Biology and life cycle of *Tmetonyx similis* (G. O. Sars, 1891) (Amphipoda, Lysianassidae), a scavenging amphipod from the continental slope of the Mediterranean

R. A. KAÏM-MALKA

*Université d’Aix-Marseille II, Centre d’Océanologie de Marseille, Marseille, France*

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**Abstract**

The present study focused on the biology and life cycle of *Tmetonyx similis*, a scavenging amphipod inhabiting the continental slope of the north-western Mediterranean. All the categories of individuals were observed in the samples. The emergence of offspring occurs in successive cohorts. The lifespan of the females is longer than that of the males, but the sex ratio is strongly in favour of the males. The fecundity was found to be lower than that of the other female crustaceans present in these samples. The growth pattern was modelled. A strong correlation was observed between the length and the weight of the animals collected. Several hypotheses are proposed to explain a sex ratio in favour of males. This result may be explained by a migratory process of the females of *T. similis*. A comparison of the reproduction strategy is given for the three main scavenger crustacean species (amphipods and isopod) collected in this area.

**Keywords:** Amphipod, biology, continental slope, life cycle, Mediterranean Sea, scavenger, *Tmetonyx similis*

**Résumé**

La biologie et le cycle de vie de l’amphipode nécrophage *Tmetonyx similis*, vivant sur la pente continentale, ont été étudiés. Les différentes catégories d’individus ont été récoltées au cours des prélèvements. Les juvéniles sont émis en cohortes successives. La durée de vie des femelles est plus longue que celle des mâles, mais la sex ratio est fortement en faveur des mâles. La fécondité est plus faible que celle de femelles appartenant à d’autres espèces de crustacés présentes dans ces prélèvements. Un modèle de croissance a pu être établi. Il existe une étroite corrélation entre la taille et le poids. Différentes hypothèses sont avancées pour expliquer une sex ratio en faveur des mâles. Ce résultat peut s’interpréter par l’existence d’un processus de migration des femelles de *T. similis*. La stratégie de reproduction des trois principales espèces de crustacés nécrophages (amphipodes et isopode) récoltées dans ce milieu est étudiée.

**Mots clés:** Amphipode, biologie, cycle, Méditerranée, nécrophage, pente continentale, *Tmetonyx similis*

**Introduction**

In deep-sea habitats, the food available becomes more scarce, and the search for food determines the animals’ activities, reproduction, development, juvenile recruitment and the
maintenance of the species. Scavenging is a widespread feeding mode in deep-sea species. Scavenger species play an important role because they contribute to the conversion and recycling of organic matter and pollutants. They also contribute to the exchange of material between the sea floor and the water column.

Amphipods are one of the main groups of scavengers in deep-sea habitats. Most of them belong to the family Lysianassidae. One of the best known scavenging species is the amphipod *Eurythenes gryllus* (Lichtenstein, 1822) (see Hessler et al. 1978; Ingram and Hessler 1983, 1987; Gage and Tyler 1991; Hargrave et al. 1995; Thurston and Bett 1995; Thurston et al. 1995).

Scavengers on the continental slope of the north-western Mediterranean were studied for 2 years, in 1990 and 1991. Seasonal samples were collected with baited traps (Kaïm-Malka 1997, 2003), and numerous crustaceans, isopods and amphipods belonging mainly to the species *Natatolana borealis* (Lilljeborg, 1851), *Scopelocheirus hopei* (A. Costa, 1851), and *Tmetonyx similis* (G. O. Sars, 1891) were collected.

Studies on *N. borealis* have improved our knowledge about the biology (Kaïm-Malka 1997), biochemistry (Kaïm-Malka 1993), behaviour (Macquart-Moulin and Kaïm-Malka 1994; Maebe 1994), and morphology (Maebe 1994; Kaïm-Malka et al. 1999) of this species. Studies on *S. hopei* have also extended biological data available on this scavenger amphipod species.

Besides these two species, which were the main species present in these samples, there was another less numerically predominant species. This was a Lysianassidae amphipod, *Tmetonyx similis* (G. O. Sars, 1891). This species is present within a wide bathymetric range, and is to be found in both *Posidonia* beds and coralline bottoms (Ledoyer 1968; Diviacco and Ruffo 1989) to 2540 m (Bellan-Santini 1998). It also has a wide geographical distribution, since it has been reported to occur in the Arctic Ocean, the North Sea, the Norwegian Sea, the English Channel, and on both the North American and European shores of the North Atlantic Ocean (Sars 1891; Norman 1900; Chevreux and Fage 1925; Moore 1984; Vader and Romppainen 1985; Diviacco and Ruffo 1989; Bellan-Santini and Ruffo 1998), in the western Mediterranean, and the Adriatic (Chevreux and Fage 1925; Picard 1965; Ledoyer 1970; Diviacco and Ruffo 1989; Bellan-Santini and Ruffo 1998). Reys (1960) reported that this species was present in the stomach of demersal fishes belonging to the genera *Raja* and *Trigla*. The species *T. similis*, along with other peracarid species, are known to damage seriously commercial fishes caught in nets and on long lines (Vader and Romppainen 1985).

In a previous study on *Tmetonyx similis*, collected in the Toulon area, the present author observed that the sexual maturation of the females is a complex process. The development of the oostegites involves a series of variably long sequences (Kaïm-Malka 2004). Except for the few studies mentioned above, there are very few biological data available on this species. Despite the small numbers present in these samples, it therefore seemed to be worth investigating some interesting biological aspects of *Tmetonyx similis*, based on the data obtained on the individuals collected in the Toulon Canyon.

**Materials and methods**

**Sites and techniques**

Samples were collected with baited traps (Kaïm-Malka 1997, 2003), at a station located at a depth of 500 m on the north-western Mediterranean slope in the Toulon Canyon. The baits consisted of heads of tuna (*Thunnus thynnus* L.), hake (*Merluccius merluccius* L.) and
anglerfish (Lophius piscatorius L.), and whole mackerel (Scomber scombrus L.). Samples were taken at 4-month intervals during the year 1990 and at the beginning of 1991. The sampling time ranged from 3 to 4 h, between 11:00 and 15:00 h (local time), depending on the weather conditions.

Processing

Animals were fixed with alcohol and weighed to the nearest 0.01 mg after being carefully dried on filter paper. They were measured dorsally from the extremity of the head to the extremity of urosome segment 3, using a digitizing tablet connected to a computer (Kaim-Malka 2003). The eggs carried by the females were also measured, taking the longer axis.

Sex was determined by external examination. Up to a size of 5.6 mm, animals were classified as juveniles, as they lacked secondary sexual characters, except for some of the females. The males were identified based on the presence of calceoli on the antennae and the presence of penile papillae on the ventral part of pereon segment 7. The stage of development reached by the females was determined by observing the oostegites on coxa 3 (Kaim-Malka 2004).

Size class determinations were performed using two methods: (1) by separating the size classes into Gaussian components (Harding 1949; Cassie 1954); (2) using the successive maximum method (Ghéno and Le Guen 1968; Daget and Le Guen 1975 in Barbault 1981). All of the animals collected during 1990–1991 were measured. For each category of them (juveniles, males, females), the measures obtained, for the whole cycle, were pooled. After this, the size classes of each category were separated from these pools of measures. This method permits all the size classes of each category of animal for the cycle to be known. It permits also all size classes to be taken into account, even if, for a given size class, no animal was present in a sample. Growth curves were established using the Von Bertalanffy (1938) growth pattern.

Results

All 1066 animals collected at this site were measured. Juveniles amounted to 9.94% of the collection, and the remaining 90.06% were adults; 54.97% were males (accounting for 61.04% of the adults) and 35.08% were females (accounting for 38.95% of the adults). Except for February 1990, three groups of individuals (juveniles, male and female adults) were always present in the samples (Table I).

| Date             | 23 February 1990 | 11 June 1990 | 7 October 1990 | 21 January 1991 | Total |
|------------------|------------------|--------------|----------------|-----------------|-------|
| Total            | 22               | 921          | 91             | 32              | 1066  |
| Juveniles        | 0                | 91           | 12             | 3               | 106   |
| Males            | 14               | 493 (449)    | 55             | 24              | 586   |
| Females          | 8                | 337 (117)    | 24             | 5               | 374   |
| M + F            | 22               | 830          | 79             | 29              | 960   |
| % Juveniles      | 0                | 9.88         | 13.19          | 9.37            | 9.94  |
| % Males          | 63.63            | 53.53        | 60.44          | 75.00           | 54.97 |
| % Females        | 36.37            | 36.59        | 26.37          | 15.63           | 35.08 |
| % M + F          | 100              | 90.12        | 86.81          | 90.63           | 90.06 |

The numbers in parentheses indicate the mature individuals, i.e. ♂>7.3 mm and ♀>7 mm. Under these conditions, the sex ratio was 3.84 in this sample.
Sexual development

Juveniles. The sizes of the juvenile animals collected ranged between 2.7 and 5.6 mm. Beyond this size, it was possible to determine the sex of each individual. In some cases, it was possible to distinguish the females at a size of less than 4.8 mm.

Males. The size of the males ranged between 5.5 and 11.6 mm. The penile papillae were observed on the ventral part of pereon segment 7. Calceoli were distinguished on antennae 1 and 2. These were rarely present in the young animals, and were more numerous and more easily visible in the adults (in the older ones) (Figure 1). Three other characteristics can be used to differentiate between the sexes:

- Antennae 1 (A1) can be longer than half the length of the flagellum of antennae 2.
- Antennae 2 (A2) are a little longer in males than in females, they reach the posterior margin of pereon segment 5.
- The lateral body surface of males is flat.

Three stages were defined in the males’ sexual maturation process, depending on the development of the sexual characteristics:

- Stage 1: this stage includes young animals, A1 reach half the length of the A2 flagellum; A2 reach the posterior margin of pereon segment 4. Calceoli are hardly visible at all on A2. The penile papillae are hardly visible on the ventral part of pereon segment 7.
- Stage 2: A1 reach half the length of the A2 flagellum; A2 reach the posterior margin of pereon segment 4 or the middle of pereon segment 5. Calceoli are more numerous and mainly located on the proximal half of the A2 flagellum. The penile papillae are visible on the ventral part of pereon segment 7, and more highly developed than in St 1.
- Stage 3: A1 reach half the length of the A2 flagellum; A2 reach the posterior margin of pereon segment 5. Calceoli are numerous, and easily visible along the whole A2 flagellum. The penile papillae are well developed and clearly visible on the ventral part of pereon segment 7.

Figure 1. Sexual characteristic of a male. Calceoli on antennae 2 of a male.
Females. The size of the females ranged between 4.8 (female Stage 2) and 12.4 mm (female Stage 5C). Females can be distinguished from males by the following characteristics:

- There are no calceoli on antennae 1 and 2.
- The A1 reach one-third to half of the length of the A2 flagellum.
- Antennae 2 never reach beyond the posterior margin of pereon segment 4.
- The lateral body surface of females is convex. This feature becomes visible from Stage 3, and increases with the age of the female and the development of the brood pouch.
- The presence of variably well-developed oostegites.

Depending on the stage of oostegite development reached, 11 stages were defined in the females’ sexual maturation process. The development of the oostegites, the various stages of development, and the females’ sexual maturation process have been studied separately in *Tmetonyx similis* (Kaim-Malka 2004).

Developmental pattern of the population

The length frequency histograms were polymodal (Figure 2). The various components of the population were determined using two methods: (1) by separating the size classes into Gaussian components (Harding 1949; Cassie 1954); (2) using the successive maximum method (Ghéno and Le Guen 1968; Daget and Le Guen 1975 in Barbault 1981). Under these conditions, it was possible to identify:

- Juveniles: between lengths of 2.66 and 5.6 mm eight size classes were defined (Figure 2; Table IIb). The last three classes sometimes included a few small females at oostegite development St 2 or St 2A (Kaim-Malka 2004). During this period, each individual probably effects seven moults before reaching a size of 5.6 mm (Table IIb). Judging from the size of the eggs, it seems probable that newly released juveniles are about 1.6–1.7 mm in length. The smallest individual collected was 2.66 mm, which indicates that some time had elapsed since it was released, and that it had already moulted several times. The first size classes were not captured. From these data, it is possible to conclude that: (1) between their release and reaching a size of 2.66 mm, juveniles probably effect five moults; (2) between their release and reaching a size of 5.43 mm, i.e. during the whole juvenile stage, individuals probably effect 12 moults (Table II).

- Males: the size of the males ranged between 5.5 and 11.6 mm. The males could be divided into 17 or 18 size classes, the first of which tended to merge with the last juvenile size class (Figure 2; Table III). During this period, each individual probably effects about 17 moults before reaching a size of 11.6 mm. On the whole, the males measuring between 2.66 and 11.6 mm were divided into 25 size classes (8 + 17), and probably effected 24 moults (Tables IIb, III). Between their release and reaching a size of 11.6 mm, the males probably effect 29 moults (Tables II, III). In the majority of the males, sexual maturity is probably reached 17 moults after their release, at a size of 7.3 mm (Table III).

- Females: the size of the females ranged between 4.8 mm (female Stage 2) and 12.39 mm. The females could be divided into 27 size classes, the first three of which tended to merge with the last three juvenile size classes (Figure 2; Table IV). During this period, each individual probably effects 26 moults before reaching a size of 12.4 mm (Table IV).
On the whole, the females measuring between 2.66 and 12.4 mm were divided into 32 size classes and they probably effected 31 moults. Between their release and reaching a size of 12.4 mm, the females probably effect 36 moults (Tables II, IV). Sexual maturity is probably reached 16 moults after their release, at a size of 7 mm (Table IV).

Classifying the animals into size classes was a much more complex task in the case of the females, due to the existence of many stages in the female sexual maturation process.
Table II. Juvenile size classes. A possible distribution of the size classes in the first juvenile stages (not collected), is indicated in Table IIa.

Table IIa

| Moult no. | 1 | 2 | 3 | 4 | 5 | 6 |
|-----------|---|---|---|---|---|---|
| Size-class no. | Cl 1 | Cl 2 | Cl 3 | Cl 4 | Cl 5 | Cl 6 |
| Mean | 1.7 | 1.85 | 2.1 | 2.3 | 2.5 | 2.7 |
| Growth factor | 1.088 | 1.135 | 1.095 | 1.087 | 1.08 |

Table IIb

| Moult no. | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|-----------|---|---|---|---|----|----|----|----|
| Size-class no. | Cl 6 | Cl 7 | Cl 8 | Cl 9 | Cl 10 | Cl 11 | Cl 12 | Cl 13 |
| % | 0.94 | 14.15 | 20.76 | 15.09 | 16.04 | 8.49 | 18.87 | 5.66 |
| N | 1 | 15 | 22 | 16 | 17 | 9 | 20 | 6 |
| Sum | 2.66 | 46.7 | 77.5 | 62.9 | 72.3 | 42.4 | 101.6 | 32.6 |
| Mean | 2.66 | 3.11 | 3.52 | 3.93 | 4.25 | 4.71 | 5.08 | 5.43 |
| SD | 0.000 | 0.106 | 0.119 | 0.149 | 0.128 | 0.154 | 0.106 | 0.103 |
| Range | 2.65–2.75 | 2.75–3.35 | 3.35–3.7 | 3.7–4.1 | 4.1–4.5 | 4.5–4.9 | 4.9–5.2 | 5.3–5.6 |
| Growth factor | 1.169 | 1.132 | 1.116 | 1.082 | 1.108 | 1.078 | 1.069 |
### Table III. Male size classes.

| Moult no. | Cl 13 | Cl 14 | Cl 15 | Cl 16 | Cl 17 | Cl 18 |
|-----------|-------|-------|-------|-------|-------|-------|
| %         | 0.170 | 1.195 | 2.901 | 1.706 | 2.389 | 3.242 |
| N         | 1     | 7     | 17    | 10    | 14    | 19    |
| Sum       | 5.5   | 39.6  | 103.5 | 64.3  | 95.1  | 136.6 |
| Mean      | 5.5   | 5.66  | 6.09  | 6.43  | 6.79  | 7.19  |
| SD        | 0.000 | 0.098 | 0.127 | 0.082 | 0.114 | 0.11  |
| Range     | 5.5–5.6 | 5.5–5.85 | 5.85–6.35 | 6.35–6.65 | 6.65–7.05 | 7.05–7.45 |
| Growth factor | 1.024 | 1.076 | 1.056 | 1.056 | 1.059 | 1.058 |

| Moult no. | Cl 19 | Cl 20 | Cl 21 | Cl 22 | Cl 23 |
|-----------|-------|-------|-------|-------|-------|
| %         | 5.802 | 8.020 | 16.212 | 32.594 | 17.235 |
| N         | 34    | 47    | 95    | 191   | 101   |
| Sum       | 258.8 | 375.4 | 798   | 1700  | 955.4 |
| Mean      | 7.61  | 7.99  | 8.40  | 8.90  | 9.46  |
| SD        | 0.125 | 0.13  | 0.171 | 0.198 | 0.142 |
| Range     | 7.45–7.85 | 7.85–8.25 | 8.15–8.75 | 8.55–9.35 | 9.15–9.75 |
| Growth factor | 1.050 | 1.051 | 1.060 | 1.063 | 1.051 |

| Moult no. | Cl 24 | Cl 25 | Cl 26 | Cl 27 | Cl 28 | Cl 29 | Cl 30 |
|-----------|-------|-------|-------|-------|-------|-------|-------|
| %         | 4.266 | 1.195 | 1.877 | 0.683 | 0.170 | 0.170 | 0.170 |
| N         | 25    | 7     | 11    | 4     | 1     | 1     | 1     |
| Sum       | 248.5 | 71.4  | 115.3 | 42.8  | 11.1  | 11.4  | 11.6  |
| Mean      | 9.94  | 10.20 | 10.48 | 10.70 | 11.1  | 11.4  | 11.6  |
| SD        | 0.091 | 0.058 | 0.075 | 0.000 | 0     | 0     | 0     |
| Range     | 9.75–10.15 | 10.15–10.35 | 10.35–10.65 | 10.65–10.95 | 10.95–11.25 | 11.25–11.55 | 11.55–11.85 |
| Growth factor | 1.026 | 1.027 | 1.021 | 1.037 | 1.027 | 1.018 |
### Table IV. Female size classes.

| Moult no. | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
|----------|----|----|----|----|----|----|----|----|----|
| Size-class no. | Cl 11 | Cl 12 | Cl 13 | Cl 14 | Cl 15 | Cl 16 | Cl 17 | Cl 18 | Cl 19 |
| % | 1.070 | 1.070 | 2.941 | 5.08 | 6.417 | 3.743 | 2.406 | 12.032 | 8.824 |
| N | 4 | 4 | 11 | 19 | 24 | 14 | 9 | 45 | 33 |
| Sum | 19.6 | 20.8 | 61.2 | 114.4 | 153.2 | 93.8 | 62.1 | 324 | 250.8 |
| Mean | 4.90 | 5.20 | 5.56 | 6.02 | 6.38 | 6.70 | 6.90 | 7.20 | 7.60 |
| SD | 0.0816 | 0.0816 | 0.0924 | 0.1316 | 0.1204 | 0.0784 | 0.05 | 0.1314 | 0.1118 |
| Range | 4.8–5.05 | 5.05–5.35 | 5.35–5.75 | 5.75–6.2 | 6.2–6.6 | 6.6–6.8 | 6.8–7 | 7–7.4 | 7.4–7.8 |
| Growth factor | 1.061 | 1.069 | 1.083 | 1.060 | 1.050 | 1.030 | 1.043 | 1.055 | 1.039 |

| Moult no. | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 |
|----------|----|----|----|----|----|----|----|----|----|
| Size-class no. | Cl 20 | Cl 21 | Cl 22 | Cl 23 | Cl 24 | Cl 25 | Cl 26 | Cl 27 | Cl 28 |
| % | 7.219 | 7.754 | 10.963 | 2.941 | 4.813 | 1.872 | 2.674 | 6.417 | 2.941 |
| N | 27 | 29 | 41 | 11 | 18 | 7 | 10 | 24 | 11 |
| Sum | 213.3 | 237.7 | 353.1 | 96.8 | 162 | 64.4 | 93.9 | 235.6 | 110.9 |
| Mean | 7.90 | 8.20 | 8.61 | 8.80 | 9.00 | 9.20 | 9.39 | 9.82 | 10.08 |
| SD | 0.1387 | 0.118 | 0.1418 | 0.0775 | 0.0686 | 0.0577 | 0.0876 | 0.1341 | 0.0751 |
| Range | 7.7–8.1 | 8–8.4 | 8.4–8.8 | 8.7–8.9 | 8.9–9.1 | 9.1–9.3 | 9.3–9.55 | 9.55–10.05 | 10.05–10.25 |
| Growth factor | 1.038 | 1.050 | 1.022 | 1.023 | 1.022 | 1.021 | 1.046 | 1.026 | 1.022 |
Table IV. (continued).

| Moul no. | 29  | 30  | 31  | 32  | 33  | 34  | 35  | 36  | Cl 37 |
|----------|-----|-----|-----|-----|-----|-----|-----|-----|-------|
| %        | 2.406 | 1.337 | 1.872 | 1.070 | 0.535 | 1.337 | 0   | 0   | 0.267 |
| N        | 9   | 5   | 7   | 4   | 2   | 5   | 0   | 0   | 1     |
| Sum      | 92.7 | 52.5 | 75  | 43.8 | 22.6 | 58.4 | 0   | 0   | 12.39 |
| Mean     | 10.30 | 10.50 | 10.71 | 10.95 | 11.3 | 11.68 | 0   | 0   | 12.39 |
| SD       | 0.05 | 0.0707 | 0.069 | 0.1291 | 0   | 0.1643 | 0   | 0   | 0     |
| Range    | 10.25–10.45 | 10.45–10.65 | 10.65–10.85 | 10.85–11.15 | 11.15–11.45 | 11.45–11.75 | 11.75–12.05 | 12.05–12.35 | 12.35–12.65 |
| Growth factor | 1.019 | 1.020 | 1.022 | 1.032 | 1.034 |
The distribution of the females in terms of their sexual maturation stage (based on coxa 3) is given in Table V. Note the large number of size classes (21) obtained in the case of the females at Stage 5C, which were sexually mature females bearing eggs.

**Sex ratio**

In the samples collected, the males of *T. similis* are always present, and males were always more numerous than females (Table I). Apart from the sample collected in June 1990, the number of individuals belonging to the species *T. similis* was not very large. It is therefore impossible to reach any definite conclusions as to whether this sex ratio was representative of the species as a whole. However, in the June 1990 sample, where a large number of these individuals was collected, the sex ratio worked out at 1.46 in the whole population of individuals (493 males, 337 females). From the reproductive point of view, the most important sexual ratio is the number of mature males to mature females. This ratio was based on the number of males length $\geq 7.3$ mm in size (449 individuals) and the number of females at St 5–8 length $\geq 7$ mm in size (117 individuals), and worked out at 3.84, strongly in favour of the males.

**Size-to-weight ratio**

The size-to-weight ratio was established using the 909 animals collected on 11 June 1990. This sample included 88 juveniles, 488 males, and 333 females. The difference with Table I is due to the rejection of some animals in poor condition. The weights ranged from 0.14 mg in the case of a juvenile measuring 3.1 mm to 24.33 mg in that of a female measuring 12.39 mm. The size-to-weight ratio is given by the following formula: $W = aL^b$, where $W$ is the weight in mg; $L$, the length in mm; and $a$ and $b$ are calculated coefficients. In the whole sample, this relationship was found to be (1) $W = 0.017L^{3.003}$. These results are given in detail in Table VI and Figure 3.

- **Juveniles.** The weights of the juveniles ranged from 0.14 mg ($L=3.1$ mm) to 3.62 mg ($L=5.0$ mm). The best fitting relationship between 2.7 and 5.6 mm was (2) $W = 0.0052L^{3.798}$. 

| Stage coxa 3 | Size (mm) | Classes | No. of classes |
|--------------|-----------|---------|----------------|
| St 0         | 6.8       | 11–16   | 6              |
| St 2(−)      | 6         | 11–14   | 4              |
| St 2         | 4.8–7.7   | 11–19   | 9              |
| St 2A        | 4.9–8.6   | 11–22   | 12             |
| St 3         | 5.6–8.8   | 13–23   | 11             |
| St 3A        | 5.9–9.1   | 14–24   | 11             |
| St 4         | 6.4–10.3  | 15–29   | 15             |
| St 4A        | 6.9–10.3  | 17–29   | 13             |
| St 5A–B      | 7–11.7    | 17–34   | 18             |
| St 5C        | 7–12.4    | 17–37   | 21             |

Note the large number of size classes (21) obtained among the females at Stage 5C (St 5C).
The weights ranged between 2.39 mg ($L=5.5$ mm) and 19.41 mg ($L=10.6$ mm).

The best fitting relationship between 5.5 and 11.4 mm was $W=0.0495 L^{2.5011}$.

The weights of the females ranged from 1.99 mg ($L=4.9$ mm) to 24.33 mg ($L=12.39$ mm). The best fitting relationship between 4.8 and 12.4 mm was $W=0.0269 L^{2.7946}$.

- **Males.** The weights ranged between 2.39 mg ($L=5.5$ mm) and 19.41 mg ($L=10.6$ mm).
  - The best fitting relationship between 5.5 and 11.4 mm was $W=0.0495 L^{2.5011}$.
- **Females.** The weights of the females ranged from 1.99 mg ($L=4.9$ mm) to 24.33 mg ($L=12.39$ mm). The best fitting relationship between 4.8 and 12.4 mm was $W=0.0269 L^{2.7946}$.
Fecundity

During the year 1990–1991, 374 females were collected in the Toulon Canyon (Table I), 89 of which were ovigerous females (Stage 5C). Their sizes ranged between 7 and 12.39 mm, which corresponds to 21 size classes from size class 17 to 37 (Table V). The egg sizes measured on the long axis ranged between 519 µm (produced by a female 8.6 mm in size with an incomplete brood of three eggs, collected on 11 June 1990) and 1030 µm (produced by a female 9.7 mm in size with a complete brood of six eggs, collected on 7 October 1990). However, the most frequent sizes ranged between 700 and 800 µm.

The fecundity of this species is difficult to assess because there were too few females with an entire brood (40). The number of eggs produced by a female was variable, and it is possible to distinguish between two kinds of broods:

- The minimum brood: this is the smallest number of eggs laid by a female of a given size. This number ranged between four eggs per brood (produced by a female 8 mm in size) and nine eggs per brood (produced by a female 11.8 mm in size).
- The maximum brood size: this corresponds to the largest number of eggs produced by a female of a given size. This number ranged between seven eggs per brood (produced by a female 8.4 mm in size) and 13 eggs per brood (produced by a female 11.7 mm in size).

In each kind of brood, it was possible to establish a correlation between the size of the female and the number of eggs per brood. Based on these correlations, between reaching lengths of 7 and 12.39 mm, a female could produce 117–181 eggs (Figure 4; Table VII).

![Figure 4. Maximum and minimum number of eggs per female, depending on the size. L, length in mm; N, number of eggs.](image-url)
Lifespan

Ovigerous females and juveniles were present in all the samples collected, all the year round. This means that the individuals in each generation were born at very different times in successive cohorts. By applying the Von Bertalanffy (1938) growth pattern, \( L_t = L_\infty [1 - e^{-k(t-t_0)}] \), to the data obtained on all the animals of each sex, an equation and a growth curve were obtained (Figure 5), from which it was possible to estimate the potential lifespan of each sex. It was also possible to estimate the age of each individual, and the duration of each of the main stages in the species’ life from these equations (Table VIII).

In the majority of the males (length ≤ 10.7 mm; Table III), the lifespan was estimated to be 35–37 months (around 3 years). The largest male (12.1 mm in length) collected in Planier Canyon, was estimated to be aged 55–56 months (4 years and 7.5 months) (Figure 5; Table VIII).

In the majority of the females (length ≤ 11.68 mm; Table IV), the lifespan was estimated to be 47 months (3 years and 11 months), i.e. around 1 year longer than that of the males. The largest female collected (12.39 mm in length) was estimated to be aged 64 months (5 years and 4 months) (Figure 5; Table VIII). It is possible that the lifespan of the females may be greater because, during their sexual maturation, some moult may occur without any size increase (Kaim-Malka 2004).

Depending on the sex, five or six generations occurred during the observation period in the Toulon Canyon (Figure 6).

| Class no. | Mean size | Range  | Minimum | Maximum |
|-----------|-----------|--------|---------|---------|
| 12        | 6.9       | 6.8–7.05| 2       | 2       |
| 13        | 7.2       | 7.05–7.45| 2       | 2       |
| 14        | 7.6       | 7.45–7.8| 3       | 3       |
| 15        | 7.9       | 7.7–8.1 | 3       | 4       |
| 16        | 8.2       | 8–8.45  | 3       | 5       |
| 17        | 8.61      | 8.45–8.8| 4       | 6       |
| 18        | 8.8       | 8.47–8.95| 4       | 6       |
| 19        | 9         | 8.95–9.15| 5       | 7       |
| 20        | 9.2       | 9.15–9.35| 5       | 7       |
| 21        | 9.39      | 9.35–9.55| 5       | 8       |
| 22        | 9.82      | 9.55–10.05| 6       | 9       |
| 23        | 10.08     | 10.05–10.25| 6       | 9       |
| 24        | 10.3      | 10.25–10.45| 6       | 10      |
| 25        | 10.5      | 10.45–10.65| 7       | 10      |
| 26        | 10.71     | 10.65–10.85| 7       | 11      |
| 27        | 10.95     | 10.85–11.15| 7       | 12      |
| 28        | 11.3      | 11.15–11.45| 8       | 12      |
| 29        | 11.68     | 11.45–11.75| 8       | 13      |
| 30        | 11.9      | 11.75–12.05| 9       | 14      |
| 31        | 12.2      | 12.05–12.35| 9       | 15      |
| 32        | 12.39     | 12.35–12.65| 9       | 15      |
| Total     |           |         | 117     | 181     |
Only a small number of individuals was collected in this study, except for the June 1990 sample (Table I). It is therefore difficult to reach any conclusions about the development of the various groups during the year 1990. However, the following main points are worth mentioning:

Table VIII. Potential lifespan of *Tmetonyx similis* (estimated duration of the main stages of development in this species).

| Stages                  | Males          | Females        |
|-------------------------|----------------|----------------|
| Releasing               | 1.68           | 1.7            |
| In sample               | 2.66           | 2.66           |
| Juvenile in sample      | 2.66–5.43      | 2.66–4.8       |
| Total juvenile          | 1.68–5.43      | 1.7–4.8        |
| Sexual maturation       | 5.43–7.3       | 4.8–7          |
| Releasing–end maturation| 1.68–7.3       | 1.7–7          |
| Lifespan                | \( L \leq 10.7 \) | \( L \leq 11.68 \) |
| Maximum lifespan        | 12.1           | 12.39          |

*Life cycle*

Only a small number of individuals was collected in this study, except for the June 1990 sample (Table I). It is therefore difficult to reach any conclusions about the development of the various groups during the year 1990. However, the following main points are worth mentioning:
Juveniles seem to be present all the year round (this is the case in the Planier Canyon). However, they were caught only at lengths of 2.66 mm upwards.

Males were present all the year round, and they were always more numerous than the females and juveniles.

Females without eggs, and ovigerous females, were permanently present. This means that the reproduction process occurs all the year round.

The males belonging to one generation, M0, which had reached sexual maturity, would have to compete with the younger males M(+1) of the following generation, as well as with older males belonging to generation M(−1) (Figure 7).

The females belonging to generation F0 reached sexual maturity a little before the males of the same generation (M0). Most of them would be fecundated by males belonging to the same generation (M0). The females have a greater lifespan than the males (see above), and therefore, after reaching a certain size, they will be fecundated by males of a larger size belonging to generation M(+1), or exceptionally by males belonging to generations M0 and M(−1) showing a greater longevity than their conspecifics.

At the beginning of their reproduction period, the smaller generation F0 females will be fecundated by the larger generation M(−1) males, or possibly by young males M0 of the same generation, born a little before them and reaching maturity at the same time. To
understand the latter possibility, it should be remembered that the reproduction process occurs all the year round (Figure 7).

**Discussion**

*Bias linked to the samples*

Samples collected with baited traps are always biased, but this is the only method available for collecting scavengers in sufficiently large numbers. The following comments should be made about the use of this sampling method:

- The catch is limited to some scavenger species attracted by the bait used.
- Some stages in the development of the species may escape the sample, either because the bait used does not attract some particular classes of specimens, such as juveniles with a different diet from that of the adults, or fasting individuals (some females can fast during the brooding period).
- Some kinds of individuals may escape the traps because they are located in other areas as the result of migrations. This is probably the case with some females about to release their eggs, and that of newly released juveniles in the first stages, which will not be caught.

*Figure 7. Development of the various male and female generations.*
Based on what is known about the behaviour of the species and the method of collection used here, it can be said that the present study deals with only part of the entire population corresponding to very specific conditions.

Presence

Previous authors have mentioned that this species was collected in large numbers along with the fishes caught in nets or on long lines. The number of specimens collected using other sampling techniques was very small indeed. In the present study, the fishes used to bait the traps were not always of the same kind, since this depended on the supplies available. The differences between the kind of bait used may partly explain the differences in the size of the catch (Kaïm-Malka 1997, 2004).

Size classes

The reason why two methods were used to determine the size classes was that the Harding method does not include those classes containing no individuals, particularly in the case of the largest size classes, which often contained very few if any individuals, and this reduces the number of classes. As mentioned above, the number of moults effected by the females and their potential lifespan are minimum assessments because they may have effected some moults without any corresponding size increase. The beginning of each stage in the sexual maturation of *T. similis* females has been defined on the basis of the oostegites on coxa 3 (Kaïm-Malka 2004).

Absence of the first juvenile stages in the samples

The juveniles of amphipods have often been studied. The main points known so far about the juveniles of scavenger species are as follows:

- Several possible reasons have been given for the absence of the juveniles of some scavenger species, such as: differences in feeding behaviour between juveniles and adults, energy savings, predation risk reduction and cannibalism (Bregazzi 1972; Johnson 1976; Hessler et al. 1978; Thurston 1979; Shafir and Field 1980; Lampitt et al. 1983; Kaïm-Malka 1997).
- Rakusa-Suszczewski (1982) indicated that the females of *Orchomene plebs* (Hurley, 1965) may effect vertical migrations during their biological cycle.
- Slattery and Oliver (1986) observed a habitat segregation between “the juveniles restricted to the shallow site … and the older animals at the deeper sites”.
- Poltermann (2001) observed the existence of a wide food spectrum in three necrophagous amphipod species in the Arctic area.

In the Introduction to this study, it was mentioned that *Tmetonyx similis* has a wide bathymetric range, since it can be collected at low tide in gravels (Chevreux and Fage 1925), in *Posidonia* beds and coralline bottoms (Ledoyer 1968; Bellan-Santini and Ledoyer 1972; Diviacco and Ruffo 1989), to 2540 m (Bellan-Santini 1998).

Based on all these findings, it is possible that when they are about to release their eggs, the females of this species may effect a migration towards the shallow waters constituting the most suitable environment for their hatchlings, and the early post-hatchlings of *T. similis* spend their early lives in shallow depths. In these sites, the newly released
juveniles probably ingest foods compatible with their enzymatic digestive equipment, and their diet probably differs from the adult diet. Later on these juveniles may migrate towards deeper areas (or towards “well areas”) where they will adopt another lifestyle. This ecological change may be correlated with physiological changes such as a diversification or an extension of the digestive enzyme spectrum, in keeping with a scavenger diet.

This would mean that relative to the whole population, a habitat segregation may exist for parts of the juveniles and females of *T. similis*, and this behaviour may be accompanied by physiological characters. This process would reduce intraspecific competition.

**Sex ratio**

The authors of many previous studies on Amphipoda have reported that in many cases, the ratio $\frac{M}{F}$ is near to 1:1, with the possibility of variations for many reasons (see Kaïm-Malka 2003). In many cases, the sex ratio is in favour of the females and many hypotheses have been put forward to explain this imbalance, based on seasonal variations, the lesser resistance of the males, sexual inversion, monogeny, photoperiod, temperature, and so on. A sex ratio in favour of the females is thought to promote the survival of the species in question (see Kaïm-Malka 2003).

The occurrence of a sex ratio in favour of the males is more unusual judging from the literature (Bone 1972; Bregazzi 1972; Rakusa-Suszczewski 1982; Ingram and Hessler 1987). An increase in the number of males has been thought to increase the chance of the eggs being fertilized when the mature females are ready to spawn. Bone (1972) considered that this particular sex ratio may be the result of a selective predation of large-sized individuals; the absence of pre-copulatory pairing may increase the chance of the two sexes meeting during a possibly short period during which the female is receptive.

However, the explanation can be ruled out that males are less resistant than females to environmental conditions, and that an increase in the number of males will therefore compensate for the selective loss of males.

Apart from this “useful” interpretation of the sex ratio in favour of the males, it might be worth looking at how the balance between the sexes may be controlled, and how the males can come to be more numerous than the females in the environment. There are two approaches which shed some light on this point: (1) the genetic approach; (2) the biological approach.

**Genetic hypotheses.** The conclusions developed in this paragraph are necessarily limited, because they need to be supported by studies on samples containing more numerous specimens. In the present samples, the *T. similis* males were always present, and they were always more numerous than the females (Table I). In June 1990, the sex ratio was 3.84, very strongly in favour of the males. This finding can be interpreted in many ways: (1) the fecundity of the males is low; (2) the chances of males meeting females are low; (3) the fecundity of the females is low, and they produce only a few eggs, which seems to be the case. The survival of this species suggests that all its egg-laying activities are carried out successfully. Under these conditions, the excess males might be necessary to ensure the complete success of the fecundation process.

Many hypotheses about monogeny could be mentioned here, but in the present state of the art, it is impossible to evaluate them, because genetic studies are required for this purpose.
The first of these hypotheses refers to a process studied by Ginsburger-Vogel (1989) in the talitrid amphipod _Orchestia gammarella_ (Pallas, 1766) (cited as _O. gammarellus_). According to this author, variations in the sex ratio may be determined by the parent male (male arrhenogeny process). In cases where males are more numerous than females, variations would be caused by a male trait exclusively transmitted by the males. All the embryos receiving this trait would become males and continue to transmit the trait to subsequent generations. However, the ecology and ethology of _Orchestia_ and _Tmetonyx_ are so different that it is difficult to compare them.

The length of the intermoult period increases gradually with time. The length of the gestation period can vary, depending on the size, and hence on the age, of the female. The younger (and smaller) females would have a shorter gestation period and would produce females. The older females would have a longer gestation period and would produce males. This process would lead to a more frequent and earlier production of female than of males (but not necessarily more important numerically); the frequency of the females coming into the environment, associated with their greater longevity, may compensate for the females’ low fecundity.

Another hypothesis, which is similar to the previous one and again involves a process of monogeny, is that only one sex is produced at each egg-laying event, and that the sex would depend on the brood: the minimum brood would correspond to females, and the maximum brood to males.

Legrand and Juchault (1994) have stated that “l’une des conséquences de la monogénie est de rendre très rares les croisements consanguins et donc de favoriser l’hétérosis” (“One of the results of monogeny is that it makes the occurrence of consanguinity very rare and thus favours heterosis”).

**Biological hypotheses.** Many studies on amphipod populations have documented the factors responsible for seasonal variations in the numbers of males. One of these factors is the occurrence of seasonal female migrations towards other areas, at the time of egg release. The areas where the newly released juveniles will develop are probably characterized by the existence of a sufficiently large food supply for the juveniles, and the low risk of predation or cannibalism, and one of the advantages of these migratory processes is that they reduce intra-specific competition.

Hessler et al. (1978), Thurston (1979), Smith and Baldwin (1984), and Christiansen (1996) studied various amphipod species and reported that the distribution depends on the sex of the specimens. The males and females are not located at the same level in the water column.

This pattern may also occur in _T. similis_, which has been reported to display a wide bathymetric range, and to be present in some very different places. The females may release juveniles in shallow waters, and later on, juveniles and females may return to deeper areas. It is worth noting that in this study, no ovigerous females were observed carrying embryos or juveniles about to be released. This argues in favour of the idea that female migrations occur towards other areas, at the time of release.

This “biological hypothesis” might also explain the preponderance of males in some places. Some of the females may be permanently established in another place because reproduction is a permanent process. Under these conditions, the diet of the species is not strictly necrophagous, and its spectrum will be wider, at least in the case of the females, which will enable them to live temporarily in other places. The presence of ovigerous
T. similis females in our samples means that in this species no fasting occurs during the period of gestation. The females go on feeding throughout their lives.

We do not have sufficient data so far to be able to argue for or against any of these hypotheses. In the case of the “biological hypothesis”, presented above, although it has been established that females do effect migrations, it is not possible to state:

- whether the normal sex ratio is near to 1:1;
- whether there is a monogeny in favour of the males;
- whether or not a biological artifact may be involved, which means that the real facts of the picture may be masked by the migration process. We may in fact be dealing here with a process of monogeny in favour of the females, masked by a migratory process. In this case, the truth may lie in the opposite direction (i.e. there is a monogeny in favour of the males), because some of the females have migrated elsewhere, and diet may have changed during the period prior to the release of the brood. During the subsequent moult and postmoult periods, the animals do not feed and the females are therefore not caught.

On account of the absence of specimens in the first juvenile stages in the samples, the small numbers of females collected, and the wide bathymetric range of the species, the variations in the sex ratio in *Tmetonyx similis* could be interpreted either in biological terms, based either on the migratory process, or on the differential distribution observed, depending on the sex or the stage of development of the individuals.

In the case of *Scopelocheirus hopei*, a species associated with *Tmetonyx similis* in the samples collected, the “genetic hypothesis” seems to provide the best means of accounting for the sex ratio variations observed in this species (Kaim-Malka 2003), because in the case of this species, all the stages and sizes of individuals from release onwards are to be found in the same place.

**Fecundity**

The reproduction strategy used by *T. similis* consists of frequent successive broods, containing only a few offspring. It should be remembered that the ovigerous females collected in the Toulon Canyon fell into 21 size classes (Table V). In the Mediterranean sea, the females collected reach a smaller maximum size (12.4 mm) than those of individuals collected in the Atlantic Ocean or in the North Sea (14 mm reported by Sars 1891; Chevreux and Fage 1925; 15 mm reported by Lincoln 1979). These size differences raise the question as to whether the fecundity of this species is the same in all these geographical areas.

**Simultaneous presence of many necrophagous species**

In the Toulon Canyon, the samples collected were characterized by the presence of three main scavenger species: *Natatolana borealis, Scopelocheirus hopei, and Tmetonyx similis*, all of which have been studied (Kaim-Malka 1997, 2003, this work). The feeding strategies used seem to differ from one species to another. It is possible to distinguish here between two cases:

1. *The first juveniles stages were not captured.* The diet of the juveniles is probably different to the adult diet. This is so in the case of the isopod *Natatolana borealis* and in that of the
amphipod *Tmetonyx similis*. *Natatolana borealis* has an annual reproductive cycle (Kaim-Malka 1997). Reproduction seems to continue all the year round in the case of *Tmetonyx similis*.

2. **Juvenile and adults at all stages were captured.** This means that the juveniles and adults have the same diet. This is also so in the case of the amphipod *Scopelocheirus hopei*. Reproduction continues in this species all the year round (Kaim-Malka 2003). In this latter case, it is possible that intra- and interspecific food competition may be stronger.

It has been reported that in *Tmetonyx similis* the sexual maturation process of the females can be accelerated or slowed down, probably depending on the food supply in the environment (Kaim-Malka 2004). A similar mechanism probably exists in the amphipod *Scopelocheirus hopei* (Kaim-Malka 2003).

Poltermann (2001) has reported that in four necrophagous amphipod species inhabiting Arctic areas, the availability of a wide food spectrum reduces intra- and interspecific competition which occurs in environments where food resources are limited. A wider spectrum, or a smaller one possibly reduced to one specific substance, would allow the simultaneous presence of many necrophagous species (see Ingram and Hessler 1983; Lowry and Stoddart 1989; Meador 1989; Nickell and Moore 1991; Moore and Wong 1995). In the same way, when several species are present in the place, the release of the juveniles in another place reduces competition for food (Bregazzi 1972), and thus increases the chances of survival of the species.

These observations may partly explain the co-existence of *Tmetonyx similis*, *Scopelocheirus hopei*, and *Natatolana borealis*, on the continental slope of the western Mediterranean.

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