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Density-dependent effects of a toxicant on life-history traits and population dynamics of a capitellid polychaete

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ABSTRACT: The toxic effects of the widespread polycyclic aromatic hydrocarbon (PAH), fluoranthene (FLU), on life-history traits of *Capitella* sp. M as a function of population density were investigated in a life-table-response-experiment (LTRE) lasting 134 d. Animals from laboratory cultures were exposed to 6 different FLU concentrations (range 0 to 80 µg FLU [g dry wt sed]$^{-1}$, ppm) at 3 population densities (range 529 to 36 842 worms m^{-2}), and survivorship, growth rate until maturity and reproductive parameters were recorded. Fluoranthene exposure significantly reduced juvenile survivorship in a concentration-dependent manner, whereas population density had no effect on this trait. In contrast, increasing density (= food limitation) was associated with significant decreases in body size at maturity and increased time to maturity, while FLU had no effect on these traits. Effects of FLU on time to first reproduction, % reproducing females, larvae per brood, broods per female and population growth rate (λ) varied in response to the intensity of density dependence. In general, interactions between FLU and density were compensatory (antagonistic) at low toxicant exposures, but synergistic at the highest. Population effects are summarised by effects on population growth rate. Our main result is that at low concentrations of FLU (0 to 40 ppm), increasing density alleviated FLU's effects on λ. Thus increasing FLU decreased λ at low density but had no effect at high density. At the highest concentrations of FLU, however, the reverse was the case ('synergistic effects'). Here, the effect of increasing density is to exacerbate the effects of FLU. This result is particularly important because it demonstrates that LTREs carried out at low density (non-food limited), as most have been in the past, may seriously underestimate effects in the field, where densities are generally high and likely to produce food limitation, as here. Our results suggest that when food availability is limiting, the impact of low levels of toxicant stress on population dynamics may be marginal. By contrast at higher toxicant exposures, food limitation exacerbates toxicant effects and may increase the likelihood of extinction.

KEY WORDS: Fluoranthene · *Capitella* sp. M · Population density · Organic pollution · Population growth rate

INTRODUCTION

Population dynamics theory provides a powerful tool for linking measured effects of toxicants on individual organism performance to consequences at the population level. Most experimental and theoretical work performed in this area has not incorporated density-dependence, however, the effects of which may be important in controlling the dynamics of natural populations (Grant 1998, Sibly 1999). Here, we present the results of an experimental analysis of the combined effects of density dependence, operating via food limitation, and toxicant exposure on the population dynamics of a sediment-dwelling polychaete. We have chosen fluoranthene (FLU) as our study toxicant, as it has previously been shown to influence growth and survival in *Capitella* species at relevant field concen-

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trations (Foss & Forbes 1997, unpubl. data). FLU is a polycyclic aromatic hydrocarbon (PAH) associated with partially combusted oil, and is one of the most abundant PAH identified in marine sediments.

The deposit feeding polychaete *Capitella capitata* is well known as an opportunistic species complex often associated with organically enriched and/or polluted environments (e.g. Grassle & Grassle 1974, 1976, Pearson & Rosenberg 1978). Recent studies suggest that this species complex is substantially more diverse in ecophysiological characteristics than has previously been recognized (Gamenick et al. 1998b). However, most sibling species, e.g. *Capitella* sp. I, are 'typical' opportunistic species with high reproductive rates, good dispersal abilities and high population growth rates. These worms can reach extremely high population densities in disturbed and oil-polluted habitats (Grassle & Grassle 1974, Sanders et al. 1980), a process which may be controlled to a large extent by demographic mechanisms, such as reduced age at maturity and increased fecundity (Bridges et al. 1994, Levin et al. 1996).

Until now ecotoxicological studies have used either unidentified *Capitella* sibling species (Bellan et al. 1972, Foret 1975, Rossi et al. 1976) or the 'most opportunistic' *Capitella* sp. I as a model organism to investigate toxicant-caused impacts on individual life-history traits and population growth rates (Bridges et al. 1994, Levin et al. 1996, Hansen et al. 1999). In this study we use another sibling species, *Capitella* sp. M, that was recently discovered in shallow hydrothermal vent areas in the Mediterranean Sea (Thiermann et al. 1997). *Capitella* sp. M reproduces via free-swimming larvae, like *Capitella* sp. I, but is far more tolerant to harsh environmental conditions, e.g. hypoxia and high sulfide concentrations, (Gamenick et al. 1998a,b). Studies of laboratory-cultured worms revealed that *Capitella* sp. M and *Capitella* sp. I have comparable life-history traits, e.g. an average time to first reproduction of about 50 d, and exposure to fluoranthene led to delayed reproduction to a similar degree in both sibling species (Rudbeck unpubl. data).

Based on simplified life-history scenarios Calow et al. (1997) recently employed an approach by which information from ecotoxicity tests can be used to explore effects on population dynamics. Using a series of life-history scenarios, the authors were able to make explicit and ecologically relevant links between test results on individual organism performance and their implications for population dynamics. Calow et al. (1997) hypothesized that density-dependent effects (e.g greater food availability for the survivors) are likely to compensate for toxicant-caused reductions in survival, growth and reproduction and therefore that predictions of toxicant effects based on low density experimental designs may provide overestimates of impacts on the dynamics of natural populations in which density dependence is the rule. Grant (1998) reached similar conclusions from models of how density dependence might affect observed effects of pollution on the copepod *Eurytemora affinis*.

In this paper we experimentally test the hypothesis proposed by Calow et al. (1997) and Grant (1998) that negative toxicant effects on population dynamics are buffered under conditions of high population density. Alternative hypotheses are (1) that the effects of toxicant stress and density-dependent effects act independently (additively) to control population growth rate, or (2) that density-dependent effects (such as food limitation) exacerbate the effects of toxicant stress, causing the population growth rate to reduce more rapidly than if the 2 stress factors operated independently. We used *Capitella* sp. M to evaluate population density-dependent effects of the widepspread PAH, FLU, on individual life-history traits (i.e. growth, maturation time, and reproductive output), as well as population growth rate (λ) of this opportunistic polychaete.

MATERIALS AND METHODS

Worms. *Capitella* sp. M was collected from sediments close to shallow hydrothermal vents off Milos, Greece (Gamenick et al. 1998a). In this habitat, low in organic content, it occurred at low densities, but as one of the dominant macrobenthic species. Worms were cultured in the laboratory in aquaria (20 × 30 cm) containing a 2 to 4 cm layer of azoic (i.e. frozen to –80°C twice) natural sediment (<250 µm grain size) and aerated seawater (32‰ S) at 16°C. The organic content of the sediment on which worms were cultured was kept high by weekly additions of ground 'worm food' (an equal mixture of Tetramin® fish food flakes, baby cereal, and dried spinach). Approximately 1 wk prior to the start of the experiment, several brood tubes were transferred to dishes with seawater and checked daily for larvae for use in the experiment.

Sediment. For the experiment, we used sieved (<250 µm), pre-frozen (to –80°C for several weeks) sediment from Roskilde Fjord, having a water content of 24.02 ± 0.31% (n = 6) and an organic content of 1.75 ± 0.47% (n = 10). FLU-contaminated sediment was prepared in 6 different nominal concentrations: 0 (= control), 5, 10, 20, 40 and 80 µg FLU (g dry wt sed)$^{-1}$ (= ppm). A known volume of FLU stock solution (crystalline FLU [98% GC grade, Aldrich] dissolved in acetone) was added to a known volume of thawed sediment in a glass flask that was subsequently shaken for ca 24 h at room temperature in the dark. Nominal FLU

concentrations were estimated by accounting for water content and organic carbon content of the sediment. The overlying water was removed by pipette and centrifuged (15 min at 4000 × *g*, 10°C) to recover any fine particles remaining in suspension. The recovered particles (i.e. the pellet) were returned to the remaining contaminated sediment. The sediment was homogenized, portioned and stored frozen until use in the experiment.

Experimental design. A total of 144 *Capitella* sp. M larvae (2 to 5 d old) were taken from 6 brood tubes and randomly assigned to 18 groups (8 larvae group^{-1}). Each group was transferred into a plastic dish with FLU-contaminated sediment (Fig. 1). To simulate different population densities, 6 groups (in 0, 5, 10, 20, 40, and 80 ppm FLU) were placed in large dishes with 29 mg of sediment and 29 ml of 31‰ S seawater (= OW density treatment), 6 groups were placed in dishes with 5 mg of sediment and 5 ml seawater (= MID density treatment), and 6 groups were placed in small dishes with 1 mg of sediment and 1 ml of seawater (= HIGH density treatment). Sediment and overlying seawater were each 1 cm in height to enhance oxygen diffusion and prevent anoxia in the sediment. All dishes were placed in a moisture chamber to keep evaporation low and kept in the dark at 18°C. The salinity was controlled every few days.

The dishes were monitored once a week for a duration of 134 d. Specimens were sieved out of the sediment, and data on survivorship, body size and reproduction were collected. Females in brood tubes were isolated and checked daily for reproductive output. All other *Capitella* sp. M were returned to their treatments prepared with fresh FLU-contaminated sediment and seawater. The following parameters were recorded: juvenile and adult survivorship, body volume at maturity (female = appearance of ovaries, male = appearance of genital spines), growth rate until maturity, time to maturity, time to first reproduction (appearance of brood tubes), percentage of reproducing females, number of broods per female, brood size (= larvae per brood), and population growth rate. Time to maturity was distinguished from time to 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.

The size of the worms was measured by videotaping them with a video camera connected to a dissecting microscope. The 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 volumes (V) were calculated, following Forbes et al. (1994), using the formula:

$$V = \pi A^2/4L$$

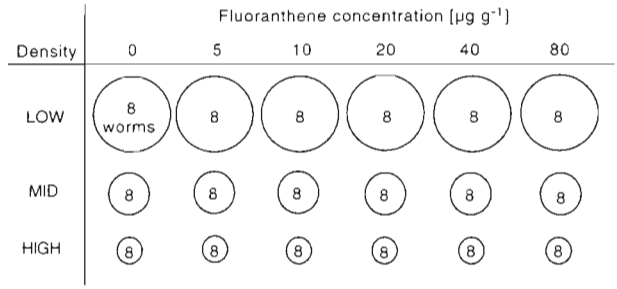

Fig. 1 Experimental design showing the different fluoranthene and population density treatments

Juvenile specific growth rates (SGR) until maturity were calculated as:

$$SGR = (\ln S_2 - \ln S_1)/(t_2 - t_1)$$

where S_1 and S_2 are body volumes at times t_1 and t_2 (in days) respectively.

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

$$1 = nS_j\lambda^{-t_j} + S_a\lambda^{-t_a}$$

where n is the number of female offspring at each breeding attempt over the adult period, S_j represents juvenile survival (percent surviving from birth to first reproduction), t_j is the average time to first breeding, S_a is adult survival (percent of adults surviving per unit time averaged over the adult period) and t_a is the time between breeding attempts. We employed a t_a of 1 wk for all treatments in the model since reproductive output was measured once per week and since our design required that we rear worms in groups, preventing individual females from being identified. Time units for the demographic analysis are expressed in terms of weeks.

FLU extraction and analysis. From each treatment (before worm addition and after 1 wk with worms) 3 to 5 sediment samples were taken and extracted as follows. From each sample 0.5 g sediment were taken, to which 1 ml methanol and 2 ml ethylacetate were added. After stirring for 5 s, the sample was exposed to ultrasonic treatment for 10 min, stirred again for 5 s, and finally centrifuged for 10 min at 3000 × *g* at 4°C. The supernatant was transferred to a new glass tube, and the extraction repeated twice (without methanol addition) as described above. After the supernatant was stirred again for 30 s, exposed to ultrasonic treatment for 10 min and stirred for another 30 s, about 7 ml were transferred into another glass tube held in a 32°C water bath. Subsequently the sample was evaporated with nitrogen gas to almost dryness, and, after addition of 1 ml ethylacetate, was stored frozen at −80°C until analysis.

Table 1. Measured fluoranthene (FLU) concentrations in the experimental sediment. n = number of replicates. 1 wk = measured after 1 wk with worms

Nominal FLU	Measured FLU (µg g^{-1} dry wt sed)	n
0	Not detectable	–
5	Not detectable	–
10	6.29 ± 1.2	4
20	16.87 ± 0.8	2
40	37.19 ± 5.3	4
80	74.94 ± 4.6	4
10 (1 wk)	2.7 ± 0.1	2
20 (1 wk)	7.68 ± 0.9	2
40 (1 wk)	24.59 ± 4.7	5
80 (1 wk)	61.80 ± 8.5	6

FLU concentrations were measured by HPLC modified after Kelley et al. (1993). The HPLC system was equipped with a Waters 600 E pump (Millipore instruments), a Wisp 700 autosampler, a Nucleosil precolumn (10 C18), a Primesphere column (4.6 mm by 25 cm, 5 µm C18-HC 110 A; Mikrolab, Aarhus, Denmark), and a Waters 994 fotodiode array detector. The mobile phase was a linear gradient of methanol-water (3 solvents, 30 to 90% methanol [vol./vol.], less than 0.5% acetic acid) running for 65 min at 0.85 ml min^{-1}. UV absorbance was measured at 254 nm, and peak areas were integrated with a Millenium computer programme (version 2.15).

Statistical analysis. Effects of population density and FLU exposure on juvenile specific growth rate (log_{10} transformed), age and size at maturity, age at first reproduction, and the number of larvae per brood were tested by 2-way ANOVA, using Statistica version 5. In cases for which 1 of the main effects was significant, Duncan's multiple range test was used to test for pairwise differences based on separate 1-way ANOVAs for subsets of the data (e.g. effects of FLU on juvenile SGR were tested separately for each density treatment). For each density × FLU treatment there was only 1 value for percent juvenile survival. Effects of density on percent juvenile survival were tested by 1-way ANOVA for data pooled among FLU treatments following visual inspection of the data (which indicated no obvious effects of density but possible effects of FLU). Differences in the survival functions and average lifespan were analyzed using Statistica's Survival Analysis Module, which is designed to handle censored data. To compare survival times among treatment groups a score is first assigned to each survival time using Mantel's procedure; next a chi-square value is computed based on the sums (for each group) of this score.

The design of the experiment prevented error estimates for percent reproducing females, broods per female, and total larvae produced. Therefore, these parameters were compared qualitatively.

Table 2. Worm density (adults), fraction of females, total numbers of broods and larvae and reproductive parameters in the different experimental treatments. – = no reproduction. + = anoxic event in the LOW density treatment

FLU	µg g^{-1}	0	5	10+	20	40	80
Low	Worms m^{-2}	1058	1235	1058	1058	882	529
	Total females (%)	33	57	50	67	40	67
	Reproducing females (%)	100	100	100	100	100	100
	Total broods	6	13	3	11	6	5
	Broods/female	3	3.3	1	3	3	2.5
	Total larvae/treatment	1281	2411	545	1374	563	555
	Larvae/total females	641	603	182	344	282	278
Mid	Worms m^{-2}	7292	7292	6250	7292	3125	3125
	Total females (%)	57	57	67	71	67	67
	Reproducing females (%)	100	75	75	100	100	0
	Total broods	6	5	6	11	5	0
	Broods/female	1.5	1.3	1.5	2.2	1.7	–
	Total larvae/treatment	594	514	520	943	551	0
	Larvae/total females	146	129	130	189	184	0
High	Worms m^{-2}	36824	36842	31579	36842	21053	15791
	Total females (%)	43	57	50	71	75	67
	Reproducing females (%)	67	40	67	60	67	0
	Total broods	2	2	1	3	2	0
	Broods/female	0.7	0.5	0.3	0.6	0.7	–
	Total larvae/treatment	66	40	39	63	68	0
	Larvae/total females	22	10	13	13	23	0

RESULTS AND DISCUSSION

General

A comparison of nominal and measured sediment FLU concentrations in the 6 different FLU treatments is shown in Table 1. The population densities after juvenile mortality (Week 4) ranged between 529 and 1058 worms m^{-2} in the LOW density treatment, from 3125 to 7292 worms m^{-2} in the MID density treatment and between 15 790 and 36 842 worms m^{-2} in the HIGH density treatment (Table 2). Once during the experiment on Day 43 an anoxic event occurred in the LOW density treatment at 10 µg FLU (g dry wt sed)$^{-1}$ that reduced the number of worms to 38 % of the starting density.

Mortality

Population density had no obvious effect on percent juvenile survival (Fig. 2). In contrast, FLU exposure at concentrations of up to 40 ppm and 80 ppm FLU, that is in the range of polluted harbor sediments, significantly (F = 16.49, df = 5, p = 0.00005) reduced juvenile survivorship at all densities.

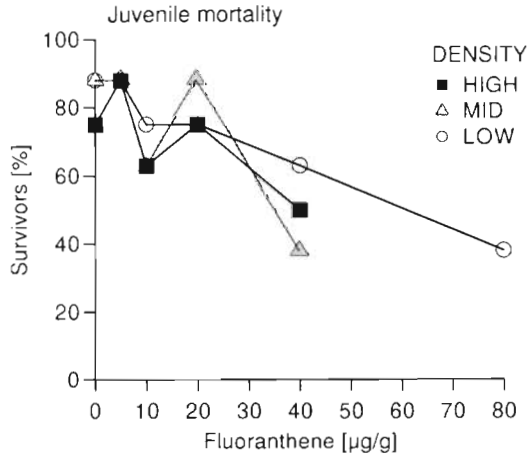

Fig. 2. Juvenile mortality: survivorship of *Capitella* sp. M from birth to first reproduction at different fluoranthene concentrations and population density treatments

Exposure to fluoranthene had no effect on adult survival and the overall lifespan of animals at LOW (χ^2 test, p = 0.607) and HIGH (χ^2 test, p = 0.121) density and a marginally significant effect (χ^2 test, p = 0.059) in the MID density treatment (Fig. 3, summary Table 3).

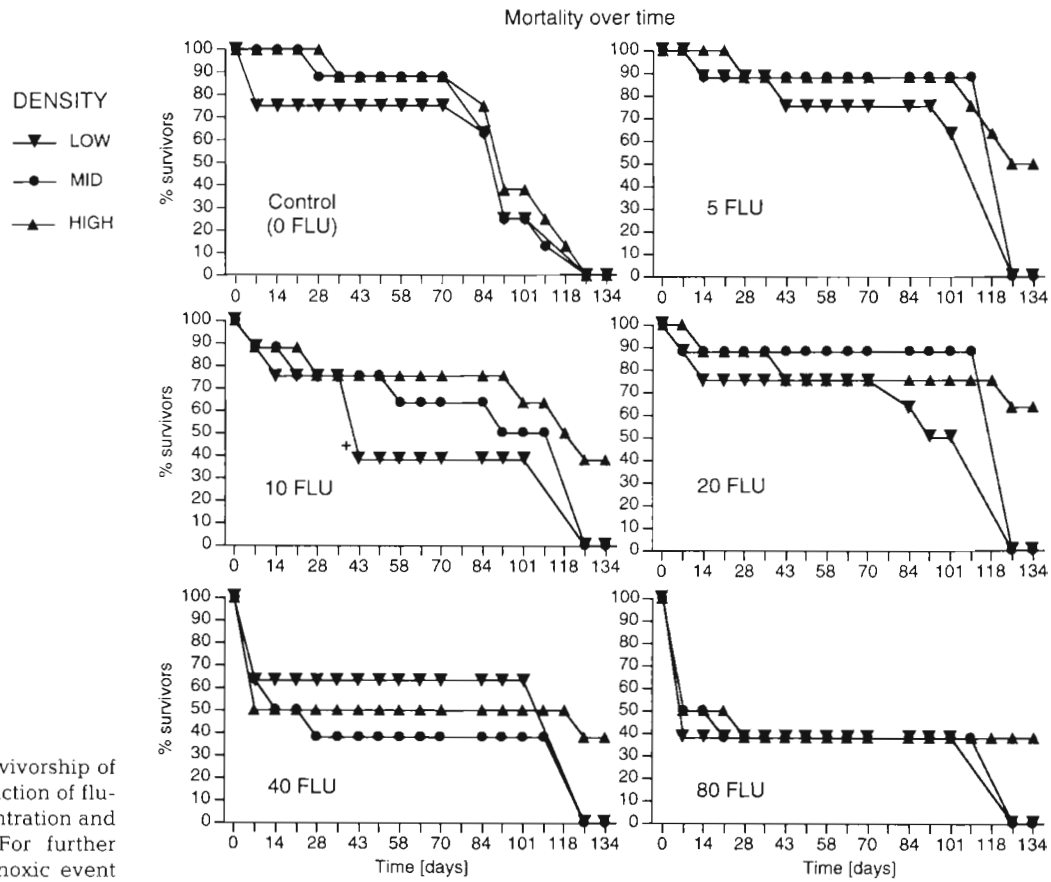

Fig. 3. Age-specific survivorship of *Capitella* sp. M as a function of fluoranthene (FLU) concentration and population densities. For further details see text. + = anoxic event

Table 3. Summary of density and fluoranthene (FLU) effects (•) and type of interactions between them on life-history traits of *Capitella* sp. M. Juv = juvenile, SGR = specific growth rate, repr = reproduction, A = antagonistic, S = synergistic

	Density effect	FLU effect	Density dependence of FLU effect	
			0–40 ppm FLU	40–80 ppm FLU
Juv survival		•		
Lifespan	•			
Juv SGR	•	•	A	A
Size at maturity	•			
Time to maturity	•			
Time to first repr	•	•	A	S
% reproducing	•	•		S
Larvae/brood	•	•	A	S
Broods/female	•	•		S
Pop growth rate	•	•	A	S

Density did not influence lifespan in control exposures. In contrast, we observed a significantly longer lifespan with increasing density at 5 (χ^2 test, p = 0.027) and 20 (χ^2 test, p = 0.012) ppm FLU. Though a similar trend was apparent in the other FLU treatments, the differences were not significant (χ^2 test, 10 ppm FLU: p = 0.19; 40 FLU: p = 0.98; 80 ppm FLU: p = 0.76).

In contrast, it has been shown for other polychaetes (i.e. *Neanthes arenaceodentata*) that high population density can have significant negative effects on adult survival (Pesch et al. 1987). The authors assigned this to aggressive behavioral interactions between worms, primarily the adults. However, it is interesting to note that in our study at increased population densities FLU-exposed worms had longer lifespans (Fig. 3), although significant only at 5 and 20 ppm FLU.

Growth

At the start of the experiment (Day 0) the average body volume of 12 randomly chosen larvae was 0.02 ± 0.002 mm^3, varying from 0.01 mm^3 (length: 0.9 mm, 2 d old) to 0.05 mm^3 (length: 2.1 mm, 5 d old).

HIGH population density had a significant negative effect on juvenile SGR (F = 43.536, df = 2, p < 0.0001), leading to smaller body volumes in *Capitella* sp. M (Figs. 4 & 5). This can be clearly attributed to limited food availability. The strong dependence of growth on food availability has been well described for *Capitella* sp. I (Tenore 1977, Forbes & Lopez 1990, Tsutsumi et al. 1990, Bridges et al. 1994).

At LOW population density high FLU concentrations of 40 and 80 ppm FLU significantly reduced juvenile SGR (F = 4.027, df = 5, p = 0.009), while, in MID and HIGH density treatments we could not detect an additional effect of FLU on juvenile SGR (MID: F = 0.316, df = 5, p = 0.898; HIGH: F = 0.873, df = 5, p = 0.515). This is consistent with studies on *Capitella* sp. I under non-food-limited conditions. For example Foss & Forbes (1997) showed that exposure to 100 ppm FLU (for 2 wk) reduced body volume specific growth rates by 50% compared to worms grown on uncontaminated sediment.

The fact that at MID and HIGH treatments juvenile SGR of *Capitella* sp. M was reduced to such an extent that an additional FLU effect was not detectable indi-

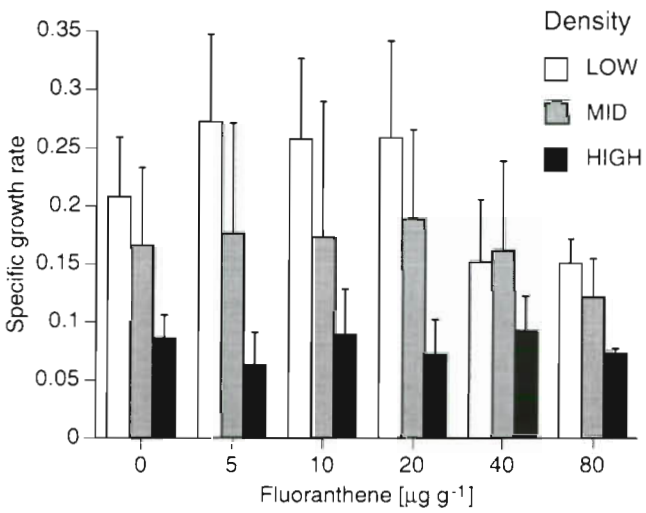

Fig. 4. Juvenile specific growth rate (proportion per day) of *Capitella* sp. M until maturity in different fluoranthene concentrations and population density. n = 2 to 7 specimens

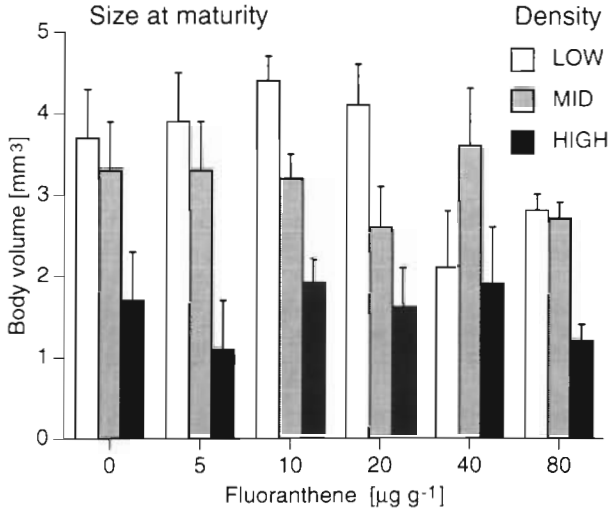

Fig. 5. Average body volume at maturity of *Capitella* sp. M as a function of fluoranthene concentration and population density. n = 2 to 7 specimens

cates an antagonistic (compensatory) interaction betweeen density and toxicant effects (see also Table 3).

Size and age at maturity

Density also strongly affected size at maturity (F = 18.31, df = 2, $p < 0.0001$), with largest body volumes in LOW density and smallest body volumes in HIGH density treatments (Fig. 5). In contrast, FLU had no effect on the average body volume at maturity in any of the density treatments (LOW: F = 1.387, df = 5, p = 0.266; MID: F = 0.578, df = 5, p = 0.716; HIGH: F = 2.399, df = 5, p = 0.070).

Likewise, time to maturity was strongly influenced by population density (F = 31.054, df = 2, $p < 0.0001$), with shortest maturation times at LOW density (28.8 ± 5 d, n = 6) and longest at HIGH density (62.2 ± 7 d, n = 6, Fig. 6). FLU had no effect on time to maturity at any density (LOW: F = 1.976, df = 5, p = 0.120; MID: F = 0.393, df = 5, p = 0.849; HIGH: F = 0.413, df = 5, p = 0.835).

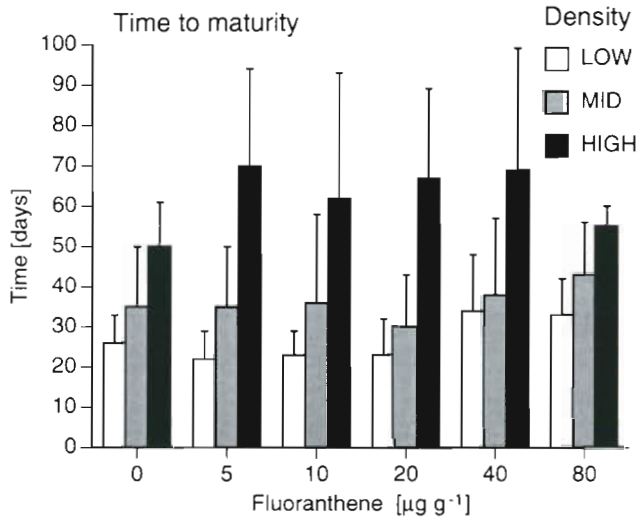

Fig. 6. Average time to maturity of *Capitella* sp. M as a function of fluoranthene concentration and population density. n = 2 to 7 specimens

Reproductive parameters

Population density had a highly significant effect on time to first reproduction (F = 57.686, df = 2, $p < 0.0001$, omitting 80 ppm FLU treatments, Fig. 7). Time to first breeding was shortest in LOW and MID density treatments and markedly delayed at HIGH population density, especially at higher FLU. Exposure to FLU significantly affected time to first reproduction at LOW density (F = 3.54, df = 5, p = 0.037). At MID density effects of FLU up to 40 ppm FLU were marginal (F = 0.06, df = 4, p = 0.062) and at HIGH density there was no effect of FLU up to 40 ppm FLU (F = 0.675, df = 4, p = 0.633). However, in both MID and HIGH density reproduction was completely inhibited at the highest FLU concentrations of 80 µg (g dry wt sed)$^{-1}$.

FLU exposure had no effect on the percentage of reproducing females at LOW density, whereas at MID and HIGH density 80 ppm FLU inhibited reproduction (Table 2). Population density had a strong effect with 100% of female *Capitella* sp. M reproducing at LOW density and only 40 to 67% of females reproducing at HIGH density in all treatments.

FLU decreased the number of larvae per brood at LOW density (F = 2.522, df = 5, p = 0.046, Fig. 8). Duncan's test showed 40 and 80 ppm FLU to be significantly different from 0, 5, 10 and 20 ppm FLU. At MID and HIGH densities, no effect of FLU was detectable until 80 ppm FLU, at which no reproduction occurred (omitting 80 ppm FLU gives for MID: F = 0.485, df = 4, p = 0.746; for HIGH: F = 0.499, df = 4, p = 0.740). Population density significantly affected brood size (F = 17.487, df = 2, $p < 0.0001$) with the highest number of larvae per brood produced at LOW density (214 ± 75 SD, 0 FLU, n = 6), while at HIGH density an average of 34 ± 4 SD larvae per brood (40 ppm FLU, n = 2) were produced.

Exposure to FLU had no effect on the estimated number of broods per female at LOW density, and at MID and HIGH densities, no effects were observed until 80 ppm FLU at which no reproduction occurred (Table 2). The number of broods per female were markedly influenced by population density, with the

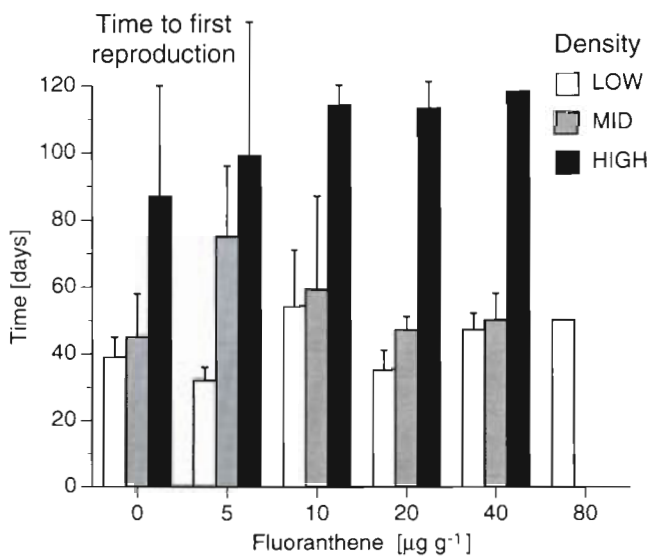

Fig. 7. Average time to first reproduction of female *Capitella* sp. M as a function of fluoranthene concentration and population density. n = 2 to 5 specimens

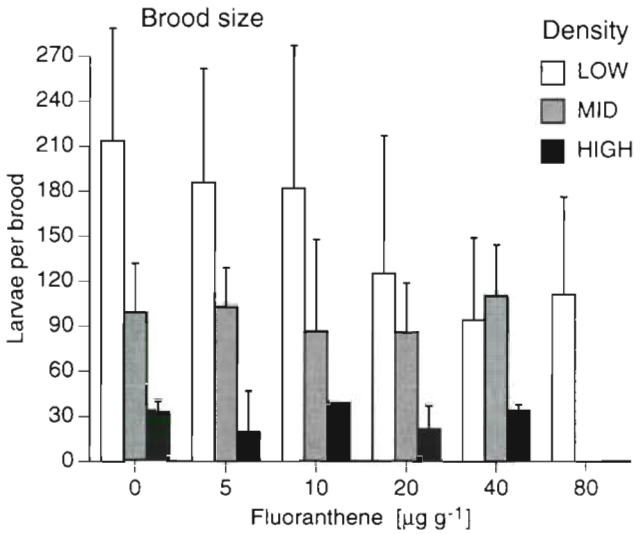

Fig. 8. Average number of larvae per brood as a function of fluoranthene concentration and population density. n = 2 (HIGH) to 13 (LOW) broods

largest number of broods produced at LOW density (up to 3.3 broods female^{-1}) and the smallest number of broods at HIGH density (between 0 and 0.7 broods female^{-1}). The anoxic event in 10 FLU at LOW density reduced the number of broods drastically to 1 female^{-1}.

A strong dependence of reproduction on food availability is also well described for other sibling species of the *Capitella capitata* complex. Bridges et al. (1994) demonstrated a 3- to 4-fold higher average per brood fecundity for *Capitella* sp. I grown in sewage and cyanobacteria treatments compared to marsh mud (i.e. control) and hydrocarbon treatments. Moreover, Levin et al. (1996) confirmed for the same species that total lifetime fecundities were elevated in organically enriched treatments. For an unidentified sibling species Qian (1994) reported that size and egg production increased with increasing food rations, and thus individuals fed a high food ration grew to a larger body size and produced more offspring.

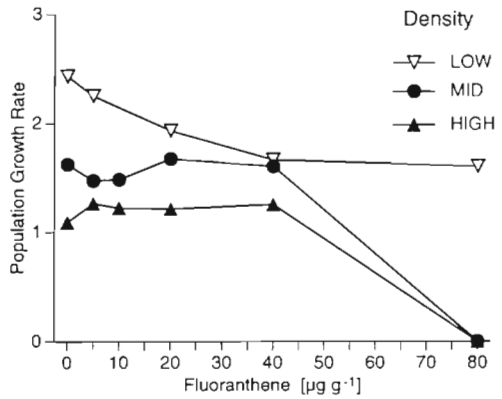

Fig. 9. Population growth rate (λ) as a function of fluoranthene concentration and population density

Population growth rates (λ)

The highest λ of up to 2.43 occurred at LOW density, whereas at MID and HIGH densities λ was substantially lower, never exceeding values of 1.67 and 1.25, respectively (Fig. 9). At LOW density, λ showed a generally decreasing trend with increasing FLU concentration. At MID and HIGH densities, however, λ remained more or less constant until the highest exposure of 80 ppm FLU at which λ dropped to zero, indicating population extinction.

One advantage of life-table-response-experiments (LTREs) is that the contributions of changes in individual life-history traits to changes in λ can be determined. For *Capitella* sp. I, Levin et al. (1996) showed that hydrocarbons, having little effects on survivorship or growth, can have enormous consequences for population dynamics through delayed maturation and reduced fecundity. The authors showed that treatment effects on older individuals had little or no impact on the population dynamics of their rapidly expanding populations. Also Hansen et al. (1999) showed for *Capitella* sp. I that toxicant effects on juvenile mortality and time to first reproduction were very important in terms of their influence on λ. The sensitivity of λ to individual life-history traits cannot in general be predicted *a priori*, however, and depends on the starting value of λ, the life-history type of the study organism, and a host of other factors (Caswell 1989, Calow et al. 1997, Kammenga et al. 1996). However, an important advantage of employing λ as an effect endpoint is that it integrates complex and/or conflicting effects of toxicants on different individual-level traits (Forbes & Calow in press).

DISCUSSION

Table 3 summarises the main results. FLU exposure significantly reduced juvenile survivorship and juvenile SGR in a concentration-dependent manner, and affected all the reproductive parameters, but had no effect on lifespan or size or age at maturity. Population density however affected all measured variables with the exception of juvenile survivorship.

The last 2 columns of Table 3 indicate whether there was a significant interaction between the effects of FLU and population density, i.e. whether the FLU effect was density-dependent. Where there were effects at low concentrations of FLU (0 to 40 ppm,

penultimate column), these were without exception antagonistic. The effect of this on the population would be compensatory, in the sense that density dependence would compensate at least to some extent for the direct effects of FLU. Thus although we have demonstrated low-density effects of low concentrations of FLU on juvenile SGR, time to first reproduction, larvae/brood and population growth rate, the population would not necessarily suffer, because the effects of FLU lessened as density increased.

At the highest concentration of FLU, however, the effects of density dependence were synergistic, so that the effects of density exacerbated those of FLU. This is the reverse of compensation; here the population suffers even more at high density than at low.

λ is the crucial summary variable that integrates data from individual life-history characters to the population level, and shows how the population's dynamics will be affected by FLU and density. The effects of FLU and density on λ are shown in the bottom row of Table 3 and Fig. 9. Our main result is that at low concentrations of FLU (0 to 40 ppm), increasing density alleviated FLU's effects. Thus increasing FLU decreased λ at low density but had no effect at high density (Fig. 9), so density-dependence completely compensated for the effects of FLU in the range 0 to 40 ppm. At the highest concentrations of FLU, however, the reverse is the case ('synergistic effects'). Here the effect of increasing density is to exacerbate the effects of FLU. This result is particularly important because it demonstrates that LTREs carried out at low density, as most have been in the past, may seriously underestimate effects in the field, where densities are generally high and likely to produce food limitation, as here.

To date few attempts have been made to explore the combined effects of toxicant stress and density dependence on λ. Grant (1998) simulated density dependence to explore its influence on the population dynamics of *Eurytemora affinis* exposed to dieldrin. His results indicated compensatory effects on some of the life-history traits that reduced the intensity of density dependence and hence reduced the sensitivity of λ to changes in the individual life-history traits in density-dependent relative to density-independent simulations. In our study, the combined effects of FLU exposure and population density on population growth rate mirror the results obtained for the individual reproductive parameters (Table 3).

CONCLUSIONS

Both population density and FLU exposure adversely affected some life-history parameters of *Capitella* sp. M, leading to a reduction in population growth rate. Our results suggest that when food availability is limiting, the impact of low levels of toxicant stress on population dynamics may be marginal. However, at higher toxicant exposures, food limitation exacerbates toxicant effects and may increase the likelihood of extinction. In nature, populations of deposit feeders generally exist under conditions of food limitation (Lopez & Levinton 1987). Our results suggest that in these conditions the maximum toxicant concentration at which populations can persist is less than previously believed, because of the synergistic interaction of the effects of the toxicant with those of density. However, the frequent association of xenobiotic contamination with organic enrichment may help to buffer the effects of the former and facilitate the persistence of *C. capitata* in extremely polluted sediments.

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