Morphological variation and sexual dimorphism in the California skate, *Raja inornata* Jordan and Gilbert, 1881 from the Gulf of California, Mexico

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Abstract

Knowledge of taxonomy, systematics and life histories of the skates that inhabit the Gulf of California is scarce. Five species have been documented in the Sea of Cortez: *R. cortezensis, R. equatorialis, Raja inornata, R. rhina* and *R. velezi*. The California skate (*R. inornata*) is the most abundant species caught as by-catch during the hake trawl fishery in the Gulf. Intraspecific variation in the external morphology of *R. inornata* from the northern Gulf of California, México is described on the basis of 24 proportional morphometric variables from 45 males (227–525 mm total length TL) and 52 females (226-690 mm TL). Males and females had 9 and 14 proportional dimensions respectively that were isometric with total length (TL). Regression slope and elevation analysis revealed that 9 relationships between TL and morphometric variables were sexually dimorphic. A stepwise discriminant function separated three groups of skates (females and males of *R. inornata* and males of *Raja cortezensis*) and was able to correctly classify 97%, 100% and 100% of the original grouped cases, respectively. The variables that best discriminated between species and sexes were preorbital length, preoral length, distance between fifth gill openings, maximum distance between pelvic fins, and distance from cloaca to anterior caudal fin. The study also revealed that several of the meristic characters examined showed considerable variation and, therefore, should be used with caution in taxonomic studies.

Key words: morphometrics; allometry; sexual dimorphism; *Raja*; Rajiformes; Gulf of California

Introduction

Skates have a wide distribution and occur shallower than 50 m deep (McEachran & Miyake, 1990). In temperate and subpolar seas they are commonly found in shallow waters. At tropical latitudes they are generally restricted to the outer shelf to abyssal depths (< 3,000 m) (Ishiyama, 1967; McEachran & Miyake, 1990). There are at least 15 genera of rajids and at least 136 species, comprising the largest chondrichthyan family (Compagno, 2005).

Although the skate fauna in eastern Tropical Pacific waters is apparently poor in species richness in comparison with other regions, this may, in part, be due to misidentification (McEachran & Miyake, 1984). Knowledge of taxonomy, systematics and life histories of the skates inhabiting the Gulf of California (Sea of Cortez) is scarce. One of the main problems that biologists face in Mexico is the difficulty of correctly identifying the diverse species of elasmobranchs caught by artisanal fleets and fishery vessels (Castillo, 1992). Skates are no exception. Ishiyama (1958, 1967) mentioned the complexity of distinguishing among the differ-

ent species and life stages of rajids (Rajidae), using external morphology. Ishihara & Ishiyama (1985) and Ishihara (1987) stated that the taxonomy of the North Pacific skates remains, confused largely as a result of ambiguous specific characters and insufficient information on the morphological variation of each species.

Few works describing allometric growth and sexual dimorphism in elasmobranches exist. There is scarce information on the variability of the morphometric dimensions of skates with size and between sexes (Braccini & Chiaramonte, 2002). Hubbs & Ishiyama (1968) found that several species of skates often differ in the relative size of many parts of the head, trunk, tail and fins between sexes. Most of the studies of sexual dimorphism in skates and rays have focused on differences in tooth shape (Feduccia & Slaughter, 1974; McEachran, 1976; and Kajiura & Tricas, 1996). Braccini & Chiaramonte (2002) conducted a thorough study of the intraspecific variation in the external morphology of the sand skate, *Psammobatis extenta*, in Argentina.

Thirty–five rajiforms have been documented in Mexican waters (Castro-Aguirre & Espinosa-Pérez, 1996). During the Pacific hake (*Merluccius productus*) trawl fishery in the northern part of the Gulf of California, specimens of 5 skates species are commonly caught as by-catch, the California skate, *R. inornata* (Jordan and Gilbert, 1881); rasptail skate, *R. velezi* (Chirichigno 1973); longnose skate, *R. rhina* (Jordan and Gilbert, 1880); equatorial skate, *R. equatorialis*, (Jordan and Bollman, 1890); and Cortez skate, *R. cortezensis*, McEachran and Miyake, 1988. *R. inornata*, and *R. rhina* are part of the North Pacific *Raja* assemblage ranging from the Bering Sea to the Baja California Peninsula coast (McEachran & Miyake, 1990). These two species also occur in the Gulf of California with *R. cortezensis* considered endemic to the Gulf (McEachran & Miyake, 1988).

R. inornata is the most abundant rajid species caught incidentally during trawling targeting Pacific hake in the northern Gulf of California. It occurs from the Strait of Juan de Fuca, Washington, to central Baja California (Eschmeyer *et al.*, 1983). The first record of *R. inornata* from the Gulf of California was presented by Castro-Aguirre *et al.* (1970) after having captured five skates off Puerto Peñasco, Punta Lobos, and Angel de la Guarda Island (from the north-central Gulf region). Since then, no records or accounts of distribution, life history and ecology of *R. inornata* from the Gulf of California exist.

This contribution is part of a more extensive management-oriented study of *R. inornata* (life history, fisheries, conservation). In this study, morphometric and meristic characters of *R. inornata* were analysed in order to determine changes with growth (ontogenetic) and differences between sexes. Because of the similarity in external morphology between *R. inornata* and *R. cortezensis* (McEachran & Miyake, 1988), additional analysis were conducted between both species, comparing specimens recently collected from the northern Gulf of California and museum specimens, with the aim of finding characters of the external morphology that can be used for a rapid and reliable field identification of both skates.

Material and methods

Sample collection

Samples were collected during March 2003-April 2004 from six commercial fishery trips on board the bottom-trawler "ESCAMA VI" of Puerto Peñasco, Sonora (113°35'N; 31°20'W), and from one trip on the shrimp-trawler "OVIEDO III" of San Felipe, Baja California (31°01'N; 114°49'W), Mexico. Most of the skates collected were obtained from the catches of the "ESCAMA VI", which operated in depths of c. 68-276 m in the northern Gulf of California. The "OVIEDO III" fished in a depth range of c. 28.8–216 m.

Forty-five male (227–525 mm total length, TL) and fifty-two female (226–690 mm TL) *R. inornata* were collected and examined for morphometric and meristic analyses. Abbreviations of 26 morphometric variables used in this study are given in Table 1. The morphometric variables were measured following Bigelow & Schroeder (1953), Hubbs & Ishiyama (1968) and Leible (1988) (Fig. 1). Total length (TL) was measured to the nearest mm. The other morphological variables were measured to the nearest 0.1 mm. The total body mass was also measured to the nearest 1.0 gr. Standard statistics were used for comparisons (*t*-test, ANCOVA's).

TABLE 1. List of morphometric measurements made on *R. inornata* and *R. cortezensis*. Abbreviations are those used in text.

Abbreviation	Description
TL	Total length
DW	Disc width
DL	Disc length
SMW	Snout to maximum width
APECL	Anterior pectoral length
PPL	Posterior pectoral length
PORBL	Preorbital length
IOD	Interorbital distance
OD	Orbital diameter
SL	Spiracle length
ISD	Interspiracular distance
PNL	Prenasal length
PORAL	Preoral length
INL	Internarial length
MW	Mouth width
D1GO	Distance between first gill openings
D5GO	Distance betweenfifth gill openings
DSC	Distance- snout to cloaca
APELL	Anterior pelvic lobe length
PIPL	Posterior internal pelvic lobe length
DPF	Maximum distance between pelvic fins
C1D	Distance cloaca to 1st dorsal fin
C2D	Distance cloaca to 2nd dorsal fin
1DF	1st dorsal fin base
2DF	2nd dorsal fin base
DCC	Distance cloaca to caudal tip

Since *Raja inornata* and *Raja cortezensis* are remarkably similar in external morphology, 13 specimens of *R. cortezensis* were additionally examined to revise the diagnostic characteristics used in its original description. Four specimens were collected during field sampling in the present work, eight were examined from the Ichthyology Collection of the Los Angeles County Museum of Natural History and one was obtained from the Marine Vertebrate Collection of the SCRIPPS Institution of Oceanography.

Data analyses

Allometry. For each morphometric measurement, the mean, standard deviation and coefficient of variation (CV) were calculated separately for each sex. The morphometric dimensions were plotted against TL. To determine their allometric relationships with TL, the variables and TL were $\log_{10}$ transformed and the regression slopes calculated (Peters, 1983). The statistical significance of the resulting slopes were tested using a *t*-test (Braccini & Chiaramonte, 2002). The morphometric variables were then divided into three categories according to Gould (1965) and Fairbairn (1997): positive allometry (+*A*), also called "hyperallometry", when the slope (the allometry coefficient) was significantly >1.0 and the proportional variable increased relative to TL; negative allometry (-*A*) ("hypoallometry"), when the slope was significantly <1.0 and the proportional

variable decreased relative to TL; and isometry or "geometric similarity" (*I*) when the slope showed a non-significant difference from 1.0, indicating direct proportionality between the variable and TL.
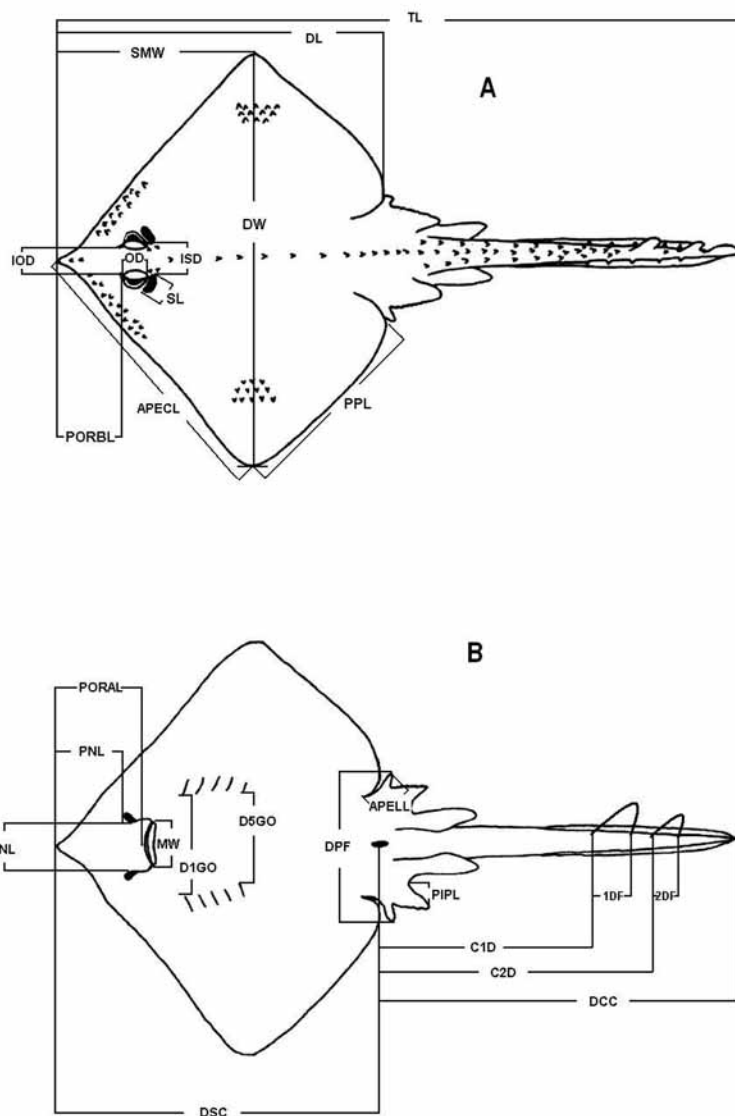

FIGURE 1. Morphometric measurements made on *R. inornata* and *R. cortezensis*. (A) Dorsal and (B) ventral views (see table 1 for definitions)(Figure from McEachran & Notarbartolo di Sciara, 1995).

Sexual dimorphism

To examine sexual differences in the morphometric dimensions of *R. inornata* each variable was plotted against TL and the regression slope and elevation were calculated. The possible differences among the linear regressions (if slopes and elevations are homeogeneous) between males and females were tested by ANCO-VAs (Zar, 1999).

Meristics

Orbital, middorsal and interdorsal thorns were counted in both sexes of *R. inornata*. Malar and alar spines were counted in males. Numbers of precaudal and total vertebrae were recorded from 33 females (354–589 mm TL) and 30 males (435–520 mm TL). The jaws of 33 males (228–560 mm TL) and 55 females (170–613 mm TL) of *R. inornata* were extracted, cleaned, dried and examined. The number of rows of teeth each jaw

was counted, and the variation in dentition between sexes and sizes was documented. Teeth were classified into two groups on the basis of morphology: 1) teeth with rounded cusps (*R*) and, 2) teeth with pointed cusps (*P*) (McEachran & Stehmann, 1984; Braccini & Chiaramonte, 2002).

Comparison between *R. inornata* and *R. cortezensis*

To investigate morphometric differences between *R. inornata* and *R. cortezensis* a forward stepwise discriminant analysis (DA stepwise) was conducted for three groups of individuals: males and females of *R. inornata* and males of *R. cortezensis*; using 18 morphometric variables. Discriminant analysis assumes that groups have equal dispersions, specifically that the variances of the discriminant variables be the same in the respective populations from which the groups of entities have been drawn (McGarigal *et al.* 2000). To test the normality of canonical scores homogeneity of variance between groups, the Levene's test was used upon the distribution of the residuals from an analysis of variance (ANOVA) conducted on each discriminant variable. To test the multivariate normality of the original data structure skewness, kurtosis and normality of the canonical scores were evaluated. Normal probability plots of the same scores also were examined. To interpret the canonical functions the signs and magnitudes of the standardized canonical coefficients were used. To compare the relative magnitudes of the eigenvalues and determine the amount of the total discriminatory power is accounted for each function the relative percent variance (Φ_i) was calculated. The canonical correlation coefficient (R_{ci}), a measure of the multiple correlation between the set of discriminating variables and the corresponding canonical function, also was computed (McGarigal *et al.* 2000).

To diminish the effect of allometry and because sexual dimorphism is generally more conspicuous in mature individuals (Braccini & Chiaramonte, 2002), only mature specimens were used. These comprised 35 males and 39 females of *R. inornata* and 11 males of *R. cortezensis*; maturity was based on relative clasper calcification, testes length and clasper gland length in males and relative oviducal gland width, oocyte diameter, ovaries development or the presence of egg capsules in females. Mature male *R. inornata* was ≥ 447 mm TL, whereas mature females were ≥ 470 mm TL. The 11 males of *R. cortezensis* examined in this study were all mature (≥ 321 mm TL).

Results

Morphometrics

A summary of the descriptive statistics of the morphometric variables expressed as proportional dimensions (percentage of TL) is given in Table 2. The morphometric variables that showed a CV>10% were SL, 2DF, IOD, and APECL in males, and SL, and APECL in females. Conversely, the largest measurements (DW, DL, DSC, and DCC) presented a CV<4.2% in both sexes (Table 2).

Allometry

Females presented the larger %TL in sixteen morphometric characters, whereas males showed higher proportions in eight. (Table 2). Males presented twelve dimensions with negative allometry (–A) (*t*- test, d.f.=43, $P < 0.05$), and the rest had isometric relationships (*I*) (Table 3). In females five dimensions had +A relationships ($P < 0.05$) and two measurements –A relationships with TL (*t*-test, d.f.=50, $P < 0.05$). Fourteen dimensions showed *I* with TL (Table 3).

Sexual dimorphism

An ANCOVA test on 26 morphometric variables revealed that SMW, APECL, PPL, PORBL, PNL, PORAL, D1GO, D5GO, and DCC were significantly different ($P < 0.05$) between males and females (dimorphic). Only the dimensions SMW, APECL and DCC were larger in males

TABLE 2. Morphometric variables expressed as proportional dimensions (percentage of al length).

	Males (n = 45)				Females (n = 52)			
	Range	Mean.	S.D.	CV	Range	Mean	S.D.	CV
TL (mm)	227.0–525.0	476.1	61.4	13.0	226.0–690.0	505.0	101.0	20.0
DW	60.0–70.8	65.3	2.6	4.1	60.8–71.7	67.8	2.0	2.9
DL	48.4–58.4	53.3	2.2	4.2	48.5–58.1	55.1	1.6	3.0
SMW	28.4–37.2	32.7	2.4	7.5	27.2–38.8	34.0	2.2	6.5
APECL	41.6–51.7	46.1	2.0	4.4	42.7–51.3	47.5	1.7	3.7
PPL	25.5–34.3	29.3	2.3	8.0	25.6–35.3	31.0	1.8	5.8
PORBL	11.4–15.8	13.2	1.0	7.3	13.0–17.2	15.5	0.7	4.7
IOD	3.4–5.7	4.3	0.5	11.1	3.8–6.6	4.7	0.4	8.6
OD	1.6–3.8	2.8	0.5	17.3	1.5–3.8	2.6	0.4	17.5
SL	2.4–4.0	3.2	0.4	12.0	2.5–4.8	3.4	0.4	12.0
ISD	5.2–7.0	6.0	0.3	6.1	5.2–6.8	6.2	0.3	4.8
PNL	9.0–12.5	10.3	0.7	7.5	10.6–13.3	12.3	0.5	4.2
PORAL	12.0–16.1	13.5	0.8	6.7	13.5–17.3	16.0	0.6	4.0
INL	6.2–8.5	7.3	0.4	6.4	6.5–9.0	8.0	0.3	4.6
MW	7.2–9.9	8.4	0.5	5.8	7.5–9.6	8.5	0.4	5.1
D1GO	13.6–17.3	15.5	0.8	5.6	15.5–18.7	17.0	0.7	4.6
D5GO	6.3–8.7	7.7	0.6	8.0	7.7–11.0	9.5	0.6	6.6
DSC	47.0–54.6	49.6	1.4	3.0	47.1–56.4	52.7	2.0	4.0
APELL	8.3–14.3	11.8	1.2	10.4	9.2–14.4	11.2	1.2	11.1
PIPL	1.2–5.8	4.4	1.0	22.5	4.1–9.3	6.7	1.0	15.4
DPF	27.7–35.3	32.0	2.0	6.0	21.3–37.6	32.3	3.1	9.7
C1D	30.0–37.0	33.2	1.6	4.9	24.6–35.8	30.4	1.9	6.5
C2D	30.0–37.0	33.2	1.6	4.9	24.5–35.8	30.4	2.0	6.5
1DF	4.2–6.0	5.0	0.3	6.6	3.7–5.6	4.7	0.3	8.0
2DF	3.3–6.5	5.5	0.6	11.1	3.7–5.6	4.7	0.3	8.0
DCC	47.2–53.7	49.8	1.2	2.6	39.8–51.2	46.0	2.0	4.2

Meristics

The counts of spines and thorns series revealed a significant variability among sizes and sexes. Females showed a larger number of orbital, middorsal and interdorsal thorns (Table 4). For the orbital thorns series, which in this study included preorbital, postorbital and spiracular thorns, there was a significant relationship between TL and thorn number in both sexes (females, $r^2=0.64$, $F_{1,52}=95.78$, $P <0.05$; males, $r^2=0.16$, $F_{1,45}=8.58$, $P <0.05$) (Fig. 2). Only in females a significant relationship was observed between the number of middorsal thorns and TL (females, $r^2=0.32$, $F_{1,55}= 25.97$, $P <0.005$; males, $r^2=0.015$, $F_{1,46}=0.70$, $P <0.404$) (Fig. 3). Males presented 1 to 3 thorn rows in the tail, two lateral rows and one median row. The smallest specimens (291–493 mm TL) did not present lateral rows. In most females 3 thorn rows were observed in the tail, although some larger females (492–613 mm TL) had 5 thorn rows (parallel and lateral rows). The males presented a range of 7–24 malar thorns arranged in a path of 2–3 rows with 11–21 alar thorns per row. Malar and alar thorns were not observed in males <394 mm TL. The number of pectoral radials, precaudal vertebrae and total number of vertebrae between sexes were similar (Table 4).
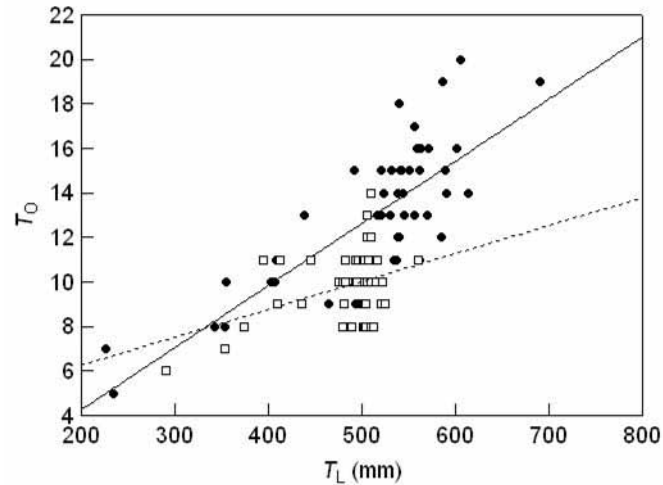
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FIGURE 2. Relationship between the number of orbital thorns (T_O) and total length. Males (□), T_O =0.01 TL+3.75; r^2=0.16; females (●), T_O=0.02 TL+1.31; r^2=0.64.

TABLE 3. Allometric analysis on morphometric measurements for male and female *R. inornata*. Values given for log *a* (intercept) and *b* (slope of the regression, "allometry coefficient") are from the equation log (dimension) = log *a* + *b** log (TL). Increment patterns are: +*A*, positive allometry; -*A*, negative allometry; *I*, isometry.

Dimensión	Males (n = 45)				Females (n = 52)			
	Log *a*	*b*	*r²*	Increment	Log *a*	*b*	*r²*	Increment
DW	0.053	0.910	0.93	- *A* (*P*<0.05)	-0.178	1.004	0.99	*I* (*P*=0.28)
DL	-0.305	1.011	0.93	*I* (*P*=0.47)	-0.324	1.024	0.99	*I* (*P*=1.0)
SMW	-0.586	1.037	0.71	*I* (*P*=0.67)	-0.728	1.096	0.94	+ *A* (*P*<0.05)
APECL	0.093	0.839	0.83	- *A* (*P*<0.05)	-0.399	1.028	0.98	*I* (*P*=1.0)
PPL	0.704	0.539	0.36	- *A* (*P*<0.05)	-0.346	0.939	0.93	*I* (*P*=1.0)
PORBL	-0.091	0.705	0.80	- *A* (*P*<0.05)	-0.841	1.011	0.96	*I* (*P*=0.88)
IOD	-0.769	0.777	0.59	- *A* (*P*<0.05)	-1.560	1.088	0.92	+ *A* (*P*<0.05)
ISD	-0.562	0.753	0.85	- *A* (*P*<0.05)	-0.837	0.861	0.92	- *A* (*P*<0.05)
PNL	-0.157	0.691	0.67	- *A* (*P*<0.05)	-0.875	0.987	0.96	*I* (*P*=0.96)
PORAL	-0.125	0.721	0.84	- *A* (*P*<0.05)	-0.709	0.967	0.96	*I* (*P*=1.0)
INL	-0.602	0.800	0.68	- *A* (*P*<0.05)	-1.356	1.096	0.93	+ *A* (*P*<0.05)
MW	-0.921	0.942	0.87	*I* (*P*=1.0)	-0.992	0.971	0.95	*I* (*P*=1.0)
D1GO	-0.209	0.776	0.75	- *A* (*P*<0.05)	-0.855	1.031	0.96	*I* (*P*=1.0)
D5GO	0.186	0.515	0.38	- *A* (*P*<0.05)	-1.297	1.101	0.94	+ *A* (*P*<0.05)
DSC	-0.015	0.893	0.85	- *A* (*P*<0.05)	-0.509	1.085	0.97	+ *A* (*P*<0.05)
DPF	-0.219	0.897	0.74	*I* (*P*=1.0)	-0.727	1.087	0.83	*I* (*P*=1.0)
C1D	-0.564	1.031	0.85	*I* (*P*=0.88)	-0.207	0.891	0.49	*I* (*P*=1.0)
C2D	-0.225	0.937	0.54	*I* (*P*=0.90)	-0.080	0.876	0.55	*I* (*P*=1.0)
1DF	-1.529	1.082	0.40	*I* (*P*=0.68)	-1.452	1.047	0.90	*I* (*P*=0.99)
2DF	-1.297	1.014	0.44	*I* (*P*=0.07)	-1.029	0.897	0.76	*I* (*P*=1.0)
DCC	-0.377	1.028	0.97	*I* (*P*=1.0)	-0.017	0.881	0.98	- *A* (*P*<0.05)

TABLE 4. Meristic values of *R. inornata*, number of thorns, hooks, pectoral radials, vertebrae and tooth rows. Values in parentheses are sample size.

	Males (Range)	Females (Range)
Orbital thorns	6–14 (47)	5–20 (56)
Middorsal thorns	0–8 (48)	2–13 (57)
Interdorsal thorns	1–6 (40)	1–9 (43)
Alar hooks	11–21 (40)	
Malar hooks	7–24 (40)	
Pectoral radials	72–78 (35)	66–78 (34)
Precaudal vertebrae	23–28 (30)	23–28 (33)
Total vertebrae	96–114 (11)	102–116 (10)
Tooth rows (upper jaw)	34–46 (33)	32–47 (55)
Tooth rows (lower jaw)	34–43 (33)	36–46 (55)

Raja inornata shows a conspicuous sexual dimorphism in dental morphology. Teeth in both sexes are arranged in transverse parallel rows. Rhomboidal teeth with pointed cusps oriented posteriorly are presented in adult and juvenile females. Symphysial teeth have developed a longer cusp than the commissural teeth (Fig. 4A and 4B). In males there was a transition from rounded cusps (in males <412 mm TL) to teeth with a long sharp (pointed) cusp (in males >480 mm TL) (Fig. 4C and 4D). Male commissural teeth are rhomboidal like those observed in females. Tooth row counts in superior jaws do not differ significantly between sexes, but inferior jaws row counts did ($t= 3.571$, df= 84, $P< 0.001$). Number of tooth rows was not related to size of fish in either sex (females: $r^2= 0.001$, $F_{1,53}= 0.094$, $P= 0.759$; males: $r^2= 0.003$, $F_{1,31} =0.012$, $P= 0.913$).
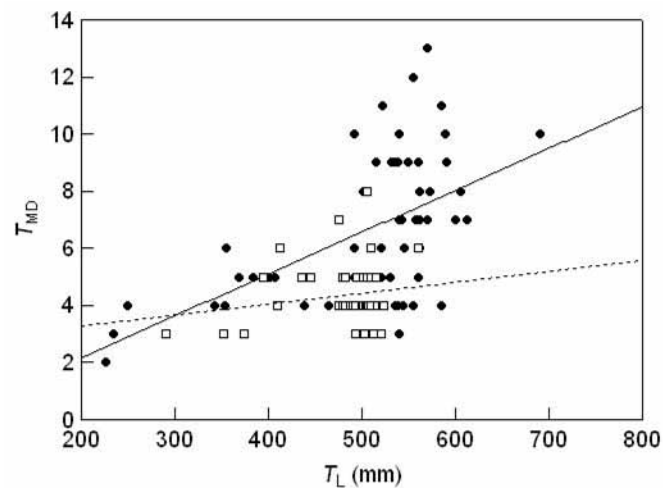

FIGURE 3. Relationship between the number of middorsal thorns (T_{MD}) and total length. Males (□), $T_{MD} =0.003$ TL + 2.51; r^2=0.16; females (●), $T_{MD} =0.01$ TL – 0.76; r^2=0.32.

R.inornata versus *R. cortezensis*

Shea (1985) pointed out the advantage of multivariate analysis in simultaneously considering large sets of variables, and the potential for discovering biologically meaningful patterns of covariation among interrelated variables that are not necessarily discernible in the original data. Taxonomic groups can be identified using multivariate statistical analyses such as discriminant analysis (Siqueiros-Beltrones, 1990, Braccini & Chiaramonte, 2002 and Aguiar *et al.* 2004).
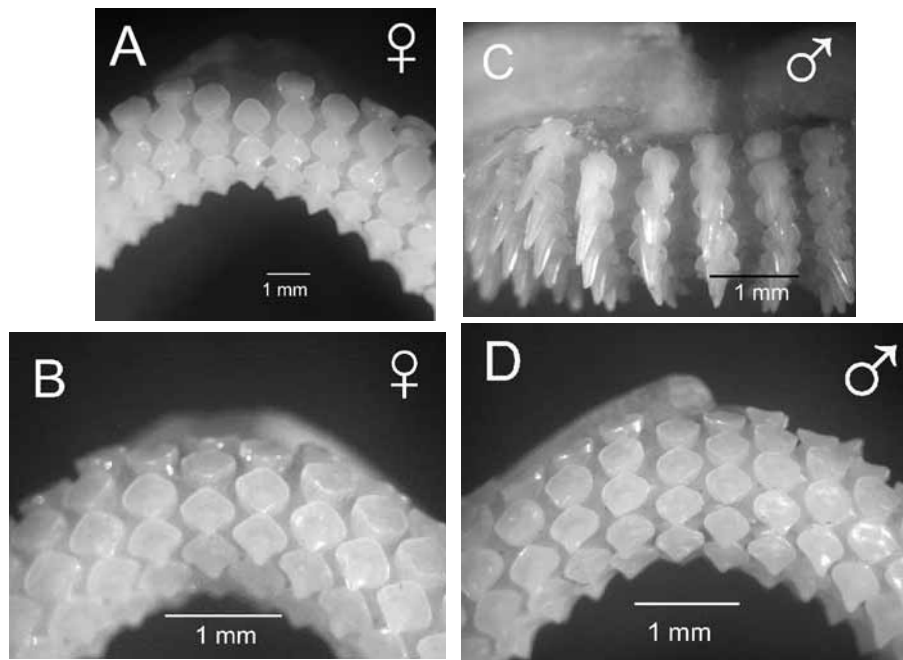
FIGURE 4. Photographs of male and female upper jaw teeth (symphysial teeth) of juveniles and adults of *Raja inornata*: (A) mature female, 570 mm LT; (B) juvenile female, 262 mm LT; (C) mature male, 500 LT and (D) juvenile male, 262 mm LT (photographs 25 X).

From the 18 original morphometric characters intended to be used for the discriminant analysis, TL, DW, DL and APECL were eliminated because they showed a strong pairwise correlations ($r= 0.7$) () and 2 more (C1D and C2D) because the analysis of their residuals (ANOVAs) showed a lack of normality. The discriminant analysis therefore used 12 morphometric characters. The generated model that best discriminated among groups was highly significant (Wilks´ Lambda $=0.023$; $F=86.75$, $P<0.000$). The variables that best distinguished among the three groups were: DCC, D5GO, PORBL, DPF and PORAL. The highest partial Wilk's was determined for PORAL, 0.943 (Table 5).

TABLE 5. Variables selected by the stepwise canonical discriminant analysis. Wilks'lambda = 0.023, $F= 86.753$, $p= 0.000$.

Variables	Wilks´ Lambda	Partial Wilks´Lambda	P
LPORB	0.025	0.900	0.016
PORAL	0.024	0.943	0.246
D5GO	0.026	0.882	0.007
DPF	0.025	0.901	0.017
DCC	0.051	0.453	0.000

The DA generated two discriminant functions (canonical variables) that were formed by five variables with their respective coefficients, both unstandardized and standardized. The first discriminant function clearly separated females of *R. inornata* from males of *R. inornata* and *R. cortezensis* (Fig. 6). The negative canonical coefficients of males (both species) contrast with the positive values calculated for females of *R. inornata*. The first discriminant function showed that DCC was the main character which discriminated between females and males of either species. The second function separated each group of males using mainly the variables PORAL and D5GO, which showed negative coefficients. The relative percent variance (Φ_1) of

the first discriminant function was 80.4% and 19.6% for the second. The canonical correlation coefficient (R_{CI}) of the first function was 0.957 and 0.616 for the second function.

The classification of specimens based on classification coefficients was correct in 97% of females of *R. inornata* (1 female misclassified), 100% of *R. inornata* males and 100% of males of *R. cortezensis.* Means of canonical variables for the first discriminant function were: *R. inornata* males -1.756, *R. inornata* females 3.224 and *R. cortezensis* males -5.841. The canonical scores of group means for the second discriminant function were: *R. inornata* males 1.698, *R. inornata* females -0.687 and *R. cortezensis* -2.969. The statistic test for normality, Shapiro-Wilk (W) showed that all the canonical scores for both discriminant functions were distributed normally.
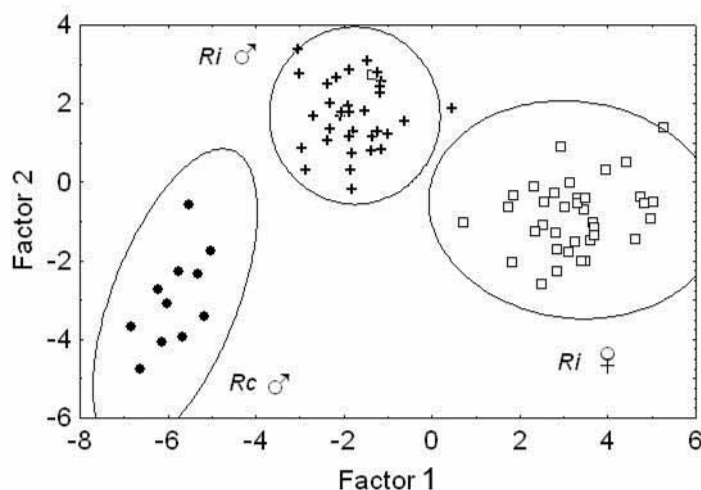
FIGURE 5. Bi-plot of canonical scores for factors 1 and 2 from DA of female and male *R. inornata* and male *R. cortezensis*. Discriminant analysis based on 12 morphometric characters. (+) *R. inornata*-males; (□) *R. inornata*-females and (o) *R. cortezensis*-males. (read text for explaination).

Discussion

Morphometric data

The proportional dimensions of *R. inornata* recorded by McEachran & Miyake (1988) were obtained from 24 specimens collected from southern California waters (USA) and the west coast of Baja Peninsula, including the central region of the Gulf of California (Mexico). Although McEachran & Miyake (1988) combined the morphometric data of both sexes, TL ranges from their study (220–658 mm TL) and the present work (males=227–525, females=226–690 mm TL) were similar. We obtained morphometric data for *R. inornata* from 45 males and 52 females collected exclusively from the northern Gulf of California. Comparing 20 morphological dimensions expressed as percentage of total length from McEachran & Miyake (1988) with those of the present study we found that 18 measurements have similar range of percentage.

Mamuris *et al.* (1998) suggested that low within–sex variation in morphological characters indicates that each sex sample consist of a phenotypically homogeneous group. In the present study, 26 morphological dimensions of males and females of *R. inornata* showed low %CV values, the majority ranging from 2.6 to 15% which corresponds to a homogeneous sample. This homogeneity is likely accentuated because 86.6% *R. inornata* individuals were mature. Because McEachran & Miyake (1988) did not provide the standard desviations of proportional measurements of *Raja inornata* used in their description of *R. cortezensis*, it was not possible to compare the present data in terms of %CV.

Braccini & Chiaramonte (2002) found in their study on variation in the external morphology of the sand skate *Psammobatis extenta*, that the morphological characters that showed the lowest CV values were DL,

DW, DSC and DCC. In the present study the same characters in *Raja inornata* showed the lowest CV percentages. As mentioned in Bass (1973) and Braccini & Chiaramonte (2002), this is what would be expected for the longest proportional dimensions. These low CV% values contrast with the high CV percentages (23–41%) that were calculated using the mean and standard deviation of 20 morphological characters measured in two species of *Myliobatis* that occur on the Brazilian coast (Aguiar *et al.* 2004). Those differences in the pattern of the CV can be explained on basis of the size and body form differences between skates and rays.

Allometry

During the last two decades, morphological analyses conducted on rajiformes comprise the description of new species (McEachran & Miyake, 1984, Ishihara & Ishiyama, 1985, McEachran & Matheson, 1985, McEachran & Miyake, 1988), updated revisions of genera (e.g., Ishihara, 1987), and studies on morphological variation over the geographic distribution (e.g., McEachran, 1977, McEachran & Compagno, 1979, McEachran *et al.* 1989). In these studies, the authors provided lists of several morphological characters examined and measured on a few museum specimens or recently collected skates, mostly adult specimens. Because of the difficulty of collecting skates in different developmental stages, there are few studies that describe the ontogenetic changes in rajiformes. In their morphometric analysis by sex of *Psammobatis extenta*, Braccini & Chiaramonte (2002) found that in males there was a tendency for 2 of 15 measurements to increase and for 5 of 15 measurements to decrease with TL. In females the tendency was similar, 2 dimensions showing +*A* and 4, -*A*. In *Raja inornata* from 21 proportional dimensions, males presented twelve –*A* relationships with TL, females had five +*A* and two –*A* relationships. Most of the morphological characters in both sexes presented an isometric growth.

Comparing the allometric patterns between *P. extenta* and *R. inornata*, we observed that PORBL, ISD, and PNL showed a negative allometric coefficient in males. In females of both species, ISD was the only character that presented a negative allometric coefficient. PORBL and PNL are morphometric characters with diagnostic value to compare *Raja* species of the Eastern Pacific, including the Gulf of California (McEachran & Notarbartolo, 1995).

Sexual dimorphism

Results indicated that there is a significant amount of sexual dimorphism in *R. inornata*. The dimorphic measurements that presented a higher slope in females were D5GO, IOD, DPF, and DSC. All were isometric with the exception of DSC and D5GO which exhibited a +*A* relationship with TL. The measurements of DSC and D5GO comprise part of the central disc area inside of which is the body cavity, containing the digestive and urogenital tracts. Being oviparous, females need a large space inside the cavity to afford and produce large egg capsules that contain sufficient yolk to nourish the embryo through development. A positive allometric growth in this area can be explained in terms of reproduction efficiency. Also there is a relative displacement of the position of the cloaca in adult females of *R. inornata*, similar to that observed in females of *P. extenta* by Braccini & Chiaramonte (2002).

Badyaev (2002) stated that in many species, the most sexually dimorphic growth occurs during short periods late in development, when animals reach sexual maturity. The few juvenile *R. inornata* examined in the present study (8 females and 3 males) showed similar dimensions in morphometric measurements suggesting that the dimorphic differences begin during sexual maturation. Badyaev (2002) mentioned that the sexual size dimorphism is favored by selection acting during adult stages when differences in size contribute to the reproductive success of each sex. Because female skates produce large capsules (oviparity) they need to develop a significantly enlarged coelomic cavity. In contrast, male morphology appear to be directed towards efficiency during the mating process, having smaller bodies than females with elongate copulatory organs (claspers) to reach the cloaca in the ventral posterior area of the females body. Those differences in adult sizes observed in the sexes of *R. inornata* could contribute to its reproductive success as have been reported in other species.

Braccini & Chiaramonte (2002) observed in *Psammobatis extenta* significant differences in skull and jaw of adult males with PORBL, PORAL, PNL decreasing relative to increasing TL, whereas WM and INL increased proportionately. In adult males of *R. inornata,* also showed similar negative allometry relationships PORBL, PNL and PORAL. Females presented an isometric pattern for the same variables. Sexual dimorphism in *R. inornata* is reflected in the size and form of the disc and rostrum of the skate, which are conspicuously larger in females. Those variables were used by McEachran and Miyake (1988) for the main diagnostic differences between *R. inornata* and *R. cortezensis*.

Meristics

Leible (1988), observing skates of South America waters, (*Raja flavirostris*, *R. trachyderma*, *R. miraletus*, *Bathyraja magellanica*, *B. sp.*, *Sympterygia lima*, *S. brevicaudata*, and *Psammobatis scobina*) found thorns and spines to have no taxonomic value because of the high variability in number between sizes and sexes. In *P. extenta* the number of spines varied within each sex (Braccini & Chiaramonte, 2002). However in *R. inornata* a significant positive relationship was found between size and number of thorns (orbital series) in both sexes. The same pattern was observed in the midline dorsal thorns of *P. extenta*, which increase with TL.(Braccini & Chiaramonte, 2002). Malar thorns and alar thorns were observed only in adult males of *Raja inornata* (> 394 mm TL) suggesting its use during courtship (McEachran 1976).

McEachran & Miyake (1988) counted 36–45 tooth rows in the upper jaw of males and females (mean=40.7 rows) of *R. inornata*. The original description and type series for *R. inornata* was 38 tooth rows (Jordan & Gilbert, 1881). In this study, mature males and females of *R. inornata* showed a sexual heterodonty but in juveniles the teeth were similar between sexes (homodonty). This pattern of dental sexual dimorphism has been observed in other batoids (Kajimura & Tricas, 1996, Sáez & Lamilla, 2004, and Braccini & Chiaramonte, 2002). McEachran (1976), described changes in the dentition and shape of the mouth of some skate species upon reaching maturity. Sexual dimorphism in the dentition of skates has been attributed to differences in feeding habits (Feduccia & Slaughter, 1974), although McEachran (1976) refuted this and concluded that males used their jaws to hold the female during copulation. The differences in dental morphology observed in adult males and females of *R. inornata* agree with the observations of Braccini & Chiaramonte, 2002 on *P. extenta*, which were interpreted as an adaptation of males and females to their different reproductive roles. With mature females of *R. inornata* possessing larger bodies it is apparently necessary that males develop additional structures such as alar spines and tooth with long and pointed cusps, to hold females during mating. Supporting this conclusion is that adult males and females *R. inornata* have similar diets (Castillo & Mendez, unpub. data).

R. inornata versus *R. cortezensis*

The DA performed on morphometric characters between male and female *R. inornata* and male *R. cortezensis* was consistent with the dimorphic analysis performed between both sexes of *R. inornata,* because the first discriminant function discriminated perfectly between females of *R. inornata* and males of both species. From the 9 variables statistically dimorphic, 3 where used in the DA model (DCC, D5GO and PORBL) to separate the three groups.

The variables that were most variable between groups were DCC, D5GO, PORBL, DPF, and PORAL. Those variables include some with largest dimensions, and some from the cranium. A Wilks' lambda of 0.0 denotes perfect discriminatory power of the model, meanwhile the partial Wilks' lambda accounts for the unique contribution of each variable to the discrimination between groups (StatSoft, 1998). According to the DA model, PORAL was the variable with the lowest Wilk's lambda and the highest partial Wilk's lambda. PORAL was therefore the variable that contributed most to group discrimination.

Converting the eigenvalues of the canonical functions obtained by the model to relative percentages (relative percent variance, RPV), it was possible to determine how much of the total discriminatory power was

accounted by the first discriminant function (80.4%), which was sufficient to explain group differences. Using the canonical correlation criterion (R_c), we measured the multiple correlation between the set of discriminating variables and the corresponding canonical function (McGarigal *et al.* 2000). The multiple correlation between the five discriminating variables and the first canonical function was 0.957. The squared canonical correlation indicated that 91.6 percent of the total canonical variation is explained by group differences (females and males groups). The gradient defined by the first canonical function is therefore very much a function of group differences.

The second canonical function discriminated males of *R. inornata* and *R. cortezensis*, which are highly similar in their external morphology. This similarity was reflected in the low relative percent variance of this function (19.6%). The correlation between variables and the second function was 0.616 and the squared correlation accounted 37.9% of the canonical variation. The PORAL and D5GO dimensions were the primary variables that the DA model used to discriminate between males of the two species.

The morphometric characters selected by the DA model coincided with those found through a principal component analysis conducted by McEachran & Miyake (1988), which separated the two species based in 21 morphometric variables. In their analysis the two species were separated along the first principal component axis, which was heavily loaded on three snout measurements (PORBL, PORAL and PNL) and two disc measurements (DW and DL). For the correct separation of males of *R. inornata* and *R. cortezensis* in the field, the dimensions of the rostrum are the diagnostic features as McEachran & Miyake suggested in 1988.

There was also a striking difference in the claspers of the two species. The accessory terminal 1 cartilage (atr_1) in *R. inornata* is acutely pointed, whereas in *R. cortezensis* it is rounded. McEachran & Miyake (1988) found differences in claspers of the two species, particularly in the dorsal terminal 1 cartilage (dtr_1) and the ventral terminal cartilage (vtr), but they did not observe any difference in atr_1 cartilage. McEachran & Miyake (1988) based their description of *R. cortezensis* on the examination nine males. During the present study the authors had the opportunity to collect two adult females of *R. cortezensis* in March 2004 (375 mm TL and 370 mm TL). The smaller disc size (narrower and shorter disc) and the short rostral cartilage in males and females of adults identified *R. cortezensis* from *R. inornata* in the field. The correct identification of newborn and juveniles stages from both skates continues to be problematic. In the present work, we examined only 11 juveniles and 1 embryo of *R. inornata,* so comparisons with early life stages of *R. cortezensis* were not possible.

This study describes in detail variation in the external morphology of *R. inornata*, to characterize its pattern of sexual dimorphism and to model allometry in several morphometric variables. This statistical approach used to investigate the allometric nature of diverse morphometric characters was useful in understanding why some morphological characters possess a major diagnostic value in skate taxonomy. In *R. inornata*, these diagnostic characters are the snout dimensions. The great individual variation of spination and tooth rows in both sexes of *R. inornata* confirmed Leible´s (1988) assertion that these are not accurate tools in determining species, particularly in the case of the comparison with *R. cortezensis* and other skates common in the area.

The study of intraspecific morphological variation among skates continues to be essential, particularly in regions where knowledge of their taxonomy and life histories is poor. Even in recent years, in which ecological and evolutionary studies have been advanced by the new techniques in molecular genetics, molecular phylogenetic studies are dependent on morphological data because genetic samples are typically collected from specimens that have been identified as belonging to morphologically defined species on the basis of shared morphological attributes (MacLeod & Forey, 2002).

The correct identification of exploited skates from the northern Gulf of California will contribute to the collection of reliable life history data on those species.

Material examined

Raja cortezensis.- LACM W53-82, 2 (paratypes), 387 and 387 mm, mature males, Bahía de San Rafael, Gulf of California, 24 April 1953; LACM 8836-15, 5 (paratypes) 347, 324 , 321, 326 and 345, mm, matures males, San Inés Bay, Gulf of California, 11 April 1964; LACM 8842-16 (holotype), 358 mm, mature male, off Punta Conception, Gulf of California 12 April 1964; SIO 65-250 (paratype), 340 mm, mature male, off Punta Gorda, 24° 11.5' N, 109° 59.4' W, 2 July, 1965.

Acknowledgements

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