Effects of Salinity and Temperature on Embryonic Development of the Petrale Sole (*Eopsetta jordani*)

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Newly fertilized eggs were incubated at 13 combinations of levels of salinity and temperature between 20 and 35‰, and 4.1 and 8.5 C. Average egg density throughout development was 1.0252, and the incubation period ranged from 6.2 to 13.5 days. Larval length at mean hatching time averaged 2.84 mm for all trials. External features of the larvae are described. The percentages of eggs hatching (total hatch) and producing viable larvae (viable hatch) are examined with respect to salinities and temperatures of incubation. Calculated optima were: total hatch 29.47‰ S, 6.65 C; viable hatch 27.93‰ S, 7.00 C. At 6.3, 7.2, and 8.1 C, larvae grew to 5.5–5.7 mm total length prior to exhaustion of yolk 246–393 hr after hatching. It was concluded that greatest numbers of viable larvae of largest size at yolk exhaustion would occur from incubation at 27.5–29.5‰ S and 6–7 C.

Laboratory results are related to available hydrographic and meteorological data for a spawning area off the west coast of Vancouver Island. Estimates are given of direction, depth, and duration of drift of the pelagic stages until exhaustion of the yolk. Environmental variability in the spawning period is related to existing measures of year-class strength. Effect of temperature on egg development is related to the range of the species in terms of estimated temperatures available at spawning depths.

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THE petrale sole, or brill (*Eopsetta jordani*), is a relatively large member of the family Pleuronectidae, closely related to the genus *Hippoglossoides*. Its range is reported to extend from Kodiak Island (58°N, 152°W) in Alaskan waters to the Coronado Islands (32°26′N, 117°16′W) off Baja California (Roedel 1953; Hitz and Rathjen 1965; Alverson MS 1967). One other member of the genus (*Eopsetta grigorjewi*) occurs in the western Pacific between northern Japan and Formosa (Norman 1934 p. 309).

The petrale sole is a highly valued flatfish to the Canadian and United States trawl fishery, and fishing grounds extend from northern British Columbia to southern California (Alverson and Chatwin 1957; Ketchen and Forrester 1966). Tagging studies and catch statistics (Alverson and Chatwin 1957; Alverson MS 1967) indicate that the species may migrate considerable distances while exhibiting marked seasonal changes in bathymetric distribution. A small proportion of petrale sole tagged in California waters subsequently has been recovered in British Columbia waters (Best 1963) and vice versa (Forrester and Holmberg MS 1967). Spawning takes place in relatively deep water (311–457 m) during the period of December to April. Postspawning migration occurs into shallower water (57–128 m).

Off the British Columbia and Washington State coasts, variations in abundance of the species appear to be correlated with variations in the environment at the time of incubation and development of the pelagic egg and larval stages (Ketchen and Forrester 1966). Examination of some of the factors that might affect abundance was the object of laboratory experiments initiated earlier (Forrester and Alderdice MS 1967). These first studies showed the eggs to be extremely fragile and susceptible to mechanical damage in early embryonic stages. Subsequently, improvements were made in experimental design and incubation procedures. These modifications were incorporated into the present study on the effects of salinity and temperature on aspects of development of the egg and early larvae.

Materials and Methods

Live petrale sole were captured by trawlnet from the *G. B. Reed* on February 28, 1968, at a depth of 300–308 m (Levings MS 1968) near the Estevan Deep spawning ground (Ketchen and Forrester 1966, their fig. 2) off

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the west coast of Vancouver Island. Characteristics of a water sample taken at the location (48°48 N, 126°31.5′W) and depth of capture were: salinity, 33.20‰; temperature, 4.0 C; dissolved oxygen, 0.93 ppm. The adult fish were transported in live tanks to Port Alberni, B.C., about 8 hr steaming from the point of capture. There, eggs were stripped, fertilized in water of 33.2‰ S collected at the point of capture, and transported to Nanaimo, B.C., in a refrigerated container held at about 7.5 C. The eggs, fertilized at 0030 hr February 29, were placed in constant salinity–temperature incubators in the laboratory 2 hr after fertilization.

Live fertilized eggs were buoyant in the water of fertilization and formed a layer at the top of the transportation containers. Salinity of neutral buoyancy of eggs 3½ hr after fertilization was 30.39‰.[1] The mean diameter of the eggs 12½ hr after fertilization was 1.24 mm (range 1.21–1.25 mm). Eggs were dispensed into incubators volumetrically (about 0.5 cc/subsample) and held at predetermined salinity–temperature levels. Each incubator (Alderdice and Velsen 1968) held four subsamples of eggs. The mean number of eggs per subsample was 393 (range 323–741). A 13-point design defined the test conditions (Table 1). Each trial of the design was assigned by a random process to an incubator in an array of environmental control tanks. Incubation conditions were held constant in each trial until completion of hatching.

Salinities employed ranged from 20 to 35‰ in the various trials. Water was prepared by making natural sea water (27–29‰ S) up to 40‰ S with synthetic sea salt[2] followed by dilution with fresh water to required salinities. Test waters were renewed every 4 days. On the basis of earlier results (Forrester and Alderdice MS 1967) incubation temperatures were restricted to a range of 4–8.5 C. In the 1967 experiments temperatures above 8.5 C resulted in early death of the eggs and no hatching occurred at temperatures of 4.3 C and below.

Perfusion velocities through the incubating eggs were held at about 500 cm/hr. This "apparent" velocity was considered sufficient to avoid both mechanical damage to the eggs, and dependence of rate of development on rate of delivery of oxygen to the eggs (see Alderdice and Forrester 1968 p. 512). As an added precaution against mechanical damage occurring to eggs in early stages of development, individual incubators were not opened until sufficient time had elapsed to permit development of eggs to the stage of blastopore closure. These tactics were assisted by monitoring samples of eggs held in supplementary containers in the incubation tanks.

Exposure of eggs to the various salinity–temperature test conditions was considered primarily in terms of the following responses: (1) rate of development (%/day $= \frac{100}{t}$), where t = days from fertilization to 50%

[1]The density of these newly fertilized eggs may be compared with earlier measurements (Forrester and Alderdice MS 1967):

	Hr after fertilization	Salinity of neutral buoyancy (‰)	Temp (C)	Density
1968	3.5	30.59	3.5	1.0242
1967	~3	32.35	3.5	1.0258
1967	3.0	31.56	4.0	1.0251

[2]Rila Marine Mix, Rila Products, Teaneck, New Jersey.

TABLE 1. Salinities and temperatures of incubation media.

Trial	Factor S (‰)	Factor Temp (C)	Dates of tests 1968	Test conditions S (‰)	Test conditions Temp (C)
1	21.33	4.5	29/2–14/3	21.33±0.01[a]	4.51±0.01[a]
2	21.33	8.1	29/2–7/3	21.31±0.01	8.14±0.02
3	33.67	4.5	29/2–13/3	33.70±0.01	4.51±0.01
4	33.67	8.1	29/2–7/3	33.70±0.01	8.10±0.02
5	27.50	6.3	29/2–10/3	27.52±0.02	6.30±0.01
6	27.50	6.3	29/2–10/3	27.52±0.02	6.30±0.01
7	20.00	6.3	29/2–9/3	20.03±0.01	6.34±0.02
8	35.00	6.3	29/2–9/3	35.00±0.03	6.31±0.00
9	27.50	4.1	29/2–15/3	27.50±0.01	4.11±0.01
10	27.50	8.5	29/2–7/3	21.31±0.04	8.52±0.01
11	24.41	5.4	29/2–11/3	24.41±0.02	5.40±0.00
12	24.41	7.2	29/2–8/3	24.43±0.01	7.22±0.01
13	30.59	5.4	29/2–12/3	30.59±0.02	5.41±0.01
14	30.59	7.2	29/2–7/3	30.59±0.01	7.21±0.01

[a]Mean ± 1 SE.

hatch of viable larvae; (2) mean total length of larvae at hatching, mm; (3) percent total hatch (A + B)/(A + B + C) × 100, where A = normal larvae, B = abnormal larvae, C = dead eggs or embryos that died prior to hatching; (4) percent viable hatch, A/(A + B + C) × 100.

The number of larvae hatching in consecutive observation periods provided distributions of hatching frequency for each trial. Many of these were positively skewed and all were normalized by applying a square root transformation to the observation times at which newly hatched larvae were counted. The distributions provided estimates of mean hatching time and of the incubation period — the interval between fertilization and the mean hatching time of normal larvae.

A meaningful measure of larval size is assumed to be that obtained at the mean hatching time, as the estimate applies to the greater proportion of larvae obtained for a particular incubation trial. When hatching occurs over a prolonged period, size at mean hatching time may need to be interpolated from means of samples taken over a series of observation periods (Alderdice and Forrester 1971). However, the hatching rate of petrale sole eggs was rapid, about 90% of the eggs in an incubator hatching on the average within a 16-hr period. As the larvae measured hatched on the average within $\pm 3\frac{3}{4}$ hr of the subsequently calculated mean hatching time, the estimates obtained are considered representative of larval size at mean hatching time.

Viable or normal larvae were considered to be those without pronounced curvature of the body, the most frequent type of anomaly encountered. Counts of abnormal larvae also included a number of very small larvae. These appeared either to have hatched prematurely or to have been liberated through death of the egg and disintegration of the capsule at advanced stages of development.

Further descriptions of the effects of salinity and temperature on hatching efficiency (percent total hatch and viable hatch) were carried out by response surface analysis (Lindsey et al. 1970; Lindsey and Sandnes MS 1970) using as a model a nonlinear polynomial including terms up to second degree. Hence

$$Y^{\gamma} = \beta_o x_o + \beta_1 x_1^{\alpha_1} + \beta_2 x_2^{\alpha_2} + \beta_{11} x_1^{2\alpha_1} + \beta_{22} x_2^{2\alpha_2} + \beta_{12} x_1^{\alpha_1} x_2^{\alpha_2}$$

where Y = percent response (total hatch, viable hatch); x_1 = salinity,‰; x_2 = temperature, C; α_1, α_2, γ = power parameters, obtained by maximum likelihood estimation (Lindsey et al. 1970).

For each response the relative likelihood is given of the corresponding linear model (with $\alpha_1 = \alpha_2 = \gamma = 1$) adequately representing the data, as opposed to the nonlinear model (see Tables 5, 6; transform component where power parameters are not unity).

Analysis of variance associated with each response is given on the basis of the nonlinear model. Variance is partitioned into components associated with treatment effects (14 trials) and an error. The treatment component is partitioned into components associated with regression on the $x_1^{\alpha_1}$, ..., $x_1^{2\alpha_1}$, ... $x_1^{\alpha_1} x_2^{\alpha_2}$ terms, and a component not explained by regression on these terms (lack of fit). Exact inferences regarding the effects of the listed components are provided in terms of the relative likelihoods of the various β coefficients being zero, and of the power parameters (transform) being unity (see Lindsey et al. 1970). Finally, for each response the fitted equation is plotted as a regression surface to show isopleths of response within the salinity–temperature factor space.

Samples of larvae from some of the incubation trials were held in containers in their appropriate incubation tanks. Posthatching growth was followed until absorption of the yolk and death of the larvae.

Results

Rate of Development

The length of the incubation period (Table 2) ranged from 6.2 days (trial 10) to 13.5 days (trial 9). Slight curvature is shown in the relation between rate of development and temperatures from 4 to 8.5 C (Fig. 1). The trend line in the figure is described by the relation

$$Y = 0.9364 + 1.3050x + 0.0535x^2$$

where Y = rate of development, %/day; x = temperature, C.

The effect of salinity on length of the incubation period at the five test temperatures (Fig. 2) is not entirely consistent. The differences between mean hatching times for various salinities at each tem-

TABLE 2. Rates of development of petrale sole eggs incubated under each of the 14 salinity–temperature test conditions.

Trial	Incubation period (*hr*)	Rate of development (*%/day*)
1	307.41	7.81
2	167.46	14.33
3	303.26	7.91
4	159.51	15.05
5	215.69	11.13
6	221.43	10.84
7	204.96	11.71
8	205.48	11.68
9	324.51	7.40
10	148.78	16.13
11	252.92	9.49
12	182.40	13.16
13	260.48	9.21
14	174.78	13.73

perature appear to be real, although small in magnitude. In general, higher salinities are associated with shorter incubation periods. Variations in salinity obviously are of less influence on rate of development than changes in temperature.

Size of Larvae

Total length of larvae sampled at the mean hatching time (Table 3) averaged 2.84 mm for all trials and ranged from 1.95 to 3.17 mm between trials. Largest larvae were obtained in the trial at 24.41‰ S and 7.2 C (trial 12). Estimates were also obtained of the amount of yolk available to newly hatched larvae at the mean hatching time. Measurements were made of the antero-posterior length of yolk remaining in the yolk sac (Table 3). There is a direct relation between larval length, available yolk, and temperatures from 4 to 8.5 C (Fig. 3). Largest larvae and yolk stores occur at the higher temperatures. The effect of salinity on larval size and yolk size is less well defined, although in general larval size and available yolk are both greater at the higher salinities (Fig. 3).

The data on larval size (Table 3) were subjected to preliminary response surface analysis. The relation between salinity and temperature levels and larval size at mean hatching time was poorly defined. However, the analysis supported general conclusions reached from inspection of the data — that larval size tended to be greatest at higher temperatures (7.2–8.1 C) and at intermediate to high salinities (24.4–33.7‰). There is a suggested low/low–high/high interaction between salinity and temperature with respect to larval size, largest larvae at mean hatching time being obtained at combinations of higher salinities and higher temperatures. Maximum larval size appears to occur near the upper temperature boundary of the factor space examined (8.1–8.5 C). Improved definition of larval size as a function of salinity and temperature would then require adjustment of the factor space to include further trials at higher temperatures.

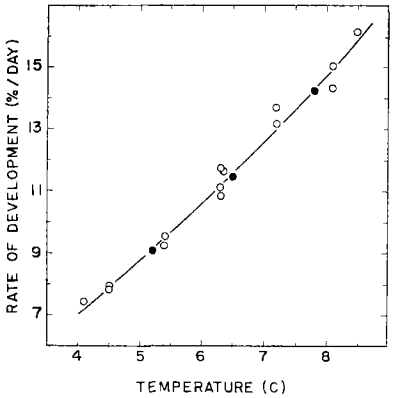


Fig. 1. Influence of temperature on rate of development from fertilization to time to 50% hatch for petrale sole eggs. Open circles, current data (Table 2); solid circles, data from Forrester and Alderdice (MS 1967); trend line, see text.

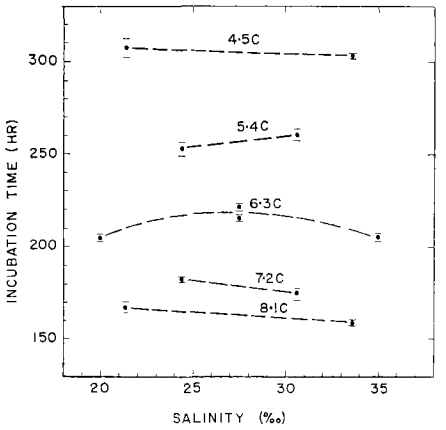


Fig. 2. Influence of salinity on time to 50% hatch of petrale sole eggs. Mean hatching time (hr) ± 2 standard deviations is shown for each trial.

Hatching Efficiency

For the particular incubation conditions examined (Table 4), total hatch was highest at 27.50‰ S and 6.3 C (trials 5, 6). Viable hatch was highest

Table 3. Mean larval length and available yolk (measured antero-posteriorly) at the mean hatching time for the 14 salinity–temperature incubation conditions.

Trial	Mean length (*mm*)	Available yolk (*mm*)	No. measurements
1	2.66	1.00	25
2	1.95	1.17	6
3	2.68	1.13	4
4	3.08	1.41	50
5	2.92	1.26	73
6	2.62	1.18	68
7	2.51	1.03	18
8	2.80	1.28	47
9	2.51	1.17	11
10	3.07	1.39	60
11	2.79	1.18	52
12	3.17	1.35	36
13	2.72	1.19	39
14	2.82	1.23	48

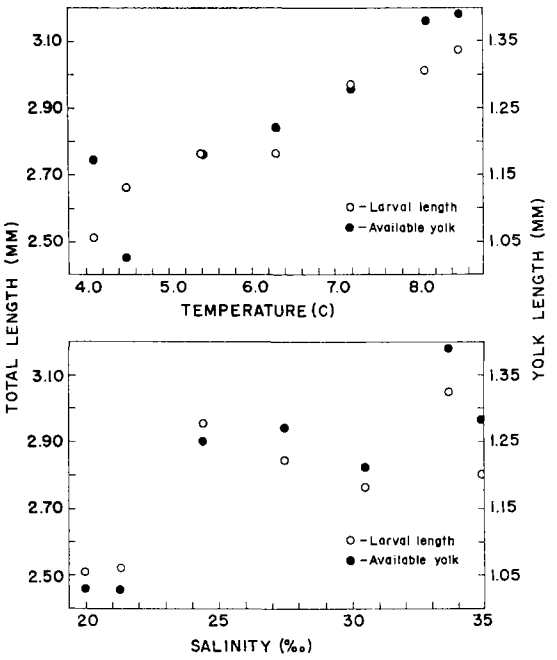


FIG. 3. Relation of larval length (open circles) and available yolk (solid circles) to salinity and temperature of incubation at the mean hatching time. Yolk length (measured antero-posteriorly) is an estimate of available stores of yolk. Some of the points shown are averages for several trials.

at 24.41‰ S and 7.2 C (trial 12). Percentages of total hatch were low (e.g., <20%) in low salinities (21.33‰, trial 2), in temperatures below 5.4 C (4.5 C, trial 3), and in combinations of low to intermediate salinity and high temperature (21.33‰ S, 8.1 C, trial 2; 27.50‰ S, 8.5 C, trial 10).

As noted earlier, incubators were not opened until after the estimated time of blastopore closure. Observations made on early developmental stages in the supplementary containers, and subsequently on eggs from the incubators, provided information on developmental anomalies (Fig. 4). In the trial at 21.33‰ S and 8.1 C many larvae had foreshortened and deformed spinal columns posterior to the vent. In the tests involving both high temperatures and high salinities mortality occurred primarily between the blastodermal cap stage and closure of the blastopore. At 27.50‰ S and 4.1 C most mortality occurred in full-term embryos that died either unhatched, or that died after producing a small rupture in the egg capsule over the region of the head of the embryo. At 21.33‰ S and 4.5 C most mortalities occurred in embryos that partly hatched tail-first (the usual process) but that died before shedding the capsule. In trial 8 an accident resulted in the eventual death of all eggs in subsample 3. The missing values were replaced by the entries shown in Table 4, which are essentially averages of the results from the other three subsamples of the trial.

TABLE 4. Incubation of petrale sole eggs at 13 salinity–temperature combinations (14 trials). Total hatch refers to the percentage of eggs that hatched. Viable hatch refers to the percentage of eggs that produced larvae of normal appearance.

	Total no. eggs				Total hatch %					Viable hatch %				
	Subsample				Subsample					Subsample				
Trial	1	2	3	4	1	2	3	4	Mean	1	2	3	4	Mean
1	326	354	388	376	12.58	12.43	10.82	23.14	14.75	0.92	0.85	0.77	1.06	0.90
2	414	381	447	475	6.52	12.86	15.66	10.32	11.36	0.00	0.00	0.00	0.00	0.00
3	437	431	348	386	0.92	1.16	0.29	0.78	0.81	0.46	0.23	0.00	0.52	0.31
4	405	385	349	385	21.73	52.21	46.70	44.42	40.88	16.05	41.56	34.96	32.21	30.91
5	399	415	381	417	81.20	77.35	78.48	78.18	78.78	48.37	60.96	44.62	47.72	50.56
6	415	432	381	530	75.66	75.69	79.27	75.09	76.28	59.28	58.56	65.35	51.32	58.02
7	412	430	444	385	73.06	69.77	63.74	64.94	67.86	3.64	2.33	0.00	0.52	1.62
8	350	323	367	384	42.57	54.80	(40.86)[a]	25.00	(40.81)	9.43	47.68	(21.90)[a]	8.85	(21.97)
9	369	417	367	410	11.92	23.50	17.44	18.54	18.04	0.27	2.88	1.91	2.44	1.92
10	420	395	338	418	8.10	15.95	13.02	16.03	13.24	4.52	11.14	10.06	12.68	9.55
11	349	460	741	389	52.15	56.96	49.26	59.38	53.64	17.48	15.87	15.92	23.91	17.79
12	342	382	333	366	65.79	74.08	75.08	74.32	72.38	50.58	66.23	68.17	71.04	64.16
13	394	354	349	363	59.90	61.02	67.34	64.74	63.15	16.50	26.55	25.50	36.09	25.96
14	392	423	395	383	57.14	68.32	59.75	62.14	61.96	44.39	59.10	43.04	56.66	50.91

[a]Missing values calculated by preliminary response surface analysis.

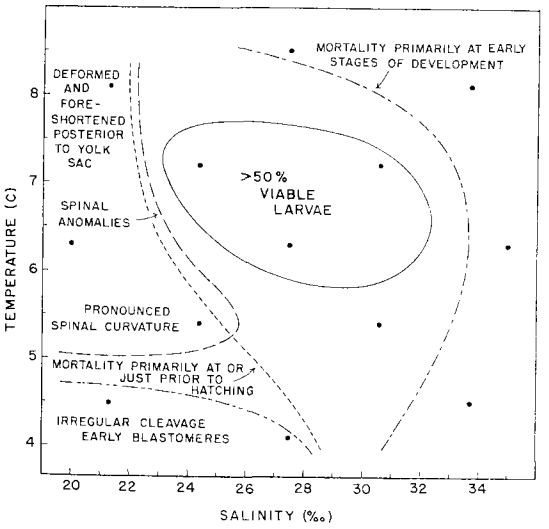


FIG. 4. Summary of the more prevalent developmental anomalies noted for petrale sole eggs in various salinity–temperature conditions of incubation. The grid of points refers to the salinity–temperature incubation trials. For example, spinal anomalies occurred in the three trials at lower salinities and higher temperatures (area within broken line).

Total hatch

Percentages of total hatch were considered in terms of the effects of salinity and temperature acting in concert. Using the nonlinear polynomial as a model

$$Y^{0.77} = -44.229 + 8.876 \times 10^{-6} x_1^{4.06} + 5.583 x_2^{1.70} - 1.236 \times 10^{-11} x_1^{8.13} - 0.122 x_2^{3.40} + 5.645 \times 10^{-7} x_1^{4.06} x_2^{1.70}$$

where Y = percentage total hatch; x_1, x_2 = salinity (‰), temperature (C); and α_1, α_2, γ = 4.0626, 1.7022, 0.7704.

Analysis of variance of the data for total hatch, given the nonlinear model, is shown in Table 5. The fifth column of the table gives approximations of the variance ratio, F. In the analysis of the nonlinear case, standard F tests are not valid as the probabilities for the ratios of sums of squares cannot be read from existing tables. Exact inferences regarding the listed components are found in the column of maximum likelihood ratios (MLR), which are relative likelihoods of the β coefficients being zero and the power parameters (transform) being unity.[3] Examination of the MLR column indicates that treatment effects explain a large portion of the variance, that the power transforms improve the fitted relation, and that none of the coefficient parameters could be eliminated without affecting the adequacy of the model. The nonlinear model provides a superior fit to that obtained by using a linear model; yet there remains a sizeable portion of the treatment variance not satisfied

[3]Ratios greater than 0.1 may be compared with a 95% probability interval for a normal theory linear model (Lindsey 1970). For example, the MLR for the x_1 component is less than 0.1 and the likelihood that the x_1 term could be replaced by zero is very small.

TABLE 5. Analysis of variance of the data for percent total hatch of petrale sole eggs (nonlinear model).

Source of variance	SS	df	MSS	Approx F	MLR[a]
Treatments	37314.86	13	2870.37	83.14	0.00
Regression	35510.79	5	7102.15	102.58	7.44×10^{-31}
Linear	1132.92	2	566.46	8.18	2.33×10^{-4}
x_1	777.06	1	777.06	11.22	2.49×10^{-3}
x_2	354.47	1	354.47	5.11	5.53×10^{-2}
Quadratic	31676.56	2	15838.27	228.76	1.37×10^{-29}
x_1^2	4031.59	1	4031.59	58.23	1.58×10^{-10}
x_2^2	29309.77	1	29309.77	423.33	9.80×10^{-29}
Interaction					
$x_1 * x_2$	2545.12	1	2545.12	36.76	9.41×10^{-8}
Transform	1590.89	3	530.29	7.65	8.64×10^{-6}
Residual	3254.04	47	69.23		
Lack of fit	1804.07	5	360.81	10.45	1.48×10^{-10}
Pure error	1449.97	42	34.52		
Total	38764.83	55			

[a]Maximum likelihood ratio.

by regression (lack of fit) on the terms of the polynomial when compared with the error term.

The likelihood also may be examined of the power parameters taking values other than their maximum likelihood estimates. Maximized relative likelihood distributions around the maximum likelihood estimates for the power parameters (Fig. 5) indicate that α_2 and γ are determined with more precision than α_1. The range of plausible estimates of the power parameters (maximum likelihood ratios >0.1) are approximately: α_1, 2.1–6.5; α_2, 1.1–2.3; γ, 0.5–1.1.

The nonlinear model is retained, employing the maximum likelihood values of the parameters as the best available estimates, from which the response surface (Fig. 6) is constructed relating percent total hatch to levels of salinity and temperature experienced throughout incubation. The canonical equation of the surface is

$$Y' - 30.065 = -0.122Z_1^2 - 0.117 \times 10^{-10}Z_2^2$$

where Y' = percent total hatch in terms of Y^γ; 30.065 = Y_s^γ, response at the centre of the surface, s; Z_1, Z_2 = canonical variables, linear combinations of the x^α variables.

The response at s is calculated as 82.91% total hatch[4] at

$$s = (29.47‰ \text{ S}, 6.65 \text{ C}).$$

The negative signs for the coefficients on the right-hand side of the canonical equation indicate that the surface is elliptical and that Y_s is a maximum. Near-maximum percent total hatch (80% or greater) occurs within salinity and temperature ranges of 27–31‰ and about 6.25–7 C, respectively. Total hatches of 50% or more would be expected within salinity and temperature ranges of approximately 20–35‰, and 5–8 C, respectively. There is also an indication of a low/low–high/high interaction between salinity and temperature. Increases in salinity are coupled with increases in temperature in maintaining maximum potential total hatch (Fig. 6).

Viable hatch

Percentage viable hatch of petrale sole eggs was highest in trials 5, 6, 12, and 14, at salinities and temperatures of about 25–30‰ and 6–7 C. Lowest results were obtained at low temperatures (4.1, 4.5 C), low salinities (21.33‰), and combined low salinity and high temperature levels (21.33‰, 8.1 C).

The relation between percent viable hatch and salinity and temperature levels during incubation is presented in the same manner as for the data on percent total hatch. Hence, for the nonlinear case

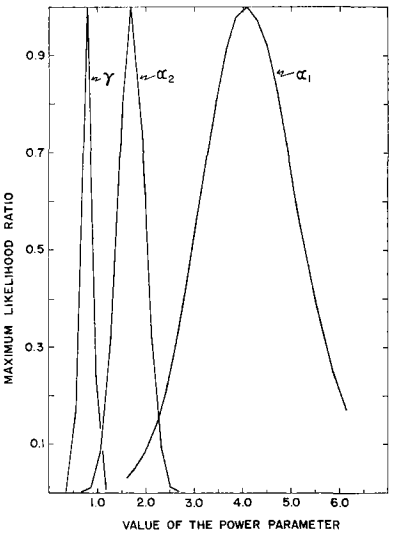


FIG. 5. Maximized relative likelihood distributions for the power parameters of the nonlinear model with respect to percent total hatch of petrale sole eggs. The likelihood of each of the α_1, α_2, and γ parameters taking other values is shown relative to the maximum likelihood estimate for each parameter.

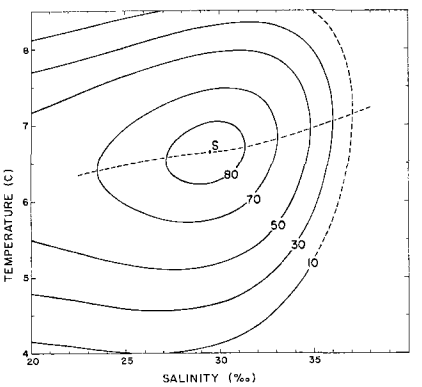


FIG. 6. Salinity–temperature response surface for percent total hatch of petrale sole eggs. Isopleths of percent total hatch are shown around the centre of the surface, s. The diagonal line through s estimates temperature at which total hatch is maximized at given salinity levels, indicating a low/low–high/high interaction with respect to salinity and temperature (see text).

[4] Y_s^γ = 30.0652; $(Y_s^\gamma)^{1/\gamma}$ = $(30.0652)^{1.2982}$; Y_s = 1.2982 ln 30.0652 = 82.91%.

$$Y^{0.23} = -8.855 + 1008.80x_1^{-1.27} + 9.776 \times 10^{-2}x_2^{2.29} - 29166.0x_1^{-2.54} - 4.133 \times 10^{-4}x_2^{4.57} - 1.866x_1^{-1.27}x_2^{2.29}$$

where Y = percent viable hatch; x_1, x_2 = salinity (‰) and temperature (C); α_1, α_2, γ = −1.2700, 2.2861, 0.2286.

Analysis of variance of the data for viable hatch (Table 6) indicates that treatment effects explain a large portion of the variance, that the nonlinear model is much more plausible than a linear model (transform component), and that none of the coefficient parameters could be eliminated without seriously affecting the adequacy of the model. As in the case of total hatch, however, there remains a substantial portion of the treatment variance not explained by regression even though the nonlinear model is more plausible than the linear model. Maximized relative likelihood distributions (not shown) around the maximum likelihood estimates of the power parameters indicate the ranges of plausible estimates to be: α_1, 0.0 to −2.5; α_2, 1.5–3.0; γ, 0.2–0.4.

For construction of the surface relating percent viable hatch to salinity and temperature levels during incubation (Fig. 7) the maximum likelihood estimates of the coefficient and power parameters in the nonlinear case again are accepted as the best available estimates. The canonical equation of the surface is

$$Y' - 2.664 = -3.835 \times 10^{-4}Z_1^2 - 29166.1Z_2^2$$

where Y' = percent viable hatch in terms of Y^{γ}; 2.664 = Y_s^{γ}, response at the centre of the surface, s; Z_1, Z_2 = canonical variables.

The response at s is calculated as 72.59‰ viable hatch, at

$$s = (27.93‰ \text{ S}, 7.00 \text{ C}).$$

The signs associated with the canonical variables are negative and thus the surface is elliptical and the response Y_s is a maximum. Near-maximum percent viable hatch (70% or greater) would be expected within salinity and temperature ranges of 26.5–29.5‰ and 6.75–7.25 C, respectively. Similarly, for 50% or greater viable hatch, the expected ranges would be 24–33‰ S and 6–7.75 C.

Posthatching Growth of Larvae

Groups of approximately 100 larvae obtained within a few hours of the mean hatching time were put into plastic and nylon-mesh containers and returned to their appropriate incubation tanks (trials 4, 5, 6, 12). Larvae were measured at 2-day intervals until exhaustion of the yolk and death of the larvae. Larvae increased in total length from about 2.84 mm (average at mean hatching time, all trials) to about 5.5–5.7 mm at exhaustion of the yolk 10–16.5 days after hatching (Fig. 8). The period from mean hatching time to exhaustion of the yolk varied inversely with temperature. Although the data are meagre, the following es-

Table 6. Analysis of variance of the data for percent viable hatch of petrale sole eggs (nonlinear model).

Source of variance	SS	df	MSS	Approx F	MLR[a]
Treatments	11557.18	13	889.01	65.82	5.80×10^{-38}
Regression	11291.23	5	2258.24	127.38	2.75×10^{-33}
Linear	2906.62	2	1453.31	81.97	5.51×10^{-19}
x_1	2319.66	1	2319.66	130.84	6.57×10^{-17}
x_2	582.18	1	582.18	32.83	3.60×10^{-7}
Quadratic	7423.83	2	3711.91	209.37	1.29×10^{-28}
x_1^2	2939.62	1	2939.62	165.81	4.31×10^{-19}
x_2^2	5134.73	1	5134.73	289.63	1.14×10^{-24}
Interaction					
$x_1 * x_2$	1196.31	1	1196.31	67.48	1.49×10^{-11}
Transform	5446.25	3	1815.41	102.40	2.60×10^{-28}
Residual	833.23	47	17.72		
Lack of fit	265.95	5	53.19	3.93	2.11×10^{-5}
Pure error	567.27	42	13.50		
Total	12124.46	55			

[a]Maximum likelihood ratio.

timates were obtained: trial 4, 8.1 C, 246 hr; trial 12, 7.2 C, 284 hr; trials 5, 6, 6.3 C, 393 hr. No feeding responses were observed. However, in terms of general development and appearance of a functional lower jaw, larvae appeared capable of feeding 216 hr (at 8.1 C) and 396 hr (at 6.3 C) after hatching.

Several stages of larval development are illustrated in Fig. 9. Newly hatched larvae lacked pigmentation, were virtually transparent, and in appearance gave the impression of having hatched prior to full-term development (Fig. 9*a*). The eyes lacked pigmentation; even though the lens and optic cup were present, the eye was difficult to discern under magnification. Sixty-three hours after hatching, larvae from the 27.50‰ S, 6.3 C incubator showed the first signs of developing pigmentation. Two rows of melanophores, located dorsally and ventrally at the base of the finfold, began to appear near the end of the tail region. At 7.2 C, 104 hr after hatching, four primary areas of melanophore development were present: 1, at the tail (as above); 2, midway between the end of the tail and the vent; 3, on the midline above the posterior margin of the yolk sac and on the hind gut; and 4, in the region of the heart between the midline of the body and the yolk sac (see Fig. 9*c*, *d*). At 8.1 C, 187 hr after hatching, a golden yellow-brown pigmentation began to appear underlying the primary areas of melanophore concentration (heavy stippled areas in Fig. 9). Eventually these areas of pigmentation and melanophore concentration became very prominent, particularly at the hind gut and vent. From 187 to 206 hr after hatching pigmentation of the eyes became evident in temperatures of 8.1 and 6.3 C. At 8.1 C at 246 hr, pigmentation of the eyes was prominent, processes of the melanophores in the tail were extending into the finfold, fin rays were beginning to appear in the finfold near the tail, and the yolk was near exhaustion.

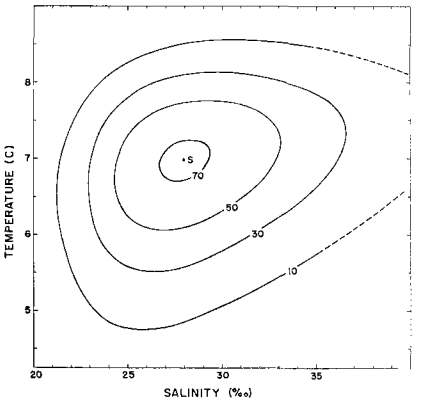


FIG. 7. Salinity–temperature response surface for percent viable hatch of petrale sole eggs (see Fig. 6).

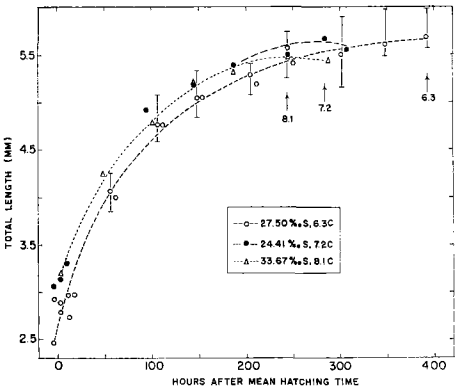


FIG. 8. Posthatching growth of petrale sole larvae held in three salinity–temperature conditions identical to those in which the samples were incubated. Times at which larvae began to die after exhaustion of the yolk are shown (8.1, 7.2, 6.3 C). The size range for some of the samples at 6.3 C is indicated by the vertical bars. Measurements at 6.3 C were discontinued before complete mortality in the sample.

A number of observations were made on the density of developing larvae. In 33.67‰ S at 8.1 C, larvae were buoyant at hatching, sank to the bottom of the container between 50 and 150 hr, and showed a decrease in density between 207 and 245 hr. At 245 hr after hatching, these larvae were suspended head down in the water with the axis of the body 10–20° from the vertical, and were virtually at neutral buoyancy. This posture was maintained until exhaustion of the yolk and death, at which time the larvae sank. Results from one of the other samples of hatched larvae indicated that density adjustments may occur in newly hatched larvae incubated at lower salinities. In the trial at 27.50‰ S and 6.3 C full-term eggs had a density higher than the incubation medium. However, newly hatched larvae were buoyant in 27.5‰ salinity.

Larvae were passive for the greater part of the posthatching period although they could be stimulated to swim rapidly for a few seconds by touching them with a probe, or by moving the container. In the 33.67‰ S, 8.1 C sample spontaneous swimming movements began about 246 hr after hatching.

At all times the larvae were very delicate. Newly hatched larvae would die within ½–1 min in an uncooled deep-well slide under the microscope. Observation time on live larvae was increased to at least 1 hr by the addition to a few drops of culture water holding the larva of an equal volume of 1:15,000 M.S. 222. Larvae treated in this manner

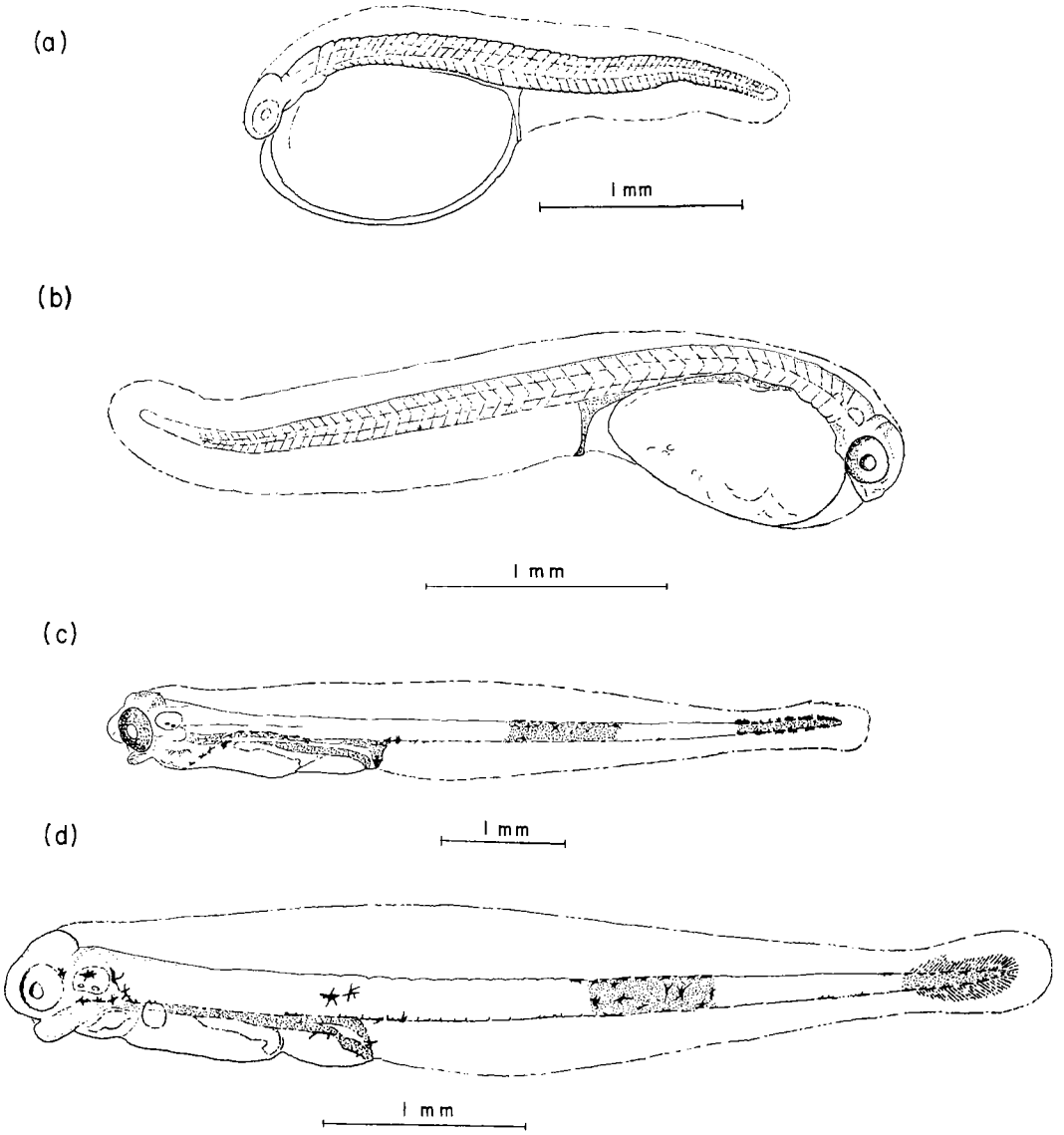


FIG. 9. Petrale sole larvae: (*a*) newly hatched (27.50‰ S, 6.3 C); (*b*) 2-day-old larva, total length 3.33 mm (33.67‰ S, 8.1 C); (*c*) and (*d*) 16½-day-old larva, total length 6.20 mm (27.50‰ S, 6.3 C). Drawn from camera lucida sketches of (*a*) preserved material in 5% formol-saline, (*b*) and (*c*) from photographs of live material, (*d*) from mounted specimen.

were returned to the holding containers after examination, without apparent ill effects.

Discussion

The direct relation between size of newly hatched larvae and of yolk supplies with temperatures in the 4.1–8.5 C range suggests an increasing efficiency of development at the higher temperatures. However, in the three instances where posthatching growth was observed, only minor differences were found in the maximum size attained by larvae at the time of yolk exhaustion (Fig. 8). These sizes were approximately: 6.3 C, 5.7 mm; 7.2 C, 5.65 mm; 8.1 C, 5.5 mm.

Percentages of total hatch and viable hatch obtained under the various incubation levels of salinity and temperature suggest that the petrale

sole egg is stenoplastic. Temperatures and salinities associated with viable hatches of 50% or greater range from 6 to 7.75 C and from 24 to 33‰, respectively (Fig. 7). However, it is doubtful that the petrale sole makes use of any but the upper portion of the salinity range. At known spawning depths salinities are of the order of 34‰. Kinne (1964) suggests that most euryhaline forms can tolerate salinity ranges of up to 10 or 15‰. The 9 parts per mille range associated with 50% viable hatch would place the petrale sole egg, conservatively speaking, among the stenohaline forms.

In terms of both larval size and hatching efficiency, the results may be summarized as follows:

Criterion	Incubation condition (‰ S, C)
Largest larvae at mean hatching time	24.41, 7.20
Largest larvae at yolk exhaustion (3 posthatching tests)	27.70, 6.30
Maximum percent total hatch	29.47, 6.65
Maximum percent viable hatch	27.93, 7.00

Therefore, even though newly hatched larvae tend to be largest at the higher temperatures, the greatest number of viable larvae of largest size at the time of yolk exhaustion would be expected at salinities of 27.5–29.5‰ and temperatures of 6–7 C.

Synthesis of factors affecting natural development

The spawning ground from which the eggs were obtained is situated on the continental slope approximately 30–35 miles offshore. Oceanographic conditions in the area (Lane 1962, 1963) and their influence on petrale sole development have been discussed by Ketchen and Forrester (1966). From the existing experimental evidence and oceanographic data, we have attempted to model the development and dispersion of eggs and larvae in the vicinity of the Estevan Deep.

In an earlier study (Forrester and Alderdice MS 1967) eggs were obtained from petrale sole caught in the Estevan Deep region at a depth of 300 m. Oceanographic data obtained at the point of capture (Table 7) and subsequent laboratory estimates of the density of developing eggs lead to calculation of *assumed* rates of rise of eggs in the natural water column. The density of developing eggs average 1.0252 (Table 8). Comparison with Table 7 indicates that such eggs would be buoyant in water from the bottom (300 m) to a depth of approximately 50 m.

The rate of ascent of the egg has been estimated using Stokes' law for the determination of settling velocity, W, of a sphere in liquid (the rate of ascent is $-W$).

$$-W = \frac{2}{9} g \cdot \frac{\rho_1 - \rho_2}{\mu} \cdot r^2 = \frac{2}{9}(981) \cdot \frac{1.0252 - 1.0263}{0.0149} \cdot (0.063)^2 = 0.06388 \text{ cm/sec, or } 55.2 \text{ m/day}$$

where $-W$ = cm/sec; ρ_1 = average density of the egg throughout development; ρ_2 = average density of the water column through which the egg is

TABLE 7. Data derived from an oceanographic station off the west coast of Vancouver Island (48°47′N, 126° 32′W) on February 28, 1967 (Forrester and Alderdice MS 1967).

Depth (*m*)	Temp (*C*)	Salinity (‰)	Density
0	8.50	32.178	1.0250
24	8.12	32.314	1.0252
49	8.08	32.347	1.0252
73	8.40	32.526	1.0253
98	8.34	33.248	1.0259
122	8.14	33.549	1.0261
147	7.83	33.752	1.0263
171	7.62	33.863	1.0264
195	7.25	33.877	1.0265
244	7.01	33.916	1.0266
264	6.76	33.939	1.0266
300 (bottom)	6.09	33.964	1.0267
Avg (73–300)	7.50	33.63	1.0263

TABLE 8. Salinities of neutral buoyancy and apparent density of petrale sole eggs incubated at 32.2‰ S and 6.5 C (Forrester and Alderdice MS 1967).

Incubation time (*hr*)	Neutral buoyancy (*S*‰)	Temp (*C*)	Apparent density[a] (g/cm^3)
3	31.56	4.0	1.0251
12	31.15	4.5	1.0247
36	31.42	3.5	1.0250
67	32.91	3.5	1.0262
84	32.47	3.5	1.0258
108	32.30	3.5	1.0257
132	31.35	3.5	1.0249
156	31.34	3.5	1.0249
184	31.35	3.5	1.0249
209	31.30	3.5	1.0249
Avg			1.0252

[a]U.S. Navy Hydrographic Office 1952.

presumed to rise; g = acceleration due to gravity; r = radius of the egg, cm; μ = dynamic viscosity of the water (Sverdrup et al. 1946) between 300 and 50 m, averaging 33.63‰ S at 7.5 C (Table 7).

Using the calculated estimate, the time required for the egg to rise to a depth of 50 m from known spawning depths of 300–450 m in the area (Alverson and Chatwin 1957) ranges from 4.5 to 7.2 days.

However, for reasons outlined by Forrester and Alderdice (MS 1967) the true rate of ascent is difficult to determine.

Changes in egg density as it passes through water of differing density will have an effect on rate of ascent as will external factors unrelated to density of the egg, e.g., processes of advection and diffusion (such as wind-driven transport, upwelling, etc.). Application of a correction for changes in water density due to pressure, and calculation of ascent time by stages, accelerated the rate of ascent to 3.1–3.9 days. However, this accelerated rate would probably be offset by increased density of the egg at depth, a factor unknown.

The ascending petrale sole eggs undoubtedly are subject to horizontal displacement by ocean currents. In the spawning season prevailing winds blow from the southeast (Lane 1962; Ketchen and Forrester 1966) and produce a net movement of surface water northward and shoreward and less saline coastal water is conserved near shore by the onshore drift of surface water (Lane, 1963). Consequently, isopleths of salinity and temperature dip under the more stable coastal water and intersect the bottom of the continental shelf seaward from shore. The isohaline upper zone is about 50–70 m deep and the oceanic halocline extends to a depth of about 200 m. Under these conditions transport of eggs northward and shoreward by wind-induced drift would begin when eggs had risen to a depth of about 200 m. It is assumed that shoreward drift below 200 m would be negligible for the first 1 or 2 days after liberation of eggs at depths of 300–450 m.[5] This assumption may be erroneous because rates of subsurface drift and shoreward transport have not been studied in the region considered. Suggested rates range between $\frac{1}{4}$ and 1 nautical mile per day and at times may be considerably greater (A. J. Dodimead and W. P. Wickett personal communication and S. J. Westrheim's personal observations aboard vessel *G. B. Reed*).

At the average temperature of the water column through which the eggs rise (7.5 C, Table 7) hatching would occur about 7.3 days after fertilization (Fig. 1). Assuming an average daily shoreward drift of 1 mile after the first day, eggs would hatch after rising to a depth of about 50 m (or 1–2 days later) and would have been transported about 6 miles toward shore. The time required for larvae to reach maximum size prior to yolk exhaustion at 7.2 and 8.1 C (Fig. 8) is estimated as 11.8 and 10.2 days, respectively. Therefore the period from egg deposition to the stage when larvae would require an external food source is estimated as about 17.5–19 days. After 17.5–19 days larvae would have been transported about 16.5–18 miles northward and shoreward.

Density changes observed in larvae after hatching would also influence the location of larvae in the water mass. Larvae would be buoyant in 32–33.5‰ S for the first few days after hatching, would tend to sink to greater depths during the next 4 days, and would become more buoyant again in the later stages of yolk absorption. Larvae held at 33.67‰ S, 8.1 C (density, 1.0256) showed near-neutral buoyancy in that medium during this latter stage. The effect of these tendencies would probably be to increase the depth of larval drift, to slow the rate of shoreward transport, and to bring larvae into proximity of the continental shelf bottom at a somewhat greater depth than would be expected from measurements of egg density alone.

The foregoing suggested relation between egg and larval development and salinity, temperature, and transport conditions is hypothetical, and is presumed to be an oversimplified version of more complex events. Nevertheless, Ketchen and Forrester (1966) show that petrale sole year-class strengths are correlated with January–March surface temperatures and atmospheric pressure differences between two points in the area in question. Higher year-class strengths are associated with increased surface temperatures[6] and with strong negative atmospheric pressure differences. The latter are associated with southeast winds whose components of surface drift are northward and shoreward. Weak negative and positive pressure differences, associated with northwest winds and lower surface temperatures, are correlated with low year-class strengths. Under the influence of northwest winds, low salinity coastal surface waters are driven seaward whereas subsurface waters below the sheer zone flow shoreward, upwell, and are reflected seaward at the coast (Lane 1963 his fig. 6).

The associations suggested by Ketchen and Forrester (1966) indicate that southeast winds favour the onshore transport of petrale sole eggs and larvae

[5]There may in fact be a reverse drift offshore at depth.

[6]Although the egg or larvae may not actually be at the surface, the surface temperatures were believed to reflect general temperature conditions in the upper mixed layer at that time of year.

to potential nursery areas. On the other hand, northwest winds could be assumed to transport eggs and larvae offshore and away from nursery areas. Under these circumstances a relation could be expected between surface temperature, atmospheric pressure differences, and year-class strength. The assumption is examined in Fig. 10, a representation of data from Ketchen and Forrester (1966 their fig. 53, 59). However, the ordered relation anticipated — a concentration of high year-class strength estimates within the correlation cloud at higher water temperatures and stronger negative pressure differences — is only marginally suggested by the limited available data. Three types of explanation may account for the absence of an obvious correlation between the three factors considered. First, estimates of the components related may be of low precision. For example, pressure differences employed by Ketchen and Forrester (1966) are averaged over a 3-month period. Such averages might not allow the detection

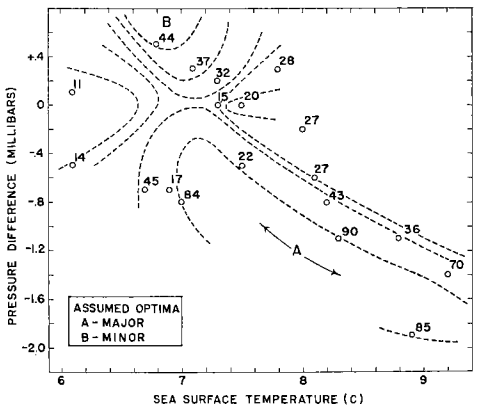
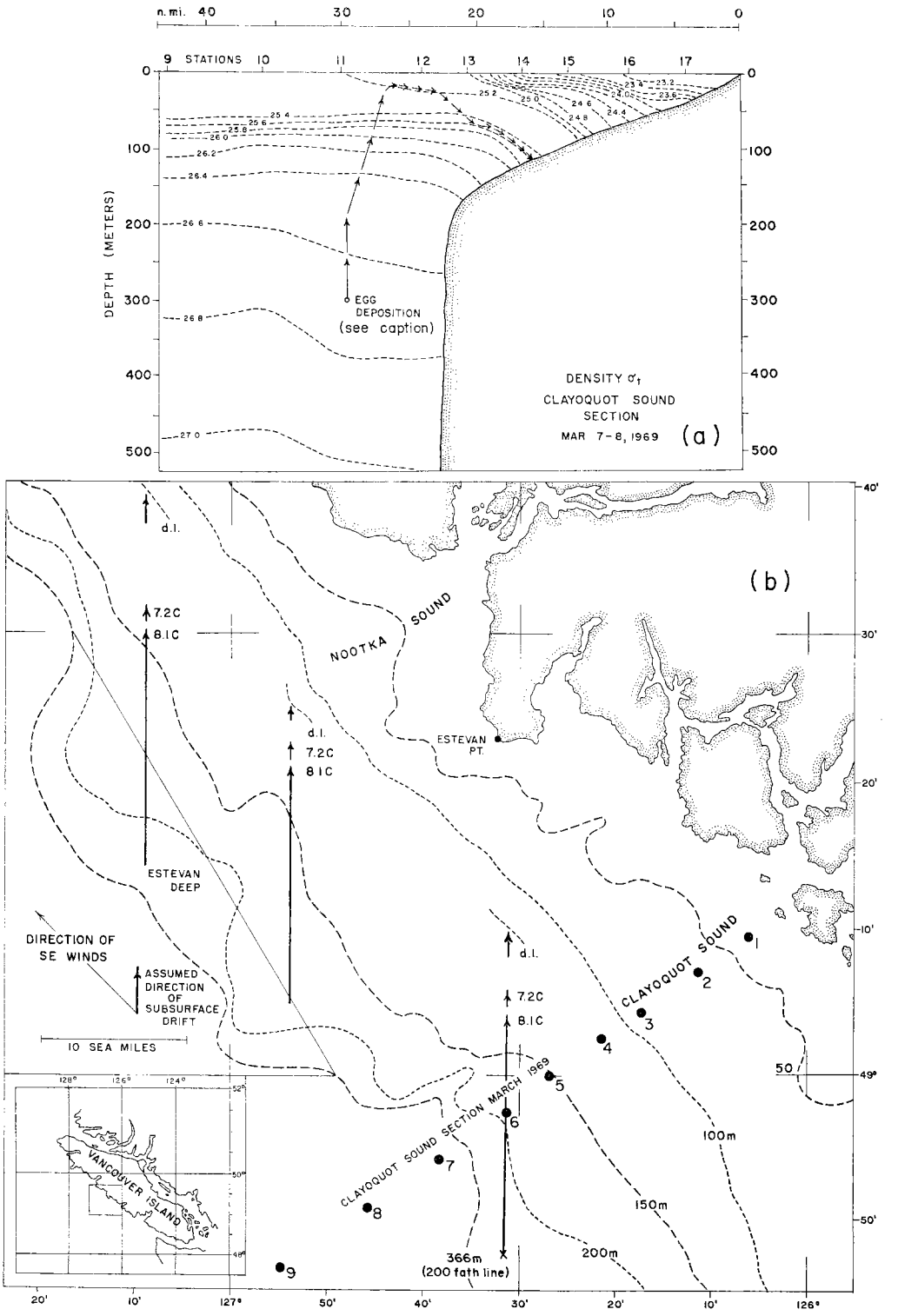


FIG. 10. Replotting of data from Ketchen and Forrester (1966). In the original presentation significant correlations were shown between year-class strength and both mean sea-surface temperature and atmospheric pressure difference, the latter providing an estimate of direction and intensity of wind-driven currents. The isopleths of year-class strength shown are based on the assumption that (1) there is a direct relation between year-class strength and temperature, (2) minimum year-class strengths are associated with near zero average pressure differences, and (3) that there are two year-class strength optima — a major optimum at higher temperatures and negative pressure differences, and a minor optimum at lower temperatures and greater positive pressure differences. The latter is assumed from measurements of egg and larval density and presumed drift of larvae relative to northwest winds (see text). Although the nature of the surface shown is considered plausible, the exact position of the isopleths of year-class strength (dotted lines) is speculative.

of unusual or short-term events, which are probably more frequent and complex than can be appreciated from limited oceanographic or meteorological data.[7] Secondly, the part of the correlation cloud (Fig. 10) relating lower surface temperatures to positive pressure differences is not associated with obvious or marked reductions in year-class strength. Examination of the relation between pressure differences and year-class strength indicated by Ketchen and Forrester (1966 their fig. 59) suggests that the relation could be nonlinear. Minimum year-class strengths appear to occur at near zero pressure differences; higher year-class strengths are associated with *both* negative and positive pressure differences and, respectively, the southeast and northwest winds with which they are related. Under the influence of northwest winds and offshore surface drift of less saline coastal waters, the density of petrale sole eggs and larvae could restrict them to the subsurface shoreward setting waters. Eggs that might become entrained in surface waters would be presumed to sink into more saline subsurface layers flowing shoreward and, in effect, be held in the coastal region. Under these circumstances eggs and larvae would be subjected to colder temperatures and development time would be prolonged; and although mortality might be increased by extension of the pelagic stage, it probably would be lower than expected if northwest winds were assumed to transport larvae away from the coastline and potential nursery grounds. Thirdly, other factors important to larval survival may not have been accounted for in the simple model presented. For example the extent and location of the Transitional Zone water mass (Dodimead et al. 1963), found off the southern British Columbia–Washington State coastline, may vary from year to year. Thus, in the spawning season the effect of local meteorological conditions on water transport could be applied from year to year on water masses of varying character. In addition, structure of the water mass in the coastal domain may be influenced by other factors not considered, such as the presence of eddy currents, tidal fluctuations, and variations in the discharge of fresh water into the coastal region.

On the basis of the various estimates of egg and larval density, rates of development associated with temperature, and rates of drift influenced by southeast winds, the hypothesis relating pelagic development to general oceanographic and meteorological conditions may be advanced as a simple model (Fig. 11). In Fig. 11*a*, arrows show the

[7]Spawning petrale sole were found over a considerable period of time (late December to early April) and thus temperatures for an extended period were used.



presumed course of eggs liberated at a depth of 300 m[8] in relation to characteristics of the water mass along a Clayoquot Sound oceanographic section (A. J. Dodimead personal communication) (Fig. 11*b*), although the direction of presumed drift is at an angle to that section. In Fig. 11*b* three arrows show the presumed extent and direction of drift of larvae developing at 7.2 and 8.1 C, assuming a subsurface transport rate of 1 nautical mile/day at an angle of 45° to the right of prevailing southeast winds. Assuming a final larval density of 1.0256 from the experimental data, the approximate position of contact of the corresponding isopycnal with the bottom is estimated from the oceanographic section (Fig. 11*a*) and is suggested as the final limit of larval drift (*d.l.* in Fig. 11*b*). In Fig. 11 the southernmost arrow originates at the point from which eggs were obtained for the current study.

The model suggests that under favorable transport conditions petrale sole larvae in the vicinity of the Estevan Deep would come into contact with the continental shelf some 15–25 miles offshore in depths of about 100–150 m. There is some evidence, though scanty, that small juvenile petrale sole occupy middle shelf depths (Ketchen and Forrester 1966 table 57) in contrast to juveniles of other species that occur in shallow water (e.g., English sole, Ketchen 1956; rock sole, Forrester and Thomson MS 1969). It is concluded, however, that a better understanding of egg and larval survival, and their influence on year-class strength, requires a more extensive accumulation of data on the physical environment and its variability from year to year during the pelagic phase of early development of the petrale sole.

Geographic distribution

The experimental evidence suggests that occurrence of the petrale sole is dependent on the availability of suitable temperatures in the period of spawning and egg incubation. To examine this assumption, Fig. 12 compares temperature effects on egg development from the laboratory data, available spawning temperatures, and measures of petrale sole abundance for approximate 300-nautical mile divisions of the coastline. The comparison is based on the following data: (A) estimates of percent viable hatch of eggs as influenced by incubation temperature, calculated from a section through the centre of the hatching surface at 27.93‰ S (Fig. 7); (B) estimates of available temperatures in the spawning period (January–March) at depths of 300 m from oceanographic records[9]; (C) estimates of abundance of petrale sole based on average annual catches by United States and Canadian fishing vessels for the period 1962–66 inclusive (Pacific Marine Fisheries Commission MS 1968).

A straightforward interpretation of the data is difficult. In the northern part of the range petrale sole spawn in deep water in area 3D (48°50′N, 126°30′W), and are caught in commercial quantities north to the British Columbia–Alaska border (54°40′N). No commercial fisheries are conducted by United States or Canadian trawl vessels north of 54°40′. A recent series of surveys (Westrheim MS 1967; Westrheim et al. MS 1968) found petrale sole north to 55°42.5′N, 135°45′W; bottom temperatures of 5.7–5.8 C were recorded in the area of most northerly capture. Most recently, one petrale sole was taken in a trawl at 57°15.9′N,

[8]The depth of capture of spawning petrale sole in 1968 was 300 m and estimates of coastal temperatures for this depth are used in the following sections. It is known, however, that spawning petrale sole may be captured in depths to 450 m. The mean depth of capture of spawning petrale sole during *G. B. Reed* cruises in the late winter and early spring months off the west coast of Vancouver Island was 370 m (Harling et al. MS 1967, MS 1968; Westrheim et al. MS 1969). The difference in bottom temperatures between depths of 300 and 370 m appears to be less than 0.5 C (Dodimead et al. 1963).

[9]Mean temperatures at 300 m for the region of the coast from southeast Alaska to Cape Mendocino (56°N to 37°30′N) were obtained from provisional printouts of oceanographic data on file at the Canadian Oceanographic Data Centre, Ottawa, Ont., and supplied by the Pacific Oceanographic Group at Nanaimo, B.C. Temperatures for the region south of 37°30′N were obtained from University of California (1961a–65).

FIG. 11. Hypothetical transport of developing petrale sole eggs and larvae in the Estevan Deep region (see text). (*a*) Density profile, Clayoquot Sound oceanographic section, March 7–8, 1969 (redrawn from A. J. Dodimead personal communication). (*b*) Bottom topography and location of the Clayoquot Sound section. In (*a*) the presumed course of drift of eggs or larvae (arrows) is shown. *Egg deposition would be at or near the bottom (300 m) at the actual spawning location.* The presumed direction of drift is northerly across the Clayoquot Sound section. In (*b*) the extent of drift (arrows) is shown relative to egg density for temperatures of 7.2 and 8.1 C, at a transport rate of 1 knot/day at 45° to the right of prevailing southeast winds. The final limit of larval drift (*d.l.* in figure) is based on density of larvae at yolk absorption (1.0256; see text) and the estimated position of that isopycnal from the density profile in (*a*).

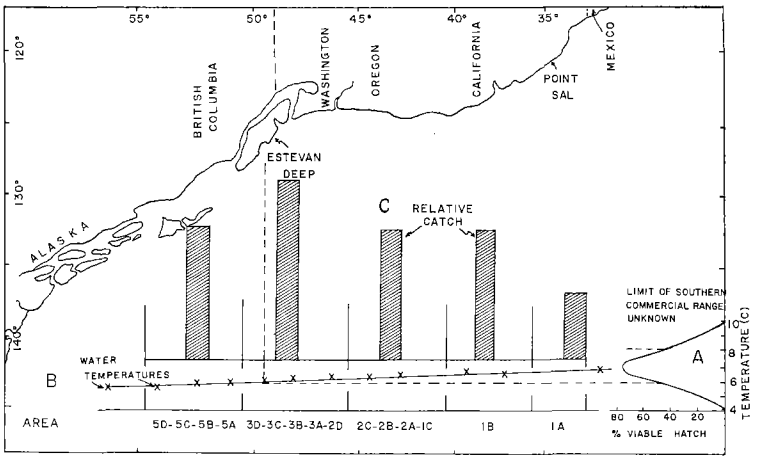


FIG. 12. Relation between (A) laboratory estimates relating temperature and percent viable hatch; (B) available environmental temperatures in the spawning period estimated for depths of 300 m; (C) estimates of average annual petrale sole landings by United States and Canadian vessels (1962–66 inclusive weighted to equal effort). The dotted line indicates the northern boundary of the area where spawning period temperatures are deemed to be most favorable for development of petrale sole eggs. There is no information with respect to petrale sole, and water-temperature records have not been examined for waters south of California.

136°12.4′W at a depth of 201–205 m. Associated with the haul, a bottom temperature of 6.1 C was recorded at a depth of 199 m (Harling et al. MS 1970).

Towards the southern part of the range there are several deepwater spawning locations (subpopulations, Best 1963). In southern California waters petrale sole are known to spawn off Point Sal (34°55′N, 120°40′W) and they are fished commercially in that area (area 1A) and northwards. However, catch figures in area 1A are not comparable with those in more northern areas because the fishery is conducted only in the northern third of the area. The region from approximately 34°30′N south to the Mexican border is closed to commercial trawling by United States vessels inside the 3-mile territorial limit and there is virtually no trawling in waters further offshore (T. Jow personal communication).

Spawning season temperatures at depths where spawning occurs (about 300 m) range from approximately 6 C in the north to 7 C in the south (Fig. 12). The stenothermal character of the petrale sole egg as found in the laboratory experiments suggests that availability of temperatures between 6 and 8 C probably plays a major role in defining distribution of spawning populations. On this basis, temperature may restrict commercial abundance of petrale sole near the northern limit of the Canadian–United States trawl fishery. Temperatures at 300 m drop below 6 C in the region north of 50°N. This might reduce survival of eggs or larvae produced but would not necessarily result in absence of adult fish. Postspawning movements of petrale sole in the region are known to be inshore or northward, or both (Ketchen and Forrester 1966).

Southward, there appear to be conditions favourable to survival in regions south of the southern limit of the trawl fishery.

In any of the areas a favourable temperature regime for egg incubation and larval development may be modified by variations in circulation of the coastal domain. It is probable that such influences as density profile, direction of drift, subsurface current velocity, eddy formation, and extent of coastal upwelling contribute substantially to annual fluctuations in larval survival within localized regions over the whole range of occurrence of the species. It is clear that models of petrale sole population dynamics must take into account the specific environmental requirements of the early developmental stages of larvae that result from the annual convergence of adult petrale sole into particular areas.

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ALDERDICE, D. F., AND C. R. FORRESTER. 1971. Effects of salinity, temperature, and dissolved oxygen on early development of the Pacific cod (*Gadus macrocephalus*). J. Fish. Res. Bd. Canada 28. (In press)

ALDERDICE, D. F., AND F. P. J. VELSEN. 1968. Design of a controlled-environment incubator for small marine fish eggs. J. Fish. Res. Bd. Canada 25: 585–588.

ALVERSON, D. L. MS 1967. A study of demersal fishes and fisheries of the northeastern Pacific ocean. Ph.D. Thesis. Univ. of Washington, Seattle, Wash. 286 p.

ALVERSON, D. L., AND B. M. CHATWIN. 1957. Results from tagging experiments on a spawning stock of petrale sole, *Eopsetta jordani* (Lockington). J. Fish. Res. Bd. Canada 14: 953–974.

BEST, E. A. 1963. Movements of petrale sole, *Eopsetta jordani* (Lockington), tagged off California. Calif. Dep. Fish Game, Pac. Mar. Fish. Comm. Bull. 6: 23–38.

DODIMEAD, A. J., F. FAVORITE, AND T. HIRANO. 1963. Salmon of the North Pacific Ocean. Part II. Review of oceanography of the subarctic Pacific region. Int. N. Pac. Fish. Comm. Bull. 13: 195 p.

FORRESTER, C. R., AND D. F. ALDERDICE. MS 1967. Preliminary observations on embryonic development of petrale sole (*Eopsetta jordani*). Fish. Res. Board Can. Tech. Rep. 41: 21 p.

FORRESTER, C. R., AND D. M. HOLMBERG. MS 1967. A summary report of the British Columbia trawl fishery in 1966 and some aspects of its investigation. Fish. Res. Board Can. Tech. Rep. 19: 32 p.

FORRESTER, C. R., AND J. A. THOMSON. MS 1969. Population studies on the rock sole (*Lepidopsetta bilineata*) of Northern Hecate Strait, British Columbia. Fish. Res. Board Can. Tech. Rep. 108: 104 p.

HARLING, W. R., D. DAVENPORT, L. E. MCLEOD, AND S. J. WESTRHEIM. MS 1968. *G. B. Reed* groundfish cruise no. 68-2, April 2 to June 11, 1968. Fish. Res. Board Can. Tech. Rep. 81: 63 p.

HARLING, W. R., D. DAVENPORT, M. S. SMITH, U. KRISTIANSON, AND S. J. WESTRHEIM. MS 1970. *G. B. Reed* groundfish cruise no. 70-1, March 5–June 18, 1970. Fish. Res. Board Can. Tech. Rep. 205: 82 p.

HARLING, W. R., D. DAVENPORT, AND S. J. WESTRHEIM. MS 1967. *G. B. Reed* groundfish cruise no 67-1, February 1–April 24, 1967. Fish. Res. Board Can. Tech. Rep. 22: 56 p.

HITZ, C. R., AND W. F. RATHJEN. 1965. Bottom trawling surveys of the northeastern Gulf of Alaska. Commer. Fish. Rev. 27(9): 1–15.

KETCHEN, K. S. 1956. Factors influencing the survival of the lemon sole (*Parophrys vetulus*) in Hecate Strait, British Columbia. J. Fish. Res. Bd. Canada 13: 647–694.

KETCHEN, K. S., AND C. R. FORRESTER. 1966. Population dynamics of the petrale sole, *Eopsetta jordani*, in waters off western Canada. Fish. Res. Board Can. Bull. 153: 195 p.

KINNE, O. 1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature salinity combinations. Oceanogr. Mar. Biol. Annu. Rev. 2: 281–339.

LANE, R. K. 1962. A review of the temperature and salinity structures in the approaches to Vancouver Island, British Columbia. J. Fish. Res. Bd. Canada 19: 45–91.

1963. A model of seawater structure near the west coast of Vancouver Island, British Columbia. J. Fish. Res. Bd. Canada 20: 939–967.

LEVINGS, C. D. MS 1968. Report on groundfish cruise of C.G.S. *G. B. Reed* to Hecate Strait in February, 1968. Fish. Res. Board Can. Tech. Rep. 62: 41 p.

LINDSEY, J. K. 1970. Exact statistical inferences about the parameter for an exponential growth curve following a Poisson distribution. J. Fish. Res. Bd. Canada 27: 172–174.

LINDSEY, J. K., D. F. ALDERDICE, AND L. V. PIENAAR. 1970. The analysis of non-linear models — the non-linear response surface. J. Fish. Res. Bd. Canada 27: 765–791.

LINDSEY, J. K., AND A. SANDNES. MS 1970. Program for the analysis of non-linear response surfaces (extended version). Fish. Res. Board Can. Tech. Rep. 173: 131 p.

NORMAN, J. R. 1934. A systematic monograph of the flatfishes (Heterosomata). Vol. I. Psettodidae, Bothidae, Pleuronectidae. Oxford University Press, London. 459 p.

PACIFIC MARINE FISHERIES COMMISSION. MS 1968. Bottom or trawl fish. Pac. Mar. Fish. Comm. Data Ser. B: 273 p.

ROEDEL, P. M. 1953. Common ocean fishes of the California coast. Calif. Div. Fish Game, Fish. Bull. 91: 184 p.

SVERDRUP, H. V., M. W. JOHNSON, AND R. H. FLEMING. 1946. The oceans. Prentice-Hall, Inc., New York, N.Y. x + 1087 p.

UNIVERSITY OF CALIFORNIA. 1961a. Data report. Scripps Institute of Oceanography. Reference 62-3.

1961b. Data report. Scripps Institute of Oceanography. Reference 62-5.

1961c. Data report. Scripps Institute of Oceanography. Reference 62-6.

1961d. Data report. Scripps Institute of Oceanography. Reference 62-15.

1962. Data report. Scripps Institute of Oceanography. Reference 62-26.

1963. Data Report. Scripps Institute of Oceanography. Reference 63-9.

1964a. Data report. Scripps Institute of Oceanography. Reference 64-2.

1964b. Data report. Scripps Institute of Oceanography. Reference 64-13.

1965. Data report. Scripps Institute of Oceanography. Reference 65-7.

U.S. NAVY HYDROGRAPHIC OFFICE. 1952. Tables for sea water density. U.S. Navy Hydrographic Office. H.O. Publ. 615: ix + 265 p.

WESTRHEIM, S. J. MS 1967. *G. B. Reed* groundfish cruise reports, 1963–66. Fish. Res. Board Can. Tech. Rep. 30: 288 p.

WESTRHEIM, S. J., D. DAVENPORT, W. R. HARLING, M. S. SMITH, AND R. M. WOWCHUK. MS 1969. *G. B. Reed* groundfish cruise no. 69-1, February 11–27, 1969. Fish. Res. Board Can. Tech. Rep. 113: 23 p.

WESTRHEIM, S. J., W. R. HARLING, AND D. DAVENPORT. MS 1968. *G. B. Reed* groundfish cruise no. 67-2, September 6 to October 4, 1967. Fish. Res. Board Can. Tech. Rep. 46: 45 p.