

Spatial patterns and movements of red king and Tanner crabs: implications for the design of marine protected areas

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ABSTRACT: Most examples of positive population responses to marine protected areas (MPAs) have been documented for tropical reef species with very small home ranges; the utility of MPAs for commercially harvested temperate species that have large movement patterns remains poorly tested. We measured the distribution and abundance of red king *Paralithodes camtschaticus* and Tanner *Chionoecetes bairdi* crabs inside and outside of MPAs in Glacier Bay National Park, Alaska, USA. By tagging a sub-sample of crabs with sonic tags, we estimated the movement of adult crabs from one of the MPAs (Muir Inlet) into the central portion of Glacier Bay where fishing still occurs. Tanner crabs and red king crabs moved similar average distances per day, although Tanner crabs had a higher transfer out of the Muir Inlet MPA into the central bay. Tanner crab movements were characterized by large variation among individual crabs, both in distance and direction traveled, while red king crabs migrated seasonally between 2 specific areas. Although Tanner crabs exhibited relatively large movements, distribution and abundance data suggest that they may be restricted at large spatial scales by habitat barriers. MPAs that are effective at protecting king and especially Tanner crab brood stock from fishing mortality will likely need to be larger than is typical of MPAs worldwide. However, by incorporating information on the seasonal movements of red king crabs and the location of habitat barriers for Tanner crabs, MPAs could likely be designed that would effectively protect adults from fishing mortality.

KEY WORDS: Marine protected area · MPA · Marine reserve · Sonic tracking · Transfer rate · Acoustic monitoring · *Paralithodes camtschaticus* · *Chionoecetes bairdi*

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INTRODUCTION

Red king *Paralithodes camtschaticus* and Tanner *Chionoecetes bairdi* crabs are 2 of the most commercially valuable crab species in Alaska, USA. Both species historically exhibited dramatic abundance oscillations followed by severely depressed populations in recent decades (Orensanz et al. 1998). The peak harvest of red king crabs occurred in the 1970s, but harvests declined 60-fold in the early 1980s, and the 4 highest production areas were subsequently closed to

fishing (Otto 1990). Tanner crab harvests peaked in 1978, and most fisheries collapsed in the mid-1990s (Orensanz et al. 1998). The causes of these severe fishery declines are not fully understood, but they have been postulated to be due to disease, increased predation (Otto 1986), environmental change (Zheng & Kruse 2000), or the direct or indirect effects of fishing (Orensanz et al. 1998, Dew & McConnaughey 2005).

Fisheries in other parts of the world have been severely depleted, and a growing number are under threat of collapse (Pauly et al. 2002). Although the

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solutions to fisheries collapses are complex, an increasing body of literature suggests that marine protected areas (MPAs) could be an important tool for conservation and fisheries management (National Research Council 2001).

Glacier Bay National Park, Alaska, has effectively been a protected area for marine birds and mammals since its establishment in 1925 (Jones 2002). However, protection for commercially fished species did not occur until 1998, when Congressional action closed approximately half of Glacier Bay's marine waters to commercial fishing (US Congress 1998). The area closed to commercial fishing is 1312 km², which is larger than 90% of the world's MPAs (Kelleher et al. 1995).

The utility of MPAs as a management tool is controversial, especially where the objective is fisheries enhancement (Willis et al. 2003, Sale et al. 2005). Although changes in size and density of fishes have been demonstrated within many MPAs, fisheries enhancement relies on the export of larvae or spillover of juveniles or adults to surrounding areas. Because testing for export is difficult (Sale et al. 2005), only a few studies have examined these effects (Abesamis & Russ 2005, Alcalá et al. 2005, Goñi et al. 2006). In general, guidelines for designing effective MPAs for fisheries enhancement are lacking (Sale et al. 2005). Additional empirical studies are needed to test the ideas generated by modeling studies (Willis et al. 2003) and to fill gaps in our understanding of MPA design (Sale et al. 2005).

Designing MPAs to facilitate the desired export of larvae or spillover of juveniles and adults requires knowledge of spatial patterns of animal abundance and movement (Palumbi 2004, Sale et al. 2005) coupled with habitat and oceanographic characteristics within and outside of the MPAs (García-Charton & Pérez-Ruzafa 1999). If the objective of the MPA is to increase larval export, a desirable site would have habitat capable of supporting abundant reproductive adults, and the configuration of the reserve would restrict adult movement out of the MPA. For example, habitat barriers along an MPA boundary can reduce the emigration of adult animals from the MPA (Tewfik & Bene 2003).

Alternatively, if the MPA objective is spillover of post-settlement individuals, including adults, habitat barriers along an MPA boundary can be counterproductive. Habitat quality inside and outside the MPA can also affect animal movement across MPA boundaries. If the optimal habitat is outside the MPA and animal distribution is influenced by density-dependent factors, animals will emigrate from the MPA to the preferred habitat as harvest removes animals from that habitat (Kramer & Chapman 1999, Abesamis & Russ 2005).

Although many populations respond to MPA protection by increasing in abundance and body size, these responses are more pronounced in animals that move less (Palumbi 2004). Tropical reef species with very small home ranges provide the most frequent examples of positive population responses to MPAs (Halpern 2003). The utility of MPAs for commercially harvested species that have large movement patterns remains unknown (FSBI 2001, Sale et al. 2005). If MPAs are to be effective at protecting animals with extensive movement patterns, large MPAs are likely needed (FSBI 2001, Palumbi 2004, Sale et al. 2005). For Atlantic cod *Gadus morhua*, a wide-ranging temperate species, an effective MPA is estimated to be at least 70 000 km² (FSBI 2001). This example, although extreme, illustrates that understanding the distribution and movements of a population is paramount to MPA design.

Glacier Bay provides a unique opportunity to study the effects of fisheries closures on fisheries populations that are highly mobile. The goals of this study were to measure the distribution and abundance of 2 mobile species, red king and Tanner crabs, inside and outside of the MPAs and to estimate the transfer rate of adult crabs from one of the MPAs (Muir Inlet) into the central portion of Glacier Bay where fishing still occurs.

MATERIALS AND METHODS

Study site. Glacier Bay (Alaska, USA) is a Y-shaped fjord system with high clay-silt sedimentation rates from streams and tidewater glaciers (Cowan et al. 1988; Fig. 1A). The Bay was formed when glaciers retreated approximately 100 km since the Little Ice Age (220 yr before present; Lawrence 1958). Deep basins (maximum depth of 450 m) occur throughout the bay and are separated by sills, including a sill 25 m deep at the mouth of the bay. Semidiurnal tides produce a maximum vertical range of 7.5 m. The primarily unconsolidated rocky coastline is highly convoluted, creating numerous small bays characterized by clay-silt bottoms that also include sand, pebble, cobble, boulder, and shell substrates (Harney et al. 2006).

Legislation initially closed commercial fishing for Tanner crabs in 5 areas that vary in shape, size, and area:boundary ratio (US Congress 1998; Fig. 1A). Fishing in central Glacier Bay is being phased out by a grandfather clause that allows continued Tanner crab harvesting only by individuals maintaining continuous ownership of their commercial fishing permit. As fishing fleet attrition occurs over the next several decades, Glacier Bay will become a single large MPA for Tanner crabs. For red king crabs, the legislation immediately closed commercial fishing in all of Glacier Bay.

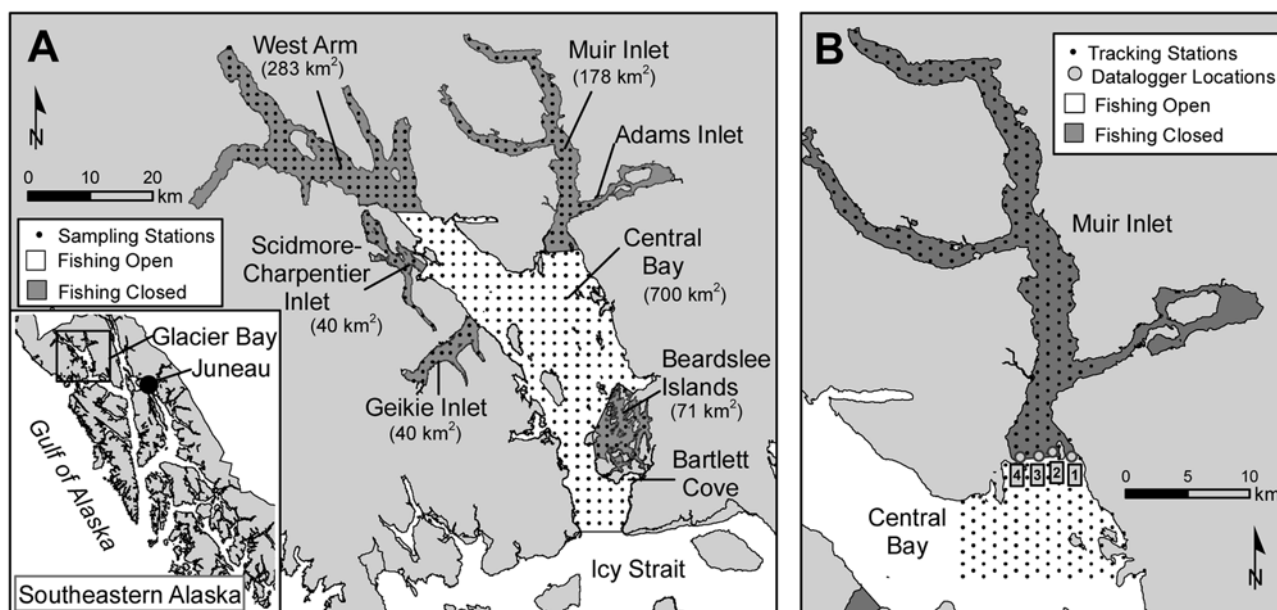


Fig. 1. Study area in Glacier Bay National Park, Alaska showing (A) sampling stations, and (B) vessel-based tracking stations and location of submerged data loggers and the associated data logger station numbers (1–4)

Field methods. Distribution and abundance: Crab abundance was estimated during July through September 2002 by sampling 415 stations located 1.5 km apart in areas closed to commercial fishing and 1.8 km apart in the area open to commercial fishing (Fig. 1A). Crabs were collected using conical, top-loading, 2.5 × 1 m commercial Tanner crab pots. To collect juvenile and female crabs, a 1 × 0.5 m commercial shrimp pot was attached with a 20 m tether to each of the conical Tanner crab pots. Pots were baited with chopped herring and pink salmon, set in the afternoon and soaked overnight (18.1 ± 2.4 h, mean ± SD). Pot placement was facilitated with an onboard Geographic Information System (GIS) that projected the research vessel's real-time position into ArcView (Environmental Systems Research Institute, ESRI). Vessel position was continuously updated with positions from a Global Positioning System (GPS; PLGR+, Rockwell Collins), and water depth (m), set and retrieval time, and GPS locations were recorded for each station.

Upon pot retrieval, the catch was counted and identified. Crabs were measured (nearest mm in carapace width for Tanner crabs and carapace length for red king crabs) with vernier calipers. Sexual maturity of female Tanner crabs was assessed by the relative size of the abdominal flap (Jadamec et al. 1999) and the presence of eggs. Sexual maturity for male Tanner crabs is not easy to classify in the field. However, in laboratory studies, all crabs larger than 80 mm produced spermatophores and fertilized mates (Paul & Paul 1990). We used this delineation to categorize

males as juvenile/small (<80 mm) or adult/large (≥80 mm).

Movement: We restricted the crab movement study to a single MPA, Muir Inlet, because of the large spatial scale of Glacier Bay. We estimated the transfer rate of crabs between Muir Inlet and the central bay, where commercial fishing for Tanner crabs continues during the phase-out period. Male Tanner crabs (N = 31) and male (N = 19) and female (N = 8) red king crabs were tagged with ultrasonic transmitters (76 kHz MAP16_2, Lotek Wireless; see Fig. 2B). Female Tanner crabs, which are significantly smaller than males, were excluded from this multi-year study because of anticipated compromised survival caused by the large size of the tag relative to female body size. The cylindrical (16 mm diameter × 88 mm long) ultrasonic tags were programmed with 20 s burst intervals with an expected operational life of 3 yr. Transmitters contained activity sensors to determine if the transmitter was still on an active crab (i.e. the crab had not molted or died); if the crab did not move for 3 d, an inactive code was broadcasted by the ultrasonic tag; the transmitter would reset to 'active' if the crab subsequently moved.

To ensure that movement rates of tagged crabs would be representative of the population, the tags were distributed proportionally to the spatial abundance determined by the pot survey. Ultrasonic tags were attached while we conducted the density sampling in September 2002. During October 2003, we attached additional tags to crabs in Muir Inlet, with tags distributed proportional to the 2002 crab abun-

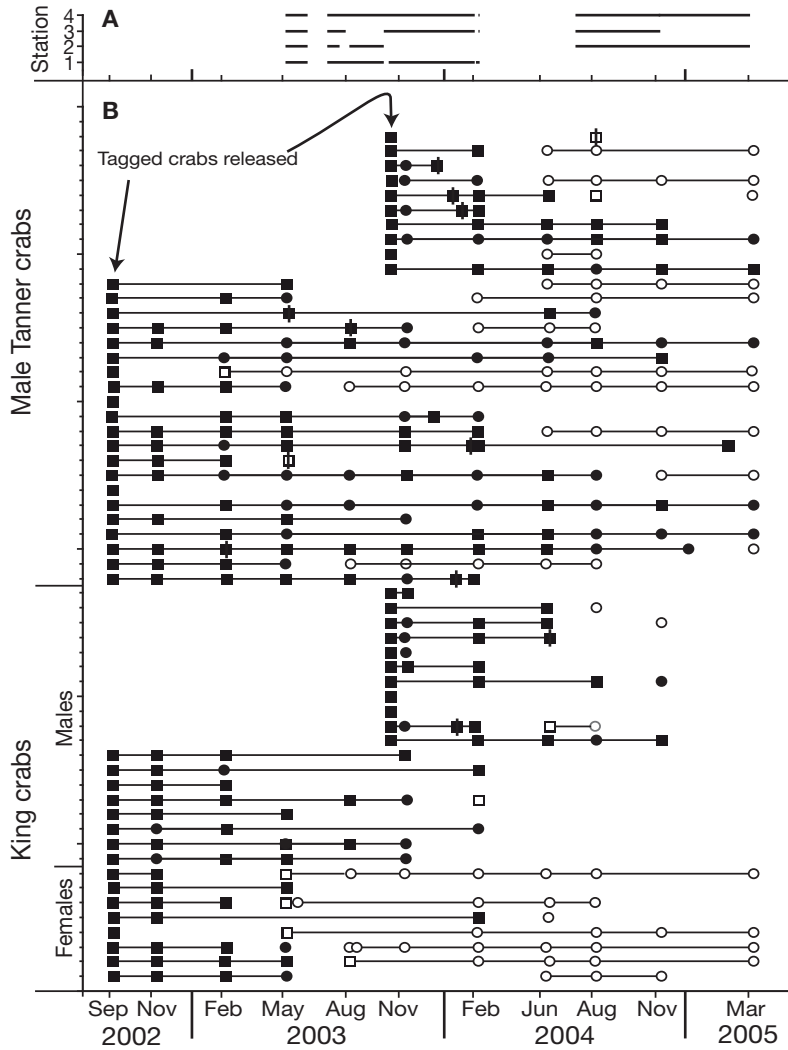


Fig. 2. *Paralithodes camtschaticus* and *Chionoecetes bairdi*. (A) Data logger deployment summary; lines show when each data logger was operational. (B) Tracking summary of sonic-tagged crabs. Each line represents a tagged crab. Symbols indicate the dates on which tags were relocated. Squares: crab had moved since it was previously located; circles: no movement since it was previously located. Solid symbols: 'active' signal from the activity sensor; open symbols: 'inactive' signal; horizontal lines: movement across the Muir Inlet marine protected area (MPA) boundary

dance. To minimize tag loss that might occur because of molting, we tagged new-shell male Tanner crabs (Jadamec et al. 1999) greater than 125 mm; these crabs were predicted to have a molt interval greater than 2 yr (Paul & Paul 1995). Similarly, we only tagged recently molted red king crabs with a carapace length larger than 140 mm. Tags were glued to the carapaces with fast cure epoxy resin (epoxy: BioFix 911, Progressive Epoxy Polymers) and fiberglass tape.

Crabs were located with a mobile tracking receiver (MAP_600 RT, Lotek Wireless) with 2 omni-directional hydrophones (LHP_1, Lotek Wireless). Surveys were

conducted 4 times per year. Initially, hydrophones were deployed from a stationary vessel at stations 0.75 km apart (Fig. 1B); after November 2003, searches were conducted by towing a hydrophone along the same search pattern. A side scan fish was used to depress the towed hydrophone to about 7 m depth.

An ultrasonic gate was deployed in May 2003 by mooring 4 submersible data loggers (WHS_3100, Lotek Wireless) along the Muir Inlet MPA boundary (Fig. 1B). Data loggers, attached to 4.8 mm stainless steel cables, were suspended 20 m off bottom using five 0.30 m center-hole trawl floats for sub-surface flotation. The moorings were secured to the bottom with disposable cement anchors (150 kg) and were placed approximately 1300 m apart to produce overlapping ranges of reception. For tagged crabs within the reception range, the data loggers recorded the unique ultrasonic tag number, date, time, and activity sensor information. Data loggers were retrieved by a remotely activated acoustic release (Oceano, IXSEA). The coverage provided by the ultrasonic gate is summarized in Fig. 2A. The gaps in coverage were caused by electronic malfunctions and mooring failures.

Data analysis. Distribution and abundance: Abundance of crabs at each station was assumed to be proportional to catch-per-unit-effort (CPUE; Quinn II & Deriso 1999) and was mapped using ArcGIS Version 9.1 (ESRI). For all stations combined, the mean CPUE and the 95% confidence intervals were calculated for Tanner and red king crabs. Differences between the spatial distributions of males and females by species were tested with a generalized 2-sample Cramer-von Mises test (Syrjala 1996). This is a non-parametric test that is sensitive to differences in the way 2 populations are distributed across the study area and is not affected by differences in abundance. The p-values were calculated with a randomization test (1000 random permutations) using a QuickBasic program, GeoDistn.BAS (Syrjala 1996).

We characterized the magnitude and range of spatial autocorrelation in CPUE data by creating a spatial

correlogram of global Moran's index (I). Moran's I indicates the degree of clustering for points within a defined distance by computing a measure of local variation relative to overall study area variation. I values close to +1 indicate positive autocorrelation where similar values (either high or low) are clustered, whereas an I close to -1 indicates negative autocorrelation where similar values are far apart; an expected value of 0 indicates the absence of autocorrelation (Moran 1950). Using the spatial statistics toolbox of ArcGIS Version 9.1 (ESRI), we calculated a global Moran's I for 9 over-water lag distances. An initial over-water lag distance of 2000 m was selected to incorporate at least 4 adjacent stations in both the area closed to commercial fishing (1.5 km sampling grid) and the area open to commercial fishing (1.8 km sampling grid). The lag distances were gradually increased to reflect the scale of the study area (Table 1). A z score, representing the significance of each Moran's I statistic, was calculated by subtracting the expected statistic generated by a random distribution from the observed statistic and dividing by the standard deviation of the expected random distribution. A Bonferroni-corrected criterion was used to ensure global significance of the correlogram; z scores were assessed at significance level of $0.05/k$, where k = the number of distance classes (Legendre & Fortin 1989). This criterion corresponds to a z score of 2.78 for $k = 9$.

Although a global Moran's I correlogram summarizes large-scale patterns in spatial autocorrelation, it does not identify local areas with high or low CPUE. A local indicator of spatial association can determine zones of high values (hotspots) and low values (coldspots) within a study area (Anselin 1995). We used the Getis-Ord G_i^* statistic to determine whether individual stations were included in clusters of high or low CPUE values for both sexes of Tanner and red king

crabs. In contrast to Moran's I , which is a measure of covariation in attribute values within a fixed distance from each station compared to overall study area variation, the G_i^* statistic provides a measure of the magnitude of attribute values within a fixed distance from each station relative to the magnitude of the attribute in the overall study area (Getis & Ord 1992). Getis & Ord (1992) stressed the value of calculating both Moran's I and Getis-Ord G_i^* to maximize understanding of local and global spatial patterns; they used the lag distance with the highest z score from Moran's I analyses as the fixed distance for G_i^* analyses. We used the Hotspot Analysis tool in the spatial statistics toolbox of ArcGIS Version 9.1 to calculate the G_i^* statistic and the corresponding z score values, which indicate the degree of departure from the expected distribution (null hypothesis) of no spatial association for each station. The fixed distance used to calculate the statistic for each species and sex was the distance lag with the maximum z score from the Moran's I correlogram (Table 1). Significant hotspots ($z > 3.48$) and coldspots ($z < -3.48$) were identified based on a Bonferroni-corrected significance level [$\alpha = 1 - (1 - 0.1)^{1/k}$] where $k = 415$, or the number of comparisons (Ord & Getis 1995). This is a conservative criterion that reveals significant clustering of high and low values (Ord & Getis 1995).

Movement: To estimate our ability to relocate tagged crabs during vessel-based searches, we summed the total number of times we located each crab between the tagging date and the last date we located the crab alive, and then divided by the number of surveys conducted during that period. Differences in the relocation probability between king and Tanner crabs were tested with a chi-squared test. For each crab, the length of time a crab was tracked was calculated as the number of days between tagging and the last date a

Table 1. *Paralithodes camtschaticus* and *Chionoecetes bairdi*. Moran's index (I) of autocorrelation and corresponding z scores at 9 over-water distance lags for female and male Tanner and red king crabs. Distance lags used to calculate Getis-Ord G_i^* for each sex and species are in **bold**

Distance lag (m)	Tanner crab				Red king crab			
	Female		Male		Female		Male	
	I	z	I	z	I	z	I	z
2000	0.111	2.91 ^a	0.354	8.73 ^a	0.084	5.01 ^a	0.434	12.19^a
2800	0.121	4.31^a	0.334	11.26 ^a	0.043	3.62 ^a	0.241	9.31 ^a
4000	0.069	3.26 ^a	0.239	10.52 ^a	0.093	9.69^a	0.219	10.98 ^a
5500	0.049	3.20 ^a	0.219	13.21 ^a	0.054	7.73 ^a	0.123	8.51 ^a
7500	0.040	3.36 ^a	0.195	15.18 ^a	0.034	6.28 ^a	0.075	6.77 ^a
10000	0.022	2.57	0.163	16.44 ^a	0.022	5.18 ^a	0.047	5.61 ^a
15000	0.014	2.43	0.114	16.50^a	0.011	3.92 ^a	0.024	4.27 ^a
30000	0.003	1.60	0.034	10.08 ^a	0.000	1.13	0.003	1.53
60000	-0.003	-0.62	-0.008	-4.10 ^a	-0.003	-0.89	0.039	11.29 ^a

^aSatisfies Bonferroni criterion, $z > 2.78$

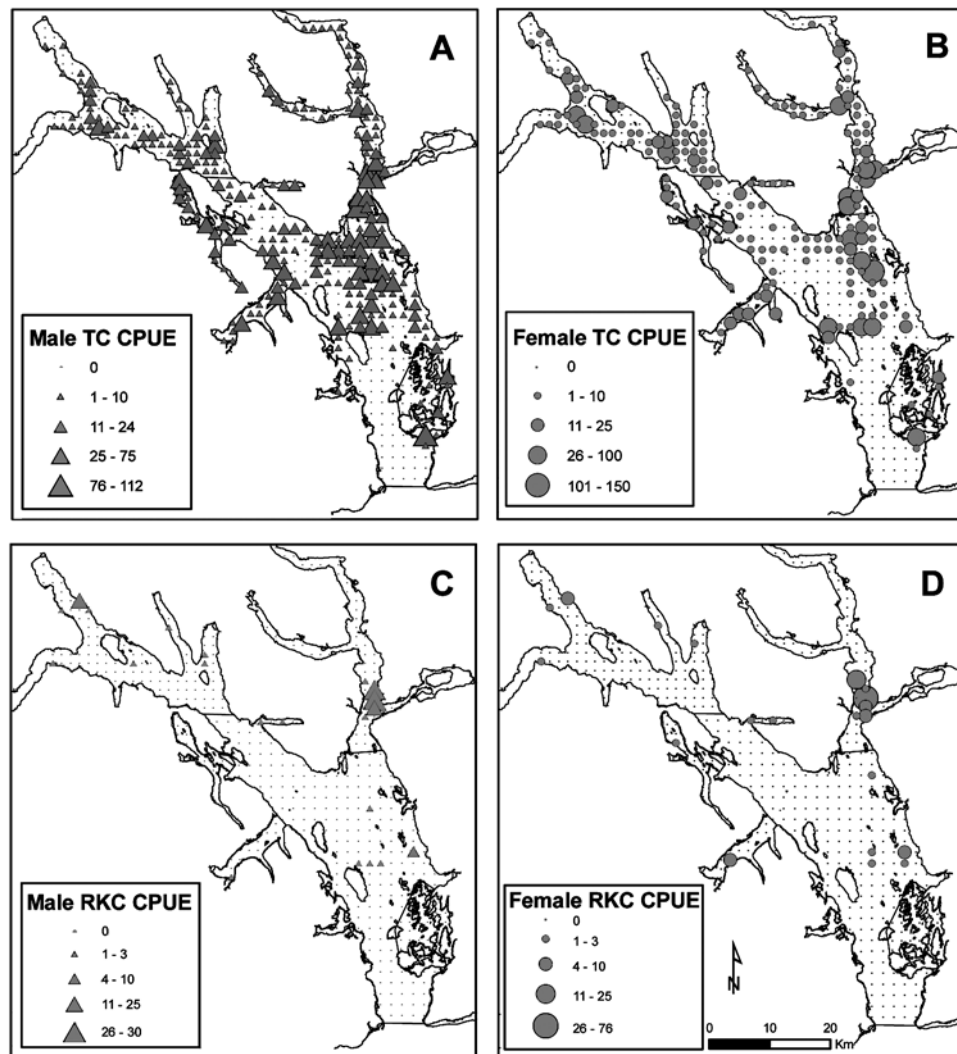


Fig. 3. *Paralithodes camtschaticus* and *Chionoecetes bairdi*. Spatial distribution of catch-per-unit-effort (CPUE) (crab per station) for (A) male Tanner crabs (TC), (B) female TC, (C) male red king crabs (RKC), and (D) female RKC during July to September 2002

crab was detected with an 'active' sensor. Analysis of variance (ANOVA) was used to compare tracking time between male and female red king crabs and between king and Tanner crabs.

The travel rate of a crab ($m d^{-1}$) was estimated by dividing the net distance moved between subsequent tracking trips by the elapsed time. To keep the duration of the segments similar, analysis was limited to crabs located on 2 consecutive tracking trips.

To determine if seasonal patterns occurred, we estimated the distance between the tagging site for each crab and the location where each crab was located on each vessel tracking survey. Because our study site was in a narrow fjord that has a north–south orientation, we simplified the analysis by estimating movement as the distance north or south from the tagging

location; for each tracking survey we calculated the mean distance and 95% CI that all crabs moved. Distances moved were compared among tracking trips with ANOVA; release locations were excluded from the analyses. Paired comparisons between tracking trips were compared with Bonferroni multiple comparison tests.

The dates that crabs moved across the Muir Inlet MPA boundary into the central bay were determined through a combination of the data logger detections and vessel-based searches (Fig. 2). If there was no detection by the data logger but a crab was located outside the Muir Inlet MPA on a tracking trip, the tracking trip date was assigned as a border crossing event.

Time-to-event statistics were used to estimate the rate at which crabs left Muir Inlet (transfer rate; Kaplan

& Meier 1958); date of tagging was 'Day 1,' and crossing the MPA boundary was the 'event.' Crabs were classified as 'censored' when a transmitter was no longer active; crabs that had not crossed the boundary at the end of the study were also censored. The transfer rates of king and Tanner crabs were compared with a log rank test (Swinscow & Campbell 2002).

RESULTS

Distribution and abundance

During July through September 2002, we captured 4968 adult Tanner crabs and 265 red king crabs. Tanner crab CPUE (12.0 ± 2.3 crabs station⁻¹, mean \pm 95% CI) was higher than red king crab CPUE (0.64 ± 0.6). When the confidence interval was calculated as a percentage of the mean, it was much larger for red king crabs than for Tanner crabs (85.5 versus 18.8%). Tanner crabs were widely distributed throughout Glacier Bay and were found at 63% of the stations surveyed (Fig. 3A,B). No Tanner crabs were captured at 51 contiguous stations in the southern part of the bay (Fig. 3A,B). Excluding this zero-catch area, crabs were captured at 72% of the remaining stations, and 90% of the stations that did not yield Tanner crabs produced crabs in an adjacent station (Fig. 3A,B). Although they were widely distributed, 80% percent of the Tanner crabs were captured in 27% of the sampling stations.

In contrast to Tanner crabs, we captured red king crabs at only 7% of the sampling stations (Fig. 3C,D).

Red king crabs were more aggregated than Tanner crabs; 79% of the red king crabs were caught in 6 adjacent pots (Fig. 3C,D).

Red king crabs were not spatially segregated by sex (Cramer-von Mises = 2.11, $p = 0.488$); male and female Tanner crabs also did not demonstrate spatial segregation by sex (Cramer-von Mises = 0.57, $p = 0.266$; but see Nielsen et al. 2007 for additional analysis on segregation by size).

In general, the correlograms for both sexes and species of crab were similar. The degree of spatial autocorrelation decreased with distance, and autocorrelation approached or reached 0 at 30 km (Table 1). Male red king crabs were most clustered and had the highest Moran's I at the 2000 m distance lag (Table 1). Female red king crabs had the highest degree of clustering at the 4000 m distance lag; however, since the majority of female red king crabs were captured in only a few adjacent pots (Fig. 3D), it is possible that they were also autocorrelated at distances less than the minimum grid resolution. Male and female Tanner crabs were also clustered at small spatial scales. Maximum I values occurred at the 2800 m distance lag for female Tanner crabs and the 2000 m distance lag for male Tanner crabs. However, the range of significant positive autocorrelation was 7.5 km for females compared to 30 km for males (Table 1).

The Getis-Ord G_i^* hotspots for male Tanner crabs occurred in a broad swath across central Glacier Bay and in lower Muir Inlet MPA (Fig. 4A). With the exception of 1 female hotspot in Bartlett Cove, the female hotspots co-occurred with male hotspots in the central

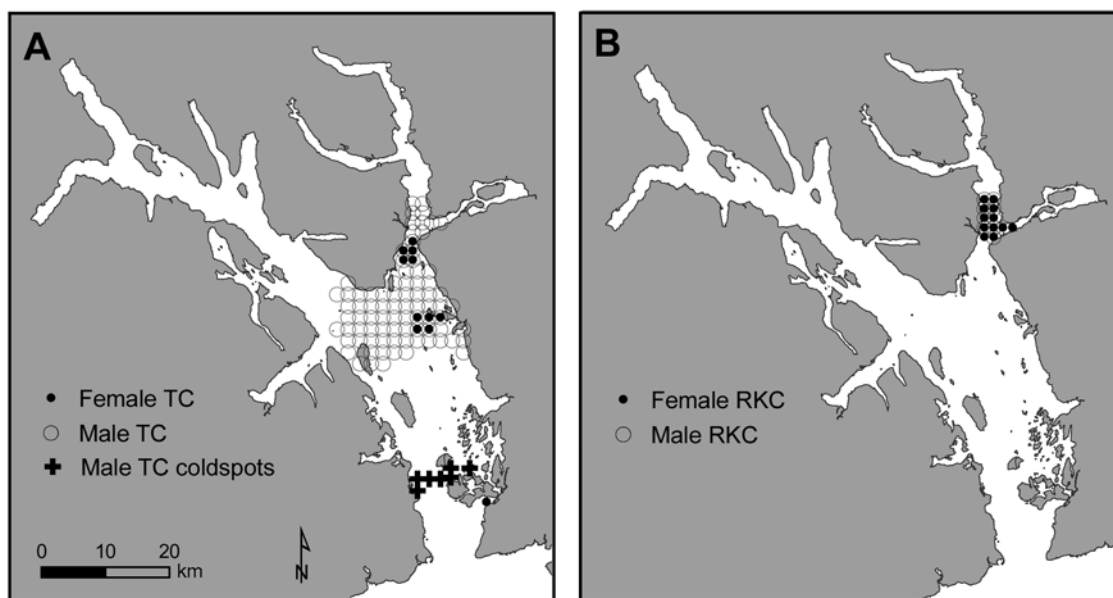


Fig. 4. *Paralithodes camtschaticus* and *Chionoecetes bairdi*. Hotspots (circles) and coldspots (crosses) for abundances of (A) Tanner crabs (TC) and (B) red king crabs (RKC) based on the Getis-Ord G_i^* statistic

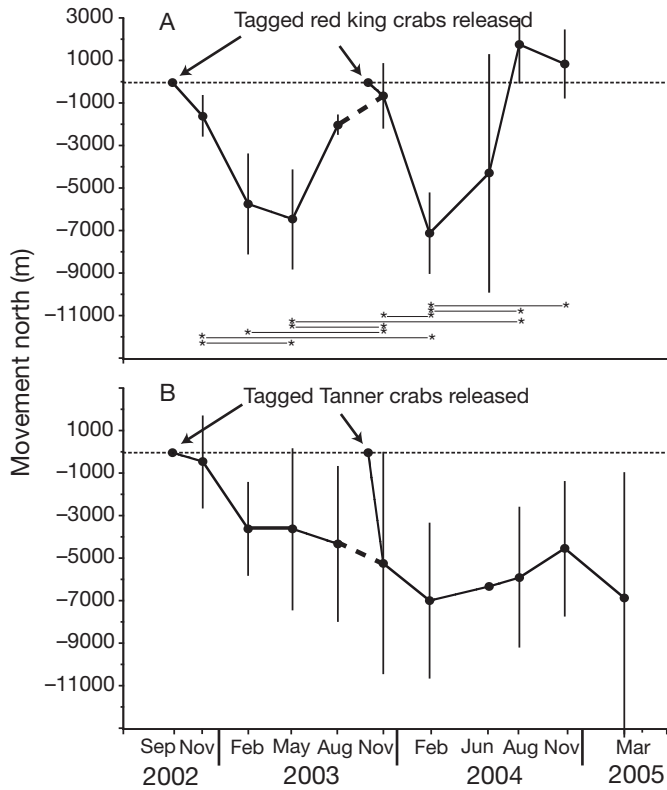


Fig. 5. *Paralithodes camtschaticus* and *Chionoecetes bairdi*. Net directional movement and 95% confidence intervals by season relative to the release locations for (A) red king crabs and (B) Tanner crabs. Southward movements are negative values and northward movements are positive values. Significant differences between pairs of tracking trips are indicated by stars for red king crabs. No significant differences were found for Tanner crabs

bay and lower Muir Inlet (Fig. 4A). Hotspots for both male and female red king crab were clustered in lower Muir Inlet (Fig. 4B). Male Tanner crabs were the only group with significant coldspots, all located near the mouth of Glacier Bay (Fig. 4A). This coldspot cluster was also observed as the low-CPUE patch in which no crabs were captured in 51 adjacent stations near the mouth of the bay (Fig. 3A,B).

Movements of crabs

Tag duration and recovery

Of the 58 tagged crabs, 2 male king and 2 male Tanner crabs were never detected after release (Fig. 2B). In addition, 3 Tanner crabs and 1 king crab molted, died, or shed their transmitters shortly after being tagged (Fig. 2B). These 8 crabs were excluded from the movement analyses. Tracking time did not differ between male (296 ± 80 d, mean \pm 95% CI) and

female red king crabs (256 ± 54 d; $F = 0.297$, $p = 0.5913$). Tanner crabs (486 ± 62 d) were tracked longer than red king crabs (284 ± 112 d; $F = 9.102$, $p = 0.0041$).

An average of 67% (range 38 to 82%) of the tagged crabs were relocated each survey. There was no significant difference in the proportion of king and Tanner crabs relocated ($\chi^2 = 2.43 \times 10^{-4}$, $p = 0.99$; Fig. 2B).

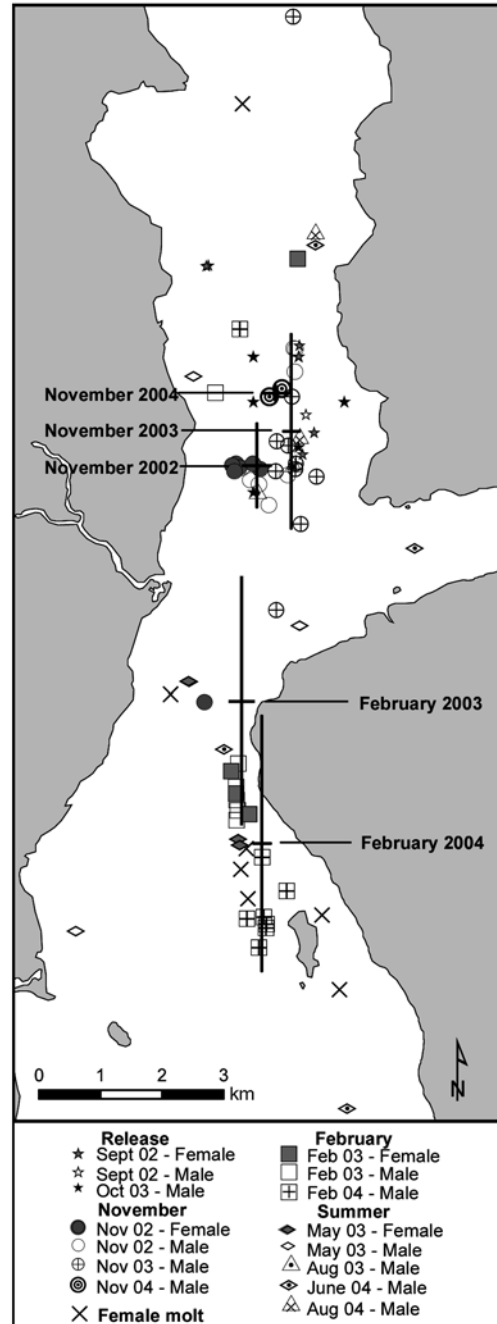


Fig. 6. *Paralithodes camtschaticus*. Seasonal red king crab locations by sex, including 95% confidence intervals for November and February vessel-based surveys, from September 2002 to November 2004

Rates and distances

Mean movement rate of Tanner crabs ($31.6 \pm 8.24 \text{ m d}^{-1}$, mean \pm 95% CI) did not differ significantly from red king crabs ($37.0 \pm 8.95 \text{ m d}^{-1}$, $p = 0.42$). Red king crabs moved southward after their release in fall (Fig. 5A; $F = 6.7$, $p < 0.0001$), and were found the following November back near their release location (Fig. 5A). Throughout a year, red king crabs completed a north–south–north migration cycle in the fjord. Tanner crabs did not demonstrate the seasonal changes in the direction of their movements (Fig. 5B; $F = 0.947$, $p = 0.49$).

Initially, 16 red king crabs were tagged in a small spatial area where they were found to be highly aggregated during the distribution and abundance survey. During the November 2002 tracking trip, 15 red king crabs were detected, generally within 2 km of the original release site. The single exception was a female that had moved approximately 6.8 km south (Fig. 6). During the February 2003 vessel survey, 8 of the 10 relocated crabs were clustered near the mouth of Muir Inlet and approximately 7.5 km south of the tagging location (Fig. 6). Crabs tagged in fall 2003 similarly moved south with a return north at summer's end to a location near the original tagging site (Figs. 5 & 6). In contrast to red king crabs, Tanner crabs did not exhibit coordinated movements. Seven of the 8 female red king crab tags were located after having molted, with 5 of the tags found along the east shore near the mouth of Muir Inlet (Fig. 6).

Proportionally, more Tanner ($N = 10$) than red king crabs ($N = 2$) moved from Muir Inlet into the central bay ($\chi^2 = 3.91$, $p = 0.049$; Fig. 7). After 350 d, the estimated transfer rate was 11% for red king crabs and 35% for Tanner crabs (Fig. 7). However, these transfer rates may be biased low. Although data loggers were effective at detecting crabs leaving the reserve, they were not in place for the entire study. In addition, 2 Tanner crabs that were detected near the gate were never relocated outside the reserve by the vessel survey, suggesting the vessel surveys may not have recovered all crabs that departed the Muir Inlet MPA.

Three of the 10 tagged Tanner crabs that left the Muir Inlet reserve were captured in the commercial harvest, explicitly demonstrating spillover into the commercial fishery. One of the harvested crabs, crab number 28500, was tagged on 1 September 2002, crossed the gate on 19 January 2004, and was captured in the commercial fishery 12 km to the south of the Muir Inlet MPA boundary on 4 February 2004 (Fig. 8). From the boundary to the point of capture the crab traveled a minimum of 440 m d^{-1} . Another crab was detected near the gate on 11 February 2004 and was captured in the fishery a year later on 24 February

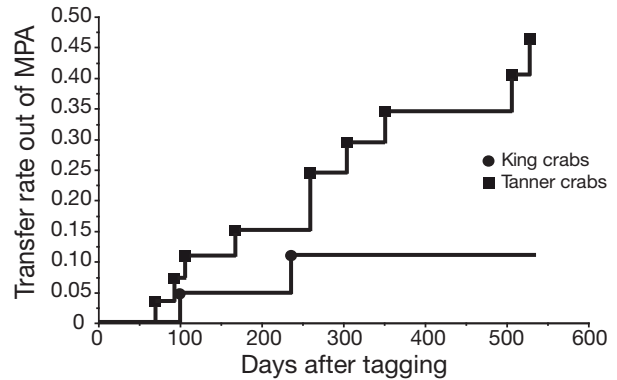


Fig. 7. *Paralithodes camtschaticus* and *Chionoecetes bairdi*. Kaplan-Meier estimated transfer rates of red king and Tanner crabs from the Muir Inlet marine protected area (MPA); symbols indicate border-crossing events

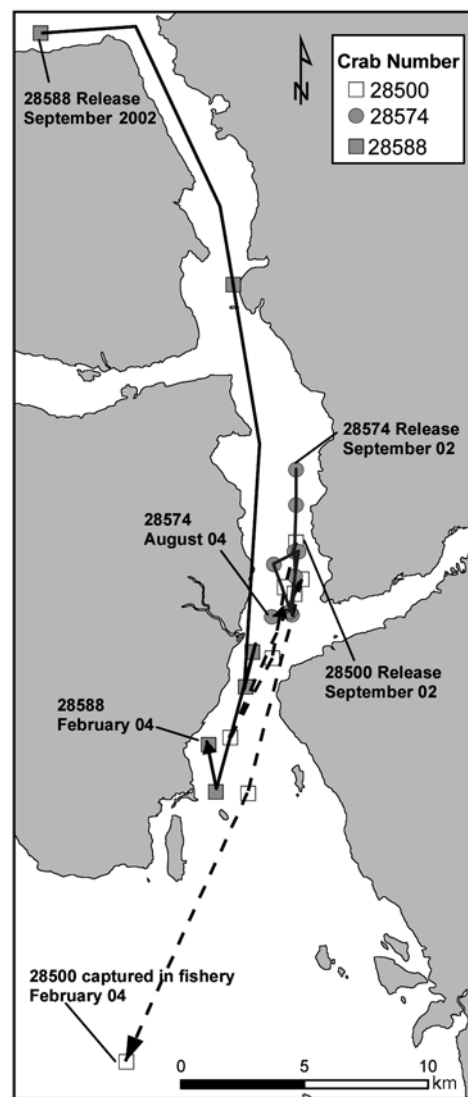


Fig. 8. *Chionoecetes bairdi*. Examples of 3 individual Tanner crab movements

2005. A third crab for which the tag identification was unknown was harvested in February 2005.

Not all crabs that moved large distances left the reserve during the time frame of our study. Crab number 28588, tagged in 2002 in upper Muir Inlet, was detected near the gate in December 2003 before moving slightly north, which means that it traversed almost the full length of Muir Inlet (32 km) in 15.6 mo (Fig. 8). In contrast, some of the Tanner crabs, such as crab number 28574, remained in Muir Inlet reserve and moved relatively small net distances (Fig. 8).

DISCUSSION

This study provides empirical data on the transfer rate of 2 commercially harvested crab species from a high-latitude MPA. The results of our combined data on transfer rates and abundance have broad implications for the design of effective MPAs for Tanner and red king crabs and other mobile benthic species.

Even though Tanner crabs and red king crabs moved similar average distances per day, Tanner crabs had a higher transfer rate from Muir Inlet into the central bay. Tanner crab movements were characterized by large variation among individual crabs, both in distance and direction traveled. In contrast, red king crabs showed cohesive movements south between fall and winter and north from spring to fall between the area north of Adams Inlet and the mouth of Muir Inlet (Fig. 6). This pattern suggests that red king crabs migrate seasonally (Fig. 5A). Seasonal movements out of and back to the original capture areas explains why red king crabs had a low net transfer rate compared to Tanner crabs. Most red king crabs found in the fall and winter were concentrated in a small area. During May and August our ability to relocate crabs was poor, and thus we do not know where the red king crabs reside during the summer or whether they remain aggregated as they move between the mouth of Muir Inlet and Adams Inlet.

Juvenile red king crabs have been observed stacked in large 3-dimensional pods during the day and then spreading out to forage at night as a mobile foraging group (Powell & Nickerson 1965, Dew 1990). Less is known about fine-scale adult behavior, because adults spend much of their lives at depths where direct observation is difficult. During the winter, when females enter shallow water, Stone et al. (1993) used SCUBA to locate ultrasonically tagged female red king crabs, which were observed to form pods and move as cohesive groups. Our study provides further support that adults have coordinated movements, and that this grouping behavior occurs in deep as well as shallow water. Since our tagged male and female red king

crabs had coordinated movements, it suggests that the adults are not segregated by sex in Glacier Bay.

The aggregated distribution of red king crabs makes them vulnerable to localized fishing pressure. This suggests that an MPA that protects red king crabs from fishing mortality may not need to be as large as one designed to protect Tanner crabs. Thus, an important objective in MPA design for red king crabs is to determine the seasonal habitats of red king crabs and include critical habitat areas in the MPA. The distances we observed red king crabs moving between spring and fall habitats were relatively small for this species and may be specific to Muir Inlet. In other locations in Alaska, red king crabs tagged with visual tags recovered in the harvest moved larger distances than we observed in Glacier Bay (Wallace et al. 1949, Hayes & Montgomery 1963, Simpson & Shippen 1968). Hence, a larger MPA for red king crabs might be required in other parts of Alaska if the intent is to provide protection from fishing mortality, especially in less bounded areas (non-fjord habitat) like the Bering Sea.

If the objective of an MPA is to protect reproductive areas of red king crabs, sonic tags can be a highly effective method for determining reproductive locations. Shortly after their eggs hatch, females molt and mate while in the soft-shelled condition (Donaldson & Byersdorfer 2005). Therefore, locations of the molted sonic tags would mark the reproductive areas of red king crabs. Since the tags can broadcast for a long time after they are molted, the locations of the molted tags can be determined at any convenient time of the year after the spring reproductive cycle. In our study, 5 of the 7 inactive tags were clustered along the east shore near the mouth of Muir Inlet (Fig. 6), and we hypothesize that this is a reproductive area for red king crabs. Additional female red king crabs should be tagged to determine if there are other reproductive locations, and they should be tagged for multiple years to determine if the crabs have site fidelity for reproductive locations among years.

The high transfer rate we found for Tanner crabs is significant because Muir Inlet is large compared to other MPAs in the world (Halpern 2003). Muir Inlet is 178 km², whereas 69% of the world's MPAs are <100 km² (Kelleher et al. 1995). As a general rule, populations in large MPAs have lower transfer rates than small MPAs because the boundary:area ratio decreases with increasing size of MPAs (Roberts & Polunin 1991, Kramer & Chapman 1999, Sale et al. 2005). In addition to being large, the Muir Inlet MPA has a very small boundary across which crabs may emigrate because it is a narrow fjord largely surrounded by a highly convoluted shoreline, making its boundary:area ratio extremely small (Fig. 1B) and effectively making it an even larger MPA. To achieve an equivalent

boundary:area ratio, a square MPA not adjacent to the shore or a square MPA with 1 side connected to the shore would need to be 17 680 and 9950 km², respectively.

The transfer rates that we observed demonstrate that MPAs can be designed to enhance Tanner crab fisheries through spillovers to nearby fished areas. Alternatively, if the goal of the MPA is to reduce fishing mortality on Tanner crab brood stock inside the MPAs and export larvae, our findings suggest that the MPA needs to be large. Despite its relatively large size and small boundary:area ratio, Muir Inlet still had a large Tanner crab transfer rate and would probably be sub-optimal as an MPA if the goal is to protect male brood stock.

The distribution data are important for interpreting the high transfer rate. The hotspot analyses showed that most of the Tanner crabs were in a contiguous patch bisected by the Muir Inlet MPA boundary. If a reserve boundary bisects a patch of good habitat, high transfer rates are likely. Many reef-dwelling species move widely within a contiguous reef, suggesting that the transfer rate will be higher if a reef is bisected by an MPA boundary (Chapman & Kramer 2000). If an MPA contains the majority of a high abundance patch, the transfer rate would presumably be lower.

Although the movement portion of our study focused on only one of the areas closed to Tanner crab fishing (Muir Inlet), eventually commercial fishing will be closed in the central portion of Glacier Bay, creating a single very large MPA (1312 km²). Like Muir Inlet, the boundary:area ratio will be very low because Glacier Bay is an enclosed body of water with a narrow entrance. One fundamental uncertainty is how the local Tanner crab population within Glacier Bay will interact with the local crab population in Icy Strait, immediately outside the future MPA (Fig. 1A). Glacier Bay and the immediately adjacent waters of Icy Strait were both productive areas for historical Tanner crab commercial fisheries; from 1996 to 1998, 13.8% of the Tanner crab harvest from all of southeastern Alaska came from Glacier Bay and 11.5% came from the adjacent waters in Icy Strait (Clark et al. 1999). It cannot be determined whether the 13% percent of the harvest that historically came from Glacier Bay will be lost to future harvests or if the loss will be mitigated by spillover from Glacier Bay into adjacent Icy Strait. Spillover may accelerate with the Glacier Bay phase-out if Tanner crabs select habitat predicted by the Ideal Free Distribution model (Fretwell 1972, Kramer & Chapman 1999). High Tanner crab mobility, as indicated by the high tag transfer rate from Muir Inlet to central Glacier Bay, supports a prediction of a high exchange rate between central Glacier Bay and Icy Strait.

When the movement data are combined with the distribution data, however, an alternate hypothesis seems more likely. Tanner crabs were widely distributed in the central and upper portions of Glacier Bay, but absent from a large continuous portion of the lower bay near the mouth (Figs. 3A,B & 4A). The edge of this empty zone marks a very abrupt transition from high CPUE to zero catch, supporting the hypothesis that this area is poor Tanner crab habitat and acts as a natural barrier. Habitat mapping with multi-beam sonar found a change from soft to hard substrate precisely where crab CPUE dropped to 0 (Harney et al. 2006). Sand has been demonstrated to be a movement barrier for the sea urchins *Strongylocentrotus purpuratus* and *S. franciscanus* (Laur et al. 1986) and blue crabs *Callinectes sapidus* (Micheli & Peterson 1999). Changes in benthic substrate have acted as a barrier to restrict MPA spillover in a variety of species including conch *Strombus gigas* (Tewfik & Bene 2003), spiny lobster *Jasus edwardsii* (Kelly et al. 2002), and numerous reef fishes (Chapman & Kramer 2000).

Movements of male Tanner crabs determined by the recovery of harvest tags suggest that habitat barriers may restrict movement near Kodiak, Alaska (Donaldson 1983). Although a few tagged crabs demonstrated the ability to move large distances, most crabs were recaptured in the areas of release. Despite a wide range in length of time between tagging and recapture, net distance moved was not correlated with time-at-large. Deep gullies and shallow ridges were suggested to act as habitat barriers to reduce the exchange rate between adjacent areas (Donaldson 1983).

If our interpretation of the mouth of Glacier Bay as a habitat barrier for adult Tanner crabs is correct, the MPA will be effective at minimizing fishing mortality for Tanner crabs in Glacier Bay following fishery phase-out. Conversely, Glacier Bay will be ineffective at supplementing the Icy Strait catch through spillover of adults. An obvious next step is to tag crabs in Icy Strait and lower Glacier Bay to explicitly test adult exchange between the 2 areas, and repeat the tagging experiment following phase-out to determine if spillover accelerates with increasing density within Glacier Bay.

Most MPAs are in tropical areas, so the majority of information on the effectiveness of MPAs comes from tropical waters. Extrapolating the success found in the tropics to higher latitude shelf habitats should be done cautiously (Sale et al. 2005). Because movement across large distances has been documented for both king and Tanner crabs (Wallace et al. 1949, Hayes & Montgomery 1963, Simpson & Shippen 1968, Donaldson 1983), it is likely that MPAs would have limited effectiveness for these species if the sizes of the reserves are

the sizes typical for coral reef habitats (Kelleher et al. 1995, Halpern 2003). Our study confirmed this conclusion by documenting a high transfer rate for Tanner crabs in an MPA that has a size much larger than the worldwide median size (15.8 km²; Kelleher et al. 1995). In contrast, we have shown that red king crabs, at least in one location, have seasonal migratory patterns that greatly reduce the net distances moved. Although Tanner crabs exhibit relatively large movements, their movements still appear to be restricted at a larger spatial scale by habitat barriers, a conclusion supported by other tagging data in Alaska (Donaldson 1983). Reserves that are effective at protecting adult king, and especially Tanner, crabs from fishing mortality will likely need to be larger than is typical of reserves worldwide. However, by incorporating information on the seasonal movements of red king crabs and the locations of habitat barriers for Tanner crabs, effective reserves can likely be designed to protect adults from fishing mortality. Although this paper focuses on red king and Tanner crabs, the data we present are applicable to the design of MPAs for other mobile species; MPAs for mobile species are more likely to be effective if seasonal movements and habitat barriers are incorporated into their design.

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