Reprinted from
CYCLIC PHENOMENA IN
MARINE PLANTS AND ANIMALS
Edited by
E. NAYLOR and R. G. HARTNOLL
PERGAMON PRESS OXFORD and NEW YORK 1979

Comparison of Events in the Seasonal Cycle for Donax vittatus and D. trunculus in European Waters

Alan D. Ansell * and A. Bodoy * *

* Dunstaffnage Marine Research Laboratory, P.O. Box No. 3, Oban, Scotland
* * Station Marine d'Endoume, Marseille 13007, France

ABSTRACT

The events of the seasonal cycle for D. vittatus from the Firth of Forth, Scotland, and D. trunculus from the Camargue coast, France, are described with relation to population structure, rate of shell growth, reproductive activities and seasonal changes in tissue weight and biochemical composition. The Mediterranean species shows a longer reproductive period, and an extended growing season, accompanied by smaller seasonal fluctuations in rates of change of tissue weight reflecting a reduced dependence on reserve storage in the seasonal cycle. The role of temperature and food supply in the cycles are discussed.

INTRODUCTION

The results described here form a part of continuing studies of the effects of temperature on the biology of molluscs from sandy sediments of the European Mediterranean and Atlantic coasts. These studies comprise determinations of the extreme upper limits of thermal tolerance, and of the upper temperature limits at which normal activities, such as the burrowing response, are retained; and the evaluation of effects of variation in temperature below these limits on aspects of reproduction, biology and energetics of common species of bivalves and gastropods. They are based on collaborative comparative investigations of the same or closely related species from the Mediterranean coast, near Marseille, and from the Scottish coast, made on the one hand at the Station Marine d'Endoume, Marseille, and on the other, at the Dunstaffnage Marine Research Laboratory, Oban, using as far as possible, comparable methods. The aim is to determine how far conclusions based on local studies can be applied to other localities on the European coastline in assessing potential effects of changes in environmental temperature which may result from such man-made disturbance as the discharge of cooling waters from electricity generating stations.

As part of this general study we are following the normal seasonal cycle of reproduction and growth, and associated biochemical changes, in a number of bivalves from beaches near Marseille, France, and in the Forth and Clyde estuaries, Scotland, in order to assess the temperature range within which the events of these seasonal cycles take place at points near the geographical and environmental extremes found in European waters. This paper reports preliminary results for two of these; Donax vittatus (da Costa), from the Forth Estuary, and D. trunculus (L.) from the Camargue coast.

DISTRIBUTION

The two species being studied are the commonest of the five representatives of the genus Donax found in European seas. D. vittatus belongs to the Mediterranean-Boreal element of the European fauna and has a distribution extending from the North African coast to the coast of Norway; D. trunculus is an Atlantic-Mediterranean warm-temperate species whose range extends through the Mediterranean and Black Seas, and from North Africa to the northern Atlantic coast of France. D. vittatus is only sparsely distributed in the southern part of its range and geographically the two species may be seen as complementary, with D. trunculus abundant in warm southern waters and D. vittatus abundant in cooler northern waters, although where their geographical ranges overlap, along the French Atlantic coast, both may occur with equal abundance. In northern waters, the distribution of D. vittatus extends into the lower part of the intertidal, although the greatest abundance is in the shallow sublittoral (1); in the tideless Mediterranean, D. trunculus is distributed in a narrow zone in shallow water (2.3). On the Atlantic coast of France, where both species are found together, D. trunculus is found in the intertidal, while D. vittatus is mainly confined to an area between low water and 5-6m depth with only the fringes of the population emerging on the lower shore or extending to greater depths (2).

MATERIALS AND METHODS

D. vittatus were collected from near low water at spring tides, from the beach at Gullane on the south shore of the Firth of Forth, Scotland, and returned living to the laboratory. The age of individuals was determined by counts of annual growth checks on the shell, and samples were taken from each age group for determination of the relationships between length and total weight, shell weight and wet and dry tissue weights, and for biochemical analysis. The methods used in these analyses wer the ame as those employed in a previous study of this species in the Firth of Cl ( ). The rate of shell growth was determined by plotting shell length against the length of the last-formed annual ring for each individual for each sampling date, and from the resulting relationship for each age group calculating the length at successive sampling dates for animals of different initial sizes.

D. trunculus were collected from a population at They de la Gracieuse on the Camargue coast of southern France, by means of a "Telliniere"; a sort of small hand dredge (3). This method is convenient for use in shallow water, but is selective in that the smallest size groups (<3mm) are not effectively sampled. It was not possible to separate the D. trunculus from this population into age groups using shell marks, and instead the size distribution of animals in the sample was determined at each sampling date to define the main modal groups present. The size frequency data was analysed using the method of Cassie (4), to provide information on growth rates of the main cohorts within the population. Analysis of shell and tissue weights were carried out for each of the major cohorts using the same methods as for D. vittatus and biochemical analyses of the tissues of two of the major groups present were also made.

ENVIRONMENTAL CONDITIONS

Temperature and Salinity

The seasonal fluctuations in mean temperature at the two sites are summarised in Fig. 1A, which also includes an indication of the range of seasonal temperature experienced in European waters between North Africa and Scotland. Seasonal temperatures along the French Mediterranean lie near the maximum for European coasts although the temperatures along the N. African coast of the Mediterranean are on average some 4°C greater throughout the year. Salinity fluctuations have not

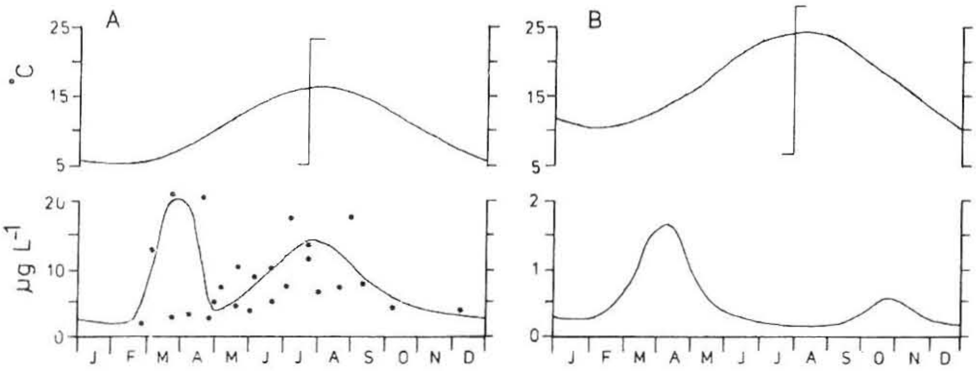

Fig. 1. Generalised mean temperature and chlorophyll a curves for A: Gullane, Firth of Forth, Scotland and B: the Mediterranean coast of France.

been studied in detail at either site: although both are affected by proximity to major estuaries (Gullane by the R. Forth, the Camargue by the R. Rhone), both are sufficiently far from the main discharge to show relatively minor effects of reduced salinity. The two sites lie, however, in areas of different mean salinity; about 32°/oo at Gullane, and about 37°/oo in the Mediterranean.

Phytoplankton Abundance

The seasonal pattern of phytoplankton abundance, as indicated by chlorophyll a concentrations, follows a normal pattern for Scottish inshore waters (Fig. 1A). High levels during the spring bloom are followed by a decline to relatively low levels in May/June followed by a gradual rise to a second peak during the late summer and autumn. Peak chlorophyll a values range up to 20 ug/l. Similar figures are not available for They de la Gracieuse, but published data for nearby waters give an indication of the general fluctuation in chlorophyll a in this region. They indicate that the form of the seasonal cycle is similar to that at Gullane, but that, a) the general level of abundance of phytoplankton is lower with peak values of chlorophyll a rarely exceeding 2 ug/l, and b) the second seasonal peak occurs later, in October/November (5).

POPULATION STRUCTURE AND RATE OF SHELL GROWTH

The population structure of the two populations during 1977 are shown in Fig. 2, which shows the mean size at each sampling date for each of the major cohorts present in each population. In the population of D. vittatus at Gullane, four main cohorts were present during the early months of 1977. Each of these was shown by analysis of the shell growth checks to consist of a single year's settlement, so that the population in early 1977 consisted of cohorts derived from settlements in 1976, 1975, 1974 and 1973. The smallest individuals were derived from the 1977 settlement, and showed a phenomenon not clearly seen in the older individuals; the separation of settlement into two separate modes deriving from

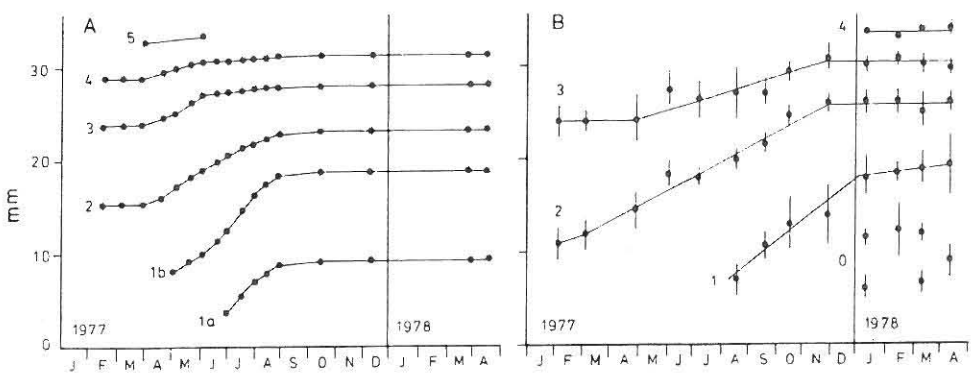

Fig. 2. The population structure for, A: D. vittatus, at Gullane, Firth of Forth and B: D. trunculus, at They de la Gracieuse, expressed as the mean shell length for each of the major cohorts present.

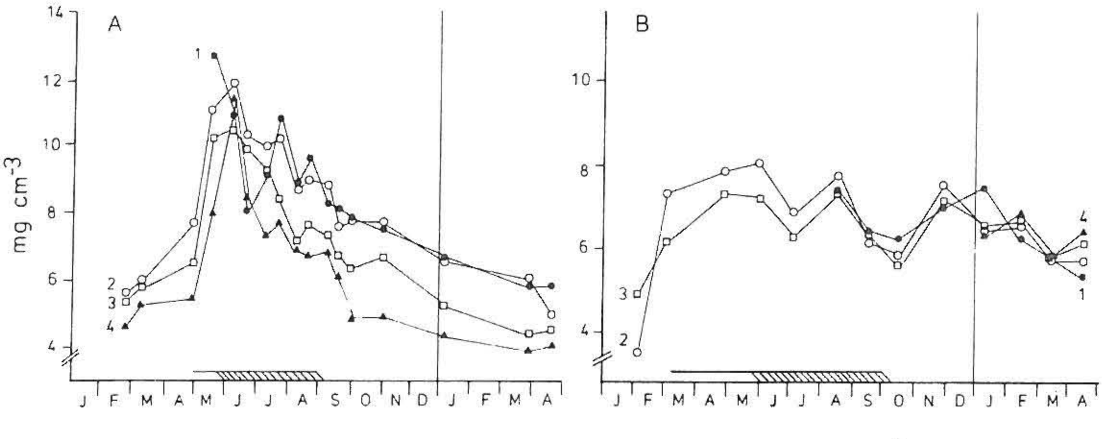

Fig. 3. Changes in condition index (mg dry tissue/cm^3) for, A: D. vittatus, at Gullane, Firth of Forth and B: D. trunculus at They de la Gracieuse.

early and late peaks of spawning within the general reproductive period.

A similar separation of settlement into separate modes within the same year is apparent in the population of D. trunculus on the Camargue coast. In early 1977, the population of D. trunculus consisted mainly of animals derived from the settlements of 1976 and 1975. The major groups which subsequently appeared in the samples, however, derived from successive peaks of settlement during 1977, with the highest intensity of settlement apparently taking place fairly early (June ?) and giving rise to the well characterised cohort which first appeared in the samples in August.

Figure 2 also illustrates the seasonal pattern of growth of the shell in the two populations. At Gullane, for D. vittatus, there was a period of cessation of shell growth between October and March; growth restarted in April and the maximum rates of growth occurred in June and July. The general pattern of shell growth was similar for all the cohorts. For D. trunculus, on the Camargue coast, the pattern was less clear because in this case, the only method available for growth measurement, (the interpretation of shell length/frequency distributions by the method of Cassie (4)), does not provide such precise information on shell growth increments as does the measurement of increments based on clearly visible shell growth checks. If the curves obtained are smoothed, the results suggest that there was only a short period of cessation of shell growth, during the period January - March, with maximum growth occurring during April/May. There is a suggestion in the unsmoothed curves, however, that in addition to the winter cessation of growth there may be a period of reduction of shell growth during the summer months. In both species the relationship between shell increment and temperature is different during the early months of growth when temperatures are rising, from that found later in the season when temperatures are higher, or falling. This phenomenon is a general one for bivalves from boreal and temperate waters and reflects the decrease in food available during the warmer months when, however, metabolic demand is increased as a result of higher temperatures and reproductive activity.

SEASONAL CHANGES IN TISSUE WEIGHT

The seasonal changes in tissue weight, expressed as a condition index (mg tissue/ cm^3), for the two populations are shown in Fig. 3. These changes in tissue weight reflect two cycles taking place in the individual animals and largely synchronised throughout the population, namely, the reproductive cycle and the related cycle of storage and utilisation of reserves.

The reproductive cycle for D. vittatus showed a period of inactivity between October and April during which the sexes were not distinguishable macroscopically. Rapid development and proliferation of the gonad accompanied the increase in tissue weight in April/May, and the gonad remained mature until August-September. During this period the gonad represented 35-40% of the total tissue weight, although the total tissue weight fluctuated as a result of successive periods of spawning and partial recovery. Beyond August the gonad did not recover following spawning and was gradually resorbed. The storage cycle consisted of a period of net increase in reserves during the summer, with maximum values occurring in September/October, followed by a period of net utilisation of reserves during the winter months, resulting in minimal values of both reserves and overall tissue weight during March.

For D. trunculus the condition index showed three successive maxima; in April/May, August and November/December. The first two represented successive peaks of gonadal development each followed by decrease as a result of spawning in the population; the third peak followed the end of the reproductive period and represented an increase in the level of stored reserves. In D. trunculus in this area the reproductive cycle showed only a short period of inactivity from October to January. Proliferation and maturation of the gonad occurred between January and March/April. Within the reproductive period, which lasted from April to September, the tissue weight fluctuated, representing the net balance between spawning activity and recovery of the gonad, while at the end of this period the gonad was depleted without recovery during August/September. The storage cycle in

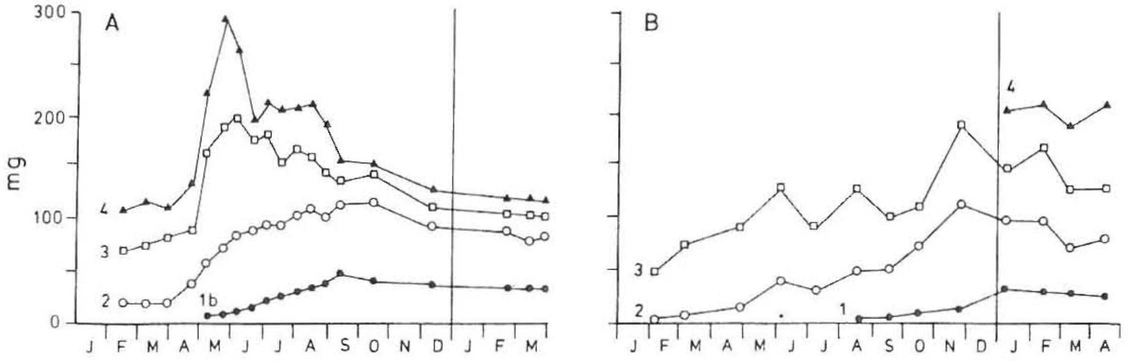

Fig. 4. Changes in dry tissue weight for each of the major cohorts present expressed as the weight corresponding to the mean shell length, for, A: D. vittatus at Gullane, Firth of Forth, and B: D. trunculus at They de la Gracieuse.

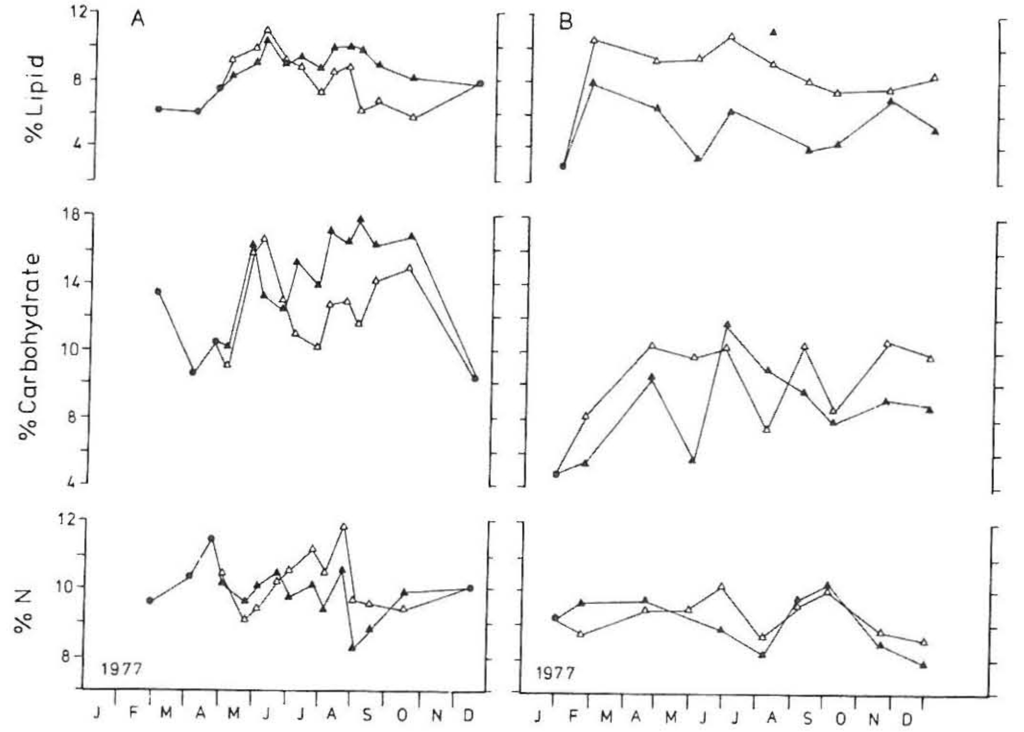

Fig. 5. Changes in percentage biochemical composition for, A: D. vittatus at Gullane, Firth of Forth, and B: D. trunculus at They de la Gracieuse. ▲ males; △ females; ● sex not determinable.

D. trunculus consisted of a net increase leading to maximum values in November/ December followed by decline during the winter months. In 1977, this resulted in minimal values in early February, and, in 1978, in a seasonal minimum in March.

Figure 4 shows the changes in dry tissue weight for an animal of the mean size for each main cohort throughout the year, combining growth in overall size and changes in condition. These changes in actual tissue weight for each cohort show most clearly a contrast between the features of the two cycles: in D. vittatus at Gullane the major increment in tissue weight took place in the period April-June, illustrating the importance of the spring phytoplankton bloom as a determining factor in the seasonal cycle; in D. trunculus at They de la Gracieuse, there was a much smaller increase during the period April-June following the spring bloom, while a second period of tissue growth in October-November coincided with the later autumn increase in phytoplankton abundance.

CHANGES IN BIOCHEMICAL COMPOSITION

In D. vittatus at Gullane there was a clear pattern of seasonal change in composition related to the reproductive and storage cycles. Fig. 5A illustrates this pattern using data for the 1974 settlement (a more detailed account of age dependent changes will be given elsewhere). The spring increase in overall tissue weight was accompanied by an increase in % carbohydrate and lipid indicating that these constituents increased relative to the protein content. Spawning (in June) resulted in a relatively greater decrease in carbohydrate and lipid than in protein and the percentage of these therefore fell. During this early period of the cycle the % lipid and carbohydrate of the females was greater than for the males, but following the spawning in June the males showed relatively higher values of carbohydrate and lipid than the females. Between June and October the percentage carbohydrate rose in both males and females, while the % lipid at first rose slightly, and then fell. The % protein (N) showed opposite changes. Finally, the % carbohydrate fell steadily during the period October to April. The changes in % carbohydrate through the summer largely reflect the increasing predominance of reserve storage resulting in maximum reserves in the autumn, followed by their utilization during the winter, while, especially in the female, the changes in lipid content reflect the reproductive cycle.

In D. trunculus from the Camargue, the extent of seasonal change in composition was less. Fig. 5B illustrates the changes found for the 26-30 mm size group in the population during 1977. % Carbohydrate rose between January and June and thereafter fluctuated, but otherwise there was relatively little consistent seasonal pattern.

DISCUSSION

The cycle of seasonal changes shown here for D. vittatus from the Firth of Forth on the east coast of Scotland is similar in essentials, and almost identical in timing, to that found earlier for this species in the Firth of Clyde, on the west coast, and similar cycles have been recorded for several other European boreal bivalves (see 6) . Major features of the cycle common to all, are the rapid increase in tissue weight during the spring; the accumulation of large reserves, particularly of glycogen; and the reliance on utilisation of these reserves during parts of the year when metabolic requirements can not be met by feeding. The availability of food must be regarded as a main factor determining the cycle, modified by the effect of, a) temperature, which sets limits to the rates at which the component processes take place, and b) the intrinsic controls of the reproductive cycle. The form of seasonal cycle shown by D. vittatus is typical of species where there is a limited reproductive period and where the major proliferation of the gonad coincides with the spring increase in tissue weight resulting in a seasonal peak of tissue weight immediately before spawning. In such species, during the reproductive period there is a dynamic balance between tissue growth and reproductive processes which, in D. vittatus, results in the mean gonad size remaining as a more or less constant proportion of the total tissue weight during the reproductive period, while the maximum levels of metabolic reserves, especially of glycogen, are found following the reproductive period.

The seasonal cycle in species from the Mediterranean Sea have been less extensively studied. The cycle for D. trunculus at They de la Gracieuse resembles that of D. vittatus in showing a limited reproductive period although in this case the inactive period is relatively short; the major proliferation of the gonad coincides, as in D. vittatus, with the spring increase in tissue weight. The cycle is similar in all essentials to that found by Moueza (7), for D. trunculus on the Algerian coast, except that in the latter, the tissue weight fell consistently to a lower level during the winter months than was the case here.

In terms of organic production, D. trunculus from the Mediterranean differs from D. vittatus from Scottish water in showing much lower seasonal fluctuations both in rates of net gain of tissue and net loss, although overall annual production is greater as a result of the extended growing season. The dampening of seasonal fluctuations in tissue weight in the southern species is also associated with generally lower levels of carbohydrate reserves, and both these differences from northern boreal species may apparently be related to the generally lower levels of phytoplankton in Mediterranean waters. These studies are continuing and it would be of great interest to extend comparisons in those areas of the Atlantic coast where the ranges of the two species overlap.

ACKNOWLEDGEMENTS

This work was carried out under Contracts No. 225-77-1-ENV. U.K. and 221-77-1-Env. F. of the 2nd Environmental Research Programme of the Commission of the European Committees.

REFERENCES

Ansell, A.D. Distribution, rate of growth and seasonal biochemical cycle of the bivalve Donax vittatus from Kames Bay, Millport. J. exp. mar. Biol. Ecol., 10, 137-150 (1972).

Lagardère, F. Les fonds de pêche de la côte ouest de l'Ile d'Oleron-Cartographie bionomique. II - Remarques systematiques, biologiques et écologiques. Tethys, 3, 265-281 (1972).

Bodoy, A. Etude de l'influence de la temperature, liee a pollution thermique sur la survie et la biologie de quelques Mollusques des substats meubles. These Doct. Specialite, Univ. Aux-Marseille II (1976).

Cassie, R.M. Some use of probability paper in the analysis of size-frequency distribution. Aust. J. Freshwater Res., 5, 513-522 (1954).

Travers, A. and M. Travers. Recherches sur le phytoplancton du Golfe de Marseille. Recl. Trav. Stn mar. Endoume, 26 (41), 7-139 (1962).

Beukema, J.J. and W. de Bruin. Seasonal changes in dry weight and chemical composition of the soft parts of the tellinid bivalve Macoma balthica in the Dutch Wadden Sea. Neth. J. Sea. Res., 11, 42-55 (1977).

Moueza, M. Contribution a l'étude de la biologie de Donax trunculus L. Mollusque Lamellibranche dans l'Algerois. These Doct. es Sciences Nat., Univ. Aix-Marseille.