Journal of Applied Ecology 2000, **37**, 388–397

PRIORITY CONTRIBUTION

How environmental stress affects density dependence and carrying capacity in a marine copepod

RICHARD M. SIBLY*, TIMOTHY D. WILLIAMS†‡ and MALCOLM B. JONES‡

*School of Animal and Microbial Sciences, University of Reading, PO Box 228, Reading RG6 6AJ, UK; †Brixham Environmental Laboratory, AstraZeneca, Freshwater Quarry, Brixham, Devon TQ5 8BA, UK; and ‡Plymouth Environmental Research Centre (Department of Biological Sciences), University of Plymouth, Drake Circus, Plymouth, Devon PL4 8AA, UK

Summary

1. Management of the effects of stress on populations – for instance in ecotoxicology – requires understanding of the effects of stressors on populations and communities. Attention to date has too rarely been directed to relevant ecological endpoints, such as carrying capacity and density dependence. Established procedures are instead based on measuring the Life Tables of individual organisms exposed to differing concentrations of a pollutant at low population density, but this approach does not take into account population effects that may occur through interactions between individuals. Here we introduce an approach that allows direct measurement of the effects of stressors on carrying capacity and density dependence.

2. Using the marine copepod Tisbe battagliai Volkmann-Rocco, we report replicated experiments establishing the effects of 100 μg L^{-1} pentachlorophenol (PCP) in combination with varying diet and food concentrations. Population density was measured as population biomass in 10 mL volumes. Diet was either the alga Isochrysis galbana Parke (here designated 'poor diet') or a mix of two algal species (I. galbana and Rhodomonas reticulata Novarino: 'good diet'). Each was given at three food concentrations (520, 1300 and 3250 μgC L^{-1}), selected on the basis that at low population density these cover the range between limited and maximal population growth.

3. Carrying capacity increased linearly with food concentration. On the poor diet the increase was 1·2 μg L^{-1} for each μgC L^{-1} increase in food concentration. On the good diet the increase was 2·3 μg L^{-1}/μgC L^{-1} in the absence of PCP, and 1·9 μg L^{-1}/μgC L^{-1} with PCP. Maximum carrying capacity was in the region of 60–80 μg per 10 mL volume. Population growth rate (pgr) decreased linearly with population biomass when the latter was plotted on a logarithmic scale. Increasing biomass reduced pgr by 1·70 $week^{-1}$ for each unit increase in $\log_{10}$ biomass. Increasing food concentration and improving diet both increased pgr, but did not affect the slope of the density-dependent relationship. Presence or absence of PCP had no effect except that at some higher food concentrations non-PCP populations initially increased faster than PCP populations, and at high concentration on the good diet the effect of density-dependence was decreased in PCP populations.

4. The results show that a stressor's effects at high population density may differ from its effects at low density, and emphasizes the importance of finding new protocols, such as those introduced here, with which to study the joint effects of a stressor and population density. Managers and researchers of threatened species,

Correspondence: Prof. R.M. Sibly, School of Animal and Microbial Sciences, University of Reading, PO Box 228, Reading RG6 6AJ, UK. Tel.: 0118 9318461. Fax: 0118 9316644, E-mail: r.m.sibly@reading.ac.uk
*To whom reprint requests should be addressed.

harvested species and pest species need to know the joint effects of stressors and population density, in order to be able to predict the effects of stressors on carrying capacity and on the course of recovery from environmental perturbations.

Key-words: diet, food, pentachlorophenol, population growth rate, scale, ecotoxicology.

Journal of Applied Ecology (2000) **37,** 388–397

A recurring theme in practical studies of the effects of stress on populations – for instance in ecotoxicology – is the need for greater insight and understanding into the effects of stressors on populations and communities (e.g. Baird et al. 1996; Walker et al. 1996). Attention to date has too rarely been directed to relevant ecological endpoints, such as carrying capacity and density dependence (Banks & Stark 1998). Established procedures are instead based on measuring the Life Tables of individual organisms in Life Table Response Experiments (LTREs, Levin et al. 1987, 1996). LTREs have, however, almost always been carried out at high food levels and low population density and, in consequence, the effects of environmental stressors, insofar as they are known, are known at low population density. This approach does not take into account population effects that may occur through interactions between individuals (competition and food availability, Van Leeuwen, Luttmer & Griffioen 1985; Van Leeuwen, Niebeek & Rijkeboer 1987). Here we use an approach that allows direct measurement of the effects of stressors on carrying capacity and density dependence.

The study organism, Tisbe battagliai Volkmann-Rocco, is a marine harpacticoid copepod of interest as an ecotoxicological test organism (Hutchinson & Williams 1989; Williams 1992; Thain & Kirby 1996; Kirby et al. 1998; Matthiessen et al. 1998). It has been studied in LTREs in relation to temperature, food concentration, diet and pentachlorophenol (PCP) (Williams 1997). These LTREs have shown that population growth rate (pgr) is sensitive to diet, being higher if the diet consists of a mixture of two algal species, Isochrysis galbana and Rhodomonas reticulata, rather than just I. galbana alone. Pgr is also sensitive to food concentration, being maximal at a concentration of 3250 μgC L^{-1}, but barely sufficient to sustain the population at 520 μgC L^{-1}. Optimal temperature has been shown to be approximately 20 °C, and Tisbe battaglia exposed to conditions of food limitation have been shown to be sensitive to PCP at a concentration of 100 μg L^{-1} (Williams 1997). However, these experimental results relate to low population density, and only limited information is available concerning the potential effects of chemical contaminants on populations of harpacticoids. Hoppenheit (1977), Hoppenheit & Sperling (1977) and Brand, Fabris & Arnott (1986) have shown that exposure to cadmium reduces population sizes of Tisbe holothuriae, and Munzinger (1994) and Van Leeuwen, Niebeek & Rijkeboer (1987) have shown that exposure to nickel and other chemicals reduces carrying capacity in Daphnia magna.

Here, we tackle the general problem of describing and characterizing ecological effects of stressors, while at the same time investigating the effects on the population dynamics of Tisbe battagliai of stressors whose effects at low density are known from LTREs. The stressors are diet, food concentration and the chemical pentachlorophenol, and the ecological effects are characterized primarily in terms of carrying capacity and density dependence.

Materials and methods

We used two diets, three food concentrations, and culture solutions with/without 100 μg L^{-1} pentachlorophenol; there were therefore $2 \times 3 \times 2 = 12$ treatments in all, each applied for 11 weeks to five replicate populations. Diet was either the alga Isochrysis galbana (here designated 'poor diet', but note that it alone will sustain cultures indefinitely) or a mix of two algal species (I. galbana and Rhodomonas reticulata: 'good diet'). Each diet was given at three food concentrations (520, 1300 and 3250 μgC L^{-1}), selected on the basis that at low density these cover the range between allowing limited and allowing maximal population growth. Previous work had shown that copepods exposed to conditions of food limitation showed an increased sensitivity to PCP at the concentration at which it is used here, 100 μg L^{-1} (Williams 1997).

The procedures for culturing Tisbe battagliai, and associated algal food species Isochrysis galbana and Rhodomonas reticulata, have been described previously (Williams & Jones 1994; International Standards Organization 1999). Pentachlorophenol (PCP) was chosen as a representative chemical stressor because it is often used as a reference toxicant (Goodfellow & Rue 1989), it has been shown to be relatively stable in test solutions within renewal periods of 48 h (Stephenson, Kaushik & Solomon 1991), and its chemistry, toxicology and fate in the environment have been reported widely (Wild, Harrad & Jones 1992; Hobbs, Howe & Dobson 1993). The chemical was obtained from Aldrich Chemicals (The

Old Brickyard, New Road, Gillingham, Dorset SP8 4XT, UK) and was stated to have a 99% purity. Stock solutions of PCP were prepared in triethylene glycol, stored in the dark and replaced weekly. Test concentrations were prepared by the addition of appropriate aliquots of stock solution in dilution water. Additions were made gradually by microlitre syringe whilst stirring by magnetic follower; solutions were stirred for 30 min prior to use.

Preparatory to setting up initial populations, for each treatment 50 nauplii were added randomly, in groups of 10 each, to 5 replicate wells of tissue culture plates, each containing 10 mL of the appropriate test solution. Nauplii were allowed to develop until females produced their first egg sacs. If sufficient animals were available, the number of adults in each replicate was then reduced to two pairs of adults (2 males and 2 females) to obtain the founding (Week 0) population. If insufficient adults were available, the founding population was supplemented with animals from other replicates, or reduced in size, but never less than one male and one female. Within each replicate population, surviving copepods were transferred daily to a duplicate culture plate well containing 10 mL of freshly prepared test solution. The number of nauplii, small copepodids, large copepodids and adults, and egg sac females in each replicate were counted weekly for the 11 weeks of the experiment. To convert population number to population biomass, the dry weights of individual nauplii, small copepodids, and large copepodids/adults with/without egg sacs were assumed to be as in the sibling species Tisbe holothuriae, measured by Heath (1994) as 0·07 μg, 0·27 μg, 1·23 μg and 4·92 μg, respectively.

Population growth rate (pgr) was calculated from population biomass, following Barlow (1992). This procedure in effect computes a weighted average of the pgrs of the different age classes, and would equate to the conventional measure calculated from the Euler–Lotka equation if the weights in the weighted average were reproductive efforts (Appendix 1). Here we were not able to estimate reproductive efforts reliably, and used instead masses of individuals in each age class.

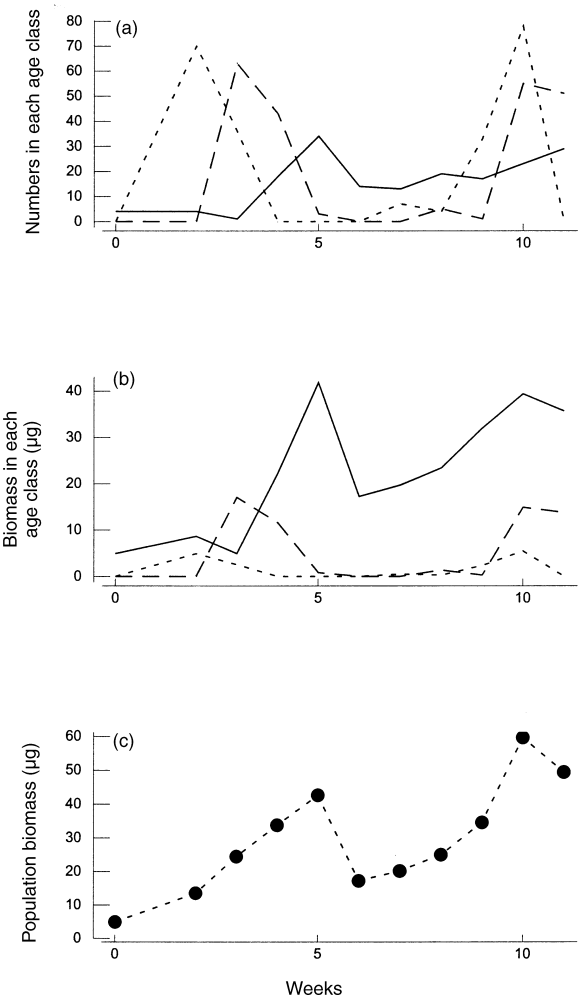

Fig. 1. Data from one replicate of one treatment for the 11 weeks of the experiment: (a) shows numbers and (b) biomass in each age class. Dotted line, nauplii; dashed line, small copepodids; solid line, adults/large copepodids, defined as in Methods. (c) Total population biomass. The population was maintained in 10 mL of test solution.

Results

An example of the data obtained from one replicate of one treatment is shown in Fig. 1a. The four founding adults bred and produced large numbers of nauplii in the first 2 weeks (numbers were not recorded in week 1). The nauplii metamorphosed into small copepodids producing a peak in copepodid numbers in week 3, and later transformed into large copepodids/adults producing a peak in their numbers in week 5. The population was then fairly stable until a second burst of reproduction in weeks 9–10. It is clear from Fig. 1a that describing population size simply in terms of total number gives undue weight to smaller copepodids. This can be avoided by describing population size in terms of biomass, following Barlow (1992) (Fig. 1b,c). In terms of biomass, the largest class is the large copepodids/adults class in every week except week 3, and the population appears to peak first in week 5 and thereafter to fluctuate about carrying capacity.

Figure 2 provides an overview of the data, showing how population biomass changed during the experiment for each of the 12 treatments. At the lowest food concentration, populations did not maintain themselves (Fig. 2e,f); other populations reached carrying capacity by about week 4 and then stayed close to carrying capacity. At the highest food concentration (Fig. 2a,b), non-PCP populations initially increased faster than PCP populations and

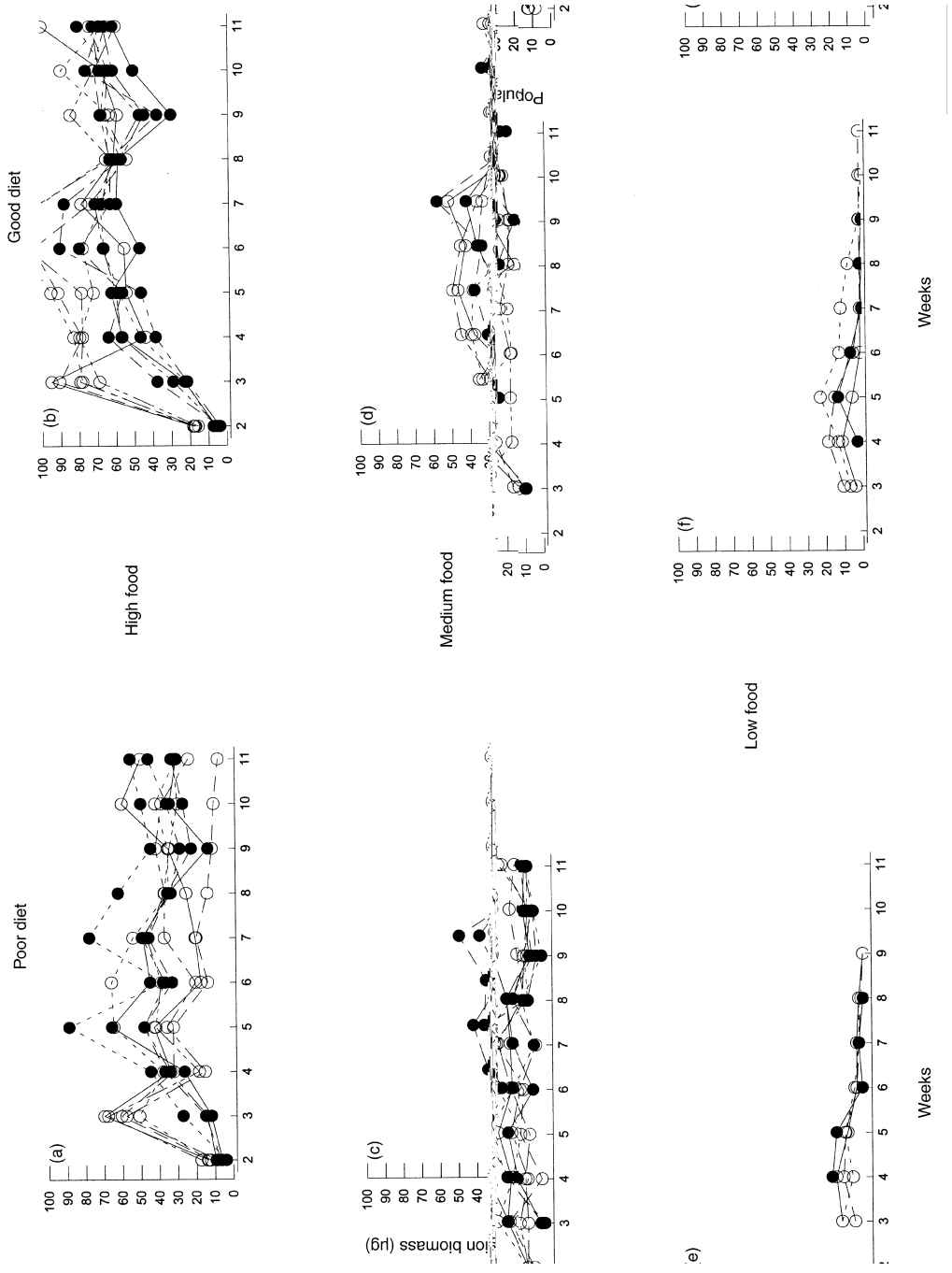

Fig. 2. Overview of the data from the 12 treatments over the 11 weeks of the experiment: top row = treatments using high concentration (3250 μgC L^{-1}); middle row = middle concentration (1300 μgC L^{-1}); bottom row = low concentration (520 μgC L^{-1}). Treatments using poor diet are in the left-hand column, those using good diet are on the right. Within each panel are shown the population biomasses of the populations with or without 100 μg L^{-1} PCP (filled and open circles, respectively). Each population was maintained in 10 mL of test solution.

reached higher peaks in week 3 (two-sample t-tests, $t_6 = 3{\cdot}72$, $P = 0{\cdot}01$ and $t_7 = 15{\cdot}30$, $P < 0{\cdot}0001$ for poor and good diets), thereafter falling back to similar levels. Week 3 populations were also higher for non-PCP than for PCP populations for the medium concentration (Fig. 2d, $t_4 = 3{\cdot}55$, $P = 0{\cdot}02$) for the good diet, though not for the poor diet (Fig. 2c, $t_5 = 2{\cdot}15$, NS).

To investigate factors affecting carrying capacity, the carrying capacity for each population in its 10 mL container was calculated as average population biomass, μg, in weeks 5–11. The carrying capacity for each population is shown in Fig. 3. Carrying capacity increased linearly with food concentration. Stepwise noconstant regression revealed that the best regression equation was:

$$\begin{aligned}\text{carrying capacity} &= 0{\cdot}0120\ (\pm 0{\cdot}0007)\ \text{concentration} \\ &\quad + 0{\cdot}0107\ (\pm 0{\cdot}0011)\ \text{concentration} \times \text{diet} \\ &\quad - 0{\cdot}00356\ (\pm 0{\cdot}00133)\ \text{concentration} \times \text{diet} \\ &\quad \times \text{PCP}. \end{aligned} \qquad \text{eqn 1}$$

Thus, carrying capacity per 10 mL test solution increased by $0{\cdot}012\,\mu$g for each μgC L^{-1} increase in concentration of the poor diet. On the good diet the increase was $0{\cdot}012 + 0{\cdot}0107 = 0{\cdot}023\,\mu$g for each μgC L^{-1} increase in concentration in the absence of PCP, and with PCP the increase was $0{\cdot}012 + 0{\cdot}0107 - 0{\cdot}00356 = 0{\cdot}019$.

To investigate the effects of population density on population growth rate (pgr), we first calculated pgr as the natural logarithm of (population biomass in week $t+1$)/(population biomass in week t). The units of pgr are therefore $week^{-1}$. This procedure is the analogue of the conventional method for populations without age structure, which calculates pgr as $r = \log_e \lambda$, where $\lambda = N_{t+1}/N_t$ and N_t represents population size at time t. Pgr is plotted against biomass in Fig. 4, where a linear relationship has been obtained by plotting biomass on a $\log_{10}$ scale. The data for the lowest concentration showed much increased variability, being based on very few individuals, and these data are not shown. General linear modelling was used to investigate the effects on pgr of log biomass, diet, PCP and concentration. Interaction terms were not significant using a stepwise procedure in which main effects were entered first. Of the main effects, that of PCP was not significant ($F_{1,299} = 0{\cdot}17$). The regression equation for the remaining main effects, all significant at $P < 0{\cdot}001$, was:

$$\begin{aligned}\text{pgr} &= 1{\cdot}27 - 1{\cdot}70\ (\pm 0{\cdot}09)\ \log_{10}\text{biomass} \\ &\quad + 0{\cdot}428\ (\pm 0{\cdot}051)\ \text{diet} \\ &\quad + 0{\cdot}000298\ (\pm 0{\cdot}000027)\ \text{concentration}. \end{aligned} \qquad \text{eqn 2}$$

Thus, increasing biomass reduced pgr by $1{\cdot}70$ $week^{-1}$ for each unit increase in $\log_{10}$ biomass. Improving diet increased pgr by $0{\cdot}428\,week^{-1}$, and increasing concentration from 1300 μgC L^{-1} to 3250 μgC L^{-1} elevated pgr by $0{\cdot}581\,week^{-1}$. The regression equation accounted for 56% of the variance (r^2_{adj}).

Discussion

This study was designed to investigate the joint effects of PCP, food concentration and diet on the population dynamics of Tisbe in controlled conditions. Carrying capacity increased linearly with food

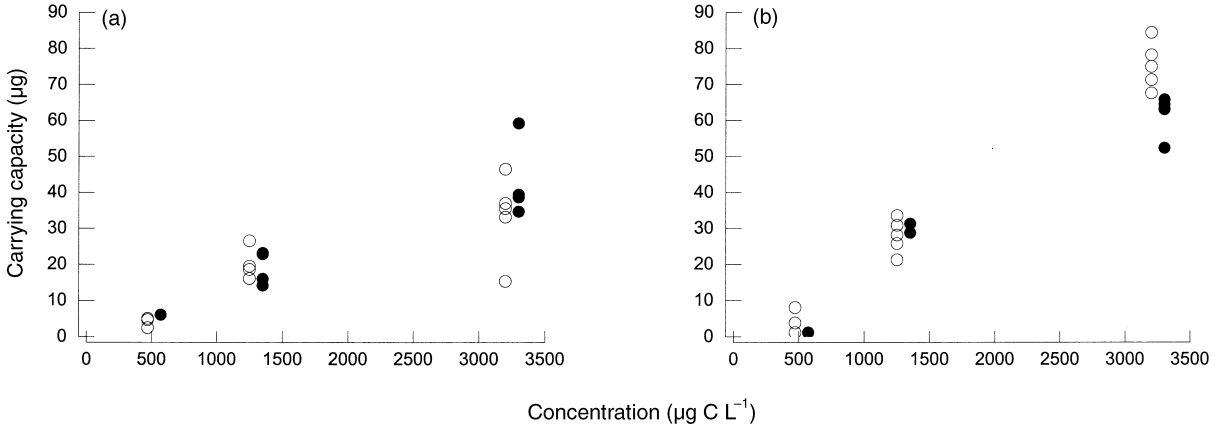

Fig. 3. Carrying capacity in relation to concentration for (a) poor, and (b) good diet. Filled and open circles show carrying capacities of populations with and without PCP, respectively, as in Fig. 2. Each population was maintained in 10 mL of test solution.

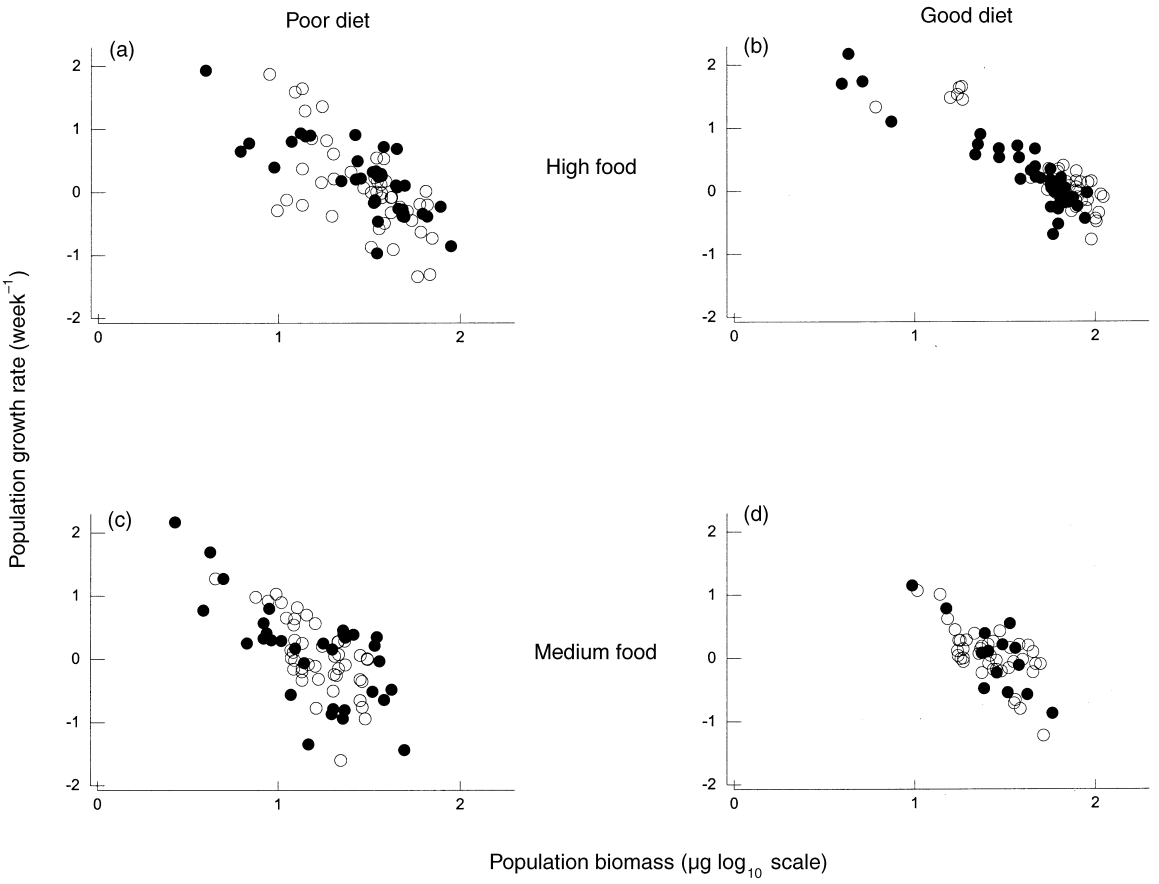

Fig. 4. Population growth rate (pgr, week^{-1}) plotted against $\log_{10}$ density, density being measured as population biomass. Layout and conventions as Fig. 2 except no data are shown for the low concentration. Thus, top and bottom rows represent high and middle concentrations; treatments using poor diet are in the left-hand column, those using good diet are on the right. Filled/open circles indicate pgrs of populations with/without 100 μg L^{-1} PCP.

concentration, more so for the good than the poor diet. The rate of increase was less on the good diet in PCP populations, but PCP had no effect on the poor diet (Fig. 3). Population growth rate (pgr) was linearly dependent on population biomass when the latter was plotted on a logarithmic scale (Fig. 4). Improving diet or food concentration increased the intercept of the line but did not affect its slope, and PCP had no effect. At some higher food concentrations, non-PCP populations initially increased faster than PCP populations and reached higher peaks in week 3 (Fig. 2a,b,d). Thus, overall food concentration had the greatest effect, diet had some effect and, rather surprisingly, PCP had relatively few effects on population dynamics. We shall discuss these in turn, but first we consider the form of density dependence in Tisbe battagliai.

The density-dependent relationships found in this study are shown in Fig. 4. To cope with the difficulty that the populations comprised different age classes, density was described by biomass. This procedure assumes body mass is invariant to either PCP or food limitation, and to the extent this assumption does not hold, the effects of PCP and/or food limitation could be underestimated. This could mean that carrying capacities are overestimated. However, this bias, if it exists, is likely to apply to all treatments, since density eventually reduced pgr to zero in all treatments.

Given its fundamental importance in population ecology, it is surprising that the dependence of pgr on density has rarely been analysed, so that there are rather few graphs in the literature with which to compare Fig. 4. Of the seven cases we found, five relationships are linear (Daphnia pulex, Frank, Boll & Kelly 1957; treehole mosquitoes Aedes triseriatus, Livdahl 1982; Edgerley & Livdahl 1992; guppies Poecilia reticulata, Barlow 1992; magpie geese Anseranas semipalmata, Bayliss 1989; wildebeest, Sinclair 1996). In the remaining cases, pgr declines as log density as in Fig. 4 (grey-sided voles Chlethrionomys rufocanus, Saitoh, Stenseth & Bjornstad 1997; wood mice Apodemus sylvaticus, Montgomery 1989). Where pgr decreases with log density, as in

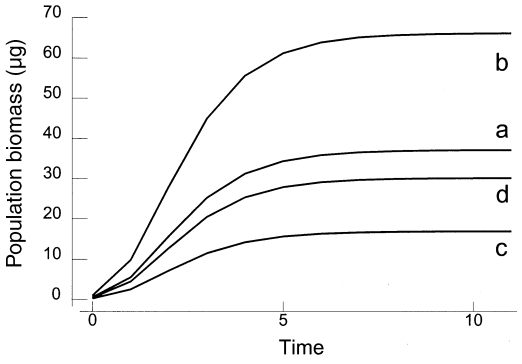

Fig. 5. The effects of logarithmic density dependence on population growth. a–d refer to graphs a–d in Fig. 4, and were calculated by fitting regression lines to the graphs in Fig. 4 and using the regression coefficients to compute the population growth curves shown here. Thus, curve a refers to poor diet, high food concentration; curve b to good diet and high food concentration; and so on. Specifically, writing population biomass as x and expressing pgr as 1/x dx/dt in eqn 2 gave an equation which was integrated to obtain $x = \alpha * \exp[-\exp(\beta - k * \text{time})]$ where α and β are parameters calculated from eqn 2 and k is a scaling parameter relating to the size of the environment, here 10 mL. Initial population size was taken to be 1.

Fig. 4, population growth is still very similar to logistic (Fig. 5). The final population biomasses in Fig. 5 correspond to carrying capacities, in effect derived from Fig. 4 as the population biomasses at which pgr = 0. Note that carrying capacities derived by this method are in good agreement with the direct estimates shown in Fig. 3.

Carrying capacity was influenced by food concentration, diet type (unialgal or mixed species diet) and, on the good diet, by PCP (Fig. 3). Populations reached a maximum stable density around 65 μg per 10 mL test solution, corresponding to approximately 13 copepods per mL^{-1} on the high concentration (3250 μgC L^{-1}) mixed species algal diet. This value is comparable to maximum densities of harpacticoids achieved in laboratory cultures in other studies. Irrespective of copepod inoculum density, populations of T. holothuriae receiving a high concentration of mixed diet of algae and an inert food, levelled out at between 10 and 20 mL^{-1} (Heath 1994); similar values were obtained by Gaudy & Guerin (1982). Our results are consistent with those from previous LTRE experiments, which showed significant reductions in fecundity of Tisbe battagliai following relatively small reductions in algal concentration (Williams 1997; Williams & Jones 1999) and significant increases in fecundity for copepods fed a mixed species algal diet compared with a unialgal diet of Isochrysis galbana (Williams 1997). The extinctions of the populations in low food concentrations (Fig. 2c,f) are also in accord with previous LTRE experiments, which revealed that low concentrations prolonged stage durations and reduced fecundity (Williams & Jones 1994, 1999).

PCP caused significant decrease in population growth at high food concentration during the first 3 weeks (Fig. 2a,b) and reduced carrying capacity on the good diet (Fig. 3). Although the effects of PCP did not appear in the density-dependent analysis of eqn 2, restricting the analysis to the case of a high concentration of good diet (Fig. 4b) does show significant effects, viz:

$$\begin{aligned} \text{pgr} = {} & 4{\cdot}34\ (\pm 0{\cdot}28) \\ & - 2{\cdot}32\ (\pm 0{\cdot}15)\ \log_{10}\ \text{biomass} \\ & - 1{\cdot}54\ (\pm 0{\cdot}32)\ \text{PCP} \\ & + 0{\cdot}759\ (\pm 0{\cdot}180)\ \text{PCP} \\ & \times\ \log_{10}\ \text{biomass.} \end{aligned} \qquad \text{eqn 3}$$

accounting for 85% of the variance (r^2_{adj}). This gives carrying capacities on good diet of 62 μg per 10 mL test solution for PCP populations and 74 μg per 10 mL test solution for populations without PCP, in broad agreement with the values estimated in Fig. 3. This analysis also shows the reduction in initial population growth that can be seen in Fig. 2b. Curiously, the reduction in initial population growth in Fig. 2a is not evident in Fig. 4a. The reason is that population biomasses were reduced in PCP populations by week 2, but this is not seen in pgrs because they were not calculated until after week 2, when there were no differences.

Stressors may be classified as acting additively, synergistically or antagonistically according to whether their joint effects are the same, more or less than the sum of their individual effects (Linke-Gamenick, Forbes & Sibly 1999; Sibly 1999). In these terms, the four stressors studied here (density, food quality, food concentration and PCP) for the most part acted additively, as evidenced by the near parallelism of the density-dependent relationships plotted in Fig. 4, and the lack of significant interaction terms in the regression analysis of eqn 2. There are suggestions of antagonism, however, in the effects of PCP, since at higher food concentrations PCP reduced pgr at low density but little if at all at carrying capacity. Thus, density dependence may to some extent compensate for effects of toxicants observed at low density, as suggested by Calow, Sibly & Forbes (1997) and Grant (1998) and observed in Capitella sp. M at low (though not at high) concentrations of fluoranthene (Linke-Gamenick, Forbes & Sibly 1999).

Several mechanisms that might give rise to density dependence in the Tisbe genus have been suggested. Bergmans (1983) considered that density effects are most likely an effect of adults on juvenile survival, and that at high population densities, nauplii may

be more sensitive than adults to crowding. Similarly, LTRE experiments suggest that adult Tisbe battagliai (Williams & Jones 1994) and freshwater calanoids (Jamieson & Burns 1988) have a higher tolerance to low food concentration than the early life-history stages. Therefore, at high density, under conditions of food limitation, the larger life stages (large copepodids and adults) may persist at lower food levels than the smaller life stages. Crowding is also known to reduce reproductive output and viability and depress larval viability in Tisbe holothuriae (Hoppenheit 1975a,b, 1976; Brand 1985). These effects could be a result of scramble competition for food and space resulting in lower food intake and increased swimming activity, with associated increase in energetic costs (Gaudy & Guerin 1982). For benthic surface-dwelling organisms such as Tisbe, the surface area of the culture vessels may therefore have a role in determining carrying capacity. Fava & Crotti (1979) reported negative effects of crowding on nauplii production by T. holothuriae but found that these effects diminished when the water medium was renewed daily. These authors concluded that a chemically mediated mechanism was the most likely explanation for reduced fertility with increased crowding. Crowding is also known to affect the sex ratio in Tisbe, from a female bias at low density to a strong male bias at high density (Hoppenheit 1976; Uhlig 1984; Heath 1994), and Kahan, Berman & Bar-el (1988) reported maternal inhibition of hatching at high population densities of the harpacticoid Tigriopus japonicus. It is not known to what extent these density-dependent processes operate in the field. However, Lopez (1982) obtained similar results to ours in a study of local population abundance of Tisbe cucumariae around dead macroinvertebrates (tunicates) in a large flowing seawater tank considered representative of field conditions. The corpses of tunicates were rapidly colonized by adults, and this was followed by a period of intense reproduction (bloom phase). This did not, however, translate into a greatly increased abundance of adults, although when the age structure stabilized it consisted largely of adults. It may be, therefore, that in field conditions as in the laboratory, reproduction is suppressed at high density. Similar results were obtained by Munzinger (1994), who observed that Daphnia magna populations at high density experienced food shortages which led to selective deaths of neonates. Only when most of the adults had died, were offspring able to reach sexual maturity and reproduce.

In conclusion, this study has demonstrated that it is relatively straightforward to measure the effects of stressors on carrying capacity and density dependence, at least when the study organism has such a short generation time and is as readily cultured as Tisbe battagliai. The quantitative description of density dependence in eqn 2 allows extrapolation to be made to other stressor values and to larger volumes, using the approach of Fig. 5. It is hoped that the results will be of interest both as an investigation of the ecological effects of stress, and as a contribution to the development of ecotoxicological test procedures for measuring the long-term effects of chemicals on populations.

Acknowledgements

We are very grateful for helpful suggestions to V. Forbes, T. Sherratt, J. Hone, I. Linke-Gamenick, T.H. Hutchinson and A.R.E. Sinclair.

References

Baird, D.J., Maltby, L., Greig-Smith, P.W. & Douben, P.E.T. (eds) (1996) Ecotoxicology: Ecological Dimensions. Chapman & Hall, London.

Banks, J.E. & Stark, J.D. (1998) What is ecotoxicology? An ad-hoc grab bag or an interdisciplinary science? Integrative Biology, **1**, 195–204.

Barlow, J. (1992) Nonlinear and logistic growth in experimental populations of guppies. Ecology, **73**, 941–950.

Bayliss, P. (1989) Population dynamics of magpie geese in relation to rainfall and density: implications for harvest models in a fluctuating environment. Journal of Applied Ecology, **26**, 913–924.

Bergmans, M. (1983) Population biology of the harpacticoid copepod Tisbe furcata (Baird, 1837). PhD Thesis, Vrije Universiteit Brussels.

Brand, G.W. (1985) Effect of crowding on larval viability in Tisbe holothuriae (Copepoda: Harpacticoida). Marine Biology, **88**, 67–72.

Brand, G.W., Fabris, G.J. & Arnott, G.H. (1986) Reduction of population growth in Tisbe holothuriae Humes (Copepoda: Harpacticoida) exposed to low cadmium concentrations. Australian Journal of Marine and Freshwater Research, **37**, 475–479.

Calow, P., Sibly, R.M. & Forbes, V. (1997) Risk assessment on the basis of simplified life-history scenarios. Environmental Toxicology and Chemistry, **16**, 1983–1989.

Charlesworth, B. (1994) Evolution in Age-Structured Populations, 2nd edn. Cambridge University Press, Cambridge.

Edgerley, J.S. & Livdahl, T.P. (1992) Density–dependent interactions within a complex life-cycle – the roles of cohort structure and mode of recruitment. Journal of Animal Ecology, **61**, 139–150.

Fava, G. & Crotti, E. (1979) Effect of crowding on nauplii production during mating time in Tisbe clodiensis and T. holothuriae (Copepoda, Harpacticoida). Helgolander Wissenschaftliche Meeresuntersuchungen, **32**, 466–475.

Frank, P.W., Boll, C.D. & Kelly, R.W. (1957) Vital statistics of laboratory cultures of Daphnia pulex DeGeer as related to density. Physiological Zoology, **30**, 287–305.

Gaudy, R. & Guerin, J.P. (1982) Population dynamics of Tisbe holothuriae (Copepoda: Harpacticoida) in exploited mass cultures. Netherlands Journal of Sea Research, **16**, 208–216.

Goodfellow, W.L. Jr & Rue, W.J. (1989) Evaluation of a chronic estimation toxicity test using Mysidopsis bahia. Aquatic Toxicology and Hazard Assessment, ASTM STP 1027 (eds U.M. Cowgill & L.R. Williams), pp. 333–344. American Society for Testing and Materials.

Grant, A. (1998) Population consequences of chronic toxicity: incorporating density dependence into the analysis of life table response experiment. Ecological Modelling, **105**, 325–335.

Heath, P.L. (1994) The development of Tisbe holothuriae as a live diet for larval flatfish rearing. PhD Thesis, Heriot-Watt University.

Hobbs, S.J., Howe, P.D. & Dobson, S. (1993) Environmental hazard assessment: pentachlorophenol. Toxic Substances Division, Directorate for Air, Climate and Toxic Substances, Department of the Environment, Building Research Establishment.

Hoppenheit, M. (1975a) Zur dynamik exploitierter populationen von Tisbe holothuriae (Copepoda, Harpacticoida). I. Methoden, verlauf der populationsentwicklung und einflub der wasserernеuerung. Helgolander Wissenschaftliche Meeresuntersuchungen, **27**, 235–253.

Hoppenheit, M. (1975b) Zur dynamik exploitierter populationen von Tisbe holothuriae (Copepoda, Harpacticoida). II. Populationsdichte, alterszusammensetzung, wachstum und ausbeute. Helgolander Wissenschaftliche Meeresuntersuchungen, **27**, 377–395.

Hoppenheit, M. (1976) Zur dynamik exploitierter populationen von Tisbe holothuriae (Copepoda, Harpacticoida). III. Reproduktion, geschlechtsverhaltnis, entwicklungsdauer und uberlebenszeit. Helgolander Wissenschaftliche Meeresuntersuchungen, **28**, 109–137.

Hoppenheit, M. (1977) On the dynamics of exploited populations of Tisbe holothuriae (Copepoda, Harpacticoida). V. The toxicity of cadmium: response to sublethal exposure. Helgolander Wissenschaftliche Meeresuntersuchungen, **29**, 503–523.

Hoppenheit, M. & Sperling, K.R. (1977) On the dynamics of exploited populations of Tisbe holothuriae (Copepoda, Harpacticoida). IV. The toxicity of cadmium: response to lethal exposure. Helgolander Wissenschaftliche Meeresuntersuchungen, **29**, 328–336.

Hutchinson, T.H. & Williams, T.D. (1989) The use of sheepshead minnow (Cyprinodon variegatus) larvae and a benthic marine copepod (Tisbe battagliai) in short-term tests for estimating the chronic toxicity of industrial effluents. Hydrobiologia, **188/189**, 567–572.

International Standards Organisation (1999) Water quality – Determination of acute lethal toxicity to marine copepods (Copepoda, Crustacea). ISO 14669.

Jamieson, C. & Burns, C.B. (1988) The effects of temperature and food on copepodite development, growth and reproduction in three species of Boeckella (Copepoda; Calanoida). Hydrobiologia, **164**, 235–257.

Kahan, D., Berman, Y., Bar-e. & l, T. (1988) Maternal inhibition of hatching at high population densities in Tigriopus japonicus (Copepoda, Crustacea). Biological Bulletin, **174**, 139–144.

Kirby, M.F., Blackburn, M.A., Thain, J.E. & Waldock, M.J. (1998) Assessment of water quality in estuarine and coastal waters of England and Wales using a contaminant concentration technique. Marine Pollution Bulletin, **36**, 631–642.

Levin, L.A., Caswell, H., De Patra, K.D. & Creed, E.L. (1987) The life table consequences of larval development mode: an intraspecific comparison for planktotrophy and lecithotrophy. Ecology, **68**, 1877–1886.

Levin, L.A., Caswell, H., Bridges, T., DiBacco, C., Cabrera & D.Plaia, G. (1996) Demographic responses of estuarine polychaetes to pollutants: life table response experiments. Ecological Applications, **6**, 1295–1313.

Linke-Gamenick, I., Forbes, V.E. & Sibly, R.M. (1999) Density-dependent effects of a toxicant on life-history traits and population dynamics of a capitellid polychaete. Marine Ecology Progress Series, **184**, 139–148.

Livdahl, T.P. (1982) Competition within and between hatching cohorts of a treehole mosquito. Ecology, **63**, 1751–1760.

Lopez, G.W. (1982) Short-term population dynamics of Tisbe cucumariae (Copepoda: Harpacticoida). Marine Biology, **68**, 333–341.

Matthiessen, P., Bifield, S., Jarrett, F., Kirby, M.F., Law, R.J., McMinn, W.R., Sheahan, D.A., Thain, J.E. & Whale, G.F. (1998) An assessment of sediment toxicity in the River Tyne estuary, UK, by means of bioassays. Marine Environmental Research, **45**, 1–15.

Montgomery, W.I. (1989) Population regulation in the wood mouse Apodemus sylvaticus I. Density dependence in the annual cycle of abundance. Journal of Animal Ecology, **58**, 465–476.

Munzinger, A. (1994) The influence of nickel on population dynamics and on some demographic parameters of Daphnia magna. Hydrobiologia, **277**, 107–120.

Saitoh, T., Stenseth, N.C. & Bjornstad, O.N. (1997) Density dependence in fluctuating grey-sided vole populations. Journal of Animal Ecology, **66**, 14–24.

Sibly, R.M. (1999) Efficient experimental designs for studying stress and population density in animal populations. Ecological Applications, **9**, 496–503.

Sibly, R.M. & Smith, R.H. (1998) Identifying key factors using -contribution analysis. Journal of Animal Ecology, **67**, 17–24.

Sinclair, A.R.E. (1996) Mammal populations: fluctuation, regulation, life history theory and their implications for conservation. Frontiers of Population Ecology (eds R.B.Floyd, A.W.Sheppard & P.J.De Barro), pp. 127–154. CSIRO Publishing, Melbourne.

Stephenson, G.L., Kaushik, N.K. & Solomon, K.R. (1991) Chronic toxicity of a pure and technical grade pentachlorophenol to Daphnia magna. Archives of Environmental Contamination and Toxicology, **21**, 388–394.

Thain, J.E. & Kirby, M.F. (1996) Improving the sensitivity of biological water quality measurements in marine waters. Proceedings of the Scientific Symposium on the North Sea Quality, Status Report 1993, April 1994, Ebeltoft, Denmark, pp. 151–156. Danish Environmental Protection Agency.

Uhlig, G. (1984) Progress in mass cultivation of harpacticoid copepods for maricultural purposes. E.M.S. Special Publication No. 8, pp. 261–273. Bredene, Belgium.

Van Leeuwen, C.J., Luttmer, W.J. & Griffioen, P.S. (1985) The use of cohorts and populations in chronic toxicity studies with Daphnia magna: a cadmium example. Ecotoxicology and Environmental Safety, **9**, 26–39.

Van Leeuwen, C.J., Niebeek, G. & Rijkeboer, M. (1987) Effects of chemical stress on the population dynamics of Daphnia magna: a comparison of two test procedures. Ecotoxicology and Environmental Safety, **14**, 1–11.

Walker, C.H., Hopkin, S.P., Sibly, R.M. & Peakall, D. (1996). Principles of Ecotoxicology. Taylor & Francis, London.

Wild, S.R., Harrad, S.J. & Jones, K.C. (1992) Pentachlorophenol in the UK environment. I. A budget and source inventory. Chemosphere, **24**, 833–845.

Williams, T.D. (1992) Survival and development of copepod larvae Tisbe battagliai in surface microlayer, water and sediment elutriates from the German Bight. Marine Ecology Progress Series, **91**, 221–228.

Williams, T.D. (1997) Life-cycle parameters of Tisbe battagliai. (Copepoda: harpacticoida) as indicators of chronic toxicity. PhD Thesis, University of Plymouth.

Williams, T.D. & Jones, M.B. (1994) Effects of temperature and food quantity on postembryonic development of Tisbe battagliai (Copepoda: harpacticoida). Journal of Experimental Marine Biology and Ecology, **183**, 283–298.

Williams, T.D. & Jones, M.B. (1999) Effects of temperature and food quantity on the reproduction of Tisbe battagliai (Copepoda: harpacticoida). Journal of Experimental Marine Biology and Ecology, **236**, 273–290.

Received 14 February 2000; revision received 24 March 2000

Appendix 1

The solution of the Euler–Lotka equation, λ, provides a measure of overall population multiplication rate even if a population is not in stable age structure (Sibly & Smith 1998). λ is equal to the multiplication rate of the total reproductive value of the population (Charlesworth 1994, p.40.). Thus, if n_i represents the number of animals in age class i at one time, and n_i' represents the number in the age class one time unit later, and if the reproductive value of each animal in age class i is v_i, then

$$\lambda = \frac{n_1'v_1 + n_2'v_2 + n_3'v_3 + \ldots}{n_1v_1 + n_2v_2 + n_3v_3 + \ldots} \qquad \text{eqn A1}$$

λ can therefore be thought of as a weighted multiplication rate, number in each age class being weighted by its reproductive value. To make use of this approach, one would measure the reproductive values, and use them in the calculation of weighted multiplication rate. Unfortunately, we experienced difficulties in estimating reproductive values, and as a substitute each age class was weighted by its dry mass.