

# Importance of spawning location and timing to successful transport to nursery areas: a simulation study of Gulf of Alaska walleye pollock

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Hinckley, S., Hermann, A. J., Mier, K. L., and Megrey, B. A. 2001. Importance of spawning location and timing to successful transport to nursery areas: a simulation study of Gulf of Alaska walleye pollock. – ICES Journal of Marine Science, 58: 1042–1052

We conducted a model experiment to examine the hypothesis that the spatial and temporal specificity of spawning of walleye pollock (*Theragra chalcogramma*) in Shelikof Strait, Alaska, evolved to optimize physical transport to the juvenile nursery area near the Shumagin Islands some 375 km to the southwest. The alternative hypothesis is that factors other than physical transport alone must also be important in the choice of spawning location and timing. We used a coupled biophysical model consisting of a three-dimensional hydrodynamic model of the currents in the region, an individual-based model of the early life stages of pollock, and a nutrient–phytoplankton–zooplankton model that provides a spatially and temporally dynamic source of food for larval pollock. Results showed that fish spawned to the south of Kodiak Island, or too early (February) or too late (July), did not reach the Shumagin Island nursery area by early September. However, the potential region and time of spawning that did allow successful transport to the nursery area was much broader than the observed spawning region and time. Therefore, factors other than physical transport alone must be considered in explaining the specificity of the location and timing of spawning for this stock.

Keywords: biophysical models, individual-based models, recruitment, spawning.

Published electronically 13 August 2001.

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## Introduction

The timing and location of spawning are integral components of the adaptation of marine fish life cycles to their environments. Maintenance of a population depends on successful recruitment of young fish to nursery areas and from nursery areas back to the parent population. The choice of spawning time and location is important, as these are likely to have evolved to optimize either the transport of planktonic stages to the nursery areas, or the conditions experienced by the young fish along the way, or both. In highly advective systems, spawning location and timing may have been selected based on the necessity of avoiding excessive transport (i.e. currents that carry them past or away from the nurseries) and the need for retention in areas conducive to survival.

In Shelikof Strait, Gulf of Alaska ([Figure 1](#)), walleye pollock (*Theragra chalcogramma*) spawns in a limited region at predictable times ([Kendall et al., 1987](#); [Schumacher and Kendall, 1991](#)). Peak spawning occurs in the deepest part of the Strait during the early part of April, but spawning begins in mid-March and continues until early May. Eggs and larvae drift to the southwest in the Alaska Coastal Current (ACC), and arrive at what appears to be the most important nursery areas near the Shumagin Islands during summer and early fall ([Hinckley et al., 1991](#); [Spring and Bailey, 1991](#); [Wilson et al., 1996](#)). In other parts of its range, notably the Bering Sea, timing and location of spawning are much broader and more variable ([Hinckley, 1987](#)).

The majority of surveys of eggs and spawning adults indicate that Shelikof Strait is the most important

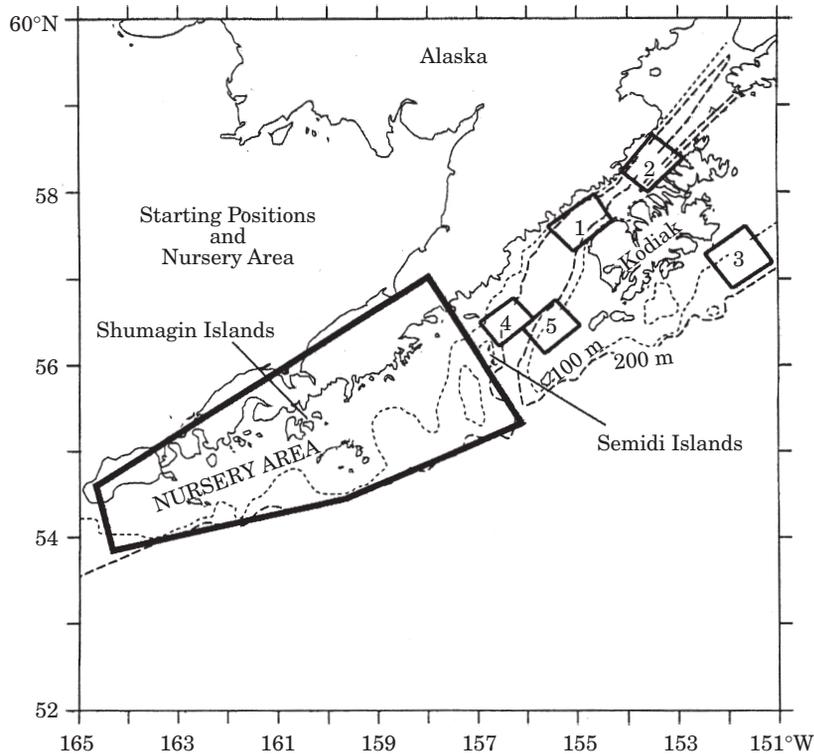


Figure 1. Spawning regions and nursery area as specified in the simulation: 1. Central Shelikof Strait, 2. Northern Shelikof Strait, 3. Outside Kodiak Island, 4. Northwest Shelikof Sea Valley, 5. Southeast Shelikof Sea Valley.

spawning region in the western Gulf of Alaska. There is some debate, however, about the relationship of anecdotal evidence of smaller spawning aggregations observed at other times and in other regions (e.g. near Chirikof Island and the Shumagin Islands) of the Gulf of Alaska to the Shelikof stock. It is not clear whether pollock in the Gulf of Alaska constitute a single stock, dominated by the spawning aggregation in Shelikof Strait, or whether separate spawning stocks exist. Nor is it clear where the nursery areas for other spawning groups are located.

Shelikof Strait may contain the largest aggregation of spawning pollock because it fosters the greatest retention of early life stages in productive coastal waters where survivorship is high. The central hypothesis of the Fisheries Oceanography Coordinated Investigations (FOCI), an interdisciplinary programme part of which is study of the recruitment of pollock in the area, is (Schumacher and Kendall, 1995) that “optimal survival and subsequent recruitment result when larvae are transported to nursery grounds in coastal regions along the Alaska Peninsula rather than into the Gulf of Alaska” (i.e. into the oceanic waters, where there is less food; Cooney, 1987).

Although eggs and larvae deriving from the Shelikof Strait spawning aggregation drift generally to the south-

west, drift does not continue indefinitely. Surface currents of only  $10 \text{ cm s}^{-1}$  could transport larvae as much as 1200 to 1800 km downstream and out of the Gulf before they become large enough to resist the flow (Strickland and Sibley, 1989). The nursery area in the Shumagin Islands is only 350–400 km downstream of the spawning location. Currents in the ACC that flow through the Strait range from 25 to  $100 \text{ cm s}^{-1}$  (Stabeno *et al.*, 1995), but the ACC bends off and flows offshore of the Shumagin Island region. Some mechanism must exist to prevent loss of eggs and larvae.

Several retention mechanisms have been proposed. One is a combination of alongshore and onshore transport. About 25% of the water in the ACC flows along the Alaska Peninsula after it leaves the Strait. Current speeds in the nearshore area, especially to the west of the Semidi Islands, are low, averaging less than  $10 \text{ cm s}^{-1}$ . The other 75% head offshore, but partly return to coastal areas (Schumacher *et al.*, 1989). If larvae were to remain in the ACC water that stays along the coast or that eventually returns to coastal waters, they would most likely be transported to the Shumagin Islands region.

The flow through Shelikof Strait is usually characterized by a high degree of mesoscale variability, some of which may aid in retention. For example, pollock larvae

have been observed in higher concentrations in meso-scale eddies (Schumacher *et al.*, 1993; Bailey *et al.*, 1995), and observations by Canino *et al.* (1991) suggest that feeding and survival conditions may be better in these eddies. It has also been hypothesized that retention in eddies, which move downstream at slower rates than the mean currents (Bograd *et al.*, 1994), aids in delivering larvae to the nurseries. Meanders and areas of weaker flow or flow reversal (e.g. caused by wind events) may also aid in retention. In years when high winds and runoff forced extremely strong currents with little meso-scale variability through Shelikof Strait (e.g. 1991), larvae appear to be carried out into offshore areas and into the Alaska Stream, the counterclockwise oceanic current circling the Gulf of Alaska offshore of the continental shelf (Bailey *et al.*, 1995).

Although the Shumagin Islands region represents an important nursery area, in some years young pollock are found in bays and coastal areas around Kodiak Island (Spring and Bailey, 1991). Their origin is not clear. Smith *et al.* (1984) concluded that it was unlikely they originated from Shelikof Strait. Alton and Deriso (1983) found no evidence of any major spawning aggregations east of Kodiak Island, nor did Kendall *et al.* (1987).

We conducted a model experiment to examine the effect of different spawning times, locations and depths on transport of juveniles to the nursery area using a coupled biophysical model of walleye pollock in the western Gulf of Alaska. Our central hypothesis is that spawning of pollock in the central Shelikof Strait in early April is not accidental, but that selection of time and location is the result of evolutionary adaptation to maximize transport of young fish to the Shumagin Islands. Spawning at other locations and at other times should result in lower rates of successful transport to this area. The alternative hypothesis is that the specificity of the location and timing of spawning of this population has to do with factors other than physical transport alone (e.g. overlap with prey and predators). To get at this question indirectly, a loglinear model was used to test whether certain factors had a significant effect on successful transport.

The model consists of an individual-based model (IBM) of the early life stages of pollock, coupled with a three-dimensional hydrodynamic model of the western Gulf of Alaska (SPEM), and a nutrient-phytoplankton-zooplankton (NPZ) model which provides food for young pollock (cf. Hermann *et al.*, 2001, this volume). This coupled model has the capability of tracking (in a Lagrangian sense) individual floats through the spatial domain, using a time-varying current field. We seeded the model with pollock eggs, represented by these floats, in different regions, at different times and depths, in two different years. We then examined whether location, time and depth of

spawning corresponding to those observed in Shelikof Strait resulted in higher numbers of juveniles reaching the nursery area by September, the time when they are normally observed there.

Different spawning depths were included in the model because this factor can affect the direction of transport, owing to vertical shear in the water column (Hinckley *et al.*, 1996). Pollock spawn at about 200-m depth (off-bottom) in Shelikof Strait, with some variability. However, spawning has also been observed both closer to the bottom and at shallower depths in other areas (e.g. parts of the Bering Sea).

This experiment was designed to give us insight into the role of transport of young fish between spawning and nursery areas. We do not specifically intend it as a test of the importance of year-to-year variation in spawning time and location, and its effect on interannual variations in recruitment to the fishery at age 2–3. However, we examined two years, 1978 and 1994, which both resulted in good year classes, but which were characterized by marked differences in physical forcing and factors thought to be important to recruitment (Megrey *et al.*, 1995). Currents in the region are mainly forced by winds and freshwater runoff. The year 1978 (January–May) was about 30% windier than 1994, while 1994 (January–May) was about 50% wetter than 1978. The cumulative integrated volume transport was 57% larger (April–September) in 1978 than in 1994.

We have not looked specifically at other factors that may affect how many fish reach the nursery area, such as food conditions, or the presence of predators along the way. However, only fish that were alive and reached the juvenile stage (i.e. had grown to 22–25 mm) by fall were considered to have been successfully transported.

## Methods

The set of coupled hydrodynamic, individual-based and nutrient-phytoplankton-zooplankton models are described in Hermann *et al.* (2001, this volume).

A balanced factorial design was used in the experiment (Table 1), with YEAR (two levels), spawning REGION (five levels), mean spawning date (SPTIME; four levels) and spawning depth (SPDEPTH; 2 levels: “On-bottom” defined as 1 m above the bottom and “Off-bottom” defined as 50 m above the bottom but not less than 20-m depth) as factors. Regions were defined by 4 × 4 grids around Kodiak island (Figure 1) and five individuals were released from each grid point for each combination of factors. Spawning has actually been observed in more northern parts of the Shelikof area, but we were not able to include a region farther away from the centre because of the physical model boundaries. The variable IN/OUT was derived from the grid point of each fish on DOY 244 (1 September), and

Table 1. Factors used in loglinear analysis.

Year
1. 1978 (~30% windier)
2. 1994 (~50% wetter)
Spawning region
1. Central Shelikof Strait–CSS
2. Northern Shelikof Strait–NSS
3. Outside Kodiak Island–OKI
4. Northwest Shelikof Strait Sea Valley–NWSV
5. Southeast Shelikof Strait Sea Valley–SESV
Spawning time
1. Early (16 Feb)
2. Middle (7 Apr)
3. Late (27 May)
4. Very late (16 Jul)
Spawning depth
1. Near-bottom
2. Off-bottom

denoted whether the fish was inside (1) or outside (0) of the polygon defining the Shumagin nursery area (Figure 1), where most juveniles are found in early fall. The “ray crossings” method (O’Rourke, 1993) was used to determine whether the point lies inside or outside the polygon: a ray is drawn from the point in an arbitrary direction; if the number of crossings with the boundary is odd, the point is inside the polygon, if even then it is outside.

To investigate the effects of REGION, SPTIME, and SPDEPTH on the success of reaching the nursery area (IN/OUT), two four-dimensional contingency tables were created for 1978 and 1994, separately. It is common to look at all possible two-way tables among all factors but this would ignore the possibility of three and four-factor interactions, and does not allow for the simultaneous expression of all factors in one model. Therefore, a loglinear model was chosen to test relationships among the factors (Fienberg, 1980). This approach was preferred to the classic ANOVA for three reasons: (1) the data are binomially distributed (fixed sample size of 80 for each combination of factors and classification as 1 or 0), and therefore the observed cells were not independent; (2) although a logarithmic transformation would linearize the model, the variances would still be unequal; and (3) a square root transformation applied to the proportional data (number of 1’s over total number of trials), would result in equal variances, but linear models on a square root scale are difficult to interpret in terms of contingency table data (Fienberg, 1970).

A loglinear model uses the formula for the estimated expected value of the frequency of a particular cell in a contingency table under the hypothesis of independence. In a two-dimensional table, the expected value of the (i, j) cell would be:

$$\hat{e}_{ij} = (r_{i+} \cdot c_{+j}) / N, \quad (1)$$

where  $r_{i+}$  is row counts,  $c_{+j}$  is column counts,  $N$  is total frequencies, and  $+$  indicates summing over levels of that particular factor. Taking the natural logarithms of both sides yields a model that is similar to a classical ANOVA. The full loglinear model used is:

$$\ln \hat{f} = \mu + \alpha_i + \beta_j + \gamma_k + \lambda_l + \alpha\beta_{ij} + \alpha\gamma_{ik} + \alpha\lambda_{il} + \beta\gamma_{jk} + \beta\lambda_{jl} + \gamma\lambda_{kl} + \alpha\beta\lambda_{ijl} + \alpha\gamma\lambda_{ikl} + \beta\gamma\lambda_{jkl} + \alpha\beta\gamma\lambda_{ijkl} \quad (2)$$

where  $\hat{f}$  is the predicted cell frequency,  $\mu$  is the mean of expected frequencies,  $i$  is the effect of REGION ( $i=1 \dots 5$ ),  $j$  is the effect of SPTIME ( $j=1 \dots 4$ ),  $k$  is the effect of SPDEPTH ( $k=1,2$ ), and  $l$  is IN/OUT of the nursery area ( $l=0,1$ ).

The loglinear model differs from the ANOVA in that it tests the independence of factors rather than the significance of main effects and therefore is used primarily for looking at interaction terms. In our model, the response is the IN/OUT effect and we are concerned with interactions with this effect. Two-way interactions involving  $\lambda_l$  are analogous to testing main effects in an ANOVA.

A likelihood ratio goodness-of-fit chi-square test was made after fitting the saturated model. Subsequent chi-square significance tests were made of (1) the fit of the model without each term (starting with the highest order interaction term) and (2) of the difference between the chi-square statistic of the full model and of the model with the term removed. Because six models were screened before ending up with the most appropriate model,  $\alpha=0.008$  (0.05/6) was used to prevent inflation of the overall type I error. If both tests were insignificant, then the term was removed from the model until the most parsimonious model was obtained. By starting with the highest-order interaction term and working downwards, the factors that are totally independent and conditionally independent of one or more variables were determined.

A similar loglinear analysis was made to determine the effects of the same factors on success of reaching the juvenile stage by 1 September by applying a critical size limit of 22–25 mm (response factor JUV/NOT JUV). This factor is independent of IN/OUT, i.e. of whether the fish reached the Shumagin nursery area. Factors affecting whether a fish reached the juvenile stage included date of spawning, whether the fish survived or died from starvation, or whether the fish remained in the model domain or was transported out of the region.

## Results

The contingency table containing the raw data (Table 2) shows that almost no fish (only ~1%) from the spawning region outside Kodiak Island were transported to

Table 2. Contingency table for percentage success in reaching the nursery (IN/OUT) and juvenile size (JUV/NOTJ), 1978 and 1994 (for factors see Table 1).

REGION	SPTIME	APDEPTH	IN/OUT		JUV/NOTJ	
			1978	1994	1978	1994
CSS	Early	Near	0	0	2.5	1.3
		Off	0	0	3.8	1.3
	Middle	Near	5.0	16.3	86.3	81.3
		Off	3.8	18.8	85.0	83.8
	Late	Near	12.5	31.3	75.0	76.3
		Off	10.0	33.8	73.8	71.3
	Very late	Near	0	0	1.3	0
		Off	0	1.3	2.5	1.3
NSS	Early	Near	0	0	2.5	1.3
		Off	0	0	1.3	0
	Middle	Near	20.0	22.5	87.5	87.5
		Off	17.5	27.5	83.8	87.5
	Late	Near	20.0	25.0	70.0	81.3
		Off	21.3	27.5	72.5	85.0
	Very late	Near	0	0	3.8	2.5
		Off	0	0	3.8	0
OKI	Early	Near	0	0	1.3	0
		Off	0	0	1.3	1.3
	Middle	Near	0	0	100.0	93.8
		Off	0	1.3	98.8	96.3
	Late	Near	0	0	100.0	87.5
		Off	0	0	97.5	93.8
	Very late	Near	0	0	1.3	0
		Off	0	0	1.3	1.3
NWSV	Early	Near	0	0	0	0
		Off	0	0	0	0
	Middle	Near	26.3	15.0	83.8	77.5
		Off	18.8	18.8	76.3	77.5
	Late	Near	37.5	35.0	80.0	83.8
		Off	36.3	33.8	77.5	86.3
	Very Late	Near	2.5	5.0	5.0	6.3
		Off	3.8	6.3	12.5	7.5
SWSV	Early	Near	0	0	0	0
		Off	0	0	0	0
	Middle	Near	7.5	1.3	88.8	83.8
		Off	6.3	0	86.3	78.8
	Late	Near	13.8	17.5	98.8	96.3
		Off	5.0	11.3	98.8	98.8
	Very Late	Near	0	0	5.0	3.8
		Off	0	1.3	2.5	5.0

the nursery area, and also that no fish from the early spawning and very few (~2%) from the very late spawning made it. Therefore, these particular levels of factors were *a priori* excluded from the loglinear model. Testing six hierarchical models based on this reduced data set revealed that SPDEPTH was independent of all factors and was therefore removed entirely from the model. This resulted in a fixed sample size of 160 for each combination of REGION and SPTIME.

In the reduced 1978 dataset, IN/OUT was dependent on SPTIME and REGION, but the three-way interaction between IN/OUT, SPTIME, and REGION was not significant. Among all regions, the highest successful transport rate was from Northwest Shelikof Sea Valley

(30%) and the lowest ones from Central Shelikof Strait and Southeast Shelikof Sea Valley (8%). Late and middle spawning time had successful transport rates of 19% and 13%, respectively.

In the reduced 1994 dataset, successful transport depended on spawning time and region jointly, mainly because of a lower than expected number of successes for the Southeast Shelikof Sea Valley and middle spawning time combination (lowest value: 1%). The highest values were found for the Northwest Shelikof Sea Valley and late spawning (34%) and for the Northern Shelikof Strait region and late spawning (33%).

In both years, at least 98% of the fish from the early spawning time did not make it to the juvenile stage.

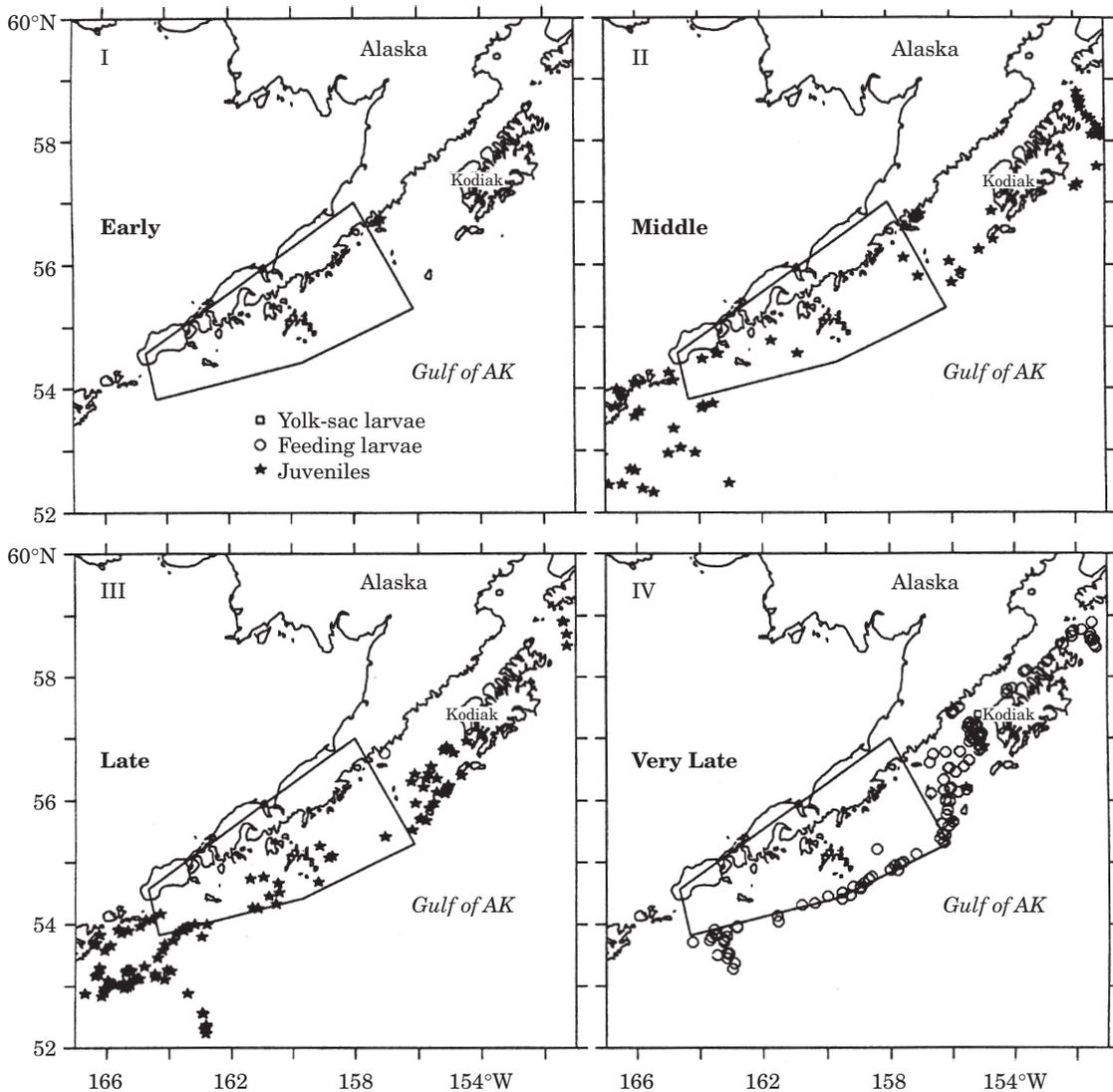


Figure 2. (a)

Figure 2. Locations (1 September) of yolk-sac larvae, feeding larvae, and juveniles originating from eggs spawned in 1978 at different times (I, Early; II, Middle; III, Late; IV, Very late): (a) Central Shelikof Strait; (b) Outside Kodiak Island; (c) Northwest Shelikof Sea Valley.

Examination of these results indicated that most of these fish died of starvation. Therefore, this spawning time was excluded also from the loglinear model. Depth was once again independent of all factors and was therefore removed entirely from the model.

In the 1978 reduced dataset, the proportion of fish reaching the juvenile stage was dependent on region and spawning time jointly. The highest proportion (99%) was found for middle and late spawning in the region outside Kodiak Island, while the lowest was found for late spawning in Central Shelikof Strait (2%). The contingency table (Table 2) shows that low proportions

are associated with early and very late spawning across regions, while higher proportions are associated with middle and late spawning times.

The proportion reaching the juvenile stage in 1994 was again dependent on region and spawning time jointly. The highest value was observed for late spawning in the Southeast Shelikof Sea Valley (98%), but the region outside Kodiak Island also showed high proportions for middle and late spawning (95% and 90%, respectively). The lowest values were found for Central Shelikof Strait and outside Kodiak Island and very late spawning (1%)

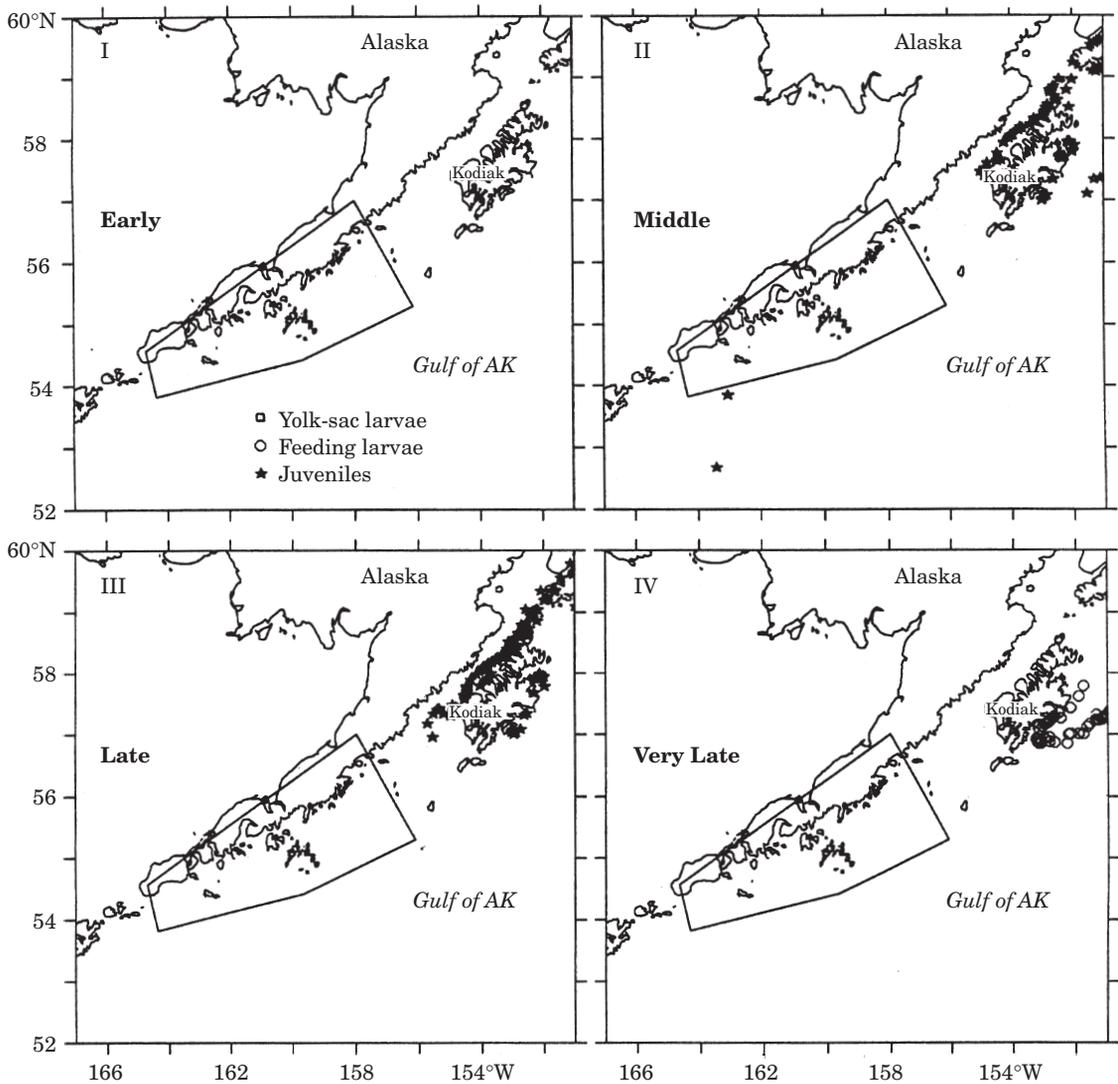


Figure 2. (b)

Examples of the locations of survivors from three spawning regions and all spawning times on 1 September for 1978 are shown in Figure 2. For Central Shelikof Strait [Figure 2(a); the observed spawning location), no survivors from the early spawning time ended up in the nursery, while only a few survivors from the middle (observed) spawning time were transported to the nursery area. Some fish ended up to the north of Kodiak Island. More fish were transported to the Shumagin area from late spawning, although many remained both upstream and downstream of the nursery and they were still in the feeding larval stage on 1 September. Patterns for 1994 were similar to 1978, except that a few more fish from both middle and late spawning ended up in the nursery. Offspring of the very late spawning was mostly still

upstream of the nursery, owing to lower overall transport rates.

For Northern Shelikof Strait, too, few fish from the early spawning survived, but many more from both the middle and the late spawning ended up in the Shumagin area by 1 September than from the Central Shelikof Strait. Again, nearly all fish spawned very late were still in the feeding larval stage. In 1994, fewer fish were swept past the nursery area owing to lower transport. In contrast, fish originating from outside Kodiak Island [Figure 2(b)] did not end up in the Shumagin area, but were retained around the island in both years.

Fish from Northwest Shelikof Sea Valley [Figure 2(c)] were successful in reaching the nursery in both years, both for middle and late spawning times. And finally,

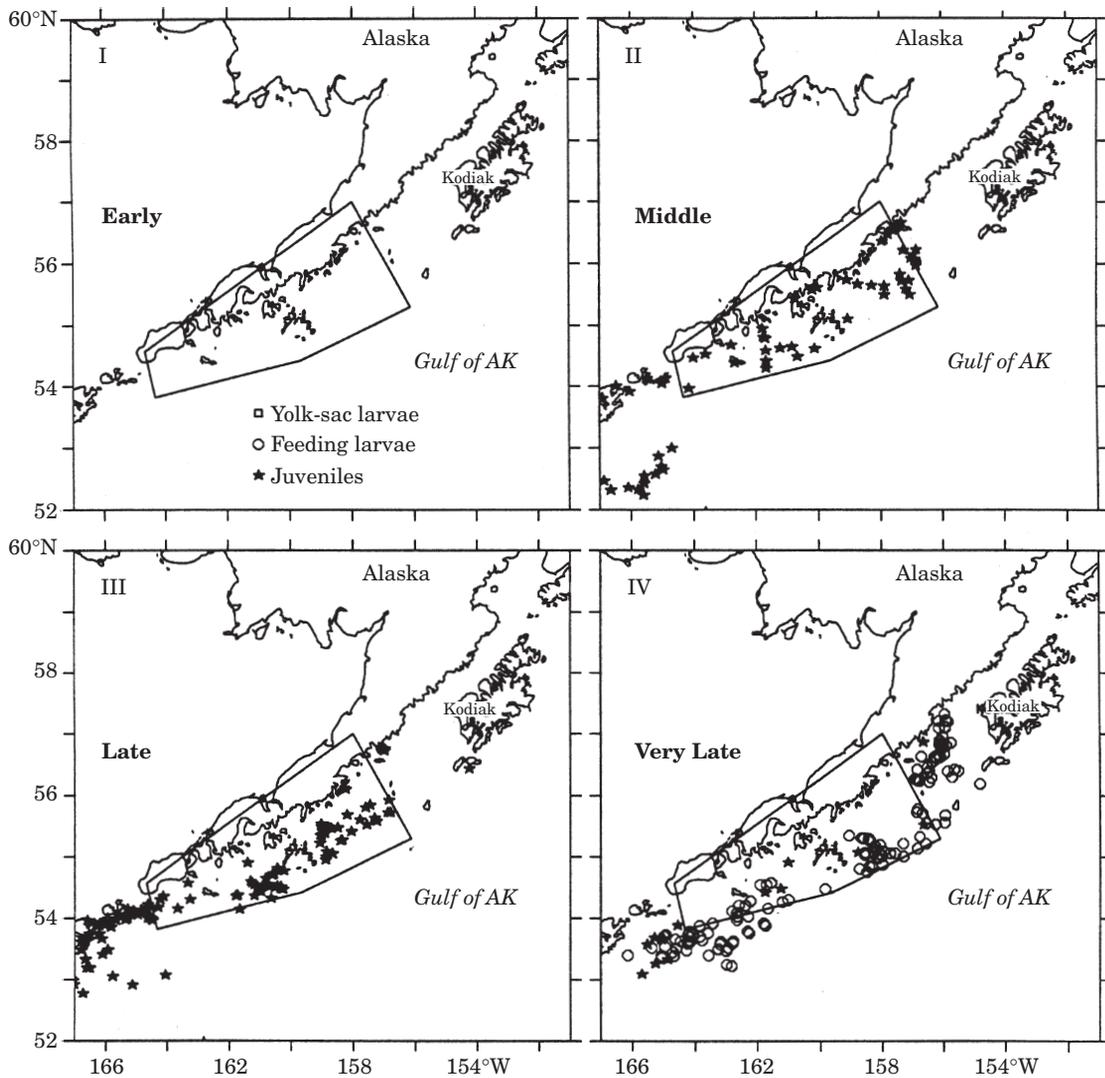


Figure 2. (c)

most of the fish originating from the Southeast Shelikof Sea Valley were swept downstream of the Shumagin area and few ended up in the nursery itself. Middle and late spawning resulted in some fish ending up to the southeast of Kodiak Island.

## Discussion

The simulations provide some very clear results. Spawning outside Kodiak Island rarely resulted in transport to the south, and no fish ended up in the polygon. Most were retained around Kodiak Island. In contrast, very few fish originating from the other spawning regions ended up around Kodiak. Our simulation therefore suggests that the large numbers of

juveniles observed in these bays in some years may originate from spawning outside of Kodiak. However, uncertainties exist in the modelled flow field in the region outside Kodiak Island because data validating the model are limited (Hermann and Stabeno, 1996; Stabeno and Hermann, 1996) and the result obtained may be biased.

Larvae originating from early spawning (February) died in the model of starvation. The common food of pollock larvae consists of nauplii of coastal copepod species (*Pseudocalanus* spp.). These species reproduce in response to the spring bloom, which generally occurs in early May (Napp *et al.*, 1996). On the other hand, larvae originating from very late spawning (July) do not grow fast enough to reach the juvenile stage by 1 September. Larval pollock grow at about  $0.2 \text{ mm d}^{-1}$  (Bailey and

Stehr, 1986; Bailey *et al.*, 1996). To make it from hatching at about 4 mm to metamorphosis at about 22–25 mm takes more than 100 days, and so the juvenile stage of fish originating from spawning in July would not be reached until late October.

Spawning depth, at least according to the definition used here, was not significant in determining whether or not a fish was transported to the Shumagin area or reached the juvenile stage. This could be because the period eggs and larvae stay at the spawning depth is relatively short. Larvae quickly rise to the upper water column not long after hatching (Kendall *et al.*, 1994).

These conclusions applied equally to the two years that were selected because of marked differences in physical forcing. Therefore, they seem to apply to a range of environmental conditions.

Of those fish that reached the Shumagin Islands nursery area, most came from the Northwest Shelikof Sea Valley and from late spawning (late May) in both years, and in 1978 also from middle spawning time (early April). This may be caused by the sluggish circulation between the Semidi Islands, near where these fish were released, and the Shumagin Islands, with average current speeds of  $10 \text{ cm s}^{-1}$  or less, compared to the middle of the Shelikof Sea Valley, where current speeds average  $25\text{--}100 \text{ cm s}^{-1}$ . Thus, the window of opportunity for spawning, if fish are to reach the Shumagin Island nursery area by September, would appear to be the region between Northern Shelikof Strait and the Northwest Shelikof Sea Valley, sometime after February (and probably not much before April) and before July.

In 1978, the established spawning region (Central Shelikof Strait) and observed spawning time (early April) resulted in fewer fish reaching the nursery area than other regions and times. Although this combination did better in 1994, the conclusion still seems to hold (Table 2). This result was counter to our initial hypothesis that spawning of pollock maximizes transport of young fish to the Shumagin Islands. We therefore have to conclude that factors other than just physical transport alone (note that spatial and temporal availability of prey probably is not an important factor because modelled prey distributions for 1978 and 1994 are relatively similar; Hinckley, 1999) must be considered as important in determining the time and location of spawning of the pollock population. These other factors could include other aspects of prey availability not included in the NPZ model, the presence or absence of predators on the early stages, or details of mesoscale or submesoscale circulation or physical factors that are not captured by the hydrodynamic model. Also, possible environmental cues (currents, temperature, salinity, etc.) that attract spawning pollock to a certain area are not known.

Examination of NPZ model simulations (Hinckley, 1999) of the distribution and timing of *Pseudocalanus* spp. naupliar production for six different years helps us

to narrow the window of opportunity for spawning further. A definite peak in naupliar production exists in most years between DOY 140 and 160. Larvae originating from the early spawning (DOY 47) reach first-feeding at about DOY 68. By this time, nauplii concentrations have not yet started to increase, and are below the  $20 \text{ l}^{-1}$  thought to be necessary (Theilacker *et al.*, 1996) for feeding and growth. Larvae originating from late spawning (DOY 168) miss the peak. The date corresponding to the observed spawning time (about DOY 90) results in first-feeding larvae about DOY 110, after naupliar production has begun to rise towards its peak.

Following the match-mismatch hypothesis of Cushing (1972, 1974), the spatial distribution of prey helps narrow potential spawning locations further. If pollock spawned in the Northwest Shelikof Sea Valley, the larvae would (as movies of their simulated movements show) be quickly carried into the coastal region between the Semidis and the Shumagins at times when naupliar abundance in this area is fairly low. Larvae originating from spawning further to the north and east, in Shelikof Strait proper, are more likely to remain in areas of high prey abundance.

It would appear that, within the constraints of the model imposed by the physical boundaries to simulate trajectories of larvae from observed spawning activity north of Shelikof Strait, a combination of advection and mean prey dynamics may be sufficient to explain the evolution of the specificity of the timing and location of spawning.

Why the Shumagin area is the preferred nursery remains unknown. Once a juvenile is carried into this area, it may be less likely to be advected either into the Bering Sea through Unimak Pass, or to be carried much further to the west by the Alaskan Stream. Retention in the nursery might ensure that the fish are able to return to the Shelikof region to spawn at age 2 or 3.

NPZ model simulations (for years not included in this model experiment) indicate a consistent peak in naupliar biomass in mid- to late May. To ensure a match between larval pollock production and that of their prey (assuming average rates of egg and larval development), spawning would need to be between early April and early May. This narrows the window of opportunity from the optimal spawning window indicated by this model experiment to what is observed, and supports the notion of the timing of spawning as a response to the average timing of prey production.

This simulation represents an examination of the optimal timing and location of spawning with respect to the probability of getting to the nursery area at the right time. By choosing two extreme years, we hoped to introduce enough variability to deal with anomalous conditions, but it would be useful to repeat the simulation using contrasting years of good and bad

recruitment. Interestingly, there is much less variability in the timing and location of spawning in the Gulf of Alaska than in the Bering Sea (Hinckley, 1987). This difference is not understood, but could relate to differences in the need to “hedge one’s bets” in the latter region. The occasional observation of spawning activity at other times and locations in the western Gulf of Alaska inferred from anecdotal evidence might also function to spread the risk of spawning within a too restricted period and area.

## Acknowledgements

This is contribution FOCI S310 to NOAA’s Fisheries-Oceanography Coordinated Investigations. The Electric Power Research Institute Fellowship Program provided partial support for S.H. to conduct the research. Many people in the FOCI program very generously provided data and participated in helpful discussions.

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