Captive biology of the pelagic stingray,
Dasyatis violacea (Bonaparte, 1832)

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Abstract. Pelagic stingrays, *Dasyatis violacea*, were collected in southern California in summer–autumn 1994–97. The smallest, 40–45 cm disc width (DW) and 2 kg, were estimated to approach age two. In captive growth and feeding experiments from March 1995 to August 2000, the largest male reached 68 cm DW and 12 kg at estimated age 7 years, and the largest female reached 96 cm DW and 49 kg at estimated age 9 years. The growth data could be fitted with both Gompertz and von Bertalanffy growth functions, but the former produced more reasonable values for size at birth, maximum size, and longevity. Consumption of squid was 6–7% of body mass (BM) per day for juveniles 2 years old and decreased to 1.25% BM day^{-1} for adults. Food intake for adults was seasonal, with 2 cycles per year with a maximum of ~2.0% and a minimum of 1.0–0.5% BM day^{-1} from July to October 1998. The data for gross conversion efficiency ($K1$, based on energy values), collected at 20°C with daily feeding to satiation, could be fitted with a linear regression in the estimated mean age range of 3–6 years ($K1 = 0.37 - 0.055$ Age).

Introduction

During the past 25 years, advancements in husbandry techniques and design of large aquarium systems have allowed public aquarium staff and scientific researchers to collect, transport and maintain elasmobranchs for extended periods in captivity (e.g. Gruber and Keyes 1981; Cliff and Thurman 1984; Andrews and Jones 1990; Murru 1990; Uchida *et al.* 1990; Smith 1992). This has allowed research into feeding rations, and age and growth of larger more active elasmobranchs and those that cannot be aged by traditional techniques using the vertebrae (Wass 1973; Gruber and Stout 1983; Casey *et al.* 1985; Cailliet *et al.* 1986; Branstetter 1987; Taylor and Wisner 1989; Schmid *et al.* 1990; Wetherbee *et al.* 1990; Van Dykhuizen and Mollet 1992; Schmid and Murru 1994; Henningsen 1996; Carlson and Parsons 1997). This has led to comparison of age and growth of captive and wild sharks, and validation of age and growth studies conducted on wild sharks. Few captive-growth studies have been published for rays (Natanson 1993; Henningsen 1996). Growth studies for rays in the wild (Babel 1967; Martin and Cailliet 1988; Villavicencio *et al.* 1994; Cowley 1997; Timmons and Bray 1997) and growth studies for skates were reviewed by Gallagher and Nolan (1999). Ezcurra (2001) reviewed available data on metabolic rates for rays.

The pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832), is a relatively small ray (maximum disc width, DW, 80 cm) in the family Dasyatidae; life-history parameters are not well known (Ranzi and Zezza 1936; Wilson and Beckett 1970; Compagno 1987; Last and Stevens 1994). Mollet (2002) collates data on its distribution off California, Central America and worldwide.

The pelagic stingray has been kept in many aquaria for almost 100 years but few data on age, growth and feeding were collected. Greenwald *et al.* (1997) recorded morphology and shed rates of teeth and of dermal denticles, this being the first shed rate recorded for any batoid. Bourdon and Mollet (1999) gave a preliminary account of the function and design of the dentition. Neer (in press) used vertebrae and estimated ages of 2–10 years for rays caught in southern California (DW 41–75 cm).

The collection of pelagic stingrays in southern California for display at the Monterey Bay Aquarium (MBA) provided an opportunity to collect data under constant temperature and feeding conditions. Here, we present the first major account of estimated age and growth, feeding and gross conversion efficiency ($K1$), reproductive data, and morphometrics of captive pelagic stingrays collected at MBA from 1995 to 2000.

Materials and methods

Collection of specimens

Several collecting trips were carried out during 1993–97. On the NOAA/NMFS shark abundance cruise in July 1994, 14 female rays out

of a total of 115 caught were brought back (Mollet 2002, table 2). These rays were measured and PIT-tagged 7 months after capture, when the first growth and feeding experiment began on 1 March 1995 (Tables 1 and 2). Three males and six females were caught on the October 1995 California Fish and Game cruise off southern California and transported by truck to MBA on 3 November 1995 (J. Neer 1995, personal communication). Three of these rays were transported to Steinhart Aquarium at the end of November and the three smallest rays remaining at MBA were weighed and measured on 5 January 1996 (Table 2). Six rays (1 male, 5 females) caught on the *Shogun* collection trip for opah (*Lampris guttatus*) near San Clemente Island were weighed and measured on 21 October 1997, the day after they were transported to MBA, which was six days after capture (Table 2).

Collection of captive feeding and growth data

Practical considerations at MBA resulted in different experimental conditions during three phases (Table 1). A short-term growth and feeding experiment was carried out from 1 March to 18 October 1995 (Table 1, No. 1). Amounts of food consumed were recorded for one ray and for the other 14 rays combined. The water temperature was lower (17.8°C) than in later experiments. The results of this short-term experiment were not as precise as those of later experiments because *(a)* measurements were taken without the benefit of anaesthesia, *(b)* food fed included fish with wide variation in size-dependent caloric content and size was not recorded, and *(c)* the density of rays was too great to ensure that all rays were fed and this also caused water quality problems at times. During three transition-experiments (T) in the 4600 m³ Outer Bay Waters exhibit, we found that the rays required daily feeding to satiation to avoid adverse interactions with ocean sunfish (*Mola mola*) (Table 1, Nos T1, T2, T3). The feeding results of phase T3 were of interest because they applied to three rays of the same size and about two years old.

A decision to postpone display in the Outer Bay Waters exhibit allowed a long-term (1175 days, 19 March 1996 to 14 April 1999) study of growth and feeding under controlled conditions. Two males and four females were kept in the same tank for most of this period, at constant temperature (20°C) with daily feeding to satiation with food of known and similar caloric content (Table 1, No. 2). This regimen, without vitamin supplements, had no negative effects. We kept the two males in a separate tank from 27 May to 24 November 1998 (Table 1, No. 2M). We recorded individual food intake; however, we compared the combined food intake for the two males during this period with that of the females. The feeding study was terminated on 14 April 1999 but

daily feeding of the two males and the two larger females was continued until 16 August 2000 and three additional growth measurements were taken (Table 1, No. 2G; Table 2). One female from the opah collection trip, soon after capture and when ~2 years old, was used to determine food intake under controlled conditions for comparison with rays of the same size in the Outer Bay Waters exhibit (Table 1, No. 3).

We hand-fed the rays daily (including most weekends). Food was weighed before and after the feeding and fed out slowly to the rays as they approached the feeding station near the overflow of the tank. At times we ran out of food (not fed to satiation), or food that was found at the bottom after 30 min had to be removed and weighed. We did not attempt to record food intake of individual rays, because it was difficult to recognize some of the females.

We attempted to weigh and measure the rays every three months (Table 2). Disc width of an anaesthetized ray was first measured with callipers, then the ray was turned on its back and over-the-curve DW and additional morphometrics were taken with a fibreglass tape as quickly as possible. All reported size data are DW, unless otherwise stated. For analyses, we used the weekly amount fed, expressed as percent of body mass (BM) per day, which was calculated from weekly food intake (kg) and a linear extrapolation of mass (kg) between the dates the rays were weighed.

Neonate growth

Because of a lack of reproductive success at MBA, we obtained data on growth of rays between 0–2 years of age from other aquaria (Table 3).

Analysis of growth and feeding data

The growth data of phase 2 were first used to estimate von Bertalanffy growth function (VBGF) parameters following the methods of Gulland and Holt (1959) and Fabens (1965). These two methods do not require age to be known and provide estimates of mean maximum disc width (DW_∞) and rate constant k $(year^{-1})$. The rate constant is best interpreted as a longevity, i.e. 7 ln2/k gives the time required for a ray to reach ~99% of its mean maximum size.

$$d[DW](t)/dt = a + b\,[DW] = k\,[DW]_\infty - k\,[DW] \qquad (1)$$

is the Gulland and Holt (1959) equation, where $d[DW](t)/dt$ is the first derivative of DW as a function of time, i.e. annualized growth rate, $b = -k$ is the slope, $a = k\,[DW]_\infty$ is the growth rate at size 0 (*y*-axis intercept), and $[DW]_\infty = -a/b$ (*x*-axis intercept) $= a/k$ is the mean maximum size.

Table 1.   Experimental phases during the collection of data on captive feeding, age and growth of pelagic stingrays at the Monterey Bay Aquarium, 1995–2000

F, Female; M, Male; HP-OBW, Holding pool of OBW; OBW, Outer Bay Water exhibit; Q, Quarantine tank. Water temperature 20°C unless specified. Light cycle: ~10 h light, ~14 h dark. Feeding: A, anchovy *Engraulis mordax* (73–189 kcal per 100 g); H, herring *Clupea harengus pallasi* (96–181 kcal per 100 g); Sa, Pacific sardine *Sardinops sagax* (97–208 kcal per 100 g); Sm, night smelt *Spirinchus starsky* (71 kcal per 100g) or day (surf) smelt *Hypomesus pretiosus* (92 kcal per 100 g); Sq, squid *Loligo opalescens* (80.0 kcal per 100 g), [*Illex* sp. (83.6 kcal per 100 g) was fed in most of 1998]

Phase	Dates	Duration (days)	No. of rays	Location	Feeding
1	01 Mar 95–18 Oct 95	231	15F (14 + 1)	Q 14 (10 m³, 3 m diameter) 17.8°C	3× per week, (A, H, Sa, Sm, Sq)
T1	19 Oct 95–03 Nov 95	15	11F	OBW (4600 m³)	Difficult
T2	04 Nov 95–24 Jan 96	81	11F	HP-OBW (70 m³, 6 m diameter)	Daily (A, H, Sa, Sm, Sq)
T3	05 Jan 96–24 Jan 96	20	2M + 1F	OBW (4600 m³)	Daily (Sm, Sq)
2	19 Mar 96–14 Apr 99	1175	2M + 4F	Q-OBW (22.5 m³)	Daily to satiation (Sq)
2M	27 May 98–24 Nov 98	182	2M	Q-17 (4.8 m³, 2.4 m diameter)	Daily to satiation (Sm, Sq)
2G	15 Apr 99–16 Aug 00	490	2M + 2F	Q-OBW, 2F were on display in OBW[A]	Daily to satiation (Sq)
3	16 Nov 97–03 Dec 97	18	1F	HP-OBW (70 m³)	Daily to satiation (Sq)

[A]The 2 females were on display in OBW in June–July 1999 (60 days).

Table 2. Schedule of pelagic stingray measurements at the Monterey Bay Aquarium, 1995–2000
F, female; M, male

Date	No. of rays	Comments
01 Mar 95	15F	1 caught September 1993, 14 caught July 1994. Start phase-1 experiment. Estimated age 2.17–5.17 years, mean 3.4 years.
02 May 95	15F	Mass only, no disc width
19 Oct 95	15F	End of phase-1 experiment. Estimated age range 2.8–5.8 years.
05 Jan 96	2M + 1F	~2 years old, caught in October 1995
19 Mar 96	2M + 4F	Start of phase-2 experiment. Estimated age 2.22–4.22 years, mean 3.05 years.
12 Aug 96	2M + 4F	
10 Dec 96	2M + 4F	
18 Mar 97	2M + 4F	
25 Jul 97	2M + 4F	
21 Oct 97	5F	New batch caught 15 October 1997, smallest ones ~2 years old[A].
24 Oct 97	2M + 4F	
14 Jan 98	2M + 4F	All 6 rays had lost weight.
15 Apr 98	2M + 4F	
21 Oct 98	2M + 4F	
14 Apr 99	2M + 4F	End of phase-2 feeding experiment. Estimated age 5.30–7.30 years, mean 6.13 years.
20 Oct 99	2M + 2F	
11 Apr 00	2M + 2F	
16 Aug 00	2M + 2F	End of phase-2 growth experiment. Estimated age 6.6–8.6 years.

[A]We only used the feeding data of one of these rays from 16 November to 3 December 1997.

$$[DW]_{END} = [DW]_{INI} + ([DW]_\infty - [DW]_{INI})(1 - e^{-kT}) \quad (2)$$

is Fabens' (1965) equation, where T is the time between two consecutive measurements $[DW]_{INI}$ and $[DW]_{END}$, and the parameters $[DW]_\infty$ and k are the same as in the Gulland and Holt (1959) equation.

The analysis based on a VBGF suggested that other growth curves should be considered, which required an age estimate for our rays. We estimated the age of each ray from its size when first measured, assuming seasonal parturition and a 1 January birth date. The resulting growth curves with growth data of our rays of age two and older were then compared with growth data of neonates born in captivity at other aquaria. These estimated ages now allowed the use of more general 3-parameter growth functions. We first used the Gompertz growth function (GGF), as an example of an S-shaped growth function, in the form used by Ricker (1975):

$$[DW](t) = [DW]_0 (e^{G(1-e^{(-kt)})})$$

where $[DW]_0$ is DW-at-birth ($t = 0$), $[DW]_\infty = [DW]_0 e^G$ is the mean-maximum-DW ($t = \infty$), and k (= g in Ricker 1975) is a rate constant which again is best interpreted in terms of longevity (7 ln2/k).

We also considered a 3-parameter VBGF for comparison with the GGF. We used the form first used by von Bertalanffy (1938), i.e. with size-at-birth $[DW]_0$, rather than t_0, as third parameter:

$$[DW](t) = [DW]_\infty - ([DW]_\infty - [DW]_0) e^{-kt}$$

where the first two parameters are $[DW]_\infty$ = mean-maximum-DW ($t = \infty$) and k = rate constant which is best interpreted in terms of longevity (7 ln2/k).

Gross conversion efficiency ($K1$) was estimated from observed growth between measurements and the caloric value of the food consumed in that period from the following equation (Brett and Groves 1979):

$$K1 = \text{growth (kcal) / food intake (kcal)}$$

No caloric values of any ray species have been reported, so the value of 1.419 kcal g^{-1} for the lemon shark (Gruber 1984) was used to convert mass gain (growth) to kcal. We used the wet-mass energy value of 0.800 kcal g^{-1} for squid (*Loligo opalescens*). During most of 1998, squid (*Illex* sp.) was fed with caloric value of 0.836 kcal g^{-1} (Ezcurra 2001). The estimated age range of the two males and four females (Table 1 No.2) was 2.22–4.22 years at the beginning of the phase-2 experiment on 19 March 1996. The mean age was 3.05 years (Table 2) but we used 3.22 years instead, to facilitate comparison of observed feeding data with calculated $K1$-values in Fig. 6. This was justified because our age estimates are approximate only. The timing of the mass measurements of the rays and the feeding cycles is critical when calculating $K1$, in particular if the rays lose mass between weighing dates and $K1$ is negative. We suspected that feeding cycles might be observable but did not anticipate two cycles per year. With regard to $K1$, we were interested in long-term values rather than values due to short-term fluctuations; therefore we combined two time-periods into one, if necessary. The timing was unfortunate from March 1997 to January 1998 (five mass measurements) and we used $K1$ values for the combined periods from 18 March 1997 to 21 October 1997 and 21 October 1997 to 14 January 1998 for the regression.

Results

Growth and estimated age

Our growth data for two males and four females indicated large growth rates for both sexes, with females reaching a larger size than males (Fig. 1). The smallest had initial DW of 40–45 cm and mass 2–3 kg. The males had initial growth of 10–15 cm year^{-1} and reached DW 63 and 68 cm and mass 9 and 12 kg five years later, with a mean growth rate of
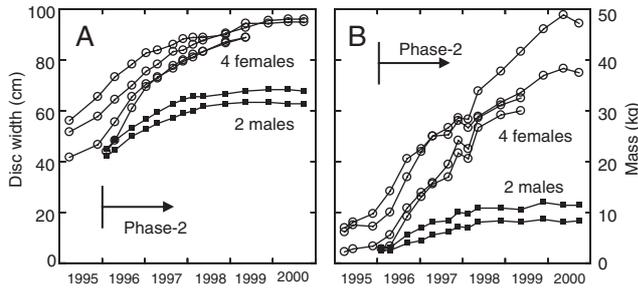
Fig. 1. Growth of captive pelagic stingrays at the Monterey Bay Aquarium, 1995–2000. *(A)* Disc width; *(B)* Mass.
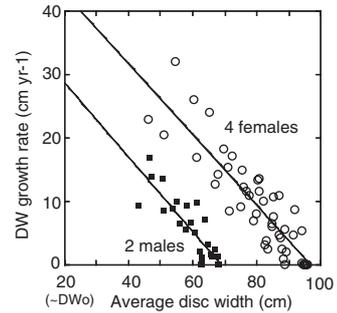

Fig. 2. Gulland and Holt (1959) graphs for male and female captive pelagic stingrays at the Monterey Bay Aquarium during phase-2 experiment, 1996–2000. Disc width at birth, $[DW]_0$, is ~20 cm.

growth rates at birth for males (28.7 cm year^{-1}) and females (42.9 cm year^{-1}) (Fig. 2).

The comparison of growth of our captive rays based on estimated ages and growth of rays born in captivity of known age indicated that the age estimates for our rays were reasonable (Fig. 3). Our smallest rays, when first measured after capture, were approaching their second birthday. One pup born at Sea World was 22 cm and reached 30, 45, 74 cm at ages 0.83, 1.44, and 3.86 years, respectively. Two pups at Keikyo Aburatsubo Marine Park were 20 cm at birth and one reached 25 cm at age 0.37 year and the other 38 cm at age 1.65 year. Only short-term growth data were available from Osaka Aquarium (Fig. 3, data near age 0 year).

The comparison of GGF and VBGF parameters showed that the GGF parameters were more reasonable overall (Fig. 4). Both growth curves fitted the data fairly well in the region with data for both males and females. However, whereas the GGF predicted reasonable size at birth of 13 and 16 cm for males and females, respectively, the VBGF predicted negative size at birth of –56 and –8 cm for males and females, respectively (Table 4). Correspondingly, the
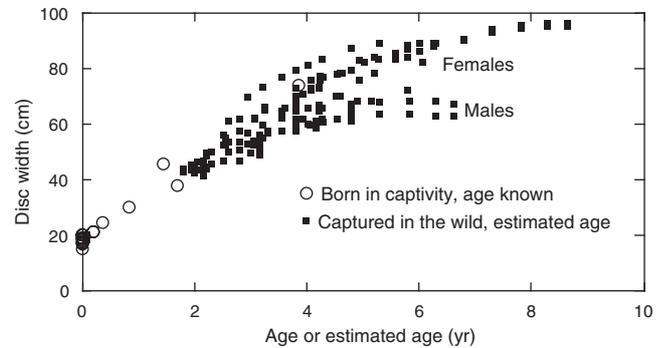

Fig. 3. Comparison of estimated ages of pelagic stingrays caught in the wild and kept in captivity at the Monterey Bay Aquarium with the known ages of rays born in captivity at other aquaria. (Data at or near age 0 are all open circles, i.e. born in captivity, age known).

GGF predicted reasonable growth rates for the first two years, whereas the VBGF predicted unreasonably large growth rates. Both GGF and VGBF predicted similar maximum size.

Table 4. Growth-function parameters (± s.e.) of captive pelagic stingrays obtained by different methods
Entries 1–4 based on two males and four females at MBA, 5–6 based on MBA specimens combined with rays born in captivity at other aquaria. Longevity (estimate), $7\ln2/k$; NA, not applicable; NS, not significant

| Method (n_{male}, n_{female})	Male DWo	Male DW∞ (a or G)	Male Longevity (k)	Female DWo	Female DW∞ (a or G)	Female Longevity (k)
1. Gulland–Holt (1959) (26, 46)	NA	69 cm ($a = 40 \pm 4$)	8.3 years (0.58 ± 0.07)	NA	97 cm ($a = 54 \pm 4$)	8.7 years (0.56 ± 0.04)
2. Fabens (1966) (26, 46)	NA	67 ± 1 cm	7.2 years (0.67 ± 0.08)	NA	97 ± 1 cm	8.5 years (0.57 ± 0.04)
3. VBGF (28, 50)	-56 ± 34 NS	67 ± 1 cm	6.0 years (0.8 ± 0.1)	-8 ± 16 NS	103 ± 5 cm	15.0 years (0.32 ± 0.07)
4. Gompertz (28, 50)	13 ± 3	68 cm (1.65 ± 0.23)	7.0 years (0.69 ± 0.07)	16 ± 6	100 cm (1.86 ± 0.33)	11.1 years 0.44 ± 0.07
5. VBGF (49, 76)	17 ± 1	74 ± 2 cm	13.9 years (0.35 ± 0.03)	17 ± 1	116 ± 5 cm	24.0 years (0.20 ± 0.02)
6. Gompertz (49, 76)	18 ± 1	70 cm (1.38 ± 0.04)	8.4 years (0.58 ± 0.04)	18 ± 1	101 cm (1.73 ± 0.05)	11.8 years (0.41 ± 0.02)
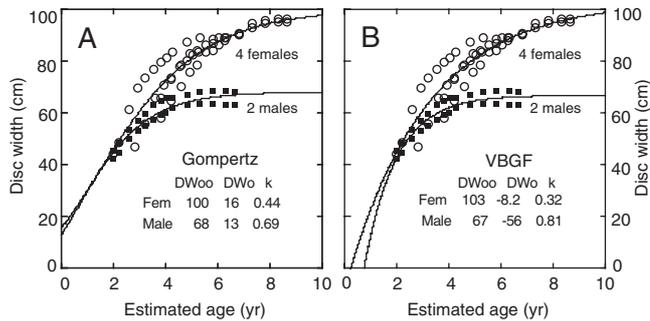
Fig. 4. Comparison of *(A)* Gompertz and *(B)* von Bertalanffy growth function fits to growth data of captive pelagic stingrays at the Monterey Bay Aquarium.
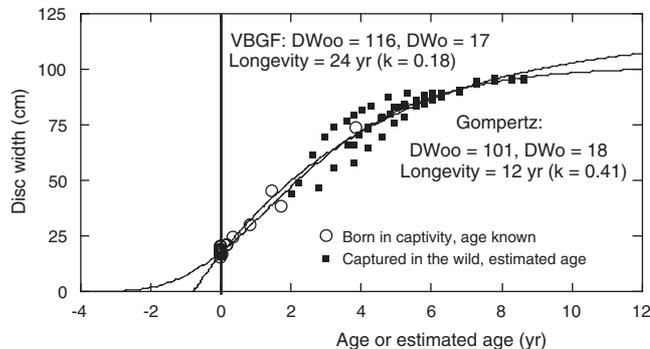

Fig. 5. Comparison of Gompertz and von Bertalanffy growth function fits to combined growth data of female captive pelagic stingrays at the Monterey Bay Aquarium and those born in other aquaria.

The inclusion of neonate data from other aquaria led to a considerable improvement of the VBGF parameters but the GGF parameters were still superior (Fig. 5, females only). The VBGF fitting curve now was forced to provide a better size at birth, but this was at the expense of a less reasonable mean maximum size of 116 cm and longevity of 24 year (Table 4). The GGF parameters which best represented growth of captive male and female pelagic stingrays are summarized in Table 4, No. 6.

Feeding and conversion

Mean weekly food intake decreased as the rays became older and showed seasonal variations for mature rays (Fig. 6A). The food intake of rays about 2 years old ('Bubbles' and 3 rays in the Outer Bay Waters exhibit) was considerably higher (6–7% BM day^{-1}) than the food intake for 2 males and 4 females during phase 2. In the phase-2 experiment, the mean food intake decreased from 2.55% BM day^{-1} in 1996 ($n = 42$, not a full year) to 1.65% BM day^{-1} in 1997 ($n = 52$) and 1.32% BM day^{-1} in 1998 ($n = 52$). Food intake by adults was greatest in January–February and July–August and decreased from 2.8 to 1.8% BM day^{-1} as the rays grew older.
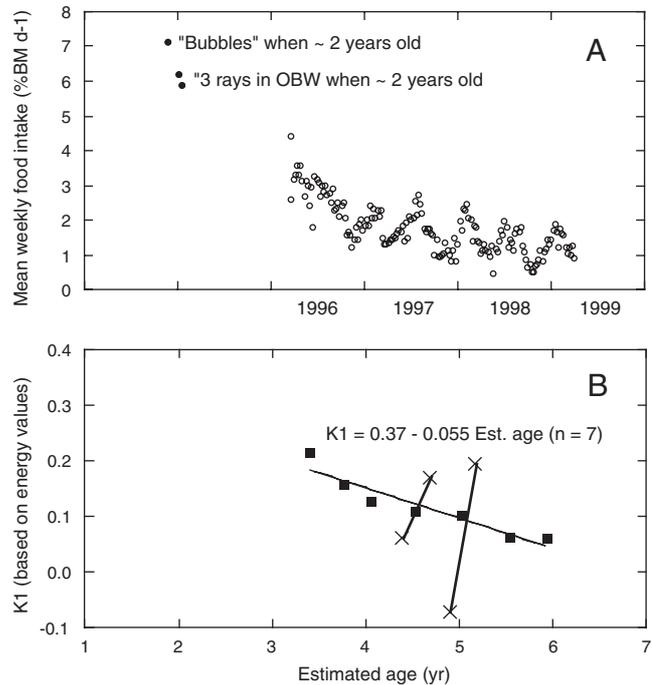

Fig. 6. Food intake and conversion efficiency of captive pelagic stingrays at the Monterey Bay Aquarium: *(A)* Mean weekly feeding amounts; *(B)* Gross conversion efficiency $K1$.

It was lowest in March–April and October–November and decreased from 1.4 to 1.0–0.5% BM day^{-1}.

The gross conversion efficiency ($K1$) decreased from 1996 to 1999, as the rays in the phase-2 experiment grew older, and there was large scatter in 1997 (Fig. 6B, top x-scale); the estimated mean age was ~3.05 years at the beginning and ~6.13 years at the end, which is close to the x-scale in Fig. 6B. The scatter is due to the timing of the mass measurements with respect to the feeding cycle. For example, the rays lost mass between 24 October 1997 and 14 January 1998 and accordingly $K1$ was negative; therefore we combined $K1$ with the following period as shown by the line connecting the two data points. The last data point is for the period 21 October 1998–14 April 1990 and represents an average over a six-month period. No mass measurements were taken in January 1999, at which time we would have expected a mass loss. We fitted a straight line for the data of phase 2:

$$K1 = 0.369 \text{ (s.e. } 0.039, P = 0.0002) - 0.0545 \text{ (s.e. } 0.008,$$
$$P = 0.001) \text{ Age } (n = 7, r^2 = 0.90).$$

If we assume that we can extrapolate to age 0 year, the predicted $K1$ value would be 37% with 95% confidence band of 24–50%. $K1$ approaches 0% for rays that no longer grow, and the linear regression is no longer applicable.

We excluded the data of the phase-1 experiment because temperature, feeding frequency and ray density were different. The results of this phase also showed large apparent scatter because of the timing of the mass measurements. The first short 62-day leg produced $K1 = 0.414$ and the following 168-day leg produced $K1 = 0.0679$ with $K1 = 0.166$ for the two legs combined. We cannot easily show these results in Fig. 6 because the data were collected earlier and these rays had a different mean age, whereas Fig. 6 used dates and approximate mean age of the rays in the phase-2 experiment. However, the regression predicted a mean age of 3.7 year (from $K = 0.166$), which was reasonably close to the calculated mean age of 3.4 year for these 14 rays at the mid point.

Our feeding data suggested that food intake is seasonal in both sexes (Fig. 7). The food intake of males and females followed the same seasonal pattern when they were in separate tanks for six months. Data for a complete year would have been required to determine unambiguously the feeding cycle for the males, but the data clearly showed the minimum in October.

Reproduction

We collected four eggcases, a 5 cm embryo, and a near-term litter at MBA (Fig. 8, Table 3). Aborted eggcases with 4–6 eggs were observed in February 1996 in the transport bag after several rays were killed. Eggcases with 2 and 7 (Fig. 8*A*) infertile eggs were observed in May 1997 and June 1996, respectively. This suggested that ovulation in captivity

might occur twice per year. An unpigmented 5 cm embryo was found on 10 December 1996 (Fig. 8*B*). Ten days earlier, an empty eggcase was found at the bottom of the tank and the two events were probably related. A mid-term litter of five was aborted at Steinhart Aquarium on 17 June 1997 after sonograms were taken (Fig. 8*C*, Table 3). A near-term litter was aborted for unknown reasons on 7 September 1995 at MBA (Fig. 8*D*) in a tank that had held 14 females since July 1994 without any males present. If we allow for a 2-month gestation period and do not consider a diapause, this suggests storage of sperm for 12 months.

Litter data from other aquaria and the field included 12 term litters, two near-term litters, and one mid-term litter (Table 3). The Osaka Aquarium recorded eight litters of 4–9 neonates with a large variation in size (140–240 mm and 100–400 g); the total mass per litter increased with time, from November 1992 to March 1993 ($P = 0.02$), which suggested that parturition in captivity might get delayed and produce larger pups and an extended parturition period. Two litters, each of 5 large pups were born at Keikyo Aburatsubo Marine Park Aquarium in March 1986, but only one litter was measured (DW 200 mm, mass 210–260 g). One pup of a litter of six at Sea World in San Diego (DW 163-203 mm, mass 93-218 g) survived and started feeding when the water temperature was increased from 16.7 to 24.8°C. A litter of two pups at the Steinhart Aquarium differed markedly in DW (150 and 235 mm) and mass (77 and 378 g).

We observed one of our males biting the posterior margin of the pectoral fin of females in a tank 1 m deep, which was probably not sufficiently deep for mating. We observed the other male chasing females in a holding pool 3 m deep; a white cloud that may have been sperm was observed but we suspect that there was no successful mating.

At Steinhart Aquarium, mating activity was observed in the Roundabout (depth 3.05 m, inside diameter 7.14 m, outside diameter 9.55 m, 391 m^3) on several occasions about 2 months prior to reproductive events (Table 3). Successful mating in captivity must have occurred because litters were observed in June 1997 and 2000, which was 1.6 and 3.6 year, respectively, after the rays had been acquired. These June litters also supported our proposal that pelagic stingrays could have two litters per year.

Morphometrics

The DW histogram of 506 measurements from 352 specimens worldwide ranged from ~0 to 96 cm and indicated a lack of data of juvenile specimens between 20 and 40 cm (Fig. 9). The majority of the measurements between 20 and 25 cm were from large neonates born in captivity. Most specimens >80 cm had been caught when small and had grown in captivity. The largest wild specimen from the Atlantic was 80 cm (Bigelow and Schroeder 1965) and we caught a 19.5 kg specimen off southern California that was not measured (estimated DW 90 cm).
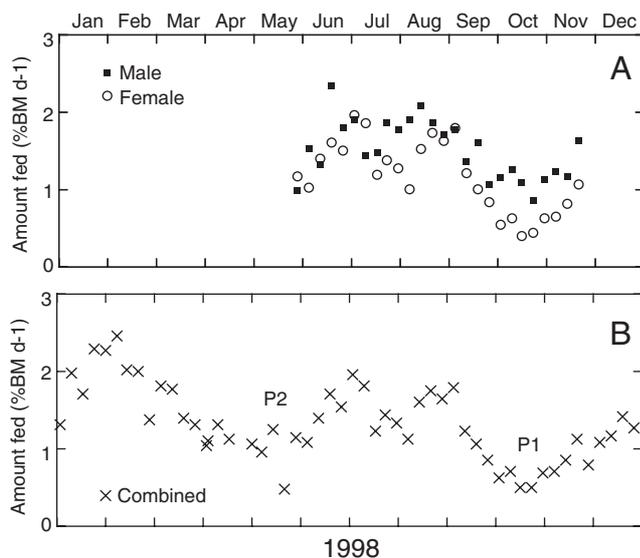

Fig. 7. Seasonal food intake for male (*n* = 2) and female (*n* = 4) pelagic stingrays at the Monterey Bay Aquarium in 1998: *(A)* Separate male and female food intake from 25 May to 24 November 1998; *(B)* Combined food intake for all of 1998. P1 & P2 are suggested parturition dates for pregnant females based on the low point of the feeding cycle.
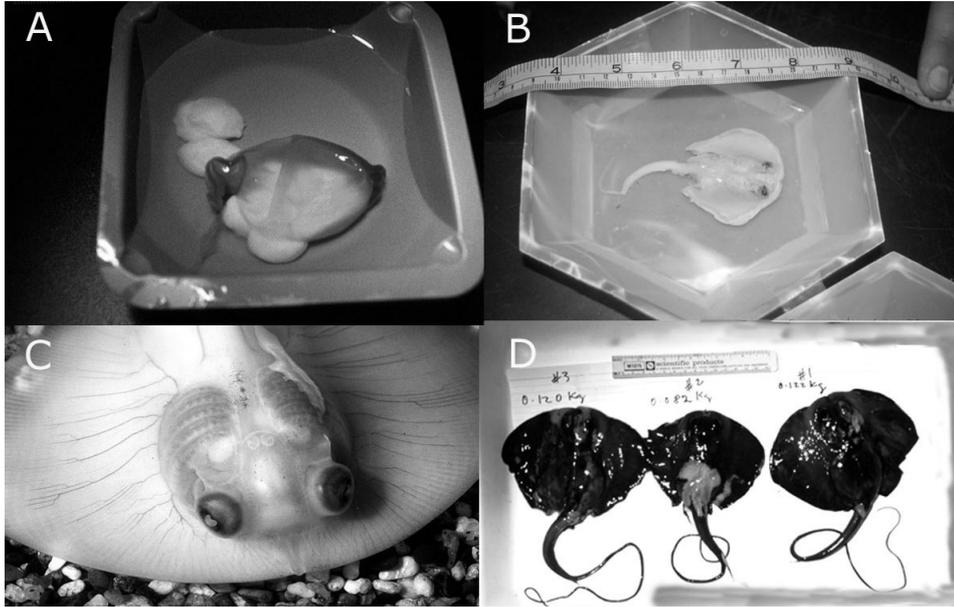
Fig. 8. Reproductive events at the Monterey Bay and Steinhart Aquariums. A) Eggcase (4.0 × 3.0 × 1.5 cm), with infertile eggs spilling out, 8 June 1996; B) mid-term embryo, 5 cm DW, 10 December 1996 at the bottom of holding tank; C) mid-term embryo, 8.5 cm DW, one of five aborted on 17 June 1997 at Steinhart Aquarium; D) Near-term embryos (DW = 128–157 mm, 82–122 g) aborted on 7 September 1995.

Disc length varied between 70% and 85% of DW but was ~90% in embryos. Total length decreased from around 300% DW in neonates to 150–250% in adults as a result of injuries to the tail and smaller differential growth, and indicated that TL is not a useful measurement.. The back-transformed power regression (Mollet and Cailliet 1996) of M (kg) *v.* DW (m) of wild-caught specimens was

$$M = 27.0 \, [\text{DW}]^{3.01} \, (n = 23, \, r^2 = 0.95, \, \text{DW } 0.43\text{--}0.77 \text{ m}).$$

The back-transformed power regression of captive specimens was

$$M = 48.4 \, [\text{DW}]^{3.471} \, (n = 159, \, r^2 = 0.97, \, \text{DW } 0.38\text{--}0.96 \text{ m}).$$
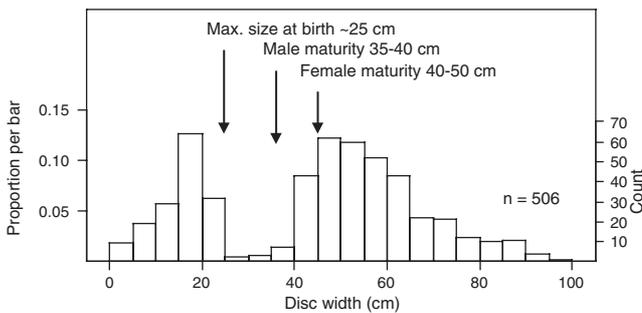

Fig. 9. Disc widths of pelagic stingrays collected from 1832 to 2000 (506 measurements from 352 specimens).

The pre-power coefficients 27.0 and 48.4 kg are estimates of the mass of a 1 m wild and captive pelagic stingray, respectively, because we used meter units in the power regression.

Discussion

Growth models

The collection of captive growth data, suitable for analysis with growth models, requires long-term data under controlled conditions, as we were able maintain during phase 2 in a quarantine tank. The only long-term growth and feeding study of rays we are aware of was for the spiny butterfly ray, *Gymnura altavela* (Henningsen 1996). Force-feeding had to be used initially as the rays were not feeding. Even after the rays were considered to have stabilized, growth rates remained small before increasing considerably and then decreasing somewhat. Such growth precludes the use of the usual growth models, in particular the VBGF, which assume that growth decreases as the rays get older.

The observed growth rates for both male (10–15 cm year^{-1}) and female pelagic stingrays (20–30 cm year^{-1}) at age 2–3 were already large and the 2-parameter VBGF predicted even larger and unreasonable growth rates at birth. We had an insufficient number of data points for a 3-parameter growth model, in particular for the males ($n = 26$) (Van Dykhuizen and Mollet 1992). However, our results suggested that the 3-parameter VBGF is not adequate as a

growth model for captive pelagic stingrays because it predicted negative size at birth. The GGF is an S-shaped model function and, accordingly, growth is linear near the inflection point. It is therefore not surprising that it produced more reasonable results. Van Dykhuizen and Mollet (1992) were unable to fit growth data of female sevengill sharks (*Notorynchus cepedianus*) with a single VBGF.

Use of the GGF required age estimates of our rays at capture. We used captive growth of neonates born in aquaria to estimate the age (~2 year) of our smallest rays (DW 40–45 cm at capture) following Van Dykhuizen and Mollet (1992). The procedure might be questioned if growth rates in captivity and in the wild differ markedly. However, our age estimate agreed with the age estimates (2 year) for the smallest rays (41–44 cm) in a study using vertebral bands (Neer in press).

We suggest that, if no growth data for neonates and/or young juveniles are available, it is more appropriate to use a 2-parameter growth function by fixing size at birth, which is usually known. If a 3-parameter VBGF is used with size at birth as the third parameter, as was done here, then it is apparent if predicted size at birth is unreasonable. With t_0 (the *x*-axis intercept) as the third parameter, it is easily overlooked that size-at-birth (*y*-axis intercept) might not be reasonable (Cailliet *et al.* 1992; Van Dykhuizen and Mollet 1992).

When we included neonate and juvenile growth data from other aquaria in our 3-parameter fits, the VBGF produced reasonable size-at-birth but less reasonable maximum size and longevity. The GGF predicted more reasonable growth parameters and is therefore better overall. The fact that the GGF predicted a much larger t_0 (infinite) in Fig. 5 is of no concern, because t_0 has no biological meaning in either growth function for elasmobranchs with well defined size at birth (Cailliet *et al.* 1992; Van Dykhuizen and Mollet 1992). Ricker (1975) suggested that the GGF is more suitable than the VBGF for computer intensive fishery work but a reluctance to use it persists.

Comparison of growth in captivity and in the wild

The 8.1 cm year^{-1} for mean growth of captive rays in this study was 5 times that (1.6 cm year^{-1}) of similarly aged (2–10 years) wild rays (Neer in press). The difference in growth of captive and wild rays when ~2 years old was considerably larger because captive growth was GGF-like, whereas the wild growth data suggested a linear relationship between DW and age (Neer in press). Captive blacktip reef sharks (*Carcharhinus melanopterus*) grew 2–3 times as much if fed rations differing by that amount (Taylor and Wisner 1989). Jones and Geen (1977) reported that first-year growth of captive spiny dogfish (*Squalus acanthias*) was 2.7 times that in the wild. Captive growth for the sandbar shark (*Carcharhinus plumbeus*) was larger than (Wass 1973; Branstetter 1987; Mohan 1996) or similar to (Schmid *et al.* 1990; Casey *et al.* 1985) growth in the wild. Growth of young

captive bull sharks (*Carcharhinus leucas*) was somewhat larger than growth in the wild (Schmid *et al.* 1990). Limited data for the nurse shark (*Ginglymostoma cirratum*) suggest that growth in captivity is larger than in the wild (Schmid *et al.* 1990). Growth in captivity was considerably larger for neonate scalloped hammerhead sharks (*Sphyrna lewini*) than for wild pups <60 days old, which lost weight (Lowe 2001, and personal communication).

In contrast, growth of captive little skates (*Raja erinacea*) was smaller than growth in the wild (Natanson 1993). Growth of wild and captive neonate Atlantic sharpnose sharks (*Rhizoprionodon terraenovea*) and sevengill sharks were similar (Branstetter 1987; Van Dykhuizen and Mollet 1992). Growth in wild and captive bonnethead shark, *Sphyrna tiburo*, were the same (Carlson and Parsons 1997). Available growth data for the sandtiger shark (*Carcharias taurus*) suggested that growth in captivity was slower than that in the field (Govender *et al.* 1991; Branstetter and Musick 1994). Comparison of growth in captivity and in the wild ought to be done cautiously because captive growth is affected by the activity level, which depends on the community make-up and stocking density in the tank (Mohan 1996).

Feeding and conversion

We documented two feeding cycles per year for both males and females. Jones and Geen (1977) reported that captive spiny dogfish consumed twice as much food in summer as in winter, but the present study is the first to measure food intake over an extended period (4 years) under constant conditions. Van Dykhuizen and Mollet (1992) collected feeding data for sevengill sharks for 5 years, but it was under ambient temperatures, and elevated temperatures in late 1987 and late 1988 coincided with increased food consumption, thereby complicating the data analysis.

Seasonal feeding is probably related to reproduction. Our seasonal feeding data in combination with captive breeding data suggested that two litters could be produced per year. Liver mass of pregnant females decreases during pregnancy (Ranzi and Zezza 1936) and we observed a loss of overall body mass in December 1998. Seasonal feeding might explain the observed growth pattern of spiny butterfly rays, with maximum growth ~1 year after capture (Henningsen 1996, fig. 1). However, another year of feeding and growth data would have been needed to substantiate this. Seasonal feeding and growth was observed for adult captive sand tiger and sandbar sharks, which fed less and lost mass from December to May (Schmid *et al.* 1990).

In our study, young (~2 years) captive pelagic stingray consumed large amounts of squid (7% of BM day^{-1}) and older adults consumed on average 1.25% BM day^{-1}. Intake probably depends on caloric value. Few data for other rays were available. Adult spiny butterfly rays began by consuming 0.67% BM day^{-1} but force feeding increased the

intake to 1.26% BM day^{-1} (Henningsen 1996). Spotted eagle rays (*Aetobatus narinari*) were fed about 2% BM daily in a large Caribbean reef display (Clippinger 1993).

Conversion coefficients should be based on long-term feeding data, and it is important to include the age of the fish. The estimated mean age of our two males and four females was 3.1 year at the beginning and 6.1 year at the end of the phase-2 feeding experiment, with $K1$ values of 21% and 6%, respectively. The $K1$ values for phase-2 in Fig. 6*B* were for sexes combined, because food intake was not recorded separately for males and females. However, the mass of the four females combined (and presumably the amounts consumed) was 5.7–7.4 times that of the two males combined, and our phase-2 data should be considered to apply to females. We calculated $K1$ of neonates to be 37%, which is close to that observed for sevengill shark pups (35%, Van Dykhuizen and Mollet 1992 from reported 29% wet-mass value). $K1$ values of 23–16% were observed for pups of blacktip reef sharks (Taylor and Wisner 1989). Wild sandbar shark pups had a $K1$ of 15.1%, which was similar to that of first-year captive spiny dogfish with a $K1$ of 12% at 10°C (Medved *et al.* 1988; Jones and Geen 1977). Older juvenile sevengill sharks, adult spiny butterfly rays, and bull sharks had $K1$ values between 15% and 7% (Van Dykhuizen and Mollet 1992; Henningsen 1996; Schmid and Murru 1994). Wild scalloped hammerhead shark pups lost mass, which produced a negative $K1$ (Lowe 2001, and personal communication).

Food consumption should be determined for individual rays if not all have the same age. This was not feasible in our feeding study because it was difficult to tell the female rays apart. This was probably the reason that the seasonal pattern was not present in the first half of 1996 when both juveniles and adults were present. However, once all the rays reached maturity, we began to observe a distinct seasonal feeding pattern.

Life-history parameters

Life history parameters for the pelagic stingray are still sparse, and they probably vary between different populations. On the basis of the data presented here, Mollet and Cailliet (2002) carried out a demographic analysis using female age-at-maturity of 3 years, maximum age of 10 years, and litter size of six. Age-at-maturity could not be determined more precisely in a study of age and growth of wild pelagic stingrays from California despite a good-sized sample of 84 (Neer in press). All males (411–565 mm) were mature and it was difficult to determine the maturity of females with a size range of 410–753 mm. With the exception of the PhD work by R. Mazzoleni, we are not aware of any studies that attempt to fill the gaps in information regarding wild pelagic stingrays.

Acknowledgments

References

Anon. (1995). Narrative Report. Townsend Cromwell, Cruise 94–10 (TC–196). Cruise Period 3–28 October 1994. US Dept. of Commerce NOAA/NMFS February 23, 1995.

Andrews, J. C., and Jones, R. T. (1990). A method for the transport of sharks for captivity. *Journal of Aquariculture and Aquatic Sciences* **5**, 70–2.

Babel, J. S. (1967). Reproduction, life history, and ecology of the round stingray, *Urolophus halleri* (Copper). California Department of Fish and Game Fish Bulletin No. 137, 1–104.

Bigelow, H. B., and Schroeder, W. C. (1965). A further account of batoid fishes from the western Atlantic. *Bulletin of the Museum of Comparative Zoology at Harvard University* **132**, 443–7.

Bourdon J. A., and Mollet, H. F. (1999). The dentition of the pelagic stingray, its design and function. Program Book and Abstracts. Joint Meeting of ASIH, AES, HL, SSAR. Pennsylvania State University, State College, Pennsylvania, USA. June 24–30, 1999. 256 pp.

Branstetter, S. (1987). Age and growth validation of newborn sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. *Copeia* **1987**, 291–300.

Branstetter, S., and Musick, J. A. (1994). Age and growth estimates for the sand tiger in the north-western Atlantic Ocean. *Transactions of the American Fisheries Society* **123**, 242–54.

Brett, J. R., and Groves, T. D. D. (1979). Physiological energetics. In 'Fish Physiology. Vol. 8. Bioenergetics and Growth'. (Eds W. S. Hoar, D. J. Randall and J. R. Brett.) pp. 279–351. (Academic Press: New York.)

Cailliet, G. M., Radtke, R. L., and Welden, B. A. (1986). Elasmobranch age determination and verification: a review. In 'Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes'. (Eds T. Uyeno, R. Arai, T. Taniuchi and K. Matsuura.) pp. 345–60. (Ichthyological Society of Japan: Tokyo.)

Cailliet, G. M., Mollet, H. F., Pittenger, G., Bedford, D., and Natanson, L. J. (1992). Growth and demography of the Pacific angel shark (*Squatina californica*), based upon tag returns off California. *Australian Journal of Marine and Freshwater Research* **43**, 1313–30.

Carlson, J. K., and Parsons, G. R. (1997). Age and growth of the bonnethead shark, *Sphyrna tiburo*, from north-west Florida, with comments on clinal variation. *Environmental Biology of Fishes* **50**, 331–41.

Casey, J. G., Pratt, H. L. Jr, and Stillwell, C. E. (1985). Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the western North Atlantic. *Canadian Journal of Fisheries and Aquatic Sciences* **42**, 963–75.

Cliff, G., and Thurman, G. D. (1984). Pathological and physiological effects of stress during capture and transport in the juvenile dusky shark, *Carcharhinus obscurus*. *Comparative Biochemistry and Physiology* **78A**, 167–73.

Clippinger, D. H. (1993). Spotted eagle rays *Aetobatus narinari* at 'The Living Seas' (Walt Disney World Co.). Program and Abstracts ASIH and AES meeting at the University of Texas at Austin, 27 May – 2 June 1993, 348 pp.

Compagno, L. J. V. (1987). Rare pelagic stingray caught off Mossel Bay. *Ichthos* **1987**(13), 6.

Cowley, P. D. (1997). Age and growth of the blue stingray, *Dasyatis chrysonota*, from the South Eastern Cape coast of South Africa. *South African Journal of Marine Science* **18**, 31–8.

Ezcurra, J. E. (2001). The mass-specific routine metabolic rate of pelagic stingrays, *Dasyatis violacea*, with comments on energetics. MS Thesis California State University, Stanislaus, through Moss Landing Marine Laboratories. 64 pp.

Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth* **29**, 265–89.

Gallagher, M., and Nolan, C. P. (1999). A novel method for the estimation of age and growth in rajids using caudal thorns. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 1590–9.

Govender, A., Kistnasamy, N., and Van der Elst, R. P. (1991). Growth of spotted ragged tooth sharks *Carcharias taurus* (Rafinesque) in captivity. *South African Journal of Marine Science* **11**, 15–19.

Greenwald, S. A., Bourdon, J. A., and Mollet, H. F. (1997). The recovery and analysis of teeth and dermal thorns from captive pelagic stingrays, *Dasyatis* (*Pteroplatytrygon*) *violacea* (Bonaparte, 1832). Poster with abstract in Program and Abstracts ASIH, AES Annual Meeting. University of Washington, Seattle WA, June 26 – July 1, 1997. 336 pp.

Gruber, S. H. (1984). Bioenergetics model of the lemon shark and overall discussion. American Association of Zoological Parks and Aquariums Annual Proceedings, Miami Fl. **1984**, 363.

Gruber, S. H., and Keyes, R. S. (1981). Keeping shark for research. In 'Aquarium Systems'. (Ed. A. D. Hawkins.) pp. 373–402. (Academy Press: New York.)

Gruber, S. H., and Stout, R. G. (1983). Biological materials for the study of age and growth in a tropical marine elasmobranch, the lemon shark, *Negaprion brevirostris* (Poey). *NOAA Technical Report NMFS* **8**, 193–205.

Gulland, J. A., and Holt, S. J. (1959). Estimation of growth parameters for data at unequal time intervals. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **25**, 47–9.

Henningsen, A. D. (1996). Captive husbandry and bioenergetics of the spiny butterfly ray *Gymnura altavela* (Linnaeus). *Zoo Biology* **15**, 135–42.

Jones, B. C., and Geen, G. H. (1977). Food and feeding of spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* **34**, 2067–78.

Last, P. R., and Stevens, J. D. (1994). 'Sharks and Rays of Australia.' (CSIRO: Australia.) 513 pp. + 84 plates.

Lowe, C. G. (2001). Metabolic rates of juvenile scalloped hammerhead sharks (*Sphyrna lewini*). *Marine Biology* **139**, 447–53.

Martin, L. K., and Cailliet, G. M. (1988). Age and growth determination of the bat ray, *Myliobatis californica*, in Central California. *Copeia* **1988**, 762–73.

Medved, R. J., Stillwell, C. E., and Casey, J. G. (1988). The rate of food consumption of young sandbar sharks (*Carcharhinus plumbeus*) in Chincotegue Bay, Virginia. *Copeia* **1988**, 956–63.

Mohan, P. (1996). Using fisheries data to manage the diets of captive elasmobranchs. American Zoo and Aquarium Association Annual Conference Proceedings Sept. 17–21 1996, Waikiki, HI. pp. 265–73.

Mollet, H. F. (2002). Distribution of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832), off California, Central America, and worldwide. *Marine and Freshwater Research* **53**, 525–30.

Mollet, H. F., and Cailliet, G. M. (1996). Using allometry to predict body mass from linear measurements of the white shark. In 'Great White Shark. The Biology of *Carcharodon carcharias*'. (Eds A. P. Klimley and D. G. Ainley.) pp. 81–9. (Academic Press: San Diego, CA.)

Mollet, H. F., and Cailliet, G. M. (2002). Comparative population demography of elasmobranchs using life history tables, Leslie matrices, and stage-based matrix models. *Marine and Freshwater Research* **53**, 503–16.

Murru, F. L. (1990). The care and maintenance of elasmobranchs in controlled environments. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of Fisheries'. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) *NOAA Technical Report NMFS* **90**, 327–46.

Natanson, L. J. (1993). Effect of temperature on band deposition in the little skate, *Raja erinacea*. *Copeia* **1993**, 199–206.

Neer, J. A. (in press). Ecology of the pelagic stingray, *Pteroplatytrygon violacea* (Bonaparte, 1832). In 'Shark of the Open Ocean'. (Eds M. Camhi and E. Pikitch.) (Blackwell Scientific: New York.)

Ranzi, S., and Zezza, P. (1936). Fegato, maturita sessuale e gestazione en *Trygon violacea*. *Pubblicazioni della Stazione Zoologica di Napoli* **15**, 355–67.

Ricker, W. E. (1975). Computation and interpretation of biological statistics of fish population. *Bulletin of the Fisheries Research Board of Canada* **191**, 1–382.

Schmid, T. H., and Murru, F. L. (1994). Bioenergetics of the bull shark, *Carcharhinus leucas*, maintained in captivity. *Zoo Biology* **13**, 177–85.

Schmid, T. H., Murru, F. L, and McDonald, F. (1990). Feeding habits and growth rates of bull (*Carcharhinus leucas* (Valenciennes)), sandbar (*Carcharhinus plumbeus* (Nardo)), sandtiger (*Eugomphodus taurus* (Rafinesque)) and nurse (*Ginglymostoma cirratum* (Bonnaterre)) sharks maintained in captivity. *Journal of Aquariculture and Aquatic Sciences* **5**, 100–5.

Smith, M. F. L. (1992). Capture and transportation of elasmobranchs, with emphasis on the grey nurse shark (*Carcharias taurus*). In 'Sharks: Biology and Fisheries'. (Ed. J. G. Pepperell.) *Australian Journal of Marine and Freshwater Research* **43**, 325–43.

Taylor, L., and Wisner, M. (1989). Growth rates of captive blacktip reef sharks (*Carcharhinus melanopterus*). *Bulletin de l'Institute Océanographique, Monaco* n special **5**, 211–17.

Timmons, M., and Bray, R. N. (1997). Age, growth, and sexual maturity of shovelnose guitarfish, *Rhinobatus productus* (Ayres). *US National Marine Fisheries Service Fishery Bulletin* **95**, 349–59.

Uchida, S., Toda, M., and Kamei, Y. (1990). Reproduction of elasmobranchs in captivity. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of Fisheries'. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) *NOAA Technical Report NMFS* **90**, 327–46.

Van Dykhuizen, G., and Mollet, H. F. (1992). Growth, age estimation, and feeding of captive sevengill sharks, *Notorynchus cepedianus*, at the Monterey Bay Aquarium. In 'Sharks: Biology and Fisheries'. (Ed. J. G. Pepperell.) *Australian Journal of Marine and Freshwater Research* **43**, 297–318.

Villavicencio, C. J., Downton, C., and Mariano, E. (1994). Tamaño y reproduccíon de la raya *Dasyatis longus* (Pisces : Dasyatidae), en Bahía Almejas, Baja California Sur, México. *Revista de Biológica Tropical* **42**, 375–7.

von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws II). *Growth* **10**, 181–213.

Wass, R. C. (1973). Size, growth, and reproduction of the sandbar shark, *Carcharhinus milberti*, in Hawaii. *Pacific Science* **27**, 305–18.

Wetherbee, B. M., Gruber, S. H., and Cortés, E. (1990). Diet, feeding habits, digestion, and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris*. In 'Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of Fisheries'. (Eds H. L. Pratt Jr, S. H. Gruber and T. Taniuchi.) *NOAA Technical Report NMFS* **90**, 29–47.

Wilson, P. C., and Beckett, J. S. (1970). Atlantic Ocean distribution of the pelagic stingray, *Dasyatis violacea*. *Copeia* **1970**, 696–707.