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Interannual variations in condition indices of larval Norwegian spring-spawning herring

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The sea water temperature off the Norwegian coast was lower in 1994 than in 1992 and 1993. RNA/DNA ratios of Norwegian spring spawning herring increased with increasing larval dry weight all years, except for larvae sampled south of 62° N in 1994. The RNA/DNA ratios indicated that each year, only a small portion ($\leq 0{\cdot}7\%$) of the larvae were starving. RNA/DNA ratios and temperature were negatively correlated in 1992, but in other years no significant correlations were found. Residuals of ln RNA *v.* ln DNA and ln W *v.* L_s were poorly correlated in all years, but residuals of ln RNA *v.* ln DNA and ln DNA *v.* ln W were negatively correlated in all years. Principal component analysis showed that the RNA/DNA ratio and DNA (% of weight) were correlated with different axes. Abundance data for herring at the early larval and 0-group stages in 1992–1994 indicated higher mortality in 1994 compared with the other years. The data do not indicate that average larval condition was poorer in 1994 than in other years. However, the variability in larval condition was higher in 1994 than in other years, and the condition of later larval stages was relatively lower in 1994 than in other years.

Key words: Nutritional condition; hydrography; RNA/DNA ratios.

INTRODUCTION

The stock of Norwegian spring-spawning herring *Clupea harengus* L., typically exhibits high interannual variability in abundance and recruitment (Hjort, 1914; Dragesund *et al.*, 1980). Initially, there is a great loss of herring larvae (70–95%) within 3 weeks post-hatch along the west coast of Norway (Dragesund & Nakken, 1971, 1973). Growth of larval fish influences survival both directly and indirectly. Starvation mortality will occur if larval growth is very low or negative over a certain time period. Also, the duration of the larval stage is related directly to growth, and thus slow-growing larvae will have a prolonged susceptibility to most predators (Bailey & Houde, 1989).

In order to evaluate the vulnerability of larval fish to mortality due to food limitation and predation, the assessment of physiological condition of fish larvae in the field has been, and continues to be, a major focus of research (Ferron & Leggett, 1994). Several condition indices have been proposed based on either morphometric, histological or biochemical measurements (Ferron & Leggett, 1994). Morphometric condition indices seek to remove the effect of larval size, and are derived by relating a variable that is responsive to larval feeding conditions (dry weight) to one that is relatively starvation-independent (standard length). Among biochemical indices, the RNA/DNA ratio has been widely used as an indicator of larval nutritional condition both in laboratory and field studies

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(Ferron & Leggett, 1994; Clemmesen, 1996). Assuming that larval condition and survival probability are correlated (Anderson, 1988), condition indices may contribute to prediction of interannual variation in recruitment. It is advisable to use several condition indices per individual in order to strengthen the inferences made (Suthers *et al.*, 1992).

In this paper, data on RNA/DNA ratios of larval Norwegian spring-spawning herring are presented for the first time. The interannual variation in nutritional condition of herring larvae collected in spring and early summer during 3 consecutive years (1992–1994) is analysed. The hypotheses are tested that several indices of condition (morphometric and biochemical) derived from the same individual are correlated, and whether there are relations between condition and recruitment indices.

MATERIALS AND METHODS

LARVAL SAMPLING AND HYDROGRAPHICAL MEASUREMENTS

A total of nine cruises were conducted in 1992–1994 to collect herring larvae off the Norwegian coast (Table I, Fig. 1). Yolk-sac herring larvae were sampled with a T-80 net (80 cm in diameter and 375 μm mesh-size). Vertical hauls were taken from 75–150 m depth to the surface, or from close to the seabed to the surface in shallow areas. In 1994, early larvae were also sampled with a Gulf III sampler (Zijlstra, 1970), or with paired Bongo nets (61 cm in diameter; 505 μm mesh-size) (Posgay *et al.*, 1968). Late larvae were sampled with a MIK net (Munk, 1988; Huse *et al.*, 1996), or with the Gulf III. The MIK net was hauled double-obliquely from a depth of 50–100 m (depth was measured with a hydroacoustic sensor) at a vessel speed of 3 kn, and the Gulf III was hauled double-obliquely from a depth of 75 m at a vessel speed of 5 kn. Each year, temperature and conductivity (converted to salinity) were measured at the same stations as herring larvae were collected, by a Neil Brown Mark III CTD sonde operated from the vessel. Mean ambient temperatures and salinities were calculated under the assumption that herring larvae stayed at depths between 0–75 m at those stations where sampling was conducted at depths >75 m (Heath *et al.*, 1988), or down to the actual sampling depth at stations with depths <75 m.

MORPHOMETRIC AND BIOCHEMICAL ANALYSES

Each year, larvae were staged according to Doyle (1977) with the inclusion of an extra stage, 1 d, representing larvae with no visible yolk sac or dorsal fin structures (Øiestad, 1983). The larvae were measured for standard length (L_s) to the nearest 0·1 mm under a stereomicroscope, or in 1-mm intervals using mm paper (cruise Ib, 1994) on board the cruise vessels, and subsequently frozen individually in 1·5-ml Eppendorf tubes in liquid nitrogen for later analysis of RNA and DNA contents. Larvae were stored later in the laboratory at −80° C. The larvae were freeze-dried and weighed individually on a Sartorius microbalance (± 1 μg). All chemicals used in the RNA/DNA analyses were analytical grade (Sigma Chemical Co.): DNA from herring sperm, RNAase from cattle pancreas, and ethidium bromide (EB). The methodology described in Raae *et al.* (1988) was used with slight modifications: prior to analysis, a drop of ice-cold Tris-EDTA buffer (0·05 M Tris, 0·1 M NaCl, 0·01 M EDTA, adjusted to pH 8·0 with HCl) was added to the larva. The larva was disintegrated by applying a short pulse of ultrasound (Virtis 50, 25 W). After adding 0·5 ml of the same buffer, the larva was completely homogenized by two separate 10-s pulses of ultrasound. After homogenization, the material was centrifuged at 9500 *g* for 15 min at −2° C. Total nucleic acid concentration (RNA+DNA) was determined fluorometrically with a Perkin–Elmer LS-5 (excitation, 360 nm; emission, 590 nm) by adding 2·8 ml EB-buffer solution (5 μg EB ml^{-1} buffer) to a 200-μl aliquot of the supernatant on larvae collected in 1992, 1993, and on 40 larvae collected in 1994. Nucleic acids from the remaining larvae (252 larvae) collected in 1994 were

TABLE I. Summary information on cruise dates, number of sampling stations, larval sampling gear, range of positions of sampling stations, and means and ranges of temperatures and salinities within study areas in 1992–1994

Year/cruise	Date	No. of stations	Sampling gears	Latitude	Temperature (° C)		Salinity (‰)	
					Mean	Range	Mean	Range
1992								
I	7–13 April	18	T-80	61°45′ N–63°23′ N	6·2	5·9–6·4	34·3	34·0–34·5
1993								
I	20–22 April	3	T-80	59°14′ N–59°19′ N	6·5	6·4–6·6	33·5	33·5–33·6
II	22–24 May	8	Gulf-III, MIK	59°34′ N–60°44′ N	7·7	7·2–8·1	33·5	31·8–34·2
1994								
<62° N								
Ia	28 April–5 May	8	T-80	59°12′ N–60°15′ N	5·4	5·0–5·8	32·1	31·2–33·0
IIa	14–16 May	8	Bongo, Gulf-III, T-80	59°24′ N–59°40′ N	6·2	5·9–6·3	32·7	32·6–32·8
IIIa	1–3 June	2	MIK	59°29′ N–59°35′ N	6·7	6·7–6·8	33·1	33·1–33·2
IVa	18–19 June	6	MIK	59°29′ N–59°58′ N	6·6	6·5–6·9	33·8	33·6–34·1
>62° N								
Ib	11–17 April	39	Gulf-III, T-80	62°50′ N–66°54′ N	5·6	4·6–6·8	34·5	33·9–35·1
IIb	25–27 May	7	MIK	63°10′ N–67°00′ N	6·8	6·7–6·9	34·8	34·7–34·9

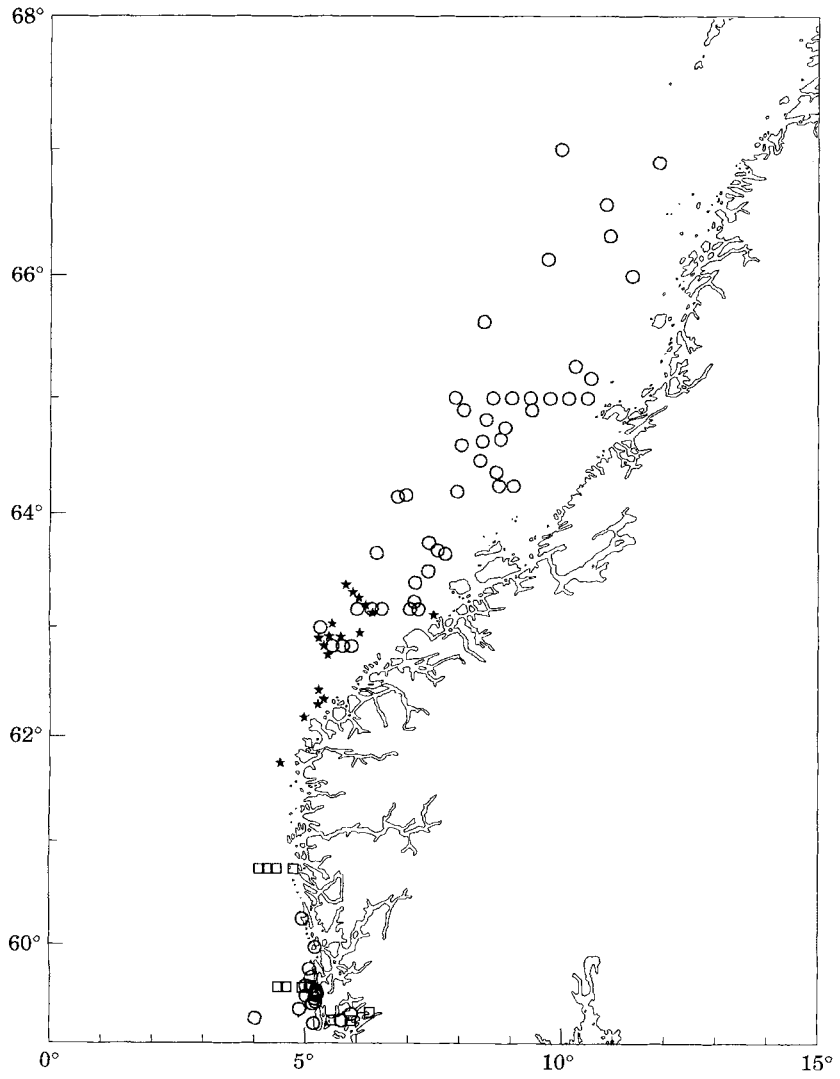

FIG. 1. Locations of sampling stations of herring larvae off the coast of Norway in 1992 (★), 1993 (□) and 1994 (○).

analysed with a Perkin-Elmer LS-30 (excitation, 360 nm; emission, 590 nm). DNA concentrations were determined in the same way after incubation of another 200-µl aliquot with 5 µg RNAase for 30 min at 37° C. The fluorescence of RNA was adjusted according to Le Pecq & Paoletti (1966), and the nucleic acid content was estimated by means of a calibrated DNA standard curve.

CALCULATIONS AND STATISTICAL ANALYSES

Only herring larvae capable of feeding (stage 1c and older) were included in the data analyses. Fulton's condition factor (F_c) was calculated as: $F_c = WL_s^{-3}$ (W, dry weight). One-way ANOVA was used to test for differences in hydrographical parameters and body size between areas and years. Differences in RNA/DNA ratios were tested (ANOVA) between fluorometers. The Tukey honestly significant difference (HSD) test with unequal sample sizes was used for *a posteriori* comparisons if the ANOVA was

significant ($P<0{\cdot}05$). ANCOVA was used to test for differences in slopes and intercepts between areas and years of relationships between ln W *v.* L_s and RNA/DNA ratios *v.* ln W, DNA (% W) *v.* ln W and RNA (% W) *v.* ln W. The analyses were restricted to common size ranges by including cruises with similar sized larvae. Due to varying spatial coverage between years, the 1992 data were compared with the 1994 data collected north of 62° N, and the 1993 data were compared with the 1994 data collected south of 62° N. In correlation analyses, Pearson product moment correlation coefficients were calculated for residuals between size measurements (morphometric and biochemical). The similarities between various size and nucleic acid measures (L_s, ln W, ln DNA, and ln RNA) and condition indices [Fulton's F_c, RNA/DNA ratio, DNA (% W), and RNA (% W)] were investigated by principal component (PC) analyses. Factors 2 and 3 were plotted after the first (size) factor had been extracted (McGurk, 1985; Suthers *et al.*, 1992), using the varimax rotation method of the normalized factor loadings.

ABUNDANCE INDICES

Abundance estimates of early larval and 0-group herring were calculated according to Map Library described by Knutsen & Westgård (unpublished data). Map Library is a tool designed for the presentation of marine data and to integrate a variable over an area to estimate total abundance.

RESULTS

HYDROGRAPHY

Mean seawater temperatures and salinities at all larval sampling stations ranged between 4·6–8·1° C and 31·2–35·1‰, respectively, during 1992–1994 (Table I). In 1994, early herring larvae collected north and south of 62° N experienced similar temperatures (ANOVA, $P=0{\cdot}17$), but higher salinities at stations north of 62° N (ANOVA, $P<0{\cdot}001$). The mean temperature differed between years on the first cruise of the year (cruise I) (ANOVA, $P<0{\cdot}001$), and it was lower in 1994 than in the other years (Tukey HSD test, $P<0{\cdot}001$). Larvae experienced lower temperatures south of 62° N in June 1994 (cruises III–IVa) than in late May 1993 (cruise II) (ANOVA, $P<0{\cdot}001$).

LENGTHS AND WEIGHTS

L_s and dry weights (W) of larvae varied from 9·0 to 29·0 mm and 0·12 to 12·6 mg, respectively, over all cruises (Table II). Larvae collected on cruise I in 1992 were longer and heavier than those collected on corresponding cruises in other years even though they were collected earlier in the year (Tukey HSD tests, $P<0{\cdot}001$). In 1994, the mean W of larvae collected north of 62° N in late May was higher than that of larvae collected south of 62° N in June (ANOVA, $P<0{\cdot}001$). Fulton's F_c ranged between 0·12–1·40 over all cruises, and increased with larval size (Table II). In 1994, the slopes and intercepts of the linear regression of ln W *v.* L_s for larvae collected north and south of 62° N were not different (ANCOVA, slopes $P=0{\cdot}75$, intercepts $P=0{\cdot}46$), and hence a common regression equation was applied. The slope of the linear relationships between ln W and L_s in 1992 was not significantly different from that of 1994 (ANCOVA, $P>0{\cdot}07$; Fig. 2), but the intercept was higher in 1992 (ANCOVA, $P<0{\cdot}001$). The slope was significantly higher in 1994 than in 1993 (ANCOVA, $P=0{\cdot}002$).

NUCLEIC ACIDS

RNA/DNA ratios ranged between 1·3–5·9 over all cruises with mean values from 2·5 to 4·0 (Table II), and they increased significantly with larval W in all

TABLE II. Means, ranges and sample sizes (n) of larval herring standard lengths, dry weights, Fulton's F_C, and RNA/DNA ratios on each cruise in 1992–1994

Year/cruise	Standard length (mm)			Dry weight (μg)			Fulton's F_C			RNA/DNA ratio		
	Mean	Range	n	Mean	Range	n	Mean	Range	n	Mean	Range	n
1992												
I	13·9	9·0–19·2	257	522	121–1800	208	0·20	0·12–0·39	208	3·0	1·8–4·7	207
1993												
I	12·6	10·8–17·0	38	360	214–968	35	0·19	0·13–0·23	35	2·5	1·8–3·4	38
II	18·5	12·9–24·5	108	1629	436–6784	106	0·28	0·13–0·49	106	3·1	1·4–4·6	106
1994												
<62° N												
Ia	11·8	9·5–15·5	11	266	135–530	10	0·17	0·14–0·27	10	—	—	—
IIa	14·0	12·0–16·0	85	498	278–1075	85	0·19	0·12–0·30	85	3·6	1·3–5·2	63
IIIa	20·8	16·5–24·0	53	3026	1292–6422	53	0·35	0·23–0·47	53	—	—	—
IVa	21·3	14·5–29·0	91	3996	740–12 555	91	0·45	0·24–1·40	91	3·3	2·1–4·3	28
>62° N												
Ib	12·6	9·5–17·5	243	367	181–1054	243	0·19	0·12–0·27	243	3·7	2·3–5·9	164
IIb	—	—	—	6088	1313–11 708	86	—	—	—	4·0	2·3–5·9	37

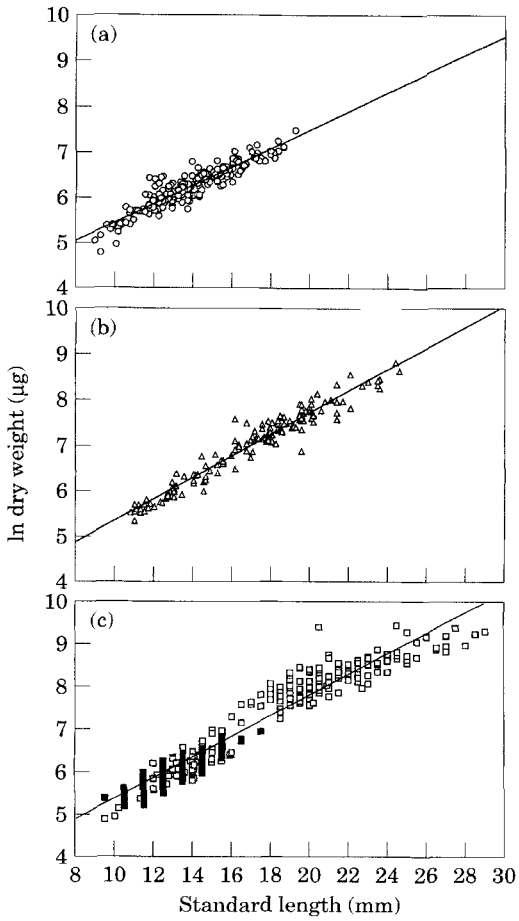

FIG. 2. Linear relationships between ln transformed dry weights (μg) and standard lengths (mm) of herring larvae collected in (a) 1992 (regression equation: ln W=0·204 L_s+3·416, r^2=0·85, P<0·001), (b) 1993 (regression equation: ln W=0·237 L_s+3·000, r^2=0·94, P<0·001), and (c) 1994 (regression equation: ln W=0·251 L_s+2·783, r^2=0·94, P<0·001); □, larvae <62° N; ■, larvae >62° N.

years except for larvae collected south of 62° N in 1994 (Fig. 3). In 1994, the slopes of the linear regressions of RNA/DNA ratios *v.* ln W in larvae collected north and south of 62° N were different (ANCOVA, P=0·004), and thus two regression equations were applied. The slope of the linear regression between RNA/DNA ratios and ln W was significantly lower in 1994 than in 1993 (ANCOVA, P<0·001). The slopes did not differ between larvae collected in 1992 and 1994 (ANCOVA, P=0·69), but the intercept was higher in 1992 (ANCOVA, P<0·001). In 1994, larvae analysed with the Perkin–Elmer LS-5 and LS-30 fluorometers gave mean RNA/DNA ratios of 4·0 (S.D.=0·8) and 3·6 (S.D.=0·7), respectively, and these mean ratios were significantly different (ANOVA, P<0·001). In 1992 and 1993, 3·4 and 5·6% of the ratios were ≤2·0, respectively, whereas in 1994 only one larva (0·3%) collected south of 62° N had a ratio ≤2·0. The residuals of the regression between RNA/DNA ratios and ln W were negatively correlated with temperature in 1992 (P<0·05), but in other years

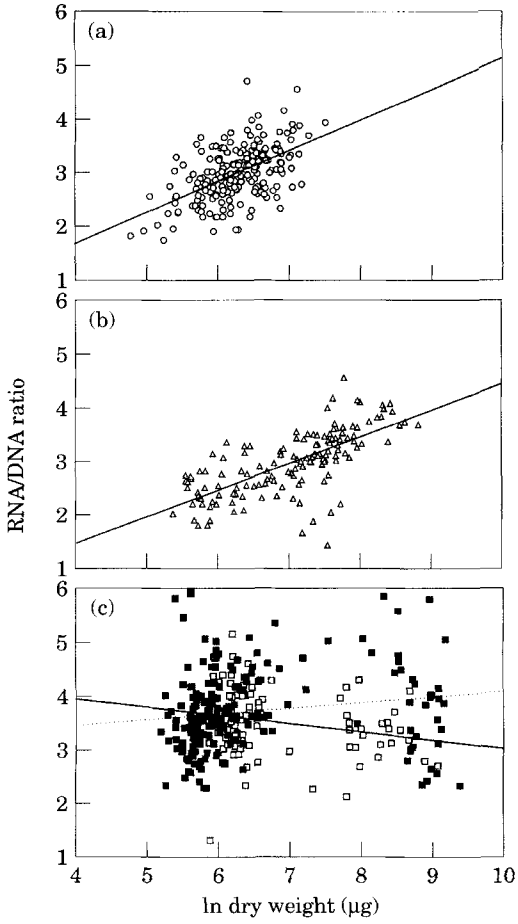

FIG. 3. Linear relationships between RNA/DNA ratios and ln transformed dry weights (μg) of herring larvae collected in (a) 1992 (regression equation: RNA/DNA=0·579 ln W − 0·617, r^2=0·29, P<0·001), (b) 1993 (regression equation: RNA/DNA=0·503 ln W − 0·555, r^2=0·48, P<0·001), and (c) 1994 (regression equations: <62° N, RNA/DNA= − 0·156 ln W+4·594, r^2=0·05, P<0·026; >62° N, RNA/DNA=0·107 ln W+3·044, r^2=0·03, P<0·022); –□–, larvae <62° N, · · ·■· · ·, >62° N.

there were no significant correlations between the corresponding residuals and temperature (P>0·05).

The content of larval DNA (% W) ranged from 0·4 to 1·4% with mean values ranging from 0·7 to 0·9%, and it decreased significantly with increasing W in all years (P<0·02). The slopes of the regressions between DNA (% W) and ln W differed between 1994 and the two other years with the most negative slopes in 1992 and 1993 (ANCOVA, P<0·001). The content of larval RNA (% W) varied from 1·0 to 4·6% with mean values from 2·5 to 2·7%. The slopes of the regressions between RNA (% W) and ln W did not differ between 1992 and 1994, but the intercept was significantly higher in 1992 (ANCOVA, P<0·001). The slopes were different between 1993 and 1994 (ANCOVA, P<0·001) with a negative slope in 1994. In 1994, there was a negative slope among larvae

TABLE III. Pearson product moment correlations between various size and nucleic acid variables of the same herring larvae in 1992–1994

Year/size variables	Size variables		
	ln *W*	ln DNA	ln RNA
1992 $n=207$			
L_s	0·92*	0·92*	0·92*
ln *W*		0·91*	0·91*
ln DNA			0·96*
1993 $n=141$			
L_s	0·97*	0·96*	0·96*
ln *W*		0·98*	0·98*
ln DNA			0·98*
1994 $n=255$			
L_s	0·96*	0·94*	0·92*
ln *W*		0·98*	0·96*
ln DNA			0·97*
All years $n=603$			
L_s	0·96*	0·95*	0·95*
ln *W*		0·97*	0·96*
ln DNA			0·97*

*$P<0·001$.

collected south of 62° N and a slope not different from 0 among larvae collected north of 62° N.

CORRELATIONS BETWEEN SIZE VARIABLES AND RESIDUAL-BASED CONDITION INDICES

Size and nucleic acid measures (L_s, ln *W*, ln DNA, and ln RNA) were positively correlated in 1992–1994 ($r>0·9$; Table III). Residuals from the ln *W* *v.* L_s regressions were poorly correlated with those from relationships between nucleic acids in all years (Table IV). Residuals of ln RNA *v.* ln DNA regressions, and ln DNA *v.* *W* regressions, were negatively correlated ($P<0·001$), and residuals of ln RNA *v.* ln DNA regressions and ln RNA *v.* ln *W* regressions were positively correlated ($P<0·001$).

PRINCIPAL COMPONENT ANALYSES

Size and nucleic acid variables (L_s, ln *W*, ln DNA, and ln RNA) were correlated strongly with PC1 in all years ($r>0·85$), and hence PC1 was interpreted as the size component. After removal of PC1, which explained from 55 to 69% of the total variance in 1992–1994, all variables were plotted on PC2 and PC3 (Fig. 4). The size and nucleic acid variables were correlated poorly with both PC2 and PC3, indicating that size was correlated mostly with PC1. A similar pattern was also found for Fulton's F_c. RNA/DNA ratio and DNA (% *W*) loaded clearly on opposite axes in all years with absolute correlations >0·79 with their respective axes, and RNA (% *W*) loaded between RNA/DNA ratio

TABLE IV. Pearson product moment correlations between residuals of condition indices derived from the same herring larvae in 1992–1994

Year/condition indices	Condition indices		
	ln RNA − ln DNA	ln DNA − ln W	ln RNA − ln W
1992 n=207			
ln $W - L_s$	−0·02	−0·47*	−0·48*
ln RNA − ln DNA		−0·23*	0·41*
ln DNA − ln W			0·79*
1993 n=141			
ln $W - L_s$	−0·09	−0·14	−0·24**
ln RNA − ln DNA		−0·44*	0·51*
ln DNA − ln W			0·55*
1994 n=225			
ln $W - L_s$	−0·09	0·02	−0·10
ln RNA − ln DNA		−0·30*	0·69*
ln DNA − ln W			0·48*
All years n=603			
ln $W - L_s$	−0·04	−0·19*	−0·22*
ln RNA − ln DNA		−0·40*	0·62*
ln DNA − ln W			0·47*

*P<0·001; **P<0·01.

and DNA (% W) on the PC plots in all years with absolute correlations from 0·38 to 0·86 with PC2 and 0·49 to 0·85 with PC3.

ABUNDANCE INDICES

The number of early herring larvae in Norwegian coastal waters in April ranged from 5×10^{12}–21×10^{12} individuals in 1992–1994, with the highest abundance recorded in 1993 (Table V). At the 0-group stage, the numbers varied between 26×10^9 and 114×10^9 individuals with the maximum in 1992. Survival between the early larval and 0-group stages was lowest in 1994, with 0·16% and highest in 1992 with 2·3%.

DISCUSSION

Each year, only a small portion ($\leq$5·6%) of the Norwegian spring-spawning herring larvae had RNA/DNA ratios $\leq$2·0. An RNA/DNA ratio of 2·0 has been used as the critical value for evaluation of condition for several species of larval fishes (Robinson & Ware, 1988; Ferron & Leggett, 1994). In a field study, Clemmesen (1996) found RNA/DNA ratios of larval herring to be between 2·3–5·4 in the northern North Sea and between 1·0–3·2 in the English Channel. She concluded that all larvae from the northern North Sea were in a very good nutritional condition, but in the English Channel 2·7% of the larvae were judged to be starving. In a laboratory study, Clemmesen (1994) proposed a critical level for the RNA/DNA ratio of 1·2 for a 10-mm herring larva, and 1·8 for a 25-mm larva. Based on the results of Clemmesen (1994), the RNA/DNA ratios given in

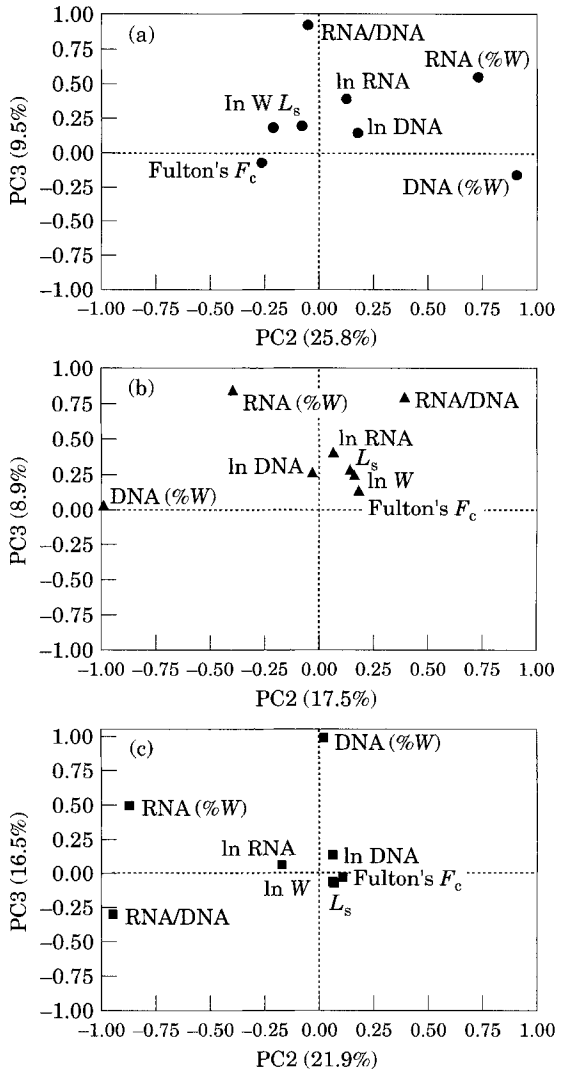

FIG. 4. Factor loadings of each larval variable on the second and third principal components (PC) in (a) 1992, (b) 1993, and (c) 1994.

our study indicate that none of the larvae was in a starving condition in 1992, and only a single larva sampled in 1993 (0·7%) and one in 1994 (0·3%) were starving. Hence, our results suggest that the nutritional condition of larval Norwegian spring-spawning herring was relatively high in 1992–1994, and starvation was of minor importance.

RNA/DNA ratios in larval fish correlate positively with prey densities (Ferron & Leggett, 1994). Prey densities in habitats of larval Norwegian spring-spawning herring varied by a factor of up to 20 during first-feeding in 1989–1993 (Fossum, 1996), and the highest prey densities were found in 1993 with a maximum of *c.* 14 copepod eggs and nauplii l^{-1}. In a mesocosm study, Folkvord *et al.* (1996) reported RNA/DNA ratios of between 0·5 and 2·0 for

TABLE V. Abundance estimates of herring (1992–1994) at the early larval stage on the Norwegian coast in April, and at the 0-group stage in the Barents Sea and in Norwegian coastal waters in August/September (Fossum, 1996, unpublished data)

Year	No. of herring	
	Early larvae ($\times 10^{12}$)	0-group ($\times 10^{9}$)
1992	5	114
1993	21	57
1994	16	26

early herring larvae at prey densities from 0·1 to 0·5 l^{-1}. They also reported that up to 70% of the larvae were in a poor nutritional condition at those prey densities. However, the RNA/DNA ratios found in early larval herring in 1992–1994 suggest that the prey densities were not below the critical limit for larval growth.

RNA/DNA ratios increased significantly with body size in all years, with the exception of larvae collected south of 62° N in 1994. Similar effects have been documented in the literature (Buckley *et al.*, 1984; Clemmesen, 1994; Rooker *et al.*, 1997). Temperature has also been shown to affect the RNA/DNA ratios (Buckley, 1982; Mathers *et al.*, 1993; Rooker *et al.*, 1997), but the relation between these variables was not clear. There was a negative relationship between RNA/DNA ratios and temperature in 1992, but in other years no significant relationships were found. Higher concentrations of RNA in fish tissues have been found at lower temperatures in some studies (Buckley, 1982; Goolish *et al.*, 1984; Mathers *et al.*, 1993), and this may be a compensatory mechanism for lower RNA activity at lower temperatures (Goolish *et al.*, 1984). However, Rooker *et al.* (1997) reported that RNA/DNA ratios increased with increasing temperature for wild larval and juvenile red drum *Sciaenops ocellatus* (L.), and suggested that this was expected because temperature controls the protein synthesis which again is directly proportional to the amount of RNA in the cell. Thus, a temperature correction factor for the comparison of RNA/DNA ratios in young fish inhabiting various thermal environments is essential (Clemmesen, 1996; Rooker *et al.*, 1997).

DNA (% W) has been suggested as a more reliable index of larval nutritional status than the RNA/DNA ratio (Richard *et al.*, 1991). DNA (% W) was always higher in starved sole *Solea solea* (L.) larvae than in well fed individuals, and increased progressively with starvation period (Richard *et al.*, 1991). Thus one should expect both higher RNA/DNA ratios and lower DNA/W ratios in well fed larvae compared to starving larvae at comparable size. The residuals of ln DNA *v.* ln W and ln RNA *v.* ln DNA for the same larvae were in fact significantly negatively correlated all years in our study, indicating that both of these residual-based indices should be suitable as condition measures. Our relationships between RNA (% W) and body size gave both positive and negative

slopes and were therefore unclear. Richard *et al.* (1991) found that in fed larval sole this index decreased from 3·4–4·3% in early larvae to 2·0–2·5% in larger larvae. In starved sole larvae, they reported that the RNA (% *W*) index decreased with size, but always stayed equal to, or higher than that in well-fed larvae. In our study, ln RNA *v.* ln *W* residuals were significantly positively correlated with ln RNA *v.* ln DNA residuals in all years, suggesting that this residual-based index can be used as a condition measure. Suthers *et al.* (1996) reported that the residuals between ln RNA and ln L_s did reveal significant effects of starvation in larval Australian bass *Macquaria novemaculeata* (Steindachner) in the laboratory, whereas the RNA/DNA ratio did not.

In this study, Fulton's F_c and the residuals between ln *W v.* L_s were poorly correlated with other condition indices from the same larvae, and the PC analyses showed that the Fulton's F_c loaded together with size and nucleic acid measures. Other studies have also shown that Fulton's F_c and relationships between *W* and L_s are poorly correlated with other condition indices (e.g. Suthers *et al.*, 1992).

The growth conditions of larval Norwegian spring-spawning herring may have been sub-optimal in 1994 compared to those in other years. Larvae collected in late May 1994 north of 62° N (cruise IIb) were considerably smaller than those collected in the same area, and at the same time in 1992 and 1993 (Fossum, unpublished data). Several larger larvae (>3 mg *W*) had RNA/DNA ratios between 2 and 3 in 1994, whereas the largest larvae (>3 mg *W*) in 1993 all had ratios >3. The RNA/DNA ratios also showed a higher variability in 1994 than in other years. These findings may be indicative of poorer growth conditions during the late larval stage in 1994 than in other years. Our data also show that the sea was generally colder in 1994 than in other years which may have slowed down larval growth that year. The abundance indices indicated that survival was lower from the early larval stage to the 0-group stage in 1994 than in other years. Sampling of late larvae north of 62° N during the end of May 1994, showed that larvae were caught from only half of the stations in which larvae had been found in high concentrations in 1993 (Fossum, unpublished data). This indicates that most herring mortality occurred between mid-April and the end of May in 1994. Based on our data giving indices of nutritional condition of larval herring from 1992 to 1994, it cannot be concluded that the average larval condition actually was worse in 1994 than in other years. However, the condition of later larval stages was relatively poorer, and more variable in 1994 than in other years. Larval growth and survival conditions may have been poor between subsequent cruises that year. A successful first-feeding period in larval herring is important for good recruitment (Fossum, 1996), but a major contribution to the determination of recruitment success also seems to be the rate of predation on late larval and early juvenile stages (Holst & Røttingen, 1994; Barros, 1995).

In conclusion, the nutritional condition of larval Norwegian spring-spawning herring was generally high in 1992–1994, and starvation seemed to be of minor importance. However, the validity of our biochemical condition indices would have been improved by incorporating otolith microstructure studies on all larvae that were analysed for nutritional condition (Clemmesen, 1996; Clemmesen & Doan, 1996), in order to obtain the growth history of the larvae as well as the condition at catch.

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