



Inference on energetics of deep-sea fish that cannot be aged: The case of the hagfish



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ABSTRACT

Dynamic Energy Budget (DEB) theory is used to estimate maximum growth rates and age at maturity for two hagfish species, the Atlantic hagfish *Myxine glutinosa* and the Pacific hagfish *Eptatretus stoutii*. Neither direct measurements on growth nor aging methods are available for these species. Only limited information on, for example, length and mass at birth and at puberty, and on oxygen consumption versus mass is available. For the Atlantic hagfish, but not for the Pacific hagfish, estimated growth rates are much higher and estimated age at maturity is much lower than previously thought, which may have implications for fisheries management. Yet, whether or not these results are due to erroneous oxygen consumption measurements remains to be seen.

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1. Introduction

Over the last decades marine fisheries have expanded to deep waters along the continental slopes. This global expansion from a traditional fishery on the continental shelves toward fishing in deeper waters also implied that entirely new taxonomic groups were targeted, other than the relatively well-known taxa such as for example the gadoids, clupeoids and salmonids. Deep-sea fishing started without much knowledge of the life-history characteristics of the newly exploited stocks. Not surprisingly, these unregulated or poorly controlled fisheries have repeatedly gone through a boom-and-bust cycle. Many examples are known where the fisheries flourished briefly, but then diminished due to overfishing (Koslow et al., 2000; Roberts, 2002). Slow growth and late reproduction make deep-sea fishes much more vulnerable than their coastal counterparts and it might turn out that sustainable deep-sea fishing cannot be economically viable.

One striking example of a recent fishery without much knowledge of the life-history characteristics of the stock is the fishery on Atlantic hagfish *Myxine glutinosa*. The Atlantic hagfish or slime eel is a jawless fish of an eel-like form, which is known for the huge amounts of mucus or slime that it produces when it gets stressed (Zintzen et al., 2011). All hagfishes belong to the family Myxinoidea and they are lumped together with the lampreys in the cyclostomes, previously called the Agnatha or jawless fishes (Janvier, 2010). Hagfishes live in burrows in soft-sediments at depths of 30 to more than 1200 m.

In Korea and Japan there has been a traditional fishery for Pacific hagfish *Eptatretus stoutii*, but declining stocks in the 1980s and 1990s and a growing demand on hagfish products resulted in an emerging fishery on Atlantic hagfish on the east coast of the United States and Canada in the early 1990s. The Asian market not just asks for hagfish meat, but also for hagfish skin. The skin of larger hagfish, with a length of at least 35 cm, is used as light leather alternative (Grey et al., 2006). Up to 12 million lb per year of Atlantic hagfish have been harvested off the coast of Maine and Massachusetts (Powell et al., 2005), but it is not known and even questionable whether the fisheries in the western North Atlantic are sustainable (Grant, 2006; Grant et al., 2009; Martini et al., 1997). There is lack of data on distribution and stock abundance, but especially knowledge on reproduction and growth is lacking. One of the major problems to get reliable field growth data is that the animals cannot be aged (Honma, 1998; Martini, 1998). Age at maturity and longevity are therefore also unknown. A further problem is that hagfish tend to behave abnormally in captivity, refuse to eat, exhibit very little growth and demonstrate no reproductive tendencies (Northeast Fisheries Science Center, 2003, p. 591).

The example of the hagfish is thus particularly interesting as it gives rise to the question whether we can say something at all about growth and age at maturity without being able to age specimens or to raise them in the laboratory.

Dynamic Energy Budget (DEB) theory is a mechanistic theory that resulted in the so-called standard DEB model, which assumes that the various energetic processes, such as assimilation rate and maintenance, are dependent either on the surface area or the volume of the structural body. The model further assumes that the assimilated products first

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Table 1

Data used to fit the standard Dynamic Energy Budget model. Data in the upper part of the table are true zero-dimensional data, the middle part gives pseudo-data. These pseudo-data are a-priori estimates of the parameters and might be needed to avoid overfitting. The lower part gives true univariate data. The last column gives the model equations that link the data to the model parameters; L_m^{ref} is a reference length and equals 1 cm, z is the zoom factor, and δ_M the shape coefficient. Section (Sn) and equation (Eq) numbers refer to Kooijman (2010).

Variable	Explanation	Model
a_m	Maximum life span	Sn 6.1.1
$L_{w,b}$	Physical length at birth	Sn 2.6.2; Eqs. 2.32, 2.46
$L_{w,p}$	Physical length at puberty	Sn 2.6.3; Eq. 2.54
$L_{w,\infty}$	Ultimate physical length	$fL_m^{\text{ref}}z/\delta_M$
W_b	Wet mass at birth	Sns 1.2.3, 2.6.2; Eq. 3.2
W_p	Wet mass at puberty	Sns 1.2.3, 2.6.2; Eq. 3.2
W_∞	Ultimate wet mass	Sns 1.2.3, 3.2.1; Eq. 3.2
\dot{R}_∞	Ultimate reproductive rate	Eq. 2.58
\dot{v}	Energy conductance	
κ	Allocation fraction to soma	
κ_R	Reproduction efficiency	
$[\dot{p}_M]$	Volume-specific somatic maintenance rate	
$\{\dot{p}_T\}$	Area-specific somatic maintenance rate	
k_j	Maturity maintenance rate coefficient	
κ_G	Growth efficiency	
W_w, L_w	Wet mass versus physical length	Sns 1.2.3, 3.2.1; Eq. 3.2
J_O, W_w	Oxygen consumption versus wet mass	Sn 4.4
\dot{R}, L_w	Reproductive rate versus physical length	Eqs. 2.56, 2.57

enter a reserve pool, from which they are allocated to maintenance, growth and reproduction. The κ -rule says that a fixed fraction κ is allocated to maintenance and growth of the structural body and that the remaining fraction $1-\kappa$ is available for development, reproduction and maturity maintenance. The standard DEB model predicts that under constant food conditions growth follows the well-known von Bertalanffy growth model (von Bertalanffy, 1934). But what's more, the DEB model also shows how the two parameters of the von Bertalanffy growth model, ultimate length $L_{w,\infty}$ and the von Bertalanffy growth coefficient \dot{r}_B , depend upon underlying more basic physiological parameters, the so-called primary parameters of the standard DEB model. Ultimate physical length is given by

$$L_{w,\infty} = \frac{fL_m^{\text{ref}}z}{\delta_M} \tag{1}$$

where f is the scaled functional response that varies between 0 and 1 and depends upon the food availability, L_m^{ref} is a reference length set at 1 cm, z is a dimensionless zoom factor that gives the maximum length of the structural body of the animal relative to the reference length, and δ_M is the shape coefficient that relates the length of the structural

body to some physical length measure, which in this case is the body length of the fish. The zoom factor z is related to the primary parameters of the DEB model by

$$z = \frac{L_m}{L_m^{\text{ref}}} = \frac{\kappa\{\dot{p}_{Am}\}}{[\dot{p}_M]} \frac{1}{L_m^{\text{ref}}} \tag{2}$$

where L_m is the maximum volumetric length, κ is the fraction of the energy mobilized from the reserves that is spent on maintenance and growth of the structural body of the animal, $\{\dot{p}_{Am}\}$ is the surface-area-specific maximum assimilation rate that relates assimilation to the surface area of the structural body, and $[\dot{p}_M]$ is the volume-specific maintenance rate that links the maintenance rate to the volume of the structural body. The parameters κ , $\{\dot{p}_{Am}\}$, and $[\dot{p}_M]$ are primary parameters within DEB theory, but L_m is a so-called compound parameter. Similarly, the von Bertalanffy growth coefficient is also a compound parameter and at optimal food conditions it is given by

$$\dot{r}_B = \frac{1}{3} \frac{[\dot{p}_M]}{\kappa\{\dot{p}_{Am}\}\dot{v}^{-1} + [E_G]} \tag{3}$$

where \dot{v} is the energy conductance, a parameter that more or less indicates how fast energy within the reserves can be mobilized, and finally $[E_G]$ gives the volume-specific costs of growth. The parameters \dot{v} and $[E_G]$ are also primary parameters.

These primary parameters turn up in many other relationships as well, for example the relation between respiration and body mass also contains the parameters $\{\dot{p}_{Am}\}$, κ , $[\dot{p}_M]$, \dot{v} , and $[E_G]$. Studying the respiration rate of salmon eggs, Smith (1957) observed already in 1957 that respiration is proportional to a weighted sum of volume and volume growth rate, and such relationship is confirmed by DEB theory. DEB theory thus offers the possibility to predict growth rates in response to food and temperature even if growth has never been measured, but of course only if enough other types of data, some of which have to be rates, are available enabling estimation of the primary parameters. We use this possibility to predict the growth and the age at maturity of the Atlantic hagfish *M. glutinosa*, using a variety of other information available in the literature. For comparison, the primary parameters of the DEB model are also estimated for the Pacific hagfish *E. stoutii*.

2. Materials and methods

Using various datasets on life-history parameters a total of eight DEB model parameters are estimated according to a procedure described by Lika et al. (2011). The remaining DEB parameters were set to predefined values taken from Kooijman (2010). See Table 4 for an overview. The DEB parameter estimation procedure starts with 8 so-called zero-

Table 2

Observed versus predicted zero-dimensional data for the Atlantic hagfish *M. glutinosa*. Data in the upper part of the table are true data, the lower part gives pseudo-data. Weight refers to the weighing of the squared relative differences in the optimization procedure. Maximum age and reproduction rate are observed at a temperature of 6 °C, whereas the pseudo-data are given for a reference temperature of 20 °C.

Variable	Observed	Predicted	Unit	Weight	Source
a_m	7300	7300	d	1	Department Fisheries and Oceans Canada (DFO) (2009)
$L_{w,b}$	9.8	10.62	cm	1	Scott M. Grant (pers. comm.)
$L_{w,p}$	34.3	37.12	cm	1	Scott M. Grant (pers. comm.)
$L_{w,\infty}$	65	64.07	cm	1	Grant (2006)
W_b	0.9	1.207	g	2	Scott M. Grant (pers. comm.)
W_p	47	51.49	g	2	Scott M. Grant (pers. comm.)
W_∞	275	264.8	g	20	Grant (2006)
\dot{R}_m	0.1041	0.1181	d ⁻¹	1	(Grant (2006); Department Fisheries and Oceans Canada (DFO) (2009))
\dot{v}	0.02	0.113	cm d ⁻¹	0.004	Kooijman (2010)
κ	0.8	0.7322	-	1	Kooijman (2010)
κ_R	0.95	0.95	-	0.1	Kooijman (2010)
$[\dot{p}_M]$	18	72.76	J d ⁻¹ cm ⁻³	0.1	Kooijman (2010)
k_j	0.002	0.002	d ⁻¹	0.00004	Kooijman (2010)
κ_G	0.8	0.805	-	0.2	Kooijman (2010)

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