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Gape morphology of cod *Gadus morhua* L., haddock *Melanogrammus aeglefinus* (L.) and whiting *Merlangius merlangus* (L.) through metamorphosis from larvae to juveniles in the western Irish Sea

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Variations in standard length (L_S), gape size (S_G) and jaw length (L_J) were studied in larval and juvenile gadoids (cod *Gadus morhua*, haddock *Melanogrammus aeglefinus* and whiting *Merlangius merlangus*) from 4 to 70 mm. The increase in S_G and L_J was not linear with respect to L_S . The relationship was best described by segmented regression lines in all three species, with an inflection point at c. 10.5 mm. The S_G and L_J increased more rapidly in relation to larval L_S for individuals smaller than this inflection point size. The rates of increase slowed significantly post-inflection, an effect more noticeable in S_G data compared to L_J data. In each case, the inflection point fell in the intermediate period of development between the larval and juvenile stages, which could be considered as metamorphosis. Published equations that have been used to predict S_G from L_J lead to the overestimation of gape. New relationships are presented, which may be used to predict S_G from measurements of either L_S or upper jaw length in cod, haddock and whiting.

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Key words: development; gadoid; gape; jaw; larvae.

INTRODUCTION

Cod *Gadus morhua* L., haddock *Melanogrammus aeglefinus* (L.) and whiting *Merlangius merlangus* (L.) are commercially important whitefish which spawn between March and May in the Irish Sea (Bal, 1941; Wheeler, 1969; Nichols *et al.*, 1993; Brander, 1994). Due to similarities in spawning times and locations, there is a considerable overlap in the distribution of the pelagic

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MATERIALS AND METHODS

SAMPLE COLLECTION AND PRESERVATION

Samples of fish larvae were collected on two occasions (April and May 2001) in the north-western Irish Sea from the Department of Agriculture and Rural Development – Northern Ireland research vessel, the M.R.V. *Lough Foyle*. The full range of developmental stages, yolk-sac larvae to juveniles, were sampled with a Hydrobios Multiplankton (MP) Sampler with 280 µm mesh (Weikert & John, 1981) to capture yolk-sac larvae in both April and May, a Multiple Opening and Closing Net and Environmental Sensing System (MOCNESS) sampler (Wiebe *et al.*, 1976; Roe & Shale, 1979) with 1000 µm mesh to sample larger larvae in May only and a German pelagic juvenile trawl in May only to sample juveniles. The first two samplers were towed for 20 min using a stepwise oblique profile at 3 knots (1.5 m s^{-1}). The pelagic juvenile trawl was towed for 20 min between 4 and 5 knots ($2\text{--}2.6 \text{ m s}^{-1}$). Over a 24 h period, the MP was deployed with two replicates every 4 h, the MOCNESS six times, and the pelagic juvenile trawl only once. This sampling strategy was part of a larger project and these deployments were carried out at four different stations in the north-western Irish Sea (Fig. 1). The high numbers of deployments gave a relatively large catch of larval and juvenile gadoids.

All samples were preserved immediately in 4% buffered (sodium acetate trihydrate) formaldehyde to reduce larval shrinkage (Blaxter, 1971; Hay, 1981).

MORPHOLOGICAL AND DEVELOPMENTAL MEASUREMENTS

Standard lengths (L_S) of cod, haddock and whiting larvae were measured in the laboratory, either under a dissecting microscope with a graticule (with a precision of 0.02 mm), or in the case of larger juveniles with vernier calipers (with a precision of 0.05 mm).

The S_G were calculated using a method similar to that of Wong & Ward (1972), which allowed the limiting dimension to be measured, in this case with differently sized disposable plastic pipette tips ranging from 0.3 to 10.0 mm in diameter. The pipette tips were placed under a microscope and scored along their length using a scalpel at 0.5 mm intervals. The scored marks were then rubbed with permanent ink to leave a clearly identifiable line. The diameter of the pipette tip at each scored interval was measured using a dissecting microscope with graticule to give a range of sizes (diameters) along the pipette tip with an accuracy of 0.05 mm.

The S_G was measured by holding a larva under the microscope, while inserting a calibrated pipette tip into the mouth until a jaw angle of 90° was achieved. The diameter of the cone at the scored mark where the front tips of the upper and lower jaws touched the cone was taken to be the gape. The measurement was made at a mouth angle of 90° as this has been assumed to give the maximum gape for larval fishes (Shirota, 1970). Care had to be taken not to insert the cones too far, as this caused the pipette tip to reach the back of the mouth before the jaws were fully opened, thus giving false readings (Arts & Evans, 1987). In order to avoid this problem, a slightly larger sized tip was used if a tip went too far into the mouth.

The upper (L_{UJ}) and lower jaw (L_{LJ}) lengths of the larvae were measured under a dissection microscope with a graticule and defined as the distance from the tip of the jaw to where the upper and lower jaws joined. Jaw lengths were measured with the mouth in the closed position.

The measurement of the jaws also allowed S_G to be calculated using equations given by Shirota (1970): $S_G = \sqrt{2(L_{UJ})}$ and later modified by Guma'a (1978): $S_G = \sqrt{(L_{UJ}^2 + L_{LJ}^2)}$.

Basic developmental features of each larva were also recorded using external and internal morphology (Balon, 1975; Timmermans, 1987; Kjørsvik *et al.*, 1991; Osse & van den Boogaart, 1995). A score was allocated to each developmental observation

TABLE 1. Developmental features and assigned scores for the determination of a developmental index for larval fishes

Score	Developmental feature
External features	
1	Yolk-sac larvae with mouth closed
2	Yolk-sac larvae with mouth open
3	Exogenous feeding larvae: finfold complete
4	Exogenous feeding larvae: finrays visible
5	Exogenous feeding larvae: all fins present
Internal features	
6	Teeth not visible in mouth
7	Teeth visible in mouth
8	Incipient gut
9	Gut looped but stomach not visible
10	Stomach visible
11	Pyloric caeca visible

Developmental features based on observations from Balon (1975), Timmermans (1987), Kjørsvik *et al.* (1991) and Osse & van den Boogaart (1995).

the residual sum of squares (RSS), testing each inflection point iteratively to obtain the lowest RSS value (Somerton, 1980).

The significance of each segmented regression line was tested and comparisons between regression lines were made using the General Linear Model (GLM) assuming normality and homogeneity of variance. All calculations were made using MINITAB® release 13.1 (www.minitab.com).

RESULTS

GAPE SIZE AND STANDARD LENGTH RELATIONSHIP

The S_G increased allometrically with L_S and when transformed using \ln , a segmented relationship with a single inflection point was observed (Fig. 3). Although a single line linear regression could be fitted to these data, it obscured the true relationship between S_G and L_S [Table II(a), shown by the lower F -statistic values]. The inflection points were located at a L_S of 9.84 mm for whiting, 10.21 mm for haddock and 11.72 mm for cod. The differences between species were not significant, suggesting a global gadoid 'breakpoint' of 10.56 mm.

In all three species, the slope of the regression of S_G and L_S for fish pre-inflection point was >1 (positive allometry) and for post-inflection point, the slope was <1 (negative allometry), [Table II(a)]. In all cases, the relationship between pre- and post-inflection points was significantly different (GLM, d.f. = 2, n = 141, P < 0.001; d.f. = 2, n = 258, P < 0.001; d.f. = 2, n = 553, P < 0.001, for cod, haddock and whiting, respectively).

Among smaller larvae (pre-inflection point), the S_G of whiting increased at a significantly slower rate than that of haddock (GLM, d.f. = 2, n = 520, P < 0.001), while the rate of S_G increase of cod fell between that of whiting and haddock and was not significantly different to either. In larger larvae

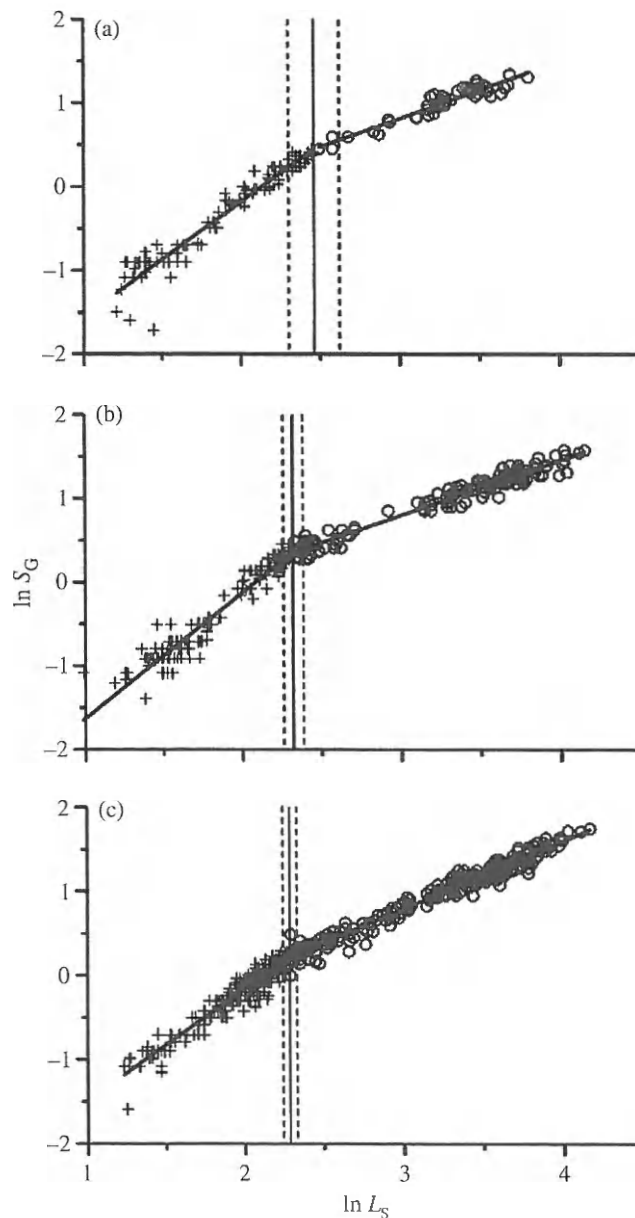


FIG. 3. Natural logarithmic transformed standard length (L_S) and gape size (S_G) for (a) cod, (b) haddock and (c) whiting. The inflection point position at L_S (solid vertical line) $\pm 95\%$ CI (dashed vertical line) for cod (2.46 ± 0.16), haddock (2.32 ± 0.06) and whiting (2.29 ± 0.05) is shown (see Table II for regression analysis).

GAPE SIZE AND JAW LENGTH RELATIONSHIP

The L_{UJ} was used for analysis, as it was the easier dimension to measure, and therefore most reliable. When compared, L_{UJ} and S_G again produced a curved relationship, which was transformed using \ln . A segmented relationship with

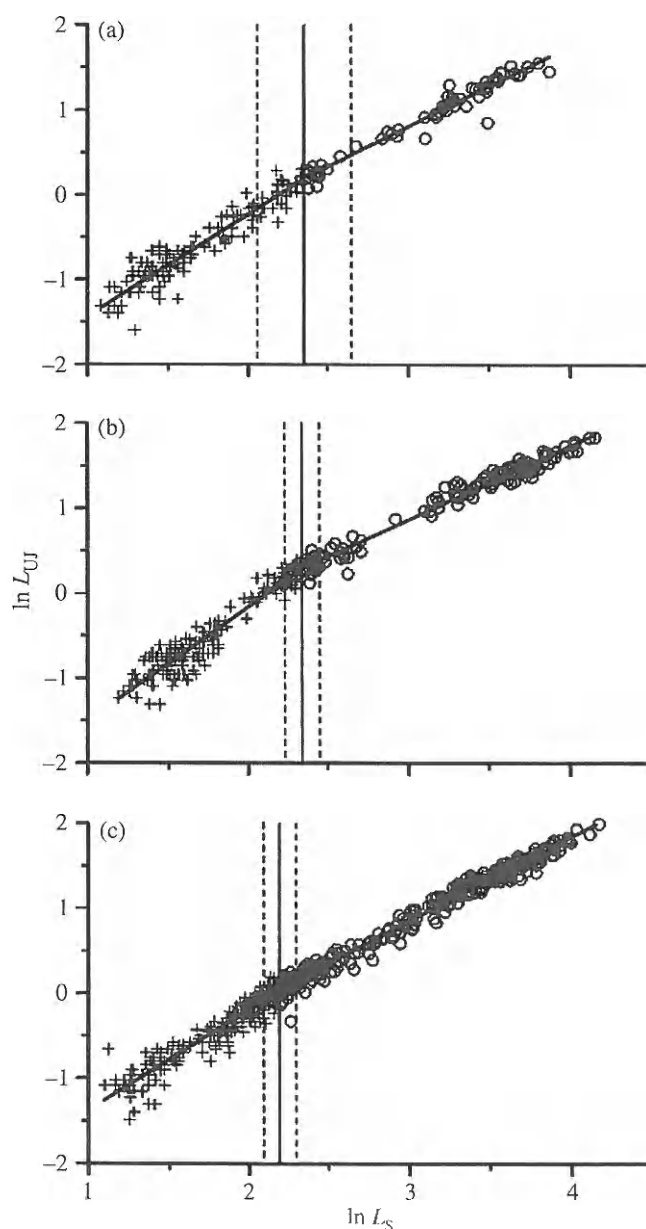


FIG. 4. Natural logarithmic transformed standard length (L_S) and upper jaw length (L_{UJ}) for (a) cod, (b) haddock and (c) whiting. The inflection point position at L_S (solid vertical line) $\pm 95\%$ CI (dashed vertical line) for cod (2.34 ± 0.29), haddock (2.34 ± 0.11) and whiting (2.19 ± 0.10) is shown (see Table II for regression analysis).

single inflection point (Fig. 5) was a better fit to the data than a single linear regression [F statistic greater in segmented relationships; Table II(c)]. The positions of these inflection points were compared and no differences were observed between species, occurring at a L_{UJ} of 1.27 mm.

of the regression lines below the inflection point showed no differences. Regressions above the inflection point, however, suggested that S_G increased at a significantly faster rate with jaw length for cod compared to either haddock or whiting (GLM, d.f. = 2, $n = 411$, $P < 0.05$), with no difference between the haddock and whiting.

MODELS FOR ESTIMATING GAPE

The S_G was calculated from L_{UJ} , following equations in Shirota (1970) and Guma'a (1978) and compared to the actual measurements of S_G . The calculated S_G were significantly larger than actual gape measurements (GLM, d.f. = 2, $n = 1801$, $P < 0.001$), with post-inflection point data (those >9.84 mm, taken from Fig. 4) showing increased overestimation.

From data in this study, individual models converting L_S , L_{UJ} and L_{LJ} to S_G could be calculated and are shown below. The associated variables (a and b) for each gadoid species pre- and post-inflection point are given in Table III: $S_G = (L_S^a)b$, $S_G = (L_{UJ}^a)b$ and $S_G = (L_{LJ}^a)b$.

Each model is subject to size constraints due to the segmented nature of the data and the size range of larvae used. Pre-inflection equations for all models are limited to larvae of L_S and L_{UJ} and L_{LJ} below the size at inflection. The L_S model, post-inflection equations have an upper size limit of 50 mm for cod, and 65 mm for haddock and whiting. The L_{UJ} and L_{LJ} models, post-inflection equations have an upper limit of 4.5 mm for cod, 6.5 mm for haddock and 7.5 mm for whiting.

TABLE III. Associated coefficients used for the calculation of larval gape size, when using 1) standard length, 2) upper jaw length and 3) lower jaw length measurements

	Species	Size range (mm)	Coefficients	
			a	b
1)	Cod	<10.56	1.376	5.297×10^{-2}
		>10.56	0.768	2.952×10^{-1}
	Haddock	<10.56	1.500	4.381×10^{-2}
		>10.56	0.654	3.122×10^{-1}
	Whiting	<10.56	1.331	5.937×10^{-2}
		>10.56	0.803	1.987×10^{-1}
2)	Cod	<1.27	1.134	1.089
		>1.27	0.773	1.174
	Haddock	<1.27	1.100	1.044
		>1.27	0.758	1.146
	Whiting	<1.27	1.063	1.040
		>1.27	0.807	1.109
3)	Cod	<1.27	1.030	1.207
		>1.27	0.672	1.439
	Haddock	<1.27	1.050	1.095
		>1.27	0.782	1.246
	Whiting	<1.27	1.010	1.078
		>1.27	0.804	1.213

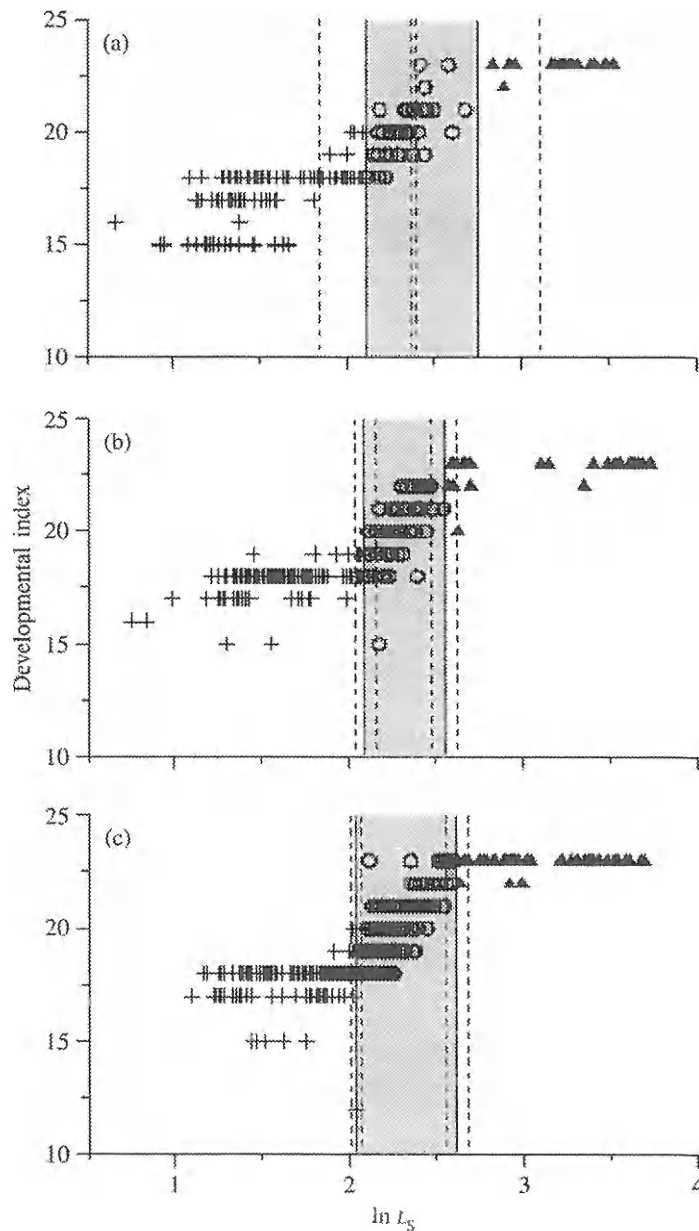


FIG. 6. Relationship between developmental index and \ln -transformed standard length (L_S) data for (a) cod, (b) haddock and (c) whiting. Inflection points at L_S for the change of larval stage are shown as solid vertical lines, $\pm 95\%$ CI shown as dashed vertical lines. Shaded area equates to the region of 'intermediate' stage (O) after the larval stage (+) and before the juvenile stage (▲).

marine larvae by Shirota (1978), where the point of inflection was seen to differ between species. In this study, however, the inflection point occurred at the same L_S for all species for S_G , and L_{UJ} data, implying a general gadoid model, certainly for these gadoids in the Irish Sea. In these fish, the inflection points

available will occur and affect the prediction of larval survival in relation to prey present.

Shirota's (1970) and Guma'a's (1978) calculations rely on a single relationship to derive S_G from jaw length. When post-inflection point data were compared to pre-inflection point data from this study, there was a $25 \pm 5\%$ ($\pm 95\%$ CI) reduction in the rate of jaw length increase compared to a $50 \pm 5\%$ reduction in the rate of S_G increase for the same increase in L_S . Thus, the real segmented allometric effect was not fully translated into the S_G calculations of Shirota (1970) and Guma'a (1978), leading to overestimations of S_G , especially during both the later intermediate and juvenile stages. Two non-linear models (one pre-inflection and one post-inflection) for each gadoid species that incorporate the relative changes of S_G in relation to either jaw length or fish L_S produces better estimates where S_G cannot be measured directly. This method of S_G calculation on unpreserved larvae would have to be carried out with caution as 10% shrinkage has been observed in the L_S of other gadoid species preserved in formalin (Porter *et al.*, 2001).

In conclusion, S_G can be a useful tool in establishing prey niche size of fish larvae, and in helping to developmentally stage larval fishes. If S_G is calculated from jaw length, however, the allometric relationships as larvae grow and develop must be incorporated. Although S_G and rates of S_G increase have been shown to vary between species, similarities suggesting the existence of a global gadoid model were also observed. These similarities were related to larval development, where in all species, larval L_S at changes in jaw and gape allometry did not differ significantly. In every case, these changes in allometry occurred in the same period of development, the intermediate stage, equating to the period of most rapid development implying metamorphosis. This was found not to differ between species implying a general gadoid L_S for the start of metamorphosis at 8 mm, with rapid development ceasing at a L_S of 14 mm. Further experimentation of interest would therefore be the larval study of other gadoid species to see if they too adhered to these developmental patterns. Another interesting comparison would be the application of the newly derived gape calculation equations to adult cod, haddock and whiting.

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