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Reproductive biology of deep-sea catsharks (Chondrichthyes: Scyliorhinidae) in the eastern North Pacific

Brooke E. Flammang · David A. Ebert · Gregor M. Cailliet

Abstract *Apristurus brunneus*, *A. kampae*, and *Parmaturus xaniurus* were caught by trawl and longline between Washington and southern California (48°N to 32°N latitude) from June 2001 through October 2004. In females, oviducal gland width increased with TL in all three species but remained within 4 to 6% of TL. Oocyte diameter increased with TL during reproductive development in all species, and continued to increase with size after reproductive maturity was reached. The weight-length relationships differed significantly among species but not between sexes of any species from the eastern North Pacific combined. Using logistic regression, it was determined that total length at 50% maturity (TL_{50}) of *A. brunneus* males was 514 mm TL and all *A. brunneus* males were mature at 547 mm TL. Female *A. brunneus* reached TL_{50} at 501 mm TL and all female *A. brunneus* were mature at 581 mm TL. *Apristurus kampae* males and females reached TL_{50} at approximately 485 mm TL and 490 mm TL, respectively. *Parmaturus xaniurus* males reached TL_{50} at 444 mm TL and females at 501 mm TL. Gravid female *A. brunneus* were found in all months of the year, but gravid *P. xaniurus* were found primarily June through September. Adult *A. kampae* females were found only in July through November and there were gravid females in all these months. Based upon gonadosomatic indices, I_G, these species may mate within a defined period of time (April through June); however, *A. brunneus* appear to reproduce throughout the year and *P. xaniurus* reproduce within a defined season (approximately July through September).

Keywords Maturity · Seasonality · Reproduction · Egg case · Weight–length regression · Gonadosomatic index

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Introduction

Catsharks (Chondrichthyes: Scyliorhinidae) are the largest and the most diverse family of living sharks, totaling 16 genera and approximately 134 species distributed worldwide (Compagno et al. 2005). With the exception of morphological information provided in species descriptions, the reproductive biology of the species within this family is poorly known, despite their global

distribution (Springer 1979; Ebert et al. 2006). A major contributing factor to this is the depth at which many of these species are found (Springer 1979). In the eastern North Pacific (ENP), there are three deep-sea scyliorhinids reported in the deep-water slope habitats: brown catshark, *Apristurus brunneus* (Gilbert 1892), white-edge catshark, *Apristurus kampae* Taylor 1972, and filetail catshark, *Parmaturus xaniurus* (Gilbert 1892).

The occurrence of these scyliorhinids as incidental catch in commercial fishing operations (Rogers and Ellis 2000; Ebert 2003) warrants research into their biology and distribution to gauge the need for fisheries management. There are no data on *A. brunneus*, *A. kampae*, or *P. xaniurus* between Cape Flattery, Washington (48°N) and Point Dume, California (34°N) for comparison with the studies conducted in more northern and southern regions (Jones and Geen 1977; Cross 1988; Balart et al. 2000). By examining the biology of these deep-sea species throughout the extent of their range, we can better understand their life history. The aim of this project was to describe the reproductive biology of *A. brunneus, A. kampae* and *P. xaniurus* in the eastern North Pacific, between 48°N and 32°N latitude.

Methods

Field sampling

Samples were obtained annually from fishery-independent bottom trawl survey cruises conducted by the National Oceanic and Atmospheric Administration (NOAA) Fisheries Service Northwest Fisheries Science Center (NWFSC) laboratories in Newport, OR and Seattle, WA. The NWFSC provided samples from their annual slope and shelf Fisheries Research and Monitoring (FRAM) cruises during the months of June through October from 2001 to 2004, between Cape Flattery, Washington (48°N latitude) and San Diego, California (32°N latitude, Fig. 1). Six hundred sample locations were randomly chosen each year from a map of the survey area divided into grids 2 nautical miles by 1.5 nautical miles in length. The NWFSC survey was designed to cover
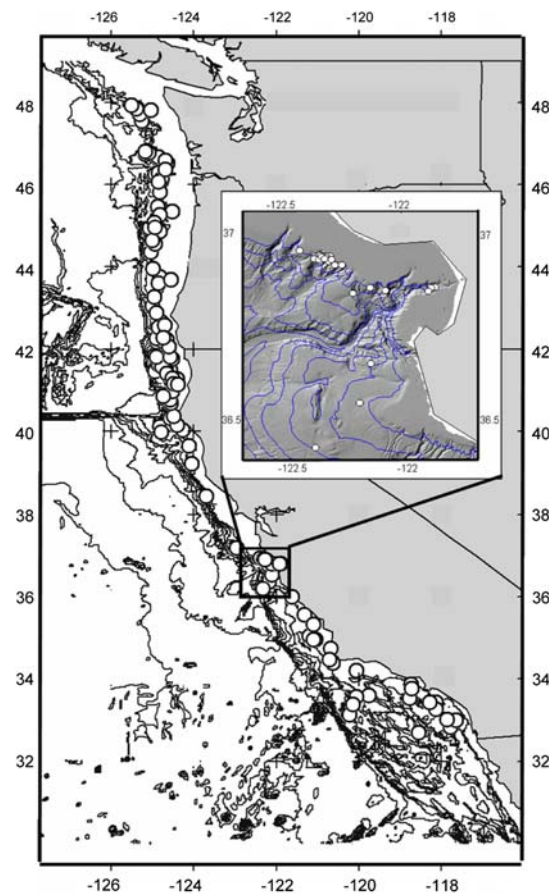
Fig. 1 Catch locations of all *Apristurus brunneus* (*n* = 711), *A. kampae* (*n* = 97), and *Parmaturus xaniurus* (*n* = 376) studied from the eastern North Pacific from June 2001 through October 2004. Inset is of catch locations of trawl and longline surveys by NOAA Fisheries Northwest and Santa Cruz labs in Monterey Bay off central California from June 2001 through October 2004. Bathymetric contours are scaled at 500 m depths

three depth strata they defined as shelf (20–183 m), shallow slope (184–549 m), and deep slope (550–1350 m), with the aim of sampling as many different habitat types as possible while minimizing damage to trawl gear.

The Federal Ecology Division (FED) of the NOAA Fisheries Service Southwest Fisheries Science Center (SWFSC) laboratory in Santa Cruz, CA provided samples obtained monthly by fishery-independent bottom trawl and longline survey cruises targeting commercial groundfish species between Davenport, CA (approximately 37°N latitude) and Monterey, CA (approximately

36°N latitude) from June 2002 to March 2004 (Fig. 1, inset). Using a depth-stratified sampling method, five stations at arbitrarily designated depth gradients were surveyed monthly off central California, dependent on weather. Bottom trawls were conducted from 170 to 667 m depth. Longlines had between 750 and 7250 hooks per haul and longline haul depths ranged from 373 to 503 m. No sampling was undertaken in the month of May of any year because SWFSC/FED resources were focused on another survey, the annual California Cooperative Oceanic Fisheries Investigations (CalCOFI) larval fish survey.

Samples opportunistically collected by observers with the Pacific States Marine Fisheries Commission (PSMFC) between Monterey Bay (37°N) and Big Sur, California (36°N) were dependent upon cooperation of individual commercial fishing operations and observer availability. Additionally, specimens in collections at the California Academy of Sciences (CAS), Commonwealth Scientific and Industrial Research Organization (CSIRO) Hobart, Tasmania, Los Angeles County Museum (LACM), Museum of Comparative Zoology (MCZ), Scripps Institute of Oceanography (SIO), Smithsonian National Museum of Natural History (USNM), and the University of Washington (UW) were examined to augment field samples. Institutional codes are as designated in Leviton et al. (1985).

Biological data

Field samples were frozen upon capture and returned to Moss Landing Marine Laboratories (MLML) for examination. Specimens were thawed, measured, and weighed. Total length (TL) was measured to the nearest millimeter (mm), with the tail of the specimen in line with the body (Ricker and Merriman 1945). Specimen weight was determined to the nearest gram (g). Geometric weight-length regressions were calculated for males and females of each species using the equation $W = aL^b$, where W is the weight in g, L is the total length in mm, and a and b are fitted constants (Ricker 1979). Analysis of variance (ANOVA) was used to determine difference in weight–length regressions among species, sex, and geographic region.

Sexual maturity of specimens was determined by visual analysis of gonads and reproductive organs. In males, sexual maturity was determined by clasper development and calcification. Juvenile males had flaccid claspers that did not extend past the posterior end of the pelvic fins. Adolescent males had claspers that had grown past the pelvic fin edge but were not calcified. The terminal clasper elements are fully calcified in mature individuals. Clasper length was measured to the nearest mm along the inner length of the clasper, from the clasper origin at the apex of the cloaca, to the distal tip of the clasper (Compagno 1984).

Maturity status in females was determined by vascularization of the ovary and development of the oviducal gland, which produces the egg case. In juvenile females, there was no discernible oviducal gland and no oocytes were visible in the ovary. Development of the small, heart-shaped oviducal gland began in adolescents. The oviducal gland in adult females was large and bulbous, and oocytes are ≥14 mm in diameter. The widths of the uterus, the left oviducal gland, and mature oocytes were measured to the nearest mm. In these scyliorhinids, only the right ovary was developed and reproductively functional. The left ovary was vestigial (Springer 1966). Ovary mass was recorded to the nearest tenth of a gram. Changes in gonad mass, mature oocyte diameter and number, and liver mass were analyzed for developmental and seasonal variation.

Egg case size and fecundity were evaluated for each species. Egg case length relative to female TL was compared to determine if a relationship exists, as purported in Cross (1988). The proportion of gravid females was calculated for each month to investigate reproductive seasonality.

Total length at first, 50% (TL_{50}) and 100% (TL_{100}) maturity was determined for males and females of all species. Size at first maturity was determined to be the length of the smallest mature individual for each sex of each species. Size at 50% maturity was determined using the logistic equation detailed in Roa et al. (1999), $P(L) = a(1 - e^{\beta_0 + \beta_1 L})^{-1}$, where $P(L)$ is the proportion of mature individuals at length L, α is the asymptote, β_0 is the intercept, and β_1 is the slope parameter. This logistic model provided the best fit to the biological data. Significant differences

between male and female maturity sizes were determined by plotting 95% confidence intervals (CI) around the logistic regression; overlap of 95% CI indicated the values were not significantly different ($P > 0.05$). All specimens from the entire study range were arbitrarily grouped by geographic area and designated as Washington (48°N to 46°N latitude), Oregon (46°N to 42°N latitude), northern California (42°N to 38°N latitude), central California (38°N to 34°N latitude), and southern California (34°N to 32°N latitude). This was done to allow comparisons with previous studies and to investigate clinal variability in reproductive maturity. Size of the smallest mature and largest immature males and females were evaluated for significant difference by geographical region using an ANOVA.

Seasonal variability of reproductive status in adults was quantified using the gonadosomatic index (I_G), $I_G = (GB^{-1}) \times 100$, where G is the total gonad mass and B is the total body mass of the specimen. Gonadosomatic index was determined using testis mass in males and ovary mass (including oocytes) in females and compared throughout the year to see if there was a seasonal fluctuation in gonad mass. Changes in liver mass were analyzed using the hepatosomatic index (I_H), $I_H = (HB^{-1}) \times 100$, where H is the total liver mass and B is the total body mass of the specimen. Hepatic lipids are used in vitellogenesis, the formation of oocyte yolk (Craik 1978; Hamlett and Koob 1999), and it was expected that any seasonal variability in I_H would coincide with inverse fluctuations in I_G. Gonadosomatic and hepatosomatic indices were compared by month, with significant difference determined by plotting

standard error (S.E.) around the mean index value.

Results

Apristurus brunneus

A total of 711 *A. brunneus* (317 males and 394 females) was examined, of these 62% were juvenile males ($n = 224$) and females ($n = 218$). Of the remainder, 10% (16 males and 58 females) were adolescents and 27% (77 males and 118 females) were adults, including 63 gravid females. Geometric mean weight–length relationships were not significant among geographic regions (ANOVA, d.f. = 4, $P = 0.648$) or sex (ANOVA, d.f. = 1, $P = 0.958$; Table 1).

Males

Clasper length increased curvilinearly with TL from 400 mm TL, and a maximum inner clasper length of 10% TL was attained between 490 and 540 mm TL. Claspers did not increase further in relative length for individuals >540 mm TL (Fig. 2). Specimens >550 mm TL showed negative allometry in the ratio of clasper length to TL. Therefore, some *A. brunneus* males had fully calcified terminal clasper cartilages and were considered mature with an inner clasper length 6% TL.

Total length at first maturity, 50% (TL_{50}), and 100% (TL_{100}) was based on study of 317 males (Table 1). The smallest mature male, which was determined to be size at first maturity, was

Table 1 Geometric mean weight–length relationships, total length (TL) at first maturity, TL at 50% maturity (TL_{50}), and TL at 100% maturity (TL_{100}), for *Apristurus brunneus*, *Apristurus kampae*, and *Parmaturus xaniurus* from the eastern North Pacific

Species	Sex	n total	Weight–length relationship	r^2	n mature	TL at first maturity (cm)	TL_{50} (cm)	TL_{100} (cm)
Apristurus brunneus	Male	317	$W = 2.444 \times 10^{-6} L^{3.027}$	0.950	77	488	514	547
	Female	394	$W = 3.679 \times 10^{-7} L^{3.341}$	0.949	118	485	501	581
Apristurus kampae	Male	54	$W = 1.140 \times 10^{-3} L^{2.090}$	0.831	43	486	*c.* 485	486
	Female	43	$W = 1.849 \times 10^{-4} L^{2.421}$	0.830	28	484	490	539
Parmaturus xaniurus	Male	140	$W = 4.538 \times 10^{-5} L^{2.600}$	0.905	48	409	444	478
	Female	236	$W = 1.076 \times 10^{-5} L^{2.845}$	0.831	89	369	501	543

The estimate for 50% maturity for *A. kampae* males is based on mathematical estimate, because there was no overlap in sexual maturity among size classes in the specimens available

Fig. 2 Inner clasper length as a percentage of total length for adult (closed triangles) and juvenile and adolescent (open triangles) male *Apristurus brunneus* ($n = 317$)
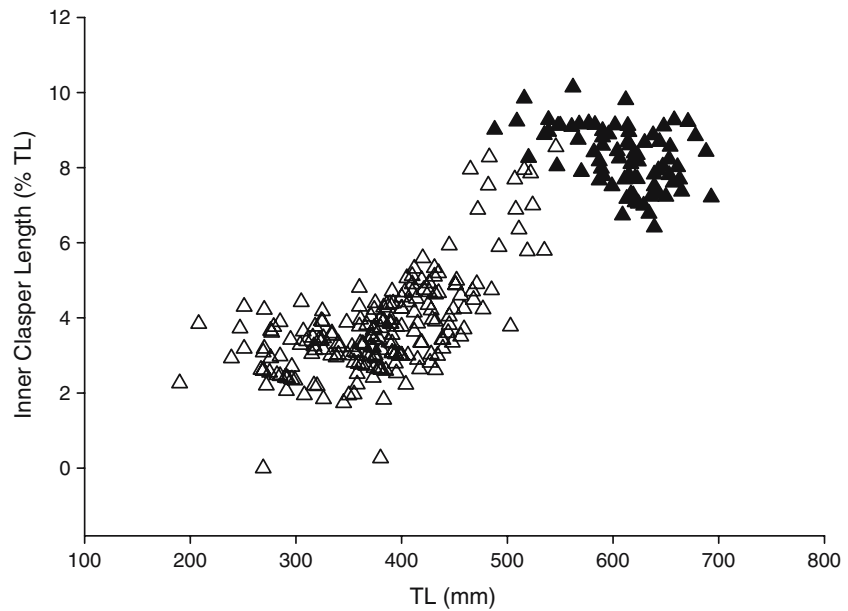
488 mm TL or 70.4% of maximum total length (TL$_{max}$). Using logistic regression, it was determined that TL$_{50}$ of males was 514 mm TL or 74.2% of TL$_{max}$. Total length at 100% maturity in *A. brunneus* males was 547 mm TL (78.9% of TL$_{max}$). The largest male was 693 mm TL.

Size of the smallest mature and largest immature male *A. brunneus* varied by latitudinal region (Table 2). The smallest mature male (488 mm TL) was from central California and the largest immature male was from Washington (546 mm TL). Size at first maturity was not significantly different by latitudinal region (ANOVA, d.f. = 5, $P > 0.25$). Size of the largest immature male increased with latitude but was not statistically different among regions (ANOVA, d.f. = 5, $P > 0.25$).

Based on S.E. bars, the I_G in adult male *A. brunneus* was significantly elevated in April ($n = 11$) and May ($n = 2$) as compared to other months (Fig. 3). However, there was no corresponding decrease in I_H, suggesting that there is no relationship between I_G and I_H in the males of this species.

Females

Oviducal gland width increased with TL to a maximum of 5% of TL (Fig. 4a). At approximately 400 mm TL, *A. brunneus* oviducal gland width began to increase from 1% of TL to between 2.75 and 5% TL in adult and gravid female specimens ≥475 mm TL. The oviducal gland width percentage of TL remained in the

Table 2 Size at first maturity and largest immature male and female *Apristurus brunneus* (mm TL) by latitudinal region (Washington (48°N to 46°N latitude), Oregon (46°N to 42°N latitude), and northern (42°N to 38°N latitude), central (38°N to 34°N latitude), and southern California (34°N to 32°N latitude))

	Males (mm TL)				Females (mm TL)			
	n	Smallest mature	n	Largest immature	n	Smallest mature	n	Largest immature
Washington	3	550	36	546	0	–	53	544
Oregon	6	587	66	522	14	540	55	566
Northern California	6	520	55	507	15	541	72	581
Central California	50	547	54	492	97	485	55	527
Southern California	8	488	28	408	7	486	29	501

No mature females were caught in the Washington region
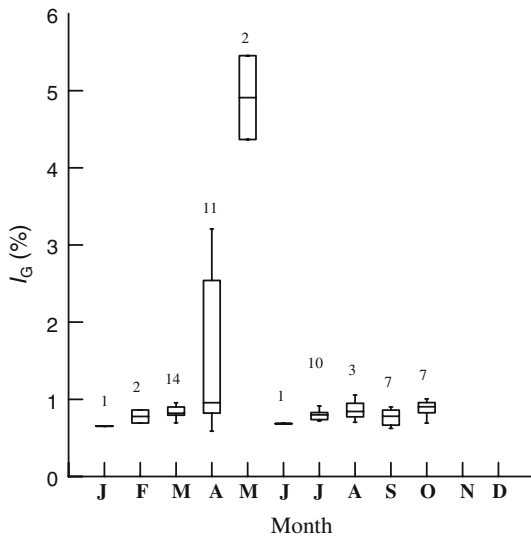
Fig. 3 Gonadosomatic index (I_G) for adult male *Apristurus brunneus*. $I_G = (G/B) \times 100$, where G is the total gonad mass, and B is the total body mass of the specimen. The horizontal line within each box denotes the median for the sample and the box encompasses the range of the central 50% of the values. Bars extending vertically from the box denote 95% confidence from the mean. The number of samples per month is designated above each box plot

2.75–5% of TL range for mature females, even as TL continued to increase. Oocyte diameter increased with TL during reproductive development, and continued to increase with size after reproductive maturity was reached (Fig. 4b). The smallest adult *A. brunneus* females (approximately 480 mm TL) had oocyte diameters 12–17 mm and the largest adults (≥680 mm TL) had oocytes 15–20 mm in diameter. Adult *A. brunneus* females had between 1 and 16 mature oocytes. There was no relationship between the number of mature oocytes and adult female TL (Fig. 4c). Egg case length did not appear to increase relative to female TL. Egg case lengths of *A. brunneus* remained consistent ($n = 38$ females, mean = 63.0 ± 4.7 mm), and were not significantly related to female TL ($R^2 = 0.08$, Fig. 4d).

Total length at first maturity, TL_{50} and TL_{100} was based on study of 394 females (Table 1). The smallest mature female was 485 mm TL (73.5% of TL_{max}). Fifty percent of females were mature at 501 mm TL (75.9% of TL_{max}). All female *A. brunneus* were mature at 581 mm TL (88.0%

of TL_{max}). The largest female was 660 mm TL. Male and female size at 50% maturity estimates were significantly different from each other based upon 95% CI ($P < 0.05$).

Female *A. brunneus* matured at a smaller size in lower latitudes than at higher latitudes (Table 2). The smallest mature female (485 mm TL) was from central California and the largest immature female was from northern California (581 mm TL). No mature females were found in the Washington region. Size at first maturity varied between 46°N to 38°N latitude (mean = 540.5) and 38°N to 32°N latitude (mean = 485.5) but was not significantly different by latitudinal region (ANOVA, d.f. = 4, $P > 0.25$). Sizes of the largest immature females were not statistically different among regions (ANOVA, d.f. = 5, $P > 0.25$).

Adult female *A. brunneus* had had a significantly elevated I_G in May and June, but there was no corresponding decrease in I_H (Fig. 5). The significant increase in I_G in May ($n = 1$) and June ($n = 4$) is apparent based on S.E. bars as compared to other months. As with the males, there was no significant associated seasonal variability in I_H values based on overlap of S.E. bars. Gravid *A. brunneus* females were found in all months of the year (Table 3). From March through August, ≥48% of all adult female *A. brunneus* had egg cases ($n = 113$).

Apristurus kampae

Seventy-four percent of *A. kampae* specimens available were adults ($n = 43$ males and 28 females, including gravid females). The remainder was 13% juveniles (6 males and 7 females) and 13% adolescents (5 males and 8 females). Geometric mean weight–length relationships were not significant when subdivided by sex (ANOVA, d.f. = 1, $P = 0.963$; Table 1).

Males

Apristurus kampae adult males also had an inner clasper length 6–10% of TL, which was reached at ≥500 mm TL (Fig. 6). The sample size was insufficient to determine the change in clasper
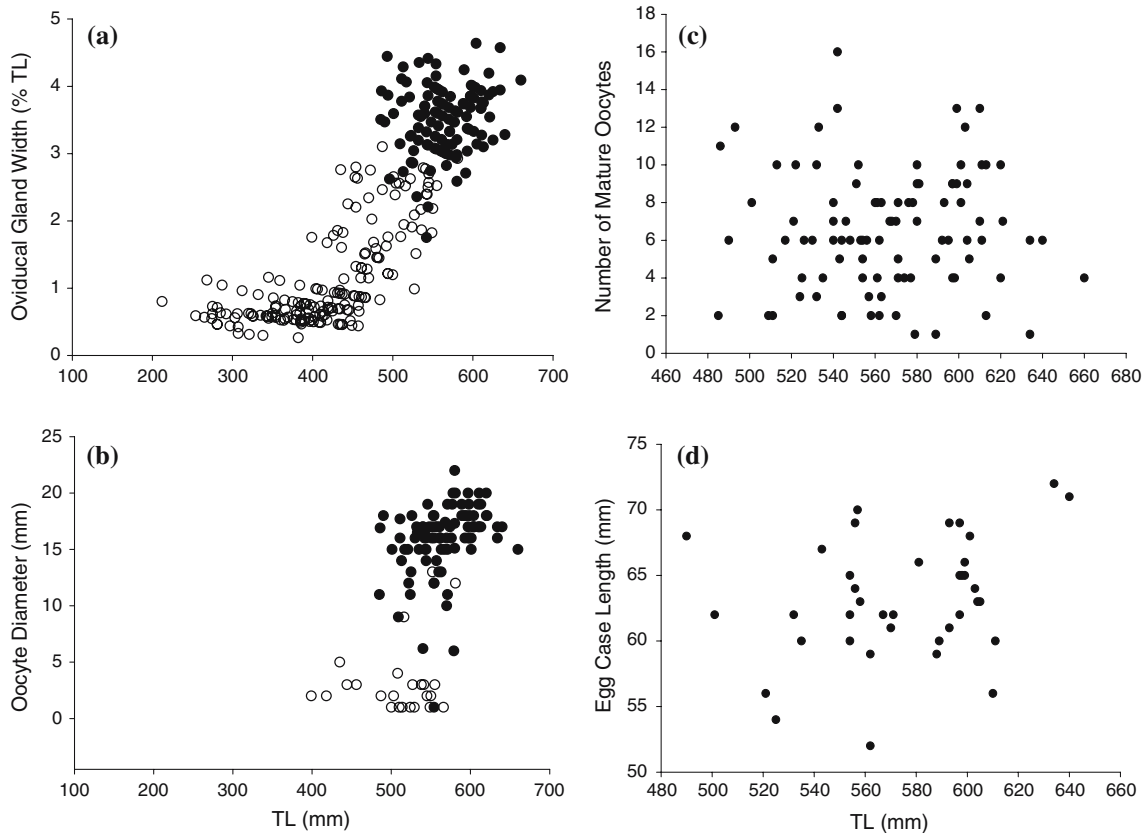
Fig. 4 (**a**) Oviducal gland width as a percentage of total length for adult (including gravid; closed circles) and juvenile and adolescent (open circles) female *Apristurus brunneus* (*n* = 394). (**b**) Maximum oocyte diameter versus total length of adult (including gravid; closed circles) and juvenile and adolescent (open circles) female *Apristurus brunneus* (*n* = 394). (**c**) Number of mature oocytes versus total length of adult female *Apristurus brunneus* (*n* = 118). (**d**) Egg case length versus female total length for *Apristurus brunneus* (*n* = 38)

length ratio in *A. kampae* juveniles and adolescents as compared to adults.

Estimates of TL at first maturity, TL_{50} and TL_{100} were based on 52 male *A. kampae* (Table 1). The smallest mature male was 486 mm TL (75.1% of TL_{max}) and the largest immature male was 484 mm TL (74.8% of TL_{max}). Males reached TL_{50} at approximately 485 mm TL (75.0% of TL_{max}). This estimate was based on the average between the largest immature and smallest mature individuals, because there was no overlap in sexual maturity among size classes in the male specimens available. All *A. kampae* males were mature at 486 mm TL (75.1% of TL_{max}). The largest male was 647 mm TL.

The majority of *A. kampae* specimens were obtained from preserved museum collections

(37 of 52 males examined); therefore, I_G's and I_H's could not be measured or calculated for this species.

Females

Apristurus kampae adult females (including gravid individuals) had an oviducal gland width 2.5–4% of TL (Fig. 7a). These adult females were ≥500 mm TL. Oviducal gland measurements were available for only five immature (juvenile and adolescent) females. *Apristurus kampae* females had mature oocytes between 15 and 20 mm diameter (Fig. 7b). These females with mature oocytes were ≥475 mm TL. Three juvenile and adolescent females had immature oocytes 3–4 mm diameter. *Apristurus kampae* adult females had 4–8 mature oocytes (Fig. 7c). Egg case
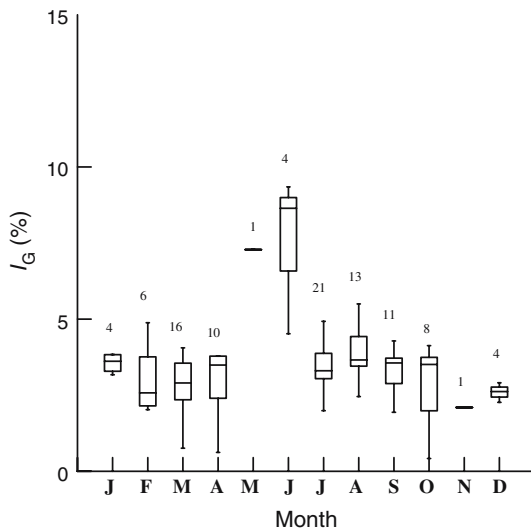
Fig. 5 Gonadosomatic index (I_G) for adult female *Apristurus brunneus*. $I_G = (GB^{-1}) \times 100$, where G is the total gonad mass, and B is the total body mass of the specimen. The horizontal line within each box denotes the median for the sample and the box encompasses the range of the central 50% of the values. Bars extending vertically from the box denote 95% confidence from the mean. The number of samples per month is designated above each box plot

lengths of *A. kampae* varied ($n = 8$ females, mean = 63.4 mm ± 3.5 mm), and were not significantly related to female TL ($R^2 = 0.34$, Fig. 7d).

Table 3 Proportion of gravid females of total mature *Apristurus brunneus*, *A. kampae*, and *Parmaturus xaniurus* females by month

Month	*Apristurus brunneus*		*Apristurus kampae*		*Parmaturus xaniurus*	
	n	Proportion gravid	n	Proportion gravid	n	Proportion gravid
January	4	*0.50*	0	–	1	0.00
February	6	0.33	0	–	9	0.00
March	17	*0.85*	0	–	6	0.00
April	15	*0.67*	0	–	15	0.20
May	4	*0.50*	0	–	0	–
June	6	*0.67*	0	–	7	0.14
July	21	*0.48*	3	0.33	17	*0.47*
August	15	*0.80*	2	0.00	10	*0.44*
September	12	0.17	8	*0.50*	9	*0.50*
October	12	0.25	3	*0.67*	7	0.14
November	1	*1.00*	5	0.20	6	0.00
December	3	0.33	0	–	2	1.00

Apristurus kampae adult females were only caught from July through November *Parmaturus xaniurus* were not caught in the month of May because of limited fishing resources

Estimates of TL at first maturity, TL_{50} and TL_{100} were based on 52 male and 45 female *A. kampae* (Table 1). The smallest mature female was 484 mm TL (82.0% of TL_{max}) and all females were mature at 539 mm TL (91.4% of TL_{max}). The largest immature female was 537 mm TL (91.0% of TL_{max}). Fifty percent maturity of females was reached at 490 mm TL (83.0% of TL_{max}). Maximum length of females was 590 mm TL. Male and female TL_{50} estimates were not significantly different from each other based upon 95% CI ($P > 0.05$).

The majority of *A. kampae* specimens were obtained from preserved museum collections (35 of 45 females examined); therefore I_G's and I_H's could not be measured or calculated for this species. Adult females were collected in July through November only, and gravid females were found in all months except August (Table 3). In September and October, ≥50% of adult *A. kampae* females were gravid.

Parmaturus xaniurus

Specimens representative of each maturity class (juvenile, adolescent, adult, and gravid female) were obtained for all species. *Parmaturus xaniurus* males were evenly distributed among maturity classes, but females collected consisted mostly of adolescents (109 of 236 specimens). The number of adolescent females collected was twice the number of adolescent males ($n = 49$). Of the rest of the *P. xaniurus*, juveniles comprised 22%, and the remaining 36% was adults and gravid females. Geometric mean weight–length relationships were not significant when subdivided by sex (ANOVA, d.f. = 1, $P = 0.984$; Table 1).

Males

Clasper length increased curvilinearly with TL (Fig. 8). *Parmaturus xaniurus* adult males had an inner clasper length 10–16% of their TL. Clasper length increased rapidly after 375 mm TL and maximum clasper length occurred at approximately 400 mm TL. However, calcification of the terminal clasper elements was not always present in specimens 400–450 mm TL. There was no

Fig. 6 Inner clasper length as a percentage of total length for adult (closed triangles) and juvenile and adolescent (open triangles) male *Apristurus kampae* ($n = 54$)
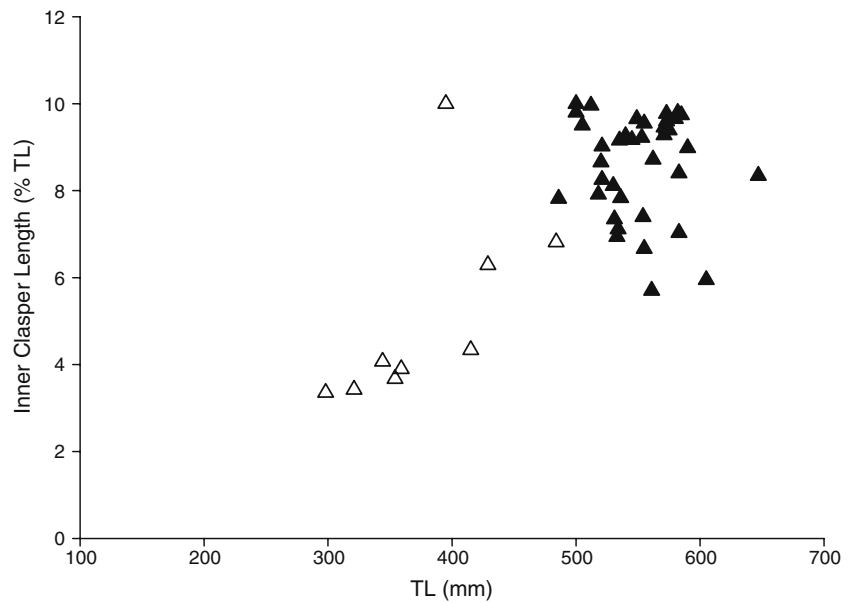
evidence of negative allometry in the clasper ratio of *P. xaniurus*.

Size at first maturity, TL_{50}, and TL_{100} was determined from 140 male specimens (Table 1). The smallest mature male was 409 mm TL (80.0% of TL_{max}) and all males were mature at 478 mm TL (93.3% of TL_{max}). Male TL_{50} was reached at 444 mm TL (86.7% of TL_{max}). The largest male was 512 mm TL.

Parmaturus xaniurus males exhibited an increased trend in I_G in April through July when compared to S.E. of other months (Fig. 9). Male HSI values remained relatively consistent throughout the year and were not significantly different. Gonadosomatic indices and I_H for adult *P. xaniurus* males did not reflect a relationship between gonad and liver mass.

Females

Oviducal gland width increased with TL to a maximum of 6% of TL (Fig. 10a). *Parmaturus xaniurus* adult and gravid females had an oviducal gland width between 2.5 and 6% of TL. Some *P. xaniurus* females of size similar to adolescents had an oviducal gland width in this range and an oviducal gland that appeared to be developed, but were determined to be immature

based upon oocyte size and ovary development. Oocyte diameter increased with TL during reproductive development, and continued to increase with size after reproductive maturity was reached (Fig. 10b). In *P. xaniurus*, oocyte diameter first began to increase at approximately 400 mm TL. The smallest adult females (approximately 425–450 mm TL) had mature oocytes 10–15 mm diameter. The largest *P. xaniurus* females (≥525 mm TL) had 20–25 mm diameter oocytes. There was no relationship between the number of mature oocytes and adult female TL (Fig. 10c). *Parmaturus xaniurus* adult females had between 1 and 11 mature oocytes. Some adolescent female *P. xaniurus* had fully developed, vascularized ovaries before their oviducal glands were fully developed or they were reproductively mature. This was not observed for either species of *Apristurus*. There was a trend of increasing *P. xaniurus* egg case length with female TL (Fig. 10d); however, it was not significantly correlated ($R^2 = 0.34$, $n = 22$ females).

Size at first maturity, TL_{50}, and TL_{100} was determined from 236 female specimens (Table 1). The smallest mature female was 369 mm TL (63.7% of TL_{max}) and all females were mature at 543 m TL (93.8% of TL_{max}). The largest immature female was 542 mm TL (93.6% of TL_{max}).
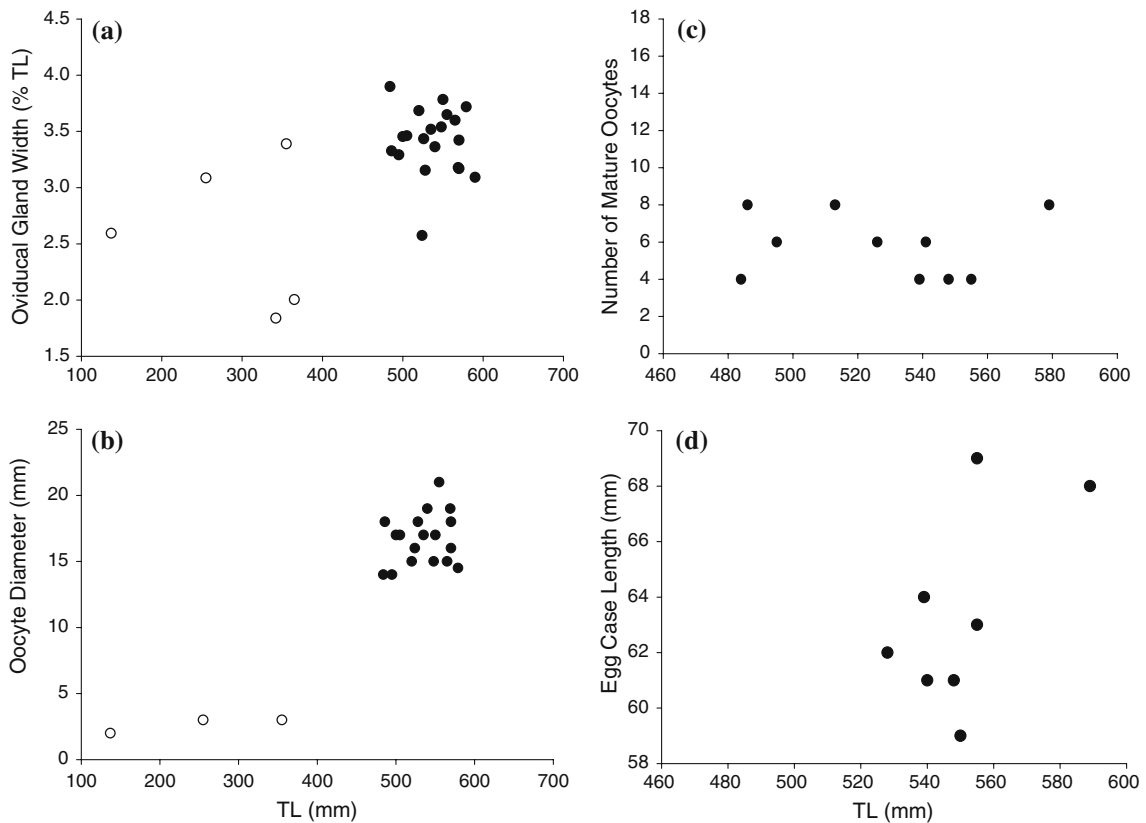
Fig. 7 (a) Oviducal gland width as a percentage of total length for adult (including gravid; closed circles) and juvenile and adolescent (open circles) female *Apristurus kampae* (*n* = 43). (b) Maximum oocyte diameter versus total length of adult (including gravid; closed circles) and juvenile and adolescent (open circles) female *Apristurus kampae* (*n* = 43). (c) Number of mature oocytes versus total length of adult female *Apristurus kampae* (*n* = 11). (d) Egg case length versus female total length for *Apristurus kampae* (*n* = 8)
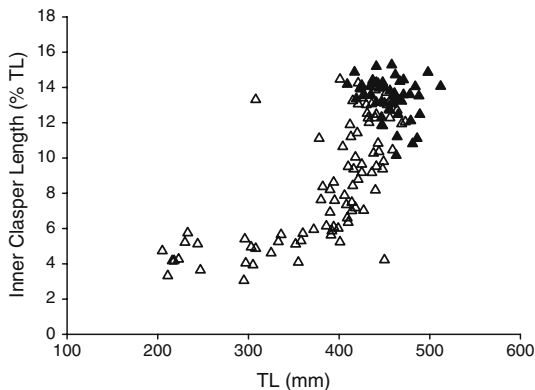
Fig. 8 Inner clasper length as a percentage of total length for adult (closed triangles) and juvenile and adolescent (open triangles) male *Parmaturus xaniurus* (*n* = 140)

Fifty percent maturity of females was reached at 501 mm TL (86.5% of TL_{max}). The largest female was 579 mm TL.

Adult females had a significant an increase in I_G in June (*n* = 7) as compared to the S.E. of other months (Fig. 11). There was no significant associated seasonal variability in I_H values. Gonadosomatic indices and I_H for adult *P. xaniurus* females did not reflect a relationship between gonad and liver mass. The greatest proportion (44–50%) of gravid *P. xaniurus* was found from July through August, and no gravid females were found January through March or November (*n* = 89, Table 3).

Discussion

Weight–length relationships

Weight–length relationships among all species from the entire study range were similar and were
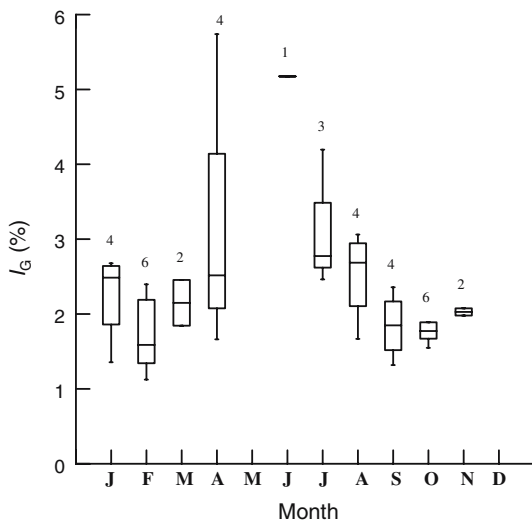
Fig. 9 Gonadosomatic index (I_G) for adult male *Parmaturus xaniurus*. $I_G = (GB^{-1}) \times 100$, where G is the total gonad mass, and B is the total body mass of the specimen. The horizontal line within each box denotes the median for the sample and the box encompasses the range of the central 50% of the values. Bars extending vertically from the box denote 95% confidence from the mean. The number of samples per month is designated above each box plot

only significantly different among species with sexes combined, but not by species or sexes alone. The regression coefficients in female and male *Apristurus brunneus* appeared greater in southern California than in Washington, but there was no significant difference or clear gradient in change of regression coefficients latitudinally. When compared to weight–length relationships determined by Cross (1988) and Balart et al. (2000), there was no significant difference in weight–length relationship regression coefficients among latitudinal regions of *P. xaniurus* (ANOVA, d.f. = 2, $P > 0.25$).

Egg cases

Apristurus brunneus and *P. xaniurus* egg case lengths were not correlated to female TL, contrary to Cross's (1988) findings in southern California. This was most likely a coincidence of smaller sample sizes used in the southern California study. In fact, *A. brunneus* egg cases were almost the same size regardless of female TL. Increase in egg case size is assumed to allow

embryos to attain larger sizes before hatching, which would be beneficial in avoiding predation.

Deposition of the right egg case before the left may be a reproductive characteristic for these fishes, as it is in some skates (Templeman 1982). A few females of each species had only one egg case, in the left oviduct, presumably the egg case from the right oviduct had already been deposited before capture. In most scyliorhinids, only the right ovary is functional (Hamlett and Koob 1999), and egg cases on the right side were always more developed and farther down the uterus than the left.

Variability in reproductive development and size at maturity

Sizes at maturity determined in this study were different from those determined at lower latitudes by Cross (1988) and Balart et al. (2000). In southern California, Cross (1988) determined that *A. brunneus* males reached sexual maturity between 450 and 500 mm TL and *P. xaniurus* between 375 and 425 mm TL. Balart et al. (2000) determined reproductive maturity in *P. xaniurus* to occur at 340 mm TL off Baja California Sur. These estimated sizes are substantially less than values for TL_{50} determined in this study for *A. brunneus* and *P. xaniurus*, although the estimate by Cross (1988) for *A. brunneus* falls within the range of the smallest mature and largest immature males found in southern California. Size at sexual maturity can vary over time, as a result of changes in population size, environmental conditions, or geographic clines (Horie and Tanaka 2000). The studies by Cross (1988) and Balart et al. (2000) may have provided different size at maturity results because of smaller sample sizes or fluctuation in population structure or temperature since the time of their research.

Maturity estimates may also be biased by the technique used. Cross (1988) used relative change in clasper length and gonad weight, while Balart et al. (2000) used clasper length alone. Balart et al. (2000) examined male individuals 117–380 mm TL, which were smaller than the first mature *P. xaniurus* in central California. Adolescent *P. xaniurus* males exhibited asynchronous development of reproductive structures; these
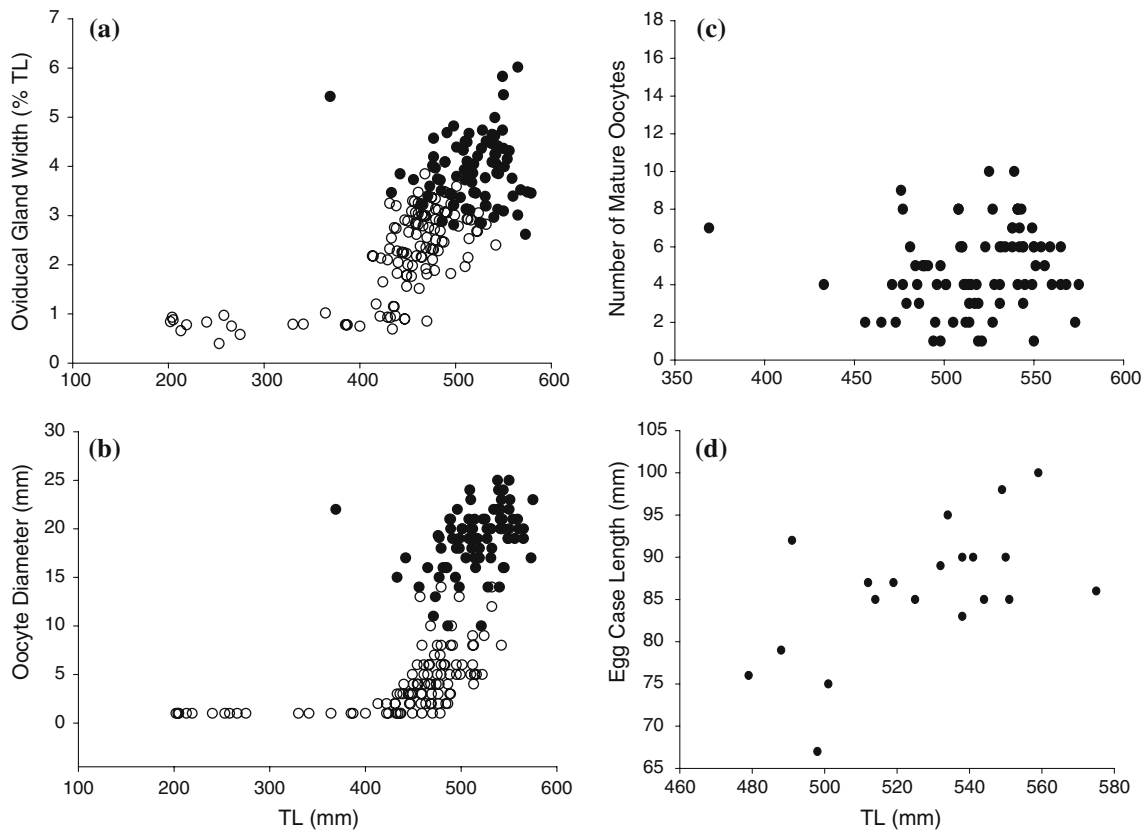
Fig. 10 (a) Oviducal gland width as a percentage of total length for adult (including gravid; closed circles) and juvenile and adolescent (open circles) female *Parmaturus xaniurus* (*n* = 236). (b) Maximum oocyte diameter versus total length of adult (including gravid; closed circles) and juvenile and adolescent (open circles) female *Parmaturus xaniurus* (*n* = 236). (c) Number of mature oocytes versus total length of adult female *Parmaturus xaniurus* (*n* = 89). (d) Egg case length versus female total length for *Parmaturus xaniurus* (*n* = 22)

small individuals had claspers that were not calcified, although of equal lengths as adult claspers, and smaller testes than the adult males. The estimate by Balart et al. (2000) was based only on clasper length, and did not mention calcification of clasper elements. Therefore, it is possible that those individuals were not actually reproductively competent.

As with the males, female *A. brunneus* and *P. xaniurus* also reached TL_{50} at a greater TL than females in previous studies. In British Columbia coastal waters, all females over 450 mm TL were determined to be mature and had vascularized ovaries with oocytes; some also had egg cases (Jones and Geen 1977). These mature females are considerably smaller than the smallest mature *A. brunneus* found from Washington to San Diego (477 mm TL). The

largest *A. brunneus* female found in Washington was immature at 544 mm TL. *Apristurus brunneus* studied by Jones and Geen (1977) were collected in shallower waters, to 369 m depth, where water temperature was approximately 8°C. Elevated seawater temperatures in this shallower region may facilitate faster growth and maturation rates in scyliorhinids, as it does in other elasmobranchs (Parsons 1993). Size at first maturity for female *A. brunneus* tended to be larger above and smaller below 38°N latitude, although this difference was not significant. All female *P. xaniurus* studied by Balart et al. (2000) in Baja California Sur (*n* = 22) were between 108 and 350 mm TL and sexually immature.

Cross (1988) estimated maturity of female *A. brunneus* and *P. xaniurus* between 425 and 475 mm TL in southern California, using oocyte
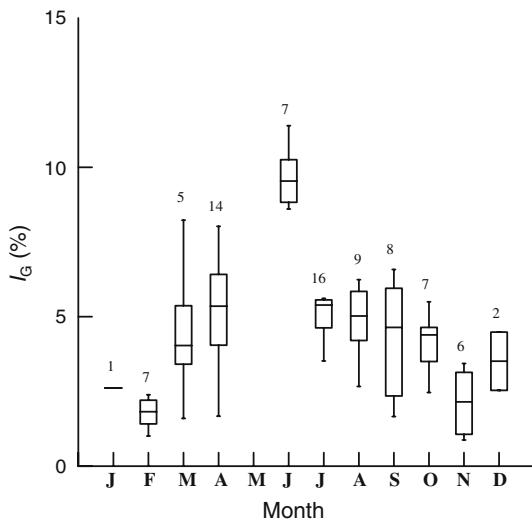
Fig. 11 Gonadosomatic index (I_G) for adult female *Parmaturus xaniurus*. $I_G = (GB^{-1}) \times 100$, where G is the total gonad mass, and B is the total body mass of the specimen. The horizontal line within each box denotes the median for the sample and the box encompasses the range of the central 50% of the values. Bars extending vertically from the box denote 95% confidence from the mean. The number of samples per month is designated above each box plot

number and diameter to determine maturity, whereas this study used oviducal gland development. Using oocyte diameter in the case of *P. xaniurus* is inadequate because females of this species also develop asynchronously and exhibit fully developed and vascularized oocytes while still juveniles. The oocytes in immature *P. xaniurus* females reach diameters comparable with mature females well before the oviducal gland is fully formed.

In most shark species, males reach sexual maturity at a smaller size than females of the same species (Taniuchi 1988; Ellis and Shackley 1997; Cortés 2000; Ebert 2003). One benefit of females maturing at larger sizes is that females that are larger in size tend to have larger or more numerous young, which are less susceptible to predation (Branstetter 1990). Cortés (2000) stated that the number and size of offspring of *A. brunneus* may increase with female TL and that the number of offspring produced by *P. xaniurus* may increase with female TL. *Parmaturus xaniurus* male TL_{50} was 57 mm

shorter than female TL_{50}, whereas sexual maturity was reached at approximately the same lengths for males and females in both *A. brunneus* and *A. kampae*. Within the family Scyliorhinidae, male reproductive maturity occurred at an equal or larger size than females in 10 of 17 oviparous species, although there was no trend among the different genera represented (Cortés 2000).

Male scyliorhinids may grow to an equal or longer maximum TL than females of the same species, whereas females often attain the larger maximum size in most other shark families (Compagno 1984, 1988; Cortés 2000; Ebert 2005). In both *A. brunneus* and *A. kampae*, males reached greater maximum TL than females. However, in *P. xaniurus*, the male maximum TL was smaller than the maximum TL for females. Males in both *Aprosturus* species were approximately the same size as females at TL_{50}, and grew to a longer maximum TL. Cortés (2000) suggested that the males of some elasmobranch species may grow at a faster rate than females of the same species.

There may be distinctions in growth, reproductive maturity, and seasonality based upon variations in bathymetric distribution (Bullis 1967; Carrassón et al. 1992), latitude (Parsons 1993; Horie and Tanaka 2002), or isolation by environmental variables (Horie and Tanaka 2000). Smaller size at maturity estimates could be a factor of the lower latitude of the study areas in Cross (1988) and Balart et al. (2000). Differences in maturity estimates could also be an artifact of the smaller sample sizes in previous studies. It was not possible to determine TL_{50} by regional distribution throughout the entire eastern North Pacific because the sample sizes were too small when subdivided by geographic location.

Reproductive seasonality and fecundity

Previous studies suggested that gonadosomatic and hepatosomatic indices may fluctuate as a result of the production of gametes and the metabolic costs incurred through reproduction (Craik 1978; Sumpter and Dodd 1979; Parsons and Grier 1992; Maruska et al. 1996; Richardson et al. 2000). An increase in I_G implies reproductive readiness, which may occur at first reproductive maturity or at peak times of reproductive activity

(Parsons and Grier 1992; Maruska et al. 1996). Hepatosomatic index values were thought to vary because of the use of hepatic lipids in the formation of gametes or because of metabolic costs incurred during the processes of mate location and copulation (Craik 1978; Sumpter and Dodd 1979). There is an inverse I_G–I_H relationship in some scyliorhinids at the onset of reproductive maturity (Craik 1978; Richardson et al. 2000). In *S. canicula*, I_G increases as I_H decreases during mating seasons, presumably because hepatic lipids are involved in formation of the egg yolk during vitellogenesis (Craik 1978; Sumpter and Dodd 1979; Hamlett and Koob 1999; Koob and Callard 1999). Therefore, variation in the I_H was investigated as an indicator of mating period, because coincident trends of the I_G and I_H should illustrate a seasonal trend of reproductive productivity and metabolic effort. However, it was determined in all three species studied that the I_H did not exhibit significant fluctuation and was not a good indicator of reproductive season or maturity in these deep-sea catsharks.

In contrast, there was a significant seasonal increase in I_G, which may be indicative of the mating period for these species. Other scyliorhinids, including *Cephaloscyllium umbratile* (Taniuchi 1988), *Galeus sauteri* (Chen et al. 1996), and *Scyliorhinus canicula* (Ellis and Shackley 1997), exhibit a seasonal peak in GSI but deposit egg cases year round. *Apristurus brunneus* had an increase in I_G in May and June, but this did not necessarily coincide with an increase in gravid females, as the highest proportion of gravid females was found in the months both preceding and following the increase in I_G. The presence of egg cases in *A. brunneus* year-round coincides with the findings of Cross (1988). *Parmaturus xaniurus* females had in increase in I_G in June and were gravid in subsequent months. However, *P. xaniurus* in captivity at the Monterey Bay Aquarium, Monterey, California, did deposit fertile egg cases in all months during the time in which egg cases were collected for this study. Cross (1988) reported gravid female *P. xaniurus* in January, August, November, and December. Gravid females of all species had fully developed, mature oocytes; therefore, exhibit continuous

oviposition and would be capable of reproducing again after egg case deposition.

The most congruent conclusion is that these species may mate within a defined period of time (April through June) but *A. brunneus* reproduce throughout the year and *P. xaniurus* reproduce within a defined season (approximately July through September). Mature females of both species were either gravid or had mature oocytes throughout the year. Egg vitellogenesis is controlled by the pituitary gland which is in turn controlled by the hypothalamus (Dodd 1972, 1983). Seasonal cues that might stimulate hypothalamus activity and incite reproductive periodicity, such as light or temperature, may not fluctuate seasonally in the deep sea. Therefore, it may be that *A. brunneus*, which are found at greater depths than *P. xaniurus*, are less affected by seasonal reproductive cues.

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