Reproductive biology of two commercially exploited skates, *Raja binoculata* and *R. rhina*, in the western Gulf of Alaska

David A. Ebert [a,*], Wade D. Smith [a,b], Gregor M. Cailliet [a]

[a] *Pacific Shark Research Center, Moss Landing Marine Laboratories, 8272 Moss Landing Road, Moss Landing, CA 95039, USA*
[b] *Oregon State University, Dept. of Fisheries and Wildlife, 104 Nash Hall, Corvallis, OR 97331, USA*

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ABSTRACT

This study provides the first detailed information on the reproductive biology of two large and abundant eastern North Pacific Ocean skate species: big skate (*Raja binoculata*) and longnose skate (*Raja rhina*). Skates were collected in the western Gulf of Alaska during 2005 and 2006 after a targeted fishery for these two species developed around Kodiak Island, Alaska; both species are also taken as by-catch to other fisheries. A total of 307 females (20.1–183.3 cm TL) and 138 males (19.5–143.7 cm TL) *R. binoculata*, and 354 females (18.1–145.0 cm TL) and 318 males (21.1–135.8 cm TL) *R. rhina* were collected. Female *R. binoculata* were found to attain first (e.g., smallest individual) maturity at 125.8 cm TL and 50% at 148.6 cm TL. Males were found to attain first and 50% maturity at 124.0 and 119.2 cm TL, respectively. No gravid female *R. binoculata*, with egg cases *in utero*, were encountered during the study. Female *R. rhina* were found to attain first and 50% maturity at 102.2 and 113.1 cm TL, respectively. Gravid female *R. rhina*, with egg cases *in utero*, were recorded throughout the sampling period. Males attained first maturity at 101.0 cm TL and 50% maturity at 102.9 cm TL. Histological analysis did not reveal significant changes in spermatocyst production for either species during the sampling period. Both species appear to be reproductively active year-round as no seasonal cycle was evident. This study provides new and essential information on the reproductive biology of these two commercially targeted skate species.

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1. Introduction

The life histories and population status of skates have become an area of rapidly growing interest because of their prevalence as bycatch in groundfish fisheries throughout the world (Walker and Heesen, 1996; Walker and Hislop, 1998; Stevens et al., 2000; Gaichas et al., 2003; Raje, 2006; Tamini et al., 2006). They are especially vulnerable to trawl fisheries because of their large size and demersal life-style. In addition, skates may exhibit life history characteristics, e.g., slow growth, late attainment of sexual maturity, which may make them particularly vulnerable to over-exploitation (Holden, 1974; Jennings et al., 1998). An example of skate susceptibility to fishing pressure is highlighted in the North Atlantic, where increased mortality has dramatically altered the relative abundance and population structure of North Sea skates (Walker and Hislop, 1998; Dulvy et al., 2000; Frisk et al., 2002). Mortality of discarded skates and rays from trawl fisheries may be high, ranging between 41% and 65% (Stobutzki et al., 2002; Laptikhovsky, 2004). Because skate species are often discretely distributed and vary widely in

length and age at maturity, populations may be differentially susceptible to exploitation and the potential for altering abundance and population structure may be great (Walker and Hislop, 1998; Dulvy and Reynolds, 2002).

In Alaskan waters, skate landings greatly exceed those of all other North American states combined. During 2005, an estimated 23,000 metric tons of skates, most of it discarded, were taken as bycatch in Alaskan groundfish fisheries in the Bering Sea and Aleutian Islands (Matta et al., 2006). Little, however, is known about the life histories of the local fauna or the impact of fishery exploitation on these species. Prior to 2005, only two skate species were recognized in National Marine Fisheries Service, Alaska Fisheries Science Center (NMFS-AFSC) taxonomic categories for landings statistics, and fishery observers had only identified skates to gross taxa ("skate unidentified") (Gaichas et al., 2005; Matta et al., 2006). Current and historic species composition and relative abundance of skate landings are therefore essentially unknown.

Incidental capture and landings of Alaskan skates have increased in recent years and in 2003, a directed fishery for two species, the big (*Raja binoculata*) and longnose (*Raja rhina*) skates developed in the Gulf of Alaska (GOA) off Kodiak Island (NPFMC, 1999; Gaichas et al., 2003). Despite precautionary management of this incipient fishery (Matta et al., 2006), it is likely that directed fisheries for
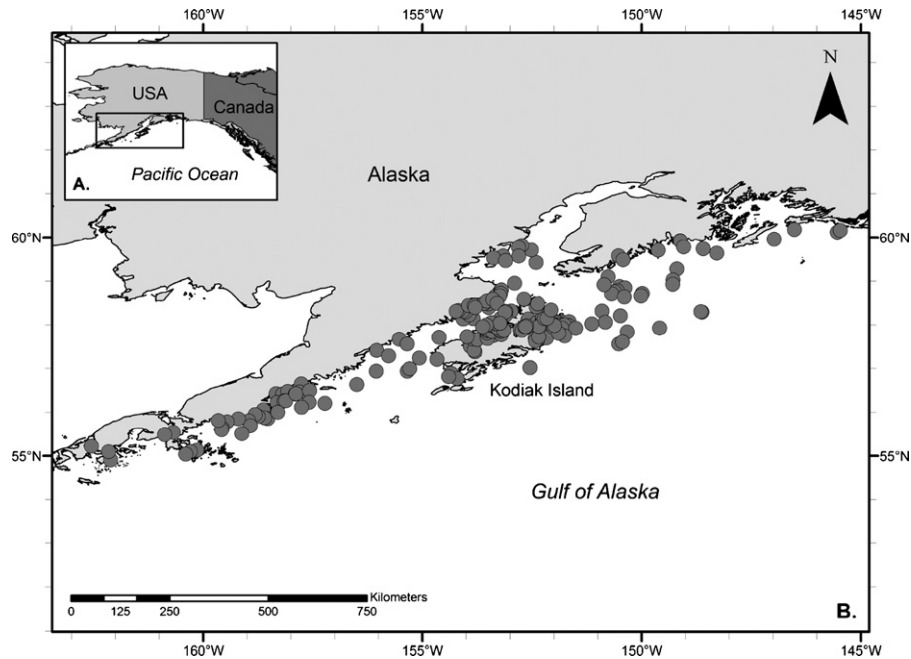
Fig. 1. Areas sampled within the Gulf of Alaska.

skates are likely to expand in other areas of Alaska in response to the relatively large take and amount of currently unutilized biomass. Given the paucity of published life history information, increasing bycatch concerns, and the likelihood of an expanding directed fishery, we investigated the reproductive biology of *R. binoculata* and *R. rhina*, in the GOA to provide critical details necessary for developing population assessments of these exploited species.

2. Materials and methods

2.1. Data collection

Skates were collected between April and September of 2005 and 2006 from surveys conducted by the Alaska Department of Fish and Game and the NMFS-AFSC in the western GOA. The survey area extended from along the Alaskan Peninsula to Kamishak Bay and eastwards to the Kenai Peninsula (Fig. 1). Much of the survey effort was concentrated around Kodiak Island where the fishery was centered. Samples were also obtained from specimens landed on Kodiak Island.

Morphological measurements taken at the time of collection included sex, maturity, total length (TL), disc width (DW), and weight (W). Measurements for TL and DW were made to the nearest millimeter (mm) in a straight line with the skate lying in its natural position from the snout tip to the tail tip. The relationship between TL and DW is described (Table 1) by the equation: $DW = aTL^b$, where DW is the disc width, TL the total length, and a and b are fitted constants (Ricker, 1973). Weights were taken to the nearest 0.1 kg and the relationship between TL and W was also described (Table 1) by the equation $W = aTL^b$,

where W is the weight, TL the total length, and a and b are fitted constants (Ricker, 1973). Additional biological measurements taken included: inner clasper length on males as measured from the point of insertion of the clasper shaft to the clasper tip and for females the width of the oviducal gland, and maximum ova width.

2.2. Maturity determination

Maturity status was assessed by visual inspection of the reproductive organs following Ebert (2005). Three reproductive classifications were determined for each sex: juvenile, adolescent, and adult. Changes in the reproductive organs, e.g., clasper length and oviducal gland width, as measured to the nearest mm and plotted against TL, were used to further assess the onset of maturity. A sharp increase in growth of each structure relative to TL was determined to correspond to the onset of maturity, followed by a slowing of growth, which was assumed to correspond with full maturation of the individual. Males were considered to be adult when the claspers were elongated and the terminal cartilage elements were calcified. Adolescent individuals are those whose claspers extend beyond the posterior edge of the pelvic fins, but lack calcification of the terminal cartilage elements. Juveniles had short, flexible claspers that did not extend beyond the posterior edge of the pelvic fins. Internally, coiling of the epididymides and testes development were also good indicators of maturation. Females were determined to be mature by the presence of large, vitellogenic mature ova, an oviducal gland that was distinctly differentiated from the uterus, and the posterior portion of the uteri were pendulous. The number of mature ova per ovary was also recorded from mature females. Adolescent individuals had smaller

Table 1
The TL–DW and TL–W equations for *Raja binoculata* and *R. rhina*

Species	n	TL to DW equation	r^2	n	TL to W equation	r^2
Raja binoculata	438	DW = 0.7393(TL) + 2.4974	0.98	143	$W = (5 \times 10^{-6})TL^{3.1064}$	0.99
Raja rhina	527	DW = 0.6946(TL) + 1.4049	0.99	153	$W = (4 \times 10^{-6})TL^{3.091}$	0.98
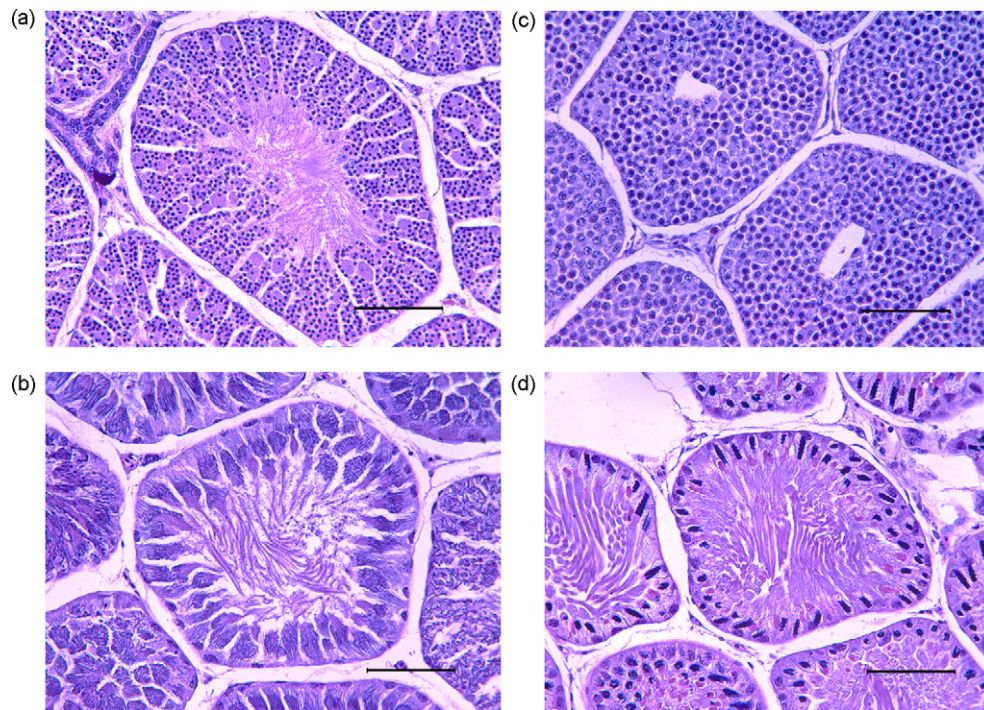
Fig. 2. Stages III–VI of spermatogenesis used to classify spermatocysts in skate testes at 200× magnification. Classification follows Maruska et al. (1996): (a) stage III spermatocytes; (b) stage IV spermatids; (c) stage V immature spermatozoa; and (d) stage VI mature spermatocysts. Bar = 100 μm.

ovaries, with some differentiation, but lacked mature ova. The oviducal gland was undeveloped and the uteri were narrow and constricted. Juveniles lacked any differentiation of the ovaries, and the oviducal gland was not differentiated from the uterus (Ebert, 2005).

2.3. Histology

Histological assays of male reproductive tracts were conducted to examine potential seasonal changes in the reproductive cycle and to verify macroscopic maturity assessments of each skate species. Sections (3–4 mm thick) of fixed testes were removed from preserved reproductive tracts, placed in tissue cassettes for sectioning, and stored in 70% ethanol. Gonad sections were shipped to the University of New Hampshire and Louisiana State University veterinary laboratories for processing using standard hematoxylin and eosin staining (e.g., Maruska et al., 1996). Maturity stages of sperm in the testes were evaluated for samples from each available month. Prepared slides were then examined under a compound microscope. The developmental stages of spermatogenesis have been well described for several elasmobranch groups, including skates, and hormonal analysis have confirmed that spermatocyst and spermatid stages are associated with reproductive readiness (Heupel et al., 1999; Sulikowski et al., 2004). Therefore, we concentrated on these specific stages: stage III, spermatocytes; stage IV, spermatids; stage V, immature spermatozoa; stage VI, mature spermatocysts (Fig. 2; Maruska et al., 1996; Conrath and Musick, 2002). Stage VII, consisting of empty spermatocysts and free spermatogonia, were considered mature and combined with stage VI estimates. Mean proportion of mature spermatocysts was estimated along a transect crossing a full, representative section of testis lobe. The tightness and organization of sperm packets in the spermatocysts were used to determine maturity (Sulikowski et al., 2005a,b). The mean proportion of testes occupied by each stage per month was compared to discern any seasonal pattern in testis development.

2.4. Data analyses

Size at maturity was determined using maturity ogives. Median TL at 50% maturity was estimated by fitting binomial maturity (0 = immature; 1 = mature) to length data (Mollet et al., 2000). Maturity data were binned into 5 cm TL size classes. Males and females were analyzed separately for each species. A logistic equation was fitted using least squares non-linear regression and SigmaPlot graphical software (SPSS Inc., version 8.0, Chicago, IL) in the following form:

$$Y = \frac{1}{(1 + e^{-(a+bx)})}$$

where Y is the maturity status and x is the TL in cm. Median TL at 50% maturity was calculated as $-a/b$.

Ovulation cycles may be detected by comparing ova size among months in mature females (Conrath, 2004). In females, all mature ova visible on the surface of each ovary were enumerated, and the diameter of the largest ovum was measured to the nearest mm. Mature ova were characterized by their yolky appearance and size, typically exceeded 10 mm in diameter (Ebert, 2005). To discern any peaks in reproductive activity, mean maximum ova diameter and number of mature ova were plotted against month of capture. Differences between months in maximum ova diameter and number of mature ova were each tested using one-way ANOVA or non-parametric Kruskal–Wallis tests (Zar, 1999).

3. Results

3.1. R. binoculata

A total of 307 females ranging in size from 20.1 to 183.3 cm TL was sampled (Fig. 3a). Female *R. binoculata* attained greater lengths, including length at maturity, than males. A gradual increase in the relationships between the width of female reproductive organs
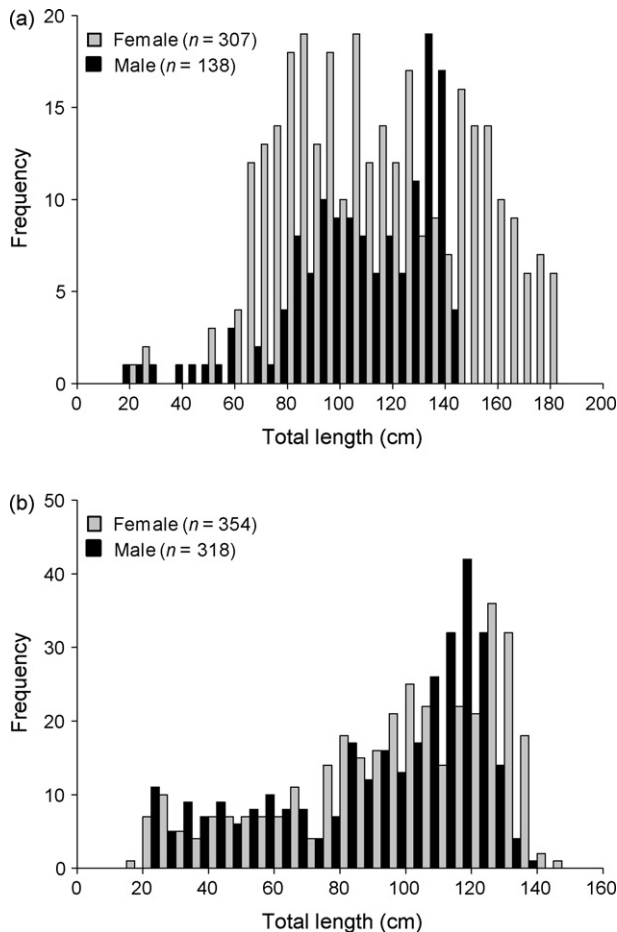
Fig. 3. Length frequency distribution of female ($n = 307$) and male ($n = 138$) *Raja binoculata* (a) and female ($n = 354$) and male ($n = 318$) *Raja rhina* (b) examined between 2004 and 2006. Female specimens are represented by grey bars and male specimens by black bars.

and TL generally coincided with the onset of maturity. A gradual increase in the relationship between oviducal gland width and TL was observed at approximately 100 cm TL (Fig. 4a). Oviducal gland widths of mature individuals ranged from approximately 50 to 125 mm. Uterus widths increased markedly among specimens in excess of 140 cm TL, but were also associated with high variability among specimens (Fig. 4b). Considerable overlap was observed among maturity groups based on their maturity classifications, and both oviducal gland and uterus widths in relation to TL. The smallest mature individual measured 117.5 cm TL and the largest immature was 163.6 cm TL. All females >164.0 cm TL were considered to be mature. Total length at 50% maturity was estimated at 148.6 cm (Fig. 5a). First maturity and 50% maturity were estimated to occur at 68.6% and 81.1%, respectively, of the maximum TL observed in this study. An insufficient sample size of adult females precluded determining whether monthly changes in maximum ovarian diameter occurred and estimating ovarian fecundity. No gravid females were observed.

A total of 138 males ranging in size from 19.5 to 143.7 cm TL was sampled (Fig. 3a). A gradual increase in the proportion of clasper length to TL was evident between approximately 99 and 119 cm TL indicating the onset of male sexual maturity in male *R. binoculata* (Fig. 6a). Mature males were found to have clasper lengths that exceeded 200 mm. Clasper length for specimens classified as juveniles did not exceed 100 mm. The smallest mature individual measured 124.0 cm TL and the largest immature was 126.1 cm TL.

All males >127.0 cm TL were considered to be mature. Total length at 50% maturity was estimated at 119.2 cm (Fig. 5a). First maturity and 50% maturity were estimated to occur at 86.3% and 83.0%, respectively, of the maximum TL observed in this study.

Testis samples for histological analysis of *R. binoculata* were collected from 3 months: April, August, and September. Examination of histological stages III–VI of spermatogenesis did not reveal any significant differences in the relative proportion of these four stages among the 3 months sampled (Fig. 7a). The production and maintenance of mature spermatocysts within the testes appears to persist during these 3 months. There did not appear to be any notable reduction of mature spermatocysts between the spring (April) and late summer (August and September) months. The percentage increase in mature spermatocysts corresponded closely with clasper development (Fig. 7a).

3.2. R. rhina

A total of 354 females ranging in size from 18.1 to 145.0 cm TL was sampled (Fig. 3b). Females were found to attain first maturity at about the same TL as males. The smallest mature individual measured 102.2 cm TL and the largest immature was 137.1 cm TL. Oviducal gland width and uterus width to TL relationships revealed sharp increases in size of these reproductive organs at or near 110 cm TL (Fig. 4c). Oviducal gland widths measuring approximately ≥40 mm were among those females that were assigned a maturity status of adults. Greater variability among uterus width to TL and maturity status was more evident than that observed within oviducal gland width to TL relationships. A range of uterine widths of 4 mm to greater than 70 mm was recorded among adult females. Differences among uterus widths between juveniles and adolescents were minimal (Fig. 4d). Total length at 50% maturity was estimated at 113.1 cm (Fig. 5b), a length slightly greater than that observed for males. First maturity and 50% maturity were estimated to occur at 70.5% and 78.0%, respectively, of the maximum TL recorded in this study.

No trend was detected between maximum ovarian diameter and month (Fig. 8a). Average maximum ova diameter values were largest among June specimens. However, variance among specimens and months was high. Among the 74 mature females examined, maximum ovum diameters ranged from 10 to 57 mm in diameter. Mature ova were observed in females during all months sampled.

No trend was observed between maximum ovarian fecundity and female TL (Fig. 8b). Ovarian ova were frequently damaged during collection or as a result of extended periods of time following specimen capture and processing, limiting the number of specimens from which accurate counts could be obtained to 49 individuals. Maximum average ovarian fecundity was highly variable among months. Counts ranged from 2 to 61 ova. Examination of 74 adult females revealed 21 (28.4%) to contain egg cases *in utero*.

A total of 318 males ranging in size from 21.1 to 135.8 cm TL was sampled (Fig. 3b). A notable upward trend in the clasper length to TL relationship occurred at about 105 cm TL, indicating the onset of maturity (Fig. 6b). Individuals classified as adults had clasper lengths measuring >250 mm. Overlap in the clasper length of adults, adolescents, and juveniles were evident between 70 and 110 mm. The smallest mature individual measured 93.0 cm TL and the largest immature was 118.6 cm TL. All males >120.0 cm TL were considered to be mature. Total length at 50% maturity was estimated at 102.9 cm (Fig. 5b). First maturity and 50% maturity were estimated to occur at 74.4% and 75.8%, respectively, of the maximum TL observed in this study.

Testis samples for histological analysis of *R. rhina* were collected from 5 months, between April and September. Examination of his-
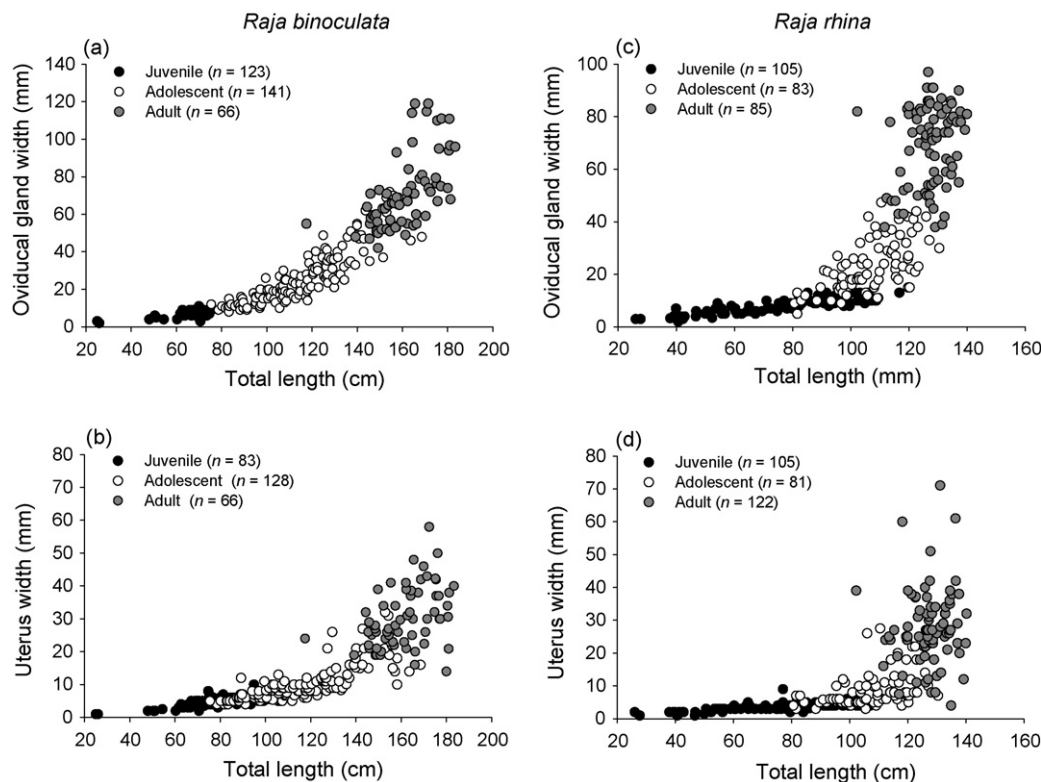
Fig. 4. Relationships between oviducal gland width (a and c) and uterus width (b and d) and total length based on reproductive classifications of *Raja binoculata* and *Raja rhina*.
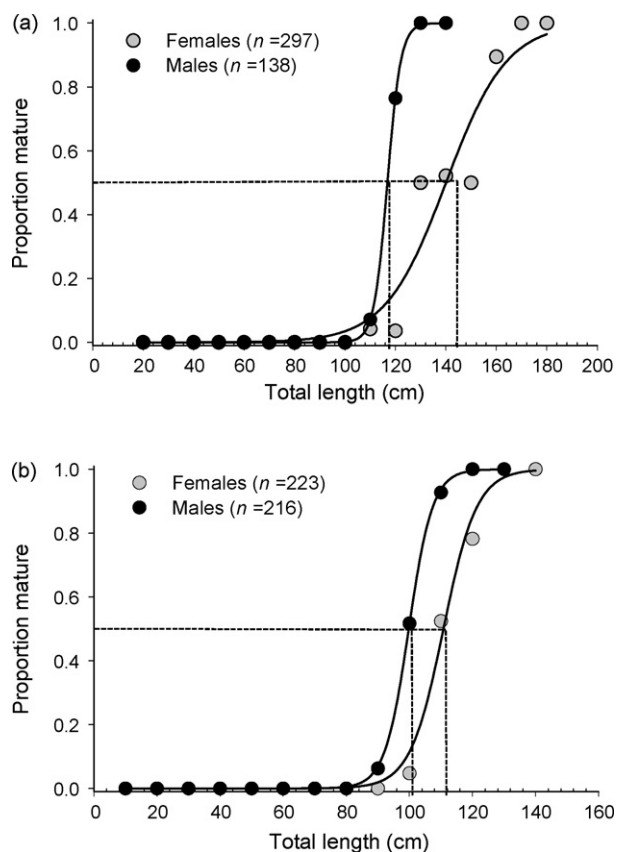

Fig. 5. Estimated median size at maturity for female and male *Raja binoculata* (a) and *Raja rhina* (b).

tological stages III–VI of spermatogenesis did not reveal any notable change in the relative proportion of these four stages among the 5 months sampled (Fig. 9a). The production and maintenance of mature spermatocysts within the testes appears to persist throughout the spring and summer, with no notable changes among those examined. The increase in the proportion of mature spermatocysts occurred primarily in those individuals over 100 cm TL and appeared to mirror development of the claspers (Fig. 9b).

4. Discussion

R. binoculata is generally considered the largest skate species occurring in the eastern North Pacific with an estimated maximum TL of 240 cm (Mecklenburg et al., 2002; Ebert, 2003). The maximum TL reported for *R. binoculata* is comparable to that of some of the largest known extant skate species, including *Dipturus batis*, *Dipturus innominatus*, *Dipturus trachyderma*, and *Rostroraja alba*, each known to reach a maximum TL of 240 cm or more (Stehmann and Bürkel, 1984; Cox and Francis, 1997; Licandeo et al., 2007; Ebert et al., 2008). However, to the best of our knowledge, there are no verifiable records of *R. binoculata* specimens attaining this length. The maximum confirmed TL of this species is 203.9 cm for females and 183.6 cm for males (McFarlane and King, 2006); both documented from specimens captured in the waters off British Columbia (BC), Canada. The maximum TL observed in the present study, although less than those found in BC waters, was similar to the maximum TL reported from central California (Zeiner and Wolf, 1993) and the western GOA (Gburski et al., 2007).

The maximum TL for *R. rhina* examined in this study slightly exceeded the previously reported maximum size for males and females of this species (Gburski et al., 2007; Stevenson et al., 2007). Maximum TL was 135.8 and 145.0 cm for male and female *R. rhina*, respectively, slightly exceeding the 129.0 and 142.0 cm TL for males
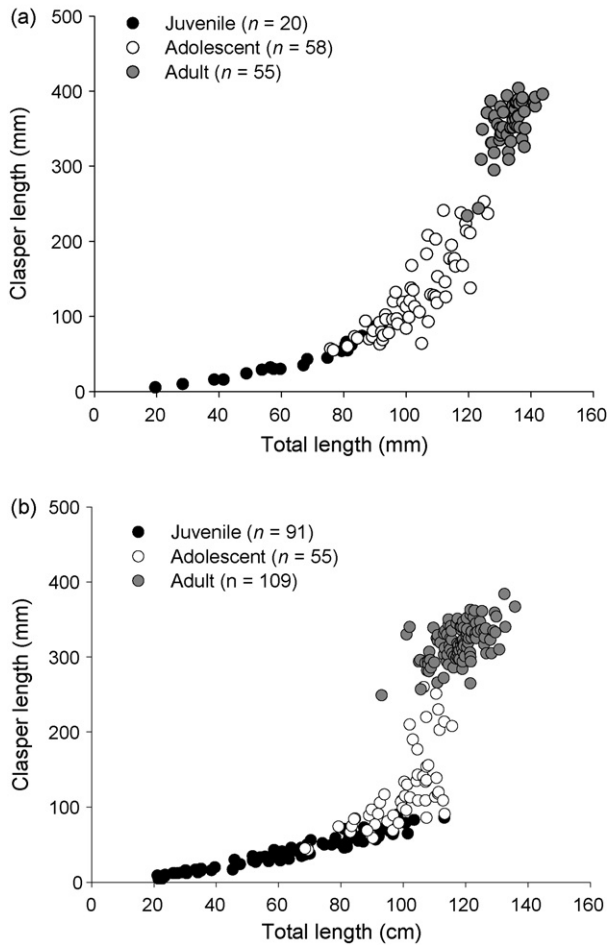
Fig. 6. . Relationships between clasper length and total length for *Raja binoculata* (a) and *Raja rhina* (b).

phism in maximum TL among medium sized and smaller skates is in contrast to the typical pattern among elasmobranchs for females to attain greater sizes than males (Cortés, 2000). Indeed, there is a growing body of evidence that suggests such size differentials do not hold for many oviparous species. Males and females of most scyliorhinid sharks (family Scyliorhinidae), for example, also grow to approximately the same maximum TL, or in some cases, the males attain a larger maximum TL (Ebert et al., 2006; Flammang et al., 2008).

Previous details on the reproductive biology of *R. binoculata* are sparse, and comparisons with other studies of relatively low sample sizes provide differing perspectives on sizes at maturity. McFarlane and King (2006) reported first maturity and 50% maturity for females and males as 60.0, 90.0, 50.0, and 72.0 cm TL, respectively, from BC. In contrast, we found first maturity of females (125.8 cm TL) and males (124.0 cm TL) to occur at much greater sizes. Among females, notable increases in oviducal gland width and uterus width did not occur until specimens attained total lengths in excess of 100.0 cm. Similarly, a shift in clasper length and the presence of mature spermatocysts within the testes were not apparent in specimens <115 cm TL. However, few mature fish were obtained from the GOA, and the resulting estimate of 50% maturity was less than the size of the smallest mature male. In a study of *R. binoculata* from central California, Zeiner and Wolf (1993) reported sizes at first maturity of approximately 129.0 and 100.0 cm TL for females and males, respectively. The maturity estimates of Gburski et al. (2007) also indicate maturation at much smaller sizes in BC than off the central California coast or from the GOA, a trend that is opposite of most reported latitudinal differences in maturity (e.g., Templeman, 1987; Frisk and Miller, 2006). These inconsistencies
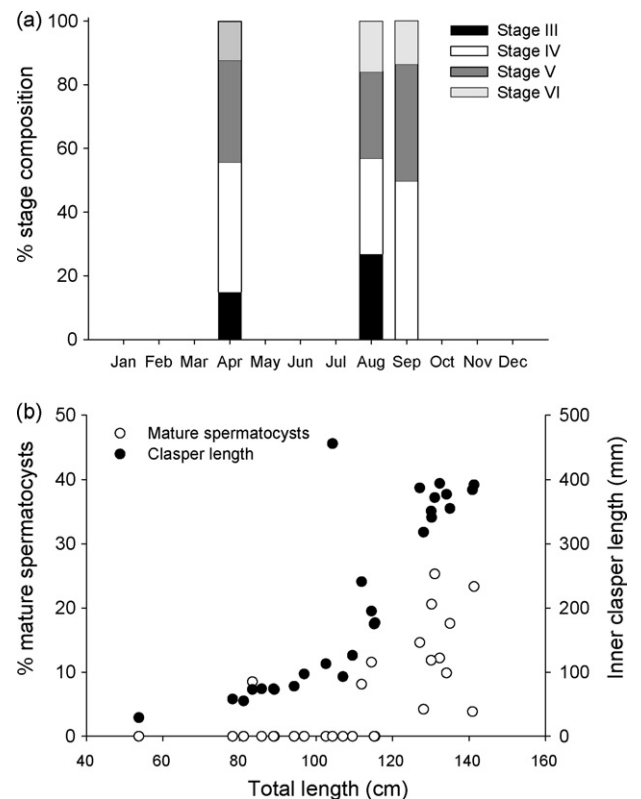
and females reported by Gburski et al. (2007) from the United States (US) west coast. Other studies have found maximum sizes of 122.0 cm TL for males and 124.6 cm TL for females from BC (McFarlane and King, 2006) and as 132.2 and 106.8 cm TL for males and females, respectively, from central California (Zeiner and Wolf, 1993). Ebert (2003) noted a maximum length of 105 cm for males and 137 cm for females from California waters. Stevenson et al. (2007) reported an unconfirmed maximum TL of 180 cm for this species, but stated it was unverified.

The smallest free swimming neonates of both *R. binoculata* (19.5 cm TL) and *R. rhina* (18.1 cm TL) observed in this study were comparable to the smallest individuals found from BC and southwards along the US west coast (McFarlane and King, 2006; Gburski et al., 2007). These sizes correspond to the estimated size at birth for *R. binoculata* as 18–23 cm TL and for *R. rhina* as 12–17 cm TL (DeLacy and Chapman, 1935; Hitz, 1964; Ebert, 2003).

The maximum observed TL of the two species studied revealed greater size disparity between male and female *R. binoculata* (39.6 cm), than between male and female *R. rhina* (9.2 cm). The similarity in maximum sizes for both sexes in *R. rhina* is consistent with the findings of other studies whereby male and female small to medium sized skates (<150 cm maximum TL) grow to approximately the same lengths (Templeman, 1987; Braccini and Chiaramonte, 2002; Mabragaña and Cousseau, 2004; Ebert, 2005; Ebert et al., 2008). Conversely, those species that exceed 150 cm TL tend to have substantial size differentials between the sexes (Francis et al., 2001; Ebert et al., 2008). This lack of sexual dimor-

Fig. 7. Monthly changes in spermatogenesis in male *Raja binoculata* (a). The percent stage composition is the mean proportion of each stage occupied along a transect line across one representative full lobe cross section of a testes, and expressed as the mean. Relationship between the proportion of mature spermatocysts, clasper length, and total length in *Raja binoculata* (*n* = 26) (b).
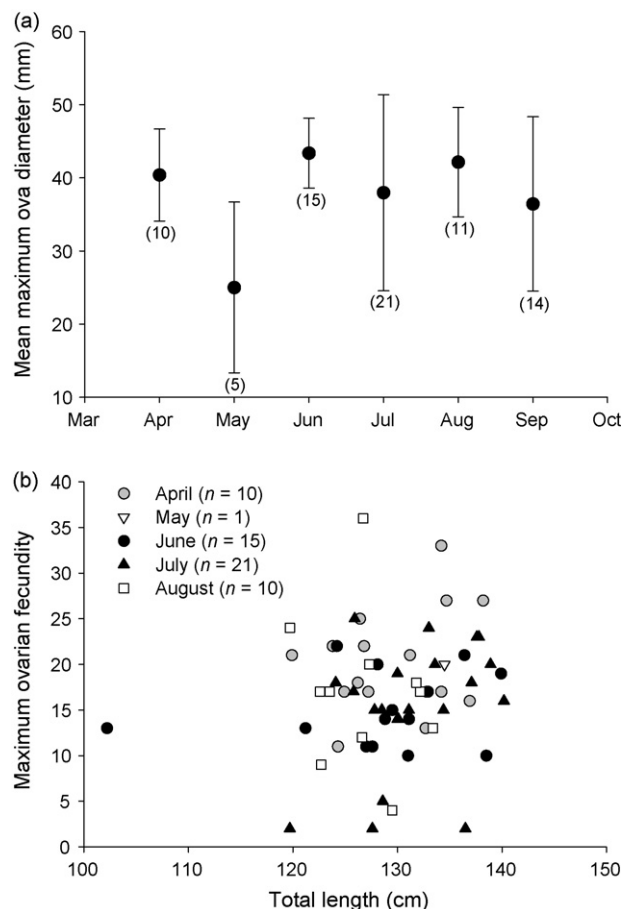
Fig. 8. Relationship between mean maximum ova diameter and month ($n = 74$) (a) and maximum number of mature ova recorded by total length and month for mature *Raja rhina* (b). Error bars represent ±one standard deviation. Counts of mature ova were summed from both ovaries.

may have arisen due to differing criteria for reproductive classifications, relatively small sample sizes, or regional environmental differences. Further research is required to clarify potential regional differences in maturation and improve our knowledge of the reproductive biology of this species.

Regional differences in the size at first and 50% maturity were also evident for *R. rhina*. Off central California, the onset of maturity in male *R. rhina* is reported to occur at 61.5 cm TL and for females >130.0 cm TL (Zeiner and Wolf, 1993). McFarlane and King (2006) calculated 50% maturity as 83.0 cm TL for females and 65.0 cm for males. These estimates are considerably less than the 50% maturity estimates of 113.1 cm TL for females and 102.0 cm TL for males determined in this study, but agree with our observation that female *R. rhina* mature at greater sizes than males. Because maturity ogives were not calculated by Zeiner and Wolf (1993), 50% maturity cannot be statistically compared between these regions. Sizes at first maturity and 50% maturity indicate greater sizes of maturity in general for *R. rhina* in the GOA. As observed for *R. binoculata*, these observed latitudinal differences in maturity may have been influenced by differing criteria for reproductive classifications, sample sizes, or the sample size range. Also, this latitudinal increase in body size may be due to biological influences.

Histological analysis of gonads has been used to corroborate maturity stages determined by morphological examination in several species (Sulikowski et al., 2006, 2007). The increase in clasper size relative to TL corresponded with the increase in mature spermatocysts in males of both species. A slight lag occurred as claspers

developed more gradually than the spermatocysts. This observation is in agreement with those of Sulikowski et al. (2005b, 2006, 2007) for skates from the Gulf of Maine.

Skates display three types of reproductive cycles: (1) reproductively active throughout the year; (2) a partially defined annual cycle with one or two peaks; and (3) a well-defined annual or biennial cycle (Holden, 1975; Mabragaña et al., 2002; Ebert et al., 2008). The absence of gravid *R. binoculata* in our samples and a limited number of mature specimens in general constrains our ability to assess reproductive seasonality in this species. Segregation by size and sex is common among elasmobranchs (Springer, 1967), and the lack of gravid females within the study area may be reflective of segregation or indicate a broader movement pattern or differential habitat use by adults of this species. Data on reproductive seasonality for *R. rhina* were inconclusive, but suggest an extended reproductive season lasting at least 6 months, if not the occurrence of egg deposition throughout the year. Mature ova and sperm were found in *R. rhina* during all months sampled. There did not appear to be any definitive peaks in reproductive activity during the months sampled. Although, Sulikowski et al. (2007) did not find egg cases in all months, *Malacoraja senta* was considered to be reproductively capable year-round using the criteria of minimum ovum diameter and oviducal weight, as well as synchronicity of mature sperm with percent gravid females per month. Additional sampling is needed to confirm these observed reproductive trends during the remainder of the year. Expanded histological analyses or hormonal assays may be necessary to further evaluate the reproductive cycles of these species (Parsons and Grier, 1992; Tricas et al., 2000; Sulikowski et al., 2005b; Awruch et al., 2008).
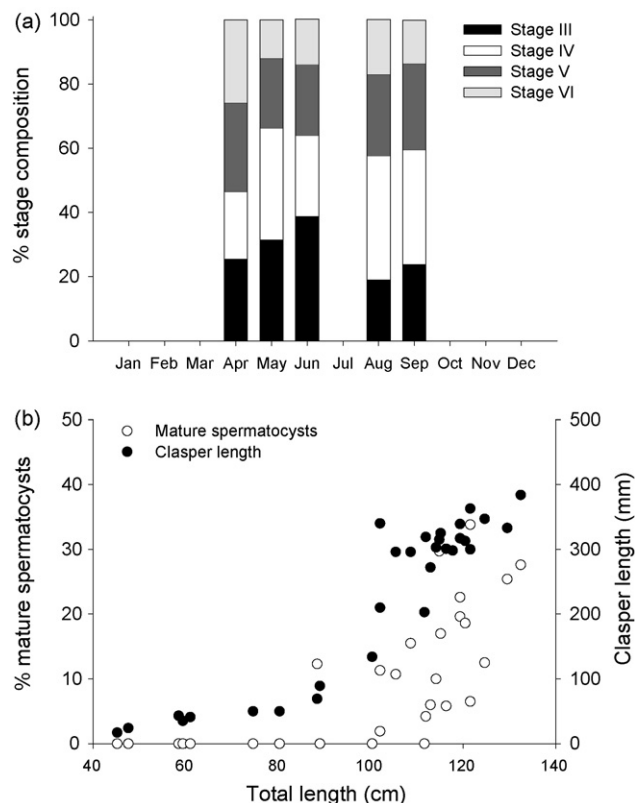
Fig. 9. Monthly changes in spermatogenesis (a) and relationship between the proportion of mature spermatocysts, clasper length, and total length (b) in male *Raja rhina* ($n = 30$). The percent stage composition is the mean proportion of each stage occupied along a transect line across one representative full lobe cross section of a testes, and expressed as the mean.

Visual assessments of reproductive condition provide limited insight into the reproductive biology of a species and may be prone to inconsistencies, particularly during recovering phases of gonadal development (Gerristen and McGrath, 2006; Vitale et al., 2006). Criteria for reproductive classifications typically outline distinctions among immature individuals or distinguish categories for mature, actively reproductive specimens, but lack descriptions or separate stages for resting and post-partum conditions or the possibility of senescence (e.g., Pratt, 1979; Martin and Cailliet, 1988; Stehmann, 2002; Ebert, 2005). As a result, the potential for misclassifying mature, but reproductively inactive, specimens such as those undergoing recrudescence of gonads or resorption of ova, as immature is increased. Such errors may lead to systematic over- or under-estimation of 50% maturity, skewing estimates of a population's reproductive potential and growth. To limit misclassifications and generate improved details on the reproductive cycle and biology of skates and other elasmobranchs, expanded reproductive categories should be considered. Future studies should incorporate combined visual, hormonal, and histological assessments to identify mature, reproductively inactive individuals to confirm gonadal characteristics during spent, recovering, and resting phases.

The relationship between mature ovum diameter or ovarian fecundity and maternal size for *R. rhina* in the GOA did not indicate any consistent pattern. Ebert (2005), however, did find a relationship between number of mature ova and maternal size for several eastern Bering Sea skates, and Matta and Gunderson (2007) found a slight but significant relationship for *Bathyraja parmifera*. Elsewhere, an increase in maximum ovum diameter with increasing maternal TL has also been reported for *Psammobatis extenta* (Braccini and Chiaramonte, 2002) from the southwest Atlantic, *Dipturus laevis* (Gedamke et al., 2005) from the western North Atlantic, and *Zearaja chilensis* (Licandeo et al., 2006) from the southeastern Pacific.

Fecundity estimates in skates, and most oviparous elasmobranchs, are poorly known. However, observations on captive *R. binoculata* have revealed these skates to deposit >350 egg cases annually in captive specimens (Kevin Lewand, Monterey Bay Aquarium, personal communication); the number of egg cases containing viable embryos was not determined. The egg cases of *R. binoculata* are unusual in that it is one of only two known skate species, the other being *Raja pulchra*, to deposit multiple embyos in each egg case (Ebert and Davis, 2007). Therefore, based on an estimated maturity of 8 years and longevity of 26 years (McFarlane and King, 2006) a single individual *R. binoculata* may be capable of producing >6000 egg cases during its life. Given that a single *R. binoculata* egg case may contain up to eight embryos (Ford, 1971), a single individual adult female may potentially produce >48,000 embryos during its life-span; making it perhaps the most fecund of any modern elasmobranch species. Holden (1975) estimated an average annual fecundity of 140 eggs for *Raja clavata* based on the number of ovarian eggs present throughout the year. Captive studies indicate that the fecundity of some species may be relatively high not just annually, but over the life span of an individual skate (Holden et al., 1971; Ishihara et al., 2002; Koop, 2005). Although, data are limited, skates, and other oviparous elasmobranchs, appear to possess a reproductive strategy that produces relatively smaller offspring and notably higher fecundities than observed among their viviparous relatives (Lucifora and García, 2004; Musick and Ellis, 2005).

It has been suggested that skates may become less fecund, and perhaps may even senesce, with age. Ebert (2005) noted the possibility of senescence in three species of eastern Bering Sea skates and mentioned several other possible instances of senescence in eastern and southwestern Pacific Ocean skate species. The only other record of senescence in an elasmobranch was reported in *Galeorhinus galeus* off southern Brazil (Peres and Vooren, 1991). It is possible that individuals within a given population go through a period of diapause or reproductive inactivity that may be misinterpreted as senescence, but it may also suggest these individuals have reached the end of their reproductive viability.

5. Conclusions

It is a commonly held paradigm that large skate species maturing at a large size relative to their maximum TL are considered to be late maturing (Dulvy et al., 2000), and thus potentially highly vulnerable to over-exploitation. Contrary to this line of reasoning, the size at maturity relative to maximum TL is in fact a poor indicator of the rate at which maturity is achieved. Skates, like other oviparous elasmobranchs, tend to grow very little once mature, instead concentrating their energies into reproduction. As a result many species tend to mature between 75% and 90% of their maximum TL (Dulvy et al., 2000; Ishihara et al., 2002; Ebert, 2005; Ebert et al., 2008). Using percentages based on female 50% maturity and the maximum TL observed in the present study, both *R. binoculata* (81%) and *R. rhina* (78%) appear to follow this trend. However, *R. binoculata*, unlike other large skate species matures relatively early, between 5 and 9 years, and has a longevity approximating 26 years (McFarlane and King, 2006). *R. rhina* by comparison matures much older, between 9 and 12 years, but with a similar longevity also estimated at 26 years (McFarlane and King, 2006). Furthermore, as discussed above, *R. binoculata* is unique in that it has multiple embryos per egg case, whereas *R. rhina* only has a single embryo per egg case. The striking difference in life history traits between these two relatively large and abundant species only emphasizes the critical need for species-specific information when developing a management plan. The lack of detailed biological information for most skate species greatly impedes the development of species-specific management strategies for this group. This study, although limited, does provide new and essential information on the reproductive biology of these two commercially targeted eastern North Pacific skates.

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