



Biodiversity of tactics used by three Gobiidae (Pisces; Teleostei): Pomatoschistus minutus (Pallas, 1770), P. microps (Krøyer, 1838), Gobius niger Linnaeus, 1758, to survive in a mediterranean lagoon environment.

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**BIODIVERSITY OF TACTICS USED BY THREE GOBIIDAE
(PISCES; TELEOSTEI): *POMATOSCHISTUS MINUTUS*
(PALLAS, 1770), *P. MICROPS* (KRØYER, 1838),
GOBIUS NIGER LINNAEUS, 1758, TO SURVIVE IN
A MEDITERRANEAN LAGOON ENVIRONMENT**

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Key words: Sedentary fishes, Gulf of Lions, occupying tactics, lagoon

Abstract

Each population studied employs a personal strategy to ensure its successful occupation of and reproduction in a very harsh Mediterranean ecosystem, the Mauguio lagoon (Gulf of Lions). *P. minutus* undertakes relocation to search for quality biotopes and to ensure success in the various stages of its life cycle by genescic migration (for reproduction) to the sea of adults for spawning, and by postlarval trophic immigration within the lagoon. However, *P. microps*, more euryvalent, is completely sedentary. Although *G. niger* has adaptive capacities potentially similar to those of *P. microps*, and makes a considerable reproductive effort, this species is subject to relative demographic failure, mainly owing to the scarcity of nesting areas both in the lagoon and at sea. The spatial and trophic co-exploitation of the lagoon is facilitated for these three populations by the migrational behaviour of *P. minutus*, the different static and dynamic characteristics of each species studied, and the evolution of the seasonal vegetation in this environment.

INTRODUCTION

The Mediterranean Sea is surrounded by lagoons (Quignard, Zaouali 1980, Quignard, 1984) representing 0.2 % of its surface area and 3 % of its continental shelf. Transitional formations between sea and land, these lagoons are permanently oscillating between artificial support and disappearance. To maintain their existence for human purposes, communications (the *grau*) linking them to the sea have been so arranged that very few lagoons can at present be considered "natural". They are characterised by high temporal-spatial variations (Quignard, Zaouali 1980, Quignard 1984) in their hydroclimate (temperature, salinity, etc.) and tend at present to be subject to eutrophication. In certain circumstances, they suffer from dystrophic anoxic crises leading to large-scale mortality. Moreover, because they are shallow and the bottom is covered by fine, often muddy, sediment, the water becomes extremely turbid (nephelo-sedimentary crises) at the slightest æolian mixing. The lagoon can therefore be considered an extremely harsh environment for living organisms. Thus, sedentary lagoon fishes only number about ten species, whereas the migrants able to escape these adverse circumstances are more numerous, 20 to 80 species depending on the type of the lagoon (Quignard, Zaouali 1980). The lagoon life organises itself with these two main functional units, the migrant and the sedentary fishes. The migrants divide their life between the lagoons and the sea. They spawn in the sea. They penetrate the lagoon via the *grau* at the larval, juvenile, or adult stage according to the species and type of lagoon. They stay from several weeks to several months, exceptionally several years. Their recruitment and thus their presence in the lagoon depends on the quality of the lagoon as well as on that of the *graus* and the sea, and the state of their original marine stocks. These migrant fishes generally represent a good market value.

The sedentary species hatch, grow, spawn and die in the lagoons. Being of a smaller size, they have not really attracted attention up to now, although they are the ones who determine the attractive power, as it were, of these water masses for the migrants. Finally it is noticeable, that since these specimens and their populations spend their whole existence in the lagoons, they can be useful bio-indicators of their quality.

Based on our recent research, we have attempted in this study to evaluate and understand the original features and tactics used by *P. minutus*, *P. microps*, *G. niger* to occupy, survive, and eventually spawn in such a relatively constraining environment as the Mediterranean lagoons.

MATERIAL AND METHODS

The three goby species were studied in the Manguio lagoon, located on the French Mediterranean coast, south of Montpellier between 43°33'30" N and 43°37'17"

N and between 3°57'50"E and 4°05'00" E. The lagoon is shallow (mean 0,80 m), ranked seventh among French lagoons in surface area (31.66 km²), separated from the sea by a kilometre-wide stretch of land (*lido*) and linked to it by a channel 1050 m long, 10 m wide and 1.50 m depth. The temperature of the water is closely related to that of the air (Bouchereau *et al.* 1990a). The mean monthly water temperature lies between 5°C (exceptionally 3°C) in January and 25°C in July or August. Although winters are usually mild, low temperatures in mid-January can cause the lagoon to freeze. It is an environment subject to high spatial-temporal variations in chemical and physical conditions. The N, NE winds (Mistral and Tramontana), and those from the SSE (120°–159°) contribute to the instability of the lagoon water. Windy episodes reaching 8 metres per second are frequent all the year round, but especially during April, August and November; however, there are high interannual variations. Water circulation is complex and depends upon various factors (Ringuelet 1974, Pons 1976, C.E.M.A.G.R.E.F. 1989). These strong winds cause temporary differences of depth (Æolian tides) between the lagoon's northern and southern shores, greater than those due to the normal semi-diurnal tides and those due to possible barometric tides. The run-off from often torrential rains enriches the lagoon environment with nutritional elements promoting primary production (Hénard, Vaulot 1979, Quignard 1989) which is 7 to 10 times greater than that of the sea. The meiobenthos can be found in almost unlimited quantities. According to Hénard and Vaulot (1979), the lagoon's water volume, estimated at 31.6×10^6 m³, is renewed on average, every three months. The green alga of the *Ulva*, *Ulvopsis*, *Chaetomorpha*, *Enteromorpha* genera and red alga such as *Gracilaria verrucosa* grow considerably from the beginning of spring until summer, invading the entire depth of water (Cugnen 1980). These proliferations can generate an algal overcharge reaching for example 9 400 g · pm⁻¹ of fresh wet alg in the neighbouring lagoon of Prévost (Riouall 1976). Also, they can cause a dystrophic crisis of varying intensity, called "*malaïgues*" in the Languedoc region, leading to the large-scale disappearance (death or departure) of lagoon organisms, such as happened in August 1988 (Quignard *et al.* 1989, Bouchereau *et al.* 1990a, 1990b, 1993b) and in August 1992 (Bouchereau 1994). The global biomass is at its minimum from September to February. Several bird species, potential predators of fish, are permanently present in the Languedocian lagoons. In the Mauguio lagoon, fishing is an intervening factor in the structuring and the evolution of its fish populations (Quignard *et al.* 1989, Bouchereau *et al.* 1990a). The dominant species caught between 1986 and 1989 are the following in decreasing order: eels, mullets, sand-smelts, gobies, flat fishes and sardines. The halieutic production has declined significantly since 1970 (Quignard *et al.* 1989, Bouchereau *et al.* 1990a). This decrease has been mainly due to the modernisation of fishing methods (motor-boats, rot-proof fishing nets) and the breaking of fishing regulations (a limited number of fixed nets, called *capéchades*, per fisher-

man) leading to the over-exploitation of the lagoon; however, it is also due to the deterioration of the lagoon water quality.

The three goby species studied here are small in-shore epi- and cryptobenthic Teleostean fishes, in which the males are the nest-keepers. One or several females lay their eggs in the interior of an empty upside-down Lamellibranchia valve (*P. minutus* and *P. microps*), or on a rock surface (*G. niger*).

P. minutus, the sand goby, is a small fish, 89 mm in the Mediterranean, Bouchereau *et al.* 1989c, 1990c), essentially living near the shore. It is common in the north-eastern Atlantic from Norway to southern Spain, in some sectors of the western Mediterranean (Gulfs of Lions and Genoa), in the Adriatic (Gulf of Venice) and along western Black Sea coasts. The precise geographic distribution of this fish is difficult to define because it has often been mistaken for other gobies species (Guitel 1892, Swedmark 1968, Vaas *et al.* 1975, Vaas 1979, Webb 1980). *P. minutus* lives in estuaries, salty lagoons, and inshore waters up to 26 metres in depth (Johnsen 1936). This goby does not generally spend all its life in lagoons or estuaries because it leaves them to reproduce in the sea to avoid low temperatures. Throughout its distribution range, this species does not appear to be fished commercially, but is accidentally caught in great numbers in the French Mediterranean lagoons (Quignard *et al.* 1983), mainly during autumn and winter. Over 40 studies refer to the biology of *P. minutus* from the Atlantic; of those dealing with this species in the Mediterranean, *e.g.* Gourret (1897), Mathias and Dolique (1962), Lo Bianco (1909), Ninni (1938), Cavinato (1952), Padoa (1953), only one (Hervé, 1978) considers its biology there. Characteristic of this fish is the fact that it is the only annual species of the environment under study to undergo genescic and ontogenic lagoon-sea migration (reproduction migration). *P. minutus* is highly interesting because of its subresident position between high-longevity migrating fish such as soles, sea bream, sea-bass, and gilt-head sea bream, which occupy the lagoon in their first or second year of life, and sedentary fish. Both the following species, *P. microps* and *G. niger*, spend their entire life cycle in the lagoon, even though they are not endemic to these lagoons.

P. microps, the common goby, is a small fish (64 mm on the British coasts, Jones and Miller 1966; 53 mm in the Mediterranean, Bouchereau *et al.* 1989a), and is usually found on the Atlantic coasts from Norway to Morocco (Miller 1986). In the Mediterranean, its presence is limited from the Gulf of Lions to Corsica. In the whole of its distribution area, it lives in estuaries, salty lagoons and along sea shores up to 11 metres in depth in the Atlantic (Fonds, 1961–1962 in Jones and Miller 1966). Although in some parts of the Atlantic this fish has a migratory behaviour, it is sedentary in the Gulf of Lions. It is not commercially fished but may be caught locally by fishermen looking for other species. Although studies of the biology of *P. microps* are numerous in northern Europe (over 34; see Webb (1986) and Al Hassan *et al.* (1987) for genetic studies of this species), only one has provided data on its biology in the Mediterranean sea (Hervé 1978).

G. niger is a larger fish than both the *Pomatoschistus* species previously described in this paper (165 mm, Fabi and Giannetti, 1984), and its geographical distribution is very wide (Miller 1986). It inhabits an area from Norway to Mauritania as well as all of the Mediterranean and Black Seas. It is often caught in the sea at 75 metres depth as well as in lagoons and estuaries. Although wholly sedentary in its distribution area, it congregates in coastal waters at spawning time and moves in the circalittoral muds in winter (Fabi, Frogliia 1984). The male watches over the eggs laid on an inert substratum usually of rock. In some areas, this goby is locally subjected to commercial fishing and represents (as in the central Adriatic) the principal catch of fishing boats working at times at a depth of 35 metres (Fabi, Frogliia 1983). Comparatively few studies are devoted to this species, whether from the Atlantic or the Mediterranean. In the latter, growth (Fabi, Giannetti 1984), feeding (De Casabianca and Kiener 1969, Fabi, Frogliia 1983), and reproduction, along with embryogenesis and fecundity (Ballard 1969) have been briefly studied. For the Atlantic, Nash (1984) and Vesey and Langford (1985) each studied the main aspects (age, growth, reproduction) of *G. niger* biology; Le Menn (1974) only discussed vitellogenesis. Benharrat *et al.* (1981) and Benharrat (1983) studied enzymatic polymorphism of marine and lagoon populations of *G. niger* in the Gulf of Lions where it occurs erratically.

Fish were sampled every week from landings by fishermen at Cabanes de Pérols (Mauguio lagoon). They catch fish with non-selective fixed nets called "capéchades" (Fig. 2) set all over the lagoon. Nests of *Pomatoschistus* were collected by diving or with a manual trawl (Fig. 3) either in Mauguio lagoon or in the sea beside the *grau* of this lagoon (Fig. 1). Sampling and treatment of the biological material methods used are detailed in Bouchereau (1994). To demonstrate and verify the tactics displayed by these three gobies to ensure occupation success in the Mauguio lagoon, we studied the following life history aspects: sex, demographic structure in size and age, growth, condition factors, reproduction: spawning sites, reproduction period, size and age at first maturity, sexual behaviour, female and nest fecundities, number of spawns, time of interspawnings. The determinism of migration of *P. minutus* and the sedentarity of *P. microps* and *G. niger* have been considered.

RESULTS

Between 1986 and 1990, a large number of samples were taken: ca 31 000 *P. minutus*, 26 000 *P. microps* and 8 500 *G. niger* from landings at Cabanes de Pérols, Mauguio lagoon (Quignard *et al.* 1989, Bouchereau *et al.* 1990a). More than one hundred nests of *Pomatoschistus* were collected by diving or with a manual ski-trawl either in Mauguio lagoon or in the sea adjoining the *grau* of this lagoon (Table 1).

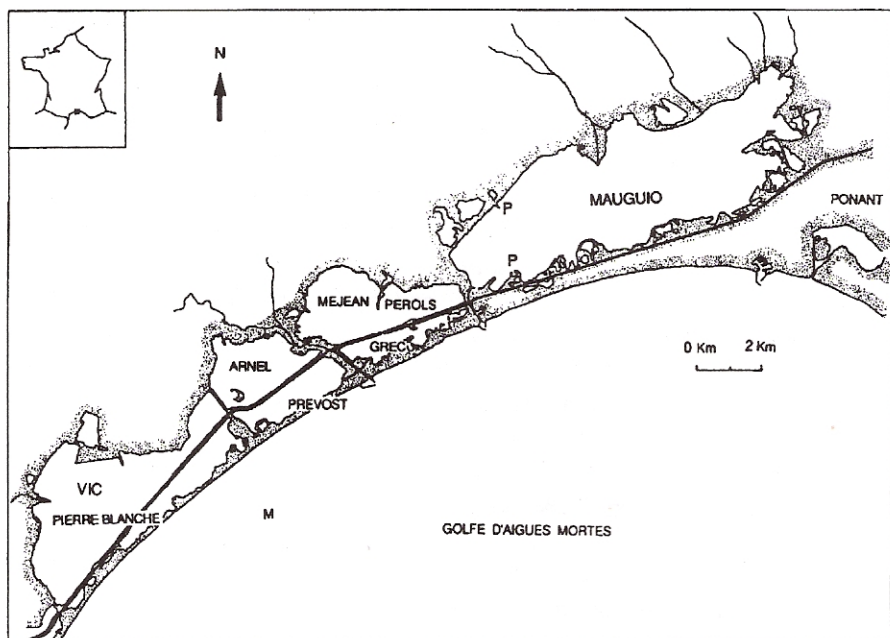


Fig. 1. Mauguio lagoon in the Palavasian lagoon complex, fishing landing place D, and nest collection sites of *P. microps* in the lagoon (P) and *P. minutus* near the shore (M)

Main results are summarised in Table 2 and Figs. 4 and 5. The maximum sizes caught were smaller than those found in the Adriatic for each species: *P. minutus* 89mm, *P. microps* 53mm, *G. niger* (136 mm). Even if there is no significant statistical difference between the sexes in each size class, males are always larger than females. Both *Pomatoschistus* species are annual and spawn once. They do not live more than one year. Very exceptionally *P. microps* can live two years. The life span of *G. niger* is 3 or 4 years according to sex. Ages at first maturity are less than one year for each species but part of the *P. microps* population can reproduce at 4 months. Sizes at first maturity are small for *P. microps* (27 mm) and *G. niger* (43mm: males; 54 mm: females). The size of *P. minutus* at first maturity has not been measured since it migrates seawards to reproduce.

Somatic and gonadic growth occurs separately in *P. minutus* but almost concurrently in *P. microps* and *G. niger*. During the spawning season, which in *P. minutus* takes place in winter but in *P. microps* and *G. niger* in spring and summer, reproductive investment is high for the three species. They can breed more than 11 times per season. Fecundity is high according to size and weight. During the reproductive period, the sex ratio is in favour of *P. microps* females

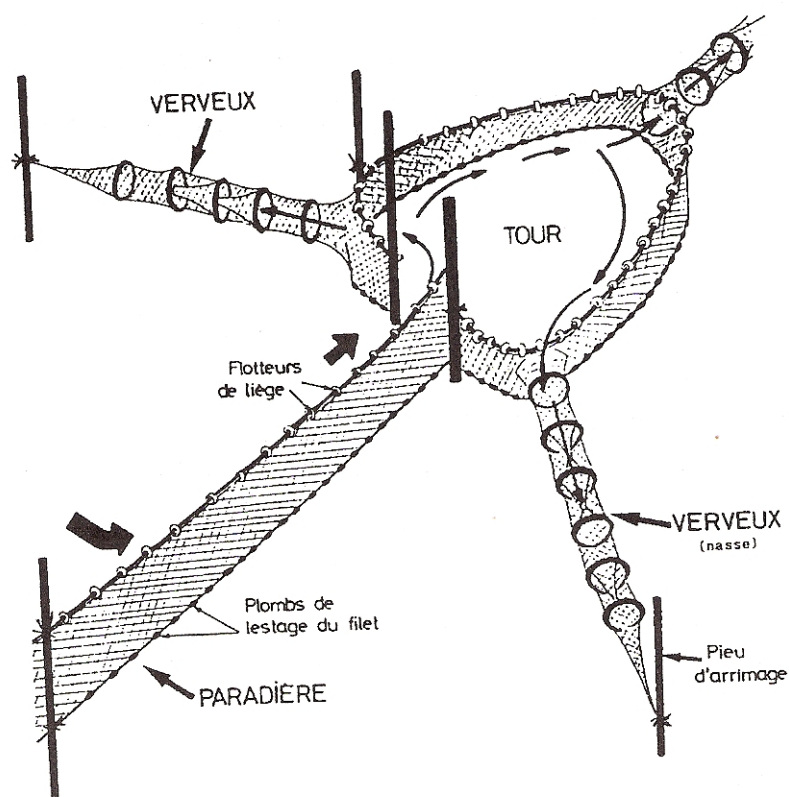


Fig. 2. Fixed *capéchade* nets. Direction of fish movement is indicated by arrows (after Bouchereau, 1994)

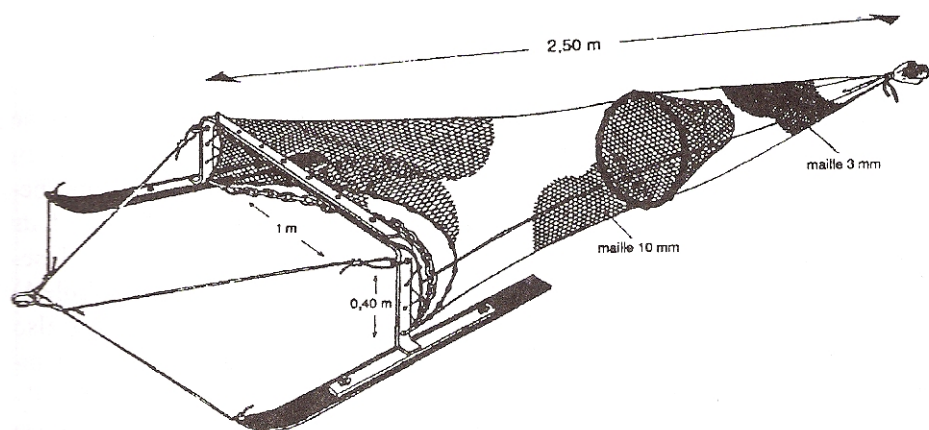


Fig. 3. Manual bentkhic ski-trawl net (after Bouchereau, 1994)

and of *G. niger* males. During that time, *P. minutus* has to migrate to sea, whereas *P. microps* is sedentary in the lagoon and *G. niger* has the status of a rather erratic species. Suitable substrata for nesting are absent in the lagoon for *P. minutus* but present for *P. microps*; for *G. niger* such substrata are rather rare in both the lagoon and the Gulf of Lions.

Table 1

Length of sampling periods, number of individuals sampled for each species studied according to sex (m: male; f: female) and limit values of total length (TL in mm) observed

Species	Duration	number	males	females	TL limits
<i>P. minutus</i>	09-1985	30758	15679	15109	(m) 27-83
	10-1987				(f) 25-81
<i>P. microps</i>	10-1985	25363	7438	17925	(m) 19-53
	10-1987				(f) 20-49
<i>G. niger</i>	12-1985	8436	4195	4291	(m) 33-135
	12-1989				(f) 33-122

DISCUSSION

Specific tactics of each species

Each of the three species described above displays a specific strategy for living in the lagoon.

Pomatoschistus minutus

In Mauguio lagoon, *P. minutus* is different from *P. microps* and *G. niger* because of its trophic and genestic migrations (Bouchereau *et al.* 1990c) undertaken when the environmental circumstances are not adapted to their requirements, and because of the very evolutive statural structure (Bouchereau *et al.* 1989c) of its annual population (Table 1, Fig. 1). The necessity of spawning in the sea is closely linked to the scarcity in the lagoon of compatible substrata for nesting (Table 1) and of suitably-sized Lamellibranchia valves (Bouchereau *et al.* 1991); it is also due to the contrary ($< 10^{\circ}\text{C}$) hydroclimatic conditions encountered from November to the end of January (Bouchereau 1994). This seaward migration not only generates advantages in reproduction: for example, the spawning which takes place at 10 metres depth limits predation on the parents which are not mobile enough.

Table 2

Comparison of demographic variables for the three species studied in the Mauguio lagoon; TL: total length; references are: (1) Bouchereau, 1994; (2) Bouchereau *et al.*, 1990a; (3) Bouchereau *et al.*, 1989a; (4) Bouchereau *et al.*, 1989b; (5) Bouchereau *et al.*, 1990b; (6) Bouchereau *et al.*, 1989c; (7) Bouchereau *et al.*, 1993a; (8) Bouchereau *et al.*, 1990c; (9) Bouchereau *et al.*, 1991; (10) Joyeux *et al.*, 1991a; (11) Joyeux *et al.*, 1991b; (12) Joyeux *et al.*, 1992; (13) Quignard *et al.*, 1989

VARIABLES	<i>P. minutus</i>	<i>P. microps</i>	<i>G. niger</i>
Maximum size (TL in mm)	89 (5)	53 (3)	136 (10)
Life span	annual (6)	annual (3)	4 years, m 3 years, f (10)
Age at first maturity	10 months (8)	4 months (7)	7 - 13 months (11) (12)
Size at first maturity	-	27 mm (7)	43 mm, m 54 mm, f (11) (12)
Spawning period	Dec. - Mar. (8)	Mar. - Sep. (4)	Mar. - Sep. (11)
Duration of spawning periods	4 - 5 months (8)	6 - 7 months (4)	7 months (11)
Number of spawning periods	12 (1)	11 (1) (7)	12 - 18 (11)
Relative fecundity	883 - 1575 47 ≤ TL ≤ 73 (8)	766 - 2333 31 ≤ TL ≤ 46 (4)	1372 - 1754 122 ≤ TL ≤ 54 (11)
Sex ratio (in reproductive period)	-	1 m : 3 f (3)	1,5 m : 1 f (10) (12)
Migration / Sedentariness	genesic (6)	sedentary (5)	erratic (1)
Nesting substrata (valves)	abundant (sea) (9)	abundant (lagoon) (9)	rare (lagoon+sea) (1)
Population structure	unimodal (dynamic) (6)	unimodal (static) (3)	polymodal (static) (10)
Relative reproductive potentials of the population	important (8) (9)	important (4) (9)	important (11) (12)
Numerical density	high (2) (13)	high (2) (13)	low (2) (13)

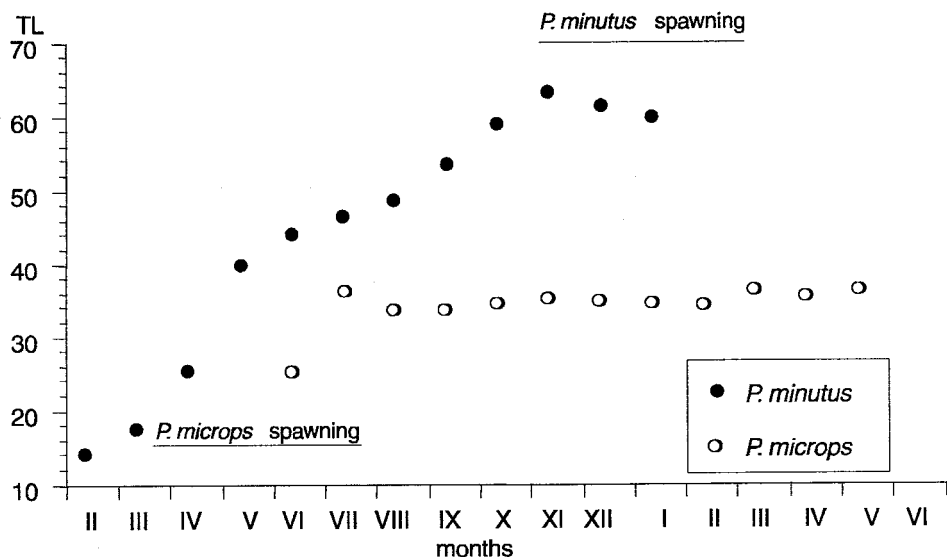


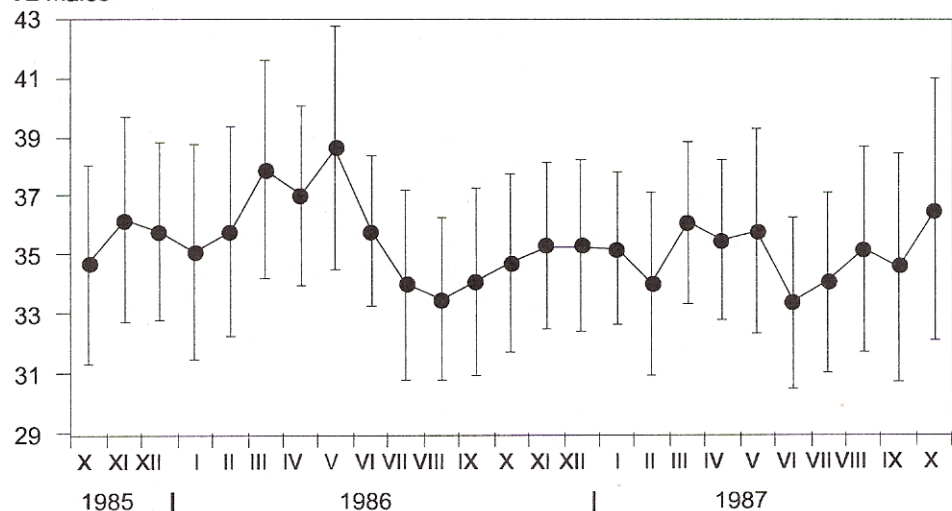
Fig. 4. Monthly mean linear growth (Total length: TL) and spawning periods of *Pomatoschistus minutus* and *P. microps* populations during a fictive year in Manguio lagoon

The offshore location of the spawning grounds provides *P. minutus* with a substantial capacity for colonising various seashore sites. This advantage became obvious after the anoxic crisis of August 1988, which annihilated the Manguio lagoon population (Quignard *et al.* 1989, Bouchereau *et al.* 1990b). Indeed, at the end of the spawning period (winter 1998-89) following this crisis, some 0⁺ fertilised by sea spawning parents originating from other lagoons were already colonising the Manguio lagoon, while the *P. microps* population, a sedentary species, remained very sparse (Bouchereau *et al.* 1990b). The migration bringing juveniles 0⁺ to occupy the lagoon at the end of winter came about mainly as a result of trophic opportunism, since its environment is relatively richer than that of the sea. This residence time in the lagoon has repercussions on a populational and individual level, as it enhances the reproductive capacities of the local population. Indeed, in the lagoon, the abundance of vegetation in the spring keeps predation within limits, and, depending on the hydroclimatic conditions, the amount of available food allows most specimens to reach their maximum size before their gonad products mature, and to acquire a fecundity and a nest-keeping ability at their highest potential.

Pomatoschistus microps

In the Mediterranean, the adaptive capacity (euryvalence) of this species seems superior to that of Atlantic specimens since, contrary to what happens there, the sedentarism (Table 1) remains even when the conditions in Manguio lagoon (frost,

TL males



TL females

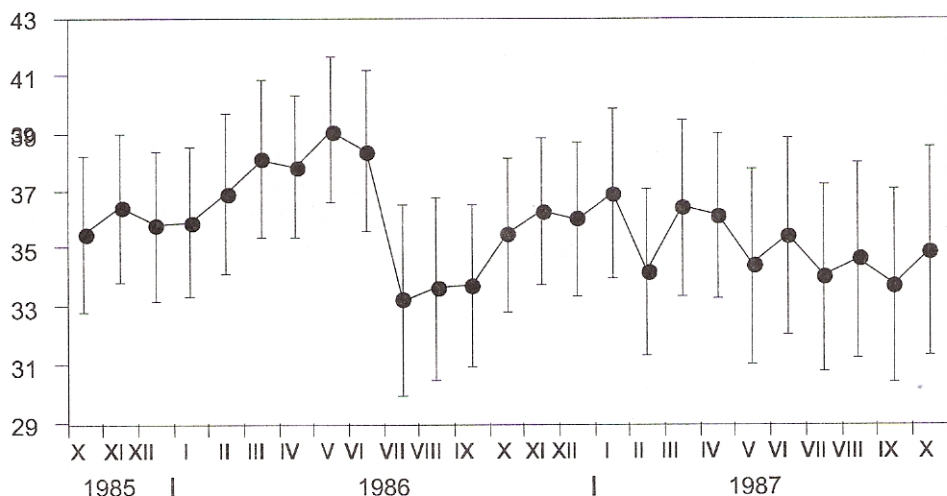


Fig. 5. Evolution, according to sex of *P. microps*, of monthly mean length (TL, in mm) and their standard deviation, from October 1985 to October 1987

dystrophy) become unfavourable (Bouchereau *et al.* 1989a, 1989b). This sedentarism is certainly favoured by the abundance of food and nesting substrata, such as valves (Bouchereau *et al.* 1991). *P. microps* uses several original tactics to remain permanently in the Mauguio environment. The most original one is certainly the onset of first sexual maturity (Table 1), enabling some specimens

to spawn for two seasons (Bouchereau *et al.* 1993a). The first time can take place four months after hatching, the second, at the age of twelve months (contracted iteroparity). The reproductive success is also optimised by a lengthening of the spawning period and individual fractioned laying. This tactic ensures that spawning coincides with environmental conditions propitious to embryonic or larval development. Even if we do not know the reason for its value and how it is maintained, the sex-ratio (Bouchereau *et al.* 1989a) favouring females (1:2.4 to 1:3.6) is also a factor intensifying their reproductive potential. The significantly larger number of females eliminates any competition between males to reach a spawn. Furthermore, in the case of nest destruction, it enables males to quickly restart the incubation cycle. Lastly, because this fish is basically dominated by the subsympatric species *P. minutus* (Edlung, Magnhagen 1981), sedentarism and the great statural stability of the population (Fig. 1) are no doubt the basis of its successful occupation of the lagoon. The importance of this tactic was revealed after the dystrophic crisis of August 1988, when the decimated *P. microps* population was overwhelmed by *P. minutus* for many months (Bouchereau *et al.* 1990b, 1993b). This example shows that the advantages of sedentarism have their limits.

Gobius niger

G. niger is a relatively euryvalent species, as is shown by its geographical distribution and its capacity to occupy both marine and lagoon environments. In the Mauguio lagoon, this fish shows an adaptability comparable (Table 1) to that of *P. microps*. It has a sexual life covering several spawning periods; this species is, moreover, sexually precocious, as the first maturity is reached at the age of one, whereas in the Atlantic it is reached at the age of two and sometimes three years. It also undergoes sequential individual spawning, which stretches over a long, six-month period (Joyeux *et al.* 1991b, 1992), and the statural stability in the Mauguio lagoon population (Joyeux *et al.* 1991a). *G. niger* differs (Table 1) by an absolute and relative fecundity superior to that of *P. microps* and *P. minutus* because of its sex-ratio favouring males (Joyeux *et al.* 1991a) and the presence of "parasitic" males (spawn sneaks). Both of these last characteristics could be taken as adaptative phenomena in the local environment, particularly in view of the scarcity of nesting sites. Indeed, they not only allow maximum occupation of available sites but they also ensure egg fertility; the "parasitic" males (egg sneakers) could compensate for a deficiency in nest keepers. In spite of these tactics and strategies, *G. niger* never reaches the population level of *P. minutus* and *P. microps*. The only explanation which can currently be considered is the relative scarcity of potential nests, whether in the lagoon or at sea, which could limit reproduction possibilities. With regard to *P. minutus* or *P. microps* this factor cannot be taken into consideration (Table 1), as in their case we find an important stratum or bed of potential nests at sea or in the lagoon (Bouchereau *et al.*, 1991).

Factors influencing the coexistence of the three species

Various elements favour the coexistence of these three species in Manguio lagoon that allows them to share the spatial and trophic resources during the year. The most important factor in this respect is certainly the genescic migration to sea of *P. minutus* (Bouchereau *et al.* 1989c), which prevents heavy competition between the three goby species present in the lagoon at a crucial time (Bouchereau *et al.* 1993b). This has noticeable repercussions on the *P. microps* population occupying the same environment and using the same trophic spectrum as *P. minutus* (Bouchereau *et al.* 1990b). Indeed, the departure of the latter coincides with the increasing needs of the growing *P. microps* population (Fig. 1) and promotes gonad maturity. However, during that season, the trophic richness in the lagoon is relatively low. The departure of *P. minutus* also has consequences for the *G. niger* population, whose spawning period begins in March. But the relative impact on this goby is certainly less as its quite large size enables it to explore a wider food spectrum. This departure also releases some space (not only nests) which can be used by the other two goby species during their spawning periods. The size/age differences existing at a given time between specimens of *P. minutus*, *P. microps* (Fig. 1) and *G. niger* (Table 1), induce in each species a shift in its temporal and spatial requirements, thus enhancing the likelihood of coexistence (Bouchereau *et al.*, 1993b) and diminishing competition.

The observed differences concerning each of the life cycles, encountered according to their geographical site, can be explained by the latitude of the Mediterranean area (Gulf of Lions), where daylight and thermal variations are less noticeable than at the northern limits of the three species' ranges, and by the hydroclimate of the area which governs the shifting and lengthening of spawning and growth times in these studied populations compared to those living in the Atlantic. Other differences arise from the general characteristics of the shallow and highly trophic lagoons, which attract inshore species such as *P. minutus*, and from the unstable hydroclimatic environment of the Manguio lagoon. The latter entails a greater euryvalence from sedentary species such as *P. microps* and *G. niger*. The configuration of the local biotope of the Manguio lagoon is also the source of other differences. The variable density of the vegetative structure in the lagoon affects of *P. microps* and *G. niger*. If there is, as in the Gulf of Lions, a reduction in nesting substrata (rocks) for *G. niger* prejudicial to the numerical success of this population in the lagoon, the muddy to silty habitat and abundant nesting sites are positively attractive to *P. microps* (Bouchereau *et al.* 1991). The lack of nesting sites and the quality of the nearby sea floor (deeper and clearer waters than in the lagoon, the presence of large Lamellibranchia valva) compels *P. minutus* to reproduce at sea, and therefore to migrate (Bouchereau 1994). The influence of dystrophic crises (Bouchereau *et al.* 1990b, 1993b) and the important

threat from predators in Mauguio lagoon (natural and by fishermen) are two of the main mortality factors in the area, causing a decrease in size and age at first sexual maturity of *P. microps* (Bouchereau *et al.* 1989b, 1993a) and *G. niger* (Joyeux *et al.* 1991b, 1992) compared to other populations.

The different tactics employed to occupy this lagoon can be explained by the different origins of the 3 species (2 Boreal, 1 Mediterranean). But the latitudinal position and the local biotope of Mauguio lagoon at the southern limit of the geographical range of the 3 species must also be taken into account.

SUMMARY

This work on three goby species living in a north Mediterranean lagoon has enabled us to clarify some aspects of our knowledge of their population through their biological characteristics. On the whole, the results confirm the great adaptability of these gobies and their potential capacity to occupy varying biotopes successfully. Depending on local climatic conditions, each population displays a particular strategy to ensure its reproductive success and to reside the longest possible time in the lagoon. *P. minutus* does not appear to attempt any adaptation to occupy the lagoon environment permanently but rather uses its ability to undertake trophic and genestic (for reproduction) migrations to ensure the success of the various stages of its life cycle in two different biotopes. *P. microps*, a more euryvalent species, uses its adaptability to exploit the lagoon to the full, and has become sedentary. The success of this strategy is expressed in the numerical importance of its population. Such success is less obvious in *G. niger* because of the scarcity of nesting sites, despite adaptative capacities similar to those of the biannual species *P. microps*. Finally, the coexistence of these three species in the lagoon is facilitated by the age and size-structure dynamics, and by the migration of *P. minutus*, which, while avoiding overlapping all year long, enables each species to make optimum use of space and the trophic environment.

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