Wind-mixing effects on feeding success and condition of blue whiting larvae in the Porcupine Bank area

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ABSTRACT: Prey environment, feeding success and condition of blue whiting *Micromesistius poutassou* larvae were analysed in contrasting meteorological situations west of Ireland in the spring of 2 consecutive years (1994 and 1995). While larval abundance in both years of the study was approximately equal, there were marked differences in the physical and biological environment between the 2 years. 1994 was characterised by strong, unidirectional wind stress, which probably caused the low overall abundance of prey organisms recorded in this year. Abundance of copepod eggs and nauplii was considerably higher in 1995, when wind speeds were lower and wind direction was more variable. Copepod nauplii were also significantly larger than in 1994. Larval feeding success in both years was highly variable, but with considerably higher feeding intensities in 1995 than in 1994. For the determination of larval condition, 3 different condition indices were used, Fulton's *K* index (FCI) and body height to body length ratio for between-year comparison, and carbon and nitrogen content for estimation of immediate effects of wind stress on larval condition. In 1994, the FCI of blue whiting larvae was significantly lower than in 1995, and 11% of the larvae were significantly lighter at length than their conspecifics, suggesting that a part (11%) of the larval population at any one time fed less successfully at low prey density and high turbulence levels. No differences between the years were observed using the index of body height at the anus versus standard length. Analyses of relative C and N content of blue whiting larvae in relation to varying wind stress showed that while wind stress had a minor negative effect on C content, relative N content was significantly reduced with increasing wind speed, indicating that at periods of high wind-mixing more protein is catabolised in order to satisfy increasing energy demands, thus leaving less material to be assimilated for growth.

KEY WORDS: Blue whiting · Fish larvae · Condition · Wind-mixing · Carbon and nitrogen content

INTRODUCTION

Temporal or spatial match or mismatch of fish larvae with their potential prey organisms (e.g. Lasker 1975, Cushing 1990) is considered to be one of the major factors regulating year-class strength in marine fish populations. While adequate numerical abundance of

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potential prey organisms alone often has failed to support a corresponding high survival of fish larvae, adequate microscale turbulence has appeared to be necessary to generate a positive effect on the availability of food organisms to planktonic predators (Rothschild & Osborn 1988). Over the last decade, considerable work has been published supporting this theory to various degrees (e.g. Sundby & Fossum 1990, Kiørboe & Saiz 1995, Sundby 1995, Dower et al. 1997 and literature therein). Several studies have indicated that the relationship between turbulence, successful feeding, survival, and subsequent recruitment is in most cases non-linear (e.g. Cury & Roy 1989, MacKenzie et al. 1994, Leising & Franks 1999), suggesting that benefi-

cial effects of turbulence only occur at intermediate levels, while at higher levels the speed of the predator relative to its prey might be too fast for a successful capture (Fiksen et al. 1998, MacKenzie & Kiørboe 2000).

Strong wind-mixing can have a multitude of effects that might in turn influence survival of larval blue whiting. Wind-mixing is known to (e.g.) disrupt layers of high prey concentrations (Lasker 1975) and reduce the efficiency of energy transfer from phytoplankton production to higher trophic levels (Lewis et al. 1994).

The waters west of the British Isles comprise the major spawning area of blue whiting (Bailey 1982, Isaev & Seliverstov 1991) at a time (March & April) when the risk of strong wind-mixing is relatively high (DHI 1967). Low prey density at the time of high blue whiting larval abundance (Hillgruber et al. 1997, Hillgruber & Kloppmann 1999) might imply that, in order to survive, the larvae have to benefit from enhanced encounter rates associated with wind-induced turbulence. However, Hillgruber & Kloppmann (2000) found that feeding at moderate wind speeds, slightly higher than 10 m s^{-1}, was significantly reduced compared to almost calm situations. These results suggest that in years of high storm activities, particularly around the early larval phase, blue whiting survival might be poor due to turbulence-induced malnutrition.

1994 and 1995 were characterised by contrasting wind situations at the time of high abundance of larval blue whiting. Particularly during the early larval stage of blue whiting in March and April, relatively strong westerly to south-westerly winds prevailed in 1994, while wind stress was much lower and of high directional variability in 1995 (Bartsch & Coombs 1997). Even though both years were characterised by equally high blue whiting egg and larval abundances west of the British Isles (SEFOS 1997, Kloppmann et al. 2001, S. Coombs, Marine Biological Association of the

United Kingdom, pers. comm.), recruitment success differed significantly (Anonymous 1996). In 1994, blue whiting recruitment was slightly below the long-term mean, while recruitment in 1995 was (at that time) the highest on record (Anonymous 1996). Similar observations were made for larval walleye pollock *Theragra chalcogramma* in Shelikof Strait, Alaska, namely an association of strong wind-mixing events in the first-feeding larval period with lower recruitment and a linking of calm wind situations with strong survival periods (Bailey & Macklin 1994). Thus, it appears that the higher blue whiting recruitment success in 1995 might be the result of the lower wind-mixing in that year, either translating to higher prey concentrations and, thus, better feeding success, or improving the availability of prey organisms due to reduced wind-generated turbulence. Both mechanisms would result in better larval condition and, thus, could enhance survival through the first critical period of early life.

In this paper we investigate prey field, feeding success and condition of blue whiting larvae in relation to differing wind-mixing patterns during the period of first-feeding. Based on these comparisons we attempt to test the hypothesis that there is a causal relationship between wind stress and survival of blue whiting larvae via food availability.

MATERIALS AND METHODS

Shipboard sampling. During 2 cruises with RV 'Heincke' in March/April 1994 and April 1995 (Table 1) to the west of Ireland, blue whiting *Micromesistius poutassou* larvae were sampled with a towed HydroBios multiple-opening-closing-net (MCN) with a 50 × 50 cm opening and 150 (1994) to 200 μm (1995) mesh. The smaller mesh size in 1994 was chosen to efficiently catch the recently hatched and non-feeding larvae which predominantly occur at depths >100 m (Kloppmann et al. 2001). While in 1994 sampling was done on a large-scale station grid in waters above the Irish Shelf and Porcupine Bank to a maximum depth of 650 m, all samples in 1995 were taken from tows to a maximum depth of 100 m during a drift study carried out above the western slope of Porcupine Bank (Fig. 1). A bias in the feeding and condition-index results due to different sampling designs in both years is ruled out because all 1994 feeding and condition-index samples were from a rather restricted area where blue whiting larvae were very abundant (Fig 1: encircled area; and Kloppmann et al. 2001). The 1995 study was carried out almost in the centre of this area. Because this study exclusively deals with feeding of blue whiting larvae >3.0 mm occurring in the top 100 m (Kloppmann et al. 2001), no mesh size- and catch-depth-related dif-

Table 1. *Micromesistius poutassou.* Summary of survey information on cruises of RV 'Heincke' for 1994 (H56) and 1995 (H67)

	1994	1995
Dates of sampling	March 25–27, April 6, 8	April 5–7
Number of stations	13	17
Samples per stations	3	5
Depth profile (m)	100–50, 50–25, 25–0	100–80, 80–60, 60–40, 40–20, 20–0
No. of feeding samples	633	1640
Size range (mm)	2.5–8.3	2.0–7.0
Feeding larvae (%)	79.6	83.8

ferences in catch efficiency with respect to length is anticipated.

All plankton samples were preserved immediately after collection in buffered 4 % formaldehyde-seawater solution. Ichthyoplankton sampling was accompanied by routine measurements of physical data, such as temperature and salinity down the water column with a conductivity temperature depth probe (CTD). Water bottle samples were taken at 5 depths to determine abundance and composition of potential prey organisms. Wind speed was measured by an anemometer mounted on the mast of the ship and recorded every half hour. Detailed descriptions of all sampling procedures and the respective results are given in Hillgruber & Kloppmann (1999, 2000) and Kloppmann et al. (2001).

In addition to the MCN hauls in 1995, double oblique tows with a 60 cm Bongo net equipped with 200 µm-mesh nets were conducted at each station to obtain blue whiting larvae for carbon and nitrogen content analysis (see 'Condition analysis' below). Hauls were carried out down to 40 m depth in order to reduce sampling time and, thus, assure minimum damage to the larvae. Since most blue whiting larvae occurred within the top 40 m (Hillgruber & Kloppmann 2000), the representative nature of the sampling can be assumed. Immediately after recovery of the Bongo net, cod-end buckets were detached and transferred to a constant temperature (10°C) laboratory on board RV 'Heincke'. Cod-end buckets were emptied into a sorting dish placed on a bed of crushed ice to avoid instant deterioration of the larvae. Blue whiting larvae were sorted, measured to the nearest 1.0 mm standard length (SL) and triple-washed in distilled water. To meet the minimum dry wt requirements for analysis precision of the Heraeus CHN analysing system, a minimum of 5 to 15 larvae, depending on size, were pooled and deep-frozen at −35°C in pre-weighed tin capsules.

Laboratory analyses. In the laboratory, ichthyo- and microzooplankton samples as well as blue whiting larval gut contents were analysed according to standard analysing methods. Details are given in Hillgruber & Kloppmann (1999, 2000). Preserved blue whiting larvae were randomly selected from MCN samples of the 1994 and 1995 cruises to determine between-year differences in condition. For each individual larva the standard length and myotome body height above the anus (to the nearest 0.1 mm) was measured and the dry wt was determined after freeze-drying these larvae.

Condition analysis. Altogether, 3 different condition indices were determined for the comparative study: 2 morphometric indices and 1 biochemical index. Morphometric indices are generally derived by using a variable that is relatively sensitive to starvation and adjusting it with a starvation-insensitive variable like length to remove the effect of body size (Koslow et al.

1985, Suthers et al. 1992). The first morphometric index, Fulton's condition index (FCI), is defined as

$$\text{FCI} = \frac{\text{DW} \times 100}{\text{SL}^3}$$

where DW is dry wt and SL is standard length (Frank & McRuer 1989). FCI represents an isometric index that could potentially covary with length and, thus, prevent comparison of condition between different-sized larvae (Koslow et al. 1985). However, since we were comparing between-year differences in FCI of larvae of comparable size ranges, a potential co-variation of FCI with size will not alter the meaning of results.

The second morphometric index utilised was the relationship of body height above the anus over standard length. In a comparison of different morphometric indices, this index proved most sensitive to environmental conditions (Koslow et al. 1985). In addition to comparisons of between-year differences in mean condition indices, we also conducted multiple regression analysis (Chambers & Hastie 1992, MathSoft 1999) to examine the influence of standard length and year as well as the interaction of both on dry wt and body height.

Both morphometric indices were estimated with formaldehyde-preserved larvae. Formaldehyde is known to dissolve lipids from tissues and, therefore, dry wt measurements may have been influenced by this fact. However, the lipid content of young fish larvae is considered to be low, highly variable, and not necessarily linked to nutritional condition (Ferron & Leggett 1994). We therefore consider the resulting bias to be negligible.
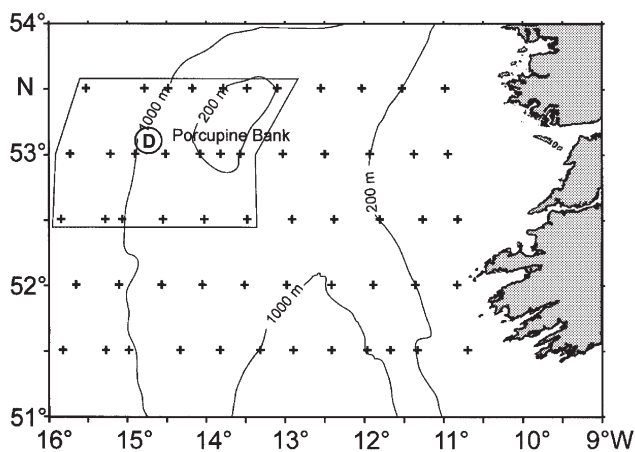

Fig. 1. Map of the study area indicating 1994 sampling stations and site of the drift study (D) in 1995. Encircled area represents the 1994 samples from which *Micromesistius poutassou* larvae were selected for stomach content and morphometric condition analysis

Table 2. Mean density of microzooplankton groups (l⁻¹) in the upper 100 m water column above Porcupine Bank in 1994 and 1995. Mean densities were calculated using square-root $(x + 0.5)$ transformed variates. ns: non-significant

Taxa	1994	1995	p
Copepod eggs	0.19	0.63	0.001
Copepod nauplii	5.99	19.09	0.001
Copepodites and adult copepods	3.03	3.14	ns

To test the immediate effect of wind stress on larval condition, a third index, the proportionate amount of C and N, was measured for blue whiting larvae caught during the continuous-patch study in 1995, providing also the C/N ratio as an index of condition. While the C/N ratio is often used as a condition index in fish larvae (Ehrlich 1974a,b, von Westernhagen et al. 1998 and literature therein), its value is questionable because of the complex and often correlated behaviour of carbon and nitrogen content in relation to individual physiology (Ferron & Leggett 1994). However, treated on their own, C and N content can give valuable insights into the *in situ* condition of fish larvae (Christensen & Korsgaard 1999, Coombs et al. 1999). Blue whiting larvae that were deep-frozen in pre-weighed tin capsules on board the RV 'Heincke' were freeze-dried in the laboratory and their dry wt determined;

they were then processed in a Heraeus CHN analyser. Acetanilide was used as the calibration agent. The effects of wind stress, time of day and individual mean dry wt plus their interaction on carbon and nitrogen content in blue whiting larvae was examined using multiple regression with routines of S-Plus software (Chambers & Hastie 1992, MathSoft 1999). Wind values were averaged over 6 h prior to sampling. Since none of the interaction terms showed any significant influence on both C and N content, these terms were dropped from the final linear models.

RESULTS

Physical environment

Temperature and salinity of the water column were quite similar in both 1994 and 1995 (White et al. 1998, Kloppmann et al. 2001). Temperatures in the top 100 m ranged between 10.2 and 10.3°C, with salinity values slightly >35.4. The water column was homogeneously mixed and no seasonal stratification was discernible.

In contrast, the wind situation differed conspicuously between both years. In 1994, relatively strong and uni-directional winds, mainly from the west to south-west, prevailed (Bartsch & Coombs 1997). Frequent storms resulted in deep mixing of the water column and a

Table 3. *Micromesistius poutassou.* % (by number) prey items ingested by larvae in 1994 and 1995

Prey items	<3.0 mm	3.0–3.9 mm	4.0–4.9 mm	5.0–5.9 mm	≥6.0 mm	Total
1994						
Tintinnids	44.0	16.5	2.1	0.0	0.0	15.6
Eggs	5.8	11.4	16.8	13.5	5.3	11.4
Cyclopoid nauplii	31.3	39.1	24.1	6.5	6.0	29.7
Harpacticoid nauplii	0.0	0.2	0.0	0.0	0.0	0.1
Calanoid nauplii	10.6	21.9	41.9	53.6	37.1	27.9
Other nauplii	4.1	3.7	3.2	1.5	13.7	4.1
Copepodites	1.3	4.0	10.2	15.4	31.7	7.5
Adults	0.1	0.2	1.0	6.9	1.5	1.0
Others	2.8	3.2	0.7	2.5	4.7	2.6
Number of larvae	85	237	107	44	31	504
1995						
Tintinnids	37.9	10.3	5.5	2.8	0.0	11.3
Eggs	18.3	30.6	30.8	34.5	33.8	29.5
Cyclopoid nauplii	14.4	32.2	40.0	34.2	17.6	32.7
Harpacticoid nauplii	1.0	0.4	0.3	0.2	0.0	0.4
Calanoid nauplii	7.8	7.5	6.3	5.7	4.0	6.9
Other nauplii	2.1	5.3	5.9	5.4	12.8	5.2
Copepodites	0.0	0.7	3.1	8.8	13.9	2.4
Adults	0.0	0.0	1.9	4.7	13.7	1.3
Others	18.4	13.1	6.2	3.8	4.2	10.3
Number of larvae	182	539	498	141	15	1375

breakdown of the anti-cyclonic circulation system above Porcupine Bank (Mohn 2000, Kloppmann et al. 2001). In 1995, moderate winds, which were very variable in direction, prevailed (Bartsch & Coombs 1997).

During the 1994 cruise, average wind speed was 14.9 ms^{-1} with maximum values up to 27.9 ms^{-1} (SD = 4.8, median = 14.8, range: 2.1 to 27.9, n = 759). In contrast, wind speeds during the 1995 cruise were much lower, with an average speed of 8.6 ms^{-1} and maximum values only up to 15.1 ms^{-1} (SD = 3.5, median = 9.0, range: 0.5 to 15.1, n = 151).

Prey environment

In March-April 1994, the densities of potential prey organisms for blue whiting larvae were substantially lower than at the same time in 1995. Specifically, copepod eggs and copepod nauplii in the upper 100 m of the water column were significantly more abundant in 1995 (Table 2). The highest differences in abundance of microzooplankton taxa were observed for copepod nauplii, the primary prey item of blue whiting larvae (Conway 1980, Hillgruber et al. 1997, Hillgruber & Kloppmann 1999).

The vertical distribution of copepod nauplii differed significantly in the 2 years of the study, with nauplii being randomly distributed in the upper 100 m in 1994. In comparison, depth had a significant effect on naupliar distribution in 1995, with peak densities at 30 m depth. Densities of copepod nauplii above and below 30 m were significantly lower (ANOVA, F = 19.352, p < 0.001).

Sizes of copepod nauplii ranged from 50 to 500 μm total length (TL) in 1994 and from 60 to 680 μm in 1995, and size-frequency distributions revealed significant differences between the 2 years (Kolmogorov-Smirnov [KS] test: p < 0.001), with significantly different means (T = 7.772, p < 0.001). Copepod nauplii in the water column were larger in 1995, with a mean TL of 167.40 μm in comparison to a mean TL of 146.87 μm in 1994. Differences in naupliar TL was mainly due to a lower proportion of smaller cyclopoid nauplii in 1994. Among the copepod nauplii, 1995 was characterised by proportionately more calanoid nauplii, such as *Calanus* sp., *Microcalanus* sp. and Metrididae.

Feeding success

A total of 633 (range: 2.5 to 8.3 mm SL) and 1640 (range: 2.0 to 7.0 mm SL) blue whiting larvae in 1994 and 1995, respectively, were analysed for their feeding
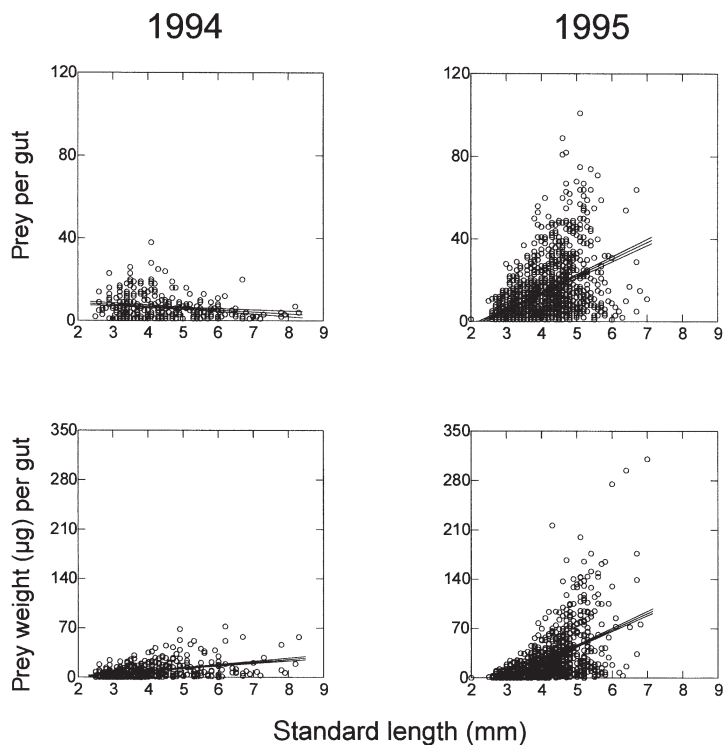

Fig. 2. *Micromesistius poutassou.* Numerical feeding intensities of larvae in 1994 and 1995

patterns (Table 1). Averaged over all sizes and sampling times, the proportion of feeding larvae did not differ significantly between 1994 and 1995, namely 79.6 and 83.8%, respectively.

In both years, the feeding incidence was lowest for first-feeding individuals, but increased thereafter. Numerical feeding intensity (i.e. the number of prey items per larval gut), however, differed for larvae in 1994 and in 1995 (Fig. 2). In 1994, highest numbers of prey items were observed in first-feeding larvae, with numerical feeding intensity decreasing thereafter ($y = -0.8883x +$ 10.508, r^2 = 0.0304, p < 0.001). In comparison, numerical feeding intensity steadily increased with increasing larval length in 1995 ($y = 8.2115x - 18.984$, r^2 = 0.0937, p < 0.001). In 1994, in spite of the contrasting pattern in numerical feeding intensities, weight-based intensities increased with increasing larval size ($y = 3.3248x -$ 2.53, r^2 = 0.0937, p < 0.001). While the same was true for weight-based feeding intensities in 1995, however, the increase with larval size was distinctly steeper ($y = 23.04x - 69.883$, r^2 = 0.3576, p < 0.001).

An analysis of the composition of the larval diet revealed distinct differences between the 2 years of our study. In 1994, first-feeding larvae <4.0 mm relied most heavily on tintinnids and cyclopoid nauplii, while in 1995 there was a high proportion of copepod eggs in their diet (Tables 3 & 4). This was apparent in both the

Table 4. *Micromesistius poutassou*. % (by weight) prey items ingested by larvae in 1994 and 1995

Prey items	<3.0 mm	3.0–3.9 mm	4.0–4.9 mm	5.0–5.9 mm	≥6.0 mm	Total
1994						
Tintinnids	21.8	6.2	0.2	0.0	0.0	6.6
Eggs	10.6	16.5	16.8	11.9	2.8	14.3
Cyclopoid nauplii	46.1	38.9	18.2	3.4	2.8	30.3
Harpacticoid nauplii	0.0	0.1	0.0	0.0	0.0	0.0
Calanoid nauplii	12.5	25.0	41.0	51.2	28.5	28.8
Other nauplii	4.4	4.4	2.7	1.1	12.5	4.3
Copepodites	3.4	5.8	17.9	21.1	41.6	11.6
Adults	0.4	0.8	2.9	10.3	5.0	2.3
Others	0.8	2.4	0.2	1.0	6.8	1.8
Number of larvae	84	237	107	44	32	504
1995						
Tintinnids	32.4	6.1	1.2	0.6	0.0	7.1
Eggs	32.4	46.1	43.4	35.1	18.7	41.9
Cyclopoid nauplii	16.8	31.9	32.3	22.5	6.3	28.8
Harpacticoid nauplii	1.3	0.3	0.1	0.0	0.0	0.3
Calanoid nauplii	6.7	5.8	2.9	2.9	1.7	4.5
Other nauplii	1.8	4.4	3.9	3.3	18.6	3.9
Copepodites	0.0	1.2	7.3	17.3	18.3	5.1
Adults	0.0	0.2	8.5	16.0	30.1	5.1
Others	8.6	4.0	0.6	2.3	6.2	3.2
Number of larvae	182	538	498	141	15	1374

numerical and the weight-based proportion of prey items. Later-stage larvae in 1994 shifted feeding towards the larger calanoid nauplii and copepodite stages. In comparison, in 1995, larvae of all size classes analysed continued to prey on cyclopoid nauplii and copepod eggs. While they did include copepodite stages and adult copepods in their diet, proportions rarely reached the values observed in 1994.

Fig. 3. *Micromesistius poutassou*. Length frequency distribution of larvae selected for morphometric condition analysis

Comparison of 1994 and 1995 morphometric condition factors

A total of 168 formaldehyde-preserved blue whiting larvae (1994: 82 larvae, 1995: 86 larvae) were randomly selected, measured, freeze-dried and weighed. Even though larvae from the 1994 samples covered a wider length range (2.7 to 7.9 mm) than those from the 1995 samples (3.0 to 7.1 mm), the difference in mean lengths (1994: mean = 4.694, SD = 1.378; 1995: mean = 4.437, SD = 0.844) was not significant (Student's *t*-test: $t = 1.4664$, df = 166, p = 0.144). Length-frequency distribution of both larval samples revealed conspicuous differences (Fig. 3). While the 1994 histogram showed a distinct mode in the 3.0 to 3.5 mm length class and an almost equal distribution over the remaining length range, the 1995 histogram revealed a mode in the 4.0 to 4.5 mm length class, with the majority of the larvae being <5.0 mm in size. Thus, while more larvae of intermediate length were analysed from the 1995 samples, proportionately more small and large larvae were weighed and measured from the 1994 samples.
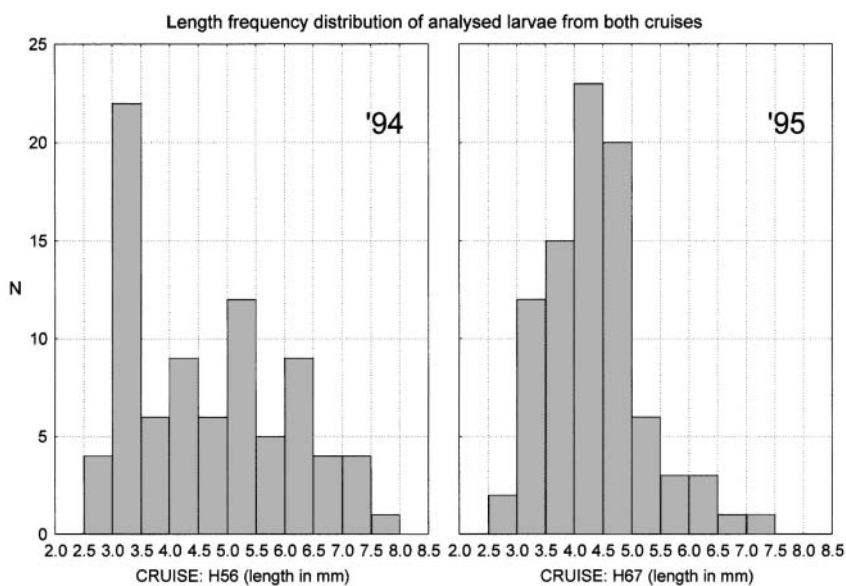
Table 5. *Micromesistius poutassou.* Morphological condition indices for cruises H56 and H67 larvae. FCI: Fultons's condition index; Body h/L ratio: body height/length ratio

Index	H56	H67
FCI		
Mean	0.0964	0.1151
SD	0.0290	0.0232
Median	0.0928	0.1100
Range	0.0288–0.1712	0.0746–0.1855
Body h/L ratio		
Mean	0.0852	0.0893
SD	0.0155	0.0097
Median	0.0839	0.0899
Range	0.0566–0.1216	0.0588–0.1129
Number of larvae	82	86

Larval dry wt and Fulton's condition index

The dry wt of the 1994 formaldehyde-preserved blue whiting larvae ranged between 13 and 439 µg (mean = 116.2 µg, SD = 102.5 µg), while in 1995 formaldehyde-preserved larvae weighed between 30 and 498 µg (mean = 110.9, SD = 73.6 µg). For both cruises, dry wt significantly increased with increasing length, and the resulting regression equations were:

1994: $DW = 0.0018 \times SL^{2.5484}$, $r^2 = 0.8484$, $p \ll 0.001$
1995: $DW = 0.0013 \times SL^{2.9041}$, $r^2 = 0.8914$, $p \ll 0.001$

where DW = dry wt in mg and SL = standard length in mm (Fig. 4). There was a conspicuous difference between both regression coefficients, and Fulton's condition index was significantly higher for 1995 blue whiting larvae than for the 1994 individuals (Table 5; δ = 0.0187; Student's *t*-test: $t = -4.620$, df = 166, $p \ll 0.0001$). However, while for 1995 larvae there was no significant relationship between length and FCI ($r^2 = 0.0062$, $p = 0.4700$), in 1994 larvae FCI decreased significantly with increasing length, indicating that, in contrast to 1995, the larvae were not growing isometrically. The regression equation for 1994 was:

$$FCI = 0.1371 - 0.0087 \times SL, r^2 = 0.1697, p < 0.001$$

where FCI = Fulton's condition index in 1994 and SL = standard length in mm.

The distribution of the variates around the 1994 length to dry wt regression curve suggests that the lower regression coefficient in 1994 was caused by an 11% proportion of poorly conditioned larvae (i.e. 9 individuals with comparatively low dry wt; Fig. 4a: data enclosed by dashed line). These larvae were from different stations, so that a spatial effect could be ruled out. Indeed, without these values the regression coefficient of the 1994 values increased to β = 2.6891 (Fig. 4a: dashed curve).

To analyse the effect of standard length, year and the interaction of both on dry wt, we conducted multiple regression analyses with all data, a data set without the above-mentioned 'poor' variates, and a data set consisting of the 'poor' variates only (for the 1994 data). The resulting models revealed that in all 3 tests, standard length had the strongest effect on dry wt, explaining 84.1, 91.3 and 65.4%, respectively, of the total variability in dry wt. Within the first 2 set-ups, i.e. full data set and the data set without 'poor' variates, year and interaction of year with standard length had no significant influence on dry wt. However, sampling year had a significant effect ($p = 0.0143$) on dry wt for the 1994 data set consisting of 'poor' variates only, for which it explained 24.3% of total dry wt variability, suggesting that 11% of the 1994 blue whiting larvae were significantly lighter than their conspecifics.
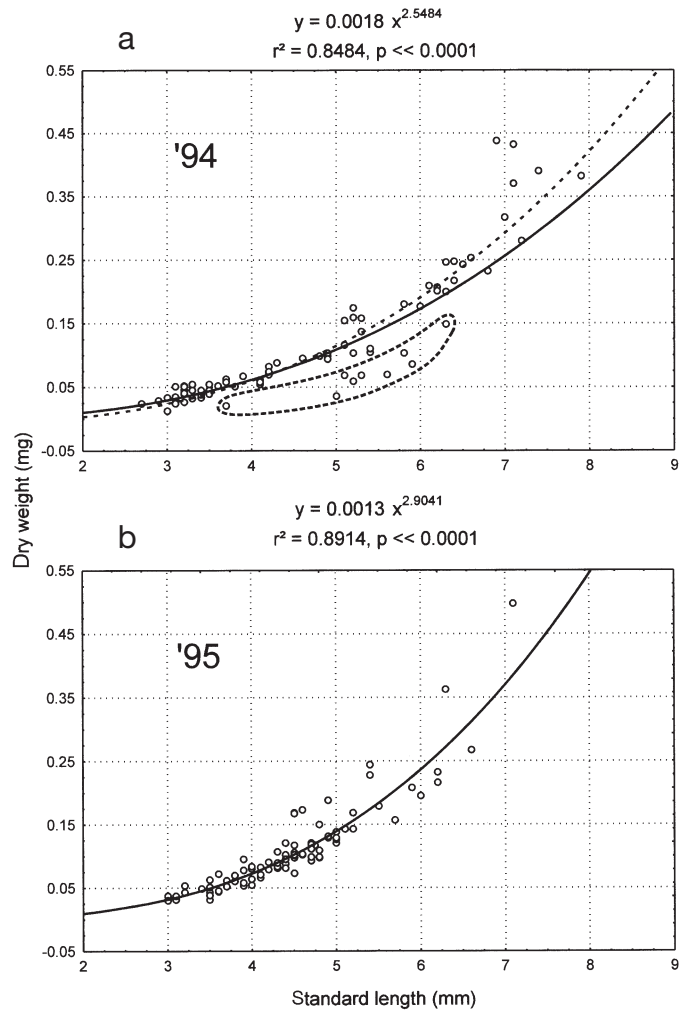

Fig. 4. *Micromesistius poutassou.* Standard length to dry wt relation in larvae in 1994 (upper graph) and in 1995 (lower graph). Continuous line: regression curve for length/dry wt relationship; dashed line in upper graph: regression curve estimated without encircled data
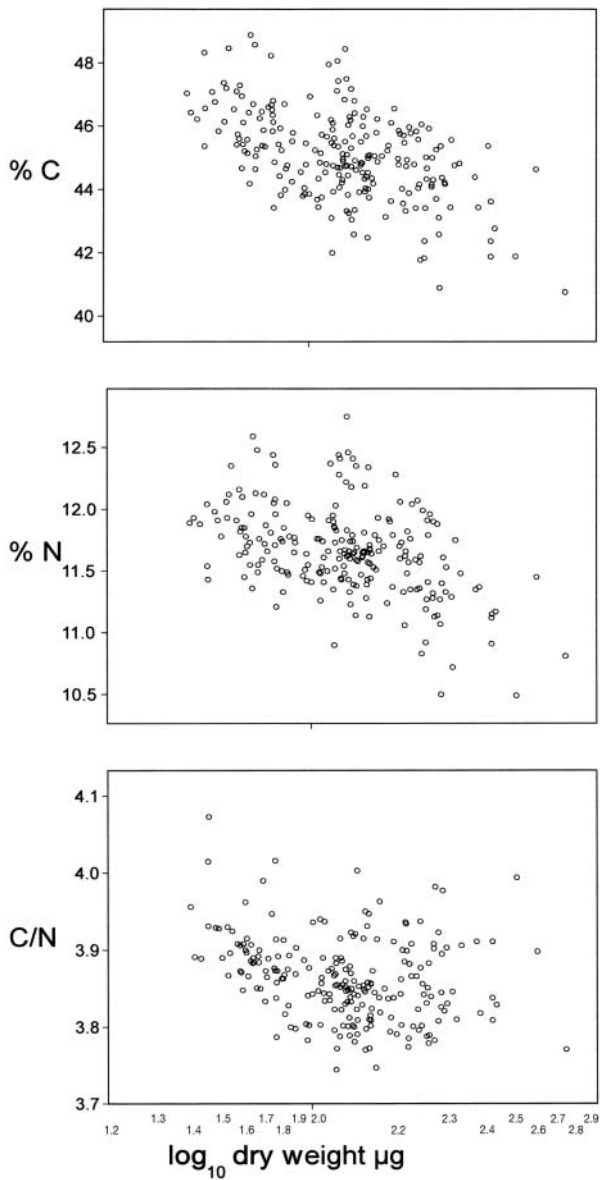
Fig. 5. *Micromesistius poutassou*. Scatterplots for relationship of $\log_{10}$ dry wt to C, N, and CN ratio

Thus, FCI and the length to dry wt relationship revealed that in 1994 blue whiting larvae had a significantly poorer condition than those in 1995.

Body height-standard length relationship

Body height above the anus increased significantly and linearly with increasing length on both cruises. The resulting regression equations are:

1994: AH = 0.133 + 0.116 × SL, r^2 = 0.8526, p ≪ 0.0001
1995: AH = 0.107 + 0.114 × SL, r^2 = 0.7931, p ≪ 0.0001

where AH = body height above anus in mm, SL = standard length in mm. These equations indicate an almost identical body height to length relationship for both years. Indeed, correlation coefficients for both years did not differ significantly (t = −0.2207, p = 0.8256). However, there was a significantly higher body height to length ratio for 1995 larvae (t = −2.04398, p = 0.0425, Table 5). On the other hand, in both years the body height to length ratio was positively and significantly correlated to length (r^2 = 0.2743, p ≪ 0.0001 for 1994, and r^2 = 0.1762, p ≪ 0.0001 for 1995) so that a bias due to the higher number of smaller larvae in 1994 must be taken into account.
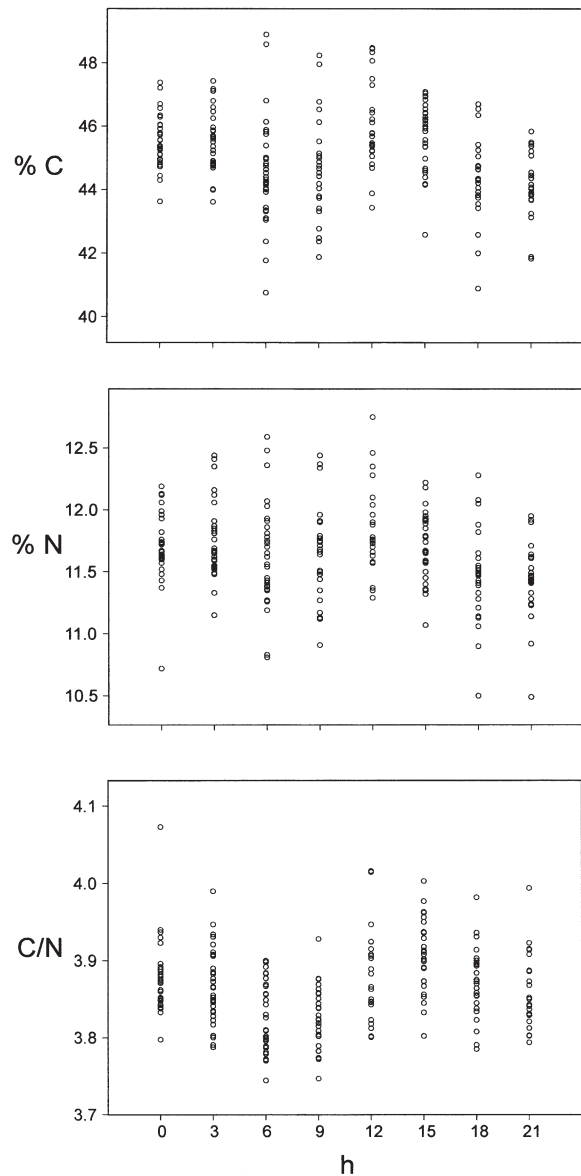

Fig. 6. *Micromesistius poutassou*. Scatterplots for relationship of time of day to C, N, and C/N ratio

Table 6. *Micromesistius poutassou*. Statistics of C and N contents (%) and C/N ratio in larvae of the different length classes

Parameter	3 mm	4 mm	5 mm	6 mm	7 mm
C content					
Mean	45.59	45.13	44.79	43.71	43.59
SD	1.47	1.13	1.47	1.17	2.47
Median	45.52	44.98	44.79	43.62	44.64
Range	42.00–48.90	42.48–47.96	40.89–48.45	41.88–45.56	40.76–45.36
N content					
Mean	11.75	11.72	11.57	11.21	11.22
SD	0.33	0.30	0.39	0.34	0.36
Median	11.73	11.67	11.60	11.28	11.40
Range	10.90–12.59	11.13–12.46	10.50–12.75	10.49–11.75	10.81–11.45
C/N ratio					
Mean	3.88	3.85	3.87	3.86	3.88
SD	0.05	0.05	0.06	0.06	0.10
Median	3.87	3.85	3.87	3.84	3.90
Range	3.78–4.07	3.74–3.99	3.77–4.00	3.80–3.99	3.77–3.98
Number of samples	63	89	50	15	3

C and N analysis of 1995 blue whiting larvae

Mean relative carbon (C) content in blue whiting larvae was 45.07 % (SD = 1.42, median = 45.05, range: 40.76 to 48.90, N = 220) while nitrogen (N) content varied between 10.49 and 12.75 % (mean = 11.66, SD = 0.05, median = 11.65, N = 220). The resulting mean C/N ratio was 3.86 (SD = 0.36, median = 3.86, range = 3.74 to 4.07, N = 220). While the C/N ratio remained almost constant with increasing length (Spearman rank-order correlation: $t = 0.1786$, $p = 0.8696$; Table 6), the mean C and N contents appeared to decrease significantly (Spearman rank-order correlation: C: $t = \infty$, $p = 0$; N: $t = -3.5762$, $p < 0.05$; Table 6).

Both C and N content decreased with increasing mean dry wt of the larvae (Fig. 5), while their ratio was not conspicuously affected by dry wt. However, there was a decrease discernible for larvae up to 100 μg dry wt. Daytime had an effect on both C and N. At sunrise, after 03:00 h, carbon content decreased and tended to rise again towards noon. There was a distinct decline in carbon content after 15:00 h (Fig. 6). Nitrogen content remained almost constant between 00:00 and 15:00 h, after which it also dropped conspicuously. The C/N ratio (Fig. 6) showed a similar distribution pattern during the day to C content. Wind stress appeared to have an effect on both C and N content, in that both decreased with increasing 6-hourly mean wind speed. The C/N ratio appeared to increase slightly up to a wind speed of 6 to 8 m s^{-1}, after which it remained almost constant (Fig. 7).

To analyse the combined influence of wind, dry wt and time of day on C and N contents of larval blue whiting, we conducted multiple regression analyses. C and N data were tested for the underlying distribution.

Both distributions did not differ significantly from a normal distribution (C: K-S test: d = 0.025, not significant [ns]; chi-square: 6.62, df = 9, p = 0.677; N: K-S test: d = 0.051, ns; chi-square: 18.84, df = 12, p = 0.093). Six-hourly wind values and weight data were used as linear continuous variables, whereas time of day was used as a factor. Weight data were $\log_{10}$-transformed prior to analysis. To test the significance of the influence of the covariates, sequential analysis of variance (ANOVA) was carried out.

The resulting regression model for C was:

$$C = 52.421 - 0.201 \times wind - 2.645 \times \log_{10}(weight) + T$$
$$r^2 = 0.5769, \ p \ll 0.0001$$

where C = carbon content in %, wind = 6-hourly wind speed in m s^{-1}, weight = mean dry wt in μg and T = the categorical factor for each sampling time (see Table 5). Partial residual analysis revealed that the model sufficiently represented the behaviour of C in relation to wind, body weight and daytime (Fig. 7) and explained 57.7 % of its variability. All 3 covariates contributed significantly to total C content variability. Sequential

Table 7. *Micromesistius poutassou*. Categorical factors in C and N linear models for each sampling time

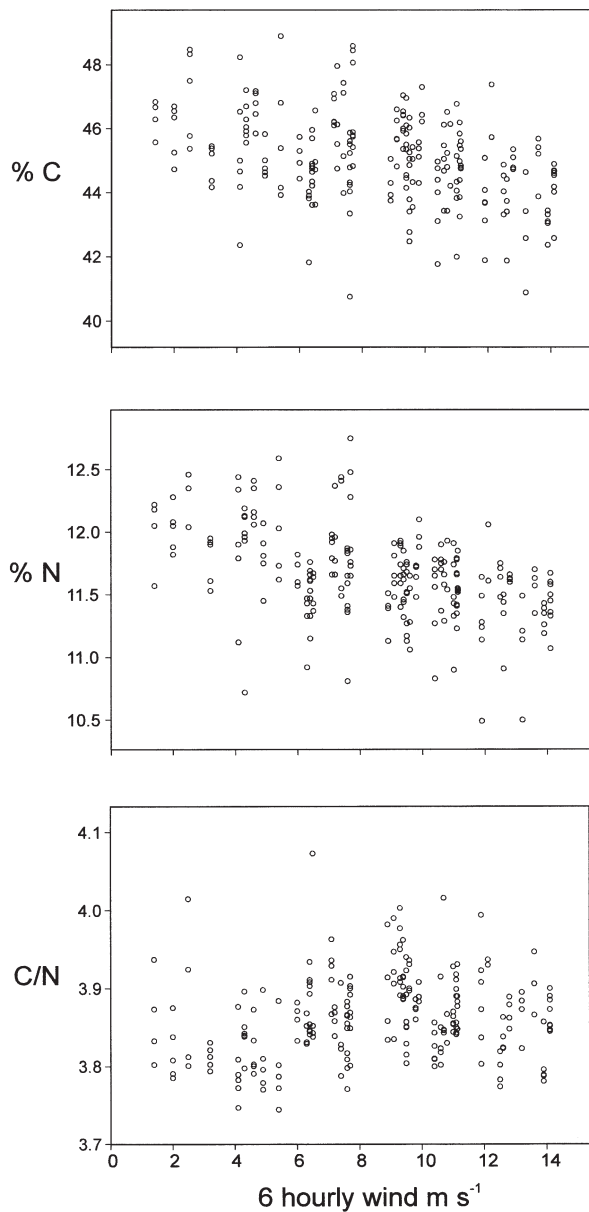| Sampling hour	C	N
00:00	0.1365	−0.0046
03:00	0.3091	0.0818
06:00	−0.2394	0.0462
09:00	−0.0546	0.0769
12:00	0.7112	0.1360
15:00	0.5961	0.0491
18:00	−0.7210	−0.2023
21:00	−0.7379	−0.1835

Fig. 7. *Micromesistius poutassou*. Scatterplots for relationship of wind stress to C, N, and C/N ratio

ANOVA revealed that body weight had the most important influence on C content, explaining 26.8% of its variability ($F = 132.91$, $p \ll 0.0001$), while wind only accounted for 18.1% variability ($F = 90.01$, $p \ll 0.0001$). Daytime had the least influence, explaining only 12.8% variability ($F = 9.06$, $p \ll 0.0001$).

The regression model for N was:

$$N = 13.260 - 0.061 \times weight - 0.496 \times \log_{10}(weight) + T$$
$$r^2 = 0.5570, \; p \ll 0.0001$$

where N = nitrogen content in % and all other variables are as explained above. As for C, the residual

analysis showed that the model represented the behaviour of N in relation to wind, body weight and daytime well (Fig. 8) and explained 55.7% of its variability. However, for the wind parameter, partial residual analysis showed that at wind speeds between 6 and 8 m s^{-1} residuals were not evenly distributed around the regression line but were predominantly below it, indicating that the model overestimates the N contents at these particular wind speeds. Partially, this finding is explained by the fact that most observations of wind speeds between 6 and 8 m s^{-1} were done at 18:00 and 21:00 h, the time of day when a conspicuous reduction in N content was found. Again, all 3 parameters contributed significantly to total N content variability. In contrast to C, wind speed had the most important influence on N content and accounted for 30.0% of its variability ($F = 141.62$, $p \ll 0.0001$) while only 14.1% was explained entirely through body weight ($F = 53.68$, $p \ll 0.0001$). Time of day had the least influence, and accounted for only 11.6% of total variability ($F = 7.82$, $p \ll 0.0001$).

DISCUSSION

In order to judge the impact of wind stress on blue whiting larval condition we carried out 3 different types of condition measurements, 2 of which were morphometric indices (Fulton's K index and body height to standard length ratio) which have latency times of several days (Ferron & Leggett 1994 and literature therein) and were therefore chosen for between-year comparison of contrasting wind stress. The other was carbon and nitrogen content analysis, which is known for its short reaction time (<12 h: von Westernhagen et al. 1998) and was therefore chosen for the continuous-drift study. For interpretation of condition results, data on differential feeding success due to wind stress were utilised.

Morphological condition indices

Though there was a significant difference in feeding success between years (see above), the morphometric condition measurements revealed somewhat contradictory differences in the nutritional state of the larvae. Fulton's condition index was significantly lower for blue whiting larvae in 1994 than in 1995 because isometric growth of the 1994 larvae was restricted. The dry wt measurements indicated that approximately 11% of the larvae showed serious signs of malnutrition. Within the same year, these larvae were significantly lighter than their conspecifics at similar lengths. However, these results were not corroborated by the
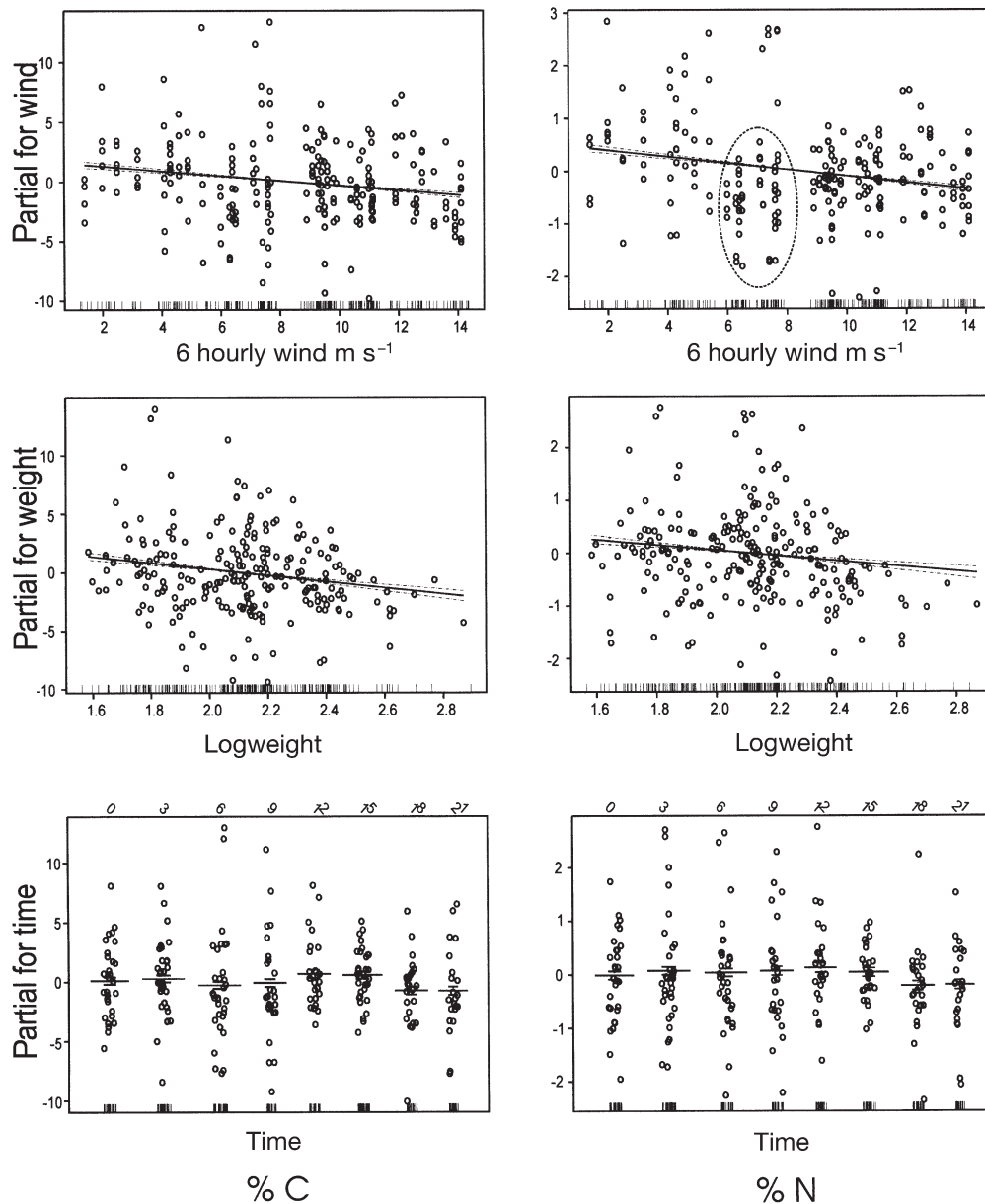
Fig. 8. *Micromesistius poutassou.* Partial residuals for C and N relationships to wind stress, weight and time of day. Whiskers on abscissa represent data density for a given interval of predictor values

standard length/body height ratio, which only showed slight and probably biased differences between both years. These somewhat contradictory results may have been caused by different latency times for both condition factors examined. During starvation, fish larvae are able to utilise energy by metabolising protein from muscle tissue (Love 1970), which is replaced by an increase in intercellular space and cellular water content, resulting in a reduced body dry wt but presumably not body height. Only after prolonged starvation, due to a breakdown of the osmoregulatory system, do fish larvae lose water to the environment (Sclafani et

al. 1997) and become thinner. As a consequence, larvae become less buoyant and sink. Larvae examined for condition in the present study were all captured in the top 50 (1994) to 60 m (1995) of the water column. Larvae in poor condition with respect to body height might have sunk below the investigated depth strata, thus reducing the probability of capturing them within the top 50 to 60 m. This fact may explain the apparent contradictory results between morphometric condition factors, suggesting that in 1994 the proportion of malnourished larvae may have been even larger than the observed 11 %.

Carbon and nitrogen contents

Multiple regression analysis indicated that relative C content, a measure that has previously been postulated as an indicator for larval condition (Coombs et al. 1999), was primarily and negatively influenced by body weight. This appears contradictory to most other studies on C content in fish larvae in which it was observed to increase with growth (Ehrlich 1974a, Harris et al. 1986, Ikeda 1996, Coombs et al. 1999). However, Ehrlich (1974b) found that a constant increase in relative C content with growth is not the rule. Also, absolute C and N contents for growing *Blennius pavo* larvae indicated a possible decrease in relative C and N content with age (Freitas 1993). Indeed, fishes do show quite different behaviour in energy deposition with respect to lipid content (Anthony et al. 2000). Thus, a decrease in relative C content of fish larvae with age may not be a sign of deteriorating condition, but reflects a species-specific behaviour of energy storage.

Approximately 18% of the total C content variability was explained by wind stress, indicating that turbulence has a slight but significant negative effect on C deposition. This might be the result of reduced feeding intensity with increasing wind speed (Hillgruber & Kloppmann 2000) and, thus, an increased utilisation of reserve carbohydrates. The fact that the time of day to C content relationship significantly reflected the daily feeding rhythm of blue whiting larvae, as described by Hillgruber & Kloppmann (2000), suggests that gut contents might influence relative C content (Lochmann et al. 1996). However, C content in early developmental stages of copepods (the primary prey of blue whiting larvae: Hillgruber & Kloppmann 1999, 2000) at that particular time of year is lower (<40%, Bottrell & Robins 1984) than that of blue whiting larvae (about 45%); thus, C content would be more likely to decrease with increasing feeding intensity.

In contrast to larval C content, relative N content was predominantly and significantly influenced by wind speed. This was not due to the reduction in feeding intensity with increasing wind stress (Hillgruber & Kloppmann 2000), since time of day contributed less to the variability of N content than to C content and appeared to be more constant during the day, with the only significant reduction occurring in the late evening hours. Furthermore, with a relative N content of 8 to 9% in early developmental stages of copepods (Bottrell & Robins 1984) the N content of blue whiting larvae (about 11% N) is more likely to increase with reduced feeding success if gut contents have a significant influence.

Proteins are considered to be the primary energy resource for fish larvae (Ehrlich 1974a,b, Klumpp & Westernhagen 1986, Torres et al. 1996), supplying the majority of material for the assimilation of new body tissue during growth. Since N is predominantly found in proteins, the relative N content of fish larvae may give insight into the rate of ingested protein retained for growth (Linton et al. 1998). N retention is depressed during critical periods of increased physiological stress, e.g. during transition from endogenous to exogenous feeding or during metamorphosis, when more protein is utilised for energy expenditure (Yúfera et al. 1993, Christensen & Korsgaard 1999, Yúfera et al. 2000). Similarly, wind stress might also increase energy demands on a fish larva since more resources are needed for behaviour such as maintaining a preferred depth (Hillgruber & Kloppmann 2000) or successfully capturing prey organisms (MacKenzie & Kiørboe 2000). As a consequence, more protein will be catabolised, leaving less for assimilation into new body tissue. This might explain the decline in N content with increasing wind stress.

Thus, while C content in blue whiting larvae may be primarily explained by changing energy storage mechanisms characteristic for a developing larva and be only partially due to differential feeding success, N content clearly reflects changes in nutritional condition imposed by external stress such as intensive wind-mixing. It appears that gross growth efficiency in blue whiting larvae is maximised during calm wind situations.

Feeding and wind stress

Increased wind stress can significantly reduce feeding success in larval blue whiting despite the persistence of sufficiently large prey patches (Hillgruber & Kloppmann 2000). However, fish larvae are probably able to survive short periods of high wind stress, if these do not affect the prey environment, and to recover from such reductions in condition and growth (e.g. Dabrowski et al. 1986). Problems may only arise if high wind stress persists over a longer time period and prey abundance and production are continuously affected. Especially at the time of year of our study, strong and unidirectional wind stress may have affected the timing of the spring bloom and may also have resulted in expatriation of the copepod spawning stock (Lewis et al. 1994), both having led to reduced naupliar production and, hence, the observed reduced abundance of food in 1994. Furthermore, strong wind-mixing in 1994 would have destroyed or prevented any concentration of prey items, as has been previously shown for other areas (Lagadeuc et al. 1997, Conway et al. 1998). In 1995 the comparatively low and directionally variable wind stress resulted in higher nau-

pliar production and the formation of layers of high prey densities at 30 m depth.

The considerable difference in feeding intensity, both in numbers of prey items and in weight of gut contents (Fig. 2), clearly shows that blue whiting larvae benefited from higher prey densities in April 1995. While the analysis of larval dry wt revealed that in both years of our study a high proportion of blue whiting larvae were probably not starving, the FCI analysis indicated that certain larvae did not grow isometrically, suggesting that a proportion of the larval population was affected by the low prey density in 1994. This has already been shown for larval walleye pollock *Theragra chalcogramma* for contrasting years of wind stress and prey abundance (Bailey et al. 1995). Mortality of pollock larvae almost doubled in the year of higher wind stress and lower food abundance. Bailey et al. concluded that the prey levels in the year of high wind-mixing were too low for the larvae to benefit from the increased turbulence. However, in laboratory observations, cod *Gadus morhua* larvae were observed to cope with low prey densities (<10 nauplii l^{-1}) particularly well by adjusting their prey-search and prey-selection behaviour (Munk 1995). Similar results were obtained in a study on the walleye pollock, whereby prey concentrations of as low as 8 nauplii l^{-1} still provided a sufficiently dense prey environment for initiation of feeding (Paul 1983). Even at densities of 2 nauplii l^{-1}, 2% of the larvae were feeding, suggesting that within any larval population individual variation in prey-capture success is considerable and highly dependent on prey concentration. Switching to larger food items such as calanoid nauplii and copepodites (Tables 3 & 4) might, at some stage, have helped blue whiting larvae to compensate for the lower naupliar prey abundance in 1994. Larval blue whiting, like other gadoid larvae, might therefore be considered as 'prey-insensitive' larvae (Houde 1987) which have adapted to food-limiting situations, since they normally hatch prior to the seasonal copepod peak into a comparatively poor prey environment (Hillgruber & Kloppmann 1997, Hillgruber et al. 1999).

However, while starvation might not be the sole source of larval mortality, small declines in growth rates due to lower than optimum food levels might prolong the larval stage duration over which high mortality rates can operate (Houde 1987). While no information on larval growth rates are available for 1994, there is an indication of such a process operating in 1994, when a proportion (11%) of blue whiting larvae exhibited significantly lower growth in weight between 4.0 and 6.0 mm than larvae in 1995. Furthermore, it was evident that isometric growth was already restricted in at least some of the 1994 larvae, i.e. the larvae were already losing weight relative to their size. However,

growth can be inhibited long before weight-at-length is affected (see e.g. Bailey & Heath 2001); therefore, these larvae might have already shown reduced growth rates for quite some time. Thus, the low feeding intensities, particularly of larvae >3.5 mm, suggest that in 1994 a considerable proportion of blue whiting larvae was growth-limited. Because C and N analysis clearly demonstrated a decreased N assimilation efficiency at high wind stress, we conclude that it was more likely the combination of increased wind stress and low prey abundance than the poor prey levels alone that had a detrimental effect on condition, growth, and, hence, survival of blue whiting larvae in 1994.

In summary, it is evident that prolonged high wind stress affects blue whiting larval biology in multiple ways. It increases the energy demands in blue whiting larvae, which immediately has an effect on growth as indicated by a reduction in N retention under high wind stress. It disperses existing prey patches and prevents restoration of these, while it also reduces larval feeding success (MacKenzie & Kiørboe 2000). The current study supports the conclusion that the unusually calm wind situation in 1995 resulted in higher prey concentration, and consequently better feeding success and condition of larval blue whiting and, thus, most probably in higher larval survival rates. Therefore, one of the reasons for the success of the 1995 blue whiting year-class may have been the favourable wind conditions during the larval phase; however, in order to have a bearing on recruitment, conditions during the juvenile phase must have been favourable also.

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