Secondary production and reproduction of *Capitella capitata* type I (Annelida: Polychaeta) during a population cycle

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ABSTRACT: We monitored secondary production, individual reproductive characteristics (i.e. reproductive periodicity, female size, fecundity, reproductive output), and oocyte standing crop during an oscillation cycle of a laboratory population of the opportunistic polychaete *Capitella capitata* type I. Biomass oscillation resulted from changes in the amount of food available per unit standing biomass of *C. capitata*. During population decline, reproduction and secondary production were reduced; this confirms that the population cycle was driven by food availability. Comparisons of actual supplied ration vs theoretical estimate maintenance ration needed to support the population, suggested that the population was overshooting its carrying capacity. However, maximal population biomass and density did not decline sharply and were sustained over an 8 wk period. Decreases in production and reproduction rates preceding population decline are indicative of metabolic regulation to adjust energetic requirements to available resources. This observation suggests that the population would not overshoot its carrying capacity. When density was low, daily food ration exceeded the whole community requirements and food accumulated in the tray. Until used, such build-up increases the amount of food available to *C. capitata*, resulting in an oscillating (actual) carrying capacity above the static (theoretical) carrying capacity calculated relative to the daily food-ration. Our results suggest that the population did overshoot this 'theoretical' carrying capacity but not the 'actual' carrying capacity.

INTRODUCTION

The opportunistic polychaete *Capitella capitata* type I has received considerable attention because of its ability to colonize disturbed sediments. Field studies of the population dynamics of *C. capitata* describe early colonization of azoic areas, rapid population growth and then subsequent rapid declines in population size (Grassle & Grassle 1974, McCall 1977, Tsutsumi 1987). These dynamics are important to models of community succession where early colonizers are displaced from a community as other species gradually become established. Although displacements of early colonizers have often been attributed to competitive interactions (Grassle & Grassle 1974, McCall 1977, Pearson & Rosenberg 1978), recent studies have suggested that

the exclusion of opportunistic species from later seral stages is independent of interspecific interactions (Petersen 1980, Gray 1981, Chesney 1985, Tsutsumi 1987).

The population dynamics of *Capitella capitata* have been studied in laboratory cultures to ascertain the role of food availability in controlling these 'boom and bust' patterns (Chesney & Tenore 1985a, b). In the absence of macrofaunal competitors, *C. capitata* populations oscillate between low and high densities in relation to food availability. Chesney & Tenore suggest that when food is abundant, rapid growth and reproduction push the population above its carrying capacity, resulting in rapid population declines as the nutritional needs of the population can no longer be met. However, in all experimental cultures, population declines occur over a period of at least 10 wk. An important question concerning these dynamics needs to be addressed: if the population declines are due to an overshoot of the

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carrying capacity, why does it take so long for the populations to decline?

In opportunistic polychaetes, reproductive output (Wible 1984, Levin 1986, Levin & Creed 1986, Zajac 1986), energy partitioning (Grémare et al. in press a), and growth (Tenore 1981, 1983) are highly sensitive to food availability, which sustains rapid population increases. However, such sensitivity to food availability provides a mechanism for a population to adjust its reproduction and growth rates relative to available food resources. With this level of regulation it could be possible for *Capitella capitata* to avoid an increase in population size which would push the population's energetic requirements above the level of available resources.

To determine whether the oscillation cycle is due to an overshoot of the carrying capacity requires: (1) an estimation of the carrying capacity of the population, and (2) a measure of changes in growth and reproduction rate as a function of time (Chesney & Tenore 1985a). Previous studies on the oscillation cycles of *Capitella capitata* have mainly considered changes in secondary production and have not measured changes in reproduction rate (Chesney & Tenore 1985a, b). Chesney & Tenore (1985a) measured changes in reproductive output through changes in larval settlement rates. However such an index is likely to be correlated with population density and provides no information about the reproductive responses of individual females. This study examines changes in secondary production and reproduction rates in *C. capitata* relative to available resources during a population cycle.

MATERIALS AND METHODS

Tray data. A population of the polychaete *Capitella capitata* type I was cultured on a 2 cm layer of sieved (<0.3 mm) beach sand placed in a small tray (0.25 m^2) receiving recirculating artificial seawater (Instant Ocean, 20 °C, 25 ‰). The tray was stocked with 100 non-sexed juveniles (originating from our stock cultures) and the population was fed Gerber's mixed cereals at a rate of 120 mg N m^{-2} d^{-1}. The experiment was unreplicated. The population was sampled once a week (three 541 mm^2 cylindrical cores). Each sample was sieved (0.3 mm mesh). The worms were narcotized (1 % MgCl$_2$ in artificial seawater) and then removed from their tubes to be counted and measured (width and length of the 5th setiger). Number of fertile segments, and number of maturing oocytes were determined for each gravid female. Dry weights were estimated using multiple-linear regression models between width and length of the 5th setiger, number of fertile segments, and dry weight (Grémare et al. in

press b). Weight-specific reproductive outputs (reproductive outputs) were computed after Grémare et al. (in press b). Because the distribution of *C. capitata* was not uniform in the tray (edge effects due to water circulation), we used the sampling strategy described by Chesney & Tenore (1985a).

Secondary production was calculated with a size-frequency summation technique (after Krueger & Martin 1980) modified to estimate production at between-sample intervals. Let i index sampling dates (i = 1, 2, . ., n), j index size classes (j = 1, 2, . ., a), and $Y_{i,j}$ represent the mean abundance of all replicates for size class j on date i. Secondary production for a sampling interval i to i + 1 is estimated by:

$$P = \sum_{j=1}^{a-1} 0.5 \left[(Y_{i,j} + Y_{i+1,j}) - (Y_{i,j+1} + Y_{i+1,j+1}) \right] \times (W_j \times W_{j+1})^{0.5} \times (t)^{-1},$$

where P = daily production rate; W_j = mass of size class j; t = number of days between samples i and i + 1. A size-frequency summation technique is justified because *Capitella capitata* reproduces continuously, and cohorts were indistinguishable within the population (Morin et al. 1987). To compare *C. capitata* nitrogen requirements with daily ration, growth and reproduction requirements of *C. capitata* were measured as described above. Respiration was estimated from secondary production values using the equation of Humphreys (1979). A metabolic turnover rate of 8 % of the nitrogen biomass was estimated from the minimum daily-nitrogen requirements reported by Chesney & Tenore (1985a).

Growth experiment. In a separate experiment we assessed the effect of different rations of Gerber's mixed cereals on the growth of *Capitella capitata* juveniles. Juveniles (between 10 and 40 µg individual dry weight) were sampled from culture trays receiving recirculating artificial (Instant Ocean) seawater (20 °C, 25/1000). They were narcotized in isotonic artificial seawater with 1 % MgCl$_2$ (750 mOsm); 20 juveniles of approximately the same size were measured (width and length of the 5th setiger) and introduced in a 3.5 cm diameter plastic dish containing a 1 cm layer of clean beach sand (<0.3 mm, rinsed in running tap water for 2 d). These cups were placed in a tray on a recirculating seawater table (20 °C, 25 ‰) and given a 3 d food ration of Gerber's mixed cereals. After 3 d, cups were removed, worms measured as above, and the cups were returned to the sea table. This procedure was repeated 2 more times for each cup. A total of 24 cups were used during this experiment.

A multiple linear regression between width, length of the 5th setiger, and dry weight, (µg DW = −49.509 + 0.280 (width)^2 + 9.205 (length)^2; r = 0.907, n = 60)

allowed for the computation of average initial and final biomasses in each cup. The average change in individual biomass was used to estimate a daily weight-specific growth rate.

$$G = (B_{Final} - B_{Initial}) / 0.5 (B_{Initial} + B_{Final}).$$

The ratio ration to population biomass (R:B) was computed as the mass ratio of organic nitrogen provided to the average nitrogen biomass of *Capitella capitata* present in a cup between 2 successive measurements (8 % dry wt as determined with a Perkin-Elmer analyzer; Tenore & Chesney 1985, Marsh et al. unpubl.).

RESULTS

Population dynamics

Density and biomass in the tray oscillated from 10 000 to 205 000 individuals m^{-2}, and 1 to 12.5 g dry weight m^{-2}, respectively, during a period of 28 wk (Fig. 1). Maxima in density and biomass were not sharp peaks. The population remained at its higher density between Week 4 and Week 12, and at its higher biomass between Week 5 and Week 13. Because food input was constant, changes in biomass resulted in changes in the amount of food available per unit of standing biomass of *Capitella capitata* (R:B ratio). The R:B ratio ranged from 0.12 (Week 5) to 1.56 (Week 23) (Fig. 1). Population dynamics were dominated by
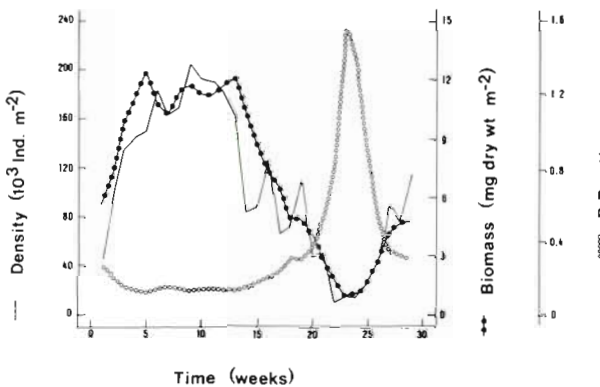

Fig. 1. *Capitella capitata*. Changes in density, biomass, and R:B ratio in the population examined

changes in abundances of small size classes (dry wt <50 µg) (Fig. 2). Larger worms were dominant only between Weeks 9 and 16. The 2 density peaks corresponded to periods of recruitment of small juveniles.

Secondary production oscillated from 10 to 150 mg ash-free dry wt m^{-2} d^{-1}. Secondary production was almost constant between Week 5 and Week 9, then declined to a minimum at Week 22 (Fig. 3). The P:B ratio

(average daily production: average weekly biomass) fluctuated from 0.17 to 0.39 (Fig. 3). The P:B ratio was low during population decline (Weeks 10 to 14). After Week 15, the P:B ratio started increasing as food availability (i.e. R:B ratio) increased. During another experiment we assessed the influence of food availability on *Capitella capitata* juvenile growth rates. The relation between growth rate and R:B ratio was best described by an
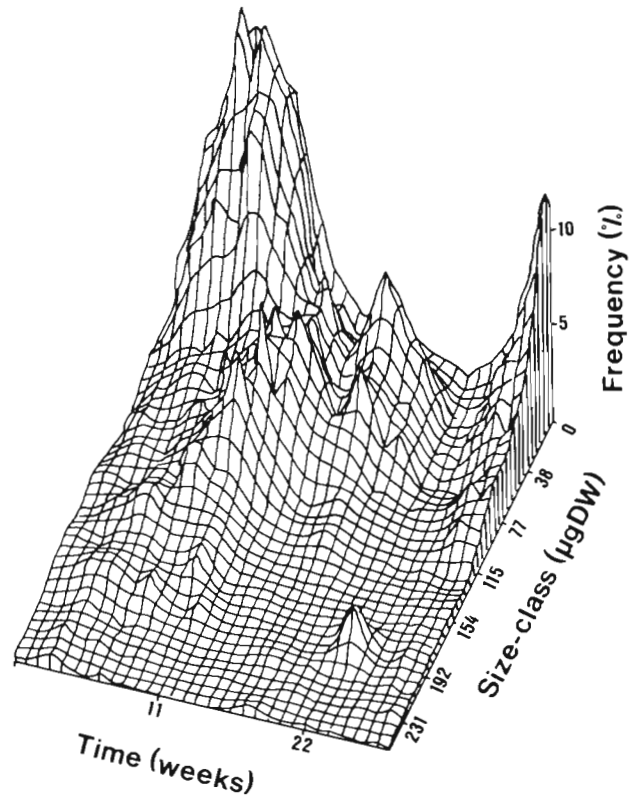

Fig. 2. *Capitella capitata*. Changes in size-frequency distribution
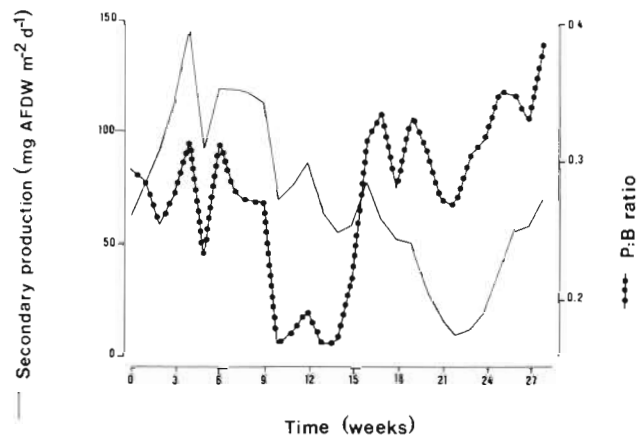

Fig. 3. *Capitella capitata*. Changes in secondary production, and P:B ratio

hyperbolic tangent function (Fig. 4, see also Tenore & Chesney 1985). When the R : B ratio was lower than 0.2, juvenile growth rates were negligible (less than 5 % d^{-1}). However, it should be pointed out that the values of the R : B ratio obtained in the tray did not account for the presence of meiofauna and microheterotrophs.
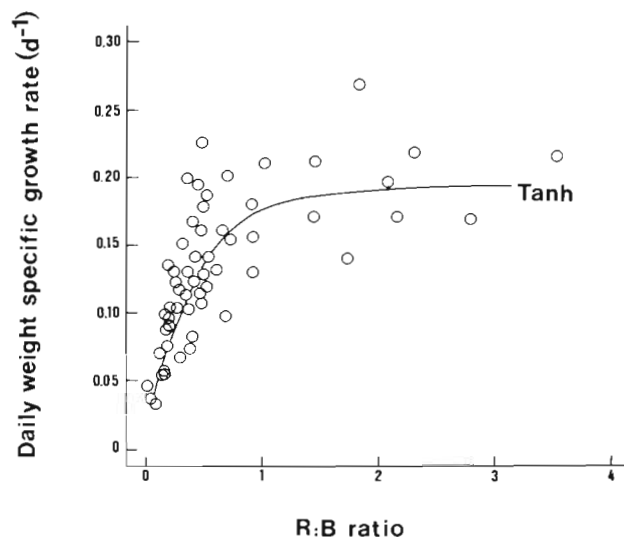

Fig. 4. *Capitella capitata*. Relation between juvenile growth rates (% d^{-1}) and food availability (separate experiment)

Reproductive activity

The proportion of gravid females in the tray oscillated from 2 to 24 % (Fig. 5). The proportion of brooding females (i.e. the proportion of gravid females found in brood-tubes) ranged from 0 (Weeks 22 to 26) to 12 % (Week 9). The proportion of brooding females is
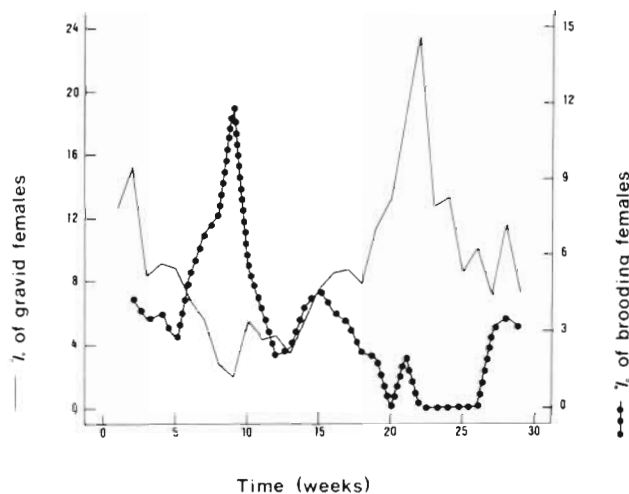

Fig. 5. *Capitella capitata*. Changes in the proportion of gravid and brooding females within the population
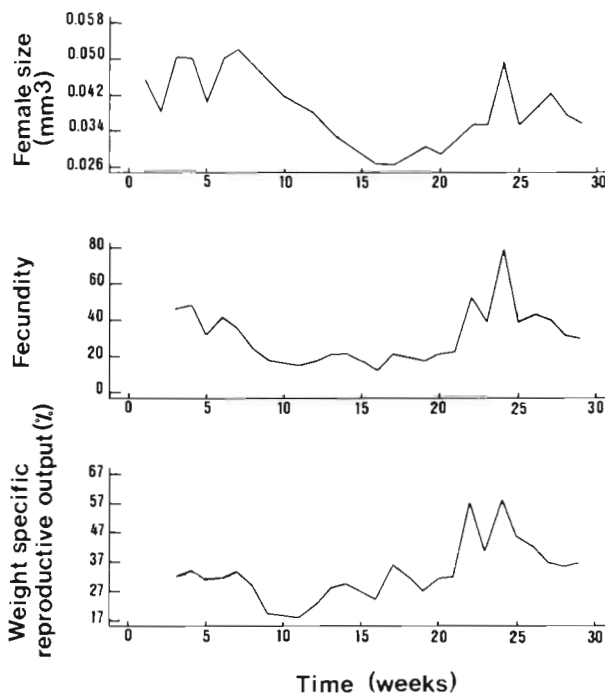

Fig. 6. *Capitella capitata*. Changes in female size, fecundity, and reproductive output

indicative of the frequency of reproduction (for details see Grémare et al. in press a). The diminution of the reproductive periodicity (Weeks 9 to 12) preceeded the decline of the population (Weeks 13 to 22).

We used female size, fecundity, and reproductive output as indices of individual reproductive responses of gravid females (Fig. 6). Female size, as measured by the volume of the 5th setiger ranged from 0.50 (Weeks 3 to 7) to 0.28 mm^3 (Week 16). Average fecundity oscillated from 11.5 (Week 16) to 79 eggs per female (Week 24). Fecundities started to decrease at Week 6. Average reproductive output ranged between 17.8 (Week 11) and 58 % (Week 24). Reproductive output began to decline in Week 7.

The standing crop of oocytes produced by all females in the population ranged from 58 200 (Week 8) to 665 400 oocytes m^{-2} (Week 4), differing by a factor of 11× (Fig. 7). Density of brooded larvae oscillated between 0 (Weeks 22 to 26) and 257 300 larvae m^{-2} (Week 6) (Fig. 7); it was less than expected on the basis of oocyte standing crop (with the assumption that these 2 stages have about the same duration). Differences between standing crop of oocytes and density of brooded larvae suggest that oosorption may occur in the population. The density of post-metamorphic juveniles (dry weight < 40 μg) ranged from 1900 (Week 22) to 64 200 individuals m^{-2} (Week 6), differing by a factor of 34× (Fig. 7).

Given that our estimates of nitrogen requirements of

Capitella capitata do not account for possible oosorption, we can confidently say that the requirements of the population probably never greatly exceeded the daily ration of organic nitrogen (Fig. 8). However, during the period of maximal biomass (Weeks 5 to 13) these requirements were at least equivalent to the daily input of nitrogen. Chesney & Tenore (1985a, b) reported a similar result for other laboratory populations of *C. capitata* fed on different rations of Gerber's mixed cereals.

DISCUSSION AND CONCLUSION

Oscillation cycle and food availability

Because the food ration was constant, variations in density and biomass modified the food available per unit of standing biomass of *Capitella capitata* (R:B
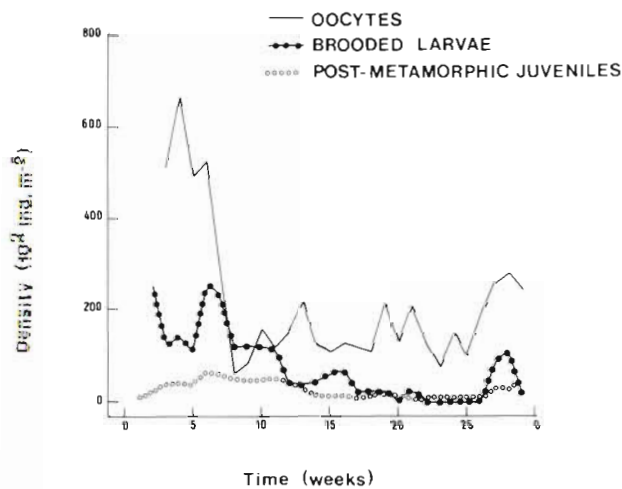

Fig. 7. *Capitella capitata.* Changes in total reproductive output (i.e. oocytes, larvae, post-metamorphic juveniles)
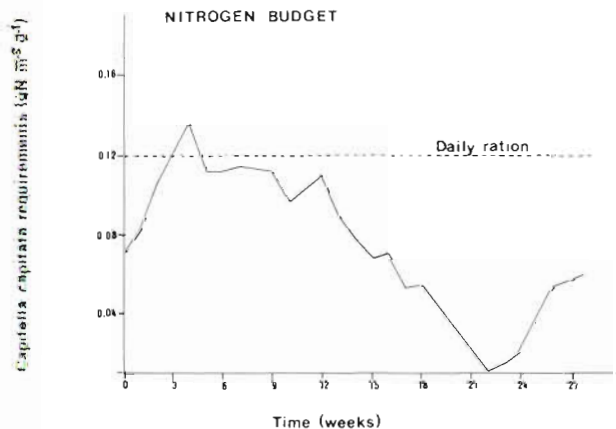

Fig. 8. *Capitella capitata.* Comparison of nitrogen requirements vs daily nitrogen input (theoretical carrying capacity)

ratio). Decline of the population took place when the R:B ratio was low (about 0.20). The decline coincided with diminished growth and reproduction. Variations in reproductive characteristics during the crash (i.e. diminution of the proportion of brooding females, female size, fecundity, and reproductive output) were equivalent to values obtained by experimentally reducing food availability (Grémare et al. in press a). The same is true for the decrease in growth rate (Marsh et al. unpubl.). These data confirm that the oscillation cycle is driven by changes in food availability (Chesney & Tenore 1985a).

Oscillation cycle and carrying capacity

Our results show that, on a daily basis, the nitrogen requirements of the *Capitella capitata* population never greatly exceeded the nitrogen input; this is similar to what has been reported by Chesney & Tenore (1985a). Because bacteria and meiofauna are always present in the tray (Alongi & Hanson 1985, Alongi & Tenore 1985) and compete for food with *C. capitata*, Chesney & Tenore (1985a) suggested that when food is abundant, rapid growth and reproduction push the population above its carrying capacity, resulting in rapid population declines as the nutritional needs of the population can no longer be met.

However, during our experiment, the population maintained its highest biomass for 8 wk and then declined during the next 9 wk. Similar patterns of biomass plateaus and gradual declines can be seen in *C. capitata* oscillation cycles corresponding to other daily food rations (Chesney & Tenore 1985a, b). Moreover, our results show that growth and reproduction rates of *C. capitata* responded closely to changes in food availability (Grémare et al. in press a, Marsh et al. unpubl.), and that these rates were actually adjusted (i.e. diminished) before the population began to decline. Given the duration at which populations remain at their higher density, it is unlikely that this density is in great excess of the carrying capacity value.

Fixing the carrying capacity to a constant value corresponding to a ration of 120 mg N m^{-2} d^{-1} is probably an oversimplification of the system. During the period of low density, the ration is in great excess of the *Capitella capitata* requirements (Fig. 7) and also exceeds the whole community requirements (i.e. *C. capitata* plus bacteria and meiofauna), thus accumulating food in the tray (Grémare pers. obs.). Before it is ingested, this food accumulation increases the carrying capacity of the population. Non-ingested (or non-digested) cereals would act like an external storage compartment and the actual carrying capacity of the population would oscillate above a static value

(theoretical carrying capacity) which is set by the daily food ration. At its higher density, the population would overshoot its theoretical carrying capacity as more food was consumed than supplied by the daily ration, but not its actual carrying capacity, as the food remaining in the tray was utilized.

There is some experimental evidence to suggest that, when the R:B ratio is low, it does not adequately describe the quantity of food available to the worms. In another set of experiments we showed that there is a tight correlation between fecundity and the daily nitrogen ration provided to *Capitella capitata* ($r = 0.929$, $N = 24$, $p < 0.001$; Grémare et al. in press a). In the tray, this correlation is high when the R:B ratio is greater than 0.3 ($r = 0.674$, $N = 12$, $p = 0.016$) (Fig. 9), however, when the ratio becomes lower than 0.3 (i.e. between Weeks 3 and 7), fecundity is greater than what would be expected from this regression (Fig. 9). We calculated that between Weeks 3 and 7, an R:B ratio of 1.0 was necessary to sustain the reproductive rates of the population, whereas the R:B ratio corresponding to the daily food ration was only 0.15. The period of maximal biomass is characterized by low R:B ratios; this suggests that the plateau of the biomass is partly due to the exploitation of a food source which is not accounted for in the R:B ratio (i.e. internal or external storage). Because internal storages (with the exception of oosorption) seem to be very restricted in *C. capitata* (Marsh unpubl.), the non-accounted food source probably results from an accumulation of cereals in the tray. Unfortunately, this hypothesis cannot be directly assessed by the measure of organic nitrogen (or even carbon) in the tray. Both nitrogen and carbon concentrations steadily increase with time in the presence of *C. capitata* because of its intensive mucous production (Alongi & Hanson 1985).

Oscillation cycle and time lags

Our explanation of the population cycle is similar to the one proposed by Chesney & Tenore (1985a) in the sense that they both consider: (1) that population cycles are driven by food availability, and (2) that populations overshoot their theoretical carrying capacity. However the models are very different when it comes to the mechanisms causing this overshoot. Classically, overshooting the carrying capacity is attributed to the existence of a time lag between changes in food availability and the demographic response of a population (Chesney & Tenore 1985a). Previous models (Chesney & Tenore 1985a) of oscillations in *Capitella capitata* suggested that a time lag resulted from a lack of regulation of secondary production and reproduction rates relative to food availability, eventually leading to overexploitation. Because of its life-history characteristics, *C. capitata* is likely to react rapidly to changes in food availability. Our results show that *C. capitata* quickly adjusts its growth and reproduction rates relative to food availability. The population dynamics of *C. capitata* can be separated into 2 phases, a boom and a bust. We believe that the overshoot of the theoretical carrying capacity of the population is due to the exploitation of accumulated food and that the subsequent crash of the population results from the depletion of this second food source.

Although there does not appear to be a significant time lag between decreases in food availability and decreases in population requirements, there is a time lag between increasing a resource availability and demographic population responses. Although individual characteristics (i.e. reproductive periodicity, size, fecundity, and reproductive output) of the gravid females are affected almost immediatly by an increase of the R.B ratio as populations decline, population reproductive responses are much slower (Week 25 vs Week 21). Although *Capitella capitata* (Grémare et al. in press a, b) in particular, and opportunists in general (Wible 1984, Levin 1986, Levin & Creed 1986, Zajac 1986) are able to rapidly adjust individual reproductive responses to food availability, the density of females will determine the initial rate at which the population will utilize increasing resources for reproduction.
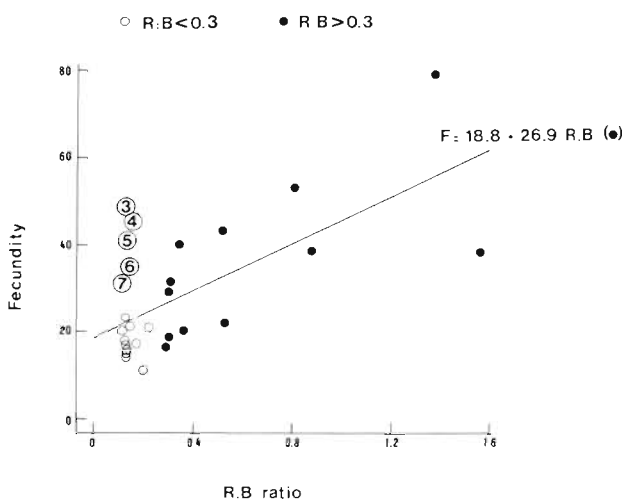

Fig. 9. *Capitella capitata*. Relation between fecundity and R:B ratio during 2 different periods of the oscillation cycle. R:B < 0.3 corresponds to the time between Week 3 and Week 17; R:B ratio > 0.3, between Week 18 and 29. Numbers in open circles indicate the week of observation

Oscillation cycle and secondary succession

Understanding the causes of the oscillations of laboratory populations of *Capitella capitata* may contribute to a better comprehension of the mechanisms of

secondary succession in soft-bottom communities. *C. capitata* adjusted its reproduction and secondary production rates relative to the amount of food available, enabling it to maintain a maximal biomass for a period of 8 wk. Because of this level of regulation, the oscillations of the laboratory populations of *C. capitata* probably did not result from an overshoot of their (actual) carrying capacity. However, the oscillation cycle is driven by food availability which suggests that in the field, replacement of opportunistic species by later colonists may be due to the opportunist's high energetic requirements (Shumway & Newell 1984) in conjunction with a diminution of food availability (Tilman 1985, Huston & Smith 1987). Diminution of food availability relative to energetic requirements can be due to: (1) changes in physical factor(s) (i.e. an increase in temperature will result in an augmentation of energetic requirements). (2) a reduction in the available resources, or (3) competition (for food) with later colonists. In this last case, it is important to note that the decline of opportunists does not necessarily imply that they are outcompeted for the food resources, but are simply not able to meet their (high) energetic requirements.

LITERATURE CITED

Alongi, D. M., Hanson, R. B. (1985). Effect of detritus supply on trophic relationships within experimental benthic food webs. II. Microbial responses, fate and composition of decomposing detritus. J. exp. mar. Biol. Ecol. 88: 167–182

Alongi, D. M., Tenore, K. R. (1985). Effect of detritus supply on trophic relationships within experimental benthic food webs. I. Meiofauna-polychaete [*Capitella capitata* (type I) Fabricius] interactions. J. exp. mar. Biol. Ecol. 88: 153–166

Chesney, E. J. (1985). Succession in soft-bottom benthic environments: are pioneering species really outcompeted? In: Gibbs, P. E. (ed.) Proceedings 19th European Marine Biology Symposium. Cambridge University Press, Cambridge, p. 277–286

Chesney, E. J., Tenore, K. R. (1985a). Oscillations of laboratory populations of the polychaete *Capitella capitata* (type I): their cause and implications for natural populations. Mar Ecol. Prog. Ser. 20: 289–296

Chesney, E. J., Tenore, K. R. (1985b). Effects of predation and disturbance on the population growth and dynamics of the polychaete *Capitella capitata* (type I). Mar. Biol. 85: 77–82

Krueger, C., Martin, F. (1980). Computation of confidence intervals for the size-frequency (HYNES) method of estimating secondary production. Limnol. Oceanogr 25: 773–777

Grassle, J. F., Grassle, J. P. (1974). Opportunistic life-histories and genetic systems in marine benthic polychaetes. J. mar Res. 32: 253–284

Gray, J. S. (1981). The ecology of marine sediments. Cambridge University Press, Cambridge

Grémare, A., Marsh, A. G., Tenore, K. R. (in press a). Short-term reproductive responses of *Capitella capitata* spl (Annelida: Polychaeta) fed on different diets. J. exp. mar Biol. Ecol.

Grémare, A., Marsh, A. G., Tenore, K. R. (in press b). Fecundity and energy partitioning in *Capitella capitata* type I (Annelida: Polychaeta). Mar Biol.

Humphrey, W (1979). Production and respiration in animal populations. J. Anim. Ecol. 48: 427–453

Huston, M., Smith, T (1987). Plant succession: Life history and competition. Am. Nat. 130: 168–198

Levin, L. A. (1986). Effects of enrichment on reproduction in the opportunistic polychaete *Streblospio benedicti* (Webster): a mesocosm study. Biol. Bull. mar. biol. Lab., Woods Hole 171: 143–160

Levin, L. A., Creed, E. I. (1986). Effect of temperature and food availability on reproductive responses of *Streblospio benedicti* (polychaeta: spionidae) with planktotrophic or lecithotrophic development. Mar Biol. 92: 103–113

McCall, P. L. (1977). Community patterns and adaptive strategies of the infaunal benthos of Long Island Sound. J. mar. Res. 35: 221–265

Morin, A., Mousseau, T., Roff, D. (1987). Accuracy and precision of secondary production estimates. Limnol. Oceanogr. 32: 1342–1352

Pearson, T H., Rosenberg, R. (1978). Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. Oceanogr. Mar Biol. A. Rev. 16: 229–311

Petersen, C. H. (1980). Approaches to the study of competition in benthic communities in soft sediments. In: Kennedy, V S. (ed.) Estuarine perspectives. Academic Press, New York, p. 291–301

Shumway, S. E., Newell, R. C. (1984). Energy resource allocation in *Mulinia lateralis* (Say) an opportunist bivalve from shallow water sediment. Ophelia 23: 101–108

Tenore, K. R. (1981). Organic nitrogen and caloric content of detritus. I. Utilization by the deposit-feeding polychaete, *Capitella capitata*. Estuar coast. Shelf Sci. 12: 39–47

Tenore, K. R. (1983). Organic nitrogen and caloric content of detritus. III. Effects on growth of a deposit-feeding polychaete. *Capitella capitata*. Estuar coast. Shelf Sci. 17: 733–742

Tenore, K. R., Chesney, E. J. (1985). The interaction of rate of food supply and population density upon the bioenergetics of the opportunistic polychaete. *Capitella capitata* (type I). Limnol. Oceanogr 30: 1188–1195

Tilman, D. (1985). The resource limitation hypothesis of plant succession. Am. Nat. 125: 827–852

Tsutsumi, H. (1987). Population dynamics of *Capitella capitata* (Polychaeta; Capitellidae) in an organic polluted cove. Mar. Ecol. Prog. Ser. 36: 139–149

Wible, J. G. (1984). The effects of salinity, temperature, and food on the growth and reproductive output of *Polydora nuchalis* Woodwick, 1953 (Polychaeta: Spionidae). Ph. D. dissertation, University of South California, Los Angeles

Zajac, R. N. (1986). The effect of intra-specific density and food supply on growth and reproduction in an infaunal polychaete, *Polydora ligni*, Webster J mar. Res. 44: 339–359