Effects of small-scale turbulence on development time and growth of *Acartia grani* (Copepoda: Calanoida)

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**Abstract.** To test the effects of small-scale turbulence on development and growth of marine copepods, a series of 10 l laboratory microcosms were used to follow the development, under turbulent and calm conditions, of a cohort of *Acartia grani*, a common coastal planktonic copepod of temperate zones. Aside from possible indirect effects due to differences in food availability, turbulence significantly shortened development times and modified growth rates. These influences seem to vary throughout its life history, late nauplii and early copepodites being more affected.

**Introduction**

Turbulence plays a prime role in the regulation of primary production, spatial distribution, and selection of 'life forms' of phytoplankton (Margalef, 1978; Legendre, 1981; Tett and Edwards, 1984; Mackas et al., 1985; Estrada et al., 1987, 1988). At smaller scales, turbulence increases encounter rates between planktonic predators and prey (Rothschild and Osborn, 1988; Evans, 1989), modifies copepod feeding activity (Perez et al., 1977; Oviatt, 1981; Strickler, 1985; Costello et al., 1990), and appears to enhance their development rates (Alcaraz et al., 1988, 1989) and metabolism (Marrase et al., 1990; Alcaraz and Saiz, 1991). These multiple effects may result in changes in biomass and demographic parameters of copepod populations (i.e. sexual proportion or age structure) (Alcaraz et al., 1988), thereby modulating population dynamics and consequently the pressure exerted by copepods on phytoplankton.

Alcaraz et al. (1988) suggested that turbulence accelerates zooplankton development and metabolism. Their experimental design, however, was not appropriate for zooplankton development and growth rates. Here, we examine whether small-scale turbulence significantly enhances the development and growth of planktonic copepods. To achieve our goal, we used 10 l laboratory microcosms to observe the development, under non-limited food conditions, of a cohort of *Acartia grani*, a common coastal copepod in temperate seas, and compared the differences in development and growth rates of individuals under agitated versus calm water conditions.

**Method**

**Microcosms and experimental design**

The laboratory microcosms were a modified version of those described by Estrada et al. (1987) and Alcaraz et al. (1988). They consisted of 15 10.3 l Perspex tubes (100 cm high and 11.5 cm i.d.) placed in a temperature-controlled chamber (20 ± 1°C). A 35 W, 60 cm fluorescent lamp illuminated each
microcosm over their whole length with a 12:12 h light:dark photoperiod with a photosynthetically available radiation ranging from 500 to 650 μE m⁻² s⁻¹.

The microcosms were filled with seawater from Masnou harbour (20 km N of Barcelona) which had been filtered through a 39 μm nylon netting to exclude eggs and the different stages of copepods, as well as other zooplankters, and were allowed to acclimatize overnight. The experimental organisms (Acartia granii) were obtained simultaneously with the collection of seawater, by means of short (5 min) horizontal tows made with a 38 cm wide-mouth plankton net fitted with 250 μm mesh nylon netting. Samples were diluted in seawater and transported to the laboratory in 10 l carboys.

Two experimental conditions were considered, and included two sets of seven microcosms each: no turbulence ('Q' microcosms, unstirred) and turbulence ('A' microcosms, stirred). An additional microcosm (the 'initial' microcosm) provided data concerning the new cohort at the start of the experiment. Turbulence was generated by two oscillating (20 oscillations/min) circular Netlon grids of 6 mm mesh size per tube. A similar setup (Estrada et al., 1987) provided a range of vertical eddy diffusivity coefficients ('Q' microcosms, 0.5 cm² s⁻¹; 'A' microcosms, 1-5 cm² s⁻¹) comparable to those found in natural systems (Denman and Gargett, 1983).

Adult males and females of A.grani were sorted from the zooplankton samples, placed in 1 l jars filled with 39 μm filtered sea water and left overnight in a Ferris-Wheel at 1 r.p.m. Then, 15 parental populations, each consisting of 13 males and 13 females of A.grani, were introduced into the microcosms in chambers designed to keep adults apart from eggs and to remove the adults from the microcosms easily, thereby providing a new cohort without generational overlap. The chambers were Plexiglas cylinders (15 cm high, 5 cm diameter) bottom screened (150 μm mesh netting) and suspended half submerged in the upper part of each microcosm. After 2 days, the chambers with the parental populations were carefully removed. Following the removal of the adults, the abundance of the new cohort (eggs plus first naupliar stages) was determined in one of the microcosms (the 'initial' microcosm) by gently filtering its contents through 39 μm netting. In the 'A' microcosms, the stirring systems were switched on and turbulent conditions started (day 0).

Every 2 days, 50 ml of a nutrient solution was added to each microcosm, providing an increase of 5 μM of nitrate, 0.2 μM of silicate and 0.5 μM of phosphate, in order to ensure non-limiting food conditions throughout the experiment.

Sampling strategy and variables studied

Food availability was estimated daily in all microcosms by the concentration and size spectrum of particulate matter (Coulter Counter model TA fitted with a 140 μm tube).

The development and growth of A.grani were studied following the time course of the age structure of the population. At 2 day intervals, the whole contents of each of two microcosms, one stirred and one unstirred, was filtered
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through 39 μm nettings to collect the copepods, as in the 'initial' microcosm. The instar composition of *A. granii* was estimated in either total samples or in aliquots, for the most abundant developmental stages. Individuals were counted and measured using a stereomicroscope. Metasome length (adults and copepodites), total length (nauplii) or diameter (eggs) were used to estimate specific biomass from a modified length–dry weight relation described for *Acartia clausi* by Durbin and Durbin (1978) and from egg dry weight estimates by Kiorboe et al. (1985). For further details of the procedures see Alcaraz *et al.* (1988).

Development times corresponding to the different naupliar and copepodite stages were estimated as the time corresponding to the gravitational centre of pulses of successive instars (Rigler and Cooley, 1974). To avoid any differences in the absolute number of individuals, we analysed stage composition on the basis of frequency data (after arcsin transformation) (Sokal and Rohlf, 1969; Landry, 1983).

Growth patterns were described by comparing the specific body masses with the relative specific development time (i.e. the ratio between the development time of the instar and that corresponding to adult females for each condition) (Ivanova, 1973; Miller *et al.*, 1977). This procedure allowed us to compare growth patterns independent of the absolute development time of the species.

**Results**

**Food availability**

Particulate matter concentration (as volume, mm$^3$ l$^{-1}$, Figure 1) increased after enclosure and experienced a subsequent decline, followed by a later increase. For most of the experiment ‘Q’ and ‘A’ microcosms had similar food concentrations, but after the 10th day variability increased and particulate volume concentrations were higher in ‘A’ microcosms.

The size spectrum of particles was similar in ‘A’ and ‘Q’ microcosms until the 7–8th day (Figure 2). Afterwards they diverged, the proportion of >10 micron particles raising in ‘A’ microcosms.

**Development and growth of *A. granii***

The abundance peaks for the different instars in stirred conditions preceded those in unstirred conditions (Figure 3), as found by Alcaraz *et al.* (1988) for *Acartia italica*. Consequently, instar development times were consistently shorter in ‘A’ microcosms (two-tailed Wilcoxon rank test, *P* < 0.005). However, to avoid possible indirect effects of turbulence that could result in a shorter total development time in ‘A’ microcosms (maybe a stimulating effect of stirring on egg hatching by i.e. changes in oxygen availability) (Uye *et al.*, 1979), we compared instar development time as a percentage of time required to develop adult females in each condition. This analysis also demonstrated a quickening effect of turbulence on development (two-tailed Wilcoxon rank test, *P* < 0.011). The gap in development time between ‘A’ and ‘Q’ microcosms increased until nauplius V–VI, then decreased toward adulthood (Figures 4 and 5).
Stage-specific sizes of *A. grani* (Table I) agreed with those reported by Vilela (1972) for the same species in a similar temperature range. For organisms at copepodite II or older, possible differences in size between treatments were checked. Adult males were significantly smaller in 'A' microcosms (Table I). The same tendency was observed for adult females, although the differences between 'Q' and 'A' microcosms were not significant, as occurred in the case of copepodite stages.

Growth was exponential throughout development, but shifted in the transitions from nauplius V–VI to copepodite I and from copepodite V–VI to adult (Figure 5), following a pattern similar to that described by Ivanova (1973) and Miller *et al.* (1977). In general, copepodites had higher growth rates (estimated from the slope of the linear regression equations for log body mass versus relative development time; Table II) than nauplii (2.5 and 1.5 times higher in ‘Q’ and ‘A’ microcosms respectively). Naupliar growth rates were higher in ‘A’ microcosms than in ‘Q’ microcosms (1.3 times), but for copepodites the trend was in the opposite direction (1.3 times lower in ‘A’ microcosms).

**Discussion**

Isochronal development (equal duration of all life history stages) has been
considered as an evolutionary strategy for *Acartia* and other copepods occupying neritic and estuarine habitats, where predation would concentrate on adults (Miller *et al.*, 1977). Although the instar–development time relationship for *A. grani* followed approximately a linear trend, there were step transitions at the stages experiencing the deepest morphological changes (i.e. NV–VI and CI; CIV and CV–VI). Differences in food availability throughout the experiment do not seem to explain this lack of linearity because, in most of the experiment, particulate matter concentration was >2–3 mm$^3$l$^{-1}$, well above the saturation level reported for ingestion, egg production and specific growth rates of different *Acartia* species [1.7 mm$^3$l$^{-1}$ for *A. clausi* (Ayukai, 1987); 1.8 mm$^3$l$^{-1}$ for *A. tonsa*]
Fig. 3. Mean numbers over time of the different developmental stages of *A. granii* in 'Q' (continuous line) and 'A' (broken line) microcosms. The dashed area indicates the starting of a second cohort.
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Fig. 4. Mean specific developmental times estimated from stage frequency data under turbulent and non-turbulent conditions

Table I. Size (µm) and estimated specific mean biomass (µg dry weight)

<table>
<thead>
<tr>
<th>Instar</th>
<th>Length</th>
<th>Biomass</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>77.8</td>
<td>0.04</td>
</tr>
<tr>
<td>N1-II</td>
<td>123.0 (101-145)</td>
<td>0.049</td>
</tr>
<tr>
<td>NIII</td>
<td>158.0 (145-171)</td>
<td>0.099</td>
</tr>
<tr>
<td>NIV</td>
<td>184.5 (171-198)</td>
<td>0.154</td>
</tr>
<tr>
<td>NV-VI</td>
<td>235.0 (198-272)</td>
<td>0.307</td>
</tr>
<tr>
<td>CI</td>
<td>337 ± 15.1</td>
<td>0.385</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>'Q'</th>
<th>'A'</th>
<th>'Q'</th>
<th>'A'</th>
</tr>
</thead>
<tbody>
<tr>
<td>CII</td>
<td>450.9 ± 23.2</td>
<td>441.4 ± 20.0</td>
<td>0.938</td>
<td>0.879</td>
</tr>
<tr>
<td>CIII</td>
<td>555.3 ± 19.3</td>
<td>555.9 ± 23.7</td>
<td>1.776</td>
<td>1.782</td>
</tr>
<tr>
<td>CIV</td>
<td>677.0 ± 32.4</td>
<td>672.5 ± 28.2</td>
<td>3.259</td>
<td>3.194</td>
</tr>
<tr>
<td>CV-Vlm</td>
<td>787.2 ± 16.2</td>
<td>788.2 ± 21.6</td>
<td>5.176</td>
<td>5.197</td>
</tr>
<tr>
<td>CV-Vlf</td>
<td>863.5 ± 32.1</td>
<td>855.3 ± 26.3</td>
<td>6.873</td>
<td>6.675</td>
</tr>
<tr>
<td>m</td>
<td>883.7 ± 25.8</td>
<td>873.6 ± 23.2*</td>
<td>7.378</td>
<td>7.123</td>
</tr>
<tr>
<td>f</td>
<td>1013.7 ± 32.5</td>
<td>1006.6 ± 37.2</td>
<td>11.235</td>
<td>10.997</td>
</tr>
</tbody>
</table>

From egg to CI instar, mean values and size ranges correspond to data pooled for 'Q' and 'A' conditions. From CII afterwards, mean values and standard deviations for each condition: not turbulent ('Q') and turbulent ('A') microcosms.

*Significant at the 0.01 level.
Fig. 5. Growth pattern of *A. granii* in 'Q' and 'A' microcosms. Continuous and broken lines are the fitted regression lines for 'Q' and 'A' microcosm data respectively.

Table II. Growth rates (regression slopes ± standard error) from the linear relationship between log body mass and relative instar development time (Figure 5)

<table>
<thead>
<tr>
<th>Growth rates</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>'Q' microcosms</td>
<td>Naupli</td>
</tr>
<tr>
<td></td>
<td>Copepodes (CI to CV-VI)</td>
</tr>
<tr>
<td>'A' microcosms</td>
<td>Naupli</td>
</tr>
<tr>
<td></td>
<td>Copepodes (CI to CV-VI)</td>
</tr>
</tbody>
</table>

(Kjørboe *et al.*, 1985; Berggreen *et al.*, 1988). As a consequence, the development of *A. granii* cannot be considered as strictly isochronal (sensu Landry, 1983) in our experiment.

Development times were significantly shorter in 'A' microcosms for the different stages in our experiment. Although changes in food quality and quantity due to turbulence [as in the shift in food size spectrum in natural systems reported by Kjørboe *et al.* (1990)] could also play an important role in copepod life history, in our experiment the particulate matter concentration and
size spectrum were similar until the 7–8th day, when CI copepodites had just molted and the dissimilarities in development were more marked. Consequently, the changes in development observed in this period must be mainly attributed to a direct effect of turbulence (sensu Alcaraz et al., 1988). Afterwards, when differences in particulate matter started to manifest themselves, discrepancies in development time smoothed progressively. It is not clear whether or not differences in particulate matter concentration were really of importance in this period. If they were, poorer food conditions at the end of the experiment in 'Q' microcosms should have caused longer development times and curtailed sizes of later stages (Klein Breteler et al., 1982, 1990). But in spite of that, in this period instar development times in 'Q' and 'A' microcosms tended to be equal and sizes were not significantly shorter in 'Q' microcosms.

Thus, we must conclude that even though differences in food availability could play a minor role in the faster development observed in our experiment, a direct effect of turbulence must be the main explanation for the differences found.

Regarding the changes in growth rates found in 'A' microcosms, they seem to reflect the more conspicuous differences in development rate in late nauplii and early copepodites mentioned above. On the other hand, the fact that in both treatments copepodite growth rates were higher than the naupliar ones, contrasts with the constant relationship found for other Acartia species in a wide range of food concentrations, from starvation to saturation (Berggreen et al., 1988), and agrees with the development pattern showed by A.grani in our experiment.

The occurrence of the maximum acceleration of development in nauplii and the progressive decrease for the successive copepodite stages, points to possible differences in the way turbulence affects copepods throughout life. How turbulence really does affect copepods is still unclear, but recent works (Costello et al., 1990; Marrasé et al., 1990; Alcaraz and Saiz, 1991) indicate that either an enhanced grazing activity due to higher encounter rates in turbulent situations or an increased metabolism due to a higher frequency of escape reactions might play an important role. Either mechanism could be responsible for an acceleration of development, in a way similar to increasing temperature (Ikeda, 1985; Landry, 1975; Uye, 1988).

The importance of small-scale turbulence in natural plankton communities is still uncertain, particularly for zooplankton (Marine Zooplankton Colloquium 1, 1989). Although there is no reason to expect qualitative differences between the effects of small-scale turbulence in laboratory microcosms and natural systems, this point is not yet resolved. The measurement of turbulence itself is one of the main problems (Soloviev et al., 1988). Changes in size, quantity or quality of particulate matter (Kierboe et al., 1990) mediated by small-scale turbulence could affect copepod activity indirectly, and one must be cautious in interpreting experimental data.

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