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JOINT EFFECTS OF POPULATION DENSITY AND TOXICANT EXPOSURE ON POPULATION DYNAMICS OF *CAPITELLA* SP. I

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Abstract. Very few studies have analyzed the dependence of population growth rate on population density, and even fewer have considered interaction effects of density and other stresses, such as exposure to toxic chemicals. Yet without such studies we cannot know whether chemicals harmful at low density have effects on carrying capacity or, conversely, whether chemicals reducing carrying capacity are also harmful at low density, impeding a population's capacity to recover from disturbance. This study examines the combined effects of population density and a toxicant (fluoranthene) on population growth rate (pgr) and carrying capacity using the deposit-feeding polychaete *Capitella* sp. I as a test organism. Populations were initiated with a stable age distribution, and population density and age/size distribution were followed during a period of 28 wk. Fluoranthene (FLU), population density, and their interaction influenced population growth rate. Population growth rate declined linearly with the logarithm of population biomass, but the slope of the relationship was steeper for the control populations than for populations exposed to 50 μg FLU/(g sediment dry mass). Populations exposed to 150 μg FLU/(g sediment dry mass) went extinct after 8 wk of exposure. Despite concerns that toxicant effects would be exacerbated at high density, we found the reverse to be the case, and effects of fluoranthene on population growth rate were much reduced in the region of carrying capacity. Fluoranthene did reduce carrying capacity by 46%, and this could have important implications for interacting species and/or sediment biogeochemical processes.

Key words: Capitella *sp. 1; carrying capacity; ecotoxicology; fluoranthene; life table response experiment; population growth rate.*

INTRODUCTION

Population effects of toxicants have generally been examined at low population density and high food availability, and effects on carrying capacity have only rarely been addressed (Forbes and Calow 1999, Sibly et al. 2000). Population responses at low density may, however, be a poor guide to population responses in the field for populations close to carrying capacity where resources are limiting. Toxicant exposure may reduce carrying capacity, and this could have important effects on other species in the system. Here we examine the joint effects of density and a toxicant in populations close to carrying capacity.

Interactions between population density and toxicants on population dynamics have been explored theoretically, experimentally, and by simulation. These analyses emphasize that population density may influence the effects of toxic chemicals on population dynamics in complex ways. Theoretical considerations do not provide clear answers in that many types of interactions between density and toxicant effects appear to be possible in theory (Forbes et al. 2001*a*). Some results of simulation studies suggest that toxicant effects are likely to be ameliorated at high population densities largely because toxicant-caused mortalities should reduce the negative effects of density on population dynamics (Grant 1998, Hansen et al. 1999).

The few experiments that have explored density (usually simulated by controlling food availability), toxicant interactions have shown mixed results. Some studies found toxicant effects to be exacerbated under high-density conditions (Chandini 1988, Cecchine and Snell 1999), others found an amelioration of toxicant effects at high densities (Marshall 1978, Sibly et al. 2000), whereas others found additive effects of density and toxicants on population growth rate (Winner et al. 1977, Klüttgen and Ratte 1994). In a recent life-table response experiment examining effects of food supply and density on the cladoceran *Moinodaphnia macleayi* to cadmium, Barata et al. (2002) showed that cadmium increases extinction probability at low density and high food availability, but has less effect at high density and low food availability, as a result of ecological compensation.

Part of the reason for discrepancies among studies appears to be due to differences in experimental design, which influences the kinds of interactions that are possible (Forbes et al. 2001*a*). In addition, the form of the

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interaction between density and toxicants is likely to depend on the relative intensities of density and toxicant effects on individual performance. For example, low to moderate toxicant exposure may remove weak individuals from the population and enhance resource availability for survivors. However, as toxicant concentration increases and an increasing fraction of the population is impaired, survivors will eventually be unable to take advantage of additional resources. Models of fish populations (Power 1997) and experimental work with polychaetes (Linke-Gamenick et al. 1999) have indicated amelioration of toxicant effects in dense populations at low toxicant exposures and exacerbation at high toxicant exposures.

We have previously conducted experiments on the effect of the polycyclic aromatic hydrocarbon (PAH), fluoranthene, on life-history traits and population dynamics of the polychaete *Capitella* sp. I. This species is of interest as a marine pollution indicator (Grassle and Grassle 1976). It has an opportunistic life history and exhibits boom-and-bust population dynamics. In the field, this cosmopolitan species is frequently found at low densities (~100 individuals/m^2) in clean sediments, but in sediments contaminated with, e.g., organic waste, sewage, or oil, it can reach densities of up to ~200 000 individuals/m^2 (Sanders et al. 1980, Tsutsumi 1987, Gamenick and Giere 1994). Fluoranthene is derived from the partial combustion of oil and is one of the most abundant PAHs identified in marine sediments. Its concentration in oil-polluted sediments can range from tens to hundreds of micrograms per gram of sediment dry mass (Shiaris and Jambard-Sweet 1986, National Oceanic and Atmospheric Administration 1989). Fluoranthene is highly bioaccumulative and toxic to a range of aquatic species at concentrations down to about 10 μg/(g sediment dry mass) (Swartz et al. 1990).

In previous studies, we have described the effects of fluoranthene under low-density conditions (Linke-Gamenick et al. 2000) and investigated some density-dependent effects on life-history traits using a modified life-table response experiment (Linke-Gamenick et al. 1999). Those experiments did not, however, adequately describe the effects of fluoranthene in the region of carrying capacity. This deficiency is remedied in the study presented here, which retains the juveniles in the populations, and so gives a closer approximation to natural conditions. The results allow us to predict the effects of fluoranthene on carrying capacity and on a population's ability to recover from disturbance.

Methods

Test species

All experiments were performed with laboratory-cultured worms. Stock cultures of *Capitella capitata* sp. I (identified by J. P. Grassle) were reared in aquaria with sediment (2–4 cm layer, <250 μm particle size) and 31‰ salinity aerated seawater at 16°C. The sediment was enriched with a supplemental food source comprised of commercial fish food (Tetramin; Tetra Werke, Melle, Germany) mixed with baby cereal (Milpo; Milupa, Hørsholm, Denmark) and dried spinach in equal ratios, added weekly. Approximately one week prior to the start of the experiment, several brood tubes from *Capitella* sp. I were transferred to dishes with a thin layer of sediment and seawater and checked daily for larvae for use in the experiments.

Sediment

For the experiments, sieved (at <125-μm mesh size), prefrozen (−80°C for several weeks) sediment from Roskilde Fjord, Denmark, with a water content of 35.7 ± 0.37% (mean ± 1 SD; $n = 6$) and an organic content of 3.09 ± 0.11% ($n = 6$) was used. Fluoranthene-spiked (FLU) sediment with concentrations of 50 and 150 μg FLU/(g sediment dry mass) was prepared as follows. The wet mass and dry mass of a known volume of sediment were estimated. A known volume of FLU stock solution (crystalline fluoranthene, 98% GC grade, [Sigma-Aldrich, Vallensbæk Strand], dissolved in 2 mL acetone) was added to a known volume of thawed sediment in a glass flask that was subsequently shaken for ~17 h at room temperature in the dark. For the control, 2 mL of acetone was added to the sediment, which was prepared similarly. Once the sediment was contaminated, the overlying water was decanted (to remove any unevaporated acetone) and replaced with an equivalent amount of fresh seawater. The sediment was divided into 12 g (wet mass) portions and stored frozen (−20°C) until use in experiments. Previous analyses demonstrated that sediment fluoranthene concentrations were stable and not influenced by varying periods of freezing (I. Linke-Gamenick, *unpublished results*).

Experiments

Experiments were started with replicate populations of 20 *Capitella* specimens representing a stable age distribution containing 30% swimming larvae (1 d old), 60% juveniles (1–4 wk old), and 10% adult specimens (with equal numbers of males and females). The adults were sexually mature, but had not yet reproduced. Mature males were identified by the presence of genital spines, whereas mature females were characterized by the presence of oocytes in the coelomic cavity.

Three replicate populations for each FLU treatment were exposed in petri dishes (8.4 cm diameter; 55.4 cm^2 area) with 12 g wet mass of sediment and 20 mL of 31‰ salinity seawater. The measured FLU concentrations at sediment addition were 0.50 ± 0.12 μg/g FLU (mean ± 1 SD) (control), 48.21 ± 2.12 μg/g FLU (50 FLU), and 146.29 ± 5.98 μg/g FLU (150 FLU), respectively, based on four replicate measurements per

concentration. All dishes were placed in a moisture chamber to reduce evaporation and kept in the dark at 18°C. The salinity was checked every few days and adjusted as necessary.

The populations were censused every 2–3 wk for a duration of 28 wk. On each census day, worms were removed from the sediment using a 250-μm sieve, assigned to different life stages, and data on population density and reproduction were collected. Pilot experiments indicated that this frequency of sampling was sufficient for assessing changes in population size, and that more frequent handling of (particularly juvenile) worms led to reduced survival. Individual worms from each population were divided into the following life stages: 1, white juveniles (<3 wk old); 2, larger juveniles containing some hemoglobin; 3, young adults (red, no sexual features); 4, sexually mature adults (males with genital spines, females with oocytes or eggs, or hermaphrodites with both features); 5, old worms (had already reproduced, brownish color). After censusing, worms were returned to their corresponding treatments with new experimental sediment and seawater.

To obtain a mean wet mass for each life stage, we measured the wet mass of 10–15 individuals of each stage on each census day. Dry mass was calculated as wet weight ×0.14 (Méndez et al. 2001)

Fluoranthene extraction and analysis

Extraction of fluoranthene from sediment followed Forbes et al. (2001*b*) with minor modifications. From each sediment treatment, four replicate samples of 0.5 g were taken, and 1 mL methanol and 2 mL ethylacetate added to each. After stirring (5 s), the sample was exposed to ultrasonic treatment (10 min), stirred again (5 s), and finally centrifuged (10 min) at 3000× g (1 g = 9.80665 m/s^2) at 4°C. The supernatant was transferred to a new 8 mL pyrex tube, and the extraction repeated twice (without methanol addition). Subsequently, the supernatant was stirred again (30 s), exposed to ultrasonic treatment (10 min) and stirred for another 30 s, and 7 mL was transferred into a new glass tube in a 35°C water bath. Samples were evaporated with nitrogen gas to almost dryness, resuspended with 1 mL ethylacetate, and stored frozen at −80°C until analysis.

After sample centrifugation (5 min), FLU concentrations were measured with high-performance liquid chromatography (HPLC) following Kelley et al. (1993) with slight modifications. The HPLC system was equipped with a Waters 600 E pump (Millipore Instruments, Glostrup, Denmark), a Wisp 700 autosampler, a Nucleosil precolumn (10 C18), a Primesphere column (4.6 mm by 25 cm, 5 μm C18-HC 110 A) (all three from Mikrolab, Aarhus, Denmark), and a Waters 994 photodiode array detector (Waters, Hedehusene, Denmark). The mobile phase was a linear gradient of methanol–water (30, 60, and 90% methanol [by volume], plus 0.5% acetic acid) run for 80 min at 0.85 mL/min. UV absorbance was measured at 254 nm, and peak areas were integrated with the computer program Millenium, version 2.15 (Waters, Hedehusene, Denmark).

Calculations and statistical analysis

Population growth rate (pgr) was defined as

$$\frac{1}{\Delta}\ln\frac{\text{population size at time } t+\Delta}{\text{population size at time } t}$$

following Sibly and Hone (2002). Time was measured in weeks and Δ refers to the census period (2–3 wk). Following others (e.g., Barlow 1992, Sibly et al. 2000), we measured population size by population biomass because there is no other sensible way to account for between-individual variation in size and reproductive value. Biomass of each stage was estimated by multiplying the total number of individuals in the stage by their mean dry mass. Total population biomass was estimated by summing the biomasses of the five stages.

Effects of FLU and population biomass (as covariate) on pgr were analyzed by analysis of covariance. Such analyses are generally adopted for analysis of density dependence, but it should be borne in mind that they do not allow for possible effects of measurement errors, which could exaggerate the effects of density dependence or produce the illusion of density dependence in invariant populations (Woiwod and Hanski 1992, Sibly and Hone 2002). However, in the present case, measurement errors are unlikely. Prior to ANCOVA, the biomass data were transformed to a $\log_{10}$ scale, as this resulted in a more linear relationship with the dependent variable, pgr. Studentized residuals were estimated and plotted against the estimated values, as well as against $\log_{10}$(biomass) and week. Serial correlations of residuals were examined with an autocorrelation plot, and all but one of the residuals (11 wk) were within acceptable confidence bands, indicating that the majority of residuals were not correlated in time. All statistical analyses were performed with Systat version 9.0 (SPSS, Chicago, Illinois, USA).

Results

In both the control and 50-FLU treatment, populations persisted for 28 wk, at which time the experiment was terminated. In the 150-FLU treatment, all three populations went extinct by week 8. When the 150-FLU populations were censused for the first time (after 3 weeks of exposure), all of the surviving worms were in stages 3 and 4, indicating a preferential mortality of larvae and juveniles. Mean total mortality for the 150-FLU treatment was 87% after 3 weeks of exposure.

In the control, population size fluctuated with the highest number of worms in week 11, a trough in week 16, and a second maximum in week 21 (Fig. 1A). From

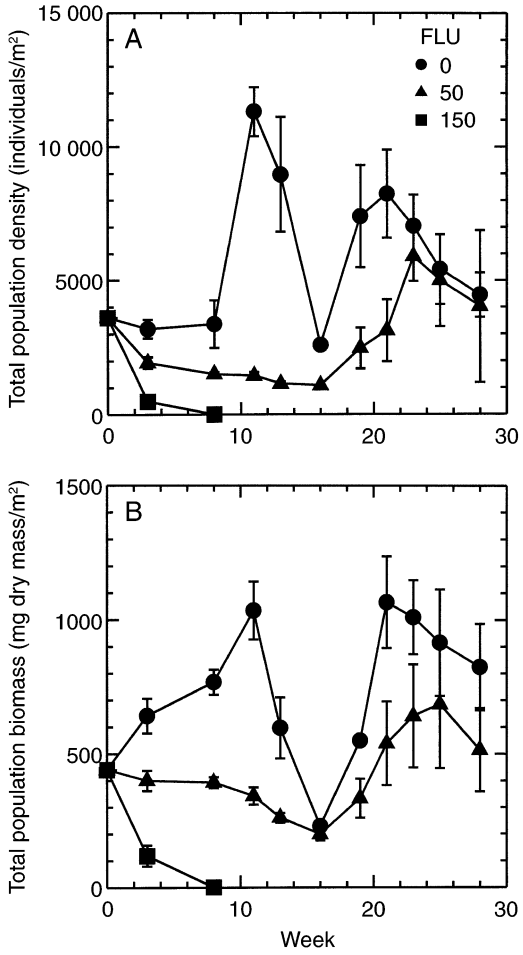

FIG. 1. Effects of fluoranthene on population size of *Capitella* sp. I. (A) Total worm density and (B) total worm biomass in the three fluoranthene treatments as a function of time. Control treatment, circles; 50 FLU, triangles; 150 FLU, squares. Error bars represent ±1 SE.

week 13 on, the sediment was completely processed at each census day indicating that the populations were food limited. In the 50-FLU treatment, population size was reduced and remained low until week 16, after which it increased to a maximum (lower compared to the control) in week 23.

The mean wet masses for each stage class are shown in Table 1. The measurable decreases in wet mass for the adult stages during the latter part of the experiment, which was particularly noticeable in control worms, corresponded to the point at which the populations became food limited.

Describing population size in terms of numbers of individuals gives undue weight to smaller age classes. This can be avoided by describing population size in terms of biomass (Barlow 1992, Sibly et al. 2000). Conversion of the measured wet masses to dry masses was used to estimate population biomass, which showed a pattern generally similar to that of population density with two maxima in the control (though these were more equal in size than when population size was expressed as worm numbers) and one lower maximum at a later time in the 50-FLU treatment (Fig. 1B). However, toward the end of the experiment, biomass differences between control and fluoranthene-exposed populations became apparent in contrast to the pattern for worm numbers. This is due to the larger proportion of relatively heavy stage-3 and stage-4 worms in the control compared to the FLU populations (Figs. 2A and 3A) and occurred despite the larger mass reduction in stage-4 and stage-5 worms in the control relative to the FLU treatment toward the end of the experiment (Table 1).

To determine the contribution of the different stages to the population, we plotted the densities and biomasses of each stage class separately as a function of time (Figs. 2 and 3). In the control, both density maxima were due to juvenile stages 1 and 2 (Fig. 2A), and the juveniles comprised >70% of the population between week 11 and week 21. Young adults and mature adults (stages 3 and 4) were more abundant at the beginning of the experiment (~80%, until week 8) and after week 23. In the 50-FLU treatment, all juveniles initially disappeared, whereas the older stages had a higher survival (Fig. 3A). The first newly hatched juveniles were found in week 16. The older stages were relatively more abundant in the 50-FLU population. The importance of the youngest age classes is noticeably reduced when their contribution is expressed in terms of biomass (compare Fig. 2A vs. 2B and Fig. 3A vs. 3B). In terms of biomass, the contribution of stage-1 juveniles is minor, whereas the contributions of stages 3 and 4 are increased. The contribution of stage-5 adults is minimal, whether expressed in terms of density or biomass.

Fluoranthene exposure, population biomass, and their interaction explained 61% of the variance in population growth rate when all three exposure groups (0, 50, and 150 FLU) were included in the analysis (Table 2a). FLU level had a marked negative effect on pgr at the lowest observed densities (Fig. 4), reducing pgr from 0.38/wk (control) to 0.07/wk (50 FLU), and at 150 FLU, pgr was severely negative (~−0.5/wk), as

TABLE 1. Mean wet mass for each of the stage classes at different times.

	Control		50 FLU	
Stage	Mean wet mass (mg)	Week	Mean wet mass (mg)	Week
1	0.03		0.03	
2	0.14		0.14	
3	0.20		0.20	
4	0.29	0–12	0.29	0–10
	0.17	13–28	0.26	11–28
5	0.23	0–12	0.23	0–10
	0.14	13–28	0.21	11–28

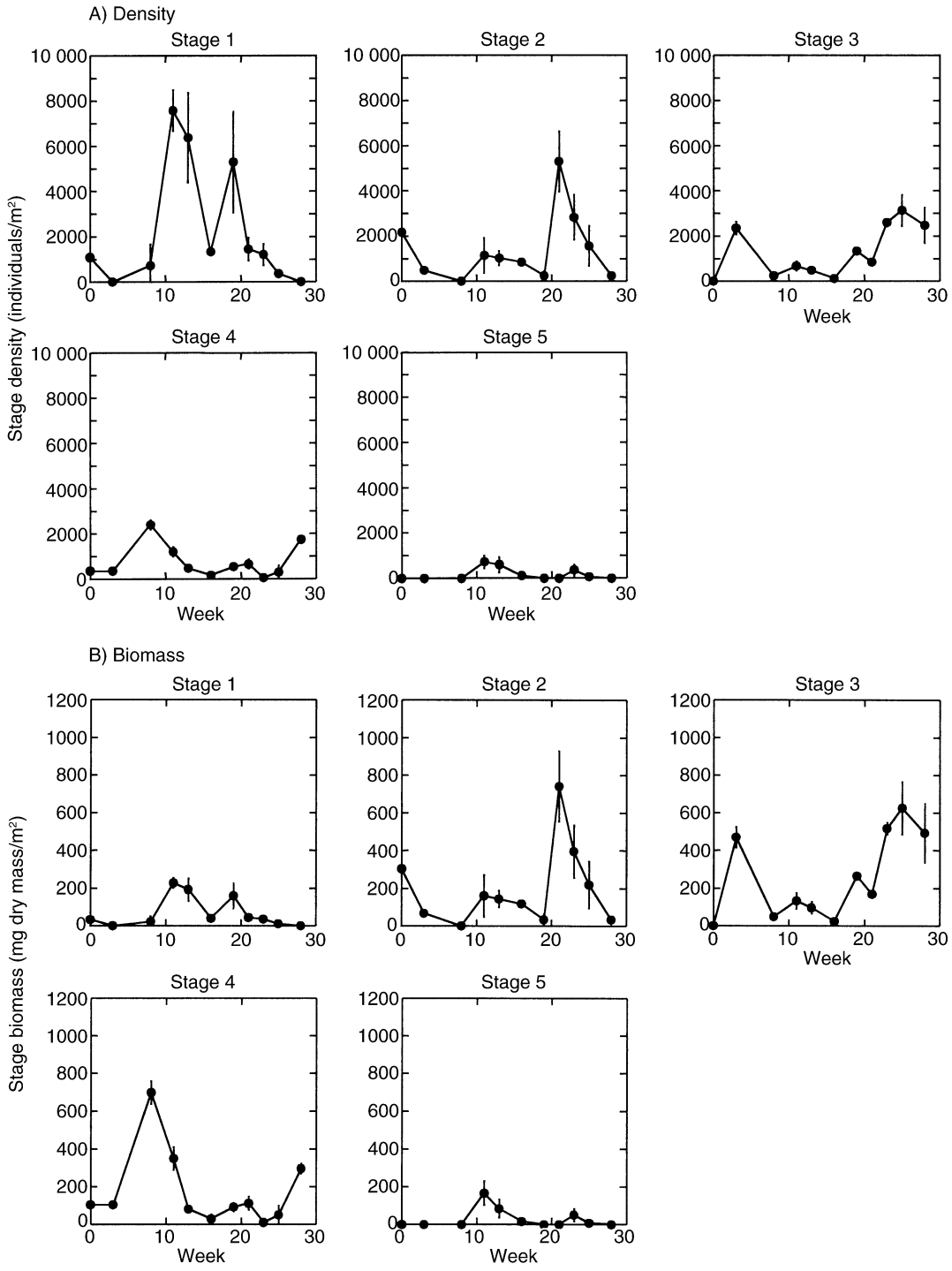

FIG. 2. Age structure of control populations over time: (A) density and (B) biomass of each of the five life-history stages. Error bars represent ±1 SE.

expected, given the rapid extinction of these populations. Because of the paucity of data, density dependence cannot sensibly be evaluated at 150 FLU. Rerunning the ANCOVA, omitting the 150-FLU group (Table 2b), showed that fluoranthene, biomass, and their interaction explained 25% of the variance in pgr. In the control populations, pgr declined linearly and significantly with $\log_{10}$(biomass), but the decline with density was slight and not statistically significant in 50-FLU populations (Fig. 4). Increasing biomass re-

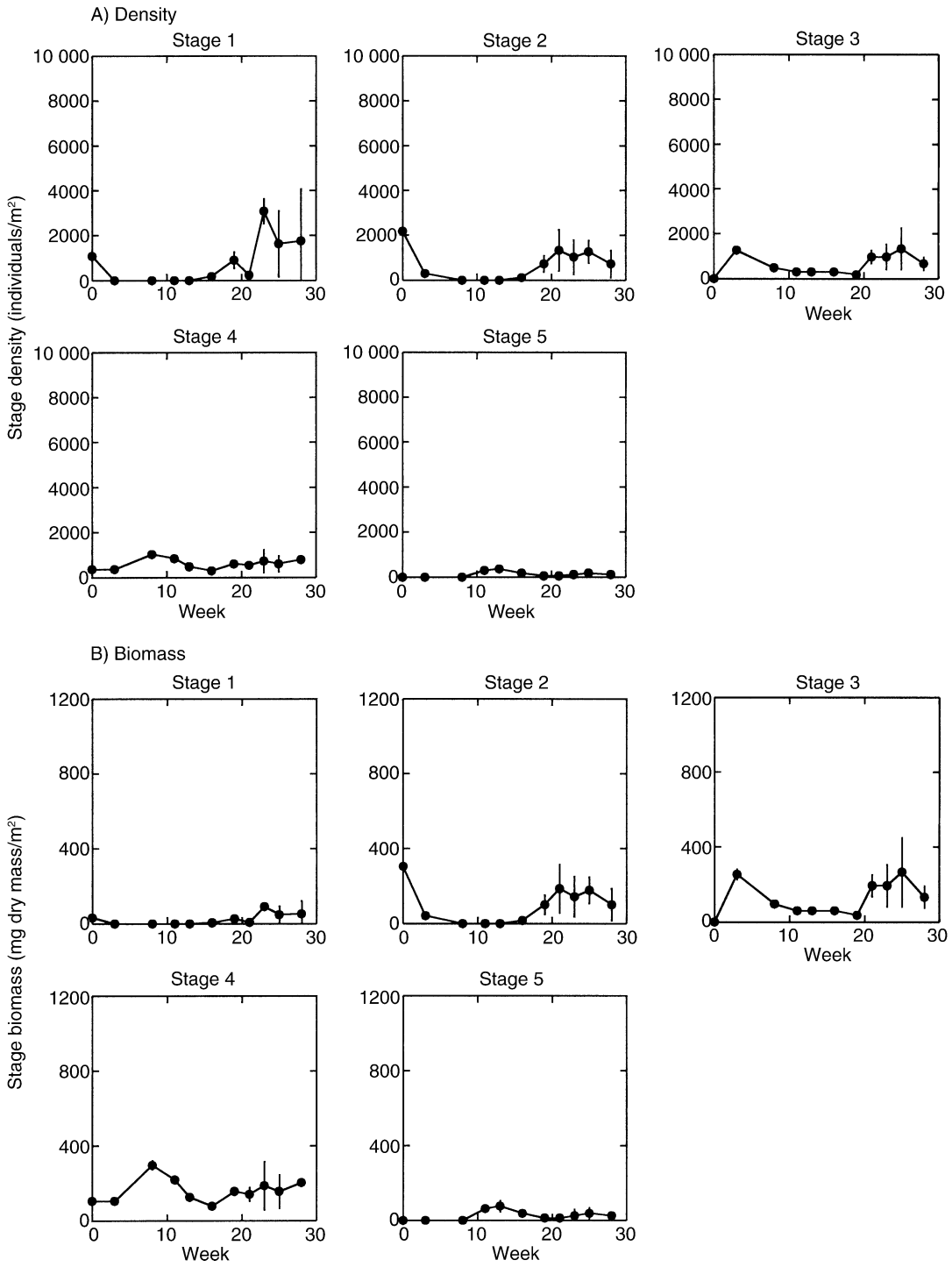

FIG. 3. Age structure of control populations exposed to 50 μg/g of fluoranthene over time: (A) density and (B) biomass of each of the five life-history stages. Error bars are means ± 1 SE.

duced pgr by 0.57/wk for each unit increase in $\log_{10}$(biomass) in the control and by 0.17/wk at 50 FLU. Carrying capacity, estimated from the regression lines as biomass at zero pgr, was 0.72 g/m² in control and 0.39 g/m² in the 50-FLU treatment. Although there is substantial scatter about the regression lines (Fig. 4), this is not due to variation among replicates within control and FLU-exposed populations. The replicates

TABLE 2. Analysis of covariance of the effects of fluoranthene exposure (0, 50, or 150 FLU), population biomass (log_{10}-transformed), and their interaction on population growth rate in *Capitella* sp. I.

Source	SS	df	MS	*F*	*P*
a) Three treatment levels					
log(Biomass)	0.09	1	0.09	4.02	0.050
FLU	0.42	2	0.21	9.38	<0.001
FLU × log(Biomass)	0.24	2	0.12	5.40	0.007
Error	1.34	60	0.02		
b) Two treatment levels†					
log(Biomass)	0.29	1	0.29	12.86	<0.01
FLU	0.10	1	0.10	4.59	0.04
FLU × log(Biomass)	0.09	1	0.09	3.90	0.05
Error	1.28	56	0.02		

† (b) Same as above, but omitting the 150-FLU treatment.

were, in general, remarkably similar, as can be seen from the size of the error bars in Figs. 1–3.

DISCUSSION

Population density, FLU exposure, and their interaction influenced the population growth rate of *Capitella* sp. I, and FLU exposure reduced the carrying capacity of worm populations. Carrying capacity in the present study, estimated from the lines fitted to the data in Fig. 4, was reduced by 46%, from 0.72 g/m^2 in the control to 0.39 g/m^2 in the 50 μg/g FLU treatment. Possible explanations for this reduction include direct toxic effects, resulting in reductions in fecundity and/or survival, as well as increased energy costs of detoxification (Calow and Sibly 1990). The implications of such reductions for other trophic groups or sediment biogeochemical processes may be significant. *Capitella* sp. I is a cosmopolitan species that is particularly important as an initial colonizer of polluted sediments. By feeding on and burrowing in surface sediment, *Capitella* species increase oxygenation of surface sediment, play a key role in organic-matter breakdown, and are prey to bottom-feeding fish and invertebrates (Grassle and Grassle 1976, Sanders et al. 1980, Tsutsumi 1987, Gamenick and Giere 1994). Carrying capacity of *Capitella* populations appears to be strongly influenced by the organic matter content of the sediment. In organic-poor sediments population densities may be only a few hundred individuals per square meter, whereas in sediments contaminated with organic waste (e.g., from fish farming, sewage, or oil) *Capitella* sp. I characteristically exhibits boom-and-bust population dynamics with densities reaching as high as 200 000 worms/m^2 or more (Sanders et al. 1980, Tsutsumi 1987, Gamenick and Giere 1994). More often than not, sediments contaminated with toxic chemicals are also enriched in organic material (e.g., in harbors, near sewage outfalls, in areas receiving agricultural runoff), and *Capitella* sp. I is one of few species likely to dominate in such habitats. In addition, this species has been shown to effectively metabolize PAH, such as fluoranthene, and may be important in reducing contaminant concentrations in sediments (Forbes et al. 2001*b*; Selck et al., *in press*). Therefore interactions between toxicants and density on the population dynamics of *Capitella* can be of critical importance for organic matter cycling in and contaminant remediation of polluted sediments.

This paper is among very few to establish the combined effects of population density and a toxicant on population growth rate and carrying capacity of intact populations. Despite concerns that toxicant effects on pgr would be exacerbated at high density compared to low density (Sibly et al. 2000, Forbes et al. 2001*a*), here we find the reverse to be the case. Effects of FLU on pgr are very much reduced in the region of carrying capacity as indicated by the convergence of lines in Fig. 4. While the present design does not allow identification of the specific mechanism(s), examination of Fig. 2B suggests that pgr may decline more slowly with biomass in the FLU populations compared to the controls as a result of a time lag in the input of offspring to the populations. Whether this is due to slower growth (e.g., leading to a longer time to first reproduction or between broods), lower fecundity, and/or reduced offspring survival) cannot be determined from the present results. However, results of life table response experiments (LTRE) (Linke-Gamenick et al. 2000) showed that juvenile survival of *Capitella* sp. I was not reduced significantly by exposure to 50 FLU, but that exposed worms had a significantly smaller body size at maturity compared to control worms and took longer to reach the age of first reproduction. Thus, we suggest that FLU acts to weaken the density dependence of pgr primarily by decreasing individual worm growth and develop-

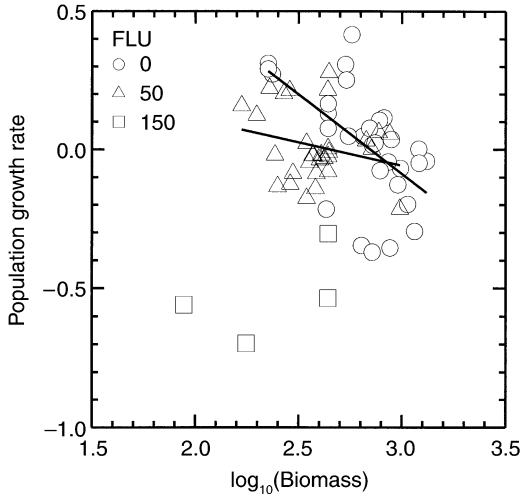

FIG. 4. Population growth rate per week as a function of (log_{10}-transformed) population biomass. Lines were fitted to the control and 50-FLU treatments using linear regressions: Control, pgr = 1.63 − 0.57(log[biomass]), n = 30, r = 0.57, P = 0.001; 50 FLU, pgr = 0.44 − 0.17(log[biomass]), n = 30, r = 0.24, P = 0.20. For lack of data, no line was fitted at 150 FLU.

ment, which thereby creates time lags in the dynamics of worm populations.

Similar, though weaker, amelioration of the effects of a toxicant were found by Sibly et al. (2000) for the marine copepod, *Tisbe battagliai*. These authors examined the joint effects of diet quality, food concentration, and the toxicant pentachlorophenol (PCP). In the high diet-quality and food-concentration treatment, they found that PCP reduced population growth rate at low density and carrying capacity, but that, as here, the effects of the toxicant were ameliorated near carrying capacity.

Using an LTRE approach, Barata et al. (2002) also showed that negative effects of a toxicant (Cd) on the cladoceran *Moinodaphnia macleayi* were buffered by increasing population density. At low food levels, effects seemed to be due to interactions between juvenile survival (reduced by density) and reproduction (reduced by Cd), whereas, at moderate food levels, the buffering appeared to result from less-than-additive effects between the contributions of age at first reproduction and daily reproduction on pgr. These authors suggested that, at high densities and low food levels, ecological compensation will prevent populations at carrying capacity from being driven to extinction by toxicity effects at the individual level, but that, at low densities when food availability is not limiting, exposure to toxicants will increase extinction probability.

Clearly, the combined effects of toxicants and density on pgr will depend on the relative strengths of the effects of the two stressors on individual performance. For example, in the present study, we observed an amelioration of density effects on pgr at 50 FLU, but as fluoranthene concentration increased beyond this level (i.e., to 150 FLU), the strength of the toxicant stress masked any density effect, and populations rapidly went extinct. In general, we hypothesize that low toxicant concentrations will have less of an effect on pgr when density effects are strong (i.e., near carrying capacity) than when they are weak (i.e., when pgr is close to its maximum intrinsic rate) because mild toxicant-caused reductions in population density will act to reduce the negative effect of density on pgr. Further, we suggest that moderate increases in density will have less of a negative effect on pgr in toxicant-exposed (i.e., the decline in pgr per unit increasing density will be less) than in unexposed populations if the increased density reduces toxicant exposure per individual. This kind of exposure scenario has been demonstrated to occur in many aquatic populations that are exposed to toxicants via contact of body surfaces with the external environment (e.g., Chen 1994). As the strength of toxicant stress on pgr increases, however, the negative effects on individual performance will eventually outweigh any ameliorating effects of reductions in density.

Partial support for the above hypotheses is provided by Linke-Gamenick et al. (1999). Effects of starting population density and fluoranthene on life-history traits of *Capitella* sp. I were assessed in a modified LTRE. Density treatments were 529–1058 worms/m^2 (defined as low density), 3125–7292 worms/m^2 (defined as medium density), and 15 790–36 842 worms/m^2 (defined as high density). There was evidence for less-than-additive effects between density and fluoranthene at exposure concentrations up to 40 μg FLU/g on juvenile growth, time to first reproduction, number of larvae per brood, and population growth rate, and more-than-additive effects on these same traits (as well as on the percent of worms reproducing and number of broods per female) at exposure concentrations of 40–80 μg FLU/g. At low density, pgr declined from 0.89/wk in the control to 0.51/wk at 40 FLU and 0.47/wk at 80 FLU. At medium density, pgr was fairly stable between the control (0.48/wk) and 40 FLU (0.47/wk), but worms failed to reproduce entirely at 80 FLU. At high density, pgr increased from 0.08/wk in the control to 0.22/wk at 40 FLU before decreasing to extinction at 80 FLU.

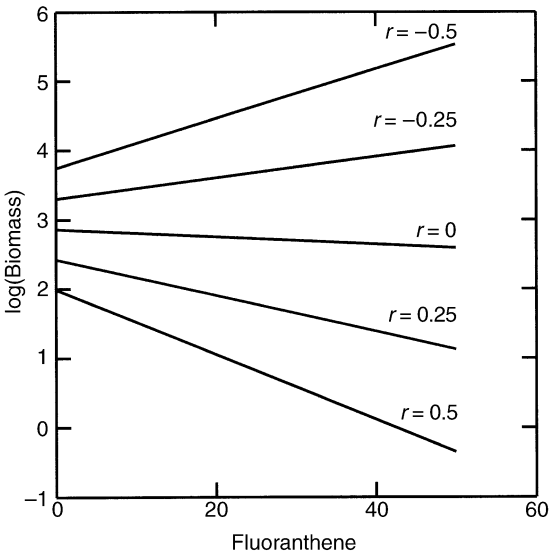

FIG. 5. Isoclines of equal pgr as a function of density and FLU. PGR values were derived from regression equations for control and 50 FLU (see Fig. 4 caption), and the isoclines were drawn by interpolating between the calculated PGR values.

Overall, our results show that, within certain limits, density can render the dynamics of populations less sensitive to toxicants. Alternatively, toxicants can make populations less responsive to changes in density. This latter consequence is illustrated in Fig. 5. Here we have used the best-fit regressions for the relationship between biomass and pgr for the 0 and 50 FLU populations (i.e., see Fig. 4) to generate isoclines of equal pgr as a function of biomass and FLU (Sibly 1999). The closer together that the isoclines are, the more responsive (in terms of pgr) the populations will be to changes in density. This figure shows that when populations are perturbed away from carrying capacity

(i.e., $r = 0$ isocline), it will take exposed populations longer than unexposed populations to return to carrying capacity. This means that exposed populations may be more susceptible to other perturbations that reduce density (e.g., predation, hypoxia, etc.). Likewise, if conditions improve, for example if food supply is increased, it may take toxicant-exposed populations longer to respond, and they would reach a lower carrying capacity than unexposed populations. These kinds of effect could have important implications, particularly for species such as *Capitella* that plays a key role in organic matter processing in marine sediments.

The results of the present study suggest that the effects of toxicants on pgr estimated in LTREs at low population densities may overestimate the effects of toxicants on populations close to carrying capacity and thus provide an added element of conservatism in ecotoxicological effects assessment. However, LTREs cannot address the issue of how toxicants affect carrying capacity itself, and this may be an important endpoint for ecological risk assessment. There are very few studies that have analyzed the dependence of pgr on density (reviewed in Sibly and Hone 2002) and even fewer that have considered interaction effects of density and other stresses, such as toxicants, on pgr. Those that have addressed these issues either experimentally or by modeling (Power 1997, Grant 1998, Hansen et al. 1999, Forbes et al. 2001*a*, Barata et al. 2002) highlight the potential complexity of the interactions that may occur. Given the theoretical and practical importance of such relationships for population ecology and ecotoxicology, it is our hope that more experimental efforts will be devoted to this area.

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