

Abstract.—The spatio-temporal structure of a population of the deep-water shrimp *Aristeus antennatus* on the fishing grounds off Barcelona, Spain, in the western Mediterranean Sea was studied, and the relationship between fluctuations in catch of this species and spatio-temporal changes in the size and sex composition of shoals is described. Fluctuations were monitored by using a sample design based on fixed seasonal sampling of three different habitats (upper submarine canyon, middle slope, and lower slope). The results explain changes in fishing fleet and fishing location. The stock appears to remain constant at approximately optimum levels of exploitation because part of it is unexploited below 1,000 m.

Factorial correspondence analysis indicated a generally strong influence of depth on the abundance of deep-water shrimp, explaining 63.14% of the variance. However, the influence of seasonality was stronger when only samples taken at depths shallower than 1,000 m (75.22%) were considered. Females contributed most to the catches on the upper and middle slope throughout the year, and catches of females were strongly related to seasonality ($P < 0.05$). The combined interaction of depth and seasonality on the abundance of males was significant ($P < 0.05$). Juveniles were present in the catches from autumn to spring, and the combined effect of depth and seasonality on the abundance of juveniles was also significant ($P < 0.05$). The role of the regional submarine canyon as a zone of higher energy and biomass in the recruitment of this species is discussed, and the importance of spatio-temporal factors linked to the life cycle of deep-water shrimps is highlighted. The results demonstrate that comprehensive ecological studies of exploited species are essential to proper fisheries management.

Spatio-temporal structure of the deep-water shrimp *Aristeus antennatus* (Decapoda: Aristeidae) population in the western Mediterranean

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As fishing activity has expanded into deeper waters, deep-water shrimps (Dendrobranchiata and Caridea) have become an important resource in different parts of the world, e.g. Australia (King, 1981; King and Butler, 1985) northern Europe (Anon., 1992), and the Pacific (Gooding, 1984) and Indian (Jones, 1969) oceans. In the Mediterranean Sea in particular, these shrimps are the target of a traditional fishery (Relini and Orsi Relini, 1987; Tobar and Sardà, 1987; Campillo et al., 1990; Demestre, 1990; Demestre and Leonart, 1993). In addition, deep-water shrimps, particularly aristeid species (Dendrobranchiata, Penaeoidea: *Aristeus antennatus* Risso, 1816), play an important ecological role in Mediterranean deep-sea communities at depths below 400 m (Pérès, 1985; Abelló et al., 1988; Abelló and Valladares, 1988; Cartes and Sardà, 1993). Population structure, biological cycles, life history, and spawning strategies of deep-water shrimps differ from those of littoral species (García and Le Reste, 1987)

and are poorly understood. The life history of deep-water penaeoidean species is not dependent upon lagoonal or littoral systems, and growth in such species tends to be slower than that in littoral penaeid species (García and Le Reste, 1987; Demestre, 1990). The presence and abundance of such species are linked to the topography of the continental slope and submarine canyons. However, their behavioral patterns are complex and not well understood (Tobar and Sardà, 1987; Cartes et al., 1993).

Pandalus borealis (Anon., 1992) (Pandalidae, Caridea) is the most extensively studied shrimp species from a fisheries perspective. This species exhibits major differences with respect to species of other genera inhabiting subtropical deep-sea regions, such as *Aristeus*, *Aristaeomorpha*, *Parapandalus*, and *Plesionika*; it is protandrously hermaphroditic and distributed in shallower waters. Migratory patterns, short and medium-term fluctuations in abundance, aggregating behavior, recruitment, and larval and postlarval dis-

tribution patterns are to a large extent still unknown in deep-water species of the latter genera.

Moreover, recently published data on the distribution and abundance of deep-water shrimps in the western Mediterranean (*Aristeus antennatus*, *Acanthephyra eximia*, *Nematocarcinus exilis*) indicate relatively high biomass levels for these species at depths down to 2,200 m (Abelló and Valladares, 1988; Cartes and Sardà, 1992, 1993; Sardà and Cartes, 1993a). Fishing pressure in shallow waters has resulted in a shift of effort to deeper regions, making the study of deepwater species extremely important, while exploitation of these resources is still low (King, 1981; Demestre, 1990; Demestre and Lleonart, 1993). Growth, reproductive biology and morphometry of *Aristeus antennatus* in particular has been studied by several authors (e.g. Bas, 1965; Relini Orsi and Relini, 1979; Arrobas and Ribeiro-Cascalho, 1987; Sardà and Demestre, 1987; Demestre and Fortuño, 1992; Sardà et al., in press). In contrast, the only available information on population structure (sex-ratio, size distribution, proportion of juveniles) and spatio-temporal migrations has been compiled from commercial fisheries data (Relini and Orsi Relini, 1987; Tobar and Sardà, 1987, 1992).

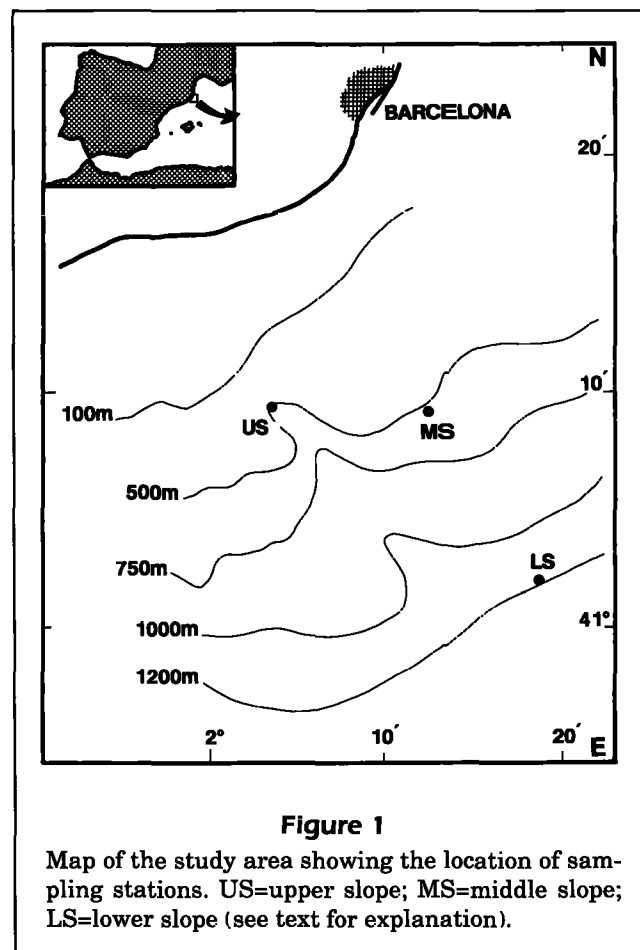
The objective of the present study is to examine the relationship between fisheries exploitation and the distribution and spatio-temporal structure of a population of *A. antennatus* in the three different habitats occupied by this species: submarine canyons on the upper slope, the middle slope, and lower slope. The study attempts to integrate our basic knowledge of the biology and population structure of this species with the pattern of fishing activity in the region. We provide a basis for interpreting catch fluctuations observed during the year and for managing this fishery consistent with the general ecology of the species.

Materials and methods

Sampling was designed to survey spatio-temporal features in two different habitats (one station in each) where commercial catches of *A. antennatus* were common: the submarine canyon known as "La Merenguera" located on the upper slope (US) at a depth of approximately 450 m (41°07'75"N, 02°04'43"E) and the area known as the "Abisinia" fishing grounds on the middle slope (MS) at a depth of 600–650 m (41°06'34"N, 02°12'05"E). A third station was located on the upper portion of the lower slope (LS) at a depth of about 1,200 m (41°54'63"N, 02°06'90"E), where no fishing activity takes place (Fig. 1). Habitat nomenclature follows Pérès (1985). Three replicate tows were carried out within a period of less than 12 hours

at each sampling station in summer, autumn, winter, and spring (Table 1). The trawl gear was a "Maireta system" (Spanish patent: 9200614, Inst. Ciencias del Mar [CSIC], consisting of a semi-balloon otter trawl with square panels and wings and a 25-m headline. The gear was towed by a single warp line attached to a V-shaped backstrop, which was in turn connected to two 450-kg iron doors. The horizontal gear opening (the wing-end spread of 14 m) was measured by using a SCANMAR system. Codend stretch mesh size was 2 mm (Sardà et al., 1993). Trawls were conducted by the Research Ship *García del Cid*.

Towing speed was 2.5 knots for all trawls. Starting and ending positions of each tow were recorded by using a GPS system. Specimens of *A. antennatus* were weighed and sexed (M=males; F=females), and short carapace length (CL) in mm was measured (rear edge of ocular orbit to rear edge of carapace). Male and female individuals smaller than 23 mm CL were classified as juveniles (J) (Sardà and Demestre, 1987; Demestre, 1990). Smaller individuals (CL <15 mm) were uncommon in the samples; such



individuals were considered to represent the early juvenile stages (L) and were analyzed separately to obtain information on the earliest stages of recruitment.

Spatio-temporal changes in population structure were analyzed by using factorial correspondence analysis (FCA) (Benzecri, 1980; Greenacre, 1984). Data were logarithmically transformed and a data matrix was constructed by using the three habitats sampled and the following variables: number of males (M), number of females (F), number of juveniles (J), number of smaller juveniles (L), and total number. Because the LS below 1,000 m is a stable habitat that, unlike the US and MS, is less affected by sea-

sonal factors (Hopkins, 1984; Tyler, 1988; Gage and Tyler, 1991) and is not exploited by the fishery (Demestre, 1986; Sardà and Martín, 1986), the analysis was repeated excluding samples taken on the LS (Table 2).

Multifactorial nonparametric analysis of variance (Zar, 1984) was used to calculate differences between variable and habitat combinations in each season (spring, summer, fall, and winter). The Mood nonparametric median test (Conover, 1980) was also used to determine differences in total number of individuals by habitat.

Results

The first two inertial axes of the correspondence analysis explained 63.14% and 26.84% of the variance in abundance of shrimp, respectively (Fig. 2). Along the first axis, LS samples were associated with a higher proportion of males and early juvenile stages (L), which did not exhibit any marked seasonal pattern in the deepest region. However, the samples collected in summer on both the US and MS were mainly females and were located in the region opposite the LS samples (Fig. 2). In summary, the first axis was mainly related to depth and juveniles predominated in the US and MS samples collected in spring, autumn, and winter.

The results of the analysis, excluding samples taken on the LS (Fig. 3), yielded a cluster of data points for spring samples associated with the presence of juveniles (recruits); in contrast, data points for summer samples were again associated with adult females. Autumn and winter samples were less clearly discriminated but shifted to the right from the origin and were associated with males. This may be interpreted as a seasonal effect that alters the population structure and is discriminated by the first axis, which explained 75.22% of the total variance (Fig. 3A). The distribution of juveniles appeared to be linked to the topography of the submarine canyons (black points in Fig. 3B), mainly during winter and spring, while the proportion of males rose on the middle slope out to the canyon in autumn and winter (open symbols, Fig. 3B). Juveniles and early juvenile stages (L) were caught in the deepest region sampled (Table 2 and Fig. 2). In summer females were distributed extensively on both the MS and the US. In this second analysis the first axis may be related to seasonality. The second axis (20.27%) probably represents a depth-related component, because the samples from the MS were taken at slightly greater depths (600–650 m) than those taken from the US (400–500 m).

Table 1

Sample list and specific haul data for collections of rose shrimp, *Aristeus antennatus*. P=spring; W=winter; A=autumn, and S=summer. US=upper slope; MS=middle slope, and LS=lower slope.

Ref. code	Season	Habitat	Date	Haul time (h)	Mean depth (m)
R1/1	P	MS	04/23/91	1.00	570
R1/2	P	MS	04/23/91	1.50	600
R1/3	P	MS	04/23/91	1.67	692
R1/4	P	US	04/23/91	1.00	455
R1/5	P	US	04/23/91	1.00	459
R1/6	P	US	04/23/91	1.00	390
R1/7	P	LS	04/25/91	1.00	1160
R1/8	P	LS	04/25/91	1.00	1210
R1/9	P	LS	04/25/91	1.00	1230
R2/7	A	MS	12/09/91	1.00	625
R2/8	A	MS	12/09/91	1.00	613
R2/9	A	MS	12/09/91	2.00	562
R2/1	A	US	12/08/91	0.42	433
R2/2	A	US	12/08/91	0.50	455
R2/3	A	US	12/08/91	0.50	504
R2/4	A	LS	12/08/91	1.00	1265
R2/5	A	LS	12/09/91	1.00	1274
R2/6	A	LS	12/09/91	0.50	1252
R3/1	W	MS	03/12/92	0.83	565
R3/2	W	MS	03/12/92	0.75	545
R3/3	W	MS	03/12/92	0.75	545
R3/4	W	US	03/12/92	0.50	355
R3/5	W	US	03/12/92	0.50	447
R3/6	W	US	03/12/92	0.50	508
R3/7	W	LS	03/13/92	1.00	1235
R3/8	W	LS	03/13/92	1.00	1275
R3/9	W	LS	03/13/92	1.00	1210
R4/1	S	MS	07/26/92	1.00	605
R4/2	S	MS	07/26/92	1.00	611
R4/3	S	MS	07/26/92	1.00	616
R4/4	S	US	07/26/92	0.50	426
R4/5	S	US	07/26/92	0.42	400
R4/6	S	US	07/26/92	0.50	440
R4/7	S	LS	07/27/92	1.00	1260
R4/8	S	LS	07/27/92	1.00	1286
R4/9	S	LS	07/27/92	1.00	1272

Table 2

Basic data matrix in number of individuals per sample of *Aristeus antennatus*: M=males; F=females; J=juveniles (CL<23 mm); L=early juvenile stages (CL<15 mm); n=total number; US=upper slope; MS=middle slope; LS=lower slope. P=spring; A=autumn; W=winter and S=summer, (—)=no data.

Replicates	US			MS			LS		
	1	2	3	1	2	3	1	2	3
M	74	15	48	153	51	31	—	39	19
F	359	113	298	178	314	132	—	21	15
P J	241	60	166	198	86	73	—	40	24
L	0	0	0	0	0	0	—	0	0
n	433	128	346	331	265	163	—	60	34
M	40	82	44	7	5	4	11	24	36
F	160	378	166	5	8	17	14	11	14
A J	112	160	94	8	5	4	19	29	42
L	0	0	0	0	0	0	1	0	0
n	200	460	160	12	13	21	25	35	50
M	0	12	6	130	11	24	4	26	25
F	0	62	42	212	30	107	3	15	12
W J	0	32	32	102	11	20	4	23	22
L	0	0	0	0	0	0	0	3	3
n	0	74	48	342	41	131	7	41	37
M	18	12	0	0	4	0	63	51	353
F	820	144	166	53	104	196	45	14	120
S J	52	30	4	41	5	5	65	40	285
L	0	0	0	0	0	0	4	2	6
n	838	156	166	53	108	196	108	65	473

Seasonal groupings of samples revealed significant differences in the analysis of variance (Table 3). When the deepest station (LS) was included in the analysis, the total number of individuals were significantly different with depth ($P<0.05$). This variation with depth can be explained by the fact that, on average, fewer individuals were collected at the station on the LS ($P<0.01$) (Fig. 4).

Differences in the number of females were also significantly related to depth ($P<0.05$); females were more abundant at shallower stations on the MS and US. Males collected from the three habitats exhibited significant differences for interaction between depth and seasonality ($P<0.05$) (Table 3), which resulted from the higher percentage of males on the LS all year and on the MS in autumn and winter.

When the deepest samples (LS) were excluded, differences between the number of males and the total number of individuals were significant between seasons ($P<0.05$) and for the interaction between depth and season ($P<0.05$).

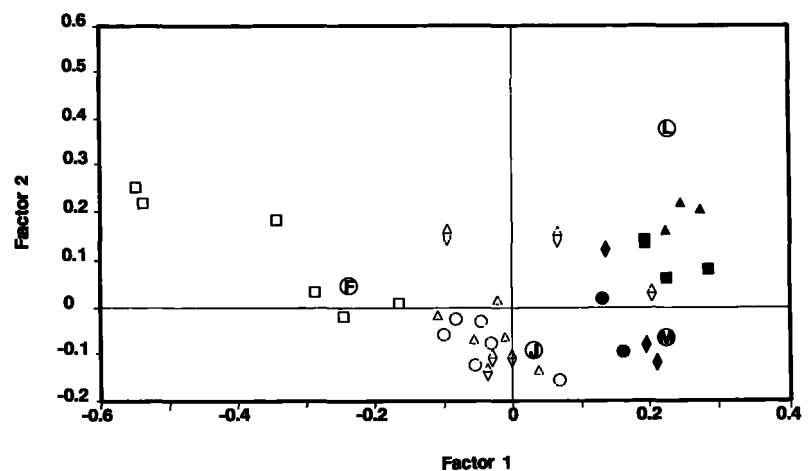


Figure 2

Plots of scores on the first two correspondence axes for the entire set of samples of rose shrimp, *Aristeus antennatus*. F=females; M=males; J=juveniles; L=early juvenile stages; circle=spring; square=summer; triangle=autumn; diamond=winter.

Discussion

The distribution of *A. antennatus* extended to a depth of more than 2,200 m. The population structure in

the deeper region between 1,000 and 2,200 m consisted of a higher proportion of juveniles and males (Cartes and Sardà, 1992; Sardà and Cartes, 1993b; Cartes, in press). This contrasts with the high proportion of females collected at depths of less than 1,000 m.

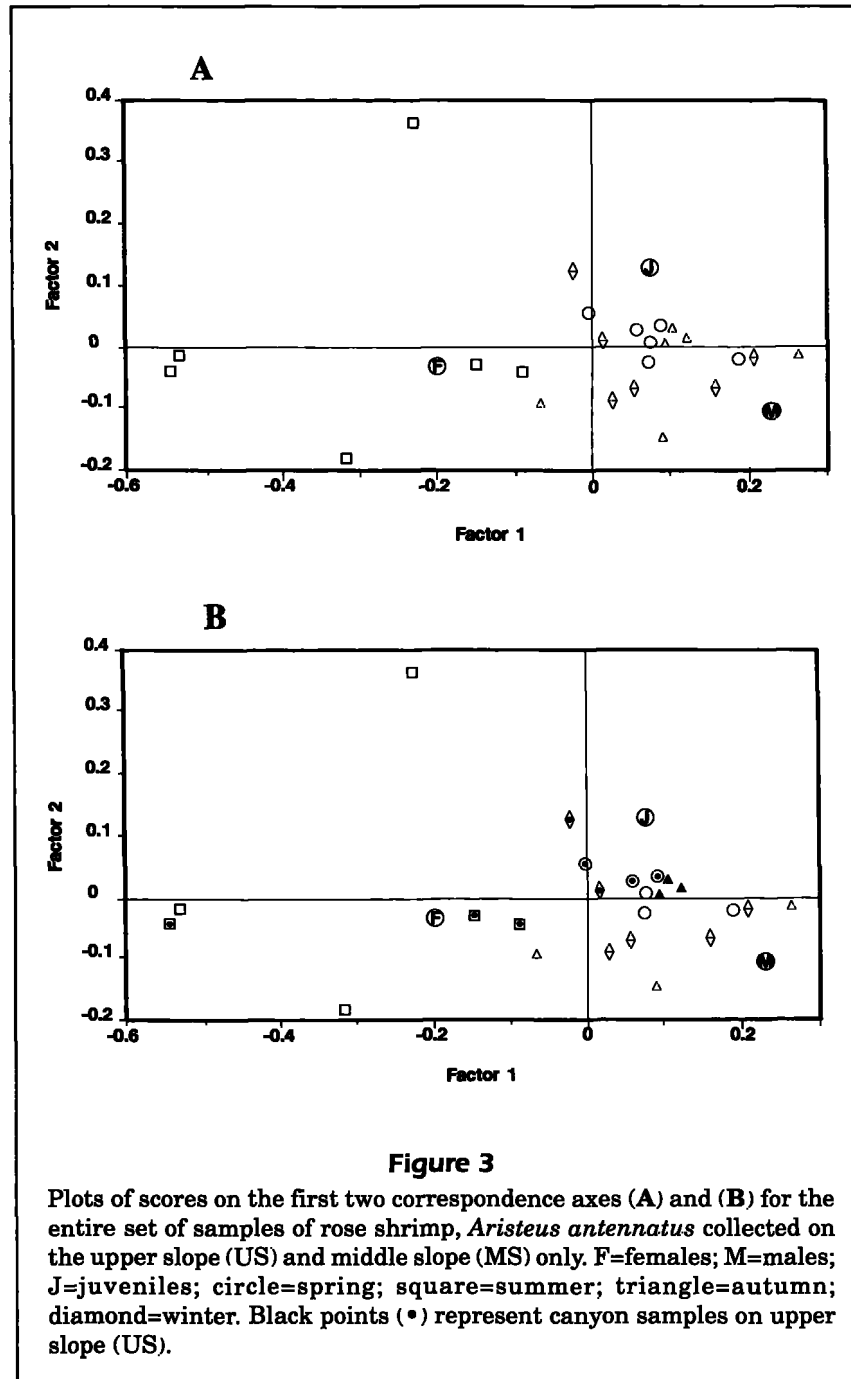
The present results support the hypothesis that two different populations of *A. antennatus* persist in the western Mediterranean. One population is unexploited and stable throughout the year at depths below 1,000 m and is characterized by lower densities and higher percentages of males and juveniles.

The other population is commercially exploited and variable over the year at shallower depths between 400 and 1,000 m. It is characterized by high abundance and by seasonal variations in total number, sex ratio, and depth distribution.

The *A. antennatus* stock, though subjected to considerable fishing pressure, has remained at near optimum equilibrium levels (Demestre and Lleonart, 1993). Sardà (1993) and Sardà and Cartes (1993a) attributed this equilibrium to the presence of unexploited biomass at depths below 1,000 m, which annually renews the exploited portion of the stock.

Though sampling was localized and did not cover extensive areas of each habitat, the samples from the US and MS nonetheless reflected specific spatio-temporal patterns in population structure: females completely dominated the population all year, forming aggregations on the MS in spring and summer. Earlier studies on fishing patterns during the year (Figure 5A, revised after Tobar and Sardà, 1987) have referred to this population migration pattern. Changes in the coefficient of variation of catch rate illustrated in Figure 5B reflect a scattering of the shoals in spring and summer (from April to August) and a more highly aggregated stock structure in autumn and winter. Figure 6 summarizes our conclusions regarding the distribution and movement of *A. antennatus*.

The increase in number of females on the MS in spring and summer coincides with the period of gonadal ripening and fertilization (Relini Orsi and Relini, 1979; Arrobas and Ribeiro-Cascalho, 1987; Sardà and Demestre, 1987; Demestre and Fortuño, 1992) and shortening of the male rostrum (Sardà and Demestre, 1989). These authors also reported that shoals disperse after spawning, which occurs mainly from June to September. This might suggest a specific mating area in the MS. After September, shrimps spread out over the slope and submarine canyons, leading to a decrease in density and increase in the proportion of males on the slope. Processes linked to the transfer of energy through the slope and submarine canyon systems (Reyss, 1971, 1973; or Rowe, 1971;



Koslow and Ota, 1981; Houston and Haedrich, 1984), and feeding habits (Cartes and Sardà, 1989; Cartes, 1991) may also be related to distribution of *A. antennatus*. Ghidalia and Bourgois (1961) and Bombace (1975) associated certain shrimp species with water masses that were of a characteristic septentrional type, with a low temperature of 12.8°C and high salinity (38.1–38.8 ppt). However, it has not been possible to confirm these hydrographic hypotheses for *A. antennatus*, because the study by Ghidalia and Bourgois (1961) reported few catch data of this species. No other studies on related species have established more specific hypotheses.

The growth, abundance, parent stock biomass, and recruitment of commercial species are important when calculating parameters directly related to their population dynamics and exploitation (Caddy and

Sharp, 1988; Sardà, 1993). Size-frequency data for *A. antennatus* caught by commercial fishing vessels (Demestre, 1990; Fig. 7) do not show progressions in monthly length-frequency modes. Apparent “negative growth rates” between different months suggest that vessels were following a moving stock and that catches were taken at the most commercially profitable locations. Procedures for analyzing this type of stock have been considered by Jones (1984), Caddy (1982, 1987), and Caddy and García (1986) from fishery catches. Procedures for treating migratory stocks have been considered primarily by Sousa (1988) in the fish *Decapterus russelli*. Bias in size frequencies due to migratory effects in *D. russelli* is similar to

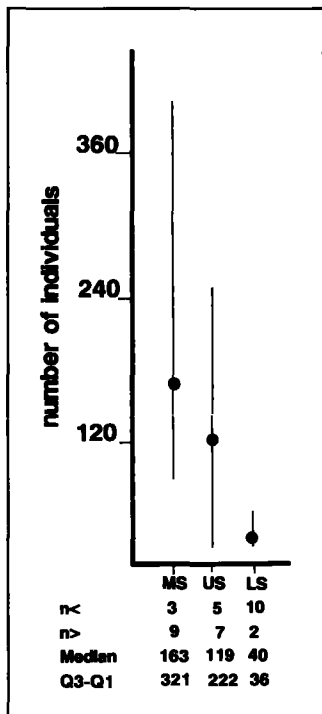


Figure 4
Mean number of individuals of rose shrimp, *Aristeus antennatus*, showing 95% confidence intervals ($\chi^2=8.67$; $P < 0.01$): 'n' = number of samples below median; 'n' = number of samples above median; Q3-Q1 = difference between maximum and minimum value. US=upper slope; MS=middle slope; LS=lower slope.

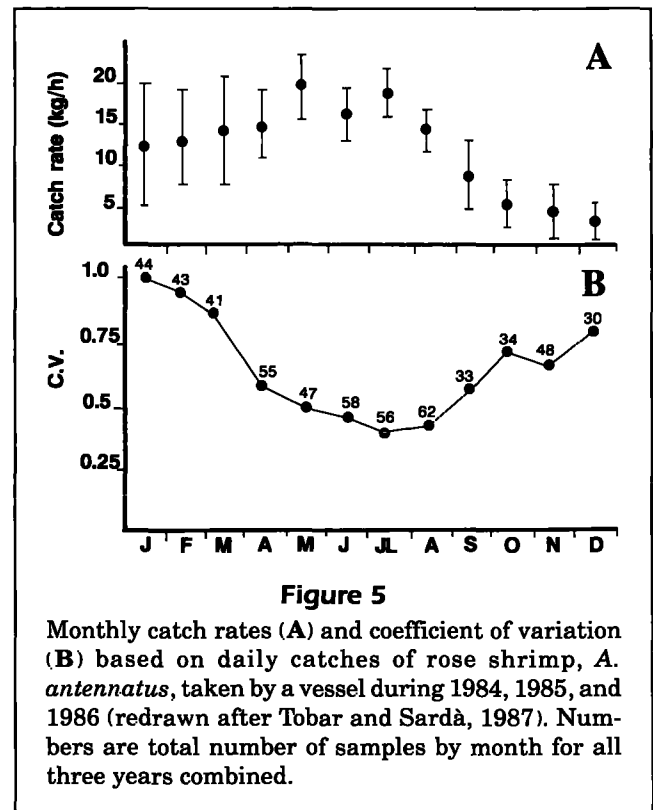


Figure 5
Monthly catch rates (A) and coefficient of variation (B) based on daily catches of rose shrimp, *A. antennatus*, taken by a vessel during 1984, 1985, and 1986 (redrawn after Tobar and Sardà, 1987). Numbers are total number of samples by month for all three years combined.

Table 3

Results of applying multifactorial nonparametric analysis of variance to the basic data matrix presented in Table 2 for collections of rose shrimp, *Aristeus antennatus*, with and without lower slope (LS) data. M = males; F = females; J=juveniles, n=total number; (+)=significant difference ($P < 0.05$); (—)=nonsignificant difference.

	With LS data				Without LS data			
	M	F	J	n	M	F	J	n
Seasonality	+	—	—	+	—	—	—	—
Depth	—	—	—	—	—	+	—	+
Interaction	+	—	—	+	+	—	+	—

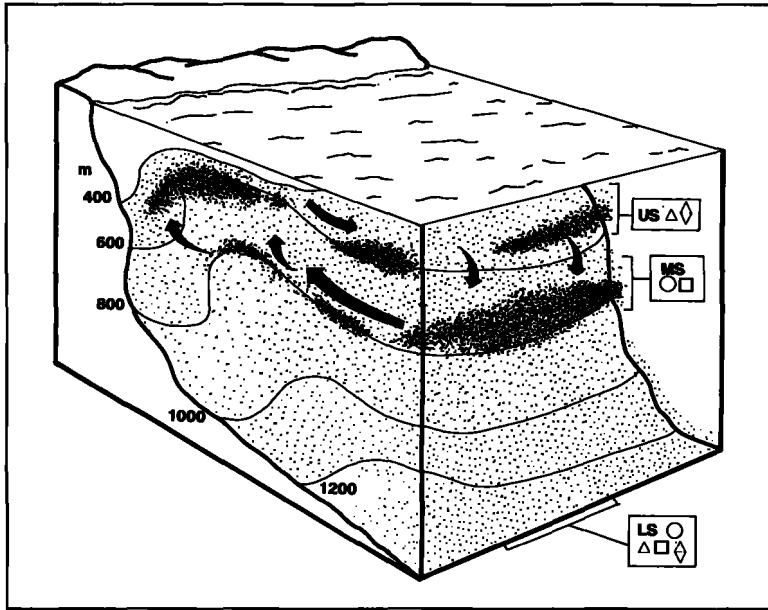


Figure 6

Conceptual model of the spatio-temporal dynamics of *Aristeus antennatus* in the study area (see text for more details). MS=middle slope; US=upper slope, and LS=lower slope; circle=spring; square=summer; triangle=autumn; diamond=winter.

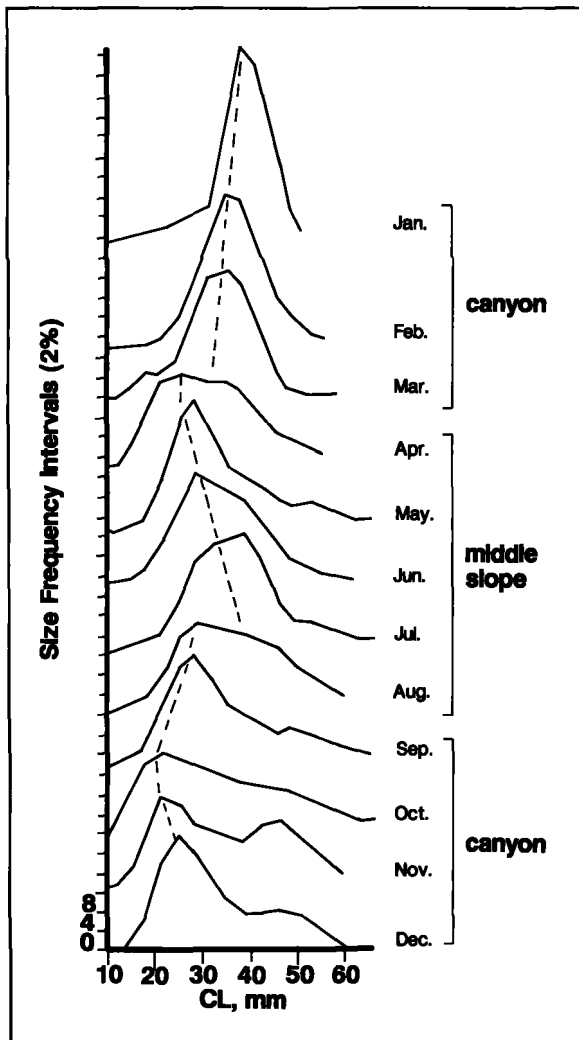


Figure 7

Monthly size frequencies for rose shrimp, *Aristeus antennatus* (carapace length) taken in commercial catches from the upper slope (US) and middle slope (MS) (data from Demestre, 1990).

that observed for *A. antennatus*. Size-frequency modes were evident in spring and summer but did not progress in autumn and winter (Fig. 6). Sparre et al. (1989) advised using the annual-return matched sample method to estimate growth parameters in such cases. Failing to take these aspects into account when considering a population exploited by a given fleet in a given area may lead to errors in calculating biological parameters and, consequently, in decision-making for fishery management.

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