

Abstract—We examined the effects of gear selectivity and the consequences of a chosen method for estimating growth parameters of bluefish, *Pomatomus saltatrix*, from southern Brazil. Samples were obtained from commercial landings at Rio Grande (1992–97). Age determination for 1159 fish indicated that gill-net and purse-seine fisheries caught 1–5 year-old and 1–7 year-old fish, respectively. Trawlers caught fish from ages 1 to 7. Because of their high degree of selectivity, the gill nets caught the larger individuals of ages 1 and 2, as well as the smaller individuals of ages 3–5. Faster-growing fish captured with gill nets had smaller scales than fish of a similar length caught with purse seines. By contrast, the slower-growing fish captured with gill nets had larger scale size than fish of a similar length caught with purse seines. For gill nets and purse seines, there were differences between the von Bertalanffy growth estimates derived from both mean values of back-calculated length-at-age and individual back-calculated length-at-age. We also recorded differences in growth parameters obtained from back-calculated length-at-age derived from measurements to the last annulus only and from measurements of all annuli up to the sampling age. Selectivity-related bias was incorporated in the estimation of growth parameters, yielding unrealistic estimates of L_{∞} and k for the gill-net growth curve.

Effects of gear selectivity and different calculation methods on estimating growth parameters of bluefish, *Pomatomus saltatrix* (Pisces: Pomatomidae), from southern Brazil

Flávia M. Lucena

Carl M. O'Brien

CEFAS Lowestoft Laboratory

Pakefield Road

Lowestoft, Suffolk NR33 OHT, United Kingdom

Present address (for F. M. Lucena): Universidade Federal Rural de Pernambuco

Departamento de Pesca. Av. Dom Manoel s/n

Dois Irmãos. Recife, PE. Cep: 52171-900, Brazil

E-mail address (for F. M. Lucena): flavialucena@hotmail.com

The bluefish, *Pomatomus saltatrix* (L.) (Pomatomidae), is a highly mobile pelagic predator (Haimovici and Krug, 1996), widely distributed along the continental shelf in the temperate and warm waters of the Atlantic, Pacific, and Indian oceans (Wilk, 1977). Abundant in Brazilian waters, this species is commercially exploited by purse-seine and gill-net fleets operating in the subtropical coastal waters of Rio Grande do Sul between Conceição (31°42'S) and Chuí (33°43'S), at depths between 8 and 100 m (Lucena and Reis, 1998) (Fig. 1). Purse-seine boats are approximately 23 m in length and have 220–330 HP engines, whereas gill-net boats are usually 14–16 m in length and have 90–150 HP engines (Boffo and Reis, 1997). Gill nets used in the bluefish fishery are drift gill nets 1800 m in length and that have a stretched mesh size of 90 mm.

Commercial catches of bluefish were first monitored from 1976 to 1983 on the fishing grounds from Sarita (32°37'S) to Conceição at depths up to 35 m (Krug and Haimovici, 1991). Bluefish were then primarily exploited by purse seine but were also taken as bycatch in a gill-net fishery targeting wreckfish (*Polyprion americanus*) and elasmobranchs. Commercial catches were dominated by fish between 1 and 3 years old for the purse-seine fleet and by fish aged 2–4 years old for the gill-net fleet (Krug and Haimovici, 1989).

As catches from the estuarine Patos Lagoon declined, beginning in 1982, the artisanal fleet began exploiting new

fishing grounds and a fishery developed in shallow coastal waters (Reis, 1992). Since 1990, bluefish have been caught primarily by gill net (up to 72% of landings by weight) and the fishing grounds now extend southward into waters up to 100 m (Lucena and Reis, 1998). For the period 1991–95, commercial catches have included individuals to age 10 (Lucena, 1997).

Since the emergence of the gill-net fleet, the exploitation of the bluefish has been increasing. From 1991 to 1996, there has been an 87% increase in the length of netting deployed and a 166% increase in the soak time of the gear (Lucena and Reis, 1998). In addition, there has been a decrease in mean length of fish caught by purse seines and gill nets from 1992 to 1995 (Lucena, 1997). Average annual landings of the bluefish decreased from 3100 (during the period 1990–95) to 1700 tonnes (during 1996–98) (IBAMA¹).

The growth parameters of the southern Brazilian bluefish population were estimated by Krug and Haimovici (1989), using scales from fish landed commercially by several gears (gill nets, purse seines, trawlers, long lines, and beach netting) from 1976 to 1983. Their study excluded individuals larger than 63 cm TL because the larger fish lived

¹ IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis). 1990–1998. Unpubl. data. Centro de Pesquisa do Rio Grande (CEPERG)—RS, IBAMA, Brazil. Cep: 96201-900.

at depths greater than 35 m, the operational limit of the fleet at that time. Given today's increased exploitation of bluefish, and the lack of older fish in the earlier study, we decided to examine the age structure and growth parameters of the bluefish stock off southern Brazil. New data are compared to previously published information and the effects of gear selectivity on the estimation of growth parameters are also evaluated.

Annulus formation occurs in winter (June to September) and is associated with lower water temperature (Haimovici and Krug, 1996). Rings do not become visible until growth resumes in January or February. During peak spawning, January–February, the true age of individuals with one ring is 7 months on average (Haimovici and Krug, 1992).

Even though most sampled bluefish have usually been caught during the short period of the fishing season (June to September), the real age of a fish may vary by between 4 and 9 months from that notionally adopted because the bluefish is a multiple spawner and because this species' scale ring formation is associated with lower temperatures (the exact timing of ring formation varies from year to year and can also be influenced by environmental phenomena such as El Niño events). Hence, because sample collections were spaced unevenly throughout the fishing season for both within-year and between-period comparisons, growth rates based on changes in observed lengths were deemed inappropriate and the estimation of growth parameters was based on back-calculated lengths.

Many early writers, using the back-calculation technique, made no mention of the reason for choosing a particular procedure (e.g. Johnson and Saloman, 1984; Barger, 1990; Vieira and Haimovici, 1993). Valuable reviews on back-calculation were carried out by Hile (1970), Tesch (1971), Casselman (1987) and Francis (1990) and, although this technique is widespread, it still does not appear to be well understood. Moreover, there is a common tendency to plot only mean, rather than individual, back-calculated length-at-age to produce the growth curve (Hilborn and Walters, 1992). The effects of different approaches on growth parameter estimates are discussed in this paper.

Materials and methods

Sampling, age structure, and scale reading

We sampled commercial landings from three fleets at Rio Grande from 1992 to 1997: catch from the gill-net fleet,

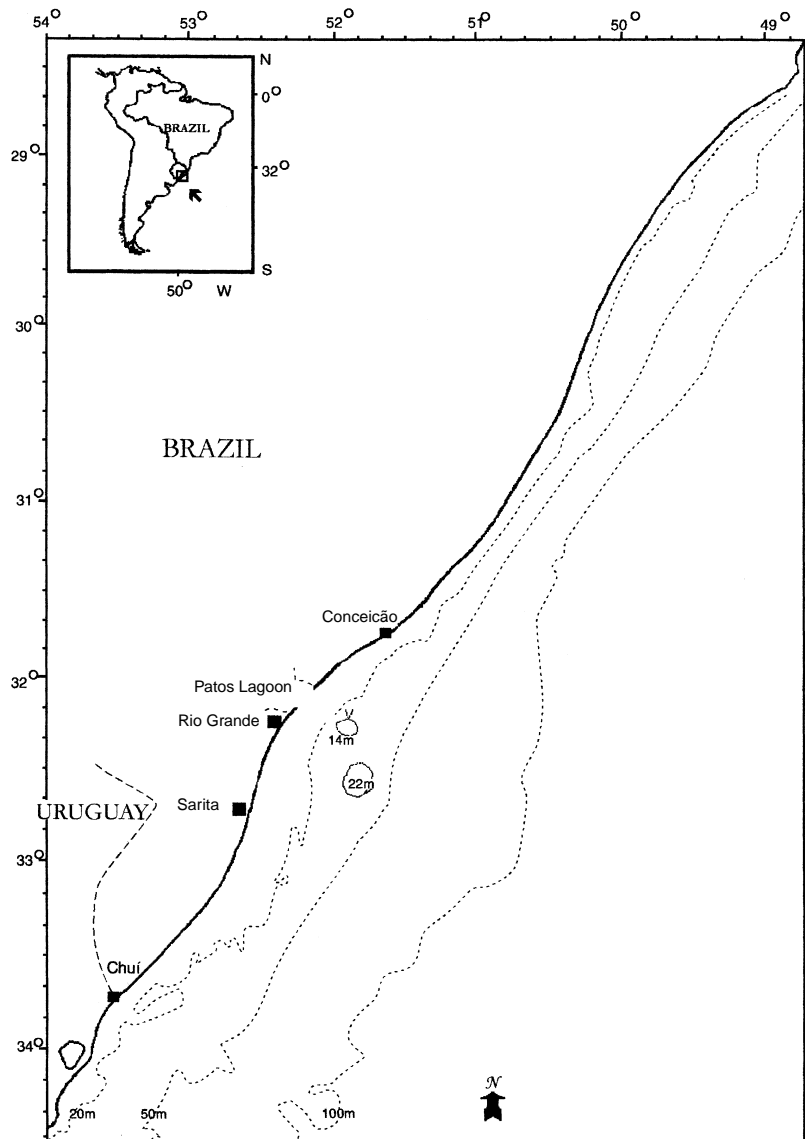


Figure 1

Map of the southern coast of Brazil and sampling area for bluefish.

catch from the purse-seine fleet, and bycatch from the trawl (pair and otter) fleet (Table 1). We sampled 13 additional bluefish from the gill-net fishery targeting wreckfish (*Polyprion americanus*), choosing larger (older) fish in order to investigate the size of the bluefish that move along the shelf break at depths >200 m, where the wreckfish fishery operates. We collected an additional 57 individuals (75–135 mm in TL) with experimental trawls in the estuary of Patos Lagoon in order to calibrate the weight-length relationship for juveniles.

Total length (TL) in mm of 1159 fish (260 to 711 in TL), measured to the end of the extended tail were recorded. The total weight (TW, in grams) and sex (macroscopically determined) of 580 bluefish, ranging in size from 75 to 711 mm TL, were determined to calculate the weight-length relationship, by using nonlinear least-squares regression

Table 1

Depth, sampling period, length and age range, and number of boats and individuals examined as part of the bluefish sampling in southern Brazil during the 1992–97 period.

	Bluefish target species		Bluefish bycatch	
	Gill net	Purse seine	Gill net	Trawl (pair and otter) net
Depth (m)	10–35	8–100	270	8–68
Sampling period	Jun–Aug	May–Sep	Sep	Jan–Mar, May
Length range (mm)	301–602	265–711	650–770	262–711
Age range (years)	1–5	1–7	5–10	1–7
Number of boats examined	33	11	1	7
Number of individuals examined	853	233	13	60

(SPSS, 1998). *T*-tests were used to test for gear- and sex-specific length-weight relationships.

Scales of captured bluefish were removed from under the pectoral fin and stored in a coin envelop. The scales of 1159 fish were mounted between glass slides and fish age was determined by following Krug and Haimovici (1989). Fish were considered to be 1 year old after the formation of the first winter ring and a further year was added to the age of the fish for each subsequent ring (Krug and Haimovici, 1989).

Two different readers assigned ages for the fish, with no knowledge of fish length or month and gear of capture. If two readings agreed, then the age of that reading was adopted as definitive. If not, the scale was reread after two months, concurrently by both readers. If two of the three readings were the same, the age of these two readings was assumed as definitive. If all three readings differed, the scale was omitted from further analysis. On some scales, a single reader assigned ages. This method was followed with a time lag (2 months) between readings.

Estimation of growth parameters

Sample sizes were sufficient for estimation of growth parameters from gill-net and purse-seine samples. Ages from the direct reading of scales were obtained for 816 bluefish from gill-net samples and for 212 bluefish from purse-seine samples.

Ricker (1992) pointed out that the inclusion of sampled fish taken at different times during the growing season should be avoided and that preferably fish collected between the formation of an annulus and the start of the next year's growth should be used in analysis. Only data obtained during the fishing season were included for estimation of growth parameters derived from direct reading, and data derived from purse-seine samples (the less selective gear) were used to compare the growth parameters derived from mean observed lengths-at-age and back-calculated lengths-at-age.

For back-calculation of growth parameters, 283 specimens (174 from gill-net samples and 109 from purse-seine samples) were used. Fish were processed by sex and gears used in their capture to avoid bias in results.

We determined the relationship between fish length (*TL*) and scale radius (*S*). Krug and Haimovici (1989) previously identified a nonlinear relationship between fish length and scale radius for the southern Brazilian bluefish ($TL = aS^b$). Back-calculated total lengths at age were determined by using the formula of Monastyrsky (see Bagenal and Tesch, 1978; Francis, 1990):

$$L_n = (S_n/S)^b \times TL,$$

where L_n = the length of fish when annulus "n" was formed;

S_n = the radius of annulus "n" (at fish length L_n);
and

b = the slope from the body-scale relationship *TL* on *S*.

This nonlinear method for back-calculation assumes that the relationship *TL* on *S* is of the form $TL = aS^b$ where a and b are parameters to be estimated usually by nonlinear least squares.

The periodicity of growth increments was examined by using analysis of marginal increments $[(S - S_n)/(S_n - S_{n-1})]$ from fish 2–7 years old (mainly 2–3 years old) (following Krug and Haimovici, 1989). Because of the limited temporal range of samples, no marginal increments analysis was done for the months March–April and November–December.

We derived theoretical growth parameters by fitting back-calculated lengths-at-age to the von Bertalanffy (1934) growth equation

$$L_t = L_\infty (1 - \exp^{-k(t-t_0)}),$$

where L_t = the length at age t ;

L_∞ = the asymptotic length;

k = the brody growth coefficient; and

t_0 = the age when length would theoretically be zero.

Estimation of growth parameters was based upon two criteria. Criterion I identified the type of summary statistic to be used:

- Ia corresponded to mean values of back-calculated lengths-at-age; and
 Ib represented individual back-calculated lengths-at-age.

Criterion II identified the type of data to be used:

- IIa corresponded to the back-calculated length-at-age derived from the last annulus only; and
 IIb represented the back-calculated lengths-at-age derived from all the annuli up to the sampling age.

We calculated growth parameters by using four methods for each gear: method 1 (where criteria Ia and IIa were used), method 2 (where criteria Ia and IIb were used), method 3 (where criteria Ib and IIa were used), and method 4 (where criteria Ib and IIb were used).

The growth curves were estimated with the program AD Model Builder (Otter Research, 1996), which uses an automatic differentiation algorithm to estimate the parameters of a nonlinear function with an appropriate objective function. The software allows the calculation of confidence intervals for parameter estimates with asymptotic normal approximations.

The objective function considered is the nonlinear least-squares regression criterion, $R(\cdot)$, either given by

$$R(L_\infty, k, t_0 | O_t) = \sum_{t=1}^T (O_t - L_t)^2,$$

when mean values are considered, or given by

$$R(L_\infty, k, t_0 | O_{it}) = \sum_{t=1}^T \sum_{i=1}^{n_t} (O_{it} - L_t)^2,$$

when individual values are considered.

Note that O_t is the mean back-calculated length-at-age t , O_{it} is the i th individual back-calculated length-at-age t , T denotes the maximum number of distinct ages, and n_t is the number of observations at age t . To compare growth curves between gears, Hotelling's t -test (1979) was used.

Results

Age structure of the stock

We examined a total of 1159 fish and 94% of samples were collected during the fishing season (June to September)—the remaining numbers represented bycatch during the off-peak season. Age determination (Fig. 2) indicated that the gill-net fisheries caught fish of ages 1–5 (mode=

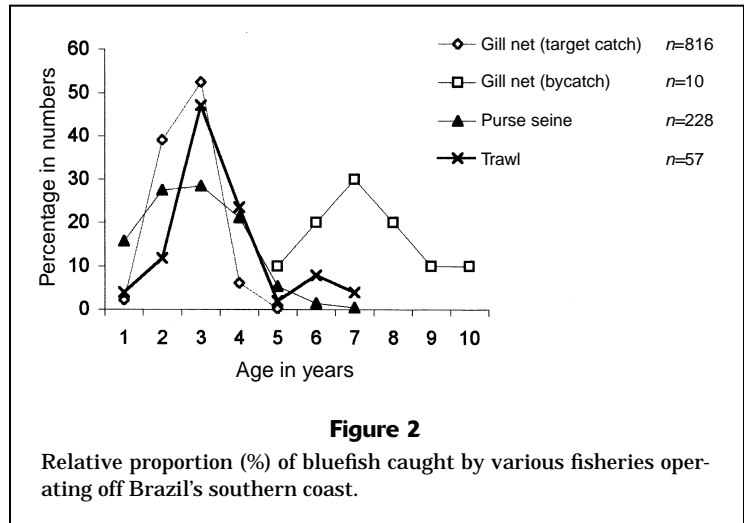


Figure 2
Relative proportion (%) of bluefish caught by various fisheries operating off Brazil's southern coast.

3 yr) and purse-seine fisheries caught fish of ages 1–7 (mode=2–3 yr). Trawlers caught fish of ages 1–7. Individuals of ages 5 to 7 represented less than 2% of samples (individuals of 5 to 7 years old were underrepresented also in the back-calculation procedures). The deep-water (to 200 m) gill-net fishery targeting *P. americanus* caught individuals of age 5–10 and the only fish older than age 7. There was a considerable overlap in the range of observed lengths-at-age (Table 2), nevertheless significant differences between gears were detected for some ages. Gill nets caught larger individuals of ages 1 and 2 and smaller individuals of ages 3–5 than purse seines. Trawls, on the other hand, appear to catch smaller individuals in all age classes.

Weight-length relationship

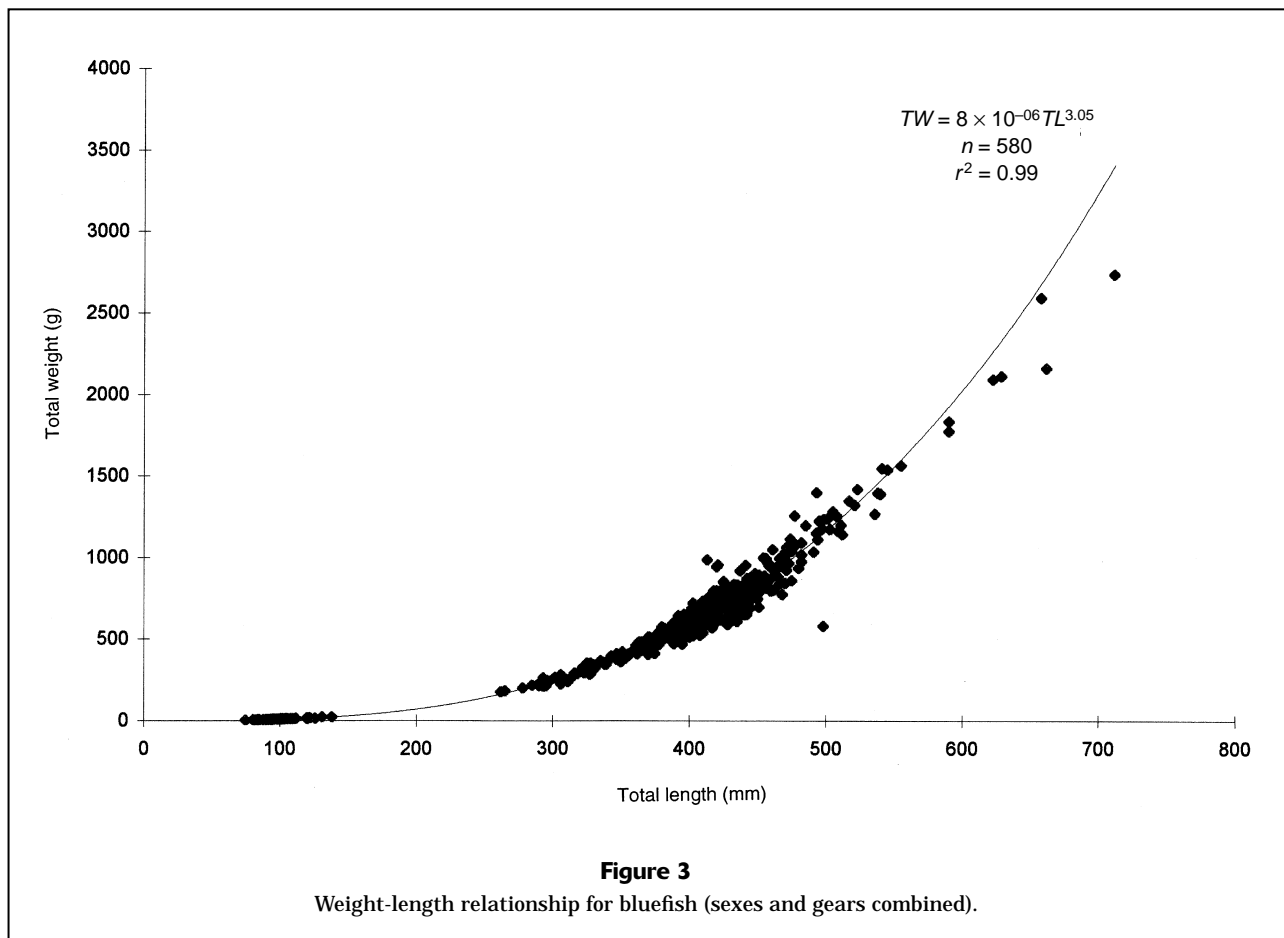
We found no statistically significant differences in length-weight relationships between gear types or between sexes (t -test, $P > 0.05$). The relationship for both sexes and all gears combined is illustrated in Figure 3.

Body-scale relationship

Gear-specific regressions of TL on S (Fig. 4) showed that gill nets tended to catch the fast-growing fish of younger ages and the slow-growing individuals of older ages. These faster-growing younger fish (<360 mm TL , 1–2 years) have smaller scales than similar-size purse-seine-caught fish (t -test; $P < 0.05$). By contrast, the slower-growing fish (>410 mm TL , 4–5 yr) had larger scales than fish of a similar length caught by the purse-seine fleet. For the length range that the gill nets target most efficiently (360–410 mm TL , age 3), the TL - S relationship for both gill net and purse seine was similar.

Periodicity of growth increments

Our limited data showed marginal increment to be lowest in January–February, corresponding to ring deposition.

**Table 2**

Mean observed length-at-age for gill-net (targeted catch), purse-seine, and trawl catches. The symbol SD denotes the standard deviation, *n* denotes the number of individuals examined and “—” denotes that a value could not be calculated. ANOVA was performed only for the age classes with *n* greater than 10.

Age (yr)	Gill net length at age (mm)			Purse-seine length at age (mm)			Trawl length at age (mm)		
	Average	Range	SD (<i>n</i>)	Average	Range	SD (<i>n</i>)	Average	Range	SD (<i>n</i>)
1	354.3 ^{1,2}	301–417	30.8 (33)	313.5 ¹	276–385	23.4 (31)	278.5	265–292	19.0 (2)
2	408.7 ¹	293–495	32.6 (286)	385.0 ¹	290–485	44.5 (49)	372.8	285–409	47.0 (6)
3	438.9 ¹	328–543	31.0 (431)	460.4 ^{1,3}	364–520	40.7 (61)	419.4 ³	361–498	30.6 (24)
4	467.7 ¹	410–602	42.3 (65)	518.1 ^{1,3}	451–622	38.3 (62)	451.5 ³	342–554	54.7 (12)
5	498.0		— (1)	552.5	418–711	54.4 (17)	474	—	— (1)
6				622.7	556–661	38.7 (7)	507	477–661	89.3 (4)
7				664.5	657–672	10.6 (2)	651	642–660	12.72 (2)

¹ Significant difference between lengths-at-age for gill-net and purse-seine catches (ANOVA, $P < 0.05$).

² Significant difference between lengths-at-age for gill-net and trawl catches (ANOVA, $P < 0.05$).

³ Significant differences between lengths-at-age for purse-seine and trawl catches (ANOVA, $P < 0.05$).

Table 3

Mean back-calculated total lengths (mm) of bluefish for the purse-seine and gill-net fishery. *Lc* = Mean observed lengths-at-age. Mean back-calculated lengths-at-age derived from the last annulus are shown in bold.

Age-group	<i>Lc</i>	<i>n</i>	SD (last annulus only)	Method						
				1	2	3	4	5	6	7
Purse-seine fishery										
1	313.5	22	27	202.2						
2	385.0	26	31	189.0	315.5					
3	460.4	23	36	227.9	358.0	437.3				
4	518.1	26	35	234.5	373.1	462.4	504.3			
5	552.5	8	72	225.4	366.9	455.4	504.5	547.1		
6	622.7	3	30	219.1	352.5	447.2	502.0	552.7	607.9	
7	664.5	1	—	247.9	352.6	512.1	574.6	615.9	636.5	647.4
Mean (all annuli)		109		214.6	350.6	451.3	506.1	554.4	615.4	647.4
SD				36	47	45	46	64	28	—
Gill-net fishery										
1	354.3	18	27	236.2						
2	408.7	59	46	230.4	346.1					
3	438.9	75	30	239.8	358.2	430.3				
4	467.7	21	41	244.9	366.2	445.5	480.8			
5	498.0	1	—	196.3	350.3	403.7	426.5	460.0		
Mean (all annuli)		174		236.7	354.9	433.3	483.4	460.0		
SD				41	39	58	41	—		

Growth occurs from May to October and peaks in August. From these data, we believe that the growth increments are annuli.

Back-calculated length-at-age and estimation of growth parameters

Back-calculated lengths-at-age calculated by using the last annulus only (IIa) were smaller than lengths-at-age calculated by using all annuli (IIb) (Table 3). There were also significant differences in lengths-at-age for these two criteria between gear types (*t*-test, *P*<0.05 for all age classes). Sexes were combined because there was no significant difference between them (*t*-test, *P*<0.05). Back-calculated lengths-at-age for gill-net samples showed a decreasing pattern for older fish (5 years old), indicating the presence of Lee's phenomenon and the selective effects of this gear.

Estimates of theoretical growth parameters indicated differences by gear and method of estimation (Table 4, Fig. 5). For criterion I, estimates with mean back-calculated lengths-at-age (criterion Ia) produced higher values of *L*_∞ (and smaller values of *k*) for purse-seine samples than estimates with individual back-calculated lengths-at-age (criterion Ib). The opposite trend was observed for the gill-net samples.

On the other hand, for criterion II, especially for purse-seine samples, estimates of mean back-calculated lengths-at-age derived from the last annulus only (criterion IIa) produced smaller values of *L*_∞ (and higher values of *k*)

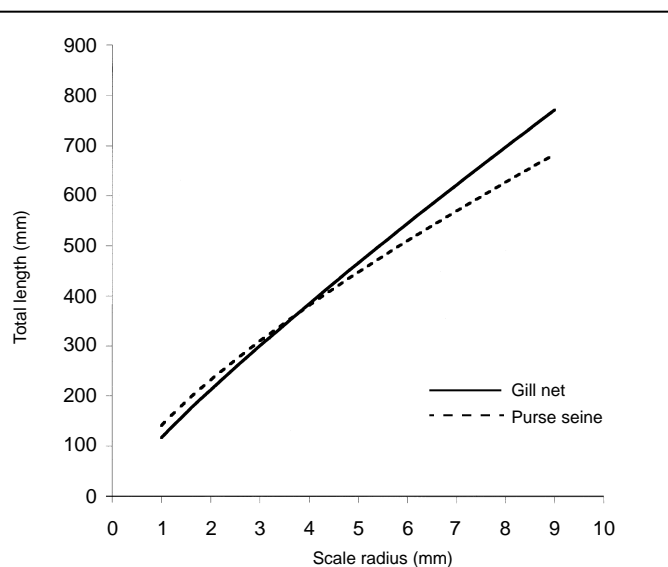
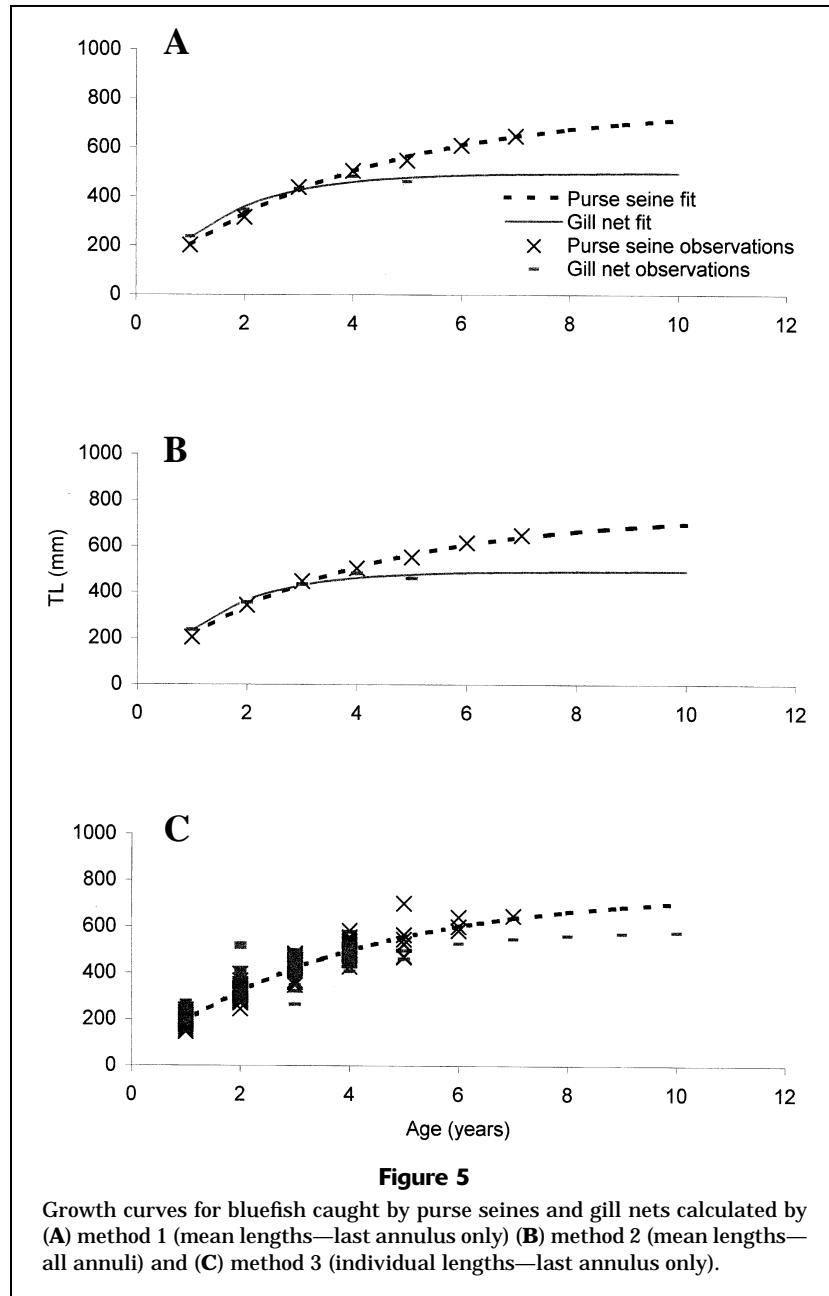


Figure 4

Total length-scale relationship derived from gill-net samples (*TL*=140.5*S*^{0.72}, *n*=174) and purse-seine samples (*TL*=116.7*S*^{0.86}, *n*=109).

than estimates with mean back-calculated lengths-at-age for all annuli (criterion IIb) (Table 4). Furthermore, for the purse seine, the growth parameters derived from methods 3 (Ib, IIa) and 4 (Ib, IIb) were distinct (Table 4). The at-



tempt to fit the von Bertalanffy growth curve by method 4 for the gill net failed because no feasible solution could be found for the parameters of the curve.

For all methods there were significant differences in growth parameter estimates between the gill-net and the purse-seine samples (Hotelling's t -test, $P < 0.05$).

The comparison between mean back-calculated (especially criterion IIa) and mean observed length-at-age showed that the latter is systematically larger than the former (Table 3). This difference was expected because the mean back-calculated lengths-at-age were obtained for length at time of annulus formation (where spawning season and time of annulus formation are considered uni-

form for all fish). The differences between both means may be attributed to growth after the growth mark formation. Moreover, the mean observed length-at-age calculated from sampled fish was obtained from individuals that may have spawned at different times of the year or whose ring formation may have been distinctly visible in time, resulting in fish with distinct real ages. Hence, growth parameters obtained from mean observed lengths-at-age of purse-seine catches during the fishing season ($L_{\infty} = 985$ mm, $k = 0.12$ and $t_0 = 2.17$) were significantly different from the growth parameters derived from back-calculated lengths-at-age (also from purse-seine catches) (Hotelling's t -test, $P < 0.001$ for all methods).

Table 4

Growth parameters and correlation between k and L_{∞} for different methods (1–4), and respective criteria (Ia, Ib, IIa, IIb) of back-calculation. Standard errors are given in parenthesis. “—” denotes that parameter estimates did not converge to a solution.

Parameters	Purse seine				Gill net			
	[1] Ia-IIa	[2] Ia-IIb	[3] Ib-IIa	[4] Ib-IIb	[1] Ia-IIa	[2] Ia-IIb	[3] Ib-IIa	[4] Ib-IIb
L_{∞}	773 (32.6)	743 (26.6)	754 (53.8)	670 (55.2)	496 (21.3)	491 (17.1)	589 (45.3)	—
k	0.25 (0.03)	0.27 (0.03)	0.26 (0.04)	0.35 (0.07)	0.65 (0.14)	0.71 (0.13)	0.39 (0.08)	—
t_0	-0.21 (0.12)	-0.27 (0.12)	-0.15 (0.12)	-0.09 (0.13)	0.03 (0.20)	0.09 (0.17)	0.27 (0.2)	—
$r(k, L_{\infty})$	-0.97	-0.97	-0.98	-0.98	-0.89	-0.87	-0.98	—

Discussion

Back-calculation of length is widely used to obtain growth curves, to estimate length-at-age of individuals that are rarely observed, to compare growth differences among populations or sexes of the same species, and even to illustrate gear selectivity (Francis, 1990). However, this technique is poorly understood (Francis, 1990; Rijnsdorp et al., 1990) and some of the sources of bias in using the technique are 1) inaccurate counts of annuli and incorrect estimation of time of formation of the growth mark; and 2) an erroneous choice of the mathematical function to describe the body-scale relationship. In respect to the first source of bias, our results corroborate the findings of Krug and Haimovici (1989). In respect to the body-scale relationship, the main concern of Francis (1990) was to decide whether the appropriate regression was TL on S (body proportional) or S on TL (scale proportional). The small difference between the back-calculation derived from the two approaches for the bluefish can be a minimum measure of precision of the back-calculation procedure (Francis, 1990). Campana (1990) and Wright et al. (1990) pointed out that slow-growing fish have larger bony structures (scales or otoliths) than fast-growing fish of the same size. For the bluefish body-scale relationship, we attribute this effect to gear selectivity. The fast-growing fish (ages 1 and 2 from the gill-net catches) tend to occur above the purse-seine curve and the slow-growing fish (ages 4 and 5 from the gill-net catches) tend to occur below the purse-seine curve in a TL - S relationship.

An additional source of bias may be introduced depending on whether mean back-calculated lengths-at-ages or individual lengths-at-age are used to fit the von Bertalanffy equation. The estimated growth parameters derived from the two methods may differ considerably (Hilborn and Walters, 1992). Use of mean values would ignore individual variability in length-at-age, giving the same weight for possibly uncertain ages because of low sample sizes.

We suggest that back-calculated lengths-at-age derived from the last annulus only (criterion IIa) be used rather than the back-calculated lengths-at-age derived from all annuli (criterion IIb). Many investigators continue to use mean-weighted data (all annuli) (e.g. Krug and Haimov-

ici, 1989; Barger, 1990)—a procedure in violation of the least-squares assumption of independence of sample elements (Draper and Smith, 1966). This assumption is violated when multiple measures from a single fish are used. Use of the last annulus only does not use all information available about growth of all cohorts and may result in an incorrect estimate of lengths-at-age for age classes absent or infrequently caught. However, if representative samples are available for younger age groups, the use of back-calculated lengths-at-age derived from the last annulus only is to be preferred.

Ricker (1969) noted that where differential mortality exists, the calculated average length of a particular age class calculated from the last annulus differs from the calculated average length of an age class calculated from previous annuli—the latter representing the former size of the fish that has survived to the sampling age. The differential mortality may be due to natural or fishing causes but under these circumstances, the average size of fish in the year class becomes different as time passes and the frequency distribution of the survivors would become progressively skewed. Gutreuter (1987) suggested that back-calculation should be restricted to the most recent annulus to avoid bias from size-selective sampling.

Gear selectivity can influence estimates of growth parameters (Ricker, 1969; Potts et al., 1998), and we found that gear-related differences in parameters were significant. Gill nets, on the basis of their mesh size, are a selective gear. Trawls are selective for smaller fish that may not be able to avoid the nets because of slower swimming speed (Hilborn and Walters, 1992). Purse seines are probably a less selective gear (Cushing, 1968). Observed lengths-at-age reflect the differences in selectivity between gears. Gill nets catch the faster-growing fish at age 1 and 2 and the slower-growing fish at age 4 and 5, and trawls catch the smaller individuals for each age.

The high selectivity of gill nets is visible in the body-scale relationship, the mean observed length-at-age, and in the back-calculated lengths-at-age which indicate the presence of Lee's phenomenon (Lee, 1920). Size-selective mortality—caused by the differing catchabilities of fish at different sizes—is the probable reason for Lee's phenomenon in back-calculation of lengths from gill-net catches.

Table 5

Back-calculated length-at-age and growth parameters obtained by various authors and at a number of locations. Probability values calculated from tests between means ($P < 0.05$) for the bluefish in southern Brazil (our study and published studies) are given in parentheses. Mean back-calculated length-at-age derived from all annuli was used to allow comparison between studies.

Location	Age class										L_{∞}	k	Source
	1	2	3	4	5	6	7	8	9				
Black Sea	212	322	409	562	615	663					1080	0.150	Kolarov (1963)
Senegal	209	375	500	604	689	758	913	858	893		1044	0.018	Champagnat (1983)
Long Island, USA	230	400	490	580	640	690	710				795	0.340	Richards (1976) ^{1,2}
Mexico	308	413	509	576	627	675	715	766			944	0.180	Barger (1990) ¹
West Atlantic	290	361	415	473							1019	0.096	Barger (1990) ¹
South Africa	165	279	369	437	480						840	0.196	Van de Elst (1976)
Southern Brazil	196	356	438	506	562	600	618				662	0.380	Krug and Haimovici (1989)
Southern Brazil	214	351	451	506	554	615	647				754	0.260	Our study
	($P=0.0$)	($P=0.21$)	($P=0.03$)	($P=0.99$)	($P=0.57$)	($P=0.39$)	— ³						

¹ Fork length was considered.

² Growth parameters were calculated from published mean back-calculated length-at-age.

³ Sample size was 1.

Selectivity-related bias from gill-net back-calculation is thus incorporated in the growth parameter estimation. The growth curve calculated from gill-net back-calculation reports unrealistic L_{∞} and k . Method 4 (individual back-calculated lengths-at-age derived from all annuli) for the gill net failed because no feasible solution could be found for the parameters of the curve. High variability of back-calculated lengths-at-age derived from all annuli (see standard deviations in Table 3) in the presence of Lee's phenomenon may have been the reason for the unsuccessful attempt to obtain estimates of the parameters of the von Bertalanffy growth curve with this method.

In our study, the growth parameters estimated from individual back-calculated length-at-age derived from the last annulus only (method 3) on purse-seine samples were considered to be the most appropriate for future assessment of the southern Brazilian bluefish stock. This gear is less selective than others and data comprise a wider range of total length groups and age groups.

Changes in Brazilian commercial fishing operations for the bluefish over the last decade have led to changes in the length and age structure of commercial landings. From 1976 to 1983 the maximum age and total length of bluefish in the fishery were 7 years and 630 mm TL, respectively, and less than 5% of fish were 4 years and older (Krug and Haimovici, 1989). Currently the fishery lands fish up to age 10, and 16% of fish are aged 4 and older. The inclusion of older individuals in recent catches is due to the expansion of the fishery into deeper areas. In 1990, the purse-seine fishery began moving to deeper waters, catching a wider range of sizes of bluefish. Hilborn and Walters (1992) have pointed out the necessity to understand fleet dynamics in order to assess the population dynamics of a species.

Our mean back-calculated lengths-at-age (calculated from the last annulus only) are similar to those found by Krug and Haimovici (1989) (except for ages 1 and 3) (Table 5), but estimated growth parameters for the two studies are different. We believe these differences are due to differences in fishing operation between the two periods (fleet operated in shallower water in 1977–83 than in 1992–97) rather than to fishing pressure. Also, the use of individual back-calculated lengths-at-age for the last annulus only (method 3) rather than the mean back-calculated lengths-at-age for all annuli (weighted mean, method 2, Krug and Haimovici, 1989) could have led to such a difference.

Data from the literature indicate considerable variation in length-at-age of bluefish between areas (Table 5). Terceiro and Ross (1993) attributed this variation to a sampling bias in available fish and to the differential proportion of spawned fishes in collected samples (e.g. due to multiple spawning). Champagnat (1983) suggested that differences in size at first maturity could lead to differences in growth parameters. The reported size at first maturity of bluefish varies from 250 mm TL in South Africa (Van der Elst, 1976)

to 430 mm TL in Senegal (Conand, 1975, Champagnat, 1983). In southern Brazil, length at first maturity for bluefish is between 350 to 400 mm TL (Haimovici and Krug, 1992) and this stock is considered to be relatively fast growing.

It is difficult to obtain samples representative of the population's age structure when using a single gear because of the size selectivity of most gears (Bagenal and Tesch, 1978). Also, the ranges of fish length and age represented in a study may affect the estimation of population parameters if they are not representative of the stock (Goodyear, 1995). Our study suggests that the data used for the estimation of the growth parameters for a fish stock should allow for the possible effects of gear selectivity. Data from different gears should be analyzed and should cover as wide an area of the stock distribution as possible. Moreover, the technique applied for estimation of growth parameters should be carefully assessed and the one chosen, strongly justified. Verification of the validity of the back-calculation method and validation of the annual nature of increment formation are also strongly recommended.

Acknowledgments

The authors are grateful to Gladimir Barenho for technical field assistance in Brazil and to Jim Ellis, Richard Millner, Simon Jennings, Paul Kinas, and Verena Trenkel for their comments on earlier drafts of the paper. The authors are also grateful to Manoel Haimovici for providing additional sample data for our analysis. This study was partially financed by CAPES, Brazil, through a grant to the first author (FML) and by the Ministry of Agriculture, Fisheries and Food, UK, with funding support (contracts MF0310 and MF0316) provided to the second author (CMO'B).

Literature cited

- Bagenal, T. B., and F. W. Tesch.
1978. Age and growth. *In* Methods for assessment of fish production in fresh waters (T. B. Bagenal, ed.), p. 101–136. Blackwell Scientific Publications, Oxford.
- Barger, L. E.
1990. Age and growth of the bluefish *Pomatomus saltatrix* from the northern Gulf of Mexico and U.S. South Atlantic coast. *Fish. Bull.* 88:805–809.
- Bernard, D. R.
1981. Multivariate analysis as a mean of comparing growth in fish. *Can. J. Fish. Aquat. Sci.* 38: 233–236.
- Boffo, M., and E. G. Reis.
1997. Estrutura da pesca artesanal costeira no extremo sul do Brasil. *In* VII Congresso Latino-Americano de Ciências del Mar, p. 88–90. Instituto Oceanográfico da Universidade de São Paulo, São Paulo, Brazil.
- Campana, S. E.
1990. How reliable are growth back-calculation based on otoliths? *Can. J. Fish. Aquat. Sci.* 47: 2219–2227.
- Casselman, J. M.
1987. Determination of age and growth. *In* The biology of fish growth (A. H. Weatherley and H. S. Gill, eds.), p. 209–242. Academic Press, New York, NY.
- Champagnat, C.
1983. Pêche, biologie et dynamique du tassergal (*Pomatomus saltator*, Linnaeus, 1766) sur les côtes sénégalomauretaniennes. Travaux et Documents du l'ORSTOM (Office de la Recherche Scientifique et Technique Outre Mer) 168: 1–279.
- Conand, C.
1975. Maturité sexuelle et fécondité du tassergal (*Pomatomus saltator*) (L., 1766), Poissons: Pomatomidae. Bull. L.I.F.A.N. (l'Institut français de l'Afrique noir), tome 37, ser. A, p. 2.
- Cushing, D. H.
1968. Fisheries biology. Univ. Wisconsin Press, London, 199 p.
- Draper, N. R., and H. Smith.
1966. Applied regression analysis. John Wiley and Sons Press, London, 407 p.
- Francis, R. I. C. C.
1990. Back-calculation of fish length: a critical review. *Fish. Biol.* 3:883–902.
- Goodyear, C. P.
1995. Mean size at age: an evaluation of sampling strategies with simulated red grouper data. *Trans. Am. Fish. Soc.* 124:454–456.
- Gutreuter, S.
1987. Consideration for estimation and interpretation of annual growth rates. *In* Age and growth in fish (R. C. Sommerfelt and R. C. Hall, eds.), p. 115–126. Iowa State Univ. Press, Ames, IA.
- Haimovici, M., and L. C. Krug.
1992. Alimentação e reprodução da enchova *Pomatomus saltatrix* no litoral sul do Brasil. *Rev. Bras. Biol.* 52(3): 530–513.
1996. Life history and fishery of the enchova *Pomatomus saltatrix* in southern Brazil. *Mar. Freshwater Res.* 47: 357–363.
- Hilborn, R., and C. Walters.
1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York, NY, 570 p.
- Hile, R.
1970. Body-scale relation and calculation of growth in fishes. *Trans. Am. Fish. Soc.* 99:468–474.
- Johnson, A. G., and C. H. Saloman.
1984. Age, growth, and mortality of gray triggerfish, *Balistes capricus*, from the northeastern Gulf of Mexico. *Fish. Bull.* 82(3):485–492.
- Kolarov, P.
1963. Narastvane na lefera (*Pomatomus saltatrix*). *Izv. Inst. Rib. Varna* 3:103–126.
- Krug, L. C., and M. Haimovici.
1989. Crescimento da enchova *Pomatomus saltatrix* do sul do Brasil. *Atlântica* 11(1):47–61.
1991. A pesca da enchova *Pomatomus saltatrix* no Sul do Brasil. Anais do simpósio da FURG sobre pesquisa pesqueira. *Atlântica* 13 (1):119–130.
- Lee, R. M.
1920. A review of methods of age and growth determination in fishes by means of scale. *Fish. Invest. Lond. Ser.* 4:1–32.
- Lucena, F. M.
1997. Pesca da anchova *Pomatomus saltatrix* (Pisces: Pomatomidae) na costa do Rio Grande do Sul: estrutura do estoque e seletividade da rede de emalhar. MSc. thesis, Univ. Rio Grande, Brazil, 153 p.

- Lucena, F. M., and E. G. Reis.
1998. Estrutura e estratégia de pesca da anchova *Pomatomus saltatrix* (Pisces: Pomatomidae) na costa do Rio Grande do Sul. *Atlântica* 20:87–103.
- Otter Research.
1996. An introduction to AD model builder for use in non-linear modelling and statistics. Otter Research Ltd, Vancouver, British Columbia, Canada, 40 p.
- Potts, J., C. S. Manooch III., and D. S. Vaughan.
1998. Age and growth of vermilion snapper from the southeastern United States. *Trans. Am. Fish. Soc.* 127: 787–795.
- Reis, E. G.
1992. An assessment of the exploitation of the white croaker *Micropogonias furnieri* (Pisces, Sciaenidae) by the artisanal and industrial fisheries in coastal waters of southern Brazil. Ph.D. diss., Univ. East Anglia, UK, 219 p.
- Richards, S. W.
1976. Age, growth and food of bluefish *Pomatomus saltatrix* from east-central Long Island Sound from July through November 1975. *Trans. Am. Fish. Soc.* 105:523–525.
- Ricker, W. E.
1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *J. Fish. Res. Board Can.* 26:479–541.
1992. Back-calculation of fish lengths based on proportionality between scale and length increments. *Can. J. Fish. Aquat. Sci.* 49:1018–1026.
- Rijnsdorp, A. D., P. I. van Leeuwen., and T. A. M. Visser.
1990. On the validity and precision of back-calculation of growth from otoliths of the plaice, *Pleuronectes platessa* L. *Fish. Res.* 9:97–117.
- SPSS.
1998. SPSS (Statistical Package for Social Sciences). SPSS Inc., Chicago, IL.
- Terceiro, M., and J. L. Ross.
1993. A comparison of alternative methods for the estimation of age from length data for Atlantic coast bluefish (*Pomatomus saltatrix*). *Fish. Bull.* 91:534–549.
- Tesch, F. W.
1971. Age and growth. In *Methods for assessment of fish production in fresh waters* (W. E. Ricker, ed.), p. 98–130. IBP Handbook 3, Blackwell, Oxford.
- Van der Elst, R.
1976. Game fish of the east coast of Southern Africa. I. The biology of the elf *Pomatomus saltatrix* (Linnaeus), in the coastal waters of Natal. *South African Assoc. Mar. Biol. Res. Invest. Report* 44:1–59.
- Vieira, P. C., and M. Haimovici.
1993. Idade e crescimento da pescada-olhuda *Cynoscion striatus* (Pisces, Sciaenidae) no sul do Brasil. *Atlântica* 15: 73–91.
- von Bertalanffy, L.
1934. Untersuchungen über die Gesetzmäßigkeiten des Wachstums. 1. Allgemeine Grundlagen der Theorie *Roux Arch. Entwicklungsmech. Org.* 131:613–653.
- Wilk, S. J.
1977. Biological and fisheries data on bluefish, *Pomatomus saltatrix* (Linnaeus). Tech. Ser. Rep. 11, Sandy Hook Lab., Northeast Fish. Science Cent., Natl. Mar. Fish. Serv., NOAA, Highlands, NJ, 56 p.
- Wright, P. J., N. B. Metcalfe., and J. E. Thorpe.
1990. Otolith and somatic growth rates in Atlantic salmon parr, *Salmo salar* L: evidence against coupling. *J. Fish. Biol.* 36:241–249.