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Abstract.—To estimate mortality and abundance of walleye pollock *Theragra chalcogramma* larvae in Shelikof Strait, Alaska, during spring 1981, a diffusion-advection model, combined with growth and death of fish larvae, was applied. Physical parameters (diffusion coefficients and advection rates) were derived from the distributional variances and centroids of fish larvae collected in ichthyoplankton surveys. The diffusion coefficient and the advection rate in the along-strait direction were 65.2 km²/day and 2.7–4.2 km/day, respectively, which compared favorably with values obtained from moored current-meter data. Simulation revealed that the expected distribution of larvae was similar to that observed from ichthyoplankton samplings, and that around 20% of the larvae drifted out of the survey area in Shelikof Strait within the 1-month sampling period. The larval fraction dispersed out of the survey area was used to revise larval mortality and abundance estimates. Revised mortality (0.070/day) was close to that (0.063/day) determined from examining larval patches. The simulation in this paper resulted in an increase by a factor of 1.5 in the estimated total larval abundance compared with earlier estimates and field observations.

Oceanic Dispersion of Larval Fish and its Implication for Mortality Estimates: Case Study of Walleye Pollock Larvae in Shelikof Strait, Alaska

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Most marine fish have a period of planktonic existence during egg and larval stages. Since early in this century it has been believed that survival during early life determines year-class strength and recruitment variability to fisheries (Hjort 1914). Furthermore, recruitment processes are quite complex because the biological and environmental factors which act on eggs and larvae are closely related (Wooster et al. 1983). Hence, the relationship between organisms and their environment is critical for understanding recruitment variability. The observed patterns of egg and larval distributions can be considered to be the result of a combination of fundamental processes, including spawning time and location, advection, diffusion, growth and mortality. These parameters could be identified using biological data.

The early-life stages of walleye pollock *Theragra chalcogramma* whose biomass is the largest of a single species in world fisheries (Sharp 1987), have been the objects of considerable research in recent years. In Shelikof Strait (Fig. 1), about 90% of the eggs were produced between 25 March and 15 April 1981, and they have

approximately a 2-week embryonic period at 5°C (Kim 1989). Spawning produces a patch of planktonic eggs and larvae that can be followed as they develop and are advected in prevailing currents toward the southwest. In Shelikof Strait walleye pollock eggs exist at depths below 150 m due to their high specific gravity. Their transport rate from the spawning area is very small because of weak circulation in deep water (Kendall and Kim 1989).

Eggs of late developmental stage would move upward fast due to the decreased specific gravity of old eggs, and the eggs hatch mid-depth in the water column (Kim 1987). Also the specific gravity of newly hatched larvae is continuously decreasing, so that most larvae are found within the upper 60 m of the surface (Kendall et al. 1987). Kim and Kendall (1989) described the distribution and transport pattern of larvae in Shelikof Strait during spring. Young larvae occupy a relatively small area and form a dense patch, while older larvae spread over a broader area in Shelikof Strait, showing the importance of diffusion on the larval patch. These larval patches have been identified for at

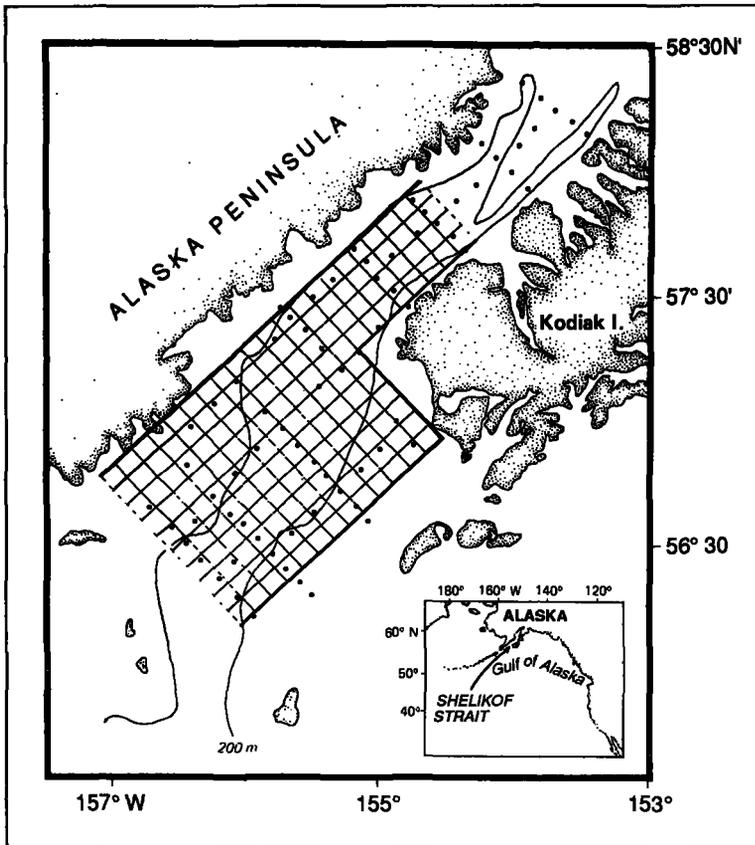


Figure 1
Typical locations of sampling stations (*) and the grid pattern used for the computer simulation. The flux of larvae through the solid lines is zero. The dashed lines are open boundaries of the model that permit the loss of larvae.

least a month after hatching (Incze et al. 1989). Assuming no drift or dispersion of larvae away from the sampling area, the instantaneous daily mortality was estimated as 0.086 (Kim and Gunderson 1989). The effects of advection and diffusion on the larval mass, however, can cause errors in estimation of mortality and abundance. Hence, the distribution and abundance of walleye pollock larvae in Shelikof Strait should be reconsidered in the light of oceanic diffusion-advection theory (McGurk 1989).

The main objectives of this paper are:

- 1 Estimation of diffusion coefficients and advection rates of walleye pollock larvae based on ichthyoplankton distribution in Shelikof Strait;
- 2 Description of expected larval distribution and abundance with time from a computer simulation using a diffusion-advection model; and
- 3 Reestimation of larval mortality and expected larval abundance reported in Kim and Gunderson (1989) and comparison of these results with field observations.

Background of theories and model

In general, the simplest approach to the diffusion problem for particles in a fluid medium follows from the

assumption that the rate of diffusion is directly proportional to the local concentration gradient (Okubo 1980). Walleye pollock larvae in Shelikof Strait are advected and diffused in the upper 60 m during early larval stages (Kendall et al. 1987), and the swimming ability of larvae less than 10 mm is assumed to be inconsequential. Therefore, a horizontal two-dimensional diffusion-advection model is applicable to changes in the distribution and abundance of young walleye pollock larvae in Shelikof Strait. Current speeds (u and v) and diffusion coefficients (K_x and K_y) are set constant, with the assumption of a homogeneous turbulence field and negligible horizontal divergence. Newly hatched larvae (i.e., the source material in the diffusion-advection model) are assumed to be produced daily at a fixed location near the center of Shelikof Strait (Kim and Kendall 1989). Once larvae that dispersed from the source point arrived at the Alaska Peninsula coast, they were required to remain there, since the shallow coastal region is considered a nursery area of young fish (Walters et al. 1985). Since larvae grow as they drift, the simulated distribution and abundance of larvae can be divided into several size groups. The partial differential equation, with initial condition $C_i(x, y, T_1) = 0$ and boundary conditions as described above, is

$$\frac{\partial C_i}{\partial t} = K_x \frac{\partial^2 C_i}{\partial x^2} + K_y \frac{\partial^2 C_i}{\partial y^2} - u \frac{\partial C_i}{\partial x} - v \frac{\partial C_i}{\partial y} - r C_i \quad (1)$$

where C_i = larval concentration of i -th cohort (number/m²),
 x and y = along- and cross-strait coordinates,
 K_x and K_y = along- and cross-strait turbulence diffusion coefficients,
 u and v = along- and cross-strait velocity components,
 r = instantaneous daily mortality of larvae, and
 T_1 = starting time of i -th cohort larval production.

The solution using Laplace transform is

$$C_i(x, y, t) = \frac{1}{4\pi\sqrt{K_x K_y}} \int_{T_1}^t \frac{P_i(T)}{(t-T)} e^{r(t-T)} \left\{ \sum_a e^{-\frac{(x-A_a)^2}{4K_x(t-T)}} \right\} \left\{ \sum_b e^{-\frac{(y-B_b)^2}{4K_y(t-T)}} \right\} dT \quad (2)$$

where $C_i(x, y, t)$ = larval concentration of i -th cohort at time t at point (x, y) ,
 $P_i(T)$ = i -th cohort's larval production rate at time T ($T_1 < T < t$) and at source point (x_0, y_0) .
 $A_a = (-1)^{|a|} X^* + a(x_{+L} - x_{-L}) + \text{mod}(|a|, 2)(x_{+L} + x_{-L})$
 $B_b = (-1)^{|b|} Y^* + b(y_{+L} - y_{-L}) + \text{mod}(|b|, 2)(y_{+L} + y_{-L})$

where a and b = indices of symbol summation (Σ)

- if there is no boundary, a or $b = 0$
- if there is negative-side ($-L$) boundary only, $a = -1, 0; b = -1, 0$
- if there is positive-side ($+L$) boundary only, $a = 0, 1; b = 0, 1$,
- if there are boundaries at both sides, $a = -\infty, \dots, 0, \dots, +\infty$
 $b = -\infty, \dots, 0, \dots, +\infty$

$$X^* = x_0 + u(t - T)$$

$$Y^* = y_0 + v(t - T)$$

x_{+L}, x_{-L}, y_{+L} , and y_{-L} = positive and negative side boundaries in x and y coordinates,

$\text{mod}(|a|, 2)$ = remainder of $|a|$ divided by 2, and
 $\text{mod}(|b|, 2)$ = remainder of $|b|$ divided by 2.

The area of Shelikof Strait used in the computer simulation was divided into 162 10×10 km grid areas with boundaries along the Alaska Peninsula and Kodiak Island (Fig. 1). The grid scheme was used to obtain contour patterns of results and to compare the simulated values with observations. To obtain larval abundance for each grid area from Equation (2), numerical integration was used, since the integration could not be handled by further analytic approach. For time integration, an 8-point Gaussian Quadrature is used (Scheid 1968), and for spatial integration an error-function infinite series is used (Gradshteyn and Ryzhik 1980).

Once all parameters were selected for the diffusion-advection equation, the simulation program was run for 50 days starting on 5 April (Julian day 95) and continuing until 24 May (Julian day 144). Larvae were produced near the central strait every day. They then were advected and diffused in the grid area according to given values of the parameters. Finally the concentration obtained from the model for each size group during the 5-day period of 20–24 May was averaged to show the expected larval abundance of each size group in late May 1981.

The mortality parameter in Equations (1) and (2) was derived in Kim and Gunderson (1989) from observed data during two consecutive surveys (i.e., 26–30 April and 20–24 May, 1981) assuming that larvae stayed in the survey area and that the larval population decreased exponentially with time. If, however, some of the larval cohort that existed in the sampling area during the first survey drifted out of the area by the second survey (called out-fraction in this paper), then the mortality rate must be an overestimate. The out-fraction of larval abundance—which is the ratio of the larval abundance evicted from the simulation box in Figure 1 to the total larval abundance assuming no dispersion—is computed after simulation, and this computation can be used to estimate a new mortality value in an exponentially decreasing population with time:

$$Z^*(L) = -\frac{1}{\Delta T} \ln \left\{ \frac{d_2/(1-f)}{d_1} \right\}$$

$$= -\frac{1}{\Delta T} \ln \left\{ \frac{d_2}{d_1} \right\} + \frac{1}{\Delta T} \ln(1-f) \quad (3)$$

where $Z^*(L)$ = revised instantaneous daily larval mortality,
 ΔT = time difference in days (24 days) between surveys,

d_1 and d_2 = observed larval densities during late April and late May surveys, respectively, and
 f = out-fraction.

Note that the first term of the right side means the daily mortality rate for the closed population, which was used in Kim and Gunderson (1989), and that the second term is the correction factor due to dispersion. Once the new mortality rate was determined, it was used for the second simulation to obtain a revised estimate of larval abundance in late May 1981.

Parameter estimation

Some parameters for the model were available from other studies. Kim and Gunderson (1989) found two dominant larval cohorts during April and May surveys, and assumed that 4–5 mm larvae in late April had grown to 8–9 mm, and regarded this group as cohort 1. Also, the 5–6 mm size class in late April and the 9–10 mm size class in late May were treated as cohort 2. By comparing the larval abundances of these two cohorts, they estimated an instantaneous daily larval mortality of 0.086 and a daily growth rate of 0.17 mm.

Daily larval production was derived from daily egg production and time-specific egg mortality during development (Kim and Gunderson 1989). A rapid increase in daily larval production occurred in mid-April, and most larvae were produced during late April (Table 1). Toward the end of the spawning season, larval production decreased but tended to be prolonged due to decreased egg mortality late in the spawning season.

Advective velocities and turbulent diffusivities were derived by examining changes in the distributional centroids and variances of several larval size groups. We treated the distribution of a certain size of larvae at a specific time as a single dispersing system in Shelikof

Table 1

Estimates of daily larval production of walleye pollock after 14-day incubation period in Shelikof Strait during spring 1981, using estimated daily egg production and time-specific egg mortality in Kim and Gunderson (1989). Dates 95 and 144 denote 5 April and 24 May, respectively.

Date of year	Daily larval production ($\times 10^6$)	Date of year	Daily larval production ($\times 10^6$)
95	23	120	1103
96	48	121	1027
97	77	122	938
98	111	123	835
99	151	124	717
100	197	125	584
101	250	126	435
102	311	127	270
103	380	128	37
104	458	129	38
105	546	130	37
106	1016	131	38
107	1557	132	38
108	2174	133	39
109	2873	134	39
110	3087	135	38
111	3311	136	38
112	3545	137	38
113	3790	138	37
114	3294	139	37
115	2711	140	36
116	2034	141	35
117	1257	142	34
118	1217	143	33
119	1166	144	32

Strait. The change in the centroids in along- and cross-strait coordinates for three size groups (4–5, 5–6, and 6–7 mm) from each survey was used to estimate advection, assuming that larvae were hatched in the same area and that these larvae were not flushed out of

Table 2

Comparison of walleye pollock larval mortality rates, advection rates, and diffusion coefficients in Shelikof Strait during spring 1981.

	Instantaneous daily mortality	Advection rate (km/day)				Diffusion coefficients (km ² /day)	
		<i>u</i>		<i>v</i>		K_x	K_y
		April	May	April	May		
This paper	0.070	4.2	2.7	1.3	0.4	65.2	3.6
Reed et al. (1989)	0.063	4.3	—	—	—	43.2	—

Shelikof Strait. Estimates of u and v , from regression analysis (see Table 1 in Kim and Kendall (1988) for data) were 4.2 and 1.3 km/day in April, and 2.7 and 0.4 km/day in May, respectively (Table 2). Because the variance of the horizontal distribution is a suitable measure of the spread of the substance (Bowden 1983, Okubo 1971), the change in variance (i.e., S_x^2 and S_y^2 for along- and cross-strait directions) with time provides a reasonable measure of the diffusion coefficient;

$$K_x = \frac{1}{2} \frac{dS_x^2}{dt} \cong \frac{S_{x,t1}^2 - S_{x,t0}^2}{2\Delta t} \quad (4)$$

$$K_y = \frac{1}{2} \frac{dS_y^2}{dt} \cong \frac{S_{y,t1}^2 - S_{y,t0}^2}{2\Delta t} \quad (5)$$

where $S_{x,t0}^2$, $S_{x,t1}^2$, $S_{y,t0}^2$, and $S_{y,t1}^2$ are the spatial variances at time t_0 and time t_1 in along- and cross-strait directions, and $\Delta t = t_1 - t_0$. The variances of two dominant larval cohorts were calculated as in Kim (1987). Variances of larval distribution were much increased in a month, and along-strait components were dominant compared with those in the cross-strait direction (Table 3). The estimated K_x for these two cohorts were 79.6 and 50.7 km²/day (average 65.2). For K_y , the values were 1.0 and 6.3 km²/day (average 3.6) (Table 2).

Simulation results

Spatial distribution and abundance of larvae

The model distribution of larvae in late May after 50 days of simulation was similar to that observed. Two major larval cohorts, 8–9 mm and 9–10 mm size groups, were selected for comparing the model and observed distributions (Fig. 2). In general, the simulated centroids of distribution were close to the densest patches of the larvae, and the area of larval distribution and contour levels of the larval concentrations were not very different from those observed. The simulation demonstrated the elliptical pattern of distribution, which was elongated in the along-strait direction, and the southwesterly movement of centroids from the main hatching area. The first (8–9 mm) and second (9–10 mm) cohorts drifted 92 km and 114 km, respectively, from the source point after hatching.

The maximum size of larvae was 12 mm, and the abundance of larvae and the out-fraction in each size group were computed. Comparing the simulated values with the observed ones, we found that the results were very close (Table 4). Also, as expected, the effect of out-fraction on larval distribution was more important for the larger size group than the smaller group. This

Table 3

Spatial variances of larval distributions of two major cohorts of walleye pollock larvae in Shelikof Strait during late April and late May 1981. The larval sizes of cohorts 1 and 2 in late April are 4–5 mm and 5–6 mm, and they grow to 8–9 mm and 9–10 mm in late May, respectively.

		Variance (km ²)	
		late April	late May
Cohort 1	S_x^2	1292	5114
	S_y^2	563	609
Cohort 2	S_x^2	3066	5500
	S_y^2	302	606

was caused by the larger larval size having a higher out-fraction value. Negligible amounts of small larvae were advected from the simulation box, but over 50% of the large larvae were removed. Among total larval abundance, about 20% were flushed out of the simulation area. This concept of out-fraction due to diffusion and advection might change the larval abundance and mortality previously reported by Kim and Gunderson (1989). Even though their derived estimates agreed well with observed ones, their results should be reconsidered because the areas involved for abundance estimates were not the same. Our study revealed that their sampling area, which was similar to our simulation box, was only part of the area of larval occurrence in Shelikof Strait. Therefore the total larval abundance should be higher than they observed, and the simulated abundance within the simulation box should be close to that observed. In Table 4, the reason for the smaller larval abundance in the simulation box (3.37×10^{12}) than observed (4.15×10^{12}) might be due to their overestimate of the mortality rate.

Re-estimation of larval mortality and abundance

The first approximation of larval mortality has been recalculated using the out-fraction in Table 4. By applying the out-fractions of the two major cohorts to Equation (3), we computed revised instantaneous daily mortalities of 0.081 and 0.059 from the first and second cohorts, respectively (average 0.070). Assuming no significant change in diffusion coefficients, the revised mortality rate was used for the second computer simulation of the diffusion-advection model. Figure 3 revealed that the second simulation resulted in a 50% increase in the total larval abundance (6.21×10^{12}) in Shelikof Strait, compared with the first simulation (4.23×10^{12} from Table 4). The size-specific abundance

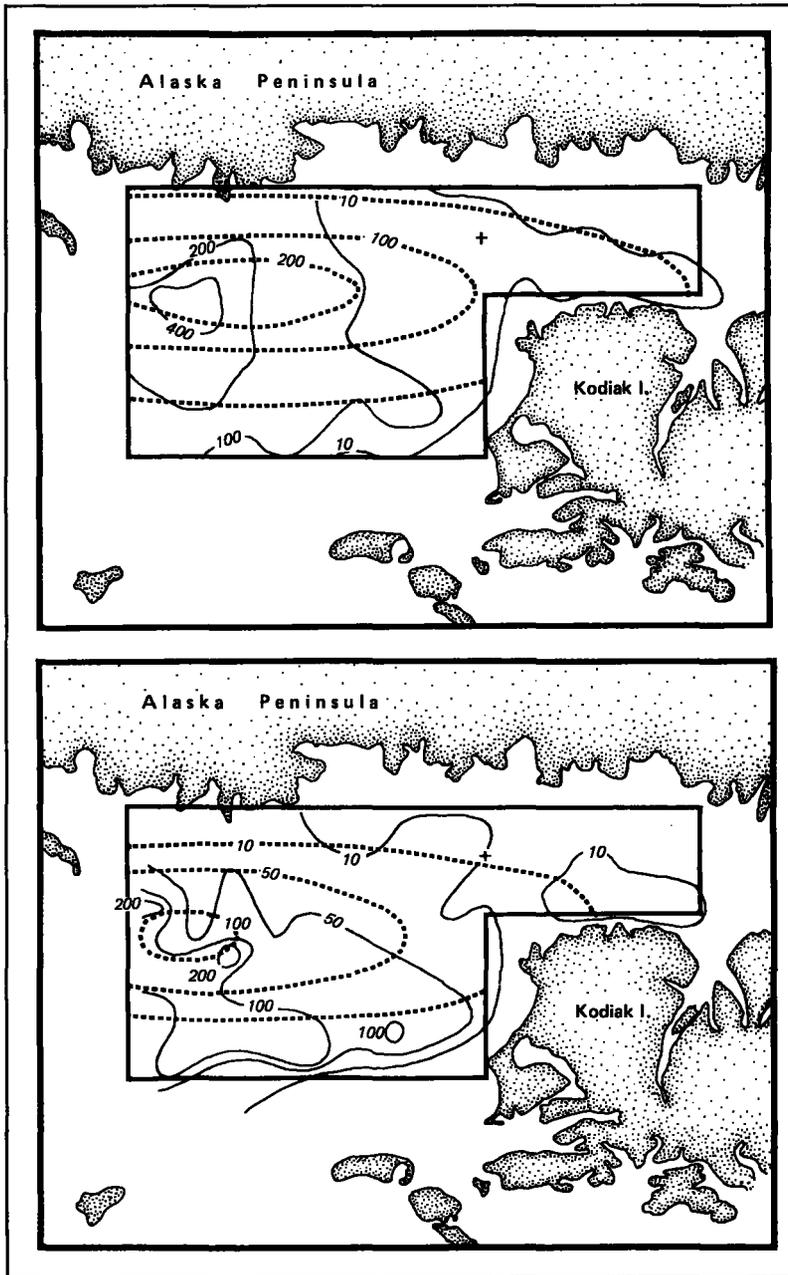


Figure 2
Contours of observed (—) and estimated (---) distributions of (a) 8-9 mm and (b) 9-10 mm walleye pollock larvae during late May 1981. Source points of larvae are indicated by (+) in each map.

of larvae within the simulation box was compared with the observed values, because the area used in the simulation could be regarded as the survey area. In general, the trends in size abundance curves, as well as the absolute abundances, were very similar to one another. The abundance of two major cohorts, both observed and simulated, consisted of about 50% of the total abundance.

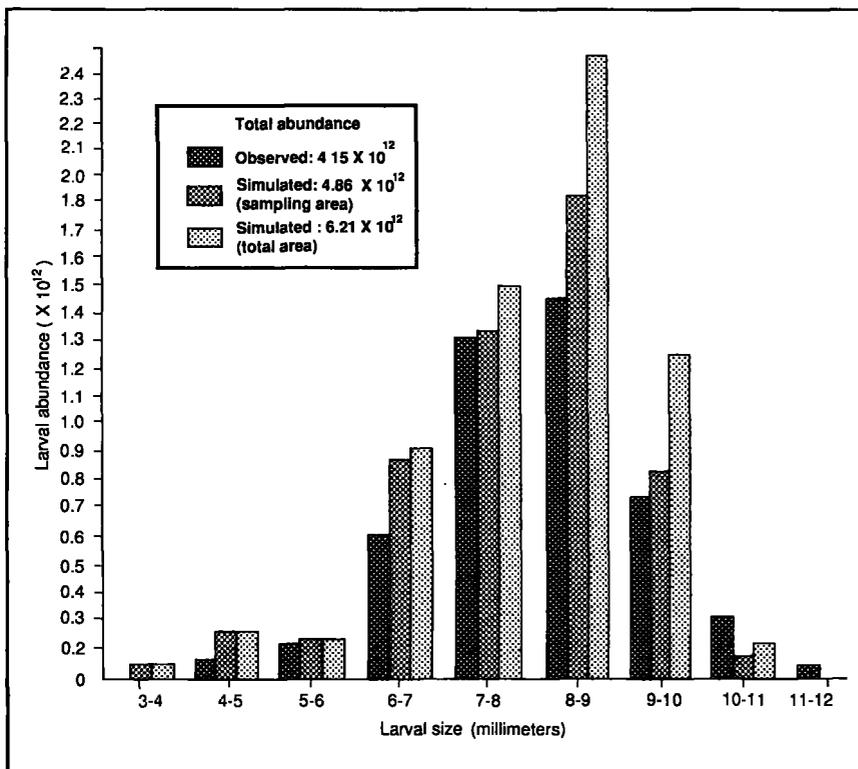
Discussion

The application of a diffusion-advection model to examine the dispersal of larvae helps not only to explain spatiotemporal distribution of abundance but also to revise estimates of population parameters such as larval mortality. Difficulties in determining parameter values, however, often arise in this kind of study. In describing plankton distribution, the physical properties (diffusion coefficients and advection rates) often

Table 4

Simulated abundances of walleye pollock larvae in Shelikof Strait during late May 1981 resulted from the first computer simulation, using a daily instantaneous mortality rate of 0.086 and observed values derived from Kim (1987).

Larval size (mm)	Simulated larval abundance ($\times 10^{12}$)			Observed larval abundance ($\times 10^{12}$)
	Total	Simulation box	Out-fraction	
<4	0.033	0.033	0.0000	0.004
4-5	0.157	0.157	0.0006	0.057
5-6	0.112	0.111	0.0128	0.111
6-7	0.627	0.593	0.0538	0.496
7-8	1.011	0.881	0.1281	1.221
8-9	1.509	1.120	0.2576	1.350
9-10	0.701	0.436	0.3786	0.627
10-11	0.073	0.035	0.5200	0.204
11-12	0.008	0.003	0.6367	0.058
Total	4.230	3.369	0.2036	4.149

**Figure 3**

Simulated larval abundance from the second computer simulation using a revised mortality rate of 0.070/day, and observed larval abundance in Table 3. Notice the difference in the simulated abundances from the sampling area and the total area.

are calculated from oceanic current data, wind speed, temperature distribution, or results of dye experiments (Talbot 1974, Talbot 1977, Power and McCleave 1983, Sundby 1983), even though they do not represent the actual diffusion and advection of dispersing organisms. The collection of diffusion coefficients and advection rates from several sources is very important to understand the characteristics of the oceanic situation. Aside

from measuring the dispersion using inert tracers, the use of plankton sampling data to derive these parameters has been limited because of the complexity of biological systems in the sea. The mobility and mortality of larvae may bias in estimating such parameters. The emphasis of this paper is how biological sampling data can be used for estimating physical properties, when the swimming ability of the larvae is not significant.

Reed et al. (1989) estimated parameters based on current measurement and larval patch in Shelikof Strait. By examining the abundance in small areas around the densest larval patches found in April and May surveys, they estimated an instantaneous mortality rate of 0.063/day and an advection rate of 4.3 km/day (Table 2), which are in excellent agreement with our estimates. Also, the estimation of eddy diffusivity in the along-strait direction of 43.2 km²/day by Reed et al. (1989) did not differ greatly from our mean value of 65.2 km² (Table 2), even though the former was derived from moored current meter data in the surface layer (56 m) and the latter from larval distribution. These estimates are realistic only in a mean sense, because they vary in both time and space.

The diffusion process tends to destroy larval aggregation until larvae reach a certain size, so that patchiness will decrease with time. The Lloyd Patchiness Index (LPI) has been frequently used for describing aggregations of organisms (Lloyd 1967), and Kim (1987) discussed changes in LPI of walleye pollock larvae as they grew. The smaller size groups of larvae usually had a higher LPI, but it decreased until a size of about 10 mm because of dispersal of the larval patch. For sizes greater than 10 mm, although their contribution to the total larval abundance was very small, the LPI increased with length, perhaps because of reaggregation of the larvae as their swimming ability increased. If a larval retention mechanism worked for large larvae (10–12 mm) in Shelikof Strait due to increased swimming ability, that might explain the higher larval abundance from field samplings than that from the simulation shown in Figure 3. Similar examples of larval aggregation (i.e., initially patchy, dispersing until a larval size of around 10 mm, and then patchy again) were reported for northern anchovy and jack mackerel off California (Hewitt 1982).

The expected total larval abundance from the first simulation was almost identical to that in Kim and Gunderson (1989) because the same parameter values were used. By adding the concept of diffusion and advection to their model, elaborations on mortality and expected abundance of walleye pollock larvae were made. Based upon good agreement between observed and simulated results, this paper has emphasized that dispersion (or emigration) of organisms is important in the field of population dynamics.

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