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Energetics of Pacific Herring (*Clupea harengus pallasi*) Embryos and Larvae Exposed to Low Conentrations of Benzene, a Monoaromatic Component of Crude Oil

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ABSTRACT

Interest in the energetic processes of critical early life stages of Pacific herring (*Clupea harengus pallasi*) and the potential effects from sublethal exposure to benzene, a monoaromatic component of crude oil, led to a series of experiments which examined metabolism of herring embryos, yolk-sac larvae, and post-yolk-sac larvae. Yolk caloric content was 6,020 cal/g or 1.3 calories per egg. This energy was consumed rapidly during incubation; total yolk absorption occurred 12 days after fertilization. Anabolic rates varied but at no time was there an energy deficit. Oxygen consumption of embryos increased prior to hatching, then a 10-fold rise was seen in newly hatched yolk-sac larvae. Exogenous calories were estimated from ingested rotifers and were less definable than endogenous energy due to variable grazing rates. Sublethal concentrations of benzene caused (a) significantly less embryonic tissue growth, (b) significantly different oxygen consumption in embryos, and (c) significantly greater assimilation in feeding larvae. It is believed activity of larvae played an important role in accounting for increased metabolism of later stages.

When fish eggs and larvae are viewed as open systems through which energy enters and exits (Von Bertalanffy 1950), they exhibit unique differences from older life stages. Eggs, embryos, and yolk-sac larvae rely solely on endogenous energy sources in their primary energy expenditures for growth and development. Later larval stages must obtain energy from exogenous food sources. Near yolk absorption, larvae must develop to the stage where they can successfully make the transition to exogenous energy utilization by locating, capturing, and metabolizing food (see "critical period," May 1974). Survival of these early life stages is often tenuous, and an understanding of the energetic processes and the environmental and inherent factors affecting them is ecologically important.

In addition to naturally occurring environmental stress on early stages, there are stresses resulting from man's alteration of the environment, such as pollution. Among the increasing hazards to fish eggs and larvae in this regard is the potential exposure to crude oil and petroleum products. Eggs and larvae of phylogenetically divergent species have exhibited lethal and sublethal responses when challenged with crude oil, oil dispersants, and oil/dispersant mixtures (Chipman and Galtsoff 1949; Mironov 1967, 1969; Kühnhold 1969, 1972, 1974; Wilson 1970; Lindén 1974, 1975, 1976). Our studies on effects of petroleum hydrocarbons on fishes have emphasized the critical early life stages and single oil components among the more toxic aromatic fractions of crude oil. In most experiments we tested the effects of benzene, a principal aromatic component of crude oil (Anderson et al. 1974) which is relatively water-soluble (Benville and Korn 1974), highly lipid-soluble, and is toxic to Pacific herring eggs and larvae in initial exposure concentrations from 5 to 50 μl/liter (Struhsaker et al. 1974).

Considerable research has been done on the energetics of fish larvae in relation to the "critical period" (Lasker 1962; Toetz 1966; Laurence 1969; Cooney 1973; May 1974). In addition, several researchers have defined the effects of varying physical-chemical conditions, primarily temperature and salinity, on various metabolic parameters and energy utilization (Holliday et al. 1964; Blaxter and Hempel 1966). Little work, however, has been done on the effects of oil pollutants on metabolism and energy utilization of early stages.

The research reported here had three objectives: (1) to outline the energetics of

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TABLE 1.—*Independent variables in benzene toxicity experiments with Pacific herring.*

Experiment	Developmental stage	Duration of experiment (after fertilization)		Exposure times	Mean initial benzene concentration (μl/liter)			Mean temperature (C)	Mean salinity (‰)
		Days	Hours		Control	Low	High		
1	Embryo	0–7	0–168	Initial exposure only	0	0.06	0.56	13.5	23.0
2	Yolk-sac larva	7–12	168–288	Initial exposure only	0	0.04	0.52	12.5	23.0
3	Post-yolk-sac larva	12–24	288–576	Initial exposure only	0	0.14	2.10	12.2	23.0

Pacific herring eggs and larvae; (2) to demonstrate effects, if any, of exposure to sublethal concentrations (approximating chronic levels) of benzene on various energetic parameters; and (3) to contrast the energy budgets of larvae in the above experimental conditions.

METHODS

Three individual experiments were conducted, each concerned with a different early life stage—embryo, yolk-sac larva and post-yolk-sac larva.

For experiments on embryos we needed to establish the exact time of fertilization, and to expose the embryos as soon as possible after fertilization. To do this, sexually mature Pacific herring were collected from San Francisco Bay in December 1974, and artificially spawned in the laboratory. Eggs were extruded by stripping, and distributed in single-egg rows on 10 × 25 cm clear glass plates. The plates were immersed in containers filled with a milt-seawater mixture for about 1 min. The plates were then rinsed in triple-Cuno[2] filtered (pore size 5 μ) seawater and placed in rectangular 8-liter test containers.

For experiments on larvae, test organisms were obtained from naturally spawned eggs collected within 24 h after spawning in San Francisco Bay. The eggs from two different spawns (December 1974 and January 1975) were used in the yolk-sac and post-yolk-sac larva experiments. Eggs were rinsed after being brought from the field and placed in the same 8-liter test containers for incubation. Larvae hatched after 168 h (7 days). Newly hatched larvae were used for the yolk-sac larval experiment (7.2–9.0 mm standard lengths). After the yolk was consumed and feeding established at 288 h (12 days) after fertilization, the post-yolk-sac larval (9.4–13.4 mm standard lengths) experiment was conducted with the remaining larvae.

In all cases water in the test containers was changed prior to benzene exposure. At the beginning of incubation, in all 3 experiments, an antibiotic treatment of 5 ppm erythromycin gluceptate was given to reduce excessive bacterial epifloral growth on the chorion. Other physical-chemical conditions in the test containers are presented in Table 1.

Post-yolk-sac larvae were fed the marine rotifer, *Brachionus plicatilis*. Rotifers were reared according to methods of Theilacker and McMaster (1971) except that *Nephroselmis* sp., a small green flagellate, was used for rotifer food. We estimated the feeding rate of the larvae by measuring the decline in rotifer concentrations (Coulter Counter, Model ZBI) in the test containers and adjusted them according to fluctuations in a control rotifer population held in a similar container without larvae.

All exposures to benzene were single doses under static conditions. Benzene was introduced in the form of precalculated amounts of benzene-saturated seawater. We attempted to expose the herring to two chronic concentrations of approximately 1.0 and 0.1 μl/liter, subsequently referred to as "high" and "low," respectively. Exposed larvae were contrasted to controls; that is, embryos or larvae held under similar conditions except for the absence of benzene. The actual amount of benzene in the water varied,

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

TABLE 2.—*Dependent variables in benzene toxicity experiments with Pacific herring.*

		Yolk volume, dry weight, growth and development		Oxygen consumption			Caloric content		
Experiment	Stage	Sampling frequency	Sample size individuals/ treatment	Ages when tested (hours after fertilization)	Duration of test (hours)	Number of replicates/ treatment	Sampling frequency	Number of individuals per sample	Number of samples/ treatment
1	Egg	Daily	5	48, 72, 96, 120, 144	24	5	Daily	20	3
2	Yolk-sac	Daily	5	168, 192, 216, 240	24	5	Daily	3	3
3	Post-yolk-sac	Daily	5	312, 360, 456	24	5	Daily	3	3

however, due mostly to its volatile nature. Concentrations were determined on a Tracor MT 220 gas chromatograph (GC); water samples were taken immediately after the benzene-water mixture was added. The mean initial concentrations are presented in Table 1 and were 0.04 to 0.14 (low) and 0.52 to 2.10 μl/liter (high). Measurements of benzene in our 8-liter test containers have shown that the benzene concentration declines exponentially to an average of 25 to 30% of the initial concentration (Struhsaker et al. 1974) by the end of 24 h and is below the detectable level of our method (0.01 μl/liter) after 48 h.

Dependent variables measured in these experiments are outlined in Table 2 along with the sampling frequencies, sample sizes, and replicates per treatment. Yolk volumes (V) were calculated by making length (L) and height (H) measurements of the ovoid yolk sacs with an ocular micrometer and using the ellipsoid volume formula, $V = (\pi LH^2)/6$. In the dry weight determinations, samples were rinsed in distilled water, dried 24 h at 66 C and weighed on a Cahn electrobalance to ±0.1 μg. Since the egg chorions comprise over 30% of the dry weight of Atlantic herring eggs (Blaxter and Hempel 1966) and our estimates for six samples of 25 Pacific herring eggs each amounted to 29%, we subtracted the

TABLE 3.—*Descriptive equations of yolk calories, tissue calories, and catabolic calories in Pacific herring embryos and yolk-sac larvae exposed to 0 (control), low, and high concentrations of benzene. Y is calories; X is days post-fertilization.*[a]

Stage	Benzene concentrations	Equation	Curve type	r
		Yolk Calories		
Embryo (days 1–7)	Control	$Y = 1.473\ e^{0.16263X}$	Exponential	0.96
	Low	$Y = 1.484\ e^{0.17273X}$	Exponential	0.96
	High	$Y = 1.506\ X^{0.61948X}$	Power	0.94
Yolk-sac larvae (days 7–12)	Control	$Y = 0.879 - 0.0642X$	Linear	0.97
	Low	$Y = 0.865 - 0.0652X$	Linear	0.97
	High	$Y = 0.954 - 0.0725X$	Linear	0.99
		Tissue Calories		
Embryo	Control	$Y = 0.742 + (-0.8095/X)$	Hyperbolic	0.98
	Low	$Y = -0.077 + 0.0865X$	Linear	0.94
	High	$Y = -0.118 + 0.1034X$	Linear	0.91
Yolk-sac larvae	Control	$Y = 1/(2.351 - 0.0350X)$	Hyperbolic	0.29
	Low	$Y = 0.0822 + 0.0420X$	Linear	0.88
	High	$Y = 0.1484 + 0.0350X$	Linear	0.93
		Catabolic Calories		
Embryo	Control	$Y = -0.0039 + 0.0137X$	Linear	0.51
	Low	$Y = 0.1150 - 0.0118X$	Linear	0.40
	High	$Y = 0.0801 - 0.00564X$	Linear	0.22
Yolk-sac larvae	Control	$Y = -0.2516 + (3.679/X)$	Hyperbolic	0.72
	Low	$Y = -0.4326 + (5.367/X)$	Hyperbolic	0.89
	High	$Y = -0.7706 + (9.512/X)$	Hyperbolic	0.79

[a] These best-fit equations are one day out of phase with the graphs of Figure 2. The equations were calculated for the end of each 24-h period, and the graphs were calculated for the beginning of each period.

chorion weights from the total egg weights throughout the study.

Oxygen consumption as a measure of catabolism was determined with a Gilson differential respirometer. Either 25 eggs or 10 larvae were placed in each 25-ml vial with 10 ml of fresh filtered seawater, 24 h after their exposure to benzene. Five replicate vials per treatment were run for 24 continuous h and consumption values averaged over that period. After each 24-h measurement a new experiment was begun as soon as the respirometer could be refilled with new test animals and fresh seawater.

Yolk, tissue, and rotifer caloric contents were determined my means of a Parr adiabatic microbomb calorimeter. Measurements of three replicate samples per treatment were made daily (Table 2).

Energy budgets of the embryo and yolk-sac larvae were computed by the dry weight method, explained in detail by Laurence (1969). The percent decrease in yolk volume was multiplied by the original yolk weight, and this value was multiplied by the caloric value per gram dry weight of original yolk to obtain the caloric value per unit weight of yolk. Tissue weight was calculated by subtraction of yolk weight from the daily total weight of the embryo (or larva) and yolk complex. Then, the product of tissue weight and tissue caloric value per unit weight (i.e., 6,034 cal/g) yielded calories involved in anabolism.

Constructing an energy budget for feeding larvae involved determining the amount of rotifers consumed, estimating the calories ingested, and comparing this value with the tissue growth (in weight). Catabolism was estimated through the difference in tissue formed minus food ingested.

Data were analyzed by analysis of covariance, using the University of California Biomedical programs, BMD 1R (Dixon 1971) and methods of Snedecor and Cochran (1968).

RESULTS

Energy Utilization in Unexposed, Control Embryos and Larvae

Energy utilization of embryos and larvae reared under experimental conditions, with no exposure to benzene are described here. The average herring egg weighed 216 μg and contained 1.3 calories, prior to fertilization. The caloric content per unit of dry weight averaged 6,020 cal/g. For comparison, Lasker (1962) found an average of 5,386 cal/g in unfertilized sardine eggs, and Paffenhöfer and Rosenthal (1968) estimated 6,585 cal/g in Atlantic herring (yolk only).

TABLE 4.—*Calories consumed in food and tissue calories of feeding Pacific herring.*

Age (Days)	Food energy (cal) per larva			Larval tissue energy (cal) per larva		
	Control	Low concentration	High concentration	Control	Low concentration	High concentration
12–14	0.73	1.38	1.53	0.71	0.79	0.77
14–16	0.49	1.01	1.23	0.66	0.75	0.75
16–18	2.67	1.39	1.67	0.88	0.80	0.85
18–20	0.50	0.61	0.56	1.04	1.65	0.78
20–22	1.78	0.45	1.45	1.11	1.60	1.08
Totals	6.17	4.84	6.44	4.40	5.59	4.23

During incubation the energy available to developing embryos (yolk weight and yolk calories) declined exponentially to about 30% of the original amount (Figs. 1A, 2; Table 3). After hatching, 7 days (168 h) after fertilization, larvae continued yolk consumption linearly to completion of yolk absorption on day 12 (Figs. 1A, 2; Table 3).

Anabolic energy in terms of embryo tissue weight (tissue calories followed a similar trend) increased hyperbolically to day 5, then decreased just prior to hatching (Fig. 1B, Table 3). From day 6 to hatching on day 7, weight again increased. After hatching, larval tissue weight declined until day 9, then gradually increased linearly until feeding on day 12 (Fig. 1B, Table 3). After initiation of feeding, tissue weight increased more rapidly (Fig. 1B, Table 4).

Catabolic energy (difference between yolk or food calories used and tissue calories formed) was highly variable. Catabolic calories in embryos were low until day 2, then increased on day 3 to almost 0.2 calories (Fig. 2). They then varied daily with no significant discernible pattern through hatching until energy in the yolk was essentially depleted on day 12. No energy deficit (catabolic calories exceeding anabolic calories) occurred through the period of en-

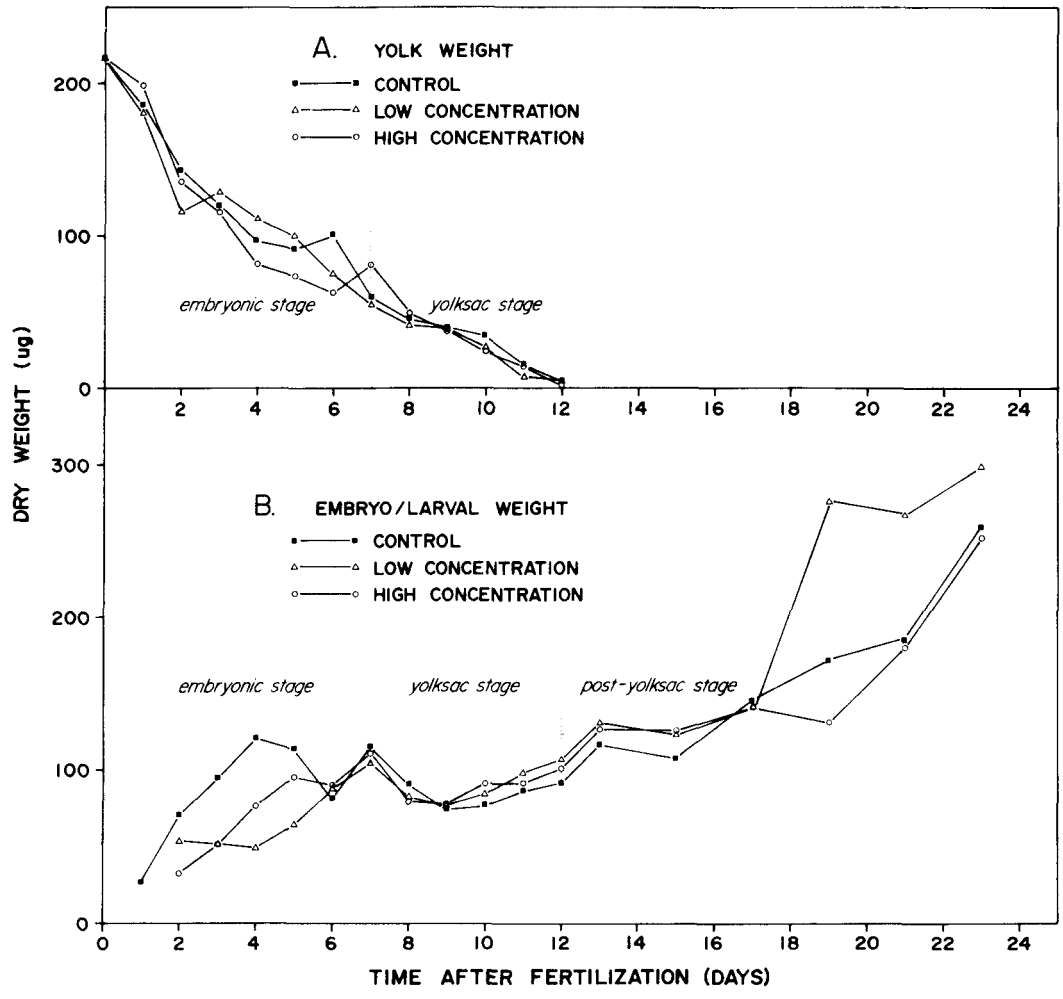

FIGURE 1.—*Dry weights (μg) of yolk (A) and embryonic and larval tissues (B) from Pacific herring exposed to high, low, and zero (control) benzene concentrations.*

dogenous energy utilization in control embryos and larvae.

Embryonic metabolic rates estimated from measurement of oxygen consumption showed a rapid prehatch increase on day 6, then declined (Fig. 3). After hatching on day 7, larval metabolism increased rapidly by approximately tenfold. Another decline occurred on day 10 prior to feeding; then consumption gradually increased through yolk absorption on day 12 into feeding (day 12 to end of experiment on day 21).

Feeding began on day 12 (288 h). Trends in calories of food energy consumed were less definable than those of endogenous yolk energy consumed, primarily due to the highly variable grazing rate of larvae (Table 4). The larvae were provided rotifers at an initial concentration of 14–20 rotifers/ml, a density found adequate for *Engraulis mordax* larvae (Theilacker and McMaster 1971). The caloric value of the rotifers was established by bomb calorimetry to be 11.6×10^{-4} cal/rotifer; an average of three samples (mean dry weight = 0.905 μg). This value was slightly higher than that of Theilacker and McMaster's (1971) value of 8.0×10^{-4} cal/rotifer, the difference possibly due to the greater weights of our egg-bearing adult rotifers. The herring larvae grazed nearly all the rotifers within 24 h. When we increased the density to over 20 rotifers/ml

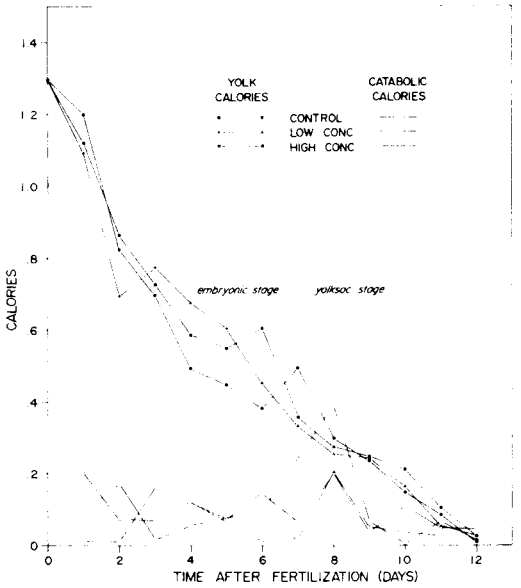

FIGURE 2.—*Catabolic and yolk calories of Pacific herring embryos and yolk-sac larvae exposed to high, low, and zero (control) benzene concentrations.*

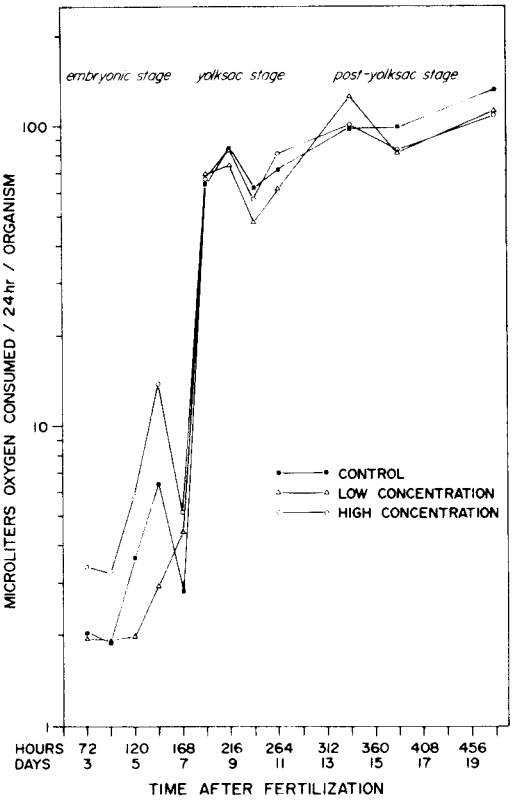

FIGURE 3.—*Oxygen consumption of Pacific herring embryos, yolk-sac larvae and post-yolk-sac larvae exposed to high, low and zero (control) benzene concentrations.*

on day 16, they still ate all that was available up to a maximum of 45 rotifers/ml in one container. This indicates that the satiation level may never have been reached during the experimental period. The estimates of energy intake were calculated directly from numbers consumed per larva per unit time. These estimates, however, may be biased because no corrections for assimilation and digestive efficiency were included.

Feeding larvae grew steadily and appeared to increase their assimilation rates near the end of the experiment (Fig. 1B, Table 4). Metabolic rates also were increasing (Fig. 3) as indicated by respiration, a result of, among other things, increased size and activity.

Effects of Benzene on Energy Utilization in Embryos and Larvae

The effects of exposure to benzene on energy utilization were determined by contrasting exposed with control embryos and larvae. Relatively low sublethal concentrations of benzene were chosen in an attempt to approximate field concentrations and to test for limiting or controlling effects on energy utilization in sensitive stages of embryos and larvae. No mortality occurred over the experimental period. However, some significant effects were found on embryonic and post-yolk-sac larval growth and oxygen consumption.

During incubation, days 1 to 7, it appeared that embryos exposed to the higher concentration of benzene consumed yolk (weight and calories) more rapidly than controls (Fig. 1A, 2; Table 3). The difference, however, was not significant when tested. No significant differences in yolk consumption occurred between exposed and control yolk-sac larvae.

Anabolism in embryos exposed to both low and high concentrations increased linearly from days 1 to 6 (Fig. 1B, Table 3). However, tissue weights of exposed embryos were significantly less than in controls. Both high and low concentrations caused significantly delayed growth (Table

TABLE 5.—*Analysis of covariance comparing tissue dry weights of Pacific herring embryos and post-yolk-sac larvae exposed to 0, 1.0, and 0.1 μl/liter benzene.*

Stage	Treatment	df	Σx^2	Σxy	Σy^2	Deviation from regression: df	Deviation from regression: Sums of squares	Deviation from regression: Mean square
Embryo	Control	7	0.420	61.975	13,608.709	6	4,463.707	743.951
	Low concentration	7	0.420	60.250	9,705.680	6	1,062.674	177.112
	High concentration	7	0.420	71.965	12,966.329	6	635.469	105.911
						18	6,161.850	342.325
	Pooled, W	21	1.260	194.190	12,966.329	20	6,352.340	317.617
	Difference between slopes					2	190.490	95.245
	Between, B	2	0.000	0.000	3,048.468			
	W & B	23	1.260	194.190	39,329.185	22	9,400.807	427.309
	Between adjusted means					2	3,048.467	1,524.234
	Comparison of slopes:	$F = 95.245/342.325 = 0.278(df = 2,18)$; $P > 0.05$						
	Comparison of elevations:	$F = 1,524.234/317.617 = 4.780(df = 2,20)$; $P \leq 0.05$						
Post-yolk-sac	Control	5	0.700	95.820	15,026.000	4	1,909.611	477.403
	Low concentration	5	0.700	140.710	33,951.495	4	5,666.770	1,416.694
	High concentration	5	0.700	78.240	12,459.973	4	3,714.977	928.744
						12	11,291.358	940.947
	Pooled, W	15	2.100	314.770	61,437.468	14	14,256.443	1,018.317
	Difference between slopes					2	2,965.085	1,482.543
	Between, B	2	0.000	0.000	7,905.788			
	W & B	17	2.100	314.770	69,343.256	16	22,162.231	1,385.139
	Between adjusted means					2	7,905.788	3,952.894
	Comparison of slopes:	$F = 1,482.543/940.947 = 1.576(df = 2,12)$; $P \geq 0.05$						
	Comparison of elevations:	$F = 3,952.894/1,018.317 = 3.882(df = 2,14)$; $P \leq 0.05$						

5). By hatching, 7 days after the initial exposure, the anabolic differences between exposed and control embryos were insignificant. As in yolk consumption, there were no significant differences in tissue weight and growth between exposed and control yolk-sac larvae. The effects of benzene exposure (at these concentrations) would appear to be minimal at this stage after hatching.

Feeding post-yolk-sac larvae were exposed to benzene on day 13. Until day 17 exposed larvae ingested more food than unexposed larvae (Table 4). Corresponding tissue weights of exposed larvae were heavier during that period but not significantly different. However, after day 18, larvae exposed to low benzene concentration demonstrated much higher growth and assimilation which proved to be significant (Fig. 1B, Table 5).

Catabolic calories were as variable in exposed embryos and larvae as in controls (Fig. 2). No significant differences between exposed and control embryos and yolk-sac larvae occurred except on day 8, when yolk-sac larvae exposed to the higher concentration showed higher catabolism, at that time exceeding anabolism, and an energy deficit.

Embryos exposed to benzene also showed significant differences in oxygen consumption from day 1 to hatching (Fig. 3; Table 6). High benzene concentration caused greater oxygen consumption while low concentration caused depressed consumption relative to controls. Differences at later larval stages were not significant, except toward the end of the experiment when control post-yolk-sac larvae appeared to respire more rapidly than exposed larvae.

DISCUSSION

The amount of endogenous energy available to Pacific herring embryos and larvae differed considerably from their Atlantic counterparts. Paffenhöfer and Rosenthal (1968) found the smaller Atlantic herring

TABLE 6.—*Analysis of covariance comparing oxygen consumption of Pacific herring embryos (days 1–7).*

Treatment	df	Σx^2	Σxy	Σy^2	Deviation from regression: df	Deviation from regression: Sums of squares	Deviation from regression: Mean square
Control	20	3.412	3.856	152.536	19	148.178	7.799
Low concentration	24	4.262	9.281	49.018	23	28.810	1.253
High concentration	24	4.262	15.849	620.106	23	561.173	24.399
					65	738.161	11.356
Pooled, W	68	11.937	28.986	821.659	67	751.273	11.213
Difference between slopes					2	13.112	6.556
Between, B	2	0.009	−0.980	180.98			
W & B	70	11.946	28.006	1,002.639	69	936.982	
Between adjusted means					2	185.709	92.855
Comparison of slopes:	F = 6.556/11.356 = 0.577(df = 2,65); $P > 0.05$						
Comparison of elevations:	F = 92.855/11.213 = 8.281(df = 2,67); $P < 0.01$						

(216 vs. 170 μg) to contain 0.748 calories vs. 1.298 calories for Pacific herring. The magnitude of the difference may change since egg size was found to vary by a factor of 1.5 within the same female (Blaxter and Hempel 1963). The amount contained in other marine species indicates a very wide range of values with Pacific herring tending towards the upper end of the range. Cooney's (1973) study of three tropical Hawaiian species showed *Caranx mate* to have 1.131, *Etrumeus micropus* 1.007, and *Abudefduf abdominalis* 0.344 cal/egg. Lasker (1962) found the clupeid *Sardinops caerulea* to have only 0.300 cal/egg. Freshwater fishes also show wide variability. *Lepomis macrochirus* had 0.924, according to Toetz (1966), while *Micropterus salmoides* had 2.284 cal/egg (Laurence 1969).

Developing embryos consumed yolk in a linear fashion, and despite the greater metabolic rate demonstrated by the prehatch rise in oxygen consumption no energy deficit was seen. The prehatch rise in oxygen consumption has been observed in Atlantic herring (Holliday et al. 1964) and is mostly attributable to embryonic activity associated with hatching.

The order of magnitude increase in yolk-sac larval metabolism over embryonic metabolism (Fig. 3) is best explained by increased activity since the respiring biomass of the about-to-hatch embryos and the newly hatched larvae are not so dissimilar as to account for the difference in oxygen consumption. The metabolism measured by the Gilson differential respirometer was "routine" metabolism, defined by Fry (1971) to be the rate influenced by random activity under experimental conditions. The restrictive confines of the 25 ml respiratory flasks appear to have increased larval activity. Holliday et al. (1964) and Lasker (1962) demonstrated that activity was the most influential factor affecting oxygen uptake in both embryos and larvae. Active Q_{O_2}s exceeded resting values by as much as 5 to 10 times.

Significant effects of benzene on herring eggs and larvae were confined to anabolism and oxygen consumption. The suppressed embryonic growth, increased growth of post-yolk-sac larvae, and divergent oxygen consumption rates reflected alterations in the metabolic rate, yolk energy being diverted from assimilation to detoxification of benzene and/or its metabolites. Both increased and decreased metabolic rates were seen in juvenile chinook salmon and striped bass exposed to benzene (Brocksen and Bailey 1973). Other oil compounds also have affected embryonic metabolism. Lindén (1974, 1976) found oil dispersants and dispersant and oil mixtures slowed heartbeat rates in Baltic herring (*Clupea harengus*), indicating reduced metabolism.

By increasing growth in feeding larvae low benzene concentration appears to have a beneficial effect. We have also seen cases where low concentrations of both benzene and xylene caused higher hatching percentages in herring. This phenomenon has been

TABLE 7.—*Percent yolk utilization efficiency of ten species of fish.*

Species	% efficiency	State of development	Reference
Micropterus salmoides	35.2	To hatching	Laurence (1969)
Salmo salar	41.0	To hatching	Hollett and Hayes (1946)
Clupea harengus	67.8	To hatching	Paffenhöfer and Rosenthal (1968)
Clupea harengus	50.0 to 74.0	To hatching	Blaxter and Hempel (1966)
Clupea pallasi	74.4	To hatching	Eldridge et al. (this study)
Clupea pallasi	43.9	To yolk absorption	Eldridge et al. (this study)
Micropterus salmoides	44.4	To yolk absorption	Laurence (1969)
Salmo fario	56.0	To yolk absorption	Gray (1928)
Etrumeus micropus	57.9	To yolk absorption	Cooney (1973)
Salmo gairdneri	60.2	To yolk absorption	Smith (1957)
Caranx mate	75.1	To yolk absorption	Cooney (1973)
Abudefduf abdominalis	75.3	To yolk absorption	Cooney (1973)
Sardinops caerulea	77.0 to 79.0	To yolk absorption	Lasker (1962)

noted in many toxicological experiments wherein animals receiving small doses appeared healthier than controls. Smyth (1967) proposed an explanation in the form of "sufficient challenge." Small chronic doses of a toxicant exercise adaptive physiological functions which serve in healthy organisms to maintain homeostasis. In some instances this adaptive response can be measured in a positive mode, resulting in an apparent benefit to the test organism.

Yolk utilization efficiencies of controls declined when incubation period is compared to the entire yolk-sac period (Table 7). This agrees with dry weight and metabolic measurements in that larval activity and its high metabolic demand resulted in conversion efficiencies lower than in embryos. This pattern also coincides with Blaxter and Hempel's (1966) Atlantic herring observations. In comparison to developmental efficiencies in other fishes, our results tend toward the high end during incubation and the low end through yolk absorption (Table 7). At least during incubation unexposed Pacific herring were slightly more efficient than Atlantic herring.

If one considers the early life forms as "the expression of a pattern of processes of an ordered system of forces" (Von Bertalanffy 1950), it is necessary to understand the factors controlling, directing, masking, and otherwise affecting these dynamic systems. Hjort (1926) has hypothesized that year-class strength is largely determined by mortality in the early developmental stages. It therefore follows that any potential pollutant which can be shown to affect this dynamic system has implications for the organism's survival and ultimately its population. We have found that benzene in low concentrations can modify the metabolic processes of Pacific herring embryos and larvae. It remains to be determined whether the extent of the effect is sufficient to disrupt fatally the internal "ordered system."

LITERATURE CITED

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