REPORT

Regional warming-induced species shift in north-west Mediterranean marine caves

P. Chevaldonné* and C. Lejeusne

UMR CNRS 6540 'DIMAR',
Centre d'Océanologie de
Marseille, Station Marine
d'Endoume, Rue de la Batterie
des Lions, 13007 Marseille,
France
*Correspondence: E-mail:
chevaldonne@com.univ-mrs.fr

Abstract

The north-western Mediterranean Sea's high biodiversity originates from a mixture of temperate and subtropical species. Large-scale warming has been detected through northward range shifts of 'warm-water' species, and mass-mortality events for 'cold-water' invertebrates. Marine caves are affected in a more subtle way. By monitoring endemic species of cave mysids (Crustacea) and comparing our results with data in the literature, we observed a strong decline in one species, coupled with the success of another. Near Marseille (France), this phenomenon began while two major thermal anomalies were reported. Different tolerances to temperature were demonstrated by both the species distribution ranges and laboratory experimentation. We provide a possible physiological explanation for populations of cold stenothermal species of endemic cave mysids being replaced by congeners of warmer affinities, with a high risk of extinction. We also found strong support for the view that Mediterranean marine biodiversity is already under the threat of global warming.

Keywords

Hemimysis, marine caves, Mysidacea, NW Mediterranean, regional warming, species shift, thermotolerance.

Ecology Letters (2003) 6: 371–379

INTRODUCTION

The north-western Mediterranean Sea is biologically diverse because of the presence of both temperate and subtropical species, and also because of its complex geological history, a legacy from the Tethys Ocean (Bianchi & Morri 2000). Recent evidence however undoubtedly points to large-scale warming of this region (Bethoux *et al.* 1990; Astraldi *et al.* 1995; Bethoux & Gentili 1996; Walther *et al.* 2002), although Morri & Bianchi (2001) often found difficulties in distinguishing modifications caused by climate change from local human disturbance. The biological response observed so far includes the northward migration of conspicuous species of warmer affinities (Bianchi & Morri, 1994a; Francour *et al.* 1994), and more recently the mass mortalities of 'cold-water' sessile macro-invertebrates during episodes of unusually long warm and quiet weather (Cerrano *et al.* 2000; Perez *et al.* 2000; Romano *et al.* 2000; Garrabou *et al.* 2001).

According to Southward *et al.* (1995) followed by Bianchi (1997), climate change can influence marine communities by a combination of: (1) direct effects on the organisms, such as the influence of temperature on survival, reproductive success, dispersal or behaviour, (2) effects mediated by biotic interactions, e.g. conferral of competitive advantage to one of a pair of overlapping species, and (3) indirect effects through ocean currents, whose patterns may be altered. In the Mediterranean, only the latter have been adequately described (Astraldi *et al.* 1995; Aliani & Meloni 1999). Here, we present the first convincing illustration of the first and, possibly, the second mechanism.

Cave communities are particularly at risk as they are naturally fragmented and poorly resilient, and therefore more sensitive to large-scale perturbations (Harmelin 1980). Among the most fragile habitats of the littoral zone, caves harbour several endemic and specialized species (Harmelin *et al.* 1985). To detect potential effects of the ongoing regional warming of the north-western Mediterranean, we focused our study on shallow marine caves commonly inhabited by swarms of the mysid genus *Hemimysis* (Crustacea: Mysidacea), small shrimp-like crustaceans confined to the darkest reaches of those cavities (Ledoyer 1989). We report on the profound changes exhibited by populations of two sympatric species of this genus, *Hemimysis speluncola* Ledoyer and *Hemimysis margalefi* Alcaraz, Riera & Gili, following recent episodes of thermal anomalies near

Marseille (France). To test the relationship between these changes and environmental temperatures, we (1) documented the temporal sequence of species replacement in caves of known thermal conditions, (2) compiled information on the distribution ranges of both species, and (3) conducted replicated laboratory experiments to establish whether there are differences in the relative thermotolerance of these mysid species. Prior to this, no published data existed on the comparative tolerance to high temperatures of the two species. Only one previous study established that *H. speluncola* has a more stenothermal behaviour than a non-cave shallow-water mysid, *Leptomysis lingvura* (Gaudy & Guérin 1979), and no data existed on *H. margalefi*.

MATERIAL AND METHODS

Cave monitoring and mysid sampling

The caves mentioned in this study have been monitored by SCUBA diving. All of the 35 caves explored and sampled between 1998 and 2003 are located between 0 and 55-m depth, and are long enough (from 10 to over 100 m long) to include totally dark rooms where mysids can be found. Caves were studied throughout the NW Mediterranean from Spain to Croatia, but our attention was particularly focused on two large caves on the French Mediterranean coast (Fig. 1): Jarre (depth 15 m, latitude 43.2°N, longitude 5.4°E) and 3PP (depth 25 m, latitude 43.17°N, longitude 5.6°E). Jarre cave has been well described by Passelaigue (1989) and presents a mostly ascending profile from the entrance, allowing water homogenization with the outside. 3PP cave has been described by Vacelet *et al.* (1994) and Vacelet (1996), and presents a peculiar descending profile trapping cold water by density year-round.
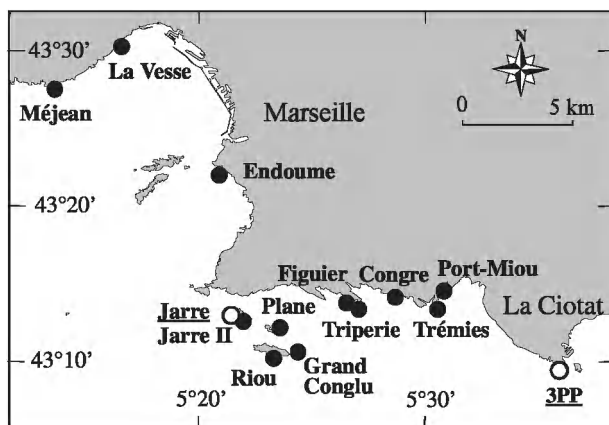

Figure 1 Map of the Marseille area (France, NW Mediterranean) with the position of the two main caves studied in this paper (open circles, underlined), Jarre and 3PP, together with 12 other caves surveyed nearby (black circles).

Prior to 1998, information on mysid occurrence relied on scattered literature data as well as published and unpublished reports and occasional sampling by members of our laboratory (F. Passelaigue, J.G. Harmelin, J. Vacelet, H. Zibrowius, T. Perez, C. Jalong). In 1998 and 1999, sampling was conducted by one of us (P.C.) at least every 4 months in Jarre, and once a year in the more stable 3PP cave. From January 2000, monthly sampling began in Jarre (still uninterrupted). Temperature was regularly monitored in Jarre and 3PP caves using digital data-logging thermographs.

Mysids were collected using diver-operated, specially-designed, hand nets and suction bottles, and species were identified *in vivo* under a dissecting microscope. Whenever mysid densities made it possible, at least 100 individuals were identified under the microscope.

Thermotolerance experiments

Two experiments were conducted at different times of the year, one in late winter (26 March 2002), and one in early winter (17 December 2002). Each time, a mysid sample was collected in the 3PP cave (to obtain the species *Hemimysis speluncola*) on the same day as a sample from the Jarre cave (for *Hemimysis margalefi*). Sampling was conducted during winter to ensure that *in situ* temperature was the same in both caves, i.e. *c.* 13–15 °C, but experimenting with late- and early-winter populations allowed us to work on individuals with contrasted environmental histories: late-winter mysids mostly experienced the cold, rather constant winter conditions, whereas most of the early-winter mysids would have experienced more variable, often warmer conditions. Samples were brought back to the laboratory in insulated baskets, and were allowed to acclimate in a cold room at 15 °C in the dark for 17 h.

In the preliminary March experiment, roughly 100 individuals from each cave were divided into two subsamples of identical size (*c.* 50). These subsamples were kept in identical aquaria. One subsample of each species was kept as a control at 15 °C. The other subsample of each species was placed in a temperature-controlled cabinet. The temperature in the water of a fifth aquarium placed in the cabinet was monitored with a digital data-logging thermograph recording temperature every minute. Additional discrete temperature measurements were performed with a digital probe at each temperature increment. The experiment was designed to be simple and performed within a day, so that mysids would not be subject to too many other potential sources of mortality. We believed that the upper temperature limit for both species would probably be lower than 40 °C. Because we started the experiment at 15 °C, after set-up time allowed for the resulting 25 °C temperature range had to be covered in *c.* 17 h. Closet temperature control was therefore regularly adjusted so that the measured temperature in the

water increased by 0.75 °C every 30 min. Every 30 min, the aquaria in the closet and in the control room were checked for dead individuals, which were immediately removed and counted.

The December experiment was conducted in a very similar fashion, the main difference being the search for a more robust conclusion. Therefore, more mysids (subsamples of *c.* 100 individuals vs. 50 in March) were placed in each aquarium, and thermal manipulations were performed on two replicates of each cave.

To test for differences in mortality curves, a log-rank statistic was used (STATISTICA® 5.1 package; StatSoft France, Paris).

RESULTS

Temporal changes in species distribution near Marseille

The elusive nature of the two main species of *Hemimysis* in north-western Mediterranean caves, and their unusual habitat allowed them to remain unknown to science until very recent times: *H. speluncola* was discovered in caves near

Marseille in 1962, and *H. margalefi* in the Balearic Islands in 1984 (Ledoyer 1963; Alcaraz *et al.* 1986). *Hemimysis speluncola*, then the dominant cave mysid near Marseille, was the focus of many (mostly ecophysiological) studies from 1962 through the mid-1990s (e.g. Gaudy & Guérin 1979; Macquart-Moulin & Passelaigue 1982; Bourdillon & Castelbon 1983; David *et al.* 1999), and large monospecific *H. speluncola* swarms occurred in many caves of the area (Ledoyer 1989). The very long cave of Jarre Island was discovered in 1977. A particularly large swarm was found there; this became the main focus of studies and sampling efforts until January 1997. Throughout this whole 20-year period, this particular swarm never seemed to have decreased or disappeared. By the end of 1988, according to Ledoyer (1989) this swarm had always been there, and was only composed of *H. speluncola*. All information that could be gathered on the documented occurrence of this species in Jarre cave between its discovery and 1997 has been compiled and summarized in Table 1. On 68 documented occasions, at the very least, the huge swarm was spotted over this period, and the species positively identified as *H. speluncola*. It is most likely that the *H. speluncola* swarm

Table 1 Compilation of the information available on the documented occurrence of the mysid *Hemimysis speluncola* in Jarre cave near Marseille (France) between the cave discovery in June 1977 and the beginning of periodic surveys in May 1988

Year	Dates	Source
1977	29 June	H. Zibrowius, coll.
1979	17 January; 29 May; 3 October; 9 November; 6 December; 13 December	Monteiro-Marques (1981); Passelaigue (1989); F. Passelaigue, coll. & pers. comm.
1980	9 January; 8 February; 1 April; 29 April; 2 May; 25 May; 24 June; 14 July; 18 August; 4 September	Passelaigue (1989); F. Passelaigue, coll. & pers. comm.
1984	April; 8 May; 29 June; 6 July; 20 July; August	Passelaigue & Bourdillon (1986); Passelaigue (1989); F. Passelaigue, coll. & pers. comm.
1985	7 February; 22 February; 19 April; 4 June; 7 June; 19 July; 26 July; 14 September; 28 September; 11 October; 15 October; 29 October	Passelaigue (1989); Passelaigue, coll. & pers. comm.
1986	30 September; October	Fichez (1989); Passelaigue (1989)
1987	February; 12 March; 16 April; July; 8 September	Fichez (1989); Passelaigue (1989); J. Vacelet, pers. comm.
1988	26 February; 7 July; 26 July; 1 September	Fichez (1989); J. Vacelet, pers. comm.; J.G. Harmelin, pers. comm.
1989	26 January; 27 January; 11 July	J. Vacelet, pers. comm.
1990	20 February; 7 May; 3 June	David *et al.* (1999); J.G. Harmelin, pers. comm.
1991	14 August; 29 November; 12 December; 15 December	David *et al.* (1999); J.G. Harmelin, pers. comm.
1993	7 June; 17 June	J. Vacelet, pers. comm.; J.G. Harmelin, pers. comm.
1994	1 May; 8 December	De Jong-Moreau *et al.* (2001); J.G. Harmelin, pers. comm.
1995	April; 5 May; 9 May; 6 November	T. Perez, coll. & pers. comm.; C. Jalong, coll.; J. Vacelet, pers. comm.
1996	May; June; 23 July	T. Perez, coll. & pers. comm.; J. Vacelet, pers. comm.
1997	13 January	J. Vacelet, coll. & pers. comm.

Dates are reported when the large mysid swarm was observed, and the species positively identified as *H. speluncola*. This swarm was never noted to be absent during this period. Sources are published reports, samples in collection in our laboratory (mentioned as 'coll.'), or personal communications ('pers. comm.') from experienced scientific divers used to observe *H. speluncola* swarms.

existed in Jarre prior to 1977, as such swarms have been reported from nearby caves (some at distances of only 2 km) between 1962 and 1977 (see for example Ledoyer 1963, 1965, 1966, 1969, 1989; Macquart-Moulin & Patriti 1966; Macquart-Moulin & Passelaigue 1982).

In May 1998 one of us (PC) began a more regular survey of the Jarre cave: every 4 months in 1998 and 1999, and monthly from January 2000. Between January 1997 and May 1998, however, the Jarre cave swarm had disappeared, with only a few scattered individuals left. The sample we obtained of these scattered individuals revealed only 8% *H. speluncola* vs. 92% *H. margalefi* (Table 2). The last individual *H. speluncola* was seen in a June 1999 sample. This information, and the data gathered from Table 1, were used to construct a synthetic diagram of the hypothetical relative abundances of both *Hemimysis* species in Jarre, which helps visualize the likely scenario (Fig. 2). Since June 1999, although samples of 100+ individuals have been examined each month, *H. speluncola* has totally disappeared from the Jarre cave. A survey of the mysid populations in 12 other caves of the Marseille area (Fig. 1) during the years 1998–2003, interestingly showed the same pattern of replacement of *H. speluncola* by *H. margalefi*

(Table 2). The 3PP cave (near La Ciotat, 30 km east of Marseille, see Fig. 1) is the only exception to this pattern, but it is a most peculiar cave, with a constant, cold (13–15 °C) temperature throughout the year (Fig. 3a), which mimics Mediterranean deep-sea environmental conditions (Vacelet *et al.* 1994; Vacelet & Boury-Esnault 1995; Vacelet 1996; Harmelin 1997). Indeed, the temperature of deep waters throughout the Mediterranean is *c.* 13 °C while superficial waters often reach *c.* 24 °C in the summer near Marseille (Fig. 3). To date, only the 3PP cave, associated with constant cold conditions, seems not to have experienced this species shift along the French Mediterranean coast.

Spatial distribution patterns of Hemimysis species

Outside the Marseille area, the geographical distribution of the two mysid species is poorly known but offers significant insights (Fig. 4). *Hemimysis speluncola* has only been reported from the coldest gulfs of the Mediterranean: in the Medes Islands, marking the western border of the Gulf of Lions, and in the Croatian island of Krk in the northernmost part of the Adriatic Sea. It was also earlier reported from Ischia,

Table 2 Cave mysid species composition in Jarre cave (upper table, main object of this study), compared with that of the main 12 other caves surveyed in the Marseille area, and to the 3PP cave (lower table) in La Ciotat, NW Mediterranean, France (see Fig. 1 for location)

Cave	Species composition before this study (1962–1998)	Captures of *H. speluncola* vs. *H. margalefi* in 1998–1999 (**H. speluncola** : *H. margalefi*)						Current species composition
		5/98	6/98	8/98	9/98	3/99	6/99	
Jarre	***Hemimysis speluncola*** (1977–1997)		1 : 10	1 : 11			1 : 18	*H. margalefi* (1999–2003)
Méjean	Unknown							*H. margalefi* (1998–1999)
La Vesse	Unknown							*H. margalefi* (1998–2003)
Endoume	*H. margalefi* (*c.* 1985–1989)					1 : 24		*H. margalefi* (1998–2002)
Jarre II	Not observed (1964–1977)							*H. margalefi* (1998–2002)
Plane	***H. speluncola*** (1962–1989)							None (1998–2002)
Riou	***H. speluncola*** dominant over *H. margalefi* (*c.* 1980–1989)							None (1998–2003)
Gd. Conglu	***H. speluncola*** (1992)							None (2001–2002)
Figuier	***H. speluncola*** (1962–1989)	**19 : 0**			2 : 5			*H. margalefi* (1998–2001)
Triperie	***H. speluncola*** (1962–1993)							*H. margalefi* (1998–1999)
Congre	***H. speluncola*** dominant over *H. margalefi* (1977–1986)							*H. margalefi* (1998–2000)
Trémies	***H. speluncola*** (1968–1986)							*H. margalefi* (1998–2000)
Port-Miou	*H. margalefi* dominant over ***H. speluncola*** (1981–1994)							*H. margalefi* (1998–1999)
3PP	Unknown							***H. speluncola*** dominant over *H. margalefi* (1998–2003)

Entries for *Hemimysis speluncola* are reported in bold for a better reading. Captures during the transition period (1998–1999) were scattered and rare, but show that *H. speluncola* did persist in very low numbers until then. From June 1999, repeated sampling and observation of thousands of individuals, revealed 100% *Hemimysis margalefi* in all caves but the 3PP cave. Information on species composition and known years of occurrence prior to this study (first column) come mostly from Ledoyer (1966, 1989), personal observations of mysids collected at Grand Conglu cave by H. Zibrowius in 1992, and the literature and communication cited in Table 1.
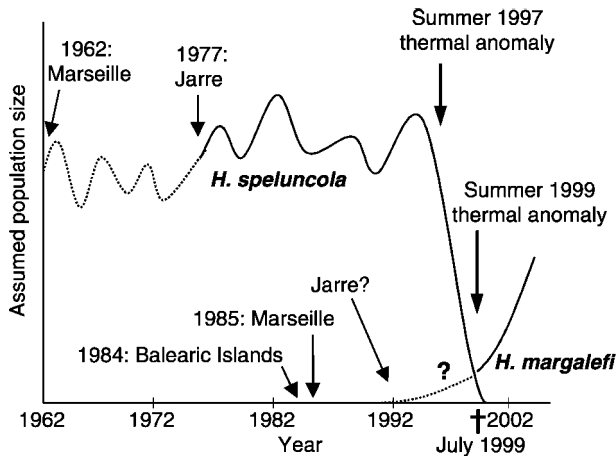
Figure 2 Proposed scenario (schematic representation) of changes in the populations of two Mediterranean species of Mysidacea (Crustacea) in a shallow-water marine cave of Jarre Island, near Marseille, France, over the past 40 years, based on regular observations by SCUBA diving, and the compiled information from Tables 1 and 2. The years the two species were discovered are also reported, as well as the first report of *Hemimysis margalefi* in the Marseille area. Because, actual population sizes were impossible to measure or even estimate, this figure is mostly based on presence/absence data.

in the Gulf of Naples by Wittmann (1978, 2001), but the species was never found there after 1976, despite periodic sampling conducted until 1994 (K.J. Wittmann, pers. comm.), and *H. speluncola* seems to have been replaced by *Hemimysis margalefi* there too. *H. speluncola* was also found in the Bergeggi cave near Savona in the Ligurian Sea, but it has now also disappeared and been replaced by *H. margalefi* between the early 1990s (C.N. Bianchi, pers. comm.) and 2002 (P.C., pers. obs.). Outside France, *H. margalefi* is reported from most of the NW Mediterranean (Fig. 4), and its southernmost known occurrence is in Malta (M.A. Faasse, pers. comm.).

Comparative temperature tolerances

Our experiments were designed to compare the upper thermal tolerance of both species by gradually heating the individuals by 0.75 °C every 30 min. Only four individuals (all *H. speluncola*) died in the control during the March experiment, and none during the December experiment. Interestingly, whereas the March 3PP sample contained only *H. speluncola*, the December sample was a mixture of both species (*c.* 47% *H. speluncola*), as it sometimes happens. This allowed us to also compare the thermotolerance of individuals of the two species, originating from the same cave environment and taken at the exact same place and time. Figure 5 summarizes the experiments, which unam-
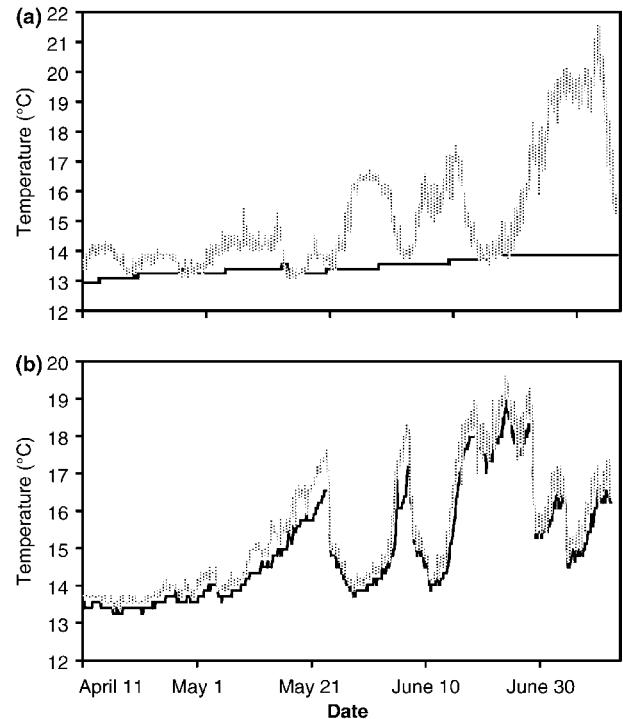

Figure 3 Examples of temperature time-series obtained from the two contrasted cave environments of Jarre and 3PP (NW Mediterranean). (a) 3-month record of temperature (11 April–6 July 1995) 100 m inside the 3PP cave at a depth of 24 m (black) compared with the temperature recorded just outside the cave at 18 m depth (grey). Beginning in spring, outside temperatures display large fluctuations due to alternating wind regimes, but may rise to over 20 °C, while it remains constant and cold inside the cave (Data modified from Vacelet (1996), courtesy of J. Vacelet and J.G. Harmelin). (b) Temperatures recorded during the same season (11 April–12 July 2002) 60 m inside Jarre cave at a depth of 15 m (black) compared with those recorded immediately outside the cave at the same depth (grey). Temperature fluctuations inside the cave (only slightly buffered) follow those of the outside environment. On some occasions (e.g. July 2001) it has been observed to rise to 24 °C (not shown here).

biguously always show a much higher tolerance to acute thermal stress in *H. margalefi*. The difference observed between the two species is always significant, in the March experiment (log-rank = 10.81, $P < 0.0001$), in December (log-rank = 10.57, $P < 0.0001$), and all experiments together (log-rank = 14.84, $P < 0.0001$). In the December experiment, there were no significant differences between samples of a given species, whether from different replicates (log-rank = 1.45, $P = 0.1474$ for *H. speluncola*) or from different caves and replicates (log-rank = 1.41, $P = 0.1588$ for *H. margalefi*).

The lowest experimental temperature at which first signs of mortality begin to affect *H. speluncola* was 22 °C in the March experiment compared with 31 °C for *H. margalefi* in
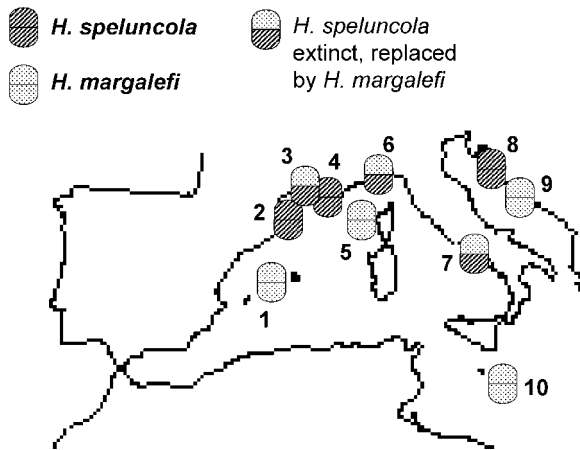
Figure 4 Present distribution map of the two north-western Mediterranean cave mysids *Hemimysis speluncola* and *Hemimysis margalefi* obtained from personal (PC) field observations (with years of observation), or from literature records and personal communications when stated. 1, Menorca, Balearic Islands, Spain (1998); 2, Medes Islands, Spain (2000, 2002); 3, Marseille, France (1998–2003); 4, 3PP cave, La Ciotat, France (1998–2003); 5, Corsica, France (Ledoyer 1989); 6, Bergeggi, Savona, Italy (pers. obs. 2002, Bianchi *et al.* 1986, Bianchi & Morri 1994b); 7, Gulf of Naples, Italy (pers. obs. 1999, K.J. Wittmann pers. comm., Wittmann 1978, 2001); 8, Krk Island, Croatia (Arko-Pijevac *et al.* 2001); 9, Premuda, Dugi Otok and Kornati Islands, Croatia (2000); 10, Gozo, Malta (M.A. Faasse, pers. comm.).

that same experiment. In December, mortality appears at more similar temperatures for the two species (27.5 °C vs. 28.3 °C, respectively), but the subsequent inflexion of the curve is very different. This is best illustrated (Fig. 5) by the two species' acute LT_{50} (lethal temperature for 50% of the experimental sample) which show a 2.7 °C difference in December (mean ± SE: 29.50 ± 0.02 vs. 32.19 ± 0.21 °C), and 3 °C in March (29.6 °C vs. 32.6 °C). In that same March experiment, over 90% of *H. speluncola* were dead at 31 °C, a temperature which, in this particular experiment, caused no mortality to *H. margalefi*. Similarly, in December, almost all *H. speluncola* were dead at 31 °C, when less than 10% of the *H. margalefi* were affected.

DISCUSSION

From the species distribution data, *Hemimysis speluncola* now significantly appears to be restricted to the two coldest regions of the Mediterranean (Fig. 4): the Gulf of Lions (Medes Is., only one cave near Marseille) and the northernmost Adriatic Sea (Krk). It has disappeared from the warmer Tyrrhenian Sea (Naples) in the late-1970s, from the Ligurian Sea in the 1990s, and has recently started declining near Marseille, where it can no longer be found in the many caves of the area, and only seems to survive in one peculiar
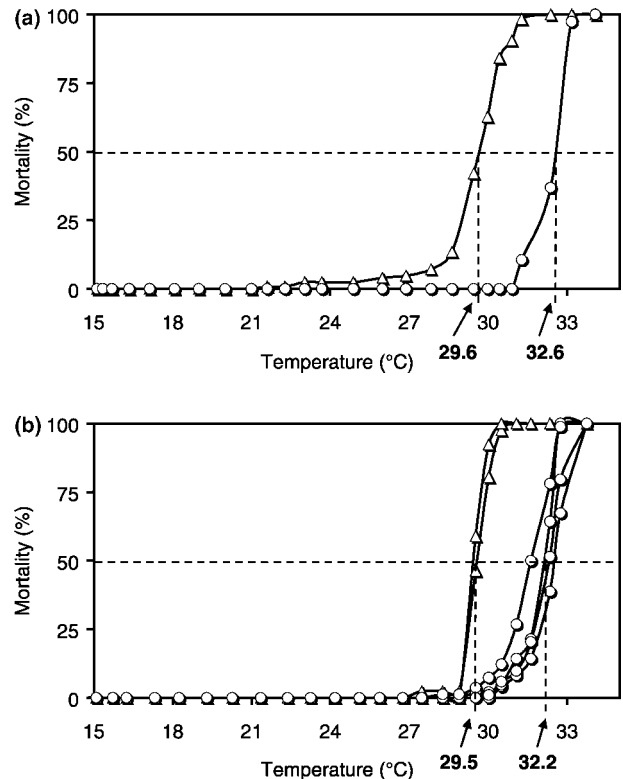

Figure 5 Experimental determination of the different tolerance to acute temperature increase in *Hemimysis speluncola* and *Hemimysis margalefi*, two species of cave mysids with different thermal habitat requirements. Triangles represent *H. speluncola*, circles are for *H. margalefi*. Dotted lines indicate the acute LT_{50} (lethal temperature for 50% of an experimental population) determined for each species. (a) March 2002 experiment with only one replicate per species. (b) December 2002 experiment, with two replicates for *H. speluncola* (from 3PP cave), and four for *H. margalefi* (two from 3PP, two from Jarre cave). LT_{50} in the December experiment is an average value.

cold-water cave system. We suggest that the dramatic reduction of this species' geographical range has been caused by its lower temperature tolerance as compared with its congener *Hemimysis margalefi*.

This was tested in our comparative thermotolerance experiments. This type of experiment does not intend to reproduce *in situ* environmental conditions in the caves, nor does it determine *in situ* survival limits for the two species (see for example Stirling 1982). It however clearly provides the *comparative* evidence that *H. speluncola*, a species with a geographical distribution limited to colder regions, has indeed a significantly lower tolerance to acute thermal stress than its widely distributed congener *H. margalefi* (Fig. 5). In the literature, *H. speluncola* has been considered stenothermal for a temperate mysid species (Gaudy & Guérin 1979). Behavioural observations both in experimental tanks

(Bourdillon & Castelbon 1983) and *in situ* (Passelaigue 1989) furthermore indicated that *H. speluncola* actively escapes warmer layers when water is stratified. No data existed on *H. margalefi*, nor on the comparative tolerance to high temperatures of the two species.

When looking at the possible cause for the sudden collapse of the Jarre population between January 1997 and May 1998, this period strikingly encompasses (Fig. 2) the first of two thermal anomalies (summer 1997 and 1999) recorded in the Marseille area that have been related to mass mortalities of sessile benthic invertebrates, especially in 1999 (Perez *et al.* 2000; Romano *et al.* 2000; Garrabou *et al.* 2001). These events were characterized by unusually-long periods of high temperatures, and a very deep-plunging thermocline. Coastal waters in this area are usually regularly cooled down (see Fig. 3) during the summer by episodes of upwelling related to a strong dominant north-western wind (Mistral). This did not happen in 1997 and 1999 across periods of time long enough to cause damage to many sessile invertebrates with cold-water affinities (Perez *et al.* 2000; Garrabou *et al.* 2001). The maximum temperatures recorded thus far in the ascending caves (i.e. except the 3PP cave) near Marseille can reach up to 24 °C, usually for relatively short periods (Passelaigue, 1989; personal observations from July 2001). However, during the 1999 thermal anomaly, Perez *et al.* (2000) reported temperatures outside caves remaining stable at *c.* 24 °C for a whole month at 24 m near Marseille. Undoubtedly, the temperature in the Jarre cave, at the shallower depth of 15 m, must have risen to at least 24 °C for the same period. Interestingly, in our experiments, 24 °C is a temperature at which some increases in mortality have already begun to affect *H. speluncola* (Fig. 5a). Therefore, it seems very likely that the NW Mediterranean 1997 and 1999 thermal events have produced long-term (*c.* 1 month) sub-optimal or even sub-lethal environmental conditions for *H. speluncola*, in the depth zone where the vast majority of caves are found. It is likely that prolonged periods of high temperatures in summer 1997 led to the decline of the large *H. speluncola* swarms in Jarre and other caves along the coast. The second, even stronger event in 1999, might have ruined the chances of recovery of these already weakened populations.

This temperature-based scenario is, however, only supported by indirect, albeit abundant evidence. Alternative causes, particularly competitive replacement, or natural population fluctuations, cannot totally be ruled out. But the status of *H. margalefi* as a better competitor, or recent colonizer of the Mediterranean caves cannot be assessed, because virtually no information existed on this species before the present study, except the very fragmented information available in the systematic accounts of Alcaraz *et al.* (1986) and Ledoyer (1989). Work is currently underway to elucidate the comparative life-history traits, population

genetic and demographic structures, as well as the phylogeography of those two species (C.L. and P.C.). Considering all the data gathered so far, the temperature effect however appears more likely. If competitive exclusion were responsible, it should have eliminated *H. speluncola* from the 3PP cave, as the two species co-exist there. Natural fluctuations are also unlikely. Unfortunately, there is no information available on natural population fluctuations in those *Hemimysis* species in a normal context. They have only been known to science for a few decades, they are rather elusive to the average observer (being small, living in caves, etc.), and their abundance cannot be quantitated. Trained observers can however detect obvious changes between two visits to a cave (pers. obs.), in a semi-quantitative way (e.g. very abundant, abundant, highly dispersed, scarce). In that way, Ledoyer (1989) mentioned *H. speluncola* population fluctuations (but never extinctions, nor species shifts) in a particular cave. What we report here is of a different nature, as all the caves in the area, with a few significant exceptions, have seen their populations collapse, and have not recovered since.

With the likely increase in frequency of thermal anomalies in the context of global climate change, and signs already detectable that the general temperature of the Mediterranean Sea is increasing (Bethoux *et al.* 1990; Astraldi *et al.* 1995; Bethoux & Gentili 1996), *H. speluncola*, an endemic of this region, might soon be driven to extinction, as may many of the temperate components of NW Mediterranean marine biodiversity. In contrast, species considered as indicators of the warmer parts of the Mediterranean, are gradually becoming more frequent and widespread (Bianchi & Morri, 1994a; Francour *et al.* 1994).

The particular geographical context of the Mediterranean Sea makes it impossible for shallow-water temperate species already trapped in the northernmost, coldest parts of the basin to migrate or disperse northward to accommodate temperature changes. Potential refuges for such cold-loving species exist however, where low temperature can be maintained even in the summer period. Such refuges can include topographical peculiarities such as the 3PP cave, which maintains a low temperature throughout the year, or habitats situated well below the summer thermocline, i.e. 40–50 m in the Marseille area. It is highly unlikely that a viable population may be maintained in the NW Mediterranean, without genetic bottleneck, if it relies entirely upon exceptional habitats such as the 3PP cave. The deep-water hypothesis, on the other hand, remains to be tested by looking for *Hemimysis* occurrences in deeper caves or other cryptic habitats, but to date, no such occurrence has been reported. Many terrestrial or freshwater species confronted with environmental warming are forced to move upward in altitude when they cannot move northward, which increases their habitat fragmentation in small patches (Rahel *et al.*

1996; Hughes 2000). Similarly, cold stenothermal marine species will be pushed to deeper, colder waters, until habitat requirements are no longer met. Whereas some cave-dwelling organisms do find their origins in the deep sea (Harmelin *et al.* 1985; Hart *et al.* 1985; Vacelet *et al.* 1994; Vacelet 1996; Harmelin 1997), not all of them will be able to cope with such a habitat change. A significant component of the biodiversity of the Mediterranean Sea is clearly under the threat of global warming, and some cave species such as mysids, as recently demonstrated for the North Sea plankton (Taylor *et al.* 2002), will prove useful in detecting and monitoring the changes to come.

ACKNOWLEDGEMENTS

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