Journal of Fish Biology (2001) **59,** 1111–1125
doi:10.1006/jfbi.2001.1724, available online at http://www.idealibrary.com on IDEAL®

REGULAR PAPERS

Diet breadth variability in larval blue whiting as a response to plankton size structure

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(*Received 7 October 2000, Accepted 19 July 2001*)

Diet breadth (measured as the S.D. of the log of prey size per larvae; SLH) of blue whiting *micromesistius poutassou* larvae followed a quadratic equation with larval size. In small larvae, diet breadth in terms of size (SLH), the mean and the maximum of the log of prey size per larvae (MLH and XLH, respectively) increased with larval size as prey size selection shifted to larger prey. In contrast, large larvae tended to reduce diet breadth of prey sizes ingested, focusing on the larger prey that were abundant, instead of raising the upper limit of prey sizes because of the low abundance of larger prey. Except for larvae at the onset of first feeding, number of prey stayed constant or decreased in relation to larval size. Both patterns (in small and large larvae) maintained a constant rate of increase of gut carbon content with increase in larval size. Large larvae appear to maintain the increase in gut carbon content during ontogenetic development by reducing diet breadth (SLH) and increasing selection towards the larger prey that are abundant.

Key words: fish larvae; blue whiting; feeding ecology; prey size; diet breadth.

INTRODUCTION

During the relatively brief larval stage, fishes can increase their biomass by a factor of $\times 10^3$ (Houde, 1987); energetic demands for maintenance of this high growth rate have to change dramatically as a consequence of size. The availability of prey during larval development will be defined by changes in diet breadth. Diet breadth is ultimately dependent on changes of the prey that larva are capable of feeding upon. Mouth gape has been proposed as the main morphological constraint to maximum prey size. Also, other rapid morphological and physiological changes ocurring in larval development modify detection capability or swimming speed that have important consequences on components of the foraging process such as searching and handling (Munk, 1992, 1997).

As fishes grow, they increase the capability to consume a wider range of prey sizes in absolute terms. Maximum prey size usually increases with predator size while minimum size remains constant or increases slightly (Peters, 1983). Pearre (1986) argues that using the range of prey size to define diet breadth as fishes grow has fostered the impression that larger fish have a competitive advantage.

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0022–1112/01/111111+15 $35.00/0

Range is dependent on sample size that in turn is dependent on the size structure of the predator population, gear selectivity and on the fact that number of prey within the gut often increases with fish size. Standard deviation (S.D.) of prey size, although independent of sample size, does not take into account changes in fish size as they grow. Instead, Pearre (1986) proposed the S.D. of the logarithm of prey size (SLH) as the most adequate parameter to represent diet breadth. The variance of prey size is often proportional to the mean, so a log transformation is adequate to make variance and mean independent for testing significance. In addition, logarithmic interval recording of prey sizes adjusts, at least partially, to the scale of perception of fish larvae, that, as referred to above, they increase their mass $\times 10^3$ during the larval period (Houde, 1987).

Pearre (1986) formulated the hypothesis that the ratio of prey size to larval size is a constant, showing constant SLH against fish size for several species. Other studies support this hypothesis (Munk 1992, 1997, Sabatés & Sáiz, 2000). However, Pepin & Penney (1997) observed variability in SLH with respect to fish larval size for six out of 11 species. This variability was maintained in fishes for which SLH remained relatively constant and mean prey size increased, to the other extreme, where animals increased SLH but with a low increase on mean prey size. They observed a negative relationship between the rate of change in mean prey size and the rate of change in SLH.

Gut content analysis was carried out on blue whiting *Micromesistius poutassou* (Risso) larvae in the present study. This gadoid spawns from February to June along the edge of the European shelf from Portugal to the Faeroe Islands (Bailey, 1974), progressively later as spawning activities move northwards (Coombs, 1980). Blue whiting larvae occur in the Cantabrian Sea from February to April, being most abundant in March (Dicenta, 1984; González-Quirós, 1999). Only two studies have been published on feeding of larval blue whiting. Conway (1980) analysed the gut contents of larvae and juveniles from Rockall and Hillgruber *et al.* (1997) from the Porcupine Bank, both areas located far from the coast and north or midpoint in the latitudinal range of the species. This study is the first on larval feeding from the southern part of the blue whiting range and also the first to include coastal sampling.

The hypothesis of a constant diet breadth in terms of the ratio of prey size to blue whiting larval size was tested. The effect of SLH and the number and type of prey on the rate of increase in gut carbon content was analysed in relation to larval size and the range in plankton size.

MATERIALS AND METHODS

Sampling was carried out from the RV José Rioja at three stations off the central Cantabrian coast (Fig. 1) in March 1994. Stations 2 and 3 were sampled on 18 March and station 1 on 19 March, all during daytime, between 0900–1130 hours. Temperature and salinity distribution was determined by a CTD (conductivity, temperature and depth sensor) probe.

Sampling for larval blue whiting and their potential food was carried out by a variety of methods. Only organisms observed during gut contents analysis were considered. The abundance of microplankton <53 μm was estimated from 125 ml water samples preserved in lugol's solution, obtained with Niskin bottles from 0, 20 and 40 m depth. Fish larvae and mesozooplankton were sampled with a 40 cm diameter bongo net with a

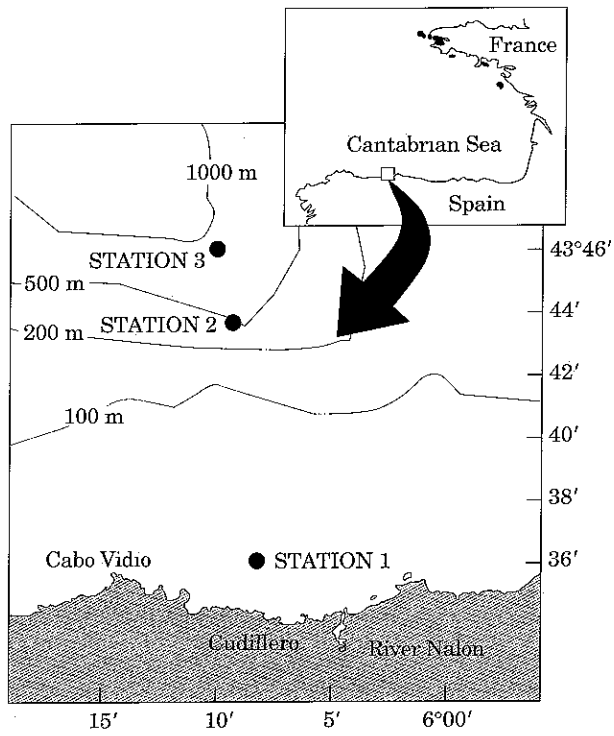

FIG 1 Area of study

200 μm mesh net. Abundance of copepod copepodites with a cephalothorax length >800 μm was estimated from 0·02 of the sample volume obtained with a Stemple pipette. Microplankton >53 μm was sampled with a 10 cm diameter bongo net of 53 μm mesh, attached above the larger bongo net. Abundance of copepodites with cephalothorax length <800 μm, copepod nauplii and copepod eggs were estimated from 0·01 of the sample volume obtained with a Stemple pipette. Bongo tows were hauled to 55 m depth at station 1 and to 120 m at the other two stations. Calibrated flowmeters were mounted on both bongo nets to calculate volume of water filtered. A depth monitor was attached to the bongo frame to determine maximum tow depth. Ship speed during bongo tows was maintained at 3–3·5 knots. Samples were preserved in freshwater, borax buffered 4% formalin.

Mandible length was chosen as an index of mouth gape, assuming an isometric relationship between both variables. The mandible length and the standard length (L_s) of 100 blue whiting larvae were measured with a micrometer under an steromicroscope to the nearest 0·01 mm to analyse the relationship between variables.

GUT CONTENT ANALYSIS

Gut content analysis was carried out on larvae from all stations. L_s of larvae selected for gut content analysis was measured as above. The number of prey within the gut of each larva was noted and sorted into four different prey types: tintinnids, and copepod eggs, nauplii and copepodites. Several nauplii and copepodites within the gut contents were deformed (see below), which made further identification difficult.

For prey size analysis, maximum width of tintinnids, copepod egg diameter, and cephalothorax width of copepod nauplii and copepodites were measured with a micrometer under a steromicroscope.

Several copepod nauplii and copepodites within the guts were laterally and dorso-ventrally flattened. The relationship between body width (L_w) and length (L) of prey from

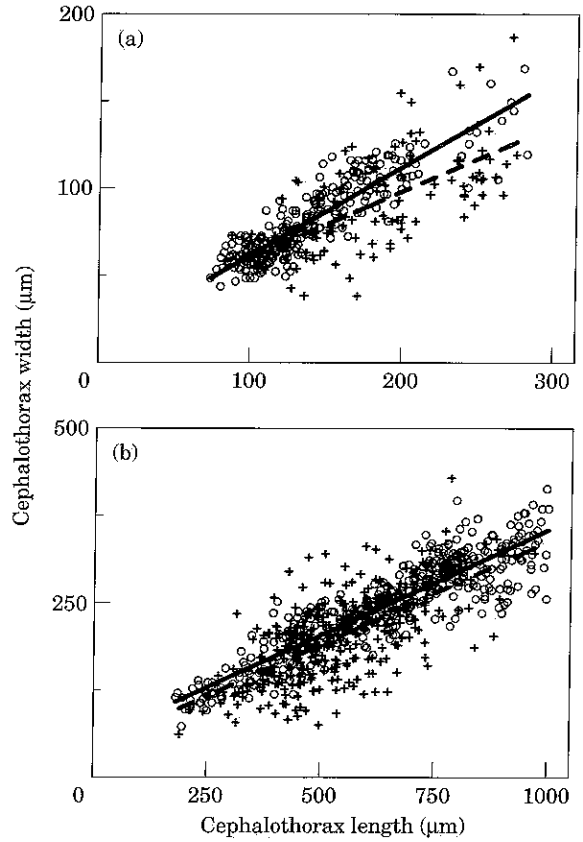

FIG 2 Relationship between cephalothorax width and length for copepod nauplii (a) and copepod copepodites (b). ○, from the plankton samples; + from gut contents. Regression lines are given for prey from the gut (——) and from the plankton samples (– – –).

the guts and from the plankton samples were compared to test the feasibility of direct comparisons between prey widths in the plankton and in the gut contents. It was assumed that there was no alteration in prey length due to digestion. A sub-sample of 35 nauplii and 100 copepodites from the gut contents, and 100 nauplii and 150 copepodites from the plankton samples were taken from each station and measured. Higher dispersion of data from the length-width relationship is observed for the prey from the guts (Fig. 2). This is consistent with the lower coefficients of determination of the regressions obtained for the prey within the guts, compared with prey from the plankton samples: $L_w=0{\cdot}38\,L+22{\cdot}16$, $n=116$, $r^2=0{\cdot}44$, for nauplii in the gut contents; $L_w=0{\cdot}51\,L+10{\cdot}72$, $n=300$, $r^2=0{\cdot}80$, for nauplii from the plankton; $L_w=0{\cdot}30\,L+41{\cdot}89$; $n=332$, $r^2=0{\cdot}44$, for copepodites in the gut contents; and $L_w=0{\cdot}30\,L+53{\cdot}15$; $n=450$, $r^2=0{\cdot}82$, for copepodites from the plankton. Therefore, width of nauplii and copepodites in the guts was recalculated from lengths using the plankton sample regressions.

Descriptive statistics were used to analyse the patterns of prey size within the guts. Prey width was logarithmically transformed as the variance of prey width was proportional to the mean. The maximum, the mean and the S D of the logarithm of prey width per larvae were calculated, referred hereafter as XLH, MLH and SLH respectively. SLH is used as a measure of diet breadth of prey sizes. The adequacy of SLH as an index of diet bredth of prey sizes has been discussed by Pearre (1986). MLH and SLH were only calculated for larvae with at least three prey in their gut.

ESTIMATION OF GUT CARBON CONTENT

The carbon equivalent mass (W_c, µg C) of the gut content was estimated from different allometric equations for the different types of prey. W_c of tintinnids was calculated from $W_c = 0{\cdot}053\ V_L$ (Verity & Langdon, 1984); V_L is the volume of the loricae. This volume was calculated as an hemi-ellipsoid as all the tintinnids observed within the guts had a shape very similar to this geometric form. W_c of copepod eggs was estimated from: $W_c = 160\ V_e$, V_e is egg volume (mm^3) (Kleppel *et al*., 1991). The carbon mass value given by Mullin & Brooks (1970) for copepodite III of *Calanus helgolandicus* (4·9 µg) was used for those copepodites observed in the guts. Carbon mass for the remainder of the copepod copepodites and nauplii (W_c, µg C) was estimated from $W_c = 0{\cdot}4\ W$ (Parsons *et al*., 1984), where dry mass (W, µg) was calculated from $W = e^{(4{\cdot}964\ L_c - 2{\cdot}168)}$, L_c is the cephalothorax length (µm); this equation was calculated by Hay *et al*. (1988) from nauplii and copepodites of *Pseudocalanus elongatus*.

PREY SIZE SELECTION

Chesson's electivity index (Chesson, 1978) was chosen to analyse feeding preferences.

$$\alpha_i = (d_j p_j^{-1})[\Sigma(d_i p_i^{-1})]^{-1}, \text{ for } i = 1, \quad , n$$

where n = number of prey items considered; d_j and p_j = frequencies of prey in the diet and in the plankton respectively; and d_i and p_i = the same frequencies for the ith prey. The index for a prey size class was first computed for each larvae and then averaged for the different length categories of larvae. It is independent of the fluctuations in the absolute abundance of the plankton and varies only with changes in the feeding behaviour of the larvae.

RESULTS

COMPOSITION AND ABUNDANCE OF POTENTIAL PREY IN THE PLANKTON

High abundance of tintinnids was observed at station 1 (Table I). Copepod eggs and nauplii dominated microplankton >50 µm. Mesozooplankton >200 µm was dominated by copepod copepodites, which comprised >80% at station 1 and >90% at stations 2 and 3 (unpubl. data). In relation to the abundance of sizes of potential prey (Table I), two features are apparent, the high abundance of 0–50 µm prey at station 1 (mostly tintinnids) and the low abundance of large prey observed at all the stations. There is a significant decrease, almost two orders of magnitude, in the abundance of prey from the 250–350 to the >450 µm prey size class.

GUT CONTENTS

Carbon content

Total carbon within the gut related to larval length followed a power function at stations 1, 2 and 3 and for all the data together (Fig. 3; Table II). There were significant differences between slopes of the regression lines of the logarithmic transformed variables ($\alpha < 0{\cdot}01$, $F_{2,123} = 10{\cdot}60$, $n = 129$). There were pairwise differences between station 1 and 2 (Tukey test; $q = 4{\cdot}961 > q_{0{\cdot}001,80,2}$) and between station 1 and 3 (Tukey test; $q = 6{\cdot}508 > q_{0{\cdot}001,79,2}$). No significant differences were found between stations 2 and 3 (Tuckey test; $q_{0{\cdot}2,87,2} < q = 2{\cdot}23 < q_{0{\cdot}1,87,2}$). Gut carbon content data for larvae from station 1, which ingested tintinnids (see below), showed lower gut carbon content values than for larvae of the same size range from the other stations (Fig. 3). This is the major cause of the higher slope

TABLE I. Abundance (individuals m^{-3}) of prey types and prey sizes in the plankton (only prey types and prey sizes that were observed within the gut contents)

Station	Prey size (μm)	Prey type				
		Tintinnids	Nauplii	Copepodites	Copepod eggs	Total
1	0–50	55 000 (1)	162	—	—	55 162
	50–100	—	4365	165	1530	6060
	100–150	—	754	892	568	2215
	150–250	—	108	1454	87	1650
	250–350	—	—	2354	—	2354
	350–450	—	—	555	—	555
	>450	—	—	53	—	53
	Total	55 000	5389	5474	2185	68 049
2	0–50	—	—	—	—	—
	50–100	—	2129	327	471	2927
	100–150	—	539	682	80	1301
	150–250	—	27	1310	23	1360
	250–350	—	—	872		872
	350–450	—	—	176		176
	>450	—	—	45		45
	Total	—	2694	3412	574	6680
3	0–50	—	75	—	—	75
	50–100	—	2695	82	521	3297
	100–150	—	936	1224	193	2353
	150–250	—	37	1877	30	1944
	250–350	—	—	1926	—	1926
	350–450	—	—	175	—	175
	>450	—	—	44	—	44
	Total	—	3743	5328	744	9814

(1) Average value from samples at 0, 20 and 40 m depth. All other values were calculated from samples obtained by tows down to 50 m at station 1 and down to 120 m at stations 2 and 3

obtained for station 1. Increasing the amount of carbon ingested can be achieved in two ways, an increase in the number of prey or an increase in prey carbon content.

Number of prey in the gut

Feeding incidence of all blue whiting larvae analysed was 95·6%. Small larvae at station 1 had empty guts or were nearly empty, but slightly larger larvae, which had ingested tintinnids, had high numbers of prey (a maximum of 58 tintinnids $larvae^{-1}$) [Fig. 4(a)]. The number of prey ingested declined with larval size and this pattern persisted in larvae with no tintinnids in their guts [Fig 4(a)]. Mean number of prey for larvae >3 mm at station 1 was *c.* 16·47 prey $larvae^{-1}$ (S.D. 13·13). At stations 2 and 3 there was a different pattern, for larvae >3 mm, the number of prey items reached an asymptotic value *c.* 18 per larvae, although

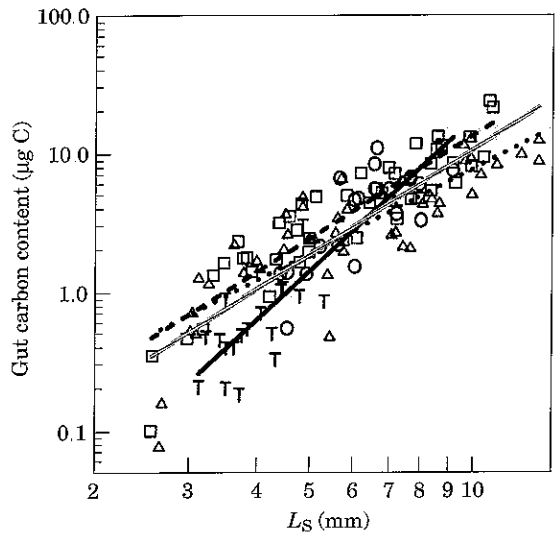

FIG 3 Gut carbon content and larval length (note logarithmic scales). T, ○, Data from station 1, with and without tintinnids in the guts, respectively; □, data from station 2; △, data from station 3. Regression lines fitted by a power function: ——, data from larvae from station 1; – – –, from station 2; • • •, from station 3; ≈≈≈, data from all three stations

TABLE II. Results of the regression analysis between the logarithms of gut carbon content ($\log_{10} W_c$, µg C) and larval length ($\log_{10} L_s$; mm)

Station	n	Linear regression equation	r^2	F
1	38	$\log_{10} W_c = 3{\cdot}65 \log_{10} L_s - 2\,38$	0·80	145 1
2	46	$\log_{10} W_c = 2\,48 \log_{10} L_s - 1{\cdot}33$	0 82	207·7
3	45	$\log_{10} W_c = 2{\cdot}02 \log_{10} L_s - 1{\cdot}12$	0·69	96 9

n, Number of larvae analysed. All F values were significant at $\alpha < 0{\cdot}0001$

there was high variability [Fig. 4(b)]; at station 2, the mean number per larvae >3 mm was 13·53 prey larvae^{-1} (S.D. 5·27), and at station 3, 9·91 prey larvae^{-1} (S.D. 4·47). Both patterns, a decrease in the number of prey and no variation with larval size, suggest that the direct proportionality that was observed between gut carbon content and larval size (Fig. 3) has to be a major consequence of shifts in the carbon content of the ingested prey.

Prey type

Blue whiting larvae fed almost exclusively on the life stages of copepods: eggs, nauplii and copepodites (Fig. 5). There was a shift from copepod nauplii to copepod copepodites with increasing larval size at every station. Differences between their percentage in number and in carbon within the guts are a consequence of differences in prey size, as carbon prey content was calculated from allometric equations. Only larvae <5·5 mm at coastal station 1 fed on tintinnids. For this prey type there was an important contrast between their

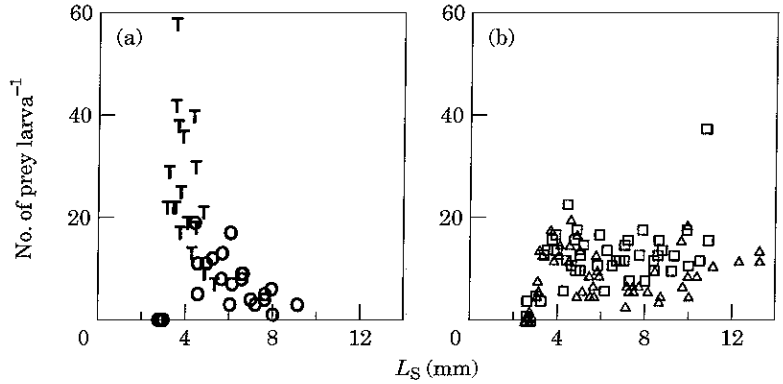

FIG 4. Number of prey per larvae. (a) larvae from station 1, T, larvae that have at least one tintinnid within the gut; ○, larvae without tintinnids; (b) □, larvae from station 2; △, larvae from station 3

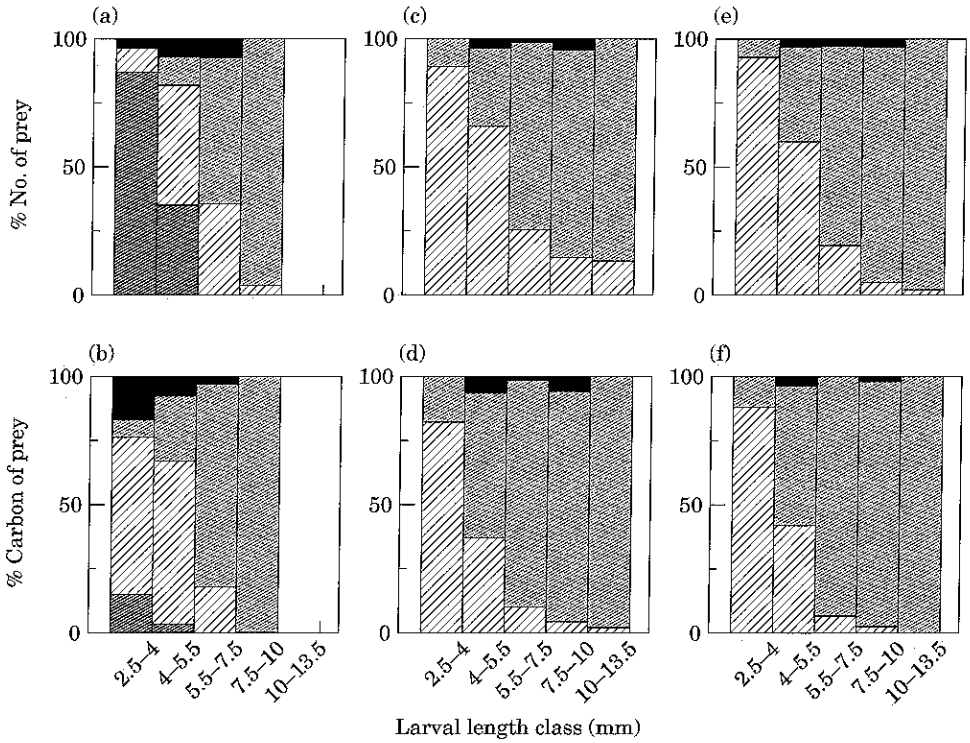

FIG 5. Percentage by number and percentage by carbon of each prey type in the guts of the blue whiting larval length classes at stations 1 (a), (b), 2 (c), (d) and 3 (e), (f). ▩, tintinnids, ■, copepod eggs; ▨, copepod nauplii; ⊞, copepodites.

percentage in number and their corresponding percentage in carbon (Fig. 5). Copepod eggs did not represent an important percentage of the diet and no clear pattern in relation to larval size was observed.

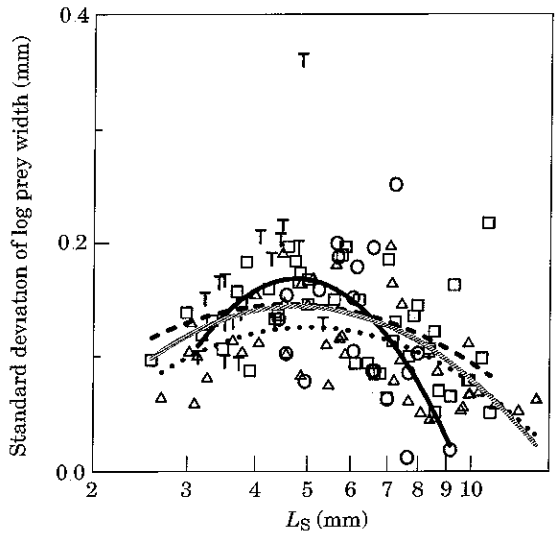

FIG 6. Standard deviation of the logarithm of prey width (SLH) against larval length (note logarithmic *x*-axis scale). T, ○, Larvae from station 1, with and without tintinnids in their guts, respectively; □, larvae from station 2; △, larvae from station 3. Lines represent fits to a second degree polymomial equation after logarithmic transformation of larval length; ——, data for larvae from station 1; – – –, from station 2; • • •, from station 3; ~~~, data for all three stations.

Diet breadth

The relationship between SLH and larval length followed a quadratic function (Fig. 6). Regression analysis on other functions (linear, power and exponential) resulted in higher residual sum-of-squares error and significance levels and lower coefficients of determination. As stated above, the rate of increase in gut carbon content against larval size (Fig. 3) was a consequence of changes in prey carbon content because the number of prey was fairly constant, or decreased, for larvae >3 mm (Fig. 4). The reduction in SLH in large larvae (Fig. 6) did not affect the rate of increase in gut carbon content against larval size. As stated above gut carbon content against larval size followed a power function and the resultant residuals were uniformly distributed around zero against logarithm of larval size.

Mouth gape and prey size

Mouth gape may be a morphological constraint to log prey maximum width (XLH). Should this be the case, it can be expected that slopes of the regression lines between mouth gape and XLH against larval length, or at least the upper limit of XLH, would be parallel. The regressions obtained between larval length (L_s) and mandible length (M), both in mm, and between both log-transformed variables were: $M=0{\cdot}177L_s-0{\cdot}126$ ($n=100$; $r^2=0{\cdot}92$, and log $M=1{\cdot}22$ log $L_s-0{\cdot}989$ ($n=100$, $r^2=0{\cdot}94$).

The slope of the latter is different from that obtained from the regression of XLH and log L_s, XLH$=0{\cdot}80$ log $L_s-1{\cdot}28$ ($n=129$, $r^2=0{\cdot}62$) and log prey mean width (MLH) (excluding larvae with tintinnids) and log L_s, MLH$=0{\cdot}87$ log $L_s-1{\cdot}49$ ($n=111$, $r^2=0{\cdot}76$) (Fig. 7). Although different, it was not possible to

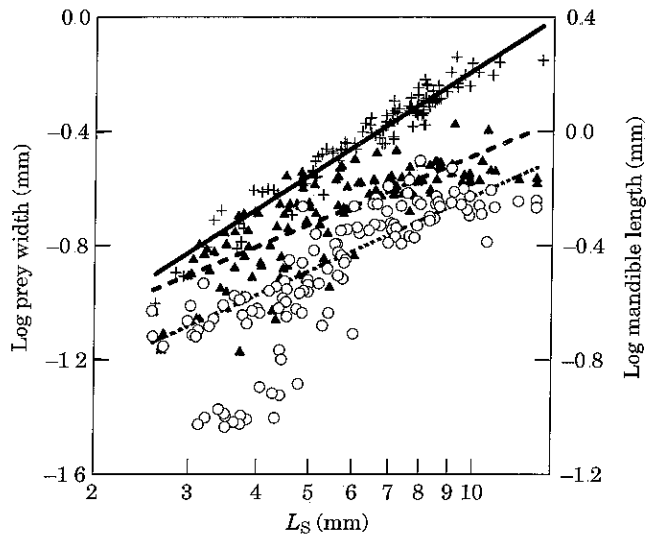

FIG. 7 Relationship between larval length and maximum of log prey width (XLH, ▲, – – –), mean of log prey width (MLH, ○, • • •) and log mandible length (+, ——) Note log scales. Regression lines have been fitted to the data.

compare them by ANCOVA because of significant heterogeneity of variance (Chocran's test; $P<0{\cdot}0001$). However, for small larvae, the higher observed values of XLH for a certain larval size seem to be related to mandible length (Fig. 7). In contrast, for large larvae, XLH and MLH do not increase with larval size as does mandible length. This pattern may be a consequence of the low abundance of large prey size classes observed in the plankton. Also, less dispersion of XLH and MLH data is also observed in large larvae (Fig. 7), which is consistent with the observed reduction of SLH for large larvae (Fig 6) At least for small larvae, XLH and mouth gape are related, but the low abundance of large prey sizes seems to be regulating XLH in large larvae.

Prey size selection

In small larvae there is a shift in selection for larger prey size classes with increasing larval size (Table III). However, above the 5·5–7·5 mm larval length class, although with some variability between stations, size prey selection remains constant or shifts slightly towards larger prey sizes, taking into account that at the coastal station no larvae of the largest size fraction were found

DISCUSSION

The gut content analysis in this study does not support the hypothesis of a constant diet breadth on a scale dependent on fish size (Pearre, 1986) across the range of blue whiting larval sizes. In small larvae, diet breadth in terms of size (SLH), MLH and XLH increase with larval size as prey size selection shifts to larger prey. In contrast, large larvae tend to reduce SLH, focusing on the larger prey that are abundant, instead of raising the upper limit of prey sizes because of

TABLE III Larval selectivity for prey sizes

Station	Larval length class (mm)	*n*	Prey size class (μm)				
			0–50	50–100	100–150	150–250	250–350
1	2·5–4	10	0·418 (+)	0·273 (+)	0·244 (+)	0·065 (−)	—
	4–5·5	10	0·068 (−)	0·450 (+)	0·331 (+)	0·151 (−)	—
	5·5–7·5	10	—	0·105 (−)	0·185 (−)	0·347 (+)	0·364 (+)
	7·5–10	6	—	—	0·038 (−)	0·225 (+)	0·737 (+)
	10–13·5	—	—	—	—	—	—
2	2·5–4	10	—	0·560 (+)	0·378 (+)	0·061 (−)	—
	4–5·5	10	—	0·335 (+)	0·314 (+)	0·328 (+)	0·024 (−)
	5·5–7·5	10	—	0·046 (−)	0·201 (+)	0·665 (+)	0·087 (−)
	7·5–10	10	—	0·012 (−)	0·115 (−)	0·685 (+)	0·189 (−)
	10–13·5	3	—	0·041 (−)	0·086 (−)	0·504 (+)	0·370 (+)
3	2·5–4	10	—	0·715 (+)	0·254 (+)	0·031 (−)	—
	4–5·5	10	—	0·308 (+)	0·287 (+)	0·376 (+)	0·028 (−)
	5·5–7·5	10	—	0·042 (−)	0·194 (−)	0·601 (+)	0·164 (−)
	7·5–10	10	—	—	0·026 (−)	0·729 (+)	0·245 (+)
	10–13·5	5	—	—	—	0·786 (+)	0·214 (+)

n, Number of larvae included in the analysis for each larval size class; (+), positive selection, (−), negative selection

the low abundance of larger prey. These different feeding patterns do not reflect a change in the rate of increase of gut carbon content that is constant with larval size.

The number of prey within the guts of blue whiting larvae was within the values reported by Conway (1980) and Hillgruber *et al.* (1997) for this species. However, a high number of prey was observed in small larvae at station 1 because of the high number of tintinnids consumed. Length of blue whiting larvae at hatching is *c.* 2·5 mm (Coombs & Hiby, 1979), hence the small larvae with empty stomachs or with low number of prey would be at the onset of first feeding.

The daily feeding cycle for blue whiting larvae reported by Conway (1980), indicated that the highest percentage of empty guts ocurred at night, between 0300 and 0500 hours. Wet mass of the gut contents also decreased during the night, with minimum values between 0500 and 0700 hours. This pattern was consistent for both small (3–6 mm L_s) and large larvae (7–15 mm L_s). Apart from latitude and seasonal differences, carbon content and number of prey in the present study may be below mean daily values. It can be argued that sampling larvae at the time of low gut contents may not reflect their feeding pattern adequately and that the decrease in SLH in large larvae may be a consequence of it. Gut contents are the consequence of the balance between ingestion rate and gut passage time or digestion rates. It has been suggested that digestion time is dependent on particle sizes ingested (Hall *et al.*, 1995, Salvanes *et al.*, 1995) In case this affects the prey size spectra within the gut (as an indirect measurement of feeding behaviour), sampling at the time of low gut contents (consequence of

a decrease in the ingestion rate and continuation of digestion) would reflect bias towards higher percentage of large prey. Concurrently, the absence of large prey in the guts of large larvae would not be a consequence of sampling larvae at a time with gut contents below the mean and, therefore, the general conclusion of a diet breadth reduction in larger blue whiting larvae would be reinforced.

The diet of blue whiting larvae in this study consisted mainly of copepod nauplii and copepodites. The gradual ontogenetic change in feeding, from ingestion of nauplii by small larvae to copepodites by larger larvae, have been previously reported for blue whiting (Conway, 1980) and other larval fishes (Last, 1980). The fact that at stations 2 and 3 the number of prey remained fairly constant with increase in larval size, and that it decreased in larvae from station 1, suggests that the direct proportionality between gut carbon content and larval size is a major consequence of shifts in the size of copepod nauplii and copepod copepodites ingested. In the case of tintinnids, for which large differences between the percentage of ingested prey and the percentage of gut carbon content were observed, other non size-dependent aspects involved in the foraging process may have an important role Copepod eggs had a low percentage occurrence in the guts and there was no clear feeding pattern related to larval size. The cause of the low percentage could be, as suggested by Peterson & Ausubel (1984) for mackerel *Scomber scombrus* L., that blue whiting larvae preferentially hunt and consume prey that are active. A combination of feeding on free copepod eggs and egg-bearing copepod females may explain the absence of an ontogenetic pattern. Copepod eggs are frequently ingested by first feeding and by small fish larvae (Last, 1980), although increasing ingestion with increase in larval size has also been observed (Fortier & Harris, 1989; Fortier & Villeneuve, 1996). Fortier & Villeneuve (1996) suggested that this increase may have reflected the ingestion of egg-bearing female copepods. Conway (1980) observed that in blue whiting larvae <8 mm, *Calanus* eggs formed the largest proportion of the copepod eggs within the guts, and larger larvae ingested mainly *Pseudocalanus* eggs, which is an egg-bearing female copepod.

Larval mouth gape determines the maximum prey size that can be ingested and has been frequently used to analyse changes in size of prey in the diet in relation to larval length (Economou, 1991; Pepin & Penney, 1997). In this study, maximum prey size within the guts of small larvae seems to be related to mouth gape, although high dispersion of the data was observed. Pepin & Penney (1997) observed that the maximum increase in mean prey size for 11 species did not increase in the proportion to the fish capacity to ingest prey. Munk (1997) concluded that for prey sizes over the size of maximal preference, the rate of decrease in catchability, influenced by prey avoidance and escape, overrides the rate of increase in visibility. Even though for small larvae, maximum prey size has a similar relationship as mandible size to L_s, other ontogenetic related constraints such as relative mobility of larval blue whiting and their prey and size dependent catchability, may restrict the maximum prey size ingested.

For large larvae, maximum prey size ingested did not increase with larval size From the present study, the maximum prey width for larvae of 8, 10 and 13 mm, is 0·5, 0 7 and 0 9 mm, respectively Only adults and copepodites V of the genera *Calanus*, *Euchaeta*, *Centropages* and *Candacia,* which had low abundance in the

study area, have widths >0 5 mm. The fact that maximum prey size did not increase with larval size and that the rate of increase of mean prey size also declined, appeared to be a consequence of the low concentration of prey >350 μm in width in the plankton, and subsequently of a lower encounter rate for these prey sizes. As suggested by Munk (1997), the low abundance of large prey implies that SLH and prey selection calculations underestimate larval capability. However, at least in the present study, it does not seem to be a consequence of an underestimate of prey size of maximal preference. The reduction in SLH is at least partially a consequence of the larval feeding behaviour. Otherwise, the observed decrease in SLH would have led to a reduction in the rate of increase in gut carbon content for larger larvae in contrast to the present results The maintenance of the rate of ontogenetic increase in carbon gut content of large blue whiting larvae was achieved by reducing diet breadth in terms of prey size (SLH) and increasing selection towards the larger prey that are abundant In contrast, Pepin & Penney (1997) observed high abundance of all prey size classes in the plankton and that the constant rate of increase in gut content dry mass (Pepin & Penney, 2000) was maintained by increasing mean prey size or SLH. Pepin & Penney (1997) showed a negative relationship between the rate of change (slope) in mean prey size and the rate of change in SLH (niche breadth), as a function of the length of maxillae for 11 species; mean prey size increased for species for which SLH remained relatively constant, whereas species with low increase in mean prey size increased SLH. The present data on large blue whiting larvae did not follow the gradient between both extreme feeding patterns Larval size had a negative relationship with SLH [cf. Pepin & Penney (1997) where it was always positive] coincident with a low increase in mean prey size. Different plankton size structures seem to be related to the differences in feeding patterns but in both cases the rate of increase in gut content is maintained

A similar situation with a prey size structure reflecting low abundance large prey has been described by Sabates & Saiz (2000). They observed high variability in six myctophiform species between mean prey size and mouth size of the larvae; mouth size was a linear function of larval size. However, not all the species had the same range of mouth sizes and, subsequently, they were not consuming the same range of prey sizes. Considering all the myctophiform larvae together, over a certain mouth size (*c.* 1000 μm), mean prey size seemed to reach an asymptote, which was *c.* 250 μm prey width This prey size was low in abundance in the plankton Larger prey sizes decreased further in abundance. Species feeding on a range of larger prey sizes showed lower increase in mean prey size against larval size. Although some of the differences between species in the pattern of the prey and mouth size relationship may be a consequence of physiological and morphological differences between species (Sabates & Saiz, 2000), there seems to be a general limit to maximum prey size that can be related, as in the present study, to the prey size structure observed in the plankton. In contrast to the present study, SLH was constant with larval size and Sabates & Saiz (2000) argue, that for the species that displayed the lowest rate of increase in prey size as they grew, ingestion in terms of biomass was compensated by higher frequency of prey items in the gut, although they did not carry out an analysis on the total dry mass or carbon gut content. It seems that facing a similar prey size

structure availability, the larvae of myctophiforms increase the number of prey to compensate for the low availability of large prey.

Low coefficients of determination of regression analysis for SLH and larval size reported by Pepin & Penney (1997) and Sabates & Saiz (2000) suggest that the linear regression approach used by Pearre (1986), may not always be adequate. Pearre's (1986) data showed high variability in the slope of SLH against fish size. He assumed constant plankton biomass within equal logarithmic intervals of particle diameter (Sheldon *et al.*, 1972), based on global spatial and long temporal scale. Mean prey sizes in specific spawning grounds and seasons are likely to differ from this situation, particularly for species with well defined temporal spawning periods as is the case for blue whiting (Coombs, 1980). The feeding pattern presented here, based on just one specie, is not enough to reject Pearre's (1986) hypothesis of a linear relationship. Variability in plankton size structure and composition that is consumed by fish during the larval period, combined with specific feeding behaviour, may result in variable diet breadth patterns which are not always adequately represented by linear models. Flexibility in feeding patterns during the larval stages, as seems to be the case for blue whiting larvae, and might be the case for other species, may leed to less vulnerability to growth reduction and thus to recruitment variability (Houde, 1987).

We want to thank the crew of the RV Jose Rioja from the I E O. for their help during sampling procedures We also thank J. L. Acuña for his suggestions during data analysis D. Conway and J. L. Acuña made helpful critical comments on previous drafts of the manuscript and corrected the English. Comments and suggestions of the referees greatly improved the manuscript. Financial support for this project was provided by the Consejería de Agricultura y Pesca (Gobierno del Principado de Asturias; Spain) and the cooperation programme *El control de las condiciones químico-biológicas en la plataforma continental de Asturias* between the Instituto Español de Oceanografía and the Universidad de Oviedo. A fellowship to R G -Q was provided by the Consejería de Agricultura y Pesca (Gobierno del Principado de Asturias; Spain).

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