

POINTS OF VIEW

Inertia as a 'safe harbour': do fish larvae increase length growth to escape viscous drag?

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Introduction

Fish larvae differ from adults in their interaction with the physical environment. They hatch at a size small enough to experience water as a mainly viscous medium. Their external morphology and development are adapted accordingly (Osse and Drost, 1989). The boundary layer around the gill filaments would be too thick to allow efficient gas exchange. Only as the larvae grow bigger do the gills become functional in breathing (Osse, 1989). Viscosity also affects swimming. The flow regime around an organism depends on its size and swimming speed and can be characterized by the dimensionless Reynolds number (the ratio of inertial to viscous forces). Fish larvae hatch in the viscous flow regime and reach the inertial regime around first feeding. Experimental evidence (Vlymen, 1974) and theoretical considerations (Weihs, 1980) indicate a change of swimming style as the fish larva passes from a viscous to an inertial flow regime. The fish larva responds to the changing regime, not only by changing its swimming style, but also by adjusting its growth pattern. Fish larvae delay the gut development to keep their body flexible enough to achieve the high body wave amplitudes suitable for swimming in a more viscous regime (Osse, 1990). In spite of the obvious adjustments to the viscous flow regime, small fish larvae still experience mortality close to that of eggs (Pepin, 1991). The mortality drops drastically as the larvae grow and swimming performance improves (Bailey and Batty, 1984; Pepin, 1991). This hints at the possibility that fish larvae, instead of adapting optimally to the viscous flow regime, invest into outgrowing viscosity as quickly as possible ('safe harbour' hypothesis of Shine, 1978). To escape the viscous flow regime, a fish larva can increase its swimming speed or its size. Webb and Weihs (1986) suggest that fish larvae escape the viscous flow regime by increasing their body length. Fuiman (1983) and Osse (1990) found some indication to support this idea in the fish larvae's allometric growth patterns.

This review tries to test the hypothesis that fish larvae increase their growth in length to escape the viscous flow regime. It does so by looking at the weight-length relationship of larvae from 23 species. Fish larvae should increase their growth in length until they reach the inertial flow regime at some critical length. The allometric exponent of the weight-length relationship below this critical length should be lower

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than the allometric exponent above this length. The critical length is defined by the transition from a viscous to an inertial flow regime. Considering that the swimming speed of fish larvae increases linearly over the relevant size range (Blaxter, 1986), the factor determining the Reynolds number in fish larvae becomes their size. Weihs (1980) predicts this threshold at a Reynolds number of about 200. If cruising speeds of one to two body lengths per second are the determining factor, this would correspond to a critical length of around 15 mm. The critical length would be considerably smaller if the inflexion point were to be dominated by burst swimming speeds.

This critical length depends entirely on the hydrodynamics. The inflexion point of the allometric relationship should therefore not correlate with other ontogenetic events. Because there are hardly any data on the volume of fish larvae, weight was used in spite of the fact that the density of fish larvae increases exponentially during ontogeny (Power and Walsh, 1992). As a result, the allometric exponent of the weight-length relationship will be an overestimate, rather than an underestimate, of the volume-length relationship.

Material and methods

All 37 data sets of 23 marine species from four orders were gathered from the literature (Table 1). The weight-length data of each data set were log-transformed and fitted geometrically (Ricker, 1984) with a linear function to obtain the allometric exponent of the weight-length relationship. Possible inflexion points in the weight-length relationship were detected by repeated fitting, first starting from the lowest, subsequently from the highest x value including one more data point each time. The two allometric exponents obtained from the fitting procedures up to a certain data point were compared. If the exponents were significantly different (t -test, $\alpha \leq 0.05$), the inflexion point was assumed to be at the last data point included in both fitting procedures. If several pairs of exponents exhibited a significant difference, the inflexion point was assumed to be at the highest t -value.

The values for the inflexion points were compared with temperature data, the length at hatch, and the length at yolk sac exhaustion (Pearson correlation). To test whether the inflexion points correlate with ontogenetic events, it was necessary to calculate temperature residuals for the inflexion points, the length at hatch and the length at yolk sac exhaustion. The calculation of residuals excludes temperature and size effects on the relationship of inflexion point and length at yolk sac exhaustion. The calculations were based on the linear regression equations of the temperature versus the variable concerned. The yolk sac exhaustion data were furthermore corrected for size effects. This correction accounts for the effect of the egg size that shows throughout the whole ontogeny (Pepin, 1991). There were not, however, sufficient data on egg size. Therefore length at hatch was chosen instead, because it correlates significantly with egg size (Pepin, 1991).

Results

An inflexion point could be found in all data sets that range from hatching to well after first feeding. Clupeiformes have the highest inflexion point at 11.4 ± 4.5 mm (means calculated for a standard temperature of 10 °C, $n = 14$). The values for Pleuronectiformes

Table 1. Data for the weight-length relationship $W = aL^b$, where b is the allometric exponent (given with standard error and number of data points), and inflexion points

Species	Source data set*	Allometric exponent				Inflexion point (mm)
		Before inflexion	n	After inflexion	n	
Clupeiformes						
<i>Anchoa mitchilli</i>	7	2.9 ± 12.0	6	4.5 ± 0.2	28	3.7
<i>Clupea harengus</i>	5	2.3 ± 0.8	6	3.6 ± 0.4	10	10.2
<i>Clupea harengus</i>	5	1.2 ± 0.4	5	4.5 ± 0.2	13	10.7
<i>Clupea harengus</i>	4	1.9 ± 0.2	9	4.5 ± 0.7	15	10.0
<i>Clupea harengus</i>	12	6.1 ± 2.9	15	4.3 ± 0.1	72	10.4
<i>Clupea harengus</i>	3	3.2 ± 0.5	8	4.6 ± 0.0	60	12.5
<i>Clupea harengus pallasii</i>	15	2.4 ± 0.2	16	6.1 ± 0.2	29	15.5
<i>Clupea harengus pallasii</i>	15	2.1 ± 0.5	6	6.2 ± 0.6	18	16.8
<i>Clupea harengus pallasii</i>	15	1.7 ± 0.1	7	4.4 ± 0.3	34	12.6
<i>Clupea harengus pallasii</i>	14	1.3 ± 0.9	11	4.8 ± 0.2	12	10.1
<i>Clupea harengus pallasii</i>	23	1.8 ± 0.5	9	4.3 ± 0.1	20	13.0
<i>Clupea harengus pallasii</i>	24	-1.0 ± 1.0	9	10.6 ± 0.3	4	12.9
<i>Engraulis mordax</i>	21	2.9 ± 0.2	16	3.3 ± 0.3	12	7.0
<i>Engraulis mordax</i>	9	3.3 ± 0.1	15	6.0 ± 0.2	21	18.1
Gadiformes						
<i>Gadus morhua</i>	12	6.7 ± 0.6	42	3.9 ± 0.2	53	6.9
<i>Melanogrammus aeglefinus</i>	12	6.8 ± 1.0	9	3.9 ± 0.2	10	6.0
<i>Melanogrammus aeglefinus</i>	11	5.4 ± 0.5	12	3.0 ± 0.5	7	7.3
<i>Merluccius productus</i>	1	7.2 ± 2.0	16	3.2 ± 0.1	36	4.0
Pleuronectiformes						
<i>Achirus lineatus</i>	7	6.9 ± 0.7	13	4.7 ± 0.8	13	2.8
<i>Limanda ferruginea</i>	12	2.5 ± 0.5	15	4.0 ± 0.1	56	5.6
<i>Paralichthys dentatus</i>	12	2.7 ± 0.3	25	4.6 ± 0.2	27	5.4
<i>Pleuronectes platessa</i>	8	3.4 ± 0.7	15	7.4 ± 1.2	21	10.1
<i>Pleuronectes platessa</i>	8	5.0 ± 0.8	16	11.3 ± 6.4	5	11.9
<i>Pleuronectes platessa</i>	3	2.4 ± 0.7	7	4.0 ± 0.1	37	7.5
<i>Pleuronectes platessa</i>	19	6.4 ± 0.5	75	4.7 ± 0.2	99	9.6
<i>Pseudopleuronectes americanus</i>	12	7.3 ± 0.8	13	4.3 ± 0.4	25	4.1
<i>Scophthalmus maximus</i>	18	none		none		none
Perciformes						
<i>Ammodytes americanus</i>	20	3.1 ± 0.3	7	4.4 ± 0.3	7	10.0
<i>Archosargus rhomboidalis</i>	7	4.3 ± 0.5	16	7.6 ± 0.9	9	3.5
<i>Chloroscombrus chrysurus</i>	13	3.4 ± 0.3	27	3.0 ± 0.1	56	15.0
<i>Leiostomus xanthurus</i>	22	4.6 ± 0.1	34	3.4 ± 0.1	88	6.5
<i>Menticirrhus americanus</i>	2	2.8 ± 0.1	129	3.3 ± 0.1	244	7.4
<i>Morone americana</i>	16	1.7 ± 0.2	37	3.5 ± 0.1	24	3.7
<i>Morone saxatilis</i>	6	5.0 ± 0.2	18	2.7 ± 0.5	6	10.0
<i>Pagrus major</i>	17	0.0 ± 0.4	7	3.2 ± 0.0	81	3.3
<i>Scomber japonicus</i>	10	4.1 ± 0.1	25	3.1 ± 0.0	72	11.1
<i>Stenotomus chrysops</i>	12	1.5 ± 0.3	33	3.8 ± 0.1	57	3.9

* See literature cited for numbers.

(6.9 ± 4.6 mm, $n = 8$), Gadiformes (6.4 ± 2.2 mm, $n = 4$) and Perciformes (5.3 ± 4.5 mm, $n = 10$) are significantly lower. The length at the inflexion point correlates negatively with temperature ($r = -0.40$, $p < 0.0001$, $n = 36$). The temperature residuals of the inflexion point correlate positively with the temperature residuals of the length at hatch ($r = 0.65$, $p < 0.0001$, $n = 30$). After correcting the length at yolk sac exhaustion for the temperature and the size effect by calculating the respective residuals, no significant correlation between length at yolk sac exhaustion and length at the inflexion point can be found (Fig. 1).

The allometric exponent before the inflexion point (2.3 ± 1.5 , $n = 14$; 4.6 ± 2.1 , $n = 8$; 3.1 ± 1.6 , $n = 10$ respectively) is smaller than the exponent after the inflexion point (5.1 ± 1.8 , $n = 14$; 5.6 ± 2.5 , $n = 8$; 3.7 ± 1.4 , $n = 10$ respectively) in Clupeiformes, Pleuronectiformes, and Perciformes. In the Gadiformes the allometric exponent before the inflexion point (6.5 ± 0.8 , $n = 4$) is bigger than the exponent after the inflexion point (3.5 ± 0.5 , $n = 4$).

Discussion

Fish larvae undergo niche shifts during their ontogeny with consequences for their growth and development. Some authors (Zweifel and Lasker, 1976) assume gradual transition, whereas other (Balon 1985; Safran, 1992) advocate an essentially saltatory ontogeny. Although the exact position of the inflexion point will be affected by whether a sigmoidal or piecewise linear growth model is used, the qualitative prediction about the change in the allometric exponent will not be affected. This change in allometric relationships can be a valuable indicator for transitions in the ecology of an organism and thereby help to detect transitions in the ontogeny (Safran, 1992). Trying to link those transitions to changes in the environment of the organism, like a shift in the hydrodynamic constraints, may help to understand what causes a particular transition in the ontogeny.

The predictions based on the shift in hydrodynamics are confirmed in most points. The allometric exponent after the inflexion point increases in all orders considered except the Gadiformes. The length at the inflexion point does not correlate with the ontogenetic event of yolk sac exhaustion and is therefore not simply a geometrical effect of the yolk sac exhaustion. This weakens Webb and Weihs' (1986) explanation that the fast transition to the inertial flow regime is achieved mainly by the streamlining effect of yolk sac exhaustion.

An alternative explanation for the change in the allometric weight-length relationship arises from metabolism being constrained by the surfaces of exchange. In fish larvae, metabolism scales isometrically with size (Giguère *et al.*, 1988). Early larvae use the skin and the underlying red muscle layer as the surface for oxygen uptake (El-Fiky *et al.*, 1987). Only later in their development do they switch to gill breathing. For the time before this transition, Safran (1992) predicts an exponent of less than 3 for the length-weight relationship as optimal to accommodate a proportional growth of surface and volume. As soon as the fish larvae changes to gill breathing, the growth of body surface no longer needs to match the growth in volume and the exponent might increase. Only the Clupeiformes conform to this prediction. In the other orders, the allometric exponent before the inflexion point is above or around 3. This makes the

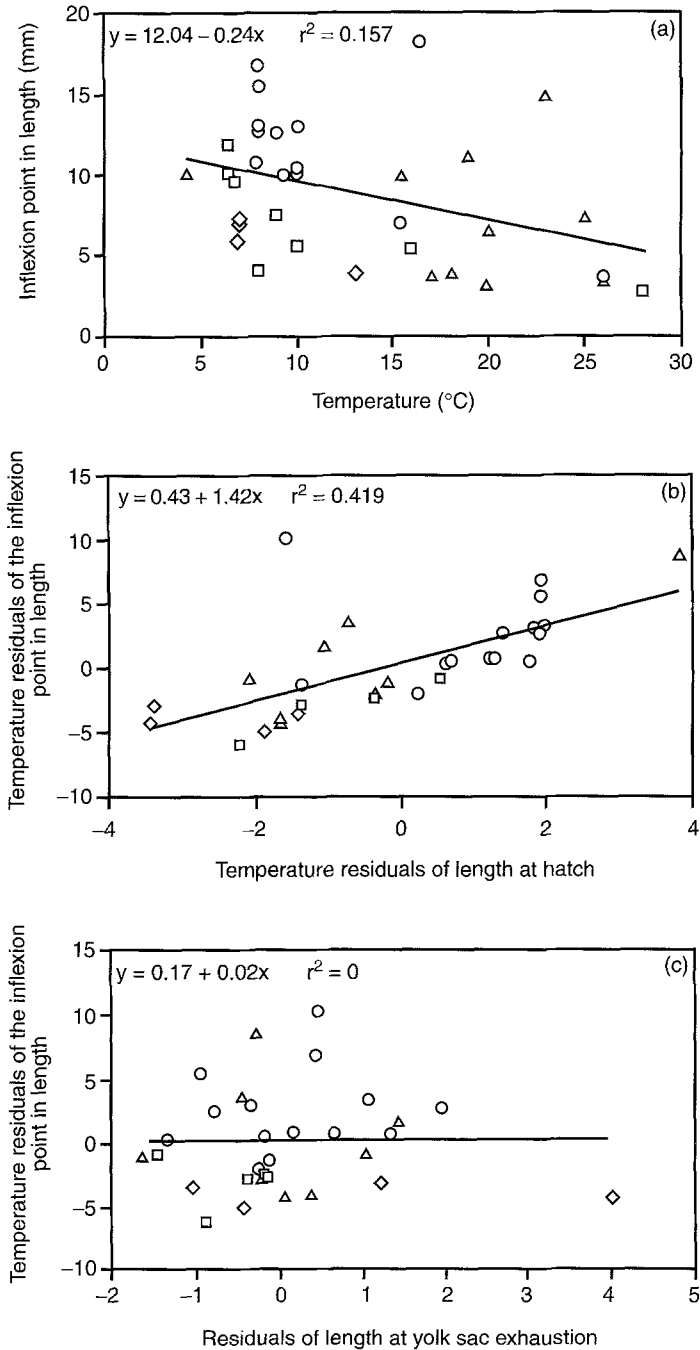


Fig. 1. (a) Inflexion point in length plotted in relation to temperature. (b) Temperature residuals of the inflexion point in length plotted in relation to the temperature residuals of the length at hatch. (c) Temperature residuals of the inflexion point in length plotted in relation to the temperature and length at hatch residuals of the length at yolk sac exhaustion. \square Pleuronectiformes, \circ Clupeiformes, \triangle Perciformes, \diamond Gadiformes.

hydrodynamic constraints a more likely candidate to explain the change in the allometric relationship of length and weight despite the fact that the large variability in length at the inflexion point weakens a hydrodynamic explanation, and so does the deviation of the Gadiformes from the overall pattern.

The data suggest that at least some fish larvae, instead of adapting, grow out of the viscous flow regime as fast as possible to reach the inertial flow regime. This is the regime to which the adult swimming morphology is optimally adjusted.

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