Abundance, Population Structure and Production of Scrobicularia plana and Abra tenuis (Bivalvia: Scrobiculariidae) in a Mediterranean Brackish Lagoon, Lake Ichkeul, Tunisia

key words: Scrobicularia plana, Abra tenuis, population structure, secondary production, Mediterranean lagoon

Abstract

Abundance, growth and production of the deposit-feeding bivalves were studied in the Ichkeul wetland, northern Tunisia, from July 1993 – April 1994. Scrobicularia plana (DA COSTA, 1778) occurred at annual mean densities (biomasses) of 299 ± 65 to 400 ± 100 individuals/m² (22.54 ± 3.00 to 34.27 ± 3.96 g ash-free dry mass (AFDM)/m²) depending on the study area. The annual mean density of Abra tenuis (MONTAGU, 1803) amounted to 640 ± 74 individuals/m² during the whole study period, in contrast the biomass rose from 2.87 g AFDM/m² in July to 10.29 g AFDM/m² in April. Both species were largely dominated by age class I. Although not very successful, recruitment presented a two-period pattern: the main period at the beginning of spring, and a secondary one in late summer/autumn. S. plana rarely exceeded 40 mm and lived for only 2 years, while most individuals of A. tenuis lived for only 15–18 months growing to a length of 12 mm. The annual bivalve deposit-feeder production for the whole lagoon system (90 km²) was 8.24 g AFDM/m² (5.26 g C/m², 0.65 g N/m²). The annual P/B ratio was about 0.4 and therefore in the same order of magnitude as estimates from other brackish coastal waters.

1. Introduction

Scrobicularia plana (DA COSTA, 1778) and Abra tenuis (MONTAGU, 1803) are ecologically closely related marine infaunal bivalves of the family Scrobiculariidae. Their main ecological characteristics are tolerance of physical and chemical changes in the sediment and rapid demographic adaptability to variations in the environment (HUGHES, 1970a; NOTT, 1980). They both inhabit similar types of soft bottoms of clay or mud, with abundant organic detritus, where freshwater input produces conditions of varying salinity. Their range extends from the Norwegian Sea to Senegal including the Mediterranean (TEBBLE, 1976). But they differ with regard to habitat preference. A. tenuis is localized in its distribution, tending to occur in lagoons or sites partly cut off from the sea, just below the surface of the sediment or amongst macrophytes. S. plana is more widely distributed, inhabits the intertidal coastal waters in great abundance and is often the dominant species of shallow water benthic communities (TEBBLE, 1976). In many of these coastal waters, benthic macrophytes form large dense stands from late spring to early autumn. Often only a small proportion of this biomass is directly consumed by herbivores, the remaining part enters the detritical pool and becomes
available to deposit-feeders. Living micro-organisms are commonly much better absorbed than detritus, suggesting that they constitute the main food source of deposit-feeding bivalves (Matthews et al., 1989). Although they primarily suck up surface deposits, S. plana and A. tenuis obtain some of their food by filtering suspended matter from the water column (Hughes, 1970a; Hughes, 1973). The bivalves play an important role in the coupling between the benthic and pelagic systems by removing large amounts of particulate material from the water column (Alpine and Cloern, 1992), partly sequestrating the nitrogen and phosphorus (Nalepa et al., 1991) and releasing inorganic nutrients into the water column from direct excretion and from production of pseudofeces (Prins and Smal, 1994). The sediment enrichment with biodeposits provides a nutrient source for other biotic components such as macrophytes and epibenthic deposit-feeders.

An estimate of the annual bivalve deposit-feeder production is needed in order to obtain a quantitative measure of their role in the benthic-pelagic coupling in the Ichkeul ecosystem. Secondary production of Scrobicularia plana has been investigated by Hughes (1970a, b), Warwick and Price (1975), Bachelet (1982), Guelorget and Mazoyer-Mayère (1983), Sola (1997) and Guerreiro (1998). Abra alba (Wood, 1802) has received a lot of attention on account of its wide geographical distribution and its high density permitting production studies (Hily, 1976; Meneguen, 1980; Warwick and George, 1980; Bachelet, 1981b; Glemarec and Meneguen, 1980; Cornet, 1986; Daunin, 1986; Francesch and López-Jamar, 1991; Lastra et al., 1993). Little is known about the secondary production of Abra ovata (Philippi, 1893) (Guelorget and Mazoyer-Mayère, 1982; Kevrekidis and Koukouras, 1992) and Abra nitida ( Müller, 1776) (Buchanan and Warwick, 1974; Francesch and López-Jamar, 1991). No production investigation of Abra tenuis was found in the literature.

The present study is part of a more extensive research programme on the functioning of the Ichkeul (Tunisia) which has the objective of identifying the ecological and physical characteristics of the ecosystem in order to draw up a predictive forecasting model with a view to devising a conservation management programme which takes into account the social and economic development of the region. The Ichkeul lagoon is a rare example of an oligotrophic functioning coastal lagoon in the Mediterranean basin (Tamisier and Bouduresque, 1994). What is the fate of the macrophyte biomass since a dystrophic crisis has never been described at Ichkeul lagoon? We investigate the contribution of the deposit-feeding bivalves to the functioning of the ecosystem. Our study describes the abundance and biomass of Scrobicularia plana and Abra tenuis, and estimates their life span, growth and production in this temperate brackish lagoon which harbours a conspicuous population of wintering waterfowl (Tamisier et al., 1987; Tamisier and Bouduresque, 1994; Tamisier et al., 2000).

2. Materials and Methods

2.1. Study Site

The study was carried out at Lake Ichkeul, an inland brackish lagoon of 9000 ha surrounded by 3000 ha of temporary marshes on the northern coast of Tunisia (Fig. 1). It is linked by a narrow channel (Tinja channel) to the Lagoon of Bizerte which in turn has an outlet to the Mediterranean sea. The wetland is shallow with a mean depth of 2–3 m in winter and 1 m in summer. It is filled up with freshwater from autumn and winter rainfall (from 7 wadis, i.e. temporary rivers) that overflows into the Lagoon of Bizerte. In summer, high evaporation lowers the water level and allows seawater to enter the lagoon. Salinity displays considerable seasonal changes from 3 psu in the innermost parts in spring to 38 psu at the mouth of the Tinja channel in autumn. The western and the southern areas, supplied with freshwater from the wadis, are covered by extensive beds of Potamogeton pectinatus L. The eastern area close to the Tinja channel and supplied with seawater is covered by a meadow of Ruppia cirrhosa (Petagna) Grande. The central area of the Ichkeul lagoon is completely vegetation-free. The faunal investigation carried out by Hollis (1986) by means of two cores in the eastern and central lagoon areas dated in a
210Pb analysis showed that before the widening of the channel which links the Bizerte lagoon to the sea during the 1880's, the bivalve community of Ichkeul was represented by two species, *Cerastoderma glaucum* (POIRET, 1789) and *A. tenuis*. In the strata following the 1890's, *S. plana* was then present and has progressively replaced *A. tenuis* since then. *A. tenuis* nowadays inhabits the eastern area of the Ichkeul lagoon whereas *S. plana* occupies the eastern and the central area (HOLLIS, 1986).

During the study period from July 1993 to April 1994 mean aboveground macrophyte biomass was maximum in September (BCEOM *et al*. 1995) followed by the macrophyte fall from October onward. Only negligible autumn and winter rainfall was registered, the inflow of seawater into the lagoon continued from summer to winter and was reversed only in February and March 1994 (2 months instead of 8 in average years). While water temperature did not deviate from its usual mean values (27.2 ± 0.8 °C in August and 10.6 ± 0.2 °C in January), salinity continued to increase from 26.0 ± 4.1 psu in August to 36.2 ± 1.1 psu (BCEOM *et al*. 1995) in December with a slight decrease during January and February due to some precipitation. In December the *P. pectinatus* meadow had completely disappeared at Sejnene and Joumine and did not regrow in spring. Thick layers of dead vegetation piled up in particular along the southern shores. The *R. cirrhosa* meadow reached its minimum in February and regrew from March onward. At the end of the study period in April 1994, unusually high average salinity of 28.3 ± 0.4 psu (BCEOM *et al*. 1995) and low water level were observed. The mean salinity rose to 43.2 ± 0.5 psu in June 1994 (BCEOM *et al*. 1995). *C. glaucum* and other endobenthic deposit-feeder species such as *Cyathura carinata* (KROYER, 1847), *Corophium volutator* (PALLAS, 1766) and *Nereis diversicolor* MÜLLER, 1776 were also present in the lagoon but occurred in too low density to allow demographic studies and were therefore not taken into consideration.

2.2. Sampling

The lagoon was divided into 4 study areas on the basis of the macrophytal cover (Fig. 1). The western and the southern areas were called “Sejnene” and “Joumine” after the main wadi supplying the lagoon.

© 2005 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim
with freshwater. The eastern area close to the Tinja channel was henceforth called “Tinja” and the vegetation free area “Centre”. From July 1993 to April 1994, three replicate samples were taken monthly (with the exception of August and September 1993) at a total of 21 sites, at Sejnene 6 (sites 1–5), in the Centre 3 (sites 6–8), at Tinja 6 (sites 9–14) and at Joumine 6 (sites 15–20) (Fig. 1) using a 15 cm inner diameter cylindrical Plexiglas coring tube containing a 20 cm thick substrate layer. The sediment cores were rinsed in a 300 μm gauze hand-net. All samples were preserved in 75% ethanol.

2.3. Size Frequency Distribution, Biomass and CHN Content

Only live bivalves were measured and counted. In the Ichkeul lagoon clear visible growth rings on the S. plana and A. tenuis shells are produced between July and August when water temperature and salinity are highest. These summer rings are often accompanied by weak extra rings produced during winter. The group of specimens which had not yet passed its first summer has been classified as age class 0; age class I is the group which had passed only one summer, etc. The ash-free dry mass (AFDM) [g] was estimated as a general power function of shell length (SL) [mm].

Scrobicularia plana:

\[ \text{AFDM} = e^{-11.2009} \cdot SL^{2.64089} \quad (R^2 = 85.21\%, n = 18) \]

Abra tenuis:

\[ \text{AFDM} = e^{-10.7109} \cdot SL^{2.8038} \quad (R^2 = 61.19\%, n = 38) \]

The AFDM was measured as weight loss after 4 h of incineration at 600 °C (BACHELET, 1982) of unconserved specimens dried at 60 °C for 48 h. The average CHN content was measured with a LECO 800 analyser as described by CASAGRANDA and BOUDOURESQUE (2002). The C- and N-content for S. plana yielded 64.3% C and 8.0% N of the AFDM, for A. tenuis 29.4% C and 2.9% N respectively.

2.4. Production

The different age classes were regarded as separate cohorts, and production was calculated separately for each of these cohorts. The cohorts were separated according to HARDING (1949), assuming that the size-frequency distributions of the cohorts were normally distributed. Production was estimated by two methods using (1) the loss summation method described by BOYSEN-JENSEN (1919) and (2) the increment summation method which MASSÉ (1968) derived from the BOYSEN-JENSEN (1919) method. Another method, the mass specific growth rate method (CRISP, 1984; BREY, 2001) was not considered here since comparing methods was not the aim of the present work and results from direct methods are usually equivalent (MEDERNACH and GREMARE, 1999).

(1) According to BOYSEN-JENSEN (1919), the production \( \Delta P \) of a cohort can be calculated as the sum of the standing stock gain (\( \Delta B \)) and the biomass produced but eliminated (E) due to mortality or emigration from time t to time \( t+\Delta t \):

\[
\Delta P = \Delta B + E
\]

with \( \Delta B = B_{t+\Delta t} - B_t \) and \( E = \Delta N \cdot \bar{w} \) where \( \Delta N = N_t - N_{t+\Delta t} \) and \( \bar{w} = \frac{1}{2} (w_t + w_{t+\Delta t}) \). \( N \) is the individual number and \( w \) the mean individual biomass. Total cohort production is expressed as the sum of all produced biomass over all time intervals:

\[
P_1 = \sum (B_{t+\Delta t} - B_t) + (N_t - N_{t+\Delta t}) \cdot \frac{1}{2}(w_t + w_{t+\Delta t}).
\]

(2) According to MASSÉ (1968), the production \( \Delta P \) of a cohort can be calculated as biomass gain from time t to time \( t+\Delta t \):

\[
\Delta P = \bar{N} \cdot \Delta w
\]

with \( \bar{N} = \frac{1}{2} (N_t + N_{t+\Delta t}) \) and \( \Delta w = w_{t+\Delta t} - w_t \). The total production of the cohort is calculated as the sum of the production increments over all time intervals:

\[
P_2 = \sum (\frac{1}{2}(N_t + N_{t+\Delta t})) \cdot (w_{t+\Delta t} - w_t).
\]
The energy budget of the deposit-feeding bivalves was estimated from literature using the calorific value of 18.74 kJ/g AFDM, the growth efficiency (P/A) of 21.07% and 12.78% consumption (C) used for production according to HUGHES (1970b). The organic income from the macrophyte meadows of the Ichkeul lagoon was calculated to be 5306 kJ/m² (BOUDOURESQUE et al., 1994; BCEOM et al., 1995; DEFOSSE and POYDENOT, 1995).

3. Results

3.1. Spatial and Temporal Fluctuations of Abundance and Biomass

*S. plana* and *A. tenuis* were never found at Sejnene and Joumine. *S. plana* occurred at annual mean densities (biomasses) of 400 ± 100 individuals/m² (34.27 ± 3.96 g AFDM/m²) at Centre and 299 ± 65 individuals/m² (22.54 ± 3.00 g AFDM/m²) at Tinja. At the Centre (3 sites*3 replicates) *S. plana* was the most abundant in November and December with a mean density (biomass) of 577 and 621 individuals/m² (22.75 and 36.61 g AFDM/m²), respectively (Fig. 2). At Tinja (6 sites*3 replicates), the maximum was reached in July with a mean density (biomass) of 515 individuals/m² (27.22 g AFDM/m²) and the minimum in October with a mean density (biomass) of 146 individuals/m² (9.96 g AFDM/m²) when the autumnal macrophyte fall started. Monthly estimates of density were highly variable during the macrophyte fall in autumn and stabilized once the leaf fall finished, i.e. from January. *A. tenuis* was only present at Tinja. Mean density (6 sites*3 replicates) was around 640 ± 74 individuals/m² during the whole study period; in contrast the biomass rose from 2.87 g AFDM/m² in July to 10.29 g AFDM/m² in April. The abundance and biomass of *S. plana* were only significantly higher in July, that of *A. tenuis* only in October (Table 1). No significant difference in the temporal variation of *S. plana* was found between the Centre and Tinja by the Mann-Whitney test.

3.2. Population Structure and Growth

Both species were largely dominated by age class I composed of 2 cohorts (I–1 and I–2) (Figs. 3 and 4). Specimens which had passed the second summer merged into a single class. This is due to the lowering of the growth rate as the animals become larger so that younger and faster growing animals could catch them up. In October, an increase of large numbers of one-year-old *S. plana* individuals was observed in the central lagoon (Fig. 3). For *S. plana*, a first spat settlement (0–1 cohort) was observed in October at Tinja (Fig. 4), in November through December in the Centre, which was eliminated during winter, and a second settlement (0–2 cohort) in March only in the Centre. For *A. tenuis*, a first recruit-

Table 1. Kruskal-Wallis analysis of temporal variation in abundance [individuals/m²] and biomass [g AFDM/m²] of each species in each area. H = Kruskal-Wallis test statistic, 

<table>
<thead>
<tr>
<th>Species</th>
<th>Area</th>
<th>Data</th>
<th>H</th>
<th>p</th>
<th>SNK test between months</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Scrobicularia plana</em></td>
<td>Centre</td>
<td>Abundance</td>
<td>6.95</td>
<td>0.33</td>
<td>Jul &gt; Oct = Nov = Dec = Jan = Feb = Mar = Apr</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Biomass</td>
<td>11.24</td>
<td>0.08</td>
<td>Jul &gt; Oct = Nov = Dec = Jan = Feb = Mar = Apr</td>
</tr>
<tr>
<td><em>Abra tenuis</em></td>
<td>Tinja</td>
<td>Abundance</td>
<td>9.69</td>
<td>0.21</td>
<td>Jul &gt; Oct = Nov = Dec = Jan = Feb = Mar = Apr</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Biomass</td>
<td>9.16</td>
<td>0.24</td>
<td>Jul &gt; Oct = Nov = Dec = Jan = Feb = Mar = Apr</td>
</tr>
</tbody>
</table>

© 2005 WILEY-VCH Verlag GmbH & Co. KGaA, Weinheim
Figure 2. Over time changes in abundance [individuals/m$^2$] and biomass [g AFDM/m$^2$] of Scrobicularia plana and Abra tenuis at each study area. Bars = standard error. No samples were taken in August and September nor in January for Centre due to stormy weather.

Figure 3. Over time changes in size-frequency distribution and growth of age classes of Scrobicularia plana at Centre. Bars = standard error. Cohorts detected by the HARDING (1949) method are indicated. No samples were taken in August and September nor in January due to stormy weather.
Figure 4. Over time changes in size-frequency distribution of *Scrobicularia plana* and *Abra tenuis* at Tinja. Cohorts detected by the HARDING (1949) method are indicated. No samples were taken in August and September.
ment was recorded in October (0–1 cohort) and a second one in April (0–2 cohort) (Fig. 4). Although not very successful, recruitment of both species presented two periods: the main period at the beginning of spring, and a second one in late summer/autumn. The data set indicated high losses during summer. The youngest age class (0) underwent high losses during winter, resulting in a dominance of age class I in both species. *S. plana* rarely exceeded 40 mm and lived 2 years although maximum life span observed was 5 years with growth to a length of 52 mm (Fig. 5). The maximum life span of *A. tenuis* was 2 years, and the maximum length observed 15 mm respectively, but most individuals lived only 15–18 months growing to a length of 12 mm.

### 3.3. Production

Production estimates for *S. plana* varied according to the area. The *S. plana* production achieved by loss summation was 13.45 g AFDM/m² in the Centre and 21.23 at Tinja (Table 2). The *A. tenuis* production at Tinja amounted to 3.44 g AFDM/m². The major production (81–94%) of the deposit-feeding bivalves took place in age class I. Within this age class, about 60% was achieved in *S. plana* by the second recruited cohort (I–2) (Table 2). In *A. tenuis*, 67% was achieved by the first recruited cohort (I–1). Production mainly occurred before November, when growth ceased. During winter, production was almost zero. Production of the remaining age classes was negligible. The P/B values decreased whereas age increased (Table 2). A mean estimate of bivalve deposit-feeder production and biomass was determined for the whole lagoon. In order to obtain this overall figure, the production and biomass estimates for each sampling area were weighted by their contribution (Centre, 55%; Tinja, 3%) to the total surface area of the wetland (Table 2). Mean production (biomass) from July to April for the deposit-feeding bivalves achieved by loss summation amounted to 8.24 g AFDM/m² (19.90 g AFDM/m²). The mean C- and N-production from July to April yielded 5.26 g C/m² and 0.65 g N/m² in the lagoon. The resulting turnover (P/B ratio) was about 0.4 (Table 2). The estimate according to Massé’s (1968) method, 7.40 g AFDM/m², was about 10% lower. The total bivalve deposit-feeding production (biomass) over the whole lagoon surface was 741 t AFDM (1791 t AFDM).

The calorific value of the infaunal tissue production was calculated to be 154 kJ/m². The total bivalve deposit-feeder assimilation amounted to 733 kJ/m² and the total consumption (C) was to 1208 kJ/m². On the basis of this value the deposit-feeding bivalves would have consumed 23% of this energy income during the study period. The elimination (E) calcula-
ted by the BOYSEN-JENSEN (1919) method amounted to 104 kJ/m², rendering the ecological efficiency (E/C) of the deposit-feeding bivalves as 9%.

4. Discussion

4.1. Spatial and Temporal Fluctuations of Abundance and Biomass

Density and biomass of the deposit-feeding bivalves in the Ichkeul lagoon are high compared with results from other studies (GUELORGET and MAZOYER-MAYÈRE, 1982; GUERREIRO, 1998; HUGHES, 1970b; KEVREKIDIS and KOUKOURAS, 1992; SOLA, 1997). Among the local factors that could influence high abundance in the Ichkeul lagoon, we can point to (1) the stability of the sediment; (2) the high organic matter content of the sediment favouring the development of bacterial populations that form the basis of the diet of deposit-feeders; (3) the low number of competing bivalve species and predators on adult individuals (BCEOM et al., 1995).
The reproductive strategies differ considerably for the two species. *S. plana* has a planktotrophic development with a long pelagic stage (HUGHES, 1970a). The unfavourable environmental conditions at Sejnene and Joumine such as low salinity, dense *Potamogeton pectinatus* stands, coarser sediment, high temperature and low dissolved oxygen especially at the time of settlement in summer prevent *S. plana* from colonizing these areas. *A. tenuis* has a lecithotrophic development (NOTT, 1980) which is interpreted as ensuring the maintenance of populations but population dispersal is very limited.

The strong biomass decrease observed in October can be interpreted as the result of lower condition factor linked with spawning. Gamete release significantly affects biomass. HUGHES (1970b) estimated that gametic production could account for 24 to 52% of the total production which is in line with BACHELET (1982). However, in the Ichkeul lagoon the effect of summer stress on biomass outweighed the effect of spawning on biomass. *S. plana* is unable to osmoregulate physiologically (HUGHES, 1970a) and highest mortality occurred essentially during summer when temperature, salinity and macrophyte development were highest and dissolved oxygen lowest in the lagoon (BCEOM et al., 1995). High mortality following spat settlement and spawning is not unusual. The *S. plana* population of the Prévost lagoon (GUELORET and MAZOYER-MAYÈRE, 1983) was almost eliminated during summer. HUGHES (1970a) found in an *S. plana* population a mortality rate of 50% that he attributed to unfavourable environmental conditions which is consistent with the results of BACHELET (1982) and SOLA (1997).

### 4.2. Life History and Recruitment

The high density and biomass of the Ichkeul deposit-feeding bivalves could also be related to the temperature regime in the southern part of the geographical range of both *S. plana* and *A. tenuis*. This may result in faster growth, higher density of individuals of smaller size and a shorter life span. Although *S. plana* is obviously capable of substantial horizontal migration it appears to do so only rarely (HUGHES, 1970a; BACHELET, 1982; GUELORET and MAZOYER-MAYÈRE, 1983). In October, the arrival in the central lagoon of large numbers of one-year-old *S. plana* individuals which had already passed a summer (Fig. 3) can only be explained by migration as a response to unfavourable conditions. The highly adverse environmental conditions during late summer eliminate the possible interpretation of the rapid growth of a new settlement.

The Ichkeul population of *S. plana* showed a reproduction pattern similar to that of the Arcachon bay population (BACHELET, 1981a) and the Tagus and Mira estuary populations (GUERREIRO, 1998) with two recruitment events, one in spring and one in autumn. The reproduction pattern of the Ichkeul *A. tenuis* population differs from that of northern regions (NOTT, 1980; GIBBS, 1984; DEKKER and BEUKEMA, 1993) by the occurrence of 2 recruitments in spring and autumn. According to HUGHES (1970a) the differences in the reproductive cycle of *S. plana* may be due to latitudinal, i.e. thermal differences along the Atlantic coast. Northern populations of *S. plana* are characterised by short, mid-summer spawning periods (HUGHES, 1970a; WARWICK and PRICE, 1975). Further south, spawning periods are extended and occur later, sometimes throughout the winter, but with negligible or no activity in mid-summer (SOLA, 1997). One cohort per year occurs mostly in northern areas (HUGHES, 1970a; WARWICK and PRICE, 1975), versus 2–3 cohorts per year in southern regions (BACHELET, 1981a; GUERREIRO, 1998). DAUVIN (1986) compared his results to other *A. alba* populations and his conclusions seem to confirm this pattern.

These latitudinal differences in reproductive cycles are related to varying local conditions at times of settlement and during the first six months after settlement which affect the success of recruitment (HUGHES, 1970a). At densities found in the Ichkeul lagoon, pediveliger or spats could be consumed by adults while deposit-feeding. Thus the poor recruitment has
lead to a dominant age class at Ichkeul. In fact, if one very successful spawning event takes place, recruitment in the following years may be suppressed due to intraspecific competition for food and space. Hughes (1970a) and Guerreiro (1998) postulated a dominant age class phenomenon where a population may be numerically dominated by one or a few large older classes. Successful recruitment does not seem to be a regular annual phenomenon (Dekker and Beukema, 1993; Guerreiro, 1998). In southern Europe, the pattern of population dynamics of at least S. plana may possibly be dominated by periods of highly successful recruitment and high production followed by large periods of unsuccessful recruitment and low production (Guerreiro, 1998; this study).

4.3. Production

The S. plana P/B ratio in the Centre was much lower (0.39) than at Tinja (0.94, Table 2) due to a faster growth in age class I from March on at Tinja (Fig. 5) than in the Centre (Fig. 3). At Tinja, growth is favoured by much better food availability in spring than in the vegetation-free Centre. The P/B of A. tenuis at Tinja is in the same order as that of S. plana in the Centre which is interpreted as a consequence of the poor recruitment during the study period. As has been pointed out by Siegismund (1982), the method described by Massé (1968) underestimates the production of a cohort during a period of recruitment in which the density is increasing. The Siegismund (1982) modification probably still underestimates production as it neglects the production of individuals recruited during the period of increasing density and eliminated before observation at the end of the period. For these reasons and also because of migration phenomenon within the system, the production estimates achieved by the loss summation method (Boysen-Jensen, 1919) were favoured here. The production of S. plana from July 1993 to April 1994 amounted to 17.34 g AFDM/m², and that of A. tenuis to 3.44 g AFDM/m² (Table 3). Although determined for only 10 months, this probably approximates the total annual production since the highly adverse environmental conditions from October onward did not improve but worsened. The P/B ratio estimates of S. plana in the Ichkeul lagoon were of the same order of magnitude as estimates in other brackish coastal areas (Hughes, 1970b; Warwick and Price, 1975; Bachelet, 1982; Guerreiro, 1998) (Table 3). In the Prévost lagoon, Guelorget and Mazoyer-Mayère (1983) found exceptionally high P/B values which are due to particularly fast growth and short but very abundant recruitment. The P/B ratio of A. tenuis in the Ichkeul lagoon is low compared to other Abra species which may be due to the weak recruitment during the study period and a very slow growth rate of the settling juveniles until a length of 1 mm was reached (Bachelet, 1989). Along the Atlantic coast, a southward increase in secondary production can be observed for populations of S. plana whereas P/B is constant (Table 3). This could be related to faster growth in southern latitudes (Bachelet, 1981a), high densities of small individuals, more than one annual generation and a shorter life span.

The high energy flow through the deposit-feeding bivalves indicates the importance of this functional group in the Ichkeul ecosystem. Hughes (1970b) estimated as much as 1336 and 1407 kJ/m² for S. plana on a Welsh tidal flat, which seems to be very high. The assimilation in the Ichkeul lagoon was locally close to the above values but weighted to the whole lagoon surface, the estimate of the average energy flow amounted to 733 kJ/m² during the study period. The consumption was 23% of the total energy input from the lagoon macrophytes during the study period. Other energy sources may be available in the Ichkeul lagoon, e.g. the excrements of the wintering waterfowl and the input through the Tinja channel. As the autumn and winter rainfall was very low during the study period, the nutrient input from the wadis was negligible. Input of inorganic nutrients can also be attributed to bivalve activity. Through their feeding and burrowing activities, Scrobicularids stimulate mineralization processes in the adjacent sediment. In addition to mixing nutrient-rich pore
waters with overlying waters, the deposit-feeders remove organic material from the water column and excrete remineralized nutrients in form of pseudofeces and through direct excretion (ALPINE and CLOERN, 1992). Bivalves can also sequestrate nitrogen and phosphorus. The reduction of total phosphorus (TP) content in the Centre and at Tinja during winter (e.g., from 142 \( \mu g \) TP/l in August to 70 \( \mu g \) TP/l in October throughout the winter; BCEOM et al., 1995) indicated a high potential for phosphorus storage in the bivalves. The nutrient cycling

<table>
<thead>
<tr>
<th>Study area</th>
<th>B</th>
<th>P</th>
<th>P/B</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abra tenuis</td>
<td>AFDM</td>
<td>7.78</td>
<td>3.44</td>
<td>0.44 this study</td>
</tr>
<tr>
<td>Ichkeul lagoon (Tunisia)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abra ovata</td>
<td>DM</td>
<td>0.70</td>
<td>1.50</td>
<td>2.14 GUELORGET and MAZOYER-MAYÈRE (1982)</td>
</tr>
<tr>
<td>Prévost lagoon (France)</td>
<td>DM</td>
<td>14.33</td>
<td>26.10</td>
<td>1.82 GUELORGET and MAZOYER-MAYÈRE (1982)</td>
</tr>
<tr>
<td>Mauguio lagoon (France)</td>
<td>DM</td>
<td>29.22</td>
<td>17.09</td>
<td>0.59 KEVREKIDIS and KOUKOURAS (1992)</td>
</tr>
<tr>
<td>Evros Delta (Greece)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abra alba</td>
<td>DM</td>
<td>1.04</td>
<td>0.81</td>
<td>0.77 HILY (1976)</td>
</tr>
<tr>
<td>Charente straits (France)</td>
<td>DM</td>
<td>0.35</td>
<td>1.34</td>
<td>3.83 MENESGUEN (1980)</td>
</tr>
<tr>
<td>Concarneau Bay (France)</td>
<td>ADFM</td>
<td>0.30</td>
<td>0.41</td>
<td>1.35 WARWICK and GEORGE (1980)</td>
</tr>
<tr>
<td>Bristol channel (U.K.)</td>
<td>ADFM</td>
<td>0.80</td>
<td>2.91</td>
<td>3.63 BACHELET (1981b)</td>
</tr>
<tr>
<td>Gironde estuary (France)</td>
<td>DM</td>
<td>0.72</td>
<td>1.45</td>
<td>2.01 GLÈMAREC and MENESGUEN (1980)</td>
</tr>
<tr>
<td>Concarneau Bay (France)</td>
<td>ADFM</td>
<td>0.81</td>
<td>2.34</td>
<td>2.87 CORNET (1986)d</td>
</tr>
<tr>
<td>Arcachon Bay (France)</td>
<td>ADFM</td>
<td>4.44</td>
<td>7.31</td>
<td>1.65 CORNET (1986)b,d</td>
</tr>
<tr>
<td>Gironde estuary (France)</td>
<td>DM</td>
<td>0.77</td>
<td>1.58</td>
<td>2.04 DAUVIN (1986)</td>
</tr>
<tr>
<td>Morlaix Bay (France)</td>
<td>ADFM</td>
<td>2.86</td>
<td>8.80</td>
<td>3.08 FRANCESCH and LOPEZ-JAMAR (1991)</td>
</tr>
<tr>
<td>Ria de La Coruna (Spain)</td>
<td>ADFM</td>
<td>0.30</td>
<td>0.85</td>
<td>2.82 LASTRA et al. (1993)</td>
</tr>
<tr>
<td>Abra nitida</td>
<td>ADFM</td>
<td>0.11</td>
<td>0.12</td>
<td>0.11 BUCHANAN and WARWICK (1974)</td>
</tr>
<tr>
<td>Northumberland coast (U.K.)</td>
<td>ADFM</td>
<td>0.35</td>
<td>0.93</td>
<td>2.63 FRANCESCH and LOPEZ-JAMAR (1991)</td>
</tr>
<tr>
<td>Ria de La Coruna (Spain)</td>
<td>ADFM</td>
<td>4.37</td>
<td>2.97</td>
<td>0.68 HUGHES (1970 b)a</td>
</tr>
<tr>
<td>Conway Bay, marshward (U.K.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conway Bay, seaward (U.K.)</td>
<td>ADFM</td>
<td>46.24</td>
<td>13.41</td>
<td>0.29 HUGHES (1970 b)a</td>
</tr>
<tr>
<td>Lynher estuary (U.K.)</td>
<td>ADFM</td>
<td>2.15</td>
<td>0.48</td>
<td>0.22 WARWICK and PRICE (1975)b</td>
</tr>
<tr>
<td>Gironde estuary (France)</td>
<td>ADFM</td>
<td>11.60</td>
<td>9.13</td>
<td>0.79 BACHELET (1982)a,b</td>
</tr>
<tr>
<td>Arcachon Bay (France)</td>
<td>ADFM</td>
<td>9.65</td>
<td>12.28</td>
<td>1.27 BACHELET (1982)a,b</td>
</tr>
<tr>
<td>Prévost lagoon, marshward (France)</td>
<td>ADFM</td>
<td>7.98</td>
<td>31.69</td>
<td>3.97 GUELORGET and MAZOYER-MAYÈRE (1983)</td>
</tr>
<tr>
<td>Prévost lagoon, seaward (France)</td>
<td>ADFM</td>
<td>122.87</td>
<td>451.92</td>
<td>3.68 GUELORGET and MAZOYER-MAYÈRE (1983)</td>
</tr>
<tr>
<td>Bidasoa estuary (Spain)</td>
<td>ADFM</td>
<td>69.20</td>
<td>83.62</td>
<td>1.21 SOLA (1997)b</td>
</tr>
<tr>
<td>Mira estuary (Portugal)</td>
<td>ADFM</td>
<td>7.29</td>
<td>4.20</td>
<td>0.58 GUERREIRO (1998)c</td>
</tr>
<tr>
<td>Tagus estuary (Portugal)</td>
<td>ADFM</td>
<td>28.93</td>
<td>24.71</td>
<td>0.85 GUERREIRO (1998)c</td>
</tr>
<tr>
<td>Ichkeul lagoon (Tunisia)</td>
<td>ADFM</td>
<td>28.40</td>
<td>17.34</td>
<td>0.61 this study</td>
</tr>
</tbody>
</table>
and the phosphorus storage by bivalves has been described for different aquatic ecosystems (NALEPA et al., 1991; PRINS and SMAAL, 1994) suggesting the potential of bivalves for eutrophication control. It is difficult to quantify the amount of ingested material derived from the sediment. More studies are necessary to determine food preferences and to quantify actual ingestion rates. However, our study allowed quantification of the amounts of organic matter which passed through the deposit-feeding bivalves (short-term energy budget). Only 9% of the bivalve deposit-feeding production was available to the next trophic level such as common pochards, oystercatchers, eels and gilthead seabream.

5. Acknowledgements

This study was carried out within the international programme “Etude pour la sauvegarde du Parc National de l’Ichkeul” financed by the Kreditanstalt für Wiederaufbau (KfW) under the aegis of the Tunisian authorities, in particular the Agence Nationale pour la Protection de l’Environnement. Thanks are due to members of the Groupement d’Intérêt Scientifique (GIS) Posidonie for field assistance, to the colleagues at UMR 6540 CNRS Dimar (Diversité, Evolution et Ecologie fonctionnelle marine) for advice and work facilities, and to Prof. GERHARD BAUER of the University of Freiburg for critical revision of the manuscript. The present research was supported by a Ph. D. grant from the Landesgraduiertenförderungsgesetzes (LGFG) Germany. The study would not have been possible without the support of Prof. JÜRGEN SCHWOERBEL, mentor and friend. Finally, the authors are grateful to two anonymous referees for very valuable comments and to MICHAEL PAUL for improving the English text.

6. References

C. CASAGRANDA and C. F. BOUDOURESQUE


Manuscript received July 24th, 2004; revised February 19th, 2005; accepted March 9th, 2005