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FISHERIES OCEANOGRAPHY OF THE SOUTHEAST BERING SEA:

Simulated dispersal of herring and sand lance larvae in Port Moller, Alaska, using a three-dimensional hydrodynamic model

FINAL REPORT

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ABSTRACT

Studies of Pacific herring and sand lance larvae in the Port Moller estuary have shown that these larvae are retained within the estuary, suggesting that retention may be important for successful year-class formation. To determine the physical and biological mechanisms involved in retention, a three-dimensional numerical hydrodynamic model of the Port Moller estuary was used to simulate dispersal of fish larvae.

Directed motion modeling reproduced the observed densities of herring larvae far better than passive modeling. The best fit ($r^2 = 0.30$) between observed and computed herring densities was obtained by assuming that herring swam against the current at all times. The fit increased substantially ($r^2 = 0.52$) when comparisons were restricted to observed densities measured after larvae were fully-recruited to the sampling gear.

In contrast to herring, passive drift of sand lance larvae produced roughly the same fit ($r^2 = 0.54$) between observed and computed densities as did various hypotheses of directed-motion ($r^2 = 0.51$ to 0.57). The fit was most sensitive to location of hatch; the worst fit ($r^2 = 0.37$) occurred when hatching was placed close to the eastern shore of lower Moller Bay, and the best fit ($r^2 = 0.57$) occurred when hatching was placed close to the western shore near the entrance to Herendeen Bay.

We conclude that herring and sand lance have different strategies for larval retention in Port Moller, and that these strategies may have evolved in response to their need to stay inside specific nursery areas of the estuary. Most herring larvae are retained in upper Moller Bay, so directed motion may be a necessary strategy to stay in those relatively turbulent waters, but most sand lance larvae are retained in the quieter waters of Herendeen Bay and they can move there by passive drift on tidal currents. For both species, the location of the eggs in relation to local oceanographic features appears to be crucial for larval retention.

Key words: Pacific herring, *Clupea pallasi*, Pacific sand lance, *Ammodytes hexapterus*, larvae, dispersal, numerical hydrodynamic modeling, southeastern Bering Sea

NOTICE

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

This is the final report of computer simulations of larval fish dispersal in the Port Moller estuary of the southeastern Bering Sea. This research program was supported by the U.S. Minerals Management Service (MMS) for the purpose of collecting information on the early life history of forage fishes in the southeastern Bering Sea. This information will be used by MMS to assess the potential impact of oil and gas development in the Bering Sea on population dynamics of forage fishes.

Target Species

Two species of fish were chosen for study: Pacific herring, *Clupea pallasi*, and Pacific sand lance, *Ammodytes hexapterus*. Herring was chosen because it is commercially important, it is prey for larger animals of commercial, ecological and cultural importance such as salmon and marine mammals, and because its eggs are laid in intertidal and subtidal habitat and its larvae rear in coastal bays and estuaries (Alderdice and Hourston 1985; Haegele and Schweigert 1985; Hay 1985). This is the same habitat that is most vulnerable to damage from short-term spills of hydrocarbons from offshore oil and gas wells or from long-term contamination from shoreline industrial development such as pipelines and oil terminals.

Although sand lance are not commercially fished, they are, like herring, an abundant prey species for larger animals. They also lay their eggs in subtidal habitat in coastal waters, and their larvae rear in coastal embayments, at least in the southeastern Bering Sea (McGurk and Warburton 1992a, 1992b).

Study Area

The Port Moller estuary was chosen as the study area partly because it supports the largest herring sac roe fishery on the northern shore of the Alaska Peninsula (McCullough 1990), and so there would be sufficient numbers of herring larvae to justify an intensive study of their population dynamics (McGurk 1989c, 1991). Just as important, however, was the unique physical oceanography of Port Moller - it is an enclosed body of water that forms a natural study unit (Figure 1) - and the fact that Herendeen Bay, one of the two major bays that make up the Port Moller estuary (Moller Bay is the other), supports populations of red king crab (*Paralithodes camtschaticus*) and blue king crab (*P. platypus*). These crabs were the subject of a parallel study, also supported by MMS, conducted by the Crustacean Ecology Group of the University of Washington (Wainwright et al. 1992).

Port Moller is the largest embayment on the northern shore of the Alaska Peninsula. It exchanges water with Bristol Bay, the southeastern part of the Bering Sea. The estuary has a total area of 876 km^2 enclosed in four bays: Mud Bay, Nelson Lagoon, Herendeen Bay and Moller Bay. At low tides, Mud Bay and Nelson Lagoon are dewatered and the rest of the estuary can only be navigated through three narrow channels. Almost all plankton stations were placed in these channels.

The estuary contains two distinctly different physical and biological environments (McGurk et al. 1992). Moller Bay contains extensive mud flats which are dewatered at low tides, a shelf region that is rarely dewatered, and a narrow channel that is never deeper than about 30 m. The lower and middle sections of Herendeen Bay also contain mud flats, a shelf region and two narrow channels: Hague and Johnston Channels. The water in these areas is well-mixed due to strong tidal flushing and frequent storm events, and there is little or no vertical stratification.

Upper Herendeen Bay contains a 100 m-deep fjord-like basin. This basin has the lowest flushing rate of any part of the estuary and it is the only part of the estuary that has significant vertical stratification, with a thermocline at about 30 m depth. Concentration of prey for herring and sand lance larvae is higher in the basin than in any other part of the estuary.

Numerical modeling of the hydrodynamics of Port Moller showed the presence of two convergences of surface currents (McGurk et al. 1992: Appendix C). Both are caused by the collision of an anti-seaward current from the north with a baroclinic seaward current from the south. The strongest convergence is located south of Harbor Point in upper Moller Bay. The weaker convergence is located at the northern lip of the deep basin in Herendeen Bay.

Previous Research

This is the fifth report in a series of five on the fisheries oceanography of the southeastern Bering Sea. The series was preceded by a pilot study of larval herring population dynamics conducted in Auke Bay, Alaska (McGurk 1989b; McGurk et al. in press). The first report in this series described the growth, mortality and dispersion of Pacific herring larvae in Port Moller, based on a 2 wk reconnaissance of the estuary in early June, 1989 (McGurk 1989c, 1991). This was followed by a plan for fisheries oceanographic research in Port Moller (McGurk et al. 1989). The third report described the population dynamics of herring larvae in the estuary, based on a 4 month long survey in spring-summer of 1990 (McGurk et al. 1992). It also described the biological and physical oceanography of the estuary with the assistance of a numerical hydrodynamic model. The fourth report described the population dynamics of sand lance larvae in the estuary, based on ichthyoplankton catches taken in 1990 (McGurk and Warburton 1992a, 1992b).

One of the most important conclusions of the last three studies was that Port Moller is a nursery for herring and sand lance larvae. Wainwright et al. (1992) have shown that it is also a nursery for red king crab and blue king crab larvae. This suggested that some physical or biological features of the estuary were important to survival of herring and sand lance larvae, and so may be important factors controlling year-class strength of the local stock of herring and sand lance.

Herring

Analysis of ichthyoplankton surveys showed that spawning herring entered the estuary in May-June, 1990, in five waves. Each wave split into two groups, one spawning at the head of Moller Bay and the other spawning at the head of Herendeen Bay. After incubating for several weeks, the demersal eggs hatched and larvae dispersed into the estuary. Despite the high flushing rate of the outer estuary, the centroids (= centers of distribution) of herring larvae in Moller and Herendeen Bays never crossed the boundary between the estuary and Bristol Bay, although there was some leakage of larvae across the boundary. In fact, the herring larval centroids never moved seaward of convergences of surface currents that lie within the estuary about one-half to one-third of the distance between the heads of the bays and the boundary of the estuary.

These results strongly suggested that Port Moller has at least one, and perhaps two, herring larval retention zones as defined by Iles and Sinclair (1982). The central ideas of their hypothesis, which was actually first proposed in a less developed form by Stevenson (1962), are that retention zones are physical oceanographic features defined by fronts or convergences, that herring spawning takes place only inside retention zones, and that herring larvae that are transported out of a zone do not spend enough time in it to imprint on it and so they do not return there to spawn. In effect, they are lost to the population even though they may survive to spawn elsewhere. This hypothesis predicts that recruitment to a herring stock is controlled by annual changes in the size of the retention zone or in the rate at which herring larvae "leak" from the zone. The size of a zone is defined by physical oceanographic processes driven by oceanographic or meteorological forcing.

Sand lance

Analysis of ichthyoplankton samples taken in 1990 showed that three waves of sand lance spawners entered Port Moller from mid-January to late May and laid their eggs on sand somewhere within lower Moller Bay north of Harbor Point. After incubating for 45 to 94 d, the eggs hatched and sand lance larvae dispersed within the estuary. Some sand lance larvae dispersed into Moller Bay, but most moved directly towards the head of Herendeen Bay in the opposite direction to the boundary of the estuary.

There is no "retention zone" theory for sand lance that can be used as a framework to understand the movements of their larvae. This is due to the fact that much less is known of the population dynamics of sand lances than the population dynamics of herring because sand lances are not commercially valuable fish.

Our Port Moller investigations showed clearly that the life history strategy of Pacific sand lance in Port Moller is different from that of herring. The most important difference is that sand lance and herring larvae are separated in space and time. Sand lance spawn in January-May, several months before the spring bloom, while herring spawn in May-July during the spring bloom. Sand lance spawn in the outer estuary, whereas herring spawn at the heads of the estuary. The major nursery area for sand lance larvae and juveniles is the deep basin at the head of Herendeen Bay, but the major nursery area for herring larvae in 1990 was upper Moller Bay, south of Harbor Point. We suggest that this segregation evolved to reduce competition for food between the larvae of the two species, since they feed on the same prey, mainly the naupliar, copepodite and small adult stages of pelagic copepods (McGurk et al. 1992).

Another feature that separates sand lance larvae and herring larvae is that the centroids of sand lance larvae crossed the weak convergence zone in Herendeen Bay on their way to the head of that bay, although the centroids did not cross the major convergence south of Harbor Point in Moller Bay. The centroids of herring larvae did not cross either convergence.

These observations suggest that herring and sand lance larvae may have different mechanisms of dispersal and retention.

Objective

The findings of the previous three studies on forage fishes in Port Moller raised new questions: did larvae of both species drift passively, so that their dispersal in the estuary was entirely dependent on waterbody dynamics? or did larvae employ a combination of passive drift and directed motion? If some portion of their transport was self-directed, then what strategy of horizontal and vertical movement did larvae follow to avoid being flushed into the southeastern Bering Sea?

Answers to these questions would assist in any future understanding of year-class variation in the Port Moller stocks of herring and sand lance, particularly with regard to the role of hydrodynamic and meteorological forcing. This "understanding" may take the form of a conceptual model of year-class formation, or of simulation models of herring and sand lance population dynamics that incorporate hydrodynamics. It would be a step towards successful long-term management of the stocks, and towards accurate assessments of the impacts of industrial development in the southeastern Bering Sea on herring and sand lance.

Since Port Moller has a complex current pattern, these questions could only be answered by simulation experiments with a hydrodynamic model of the estuary.

Therefore, the primary objective of this component of our Port Moller studies was to model larval fish dispersal in the estuary using a three-dimensional model of waterbody dynamics. By doing so, we hoped to identify which physical features of the estuary were crucial for larval fish retention, and which mechanisms were used by larvae to retain themselves within the estuary.

Organization of Report

In this report, we describe how the General Longitudinal, Lateral and Vertical Hydrodynamic and Transport (GLLVHT) model that was originally used to describe the physical oceanography of Port Moller was modified to simulate the motion of fish larvae. Then, we describe how the dispersal of herring and sand lance larvae was simulated under a variety of hypotheses about the mechanism of dispersal.

Experiments were done separately for herring and sand lance by Triton's primary sub-contractor: Dr. John E. Edinger and Mr. Edward M. Buchak of J. E. Edinger Associates, Inc. The two sets of experiments are reported separately in the next two chapters of this report. The chapter on herring contains most details of the model setup, and the chapter on sand lance describes its application to sand lance. The main findings of the two sets of experiments are discussed together in the Discussion.

The larval transport modeling described in this study was based on the standard approach used to model waterbody dynamics - the Eulerian form of the advective-dispersive transport relationship in three spatial dimensions and time. It was modified for fish larvae by assigning swimming speeds and a mortality rate to the larvae, instead of allowing them to drift as passive, immortal particles. The major technical problem of this kind of modeling was relating larval swimming speeds to waterbody velocities. This was done by developing directed motion modeling, which assumes that the direction in which larvae move is related to the waterbody current direction.

DIRECTED MOTION MODELING OF HERRING LARVAE

In this section of the report, we describe the basic transport relationships for fish larvae in the GLLVHT hydrodynamic model, and then we test various assumptions for herring larvae, beginning with passive transport with and without mortality, proceeding to directed motion, and ending with the inclusion of vertical motion.

Larval Transport Theory

Advective-dispersive transport relationships were originally developed to study dissolved constituents of water such as salinity. These models have been quite successful in predicting transport of these constituents because their temporal and spatial distributions are usually smooth and continuous. These relationships have been used with varying degrees of success for ecological problems concerning animal and plant dispersion (Pielou 1969; Okubo 1980; McGurk 1989a). They are reasonable descriptions as long as distributions of animals and plants are not too patchy in space and time.

Basic transport relationship

In our model, the advective-dispersive transport relationship in three dimensions and time was extended to include fish velocities in three dimensions (u_f, v_f, w_f) and mortality (Z). The modified advective-dispersive relationship was

$$\partial N/\partial t + \partial UN/\partial x + \partial VN/\partial y + \partial WN/\ z - \partial(D_x \partial N/\partial x)/\ x - \partial(D_y \partial N/\partial y)/\partial y - \partial(D_z \partial N/\partial z)/\partial z = -\partial u_f N/\partial x - \partial v_f N/\partial y - \partial w_f N/\partial y - ZN \qquad (1)$$

where U, V, and W were longitudinal, lateral and vertical water velocities, D_x, D_y, and D_z were longitudinal, lateral and vertical water diffusion coefficients, and N is larval density.

The solution of equation (1) was known to the same detail with which the velocity field (U, V, W) is known as a function of time and space. In the case of numerical modeling of a waterbody, the velocity field was determined from hydrodynamic relationships as described in Appendix C of McGurk et al. (1992). The longitudinal dispersion coefficients were a function of the scale of modeling (Okubo 1971, 1980).

The vertical dispersion coefficient was a function of the vertical shear of the horizontal velocities and of the local Richardson number, which in turn was a function of the vertical density gradient determined from salinity and temperature.

The larval transport problem required describing the larval velocity components as a function of age, space and time. The directed motion modeling developed in this study was based on examining different possible relationships between the larval velocity components and the waterbody current direction.

Summary of hydrodynamic computations for U, V and W

The GLLVHT model is based on the longitudinal, lateral and vertical equations of momentum, continuity and constituent transport described by Edinger and Buchak (1980, 1985, 1989) and McGurk et al. (1989). The formulation includes the vertically varying longitudinal and lateral momentum balances, the vertical momentum in the form of the hydrostatic approximation, local continuity, the free-water surface condition based on vertically integrated continuity, and longitudinal, lateral and vertical transport of any number of constituents. Constituents that determine density such as temperature and salinity are related to momentum through an equation of state. The vertically varying longitudinal and lateral momentum balances include local acceleration of horizontal velocity, horizontal and vertical advective momentum transfer, the horizontal pressure gradient, and horizontal and vertical shear stress. Included in the latter are the surface wind stress and the bottom stress due to friction. The horizontal pressure gradient includes the barotropic surface slope and the baroclinic vertical integral of the horizontal density gradient, which is the dominant term of density-induced convective circulation.

The time-varying solution technique of the model is based on an implicit scheme that results from the simultaneous solution of the longitudinal and lateral momentum equations and the free-water surface equation of vertically integrated continuity. This technique results in the surface long wave equation that is solved on each time step to give the water surface elevations, from which the vertical pressure distribution can be determined. The longitudinal and lateral momentum balances are then computed, followed by internal continuity and then constituent transport. Upwind differencing is used for the advective processes in the momentum and constituent transport balances. Vertical turbulent transfer of momentum and constituents is determined from the vertical shear of horizontal velocity and a density gradient dependent Richardson number function.

Setup of the GLLVHT model for the Port Moller Estuaries is given in Appendix C of McGurk et al. (1992). The time varying input data are tides at the mouth, freshwater inflows at the heads of the arms, and meteorological data for wind-shear and surface heat exchange computations.

Difference form of GLLVHT model

The numerical computations of advective and dispersive transport in GLLVHT are in the form of a box model with the velocities and dispersion coefficients given at the faces of the box and the larval densities in the center of the box. This arrangement is called a space-staggered grid. An undesirable consequence of this arrangement is that upwind differencing can lead to numerical dispersion. All numerical models suffer from this problem. In GLLVHT, numerical dispersion was minimized by the use of implicit computation, which allowed the use of large time steps. To learn of the significance of numerical dispersion to our computations, we tested the case in which herring larval velocities were assumed to be directly opposite the current velocities. For example, $u_f = -U$. Any dispersion in that case could only be due to numerical dispersion. The test showed no significant influence of numerical dispersion. Higher order methods of transport computation are presently under investigation to eliminate the problem of numerical dispersion (Buchak et al. 1990, 1991).

Passive Transport Modeling

The first test of the suitability of equation (1) in numerical form was to calculate densities of herring larvae that resulted from the assumption of no larval motion ($u_f = 0$, $v_f = 0$, and $w_f = 0$) and no mortality ($Z = 0$). Thus, the number of herring larvae at hatch for each sub-cohort was distributed over time and space as if the larvae were a conservative substance like salt.

The second test of equation (1) in numerical form was to assume no larval motion, but non-zero larval mortality. The inclusion of mortality in the modeling was expected to improve the results over the conservative case.

In the model and data comparisons run in these and other analyses, the model was run completely independent of the data. A modeling formulation was stated, the model was tested and run on an i860-based mini-computer, and the results were copied to a file of densities for each survey date and station for each sub-cohort. This file was transferred by disk to a 286 PC for comparison to the data. The field data were kept in the 286 PC and were compared to the model results only when making plots of observed versus computed densities or when computing the correlation coefficient of the observed versus computed comparisons.

Model input data

The required input for each sub-cohort was the hatch date, the location of the hatch, the initial number in the hatch and the mortality rate (Table 1). The numerical model also required specifying the depth of water column over which the initial number in the hatch is distributed. Sensitivity of the results to different values of the initial depth were examined in this report.

Basis of comparison of cases

The statistic used for determining the significance of results for each case and for comparing one case to another was the coefficient of determination, r^2, computed from a regression of the logarithm of computed density on the logarithm of observed density. It is useful because it is easy to compute, and the critical r^2 that marks the edge of statistical significance is known. For 100 or more data points, which was the case for almost all of our comparisons, the critical r^2 was 0.195 at a 5% level of significance and 0.254 at a 1% level of significance (Neville and Kennedy 1966).

Comparisons without and with mortality

The comparison of computed and observed values without mortality had an r^2 of 0.11 (Figure 2). Almost all the computed values were above the line of equality, showing that this case overcomputes the observed densities by almost an order of magnitude throughout the full range of densities.

The comparison with mortality had an r^2 of 0.19 (Figure 3). Inclusion of mortality reduced the computed values by almost an order of magnitude and gave a relatively even distribution of points about the line of equality.

Neither of these two r^2 were statistically significant. Thus, the case of passive motion does not appear to be a reasonable description of the transport of herring larvae in the Port Moller estuary.

Directed Motion Modeling

Directed motion modeling assumed that larval fishes swim in a direction related to the direction of the local water current. For example, larval fish may swim with the current, or swim against the current, or swim at an angle to the direction of the current. The only rule followed in all cases was not to introduce any arbitrary or artificial empirical parameter into the modeling beyond those necessary for describing the larval length-age relationship.

Derivation of directed motion modeling

Larval velocities were incorporated in the advection terms of equation (1) by modifying the standard expression for the sinking velocity of a particle and using it for all three spatial dimensions, not just the vertical dimension. Our reasoning was: (1) the term $(U^2 + V^2 + W^2)^{0.5}$ is the current speed at a point in the grid of the model; (2) the ratio of U, V or W to current speed is the proportion of current speed in each coordinate direction; (3) let L_{ss} be larval swimming speed, which is usually a function of length or age; (4) therefore, multiplying L_{ss} by the proportion of current speed in any one direction gives the larval fish velocities:

$$u_f = L_{ss} \cdot U/(U^2 + V^2 + W^2)^{0.5} \tag{2}$$

$$v_f = L_{ss} \cdot V/(U^2 + V^2 + W^2)^{0.5} \tag{3}$$

$$w_f = L_{ss} \cdot W/(U^2 + V^2 + W^2)^{0.5} \tag{4}$$

The algebraic sign assigned to L_{ss} determines if the larval motion is against or with the current.

L_{ss} is the most important parameter of the directed motion computation. As a general rule, cruising speeds of fish are about one body length·s^{-1} (BL·s^{-1}), giving a swimming speed for older herring larvae (20-40 mm long) of 2 to 4 cm·s^{-1}.

Hypotheses of directed motion

Different hypotheses of directed motion were first tested using all larval densities from all nine sub-cohorts. Then, the most reasonable hypotheses were tested for individual sub-cohorts (Table 2).

Run 3.04 was the case of transport with mortality and with larval motion in the direction of the current. L_{ss} was assumed to be one BL·s^{-1}. This case had an r^2 of 0.06, which was not significant, and which suggests that larval motion in the direction of the current is not a viable hypothesis.

Run 3.05 was the case for larval motion directed against the current. L_{ss} was assumed to be one BL·s^{-1}. This case had an r^2 of 0.29, which was highly significant, and which suggests that herring larvae were generally oriented into the current.

Run 3.06 was the case in which larval swimming speed was the exact negative of current speed, for example $u_f = -U$. Thus, any dispersal of larvae could only be due to numerical dispersion caused by the setup of the model. As discussed above, this case has little biological value - it was tested for the sake of determining the influence of numerical dispersion, which is an undesirable side-effect of evaluating the model with upwind differencing techniques. As shown in Table 2, the r^2 for this case is 0.15, which was not statistically significant. We concluded that numerical dispersion was not significantly influencing the results of the simulation experiments.

Runs 3.07 and 3.13 were similar to Run 3.05 except that they had larval swimming speeds of 2 BL·s^{-1} and 0.5 BL·s^{-1}, respectively. Both runs gave r^2 similar to that of Run 3.05, indicating that the speed of larvae was less important than their orientation in relation to currents.

Runs 3.08 and 3.14 assumed that the initial densities of larval herring were distributed with depth in different ways. Run 3.08 assumed that larvae hatched into shallow water <20 m deep, but Run 3.14 assumed that larvae were distributed up to

40 m deep at hatch. The results of these cases were similar to that of Run 3.05, indicating that the vertical distribution of initial densities had a limited influence on the final results.

Run 3.09 included the effect of daily vertical migration of larvae. It is discussed in more detail below in the section on vertical motion.

Run 3.11 included advected vertical transport of larvae and is an extension of Run 3.05. Since this run gave similar results to Run 3.05, we conclude that vertical advection on the order of $1.0\ \mathrm{mm \cdot s^{-1}}$ is not important in larval transport.

Run 3.12 assumed a Gompertz growth curve, rather than linear growth as was assumed for all previous runs. The r^2 was 0.29, which was similar to that of Runs 3.05, 3.07 and 3.13, indicating that the form of the growth curve was less important than orientation to current.

We conclude that the best directed motion model is the case of larval motion against the current that was examined in Runs 3.05 and 3.11 (Figure 4). This case is chosen as the model to be examined in more detail below.

Model results over time and station

Not only should the chosen model (Run 3.05) result in a high r^2 when comparing observed and computed densities, the results should also be reasonable through space and time. Space-time comparisons were made using station versus time tables (Appendix A). In these tables, the sampling stations are across the top. Stations 21 to 23 are at the open boundary of the model; stations 38 to 47 go up Moller Bay and stations 25 to 37 go up Herendeen Bay. The results given in the tables are average densities over the depth of sampling at each station.

There is one important aspect to the observed larval densities that should be noted when comparing their temporal and spatial distributions to those computed by the model. In almost all sub-cohorts of herring, larval densities increased to a maximum over the first three weeks and then decreased with time after the maximum. The initial low densities were most likely due to incomplete recruitment of larvae to sampling gear because newly-hatched herring larvae dispersed first onto the shelves of the bays and then into the centers of the deep channels where plankton nets were used (McGurk et al. 1992). The decay of larval density with time after the date of full recruitment was due to a combination of mortality and dispersal.

Examination of the observed densities for the Moller Bay sub-cohorts 1M through 5M indicated that most larvae stayed in Moller Bay, although some larvae reached the boundary of the estuary within one or two weeks after hatching (McGurk et al. 1992). For the sake of convenience in regression analysis, herring larvae were divided into Moller and Herendeen Bay sub-cohorts by assuming that Moller Bay herring larvae did not enter Herendeen Bay.

The model reproduced some of these features, but not others. Most larvae were retained within Moller Bay, but some reached the open boundary a week or two after hatch. In contrast to our simple analyses of observed larval density, the model showed larvae from Moller Bay moving into Herendeen Bay as far south as station 37 within a few weeks of hatch. However, the densities of Moller Bay larvae at station 37 were an order of magnitude lower than the densities at station 27.

There is a transport mechanism that could carry Moller Bay larvae from around station 39 near Harbor Point into the mouth of Herendeen Bay near the junction of Johnson Channel and Hague Channel. In every tidal cycle the flood tide current entering off Port Moller deflects the intertidal surface current moving outward from Harbor Point toward Deer Island. This current could carry Moller Bay larvae from near station 39 in Moller Bay to station 27 in Herendeen Bay.

Examination of the observed densities of herring larvae for Herendeen Bay sub-cohorts 1H through 4H showed that most larvae were caught between stations 37 and 27 with the highest densities near stations 31 to 33. Herendeen Bay larvae did not reach the open boundary over the study period. Comparing computed larval densities at stations 37 and 27, we found sub-cohorts 1H and 2H showed densities over time about the same for the two stations, but sub-cohorts 3H and 4H showed densities higher at stations 37 than 27. Except for the latter discrepancies, the spatial and temporal distributions for the model and data in Herendeen Bay appeared reasonable.

Model comparisons for each sub-cohort

From the kind of scatter shown in Figure 3 we expected that the model reproduced the observed pattern of larval densities better for one sub-cohort than for others. Therefore, we examined the ability of the model to reproduce observed densities for each sub-cohort individually:

Cohort	1M	1H	2M	2H	3M	3H	4M	4H	5M
r^2	0.14	0.30	0.65	0.45	0.66	0.06	0.41	0.04	-
n	53	41	49	51	46	32	30	18	0

These results show that there were sub-cohorts for which the r^2 were much higher than the r^2 for the whole data set. This occurred for sub-cohorts from both Moller and Herendeen Bays, hence there was no bias toward one bay over the other.

Comparisons for fully-recruited data

We repeated the comparison of observed and computed larval densities for whole data sets, but included only those densities measured at or after the date of full recruitment of larvae to the sampling gear. The dates of full recruitment were:

Cohort	1M	2M	3M	4M	5M	1H	2H	3H	4H
Day	168	168	180	192	207	168	168	180	203

The results of the model with directed motion into the current (Run 3.07 in Table 2), were evaluated using only the fully-recruited data. The result was almost a doubling of the fit, to an r^2 of 0.52.

Comparison between Moller and Herendeen Bays

In Herendeen Bay, the mean horizontal water velocities estimated by GLLVHT ranged from 0.1 to 3 $cm \cdot s^{-1}$ (Appendix C of McGurk et al. 1992), much less than larval swimming speeds of 2 to 4 $cm \cdot s^{-1}$. Therefore, larvae could stem the current and move anywhere in Herendeen Bay from a very early age.

The hydrodynamics of Moller Bay are more complicated then Herendeen Bay. There is a major vertical flow reversal (= upwelling) between stations 39 and 38 with a surface current toward the head of the estuary and a bottom current toward the mouth. The magnitudes of the currents in this region are 5 to 15 $cm \cdot s^{-1}$, much greater than herring larval swimming speeds. Therefore, larvae in this area would tend to be forced up-estuary toward the spawning locations at the head of Moller Bay.

This reasoning leads to the prediction that the passive motion model (Run 3.03) would provide a better fit to the observed herring densities in Herendeen Bay than in Moller Bay, and that the directed motion model (Run 3.05) would provide a better fit to the observed herring densities in Moller Bay than in Herendeen Bay.

Running each model separately for each bay supported these predictions. The table below shows the r^2 (sample size) for each comparison:

Run	Both Bays	Moller Bay	Herendeen Bay
3.03	0.19 (320)	0.20 (178)	0.28 (142)
3.05	0.32 (320)	0.35 (178)	0.18 (142)

Inclusion of Vertical Motion

All modeling to this point has excluded daily vertical migration of fish larvae. However, most fish larvae have definite daily vertical migration patterns, and these patterns may influence their horizontal dispersal (Neilson and Perry 1990). In this section of the report, we describe simulations that incorporate vertical migration of herring larvae.

To describe vertical migration of herring and sand lance larvae in Port Moller, we measured densities of larval herring with Tucker trawls at 10 m-deep intervals at station 36 in the deep basin of Herendeen Bay and at station 39 in Moller Bay (McGurk and Warburton 1992a; McGurk et al. 1992). The trawls were repeated at 6 h intervals over a period of 24 to 36 h.

Vertical migration in herring was only observed at station 36, and it was quite shallow - never exceeding a movement of about 10 $m \cdot d^{-1}$. Vertical migration of herring was not observed at station 39, and vertical migration of sand lance larvae was not observed at either station. We concluded that the shallow water and tide-driven turbulence of most of Port Moller suppresses vertical migration in both species. The exception is the head of Herendeen Bay, and even there vertical migration of herring larvae was barely detectable.

To model the possible contribution of vertical migration of herring larvae to horizontal dispersal, we modeled the daily cycle of the depth of the centroids at station 36 with a diurnal harmonic relationship

$$z = 9.5 - 2.4\cos(2\pi wt) \tag{5}$$

where z is average depth (m) of the centroid, w is the period of diurnal variation (1 d^{-1}), and t is time in fractions of a day.

The vertical migration larval velocity was computed from equation (5) as

$$w_f = dz/dt = 4.8\pi w\sin(2\pi wt) \tag{6}$$

According to equation (6), vertical migration velocity was maximum downward at 06:00 in the morning, zero at the maximum depth at 12:00, maximum upward at 18:00, and zero at the minimum depth at 24:00.

Vertical migration velocity was incorporated in Run 3.09 (Table 2). Comparison of Run 3.05 to Run 3.09 indicates less agreement between computed and observed larval densities with vertical migration than without.

One possible reason for this finding is that the weekly larval sampling was conducted with oblique tows over a depth of 30 to 60 m. If there was an effect of vertical migration on observed larval density, then it could only happen if there was significant numbers of larvae entering or leaving from the bottom of the water column. Larvae leaving at the bottom should lower average water column densities and larvae entering should increase average water column densities. The horizontal trawl data, however, shows that the mean depth of the larvae was only 9.7 meters and there were much lower densities near the bottom of the water column. Thus, the effects of vertical migration might not be detectable from the average column densities used in the model and data comparisons.

DIRECTED MOTION MODELING OF SAND LANCE LARVAE

In this section of the report, we tested how well the three-dimensional hydrodynamic and transport model described in the previous section of the report predicted the distribution of sand lance larvae in Port Moller.

Hatch Rates, Mortality and Growth

In order to apply GLLVHT to each cohort of sand lance larvae it was necessary to know the: (1) rate of hatch over time; (2) larval mortality rate; (3) larval growth rate (from which to determine swimming speed); and (4) location of hatch.

Hatching of Pacific herring larvae was virtually instantaneous, and the locations of hatch of herring were known reasonably accurately. In contrast, the hatch rate of sand lance varied with time and the hatch location was known with much less accuracy.

McGurk and Warburton (1992a, 1992b) showed that the rate of sand lance hatching for each cohort is a Gaussian distribution with time

$$R(t) = [NT/(SD(2\pi)^{0.5})]\exp\{-[(t - t_m)/SD]^2\} \qquad (7)$$

where $R(t)$ = rate of hatching (number·d^{-1}) at day of year t, NT = total number hatched from beginning of hatch to end of hatch, t_m = mean day of year of hatch, and SD = standard deviation of the distribution of hatching (Table 3).

McGurk and Warburton (1992a, 1992b) showed that the three cohorts of sand lance started hatching into Port Moller on calendar days of 66, 113 and 142. However, the hydrodynamic and transport model simulations only began on day 126 because that was when the first temperature-salinity profiles and water surface elevations were taken. This meant that all hatching of cohort 1 was over by the time the model could run, and so all modeling described in this report was concerned solely with data from cohorts 2 and 3.

By starting on day 126, we lost about 13 d out of a total of 47 d from the hatching period of the second cohort, but since the rate of hatching during the first 13 d was relatively low due to its Gaussian nature, only about 3% of the total hatch of cohort 2 was lost.

Natural mortality of sand lance larvae in Port Moller in 1990 was set at 0.177 d^{-1} for all three cohorts (McGurk and Warburton 1992a, 1992b).

The swimming speed of larvae in the model was determined from their larval length. McGurk and Warburton (1992a, 1992b) developed a Gompertz growth curve for sand lance that enabled us to calculate an average length for a larva of a given age. However, the use of any growth relationship that is a function of age in conjunction with a hatch rate that varies from day to day essentially requires labeling each daily hatch as new cohort. Thus, 34 daily cohorts would be required to describe the second cohort alone, which meant that the computational problem would become unmanageable. We overcame this problem by assuming a constant length for all larvae of a cohort on the same date. Sensitivity simulations were made to test the impact of this assumption.

Location of Hatch

Hatch locations for the sand lance larvae are not known as accurately as they are for Pacific herring. McGurk and Warburton (1992a, 1992b) reported that the highest densities of young sand lance larvae were in lower Moller Bay between Point Divide and Harbor Point. The region near Point Divide is a good candidate for a hatching site because the tidal currents computed by the hydrodynamic model show that the incoming tide usually enters Herendeen Bay before Moller Bay, and that there is a cross-current out of Moller Bay onto the Point Divide flats. Also, the tidal currents out of Herendeen Bay are not as strong as the tidal currents off Point Divide, suggesting that fish larvae transported into Herendeen Bay on flooding tides are not as readily transported out on falling tides. The tidal currents into and out of Moller Bay tend to be as strong as the currents across Point Divide and it would be expected that larvae would not be as readily retained in Moller Bay as in Herendeen Bay.

The tidal currents across the Point Divide flats would tend to disperse newly hatched sand lance larvae over a wide area. This is opposite to the pattern of dispersion of Pacific herring up and down the channels from specific hatching sites in upper Moller Bay and Herendeen Bay.

The initial hatch of sand lance larvae was limited to the top 40 meters of water column.

Results

Unlike herring, all sand lance larvae were fully recruited to the sampling gear soon after hatch, most likely because sand lance larvae hatched directly into the central channels of the estuary from their hatch site in lower Moller Bay. Thus, the plots of observed sand lance larval density against age or date did not show the ascending left limb that was characteristic of herring larval catch curves. In turn, this means that the simulations of sand lance dispersal should only be compared to those simulations of Pacific herring larvae that were evaluated for falling limb data, i.e. those herring cases that had an r^2 of 0.52.

Transport with mortality

The first case was advective-dispersive transport with mortality, but with no larval motion relative to currents. The location of hatch for this case was a square with a side length of 8.4 km in central lower Moller Bay. In the model, the hatch site was contained within cells J10-J13 and I3-I6, as shown on Table 1 of Appendix C of McGurk et al. (1992). (Each cell had a length of 2.1 km.) This case gave an r^2 of 0.54 for both cohorts, 0.69 for the second cohort (L2), and 0.16 for the third cohort (L3) (Table 4 and Figures 5 and 6).

The second cohort covered a wider range of densities, and contained about 20 times the number of larvae, than the third cohort, which may explain why the second cohort had a higher r^2 than the third cohort. Both Figures 5 and 6 show that the total observed number of larvae may have been underestimated by about a factor of 8.

Directed motion cases

The cases of directed motion into the current were run for large fish (Run 3.52) and small fish (Run 3.53). There were no significant differences between these two cases or between the case with no directed larval motion (Run 3.51). The comparable case for Pacific herring larvae (for densities on the descending right-hand limb of the catch curve only) had an r^2 of 0.52.

Run 3.54 tested the case of larval motion in the direction of the current for small fish. It showed no significant differences from the preceding runs.

Hatch locations

Runs 3.51 through 3.54 were run for a 12 cell model region in central lower Moller Bay. To test the effect of altering the hatch site, we ran the model for two other locations: one near the channel into Herendeen Bay and another near the channel into Moller Bay.

The hatch location near the channels into Herendeen Bay (Run 3.55) gives results similar to the previous cases. However, the hatch location near the channels to Moller Bay showed a significant reduction in r^2 from the previous cases.

DISCUSSION

Comparison of model and data

This study shows that the hydrodynamic model was capable of reproducing the observed horizontal dispersal of herring and sand lance larvae within Port Moller. We consider an r^2 of 0.5 to 0.6 to be a good fit between model and data, considering the possible sources of error.

However, this still leaves unexplained 40-50% of the variance in larval densities. Part of the unexplained variance was due to unavoidable error in measurement of larval density, part was due to differences in the spatial scales used to measure fish density and to estimate current speed and direction, and part was due to differences between modeled currents and actual currents.

Variance in larval densities

The difficulty of accurately measuring density of larval fish is due in large part to the ability of larvae to direct their own movements. Both herring and sand lance larvae are capable of detecting and avoiding towed sampling gear. In our Port Moller studies we corrected larval fish density for net avoidance (McGurk and Warburton 1992a, 1992b; McGurk et al. 1992) using night-day catch ratios taken from the scientific literature (McGurk 1992). Although the average night-day catch ratio is the best available estimate of net avoidance, we cannot guarantee that it is directly applicable to all times and places in Port Moller because the estuary contains a wide variety of physical habitat and this habitat changes with time. For example, Moller Bay is so turbid that one would expect net avoidance to be reduced close to zero due to the inability of larvae to see an approaching plankton net. On the other hand, larvae in the deep, relatively clear water of upper Herendeen Bay are probably able to detect and avoid nets at maximum range.

The problems associated with the measurement of larval density are well known (Smith and Richardson 1977), and since they are unavoidable for practical purposes, they will not be discussed further. Instead, we focus our attention on the hydrodynamic model.

Spatial scales of larval density and the hydrodynamic model

Fish larvae are distributed in horizontal and vertical patches at scales ranging from 1 to 10,000 m. An estimate of larval density at a station was an integration of this patchy distribution over a horizontal distance of about 600 km (= 1 $m \cdot s^{-1}$ tow speed x 10 min tow duration) and a vertical distance of 10-30 m. In contrast, the smallest horizontal scale of the hydrodynamic model was 2100 m, the length of a cell, and the smallest vertical sale was 2 m, the depth of a cell. Thus the scale of measurement of larval density was three times smaller in the horizontal direction, and 5-15 times greater in the vertical direction, than the scale of hydrodynamic modeling. This difference in scaling may have contributed an unknown amount of unexplained variance when measured larval densities were compared to computed larval densities.

The only way to measure the importance of the scaling effect would be to run a model with smaller horizontal cell size and see if it resulted in an increase in r^2 when measured larval densities were compared to predicted larval densities. This was not possible in this study for reasons of time and cost. Set-up of model structure is one of the most time-consuming and expensive aspects of hydrodynamic modeling, and once it is established it is rarely ever altered. The choice of spatial resolution of this model was a compromise between detail and practical limits of computer time; greater resolution would have substantially increased the time required for each run of the model.

Variances in modeled currents

We cannot directly assess the degree of fit between actual and modeled currents because there were no direct current measurements in the estuary in 1990. Instead, we used indirect means to validate the Port Moller model: (1) comparison of actual and modeled currents in other studies that used both the GLLVHT model and current meters; and (2) comparison of actual and modeled tide heights and comparison of actual and modeled temperature-salinity profiles.

Numerous applications of GLLVHT over the last 20 years have shown that it is a reliable model for calculation of water velocities from boundary condition data. For example, GLLVHT was recently used to model hydrodynamics of the Patuxent River estuary (Chesapeake Bay, Maryland), the Raritan River estuary (New York City Harbor, New York) and the Arthur Kill (New York City Harbor, New York) (Edinger and Buchak 1989). Modeling procedures were similar to those used in Port Moller in that tides and salinities were specified at the mouths of the estuaries and meteorological variables and freshwater inflows were specified along the length of the estuaries. Arthur Kill was a more complex situation than Port Moller because it had two tidal boundaries. Current meter data were collected at all three areas either as an adjunct to transport studies or as separate studies conducted by other investigators. Statistical comparison of observed and modeled water velocities showed that the ratios of computed to observed velocities ranged from 0.6 to 1.0, which is considered to be good agreement by hydrodynamicists.

In this regard, it should be noted that there are at present no commonly accepted standards for verification of a hydrodynamic model. The level of agreement between observed and computed results that is acceptable or unacceptable to regulatory agencies has yet to be defined.

Although current meter data is not available for Port Moller for 1990, water surface elevation at the boundary and at the head of Herendeen Bay was measured indirectly with water pressure sensors. Temperature and salinity profiles at the heads of Moller and Herendeen Bay were also measured. The agreement between tide heights measured at the head of Herendeen Bay and tide heights predicted by the model from boundary conditions was considered to range from good to excellent (McGurk et al. 1992; Appendix D).

On the other hand, the measured temperature and salinity profiles differed slightly from those predicted by the model. In general, measured temperatures were 1-2°C higher than computed temperatures in both Moller and Herendeen Bays, and measured salinities were about 0.1-0.5 ppt lower than computed salinities in Moller Bay and 0.1-0.5 ppt higher than computed salinities in Herendeen Bay. The cause of these discrepancies was uncertainty about the amount, timing and site of entry of freshwater into the estuary. This was unavoidable because none of the streams entering Port Moller were gaged, and we had no information on the spring melt of snowpack on the mountains surrounding Port Moller. In the absence of this data, freshwater input was estimated from rainfall records at Cold Bay, Alaska, using simple assumptions about time lags of run-off, and the proportion of water lost to evaporation and absorption into the ground.

To obtain a rough estimate of the sensitivity of the model to error in freshwater inflow rates, we ran a case in which flow was increased by a factor of four. This decreased the r^2 of the best larval herring transport model from 0.52 to 0.20. As a comparison, we ran the case in which surface wind speed was set to zero; this also reduced r^2 from 0.52 to 0.20. We conclude that the lack of accurate data on freshwater input was the single weakest point in hydrodynamic modeling of Port Moller. In theory, it can be fixed by repeatedly running the model with small changes in freshwater flow rates until a good agreement is obtained between observed and predicted temperature-salinity profiles. However, this is a time-consuming and costly process. The freshwater flow rates used in the current version of the model were our best guesses under this project's constraints.

The problem of measuring the best fit

Related to the problem of obtaining the "best" hydrodynamic model is the problem of how one defines a good fit between observation and prediction. In this study we used the coefficient of determination, r^2, which measured the percent of variance in the observed larval densities that was explained by the model. However, both the dynamics of fish larvae and the dynamics of the model are too complex to be adequately summed by a single number. Larval dynamics were the result of growth, mortality, vertical migration and directed motion, and the model contained six equations and six unknowns solved over space and time. An example of the practical difficulty in attaching meaning to the r^2 statistic is the fact that soon after hatching most herring larvae were contained within a few model cells, so model accuracy was based on predictions from a small percentage of the model area. However, at the end of each run, larvae were spread over 170 cells and model accuracy was based on most of the modeled area. r^2 was not weighted to take this into account.

There is no consensus in the scientific literature on how to resolve this problem because the field is so new that few scientists have had to grapple with the problem.

Implications of model results for Port Moller hydrology

One immediate result of the modeling study is that it gives a good indication of where continuous current observations should be made in future studies, both to verify the hydrodynamic model and to aid in larval transport studies. For example, the model predicts the presence of upwelling in Moller Bay and a weak convergence in Herendeen Bay that should be verified by current meters. It also shows that vertical velocity profiles at the boundary to the estuary may be important to retention and loss of herring larvae from the estuary.

Another use of the model is to predict the distribution and fate of water-borne contaminants within the estuary. The obvious candidate is hydrocarbons, since the rationale for this study was based on anticipated oil and gas exploration and development in the southeastern Bering Sea.

Implications of model results for herring and sand lance larval dynamics

These simulations support our argument that the Port Moller stocks of herring and sand lance follow different early life history strategies. This argument was briefly summarized in the Introduction of this report; it is based on data in McGurk and Warburton (1992a) and McGurk et al. (1992). While herring larvae swim against the current to maintain themselves south of Harbor Point in Moller Bay, sand lance appear to disperse into Herendeen Bay entirely by passive drift, or at least directed motion does not enhance a strategy of passive drift.

This simple picture is complicated by the finding that while directed motion increased the fit between observed and computed herring larval densities in Moller Bay, it decreased the fit for herring larval densities in Herendeen Bay. This finding suggests that herring larvae may have followed different strategies depending on local water velocity: in areas of relatively quiet water such as Herendeen Bay, herring larvae dispersed in a way that was indistinguishable from passive dispersal, but in areas of turbulence they actively swam against the current. It also suggests that the location of spawning in relation to oceanographic features is important to the subsequent behavior of herring larvae and to their ability to retain themselves in sheltered areas of their nursery.

We are unable to determine if sand lance larvae exhibit the same flexibility as herring larvae appear to exhibit because most sand lance larvae dispersed into Herendeen Bay. However, regardless of whether sand lance exhibit herring-like flexibility, or are passive drifters under all circumstances, the dispersal of sand lance larvae is also highly sensitive to the location of their hatch sites. Even if sand lance are capable of directed motion, but only employ it when necessary, Run 3.56 shows that the location of their hatch sites is still crucial to their successful dispersal into Herendeen Bay.

Consequences for management of Alaska herring and sand lance

Our work has at least two consequences for management of herring and sand lance in Alaska. First, we have shown that herring and sand lance larvae are substantially retained in Port Moller. Retention of Pacific herring larvae in coastal embayments has been reported ever since larval surveys began in the 1950s (Stevenson 1962; Robinson 1988; McGurk 1989; Haldorson and Collie 1991; Hay and McCarter 1991; McGurk 1991; McGurk et al. in press). Our study is the first to demonstrate its existence in the Bering Sea. It is also the first to demonstrate retention of Pacific sand lance larvae in an estuary. The only other report of larval retention in any species of sand lance was by Fujiwara et al. (1990) for Japanese sand eel, *Ammodytes personatus*.

A second related consequence for fisheries management is that we have shown that the distribution of herring and sand lance larvae in Port Moller coincides with specific physical features of the estuary, mainly two convergences of currents. To the best of our knowledge, this is the first time such a linkage has been made for either species. It was possible only because we combined biological surveys with hydrodynamic modeling of the estuary.

These findings suggest a new means of identifying spawning stocks of herring and sand lance in the Bering Sea. The stock structure of Bering Sea herring is poorly understood (Fried and Wespestad 1985), and the stock structure of Pacific sand lance is completely unknown (McGurk and Warburton 1992a, 1992b). Stocks of fish are usually identified by the amount of geographic separation between fishing grounds, by tagging studies, or by genetic studies. However, tagging is currently considered to be too expensive or impractical to perform in the Bering Sea (K. Rowell, Alaska Department of Fish and Game, Anchorage, AK, pers. comm.), and genetic studies may not have the resolution necessary to distinguish neighboring stocks. In this situation, we suggest that the link between a spawning population and retention of its larvae may be a useful means of identifying stocks. To date, no one has yet studied the distribution of herring or sand lance larvae in the coastal waters of the entire Bering Sea. Our results in Port Moller indicate that if such a study were performed it may reveal a mosaic of concentrations of larval herring and sand lance, each concentration corresponding to a separate spawning population. Whether a spawning population can be considered a stock is controversial because the current concept of stock is not solely genetic but is confounded by the requirements of fisheries management.

Consequences for the environmental impact of oil and gas development

If the hypothesis that Port Moller herring and sand lance have evolved behaviors specific to the hydrodynamics of Port Moller is correct, and we stress that we have no information on this matter other than our simulation experiments, then degradation of herring and sand lance spawning habitat in Port Moller could have serious consequences for the two stocks of fish. In the event of a loss of spawning habitat, fish would be forced to spawn in areas of the estuary that do not lead to optimal retention of larvae, or they might not spawn in the estuary at all. Transplantation of eggs in an attempt to restore a stock injured by degradation of its spawning habitat may not be a viable alternative to preventing the damage in the first place.

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