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ARTICLE

Size at maturity, reproductive cycle, and fecundity of the southern California brown box crab *Lopholithodes foraminatus* and implications for developing a new targeted fishery

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Abstract

Objective: The brown box crab *Lopholithodes foraminatus* is a member of the king and stone crab family (Lithodidae) that occurs in deepwater along the eastern Pacific coast. Historically, landings in California have been low for this species, but an increase in fishing pressure prompted the state to designate it as an emerging fishery and implement an experimental fishery program. With no known biological studies of California brown box crab, essential fisheries information is needed to evaluate the feasibility of a new targeted fishery.

Methods: Using field sampling and observations, along with laboratory studies, we investigated elements of reproductive capacity of the brown box crab in southern California.

Result: We found that females reach physiological maturity at a carapace width (CW) between 50.8 and 71.7 mm, and males do so at a CW between 43.3 and 66.3 mm. Morphometric maturity analysis showed a clear inflection point of abdomen width between immature and mature females. Females were 50% functionally mature at 75 mm CW. Morphometric and functional maturity was not detected for males, albeit samples of small male crabs were extremely limited, thus warranting further study. Females followed a biennial reproduction pattern: mating occurred in the fall, followed by an approximately 18-month brooding period, with hatching in the second spring after mating. Fecundity was positively related to size and ranged from 8352 eggs/brood for a 67.8-mm-CW female to 62,181 eggs/brood for a 130.5-mm-CW female.

Conclusion: These findings can inform the evaluation of a fishery for the brown box crab, including potential management strategies and models for assessing stock condition.

KEYWORDS

brown box crab, fecundity, fisheries, reproduction

INTRODUCTION

In recent years, southern California commercial fishermen have expanded fishing effort (California Department of Fish and Wildlife [CDFW] 2017) for the brown box crab *Lopholithodes foraminatus*, a relative of king crabs, to diversify their businesses and take advantage of new marketing opportunities. Fishing for the brown box crab is not new; the species has been commercially landed throughout its distribution along the eastern Pacific coast of North America for decades. Historically, coastwide landings have been small and incidental to other fisheries. Spikes in brown box crab landings, although rare, typically resulted when effort shifted to deeper fishing grounds in search of target species, as occurred with Dungeness crab *Metacarcinus magister* fishing during the 1983 El Niño in Oregon (Kato 1992). A similar dramatic increase in brown box crab landings occurred in California after the El Niño, warmwater blob, and domoic acid events of 2014–2016 that negatively affected rock crab fishing effort. California brown box crab landings increased fivefold from about 6000 kg in 2016 to nearly 32,000 kg in 2017 (Figure 1; CDFW 2017). During that time, the price per kilogram reached a high of US$15.00 at newly developed direct-to-consumer markets.

The new market demand for and increased landings of brown box crabs, however, have raised some concerns. A designated fishery for this species did not exist; thus, only incidental take, not targeted take, was permitted. To address this issue, in 2018, the CDFW designated the brown box crab as an emerging fishery and limited incidental take to 11.35 kg/trip (Coates 2018). In 2019, the CDFW implemented an experimental fishery program (EFP) for the brown box crab. The EFP provides 4 years to evaluate and determine whether a commercial fishery is feasible. Making this determination requires having the necessary information with which to evaluate the sustainability of the resource. Such information includes but is not limited to estimates of biomass, sustainable yield, movements, growth, and reproduction.

To help inform this evaluation, we examined the reproductive capacity of southern California brown box crabs. Although studies have reported on the distribution and catch rates of brown box crabs (Colomy 1989; McCrae and Hoover 1997; Zhang 2001), there have been few studies of their reproductive biology, and no studies of their reproduction have been conducted in California. The early studies conducted in Oregon and British Columbia reported limited information on size at maturity and fecundity for this sexually dimorphic species in which the males are larger than the females (Goddard 1997; McCrae and Hoover 1997; Zhang 2001). Most recently, Duguid and Page (2011) detailed egg development and egg seasonality of brown box crabs in British Columbia. To expand the biological information describing brown box crabs, we investigated elements of southern California brown box crab reproductive capacity, including (1) size at maturity; (2) fecundity; and (3) reproductive cycle, brood duration, and seasonality.

Impact statement

New information was generated about the reproduction of the deepwater brown box crab to help evaluate the potential for a new California commercial fishery. The results are informing discussions about ways to manage such a fishery, including limits on the size, number, and/or time of year crabs may be fished.

Size at maturity is defined in three ways: physiological maturity, morphometric maturity, and functional maturity (Hartnoll 1969). The presence of mature gonads, in which the reproductive organs are producing gametes, is taken to indicate physiological maturity, but physiological maturity alone does not infer that a crab is ready to mate. Morphometric maturity is the development of secondary sexual characteristics that enable an animal to be physically capable of mating (Hartnoll 1974, 1978). In many species of Anomura and Brachyura, this is denoted by an increase in the abdominal flap width in females and a change in the claw characteristics (e.g., length, height, and gape) in males (Jewett et al. 1985; Haefner 1990; Culver 1991; Alunno-Bruscia and Sainte-Marie 1998). A successful mating event (functional maturity), though often harder to determine in males (e.g., mating marks) than in females (presence of eggs), is the most conclusive sign of sexual maturity (Boolootian et al. 1959; Butler 1960). Taken together, the three parameters present a clear indication of size at maturity.

Determining reproductive capacity includes assessments of fecundity, brood duration and mortality, and reproductive seasonality. Fecundity (the number of eggs per brood) varies among as well as within species (Haynes 1968; Hartnoll 1985; Otto 1990). In general, fecundity increases with increasing size (Otto 1990; Shields 1991). In addition to size, regional differences in environmental conditions, such as water temperature, can influence brooding time and seasonality (Wear 1974; Shields 1991). Duguid and Page (2011) found that brown box crabs in British Columbia underwent a 12-month diapause, with an approximately 18-month overall brooding period and biennial reproduction. Whether California brown box crabs have a similar reproductive cycle is unknown. Brood mortality, particularly due to egg predators, has impacted egg production for other lithodid crab fisheries (Kuris and Wickham 1987; Kuris et al. 1991). This has not been investigated for brown box

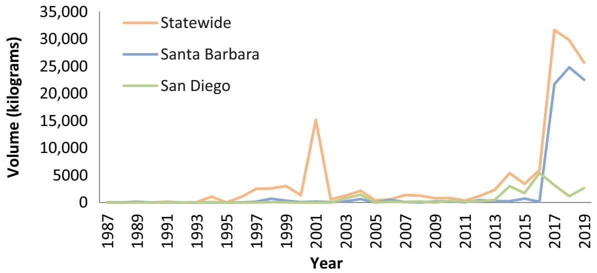

FIGURE 1 Statewide (California) and regional (Santa Barbara and San Diego) fisheries landings of brown box crabs from 1987 to 2017 (CDFW 2017).

crabs. Together, these reproductive parameters could contribute to future assessments of egg production.

Our findings provide information on the reproductive capacity of brown box crabs, which is needed for evaluating the feasibility of a targeted fishery for this species. Study results will inform discussions about potential management options, such as size limits, quotas, and seasonal closures. The results may also be used to develop models (e.g., eggs per recruit and spawning potential ratios) for assessing stock condition.

METHODS

Sampling and measurements

Crab samples were obtained from and in collaboration with commercial fishermen participating in the brown box crab EFP. Samples were collected from the Southern California Bight, south of Point Conception and north of the Mexican border, including both island and coastal mainland areas at depths ranging from 120 to 245 m. Data were collected over the course of 3 years (March 10, 2018–August 31, 2021), excluding a 5-month period (March–July 2020) that was impacted by research and travel restrictions associated with the COVID-19 pandemic. Each participating fisherman provided a monthly sample of 15 males and 15 females as weather permitted; supplemental samples of small crabs (<75 mm carapace width [CW]) and molting crabs were provided as available. Additional crabs were also provided by the CDFW. Sample crabs were caught using commercial lobster traps (5- × 10-cm mesh) and custom research or prawn traps, which were traps with a smaller mesh size (2.5- × 2.5-cm mesh) and closed or no escape ports. Traps were generally 122 cm long × 91 cm wide × 35.5–61.0 cm high. The research and prawn traps (referred to as "experimental traps") were designed to collect a wider size range of crabs that were representative of the brown box crab population as compared to crabs that were captured and retained in the commercial traps, based on observations that small brown box crabs were caught in the spot prawn *Pandalus platyceros* fishery, which uses smaller mesh traps in deeper waters. Although the smallest crabs likely came from the small-mesh (experimental and prawn) traps, trap type was not recorded for each crab. Brown box crab samples could not be obtained from the spot prawn fishery because it is illegal to land bycatch, such as brown box crabs, in that California fishery.

Size at maturity

Carapace width (the widest point not including spines), abdomen width (AW; at the suture line near the widest part), left and right propodus lengths (PLs; posterior surface from tip to joint), and left and right propodus heights (PHs; posterior surface from joint to base) were measured to investigate morphometric maturity. Measurements were recorded using a digital caliper (0.01 mm). Although maximum CW (including the spines) is used for the fishery, CW is used in this study to avoid the inherent issues caused by worn and damaged spines. Additional size measurements were taken and conversion equations were calculated (Appendix) to enable comparisons with measurements from other studies and California fisheries data. Since the claws of brown box crabs are dimorphic, claw measurements for only those crabs having a right claw that was larger (dominant) than the left claw were included, as these represented virtually all crabs encountered. Crabs with damaged or noticeably small regenerated claws were removed prior to analysis.

Crabs were categorized as immature or mature for physiological, morphometric, and functional maturity analyses. Female crabs were categorized as mature when eggs or a mat of remnant brood setae, filaments to which eggs were attached and that remained with empty egg cases (also referred to as "moss" per Zhang et al. 1999), were present. When such was not the case, the crab was dissected and the gonads were examined. Those with colored (yellow, orange, or red) gonads were categorized as mature. Translucent or white gonads were categorized as immature. Males were categorized as mature when the reproductive system (vas deferens and testes) was white and filled. For males in which the vas deferens was not in this state, gonad tissue was removed and examined microscopically at 100× magnification to determine the presence of spermatophores (indicating maturity); maturity was further confirmed by pressing on the gonopore to see if sperm was released. A small subset of mature and immature male crabs representing a range of sizes were further examined both visually and with a microscope for setae abrasion of the genital pore and mating marks, which are believed to be associated with functional maturity.

Egg development

Egg development of captive brooding females was assessed from September 2019 through March 2020, after which time research restrictions associated with the COVID-19 pandemic precluded further observations. Crabs were held in chilled (8–10°C), filtered seawater tanks at the University of California Santa Barbara and at the Scripps Institution of Oceanography, University of California San Diego. Eleven crabs were monitored at the Scripps Institution of Oceanography over the 7-month period. At the University of California Santa Barbara, 11 crabs were monitored for the first 5 months. Due to a tank malfunction that caused a complete die-off of the crabs, a replacement cohort of 16 crabs having similar egg stages were monitored for the final 2 months. Each individual was assigned a unique identifier by affixing vinyl tags to the carapace with ethyl cyanoacrylate gel (bSi Insta-Cure). Crabs were fed a variety of foods, including mussels, squid, shrimp, scallops, brittle stars, and an occasional fish carcass, every 7–10 days. Samples of at least 20 eggs were retrieved from each captive crab by separating two of their limbs and inserting forceps under the abdominal flap, as we found it to be less damaging to the flap. Because Duguid and Page (2011) reported a lengthy diapause stage (up to 12 months of no development), eggs were sampled once per month until egg development was initiated and then twice per month when eggs were developing. Eggs were observed through a 100× magnified lens on a dissecting microscope. We categorized six egg development stages (Table 1) in addition to the hatching and moss stages for captive crabs, based on descriptions from Duguid and Page (2011). Development stage was recorded, and the number of eggs per stage was totaled and used to calculate the proportion of eggs per stage by month among crabs.

Egg stage observations were also recorded for all monthly field samples to assess reproductive status in nature. Observations were made visually (rather than using a microscope) to mimic field techniques and included four broad categories: bright orange (diapause), dark orange/eye spot (developing and/or hatching), moss (fully hatched), and empty (absence of eggs or moss; clean pleopods).

Fecundity

To assess fecundity, crabs from field samples were measured as described above, and abdominal flaps containing full broods of undeveloped eggs (no eye spots visible by eye) were removed and frozen for processing at a later date. Full broods were defined as egg masses that extended close to or were at the edge of the abdominal flap (Figure 2A). Although encountered rarely ($n = 5$), small broods (Figure 2B) were also assessed to provide baseline data. Upon processing, the abdominal flap with the intact brood was defrosted and the uneyed diapause stage was confirmed via microscopic (100×) examination. All pleopods were numbered clockwise starting with the small pleopod on the side of the dominant right claw and the side opposite from the other pleopods, and they were detached according to this sequence (Figure 2C). Eggs were removed from each pleopod by gently scraping the setae with a spatula in a petri dish of shallow seawater and subsequently separating the clusters with forceps. In preparation for manual and digital counts, the eggs were spread in a single layer covering 75% of a petri dish, avoiding the edges. Multiple dishes were used as needed based on the quantity of eggs removed per pleopod. Photographs of the separated eggs in the petri dishes were taken using a digital camera (Olympus Stylus) magnified to 3.0× and mounted on a frame with a sheet of blue paper and tracing light underneath using methods modified from Bohenek and Resetarits (2017). Egg counts were then calculated for each pleopod from the photographs using ImageJ version 1.52q (particle analysis; https://imagej.nih.gov/ij/) following a validation period during which manual and digital counts were compared for 45 petri dishes totaling 23,000 eggs. Because the manual and digital counts were found to be nearly identical, averaging 1.08% error (median = 0.29%), only digital counts were used for this analysis ($n = 99$). A relationship ($R^2 = 0.96$) was found between the number of eggs on pleopod 3 and total fecundity ($n = 81$): total number of eggs = [(number of eggs on pleopod 3) × 4] + 2085. For 13 crabs, only the eggs that were attached to pleopod 3 were counted and the equation was applied to calculate the total number of eggs.

Analysis

Statistical analyses were performed using R version 1.4.1 (R Core Team 2020) and Microsoft Excel. The significance level α used for all analyses was 0.05. Relative growth was evaluated based on claw size for males and the AW for females, as these are the structures that undergo the most striking morphological changes (Teissier 1960; Hartnoll 1963), using regression and analysis of covariance (ANCOVA) statistics on log-transformed data. Per ANCOVA, intercepts were not tested for significance if slopes were different and/or if there was little overlap in the range of data being analyzed (Snedecor and Cochran 1980). Relative growth was considered isometric if β was greater than 0.9 and

TABLE 1 Egg development categories compared to the embryogenesis illustrated in Figure 3 of Duguid and Page (2011).

Duguid and Page (2011) code	Egg development category
C/D	Diapause; no development occurring
E/F/G	Development initiated
H	Eye spots present, with >80% yolk
I	Eye spots present, with ~75% yolk
NA	Eye spots present, with ~50% yolk (not pictured in the figure)
K	Eye spots present, with ≤25% yolk

less than 1.1 (Kuris and Carlton 1977). The relationship between size (CW) and fecundity was determined using linear regression, and an ANCOVA on log-transformed data was used to analyze the influence of location on fecundity, with data back-transformed for visualization. Size-at-maturity estimates were performed by fitting a maturity curve to binary maturity status for CW data. The maturity curve was fitted and illustrated using a generalized linear model and a logit link function in the R statistical package AquaticLifeHistory version 0.0.9000 (J. Smart; https://github.com/jonathansmart/AquaticLifeHistory). Due to limitations on receiving a full size range of crabs, the effect of location on size at maturity could not be analyzed. Fisher's exact test was used to evaluate differences in seasonal egg development between locations. Because there were gaps in our monthly field sampling, we used only two categories for season: winter/spring (February–April) and summer/fall (June–November).

RESULTS

Size at maturity

In total, 767 female and 870 male brown box crabs from the Southern California Bight were examined. Females ranged from 45.3 to 134.0 mm CW. Males ranged from 43.7 to 188.5 mm CW.

Physiological maturity

Thirty-three females were classified as immature. The largest immature female was 71.7 mm CW, while the smallest female with mature gonads was 50.8 mm CW. We identified only four immature males, with measurements of 43.7, 47.0, 60.5, and 63.6 mm CW. The smallest mature

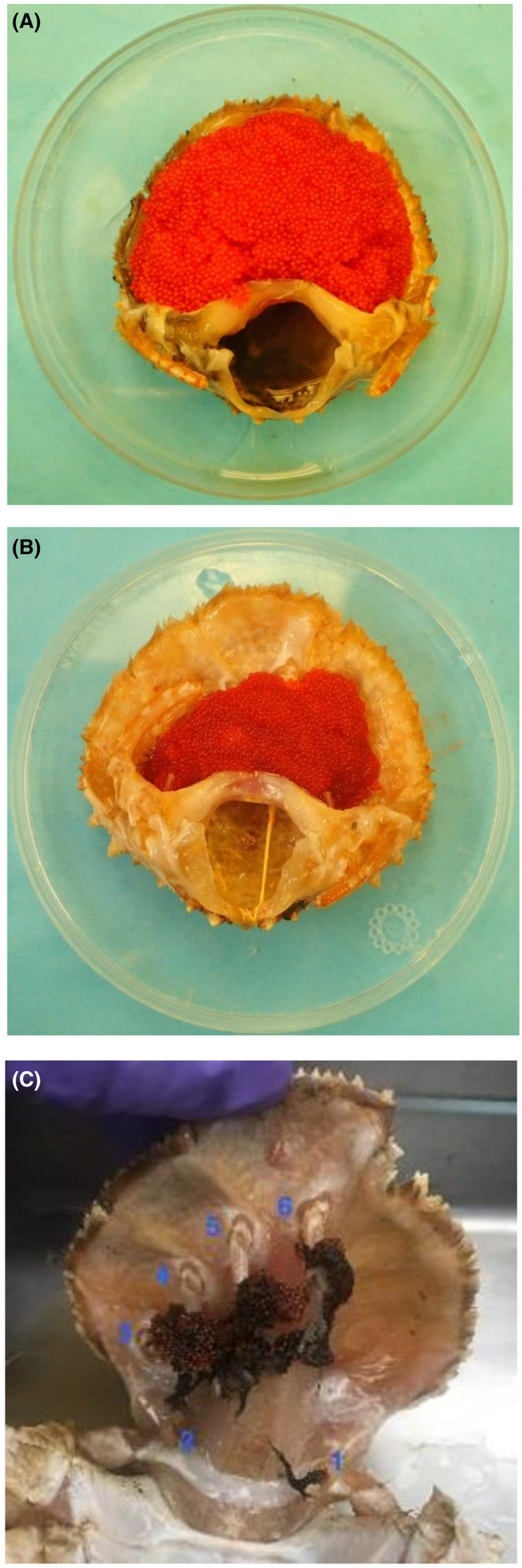

FIGURE 2 Egg masses of brown box crabs: (A) full brood of eggs in the diapause stage; (B) small brood of eggs in the diapause stage; and (C) abnormal clusters of eggs in the developing stage. Numerical labels (1–6) in panel C represent assigned pleopod numbers.

male was 47.3 mm CW, and all males at or above 66.3 mm CW were mature.

Morphometric maturity

A significant allometric shift in AW was identified for immature and mature females ($F_{1,\ 731} = 47.34$, $p < 0.001$; Figure 3). Immature and mature crabs overlapped in size between 50 and 72 mm CW, with crabs below 50 mm CW being immature and those above 72 mm CW being mature. Mature females exhibited positive allometric growth ($\beta = 1.2$) of the abdomen, whereas the immature females exhibited isometric growth ($\beta = 1.1$). We did not detect a significant allometric shift in either PL ($F_{1,\ 566} = 0.94$, $p = 0.33$) or PH ($F_{1,\ 487} = 0.875$, $p = 0.35$) for immature and mature males, albeit the sample size of immature male crabs was very small ($n = 4$). Both mature and immature males exhibited isometric growth in PL ($\beta = 0.99$ and 1.10, respectively; Figure 4). Positive allometric growth of PH was detected for mature males ($\beta = 1.2$), while immature males exhibited isometric growth ($\beta = 0.98$; Figure 5).

Functional maturity

Females were 50% functionally mature (i.e., presence of eggs or moss) at 75.0 ± 1.01 mm CW and were 95% functionally mature at 88.9 ± 1.26 mm CW (Figure 6). The smallest ovigerous female was 67.8 mm CW. Functional maturity could not be estimated for males due to the lack of indicator(s). No mating marks or setae abrasion of the genital pore were observed in males.

Reproductive seasonality and egg development

Egg-bearing females (diapause and developing eggs) occurred year-round but were most prevalent (>90% of samples) from October through March (Figure 7). Females with eggs in diapause were present year-round. Those with developing eggs were most prevalent from November through March and, with the exception of one crab, were nonexistent from June through September. There was a shift in the percentages of moss females and egg-bearing

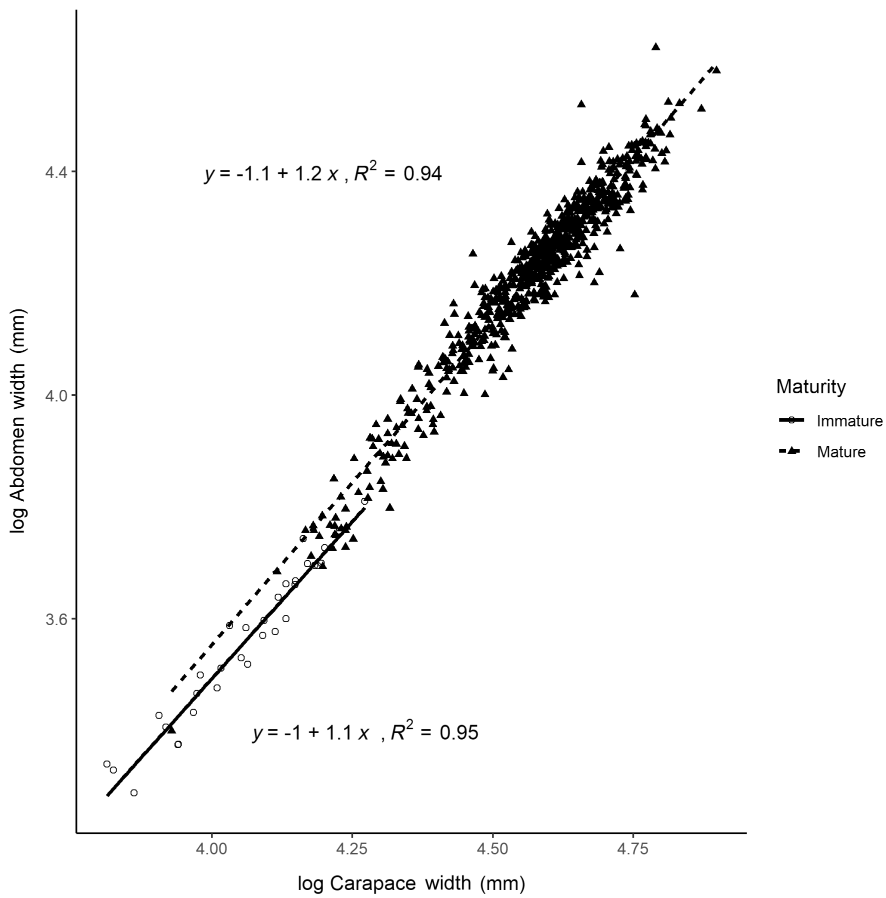

FIGURE 3 The relationship between the natural log of abdomen width and the natural log of carapace width (CW) for female brown box crabs by maturity group. Separate allometric equations were fitted for immature (open circles and solid line) and mature (closed triangles and dashed line) groups that were based on physiological maturity. (Note: All data points are below the legal size of 144.6 mm CW).

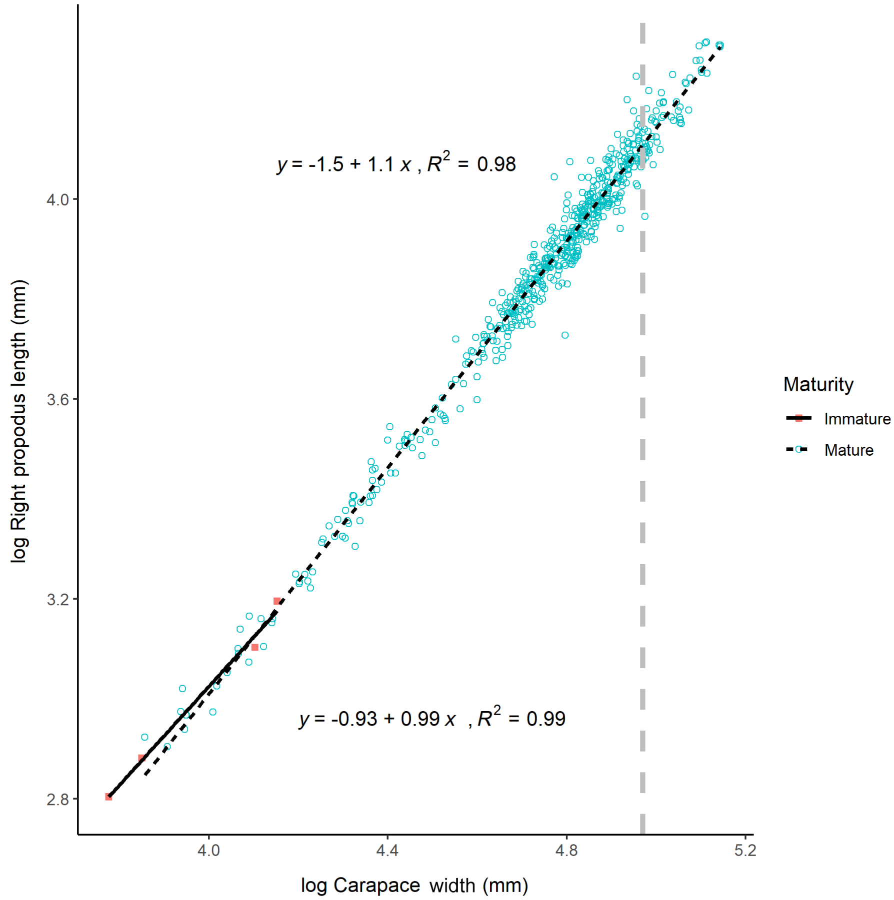

FIGURE 4 The relationship between the natural log of carapace width (CW) to the natural log of propodus length for male brown box crabs by maturity group. Separate allometric equations were fitted for immature (red closed squares and solid black line) and mature (blue open circles and dashed black line) groups based on physiological maturity. The gray dashed line denotes the legal size (144.6 mm CW).

females from September to October, with nearly all females bearing eggs in October (Figure 7). Fully hatched broods (moss) were common from May through September, with just a few in October and November, and were absent from December through March. There was no difference in egg development between locations in either season (winter/spring: $p = 0.484$; summer/fall: $p = 1.0$).

For crabs that were held in the laboratory, broods developed over an approximately 6–7-month period (Figure 8). They began developing in October, with the first signs of hatching observed in February. Eggs that were adjacent to one another developed at differing rates. Asynchronous development and hatching were not localized to areas within a brood but rather were dispersed throughout.

Fecundity

Fecundity ranged from 8352 to 62,181 eggs/brood for field-sampled brown box crabs ($n = 94$) ranging in size from 67.8 to 130.5 mm CW (Figure 9). The slopes of the size–fecundity relationship did not differ significantly between locations ($F_{1, 96} = 0.83$, $p = 0.365$). There was a positive relationship between brood size and CW that was generally linear ($y = 753.93[\mathrm{CW}] - 43{,}974.62$; $R^2 = 0.79$). There was high variation in fecundity within size-classes (Table 2). For atypically small broods ($n = 5$), fecundity ranged from 7813 to 40,787 for crabs from 94.4 to 125.5 mm CW (Figure 9).

DISCUSSION

Our results provide essential biological information that can be used to inform the evaluation of a fishery targeting the California brown box crab. Female size at maturity was smaller in southern California compared to reports from studies farther north. In British Columbia (Zhang 2001), 50% functional maturity was reported at 80 mm carapace length (CL) as compared to 68 mm

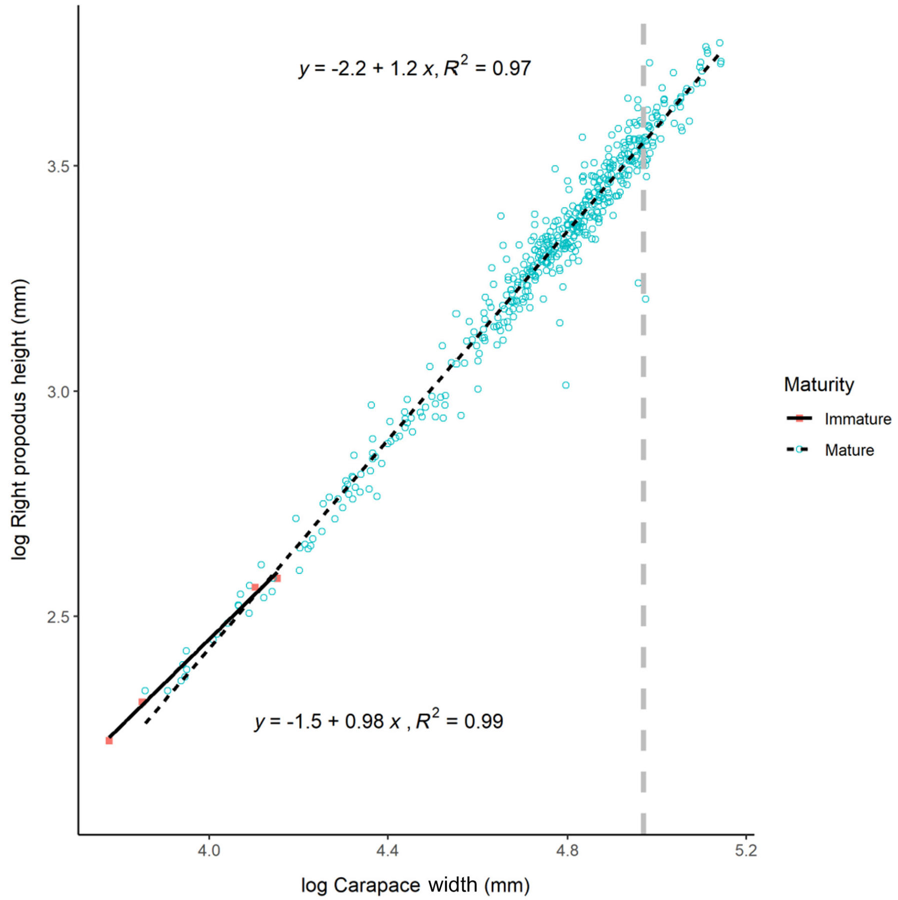

FIGURE 5 The relationship between the natural log of carapace width (CW) to the natural log of propodus height for male brown box crabs by maturity group. Separate allometric equations were fitted for immature (red closed squares and solid black line) and mature (blue open circles and black dashed line) groups based on physiological maturity. The gray dashed line denotes the legal size (144.6 mm CW).

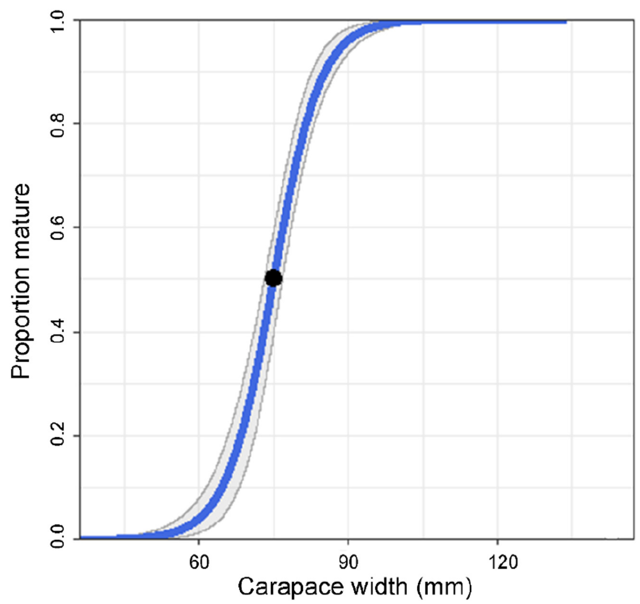

FIGURE 6 Curve fitted to obtain the proportion of female brown box crabs that were mature at a given carapace width (mm). The calculated size at 50% maturity is denoted by the black filled circle.

CL (75 mm CW) in our study. Likewise, 95% functional maturity was 90 mm CL for crabs in British Columbia (Zhang 2001) as compared to 79 mm CL (89 mm CW) for crabs in our study. The smallest gravid female reported in British Columbia was between 65 and 75 mm CL (specific size was not cited; Zhang 2001) and the smallest gravid female reported in Oregon was 68 mm CL (McCrae and Hoover 1997), whereas in our study, the smallest gravid female was 62.3 mm CL (67.8 mm CW). These comparisons follow the general pattern of size at maturity decreasing with lower latitude (Hines 1989; Dugan et al. 1991), a pattern that was also found in North Pacific populations of some king crab species (Olson et al. 2018). However, trap biases may also explain this finding, as we obtained small immature crabs from smaller mesh traps (2.5 × 2.5 cm) used in deeper waters (~250 m) than where legal-sized crabs were fished (~150–200 m), which may have influenced the smaller size at maturity that we identified as compared to other studies. The encounters with small brown box crabs by spot prawn trappers in deeper water may suggest an ontogenetic distribution shift (e.g., Somerton and Otto 1986) of brown box crabs. However,

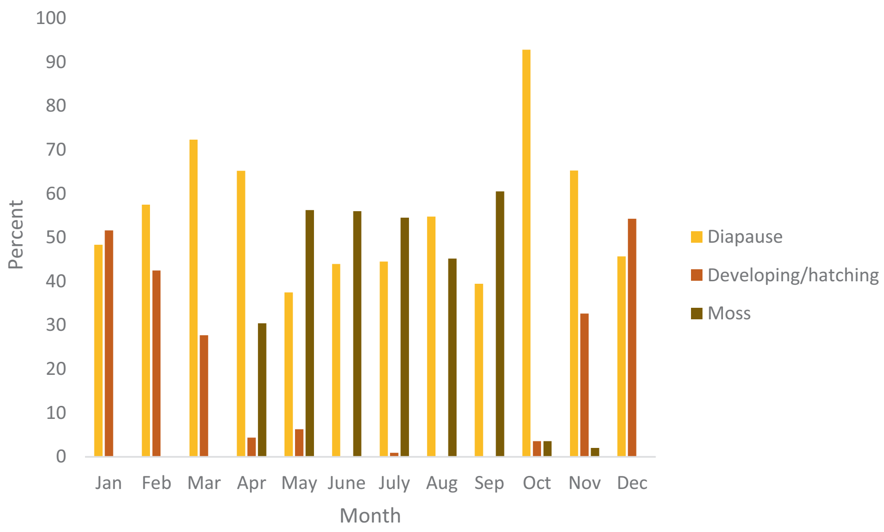

FIGURE 7 Seasonality of egg stages in southern California brown box crabs from field collections.

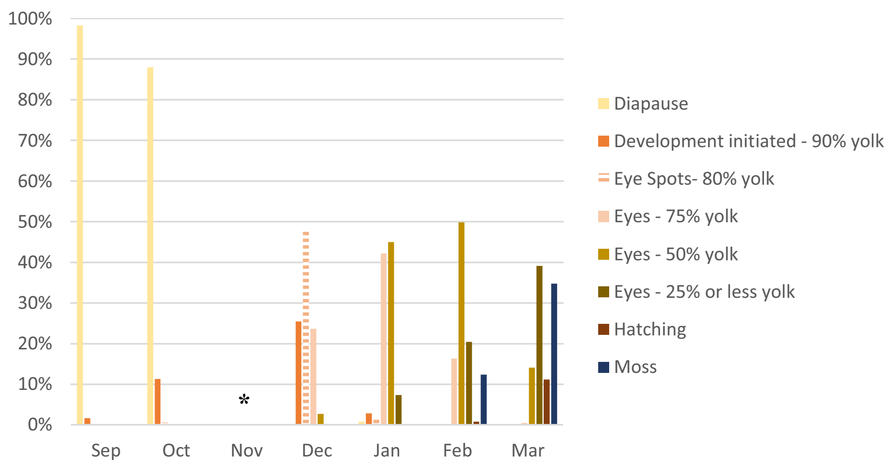

FIGURE 8 Time course of egg development for laboratory-held brown box crabs. The asterisk indicates that samples were not taken in November.

specifically targeted sampling is necessary to fully evaluate this hypothesis.

We report the first evidence for female morphometric maturity in the brown box crab. Previously, coverage of the coxa by the abdominal flap and the presence of setae on the pleopods have been used to distinguish immature from mature female king crabs (Donaldson and Byersdorfer 2005). Our examination of these features did not coincide with maturation as determined by observation of gonad status. Although the change in female AW relative to CW was not as readily evident as it is with brachyuran crabs, a clear relative width inflection between the two groups was consistent with physiologically based categories of mature and immature female brown box crabs. Since the morphometric differences are subtle, the presence of eggs and moss will still be the most readily available technique to identify mature female crabs in the field despite the overlap in immature and mature sizes.

Male size at maturity could only be recognized physiologically—not morphometrically or functionally. Our findings on physiological maturity agree with and further refine those of Goddard (1997) for Oregon. All of the male crabs ($n = 33$) examined by Goddard (1997) were 67 mm CW or larger and were mature. Our data confirm that male brown box crabs above 66 mm CW are mature and that maturity occurs between 47 and 66 mm CW. In agreement with the Goddard (1997) study, no inflection point was detected when evaluating the relationship between crab size and the two claw morphology parameters (PL and PH) for immature and mature male crabs. Notably, none of the crabs examined by Goddard (1997) were immature, and we only evaluated four immature male crabs. Additionally, although Goddard (1997) suggested that

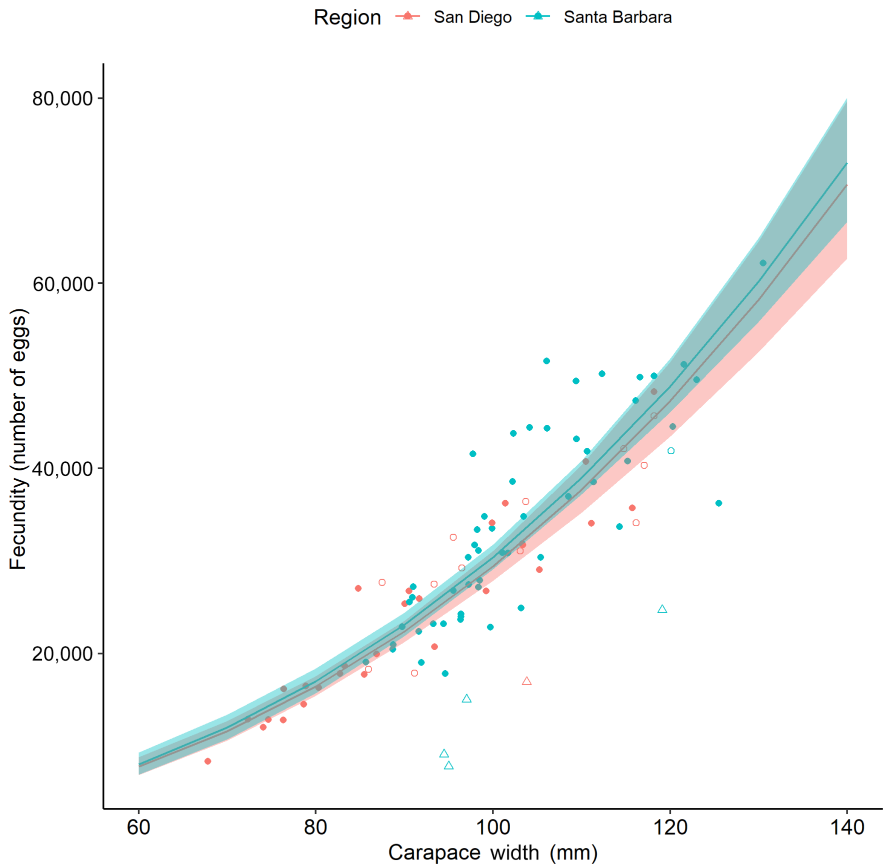

FIGURE 9 Relationship between fecundity and carapace width of brown box crabs ($n = 94$) at two locations in California. Circles represent egg counts for full broods: closed circles represent counts determined using our standard method ($n = 81$), whereas open circles represent counts determined using the pleopod 3 regression equation described in the Methods ($n = 13$). The shaded area indicates the 95% confidence interval. Small broods ($n = 5$), represented by open triangles, were not included in the analysis.

TABLE 2 Fecundity (number of eggs per brood per female) of southern California brown box crabs for 10-mm-interval size-classes based on carapace width (CW). Max, maximum; Min, minimum; *n*, number of females examined; SD, standard deviation.

Size-class (mm CW)	*n*	Min	Max	Mean	SD
60.0–69.9	1	8352	8352	8352	NA
70.0–79.9	7	12,023	16,492	13,974	1778
80.0–89.9	12	16,318	27,697	20,574	3612
90.0–99.9	33	17,830	41,588	27,028	5208
100.0–109.9	19	24,895	51,587	36,871	7404
110.0–119.9	16	33,694	50,202	42,081	5913
120.0–129.9	5	36,236	51,245	46,690	6042
130.0–139.9	1	62,181	62,181	62,181	NA

setae abrasion of the male genital pore may be a useful indicator of functional maturity, we did not find this to be the case. Setae were observed over a wide range of sizes, with no distinguishable differences in wear. The large size range of physiologically mature males (47–189 mm CW) and the extremely small sample size of immature males ($n = 4$), however, necessitate further investigations of morphometric indicators and functional maturity to determine the size at which male crabs can successfully mate.

Our study provides the most comprehensive fecundity analysis of brown box crabs. We documented the highest reported egg count (>62,000 eggs) for this species and demonstrated the similarity in fecundity for crabs

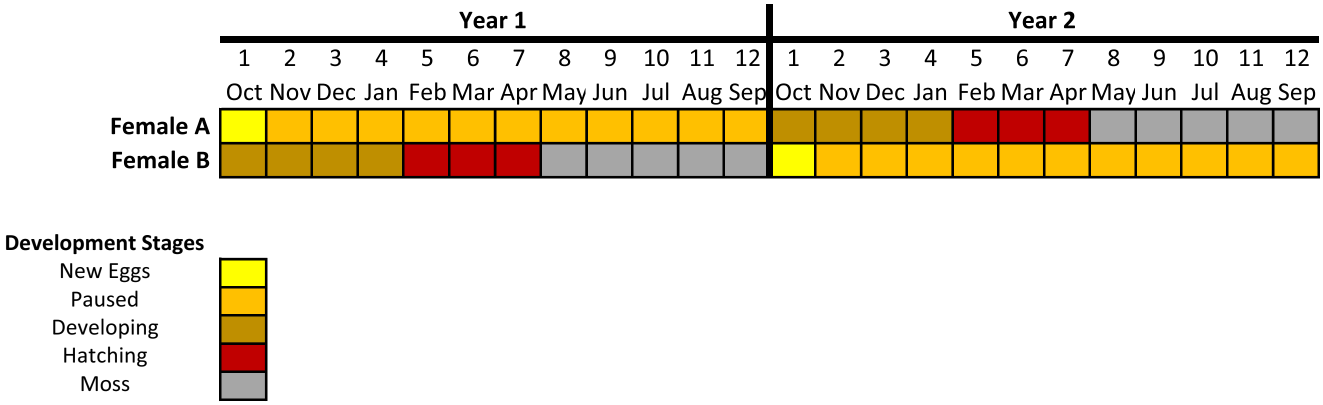

FIGURE 10 Simultaneous timelines depicting the general duration of egg development phases during biennial reproduction based on the timing of mating events for brown box crabs in southern California. Female A mated and extruded new eggs in October of year 1. Female B mated during October of the prior year (year 0; not shown).

throughout southern California. As expected, the number of eggs increased with increasing crab size, with no indication of senescence as seen with other crab species (Swiney et al. 2012; Danielsen et al. 2019). Fecundity estimates from Oregon ($n = 4$; McCrae and Hoover 1997) were similar to ours for large (~120-mm CW) crabs: 48,100 and 51,200 eggs, respectively. However, the estimates from McCrae and Hoover (1997) were a bit higher for small (~75-mm CW) crabs: 20,100 and 16,000 eggs, respectively. Given variation within a size-class and the small sample size from the McCrae and Hoover (1997) study, size–fecundity relationships may be similar for crabs from California and Oregon. Taken together, we conclude that the resulting size–fecundity relationship can be used to evaluate the reproductive capacity of brown box crabs throughout southern California and potentially elsewhere.

Brood mortality can have a significant effect on reproductive output (Kuris 1991). In particular, red king crabs *Paralithodes camtschaticus* can experience high brood mortality, losing the majority of broods to a nemertean egg predator (Shields et al. 1990; Kuris et al. 1991). Even though we did not directly study brood mortality, we did not observe empty egg cases or egg predators during our fecundity assessments, even for broods that were further along in diapause (~8–10 months brooding time) and that presumably had a longer time of exposure to potential mortality sources. However, a few times we observed females with small clusters of eggs on just a few pleopods (Figure 2C). These were not partially hatched broods as described by Zhang et al. (1999), given that there was no moss on the pleopods lacking eggs and, in most cases, the eggs were bright orange and not developing. It is unknown whether these instances were the result of poor fertilization or delayed mating that negatively impacted extrusion. Laboratory studies have illustrated negative impacts of delayed mating after molting on egg extrusion and development in lithodids (McMullen 1969; Sato et al. 2005), and those authors further hypothesized that this could be an issue as the breeding population is harvested and becomes less available.

On a few occasions, we observed barren females—crabs with mature ovaries but lacking both eggs and moss on the pleopods. Many of these females were part of two summer samples and were 60–80 mm CW, overlapping with the size of functional maturity and the sizes of the smallest ovigerous and largest immature female crabs. Given their size and the season in which they were obtained, these females may have recently matured and never mated. This hypothesis is further supported by the fact that these samples came from a deeper water area known to have smaller immature brown box crabs. However, we also observed a few barren females during other seasons and at larger sizes. The occurrence of this condition in larger (>90-mm CW) mature crabs that should have mated previously may be an indication of unsuccessful or delayed mating. Alternatively, these crabs may have reached maturity at a very large size and had not mated yet. Although we rarely encountered barren females, suggesting that this phenomenon likely has little impact on the reproductive capacity of the population, we recommend future monitoring of brood presence and size and, if warranted, the potential factors influencing this condition.

Our field observations of the southern California brown box crab support an approximately 18-month biennial reproductive cycle (Figure 10; Duguid and Page 2011). Since (1) females must molt prior to mating, (2) molting occurs in the late summer or fall (our unpublished data), and (3) fertilization occurs shortly after mating (sperm is not stored; Duguid and Page 2011), the occurrence of many crabs with eggs in diapause throughout the year is best explained by a 12-month diapause period. The mix of some crabs with eggs in diapause and some with eggs developing and hatching in the winter and spring further suggests a staggered biennial cycle, with recently molted and mated crabs having eggs in diapause and crabs that mated in the previous year having developing or hatching eggs.

Development (once initiated) to hatch time in the laboratory supported our observations in the field and was similar to the British Columbia laboratory results (Duguid and Page 2011) despite the notable geographic distance between the two studies. Others (Shirley et al. 1989; Stevens et al. 2008) have shown that temperature can affect the duration of embryonic development. Both laboratory studies (Duguid and Page 2011 and the present study) were conducted at temperatures that were representative of the respective regions. The similarity in the duration of the reproductive cycle between our California field and laboratory studies and the British Columbia study may be partially explained by the minimal difference in temperatures of deepwater habitat in the two locations (Duguid and Page 2011; our unpublished data), which was far less than the temperature difference between shallow waters in these regions. Although the duration of the cycle is similar in the two regions, the timing differs. In British Columbia, mating and egg development commence during late summer, whereas in California, these events take place largely in the fall. Investigating other environmental parameters (e.g., ocean productivity, day length, and seasonal temperature changes) that differ between the two locations and that can influence the timing of mating and reproduction may reveal why the cycles commence at different times.

Our findings can inform the evaluation of management strategies for a fishery targeting brown box crabs. Currently, the EFP is managed primarily through the use of a size limit and a quota. The minimum legal size for brown box crabs is 146 mm maximum CW (i.e., including spines), which converts to 144.6 mm CW (i.e., excluding spines). This size limit was based largely on market demand. As female brown box crabs typically are smaller than the legal size, they are not currently being harvested and likely will not be considered for harvest in the future. As a result, females are able to contribute reproductively to the population throughout their lives. For males, our current research supports this size limit in terms of physiological maturity, which occurs at a much smaller size, thus allowing them to contribute reproductively prior to harvest. Further, our preliminary analyses of growth rates (Culver and Page 2021), albeit extremely limited, suggested that male brown box crabs may be able to reproduce for many years prior to harvest. Molt increments decreased from around 16% for males between 62 and 98 mm CW to less than half that (~7%) for males larger than 125 mm CW. Additionally, the presence of soft-shelled males in our monthly samples indicated that males likely molt only once per year. Based on these molt increments and interval, if functional maturity is close to physiological maturity, then a 66-mm-CW male brown box crab (the size at which all male crabs were found to be mature) would have at least 5 years to contribute to the population before reaching legal size.

Although the catch size limit seems appropriate, size-selective fisheries using a minimum size can have drawbacks (Conover and Munch 2002; Fenberg and Roy 2008; Varisco et al. 2019). By selecting for large males, there is a long-term potential for harvest to drive the population toward a smaller size at maturity and slower-growing individuals, evolving toward a small body size and lower fecundity. Some fisheries have implemented a slot limit (Ahrens et al. 2020; Pellowe and Leslie 2020) restricting harvest to intermediate sizes, a measure that allows reproduction prior to harvest while also protecting the genetics and reproductive potential of the larger individuals. Future studies on growth rates and mating success would help to inform the determination of the most appropriate size limits for a sustainable fishery.

Another management strategy that could be considered is seasonal closure. Many fisheries use seasonal closures to protect stocks when crabs are molting and/or reproducing (mating; eggs hatching). Since female brown box crabs are not of harvestable size and thus are not retained, protection of the hatching season is likely not needed. Instead, closing the fishery during the molting and mating season might be considered. Given that molting and mating are basically synchronous and quite seasonal, a short-term closure during September and October may be sufficient to protect the majority of the mating/molting population if additional measures are required. Given that fishermen select for heavier, hard-shelled brown box crabs to maximize meat return, such a closure could have the added benefit of preventing low-quality crab from entering the market. The specific timing and duration of the closure would need to be periodically reassessed in light of ongoing environmental changes that may impact molting seasonality and, thus, mating seasonality.

Lastly, if California brown box crabs do indeed have limited movement (Colomy 1989; Kato 1992), another option could be rotational zone management. Density can play a large role in the reproductive potential of marine organisms. Populations with a low density of reproductive males may lead to lower reproductive success due to limited sperm transfer from increased mating delays and decreased mating encounters associated with higher mate search and encounter times (Powell et al. 1974; Kendall et al. 2001; Sato et al. 2005). Use of rotating area closures could help to slow the reductions of localized densities, as seen with the sea cucumber fishery (Plagányi et al. 2015). Ongoing investigations of brown box crab movement by resource managers, together with investigations of density-dependent reproductive success (e.g., tracking the number of barren mature females), are needed to better understand the potential utility of this management strategy for the brown box crab fishery.

The EFP for brown box crabs provided a unique opportunity to collect information prior to having a large-scale fishery underway. Valuable data have been collected, but research was limited for a variety of reasons. The continued strong market for the brown box crab (with the price per kilogram at $22.00 for direct-to-consumer markets) suggests that such a fishery will likely be economically viable. However, questions remain about (1) how sustainable the population will be as large males are harvested and (2) which management strategies will be most effective in light of this and other biological characteristics. More information is clearly needed to evaluate the potential for a long-term fishery for brown box crabs in California and elsewhere.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author, C. S. Culver, upon reasonable request, although some data in raw form may be withheld due to state data confidentiality rules.

ETHICS STATEMENT

This study was conducted according to the permit guidelines and requirements set by the California Department of Fish and Wildlife.

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APPENDIX

CONVERSION EQUATIONS

Brown box crab measurements

Studies of brown box crabs use a variety of measurements to define crab size and associated anatomical attributes. To address this issue and to enable comparisons across studies, we took additional measurements and developed calibration equations by using linear regression. Measurements were taken as described and shown in Table A.1 and Figure A.1 using a digital caliper (nearest 0.01 mm) or scale (nearest 0.5 g). All measurements were compared to carapace width (CW), our standard measurement for this study, with males and females reported separately. Our equations complement those provided by Zhang et al. (1999), which represented female and male crab measurements combined (Figures A.2–A.8).

TABLE A.1 Definition of measurements for the brown box crab. Numbers 1–7 correspond to the measurements depicted in Figure A.1.

Attribute (abbreviation)	Number	Measurement
Carapace length (CL)	1	Rostral teeth to posterior carapace edge
Orbit length (OL)	2	Right eye orbit to posterior carapace edge
Mid carapace width (mid CW)	3	Midsection not including spines
Carapace width (CW)	4	Widest point not including spines
Maximum carapace width (max CW)	5	Widest point including spines
Propodus length (PL)	6	Posterior surface from tip to joint
Propodus height (PH)	7	Posterior surface from joint to base
Total body wet weight (wgt)	8	Measured to the nearest 0.5g

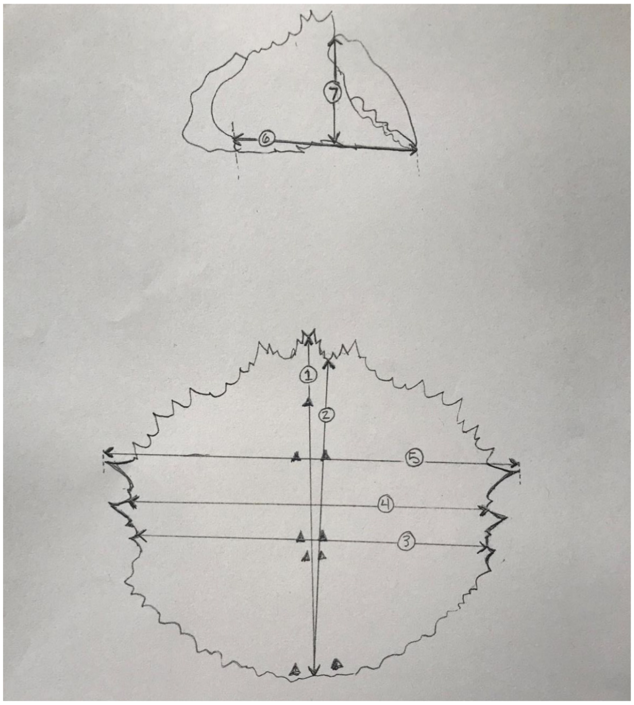

FIGURE A.1 Illustration of brown box crab measurements. Numbers correspond to the measurements defined in Table A.1 (Drawing adapted from Goddard 1997).

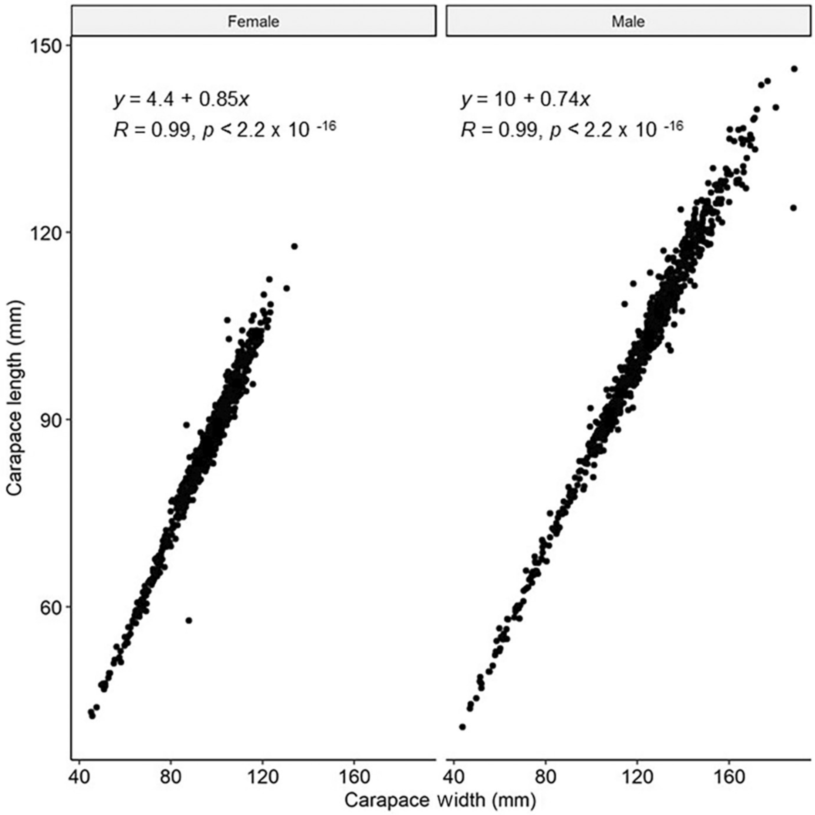

FIGURE A.2 The relationship between carapace width and carapace length for female and male brown box crabs.

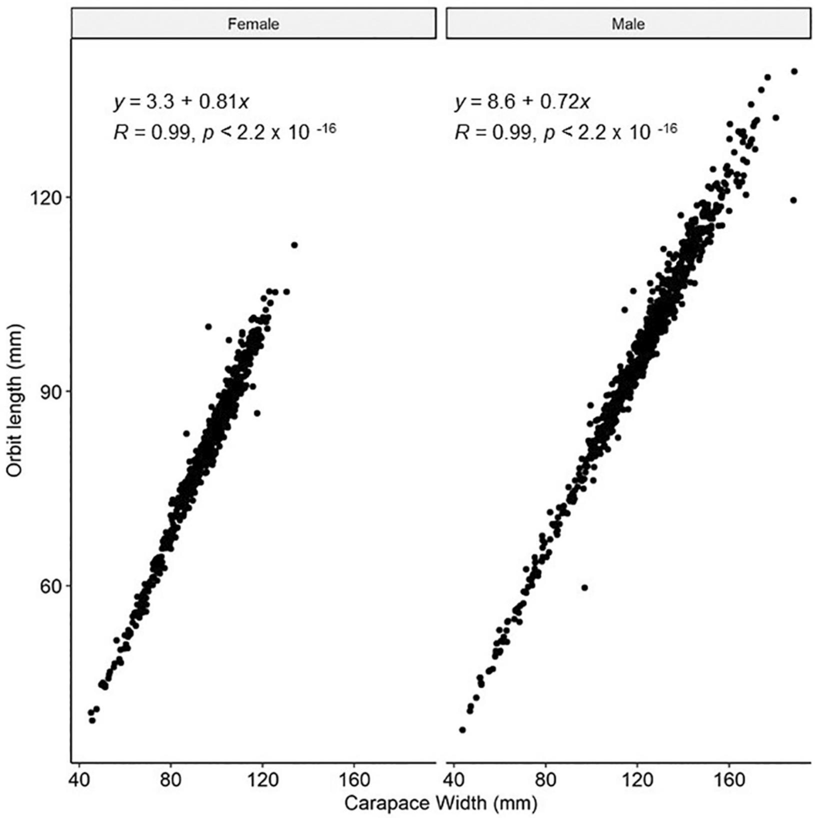

FIGURE A.3 The relationship between carapace width and orbit length for female and male brown box crabs.

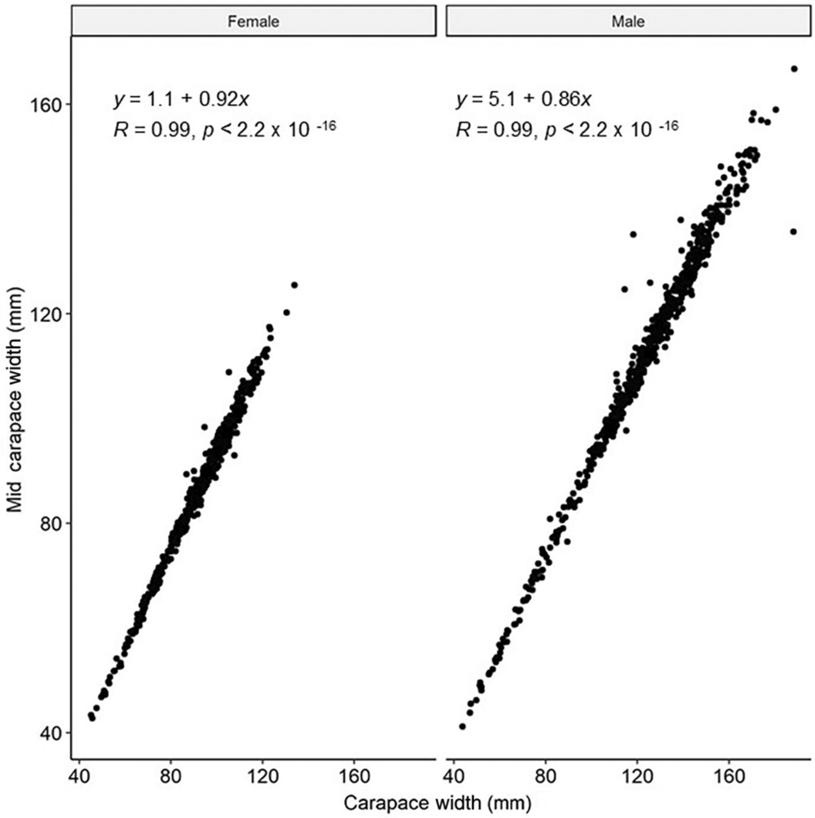

FIGURE A.4 The relationship between carapace width and mid carapace width for female and male brown box crabs.

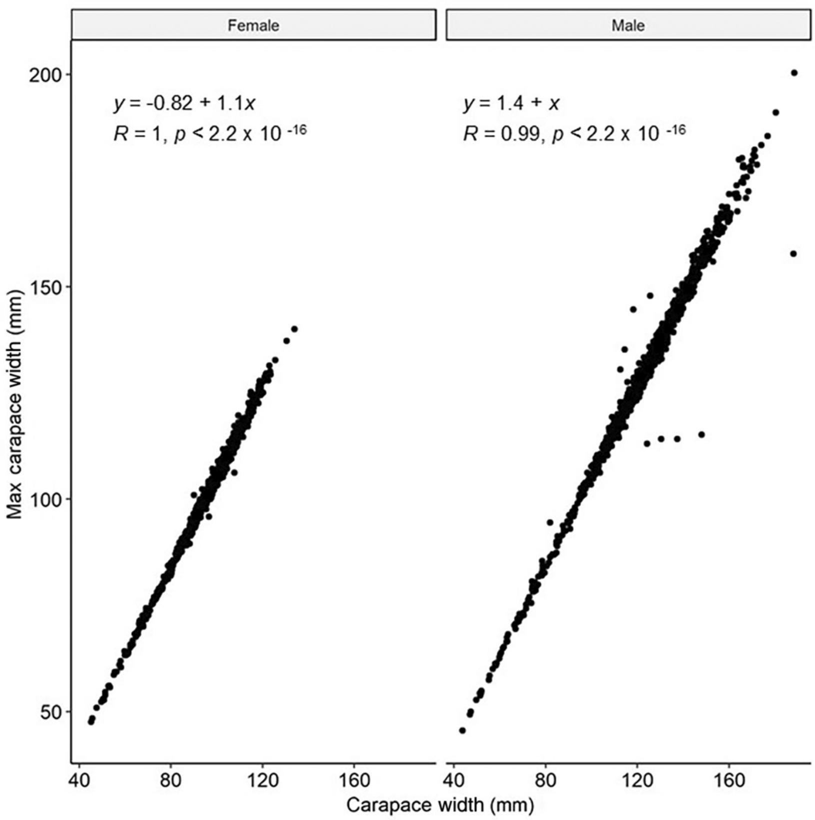

FIGURE A.5 The relationship between carapace width and maximum (max) carapace width for female and male brown box crabs.

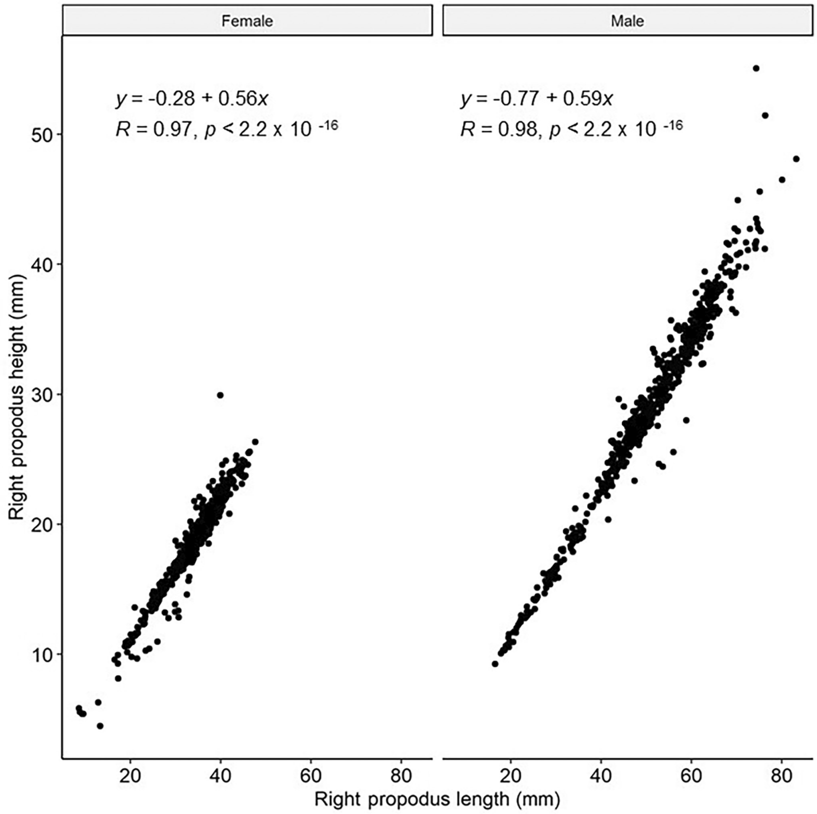

FIGURE A.6 The relationship between right propodus length and right propodus height for female and male brown box crabs.

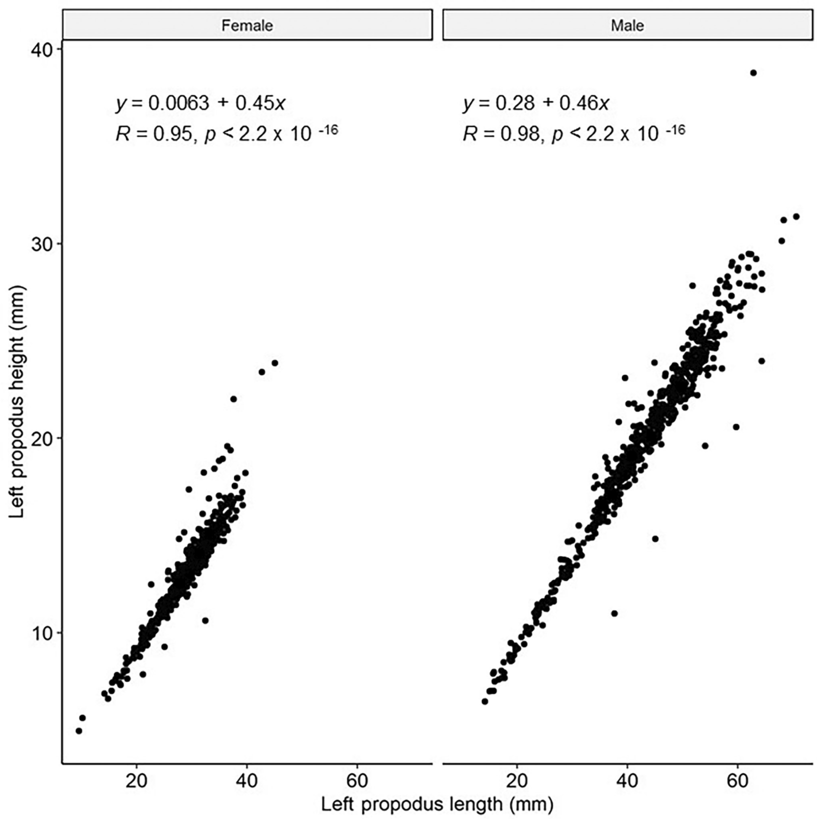

FIGURE A.7 The relationship between left propodus length and left propodus height for female and male brown box crabs.

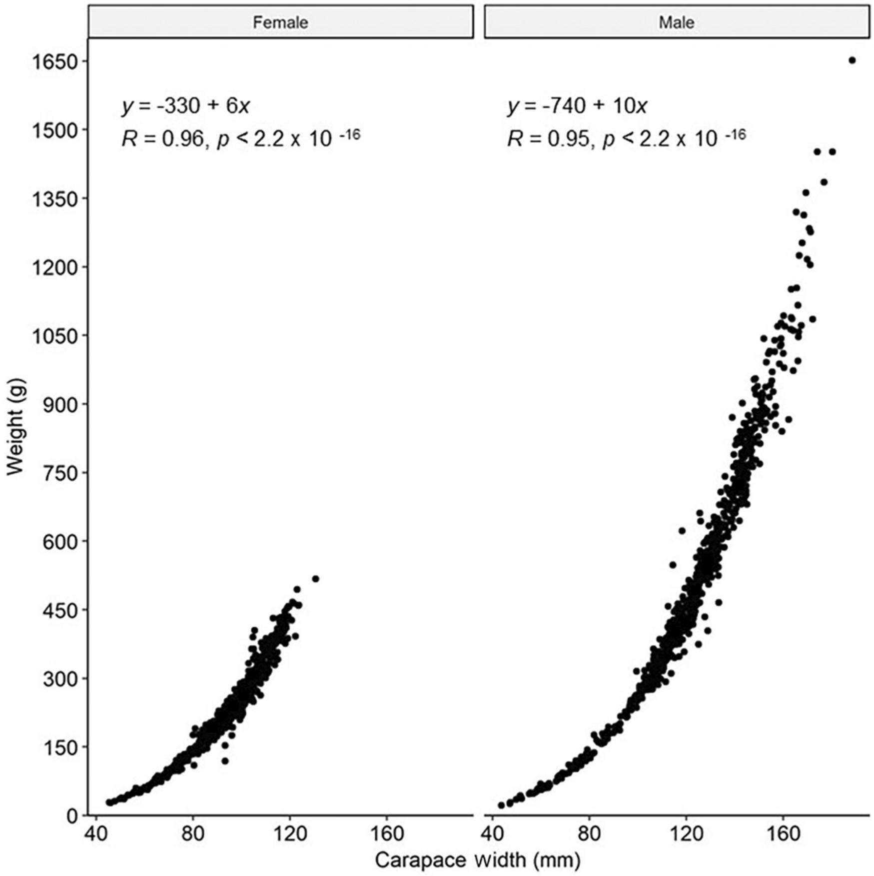

FIGURE A.8 The relationship between carapace width and weight for female and male brown box crabs.