*Journal of Fish Biology* (1993) **42,** 851–863

# Life history of the silverside *Atherinomorus lacunosus* (Atherinidae) in New Caledonia

F. Conand

*Centre ORSTOM de Brest, B.P. 70, 29280 Plouzané, France*

(*Received 12 May 1992, Accepted 26 September 1992*)

The abundance, the seasonal variation and the life history of the silverside, *Atherinomorus lacunosus*, are studied from fish caught in the lagoons around New Caledonia. About 270 nights of fishing were carried out between 1980 and 1983. The silverside is present in most of the fishing hauls but seldom in large quantities. Fish reproduce from September to December at 1 year of age. At this time their size is about 10 cm. Mortality is high and a few individuals can survive a second year and reach 13 cm. Results from other studies indicate that in a less seasonally contrasted environment than the lagoons of New Caledonia, *A. lacunosus* has several spawning periods during the year. This species is thus able to adjust its phenology to the environmental conditions.

Key words: *Atherinomorus lacunosus*; Atherinidae; silverside; life history; lagoon; New Caledonia.

## I. INTRODUCTION

The small pelagic fish from the lagoon of New Caledonia were studied at the Centre ORSTOM of Noumea from 1980 to 1983 to estimate the resources for tuna bait fishing (Conand, 1988). About 20 species of small pelagics occur frequently in the catches. One atherinid, *Atherinomorus lacunosus* (Schneider, 1801), (synonym: *Pranesus pinguis* Lacépède, 1803) commonly named silverside, which reaches a maximum length of 14 cm, occurs in most of the catches. Its geographical distribution is very wide, from the Mediterranean, immigrant from the Indian Ocean through the Suez Canal, to the Pacific Ocean eastward of the Samoa Islands. Studies have been conducted on its biology or life history, in South Africa (Harman *et al.*, 1982), in the Seychelles Islands (Anon., 1983; Hallier, 1990), in India (Thangaraja, 1985), and in the Marshall Islands (Hida & Uchiyama, 1977). This article presents results obtained in the lagoons of New Caledonia on the occurrence and abundance, and the population parameters of the species; its life cycle is then considered.



## II. MATERIALS AND METHODS

Eighteen fishing cruises, each lasting 2 weeks were made every other month, from March 1980 till June 1983, in the lagoons all around New Caledonia. About 80 different sites were surveyed and the good ones were visited regularly. Fishing was done at night, with a boke ami (a Japanese kind of lift-net), after attracting the fish with light. The most commonly used net was 11 m wide and 13 m deep and the mesh size was 5 mm. Usually two hauls were made: the first in the middle of the night and the second before sunrise. In addition, from July 1981, the Dumbea Bay near Noumea was visited monthly.



0022–1112/93/060851+13 $08.00/0

The whole catch was weighed and size frequency distributions were made on the different species (total length to the nearest lower half centimetre). A sample was taken to determine the species and weight composition of the catch. Then samples of different species were frozen and brought back to the laboratory for reproductive studies.

Biometric relationships were adjusted. Linear relations describe the relationships among standard length, fork length and total length. The length–weight relationship $W=aL^b$ was determined by logarithmic regression.

For the study of growth, the Multifan software has been used for estimating the parameters of the von Bertalanffy growth function (VBGF). Multifan utilizes a likelihood method based on the approach of Schnute & Fournier (1980) and Fournier & Breen (1983) to analyse simultaneously several length frequency samples. Several estimates were made either accumulating the size distribution frequency on a monthly basis for the whole of New Caledonia, or with observations of one night per month in Dumbea Bay.

For the study of reproduction the parameters recorded on samples brought to the laboratory were the total length (mm), the total weight (g) and the gonad weight (cg). The sex and the maturity stage of the gonads were noted using the Nikolsky (1963) scale which comprises six stages (1: immature; 2: resting; 3: developing; 4: mature; 5: spawning; 6: post-spawning). The gonad index (GI) given by the relation:

$$\text{gonad weight} \times 100/\text{total weight}$$

has been calculated and the variation of its monthly mean analysed. Size at first maturity has been defined as that of which 50% of females were mature during the spawning season. The purpose of such a definition is to adopt a value corresponding to a mean situation. Another interesting index is given by the size at which the sex can be identified by the naked eye.

Natural mortality can be inferred from the catch curve (Ricker, 1975). To set this curve, the monthly mean of the number of fish caught per fishing haul has first been calculated for each size class. Then, considering the consistency of the variations of the yield and the sizes, during the 3 years, observations were grouped per month on a yearly basis. Finally, with the back calculated ages the catch curve has been established.

Using the natural mortality, the length–weight relationship and the growth function, it is possible to estimate the theoretical changes of the instant biomass of a cohort, with the relation:

$$B_t = N \,.\, e^{-Zt} W_t$$

where $B_t$=biomass at instant $t$, $N$=initial population number, $Z$=total mortality, and $W_t$=mean weight of a fish at instant $t$.

## III. RESULTS

### OCCURRENCE

Some 20 species were present regularly in the catches. They belong to seven families: Engraulidae [*Stolephorus heterolobus* (Rüppel, 1837), *S. devisi* (Whitley, 1940), *S. puctifer* (Fowler, 1938), *S. indicus* (van Hasselt, 1923), *S. insularis* (Hardenberg, 1933), *Thrissina baelama* (Forsskål, 1775)], Clupeidae [*Herklotsichthys quadrimaculatus* (Rüppel, 1837), *Amblygaster sirm* (Walbaum, 1792), *A. clupeoides* (Bleeker, 1849)], Dussumieriidae [*Dussumieria* spp., *Spratelloides delicatulus* (Bennet, 1831), *S. gracilis* (Schleger, 1846)], Atherinidae [*Atherinomorus lacunosus* (Schneider, 1801), *Hypoatherina ovalaua* (Herre, 1935)), Leiognathidae (*Leiognathus bindus* (Valenciennes, 1835), *Gazza minuta* (Bloch, 1797)], Carangidae [*Decapterus russelli* (Rüppel, 1828), *Selar crumenophthalmus* (Bloch, 1793), *Scomberoides lysan* (Forsskål, 1775)], and Scombridae [*Rastrelliger kanagurta* (Cuvier, 1829)].

TABLE I. Occurrence of the silverside and rank amongst the different species

| Environment | Number of species occurring | Number of fishing nights | Occurrence of silverside | |
|---|---|---|---|---|
| | | | Number | Rank |
| Mangrove influence | 19 | 41 | 33 | 2 |
| Coral reef areas | 16 | 44 | 39 | 1 |
| Deep bays | 21 | 38 | 37 | 1 |

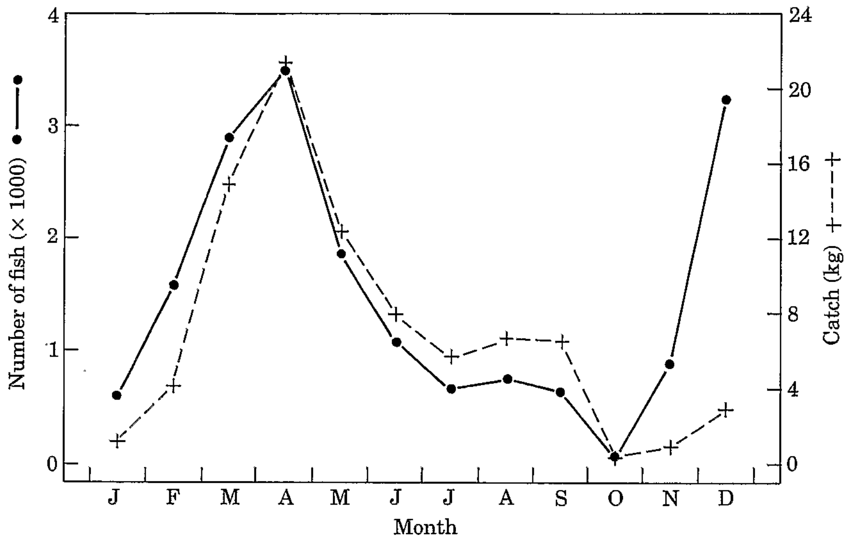


FIG. 1. Mean monthly catch of *Atherinomorus lacunosus* per fishing haul.

An analysis was made on the occurrence of the silverside in the three characteristic types of biotopes (Table I). These biotopes were defined in a previous study (Conand, 1988): shallow waters under the influence of mangroves, coral reef areas, deep bays and channels of the lagoon. *Atherinomorus lacunosus* and *H. quadrimaculatus* were ubiquitous species occurring the most regularly in the catch.

## ABUNDANCE

The changes during a year of the mean monthly catch of the silverside, in weight and in number of individuals (Fig. 1), show that recruitment started in November but was completed only in April. Catch then gradually decreased until October.

The abundance of the silverside in the catch of the 273 nights of fishing made during the study is analysed and results are given for the four main species in Table II. The more characteristic features are that *A. lacunosus* occurred in most of the fishing hauls in small quantities and that large catches were very uncommon.

TABLE II. Abundance of the silverside in the catches in comparison to the most important species

| Species | Mean catch (kg) per night when occurring | Number of nights with catch >100 kg | Occurrence in the hauls (%) |
|---|---|---|---|
| *Atherinomorus lacunosus* | 17·8 | 5 | 88 |
| *Herklotsichthys quadrimaculatus* | 49·7 | 41 | 88 |
| *Amblygaster sirm* | 57·0 | 23 | 64 |
| *Stolephorus heterolobus* | 72·8 | 23 | 39 |

TABLE III. Length weight relationship; weight in grams, total length in millimeters, $n$: number, $L_{min}$ and $L_{max}$: size interval of observations

| | $n$ | $L_{min}$ | $L_{max}$ | $r$ | $a \times 10^{-6}$ | $b$ |
|---|---|---|---|---|---|---|
| Males | 107 | 72 | 131 | 0·978 | 2·80 | 3·248 |
| Females | 139 | 65 | 143 | 0·987 | 3·42 | 3·212 |
| Males Females Juveniles | 208 | 42 | 143 | 0·994 | 1·69 | 3·364 |

BIOMETRIC RELATIONSHIPS

Relations between fork length (F.L.), total length (T.L.) and standard length (S.L.), calculated from 66 individuals with a T.L. between 55 and 109 mm were:

$$\text{F.L.} = 0{\cdot}93\ \text{T.L.} - 0{\cdot}66\ (r = 0{\cdot}993)$$

and

$$\text{S.L.} = 0{\cdot}96\ \text{T.L.} - 9{\cdot}16\ (r = 0{\cdot}989)$$

The length–weight functions $W = aL^n$ given in Table III were established for males, females, and a balanced sample of juveniles and adults of both sexes.

GROWTH

VBGF adjustments were made, on monthly samples from Dumbea Bay in 1982 and 1983, and the monthly grouping of all the observations made in New Caledonia. Histograms and back-calculated modal lengths are given in Fig. 2. Parameters of the functions and back-calculated age-length values are given in Table IV. *Atherinomorus lacunosus* in New Caledonia reached about 6·5 cm at 6 months, 10 cm at 1 year and 13 cm at 2 years, with slight variations according to sites and years.

REPRODUCTION

Studies of sex-ratio were limited to a few observations. They showed that one sex was usually dominant in a fishing haul, which could result from the dominance of one sex in a school. Observations indicated also that females were less abundant amongst small fish, but more abundant than males amongst large ones.

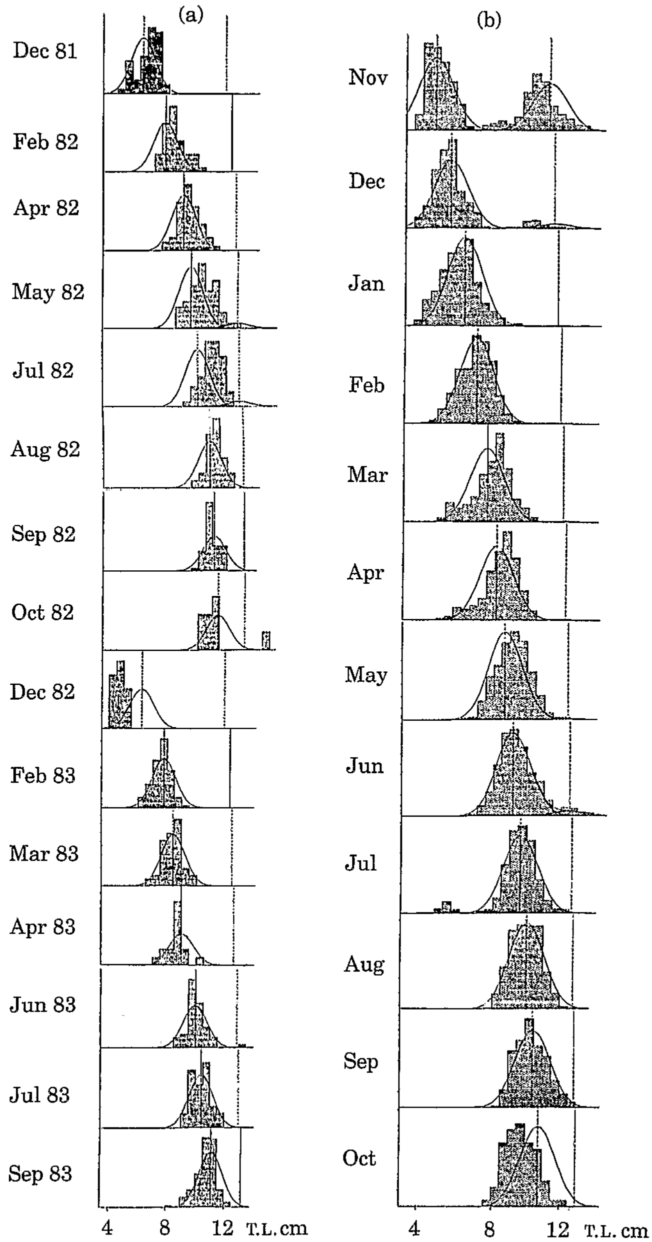


FIG. 2. Length–frequency histograms and back-calculated size from von Bertalanffy growth functions; (a) Dumbea Bay in 1982 and 1983; (b) New Caledonia, monthly grouping from 1980 to 1982.

The variations of the GI from 1980 to 1982 (Fig. 3) show clearly that the sexual cycle of *A. lacunosus* in New Caledonia was regular and annual. This allowed the calculation of a mean on a monthly basis for the 3 years of observations (Fig. 4). In January and February, almost all silversides were small juveniles, and gonads developed gradually from March till August. Spawning occurred from late August to December.

TABLE IV. Parameters of the von Bertalanffy growth equation and back-calculated lengths

| Location, year | Parameters | | | Back-calculated length/age | | | |
|---|---|---|---|---|---|---|---|
| | $L_{\alpha}$ | $K$ | $t_0$ | 3 mth | 6 mth | 1 y | 2 yrs |
| Dumbea 1982 | 136·4 | 1·34 | −0·003 | 39 | 67 | 101 | 127 |
| New Caledonia | 141·1 | 1·22 | −0·002 | 37 | 65 | 100 | 129 |

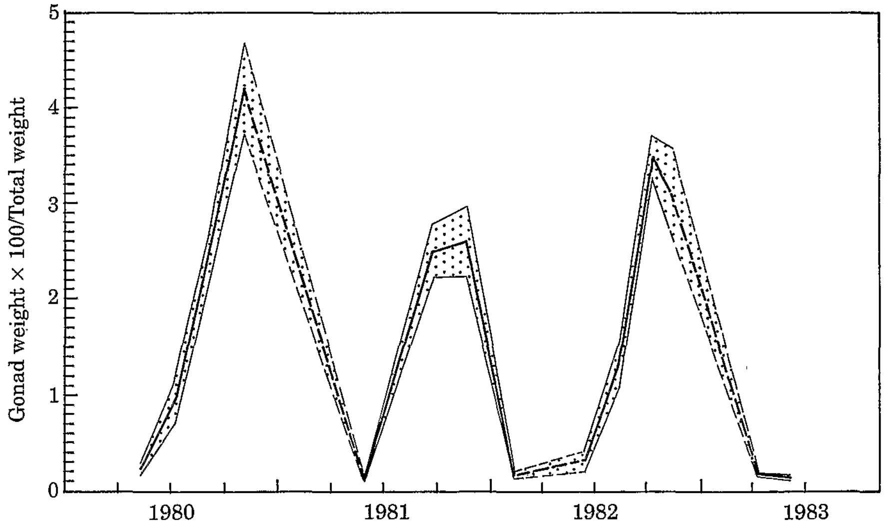


FIG. 3. Three consecutive years of female gonad index; mean gonad index computed per fishing cruise; shaded area for 95% confidence interval.

During the spawning season, the sex could be identified at a mean size of 7·5 cm and first maturity was reached at 8·5 cm (Fig. 5).

To estimate the batch fecundity, the oocytes of the last mode of their size distribution, were counted for 10 females measuring between 99 and 148 mm (T.L.) caught in September. Fish were at stage 4. The relation between batch fecundity (F) and weight (in grams) was linear:

$$F=78\ W-138$$

with S.D.$=\pm 13$ and $r=0{\cdot}94$. It was not possible to establish how many batches of eggs were laid in a spawning season, so the total fecundity is still unknown.

## MORTALITY AND THEORETICAL EVOLUTION OF A COHORT

From monthly observations of size frequency and CPUE, expressed in number of fish per fishing haul, a CPUE per size class for each month and for the year was calculated (Table V). With this figure and the growth function, the catch per age was calculated (Table VI), the catch curve drawn (Fig. 6) and the total mortality estimated:

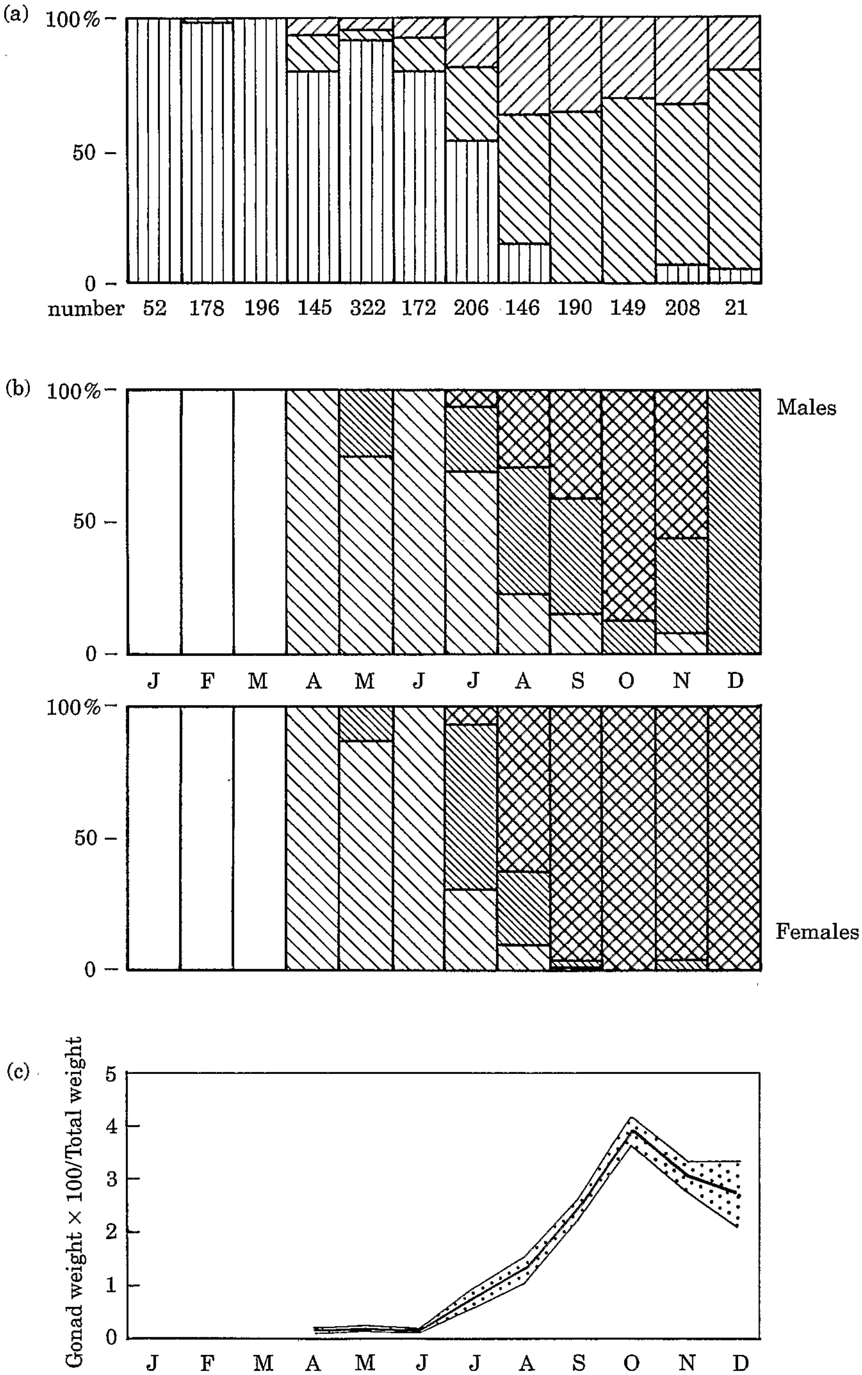


FIG. 4. Reproduction of *Atherinomorus lacunosus*. Mean of 3 years of observations: (a) monthly proportion of males, ▨, and females ▧ (▥, undetermined); (b) monthly proportion of maturity stages for males and females, sexual stages: ▧, 2; ▧, 3; ⊠, 4, 5, 6; (c) GI as a function of month for females, ⚃ 95% confidence interval.

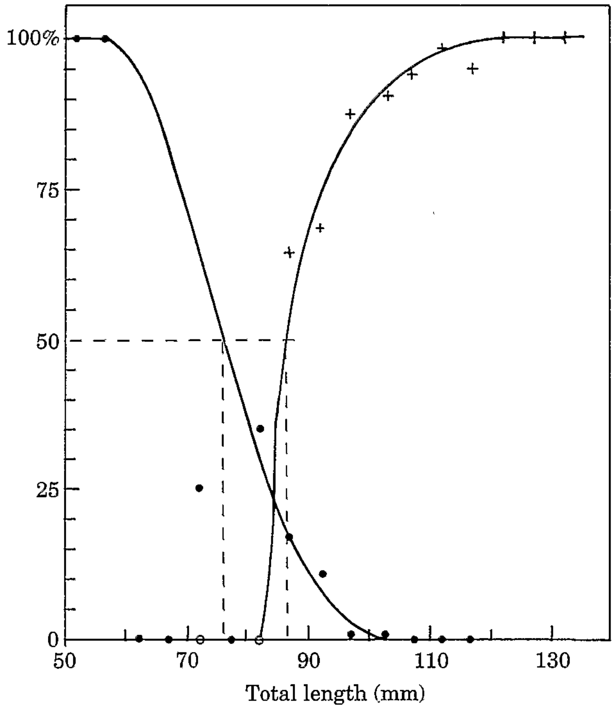


FIG. 5. Size at first maturity of *Atherinomorus lacunosus*. ●, percent immatures (months 8–12); +, percent females at stage 4–6.

$$Z = 4{\cdot}0 \pm 0{\cdot}2$$

As there was almost no fishery for the silverside, the total mortality was also the natural mortality.

The theoretical changes of the biomass of a cohort of 100 000 fish of 1-month-old, is shown in Fig. 7. The maximum biomass occurred at 7 months and this critical size was attained slightly before first maturity.

LIFE CYCLE

In New Caledonia, the silverside attained sexual maturity towards the end of the first year and the spawning season lasted from late August till December. The low batch fecundity and relatively long duration of the spawning season, argue in favour of a serial spawning strategy. The lifespan was short and the fish usually died after the spawning season, however some individuals reached a second year.

## IV. DISCUSSION

The analysis of occurrence confirms a previous result (Conand, 1988) given by a correspondence analysis made from the 273 nights of fishing and the 20 species, which led to the identification of five ecological groups. One of them, including *A. lacunosus*, was of ubiquitous species.

TABLE V. Catch per unit effort (number of individuals per fishing hauls). Monthly value and total, per size class

| Class midlength | Month | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 01 | 02 | 03 | 04 | 05 | 06 | 07 | 08 | 09 | 10 | 11 | 12 | Total |
| 32 | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 26 | 100 | 133 |
| 37 | 32 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 150 | 211 | 399 |
| 42 | 42 | 13 | 0 | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 142 | 536 | 738 |
| 47 | 68 | 52 | 32 | 18 | 0 | 0 | 8 | 0 | 0 | 0 | 117 | 713 | 1008 |
| 52 | 89 | 110 | 147 | 35 | 0 | 0 | 20 | 0 | 0 | 0 | 83 | 807 | 1291 |
| 57 | 96 | 198 | 104 | 116 | 4 | 0 | 7 | 0 | 0 | 0 | 44 | 342 | 911 |
| 62 | 106 | 200 | 133 | 102 | 8 | 1 | 1 | 0 | 0 | 0 | 7 | 238 | 795 |
| 67 | 53 | 319 | 193 | 133 | 13 | 5 | 0 | 0 | 0 | 0 | 1 | 144 | 863 |
| 72 | 28 | 297 | 364 | 203 | 81 | 26 | 4 | 0 | 1 | 0 | 9 | 17 | 1030 |
| 77 | 18 | 227 | 465 | 459 | 185 | 59 | 7 | 2 | 0 | 1 | 12 | 0 | 1435 |
| 82 | 10 | 102 | 681 | 635 | 231 | 125 | 26 | 25 | 3 | 3 | 16 | 0 | 1856 |
| 87 | 1 | 37 | 407 | 817 | 327 | 203 | 82 | 71 | 29 | 10 | 11 | 10 | 2004 |
| 92 | 3 | 10 | 176 | 575 | 375 | 212 | 137 | 134 | 92 | 12 | 23 | 10 | 1759 |
| 97 | 0 | 2 | 107 | 277 | 333 | 169 | 145 | 143 | 109 | 13 | 65 | 67 | 1629 |
| 102 | 0 | 2 | 38 | 88 | 204 | 105 | 121 | 141 | 145 | 10 | 98 | 77 | 1028 |
| 107 | 0 | 3 | 9 | 4 | 104 | 84 | 57 | 141 | 100 | 9 | 84 | 33 | 628 |
| 112 | 0 | 5 | 9 | 11 | 31 | 38 | 22 | 62 | 83 | 4 | 42 | 17 | 322 |
| 117 | 0 | 3 | 6 | 11 | 12 | 12 | 8 | 26 | 44 | 1 | 28 | 17 | 167 |
| 122 | 0 | 3 | 12 | 14 | 13 | 21 | 7 | 4 | 22 | 1 | 20 | 0 | 115 |
| 127 | 0 | 0 | 6 | 0 | 2 | 18 | 1 | 0 | 9 | 0 | 10 | 0 | 46 |
| 132 | 1 | 0 | 0 | 4 | 2 | 9 | 1 | 0 | 0 | 0 | 9 | 10 | 36 |
| 137 | 0 | 0 | 0 | 4 | 0 | 8 | 0 | 0 | 0 | 0 | 3 | 0 | 14 |
| 142 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 3 |
| 147 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 |

Movements and spatial distribution of *A. lacunosus* were studied by Hobson & Chess (1972) and Conand *et al.* (1990) and the schooling behaviour of *Atherinomorus insularum*, a closely related species, was analysed in Hawaii by Major (1977). During the day, the fish school quietly in shallow waters over reef flats or along the coast in sheltered bays. Schools are usually small. At sunset they migrate offshore in the lagoon and spread out just below the surface. This dispersion of the silverside could explain why it was almost always present in fishing hauls. The dispersion also explains why we never caught large number of silversides, as happened for several species of sardines or anchovies.

The silversides in New Caledonia grew slightly larger and faster than those in the Seychelles (Anon., 1983; Hallier, 1990) and in the Marshall Islands (Hida & Uchiyama, 1977). They reproduced annually in New Caledonia with a precisely determined season between September and December, which corresponds to the warming of the waters. In south-east Africa, approximately at the same latitude, Harman *et al.* (1982) observed a similar annual periodicity. In the Seychelles, two well marked seasons of spawning were observed in April–June and September–December (Anon., 1983; Hallier, 1990). They correspond to the inter-monsoons. In the Marshall Islands, fish with ripe ovaries occurred throughout the year (Hida & Uchiyama, 1977). Size of first reproduction was

TABLE VI. Showing the steps for the construction of the catch curve of *Atherinomorus lacunosus*; with $L_\alpha$=136·4, $K$=1·34, $t_0$=−0·003; Dt: time spent in the size class; *n*: number of fish

| Class limits | | Age | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Lower | Upper | In | Out | Dt | *n* | *n*/Dt | Log e *n*/Dt | Mean age |
| 32 | 37 | 0·197 | 0·234 | 0·037 | 133 | 3 595 | 8·18 | 0·22 |
| 37 | 42 | 0·234 | 0·272 | 0·038 | 399 | 10 500 | 9·26 | 0·26 |
| 42 | 47 | 0·272 | 0·312 | 0·040 | 738 | 18 450 | 9·82 | 0·30 |
| 47 | 52 | 0·312 | 0·356 | 0·044 | 1008 | 22 909 | 10·04 | 0·34 |
| 52 | 57 | 0·356 | 0·401 | 0·045 | 1291 | 28 689 | 10·26 | 0·38 |
| 57 | 62 | 0·401 | 0·449 | 0·048 | 911 | 18 979 | 9·87 | 0·43 |
| 62 | 67 | 0·449 | 0·501 | 0·052 | 795 | 15 288 | 9·63 | 0·48 |
| 67 | 72 | 0·501 | 0·557 | 0·056 | 863 | 15 411 | 9·64 | 0·53 |
| 72 | 77 | 0·557 | 0·617 | 0·060 | 1030 | 17 167 | 9·75 | 0·59 |
| 77 | 82 | 0·617 | 0·683 | 0·066 | 1435 | 21 742 | 9·99 | 0·68 |
| 82 | 87 | 0·683 | 0·755 | 0·072 | 1856 | 25 778 | 10·16 | 0·73 |
| 87 | 92 | 0·755 | 0·835 | 0·080 | 2004 | 25 050 | 10·13 | 0·80 |
| 92 | 97 | 0·835 | 0·924 | 0·089 | 1759 | 19 764 | 9·89 | 0·89 |
| 97 | 102 | 0·924 | 1·025 | 0·101 | 1629 | 16 129 | 9·69 | 0·98 |
| 102 | 107 | 1·025 | 1·142 | 0·117 | 1028 | 8 786 | 9·08 | 1·09 |
| 107 | 112 | 1·142 | 0·140 | 1·282 | 628 | 4 486 | 8·41 | 1·22 |
| 112 | 117 | 1·282 | 1·452 | 0·170 | 322 | 1 894 | 7·54 | 1·38 |
| 117 | 122 | 1·452 | 1·675 | 0·223 | 167 | 749 | 6·62 | 1·58 |
| 122 | 127 | 1·675 | 1·993 | 0·318 | 115 | 362 | 5·89 | 1·85 |
| 127 | 132 | 1·993 | 2·560 | 0·567 | 46 | 81 | 4·39 | 2·28 |
| 132 | 137 | 2·560 | | | 36 | | | |

larger in New Caledonia, smaller in the Marshall Islands and intermediate in the Seychelles. In tropical regions like the south-east African coast or New Caledonia where the coastal seawater temperature varies during the year with a relatively large amplitude (between 20 and 29° C), populations have a relatively protracted spawning period. In equatorial regions, like the Seychelles and the Marshall Islands, breeding does not reveal such a clear pattern.

A similar and even stronger latitudinal variation has been observed by Henderson & Bamber (1987) in temperate regions on another atherinid, *Atherina boyeri* Risso, a species living in coastal and estuarine waters from the north-west coast of Scotland throughout the Mediterranean and adjacent seas. They compared the life history of several populations and observed a trend of reduced maximum size, longevity, and size and age at first maturity in a north–south direction. Fish from the English channel population can live up to 4 years with one annual spawning season and achieve a length of 13 cm. In the populations from the coasts of the south of France, fish live for a maximum of 2 years, have two peaks of spawning during the year and achieve 9 cm. Finally, *A. boyeri* from the Sinai coast population can mature at 3·5 cm, which corresponds to 2–3-months-old and the maximum length recorded was 6·3 cm (age 12–13 months).

Two basic life cycle strategies of small pelagic fish from coral reef areas were recognized by Lewis *et al.* (1983) and Conand (1988): (i) species with a short life cycle (less than 1 year) which are small in size (less than 10 cm), attain sexual

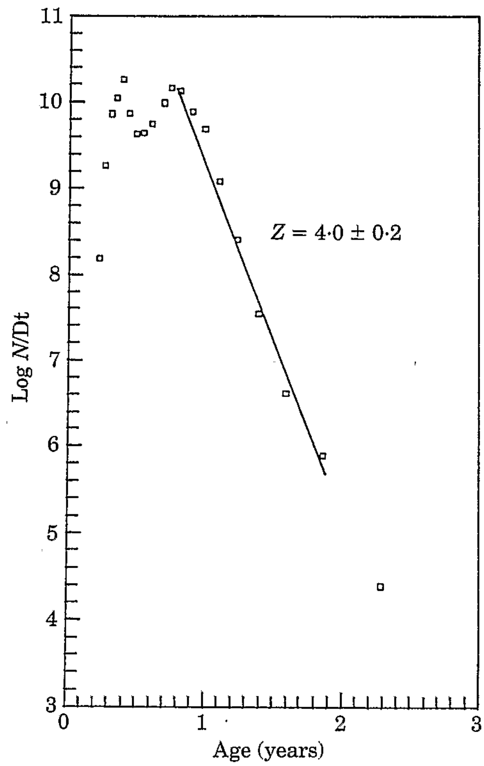


FIG. 6. Catch curve used to infer mortality.

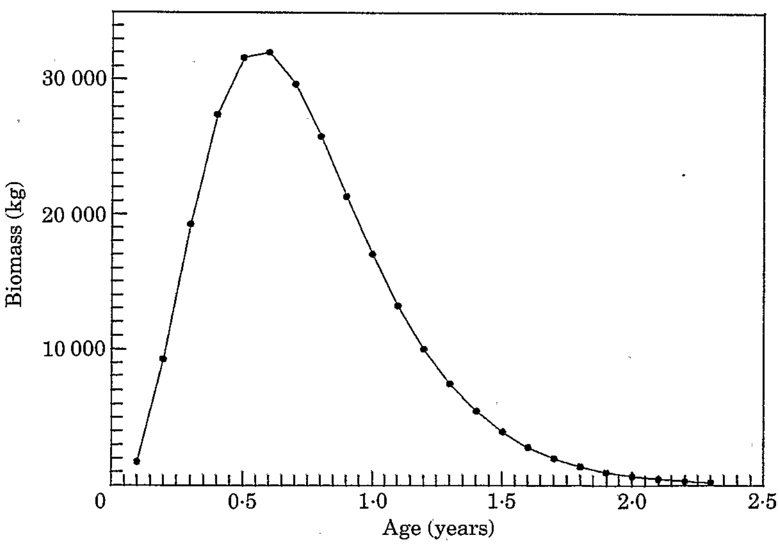


FIG. 7. Theoretical changes in the instantaneous biomass of a cohort of 100 000 1-month-old individuals.

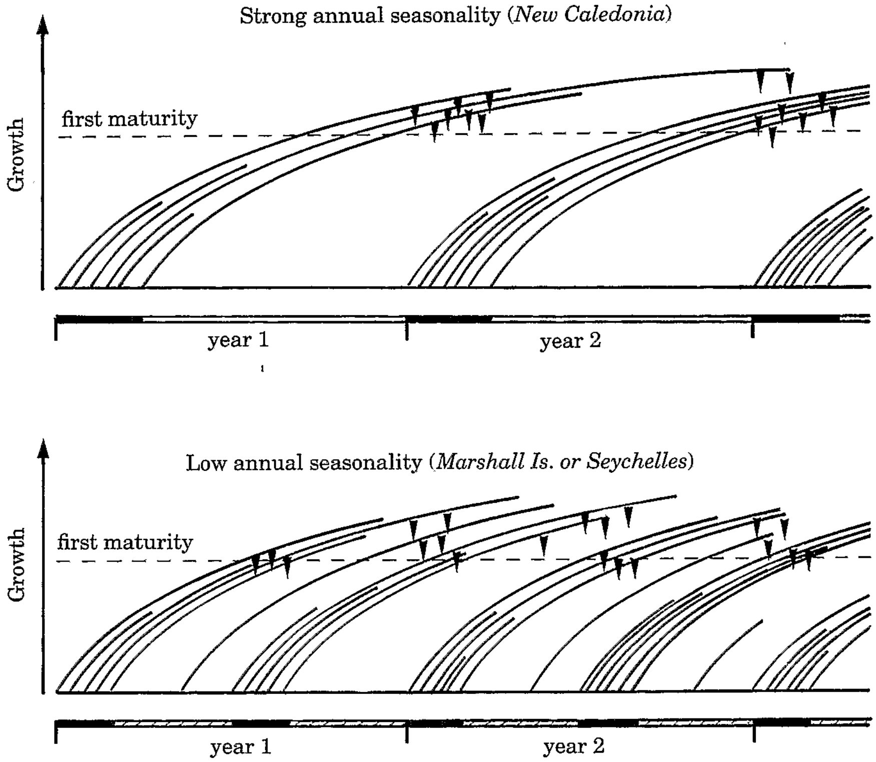


FIG. 8. Phenological response of *Atherinomorus lacunosus* to the intensity of seasonal environmental variation. ▬, environmental conditions optimal for spawning; ▨, conditions allowing spawning but not optimal; □, conditions unfavourable for spawning; ▼, spawning.

maturity in 3–4 months and spawn over an extended period; and (ii) species with an annual life cycle (but with some individuals surviving to 2 years of age), which are larger in size (10–24 cm), attain sexual maturity towards the end of the first year and spawn on a restricted seasonal basis. *Atherinomorus lacunosus* is intermediate between these two categories and adjusts its phenology according to the presence or the absence of well-defined seasons (Fig. 8).

A study on the life-cycle, growth and spawning time of five species of atherinids in a subtropical estuary of Western Australia, by Prince & Potter (1983), showed that in the same habitat the various species can experience two different life strategies related to their size. Four of them reaching a maximum length of 9 cm, have a 1-year life cycle with a precise season of breeding. The fifth species, *Atherinomorus ogilbyi* (Whitley), reaches 18 cm and typically lives 2 years.

The 1-year life cycle of *A. lacunosus* is also related to a tendency to semelparity, as even if the fish spawns several times, it generally dies after a single breeding period. This phenology is frequently observed in tropical fish of small size (Prince & Potter, 1983; Conand, 1991).

## References

Anon. (1983). L'appât vivant aux Seychelles: synthèse des connaissances acquises. *Rapport scientifique Mission ORSTOM Seychelles* **1**.

Conand, F. (1988). *Biologie et écologie des poisson pélagiques du lagon de Nouvelle-Calédonie utilisables comme appât thonier.* Paris: ORSTOM.

Conand, F. (1991). Biology and phenology of *Amblygaster sirm* (Clupeidae) in New Caledonia, a sardine of the coral environment. *Bulletin of Marine Science* **48,** 137–149.

Conand, F., Boely, T. & Petit, D. (1990). Spatial distribution of small pelagic fish in the lagoon of New Caledonia. *Proceedings of the 6th International Coral Reef Symposium,* Townsville, Australia **2,** 65–69.

Fournier, D. A. & Breen, P. A. (1983). Estimation of abalone mortality rates growth analysis. *Transaction of the American Fisheries Society* **112,** 403–411.

Hallier, J. P. (1990). Biology of tuna baitfish of Seychelles. In *Tuna Baitfish in the Indo-Pacific Region* (Blaber S. J. M. & Copland J. W., eds), pp. 60–69. Canberra: ACIAR.

Harman, M. A. J., Blaber, S. J. M. & Cyrus, D. P. (1982). The biology and taxonomic status of an estuarine population of *Pranesus pinguis* (Lacépède) (Teleostei: Atherinidae) in south east Africa. *South African Journal of Zoology* **17,** 15–23.

Henderson, P. A. & Bamber, R. N. (1987). On the reproductive biology of the sand smelt *Atherina boyeri* Risso (Pisces: Atherinidae) and its evolutionary potential. *Biological Journal of the Linnean Society* **32,** 395–415.

Hida, T. S. & Uchiyama, J. H. (1977). Biology of the bait fishes *Herklotichthys punctatus* and *Pranesus pinguis* in Majuro, Marshall Islands. In *Collection of Tuna Baitfish Papers* (Shomura,R., ed.). Technical Report NMFS Circ. **408,** 63–68

Hobson, E. S. & Chess, J. R. (1973). Feeding oriented movements of the Atherinid fish *Pranesus pinguis* at Majuro atoll, Marshall Island. *U.S. Fishery Bulletin* **71,** 777–786.

Lewis, A. D., Sharma, S., Prakash, J. & Tikomainiusiladi, B. (1983). The Fiji baitfishery 1981–82, with notes on the biology of the gold spot herring *Herklotsichthys quadrimaculatus* (Clupeidae) and the blue sprat *Spratelloides delicatulus* (Dussumieriidae). Fisheries Division, M.A.F., Suva, Fiji, Technical Report 6.

Major, P. F. (1977). Predator–prey interactions in schooling fishes during periods of twilight: a study of the silverside *Pranesus insularum* in Hawaii. *U.S. Fishery Bulletin* **75,** 415–426.

Nikolsky, C. V. (1963). *The Ecology of Fisheries.* New York: Academic Press.

Prince, J. D. & Potter, I. C. (1983). Life-cycle duration, growth and spawning times of five species of Atherinidae (Teleostei) found in a Western Australian estuary. *Australian Journal of Marine and Freshwater Research* **34,** 287–301.

Ricker, W. E. (1975). Computations and interpretation of biological statistics of fish populations. *Bulletin of the Fisheries Research Board of Canada* **191.**

Schnute, J. & Fournier, D. (1980). A new approach to length frequency analysis: growth structure. *Journal of the Fisheries Research Board of Canada* **37,** 1337–1351.

Thangaraja, M. (1985). Some observations on life history of the silverside *Pranesus pinguis* (Lacépède) from Velar estuary. *Mahasagar-Bulletin of the National Institute of Oceanography* (India) **18,** 49–56.