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ABSTRACT: Understanding the spatial and bathymetric extent of the reproductive habitat of Atka mackerel *Pleurogrammus monopterygius* is basic and fundamental information for managing and conserving the species. From 1998 to 2004, scuba diving and *in situ* and towed underwater cameras were used to document reproductive behavior of Atka mackerel and to map the geographic and depth ranges of their spawning and nesting habitat in Alaska. This study extended the geographic range of nesting sites from the Kamchatka Peninsula to the Gulf of Alaska, and extended the lower depth limit from 32 to 144 m. Male Atka mackerel guarding egg masses were observed during October—indicating that the duration of the nesting period in Alaska is more protracted than in the western Pacific. Results from this study also suggest that nearshore nesting sites constitute only a fraction of the nesting habitat and that there is no concerted nearshore spawning migration for Atka mackerel in Alaska. Nesting sites were widespread across the continental shelf and found over a much broader depth range than in the western Pacific. Nesting habitat was invariably associated with rocky substrates and water currents; however, smaller-scale geomorphic and oceanographic features as well as physical properties of the rocky substrate were variable between different island groups and nesting sites. Water temperatures for nesting sites ranged from 3.9°C to 10.5°C. Water temperatures within nesting sites varied little and did not appear to be limiting the upper or lower depth boundaries of nesting. Results from dive transects showed significantly fewer egg masses above 20 m water depth. Other possible factors limiting the upper or lower depth limit of nesting sites are discussed.

INTRODUCTION

Atka mackerel *Pleurogrammus monopterygius* is a gregarious, semi-pelagic and semi-demersal hexagrammid that is distributed in the continental shelf regions across the North Pacific Ocean and Bering Sea from Asia to North America. On the Asian side their distribution extends from the Kurile Islands to the Gulf of Anadyrskiy (Rutenberg 1962). From Kamchatka, they extend eastward through the Komandorskiye (Rutenberg 1962) and Aleutian Islands (Zenger 2004), north to the Pribilof Islands in the eastern Bering Sea (Acuna and Kotwicki 2004), and eastward through the Gulf of Alaska to southeast Alaska (Lowe et al. 2005). Their center of abundance is in the central and western Aleutian archipelago where a directed commercial trawl fishery operates (Lowe et al. 2004). Atka mackerel is a key prey item for marine fishes, birds, and mammals, including the endangered Steller sea lion (Murie 1959, Kenyon 1965, Merrick et al. 1997, Yang 1999, Sinclair and Zeppelin 2002, Dragoo et al. 2004).

Atka mackerel are obligate demersal spawners. Females lay adhesive eggs on rocky substrate and males guard the nests to protect eggs against predation and cannibalism (Zolotov 1993). Locations of spawning and nesting grounds within Alaska are unknown. The only published account of an Atka mackerel spawning site in Alaska is by Turner (1886). Turner (1886) noted that spawning Atka mackerel, when observed from the water's surface, appeared to form several strata with the least mature fish in the top layer and spawning

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"vigorous males and females" in the bottom stratum. He reported that females deposited eggs on kelp and that both sexes remained for one month, from June to July, and then departed. Turner's (1886) observations contradict the more recent accounts by Gorbunova (1962) and Zolotov (1993), who used scuba for direct observation of nesting grounds in Kamchatkan waters. Their observations of spawning and nesting sites were confined to coastal areas, and the minimum and maximum depths for spawning and nesting ranged from 10 m to 32 m. Both authors report that Atka mackerel were segregated by sex and size, that eggs were laid only on rocky substrates, and that males guarded nests for protracted periods lasting months. Bottom type, depth, and temperature along with moderate tidal current were reported as being important factors for a nesting site. The temperature range for nesting sites was between 5°C and 8°C. The Russian studies, however, were limited in scope both in terms of methodology and spatial coverage. Characteristics of nesting sites off the Kamchatka Peninsula may not be representative of nesting sites over the entire geographic range of Atka mackerel, and scuba has depth limitations that could have prohibited direct observations of nesting sites in deeper water.

There is a directed commercial trawl fishery for Atka mackerel in the Aleutian Islands, Alaska (Lowe et al. 2004). Bottom trawling can negatively impact the sustainability of the fishery through destruction of nests or nesting habitat and direct removal of guardian males during the nesting period. Understanding the spatial or bathymetric extent of the Atka mackerel reproductive habitat is basic and fundamental information for managing and conserving the species.

METHOD AND MATERIALS

Vessels and Study Area and Period

Observations were conducted at various dates between June and October from 1998 to 2004, except 2001, using National Marine Fisheries Service (NMFS) charters M/V *Grand Aleutian*, F/V *Pacific Explorer*, F/V *Sea Storm*, F/V *Morning Star,* F/V *Gladiator,* F/V *Seafisher*, F/V *Vesteraalen*, and the U.S. Fish and Wildlife R/V *Tîglâx*. Only one of these vessels was chartered exclusively for this research, the M/V *Grand Aleutian* in 1998. All others were vessels-of-opportunity that had other primary cruise objectives.

The study area included the continental shelf regions of the Aleutian archipelago and the central Gulf of Alaska (Figure 1). A summary of charter periods, study areas, and methodologies can be found in Table 1. The study area spanned over 2,500 km so it was subdivided into 6 different island groups and the Gulf of Alaska. From west to east, the 6 island groups include Stalemate Bank and the Near Islands, Rat Islands, Delarof Islands, Andreanof Islands, Islands of Four Mountains, and Fox Islands (Figure 1).

Reconnaissance and Transect Dives

All dives were made at a nearshore nesting site off the eastern side of Seguam Island in the Andreanof Islands Group (Figure 2). This site was chosen for dive studies because it was the first nesting site to be located, it covered a relatively large area along the shore (see results), and the nesting area was within the depth limits of scuba. All dives were less than 40 m depth, non-saturation, and used open circuit scuba with regular air.

Reconnaissance scuba dives were made to verify that aggregations of males and the observed behaviors seen with a towed video camera (see below) were associated with the presence of egg masses, and to make general notes about the substrate, biota, and depth limits of egg masses. An "egg mass" is a distinct and continuous mass of fertilized embryos spatially separate from others. Single or multiple egg masses comprise a "nest." Nine dives were made for reconnoitering the Seguam Island nesting site. There were a total of 5 reconnaissance dives on 13 and 16 August 1999, and an additional 3 dives on 9 and 11 August 2000.

Transect scuba dives were done to determine if egg mass density varied by depth. Eight dive transects were made from 9 to 10 August 2000 at randomly chosen locations within the nearshore Seguam Island nesting site. A Branker XL200[1] data recorder was used to record depth and temperature. A 50 m plastic tape measure was stretched along the target depth contour and individual egg masses 1 m to either side of the entire length of the tape measure were counted and their depths recorded. The total area covered for each transect was 100 m^2 so egg mass density was expressed as number/100 m^2. Egg mass densities were pooled into 2 depth bins according to average transect depths less than and greater than 20 m. The mean and standard deviation of egg mass density and depth was calculated for each set of pooled data. A plot of mean egg mass density and transect depth was used to see how density varied by depth at the nearshore nesting site at Seguam Island. A one-tailed Student's *t*-test was used to determine if mean egg mass density increased with depth.

[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

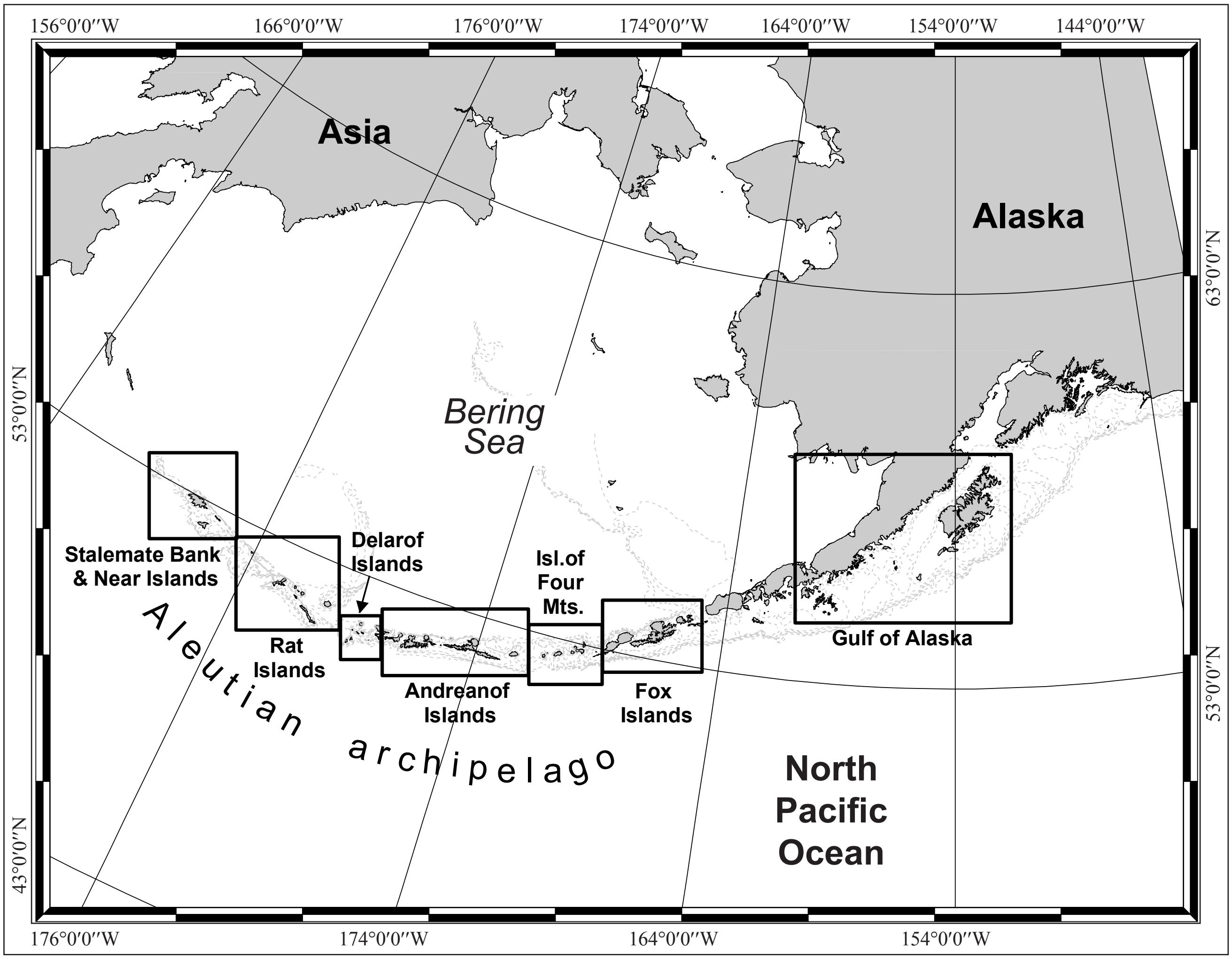

Figure 1. The study area subdivided into 6 different island groups and the Gulf of Alaska. From west to east, the 6 island groups include Stalemate Bank and the Near Islands, Rat Islands, Delarof Islands, Andreanof Islands, Islands of Four Mountains, and Fox Islands.

Table 1. Dates, vessels and methodology used for studying and locating nesting sites (CT = Video camera tow, SC = stationary underwater camera, DV = scuba).

Year	Vessel	Dates	Methodolgy	Cumulative CT Distance (km)	Island Group
1998	Grand Aleutian	20 Jun & 27 Jul–2 Aug	CT	15.3	Fox
1999	F/V *Vesteraalen*	10–15 Aug	CT, SC, DV	20.4	Andreanof
2000	F/V *Morning Star*	7–10 Aug	CT, SC, DV	7.64	Andreanof
2002	R/V *Tĭglâx*	30 Aug–9 Sep	CT, SC	16.9	Near & Andreanof
2003	F/V *Pacific Explorer*	23–26 July	CT	15.2	Rat & Andreanof
2004	F/V *Sea Storm*	26 Jun–16 Jul	CT	31.7	Four Mountains, Andreanof, Delarof & Rat
2004	F/V *Gladiator*	20 Jul–6 Aug	CT	44.2	Andreanof, Rat & Near
2004	R/V *Tĭglâx*	2–9 Sep	CT	15.8	Fox, eastern & central Gulf of Alaska
2004	F/V *Seafisher*	10–21 Oct	CT	30.9	Andreanof & Rat

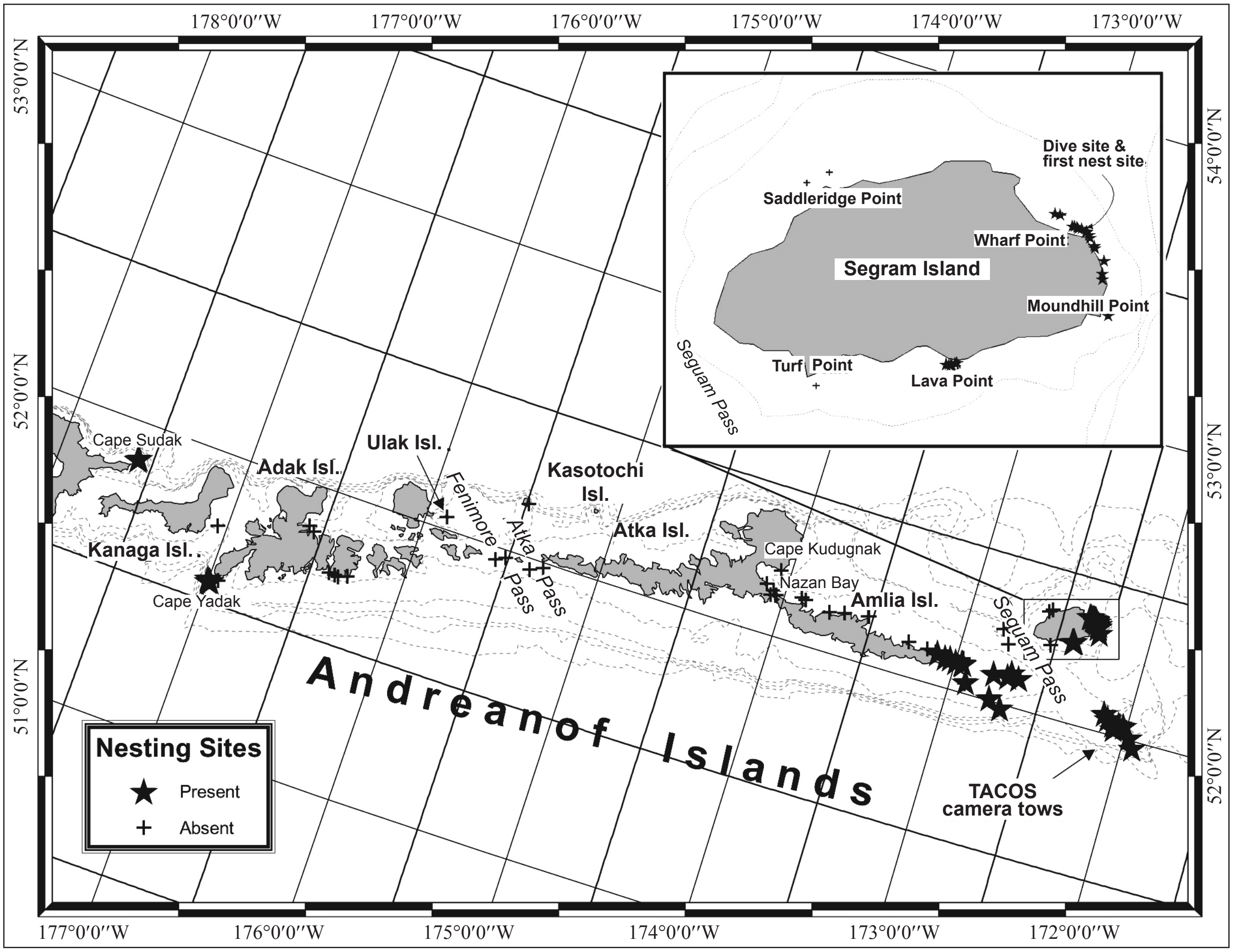

Figure 2. Map of the Andreanof Islands showing locations of video camera tows and whether Atka mackerel nesting sites were present or absent. The labeled arrow indicates the location of 3 tows made with the towed automatically compensating observation system (TACOS). Inset map is a detail showing the location of nearshore coastal nesting sites around Seguam Island where the first nesting site was found and dive transects were made.

In situ Camera

Atka mackerel were absent when divers were present so *in situ* stationary underwater cameras were necessary to observe Atka mackerel spawning and nesting behavior. Either a SONY[2] HI8 or mini-DV video camera was placed inside a Plexiglas housing and placed by a diver on the seafloor near a nest at the Seguam Island nesting site. Recording was continuous for a 1 h to 2 h period or discontinuous for varying periods (e.g. 30 s every 30 min for 2 d) using a time-lapse controller.

Atka mackerel are sexually dichromatic (Medveditsyna 1962, Rutenberg 1962) and sexually dimorphic (Zolotov 1981). During their spawning period, the males change from a greenish gray color to bright yellow or orange and the dark vertical stripes become jet black (Medveditsyna 1962). Compared to females, the dorsal fins of reproductive males are higher, their pectoral and pelvic fins are longer, and they have greater body depth and less head length (Zolotov 1981).

Sexual dichromatism was used to distinguish between males and females when documenting nesting, courtship, or spawning behaviors. Documented behaviors were used as criteria for identifying and documenting nesting sites from towed video camera footage.

[2] Ibid.

Towed video camera

A towed underwater video camera was the primary research tool for locating spawning and nesting sites and determining their overall depth range. Charged coupled device (CCD) video cameras were put into stainless steel housings and were clamped onto the drop camera frame (Figure 3). One of 2 different cameras was used to take advantage of the ambient light conditions expected during the camera tow. A color CCD camera was used with available light during the daytime and at shallow depths. A low-light black and white CCD camera (0.0003 lux) was used in low light conditions (e.g. dusk or at depth). At night or near darkness, a red light emitting diode (LED) array was used in conjunction with the low-light CCD camera to illuminate the area viewed by the camera. The camera and lights were powered with a 13.2V nickel metal hydride battery. A custom variable speed electric winch with a small boom was built for deploying the camera. It was portable and could be adapted for use on a small inflatable boat (4.9 m or 6.1 m) or directly from chartered vessels.

Doing a large number of towed camera samples over a vast geographical area provided observations representing a wide range of nesting habitats for Atka mackerel. However, it was neither practical nor cost effective to use a traditional survey design for selecting towed camera stations because of the remote and expansive study area, the high cost of vessel charter time, and the uncertainty of locating Atka mackerel nesting sites.

During the first year, towed camera sites were limited to locations in the eastern Fox Islands in the exposed rocky nearshore areas with water current at least 20 cm/sec and water depths less than 70 m. The scientific literature reported that spawning and nesting was exclusive to these types of coastal areas in water depths above 35 m (see introduction).

During subsequent years, vessels-of-opportunity were used and site selection of towed camera samples was a consequence of the vessel's location when time was available and if the weather was conducive for doing camera tows. Nautical charts were used for identifying and selecting towed camera sites in the vicinity

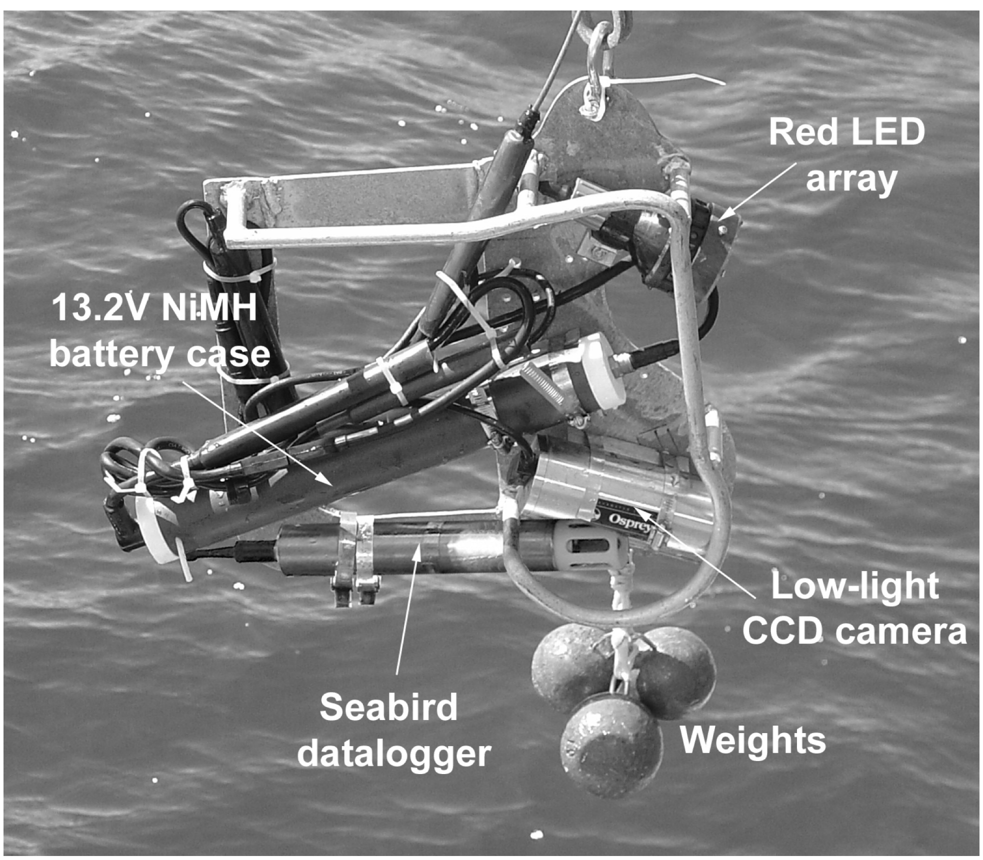

Figure 3. The towed video camera and frame.

of the vessels. Site selection was confined to within 20 km of the vessel to areas with water currents at least 20 cm/sec and a rocky bottom substrate. Through 2002, camera tows were limited to nearshore areas less than 70 m water depth. Starting in 2003, the depth limit for towed camera samples was extended to 200 m anywhere on the continental shelf.

Vessels were not under power during camera tows—they were allowed to drift in the direction of the current, wind, or a combination of both. The depth profile of a camera tow varied depending on bathymetry of the site and the direction of vessel drift. Real-time video feed to a topside video monitor was recorded for later viewing and analyses. Real-time monitoring was necessary to avoid obstacles while the towed video camera drifted over the irregular bottom. The camera frame height-off-bottom was kept at about 1 m and was raised and lowered using the variable speed electric winch.

Beginning and ending times and global positional system (GPS) positions were recorded for each video camera tow. Starting in 2002, positions and times were recorded directly onto the video using a GPS overlay board. The GPS positions were taken relative to the support vessel and the camera was assumed to be directly under the vessel. Temperature and depth of tows was recorded using a Brancker XL200, Lotek data logger, or a Seabird SBE 39 that was attached to the drop camera frame. Means and standard deviations were calculated for the depths and temperatures of camera tows. The depth range of each camera tow by presence and absence of nest-guarding males was depicted using a bar graph with camera tows ordered by increasing average depth of the camera tow. For analyzing the depth distribution of nesting sites, average camera tow depths were pooled into 20 m depth bins (e.g. 0–20 m, >20–40 m, >40–60 m) and the number of tows with nests present and absent were graphed as a percentage of the total number of camera tows made during the study.

Documented behaviors from the *in situ* cameras were used for identifying nesting sites from the towed camera videotape footage. Each tape was examined for the presence of male Atka mackerel exhibiting spawning and nesting coloration and behaviors. To be considered a nesting site, an aggregation of nesting males had to be present during some portion of the camera tow.

Ancillary Towed Video Camera Data

Towed video camera footage from a 1999 study was examined for the presence of Atka mackerel nesting sites and combined with results from this study. In August 1999, the Towed Automatically Compensating Observation System (TACOS; Barker et al. 1999) was used by the Alaska Fisheries Science Center in Seguam Pass aboard the F/V *Vesteraalen* to study demersal habitat and the impacts of trawling. Three camera tows, centered at lat 52°N and long 172°W, showed the presence of nesting sites (Figure 2). Like the other towed camera footage earlier, the location, depth, and water temperature of Atka mackerel nesting sites were recorded.

RESULTS

Reconnaissance and Transect Dives

The first observation of a nesting site was made with a towed video camera on 13 August 1999 in the nearshore region on the northeast side of Seguam Island (Figure 2). A reconnaissance dive at this site confirmed the presence of nests. Additional camera tows and reconnaissance dives to the south along the eastern shore showed that the Seguam Island nesting site extended to Moundhill Point (Figure 2). Nests were present and consisted of one or more non-overlapping fist-sized egg masses. Egg masses were generally oblong, irregularly shaped, and conformed to the rock crevice where they were deposited. No egg masses were observed below 32 m during reconnaissance dives anywhere at the Seguam nesting site, and 32 m was the general depth where the seafloor habitat made a transition from boulders and consolidated rock to unconsolidated sand, shells, and cobble (Figure 4). The shallowest egg mass observed during reconnaissance dives at the Seguam nesting site was 15 m, even though the rocky habitat continued above this depth to the shoreline. Wave surge intensified and brown kelp *Alaria* spp., *Laminaria* spp. *Thalassiophyllum* spp., and *Agarum* spp. and green sea urchins *Strongylocentrotus droebachiensis* were abundant where the shallowest egg mass was observed (Figure 4).

The water depth for transect dives ranged from 14.5 m to 26.6 m and the number of egg masses observed along transects ranged from 0 to 38. The average water temperature for all dives was 4.7°C and ranged from 4.4°C to 5.0°C. The mean depth for pooled transect dives <20 m was 17.9 m (n=5), and for transect dives >20 m it was 23.1 m (n=3). Mean egg mass densities were about 5 times greater at the transects > 20 m compared to the transects < 20 m ($p = 0.0003$; Figure 4).

In situ Observations

Spawning and nesting behaviors were based on general observations obtained from viewing 22 h of *in situ* video camera footage and 56 h of towed camera video footage of Atka mackerel nesting sites.

Individuals involved in courtship displays were sexually dichromatic. The coloration pattern of males was conspicuous and contrasted with the surrounding seascape. From the dorsal to the ventral side, the overall color made a transition from golden to lemon yellow. The length of the body was interspersed with prominent black vertical bands that varied in width. Posterior to the pectoral fins, there were usually 3 narrow followed by 2 broad black vertical bands. The lower half of the pectoral fin and the entire pelvic and anal fins were also black. The bold contrast in vertical banding was easily observable using either a color or black-and-white camera. The coloration of spawning females was mottled grey-blue with white blotches on the head and dorsum and low contrast vertical bars across the body. Females observed sitting motionless within a male's nesting territory blended in with the background and were difficult to see on camera with available light. The dorsal fins on females were generally not erect except during courtship or when making forays into a male's nesting area.

Nesting territories of individual males were generally adjacent to one another; however, there was no way with the methods used to delineate individual nest boundaries. Nest-guarding males avoided divers and temporarily abandoned their nests when divers were present, so divers were not able to observe the extent to which males tended individual egg masses within a nest. The *in situ* camera was able to observe general nesting behavior, but the camera was not close enough or of sufficient resolution to discern individual egg masses. As a result, the perimeter of a single male's nest and the number of masses within it were ambiguous. However, using the average size of a sexually mature male as a gauge (about 35 cm to 40 cm, Fritz and Lowe 1998), territorial males guarded rocky nest patches with estimated areas of about 2 m^2.

Courtship behavior between a nesting male and gravid female was frequently observed with the *in situ* and towed video cameras. Individuals involved in courtship displays had different behaviors and were sexually dichromatic. To attract passing females, males swam vertically into the water column, turned sharply downward, and descended back towards the nest with

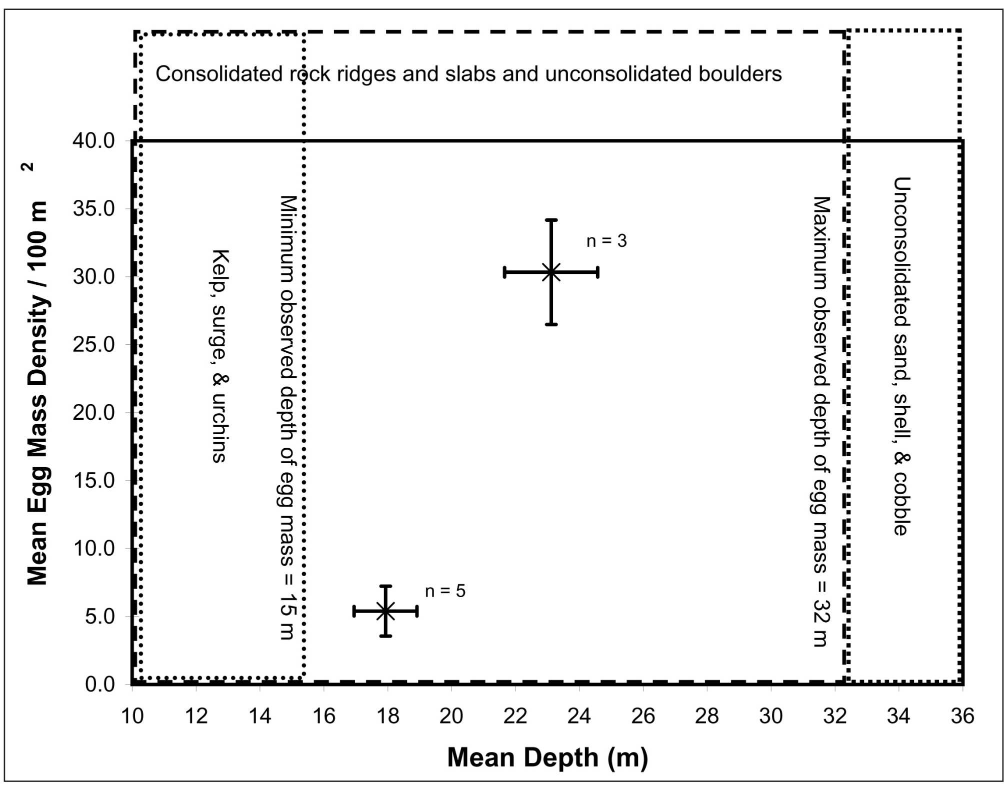

Figure 4. Graph showing the mean and standard deviation for egg mass density/100 m^2 by depth for pooled dive transect depths <20 m and >20 m at the nearshore nesting site at Seguam Island. The boxes with dashed borders represent the different habitat types by depth at the Seguam nesting site, and show the minimum and maximum depths that egg masses were observed during reconnaissance dives.

a rapid dorsal-ventral tail wag. Once the female was inside a male's nesting territory, the male swam tight circles around the female to corral her within a specific area of the nest. Males would use their snout to butt against a female's abdomen and point towards a particular spot on the rocky substrate accompanied by short tail wags. Two male behaviors were observed while a female laid motionless in a nest: circling overhead with an erect dorsal fin, and slow passes alongside the female accompanied by quivering of the dorsal fin. The *in situ* camera was not close enough to discern if these behaviors were associated with the release of gametes by either the male or female.

Each nest-guarding male exhibited territorial behavior for his patch of rocky bottom and was aggressive towards neighboring males and other fishes. Most often males were observed sedentary on the seafloor or hovering or circling overhead the nesting patch. Males used their mouths to remove miscellaneous debris or invertebrates from their nest. Marine invertebrates observed being removed included the green sea urchin *S. droebachiensis*, gumboot chiton *Cryptochiton stelleri*, and *Henricia* sp. starfish. Green urchins were observed moving over the front of the camera housing during one of the longer *in situ* camera deployments and urchin "bite" marks were evident on the lashing holding down the camera.

Females and non-mating Atka mackerels typically formed schools and were generally on the move during the day. When swimming through a nesting site, these schools were vertically stratified above the territorial males. During the night, schools became sedentary and settled to the bottom in areas adjacent or close to nesting sites, and sometimes directly onto nesting sites. Nighttime was the only time of day that nest-guarding males were observed co-mingling with other Atka mackerel, except when involved with courtship or spawning.

Towed Video Camera

Video recordings were obtained from 283 video camera tows made between June 1998 and October 2004. Aggregations of males exhibiting nesting behavior and the nesting color pattern were observed during 106 (37.5%) of the video camera tows. Males guarding nests were present at 26.8% of the 143 camera tows made in coastal waters, and at 49.3% of the 140 camera tows made offshore. The average bottom time for all camera tows was 21.5 min and ranged in duration from 1 min to 163 min. The red light from the LED appeared to have little effect on Atka mackerel behavior.

Drift speeds averaged 57.5 cm s^{-1} and ranged from 0 cm s^{-1} to 194 cm s^{-1}, and distances towed averaged 0.75 km and ranged from 1 m to 5.47 km. The video camera was towed at sites between Stalemate Bank (Figure 5, 170°56′E) and the Barren Islands (Figure 6, 152°00′W). Stalemate Bank was the farthest west, and Unga Island (160°55′W) the farthest east, that an aggregation of nesting males was observed (Figures 5 and 6).

The general habitat for the overall study area was characterized by a narrow continental shelf, a mostly hard and irregular seafloor, and channels and passes with strong currents. On smaller scales, there was much greater diversity of habitats across the geographic range of this study. Aggregations of nesting males were always observed at sites having rocky substrate and current; however, there was tremendous variability regarding geomorphic and oceanographic features and the physical properties of the rocky substrate. Examples of geomorphic and oceanographic features that varied between sampling sites were proximity to shore, shelf break, headland, rivers (turbidity), ocean current or island pass, width and depth of a channel or pass, and duration, speed, and direction of currents and eddies.

Physical properties of the rocky substrate, such as relief, slope, consolidation, and continuity also varied among the different nesting sites. Aggregations of nesting males were observed at sites with rocky substrate having many combinations of these physical properties. Nesting sites were observed on rocky substrate consisting of unconsolidated cobble and boulders, and at sites with consolidated slabs and ridges. The rock seafloor at nesting sites could be either continuous or with channels or patches of sand, shell, and gravel interspersing the rocky spots. Bottom relief, seafloor slope, and the density of sessile invertebrates were also variable between nesting sites.

Nesting behavior was observed at water depths between 15.5 m and 143.8 m (Figure 7). Average depths for camera tows where nesting was observed ranged from 16.6 m to 136.7 m, and the overall mean and standard deviation for all nesting sites combined was 61.3 ± 34.0 m (Figure 7). No aggregations of nest-guarding males were found at mean depths deeper than 140 m and only 1% of tows with mean depths of <20 m had nesters (Figure 8). Aggregations of nest-guarding males were absent at a larger percentage of tows at mean depths <40 m compared to tows with mean depths between 40 m and 140 m.

The greatest range in depth within a single nesting area was 52 m observed at Middle Reef (Figure 7, 175°59′E). Other nesting areas with broad depth

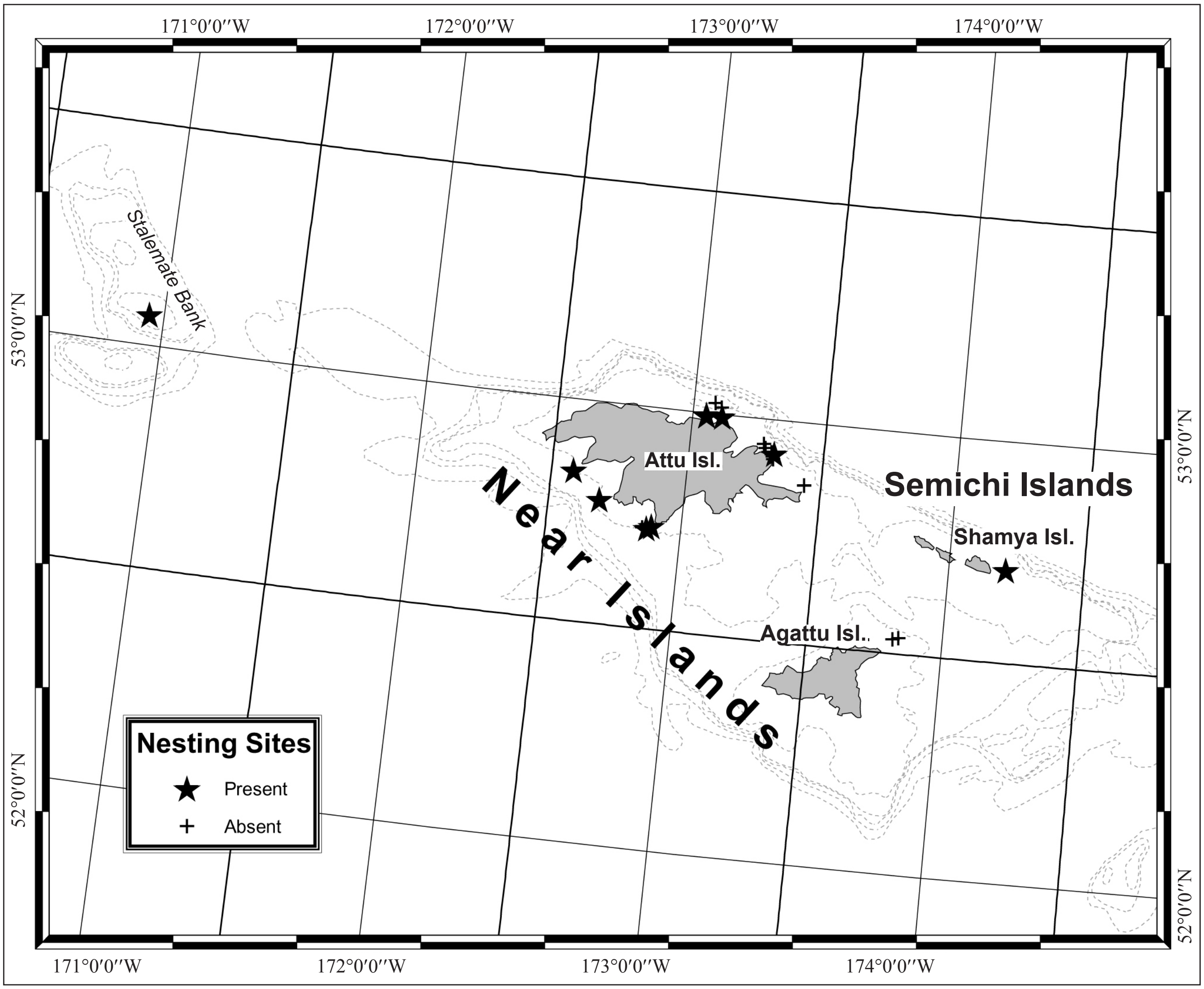

Figure 5. Map of the Near Islands and Stalemate Bank showing locations of video camera tows and Atka mackerel nesting sites.

ranges were Stalemate Bank (45 m), Cape Yakak (43 m, 177°00′W), Lava Point (38 m, 172°24.5′W), and Egg Island Reef (29 m, 165°57.5′W). The 10 deepest nesting areas were observed at Wall's Plateau (121 m to 135 m, 175°12.5′E), Cape Yakak (92 m to 136 m), and in Seguam Pass (99 m to 143.8 m).

Average water temperatures for camera tows at nesting sites ranged from 3.9°C to 10.7°C, and the overall mean and standard deviation of all tows combined was 5.4°C ± 1.2°C. The average range of water temperatures was similar for camera tows at non-nesting sites (4.1°C to 10.8°C) and the overall mean was 0.8°C higher. Within-tow variability of temperatures was surprisingly low for all camera tows, regardless of the depth range of the camera tow, which varied greatly at some sites (Figure 7). The temperatures from 42% of the camera tows varied by ≤0.1°C, and the temperatures from 79% of the camera tows varied by ≤0.5°C.

Descriptive Observations by Island Group

Stalemate Bank and the Near Islands

Twenty-two camera tows were conducted in this area and aggregations of nesting males were observed in 45% of the tows on Stalemate Bank and off Attu and Shemya Islands (Figure 5). Nesting sites ranged in depth from 15.9 m to 111.5 m (Appendix 1a). Nesting sites on the north side of Attu Island were in coastal (<44 m) areas and nesting sites on the south side of Attu were much deeper (64.5 m to 111.5 m) and about 2 km to 3 km from shore. The nesting site at Stalemate Bank, situated about 100 km west of Attu Island in Near Strait, was the farthest out on the continental

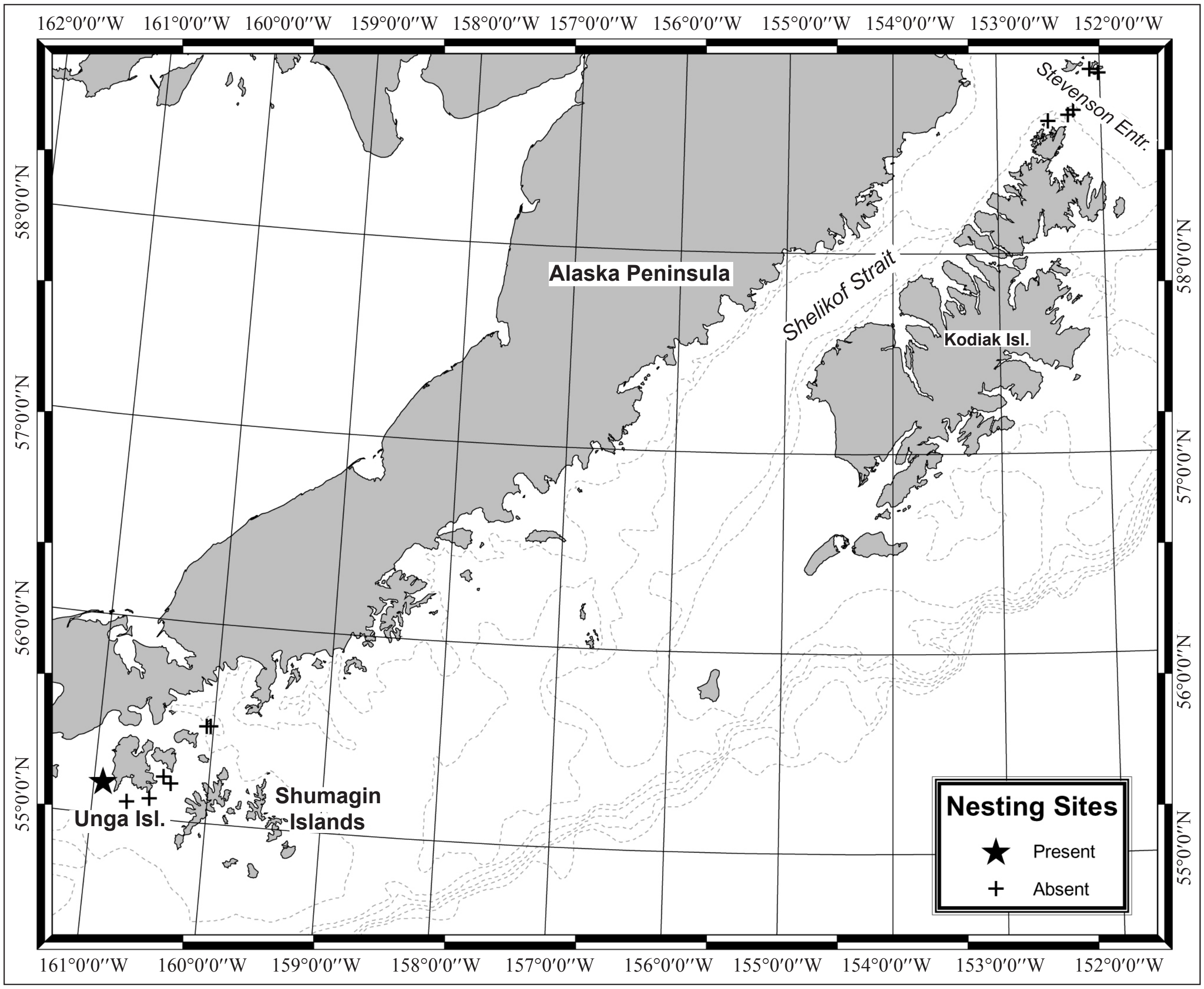

Figure 6. Map of the central and western Gulf of Alaska showing locations of video camera tows and Atka mackerel nesting sites.

shelf of any nesting site and was also the farthest west sampled in this study.

Nesting sites at Stalemate Bank and near Shemya Island covered large areas. The Stalemate Bank camera tow was 2.75 km in length and the bottom substrate was consolidated rock with high relief and some patches of unconsolidated boulders and cobble. Nesting males were observed during the entire camera tow. The current velocity of the water based on the average drift speed of the vessel was 34.0 cm/sec.

The Shemya Island camera tow was 4.6 km in length and was similar to Stalemate Bank except there were large stretches with a gravel, sand, and shell bottom. Male nesters were observed in areas with rocky bottom and absent in areas with gravel, sand, and shell bottom. The current velocity at Shemya based on the average drift speed of the vessel was 66.9 cm/sec.

Rat Islands

There was nesting activity at 41% of the 68 sites towed with the camera in the Rat Islands (Figure 9). Aggregations of nesting males were not seen at the eastern end of Amchitka Island, but were present at the southwestern end, as well as in areas offshore of Kiska and Buldir Islands. Nesting males were also observed in Oglala and Sealion Passes, and on Middle and Buldir Reefs, Wall's Plateau, and Petrel Bank. The depth range for all 28 nesting sites was 24 m to 128 m (Appendix 1b).

Camera tows made around Amchitka, Tanaga, and Seguam Islands from 10 to 21 October 2004 (Table 1) were the latest date sampled during this study.

The nesting habitat at Petrel Bank was unique in that it was almost entirely large unconsolidated boul-

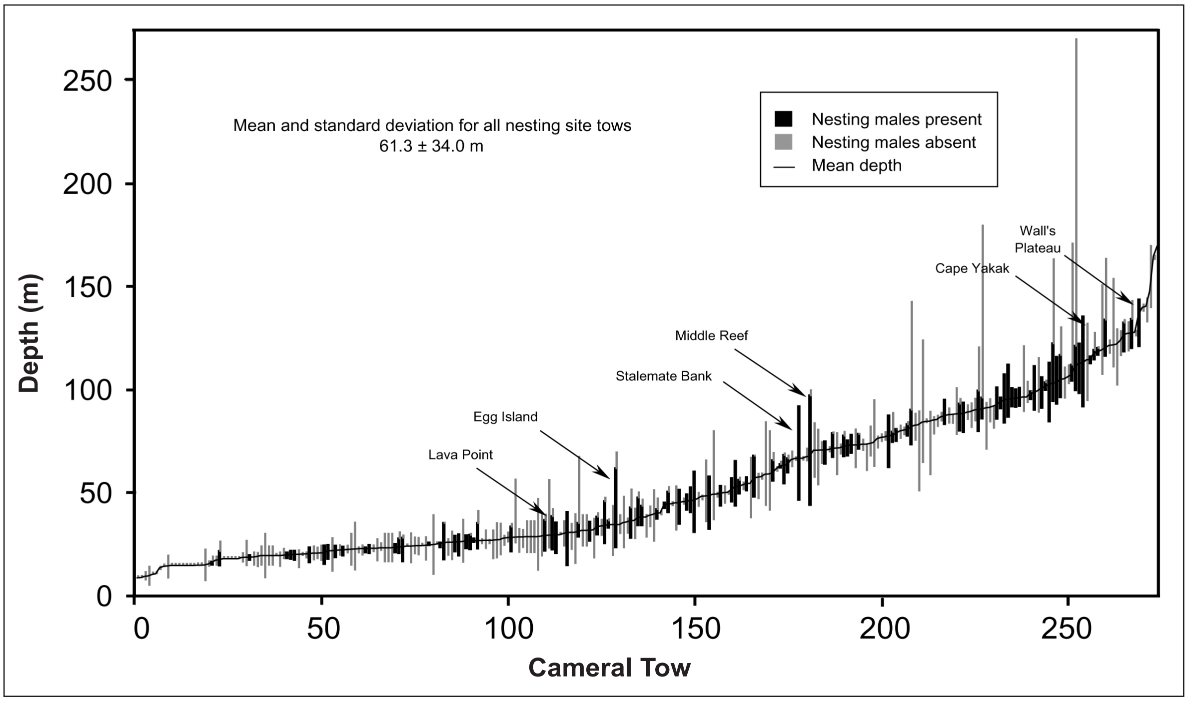

Figure 7. Bar graph depicting depth range of each camera tow by presence and absence of nest-guarding males. Tows are ordered by increasing average depth (solid line).

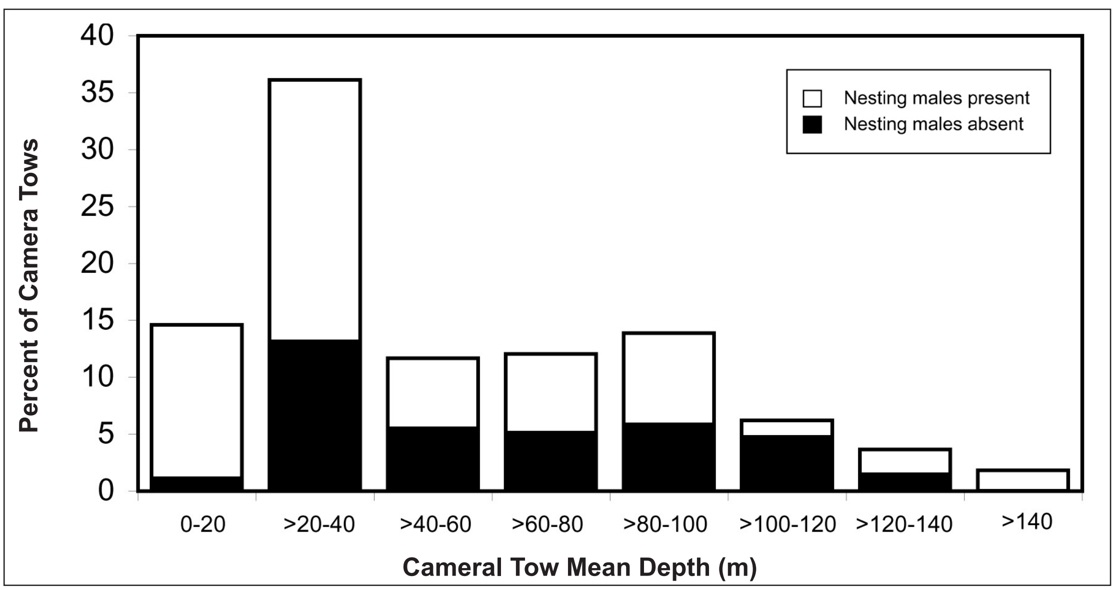

Figure 8. Bar graph showing percentage of all camera tows, by 20 m mean depth bins, in which nest-guarding males were present and absent.

ders interspersed with volcanic sand. Nest-guarding males were observed on boulders for the duration of 2 camera tows covering a total distance of 0.81 km. Six camera tows totaling a distance of 13.07 km were done at Middle Reef and Walls Plateau. The seafloor at both these reefs was a combination of consolidated and unconsolidated rock scattered with sand channels. Nest-guarding males had patchy distribution in some of these rocky areas. Vertical relief and sessile invertebrate coverage (e.g., sponges and corals) on rocky substrate was variable and did not appear to be related to presence or absence of nest-guarding males.

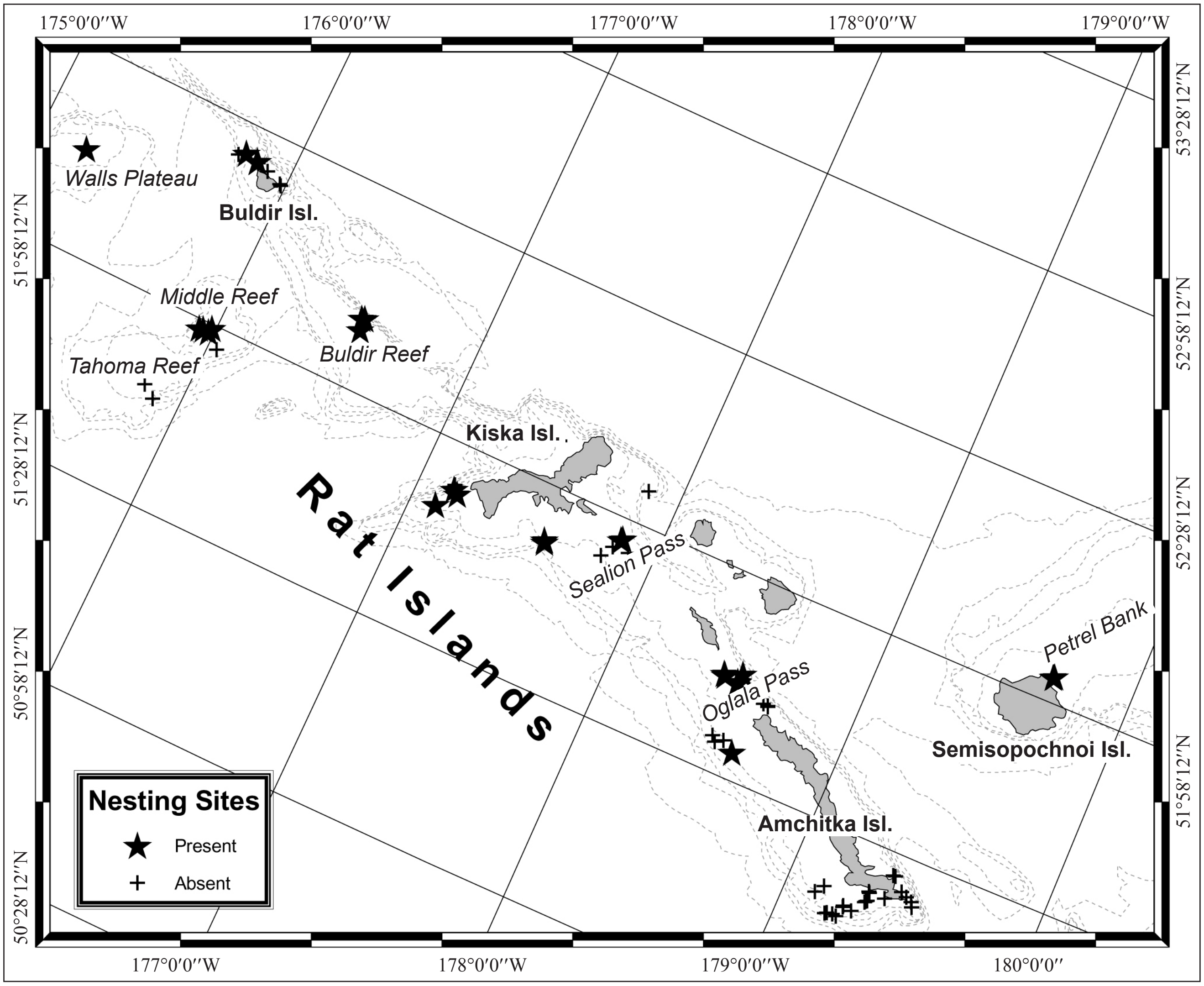

Figure 9. Map of the Rat Islands showing locations of video camera tows and Atka mackerel nesting sites.

Delarof Islands

There were nest-guarding male Atka mackerel in all but 1 of the 8 video camera tows in the Delarof Islands (Figure 10). Nesting sites ranged in depth from 30.2 m to 101.2 m (Appendix 1c). Six of the nesting sites were on the edges of Tanaga Pass and the seventh was on a shallow bank in Amchitka Pass (Nameless Reef number 1). This was the southern extent of our study area and the farthest south that a nesting site was observed.

Andreanof Islands

Nesting sites were concentrated at either end of the Andreanof Island chain off Capes Yakak and Sudak, and in the Seguam Pass area (Figure 2). No nesting sites were observed in 30 camera tows made between those 2 areas. Nest-guarding males were not observed at Kasotochi and Ulak Islands, Fenimore and Atka Passes, and between Cape Kudugnak at the north end of Nazan Bay on Atka Island to the eastern end of the north side of Amlia Island. Currents exceeding 150 cm/sec were observed in Fenimore and Atka Passes. A large surface aggregation of Atka mackerel feeding on krill was encountered at the north end of Amlia Pass, but no nesting activity was observed when the camera was dropped to the bottom.

Cape Yakak and Seguam Pass nesting sites were consistently among the deepest observed during this study (92 m to 143.8 m). By far, the nearshore area of Seguam Island had the most extensive nesting activity of all the nearshore coastal areas investigated during this study. The Seguam Island nesting site extended along the northern and eastern shore for 8 km from

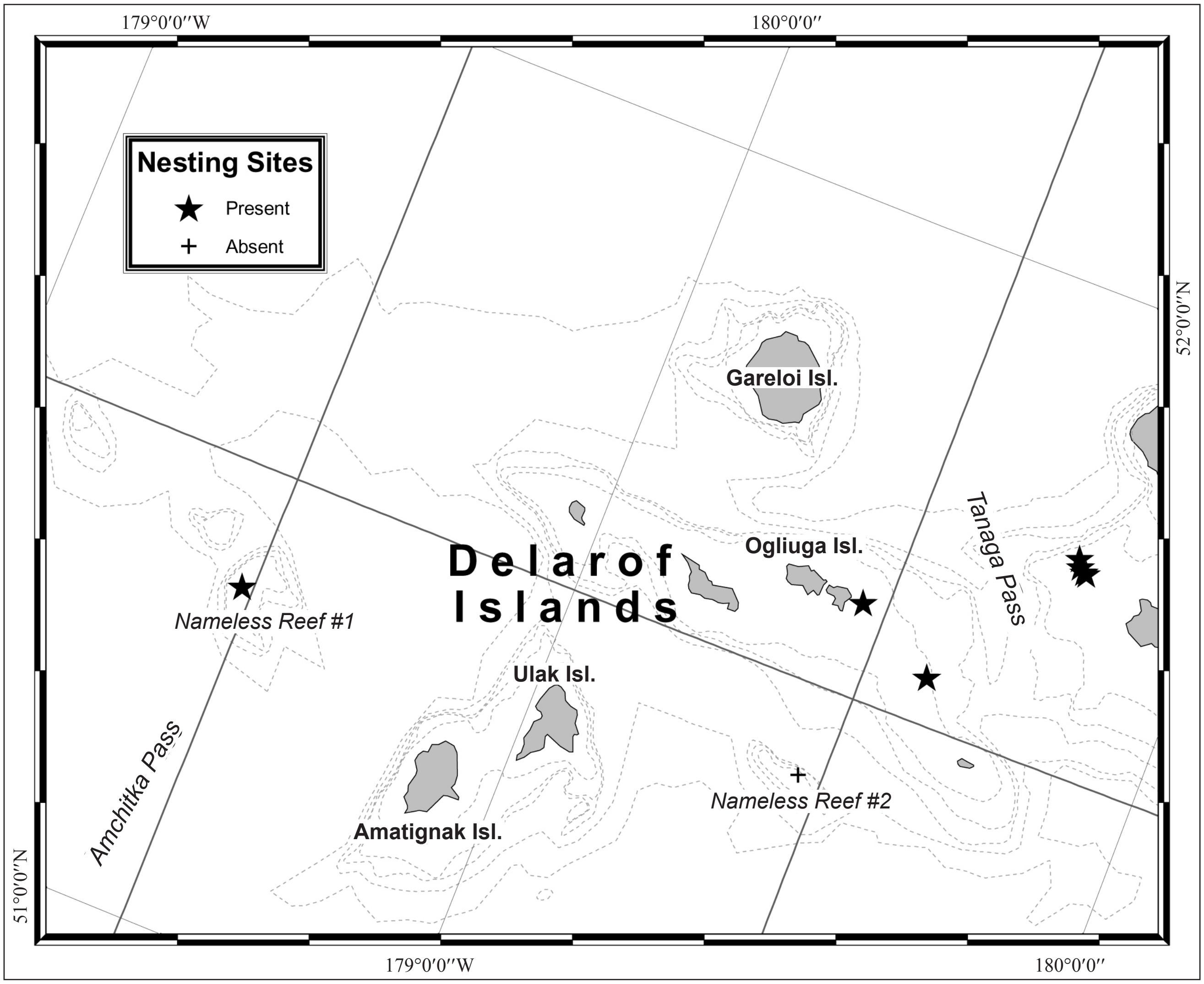

Figure 10. Map of Delarof Islands showing locations of video camera tows and Atka mackerel nesting sites.

northwest of Wharf Point to Moundhill Point (Figure 2), and another nesting area was observed at Lava Point on the south side of Seguam Island. No nesting activity was seen on the north side of the island at Saddleridge Point or at Turf Point on the southwestern side. The lower depth boundary of the nearshore nesting sites on Seguam Island was habitat limited. Nesting behavior disappeared at the same depth where the seafloor made a transition from boulders and consolidated rock to unconsolidated sand, shell, and cobble. Between Wharf Point and Moundhill Point, the lower depth boundary for the rocky habitat was typically from 30 m to 35 m, and at Lava Point and on the east side of Amukta Island, it ranged from 45 m to 50 m (Appendix 1d).

Islands of Four Mountains

Nesting sites were seen in 2 general areas in the Islands of Four Mountains: one on a large reef south of Chuginadak Island and the other off the southwest coast of Amukta Island (Figure 11). The nearshore nesting site was similar to what was seen at the nearshore Seguam Island nesting site in terms of habitat and depth. At the large offshore reef, there was nesting activity between 43 m and 81 m (Appendix 1e).

Fox Islands

A large percentage of all video camera tows (22%) were made in the Fox Islands, but nesting sites were observed in only 3% of these tows (Figure 12). Atka mackerel

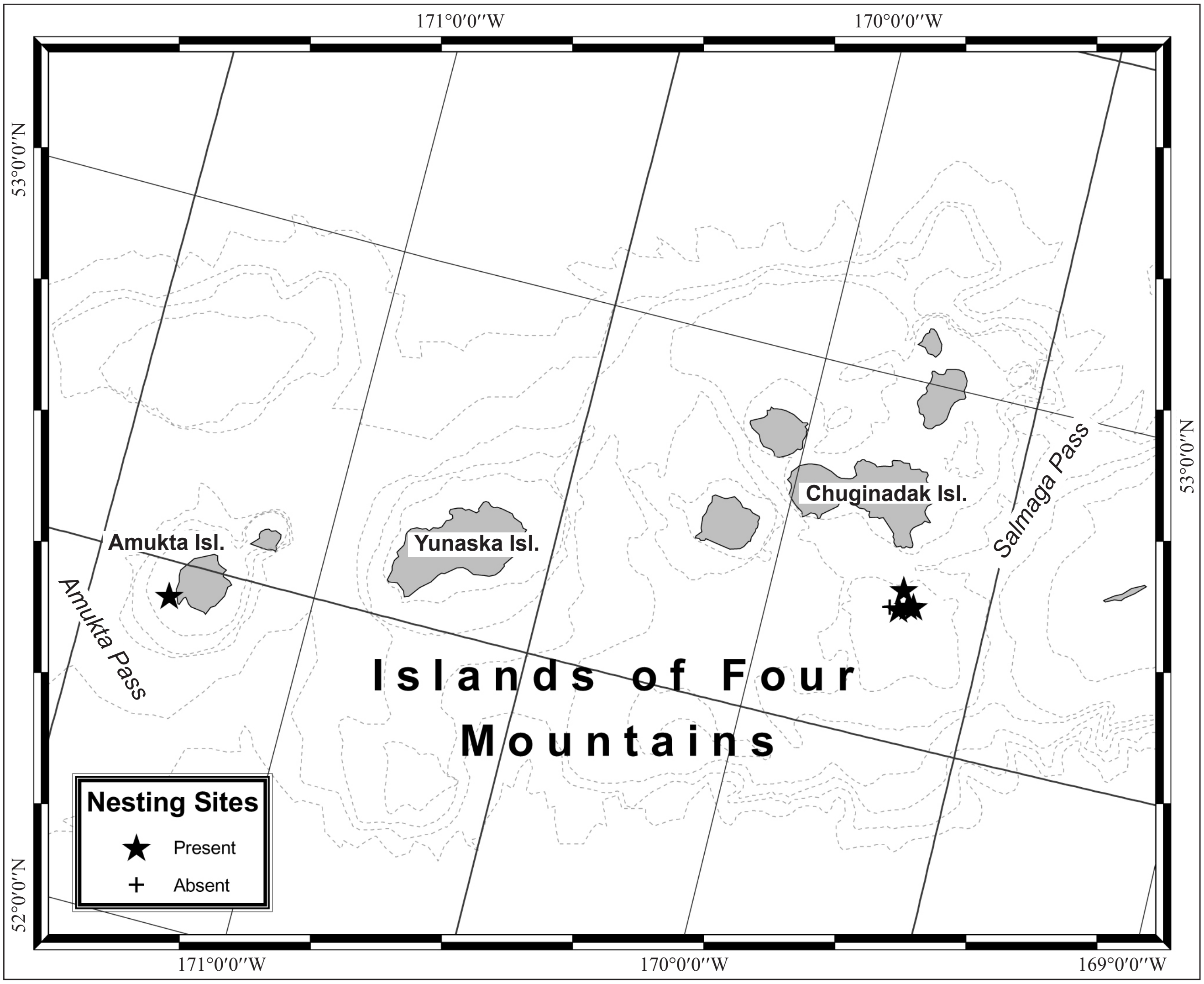

Figure 11. Map of the Islands of Four Mountains showing locations of video camera tows and Atka mackerel nesting sites.

were absent from camera tows made along the northwestern side of Unimak Pass and in the nearshore areas around the eastern half of Unalaska Island, the southern side of Akutan Island, and on the southwest shore of Umnak Island. Two areas, one in Umnak Pass and the other on a rocky reef south of Akutan Pass, showed large aggregations of nesting males. Depths for these sites ranged from 15 m to 42 m (Appendix 1f).

Gulf of Alaska

Towed video camera effort over the large continental shelf area south of the Alaska Peninsula was sparse and centered on Unga Island in the Shumagin Island group and Stevenson Entrance between Kodiak Island and the Kenai Peninsula (Figure 6). Of the 14 video camera tows, there was only 1 small nesting aggregation off the southwest side of Unga Island. During a 4 min period of a 21 min camera tow, 6 males exhibiting nesting color and behavior were observed. Average depth and temperature during this 4 min period was 44.9 m and 10.7°C (Appendix 1g). The water temperatures at this small nesting site were several degrees higher than any other nesting site.

DISCUSSION

This study expands the known depth and geographic range of Atka mackerel spawning and nesting habitat. Zolotov (1993) and Gorbunova (1962) concluded that Atka mackerel spawning and nesting off Kamchatka were confined to rocky coastal areas down to an absolute depth limit of 32 m. This study extends the known geographic range of nesting sites eastward from the

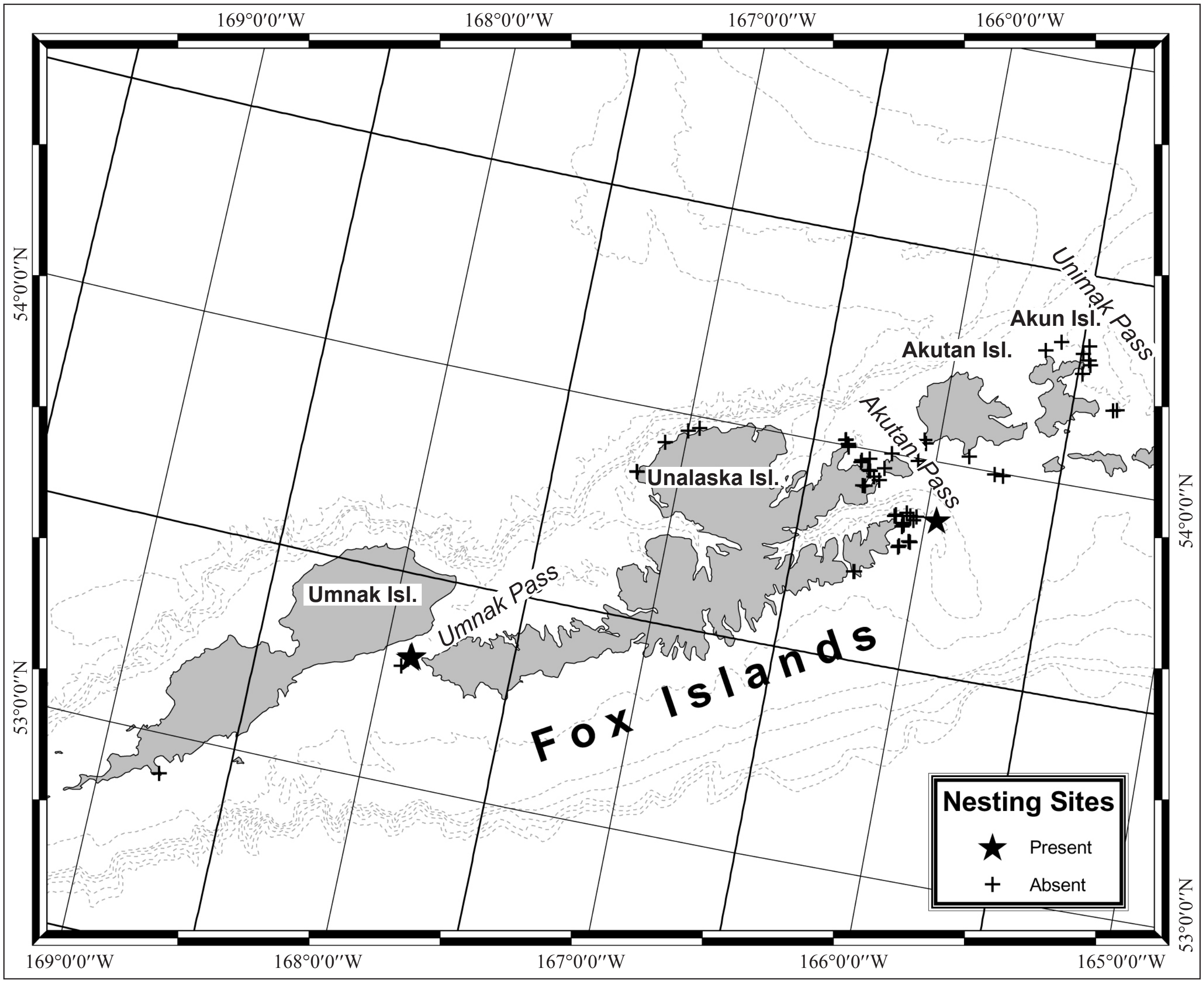

Figure 12. Map of the Fox Islands showing locations of video camera tows and Atka mackerel nesting sites.

Kamchatka Peninsula to Unga Island and the lower depth limit to 144 m.

Nesting habitat was invariably associated with rocky substrates and water currents; however, smaller-scale geomorphic and oceanographic features and physical properties of the rocky substrate were variable between different island groups and nesting sites. Determining the effect and interactions of these factors on the presence or absence of an Atka mackerel nesting site will require much more detailed analysis of physical features and the towed video camera footage.

This study showed that nesting was also present in the western Gulf of Alaska (GOA). It appears that nesting sites were less common and shallower in the western GOA compared to the continental shelf areas farther west; however, results about the depth limits and geographic extent of spawning and nesting sites in the GOA are unclear because sampling effort in the GOA was sparse and the lack of a strict survey design did not permit comparison of camera tow sampling effort.

Ronholt (1989) believed that the central GOA was the eastern geographical range of Atka mackerel distribution because the population was not resilient to fishing pressure. By mid-1980s, the GOA population of Atka mackerel in the Shumagin, Chirikof, and Kodiak areas disappeared after more than a decade of commercial fishing by foreign boats (Ronholt 1989). Since 1990, summer bottom trawl surveys conducted by the Alaska Fisheries Science Center have had an increasing percentage of tows catching Atka mackerel in the Shumagin area (Lowe et al. 2005). Atka mackerel were not caught in surveys east of the Shumagins until 2003, and catches in the central GOA still remain relatively small and patchy (Lowe et al. 2005).

The stock structure of the historical and existing populations is unknown, and genetics research will be required to determine if the existing population was recruited from a local remnant population, or from migrating juveniles or adults originating in the western GOA or eastern Aleutian Islands (Lowe et al. 2005). The westerly flowing Alaska Coastal and Alaska Stream Currents (Stabeno et al. 1999) make it very unlikely that larvae or juveniles are passively transported into the GOA from the Aleutian Islands region.

Historical data suggest a self-sustaining population of Atka mackerel was once present in the central GOA. On the outer shelf of Kodiak Island in the 1970s, Atka mackerel larvae, 10.3 mm in size, occurred in 80% of neuston tows during the fall sampling period (Kendall and Dunn 1985). Larvae of that size are days or weeks old (Gorbonuva 1962) and would indicate a spawning and nesting population of Atka mackerel in the same area. Further evidence that Atka mackerel recruited from the central Gulf are accounts of juvenile Atka mackerel reported in the burrows of puffins at Chowiet and Middleton Islands (Scott Hatch, USGS, unpublished data).

Alaskan Atka mackerel appear to have a more protracted nesting period than previously observed in the western Pacific Ocean. In Kamchatka, Zolotov (1993) found that spawning lasted until September, and Gorbunova (1962) determined that the incubation for Atka mackerel eggs was 40 d to 45 d, hence it was inferred that the nesting season lasted until early October. In Alaska, aggregations of nest-guarding males were observed at nesting areas during late October and histological studies show that female Atka mackerel are still spawning in October (McDermott and Lowe 1997). If incubation rates are the same or slower (as suggested by lower water temperatures) than reported by Gorbunova (1962), it is likely that aggregations of nest-guarding males remain one or two months beyond October.

Studies from the western Pacific Ocean conclude that from June to September Atka mackerel undergo a migration to shallow coastal waters (< 40 m) for spawning and nesting (Gorbunova 1962, Rutenburg 1962, and Zolotov 1993). This, and the questionable anecdotal account by Turner (1886) mentioned in the introduction, is the basis for suppositions made about a similar migration for Atka mackerel in Alaska (McDermott and Lowe 1997, Fritz and Lowe 1998, Lowe et al. 1998, Mecklenberg et al. 2002).

Observations of the distribution and depth of nesting sites from this study clearly show that a concerted nearshore migration is not taking place in Alaska. Results suggest that the nearshore nesting sites constitute only a fraction of the nesting habitat. Studies from the western Pacific Ocean were based on relatively few nesting sites over a much smaller geographical area (Gorbunova 1962, Rutenburg 1962, and Zolotov 1993) and favorable nesting habitat may have been limited to nearshore areas.

Compared to the western Pacific, nesting sites in Alaska were widespread across the continental shelf over a much broader depth range, and a majority of the sites were well beyond the maximum depth cited for nesting in the western Pacific Ocean (Gorbunova 1962, Rutenburg 1962, and Zolotov 1993). Furthermore, many of the nesting sites in our study—like Stalemate Bank, Wall's Plateau, Middle Reef, and Seguam Pass—were located far from any island or coastline at places.

Historical commercial fishing data from Alaska (Fritz and Lowe 1998) also do not support the thesis of a mass migration to coastal areas. These data show no shoreward shift in fishing effort during the summer and fall months and all sizes of Atka mackerel of both sexes are fished year-round in offshore waters (Fritz and Lowe 1998). This is during the same time period that a migration would have already taken place. Extensive nesting sites located during this study overlap with many of the offshore commercial fishing areas (Fritz and Lowe 1998), indicating no shoreward movement pattern of nesting males during the spawning period. A more consistent explanation for observations from this study and the commercial fishery data is that Atka mackerel populations become highly segregated during the spawning and nesting season and that males seek out favorable nesting habitat throughout their depth range.

It is probable that large schools of Atka mackerel observed on the surface in Alaskan coastal areas during the spring and summer (Turner 1886, Tanner 1890) may have been mistaken for a spawning migration or aggregation. Non-nesting Atka mackerel undergo diurnal vertical migrations (Nichol and Somerton 2002) and large surface aggregations may be non-nesting Atka mackerel (including reproductively mature and gravid females) making mesoscale movements to highly productive feeding areas in the vicinity of spawning and nesting grounds. This is supported by direct observations of surface aggregations, both inshore and offshore, by the principal author and others (M-S Yang, Alaska Fisheries Science Center, personal communication), where the aggregations were associated with the presence of euphausids (or some other zooplankton), current boundaries, or both. On two occasions, the towed video camera was dropped to the bottom in the midst of a surface aggregation and there was no evidence of nesting activity on the bottom.

Several possibilities may explain the remarkable difference in spawning depth range between this and the previous studies in Kamchatka. The most obvious is that researchers may have been constrained by depth. Another possibility is that nesting habitat in deeper areas was unsuitable within the smaller geographic range of the study. A thorough discussion of the definition of "suitable" nesting habitat is beyond the scope of this paper, but lack of rocky substrate or favorable water temperature are two possibilities. For example, at the nearshore Seguam Island nesting site, there was a transition to unconsolidated sand, shell, and cobble beyond 32 m and this was obviously not favorable habitat for spawning and nesting. The coastal areas off Kamchatka Peninsula may have similar transitions in substrate with depth.

Water temperature did not appear to limit the upper or lower depth boundaries of Atka mackerel nesting sites in this study because the temperature ranges observed varied little and were not within the range considered lethal to embryos. Gorbunova (1962) notes that water temperatures below 3°C and above 15°C can be lethal to eggs or unfavorable for embryonic development depending on the exposure time. Water temperatures exceeding those thresholds may be a thermal barrier for spawning and nesting. The lowest water temperature observed in this study was 3.9°C and typical spawning ground temperatures ranged from 4.0°C to 5.5°C. Low water temperatures may have limited the lower depth boundary of nesting sites off Kamchatka because Gorbunova (1962) reported episodic water temperatures below 3.0°C at some nesting sites at depths ranging from 20 m to 30 m. The lack of temperature stratification over a wide depth range in this study indicates that there is a high degree of vertical mixing at nesting sites, which is likely due, in part, to strong tidal and ocean currents (Stabeno et al. 1999). The relative homogeneity of temperature with depth seen in the Aleutian archipelago during this study suggests that factors besides temperature may limit the lower depth range of Atka mackerel spawning and nesting.

Increasing depth or turbidity, which can reduce light levels, may be among the factors limiting the maximum nesting site depth. Water clarity and light penetration of the marine environment can vary significantly by area. Light intensity decreases with increasing water depth and the loss of intensity varies by wavelength depending on the quality and amount of organic and inorganic material in the water (Levine and MacNichol 1982). Many of the Atka mackerel's behavioral responses are elicited by visual stimuli. They show a diurnal vertical migration in response to changing light levels (Nichol and Somerton 2002) and they have an elaborate reproductive behavior involving sexual dichromatism, territorial behavior, and mating displays. Behavioral responses to visual cues suggest that adequate light of the proper intensity and wavelength is a requisite for nesting. Water turbidity in the Aleutian archipelago, in places like Wall's Plateau, Seguam Pass and Cape Yakak, was very low; nesting sites at these locations were some of the deepest observed. The Aleutian archipelago is comprised of relatively small, rocky, volcanic islands that do not provide as large a source of runoff as the Alaska mainland or Kamchatka Peninsula. This results in lower turbidity and better light penetration.

Results from dive transects showed a trend towards significantly fewer egg masses above 20 m water depth. Potential factors limiting the shallow end of the distribution of nesting sites include kelp, green sea urchins, and wave surge. Gorbunova (1962) and Zolotov (1993) discuss how kelp and algae at shallow depths can have a negative effect on eggs by aiding stagnation and reducing egg aeration. Giorgi and Congleton (1984) investigated the effects of current velocities on the development and survival of embryos in another hexagrammid with similar nesting behavior, the lingcod *Ophiodon elongatus*. They found that current velocities of 10 cm s^{-1} to 15 cm s^{-1} were necessary for keeping oxygen levels within the interstices of an egg mass the same as the surrounding water. Low current velocities resulted in mortality or retarded embryo development. All the nesting sites in this study and those in Kamchatka (Gorbunova 1962, Zolotov 1993) were located in areas with noticeable current. Many of the sites were situated in or near island passes where tidal flow between the North Pacific Ocean and the Bering Sea generate strong currents. Nesting sites farther from shore are also affected by currents generated by the general circulation of the GOA and Aleutian archipelago with the westward flowing Alaska Stream on the Pacific side and the eastward flowing Aleutian North Slope Current on the Bering Sea side (Stabeno et al. 1999). The maximum average daily buoy speeds of the Alaska Stream range from 40 cm s^{-1} to 95 cm s^{-1}, and the strongest daily average currents for the Aleutian North Slope Current (measured at 100 m) are > 40 cm s^{-1} (Stabeno et al. 1999).

In the shallow coastal areas, wave surge may also limit the upper depth boundary of nesting sites. Waves approaching the shore cause water near the bottom to move in a horizontal, back and forth motion known as wave surge. The depth and force of wave surge increases with the wave period and with a decrease in depth. Gorbunova (1962) notes that wave surge could wash away eggs at depths less than 10 m. Wave surge was experienced firsthand during dives at the nearshore coastal nesting site at Seguam Island. On a particularly stormy day, its effects were also observed on the underwater *in situ* camera at 23 m. Closer to shore, where the wave surge intensifies, the constant back and forth motion could dislodge eggs, and it would also make it difficult or impossible for a male and female Atka mackerel to remain still for the purposes of spawning or guarding a nest.

The green sea urchin, *S. droebachiensis*, plays a key role in nearshore benthic communities (Estes and Harrold 1988) and its high densities in Alaska coastal areas may be unfavorable for Atka mackerel nesting in shallow water habitat. The primary food of green sea urchins is macro and microalgae, but they are opportunists and can also browse or scavenge for animal material (Briscoe and Sebans 1988). The list of potential food items includes sponges, bryozoans, ascidians, young mussels, polychaetes, sand dollars, barnacles, whelks, periwinkles, and dead fish (Himmelman 1971; Briscoe and Sebans 1988).

Atka mackerel eggs are another available food item for the green urchin. The *in situ* camera showed nest-guarding males removing urchins from their nesting territory, and urchin bite marks on the camera rigging demonstrate their potential for damaging egg masses. When placed in an aquarium with egg masses, the urchins grazed on the eggs and damaged the outer layers. Green sea urchins are efficient feeders and when they are in dense aggregations, as they are in some nearshore kelp beds or barrens in Alaska, they can sweep the bottom and dramatically affect the benthic community by completely denuding it of kelp (Lawrence 1975; Estes and Duggins 1995). Furthermore, the higher the urchin density, the higher the risk of injury and bioenergetic cost to guardian males, who must remove urchins from their nests. There is a high energetic cost to male parental care (Marconato et al. 1993), so it is important that nest-guarding males conserve their energy during a protracted nesting period with limited feeding opportunities (Zolotov 1993).

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APPENDIX

Appendix 1. Table listing the midpoint positions of camera tows by island group, and the averages and ranges for the depth and temperature where nest-guarding males were seen.

a) Stalemate Bank and the Near Islands

Tow midpoint		Depth (m)			Temperature (°C)		
Latitude	Longitude	Mean	Min.	Max	Mean	Min.	Max
53°04.2′N	170°56.6′E	67.0	47.0	92.0	4.3	4.1	5.1
52°59.8′N	173°03.0′E	29.6	22.3	36.8	7.9	7.7	7.9
52°59.8′N	173°06.6′E	26.0	18.1	35.4	8.3	8.3	8.7
52°59.7′N	173°03.0′E	21.2	15.9	24.5	8.2	8.1	8.3
52°55.5′N	173°19.0′E	38.5	34.7	43.8	8.2	8.1	8.9
52°50.4′N	172°34.9′E	87.6	83.7	95.2	6.1	6.0	6.2
52°46.8′N	172°41.2′E	98.9	90.7	111.5	6.4	6.1	6.7
52°44.0N	172°53.4′E	71.0	64.5	75.0	6.9	6.7	7.3
52°43.6′N	172°52.3′E	88.7	80.6	93.3	5.8	5.7	6.4
52°42.8′N	174°12.5′E	49.0	32.9	58.0	7.0	6.3	7.5

b) Rat Islands

Tow midpoint		Depth (m)			Temperature (°C)		
Latitude	Longitude	Mean	Min.	Max	Mean	Min.	Max
52°02.1′N	179°40.5′E	50.0	44.2	53.4	4.7	4.7	4.7
52°02.0′N	179°40.3′E	46.1	42.2	49.3	4.7	4.7	4.7
52°00.0′N	179°00.7′E	72.8	68.1	77.9	4.8	4.7	4.8
51°32.4′N	178°35.8′E	96.4	92.5	101.0	5.9	5.9	5.9
51°33.5′N	178°33.0′E	96.2	92.1	100.3	5.9	5.9	5.9
51°43.8′N	178°31.1′E	90.9	86.4	96.3	5.2	5.1	5.2
51°42.4′N	178°30.5′E	71.8	67.8	79.0	4.3	4.3	4.5
51°42.7′N	178°27.0′E	29.9	22.9	38.8	4.3	4.3	4.7
51°42.9′N	178°26.6′E	27.1	23.4	35.4	4.4	4.3	4.7
51°51.4′N	177°08.8′E	94.4	91.3	96.3	4.5	4.5	4.5
51°55.2′N	177°51.0′E	54.8	51.6	57.7	4.5	4.5	4.5
51°55.0′N	177°50.7′E	27.1	23.0	29.7	4.5	4.5	4.5
51°51.5′N	177°47.8′E	101.8	100.3	103.7	5.0	5.0	5.0
51°49.9′N	177°34.0′E	103.6	93.6	116.0	4.9	4.9	4.9
51°50.2′N	177°33.7′E	95.9	92.3	100.9	4.9	4.9	4.9
51°50.9′N	177°10.0′E	73.1	68.4	75.5	4.9	4.9	4.9
52°07.2′N	176°31.6′E	63.9	60.2	66.8	5.4	5.4	5.4
52°09.0′N	176°31.5′E	90.8	80.3	99.7	5.1	5.0	5.1
52°08.8′N	176°30.9′E	88.7	79.9	93.8	5.3	5.2	5.3
51°55.1′N	176°02.3′E	81.0	78.1	83.4	5.1	5.1	5.2
51°57.6′N	175°59.0′E	59.9	56.2	65.9	5.4	5.3	5.6
51°57.0′N	175°58.2′E	68.1	44.5	97.4	4.8	4.6	5.1
51°57.4′N	175°57.7′E	78.1	62.8	87.6	5.0	4.9	5.3
51°56.9′N	175°56.2′E	98.3	95.8	99.3	4.8	4.8	4.8
52°23.4′N	175°51.2′E	27.1	26.5	27.9	5.0	5.0	5.0
52°23.4′N	175°51.1′E	24.1	17.2	28.3	5.0	4.8	6.3
52°23.8′N	175°47.9′E	78.1	75.0	79.7	4.4	4.4	4.4
52°13.7′N	175°12.3′E	127.8	120.6	134.4	4.5	4.4	4.5

c) Delarof Islands

Tow midpoint		Depth (m)			Temperature (°C)		
Latitude	Longitude	Mean	Min.	Max	Mean	Min.	Max
51°22.4′N	179°31.2′W	93.1	86.3	101.2	5.2	5.1	5.3
51°36.0′N	178°32.6′W	33.9	30.2	40.6	5.8	5.8	6.3
51°33.0′N	178°23.8′W	82.2	73.8	90.4	4.5	4.4	4.5
51°43.5′N	178°13.8′W	74.2	71.8	79.1	5.1	5.0	5.2
51°43.0′N	178°13.4′W	57.3	48.5	68.4	5.2	5.2	5.2
51°42.8′N	178°12.8′W	52.1	46.1	57.2	5.8	5.8	6.0
51°42.8′N	178°12.6′W	54.2	49.7	57.8	5.4	5.2	5.4

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d) Andreanof Islands

Tow midpoint		Depth (m)			Temperature (°C)		
Latitude	Longitude	Mean	Min.	Max	Mean	Min.	Max
51°52.5′N	177°35.1′W	46.6	41.0	52.7	5.3	5.3	5.4
51°52.8′N	177°34.8′W	63.6	55.0	68.4	5.4	5.4	5.4
51°34.1′N	177°00.1′W	113.2	92.3	135.6	5.0	5.0	5.1
51°34.7′N	177°00.5′W	103.6	94.9	122.6	5.4	5.4	5.4
51°34.3′N	177°00.0′W	105.3	96.7	116.9	5.4	5.3	5.4
51°34.2′N	176°59.4′W	101.1	91.6	106.2	5.4	5.4	5.4
52°06.6′N	173°06.5′W	32.2	27.1	36.0	7.1	7.1	7.1
52°06.1′N	173°03.8′W	22.2	18.3	24.8	7.3	7.3	7.4
52°06.2′N	173°02.1′W	25.0	25.0	25.0	7.1	7.1	7.1
52°05.9′N	173°00.1′W	20.2	18.7	21.1	7.1	7.1	7.2
52°04.1′N	172°08.5′W	136.7	121.5	143.8	5.2	5.2	5.2
52°06.0′N	172°57.9′W	20.5	20.5	20.5	7.1	7.1	7.1
52°05.9′N	172°57.7′W	22.3	19.1	24.4	7.2	7.1	7.3
52°05.9′N	172°57.6′W	20.7	16.7	23.6	7.3	7.3	7.3
52°02.5′N	172°55.1′W	63.5	62.6	64.0	4.1	4.1	4.1
52°05.7′N	172°47.0′W	73.5	69.8	78.2	5.2	5.2	5.2
52°00.7′N	172°46.2′W	95.5	84.4	107.5	3.9	3.9	3.9
52°06.1′N	172°42.4′W	95.7	87.3	112.3	4.8	4.7	5.0
51°59.3′N	172°42.0′W	107.7	104.7	112.3	4.2	3.9	4.3
52°06.8′N	172°41.3′W	113.2	98.8	122.5	4.6	4.5	4.7
52°02.4′N	172°04.9′W	115.0	113.2	116.3	4.5	4.5	4.5
52°06.1′N	172°38.6′W	126.9	118.9	132.7	5.3	5.0	5.8
52°16.4′N	172°25.0′W	38.2	34.6	47.8	5.2	4.8	5.9
52°16.4′N	172°24.9′W	36.8	28.5	43.0	5.6	5.2	6.3
52°16.4′N	172°24.8′W	34.9	24.0	62.0	4.7	4.6	5.1
52°16.4′N	172°24.7′W	34.7	33.5	36.7	6.4	5.9	6.7
52°16.5′N	172°24.7′W	31.6	29.1	35.5	6.1	6.0	6.1
52°16.6′N	172°24.5′W	27.0	23.5	29.5	5.1	5.0	5.9
52°16.6′N	172°24.4′W	-	-	-	-	-	-
52°22.4′N	172°21.5′W	24.1	21.1	28.0	4.6	4.5	4.7
52°22.4′N	172°21.2′W	28.7	21.9	33.7	5.0	5.0	5.0
52°22.1′N	172°20.4′W	20.4	17.9	21.9	4.5	4.5	4.5
52°22.1′N	172°20.3′W	23.3	21.5	23.6	4.4	4.4	4.4
52°22.1′N	172°20.1′W	-	-	-	-	-	-
52°22.1′N	172°20.1′W	19.0	17.9	19.9	4.4	4.3	4.4
52°22.1′N	172°19.9′W	25.8	24.0	26.0	4.6	4.5	4.8
52°22.0′N	172°19.6′W	-	-	-	-	-	-
52°22.1′N	172°19.6′W	22.6	20.0	24.0	5.3	5.1	5.6
52°22.1′N	172°19.6′W	26.6	20.0	30.0	4.7	4.5	4.9
52°22.0′N	172°19.4′W	20.3	18.3	21.9	5.0	5.0	5.0
52°21.9′N	172°19.3′W	29.9	21.1	35.7	5.0	5.0	5.0
52°21.7′N	172°18.9′W	26.5	21.9	29.2	5.0	4.9	5.0
52°21.6′N	172°18.9′W	23.3	21.1	24.8	5.0	4.9	5.3
52°21.3′N	172°18.2′W	24.0	21.5	25.2	5.1	5.0	5.3
52°20.6′N	172°18.0′W	16.6	15.5	16.7	4.9	4.8	4.9
52°19.5′N	172°17.2′W	34.4	26.0	46.0	4.4	4.4	4.5
52°03.2′N	172°06.9′W	117.9	115.1	119.4	4.5	4.4	4.5
52°01.5′N	172°04.3′W	102.8	85.0	113.2	4.1	4.1	4.2
52°02.5′N	172°02.9′W	118.7	117.3	120.4	4.4	4.4	4.4
52°02.6′N	172°01.3′W	111.4	100.2	121.4	4.5	4.4	4.5
52°01.0′N	172°0.0′W	111.4	105.7	121.3	4.5	4.4	4.5
52°00.6′N	171°58.5′W	123.5	116.8	134.1	-	-	-

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e) Islands of Four Mountains

Tow midpoint		Depth (m)			Temperature (°C)		
Latitude	Longitude	Mean	Min.	Max	Mean	Min.	Max
52°27.2′N	171°19.2′W						
52°41.5′N	169°40.9′W	44.3	43.0	45.3	4.8	4.8	4.8
52°41.1′N	169°42.1′W	53.4	44.1	65.5	4.8	4.8	4.8
52°42.8′N	169°42.1′W	79.0	75.5	81.0	4.7	4.7	4.7
52°41.6′N	169°40.2′W	45.5	35.3	51.5	4.7	4.6	4.7

f) Fox Islands

Tow midpoint		Depth (m)			Temperature (°C)		
Latitude	Longitude	Mean	Min.	Max	Mean	Min.	Max
53°18.3′N	167°54.1′W	17.8	15.1	21.8	7.2	7.2	7.4
53°18.5′N	167°53.7′W	40.5	37.8	42.2	7.0	7.0	7.0
53°18.5′N	167°53.9′W	31.0	15.3	40.8	7.2	7.0	7.2
53°52.0′N	165°57.4′W	46.7	31.3	60.3	7.9	7.7	7.9

g) Gulf of Alaska

Tow midpoint		Depth (m)			Temperature (°C)		
Latitude	Longitude	Mean	Min.	Max	Mean	Min.	Max
55°12.2′N	160°34.5′W	44.9	41.0	50.6	10.7	10.2	11.0