

Reproductive investment of the bivalves *Cerastoderma edule* (L.) and *Mya arenaria* L. in the Dutch Wadden Sea

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Abstract

Cerastoderma edule and *Mya arenaria* are two common bivalve species in European waters. In the Dutch Wadden Sea, these species are abundant in intertidal and subtidal areas, and recruitment success is usually higher in *C. edule* than in *M. arenaria*. Differences in reproductive output or in larval and post-larval processes could be responsible for the observed differences in recruitment success between species. In the present paper, the timing of spawning and the reproductive investment of the two bivalve species was studied at intertidal and subtidal areas of the western Dutch Wadden Sea. *M. arenaria* showed higher growth than *C. edule*, in both locations. This resulted in a maximum gonadal mass of 60 mg AFDM in *C. edule* and 2000 mg AFDM in *M. arenaria* at the intertidal, and 20 mg AFDM in *C. edule* and 1300 mg AFDM in *M. arenaria* at the subtidal. Individual reproductive investment was higher in *M. arenaria* than in *C. edule*. *M. arenaria* invested more energy in gonadal mass than *C. edule* both in the intertidal (20% versus 15%) and in the subtidal (13% versus 10%). Timing of spawning was similar in both species, around May, except for *M. arenaria* in the intertidal which seemed to spawn in August. Most *C. edule* showed empty gonads after the spawning season while *M. arenaria* did not spawn completely. However, due to the differences in mass composition between species, absolute reproductive output of the *M. arenaria* population in the western Wadden Sea must be much higher than that of the *C. edule* population. The observed differences in recruitment success between the two species cannot be due to differences in reproductive output since *M. arenaria* has a higher reproductive output. Since egg and larval stage duration are similar between species, differences in post-larval processes are more likely to be the cause for the observed recruitment patterns.

Introduction

The Dutch Wadden Sea, in north-western Europe, is an important nursery area for many pelagic and epibenthic organisms, and a feeding area for migrating shorebirds (Wolff 1983). Bivalves play an important role in the ecosystem, both in terms of biomass as well as in terms of productivity, whereby a few species account for most of the numbers and biomass (Beukema 1991, Dekker et al. 2002, 2003; Dekker and Waasdorp 2004). The life cycle of the various bivalve species is in general similar: after the release of gametes in the water column, a planktonic larval stage occurs, followed by settlement on the seafloor and a demersal juvenile and adult stage. Nevertheless, the various species show large differences in distribution and abundance patterns over the various habitats in the Dutch Wadden Sea. For instance, settlement of the Baltic tellin *Macoma balthica* occurs mostly at intertidal areas, but before or during their first winter, spat migrates in the opposite direction and redistributes into deeper intertidal, subtidal and coastal waters (Beukema 1993). On the other hand, the Pacific oyster *Crassostrea gigas* is more restricted to the intertidal area (Dekker and Waasdorp 2005, 2006) while the blue mussel *Mytilus edulis* can be found in wild beds in the intertidal and subtidal (Dankers and Koelemaij 1989, Dankers and Zuidema 1995, Dankers et al. 1999).

In two other species, the common cockle *Cerastoderma edule* and the soft-shell clam *Mya arenaria* such an intermediate distribution pattern is also observed. *C. edule* and *M. arenaria* are common suspension-feeding bivalves along the European coast. *M. arenaria* occurs from the White Sea to the Gironde estuary and *C. edule* can be found from the western Barents Sea to Mauritania in West Africa (Tebble 1966, Wolff unpubl. observ.). They present large differences in maximum size and age: *M. arenaria* reaches a maximum shell length of about 15 cm while *C. edule* usually grows until a maximum size of 5 cm (Tebble 1966, Hayward and Ryland 1995); and the oldest age reported for *M. arenaria* is 28 years (MacDonald and Thomas 1980) in contrast to 10 years in *C. edule* (Seed and Brown 1978).

In the western Wadden Sea, spat settlement of these species occurs in intertidal and subtidal areas and, as a result, juveniles and adults of both species are found in these areas (Dekker 1989, Dekker et al. 2002, 2003; Dekker and Waasdorp 2004, 2005). Biomass of *C. edule* shows strong fluctuations from year to year, from more than 6 g m⁻² ash-free dry mass (AFDM) in some years to almost 0 in others. Biomass of *M. arenaria* has been increasing during the last decade, from almost 0 g m⁻² AFDM in 1991 to more than 30 g m⁻² AFDM in recent years, in some areas of the western Wadden Sea (Dekker and Waasdorp 2006). In terms of recruitment success, both species show fluctuations from year to year (Beukema et al. 2001). However, during the last 40 years, recruit numbers in intertidal and subtidal areas at the end of the summer are usually higher in *C. edule* than in *M. arenaria* (Beukema et al. 2001, Dekker et al. 2002, 2003; Dekker and Waasdorp 2004, 2005, 2006). Differences in recruitment can result from a number of factors, starting with differences in reproductive output and/or differences in larval and post-larval processes (such as pelagic stage duration,

mortality, growth). Egg size is rather similar between these species (*C. edule*: 65 μm ; *M. arenaria*: 57 μm), considering that egg sizes in bivalves can vary between 40 μm and 270 μm (Loosanoff and Davis 1963, Brousseau 1979, 1987; Nott 1981, Strathman 1977, Honkoop and Van der Meer 1998, Kenchington et al. 1998, Cardoso et al. 2007a,b). The fact that egg size of *C. edule* and *M. arenaria* is similar suggests that larval size and pelagic stage duration should also be similar (Kooijman 2000).

Therefore, differences in larval processes between species are not likely to be responsible for the observed differences in recruitment. Lower reproductive success in *M. arenaria* could be related to lower recruitment, although post-larval processes such as higher predation on settled larvae can not be excluded. In the present paper, we focussed, as a starting point, on the reproductive output of *C. edule* and *M. arenaria* in two habitats of the western Wadden Sea. The aim was to find out if differences in reproductive investment between these two species could be the cause for the observed differences in recruitment success in the western Wadden Sea. Regular sampling of both species was carried out in intertidal and subtidal areas to reveal:

- [1] the timing of spawning by analysing the seasonal patterns in gonadal mass; and
- [2] the reproductive investment by determining the energy investment into somatic and gonadal mass in relation to size and age.

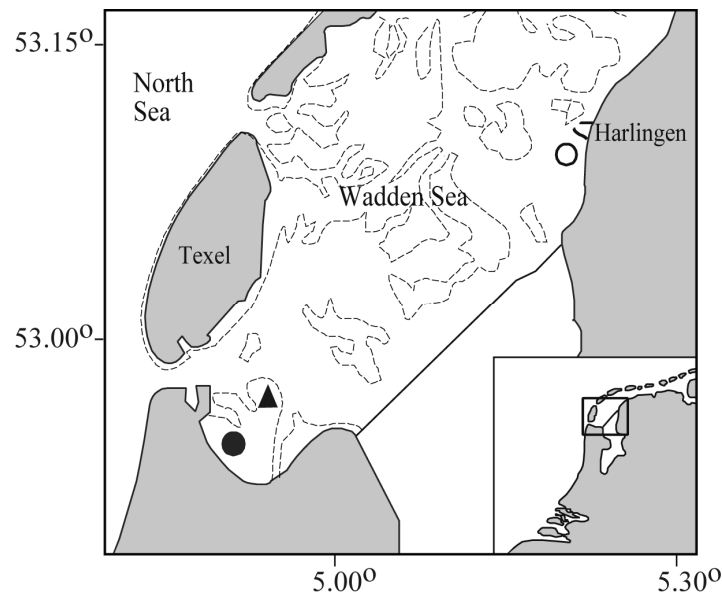


Fig. 3.1. Sampling locations of intertidal *C. edule* (●) and *M. arenaria* (▲). Subtidal sampling was done in the same area for both species (○). Striped lines mark the limits of the intertidal areas.

Materials and Methods

Field sampling

From September 2001 to April 2003, *Mya arenaria* and *Cerastoderma edule* were collected, if possible, every month in intertidal and subtidal areas in the western Wadden Sea (Fig. 3.1; for characteristics see Table 3.1). At each sampling date, around 100 individuals were sampled in an area of a few km². Individuals of all size classes were sampled. Intertidal *M. arenaria* and *C. edule* were collected by hand at the Balgzand area during low tide. The intertidal sites are emerged for an average of 4 h per tidal cycle. Subtidal samples were collected near Harlingen during high tide. Since *M. arenaria* lives buried in the sediment, sampling was done with a ‘Reineck’ box corer (0.06 m²). For *C. edule*, which lives on the sediment surface, sampling was done with a 1.9 m beam trawl (for description see Van der Veer and Witte 1999). In the laboratory, all animals were stored in seawater at 5 °C and processed within the next 48 h.

Table 3.1. Characteristics of the locations where *C. edule* and *M. arenaria* were sampled. Depth values are expressed as the difference between MTL and the mean intertidal level of each sampling site.

Species	Location	Latitude (°N)	Longitude (°E)	Depth (m)	Density (ind m ⁻²)* ¹
<i>C. edule</i>	intertidal	52° 56'	4° 48'	-0.4	19
<i>C. edule</i>	subtidal	53° 09'	5° 19'	-2.5	103
<i>M. arenaria</i>	intertidal	52° 57'	4° 55'	-0.5	14
<i>M. arenaria</i>	subtidal	53° 09'	5° 19'	-2.5	102

*1 data from Dekker and Waasdorp (2003)

Data analysis

Of each individual bivalve, shell length was measured to the nearest 0.01 mm with electronic callipers, and subsequently, bivalves were opened and all flesh was removed. Gonads were separated from somatic mass under a microscope. Ash-free dry mass (AFDM) of each part was determined to the nearest 0.01 mg. Age was estimated by counting the external year marks on the shell (following Seed and Brown 1978, Brousseau 1979, Iglesias and Navarro 1990, Van Moorsel 2003). Shell length (mm), somatic AFDM (mg) and gonadal AFDM were plotted against age. Von Bertalanffy Growth (VBG) parameters were iteratively estimated for length-at-age growth curves.

The energy investment in somatic and gonadal mass was determined by estimating, respectively, the Somatic Mass Index (SMI), expressed as the AFDM of the soma divided by cubic shell length (cm³), and the Gonadal Mass Index (GMI) expressed as the gonadal AFDM divided by cubic shell length (cm³). The relative investment in reproduction was determined

by calculating the Gonadosomatic Ratio (GSR), described as the gonadal AFDM divided by the total body AFDM (soma + gonads).

By dividing mass by cubic shell length, animals of different size could be compared in terms of condition. The extent to which variability in condition was accounted for by seasonal variability and by differences among age classes and among locations was examined by analysis of variance ANOVA. Due to an unbalance in the sampling scheme over the year, the effect of time could not be described in terms of differences among all sampling months (that is, by using sampling month as a categorical variable). Instead we used a linear trend over time in combination with a sinusoidal seasonal effect. The overall time effect was modelled as:

$$\beta_1 \text{ Time} + \beta_2 \sin(2\pi ((\text{Month} - \beta_3)/12)),$$

in which β_1 , β_2 , and β_3 are parameters, *Time* is a continuous variable that runs from the first day of observation till the last day, and *Month* is a continuous variable running from the first month of observation till the last month. Note that this model is only a linear model when β_3 is known beforehand. For that, we ran this linear model, which further included the factor site and the covariate age, for all 12 possible values of β_3 (i.e. the values 1 to 12) and selected the model with the lowest residual mean squares. Subsequently, the selected model was used to correct somatic and gonad mass indices for seasonal and age differences, and adjusted to the average month and age. In order to obtain Normality, GMI data were transformed using the squared root transformation.

All statistical analyses were made using the software package SYSTAT (Wilkinson 1996).

Results

Growth

In both species, shell length, somatic and gonadal mass showed an increase over time (Fig. 3.2). A decrease in mean shell length between successive sampling occasions was sometimes observed but this was due to sampling errors (Fig. 3.2a and 3.2d). In *C. edule*, growth in somatic mass occurred from mid spring to the end of the summer (Fig. 3.2b). Weight loss occurred in winter, as indicated by the decrease in mean somatic mass values. Gonadal mass increased in spring, after which it rapidly decreased due to spawning (Fig. 3.2c). For most year classes, a slight increase in gonadal mass was also observed at the end of the summer. In autumn, most individuals had empty gonads. Patterns of growth in shell length were similar between intertidal and subtidal individuals but somatic growth in the subtidal did not show very clear patterns due to the variability in data. Gonadal mass in the subtidal followed the same pattern as in the intertidal but only one peak in mass was observed in mid spring, except for 1 year old individuals which showed a peak in gonads in late spring.

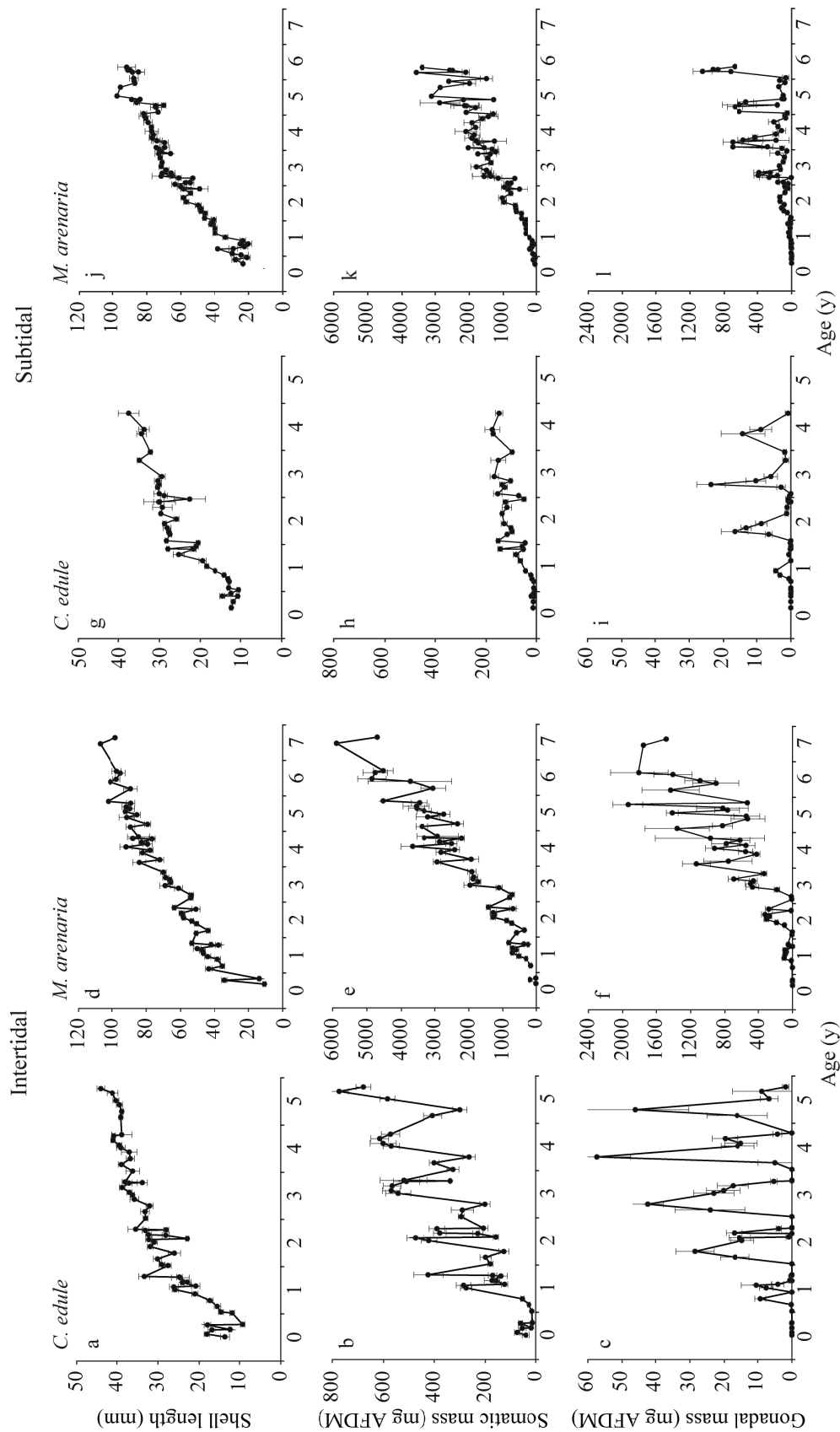


Fig. 3.2. Shell length (mm, mean $\pm$ SE), somatic mass (mg AFDM, mean $\pm$ SE) and gonadal mass (mg AFDM, mean $\pm$ SE) of *C. edule* and *M. arenaria* plotted against age (years) in intertidal (a-f) and subtidal (g-l) locations. The transition between two age classes is considered to be on the 1st of January.

The observed maximum mean shell length, somatic mass and gonadal mass for *C. edule* were, respectively, about 43 mm, 700 mg AFDM and 60 mg AFDM in the intertidal, and 41 mm, 100 mg AFDM and 20 mg AFDM in the subtidal. The estimated maximum length for the intertidal and subtidal stations was, respectively, 43.4 mm and 43.3 mm (Table 3.2).

Table 3.2. Parameters of the Von Bertalanffy growth curve for maximum length (mm) of *C. edule* and *M. arenaria* at the subtidal and intertidal locations. L_{∞} is the estimated maximum shell length (mm), k is the Von Bertalanffy growth coefficient and $\omega = L_{\infty} * k$.

Species	n	L_{∞} ($\pm$ SE, mm)	$10^3 * k$ ($\pm$ SE, d^{-1}) r^2	ω (mm d^{-1})
Intertidal				
<i>C. edule</i>	56	43.40 $\pm$ 1.42	0.33 $\pm$ 0.10	0.90 $\pm$ 0.06
<i>M. arenaria</i>	55	119.34 $\pm$ 5.88	0.68 $\pm$ 0.06	0.93 $\pm$ 0.08
Subtidal				
<i>C. edule</i>	40	43.26 $\pm$ 3.19	1.04 $\pm$ 0.13	0.90 $\pm$ 0.05
<i>M. arenaria</i>	77	115.74 $\pm$ 5.24	0.65 $\pm$ 0.05	0.95 $\pm$ 0.08

In *M. arenaria*, growth in somatic mass occurred earlier, from spring to mid summer at the two stations, although the large variability in older age classes partly disturbed the patterns, especially in the intertidal (Fig. 3.2e). Weight loss occurred usually between the end of the summer and the beginning of the following year. Large variability in gonadal mass was also observed in the intertidal location. In the intertidal, highest gonadal masses were found in mid summer (Fig. 3.2f). In the subtidal, gonadal mass reached maximum values in spring. Complete spawning was only observed during the first years of life at both locations. Maximum shell length, somatic mass and gonadal mass were in the intertidal 108 mm, 6000 mg ADFM and 2000 mg AFDM, respectively, while in the subtidal they were 100 mm, 4800 mg AFDM and 1300 mg AFDM, respectively. Length-at-age curves resulted in an estimated maximum length of 119.3 mm in the intertidal and 115.7 mm in the subtidal (Table 3.2).

C. edule reached a maximum age of 5 years in the intertidal and 4 in the subtidal while in *M. arenaria* the maximum age was 7 years in the intertidal and 6 in the subtidal. For both species and locations, individuals of all size ranges from 0-group to maximum age were found. To compare growth rates between the two species, the parameter ω was estimated by multiplying L_{∞} with the Von Bertalanffy growth rate k (Appeldoorn 1983, Beukema and Meehan 1985). *M. arenaria* had higher growth rates than *C. edule*, both in intertidal and subtidal locations (Table 3.2).

Body mass cycles

For both species, sexes were treated together because no differences in somatic mass index (SMI) and gonadal mass index (GMI) were found between males and females (ANOVA, $p >$

0.05). Somatic mass index showed a clear seasonal pattern in both species (Fig. 3.3) although *C. edule* showed a stronger pattern than *M. arenaria*. The peak in SMI was in July at intertidal locations for both species (Fig. 3.3a and 3.3c), and in June/July in subtidal *C. edule* (Fig. 3.3b) and between April and June in subtidal *M. arenaria* (Fig. 3.3d).

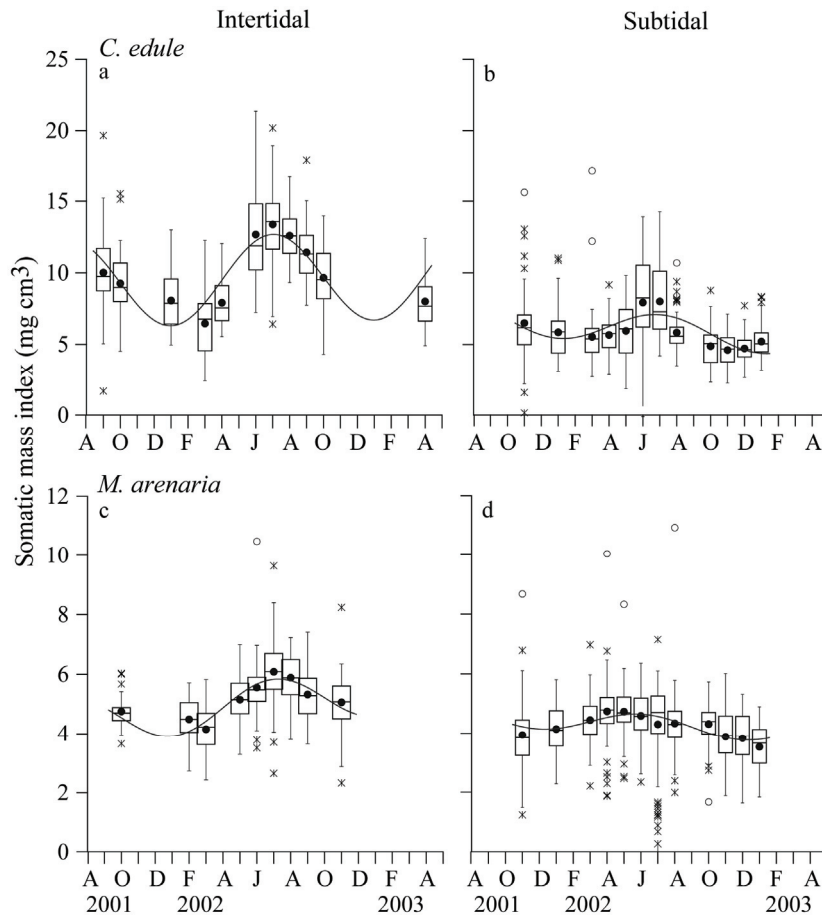


Fig. 3.3. Somatic mass index (mg cm^{-3}) of *C. edule* (a and b) and *M. arenaria* (c and d) along the year in intertidal and subtidal locations.

The period with lowest somatic mass index was between December and February for *M. arenaria* and around February/March for *C. edule*. Both in *M. arenaria* and *C. edule*, significant differences in SMI between intertidal and subtidal stations were found between months (ANOVA, $p < 0.001$) but not between age groups (ANOVA, $p > 0.05$). In *C. edule*, SMI increased during the first year of life and decreased from then onwards (not shown) while in *M. arenaria*, SMI increased during the first 2 to 3 years of life (not shown).

In relation to the gonadal mass index, clear seasonal cycles were also seen in the two species (Fig. 3.4). *C. edule* presented, for both stations, a peak in April and minimum values in October/November (Fig. 3.4a and 3.4b). *M. arenaria* showed maximum values around July in the intertidal and April in the subtidal (Fig. 3.4c and 3.4d). GMI decreased with age in *C.*

edule (not shown) while it increased with age in *M. arenaria* (not shown). In *C. edule*, differences in GMI between stations were significant with age (ANOVA, $p < 0.001$) but not between months (ANOVA, $p > 0.05$). In contrast, *M. arenaria* showed significant differences both between months and age groups (ANOVA, $p < 0.001$).

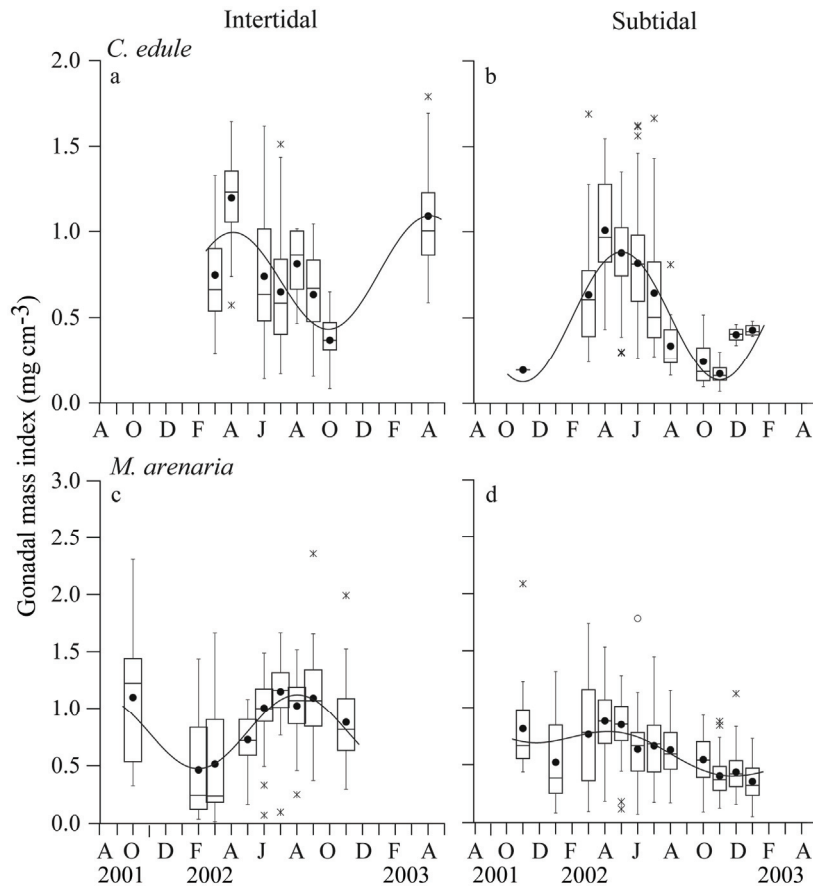


Fig. 3.4. Gonadal mass index (mg cm^{-3}) of *C. edule* (a and b) and *M. arenaria* (c and d) along the year in intertidal and subtidal locations. GMI values are square-root transformed. Note that only individuals that had gonadal mass are represented.

Timing of spawning and gonadosomatic ratio

From the decrease in GMI after the peak in spring/summer, spawning was estimated to occur around May for subtidal *M. arenaria* and for intertidal and subtidal *C. edule*, and around August for intertidal *M. arenaria* (Fig. 3.4). In *C. edule*, there was a suggestion of a second spawning period in September, as seen by an increase in GMI between July and August and a decrease in September (Fig. 3.4a).

The seasonal pattern in gonadosomatic ratio (GSR) was different between species. Overall, *M. arenaria* had a higher GSR than *C. edule*, both in the intertidal and the subtidal (Fig. 3.5). In the intertidal, the amount of gonads in *M. arenaria* was about 20% of the total body mass

while in *C. edule*, about 15% of the body was composed of gonadal mass. In the subtidal, the investment in gonads amounted to roughly 13% of the total body mass in *M. arenaria* and only about 10% in *C. edule*. Overall, *M. arenaria* invested more energy in gonadal mass than *C. edule*. However, most *C. edule* seemed to have spawned completely during the spawning season, as suggested by the very low or even null values in gonadal mass after the spawning season (Fig. 3.5a). In contrast, most *M. arenaria* did not seem to spawn completely, due to the relatively high values in GSR after the spawning season (Fig. 3.5b).

An overview of the main data collected in the present study is presented in Table 3.3.

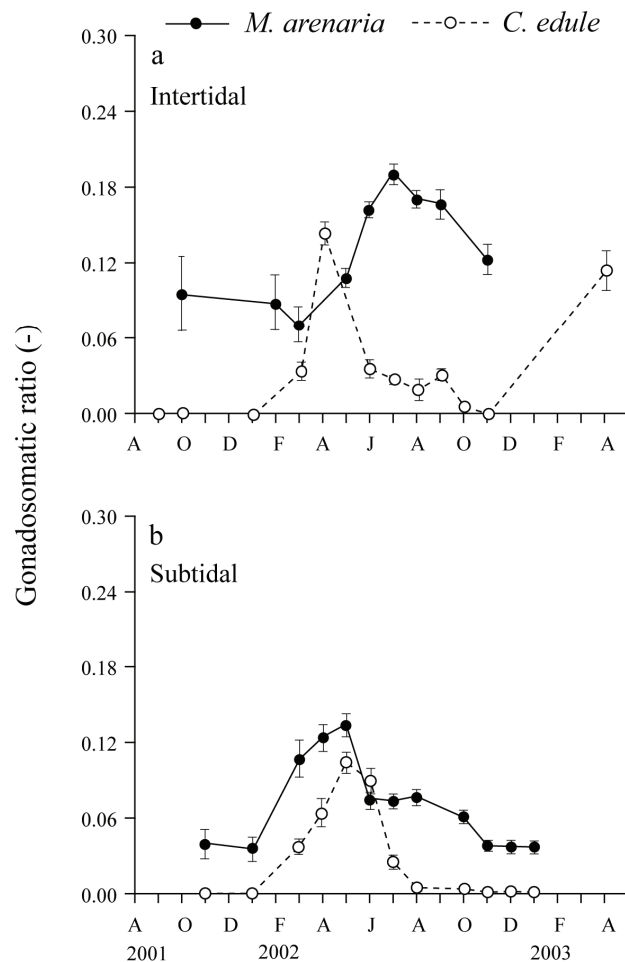


Fig. 3.5. Gonadosomatic ratio (-) of *C. edule* (a) and *M. arenaria* (b) along the year, in intertidal and subtidal locations.

Table 3.3. Overview of data from this study.

	Intertidal	Subtidal
Maximum observed length		
<i>C. edule</i>	43 mm	41 mm
<i>M. arenaria</i>	108 mm	100 mm
Max. observed somatic mass		
<i>C. edule</i>	700 mg AFDM	100 mg AFDM
<i>M. arenaria</i>	6000 mg AFDM	4800 mg AFDM
Max. observed gonadal mass		
<i>C. edule</i>	60 mg AFDM	20 mg AFDM
<i>M. arenaria</i>	2000 mg AFDM	1300 mg AFDM
Individual reproductive investment		
<i>C. edule</i>	15%	10%
<i>M. arenaria</i>	20%	13%
Timing of spawning		
<i>C. edule</i>	May	May
<i>M. arenaria</i>	August	May

Discussion

Age determination

Age determination in *C. edule* and *M. arenaria* was done by counting the external shell marks. Growth marks on shells are usually related to cessation of growth during winter months, due to low food availability and low temperatures. In Dutch waters, growth of bivalves stops during winter and they usually lose weight in autumn/winter (Lammens 1967, Pieters et al. 1979, Beukema et al. 1985, Zwarts 1991, Honkoop and Beukema 1997). In the present study, this seasonal pattern in growth was confirmed by the decrease in somatic mass during winter and the increase in shell length and somatic mass during the spring/summer. Therefore, a clear winter mark on the shell surface can be expected. However, sudden changes in temperature or food conditions, spawning, and other stressing factors may also lead to a temporary cessation of growth and the formation of disturbance marks. Such marks are not always visually distinguishable from real growth marks and can be mistaken for year rings, leading to errors in age determination. This will mainly occur in older individuals, in which the last growth marks are very close to each other and difficult to visualize. An overestimation of age will result in an underestimation of the growth rate. Nevertheless, examples from the literature show that in these two species, the use of external shell marks to determine age does

not cause a large error and is mostly correct (Newcombe 1936, Seed and Brown 1978, Brousseau 1979, MacDonald and Thomas 1980, Brêthes and Desrosiers 1981, Brousseau and Baglivo 1987, Iglesias and Navarro 1990, Roseberry et al. 1991, Maximovich and Guerassimova 2003). However, Van Moorsel (2003) found that reading internal shell rings in *M. arenaria* yielded better results. But he analyzed only 6 clams.

A comparison of the age data of *M. arenaria* from this study with data from the 1991 cohort (Dekker unpubl. data), which was a year with strong recruitment, and data of Philipp et al. (2005) for the same subtidal location, illustrates the large variability in the estimated size-at-age in *M. arenaria* (Fig. 3.6).

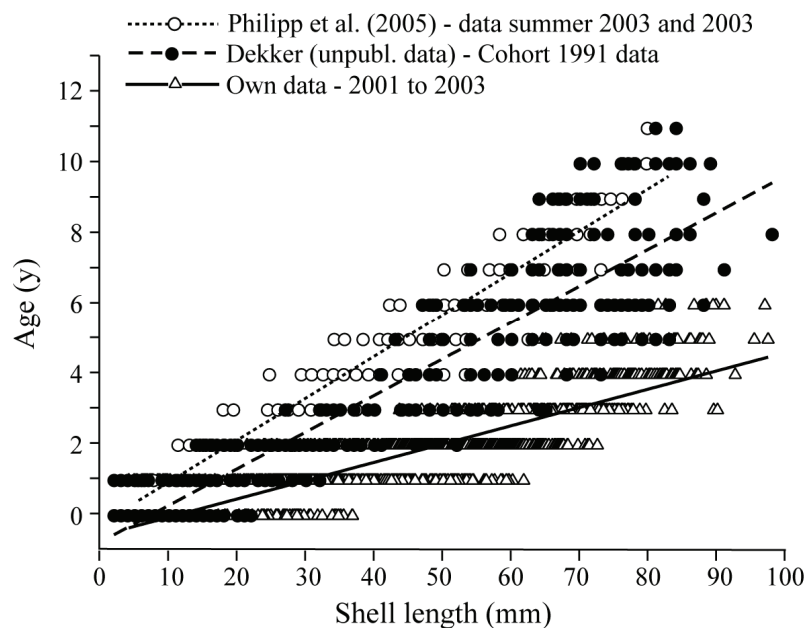


Fig. 3.6. Shell length (mm) – age (y) relationship for subtidal *M. arenaria* resulting from different methods of age determination. ●: data of Dekker (unpubl. data; 1991 cohort); Δ: own data (2001-2003); ○: data from Philipp et al. (2005; summer 2002 and 2003).

In relation to the 1991 cohort data, age estimated in the present study seems to be underestimated, especially in older individuals, while age determined by Philipp et al. (2005) seems to be overestimated. Although Philipp et al. (2005) validated the growth rings in the umbo with isotope analysis, this was done in only 4 individuals. It should also be kept in mind that variability between datasets can be due to the time difference. However, for the first years of life the differences are relatively small. The large difference in age determination between different methods points out to the necessity of validating age determination in *M. arenaria* for different areas.

Growth

In both species, 0-group individuals were found in intertidal and subtidal areas. This means that recruitment of *M. arenaria* and *C. edule* occurs in both areas as observed by Dekker et al. (2003) and Dekker and Waasdorp (2004, 2005, 2006). The reported maximum age of *C. edule* varies along the European coast: 7 years old in northern Spain (Iglesias and Navarro 1990), 6 in the Dutch Wadden Sea (Dekker et al. 2003), 9 in Wales (Jones 1979) and 10 in Ireland (Seed and Brown 1978). In *M. arenaria*, maximum observed age in the southern Baltic Sea and East American coast was 13 years (Brousseau 1979, Kube 1996), in Canada 28 years (MacDonald and Thomas 1980) and in the White Sea 17 years (Maximovich and Guerassimova 2003). In the present study, the oldest *M. arenaria* was 7 years old and the oldest *C. edule* was 5. However, only two locations were sampled during a little bit more than a year. For an overview of the population dynamics of these species in the western Wadden Sea, more locations should be sampled over a longer time period. In addition, age determination in *M. arenaria* is preliminary until age has been studied in more detail and validated (see above).

Within each habitat, differences in growth between species could be due to competition for food or differences in predation pressure. Competition for food is likely to occur between bivalve species living in the same area (Kamermans 1994). *C. edule* and *M. arenaria* are both suspension-feeding species and therefore they compete for the same food source. Density-dependent regulation of growth rates, by local depletion of phytoplankton, has been observed in populations of suspension-feeding bivalves (Peterson 1982, Olafsson 1986, Vincent et al. 1989, Jensen 1992, Peterson and Black 1993, De Montaudouin and Bachelet 1996). However, body condition and growth of *C. edule* was seen to be independent of density (Kamermans et al. 1992, De Montaudouin 1996), except when high densities occur over areas of several km² (Jensen 1992). Intraspecific competition in 10 mm *C. edule* seems to occur only at densities above 2000 individual m⁻² (Jensen 1992, 1993), which are much higher densities than observed in the present study. In *M. arenaria*, significant negative effects of increasing clam density on growth were observed in individuals between 9 and 12 mm, especially at densities above 1000 individual m⁻² (Beal and Kraus 2002). Since densities of both species were similar during the study period, an effect of density on growth of *C. edule* and *M. arenaria* does not seem likely to have occurred.

The fact that *M. arenaria* lives deeply buried in the sediment while *C. edule* lives just under the sediment surface, suggest that differences in predation pressure may occur between species. Two different types of predation are possible: predation on complete individuals, resulting in direct mortality, and predation on regenerating body parts such as siphon and foot tips, which affects food intake and condition. Predation on complete individuals occurs by birds (Fréchette and Bourget 1985, Wanink and Zwarts 1993, Zwarts et al. 1996), shrimps *Crangon crangon*, crabs *Carcinus maenas* and fish species (Seed and Brown 1978, De Vlas 1979, Phil and Rosenberg 1982, Möller and Røsenberg 1983, Kube 1996, Van der Veer et al.

1998, Mackenzie and McLaughlin 2000, Mascaró and Seed 2000, Beukema and Dekker 2005). Various fish species, shrimps and crabs are also responsible for predation on regenerating body parts (De Vlas 1979). It is possible that by burying shallower, *C. edule* is more susceptible to predation.

Timing of spawning and reproductive investment

Seasonal patterns in somatic and gonadal mass indices, as well as in gonadosomatic ratio, were used to determine the timing of spawning and the reproductive investment of each species. As observed in other intertidal areas of the Wadden Sea (Zwarts 1991, Honkoop and Beukema 1997), body mass indices increased from early spring to mid summer and decreased in winter. Somatic growth started in early spring in both species, corresponding with the annual April/ May peak in chlorophyll-*a* in the water (Cadée and Hegeman 2002). At this time of the year, the amount of chlorophyll-*a* (from benthic and pelagic algae) in the stomachs of bivalves was also high (Kamermans, 1994). The increase in gonadal mass started in the beginning of the year suggesting that gametogenesis takes place during the beginning of the growing season, as observed in other areas (Newell and Bayne 1980, Rosenblum and Niesen 1985, Iglesias and Navarro 1991). Gonadal mass index showed a stronger pattern in *C. edule* than in *M. arenaria*. In the intertidal, timing of spawning was earlier in *C. edule* (around May) than in *M. arenaria* (around August). In the subtidal, both species spawned in the same period (around May). In a nearby intertidal area, *C. edule* was also seen to spawn in May/June (Honkoop and Van der Meer 1998). Spawning in late spring (around May) has the advantage that temperatures and algal concentration in the water are relatively high and, therefore, larval growth can be fast. The fact that gonadal mass index in *M. arenaria* increases with age also indicates that large animals, suffering lower predation, are able to invest more energy in reproduction.

GSR was higher in *M. arenaria* than in *C. edule*, both in the intertidal and subtidal. Despite the similarities in egg size between the two species, within the same habitat conditions *M. arenaria* invests more energy in reproduction than *C. edule*. During the peak in gonadosomatic ratio, *M. arenaria* showed a maximum of about 20% of gonadal mass in relation to the total body mass in contrast to *C. edule* with a maximum of about 15%. Although intertidal *M. arenaria* spawns in late summer, this does not seem to affect its reproductive output. However, in contrast to *M. arenaria*, most *C. edule* spawned completely during the spawning season. In terms of individual reproductive output, *C. edule* seems to be more successful than *M. arenaria*, since all the energy put in gonadal mass is released in the form of gametes. Nevertheless, the absolute amount of gonadal mass produced by individual is more than 30 times higher in *M. arenaria* than in *C. edule*. If densities of both species are similar, then the amount of gametes released by the *M. arenaria* population, both in the intertidal and subtidal, must be higher than the amount released by the *C. edule* population.

Long-term trends in recruit density in the western Dutch Wadden Sea show that densities of *C. edule* are, most of the years, larger than those of *M. arenaria* (Beukema et al. 2001, Dekker et al. 2003, Dekker and Waasdorp 2004, Beukema and Dekker 2005). Since absolute reproductive investment is higher in *M. arenaria* than in *C. edule*, differences in recruitment success between species cannot be caused by differences in reproductive output. Due to the similarity in egg size between species, characteristics of the larvae (such as size and pelagic stage duration) are also thought to be similar. Therefore, differences in post-larval processes (such as differential predation pressure in early life stages) are more likely to be the reason for the observed differences in recruitment between *C. edule* and *M. arenaria*.

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