

Seasonal, Small-Scale Distribution of Atka Mackerel in the Aleutian Islands, Alaska, with Respect to Reproduction

Authors: Cooper, Daniel, and McDermott, Susanne

Source: Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science, 3(1) : 10-20

Published By: American Fisheries Society

URL: <https://doi.org/10.1080/19425120.2011.558439>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

SPECIAL SECTION: ATKA MACKEREL

Seasonal, Small-Scale Distribution of Atka Mackerel in the Aleutian Islands, Alaska, with Respect to Reproduction

Daniel Cooper* and Susanne McDermott

National Marine Fisheries Service, Alaska Fisheries Science Center,
7600 Sand Point Way Northeast, Seattle, Washington 98115, USA

Abstract

We investigated the spatial distribution of Atka mackerel *Pleurogrammus monopterygius* with respect to maturity stage at Seguam Pass in the Aleutian Islands as well as their spawning locations within trawlable areas at three small-scale (10–20-nautical mile or 18.5–37.0-km) sites. Histological methods were used to determine maturity stages, and male maturity stages are described for the first time. Spawning areas were identified by catch per unit effort of demersal egg masses. At Seguam Pass, spawning was concentrated in the area adjacent to the east side of Amlia Island and between Amlia and Seguam islands. The observed spatial segregation of Atka mackerel by sex and maturity stage appears to interact with the boundaries of the trawl exclusion zone (TEZ) at Seguam Pass. During spawning, mature fish aggregate inside the closed area and immature fish and nonreproductively active mature males aggregate outside the TEZ in the area open to fishing. This increased the commercial catch selectivity of nonreproductively active males and immature fish during the September fishery. The spawning areas observed at Seguam and Tanaga passes and near Amchitka Island were within TEZs, which may serve as de facto marine protected areas for spawning Atka mackerel.

Many marine fish species use only a portion of their range for spawning (Miller and Kendall 2009), and some species segregate spatially by reproductive stage or sex during spawning: Atlantic cod *Gadus morhua* (Morgan and Trippel 1996), plaice *Pleuronectes platessa* (Solmundsson et al. 2003), and Argentine hake *Merluccius hubbsi* (Pajaro et al. 2005). Spatial restrictions on commercial fishing can affect whether spawning fish are targeted and whether fishing impacts demersal spawning habitat.

Atka mackerel *Pleurogrammus monopterygius* have been observed in situ to segregate by size and sex at a very small (1–100-m) spatial scale during the spawning and nest-guarding season, males guarding demersal nesting territories and females schooling nearby and moving to these territories to deposit batches of demersal egg masses (Zolotov 1993; Lauth et al. 2007). At a larger scale (10–20 nautical miles), Fritz and Lowe (1998) observed partial segregation by sex and size at four Atka mackerel aggregations in the Aleutian Islands, Alaska, and con-

cluded that Atka mackerel have separate feeding and spawning areas. Fritz and Lowe (1998) noted a reduced percentage of Atka mackerel females in the commercial catch during the spawning period, which they attributed to higher fishery selectivity of nonreproducing males during the spawning season. Fritz and Lowe (1998) inferred spatial maturity patterns from fishery catch data; however, small-scale spatial patterns based on observed maturity stages have not been studied for Atka mackerel.

The histology of female maturity stages has been described for Atka mackerel (McDermott and Lowe 1997), but male maturity stages have not been examined and defined with histological methods.

Spatial and temporal harvest regulations attempt to limit possible localized depletion of Atka mackerel, which are a prey resource of Steller sea lions *Eumetopias jubatus*. Total allowable catch (TAC) is divided equally between a winter season beginning in January and a fall season beginning in September.

Subject editor: Guy Fleischer, National Marine Fisheries Service, Alaska Fisheries Science Center, Seattle

*Corresponding author: dan.cooper@noaa.gov

Received June 14, 2010; accepted November 1, 2010

The fall season occurs when Atka mackerel are spawning. Spatially, TAC is divided among three areas in the Aleutian Islands (North Pacific Fishery Management Council management areas 541, 542, and 543), and only 60% of the TAC may come from areas designated as Steller sea lion critical habitat. Trawl exclusion zones (TEZs) in radii of 10 or 20 nautical miles from sea lion rookeries prohibit all directed Atka mackerel fishing within a subset of Steller sea lion critical habitat. Because of the complex spatial and temporal restrictions on Atka mackerel commercial fishing, it is important to understand spatial and temporal segregation by sex, length, and reproductive stage for Atka mackerel and their potential effects on the fishery. In addition, it is important to identify Atka mackerel nesting habitat at the local scale of the commercial bottom trawl fishery to examine potential effects of fishing on the spawning grounds. The objectives of this study were to (1) describe male maturity stages using histology, (2) examine the small-scale spatial distribution of male and female Atka mackerel by reproductive stage before, during, and at the completion of the spawning season at Seguam Pass, and (3) examine the small-scale spatial distribution of Atka mackerel nesting habitat within three sites in the Aleutian Islands.

This study was done in conjunction with a study of the spatial and temporal feeding habits of Atka mackerel (Rand and Lowe 2011, this issue). Both studies incorporated the same individual fish specimens from Seguam Pass in 2002 into their analyses.

STUDY SITES

We examined three areas (Figure 1a) with dense Atka mackerel aggregations: Seguam Pass, Tanaga Pass, and the Amchitka Island area. Atka mackerel were collected during National Marine Fisheries Service (NMFS) tagging and tag recovery cruises. Hauls were conducted both inside and outside of TEZs in each area.

The Seguam Pass study area was further divided into four study strata (Figure 1b). Strata 1 and 2, which comprise the northwestern area of Seguam Pass, historically had Atka mackerel catches but are now inside the TEZ; these two strata were subdivided into areas of relatively high catch per unit of effort (CPUE; stratum 1) and lower CPUE (stratum 2) based on historical catches. Strata 3 and 4 cover the southeastern portion of the pass, both having historical Atka mackerel catches. Stratum 3 is located inside the TEZ, while stratum 4 is outside the TEZ in the area open to the fishery.

METHODS

Gonad collection methods.— Five males and five females were randomly sampled from each trawl haul during Atka mackerel tagging and tag recovery cruises in 2002, 2003, and 2004 (Table 1). Total weight (± 2 g) and fork length (± 1 cm) were recorded, and gonads were removed and preserved in a 10% solution of formalin in seawater buffered with sodium bicarbonate. To increase sample size for male gonads during the spawning

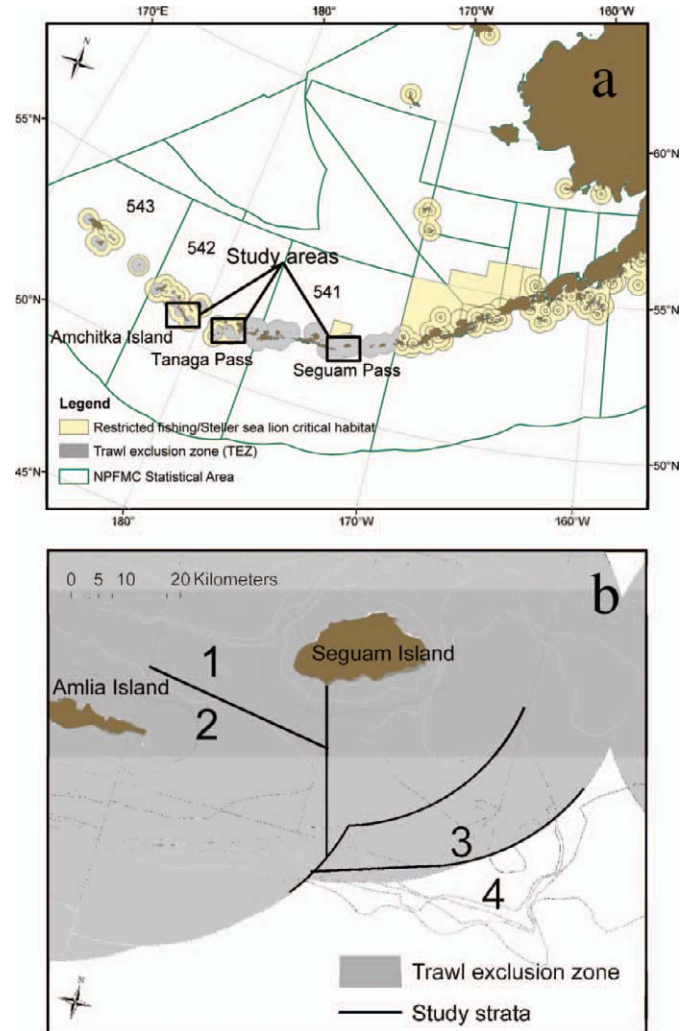


FIGURE 1. Maps showing (a) the locations of the three small-scale study sites where Atka mackerel were sampled and (b) the Seguam Pass study site divided into four study strata. North Pacific Fishery Management Council (NPFMC) statistical areas are delineated.

season, testes from 10 to 15 males per haul were collected aboard the *FT Seafisher* during commercial fishing operations in August 2005 in areas outside the TEZs at Seguam Pass, Tanaga Pass, Amchitka Island, and Petrel Bank (Table 1).

Length frequencies.— From each haul during the tag-release and tag recovery cruises, at least 150 randomly sampled Atka mackerel were measured (fork length; ± 1.0 cm) and their sex was determined. Additional length frequency data from seven commercial vessels during the 2002 September Atka mackerel fishery at Seguam Pass were obtained from the NMFS North Pacific Observer Program database. Female length at 50% maturity (35.9 cm) from Seguam Pass (McDermott and Lowe 1997) was used to calculate the percentage of females larger than size at 50% maturity within each stratum during each cruise at Seguam Pass.

TABLE 1. Number of Atka mackerel gonad samples collected in the Aleutian Islands, by sex, area, and date.

Area	June–July 2002		August 2002		October 2002		July 2003		October 2003		October 2004		August 2005	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Total
Seguam Pass	143	141	95	91	69	75	0	0	171	172	150	150	55	1,312
Tanaga Pass	63	64	0	0	152	149	0	0	0	0	65	66	75	634
Amchitka Island	0	0	0	0	0	0	98	104	205	207	121	119	25	879
Petral Bank	0	0	0	0	0	0	0	0	0	0	0	0	46	46
Total	206	205	95	91	221	224	98	104	376	379	336	335	201	2,871

Sex ratios.— Sex ratios during all the NMFS cruises were obtained from the 150 fish used in the length frequency analysis. During the August and October cruises, numbers of Atka mackerel in the catch were estimated for each haul and were used to weight the mean sex ratios for stratum 4 at Seguam Pass. Numbers of Atka mackerel per haul were not estimated during the cruise in June–July 2002, so the reported mean sex ratio for stratum 4 is unweighted for that cruise. Sex ratios of the commercial catch from 1998 to 2007 were collected by fishery observers and obtained from the NMFS North Pacific Observer Program database.

Gonad histological analysis.— After storage of specimens for 1–2 years in 10% formalin, samples were soaked in water for a minimum of 4 h before further handling. Gonads were blotted dry and weighed (± 0.0001 g). Gonad cross sections were embedded in paraffin, sectioned at 4 μ m, mounted on slides, and stained with hematoxylin and eosin (McDermott and Lowe 1997).

Ovary cross sections were examined at 40 \times and 100 \times magnifications. Presence of all oocyte stages, postovulatory follicles, and atretic yolked and hydrated oocytes (McDermott and Lowe 1997) were recorded. Maturity stages were assigned according to McDermott and Lowe (1997). Females were divided into four maturity stage categories for mapping: (1) immature, (2) imma-

ture or early developing, (3) developing through spawning, and (4) spent. The immature or developing group was created because it was not possible to differentiate all immature or early developing females collected during the summer.

Testes were staged using the five-stage classification system developed by Grier and Taylor (1998) for the common snook *Centropomus undecimalis* and were grouped into four maturity classes for mapping.

Egg masses.— We used CPUE (kg/h of trawling) of Atka mackerel demersal egg masses collected in trawl hauls as an indication of spawning activity. Egg masses were identified and recorded for each trawl haul during the cruise in October 2004. Catch sampling aboard the commercial fishing vessel followed standardized NMFS observer sampling procedures (AFSC 2002). Total haul weight was determined with a flow scale over which the entire catch passed during processing. Three 1,000–3,000-kg subsamples were randomly taken during the processing of each haul in the ship's factory. Samples were sorted and weighed by species. Atka mackerel egg masses were treated as a separate species, which allowed total egg mass weight estimates per haul. The egg mass weight was then divided by the hours trawled to estimate egg mass CPUE for each haul. Egg mass CPUE by haul was plotted using geographical information systems (GIS).

TABLE 2. Atka mackerel male gonadal maturity stages based on Grier and Taylor (1998).

Maturation stage	Description
Early maturation	All stages of spermatogenesis in spermatocysts. Some spermatozoa may be in ducts. Continuous germinal epithelium throughout testes.
Midmaturation	All stages of spermatogenesis in spermatocysts. Spermatozoa in ducts. Germinal epithelium continuous at periphery, discontinuous near ducts.
Late maturation	Spermatocytes, spermatids, and spermatozoa in spermatocysts. Discontinuous germinal epithelium extends to periphery of testes in at least one lobule.
Regression	Spermatocysts are widely scattered. Discontinuous germinal epithelium from ducts to the testis periphery. Lobules contain varying amounts of spermatozoa.
Regressed or immature	Spermatogonia are the only germ cells present in large amounts. There may be a few spermatocysts containing germ cells advanced beyond spermatogonia. It is unclear if these will be developed for the next year or destined to become necrotic. Residual spermatozoa often present.

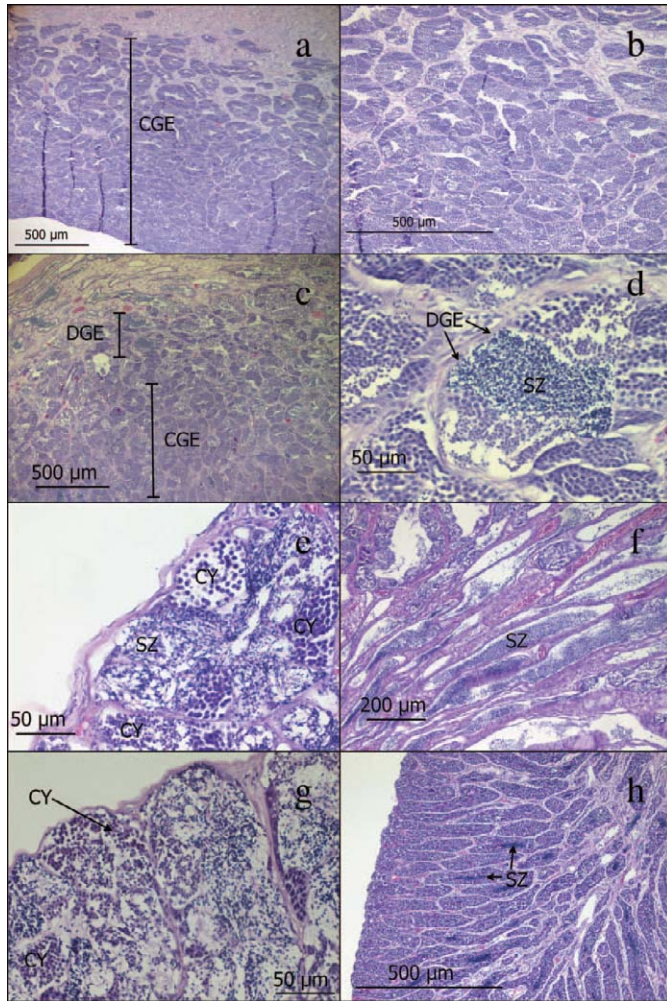


FIGURE 2. Images of the stages used to classify Atka mackerel testes. Panel (a) shows a portion of a testis in the early maturation stage from near the ducts (top) to the testis periphery (bottom); spermatocysts containing developing sperm line the lobules to form a continuous germinal epithelium (CGE) from the ducts to the testis periphery. Panel (b) shows a portion of a testis in the early maturation stage near the ducts with the CGE bordering each lobule. Panel (c) shows a testis in the midmaturation stage; some spermatocysts near the ducts have completed development to become spermatozoa and entered the lobules, creating a discontinuous germinal epithelium (DGE), while the CGE is still present in the distal area of the testis. Panel (d) shows a portion of a testis in the midmaturation stage with a DGE (arrows) and spermatozoa (SZ). Panel (e) shows a portion of a testis in the late maturation stage at the testis periphery; spermatocysts have completed development to become spermatozoa and entered the lobules, creating a DGE at the testis periphery, while spermatocysts (CY) containing developing sperm remain in the testis. Panel (f) shows ducts and proximal lobules filled with SZ in a testis in the late maturation stage. Panel (g) shows a portion of a testis in the regression stage at the testis periphery; a few scattered CY containing developing sperm remain in the testis and spermatozoa are present in lobules to the testis periphery. Panel (h) shows a regressed-stage testis from the ducts to the testis periphery; spermatogonia are the only developing germ cells present, along with residual SZ from the previous spawning season.

TABLE 3. Atka mackerel male maturity classes used to create maps.

Maturity class	Maturity stage
Inactive or immature	Regressed; in samples collected after completion of the spawning season, this category also contains testes just beginning the early maturation stage for the next spawning season
Early maturation	Early maturation
Sperm production and storage	Mid- and late maturation
Ending sperm production	Regression

RESULTS

Male Maturity

Atka mackerel testes were determined to be of the unrestricted lobular type (Parenti and Grier 2004). Ducts for storing and transporting sperm are located in the center of the testes, and spermatogenesis occurs in germinal compartments lining lobules in the distal portion of the testes. Males were classified into five maturity stages based on germ cell stages present and continuity or discontinuity of the germinal epithelium lining the lobules (Table 2; Figure 2). To spatially represent male maturity stages, mid and late maturation stages (Table 3) were combined in Figure 3 (using Arcmap GIS).

Seasonal Distribution at Seguam Pass

In June–July 2002, prior to the onset of spawning (Figure 4a), there was little evidence of distributional differences by maturity stage among the four study strata. Mature females and reproductively active males (early maturation, sperm production and storage, and ending sperm production) were both present in all hauls in all study strata (Figures 3a, 4a). The presence of mature and immature fish of both sexes in all Seguam Pass strata is further evidenced by bimodal length distributions for both sexes, peaks centered at about 37 and 43 cm in all strata (Figures 5a, 6a). Outside the TEZ in stratum 4, 79% of all females were larger than the length of 50% maturity (Table 4). Except for one haul that was predominately male,

TABLE 4. Percent of females larger than the length of 50% maturity (35.9 cm) collected in the Seguam study area, by stratum and date. Combined percent females is weighted by catch in each stratum.

Stratum	June–July	August	October
1	94	86	68
2	82	49	44
3	86	24	47
4	79	7	22
Combined	86	50	47

prespawning sex ratios for all hauls in all strata were mostly balanced (40–60% male) or predominately female (Figure 7a). The mean percentage of males in the catch outside the TEZ was 47%.

In August 2002, when most mature females were spawning (Figure 4c), differences in distribution by maturity stage among the four study strata were observed. Mature females were present in strata 1 and 2 in every haul, but few mature females were found in stratum 3 and no mature females were found outside of the TEZ in stratum 4 (Figure 4d). Females greater than 41 cm were absent from outside the TEZ in stratum 4 (Figure 5b), and only 7% of females from stratum 4 were larger than the length of 50% maturity (Table 4). Similar to the females, reproductively active males (early maturation, sperm production and storage, and ending sperm production) were also present in strata 1 and 2 and were absent in strata 3 and 4, except for one haul in stratum 3 (Figure 3b). The frequency of males larger than 41 cm in strata 4 was also lower than prior to spawning (Figure 6b). Hauls in the areas outside of the TEZ had either a balanced sex ratio or were predominantly male (Figure 7b), which differed from the prespawning period. The overall mean sex ratio weighted by numbers of fish in each haul was 65% male. Fishery length frequency and sex ratio data from the September 2002 fishery (outside the TEZ) also indicated a lower percentage of fish of both sexes greater than 41 cm outside the TEZ during the spawning period (Figures 5c, 6c) and a higher percentage of males in the catch (62%). When the sexed length frequencies of the commercial fishery data were examined for 1998–2007, the percentage of males in the catch at Seguam Pass was consistently higher in September (spawning) than in January (prespawning; Figure 8).

In October, 78% of mature females had completed spawning (Figure 4e), and mature females were again found in all study strata (Figure 4f). At this same time, no reproductively active males (early maturation, sperm production and storage, and ending sperm production) were present in the histology samples (Figure 3c). Outside the TEZ, the frequency of both sexes larger than 41 cm increased slightly from the spawning season (Figures 5d, 6d), and the percent of females larger than the 50% mature length increased to 22% (Table 4). The sex ratios were predominantly balanced (Figure 7c), and the weighted mean sex ratio from the area outside the TEZ was 54% male.

In addition to spatial changes in length frequency, the frequency of females larger than the length at 50% maturity decreased (all strata combined) from 86% in June 2002 to 50% in August (Table 4).

Nest-Guarding Areas in Three Small-Scale Sites

At Seguam Pass, the October 2004 trawl catches of egg masses suggested a high concentration of nest-guarding activity adjacent to the eastern end of Amlia Island and between Amlia and Seguam islands (stratum 2). Most hauls (71%) in stratum 2 contained egg masses (Figure 9a). Hauls in the other strata also contained egg masses but in a smaller fraction of the hauls and at lower levels than stratum 2 (Figure 9a).

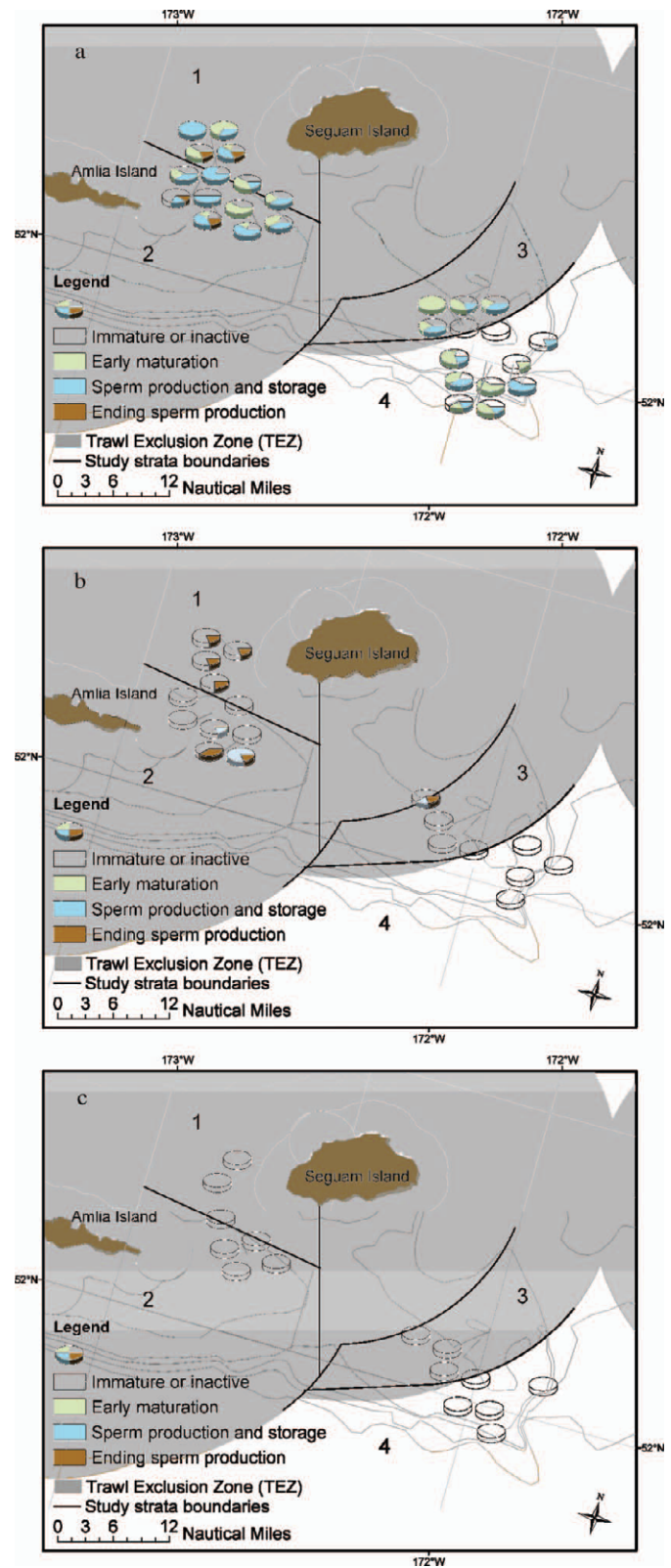


FIGURE 3. Individual trawl haul proportions of male Atka mackerel by maturity class across the Seguam Pass sample area during (a) June–July 2002, (b) August 2002, and (c) October 2002. Each pie chart represents one trawl haul.

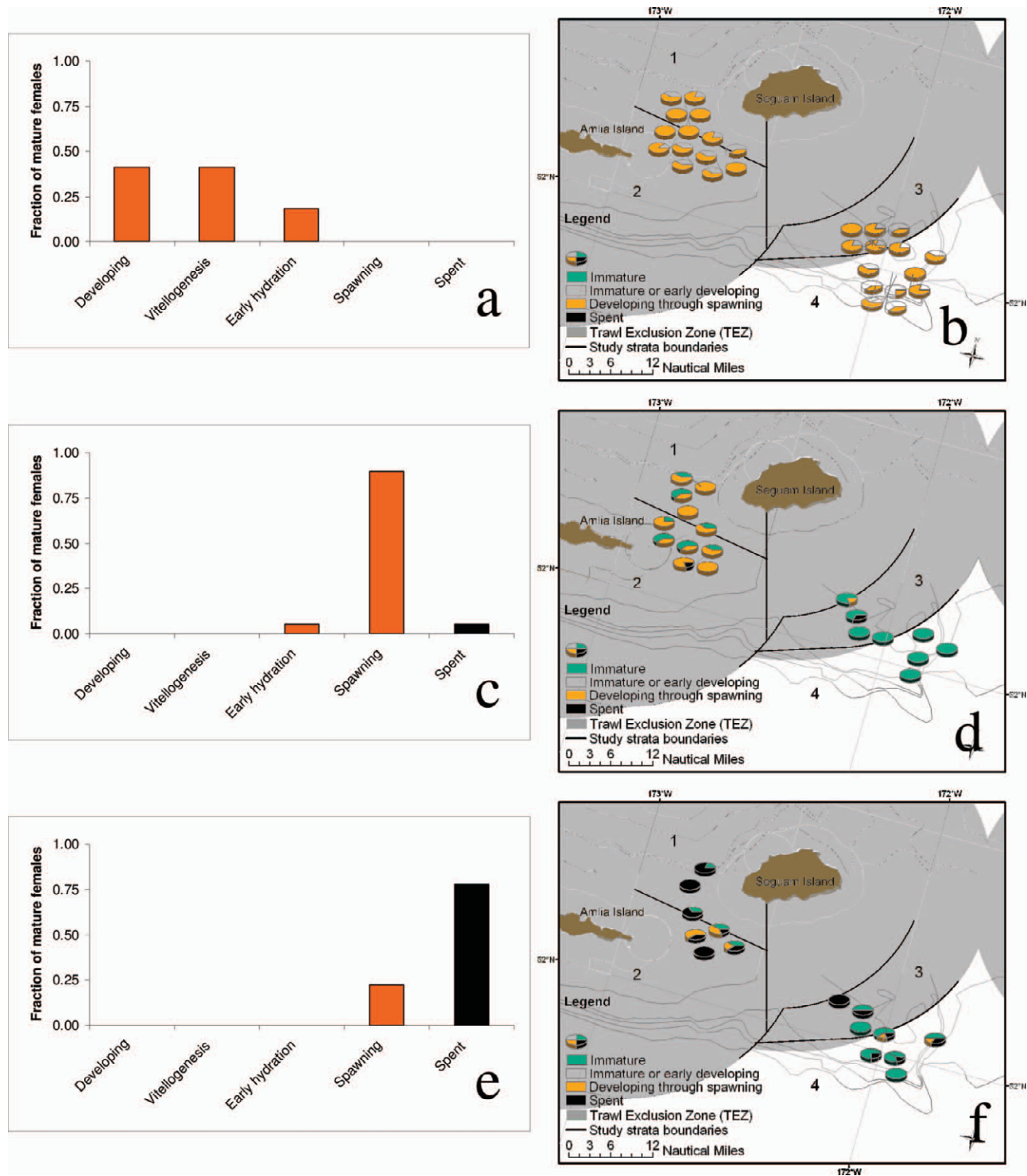


FIGURE 4. Proportions of female Atka mackerel at each maturity stage (immature, immature to early developing, developing through spawning, and spent) for all samples combined compared with the proportions by individual trawl haul across the Seguan Pass sample area in (a)–(b) June–July 2002, (c)–(d) August 2002, and (e)–(f) October 2002. Each pie chart represents one trawl haul.

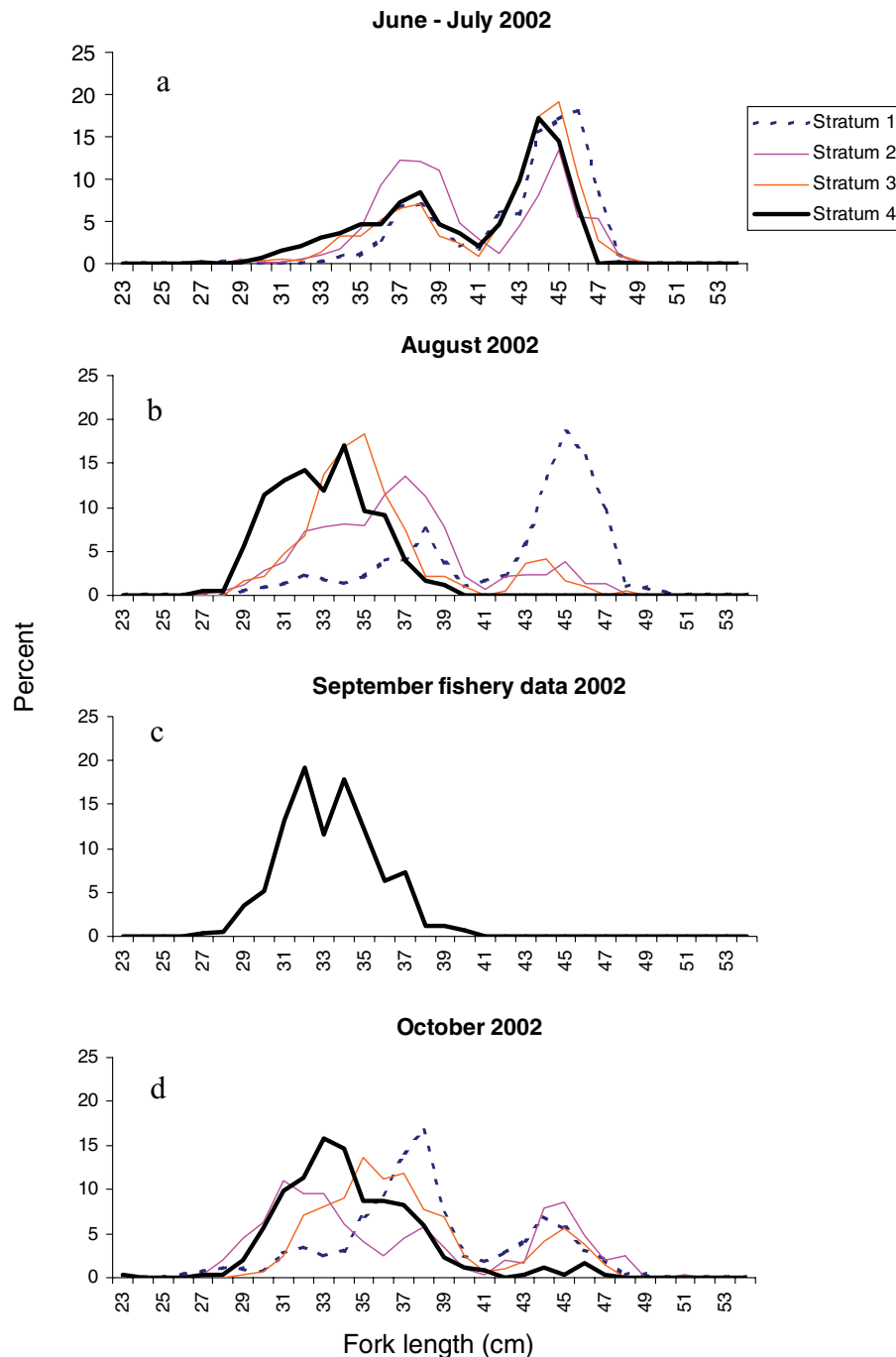


FIGURE 5. Female Atka mackerel length frequencies for the four study strata in Seguam Pass during (a) June–July 2002 (before spawning), (b) August 2002 (during spawning), (c) September 2002 (during spawning; stratum 4), and (d) October 2002 (after most spawning was completed). All data were collected during Atka mackerel tagging and tag recovery cruises except for the September data, which are from the fishery.

At Tanaga Pass, egg masses were found only in one location, southwest of Gareloi Island (Figure 9b). At Amchitka Island, egg masses were present in nearly every haul within the northern TEZ and in two hauls in the southern TEZ but were absent from all hauls outside the TEZs. (Figure 9c).

DISCUSSION

In our study, the shallow-water area east of Amlia Island was the predominant spawning area for Atka mackerel within trawlable grounds near Seguam Pass, as suggested by Fritz and Lowe (1998) and as observed by Lauth et al. (2007), who

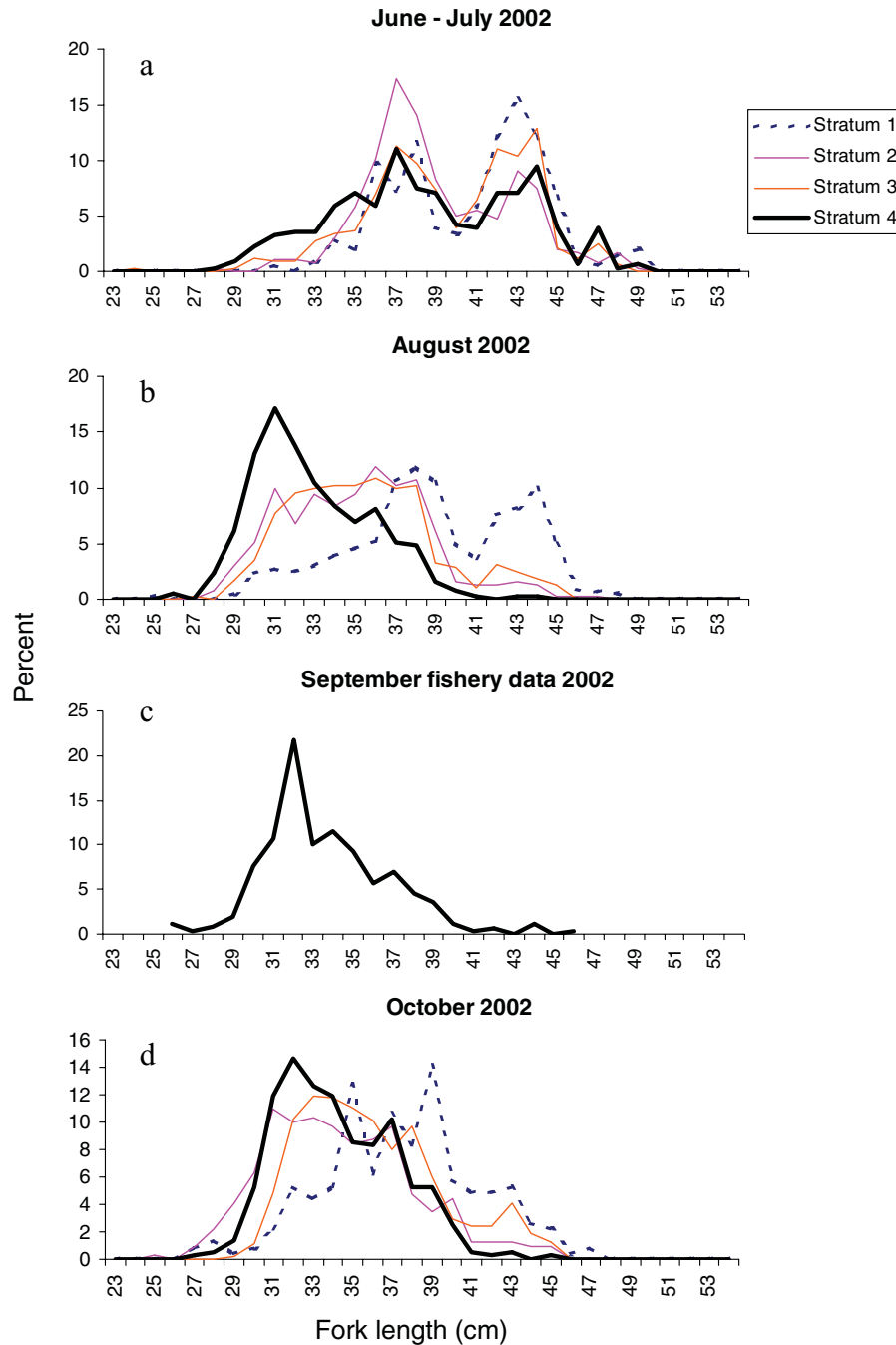


FIGURE 6. Male Atka mackerel length frequencies for the four study strata in Seguam Pass during (a) June–July 2002 (before spawning), (b) August 2002 (during spawning), (c) September 2002 (during spawning; stratum 4), and (d) October 2002 (after most spawning was completed). See Figure 5 for additional details.

reported nesting sites outside the TEZ in Seguam Pass. Egg masses were also present outside the TEZ at Seguam Pass in trawl hauls in our study. However, egg mass densities were highest adjacent to the east side of Amlia Island and between Amlia and Seguam islands. The reduction of large fish in the catch outside the TEZ during spawning suggests that during the spawning season most reproductively active fish abandon this area and move to areas on or near nesting sites, either adjacent

to Amlia Island or to other nontrawlable areas. It appears the females do not move outside the TEZ between batch spawning events but, rather, stay near the nesting sites for the duration of the spawning season. These females could feed at productive feeding areas located inside Seguam Pass (Rand and Lowe 2011).

The spatial segregation of males and females by reproductive stage seems to interact with the TEZ during the spawning

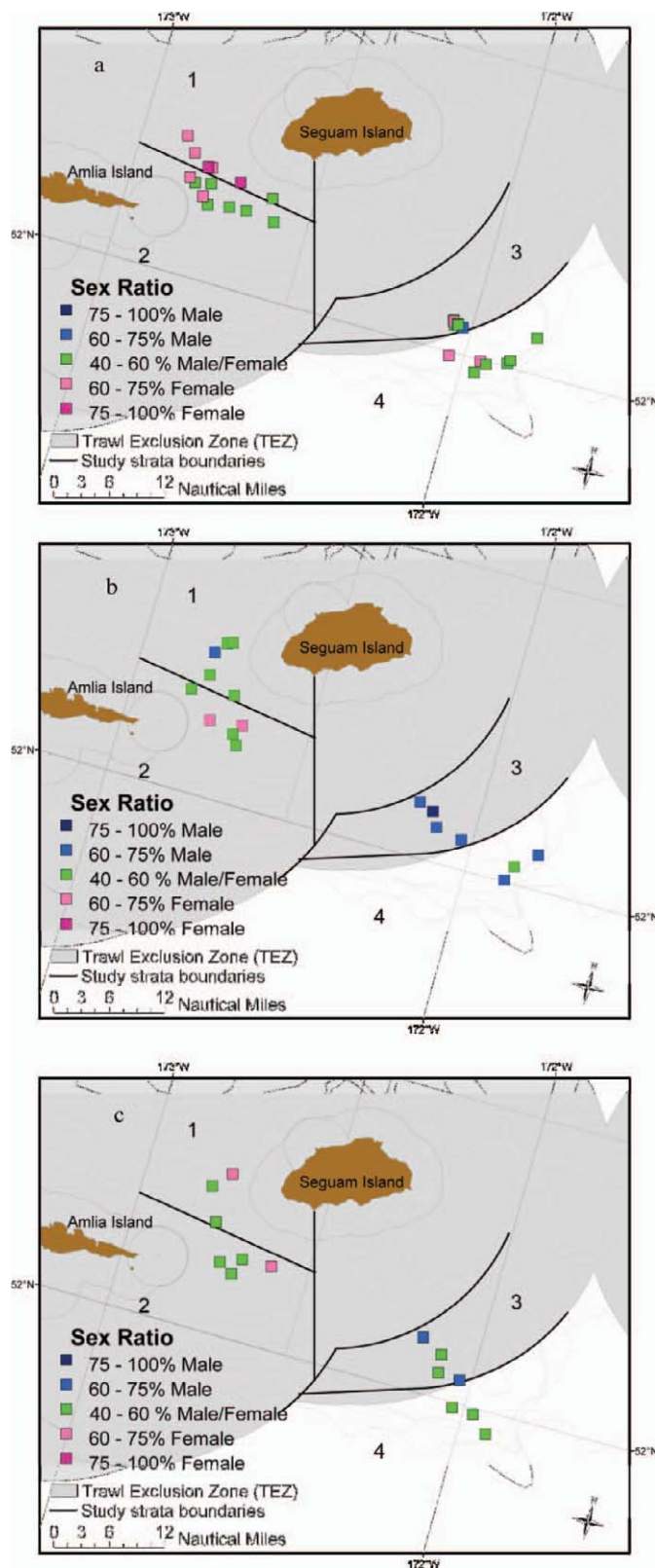


FIGURE 7. Atka mackerel sex ratios by trawl haul at Segum Pass in (a) June–July 2002 (before spawning), (b) August 2002 (during spawning), and (c) October 2002 (after most spawning was completed).

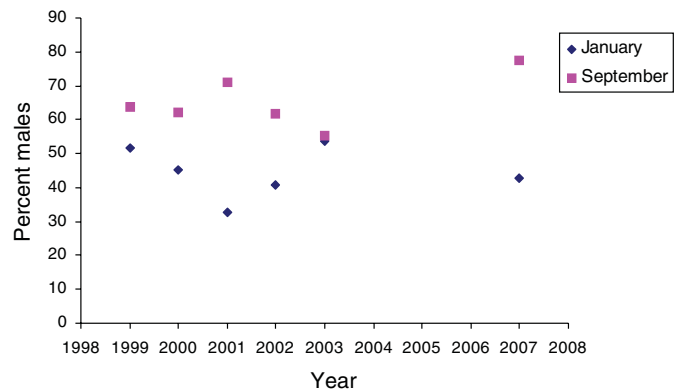


FIGURE 8. Percent of males in the Atka mackerel commercial fishery catch at Segum Pass in September and January of 1999–2007.

season. A higher percentage of males and immature fish are present outside the TEZ, causing the fishery to increase selectivity on these population segments. Sex ratio data from the commercial fishery at Segum Pass from 1998 to 2007 indicate that the increased male selectivity of the fishery during spawning is consistent over time. There is little understanding of how distorted sex ratios affect population dynamics (Hilborn and Walters 1992), and this could be especially important for Atka mackerel because of the male parental care (i.e., nest guarding). The Segum Pass study area is a relatively small geographical area in the Aleutian Islands; however, it has one of the largest small-scale aggregations of Atka mackerel (McDermott et al. 2005) and has been historically important to the fishery. Prior to spatial restrictions on fishing to limit localized depletions of Steller sea lion prey, the Segum Pass study area accounted for 73% of the entire 1984 Atka mackerel catch in the eastern Bering Sea and Aleutian Islands, and 52% of the catch in 1985 (Lowe et al. 2008).

Some of the observed segregation of reproductively active fish near Amlia Island and immature females in the area open to fishing could have been caused by the recruitment of immature fish to the area outside the TEZ. The observed absence of females greater than 41 cm outside the TEZ during spawning season and the consistent reduction of females outside the TEZ during spawning season suggest a movement of mature females rather than merely a dilution of the large females in the catch by newly recruited immature females.

As at Segum Pass, nesting sites were clustered only in certain portions of the trawlable Atka mackerel habitat at Amchitka Island and Tanaga Pass, and most of the nests observed in this study were inside the TEZs. One reason for this could be that trawling disrupts active nest guarding. Lauth et al. (2007) observed nest-guarding males in areas open to fishing; however six of their nine research cruises occurred prior to the September fishery, and before trawling could potentially disrupt the nest-guarding males. It is also possible that repeated trawling in an area over multiple years inhibits nest guarding altogether. Another potential reason spawning occurred mostly within TEZs

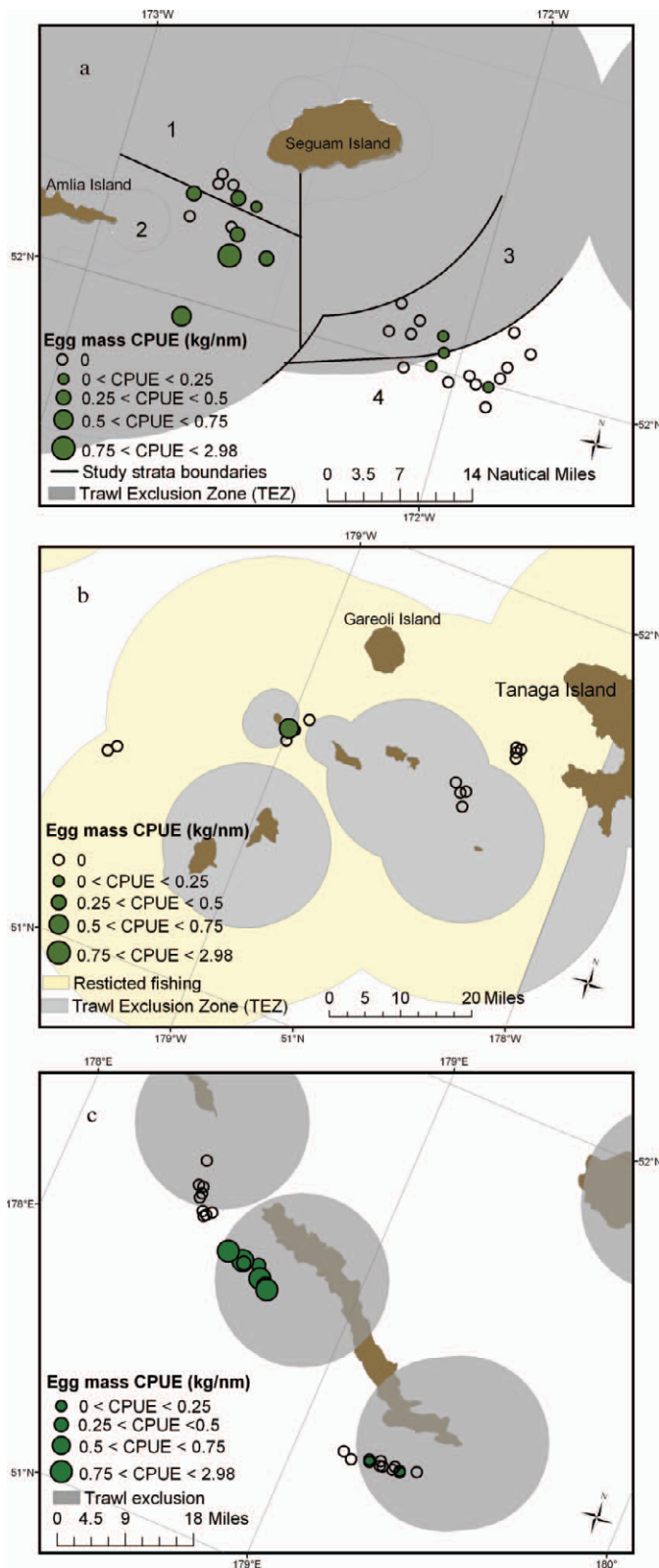


FIGURE 9. Atka mackerel egg mass CPUE per trawl haul in October 2004 at (a) Segum Pass, (b) Tanaga Pass, and (c) Amchitka Island.

could be that Steller sea lions choose rookeries in proximity to Atka mackerel spawning locations because of foraging advantages. This could lead to spawning grounds being within TEZs simply because TEZs were promulgated to provide 10–20-nautical mile (18.5–37.0-km) sanctuaries around rookeries.

Regardless of the reason, TEZs contained most of the observed nesting sites and thereby created de facto marine protected areas, protecting the nesting sites from the effects of trawling. Rand and Lowe (2011) observed higher Atka mackerel feeding rates inside the TEZs, partly due to cannibalism in October.

Undisturbed Atka mackerel spawning areas may also be important for Steller sea lions. During the Atka mackerel nest-guarding season, Steller sea lion females give birth at rookeries and must forage nearby while they nurse their pups. Spatial and temporal predictability of prey sources is an important factor in Steller sea lion foraging success (Gende and Sigler 2006; Womble et al. 2009). Nest-guarding males and nearby schools of spawning females may offer an annually recurring and spatially predictable potential prey resource for female sea lions while nursing pups. Two such rookeries (on Segum and Agligadak islands) are located near the Atka mackerel nesting area east of Amlia Island, and other Steller sea lion rookeries in the Aleutians are located near Atka mackerel aggregations (Fritz and Lowe 1998).

Although Atka mackerel are known to spawn in high-relief areas, some of which are not accessible to trawl gear (Lauth et al. 2007), the sampling tool for this study was trawl gear and the sampling platforms were chartered commercial trawlers. Therefore the data gathered in this study are assumed to represent the Atka mackerel population that is accessible to commercial trawl gear.

Our study shows that small-scale spatial segregation by sex and maturity stage can overlap with spatial fishery management controls such as TEZs and have unexpected consequences. In the case of Atka mackerel, the TEZs created de facto marine protected areas for nest-guarding males and affected the fishery sex selectivity. The consequences of both effects need further study. These results imply that it is of great benefit to understand the small-scale spatial patterns in fish distribution—which are often linked to the species' life history and reproductive cycle—when using management tools such as spatial and temporal restrictions on fishing effort.

ACKNOWLEDGMENTS

We thank Cascade Fishing for the opportunity to sample gonads during commercial fishing operations. We also thank Kimberly Rand, Peter Munro, and Bob Lauth of the Alaska Fisheries Science Center (AFSC) for fruitful discussions. This study could not have been completed without diligent sample collection by many AFSC and contract biologists.

REFERENCES

- AFSC (Alaska Fisheries Science Center). 2002. North Pacific groundfish observer manual. AFSC, Seattle.
- Fritz, L., and S. A. Lowe. 1998. Seasonal distributions of Atka mackerel (*Pleurogrammus monopterygius*) in commercially fished areas of the Aleutian Islands and Gulf of Alaska. NOAA Technical Memorandum NMFS-AFSC-92.
- Gende, S. M., and M. F. Sigler. 2006. Predictability of prey available to Steller sea lions in Southeastern Alaska. Pages 69–81 in A. Trites, S. Atkinson, D. Demaster, L. Fritz, T. Gelatt, L. Rea, and K. Wynne, editors. Sea lions of the world. University of Alaska, Alaska Sea Grant College Program, Fairbanks.
- Grier, H. J., and R. G. Taylor. 1998. Testicular maturation and regression in the common snook. *Journal of Fish Biology* 53:521–542.
- Hilborn, R., and C. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York.
- Lauth, R. R., S. W. McEntire, and H. H. Zenger, Jr. 2007. Geographic distribution, depth range, and description of Atka mackerel *Pleurogrammus monopterygius* nesting habitats in Alaska. *Alaska Fishery Research Bulletin* 12:165–186.
- Lowe, S. A., J. Ianelli, M. Wilkins, K. Aydin, R. Lauth, and I. Spies. 2008. Stock assessment of Bering Sea/Aleutian Islands Atka mackerel. Pages 1119–1198 in Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. North Pacific Fishery Management Council, Anchorage.
- McDermott, S. F., L. W. Fritz, and V. Haist. 2005. Estimating movement and abundance of Atka mackerel (*Pleurogrammus monopterygius*) with tag–release–recapture data. *Fisheries Oceanography* 14(Supplement 1):113–130.
- McDermott, S. F., and S. A. Lowe. 1997. The reproductive cycle of Atka mackerel (*Pleurogrammus monopterygius*) in Alaska waters. U.S. National Marine Fisheries Service Fishery Bulletin 95:231–333.
- Miller, B. S., and A. W. Kendall. 2009. Early life history of marine fishes. University of California Press, Berkeley.
- Morgan, M. J., and E. A. Trippel. 1996. Skewed sex ratio in Atlantic cod (*Gadus morhua*). *ICES (International Council for the Exploration of the Sea) Journal of Marine Science* 53:820–826.
- Pajaro, M., G. J. Maachi, and P. Martos. 2005. Reproductive pattern of the Patagonian stock of Argentine hake (*Merluccius hubbsi*). *Fisheries Research (Amsterdam)* 72:97–108.
- Parenti, L. R., and H. J. Grier. 2004. Evolution and phylogeny of gonad morphology in bony fishes. *Integrative and Comparative Biology* 44:333–348.
- Rand, K. M., and S. A. Lowe. 2011. Defining essential fish habitat for Atka mackerel with respect to feeding within and adjacent to Aleutian Islands trawl exclusion zones. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* [online serial] 3:21–31.
- Solmundsson, J., H. Karlsson, and J. Pálsson. 2003. Sexual differences in spawning behavior and catchability of plaice (*Pleuronectes platessa*) west of Iceland. *Fisheries Research (Amsterdam)* 61:57–71.
- Womble, J. N., M. F. Sigler, and M. F. Wilson. 2009. Linking seasonal distribution patterns with prey availability in a central-place forager, the Steller sea lion. *Journal of Biogeography* 36:439–451.
- Zolotov, O. G. 1993. Notes on the reproductive biology of *Pleurogrammus monopterygius* in Kamchatkan waters. *Journal of Ichthyology* 33(4):25–37.