Size at maturity for grooved Tanner crab (Chionoecetes tanneri) along the U.S. west coast (Washington to California)

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ABSTRACT
We conducted a multiyear study to examine interannual variability in the mean size (carapace width, mm), maturity size (mm) and depth (m) for grooved Tanner crab (Chionoecetes tanneri (Rathbun, 1893)) along the U.S. west coast. An additional goal was to provide updated estimates of carapace width (mm) at 50% maturity (W50) for male and female grooved Tanner crab and assess changes over time. Randomly selected samples came from trawl surveys undertaken annually by the Northwest Fisheries Science Center at depths of 55 to 1280 m. We used allometric relationships between carapace width (CW) and either abdominal width (AW) (females) or chela length (CL) (males) to determine functional maturity by sex. We evaluated maturity by fitting logistic regression models to proportion mature grooved Tanner crab. W50 varied significantly between males (125.2 mm) and females (89.1 mm) but interannual differences were slight. The annual mean CW were greater for mature males (139.9–143.4 mm) relative to females (98.8–100.4 mm). The average sizes of immature grooved Tanner crab varied between sexes with males (75.7–84.6 mm) larger than females (66.7–71.9 mm). Size frequency distributions indicated little overlap in the size of mature male and female grooved Tanner crab but considerable overlap between immature grooved Tanner crab. The best model expressing complexity in growth incorporated width, sex and maturity stage. Depth ranged from 195–1254 m with the average depth of a mature grooved Tanner crab (females, 737 m; males, 767 m) significantly shallower than an immature (females, 949 m; males, 918 m) grooved Tanner crab.

Key words: abdominal width, allometric relationships, carapace width, chela length, size at 50% maturity

INTRODUCTION
The push to explore new resources and increase economic opportunities for fishermen kindled an interest in grooved Tanner crab (Chionoecetes tanneri Rathbun, 1893) in the NE Pacific Ocean in recent years (Gillespie et al., 2004; Keller et al., 2012a). Obtaining up-to-date knowledge of species life-history traits is fundamentally important for the management of these potentially valuable grooved Tanner crab populations. In particular, providing improved information on size at maturity and interrelationships with growth and depth will prove vital in assessing both the status of this species and the vulnerability of grooved Tanner crab to commercial fishing.

Grooved Tanner crab are a widespread species, occurring at depths of 53–1944 m from northern Mexico to the Gulf of Alaska (Rathbun, 1925; Pereyra, 1968; Hart, 1982). They are primarily a deep-water species with a recently reported maximum abundance along the U.S. west coast occurring at depths of 601–800 m (Keller et al., 2012a), somewhat deeper than previously reported (500–775 m) (Pereyra, 1966). Summaries on the biology, distribution and abundance of grooved Tanner crab are described for a variety of locations: offshore northern Oregon near the mouth of the Columbia River (Pereyra, 1966), off the southern Oregon coast (Tester and Carey, 1986), off the coast of British Columbia (Jamieson, 1990), in the eastern Bering Sea (Somerton and Donaldson, 1996) and along the U.S. west coast from California to Washington (Keller et al., 2012a). Valuable commercial fisheries occur for
Tanner and snow crab (Chionoecetes spp.) in Alaska, Japan and the Atlantic region of Canada (Fong and Dunham, 2007). Pereyra (1966) recognized a potential for establishing a commercial C. tanneri fishery along the U.S. west coast, but the value of the catch, at that time, did not offset the prohibitively high cost of fishing in relatively deep water. Somerton and Donaldson (1996), however, noted that as populations of the shallowwater, commercially harvested C. bairdi Rathbun 1925 and snow crab (C. opilio Fabricius 1788) declined during the mid-1990s in Alaska there was a shift to fishing in deeper water despite higher costs. In recent years, an experimental fishery in British Columbia determined the feasibility of establishing a commercial grooved Tanner crab fishery along the west coast of Vancouver Island (Gillespie et al., 2004). An experimental fishery off California in 2004 and 2005 also indicated the feasibility of conducting a commercial venture (Kalvass and Patyten, 2005). But before developing a sustainable, deep-sea fishery for grooved Tanner crab, we require sufficient understanding of their biology to evaluate potential overharvesting risks and establish appropriate management strategies (Boutillier and Gillespie, 2005). In particular, evaluating the reproductive biology of grooved Tanner crab over time can improve the accuracy of spawning biomass and related recruitment estimates and subsequent projections used by fisheries managers to determine harvest levels.

Despite the deep-water habitat occupied by grooved Tanner crab, various aspects of their reproductive biology have previously been described, although rarely across such a wide geographic range as undertaken here. Prior studies indicated that grooved Tanner crab segregate by depth based on maturity stage and gender (Pereyra, 1966; Jamieson et al., 1990; Somerton and Donaldson, 1996; Gillespie et al., 2004; Keller et al., 2012a) and that seasonality or oceanographic conditions may impact the variation in depth distribution among geographic areas (Pereyra, 1966; Phillips and Lauzier, 1997; Keller et al., 2012a). As prior studies suggested shifts in depth distributions are related to changing climatic regimes, we compared variation in depth for grooved Tanner crab to the annual average Pacific Decadal Oscillation (PDO) index, a widely used index of climate variability for the California Current system (Mantua et al., 1997; Schwing et al., 2009). The PDO is detected as warm or cool surface waters in the Pacific Ocean, north of 20°N, that historically shift phases on a scale of about 10–30 years. Shifts in the PDO are accompanied by changes in productivity of waters off the U.S. west coast (Schwing et al., 2009). Here we update and refine our earlier research examining the role of environmental effects on the depth distribution of grooved Tanner crab (Keller et al., 2012a). We included data from additional years (2012–2014) and incorporated the annual variation in sampling depth, introduced by our stratified, random sampling design, into the analysis.

Our prior research also revealed a gap in information on carapace width at 50% maturity along the extent of the U.S. west coast which we address here. Several older investigations indicated only slight variations in maturity, fecundity and reproduction over large geographic areas, extending from southern Oregon to the eastern Bering Sea (Pereyra, 1966; Tester and Carey, 1986; Somerton and Donaldson, 1996; Workman et al., 2000, 2002). However, the validity of these conclusions is somewhat questionable as historical comparisons were not always based on the same metric, with carapace width at 50% maturity (W50) in some cases being compared with either minimum or average size at maturity. Our focus on updating W50 was driven by a desire to examine any changes over time and against the backdrop of a changing environment.

In our prior study, we substantially enhanced the available information on grooved Tanner crab biology, size and distribution along the U.S. west coast (Keller et al., 2012a). However, we concluded that additional information was needed given the goal of managing a sustainable fishery in U.S. waters. In particular, we recommended that data on maturity be collected directly. Previously, we examined the variation in growth and depth of grooved Tanner crab, by sex and maturity stage, based on sizes at maturity reported off Oregon in 1973–1975 (Tester and Carey, 1986). Here we use allometric relationships to identify male and female grooved Tanner crab as mature or immature (Watson, 1970; Brown and Powell, 1972). Specifically, we used relationships between the abdominal width (AW) (females) and chela length (males) versus carapace width to segregate mature and immature grooved Tanner crab (Jamieson et al., 1990). We then examined interannual variations in size, growth and depth based on actual, rather than estimated maturity stages for comparison with earlier findings. We additionally determined updated size at 50% maturity (W50) for comparison with prior estimates of W50 from the Bering Sea (Somerton and Donaldson, 1996) and British Columbia (Workman et al., 2000, 2002), while using average carapace width to compare results with past estimates of minimum and average size at maturity on the Oregon coast (Pereyra, 1966, 1968; Tester and Carey, 1986).
This study consequently updates previous maturity work for this species and provides information of value to support the reliability of future stock assessments.

METHODS

Survey design and methods
Grooved Tanner crab were sampled annually during the NWFSC’s fishery-independent bottom trawl survey of the eastern North Pacific (Keller et al., 2008). The annual survey covered the area between the U.S.–Canada border (48°30’N) and the U.S.–Mexico border (32°30’N) at depths of 55–1280 m (30–700 fm). The survey utilized a stratified random sampling design with two geographic strata (N and S of Pt. Conception, CA) and three depth strata (55–182 m, 183–549 m and 550–1280 m). The geographic extent was sampled twice (N to S coast-wide sweeps), with two chartered west coast commercial fishing vessels (20- to 28-m length) utilized each period. Sampling occurred from late May through to late July for the first period and mid-August through to late October for the second. Trawling occurred at about 750 locations per year based on a stratified-random sampling design. Sites were randomly selected from a grid of 1.5 × 2 nautical mile cells that span the entire survey area. Vessels utilized modified Aberdeen-style trawl nets equipped with a small mesh (3.8 cm stretched measure) liner in the codend, a 25.9 m headrope and a 31.7 m foot rope. The Simrad Integrated Trawl Instrumentation (ITI Kongsberg Simrad Mesotech Ltd., Port Coquitlam, BC, Canada) was used to monitor and record net performance and position for each haul. A differential global positioning system (DGPS) navigation unit was used to monitor towing speed during each haul. Standardized survey haul positions were estimated from DGPS and Simrad data – generally the mid-point between the net touchdown and net liftoff positions. Average net speed over the ground and the distance fished were calculated from trawl position and actual bottom time (Keller et al., 2008). Samples were collected by trawling within the randomly selected cells for a target tow time of 15 min at a target speed of 1.13 m s\(^{-1}\) (2.2 knots). All fishing operations are conducted in strict compliance with national and regional protocols detailed in Stauffer (2004).

Catch per unit effort and environmental effects
Grooved Tanner crab captured during trawling (2003–2014) were identified to species, weighed and enumerated. Catch per unit effort (CPUE, kg ha\(^{-1}\)) was calculated by dividing grooved Tanner crab catch (kg) by area swept (ha) per tow. Area swept was computed from the mean net width for each tow multiplied by the distance fished. Standard deviations for annual average CPUE were calculated using standard statistical techniques (Cochran, 1977; SAS, 1999). CPUE was compared among depth strata (55–182 m, 183–549 m and 550–1280 m) and across years with analysis of variance (Sokal and Rohlff, 1981) conducted using SAS PROC ANOVA (Littell et al., 1996). Significant ANOVA was followed by a multiple comparison test (Duncan’s multiple means test, Duncan, 1955).

To examine the relationship between the average capture depth for grooved Tanner crab in each year as a function of climate variables, we first calculated coast-wide CPUE-weighted average depths (m) as:

\[
D = \frac{\sum_{i=1}^{n} (\text{CPUE}_i \times d_i)}{\sum_{i=1}^{n} \text{CPUE}_i} (1)
\]

where \(D\) is catch-weighted average depth (m), CPUE is (kg ha\(^{-1}\)) for each station \(i\) and \(d\) is depth for each station \(i\). To account for variations in sampling depths within the range of occurrence for grooved Tanner crab (195–1254 m), we calculated the mean depth by year and the year-to-year differences (Δ-depth, m) in these values versus mean CPUE-weighted annual depths. We compared the Δ-depth values to average annual PDO indices (2003–2014) using standard regression analysis (SAS, 1999).

Allometric measurements and size
From 2012 to 2014, we selected a random subsample of individuals (\(n = 5\) for each sex per tow or all if fewer than five captured per tow) to measure weight (g) and CW (mm). For female grooved Tanner crab, we additionally measured the width of the 5th abdominal segment (AW, mm) and for males, we measured chela length (CL, mm) and chela height (CH, mm). CW measurements for both sexes were taken at the widest part of the carapace exclusive of lateral spines. For females, the measured AW represents the widest segment of the abdomen. For males, we measured the length of the right chela diagonally from the notch at the base of the thumb to the base of the large spine on the ventral surface of the chela at the joint between the chela and the cheliped (adapted from Jadamec et al., 1999; Workman et al., 2001). We also measured the height of the chela at the widest extent. Grooved Tanner crab with missing legs or physical damage were excluded from the study.
Maturity was assigned based on morphometric measurements. For females, we determined two stages of maturity (mature and immature) based on the fitted CW to AW relationships. We further compared these results with maturity visually determined in the field, based on an increase in the AW, the presence of eggs or empty egg cases. For males, we assigned maturity based on examination of the CL to CW relationship. For both females and males, the onset of maturity is detected by discontinuities in the above morphometric relationships (Pereyra, 1966; Tester and Carey, 1986; Jamieson et al., 1990).

Analysis of covariance, ANCOVA, conducted using SAS PROC MIXED (SAS v. 9.3; SAS Institute, Inc., Cary, NC, USA) was used to examine stage-specific variations in AW (females) or CL (males) relative to year and CW (Sokal and Rohlf, 1981). The main factor in the ANCOVA was the year (2012–2014). The null hypothesis tested was that no difference in morphometric relationships occurred among years. CW was incorporated in the model as a covariate. After assigning maturity, we additionally examined variation in CW by sex and maturity stage using analysis of variance (ANOVA) in SAS for Windows (PROC GLM; SAS Institute, Inc.). Significant results were followed by a multiple comparison test (Duncan’s multiple means test, Duncan, 1955).

Weight–width relationships for grooved Tanner crab were based on the allometric equation:

\[ W = aCW^b \]  

where \( W \) is grooved Tanner crab weight in g, \( CW \) is carapace width in mm, and \( a \) and \( b \) are constants. Regression equations for natural log transformed weight and width were generated using least-squares regression techniques (conducted in SAS). Obvious outliers (e.g., unrealistic measurements) were removed from the dataset after examination of plots of raw and natural log-transformed variables (< 0.5% of the observations). ANCOVA (Sokal and Rohlf, 1981) conducted using SAS PROC MIXED (Littell et al., 1996) was used to test for differences between linear regression models by gender and stage. Each sex was subdivided into two stages, immature and mature, based on the previously defined morphometric relationships. The natural log-transformed width was fitted as a continuous variable while sex and/or stage were fitted as factors. Akaike’s Information Criterion (AIC) (Sakamoto et al., 1986) was used to select the most appropriate model to describe the weight versus CW relationship for grooved Tanner crab. AIC values are based on the residual sum of squares, the number of parameters estimated in the models (\( P \)) and the number of data points included in each analysis (\( N \)) according to Burnham and Anderson (2002):

\[ \text{AIC} = N \cdot [\log(\text{SSR}/N)] + 2P \]  

where SSR is the minimum residual sum of squares, \( P \) the number of parameters estimated in the regression and \( N \) the total sample size. The best model was selected by the smallest AIC value (\( \text{AIC}_{\text{min}} \)). To determine if a model other than the best model was plausible, the difference in AIC values for each model was calculated as:

\[ \Delta_{\text{AIC}} = \text{AIC}_i - \text{AIC}_{\text{min}} \]  

Models with \( \Delta_{\text{AIC}} > 10 \) are recommended for omission from consideration as alternates (Burnham and Anderson, 2002).

Carapace width at 50% maturity

\( CW \) at 50% maturity (\( W_{50} \)) is based on the fit of the logistic regression to the proportion of male and female grooved Tanner crab mature at a given width (mm) as:

\[ P = \frac{1}{1 + e^{-(a+b\text{CW})}} \]  

where \( P \) is the proportion mature at width \( x \), and \( a \) and \( \beta \) are parameters that define the shape and location of the fitted sigmoid curve. Parameters \( a \) and \( \beta \) were estimated using a generalized linear model (GLM) in R ver. 2.15.1 statistical programming language (R Core Team, 2012). Residual values (observed–predicted proportion mature) were calculated for models fitted using Eqn (5) for both female and male grooved Tanner crab and compared to predicted proportion mature to assess the adequacy of the model fit. The width at 50% maturity for males and females (\( W_{50} \)) were calculated as:

\[ W_{50} = -\frac{a}{\beta} \]  

Variance and 95% confidence intervals for \( W_{50} \) were estimated using the delta method (Seber, 1982):  

\[ S^2(W_{50}) = \frac{S^2(\hat{a})}{\hat{\beta}^2} - \frac{2\hat{a}S(\hat{a})S(\hat{\beta})r}{\hat{\beta}^3} + \frac{\hat{\beta}^2S^2(\hat{\beta})}{\hat{\beta}^4} \]  

where \( S^2(W_{50}) \) is the variance of \( W_{50} \), \( \hat{a} \) and \( \hat{\beta} \) are estimates of parameters \( a \) and \( \beta \) generated by the GLM model, \( S(\hat{a}) \) and \( S(\hat{\beta}) \) are the standard errors of \( \hat{a} \) and \( \hat{\beta} \), and \( r \) is the correlation coefficient.
Depth distribution by stage
After categorizing grooved Tanner crab by sex and stage based on morphometric relationships, we examined the average depth (m) for each subgroup (mature and immature males and females). We compared average depths by sex and stage overall, and by year, using analysis of variance (ANOVA) in SAS for Windows (PROC GLM; SAS Institute, Inc.). Significant results were followed by a multiple comparison test (Duncan’s multiple means test; Duncan, 1955).

RESULTS
CPUE and environmental effects
Grooved Tanner crab were present in 2180 of 7608 trawl sets (29%) conducted during a series of 12 annual fishery-independent surveys (2003–2014) using standardized techniques along the U.S. west coast. Grooved Tanner crab occurred primarily in the deepest depth stratum (550–1280 m) where they were present in 82% of the tows (1729 of 2102 tows) over the study period versus 8% in other strata (451 of 5506 tows). The mean annual CPUE ranged from 5.5 to 11.7 kg ha\(^{-1}\)/C0 (Fig. 1). Significant differences occurred in the mean CPUE by year (ANOVA \(F = 2.61, P = 0.003\)) with 2005 significantly greater than 2007, 2008, 2009, 2011 and 2012. Additionally, the mean CPUE in 2011 was significantly smaller than in 2003 and 2005 but all other years were not significantly different from each other (Duncan’s multiple means test, \(a = 0.05\)). CPUE also varied significantly by depth strata (ANOVA \(F = 109.15, P < 0.0001, \text{d.f.} = 26\)) for all years combined with CPUE in the deepest depth stratum significantly greater than other depth strata. We saw similar differences in CPUE by depth strata for all years individually from 2003 to 2014. The average annual CPUE (kg ha\(^{-1}\)) was significantly (\(P = 0.01; R^2 = 0.50\)) and positively related to the PDO index as well (Fig. 2a).

The annual differences in \(\Delta\)-depth (m), i.e., coast-wide CPUE-weighted average depths (m) adjusted for the mean depth of sampling within the range at which grooved Tanner crab were taken (195–1254 m), were significantly (\(P = 0.005; R^2 = 0.56\)) and positively related to average annual (PDO) indices over the study period (2003–2014) (Fig. 2b). The results are very similar if CPUE-weighted average depths (m) are directly compared to PDO values (\(P = 0.006; R^2 = 0.54\)), without accounting for differences in sampling depths among years. Grooved Tanner crab populations occur at greater depths during the warmer phases of the PDO (2003 to 2006 and 2014). We found a similar significant trend between \(\Delta\)-depth (m) and the multivariate El Niño–Southern Oscillation Index (\(P = 0.04, R^2 = 0.35\)), but not the North Pacific Gyre Oscillation Index (\(P = 0.37\)) (data not shown).

Allometric measurements and size
According to Tester and Carey (1986), Somerton and Donaldson (1996) and Workman et al. (2001), we assigned morphometric (functional) maturity to female grooved Tanner crab by plotting AW (mm) versus CW (mm) for each year. The results clearly demonstrated the presence of two distinct groups (Fig. 3a). The discontinuity in the AW to CW relationships was used to assign maturity to female grooved Tanner crab; grooved Tanner crab with wider abdominal segments and larger CW (open circles, Fig. 3a) were defined as functionally mature.
ANCOVA revealed significant (ANCOVA $F = 3.02$, $P = 0.05$) year-to-year variation in the AW to CW relationship for immature female grooved Tanner crab with 2013 being different from other years. No significant differences in the AW versus CW regressions occurred for mature female grooved Tanner crab among the years (ANCOVA $F = 1.5$, $P = 0.22$). Allometric determination of maturity for female grooved Tanner crab always agreed with field determinations when the abdomen was noticeably narrow and flattened (immature) and when eggs or empty egg cases were present (mature). But visual assessments based on changes to the shape of the abdomen were incorrectly classified as mature about 49% of the time.

Similarly, for male grooved Tanner crab, we examined allometric relationships between CL (mm) and CH (mm) versus CW (mm) (Tester and Carey, 1986; Somerton and Donaldson, 1996; Workman et al., 2001). The dispersion of values for both CL and CH (not shown) plotted against CW fell into two distinct groups (Fig. 3b). Functionally mature male grooved Tanner crab are defined as those with larger CL versus CW (open circles, Fig. 3b). Immature males (subadults) had smaller CL relative to CW (closed circles, Fig. 3b). For male grooved Tanner crab, we found stage-specific interannual variation in the CL to CW relationships. ANCOVA revealed no significant differences (ANCOVA $F = 1.52$, $P = 0.22$) among years for mature male grooved Tanner crab but significant (ANCOVA $F = 3.38$, $P = 0.03$) interannual differences in the relationship for immature males with 2013 different from other years.

We examined variation in CW by sex and stage and found significant differences (ANOVA $F = 493$, $P < 0.0001$, d.f. = 1049) between male and female grooved Tanner crab (Table 1). The mean CW for males were always significantly greater relative to females regardless of stage (immature and mature). The mean CW by stage and sex did not differ significantly ($P > 0.05$) among the years (2012–2014).

Figure 2. (a) The mean catch per unit effort (CPUE) (kg ha$^{-1}$ ± standard error) for grooved Tanner crab collected during the 2003–2014 west coast groundfish bottom trawl survey; and (b) differences ($\Delta$-depth, m) between the mean coast-wide CPUE-weighted depths (m) and the mean annual depth (m) are shown relative to an annual index for climate change in the northeast Pacific Ocean, the Pacific Decadal Oscillation (PDO) during corresponding years.
Size frequency distributions (CW, mm) varied by sex and stage with males (29–168 mm) exhibiting a wider range of sizes than females (30–122 mm) (Fig. 4). Immature females measured 30–102 mm and exhibited considerable overlap with immature males (range: 29–143 mm) (Fig. 4a). Mature females ranged from 83 to 122 mm with very little overlap with mature males (range: 99–168 mm) (Fig. 4b).

**Figure 3.** (a) Morphometric relationships between (a) abdominal width (mm) for female; and (b) chela length (mm) for male grooved Tanner crab versus carapace width (mm) showing distinct groups used to determine maturity stage (immature: closed circles and mature: open circles) by year (2012–2014). Regression equations shown for mature (m) and immature (i) grooved Tanner crab by year and sex.
The best model for expressing the variation in the weight versus width relationship incorporated width, sex and stage, as determined using AIC. The best model was selected by the smallest AIC value ($AIC = 797.4$) (Table 3). The $\Delta AIC$ values for models incorporating fewer variables were $\Delta AIC = 54.4$ (width) and $\Delta AIC = 53.6$ (width and gender) (Table 3). Both models were omitted from consideration as alternative models since $\Delta AIC < 10$ (Burnham and Anderson, 2002).

### Table 1. The mean carapace width (mm) with standard error (± SE) for male and female grooved Tanner crab by stage and year.

<table>
<thead>
<tr>
<th>Stage and sex</th>
<th>Year: 2012</th>
<th>2013</th>
<th>2014</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Immature females</td>
<td>66.7 (±3.4)</td>
<td>67.9 (±2.1)</td>
<td>71.9 (±1.5)</td>
<td>69.9 (±1.2)</td>
</tr>
<tr>
<td></td>
<td>n = 29</td>
<td>n = 64</td>
<td>n = 114</td>
<td>n = 207</td>
</tr>
<tr>
<td>Mature females</td>
<td>98.8 (±1.3)</td>
<td>100.1 (±0.8)</td>
<td>100.4 (±0.6)</td>
<td>100.1 (±0.4)</td>
</tr>
<tr>
<td></td>
<td>n = 28</td>
<td>n = 87</td>
<td>n = 171</td>
<td>n = 286</td>
</tr>
<tr>
<td>Immature males</td>
<td>79.9 (±4.2)</td>
<td>75.7 (±1.9)</td>
<td>84.6 (±1.6)</td>
<td>81.1 (±1.2)</td>
</tr>
<tr>
<td></td>
<td>n = 45</td>
<td>n = 144</td>
<td>n = 236</td>
<td>n = 425</td>
</tr>
<tr>
<td>Mature males</td>
<td>140.3 (±2.4)</td>
<td>139.9 (±1.7)</td>
<td>143.4 (±2.0)</td>
<td>141.0 (±1.2)</td>
</tr>
<tr>
<td></td>
<td>n = 43</td>
<td>n = 52</td>
<td>n = 36</td>
<td>n = 131</td>
</tr>
</tbody>
</table>

### Figure 4. Size frequency distributions (percent) based on carapace width (mm) for: (a) immature; and (b) mature female (black bars) and male (gray bars) grooved Tanner crab from the 2012–2014 NWFSC’s west coast groundfish bottom trawl surveys. Only those grooved Tanner crab with maturity stages assigned morphometrically are included in the figures.

**Carapace width at 50% maturity**

For female grooved Tanner crab, 286 were classified as mature and 207 as immature. The CW (mm) at 50% maturity ($W_{50}$, mm) for female grooved Tanner crab was estimated as 89.1 mm [95% confidence interval (CI) = 87.5–90.7 mm] for all years pooled (Fig. 5a, Table 4). $W_{50}$ ranged from 88.3 to 89.6 mm across years with no significant differences among years (Table 4). For male grooved Tanner crab, 131 were classified as mature and 425 as immature.
immature. The CW (mm) at 50% maturity for male grooved Tanner crab was estimated as 125.2 mm (95% CI = 122.9–127.4 mm) for all years pooled (Fig. 5b, Table 4). $W_{50}$ ranged from 117.1 to 131.4 mm across years with no significant differences among years (Table 4). Based on residual (observed – predicted) versus predicted values for female (Fig. 6a) and male grooved Tanner crab (Fig. 6b) the logistic regression provided an adequate fit for the proportion mature.

**Depth distribution by stage**

The mean depths (m) for grooved Tanner crab varied significantly (ANOVA $F = 61.5$, $P < 0.0001$, d.f. = 1021) by stage (mature and immature) but not by sex (male and female), with mature grooved Tanner crab at significantly shallower depths than immature grooved Tanner crab. The average depth of mature female (737 m) and male (767 m) grooved Tanner crab differed significantly from immature female (947 m) and male (918 m) grooved Tanner crab based on Duncan’s multiple mean test. Similar results occurred in all years, with a tendency ($P > 0.05$) for all groups to be deeper in 2014 relative to earlier years.

**DISCUSSION**

The focus of our current research was to reduce uncertainty about the size ($W_{50}$, mm) at functional maturity throughout the region studied through a collection of morphometric measurements and subsequently fitting the newly acquired data to the logistic maturity model. Somerton and Donaldson (1996) and Workman et al. (2001) used a similar approach to determine maturity ogives for grooved Tanner crab in Alaska and Canada. Although Pereyra (1966) and Tester and Carey (1986) also reported size at maturity for grooved Tanner crab along the U.S. west coast, their results were average or minimum sizes (CW, mm) at maturity rather than $W_{50}$ from fitting a logistic model to the proportion mature. In addition to presenting new findings, a secondary focus was to utilize data collected from 2011 to 2014 to update and confirm our earlier results (Keller et al., 2012a).

**CPUE and environmental effects**

Differences in the mean CPUE were relatively minor between years and represent the range of interannual variability expected in catch along the U.S. west coast. The catch is also tied to environmental factors, as evidenced by the significant increase in annual average CPUE with warmer conditions as measured by the PDO index (Fig. 2a). Also, as noted in our earlier work, we saw a significant variation in the annual average catch-weighted depth of grooved Tanner crab among years, expressed here as $\Delta$-depth (m), to account for variation in sampling depth among the years (Fig. 2b). Within the extended time period examined here (2003–2014), we saw $\Delta$-depth vary from an annual minimum of 161 m in 2010 to a maximum of 319 m observed in 2003. Interestingly, $\Delta$-depth for 2014 (272 m) is among the deepest recorded during the period studied. This increase in $\Delta$-depth occurred during a year when the average PDO index increased from a negative value of $-0.52$ in 2013 to a positive value of 1.13 in 2014, the highest average recorded during the time frame of the current study. The relative increase in catch-weighted depth in 2014 reversed the trend of shallower depths observed from 2008 to 2013. Although some of the variation in $\Delta$-depth is tied to the number of immature grooved Tanner crab encountered each year, an additional component is tied to changing environmental conditions.
We expanded our analysis on the relationship between annual shifts in grooved Tanner crab distribution and environmental conditions by adding data from 2011–2014 to the earlier analysis. Our results confirm that annual shifts in catch-weighted depth appear related to shifts in environmental conditions such as temperature and productivity, with a significant relationship to the PDO index ($P = 0.003$). Mueter and Litzow (2008) observed shifts in the catch of snow crab ($C. opilio$) in association with climate-related changes in the Bering Sea. Recruitment success may also contribute to annual variation in the depth distribution of grooved Tanner crab. Strong recruitment, even in the absence of environmental effects, would impact depth distribution as immature grooved Tanner crab occur at greater depths than mature grooved Tanner crab.

Table 4. Carapace width ($W_{50}$, mm) at 50% maturity for female and male grooved Tanner crab by year (2012–2014) and with all years pooled. $\alpha$ and $\beta$ are estimated parameters defining the shape and location of fitted sigmoid curves with standard errors shown in parentheses.

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Size and allometric measurements
According to Tester and Carey (1986), Somerton and Donaldson (1996) and Workman et al. (2001), we estimated male and female functional maturity based on allometry. The development of secondary sexual characteristics in male $Chionoecetes$ results in a relative increase in CL compared with CW and corresponds with functional maturity (Watson, 1970; Brown and Powell, 1972). An enlarged chela is used to grasp females during breeding activity (Workman et al., 2001). For females, there is an enlargement in the AW relative to carapace width that occurs at maturity and is related to egg carrying ability. For both males and females, plots of these measurements revealed clear separation between mature and immature individuals (Fig. 3). For female grooved Tanner
crab, the at-sea assignment of maturity based on the presence of eggs or empty egg cases consistently matched determination of stage through later comparison of the measured abdominal and carapace widths. However, determination of maturity based on visual assessment of AW (narrow versus wide) was frequently incorrect and suggests that morphometric measurements are essential to accurately assess $W_{50}$ for females. Visually assigning maturity stage for male grooved Tanner crab was not attempted at sea.

We saw no variation in the AW or CL relationships among years for mature male or female grooved Tanner crab. However, we noted significant differences in these relationships among years for immature male and female grooved Tanner crab. Interannual variations in morphometric relations for immature grooved Tanner crab are likely the effect of complex interactions such as variation in growth rate, recruitment and instar at terminal molt as similarly noted for snow crab (Sainte-Marie et al., 1995; Orensanz et al., 2007). Following assignment of maturity stages, we compared CW for male and female mature and immature grooved Tanner crab and noted significant differences with males always larger than females regardless of stage. Tester and Carey (1986) and Workman et al. (2001) presented size information for grooved Tanner crab collected along the Oregon coast and off British Columbia and both reported larger sizes for males relative to females. Size distributions for grooved Tanner crab CWs from the Bering Sea (Somerton and Donaldson, 1996) show patterns similar to those observed here.

**Weight–size relationship**

Relationships derived here indicate significant differences in growth between mature and immature grooved Tanner crab, as well as between male and female mature grooved Tanner crab. However, unlike our earlier study (Keller et al., 2012a), we saw that when stage is determined allometrically, immature grooved Tanner crab grew at similar rates regardless of sex. Yet similar to our prior results, we noted that adding sex and stage reduced AIC values relative to including width as the sole explanatory variable for weight. Delta AIC values revealed that all other models should be eliminated from consideration. Tester and Carey (1986) reported two growth phases, one for juveniles and one for mature grooved Tanner crab, but they did not fit weight versus size curves for either group. Somerton and Donaldson (1996) presented parameter estimates for the weight–CW relationship for mature male grooved Tanner crab ($a = -9.039; b = 3.189$) and Workman et al. (2001) reported estimates for males ($a = -8.100, b = 3.101$) and females ($a = -7.899, b = 2.718$). For comparison, we fit the weight–width relationship for mature males versus females in our current study and found parameter estimates for males ($a = -7.899$ and $b = 2.939$) and females ($a = -6.112$ and $b = 2.530$). Comparing parameters for males among the three studies confirmed the decreasing tendency in the slopes ($b$) of the weight–width relationship moving from the north (eastern Bering Sea) to the south (U.S. west coast) that we previously reported (Keller et al., 2012a). Variations in the weight–width relationships are often correlated with changes in regional productivity with weight at size greatest in areas of higher productivity (Juan-Jordá et al., 2009; Keller et al., 2012b). A similar trend is also suggested for females although data are limited to two geographic areas rather than three. Based on these apparent patterns, our results suggest that separate curves should be developed for mature male and female grooved Tanner crab but not immature grooved Tanner crab within our study area.
Workman et al. (2002) estimated 50% morphometric maturity to be 112 mm for male and 88 mm for female grooved Tanner crab (Table 5). For males this is slightly less than the value reported from Alaska (118.7 mm) whereas for females it is significantly greater (79.2 mm) (Somerton and Donaldson, 1996). When compared to the size at 50% maturity determined here, both males ($W_{50} = 125.2$ mm) and females ($W_{50} = 89.1$ mm) are maturing at larger sizes along the U.S. west coast than at either other location. There seems to be a tendency for $W_{50}$ to increase from the north (Bering Sea) to the south or perhaps from the earlier (1982–1999) to the current time period (2012–2014). $W_{50}$ has not previously been determined for grooved Tanner crab along the U.S. west coast, although the mean size at maturity ($W_m$) was reported off the Oregon coast (Pereyra, 1966; Tester and Carey, 1986). The mean CW for morphometrically mature females ranged from 99.5 to 102.3 mm and was relatively constant regardless of the location (Table 5). Although somewhat more variable, the mean values for morphometrically mature males (136–148.9 mm) exhibited no discernable trends by latitude or over time. The mean values of mature grooved Tanner crab may, however, be affected by variations in recruitment and mortality. For male inshore Tanner crab, the mean values may change with fishing pressure in areas where there is an active fishery (ex. Alaska). This scenario is also likely for male grooved Tanner crab if, like other species of Chionoecetes sp. (Fong and Dunham, 2007), they cease growing when they undergo their terminal molt and attain the secondary sexual characteristic of enlarged claws. As males will likely experience fishing mortality on only mature individuals within a size class then the relative abundance of mature to immature crab decreases and the size of maturity declines as the fishing rate increases (personal communication, anonymous reviewer).

**Table 5.** Estimated carapace width ($W_{50}$, mm) at 50% maturity and average carapace width ($W_m$, mm) for mature female and male grooved Tanner crab in the present study compared with previously reported values along the U.S. west coast.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sample period</th>
<th>Sample latitude</th>
<th>Female $W_{50}$ ($W_m$)</th>
<th>Male $W_{50}$ ($W_m$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Somerton and Donaldson (1996)</td>
<td>1982</td>
<td>Bering Sea, Alaska (58.3–60.9°N)</td>
<td>79.2 (99.5)</td>
<td>118.7 (137.9)</td>
</tr>
<tr>
<td>Workman et al. (2002)</td>
<td>1999</td>
<td>British Columbia (49.0–49.8°N)</td>
<td>88 (102)</td>
<td>112 (136)</td>
</tr>
<tr>
<td>Pereyra (1966)</td>
<td>1961–1965</td>
<td>N. Oregon (46.2°N)</td>
<td>– (102.5)</td>
<td>– (148.9)</td>
</tr>
<tr>
<td>Tester and Carey (1986)</td>
<td>1973–1975</td>
<td>S. Oregon (42.4°N)</td>
<td>– (102.3)</td>
<td>– (142.7)</td>
</tr>
<tr>
<td>Present Study</td>
<td>2012–2014</td>
<td>CA to WA (32.0–48.4°N)</td>
<td>89.1 (100.1)</td>
<td>125.2 (141.0)</td>
</tr>
</tbody>
</table>

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contributing to apparent changes in abundance (personal communication, anonymous reviewer).

CONCLUSIONS
Although prior studies remarked on the consistency of W50 from the Bering Sea to off-shore Oregon, the historical comparison was based on two different metrics (W50 and minimum size at maturity). We observed significant variations in W50 along a latitudinal gradient with increases observed for both male and female grooved Tanner crab from the north (Bering Sea) to the south (U.S. west coast) and potentially over time (1982–2014). Determining the expected temporal and spatial variability in the size at maturity is essential prior to establishing a fishery for grooved Tanner crab along the U.S. west coast. A size limit greater than the size of 50% maturity would protect breeding stocks and prevent recruitment overfishing. In addition to size limits, all crab fisheries in Alaska are restricted to male-only fisheries. Similar restrictions should be considered for grooved Tanner crab catch along the west coast (U.S.–Canada to U.S.–Mexico) as an additional conservation measure. Although only slight variations in W50 occurred throughout the study period (2012–2014), continued observations across multiple years and areas are recommended to see if geographic differences occur along the extent of the coast and to confirm the suggested long-term changes observed in W50 over the last few decades.

ACKNOWLEDGEMENTS
The authors are indebted to the captains and the crew of the chartered fishing vessels Excalibur, Ms. Julie, Noah’s Ark, and Last Straw for providing at-sea support. We especially thank Victor Simon, Keith Bosley, Dan Kamikawa and John Harms, members of the West Coast Groundfish Bottom Trawl Survey team, and numerous volunteers for their skill and dedication in collecting high-quality grooved Tanner crab data for the current analysis. We also thank the reviewers for their constructive comments.

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