
#### Abstract

Over 34,000 age $0-2$ juvenile sablefish (Anoplopoma fimbria) were tagged and released in southeast Alaska waters during 1985-2005. The data set resulting from this tagging study was unusual because of its time span ( 20 years) and because age could be reliably inferred from release length (i.e., tagged and released fish were of known age); thus, age-specific movement patterns could be examined. The depth- and area-related recovery patterns supported the concepts that sablefish move to deeper water with age and migrate counterclockwise in the Gulf of Alaska. Availability to the fishery increased rapidly for fish of younger ages, peaked at age 5 to 6 , and then gradually declined as sablefish moved deeper with age. Decreased availability with age may occur because of lower fishing effort in deep water and could have substantial implications for sablefish stock assessments because "domeshaped" availability influences the reliability of abundance estimates. The area-related recovery pattern was not affected by year-class strength; i.e., there was no significant densitydependent relationship.


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# Age-specific movement patterns of sablefish (Anoplopoma fimbria) in Alaska 

Nancy E. Maloney (contact author)<br>Michael F. Sigler<br>Email address for N. E. Maloney: Nancy.Maloney@noaa.gov<br>National Oceanic and Atmospheric Administration<br>National Marine Fisheries Service<br>Alaska Fisheries Science Center, Auke Bay Laboratories<br>Ted Stevens Marine Research Institute<br>17109 Point Lena Loop Road<br>Juneau, Alaska 99801

The general migration pattern of sablefish (Anoplopoma fimbria) in the northeast Pacific Ocean was deduced in the 1980s from several tagging studies (Bracken, 1983; Beamish and McFarlane, 1988; Fujioka et al., 1988;) and enlarged upon in further studies over the following two decades (Heifetz and Fujioka, 1991; Rutecki and Varosi, 1997; Kimura et al., 1998; Maloney, 2004). In southeast Alaska, juvenile sablefish that are spawned offshore appear in inshore waters in late summer or early fall and spend the first year or two of life in shallow coastal bays and inlets before moving into progressively deeper water. At the same time that they are moving into deeper water, many young sablefish move north and west on a migration path that takes them across the Gulf of Alaska to the Aleutian Islands and Bering Sea. Eventually, most will return to the eastern Gulf of Alaska as adults.

The sablefish fishery in the Gulf of Alaska (GOA), eastern Bering Sea, and Aleutian Islands is managed by the National Marine Fisheries Service (NMFS) in cooperation with the North Pacific Fishery Management Council. Sablefish in these areas are assumed to belong to one population (Kimura et al., 1998), for which a total allowable catch is calculated each year and apportioned among six management areas. The annual quotas for each area are based on the distribution of biomass among the areas, which is estimated from longline surveys and commercial catches (Heifetz et al., 1997). Because sablefish are
known to be migratory, estimates of the rates of migration between areas could affect the apportionment of quotas among management areas (Heifetz et al., 1997).
Migration rates between areas have been estimated from tag data by using fish-length classes in the modeling process (Heifetz and Fujioka, 1991). Although fish-length data are commonly available, actual age data are generally scarce. Age data are preferable to length data for estimating population age structure (Sigler, 1999), but sablefish are difficult to age, especially for ages greater than 5 or 6 years (Kimura and Lyons, 1991). Tagging of known-age juveniles before they leave coastal areas offers an opportunity to document age-specific movements. Age $0-2$ (mostly age 1) sablefish have been tagged annually since 1985 in bays and inlets of southeast Alaska. The objective of our study was to determine movement patterns of sablefish based on these known-age fish, using a unique 20-year data set of age-specific mark-recapture data. Specifically, we determined 1) how the depth inhabited by sablefish changes with age; 2) how the area inhabited changes with age; 3) how availability to the primary fishery (longline) changes with age; and 4) whether there is a density-dependent effect of year-class strength on the extent of migration of young sablefish. Results of objectives 1 and 2 largely confirmed the results of previous studies, whereas objectives 3 and 4 were new.


Figure 1
Recovery locations (o) of sablefish (Anoplopoma fimbria) tagged and released as juveniles in southeast Alaska. St. John Baptist Bay was the most common release site. Vertical and horizontal bars are regulatory area boundaries. Gulf of Alaska is shown as GOA for the Western, Central, and Eastern areas.

## Materials and methods

Juvenile sablefish were captured, primarily with jigging gear (Rutecki and Varosi, 1997) in various bays and inlets of southeast Alaska, for tagging and release from 1985 to 2005 . A total of 74 sites were selected during that period, but most tagging after 1987 was undertaken in St. John Baptist Bay near Sitka, Alaska (Fig. 1), because it was easily accessible and juvenile sablefish were consistently found there. Bottom depth is about 30 m and fish were caught on the bottom and throughout the water column. Release and recovery data for these fish are maintained in the NMFS Alaska Sablefish Tag Database, which is described in detail by Fujioka et al. (1988).

## Data criteria

Recovered fish had to meet several criteria to be included in this study: recovery year had to be known, recovery depth and location had to be accurate, and the fish had to be at liberty for at least one year. Recovery year was necessary to calculate age at recapture. Accurate recovery depth and location were necessary to reliably assign recovery depth strata and areas. Only recoveries for which there were reported positions that were precise to within 10 minutes of latitude and longitude were used; this criterion was used to judge the reliability of the recovery information. Some tag recoveries had accurate recovery location but no depth information; these tag recoveries were included in the area
analysis, but not the depth analysis. Recovery depths were classified into seven depth strata chosen to reflect general habitat type: $1-100 \mathrm{~m}$ (nearshore), $101-200 \mathrm{~m}$ (continental shelf), 201-300 m (shelf break), 301-500 m (upper continental slope), $501-700 \mathrm{~m}$ (middle slope), $701-1000 \mathrm{~m}$ (lower slope), and $>1000 \mathrm{~m}$ (deep water). Recovery locations were classified into seven areas: Aleutian Islands, Bering Sea, western Gulf of Alaska (western GOA), central Gulf of Alaska (central GOA), eastern Gulf of Alaska outside waters (eastern GOA outside), eastern Gulf of Alaska inside waters (eastern GOA inside), and British Columbia. For some analyses, inside and outside waters were pooled and referred to as eastern GOA. The minimum time at liberty of one year was imposed to exclude short-term movements and to focus on migration.

Age at release was determined from fish size and time of year. Depending on the time of year, in most years and tagging areas, no more than two ages of fish, and usually only one, were present at the time of tagging. Ages were readily separable by means of non-overlapping length frequencies and by time of year. Age-0 fish enter into bays from the ocean in the fall of their first year of life, and they average $21-23 \mathrm{~cm}$ in length (Rutecki and Varosi, 1997). One-year-old fish in the middle of summer average $31-35 \mathrm{~cm}$ and 2 -year-old fish average $40-45 \mathrm{~cm}$. The number of years at liberty after release was calculated by subtracting the release year from the recovery year; adding this number to the release age supplied the recovery age.

## Availability to the fishery by age

Sablefish move progressively deeper with age, and as they do so, become available to the main commercial fishery (longline), which operates primarily on the continental slope. The fraction of the total population available by age to the commercial fishery was estimated by the following method. The initial number of tagged fish released in year $t$ of age $a$ is $N_{a t}^{\prime}$. A fraction of the tags, $l=0.048$ (Lenarz and Shaw, 1997), are immediately lost or the fish die from tagging, such that a short time after tagging, some smaller number of tagged fish survive,

$$
N_{a t}=(1-l) N_{a t}^{\prime}
$$

The year following tagging, the number of tagged fish is

$$
N_{a+1, t+1}=N_{a t} \exp \left(-\left(M+\lambda s_{a} F_{t}+H\right)\right)
$$

where $M=0.1$ (Sigler, 1999; Hanselman et al., 2006) is the instantaneous rate of natural mortality;
$\lambda=$ a calibration parameter (Heifetz and Fujioka, 1991) to account for bias in assumed values for the instantaneous rates of annual fishing mortality ( $F_{t}$ );
$s_{a}=$ availability (selectivity) to the commercial fishery; and
$H=0.03$ (Lenarz and Shaw, 1997) is the instantaneous rate of tag shedding.

The $F_{t}$ values were estimated independently in the Alaska sablefish stock assessment (Hanselman et al., 2006). The fishery captures a number of the tagged fish, $C_{a t}$, where

$$
\begin{gathered}
C_{a t}=\lambda s_{a} F_{t} /\left(M+\lambda s_{a} F_{t}+H\right) \\
\left(1-\exp \left(-\left(M+\lambda s_{a} F_{t}+H\right)\right)\right) N_{a t}
\end{gathered}
$$

The relationship between availability and age was represented by the exponential-logistic function (Thompson, 1994; Sigler, 1999)

$$
\begin{gathered}
s_{a}=1 /(1-\gamma)((1-\gamma) / \gamma)^{\gamma} \\
\exp (\beta \gamma(\alpha-a)) /(1+\exp (\beta(\alpha-a)))
\end{gathered}
$$

The exponential-logistic function is flexible, allowing both asymptotic availability when availability increases with age to an asymptote, and dome-shaped availability when availability increases with age to a maximum and then decreases for older fish. The exponential-logistic function automatically scales maximum availability to 1.0 and reduces to asymptotic availability as the parameter $\gamma$ approaches zero. When $\gamma=0$, the parameter $\alpha$ is the age of $50 \%$ availability and the slope of the curve equals $1 / 4 \beta$ at $\alpha=\alpha$. When $\gamma>0$, then $\alpha$ and $\beta$ lose biological meaning because $\alpha$ no longer represents the age
at $50 \%$ availability, and $\gamma$ is a parameter that allows availability to decrease (and form the "dome-shape") for older ages The fishery switched from open access to individual fishing quotas (IFQ) in 1995. This switch has been shown to affect availability of the fish to the fishery (Sigler and Lunsford, 2001). Thus, we estimated availability parameters, $\alpha, \beta$, and $\gamma$, as well as the fishing mortality calibration parameter, $\lambda$, separately for each time period (1984-94, 1995-2005). We assumed that the estimated availability curves represent the commercial longline fishery because most tags ( $93 \%$ ) were recovered by longline or other fixed gear types.

Not all tagged fish caught in the sablefish fishery are reported (Heifetz and Maloney, 2001). The number of tags reported, $R$, is related to the number of tagged fish caught, $C_{a t}$, where $R_{a t}=w_{t} C_{a t}$ and $w_{t}$ is the reporting rate. Heifetz and Maloney (2001) estimated annual reporting rates for 1980-98 and subsequent reporting rates were estimated of 0.43 for 1999-2001 and 0.52 for $2002-05$, which we applied in our analysis.

The model parameters ( $\alpha, \beta, \gamma$, and $\lambda$ for 1984-94 and 1995-2005) were estimated by maximum likelihood. The observed number of tag recoveries in any year-cohort grouping was small (mean of 6 , range of 0 to 27); therefore the expected number of tag recoveries, $Q$, could be approximated by the Poisson distribution (Hilborn, 1990). The negative log-likelihood $\left(-\log _{e} L\right)$ for all observed recoveries was

$$
\begin{gathered}
-\log _{e} L\left(Q_{a t} \mid R_{a t}\right) \\
=\sum_{a} \sum_{t}\left(Q_{a t}-R_{a t} \log _{e}\left(Q_{a t}\right)+\log _{e}\left(R_{a t}!\right)\right)
\end{gathered}
$$

which was minimized to find the most likely set of parameter estimates. We examined model fit using deviance (McCullagh and Nelder, 1983), which for any observation of tag recoveries is

$$
\text { deviance }(a, t)=-2\left\{\log _{e} L\left(Q_{a t} \mid R_{a t}\right)-\log _{e} L\left(R_{a t} \mid R_{a t}\right\}\right.
$$

(Heifetz and Fujioka, 1991). We applied the likelihood ratio test for nested models (Hilborn and Mangel, 1997) to determine whether model fit was significantly improved by assuming separate parameter sets for the open access and IFQ fisheries. We estimated the 95\% confidence intervals of the parameters from their likelihood profiles (Hilborn and Mangel, 1997).

## Density-dependent effect on migration

Migration may be affected by abundance if sablefish tend to disperse when abundant. We tested for a den-sity-dependent effect by examining whether recovery patterns by area were influenced by cohort abundance (recruitment strength). Recruitment strength is estimated through age-structured population modeling (Hanselman et al., 2006) and is expressed as the number of fish at age 2 (in millions). We tested by linear regression whether more recoveries occurred in western areas for stronger year classes, hypothesizing that more mem-

## Table 1

Total numbers of juvenile sablefish (Anoplopoma fimbria) released and recovered in southeast Alaska, 1985-2005, by release age (age 0, age 1, and age 2). Also shown are numbers of recoveries of fish with known recovery year, with accurate recovery location and accurate recovery depth, for fish at liberty longer than one year.

| Year | Age 0 | Age 1 | Age 2 | Total releases | Total recoveries | Accurate recovery location | Accurate recovery depth |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1985 | 0 | 6168 | 0 | 6168 | 853 |  |  |
| 1986 | 0 | 240 | 936 | 1176 | 68 | 2 | 1 |
| 1987 | 0 | 7916 | 0 | 7916 | 314 | 8 | 7 |
| 1988 | 1762 | 2142 | 1 | 3905 | 153 | 26 | 20 |
| 1989 | 0 | 530 | 1 | 531 | 35 | 47 | 41 |
| 1990 | 0 | 0 | 0 | 0 | 0 | 65 | 53 |
| 1991 | 789 | 2580 | 1 | 3370 | 154 | 56 | 39 |
| 1992 | 0 | 1658 | 0 | 1658 | 68 | 57 | 47 |
| 1993 | 0 | 568 | 26 | 594 | 48 | 66 | 59 |
| 1994 | 0 | 1190 | 8 | 1198 | 44 | 31 | 27 |
| 1995 | 0 | 986 | 0 | 986 | 75 | 50 | 42 |
| 1996 | 0 | 1735 | 0 | 1735 | 62 | 46 | 42 |
| 1997 | 0 | 58 | 0 | 58 | 4 | 59 | 55 |
| 1998 | 0 | 1174 | 0 | 1174 | 37 | 43 | 38 |
| 1999 | 0 | 859 | 5 | 864 | 41 | 61 | 56 |
| 2000 | 0 | 559 | 178 | 737 | 41 | 40 | 31 |
| 2001 | 0 | 105 | 1 | 106 | 3 | 41 | 34 |
| 2002 | 0 | 471 | 2 | 473 | 8 | 37 | 29 |
| 2003 | 766 | 0 | 0 | 766 | 0 | 56 | 49 |
| 2004 | 0 | 290 | 1 | 291 | 0 | 40 | 34 |
| 2005 | 0 | 610 | 0 | 610 | 3 | 29 | 26 |
| Totals | 3317 | 29,839 | 1160 | 34,316 | 2011 | 860 | 730 |

bers of strong year classes would move westward if cohort density affected migration.

## Results

Over 34,000 juvenile sablefish were tagged and released in southeast Alaska from 1985 to 2005 (Table 1). Most ( $87 \%$ ) were tagged and released at age 1. A total of 2011 sablefish tagged as juveniles were recovered, most by the commercial fishery and a few by research vessels. Of these 2011 recoveries, 860 fish had a known recovery year, accurate recovery information, and were at liberty for at least one year, thus qualifying for area-based analyses; 730 fish also had known recovery depth and qualified for depth-based analyses (Table 1). Of the 860 fish recovered, most ( $85 \%$ ) were caught by longline, $8 \%$ by pots, $6 \%$ by bottom trawl, and the remainder ( $1 \%$ ) by jig, purse seine, sport fishing gear, or by unknown gear. The largest percentage ( $45 \%$ ) of recoveries occurred in the eastern Gulf of Alaska (Table 2). Large percentages of tagged fish also were recovered in the central Gulf of Alaska ( $30 \%$ ) and farther westward ( $18 \%$ ). About half ( $51 \%$ ) of recoveries occurred at depths $501-700 \mathrm{~m}$ and
nearly all (93\%) recoveries occurred at depths from 201 to 1000 m .

Sablefish tagged as juveniles in southeast Alaska were recovered as far west as $177^{\circ} \mathrm{E}$ along the Aleutian Islands, as far north as $60^{\circ} \mathrm{N}$ in the eastern Bering Sea, and as far south as $48.5^{\circ} \mathrm{N}$ off Vancouver Island (Fig. 1). Most recoveries were located along the upper continental slope or in cross-shelf gullies such as Spencer and Seward Gullies. Having originated in coastal bays, these fish had to cross the continental shelf to reach these areas. Fish recovered in Chatham Strait may have moved there by way of inland waters or may have migrated first to outer coastal waters before moving into the strait.

## Recovery locations by depth and area

Generally, young fish were more common at shallower depths and older fish were more common at greater depths. In depths shallower than 200 m , the most common ages of tagged juvenile sablefish recoveries were 3 and 4 years, and in depths greater than 200 m , the most common ages were $5-8$ years (Fig. 2). Median recovery age increased with depth from shallow (2 years)

## Table 2

Recovery area and depth strata ( m ) for recovered sablefish (Anoplopoma fimbria) tagged as juveniles, number of fish for which depth was unknown, and total number of tagged fish captured in the recovery area. Proportion of recoveries at depth (bottom row) excludes recoveries with unknown depth. Proportion of recoveries by recovery area (rightmost column) includes recoveries with unknown depth. GOA = Gulf of Alaska.

|  | Depth strata $(\mathrm{m})$ |  |  |  |  |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Recovery area | $1-100$ | $101-200$ | $201-300$ | $301-500$ | $501-700$ | $701-1000$ | $>1000$ | Unknown | Total | Proportion |
| Bering Sea |  |  |  | 4 | 9 | 4 |  | 1 | 18 | 0.02 |  |
| Aleutian Islands |  | 3 |  | 5 | 39 | 7 |  | 8 | 62 | 0.07 |  |
| Western GOA |  | 4 | 6 | 19 | 28 | 7 |  | 10 | 74 | 0.09 |  |
| Central GOA |  | 25 | 43 | 48 | 90 | 19 | 2 | 28 | 255 | 0.30 |  |
| Eastern GOA | 2 | 12 | 8 | 67 | 177 | 45 | 1 | 75 | 387 | 0.45 |  |
| British Columbia |  |  | 6 | 11 | 26 | 12 | 1 | 8 | 64 | 0.07 |  |
| Total | 2 | 44 | 63 | 154 | 369 | 94 | 4 | 130 | 860 |  |  |
| Proportion | 0.00 | 0.06 | 0.09 | 0.21 | 0.51 | 0.13 | 0.01 |  | 730 |  |  |

to deep (5-6 years). Only two 2-year-old sablefish that had traveled $<6 \mathrm{~km}$ from their release location in St. John Baptist Bay were recovered in nearshore waters ( $<100 \mathrm{~m}$ water depth); no fish older than 2 years were recovered in nearshore waters. Only one sablefish older than 13 years was found in depths $<300 \mathrm{~m}$ and most were found deeper than 500 m .

The most common areas of recovery were the central GOA and the eastern GOA, which together accounted for $75 \%$ of all recoveries (Table 2). There were more than twice as many recoveries in outside waters as in inside waters of the eastern GOA. The most common ages of recovered fish in all areas except eastern GOA and British Columbia were 5 to 7 years (Fig. 3). In eastern GOA the most common ages at recovery were 3 to 6 years, and in British Columbia 6 to 9 years. Fish of all ages from $3-10$ years old were recovered in all areas except the Bering Sea, where no fish younger than 4 years old were recovered. The Bering Sea had the fewest recoveries (only 18) and the smallest range of ages (4-10 years, except for one recovery of a 19-year-old fish). Most fish 2 years old and most fish older than 12 years were recovered in the eastern GOA (Fig. 3). Most recoveries in western areas (Bering Sea, Aleutian Islands, western Gulf of Alaska) were 12 years old or less. The large number of recoveries that occurred in the central Gulf of Alaska ( $30 \%$ ) and farther west ( $18 \%$ ) indicated that nearly half of the population had moved westward from the eastern Gulf of Alaska (Table 2).


(Fig. 3). By ages 5 and 6 years, many fish had reached the western areas. Age 5 was the most common age of recovery for the western GOA and Aleutian Islands, and age 6 for the Bering Sea. Some fish aged 7-9 years remained in the western areas, but most had begun a return to the east. In the central GOA and eastern GOA outside waters, the $7-9$-year-olds were mostly found in the $501-700 \mathrm{~m}$ depth range and were some of the most numerous fish. Fish aged 6-9 years were the most commonly recovered in the waters off British Columbia and may also have been fish returned from a westward migration (Fig. 4). A few fish may have come from eastern GOA inside waters (Chatham Strait), but Maloney and Heifetz (1997) found that this area has a high proportion of non-migrating fish. The most common depth stratum for fish recovered in British Columbia was the $501-700 \mathrm{~m}$ stratum.

## Availability to the fishery by age

The model of availability at age fit the observed pattern of tag recoveries well. Deviances were scattered symmetrically around zero for most ages (Fig. 5). Only for ages 2 and 13 were there noticeable biases. The full model that assumed separate selectivity functions for the open access and IFQ fisheries significantly improved model fit, compared to a single selectivity function (Likelihood ratio test, $\chi^{2}=220.1, \mathrm{df}=3, P<0.001$ ). The assumption of separate calibration coefficients rather than a single calibration coefficient also significantly improved fit (likelihood ratio test, $\chi^{2}=189.7, \mathrm{df}=1, P<0.001$ ). Including parameters to allow availability to decrease
for older ages ( $\gamma$ for 1985-94 and 1995-2005) significantly improved fit compared to a reduced model with asymptotic availability (likelihood ratio test, $\chi^{2}=686.7$, $\mathrm{df}=2, P<0.001$ ).

Juvenile sablefish first became available to the commercial fishery at age 2 . Availability rapidly increased such that by age 5, nearly all sablefish were available to the commercial fishery (Fig. 6). Both the age at $50 \%$ availability and the age at $100 \%$ availability values were one year greater (older) in the IFQ fishery than in the open access fishery (4 years versus 3 years and 6 years versus 5 years, respectively). Availability decreased for older ages, such that by 15 years, availability was $50 \%$ for the open access fishery and $20 \%$ for the IFQ fishery. The degree of dome shape was sensitive to the assumed value of $M$; for example, by 15 years, availability for the open access fishery was $70 \%$ for $M=0.12$ compared to $50 \%$ for the assumed value of $M=0.10$.

## Density-dependent effect on migration

We tested whether year-class strength affected the proportion of recoveries in the western areas, hypothesizing that a density-dependent effect would cause more recoveries in western areas for strong year classes. There was no significant relationship (regression, $\mathrm{df}=14, P=0.18$ ) because about $20 \%$ of recoveries occurred in western areas, regardless of year-class strength (Fig. 7). In the regression, the proportion was transformed by arcsin squareroot, as is recommended to normalize data expressed as proportions (Zar, 1984).


## Discussion

## Movement by depth and area with age

Sablefish spend 1-2 years nearshore before moving onto the continental shelf where they reside as adults and spawn. In this study, the most common ages in the shallower depths were $3-4$ years and in the deeper depths $5-8$ years, indicating that sablefish are younger on the continental shelf than on the continental slope. This result confirmed other sablefish age data that indicated that fewer sablefish older than 10 years are found on the continental shelf than on the continental slope (Sigler et al., 1997). Concurrent with the offshore movement with age, many young fish from the eastern areas (British Columbia, eastern GOA) moved in a northerly and westerly direction through the central GOA to the western areas (western GOA, Bering Sea, and Aleutian Islands).

The simultaneous depth and area movements resulted in a general age distribution of younger fish in shallower water in the east, mid-age fish in middle depths in the west, and older fish in deeper waters on the return from western to eastern areas.

Age pattern variability was high; there was a substantial overlap of ages within and between depths and areas. For example, fish of ages $2-13$ years were recovered in $101-200 \mathrm{~m}$ and fish aged $2-20$ years were caught in 501-700 m. Likewise, fish of all ages from 3 to 10 years were recovered in all areas except the Bering Sea where the youngest fish recovered was 4 years old. However, the separation of ages by depth, although incomplete, was quite pronounced within some areas, most notably the eastern GOA outside and the central GOA (Fig. 4). In both of these areas the distribution of younger fish in shallower water and older fish in deeper water was evident and, taken together with the general


Figure 5
Scatterplot representing the fit of observed and predicted availability of sablefish (Anoplopoma fimbria) to the fishery by age. Deviance is a function of the difference between observed and predicted values; a smaller deviance indicates a better fit of the exponential-logistic model to the observation.


Figure 6
Estimated availability (fraction of the total population) of sablefish (Anoplopoma fimbria) to the fishery by age (years) for the open-access (1985-94, ———) and individual fishing quota (IFQ) (1995-2005, ----) fisheries. Parameter estimates and $95 \%$ confidence intervals for 1985-94 are $\alpha=1.50$ (1.26, 1.87), $\beta=3.33$ (3.04, 3.69), $\gamma=0.050$ ( $0.023,0.092$ ), and $\lambda=0.23(0.22,0.25)$ and for 1995-2005 are $\alpha=1.14$ (1.05, 1.24), $\beta=4.76$ (4.53, 5.01), $\gamma=0.18$ ( $0.15,0.21$ ), and $\lambda=0.38(0.36,0.39)$.
age distribution by area, corroborated the counterclockwise pattern of sablefish migration in the northeast Pacific Ocean.

## Availability to the fishery by age

The pattern of movement from shallow to deep water with age (Fig. 2) results in increased availability to the fishery as sablefish grow older (Fig. 6). Estimates of availability at age have shown that about half of sablefish are available to the fishery by age 3 or 4 , depending on the fishery management system, and that most are available by age 5 or 6. The later availability of fish (at ages 5 or 6 ) under the IFQ management system (compared to earlier availability of younger fish under the open access system) also was also found to be the case in an analysis of length-frequency data from the two fisheries, and this pattern of availability was likely created because the crowding of fishing vessels during the open access fishery pushed fishermen into areas and depths where there were smaller fish (Sigler and Lunsford, 2001). The IFQ fishery, with a longer season and fewer vessels, reduced crowding so that fishermen were able to avoid shallower depths with smaller, younger fish.

Unlike previous analyses, where availability was assumed not to decrease with age (e.g., Sigler, 1999), our analysis of known-age tag recoveries showed that sablefish availability decreases with age. An alternate explanation is that tag loss increased with time. However, dou-ble-tagging experiments have shown that the rate of tag loss is constant with time (Beamish and McFarlane, 1988; Lenarz and Shaw, 1997). Decreased availability with age may occur because of reduced fishing effort for older age fish. Fishing effort is concentrated at intermediate depths (e.g., half of the recoveries occurred at depths 501-700 m [Table 2]) but fish exit these depths as they age and move deeper. In addition, older fish were less available for IFQ management compared to open access management, which also may have been due to reduced crowding of fishing grounds during IFQ man-
agement; for example, recoveries at depths $>700 \mathrm{~m}$ were fewer during IFQ management ( $16 \%$ of recoveries during 2003-05) than during open access management ( $25 \%$ during 1992-94). This result has potentially substantial implications for a stock assessment because "domeshaped" availability influences the reliability of abundance estimates (Bence et al., 1993; Sigler, 1999). A logical next step for other researchers to understand these effects is to complete a migratory catch-age analysis (e.g., Quinn et al., 1990) that melds sablefish migration (Heifetz and Fujioka, 1991) and agestructured (Sigler, 1999; Hanselman et al., 2006) analyses.

## Density-dependent effect on migration

Migration is a prominent feature in the life history of many fishes. Well-known examples of migratory fish are Pacific salmon (Oncorhynchus spp.) that return to their natal stream to spawn (Burgner, 1991; Heard, 1991) and Pacific herring (Clupea harengus) that consistently follow routes from spawning to feeding grounds (Hourston, 1982; Wheeler and Winters, 1984; Corten, 2002). Presumably the energy expended during migration is compensated for by other benefits. Demonstrated benefits include the ability to take advantage of seasonally available prey (Walters et al., 1986; Livingston, 1993) and avoidance of predation (Carlson, 1980). Benefits of migration for sablefish are not immediately obvious because they are opportunistic feeders and have no need to pursue specific prey, and their rapid growth rate in early life quickly lessens their vulnerability as prey. Nevertheless, a substantial proportion of the population migrates each year (Heifetz and Fujioka, 1991; Kimura et al., 1998).

Sablefish are characterized by great variability in year-class strength; and occasional strong year classes dominate the fishery for several years in a row (Sigler, 1999; Hanselman et al., 2006). A higher proportion of a strong year class may migrate and young fish may move farther and faster in order to occupy less crowded areas (density-dependent habitat selection; e.g., MacCall, 1990). Beamish and McFarlane (1988) noted differing rates of sablefish movement out of release areas from 1977 to 1985 and theorized that increased density resulting from recruitment of the large 1977 year class may have contributed to an increased rate of movement. However, we found no significant effect of year-class strength on the proportion of recoveries in the western areas, and therefore cohort density does not appear to affect the proportion of a cohort that will
migrate. Although we tested a long time series, this time series does not span the full range of observed recruitment variability. Some earlier year classes were substantially stronger (e.g., the exceptional 1977 year class was $44 \%$ larger than the strongest year class (1984) that we tested). Migration may be stronger for year classes of such magnitude. Further, movement rates may be affected by total abundance-a possibility that could be tested in a sablefish migratory catch-age analysis such as we suggested earlier.

Observed sablefish abundance trends by area during the last 25 years can be explained by their counterclockwise migration pattern. Overall sablefish abundance peaked in the late 1980s and then decreased. The western areas of Bering Sea, Aleutian Islands, and western GOA decreased quickest, as migrating fish matured and turned eastward (Fig. 8). Abundance declined more slowly in the eastern GOA, presumably because fish that migrated westward returned to the eastern GOA. The abundance decline in the central GOA was intermediate, probably because migrating fish pass through in both directions (westward and eastward). This pattern of abundance changes (faster in western areas, slower in central and eastern GOA) supports the conclusion that the eastern GOA and the eastern part of the central GOA are the center of the range for Alaska sablefish (Bracken, 1983; Beamish and McFarlane, 1988; Sigler et al., 2001).

## Currents and sablefish migration

Prevailing currents may play an important role in determining the direction of migration for most young sable-

fish. From the time they first venture out of coastal bays onto the continental shelf of northern British Columbia or the eastern GOA, young fish are subject to northward or westward flowing currents. Driven by fresh water runoff, the Alaska Coastal Current (ACC) flows northwestward close to shore toward the head of the Gulf of Alaska (Royer, 1981). From Icy Bay at about $137^{\circ} \mathrm{W}$ the ACC flows 1500 km to Unimak Pass at the eastern end of the Aleutian Island chain (Stabeno et al., 2004). This inshore current is likely the initial route of most young sablefish leaving nursery areas in southeast Alaska. As the fish move westward, cross-shelf gullies and canyons provide avenues of deeper water leading to the shelf break and the upper continental slope, along which runs the westward-flowing Alaskan Stream. The potential ease of transit from the Alaska Coastal Current on the shelf to the Alaskan Stream on the upper slope may help
to explain the considerable overlap in fish ages that we found within and between depths.
The direction of migratory movement by young sablefish may be influenced by prevailing current direction, but the return of adult sablefish along the continental slope to the eastern areas of the GOA is presumably made against the westward-flowing Alaskan Stream and from a lower density area to a higher one. Reed and Schumacher (1987) believed that velocities of the Alaskan Stream are low in water deeper than 300 m , and most of the fish travel within a $500-700 \mathrm{~m}$ depth when returning; therefore swimming against the current would not pose a problem for adult fish. The return of most adults to the eastern GOA serves to maintain the center of the population there and likely increases the chance of successful spawning in that area.

One factor that may make the eastern GOA and British Columbia spawning grounds more favorable is that spawning depths in these areas are closer to the coast than those farther west because of the narrow continental shelf in much of the eastern GOA. Also, the prevailing north-flowing Alaska Current in the eastern GOA may carry pelagic larvae and young fish closer inshore for easier access to coastal nursery areas. In the central and western GOA, spawning depths are farther offshore, increasing predation risk for larvae, and there is no prevailing northerly current to transport larvae shoreward. Instead, the Alaskan Stream, up to 100 km wide, flows westward along the shelf break, more or less perpendicular to the route that offshore-spawned larval and juvenile sablefish must travel to reach inshore nursery grounds. Tokranov (2002) believes this current is the source of periodic occurrences of juvenile sablefish off Kamchatka and the Kuril Islands. Winter current direction and sablefish recruitment success are related, and above-average recruitment is more likely in years with northerly drift ( $59 \%$ ) than for years with an easterly or southerly drift (25\%) (Sigler et al., 2001).

All the sablefish in this study originated in the eastern GOA, but young-of-the-year sablefish have been caught in small numbers on various cruises in the Bering Sea, Aleutian Islands, western and central GOA, as well as the eastern GOA from 1955 to 1999 (Kendall and Matarese, 1987; Sigler et al., 2001). These observations indicate the likelihood of some direct recruitment into each of these areas, in addition to recruitment resulting from migration. Spawners contributing to each area may be migrants returning to the eastern GOA, adult fish that are resident in the area, or adult fish in an adjoining upstream area whose larvae are caught up in the prevailing currents and are carried westward. Although most fish in our study older than 12 years were recovered in eastern GOA outside waters, older fish ( 13 to 21 years) also were recovered in each of the other areas, indicating that they may have become resident in the new area at some point during migration.

Our study corroborated much that is already known or suspected about sablefish migration in Alaska waters. In addition, our data on age by depth and area have refined our knowledge of sablefish movements. Further studies to locate sablefish nursery grounds throughout the GOA and in the Bering Sea and Aleutian Islands and to tag juveniles on these grounds as was done in the eastern GOA for our study would determine whether these movement patterns observed in the present study are similar to movement patterns of sablefish originating in other regions of Alaska.

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