

**Abstract.** — Approximately 12,396 Pacific cod, *Gadus macrocephalus*, were tagged and released from fishery research vessels in the eastern Bering Sea and adjacent waters between 1982 and 1990. Recapture data from 373 tags recovered through the first quarter of 1992 revealed a strong seasonal component in fish movement between summer and winter areas. Prespawning fish were tagged throughout their summer distribution, primarily over the inner and middle shelf (<30–100 m depths), and recaptured on the outer shelf (>100–200 m) and upper continental slope (>200 m) in subsequent quarters. Recoveries from the winter quarter (January–March) showed the most directed movement, when Pacific cod aggregated in major spawning areas between Unalaska and Unimak islands in the eastern Aleutian Islands, seaward of the Pribilof Islands along the shelf edge in the eastern Bering Sea, and near the Shumagin Islands in the western Gulf of Alaska. By early summer, a hypothesized postspawning dispersal was observed from these overwintering areas, when tagged Pacific cod moved from deep off-shelf waters to shallower depths on the eastern Bering Sea shelf. The importance of seasonal migration was examined statistically by contingency table analysis, which indicated that season of recovery affected area of recovery more than either the season or area of tagging. Seasonal movements were further quantified by modeling the population dynamics of tagged individuals, which allowed estimation of the seasonal distribution in the eastern Bering Sea population. These estimated seasonal distributions compare well with the seasonal distribution of catches from the commercial fisheries. This analysis of tag-recapture data suggests a single winter spawning population in the eastern Bering Sea, nearby waters of the Aleutian Islands, and western Gulf of Alaska waters between longitude 157°W and 170°W

## Seasonal movements of Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea and adjacent waters based on tag-recapture data

**Allen M. Shimada**

Alaska Fisheries Science Center  
National Marine Fisheries Service, NOAA  
7600 Sand Point Way NE, Seattle, Washington 98115-0070  
Present address: Office of Research and Environmental Information  
National Marine Fisheries Service, NOAA  
1335 East-West Highway, Silver Spring, Maryland 20910

**Daniel K. Kimura**

Alaska Fisheries Science Center  
National Marine Fisheries Service, NOAA  
7600 Sand Point Way NE, Seattle, Washington 98115-0070

Pacific cod, *Gadus macrocephalus*, are widely distributed throughout the North Pacific Ocean. Off North America, Pacific cod range from California north through British Columbia and southeast Alaska, into the Bering Sea, and west along the Aleutian Islands (Bakkala et al., 1984). Pacific cod are found epibenthically over the Bering Sea shelf and slope. The Bering Sea represents the center of greatest regional abundance, although Pacific cod are also abundant in the neighboring Aleutian Islands and Gulf of Alaska waters (OCSEAP, 1987). Pacific cod catches rank third among the eastern Bering Sea groundfish resources following walleye pollock, *Theragra chalcogramma*, and yellowfin sole, *Pleuronectes asper* (Low, 1991).

Beginning in the early 1980's, Pacific cod catches increased substantially above the 10,000 to 50,000 metric tons (t) landed annually between 1958 and 1979. Eastern Bering Sea and Aleutian Islands catches over the last decade have averaged 132,500 t; a historic high

of 198,000 t was taken in 1988 (Thompson, 1994). Much of this growth was due to the recruitment of exceptionally strong 1977–78 year classes, in combination with greater fishing effort from joint-venture (i.e. U.S. fishing vessels delivering catches to foreign processors at sea) and new domestic groundfish fisheries (Bakkala, 1984; Shimada, 1985). More recently, the eastern Bering Sea and Aleutian Islands Pacific cod fishery generated a catch of 177,300 t, valued at \$90 million in 1991 (NMFS, 1992). These developments in resource availability and in expanding fishery exploitation patterns provided the impetus for new studies into the biology of Pacific cod in Alaskan waters.

In September 1982, a pilot tagging experiment for Pacific cod and walleye pollock in the eastern Bering Sea was conducted by National Marine Fisheries Service (NMFS) scientists from the Alaska Fisheries Science Center (AFSC). The initial objective of this experi-

ment was to evaluate the feasibility of a tag-recapture program for Pacific cod and walleye pollock (Shimada<sup>1</sup>). During the second year, as tag-recovery information accumulated, field efforts focused exclusively on Pacific cod because few tagged walleye pollock were recovered. Growth-increment data obtained from these tag returns have been analyzed by Kimura et al. (1993). This paper presents new information on the seasonal movements and long-range migration of Pacific cod in the eastern Bering Sea and adjacent waters.

## Materials and methods

Between 1982 and 1990, Pacific cod were successfully captured and released from AFSC-chartered fishing vessels engaged in summer bottom trawl surveys off Alaska. Pacific cod were tagged throughout their eastern Bering Sea distribution (Fig. 1). This effort was augmented by tag releases from cooperating Japanese, Korean, and U.S. research vessels operating in the Aleutian Islands and Gulf of Alaska (Fig. 1).

Capture gear included bottom trawls, pots, and hook-and-line. For the bottom trawl, predetermined stations were sampled each year across the eastern Bering Sea shelf (Bakkala, 1993). Thirty-minute trawl hauls and biological samplings were performed at each station. Occasional opportunistic hauls of 10 to 30-minute durations were made to obtain additional tag releases. On retrieval of the trawl net, Pacific cod were taken from the unprocessed portion of the catch and placed in on-deck holding tanks supplied with running sea water. After a recovery period (typically 1–2 h), fish were removed with a dip net and examined for visible signs of injury or stress. Those not seriously harmed during capture were placed in a padded cradle, tagged, and measured for fork length to the nearest 0.5 cm. General condition was noted, and fish were quickly returned to the sea.

Two tag types were used in this study: 3.5-inch anchor tags and 8-inch lock-on spaghetti tags.<sup>2</sup> Both types were constructed from international orange #20 vinyl tubing and labeled with a tag serial number and return address. The majority of releases were made with the spaghetti tag (69%). This tag was applied through the dorsal musculature, behind the head and anterior to the first dorsal fin, with a hollow needle applicator and secured by interlocking

plastic terminals. Anchor tags were inserted between individual fin rays at the base of the first or second dorsal fin.

Pacific cod were tagged across the entire size range available to the capture gears (Fig. 2); priority was placed on the release of fish less than 55 cm (i.e. younger than about age 5 yr; conversion from length to age in this paper is based on growth data in Kimura and Lyons [1990]). Pacific cod smaller than about 42 cm (i.e. age 3 yr or younger) were not recruited to the commercial fisheries and were of particular interest as the preexploited population component; however, owing to availability larger fish made up the majority of tagged fish. Data recorded at release included date, haul or set number, gear type, depth fished, bottom water temperature, release position, fork length, and general fish health.

Tag information from Pacific cod recovered by commercial trawl, longline, and pot fisheries (Table 1) through the first quarter of 1992 were used in this paper. The Bering Sea groundfish fishery was dominated by foreign fishing until 1987, when harvest allocations shifted to joint-venture and domestic fisheries. By early 1991, the Pacific cod fishery had evolved into an exclusively U.S. enterprise. Mirroring this transition in fleet involvement, tag recoveries initially came from foreign and joint-venture trawl and foreign longline fisheries. More recent tag returns have come from the domestic trawl and longline fisheries. Tag recovery reports provided information regarding capture date, catch location, and body length. Some tag returns also included capture method, depth fished, sex, body weight, maturity, and a collection of scales or otoliths.

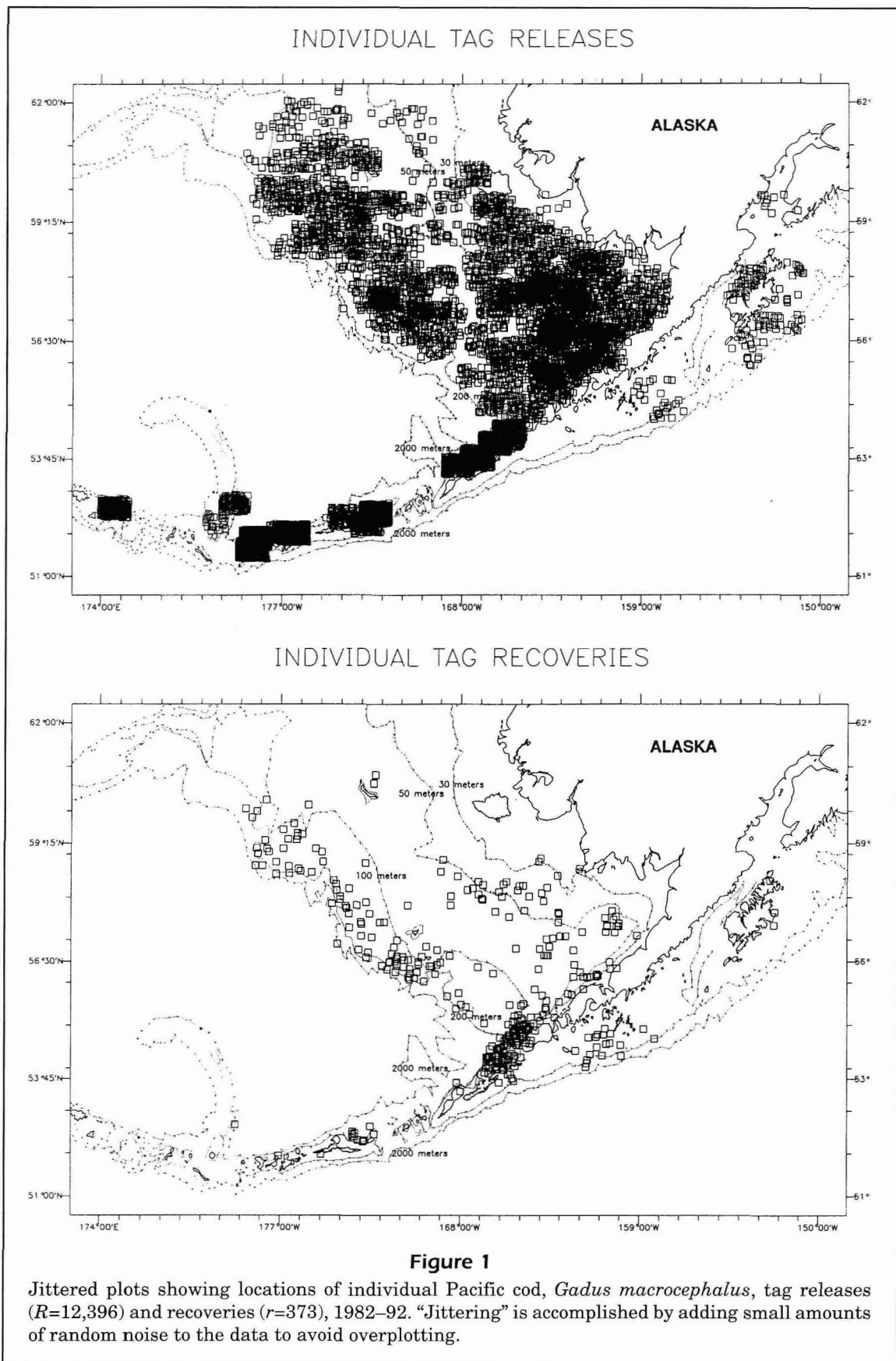
Tag recovery data were analyzed by three complementary methods: 1) mapping, which described the location of release or recovery or the movement of fish from the area of tagging to the area of recovery; 2) multiway contingency table analysis (Fienberg, 1977), which was used to analyze the strength of relationships between the season and area of tagging and the season and area of recovery; and 3) direct population dynamics modeling of the tagged population.

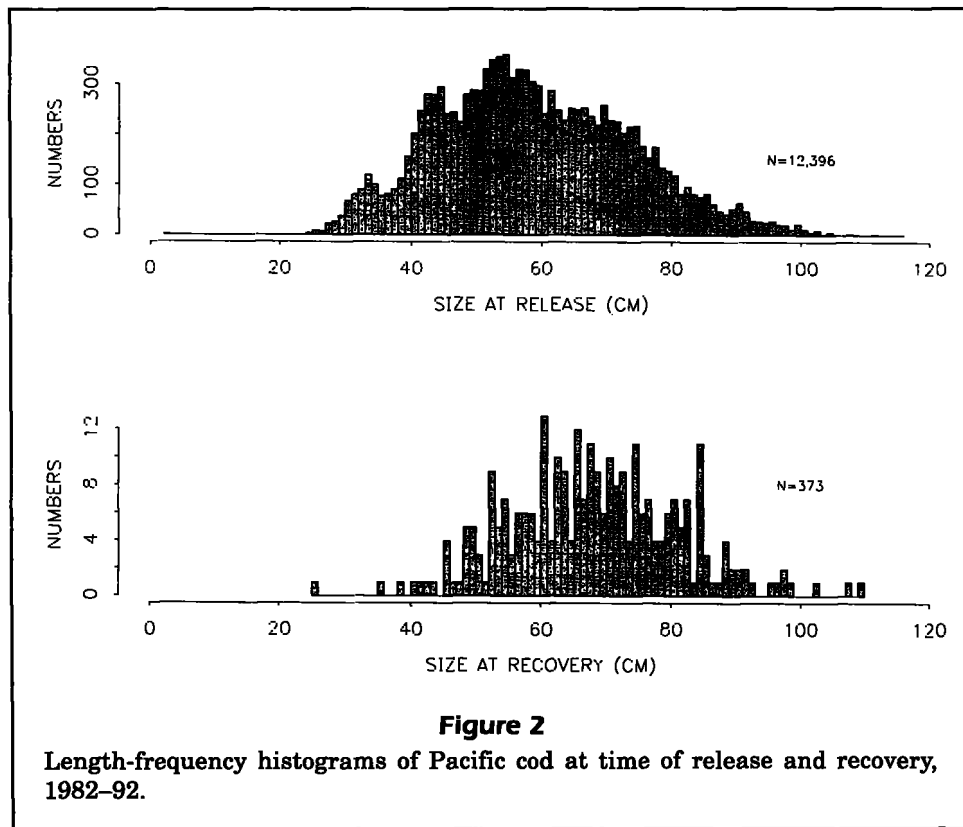
Three primary areas of interest (Fig. 3) were defined for use in the mapping, contingency table analysis, and the population dynamics model: 1) the inner shelf from depths <30 m to 100 m [Area 1]; 2) the outer shelf between >100 m and 200 m and incorporating the upper continental slope at depths greater than 200 m [Area 2]; and 3) winter spawning grounds surrounding Unimak Pass and adjacent waters [Area 3].

To emphasize the main features in the data, release-recovery positions were plotted individually (Fig. 4) and as mean-movement vectors based on tags released over blocks of 2° latitude × 5° longitude (Fig.

<sup>1</sup> Shimada, A. M. 1982. Cruise results, NOAA ship *Chapman*, Cruise CH-82-06, 7 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., Bin C15700, Seattle, WA 98115-0070.

<sup>2</sup> Floy FD68BC anchor tag and FT-4C lock-on spaghetti tag.





5) and aggregated by recovery season (winter=Jan-Mar, spring=Apr-Jun, summer=Jul-Sept, and fall=Oct-Dec; this definition of seasons is used throughout the paper). For these plots each 2° × 5° block is associated with just one arrow.

The modeling of the tagged population was performed similarly to that done by Hilborn (1990) and by Heifetz and Fujioka (1991). However, rather than describing movement through time as a Markov process, we only estimated seasonal distribution, a much easier task. Our model assumed that the quarterly natural mortality rate ( $M$ ) was the same in all seasons and areas, and that the instantaneous fishing mortality rate ( $F$ ) varied by season but not by area. Years were assumed to be homogeneous (i.e. we assumed no year effects). Modeling the tagged population allowed the estimation of seasonal distribution by taking into account the actual time and area of tagging and recovery.

The model assumed that time ( $i$ ) is divided into seasons (four per year over all years, so that the subscript  $i$  runs from 1 to 4 × nyr, where nyr=10, the number of years being modeled) and that there are three areas ( $j$ ) being modeled.

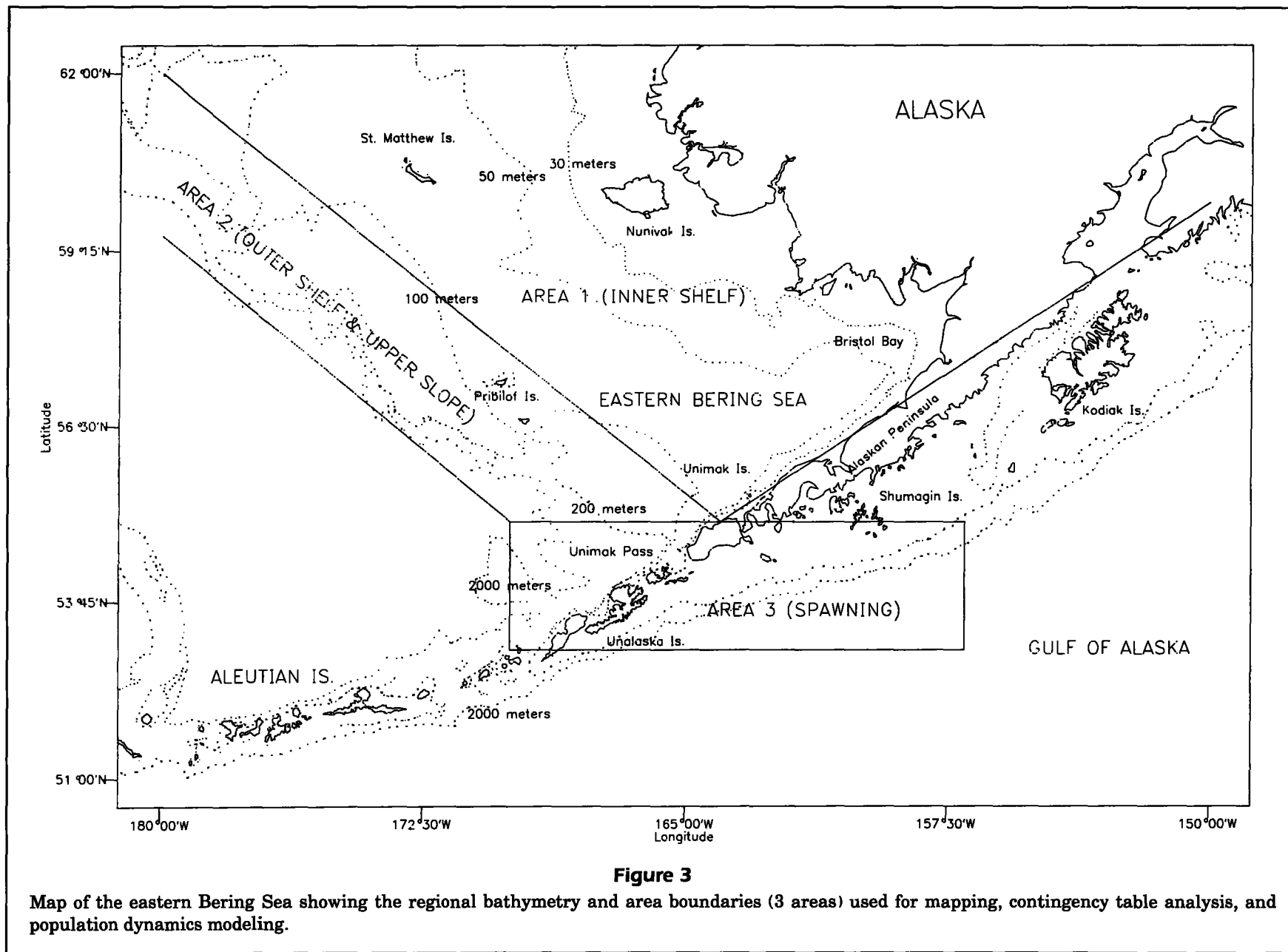
**Table 1**

Tabulations of tag releases and tag recoveries (top) by areas described in Figure 3 (Area 1=the eastern Bering Sea shelf, Area 2=the outer eastern Bering Sea shelf and upper slope, Area 3= the main spawning area) for Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea. Percentage release and recoveries by fishing gear (bottom).

Area	Release		Recovery	
	Number	Percent	Number	Percent
1	4,967	40.1	91	24.4
2	1,303	10.5	107	28.7
3	3,048	24.6	158	42.4
Other	3,078	24.8	17	4.5
<b>Total</b>	<b>12,396</b>		<b>373</b>	

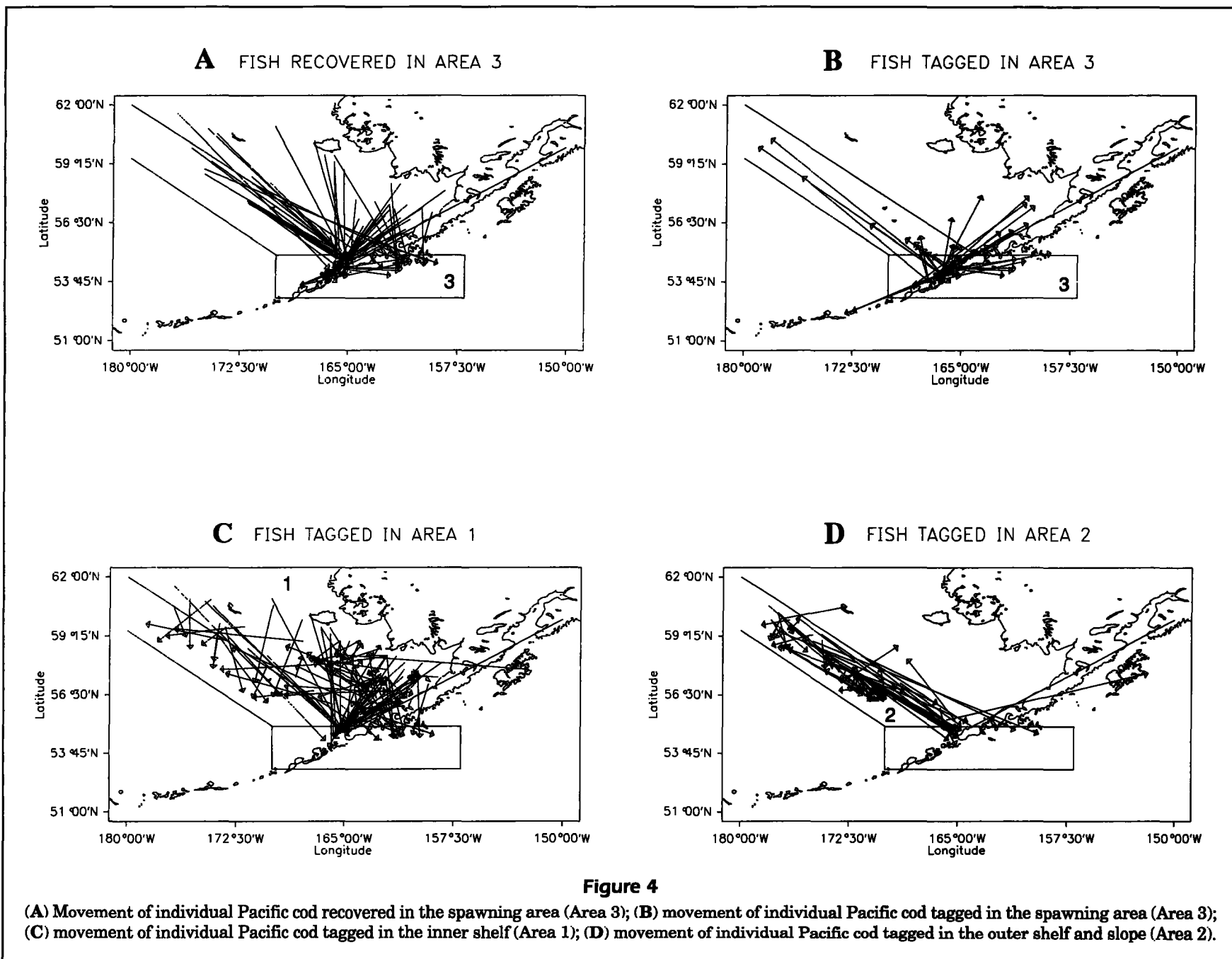
  

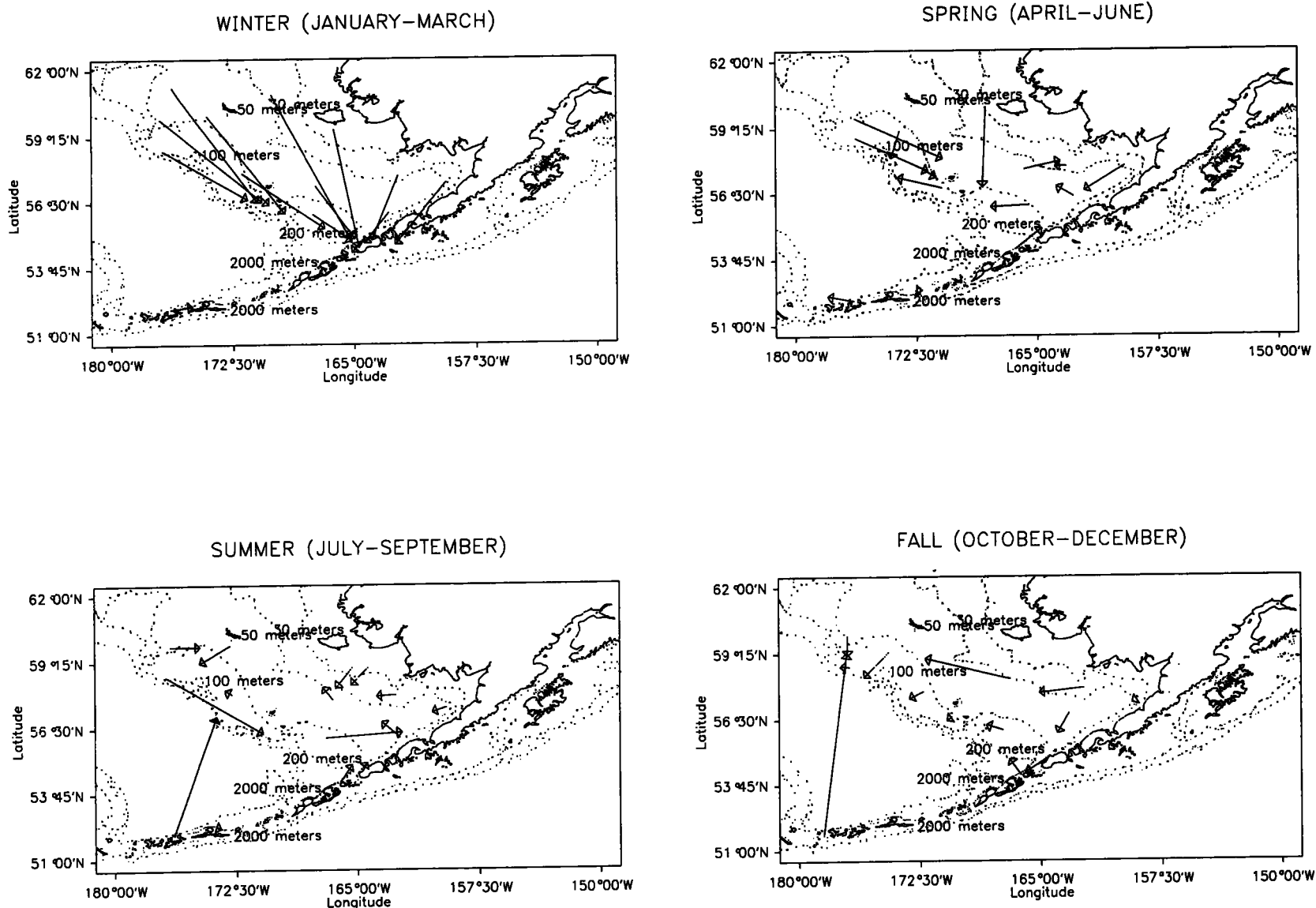
Gear	Release		Recovery	
		Percent	Gear	Percent
Trawl		97.2	trawl	62
Hook and line		0.6	longline	24
Pot		2.2	pot	2
Unknown		0.0	unknown	12



**Figure 3**

Map of the eastern Bering Sea showing the regional bathymetry and area boundaries (3 areas) used for mapping, contingency table analysis, and population dynamics modeling.





**Figure 5**

Average seasonal movement of Pacific cod from release to recapture locations. Average movement calculated from all tags released from 2° latitude × 5° longitude reporting blocks and recovered during a specific season.

Let

$R_{ij}$  = the number of fish tagged in time period  $i$  in area  $j$ ,

$r_{ij}$  = the recoveries of tagged fish in time period  $i$  in area  $j$ ,

$N_{ij}^b$  = the number of tags at the beginning of time period  $i$  in area  $j$ , after tags have been redistributed according to estimates of their seasonal distribution,

$N_{ij}^e$  = the number of tags at the end of time period  $i$  in area  $j$ ,

$s_{ij} = s_i = \exp(-M - F_{s(i)})$  the survival of tagged fish in time period  $i$  and area  $j$ ,

$u_{ij} = u_i = F_{s(i)}(1.0 - \exp(-M - F_{s(i)}))/(M + F_{s(i)})$  the exploitation rate of tagged fish in time period  $i$  and area  $j$ , and

$p_{s(i)}$  = the areal distribution by seasonal time period.

Here, the subscript  $s(i)$  refers to the season corresponding to the time period subscript  $i$ . Therefore  $s(i)$  could be  $w$ =winter,  $sp$ =spring,  $su$ =summer, or  $f$ =fall. Each seasonal area-distribution vector ( $p_w$  for example) is a vector containing one element for each of the three areas.

There are 13 parameters to be estimated in this model: the seasonal distribution vectors ( $p_w, p_{sp}, p_{su}, p_f$ ); the seasonal instantaneous rates of fishing mortality ( $F_w, F_{sp}, F_{su}, F_f$ ); and the seasonal instantaneous natural mortality rate ( $M$ ). The seasonal area-distribution vectors each contain only two parameters to be estimated because they are probability distributions that must sum to one. The model is tied together by three simple equations:

$$\begin{aligned} \hat{N}_{ij}^e &= \hat{N}_{ij}^b \hat{s}_i + R_{ij} \sqrt{\hat{s}_i}, \\ \hat{r}_{ij} &= \hat{N}_{ij}^b \hat{u}_i + R_{ij} \hat{u}_i / 2, \\ \hat{N}_{i+1,j}^b &= \left( \sum_j \hat{N}_{ij}^e \right) \hat{p}_{j[s(i+1)]}. \end{aligned}$$

Here,  $\hat{p}_{j[s(i+1)]}$  represents the estimated proportion of tags in area  $j$  in season  $s(i+1)$ . Note that  $\sqrt{\hat{s}_i}$  and  $\hat{u}_i / 2$  are the estimated survival and exploitation rates, respectively, over half a season.

Following Hilborn (1990) and Heifetz and Fujioka (1991), the model was fit by using maximum likelihood and by assuming recoveries were distributed as Poisson random variables. That is, the parameters were estimated by minimizing minus the log-likelihood:

$$-L = \sum_{ij} \hat{r}_{ij} - r_{ij} \log(\hat{r}_{ij}) + const.$$

The probabilities in ( $p_w, p_{sp}, p_{su}, p_f$ ) were modeled as expressions similar to exploitation rates following the method of Heifetz and Fujioka (1991). Parameters were estimated on the logarithmic scale and coefficients of variation were estimated by using the inverse Hessian of the minus log-likelihood and the delta method.

Our seasonal population dynamics model of the tagged population was applied to the areas described in Figure 3. For modeling purposes, we used only fish tagged and recovered in these three areas. Thus, 9,318 releases,

$$\left( \sum_{ij} R_{ij} \right),$$

and 353 recoveries,

$$\left( \sum_{ij} r_{ij} \right),$$

were available for analysis.

A problem associated with our population dynamics model is the strong assumption that the  $F_{s(i)}$  are constant across areas. An attempt was made to use existing commercial trawl and longline data to determine recovery effort, but these data varied too much in their seasonal coverage, and gears and areas were confounded.

Nevertheless, the population dynamics model provides evidence that our tag data are representative of the entire eastern Bering Sea population. In the following sections we present evidence that our tagging study probably suffered from significant tag loss, tag mortality, or under-reporting of tag recoveries. By comparing the estimated seasonal distribution of the tagged population with the distribution from commercial catches, we can verify that the tagged population and untagged population were distributed similarly. Since catch distribution should reflect abundance in a heavily fished region such as the eastern Bering Sea, we interpret this as meaning that the behavior of the tagged Pacific cod population largely reflected similar patterns in the entire Bering Sea population. Commercial catch statistics were taken from the Alaska and Pacific Northwest Historical Groundfish Database (Berger<sup>3</sup>), from which we calculated the areal trawl and longline catch distribution (for numbers), by season, for the 1982–92 study period.

## Results

Approximately 12,396 tagged fish were released between 1982 and 1990 (Table 1; Fig. 1). A total of 373

<sup>3</sup> Berger, J. Alaska Fish. Sci. Cent., Seattle, WA 98115-0070. Personal commun., January 1993.



tag recaptures with useful information were reported to the AFSC through March 1992 for a recovery rate of 3.0%. Although tag returns occurred over a broad area and time period, this rate is much lower than the 24–26% recovery rate reported by Canadian and U.S. researchers working off British Columbia, Canada, and in Puget Sound, Washington (Westrheim, 1984; Karp, 1982). In our study, research trawl-caught fish accounted for the majority of tag releases (97%), and commercially fished bottom trawls and longlines accounted for the majority of tag recoveries (Table 1). Thompson (1994) estimated that the exploitation rate for Pacific cod in the eastern Bering Sea during 1981–1992 averaged 9–11% annually. This suggests additional tag loss, tagging mortality, or under-reporting of rates which sum to about 2/3 in some combination.

Fish lengths at release were between 25 and 118 cm, representing fish as young as age 2 yr as well as very large, mature fish. The distribution of lengths at recovery corresponds well with the overall tag-release size frequency but is shifted to the right due to growth and gear selectivity (Fig. 2).

In the commercial fisheries, Pacific cod are first recruited at about 40 cm or age 3 yr. They become available to different gear types (i.e. initially to bottom trawls, then to longline gear) at progressively older ages and larger mean size (Shimada, 1985). Most tag recaptures were of commercially recruited, sexually mature fish, older than age 5 yr, and larger than about 60 cm, as defined by Teshima (1985).

More than 75% of all tag releases were from U.S. survey vessels in the eastern Bering Sea (Table 1; Fig. 1). Cooperative foreign research vessels operating in the Aleutian Islands and Gulf of Alaska were responsible for the remaining 25%. Twenty-four percent of recoveries were made over the inner shelf, and 29% over the outer shelf and upper slope (Table 1; Fig. 1). Of particular note was the high concentration of tag recoveries (>42%) in Unimak Pass and its surrounding waters (including the adjacent western Gulf of Alaska) during the winter months (Fig. 1). Only 17 tags (<5%) were recovered from outside the three primary study areas (i.e. from the outer Aleutian Islands and the central Gulf of Alaska).

## Mapping seasonal movements

Tagged Pacific cod exhibited marked spatial and temporal displacement from their point of initial release (Fig. 4). Individual movements generally conformed to seasonal shifts in centers of Pacific cod abundance (Ketchen, 1961; Bakkala, 1984) and to the corresponding movement of fishing effort (Shimada, 1985).

We attribute the observed pattern in tagged fish movements to hypothesized migratory shifts between perennial summer (feeding) and winter (spawning) areas (Moiseev, 1952, 1953; Ketchen, 1961). This is most easily seen in the vector movements of individual fish into and out of the main spawning area, Area 3. These data were grouped in two ways to show 1) the origin of fish released in all areas and recovered within Area 3 [Fig. 4A]; and 2) the outward recoveries of fish tagged within Area 3 [Fig. 4B]. Although the movement into and out of Area 3 is clear, the movement into the spawning areas seems to occur in two stages: 1) movement off the inner shelf [Area 1] into slope areas [Area 2] [Fig. 4C]; and 2) subsequent movement into spawning areas in Areas 2 and 3 [Fig. 4D]. This shift is counterbalanced by spring and summer recaptures on the inner shelf [Fig. 4B].

The annual cycle of Pacific cod migration appears to begin in late September, when tagged fish move off the eastern Bering Sea shelf and seaward to the 200 m shelf break. By fall, tags were recovered, primarily along the outer shelf edge. In winter, Pacific cod converged in large spawning masses over relatively small areas. Major aggregations were usually encountered between Unalaska and Unimak islands on the Bering Sea side of Unimak Pass. Other recurring centers of abundance were located southwest of the Pribilof Islands along the shelf edge and near the Shumagin Island group in the western Gulf of Alaska (Fig. 1).

Following the spawning season, tagged Pacific cod dispersed from these overwintering areas and were recaptured farther inshore in concert with seasonal warming of the inner shelf environment. For example, fish tagged in areas of deep off-shelf waters adjoining Unimak Pass, close to the time of winter spawning, were recaptured progressively over the shelf (and especially north of the Alaska Peninsula following the 30-m isobath) beginning in late spring. Tagged Pacific cod also moved to the northwest outer shelf (100–200 m) during the spring quarter. By summer, the feeding range was well established back in central Bristol Bay (30–50 m) and the outer shelf. This distribution persisted until late fall and the beginning of the next yearly cycle.

The seasonal nature of Pacific cod movement is most easily seen in the average vector movement of fish tagged within a particular 2° latitude and 5° longitude rectangle and recovered during a specific season (Fig. 5). From these maps, the off-shelf movement is clearly visible in fall, and movement to the spawning ground is clearly visible in winter. However, spring and summer maps show relatively little directed movement, because during these time peri-

ods, Pacific cod have presumably returned to the feeding grounds on which they were originally tagged. The absence of any definitive within-season pattern is further illustrated in Figure 6. Pacific cod released and recaptured during the same three-month period (i.e. within the same season, perhaps in different years) showed only random movement and little directional bearing. This is in marked contrast to the strong interseasonal movements traced between fall-winter and winter-spring quarter tag recaptures.

**Multiway contingency analysis**

Results from a multiway contingency table analysis (Table 2) indicated that month of recovery most strongly influenced the area of recovery. Although area of tagging also had a significant affect on the area of recovery, the month of tagging was seen to have only a relatively small affect on the area of recovery. Thus season of recovery appeared as the strongest correlate to area of recovery, which further supports our finding of strong seasonal migrations in Pacific cod.

**Seasonal-areal population dynamics modeling and catch distribution**

A histogram of residuals from predicted tag recoveries indicates that the 13-parameter population dynamics model of the tagged population fit the data quite well (Fig. 7). The parameter estimates from the tagging model (Table 3) show strong movement from

**Table 3**  
Estimates of parameters (and coefficients of variation measured as proportions) for the population dynamics model for tagged Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea. Areas are shown in Figure 3.

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1 Quarterly instantaneous natural mortality rate:  
 $\hat{M} = 0.235 (0.109)$ .

2 Seasonal instantaneous fishing mortality rates:  
 $\hat{F}_w = 0.01389 (0.149)$ ,  $\hat{F}_{sp} = 0.0082 (0.176)$ ,  
 $\hat{F}_{su} = 0.0075 (0.152)$ ,  $\hat{F}_f = 0.0087 (0.141)$

3 Seasonal distribution over (Area 1, Area 2, Area 3):  
a  $\hat{p}_w = [0.0246 (0.570), 0.1884 (0.188), 0.7870 (0.047)]$   
b  $\hat{p}_{sp} = [0.4849 (0.148), 0.3937 (0.175), 0.1214 (0.371)]$   
c  $\hat{p}_{su} = [0.5830 (0.122), 0.2330 (0.255), 0.1840 (0.318)]$   
d  $\hat{p}_f = [0.1103 (0.304), 0.5167 (0.105), 0.3730 (0.143)]$

the major spawning area (Area 3) in spring, further movement onto the shelf (Area 1) in summer, movement off the shelf in fall, and movement to the spawning areas in winter. Furthermore, the model results confirm strong seasonal movement between areas in a manner consistent with our previously described pattern of seasonal Pacific cod movements.

The apparent high annual instantaneous natural mortality rate ( $\hat{M} = 0.96$ ) and low annual fishing mortality rate ( $\hat{F} = 0.038$ ) of the tagged population can be noted. This is probably due to tag loss, tagging mortality, or the under-reporting of tag recoveries as previously discussed. Multiplying releases by 1/3, or multiplying recoveries by 3 would lower  $\hat{M}$  and increase  $\hat{F}$  nearer to expected levels ( $\hat{M} = 0.87, \hat{F} = 0.11$ ). However, the model fit and estimated seasonal distribution of the tagged population were not affected by this scaling of observed releases or recoveries. Therefore, the population dynamics model estimates of seasonal distribution appear to be robust to tag loss, tag mortality, or under-reporting of recoveries.

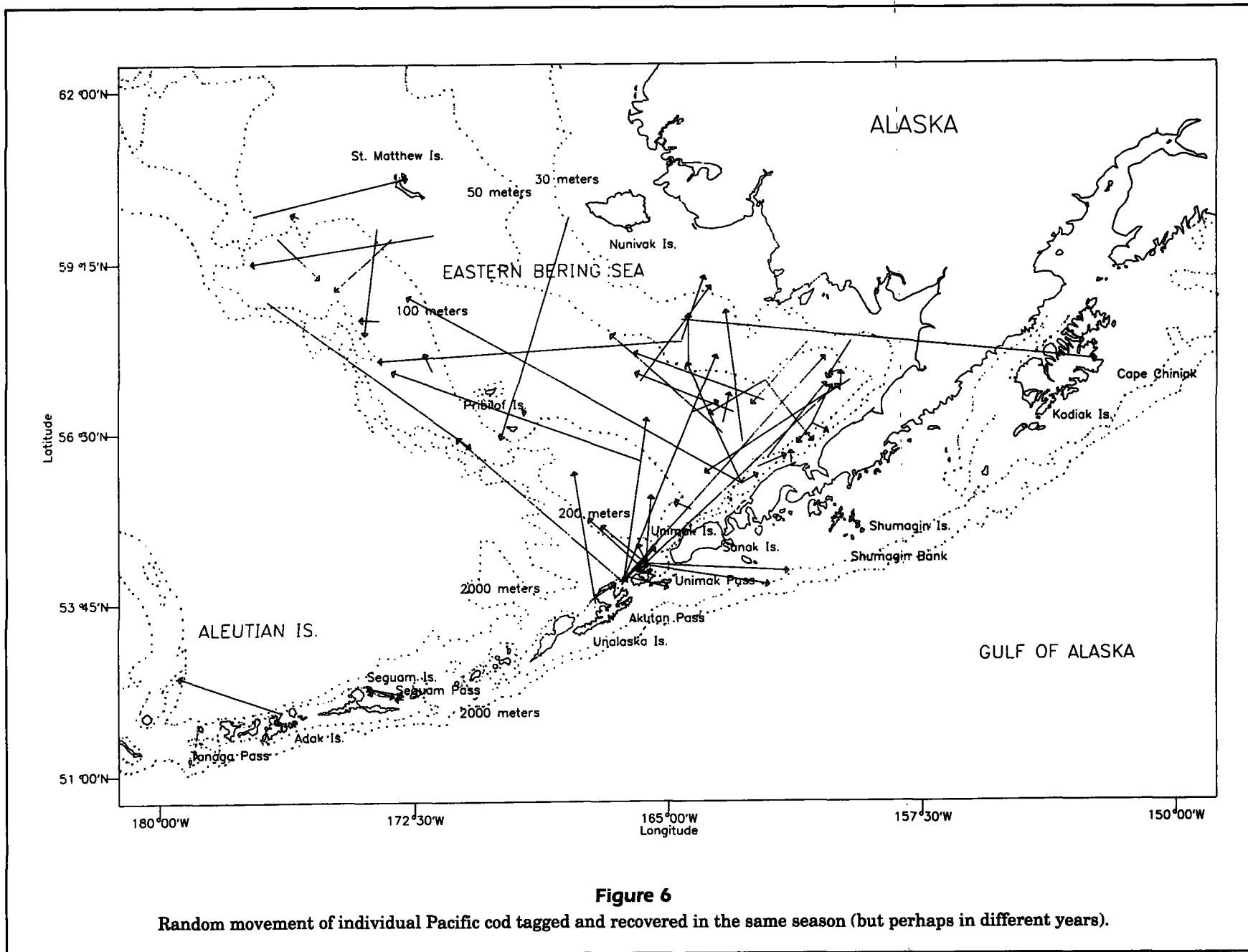
The estimated areal distributions (within seasons) of the tagged population largely reflect the areal distribution of tag recoveries. Also, although no catch data were used in the population dynamics model, the results coincide well with the estimated seasonal distribution of the commercial catches (Table 4). The main difference appears to be that the hypothesized fall season off-shelf movement, and subsequent movement into the winter spawning area (Fig. 4, C and D), is more pronounced in the commercial catch data

**Table 2**

Multiway contingency table analysis of tag recovery data for Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea. The model examined all two-factor interactions (i.e. no factor deletions). Each two-factor interaction was tested for significance by deleting it from the model. Factor 1 = season of release (4 levels), 2 = area of release (3 levels), 3 = season of recovery (4 levels), 4 = area of recovery (3 levels).

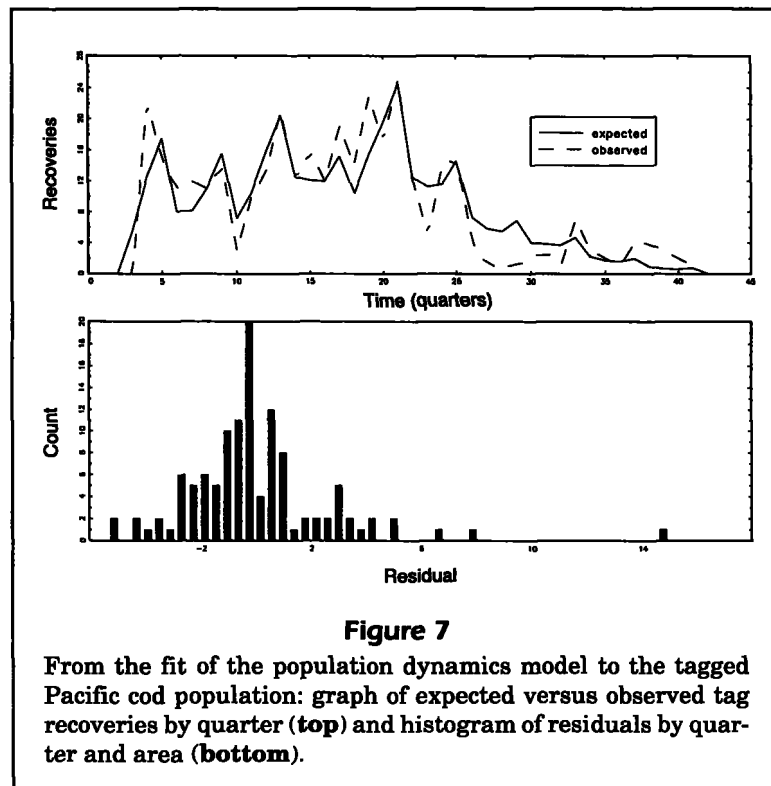
Factor deleted	Likelihood ratio stat.	df	P	Test of interaction
none	66.150	96	0.0087	not applicable
[12]	139.382	102	0.9917	(Z=8.786) <sup>1</sup>
[13]	75.892	105	0.0145	(Z=0.291)
[14]	79.206	102	0.0459	(Z=1.793)
[23]	118.317	102	0.8713	(Z=6.898)
[24]	209.201	100	1.0000	(Z=14.269)***
[34]	245.890	102	1.0000	(Z=15.643)***

<sup>1</sup> Interaction large but fixed by design. Z-statistic is a standard normalization of the hierarchical chi-square test.  
\*\*\* Interactions were significant;  $\alpha=0.0001$ .



**Figure 6**

Random movement of individual Pacific cod tagged and recovered in the same season (but perhaps in different years).



(Hollowed and Low<sup>4</sup>) than the tagging data. Therefore, we conclude that observed movements in the tagged population generally reflect the population movements of Pacific cod in the eastern Bering Sea.

#### Emigration and immigration relative to the study area

We provide direct evidence that Pacific cod migrate from the eastern Bering Sea into the Gulf of Alaska. Of the 95 winter recoveries made in Area 3, 21 of these occurred in the Gulf of Alaska (Fig. 8; note that Fig. 8 includes 30 Gulf of Alaska recoveries from all seasons). Longline vessels operating in the winter quarter between Sanak Island and Shumagin Bank were the main source of returns. These data suggest that 22% of fish found in Area 3 in winter may migrate into the Gulf of Alaska. Multiplying this figure by the population dynamics estimate of 78% (which is the total eastern Bering Sea winter population within Area 3), or by the 68% of the winter commercial catch that is taken in Area 3, suggests that 15 to

<sup>4</sup> Hollowed, A. B., and L. L. Low. 1986. Productive gadoid fishing grounds based on species assemblage analysis. In M. A. Alton (ed.), A workshop on comparative biology, assessment, and management of gadoids from the North Pacific and Atlantic oceans. Proceedings: part II, p. 681-712. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., Bin C15700, Seattle, WA 98115-0070.

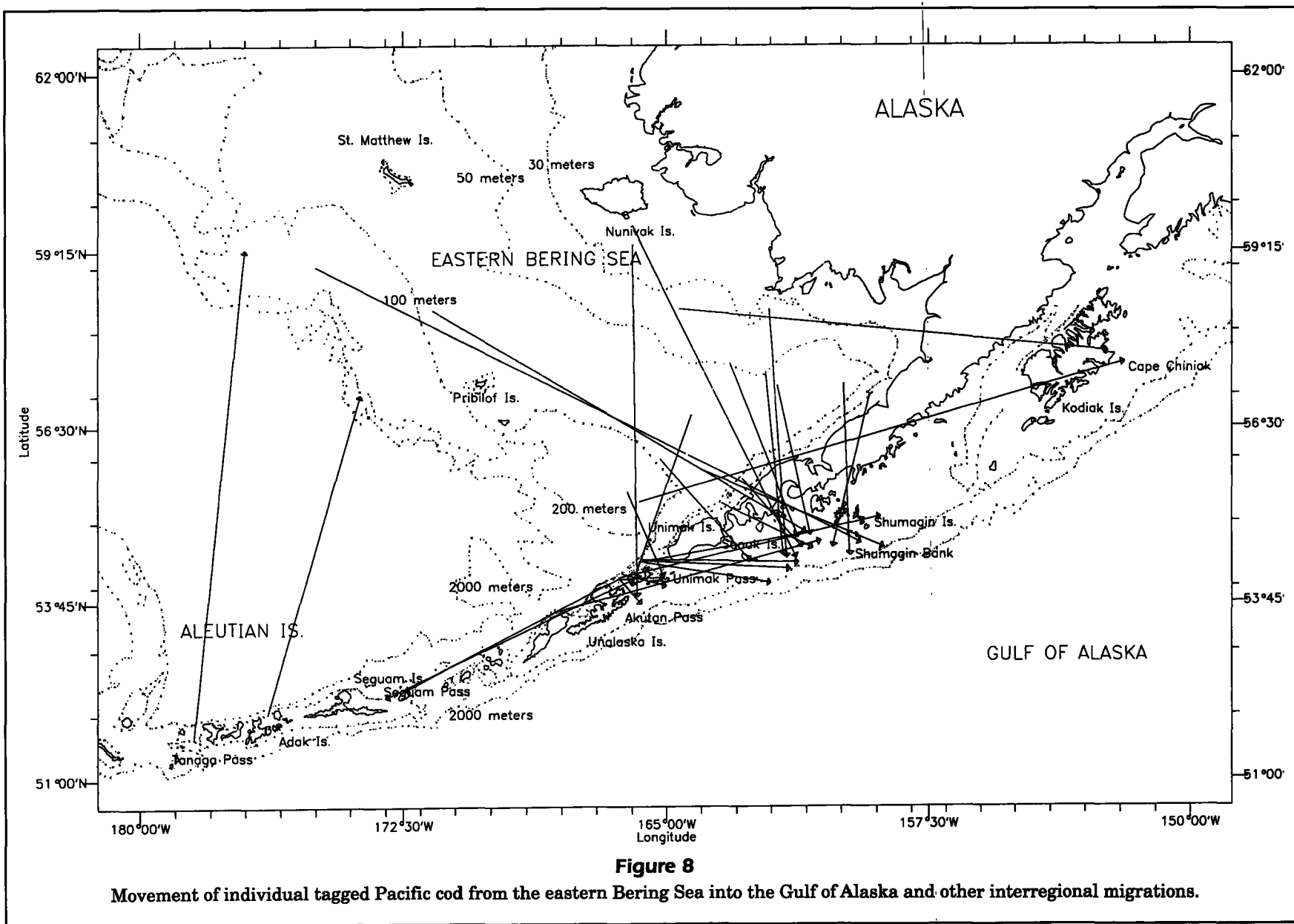
**Table 4**

Distribution of catch (numbers) by season and area (Area 1=the eastern Bering Sea shelf, Area 2=the outer eastern Bering Sea shelf and upper slope, Area 3= the main spawning area), from 1982 to 1992, for Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea. Estimated from the Alaska and Pacific Northwest Historical Groundfish Database (J. Berger, Alaska Fish. Sci. Cent., Seattle, WA 98115-0070, Personal commun., January 1993) and from the relative magnitude of trawl and longline catches.

Season	Area 1	Area 2	Area 3
Winter	0.085	0.235	0.680
Spring	0.496	0.393	0.111
Summer	0.703	0.276	0.021
Fall	0.176	0.651	0.173

17% of the total population in the eastern Bering Sea may migrate into the Gulf of Alaska during winter.

A number of individual longer-range migrations tie together the Pacific cod population from 150° W to 180° W longitude (Fig. 8). We note with interest the recovery of two Bering Sea tags in the central Gulf of Alaska near Cape Chiniak on Kodiak Island, after 103 and 334 days. Other tagged Bering Sea emigrants have been recaptured on the North



Pacific side of Akutan Pass and Unimak Pass in the Aleutian Islands. Additionally, two fish tagged in the major spawning area (Area 3) were recaptured to the west in Seguam Pass within 250 days. In a striking occurrence of immigration to the Bering Sea, a pair of Pacific cod (65 cm fork length) tagged in Tanaga Pass near Adak Island were recaptured on the outer northwest shelf (above 57°N) after 3 and 5 years at liberty (Fig. 8).

Although substantial numbers of Pacific cod were tagged along the Aleutian Islands west of 170°W, including to about 174°E (Fig. 1), few recoveries have been made. These releases came from a single 1986 summer trawl survey and tagged fish were in poor condition because commercial foreign fishing operations were employed.

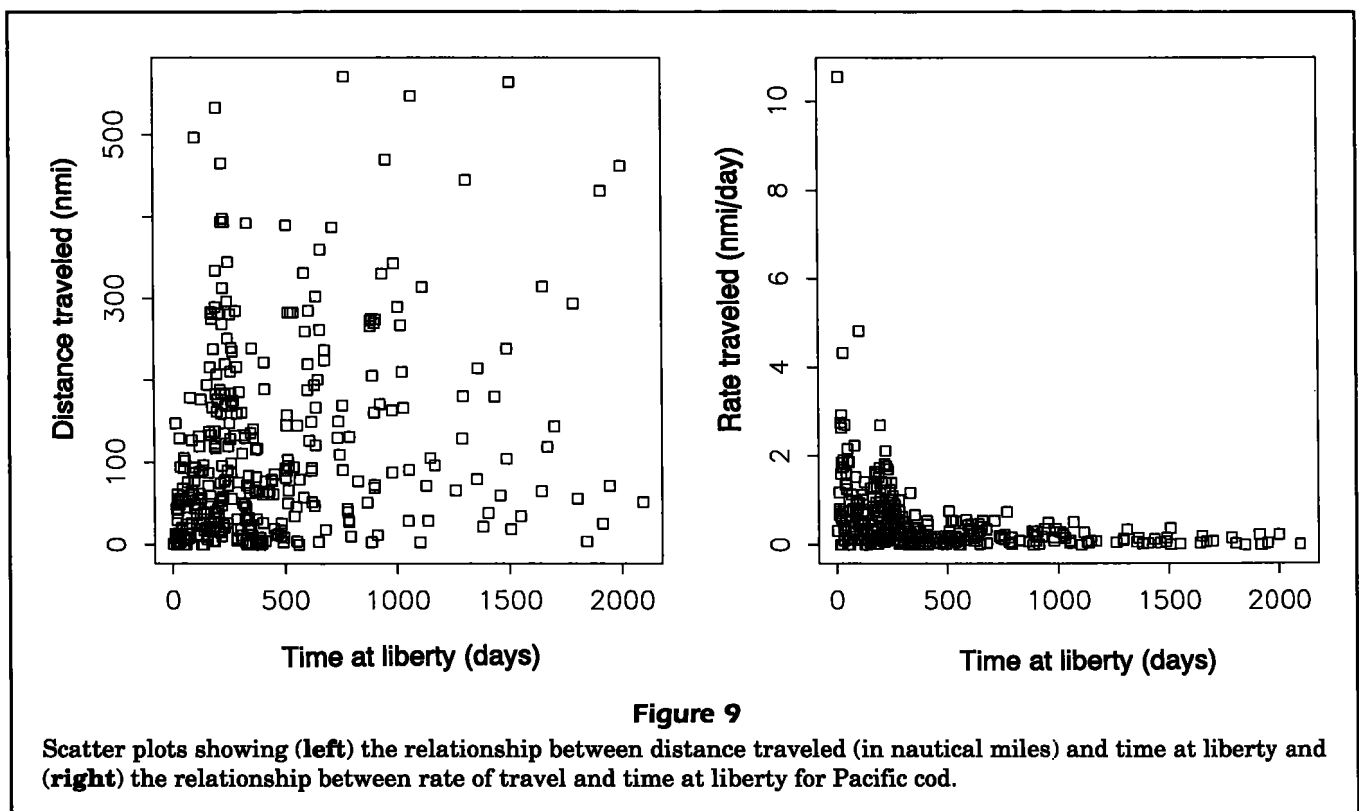
## Discussion

Our analysis identified a seasonal circuit that we attribute to annual migrations for spawning and feeding; it also provided preliminary indications of emigration from the eastern Bering Sea. The former is described in terms of three eastern Bering Sea areas. The latter ties together more expansive distances as defined by regional geography or fishery management boundaries, or both (OCSEAP, 1987). Although

the majority of tagged Pacific cod exhibited the seasonal character of short-term cross-shelf movements, a small number of tagged individuals provided empirical evidence for much longer transits.

We recognize that emigration and immigration probably occur with respect to the main study area (i.e. Areas 1–3). However, the locations of tag releases and numbers of tag recoveries received to date make it difficult either to quantify the amount of emigration from the eastern Bering Sea, or to conclude with certainty that return immigration to the eastern Bering Sea is significant. At this time, we believe there is some eastern Bering Sea immigration from the surrounding regions. However, considerable uncertainty exists because so few Pacific cod were tagged outside the study region, most importantly in the central and eastern Gulf of Alaska (Fig. 1). Also, we have some evidence that the western Aleutian Islands stock(s) may be fairly independent of the eastern Bering Sea, but this evidence is far from conclusive.

Despite these conjectures, statistics such as “distance traveled” and “rate traveled” versus “time at liberty” (Fig. 9) generally support our seasonal movement model. Observed “distance traveled” already is maximized within the first year of freedom. Similarly, observed “rate traveled” is maximized within the first year at liberty. This behavior is consistent



with seasonal migrations within a closed system. Other movements occur against a backdrop which is dominated by regular seasonal movements.

Movements of Pacific cod may be better understood in the context of the general life history, population dynamics and physical environment requirements of this species. Bakkala (1984) examined distribution patterns based on an analysis of research survey and commercial fishery catch per unit of effort and size composition data. He described a gradual shift over the southeast shelf with time, corresponding to a progression in cohort ages and the influence of year-class abundance. A tendency towards the offshore environment was noted from coastal waters to the outer shelf and slope edge. This was based on an areal transition stemming from ontogenetic development in younger age (1–3 yr) to older age (4+ yr) groups. Further, during years of higher than average abundance, the population range was much more extensive than that in years of low abundance (Bakkala, 1984).

From Russian trawl surveys, Stepanenko<sup>5</sup> described winter concentrations along the upper slope at depths between 400 and 545 m. Prespawning and spawning aggregations were consistently found northwest of Unimak Island, in the Pribilof Islands sector, and along the northern slope on either side of the U.S.-Russia Convention Line. The most significant spawning aggregations occurred in the vicinity of Unimak Pass along the outer shelf edge.

The literature indicates that preferred water temperatures (0 to 10°C) are the primary factor for determining centers of Pacific cod abundance. Towards its southern range off British Columbia, Ketchen (1961) reported highest catch rates at bottom temperatures of between 6 and 9°C. Off Russia, Moiseev (1953) noted that spawning Asian Pacific cod preferred 80–290 m depths and water temperatures between 0 and 2 to 3°C; optimal summer temperatures were between 0.2 and 4.5°C. Hirschberger and Smith (1983) reported water temperatures around 5.4°C for spawning Gulf of Alaska Pacific cod at 150–250 m.

In the eastern Bering Sea, high winter concentrations of Pacific cod coincide with warmer water (mean 4.0°C) found year-round in depths off Unimak Pass and the upper slope (Kihara, 1982, a and b; Bakkala, 1984). Bottom temperatures on the shelf drop from the 0.2 to 4.5°C range in summer to below 0°C in winter (Schumacher and Reed, 1983). Thus at the high latitudes of the Bering Sea, the stimulus for

offshore migration appears to be avoidance of the intense cooling of inshore waters that accompany advancing ice formation from the Bering Strait in favor of warmer temperatures at depth. The spring feeding migration, shoreward, is most likely timed to the warming of the coastal shelf environment and a return to summer norms (Bakkala, 1984).

Interestingly, at lower latitudes, seasonal migrations are reversed. At the southernmost edge of its range, off Korea, Japan, and in Puget Sound, Washington (Karp, 1982; Mishima, 1984; Zhang, 1984), Pacific cod migrate to deep offshore waters during summer months to avoid excessively heated (>10°C coastal waters). A returning inshore spawning migration occurs each winter.

Moiseev (1953) noted very limited along-shore migrations in Russian waters. However, active seasonal migrations between coastal shallows and offshore depths perpendicular to the shoreline (mainly in response to inshore and offshore temperature shifts) were found. He further hypothesized that the potential for stock intermingling was reduced because of limited along-shore movement. Winter offshore movements were observed throughout the northern range of Pacific cod. Local abundance centers were always in the direction of the preferred temperature regime in response to the pronounced cooling of their onshelf environment. Westheim (1984) noted that Pacific cod off Vancouver Island, British Columbia, exhibited the same bathymetric seasonal movements as Pacific cod in Alaska but very limited along-shore movements.

In all of the cases described above, seasonal migrations of Pacific cod appear to be triggered by the desire to avoid temperature extremes that accompany the changing seasons. In the eastern Bering Sea, movements represent necessarily long-range migrations across the Bering Sea shelf which on average is 300 nmi wide. For southern coastal stocks, the same result can be achieved with much shorter offshore migrations to depth. It is likely that inter-regional along-shore migrations seldom are found because they are unnecessary for achieving the preferred temperature regime (Moiseev, 1952).

Rose (1993) found a similar pattern in Atlantic cod, *Gadus morhua*, based on hydroacoustic surveys. He attributed seasonal movement to springtime feeding migrations, which shifted Atlantic cod from offshore winter spawning grounds shoreward. Migration pathways were facilitated by stable bottom temperature regimes (2–3°C) associated with trenches on the north-eastern Newfoundland shelf.

How large-scale stock structure is affected by migrations motivated by preferred temperatures is unclear. Grant et al. (1987) screened Pacific cod genetic samples from throughout their range. Two ge-

<sup>5</sup> Stepanenko, M. A. 1989. Condition of stocks, interannual variability of catch per unit of effort and fishing of cod in the eastern part of the Bering Sea. Pacific Research Institute of Fisheries and Oceanography (TINRO), Vladivostok, USSR. Document submitted to the US-USSR bilateral meetings, November 1989, 35 p. Available: Alaska Fish. Sci. Cent., NOAA, NMFS, 7600 Sand Point Way NE., Bin C15700, Seattle, WA 98115-0070.

netically distinct stocks were detected: a western North Pacific Ocean (Asian) group, and an eastern North Pacific group which included the Bering Sea, Aleutians Islands, and Gulf of Alaska regions. There were virtually no regional genetic differences among any of the North American samples. These authors were unable to identify where the effective northern boundary between the western and eastern groups lies, though the western Bering Sea was considered most likely. Grant et al. (1987) attributed this lack of genetic differentiation to gene flow between various subareas and regions on either side of the Pacific. Grant et al. (1987) were puzzled that most of the literature on Pacific cod pointed toward locally isolated stocks (Moiseev, 1953; Svetovidov, 1948; Ketchen, 1961; Wilimovsky et al., 1967). Our tagging study confirms sufficient migration to explain Grant et al.'s findings of genetic homogeneity in Pacific cod over broad areas of the North Pacific.

We have confirmed from tagging that Pacific cod migration occurs between the Bering Sea and Aleutian Islands. Because of the experimental design, the majority of tag returns demonstrate emigration from the Bering Sea but have not shown conclusively that immigration to the Bering Sea takes place. Even so, this study shows that significant exchange may occur within the open ocean populations of Pacific cod off Alaska. Whether Bering Sea Pacific cod have a reciprocal exchange to the wider Gulf of Alaska beyond the nearby waters of major Aleutian passes remains an open question. Lack of data precludes any further statement or quantification of exchanges between these regions. Further elucidation must await additional tagging results, particularly from the eastern Gulf of Alaska and western Aleutian Islands.

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