

Growth and Demography of the Pacific Angel Shark (*Squatina californica*), Based upon Tag Returns off California

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Abstract

Knowledge of the age, growth and demography of an organism can be quite useful for managing its fishery. However, for many elasmobranch species, no valid estimates of age, growth and therefore age-specific mortality and natality rates are available. Thus, even though the distribution, abundance, habits and reproduction of a population may be known, no reliable estimates of population growth are possible. As a result, detailed demographic analysis has been completed for only a few shark species (e.g. the California leopard shark, *Triakis semifasciata*). All age-determination techniques attempted for the Pacific angel shark (*Squatina californica*) have met with difficulties. Recently, however, we have accumulated data on 69 tag-recaptures and have used this information to model a von Bertalanffy growth function (VBGF) to predict the growth of this commercially exploited shark species. We performed a demographic analysis of this species, which yielded a net reproductive rate (R_0) of 2.25, a generation time (G) of 14.5 years, and an estimate of the instantaneous population growth coefficient (r) of 0.056 year⁻¹, assuming that only natural mortality (M) was occurring, estimated to be 0.2 year⁻¹. When reasonable estimates of fishing mortality (F) are included in the survivorship function, R_0 and r are reduced considerably. Presently, Pacific angel sharks first enter the fishery at the same size and age at which they first reproduce. Until accurate estimates of M and F are available, it would be prudent to set a size limit considerably above the size at first reproduction to protect the Pacific angel shark in California.

Introduction

The Pacific angel shark, *Squatina californica*, is a relatively abundant, nearshore elasmobranch in California (Miller and Lea 1972; Eschmeyer *et al.* 1983; Compagno 1984) and is caught in a commercial gill-net fishery that also targets the California halibut, *Paralichthys californicus* (Pleshner 1983; Natanson and Cailliet 1986, 1990; Richards 1987; Holts 1988). Some aspects of the shark's life history have been well studied, including its distribution and abundance, feeding habits and reproduction (Natanson and Cailliet 1986). However, age and growth studies have been hampered by the lack of valid annual growth zones in the vertebrae (Cailliet 1990; Natanson and Cailliet 1990).

Because of the increased interest in this (and other) elasmobranch species, it is important to understand as much about its population dynamics as possible. This is only possible if sufficient details are available about the age, growth and mortality (Hoenig and Gruber 1990) and reproduction (Pratt and Casey 1990; Pratt and Otake 1990) of elasmobranchs. These estimates should be accompanied by validated age estimates (Cailliet *et al.* 1986; Cailliet 1990). Anderson and Teshima (1990) and Hoff and Musick (1990) provide complete lists of the biological, ecological and fishery details that are necessary to completely understand the dynamics of fished elasmobranch populations.

Because no valid age estimates have been available for Pacific angel sharks (Welden *et al.* 1987; Natanson and Cailliet 1990), the approach taken by Smith and Abramson (1990) and Cailliet (1992) of utilizing life-history features of the central California population of the leopard shark (*Triakis semifasciata*) to calculate mortality rates, yield and stock-replenishment estimates, and demographic parameters has not been possible for Pacific angel sharks.

However, tag-recapture results can be used to fill this gap in knowledge about growth rates (Gulland and Holt 1959; Fabens 1965; Francis 1988a, 1988b; Cailliet and Tanaka 1990; Smith and Abramson 1990; Kusher *et al.* 1992), which can then be useful for estimating parameters of population dynamics (Anderson 1990). Once reasonable estimates of ages and growth characteristics are available, they can be used in a demographic analysis by incorporating age-specific mortality and natality rates to produce estimates of the net reproductive rate (R_0), generation time (G), and intrinsic (instantaneous) rate of increase (r) (Caughley 1977; Charlesworth 1980; Krebs 1985; Hoenig and Gruber 1990; Cailliet 1992).

Such a demographic analysis involves the construction of either a cohort or a static life table for the population, based upon the best available estimates of mortality, fecundity and longevity. It also usually assumes a stable age distribution, equal sex ratios, and a constant recruitment rate (Caughley 1977; Jenkins 1988). The estimate of the intrinsic rate of increase, proposed by Caughley (1977) as a 'measure of demographic vigour', has often been used in exponential and logistic models of population growth (Krebs 1985; Jenkins 1988; Hoenig and Gruber 1990). When used for gill-net fisheries, demographic analyses also must make assumptions about knife-edge selection and age-specific fishing mortality (Kirkwood and Walker 1986).

Because detailed, basic ecological information is often lacking, detailed demographic analyses have been completed for only three shark species: the spiny dogfish, *Squalus acanthias* (Jones and Geen 1977; Wood *et al.* 1979; Hanchet 1988); the lemon shark, *Negaprion brevirostris* (Hoenig and Gruber 1990); and, most recently, the leopard shark, *Triakis semifasciata* (Cailliet 1992). Limited aspects of demography have been considered for the soupfin or school shark, *Galeorhinus galeus* (= *australis*; Grant *et al.* 1979).

In the present paper, we use the available tag-recapture data and limited laboratory growth information (Natanson and Cailliet 1990) as the only possible means of estimating age and growth of the Pacific angel shark since age-length data are not available (Francis 1988a). Once a reasonable von Bertalanffy growth function (VBGF) has been determined, we can combine growth with estimates of natural mortality and fecundity (Natanson and Cailliet 1990) to demographically analyse the California population of the Pacific angel shark. This may prove to be the only possible way to model this population relative to the fishery that has developed for this species and that may already have deleteriously affected it (Richards 1987; Holts 1988).

Materials and Methods

To construct the most plausible life table, we first estimated growth characteristics of the Pacific angel shark by using tag-recapture data to estimate parameters of the VBGF (von Bertalanffy 1938). Sharks were tagged by following two different procedures in separate studies. First, Pittenger (1984) tagged sharks *in situ*, using SCUBA at depths between 29 and 38 m near Ship Rock, Catalina Island, California, in 1981 and 1982. The animals were usually found lying on the sandy bottom, well

camouflaged and partially buried. Colour-coded tags were made by attaching Floy FH-69 stainless-steel dart tags to monofilament fishing line, over which were four 3-cm sections of coloured vinyl tubing, creating a unique four-colour pattern for each tagged animal.

Date, locality, total length (TL) and sex were recorded for each animal prior to tag implantation. Length measurements were obtained by using a 1.5-m fibreglass measuring tape positioned from the tip of the shark's snout to the trailing edge of the lower lobe of the caudal fin. Individual sharks could not be weighed prior to tagging and release. Tags were implanted into the musculature near the base of the tail with a modified pole spear. Most of the sharks did not flee upon tag implantation, indicating a relatively small amount of trauma involved in the tagging process.

In another study, we collected Pacific angel sharks off Santa Barbara, California, between Gaviota and Ventura between 1979 and 1983 (Natanson and Cailliet 1990). Most specimens were taken from commercial, 20-cm-mesh, California halibut (*Paralichthys californicus*) gill- or trammel-nets operating at depths of 6–37 m or otter trawls at depths of 58–77 m. Pacific angel sharks from commercial gill-nets were sexed, measured, tagged, injected with tetracycline, and released alive off the coast north of Santa Barbara and the Channel Islands. We have already presented the data on variable growth-zone formation in the centra of six recaptured specimens (Natanson and Cailliet 1990).

Also, some growth-rate data were available from laboratory-grown Pacific angel shark pups, some of which were originally reported in Pittenger (1984) and Natanson and Cailliet (1990). Data from two pups that did not feed or were not fed (codes MLML951 and CSULBMcK in Table 1) were not included, whereas data from the other four pups (MLML285, MLML333, CSULB6MO and CMM24MO), yielding five growth rates, were included in the VBGF analysis. It should be noted here that the results might have been different if we had weighed all sharks in addition to measuring their lengths. Indeed, MLML951 had the highest growth rate but lost weight (see Table 1).

At the end of Pittenger's (1984) Catalina Island study, a gill-net was set five times at Ship Rock. The net was 31.5 m long and 2.5 m high, with a 12-cm square mesh. It was set prior to sunset and hauled shortly after sunrise. Several additional tagged sharks were captured by commercial squid purse-seiners and California halibut gill-netters and were returned to the California Department of Fish and Game. Many sharks were observed by SCUBA divers up to three years after tagging and none showed any indication of tissue irritation surrounding the tag. Based upon scar-tissue formation around the base of the tag, the wound healed within three to four weeks. The sharks did not appear to shed the tags, based upon the lack of scar tissue in subsequently observed sharks.

Data on the growth of individuals from tag-recaptures (field growth) and laboratory data were standardized to include length at tagging or capture (TLTAG, cm TL); length at recapture, release or termination (TLCAP, cm TL); average TL ($TL_{ave} \text{ cm} = (TL_{tag} + TL_{recapture})/2$); time at large or in captivity (T-A-L, years); and annualized growth rate (G-RATE, cm year^{-1}) (see Table 1).

These data were then used to estimate VBGF parameters primarily by following the technique given by Gulland and Holt (1959) for 'data at unequal time intervals' according to the VBGF in the form $L'(L) = dL/dt = KL_{\infty} - KL = a + bL$. We plotted annualized growth rate (cm year^{-1}) versus average TL (cm) between tagging/capture and recapture/termination and calculated the linear regression coefficients by using the MGLH module of SYSTAT (Wilkinson 1988a).

Gulland and Holt (1959) recommended correcting calculated growth rates based on long times at large ($T = T\text{-A-L}$, Table 1) according to the criterion that $b = \frac{1}{2}KT$ and must be more than 0.4 (e.g. GGP1113 and GGP1343 in Table 1). However, a regression based upon corrected growth rates yielded almost identical results. Thus, only the uncorrected results for K (slope) and L_{∞} (x-axis intercept) are reported. This method is identical to the 'derivative method' used by Van Dykhuizen and Mollet (1992) but is more refined since it gives the exact criterion for its use and the correlation term to be used in case of very long times at large.

The predictive y -on- x regression was chosen for the analysis because the percentage error from using growth rate as the y -axis was much larger than that from using average TL as the x -axis (Ricker 1973). Since y and x are correlated, we relied on the standard error of estimate (s.e.e.) rather than the correlation coefficient r to evaluate the quality of the fit (Sokal and Rohlf 1981).

Results were plotted by using SYGRAPH (Wilkinson 1988b), which produces a regression line and 95% confidence band (CB) (Neter *et al.* 1983). This confidence band is between that for the line and that for a new observation (Wallis and Roberts 1956). The regression parameter (b = slope) provides an estimate of K . The x -axis intercept (an estimate of L_{∞}) equals $-a/b$. Its standard error was estimated graphically by using the average distance of upper and lower confidence limits from the line and is not symmetrical.

We also used Fabens' (1965) method to determine K and L_{∞} values for comparison with Gulland and Holt's (1959) method in order to test whether the distribution of data influenced the results. We inserted Fabens' equation for fitting the VBGF in the NONLIN module of SYSTAT (Wilkinson 1988a) and in addition got asymptotic standard errors for the parameters. We ran analyses with and without the largest outlier (MLML335). For comparison purposes, we have listed the results of both methods in Table 2.

Once we derived reasonable values for the two VBGF parameters, we used them in combination with the observed length at birth $L_0 = 24$ cm (Natanson and Cailliet 1986), to generate a von Bertalanffy growth (or length-at-age) curve (VBGC). The size at capture and the calculated age at capture served to place each shark on the curve. The size at recapture and the time at large defined the end point and illustrated the deviation from the VBGF for individual sharks. This is a similar approach to that of Kusher *et al.* (1992), in which the growth of individual leopard sharks (*Triakis semifasciata*) was compared with the VBGC based upon growth zones in vertebral centra.

The maximum age (longevity) of the Pacific angel shark was estimated from the TL at which $>99\%$ of the L_{∞} was reached (this is equivalent to seven half-lives, i.e. $7(\ln 2)/K \approx 35$ years; after Fabens 1965), not at 95% of L_{∞} (five half-lives, Ricker 1979).

The length at first maturity has been estimated at between 101 and 103 cm TL (Natanson and Cailliet 1986). Based upon the VBGF calculated from tag return data, confidence intervals for the age at first maturity would range between 8 and 13 years. We thus used approximately 10 years for our demographic analysis.

The estimate of natural mortality ($M = 0.2 \text{ year}^{-1}$) was based upon the relationship between mortality rate and maximum age presented by Hoenig (1983) and Hoenig and Gruber (1990). This rate was used to estimate the natural survivorship function $l_x = N_0(e^{-(M)x})$.

The gestation period was assumed to be approximately 12 months and birth events annual (Natanson and Cailliet 1986). Estimates of fecundity were also taken from Natanson and Cailliet (1986), and this relationship was used to estimate age-specific natality (m_x). Because we were not able to find a significant relationship between number of offspring and either size or age of parent for this species, we used a mean of six offspring (95% CL = 0.43) per female parent to estimate age-specific fecundity, or three female offspring per female parent because sex ratios are very close to 1:1 (Natanson and Cailliet 1986). The confidence intervals were narrower than those for the age-at-maturity estimate, so only this value of fecundity was used.

Using the life table constructed from the above values, we calculated estimates of net reproductive rate (R_0 : multiplication rate per generation), generation time (G , years), and instantaneous growth rate (r , year^{-1}), following Mertz (1970), Krebs (1985) and Cailliet (1992).

To simulate what would happen to the demography of the Pacific angel shark population under a range of natural and fishing mortalities, the survivorship function (l_x) was modified to include estimates of the instantaneous fishing mortality rate (F), which varied from 0 to 0.22 year^{-1} to cover seven possible outcomes. M values always started at age 0 and continued throughout life, whereas F values always started at age 10, which is equivalent to the average size at entry into the gill-net fishery (1000 mm TL; Richards 1987). Life tables were calculated first by using three M values alone (0.10, 0.15 and 0.20 year^{-1}) and then by combining an M value of 0.2 year^{-1} with four F values (0.05, 0.10, 0.20 and 0.22 year^{-1}). In this analysis, both the natural and the fishing mortality rates were used to estimate the survivorship function $l_x = N_0(e^{-(M+F)x})$. This new survivorship was then coupled with the natality function to simulate the effect on the age-specific reproduction rate and demography that various combinations of natural and fishing mortality might have.

The net reproductive rate, generation time, and intrinsic rate of increase were then recalculated and tabulated. With these seven combinations of M and F , the age-specific reproductive rates ($l_x m_x$) were plotted against age (x) to graphically demonstrate the effect on the population of M values below 0.20 and of initiating different intensities of fishing at ages ranging from 6 to 10 years old, assuming $M = 0.20$. By noting where the net reproductive rate falls below 1 and the intrinsic rate of increase changes signs, one can estimate where to set the minimum size of shark that could be fished and still maintain a viable, reproducing population.

Results

The growth rates of the pups in captivity were considerably higher than those of adults (TL at tagging more than 90 cm) in the field (Table 1). The five pups with a mean size

Table 1. List of all 69 tag-recaptures of Pacific angel sharks used in this analysis, including identification number, sex, total length at tagging (TLTAG), total length at recapture (TLCAP), time at large (T-A-L), annualized growth rate (G-RATE), and *b* value (Gulland and Holt 1959; see Materials and Methods)

GGP, G. G. Pittenger; DB, D. Bedford; MLML, Moss Landing Marine Laboratories; CSULB, California State University, Long Beach; CMM, Cabrillo Marine Museum; M, male; F, female; ?, sex unknown. The two sharks in brackets at the end of the table were kept in captivity but were not used for reasons that are explained in the text. The sharks marked with asterisks are two field-grown sharks and one laboratory-grown shark, each of which was recaptured once, remeasured, released and recaptured again. Laboratory-reared sharks are denoted by (L) in the G-RATE column

ID No.	Sex	TLTAG (cm)	TLCAP (cm)	T-A-L (years)	G-RATE (cm year ⁻¹)	<i>b</i>
GGP1112	M	113.0	120.0	1.685	4.15	0.123
1113	M	101.0	109.3	5.921	1.40	0.431
1123	M	108.0	113.0	1.989	2.51	0.145
1215	M	106.0	109.0	0.644	4.66	0.047
1223	F	113.0	115.5	0.967	2.58	0.070
1242	M	108.0	110.5	2.175	1.15	0.158
1315	F	106.0	110.0	0.948	4.22	0.069
1322	M	107.0	114.5	1.885	3.98	0.137
1331	M	114.0	115.5	1.148	1.31	0.084
1333	M	104.0	110.7	2.041	3.28	0.149
1343	M	104.0	108.9	5.578	0.88	0.406
1413	M	121.5	121.5	1.888	0.00	0.137
1415	F	111.0	113.2	1.101	2.00	0.080
1421	M	103.0	115.0	3.003	4.00	0.218
1443	F	94.5	100.0	1.082	5.08	0.079
1512	F	108.0	111.0	1.241	2.42	0.090
1523	M	113.0	114.5	0.964	1.56	0.070
1531	M	112.5	115.5	1.510	1.99	0.110
1534	M	120.0	124.0	1.910	2.09	0.139
1543	M	79.0	88.5	0.778	12.21	0.057
2221	M	113.0	115.5	2.923	0.86	0.213
2243	F	105.0	108.0	0.866	3.47	0.063
2322	M	109.0	110.3	1.660	0.78	0.121
2323	F	100.5	104.0	0.770	4.55	0.056
2351	F	106.0	110.0	1.088	3.68	0.079
2444	F	114.5	118.0	2.392	1.46	0.174
2454	M	111.0	113.3	4.411	0.52	0.321
2512	M	109.5	110.1	0.499	1.20	0.036
2551	F	116.0	119.8	1.564	2.43	0.114
2552	F	110.5	112.5	1.118	1.79	0.081
3112	M	115.5	119.7	1.060	3.96	0.077
3114	M	116.0	118.5	1.225	2.04	0.089
3123	M	100.5	104.5	1.197	3.34	0.087
3125	M	100.5	105.0	1.033	4.36	0.075
3141	F	105.0	110.0	1.170	4.27	0.085
3144	M	113.0	113.5	1.060	0.47	0.077
3151	F	93.0	99.5	1.170	5.56	0.085
3154	M	120.0	121.5	1.164	1.29	0.085
3215	M	117.0	121.5	1.488	3.02	0.108
3224	M	109.0	108.5	0.474	-1.05	0.034
3253	F	110.5	114.5	1.126	3.55	0.082
3351	F	112.0	113.8	1.112	1.62	0.081
3411	M	118.5	118.0	1.000	-0.50	0.073

Table 1 (continued)

ID No.	Sex	TLTAG (cm)	TLCAP (cm)	T-A-L (years)	G-RATE (cm year ⁻¹)	<i>b</i>
3422	M	113.5	115.8	1.115	2.06	0.081
3423*	M	98.0	103.2	1.110	4.69	0.081
3423*	M	103.2	108.1	3.074	1.59	0.224
3445	M	117.0	118.0	1.077	0.93	0.078
3514	M	114.5	117.7	1.400	2.29	0.102
3521	M	117.0	121.2	0.912	4.60	0.066
3533	M	112.0	112.7	0.896	0.78	0.065
3544	F	79.5	88.0	1.071	7.93	0.078
4113*	M	110.0	111.0	0.896	1.12	0.065
4113*	M	111.0	113.5	2.082	1.20	0.151
4114	M	114.5	116.3	0.904	1.99	0.066
4123	M	114.5	116.5	1.329	1.51	0.097
4134	F	120.0	119.5	0.899	-0.56	0.065
4151	M	96.7	100.5	3.995	0.95	0.291
DB28	M	81.0	90.0	1.627	5.53	0.118
MLML335	F	65.2	71.0	3.526	1.64	0.257
336	F	97.0	98.0	3.693	0.27	0.269
337	M	110.2	113.6	0.885	3.84	0.064
338	F	112.0	115.1	0.877	3.54	0.064
339	M	112.9	113.0	0.953	0.10	0.069
285	F	25.4	34.8	0.474	19.83 (L)	0.034
333	F	25.0	41.2	1.104	14.67 (L)	0.080
CSULB6MO	?	26.0	31.0	0.500	10.00 (L)	0.036
CMM24MO*	M	24.0	39.4	1.167	13.19 (L)	0.085
CMM24MO*	M	39.4	50.6	0.836	13.40 (L)	0.061
[MLML951]	?	59.2	61.5	0.110	21.53 (L)	
[CSULBMcK]	?	24.0	29.0	0.929	5.38 (L)	

of 33.7 (s.d. = 6.7) cm TL had a mean growth rate of 14.2 (s.d. = 3.6) cm year⁻¹. The 60 adults had a mean size of 111 (s.d. = 6) cm TL and a mean growth rate of 2.2 (s.d. = 1.2) cm year⁻¹.

The regression analysis of annualized growth rate versus average size estimated the VBGF parameter K to be 0.146 year⁻¹ (s.e. = 0.011) and the asymptotic length (L_{∞} = x-axis intercept) to be 127 cm TL (s.e. = 2.5). This was derived from the regression equation $y = (18.5; \text{s.e.} = 1.2) - (0.146; \text{s.e.} = 0.011)x$ ($n = 69$, $r^2 = 0.714$, s.e.e. = 2.04) (Fig. 1). Note that K is often referred to as the Brody growth coefficient, but its units are time⁻¹ and its meaning is best illustrated by pointing out that $\ln(2)/K$ is a 'half-life' (Fabens 1965; Van Dykhuizen and Mollet 1992). With an L_0 of 24 cm TL for the Pacific angel shark (Natanson and Cailliet 1986, 1990), the complete VBGF is $L_t = 127 - (124 - 24)e^{-0.146t}$, with TL in centimetres and t in years.

Analysis of the residuals showed that all five pup data points had large leverage (defined as more than 0.1, after Sokal and Rohlf 1981 and Wilkinson 1990). Of these five, one (MLML285) was an outlier (defined as having a Studentized residual of more than 3, after Wilkinson 1990). Two additional subadult data points were also identified as outliers. However, the Gulland and Holt (1959) regression parameters changed only slightly and influenced the VBGF parameters little ($K = 0.134$ year⁻¹ and $L_{\infty} = 128.4$ cm) when these three outliers were excluded.

No statistical differences were found in the VBGF parameters between males ($n = 46$) and females ($n = 22$) (Fig. 1, Table 2). The K values were 0.152 and 0.162 year⁻¹ and the L_{∞} values were 125.9 and 126.0 cm TL, respectively.

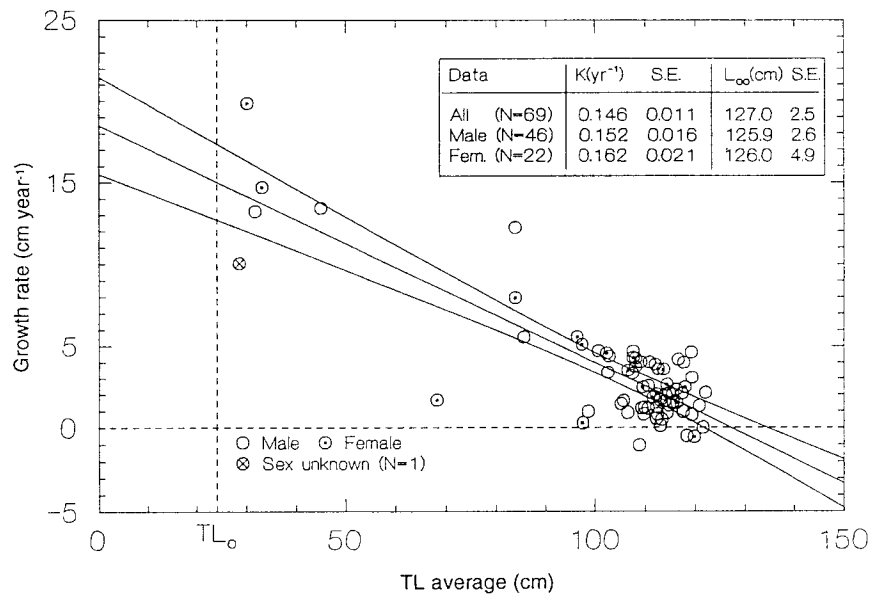


Fig. 1. Gulland and Holt (1959) plot of average total length and subsequent annualized growth of recaptured Pacific angel sharks. All 69 data points are shown, with males depicted as open circles and females as dots within open circles. The solid straight line is the regression calculated for these data, and the upper and lower curved lines are 95% confident limits (bands). The slope of the regression line provides an estimate of the VBGF growth coefficient K , and the intercept on the x -axis is an estimate of asymptotic length (L_{∞}). Estimates of K and L_{∞} are given for all sharks and for males ($n=46$) and females ($n=22$) separately.

Table 2. VBGF parameters calculated by using two different methods (Gulland and Holt 1959 and Fabens 1965)

Units: K , year⁻¹; L_{∞} , cm. Values in parentheses are standard errors and asymptotic standards, by method, respectively. Analyses were run on the total data set and with the outermost outlier (MLML335) excluded

Sample used	Gulland and Holt (1959)		Fabens (1965)	
	K	L_{∞}	K	L_{∞}
Sexes combined				
All ($n=69$)	0.146 (0.011)	127.0 (2.5)	0.101 (0.017)	125.2 (3.8)
Excluding MLML335 ($n=68$)	0.153 (0.010)	126.5 (2.5)	0.148 (0.016)	121.4 (2.0)
Sexes separate				
Females (all) ($n=22$)	0.162 (0.021)	126.0 (4.9)	0.072 (0.031)	129.4 (16.1)
Females (excluding MLML335) ($n=21$)	0.182 (0.014)	125.2 (2.5)	0.164 (0.031)	120.6 (4.2)
Males ($n=46$)	0.152 (0.016)	125.9 (2.6)	0.143 (0.022)	121.7 (2.4)

The Gulland and Holt (1959) method produced consistent VBGF estimates, whereas Fabens' (1965) approach appeared to underestimate K but produced similar estimates of L_{∞} (Table 2). Exclusion of the outermost outlier (MLML335) had a very strong influence on both parameters with Fabens' (1965) approach but not with Gulland and Holt's (1959) method. The effect of excluding this outlier was especially large when only females, represented by a smaller sample, were considered. For example, with Fabens' (1965) method, the K value changed from 0.072 to 0.164, whereas Gulland and Holt's (1959) technique produced K estimates of 0.162 and 0.182, respectively.

Changes in the total lengths of the 69 Pacific angel sharks corresponded well with the growth curve generated by the VBGF from tag-recapture data (Fig. 2). Individual growth rates varied somewhat, and times at large ranged from less than a year to more than five years. However, the majority of lines for individual sharks had slopes that very closely approximated those of the theoretical curve. Several sharks of intermediate size and one of smaller size had growth rates that were lower than predicted, and a few had slopes that were somewhat higher than predicted.

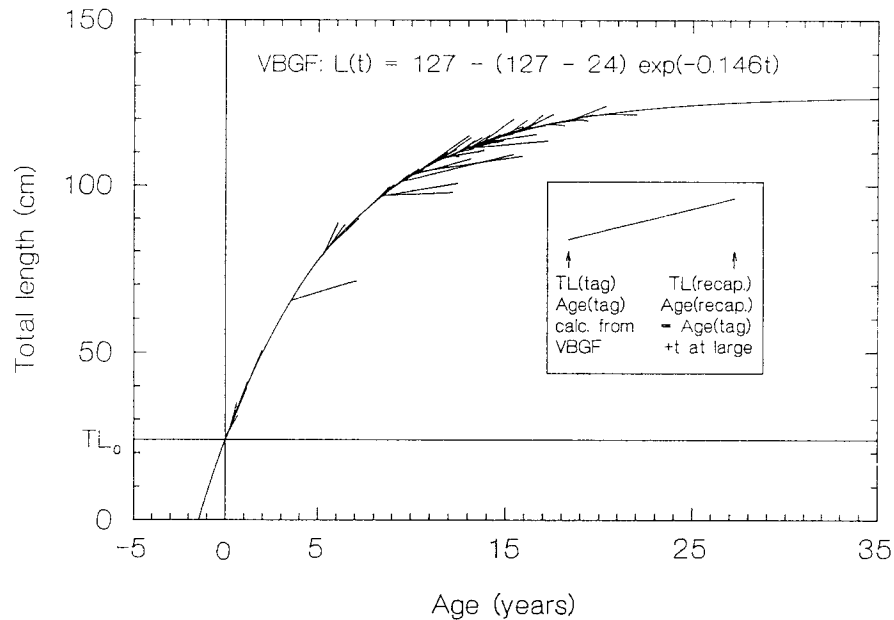


Fig. 2. The von Bertalanffy growth curve for both sexes of Pacific angel shark as predicted from the parameters K and L_{∞} estimated by using the Gulland and Holt (1959) method shown in Fig. 1. L_0 is estimated from the size at birth in the literature (Natanson and Cailliet 1986). The short lines are actual growth data from the 69 tag-recaptures of Pacific angel sharks, with their initial length and age estimate from the VBGF being used as the point of attachment to the predicted line (see insert).

The life table constructed for the Pacific angel shark population off California, using only natural age-specific mortality and natality, indicates that the population is healthy and capable of increasing (Table 3). The net reproductive rate (R_0) was 2.25 per generation, the generation length (G) 14.5 years, and the intrinsic rate of population increase (r) 0.056 year^{-1} . This would suggest that the population could increase at about $6\% \text{ year}^{-1}$ without fishing. When the lower and upper 95% confidence limits of age at maturity (8 and 13 years) were used in the demographic analysis, R_0 values were 3.33 and 1.22, G values

were 12.41 and 17.28 years, and r estimates were 0.098 and 0.012 year⁻¹, respectively. Thus, an earlier age at maturity increased R_0 and r estimates but decreased G estimates, with opposite trends for later ages at maturity.

Table 3. Life-history table of *Squatina californica*
Natural mortality (M) is assumed to be 0.2. No fishing mortality (F)
is included

x	TL (cm)	l_x	m_x	$l_x m_x$	$l_x m_x x$
0	24.0	1.000	0	0	0
1	37.9	0.819	0	0	0
2	50.0	0.670	0	0	0
3	60.4	0.549	0	0	0
4	69.4	0.449	0	0	0
5	77.2	0.368	0	0	0
6	84.0	0.301	0	0	0
7	89.8	0.247	0	0	0
8	94.8	0.202	0	0	0
9	99.2	0.165	0	0	0
10	103.0	0.135	3	0.405	4.050
11	106.2	0.111	3	0.333	3.663
12	109.0	0.091	3	0.273	3.276
13	111.5	0.075	3	0.225	2.925
14	113.6	0.061	3	0.183	2.562
15	115.4	0.050	3	0.150	2.250
16	117.0	0.041	3	0.123	1.968
17	118.3	0.034	3	0.102	1.734
18	119.5	0.028	3	0.084	1.512
19	120.5	0.023	3	0.069	1.311
20	121.4	0.018	3	0.057	1.140
21	122.1	0.018	3	0.048	1.008
22	122.8	0.013	3	0.039	0.858
23	123.4	0.011	3	0.033	0.759
24	123.9	0.009	3	0.027	0.648
25	124.3	0.007	3	0.021	0.525
26	124.7	0.006	3	0.018	0.468
27	125.0	0.005	3	0.015	0.405
28	125.2	0.004	3	0.012	0.336
29	125.5	0.003	3	0.009	0.261
30	125.7	0.002	3	0.006	0.180
31	125.9	0.002	3	0.006	0.169
32	126.0	0.0017	3	0.005	0.159
33	126.2	0.0014	3	0.004	0.135
34	126.3	0.0011	3	0.003	0.113
35	126.4	0.0009	3	0.003	0.096

$R_0 = 2.25$
 $G = 14.51$ years
 $r = 0.056$ year⁻¹
 $e^r = 1.06$

The two lower estimates of natural mortality ($M=0.10$ and 0.15 year⁻¹) produced higher R_0 , G and r estimates, whereas the addition of fishing mortalities to our best estimate of M (0.20 year⁻¹) reduced these demographic parameters (Table 4) mainly through

Table 4. Life-history parameters for *Squatina californica* under three natural mortalities alone ($M=0.1, 0.15$ and 0.20 year^{-1}) and under an M value of 0.2 year^{-1} combined with $F=0.05, 0.10, 0.20$ and 0.22 year^{-1}

M always starts during the first year and continues throughout life, whereas F always starts at age 10 (about 103 cm TL)

	$M: 0.10$	0.15	0.20	0.20	0.20	0.20	0.20
$F:$	0	0	0	0.05	0.10	0.20	0.22
R_0	10.67	4.67	2.26	1.79	1.42	1.05	0.99
G	17.4	15.6	14.5	13.8	13.0	12.6	12.6
r	0.136	0.099	0.056	0.042	0.027	0.004	-0.001

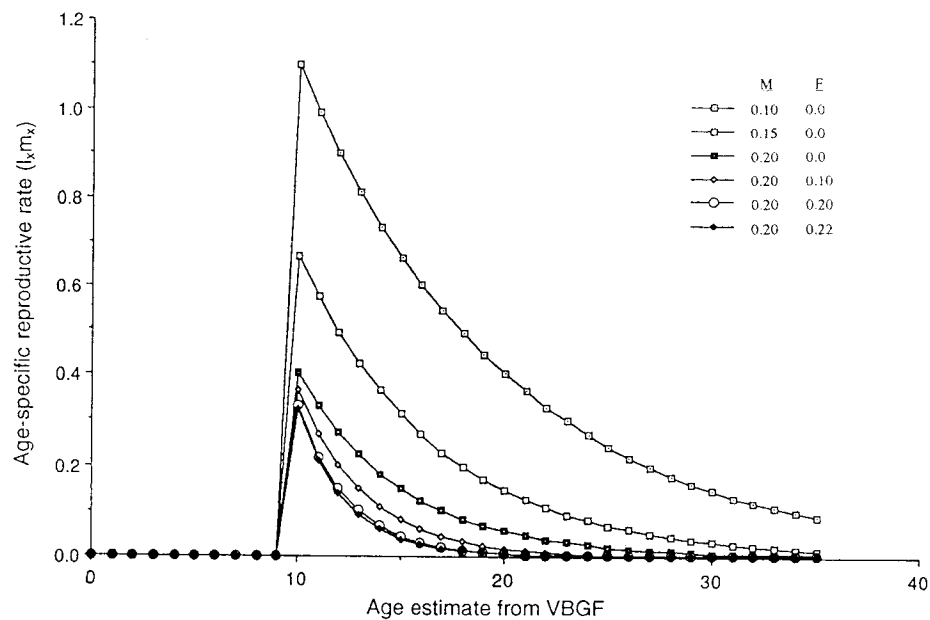


Fig. 3. Age-specific reproductive rates of *Squatina californica* under M values of $0.10, 0.15$ and 0.20 year^{-1} and under an M value of 0.20 year^{-1} coupled with F values of $0.10, 0.20$ and 0.22 year^{-1} . Age estimate is equivalent to x in Table 3.

decreases in age-specific reproductive rates (Fig. 3). The lowest natural mortality estimate (0.1 year^{-1}) produced unreasonably high parameters, whereas those at higher M values (0.15 and 0.20 year^{-1}) were similar. Fishing mortalities of up to 0.20 year^{-1} (in combination with an M value of 0.20 year^{-1}) result in R_0 values of more than 1 and thus predict a slowly growing population. However, this would also predict a doubling time for the population of 173 years!

Discussion

It is generally agreed that the Fabens (1965) nonlinear method of analysing tag-recapture data to obtain VBGF parameters is preferable to the other, linear methods (Vaughan and Kanciruk 1982; Sundberg 1984; Francis 1988b). Further improvements have involved

calculating statistical variability around the VBGF parameters (Francis 1988b), a process successfully utilized by Van Dykhuizen and Mollet (1992) on captive sevengill sharks (*Notorhynchus cepedianus*).

We suggest that Gulland and Holt's (1959) method is also good and that the comparisons by Vaughan and Kanciruk (1982), Sundberg (1984) and Stamatopoulos and Caddy (1989) are inappropriate for long-lived organisms like sharks. We found that the Gulland and Holt (1959) method produced more consistent results for the Pacific angel shark than did the Fabens (1965) method, which inexplicably was influenced by a single outlier (as identified in the linear regression) in the midrange of values for starting size and incremental growth rate.

Vaughan and Kanciruk (1982) concluded from their very systematic comparison that the nonlinear Fabens (1965) technique produced better results than did the Ford-Walford (Walford 1946) and Bayley (1977) methods. However, their Monte Carlo simulations testing these three methods covered only seven years, which would represent only the ascending part of early growth in such long-lived organisms as sharks (Pratt and Casey 1990). This would certainly be true for the Pacific angel shark, which we estimate to have a longevity of 25–35 years. The Ford-Walford plot requires equal times at large and is therefore not suitable for most shark tag-recapture data. Bayley's method is basically the same as that of Gulland and Holt (1959) and is expressed by the equation $L'/L = (kL_{\infty}/L - K)$, which is equivalent to a fractional growth rate.

Sundberg (1984) also found Fabens' (1965) method to be more accurate than those of Gulland and Holt (1959) and Munro (1982). However, Sundberg's (1984) Monte Carlo simulations were not appropriate for typical shark growth data either. Only eight of his 80 calculations had a K value (converted from day⁻¹ to year⁻¹) that would be relevant to shark growth (0.1–0.4 year⁻¹), the time period used was too short, and it covered only the early growth phase. We do not agree with Sundberg's contention that the Gulland and Holt (1959) method is problematic because it requires a geometric-mean regression and a value of b that falls within a certain range. For our shark data, we therefore used an ordinary regression, and all but two of our b values were less than 0.4. We agree with Sundberg (1984) that the Munro (1982) method, because it uses a coefficient of variation to derive the best estimate of K , is not well established.

Stamatopoulos and Caddy (1989) used simulated data to test their new linear regression method for estimating VBGF parameters and concluded that it produced lower error and bias and was more flexible than the Munro (1982) and Gulland and Holt (1959) methods. We do not feel that their new method was properly compared with that of Gulland and Holt (1959) because they used an inadequate sample in which all data pairs had b values that were larger than 0.4 and that ranged from 0.54 to 0.94. In addition, they should have applied the correction factor ($b/\tanh[b]$), as suggested by Gulland and Holt (1959). Finally, their analysis did not include Fabens' (1965) method, which produces virtually the same estimates.

The difficulty that our analysis had with Fabens' (1965) method should be investigated in more detail. The problem is of a different nature from the one reported by Chien and Condrey (1987), who showed that the Fabens (1965) technique systematically overestimated K and underestimated L_{∞} . The 'worst' of three outliers in the midrange caused our Fabens (1965) analysis to produce a K value that was 31% lower than that produced by following Gulland and Holt (1959). This outlier, a female, produced a K value that was a factor of two lower, and quite unrealistic, when only female data ($n=22$) were analysed. Once this one outlier was excluded, the two methods produced almost identical results.

The fact that we used y and x variables, which were correlated, in our Gulland and Holt (1959) linear regression appeared to reduce the standard errors of the VBGF parameters (K and L_{∞}) resulting from this regression. The standard error for K from the Fabens (1965) method was indeed higher than that from the Gulland and Holt (1959) method, but this difference was not large (Table 2).

Another way to evaluate this potential standard-error problem is to independently calculate the VBGF parameter K by a different technique. Therefore, we used Munro's (1982) method of calculating a K value for each tag-recapture data pair, using our best estimate of L_{∞} (127 cm). The results (mean $K=0.155$; s.e. = 0.014) were only slightly higher than the standard error for K resulting from the Gulland and Holt (1959) linear regression (Table 2).

The VBGC plotted by using the parameters K and L_{∞} derived from Gulland and Holt's (1959) method, and the observed length at birth (L_0), produced a reasonable growth curve. The use of L_0 is feasible considering the viviparous nature of shark reproduction and the well established data on size at birth of most sharks (Van Dykhuizen and Mollet 1992).

As pointed out by Sainsbury (1980) and Kusher *et al.* (1992), individual growth rates do not always fit the curve predicted by a model such as the VBGF, a fact that is not unusual in sharks. In the case of the Pacific angel shark, the growth rates of individuals generally conformed to the VBGC predicted from tag-recapture data (Figs 1 and 2). The main exception was one small shark that did not grow as fast as the VBGF predicted, but in all other cases, even though the growth rates of individuals did not fit right on the line, the slopes of the growth rates were very similar to that of the predicted curve.

The growth of the Pacific angel shark, in agreement with other studies on other species (Pratt and Casey 1990), has at least two growth phases, embryonic and post-partum. For example, the range of embryonic-growth rates of 54 to 12 cm year⁻¹ reported by Natanson and Cailliet (1986) is much larger than the range of predicted growth rates of 18.5 to 15 cm year⁻¹ for $TL_0=0$ to 24 cm based on the observed growth rates of the sharks included in the present study. Thus, the characteristics of embryonic growth can not serve as an accurate model for free-living growth, or vice versa (Pratt and Casey 1990; Van Dykhuizen and Mollet 1992), as originally proposed in general by Holden (1974) and for smoothhound sharks by Francis (1981).

The only other check on our VBGF would be the work of Welden *et al.* (1987), who used radiometric techniques to analyse naturally occurring ²¹⁰Pb isotopes in vertebral centra in order to estimate ages for four species, including the Pacific angel shark. Unfortunately, this radiometric study suffered from a small sample size (only two specimens), a high count variability, and two unsupported assumptions (constant incorporation and a closed system). Therefore, the age estimates in that study were lower than those that would be predicted by the VBGF generated from our tag-recapture data for the same species.

There is evidence that tagging may reduce or halt growth in sharks such as the lemon shark (*Negaprion brevirostris*), studied by Manire and Gruber (1991). Our tag-recapture data support tagging effects (Table 1), but they are difficult to substantiate. Pittenger (1984) tagged all of his 56 recaptured sharks by using SCUBA in the field, and most did not even move after being tagged. They had a mean size of 110.6 (s.d. = 7.9) cm TL and a mean growth rate of 2.5 (s.d. = 2.2) cm year⁻¹, and only five had growth rates of less than 0.5 cm year⁻¹. On the other hand, the five tagged by Natanson and Cailliet (1990), after being caught in gill-nets and brought aboard a fishing vessel, were somewhat smaller (100.8, s.d. = 19.5, cm TL) yet had a low mean growth rate of 1.9 (s.d. = 1.8) cm year⁻¹, slower than what the VBGF would predict for this size. Indeed, three of these five sharks had very low growth rates, ranging from 0.1 to 1.6 cm year⁻¹.

To determine the effect of data representing unusually small growth rates on the Gulland and Holt (1959) linear regression, we followed Pauly's (1984) suggestion of eliminating growth increments lower than 0.2 cm. However, the regression excluding growth rates of less than 0.5 cm year⁻¹ produced very similar results ($K=0.141$ year⁻¹ and $L_{\infty}=129.8$ cm TL; $n=62$, $r^2=0.735$, s.e.e. = 1.96). Thus, we do not believe that negative or small growth increments had any influence on our conclusions.

Demography studies are useful for determining whether a population will increase or decrease and for diagnosing how susceptible it may be to exploitation (Caughley 1977; Hoenig and Gruber 1990). In this case, demographic analysis indicates that the Pacific angel

shark population may not be very resilient and also could be quite susceptible to fishing. This would be especially true if fishing started on smaller/younger individuals and was more intense than at present. Thus, depending upon the actual level of natural mortality, care should be taken to keep fishing mortality as low as possible to prevent overexploitation.

Varying the size (and age) at which fishing starts also would have serious implications on the age-specific reproductive rates (Fig. 3) and demography (Tables 3 and 4) of the Pacific angel shark. Assuming that M is constant from birth onwards, the age at which fishing could start and still result in a growing population would be later with higher values of F . Assuming that $M = 0.2 \text{ year}^{-1}$ and $F = 0.22 \text{ year}^{-1}$ (which equals a total mortality, Z , of 0.42 year^{-1} starting at age 10 and a TL of 84 cm), the net reproductive rate would be only 0.99, with $G = 12.60$ years and $r = -0.001 \text{ year}^{-1}$. With M constant at 0.2 year^{-1} , to keep the population growing fishing could not start until age 8 and 9 for F values of 0.15 and 0.2 year^{-1} , respectively.

Data on reproduction (Natanson and Cailliet 1986) indicate that female Pacific angel sharks do not reproduce for the first time until they are about 10 years old (CB = 8–13 years) and that their fecundity does not vary much with increased age or size. This is based on the examination of many specimens of a variety of sizes. However, further studies are needed to determine the proportion of adults in each age class that are actually breeding and whether adults breed every year. Although we now have estimates of the present sizes (and ages) at first capture, we do not know the proportion of sharks subject to fishing at these different sizes and ages.

Some of the parameters used in the present study could be inaccurate. For example, the constant natural mortality value of 0.2 that we used, although reasonable, was taken from Hoenig's (1983) regression equation between instantaneous mortality coefficients and the longevity of many organisms and may not apply to the Pacific angel shark.

The fishing-mortality estimates were arbitrarily chosen, and we have no independent way to estimate them. It was impossible to use the approach taken by Smith and Abramson (1990) for tag returns of leopard sharks in San Francisco Bay because no organized original-capture, tagging or recovery strategy was used. Sharks were tagged in several places over several years, and the tag-return data were taken by various people in different years and localities.

Another problem might be that M or F do not operate uniformly during all ages. That is, one or more years of life might be susceptible to higher or lower natural mortalities than are accounted for in the present model. Once they have started operating, M and F have been assumed to be constant throughout the life of Pacific angel sharks. In this shark, reproductive maturity and F start at the same age and size. However, in the future, regulations could be imposed that would limit the size at which the sharks should first be taken by the fishery, thus ensuring adequate reproduction for replacement.

Stable age distributions were not calculated from the life table because there were few data from the commercial fishery with which to compare them. However, the size frequencies presented by Pittenger (1984) from SCUBA observations off Catalina Island, and unpublished data of Natanson and Bedford from the commercial gill-net fishery off Santa Barbara and the Channel Islands, indicate that the majority of sharks were over 100 cm TL and therefore mature. In general, very few sharks between 24 and 100 cm TL have been encountered, indicating either that the population grows rapidly through this size category, which would contradict our VBGF assumptions, or that these size classes live elsewhere.

It would be impossible to evaluate how close our estimates of net reproductive rate, generation time and intrinsic rate of increase are to the true values. Yet, they conform to the published life-history parameters of other elasmobranchs. For example, Hoenig and Gruber (1990), after modifying data from Heron (1972), Blueweiss *et al.* (1978) and Pauly (1982), proposed that statistical relationships between r (day^{-1}) and (1) adult body weight (kg) and (2) generation time (days) could be used to predict these population parameters

for elasmobranchs. Indeed, our values for Pacific angel sharks (Table 1), when converted to daily rates ($r = 1.54 \times 10^{-4} \text{ day}^{-1}$; $G = 5293 \text{ days}$), fit right on both of the curves modified by Hoenig and Gruber (1990).

A comparison of the Pacific angel shark and the leopard shark off central California indicates that they have different life histories. The net reproductive rate ($R_0 = 2.26$) and generation time ($G = 14.51 \text{ years}$) of the Pacific angel shark are considerably lower than those estimated for leopard sharks ($R_0 = 4.47$; $G = 22.3 \text{ years}$), although the two intrinsic rates of increase are similar ($r = 0.06$ and 0.07 year^{-1} , respectively). However, the Pacific angel shark is similar to the leopard shark in its distribution, size composition, reproductive seasonality, and apparently natural mortality (Smith and Abramson 1990; Cailliet 1992).

It is not necessarily legitimate to compare directly the life-history parameters R_0 , G and r obtained in the present study with those published in the literature for other species of elasmobranchs, mainly because of the differences in approaches and assumptions made (Cailliet 1992). Nevertheless, Hoenig and Gruber (1990) derived an estimate of 0.015 year^{-1} for the observed intrinsic rate of increase in the lemon shark, which is a much smaller value than that calculated for either leopard or Pacific angel sharks. Perhaps this is related to the lower fecundity or higher estimate of natural mortality they assumed for the lemon shark.

Whether the demographic parameters derived in the present analysis would fit Pacific angel shark populations throughout their range is uncertain. We are reasonably sure, however, that the population studied off Santa Barbara and the Channel Islands is sufficiently related genetically to be considered as a single unit. Tagged Pacific angel sharks have been caught both along the Californian coast and at the Channel Islands, but there is no genetic information, such as that found by Lavery and Shaklee (1989) for Australian sharks, that indicates that separate stocks exist.

Before incorporating the results of the present study into fishery management, one would have to know more about (1) the possible relationship between recruitment and parent stock size and (2) whether there might be density-dependent changes in the reproduction rate, mortality rate or growth rate in response to reduced stock abundance. Although we know that the Pacific angel shark fishery has declined (Richards 1987; Holts 1988), we have no idea about either of these relationships or about the population dynamics of this species (Wood *et al.* 1979). We hope we have clearly enough stated the assumptions we have made to demographically model this population so that new parameters can be incorporated into future models once they are available.

Thus, we have used tag-recapture information, a conservative estimate of natural mortality, and reproductive information (Natanson and Cailliet 1986) in a demographic analysis to produce estimates of life-history parameters that may be useful for further understanding the Pacific angel shark. If the fishing pressure were to increase in intensity or start to effectively target the smaller, and younger, sharks, there would be strong potential for this nearshore and residential shark population to decrease.

Indeed, this fishery already has peaked and declined (Richards 1987; Holts 1988), and it should be watched carefully in the future. Until accurate estimates of M and F are available, it would be prudent to set a size limit considerably above the size at first reproduction in order to protect the Pacific angel shark in California.

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References

- Anderson, E. D. (1990). Fishery models as applied to elasmobranch fisheries. In 'Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries'. (Eds H. L. Pratt, Jr, S. H. Gruber and T. Taniuchi.) pp. 473-84. United States Department of Commerce, NOAA Technical Report NMFS Circular No. 90.
- Anderson, E. D., and Teshima, K. (1990). Workshop on fisheries management. In 'Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries'. (Eds H. L. Pratt, Jr, S. H. Gruber and T. Taniuchi.) pp. 499-503. United States Department of Commerce, NOAA Technical Report NMFS Circular No. 90.
- Bayley, P. B. (1977). A method for finding the limits of application of the von Bertalanffy growth model and statistical estimates of the parameters. *Journal of the Fisheries Research Board of Canada* 34, 1079-84.
- Blueweiss, L., Fox, L. H., Kudzma, V., Nakashima, D., Peters, R., and Sams, S. (1978). Relationship between body size and some life-history parameters. *Oecologia (Berlin)* 37, 257-72.
- Cailliet, G. M. (1990). Elasmobranch age determination and verification: an updated review. In 'Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries'. (Eds H. L. Pratt, Jr, S. H. Gruber and T. Taniuchi.) pp. 157-65. United States Department of Commerce, NOAA Technical Report NMFS Circular No. 90.
- Cailliet, G. M. (1992). Demography of the central California population of the leopard shark (*Triakis semifasciata*). In 'Sharks: Biology and Fisheries'. (Ed. J. G. Pepperell.) *Australian Journal of Marine and Freshwater Research* 43, 183-93.
- Cailliet, G. M., and Tanaka, S. (1990). Recommendations for research needed to better understand the age and growth of elasmobranchs. In 'Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries'. (Eds H. L. Pratt, Jr, S. H. Gruber and T. Taniuchi.) pp. 505-7. United States Department of Commerce, NOAA Technical Report NMFS Circular No. 90.
- 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. Yeno, R. Arai, T. Taniuchi and K. Matsuura.) pp. 345-60. (Ichthyological Society of Japan: Tokyo.)
- Caughley, G. (1977). 'Analysis of Vertebrate Populations.' (Wiley: New York.)
- Charlesworth, B. (1980). 'Evolution in Age-structured Populations.' (Wiley: New York.)
- Chien, Y.-H., and Condrey, R. E. (1987). Bias in estimating growth parameters using Fabens' mark-recapture procedures. *Asian Fisheries Science* 1, 65-74.
- Compagno, L. J. V. (1984). Sharks of the world: an annotated and illustrated catalogue of shark species known to date. FAO Fisheries Synopsis No. 125, Vol. 4, Parts 1 and 2. 655 pp.
- Eschmeyer, W. H., Herald, E. S., and Hammann, H. (1983). 'A Field Guide to the Pacific Coast Fishes of North America from the Gulf of Alaska to Baja California.' (Houghton Mifflin: Boston.) 336 pp.

- Fabens, A. J. (1965). Properties and fitting of the von Bertalanffy growth curve. *Growth* **29**, 265–89.
- Francis, M. P. (1981). von Bertalanffy growth rates in species of *Mustelus* (Elasmobranchii: Triakidae). *Copeia* **1981**(1), 189–92.
- Francis, R. I. C. C. (1988a). Are growth parameters estimated from tagging and age-length data comparable? *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 936–42.
- Francis, R. I. C. C. (1988b). Maximum likelihood estimation of growth and growth variability from tagging data. *New Zealand Journal of Marine and Freshwater Research* **22**, 42–51.
- Grant, C. J., Sandland, R. O., and Olsen, A. M. (1979). Estimation of growth, mortality and yield per recruit of the Australian school shark, *Galeorhinus australis* (Macleay), from tag recoveries. *Australian Journal of Marine and Freshwater Research* **30**, 625–37.
- 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.
- Hanchet, S. (1988). Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **22**, 537–49.
- Heron, A. C. (1972). Population ecology of a colonizing species: the pelagic tunicate *Thalia democratica*. II. Population growth rate. *Oecologia (Berlin)* **10**, 294–312.
- Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. *US National Marine Fisheries Service Fishery Bulletin* **81**, 898–903.
- Hoenig, J. M., and Gruber, S. H. (1990). Life-history patterns in the elasmobranchs: implications for fisheries management. In 'Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries'. (Eds H. L. Pratt, Jr, S. H. Gruber and T. Taniuchi.) pp. 1–16. United States Department of Commerce, NOAA Technical Report NMFS Circular No. 90.
- Hoff, T. B., and Musick, J. A. (1990). Western North Atlantic shark-fishery management problems and informational requirements. In 'Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries'. (Eds H. L. Pratt, Jr, S. H. Gruber and T. Taniuchi.) pp. 455–72. United States Department of Commerce, NOAA Technical Report NMFS Circular No. 90.
- Holden, M. J. (1974). Problems in the rational exploitation of elasmobranch populations and some suggested solutions. In 'Sea-fisheries Research'. (Ed. F. R. Harden Jones.) pp. 117–37. (Wiley: New York.)
- Holts, D. (1988). Review of US West Coast commercial shark fisheries. *US National Marine Fisheries Service Marine Fisheries Review* **50**(1), 1–8.
- Jenkins, S. H. (1988). Use and abuse of demographic models of population growth. *Bulletin, Ecological Society of America* **69**(4), 201–7.
- Jones, B. C., and Geen, G. H. (1977). Reproduction and embryonic development of spiny dogfish (*Squalus acanthias*) in the Strait of Georgia, British Columbia. *Journal of the Fisheries Research Board of Canada* **34**, 1286–92.
- Kirkwood, G. P., and Walker, T. I. (1986). Gill net mesh selectivities for gummy shark, *Mustelus antarcticus* Günther, taken in south-eastern Australian waters. *Australian Journal of Marine and Freshwater Research* **37**, 689–97.
- Krebs, C. J. (1985). 'Ecology, the Experimental Analysis of Distribution and Abundance.' 3rd edn. (Harper and Row: New York.)
- Kusher, D. I., Smith, S. E., and Cailliet, G. M. (1992). Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. *Environmental Biology of Fishes* **35**(2), 187–203.
- Lavery, S., and Shaklee, J. B. (1989). Population genetics of two tropical sharks, *Carcharhinus tilstoni* and *C. sorrah*, in northern Australia. *Australian Journal of Marine and Freshwater Research* **40**, 541–57.
- Manire, C. A., and Gruber, S. H. (1991). Effect of M-type dart tags on field growth of juvenile lemon sharks. *Transactions of the American Fisheries Society* **120**, 776–80.
- Mertz, D. B. (1970). Notes on methods used in life-history studies. In 'Readings in Ecology and Ecological Genetics'. (Eds J. H. Connell, D. B. Mertz and W. W. Murdoch.) pp. 4–17. (Harper and Row: New York.)
- Miller, D. J., and Lea, R. N. (1972). Guide to the coastal marine fishes of California. *California Department of Fish and Game Fish Bulletin* **157**, 1–235.

- Munro, J. L. (1982). Short notes: estimation of the parameters of the von Bertalanffy growth equation from recapture data at variable time intervals. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **40**, 199–200.
- Natanson, L. J., and Cailliet, G. M. (1986). Reproduction and development of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. *Copeia* **1986**(4), 987–94.
- Natanson, L. J., and Cailliet, G. M. (1990). Vertebral growth zone deposition in Pacific angel sharks. *Copeia* **1990**(4), 1133–45.
- Neter, J., Wassermann, M. H., and Kutner, M. H. (1983). 'Applied Linear Regression Models.' (Irwin: Homewood, Illinois.) p. 154.
- Pauly, D. (1982). Studying single-species dynamics in a tropical multi-species context. In 'Theory and Management of Tropical Fisheries'. (Eds D. Pauly and G. I. Murphy.) Conference Proceedings No. 9, pp. 33–70. (International Centre for Living Aquatic Resources Management/CSIRO Division of Fisheries Research: Manila/Sydney.)
- Pauly, D. (1984). 'Fish Population Dynamics in Tropical Waters: A Manual for Use with Programmable Calculators.' (International Centre for Living Aquatic Resources Management: Manila.)
- Pittenger, G. G. (1984). Movements, distribution, feeding, and growth of the Pacific angel shark, *Squatina californica*, at Catalina Island, California. M.S. Thesis, California State University, Long Beach. 83 pp.
- Pleshner, D. B. (1983). Pacific angel shark. *Pacific Fishing* February, 55–9.
- Pratt, H. L., Jr, and Casey, J. G. (1990). Shark reproductive strategies as a limiting factor in directed fisheries, with a review of Holden's method of estimating growth parameters. In 'Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries'. (Eds H. L. Pratt, Jr, S. H. Gruber and T. Taniuchi.) pp. 97–109. United States Department of Commerce, NOAA Technical Report NMFS Circular No. 90.
- Pratt, H. L., Jr, and Otake, T. (1990). Recommendations for work needed to increase our knowledge of reproduction relative to fishery management. In 'Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries'. (Eds H. L. Pratt, Jr, S. H. Gruber and T. Taniuchi.) pp. 509–10. United States Department of Commerce, NOAA Technical Report NMFS Circular No. 90.
- Richards, J. B. (1987). Developing a localized fishery: the Pacific angel shark. In 'Sharks: An Inquiry into Biology, Behavior, Fisheries, and Use'. (Ed. S. Cook.) pp. 147–60. (Oregon State University: Corvallis.)
- Ricker, W. E. (1973). Linear regression in fishery research. *Journal of the Fisheries Research Board of Canada* **30**, 409–34.
- Ricker, W. E. (1979). Growth rates and models. In 'Fish Physiology. Vol. VIII. Bioenergetics and Growth'. (Eds W. S. Hoar, D. J. Randall and J. R. Brett.) pp. 677–743. (Academic Press: New York.)
- Sainsbury, K. J. (1980). Effect of individual variability on the von Bertalanffy growth equation. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 241–7.
- Smith, S. E., and Abramson, N. J. (1990). Leopard shark *Triakis semifasciata* distribution, mortality rate, yield, and stock replenishment estimates based on a tagging study in San Francisco Bay. *US National Marine Fisheries Service Fishery Bulletin* **88**, 371–81.
- Sokal, R. R., and Rohlf, F. J. (1981). 'Biometry: The Principles of Statistics in Biological Research'. 2nd edn. (Freeman: New York.)
- Stamatopoulos, C., and Caddy, J. F. (1989). Estimation of von Bertalanffy growth parameters: a versatile linear regression approach. *Journal du Conseil. Conseil International pour l'Exploration de la Mer* **45**, 200–8.
- Sundberg, P. (1984). A Monte Carlo study of three methods for estimating the parameters in the von Bertalanffy growth equation. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **41**, 248–58.
- 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.
- Vaughan, D. S., and Kanciruk, P. (1982). An empirical comparison of estimation procedures for the von Bertalanffy growth equation. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **40**, 211–19.

- von Bertalanffy, L. (1938). A quantitative theory of organic growth (inquiries on growth laws. II). *Human Biology* 10(2), 181–213.
- Walford, L. A. (1946). A new graphic method of describing the growth of animals. *Biological Bulletin (Woods Hole)* 90, 141–7.
- Wallis, W. A., and Roberts, H. V. (1956). 'Statistics, a New Approach.' (The Free Press: New York.)
- Welden, B. A., Cailliet, G. M., and Flegal, A. R. (1987). Comparison of radiometric with vertebral band age estimates in four California elasmobranchs. In 'Age and Growth of Fish'. (Eds R. C. Summerfelt and G. E. Hall.) pp. 301–15. (Iowa State University Press: Ames, Iowa.)
- Wilkinson, L. (1988a). 'SYSTAT: The System for Statistics.' (SYSTAT, Inc.: Evanston, Illinois.)
- Wilkinson, L. (1988b). 'SYGRAPH: The System for Graphics.' (SYSTAT, Inc.: Evanston, Illinois.)
- Wilkinson, L. (1990). 'SYSTAT: The System for Statistics.' (SYSTAT, Inc.: Evanston, Illinois.) 677 pp.
- Wood, C. C., Ketchen, K. S., and Beamish, R. J. (1979). Population dynamics of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada* 36, 647–56.