Aspects of the reproductive biology of the North Pacific giant octopus (*Enteroctopus dofleini*) in the Gulf of Alaska

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Abstract—In 2011, octopuses in the Gulf of Alaska were removed from the "other species" group and are now managed by the North Pacific Fishery Management Council as a complex that includes all octopus species within this region. Management of this complex includes the specification of annual catch limits and overfishing limits. Understanding the life history of octopuses is important for establishment of appropriate management strategies. The North Pacific giant octopus (*Enteroctopus dofleini*) is the most abundant octopus species found on the continental shelf and dominates the commercial catch of octopuses within the Gulf of Alaska. Specimens of the North Pacific giant octopus were obtained from charter operations, commercial fishermen, and scientific surveys within the Gulf of Alaska. This species has a protracted reproductive cycle and peak spawning occurs from winter to early spring months. In the Gulf of Alaska, this species matures at weights from 10 to 20 kg; weight at 50% maturity is 13.7 kg (95% confidence interval [CI]=12.5–15.5 kg) for females and 14.2 kg (95% CI=12.6–15.9 kg) for males. Estimates of fecundity for this species range from 41,600 to 239,000 eggs per female and average fecundity is estimated at 106,800 eggs per female. Fecundity was positively related to the weight of the female (n=33, P<0.001). Determination of reproductive parameters is necessary to assess the vulnerability of octopuses within this region to overfishing and to establish appropriate management strategies for this species group within the Gulf of Alaska.

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Recent changes in the management of commercial fisheries in Alaska have included increased monitoring and regulation of several species groups that are not directly targeted but are incidentally taken in fisheries managed by federal and state agencies. An octopus management complex, with its own annual catch limits and overfishing limits was created by the North Pacific Fishery Management Council in 2011 in both the Bering Sea and Gulf of Alaska regions. There is no fishery that directly targets this complex, but octopuses are taken as bycatch in trawl, longline, and pot fisheries throughout Alaska—the majority of catch coming from pot fisheries targeting Pacific cod (*Gadus macrocephalus*) (Sagalkin and Spalinger, 2011; Conners et al., 2012). At least 8 species of octopuses are found within the Gulf of Alaska and are members of this complex, but the North Pacific giant octopus (*Enteroctopus dofleini*) is the most abundant species in continental shelf waters within this region (Jorgensen, 2009; Conners et al., 2012). This species dominates incidental catch of octopuses in commercial fisheries managed by the North Pacific Fishery Management Council and by the state of Alaska (Conners et al., 2012).

The North Pacific giant octopus is found throughout the North Pacific Ocean from Japanese waters to the Aleutian Islands, Bering Sea, and the Gulf of Alaska and in coastal waters in the eastern Pacific as far south as Southern California (Jorgensen, 2009). It is the largest species of octopuss in the world, reaching a maximum size of around 50 kg (Roper et al., 1984). The life expectancy of this species appears to be 4.5 to 5 years on the basis of aquarium studies conducted within the Puget Sound region of Washington state. Like most incirrate octopuses, this species is semelparous and, therefore, females die after a single batch of eggs hatch (High, 1976). This species is estimated to have up to 100,000 eggs per female and a large number of planktotrophic larvae (Kanamaru, 1964; Sato, 1996). Hatchlings have been found to be about 3.5 mm in length (Kubodera, 1991). It has been assumed that females of this species have the ability to store sperm (Kanamaru, 1964), and this phenomenon has been documented in an aquarium setting (Gabe, 1975).

The life history of the North Pacific giant octopus has been examined in other parts of their range, particularly in Japanese waters (Kanamaru, 1964; Kanamaru and Yamashita, 1967; Sano et al., 2011) and in Canadian waters near British Columbia (Gabe, 1975; Robinson, 1983). However, there is a lack of information on the biology and ecology of all octopus species in the Gulf of Alaska. These data are needed to determine bycatch limits and management strategies for octopus species within this region. The objective of this study was to examine the reproductive biology of the North Pacific giant octopus within the Gulf of Alaska, specifically to determine the seasonality of reproduction, size at maturity, and fecundity of this species in this region.

Materials and methods

Maturity stages

Specimens of the North Pacific giant octopus were obtained from the Gulf of Alaska from commercial fishermen during February 2010, the Alaska Fisheries Science Center bottom-trawl survey of the Gulf of Alaska in the summer of 2011, and charter operations near Kodiak Island during the period from May 2010 to December 2011. Octopuses were identified as North Pacific giant octopus on the basis of characteristics presented in Jorgensen (2009). Charter operations occurred within Chiniak Bay and specimens from the bottom-trawl survey were collected at 4 locations in the western and central Gulf of Alaska (Fig. 1). The exact location of specimens donated from commercial fishermen is unknown, but specimens were captured in the Gulf of Alaska near Kodiak Island. A total of 154 specimens were collected. These specimens, including both females (n=71) and males (n=83), ranged in size from 1.2 to 25.2 kg.

All sampled octopuses were weighed, their sex was determined, and their reproductive tracts were removed and weighed. The weight and diameter of each gonad was measured, and the condition of the reproductive tract was noted. Female reproductive structures were examined for the presence of spermatophores or other evidence of mating activity. A 3-stage maturity classification system was developed as part of this study for both male and female North Pacific giant octopuses on the basis of characteristics of the reproductive tract and the presence or absence of well-developed eggs or spermatophores.

On the basis of this classification system, which is a modification of the classification system presented in a report by the Fisheries and Oceans Canada,[1] each specimen was assigned a maturity stage of 1 (immature), 2 (maturing), or 3 (mature). A female was considered immature (stage 1) if it possessed an ovary that was small (diameter ≤65 mm) and white and had eggs not easily visible; maturing (stage 2) if its ovary was larger (diameter 69–90 mm) and had small, white, or pale-yellow eggs; and mature (stage 3) if its ovary was large (≥100 mm) and yellow and the majority of eggs were large (≥5 mm), dark, and yellow. A male was considered immature (stage 1) if its reproductive tract was transparent and undifferentiated, maturing (stage 2) if its reproductive tract contained well-developed accessory structures but had no fully developed spermatophores, and mature (stage 3) if visible and fully developed spermatophores were present within its reproductive tract.

For all specimens, all or part of the gonad was preserved. Thin sections of these tissues were embedded in paraffin and stained through the use of standard histological techniques (Sheehan and Hrapchak, 1980). These sections were used to verify the visual assessment of the gonad and to measure egg size in female octopuses.

Size at maturity

Octopus size at maturity was assessed because aging of cephalopods is difficult (Guerra et al., 2010) and there is no established procedure for aging of the North Pacific giant octopus. Octopus lengths are difficult to measure consistently because of the fluidity of octopus movement and differences found in measurement of live (mantle contracting) and dead (mantle not contracting) octopuses. The weight at maturity of octopuses is generally assessed in studies of octopus biology (Hernández-García et al., 2002). A gonadosomatic index (GSI) was calculated for each octopus sampled by dividing the wet weight of the reproductive tract by the total wet weight of the octopus. A variety of GSI-type indices have been used in octopus reproductive studies (Perez and Haimovici, 1991; Cortez et al., 1995; Quetglas et al., 2005). For this study, the simplest method was chosen. Gonadosomatic index values for both males and females were examined across all size ranges to see if there was a pattern in development.

Weight at 50% maturity (W_{50}) was estimated by fitting the data to the following logistic equation:

$$Y = 1 / (1 + e - (a + bX)),$$

where Y = the proportion of specimens that were mature at weight X;
a and b = parameters of the model; and
X = the weight of the octopus.

This model was chosen because of its wide application in fisheries research and because logistic models are prevalent in recent octopus research (Quetglas et al., 2009; Šifner and Vrgoć, 2009). Parameters were fitted to the logistic equation with a generalized linear

[1] Fisheries and Oceans Canada. 2003. Pacific regions: 2003 experimental harvest guidelines, octopus by dive, January 16, 2003 to July 31, 2003, 21 p. [Available from http://www.dfo-mpo.gc.ca/Library/315447.pdf.]

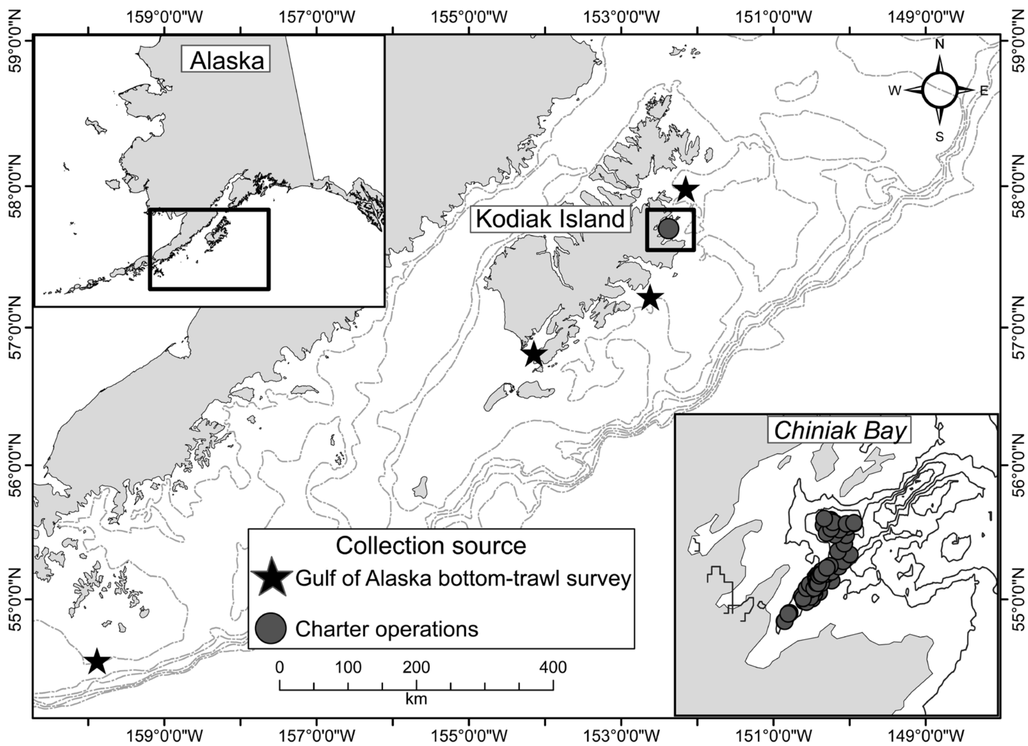

Figure 1

Map of sampling locations where North Pacific giant octopuses (*Enteroctopus dofleini*) were collected during 2010–2011 in the central and western Gulf of Alaska from both charter operations and the bottom-trawl survey conducted by the Alaska Fisheries Science Center in the Gulf of Alaska. The inset on the upper left of the figure shows the location of the sampling area in relation to the state of Alaska. The inset on the lower right of the figure provides greater detail on the locations where octopuses were sampled during charter operations in Chiniak Bay.

model, and the equation was solved for Y=0.5 to yield W_{50}. Bootstrapping methods were used to estimate confidence intervals and the variance of W_{50} (Efron and Tibshirani, 1993). These statistical tests were completed with TIBCO Spotfire S+ statistical software,[2] vers. 8.2 (TIBCO Software, Palo Alto, CA). In addition, for maturing and mature female specimens, the histological sections were examined to determine the longest ova: 5 large ova in each section were measured with a micrometer, and the largest was determined to be the maximum ova length (MOL).

Seasonality

Seasonality of reproduction in this species was examined by noting the presence or absence of spermatophores and well-developed, yolked (stage-3) ovarian eggs during each season of the year. Seasons were defined on the basis of daily measurements of sea-surface temperatures in Chiniak Bay taken at the Kodiak Fisheries Research Center: spring had rising temperatures (April–June), summer had rising temperatures to a maximum (July–September), fall had falling temperatures (October–December), and winter temperatures were steady and coldest (January–March). The GSI values for maturing and mature North Pacific giant octopuses were averaged by season to determine a mean seasonal GSI values for males and females. This seasonal examination of gonad growth was limited to individuals with developing reproductive tracts and, therefore, did not include immature specimens that may remain immature for a period of years. The mean MOL also was determined for each season of the year. A one-way analysis of variance (ANOVA) was used to test for significant differences in GSI and female MOL values during each season of the year. If results were found to significantly differ, the Tukey honest significant difference (HSD) test was used to compare the GSI and MOL values between individual seasons. The ANOVA and Tukey HSD tests were completed with R statistical software, vers. 2.15.1 (R Core Team, 2012).

[2] Reference to trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Fecundity

Fecundity was estimated for stage-2 and stage-3 females with developing eggs within their ovaries. The fecundity of stage-1 females was not examined because of a lack of development of some stage-1 females and the small size of eggs found within the ovaries of these females. For each female classified as stage 2 or 3, a sample that weighed between 1.5 and 3 g was removed from the ovary and all eggs within it were counted with a dissecting microscope. This subsample was used to estimate the total number of eggs within an ovary by applying a gravimetric approach. With this approach, the estimated individual egg weight was used in combination with the weight of the whole ovary to estimate the number of eggs found within each ovary. The relationship between total body weight and fecundity for females was plotted, and an exponential regression line was fitted to the data with R software.

Results

Size at maturity

Female GSI values ranged from <0.001 to 0.083 and overlapped between stages (Fig. 2A). Female North Pacific giant octopuses had MOL values ranging from 0.1 to 8.1 mm. Stage-1 females had MOLs that were <2 mm, stage-2 females had MOLs ranging from 2.6 to 7.8 mm, and stage-3 females had MOLs ranging from 3.6 to 8.1 mm. MOLs of stage-2 females were predominately ≤5.0 mm with one exception, and most MOLs of stage-3 females were >5.0 mm.

Male North Pacific giant octopuses had GSI values that ranged from <0.003 to 0.082 (Fig. 2B). The overlap in GSI values for all stages is a reflection of the large size range of stage-2 males. Many stage-2 males possessed reproductive structures that were well-developed and large but lacked spermatophores. Because spermatophores are necessary for successful mating, these male octopuses were determined to be stage 2. They all appeared to be healthy— without any obvious signs of senescence (reduced body condition or uncoordinated body movements), and we assumed that they had been captured before maturation rather than after mating.

Size at maturity was highly variable for both sexes, but it was particularly so for male North Pacific giant octopuses. The smallest mature male was 7.5 kg, and the largest immature male was 22.5 kg (Fig. 2A). The smallest mature female was 9.2 kg, and the largest immature female was 18.0 kg (Fig. 2B). North Pacific giant octopuses <10 kg tended to be immature, but male and female members of this species in the size range of 10–20 kg were found at all 3 maturity stages. Weight at 50% maturity for males and females fitted the logistic model and was found to be near 14 kg for both sexes, but it was highly variable between individuals (males, W_{50}=14.2 kg, P<0.001, 95% confidence interval [CI]=12.6–15.9 kg; females, W_{50}=13.7 kg, P<0.001, 95% CI=12.5–15.5 kg; Fig. 3).

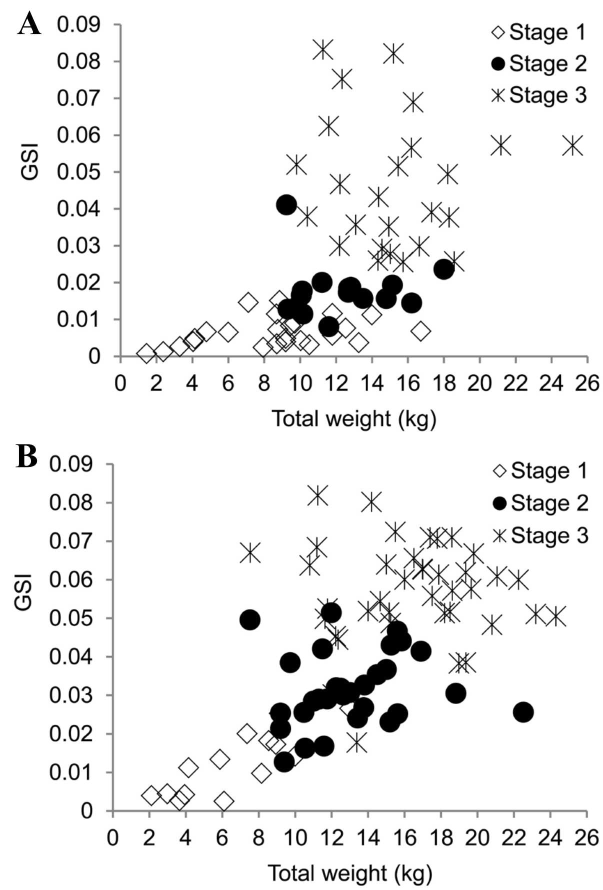

Figure 2

Gonadosomatic index (GSI) by total weight for (**A**) all female specimens and (**B**) all male specimens of the North Pacific giant octopus (*Enteroctopus dofleini*) collected from the central and western Gulf of Alaska in 2010–2011. Values are shown for 3 maturity stages: immature (stage 1), maturing (stage 2), and mature (stage 3).

Seasonality

Mature males and females were observed within each sampling season (Table 1). The seasonal GSI for females peaked in the winter season, was at a minimum during spring months, and increased steadily throughout the summer and fall (Fig. 4A). The seasonal GSI values were significantly different between seasons (P<0.001); significant differences were found between 3 seasonal comparisons: spring and fall (P=0.004); winter and spring (P=0.001); and winter and summer (P=0.011). These results indicate a significant increase

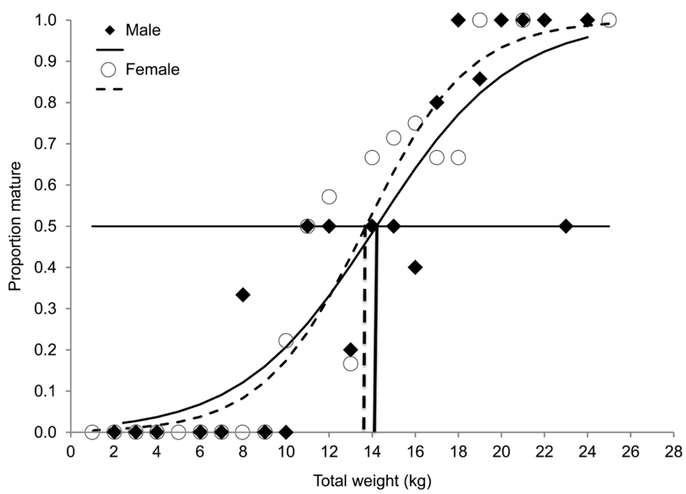

Figure 3

The proportion mature as a function of body weight of male (diamonds) and female (circles) North Pacific giant octopuses (*Enteroctopus dofleini*) collected from the central and western Gulf of Alaska in 2010–11. The vertical lines indicate the weights at which 50% of the males (solid line) and females (dotted line) were mature. The curved lines are the logistic curves fitted to the data for males (dotted line) and females (solid line).

in GSI values during the fall and winter months in comparison with the spring and summer months. The number of samples used in this analysis was small, but these results provide evidence that reproduction for this species is weakly synchronous with a peak in egg development in the coldest months of the year.

A similar pattern is evident in the MOL data, with peak egg size occurring in the fall and winter months. The seasonal MOL values also were significantly different between seasons (P=0.003), with significant differences found between the spring and fall (P=0.002) and the summer and spring (P=0.033). This evidence indicates that the majority of females lay eggs in late winter in this region. Spermatophores or other evidence of mating was not found within female octopuses during any of the sampling periods. These patterns are not found in the males of this species. Male GSI values were highest in winter and spring but did not vary as much as the female values throughout the year (Fig. 4B). The seasonal GSI values for males were not found to be significantly different between seasons (P=0.452).

Fecundity

Estimated fecundity of mature and maturing North Pacific giant octopuses ranged from 41,600 to 239,000 eggs per female and mean fecundity was 106,800 eggs per female (n=33, standard error=7900). There was a positive relationship between fecundity and total weight of female North Pacific giant octopuses, but there was a high amount of individual variability in fecundity (Fig. 5). Exponential regression of fecundity on total weight of female octopuses was highly significant (P<0.001), but the predictive value of this relationship was low, as indicated by a low coefficient of multiple determination (R^2=0.471).

Discussion

Size at maturity

We found that North Pacific giant octopuses in the Gulf of Alaska mature at a size of about 14 kg—a finding similar to results from another study in Japanese waters, a study in which females of this species were estimated to mature at 10–15 kg and males at 7–17 kg (Kanamaru and Yamashita, 1967). Recent research indicated size at maturity of this species is smaller within the Bering Sea, with a calculated W_{50} of 12.8 kg for females and 10.8 kg for males (Brewer[3]). In British Columbia waters, male North Pacific giant octopuses were also found to mature at around 12.5 kg and at a smaller size than females (Robinson, 1983), but that study did not include mature females.

Although our value for weight at 50% maturity was larger for males than for females, male size at maturity was more variable and there were larger

[3] Brewer, R. 2012. Personal commun. Univ. Alaska Fairbanks, Unalaska, AK 99685.

Table 1

Frequency of maturity stage observed during each season of the year for male and female North Pacific giant octopuses (*Enteroctopus dofleini*) captured in the western and central Gulf of Alaska in 2010–11. The spring season was from April to June, the summer season was from July to September, the fall season was from October to December, and the winter season was from January to March.

Season	Immature	Maturing	Mature
Male			
Spring	2	2	13
Summer	8	3	9
Fall	1	11	5
Winter	3	14	12
Female			
Spring	8	4	2
Summer	10	7	4
Fall	2	4	11
Winter	7	2	9

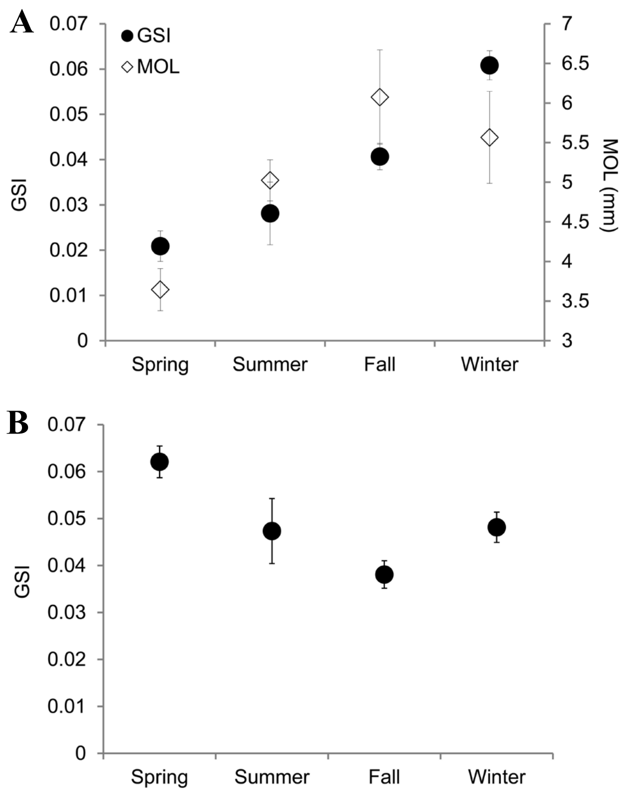

Figure 4

(**A**) Gonadosomatic index (GSI) and maximum ova length (MOL) by season for maturing and mature female specimens of North Pacific giant octopuses (*Enteroctopus dofleini*) and (**B**) GSI by season for maturing and mature male North Pacific giant octopuses. Specimens were collected from the central and western Gulf of Alaska in 2010–2011. Error bars indicate standard error of the mean.

fractions of both small mature males and large immature males. Growth and maturity of this species appear to be quite variable, and regional differences in size at maturity may reflect differences in environmental conditions, food availability, or genetic differences between stocks.

Seasonality

The life history of the North Pacific giant octopus in the Gulf of Alaska is similar to that in Japanese and Canadian waters of the North Pacific Ocean, but the timing of reproductive events is different for members of this species in the Gulf of Alaska. In Japanese waters, this species has been reported to mate during summer and early fall (July–October) and to lay eggs or spawn during fall and winter (October–January) with a 2-month lag between mating and spawning (Kanamaru, 1964). Another study in Japanese waters found that the spawning season occurred in early summer (Sano et al., 2011). In the Bering Sea during a recent study, female development was most advanced in the fall months and male development did not show a seasonal pattern (Brewer[3]). Our study indicates that peak spawning in the Gulf of Alaska occurs during the winter months (January–March). The development of male gonads indicates that mating may peak earlier in the spring months.

Results from our study indicate that mating occurs predominately in the spring and summer months but may be very protracted and occur throughout the year. It is assumed that females of this species are capable of storing sperm. This phenomenon has been documented in an aquarium study of North Pacific giant octopuses in British Columbia (Gabe, 1975) and has been observed in several other octopus species (Joll, 1976; Perez et al., 1990). The seasonal differences in the timing of peak GSI values between male and female North Pacific giant octopuses indicate that storage of sperm may occur in octopuses in the Gulf of Alaska between spring mating and winter spawning. Females of this species appear to lay eggs predominately during winter, although the presence of mature females throughout the year indicates that some spawning may occur during other periods of the year.

This species is found throughout the North Pacific Ocean, but there is little information available about its seasonal movements in Alaska waters. It is, therefore, difficult to interpret how the habitat of these octopuses differs during periods of the year when octopuses are mating and spawning. Japanese studies indicate that North Pacific giant octopuses in waters off of the coast of Hokkaido, Japan, move to deeper waters in summer to mate and move into shallower waters to spawn (Kanamaru, 1964). However, no evidence of a seasonal or directed migration for this species has been found in studies of this species in British Columbia (Hartwick et al., 1984) and south central Alaska (Scheel and Bisson, 2012). Long-term tagging studies are needed to obtain a more complete understanding of the migratory pattern of this species.

Another complicating factor that may contribute to the variability in both size at maturity and seasonality of the reproduction of the North Pacific giant octopus is the complicated stock structure and phylogenetic relationships of this species throughout its range. Three subspecies have been identified on the basis of large geographic ranges and morphological characteristics: *Enteroctopus dofleini dofleini* (far western North Pacific Ocean), *E. dofleini apollyon* (waters near Japan, Bering Sea, Gulf of Alaska), and *E. dofleini martini* (eastern part of range [Pickford, 1964]). A recent genetic study (Toussaint et al., 2012) indicated the presence of a cryptic species of North Pacific giant octopus in Prince William Sound, Alaska, and raises additional questions about the stock structure of this species. More data are needed to define the stock structure of this

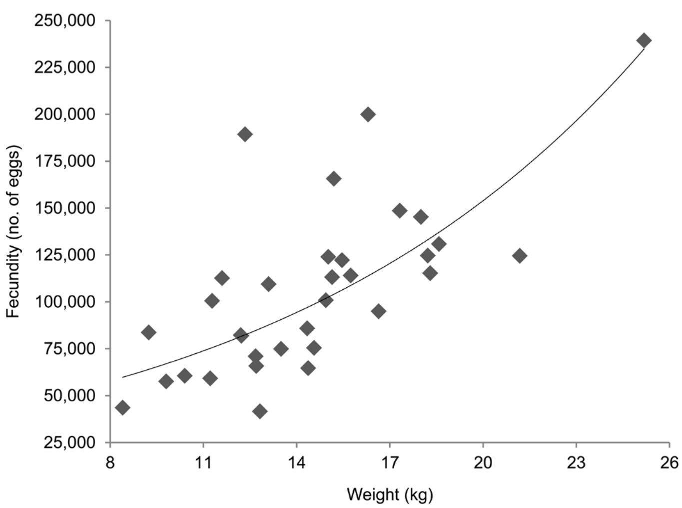

Figure 5

Fecundity, measured as number of eggs per female, by total body weight for North Pacific giant octopuses (*Enteroctopus dofleini*) classified as stage 2 (maturing) and stage 3 (mature) and collected from the central and western Gulf of Alaska during 2010–11. The exponential regression line is presented.

species in Alaska waters, and additional data may aid in reduction of the variability of estimates of reproductive parameters.

Fecundity

Fecundity in the Gulf of Alaska was found to be greater than previously reported for this species, although results of this study did have some overlap with values reported from studies in Canada and Japan. The fecundity of this species in Japanese waters has been estimated to be from 30,000 to 100,000 eggs per female (Kanamaru, 1964; Mottet, 1975; Sato, 1996). Gabe (1975) estimated a female in captivity in British Columbia had a realized fecundity of 35,000 eggs. We found higher mean fecundity values of 106,800 eggs per female in the Gulf of Alaska and these values had a significant positive relationship with the overall weight of the female. The values of fecundity from our study and the Japanese studies were estimates of potential fecundity and did not account for any losses that may have occurred because of either atresia or eggs not released by a female. Realized or actual fecundity will be smaller than these values, although, for a semelparous species, the difference may not be significant. The high fecundity of the North Pacific giant octopus, in combination with its short life span and relatively fast growth rate (High, 1976), indicates a potentially high rate of population productivity. However, commercial harvest should be managed conservatively because of a lack of knowledge about a variety of population parameters for this species in Alaska waters, including recruitment rates, abundance, movement, and natural mortality.

Conclusions

This study improves our understanding of the reproductive biology of the North Pacific giant octopus in the Gulf of Alaska. The weight at maturity of about 14 kg for both males and females is larger than values reported for this species within other regions of the North Pacific Ocean. The seasonality of reproduction also appears to be somewhat different in the Gulf of Alaska as well, where reproductive events occur a few months later than they do in Japanese waters. We also found higher fecundity for this species in this region. These data will aid in the management of this species complex and will be particularly important in guiding management decisions if fisheries for octopuses develop within the Gulf of Alaska.

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