Effects of chronic fluoranthene exposure on sibling species of *Capitella* with different development modes

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ABSTRACT: Toxic effects of the polycyclic aromatic hydrocarbon fluoranthene (FLU) on life-history traits and their demographic consequences were investigated in 3 non-interbreeding *Capitella* sibling species with different physiological tolerances and developmental modes: sensitive *Capitella* sp. S from oxygen-rich intertidal sediments of the North Sea (Germany); tolerant *Capitella* sp. M from sediments near shallow hydrothermal vents off Milos (Greece), a habitat low in organic matter with steep abiotic gradients and high sulfide concentrations; tolerant *Capitella* sp. I from New York (USA), known to dominate eutrophicated/polluted environments. Both *Capitella* spp. M and I can develop into hermaphrodites and have lecithotrophic larval development. In contrast, *Capitella* sp. S appears to be dioecious and has direct development with benthic juveniles. In life-table-response experiments (LTRE), juveniles from the 3 species were raised under different FLU concentrations (0 to 95 µg g^{-1} FLU), and data on age-specific survival, growth and life-history parameters were recorded at weekly intervals. Under control conditions, the 3 *Capitella* species differed markedly in a number of life-history traits and population growth rates (λ), with *Capitella* sp. S showing the lowest λ (1.05), and *Capitella* sp. M the highest (1.42). Chronic exposure to inreasing FLU concentrations also revealed species-specific differences in individual- and population-level toxic responses. Highest FLU concentrations (95 µg g^{-1}) markedly reduced juvenile survival and completely inhibited reproduction in *Capitella* sp. S, whereas individual life-history traits in *Capitella* spp. M and I were affected little, if at all. At the population level, the highest FLU exposures resulted in λ values of effectively zero in *Capitella* sp. S, whereas λ of *Capitella* spp. M and I remained >1. In conclusion, the combination of opportunistic life-history features, reproductive flexibility, and physiological adaptations enables *Capitella* spp. M and I to colonize habitats rapidly after local disturbance and to persist in stressed and unpredictable environments; whereas in *Capitella* sp. S, population extinction under toxicant stress mainly results from its physiological sensitivity.

KEY WORDS: *Capitella* sibling species complex · Fluoranthene · Life-history traits · Benthic and lecithotrophic development · Population growth rate

INTRODUCTION

Life-table-response experiments (LTRE) provide information on age-specific survival, growth, and fecundity in individuals raised under controlled laboratory conditions that can be translated to the population level by calculating population growth rate (λ).

This experimental approach is a powerful tool in analysing the responses of life-history variables to pollutants and can be used to explore demographic consequences of sublethal toxic effects on populations (e.g., Levin et al. 1987, 1996, Caswell 1989, 1996, Forbes & Calow 1999). λ expresses the population multiplication rate per unit time; in an increasing population λ is >1, in a constant size population λ = 1, in a declining population λ is <1. Toxic effects may include

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reduced growth, increased mortality, delayed repro-duction, and reduced reproductive output, leading to declines in λ or even population extinction. Changes in λ in response to changes in individual life-history traits depend on the life-history of the study organism, the severity of the toxic effect on each individual trait, as well as on the sensitivity of λ to changes in the life-history traits contributing to it (e.g., Levin et al. 1987, 1996, Caswell 1989, Kammenga et al. 1996, Hansen et al. 1999). Recent studies have shown the importance of density-dependence (i.e., food limitation) that may compensate or exacerbate negative toxic effects on population dynamics, and have suggested that den-sity-dependence should be incorporated into LTRE analyses (Grant 1998, Linke-Gamenick et al. 1999, Sibly 1999).

The polychaete species complex *Capitella capitata* is widely used as a pollution indicator, because it domi-nates the benthic communities of organically enriched or polluted marine sediments, where it can reach extremely high population densities (e.g. Grassle & Grassle 1974, 1976, Pearson & Rosenberg 1978, Mén-dez et al. 1997). *C. capitata* plays an important role in improving physicochemical properties of polluted sediments through its bioturbating activities (Gardner et al. 1979, Chareonpanich et al. 1993, 1994, Madsen et al. 1997). *C. capitata* represents a cryptic species com-plex, in which adult morphology is so similar among species that no effort has been made to separate this complex with proper taxonomical species-descriptions. Nevertheless, the so-called *Capitella* sibling species are reproductively isolated and differ substantially in a host of other parameters, e.g., in karyotypes and enzyme patterns (Grassle & Grassle 1976, Grassle et al. 1987, Wu et al. 1991), in ultrastructure of eggs and ovarian follicle cells, in larval, genital spine and sperm morphology (Eckelbarger & Grassle 1983, 1987), in eco-physiological characteristics (Gamenick et al. 1998b), in sediment-processing rates (Méndez et al. unpubl. data), and in reproductive features. For several co-occurring *Capitella* species of the North American East Coast, Grassle & Grassle (1976) described differences in numbers of larvae per brood, in egg size, in larval dispersal mode, and in the occurrence of hermaphro-dites. *Capitella* sibling species also show differences in larval mode, i.e., planktotrophic, lecithotrophic, and benthic development, depending on the larval stage hatching from the maternal brood tube (Grassle et al. 1987). These differences have been further explored by Méndez et al. (unpubl. data) to include *Capitella* species from other geographical regions.

One of the best known species of the complex is the opportunistic *Capitella* sp. I (Grassle & Grassle 1974, 1976). It has lecithotrophic development, and repro-duces via dispersing larvae with high survivorship that mature rapidly after settlement. Hence, this species exhibits rapid population explosions following local disturbances. From LTRE, Bridges et al. (1994) and Levin et al. (1996) concluded that *Capitella* sp. I's suc-cessful persistence in disturbed and oil-polluted habi-tats may result to a large extent from demographic adaptations, i.e., reduced age at first reproduction and increased fecundity under eutrophic conditions. In terms of physiological mechanisms, Forbes et al. (1994) stated that the physiology of *Capitella* sp. I is well-adapted to exploit low oxygen, high food conditions. Gamenick et al. (1998b) confirmed effective metabolic regulation of this species under stressed conditions, i.e., hypoxia and sulfide. For the first time, these authors compared several species of the *Capitella* com-plex, and found that *Capitella* sp. S originating from oxygen-rich low-sulfide habitats (Gamenick & Giere 1994) has no such regulatory abilities (i.e., is an oxy-conformer) and displays significantly lower survival rates under hypoxia and sulfide. Interspecific physio-logical differences were also found in response to xenobiotic toxicants, i.e., the polycyclic aromatic hydrocarbon fluoranthene (FLU), which is common in oil-polluted sediments (Linke-Gamenick et al. 2000). *Capitella* sp. I was found to be physiologically the best adapted, and showed the highest survival rates, whereas *Capitella* sp. S increased its metabolic rate and simultaneously reduced its food intake, resulting in high mortality rates. Morphologically the 2 species are indistinguishable, but they differ markedly in reproductive and larval modes. *Capitella* sp. S matures into females and males and hatches benthic juveniles that emerge from the parental brood tube after meta-morphosis (= direct development) in low numbers of 16 to 50 (Gamenick & Giere 1994, Méndez et al. unpubl. data). *Capitella* sp. I develops into females, males and hermaphrodites, and reproduces via free-swimming metatrochophore larvae (= lecithotrophic develop-ment) with up to 220 larvae per brood (Grassle & Grassle 1976, Méndez et al. unpubl. data).

In this study, we used these 2 species as examples of different life-history types and physiological toler-ances, and compared the effects of toxic stress (i.e., exposure to sublethal FLU concentrations) on several life-history parameters, and their demographic conse-quences. For comparison, we included an additional species with lecithotrophic development, *Capitella* sp. M (Gamenick et al. 1998a,b).

The purpose of this study was to determine whether *Capitella* species that differ in physiological tolerance and life-history features achieve similar λ under uni-form conditions. Are life-cycle variables of a physio-logically sensitive species necessarily more impaired under toxic stress, and what are the implications for its population dynamics? Knowing that *Capitella* species

vary physiologically and with respect to their life-history, another objective was to determine the relative importance of physiological adaptation versus life-history strategies in explaining demographic effects of toxic stress.

MATERIALS AND METHODS

***Capitella* spp.** Three previously identified, non-interbreeding sibling species from different geographical regions and habitat types were used in this study: *Capitella* sp. S (Gamenick & Giere 1994), from intertidal sediments of the Island of Sylt, North Sea, Germany; *Capitella* sp. M (Gamenick et al. 1998a) obtained from shallow hydrothermal vent areas in the Mediterranean Sea (Milos, Greece), an unpredictable environment characterized by steep gradients of temperature, salinity and pH and high sulfide concentrations (Dando et al. 1995, Thiermann et al. 1997); *Capitella* sp. I (Grassle & Grassle 1976), originally obtained from Setauket Harbor, New York, USA. These species reproduce readily in culture, and have been reared under identical conditions in our laboratory for many generations.

Worms were cultured in aquaria (20 × 30 cm) containing a 2 to 4 cm layer of azoic (i.e., frozen to –80°C twice) natural sediment (grain size of < 250 µm) and aerated seawater (32‰ S) at 16°C. The organic content of the sediment on which the worms were cultured was kept high by weekly additions of a 1:1:1 mixture of commercial fish-food flakes (Tetramin©), baby cereal (Beauvais©), and dried spinach (Forbes et al. 1996). Approximately 1 wk prior to the start of the experiment, several brood tubes from each species were transferred to dishes with a small amount of sediment and seawater and checked daily for larvae for use in the experiment.

Sediment. For the experiment, we used sieved (<63 µm), pre-frozen (to –80°C for several weeks) sediment from Roskilde Fjord (Denmark) with a water content of 67.79 ± 0.43% and an organic content of 6.62 ± 1.30% (n = 6). FLU sediment was prepared in 6 nominal concentrations: 0 [= control], 5, 10, 20, 40 and 80 µg g^{-1} dry wt sediment (= µg g^{-1}). A known volume of FLU stock solution (crystalline FLU [98% GC grade, Aldrich] in acetone carrier) was added to a known volume of thawed sediment in a glass flask that was subsequently shaken overnight (18 h) at room temperature. Nominal FLU concentrations were estimated by accounting for water content of the sediment. The sediment was homogenized and portioned (2 g portions). Sediment samples for FLU analysis were taken (see below), and the sediment was stored frozen (–20°C) until use in the experiment.

Experimental design. A total of 180 *Capitella* sp. S, 156 *Capitella* sp. M, and 144 *Capitella* sp. I juveniles (3 to 6 d old) were taken from the brood tubes and, for each species, randomly assigned to 6 FLU treatment groups (30 *Capitella* sp. S per group, 26 *Capitella* sp. M per group, and 24 *Capitella* sp. I per group). Each group was transferred into a petri dish containing 4 g of experimental sediment (with nominal concentrations of 0, 5, 10, 20, 40, and 80 µg g^{-1} FLU, respectively) and 7 ml seawater (30‰ S). The sediment and overlying seawater were 0.5 cm in height to enhance oxygen diffusion and prevent anoxia in the sediment. The 18 dishes were placed in a moisture chamber to reduce evaporation and kept in the dark at 18°C. The salinity was controlled every few days.

When juveniles became sexually mature (female = appearance of ovaries; male = appearance of genital spines), a female and a male were paired and transferred to new separate experimental dishes (= replicate pairs of worms per FLU concentration, i.e., up to 9 pairs), each with 2 g of experimental sediment and seawater, as described above. All dishes were monitored once a week for 175 d (*Capitella* sp. S), 133 d (*Capitella* sp. M), and 161 d (*Capitella* sp. I). On each census day, worms were removed from the sediment. The remaining sediment (pellets, tubes, mucus) was fixed in 75% ethyl alcohol, and data on worm survivorship, body size, wet weight, and reproduction were recorded. Worms were returned to their corresponding treatments with new experimental sediment and seawater. The following life-table parameters were estimated: age-specific survival, body volume over time until sexual maturity (= last measurement), juvenile specific growth rate (SGR), age at maturity, age at first reproduction (appearance of brood tubes), percentage of reproducing females/hermaphrodites, numbers of broods per female/hermaphrodite, age-specific fecundity, numbers of offspring per brood, time between broods, λ, and size-specific sediment processing rate (SSPR, feeding rate). Age at sexual maturity was distinguished from age at first reproduction in order to test whether FLU influenced the fraction of worms reaching maturity as well as the fraction of mature worms that actually reproduced.

FLU extraction and analysis. To measure FLU concentrations in the experimental sediments, 4 replicate sediment samples (0.5 g) were taken from each nominal FLU concentration and extracted with methanol and ethylacetate as described by Linke-Gamenick et al. (1999). Subsequently samples were processed and analyzed by HPLC (Kelley et al. 1993, Linke-Gamenick et al. 1999).

Data analysis. For each species, the body volume of randomly chosen individuals was measured at the start of the experiment (n = 10) and subsequently every 2 wk (n = 5) for each FLU treatment, until worms

reached the mature stage. Individual worms were videotaped with a camera connected to a dissecting microscope. Body length (L) and area (A) were measured (3 replicates per individual) using an image-analysis software program (Sigma Scan Pro, Jandel Inc., Erkrath, Germany). Worm body-volume (V) calculations were based on Forbes et al. (1994):

$$V = \pi A^2/4L \qquad (1)$$

Juvenile SGR until maturity was estimated as

$$\text{SGR} = (\ln S_2 - \ln S_1)/(t_2 - t_1) \qquad (2)$$

where S_1 and S_2 are body volumes at times t_1 (start) and t_2 (maturity) in days, giving the proportion grown per day.

Age-specific fecundity (m_x) was expressed as the number of offspring per week per reproducing female and hermaphrodite (modified after Levin et al. 1987).

For demographic analysis, λ was calculated directly from age-specific data on longevity and fecundity in the different FLU treatments using a simplified 2-stage model (Calow et al. 1997):

$$1 = nS_j\lambda^{-t_j} + S_a\lambda^{-t_a} \qquad (3)$$

where n = average number of offspring per brood per reproductive individual, S_j = juvenile survival (proportion surviving from birth to first reproduction), t_j = mean age at first reproduction, S_a adult survival (average proportion of adult females/hermaphrodites surviving between broods estimated over reproductive period) and t_a = average time between broods. All time units used to calculate λ are in weeks. The reproductive period is defined as the time between first and last breeding attempt averaged for each treatment. In cases of 1 brood per female, the second term to the right of the plus sign drops out of Eq. (3).

For SSPR, the fixed sediment samples were sieved through a 130 µm mesh to retrieve the fecal pellets (= sediment processed), and tubes and mucus without attached pellets were removed with forceps. The pellet samples were dried at 105°C (24 h) and subsequently weighed. Worm wet wt was converted to dry wt by multiplying by 0.13 (Méndez et al. unpubl. data). We estimated SSPR (feeding rate) as:

$$\text{SSPR} = (\text{dry wt of pellets})/ \\ (\text{mean worm dry wt} \times \text{time in days}) \qquad (4)$$

This gives a measure of feeding rate per unit worm body-size per day.

Statistics. Effects of FLU exposure on age and size at maturity, age at first reproduction, brood size, time between broods, and SSPR were analyzed separately for each species using 1-way ANOVA. Multiple comparisons were performed using Tukey's HSD test. In most cases the data deviated somewhat from normality and were not improved by transformation. Therefore ANOVA results were confirmed by Kruskal-Wallis analyses and by examination of notched box plots (McGill et al. 1978). These analyses were performed using SYSTAT Version 8.02. Effects of FLU exposure on survival were analyzed using Statistica Version 5, Survival Analysis Module, which is designed to handle censored data. To compare survival times among treatment groups, a score was first assigned to each survival time using Mantel's procedure; next a chi-square value was computed based on the sums (for each group) of this score. A significance level of 0.05 was employed throughout.

Parameters for which we obtained single values per treatment (i.e., survival times, percent total females, % reproducing females and/or hermaphrodites, fecundity, and λ) were compared qualitatively.

RESULTS

Fluoranthene

The measured FLU concentrations in the experimental sediments were generally close to nominal concentrations (Table 1). They differed considerably only from nominal 40 and 80 µg g^{-1} FLU, and these will be referred to as 50 and 95 µg g^{-1} FLU treatments, respectively.

Survival

No significant differences in the age-specific survival curves of the 3 *Capitella* species among the controls and lower FLU exposures (up to 50 µg g^{-1} FLU: Fig. 1) could be detected. At 95 µg g^{-1} FLU; median survival time (LT$_{50}$) was lowest in *Capitella* sp. S,

Table 1. Nominal and average (± 1 SD) measured fluoranthene concentrations (FLU; µg g^{-1}) in the experimental sediment (n = 4 repeated measurements)

Nominal FLU	Measured FLU
0	1.79 ± 1.07
5	6.61 ± 1.46
10	10.24 ± 0.77
20	21.50 ± 1.64
40	51.83 ± 4.60
80	94.79 ± 25.09

whereas *Capitella* sp. M showed a considerably higher LT_{50}, and *Capitella* sp. I was most tolerant to FLU (Table 2).

Chronic FLU exposure significantly reduced survival time in *Capitella* sp. S ($\chi^2 = 11.986$, df = 5, p = 0.035), but not in *Capitella* sp. M ($\chi^2 = 7.112$, df = 5, p = 0.213) or *Capitella* sp. I ($\chi^2 = 7.097$, df = 5, p = 0.214).

Growth

At the start of the experiments (Day 0), the average body volume of 10 randomly chosen juveniles was 0.007 ± 0.003 mm^3 in *Capitella* sp. S (3 to 4 d old), 0.015 ± 0.024 mm^3 in *Capitella* sp. M (5 to 6 d old), and 0.009 ± 0.002 mm^3 in *Capitella* sp. I (5 to 6 d old).

Body volumes over time differed significantly among species (Fig. 2). In all treatments (n = 6) *Capitella* sp. S grew more slowly and became mature at the smallest size, whereas *Capitella* sp. M and *Capitella* sp. I matured at larger body volumes. FLU had no detectable effect on body volume at maturity in *Capitella* sp. S (ANOVA: df = 5, 23; $F = 1.374$; p = 0.270) or in *Capitella* sp. M (ANOVA: df = 5, 24; $F = 2.021$; p = 0.112), but significantly reduced body volume at maturity in *Capitella* sp. I (ANOVA: df = 5, 24; $F = 3.762$; p = 0.012), with worms exposed to 50 and 95 µg g^{-1} FLU having smaller body volumes than control-group worms.

Juvenile SGR until maturity was lowest in *Capitella* sp. S, whereas *Capitella* sp. I showed highest growth rates (Fig. 3). FLU exposure significantly reduced juve-
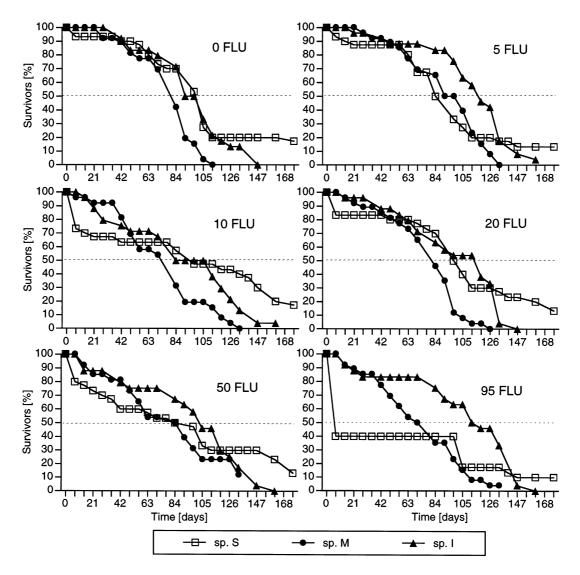

Fig. 1. *Capitella* sp. S, *Capitella* sp. M, and *Capitella* sp. I. Age-specific survivorship in different fluoranthene (FLU) treatments. Dashed lines = graphic median survival times (LT_{50})

Table 2. *Capitella* sp. S, *Capitella* sp. M, and *Capitella* sp. I. Median survival times (LT_{50}) and average (± 1 SD) vital rates in different FLU treatments (S_j: juvenile survival, S_a: adult survival, age at maturity (n = 6 to 24 worms), t_j: age at first reproduction (n = 2 to 15 worms), t_a: time between broods (n = 2 to 16 broods), 1: 1 brood, ×: no reproduction). See 'Materials and methods' for further details

Parameter	FLU ($\mu g\ g^{-1}$)					
	0	5	10	20	50	95
Capitella **sp. S**						
LT_{50} (d)	108	101	101	104	94	10
S_j (proportion)	0.20	0.20	0.47	0.30	0.30	×
S_a (proportion)	0	0	0	0	0	×
Age at maturity (d)	59 ± 1	63 ± 7	61 ± 5	62 ± 5	62 ± 5	67 ± 7
t_j (d)	115 ± 20	129	110 ± 17	115 ± 20	115 ± 21	×
t_a (d)	1	1	1	1	1	1
Capitella **sp. M**						
LT_{50} (d)	90	105	90	90	94	83
S_j (proportion)	0.77	0.77	0.54	0.65	0.54	0.35
S_a (proportion)	0.61	0.76	0.75	0.75	0.75	0
Age at maturity (d)	53 ± 11	55 ± 3	55 ± 3	51 ± 8	52 ± 9	59 ± 8
t_j (d)	58 ± 5	70 ± 23	80 ± 34	74 ± 14	67 ± 10	84 ± 21
t_a (d)	11 ± 4	8 ± 3	12	8	16 ± 11	1
Capitella **sp. I**						
LT_{50} (d)	104	124	103	124	110	131
S_j (proportion)	0.79	0.83	0.50	0.58	0.67	0.67
S_a (proportion)	0.79	0.72	0.68	0.70	0.63	0.74
Age at maturity (d)	41 ± 10	44 ± 11	56 ± 13	54 ± 10	58 ± 12	62 ± 13
t_j (d)	76 ± 10	85 ± 12	88 ± 11	97 ± 13	88 ± 14	96 ± 14
t_a (d)	19 ± 9	13 ± 5	13 ± 6	11 ± 4	10 ± 4	7 ± 10

nile SGR in *Capitella* sp. S (ANOVA: df = 5, 23; F = 7.666; p = 0.0002) and *Capitella* sp. I (ANOVA: df = 5, 24; F = 22.208; p < 0.0001), with worms exposed to 95 $\mu g\ g^{-1}$ FLU having significantly lower growth rates than worms in all other treatment groups. In *Capitella* sp. M toxic exposure did not significantly reduce the control SGR (ANOVA: df = 5, 24; F = 1.463; p = 0.239).

Reproductive parameters

In all treatments, *Capitella* sp. S matured either into females (F) (Table 3) or males. In *Capitella* spp. M and I, also hermaphrodites (H) were found in the controls as well as in the toxic exposures (except for no H in *Capitella* sp. M at 95 $\mu g\ g^{-1}$ FLU). It is interesting to note that in *Capitella* sp. I all H showed genital spines first (protandrous), whereas in H of *Capitella* sp. M female features appeared first (proterogynous), before developing into simultaneous H.

The average age at maturity (n = 6) was highest in *Capitella* sp. S, whereas *Capitella* sp. M and *Capitella* sp. I matured earlier (Table 2). Exposure to FLU significantly increased age at maturity in *Capitella* sp. S (ANOVA: df = 5, 95; F = 3.173; p = 0.011; 95 $\mu g\ g^{-1}$ FLU significantly longer than control) and in *Capitella* sp. I (ANOVA: df = 5, 100; F = 13.104; p < 0.001; 50 and 95 $\mu g\ g^{-1}$ FLU significantly longer than control and

5 $\mu g\ g^{-1}$ FLU significantly shorter than all higher concentrations). FLU had no detectable effect on age at maturity in *Capitella* sp. M (ANOVA: df = 5, 39; F = 0.605; p = 0.696).

In *Capitella* sp. S a low percentage of F reproduced successfully (Table 3), whereas in *Capitella* sp. M a higher percentage of F/H reproduced and in *Capitella* sp. I almost all F/H reproduced successfully. Highest FLU exposures completely inhibited reproduction in *Capitella* sp. S, whereas no significant FLU effect on the fraction of individuals that reproduced was observed in the 2 other species.

In all treatments, *Capitella* sp. S started to reproduce latest, whereas first reproduction occurred markedly earlier in *Capitella* spp. M and I (Table 2). For those worms that reproduced, exposure to FLU had no detectable effect on age at first reproduction in *Capitella* sp. S (ANOVA for 0 to 50 $\mu g\ g^{-1}$ FLU: df = 4, 14; F = 0.236; p = 0.914). Exposure to FLU had no detectable effect on age at first reproduction in *Capitella* sp. M (ANOVA: df = 5, 17; F = 1.221; p = 0.342), but significantly increased age at first reproduction in *Capitella* sp. I (ANOVA: df = 5, 37; F = 2.767; p = 0.032).

Capitella sp. S reproduced only once per female, whereas *Capitella* spp. M and I females and hermaphrodites made several breeding attempts during their adult period (Table 3). Time between broods in these 2
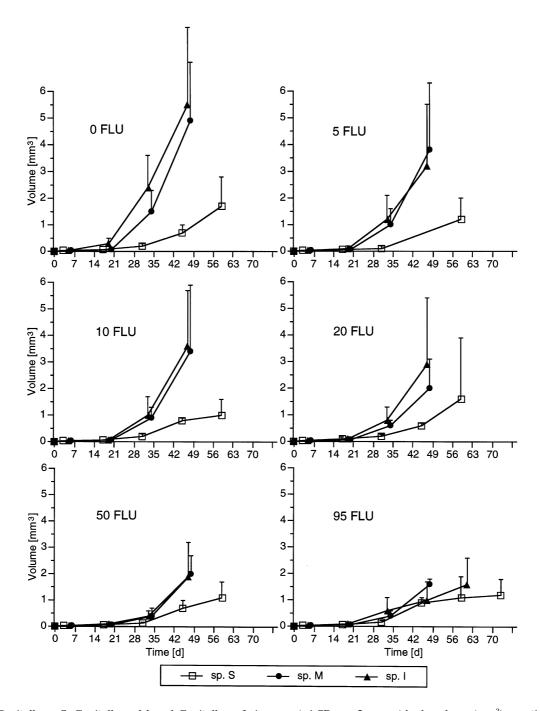
Fig. 2. *Capitella* sp. S, *Capitella* sp. M, and *Capitella* sp. I. Average (+1 SD, n = 5 worms) body volume (mm^3) over time in different FLU treatments

species was similar (Table 2). *Capitella* sp. I was the only species for which enough data were available for statistical analysis (in *Capitella* sp. M only 1 individual had >1 brood in the 10 and 20 µg g^{-1} FLU exposure groups, and no individuals reproduced more than once at 95 µg g^{-1} FLU). Effects of FLU on time between broods in *Capitella* sp. I were not significant (ANOVA: df = 5, 52; F = 2.174; p = 0.071).

Comparisons of age-specific fecundity in the controls indicate that *Capitella* sp. S with benthic juveniles had the lowest reproductive output, with a low lifetime fecundity per reproducing female and the shortest reproductive period (Fig. 4). In contrast, the lecithotroph *Capitella* spp. M and I showed substantially higher fecundities and longer reproductive periods.

Table 3. *Capitella* sp. S, *Capitella* sp. M, and *Capitella* sp. I. Fraction of females (F) and hermaphrodites (H), and reproductive parameters in different FLU treatments (n: number of offspring per brood per reproductive individual, ×: no reproduction)

Parameter	FLU (μg g^{-1})					
	0	5	10	20	50	95
***Capitella* sp. S**						
Total F (%)	69	63	84	74	69	75
Reproducing F (%)	17	7	19	6	18	×
Broods/reproducing F	1	1	1	1	1	×
Total offspring	41	18	41	13	55	×
n	10.3	18	4.6	13	13.8	×
***Capitella* sp. M**						
Total F (%)	25	10	14	12	12	19
Total H (%)	20	20	21	12	6	0
Reproducing F/H (%)	67	83	20	50	67	33
Broods/reproducing F/H	1.5	2.0	2.0	1.5	2.0	1.0
Total offspring	843	657	119	210	85	52
n	15.6	13.1	59.5	35	10.6	52
***Capitella* sp. I**						
Total F (%)	5	6	8	8	7	6
Total H (%)	42	39	42	39	53	50
Reproducing F/H (%)	78	100	100	100	100	78
Broods/reproducing F/H	2.1	2.7	2.0	2.2	2.0	2.3
Total offspring	1408	1842	541	516	1181	524
n	13.4	8.5	7.5	6.6	12.1	4.7

In all treatments, *Capitella* sp. S had smallest brood sizes, whereas *Capitella* spp. M and I reproduced with substantially higher numbers of larvae per brood (Fig. 5). So few individuals of *Capitella* sp. S reproduced that statistical analysis of FLU effects could not be performed. Exposure to FLU had no effect on brood size in *Capitella* sp. M (ANOVA: df = 5, 25; F = 0.784; p = 0.571), but significantly reduced number of larvae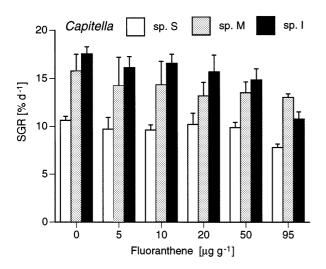 per brood in *Capitella* sp. I (ANOVA: df = 5, 86; F = 3.705; p = 0.004; control higher than 20 and 95 μg g^{-1} FLU).
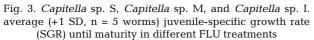
Under control conditions, *Capitella* sp. S showed the lowest λ, having values just above 1, whereas *Capitella* spp. M and I had higher λ values, indicating increasing population sizes (Fig. 6). At the highest FLU exposure, λ of *Capitella* sp. S dropped to zero (indicating population extinction), whereas λ of *Capitella* spp. M and I were reduced by ~11% but remained above 1.
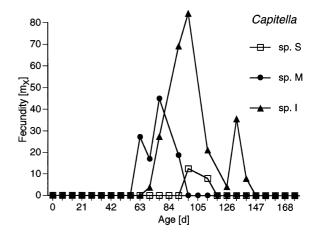

Fig. 3. *Capitella* sp. S, *Capitella* sp. M, and *Capitella* sp. I. average (+1 SD, n = 5 worms) juvenile-specific growth rate (SGR) until maturity in different FLU treatments

Fig. 4. *Capitella* sp. S, *Capitella* sp. M, and *Capitella* sp. I. Age-specific weekly offspring per reproducing female and hermaphrodite (= fecundity, m_x) in control treatments
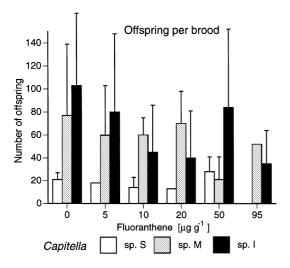
Fig. 5. *Capitella* sp. S, *Capitella* sp. M, and *Capitella* sp. I. Average (+1 SD, n = 2 to 23 broods) number of offspring per brood (= brood size) in different FLU treatments
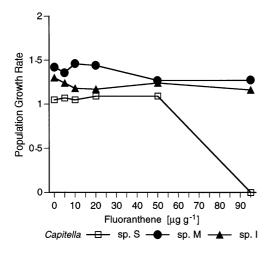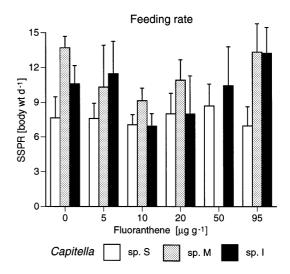

Fig. 7. *Capitella* sp. S, *Capitella* sp. M, and *Capitella* sp. I. Average (+1 SD, n = 3 to 17 worms) size-specific sediment-processing rate (SSPR = feeding rate) in different FLU treatments

Fig. 6. *Capitella* sp. S, *Capitella* sp. M, and *Capitella* sp. I. Population growth rates (λ) in different FLU treatments

Feeding rates

There were marked differences in SSPR among the *Capitella* species (Fig. 7). In all treatments, *Capitella* sp. S showed lower feeding rates than *Capitella* spp. M and I. There were no detectable effects of FLU on SSPR in *Capitella* sp. S (ANOVA: df = 5, 31; F = 1.035; p = 0.414). For *Capitella* sp. M (ANOVA [no data for 50 µg g^{-1} FLU]: df = 4, 14; F = 3.231; p = 0.045; control rates >10 µg g^{-1} FLU) and *Capitella* sp. I (ANOVA: df = 5, 39; F = 5.091; p = 0.001; 5 µg g^{-1} FLU feeding rates >10 µg g^{-1} FLU, and 10 and 20 µg g^{-1} FLU feeding rates <95 µg g^{-1} FLU), FLU had a significant effect on SSPR but the effects were not monotonic with respect to increasing FLU exposure (Fig. 7).

DISCUSSION

Interspecific differences

This study has shown that the 3 *Capitella* species differ markedly in a number of life-history traits and hence in their λ under identical non-toxic and density-independent laboratory conditions (see also summary in Table 4). *Capitella* sp. S with direct larval development grew slowest, matured at the smallest body volume, and reproduced latest with lowest fecundity, thus having the lowest λ. The lecithotrophic *Capitella* sp. M matured at an intermediate body volume, reproduced earliest with an intermediate fecundity, and had the highest λ under control conditions. *Capitella* sp. I, also with lecithotrophic free-swimming larvae, showed highest juvenile SGR, and matured at the largest body volume. This species had an intermediate reproductive age, the highest fecundity, longest reproductive period, and intermediate λ under control conditions. Despite the occurrence of hermaphrodites in *Capitella* spp. M and I, the proportion of potential egg-laying individuals was not higher in these 2 species than in *Capitella* sp. S. However, the percentage of F/H that actually laid eggs was substantially lower in *Capitella* sp. S than in the other 2 species (Table 3).

The marked differences in life-history variables, as shown in detail in this study, are of particular interest for this taxonomically difficult species group. They confirm interspecific differences within the complex in reproductive biology as first shown by Grassle & Grassle (1976) and recently by Méndez et al. (unpubl. data) that should be included in further species

Table 4. *Capitella* spp. Summary of differences in developmental modes and life-history parameters under control conditions and FLU effects. F: female; M: male; H: hermaphrodite; SGR: juvenile specific growth rate; –: reduced; +: increased; ne: no effect

	Capitella sp. S	*Capitella* sp. M	*Capitella* sp. I
Larval mode	Direct	Lecithotroph	Lecithotroph
Reproductive mode	F, M	F, M, H	F, M, H
Maturation size (mm^3)	2.0 ± 0.4	5.0 ± 2.2	6.2 ± 1.7
SGR (% d^{-1})	9.7 ± 1.0	14.0 ± 1.0	15.3 ± 2.4
Reproduction age (d)	115 ± 20	58 ± 5	76 ± 10
Lifetime fecundity (offspring per reproductive individual)	22	97	221
Offspring per brood	22 ± 6	77 ± 62	103 ± 63
Population growth rate	1.05	1.42	1.30
FLU effects			
LT$_{50}$	–	ne	ne
Maturation size	ne	ne	–
SGR	–	ne	–
Maturation age	+	ne	+
Reproduction age	ne	ne	+
Inhibition of reproduction	yes	ne	ne
Brood size	ne	ne	–

descriptions. In the *Capitella* complex a third developmental mode exists, with extremely high numbers of planktotrophic trochophore larvae leaving the maternal tube (Grassle & Grassle 1976, Méndez et al. unpubl. data), which are believed to have greatest dispersal capabilities. Attempts to get such larvae to metamorphose in the laboratory failed, and thus lifetable data are not available. However, these species have an enormous fecundity with brood sizes of >3500 larvae, and the potential for a long-dispersal larval stage (up to several weeks). Following the early study of Grassle & Grassle (1974), in which different benthic polychaete species were ranked in terms of their degree of opportunism defined by early maturation, their ability to increase rapidly to large population sizes, and their dispersal capabilities, we suggest a similar ranking in order of decreasing degree of opportunism within the *Capitella* complex according to life-history type. We suggest that the majority of described *Capitella* species for which reproductive data exist can be assigned to 1 of 3 groups: (1) Most opportunistic — *Capitella* spp. Ia, III (Grassle & Grassle 1976), *Capitella capitata* Type 2 (Pearson & Pearson 1991), *Capitella* sp. L (Gamenick & Giere 1994), *Capitella* Types K and Ct (Méndez et al. unpubl. data), with large brood sizes of small eggs and trochophore larvae that have a long dispersal time in the plankton; (2) *Capitella* spp. I, II (Grassle & Grassle 1976, this study), *Capitella* sp. M (Gamenick et al. 1998a, and this study) with lecithotrophic metatrochophore larve, with a shorter dispersal

stage (up to several days); (3) less opportunistic — *Capitella* spp. IIIa, II (Grassle & Grassle 1976), and *Capitella* sp. S (Méndez et al. unpubl. data, and this study), with direct benthic development and small brood sizes.

In the present study, the combination of differences in vital rates among species led to different population growth rates under identical non-toxic conditions. *Capitella* sp. S showed the lowest λ of (1.05), suggesting that this species has a low recolonization potential. From an ecological perspective this means that as a consequence of its demographic characteristics *Capitella* sp. S, and presumably the other species of this complex with a benthic developmental mode, may not belong to the 'typical' early colonizers following habitat disturbances.

In contrast, both lecithotrophic species *Capitella* spp. M (λ of 1.42) and I (λ of 1.30) have higher λ under identical conditions, which can be basically explained through earlier reproduction (*Capitella* sp. M), and higher fecundity (*Capitella* sp. I), as indicated previously for *Capitella* sp. I (Bridges et al. 1994, Levin et al. 1996). The lecithotrophic larvae of *Capitella* sp. I are able to delay metamorphosis and can select suitable settlement habitats, thus enhancing their survival capabilities (Grassle & Butman 1989, Pechenik & Cerulli 1991). All these life-history characters favour the ability of *Capitella* sp. I, and presumably *Capitella* sp. M, to achieve high population densities within short time periods, enabling them to colonize and persist in extreme habitats, such as unpredictable hydrothermal vent areas and eutrophic sewage outfalls.

Toxic effects

Chronic exposure to inreasing FLU concentrations revealed species differences in individual- and population-level toxic responses (Table 4). The highest FLU concentrations of 95 µg g^{-1} reduced juvenile survival markedly, and completely inhibited reproduction only in *Capitella* sp. S. The toxicant reduced juvenile SGR and delayed maturation in *Capitella* spp. S and I, and delayed reproduction as well as adult body size and brood size in *Capitella* sp. I, whereas individual life-history traits of *Capitella* sp. M were not affected. In terms of λ, this means that highest FLU exposures would be likely to lead to population extinction in

Capitella sp. S, while population dynamics of *Capitella* spp. I and M would suffer less impairment. We expect these patterns to be more complicated under density-dependent field conditions (i.e., food limitation), which might mask toxic effects on population dynamics at low FLU concentrations and magnify them at high levels (Linke-Gamenick et al. 1999).

However, the demographic results of this study basically mirror data on individual physiological performance (i.e., survival, respiration rates, anaerobiosis) under FLU exposure, and indicate a high sensitivity of *Capitella* sp. S relative to *Capitella* spp. M and I (Linke-Gamenick et al. 2000). At FLU concentrations of 100 µg g^{-1}, *Capitella* sp. S showed enhanced total metabolism associated with decreased survival. Linke-Gamenick et al. postulated that increased metabolic costs combined with apparently negligible food intake, as observed in *Capitella* sp. S, could explain the high mortality rates. In this study, slightly lower FLU levels were used, and adult survival and feeding rates of *Capitella* sp. S (and of the other 2 species) were not affected, as shown also by Méndez et al. (unpubl. data) under similar conditions. However, these sublethal concentrations nevertheless inhibited reproduction completely, leading to population extinction. Thus, toxicity tests of mortality alone would have severely underestimated population-level consequences of toxic exposure.

Some life-history traits of *Capitella* sp. I were affected by FLU exposure, whereas reproductive parameters in *Capitella* sp. M showed no toxic response. In *Capitella* sp. I, reproduction was delayed and brood size impaired, parameters that are important contributors to λ in this species (Levin et al. 1996, Hansen et al. 1999). However, in both species an 11% decline in λ with increasing toxic exposure was observed. We believe the reason why for *Capitella* sp. M we detected no significant effects on individual vital rates but a decline in λ, is the result of reduced sample size with increasing toxic concentration, resulting in very low statistical power for some of the vital rate comparisons.

In ecotoxicological terms, this case study on different *Capitella* species confirms that toxic responses of single individual-level traits cannot directly be translated to population-level responses as shown by several authors using decomposition and sensitivity analyses (Caswell 1989, Kammenga et al. 1996, Levin et al. 1996, Hansen et al. 1999), and recently reviewed by Forbes & Calow (1999). We would like to postulate this also for the linkage of individual feeding rates to λ. In this study, no clear toxic effects on individual feeding rates were detected, even at FLU exposures that led to population extinction in one of the species (i.e., *Capitella* sp. S). This is of particular interest in the use of energy budget models as a tool for linking individ-
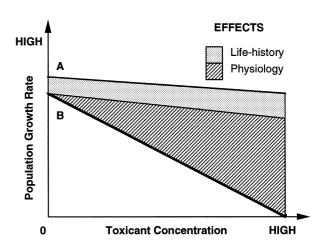

Fig. 8. Schematic approach to partition effects of life-history strategy and physiological sensitivity on λ differences in Species A and B in relation to toxicant exposure. (Species A represents *Capitella* spp. M or I, Species B *Capitella* sp. S)

ual-level effects on e.g., energy intake, to population-level consequences (Kooijman 1985). If based on the general assumption that toxic exposure results at first in a decrease in food intake, such models could underestimate population-level effects.

If we assume that all the differences in λ among species under control conditions are entirely due to different life-history strategies, and that changes in λ (within species) with increasing toxic exposure are due to physiological sensitivities of one or more vital rates, then changes in the magnitude of λ differences among species as toxic concentration increases can be attributed to differences in physiological sensitivity among species. This is shown conceptually in Fig. 8, where species A represents *Capitella* spp. M or I, while species B represents *Capitella* sp. S. We assume in the present study that there are no major differences among species in which vital rates are affected by toxic exposure and that these have different elasticities with respect to λ. This schematic approach allows us to partition the effects of life-history and physiology effects on λ differences among species in relation to toxic exposure. With respect to *Capitella* spp. I and S, the higher physiological sensitivity of *Capitella* sp. S exacerbates life-history differences under toxic exposure. A total of 67% of the λ differences found between *Capitella* spp. I and S at the highest toxic exposure could be attributed to physiology, whereas 33% could be attributed to life-history (Fig. 8).

Conclusions

In *Capitella* spp. M and I, the combination of opportunistic life-history features, reproductive flexibility,

and physiological adaptations enables them to colonize habitats rapidly after local disturbance and to persist in stressed and unpredictable environments, whereas in *Capitella* sp. S population extinction under FLU stress results mainly from the physiological sensitivity of this species.

Examining changes in λ differences among *Capitella* species with increasing toxic exposure may provide insight into the relative importance of life-history and physiology in explaining differences in population dynamics.

In addition, we would like to stress that some species of this complex, e.g., *Capitella* sp. S, cannot be regarded as a 'typical' opportunistic species, because of their physiological sensitivity in combination with their demographic characteristics (i.e., low population growth-potential).

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