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Seventeen instars of adult life in female *Aristeus antennatus* (Crustacea: Decapoda: Aristeidae). A new interpretation of life span and growth

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A new interpretation of growth in *A. antennatus* is proposed on the basis of data recorded over a period of twenty years on the fishing grounds off Portofino. Detailed size-frequency distributions of female *A. antennatus,* obtained from on board measurements of large numbers per haul or per day of fishing, have been interpreted as formed of about 17 growth instars. Five of these, in the range 38–53 mm CL, were traced in their growth after the apparently fortuitous event of a massive recruitment which took place in 1987. The shift indicated above of five instars occurred in 3 years; a long life span, of about 8–9 years, was then assigned to the female red shrimp. Males were supposed to have an identical life span, with smaller sizes at age. The '1987 shrimps' were and remained for years distinct from the previous ones, in terms of both their size structure and reproductive characteristics. They were similar to southern Mediterranean stock(s) and slowly evolved towards a northern pattern. This fact points to a substantial affinity among *A. antennatus* populations in different Mediterranean areas.

KEYWORDS: *A. antennatus,* length–frequency distributions, growth, reproduction, age.

Introduction

Given that *Aristeus antennatus* (Risso, 1816) is a highly valuable resource for Mediterranean trawl fisheries, its growth parameters have important management implications. As tagging has never been attempted in this species, all available growth studies are based on length–frequency distributions. These are generally difficult to divide into age groups; first of all, because of the difficulties in taking exhaustive samples, and secondly because the shrimps which are caught in significant quantities are mainly spawners (Relini Orsi and Relini, 1979). This makes it impossible to trace the growth of juveniles, as can generally be done with fish. The location of very young *A. antennatus* is unknown, except for small quantities: specimens of less than 20 mm CL were found both at depth > 1000 m (Sardà *et al.*, 1994) and on trawlable bottoms (< 800 and < 750 m) (Martinez Baños and Mas, 1994; D'Onghia *et al.*, 1997).

Given the impossibility of using juveniles as the starting point for growth studies, we have taken the size (or range of sizes) of the first maturation in females as a 'certain' reference point for the description of adult growth. An opportunity to

relate sizes to time was presented by an apparently fortuitous event: a massive recruitment on the Ligurian fishing grounds which took place in 1987. A fraction of the stock composed mainly of large females could be distinguished from the 'new' shrimps. The latter cohort(s) was traced over a period of 3 years. Using field data, consisting of length–frequency distributions of large numbers of shrimps recorded on board, and with the reference point of the onset of adult life, we were able to reconstruct a possible life span of the female red shrimp.

Study area, materials and methods

Measurements of shrimps were obtained over a period of more than 20 years on bathyal fishing grounds off Portofino. The Gulf of Genoa has at its centre a system of two submarine canyons, corresponding to two rivers which flow into the sea at Genoa: the Polcevera and the Bisagno. The latter canyon has an eastern branch towards the Portofino Promontory which includes shrimp fishing grounds located on its steep northern wall (figure 1). Shrimps in commercial quantities are now present in the 480–700 m range; in the past (the exploitation began in the thirties), they were fished during the winter even at epibathyal levels and rarely at the edges of the shelf.

The demographic structures of fished stock were recorded on board trawlers operating out of the port of S. Margherita (Portofino Promontory). Large numbers of shrimps, corresponding to one haul or several hauls of the same day's fishing on the above-mentioned steep bottom, were sexed and measured in terms of carapace length (CL) with callipers. In addition, their reproductive condition was assessed: in particular, in the female the ovarian maturative stage in terms of storage of carotenoproteins (white, pink, light violet, dark violet ovary). Measures utilized for this text correspond to a total of 15,882.

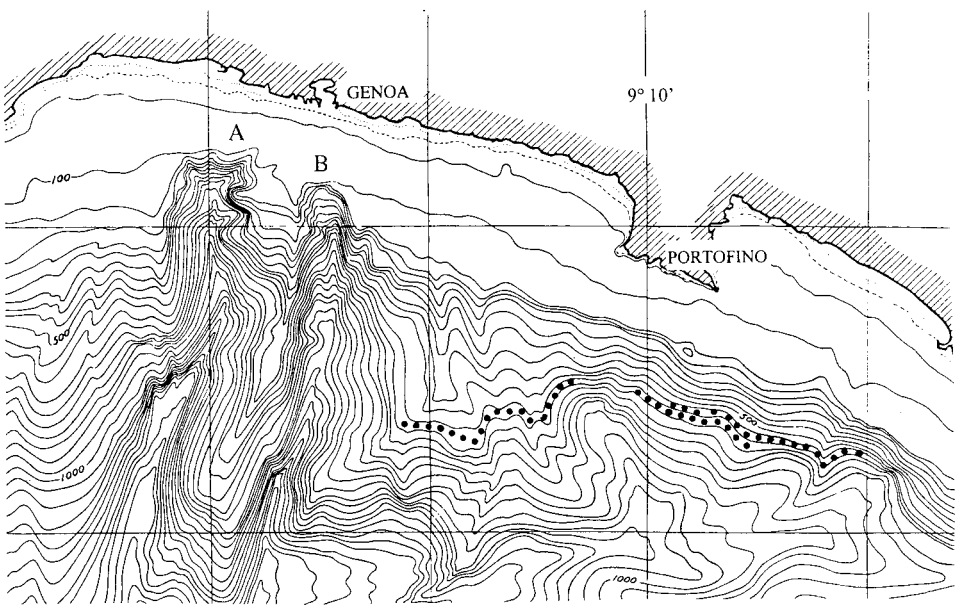

FIG. 1. The Portofino fishing grounds for red shrimps are represented by black points. The marine canyon of Polcevera (A) and Bisagno (B) are indicated.

From 1976–1981 studies of red shrimps were conducted within the framework of a Consiglio Nazionale delle Ricerche programme ('Oceanografia e fondi marini, Risorse biologiche'). Sampling was carried out by the trawler *Lavoratore Secondo*, using a net with meshes of 40 mm at the cod end.

After 1980 it became impossible to obtain substantial samples of the population because in the meantime shrimps had become extremely scarce, to the extent that commercial fishery was discontinued. In 1985 and 1986 fishing activity returned to moderate levels and samples were obtained by the same trawler. In 1987, after a massive recruitment of red shrimps, there was a period of flourishing activity for the S. Margherita fleet. Measurements of shrimps were made in summer 1987; winter, spring, summer, autumn 1988; spring and summer 1989; and summer 1990, again on board the same trawler.

Year 1985 saw the beginning of a new research plan (Ministero della Marina Mercantile, Valutazione delle risorse demersali). The trawler *Elisabetta* was used, which had fishing gear similar to that used on the previous trawler. Measures of this period are not shown here, but only mentioned for comparison purposes.

Results and discussion

Catch composition prior to 1987

In the seventies and eighties commercial concentrations of shrimps were mostly made up of large-sized females (figure 2). In the period 1976–1980 the population decreased progressively until commercial fishing in the area was suspended. Only in 1985 did shrimp catches pick up again; quantities, however, were modest and the demographic structure virtually unchanged from previous years (figure 2), i.e. the catches consisted mainly of large females (main modal sizes 53–56 mm CL, largest

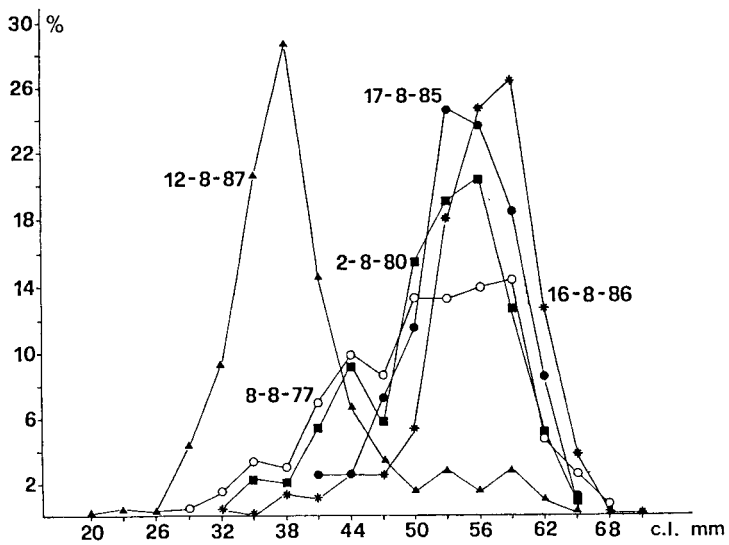

FIG. 2. Length–frequency distributions of female *A. antennatus* recorded in Portofino area. Trawler, boat, skipper and gear remained unchanged in the period of time indicated (from Orsi Relini and Relini, 1988). Numbers of females in chronological order are: 423, 521, 451, 354, 391.

size 65 mm CL). In 1986 the shrimps were a little larger (main modal size 56–59 mm, largest size 71 mm).

The 1987 recruitment

In 1987 large numbers of shrimps per day's fishing became available; among them small sizes, not present or scarcely present in the previous years, dominated. The 'new shrimps' were recorded both in the present study area and about 150 km to the west, in the Ventimiglia Canyon (figures 3–4); therefore the appearance of a

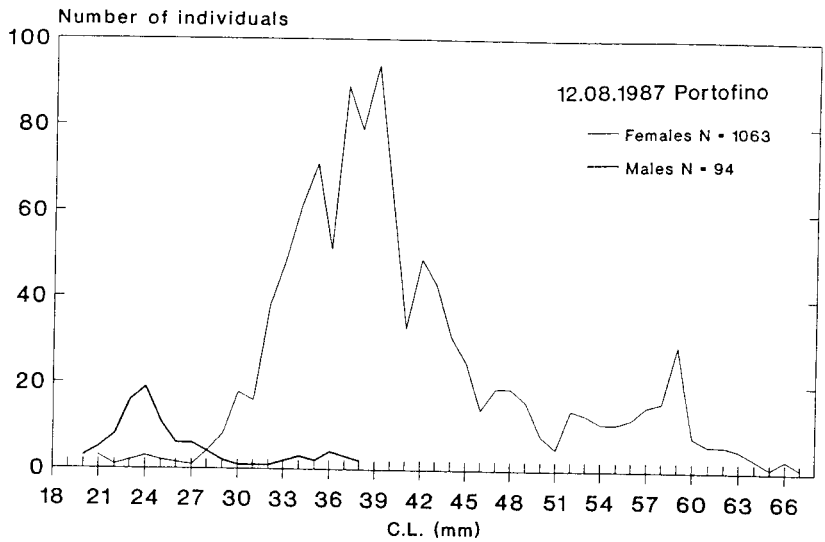

FIG. 3. Length–frequency distributions of male and female *A. antennatus* fished off Portofino on 12 August 1987.

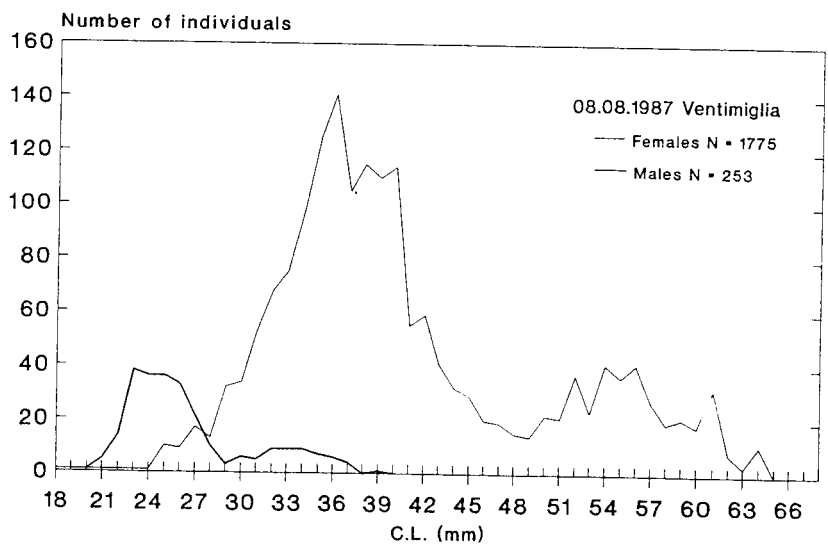

FIG. 4. Length–frequency distributions of male and female *A. antennatus* fished off Ventimiglia on 8 August 1987.

massive recruitment was a phenomenon to be found in all Ligurian red shrimp fishing grounds. In the length–frequency distributions definite peaks in abundance occur at regular intervals of 2–3 mm (figures 3–4). We assume that each peak represents a growth instar in the life of female shrimps. It is interesting to note that the length–frequency distribution of males has the same general shape as that of females, but peaks are less evident, owing to their reduced size.

If reproductive data are added to length–frequency distributions (figures 5–6),

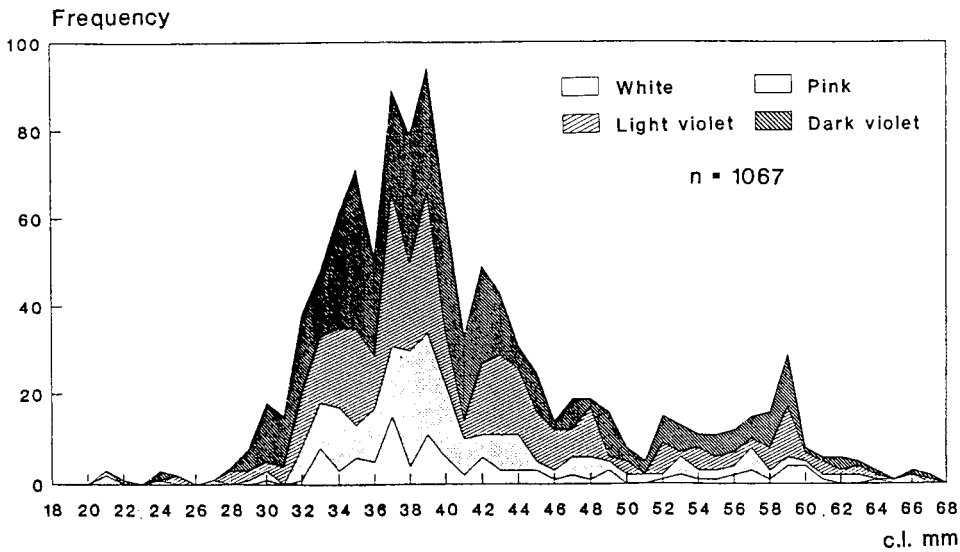

FIG. 5. Detailed size-structure and reproductive stages of female *A. antennatus* recorded in August 1987 in Portofino area.

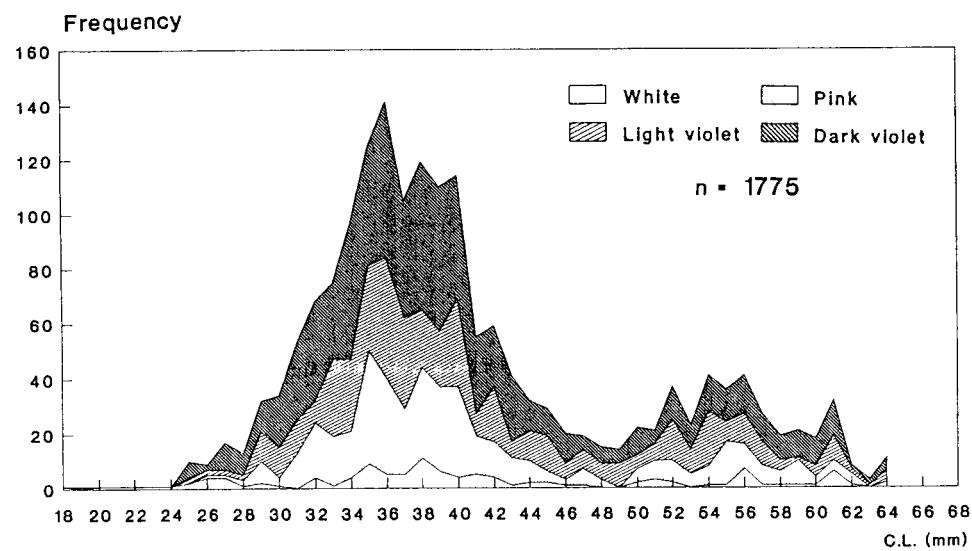

FIG. 6. Detailed size-structure and reproductive stages of female *A. antennatus* recorded in August 1987 in Ventimiglia area.

it can be readily observed that female spawners are represented by 15–17 instars, the first at 24–25 mm CL, the last at 64–66 mm CL. The 1987 recruits are made up of about seven–nine instars in the 25–45 mm CL range: in fact, this size range was absent or present only in small numbers in previous years (figure 2). These recently arrived females are both 'recruits', in the sense that they were just entering the fished stock, and spawners, all or some of them, at the beginning of their reproductive lives.

The meaning of a plurality of instars

The plurality of instars of the new shrimps must be related to a period of births. The reproductive season of *A. antennatus* lasts about 6 months (figure 7), with a beginning (June or July in the seventies in the present study area), a peak that extends for about three months and a tail. In southern Mediterranean areas the beginning may be brought forward to April or May but the overall length is the same. Can the instars of 1987 recruits be referred to one or more reproductive seasons? In attempting to answer this question, we feel it may be useful to describe some general features of shrimp reproduction.

In coastal and bathyal penaeid species spawning occurs during the night and in a short time ovaries become completely empty (Heldt, 1938; Ogle, 1992). Shrimps are therefore total spawners; moreover, coastal species maintained in captivity for aquaculture purposes proved to be multispawners in the sense that after each spawning event a new maturation cycle can start a few days later (Ogle, 1992). At the beginning of the season (figure 7), reproduction in *A. antennatus* seems synchronized in small and large females, probably on the basis of the photoperiod (Mura and Cau, 1989; Mura *et al.*, 1992). The interval between the first pink ovaries and the first dark violet ovaries can be estimated at about 1.5–2 months (figure 7a–b). In the following 3 months the co-occurrence of four ovarian stages is the rule (figure 7b–c); then, in the tail (figure 7d), the 'pink ovary' stage is missing, meaning that new maturative processes have stopped, but those already started are in the course of completion. The histology of ovaries indicates that after a spawning event new oocytes rapidly grow to refill the empty spaces (Relini Orsi and Relini, 1979; Orsi Relini and Semeria, 1983).

More than one spawning per season seems possible. However, the maximum number is probably two or three, given that maturation takes the time period referred to above and it is impossible to ascertain how long a dark violet ovary persists before releasing eggs. On this last point, it is known from penaeids in captivity that when droplets of glycoproteic materials appear in the peripheral cytoplasm of oocytes (a feature which in *A. antennatus* is associated with the dark violet stage) spawning will occur in the space of a week.

This fact does not establish the duration of the dark-violet stage, but probably indicates an absolute minimum. On the basis of the long-lasting presence of advanced maturity stages in the fished stock, it has been suggested that *A. antennatus* may become mature several times in a reproductive season (Relini Orsi and Relini, 1979) and that the moult–mating–maturation–spawning sequence could be repeated perhaps once every month (Demestre, 1995). Such a tight sequence of moults would however only be important in the transmission of the spermatophores and not for growth, which would take place through other moults in a non-reproductive season (Demestre, 1995).

The coexistence of four ovarian stages in the fished stock could also be explained as a continuous turnover of shrimps, with females arriving, maturing, spawning and

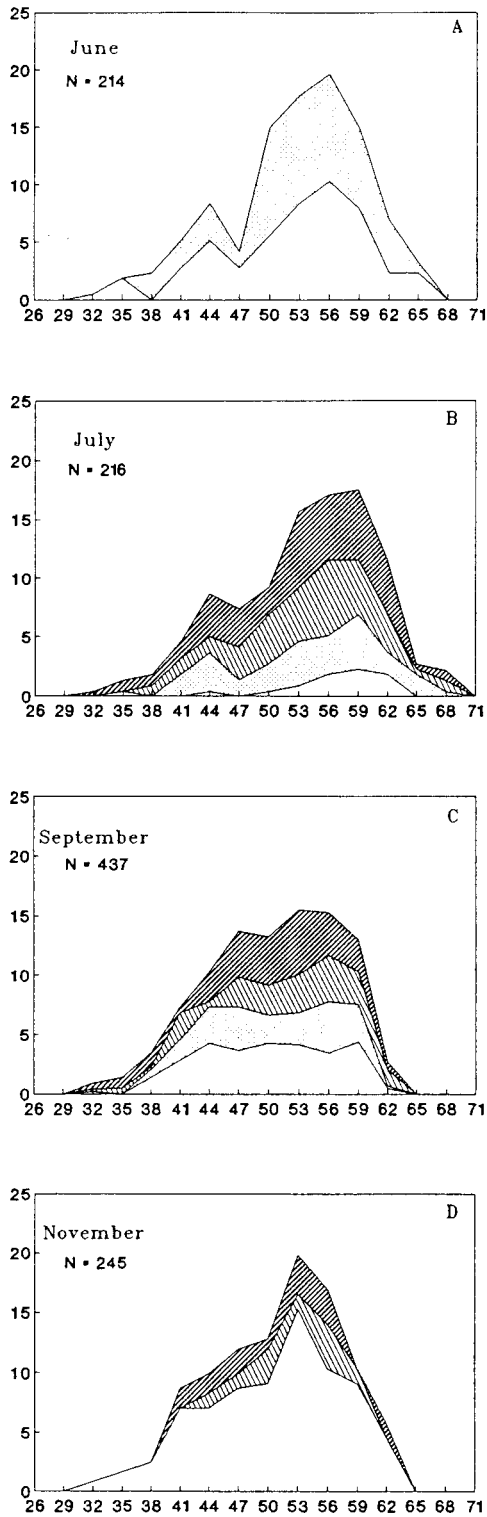

FIG. 7. Maturative sequence recorded in the seventies in the study area. Ovarian maturative stages revealed by colours white to dark violet (here white and shades of grey), are added to the length–frequency distributions.

then going away, each one remaining in place only the length of time strictly necessary for maturation and spawning, that is probably about 2–2.5 months. Both in the first and in the second case births could occur over a long period.

In conclusion, we can say there is no definite answer to the above question, although it is reasonable to suppose that every reproductive season produces not one but a group of instars. In our opinion, there are three possibilities:

scenario a: 1987 recruits were age 1
scenario b: 1987 recruits were age 1 + age 2
scenario c: 1987 recruits were age 1 + age 2 + age 3

The reference point of the onset of sexual maturity

In captivity, the spawning of Penaeidae may be obtained at an age of less than one year (10–11 months). However, in the absence of particular interventions, in some species, for instance *P. vannamei* Boone, it has been established that the majority of females are over 2 years of age when matured (Ogle, 1992).

Most authors who have studied wild populations of *Metapenaeus* assign age 1 to the first maturation (Miquel, 1982) and the same applies for *Penaeus* sp. p. of temperate waters (Dall *et al.*, 1990). In the series of reproductive instars of figure 1, we can suppose that the central value (about 38 mm CL) represents age 1, corresponding to shrimps born in the middle of the reproductive season (i.e. August) of the previous year and the other instars were born immediately before or after that month (scenario a). In this case a single reproductive season would produce the complete series of recruit instars. This is apparently the most obvious hypothesis, since it explains the sudden appearance of a lot of sizes, not registered in the area for at least 10 years. However, on the basis of the duration of maturation processes, it appears that a shift from the 24 mm CL to the 38 mm CL reproductive instars in less than 1 year is not sustainable. In fact, such a passage involves five instars, i.e. more than the number of moults which can occur in half a reproductive season even in the most optimistic interpretation of moulting and spawning processes (Demestre, 1995); in other words, if 38 is the central value of a reproductive series lasting 6 months, the time elapsed from 24 to 38 would be 3 months, into which five growth moults would have to be fitted.

In the other scenarios (b and c) we can suppose that the central value, 38 mm CL, corresponds to shrimps of age 2 or age 3. In this case every reproductive season would obviously produce a smaller number of instars, for instance two or three. Whatever its age, the main subcohort of recruits, 38 mm CL in August 1987, was traced in terms of length–frequency distributions over the following 3 years.

Growth of the 1987 main subcohort

Measures made in 1988 are shown in figure 8. The winter, spring and summer length–frequency distributions show the displacement of modal sizes indicative of growth. Observed increments, about 3 mm each, give a validation of the hypothesis of instars. Considering the central subcohort, the modal length in February was at 41 mm CL and in March at 44 mm CL, indicating the displacement of two instars. In May, July and December the modal size was unmodified.

During the following year two other instars were reached (up to 51 mm CL). After 3 years only one instar was added (53 mm CL). It is interesting to note, that there is a shift in time of moulting (from summer to spring) according to size (and

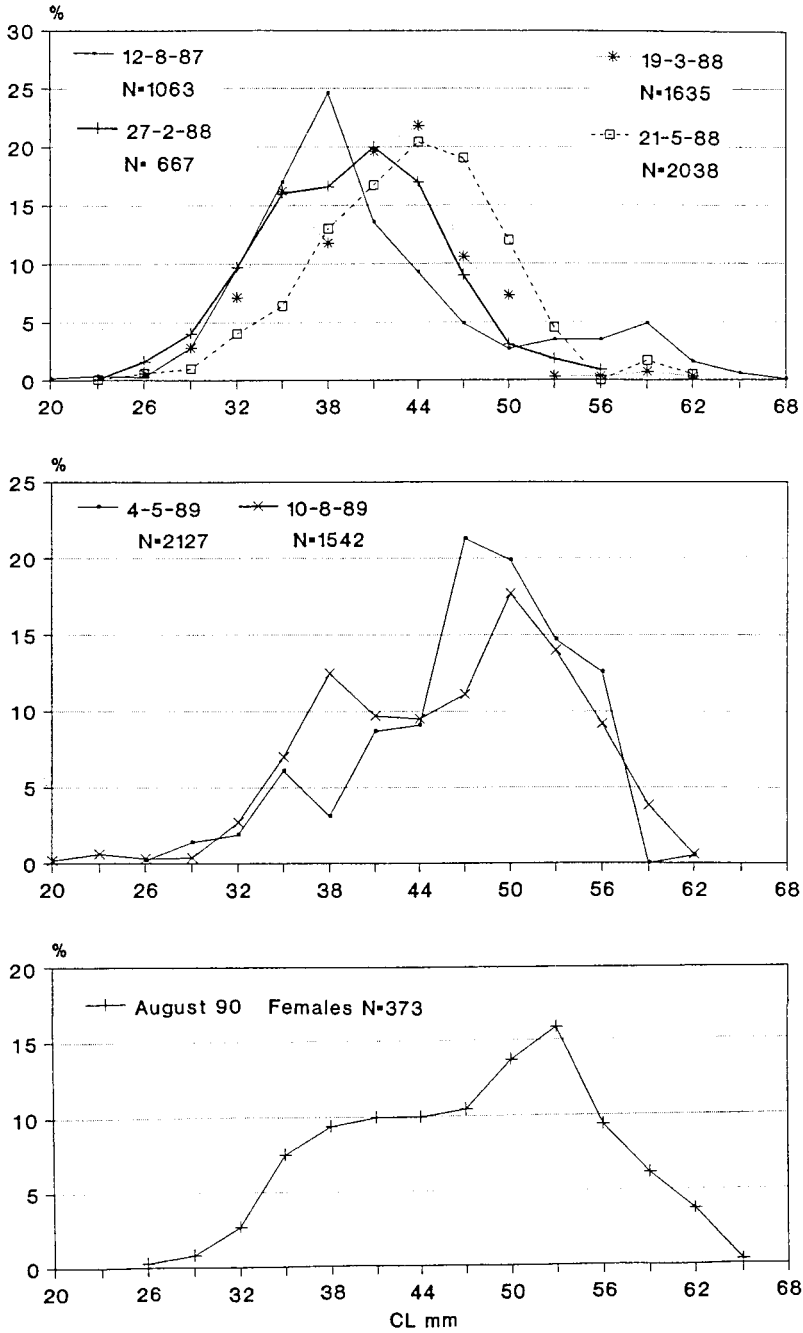

FIG. 8. Growth of the 1987 cohort in Portofino area.

age) of shrimps. It is therefore possible that the first moult after 53 mm CL will occur in summer. It is also possible that from this point onward only one moult occurs per year; in fact the increasing of intermoult period with age is of general occurrence in decapods. If so, independently of the duration of juvenile life, for

which different scenarios are envisaged, adult life appears very long, 7 or more years, if one considers the largest size recorded (71 mm CL).

Considering the overall growth registered for the main subcohort of 1987 recruits, an increase in size of 15 mm CL has been obtained in 3 years, with a shift of five instars. This figure (=5 mm CL per year) is lower than all the growth estimates available in the literature.

The growth curves

The registered growth of the 1987 main subcohort can be used to derive growth curves in the context of the different scenarios (figure 9):

a) Shrimps measuring 38 mm CL in August were 1 year old
b) Shrimps measuring 38 mm CL in August were 2 years old
c) Shrimps measuring 38 mm CL in August were 3 years old

Of these three growth hypotheses (figure 9) the first appears unnatural, and also on the basis of the above-mentioned reproductive observations is to be rejected. The other two hypotheses fit the experimental data very well. In particular, the third assigns age two to the onset of sexual maturity, a feature which, in our opinion, is consistent with the length of the subsequent life span. The growth of males can be derived on the basis of the proportion between female and male sizes (figures 3–4). Growth parameters are:

scenario a	F	L_∞	65.05	K	0.522	t_0	−0.12
	M	L_∞	39	K	0.522	t_0	−0.12
scenario b	F	L_∞	71.2	K	0.317	t_0	−0.047
	M	L_∞	42.7	K	0.317	t_0	−0.047
scenario c	F	L_∞	76.9	K	0.213	t_0	−0.019
	M	L_∞	46	K	0.213	t_0	−0.019

Evolution of the fished stock after 1987

After the 1987 recruitment, substantial changes in the fished stock and in fishing activity were registered. Shrimp distribution over the slope fishing grounds expanded, including almost epibathyal levels (480 m). Their concentration was also profitable during the winter thus making fishing activity continuous throughout the year. Part of the fleet of S. Margherita (Portofino Promontory) which worked on coastal bottoms turned to deep fishing. Also some biological characteristics of the red shrimps appeared 'new'.

From 1988 onwards the reproductive season was brought forward to the spring (May to October). These features, together with smaller mean sizes, rendered Ligurian red shrimps very similar to those of southern Mediterranean areas, such as Sardinia, Sicily, Catalonia, etc. (Sardà and Demestre, 1987; Mura *et al.*, 1992; Arculeo *et al.*, 1994; Ragonese *et al.*, 1994). Year after year a reduction of catch per unit effort is evident (Fiorentino *et al.*, submitted) while mean sizes are increasing (Orsi Relini and Relini, submitted). A more detailed account of the biological characteristics of the 'new' shrimps compared to those of the seventies–eighties is in preparation.

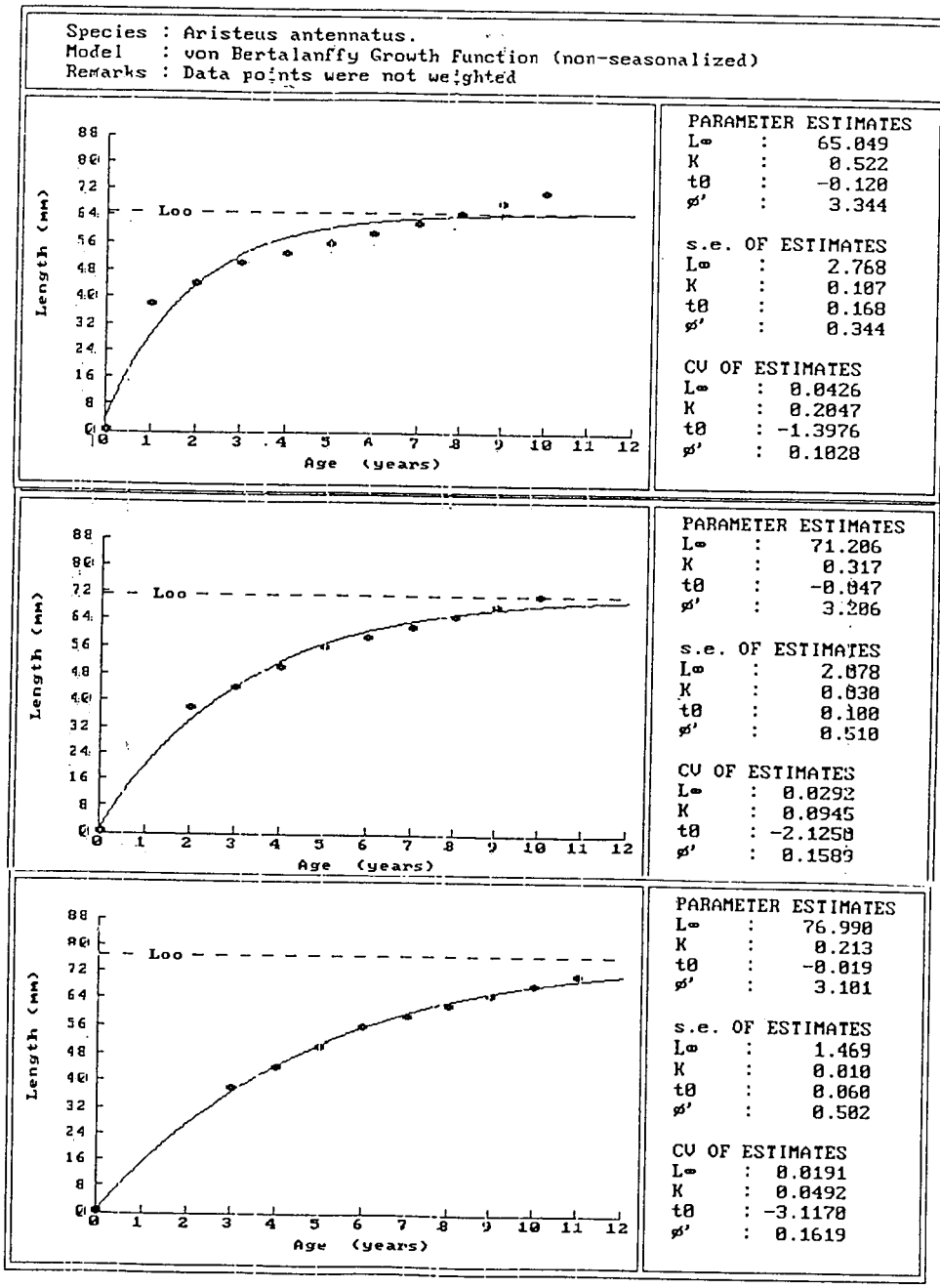

FIG. 9. Three growth hypotheses for female *A. antennatus*.

Additional remarks

A reading of length–frequency distributions in terms of instars has been proposed for good-sized deep-sea crustaceans enjoying a long life span in a unchanging environment (Childress and Price, 1978; Ingram and Hessler, 1987; Gage and Tyler, 1991).

We have supposed that *A. antennatus* might have the same characteristics, and indeed the 3-year segment of life indicated by the growth of the 1987 cohort represents proof of this. From August 1987 to August 1990 five increments of about 3 mm CL were measured, representing, in our opinion, five growth moults. Given that growth in crustaceans is discontinuous, a further moult may have occurred after a short time: in any case, 15 mm CL per 3 years or 18 mm CL per 3 years + N month(s) is a very slow growth rate compared to growth data registered in coastal penaeids. In this respect *A. antennatus* appears closer to Crustacea Reptantia of the slope, e.g. *Nephrops norvegicus* (Linnaeus) (Farmer, 1973; Froglia and Gramitto, 1988, Mytilineou and Sardà, 1995).

Previous estimates of growth rates in *A. antennatus* gave very different results. Studies began in the eighties with shrimps obtained on Portofino fishing grounds. These were very large females (figure 2) which were assigned to two age groups (Orsi Relini and Relini, 1985). When the studies were extended to southern Mediterranean areas it was evident that smaller sizes were available. Sardà (1989) promoted a comparative study which showed that the smallest shrimps were in Algarve and Mursia, those in Catalonia, Sicily and Sardinia were medium-sized, and the largest were in the Ligurian Sea. The life span was estimated at 3–4 years in Catalonia (Sardà and Demestre, 1987), 4 years in Sicily (Ragonese and Bianchini, 1996); 4–5 years in Algeria (Yahiaou, 1994) and 5 years in Murcia (Martinez-Baños, 1996).

As with other studies, the present study is unable to provide data about the first segment of life of *A. antennatus*, that is, the prematuration phase. Generally speaking it appears that in the areas where the proportion of young shrimps is largest, and therefore receives most attention, estimates tend to reduce the size at age 1 and to extend the life-span (table 1). However, the length of the first segment of life is probably still underestimated.

The available estimates of length at age 1 (table 1) seem to imply that the shrimp is able to mature before this age: in fact, only according to Martinez-Baños (1996) does age 1 coincide with the minimum spawning size. In our opinion this point deserves more attention. In fact, if in tropical and temperate penaeid species maturation occurs at age 1 and 2, it seems unlikely that a deep-sea species should have a more rapid maturation. On the other hand, we have already discussed the fact that a rapid passage from 24 to the largest adult instars is not possible in the light of observed growth (two growth instars per year in the range 38–51). The appearance of the 1987 recruits proved that a population made up of large females does not represent a unit distinct from those of the southern Mediterranean, but only a stage in a process which is identical at its origin. In fact, in 1987 shrimps with sizes similar to those found in Catalonia and Murcia arrived in the Gulf of Genoa; in the following two years the large-sized resident shrimps disappeared, and in the 1990–1993 period shrimp sizes were the same as those in the southern Mediterranean, with individuals of 61 mm CL as a maximum. The most recent survey (1996) did not produce evidence of sizes above 63 mm CL. It is difficult to understand whether this latest size limit is the result of the intensive exploitation of the resource, which certainly took place from 1988 onwards, or if other causes are at work. However, leaving aside the upper limit, the medium to large-sized shrimps are gaining in importance from year to year.

The 1987 recruitment was made up of individuals that were born in different years (scenario a has been discarded, while b and c are still possible). This means

Table 1. Chronology of growth estimates for *A. antennatus* (females only).

Year	Source	Area	Estimated life span (years)	Growth parameters			Carapace length at age (mm)			Carapace length at age (years)	
				L_∞	K/y	T_0	1	2	3	4	5
1985	Orsi Relini and Relini	Ligurian Sea	2.25	63	1.71	0.44	37	59			
1987	Sardà and Demestre	Catalan Sea	3–4	76	0.3	−0.07	29.4	39.8	53		
1994	Campillo	Gulf of Lion	5	63.57	0.525	−0.259	30.7	44.15	52.08	56.77	59.55
1994	Dos Santos and Ribeiro Cascalho	Algarve	—	75.4	0.36	−0.3	28.2	42.5	52.4	59.4	64.2
1995	Spedicato *et al.*	South Tyrrhenian	—	66.81	0.558	−0.2337	33.2	47.6	55.8	60.5	63.2
1994	Yahiaoui	Algeria	4–5	65–70	0.33–0.37	—	—	—	—	—	—
1996	Ragonese and Bianchini	Strait of Sicily	4	69.1	0.53	0	29	44	56	63	—
1996	Martinez-Baños	Murcia	5	71–75	0.38–0.4	−0.08/−0.05	25	35	44	51	57

that *A. antennatus* has a great capacity for movement, because the shrimps aged 2 or 3 in 1987 were elsewhere in the previous years. At times certain features of the fishing activity also suggest that the shrimps are groups on the move (Orsi Relini *et al.,* 1986). One could put forward the hypothesis that, as in some species of *Metapenaeus* (Miquel, 1982), once a certain concentration has been reached, the population moves away to new areas. The collapse of stock which occurred in the central-eastern part of the Gulf of Genoa in the period from 1980 to 1984 (Relini and Orsi Relini, 1987) probably created the conditions for large empty or little-populated areas to be re-occupied. Where the 1987 shrimps came from remains, however, unknown.

Even though many aspects of the biology of red shrimps and especially their migration habits, remain obscure, the picture we have drawn so far shows the large affinity that exists between the Mediterranean populations. It may be the case that we can talk of a single stock, given that the latitudinal range occupied by *A. antennatus* corresponds to that of littoral and bathyal species which have been subjected to more extensive study.

Penaeus plebejus (Hess) of Eastern Australia lives in an area that extends from 25° to 38° S. Specimens which were tagged as young shrimps in southern estuarine areas travelled as far as 900 or 1300 km towards their northern spawning areas (Ruello, 1975; Montgomery, 1981). The interesting fact is that along the same Australian coast the bathyal species *Haliporoides sibogae* de Man lives in about the same latitudinal range and migrates to the North before reaching sexual maturity (Baelde, 1992).

In another bathyal solenocerid shrimp, *Pleoticus robustus* (Smith) of the Atlantic, different sizes at different latitudes were observed (Anderson and Lindner, 1971), which could be interpreted as spawning migrations.

In our opinion the migrating abilities of *A. antennatus* in the Mediterranean are a promising subject for future research.

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