1 **Life in a warm deep sea: routine activity, burst swimming performance, and**

2 **oxygen consumption of the shrimp *Acanthephyra eximia* in the abyssal**

3 **Mediterranean**

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11 Measurements of routine swimming speed, "tail-flip" escape responses, and oxygen

12 consumptions were made of the deep-sea shrimp *Acanthephyra eximia* using autonomous

13 landers in the Rhodos Basin at depths of up to 4400 m and temperatures of 13-14.5°C.

14 Routine swimming speeds at 4200 m averaged 0.18 m · s^{-1} or 3.09 body lengths · s^{-1},

15 approximately double those of functionally similar oceanic scavengers. During escape

16 responses peak accelerations of 23 m · s^{-2} or 630.6 body lengths · s^{-2} were recorded, with

17 animals reaching speeds of 1.61 m · s^{-1} or 34.8 body lengths · s^{-2}. When compared to shallow-

18 water decapods at similar temperatures these values are low for a lightly calcified shrimp such

19 as *A. eximia* despite a maximum muscle mass specific power output of 90.0 W · kg^{-1}. The

20 mean oxygen consumption of 12 shrimp trapped at 4200 m (78.1 ml · kg^{-1} · h^{-1}) was similar to

21 that of oceanic crustacean scavengers and shallower-living Mediterranean crustaceans once

22 size and temperature had been taken into account. These animals appear to have high routine

23 swimming speeds and metabolic rates but low burst muscle performances. This suite of traits

24 can be accounted for by high competition for limited resources in the eastern Mediterranean,

25 but low selective pressure for burst swimming due to reductions in predator pressure.

1. INTRODUCTION

The deep basins of the Eastern Mediterranean are extremely unusual deep-sea systems. Although sharing many of the characteristics of the oceanic abyss (e.g. high hydrostatic pressures, lack of sunlight, and low food supply) the Mediterranean differs from the oceans in geological age and isolation (Hsü, 1972; Por, 1989), by being over 10°C warmer than equivalent oceanic depths, and by having a greatly reduced species composition (Albertelli *et al.*, 1992; Jones *et al.*, 2003).

The majority of the benthic deep-sea animals studied to date are characterised by low metabolic rates and activity levels when compared to shallow-water relatives (Smith, 1978; Smith & Baldwin, 1982; Priede *et al.*, 1991; Bailey *et al.*, 2002; Priede *et al.*, 2003). The mechanisms controlling these traits are not fully understood but possibilities include physical and ecological parameters such as direct effects of temperature and hydrostatic pressure on enzyme activity (Somero & Siebenaller, 1979), food limitation (Collins *et al.*, 1999), and the effects of low light levels on predator prey interactions (Cowles *et al.*, 1991). See Childress (1995) for a review and critique of the possible causes.

Apart from short-term experiments on vent animals (Shillito *et al.*, 2001; Ravaux *et al.*, 2003) and abyssal amphipods (Treude *et al.*, 2002) little information exists on the physiological tolerance ranges of deep-sea animals, or their abilities to adapt to environmental change. Even in shallow water, where the effects of temperature change on the activity and performance of individual animals are well understood (Rome *et al.*, 1990; Johnson & Bennett, 1995; Guderley *et al.*, 1996; Goldspink, 1998; Temple & Johnston, 1998), the factors

controlling the observed relationships between performance and habitat temperature in animals adapted to different thermal regimes (Wakeling & Johnston, 1998; Peck, 2001) are not fully explained. The question is a difficult one because the adaptive level of activity capacity will be a trade-off between the pressures of competition (Britton & Morton, 1994; Godø *et al.*, 1997; Tamburri & Barry, 1999; Morton & Yuen, 2000) and predation (Van Buskirk & Relya, 1998; O'Steen *et al.*, 2002; Angilletta Jr. *et al.*, 2003), the overall energy availability as set by the productivity of the system (Collins *et al.*, 1999; Priede *et al.*, 2003), and the effects of temperature on the energetic costs of physiological processes (Johnston & Walesby, 1979; Johnston *et al.*, 1998; Pörtner *et al.*, 1999; Fraser *et al.*, 2002). In natural situations a quantitative estimate of most of these variables is not available (e.g. the relationship between performance and survival, or a functionally relevant measure of food supply). Therefore relating the performance level of an animal to the natural temperature of the environment under which its evolution took place is fraught with difficulty.

Understanding the response of deep-ocean animals to changing temperature may be of critical importance in predicting the likely effects of environmental change in the deep-sea. Would any temperate increases result in changes in activity capacity and metabolism as observed in shallow-water animals? Or are the possible increases in energetic costs incompatible with a potentially food-limited environment such as the deep-sea? The deep Mediterranean provides for a natural experiment investigating the effects of temperature on deep-sea animals. In the present study we present new information on the swimming performance and metabolism of the shrimp *Acanthephyra eximia*, a scavenger and predator living to depths of up to 4400 m (Christiansen, 1989; Cartes & Maynou, 1998). Highly abundant at benthic food falls (Jones *et al.*, 2003), *A. eximia* has been trapped at heights of up to 500 m above the seafloor (Christiansen, 1989). The species is also known from the Indo West Pacific region, and throughout the Atlantic Ocean (Galil & Goren, 1994), where the species has also been observed around hydrothermal vents (Desbruyères *et al.*, 2001).

In the present study the results of a range of *in situ* experiments are presented, in which the routine and burst swimming performances of the shrimp *Acanthephyra eximia* were determined. A respirometry experiment was also conducted, giving an initial indication of the metabolic rates of these animals. These are the first data on locomotory performance or metabolism for any non-vent deep-sea animal under a natural high-temperature and -pressure regime.

2. METHODS

(a) *Study area*

All experiments were undertaken in the Rhodos Basin, Eastern Mediterranean (35° 45' N, 28° 15' E) between the 17th and 28th June 2002. The basin consisted of a large plain at depths of 4000-4500 m, shelving relatively steeply to the Northwest towards Rhodos.

Water temperature declined rapidly from approximately 20 ^{o}C at the sea surface to a minimum of 13.5 ^{o}C at 1000 m and then rose with increasing depth. Water temperature was 14.0^{o}C at 2400-2500 and 14.5^{o}C m at 4000-4400 m (both $\pm$ 0.2^{o}C). Current velocities averaged 0.17 $\pm$ 0.0003 m · s^{-1} at 4000-4400 m and 0.06 $\pm$ 0.0003 m · s^{-1} (mean $\pm$ 1 s.e.) at 2400-2500 m (mean $\pm$ 1 s.e).

(b) *Lander operations*

Experiments were carried out using the "FRESP" and "Sprint" lander systems (Bailey *et al.*, 2002; Bailey *et al.*, 2003), deployed from the Research Vessel *Philia*. Each lander consisted of a video camera and other instruments housed in pressure cases and mounted on an aluminium frame. Each lander was fully autonomous after deployment, and was allowed to free-fall to the seafloor where the experiments were carried out by the onboard computers. At the end of each experiment the lander was recalled by an acoustic command from the ship.

1   Animals were also collected for anatomical measurements using a free-fall fish trap consisting

2   of a 1 x 1 x 1 m wire cage with 2 funnel openings. This was deployed and recovered in the

3   same manner as the landers. The landers and fish trap were baited with mackerel (*Scomber*

4   *scombrus*).

5   (c) *Animals*

6   Twenty-four animals were collected at two trap stations and further 17 in the respirometry

7   chamber of the FRESP lander. All individuals stored in 10% formalin for transport to the

8   UK. The animals were then blotted dry and their total wet mass (M, kg) and total length (L,

9   m, from tip of telson to tip of carapace) were measured. Abdominal muscle was dissected out

10   and extensor and flexor muscle were weighed separately. Relationships between L and M (M

11   $= 7.47 \cdot L^{3.04}$, $R^2 = 8.09$, $F_{39} = 164.86$, $p < 0.001$) and between L and flexor muscle mass

12   (M_{muscle}, kg) were used to estimate M and M_{muscle} of animals observed in the video recordings

13   (M_{muscle} was on average 24.0 % of M). Video recorded shrimp were significantly larger at

14   4200 m (L of 0.059 ± 0.002 m, mean $\pm$ 1 s.e.) than at 2357 m (0.049 ± 0.002 m, mean $\pm$ 1 s.e.)

15   (ANOVA length comparison, $F_{50,52} = 10.4$, $p = 0.002$).

16   (d) *Filming*

17   Motion analyses were performed on video sequences of 52 shrimp ($L = 0.032$ to 0.077 m)

18   obtained from the Sprint lander (Bailey *et al.*, 2003). Muscle performance estimates were

19   made using video recordings of electrically stimulated and spontaneous escape responses.

20   The lander was modified for this experiment to carry a digital video (DV) camera capable of

21   50-200 Hz recording (GR-DVL 9800, JVC Ltd, Japan). Steady and burst swimming data

22   were collected using 50 and 100 Hz recordings respectively. The standard internal lens of the

23   camera was used, with automatic focus and exposure, viewing an area of seabed of 0.94 x

24   0.75 m in full frame mode.

1   (e) *Analysis of swimming and escape responses*

2   Digitised video sequences were played back frame-by-frame on a PC and the coordinates of

3   the centre of the animal's silhouette in the film plane were selected manually and recorded

4   using a program in Visual Basic 4.0 (Microsoft Inc. USA). Measurements were only made of

5   animals close to the bait and scale references (<30 cm as indicated by the animals' shadows).

6   Digitising noise was removed using piecewise quadratic regression, with the smooth-width

7   optimised according to the criteria of Wakeling and Johnston (1998). The displacement of the

8   centre of the silhouette in the x and y directions was calculated from the smoothed

9   coordinates and differentiated with respect to time to give swimming velocity in each

10   direction. Current velocity in each direction was then deducted from swimming velocity to

11   give velocity through the water. These through water velocity vs. time data were then

12   differentiated to provide through-water acceleration in the x and y directions. Total

13   (resultant) velocity and acceleration were then calculated from the x and y values.

14   Burst and routine swimming speeds are denoted by U and U_w respectively (m · s^{-1}).

15   Acceleration (A, m · s^{-2}) was only calculated for burst swimming. The inertial power output

16   required for burst swimming (P_{inert}, W) was calculated from the product of U, A and M.

17   Power output per kg muscle (P, W · kg^{-1}) was then calculated from P_{inert} and M_{musc}. Animal

18   total length (L, m), was used to calculate length-specific velocity ($\hat{U}$, *and* $\hat{U}_w$, L · s^{-1}) and

19   acceleration ($\hat{A}$, L · s^{-2}). Maximum values recorded within an individual sequence for each

20   of the above variables are denoted by the subscript $_{max}$, e.g. $\hat{U}_{max}$ for maximum length-specific

21   velocity. Full details of the equipment and procedures used are provided by Bailey et al

22   (2003).

23   Total muscle power output cannot yet be estimated as the efficiency of shrimp burst

24   swimming is not known. As filming was carried out from a single camera it is not possible to

25   determine the motion of the shrimps in the z direction (towards/away from the camera). All

1   calculations assume that the animals were swimming normal to the line of sight of the camera.

2   While observation of the videos and measurement of the positions of the animals' shadows

3   suggests that vertical movement during burst swimming was limited, a deviation of 45° from

4   horizontal swimming would result in an underestimate of total displacement of 41.4%.

5   (f) *Respirometry*

6   The FRESP vehicle (Bailey *et al.*, 2002) was capable of trapping scavenging animals and

7   measuring the oxygen concentration in the respirometry chamber (C_wO_2, ml · l^{-1}) using a

8   polarographic oxygen electrode. The precision of the sensor-logger system was ±1.03%, with

9   accuracy maintained by continual recalibration with respect to ambient O_2 concentration. For

10   this experiment the chamber volume (VOL_{resp}, litres) was 28.9 litres.

11   Respirometry measurements were obtained from one incubation at 4200 m, during which the

12   total oxygen consumption of 12 animals was measured (L 0.074 ± 0.0039 m, M 0.00298 ±

13   0.00048 kg, mean ± 1 s.e.). Control measurements without shrimps at 4050 and 4170 m

14   determined the oxygen consumption of the microbial fauna within the chamber and bait.

15   Microbial consumption was extremely low (<0.01 ml · h^{-1}).

16   The average individual oxygen consumption of the trapped shrimps (VO_2, ml · h^{-1}) was

17   calculated from the total oxygen consumption rate of all the shrimps in the chamber (ΔC_wO_2 ·

18   VOL_{resp} · Δt^{-1}, ml · h^{-1}) and the number of shrimps trapped (n)

19   $$VO_2 = \frac{\Delta C_wO_2 \cdot VOL_{resp} \cdot \Delta t^{-1}}{n}$$

20   Average mass-specific oxygen consumption (MO_2, ml · kg^{-1} · h^{-1}) was calculated from the

21   total oxygen consumption using the total mass of shrimps trapped (M, kg)

$$1 \quad MO_2 = \frac{\Delta C_w O_2 \cdot VOL_{resp} \cdot \Delta t^{-1}}{M}$$

2   The activity level of animals within the chamber was monitored for 3 minutes at 6 h intervals

3   by the onboard video camera and recorded to DV tape.

4   (g) *Statistics*

5   All analyses were performed using SPSS (Ver. 10.0.7, SPSS Inc.). Effects of depth on animal

6   size and swimming performance were investigated using ANOVA and ANCOVA. Scaling

7   relationships were determined by fitting power law functions to length and weight

8   relationships with swimming parameters.

9   **3. RESULTS**

10   (a) *Routine swimming speed*

11   Maximum and mean through-water swimming speeds, both absolute and length-specific are

12   given in Table 1. Shrimp swam at similar speeds (U_w) at both depths, despite differences in

13   animal size. Length-specific speeds ($\hat{U}_w$) were higher at the shallower station. When animal

14   size was taken into account $U_{w\,mean}$, $U_{w\,max}$ and $\hat{U}_{w\,max}$ differed significantly between depths.

15   (b) *Burst swimming speed, acceleration, and muscle performance*

16   On stimulation the shrimp performed escape responses. A rapid contraction of the abdominal

17   musculature curled the animal's tail forward and beneath its body. A brief peak in power

18   output accelerated the animal directly rearward, reaching peak velocity after around 0.05 s,

19   after which the animal decelerated before commencing normal pleopod swimming. Very few

20   animals made more than one tail-flip, and these sequences were not analysed. Examples of

1   the changes in power output, acceleration, and velocity during escape responses are given in

2   Figure 1.

3   During burst swimming shrimps produced peak power outputs (P_{max}) of up to 90.0 W · kg^{-1}

4   M_{muscle} (47.2 ± 5.5 W.kg^{-1}, mean ± 1 s.e.), and this was not related to animal length ($R^2 = 0.09$,

5    $F_{1,16} = 1.57$, $p = 0.23$). The highest A_{max} recorded was 23.1 m · s^{-2} and the highest $\hat{A}_{max}$ 630.6 L

6   · s^{-2}. The highest value of U_{max} attained was 1.6 m · s^{-1}, with a highest $\hat{U}_{max}$ of 34.8 L · s^{-1}.

7   High absolute and length-specific values did not coincide in the same animal as strong

8   negative relationships existed between body length or mass and length-specific performance

9   ($\hat{U}_{max}$ and $\hat{A}_{max}$). $\hat{U}_{max}$ was significantly related to L and M ($R^2=0.52$, $F_{11}=12.1$, $p = 0.005$)

10   according to the power law relationship where $\hat{U}_{max} = 1.57 \cdot L^{-0.89}$ or $\hat{U}_{max} = 2.86 \cdot M^{-0.29}$. The

11   relationships between $\hat{A}_{max}$ and L and M were stronger ($R^2 = 0.67$, $F_{11} = 21.9$, $p = 0.001$) where

12    $\hat{A}_{max} = 5.73 \cdot L^{-1.38}$ or $\hat{A}_{max} = 14.6 \cdot M^{-0.45}$. No significant relationships existed between animal

13   length or mass and U_{max}, A_{max} or P_{max}. Data for $\hat{U}_{max}$ values in *A. eximia* and tail flip escape

14   responses in other decapod species are presented in Figure 2. It should be noted that scaling

15   relationships were obtained over only a limited size range (32-77 mm).

16   There was no significant difference between depths in any performance parameter except $\hat{A}_{max}$

17   ($F_{1,17} = 5.391$, $p = 0.034$) which was lower at greater depth. If the effects of body length on

18   swimming were taken into account by using L as a covariate there was no significant

19   difference between depths for any performance variable.

20   c) *Oxygen consumption*

21   Oxygen levels in the respirometer (C_wO_2, ml · l^{-1}) fell sharply for the first 1 h 4 min (ΔC_wO_2 ·

22   VOL_{resp} · $\Delta t^{-1} = 9.75$ ml · h^{-1}) and then more slowly for the next 4 h (2.79 ml · h^{-1}) from a

23   background concentration of 5.1 ml · l^{-1} to a plateau at 4.47 ± 0.013 ml · l^{-1} (mean ± 1 s.e.).

24   Mean individual oxygen consumption (VO_2) of 0.23 ml · h^{-1} and mean mass specific oxygen

25   consumption (MO_2) of 78.07ml · kg^{-1} · h^{-1} were calculated from this second, lower, slope. The

1   metabolic rate of *A. eximia* was compared graphically with other, published, data for deep-

2   water crustaceans (Figure 3).

3   Video recording of the animals within the chamber revealed high levels of swimming activity

4   and apparent feeding behaviour immediately following trapping.   The condition of the

5   shrimps appeared to worsen during the incubation, with 7 active shrimps still visible after 6 h

6   (of an original 12 individuals), declining to two stationary but ventilating animals after 24 h.

7   No ventilating animals were visible after 30 h.

8   **4. DISCUSSION**

9   This study set out to examine the adaptations of deep-water shrimp *Acanthephyra eximia* to a

10   thermal regime quite different from that experienced by their nearest extant neighbours.   The

11   parameters measured were aspects of burst and routine swimming, and oxygen consumption.

12   **Swimming performance**

13   Routine swimming speeds in crustaceans can be strongly affected by acute temperature

14   changes (Lindström & Fortelius, 2001), but the effects of evolutionary adaptation to differing

15   habitat temperatures is not known.   When compared to the routine through-water swimming

16   speeds of the oceanic scavenging amphipod *Eurythenes gryllus* (at the similar depths but

17   lower temperature) the *Acanthephyra eximia* tracked here swam over twice as fast on average

18    $(0.18 \text{ m} \cdot \text{s}^{-1}$ at 4000 m) as the amphipods $(0.07 \text{ cm} \cdot \text{s}^{-1})$.   In length-specific terms an

19   individual *A. eximia* of mean size (5.7 cm) swam at 3.09 or 3.56 $L \cdot \text{s}^{-1}$ (4200 and 2357 m),

20   whereas a *E. gryllus* of the same size would swim at 1.3 $L \cdot \text{s}^{-1}$ (Laver *et al.*, 1985).   This

21   equates to a Q_{10} (2-14.5°C) of 1.99 or 2.23 and is typical for comparisons with a range of

22   amphipods and decapods (Laver *et al.*, 1985).   *Acanthephyra eximia* swims at similar speeds

23   to the krill species *Euphausia superba* (Kils, 1979) and *Euphausia* pacifica (Torres &

24   Childress, 1983).   Although high, such speeds are not unprecedented in the deep-sea, with

hydrothermal vent shrimp achieving through-water velocities of over 10 $L \cdot s^{-1}$ while holding

station in vent plumes (Kaartvedt *et al.*, 1994). *Acanthephyra eximia* has been observed at

Atlantic hydrothermal vents (Desbruyères *et al.*, 2001), so high routine activity levels under

conditions of elevated temperature may not be unusual for this species.

When compared to shallow-water decapods at the similar temperatures (Figure 2) the burst

swimming velocities and accelerations of *Acanthephyra eximia* are similar to performances

recorded for electrically stimulated tail-flips in shallow-water crayfish (Webb, 1979) and

lobster (Nauen & Shadwick, 1999). These animals have very much heavier carapaces than *A.*

eximia, and when comparisons are made with more lightly armoured decapods such as the

brown shrimp, *Crangon crangon* (Arnott *et al.*, 1998), the Mediterranean shrimp looks very

slow indeed. Peak length specific velocity ($\hat{U}_{max}$) for *A. eximia* of mean size (57 mm and 1.48

g) was 20.1 $L \cdot s^{-1}$, while $\hat{U}_{max}$ for *C. crangon* of the same length would be 32.0 $L \cdot s^{-1}$, and a

C. crangon of the same mass would have a $\hat{U}max$ of 36.5 $L \cdot s^{-1}$ (differences in length-weight

relationship mean that *C. crangon* are shorter than *A. eximia* of the same mass). The

differences in frame-rate between these studies appear unlikely to be the explanation for these

differences as Arnott *et al*'s (1998) study uses frame-rates both higher and lower than those

used in the present study without apparent effects on the velocities recorded. Few

comparative data for accelerations during tail-flip escape responses in decapods exist, but the

available evidence indicates that rates of acceleration in *A. eximia* are lower than those

measured in lobsters of the same mass (Nauen & Shadwick, 1999) despite the shrimp being of

greater length.

These data showing reductions in burst activity capacity but maintenance of routine

swimming performance would support the hypothesis that deep-water animals have reduced

selective pressure for burst activity due to the reductions in predation risk, either through

absence of suitable predators (due to the geographical isolation and recent existence of the

deep basins (Galil & Goren, 1994)), or because of reductions in light level (Childress, 1995).

1   Light-mediated effects on predation rate have been observed in the interactions between

2   shallow-living shrimp and seahorses (James & Heck Jr., 1994).

3   **Oxygen consumption**

4   As with routine swimming speed, the mass specific oxygen consumption of this species

5   appeared broadly similar to those of most oceanic deep-water crustacean species once

6   temperature and scale had been taken into account (Figure 3). The finding that temperature is

7   a strong predictor of metabolic rate at normal habitat temperature is in line with results for a

8   large range of ectothermic taxa, from bivalves (Peck & Conway, 2000; Heilmayer & Brey,

9   2003) to fish (Johnston *et al.*, 1991) across a wide temperature range.

10 Given the methodological problems encountered the oxygen consumption data for *A. eximia*

11 must be interpreted with caution. From this dataset it is not clear whether the reductions in

12 oxygen concentration within the chamber were having an effect on individual oxygen

13 consumption, or even on the number of respiring animals. Unfortunately technical difficulties

14 prevented collection of the data from other deployments that would have answered these

15 questions, and provided some much-needed replication. Variation in size between the

16 animals will have affected the proportion of the oxygen consumed by each individual, as

17 could variations in reproductive or moulting state. Further study of this species is clearly

18 required, and the existing oxygen consumption data merely provide an initial indication of

19 high metabolic activity in *A. eximia*.

20 A finding of high metabolic rate in *A. eximia* may be unsurprising, given the habitat

21 temperature of the population studied, but these data suggest that the energy consumption of

22 the Mediterranean shrimps animals is much higher than rates recorded in oceanic abyssal

23 scavenging crustaceans (Smith & Baldwin, 1982), and could therefore be associated with the

24 high routine activity levels observed in the Mediterranean species. In deep-sea fishes energy

25 supply appears to control routine swimming speed (Collins *et al.*, 1999; Priede *et al.*, 2003),

1   but as energy supply (from surface productivity) is thought to be low in the Eastern

2   Mediterranean (Psarra *et al.*, 2000) the high swimming speeds of this species are unlikely to

3   reflect a large overall energy budget.

4   If high routine swimming speeds were due to an increase in performance due to temperature-

5   related effects on muscle physiology then one might expect that burst performance would be

6   similarly affected. This is however not the case, and burst performance is rather low when

7   compared to similar shallow-living species. The discrepancy between routine and burst

8   performance tends to support an the ecological explanation that competition for scarce

9   resources drives high routine activity, while darkness and a lack of large predators over most

10   of their range have reduced the selective advantage of high burst performance.

15   **REFERENCES**

16   Albertelli, G., Arnaud, P. M., Della Croce, N., Drago, N. & Eleftheriou, A. 1992 The deep

17   Mediterranean macrofauna caught by traps and its trophic significance. *Comptes rendus de l'Académie*

18   *des sciences, Paris - Série III* 315, 139-144.

19   Angilletta Jr., M. J., Wilson, R. S., Navas, C. A. & James, R. S. 2003 Tradeoffs and the evolution of

20   thermal reaction norms. *Trends in Ecology & Evolution* 18, 234-240.

21   Arnott, S. A., Neil, D. M. & Ansell, A. D. 1998 Tail-flip mechanism and size dependent kinematics of

22   escape swimming in the brown shrimp *Crangon crangon*. *Journal of Experimental Biology* 201, 1771-

23   1784.

24   Bailey, D. M., Jamieson, A. J., Bagley, P. M., Collins, M. A. & Priede, I. G. 2002 Measurement of *in*

25   *situ* oxygen consumption of deep-sea fish using an autonomous lander vehicle. *Deep-Sea Research I*

26   49, 1519-1529.

27   Bailey, D. M., Bagley, P. M., Jamieson, A. J., Collins, M. A. & Priede, I. G. 2003 In situ investigation

28   of burst swimming and muscle performance in the deep-sea fish *Antimora rostrata*. *Journal of*

29   *Experimental Marine Biology and Ecology* 286/6, 295-311.

1   Britton, J. C. & Morton, B. 1994 Marine carrion and scavengers. *Oceanography and marine biology:*

2   *An annual review* 32, 369-434.

3   Cartes, J. E. & Maynou, F. 1998 Food consumption by bathyal decapod crustacean assemblages in the

4   western Mediterranean: predatory impact of megafauna and the food consumption-food supply balance

5   in a deep-water food web. *Marine Ecology and Progress Series* 171, 233-246.

6   Childress, J. J. 1995 Are there physiological and biochemical adaptations of metabolism in deep-sea

7   animals? *Trends in Ecology & Evolution* 10, 30-36.

8   Christiansen, B. 1989 *Acanthephyra* sp. (Crustacea: Decapoda) in the Eastern Mediterranean Sea

9   captured by baited traps. *Senkenbergiana Maritima* 20, 187-193.

10   Collins, M. A., Priede, I. G. & Bagley, P. N. 1999 *In situ* comparison of activity in two deep-sea

11   scavenging fishes occupying different depth zones. *Proceedings of the Royal Society B* 266, 2011-

12   2016.

13   Company, J. B. & Sardà, F. 1998 Metabolic rates and energy content of deep-sea benthic decapod

14   crustaceans in the western Mediterranean Sea. *Deep-Sea Research I* 45, 1861-1880.

15   Cowles, D. L., Childress, J. J. & Wells, M. E. 1991 Metabolic rates of midwater crustaceans as a

16   function of depth of occurrence off the Hawaiian islands - food availability as a selective factor.

17   *Marine Biology* 110, 75-83.

18   Desbruyères, D., Biscoito, M., Caprais, J.-C., Colaço, A., Comtet, T., Crassous, P., Fouquet, Y.,

19   Khripounoff, A., Le Bris, N., Olu, K., Riso, R., Sarradin, P.-M., Segonzac, M. & Vangriesheim, A.

20   2001 Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge near the

21   Azores plateau. *Deep-Sea Research I* 48, 1325-1346.

22   Fraser, K. P. P., Clarke, A. & Peck, L. S. 2002 Low-temperature protein metabolism: seasonal changes

23   in protein synthesis and RNA dynamics in the Antarctic limpet *Nacella concinna* Strebel 1908. *Journal*

24   *of Experimental Biology* 205, 3077-3086.

25   Galil, B. S. & Goren, M. 1994 The deep sea levantine fauna - new records and rare occurrences.

26   *Senkenbergiana Maritima* 25, 41-52.

27   Godø, O. R., Huse, I. & Michalsen, K. 1997 Bait defence behaviour of wolffish and its impact on long-

28   line catch rates. *ICES Journal of Marine Science* 54, 273-275.

29   Goldspink, G. 1998 Selective gene expression during adaptation of muscle to different physiological

30   demands. *Comparative Biochemistry and Physiology* 120, 5-15.

31   Guderley, H., A, J. & I 1996 Plasticity of fish muscle mitochondria with thermal acclimation. *The*

32   *Journal of Experimental Biology* 199, 1311-1317.

33   Heilmayer, O. & Brey, T. 2003 Saving by freezing? Metabolic rates of *Adamusium colbecki* in a

34   latitudinal context. *Marine Biology* 143, 477-484.

35   Hsü, K. J. 1972 When the Mediterranean dried up. *Scientific American* 227, 27-36.

36   James, P. L. & Heck Jr., K. L. 1994 The effects of habitat complexity and light intensity on ambush

37   predation within a simulated seagrass habitat. *Journal of Experimental Marine Biology and Ecology*

38   176, 187-200.

1   Johnson, T. P. & Bennett, A. F. 1995 The thermal acclimation of burst escape performance in fish: an
2   integrated study of molecular and cellular physiology and organismal performance. *The Journal of*
3   *Experimental Biology* 198, 2165-2175.

4   Johnston, I., Calvo, J. & Guderley, Y. H. 1998 Latitudinal variation in the abundance and oxidative
5   capacities of muscle mitochondria in perciform fishes. *Journal of Experimental Biology* 201, 1-12.

6   Johnston, I. A. & Walesby, N. J. 1979 Evolutionary temperature adaptation and the calcium regulation
7   of fish actomyosin ATPases. *Journal of Comparative Physiology - B* 129, 169-177.

8   Johnston, I. A., Clarke, A. & Ward, P. 1991 Temperature and metabolic rate in sedentary fish from the
9   Antarctic, North Sea and Indo-West Pacific Ocean. *Marine Biology* 109, 191-195.

10 Jones, E. G., Tselepides, A., Bagley, P. M., Collins, M. A. & Priede, I. G. 2003 Bathymetric
11 distribution of some benthic and benthopelagic species attracted to baited cameras and traps in the
12 eastern Mediteranean. *Marine Ecology Progress Series* 251, 75-86.

13 Kaartvedt, S., Van Dover, C. L., Mullineaux, L. S., Wiebe, P. H. & Bollens, S. M. 1994 Amphipods on
14 a deep-sea hydrothermal treadmill. *Deep-Sea Research I* 41, 179-195.

15 Kils, U. 1979 Swimming performance and escape capacity of Antarctic krill, *Euphausia superba*.
16 *Meeresforschung* 27, 264-266.

17 Laver, M. B., Olsson, M. S., Endelman, J. L. & Smith, K. L. 1985 Swimming rates of scavenging deep-
18 sea amphipods recorded with a free-vehicle video camera. *Deep-Sea Research I* 32, 1135-1142.

19 Lindström, M. & Fortelius, W. 2001 Swimming behaviour in *Monoporeia affinis* (Crustacean:
20 Amphipoda) - dependence on temperature and population density. *Journal of Experimental Marine*
21 *Biology and Ecology* 256, 73-83.

22 Morton, B. & Yuen, W. Y. 2000 The feeding behaviour and competition for carrion between two
23 sympatric scavengers on a sandy shore in Hong Kong: the gastropod *Nassarius festivus* (Powys) and
24 the hermit crab, *Diogenes edwardsii* (De Haan). *Journal of Experimental Marine Biology and Ecology*
25 246, 1-29.

26 Nauen, J. C. & Shadwick, R. E. 1999 The scaling of acceleratory aquatic locomotion: body size and
27 tail-flip performance of the California spiny lobster *Panulirus interruptus*. *Journal of Experimental*
28 *Biology* 202, 3181-3193.

29 O'Steen, S., Cullum, A. J. & Bennett, A. F. 2002 Rapid evolution of escape performance in Trinidadian
30 guppies (*Poecilia reticulata*). *Evolution* 56, 776-784.

31 Peck, L. S. & Conway, L. Z. 2000 *The myth of metabolic cold adaptation: oxygen consumption in*
32 *stenothermal Antarctic bivalves.* In: Harper E, Crame AJ (eds) The Evolutionary Biology of Bivalve
33 Molluscs. Cambridge University Press, Cambridge, p 441-450.

34 Peck, L. S. 2001 Ecophysiology of Antarctic marine ectotherms: limits to life. *Polar Biology* 25, 31-40.

35 Por, F. D. 1989 *The legacy of Tethys*. Kluwer Academic Publishers, Dordrecht.

36 Pörtner, H. O., Hardewig, I. & Peck, L. S. 1999 Mitochondrial function and critical temperature in the
37 Antarctic bivalve, *Laternula elliptica*. *Comparative Biochemistry and Physiology A* 124, 179-189.

38 Priede, I. G., Bagley, P. M., Armstrong, J. D., Smith, K. L. & Merrett, N. R. 1991 Direct measurement
39 of active dispersal of food-falls by deep-sea demersal fishes. *Nature* 351, 647-649.

1   Priede, I. G., Deary, A. R., Bailey, D. M. & Smith, K. L. 2003 Low activity and seasonal change in

2   population size structure of grenadiers in the oligotrophic abyssal Central North Pacific Ocean. *Journal*

3   *of Fish Biology* 63, 187-196.

4   Psarra, S., Tselepides, A. & Ignatiades, L. 2000 Primary productivity in the oligotrophic Cretan Sea

5   (NE Mediterranean): seasonal and interannual variability. *Progress in Oceanography* 46, 187-204.

6   Ravaux, J., Gaill, F., Le Bris, N., Sarradin, P.-M., Jollivet, D. & Shillito, B. 2003 Heat-shock response

7   and temperature resistance in the deep-sea vent shrimp *Rimicaris exoculata*. *Journal of Experimental*

8   *Biology* 206, 2345-2354.

9   Rome, L. C., Funke, R. P. & Alexander, R. M. 1990 The influence of temperature on muscle velocity

10   and sustained performance in swimming carp. *Journal of Experimental Biology* 154, 163-78.

11   Shillito, B., Jollivet, D., Sarradin, P.-M., Rodier, P., Lallier, F., Desbruyères, D. & Gaill, F. 2001

12   Temperature resistance of *Hesiolyra bergi*, a polychaetous annelid living on deep-sea vent smoker

13   walls. *Marine Ecology Progress Series* 216, 141-149.

14   Smith, K. L. 1978 Metabolism of the abyssopelagic rattail *Coryphanoides armatus*, measured *in situ*.

15   *Nature* 274, 362-364.

16   Smith, K. L. & Baldwin, R. J. 1982 Scavenging deep-sea amphipods: effects of food odor on oxygen

17   consumption and a proposed metabolic strategy. *Marine Biology* 68, 287-298.

18   Somero, G. N. & Siebenaller, J. F. 1979 Inefficient lactate dehydrogenases of deep-sea fishes. *Nature*

19   282, 100-102.

20   Tamburri, M. N. & Barry, J. P. 1999 Adaptations for scavenging by three diverse bathyal species,

21   *Eptatretus stouti*, *Neptunea amianta* and *Orchomene obtusus*. *Deep-Sea Research I* 46, 2079-2093.

22   Temple, G. K. & Johnston, I. A. 1998 Testing hypotheses concerning the phenotypic plasticity of

23   escape performance in fish of the family Cottidae. *Journal of Experimental Biology* 201, 317-331.

24   Torres, J. & Childress, J. 1983 Relationship of oxygen consumption to swimming speed in *Euphausia*

25   *pacifica*. 1. Effects of temperature and pressure. *Marine Biology* 74, 79-86.

26   Treude, T., Janßen, F., Queisser, W. & Witte, U. 2002 Metabolism and decompression tolerance of

27   scavenging lysianassoid deep-sea amphipods. *Deep-Sea Research I* 49, 1281-1289.

28   Van Buskirk, J. & Relya, R. A. 1998 Selection for phenotypic plasticity in *Rana sylvatica* tadpoles.

29   *Biological Journal of the Linnaean Society* 65, 301-328.

30   Wakeling, J. M. & Johnston, I. A. 1998 Muscle power output limits fast-start performance in fish.

31   *Journal of Experimental Biology* 201, 1505-1526.

32   Webb, P. W. 1979 Mechanics of escape response in crayfish (*Orconectes viridis*). *Journal of*

33   *Experimental Biology* 79, 245-263.

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1 **Table 1.   Maximum and mean through-water swimming speeds of *Acanthephyra eximia*.**

2 **Absolute (U) and length-specific ($\hat{U}$) steady swimming velocities are presented for animals at two**

3 **depths in the Rhodos Basin, Eastern Mediterranean. Significant differences between the depths**

4 **were detected for three of the parameters using ANCOVA.**

	Swimming velocity parameter	Depth	Swimming speed (m · s^{-1} or $L · s^{-1}$)		ANCOVA of depth distributions	
			Mean	Standard Error	$F_{31,33}$ (routine) $F_{16,18}$ (burst)	p
Routine swimming	Uw_{max}	2357 m	0.32	0.02	4.84	0.04
		4200 m	0.32	0.03		
	Uw_{mean}	2357 m	0.17	0.01	7.26	0.01
		4200 m	0.18	0.01		
	$\hat{U}w_{max}$	2357 m	6.66	0.44	5.8	0.02
		4200 m	5.61	0.38		
	$\hat{U}w_{mean}$	2357 m	3.56	0.23	3.29	0.08
			3.09	0.13		
		4200 m				
Burst swimming	U_{max}	2357 m	1.03	0.07	1.02	0.75
		4200 m	1.07	0.10		
	$\hat{U}_{max}$	2357 m	22.54	3.05	1.16	0.30
		4200 m	18.59	2.09		

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Figure Legends

Figure 1. Example of whole-animal and muscle performance during a "tail-flip" escape responses in the Mediterranean shrimp *Acanthephyra eximia* ($L = 0.059$ m) recorded at 100 Hz. A short (0.14 s) peak of power output (18 W · kg^{-1}, Figure 1A) accelerated the animal backward at up to 23 m · s^{-2} (Figure 1B). The peak velocity reached was 1.6 m · s^{-1} and occurred near the end of tail adduction (Figure 1C), after which the animal slowly decelerated and moved away using pleopod swimming.

Figure 2. Comparison of the peak length specific burst swimming speed ($\hat{U}_{max}$, L · s^{-1}) of *Acanthephyra eximia* (filled circles) to other decapod species that utilise tail-flip escape responses, over a wide range of animal sizes. There was a significant relationship between total wet mass (M, kg) and $\hat{U}_{max}$ (solid line, power law best fit, see main text for statistics). Comparative data presented are the quadratic best-fit line presented by Arnott et al (1998) for the Brown Shrimp *Crangon crangon* (dashed line) and the power law best fit for *Panulirus interruptus* (dotted line) from Nauen and Shadwick (1999).

Figure 3. Comparison of the mass specific metabolic rate of the deep Mediterranean shrimp *Acanthephyra eximia* with other active deep-water crustacean species. All data are scaled to a mass of 5 g and only experiments carried out within 1°C of normal habitat temperature for the species have been plotted. *A. eximia* is represented by the filled black circle. The solid line passing through this point indicates a calculated relationship with temperature for a Q10 of 2. Crosses indicate other *Acanthephyra* species studied by Cowles et al (1991), while the open circles are the other mid-water crustacean species investigated (Cowles *et al.*, 1991). Open triangles are data for "nektobenthic" Mediterranean species from Company and Sarda (1998). Data for deep Arabian Sea amphipods (Treude *et al.*, 2002) are indicated by the filled triangles.
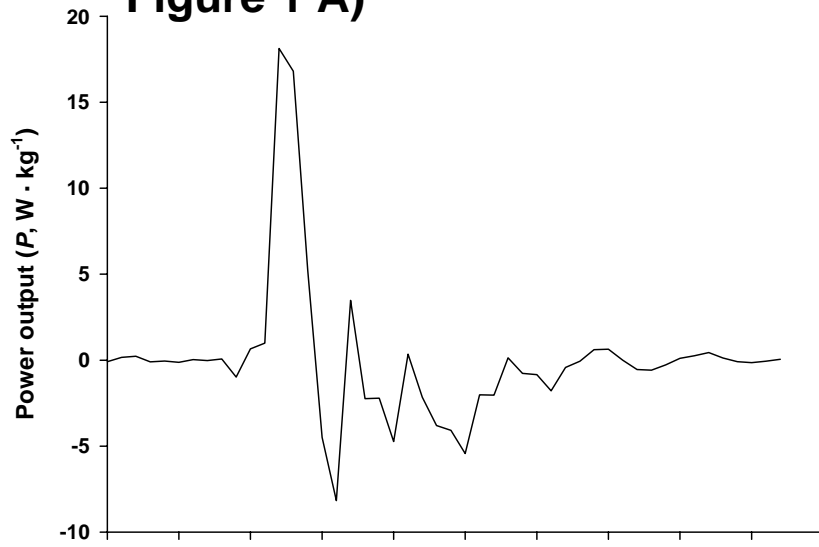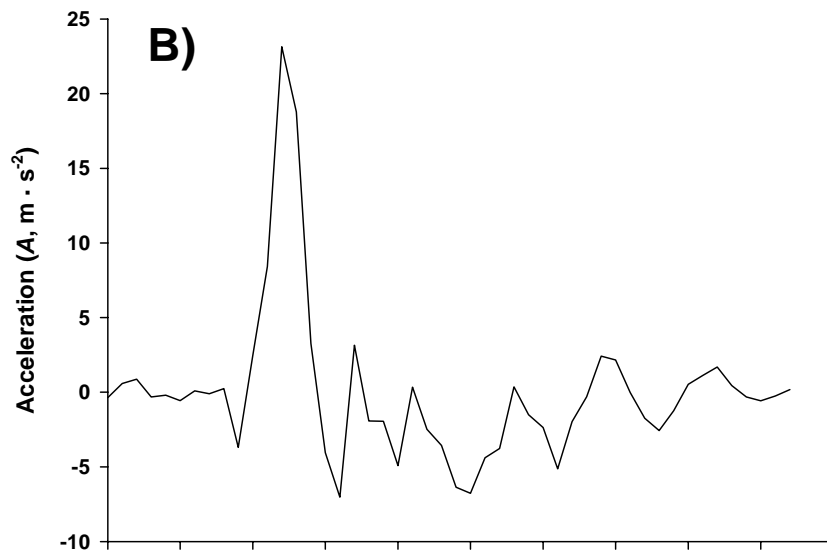
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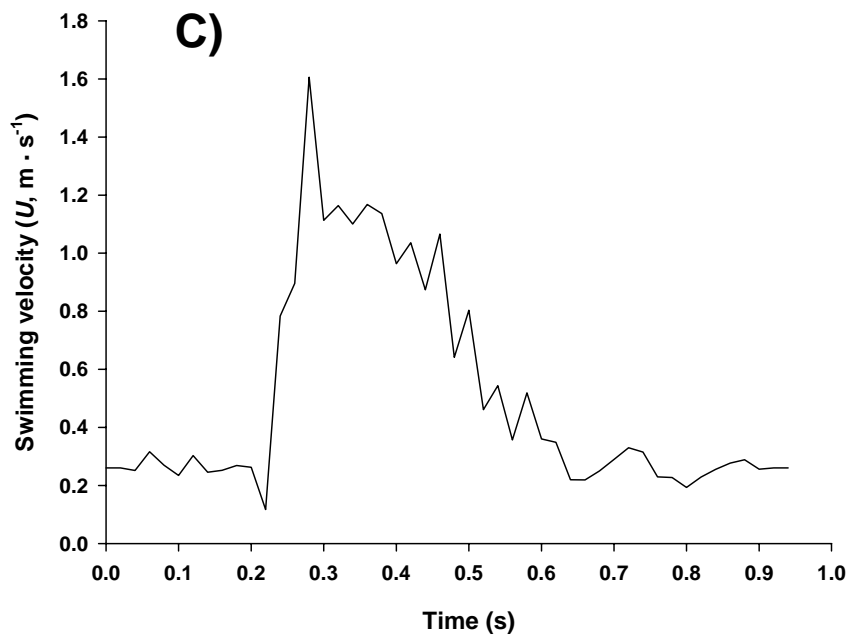2   Short title: Physiology of *Acanthephyra eximia* in the abyssal Mediterranean

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Figure 1 A)

Power output (P, W · kg^{-1})

B)

Acceleration (A, m · s^{-2})

C)

Swimming velocity (U, m · s^{-1})

Time (s)

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Figure 2

Plot showing $\hat{U}_{max}$, $L \cdot s^{-1}$ versus M (kg), with logarithmic axes ranging from 10^{-6} to 10^{0} on the horizontal axis and 1 to 100 on the vertical axis.

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Figure 3

MO$_{2, 5g}$ (ml · kg^{-1} · h^{-1})

Temperature (^{o}C)

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