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VIABLE HATCH FROM EGGS OF PACIFIC HERRING (*Clupea harengus pallasi*) DEPOSITED AT DIFFERENT INTENSITIES ON A VARIETY OF SUBSTRATES*

by

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ABSTRACT

Hourston, A. S., H. Rosenthal and H. von Westernhagen. 1984. Viable hatch from eggs of Pacific herring (Clupea harengus pallasi) deposited at different intensities on a variety of substrates. Can. Tech. Rep. Fish. Aquat. Sci. 1274: 19 p.

Hatching success, defined as the percent of eggs producing viable larvae, varied among the 14 substrates, 5 spawning intensities and 3 egg sources utilized in a series of 53 laboratory tests. Viability of the newly hatched larvae was usually high (over 80% in 47 tests) and not related to the three factors tested. Percent hatch declined and then fell off abruptly as egg density increased. The density at which this occurred varied with the substrate tested, as did the time of hatching and condition factor. Larvae from spawnings of heavier intensities hatched earlier, over a shorter period, at a shorter length and with a higher yolk volume. Length at hatching increased with the length of the incubation period, while weight, yolk volume and condition factor decreased. Minor, inconsistent differences in hatching success between natural and artificial spawn were attributed to the technique employed for the former and were not considered meaningful. No consistent differences in hatching success and other factors were found between artificially spawned eggs from large or small fish.

Key words: Clupea harengus pallasi, eggs, larvae, spawning substrates, artificial spawning, viable hatch, length, weight, yolk, condition factor.

RÉSUMÉ

Hourston, A. S., H. Rosenthal and H. von Westernhagen. 1984. Viable hatch from eggs of Pacific herring (Clupea harengus pallasi) deposited at different intensities on a variety of substrates. Can. Tech. Rep. Fish. Aquat. Sci. 1274: 19 p.

Le succès de l'éclosion, défini comme le pourcentage d'oeufs produisant des larves viables, variait entre 14 substrats, 5 niveau d'intensité de fraie et 3 sources d'oeufs au cours d'une série de 53 expériences en laboratoire. En général, la viabilité des larves nouvellement écloses était élevée (plus de 80 % dans 47 expériences) et n'était pas reliée aux trois facteurs évalués. Le pourcentage d'éclosion a d'abord décliné puis chuté en fonction de l'accroissement de la densité des oeufs. Cette densité variait, tout comme le moment de l'éclosion et le coefficient de condition, selon le substrat. Les larves provenant de fraie de forte intensité ont éclos plus tôt, plus vite, à une plus petite taille et à un plus gros volume de vitellus. La taille à l'éclosion augmentait en fonction de la longueur de la période d'incubation tandis que le poids, le volume vitellin et le coefficient de condition diminuaient. On a imputé les faibles différences incompatibles du succès de l'éclosion entre le frai naturel et le frai artificiel à la technique employée au cours de l'expérience avec le premier et, par conséquent, on ne les a pas considérées significatives. Aucune différence concordante du succès de l'éclosion et d'autres facteurs n'a été découverte entre les oeufs pondus artificiellement, provenant de petits ou de gros poissons.

Mots-clés: Clupea harengus pallasi, oeufs, larves, substrats de fraie, fraie artificielle, larves viables, taille, poids, vitellus, coefficient de condition

INTRODUCTION

Pacific herring (Clupea harengus pallasi) spawn in the intertidal and adjacent subtidal zones over the entire coast of British Columbia (Hourston and Haegele 1980; Hourston 1981). Individual fisheries for the roe market operate on the spawning grounds immediately prior to and during the early stages of spawning. Consequently it is possible to associate catches with individual spawning grounds and to regulate the fishery to provide for a target escapement to each spawning ground (e.g. Hourston 1980b).

There is no apparent relationship between the abundance of a year class at recruitment and the abundance of the spawning stocks which produced it (Taylor 1963, Hourston 1980a), or even the numbers of eggs deposited (Taylor 1964). Larval mortality is extensive and variable and appears to be related to the environmental conditions encountered by each brood (Stevenson 1962). Until the controlling factors can be identified and their effects predicted prior to spawning, it would appear desirable to aim for a level of egg deposition which would produce the maximum number of viable larvae from individual spawning grounds.

Herring spawnings in British Columbia have been surveyed annually since 1951 (Hourston et al. 1972; Hourston 1981). These survey data include the substrates utilized and assessments of the intensity of egg deposition as Very Light (VL), Light (L), Medium (M), Heavy (H) or Very Heavy (VH), which are defined in terms of eggs per linear inch on stringy substrates or eggs per square inch on leafy substrates as follows.

	Egg complement of substrate	
Spawning intensity	Per linear inch of eelgrass or japweed	Per square inch of kelp, rockweed or sea lettuce
Very light	1-25	1-50
Light	26-100	51-200
Medium	101-250	201-500
Heavy	251-500	501-1000
Very heavy	501 up	1001 up

Since the area which will be utilized by the spawners can usually be identified from the available substrates (e.g. Haegele and Hamey 1981) and past spawning practices (Hourston 1980c), the target escapements for a given spawning ground may be assessed in terms of the optimum intensity of egg deposition and the area utilized.

Egg mortality can be appreciable in heavy spawn for both Atlantic (Lea 1930) and Pacific (Hart and Tester 1934) herring. The degree of this mortality varies with the thickness of the egg deposition (Runnstrom 1941, Taylor 1971), to the extent that heavy spawnings may produce less larvae than those of intermediate intensity (Hourston and Haegele 1980). Heavy mortality

of eggs has been observed in British Columbia waters in spawn of more than 4 layers on flat substrates and in spawn of more than 10 layers on filamentous substrates. However, equally heavy spawn depositions have shown good survival (Hourston 1981), so the upper limit of egg density for good survival appears to be a function of local conditions.

Another major concern in the determination of optimum spawn intensity is the viability of the hatch. The development of the eggs in the lower layers of a multilayered egg deposition is usually retarded (Parrish et al. 1959, Baxter 1971), which may lead to abnormal development of the embryos in even the second layer. The number of such non-viable larvae can be two or three times as great as the number of dead eggs (Galkina 1971).

In addition, there is the question of the condition of the viable larvae in the hatch. If development is slowed down because of crowding and/or hatching is premature, the emerging larvae may be less successful in learning to feed effectively (Rosenthal and Hempel 1970) and escaping predators than their well developed counterparts.

Most herring eggs are spawned directly onto various types of vegetation by females and are fertilized after attachment (Hourston et al. 1977). Some are released into the water and settle onto a substrate to which they adhere (Stacey and Hourston 1982). These differences in the method of deposition, along with differences in the way eggs are deposited on different substrates, result in differences in the density of packing of eggs on the various types of substrate. In spawnings involving several layers of eggs, the more loosely packed eggs have more surface area exposed and are better able to respire, and hence are more likely to hatch successfully. Consequently the optimum number of layers of egg deposition for viable hatch will vary with the type of substrate and the strength of the current flowing over the eggs. The currents involved are primarily tidal or storm-induced and not likely to differ consistently or appreciably between most spawning grounds.

METHODS

Viability of the hatch was tested by rearing samples taken from natural spawnings to hatching under controlled laboratory conditions and examining the larvae immediately after hatching. Samples of spawn on six different substrates (Table 1) were taken from the spawnings in Mayne Bay in Barkley Sound on March 19-23, 1975 reported by Webb (1975) and Humphreys and Haegele (1976). The samples were collected by scuba divers between 0900 and 0930 hr on March 23 and transported in a holding tank by truck to the Pacific Biological Station within 6 hr. They were placed in square 40 L holding tanks of recirculating sea water (replenished every 4 days) with a salinity maintained at 26°/°° and temperature at 8°C (typical for local herring spawning grounds during incubation). At 1630 hr, the samples were distributed among six 40-litre rectangular experimental tanks according to substrate type. Throughout the experiment, sea water maintained at 8±1°C and

25±1°/.. was circulated by aeration through an air stone and approximately one-third of the water was replenished each day. Because of limitations in laboratory facilities, it was not possible to sample all spawning intensities on all substrates or to provide the replicates needed for rigorous statistical analysis of the results. In order to examine the effects of spawning intensity, each of the 5 intensity levels was sampled for the main "stringy" substrate (Zostera) and the main "leafy" substrate (Agarum), except that medium intensity was not available for the latter (Table 1). In order to examine the effects of different substrates, each of the remaining 4 substrates (Pikea, Rhodomela, Fucus and Polysiphonia) was sampled at 2 intensity levels except for Polysiphonia for which only light intensity was available. The remaining space was utilized for a replicate of medium intensity on Zostera.

Immediately before hatching commenced (April 2), a sample of about 500 eggs was taken for each of the 17 categories selected and transferred into a 200 mL aerated glass beaker which was held partially submerged on racks in three similar experimental tanks maintained at the same temperature and salinity. Beginning at 0800 hr April 3, larvae from each of the beakers were removed for examination at approximately 12-hr intervals until the peak of hatching had passed (about 10 days), and daily thereafter. The water in each of the beakers was replenished daily.

When sampled, the newly hatched larvae were examined microscopically for visible malformations such as bent body axis and retarded or abnormal development. Abnormal larvae were counted and discarded. Normal larvae were anesthetized with MS 222, measured for total length (to 0.01 mm) and maximum and minimum yolk diameters (to 0.001 mm), and mounted on glass slides. These larvae were dried at 60°C for 12 hr and 80°C for 1 hr and stored in a dessicator for subsequent dry weight determinations (to 0.001 mg) on a Cahn balance. As a basis for assessing the survival prospects of the larvae, condition factors (cf) and yolk volumes (yv) were calculated as follows:

$$cf = 1000\ \text{weight}/\text{length}^3$$

$$yv = \frac{4}{3}\left[\left(\frac{L}{2}\right)^2\left(\frac{H}{2}\right)\right]$$

where L and H are the maximum and minimum diameters respectively (Alderdice et al. 1979). Dead eggs were removed and counted throughout the sampling period.

To extend the data base and to determine differences between naturally spawned and artificially spawned eggs, the experiment was repeated beginning May 12 by artificially spawning a large and a small female at different intensities on 12 substrate types (including plastic). A large and a small fish were selected to test for indications of differences in the viability of hatch between large (older) and small (younger) females. All eggs were fertilized by milt from the same large male. Procedures employed were identical to those for the first experiment except that sampling was conducted every 24 hr. A total of 36 samples representing 27 combinations was involved in the second experiment (Table 1).

RESULTS

The numbers of viable and non-viable larvae hatched and sampled each day were recorded, along with the means and standard deviations of the length, weight, yolk volume and condition factor, for 53 combinations of substrate type, egg source and spawning intensity (Hourston and Rosenthal 1981). Average data on timing (day of 50% hatch), percent of eggs hatching, percent of the hatch which was viable, length, weight, yolk volume and condition factor were summarized by egg source, substrate type and spawning intensity (Fig. 1). Daily averages (±1 standard deviation) are shown for natural (Fig. 2) and artificial (Fig. 3) spawnings on the eelgrass substrate Zostera to illustrate time trends for different spawning intensities and egg sources. Parallel data for a kelp substrate, Agarum, are shown (Fig. 4) to illustrate differences between two types of substrate. Comparable data for the other substrates are described by Hourston et al (1981).

INCUBATION TIME

Hatching peaked at 4 to 7 days after the first larvae hatched for 36 of the 53 experiments (Fig. 1-4), giving an incubation period of 16-19 days. This is normal for an environment of 8°C and 25°/.. (Alderdice and Velsen 1971). Incubation time was shorter for 8 filamentous red algae experiments (Delesseria M, Microcladia M, and Odonthalia M for both large and small fish, Odonthalia H for large fish and natural spawning Pikea VH). It was longer (20-22 days) in 9 experiments for a variety of substrates and egg densities. However, these differences may have resulted more from differences in the egg densities represented than differences in substrates themselves. Incubation time varied inversely with spawning intensity for all substrates and showed a slight tendency to peak over a shorter period in the earlier spawnings (Hourston et al 1981).

PERCENT HATCH

Percent hatch was highly variable (Fig. 1) ranging from 16% (Rhodymenia H for large fish) to 100% (Zostera VL for natural spawning). Percent hatch tended to decrease as spawning intensity increased.

PERCENT VIABLE

Viability of the newly hatched larvae was consistently high (86-97%) in 39 of the 53 tests run. Only 6 tests gave a viability of less than 80% and in each case, the hatch was early and relatively poor (Fig. 1). All of the well sampled spawning intensities (light, medium and heavy) and all of the egg

sources (natural spawnings, large fish artificially spawned, and small fish artificially spawned) were involved in these six tests, as were three different substrates (Microcladia, Polysiphonia and Zostera). This suggests that the lower viability of the hatch for these 6 tests resulted from undetected adverse experimental conditions rather than any of the three factors being tested. There was a slight tendency for eggs with a hatching success of less than 60% to have lower larval viability than those with more than 60% hatching success (87.2% vs. 90.41%, 86.6% vs. 91.1%, 87.4% vs. 89.3%, and 87.3% vs. 90.2% for natural spawnings, artificial spawnings from large and small fish and all spawnings respectively); however these differences were not significant.

AVERAGE LENGTH AND WEIGHT

The average length of the larvae at hatching decreased with spawning intensity and increased with the length of the incubation period (Fig. 1). During that period, length at hatching increased up to the peak of hatching, dropped temporarily immediately thereafter, and then rose again (Fig. 2-4). The tendency to drop again late in the hatching period noted by Hourston et al.(1981) is evident for the spawn on kelp but appears only sporadically in the spawn on Zostera (Fig. 2, 3). Average length declined as spawning intensity increased for almost all groupings by substrate and egg source (Fig. 1). Average weight at hatching was inversely correlated with average length (Fig. 1) but the trends in the data were less evident, probably because of the much higher variability in the weight data (Fig 2-4). These relationships for both length and weight were more evident in some of the other substrates tested (Hourston et al. 1981).

YOLK VOLUME AND CONDITION FACTOR

These two interrelated characteristics were closely correlated with average weight (Hourston et al. 1981) and followed the same trends (Fig. 1). The data showed less variability than did the weight data for natural spawnings (Fig. 2, 4), but not for artificial spawnings (Fig. 3).

EGG SOURCES

Naturally spawned eggs tended to hatch later and to produce a higher percentage hatch and longer larvae than did artificially spawned eggs. This is born out by the results for all substrates as well as for the 4 substrates (Polysiphonia, Rhodomela, Zostera and Fucus) for which both natural and artificial spawnings were tested (Fig. 1).

In artificial spawnings on Zostera, eggs from large fish produced a higher percentage hatch of longer and lighter larvae with smaller yolks and

lower condition factors than did eggs from small fish. However, differences between other paired experiments on eggs from large or small fish on Neoagardhiella, Odonthalia, Fucus, Nereocystis, plastic, Sargassum and Rhodymenia showed a more or less random distribution of no differences, differences similar to and differences opposite from those for Zostera for the various characters measured. Thus the Zostera results were probably a coincidence and there would not appear to be any evidence of real differences in the production of larva from artificially spawned eggs from large and small fish.

No differences between any of the 3 egg sources were apparent in the daily time series (Fig. 2-4).

EGG DENSITY

Larvae from heavier spawn hatched earlier, over a briefer period, at a shorter length, and with a higher yolk volume (Fig. 1-4). Differences in weight and condition factor were minor or inconsistent. Hatching success (% hatch) consistently declined as egg density increased, eventually showing a sharp drop whenever sufficiently high egg densities were sampled (Microcladia, Odonthalia, Pikea, Polysiphonia, Zostera, Agarum and Rhodymenia - Fig. 1). Minor variations were associated with different egg sources, and paired experiments (same egg source) were even more consistent in this respect. The one exception to this trend was the light natural spawning on Zostera, which hatched earlier, less successfully, and with a lower proportion of viable larvae than would have been expected. This again suggests a problem with experimental conditions rather than an effect of egg density.

SUBSTRATE TYPE

The time of hatching, hatching success and condition factor varied markedly for the various substrates tested (Fig. 1). However, variability with a substrate type, (Humphreys and Hourston 1978) such as filamentous red algae (Delesseria, Microcladia, Neoagardhiella, Odonthalia, Pikea, Polysiphonia and Rhodomela - Fig. 1) was just as great as that between the other substrate types tested - sea grasses (Zostera), rockweeds (Fucus), kelps (Agarum and Nereocystis), other brown algae (Sargassum), foliose red algae (Rhodymenia) and other (plastic). It would therefore appear that these variations again represent differences in conditions between experiments more than differences in substrate type. Hatching success was very poor for very heavy spawnings on all 3 substrates sampled at this intensity and was poor on half of the 12 substrates sampled at heavy intensity. The abrupt drop in percent hatch noted above occurred at different intensities for different substrates (medium for Polysiphonia, heavy for Microcladia, Odonthalia and Rhodymenia, heavy to very heavy for Pikea and Zostera, and very heavy for Agarum).

DISCUSSION

On the basis of the limited coverage of 53 tests on a range of substrates, spawning intensities and egg sources, it would appear that hatching success for Pacific herring eggs is most seriously affected by egg density. Presumably, there is a critical egg density above which the exchange of oxygen and waste products across the egg membrane is limited by the reduced surface area of individual eggs exposed and/or the rate of exchange of the water to which the egg membrane is exposed. This critical egg density would be related to both the number of layers of eggs present and how closely they are packed together ("packing factor"). Qualitative observations in the field, along with similar observations on the material used in this study, indicate that naturally spawned eggs tend to be more loosely packed on some substrates than on others. The former substrates should, therefore, provide successful hatches from a greater thickness of eggs than would the latter. Our results indicate that there is a difference in this regard between substrate species; however, there was no evidence that these differences were consistent among substrate types. In any event, there would appear to be little adverse affect on egg survival in natural spawnings on any substrate up to the heavy level (approximately 8 layers in the new system of recording). This is consistent with observations on Atlantic herring spawnings by Parrish et al. (1959) and laboratory tests on Pacific herring by Taylor (1971).

Average weight, yolk volume and condition factor all decreased as the incubation period increased. All three factors reflect the continuing depletion of the yolk sac with development. If this depletion is a simple function of length, an earlier hatch would provide for faster growth since energy provided from the yolk sac could be supplemented earlier by energy provided from food, provided this activity begins at hatching, as would appear to be the case (Rosenthal and Hempel 1970). However, this advantage could well be negated in terms of biomass production by longer exposure to predation in the early larval stage as the early hatch grows to the equivalent size of the late hatch. On the other hand, if the rate of development is higher for the early hatch than for the late hatch, the development potential for the former would be superior.

Galkina's (1971) observation that the number of abnormal Pacific herring embryos can exceed by 2-3 times the number of dead eggs in the Okhotsk Sea was not born out for Pacific herring in this study. However, her observations included spawnings of up to 20 layers and losses through mortality in the egg stage and non-viable embryos of up to 80%. It is quite possible that had our experiments included spawnings of equivalent density, both the egg mortality and non-viable hatch would have reached comparable levels. Spawnings of such density are exceedingly rare in British Columbia waters (Hourston et al. 1972, Hourston 1981) and hence were not included in the limited series of tests included in this study.

The artificial spawning technique employed in this study approached, but did not match natural spawnings in hatching success in some (but not all) of the paired experiments. It seems likely that with further practice and

development of the technique, even the minor differences in spawning success which we observed could be eliminated. No meaningful differences in hatching success were observed between artificial spawnings from large and small females.

This study provides the basis for more specific and quantitative approaches to further research and to monitoring of the stocks. The main weakness in the data - the lack of quantitative precision in the measures of egg deposition during annual monitoring - has been addressed by replacing the qualitative assessment of spawning intensity with a system of recording layers of eggs (and fractions thereof) by substrate (Humphreys and Hourston 1978). The approximate points of sharp decreases in hatching success with increasing egg density determined herein for the various substrates suggest the potentially most productive egg densities for sampling in future work employing the needed replications and precision of measurements. This, in turn, would provide a suitable basis for the definitive statistical analyses which the authors considered unwarranted herein because of inherent weaknesses in the data base.

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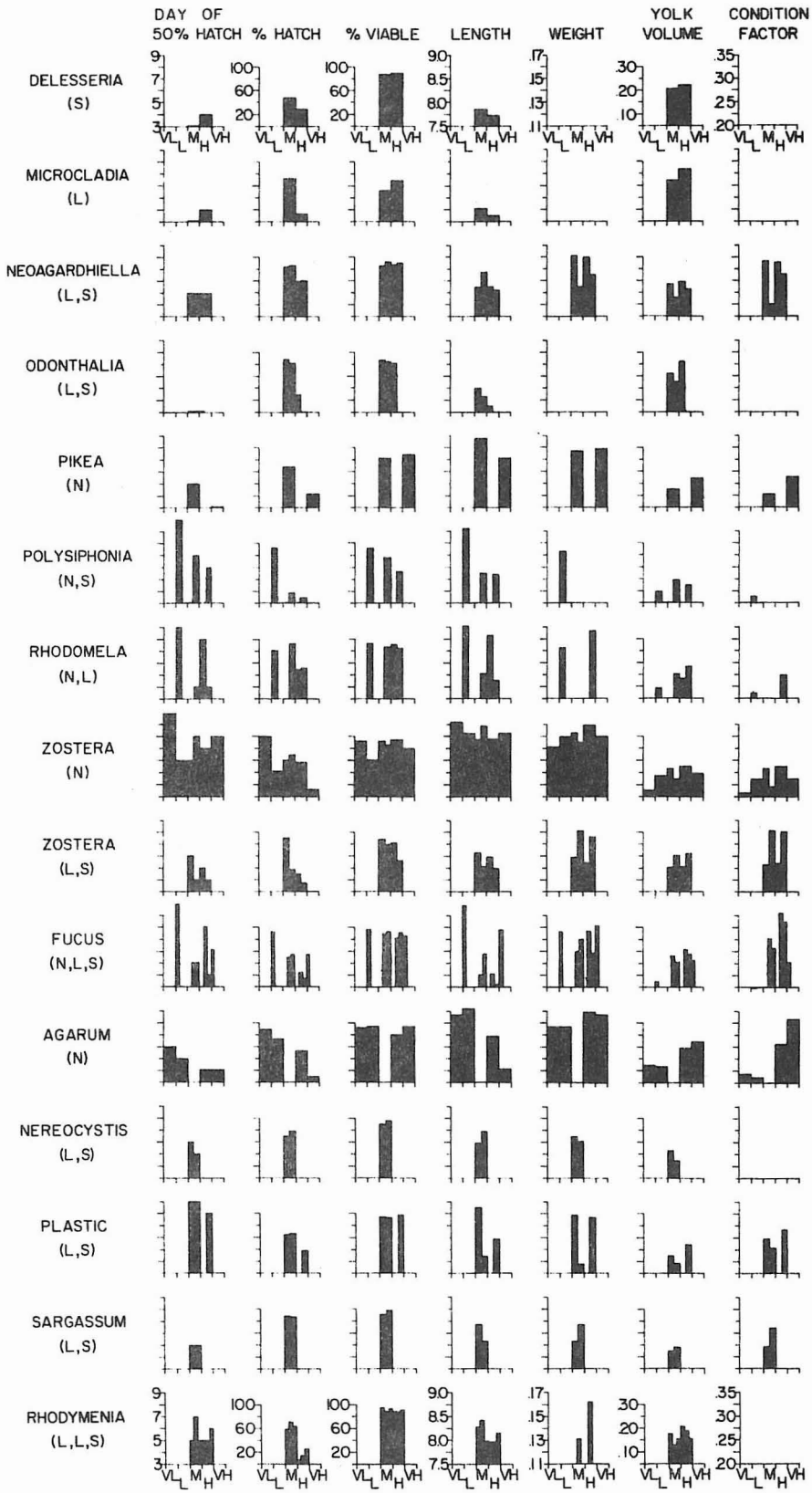
Table 1. Hatching experiments conducted on natural (N) and artificial spawnings from large (L) and small (S) fish at 5 spawning intensities on 14 different substrates.

SUBSTRATE TYPE	Spawning intensity				
Substrate	Very Light	Light	Medium	Heavy	Very Heavy
FILAMENTOUS RED ALGAE			S	S	
Delesseria			S	S	
Microcladia			L	L	
Neoagardhiella			LS	LS	
Odonthalia			LS	L	
Pikea			N		N
Polysiphonia		N	S	S	
Rhonomela		N	L	NL	
SEA GRASSES					
Zostera	N	N	NNLS	NLS	N
ROCKWEEDS					
Fucus		N	LS	LS	N
KELPS					
Agarum	N	N		N	N
Nereocystis			LS		
OTHER					
Plastic			LS	S	
OTHER BROWN ALGAE					
Sargassum			LS		
FOLIOSE RED ALGAE					
Rhodymenia			LLS	LLS	

Fig. 1. Day (numbered from the start of hatching) of 50% hatch, percent hatch, percent of hatch viable, average length (mm), average weight (mg), yolk volume (mm^3) and condition factor for natural spawn (N) and artificial spawn from large (L) and small (S) herring at very light (VL), light (L), medium (M), heavy (H), and very heavy (VH) intensities on 14 different substrates. When more than one set of data was available for a single substrate (see Table 1), the bars for that substrate were subdivided accordingly for all intensities.


DAY OF 50% HATCH
% HATCH
% VIABLE
LENGTH
WEIGHT
YOLK VOLUME
CONDITION FACTOR
DELESSERIA (S)
MICROCLADIA (L)
NEOAGARDHIELLA (L,S)
ODONTHALIA (L,S)
PIKEA (N)
POLYSIPHONIA (N,S)
RHODOMELA (N,L)
ZOSTERA (N)
ZOSTERA (L,S)
FUCUS (N,L,S)
AGARUM (N)
NEREOCYSTIS (L,S)
PLASTIC (L,S)
SARGASSUM (L,S)
RHODYMENIA (L,L,S)
VL L M H VH

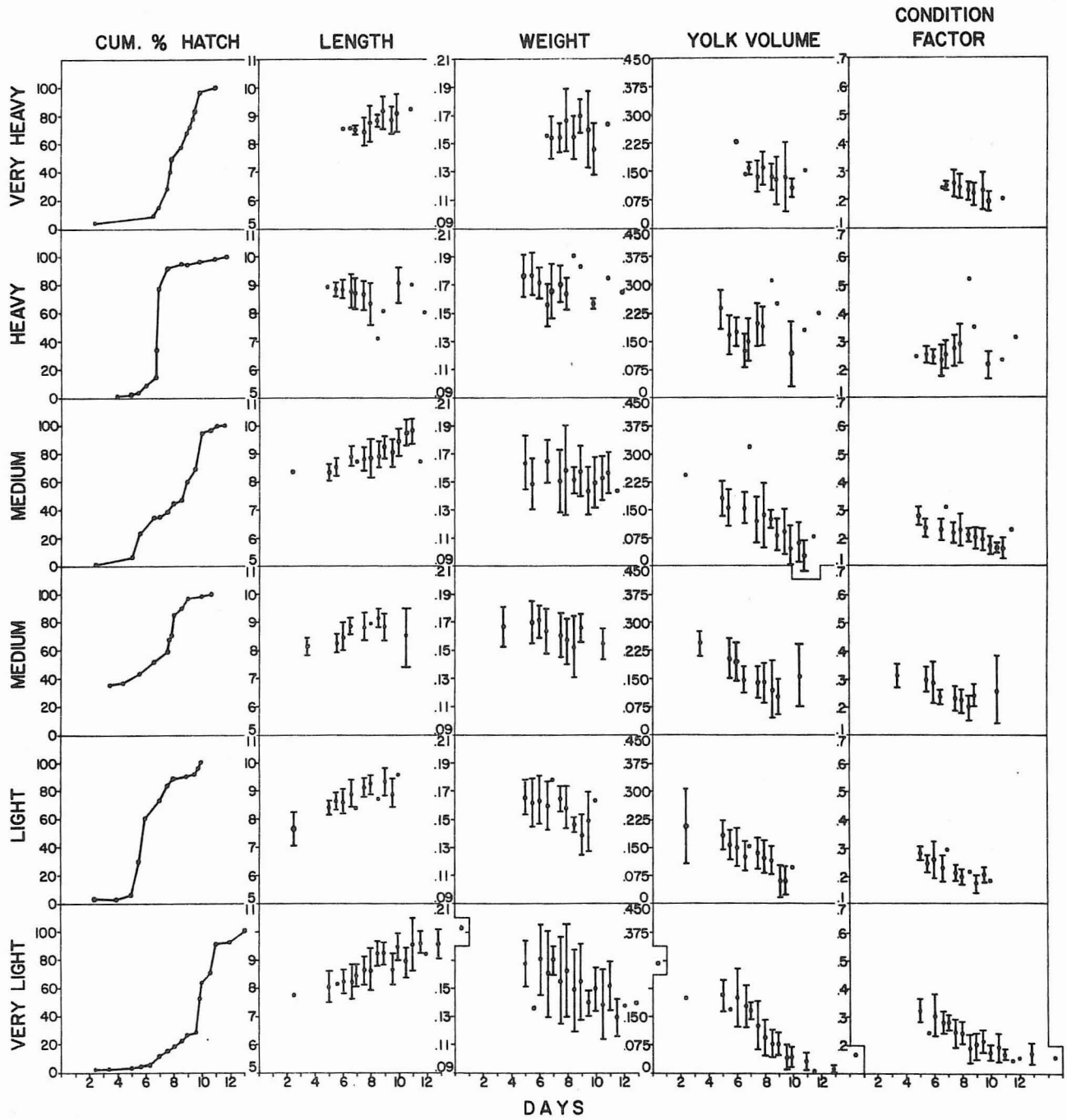


Fig. 2. Daily cumulative percent hatch and average length (mm), weight (mg), yolk volume (mm^3) and condition factor (all $\pm$ 1 standard deviation) for natural spawn of different intensities on Zostera.

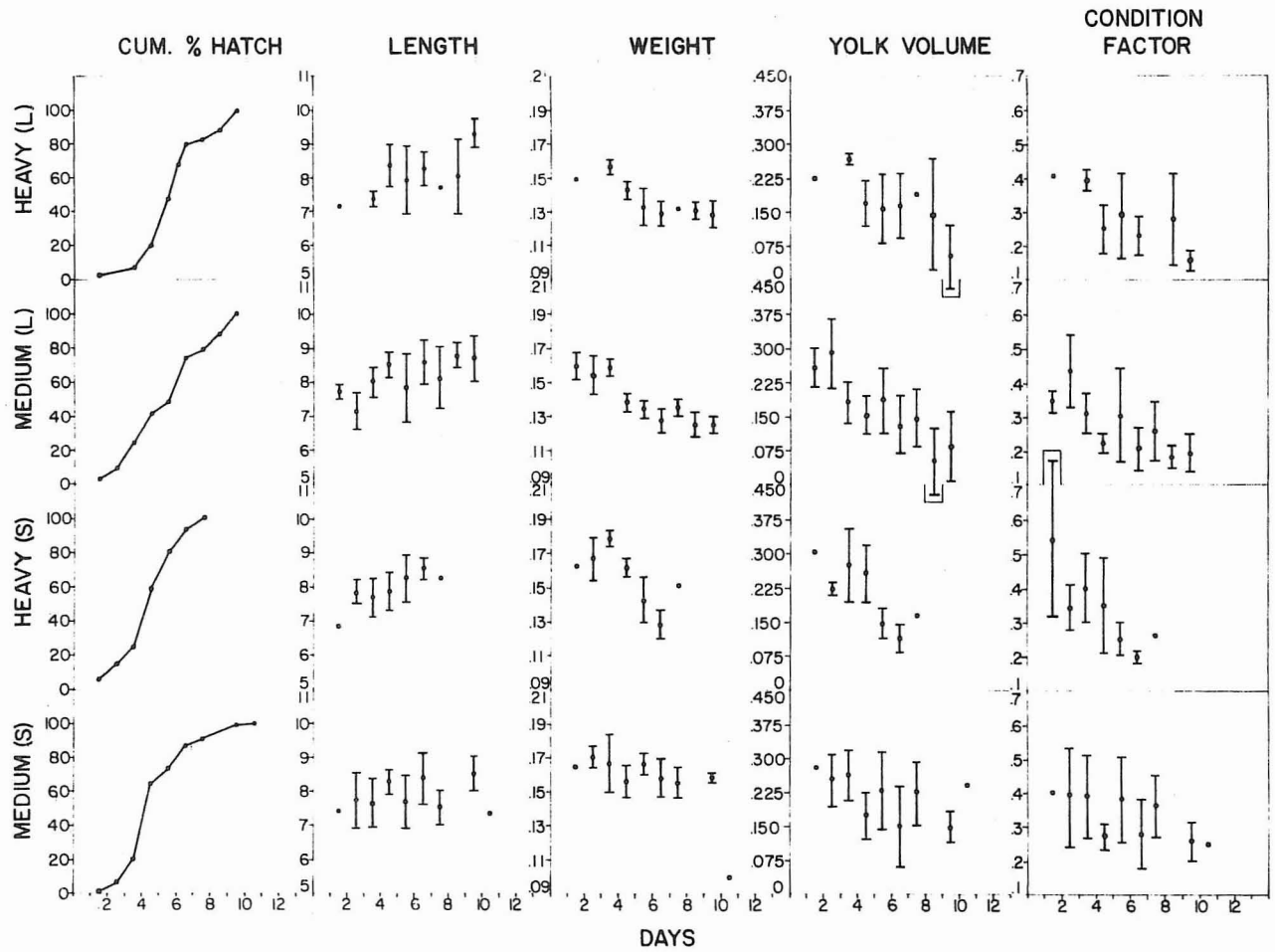


Fig. 3. Daily cumulative percent hatch and average length (mm), weight (mg), yolk volume (mm^3) and condition factor (all + 1 standard deviation) for artificial spawn from large (L) and small (S) herring of different intensities on Zostera.

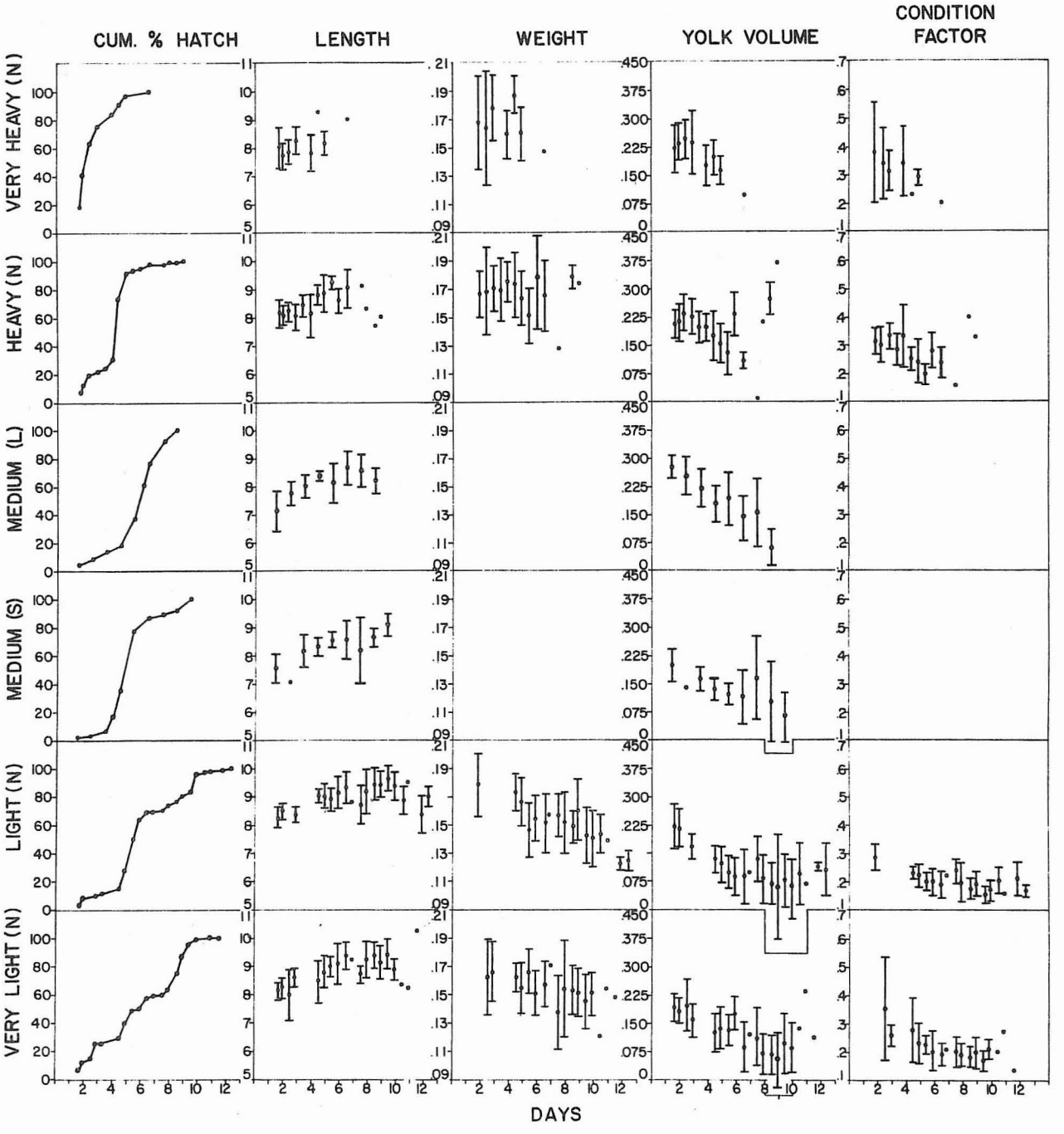


Fig. 4. Daily cumulative percent hatch and average length (mm), weight (mg), yolk volume (mm^3) and condition factor (all $\pm$ 1 standard deviation) for natural spawn of herring on the kelp Agarum (rows 1, 2, 5, and 6) and artificial spawn from large (L) and small (S) fish on another kelp Nereocystis (rows 3 and 4) at different intensities.