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Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 8(8) : 334-349

Published By: American Fisheries Society

URL: https://doi.org/10.1080/19425120.2015.1135218

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 8:334–349, 2016
Published with license by the American Fisheries Society
ISSN: 1942-5120 online
DOI: 10.1080/19425120.2015.1135218

ARTICLE

Evaluating the Efficacy of Trawl Exclusion Zones by Estimating Local Atka Mackerel Abundance and Movement Patterns in the Central and Eastern Aleutian Islands

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Abstract
Atka Mackerel *Pleurogrammus monopterygius* is the most abundant commercially exploited groundfish in the Aleutian Islands, Alaska. It is also the predominant prey of the endangered Steller sea lion *Eumetopias jubatus* in the Aleutians Islands range. In 1992, trawl exclusion zones (TEZs) that ranged from 10 to 20 nautical miles were established around rookeries to protect Steller sea lion prey abundance. This study examined the efficacy of the TEZs by estimating the movement and local abundance (10–20 nautical miles) of Atka Mackerel inside and outside of these zones using an integrated tagging model that incorporated independent data for tagging survival, recruitment, and tag reporting rates. Atka Mackerel were tagged, released, and recovered from 2000 to 2006 at four Aleutian Island locales, from both inside and outside of the TEZs. Atka Mackerel local abundance and their movement patterns across these harvest boundaries were estimated for all the study areas inside and outside the TEZs, and local exploitation rate by the fishery was calculated for each area open to fishing outside the TEZ boundary. In areas with high Atka Mackerel abundance and little movement from inside to outside the protection zones (e.g., Seguam Pass and Kiska Island), the TEZs were expected to work well to preserve the prey field for Steller sea lions. In areas of low Atka Mackerel abundance and frequent movement from the inside to the outside of the protection zone (e.g., Amchitka Island), the TEZs were expected to be less effective. Our study indicated that TEZs can be effective for preserving prey fields of Atka Mackerel for Steller sea lions, but each study area needs to be carefully evaluated in order to understand area-specific variations in abundance and movement patterns.

Subject editor: Ana Parma, Centro Nacional Patagónico, Chubut, Argentina

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Received October 21, 2014; accepted December 16, 2015

Groundfish stocks in Alaska are managed at large spatial scales; however, important ecological interactions such as predation, spawning, and habitat selection occur on a local scale. For the purpose of this study, the local scales referred to are scaled to the size of the trawl exclusion zones (TEZs), which range from 10 to 20 nautical miles (nmi; 1 nmi = 1.852 km) in diameter. Furthermore, commercial fishing in the Aleutian Islands is a local activity with the potential for localized effects. Improved understanding of the abundance in these small areas and the movement of fish is critical to understanding the potential for localized fisheries interactions within the fished system and evaluating the efficacy of TEZs as management tools in these areas.

The population decline of the Steller sea lion *Eumetopias jubatus* has been a focus of concern in the northern Pacific Ocean for many years, and a large research effort by the National Marine Fisheries Service (NMFS) has been undertaken to examine the cause of this decline (NMFS 2008). The listing of the western stock of Steller sea lions as endangered under the U.S. Endangered Species Act in 1990 prompted the need to accurately estimate the abundance of Atka Mackerel *Pleurogrammus monopterygius* on small spatial and temporal scales (McDermott et al. 2005). Several hypotheses for the Steller sea lion decline have been suggested, such as a decrease in juvenile survival and reproductive rates (Holmes et al. 2007), the impacts of climate forcing (Trites et al. 2007), and the depletion of local prey resources due to small-scale environmental variability (Lander et al. 2009). One hypothesis for the decline and lack of recovery is that the western stock of Steller Sea lion competes with the fishery at these local scales (NMFS 2008).

The dominant prey item for Steller sea lions in the Aleutian Island area is Atka Mackerel (Sinclair and Zeppelin 2002). A member of the greenling family, Atka Mackerel occurs in Alaska from the Aleutian archipelago in the west to the Shumagin Islands in the east and is the most abundant commercially exploited groundfish in the Aleutian Islands. They display highly aggregated and patchy distributions, centered near island passes and areas of high currents. Atka Mackerel are demersal batch spawners, and males often guard nests for up to 6 months of the year. Females aggregate in large schools close to the spawning grounds, presumably to feed. Atka Mackerel play an important role in the Aleutian Island ecosystem, where they are not only an important prey species for the Steller sea lion but also for other fish species, such as Pacific Cod *Gadus macrocephalus* and Arrowtooth Flounder *Atheresthes stomias* (Lowe et al. 2009).

Historically, the Atka Mackerel fishery operated close to sea lion (subfamily Otariinae) rookeries in the Aleutian Islands and largely within Steller sea lion critical habitat, which prompted scientists to speculate that commercial fishing for Atka Mackerel might cause localized depletion (Lowe and Fritz 1997). A suite of protection measures was put in place, including 10–20 nautical mile TEZs in critical habitat around sea lion rookeries and haulouts (Fritz et al. 1995). The designation of the TEZs was intended to preserve prey abundance for Steller sea lions at these smaller spatial scales. However, at the time of the implementation in 1992, it was not known whether these zones would be effective at maintaining prey on scales appropriate to foraging sea lions (e.g., 0–20 nmi). In a previous study (McDermott et al. 2005), Atka Mackerel abundance and movement were examined at Seguam Pass, which has a 20 nmi TEZ and is located in the eastern Aleutian Islands. McDermott et al. (2005) used tag–release and recovery methods, which estimated a high local biomass inside the TEZ (117,000 metric tons) and low movement between the TEZ and areas open to fishing. The high biomass estimate suggested that the TEZ was effective at protecting the prey for Steller sea lions from the effects of the local fishery. McDermott et al. (2005) also emphasized that this estimate was not transferable to other areas in the Aleutian Islands since Atka Mackerel aggregations are very patchy and abundance and movement might differ substantially between areas (e.g., passes).

To estimate the abundance at other locales in the Aleutian Islands, this study expanded the previous work by McDermott et al. (2005) and examined the small-scale abundance, movement, and local exploitation rate of Atka Mackerel in relation to the TEZs in four areas of known Atka Mackerel population centers in the Aleutian Islands (Figure 1). Specifically, the objectives were to (1) use tag–release and recovery methods to estimate local abundance and movement inside and outside the TEZs at four sites in the central and western Aleutian Islands, (2) expand the integrated maximum likelihood tagging model used in previous studies (McDermott et al. 2005) to include Atka Mackerel recruitment, and (3) estimate local exploitation rates at all four study sites.

METHODS

Study site.—The sites selected for this study were Seguam Pass, Amchitka Island, Tanaga Pass, and Kiska Island (Figure 1) located along the Aleutian Island chain in Alaska. All sites are adjacent to Steller sea lion rookeries and represent the major locations of Atka Mackerel fishing in the eastern and central Aleutian Island NMFS management areas. In the last 10 years, the majority of the commercial Atka Mackerel catch has been within these two management areas (Lowe et al. 2009). Each management area has within it several TEZs, which are circular areas of 20 nmi (Seguam Pass) or 10 nmi (Amchitka Island, Tanaga Pass, and Kiska Island) in diameter, centered on Steller sea lion rookeries or haulouts. For this study, the Amchitka and Tanaga Island study sites were further divided into two distinct subareas based on the TEZ and associated fishery locations (Figure 2). Amchitka Island was divided into Amchitka North and Amchitka South, and Tanaga Island was divided into Tanaga East and Tanaga West. The fishery at all four study sites takes place

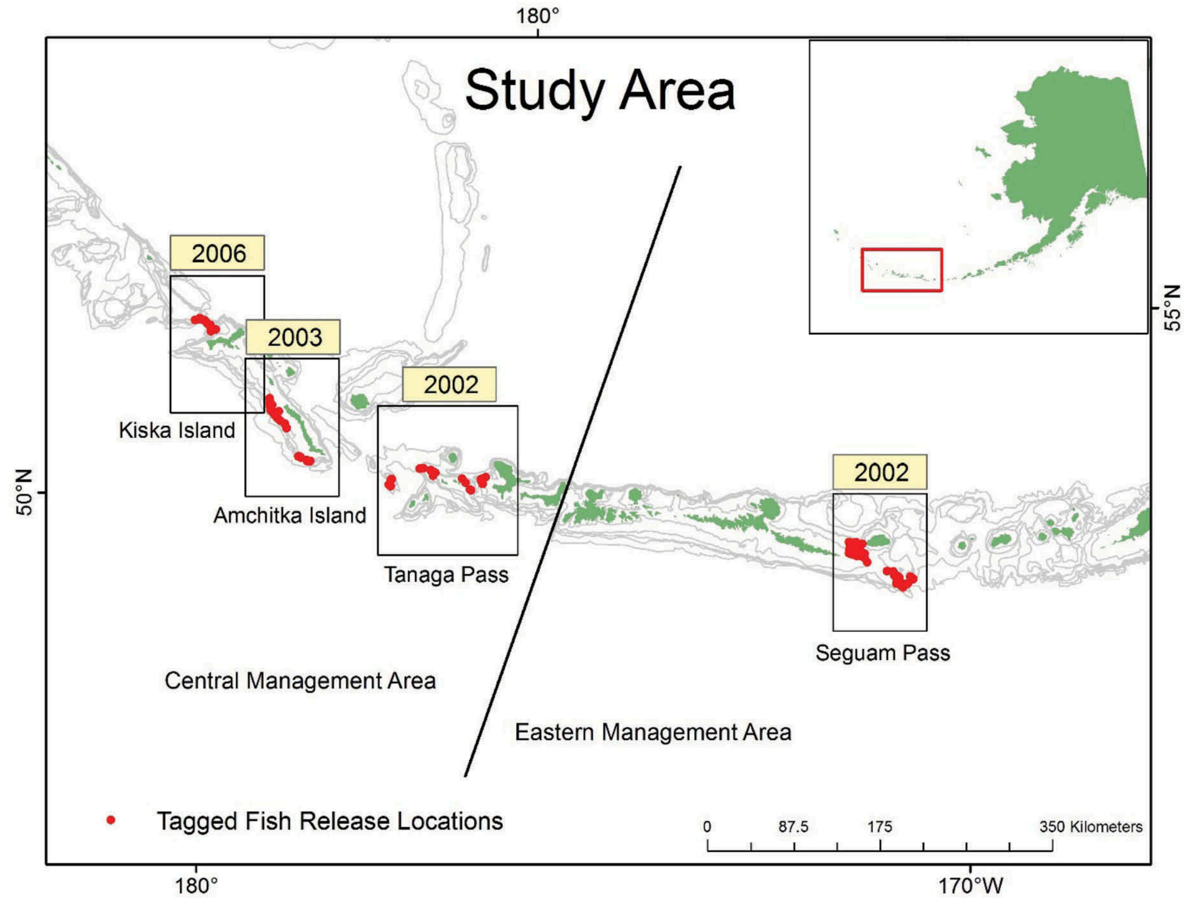

FIGURE 1. Map of the study area in the Aleutian Islands, Alaska, showing the four areas used as tag–release and recovery locations in examining Atka Mackerel abundance and movement.

outside of the TEZs, often directly adjacent to the TEZ boundary. Atka Mackerel occur mostly between 70 and 200 m deep and fishing locations are, in general, located along the shelf above a 200-m depth. At each study site, we defined the area inside the TEZ as area 1 and the area outside the TEZ as area 2; for example, Seguam Pass area 1 is the area inside the TEZ and Seguam Pass area 2 is the area outside the TEZ.

Tag–release and recovery procedures.—From 2000 to 2006, approximately 58,654 Atka Mackerel were tagged and released at Seguam Pass, Tanaga Pass, Amchitka Island, and Kiska Island (Figure 2; Table 1). Tag–release and recovery procedures were similar to the ones described by McDermott et al. (2005). The research platform used was the FV *Pacific Explorer*, a chartered commercial fishing trawler. The numbers of tagged fish released at each study site were based on the availability of charter vessel time and the estimated population size at each location using commercial catch and NMFS survey data (Table 1). We estimated the tag numbers to be released in each study area and stratum based on a rough estimate of population size (Seguam Pass with 250 million fish, all other areas with 80 million fish) and then calculated predicted tag recoveries based on the anticipated catch of the commercial fleet and the charter vessel. We then estimated the uncertainty associated with these "predicted" tag recoveries using the standard Peterson method and the Chapman estimator (Chapman 1951) and adjusted the numbers of tags to be released until all population estimates had a predicted standard deviation of less than 0.25. The predicted numbers of tags released inside the TEZs were higher than the numbers outside the TEZs for each study area since tagged fish could only be recovered by the charter vessel inside the TEZs and therefore the predicted catch of fish and resulting tag recovery numbers were much lower than in the area open to the commercial fishery.

In order to spatially reflect the population distribution with the spatial coverage of the tagged fish that were released, Atka Mackerel distributions in the bottom trawl survey and in fishery catches were used to define the extent of the study area. In all cases, Atka Mackerel tended to aggregate around island passes in less than 200 m of water, and their distribution was spatially well defined (Figures 1, 2). Fish were released within 1 nmi of the capture locations to avoid "homing" behavior.

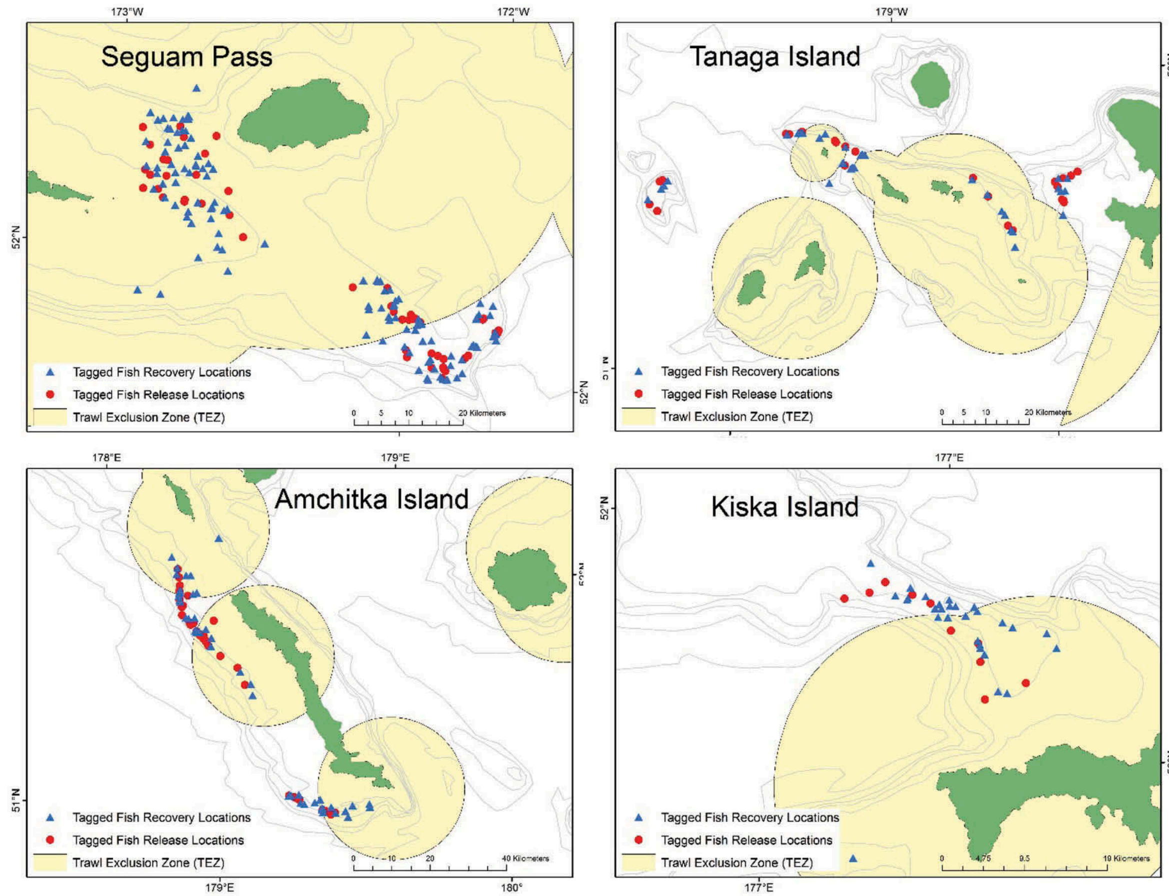

FIGURE 2. Atka Mackerel tag–release and recovery locations for each study area in the Aleutian Islands. Yellow circles denote the 20-nmi TEZs at Seguam Pass, and the 10–nmi TEZs at Tanaga Island, Amchitka Island, and Kiska Island.

The haul locations for capturing fish were spread out as far as possible within each center of Atka Mackerel abundance. Hauls were at least 2 nmi apart from the previous haul conducted during any given day. Once an area was covered sufficiently, haul locations could be repeated in order to capture the amount of fish needed for each location. Since Atka Mackerel are very patchily distributed, this ensured a good coverage in each population center.

Fish were captured for tagging with heavy-duty bottom nets at low quantities (less than 2 metric tons) by using an opening in the cod end to avoid injuring fish. Once fish were onboard, they were immediately transferred to 10 plumbed 680-L live tanks aboard the vessel with approximately 100 fish/tank, making it possible to tag and release approximately 1,000 fish/haul. The tags used were individually numbered Floy T-bar tags that were inserted into either side of the dorsal musculature of the fish near the anterior end of the dorsal fin. Roughly 20% of the tagged fish that were released were double-tagged to estimate tag loss rate. Fish were released into a 20-cm-diameter flexible hose supplied with running seawater that was secured off the side of the vessel. Injury to fish during release appeared minimal. In addition to tagging Atka Mackerel in each haul, approximately 150 randomly selected nontagged fish were sexed visually and the fork length was recorded to the nearest centimeter. To estimate the short-term effects of tagging on Atka Mackerel, a survival experiment was conducted by randomly selecting 10 fish from every haul (after they were tagged) and placing them into two dedicated 680-L running seawater tanks. Fish were held for 48–72 h and monitored for mortality every 6 h.

The recovery of tagged fish outside the TEZs was conducted by the commercial fishing fleet with the help of NMFS observers. The recovery of tagged fish from both inside and outside the TEZs was done by a NMFS-chartered factory trawler (FT *Seafisher*). On commercial vessels, the tags were recovered during the regular fishing and processing operations and the vessel crew received a small reward for finding and returning tagged fish. On the NMFS-chartered vessel, haul sizes were restricted to an average of 25 metric tons at each study site to spread out the recovery effort. In

TABLE 1. Summary of tag releases by area and the number of fish examined for tags, the estimated recruitment factors, and the tag recoveries by recovery event (RA = recovery area). Area 1 is inside the TEZ and area 2 is outside the TEZ.

	Release events (number of tags released)			Recovery events								
					Number of fish examined for tags		Recruitment factor		Release area 1		Release area 2	
Year and total recoveries	Area 1	Area 2	Month	Event	Area 1	Area 2	Area 1	Area 2	RA 1	RA 2	RA 1	RA 2
				Seguam Pass								
2002	18,621	6,378	Jun	Release								
			Jul	Fishery	115,635	417,233		1.55	4	3	0	9
			Aug	Charter	462,224	183,826	1.55	6.95	11	1	4	1
			Sep	Fishery	0	2,524,928		6.54	0	2	0	16
			Oct	Charter	465,803	194,694	2.88	5.59	7	0	0	0
Total recoveries												58
				Tanaga East								
2002	3,542	3,481	Jun	Release								
			Sep	Fishery	0	507,797		1.90	0	0	1	14
			Oct	Charter	226,555	152,228	1.57	2.60	6	0	3	5
Total recoveries												29
				Tanaga West								
2002	116	4,068	Jun									
			Oct	Charter	165,446	251,713	1.45	2.12	0	0	10	8
Total recoveries												18
				Amchitka South								
2003	3,866	3,044	Jul									
			Sep	Fishery	0	9,019,961		3.81	0	199	0	243
			Oct	Charter	489,131	308,922	5.23	3.77	15	12	3	8
Total recoveries												480
				Amchitka North								
2003	4,997	2,623	Jul	Release								
			Sep	Fishery	0	2,429,149		2.22	0	108	0	37
			Oct	Charter	605,650	167,387	3.37	2.93	15	7	10	3
2004			Jan	Fishery	0	856,231		4.85	0	15	0	6
Total recoveries												201
				Kiska Island								
2006	4,095	3,823	Jul	Release								
			Sep	Fishery	0	5,991,631		1.37	0	14	0	65
			Oct	Charter	722,248	515,089	1.37	0.64	12	8	10	20
Total recoveries												129

addition, the haul towing path was restricted to be equal to or greater than 1 nmi from the previous haul for at least 36 h. This ensured that the tagged fish recovery effort was spread out in space and time.

Tagging model parameters.—Atka Mackerel population numbers, biomass, movement rates, tagging survival rate, and tag reporting rate were estimated with an integrated model based on the one described by McDermott et al. (2005). The model uses maximum likelihood to estimate all parameters simultaneously and is described in detail in the appendix. To estimate the abundance of Atka Mackerel at each study site, the mark–recapture model requires the total number of fish examined for tags and the total number of fish recovered with tags. To estimate the number of Atka Mackerel examined for tags, we sampled the catches for species composition during commercial fishing and the

NMFS tag recovery charters. During the commercial fishing season, NMFS fishery observers onboard the commercial vessels estimate catch composition on a haul-by-haul basis (Alaska Fisheries Science Center 2002). Sampling procedures onboard the NMFS tag recovery charter vessel were similar to those during the commercial fishing season. A Scanvaegt flow-scale, over which the entire catch passed during processing, was used to obtain the total weight of the haul; the haul was then sampled for species composition. The percent of Atka Mackerel in the haul was multiplied by an average weight of Atka Mackerel to estimate the total amount of Atka Mackerel in the catch. Additionally, for each haul at least 150 Atka Mackerel were sexed and the fork length measured. The NMFS charter vessel sampling procedures for recovery of tagged Atka Mackerel are detailed further in McDermott et al. (2005). The total number of Atka Mackerel examined for tags was the total number of Atka Mackerel captured during the commercial fisheries plus the fish captured during the NMFS charter tag recovery cruises. The commercial fishing events varied for the different study sites and years and are summarized in Table 1. The main fishery event usually occurred in September, with smaller fishery events taking place in July or November. In the year 2002, there were two separate charter recoveries at Seguam Pass: one in August before the September fishery and one in October after the fishery. In all other years and areas, the charter recovery took place only in October.

The Atka Mackerel population sex ratios estimated during all NMFS charters (release and recovery) were in equal proportion during all tag–release and recovery events. Therefore, sexes were combined in the mark–recapture model.

To estimate the tag reporting rates, NMFS scientists and fishery observers tagged 10 fish/haul and randomly seeded the haul with these fish as the catch was dumped into the fish holds. The unique tag numbers were recorded and marked as test tags. Scientists and observers then recorded the number of tagged test fish reported by the processing crew. This was done for every haul during the NMFS charter cruises and for at least one haul per 12-h shift on the commercial vessels. Reporting rates were estimated separately for each of the study sites.

The tagging model used for this study makes several assumptions about the tagged fish that are released at each study site:

1. The tagged fish randomly mix with the rest of the population after a period of recovery (at least 30 d was allowed for mixing of tagged fish into the population).
2. Tagging does not affect catchability.
3. The adult population is contained within the described study sites and does not move from one broad study location to another; however, movement is allowed across the boundaries of the TEZs within one study site.
4. Recruitment of young fish is allowed into the areas between the time of tagging and the time of recovery.
5. For double-tagged fish, the probability of losing the first tag is independent of the probability of losing the second tag and both probabilities are equal.
6. All mortality associated with tagging is independent of sex and occurs within the first 4 d of tagging.
7. Natural mortality (M) is constant and predetermined (M is fixed at M = 0.3, see Lowe et al. 2009).

In 2002 and 2003, Atka Mackerel experienced a higher-than-average recruitment event of 3-year-old fish that occurred between our NMFS release charter in June–July and the recovery charter in October at Seguam Pass, Tanaga Island, and Amchitka Island (Figure 3). The large influx of young, untagged fish was most likely due to higher-than-average year-classes during 1998 and 1999 (Lowe et al. 2005). For the analysis of the data from 2002 and 2003, the model was adjusted to take recruitment into account. In 2006 at Kiska Island, similar recruitment events were not observed and the data were therefore not adjusted.

In order to account for this recruitment event, a recruitment factor was calculated to indicate the amount by which the population had increased as a whole (see appendix). The number of fish examined for tags was then adjusted by the respective recruitment factor for each area and time step to represent the fish present at the time of tag–release before the recruitment event took place (Table 1). The recruitment factor was calculated by dividing the population into two parts; these parts were separated by the two modes visible in the length frequency distribution (Figure 3A–D): older (larger) fish and younger (smaller) fish. It was assumed that the older (larger) proportion of fish did not experience an influx of fish of their size-class; the older proportion was defined as fish larger than 40 cm at Seguam Pass and as larger than 38 cm at the Tanaga and Amchitka study sites. We assumed that the abundance of large fish remained constant before and after recruitment and that the recruitment event only affected the proportion of the population of the smaller younger fish. We calculated the older (larger) population of fish ω from the proportions at length (Figure 3A–D) for all study sites and subareas before the recruitment event and after the recruitment event.

Some of the tagging data suggested that the movement rate was quite high, indicating that fish move across the TEZ boundaries defining the two subareas (for Amchitka and Tanaga study sites) on a regular basis (milling behavior). Movement was therefore modeled as a daily process. That is, each day some fraction of fish in area 1 (inside the TEZ) move to area 2 (outside the TEZ) and some fraction of fish in area 2 move to area 1. The authors suggest that this parameterization of movement captures milling behavior more closely than the previous approach presented in McDermott

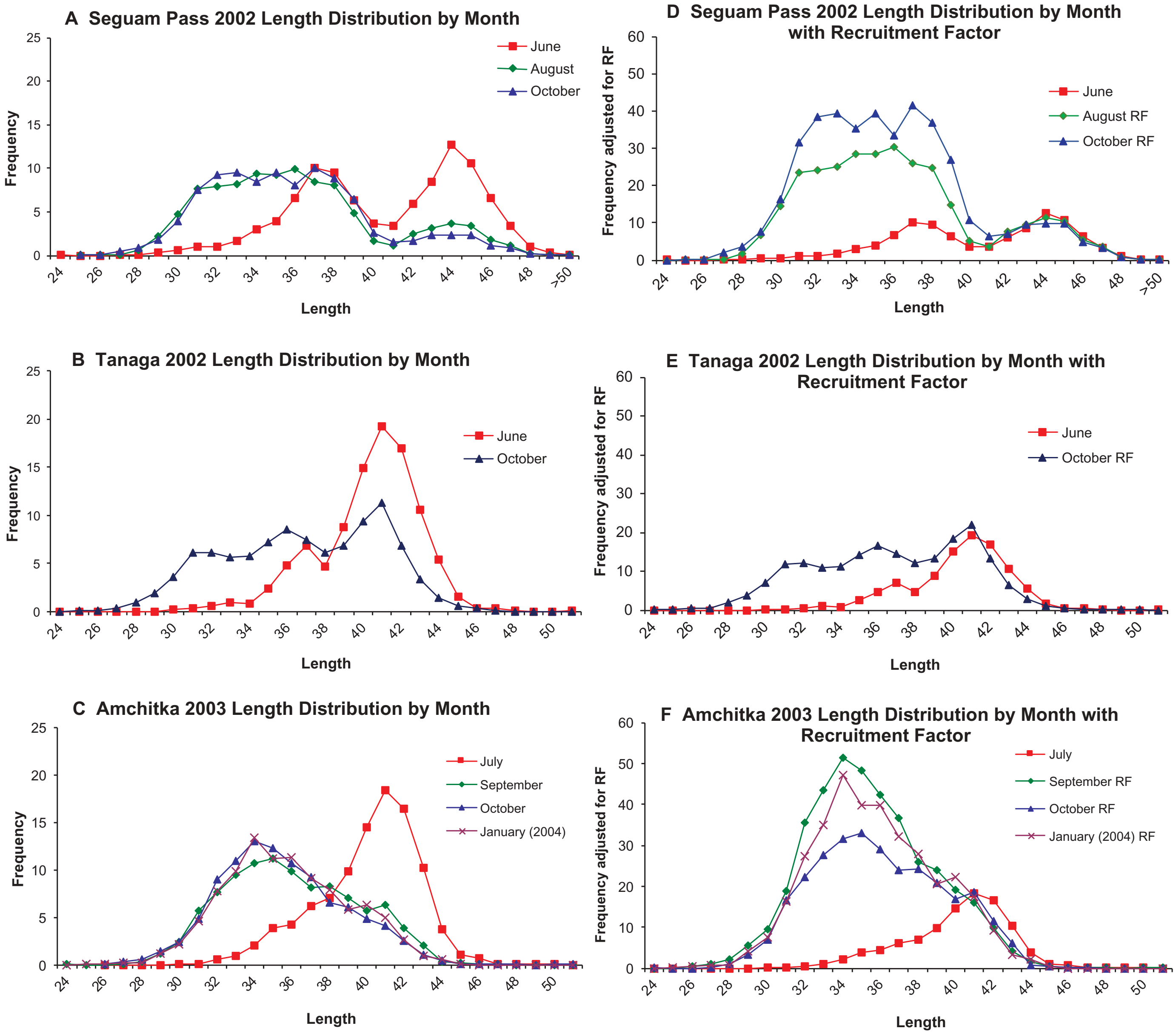

FIGURE 3. Changes in Atka Mackerel length frequency distribution in the Seguam Pass, Tanaga Island, and Amchitka Island areas from June through October, 2002 and 2003. All data were collected during the Atka Mackerel tag–release and recovery cruises. Panels **(A), (B)**, and **(C)** represent percent length frequencies from the data collected during the tag–release and recovery events. Panels **(D), (E)**, and **(F)** represent the same data after adjustment with the recruitment factor (RF). The fish length is given as fork length measured in centimeters.

et al. (2005), where movement was only modeled to happen once between the release and the recovery event. To reasonably bound the movement rates, an uninformative prior on movement rates was specified such that if tag–recapture data were absent or uninformative, the expected movement rate between areas would be equivalent to random diffusion.

Seasonal exploitation rates for each area were calculated by dividing the total tons caught by the commercial fishery during August through October by the biomass at each study site, which was estimated with tagging data for the respective year of the study. The data from which the catch statistics were derived is from the Alaska Fisheries Science Center's North Pacific observer database.

Bayesian posterior estimates of parameter values and their uncertainty were calculated using the AD Model Builder Markov chain–Monte Carlo (MCMC) algorithm and results were compared with estimates of the mode of the posterior distribution. Monte Carlo chains of 1 million in length were run. It was determined that the MCMC algorithms provided more reliable estimates of the parameter central tendencies and uncertainties than the estimates of the mode of the posterior distribution. Therefore, results presented here were derived using the MCMC algorithms and quantiles (5th, median, and 95th) of the parameter distributions.

To determine if estimates of biomass from the tagging model were within reason, we compared the NMFS groundfish survey biomass estimates with the biomass estimates from this study. Biannually NMFS conducts groundfish trawl surveys in the Aleutian Islands. Survey results are summarized by the Aleutian Island management areas and published in the Atka Mackerel stock assessment (Lowe et al. 2009). The highly aggregated and patchy distribution of Atka Mackerel results in a high uncertainty associated with the survey biomass estimates. The stock assessment uses a three-survey average to calculate the percent distribution of biomass for each NMFS statistical area. We used this 3-year average (2002–2006) as an estimate for biomass in the NMFS statistical areas of the eastern and western Aleutian Islands when comparing them to the results of our tagging study.

RESULTS

Based on our examination of large-scale movement (> 20 nmi) within the time frame of this study (≤ 1 year), only 2.3% of all the tags recovered were from fish that had moved outside of their study area (e.g., from Seguam Pass to Tanaga Pass). Specifically, the percentage of tags recovered outside their respective study areas were 1.7% in Seguam Pass, 1.3% in Tanaga Pass, 1.8% in Amchitka Island, and 7.9% in Kiska Island. The complexities of release and recovery locations of this large-scale movement were such that a more quantitative estimation of movement rate was beyond the scope of this study. Given the high fidelity of the Atka Mackerel population to their local areas (< 20 nmi), it was assumed that large-scale movement was negligible for the purposes of this study.

Tagging Model Parameters

The percentages of fish released with double tags and the number of recoveries are summarized in Table 2. Data for both the Seguam and the Tanaga study sites were combined into one estimate that was used for both sites since the number of double-tagged fish recovered at Tanaga Pass was very low. The model estimates of tag loss rates are 0.098 at Seguam and Tanaga, 0.041 and 0.045 at Amchitka, and 0.066 at Kiska (Table 3). The tagging survival rate was estimated for all study sites and years combined, and of the 573 fish included in the tag survival rate experiment, 18 fish died (Table 3).

The tag reporting rate was estimated for the fishery and the charter vessels separately. The parameter estimates and the 5th and 95th percentiles are presented in Table 3. Reporting rates for the fishery were much lower than the ones for the tag recovery charter vessels and ranged from 0.595 at Kiska to 0.804 at Amchitka North, indicating a high variability among areas and years. The tag reporting rate for the charter vessel was combined for the year 2002 for the Seguam and Tanaga areas to increase the sample size at Tanaga Pass since the commercial fishing effort there was low. The charter tag reporting rate was consistently high, ranging from 0.914 at Amchitka South to 0.948 at Amchitka North.

TABLE 2. Data for estimation of tag loss rate. The percent of double-tagged fish is for inside and outside the TEZs combined. The tag recoveries are from all recovery events in each area, combined. The data for Seguam Pass, Tanaga East, and Tanaga West were pooled.

Area	Percent double-tagged fish	Recovered with both tags	Recovered with one tag
Seguam Pass, Tanaga E, Tanaga W	0.249	41	10
Amchitka S	0.200	180	18
Amchitka N	0.245	199	18
Kiska Island	0.240	33	5

TABLE 3. Markov chain–Monte Carlo model outputs and the 5th and 95th percentiles of the posterior distribution for tagging survival, tag loss, fishery tag reporting rates, and charter tag reporting rates.

Study site (year)	Estimate	5th percentile	95th percentile
Tagging survival rate			
All study sites	0.970	0.959	0.986
Tag loss rate			
Seguam (2002)	0.098	0.040	0.156
Tanaga E (2002)	0.098	0.040	0.156
Tanaga W (2002)	0.098	0.040	0.156
Amchitka S (2003)	0.045	0.025	0.066
Amchitka N (2003)	0.041	0.023	0.060
Kiska (2006)	0.066	0.010	0.122
Fishery tag reporting rate			
Seguam (2002)	0.623	0.588	0.657
Tanaga E (2002)	0.621	0.587	0.657
Tanaga W (2002)			
Amchitka S (2003)	0.745	0.727	0.762
Amchitka N (2003)	0.804	0.794	0.814
Kiska (2006)	0.595	0.559	0.630
Charter tag reporting rate			
Seguam (2002)	0.932	0.918	0.946
Tanaga E (2002)	0.932	0.918	0.946
Tanaga W (2002)	0.932	0.918	0.946
Amchitka S (2003)	0.914	0.901	0.927
Amchitka N (2003)	0.948	0.938	0.958
Kiska (2006)	0.946	0.929	0.963

Model Estimates

Results from the model estimates for population abundance, biomass, and movement rates are presented in Table 4. For Tanaga West and Amchitka North, the model was not able to estimate movement rates without completely emptying out one area into the other, which we knew was unreasonable. Therefore we did not include the movement rates in the results. We estimated population size as a simple Peterson model and combined the areas inside and outside the TEZ into one population. The model results from 2002 and 2003 represent population sizes at the time of tagging before the recruitment event took place and are therefore conservative. Biomass estimates were highest at Seguam Pass and lowest at the south end of Amchitka Island (Figure 4; Table 4). In all areas, biomass inside the TEZs was similar to or greater than biomass outside the TEZs (Figure 4; Table 4). In all areas, movement rates from inside the TEZ to outside the TEZ were similar to or less than the movement rates from outside to inside, with the exception of Amchitka South, where movement rates were estimated to be greater from inside to outside. In addition, movement rates were greater overall at Amchitka Island than at any of the other study areas (Figure 5; Table 4).

Exploitation rates differed among study sites, ranging from 2% or less at Seguam Pass and Tanaga East to almost 60% at Amchitka South (Figure 6). Exploitation rates were calculated for the area outside the TEZ, assuming that the fishery did not affect fish inside the TEZ. Exploitation rates were also calculated for the area inside and outside the TEZ combined, assuming that both areas might be affected by fishing. Results are summarized in Figure 6 and Table 5.

The biomass estimates from the NMFS groundfish survey in both the eastern and central Aleutian Island management areas were compared to the biomass estimates derived in this study (Figure 7). The groundfish survey biomass estimate for the eastern Aleutian Island management area was somewhat lower at 261,688 metric tons than the tagging estimate of 334,917 metric tons from this study, which represents the Seguam Pass area. The groundfish biomass estimate of the central Aleutian Island management area (291,620 metric tons) was similar to the tagging biomass estimate (282,871 metric tons), which represents the combined biomass of the Tanaga, Amchitka, and Kiska study sites.

DISCUSSION

The abundance and movement results suggested that Atka Mackerel biomass varies greatly among the study sites. Seguam Pass had the largest estimated biomass and is known to have very dense aggregations in the center of the

TABLE 4. Model results for abundance (millions of fish), biomass (thousands of metric tons), and daily movement probability and the 5th and 95th percentiles of the posterior distribution for Atka Mackerel inside and outside the TEZs in the four different study areas.

	Inside TEZ (area 1)			Outside TEZ (area 2)			
Study area (year)	Model result	5th percentile	95th percentile	Model result	5th percentile	95th percentile	Total
			Abundance				
Seguam (2002)	319.04	175.60	545.58	71.29	30.79	146.34	390.34
Tanaga E (2002)	77.45	16.08	252.89	37.09	20.18	67.63	114.55
Tanaga W (2002)	23.96	2.42	64.13	24.63	20.18	64.51	48.59
Amchitka S (2003)	14.55	1.98	31.84	11.38	1.40	29.89	25.93
Amchitka N (2003)	20.97	2.34	46.57	20.11	2.11	45.31	41.09
Kiska (2006)	97.96	12.15	255.96	95.25	31.18	171.73	193.20
			Biomass				
Seguam (2002)	273.45	150.77	468.98	61.47	26.51	125.70	334.92
Tanaga E (2002)	56.23	11.85	180.54	26.91	14.63	49.34	83.13
Tanaga W (2002)	17.48	1.76	46.81	17.86	1.80	46.73	35.33
Amchitka S (2003)	10.10	1.38	22.02	7.89	0.98	20.95	17.99
Amchitka N (2003)	14.69	1.62	32.56	14.14	1.47	31.96	28.83
Kiska (2006)	59.66	7.33	157.71	57.92	18.96	105.86	117.58
			Daily movement probability				
Seguam (2002)	0.0018	0.0012	0.0028	0.0112	0.0071	0.0164	
Tanaga E (2002)	4.1×10^{-5}	3.8×10^{-5}	0.0001	0.0151	0.0125	0.0283	
Tanaga W (2002)							
Amchitka S (2003)	0.0156	0.0097	0.0087	0.0086	0.0075	0.0392	
Amchitka N (2003)							
Kiska (2006)	0.0019	0.0013	0.0021	0.0191	0.0120	0.0199	

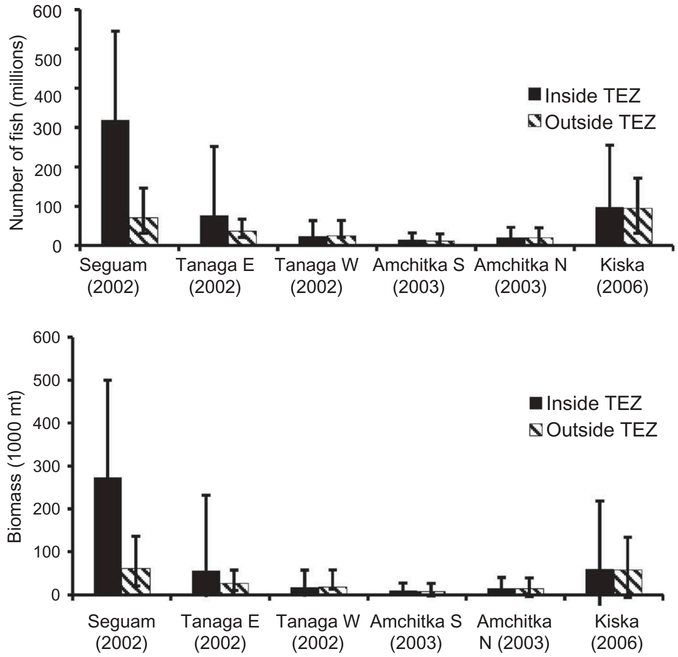

FIGURE 4. Model estimates of Atka Mackerel abundance (millions) and biomass (thousands of metric tons [mt]) inside and outside the TEZs in each study area. The error bars present the 5th and 95th percentiles of the posterior distribution.

pass. Alternatively, the Tanaga and Amchitka Island areas support smaller aggregations with biomass estimates on an order of magnitude less than those at Seguam Pass. Seguam Pass also encompasses the largest geographical area of all the study sites. The TEZ at Seguam Pass is 20 nmi in diameter, whereas it is only 10 nmi for all the other areas.

The high abundance estimates and low movement rates across the TEZs at Seguam Pass, Tanaga Island, and Kiska

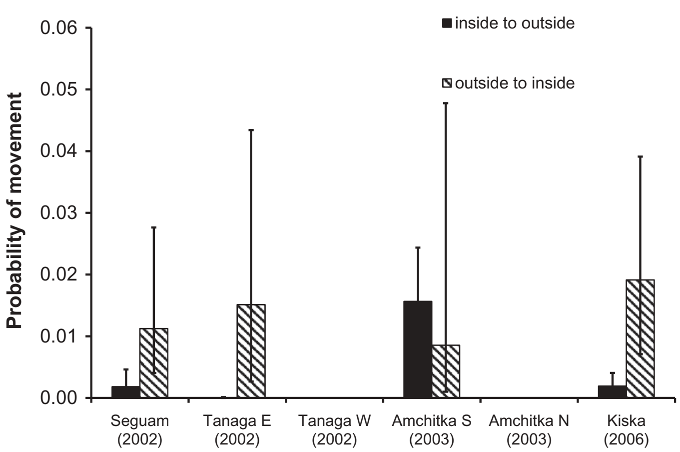

FIGURE 5. Probability of movement from inside to outside the TEZ (black bars) and from outside to inside the TEZ (hashed bars) for each study area. The error bars present the 5th and 95th percentiles of the posterior distribution.

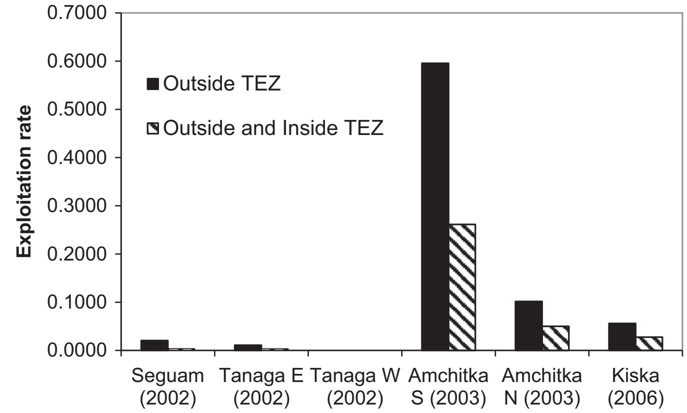

FIGURE 6. Local exploitation rates for each of the study areas. The exploitation rates for the areas outside the TEZ are depicted in black, and the exploitation rates for the areas inside and outside the TEZ combined are depicted in hashed lines.

Island suggest that TEZs may be effective at preserving local foraging areas for Steller sea lions. In contrast, the TEZ at Amchitka South, where estimated biomass is low and movement from inside to outside the TEZ is high, may be less effective at preserving prey inside the TEZ. These differences in movement relative to TEZs may be due to differences in the distribution of Atka Mackerel habitat. For example, the TEZ boundaries at Seguam Pass and Tanaga Island appear to coincide with natural Atka Mackerel habitat boundaries (by chance it follows depth contours). In contrast, the TEZ at Amchitka Island appears to bisect Atka Mackerel habitat across the depth contours. This might explain why movement rates relative to TEZ boundaries at Amchitka Island were higher than at Seguam Pass and Tanaga Island.

Atka Mackerel are an ideal species for this type of tagging experiment. Even though their population is spread out along the entire Aleutian Islands chain, subpopulation centers of

TABLE 5. Fisheries catch and calculated exploitation rate estimates for areas outside the TEZ and for areas inside and outside the TEZ combined for Atka Mackerel in the four different study areas.

Study area (year)	Outside TEZ: Fisheries catch (metric tons)	Outside TEZ: Exploitation rate	Inside and outside TEZ exploitation rate
Seguam (2002)	1,263	0.0206	0.0038
Tanaga E (2002)	299	0.0111	0.0036
Tanaga W (2002)	0		
Amchitka S (2003)	4,700	0.5956	0.2613
Amchitka N (2003)	1,439	0.1018	0.0499
Kiska (2006)	3,249	0.0561	0.0276

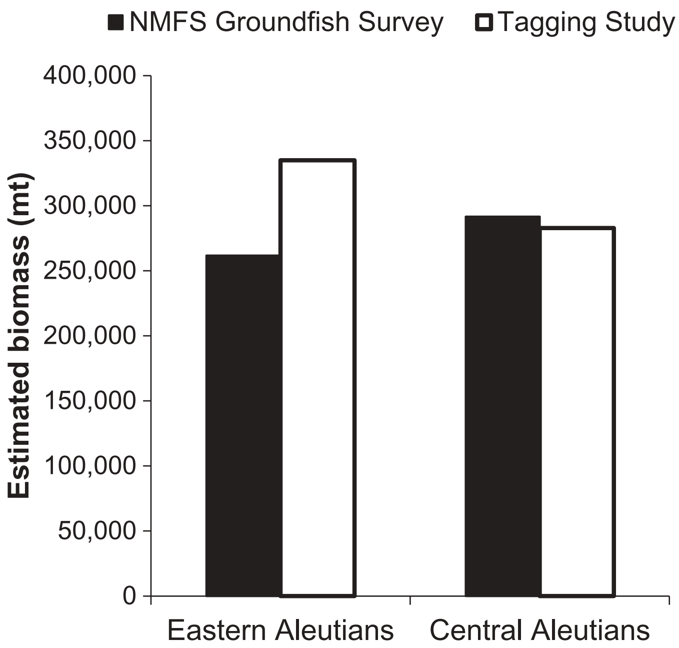

FIGURE 7. Biomass estimates of the National Marine Fisheries Service (NMFS) groundfish survey (averaged by area over the years 2002–2006) and the current tagging study. The eastern Aleutian Islands survey area encompasses the tagging study area of Seguam Pass. The central Aleutian Islands survey area encompasses the tagging study areas of Tanaga, Amchitka, and Kiska islands; mt = metric tons.

abundance can be found near or in island passes and they seem to have discrete boundaries as shown by the low occurrence of large-scale movement (< 20 nmi) by the tagged fish in this study. Atka Mackerel survive the tagging and handling procedures extremely well. The effects of inserting the tags into the fish were negligible, which is consistent with those results published in McDermott et al. (2005). Survival after tagging was estimated at 97% and is most likely attributed to the fact that Atka Mackerel do not have a swim bladder, do not experience barotrauma during capture, and do not show any significant scale loss. In addition, the small catch sizes of Atka Mackerel, the immediate transfer to the live tanks, and the gentle handling of the fish during the tagging procedures seemed to ensure good survival. The participation of the fishing fleet was an integral part of this study and the NMFS North Pacific observer program enabled us to conduct ongoing tag-reporting experiments, which enabled good participation in tag returns by the commercial fishing fleet. Chartering a commercial fishing vessel for the recovery of tagged Atka Mackerel resulted in good cooperation between the industry and the NMFS, which proved to be very successful for this study. However, the fishing fleet does not always fish in the same areas from year to year during our study time frame and there was no commercial fishing at the Tanaga West study site; therefore, abundance results were associated with large variances and movement could not be estimated reliably. At all other study sites, we could estimate local abundances, biomass, and movement.

The tag loss rate for Atka Mackerel varied by year and area, indicating the importance of consistent monitoring throughout the experiment. In areas with lower recoveries of tagged fish (Seguam Pass and Tanaga Island), the uncertainty of tag loss was high and future studies should consider releasing a higher percentage of double-tagged fish. The large differences in tag reporting by year and study site in the commercial fishery showed the importance of monitoring tag reporting throughout the recovery period. Those differences are likely due to changes in crew participation in this project rather than changes in the probability of tag detection aboard the vessel. This is supported by the high reporting rate from the tag recovery charter vessel, which processed the fish in a similar manner as the commercial vessels and therefore had a similar probability of tag detection. However, crew participation during the charter was greatly increased by the presence of scientists on the vessel, which encouraged crew members to actively participate in the experiment.

It should be noted that the local population estimates from this study represent fish aggregations in areas that are accessible to commercial trawl gear. Each of the study sites, both inside and outside the TEZs, has untrawlable habitat, especially in waters shallower than 70 m. Atka Mackerel spawning locations have been found in areas unavailable to trawl gear by using underwater cameras (Lauth et al. 2007), but it is not known what percentage of the population occupies those areas. Therefore, population estimates derived in this study may be conservative, even though the biomass estimates from tagging are within the range of the NMFS groundfish survey biomass estimates. Since both estimates are derived independently and with different estimation methods, their agreement seems to validate the general trend of population abundance presented here. The biomass estimate at Seguam Pass from the tagging study is somewhat higher than the one from the groundfish survey, which is likely due to the commercial trawl locations being located outside the central pass area, where Atka Mackerel occur in very dense aggregations. Seguam Pass is subject to high currents and displays steep bottom contours that limit the area that the NMFS groundfish survey can sample. Since our tagging study uses trawl hauls simply as a tool to recover tagged and untagged Atka Mackerel, standardized trawling procedures were not necessary. Based on our biomass estimates at Seguam Pass, it is possible that the NMFS groundfish survey biomass estimate is conservative for the eastern Aleutian Island management area.

The local exploitation rates estimated in this analysis were low for Seguam Pass, Tanaga Island, and Kiska Island (1%, 3%, and 5%, respectively) indicating that there is little to no concern for localized depletion of prey for Steller sea lions. However, lower biomass estimates and higher exploitation rates at Amchitka Island (> 50%) make this area susceptible to localized depletion outside the TEZ during the fishery. The

TEZ at Amchitka Island is 10 nmi compared with 20 nmi at Seguam Pass. The areas outside the TEZ at Tanaga and Kiska islands have limited trawlable habitat. Since the fish at Amchitka Island seemed to move freely between inside and outside the TEZ, fish may be vulnerable to the fishery outside the TEZ at both Amchitka North and Amchitka South. The exploitation rate for both inside and outside the TEZ combined at Amchitka South was estimated at 29%. Exploitation rates for the entire stock of Atka Mackerel at a projected fishing mortality of $F_{40\%}$ during the years 2002–2006 ranged from 10% in 2002 to 14% in 2010 (Lowe et al. 2009). Therefore, our estimates of exploitation rates at the Seguam Pass, Tanaga Island, and Kiska Island study sites are below the average for the entire stock, whereas the exploitation rate at the Amchitka Island study site seems unusually high. This could affect Steller sea lion foraging success if the fish inside the TEZ are also affected by this high exploitation rate. Movement at Amchitka between the north and south areas is high, indicating that the south end of Amchitka Island has a greater potential for a small-scale fishing effect on the foraging success of Steller sea lions.

In addition to preserving prey abundance inside the TEZs, these areas also serve as de facto marine protected areas for spawning (Cooper and McDermott 2011) and feeding (Rand and Lowe 2011) Atka Mackerel. The nature of the Atka Mackerel's complex spawning and nest-guarding behavior indicates that the protection of their spawning grounds is essential for the reproductive success of this species. During 2 years of this study (2002 and 2003), the recruitment of 3-year-old fish was at an all-time high (Lowe et al. 2009), with the 1999 and 2000 year-classes above average. This was not only observed in our study sites but was experienced as an Aleutian-wide event (Lowe et al. 2009). It can be hypothesized that the establishment of the Aleutian Island TEZs in 1992 has ensured high Atka Mackerel reproductive success despite a large commercial fishery operating at often high exploitation rates on a local scale (10–20 nmi). Large recruitment events are often linked to many diverse factors, such as favorable environmental conditions, larval hatching time, and predator avoidance (Duffy-Anderson et al. 2005). However, those factors can only contribute to high recruitment success after the larvae are successfully hatched. In nest-guarding species such as Atka Mackerel, it can be argued that ensuring low disturbance to the breeding colonies by establishing TEZs might enable the occurrence of large year-classes when environmental conditions are favorable.

In addition, it can be hypothesized that the Atka Mackerel nesting sites may be important for Steller sea lion foraging. As previous studies have shown (Sigler et al. 2009), Steller sea lions shift their diet composition in response to changes in prey availability, mothers and young often preferentially forage in areas close to the rookeries, and Atka Mackerel is a large portion of their diet during their breeding season (Sinclair et al. 2013). Nesting areas of Atka Mackerel are usually located in shallower water closer to the rookeries and might be easier prey than the deeper feeding aggregations of females and nonguarding males. Male Atka Mackerel can guard their nests for 3 months or more (Lauth et al. 2007). Protecting Atka Mackerel spawning grounds may also protect preferred Steller Sea lion foraging areas within local Atka Mackerel aggregations due to spawning and feeding activities in these areas (Rand and Lowe 2011).

In general, the results from this study indicate that Atka Mackerel abundance and movement and fishing patterns are variable throughout the Aleutian Islands and exploitation rates can be high on a small spatial scale (10–20 nmi). It is therefore important to understand fishery dynamics at this scale to assess the variable effect of fishing on Atka Mackerel subpopulations. This tagging experiment resulted in local (10–20 nmi) abundance estimates that were incorporated into a food web model to examine Atka Mackerel production and prey consumption by Steller sea lions with respect to these TEZs (Lowe et al. 2009). The food webs were based on the feeding habits of Steller sea lions and five fish species (Pacific Cod, Arrowtooth Flounder, Walleye Pollock *Gadus chalcogrammus*, Pacific Halibut *Hippoglossus stenolepis*, and skates [family Rajidae]) with similar prey items to those of Steller sea lions in order to quantify prey overlap and availability (Ortiz and Logerwell 2015). The ultimate goal of these studies was to evaluate the efficacy of TEZs at preserving prey abundance for Steller sea lions. Results from both of these studies suggest that understanding prey, predator, and fishery dynamics is essential for incorporating successful management tools. The complexity of the Aleutian Island habitat, such as differences in currents, productivity, prey abundance, sea lion rookery locations, weather microclimates, and fishery interactions, all should be taken into account when designing TEZs. The challenge for Steller sea lion conservation in the future will be to apply knowledge from local, small-scale studies to a large-scale recovery plan.

Management Implications

Spatial management, such as the establishing of TEZs, is a tool that can be used to control fishing effort on a small spatial scale. In this case, TEZs were used to preserve prey abundance and foraging grounds for an endangered species while allowing fishing in areas nearby. To address the potential for competition between the fisheries and Steller sea lion foraging needs, the size and location of the TEZs were determined by the location of the predator (Steller sea lion) rookeries and haulouts rather than fish distribution or associated habitat qualities. This approach works well if the fish are present in large numbers in the areas to be protected and do not move freely across the boundaries into the areas open to fishing. In the case of Atka Mackerel and Steller sea lions, this management approach worked well since Atka Mackerel do not, in general, migrate large distances (> 50 km) and tend to stay in a small "home range" once settled as adults. However, it was shown that exploitation rates were high at one of the locations where the Atka Mackerel population inside the TEZ was low, the fishing effort outside the TEZ was high, and the fish moved freely across the management boundary. This result suggests that local fish abundance, fish movement across management boundaries, and local fishing effort need to be considered when using area closures to address management issues.

ACKNOWLEDGMENTS

This study has been a multiyear effort and required a tremendous amount of field support from many people. We would like to thank all the scientists involved in the tag–release and recovery efforts; special thanks go to Libby Logerwell, Peter Munro, Daniel Cooper, Robert Lauth, and Sandi Neidetcher. We would like to thank Libby Logerwell and Sandra Lowe for critical review of the manuscript. The authors are very thankful to the captain and crew of the charter vessels *Pacific Explorer* and *Seafisher*. Special thanks go to Phil Dang for his collaborative efforts throughout all the recovery cruises and Tadichi Tamura for sharing his knowledge about Atka Mackerel fishing with us. We would like to thank the commercial Atka Mackerel fleet and all the NMFS observers that contributed to the return of the tagged fish. The authors would like to thank the North Pacific Fisheries Foundation for funding part of this study. The use of trade names does not imply endorsement by the NMFS.

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Appendix: Model Description

Data and Model Parameters

Data and model parameters are defined in Table A.1. A specific tag group T^r is defined as a group of fish tagged in the geographic area r.

Population Size and Movement

This model tracks population size and movement over the time periods in which fish were recovered. Tagged fish are assumed to be released once at the beginning of the study. The tagged fish are assumed to have mixed randomly with the nontagged population. All recovery effort is assumed to occur at the end of each time period k. Fish movement is modeled as a daily process. That is, each day some fraction of fish in area 1 move to area 2 and some fraction of fish in area 2 move to area 1. This parameterization of movement captures milling behavior more closely than the previous approach described in McDermott et al. 2005.

Population size was described using the following equations:

$$N_{i,0} = N_i \text{ for } t = 0 \tag{1}$$

TABLE A.1. Data symbols and their definition.

Symbol	Definition
	Data
T^r	Number of fish tagged and released in area r
$R^r_{i,k}$	Number of tags released in area r and recovered in area i at time period k
$C_{i,k}$	Number of fish that are examined for tags in area i at the end of time period k
$H_{i,k,v}$	Number of dummy tags reported per area i, time period k, and observation v
$\varepsilon_{i,v,k}$	Number of dummy tags released per area i, observation v, and time period k
$V_{i,k}$	Number of dummy tag–release observations in area i during time period k
D	Number of fish that died in mortality experiment
Q	Number of fish that lived in mortality experiment
F	Number of double-tagged fish recovered with one tag
G	Number of double-tagged fish recovered with both tags
x_i	Proportion of double-tagged fish among single- and double-tagged fish released in area i
d_k	Number of days fish are susceptible to movement for time period k
i	Index for area
t	Time index for daily movement (days since tagging; t = 0 is time of tagging)
k	Index for time periods
K	Number of time periods
A	Number of areas
ω	Proportion of large fish in the population that do not experience influx (recruitment) of fish in their size-class
	Fundamental parameters
N_i	Estimated initial population size at time of tagging in area i
$\theta_{j,i}$	Estimated instantaneous daily movement rate parameter for fish moving from area j to area i
$o_{i,k}$	Estimated tag reporting rate for time period k in area i
s	Estimated rate of initial survival from tagging
l	Estimated tag loss rate
	Calculated parameters
$\hat{T}^r_{i,t}$	Estimated size of tagged population in area i at time t that were released in area r
$N_{i,t}$	Estimated population size in area i at time t
B_i	Estimated biomass in area i in metric tons
w_i	Estimated average weight per fish in area i
$p_{j,i}$	Daily movement probability from area j to area i
$\alpha_{j,i,\Delta t}$	Probability of movement from area j to area i after time period Δt
$\rho_{i,t}$	Estimated recruitment factor in area i at time t
$u_{i,k}$	Estimated harvest rate in area i at time period k
$\hat{R}^r_{i,t}$	Predicted number of tags released in area r and recovered in area i at time t
y_i	Probability that a fish tagged in area i loses all its tags

$$N_{i,t} = \sum_{j=1}^{j=A} e^{-m} N_{j,t-1} p_{j,i} \text{ for } t > 0,\ t \neq d_k + 1 \quad (2)$$

$$N_{i,t} = \left(1 - u_{i,k}\right) \sum_{j=1}^{j=A} e^{-m} N_{j,t-1} p_{j,i} \text{ for } t = d_k + 1 \quad (3)$$

The daily contribution to the probability of staying in one area is modeled as follows:

$$p_{j,i} = e^{-\theta_{j,i}} \text{ for } j = i \quad (4)$$

The daily contribution to cumulative net movement is modeled as follows:

$$p_{j,i} = 1 - e^{-\theta_{j,i}} \quad \text{for } j \neq i \quad (5)$$

Recruitment factor and harvest rate.—The recruitment factor (ρ) was calculated by dividing the population into two parts; these parts were separated by the two modes visible in the length frequency distribution (Figure 3A–D): older (larger) fish and younger (smaller) fish. It was assumed that the older (larger) proportion of fish (ω) did not experience an influx of fish of their size-class and was defined as larger than 40 cm at Seguam Pass and as larger than 38 cm at the Tanaga and Amchitka study sites. We assumed that the abundance of large fish remained constant before and after recruitment and only affected the proportion of the population of the smaller younger fish. We calculated the older (larger) population of fish ω from the proportions at length (Figure 3A–D) for all study sites and subareas before the recruitment event (t) and after the recruitment event ($t + 1$).

The recruitment factor (ρ) in area i at time period t is modeled as follows:

$$\rho_{t+1} = \frac{\omega_t}{\omega_{t+1}}$$

The harvest rate $u_{i,k}$ in area i at period k was adjusted for recruitment with the recruitment factor and is modeled as follows:

$$u_{i,k} = \frac{C_{i,k}}{\rho N_{i,t}} \text{ for } t = d_k \quad (6)$$

Tagged population.—It was assumed that tag loss and mortality due to handling and tagging was instantaneous and occurred shortly after tagging, based on observations during the mortality study in 1999. The probability of not at least retaining one tag (y_i) was calculated as shown for the Peterson model (equation 7). The tagged population is modeled in the following way:

$$\hat{T}^r_{i,t} = T^r(1 - y_i)s \qquad \text{for } t = 0 \text{ and r} = \text{i} \quad (7)$$

$$\hat{T}^r_{i,t} = \sum_{j=1}^{j=A} e^{-m} T^r_{j,t-1} p_{i,j} \qquad \text{for } t > 0 \text{ and } t \neq d_k + 1 \quad (8)$$

$$\hat{T}^r_{i,t} = \left(1 - u_{i,k}\right) \sum_{j=1}^{j=A} e^{-m} T^r_{j,t-1}\, p_{j,i} \quad \text{for } t > 1 \text{ and } t = d_k + 1 \quad (9)$$

The predicted number of tags that are recovered and reported can then be expressed as follows:

$$\hat{R}^r_{i,t} = \left(\sum_{j=1}^{j=A} e^{-m} T^r_{j,t-1} p_{j,i} \right) u_{i,k} o_{i,k} \quad (10)$$

Likelihoods.—Maximum likelihood was used to estimate the parameters of this model. Maximum likelihood has become the standard technique for parameter estimation in fisheries literature when using nonlinear models (Maunder 1998). Analysis for this model consists of several components that are combined in a joint likelihood and nonlinear function minimization procedure (AD Model Builder, Fournier et al. 2012).

Tagging likelihood.—Because tag recoveries can be described as rare events, the Poisson likelihood gives similar results to a multinomial likelihood (Hilborn 1990). The tagging likelihood (L_T) is then expressed as follows:

$$L_T \text{ (parameters|tag data)} = \prod_{i=1}^{i=A} \prod_{k=1}^{k=K} \frac{e^{-\hat{R}^r_{i,d_k}}\ \hat{R}^{r\ \ R^r_{i,d_k}}_{i,d_k}}{R^r_{i,d_k}!} \quad (11)$$

Recruitment factor likelihood.—The recruitment factor likelihood was expressed as follows:

$$L_\rho(\text{parameters|data}) = 0.5 \sum_t \left[\frac{ln \rho_t / \hat{\rho}_t}{\sigma} \right]^2 \quad (12)$$

where $\hat{\rho}_t$ is the model estimate of the recruitment factor at time t, and a value of 0.2 is assumed for σ.

Tagging survival rate likelihood.—It was shown in previous studies (McDermott et al. 2005) that tagging did not affect fish survival separately from handling. Therefore, the data from the tag mortality study were pooled with 3 out of 80 fish dying. Survival rate is modeled as a binomial likelihood with fish either surviving or dying from handling procedures. The initial tag survival rate likelihood (L_s) is then expressed as follows:

$$L_s = \text{(parameters|data)} = s^Q \quad (1 - s)^D, \quad (13)$$

where Q = the number of fish that lived in the mortality experiment and D = the number of fish that died in the mortality experiment.

Tag loss rate likelihood.—In 2000, about 20% of all fish were doubly tagged. Tag loss rate can be estimated using recoveries from the doubly tagged fish. Tag loss rate likelihood (L_l) is then expressed as follows:

$$L_t(\text{parameter}|\text{data}) = (2l\ (1-l))^F\ ((1-l)(1-l)^G. \quad (14)$$

Tag reporting rate likelihood.—The reporting rates for each commercial fishing vessel were treated as individual observations. For each commercial fishing vessel, the total number of test fish tagged, recovered, and reported was compiled and treated as individual observations. Combined data from all fishing vessels were then used to estimate reporting rates on commercial vessels. The reporting rate for the charter vessel was calculated separately. Since the charter vessel recovered most tags in the closed area (area 1) and fishing vessels recovered tags in the open area (area 2) only, reporting rates by area and time stratum were calculated separately. Tag reporting rate likelihood (L_o) is then expressed as follows:

$$L_o(\text{parameters}|\text{data}) = \prod_{i=1}^{i=A}\prod_{k=1}^{k=K}\prod_{v=1}^{v=V_{i,k}} o_{i,k}{}^{H_{i,k,v}}(1-o_{i,k})^{(\varepsilon_{i,k,v}-H_{i,k,v})} \quad (15)$$

Estimation.—The parameters of the model are estimated using an iterative minimization routine (AD Model Builder, Fournier et al. 2012) to minimize the total negative log likelihood:

$$-\ln L_{tot} = -\ln L_T - \ln L_\rho - \ln L_s - lnL_i - \ln L_o \quad (16)$$

Calculated parameters.—The numbers of fish (population size) were converted to weight (biomass) using the average weight of individual Atka Mackerel at the time of recovery and multiplying it by the number of fish estimated in each area. All hauls during recovery event 2 were used to calculate average fish weight in area 1, and all hauls during recovery events 1 and 3 were used to calculate average fish weight in area 2. Average fish weight (w_i) was 1.13 kg (SD = 0.16) in area 1 and 1.02 kg (SD = 0.04) in area 2. The biomass estimate (t) and its variance were calculated with the following formula, assuming population sizeN_i and average fish weight w_i are independent (Seber 1982):

$$B_i = N_i\ \ w_i, \quad (17)$$

$$\text{var}\ (B_i) = N_i^2\ \text{var}(w_i) + (w_i)^2\ \text{var}(N_i) - \text{var}(N_i)\ \text{var}(w_i) \quad (18)$$

The instantaneous movement rate parameters were used to calculate movement probabilities over a period of time. The time elapsed in number of days since tagging is represented by Δt, and the movement probabilities for the recovery events are then calculated by Δt being equal to d_k.

$$\alpha_{j,i,\Delta t} = 1 - e^{\Delta t\,\theta_{j,i}} \quad (19)$$

Variance was calculated using the delta method (Seber 1982):

$$\text{var}(\alpha_{j,i,\Delta t}) = \text{var}(\theta_{j,i})\ \ (\Delta t^2 e^{-2\,\Delta t\,\theta_{j,i}}) \quad (20)$$

APPENDIX REFERENCES

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