



## Movement rates of morphometrically mature male snow crabs, *Chionoecetes opilio* (O. Fabricius, 1788), in the eastern Bering Sea, Alaska (Brachyura: Oregoniidae)

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### ABSTRACT

Movement rates of morphometrically mature male snow crabs, *Chionoecetes opilio*, in the eastern Bering Sea, Alaska were estimated for 33 individuals at liberty between 280 and 467 days. Using depth measurements from data storage tags attached to individual crabs, daily across-shelf movement rates were estimated as the daily change in crab depth divided by the slope (i.e., depth/horizontal distance) of the seafloor on which each crab resided each day. Rates and distances were analyzed at different time scales (day, month, year) and general additive models were used to test the significance of factors that could potentially influence the daily rate of movements. Individual crab rates averaged between 0.1 and 1.1 km/day over their time at liberty, with one individual attaining a maximum rate of 8 km/day. Rates varied significantly ( $P < 0.05$ ) with the bottom depth, season (day of year), and the release area. Although overall rates did not vary with crab size, maximum rates were highest among the smallest individuals, two of which (100–102 mm carapace width) traveled approximately 250 km in ten months. Movement rates were highest during spring when travel was directed mostly inshore, and slower during fall and winter when offshore movements occurred. In contrast to other studies that demonstrated decreased snow crab movement rates in cold water (e.g.,  $< 1$  °C), no temperature effect was found for these males in the eastern Bering Sea. Further research is necessary to determine if factors that act at shorter time scales ( $< 24$  hours), such as tidal currents and light intensity, influence snow crab movements.

**Key Words:** commercial crab fisheries, data storage tags, environmental effects, migrations

### INTRODUCTION

One focus of our research was to examine how the daily movement rates of morphometrically mature (MM) snow crab, *Chionoecetes opilio* (O. Fabricius, 1788), varies over time, and identify the biotic and abiotic factors that influence these rates. Candidate factors include water temperature, crab size, season (day of year), bottom depth, tidal current speed, and light intensity. Even though the snow crab is cold-water adapted, normally inhabiting temperatures between  $-1$  °C and  $5$  °C (Foyle *et al.*, 1989; Nichol & Somerton, 2015), metabolic costs that occur at the extremes of this range, can act to limit movements (Foyle *et al.*, 1989; Maynard, 1991). For the snow crab in eastern Canada, Maynard (1991) found, both in the laboratory and in the field, that hourly walking speeds were 2 to 3 times less at  $0$  °C to  $1$  °C compared to  $3.5$  °C to  $6$  °C. Movements may also vary with crab size, where from a

mechanistic perspective, we might expect larger crabs to move faster than smaller ones due to their longer legs. Considering seasonality and bottom depth, the expectation is that daily movement rates will increase during spring and as depths become shallower due to the inshore mating movements (Nichol & Somerton, 2015), but only if these rates are reduced or less directional during the non-mating period. Movement rates are also thought to vary with both tidal currents and with light levels, where in limited cases, adult male snow crabs have been found to preferentially move against tidal currents or during nighttime hours (Kanawa *et al.*, 2014). Greater nighttime activity levels (and less burying behavior) has been hypothesized as the reason for increased trawl catch during nighttime compared to daytime (Powles, 1968), so it might be reasonable to expect daily movement rates to be greater during nighttime compared to daytime.

Commercial-size ( $\geq 102$  mm carapace width (CW)) MM male snow crabs that reside on the outer shelf (100–200 m bottom depth) in the eastern Bering Sea undergo movements that traverse bottom depth gradients (Nichol & Somerton, 2015), although the extent of these vary widely among individuals. These large-clawed males have undergone a terminal molt and an ontogenetic migration from the middle (50–100 m) to the outer shelf. In subsequent years, the majority of MM males move seasonally inshore during spring, likely to mate with multiparous females that have a shallower distribution (Nichol & Somerton, 2015). Among 33 MM males tagged and recaptured on the outer eastern Bering Sea shelf with depth and temperature recording data storage tags (DSTs), Nichol & Somerton (2015) found that the majority moved inshore during spring, some remained within a relatively narrow bottom depth range (120–130 m), and others moved deeper before moving shallower. Two of the smallest (100–102 mm CW) males tagged, consistently moved inshore from 120 m to 90 m within a two- to three-month period, followed by a more gradual return offshore, movements that, considering the moderate slope of the eastern Bering Sea shelf, were at least 100 km in each direction.

Determining and characterizing the rate that MM male snow crabs move can help to better understand the spatio-temporal dynamics of the stock. Whether or not males observed in deeper waters can mate with mature females in shallower waters is likely dependent on the ability of males to move. The stock dynamics of the snow crab populations are highly complex (Ernst *et al.*, 2005; Sainte-Marie *et al.*, 2008; Nichol & Somerton, 2015), and many aspects of the eastern Bering Sea stock, including the movements of mature females and smaller (i.e., less than commercial size,  $< 100$  mm CW) MM males are not well known. The need for movement and ultimately the success of mating is likely dependent on the dynamics of mature male competition for mates (Comeau *et al.*, 1998; Moriyasu & Comeau, 1996; Sainte-Marie *et al.*, 1997, 2008), which in turn is dependent on mature male and female densities, distributions, and the proportion of different life-history states (e.g., primiparous *versus* multiparous females; Nichol & Somerton, 2015). Determining the extent to which MM male movement affects spawning success is further complicated by the fact that females can store sperm, and thus do not necessarily require mating every year (Sainte-Marie & Carrière, 1995). While acknowledging the complexities and unknowns, mating success is at least partly dependent on the ability and flexibility of MM males to move. The number of mature males within the population required for successful mating could be less if high mobility increases mating encounters, and given that the distributions of snow crabs are more widespread in the eastern Bering Sea compared to other snow crab populations due to the flat topography (Nichol & Somerton, 2015), mobility for the purpose of mating may be especially important for this stock. Future studies will likely rely upon spatial modeling to help predict consequences of certain management measures (Szuwalski & Punt, 2015). Knowledge of male movement rates and the factors that may affect these rates is thus needed.

This research had two objectives. The first was to express the scale of movement of snow crabs in the eastern Bering Sea, identifying how fast they move on daily, monthly, and annual time scales; the second to identify what factors, biotic and abiotic, affect these movements.

## METHODS AND MATERIALS

### Tagging

A total of 277 MM (large-clawed) male snow crabs were tagged with depth and temperature collecting data storage tags (DSTs model CEFAS G5; [www.cefastechnology.co.uk](http://www.cefastechnology.co.uk)) during winter and spring in 2010 and 2011 in the eastern Bering Sea (Fig. 1)

as described by Nichol & Somerton, 2015). Crabs were captured aboard two commercial vessels, F/V *Kiska Sea* in 2010 and F/V *Pacific Sun* in 2011, and were tagged and released within 10 min of capture. Crabs tagged in 2010 were captured and released northwest of the Pribilof Islands (57°35'N) and those tagged in 2011 were captured and released approximately 100 km farther north (58°30'N). A total of 33 of the tagged crabs, 24 from 2010 and 9 from 2011, were later recaptured by the commercial snow crab fishery after being at liberty between 280 and 467 days. DSTs recorded temperature every 30 min at a precision of 0.03 °C, and depth every 1 min at a precision of  $< 0.08$  m.

### Daily distances moved across the shelf

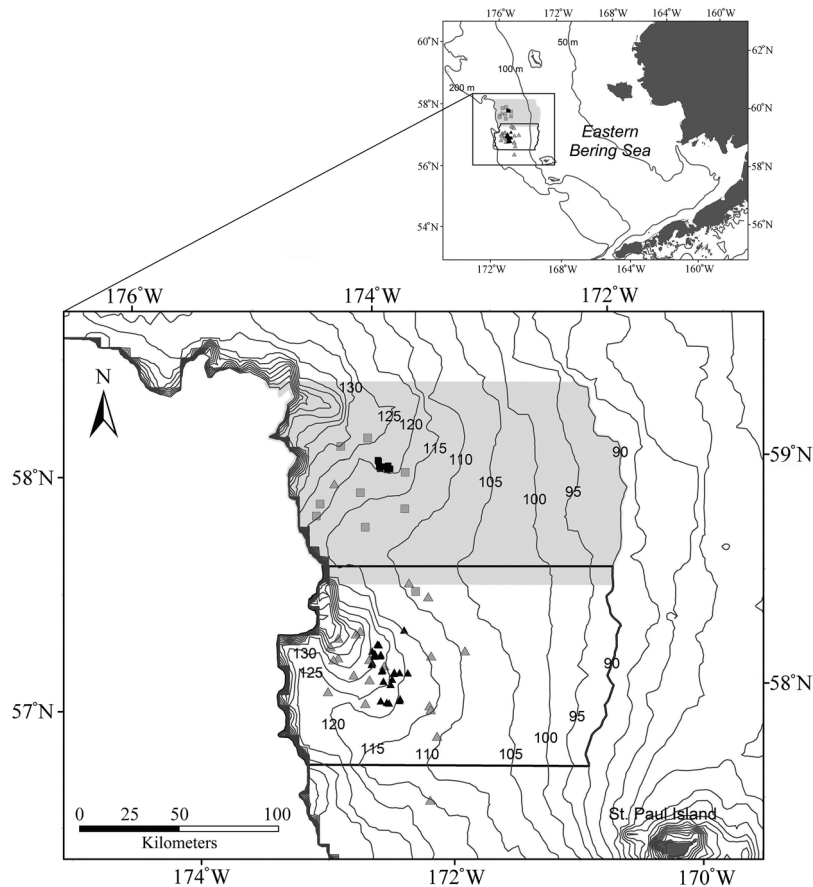
Daily movement distances were measured in the across-shelf direction (i.e., perpendicular to the depth contours). These were estimated for each tagged crab as the daily change in depth divided by the slope of the seafloor in the depth zone occupied by the crab. Tidal fluctuations were first removed from the tag depth (m) data using a low-pass filter (Flagg *et al.*, 1976; Beardsley *et al.*, 1985), then the daily depth changes were calculated by differencing the depth at 12:00 (noon) between successive days. Positive valued depth changes thus corresponded to inshore movements and negative values corresponded to offshore movements. Because this estimator does not capture movements along depth contours, daily distances should be viewed as a minimum, with overall distances moved biased low.

Across-shelf seafloor slope values, within 5 m depth intervals, were calculated by first estimating bottom depth contours at 5 m intervals using ArcGIS 10.2.2 software (ESRI, Redlands, CA). These contours were based upon spatially explicit (latitude, longitude) bottom depth data from National Imagery and Mapping Agency (NIMA) depth soundings, depths recorded during bottom trawl shelf, slope and fisheries acoustic surveys (Hoff, 2013; Lauth & Nichol, 2013; Honkalehto & McCarthy, 2015), and the tag-recorded depths at release and recapture sites. A total of 5,273 depth recordings were utilized within the release/recovery areas (31,824 km<sup>2</sup>). Depth contours were calculated first by creating a depth grid using inverse distance weighting, then creating a surface contour of the grid at 5 m intervals (Spatial Analyst Tool, ArcGIS).

Slope values specific to each 5 m contour were then calculated by first estimating the mean distance from one 5 m contour to the next, done separately for 2010 (southerly) and 2011 (northerly) release/recovery areas. Each release/recovery area was defined by a 50 km boundary north and south of the geographic center of the combined release and recovery positions (mean center tool, ArcGIS; Fig. 1). Subsequently, using vertices along each contour (mean of 205 vertices per contour) contained within the two defined areas, the minimum distance from one contour vertex to the next (e.g. 90–95 m, 95–100 m, etc.) was calculated using the “Near” analysis tool within Arc Tool Box (ArcGIS). These vertex-to-vertex distances were then averaged for each area/contour interval. The mean overall distance across each of the 17 contour intervals (per area) was lastly calculated, and the slope for each interval estimated as this distance divided by 5. Daily distance moved for each crab was then calculated as the daily change in tag depth divided by the slope for the 5 m bottom depth interval in which the crab resided that day.

### Modeling the effects of movement rate

General additive models (GAM) (Burnham & Anderson, 2010) were used to test for factors that influenced or were correlated with daily movement rate, regardless of the direction. Independent variables included five continuous variables: day of year, bottom depth, temperature, tidal strength, and crab carapace width (CW); and one categorical variable: release area (i.e., southerly



**Figure 1.** Release (small black symbols) and recapture (large grey symbols) locations of morphometrically mature male snow crabs (*Chionoecetes opilio*) tagged with timed depth-recording data storage tags (DSTs) in the eastern Bering Sea during 2010 (triangles) and 2011 (squares). The black outlined area encompasses the more southerly area for 2010 released crabs, and the shaded area the more northerly area for 2011 released crabs. Grey lines in the lower map indicate the bathymetry lines calculated at 5 m intervals, which were used to estimate the shelf slope, and subsequently to estimate the daily distance that the tagged crabs migrated across depth gradients.

2010, northerly 2011). Day of year (i.e., 1 to 365) was treated as a cyclic cubic spline (argument  $bs = "cc"$  in the “*gamm*” function) to provide continuity between January and December. Bottom depth and temperature values were those recorded by the DSTs. Because our rates are resolute to only 24 hours and both tidal currents (direction and velocity) and light levels vary over time scales less than that (e.g., semidiurnal, diurnal), we could not unfortunately directly test for their influence. We nevertheless tested if movement rates varied with tidal strength, essentially testing if rates varied between periods of stronger (spring) tides and weaker (neap) tides. Tidal strength was estimated as the daily mean absolute tide height (m), computed for the area of tagging using Tidal Inversion Software (OTIS) (Egbert *et al.*, 1994; Egbert & Erofeeva, 2002). A fixed-effects model was selected over one with a random-effects term (individual crab), so that CW could be tested.

Daily movement rate was transformed using the fourth root to normalize distributions that were strongly right skewed. To reduce autocorrelation, daily movement rates were averaged for every three-day interval. In the initial phase of modelling, however, significant autocorrelation was still detected among residuals. We therefore opted to include autocorrelation structure (*corAR1*) (Pinheiro & Bates, 2000) in the model. Models were run using the “*mgcv*” package with “*gamm*” functions in R (Wood, 2006). Independent variables were sequentially removed in a backward step-wise manner, with significant variables retained where  $P < 0.05$ .

In a separate model, a scaled response variable, daily rate divided by the mean daily rate per crab, was used to determine

if significant variables (from the model above) influenced movement rate at the individual crab level, as opposed to influence on the mean response that could result from among-crab differences. More specifically, this model was used to test whether a significant bottom-depth effect was influential for each crab, or whether significance resulted from only the fastest crab reaching the shallowest bottom depths. This model was run with the significant variables from the above model using the same transformation and structure.

## RESULTS

Cross-shelf distances moved by the 33 tagged MM male snow crabs averaged between 0.1 and 1.1 km/day, with a maximum rate of  $\sim 8$  km/day and 97 km/month (Table 1). Cumulative distances among males in which tags recorded for at least nine months ranged from 29 km for a 115 mm male at liberty for 286 days to 417 km for a 100 mm male at liberty for 467 days (Table 1). Cross-shelf movement distances were greatest during spring months (March to May in 2010 and 2011) when most movements were directed inshore, and commonly covered more than 10 km per month, although variability among individuals was high (Fig 2; Table 1). Maximum daily movement distance was negatively correlated with crab size (Fig 3), although overall rates were not dependent on crab size (see model results below).

For the two smaller male crabs that underwent clear inshore movements followed by offshore movements as indicated by the consistent change in depth over a 9–11-month period (Fig 4A, B), total

MOVEMENT RATES OF MALE SNOW CRABS

**Table 1.** Summary of the estimated distances moved by morphometrically mature (large-clawed) male snow crab (*Chionoecetes opilio*) released with data storage tags in the eastern Bering Sea. Distances reflect across-shelf movements only, estimated for each crab as the daily change in bottom depth divided by the bottom slope.

Crab identification number	Release date	Days recorded <sup>1</sup>	Carapace width (mm)	Mean overall temperature (°C)	Cumulative distance moved (km)	Mean distance per day (km)	Maximum distance per day (km)	Maximum distance per month (km)	Month/year of maximum distance <sup>2</sup>
5658	4/19/2010	309	119	3.6	63.2	0.2	3.5	19.2	5/2010
5660	4/19/2010	312	122	3.6	53.8	0.2	1.3	8.5	5/2010
5665	4/19/2010	255	126	3.2	107.9	0.4	1.9	26.7	11/2010
5749	4/19/2010	282	121	3.4	61.2	0.2	2.5	16.6	5/2010
5756	4/19/2010	298	116	3.1	267.2	0.9	5.1	38.0	5/2010
5770	4/20/2010	320	109	3.5	98.6	0.3	2.1	28.7	9/2010
5771	4/20/2010	286	115	3.6	28.8	0.1	1.1	6.5	5/2010
5776	4/20/2010	303	114	3.6	58.3	0.2	1.8	15.9	5/2010
5782	4/20/2010	286	125	3.5	101.0	0.4	2.8	21.3	7/2010
5786	4/20/2010	317	119	3.1	219.6	0.7	3.4	52.2	5/2010
5791	4/20/2010	93	111	2.5	71.9	0.8	5.6	28.6	4/2010 (8)
5792	4/20/2010	276	110	3.3	104.6	0.4	3.6	29.9	5/2010
5798	4/20/2010	293	100	2.6	260.7	0.9	8.4	47.3	9/2010
5809	4/20/2010	138	121	3.3	35.3	0.3	2.4	20.8	5/2010
5816	4/20/2010	316	123	3.6	47.9	0.2	1.4	9.7	5/2010
5819	4/20/2010	279	117	3.6	35.9	0.1	2.2	17.3	5/2010
5820	4/20/2010	279	119	3.6	48.0	0.2	1.4	8.9	5/2010
5845	4/21/2010	467	100	3.2	416.8	0.9	8.5	97.6	4/2011
5846	4/21/2010	287	110	3.4	170.7	0.6	5.9	50.9	5/2010
5851	4/22/2010	318	102	2.9	255.4	0.8	6.0	57.6	5/2010
5854	4/22/2010	278	117	3.5	147.3	0.5	7.0	24.3	11/2010
5855	4/22/2010	296	112	3.1	338.3	1.1	6.3	83.8	12/2010
5859	4/22/2010	317	125	3.4	99.2	0.3	3.0	19.5	1/2011
5860	4/22/2010	277	115	3.2	126.7	0.5	6.5	32.7	9/2010
7340	3/08/2011	440	112	2.2	242.3	0.6	5.6	38.5	11/2011
7352	3/08/2011	299	120	2.6	89.4	0.3	1.4	14.3	5/2011
7368	3/08/2011	454	123	2.3	110.6	0.2	1.4	12.2	3/2012
7371	3/08/2011	426	100	2.2	210.8	0.5	3.3	28.7	4/2011
7387	3/08/2011	45	115	2.4	16.8	0.4	1.9	8.7	3/2011 (21)
7424	3/08/2011	441	119	2.4	118.9	0.3	1.9	14.7	3/2012
7425	3/08/2011	435	117	2.3	149.1	0.3	3.1	23.6	6/2011
7448	3/08/2011	34	123	2.4	15.5	0.5	2.2	11.6	3/2011 (21)
7456	3/08/2011	69	106	2.3	77.8	1.1	3.7	44.7	4/2011

<sup>1</sup> For crab identification numbers 5665, 5791, 5809, 5845, 7387, 7448, 7456, the tag depth sensors failed after the indicated days recorded, and thus days recorded do not equal days at liberty.

<sup>2</sup> Number in parentheses indicates the total days of the month in which data was collected, for months that were not complete (i.e., the month of tag release).

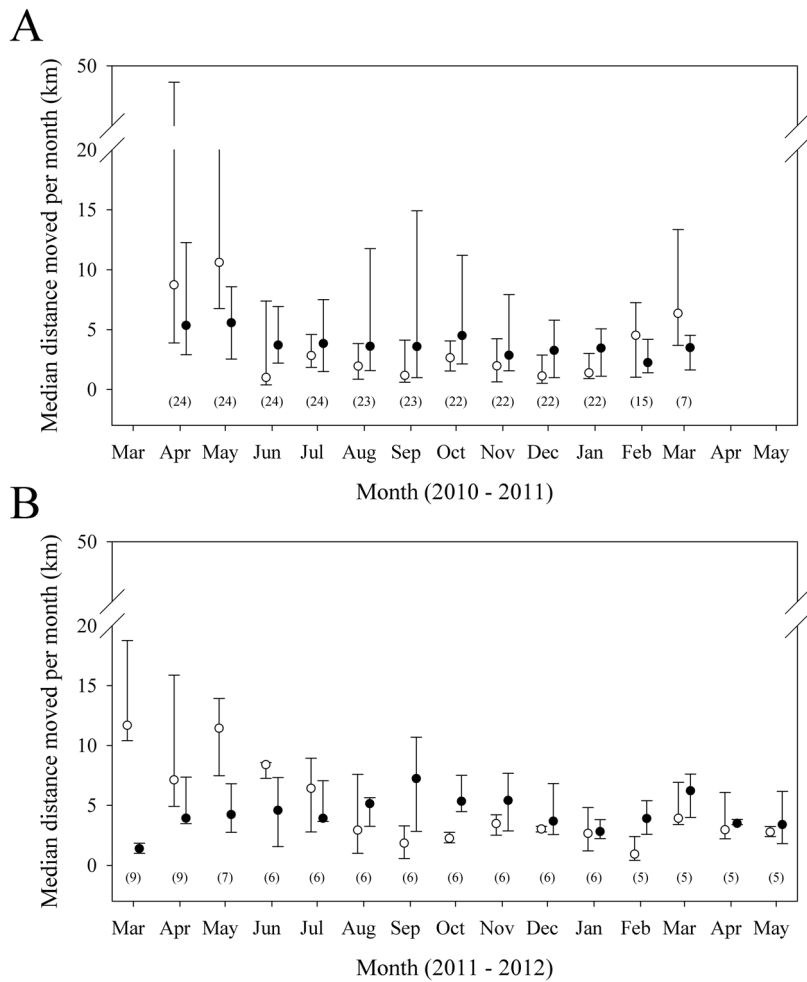
cross-shelf distances covered just over 250 km (Fig 4C, D). During the first ten days at liberty, both crabs moved inshore at a relatively fast rate averaging 3.6 km/day, followed by continued inshore movement averaging 1.0 to 1.4 km/day during spring and summer (Fig 4E, F). During summer and fall, both crabs then underwent a return offshore movement averaging about 1.0 km/day, followed by decreased rates of 0.2 km/day in winter (December to March) when only slight distances were covered in the offshore direction (Fig 4E, F).

Movement rates varied with season (day of year), bottom depth, and release area (final model  $r^2 = 0.42$ ; Fig 5), but did not vary with the temperature, crab size (CW), or tidal strength. GAM modeling indicated, as indicated above, that movements were highest during spring months (Fig 5A). Rates increased with decreasing bottom depths (Fig 5B), and were greater among crabs released at the southern site in 2010 compared to those released at the northern site in 2011 (Fig 5C). Predicted movement rates were 1 to 1.1 km/day during spring at bottom depths shallower than 110 m, and were generally less than 0.6 km/day where depths exceeded 140 m outside of the spring time period (Fig 5D).

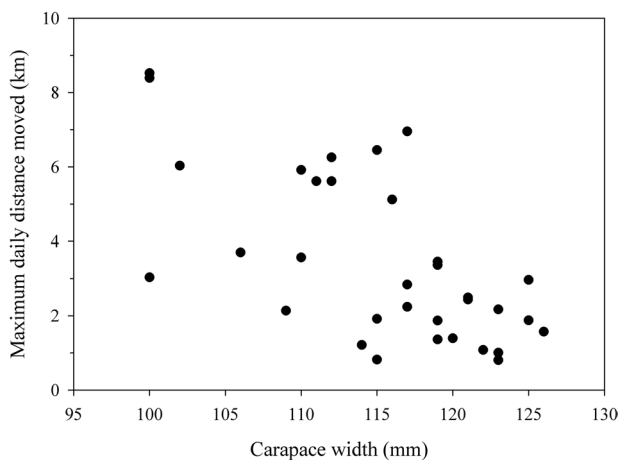
Movement rates were found to vary with bottom depth, day of year, and release area at the individual-crab level in addition to the variation due to among crab differences. Using the model in which movement rate was scaled to examine individual-crab effects (as opposed to among-crab effects), bottom depth, day of year, and release area were again significant ( $p < 0.001$ ;  $r^2 = 0.22$ ) and relationships followed the same trends as for the non-scaled movement rate model. Given the reduction in  $r^2$  (0.42 to 0.22), it is apparent that while these influences affect movement rate at the individual-crab level, they also vary among crabs. Thus, for the bottom depth variable, individuals generally moved faster when at shallower depths, but faster moving individuals generally moved to shallower depths more so than slower moving individuals.

DISCUSSION

An obvious limitation to using timed depth recordings to estimate movement rate is that we could not identify movements parallel to the depth gradients, and as such, the presented rates are biased



**Figure 2.** Median inshore (open circles) and offshore (solid circles) distances moved per month among the 33 tagged male snow crabs released in 2010 (**A**) and 2011 (**B**). Error bars indicate lower and upper quartiles. Numbers in parentheses indicate the number of crabs at liberty during each month. For months in which crabs were not at liberty for a full month (e.g., April 2010), distances were scaled up to a full month. Distances reflect across-shelf movements only, estimated for each crab as the daily change in bottom depth divided by the bottom slope.

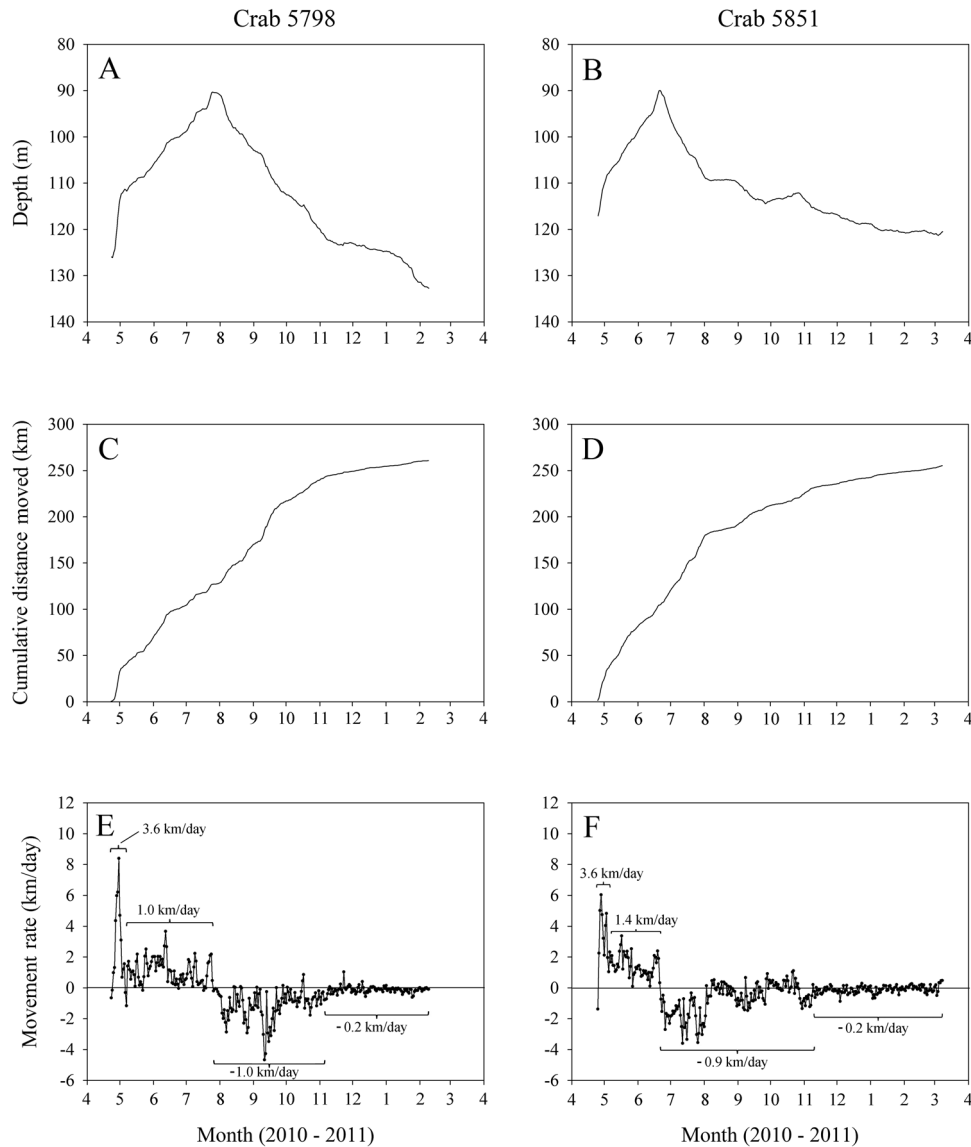


**Figure 3.** Relationship between crab carapace width (CW) and maximum daily distances moved by tagged snow crabs. Distances reflect across-shelf movements only, estimated for each crab as the daily change in bottom depth divided by the bottom slope.

low. Despite the bias, this study demonstrates that MM male snow crabs can be highly mobile. There were periods of greater than a month during which some individuals moved an average of

more than 1 km/day, and for shorter periods (e.g., three to four days) during which individuals moved an average of more than 4 km/day. Also, considering that two of the crabs traveled a minimum of 250 km within a ten-month period, the characterization of snow crab as sedentary, as observed for some other snow crab stocks (Watson, 1970; Taylor, 1992; Biron *et al.*, 2008), is inaccurate for MM males in the eastern Bering Sea.

The significant relationships of bottom depth, day of year, and release area on movement rate were in part expected, but they also provided some added detail. Logically, it makes sense that movement rates would be greater at shallower bottom depths because all the crabs were initially tagged and released in deeper water (115–120 m) just prior to or during an inshore movement (Nichol & Somerton, 2015), and the fastest crabs reached the shallowest depths (90–100 m). Our research also showed, however, that individual males moved faster while in shallower water compared to deeper water, indicating that for those males that underwent more extensive round-trips across the shelf, directional movements were not consistent spatially. Similarly, whereas it might be expected that MM male crabs move faster during spring due to known inshore spring movements, the significance of the day-of-year effect confirms that the rates of these cross-shelf movements vary across seasons. We also expected that MM males released at the southern site in 2010 had moved faster than those released at the northern site in 2011 because the southerly-released males traversed a much wider range of bottom depths than did the



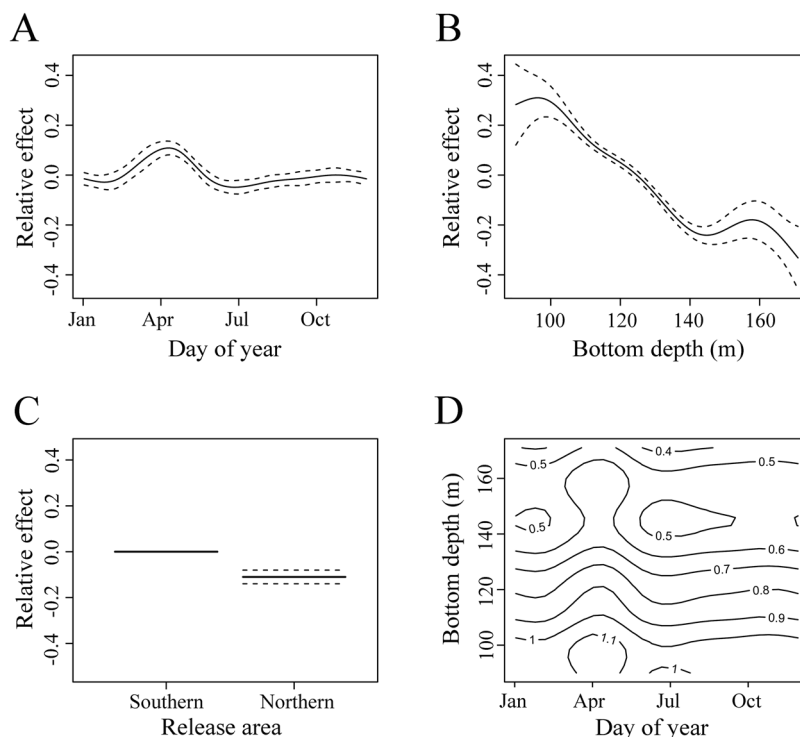
**Figure 4.** Time series of depth (**A**, **B**), cumulative absolute distance moved (**C**, **D**), and daily movement rate (**E**, **F**) for two MM male snow crabs (100–102 mm carapace width) that underwent extensive inshore followed by offshore migrations in the eastern Bering Sea. For daily distances moved (**E**, **F**), positive values indicate inshore movement and negative values indicate offshore movement. Labeled brackets indicate the average movement rate (km/day) over the period bracketed. Distances and movement rates reflect across-shelf movements only, estimated for each crab as the daily change in bottom depth divided by the bottom slope.

northerly-released males (Nichol & Somerton, 2015). Why this was the case may have more to do with the year in question than with the area of release, as potential mates (multiparous females) appeared within closer proximity to males in 2011 than 2010, perhaps lessening the need for daily movement in 2011 (Nichol & Somerton, 2015).

The lack of size-related differences in movement rate or distance traveled among commercial-sized MM males appears consistent with tagging studies of *C. opilio* in eastern Canada. Lefebvre & Brêthes (1991) and Biron *et al.* (2008) found that neither movement distances nor the direction of movement among MM male crabs ( $\geq 84$  mm CW) varied with crab size. In another tagging study, Brêthes & Coulombe (1990) found that larger MM male crab ( $> 109$  mm CW) traveled faster than smaller ( $< 90$  mm) ones; however, those differences were mostly among MM males captured and released during June and July in shallower waters ( $< 90$  m) from which movements were directed to deeper water, thus likely involved the final ontogenetic migration following their

terminal molt. In these cases, larger MM males moved to deeper water than did smaller ones, contributing to distributions in which larger MM males maintain deeper overall distributions than smaller ones, as seen in both the Gulf of St. Lawrence (Lovrich *et al.*, 1995) and the eastern Bering Sea (Nichol & Somerton, 2015). As with the present study, Brêthes & Coulombe (1990) found that among MM males that were initially tagged in deeper ( $> 130$  m) water, and subsequently underwent seasonal movements more associated with breeding, no size-related influence was found.

It is logical from a biomechanical perspective to assume that larger crabs with longer legs are capable of moving at greater speeds. This might be why adult male red king crab, *Paralithodes camtschaticus* (Tilesius, 1815), the largest of the crabs in the eastern Bering Sea, are capable of moving at the fastest speeds compared to other species, up to 18 km/day and 370 km/year (Simpson & Shippen, 1968). For the size range of snow crabs examined in this study (100–126 mm CW), daily movement rates were not significantly related to crab size, but maximum rates were higher among



**Figure 5.** Relative effects (A–C) of significant independent variables on movement rate of snow crabs in the eastern Bering Sea, as predicted by general additive modeling (R, mgcv package, function GAMM). Model predicted movement rates (km/day), as they vary with bottom depth and season (day of year), are presented for 2010 released crabs (D). Dashed lines indicate 95% confidence intervals.

the smallest individuals, opposite of the expectation considering biomechanics. Therefore, other factors that influence movement behavior are obviously involved. One such influence may involve size-related competitive exclusion for mates as suggested by Nichol & Somerton (2015) and observed for Eastern Canadian snow crabs (Moriyasu & Comeau, 1996; Sainte-Marie *et al.*, 1997; Comeau *et al.*, 1998). Two of the smallest males (100–102 mm CW) in this study underwent inshore movements that were earlier, faster, longer, and to the shallowest depths compared to larger males. A third smaller crab (100 mm CW; crab 5845) that was at liberty over two seasons, also moved at among the fastest rates (mean 0.9 km/day; Table 1) and entered some of the shallowest depths (to 101 m) during its second season (Nichol & Somerton, 2015). Given that the timing of these inshore movements and occupation of shallower waters coincided with the known mating period, it is possible they did so to secure a mate while minimizing competition from larger males (Nichol & Somerton, 2015).

Another factor that can affect the extent and speed of movements is the topography. Br  thes & Coulombe (1990), who found seasonal movements of MM male snow crabs in the northern Gulf of St. Lawrence to be less than 34 km in distance, suggested they were more sedentary than MM males of other eastern Canadian stocks because the topography included “deep holes or channels” that limited dispersion. Although this idea was questioned by Biron *et al.* (2008), who suggested dispersal among eastern Canadian snow crabs (eastern Nova Scotia, southern Gulf of St. Lawrence) is more influenced by the degree of changing water temperatures, there are examples among other Alaska crab species (e.g., *P. camtschaticus* and *Chionoecetes bairdi* (Rathbun, 1924)) that suggest movements are more extensive among crabs that inhabit more open water basins with more uniform bathymetry (Webb, 2014; McBride, 1982). In the case of the eastern Bering Sea, where the bottom slope is relatively flat and the stock is spread over a wider distance compared to eastern Canadian stocks (Nichol & Somerton, 2015; Sainte-Marie *et al.*, 2008), greater movement distances and rates among eastern Bering Sea MM

males perhaps should be expected. Given some of the observed seasonal round-trip distances observed in this study (up to 250 km), this may hold true. However, comparison among studies is difficult owing to differing methodologies used to assess movement distance (e.g., straight-line distance from release to recapture locations *versus* distances computed from change in depth), as well as the use of differing tag types (e.g., acoustic, data storage, spaghetti) that deliver data at different time scales (e.g., daily, seasonal, multi-year dispersal).

Daily movement rates of MM male crabs in the eastern Bering Sea did not vary with temperature, which ranged from  $-0.5$  °C to  $4.5$  °C during the study period (Nichol & Somerton, 2015), unlike the rates found for MM male snow crabs in eastern Canada (Foyle *et al.*, 1989; Maynard, 1991). Maynard (1991) demonstrated in the laboratory that both respiration rates and hourly walking speeds of MM males were significantly lower at temperatures of  $0$  °C compared to  $3.5$  °C and  $6$  °C. He also demonstrated in the field using acoustic tags that hourly walking speeds were less among MM males residing in  $1$  °C ( $0.14$  km/day) compared to those residing in  $4$  °C ( $0.48$  km/day). Why this apparent temperature limitation was not observed in the present study is not clear, although only 1.2% of the movements occurred at temperatures  $< 1$  °C. Still, nearly half of those  $< 1$  °C observations were from the two most mobile males that moved inshore to a depth of 90 m (Fig. 4) near the eastern Bering Sea cold pool (see Nichol & Somerton, 2015), within which each moved for approximately one month. It is possible that the temperatures were not limiting within the temperature range that most crabs were exposed. It is also possible that only smaller males chose to inhabit the colder, perhaps sub-optimal areas, again, as a way to avoid larger males.

Rates of movement are undoubtedly affected by the frequency and duration of active and inactive periods. Foyle *et al.* (1989) found that MM male snow crab (85–95 mm CW) in the laboratory were active only one to three hours per day (24 hours), and Maynard (1991) estimated that MM males in the field were active only five to eight hours per day. With inactive

periods factored in, movement rates estimated by Foyle *et al.* (1989), 0.25 to 0.74 km/day, were similar to the rates of the two smallest individuals in this study, where rates averaged between 0.2 and 1 km/day for the majority of their at-liberty period (Fig. 4E, F). Similarly, Maynard (1991), who tracked seven MM male snow crabs (81–116 mm CW) from 2 to 17 days using acoustic tags, found mean walking speeds to vary from 0.28 to 0.63 km/day for crabs living in 4 °C water, although only 0.05 to 0.22 km/day for males at 1 °C.

Movement rates were not related to tidal strength, however, it is likely that responses that occur at short-time scales (e.g., < 24 hours) could not be detected due to the temporal resolution of our data. Studies that have used acoustic array systems to examine movements of snow crabs have shown cases in which adult males moved mostly during nighttime hours and against the tidal currents (Kanawa *et al.*, 2014), or against a prevailing along-shore current (Biron *et al.*, 2008). The predominant currents where MM male snow crabs reside in the central eastern Bering Sea result from semidiurnal tides, which are rotary in direction and can achieve peak velocities of over 50 cm/s during spring-tide periods (Kowalik, 1999; Pearson *et al.*, 1981; Nichol & Somerton, 2009). Additional research, designed to measure movement rates at shorter time intervals, is necessary to determine if snow crab movements in the eastern Bering Sea vary with specific tidal current directions (i.e., with or against) or diurnally (i.e., light intensity), and whether other cases of such preferences (see Biron *et al.*, 2008; Kanawa *et al.*, 2014) were localized or temporal phenomena.

Factors other than those that limit the capacity for movement are obviously involved because of the wide differences in the magnitude of movement among different snow crab stocks, but also among individuals of the same stock as shown in this study. In addition to factors that might affect movement from an energetic or biomechanical perspective (i.e., temperature, crab size), movements are likely influenced by a crab's proximity to food, mating opportunities, and shelter. These movements may also be influenced by the mobility and concentration of prey, mates, competitors, and predators. Movement rates and distances within the same stock can consequently vary annually as the stock dynamics change. With variable annual recruitment and mortality (fishing and natural), changes in concentration and distribution of both MM males and mature females could result in changes in movement. Considering the capacity for high mobility of MM snow crabs in the eastern Bering Sea, as indicated by maximum rates observed in this study, as well as the lack of measured limitations to these movements (i.e., temperature, crab size), this capacity likely provides a flexibility that contributes to successful survival with changing environmental conditions.

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