Seasonal variations in the zooplankton and in the population structure of *Acartia tonsa* in a very eutrophic area: La Habana Bay (Cuba)

Juan Diaz Zaballa and Raymond Gaudy

*Instituto de Investigaciones del Transporte, Apartado 17029, zona postal 17, Ciudad de La Habana, Cuba and 'Centre d’Océanologie de Marseille, Station marine d’Endoume, rue de la Batterie des lions, F-130007 Marseille, France*

**Abstract.** Seasonal changes in the abundance of total zooplankton and of main components were studied at a fixed station in La Habana Bay. Special attention was given to the dominant species, *Acartia tonsa*, which constituted 89% of the total number of zooplanktonic organisms. The variations in some of its population parameters (eggs, nauplii, copepodites, adults, sex ratio, number of eggs per female) were analysed in relation to temperature, salinity and chlorophyll. The abundance of eggs was independent of the environmental factors, particularly of chlorophyll which was always present in excess. The number of eggs per female showed several peaks, but was also independent of environmental factors. Nauplii were poorly correlated with egg numbers, but depended on the abundance of chlorophyll in particles of size <55 μm. This suggested that the part of edible food suitable for them in size or quality was not always in excess in the available seston, provoking a temporary increase in naupliar mortality. The temporal evolution of the following successive stages was nearly synchronous; thus, the changes observed in their abundance were not caused by fluctuations in the reproductive potential of females, but appeared to be related to a periodic decrease in the total zooplankton density due to the flushing effect of inland water in the bay.

**Introduction**

Coastal regions which display a high degree of urban or industrial activities are often characterized by eutrophication. These conditions are generally more marked in semi-closed areas such as lagoons or bays poorly connected with the open ocean. In such environments, particularly in tropical regions, the wide range of temperature and salinity variations also contributes to affect the stability of the pelagic ecosystem. The Bay of Habana (Cuba) corresponds to this type of semi-closed ecosystem. In the present study, we analyse, during an annual cycle, the quantitative and qualitative variations in the mesozooplankton, and particularly the main species, the copepod *Acartia tonsa*, in relation to the environmental factors. This work, which is based on high-frequency data acquisitions, completes the preliminary study of Diaz Zaballa and Rodriguez (1984).

**Method**

The Bay of La Habana is located on the north coast of Cuba (23°08’N; 82°20’30”E). It is a semi-land-locked area of 5.1 km² and 9.2 m average depth, composed of three coves (Marimelena, Atares and Guasabacoa) with a river outlet in each of them (Figure 1).

The sampling station is located at the north of the bay, near the canal connecting with the sea, over 4 m depth. The samples were taken between 26 March 1991 and 30 April 1992, with an average frequency of 14 days, always in the morning.
J. Diaz Zaballa and R. Gaudy

Fig. 1. Map of the Bay of La Habana and location of the reference station

(08:40–11:20 h). Zooplankton were collected by three successive vertical hauls between the bottom and the surface, with a Juday net (opening diameter 40 cm, mesh size 55 μm). Temperature was measured in surface water. Samples of this water were taken for salinity measurements (salinometer E-202, Tsurumi Seiki) and filtered on Whatman GF/C for chlorophyll pigments (Turner fluorometer Model 1111; method of Yentsch and Menzel, 1963). The abundance of pigments was measured on a screened fraction (<55 μm) of the water and on the total water, to separate the contribution of phytoplankton (<55 μm) and detritus (fragments of macroalgae), which were generally abundant in the total sample.

The different species of zooplankton were counted. For the copepod _A. tonsa_, which was the most abundant form, eggs, naupliar stages (counted together), copepodite stages (C1–C5) and adults (males and females) were separated.

The data were compared using the Spearman correlation technique (Table I).

**Results**

**Variation in the environmental factors**

The temperature ranged between 22 and 31°C, but most values were between 26 and 30°C. Maximum values occurred from May to September (Figure 2) and the minimum, in February. Salinity varied between 28 and 34.6, with a low-salinity period during summer and a high-salinity period from the beginning of October to
<table>
<thead>
<tr>
<th></th>
<th>Temperature</th>
<th>Salinity</th>
<th>Chl a total</th>
<th>Chl a &lt;55 μm total</th>
<th>Zooplankton A. tonsa total</th>
<th>Eggs</th>
<th>Nauplii C,</th>
<th>C,</th>
<th>C,</th>
<th>C,</th>
<th>C,</th>
<th>Males</th>
<th>Females</th>
<th>Eggs per female</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salinity</td>
<td>-0.177</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chl a total</td>
<td>0.328</td>
<td>0.0847</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chl a &lt;55 μm</td>
<td>0.203</td>
<td>0.339</td>
<td>0.629**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zooplankton total</td>
<td>0.441**</td>
<td></td>
<td>-0.189</td>
<td>-0.021</td>
<td>0.233</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A. tonsa total</td>
<td>0.266</td>
<td></td>
<td>0.006</td>
<td>0.057</td>
<td>0.468*</td>
<td></td>
<td>0.875**</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eggs</td>
<td>0.197</td>
<td>0.064</td>
<td>-0.005</td>
<td>-0.022</td>
<td>0.530**</td>
<td></td>
<td>0.266</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nauplii C,</td>
<td>0.248</td>
<td>0.046</td>
<td>0.057</td>
<td>0.497**</td>
<td>0.871**</td>
<td></td>
<td>0.990**</td>
<td>0.464*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C,</td>
<td>0.257</td>
<td></td>
<td>-0.285</td>
<td>0.135</td>
<td>0.157</td>
<td>0.380</td>
<td>0.488**</td>
<td>0.307</td>
<td>0.385*</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C,</td>
<td>0.567**</td>
<td></td>
<td>-0.354</td>
<td>-0.064</td>
<td>-0.417</td>
<td>0.648**</td>
<td>0.240</td>
<td>0.056</td>
<td>0.058</td>
<td>0.559**</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C,</td>
<td>0.311</td>
<td></td>
<td>-0.441**</td>
<td>-0.018</td>
<td>-0.145</td>
<td>0.245</td>
<td>0.234</td>
<td>0.001</td>
<td>0.121</td>
<td>0.669**</td>
<td>0.814**</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C,</td>
<td>0.074</td>
<td></td>
<td>-0.243</td>
<td>-0.093</td>
<td>-0.241</td>
<td>0.158</td>
<td>0.159</td>
<td>0.129</td>
<td>0.038</td>
<td>0.625**</td>
<td>0.729**</td>
<td>0.715**</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C,</td>
<td>0.140</td>
<td></td>
<td>-0.100</td>
<td>0.047</td>
<td>-0.165</td>
<td>0.038</td>
<td>0.090</td>
<td>0.188</td>
<td>-0.031</td>
<td>0.619</td>
<td>0.669**</td>
<td>0.603**</td>
<td>0.871**</td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>0.259</td>
<td></td>
<td>-0.129</td>
<td>0.059</td>
<td>-0.138</td>
<td>0.284</td>
<td>0.255</td>
<td>0.264</td>
<td>0.140</td>
<td>0.679**</td>
<td>0.548**</td>
<td>0.687**</td>
<td>0.817**</td>
<td>0.889**</td>
</tr>
<tr>
<td>Females</td>
<td>-0.063</td>
<td></td>
<td>-0.007</td>
<td>-0.043</td>
<td>-0.157</td>
<td>0.082</td>
<td>0.026</td>
<td>0.238</td>
<td>-0.080</td>
<td>0.470*</td>
<td>0.508**</td>
<td>0.444*</td>
<td>0.743**</td>
<td>0.841**</td>
</tr>
<tr>
<td>Eggs per female</td>
<td>0.115</td>
<td></td>
<td>-0.242</td>
<td>-0.084</td>
<td>-0.256</td>
<td>-0.016</td>
<td>0.093</td>
<td>0.496*</td>
<td>-0.108</td>
<td>0.008</td>
<td>-0.030</td>
<td>-0.042</td>
<td>-0.129</td>
<td>-0.182</td>
</tr>
<tr>
<td>Sex ratio</td>
<td>0.517*</td>
<td></td>
<td>-0.139</td>
<td>0.208</td>
<td>0.041</td>
<td>0.032</td>
<td>0.431*</td>
<td>-0.007</td>
<td>0.291</td>
<td>0.329</td>
<td>0.109</td>
<td>0.339</td>
<td>0.265</td>
<td>0.231</td>
</tr>
</tbody>
</table>

*Significant at $P < 0.05$.
**Significant at $P < 0.01$.

$n = 27$ except for eggs per female ($n = 24$) and sex ratio ($n = 22$).
Fig. 2. Seasonal variations in temperature, salinity, chlorophyll (particles < 55 μm) and total chlorophyll.
the end of March. During this last period, temporary decreases in salinity were observed, particularly on 7 February, after a period of strong rains caused by a tropical depression. This minimum salinity value also corresponded to the minimal temperature. The chlorophyll of the fine (<55 μm) sestonic fraction displayed very high values (up to 150 μg L⁻¹), with a succession of rapid changes in abundance (seven peaks during the studied period). The total chlorophyll showed a parallel evolution, but with 2- to 6-fold higher values, except during the hurricane period of February when the chlorophyll concentrations of the total and <55 μm fractions were similar, because of the scarcity of large detritus in the seston.

Quantitative and qualitative variation of zooplankton

The abundance of total zooplankton was very high, from 15 000 to 255 000 ind. m⁻³, with a maximum in June–July and several other secondary peaks during the rest of the year (Figure 3). A positive, but relatively low correlation was observed with temperature (Table I).

The zooplankton were dominated by the copepod *A. tonsa* (89% of the total number of organisms, in annual average). Other notable taxa were the appendicularian *Oikopleura* sp. (5.8%) and the rotifer *Brachionus plicatilis* (3.5%). The remaining taxa were cirriped nauplii, polychaete larvae, lamellibranch larvae, other copepods and amphipods.

As a consequence of its dominance, the seasonal variation in abundance of *A. tonsa* was parallel to the evolution of total zooplankton, with a succession of six peaks (Figure 3). Correlations of total *Acartia* (swimming stages) with temperature and salinity were not significant, but a positive correlation appeared with chlorophyll <55 μm.

*Oikopleura* sp. was present all through the year, with five peaks of abundance not correlated with *A. tonsa* or total zooplankton abundances (Figure 3).

*Brachionus plicatilis* appeared only during summer, the period of the lowest salinity values. Its two main peaks corresponded to two of the phytoplankton peaks (Figure 3).

Variation in the population structure of *Acartia tonsa*

*Acartia eggs* showed a succession of eight peaks of similar size, all through the year (Figure 4). The abundance of eggs was not correlated with temperature, salinity or chlorophyll. *Acartia* nauplii were always present. They were positively correlated with the chlorophyll contained in the fine fraction (<55 μm) of seston (Table I; Figure 6) and with the proximate stages, i.e. eggs and copepodite 1. The abundance of the successive copepodites did not depend on the environmental factors, but these stages were correlated between themselves and with adult males or females.

The sex ratio (males/total number of adults) varied markedly, even showing periods of the total absence of one sex (Figure 5). It was correlated with temperature, but not with salinity or chlorophyll. The only other significant correlation was found with the total number of *Acartia* (nauplii - copepodites - adults).

The number of eggs per female, which can be considered as a fertility index of the population, presented 6–7 peaks during the study (Figure 5). No correlation
Fig. 3. Seasonal variations in abundance of total zooplankton, *A. tonsa*, *Oikopleura* sp. and *B. plicatilis*. 
Seasonal variations in zooplankton of La Habana Bay

**Eggs**

![Diagram of eggs abundance]

**Nauplii**

![Diagram of nauplii abundance]

**Copepodites**

![Diagram of copepodites abundance]

**Adults**

![Diagram of adults abundance]

**Fig. 4. Acartia tonsa: seasonal variations in abundance of eggs and nauplii, copepodites and adults.**
was found with temperature, salinity or chlorophyll. Contrary to the sex ratio, the total abundance of *Acartia* had no significant effect on this parameter.

**Discussion**

In Habana Bay, the phytoplankton cycle has no significant effect on the recruitment of *A.tonsa* estimated from the eggs per female ratio, contrary to most previous observations on *Acartia* from other temperate or tropical regions (Deevey, 1960; Landry, 1978; Lee and McAlice, 1979; Uye, 1982; Sabatini, 1990; Gaudy, 1992a,b). As a matter of fact, previous *in situ* and experimental studies show that the egg production of *A.tonsa* is narrowly related to the abundance of chlorophyll or phytoplankton in a more or less extended range of concentration and that, above a maximum food concentration (saturation level), egg production tends to be constant (Durbin *et al.*, 1983; Ambler, 1986; Beckman and Peterson, 1986; Gaudy, 1992b). This maximum value depends on the area studied. It corresponds to 20 µg m⁻³ of chlorophyll *a* in the Berre lagoon, near Marseilles (Gaudy, 1992b), to 16 µg l⁻¹ in Narrangansett Bay (Durbin *et al.*, 1983) and to only 5 µg l⁻¹ in Long Island Sound (Bellantoni and Peterson, 1987). The succession of several cohorts or generations is often observed (when the sampling frequency is sufficiently high). In *A.tonsa*, 3–11 generations can be separated according to the main temperature conditions of the different studied areas (Conover, 1956; Woodmansee, 1958; Deevey, 1960; Jeffries, 1962; Lee and McAlice, 1979; Sabatini, 1990; Gaudy, 1992a). They are generally generated by temporary increases in egg production.
Seasonal variations in zooplankton of La Habana Bay

Nauplii / m³

Chlorophyll (particles < 55 μm) µg / l

y = 455 Chl. + 24917

Fig. 6. *Acartia tonsa*: relationship between the density of nauplii and the abundance of chlorophyll (particles <55μm).

provoked by changes in the chlorophyll concentration (Gaudy, 1992a), but during summer, the increase in growth rate caused by temperature conditions leads to an overlapping of generations which makes their analysis confusing.

The succession of several peaks of numbers of eggs per female is not correlated with chlorophyll abundance. It could result from changes in the quality of the available food, independently of its abundance. Ambler (1986) showed that the egg production of *A.tonsa* in East Lagoon partly depended on the quality of algae. Similar results were given in other areas by Cahoon (1981), Stottrup and Jensen (1990), Kleppel (1992) or White and Roman (1992).

The absence of a correlation between chlorophyll and egg production in Habana Bay is the consequence of the non-limiting trophic conditions prevailing all through the year. Chlorophyll average values were 106 μg l⁻¹ for total seston and 40.62 μg l⁻¹ for seston of size <55 μm, and values <9 μg l⁻¹ were encountered on only three occasions over 27 seasonal samples. Thus, plenty of energy is available for egg production most of the year. The number of eggs per female varied between 0.6 and 120, the average value being 31.8. The corresponding egg ratio values, calculated according Edmondson *et al.* (1962), were 0.57, 133 and 32.6. These values are in the range of most literature data. For example, Gaudy (1992b) found values between 5 and 18 eggs female⁻¹ day⁻¹ in the Berre lagoon. Bellantoni and Peterson (1987) cite values between 9 and 56 in Long Island Sound, and Durbin *et al.* (1983) give an average value of 25.3 eggs female⁻¹ day⁻¹ in Narragansett Bay. Thus, the very high trophic conditions prevailing in Habana Bay do not lead to exceptional egg production rates. The relative constancy of the level of maximum egg production in various environments, characterized by very different chlorophyll richnesses, indicates that it must also depend on the physiological limit of the females, e.g. the minimal time necessary for the maturation of oocytes.

The only correlation observed between chlorophyll concentration and zooplankton was observed with nauplii of *A.tonsa*, when the fine fraction of seston
(<55 μm) was considered. This result indicates that the survival of nauplii is probably related to the presence in sufficient abundance of edible particles of suitable size for them, e.g. small phytoplankton cells. Even if naupliar stages are potentially able to feed on a large range of particle sizes (Marshall and Orr, 1956; Fernandez, 1979), their highest filtration rate is observed on particles smaller than those efficiently used by copepodites or adults. Berggreen et al. (1988) showed that the optimum particle size and the upper size limit were 7–14 and 70 μm for A. tonsa NII–NIII, respectively, instead of 14–70 and 250 μm for adults, respectively. The quality of particles should also play a role. The effect of food quality on the egg production of A. tonsa is well documented (Cahoon, 1981; Stottrup and Jensen, 1990; Kleppel, 1992; White and Roman, 1992). No information is available on this subject for naupliar feeding, but it can be supposed that, compared with older stages, they need a food containing proportionally more vitamins or oligo-elements. Possibly, although the quality and quantity of algae present in seston are never limiting for the feeding of the adults and for their egg production, the proportion in the seston of algae qualitatively favourable for the growth and survival of nauplii must be relatively low, leading to a temporary lack of favourable food when the seston abundance diminishes, with subsequent increases in the naupliar mortality. Thus, the fluctuations in the survival of nauplii, which appear to be the most sensitive developmental stage during the growth of Acartia (Heinle, 1966; Landry, 1978; Uye, 1982), regulate the quantitative abundance of the less sensitive older stages. Another hypothesis to explain the decrease in the naupliar population during low chlorophyll concentration periods could be the cannibalistic behaviour of older copepodites and adult stages. Acartia tonsa is able to feed efficiently on prey (Anraku, 1964; Lonsdale et al., 1979; Robertson, 1983; White and Roman, 1992). It could satisfy its protein requirement by feeding on its own nauplii. Such a mechanism has been advanced to explain the high naupliar mortalities periodically observed in situ for Acartia clausi (Landry, 1978) and for A. tonsa (Lonsdale et al., 1979).

The correlation between nauplii and Cl shows that the abundance of the first copepodite logically depends on the abundance of the preceding stages. The temporal variations in the successive copepodite stages and adults of A. tonsa are more or less synchronized, as demonstrated by the correlations existing between each of them. The lack of correlation between their abundance and the egg production cycle confirms that the variations in abundance of developmental stages do not indicate the succession of different cohorts, contrary to some other regions (Sabatini, 1990; Gaudy, 1992a,b), but more probably reflect the occurrence of hydrographic instability events, such as dilution or partial replacement of the bay water by riverine freshwater. The salinity variations can be used to indicate the importance of this process. For example, the large decrease in salinity observed in February corresponds to a strong decrease in the whole zooplankton population. The same trend, although not statistically significant ($r = 0.34; P = 0.08$), is also observed for chlorophyll abundance (<55 μm), which is directly related to salinity changes. The flushing effect of the freshwater in the bay is also illustrated by the disappearance of large detritus in seston, following the strong tropical rainfall event of February. Another factor associated with salinity variations could be the

Downloaded from https://academic.oup.com/plankt/article-abstract/18/7/1123/1424081/Seasonal-variations-in-the-zooplankton by guest on 16 September 2017
temporary increase in the pollution level in the bay associated with strong freshwater discharges. We have no qualitative or quantitative data on pollutants for the investigated period, but it is unlikely that the pollution impact would markedly affect the abundance of the zooplankton, which are already chronically exposed to high pollution conditions. The importance of predation by carnivorous organisms, such as ctenophores, is emphasized in several previous studies to explain populations changes of *A. tonsa* (Conover, 1956; Heinle, 1966; Beckman and Peterson, 1986): In Habana Bay, the number of crustacean predators seems to be very low: only a few amphipods and decapod larvae were collected. Gelatinous animals such as Ctenophora were never caught. Thus, it is probable that predation by other zooplankters must not be a determinant factor for the population changes.

Sex ratio variations observed in adults of *A. tonsa* could result from the greater sensitivity of males to the hydrological instability of the bay: when the total population decreases, males diminish proportionally more rapidly than females, or even disappear totally. However, this does not seem related to a particular sensitivity of males to low salinity values because their abundance is not correlated with salinity, as for females. Lee and McAlice (1979) observed in the Maine estuary that relatively more *A. tonsa* males were observed when the temperature decreased. In Habana Bay, no correlation was found between temperature and males or females, but the sex ratio was positively correlated to temperature, contrary to the observations of Lee and McAlice. The possible effect of other factors not studied there, particularly the pollutants, cannot be eliminated. The positive correlation between the sex ratio and the density of the *Acartia* population can be interpreted as a homeostatic mechanism for the regulation of the population. During periods of low abundance, a higher proportion of females is available for egg production, thus favouring a rapid recovery of the population level. Similar observations were made on the same species by Heinle (1970) in the Patuxent River estuary region and by Sabatini (1990) in the region of Bahia Blanca, and were also interpreted by these authors as a compensatory mechanism for the regulation of the population.

To summarize our main results, in an exceptionally rich environment such as Habana Bay, the short-term variations in abundance of *A. tonsa* cannot be explained by changes in its reproductive potential in relation to phytoplankton density, contrary to many other estuarine or marine coastal systems, because the food is always in excess of reproduction needs. Most of the variations in abundance mainly reflect the dilution of the total zooplankton population provoked by the flushing effect of inland freshwaters in the bay. They also depend on the survival of the naupliar stages, because nauplii numbers are directly correlated with the presence of edible phytoplanktonic particles. Thus, the importance of the quantity and quality of food appears to be different if naupliar survival or adult fertility are considered. As several other factors probably interact, it seems necessary to carry out more experimental studies to progress knowledge of the processes acting on the population dynamics in such eutrophic areas.

**Acknowledgements**

This work was carried out in the framework of the French–Cuban bilateral pro-
gramme. The authors acknowledge the administrative and scientific authorities of the two countries for their help and their financial assistance.

References


Received on August 15, 1995; accepted on January 29, 1996