (2003)
Ridge-Scaled grenadier	<i>Macrourus carinatus</i>	Macrouridae	500	1000	Cohen et al. (1990), Laptikhovsky et al. (2008)	37	12	0.08	59	85	15,000	57,000	0.80	Laptikhovsky et al. (2008)
Bigeye grenadier	<i>Macrourus holotrachys</i>	Macrouridae	670	1600	Laptikhovsky et al. (2008), Morley et al. (2004)	27	9	0.11	58	89	22,000	260,000	1.11	Laptikhovsky et al. (2008), Morley et al. (2004)
Whitson's grenadier	<i>Macrourus whitsoni</i>	Macrouridae	600	1500	Cohen et al. (1990)	55	13	0.06	46	92	9100	41,000	0.70	Alekseyeva et al. (1993), Marriott et al. (2003), 49
Hoki	<i>Macrourus novaezelandiae</i>	Merlucciidae	250	700	Bull et al. (2001)	25	4	0.17	66	120	500,000	3,000,000	3.28	Froese and Pauly (2008), Schofield and Livingston (1998)
Pacific hake	<i>Merluccius productus</i>	Merlucciidae	45	500	Cohen et al. (1990)	16	3	0.21	34	78	75,000	1,200,000	3.74	Froese and Pauly (2008), McFarlane and Saunders (1997)
Atlantic cod	<i>Gadus morhua</i>	Gadidae	50	200	Cohen et al. (1990)	25	3	0.20	41	200	300,000	9,000,000	4.20	Froese and Pauly (2008), Stares et al. (2007)
Greater forkbeard	<i>Phycis blennoides</i>	Gadidae	150	300	Hureau (1996)	20	4	0.26	33	110		750,000		Cohen et al. (1990), Froese and Pauly (2008)
Blue ling	<i>Molva dypterygia</i>	Lotidae	350	1200	Hureau (1996)	30	6	0.13	80	160	581,000	3,500,000	2.21	Froese and Pauly (2008), Thomas (1987)
Order Beryciformes														
Orange Roughy	<i>Hoplostethus atlanticus</i>	Trachichthyidae	700	1400	Francis et al. (2002)	149	29	0.06	31	75	35,000	180,000	0.36	Andrews et al. (2009), Clark et al. (1994), Tracey and Horn (1999)
Alfonsino	<i>Beryx splendens</i>	Berycidae	400	800	Lehodey et al. (1994), Menezes et al. (2009)	23	6	0.10	33	70	240,000	675,000	2.06	Froese and Pauly (2008), Lehodey et al. (1997)
Order Zeiiformes														
John dory	<i>Zeus faber</i>	Zeidae	50	150	Froese and Pauly (2008), Francis et al. (2002)	12	4	0.30	36	90		170,000		Froese and Pauly (2008)
Black oreo	<i>Alloctytus niger</i>	Oreosomatidae	600	1200	Francis et al. (2002)	153	27	0.04 ^a	27	47	9000	62,000	0.34	Conroy and Pankhurst (1989), Doonan et al. (1997), McMillan et al. (1997)
Smooth oreo	<i>Pseudocyttus maculatus</i>	Oreosomatidae	700	1400	Francis et al. (2002)	86	31	0.05 ^a	21	68	10,000	84,000	0.30	Conroy and Pankhurst (1989), Doonan et al. (1997), McMillan et al. (1997)

Order Scorpaeniformes														
Pacific Ocean perch	<i>Sebastes alutus</i>	Scorpaenidae	150	825	Love et al. (2002)	100	8	0.14 ^a	30	53	15,000	505,000	1.20	Cailliet et al. (2001), Love et al. (2002)
Splitnose rockfish	<i>Sebastes diploproa</i>	Scorpaenidae	200	600	Love et al. (2002)	84	8	0.10 ^a	19	46	14,000	255,000	1.19	Cailliet et al. (2001), Love et al. (2002)
Widow rockfish	<i>Sebastes entomelas</i>	Scorpaenidae	25	200	Love et al. (2002)	60	4	0.16	36	59	95,000	1,113,000	2.87	Cailliet et al. (2001), Love et al. (2002), Pearson and Hightower (1991)
Acadian redfish	<i>Sebastes fasciatus</i>	Scorpaenidae	130	500	Hureau (1996)	50	5	0.12	26	44	5200	70,000	1.71	Froese and Pauly (2008), St-Pierre and De Lafontaine (1995)
Yellowtail rockfish	<i>Sebastes flavidus</i>	Scorpaenidae	50	250	Love et al. (2002)	64	6	0.17 ^a	40	66	56900	1,993,000	1.82	Cailliet et al. (2001), Love et al. (2002), Pearson and Hightower (1991)
Golden redfish	<i>Sebastes marinus</i>	Scorpaenidae	100	1000	Hureau (1996)	60	10	0.09	38	100	50,000	350,000	1.08	St-Pierre and De Lafontaine (1995)
Deepwater redfish	<i>Sebastes mentella</i>	Scorpaenidae	300	900	Hureau (1996)	75	11	0.09	26	50	5200	70,000	0.78	St-Pierre and De Lafontaine (1995)
Shortspine thornyhead	<i>Sebastesomus alascanus</i>	Scorpaenidae	300	1200	Jacobson and Vetter (1996), Love et al. (2002)	80	10	0.02	22	80	11,906	1,000,000	0.94	Cooper et al. (2005), Jacobson and Vetter (1996), Kline (1996)
Longspine thornyhead	<i>Sebastesomus altivelis</i>	Scorpaenidae	500	1400	Jacobson and Vetter (1996), Love et al. (2002)	45	16	0.07	21	39	17,571	50,000	0.61	Cooper et al. (2005), Jacobson and Vetter (1996), Kline (1996)
Sablefish	<i>Anoplopoma fimbria</i>	Anoplomatidae	200	1000	Jacobson et al. (2001)	114	6	0.20	58	120	210,000	450,000	2.04	Froese and Pauly (2008), Hunter et al. (1989)
Order Perciformes														
Black cardinalfish	<i>Epigonus telescopus</i>	Epigonidae	450	1100	Francis et al. (2002)	104	36	0.03	52	76				Tracey et al. (2000)
Pelagic armorhead	<i>Pseudopentaceros wheeleri</i>	Pentaceroptidae	200	500	Humphreys (2000)	7	2	0.30	30	46		100,000		Bilim et al. (1978), Humphreys (2000)
Patagonian toothfish	<i>Dissostichus eliginoides</i>	Nototheniidae	600	2100	Laptikhovskiy et al. (2006)	53	10	0.09 ^a	100	240	80,000	350,000	1.13	Horn (2002), Nevinskii and Kozlov (2002)
Black scabbardfish	<i>Aphanopus carbo</i>	Trichiuridae	200	1600	Hureau (1996)	12	4	0.25	108	151	400,000	1,000,000	3.22	Morales-Nin and Sena-Carvalho (1996), Neves et al. (2009)
Largehead hairtail	<i>Trichiurus lepturus</i>	Trichiuridae	100	350	Froese and Pauly (2008)	15	2	0.32	65	234	4800	160,000	4.24	Froese and Pauly (2008), Khan (2006), Martins and Haimovici (2000)
Order Pleuronectiformes														
Rex sole	<i>Errex zachirus</i>	Pleuronectidae	60	500	Lauth (2000), Miller and Lea (1972)	29	5	0.28 ^a	24	51	6200	238,000	1.75	Abookire (2006), Hosie and Horton (1977)
Witch flounder	<i>Glyptocephalus cynoglossus</i>	Pleuronectidae	50	500	Bowering and Brodie (1991), Hureau (1996)	25	6	0.23	30	61	100,000	400,000	1.92	Froese and Pauly (2008), Rideout and Morgan (2007)
Pacific halibut	<i>Hippoglossus stenolepis</i>	Pleuronectidae	25	275	IPHC (1998)	55	11	0.10	85	258	220,000	3,000,000	1.12	Froese and Pauly (2008), Schmitt and Skud (1978)
Dover sole	<i>Microstomus pacificus</i>	Pleuronectidae	370	1000	Hunter et al. (1990)	58	7	0.09 ^a	33	76	22,000	160,000	1.43	Hunter et al. (1990), Hunter et al. (1992)
Greenland Halibut	<i>Rheinhardtius hippoglossoides</i>	Pleuronectidae	500	1200	Bowering and Brodie (1991), Hareide and Garnes (2001)	36	10	0.13	67	120	37,000	125,000	1.05	Cooper et al. (2007), Gregg et al. (2006)

^a Data for females.

Table 2
Regression coefficients for the relationship between life history variables and minimum, median, and maximum depth of occurrence (for adults—see Section 2). The best fit of either linear or exponential regression is shown (see Section 2).

Depth	A_{\max}	A_{50}	$\ln VB K$	L_{50}	L_{\max}	$\ln F_{50}$	$\ln F_{\max}$	$\ln r^1$
Min	0.35*	0.67***	-0.64***	0.12	-0.06	-0.30	-0.50***	-0.73***
Max	0.27	0.51***	-0.60***	0.34*	0.08	-0.19	-0.40*	-0.59***
Median	0.30	0.58***	-0.63***	0.28	0.04	-0.23	-0.44**	-0.65***

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

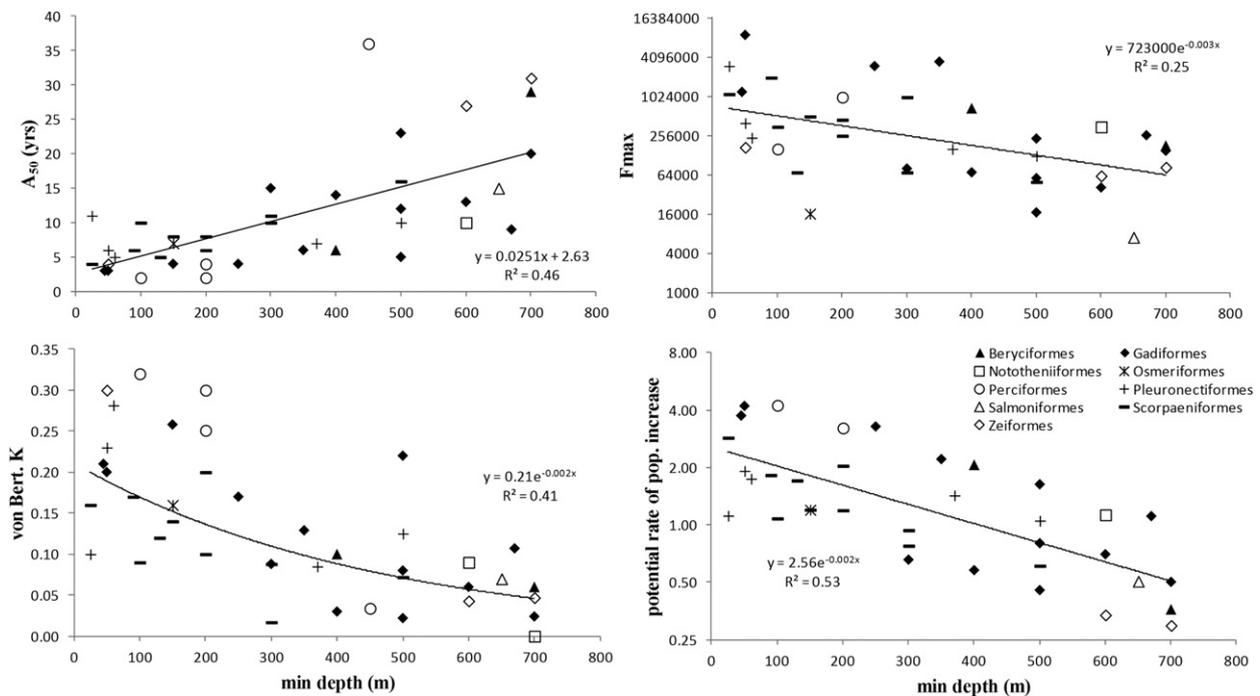


Fig. 1. Life history attributes as a function of minimum depth of occurrence. A_{50} is the age at 50% maturity, von Bertalanffy K is the von Bertalanffy growth coefficient or rate constant, F_{\max} is the maximum fecundity and potential rate of population increase (r^1) is defined as $\ln(F_{50})/A_{50}$ where F_{50} is the fecundity at the size of 50% maturity.

The regressions to A_{50} , K , F_{\max} and r^1 remained significant when the phylogenetic relationships of the individual species were taken into account (Table 3). The slopes of the regressions were very similar to the basic regressions although the intercepts differed (Fig. 1).

Two orders, Gadiformes and Scorpaeniformes, are represented by many species across a broad depth range (Table 1) making these two groups among the best for examining the competing influences of phylogeny and depth. It should be noted that within the Gadiformes, the Gadidae and Merluccidae have depth ranges primarily on the continental shelf. The Moridae and Macrouridae are represented by species primarily on the continental slope (Table 1). Within each order, minimum depth of occurrence explains large proportions of the variance in the life history attributes (Fig. 2). In many cases, when Fig. 2 is compared with Fig. 1, depth explains more of the variation within an order than across all orders. The slopes of the regressions for each order are remarkably similar to each other and to the regressions for all species (Fig. 1) although the intercepts vary.

4. Discussion

Most studies have focused on comparing deep-sea to shelf species as broad general groups (Clarke, 2003; Drazen, 2008;

Garcia et al., 2008; Koslow et al., 2000; Morato et al., 2006a) resulting in the now well-documented distinctions in terms of longevity, time to maturity and natural mortality. Our analysis shows that if species are not grouped *a priori*, then they do not naturally fall into two clear groups but range along a continuum of life history attributes.

Depth of occurrence explains a great deal of the variability in life history attributes, specifically A_{50} , K , F_{\max} , and r^1 (Fig. 1). These results are very robust given that the relationships were significant regardless of which metric of depth was used. Furthermore, while well resolved phylogenies are not available for all of the fishes in the data set, using the relationships available these trends were significant after taking phylogeny into account (Table 3) suggesting that variable representation of the species across taxa did not significantly skew the results. However, phylogeny is very likely to be important, because the predominant families in deepwater are not the same as those in shallow water preventing a robust analysis of the precise role that phylogeny plays. A greater amount of life history information for species which lie at the extreme ends of their family or generic depth distributions is what is needed. Within the orders Gadiformes and Scorpaeniformes, the trend in life history attributes with depth remained significant (Fig. 2) and the slopes of the relationships were very similar to the pattern across all orders. The results suggest that environmental factors drive much of the variation observed.

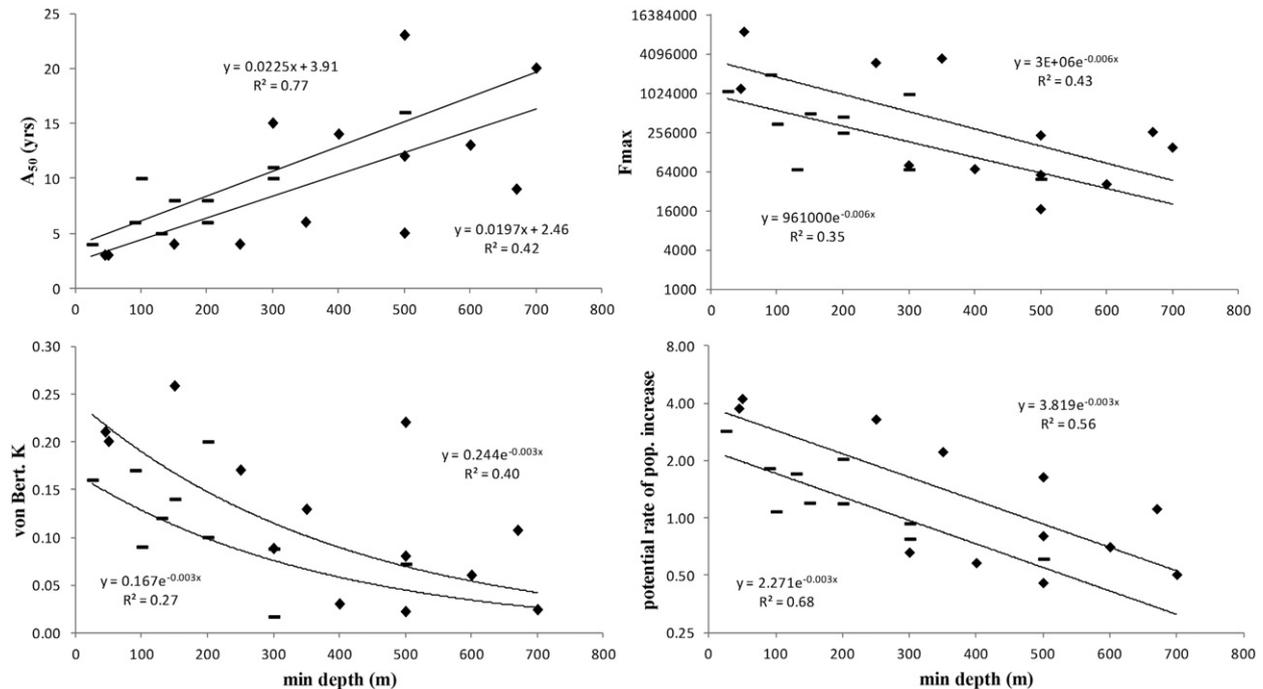


Fig. 2. Life history attributes as a function of minimum depth of occurrence in the Gadiformes (diamonds) and the Scorpaeniformes (dashes). A_{50} is the age at 50% maturity, von Bert K is the von Bertalanffy growth coefficient or rate constant, F_{max} is the maximum fecundity and potential rate of population increase (r^1) is defined as $\ln(F_{50})/A_{50}$ where F_{50} is the fecundity at the size of 50% maturity.

In the ocean, the strongest environmental gradients exist across depth: pressure increases, light levels and temperature decrease, food availability and biomass decrease exponentially, and some areas have oxygen minimums at mid-slope depths (Gage and Tyler, 1991). Deep-sea fishes are adapted physiologically to cope with these changes in a variety of ways (Samerotte et al., 2007; Seibel and Drazen, 2007; Somero, 1992; Somero and Hochachka, 1984) and their life histories also should change as a result of depth-related gradients.

Several environmental factors could be responsible for patterns observed in life history attributes, including temperature (Clarke and Johnston, 1999; Gillooly et al., 2001; Russell et al., 1996; Seibel and Drazen, 2007), reduction in predation pressure as a consequence of reduced megafaunal density (Haedrich and Rowe, 1977; Lampitt et al., 1986) and food availability. The latter has very clear effects on the growth rates of animals (Fonds et al., 1992; Jobling, 1982; Persson and De Roos, 2006), and we note that many species inhabiting the upper slope exhibit ontogenetic migration (Collins et al., 2005; Jacobson et al., 2001; Jacobson and Hunter, 1993; Yeh and Drazen, 2011); with access to warmer food-rich shallow waters early in life those species grow and mature relatively quickly. This may be part of the reason for the slightly stronger relationships between minimum depth of occurrence and the life history parameters. The trends in fecundity may be explained in a similar fashion. Intraspecific fecundity varies with ration level both in aquaculture (Coward and Bromage, 1999; Ma et al., 1998) and in the field between fish in good versus poor nutritional condition (Rideout and Morgan, 2007; Rideout et al., 2005). In addition some deep living fishes have larger eggs than shallow living species (Koslow et al., 2000) so lower absolute fecundities are expected. However if egg size were the only driving variable then F_{50} should have shown a decline with depth too but it did not. It is possible that shallower living fishes grow more, post maturity, than deep living ones and thus reach greater size and maximum fecundity. The relationship between fecundity and body size may also vary between species with different habitat depths, with lower size related increases in fecundity occurring in deeper living species.

In our results K and A_{50} showed strong trends with depth but longevity increases only weakly with minimum depth of occurrence (Table 2). A similar trend has been found in deep-sea elasmobranchs which have only modestly greater longevity but two times greater age at first maturity than their shallow water relatives (Garcia et al., 2008). Growth rate and the time to reach maturity may be better related to temperature and food supply which control the rate of energetic processes (see also below). On the other hand, greater longevity has a variety of life history advantages such as longer reproductive lifespan and a more stable population structure (Musick, 1999), which could be advantageous in many different habitats. Clearly great longevity is an attribute of deep-sea fishes (Table 1) but some shallow living species such as sturgeons and tarpon are also very long lived (Cailliet et al., 2001; Musick, 1999). Cailliet et al. (2001) did find a significant trend in longevity with depth for rockfishes in the NE Pacific, but this is not surprising since rockfishes comprise a single coherent family. Morato et al. (2006b) document an increase in longevity and age at maturity with depth across a very large number of species. However, their values are the averages for the catch in each depth horizon. Thus each species is not treated individually. The oft cited distinction in longevity between shallow and deep living species is supported by our findings but it is much weaker than trends with age at maturity.

Slow rates of growth may be the result of metabolic limitation. The metabolic rate of pelagic fishes declines exponentially by an order of magnitude with depth (Drazen and Seibel, 2007). The data for demersal deep-sea fishes are sparse but for some groups such as macrourids and morids, deeper living species have up to a 10-fold reduction in metabolic rate compared to shallow water species (Drazen and Yeh, 2012). Data using metabolic enzyme activities as proxies of metabolic capacity show an exponential decline with increasing depth (Drazen and Seibel, 2007). In other words the greatest change in metabolic capacity occurs between the shallowest living fishes and those that inhabit depths of 200–500 m in a pattern similar to what we found for growth rate and potential rate of population increase. The visual interactions

Table 3

Regression coefficients and standard errors for each equation represented in Fig. 1 after phylogenetic covariance was removed from the data.

Variable	Slope	Intercept	R ²	F	p
A ₅₀	0.019 ± 0.005	0.437	0.28	14.4	< 0.001
VB k	−0.0017 ± 0.0006	0.407	0.19	8.6	< 0.001
F _{max}	−0.0027 ± 0.0011	239000	0.13	5.6	0.02
r ¹	−0.0026 ± 0.0006	1.142	0.35	17.7	< 0.001

hypothesis states that reductions in metabolic capacity are linked with light levels and locomotory capacity rather than food supply (Childress, 1995; Seibel and Drazen, 2007).

Depth explains at most ~50% of the variation in the life history variables so other important factors remain to be elucidated. Reproductive biology is often constrained by phylogeny as in the extreme example of sharks that produce few but very large advanced stage offspring (Musick, 1999). Previous meta-analyses of deep-sea fish fecundity, one of the biological attributes we include in our analysis, have found variation between orders. Gadiformes typically have greater maximum fecundities than most other orders with deep-living representatives (Merrett and Haedrich, 1997; Fig. 2). Indeed, within orders a greater amount of variation in life history attributes was explained (up to 77%; Fig. 2) by the analysis here.

All of the environmental factors mentioned could be important and act in concert. For fisheries managers the specific reasons for the declines in productivity with depth are not as important as simply recognizing the general trend. Past studies have established that deep-sea fishes are not as productive as species from the continental shelves (Devine et al., 2006; Koslow et al., 2000; Moore, 1999; Morato et al., 2006b; Roberts, 2002). But by analyzing a suite of fishes from the shelves to the continental slope our analysis shows that there is a continuum of several life history attributes and the potential rate of population increase that is related to depth of occurrence rather than to a simple dichotomy between shelf dwelling and deep-sea fishes. The relationship we have identified suggests some level of predictive power for managers to understand the potential response of species to fishing pressure in the absence of detailed life history information, a rule that unfortunately appears only generally true. Still, effective management must be based on detailed knowledge of the particular characteristics of the species in question as well as a similar level of understanding for species involved incidentally in the fishery as by-catch.

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