Stock structure and movement of tagged sablefish, *Anoplopoma fimbria*, in offshore northeast Pacific waters and the effects of El Niño-Southern Oscillation on migration and growth

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Abstract.–Sablefish in the northeast Pacific are found in commercial quantities from the Bering Sea, the Aleutian Islands, throughout the Gulf of Alaska, and south along the west coast of Canada and the U.S. to Baja California. Tag-recovery data support a two-population hypothesis throughout the North American range: an Alaska population ranging from the Bering Sea, including the Aleutian Islands and extending down through the Gulf of Alaska to northwest Vancouver Island, Canada; and a west coast population extending from southwest Vancouver Island to Baja California. Tag recoveries indicate that these two populations mix off southwest Vancouver Island and northwest Washington, and to a lesser extent off southern Washington and Oregon.

Alaska sablefish, which commonly migrate over 500 n mi, are more mobile than west coast sablefish. Tag recoveries for sablefish tagged in Alaska have shown strong mutual exchanges between nearly all areas. In contrast, west coast sablefish have shown far less migratory behavior. Tagging data with respect to bathymetry are difficult to interpret in both regions owing to the fact that tagging and recovery effort do not cover the full bathymetric range of adults.

Results of analysis of tag-recapture growth data were consistent with patterns observed for several other pelagic and demersal species. That is, El Niño-Southern Ocean Oscillation events appeared to retard the growth of sablefish along the west coast and to enhance growth of Alaska sablefish. The timing of recoveries from sablefish tagged off Alaska and recovered off southwest Vancouver Island and Washington–Oregon suggests that movement south correlates positively with strong upwelling in this southern area. Although sablefish trap-index surveys show a north to south cline in the percentage of large sablefish (>60 cm, and possibly of Alaska origin) sampled in length frequencies along the west coast, we were unable to correlate annual fluctuations in these percentages with upwelling strength.

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Adult sablefish have a proclivity for great depths (200–1500 m) where the ocean environment is relatively constant over extensive geographic distances and consequently can be found from central Baja California along the Pacific coast through the Gulf of Alaska and Aleutian Islands, along the Bering Sea slope to the Russian coast, and down the Kamchatka Peninsula all the way to southern Japan (OCSEAP, 1986; Allen and Smith, 1988).

The marked absence of sablefish eggs and larvae from the Bering Sea above 55°N is usually attributed to an intolerance to low (<2°C) temperatures (OCSEAP, 1986). Sablefish occurrence in the Bering Sea and Aleutian Islands is thought to be dependent on egg and larval drift from the northeast Pacific, principally through westward transport from the Gulf of Alaska by the Alaskan Stream (OCSEAP, 1986). Although sablefish occur along the coast of Asia, only adult fish (>2 yr) are found (Kodolov, 1968) and they are believed to have been recruited from the northeast Pacific stock. Ocean currents from the western Bering Sea favor dispersal of sablefish along the Asian coast by means of the East Kamchatka and Oyashio Currents.

Commercial catches of sablefish appear to be absent off Japan (Chikuni, 1985). We do not know if commercial catches of sablefish occur off Russia, although Kodolov (1968) describes the adult distribution of sablefish as extending from the Bering Sea all along the Kamchatka Peninsula. In contrast, sablefish is an important commercial species throughout the northeast Pacific with average annual landings (1984–93) of 2150 t for the eastern Bering Sea, 2405 t for the Aleutian Islands, 22,590 t for the Gulf of Alaska, 4835 t for British Columbia, Canada, and 11,129 t for the U.S. West Coast.[1]

Sablefish fecundity is determinate and eggs are spawned in three or four batches (Hunter et al., 1989; Macewicz and Hunter, 1994); eggs are semipelagic (McFarlane and Beamish, 1992) and have been found at depths ranging from 200 to 800 m (Thompson, 1941; Kodolov, 1968; Moser et al. 1994). Age-0 (yr) larvae initially inhabit offshore surface waters (McFarlane and Beamish, 1992), move inshore during the

[1] Aleutian Islands and eastern Bering Sea catches (Lowe, 1995), Gulf of Alaska catches (Fujioka, 1995), Canadian west coast catches (Saunders et al., 1995), U.S. west coast catches (Methot et al., 1994).

summer of their first year (still 0-yr-old) (Rutecki and Varosi, 1997a), and usually become demersal in outer coastal waters during their second year of life at age 1 yr (Rutecki and Varosi, 1997a, 1997b). From there, it is believed that they undergo a protracted ontogenetic migration to greater depths (Saunders et al., 1997).

Adult sablefish recruit to offshore demersal fisheries at about age 3–4 yr (Sasaki, 1985; McFarlane and Saunders, 1997). Routine trawl, longline, and trap surveys by the National Marine Fisheries Service principally cover depths from 200 to 1000 m (Parks and Shaw, 1988; Lauth et al., 1998). These surveys in Alaska, and along the west coast typically indicate sablefish are abundant at the maximum depths fished. Spawning off California occurs at depths beyond 800 m (Hunter et al., 1989). In Monterey Bay, Parrish[2] measured dissolved oxygen and noted that peak longline catches occurred in the oxygen-minimum zone at around 730 m. A special longline survey targeting deeper waters (Wilkins[3]) and deep trap sets (Parks and Shaw, 1988) has shown that sablefish along the west coast occur to depths of up to ~1500 m. Beamish et al. (1979) reported exploratory catches of sablefish to depths of 2740 m. Pearcy et al. (1982) noted the occurrence of sablefish in the Astoria and Cascadia abyssal plains down to a depth of 2560 m. Deepwater trawl and photographic work by Wakefield (1990) showed that sablefish occur as far down as ~1500 m but appear to become scarce beyond this depth. Former naval dumping sites off San Francisco, at depths from 2000 to 3200 m, showed an absence of sablefish (Cailliet et al.[4]). A reasonable interpretation might be that although sablefish can occur at depths beyond 1500 m, sablefish abundance can be expected to decline considerably beyond this depth.

Because of the many interesting questions raised by their broad geographic and bathymetric distributions, sablefish have become one of the most tagged demersal fish species in the northeast Pacific. On the basis of tagging studies, authors have emphasized both the resident nature of some sablefish (Wespestad, 1983; Beamish and McFarlane, 1983, 1988; Maloney and Heifetz, 1997) and the proclivity of other sablefish to be highly migratory (Bracken, 1983; Dark, 1983; Heifetz and Fujioka, 1991; McFarlane and Saunders, 1997). Generally fish tagged inshore, off the west coast of Vancouver Island, or off the U.S. west coast were more likely to be characterized as resident and nonmigratory.

In this paper we examine several hypotheses concerning the movement of sablefish, using recapture data gathered from offshore tagging of sablefish from throughout the northeast Pacific Ocean. The first hypothesis is that sablefish off Alaska and Canada, i.e. north of 50°N latitude, are a separate population from the sablefish south of 50°N latitude found along southern Canada and the U.S. west coast. The second hypothesis is that Alaska sablefish tend to migrate much farther than west coast sablefish. Another question is whether sablefish migrate to greater depths as they become older. Such hypotheses are of practical importance because they can affect the way resource assessment survey results are interpreted.

A study in which growth curves were estimated from a sablefish tag data set has been completed (Kimura et al., 1993). In that study differences in the growth curves of Alaska and west coast populations were reported. In this paper, we examine the effects of El Niño-Southern Oscillation (ENSO) events on the growth of sablefish in the northeast Pacific Ocean.

Finally, we examine the migration of fish tagged in Alaska to areas along the west coast. Upwelling along the west coast (42–48°N latitude) appears to be positively correlated with these migrations, and possible explanations are given for why a correlation exists.

Materials and methods

In this paper we analyze tag recoveries of the sablefish tagging program conducted by the National Marine Fisheries Service (NMFS). Tagging occurred during surveys designed to measure relative abundance of sablefish throughout its range in offshore U.S. waters. From 1971 to 1993, approximately 218,255 fish were captured with trawl, trap, and longline gears and later released after having been tagged with anchor tags (Table 1). With the exception of Canadian waters, sablefish were tagged from southern California to the Bering Sea. Analyses of sablefish tagged in Canadian waters have been previously reported (e.g. Beamish et al. 1979; Beamish and McFarlane, 1983, 1988; McFarlane and Saunders, 1997).

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[2] Parrish, R. H. 1975. The relationships of oxygen concentration and depth of capture with size and abundance of sablefish (*Anoplopoma fimbria*) in Monterey Bay, California. Current address: Pacific Fisheries Environmental Lab., 1352 Lighthouse Ave., Pacific Grove, CA 93940. Unpubl. manuscript.

[3] Wilkins, M. E. 1997. RACE Division, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

[4] Cailliet, G. M., W. W. Wakefield, G. Moreno, and K. Rhodes. 1992. The deep-sea fauna from the proposed navy ocean disposal site, using trap, otter and beam trawl, and camera sled samples. Navy CLEAN Contract No. N62474-88-D-5086, prepared for PRC Environmental Management, San Francisco, CA, and Honolulu, HI, 69 p.

From 1971 to 1976, sablefish were tagged and released through a cooperative program involving the NMFS, California Department of Fish and Game, Oregon Department of Fish and Wildlife, and research vessels from Russia and the Republic of Korea. Trawls, traps, and longlines were the predominate gears used to capture sablefish, accounting for approximately 99% of the tag releases.

In Alaska from 1978 to 1993, the U.S.-Japan Cooperative Longline Survey was the primary source of sablefish tag releases; a few releases were made from NMFS trap and trawl surveys. Along the U.S. west coast from 1979 to 1993, most tagged sablefish were released through NMFS sablefish trap index surveys and the remaining fish were released during NMFS trawl surveys.

Tagging from 1971 to 1976 was carried out mainly on the west coast and in southeastern Alaska (Tables 2 and 3). In 1978, tagging operations expanded into the Gulf of Alaska; in 1979, into waters off the Aleutian Islands; and by 1982, into the eastern Bering Sea. Tag releases from 1982 onward has been fairly consistent in all areas.

Tagging

All sablefish were tagged with anchor tags (Floy FD-68). The vinyl tubing (yellow, orange, or blue) on each tag was 60 mm long, 2 mm in diameter, and bore a unique number and a legend of where to return the tag.

Captured sablefish were routinely put into "live" tanks supplied with fresh running sea water immediately after the catch was brought on board. Anesthetics were not used. Usually within 15 minutes of completion of each haul, sablefish were dipped from

Table 1

Releases and recoveries by gear and region of release. Also shown are the proportion of recoveries for each combination of gear and region of release. Bottom table shows tag recoveries by gear and region of recovery. Tag types were all anchor tags.

Gear of release	Alaska	West coast	Total
Tag releases by gear and region of release			
Trawl	10,920	28,899	39,819
Trap	7248	30,722	37,970
Longline	136,077	0	136,077
Unknown	4206	183	4389
Total	158,451	59,804	218,255
Tag recoveries by gear and region of release			
Trawl	717	1320	2037
Trap	977	3717	4694
Longline	7987	0	7987
Unknown	166	19	185
Total	9847	5056	14,903
Recovery proportions by gear and region of release			
Trawl	0.0657	0.0457	0.0512
Trap	0.1348	0.1210	0.1236
Longline	0.0587	—	0.0587
Unknown	0.0395	0.1038	0.0422
Total	0.0621	0.0845	0.0683
Tag recoveries by gear and region of recovery			
Trawl	552	1863	2415
Trap	1331	1856	3187
Longline	6342	826	7168
Unknown	1209	603	1812
Total	9434	5148	14,582

Table 2

We divided the northeast Pacific into 27 areas based on the criteria described below (Fig. 1). The historic regions: eastern Bering Sea (EBS), Aleutian Islands (AI), Gulf of Alaska (GOA), and west coast (WC) essentially maintain their integrity. Nominally, Alaska includes EBS, AI, and the GOA; whereas the west coast includes only WC. Areas are defined in decimal degrees of longitude and latitude.

Area number and region	Area definition	
	Longitude	Latitude
1. EBS	170°E–175°E	Above 55°N
2. EBS	175°E–180°E	Above 55°N
3. EBS	175°W–180°W	Above 55°N
4. EBS	170°W–175°W	Above 55°N
5. EBS	165°W–170°W	Above AK Pen.
6. EBS	160°W–165°W	Above AK Pen.
7. AI	170°E–175°E	50–55°N
8. AI	175°E–180°E	50–55°N
9. AI	175°W–180°W	50–55°N
10. AI	170°W–175°W	50–55°N
11. GOA	165°W–170°W	Below AK Pen.
12. GOA	160°W–165°W	Below AK Pen.
13. GOA	155°W–160°W	Below AK Pen.
14. GOA	150°W–155°W	Below AK Pen.
15. GOA	145°W–150°W	
16. GOA	140°W–145°W	
17. GOA	135°W–140°W	
18. GOA		52.5°N –60°N
19. GOA		50°N–52.5°N
20. WC		47.5°N–50°N
21. WC		45°N–47.5°N
22. WC		42.5°N–45°N
23. WC		40°N–42.5°N
24. WC		37.5°N–40°N
25. WC		35°N–37.5°N
26. WC		32.5°N–35°N
27. WC		30°N–32.5°N

Table 3

Tag releases tabulated by the area of release (rows) and year of release (columns). Areas are described in Table 2 and Fig. 1.

Area of release	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	Total
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	288	181	89	71	167	96	34	102	78	48	12	3	1169
4	0	0	0	0	0	0	0	0	0	0	0	1495	897	549	287	319	370	179	194	113	29	35	5	4472
5	0	0	0	0	0	20	0	0	241	131	288	5070	4488	2642	1823	1594	1025	305	451	264	50	131	20	18,543
6	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21
7	0	0	0	0	0	0	0	0	0	75	40	82	37	25	33	64	182	70	22	11	19	12	7	679
8	0	0	0	0	0	0	0	0	191	68	101	215	332	283	251	390	450	119	196	31	59	25	9	2720
9	0	0	0	0	0	0	0	0	397	768	1130	1296	701	854	617	775	767	264	410	142	230	136	180	8667
10	0	0	0	0	0	0	0	0	314	307	1071	1015	366	538	526	255	394	126	236	86	33	57	48	5372
11	0	0	0	0	0	0	0	428	414	518	846	1303	863	0	149	148	473	167	190	181	134	104	0	5918
12	0	0	0	0	0	0	0	595	822	780	1466	1380	1532	0	351	370	489	302	503	258	148	226	0	9222
13	0	0	0	0	0	0	0	633	1258	1245	1796	2321	1793	137	476	448	482	824	465	383	180	430	351	13,222
14	0	0	0	0	2	0	0	1702	1820	1984	2133	2120	2166	321	516	380	588	725	607	497	378	511	470	16,920
15	0	0	0	0	34	0	0	693	1060	1938	2703	3316	2301	0	82	0	859	562	201	568	247	452	398	15,414
16	0	0	0	0	67	0	0	705	2112	2574	2462	2257	1340	0	0	0	805	0	0	0	0	0	0	12,322
17	0	0	1523	0	0	34	0	2441	7007	2868	4651	2454	1684	0	0	0	1131	0	0	0	0	0	0	23,793
18	0	2303	5408	0	0	108	0	501	2353	1958	4047	1730	1167	0	0	0	373	49	0	0	0	0	0	19,997
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	446	2046	0	263	0	0	0	802	903	494	0	119	0	102	38	618	0	462	0	0	167	0	6460
21	0	3897	1239	475	448	122	0	0	478	1097	1519	0	524	15	48	205	849	103	810	0	0	364	0	12,193
22	0	4144	1852	541	2259	0	0	0	437	1105	322	0	875	29	0	23	180	17	92	0	0	772	0	12,648
23	0	552	253	260	443	0	0	0	0	0	0	0	464	0	0	1007	0	1670	6	0	811	78	0	5544
24	634	155	0	740	902	0	0	0	0	647	0	763	177	0	0	249	11	968	16	0	93	232	0	5587
25	581	0	0	625	145	0	0	0	0	0	0	0	0	0	0	1106	223	2576	110	0	805	42	0	6213
26	696	0	0	187	270	19	0	0	0	6455	800	475	0	0	0	0	9	0	2	0	0	11	0	8924
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	363	0	1008	0	0	864	0	0	2235
Total	1911	11,497	12,321	2828	4854	303	0	7698	19,706	25,421	25,869	27,580	22,007	5482	5332	7901	10,374	10,068	5075	2612	4128	3797	1491	218,255

the tank, placed in a padded tagging cradle, measured, tagged, and released. Each anchor tag was inserted between and engaged behind the pterygiophores of the dorsal fin. Fork length, tag number, capture depth, geographical position, and date of release were recorded for each fish. Only fish judged in viable condition were tagged. Sablefish of all sizes (20–110 cm) taken by the capture gear were tagged.

Recovery

A recovery program was promoted through the use of posters, news releases, and letters explaining the research and enlisting the cooperation of those who might encounter tagged sablefish, particularly fishermen, fish processors, and members of state fisheries agencies. Individuals finding a tagged fish were requested to return the tag with information about the date, location, fishing gear, depth of capture, and fish length. A reward and the release history of the tagged fish were provided to those who returned tags.

By the end of 1993, 14,903 recoveries had been made (6.82%). The information garnered from these recoveries constitutes the core of this paper. Owing to the widespread geographic availability of sablefish and the broad coverage of the surveys and fisheries, tagged sablefish were released and recaptured from locations throughout its range in the northeast Pacific Ocean.

Data analysis

Our philosophy in this paper is to present the data as they are and not to adjust the number of tag recoveries for exploitation rates. Such adjustments require knowing the catch and population biomass, or standardized effort measures, by area. If these are incorrectly specified, the data may be further distorted rather than corrected. When the recovery data are being adjusted over an extremely broad geographic range, where dominant gears are different and where even the same gears fish differently, such adjustments become particularly difficult.

Because of the high numbers and long time series of tag returns, basic descriptive tools appear to reveal large-scale migration and stock-structure patterns. Accordingly, we used basic descriptive tools such as mapping locations of tag recovery. Although such visual representations are useful, we also needed to aggregate the data so that general patterns could be more easily discerned. Therefore, we divided the range of sablefish (encompassing the eastern Bering Sea, the Aleutian Islands, Gulf of Alaska, and the west coast of the U.S. and Canada) into 27 areas of moderately small scale. We used large nominal regions (the eastern Bering Sea, the Aleutian Islands, and the Gulf of Alaska) to assist in these demarcations and also a straight line drawn down the Alaska Peninsula passing through 150°W, 60°N and 168.5°W, 53°N and continuing on to 170°W longitude. All areas west of 130°W longitude were divided into areas 5° wide in longitude, and areas east of 130°W longitude were divided into areas 2.5° wide in latitude (Fig. 1; Table 2). The habitat of adult sablefish includes the 400-m depth contour shown in Fig. 1.

Once these areas were described we were able to tabulate the tag recoveries in a table whose rows are the areas of release and whose columns are the areas of recovery. We feel this is the single most useful piece of information that can be garnered from any study of migration based on a tagging experiment. We also characterized net movements by mapping average positions of release and recovery. The average position of tagging and recovery was calculated for all fish tagged in area i, for each area i. An arrow was then drawn from the area of tagging to the area of recovery. The back end of the arrow was in area i, and the position of the arrow point provided some indication of the average movement of the tagged sablefish (i.e. the arrow points to where the tagged fish in area i go). Similarly, the average position of tagged and recovered fish was calculated for all fish recovered in area i, for each area i. The pointed end of these arrows were in area i, and the back end of the arrow gave some indication of where these fish, on average, originated (i.e. the arrow indicated where the tagged fish recovered in area i came from).

Distance traveled was examined by calculating a histogram and empirical cumulative distribution function (cdf) of the distance traveled between tagging and recovery. Movement of tagged fish in relation to depth was examined by simply tabulating the depth of tagging and the depth of recovery.

Modeling ENSO growth effects

Modeling approaches to analyzing ENSO growth effects was difficult because the best model for this apparently simple task was unclear. Assuming an initial size at tagging of S_1, a size at recovery of S_2, and a time at liberty of Δ_t, the most direct model would seem to be something like $S_2 = S_1 + \Delta_t \beta$. However, this model ignores the common sense notions that the growth increment per unit time would be expected to decrease as both S_1 and Δ_t increase and suggests the model $S_2 = S_1 + \Delta_t \exp(\beta_{enso} + \beta_1 S_1 + \beta_2 \Delta_t)$, where β_{enso} represents an ENSO effect, and β_1 and β_2 can be presumed negative. A tagged fish was assumed exposed to ENSO if it was at liberty anytime during a recognized ENSO event: 1972–73, 1976–77, 1982–83, 1986–87, and 1991–93.

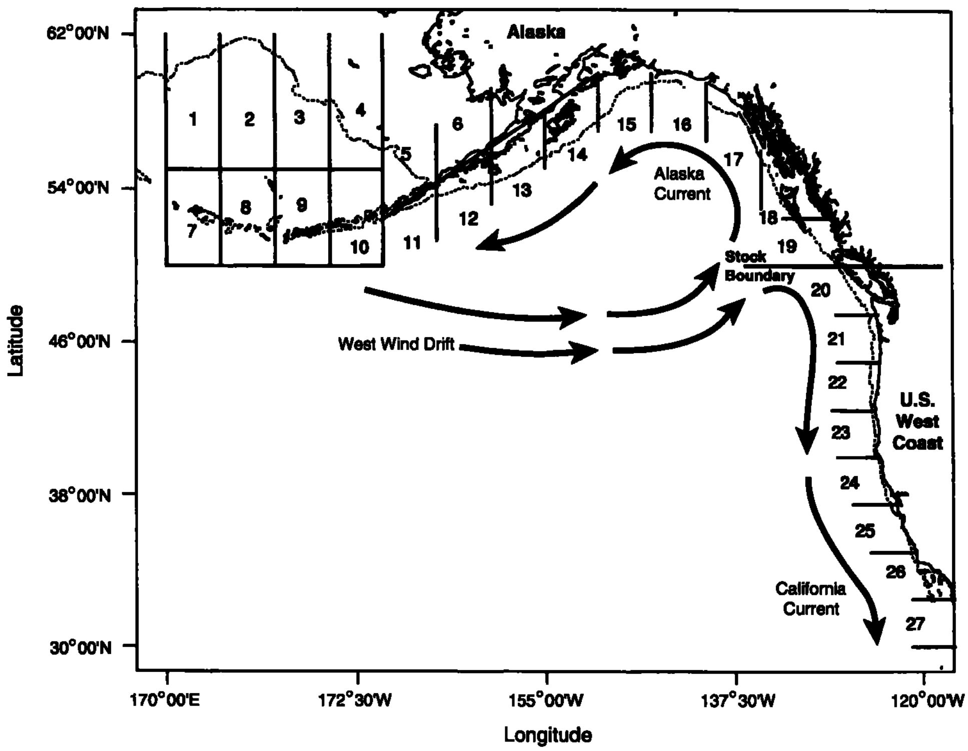

Figure 1

Map of 27 areas (described in Table 2) used in this paper to describe analysis of sablefish tag-recovery data. Principal regions are also described in Table 2. Also shown are the 400-m depth contour, which is the approximate habitat of adult sablefish, and the oceanographic circulation that are hypothesized to affect movements of sablefish.

Migration from Alaska to the west coast

A well-defined sablefish migration seems to occur from Alaska to the northern portion of the west coast. To explore this phenomenon, we plotted the number of tag recoveries from Alaska, recovered along the west coast, against upwelling strength in the northern portion of the west coast. Length frequencies from Alaska and west coast sablefish trap index surveys (Parks and Shaw, 1983) were also used to examine the hypothesis that a substantial mixing of large (>60 cm) sablefish of Alaska origin occurs in west coast sablefish stocks from Vancouver Island and Washington State to California's San Francisco Bay.

Results

Descriptive results

Tag recovery rates by fishing gear type used for initial capture show that the tag recovery rate for trap gear (12.4%) is twice that for longline (5.87%) and trawl (5.12%) gears (Table 1). Because these results hold for fish tagged in Alaska and off the west coast, it is likely that the much higher tag recovery rate for trap gear is due to the superior condition of and presumably lower mortality rate for trap-caught fish.

Tag recovery rates were remarkably consistent for all areas of tagging (Table 4). This finding would suggest that the exploitation rate for sablefish stocks are similar throughout the northeast Pacific. Recovery rates were higher along the west coast (8.4%) than from Alaska waters (6.0%). This is just about the magnitude that would be expected when taking into account the mixtures of gears used for tagging (i.e. if we apply both the recovery rates for trawl and trap caught fish observed from the west coast and the longline recovery rate observed in Alaska to the numbers released in Alaska, we would arrive at the 6% recovery rate that was actually observed in Alaska).

Sablefish are long-lived; ages over 40 yr are regularly documented (Kimura et al., 1993) and a maximum recorded age of 94 yr has been recorded at AFSC (Anderl[5]). The instantaneous natural mortality rate

[5] Anderl, D. M. 1997. Age and Growth Task, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

used for stock assessments is $M = 0.10$ or less (Methot et al., 1994). Thus fish tagged in the early 1970s were still contributing to recoveries as of 1993 (Table 5). It is also notable that sablefish tagged offshore are usually not recaptured immediately; recoveries are typically protracted over many years.

Results related to population structure

Mapping the location of the 14,903 sablefish tag recoveries shows a geographic continuity in sablefish distribution and commercial fishing effort (Fig. 2). The few offshore recoveries in midocean were located on seamounts. If we plot the source of these seamount recoveries (Fig. 3), we see that they came from virtually all areas of release (see Shaw and Parks, 1997, for details).

Table 6 lists the area of release against the area of recovery for the 27 areas in Figure 1. The data show that sablefish tagged off Alaska north of 50°N latitude have a 96.5% chance of being recaptured north of 50°N. Similarly, sablefish tagged off the west coast south of 50°N latitude have a 95.6% chance of being recovered south of 50°N.

Table 6 suggests that Alaska sablefish mix in areas 1–19. It is noteworthy that all Alaska areas show reciprocal migrations to all other Alaska areas. Mixing is also suggested from the fact that the recovery rate for fish tagged in all these areas is similar (Table 4). In contrast, west coast sablefish (areas 20–27) largely confined their movements within the area of release (64.4% of west coast tag recoveries came from the same areas as their release compared with 35.8% for Alaska).

Tag recoveries indicate that Alaska sablefish on average move considerably further than west coast sablefish (Fig. 4). More than 30% of tagged Alaska

Table 4

Table showing the percentage of tags recovered from releases in each area. Also shown by size category are the percentage of tagged fish moving north or west, staying put, and moving east or south. Areas are described in Table 2 and Figure 1.

Area	All sizes	Size less than 57 cm			Size greater than 57 cm		
	Percent recovered	Percent north or west	Percent in area of tagging	Percent east or south	Percent north or west	Percent in area of tagging	Percent east or south
1	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—
3	5.4	0.0	11.8	88.2	0.0	2.2	97.8
4	6.3	0.0	24.4	75.6	0.4	13.0	86.6
5	6.2	2.4	32.7	64.9	1.8	20.9	77.3
6	—	—	—	—	—	—	—
7	3.8	0.0	0.0	100.0	0.0	29.2	70.8
8	5.3	0.0	28.6	71.4	2.9	28.3	68.8
9	5.5	9.1	30.5	60.4	4.1	26.8	69.1
10	5.8	20.0	16.5	63.5	10.6	18.5	70.9
11	6.1	26.6	21.3	52.1	4.8	15.6	79.6
12	6.8	17.4	31.3	51.4	10.5	18.8	70.7
13	5.8	19.3	27.4	53.3	10.9	17.9	71.2
14	5.4	20.5	36.6	42.9	9.8	29.2	61.1
15	4.9	34.9	29.5	35.7	15.2	43.4	41.5
16	4.9	46.4	34.0	19.6	25.9	42.8	31.3
17	6.3	41.9	36.7	21.3	24.2	56.8	19.0
18	7.9	40.9	42.7	16.4	29.2	59.3	11.6
19	—	—	—	—	—	—	—
20	8.0	10.7	74.5	14.8	6.4	76.0	17.6
21	7.6	22.5	66.6	10.9	19.5	71.4	9.1
22	6.0	16.1	73.6	10.4	18.3	70.7	11.0
23	14.8	17.6	64.9	17.5	18.9	67.1	14.0
24	8.4	31.5	61.9	6.6	38.7	55.5	5.9
25	9.1	41.3	54.3	4.5	32.9	64.4	2.7
26	8.8	44.6	54.4	0.9	53.6	46.4	0.0
27	6.7	36.3	63.7	0.0	57.7	42.3	0.0

Table 5

Tag recoveries (1971–93) tabulated by the year of release (rows) and year of recovery (columns).

Year of release	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	Total tag recov-eries
71	4	3	1	7	8	2	5	2	6	2	0	0	0	2	0	0	0	0	1	0	0	0	0	43
72	—	72	78	39	114	75	17	31	58	19	29	39	17	6	6	4	6	3	2	0	9	1	0	625
73	—	—	100	85	86	69	23	25	44	49	34	30	14	11	10	9	13	4	12	3	5	10	7	643
74	—	—	—	9	26	16	10	11	11	6	2	1	4	1	3	0	1	0	0	0	2	2	1	106
75	—	—	—	—	49	86	30	22	64	7	21	10	10	11	3	1	3	1	0	0	0	2	3	323
76	—	—	—	—	—	1	0	0	2	0	3	0	1	1	1	2	0	0	0	1	0	0	0	12
77	—	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	—	—	—	—	—	—	—	18	98	50	65	28	37	21	21	13	12	12	3	11	10	13	15	427
79	—	—	—	—	—	—	—	—	116	219	236	160	135	112	96	76	48	59	37	47	40	35	31	1447
80	—	—	—	—	—	—	—	—	—	96	369	296	426	169	131	198	78	90	70	66	57	53	67	2166
81	—	—	—	—	—	—	—	—	—	—	102	310	247	146	173	146	100	101	77	84	74	48	61	1669
82	—	—	—	—	—	—	—	—	—	—	—	71	279	208	255	212	158	168	102	122	92	72	83	1822
83	—	—	—	—	—	—	—	—	—	—	—	—	74	237	279	204	157	152	112	134	89	88	68	1594
84	—	—	—	—	—	—	—	—	—	—	—	—	—	10	39	42	54	59	40	49	27	24	29	373
85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14	64	56	58	36	39	38	37	35	377
86	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	46	201	155	78	111	69	80	55	795
87	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	43	145	89	93	76	84	76	606
88	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32	323	262	160	151	60	988
89	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	84	81	66	64	317
90	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	35	29	24	92
91	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48	217	89	354
92	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	63	80
93	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
Total	4	75	179	140	283	249	85	109	399	448	861	945	1244	935	1031	1017	930	1039	1004	1110	912	1029	831	14,859

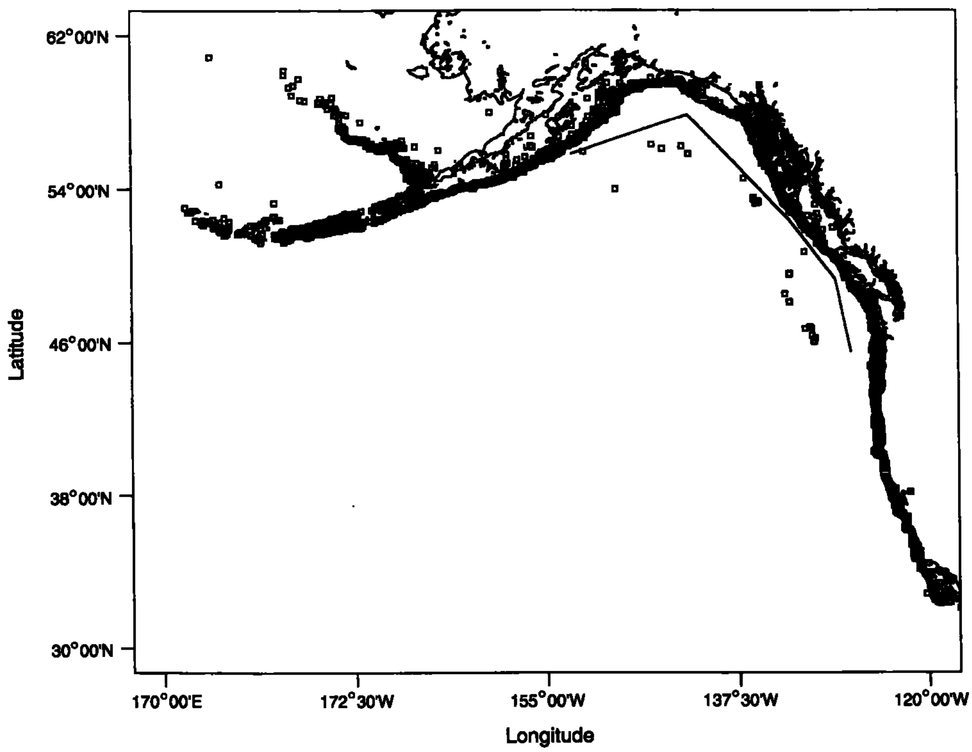

Figure 2

Position of recovery for 14,903 sablefish recovered from 1971 to 1993. Offshore recoveries, separated by line segments, were from seamounts.

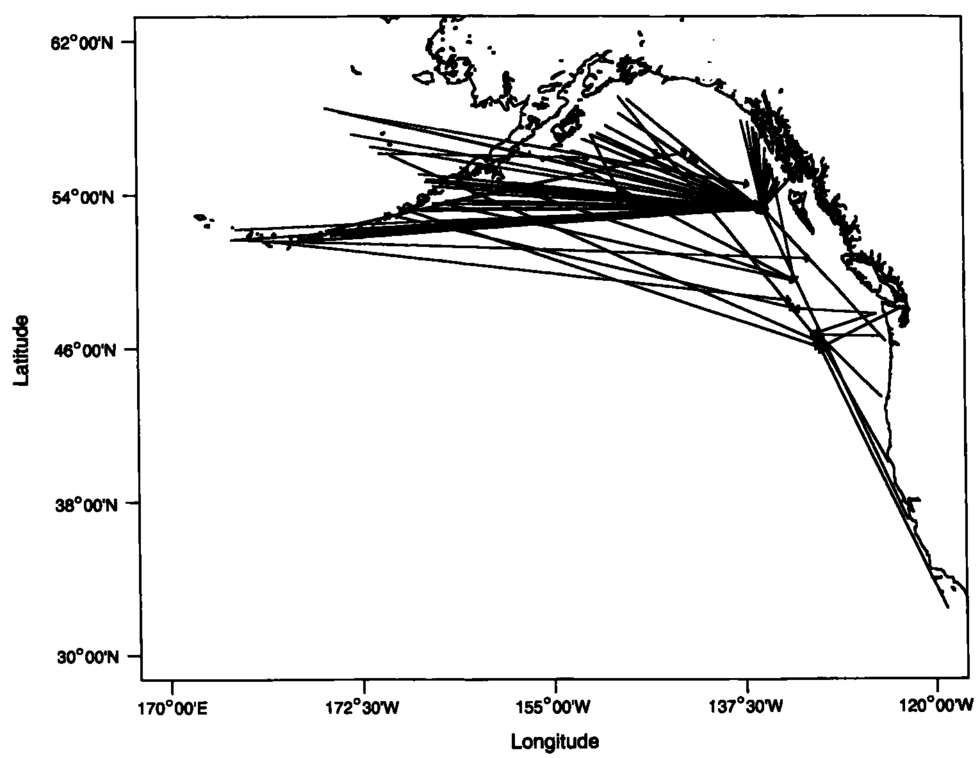

Figure 3

Source of seamount tag recoveries can be seen to be from almost all areas. Figure adapted from Shaw and Parks (1997).

Table 6

Tag recoveries tabulated by the area of release (rows) and area of recovery (columns). Areas are described in Table 2 and Figure 1.

Area of release	Area of recovery																											Total tag recoveries
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	3	6	5	0	0	1	2	1	1	3	0	1	9	2	16	7	3	2	1	0	0	0	0	0	0	63
4	0	0	1	42	18	1	0	1	8	9	2	8	13	17	46	23	42	29	14	6	1	0	1	1	0	0	0	283
5	0	0	5	18	284	1	2	5	28	19	26	60	46	84	143	115	149	109	39	4	3	3	1	0	2	0	0	1146
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	7	4	0	1	0	0	1	1	1	2	2	6	0	0	1	0	0	0	0	0	0	26
8	0	0	0	1	1	0	2	41	6	2	3	5	3	6	6	7	28	18	11	3	1	0	1	0	0	0	0	145
9	0	0	0	6	22	0	0	0	134	38	4	13	19	18	36	33	57	50	27	16	3	0	1	1	0	0	0	478
10	0	0	2	4	14	0	1	2	18	56	11	10	10	14	26	24	43	38	25	8	2	0	3	0	1	0	0	312
11	0	0	4	6	16	0	0	2	4	6	62	31	23	20	41	21	50	42	22	8	4	0	1	0	0	0	0	363
12	0	0	2	9	23	0	1	3	9	9	20	136	49	38	78	40	79	63	42	15	6	3	3	0	0	0	0	628
13	0	0	0	5	17	0	0	0	12	12	6	49	157	103	111	56	89	75	41	21	8	1	1	0	0	0	0	764
14	0	0	0	6	17	0	1	2	10	11	10	21	38	284	139	87	114	72	57	24	8	6	2	0	0	0	0	909
15	0	0	1	4	27	0	2	0	4	9	6	12	22	76	297	93	82	57	43	17	8	2	0	0	0	0	0	762
16	0	0	0	1	17	0	0	1	10	10	8	18	26	26	79	241	99	39	19	6	2	0	1	0	0	0	0	603
17	0	0	1	3	26	0	0	4	18	16	13	30	30	60	109	99	796	181	71	27	6	3	2	1	0	0	0	1496
18	1	0	0	1	13	0	0	0	17	6	1	14	13	48	34	54	299	879	115	62	9	8	3	1	1	0	0	1579
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	1	1	0	0	0	1	3	1	1	1	6	5	1	6	9	14	387	68	7	2	2	0	1	0	517
21	0	0	0	3	1	0	0	0	0	0	1	3	6	3	10	4	10	11	7	138	638	76	15	2	0	1	0	929
22	0	0	0	0	1	0	0	0	1	1	0	1	2	2	1	2	3	11	5	27	70	548	64	12	2	2	0	755
23	0	0	0	0	1	0	0	0	0	0	1	0	0	5	3	2	2	5	6	6	17	98	534	122	13	2	1	818
24	0	0	0	0	4	0	0	0	0	0	0	2	0	2	2	2	0	3	2	4	11	35	89	282	27	2	1	468
25	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	5	1	1	2	8	28	55	123	314	16	8	565
26	0	0	0	0	1	0	0	0	0	1	1	0	2	2	3	0	3	5	7	15	8	57	106	64	84	414	6	779
27	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	4	6	12	15	14	9	13	120	197
Total	1	0	19	116	509	2	16	66	283	210	177	417	461	818	1180	910	1974	1711	572	802	889	887	900	625	453	451	136	14,585

sablefish were observed to move over 500 n mi from tagging to recovery, and more than 10% moved over 1,000 n mi. In contrast fewer than 10% of west coast sablefish moved over 500 n mi.

For the Gulf of Alaska, there is a strong proclivity for fish tagged in the southeast (areas 16–18) to move north and west and for fish tagged in the west (areas 3–14) to move east and south (Tables 4 and 6). It is convenient to define movement north or west as a recovery from an area number less than the area of tagging, and movement east or south as a recovery from an area number greater than the area of tagging (Fig. 1). Several authors (Fujioka et al., 1988; Heifetz and Fujioka, 1991) point out that these directional movements are most pronounced for fish tagged at less then 57 cm in southeast Alaska, and for fish tagged at greater than 57 cm in the western Gulf of Alaska. The greater intensity of these size-selective migrations are supported by our data (Table 4).

The patterns of migration can be illustrated visually by considering maps of average movement where tag recoveries are aggregated by the area of tagging or the area of recovery. Figure 5 shows the average position of tagging (tail of arrow) for each of the 27 areas for which sablefish were tagged (i.e. 23 areas) and the average position where subsequent recoveries occurred. Similarly, Figure 6 shows the average position of recoveries (head of arrow) in each area (i.e. 24 areas) where more than 2 recoveries occurred and the average position of tagging (tail of arrow) for each aggregation of tags.

For the Alaska population, Figures 5 and 6 seem to show an expansion and return about the center of sablefish abundance in the central Gulf of Alaska. By this we mean that fish tagged away from the center of the Gulf of Alaska tend to be recovered toward the center of the Gulf, and fish recovered away from the center of the Gulf tend to have originated toward the center of the Gulf. Such a pattern could represent random movement throughout the Alaska range, with concentration of tagging and recovery effort (Tables 3 and 6) occurring in the central Gulf of Alaska. For the west coast population, the movement is more of a slight but steady northward shift whether the aggregation is by area of tagging or area of recovery. Such movement may be the result of migrations or may represent a biologically static situation, one in which recoveries are influenced by increasing fishing pressure towards the north.

As pointed out in the introduction, sablefish inhabit a very broad bathymetry. In order to try to learn something of sablefish depth migrations, we tabulated depth at release for all tagged sablefish and depth at release versus depth at recovery for sablefish that were tagged and recovered (Table 7). Fish that were tagged in Alaska and recovered off the west coast,

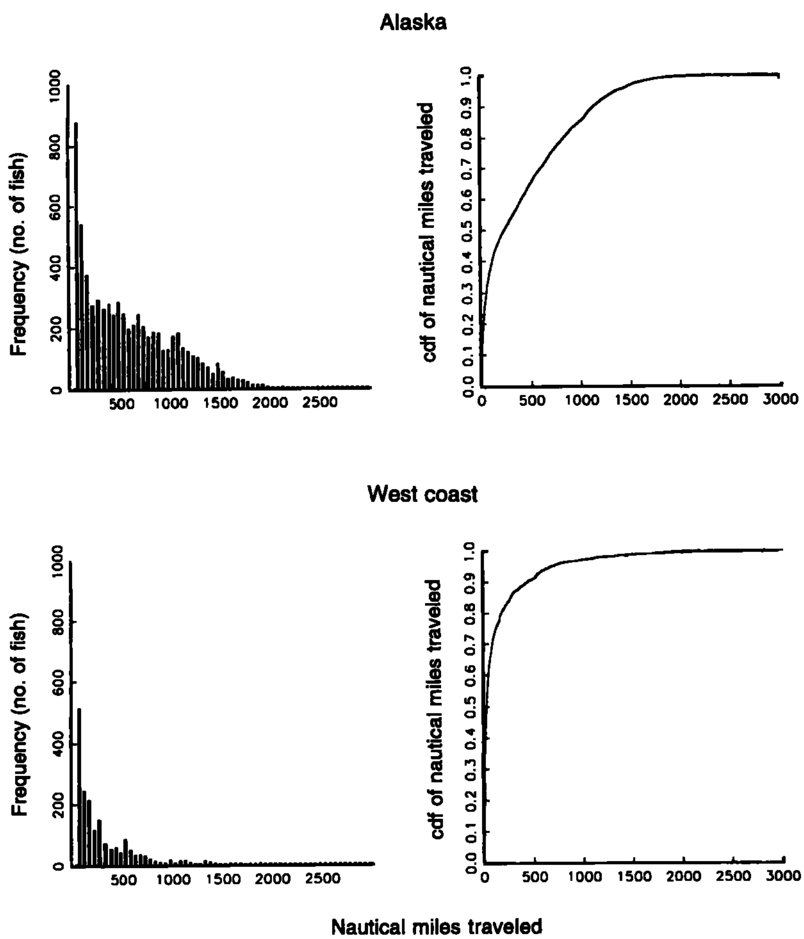

Figure 4

Histogram and cumulative distribution function (cdf) of the distance traveled (n mi) for sablefish that were tagged and recovered. Distances are straight line distances that are minimums; actual distance traveled must have been greater. Histograms are binned in 50 n mi intervals, with the 0–50 n mi bin not plotted so that more detail could be seen. For Alaska the 0–50 n mi bin count was 2744, for the west coast the 0–50 n mi bin count was 3075.

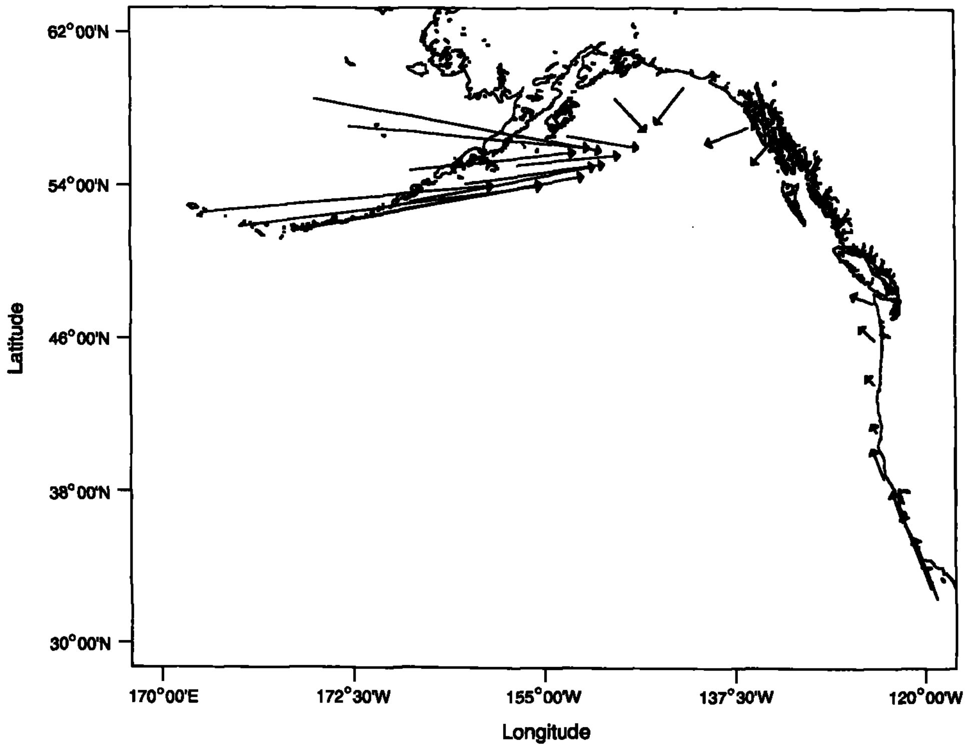

Figure 5

Average movement of tagged and recovered sablefish aggregated by area of tagging. Arrows point to the average location where sablefish tagged in a specified area were recovered (i.e. where fish were going). Tail of arrow originates in one of the 27 areas in which tagging occurred. Tagging did not occur in all areas.

or vice versa, were excluded from Table 7. For Alaska sablefish, the depth of tag recovery generally had the same distribution regardless of the depth of tagging. For west coast sablefish, recoveries tended to be in the same depth zone as the depth of tagging. However, few recoveries were made from the relatively large number of tags released in the 400–1000 m depth zone.

Results related to ENSO events and migration from Alaska to the west coast

Global-scale El Niño-Southern Oscillation (ENSO) events are the strongest climatic feature occurring in the Pacific Ocean. Along the west coast it weakens upwelling and is known to lower food availability and to stunt growth of pelagic species (Bakun, 1996). To the north, off Alaska, ENSO may have the opposite effect, enhancing growth and biological productivity (Beamish and Bouillon, 1993; Bakun, 1996). A significant negative effect on sablefish growth due to ENSO events was detected ($P[|t|>3.973] < 7.2\times10^{-5}$, df=3666) off the west coast, and a significant positive effect on growth was detected ($P[|t|>2.604] < 0.01$, df=6030) for Alaska sablefish (Table 8). In this analysis growth increment data were used only if tagging and recovery occurred in the same region. Residuals histograms suggested a normal pattern of errors for the model fits (Fig. 7).

We found that sablefish that migrate from Alaska waters to the west coast appear to concentrate in areas off Vancouver Island, Washington, and Oregon. Area 20, between 47°30' and 50°N latitude (Fig. 1), is of particular interest because it is an area of mixing for Alaska and west coast sablefish (Table 6, column 20). The question arises whether we can detect factors that might influence the migration from Alaska to areas 20 and 21 off the west coast. One factor that seems to have a positive correlation with this migration south is the strength of upwelling in these southern areas (Fig. 8, two-tailed, sign. α= 0.01).

Length frequencies from sablefish trap index surveys (1978–91), aggregated over all years, strongly distinguish between fish from Alaska (areas 17 and 18) and the west coast (areas 20–27) (Fig. 9A). However, the length frequencies for fish greater than 60 cm (Fig. 9B) suggest three groups: Alaska (areas 17 and 18), west coast north (areas 20–24), and west coast south (areas 25–27). The west coast north (ar-

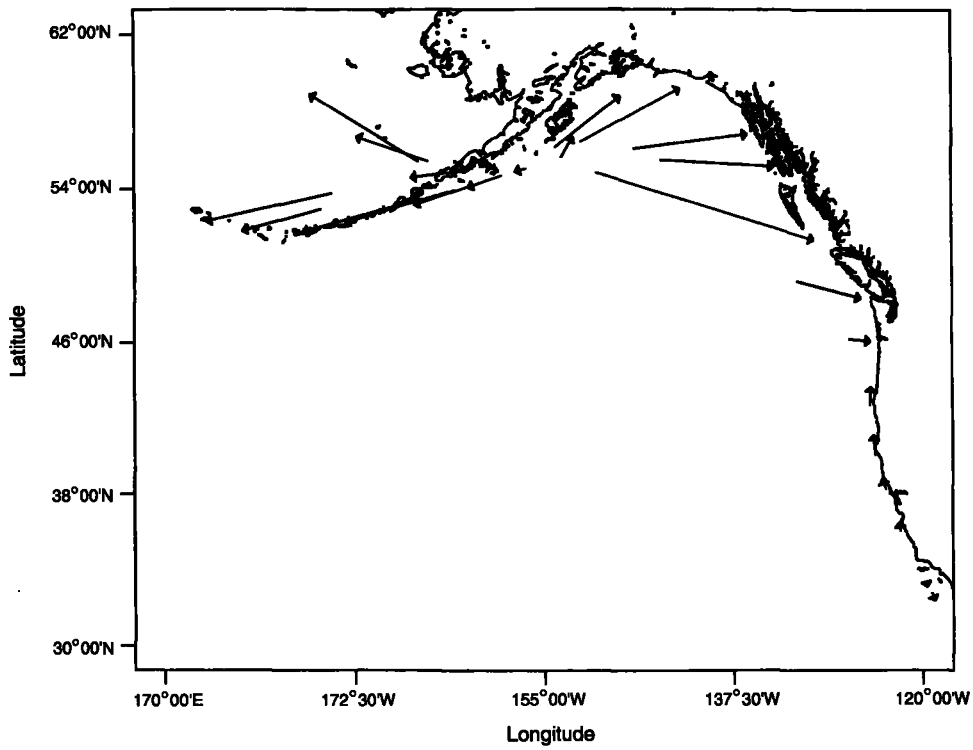

Figure 6

Average movement of tagged and recovered sablefish aggregated by area of recovery. Head of arrow lies in one of the 27 areas in which more than two tag recoveries occurred. Rear of arrows lies in the average location where sablefish were tagged (where fish were coming from).

eas 20–24) group appears to have an excess of large (>60 cm) sablefish, but we cannot be sure of their origin. We were unsuccessful in our attempt to correlate annual fluctuations in the abundance of large sablefish with upwelling, but this may have been due to limitations in the samples that were available on a biennial basis from the west coast north area.

Discussion

Comparison and interaction of Alaska and west coast populations

Our tag-recovery data alone provide compelling evidence (Table 6) that Alaska and west coast sablefish constitute separate populations that, for practical purposes, remain largely independent. In the long-term, approximately 3.5% of Alaska fish migrate to the west coast, and approximately 4.4% of west coast fish migrate to Alaska. Short-term migration rates will be small and justify the separation of these populations for fishery management purposes. However, biologically, these exchange rates are probably sufficient to consider sablefish a single biological population throughout its range, provided these populations are not reproductively isolated. Notice that these migration rates say nothing of net migration which is dependent on the absolute magnitude of the Alaska and west coast populations.

Stock assessment scientists have long felt that sablefish constitute two distinct stocks between Alaska and the U.S. west coast, largely because their von Bertalanffy growth parameters and size-at-maturity differ so dramatically (Table 9; McDevitt, 1990; Kimura et al., 1993). However, early genetic studies (Tsuyuki and Roberts, 1969; Wishard and Aebersold, 1979; Gharrett et al., 1983) indicate that although the northeast Pacific may support many "somewhat discrete" populations, a mechanism for gene transfer was expected to explain the observed polymorphism. In light of our strong evidence for migratory behavior in tagged sablefish, it is not surprising that significant gene flow occurs throughout the range.

The recapture rate for tagged sablefish appears to be remarkably similar for all areas of tagging (Table 4), especially if the differential survival rate from the fishing gears used for initial capture is taken into account. These recapture rates cannot tell us much

Table 7

Number of sablefish tag releases and recoveries by depth category (in meters). Proportions are proportion of total releases that were recovered and the proportion of recoveries that were made at each depth category. Alaska and the west coast was divided at 50°N latitude, with tagging and recovery occurring within the respective regions.

Alaska		Number recovered at depth					
Depth released	Total released	0–200	200–400	400–600	600–800	800–1000	Total recoveries
0–200	11240	75	98	264	237	49	723
200–400	19334	73	365	704	568	116	1826
400–600	108131	51	268	866	856	208	2249
600–800	17572	11	41	206	312	64	634
800–1000	683	2	0	7	31	14	54

Alaska		Number recovered at depth				
Depth released	Proportion recovered	0–200	200–400	400–600	600–800	800–1000
0–200	0.064	0.104	0.136	0.365	0.328	0.068
200–400	0.094	0.040	0.200	0.386	0.311	0.064
400–600	0.021	0.023	0.119	0.385	0.381	0.092
600–800	0.036	0.017	0.065	0.325	0.492	0.101
800–1000	0.079	0.037	0.000	0.130	0.574	0.259

West coast		Number recovered at depth					
Depth released	Total released	0–200	200–400	400–600	600–800	800–1000	Total recoveries
0–200	9208	376	386	34	3	0	799
200–400	15283	309	2054	339	12	0	2714
400–600	23624	6	108	118	7	0	239
600–800	6208	1	5	7	2	0	15
800–1000	4327	0	0	0	0	0	0

West coast		Number recovered at depth				
Depth released	Proportion recovered	0–200	200–400	400–600	600–800	800–1000
0–200	0.086	0.471	0.483	0.043	0.004	0.000
200–400	0.178	0.114	0.757	0.125	0.004	0.000
400–600	0.010	0.025	0.452	0.494	0.029	0.000
600–800	0.002	0.067	0.333	0.467	0.133	0.000
800–1000	0.000	0.000	0.000	0.000	0.000	0.000

about the absolute exploitation rate on sablefish, because tag loss, survival of tagged fish, and reporting rates are unknown. However, the data seem to indicate that the relative exploitation rate of substocks is roughly of similar magnitude throughout their range.

Adult sablefish make two types of migrations that are quite striking in nature: migrations from the continental slope across abyssal plains to seamounts, and long-range migrations along the continental slope that can extend all the way from the Bering Sea to southern California in either direction. The mechanism for accomplishing these long-range migrations has been discussed very little in the literature, although Moser et al. (1994) suggest that migration to seamounts may be midwater over the abyss.

Because adult sablefish are demersal, one possible mechanism for accomplishing these long-range migrations is that sablefish follow the continental slope, or sea floor. Because these deep areas are in the low-oxygen zone (Bakun, 1996), this route would appear to be a difficult and inefficient for long migrations. Also, it would seem that such migrations would take time, but several authors have noted that for tagged sablefish, there appears to be little relation between time at liberty and distance traveled (Bracken, 1983; Dark, 1983; Beamish and McFarlane, 1988). A second possibility is that sablefish are using the dominant ocean circulation patterns to redistribute themselves.

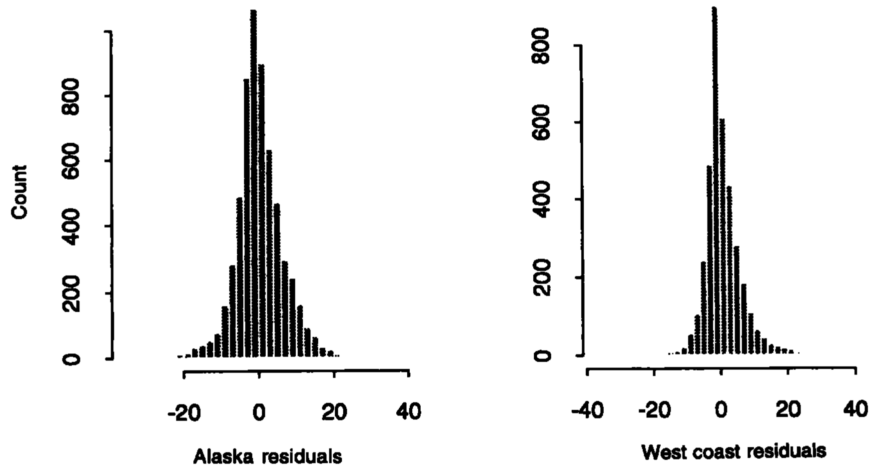

Figure 7

Histograms of residuals from fits to the growth model used to detect ENSO growth effects suggest that residuals from the model fits are approximately normally distributed.

The dominant circulation patterns in the northeast Pacific—the counter-clockwise Alaska Gyre (and Alaska Current) and the clockwise Central Pacific Gyre (and California Current)—suggest both a physical basis for separation and a mechanism for partial exchanges between Alaska and west coast stocks (Fig. 1). North of 50°N latitude, all life stages of sablefish occur in the counterclockwise rotating gyre. In contrast, south of 50°N latitude, adults live in a northward flowing undercurrent, and pelagic juveniles and benthic subadults live in the southward flowing surface current (i.e. the California Current).

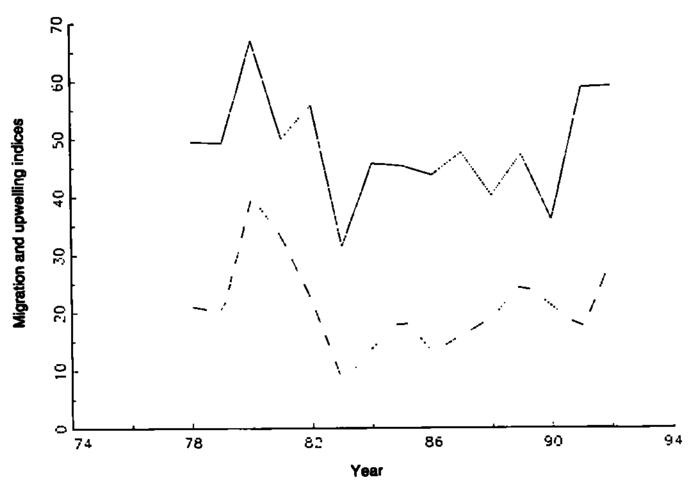

Figure 8

Plot showing correlation of the number of sablefish tagged off Alaska and recovered off the west coast (dash) with the strength of upwelling off the west coast (solid). One year was subtracted from the year of tag recovery, allowing time for the tag recovery to take place. The Bakun upwelling indices were mean coastal summer upwellings (April–August) from 42–48°N latitude (Mason and Bakun, 1986).

Tag recoveries from midocean seamounts come from all areas of tagging and appear to demonstrate that sablefish routinely migrate on (and mix on) open ocean currents from release areas along the continental slope (Fig. 3). The Alaska Current (and Gyre) could provide a passive means for sablefish to make long migrations throughout the Gulf of Alaska. Similarly, the California Current (flowing offshore and southerly on the surface) and the California Undercurrent (flowing nearshore and northerly at depth) could provide the physical conveyance for sablefish to migrate passively up and down the North American west coast.

Our findings concerning exchanges among areas in Alaska stocks corroborate earlier findings (Sasaki, 1985; Fujioka et al., 1988; Heifetz and Fujioka, 1991). Perhaps the relative strength and general timing of prevailing currents available to Alaska sablefish are what allow them to migrate farther and with greater frequency than west coast sablefish (Fig. 4). The latitudinal range of the Alaska population is only 50–60°N, half that of the west coast population which is 30–50°N. Perhaps this narrower latitudinal range also facilitates migrations.

Earlier, we described how migrations from Alaska to the west coast are reciprocated by migrations from the west coast to Alaska. Although this is true, sablefish

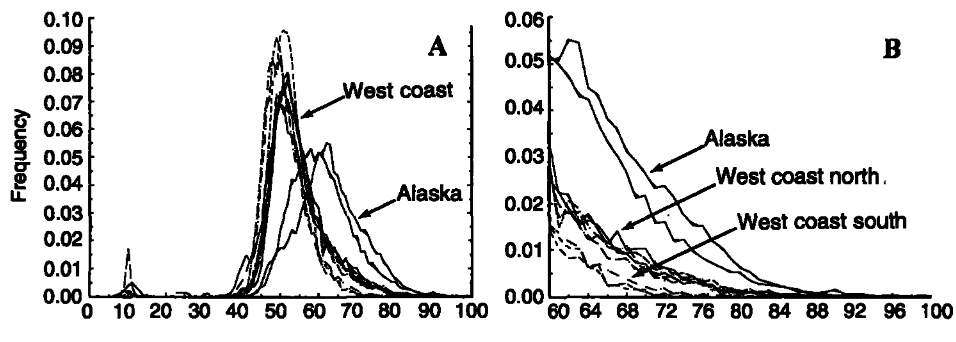

Figure 9

(**A**) Length frequencies from trap index surveys, plotted by areas, showing the dichotomy between Alaska (areas 17 and 18) and west coast (areas 20–27) sablefish. The two distributions shifted to the right are from Alaska. (**B**) The same length frequencies but only for sablefish with length greater than 60 cm. Top distributions are from Alaska (areas 17 and 18), the middle distributions are from the west coast north (areas 20–24), and the lower distributions are from the west coast south (areas 25–27).

migrating from Alaska to the U.S. west coast appear to concentrate in the northern area of the west coast (areas 20–22, Table 6).

Methot[6] recognized from fishery data that west coast sablefish varied greatly in size at age. He suggested that this was due to a commingling of southern California and Alaska "morphs." Extending this hypothesis, tag recoveries (Table 6) suggest that area 20 contains a substantial number of fish from Alaska, but that areas farther south contain substantially fewer migrants. Similarly, length frequencies of large fish from the NMFS trap index survey (Fig. 9B) suggest three populations: Alaska fish from areas 17 and 18; a mixture of Alaska and smaller southern California fish from areas 20–24; and small southern California fish from areas 25–27.

On the basis of size and age-at-depth data, adult sablefish are believed to inhabit greater depths as they grow older owing to a protracted, ontogenetic migration to greater depths (Fujioka et al., 1988; Saunders et al., 1997). Norris (1997) disagreeing with this view, conjectured that the broad bathymetric range was due to radiative evolutionary adaptation of enzyme systems to greater depths. Norris (1997) regarded the age-at-depth data as an artifact caused by varying size-selective fishing mortality with depth. He felt that reproducing populations inhabit various depth zones. Sigler et al. (1997) hypothesized that age-at-depth data could be explained by considering the movement of sablefish to greater depths as being a random walk (i.e. resulting from a sequence of random movements). From this point of view, greater age-at-depth could be viewed as an ontogenetic phenomenon resulting from statistical behavior.

Table 8

Parameter estimates and their statistical significance for a tag-recovery growth model intended to detect a growth effect due to ENSO events. Data were divided between Alaska and the west coast and the ENSO parameter was included when a particular tagged fish was at liberty during any ENSO event. The model used was $S_2 = S_1 + \Delta_t \exp(\beta_{enso} + \beta_1 S_1 + \beta_2 \Delta_t)$, where S_1 was the size of fish at the time of tagging, S_2 was the size of fish at time of recovery, Δ_t was the time elapse between tagging and recovery, and β_{enso} represents an effect from any exposure to ENSO events. Both release and recovery were in the same region for the data used.

Parameter	Estimate	SE	*t*-value
Alaska modeling results.			
Degrees of freedom for *t*–statistic=6,030.			
β_{enso}	0.05781	2.2200×10^{-2}	2.604
β_1	–0.08307	4.8603×10^{-4}	–170.910
β_2	–0.00031	9.9375×10^{-6}	–31.093
West coast modeling results.			
Degrees of freedom for *t*-statistic=3,666.			
β_{enso}	–0.12918	3.2513×10^{-2}	–3.973
β_1	–0.09636	7.4322×10^{-4}	–129.651
β_2	–0.00036	1.4059×10^{-5}	–25.853

[6] Methot, R. D. 1993. Latitudinal and bathymetric patterns in sablefish growth and maturity off the U.S. West coast. Paper presented at the international symposium on the biology and management of sablefish, Alaska Fisheries Science Center, April 13–15, 1993.

Table 9

Von Bertalanffy growth parameters and lengths at maturity for Alaska (AK) and west coast sablefish. Growth parameters are based on age data (Kimura et al., 1993). Lengths at maturity for Alaska are from Sasaki (1985), and for the west coast are from Parks and Shaw (1983).

Region	Location	Sex	L_∞ (cm)	K	t_0 (yr)	Length at maturity (cm)
Alaska		male	70.2	0.120	–8.06	
		female	86.7	0.106	–6.15	
	Bering Sea	male				65
		female				67
	Aleutian Islands	male				61
		female				65
	Gulf of AK	male				57
		female				65
West coast		male	54.7	0.472	–1.82	
		female	61.0	0.499	–0.81	
	Bodega Canyon	male				52.7
		female				55.3
	Patton Escarpment	male				54.8
		female				56.3

Depth-related tagging data for sablefish are very difficult to interpret for several reasons. First of all, surveys, and therefore tag releases, did not cover the full bathymetric distribution of sablefish. Second, commercial fishing, and therefore recovery effort, did not cover the full bathymetric distribution of sablefish. And finally, the bathymetric distribution of a species abundant across such a broad latitudinal range as sablefish, might be expected to vary by latitude.[7] Most of our evidence supports the hypothesis that sablefish seem to have a deeper, lower limit to their distribution off the west coast, compared with their distribution off Alaska.

The principal depth-related result for Alaska sablefish is that the depth distribution of recoveries is similar regardless of the depth of tagging (Table 7). Although the depth distribution of recoveries naturally follows recovery effort, it also suggests a certain amount of random movement in relation to depth over time. The depth-related data for west coast sablefish are even more difficult to decipher. These data show an extremely low recovery rate from fairly heavy tagging of fish from the 400–1000 m depth zone. The reason for this low recovery rate is unknown. Perhaps, the strongest conclusion to emerge from our study is that we still have more to learn about sablefish depth distributions.

[7] One reviewer noted the term "latitudinal emergence," where deeper dwelling species are thought to have shallower upper limits on their bathymetric distributions in the more northern limits of their range. However, we did not find this term to be widely used in the literature.

Effects of ENSO on migration and growth

It seems natural that the growth of pelagic species off the west coast, such as Pacific whiting (*Merluccius productus*) and Pacific salmon (*Onchorynchus* spp.), would be adversely affected by ENSO events (Beamish and Bouillon, 1993; MacLellan and Saunders, 1995). It is perhaps more interesting that along the west coast, the growth and somatic condition of adult rockfish have been negatively affected by ENSO (Lenarz et al., 1995). That the observed growth of a deepwater species, such as sablefish, can be negatively affected suggests that the feeding of many demersal species along the west coast may suffer some ill effects from ENSO. In the Gulf of Alaska, ENSO growth effects are thought to be opposite of those experienced off the west coast. Growth of salmon and groundfish species are thought to be significantly enhanced by ENSO events (Beamish and Bouillon, 1993; Bakun, 1996). Thus our findings that ENSO events retard growth of sablefish off the west coast but enhance growth of sablefish off Alaska are consistent with this literature. However, this may be the first documentation of this effect for a demersal species.

The question arises as to why there is a positive correlation between Bakun's upwelling index and west coast tag recoveries of Alaska fish (Fig. 8). Are migrating sablefish taking advantage of enhanced feeding opportunities presented by strong upwelling or are they displaced sablefish subject to irregular but recurring episodes of ocean-forcing events and passively entrained in strengthened currents southward?

Dorn (1992) noted two oceanographic phenomena that make west coast waters a highly productive region: coastal upwelling and the advection of cool, zooplankton-rich water from the Alaska Subarctic Gyre. These phenomena could be distinguished (Roesler and Chelton, 1987) and Hollowed and Wooster (1992) have pointed out that they are positively correlated.

Hollowed and Wooster (1992) noted that climate and ocean circulation in the northeast Pacific oscillates between a type-A pattern (i.e. weak Aleutian Low and Gulf of Alaska circulation, intensified California Current, and strong upwelling off the west coast) and type-B ENSO-associated conditions (i.e. intensified winter Aleutian Low and Gulf of Alaska circulation, weak California Current, and weak coastal upwelling). It is the more prevalent type-A scenario, with a strong California Current, that possibly facilitates the migration of sablefish south. Thus, the strength of migration from Alaska to the west coast would be negatively correlated with ENSO events. Dorn (1995) concluded that increased northward movements of Pacific whiting along the west coast during El Niño years were due to intensified northward currents. Whether or not a subset of Alaska sablefish follow enhanced feeding gradients, a strong California Current could deliver them to the west coast.

Because the California Current is a surface current and because there exists a natural boundary between the California Current and the Alaska Gyre, it is somewhat speculative to claim that a strong California Current plays an important role in the migration of Alaska sablefish to the west coast. Nevertheless, Alaska sablefish do make this migration, and the migrations coincide with an enhanced California Current and increased upwelling. It would seem difficult to conclude that these phenomena are totally unrelated.

One difficulty in discussing sablefish migration is that we cannot be sure that the larger fish found along the northern portion of the west coast are of Alaskan origin. A partial explanation could be that the strong upwelling zone from Cape Mendocino to Point Conception in central California, as measured by Ekman transport (Parrish et al. 1981), represents a physical barrier to larger (Alaska?) sablefish. This barrier seems plausible because large sablefish become relatively rare in the length frequencies for the areas where upwelling intensifies. The second part of this theory would tell us whether Alaska sablefish are able to reproduce in waters off Washington and Oregon. It is possible that the gross numbers of Alaska sablefish migrating to the west coast are not substantial enough to affect length frequencies directly but that the numbers may be substantial enough to affect the population genetically over a much broader geographic range. Bakun (1996) argued that the Southern California Bight and the Columbia River Plume offer two locations where fish larvae can survive the disruptions of a strong upwelling environment. These locations may correspond to those for northerly and southerly west coast sablefish populations.

However, Moser et al. (1994) believed that although sexually mature and spawning sablefish are encountered as far south as Baja California, virtually none of their reproductive potential survives below the Southern California Bight and they do not contribute to the standing stock in any meaningful way. They concluded that it is the advection of eggs and larvae from the north that ensures the stability of the population south of Pt. Conception. This hypothesis, that sablefish abundance off the west coast (and particularly California) is dependent on a steady "leakage" of eggs, larvae, or juvenile fish from more northern center(s) of abundance, parallels the hypothesis that Asian stocks are dependent on the migration of adult fish from northern and eastern areas of the Pacific.

Although the appearance of northern fish in the mixed-zone off the Washington–Oregon coast is well established, we cannot yet quantify the net contribution of immigrants. Also, we found little evidence of tagged adult fish migrating from areas north of central California to southern and Baja California. However, this does not preclude Moser et al.'s (1994) conjecture that the southern California population is dependent on eggs and larvae advected from the north. The dependence of sablefish stocks on spawning populations appears not to be well understood.

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pressed concerning sablefish biology and movement, it is important for us to state that the conclusions described here are those of the authors.

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