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Reprinted from the Alaska Fishery Research Bulletin
Vol. 10 No. 2, Winter 2003
The Alaska Fisheries Research Bulletin can be found on the World Wide Web at URL:
http://www.adfg.state.ak.us/pubs/afrb/afrbhome.php

Alaska Fishery Research Bulletin 10(2):104–118. 2003.
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Biological and Spatial Characteristics of the Weathervane Scallop *Patinopecten Caurinus* at Chiniak Gully in the Central Gulf of Alaska

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ABSTRACT: A manned submersible was used to collect biological and behavioral information on a deepwater population of weathervane scallops *Patinopecten caurinus* near Kodiak Island in the central Gulf of Alaska. Counts and positions of weathervane scallops and 3 additional species groups (anemones [*Cribrinopsis fernaldi* and *Metridium senile*], sunflower sea stars *Pycnopodia helianthoides*, and sea whips [*Protoptilum* sp. and *Halipteris willemoesi*]) along 20 fixed transects were compiled from video footage of the seafloor. The study site encompassed areas open to bottom trawling and scallop dredging and areas closed for 11 and 12 years. Statistical methods of circular tests, neighbor *K* analysis for one-dimensional data, analysis of variance, and Spearman rank correlation coefficient were used to assess weathervane scallop orientation, spatial characteristics, differences in abundance and size distributions between open and closed areas, and faunal associations. Orientation of weathervane scallops was directed with most oriented towards the strongest, prevailing bottom currents or the reciprocal, weaker currents. Adult weathervane scallops were aggregated in *patch lengths* ranging from less than 10 m to over 700 m. In 1999 only, the open area had higher prerecruit abundance relative to recruit abundance than the closed area. Weathervane scallop density (number of scallops m^{-2}) was not significantly lower in the open than in the closed area. There was some evidence of positive spatial associations between adult weathervane scallops and both large sea whips and anemones, and negative spatial association between adult weathervane scallops and sunflower sea stars. Juvenile weathervane scallops exhibited positive spatial association with anemones. Weathervane scallop density tended to be high in areas of high sea whip density and low in areas of high sunflower sea star density.

INTRODUCTION

Weathervane scallops *Patinopecten caurinus* (Gould, 1850) range in the northeastern Pacific Ocean from the Pribilof Islands, Alaska, and the southern Bering Sea to Point Reyes, California, at depths between 2 and 300 m (Foster 1991). Since 1967, this species has supported a relatively small but important commercial fishery in the Gulf of Alaska (GOA) and Bering Sea (Shirley and Kruse 1995) worth $2.15 million annually in the 1980s (Kruse and Shirley 1994). The 1990s brought significantly increased landings to the fishery (Kruse and Shirley 1994), which until that time, had been passively managed (i.e., gear restrictions, area and seasonal closures). Increased exploitation of weathervane scallop stocks by a growing, full-time dedicated fleet, led, in part, to the Alaska Department of Fish and Game (ADF&G) initiating a more active fishery management plan in 1994 (Kruse and Shirley 1994). Further restrictive measures were implemented, and vessels were required to have onboard, certified observers to collect biological information from scallop catches. Despite increased interest in management of the fishery in Alaska, however, little directed research on the biology of this species has been done in recent years.

Compared with other commercially exploited scallop species worldwide, little is known about the life history of weathervane scallops. Some information about weathervane scallop biology and abundance can be gathered from the few studies and biological surveys conducted in Alaska (Haynes and Powell 1968; Hennick 1970, 1971, 1973; Hammarstrom and Merritt 1985; Kaiser 1986; Ignell and Haynes 2000), British Columbia (MacDonald and Bourne 1987), Washington (Haynes and Hitz 1971), and Oregon (Starr and

Authors: MICHELE M. MASUDA is a mathematical statistician at the Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 11305 Glacier Highway, Juneau, AK 99801. Email: michele.masuda@noaa.gov. ROBERT P. STONE is a fishery research biologist at the Auke Bay Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 11305 Glacier Highway, Juneau, AK 99801.
Acknowledgments: Financial support for this project was provided by the Auke Bay Laboratory. We thank John Karinen, Jeff Regelin, Patrick Malecha, Ken Krieger, and Linc Freese of the Auke Bay Laboratory for their assistance in the field. We thank Captain Wade Loofbourrow, the crew of the Alaska Department of Fish and Game R/V *Medeia*, and the staff at Delta Oceanographics for their assistance and support. We also thank Nancy Maloney and Jerry Pella of the Auke Bay Laboratory and 3 anonymous reviewers for their helpful comments on this manuscript.

McCrae 1983; Robinson and Breese 1984). However, little is known about the behavior, faunal associations, and spatial distribution of this species. Even less is known about juvenile weathervane scallops, including their spatial relation to adults. Due to their large size and long lifespan, weathervane scallops are especially vulnerable to overharvest (Kruse and Shirley 1994); therefore, a better understanding of their behavior, faunal associations, and spatial distribution is useful to their management. In 1998 and 1999, we initiated studies to examine the effects of ambient levels of bottom trawling on soft-bottom habitat in the central GOA. Our study sites encompassed areas near Kodiak Island closed year-round to bottom trawling and scallop dredging by the North Pacific Fishery Management Council in 1987 to protect valuable habitat for Tanner *Chionoecetes bairdi* and red king *Paralithodes camtschaticus* crabs. We employed the manned submersible *Delta* to make in situ observations of the distribution and abundance of epibenthos along fixed transects in areas open and closed to bottom trawling and scallop dredging (Stone et al. In press). We identified 34 epifauna taxa in video footage of the seafloor at our primary study site in Chiniak Gully (Stone et al. In press). Due to the paucity of biological data on weathervane scallops and its commercial importance, collecting detailed in situ observations of weathervane scallops—hereafter referred to as scallops unless otherwise noted—was seen as a valuable opportunity to contribute to the limited knowledge of this species. Observations in the closed area provided biological information on scallops in an environment presumed undisturbed by bottom trawling and scallop dredging for 11 and 12 years. In addition, we used observations from the adjacent area open to bottom fishing in a control-impact study of abundance, size structure, spatial distribution, and faunal associations of a scallop population.

Chiniak Gully is one of the more heavily trawled areas in the central GOA (Rose and Jorgensen In press), although the level of trawling there is modest compared to other areas worldwide (National Research Council 2002). Precise levels of scallop dredging in Chiniak Gully prior to the start of the observer program in 1993 are unknown but were moderate in 1993 and 1994. Most dredging effort has shifted outside the study area in recent years (G. Rosenkranz, Alaska Department of Fish and Game, Kodiak, personal communication) and may indicate that other areas in the central GOA presently support larger populations of scallops than our study area (Bechtol and Gustafson 2002). Although this study was not designed to examine the effects of scallop dredging (and bottom trawling) on scallops per se, we examined differences in abundance and size distributions between areas open and closed to bottom trawling and scallop dredging. Based on previous research on weathervane scallops (Hennick 1973) and sea scallops *Placopecten magellanicus* (Langton and Robinson 1990; Thouzeau et al. 1991), we hypothesized that the open area would have lower scallop abundance and exhibit a shift in age composition to younger scallops.

In this study, we demonstrate the use of a manned submersible to make in situ observations of scallops in deep water. We investigate scallop orientation in bi-directional bottom currents, spatial distribution on transects, faunal associations, and differences in abundance and size distributions between open and closed areas to bottom trawling and scallop dredging. Juvenile scallops were investigated separately for spatial distribution, faunal associations, and differences in abundance between open and closed areas.

MATERIALS AND METHODS

Study site and sampling design

The study site, located in Chiniak Gully near Kodiak Island in the central GOA (Figure 1), slopes gently and has a uniform substratum of fine sand and silt. Median grain size of sediment sampled at the study site ranged from 101 to 241 μm (Stone and Masuda 2003). Depths at the site range from 105 to 151 m. We deployed a current meter near the study site in June, 2001, that indicated that bottom currents are strong (>0.28 m s^{-1}) and bi-directional from west to east.

Two cruises aboard the ADF&G R/V *Medeia* were conducted, 4 to 15 June 1998 and 13 to 17 August 1999. The 2-person submersible *Delta* was used to record continuous video footage of the seafloor and epifauna on 20 fixed transects (10 per year) that traversed adjacent open and closed areas to bottom trawling and scallop dredging (Figure 1). Transects were parallel, 250 to 500 m apart when years were combined, and 3,000 m in length (Figure 1). Transects were numbered 1 to 10 in both years with Transect 1 furthest east and Transect 10 furthest west. The transects in 1999 were evenly interspersed among the transects sampled in 1998. Transects 3 and 10 in 1998 were approximately 2,500 m long. Transects were purposely oriented along isobaths to minimize any biotic variation on transects due to depth differences. Maximum depth differential on any transect was 18 m. The study site encompasses approximately 12.9 km^2 of area, of which 14,500 m^2 and 23,500 m^2 of seafloor (0.3% of the total area) were

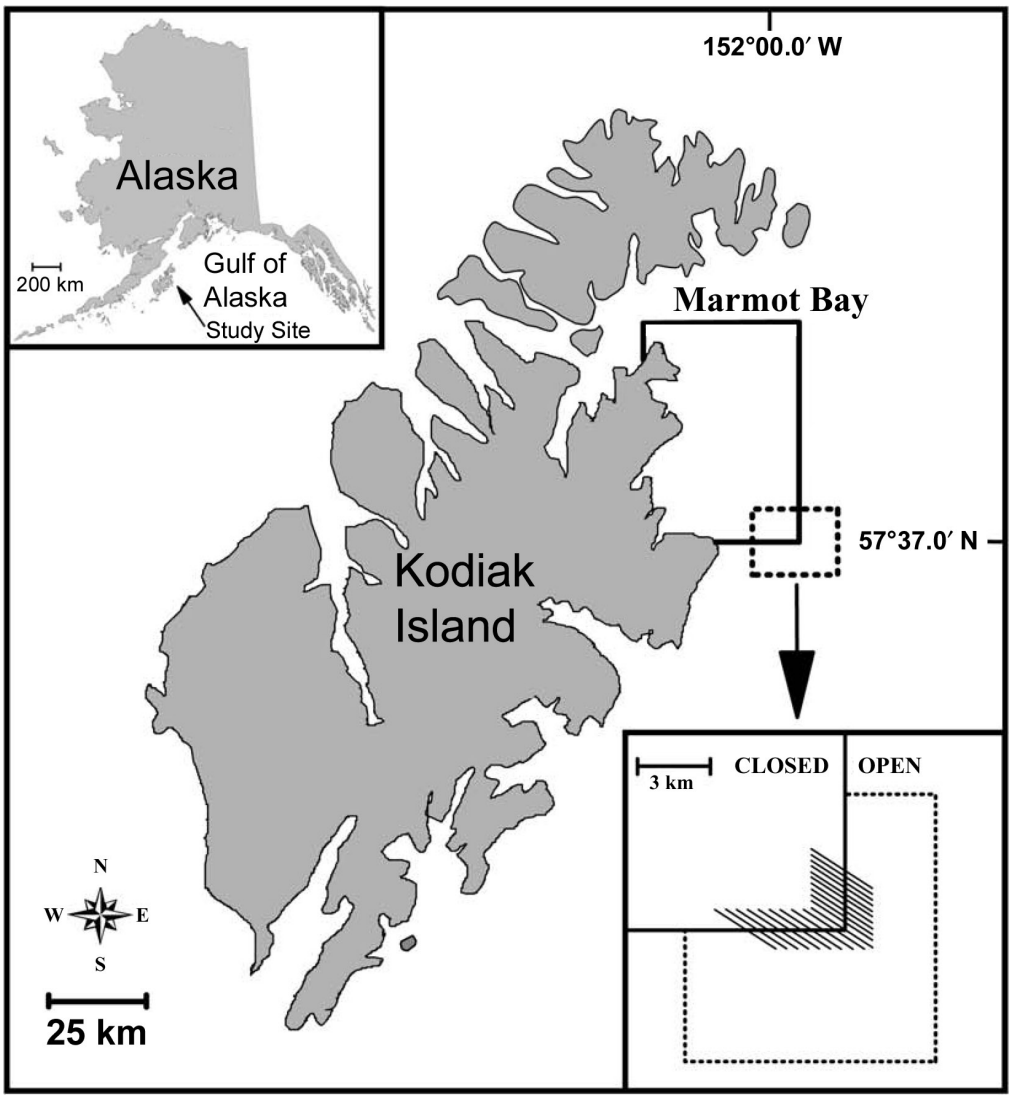

Figure 1. Map of study site (dashed line) in Chiniak Gully near Kodiak Island, Alaska and one area closed to bottom trawling and scallop dredging year-round (solid line). Ten transects per year traversed adjacent open and closed areas to bottom trawling and scallop dredging (lower inset). The transects in 1999 were evenly interspersed among the transects sampled in 1998. Bottom-trawling intensity and scallop-dredging intensity at the study site were estimated within an area approximately 3 km from transects (dashed line, lower inset).

videotaped in 1998 and 1999, respectively. Commercial trawling intensity in the open area was estimated, using the methods described in Stone and Masuda (2003), as the maximum percentage of seafloor in the study area that was trawled at least once per year. Maximum trawl intensity for the 5 years preceding the study was estimated as 29.4% of the seafloor per year (Stone and Masuda 2003). The estimate includes only the area of the seafloor potentially contacted by the footrope and can therefore be considered a conservative estimate. The maximum percentage of seafloor in the study area dredged for scallops at least once per year was estimated for the 6 years preceding the study: 17% of the seafloor in 1993 and steadily declining to less than 1% in 1998 (G. Rosenkranz, Alaska Department of Fish and Game, Kodiak, personal communication).

The submersible *Delta*, occupied by a pilot and scientific observer, is equipped with external video cameras mounted perpendicular to the seafloor and sub-to-tender vessel communication. The submersible followed a predetermined bearing at a near constant speed (0.27 to 0.82 m s^{-1}) along each transect, and its course was modified if necessary via communication with the tender vessel. The submersible's continuous contact with the seafloor maintained the camera lens at a near constant altitude above the seafloor (≈80 cm). Width of image area was approximately 0.5 m in 1998, 0.85 m for Transects 1 to 7 in 1999, and 0.63 m

for Transects 8 to 10 in 1999. Images were continuously recorded on a Hi-8 videocassette recorder. The video camera also recorded 2 parallel laser marks 20 cm apart, projected onto the seafloor. The scientific observer aboard the submersible viewed the image area laterally and vocally recorded observations.

In the laboratory, scallops partially or completely viewed on videotape were counted. Scallop abundance was assessed with scallop density (number of scallops m^{-2}), making transects of differing widths comparable. Data recorded for each scallop included shell height of the left or upper valve, position on the transect, and angle of orientation relative to true north. Shell height (i.e., the perpendicular straight-line distance from the base of the umbo to the outer shell margin) was measured on a flat screen, to the nearest 1 mm, with a vernier caliper. On-screen shell height was converted to true height using the projected laser marks as references. Each scallop's angle of orientation was measured on-screen with a protractor, to the nearest 5°, from the medial plane of the upper valve. Reported direction that the ventral margin faced was corrected to true north, assuming true north is 0° and positive angles run clockwise (east=90°, south=180°, and west=270°). Direction of bottom currents was estimated from video footage at the start and end of each transect and at 500 m intervals, based on submersible heading and movement direction of biota, debris, and sediment. Neither age, as determined by enumeration of annual growth rings on the shell (MacDonald and Bourne 1987), nor gender could be determined from video footage.

Other data recorded from video footage included recession of scallops in the sediment and presence of anemones (e.g., *Cribrinopsis fernaldi*, *Metridium senile*, and a smaller unidentified species) on the shell. Counts and positions on transects of other species groups were recorded for analyses of faunal association with scallops: anemones (*C. fernaldi* and *M. senile*), sunflower sea stars *Pycnopodia helianthoides*, and sea whips. Sea whips were classified as small (height <20 cm) (*Protoptilum* sp.) or large (height >20 cm) (*Halipteris willemoesi*). Sea whip heights were estimated using the projected laser marks as references.

Statistical analysis

Differences between open and closed areas to bottom trawling and scallop dredging

Differences in adult and juvenile scallop density and mean shell height between areas open and closed to bottom trawling and scallop dredging were tested with individual ANOVA models. The 3-factor models included fixed effects *status* (variable indicating open or closed area), *year*, *transect* (blocking variable) nested within *year*, and the interaction between *status* and *year*. Dependent variables (scallop density and mean shell height) were Box-Cox transformed (Box and Cox 1964; Venables and Ripley 1999) if necessary with a different power parameter λ estimated in the range [-2,2] for each variable. The model of scallop density was fit with ordinary least squares, and the model of mean height was fit with weighted least squares, weights equaling number of heights averaged by *status* and *transect*. Based on previous research on weathervane scallops (Hennick 1973) and sea scallops *P. magellanicus* (Langton and Robinson 1990; Thouzeau et al. 1991), we expected lower scallop density in the open than in the closed area; therefore, we used a one-tailed *t*-test.

A difference in size-frequency distributions of scallops in open and closed areas was tested with a 2-sample Kolmogorov-Smirnov (K-S) goodness-of-fit test (Mathsoft, Inc. 2000; Paddack and Estes 2000). The null hypothesis of the test is that the true distribution functions for the 2 samples compared are equal. The α-level in all tests was 0.05.

Orientation

Randomness of scallop orientation was tested with Rao's spacing test (Batschelet 1981). Scallop angles observed in the closed area were assumed a random sample and bimodally distributed based on their linear histogram (Figure 2) and a previous study of scallop orientation in an area with similar bi-directional bottom currents (Mathers 1976). Angles, θ, were assumed drawn from a mixture of 2 von Mises distributions with probability density function (pdf)

$$f(\theta \mid \mu_1,\kappa_1, \mu_2, \kappa_2, p) = p \bullet f(\theta \mid \mu_1, \kappa_1) + (1-p) \bullet f(\theta \mid \mu_2,\kappa_2),\ 0<p<1,\ 0°<\theta\leq 360°,$$

where $f(\theta \mid \mu_i, \kappa_i)$ is the pdf of a von Mises distribution, a symmetric, unimodal distribution with mean direction μ_i and concentration κ_i (Fisher 1995), and p is the mixing proportion (Spurr and Koutbeiy 1991). The von Mises distribution will hereafter be referred to as $vM(\mu,\kappa)$. Using iterative method of moments to minimize a least-squares criterion, Spurr and Koutbeiy (1991) outlined fitting the 5-parameter mixture model. Initial values of parameters were estimated from Mardia's 3-parameter model (Spurr and Koutbeiy 1991; Fisher 1995). Circular standard errors ($\hat{\sigma}_1$ and $\hat{\sigma}_2$) and approximate 95% confidence intervals were computed for $\hat{\mu}_1$ and $\hat{\mu}_2$ (Fisher 1995).

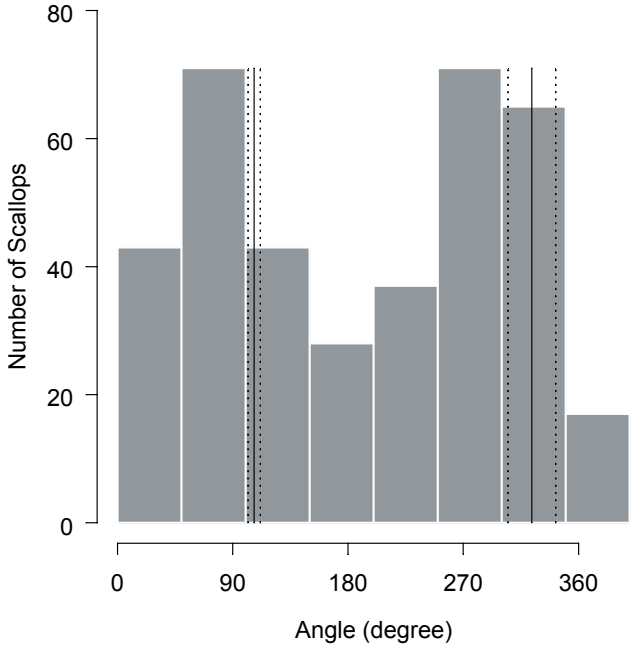

Figure 2. Linear histogram of weathervane scallop angles (degrees) of orientation relative to true north (0°) in the closed area in 1998 and 1999. Positive angles run clockwise (east = 90°, south = 180°, and west = 270°). Estimated mean angles (solid line) and corresponding 95% confidence intervals (dashed lines) of a mixture of 2 von Mises distributions are shown. Bar widths equal 50° except the last, which equals 10° (350° to 360°).

Correlation of 2 circular variables, scallop orientation and direction of bottom currents at the time of observation, was tested with a parametric circular-circular test (Batschelet 1981), called the Jupp-Mardia correlation coefficient (Jupp and Mardia 1980). Distributions of angles of scallop orientation and angles of bottom-current direction were unimodal on most transects in both years. Circular mean angles of the 2 variables were computed for each transect, and paired means were tested for correlation. The null hypothesis of the test is that the 2 variables are independent. Combined 2-year data from the closed area were analyzed, and transects were assumed independent. The α-level in all tests was 0.05.

Spatial analysis

The spatial distribution of scallops on transects was treated as one-dimensional since transect length (1,500 m in closed or open area) was large compared to transect width (0.5 to 0.85 m). Based on distances between neighboring individuals, neighbor *K* analysis (O'Driscoll 1998) provides both a test for aggregation and a spatial description of individuals on transects. An assumption of neighbor *K* analysis is that the distribution of individuals on a transect is weakly stationary (O'Driscoll 1998). That is, the spatial pattern of individuals on transects must depend on relative inter-neighbor distances, not on absolute positions of individuals in space and time (O'Driscoll 1998). Neighbor *K* statistics for one-dimensional data, developed by O'Driscoll (1998), are based on the *K* function (Ripley 1977, 1981; Cressie 1991), also known as the reduced second-moment measure of a spatial point process for mapped data. Known positions of scallops on a transect were treated as a mapped point pattern, i.e., points represented individual scallops. A spatial pattern can be described by its first- and second-order moments. The second-order moment, *K*, is defined as

$$K(h)=\lambda^{-1}E[N(h)],$$

where λ is the intensity function, or first-order property of the spatial pattern, and $E[N(h)]$ is the expected number of extra individuals within distance h of any individual (Ripley 1981; O'Driscoll 1998).

An estimate of $E[N(h)]$ is the empirical average number of individuals within distance h of an arbitrary individual:

$$\hat{E}[N(h)] = N^{-1}\sum_{\substack{i=1\\ i\neq j}}^{N}\sum_{j=1}^{N} I(d_{ij}), \qquad (1)$$

where d_{ij} is distance between individuals i and j, N is total number of individuals, and I is the indicator function:

$$I(d_{ij}) = \begin{cases} 1, & \text{if } d_{ij} < h \\ 0, & \text{otherwise.} \end{cases}$$

O'Driscoll (1998) defined Equation (1) as the statistic for testing spatial randomness of individuals on a one-dimensional transect. The test statistic was computed for varying scales, or values of h, since spatial patterns are often scale dependent (Schneider 1994). Following O'Driscoll (1998), significance of the test was measured using Monte Carlo methods. Positions of N scallops on a transect were randomly generated 999 times. $E[N(h)]$ was computed for the observed data and for the 999 simulated data sets at scales of 1 m increments: $h = 1, 2, 3, \ldots, H$, where H is transect length. For values of h, the proportion of realizations (observed data and 999 simulations) for which $E[N(h)]$ was greater than or equal to $E[N(h)]$ computed from the observed data was calculated. If the proportion at h were less than 0.05 (α-level), then individuals were considered clustered at scale h. Significant aggregation of individuals at scale h indicates individuals

have more neighbors within distance h than would be expected if individuals were randomly arranged. Following O'Driscoll (1998), we adopted an unweighted approach to edge bias, assuming no individuals occur beyond the ends of a transect. In addition to a test of spatial aggregation, neighbor K analysis provides a description of one-dimensional spatial patterns in terms of *patch length* and *crowding* (O'Driscoll 1998). *Patch length* is the spatial scale of clustering, and *crowding* is a measure of relative number of individuals in a patch. *Patch length* and *crowding* were determined from graphs of function $L(h)$, where $L(h)$ is the difference between $E[N(h)]$ computed from the data and $E[N(h)]$ averaged over the 999 simulations. Function $L(h)$ represents the average number of extra neighbors observed within distance h of any individual than would be expected under spatial randomness. *Patch length*, defined as the smallest h at which there is a local maximal difference between observed and expected number of neighbors given spatial randomness, is the distance h to the first peak of $L(h)$. *Crowding*, estimated at the scale of the *patch length*, is defined as the difference between observed and expected numbers of neighbors given spatial randomness and is the height of the first peak of *L(h)*. Values of *patch length* and *crowding*, which depend on inter-neighbor distances, may not be comparable among transects of differing widths. To lessen the effect of edge bias, significance of the test was determined only for values of h up to $H / 2$. Since bottom fishing may alter the spatial distribution of scallops (Thouzeau et al. 1991), data from open and closed areas were analyzed separately (H=1,500 m). We used a one-tailed Fisher's exact test for 2-way contingency tables (Agresti 1990) to test whether scallops were aggregated on more transects in the closed than in the open area. We used a one-tailed Wilcoxon rank sum test (Snedecor and Cochran 1973) to test whether *patch lengths* were significantly larger in the open than in the closed area. We used one-tailed tests because Thouzeau et al. (1991) observed random distribution of sea scallops *P. magellanicus* in heavily fished areas. Transects were analyzed separately, and only those transects with an arbitrary minimum of 3 scallops were tested for spatial aggregation. Adult and juvenile scallops were analyzed separately. The α-level was 0.05.

Species associations

Four species groups were tested for associations with scallops: 1) anemones (*C. fernaldi* and *M. senile*); 2) sunflower sea stars *P. helianthoides*; 3) small sea whips (height <20 cm) (*Protoptilum* sp.); and 4) large sea whips (height >20 cm) (*H. willemoesi*). The 4 species groups were chosen after data collection and prior to data analysis, based on their similar feeding mechanisms to scallops (i.e., suspension or filter feeding) or their potential predator-prey relationship with scallops. Scallops were hypothesized to have a positive association with anemones and sea whips and a negative association with sunflower sea stars. First, spatial associations on individual transects were tested between scallops and each of the 4 species groups. Second, pairwise associations between scallop density (number of scallops m^{-2}) and densities of other species were measured with Spearman rank correlation coefficients (Snedecor and Cochran 1973) as a comparison to spatial analyses. Species densities were computed by *year* and *transect* in open and closed areas. Yearly data were combined, and the α-level was 0.05.

Neighbor K analysis of spatial relationships between pairs of species is called bivariate K analysis (O'Driscoll 1998). This analysis tests whether there are significantly more individuals of one species (e.g., scallops) associated with an individual of a second species (e.g., sea whips) than would be expected if individuals of the first species were spatially random. Specifically, the empirical average number of scallops, $E[N(h)]$, Equation (1), within distance h of an arbitrary individual of another species was calculated as the test statistic. Significance of the test was evaluated using Monte Carlo methods as described previously. Spatial characteristics, *patch length* and *crowding*, of 2-species associations were determined as described previously. *Patch length* can be considered the scale of maximum 2-species association. *Crowding*, estimated at the scale of *patch length*, is the average number of extra scallops neighboring an individual of another species than would be expected if the scallops were spatially random. Since bottom fishing may alter faunal associations (Langton and Robinson 1990), data from open and closed areas were analyzed separately (H=1,500 m). Transects were analyzed separately, and only those transects with an arbitrary minimum number of 3 individuals of each species were tested for spatial association. Adult and juvenile scallops were analyzed separately. The α-level was 0.05.

Spatial association between pairs of species was summarized by the percentage of transects that showed significant association (α-level = 0.05). If 20 out of 20 transects showed significant spatial association between 2 species, then concluding that the 2 species demonstrated spatial association is trivial. With varying numbers of animals on transects and varying numbers of transects analyzed for species associations, however, drawing conclusions about species associa-

tion would unlikely be so obvious. One solution was to simulate spatially random data and compare observed results to simulation results. A single simulation consisted of randomly drawing positions of individuals from 2 species on all transects analyzed for species association. The number of random positions drawn for a species equaled the observed number of individuals of that species on a transect. Each simulated data set was analyzed for spatial association by the Monte Carlo methods described above and the number of transects with significant association recorded. Fifty simulations were conducted for each pairwise association analyzed, and the observed number of significant transects was compared to numbers of significant transects for the 50 simulations. If the observed number of significant transects equaled or exceeded the number of significant transects for, at most, 2 of the 50 simulations (P <0.05), then we concluded a significant pairwise association. That is, there was evidence of species association if the observed number of transects with significant spatial association was large compared to the expected number of significant transects given spatial randomness.

Juvenile scallops

Examination of gonads to determine sexual maturity could not be performed in this study. A shell height-sexual maturity relationship, however, allowed classification of scallops as adult or juvenile. Haynes and Hitz (1971) found shell height a good index of age, up to ages 4 to 5 years, for weathervane scallops in the Strait of Georgia and outer Washington coast. Hennick (1970) found that most 3-year-old scallops (87% of 93 scallops) collected from the Marmot Bay–Portlock Bank region (Figure 1) near Kodiak Island were sexually mature. Mean shell height of these 3-year-old scallops was 104.2 mm (range: 74 to 128 mm). Using mean shell height of 3-year-old scallops (Hennick 1970) as an index of sexual maturity, scallops in this study were classified as juvenile (shell height <104.2 mm) or adult (shell height ≥104.2 mm).

RESULTS

In 1998, 256 scallops were observed on all transects at a density of 1.8 scallops per 100 m^2. In 1999, 564 scallops (2.4 scallops per 100 m^2) were observed on all transects at 1.4 times the density observed the previous year. In both years, scallops were most dense on the westernmost and central transects (Figure 3). Mean shell heights were 126 mm (SD=48 mm, n=235, range: 22 to 193 mm) and 112 mm (SD=48 mm, n=547, range: 24 to 199 mm) in 1998 and 1999, respectively. In both years, 97% of the scallops were

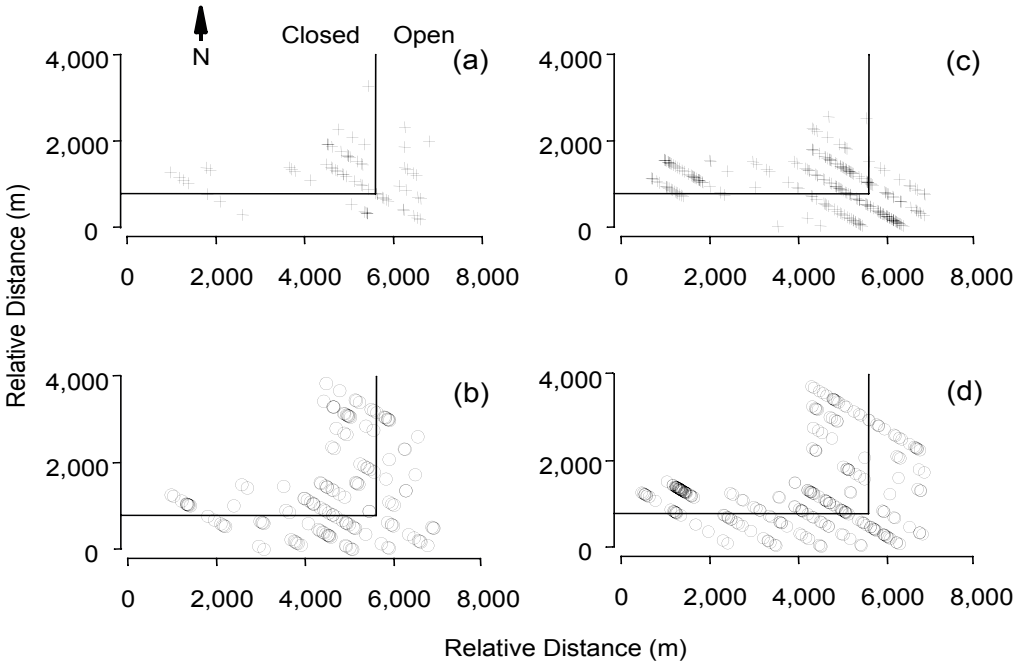

Figure 3. Distribution of (a) juvenile (+) and (b) adult (○) weathervane scallops on transects in 1998 and (c) juvenile (+) and (d) adult (○) weathervane scallops in 1999. Weathervane scallops were classified by shell height as juvenile (<104.2 mm) or adult (≥104.2 mm). The solid line indicates the fishing closure boundary.

recessed in the sediment and 17% had large epibionts (e.g., anemones) on their upper valves. Smaller species of epibionts (i.e., serpulid polychaetes and juvenile *Modiolus modiolus*) were observed on scallop upper valves; however, their numbers could not consistently be determined from video footage.

Differences between open and closed areas to bottom trawling and scallop dredging

Density of adult scallops was not significantly lower in the open than in the closed area (ANOVA, t=1.18 ~ Student's t(0.05, 19), P=0.13) (Figure 4). The interaction between variables *status* and *year* was not significant (ANOVA, F=0.88 ~ $F_{1,18}$, P=0.36). Multiple R^2 for the ANOVA model of scallop density without the interaction term was 67%. Mean shell height was not significantly different between open and closed areas (ANOVA, F=0.26 ~ $F_{1,19}$, P=0.61). The interaction between variables *status* and *year* was not significant (ANOVA, F=0.29 ~ $F_{1,18}$, P=0.60). Multiple R^2 for the ANOVA model of mean scallop height without the interaction term was 85%.

Size-frequency distributions of scallops were not significantly different between closed (n=120) and open (n=115) areas in 1998 (K-S goodness-of-fit, P=0.18) (Figures 5a, b) but were significantly different in 1999 (closed: n=310, open: n=237) (K-S goodness-of-fit, P=0.01) (Figures 5c, d). In 1999, larger scallops accounted for a greater proportion of scallops observed in the closed area (Figure 5c) than in the open area (Figure 5d). Legal-sized scallops (minimum ring size is 101.6 mm; Shirley and Kruse 1995) comprised 60% of scallops in the closed area (185/310 scallops) and 50% of scallops in the open area (119/237 scallops) in 1999.

Orientation

Scallop orientation in the closed area was significantly different from random (Rao's spacing test, n=375, U=235.2, P<0.001) (Russell and Levitin 1995). The 2 mean directions of scallop orientation were estimated to the east and northwest: 107° ($\hat{\sigma}$ =0.04°) and 324° ($\hat{\sigma}$ =0.2°) (Figure 2). Ninety-five percent confidence intervals of mean angles were non-overlapping: (101.8,111.4) and (305.0, 342.2) (Figure 2). The distribution of angles of orientation was estimated as a mixture of 10% vM(107,14.6) and 90% vM(324,0.5). Scallop orientation and direction of bottom currents at the time of observation were not significantly correlated (Jupp-Mardia correlation coefficient=2.3, P=0.69).

Spatial analysis

Significance of aggregation, and spatial characteristics of *patch length* and *crowding*, were determined from graphs of function $L(h)$ (e.g., Figure 6) computed for each transect in closed and open areas. Adult scallops exhibited aggregation on 16 of 19 transects in the closed area and on 10 of 17 transects in the open area in 1998 and 1999 (Table 1), respectively. A one-tailed Fisher's exact test showed that scallops were not sig-

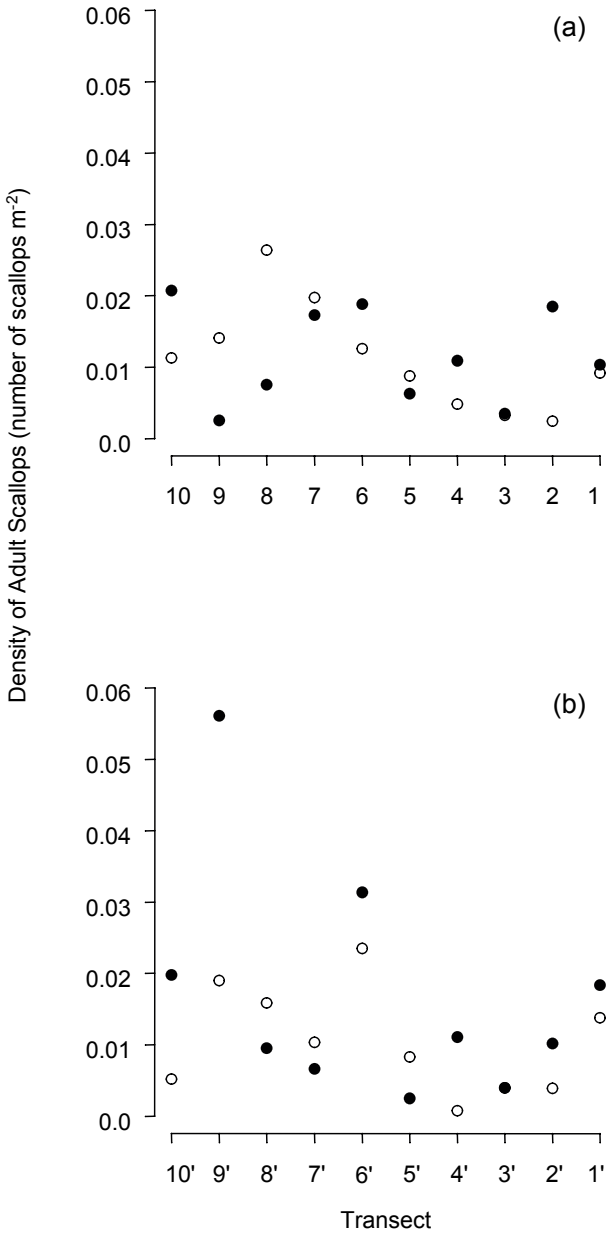

Figure 4. Densities of adult (shell height ≥104.2 mm) weathervane scallops (number of scallops m^{-2}) in the open (○) and closed (●) areas in (a) 1998 and (b) 1999.

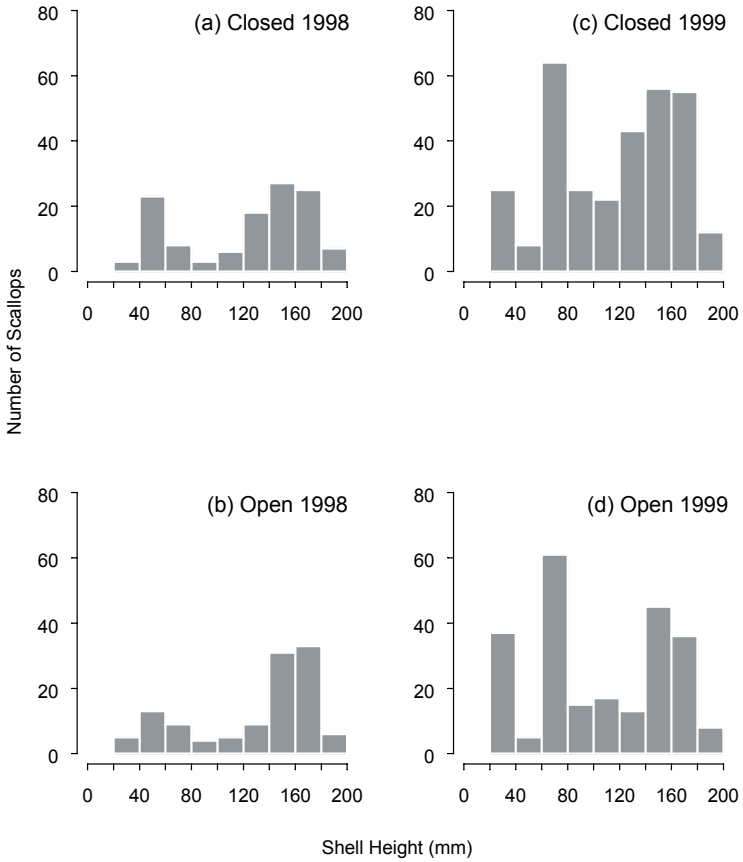

Figure 5. Histograms of weathervane scallop shell heights (mm) in the (a) closed and (b) open areas in 1998, and the (c) closed and (d) open areas in 1999.

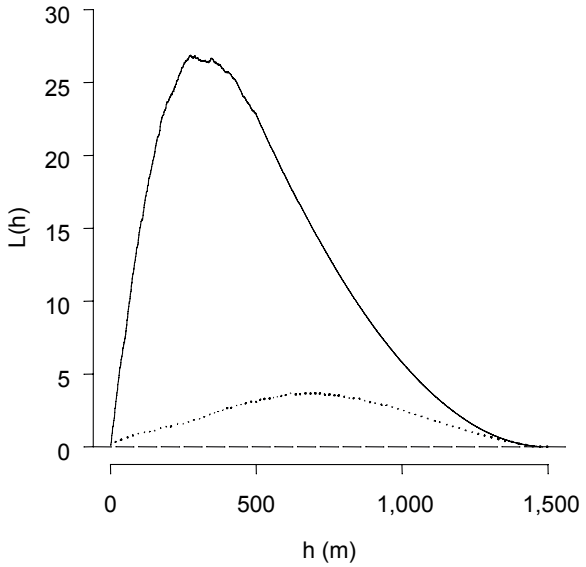

Figure 6. Function $L(h)$ (solid line) computed from the distribution of adult weathervane scallops (shell height ≥104.2 mm) in the closed area of Transect 9 in 1999. The fishing closure boundary is 0 m. The dotted line is the 95% confidence level of $L(h)$ from randomizations of the data. Individuals are significantly clustered at scale h where the solid line is above the dotted line. If individuals were spatially random, then $L(h)$ would equal zero (dashed line). *Patch length* and *crowding* were estimated as 275 m and 27 scallops, respectively.

Table 1. Number of transects that showed aggregation of adult weathervane scallops (shell height ≥104.2 mm) and associated spatial characteristics in closed and open areas. Number of transects examined is in parentheses.

			Patch length (m)		Crowding (no.)	
Year	Area	Transects (no.)	Median	Range	Median	Range
1998	Closed	7 (9)	88	11–590	2.1	0.6–3.6
	Open	5 (8)	152	8–181	2.1	1.5–3.9
1999	Closed	9 (10)	122	58–720	1.8	1.1–26.9
	Open	5 (9)	60	8–83	0.9	0.4–1.1

nificantly aggregated on more transects in the closed than in the open area, but only marginally ($P=0.09$). *Patch lengths* of scallops were variable but similar between years in the closed or open area, ranging from less than 10 m to over 700 m (Table 1). *Patch lengths* were smaller in the open than in the closed area in both 1998 and 1999 although marginally not significantly (Wilcoxon rank sum test, $z=1.34$, $P=0.09$). *Crowding* values of scallops ranged from less than 1 scallop to 27 scallops (Table 1).

Species associations

The closed area had significant numbers of transects with positive spatial association between adult scallops and both anemones and large sea whips (Table 2), and negative spatial association between adult scallops and sunflower sea stars (Table 2). Positive spatial association between adult scallops and small sea whips was found on over one-third of the transects analyzed in the closed area (Table 2); however, the number of transects was not significant. Spatial associations between adult scallops and other species groups were found on some transects in the open area (Table 2); however, the numbers of transects were not significant. Median *patch length* for the positive association between adult scallops and anemones in the closed area was 132 m (range: 1 to 704 m); median *crowding* was 0.5 scallops (range: 0.02 to 2.0 scallops). Median *patch length* for the negative association between adult scallops and sunflower sea stars in the closed area was 204 m (range: 128 to 860 m); median *crowding* was -1.2 scallops (range: –2.9 to –0.5 scallops). Median *patch length* for the positive association between adult scallops and large sea whips in the closed area was 317 m (range: 42 to 750 m); median *crowding* was 1.4 scallops (range: 0.4 to 19.0 scallops).

Table 2. Percentage of transects that showed spatial associations between weathervane scallops and species groups in the closed and open areas. Weathervane scallops were classified by shell height as juvenile (<104.2 mm) or adult (≥104.2 mm). Weathervane scallops were tested for positive association with anemones and sea whips and negative association with sunflower sea stars. Fraction of transects with significant spatial associations are shown in parentheses. Significant number of transects with spatial association is indicated by an asterisk (*).

	Weathervane Scallops	
	Adult	Juvenile
Closed Area		
Anemone	68* (13/19)	42 (5/12)
Sunflower sea star	53* (8/15)	44 (4/9)
Small sea whip	37 (7/19)	8 (1/12)
Large sea whip	69* (9/13)	55 (6/11)
Open Area		
Anemone	53 (9/17)	80* (8/10)
Sunflower sea star	43 (6/14)	56 (5/9)
Small sea whip	25 (4/16)	50 (5/10)
Large sea whip	31 (4/13)	56 (5/9)

Pairwise correlations between scallop density and densities of other species groups were consistently positive or negative among closed and open areas and among adults and juveniles (Table 3). Adult scallops had no significant faunal associations in the closed area (Table 3). In the open area, adult scallop density was low in areas of high sunflower sea star density and high in areas of small sea whip density (Table 3).

Juvenile scallops

Juvenile scallops were common in both years and comprised 28% (70/249 scallops) and 45% (254/564 scallops) of all scallops measured in 1998 and 1999, respectively. Densities of juvenile and adult scallops followed similar patterns in both years, with the notable exception that juveniles were almost completely absent from the easternmost or shallower transects (1998: Transects 1 to 3; 1999: Transects 1′ to 3′) (Figures 3 and 7). Also, juvenile scallops were dense on central transects (1998: Transect 5; 1999: Transect 5′) but adult scallops were not (Figures 3 and 7). The smallest scallop measured in either year was 22 mm. In both years, 98% of juvenile scallops were recessed in the sediment.

Density of juvenile scallops was not significantly lower in the open than in the closed area (ANOVA, $t=1.19\sim$ Student's $t(0.05, 19)$, $P=0.12$). The interaction between variables *status* and *year* was not significant (ANOVA, $F=0.87\sim F_{1,18}$, $P=0.36$). Multiple R^2 for the ANOVA model of juvenile scallop density without the interaction term was 87%.

Table 3. Spearman rank correlation coefficients between weathervane scallop density and densities of other species groups in closed and open areas. Weathervane scallops were classified by shell height as juvenile (<104.2 mm) or adult (≥104.2 mm). Densities were computed for each one-half transect, and weathervane scallops were tested for positive association with anemones and sea whips and negative association with sunflower sea stars. The critical value for a one-tailed probability is 0.38 (Zar 1972), where n=20. A significant correlation is indicated by an asterisk (*).

	Weathervane Scallops	
	Adult	Juvenile
Closed Area		
Anemone	–0.17	–0.34
Sunflower sea star	–0.36	–0.60*
Small sea whip	0.09	0.74*
Large sea whip	0.19	0.66*
Open Area		
Anemone	–0.39	-0.17
Sunflower sea star	–0.56*	-0.20
Small sea whip	0.51*	0.68*
Large sea whip	0.26	0.55*

Juvenile scallops exhibited aggregation on one-third of transects (4 of 12) in the closed area and on one-half of transects (5 of 10) in the open area. A significant number of transects in the open area exhibited positive spatial association between juvenile scallops and anemones (Table 2). Spatial associations between juvenile scallops and other species groups were found on some transects in the open and closed areas (Table 2); however, the numbers of transects were not significant. Median *patch length* for the association between juvenile scallops and anemones in the open area was 150 m (range: 10 to 600 m); median *crowding* was 0.5 scallops (range: 0.1 to 1.1 scallops). Juvenile scallop density was high in areas of high sea whip density (small and large) in both closed and open areas (Table 3). Juvenile scallop density was low in areas of high sunflower sea star density in the closed area only (Table 3).

DISCUSSION

Size–frequency distributions of scallops differed between areas open and closed to bottom trawling and scallop dredging in 1999; however, no strong evidence was found for differences in density and spatial characteristics. Mean shell height did not differ significantly between open and closed areas; however, in 1999, legal-sized scallops comprised 60% and 50% of all scallops observed in closed and open areas, respectively. Other studies have documented changes in the size structure of scallop populations as a result of fishing. Hennick (1973) observed over time a shift in age composition of commercial catches of weathervane scallops to younger scallops. Thouzeau et al. (1991) observed high prerecruit abundance relative to recruit abundance in commercially harvested *P. magellanicus*. Adult scallops were observed in smaller *patch lengths* and were clustered on fewer transects in the open than in the closed area. Both results were marginally not significant but may be evidence of fragmentation of scallop aggregations by fishing gear. Thouzeau et al.

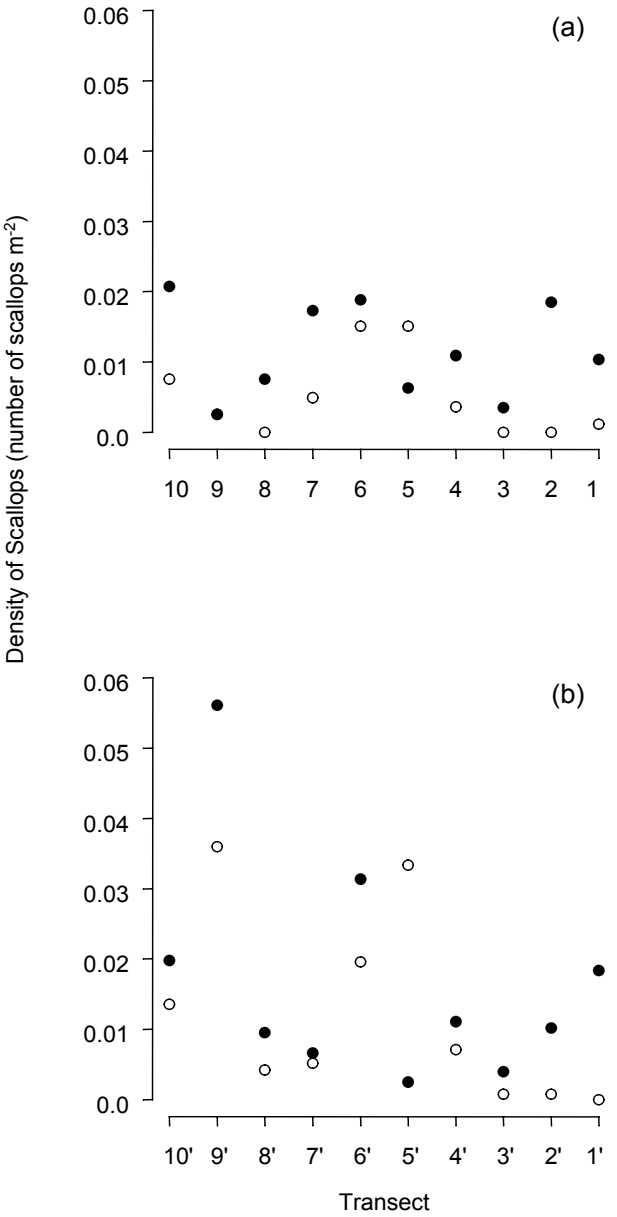

Figure 7. Densities (number of scallops m^{-2}) of juvenile (○) and adult (●) weathervane scallops in the closed area in (a) 1998 and (b) 1999. Weathervane scallops were classified by shell height as juvenile (<104.2 mm) or adult (≥104.2 mm).

(1991) observed random distribution of *P. magellanicus* in heavily fished areas.

We did not expect to find large differences in scallop density, size–frequency distribution, and spatial characteristics between open and closed areas based on the relatively low level of dredging that occurs in the open area. Certainly this work should be extended to populations in the GOA that are subjected to more intense fishing effort. Further, there are some inherent problems associated with the use of area closures as control comparisons that may bias results. We compared areas bottom trawled and dredged for approximately 30 years to areas closed for only 11 and 12 years. Weathervane scallops have life spans greater than 12 years, so their current abundance and spatial distribution may have been affected by fishing activity prior to 1987. Also, due to record-keeping limitations of the fisheries observer program, precise locations of hauls within the open areas, other than the start positions, are unknown (i.e., designated "open" samples may have been collected in areas that were not actually trawled). The in situ observations of trawl gear striations on the substrate, however, support the assumption that trawling occurred in the study area. Further, the specific differences detected in epifauna abundance, species diversity, and total organic carbon within surficial sediments between open and closed areas provide additional evidence that the open area has been disturbed (Stone et al. In press; Stone and Masuda 2003). Two other important assumptions of this study are that the closed and open areas were identical at the time of the fishery closures in 1987 and that natural disturbances have equally affected those areas.

Little is known about the distribution of juvenile weathervane scallops, especially in relation to that of adults. Juvenile scallop density was generally similar to that of adults on most transects. Juvenile scallops were observed on nearly all transects but were absent from the shallower (depth 105 to 112 m) transects in both years. Also, one central transect in both years was densely populated with juvenile scallops but not adults. The smallest scallop observed in either year had a shell height of 22 mm. Scallops around this size are likely 1-year-old scallops (Haynes and Hitz 1971; Hammarstrom and Merritt 1985) and would therefore be the youngest scallops on the grounds at the time of our surveys. We are confident that scallops smaller than 22 mm could have been identified, if present, since epifauna less than 22 mm in length (e.g., eualid shrimp) were easily identified and counted from the same video footage (Stone et al. In press). Hennick (1970) found that weathervane scallops spawn from early June through mid-July; therefore, at the time of our surveys, young-of-the-year scallops were unlikely to have yet metamorphosed to the benthos. Most juvenile scallops (98% in both years) were recessed in the sediment, indicating that juvenile scallops settle out of plankton in the general area of adults and quickly adopt their sedentary behavior.

In situ observations indicate that weathervane scallops are not highly mobile. Swimming behavior was not observed, and most scallops (>95%) were recessed in the seafloor with accumulated sediment on their upper valves. Hartnoll (1967) observed that recessed *Pecten maximus* remained in the same positions for up to 1 month and that unrecessed ones moved regularly. No studies of movement of weathervane scallops have been published, although Starr and McCrae (1983) attributed observed shifts in depth distribution to short-distance movement.

Weathervane scallops, like other scallop species (e.g., *P. magellanicus*, *Patinopecten yessoensis*), exhibit patchy distributions (Caddy 1970; Langton and Robinson 1990; MacDonald and Bajdik 1992; Stokesbury and Himmelman 1993; Goshima and Fujiwara 1994). Adult scallops in this study were clustered in *patch lengths* ranging from less than 10 m to over 700 m. Observations of scallops on narrow transects, however, provide an estimate of patch size in only one dimension. Elongated beds of other scallop species have been observed oriented with the long axis parallel to predominant current flow (Olsen 1955; Goshima and Fujiwara 1994), and transects in this study were roughly oriented in this direction. Reported *patch lengths* are therefore likely good estimates of true *patch lengths* of scallops with patch widths unknown.

Orientation of scallops was directed with most scallops facing their ventral margins towards the direction of strongest, prevailing bottom currents or the reciprocal, weaker currents. Directions of scallop orientation and bottom currents at the time of observation were unrelated, indicating that scallops do not move with daily tidal changes. Other scallop species orient their ventral margins towards predominant currents (Hartnoll 1967; Caddy 1968; Gladkov 1994). Mathers (1976) observed that *P. maximus* preferentially faced directly into flood or ebb tidal flow and further that digestion was correlated with tidal periods. In that study, scallops facing flood currents had feeding cycles 6 hours out of phase with those facing ebb currents. Feeding may be enhanced by actively directing the ventral margin towards prevailing currents (Mathers 1976), although orientation may be due to physical processes rather than due to an active, behavioral response (Grant et al. 1993). Gladkov (1994) observed in situ that 2 changes in bottom-flow direction in a 24-h

period were not followed by reorientation of *Mizuhopecten yessoensis*, but other species have shown short-term changes in orientation (Caddy 1968; Stokesbury and Himmelman 1995a). Some studies have shown that directed orientation of scallops in situ and in the laboratory requires sufficiently strong currents, otherwise orientation is random (Gladkov 1994; Stokesbury and Himmelman 1995a; Sakurai and Seto 2000). Directed orientation of weathervane scallops may be evidence that the relatively strong and predictable bottom currents observed at Chiniak Gully exceed a threshold value required to induce orientation.

Positive associations between species in a community may imply either that they are linked by dependence of one on another (e.g., symbiosis and food-chain coactions), or that they respond in similar ways to small-scale changes in environmental conditions within the community (Whittaker 1975). Negative associations may indicate either that one species tends to exclude another through competition or predation, or that they respond in different ways to changes in environment (Whittaker 1975). We restricted our analyses of fine-scale, 2-species association to only those species for which we anticipated either a predator–prey relationship or a similar feeding mechanism to scallops. Analyses were also limited to those species that were relatively abundant throughout the study site. No published studies have determined the major predators of weathervane scallops. Predators of other scallop species include sea stars, crabs, and anemones (Hartnoll 1967; Mullen and Moring 1986; Stokesbury and Himmelman 1995b; Arsenault and Himmelman 1996). Of these, only the large sunflower sea star was identified as a potential predator at our study site. Adult red king and Tanner crabs may be potential predators of weathervane scallops, but none were observed in the study area. Although Langton and Robinson (1990) found a negative association between a burrowing anemone and *P. magellanicus*, we tested for a positive spatial association between weathervane scallops and anemones (non-burrowing types) based on their similar feeding mechanisms.

There was some evidence of positive spatial associations between adult scallops and both large sea whips and anemones, and negative spatial association between adult scallops and sunflower sea stars. Juvenile scallops also exhibited a positive spatial association with anemones. We expected the positive associations because the 3 species have similar feeding mechanisms and may tend to aggregate where currents are optimal for feeding. Additionally, scallops may benefit directly from a positive association with anemones. Kaplan (1984) found that the presence of anemones *Metridium senile* on the valves of mussels *Mytilus trossulus* significantly reduced predation by the starfish *Asterias forbesii* in the laboratory. Anemones including *Metridium senile* were attached to 17% of the scallops in this study and may similarly deter predators. Conversely, epibiontic loads may hinder the mobility of scallops and their ability to escape from predators. The negative spatial association of scallops with sunflower sea stars may be evidence of a predator-prey relationship. Spatial association between scallops and small sea whips was found on some transects but not on significant numbers of transects. Faunal associations based on correlated animal densities were similar for adult and juvenile scallops. Both adult and juvenile scallops exhibited some positive association with sea whips, negative association with sunflower sea stars, and no association with anemones.

The 2 methods of assessing faunal associations—correlation of animal densities and spatial tests—yielded different results when applied specifically to area (open or closed) and maturity of scallops (adult or juvenile). In general, the methods agreed in detecting some positive association between scallops and large sea whips and negative association between scallops and sunflower sea stars. The methods disagreed in that anemones were shown to have some positive spatial association with scallops, but anemone and scallop densities were seemingly unrelated. A significant spatial relationship between scallops and small sea whips was not found, contrary to correlation analyses of animal densities. Lack of concordant results between analyses may be due to differing scales: animal densities were analyzed at a scale one-half the length of a transect which is twice the maximum scale spatial tests were performed. The Spearman rank correlation coefficient is a simple measure of a pairwise association and may be inadequate for modeling a potentially complex faunal association. Spatial analyses of paired-species associations are limited to transects with adequate numbers of both species; therefore, a potential negative association may go undetected on transects where one species is abundant and another species is completely absent. The only spatial association found with juvenile scallops was a positive association with anemones. Spatial associations with juvenile scallops may have gone undetected due to the small number of juvenile scallops (0 to 53) observed on each one-half transect. In this study, we examined paired associations of scallops with only a few potential species. Further work with faunal associations of weathervane scallops could be done as more than 30 epifauna species were identified and mapped on all transects. Also, more complex associations than paired associations could be examined.

Surveying the seafloor and epifauna with a manned submersible is a noninvasive means of assessing scallop abundance and collecting biological information. Furthermore, the submersible survey allows direct observation of behavior and community structure of deepwater scallops not possible from traditional trawl surveys (e.g., Haynes and Powell 1968). Scallops were not observed to react (i.e., swim away) to the submersible. Submersibles have previously been employed to collect scallop biological information via still-photograph subsampling (Caddy 1970; Langton and Robinson 1990). Direct observation by Scuba, a common method of assessing shallow-water scallops (Hartnoll 1967; Mathers 1976; Stokesbury and Himmelman 1993, 1995a, b; Gladkov 1994; Arsenault and Himmelman 1996), is viewed as one of the most accurate methods for studying the distribution of scallops (Stokesbury and Himmelman 1993). Scuba, however, is limited to the study of shallow-water scallops. Collection of video footage with benthic sleds (Thouzeau et al. 1991) and remotely operated vehicles, although technically and financially attractive, has limitations. For example, in this study the scientific observer voice-recorded observations simultaneously with video recordings (i.e., interpretations were recorded immediately). Siphons of large bivalves, common on 2 transects in 1999, could easily have been mistaken on videotape for small scallops (shell height <40 mm). Without interpretative observations of the scientific observer, the abundance of small scallops would have been overestimated.

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