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# **Determination and Comparison of Bivalve Growth, with Emphasis on Thailand and Other Tropical Areas**

**J.M. Vakily**

**ICLARM**

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1992



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## FOREWORD

Over the last decade, ICLARM has devoted considerable attention to bivalves, an important source of animal protein in tropical developing countries.

There appears to be, moreover, a large potential for increased production from bivalve culture - if certain stumbling blocks, especially concerning health concerns and marketing, can be resolved through research on appropriate farming systems.

Such research will have to rely on broad-based knowledge of the biological performance of various candidate species. This report, based on a doctoral thesis which I supervised, and which was submitted in mid-1991 at the Institut für Meereskunde, Universität Kiel, Germany, presents elements for such broad-based knowledge on the growth performance of bivalves.

As the reader will notice, this work consists both of a localized, very detailed study of growth in two species, based on field work conducted by Dr. Vakily in the inner Gulf of Thailand, and generalizations based on a comparative study of the growth performance of 77 species and 190 populations of bivalve scattered throughout the world, for many of which he estimated the first sets of growth parameters.

The reason for the two "axes" in this work is that it represents a test of a general theory of growth in bivalves which required both "depth", and application to a large number of cases.

As the reader will notice, this theory passed the test, enabling a number of valuable inferences to be made on the growth performance of little studied species of tropical and other bivalves.

Dr. Vakily is to be congratulated for completing a study of this scope.

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Capture Fisheries Management  
Program

International Center for Living

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Manila, June 1992

## ABSTRACT

An analysis of shell microstructure of *A. granosa* and *P. viridis* experimentally cultured in coastal waters of Thailand revealed that the formation of growth lines was closely related to tidal periodicity. It is concluded that growth lines are formed when the bivalves react with shell closure to reduced water flow, the degree of sensitivity being species-specific. The application of the methodology to tropical bivalves seems, however, not recommendable, given the rather demanding preparative work and the large degree of uncertainty involved in the interpretation of observed growth lines.

Fitting of growth data from the culture experiments to the von Bertalanffy growth function (VBGF) showed large variations of the single growth parameters, but little variance in the resulting growth index,  $\phi'$ , supporting the perception of  $\phi'$  being a species-specific parameter. This concept was further investigated by computing the index  $\phi'$  from growth parameters of 190 bivalve stocks compiled or computed from the literature. It was shown that  $\phi'$  is usually narrowly distributed around a species-specific mean. Use of  $\phi'$  for growth comparison between different genera is generally limited because of the different shell shape, which strongly influences  $\phi'$ . However, mytilids with their relative uniform shell shape displayed a linear increase of  $\phi'$  with environmental water temperature, suggesting that bivalves tend to grow larger in warm waters. This is in contrast to general observations in fish, and is explained by the difference in energy demand for the precipitation of calcium carbonate from seawater.

## CHAPTER 1

### INTRODUCTION

Throughout the world, bivalves play an important role in the national economy of many countries, be it in the form of a highly developed industry or as a cheap source of protein to the many in need of it. The management of bivalve resources and the development of culture practices has reached a level in the industrialized countries that undoubtedly matches other sectors involved in the exploitation of marine resources.

In many of the developing countries, however, bivalve resources are often underutilized, poorly managed and beset with problems arising from inappropriate culture methods. Frequently, national fisheries extension services lack the personnel familiar with the special requirements of bivalve management. Thus, it is often left to the single fisher or farm operator to find new and better methods to improve the exploitation of this resource. There is, however, little incentive for major innovations, given the high financial risks. This is even more a problem, as exploitation of bivalve resources in developing countries is mostly done on the subsistence level.

There are, of course, many research activities in developing countries, too, dealing with the biology, culturing and marketing of bivalves. The sector as a whole, though, seems to remain stagnant, to say the least. This is most unfortunate, as the exploitation of bivalve resources is usually not the only form of activity in coastal areas. In a general coastal resource management scheme, it has to stand up against strong competitors, which more often than not are given higher priority under national development programs. These competitors - e.g., development of industries in coastal areas, tourism, culture of high-priced, export oriented commodities such as shrimp - have their own specific requirements which in many cases will preclude a peaceful coexistence with other forms of utilization of coastal resources.

It is the objective of this study to investigate on the one hand the potential use of shell microstructure analysis in tropical bivalve research, which so far has only been applied systematically in research to the growth of bivalves at higher latitudes. On the other hand, it will be attempted to evaluate generally the applicability of standard growth models used in fisheries science to bivalve growth. Based on the results of culture experiments in Thailand and a large set of growth parameters compiled from the literature, means and limitations in the use of a growth index for the comparison of bivalve growth will be examined. This is to demonstrate that researchers investigating the growth of bivalves should consider such a comparison essential, as it allows them to (i) verify the results of their own research, and (ii) to assess the growth performance of cultured or wild stocks of bivalves in relation to what is generally known of the species concerned.

## CHAPTER 2

### THE ROLE OF BIVALVES AS FISHERIES RESOURCE

#### Worldwide

In the estimated total catch of  $92.7 \text{ t} \cdot 10^6$  from marine and inland fisheries worldwide in 1987, molluscs form the second most important group with  $7.5 \text{ t} \cdot 10^6$ . (These and all following statistics are based on FAO 1989, if not mentioned otherwise.) The majority of these molluscs ( $7.3 \text{ t} \cdot 10^6$ ) is of marine origin, while only a very small portion (3.6%) is produced by inland fisheries (see Table 2.1).

Out of the total catch of marine molluscs, 65.4% are bivalves. Clams are leading with  $2.1 \text{ t} \cdot 10^6$ , followed by oysters with slightly more than  $1 \text{ t} \cdot 10^6$  and mussels with  $0.9 \text{ t} \cdot 10^6$  (Table 2.2). In relation to the total fishery production worldwide, bivalves make up approximately 5% of the total catch.

Clams are almost exclusively supplied by coastal fisheries. In the USA and Canada, they include commercially important species such as *Arctica islandica* ( $188 \text{ t} \cdot 10^3$ ), *Spisula solidissima* ( $158 \text{ t} \cdot 10^3$ ) and *Mercenaria mercenaria* ( $35 \text{ t} \cdot 10^3$ ). Great Britain has an important fishery for *Cardium edule* ( $39 \text{ t} \cdot 10^3$ ). In the Mediterranean area, it is especially *Venus gallinea* ( $42 \text{ t} \cdot 10^3$ ) that supports a sustained bivalve fishery. In Asia, clam fishery has been notably successful in China,

	Marine (t)	Inland (t)	Total (t)
Finfish	69,207,000	11,630,100	80,837,100
Molluscs	7,251,700	272,400	7,524,100
Crustacea	3,692,300	283,000	3,975,300
Miscellaneous	350,100	6,800	356,900
Total	80,501,100	12,192,300	92,693,400

	Catch (t)	Share of total (%)
Oysters	1,029,851	14.20
Mussels	900,645	12.42
Scallops	692,823	9.55
Clams	2,117,597	29.20
Squids	2,265,870	31.25
Miscellaneous	244,914	3.38
Total	7,251,700	

Japan and Korea. The Chinese clam fishery reported a total production of  $885 \text{ t} \cdot 10^3$  in 1987. In the other two countries, major targets are the Japanese clam *Venerupis japonica* (= *V. semidecussata*) with  $179 \text{ t} \cdot 10^3$  and various ark clams ( $60 \text{ t} \cdot 10^3$ ). Further south, *Anadara* spp. plays an important role in Malaysia ( $46 \text{ t} \cdot 10^3$ ), Indonesia ( $35 \text{ t} \cdot 10^3$ ) and Thailand ( $12 \text{ t} \cdot 10^3$ ).

Scallops are also landed to a great deal by coastal fisheries, particularly in the North Atlantic, where *Placopecten magellanicus*, *Argopecten gibbus* and *Chlamys* spp. account for  $304 \text{ t} \cdot 10^3$ , or 44% of the total catch of scallops worldwide.

On the other hand there is the extremely highly developed scallop industry on the north of

Japan, which produced in 1987 almost 300 t·10<sup>3</sup> of *Patinopecten yessoensis*, which by itself represents another 43% of the world's total scallop catch. The enormous increase in production from 5 t·10<sup>3</sup> in 1969 to the present level is based on an efficient system of spat collection, intermediate culture, and on-growing either in hanging culture or bottom culture (Ventilla 1982).

In contrast to clams and scallops, the production of oysters and mussels depends almost entirely on coastal culture activities. Again Japan and Korea maintain a leading position with more than 50% of the total oyster production of 1 t·10<sup>6</sup> worldwide in 1987. The culture is mainly based on *Crassostrea gigas*, a species that also has replaced to a large extent the native flat oyster in the European oyster culture (Jones 1987). In 1987, 123 t·10<sup>3</sup> of this species were produced in France, while the production of *Ostrea edulis* in Europe had fallen back to around 7 t·10<sup>3</sup>. *C. gigas* has also been successfully introduced along the Pacific coast of the USA and Canada (40 t·10<sup>3</sup>), but plays still a minor role compared to the American oyster (*Crassostrea virginica*) raised on the Atlantic coast from Canada to Mexico with an annual production of 230 t·10<sup>3</sup> in 1987.

The group of mussels cultured worldwide comprises primarily two genera: *Mytilus* and *Perna*. In Europe, the culture of *Mytilus edulis* and its Mediterranean relative *M. galloprovincialis* has yielded in 1987 a total production of together 590 t·10<sup>3</sup>, or 66% of the world's total mussel production. Major producer countries are Spain, France and the Netherlands. Outside Europe, there is a well-established mussel industry in China, involving the culture of *M. edulis*, *M. crassitesta* and *Perna viridis* (Nie 1982). Operation started in the late 1950s and had reached a level of 152 t·10<sup>3</sup> in 1987. *M. crassitesta* is also cultured in Korea (30 t·10<sup>3</sup>). Among the *Perna* species, *P. viridis* plays an important role in Thailand (25 t·10<sup>3</sup>) and the Philippines (13 t·10<sup>3</sup>), while *P. canaliculus* supports a steadily increasing mussel industry in New Zealand, which had reached an annual production of 17 t·10<sup>3</sup> by 1987.

### Thailand

Table 2.3 shows the distribution of the total reported catches in 1987 listed according to the major production areas and the part of the catch pertaining to bivalves. It demonstrates the dominant role of Asia both in the total landings and in the production of bivalves, with 54% of all bivalves coming from Asia. The second largest producers, the

Table 2.3. Total marine and inland catch (in t) of bivalves in 1987 by major areas, in comparison to the total fishery production. (Source: FAO 1989).

	All species	Bivalves		
	Total production (t)	Total catch (t)	Share of total production (%)	Share of total catch of bivalves (%)
North America	9,241,783	1,025,879	11.10	22.28
South America	11,996,389	111,398	0.93	2.42
Europe	12,599,649	912,265	7.24	19.81
Africa	5,224,042	1,607	0.03	0.03
USSR	11,159,617	7,454	0.07	0.16
Asia	41,676,856	2,498,617	6.00	4.25
Oceania	795,015	48,153	6.06	1.05
Total	92,603,351	4,605,373	4.97	

USA and Canada, harvest not even half this quantity, though the share of bivalves in the total national catches is proportionally much higher (11%) than in other areas. The statistics also clearly demonstrate the extreme underutilization of the bivalve resources in Africa, which contributes only 0.03% to the total bivalve catch recorded worldwide.

According to FAO (1989) statistics, Thailand's share of bivalves produced in Asia amounts to  $135 \text{ t} \cdot 10^3$  (5.4%), which is considerably high, given that the figures reported from China, Japan and Korea together constitute almost 90% of the total landings.

The major species cultured in Thailand are oysters (*Saccostrea commercialis* and *S. lugubris*), green mussels (*Perna viridis*) and the blood cockle (*Anadara granosa*). *Paphia undulata* is the subject of an intensive commercial fishery, which landed  $90 \text{ t} \cdot 10^3$  of this species in 1987 (FAO 1989).

*S. commercialis* is commonly farmed along the east coast in the Gulf of Thailand on concrete blocks, while *S. lugubris* is primarily found in the southern provinces of Thailand (Saraya 1982) where hanging culture of this species has successfully been tried (Brohmanonda et al. 1988). The annual production was 1,300 t in 1987 (FAO 1989).

Large-scale farming of *Perna viridis* is more or less confined to the upper part of the Gulf of Thailand, close to the major markets located in the Bangkok area (Chalermwat and Lutz 1989). All operation depends completely on natural spatfall. Green mussels are harvested either from bamboo fish traps or cultured on bamboo poles, respective date palm stakes, especially set out for this purpose in leased areas. It is probably this separation into "natural" and "aquaculture" production, which has caused the apparent drop in total landings in the FAO statistics since 1986. The present level of around  $25 \text{ t} \cdot 10^3$  does by no means reflect the true production of the Thai green mussel industry, which has remained even in 1986 at a relatively constant level of approximately  $60 \text{ t} \cdot 10^3 \cdot \text{year}^{-1}$  (Chalermwat and Lutz 1989). In contrast, the  $25 \text{ t} \cdot 10^3$  listed by FAO (1989) for 1987 come quite close to the annual production of the fish traps (cf. McCoy et al. 1988, Table 5). Though the culture of green mussels in Thailand does not pose much problems from a biological point of view, its economic situation is hardly satisfying, as production and processing are only marginally profitable (McCoy et al. 1988).

*Anadara granosa* is primarily found in the southern provinces of Thailand, as the whole operation depends to a large extent on seed supply from Malaysia. The restrictions on seed export imposed by the Malaysian government has resulted in the need for Thailand to import market-size cockles from Malaysia to meet the demand for this popular bivalve species (Hansopa et al. 1988). Production in 1987 was reported to be  $12 \text{ t} \cdot 10^3$  (FAO 1989).

The very important role that bivalve culture plays in Thailand was also expressed in a multidisciplinary research project on coastal aquaculture that was initiated in 1980 at request of the Department of Fisheries (DOF) and Technical and Economic Cooperation, Government of Thailand, and carried out with the assistance of the International Center for Living Aquatic Resources Management (ICLARM), Manila, Philippines. The German government arranged funding via ICLARM through the German Agency for Technical Cooperation (GTZ). The objective of this technical assistance project was to explore new biological and socioeconomic perspectives on bivalve mollusc culture to overcome identified constraints in the production and marketing of the major bivalve species in Thailand.

In the first phase, research concentrated on four areas:

- postharvest handling;
- pollution in mollusc production areas;
- shellfish economics and marketing; and
- shellfish culture and hatchery technology.

Research emphasis during the remainder of the five-year project was shifted to problems related to seed supply for the culture of *A. granosa* and the identification of new culture areas for this species. The project has not only produced a number of valuable research reports directly related to the project (McCoy and Chongpeepien 1988) but also initiated the publication of general reviews of the biology and culture of *Anadara* spp. (Broom 1985), tropical oysters (Angell 1986), and *Perna* spp. (Vakily 1989).

## CHAPTER 3

### REVIEW OF GROWTH STUDIES ON BIVALVES

The literature on growth of bivalves is so vast that no attempt is made here to present a general overview. The references listed in Appendix 3 might be taken as a representative, though not exhaustive, selection. One aspect, however, that merits some more detailed discussion is the relationship between environmental temperature and growth of bivalves, as this is also of primary concern in the context of this study.

It has been recognized that the effect of temperature on the physiological activities of bivalves is essential to understand better the mechanisms that govern growth in bivalves. Early studies investigated the activities of oysters (Galstoff 1928; Hopkins 1931), *Venus* (= *Mercenaria*) *mercenaria* (Loosanoff 1939) and *Mytilus edulis* (Loosanoff 1942) in dependence of temperature to determine the temperature range for optimum growth respective at what temperature "hibernation" (Loosanoff 1939) would begin. It was later shown, however, that even at the coldest weather, the mussels do not hibernate (Richards 1946). Other studies describing optimum temperature ranges were presented, e.g., for *Crassostrea virginica* (Shaw 1962), *Mercenaria mercenaria* (Ansell 1968), *Mytilus californianus* (Coe and Fox 1942, 1944) and *Tivela stultorum* (Coe 1948). A number of authors have stressed the point that there is not only a lower but also an upper temperature limit at which growth will be reduced (Coe and Fox 1942; Ansell 1968).

Relating observed growth increments directly to the prevailing environmental temperature has been attempted for a large number of different bivalve species, e.g., *Cerastoderma edule* (Richardson et al. 1980a), *Chlamys opercularis* (Richardson et al. 1982), *Geukensia demissa* (Borrero and Hilbish 1988), *Macoma balthica* (Green 1973), *Mercenaria mercenaria* (Pratt and Campbell 1956), *Mytilus californianus* (Coe and Fox 1942), *Mytilus edulis diegensis* (Coe 1945), *Ostrea edulis* (Walton 1958), *Ostrea puelchana* Fernandez Castro and Bodoy (1987) and *Tridacna gigas* (Lucas et al. 1989). Ansell et al. (1964) reported *Mercenaria mercenaria* exposed to the outfall waters of a power generating station to have growth rates almost double that of other individuals in nearby, yet not so exposed, sites. The general impression, however, from the majority of these studies is that they describe a general trend of temperature being related somehow to the growth of bivalves, without this trend being precise enough to allow its mathematical formulation. Broom and Mason (1978) showed that neither temperature nor phytoplankton standing crop by itself was significantly correlated with the growth rates of *Chlamys opercularis*, but that the relationship between growth rate and the product of temperature and standing crop was significant ( $P = 0.01$ ).

With an increasing number of publications becoming available presenting detailed data on the rate of growth of bivalves from an extended geographic range, various authors have attempted to investigate the relationship between temperature and growth of a species throughout the whole range of its distribution. In a very extensive compilation of growth data for *Mercenaria mercenaria*, Ansell (1968) showed that growth in the north of the range took place only during summer, while further south growth was continuous through the year. He found that growth rates were more closely related to temperature in

the north than in the south, but that in general considerable deviations from the temperature/growth rate relationship occurred. He concluded that other factors, such as food availability, must also play an important role in determining the rate of growth.

Similarly, Gilbert (1973) compared the growth of *Macoma balthica* under widely varying climatic conditions. Her results suggest that maximum size and growth rate decreases and longevity increases with increasing latitude and relatedly cooler temperatures and shorter growing seasons. She argued that the cold-adapted *Macoma balthica* may expend more energy on respiration and less on growth compared to warm-adapted individuals. In respect to maximum size, her findings contradict the view of bivalves from low latitudes attaining a smaller maximum size than do conspecifics from higher latitudes (Newell 1964). MacDonald and Thompson (1988) obtained inconclusive results concerning the relationship between asymptotic size and latitude for *Placopecten magellanicus*, but showed that populations of this species at deeper waters reached a smaller maximum size compared to inshore stocks (see also MacDonald and Thompson 1985). A similar pattern of decreasing maximum size with increasing depth was shown, e.g., for *Macoma balthica* (Segersstrale 1960) and *Patinopecten caurinus* (MacDonald and Bourne 1987). No such pattern was found in *Chlamys opercularis* which was grown in cages at different depths in the Clyde Sea area (Richardson et al. 1982), nor in natural populations of *Pecten maximus* from the North Sea (Gruffydd (1974).

Temperature-induced seasonal growth oscillations have always presented a problem when data covering less than a one-year period were used to compute the growth parameters of the von Bertalanffy growth formula (VBGF), which in its original form has no term to consider seasonality. After Boetius (1962) had shown that the oscillating growth curve of *Mytilus edulis* (2-40 mm in length) reverts to a straight line if the age of the animals is expressed in day-degrees after settlement, Ursin (1963) presented a modified version of the VBGF that incorporated this concept and, thus, eliminated to some extent the effect of temperature from the growth curve. Application of this model to the growth of *Mytilus edulis* may be found in Theisen (1968), Davies (1969) and Dare and Davies (1975). Later modifications to the VBGF, however, abandoned the direct incorporation of temperature into the formula in favor of a more general seasonality term to compensate for seasonal growth oscillations (see, e.g., Pauly and Gaschütz 1979).

## CHAPTER 4

# MICROGROWTH ANALYSIS OF BIVALVE SHELLS - APPLICATION AND RELEVANCE TO TROPICAL BIVALVE RESOURCES MANAGEMENT

### General Theory of Growth Pattern Formation in Bivalve Shells

#### *History*

In many bivalve species, conspicuous dark-colored bands are discernible on the outer surface of the shell. Forming distinct patterns, they expand circumferential from the umbo to the shell margin. First investigations exploring the nature of shell patterns are reported to date back as far as 1799 (Schenck 1934). Since the beginning of this century a substantial amount of research has been carried out on the use of external growth patterns in both biological and paleontological studies (Lutz and Rhoads 1980).

There is no doubt that a number of bivalve species display periodic external shell patterns that are of potential relevance in ecological studies (Lutz and Rhoads 1980). Their usefulness in growth studies, though, has frequently been questioned, because of the problems associated with the occurrence of spawning or other so-called "disturbance bands" on the external shell surface, which could not reliably be distinguished from shell marks formed in a regular annual pattern (Lutz 1976).

However, during the last two decades the identification of the causative agents of observed morphological features of the shell surface was substantially improved by complementary investigations of periodic patterns within the bivalve shell (Lutz and Rhoads 1980). The discovery of the existence of internal growth lines by Barker (1964) did not only prove useful in growth-related studies, but also found wide interdisciplinary applications, ranging from geophysical, ecological and paleoecological to even archeological studies (see Lutz and Rhoads (1980) for a representative selection of relevant references).

In the following, a summary of aspects will be presented concerning the formation and significance of (i) macrostructural growth patterns on the external surface of shells and (ii) microgrowth increments within bivalve shells. This is necessary in the light of the direct impact that had the interpretation of growth patterns in form of length-at-age keys on the outcome of many growth studies. It is obvious that for any age determination of bivalves from periodic growth marks to be acceptable, it must be based on a conclusive theory that explains the mode of formation of observed growth marks. In the same time such a theory must be consistent with the time scale assigned to the periodicity with which growth increments are formed.

## External Growth Marks

The concentrically arranged marks found on the external shell surface in various bivalve species range from ridges and grooves (termed "circuli") to dark-colored rings ("annuli") that alternate with areas of lighter background coloration. Especially in freshwater bivalves belonging to the superfamily Unionacea, extensive studies have been carried out on the origin and formation of external rings (Coker et al. 1921) and the information contained in the rings used for age determination (Crowley 1957; Negus 1966; Haukioja and Hakala 1978).

Coker et al. (1921) explained the formation of marks as the doubling-up of layers at the growing edge resulting from mantle retraction due to disturbances and subsequent resumption of shell deposition in the same area after re-extension of the mantle. They reasoned that alternate warm and cold periods at the onset of the winter season in temperate latitudes would induce frequent mantle retraction and thus produce a large number of densely distributed growth checks that ultimately manifest themselves as a dark band on the shell surface. The interpretation of these rings as annual bands is often complicated by the existence of disturbance or shock rings, which to distinguish from the former rings remains rather subjective (Haukioja and Hakala 1978; Tevesz and Carter 1980a). Though various techniques have been described to help identify "true annuli" (see, e.g., Chamberlain 1931; Stansbery 1961; Haranghy et al. 1965; Tevesz and Carter 1980b), the methods still retain a large degree of uncertainty. Haukioja and Hakala (1978) showed that marked *Anodonta piscinalis* had developed between 2 and 5 "annuli" after 3 years (50% of the animals had actually developed 3 rings) and that different personnel would come up with one year difference in age determination in about 10% of the cases investigated.

Similar problems with macroscopically distinguishing annual rings from aperiodic growth checks are reported for *Placopecten magellanicus* (Stevenson and Dickie 1954; Merrill et al. 1965). Scallops are notably sensitive to sudden variation in environmental conditions such as sharp temperature or salinity changes (Merrill et al. 1965). In an attempt to obtain independent estimates of age of *Placopecten magellanicus*, Krantz et al. (1984) utilized the ratio between the stable isotopes of oxygen,  $^{18}\text{O}$  and  $^{16}\text{O}$ , in scallop shell carbonate to arrive at reliable assumptions of shell growth and age. This method takes advantage of the feature that seasonal temperature cycles produce significant variations in isotopic composition within shells (Epstein et al. 1953). The results of Krantz et al. (1984) revealed that the age interpreted from external shell lines overestimated the true age by almost 60% in a four-year old animal. They also concluded from their data that there might not be a consistent season for external line formation, hence contesting the assumption that line formation represents true annual events.

In summary, the use of external shell marks in age and growth studies might be of a certain advantage in large-scale investigations of bivalve shells. They have, however, clear limitations in those cases

- where bivalves grow very old and, thus, feature - as a result of decreased growth rates - a number of annual growth bands too densely packed at the perimeter of the shell to be reliably distinguished from each other; or
- where the bivalves are frequently exposed to drastic changes in the environment (as is typical for most tropical environments) resulting in aperiodic growth checks.

From the latter it becomes evident that the use of external growth lines in age determination is restricted almost exclusively to species from temperate latitudes. Tropical bivalves might display bands, too, but their mode of formation appears to be quite different from that in temperate species (Tevesz and Carter 1980a).

### ***Internal Growth Marks***

Since the first description of microgrowth increments in the shells of several genera of bivalves (*Anadara*, *Mactra* and *Mercenaria*) by Barker (1964), extensive research effort has yielded important new insights into how the ambient environment affects the physiology of bivalves and, in turn, the form, structure, mineralogy, chemistry, and growth pattern of their shells (Rhoads and Lutz 1980). While this issue has also proven important for a number of other scientific disciplines (see History, p. 8), the discussion of this question in the context of the present work will mainly concentrate on ontogenetic growth records within bivalve shells and their potential use in age and growth studies.

Following the definition suggested by Rhoads and Lutz (1980), ontogenetic growth pattern denotes "the life history of an individual organism as it is preserved in mineralized or otherwise refractory, tissues." Growth patterns are perceived as the result of changes in environmental conditions which had led to what can broadly be termed "ecological stress", i.e., the nonspecific response of the animal's organism to an external demand (see Selye 1980 for a general concept of stress).

For an environmental change to be recorded in the bivalve shell, the resulting ecological stress must alter the physiology of the bivalve's organism. If the metabolic response triggers biochemical reactions, for example at the interface between the animal's soft body part and the shell, i.e., in the outer mantle epithelium and its associated pallial fluid, then any drastic environmental change is very likely to express itself in changes at the inner shell surface, be it of structural or biochemical nature (Rhoads and Lutz 1980).

Manifestations of these changes that are of potential interest in the context of the present work are growth lines and their sequential arrangement within the shell's microstructure. Their pattern is revealed in sections of bivalve shells along a plane passing from the oldest part of the shell, the umbo, to the growing margin along the axis of maximum growth (Panella and MacClintock 1968; Rhoads and Panella 1970).

Prior to presenting theoretical considerations concerning the mechanisms of the formation of microgrowth increments, it seems appropriate to briefly summarize some important physiological aspects of respiration and metabolism in bivalves. New insights especially into the bivalves' ability to respire anaerobically has been crucial for a better understanding of the possible origin of growth lines within bivalve shells.

#### **ANAEROBIC METABOLISM IN BIVALVES**

It has been well documented that many bivalve species have developed adaptive mechanisms to cope with periods of insufficient oxygen supply. The most important form of this kind of adaptation is their ability to switch to anaerobic respiration. This topic has been extensively reviewed by Hochachka and Mustafa (1972) and de Zwaan and Wijsman (1976). Bivalves differ in their biochemical pathway from vertebrates insofar that the major end product of anaerobic metabolism is not lactate but primarily alanine and succinate and, to a lesser extent, volatile fatty acids such as acetate and propionate. (For a review of the biochemical pathways of the anaerobic metabolism in bivalves see de Zwaan 1977).

Other forms of adaptations include the retention of water within the shells and the use of aerial oxygen during periods of exposure, as is frequently encountered by species living in the intertidal zone. De Zwaan et al. (1976) found adult *Mytilus edulis* to retain about 3 ml of water when the valves are closed. They estimated that the oxygen contained in the water would be sufficient to meet the energy demand of *Mytilus* for about 30 minutes. In addition, aerial respiration during exposure has been demonstrated to take place in a

number of mytilids (Coleman 1973). Through a slight valve gap atmospheric O<sub>2</sub> can diffuse in the mantle cavity fluid. De Zwaan (1977), however, doubts that this means that in such a situation metabolism is principally aerobic. He concludes that upon exposure "aerobic and anaerobic pathways may operate together, with the predominance of one over the other being determined by the time of exposure (increasing desiccation, exhaustion of eventual oxygen store), the position of the tissue with regard to the mantle cavity, and humidity of the atmosphere."

Another important form of adaptation to situations where oxygen supply does not support aerobic respiration is the capability of bivalves to couple anaerobic respiration with a drastic reduction in energy demand. This differs from the situation generally found in warm-blooded vertebrates, where a drop in the energy charge of metabolic products during anaerobiosis results in an acceleration of energy generating pathways (de Zwaan 1977). This so-called "Pasteur effect", which stimulates glycogen mobilization and subsequent conversion into organic acids, is lacking in bivalves (de Zwaan 1977; de Vooy 1987). De Zwaan and Wijzman (1976) calculated the anaerobic ATP demand in *Mytilus edulis* to be lower by a factor of 18.5 compared to the energy demand during aerobiosis. Oeschger (1987) demonstrated by means of calorimetric measurements that metabolism of *Arctica islandica* and *Astarte borealis* was reduced by 35% and 40%, respectively, within the first 24 hours after the onset of anaerobic conditions. After 20 days of anaerobic respiration both species had reduced their energy demand such that metabolic heat generation was less than 1% of the original value measured during aerobiosis. Combining the results of various authors, de Zwaan (1977) lists as factors contributing to the reduced energy demand a decreased cardiac activity and filtration rate, less muscular activity, and a cease of food uptake and active transport of nutrient molecules through the intestine walls.

Though much of the research on anaerobic pathways has been concentrating on mytilids as typical representatives of an intertidal species with frequent air exposure, the tendency to switch to anaerobic metabolism is also reported for many subtidal bivalve species. Well known is the ability of certain bivalves to survive the very adverse living conditions, e.g., in the Baltic Sea, which is characterized by extended areas with bottom waters that are practically anoxic and rich in hydrogen sulfide (Theede et al. 1969; Dries and Theede 1974). Among the bottom living bivalves, whose resistance to oxygen deficiency was intensively studied were *Cyprina islandica*, *Mya arenaria*, *Astarte borealis*, *Spisula solida*, *Scrobicularia plana*, *Cardium edule* (Thamdrup 1935; Theede et al. 1969; Theede 1973) and *Macoma balthica*, *Abra alba*, *Astarte* spp., *Arctica islandica* (Dries and Theede 1974; Oeschger 1987). The investigated species show varying degrees of adaptation to insufficient oxygen supply. A 50% mortality in O<sub>2</sub>-deficient seawater was reported for *Cyprina islandica* only after 55 days (Theede et al. 1969).

However, de Zwaan (1977) is right in pointing out that bivalves switch to anaerobiosis even at moderate PO<sub>2</sub> reduction (to 120-80 mm Hg). He concludes that anaerobic metabolism should be regarded as part of a general response to ecological stress rather than an extreme response to total anoxia. Thus anaerobic metabolism may be considered as a saving mechanism in the energy budget when bivalves are confronted with adverse conditions such as O<sub>2</sub>-deficiency, food shortage, or drastic temperature or salinity changes (Coleman 1973; de Zwaan 1977).

#### FORMATION OF INTERNAL GROWTH LINES

Length-growth of bivalve shells occurs along the outer shell margin. Secretion of the shell takes place in the outer fold of the mantle, with its inner surface laying down the

periostracum and its outer surface secreting the calcereous layer (for details see, e.g., Barnes 1980). A major role in shell formation is played by the extra-cellular fluid that is enclosed between the mantle and the inner surface of the shell. Its composition is controlled by the metabolic activity of the outer mantle epithelium (Wilbur 1964, 1972; Wilbur and Simkiss 1968), and it is through this extrapallial fluid that all components needed to build up the shell have to pass (Crenshaw 1980).

Though not uncontested (see Crenshaw 1980 for a critical review of different theories of shell formation), it is now widely accepted that shell growth occurs in a manner where organic material (conchilin) is assembled to produce a relatively insoluble matrix. Inorganic material (calcium carbonate,  $\text{CaCO}_3$ , in the form of aragonite or calcite) is incorporated into this matrix to form a highly organized structure.

Microscopic views of internal shell microstructure usually present a picture of microgrowth increments arranged in a series of alternating light- and dark-colored bands (see, e.g., Fig. 4.11). Electron-microscope and optical studies have shown that in most bivalves growth lineations reflect variations in the relative proportions of organic material and calcium carbonate (Lutz and Rhoads 1980). Investigations revealed a complex relationship between the formation of growth increments and either lunar and solar cycles (Clark 1975; Panella 1975), tidal rhythms (Evans 1972, 1975; Panella 1976), or, more generally, shell valve movements (Thompson 1975; Gordon and Cariker 1978). Both observations combined have led to the conclusion that growth increments rich in calcium carbonate (relative to adjacent areas) are deposited during periods when the shells are open and the animal is actively pumping (Lutz and Rhoads 1980).

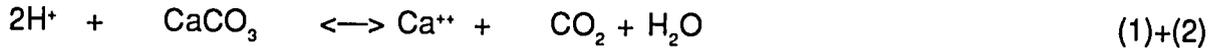
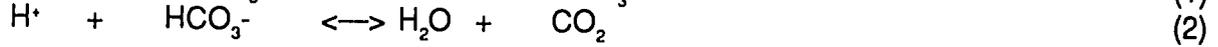
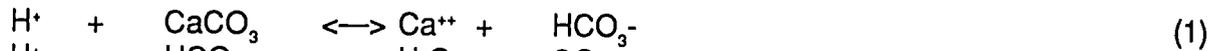
Originally, it was hypothesized that these differences occurred because calcium carbonate and organic material are deposited at variable rates, the rhythm being determined by factors described above (Panella and MacClintock 1968; Evans 1972, 1975; Panella 1975, 1976). However, with a better understanding of the biochemical pathways employed in bivalves during anaerobiosis and a clearer idea concerning the fate of the metabolic end-products, Lutz and Rhoads (1977) developed a theory that explained the variability in organic material contents of the shell (and hence the growth line formation) as being directly related to phases of aerobic and anaerobic respiration.

As mentioned before (see Anaerobic metabolism in bivalves, p. 10), the major end-products of anaerobic metabolism in bivalves are generally succinate and alanine. Extensive studies have shown that these end-products are not excreted upon return to aerobic respiration, but are mainly reconverted to glycogen (de Zwaan 1977). The fact, however, that the acids succinate and alanine accumulate in the organism's tissue during anaerobiosis results in an overall acidification of the tissues with a subsequent decrease in pH. As enzymes are sensitive to pH changes and bivalves apparently cannot regulate their internal pH, neutralization of the accumulated acids is a necessity for bivalves to maintain normal function.

It is now generally accepted that the accumulation of organic acids is at least partially buffered by shell carbonate (de Zwaan 1977). A number of early investigations in the twenties and thirties had already indicated that some bivalves dissolve previously deposited shell material when becoming anaerobic (Crenshaw 1980). By applying more refined analytical techniques, Crenshaw and Neff (1969) concluded from their experiments that shell dissolution began in minutes, rather than days, after the onset of anaerobiosis. As was later shown, a strong correlation exists between shell closure, shell movements and pH in the extrapallial fluid of *Mercenaria mercenaria* (Crenshaw 1972) and *Mytilus edulis* (Wijsman 1975).

From what is known so far, the buffering of accumulated organic acids in bivalves has to be imagined as follows:

Immediately after shell closure, there is a drop in pH. This is counteracted by hydrolysis of calcium carbonate ( $\text{CaCO}_3$ ) originating from the shell with concomitant production of  $\text{CO}_2$  and  $\text{Ca}^{++}$ , i.e. (de Zwaan 1977):



If the shells are kept closed, the accumulation of  $\text{CO}_2$  will force reaction (2) to shift towards the left, resulting again in a decrease of the pH. This is probably the reason why bivalves submerged in oxygen-free water can be observed recurrently to open their shells.  $\text{CO}_2$  can then rapidly escape and reaction (2) will shift again to the right, resuming its buffer function and, hence, stabilize the pH.

In conclusion of the above said, many bivalves can neutralize at least a portion of the organic acids produced during anaerobic metabolism by dissolving  $\text{CaCO}_3$  from their shell. Thus, periodic switches from aerobic to anaerobic metabolism should result in alternation of shell deposition and decalcification at the interface between the mantle and shell (Lutz and Rhoads 1980). With this information serving as background, Lutz and Rhoads (1977) formulated their theory of growth line formation in bivalves, which essentially states that decalcification leaves an area of relatively insoluble organic matrix at the growing margin of the shell. They hypothesized that:

*"With the return of oxygenated condition and resumption of aerobic metabolism, and assuming that shell deposition during this post-anaerobic period proceeds by a process similar to that occurring immediately prior to anaerobiosis, the deposition of calcium carbonate and organic material within an area already containing organic material should result in an increase in the ratio of organic material to calcium carbonate, within the specific shell region. The end product of this process, from a strictly structural viewpoint, is one growth increment."*

This hypothesis provides an adequate explanation for the occurrence of the dark growth lines observed in microscopic views of sectioned shells. Schematically, the formation of growth lines can be envisaged as shown in Fig. 4.1. The hypothesis was further supported by the study of Gordon and Carriker (1978), who found a causative relationship between the calculated rate of shell dissolution during anaerobiosis and the thickness of microgrowth lines observed in *Mercenaria mercenaria*.

A major objection to the idea of growth lines being solely the result of temporary anaerobiosis was formulated by Crenshaw (1980). He maintained that dissolution of the shell during anaerobiosis occurred primarily inside the pallial line and not, as assumed by Lutz and Rhoads (1977, 1980), at the growing edge. However, Lutz and Rhoads (1980) were able to present a large number of examples from the literature, that either explicitly, or by a reasonable re-interpretation of documented microgrowth patterns provided a strong support of their theory of growth line formation.

In their review, Lutz and Rhoads (1980) assigned microgrowth patterns to the following five categories: 1) semidiurnal and diurnal; 2) fortnightly; 3) monthly; 4) annual; and 5) semiperiodic or random events.

The first category refers to a pattern that is defined by the single dark lines that can be observed in acetate peels of polished and etched longitudinal shell sections of many species, meaning that one respective two lines are formed every day. The remaining

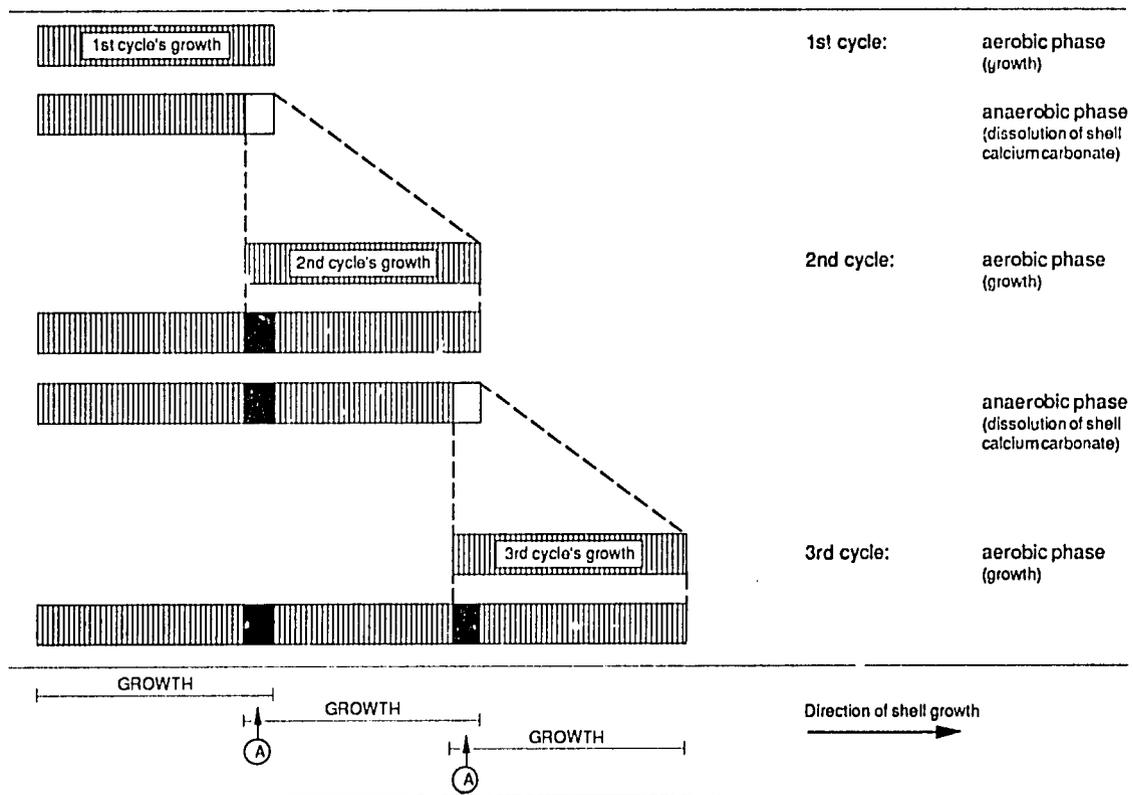


Fig. 4.1. The formation of growth lines in bivalve shells as implied by the theory of Lutz and Rhoads (1980). The graph displays three consecutive periods of aerobic growth separated from each other by a short phase of anaerobiosis. Anaerobiosis results in distal shell dissolution (lighter gray-shaded area) which is refilled with organic and inorganic matter at the onset of the next aerobic growth phase, leaving darker markings in the shell (circled A).

categories describe patterns that are formed by the "clustering" of semidiurnal or diurnal growth lines. These might be caused by the moon-phase related periodicity of the tides (e.g., the fortnightly occurrence of spring- and neap-tide) or the annual variations in hydrological factors such as temperature or oxygen content of the water. Spawning events are usually recorded in a semiperiodic pattern (Lutz and Rhoads 1980). It is possible that most, if not all, categories are present in shell sections examined, as was demonstrated by Kennish (1980) for *Mercenaria mercenaria*, a species which has proven ideally suited for microgrowth research. He also presented various applications of observed microgrowth patterns to the analysis of population dynamics.

It is important to recognize that random events can also manifest themselves in distinguishable growth lines. Such events can be, e.g., shell damage caused by predator attack or fishing gear (dredge), storm, sudden occurrence of pollution or even transplantation experiments (see Lutz and Rhoads 1980 for a review of relevant literature). As promising as the analysis of microgrowth patterns is, the occurrence of growth lines produced by random events in addition to regular patterns requires a detailed knowledge of the conditions the animal has been subjected to, before the relationship of shell microgrowth patterns to specific environmental parameters and physiological conditions can reliably be established (Kennish 1980).

## Microgrowth Analysis in Tropical Bivalves: The Thai Experience

### Introduction

Experimental field studies were conducted in 1986-1987 during an 18-month assignment with the Department of Marine Science of the Chulalongkorn University in Bangkok, Thailand. The site selected for the experiments was located at the eastern coast of the upper Gulf of Thailand at Ang Sila (see Fig. 4.2). In this area, Chulalongkorn University maintains a marine research field station that provided logistic support. Two native bivalve species, green mussel (*Perna viridis*) and cockle (*Anadara granosa*), were selected for controlled growth experiments, because of their economic importance in the Thai bivalve industry.

The design of the field experiments was to serve two purposes:

- provide the necessary shell material for an investigation into the formation of growth patterns within the microstructure of the shell; and
- provide individual growth data from tagged animals for further growth analysis and comparison.

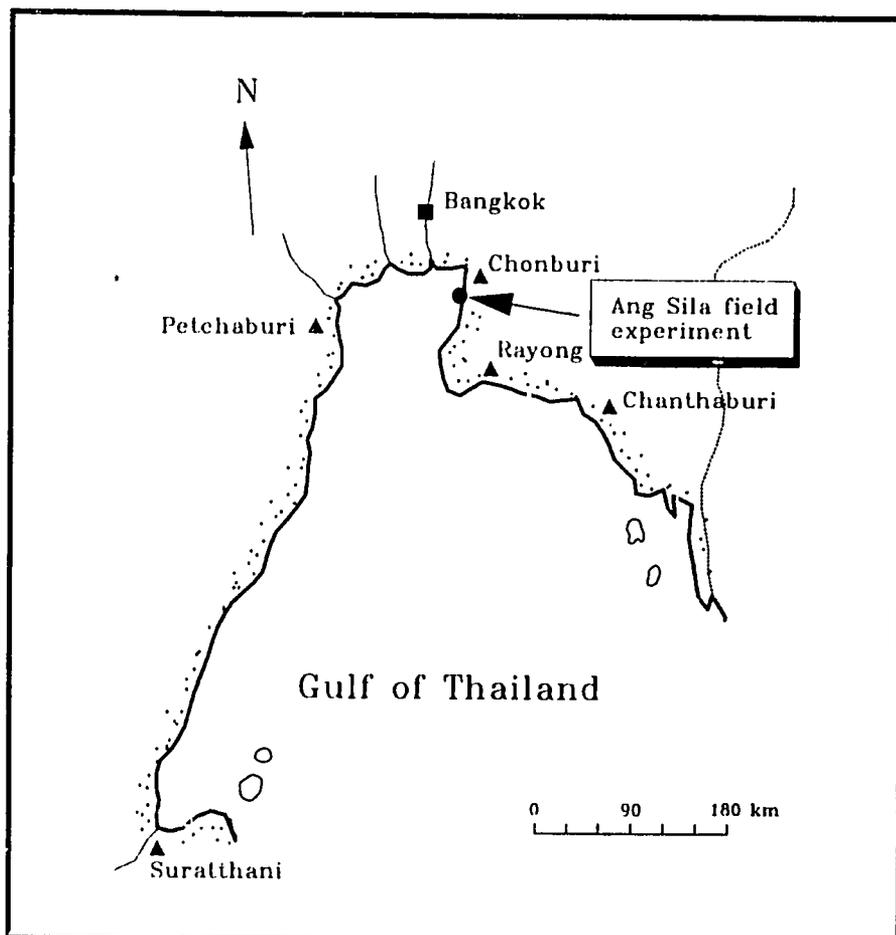


Fig. 4.2. Map of the Gulf of Thailand showing the location of the field experiments at Ang Sila, Thailand.

## Material

### *PERNA VIRIDIS*

In June 1986, about 200 green mussels were collected off Ang Sila from a mussel farm where they had been raised on bamboo poles, and brought to a fish trap some three miles from the coast. The fish trap, approximately 30 m in diameter, was built in sufficiently deep water and manned with a guard which had the advantage of providing sufficient security for the samples. The mussels were raised in net-bags which maintained a cylindrical form due to a double ring frame made of iron wire and mounted inside the net-bag (see Fig. 4.3). A supporting rope was hung between two bamboo poles approximately 10 m apart. Along the rope a total of four net-bags were evenly spaced and secured with ropes, the length of which was adjusted such that the mussels remained about 1 m below surface during low tide. Care was taken to not have the net-bags touch the ground.

The mussels collected at the farm were kept in the net-bags for one week to identify animals that might have been damaged during the process of collecting them from the bamboo poles. After this initial period of adaptation any mussel found dead was removed. Out of the remaining mussels three subsamples of 30 animals each were selected, tagged and their individual length recorded in the manner described below. Each sample was placed in its own net-bag. Another 50 specimens were selected, their length recorded, and placed in the fourth net-bag. This sample was left undisturbed during the whole period of the experiment: it was meant to serve as a control to check whether the disturbance of the other three samples brought about by the regular sampling would have any measurable effect on the overall growth performance.

### *ANADARA GRANOSA*

Cockles were obtained from a natural population off Petchaburi in the western part of the Gulf of Thailand (see Fig. 4.2). They were transferred by car to the Ang Sila research station and kept for a week in tanks for acclimatization and elimination of any animal damaged by transport.

In order to detect the possible influence of exposure on the formation of growth marks in the shell, two sites within a large oyster farm were selected: SITE I (termed "exposed") would regularly fall dry during low tide, while SITE II ("submerged") generally remained covered by water even during low tide. The difference in shore level between the two sites was calculated to be approximately 0.3 m.

The fact of setting up the experiments within an oyster farm with an extensive area covered by concrete blocks was expected to provide maximum possible protection against wave action and also give certain guarantee against accidental or intentional removal of the samples.

The cockles were to be placed in net-cages fabricated locally. The cages were made from flexible branches and featured a rectangular basis with a rounded top (see Fig. 4.4). Net material was attached to the frame with a mesh size considered small enough to prevent the cockles from escaping without obstructing free water exchange. At the top of

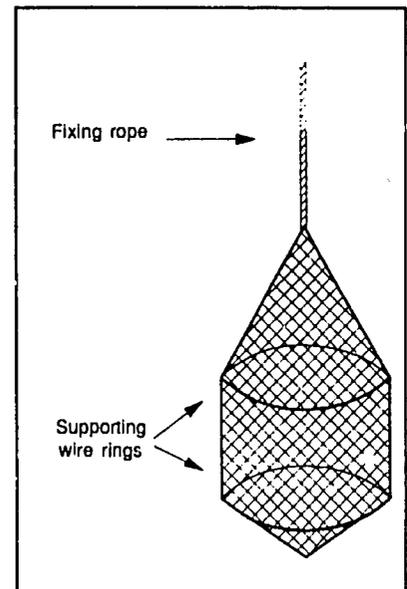


Fig. 4.3. Design of net-bags used in growth experiments with *Perna viridis* at Ang Sila, Thailand.

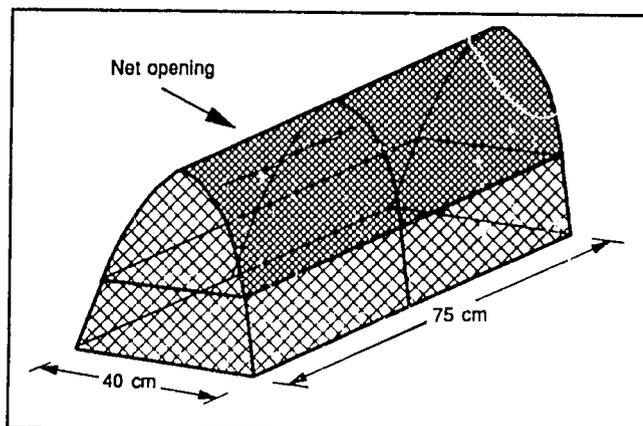


Fig. 4.4. Design of cages used in growth experiments with *Anadara granosa* at Ang Sila, Thailand.

the cage an opening was left in the net which allowed access to the cockles inside the cage.

The cages - four altogether - were of two different sizes. A larger one, measuring 75 x 40 cm base area was to contain the samples for regular monitoring, while a smaller one (50 x 30 cm) would contain the control. The height of the cages was approximately 50 cm.

In March 1986, one cage of each size was brought to SITE I and SITE II, respectively. In a preparatory step, the cockles that had been kept in the laboratory tanks of the Ang Sila field station

were transferred to the cages set-up in the oyster farm. There they were left for one week in order to let the cockles adapt to their new environment. This was meant to preclude a possible drastic reduction of the initial sample size caused by transfer-induced early mortality.

After this period, all cockles were removed from the cages and the remaining living ones separated into two samples of 90 animals each. Every animal was tagged, marked and its individual length recorded in the manner described below. Each of the large cages at SITE I and II contained one sample of 90 cockles.

From the remaining cockles two subsamples of 50 animals each were selected and the length-frequency distribution of the samples recorded. One subsample each was placed into the smaller cages at SITE I and II, respectively. These samples were to be left untouched for the whole period of the experiment in order to provide some information on the possible influence that the monthly handling of the cockles might have on their growth performance. The reduced number of bivalves in these samples was necessary to ensure a comparable initial density of cockles per unit area in the two types of cages.

The bottom of the cages was buried about 10 cm into the mud and anchored with ropes to the surrounding concrete blocks used to culture oysters. Lowering the bottom of the cage deep enough into the mud was considered essential because of the half-buried feeding position of cockles (Broom 1985).

## Methods

### TAGGING

A total of 90 *Perna viridis* and 180 *Anadara granosa* were tagged prior to the beginning of the growth experiments. Plastic stripes of the kind often found in horticulture were used in three different colors (yellow, red, white) and cut into small piece of approximately 3 x 4 mm. One set consisted of thirty tags from each color, numbered through from 1 to 30. One such set was used to tag *P. viridis*, while two sets were prepared for the two samples of *A. granosa* at SITE I and II, respectively.

The numbered plastic tabs were glued onto the shell near the umbo with cyanoacrylate adhesive. Especially in the case of *A. granosa*, the somewhat smoother area around the umbo proved to be more appropriate for the fixation of the tabs. The distal part of the shell features coarse ribs that offer only little surface onto which tabs could be glued.

The tagging method had been tested for some time under laboratory conditions prior to the beginning of the field experiments. During the testing phase only a very small number of tags had come off the shells, and the method, therefore, was considered suitable for the field experiments.

#### MARKING

In order to achieve a discernible marking in the shell microstructure, each numbered bivalve was carefully grated with a swift movement of a file across the edge of the most distal part of the shell. Care had to be taken, however, not to completely abrade the periostracum to avert a disturbance of the bivalve to a degree that would lead to anomalous growth behavior.

#### SURVEYS

##### *Perna viridis*

The growth experiment with *P. viridis* at the fish trap off Ang Sila started in June 1986. Thereafter, the site was visited regularly at one-month intervals until the termination of the experiment in December 1986.

During each survey, the net-bags containing the marked bivalves were removed from the water. However, only one bag at a time was handled to minimize the stress from exposure.

Mussels tend to attach themselves to surrounding material by means of their byssus threads. Prior to measuring the length, the mussels, therefore, had to be carefully separated from each other by dissecting the byssus threads with a sharp knife. Every precaution was taken to ensure that this separation procedure would not damage the soft part of the animal's body, from where the byssus threads are secreted. Once separated, the mussels were identified by their number. Dead animals were removed and kept for later analysis, if they still had their tags attached to the shell.

All remaining animals, including those with lost tags, had their length recorded. Length, in this context, denotes the longest distance between umbo and the outer perimeter of a shell (see Fig. 4.5). Length was measured to the lower 0.05 mm using vernier calipers.

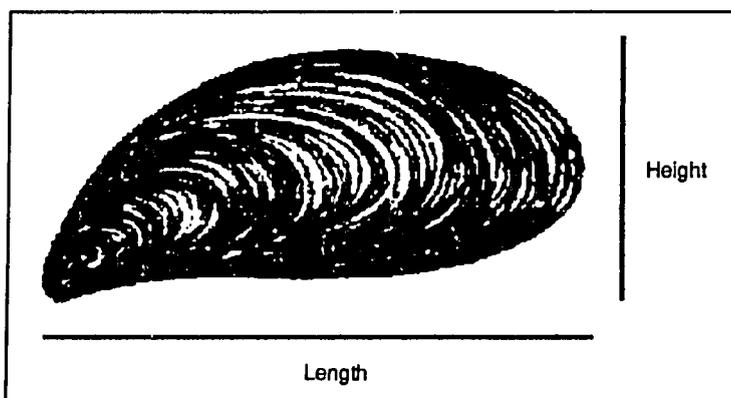


Fig. 4.5. Definition of size dimensions used for *Perna viridis*.

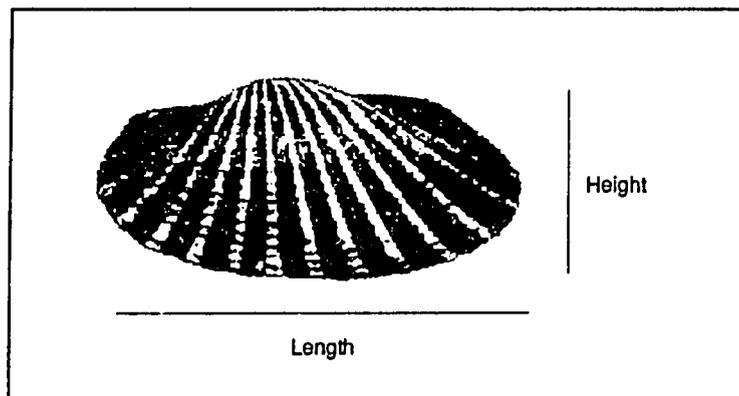


Fig. 4.6. Definition of size dimensions used for *Anadara granosa*.

Prior to placing all remaining live mussels back into their net-bags, the net material was inspected and cleaned where necessary to allow free water flow through the bags.

#### *Anadara granosa*

The growth experiment with *A. granosa* set up within the perimeters of an oyster farm at Ang Sila started in March 1986. Thereafter, regular surveys were carried out in one-month intervals until the termination of the program in February 1987.

Access to the cages was by wading through the water along the rows of concrete blocks used in the culturing of oysters. The razor-sharp edges of oyster shells attached to these blocks made it mandatory to carry out the surveys only during the time of the day when the water level was low enough to expose the rows of concrete blocks. Because of unfavorable tide conditions in September and December 1986, surveys of the cockles had to be skipped completely. In addition, SITE II ("submerged") could not be reached in November 1986.

Regular work during each of the surveys consisted of retrieving from the mud the larger one of the two cages containing the tagged cockles. These were collected from the cage and identified by their numbers. Dead cockles were retained for inclusion in later microgrowth analysis, if they still possessed their tags. The length of each animal was recorded, including those that were found to have lost their tag. Length in this context is defined as the longest distance between the anterior and posterior part of the shell (see Fig. 4.6) and was measured with vernier calipers to the lower 0.05 mm.

Measurements completed, cage and fixing ropes were inspected and, if necessary, repaired. The cage was lowered into the mud by about 10 cm and refilled with mud from the top until the cage's mud layer and the surrounding sea bottom were at same level. Only then were the cockles put back into the cage and the net opening at the top closed with a twine.

#### TIDE READINGS

*In-situ* recording of tide levels was not possible during the field studies. Instead, time tables were used for the relevant months, issued by the Thai Marine Department. These tide tables listed the predicted water heights for every full hour of the day for the area of Ko Si Chang, which is an island about 25 km southeast from where the field experiments were conducted.

The numeric data were transformed into graphs on a month by month basis to obtain a high-resolution picture of the tidal periodicity, allowing specifically to analyze the number of low and high water occurrences for a given time interval. Fig. 4.7 shows for the period March to May 1986 an example of the heterogeneous character of the tide periodicity in the Gulf of Thailand, which, according to Dietrich et al. (1980), is of the "mixed, predominantly one-day" type.

#### PREPARATION OF ACETATE PEELS

The shells of the bivalves brought back to the laboratory in Bangkok were carefully cleaned, rinsed in fresh water, left to dry for one day and then labeled for identification. In general the right valve of an animal was used for further analysis. Only in cases where this valve was obviously damaged was the left valve used.

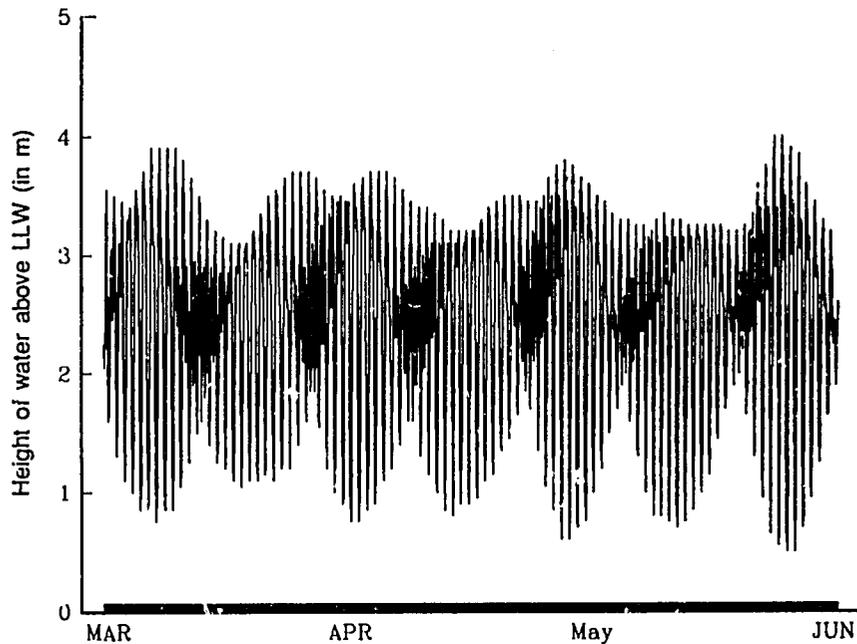


Fig. 4.7. Water levels (in m) above lowest low water (LLW) for the area of Ko Si Chang, Thailand, predicted for the period March-May 1986. (Source: Tide tables, 1986, Thai Marine Department).

The procedure applied to obtain acetate peels from the radially sectioned shell surface closely followed the methodology outlined in Kennish et al. (1980) with additional procedures in Ropes (1984). Essentially, the following steps are involved:

- embedding of the shell in epoxy resin;
- sawing of the embedded shell from the umbo to the ventral edge of the shell along the radius of maximum growth;
- sequential grinding and polishing of the sectioned surface;
- etching of the polished surface by immersion in dilute solution of hydrochloric acid (0.5-1% HCl);
- rinsing and drying of the sectioned and etched blocks;
- flooding of the etched block surface with acetone and application of an acetate sheet to the surface; and
- sandwiching of the acetate peel between glass slides.

#### *ANALYSIS OF SHELL MICROSTRUCTURE*

The slides with the acetate peels were viewed under a microscope at x4 and x10 magnification. Mounted onto the microscope's photo tube was a SONY CCD video camera connected via a frame grabber board to a microcomputer. This hardware set-up allowed the display of the video image on a large-screen monitor. Image analyzing software was used to manipulate the video image. The software includes - among others - features such as holding simultaneously two captured video images in the computer's memory, on-screen marking and counting of objects identified on the captured image, and measuring distances in calibrated units.

From the information available in the literature, it was expected to observe a more or less regular pattern of light colored bands separated from each other by darker and finer

lines, sequentially arranged along the growth axis of the bivalve's shell. Light areas represent shell growth during aerobic condition, while the dark lines result from temporary shell dissolution during anaerobiosis and ensuing refilling with organic and inorganic shell material when growth is resumed (see Formation of internal growth lines, p. 11).

It was hypothesized that the marking of the bivalves at the beginning of the growth experiments at Ang Sila, as well as the stress inflicted upon them during the monthly surveys would disturb the animals slightly more than other naturally occurring events, to which bivalve react with shell closure. Those artificial irritations were expected to induce shell closure and subsequent anaerobiosis for an extended period of time, which in turn should be reflected by more prominent dark lines in the shell microstructure.

In order to assess the periodicity of line formation in the bivalve shell, it was necessary to identify under the microscope those parts of the sample that met both of the following two criteria:

- an area could be defined that was delimited by two clearly discernible growth lines with the possibility to assess reliably their date of formation; and
- it can reasonably be assumed that the growth lines between the two delimiting lines identified under the microscope represent the true number of growth lines for the period in question, precluding the possibility that inadequate preparation had masked the existence of additional growth lines.

With these two conditions in mind, all acetate peels obtained from tagged and marked *A. granosa* and *P. viridis* were screened for their suitability for further analysis. This included checking whether the first growth line stemming from the marking could be identified beyond doubt and whether following prominent dark lines could be assigned to the sampling dates. In the case of *P. viridis*, this task was assisted to a certain extent by using the growth increments calculated from the monthly length measurements. As the length was measured along the same axis as the one along which the shell was sawn apart, growth increments could directly be utilized to help verify whether identified growth lines would indeed correspond to a certain sampling date.

In the case of *A. granosa*, only the relative size of growth increments could be employed for the identification procedure, as the axis of length measurements was different from the one followed by sectioning the shell.

When one of the prominent growth lines could reliably be identified as corresponding to a given sampling date, its position was marked on the slide. If this led to two lines being identified representing two consecutive sampling dates, the area between the two lines was checked, whether the preparation technique had most probably revealed all existing growth lines. This precondition being satisfied, the regular dark lines between the two prominent growth checks were counted. This was done by first freezing the video image on the monitor and then moving a cursor over the screen, fixing highlighted signs in sequential order to every identified growth line.

Once all lines discernible on the screen were marked and counted, the screen image was set aside in the computer's memory and the video image released. The sample was moved under the microscope until the next section adjacent to the previous view would fill the monitor's screen. Then the image was again "frozen" and the marking and counting resumed. In case of doubt whether a line had already been included in the previous view, the software allowed switching forward and backward between the actual image and the previous one stored in the computer's memory, with the possibility to check for already marked lines.

Depending on the overall length of the growth increment under investigation, this procedure was repeated several times until the second prominent growth check was

reached, indicating the end of the growth period under investigation. The total number of lines computed for this period was tabulated. Where applicable, the distances between growth lines were measured, using the appropriate options provided by the image analyzing software.

## Results

### PERNA VIRIDIS

#### Growth experiments

In the three net-bags regularly surveyed, the mussels survived fairly well during the initial four months of the field experiment with only one animal dead out of the 90 animals originally tagged. Twenty-eight specimens had lost their tag.

In November 1986, however, there was a sudden increase in mortality when in one net-bag alone eight animals had died with an additional four *P. viridis* dead in the other two net-bags. In December 1986, upon termination of the experiment, no additional mortality was observed, but it was discovered that altogether 20 bivalves were missing from the net-bags. None of the nets were damaged and the mussels were far too large to fall through the meshes of the net. It, therefore, must be assumed that the guard being housed on top of the fish trap had most probably considered the mussels a welcomed change to his monotonous daily diet, which is more than understandable in view of his sequestered life.

Table 4.1. Summary results of growth experiments with *Perna viridis*, 1986, Ang Sila, Thailand: number of mussels set out at the beginning of the experiment (16-06-86) and recovered at the completion of the field study (24-12-86).

Date	Tagged sample				Control	
	Tagged	Tag lost	Dead	Missing	Present	Missing
16-06-86	90	-	-	-	50	-
24-12-86	32	25	13	20	22	28

In the net-bag, which was filled with 50 *P. viridis* at the start of the field experiment and left undisturbed thereafter, only 22 mussels had survived. A summary on the number of bivalves recovered at the end of the experiment is presented in Table 4.1.

The marked mussels had grown during the six-month period from an average length of 63.75

mm to 84.75 mm. This represents an average increase of 0.114 mm/day. In the same time, mussels in the control net-bag grew only from 63.1 mm to 79.3 mm average length, corresponding to 0.088 mm/day.

For the analysis of the shell microstructure acetate peels were prepared from a total of 79 mussel shells. These included the 32 animals which still had their tag attached to the shell as well as the 25 mussels that had survived but had lost their tags, and the 22 mussels from the control.

When the acetate peels were inspected under the microscope, it became obvious that, if at all, only the samples originating from mussels identifiable by their tags would permit a reliable dating of the observed growth lines. As a consequence, it was decided to concentrate further analysis on the 32 mussels for which complete growth records were available from the monthly length measurements for the period 23 June to 24 December 1986.

### Analysis of the shell microstructure

The pattern of growth lines in the shell microstructure of *P. viridis* was usually fairly good visible under a microscope at x4 magnification. As expected, light-colored bands alternate with darker, narrow lines, their width being generally only one-half to one-third the width of the lighter bands. The lines run from the oldest part of the shell almost parallel to the inner shell surface for a considerable part of their total length before they bent towards the outer surface of the shell. Under normal growth condition the lines reach the area of the periostracum at an angle of about 10°-30°. With the exception of those lines created by the handling during the field experiment most lines were rather similar in respect to their width and coloration.

Generally, the preparation technique was appropriate to reveal fully the pattern of the growth lines within the shell. The only exception was a small zone along the outer margin of the shell, where the lines became frequently obscured.

In all samples the growth line created by the treatment of the shell with a file at the beginning of the field experiment could be identified without much difficulties. Its position was verified by measuring the distance of the growth line from the tip of the shell and by comparing this length with the overall growth increment recorded for the period of investigation. In most cases, the two figures were close enough to confirm the position of the first growth check.

The average increase in length of approximately 20 mm over the six-month period made the measuring of distances under the microscope a difficult task sometimes, as only a small part of the whole acetate peel could be viewed under the microscope at a time. Thus, the object had to be shifted repeatedly, before the tip of a shell was reached. In some cases, especially when the shell was of a more rounded shape, better results were obtained by measuring the distance directly from the acetate peel sandwiched between the slides by utilizing vernier calipers and leaving a mark on the slide, where the growth check was expected.

The first growth check was usually characterized by a darker coloration than all other growth lines. Its course could be fairly well traced from the outer perimeter of the shell across the section towards the inner part of the shell and then parallel to the inner shell surface right back into the area of the umbo. The location where the shell had been abraded with a file was usually marked by a small notch in the shell surface, its deepening being the beginning of the abovementioned growth check.

A few mussels either showed no visible reaction in their shell morphology to the marking or had more prominent deformations of the shell than most others. One mussel (Tag No. Y12) reacted strongly to the marking: it generated a 1-mm indentation and displayed a much reduced growth performance for the rest of the field experiment.

Beside the first growth check, the mussels featured a varying number of additional prominent growth lines developed in the course of the growth experiment. The most obvious explanation for the existence of these growth lines is that they were created by the monthly survey of the mussels. For measuring the length of the mussels the animals were kept out of the water for approximately half an hour. In principle, the stress inflicted by the exposure could have resulted in five additional "disturbance lines" formed after the first growth check at least in those mussels that had survived throughout the whole experimental period. None of the mussels, however, had that many more additional growth lines. Instead, there seemed to happen a certain form of "adaptation" to the stress caused upon by the monthly survey. In many cases the growth line corresponding to the first and second surveys after the tagging were easily identifiable. Relating sampling dates to a given growth line became, however, more and more questionable or even impossible

when investigating the part of the acetate peel corresponding to the last four months' growth. Disturbance lines were either missing altogether, or they were found in a position that was contradictory to the one expected from the growth increments calculated from the monthly length measurements.

Table 4.2 summarizes the number of growth lines counted for a specified growth period. From all investigated parts of the 32 acetate peels, only 36 areas were accepted as fulfilling the requirement of (i) being clearly identifiable in respect to the time interval they represent and (ii) having no obvious deficiencies in respect to the preparation technique. All other areas are marked with a dash in Table 4.2, meaning that either none or only one of the prerequisites were met.

Tag no.	Starting date:	Date: 25-07		Date: 23-08		Date: 26-09		Date: 27-10		Date: 24-11		Date: 24-12	
	23-06-86	GP: 32 days		GP: 29 days		GP: 34 days		GP: 31 days		GP: 28 days		GP: 30 days	
	Starting length (mm)	Incr. per month (mm)	No. of lines	Incr. per month (mm)	No. of lines	Incr. per month (mm)	No. of lines	Incr. per month (mm)	No. of lines	Incr. per month (mm)	No. of lines	Incr. per month (mm)	No. of lines
R 4	61.65	5.40	-	2.80	-	-2.35	-	5.20	-	3.90	-	2.25	-
R 6	72.50	6.00	25	2.00	-	-2.50	-	2.35	-	6.00	-	1.85	-
R 9	63.15	5.45	(>)	0.75	69 <sup>a</sup>	1.90	-	8.30	-	5.60	-	2.70	33
R 14	74.75	3.60	30	-0.50	-	-0.45	-	3.80	-	0.10	-	0.00	-
R 17	60.20	3.45	-	0.45	-	-1.15	-	4.80	-	3.70	-	1.75	-
R 21	59.45	5.25	33	1.30	27	3.30	-	3.65	-	1.65	-	2.25	-
R 22	57.75	6.90	29	0.30	30	1.05	-	4.45	-	0.40	-	0.15	-
R 25	59.30	1.15	-	1.05	-	-0.55	-	2.20	-	2.70	-	1.40	-
R 27	60.80	2.20	26	3.00	33	2.45	-	5.95	-	2.40	-	1.85	27
R 30	64.40	7.90	37	-1.20	-	-2.55	-	0.90	-	1.55	-	2.15	-
W 5	60.95	2.90	-	2.40	-	-1.50	-	1.40	-	3.05	-	1.70	-
W 9	60.90	7.95	29	3.20	-	2.50	-	3.55	-	4.45	-	1.40	-
W 13	56.65	6.65	26	1.35	-	-0.75	-	2.65	-	0.00	-	0.25	-
W 16	65.75	8.45	-	2.20	-	-2.30	-	5.30	23	0.80	-	0.75	-
W 19	65.85	9.50	30	1.85	-	1.85	36	5.35	25	6.50	28	2.55	-
W 23	67.80	3.60	-	1.90	-	0.00	-	10.10	-	3.90	-	4.50	-
W 26	60.70	4.75	-	2.95	-	-2.70	-	2.55	-	5.75	-	6.95	-
W 29	71.05	3.45	35	1.55	27	2.25	-	7.60	-	-0.10	-	1.65	32
W 30	67.95	5.50	27	4.10	-	-2.15	-	7.90	-	-2.20	-	2.60	-
Y 1	61.85	7.15	-	1.75	-	-0.80	-	3.35	-	1.70	-	1.20	-
Y 2	59.65	7.85	-	3.95	32	1.50	-	5.90	-	2.70	-	2.80	-
Y 5	65.00	7.55	27	1.60	-	2.15	37	4.25	-	2.15	-	1.60	-
Y 6	61.05	6.85	37	5.15	39	3.60	-	8.00	-	8.85	-	4.45	-
Y 10	62.35	7.75	-	2.55	-	-0.60	-	6.90	-	5.60	-	2.10	-
Y 12	59.05	5.90	-	1.85	-	-1.85	-	5.45	-	-0.20	-	2.00	-
Y 15	58.70	-1.0	-	-0.70	-	-1.65	-	7.60	-	4.70	-	0.05	-
Y 16	65.35	7.20	-	3.65	-	-1.00	-	5.20	-	7.10	-	1.70	-
Y 22	57.85	7.25	-	1.40	-	-1.90	-	9.55	-	5.85	-	3.25	-
Y 23	60.40	3.15	-	3.85	-	-1.45	-	5.55	-	11.20	-	1.80	-
Y 26	67.30	5.35	33	4.45	31	0.95	23	6.35	-	2.70	-	0.80	-
Y 28	61.60	5.05	28	1.35	-	-2.55	-	7.35	-	3.15	19	0.45	-
Y 29	76.30	7.10	-	2.25	-	-3.15	-	4.00	-	-0.70	-	1.05	-

Date: Sampling date in 1986.  
 GP: Growth period, i.e., number of days elapsed since preceding sampling date.  
 -: Growth lines not identifiable beyond reasonable doubt.  
<sup>a</sup>Number of growth lines corresponds to the period of two months.

Also tabulated in Table 4.2 are the monthly growth increments that were used to assist in locating the growth checks corresponding to a certain sampling date. Computed negative growth increments were considered artefacts that did not reflect an actual shrinking of the shell, but errors in the way the animal's length was measured. The large number of negative figures in September 1986, however, points at a systematic bias in the data recording for that month. The most probable reason is an unnoticed decalibration of the calipers used in the measurements. These calipers featured a circular analog display with index hand. This instrument had to be checked occasionally for drift when set back to its zero position, and calibrated if necessary.

#### Periodicity of growth line formation

The number of growth lines identified in each growth period were divided by the number of days of the corresponding time interval. The calculated number of growth lines per day were pooled over all months and the mean computed. This resulted in an average number of 0.962 growth lines formed every day (s.e.= 0.027, n= 32).

Fig. 4.8 shows the distribution of the single data points over the months as well as the mean number of growth lines per day computed for the whole period. The corresponding

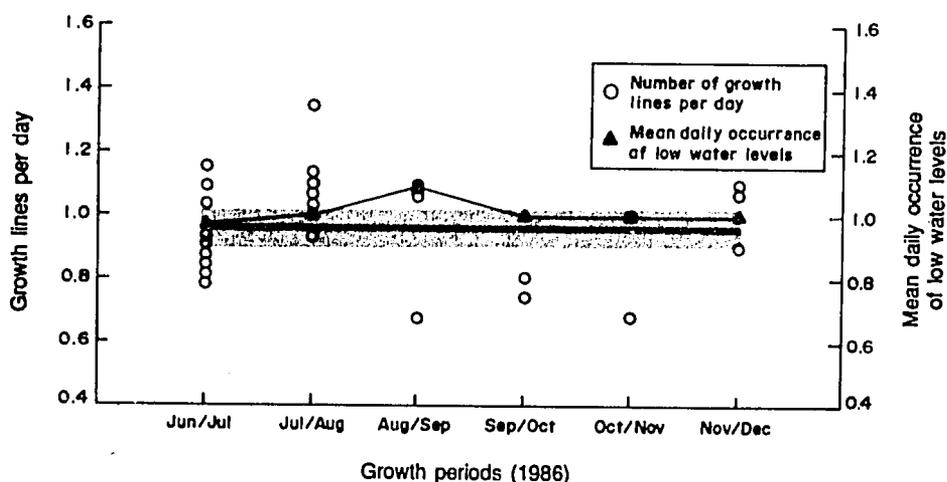


Fig. 4.8. Results of growth experiment with *Perna viridis* at Ang Sila, Thailand: observed number of growth lines per day for given growth intervals and corresponding average number of low water level occurrences for the period July to December 1986. Solid horizontal line denotes the mean number of growth lines per day, pooled over six months; the 95% confidence limit of the mean is given as shaded area.

95% confidence interval of the mean ranges from 0.9 to 1.02, classifying the growth line formation of *Perna viridis* in Thailand as an event with predominantly diurnal periodicity.

In order to assess the influence of the tidal rhythm on the periodicity of growth line formation, the number of low water level occurrences between successive sampling dates were read off from the tide graphs, expressed as number of low water levels per day, and marked for the corresponding growth period in Fig. 4.8. For the whole period July to December 1986 an average of 1.01 low water levels per day (s.e.= 0.017, n= 6) was computed. This is slightly higher than the rate at which daily growth lines were formed, but remains well inside the range defined by the 95% confidence interval of the mean number of growth lines per day.

In a direct comparison, however, the data do not yield any statistically significant correlation between the two variables growth line formation and tide periodicity. This is primarily due to the unexpected low number of growth lines counted in various samples, which definitely contributed to the masking of any possible relationship. It is not clear, if

this simply reflects an enormous variability in growth line formation within the species *P. viridis* or if a methodic inaccuracy is at the origin of the discrepancy. When looking at Fig. 4.8, it is, indeed, conspicuous that the first and the last growth periods, both being bracketed by at least one growth disturbance mark of ascertained formation time, display much less variance than the data for the remaining observation periods. Also noteworthy is a better agreement for these two periods between observed number of growth lines per day and average number of low tides per day. This suggests the possibility that even with all precautions taken the dating of some growth checks might have been erroneous and/or that some of the growth lines had not been revealed by the preparation technique.

Given the present experimental design, a more detailed analysis of the relationship between tide and growth line formation is not possible for two reasons:

- First, the tide levels used in the analysis are predicted water heights based on a theoretical tide model applied to the area. The true tide levels are largely dependent on factors such as wind and currents. These will - either positively or negatively - influence the actual water level.
- Second, the data on growth line formation are much too scarce and display too large a variance to be acceptable for a more elaborate statistical analysis.

In conclusion, from the data available the hypothesis of tide-induced growth line formation in *P. viridis* is at present not supported, at least not on the basis of correlation analysis. In the case of the complex nature of the tidal periodicity in the Gulf of Thailand a statistically more satisfying answer will be obtained only if future experiments include tide recording and an improved method of growth line identification. Nevertheless, the visual interpretation of these data in Fig. 8 which may be considered more reliable suggests a certain relationship between these two variables.

This impression is also supported by a specific observation made in quite a large number of samples: inspection of the acetate peels revealed that many mussels had formed seven to eight distinct growth lines with one or two faint lines in between just prior to the first growth check formed by the marking of the shell. It is very likely that these lines had been laid down during the "adaptation" period. This period extended from the 16 June, the day when the mussels were collected from a bamboo pole, to the 23 June 1986, when they were tagged and marked.

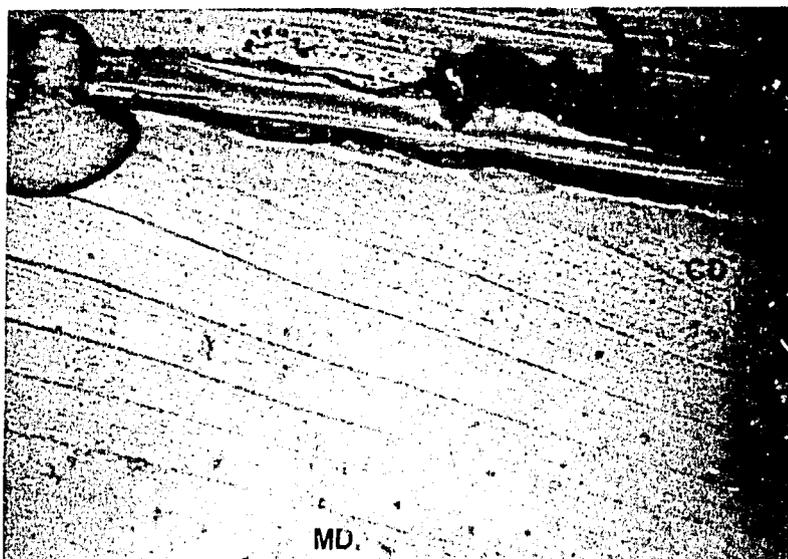


Fig. 4.9. *Perna viridis* growth experiment at Ang Sila, Thailand: cross-section through the shell, showing the nine growth lines created between 16 June (CD), when the mussel was collected at its original place, and 23 June (MD), when it was marked. Specimen with Tag. No. Y06, acetate peel technique, viewed at x4 magnification, positioned with the outer shell surface at the top. Growth is from right to left.

An example of this observation is illustrated in Fig. 4.9, showing a *P. viridis* (Tag No.: Y06) with seven prominent growth lines prior to the abovementioned growth check and two more weak lines observed after the second and fifth lines, respectively. The distances between the single lines were measured and then drawn to scale onto a time axis (Fig. 4.10) with the first line assumed to be formed late in the afternoon of 16 June, and the last line representing the growth check formed on 23 June 1986. Fig. 4.10 also displays the distribution of tidal levels for the period 16-23 June as predicted

by the tide tables. Though the same reservations as made before also apply to this theoretical tide wave, there seems to be nevertheless a synchronization between the formation of growth lines and low tide. It is also interesting to note that the two less distinct growth lines (thin, dashed lines in Fig. 4.10) appear to coincide with intermittent water still-stands that result from the complex form of the tidal periodicity in the Gulf of Thailand.

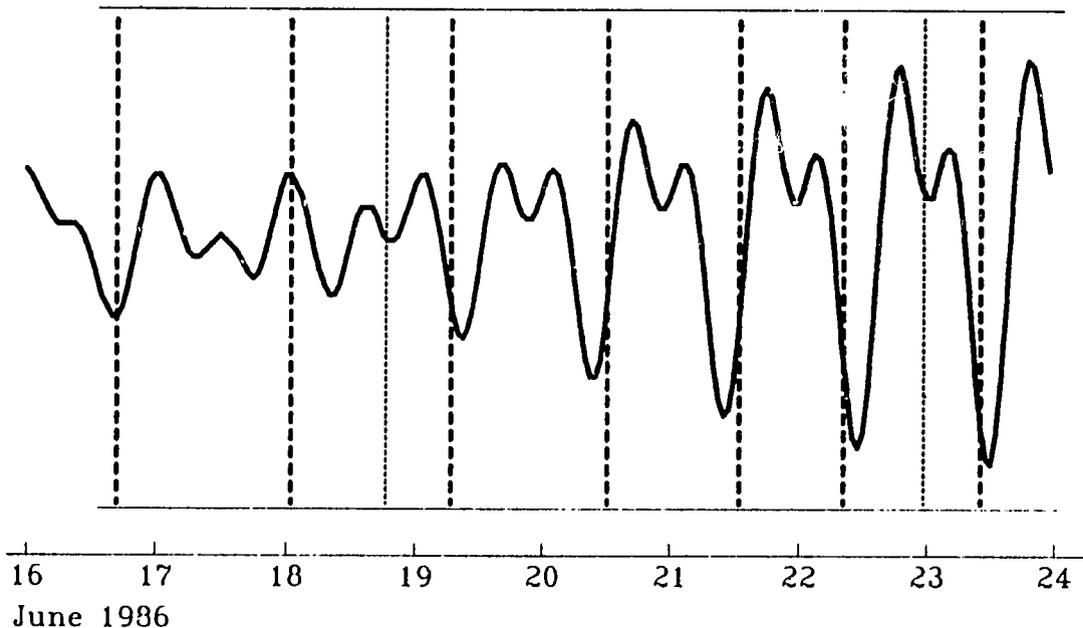


Fig. 4.10. Results of growth experiments with *Perna viridis* at Ang Sila, Thailand: distribution of identified growth lines (dashed lines) for the period 16 to 23 June 1986 with superimposed predicted tide levels (solid line) in the specimen with Tag No. Y06. Note: Thin dashed lines denote less prominent growth lines.

#### ANADARA GRANOSA

##### Growth experiments

The cockles living under exposed conditions at SITE I survived relatively well during the first five months from March to August 1986, with a total mortality of seven animals. At SITE II a very high initial mortality was observed, when seven, eight cockles died during the first and second months, respectively. Thereafter, mortality was low until August with only two additional bivalves recorded dead. While the sites could not be reached in September due to the prevailing high tide during daytime, the survey in October 1986 revealed a sudden increase in mortality with five cockles dead at SITE I and 14 at SITE II. For the rest of the experiment until February 1987, mortality was low again with one bivalve found dead per site and per month.

Upon termination of the growth experiment in February 1987, it was discovered that with the exception of one dead animal and one cockle without tag all remaining cockles at SITE I (exposed) had been stolen from both the regular surveyed cage and the control cage. As a consequence, the remaining sample from SITE I consisted almost exclusively of dead cockles collected during the previous months, out of which only nine bivalves could still be identified by their tag.

No theft had occurred at SITE II, which was situated much further away from the shore, and where the cages could not easily be detected under normal conditions. However, strong wave action during the last month of the experimental phase considerably damaged the smaller control cage, resulting in 37 out of the 50 cockles having escaped from the cage. A summary of the cockles recovered at the end of the field study is given in Table 4.3.

Growth was markedly different at the two sites. If only the period March 1986 to January 1987 is considered because of the loss of samples in February, average length of cockles at the higher shore level increased by about 6mm (22.56-28.24 mm). In the same time the cockles at SITE II grew from an average length of 22.27 mm to a length of 32.11 mm, totalling almost 10 mm. This represents an increase of 73% in growth performance compared to the cockles at the exposed site.

Table 4.3. Summary results of growth experiments with *Anadara granosa* 1986-1987, Ang Sila, Thailand: number of cockles set out at the beginning of the experiment (27-03-86) and recovered at the completion of the field study (26-02-87) at SITE I (exposed) and SITE II (submerged).

Site/ date	Tagged sample				Control	
	Tagged	Tag lost	Dead	Missing	Present	Missing
SITE I						
27-03-86	90	-	-	-	50	-
26-02-87	0	1	15	74	0	50
SITE II						
27-03-86	90	-	-	-	50	-
26-02-87	20	32	34	4	13	37

#### Analysis of the shell microstructure

From the 16 cockles recovered from SITE I, 15 were embedded for analysis of the shell microstructure. Out of this sample, only nine were still identifiable by their tag, while the other six had lost their tags. From the sample at SITE II, a total of 99 *A. granosa* were available for further analysis: 49 tagged cockles, 37 cockles without tag, and 13 cockles from the control cage.

Though the smaller size of the cross-sections of the shells had the advantage of facilitating the orientation when examining a sample, the very small growth increments (on an average 0.98 mm·month as compared to 3.50mm·month for *Perna viridis*) made the reliable identification of single growth lines an extremely difficult task. A major obstacle was the fact that the higher magnification (x10, x25) required to distinguish the growth lines from each other also made more prominent growth lines appear as a double line separated by a space not much narrower than the space between two true growth lines.

The acetate peels sandwiched between slides were viewed under a microscope at x4, x10, and x25 magnification. At low power magnification, certain parts of the cross-sections show a series of relatively clearly visible thin lines, while in other parts these lines would hardly be detectable. In areas with well documented growth lines, switching to a higher magnification (x10 or x25) would often reveal the existence of many additional, very faint, lines. On the other hand, however, this did not necessarily improve the detectability of growth lines in the areas generally lacking distinct growth lines.

It is not clear, whether these differences in the appearance of the cross-sections are caused by physiological variations in shell formation, or if it is the consequence of preparation techniques that are inappropriate for the usually very fine growth lines typical for this species.

Similar to the findings in *P. viridis*, the growth lines lead first in a 20°-40° angle from the outer shell surface across the cross-section towards the inner shell surface describing a curve that gradually slopes backwards until the growth line runs almost parallel to the inner shell surface (see Fig. 4.11). Although it looks as if the lines merge with the shell margin some place back in the older part of the shell, they are most probably still present, though hardly visible.

The growth check created by marking the shell was usually clearly discernible, both because of the line formed within the shell structure and because of the notch created at the surface of the shell. In most cases, though, it did not represent the first growth check, but was preceded by a similar, if not more prominent, growth check, which was apparently created by the transfer of the cockles from their natural habitat to the site of the field experiment at Ang Sila. This very first growth check differed from the second one created by the marking insofar that it clearly delimited the older part of the shell, which was rather different in appearance compared to the shell material added thereafter during the field experiment. Its surface structure was of a somewhat granular nature giving more plasticity to the growth lines. The fact that the appearance of the microstructure has changed with the beginning of the experiments indicates that environmental conditions play a major role in the look of the microstructure. It is not clear, though, whether this is limited to the outer look of the growth lines only, or whether this is also reflected by differences in growth performance and in the number of growth lines formed per unit time.

It was interesting to note that the line created by the marking is also well detectable in the area of the umbo. Fig. 4.12 represents a cut through this area of an *A. granosa* (Tag No.: II/R15) which died in the second month of the field experiment. Clearly visible is a dark line that reflects the marking in March 1986. The thinner line prior to the forementioned growth check is the one formed when the cockle was transferred to Ang Sila two weeks before the experiments actually started. The fact that no other growth line is visible might indicate that the animal died one month later right after the survey in April.

Most cockles had developed a varying number of additional prominent growth lines in the course of the field experiment. Attempts, however, to relate the position of these lines to the monthly surveys proved extremely difficult. Either growth lines were missing altogether, or their position made it most likely that they were created by some external disturbance other than the monthly measuring of length. The latter was especially true for the nine cockles that had remained from the samples at SITE I. This finding was in accordance with observations made already during some of the surveys, when the cages at SITE I had obviously been pulled out of the mud, most probably by people working in the oyster farm. Such handling, however, would have had the effect that for some time the bottom of the cage would have lacked any mud for the cockles to bury into. This might have caused a certain stress for the animals which would be reflected by prolonged shell closure and ensuing formation of a growth check.

After a preliminary review of all material available, it became apparent that only the experiment at SITE II represented a sufficient high number of cases that satisfied the prerequisites considered essential for further analysis: (i) the error-free assignment of sampling dates to observed growth checks and (ii) the validity of the assumption that potentially inadequate preparation technique had not masked the existence of additional growth lines within a predefined area.

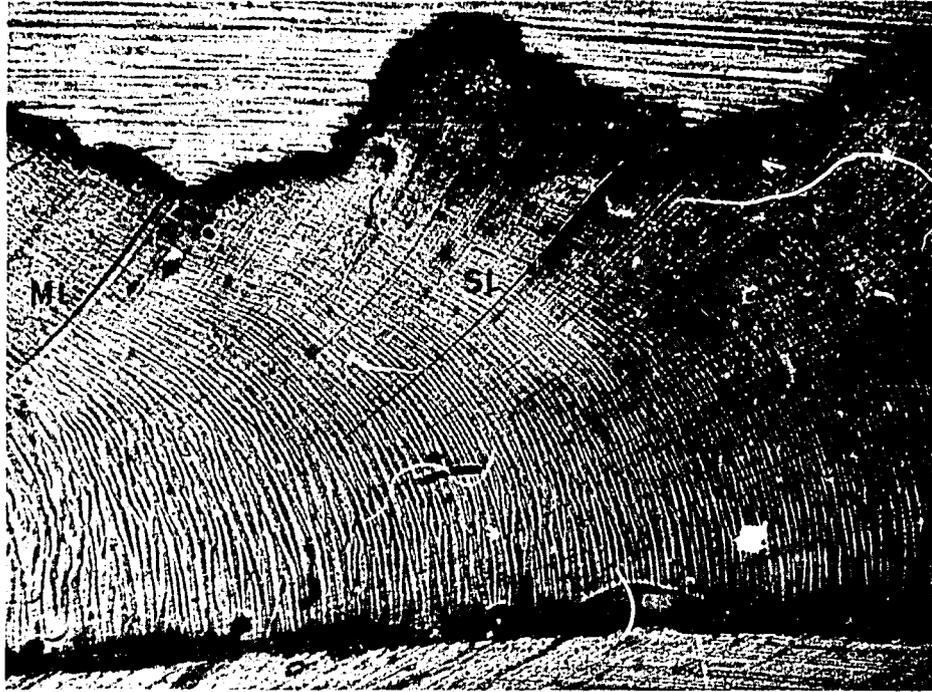


Fig. 4.11. *Anadara granosa* growth experiment at Ang Sila, Thailand: cross-section through the shell, showing the growth lines created by the marking (ML), one month later by the first survey (SL). Specimen with Tag No. II Y09, acetate peel technique, viewed at x4 magnification, positioned with the outer shell surface at the top. Growth is from left to right.



Fig. 4.12. *Anadara granosa* growth experiment at Ang Sila, Thailand: cross-section through the area of the umbo, showing a "disturbance line" (DL) caused by the transfer of the cockle to the study site, and a "growth check" (GC), resulting from the marking of the animal. Specimen Tag No. II/R15, acetate peel technique, viewed at x10 magnification.

### Periodicity of growth line formation

Given the uncertainties in the proper assignment of sampling dates to the growth checks observed in the microstructure of the shells, emphasis was laid on the analysis of the first growth interval after the cockles had been marked. This had the advantage that the formation of the first growth line - the one created by the marking on 27 March 1986 - could be dated unambiguously. While in many samples the next growth check formed on the 22 April 1986 was still identifiable with sufficient reliability, attempts to locate growth checks corresponding to any of the following sampling dates usually bore too much uncertainty to be acceptable for inclusion in the analysis.

The relatively large sample number thus available was drastically reduced, however, to a mere six acetate peels, when the area representing the first growth increment was checked for the existence of a complete record of growth lines. Except for these six, all other samples had to be considered for not reliably presenting at least partial traces of well-formed growth lines.

Table 4.4 summarizes the counts of growth lines carried out on these samples. With the values in the samples ranging from 72 to 89, an average number of 80.7 growth lines (s.e.= 2.31) were computed for the period 27 March 1986 to 22 April 1986. As this period comprised 26 days, growth lines were formed at a rate of around three lines per day.

In order to assess the influence of the tidal rhythm on the formation of growth lines in *A. granosa*, the total number of high and low water levels predicted by the time tables for the period in question were read off the tide graphs. Even though the tide tables do not accurately mirror the actual water heights that had occurred at the site of the field experiments, their general indication of a changing tide must also apply - probably with some time delay - to the area of the growth experiments.

The total number of high and low waters from the 28 March 1986 (0 hour) to the 22 April 1986 (12 hour) amounted to 80. The close conformity of this result with the average number of growth lines counted for this period in the samples of *A. granosa* (see Table 4.4) allows the conclusion that the formation of growth lines in *A. granosa* is strongly

synchronized with the tides.

This relationship is being tentatively displayed in Figs. 4.13 and 4.14. In one cockle (Tag No. II/Y09), which had an exceptionally well preserved record of growth lines for the period of the first growth increment, the distances between lines were measured and then drawn to scale onto a time axis reaching from the 28 March 1986 (0 hour) to the 22 April 1986 (12 hour). Growth lines that appeared more prominent than others are marked in the graph as thicker broken lines. The graph also displays the tide levels for the said period as extracted from the tide tables, drawn to scale onto the same time axis. As was pointed out, the actual water levels at the site were most probably slightly different from the predicted water levels, but one can

Table 4.4. Results of growth experiments with *Anadara granosa*, 1986-1987, SITE II, Ang Sila, Thailand: growth increments for the period 27 March to 22 April 1986 and corresponding number of observed growth lines from tagged animals.

Tag No. length (mm)	Starting date: 27-03-86	Sampling date: 22-04-86		
	Starting month (mm)	Incr. per of lines	Nu. per day	Lines
W 7	21.50	1.50	89	3.42
W 14 <sup>a</sup>	24.55	-0.10	84	3.23
Y 3	18.95	1.80	79	3.04
Y 9	22.55	1.40	80	3.08
Y 11	23.40	0.90	80	3.08
Y 18	22.95	0.35	72	2.77
Mean		1.19	80.67	3.10
s.d.		0.57	5.65	0.22
n		5	6	6

<sup>a</sup>The negative increment was excluded from the computation of the mean increment per month.

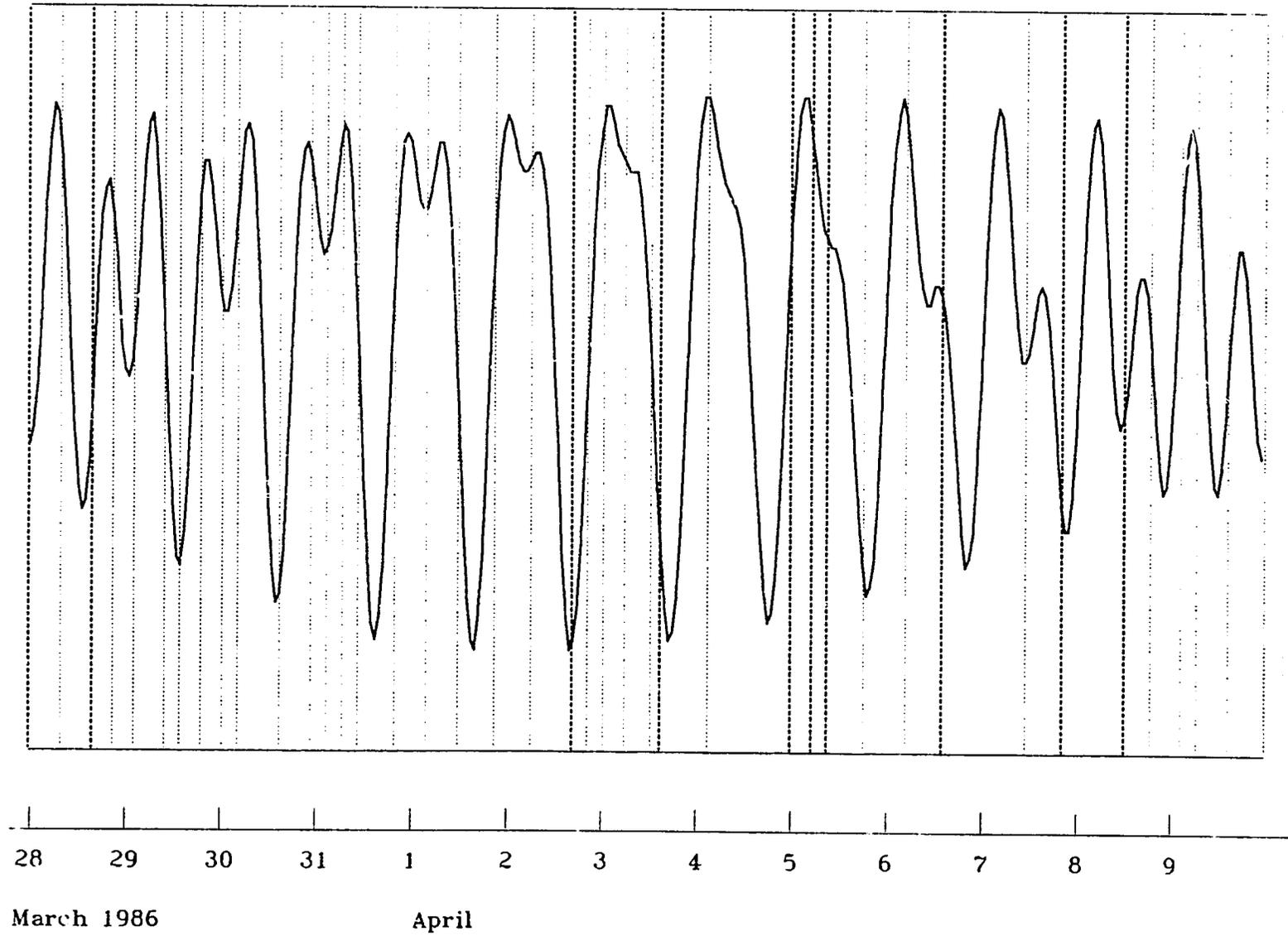


Fig. 4.13. Results of growth experiments with *Anadara granosa* at Ang Sila, Thailand: distribution of identified growth lines (dashed lines) for the period 28 March to 9 April 1986 with superimposed predicted tide levels (solid line). Note: Thick dashed lines denote more prominent growth lines.

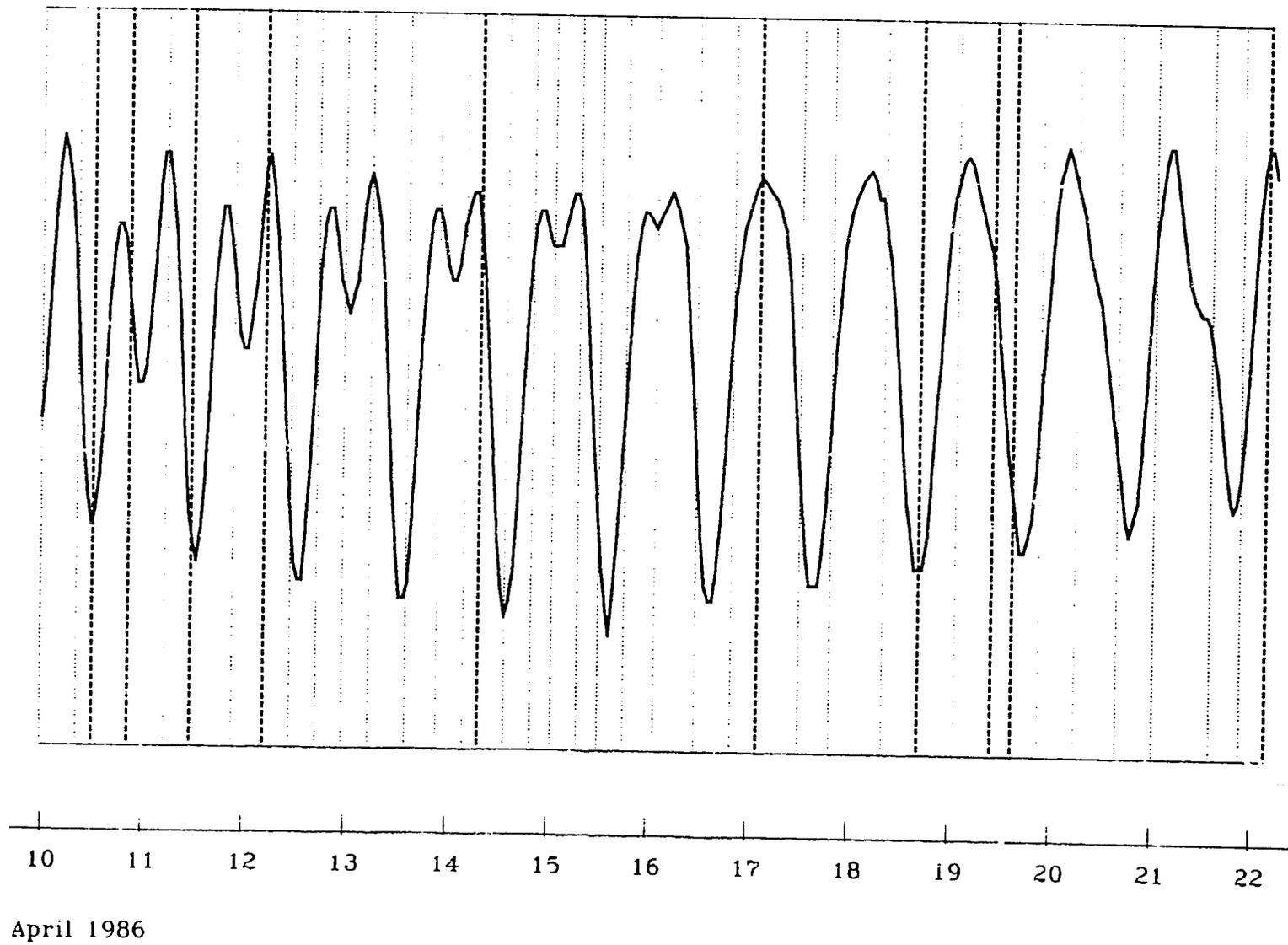


Fig. 4.14. Results of growth experiments with *Anadara granosa* at Ang Sila, Thailand: distribution of identified growth lines (dashed lines) for the period 10 to 22 April 1986 with superimposed predicted tide levels (solid line). Note: Thick dashed lines denote more prominent growth lines.

nevertheless observe in many cases a match between the position of a growth line and a peak or trough in the level of the tide.

### **Discussion**

Many of the analytical models traditionally used in fish stock assessment are age based. This reflects the fact that at higher latitudes fish, for which the models have been developed, can often readily be "aged" by means of sclerochronological records of seasonal events in hard parts of the fish body (otoliths, scales). It is only logical that scientists involved in mollusc research have looked into the potential of using the information contained in the microstructural organization of bivalve shells to analyze their life-history patterns, such as age, growth and longevity.

It seems now well accepted that the shells of many subtidal bivalve species from temperate waters possess internal records of growth increments that are characterized by the sequential occurrence of dark and light bands, one such pair being considered one year's growth. This postulated annual periodicity has been confirmed in a number of cases by concurrently investigating the periodicity of the oxygen stable isotope composition of the shell carbonate (Williams et al. 1982; Jones et al. 1983; Rollins et al. 1987).

In contrast to the relatively wide bands of subtidal bivalves, there was much more dissent in the interpretation of the periodicity behind the formation of the thin growth lines observed in intertidal species. While originally solar, lunar or daily periodicity was assumed (Lutz and Rhoads 1980), experiments both in the field and in the laboratory with an intertidal species, *Cerastoderma edule*, by Richardson et al. (1980a, 1980b, 1981), showed strong evidence of an endogenous circatidal rhythm in growth line formation which becomes entrained and reinforced by regular tidal emersions.

Though sclerochronological studies have proved valuable in the investigation of the ecology and growth of many temperate bivalve species, apparently no attempt had been made so far to extend systematically the analysis of shell microstructure to tropical bivalve species. The only exception that was brought to the attention of this author is an unpublished technical report (Richardson 1985) on the use of microstructure analysis in aging of *Anadara granosa* in Malaysia.

Obviously, the major constraint in sclerochronological studies in the tropics is the lack of strong seasonal variations, e.g., in water temperature or food availability. Though seasonality in these parameters is a reality in the tropics, too, and actually leads to seasonally changing growth rates in marine organisms, its effect is hardly strong enough to cause a complete growth stop for an extended period of time, as observed in aquatic animals of the higher latitudes. Longhurst and Pauly (1987) suggested that in general a seasonal temperature difference of 4°-5°C might be necessary to induce readable annual rings in hard parts of tropical fish. In the Gulf of Thailand, for example, the annual temperature difference does not vary by more than 2-3°C, and hence "annuli" have not been reported from any of the fish species investigated so far in the Gulf (D. Pauly, pers comm.).

While distinct annual marks are absent in the shell microstructure of *Anadara granosa* and *Perna viridis*, the present study has demonstrated that shell material in both species is added in a distinct pattern. In acetate peels of shell cross-sections this pattern consists of translucent bands delimited by faint to clearly visible dark lines, both together being assumed to represent one growth increment.

A major objective of this study was to investigate the possible factors that determine the periodicity of growth line formation in tropical bivalves. For both species investigated,

tidal rhythm was singled out as being most likely responsible for the formation of growth lines. This is based on the close relationship that became apparent between the number of growth lines formed during a given period and the corresponding tidal periodicity.

In the introduction to this chapter it was outlined that according to the theory presented by Lutz and Rhoads (1977) the formation of a growth line in the bivalve's shell microstructure must be considered as the result of a temporary switch to anaerobiosis with subsequent resumption of normal growth under aerobic condition. Any attempt to relate line formation to tidal events, while at the same time remaining consistent with the forementioned theory, therefore must identify the tide related factor that actually induces bivalves to close their valves and switch to anaerobic metabolism.

Regular exposure is definitely a factor to be taken into consideration in the case of intertidal species such as *Cerastoderma edule* (Richardson et al. 1980a, 1981) and some of the *Anadara granosa* investigated by Richardson (1985) in Malaysia. This explanation, however does not apply in the case of subtidal bivalves such as, e.g., *P. viridis* used in this experiment. Richardson (1985) speculated that in subtidal bivalves factors such as pressure change, water currents or endogenous rhythms might be the driving force behind the formation of growth lines. Though endogenous rhythms cannot completely be excluded, as has been shown by experiments of Richardson et al. (1980b), it can be assumed in the case of this study that the exogenous factors imposed on the bivalves by the frequent changes of environmental conditions of their habitat would play a dominant role in determining the periodicity of growth line formation.

With exposure and endogenous rhythms being excluded, water still-stand at the moment the tide reaches its minimum respective maximum is suggested to be the most likely factor that governs periodic shell closure, and, hence, the formation of growth lines, in subtidal populations of *A. granosa* and *P. viridis*. The obvious differences between *P. viridis* and *A. granosa* in terms of their reaction to tidal rhythm do not invalidate this hypothesis. Rather, these differences are probably well explained by ecological and physiological differences in the feeding habits of the two species.

*P. viridis* is an extremely fast growing bivalve when raised in suspended culture. Under average culture conditions it can attain a length of 70-80 mm in the first year (Vakily 1989). This obviously identifies this species as "opportunistic" (Reid 1982) in its feeding behavior, i.e., feeding is continued as long as environmentally controlled factors do not negatively affect the feeding stimuli. Such a factor could well be a high load of large sediment particles and other suspended material in the water which creates a mechanical stimulus detected by the gills or labial palps (Reid 1982). This stimulus might induce shell closure if a certain critical level is reached. In this respect, it is interesting to note that the adverse effect of increased siltation on the growth of *P. viridis* (Yap et al. 1979) and the general importance of tidal currents for the successful mass culture of this species (Cheong and Loy 1982; Cheong and Lee 1984) have long been known.

It thus could seem favorable for mussels to close - if at all - their valves at the moment of water still-stand, when the lack of water movement requires increased activity of the cilia on the gills both to transport food to the labial palps and create a sufficiently strong internal current to clear the mantle cavity from rejected particles of unsuitable size (pseudofeces).

Water still-stand occurs in the Gulf of Thailand at flood tide and ebb tide approximately twice a day. Judging from the calculated average 0.96 ( $\pm 0.027$  s.e.) growth lines formed per day, valve closure takes place only once a day, meaning that the mussels react differently to the occurrence of stagnant water.

This phenomenon might find its explanation in the differences characterizing the respective waterbody surrounding the mussels during ebb and flood tide. When the water

is receding, it carries a high load of suspended matter originating from the inshore waters with soft, muddy bottom. At water still-stand (low tide) this suspension of organic matter that usually gives the water a brownish color poses a considerable problem to any filter-feeder, the mussels being no exception. In contrast, the rising tide brings in fresh water from the open sea, which is much less turbid and, therefore, permits continuous filter-feeding, even when the water movement has come to a still-stand at the moment when the flood tide has reached its maximum.

It is, therefore, concluded that *P. viridis* is affected only by the occurrence of water still-stand during clearly discernible low tides, while high tide and the slight shifts in water movements during the less prominent tide changes have much less influence on feeding behavior and apparently do not result in temporary shell closure. From this, it follows that line formation in *P. viridis* should be related to the periodicity of low water occurrences.

In contrast to the fairly distinct, wide-spaced pattern of growth lines in *P. viridis*, *A. granosa* features a narrow-banded pattern of both clearly visible and also very faint lines, the latter only being discernible using a  $\times 10$  objective on a microscope. Richardson (1985) encountered similar problems with the cockles from Malaysia. He concluded from his investigations that the growth lines were formed at a rhythm of an average of 28 lines in 14 days, the equivalent of one spring-neap cycle in the mixed semidiurnal type of tide prevailing at the eastern coast of Malaysia with two low tides per day.

As discussed earlier the tidal periodicity in the Gulf of Thailand is of a more complex nature, without a clear-cut spring-neap cycle. The results for *A. granosa* grown in the subtidal plot indicate a very close relationship between practically all of the tidal changes and the formation of growth lines. This is clearly reflected in the number of  $80.7 (\pm 2.31 \text{ s.e.})$  growth lines formed on an average during the period 27 March to 22 April, which is closely matched by the combined total number of high and low tides (80, see Figs. 4.2 and 4.3) counted for the corresponding period.

This allows the conclusion that *A. granosa* might be more sensitive than *P. viridis* to reduced water flow and, therefore, reacts to periodic water still-stand with immediate shell closure. In the absence of dedicated investigations into this matter this hypothesis necessarily remains tentative. A closer look at the ecology of this species reveals, however, a feeding behavior which is not at variance with the hypothesis:

*A. granosa* inhabits preferably extended mud flats, where it lies in small depressions with both inhalant and exhalant openings below the surrounding level of the mud surface (Broom 1985). *A. granosa*, though a filter-feeder like *P. viridis*, seems to have well adapted to this environment and can cope with high concentrations of suspended solids (Broom 1985). One of these adaptive means might indeed be a quick response to a "fall-out" of resuspended particulates during a still-stand of the water. It could well be imagined that its accumulation in the depression formed by the half-buried position of the animal induces *A. granosa* temporarily to close its shell. At the onset of the tidal current the water flow clears the area around the bivalve from accumulated silt and feces produced by the animal, thus providing again improved conditions for feeding.

Summarizing, one can conclude that both *A. granosa* and *P. viridis* contain a record of alternating growth increments and growth stops in their shell microstructure. Further it can be suggested that growth line formation is related to the tidal rhythm to which the animals are subjected. The periodicity of the resulting growth line pattern is dependent on various ecological factors such as shore position and feeding behavior, and is characterized by extreme variability, both inter- and intraspecific.

Though the use of microstructure analysis has shown some promising results in age and growth studies of *A. granosa* in Malaysia (Richardson 1985), its general application as an instrument in routine analysis of tropical bivalve stocks seems questionable, especially

because the interpretation of the growth lines now appears to require a detailed knowledge of the animals' feeding behavior under a different water flow condition.

In addition, the preparation technique to produce acetate peels of shell cross-sections is very time consuming and the correct interpretation of observed growth line patterns requires experienced personnel (Richardson 1985). Thus, there is considerable risk that the already existing large biological variability in the samples is increased even further by misreadings or misinterpretations of growth lines. This would necessarily require larger samples and, hence, become more time consuming.

For the slow growing, long-lived, bivalve species from the temperate waters of high latitudes, age and growth studies by means of the analysis of growth lines in the shell microstructure definitely represents an advantage over methods based on length frequencies. Analysis is limited to the fewer annual growth checks, and a relative small sample size can contain information worth many years of regular length measurements. On the other hand, bivalves in the tropics will usually have achieved most of their growth during their second year, with longevity ranging from three to four years in most species. Thus, field experiments with animals of different size, whose growth in length is monitored regularly, can yield a comprehensive insight into the growth performance of a given species within a short period. Though analysis of shell microstructure should not be excluded *a priori*, its application to population dynamics of tropical bivalves will certainly be of less importance compared to length-based methods.

## CHAPTER 5

# GROWTH OF BIVALVES IN DIFFERENT CLIMATIC ZONES A COMPARATIVE APPROACH

### Introduction

For any culture operation, be it of freshwater or marine organisms, the crucial question is whether the given culture condition guarantees optimum growth of the cultured species. From a culturist's point of view, conditions have to be such that the product reaches marketable size in the shortest possible time, in order to minimize costs at a given rate of return. It follows from this that size by itself is not sufficient to describe optimum growth, but that a combination of both size and the time it takes to reach this size will determine the growth performance of a species under a given culture condition.

After a general appraisal of the applicability of the von Bertalanffy growth model to bivalves, the growth of two tropical bivalve species in experimental culture will be analyzed and possible consequences for farm management will be discussed. This will be followed by an assessment of bivalve growth on a more global scale, with the emphasis being laid on methods that allow the comparison of growth performance. Investigating the influence that environmental temperature has on the growth of bivalves is expected to expose some general factors that determine growth performance and thus might help compare growth between different species.

### The von Bertalanffy Growth Theory: Can it be Applied to Bivalve Growth?

#### *The von Bertalanffy Growth Model*

The "von Bertalanffy Growth Function" (VBGF) developed by von Bertalanffy (1934, 1938, 1951), reads for length:

$$L_t = L_{\infty} (1 - e^{-k(t-t_0)}) \quad \dots 1)$$

with  $L_{\infty}$  = asymptotic length;  
 $K$  = growth constant;  
 $L_t$  = length at age "t";  
 $t_0$  = theoretic age of an animal at a length equal to zero, if it had always grown according to the VBGF

Various authors have questioned the validity of the VBGF in general (Knight 1968; Roff 1980), or the applicability of some of the assumptions made by von Bertalanffy, e.g. Beverton and Holt (1957), Ricker (1958), Ursin (1967). Some of these criticisms, however,

might be based on misunderstandings of the basic concepts of the von Bertalanffy model (Pauly 1979).

The VBGF is, of course, not the only way to describe growth mathematically. Moreau (1987) has summarized the major properties of growth models other than the VBGF (logistic growth curve, Gompertz curve) and discussed their potential advantages compared to the VBGF. He also reviews shortcomings of the VBGF described by a number of authors. What gives, however, the VBGF a certain superiority over its competitors is not only that the parameters of the VBGF are determined with relative ease, but that they are biologically interpretable, and can serve as input to yield-per-recruit models or comparative growth studies, both tasks of major importance to fisheries scientists.

For this reason the von Bertalanffy growth model has found wide application in fisheries science, though the conceptual analysis of the underlying theory has so far mainly been based on the analysis of fish growth. No explicit validation exists for the general application of the model to the growth of invertebrates.

In order to assess whether the factors governing the growth of fish are similar to those found in bivalves, one should recall the fundamental statements of von Bertalanffy's theory of growth, which, essentially, are (cited from Pauly (1979)):

- growth is the net result of two processes with opposite tendencies (anabolism and catabolism);
- an organism approaches an asymptotic size when catabolism is equal to anabolism, and hence growth ceases;
- catabolism occurs in all living cells of an organism and is proportional to its weight (respectively the third power of its length, if isometric growth is assumed);
- anabolism is proportional to respiratory rate; and
- respiratory rate is proportional to a surface through which oxygen can penetrate into the body (i.e., proportional to a linear dimension squared, if isometric growth is assumed).

Growth, therefore, is assumed to be limited physiologically by the surface that governs the rate of oxygen supply, i.e., by the surface of the gills. For the growth of fish, Pauly (1979) discussed a number of properties of gills that support the concept of gills being the most likely physiologically effective surface limiting anabolism compared to other possible organs such as gut surface. He thus concluded that with increasing size the oxygen supply per unit body weight decreases in the same way as the relative gill size (i.e., the gill surface per body weight) decreases (a restatement and elaboration of this theory may be found in Chapter 9 of *Ecology of Tropical Oceans*, Longhurst and Pauly 1987).

In the following some evidence will be presented that in bivalves, too, gills grow more slowly than their body weight. It seems, therefore, justified to assume that bivalves will also gradually approach a point where the oxygen-supply controlled rate of synthesis of body mass is lowered to an extent where it is just sufficient to counteract the catabolic processes in the organism, the rate of which always remains proportional to body weight. Thus, bivalves should indeed also display a growth towards an asymptotic size which is typical for the von Bertalanffy growth model.

### ***Allometric Growth of Bivalve Gills***

In marine organisms, total gill area (G) relates to body weight (W) in a manner that can be described by the equation (Pauly 1979):

$$G = a \cdot W^d \quad \dots 2)$$

where "a" is a species-specific constant and  $d_g$  an exponent whose properties are such that if  $d_g = 2/3$ , the surface of the gills grow isometrically with the body weight. On the other hand, if  $d_g = 1$ , the gills would grow as fast as the body weight.

While a wealth of literature exists dealing with the relationship between gill size and body size in fish, very few studies apparently have been carried out on this matter in bivalves. Most of them primarily deal with questions related to the function of the gills as filtration apparatus. However, information is also contained on the relationship between gill size and the length of some bivalve species, namely *Mytilus edulis* (Dral 1967; Foster-Smith 1975), *Cerastoderma edule* and *Venerupis pullastra* (Foster-Smith 1975) and *Scrobicularia plana* (Hughes 1969). Though rather different techniques have been applied to measure the surface of the gills, it is generally agreed by the authors that a direct proportionality exists between the square root of gill area and length (Hughes 1969; Foster-Smith 1975), respective gill area and length (Dral 1967).

Best evidence for a declining relative gill size with increasing body size can be extracted, however, from data that have been presented by Theisen (1982). He investigated the variations in size of (among others) the gills in relation to body size in *Mytilus edulis* from Danish waters. His index of gill size was given as the area circumscribed by the outline of the outer lamella of the outer left gill, while body size is given as the size of the area circumscribed by the outline of the right shell. Irrespective of the rather nonstandard character of the selected units, the general conclusions that can be drawn from his results provide strong evidence that gill size does not increase at the same rate as body size does.

Theoretically, if isometric growth is assumed, gill area and shell area should grow in a 1:1 ratio. Theisen (1982) found the power factor of the relationship between gill size and shell area to vary between 1.08 and 1.13 if the whole size range was included in the calculation. The plot of his data (cf. Fig. 4 in Theisen 1982) demonstrates that there is a steep increase of relative gill size in very small mussels, while the curve rapidly levels off in larger specimen. Theisen, therefore, recalculated the relationship, excluding all animals with a shell area of less than 5 cm<sup>2</sup> (representing *Mytilus* of up to about 35 mm shell length). In this case, the exponents of the relationship ranged from 0.96 to 1.1, indicating that in older animals increase in gill size is directly proportional to increase in shell area, i.e., proportional to length squared.

Though Theisen (1982) has not given any measurements of body size in terms of weight, his plot of mean relative gill size against mean shell area (cf. Fig. 5 in Theisen 1982) may reasonably well be transformed into the more usual plot of gill size against weight. Once his plot is converted to numerics, absolute gill size can be calculated and shell area (T) transformed to length (L), using the power relationship given by the author ( $T = 0.0053 L^{1.92}$ ,  $N = 322$ ,  $r^2 = 0.998$ ). When the length thus obtained is expressed in terms of relative weight, using the general approximation of  $W \propto L^3$ , a new plot of relative gill size against weight can be drawn as shown in Fig. 5.1A. If both variables are transformed logarithmically, and the data fitted by least square regression ( $a = 1.3085$ ,  $b = -0.438$ ,  $r^2 = 0.9435$ ), the close negative correlation between decreasing relative gill size and increasing body size becomes evident (see Fig. 5.1B). If, instead of relative, absolute gill size is used in the above relationship, the slope b of the regression line (cf. Fig. 5.1C) represents the constant  $d_g$  as defined in equation (2).

It is most obvious that the method of measuring the size of gills is of crucial importance to the description of the relationship defined in equation (2). A comparison of datasets extracted from Dral (1967), Hughes (1969) and Theisen (1982) for *Mytilus edulis*, however, revealed that the methodic approach is apparently influencing primarily the

intercept of the regression line in a plot of log weight against log gill size. In contrast, the slope - i.e., the value of  $d_g$  - is quite similar for all three datasets as shown in Fig. 5.2. The computed values of  $b$  (see Table 5.1 for the statistics of the regression analysis) vary between 0.51 and 0.72, thus remaining within the expected range. Being clearly different from 1, these values also indicate that gills in *Mytilus edulis* increase at a slower rate than does body size, though their actual values might have to be considered with some reservation.

a	$S_Y$	b	$S_b$	$r^2$	N	Source
0.131	0.070	0.51	0.035	0.937	16	Dral (1967)
1.024	0.743	0.72	0.011	0.998	10	Hughes (1969)
-0.692	0.040	0.56	0.016	0.965	46	Theisen (1982)

The variations are due on the one hand to methodic differences and the various approximations applied to the transformation of the data (weight, e.g., is expressed as the third power of the one-dimensional unit length). On the other hand, Theisen (1982) reports a high plasticity of the relative gill size of *Mytilus edulis*. He observed a tendency of gill size to be inversely related to turbidity. In view of the function of the gills as feeding apparatus, he hypothesized that relatively large gills will predominate in waters with low turbidity and hence limited food supply. In contrast *Mytilus* living in areas of high turbidity would develop comparatively smaller gills because of good food conditions.

### Oxygen Consumption in Bivalves

Pütter (1920) already hypothesized that metabolism should be proportional to the square of a linear dimension. This was later verified in various experimental studies (see, e.g., Krüger 1940; Kittel 1941) and then comprehensively presented by von Bertalanffy (1951, 1971), showing that the dependence of the metabolism on body size could be perceived as a special case of the general rule of allometric growth. If metabolism is expressed as oxygen consumption per unit of time (Q) and body size in weight related units, the general allometric growth equation  $y = a \cdot x^b$  becomes:

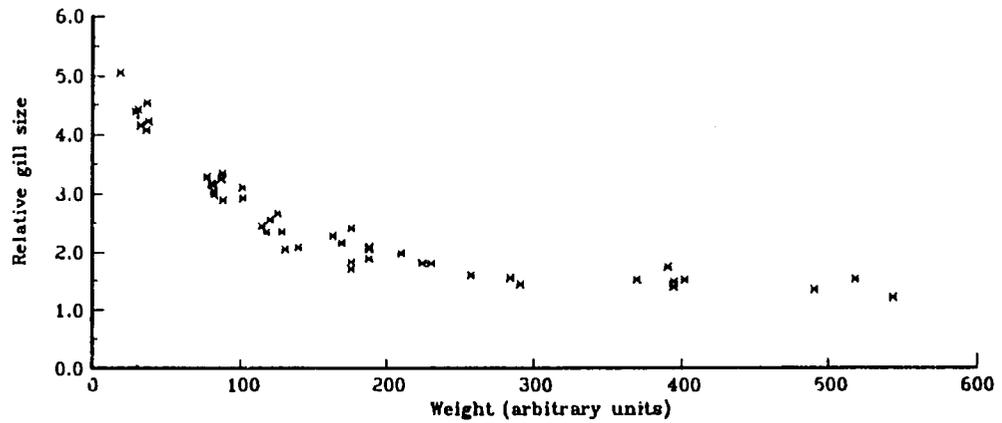
$$Q = a \cdot W^{d_o} \quad \dots 3)$$

where "a" is a species-specific constant and the exponent  $d_o$  usually ranges between 2/3 (surface-proportional respiration) and 0.95.

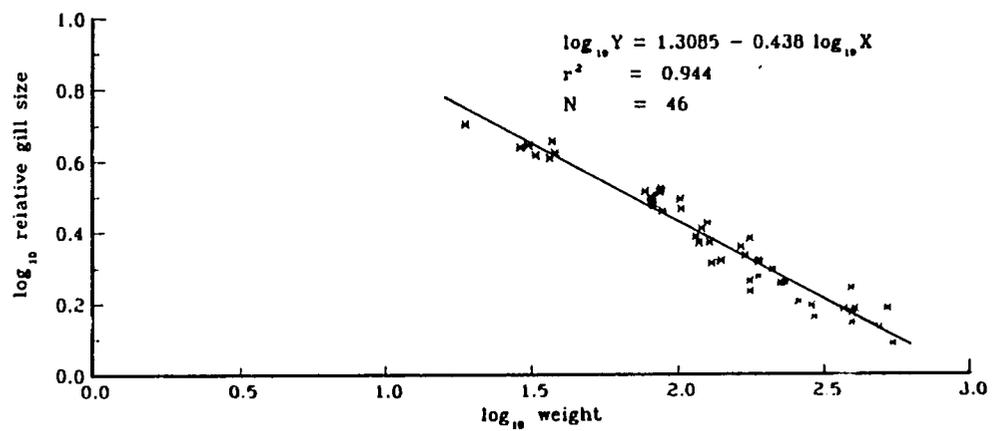
Pauly (1979) pointed out at the similarity that equation (3) has with the equation (2) which relates gill size to body weight. He also mentions that  $d_g$  should generally be equal to  $d_o$ . This means that respiration data could also be used to obtain estimates of the exponent of body weight in proportion to which the gill surfaces of bivalves increase.

Many authors have noted a considerable variation in the values of  $d_o$ , if the experiments are continued over an extended period of time. For *Mytilus edulis*, for example, Rotthauwe (1958) based his assumption of oxygen consumption being proportional to a surface ( $d_o = 0.68$ ) on data that were obtained during two months in

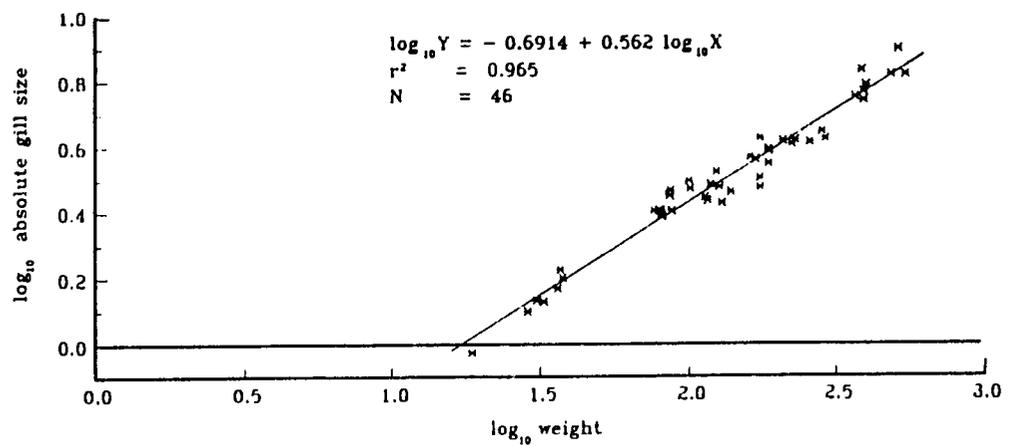
A) Plot of mean relative gill size against body size



B) Plot of relative gill size against body size



C) Plot of absolute gill size against body size

Fig. 5.1. Relationship between gill size and body size in *Mytilus edulis* (adapted from data in Theisen 1982).

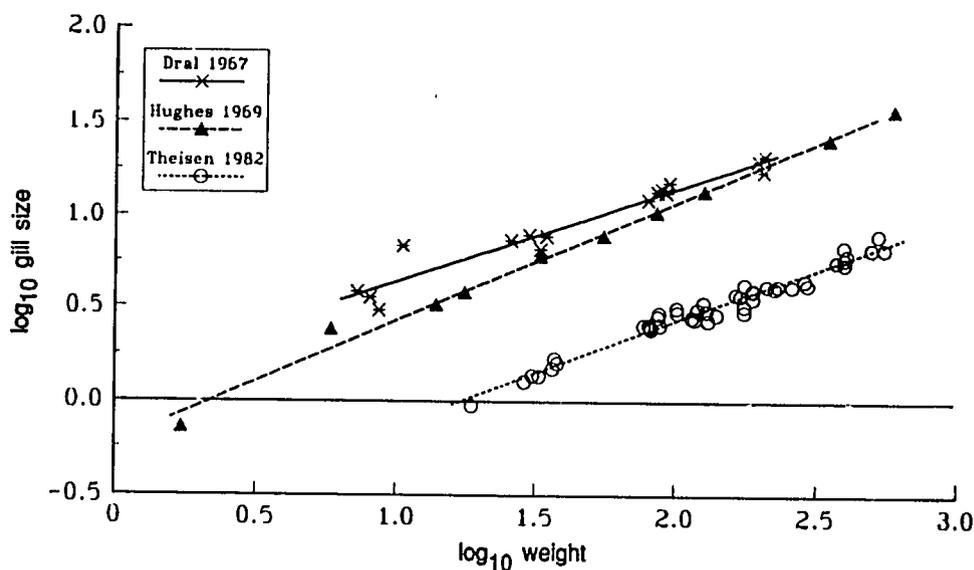


Fig. 5.2. Plot of gill size against weight in *Mytilus edulis*.

early spring. Krüger (1960) listed for the same species values ranging from 0.70 to 0.93 computed from respiration data covering the period of one year. He listed factors such as temperature, feeding condition, size range and water quality as definitely influencing the value of  $d_o$ . He suggested that a value of 0.8 would be a reasonable estimate of the mean  $d_o$  applicable to *Mytilus edulis*. Thompson and Bayne (1974), however, contended that environmental factors would primarily regulate the metabolic level "a" in equation (3) and that the weight exponent "b" (= 0.70 for *Mytilus edulis*) would remain rather stable. From this it cannot be excluded that variations in the exponent "b" might also be induced by experimental design.

Values of  $d_o$  and  $d_g$  extracted from the literature are summarized in Table 5.2. They range from 0.51 to 0.87, with the mean exponent of the allometric relationship being 0.68 (s.e.: 0.02, N: 21). This value allows the conclusion that gill growth in bivalves is in general proportional to length squared, and that the perception of gill size as the limiting factor in fish growth should also apply to the growth of bivalves. It also means that applying the original von Bertalanffy growth function to bivalves is in general physiologically correct. It should be noted that this is not the case, if the animals have consistently a  $d > 0.67$  (as in most larger fishes) which requires the introduction of an additional term (the gill surface factor D, Pauly 1979) which would make the application of the VBGF physiologically correct in all and not just the special case where  $d = 0.67$  (and hence  $D = 1$ ).

The line of arguments presented above is not invalidated by the ability of bivalves to switch to anaerobic metabolism during times of insufficient oxygen supply. As was shown earlier (see Anaerobic metabolism in bivalves, p. 10) this phenomenon is almost invariably accompanied by stagnant growth. Pamatmat (1980) demonstrated that anaerobic metabolism is proportional to body weight in that the exponent relating body weight to anaerobic heat production was equal to unity. This means that when bivalves switch to anaerobic respiration and oxygen gas exchange is no longer involved, metabolic rate scales linearly with body mass, as indeed expected in terms of the von Bertalanffy's growth theory. This clearly underlines once more the surface-limited character of aerobic

Table 5.2. Values of the exponent "d" of the weight/gill size relationship in various bivalves (based on morphometric (M) or respiratory (R) studies.)

Species	Value of d	M/R	Authority	Remarks
<i>Argopecten irradians</i>	0.87	R	Jorgensen (1976)	original data in Kirby-Smith (1970)
<i>Aulacomya ater</i>	0.66	R	Griffiths and King (1979)	
<i>Cardium edule</i>	0.58	M	Hughes (1969)	from Fig. 8A, with $W \propto L^3$
<i>Cardium edule</i>	0.63	M	Foster-Smith (1975)	from Fig. 3, with $W \propto L^3$
<i>Cardium edule</i>	0.77	R	Vahl (1972)	
<i>Chlamys islandica</i>	0.78	R	Vahl (1978)	mean of exp. 2-4, Tab. 4
<i>Chlamys opercularis</i>	0.65	R	McLusky (1973)	conv. from rel. oxyg. consumpt.
<i>Modiolus demissus</i>	0.80	R	Read (1962)	
<i>Mya arenaria</i>	0.58	M	Hughes (1969)	from Fig. 8B, with $W \propto L^3$
<i>Mytilus edulis</i>	0.51	M	Dral (1967)	from Fig. 12
<i>Mytilus edulis</i>	0.56	M	Theisen (1982)	from Fig. 5
<i>Mytilus edulis</i>	0.64	R	Read (1962)	
<i>Mytilus edulis</i>	0.65	M	Vahl (1973)	
<i>Mytilus edulis</i>	0.68	R	Rotthauwe (1958)	
<i>Mytilus edulis</i>	0.70	M	Foster-Smith (1975)	from Fig. 3, with $W \propto L^3$
<i>Mytilus edulis</i>	0.72	M	Hughes (1969)	from Fig. 8B, with $W \propto L^3$
<i>Mytilus edulis</i>	0.75	R	Vahl (1973)	
<i>Mytilus edulis</i>	0.84	R	Krüger (1960)	mean of 12 values
<i>Scrobicularia plana</i>	0.70	M	Hughes (1969)	from Fig. 8A, with $W \propto L^3$
<i>Venerupis pullastra</i>	0.65	M	Foster-Smith (1975)	from Fig. 3, with $W \propto L^3$
<i>Venus mercenaria</i>	0.65	M	Hughes (1969)	from Fig. 8A, with $W \propto L^3$
Mean	0.68			
s.e.	0.02			

metabolism, as it excludes the possibility that surface-limited metabolism is a general property of body tissues.

In conclusion, the general theory presented by von Bertalanffy can be expected to explain also the growth of bivalves well enough to allow the application of the von Bertalanffy growth function to the computation of growth parameters for bivalves.

## Materials and Methods

### Source of Data

The information on bivalve growth compiled for this study originates basically from two sources: 1) field experiments conducted in 1986-1987 by the author along the shore of the Gulf of Thailand; and 2) literature data.

The field experiments involved the culture of marked *Perna viridis* and *Anadara granosa*, two bivalve species of considerable economic importance in Thailand. The general set-up of these experiments had been described above (see p. 16). Regular monthly surveys yielded individual growth data covering a period of 6 (*P. viridis*) and 12 months (*A. granosa*), respectively.

A thorough scanning of the available literature was undertaken to obtain appropriate growth-related data from bivalves. A great deal of publications concerning the growth of bivalves from temperate waters could easily be identified through the use of the ASFA (*Aquatic Sciences and Fisheries Abstracts*) computer database, its entries for the years 1982 to 1989 being available as a CD-ROM based version at the Institut für Meereskunde, Kiel University. Reference lists given in key publications proved very

valuable in gaining access to earlier references, e.g., those published before World War II or in journals not covered by ASFA.

Identification and access to literature on the growth of tropical bivalve species turned out to be much more difficult than for those from temperate waters. Valuable information is often contained in publications that are either - technically seen - not published (internal reports, theses, manuscripts, etc.) or inadequately covered by established computer databases, thus forming the bulk of the so-called "grey literature". But even if sources have been identified, access to the information is often hampered by the lack of funds to produce and send copies of requested reports, the vagaries of mailing, or the simple fact that, especially in Southeast Asian countries, many interesting scientific reports are published in the respective national language.

Search for appropriate material on tropical bivalves, therefore, had to be based on the author's own reprint collection which contains a substantial amount of bivalve publications from Southeast Asia accrued during his stay in Thailand. Another valuable source was the personal reprint collection of Dr. Daniel Pauly, ICLARM, whose database of over 20,000 titles are available on the mainframe computer VAX V780 of the Institut für Meereskunde, Kiel, and can be accessed via the PERSONAL LIBRARIAN software.

The information searched for in the literature were either estimates of parameters of the von Bertalanffy growth function (VBGF), or "growth data" presented in such a form that they could be used to estimate those parameters. Where published, relevant data were recorded on environmental parameters, especially temperature, but also relative shore position, and growth condition.

If not mentioned otherwise, growth in the context of this work is defined as the increase in size of an animal along a given length axis. Because of the morphological particularity of bivalves, the term "length" does not necessarily refer to the anterior-posterior axis of the animal, but can also be a linear dimension along the dorso-ventral line. Which of the possible dimensions is chosen for length measurements is usually decided upon on purely practical grounds. However, for the data to remain comparable within a species, publications that contained length measurements with a dimension different from the dimension used by the majority of authors were either ignored or - when possible - transformed to the standard dimension by means of an appropriate conversion factor.

Growth data are presented in the literature either in tabular form or graphically. While data from tables could be used directly for further analysis, graphics were first converted to numeric information. This was done by measuring the X, Y-coordinates of data points on enlarged reproductions of the graphs and converting those to absolute values using the given X, Y-scales. The datasets thus obtained were essentially of three types: 1) length-frequency data; 2) length-at-time data; and 3) length increment data.

These categories might comprise quite different kinds of data but are characterized in that each of them requires its own specific method of analysis.

### ***The Seasonalized von Bertalanffy Growth Function***

The physiological aspects of bivalve growth presented above (see p. 38) give evidence enough to assume reasonably that in general the growth of bivalves is adequately described by the von Bertalanffy growth function (equation (1)).

Various authors have presented models that extend the original VBGF to express seasonal variations in growth (Ursin 1963; Pitcher and MacDonald 1973; Lockwood 1974; Cloern and Nichols 1978; Pauly and Gaschütz 1979). Among these models, the one

presented by Pauly and Gaschütz (1979) has been widely accepted, primarily because its additional parameters can be interpreted biologically and are estimated easily by means of multiple linear regression (Moreau 1987).

Pauly and Gaschütz (1979) incorporated a sine wave into the original VBGF such that equation (1) became

$$L_t = L_{\infty} (1 - e^{-K(t - t_0)}) \cdot \frac{CK}{2\pi} \sin 2\pi (t - t_s) \quad \dots 4)$$

with  $C$  = amplitude of the growth oscillation, with values ranging from 0 (no seasonal oscillation) to 1 (growth stop once per year);

$t_s$  = time between birth and the onset of the first growth oscillation; and

$L_{\infty}$ ,  $K$ , and  $t_0$  the parameters of the original VBGF as defined in equation (1).

Independently, Hoenig and Choudary Hanumara (1982) and Somers (1988) presented slight modifications of the Pauly and Gaschütz (1979) model, which were essentially of the same form and introduced an additional term to ensure that  $L_t = 0$  at  $t = t_0$ . In the model presented by Somers (1988), the equation reads:

$$L_t = L_{\infty} (1 - e^{-K(t - t_0)}) \cdot \frac{CK}{2\pi} \sin 2\pi (t - t_s) + \frac{CK}{2\pi} \sin 2\pi (t_0 - t_s) \quad \dots 5)$$

The "seasonalized VBGF" in both equations (4) and (5) reduces to the original VBGF if the parameter  $C$  is set equal to zero, i.e., if seasonality is not considered.

## ***Analysis of Growth Data***

### ***LENGTH-FREQUENCY DATA***

Length-frequency datasets were tabulated using either the original data or sets extracted from graphs. Where appropriate, length classes were regrouped into larger units to smooth the distributions and/or to make modes more clearly visible. It was checked whether the distribution of discernible modes showed any shift towards greater lengths during the time of observation. If this was not the case, some sort of sampling bias was assumed and the dataset excluded from further analysis. Similar, single mode distributions of length-frequencies covering only a relatively small part of the possible total size range of the animals were omitted, as the inferences on growth drawn from such limited samples can lead to rather erroneous results (see contributions in Pauly and Morgan 1967).

The analysis of length-frequency data was done using the ELEFAN I program of the "Compleat ELEFAN" software package of Gayanilo et al. (1988) for MS-DOS based microcomputers. The latest version of this program incorporates the seasonal oscillating growth function (equation (5)) proposed by Hoenig and Choudary Hanumara (1982) and Somers (1988). Application of the software and its various features are extensively documented in the program's manual (Gayanilo et al. 1988). In addition to the previously defined parameters  $L_{\infty}$ ,  $K$ ,  $C$ , and  $t_s$ , the program also provides an estimate of WP, the "winter point", i.e., the time of the year with minimum growth, defined as  $WP = t_s + 0.5$ . The goodness with which an identified set of growth parameters fits a given dataset is indicated by the index "Rn". This index is computed from  $Rn = 1/10 * 10(ESP/ASP)$  (ESP: explained sum of peaks, ASP: available sum of peaks), and can range from 0 (= no fit) to 1 (best fit).

The question whether the algorithms incorporated in the ELEFAN program will always find the "true" parameters of the VBGF has been object of a number of investigations. Using datasets simulated from known growth parameters, the error of the calculated parameters found to be related to the variability of the lengths about the mean ages, with high variabilities resulting in overestimates of  $L_{\infty}$  and underestimates of  $K$ . These biases are largely compensatory, however, with the effect that the overall assessment of the growth potential of organisms is generally reliable (Isaac 1989).

#### *LENGTH-AT-TIME DATA*

The bulk of datasets extracted from the literature consisted of either length-at-age data or length at a given time, with "time" expressed in standard units such as day, month or year. Except for data on individually tagged animals, the given length usually represents the mean of a number of measurements and the resulting difference in length between two data points depicts the mean growth of a population for the respective time interval. In cases where the unit of time was less than a year, and the dates pertaining to the data points were given or could be interpolated from the graphs, these were used to calculate time intervals. If only mean length per month was given without exact definition of the sampling date, sampling was assumed to have occurred on the 15th of a month, and the time elapsed between samples computed accordingly.

Aging of bivalves is generally done by interpreting growth marks on the surface or within the microstructure of shells. This method, resulting in (mean) length-at-age data, has drawn much criticism. Especially the reliability of interpreting external shell marks as annual rings or "annuli" has frequently been questioned. This point had been discussed in detail above (see p. 9).

With this criticism in mind, length-at-age data were screened with regard to their general agreement with biological data known for the species in question. If in a dataset a large deviation was detected from an assumed "standard growth" at least for the period of most prominent growth and no satisfying explanation was given by the author, the data were excluded from further analysis.

The other type of data represents a series of continuous growth increments with known time interval, with the special feature that the end date of one interval is identical with the start date of the next interval. Even though nothing is known about the absolute age of the animals, this kind of data can be turned into "length-at-relative age" data, by assigning an arbitrary "age" to the first data point and expressing all remaining data of the given set in related age units, using the known time intervals. This allows the dataset to be analyzed in the same way as true length-at-age data, with the exception that the parameter  $t_0$  would need a correction term to become meaningful.

For the purpose of the present analysis the problem arising with the interpretation of the parameter  $t_0$  was of no importance. The parameter  $t_0$  defines solely the origin of a growth curve, but does not influence its shape and, hence, a comparison of growth parameters. Both kinds of data, therefore, were grouped into the same category and analyzed with the same tools. However, to avoid any possible confusion about the meaning of the "age" data, this category was termed "length-at-time" data, and results concerning the parameter  $t_0$  omitted. Where needed, a value  $t_0$  arbitrarily set at 0 was used to allow, e.g., the graphic presentation of growth curves.

A major restriction to the use of mean length-at-time lies in the necessary statistical evaluation of the mean. No objection to its use can be made if the arithmetic mean results from a dataset with a unimodal distribution, normally distributed around the mean

and with a similar variance for all samples included. A frequent deviation from these prerequisites are distributions that are skewed to some degree, which would make it more appropriate to use the median or the mode of the distribution. Polymodal distributions should be, of course, completely rejected for use with this method.

Unfortunately, many datasets of mean length-at-time are presented in the literature in such a way that no judgement is possible of the precision and accuracy of the computed mean. Nevertheless, care was taken to identify probably inappropriate datasets by examining any additional information given such as standard deviation of the mean and range of data.

Length-at-time data were analyzed using a yet unreleased version of a program for MS-DOS based computers, which was made available to the author by courtesy of M.L. Soriano and D. Pauly, both from ICLARM. This program is a modified version of the "ETAL 1" program of Gaschütz et al. (1980), and shall here be called "ETAL 2".

ETAL 2 implements a linearized version of Somers' (1988) equation (equation (5)), presented by Soriano and Jarre (1988):

$$\ln\left(1 - \frac{L_t}{L_\infty}\right) = -Kt + Kt_0 - \frac{CK}{2\pi} \sin 2\pi(t - t_s) + \frac{CK}{2\pi} \sin 2\pi(t_0 - t_s) \quad \dots 6)$$

The program estimates iteratively the parameters of equation (6) through multiple regression analysis by minimizing the error sum of squares. The parameters thus obtained are then used as seed values to compute the final parameters via a nonlinear fit routine, which uses the Gauss-Newton method for nonlinear models. As mentioned above, setting  $C = 0$  reduces equation (6) to the linearized form of the original VBGF.

The results obtained in this fashion comprise the parameters of the VBGF and their respective standard error, as well as the sum of squares of the residuals (RSS) for an assessment of the goodness of fit of the model to the data. This information -together with a visual inspection of the position of the resulting growth curve relative to the data points - was used to decide whether a computed set of growth parameters could be accepted or had to be omitted from the database because of obviously inappropriate data.

#### LENGTH INCREMENT DATA

Length increment data are typically data obtained from mark/recapture experiments. Occasionally they also originate from growth experiments with batches of bivalves of different sizes raised separately for a specific amount of time. While in the first case the data refer to a single specimen, average length of the whole subsample might be used in the second case. These data differ from the previously described length-at-time data insofar that the observed time interval is rather short, and that growth observation usually does not carry over into a second, third, etc. observation interval. Instead, information is mainly deduced from the growth increment per unit time in relation to the starting length.

In the older literature, estimation of the growth parameters  $L_\infty$  and  $K$  from length increment data is often based on the Gulland and Holt plot, which is a plot of size increments per unit time against the mean size of the respective increment (Gulland and Holt 1959). This model is also implemented as a routine in the "Compleat ELEFAN" software, and was used with growth increment data that referred all to one and the same time interval.

In cases where growth increments pertained to varying time intervals covering the period of approximately a whole year, a test was performed to assess whether the

application of a model incorporating a seasonally oscillating growth curve improved the parameter estimation. Such a method was suggested by Soriano and Pauly (1989) and is also available as an option in the appropriate routine of the Compleat ELEFAN package. The method uses a modified version of the VBGF formulated by Appeldoorn (1987), which - after incorporation of the modification suggested by Somers (1988) - took the form:

$$L_2 - L_1 = L_{\infty} \left[ 1 - \left( 1 - \frac{L_1}{L_{\infty}} \right) e^{-K(t_2 - t_1)} + \frac{CK}{2\pi} [\sin 2\pi(t_1 - t_s) - \sin 2\pi(t_2 - t_s)] \right] \quad \dots 7)$$

Soriano and Pauly (1989) showed that equation (7) can be linearized, thus taking the form of a multiple linear regression, from which the parameters  $L_{\infty}$ ,  $K$ ,  $C$ , and  $t_s$  can be estimated iteratively by means of the least square method. The routine implemented in the Compleat ELEFAN uses a "seed" value of  $L_{\infty}$  to obtain preliminary estimates of  $K$ ,  $C$ , and  $t_s$ . The initial estimate of these parameters is then improved by altering the value of  $L_{\infty}$  in a way that maximizes the corresponding multiple coefficient of determination ( $R^2$ ).

### **Temperature Data**

Data on mean annual water temperature as well as annual minimum and maximum temperature were compiled using the following order of priority:

- published in the same source together with growth parameters or growth data;
- published in a different source but applying to the area from where growth parameters (or data) were obtained; or
- where no such data are available, temperature estimates interpolated from information contained in the *World Atlas of Sea Surface Temperatures* (Anon. 1944). For freshwater bivalves, temperatures were either those published by the cited author or annual mean air temperature at the closest weather station given in Walter and Lieth (1967), a procedure also used by Pauly (1979) in his comparison of fish growth parameters and environmental temperature.

### **Estimates of Mortality Rates from Field Experiments**

In fisheries biology, mortality of a cohort of fish or invertebrates is usually expressed as:

$$N_t = N_0 \cdot e^{-Zt} \quad \dots 8)$$

where  $N_0$  represents the number of fish at the beginning of time interval  $t$  and  $N_t$  the number of surviving fish at the end of  $t$ .  $Z$  is the instantaneous rate of total mortality, which is the sum of natural ( $M$ ) and fishing ( $F$ ) mortality, i.e.,

$$Z = M + F \quad \dots 9)$$

From the culture experiments at Ang Sila, Thailand, estimates of the parameter  $Z$  valid for the period of experimental culture were obtained from a plot of the natural logarithm of the number of bivalves surviving ( $N_t$ ) against their (relative) age ( $t$ ). This is based on a linearized version of equation (8) which has the form

$$\ln N_t = a + bt \quad \dots 10)$$

and from which the parameters  $a$  and  $b$  can be estimated by means of least square regression. The slope  $b$  of the regression, with sign changed, gives an estimate of the instantaneous rate of total mortality ( $Z$ ).

### **Estimates of Relative Yield**

In order to assess the influence of relative shore level on productivity, a comparison of the "yield potential" was made for *A. granosa* raised at SITE I and SITE II, respectively. For this purpose the parameters of  $L_{\infty}$ ,  $K$ , and  $Z$  computed for each site were used as input in a modified version of the classic yield-per-recruit model of Beverton and Holt (1957). This modified version (Beverton and Holt 1964) has the advantage of requiring less input parameters than the original one. The model consists of a plot of relative yield per recruit ( $Y'/R_r$ ) on a series of exploitation rates ( $E$ ). It has the form

$$Y'/R_r = E(1 - c)^{MK} \cdot \left( 1 - \frac{3 \cdot (1 - c)}{1 + \frac{(1 - E)}{MK}} + \frac{3 \cdot (1 - c)^2}{1 + \frac{2 \cdot (1 - E)}{MK}} - \frac{(1 - c)^3}{1 + \frac{3 \cdot (1 - E)}{MK}} \right) \quad \dots 11)$$

with  $c = L_c/L_{\infty}$ ,  $E = F/(M+F)$ , where  $M$ ,  $F$ ,  $K$ , and  $L_{\infty}$  are parameters as previously defined.  $L_c$  is the mean length at first capture. It should be noted that  $Y'/R_r$  has no dimension, yet it is proportional to the traditional yield per recruit, which is expressed in units of weight (Pauly 1984).

### **Comparison of Growth Performance**

#### *THE PHI PRIME ( $\phi'$ ) CONCEPT*

Empirically, and based on theoretical grounds as well, Pauly (1979) demonstrated that for related fishes and invertebrates whose growth can be described by the von Bertalanffy growth function, double logarithmic plots of  $K$  against  $W_{\infty}$  are linear with a mean slope of 2/3:

$$\log_{10} K = a - 0.67 \log_{10} W_{\infty} \quad \dots 12)$$

Munro and Pauly (1983) argued that this implicated that the differences in the growth performance of different organisms should be solely reflected by differences in the value of the Y-axis intercept. Renaming "a" as the parameter "phi" ( $\phi$ ), they rearranged equation (12) to the form

$$\phi = \log_{10} K + 0.67 \log_{10} W_{\infty} \quad \dots 13)$$

and showed that indeed the distribution of  $\phi$  values for a given species computed from published growth parameters were essentially normally distributed and rather sharply peaked.

Pauly and Munro (1984) showed that this concept could also be used to compare growth in terms of length, when it can reasonably be assumed that  $W \propto L^3$ . They introduced a new parameter, "phi prime" ( $\phi'$ ), which is defined as:

$$\phi' = \log_{10}K + 2\log_{10}L_{\infty} \quad \dots 14)$$

In the context of the present study, a value of  $\phi$  was computed for every pair of the growth parameters  $L_{\infty}$  and  $K$ . The distribution of these values were plotted for single species. Values of  $\phi'$  that differed markedly from other values for the same species were considered an indicator for a possible bias in the parameter estimation.

#### THE GROWTH INDEX P AND THE AUXIMETRIC GRID

In his discussion of comparison of the growth performance of fishes, Pauly (1979) argued that an index of growth performance should be independent of the actual shape of the growth curve defined by the parameters  $L_{\infty}$  and  $K$  or  $W_{\infty}$  and  $K$ . He suggested to use the growth rate at the inflection point of a weight growth curve as standard for growth comparison. Because of the mathematical properties of a sigmoid weight growth curve, this point represents in all species the maximum growth rate, irrespective of the shape of the curve.

The slope at the inflection point of a weight growth curve is defined as:

$$\left(\frac{dw}{dt}\right)_{\max} = 4/9 \cdot K \cdot W_{\infty} \quad \dots 15)$$

where  $K$  and  $W_{\infty}$  (= asymptotic weight) are parameters of the VBGF. The parameter  $P$  was defined by Pauly (1979) such that

$$\left(\frac{dw}{dt}\right)_{\max} = 4/9 \cdot 10^P \quad \dots 16)$$

with

$$P = \log_{10}(K \cdot W_{\infty}) = \log_{10}K + \log_{10}W_{\infty} \quad \dots 17)$$

Computation of the index  $P$  for bivalve species faces a problem insofar that practically no weight data are available that allow a direct estimation of  $W_{\infty}$ . As a consequence,  $W_{\infty}$  would have to be determined by converting an estimate of  $L_{\infty}$  into its equivalent  $W_{\infty}$  through use of an appropriate length-weight relationship of the form

$$W = a \cdot L^b \quad \dots 18)$$

"Weight" in bivalves, however, is a much more variable term than it is in fish. The weight of a bivalve is determined by three single components, i.e., the weight of the meat, of the shell, and of the cavity water retained inside the shell. Because the gonads make up a large part of the body mass, the "meat" weight itself is also very variable and is closely related to reproduction cycle. In order to ensure that growth parameters converted to weight remained comparable, and given the general lack of appropriate individual length-weight relationships, it was decided to use an approximation of the form  $W \propto L^3$  to convert estimates of  $L_{\infty}$  into their corresponding  $W_{\infty}$  estimate.

The values of  $P$  obtained from equation (17) are pictured in an "auximetric grid", proposed by Pauly (1979) for the comparison of fish growth. In this grid, values of  $\log_{10}W_{\infty}$  (in g) are plotted against values of  $K$  (year<sup>-1</sup>), with the scale of the abscissa being linear, while the ordinate is given on a logarithmic scale. Lines connecting pairs of  $\log_{10}W_{\infty}$  and  $K$

with the same  $P$  value are drawn at regular intervals and form the "grid". Thus, a computed parameter  $P$  represents the distance of a given pair of growth parameters from a "base line" where  $P = 0$ , which allows a direct comparison of growth performance with other species or stocks.

## Results and Discussion

### *Growth Experiments with Bivalves in Thailand*

#### *PERNA VIRIDIS*

##### Estimation of growth parameters

The experimental culture of *Perna viridis* at Ang Sila, Thailand, lasted from June to December 1986. A general overview of the experimental progress was given p. 22. The individual length measurements of the tagged mussels recorded during the monthly surveys are summarized in Appendix 1. Also given for each month is the mean length of the whole sample including those mussels that had their tag lost, but were still found in the sample. In December 1986, at the end of the growth experiment with *P. viridis*, a total of 32 mussels were recovered, which still could be identified by their tag (see Table 4.1). The length recorded for these mussels during each survey formed the dataset which was further analyzed to obtain estimates of growth parameters of the von Bertalanffy growth formula for *P. viridis*.

In order to transform the data into length-at-time data for estimation of growth parameters, it was assumed that the mussels had an age of approximately 7 months at the beginning of the experiment in June 1986. Accordingly, an age of 213 days (= 0.58 years) was assigned to the first sampling date, and all following sampling dates were expressed in corresponding ages relative to the age in June.

The ensuing analysis revealed that out of the 32 datasets available, only 15 sets allowed the estimation of growth parameters. The structure of the remaining datasets did not permit the fitting of a growth curve to the data with the method selected. This was especially the case if data increments were very irregular, which might have been produced by erroneous length readings during one of the surveys.

In a next step, the computed growth parameters were checked for consistency. Those parameters were omitted that were the result of a very poor fit, expressed by a relatively high value of the standard error, or high sum of squares of residuals. Also omitted were parameters which had values that were completely outside the range of what could reasonably be expected, such as negative values or, e.g., estimates of  $L_{\infty}$  of more than 160 mm.

This procedure reduced the original set of growth data to a subsample totaling eight specimens for which reasonable growth parameters were obtained. The large number of "failures" have most probably to be attributed to the fact that every dataset consists of a mere seven data points covering a relatively short life span of *P. viridis*. Any pronounced deviation of one of the data points from a growth curve assumed to be adequately described by the VBGF has, therefore, a much stronger influence on the computation of the parameters than it would have, if more data points were available.

The individual growth data for the eight specimens of *P. viridis* which yielded acceptable growth parameters are summarized in Table 5.3. On an average this subsample grew from 62.09 mm (s.e. = 0.66) in June 1986 to 80.53 mm (s.e. = 0.86) in

December 1986, or 3.1 mm-month. This is comparable to the general growth of the mussels in this experiment. The average length computed from all mussels in the whole sample (see Appendix 1) increased from 63.75 mm (s.e. = 0.51) in June to 84.75 mm (s.e. = 0.94) in December 1986, representing an average growth in length of 3.5 mm-month.

Computation of growth parameters for *P. viridis* was based on each of the three following length-at-time datasets:

- individual length per month of the mussels from the subsample listed in Table 5.3; this provided also a mean value (and its statistics) for each parameter, averaged from the eight single parameter estimations obtained from the subsample;
- mean monthly length computed from the mussels in the subsample (see Table 5.3);
- mean monthly length computed from the total number of mussels in the whole sample, as given in Appendix 1.

Site:	Fish trap						
Period:	June-December 1986						
Sampling month:	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Est. age (years):	0.58	0.67	0.75	0.84	0.93	1.01	1.09
Tag No.							
Y 1	61.85	69.00	70.75	71.55	74.90	76.60	77.80
Y 2	59.65	67.50	71.45	72.95	78.85	81.55	84.35
Y 5	65.00	72.55	74.15	76.30	80.55	82.70	84.30
Y 12	59.85	65.75	67.60	69.45	74.90	74.70	76.70
Y 26	67.30	72.65	77.10	78.05	84.40	87.10	87.90
R 22	57.75	64.65	64.95	66.00	70.45	70.85	71.00
R 30	64.40	72.30	71.10	73.65	74.55	76.10	78.25
W 9	60.90	68.85	72.05	74.55	78.10	82.55	83.95
N	8	8	8	8	8	8	8
Mean	62.09	69.16	71.14	72.81	77.09	79.02	80.53
s.e.	0.66	0.65	0.70	0.72	0.76	0.84	0.86

The growth parameters for the individual mussels, as computed with ETAL 2, are summarized in Table 5.4, together with their respective statistics (SE, RSS) and the calculated  $\phi'$ . Attempts to fit the data to a seasonal oscillating growth model proved impossible as expected, given the short period covered by the data.

The computed growth parameters of the individual animals display a rather large variation. The values of asymptotic length range from 73.2 mm to 107.9 mm, those of the parameter K vary between 1.46 and 4.42 year<sup>-1</sup>. This variability becomes even more obvious when the corresponding individual growth curves are plotted for a period of three years (Fig. 5.3). In contrast to the variance observed in the single growth parameters, the computed values of the parameter  $\phi'$  cover only a very limited range (4.21-4.43). The mean  $\phi'$  is 4.29 with the 95% confidence interval extending from 4.23 to 4.35.

In this respect, it is interesting to have a closer look at the growth parameters computed for the animal with Tag No. R 30 (cf. Table 5.4). While the parameter  $L_{\infty}$  has the lowest SE-value (2.99) in the subsample, the corresponding K is comparatively very high, as is its SE-value. The resulting growth curve (cf. Fig. 5.3) implies that the animal would have completed almost all of its growth within the first half year, an assumption that

Table 5.4. Suspended net culture of *Perna viridis* at Ang Sila, Thailand; summary of the parameters of the von Bertalanffy growth function (VBGF) and their corresponding  $\phi'$ . (Parameters  $L_{\infty}$  and  $K$  and their statistics computed by means of the ETAL 2 program without application of the seasonalized VBGF).

	$L_{\infty}$ (mm)	SE	K (year <sup>-1</sup> )	SE	RSS	$\phi'$
Tag No.						
Y 01	80.31	3.195	3.5321	1.364	6.678	4.36
Y 02	102.32	14.965	1.6444	0.867	8.063	4.24
Y 05	92.85	7.422	2.2463	1.034	6.654	4.29
Y 12	84.42	7.265	2.2617	1.143	6.545	4.21
Y 26	107.87	18.842	1.4629	0.965	8.073	4.23
R 22	73.17	3.079	3.9735	1.913	9.398	4.33
R 30	78.38	2.988	4.4183	2.520	12.700	4.43
W 09	96.98	9.794	1.9593	0.859	6.839	4.27
Mean:	89.54	8.444	2.687	1.333	8.119	4.29
s.d.	12.08		1.10			0.07
s.e.	3.49		0.32			0.02
Parameter from mean length in subsample	88.10	6.379	2.352	1.016	5.861	4.26
Parameter from mean length in total sample	127.47	59.687	0.768	0.879	6.293	4.10

is very unlikely, given the general growth pattern of this species (Vakily 1989). For this mussel, the fitting of the growth parameters has also produced the largest RSS, and the computed  $\phi'$  (= 4.43) is the only one that drastically deviates from the general distribution of this parameter in the subsample. This clearly demonstrates that unreliable growth parameter estimates are very likely to be associated with extreme  $\phi'$  values.

When comparing the means of  $L_{\infty}$  (= 88.1 mm) and  $K$  (= 2.352 year<sup>-1</sup>) computed from the set of eight single growth parameter estimates with the parameters estimated from the mean length in the subsample, there is only little difference between the two approaches (see Table 5.4). This expresses itself also in the very similar values of  $\phi'$  (4.26 vs. 4.29). It is, therefore, concluded that the estimation of growth parameters from average length in a sample yields reliable results, as long as the mean is approximately normally distributed and the variance stays small.

The parameters estimated from the mean of the total sample differ markedly from the two previous sets (see Table

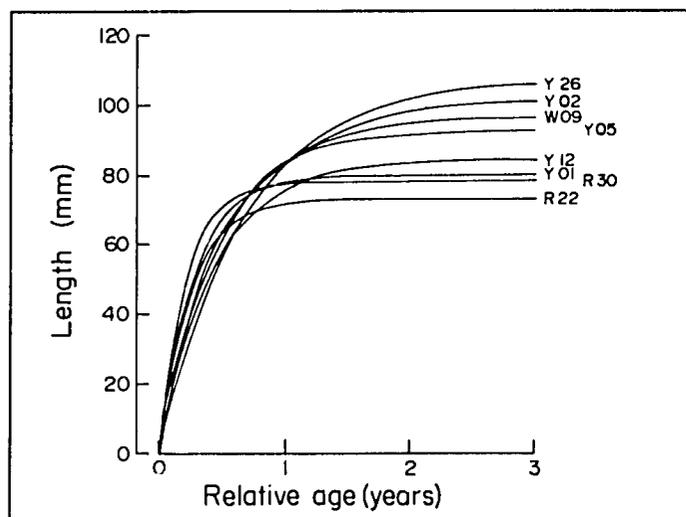


Fig. 5.3. Single growth curves of marked *Perna viridis* raised in suspended culture at Ang Sila, Thailand, in 1986. (Tag No. of specimen indicated to the right of each growth curve).

5.4). With an  $L_{\infty}$  of 127.5 mm, the estimate of asymptotic length is almost 50% higher than the one obtained from the subsample. As, on the other hand, the value of  $K$  is much lower ( $0.768 \text{ year}^{-1}$ ), the corresponding  $\phi'$  parameter ( $= 4.10$ ) still remains close to the average  $\phi'$  calculated from the subsample, though it underestimates it by approximately the same amount as previously described for the mussel with Tag No. R 30.

When attempting to assess the reliability of this growth parameter estimation, it is interesting to note that both the sum of the squares of the residuals (RSS) and also the standard error (SE) of  $K$  are well below the average, but that the SE-value of the asymptotic length ( $= 59.7 \text{ mm}$ ) exceeds the average by a factor of 7, which is a strong indication for a biased estimate of  $L_{\infty}$ .

#### Mortality

Mortality of *P. viridis* occurring in the course of the field experiments were monitored during the monthly surveys. Dead bivalves were identified by their tag and their death marked with a "D" in the survey protocol (see Appendix 1). The dead animals were removed from the sample and retained for later analysis of shell microstructures.

During the culture of *P. viridis* all mortality occurred in November 1986 with the exception of one dead mussel in October (see Appendix 1.3). Given the fact that in all other months mortality is practically nonexistent, this sudden "mass mortality" in November is, however, considered not to be naturally caused. This assumption is also supported by the observation that eight out of the twelve mussels recorded dead originated from the same net-bag, in which they were cultured. Most probably, this unexpectedly high mortality was either caused by inappropriate handling during the previous survey or through some unreported manipulation of the sample by the guard living on the fish trap. Given the uncertainties concerning the causes of the observed mortality, no attempt was made to compute estimates of the coefficient of total mortality for *P. viridis*.

#### Growth comparison

In order to display the general growth of *P. viridis* in this experiment, the parameters  $L_{\infty}$  and  $K$  were averaged for the subsample (see Table 5.4). The corresponding growth curve is displayed in Fig. 5.4 (solid line). The  $\phi'$  characterizing this growth curve is 4.33, well within the 95% confidence interval of the mean  $\phi'$  computed for the subsample.

It is now, of course, of primary interest to assess how the growth described by the growth curve in Fig. 5.4 compares with the growth of this species elsewhere. For this purpose, two questions have to be answered: (i) Are the growth parameters as such reliable? and (ii) If they are not biased, how good or how bad is the growth compared to other stocks of *P. viridis*?

An assessment of the quality of the growth parameters  $L_{\infty}$  and  $K$  obtained for *P. viridis* in the

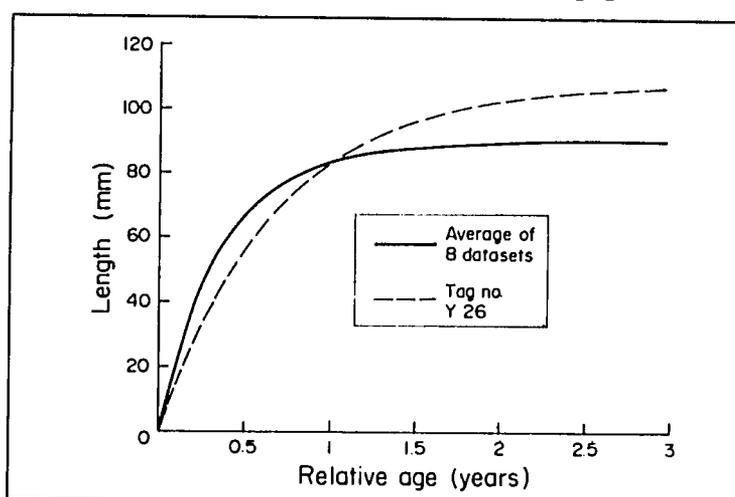


Fig. 5.4. Growth curves of marked *Perna viridis* raised in suspended culture at Ang Sila, Thailand, in 1986. Solid curve is based on parameters averaged from eight specimens ( $L_{\infty} = 89.54 \text{ mm}$ ,  $K = 2.687$ ), while the dotted curve represents the growth of a single mussel with the Tag No. Y 26 ( $L_{\infty} = 107.87 \text{ mm}$ ,  $K = 1.463$ ).

experiments is best done by comparing the resulting  $\phi'$  with an average  $\phi'$  computed for this species. This is based on the perception of  $\phi'$  as a "species-specific" parameter that varies for a given species only within a relatively narrow range. Empirical evidence for the applicability of this assumption in fish has been presented by Pauly and Munro (1984) and Longhurst and Pauly (1987). Further below, it will be demonstrated that in general this concept also applies to bivalves.

Growth parameters for *P. viridis* summarized in Appendix 4 were used to compute a number of  $\phi'$  values for this species (note that the mussel with the Ref. No. 120 was omitted for reasons that will be explained later). These combined resulted in a mean  $\phi'$  of 4.27 (s.e. = 0.01, N = 10) with the range of values extending from 4.09 to 4.57. As stated before, the curve depicting the growth of the mussels in the experiment is based on growth parameters that result in a  $\phi'$  of 4.33. This value is close enough to the average  $\phi'$  value computed for *P. viridis* to allow the conclusion that the growth parameters obtained from the field experiments are not biased but are biologically in agreement with the general growth performance of this species.

If the growth parameters as such can be accepted as reliable, the progression of the curve and especially the asymptotic length computed for this sample should give some insight on how the culture method in net-bags affected the growth. It should be recalled here that *P. viridis* in Thailand is normally grown on bamboo poles and harvested after about six to seven months, when the mussels have attained a length of 50 to 60 mm (Tuaycharoen et al. 1988). Though the experimental culture period was relatively short, it covered the second half of a year, during which the mussels usually still continue to grow before reaching their average maximum size towards the middle of the second year.

The growth curve in Fig. 5.4 depicts a very rapid decrease in growth rate between the relative age of 0.5 and 1 year and practically no growth thereafter. When compared to the growth parameters presented by Tuaycharoen et al. (1988) for *P. viridis* grown on bamboo poles in commercial mussel farms in the northern part of the Gulf of Thailand ( $L_{\infty} = 107.2$ ,  $K = 1.07$ ) the average growth of the mussels after they had been transplanted from the bamboo poles into the net-bags was similar in the second half of the first year, but is then much reduced compared to those continually raised on bamboo poles. This difference becomes apparent when looking at the growth curve representing the mussel with Tag No. Y 26, which is also included in Fig. 5.4 (dotted line). From the author's own experience and judging from the information given in Brohmanonda et al. (1988a) and Tuaycharoen et al. (1988), this growth curve seems to describe fairly well the typical growth of commercially cultured *P. viridis* in the Gulf of Thailand.

A conclusive explanation of the possible reasons of growth reduction in the net-bags cannot be offered at present. Disturbance by the monthly handling can be excluded as a cause, as the growth in the net-bag that served as control was even slower compared to those that were regularly sampled. Though the reduction in space within the net-bags with increasing size of the mussels might have played a role, other factors, such as man-induced frequent disturbances can also have contributed to the general reduction in growth performance.

#### ANADARA GRANOSA

##### Estimation of growth parameters

The experimental culture of the cockles (*Anadara granosa*) in cages at Ang Sila, Thailand, lasted for 11 months from March 1986 to February 1987. However, due to the

theft of all cockles from the nearshore site in February, growth data for SITE I are available for only 10 months. The monthly length measurements of the tagged cockles are summarized in Appendix 2. Also indicated for each month is the average length of all cockles combined, including those without tag but still present in the sample.

It should be noted that because of unfavorable tide conditions no surveys could be carried out in September and December 1986 at SITE I (exposed), and in September, November and December 1986 at SITE II (submerged). A general description of the experiment's progress was given on p. 27.

Upon completion of the growth experiment in February 1987, twenty live tagged cockles were recovered at SITE II (see summary, Table 4.3). As no cockles were available from SITE I, it was decided to use the growth data of the 26 specimens that had survived until January 1987 for further analysis.

As for *P. viridis*, the data had first to be converted into the form of length-at-time data to make them suitable for analysis with the ETAL 2 program. This was achieved by assigning the arbitrary age of 180 days (= 0.49 year) to the cockles for the first sampling date, and expressing all following sampling dates in related units. The cockles were thus assumed to have reached an "age" of 1.33 and 1.41 years at SITE I and SITE II, respectively, at the end of the experiments.

Out of the 26 datasets available for SITE I, the series of monthly length measurements of only 14 cockles proved appropriate for the analysis of the data by means of the ETAL 2 program, using a nonoscillating growth model. In all other cases, the program could not fit a standard growth curve to the data. As it became obvious during this first analysis that the distribution of the data showed a marked seasonality, all 14 datasets were re-analyzed using the option to fit the growth curve to the seasonal oscillating growth model incorporated into the ETAL 2 program. In two cases this run did not produce a fit to the data, and the two corresponding datasets were entirely excluded from analysis to retain comparability between the two approaches. Thus, the subsample finally selected contained the individual length-at-time data of 12 cockles and is presented in Table 5.5.

Table 5.5. Ang Sila growth experiment, SITE I: mean monthly length (in mm) of marked <i>Anadara granosa</i> used for the computation of the parameters of the von Bertalanffy growth function.									
Site:	Exposed (SITE I)								
Period:	March 1986-January 1987								
Sampling month:	Mar	Apr	May	Jun	Jul	Aug	Oct	Nov	Jan
Est. age (years):	0.49	0.59	0.65	0.74	0.82	0.91	1.08	1.16	1.33
Tag No.									
Y 3	24.50	26.45	28.15	28.70	29.75	30.05	31.95	32.40	32.30
Y 7	22.10	23.40	24.35	24.75	25.85	26.40	27.80	28.35	28.25
Y 14	22.60	24.00	25.75	25.70	26.45	26.95	28.10	28.40	28.40
Y 19	24.45	25.55	27.15	27.20	27.85	27.90	28.60	29.55	29.55
Y 20	21.00	22.55	23.50	23.60	24.35	24.65	25.60	26.10	26.10
Y 23	21.20	22.60	23.80	24.05	24.90	25.60	26.80	26.95	26.95
Y 24	21.30	22.80	24.30	24.30	25.30	25.70	26.55	27.65	27.65
Y 25	21.45	22.75	24.35	24.55	25.20	25.85	26.65	27.10	26.80
W 7	22.90	24.80	26.40	26.75	26.95	27.30	28.40	29.35	29.55
W 10	18.85	21.00	22.85	23.10	24.05	25.60	26.35	27.30	27.35
W 15	21.60	22.80	24.55	24.95	26.15	26.95	28.30	28.45	28.45
W 23	25.75	27.15	27.70	28.10	28.60	29.25	29.50	29.75	29.80
N	12	12	12	12	12	12	12	12	12
Mean	22.31	23.82	25.24	25.52	26.28	26.85	27.88	28.45	28.43
s.e.	0.40	0.40	0.39	0.39	0.39	0.37	0.39	0.38	0.38

The same procedure was also applied to the 20 datasets available for the cockles from SITE II. While, in seven cases, the data proved generally unsuitable for the analysis with ETAL 2, one more dataset had to be omitted, because it could not be fitted to the seasonal oscillating growth model, thus reducing the final subsample to 12 cases. The individual length of these cockles attained in each month is summarized in Table 5.6.

Comparing the computed monthly mean length in each of the subsamples demonstrates clearly the differences in growth performance at the two locations, which differed from each other primarily in their relative shore level.

At the higher shore level with regular exposure (SITE I), the mean length of the cockles increased from 22.31 mm in March 1986 to 28.43 mm in January 1987 (see Table 5.5), which represents an average increase of 0.61 mm·month. This is only slightly higher than the 0.57 mm·month computed from the mean monthly size of the whole sample listed in Appendix 2, which increased during the same period from 22.56 mm to 28.24 mm. The growth of the subsample of 12 cockles, therefore, can be regarded as representative for the whole experiment.

At SITE II, which was located at a lower shore level and remained submerged during low water, the growth in length was much better. The subsample selected for growth analysis had grown from an average length of 22.03 mm in March 1986 to 33.00 mm in January 1987 (see Table 5.6). The average 1.10 mm increase per month is almost double the relative increase recorded for the cockles at SITE I. By February 1987, these cockles had reached a mean size of 33.56 mm. The corresponding values for the whole sample (from Appendix 2) are: 22.27 mm in March 1986 and 32.11 mm in January 1987, corresponding to an average increase of 0.98 mm·month. The selected cockles in the subsample, therefore, appear to have grown on the average slightly better than the whole sample, which had reached a final mean length of 32.90 mm by the end of the experiment in February 1987.

Analogous to the proceeding followed in the case of *P. viridis* the computation of growth parameters for *A. granosa* was based on the three following length-at-time datasets:

- individual length per month of the cockles from the subsamples listed in Tables 5.5 and 5.6; from this was computed a mean value (and its statistics) for each parameter, averaged from the 12 single parameter estimations obtained from the subsample;
- mean monthly length computed from the cockles in the subsample (see Tables 5.5 and 5.6);
- mean monthly length computed from the total number of cockles in the whole sample, as given in Appendix 2.

Each analysis was done twice, using both the standard von Bertalanffy growth model and the seasonal oscillating growth model as implemented in ETAL 2. The results are summarized in Table 5.7 (SITE I) and Table 5.8 (SITE II).

The abovementioned difference in length growth at the two sites is also reflected by a sizable difference in the mean values of the parameter  $L_{\infty}$  averaged from the 12 single estimates obtained from the subsample. While the mean  $L_{\infty}$  and  $K$  at SITE I amount to 29.3 mm and 2.743 year<sup>-1</sup>, respectively, their corresponding values at SITE II are 36.9 mm and 1.867 year<sup>-1</sup>. The single growth parameters from the subsample were used to draw the corresponding growth curves. When comparing the growth curves from SITE I (Fig. 5.5) with those from SITE II (Fig. 5.6), one will note that the general trend of the growth curves at SITE I is characterized by a certain uniformity, while the growing conditions at SITE II apparently allowed the cockles to display much more variation of individual growth parameters.

Table 5.6. Ang Sila growth experiment, SITE II: mean monthly length (in mm) of marked *Anadara granosa* used for the computation of the parameters of the von Bertalanffy growth function.

Site:	Submerged (SITE II)									
Period:	March 1986-February 1987									
Sampling month:	Mar	Apr	May	Jun	Jul	Aug	Oct	Jan	Feb	
Est. age (years):	0.49	0.59	0.65	0.74	0.82	0.91	1.08	1.33	1.41	
Tag No.										
Y 4	21.50	22.20	22.85	26.20	27.80	28.95	29.30	32.00	32.90	
Y 8	20.35	22.20	22.70	25.90	27.25	27.90	28.05	31.85	33.00	
Y 9	22.55	23.95	24.20	27.35	28.10	29.40	29.50	31.95	31.45	
Y 17	20.50	22.55	22.80	26.55	28.90	29.95	30.10	31.55	31.85	
Y 23	21.00	21.80	22.95	26.05	28.35	29.50	29.95	34.55	35.40	
Y 28	21.60	22.25	22.70	26.50	27.75	28.85	29.50	32.25	33.00	
R 24	23.95	25.40	25.80	29.05	30.30	31.45	31.95	33.70	34.00	
R 26	24.35	25.20	25.60	29.35	30.80	31.90	32.10	34.35	34.80	
R 27	20.60	21.95	22.35	24.95	26.40	27.55	27.70	29.55	29.65	
W 4	23.75	24.50	25.25	28.30	29.85	31.25	31.80	34.75	35.00	
W 7	21.50	23.00	23.85	27.50	30.20	31.60	32.65	35.75	36.95	
W 15	22.75	23.50	24.10	27.80	29.50	30.85	31.55	34.30	34.70	
N	12	12	12	12	12	12	12	12	12	
Mean	22.03	23.21	23.76	27.13	28.77	29.93	30.35	33.00	33.56	
s.e.	0.35	0.33	0.33	0.34	0.35	0.36	0.38	0.40	0.42	

Table 5.7. Experimental cage culture of *Anadara granosa* at Ang Sila, Thailand: SITE I (exposed): summary of the parameters of the von Bertalanffy growth function (VBGF) and their corresponding  $\phi'$ . (Parameters  $L_{\infty}$ , K and C, and their statistics computed by means of the ETAL 2 program with the application of both the standard and the seasonalized VBGF).

Tag No.	Standard VBGF						Seasonalized VBGF							
	$L_{\infty}$ (mm)	SE (year <sup>-1</sup> )	K	SE	RSS	$\phi'$	$L_{\infty}$ (mm)	SE (year <sup>-1</sup> )	K	SE	C	SE	RSS	$\phi'$
Y 03	33.51	0.646	2.678	0.464	0.930	3.48	33.93	0.944	2.391	0.635	0.35	0.198	0.526	3.44
Y 07	30.31	0.894	1.875	0.396	0.516	3.24	29.78	0.872	2.276	0.618	0.39	0.233	0.298	3.31
Y 14	29.06	0.532	2.958	0.628	0.867	3.40	29.32	0.820	2.676	0.957	0.39	0.274	0.573	3.36
Y 19	30.00	0.622	2.802	0.788	0.998	3.40	31.27	1.533	1.575	0.233	0.92	0.559	0.513	3.19
Y 20	26.78	0.472	2.646	0.530	0.477	3.28	26.93	0.494	2.529	0.589	0.47	0.175	0.171	3.26
Y 23	28.01	0.505	2.542	0.439	0.479	3.30	27.78	0.510	2.972	0.704	0.42	0.230	0.255	3.36
Y 24	28.43	0.655	2.589	0.569	0.857	3.32	29.64	1.217	1.695	0.532	0.67	0.338	0.360	3.17
Y 25	27.42	0.385	3.303	0.579	0.633	3.40	27.52	0.636	3.179	1.137	0.23	0.287	0.545	3.38
W 07	30.02	0.779	2.789	0.785	1.545	3.40	31.63	1.079	1.595	0.422	1.01	0.292	0.262	3.20
W 10	28.59	0.769	2.609	0.491	1.209	3.33	28.30	0.091	2.982	0.899	0.37	0.290	0.852	3.38
W 15	29.79	0.641	2.559	0.457	0.788	3.36	29.45	0.842	3.003	0.981	0.27	0.352	0.681	3.42
W 23	30.09	0.155	3.561	0.371	0.126	3.51	29.92	0.114	4.480	0.573	0.46	0.143	0.041	3.60
Mean	29.33	0.588	2.743	0.541	0.785	3.37	29.62	0.763	2.613	0.690	0.50	0.281	0.423	3.34
s.d.	1.74		0.42			0.08	1.96		0.82		0.25			0.12
s.e.	0.50		0.12			0.02	0.57		0.24		0.07			0.04
From Mean length in subsample	29.29	0.471	2.681	0.439	0.497	3.36	29.49	0.669	2.511	0.645	0.31	0.189	0.300	3.34
From Mean length in total sample	29.00	0.347	2.690	0.352	0.272	3.35	29.09	0.416	2.638	0.480	0.28	0.139	0.131	3.35

Table 5.8. Experimental cage culture of *Anadara granosa* at Ang Sila, Thailand: SITE II (submerged): summary of the parameters of the von Bertalanffy growth function (VBGF) and their corresponding  $\phi'$ . (Parameters  $L_{\infty}$ , K and C, and their statistics computed by means of the ETAL 2 program with the application of both the standard and the seasonalized VBGF).

	Standard VBGF						Seasonalized VBGF							
	$L_{\infty}$ (mm)	SE	K (year <sup>-1</sup> )	SE	RSS	$\phi'$	$L_{\infty}$ (mm)	SE	K (year <sup>-1</sup> )	SE	C	SE	RSS	$\phi'$
Tag No.														
Y 04	36.26	2.824	1.588	0.555	4.586	3.32	36.08	1.286	1.468	0.257	0.97	0.182	0.428	3.28
Y 08	37.42	4.009	1.343	0.555	4.906	3.27	42.88	6.815	0.764	0.346	1.07	0.333	1.159	3.15
Y 09	32.66	1.047	2.408	0.578	2.699	3.41	32.57	0.965	2.269	0.605	0.75	0.315	0.878	3.38
Y 17	32.83	1.106	2.969	0.686	5.632	3.51	32.01	0.540	3.806	0.794	0.70	0.147	0.911	3.59
Y 23	44.81	7.330	1.016	0.475	5.534	3.31	47.37	1.454	0.787	0.064	0.97	0.056	0.057	3.25
Y 28	36.84	3.198	1.512	0.565	4.896	3.31	36.58	1.955	1.410	0.354	0.96	0.257	0.857	3.28
R 24	35.42	1.101	2.346	0.513	2.747	3.47	35.06	0.731	2.391	0.449	0.68	0.202	0.562	3.47
R 26	36.68	1.852	2.089	0.657	5.282	3.45	36.32	0.924	2.021	0.388	1.03	0.234	0.638	3.43
R 27	31.04	1.034	2.314	0.513	2.320	3.35	30.70	0.608	2.380	0.408	0.69	0.177	0.382	3.35
W 04	39.07	2.682	1.518	0.475	3.493	3.36	38.67	1.070	1.469	0.207	0.82	0.135	0.272	3.34
W 07	41.34	2.834	1.622	0.432	4.994	3.44	40.52	1.098	1.654	0.202	0.70	0.114	0.399	3.43
W 15	38.27	2.645	1.682	0.536	4.981	3.39	37.46	1.081	1.724	0.275	0.88	0.165	0.485	3.38
Mean	36.89	2.639	1.867	0.545	4.339	3.38	37.19	1.544	1.845	0.362	0.85	0.193	0.586	3.36
s.d.	3.82		0.56			0.07	4.73		0.82		0.14			0.12
s.e.	1.10		0.16			0.02	1.37		0.24		0.04			0.03
From Mean length in sub-sample	n.f.	n.f.	n.f.	n.f.	n.f.	-	36.16	1.043	1.685	0.271	0.85	0.174	0.422	3.34
From: Mean length in total sample	36.73	2.641	1.435	0.460	2.740	3.29	36.58	1.473	1.347	0.260	0.79	0.178	0.378	3.26

"n.f." implies that ETAL 2 could not fit a growth curve to the given dataset.

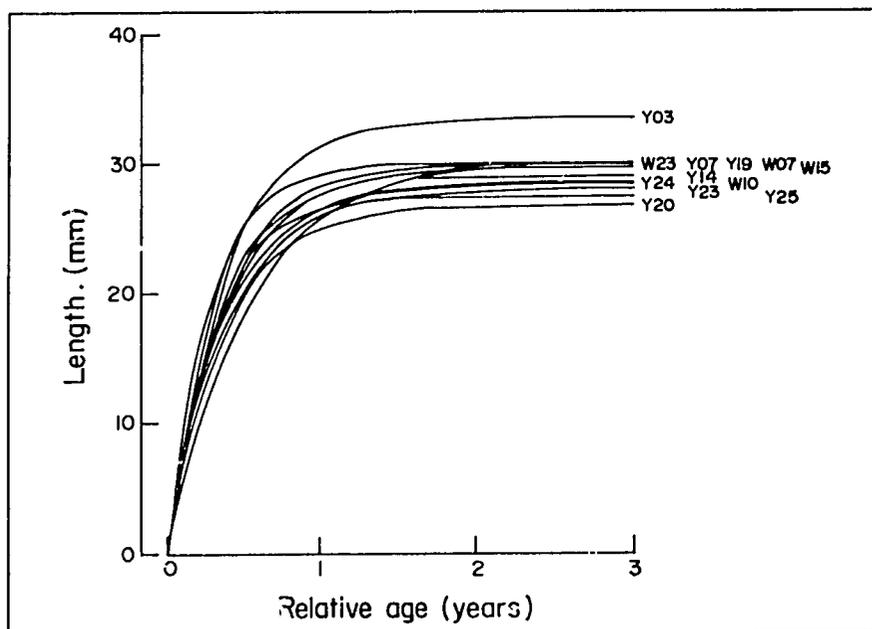


Fig. 5.5. Single growth curves of marked *Anadara granosa* raised in experimental cage culture at SITE I (exposed) at Ang Sila, Thailand, in 1986-1987. (Tag No. of specimen indicated to the right of each growth curve).

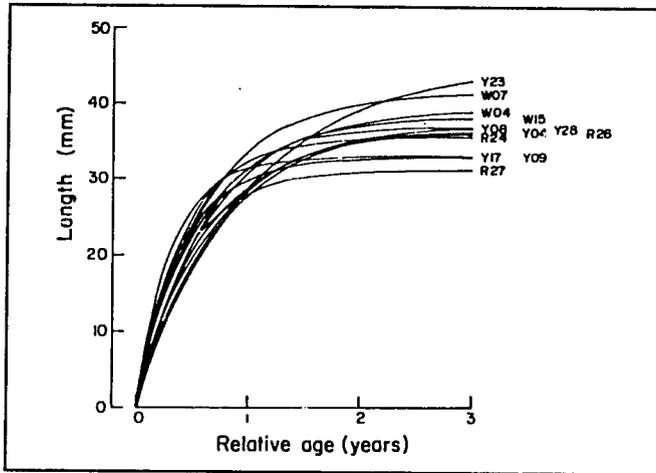


Fig. 5.6. Single growth curves of marked *Anadara granosa* raised in experimental cage culture at SITE II (submerged) at Ang Sila, Thailand, in 1986-1987. (Tag No. of specimen indicated to the right of each growth curve).

much less pronounced at SITE I where the value of  $C = 0,50 (\pm 0.07)$  denotes only moderate seasonal oscillations in growth.

This result is insofar interesting as it clearly supports the assumption that the phenomenon of seasonal growth oscillation is not limited to species of higher latitudes, but that it also can occur in tropical regions. Sedentary marine organisms in the tropics are also subjected to events with annual periodicity such as rainy seasons or increased water turbidity during the monsoon season. These might be related in a similar way to food availability as is the annual temperature regime in the waters of the higher latitudes.

On the other hand the result also shows that the general growing condition can play a role important enough to mask, by and large, any seasonal effect. The cockles at SITE I regularly had to cope with exposure during low tide, which deprived them during a substantial part of the day from the possibility of feeding. The influence on growth performance resulting from these unfavorable conditions was probably of much more importance than the additional strain exerted by seasonal fluctuations in food availability.

Though the application of the seasonalized VBGF revealed at both sites the existence of seasonal oscillating growth in the samples, the growth parameters that were thus estimated did not much differ from those produced by the standard VBGF. Yet, they differed, of course, between sites (see Tables 5.7 and 5.8). It is, however, striking to see that independent of site and method of analysis the resulting average values of the parameter  $\phi'$  in the subsamples fall within a very narrow range (3.34-3.38). The comparison of the computed means from SITE I and SITE II underlined once more the suitability of  $\phi'$  as species-specific growth index (see Table 5.9). While the parameters  $L_{\infty}$  and  $K$  were significantly different both with and without the inclusion of seasonality, the differences in the parameter  $\phi'$  were not significant in either case ( $P = 0.001$ ).

In order to test the influence of the selected model on the estimated parameters, the means of  $L_{\infty}$  and  $K$  computed from the subsample with the standard VBGF were compared with those of the seasonalized VBGF for both sites (Table 5.9). As expected, none of these were significantly different ( $P < 0.001$ ), nor were the resulting  $\phi'$  parameters.

The averaged values of  $L_{\infty}$  and  $K$  also remained similar to those obtained by calculating these parameters directly from the mean length in the subsample, respective in the total sample (note that no growth curve could be fitted to the mean length data from the subsample at SITE II using the standard VBGF). There seems to be, however, at both

When analyzing the same dataset with a seasonal oscillating growth model, a much improved fit is obtained, especially in the case of the cockles from SITE II, where the RSS-value drops from 4.339 to 0.586. This is also true for SITE I, though the improvement is less spectacular with the RSS-value reduced from 0.785 to 0.423 only. This difference becomes understandable, however, when looking at the parameter  $C$ , which is a measure of the amplitude of growth oscillation. At SITE II this parameter assumes a value of  $0.85 (\pm 0.04)$ , indicating that growth comes almost to a halt at least once a year (a value of  $C = 1$  would represent a complete growth stop). This seasonality is

Table 5.9. Summary of tests for significant differences in computed growth parameters of both the standard and the seasonalized von Bertalanffy growth formula (VBGF) obtained for *Anadara granosa* raised at different shore levels at Ang Sila, Thailand.

Parameter	Shore level Exposed vs. submerged		Growth model Standard VBGF vs. seasonalized VBGF	
	Standard VBGF	Seasonalized VBGF	SITE I	SITE II
$L_{\infty}$	different (***)	different (***)	not different	not different
K	different (***)	different (*)	not different	not different
$\phi'$	not different	not different	not different	not different

Levels of significance are  $P = 0.05$  (\*) and  $P = 0.001$  (\*\*\*)

sites, a slight tendency towards a lower asymptotic length, when the total sample is used. It is possible that this reflects a certain bias created by the mortality of predominantly larger animals towards the end of the culture experiment. At SITE II, the resulting  $\phi'$  is also slightly lower than the average from the subsample, being a further indication that the associated values of K probably underestimate this parameter.

#### Mortality

Mortality occurring in the course of the experiments was monitored during the monthly surveys. Dead cockles were identified by their tag, their death recorded (denoted by a "D" in the survey protocol in Appendix 2), and then removed from the sample to be kept for later analysis of shell microstructures.

For *A. granosa*, mortality at the two sites was quite different in absolute numbers, though the general trend was similar. As Fig. 5.7 shows, there was at both sites one peak in April/May and a second one in October. No mortality occurred in June, August and January at SITE I, respective in July, August and February at SITE II. It should be noted that the dead cockles recorded in October 1986 and January 1987 represent the accumulated mortality of two months, as no sampling was carried out in September and December, respectively.

With the data available from the two sites, the natural logarithm of surviving cockles in each month was plotted against the corresponding relative age that was assigned to the cockles for growth analysis. The coefficient of total mortality was estimated from the slope of the regression, with sign changed. Use of relative age instead of absolute age does not influence the coefficient "b" of the regression, but rather the Y-intercept of the resulting regression line. One problem, however, is caused by the number of cockles missing from the sample. Short of knowing exactly whether they had been stolen or simply escaped from the damaged cage, it was decided to consider them "alive" and their number was added to the cockles that had survived in the sample. This, of course, bears the possibility of underestimating the true mortality, as some of these missing cockles might also have died of natural causes. On the other hand, it was assumed that this bias was of approximately the same magnitude in both samples, which would make its relevance less important, when the mortalities are compared in relative terms.

Fig. 5.8 shows the plot of  $\ln N$  against age, from which the total mortality Z was estimated for the two sites. As all mortality that had occurred in the samples was considered to be of natural cause, the computed coefficient of total mortality is equivalent to the coefficient of natural mortality (M). At SITE I, a natural mortality of  $M = 0.14 \text{ year}^{-1}$

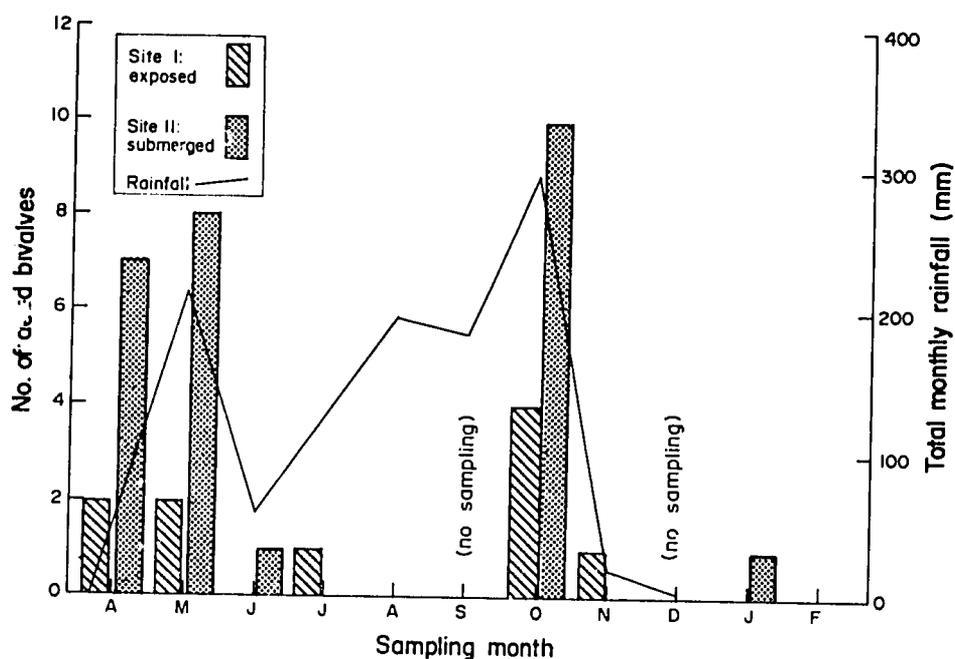


Fig. 5.7. Experimental culture of *Anadara granosa* at Ang Sila, Thailand: total number of cockles recorded dead during the monthly surveys between April 1986 and February 1987 at SITE I and SITE II. Dashed line depicts total monthly rainfall for the period April to December 1986 monitored at the meteorological station Chonburi (Source: Meteorological Department, Bangkok). Note: The columns in October 1986 and January 1987 represent the accumulated mortality of two months, as no sampling was done during the respective preceding month.

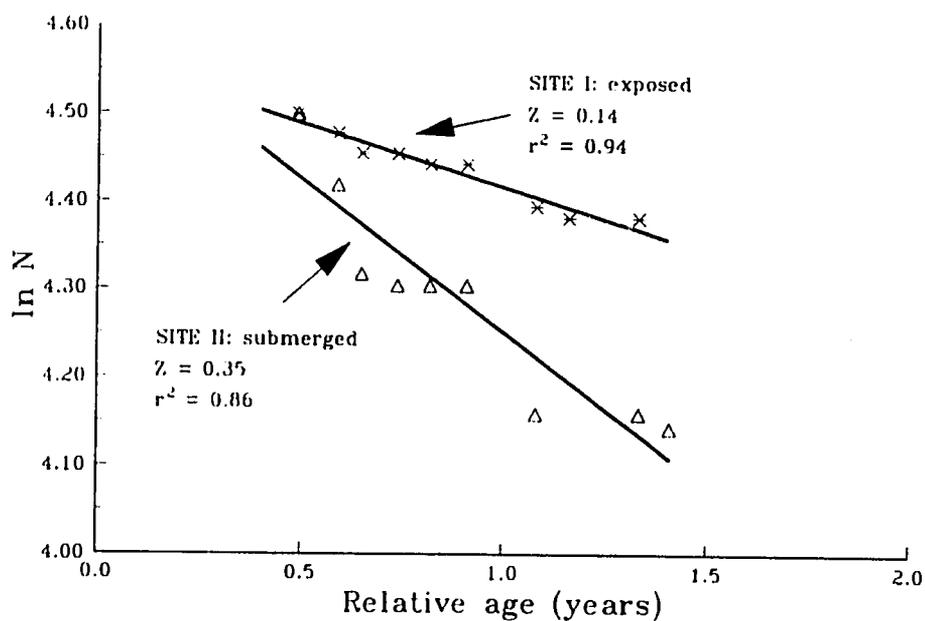


Fig. 5.8. Experimental culture of *Anadara granosa* at Ang Sila, Thailand: estimation of total mortality ( $Z$ ) for SITE I and SITE II from a plot of the natural logarithm of the number of bivalves ( $N$ ) against their corresponding relative age. (Note that  $N$  also includes missing bivalves.)

(s.e.: 0.01) is computed, which is markedly lower than the  $M = 0.35 \text{ year}^{-1}$  (s.e.: 0.05) obtained for SITE II. This implies, that at least for the selected size range (20-35 mm) and for the given culture condition, mortality is higher at the lower shore level where the cockles remain submerged during all but the lowest low water levels, while cockles at shore levels with regular exposure have a better survival.

Also displayed in Fig. 5.7 is the total monthly rainfall recorded at Chonburi, a provincial capital about 20 km north of Ang Sila (the data were kindly provided by the Meteorological Department, Bangkok). It is interesting to note that both periods of increased mortality coincide with those months when the rainfall reaches a seasonal peak, suggesting a relationship between rainfall and mortality. The effect, however, seems to be of different intensity, as survival at SITE I was better. If influences due to experimental design can be excluded, an explanation might be found in the fact that the cockles at SITE II always remained covered by water, yet the water layer became very shallow during low tide. During days of heavy rainfall the cockles had to survive for an extended period of time in water with a drastically reduced salinity. In contrast, the cockles at SITE I felt dry during low tide. Because the rising tide would bring in water of higher salinity, cockles at SITE I probably had to cope with much shorter periods of immersion in waters of reduced salinity than those at SITE II. Apparently, cockles are better adapted to the stress resulting from exposure to air than to the physiological stress ensuing from a low salinity of the surrounding waters.

#### Growth comparison

Fig. 5.9 presents the growth curves that are considered "typical" for the general growing condition characterizing the two sites and which clearly depict the site-related growth differences. When analyzing the growth performance of *A. granosa* in the experiments, there are actually three questions of interest. Similar as in the case of *P. viridis*, the reliability of the computed growth parameters as such need to be assessed,

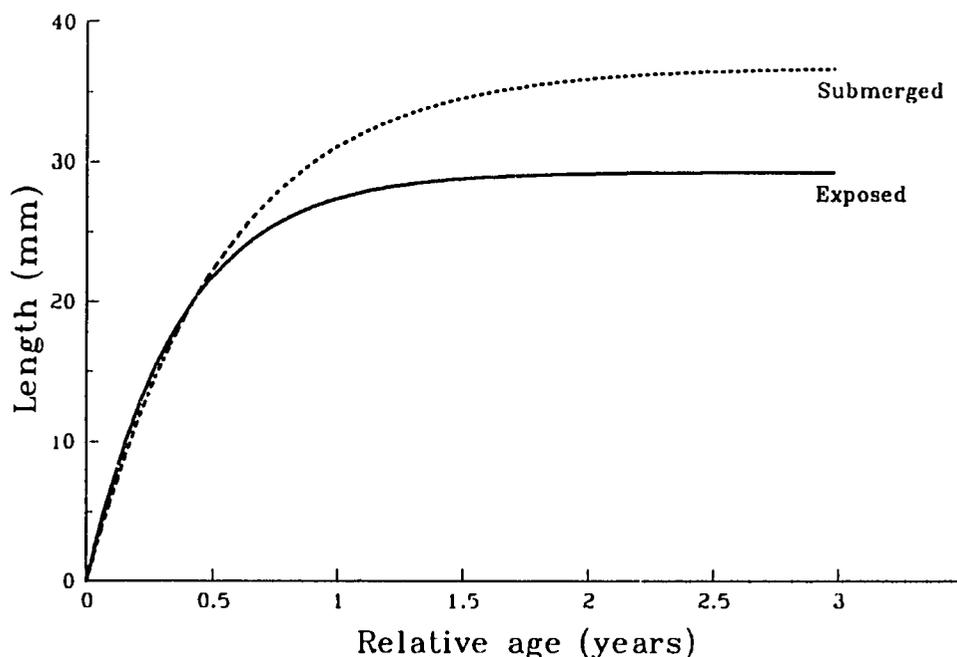


Fig. 5.9. Average growth curves of marked *Anadara granosa* raised in experimental cage culture at Ang Sila, Thailand in 1986-1987. Solid curve represents the average growth at SITE I (exposed) with  $L_{\infty} = 29.33 \text{ mm}$ ,  $K = 2.743$ , while the dotted curve represents the average growth of cockles at SITE II (submerged) with  $L_{\infty} = 36.89 \text{ mm}$ ,  $K = 1.967$ .

and the general growth performance has to be compared to what can be expected for this species in the given environment. A third aspect, however, is the effect that had the variable "SITE" on the growth of the cockles under the given culture conditions.

Appendix 4 lists a total of 21 sets of growth parameters for *A. granosa*, all originating from commercial and experimental culture of this species in Malaysia. From this set a mean  $\phi'$  of 3.27 (s.e.= 0.05) has been computed, with the single values ranging from 2.85 to 3.62. Though the average  $\phi'$  computed for SITE I (3.37) and SITE II (3.38) is slightly higher, it is nevertheless considered well inside the range of values that normally can be expected for this species. From this can be concluded that the growth parameters obtained from the experiments are biologically meaningful and that their actual values reflect the special growth conditions given in the experiment rather than being methodic artefacts.

Comparing the growth performance of the cockles in the experiment with those commercially cultured in Thailand is difficult, as data on the growth of this species in Thai cockle farms are not available. However, as cockles are commonly marketed at a length between 32 and 40 mm (Broom 1985), one can conclude that the general culture conditions both at SITE II and especially at SITE I were not very favorable for the growth in length of the cockles. This might have to be attributed, on the one hand, to the restrictions laid upon the natural behavior of *A. granosa* (borrowing in the mud, migration) caused by the use of cages. On the other hand, shore position relative to the average tide level is most probably another important factor, not only in comparison between the two experimental sites, but also in comparison of the whole experiment with sites that are located in much deeper waters.

This aspect was also reported by Broom (1982), who described an inverse relationship between the asymptotic length of *A. granosa* and the level above chart datum at which the animals were grown, which he related to differences in food availability.

While the different asymptotic sizes reached by the growth curves in Fig. 5.9 make the culture of *A. granosa* at SITE II look more favorable, one should keep in mind that "size" is one point of interest to the farmer, but what he finally sells is "yield" in terms of weight. And this, obviously, is a function of increase in size and number of bivalves surviving up to harvest time. Though growth in length is better at SITE II, as suggested by the higher  $L_{\infty}$ , mortality is also markedly higher at this site compared to the more exposed site.

Management advice for the proper selection of a culture site, therefore, must consider both aspects. For this purpose, an assessment of the relative productivity of a given site relative to another site can readily be obtained by comparing both sites on the basis of the relative yield per recruit that can be achieved at each site. If data are available of the kind presented in this study, equation (11) will produce the expected "relative yield" curve for a given species over a wide range of exploitation rates. If the mean length at first capture is kept constant, then the resulting yield curve's shape will solely depend on the three parameters  $L_{\infty}$ ,  $K$ , and  $M$ .

This approach has been used to investigate the productivity of the two sites selected for the culture of *A. granosa* (Fig. 5.10). Using the averaged growth parameters from the subsamples listed in Tables 5.7 and 5.8 and the values of natural mortality previously estimated, two "yield" curves are obtained, suggesting a higher relative productivity at SITE I (exposed) compared to SITE II, for the whole range of exploitation rates.

The point must be stressed again that this result is not a yield-per-recruit analysis in the traditional sense. This is because no information is at hand on the mortality of the younger bivalves, which is often considerably higher than the one established for the size range used in the present experiments. Also the resulting "yield" is not expressed in terms of weight, but is something proportional to it. Still, the conclusions in terms of farm

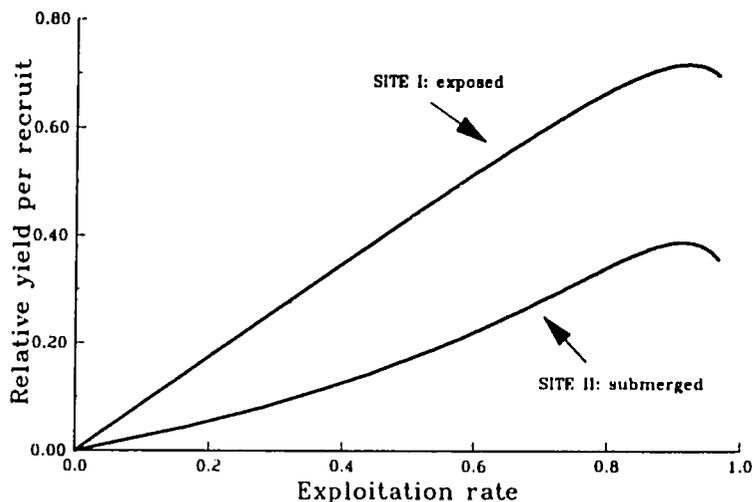


Fig. 5.10. Experimental culture of *Anadara granosa* at Ang Sila, Thailand: relative yield per recruit at different exploitation levels as indicator for the influence of shore position on the general productivity of a selected site. Input parameters of the model are for SITE I:  $L_{\infty} = 29.33$  mm,  $K = 2.743$ ,  $M = 0.14$ , and for SITE II:  $L_{\infty} = 36.89$  mm,  $K = 1.867$ ,  $M = 0.35$ ; mean length at first capture ( $L_C$ ) is 26 mm for both sites.

management that can be drawn from the relative position of the two curves in Fig. 5.10 are straightforward: if the culture operation is to maximize yield in terms of weight, then growing *A. granosa* at SITE I would be more advantageous. If, however, market preferences are such that the consumer demands primarily cockles larger than 30 mm, setting up the culture area at SITE II would be more recommendable, as the cockles would not be able to reach the desired market size at SITE I.

Both information taken together suggest that none of the two sites is well suited for the culture of cockles. If technically

feasible, the culture plots should be established at shore levels deep enough to preclude a strong fluctuations in salinity caused by rain or terrestrial runoffs. Culture of *A. granosa* in deeper waters, of course, would also be more demanding in terms of harvest gear, while the nearshore culture of this species provides the possibility to collect the bivalves from the mud during low tide, without the need for sophisticated equipment. The latter aspect might be of importance when considering the promotion of cockle culture in remote fishing communities as an additional source of income.

### **Compilation of Growth Parameters of the VBGF from the Literature**

Growth parameters for a total of 190 bivalve stocks were compiled from the literature. These cover 66 marine bivalve species and 12 freshwater species. Their geographic distribution spans from Greenland (69°N) to New Zealand (3°S), with 99 stocks being located in the tropics and subtropics (0°-40°), while the temperate zones (>40°) are represented with 91 stocks. In general, no attempt was made to verify the taxonomic nomenclature used by the authors. The only exception was *Cardium*, which was renamed *Cerastoderma* as this is the now commonly used name for this genus.

In order to tabulate the data as efficiently as possible, the compiled dataset is presented in two separate sets. The first one (Appendix 3) includes all stocks together with their geographic description (country, area, geographic coordinates), a general classification of the environment and the growing condition, as well as the literature source from which the data had been obtained. Each case is preceded by an individual reference number, which is used in all other exhibits as reference, instead of again listing the authors. Thus, a given reference number will allow tracing of general background information and authorship from Appendix 3 for the case in question.

All other information pertaining to the compiled dataset is summarized in Appendix 4. This includes: type of growth data and method of analysis, temperature data, growth and mortality parameter, estimates of their related statistics.

The type of data describes whether the original data were raw data (type 1-3) or published parameters (type 4). The raw data sets are classified according to the method of analysis applied, i.e.

Type 1 : Length frequencies.

In this category, there are 7 datasets that were analyzed with ELEFAN I.

Type 2 : Length-at-time data.

A total of 77 datasets are presented that were analyzed by means of the ETAL 2 program.

Type 3 : Growth increment data.

A total of 12 datasets are included in the database that were analyzed by means of a Gulland and Holt plot using the appropriate routine of the Compleat ELEFAN software package.

From the bulk of published growth parameters retrieved from the literature 94 sets of growth parameters could be extracted and included into the present database. Most of the published parameters of the VBGF, especially in the older literature, are based on either the Ford-Walford plot or the Gulland and Holt plot. The Ford-Walford plot consists of plotting the length at a given time ( $L_{t+1}$ ) against a previously attained length  $L_t$ . The method requires the time intervals between the two length measurements to be equidistant (i.e., 1 = year, month, etc.). The Gulland and Holt plot, as previously mentioned, allows estimation of the VBGF parameters from a plot of size increments per unit time against mean size for the increment in question (for application of these methods and a critical discussion of their limitations see Pauly (1984)). As far as possible, attempts were made to check the consistency of the published VBGF parameters with other information on growth given by the respective author(s).

Temperature data (in °C) are listed both as annual range (if available) and annual average. Also indicated is whether the data had been interpolated from a hydrographic atlas or whether the information was published together with the growth data.

The summary of growth data in Appendix 4 comprises the size range onto which the computation of the VBGF parameters was based, estimates of asymptotic length ( $L_{\infty}$ ),  $K$ , and the corresponding values of  $\phi'$ . Where available, estimates of the parameter expressing the amplitude of growth oscillation ( $C$ ) and winter point ( $WP$ ) of the seasonalized VBGF are given. The statistics block lists values which denote the quality of fit of the computed parameters to the given raw data and the standard errors for  $L_{\infty}$  and  $K$ , if they had been computed by means of the ETAL 2 program.

It should be noted that all data on shell size are given in millimeters, if not mentioned otherwise. This is insofar of importance as the value of  $\phi'$  is influenced by the dimension used for  $L_{\infty}$ . The difference, however, relates only to the integer part of  $\phi'$ . A  $\phi'$  computed for an  $L_{\infty}$  expressed in cm can be converted into the corresponding  $\phi'$  for an  $L_{\infty}$  expressed in mm by using the relationship:  $\phi'_{mm} = \phi'_{cm} + 2$ .

The interpretation of the value characterizing the goodness of fit depends on the method applied: In the case of Type 1 data, the value represents the  $R_n$ -value computed in the course of procedures included in the Compleat ELEFAN program which can range between 0 and 1. With length-at-time data, the value is the sum of squares of the residuals (RSS), which is the criterion used in the ETAL 2 program to optimize the fit of the parameters to the data. In the case of growth increment data, the value represents the coefficient of determination ( $r^2$ ) of the linear regression used in the Gulland and Holt plot.

Given the extremely small number of datasets compiled from the literature that might have been suitable for an estimation of mortality, no attempt was made to present an extensive database on bivalve mortality. However, whenever estimates of mortality were

published together with growth parameters, they were included in the summary listing in Appendix 4.

### ***Intraspecific Comparison of Growth Parameters: The Use of the Growth Index $\phi'$***

The results from the field experiments in Thailand with *Anadara granosa* and *Perna viridis* lend strong support to the perception of  $\phi'$  as a species-specific parameter.

In order to verify whether this concept would be applicable to a wide range of bivalve species from different climatic zones, the  $\phi'$  values listed in Appendix 4 were extracted for those species that are represented by at least four cases. If only one or two datasets were available for a species, but data were at hand for another species of the same genus, then the data were combined and presented under the common genus name. This resulted in a total of 14 sets of  $\phi'$  parameters for marine bivalves, comprising 35 species from 117 stocks. An additional five sets were extracted from Appendix 4 covering nine freshwater bivalve species from 28 stocks.

Fig. 5.11 shows the frequency distribution of the  $\phi'$  values (grouped in 0.2 intervals) of the 14 sets obtained for marine bivalve species. Fig. 5.14 displays the same for the freshwater bivalves. Also presented with each figure is the mean  $\phi'$  for the given species or species group, as well as the standard error and the number of cases used in the computation of the mean.

The frequency distribution of the  $\phi'$  values shows, indeed, in most cases, a tendency to aggregate within a rather narrow range. This is especially obvious in cases where the dataset pertains to a single species (e.g., *Mytilus edulis*, Fig. 5.11), but also in the case of some of the species groups (e.g., *Donax* spp., Fig. 5.11, or *Unio* spp., Fig. 5.14). On the other hand, there are also some samples with clear "outliers".

The distribution of  $\phi'$  for *Perna* spp. in Fig. 5.11 is an interesting example. While 14 observations fall within a narrow range extending from 4.09 to 4.57, there is one dataset producing a  $\phi'$  of 3.49 which is outside the usual range. The underlying growth parameters pertain to *P. viridis* from Hong Kong waters and were published by Lee (1985). The corresponding growth curve depicts this species as extremely slow-growing if compared with other growth curves of the same species in Asia (Vakily 1989). It would thus take a *P. viridis* from Hong Kong almost four years to reach a size which the same species in, e.g., Thailand would attain in one year. Though no definite statement can be made concerning the reliability of the growth parameters presented by Lee (1985), this drastic deviation from the "average growth" of this species is a strong indication of a possible bias in these parameter estimates. As indicated in the figure, this single value was therefore excluded from the computation of the mean.

Another example of a conspicuous deviation from a rather narrowly distributed  $\phi'$  is the case of *Cerastoderma* spp. (Fig. 5.11), where three data points stand apart from the rest. Interestingly enough, these three  $\phi'$  values all pertain to *Cerastoderma glaucum*, while the other five stem mainly from *Cerastoderma edule*. This could indicate that the growth of *C. glaucum* might be different enough from the other species to preclude actually their being combined in one group. However, for the time being they have been left together as the data are yet too scarce to decide finally whether these two species should be separated.

The few examples available of freshwater bivalves (Fig. 5.14) show the same tendency of clustered  $\phi'$  values, with the extreme narrow distribution for the two African species (*Caelatura* spp. and *Corbicula africana*) most probably being an artefact caused by the too limited source of information on these species.

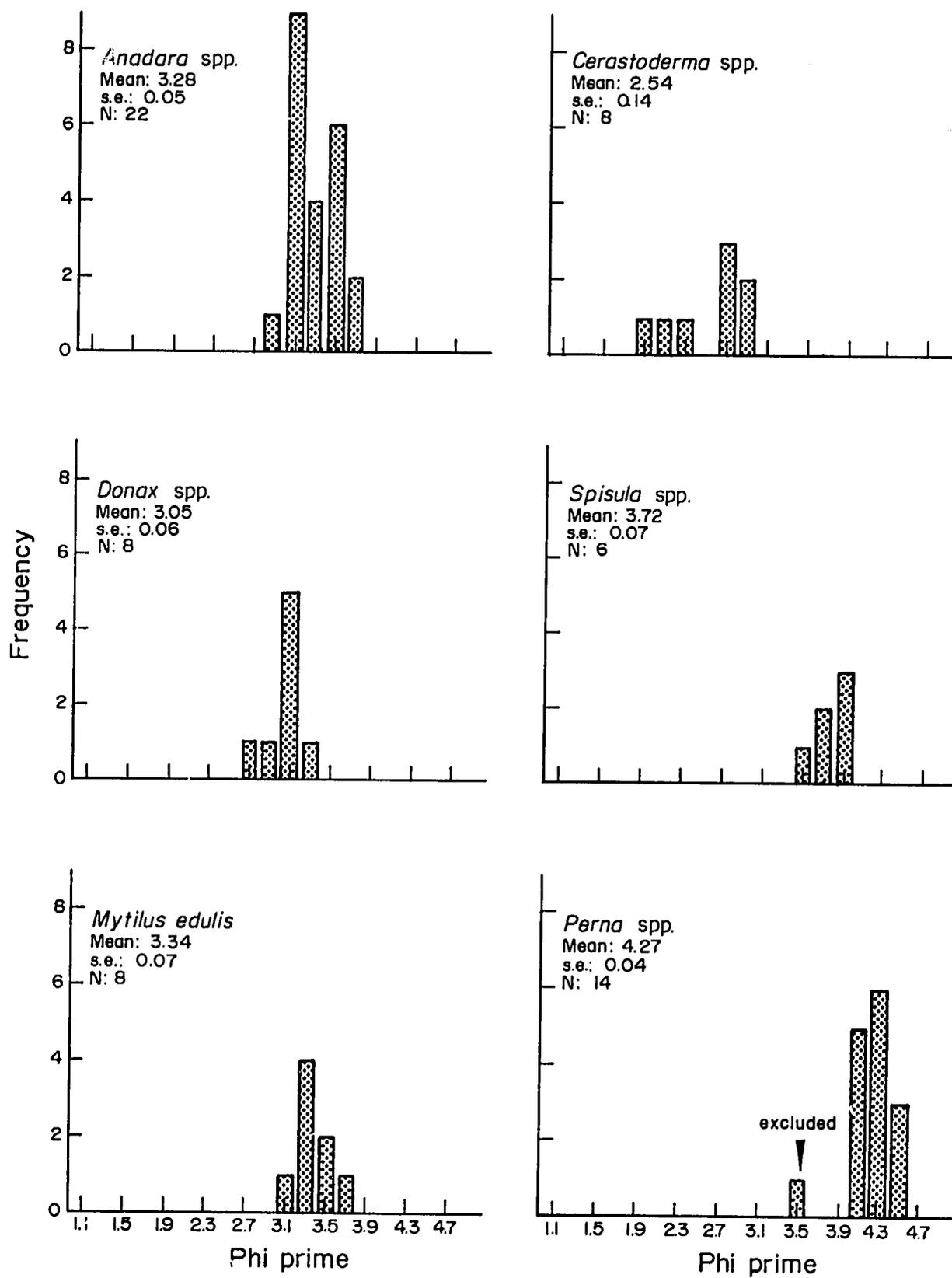


Fig. 5.11. Distribution of  $\phi'$  values for *Anadara* spp., *Cerastoderma* spp., *Donax* spp., *Spisula* spp., *Mytilus edulis* and *Perna* spp.

In conclusion, it appears that in bivalves, it is indeed acceptable to consider  $\phi'$  a parameter whose distribution around a given mean is to a large extent species specific. This has some quite important consequences for the work of a fisheries scientist investigating the growth of bivalves:

- obtained parameters of the VBGF can be checked for their general consistency with what is known of the growth potential of a given species by comparing the  $\phi'$  with a mean  $\phi'$  extracted from published growth parameters for the species in question;
- possibly erroneous sets of growth parameters in the literature can be easily identified;
- if no data are yet available to estimate reliably growth parameters for a given bivalve stock, but the average maximum length of the species to be investigated is known as well as a representative value of  $\phi'$ , a first rough approximation of the growth parameters  $L_{\infty}$  and  $K$  can be obtained by using the relationship  $\log_{10}K = \phi' - 2\log_{10}L_{\infty}$ , with  $L_{\infty}$  being estimated from  $L_{\infty} = 1/0.95L_{\max}$  (Pauly 1984).

This clearly demonstrates that the parameter  $\phi'$  can play an important role in growth studies on bivalves. Its computation, therefore, should become routine whenever parameters of the VBGF are estimated.

### ***The Growth Index $\phi'$ and Its Relationship to Environmental Temperature and Geographic Distribution***

While the previous section has demonstrated the usefulness of the  $\phi'$  concept for intraspecific growth comparison, the application of this concept to the comparison of growth between species needs careful consideration. When looking at the distribution of the  $\phi'$  values in Figs. 5.11 to 5.14 one will note that the largest values of  $\phi'$  are found for some of the tropical Tridacnidae which are known for their extraordinary size. A similar high  $\phi'$  is calculated for the genus *Perna* (Fig. 5.11), another predominantly tropical bivalve species.

On the other hand, *Anadara*, which is also a tropical bivalve, covers a range of  $\phi'$  values (cf. Fig. 5.11) that is comparable to many of the species from temperate waters. *Spisula* has even a higher mean  $\phi'$  than *Anadara*, though it occurs at the northern limits of the subtropical belt.

On the lower end of possible  $\phi'$  values one finds *Macoma* from the very cold waters of North Canada and Greenland. But then again, the lowest values of  $\phi'$  reported in this study are associated with *Corbicula africana*, a tropical freshwater bivalve from Tschad. Though there seems to be a general trend that associates higher values of  $\phi'$  with higher environmental temperature, the actual distribution of  $\phi'$  values of different bivalve species does not seem to reflect adequately this relationship. Consequently, a regression of  $\phi'$  against mean water temperature, involving all 190 cases listed in Appendix 4 does not produce any significant correlation between these two parameters ( $r^2 = 0.076$ ). This could be either because there is no relationship between  $\phi'$  and temperature, or because other factors have such a strong influence on the  $\phi'$  values that the interrelationship with temperature is masked.

One factor that comes to mind is actually methodological. Though it has been explicitly stated by Pauly and Munro (1984) when they presented their  $\phi'$  concept, it is often overlooked that  $\phi'$  can be used only to compare the growth of organisms with similar shape. This restriction follows from the fact that the whole concept was originally weight-

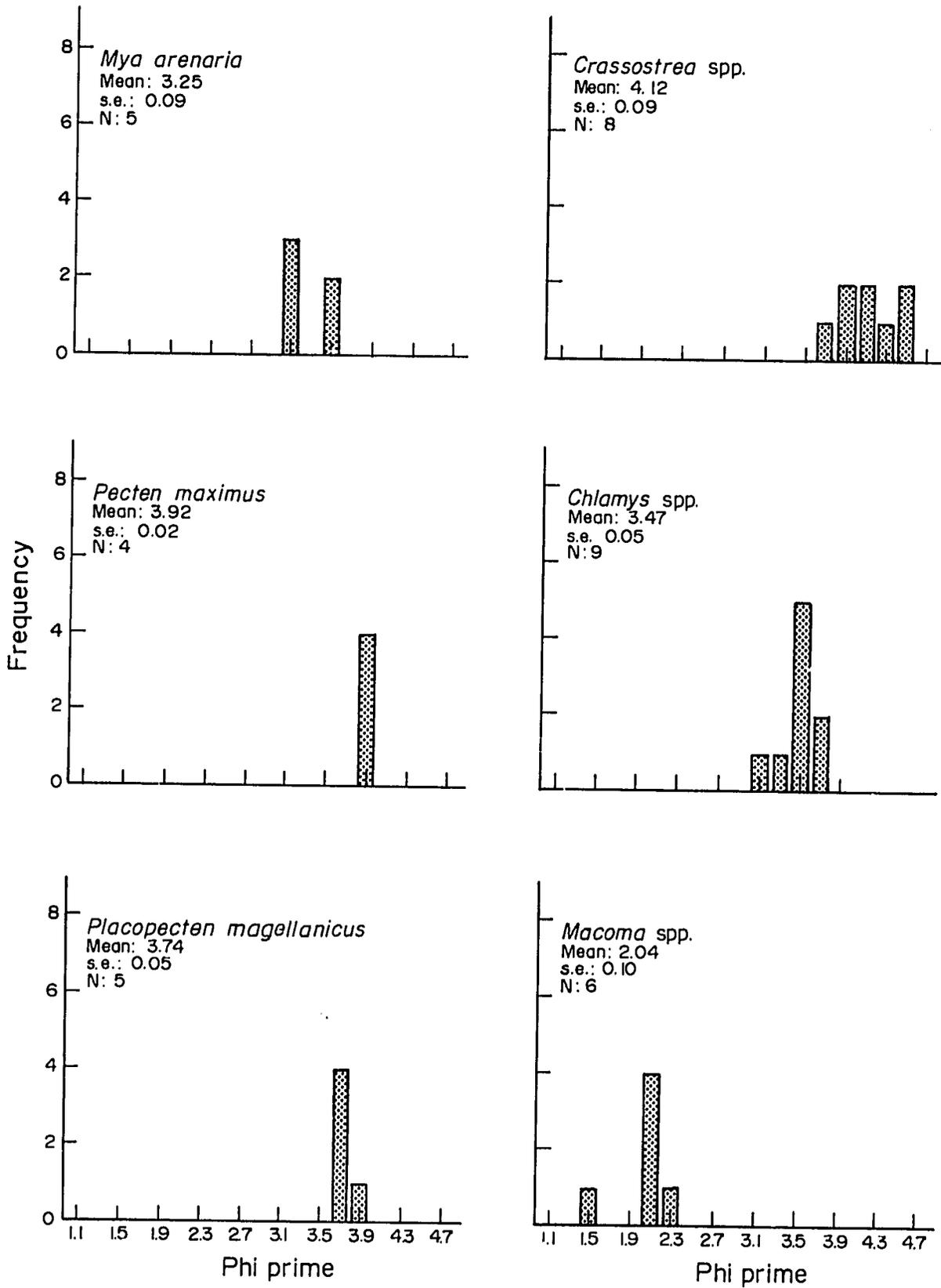


Fig. 5.12. Distribution of  $\phi'$  values for *Mya arenaria*, *Crassostrea* spp., *Pecten maximus*, *Chlamys* spp., *Placopecten magellanicus* and *Macoma* spp.

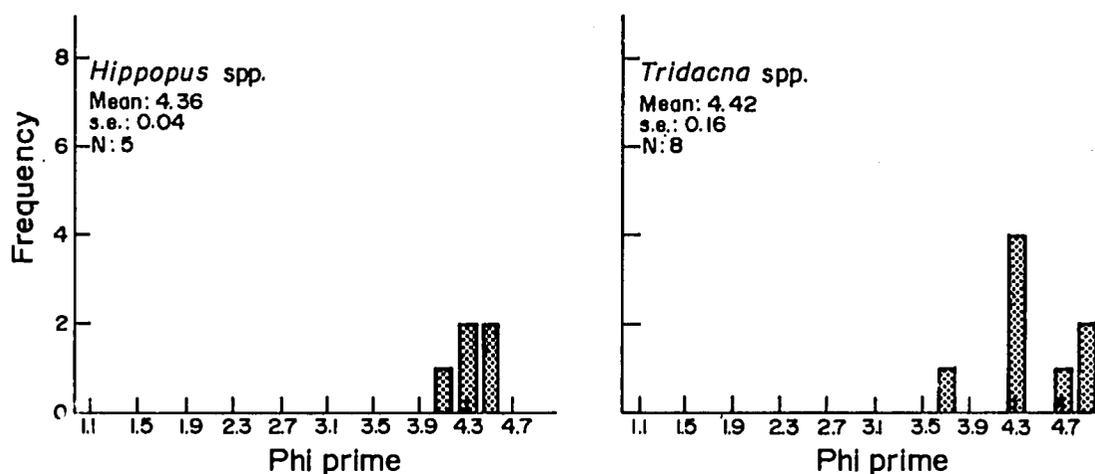


Fig. 5.13. Distribution of  $\phi'$  values for *Hippopus* spp. and *Tridacna* spp.

based and that its conversion for use with length data required the simplified assumption that  $W_{\infty} \propto L_{\infty}^3$ .

Obviously, this limitation is an important point to consider. The form of bivalve shells can be anything from almost round like *Amusium* to very elongated such as *Ensis*. Though both species might have an exponent of the length-weight relationship close to 3, the associated value of "a" will be very different. Thus, predicted weights from a given length will widely differ from each other. Strictly speaking, a comparison of the growth performance between these two species would be only possible on the basis of weight data. This type of data, however, is rarely available because of practical limitations involved in large-scale measurements of bivalve weight. The conversion of  $L_{\infty}$  into the equivalent  $W_{\infty}$  by means of a specific length-weight relationship is not always practicable either, as relevant data are usually available for a small selection of species only, and might refer to quite different units of weights (e.g., total weight, wet meat weight, or dry meat weight). The solution one is often forced to apply is to resort to the use of an approximation of the form  $W \propto L^3$ , as it was also done in the present study. This, however, will introduce a hefty bias in the computation of weight if the coefficient "a" of the length-weight relationship is normally very different from species to species.

In the following, it shall be analyzed under which circumstances the parameter  $\phi'$  can still be used to investigate the dependence of growth performance from environmental temperature. This is done by fitting the data (i) to mean annual water temperature and (ii) to geographic latitude, which, of course, also influences the mean temperature of the environment at which a species occurs. These two variables are considered important in bivalve culture, as they could indirectly be controlled to some extent through selection of the appropriate farming site. It should be noted that the investigated relationships are not necessarily causal. They may be due to other factors such as food availability, which itself is influenced by temperature cycles (Longhurst and Pauly 1987).

Together with the growth parameter obtained for a given bivalve stock, Appendix 4 lists also the mean annual water temperature (in °C) as it was either published with the growth data or extracted from a hydrographic atlas. Though the second option is a rather crude approach, occasional checking of the obtained average water temperature with published data suggested an acceptable match between the two approaches. Still, it has to be accepted that there are probably a number of cases where the actual temperature

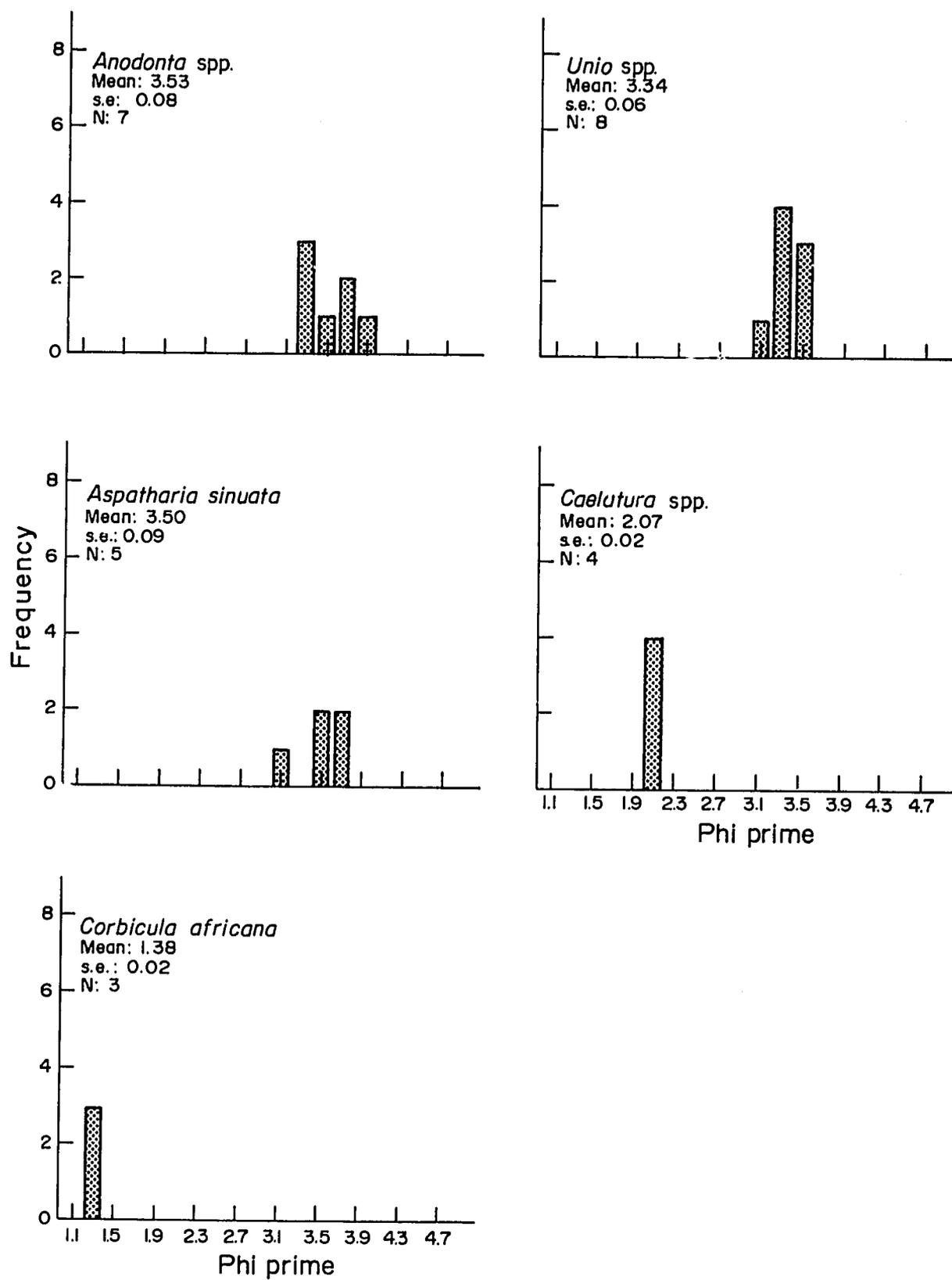


Fig. 5.14. Distribution of  $\Phi'$  values for the freshwater bivalves *Anodonta* spp., *Unio* spp., *Aspatharia sinuata*, *Caelatura* spp. and *Corbicula africana*.

to which the animals were exposed was different from the estimated mean temperature, because of site-specific peculiarities. Appendix 3 gives for each bivalve stock the geographic coordinates, from which the sample originates. Latitude, converted to decimal degrees, was used, without making specifically a difference between North or South.

As mentioned before, dissimilar shell shape is suspected to be responsible for the poor fit of the plot  $\phi'$  against temperature. The task, therefore, was to find a method that would allow testing of the relationship while excluding as much as possible the influence of shell form on the result. The way to achieve this goal is to select a group of bivalve species with similar shape that cover a sufficiently wide temperature range. Inspection of the database in Appendix 4 revealed that there were two groups available that could be used for this purpose: The first is the Mytilidae family, whose members are characterized by a relative elongated shell, and are distributed from the polar region to the tropics. The second group comprises the family Pectinidae, bivalves of almost circular shell form. This family, too, is represented in a wide range of different climatic zones.

Members of the two families selected have a specific, relatively uniform shell shape. A third group was then established, which contains bivalve species with a shell form termed "oval". This group comprised bivalve species that had shell forms in between the two previous groups, i.e., not round, but not as elongated as the mytilids. This was meant to test whether the selection of bivalve species into a group by a relatively "imprecise" term would have a discernible effect on the results.

A total of 30 stocks of bivalves belonging to the family Mytilidae were identified in the database in Appendix 4. They comprise primarily the two genera *Mytilus* and *Perna*. The set is identical with the one presented in Table 5.11, which should be consulted for specific information on the reference number of the cases selected. The corresponding values of  $\phi'$  were taken from Appendix 4, together with mean annual water temperature and geographic latitude of the locality from which the respective stock originates (Appendix 3). Similarly, 27 representatives of the family Pectinidae and 39 cases for the group with oval shell form were extracted from Appendix 4, which are identical to the sets listed in Tables 5.12 and 5.13, respectively.

Figs. 5.15, 5.16 and 5.17 show the plots of  $\phi'$  against temperature, respective geographic latitude, for Mytilidae, Pectinidae, and bivalves with oval shell form.

The statistics of the computed linear regressions for each group are summarized in Table 5.10. From all three examples, the Mytilidae group displays the best fit, with the regression function explaining 67% (temperature) to 70% (latitude) of the variation. In the group of the Pectinidae 45% respective 60% of the variation are explained by the model, while the corresponding values in the group of bivalves with oval shell form are 47% and 50% respectively.

It is interesting to note that in all three cases the plot of  $\phi'$  against geographic latitude consistently yields a higher correlation coefficient than the corresponding plot with water temperature as independent variable. Though geographic latitude and mean annual water temperature are, of course, intercorrelated, it was expected that temperature by itself would have more predictive power than latitude, which influences the growth of bivalves only indirectly through the temperature associated with a certain latitude.

Compared to the global fitting of the  $\phi'$  data to temperature, the reduction of the influence of the variable "shell form" has substantially improved the explanatory power of the model in all three cases. There are, however, gradual differences, which clearly are an expression of the variance in shell form still existing within the selected groups. This variance is probably the least in the group of the Mytilidae which consists of only few species with definitely very similar shell shape. This uniformity in shell form might be the reason for the comparatively higher correlation coefficient obtained with this dataset.

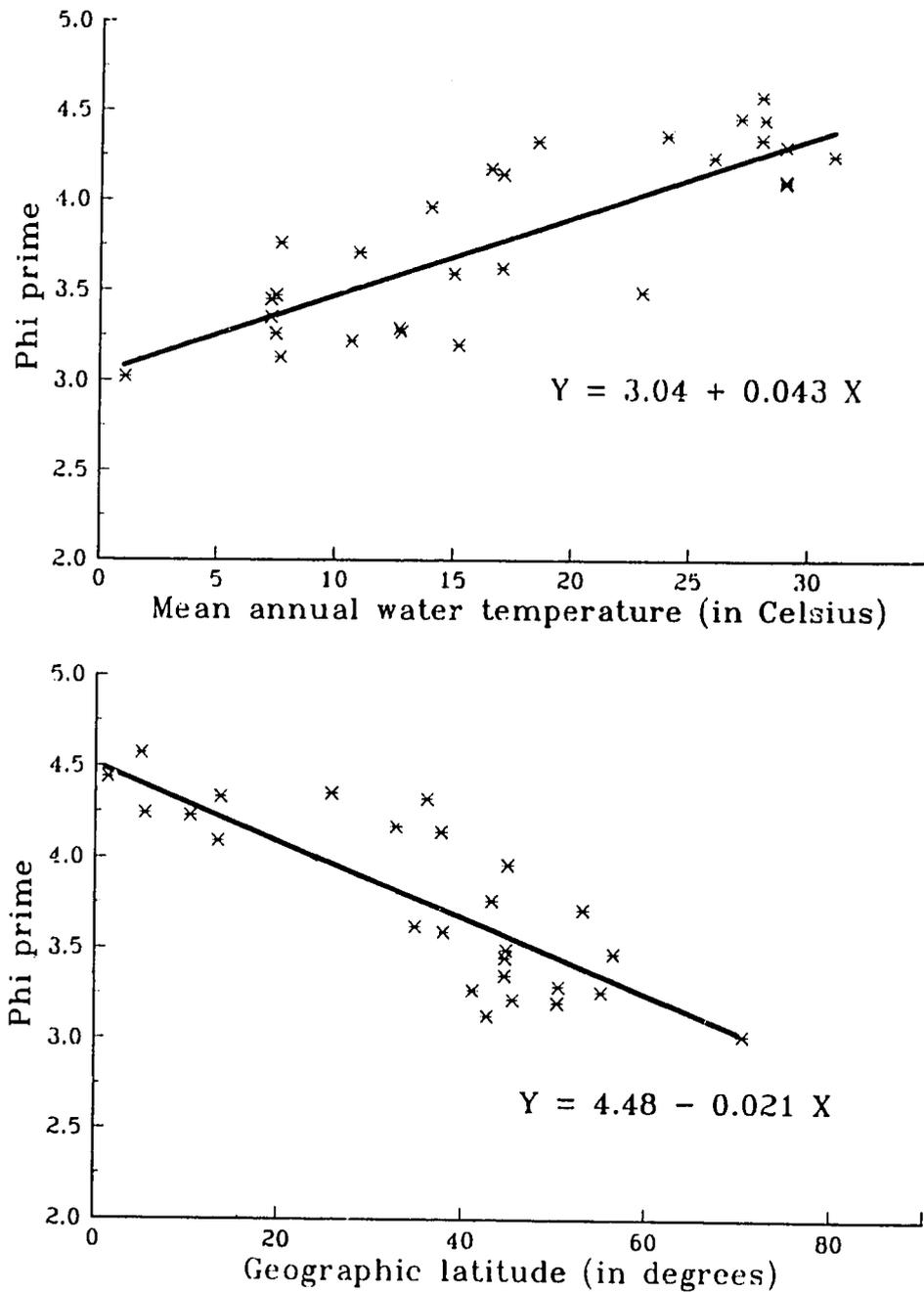


Fig. 5.15. Plot of  $\phi'$  values against temperature, respective geographic latitude (South or North), for bivalve stocks belonging to the family Mytilidae.

In the case of the other two datasets the fit of the model to the data is less conclusive, though the relationship between  $\phi'$  and temperature, respective geographic latitude, is still obvious (see Figs. 5.16 and 5.17). The computed correlation coefficient is similar in both cases, but the standard error of the regression coefficient "b" and of the Y-estimate in the Pectinidae group is only half the size of the standard errors resulting from the dataset of bivalves with oval shell form (cf. Table 5.10). This allows the conclusion that the shell form in the pectinids is probably not as uniform as in the mytilid group, but that the growth performance and its dependence on environmental temperature still can be compared to a certain extent among the different genera in this group. The low correlation

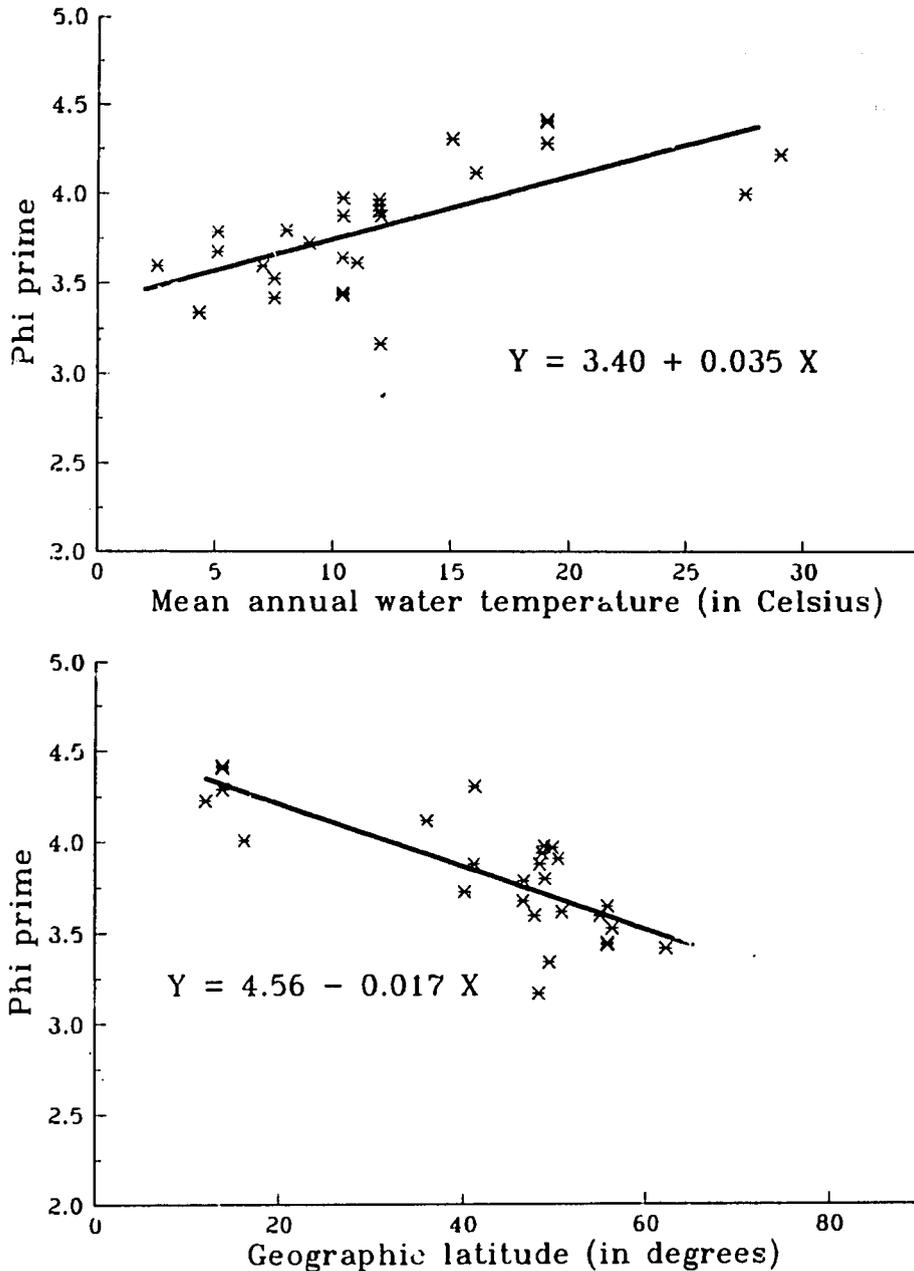


Fig. 5.16. Plot of  $\phi'$  values against temperature, respective geographic latitude (South or North), for bivalve stocks belonging to the family Pectinidae.

coefficient together with the higher standard errors in the group of bivalves with oval shell form also clearly demonstrates that this interrelationship becomes progressively masked with increasing variability of shell form within the group whose growth performance is to be compared.

The example of the mytilids shows that differences in growth performance might indeed be reflected in the parameter  $\phi'$  and that it might actually be possible to make some sort of prediction on the kind of growth that can be expected for a certain species at a given locality. As it was shown, this would require the collection of growth data together with temperature data over a wide range of climatic zones from the given species

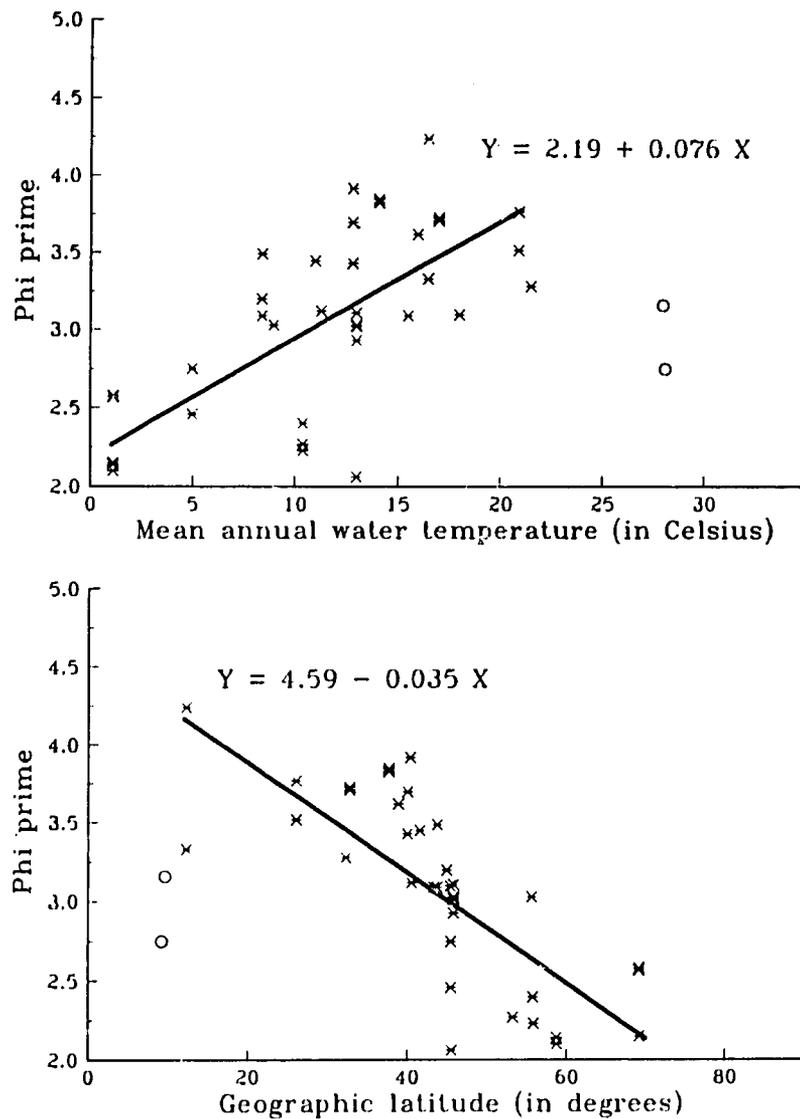


Fig. 5.17. Plot of  $\phi'$  values against temperature, respective geographic latitude (South or North), for various bivalve species that are characterized by an oval shell form. (Points depicted by an open circle have been omitted from the regression.)

Table 5.10. Linear regression of  $\phi'$  against mean annual water temperature, respective geographic latitude, for various groups of bivalves: summary of the coefficients and their standard error.

Group	Y: $\phi'$ - X: Mean temperature						Y: $\phi'$ - X: Latitude					
	a	b	$r^2$	s.e. <sub>b</sub>	s.e. <sub>y</sub>	N	a	b	$r^2$	s.e. <sub>b</sub>	s.e. <sub>y</sub>	N
Mytilidae	3.043	0.043	0.667	0.006	0.278	30	4.485	-0.021	0.706	0.002	0.261	30
Pectinidae	3.400	0.035	0.447	0.008	0.254	27	4.557	-0.017	0.599	0.003	0.216	27
Oval form	2.191	0.076	0.467	0.014	0.476	39	4.591	-0.035	0.502	0.006	0.460	39

or from very closely related species that are of similar shape. To what extent the variable temperature could simply be replaced by geographic location is still unclear and definitely would merit further investigation.

### ***Comparison of Bivalve Growth: The Potential of a Growth Index and Its Limitations***

In contrast to the  $\phi'$  concept, the comparison of growth by means of the growth index  $P$  would principally have the advantage that the method is weight-based and, therefore, independent of shell form. However, as neither weight data, nor length-weight relationships are readily available for all the bivalve species of interest, the computation of the growth index  $P$  in equation (17) had to be based on a  $W_{\infty}$  that was set proportional to  $L_{\infty}^3$ . The resulting parameter  $P$ , therefore, is once again strongly related to length. As a matter of fact, the computed  $W_{\infty}$  is probably more closely related to length than it is to the asymptotic weight.

For this reason, comparison of the parameter  $P$  in the context of the present work is hampered by the same shortcomings as described for the application of the  $\phi'$  concept. Thus, it was decided to limit the growth comparison to the same datasets as the one previously used in the evaluation of the relationship between  $\phi'$  and mean annual water temperature, as the bivalve species included in these datasets have proven to be at least to some extent comparable in their shell form, which reduced the bias introduced by the conversion of length to weight.

The advantage of the growth index  $P$  over the  $\phi'$  concept is that in a direct comparison it gives a clear answer to the question which animal grows better. The value of  $P$  is directly related to the growth rate at the point of inflexion of a weight curve. The larger the value of  $P$ , the better the animal grows.

Tables 5.11, 5.12 and 5.13 list the growth parameters and the computed values of  $W_{\infty}$  and  $P$  for the species grouped under Mytilidae, Pectinidae, and bivalves with oval shell form, respectively. The growth parameters of the VBGF were extracted from Appendix 4.  $W_{\infty}$  was computed using the already mentioned relationship  $W \propto L^3$ , with the values of  $L_{\infty}$  converted from mm to cm in order to avoid high values of  $P$ . This step facilitates the graphic presentation of the results, without affecting their interpretation.

In the summary of the data for the Mytilidae group (Table 5.11) one notes a steady increase of the  $P$ -values from the cold-water species *Mytilus* towards the tropical *Perna* species. This finding is made visible in a series of three auximetric grids that depict the general distribution of the mytilids in the auximetric grid (Fig. 5.13) as well as the position of *Mytilus* spp. (Fig. 5.19) and *Perna* spp. (Fig. 5.20) alone. In this grid,  $P$  is equal to the distance that has a data point from the "base line" (dark grid line) where  $P = 0$ . Note that  $P$  increases in the grid with the same units as  $\log_{10} W_{\infty}$ .

While the whole group of Mytilidae forms a distinct cluster extending almost parallel to the base line, there is yet a clear difference between the general position of *Mytilus* spp. and *Perna* spp. The part of the group formed by *Mytilus* is positioned consistently lower than the *Perna* species, indicating that *Perna* in general displays a better growth. There are, however, two aspects that merit special attention.

One is the rather isolated position of two stocks of *Mytilus* in Fig. 5.19. The upper of the two data point refers to *Mytilus edulis diegensis* (Ref. No. 100) from La Jolla, California (32°51'N). For this stock a growth index of  $P = 3.178$  has been computed. This makes its growth performance comparable to that of the *Perna* species, with which it shares the position in the auximetric grid. Given its comparatively high value of  $K$ , it would

Table 5.11. Growth parameters of bivalves of the family Mytilidae and corresponding values of P for use in the auximetric grid. For source of data refer to corresponding Ref. no. in Appendix A-6. (Note that  $W_{\infty}$  is computed from  $L_{\infty}$  using the relationship  $W \propto L^3$ ).

Ref. no.	Species	Country	$L_{\infty}$ (cm)	K	$W_{\infty}$ (g)	P
55	<i>Crenomytilus grayanus</i>	USSR	16.38	0.05	4,395	2.342
64	<i>Geukensia demissa</i>	USA, Connecticut	9.91	0.19	973	2.267
65	<i>Geukensia demissa</i>	USA, Virginia	10.87	0.33	1,284	2.627
83	<i>Modiolus modiolus</i>	N. Ireland, UK	14.34	0.08	2,949	2.373
91	<i>Mytilus coruscus</i>	USSR	16.52	0.21	4,508	2.976
92	<i>Mytilus edulis</i>	Canada, N.Sc.	5.42	0.95	159	2.180
93	<i>Mytilus edulis</i>	Canada, N.Sc.	7.00	0.46	343	2.169
94	<i>Mytilus edulis</i>	Denmark	8.24	0.27	559	2.179
95	<i>Mytilus edulis</i>	Denmark	8.08	0.45	528	2.375
96	<i>Mytilus edulis</i>	England, UK	9.38	0.22	825	2.259
97	<i>Mytilus edulis</i>	England, UK	8.13	0.24	537	2.110
98	<i>Mytilus edulis</i>	Greenland	14.46	0.05	3,022	2.179
99	<i>Mytilus edulis</i>	Wales, UK	6.72	1.14	313	2.539
100	<i>Mytilus edulis diegensis</i>	USA, California	10.08	1.47	1,024	2.178
101	<i>Mytilus edulis platensis</i>	Uruguay	7.28	0.78	386	2.478
102	<i>Mytilus galloprovincialis</i>	Italy	7.08	1.82	355	2.810
115	<i>Perna canaliculus</i>	New Zealand	20.26	0.51	8,316	3.527
116	<i>Perna canaliculus</i>	New Zealand	14.21	0.69	2,869	3.297
117	<i>Perna perna</i>	Mozambique	12.25	1.50	1,838	3.440
118	<i>Perna perna</i>	Venezuela	12.44	1.11	1,925	3.330
119	<i>Perna viridis</i>	Brunei	14.47	1.77	3,030	3.729
120	<i>Perna viridis</i>	Hong Kong	10.19	0.30	1,058	2.502
122	<i>Perna viridis</i>	India	9.49	2.37	855	3.307
123	<i>Perna viridis</i>	Malaysia	8.91	2.20	707	3.192
124	<i>Perna viridis</i>	Singapore	14.32	1.34	2,936	3.595
125	<i>Perna viridis</i>	Thailand	7.95	1.93	502	2.987
126	<i>Perna viridis</i>	Thailand	8.35	1.81	582	3.023
127	<i>Perna viridis</i>	Thailand	17.99	0.88	5,822	3.710
128	<i>Perna viridis</i>	Thailand	11.19	1.00	1,401	3.146
129	<i>Perna viridis</i>	Thailand	10.72	1.07	1,232	3.120

Table 5.12. Growth parameters of bivalves of the family Pectinidae and corresponding values of P for use in the auximetric grid. For source of data refer to corresponding Ref. No. in Appendix A-6. (Note that  $W_{\infty}$  is computed from  $L_{\infty}$  using the relationship  $W \propto L^3$ ).

Ref. no.	Species	Country	$L_{\infty}$ (cm)	K	$W_{\infty}$ (g)	P
1	<i>Amusium pleuronectes</i>	Philippines	10.60	0.92	1,191	3.040
2	<i>Amusium pleuronectes</i>	Thailand	11.40	1.30	1,482	3.285
27	<i>Argopecten purpuratus</i>	Peru	9.49	2.88	855	3.391
28	<i>Argopecten purpuratus</i>	Peru	9.92	1.99	976	3.288
29	<i>Argopecten purpuratus</i>	Peru	11.15	2.10	1,386	3.464
38	<i>Chlamys albidus</i>	USSR, Kuril Is.	11.72	0.16	1,610	2.411
39	<i>Chlamys opercularis</i>	Denmark	7.31	0.64	391	2.398
40	<i>Chlamys opercularis</i>	Denmark	6.99	0.54	342	2.266
41	<i>Chlamys opercularis</i>	Denmark	7.80	0.65	475	2.489
42	<i>Chlamys opercularis</i>	England, UK	5.55	1.34	171	2.360
43	<i>Chlamys opercularis</i>	Scotland, UK	6.56	1.05	282	2.472
44	<i>Chlamys opercularis</i>	Scotland, UK	7.03	0.56	347	2.289
45	<i>Chlamys opercularis</i>	Scotland, UK	7.42	0.51	409	2.319
46	<i>Chlamys varia</i>	France	5.09	0.57	132	1.876
107	<i>Patinopecten caurinus</i>	Canada	15.68	0.39	3,855	3.177
108	<i>Patinopecten caurinus</i>	Canada	11.24	0.50	1,420	2.851
109	<i>Patinopecten yessoensis</i>	Japan	14.42	0.98	2,998	3.468
110	<i>Patinopecten yessoensis</i>	Korea	12.28	0.87	1,852	3.207
111	<i>Pecten maximus</i>	France	13.89	0.48	2,680	3.109
112	<i>Pecten maximus</i>	France	10.68	0.66	1,218	2.905
113	<i>Pecten maximus</i>	France	12.35	0.53	1,884	2.999
114	<i>Pecten maximus</i>	France	12.42	0.56	916	3.031
131	<i>Placopecten magellanicus</i>	Canada, Newfdl.	17.38	0.16	5,250	2.924
132	<i>Placopecten magellanicus</i>	Canada, Newfdl.	12.76	0.38	2,078	2.897
133	<i>Placopecten magellanicus</i>	Canada, Newfdl.	15.84	0.16	3,974	2.803
134	<i>Placopecten magellanicus</i>	USA	14.36	0.37	2,961	3.040
135	<i>Placopecten magellanicus</i>	USA, New Jersey	15.59	0.22	3,789	2.921

Table 5.13. Growth parameters of bivalves from different families featuring an oval shell form, and corresponding values of P for use in the auximetric grid. For source of data refer to corresponding Ref. no. in Appendix A-6. (Note that  $W_{\infty}$  is computed from  $L_{\infty}$ , using the relationship  $W \propto L^3$ ).

Ref. no.	Species	Country	$L_{\infty}$ (cm)	K	$W_{\infty}$ (g)	P
56	<i>Donax cuneatus</i>	India	2.47	0.92	15	1.142
57	<i>Donax incarnatus</i>	India	3.11	1.50	30	1.654
58	<i>Donax peruvianus</i>	Peru	4.60	1.00	97	1.988
59	<i>Donax trunculus</i>	France	3.60	0.96	47	1.651
60	<i>Donax trunculus</i>	France	3.84	0.72	57	1.610
61	<i>Donax trunculus</i>	France	4.35	0.45	82	1.569
62	<i>Donax vittatus</i>	France	3.59	1.01	46	1.670
63	<i>Donax vittatus</i>	France	3.13	1.06	31	1.512
66	<i>Hiatella byssifera</i>	Greenland	3.85	0.25	57	1.154
72	<i>Macoma balthica</i>	Canada	2.11	0.31	9	0.464
73	<i>Macoma balthica</i>	Canada	3.73	0.09	52	0.669
74	<i>Macoma balthica</i>	Canada, Quebec	1.59	0.14	4	0.250
75	<i>Macoma balthica</i>	France	1.82	0.35	5	0.324
76	<i>Macoma balthica</i>	Netherlands	2.49	0.30	15	0.666
77	<i>Macoma calcarea</i>	Greenland	3.29	0.13	36	0.666
78	<i>Macrocallista maculata</i>	Bermuda	6.60	0.44	287	2.102
79	<i>Mercenaria campechiensis</i>	USA, Florida	9.63	0.64	893	2.757
80	<i>Mercenaria mercenaria</i>	USA, Florida	8.18	0.50	547	2.437
81	<i>Mercenaria mercenaria</i>	USA, Rhode Isl.	9.09	0.16	751	2.080
82	<i>Mesodesma donacium</i>	Peru	12.40	1.13	1,907	3.333
85	<i>Mya arenaria</i>	Canada	9.13	0.19	761	2.160
86	<i>Mya arenaria</i>	Denmark	6.01	0.30	217	1.814
87	<i>Mya arenaria</i>	USA, Maine	6.17	0.32	235	1.876
88	<i>Mya arenaria</i>	USA, Maine	14.84	0.14	3,268	2.660
89	<i>Mya arenaria</i>	USA, Massachus.	8.52	0.39	618	2.382
90	<i>Mya truncata</i>	Greenland	6.87	0.08	324	1.414
103	<i>Nucula minuta</i>	Scotland, UK	1.84	0.50	6	0.493
104	<i>Nuculana pumila</i>	Newfoundland	3.00	0.32	27	0.937
140	<i>Spisula sachalinensis</i>	Japan	9.87	0.69	962	2.822
141	<i>Spisula sachalinensis</i>	Japan	10.24	0.67	1,074	2.857
142	<i>Spisula sachalinensis</i>	Korea	12.64	0.26	2,019	2.720
143	<i>Spisula solidissima</i>	USA	19.11	0.23	6,979	3.206
144	<i>Spisula solidissima</i>	USA, New Jersey	9.15	0.32	766	2.389
145	<i>Spisula solidissima</i>	USA, New Jersey	11.82	0.36	1,651	2.774
146	<i>Tapes decussatus</i>	Italy	5.37	0.44	155	1.833
147	<i>Tivela stultorum</i>	USA, California	17.31	0.18	5,187	2.970
148	<i>Tivela stultorum</i>	USA, California	20.65	0.12	8,806	3.024
158	<i>Venus striatula</i>	Scotland, UK	3.29	0.23	36	0.913
159	<i>Yoldia thraciaformis</i>	Newfoundland	5.58	0.18	174	1.495

seem that this species could be a prime candidate for culture operation in areas where *Mytilus* is part of the native fauna and *Perna* can not be cultured or should not be cultured for ecological reasons. The second data point refers to *Mytilus coruscus* from the Vostok Bay, USSR (43°10'N) with a  $P = 2.976$ . This species also displays a growth potential slightly higher than the average for *Mytilus*. The relatively low K indicates, however, that this species outperforms other mytilids primarily by attaining larger sizes. It might be interesting to examine the growth of this species when transplanted to areas with a more elevated water temperature.

The second interesting aspect is the occurrence of an isolated data point in Fig. 5.20. This data point refers to the *Perna viridis* stock from Hong Kong waters (Ref. No. 120). In the distribution of  $\phi'$  values (see Fig. 5.11) the isolated position of the  $\phi'$  computed from the growth parameters of this stock had already given rise to the suspicion that the growth parameters might be biased. With a  $P = 2.502$  this stock again stands apart from



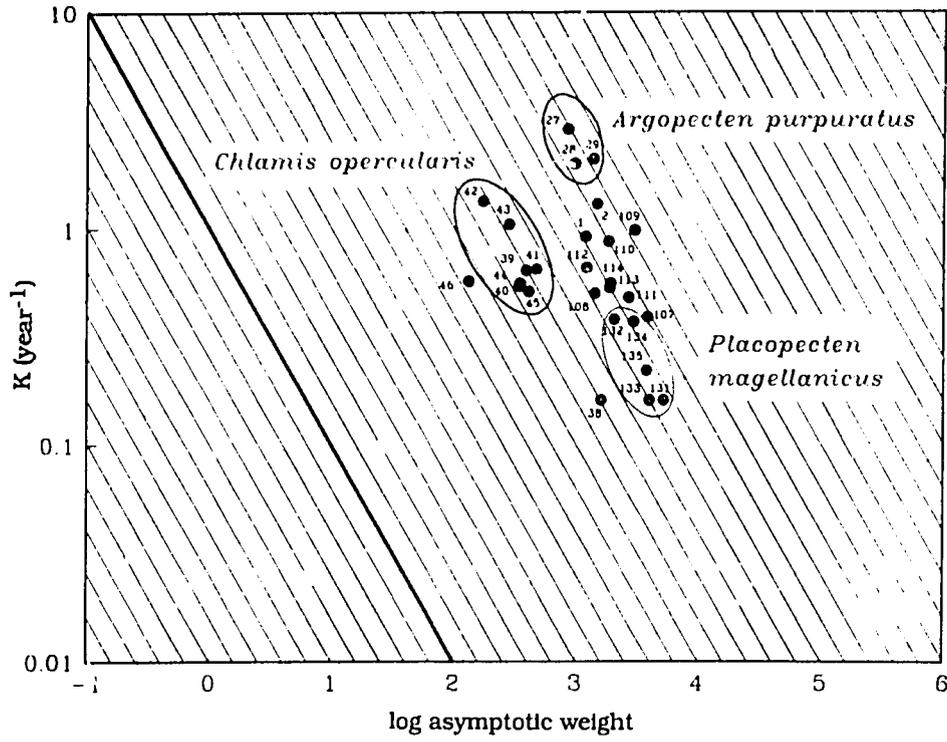


Fig. 5.21. Auximetric grid: Pectinidae, various species. Numbers refer to the Ref. No. in Table 19.

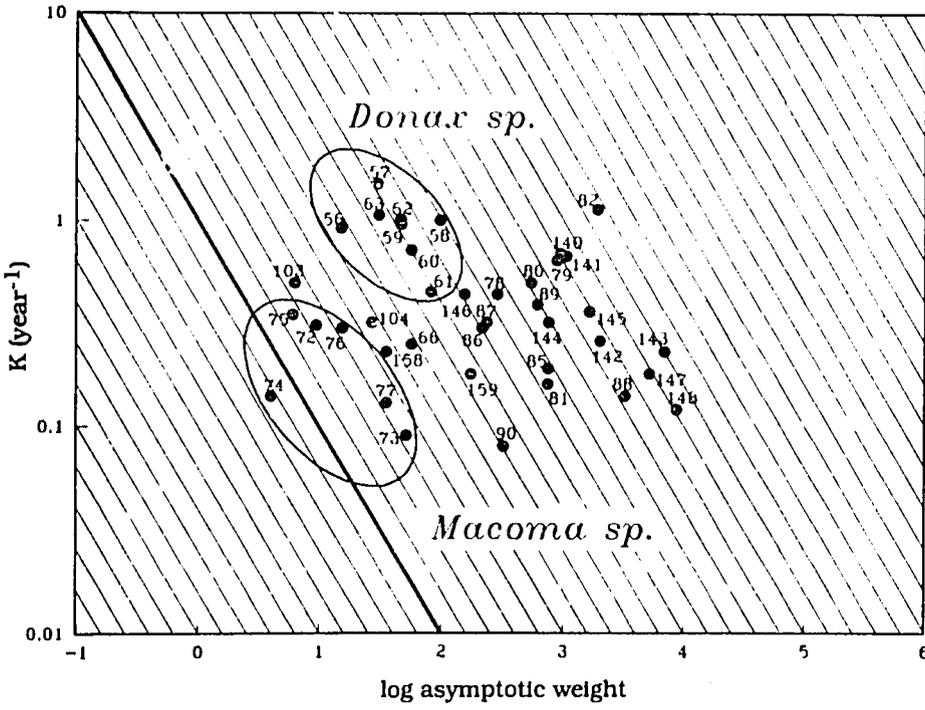


Fig. 5.22. Auximetric grid: various bivalve families with oval shell form. Numbers refer to the Ref. No. in Table 5.13.

level also refer to a *Chlamys* species, i.e., to *Chlamys albidus* (Ref. No. 38) and *Chlamys varia* (Ref. No. 46). It is interesting to observe that though the clustering of the remaining Pectinidae is rather uniform, certain species such as *Argopecten purpuratus* and *Placopecten magellanicus* occupy distinct, nonoverlapping areas within this cluster. Though similar in their general growth potential, the warm water species *A. purpuratus* must be considered fast-growing, while *P. magellanicus* from the North Atlantic is slow-growing but attains much larger sizes.

Like in the case of growth comparison based on  $\phi'$ , the presentation of the group of bivalves with oval shell form in an auximetric grid (cf. Fig. 5.22) shows the limitations of the method when applied to the comparison of bivalves with rather different shell form. It is very unlikely that the differences in the parameter  $P$  solely reflect actual growth differences but are rather artificially created by the poorly adapted transformation of length to weight. Still one can identify distinctive areas occupied predominantly by one genus, as is demonstrated for *Donax* and *Macoma*. Though it is difficult to make an assessment in absolute terms from the auximetric grid, it seems justified to consider *Macoma* as the genus with probably the lowest growth potential among the marine bivalves investigated.

Comparing the results from the three groups one realizes once more that growth comparison between bivalve species should preferably be based on actual weight data. If only length-based data are available, good estimates of individual length-weight relationships should be applied rather than a fixed relationship for all species in question to convert asymptotic length to its equivalent weight term. If, however, the length-weight transformation has to be based on a simplified assumption such as  $W \propto L^3$ , then the growth comparison has to be limited to species of very similar shape to remain meaningful.

## CHAPTER 6

### CONCLUSIONS

#### Shell Microstructure Analysis

Analysis of the shell microstructure in bivalves has proved quite valuable in long-lived species from temperate waters. Growth records retained in the shell in the form of periodic structures represent time series that can contain information worth several years of data collection. It thus can be an economic alternative to cost- and time-intensive mark and recapture programs.

This advantage, however, is countered by the possible uncertainties associated with the time scale that has to be assigned to the observed periodicity in the shell microstructure. The reliability in the interpretation of periodic structures probably lessens to the same degree as the seasonality of the causative event, e.g., temperature, changes from a distinct annual periodicity to semi-annual cycles, or even further to a daily periodicity related, e.g., to tides.

From the analysis of the shell microstructure in the two bivalve species *Anadara granosa* and *Perna viridis* is inferred that the periodicity in the formation of growth lines in tropical bivalves is primarily influenced by the tidal cycle. However, the analysis has also shown that the response to tidal changes is not necessarily uniform, but reflects the species' varying degree of adaptation to a life with constantly changing water levels and currents.

As a consequence, in the tropics this form of growth analysis seems to bear a high risk of unreliability when it comes to assigning a time scale to the periodic formation of growth lines in the shell microstructure. Without sufficient knowledge of a species' ecology, it is very unlikely that meaningful growth information can be deduced from the distribution of growth lines in the shell microstructure of tropical bivalves.

If one adds to these limitations the relative demanding preparative work involved and the requirement of sufficient practical experience with this kind of analysis, it seems hardly justified to recommend this technique in the investigation of the growth of tropical bivalves. This point needs careful consideration, all the more as the comparatively short life span of most tropical bivalve species suggests alternatives (e.g., controlled growth experiments with specimens of different size) that are less sophisticated in design and can still yield useful growth data within relatively a short time. Such methods, therefore, must be considered more appropriate in tropical bivalve research than the analysis of growth lines in the shell microstructure.

#### Comparison of Bivalve Growth

In fisheries research, growth analysis is commonly based on the von Bertalanffy growth model. Investigations into physiological aspects of bivalve growth show that the basic assumptions of the theory of growth presented by von Bertalanffy generally applies to

bivalves, too. This is insofar important as it justifies the application of most models traditionally used in fisheries science to the management of bivalve resources.

In the present study, emphasis was laid on the question, whether the growth of bivalves can be expressed in terms of a standard growth index, like e.g.  $\phi'$ , and to what extent such an index can be used to compare the growth not only within a species, but also between species.

The controlled growth experiments with *A. granosa* and *P. viridis* have demonstrated that under similar culture conditions the VBGF growth parameters of single specimens can fluctuate over a wide range, but that the resulting value of  $\phi'$  remains rather constant for the species in question. This supports the perception of  $\phi'$  being a species-specific parameter, which possibly is representative of the organism's physiological "capacity" as a whole, governed by genetically determined factors. Or, to put it simply: Any bivalve species can be assumed to have a certain characteristic growth potential, which is genetically determined and which it will try to satisfy within its normal life span. The "strategies" to reach this goal are largely dependent on environmental factors such as food availability, population density, type of sediment, shore level, annual temperature cycle, to name a few. The differences in these factors will lead to differences in longevity and maximum adult size and hence to the variance in the parameters  $L_{\infty}$  and  $K$ .

Within a certain range of ecological conditions a bivalve species at a given locality can thus be expected to realize its growth potential using one or the other strategy. This should result in a rather uniform and characteristic growth index, though the basic growth parameters might vary considerably. If methodic errors in parameter estimation can be excluded, variance in  $\phi'$ , therefore, can primarily be considered an expression of the genetic variability in the growth potential of a species. To a lesser extent they might also mirror extreme ecological conditions, to which the species at the given locality had not yet fully adapted, and which might lead to atypical (e.g., stunted) growth.

This assumption of  $\phi'$  being a species-specific parameter was further evidenced by the compilation of growth parameters for 190 bivalve stocks, which allowed the analysis of the distribution of the  $\phi'$  values for a number of different species and genera. In most cases,  $\phi'$  values were narrowly distributed around a mean that was considered characteristic for the species or genus. Deviations from this pattern were especially found if a number of different species were combined under a genus. The latter indicates that growth might in some cases be different enough between two apparently closely related species to manifest itself in differences in the growth performance index  $\phi'$ .

From the concept of  $\phi'$  being a species-specific parameter arises a potentially useful application of this growth index: It might be used to obtain first rough estimates of the growth parameters  $L_{\infty}$  and  $K$  for a given stock in cases where only one of the two parameters is known, but a mean value of  $\phi'$  can be computed from growth parameters of the same species, obtained e.g., from the literature.

As mentioned before, the present study has shown that a growth index computed on the genus level may vary to an extent that renders its use in the estimation of a missing growth parameter more than questionable. Though there are cases, where this apparently is not too much of a constraint (e.g., *Perna*), the use of different species of the same genus in the computation of a mean growth performance index should always be considered last. If it cannot be avoided on practical grounds, a thorough check should be performed for deviations in the distribution of the single values that are not purely accidental.

The use of a growth index for the comparison of growth between different bivalve species turned out to be rather limited. This finds its explanation in the fact that length-based comparison of growth requires the compared organisms to be of similar shape. If

this precondition is not met, the influence of the shape will introduce a variation large enough to mask any potential growth difference. As a consequence, growth comparison in bivalves ideally should be either based on weights or should involve the transformation of length into weight by means of adequate length-weight relationships.

Though comparison of bivalve growth on a global level was inconclusive, the limitation of such a comparison to groups of bivalves characterized by a similar shell shape has good prospects of providing valuable information on the relative growth performance of the species involved. This was successfully demonstrated in the case of the family Mytilidae. A direct relationship was observed between the growth index  $\phi'$  and either temperature or geographic latitude as predictive variable. While  $\phi'$  increased linearly with mean annual water temperature, it decreased linearly with latitude. The latter was to be expected as temperature and latitude are inversely correlated.

Given that  $L_{\infty}$  has twice the "weight" of  $K$  in the formula to compute  $\phi'$ , one has to conclude that in general the adult size bivalves can reach increases with increasing temperature, or simply spoken: bivalves grow larger in warm waters than in cold waters. The most obvious expression of this rule is the enormous size that members of the family Tridacnidae ("giant (!) clams") can reach in the tropical regions of the Pacific. In contrast, bivalve species at high latitudes stay comparatively small.

This finding is in a clear contrast to the general view that marine organisms tend to grow to a larger final size, the lower the mean water temperature of their environment (von Bertalanffy 1951, see also Laudien 1973 for examples). This rule has broadly been explained with the increased metabolism associated with warmer waters that results in a shorter life span of the organism and, hence, reduces the final size it can reach (cf. Rumohr 1975).

In most cases, when measuring the "growth" of bivalves, one actually does not look at the growth of a "body tissue" as, e.g., in fish, but rather at the growth of the shell. Obviously, shell growth and tissue growth are interrelated. A bivalve's body mass cannot increase beyond the space contained between the valves, and, on the other hand, the secretion of new shell material requires an increase of tissue surface. A major component of the bivalve's shell is calcium carbonate which is deposited in form of crystals into an organic matrix (Crenshaw 1980). From this follows necessarily that the availability of calcium carbonate is of crucial importance for shell growth, while soft tissue growth might be influenced by other factors such as food availability. An interesting example was given by Mallet et al. (1987), who investigated the winter growth of *Mytilus edulis* at ice-covered and ice-free sites. Though there was still a positive and significant correlation between shell and tissue growth, shell growth was similar at both sites while tissue growth was better at the ice-free site, which the authors related to the better feeding condition at this site.

It is a well known property of seawater that the solubility of calcium carbonate increases with decreasing temperature and high pressure (Dietrich et al. 1980). The free energy of precipitation of calcium carbonate from seawater is a function of its solubility product and increases approximately linearly from 0°C to 40°C (Clarke 1983), which means that the metabolic cost of removing calcium carbonate for the construction of shell material is greater at low than at high temperatures.

Evidence for a close relationship between calcification and temperature has been brought forward by Graus (1974). He showed that a calcification index (dry weight of the shell/internal volume) increased almost linearly with temperature in marine shallow-water gastropods. Nicol (1967) mentioned that polar molluscs tend to be small and thin shelled. On the other hand, as already mentioned, there are the enormous shells of the Tridacnidae, or - to demonstrate that this phenomenon is not limited to bivalves - the

immense coral reefs that are primarily found in the tropical and subtropical zones of the oceans.

The linear increase of the growth performance index  $\phi'$  with the mean annual water temperature reported for the Mytilidae might, therefore, be considered the result of two parallel occurring processes: one is a general acceleration of growth processes with increasing temperature. In fish, this leads to an increase in the growth constant  $K$ , but in the same time reduces  $L_{\infty}$ . The latter is a consequence of the increased routine metabolism at elevated temperatures, which let the animal reach the point at an earlier stage, where the oxygen supply through the gills is just sufficient for maintenance metabolism (Longhurst and Pauly 1987).

In bivalves (or at least in mytilids), however, this general relationship between oxygen supply and growth is masked by the second growth-related process, i.e., the increase of the solubility product of  $\text{CaCO}_3$  with decreasing temperature. This allows warmwater species during their growth period to produce relatively more shell material at any given level of oxygen supply than their coldwater relatives. Apparently, this factor has a much stronger influence on growth than the metabolic constraints associated with elevated temperature and, hence, leads to the phenomenon that bivalves tend to reach larger adult size in the tropics than in the cold waters at higher latitudes.

As discussed before, the less conclusive results for the family of the Pectinidae do not invalidate this statement, but is rather a consequence of the decreasing comparability of the species selected. Further research into this matter should bring more clarification about the influence of temperature on the growth of bivalves. Especially if data on weight were available, comparability among different species might improve. This would also probably allow to make better use of the growth index  $P$ , which loses much of its significance when based on a generalized length-weight transformation, as it had to be done in this study.

The confirmation of the postulated relationship between growth and temperature has an interesting aspect for bivalve resource management: If for a bivalve species (or family with uniform shell shape) growth parameters are known for a number of different stocks, grown under comparable conditions and covering most of the temperature range the species will normally occupy, then there is the possibility to make reasonable assumptions on the growth performance expected for a species at a given locality. Such an approach might be of considerable help in preliminary investigations into the potential of bivalve culture as an integrated part of a general coastal resource management program.

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**Appendix 1: *Perna viridis*: growth experiments 1986 at Ang Sila, Thailand.**

Appendix 1.1: *Perna viridis*, growth experiments 1986, Ang Sila, Thailand.  
Summary of field data for the period June/July 1986. Length of marked specimens, measured to the lower 0.05 mm.

DATE:	23-06-1986			25-07-1986		
SITE:	Fish Trap			Fish Trap		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	63.80	63.43	64.02	70.17	68.83	72.02
STD:	4.74	4.89	4.79	5.42	5.09	5.29
NO.: 1	61.85	64.15	59.95	69.00	68.30	M
2	59.65	60.50	66.60	67.50	67.00	76.30
3	63.60	57.85	72.95	71.85	66.60	79.35
4	67.50	61.65	58.15	75.25	67.05	M
5	65.00	64.90	60.95	72.55	69.35	63.85
6	61.05	72.50	69.00	67.90	78.50	79.30
7	72.05	70.15	70.10	77.65	74.00	M
8	63.05	63.30	67.15	68.90	70.95	M
9	64.55	63.15	60.90	70.85	68.60	68.85
10	62.35	65.30	52.20	70.10	73.55	61.55
11	67.10	61.80	58.35	73.25	66.25	M
12	59.85	63.90	63.85	65.75	70.25	M
13	62.25	61.25	56.65	72.60	66.00	63.30
14	63.45	74.75	66.80	70.55	78.35	76.60
15	58.70	68.75	65.30	57.70	68.70	73.85
16	65.35	65.45	65.75	72.55	72.40	74.20
17	77.65	60.20	60.15	84.20	63.65	67.90
18	65.90	58.60	66.95	74.20	63.85	77.30
19	61.90	74.50	65.85	63.05	80.00	75.35
20	62.15	69.60	64.20	69.05	77.45	69.80
21	64.80	59.45	66.25	67.85	64.70	73.30
22	57.85	57.75	62.60	65.10	64.65	72.40
23	60.40	63.50	67.80	63.55	70.70	71.40
24	60.45	57.75	56.00	67.30	66.60	65.75
25	62.10	59.30	69.40	71.30	60.45	81.35
26	67.30	60.95	60.70	72.65	61.65	65.45
27	56.35	60.80	62.35	65.30	63.00	68.85
28	61.60	59.80	63.80	66.65	65.50	74.05
29	76.30	56.15	71.05	83.40	63.65	74.50
30	61.00	64.40	67.95	66.70	72.30	73.45
Combined Length Measurements (incl. mussels with lost tags):						
MEAN:	63.75			70.29		
STD:	4.81			5.50		
N:	90			88		

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 1.2: *Perna viridis*, growth experiments 1986, Ang Sila, Thailand. Summary of field data for the period August/September 1986. Length of marked specimens, measured to the lower 0.05 mm.

DATE:	23-08-1986			26-09-1986		
SITE:	Fish Trap			Fish Trap		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	72.96	70.44	75.13	74.24	72.32	76.93
STD:	5.89	4.96	5.74	6.16	4.85	6.03
NO.: 1	70.75	M		71.55		
2	71.45	69.35	80.25	72.95	69.65	M
3	74.70	66.60	83.50	75.15	69.80	85.90
4	78.20	69.85		79.05	72.20	
5	74.15	72.25	66.25	76.30	72.90	67.75
6	73.05	80.50	82.25	76.65	83.00	84.75
7	78.50	74.90		M	76.45	
8	M	71.60			73.05	
9	73.65	69.35	72.05	74.20	71.25	74.55
10	72.65	74.60	65.50	73.25	75.85	69.05
11	77.20	67.90		M	71.90	
12	67.60	71.05		69.45	72.80	
13	74.75	67.15	64.65	77.05	69.40	65.40
14	73.05	77.85	79.85	74.70	78.30	M
15	57.00	71.15	M	58.65	73.10	
16	76.20	73.75	76.40	77.20	77.55	78.70
17	87.45	64.10	72.50	88.90	65.25	75.20
18	76.15	M	79.90	77.70		M
19	65.90	81.10	77.20	68.85	81.05	79.05
20	71.00	78.00	73.65	71.10	79.30	76.70
21	69.50	66.00	77.95	70.70	69.30	79.95
22	66.50	64.95	M	68.40	66.00	
23	67.40	71.60	73.30	68.85	74.70	73.30
24	71.95	68.15	68.10	73.05	70.10	M
25	74.40	61.50	83.55	M	62.05	86.75
26	77.10	M	68.40	78.05		71.10
27	M	66.00	M		68.45	
28	68.00	65.70	78.35	70.55	68.05	81.15
29	85.65	65.10	76.05	88.80	66.95	78.30
30	68.25	71.10	77.55	M	73.65	79.70
Combined Length Measurements (incl. mussels with lost tags):						
MEAN:	72.55			74.40		
STD:	5.77			5.89		
N:	88			88		

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 1.3: *Perna viridis*, growth experiments 1986, Ang Sila, Thailand. Summary of field data for the period October/November 1986. Length of marked specimens, measured to the lower 0.05 mm.

DATE:	27-10-1986			24-11-1986		
SITE:	Fish Trap			Fish Trap		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	79.38	76.25	82.04	84.58	77.79	82.19
STD:	6.39	5.47	7.72	6.23	6.24	6.54
NO.: 1	74.90			76.60		
2	78.85	70.45		81.55	75.70	
3	79.15	76.95	94.95	83.45	81.85	D
4	83.35	77.40		84.55	81.30	
5	80.55	73.00	69.15	82.70	72.20	72.20
6	84.65	85.35	92.70	93.50	91.35	D
7		77.15			M	
8		78.55			82.95	
9	79.10	79.55	78.10	86.85	85.15	82.55
10	80.15	78.20	76.75	85.75	D	80.10
11		74.90			82.30	
12	74.90	74.55		74.70	D	
13	M	75.30	68.05		D	68.05
14	M	82.10			82.20	
15	65.25	80.75		70.95	D	
16	82.40	82.50	84.00	89.50	D	84.80
17	92.10	70.05	M	96.80	73.75	
18	M					
19	M	86.70	84.40		D	90.90
20	70.75	85.30	83.15	D	M	D
21	71.85	72.95	M	M	74.60	
22	77.95	70.45		83.80	70.85	
23	74.40	79.80	83.40	85.60	M	87.30
24	79.80	76.00		85.35	D	
25		64.25	D		66.95	
26	84.40		73.65	87.10		79.40
27		74.40			76.80	
28	77.90	67.90	86.45	81.05	70.20	87.35
29	92.80	68.95	85.90	92.10	D	85.80
30		74.55	87.60		76.10	85.40
Combined Length Measurements (incl. mussels with lost tags):						
MEAN:	79.20			82.59		
STD:	6.52			6.71		
N:	86			68		

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 1.4: *Perna viridis*, growth experiments 1986, Ang Sila, Thailand. Summary of field data for the period December 1986. Length of marked specimens, measured to the lower 0.05 mm.

DATE:	24-12-1986			
SITE:	Fish Trap			
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	
MEAN: STD:	85.27 6.95	79.57 7.09	84.33 7.70	
NO.:	1	2	3	
	77.80			
	2	84.35	M	
	3	M	M	
	4	M	83.55	
	5	84.30	M	73.90
	6	97.95	93.20	
	7			
	8		M	
	9	M	87.85	83.95
	10	87.85		M
	11		M	
	12	76.70		
	13			68.30
	14		82.20	
	15	71.00		
	16	91.20		85.55
	17	M	75.50	
	18			
	19			93.45
	20			
	21		76.85	
	22	87.05	71.00	
	23	87.40		91.80
	24	M		
	25		68.35	
	26	87.90		86.35
	27		78.65	
	28	81.50	M	M
	29	93.15		87.45
	30		78.25	88.00
Combined Length Measurements (incl. mussels with lost tags):				
MEAN: STD: N:	84.75 7.10 57			

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 2: *Anadara granosa*: growth experiments 1986/87 at Ang Sila, Thailand.

Appendix 2.1: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
Summary of field data for the period March 1986. Length of marked specimens, measured to the lower 0.05 mm.

DATE:	26-03-1986			27-03-1986		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	22.77	22.56	22.35	21.65	22.15	23.00
STD:	1.43	1.27	1.75	1.55	1.27	1.35
NO.: 1	23.10	22.65	23.05	22.30	23.65	22.95
2	24.55	24.10	21.70	21.80	20.60	23.00
3	24.50	23.10	22.80	18.95	21.90	23.50
4	22.35	22.70	23.50	21.50	23.30	23.75
5	24.80	22.30	22.85	21.50	22.05	26.15
6	22.00	24.00	23.20	23.45	23.15	24.50
7	22.10	21.65	22.90	23.55	24.15	21.50
8	24.25	22.95	23.80	20.35	22.40	22.70
9	21.75	22.30	21.45	22.55	21.60	20.85
10	22.10	22.55	18.85	18.50	23.70	22.45
11	24.50	24.10	21.50	23.40	23.80	21.40
12	22.80	24.15	23.65	21.25	22.40	22.10
13	25.90	24.10	20.30	21.65	19.35	24.70
14	22.60	23.10	22.25	22.65	21.50	24.55
15	21.60	23.45	21.60	22.20	21.75	22.75
16	23.95	22.55	21.65	24.90	20.55	24.10
17	23.50	18.60	19.80	20.50	21.55	23.55
18	21.70	22.10	23.00	22.95	21.50	25.20
19	24.45	22.60	21.40	20.45	20.65	23.25
20	21.00	22.40	21.60	24.25	21.50	20.55
21	25.45	22.20	21.60	21.15	22.95	24.70
22	20.80	19.20	23.10	20.30	21.70	23.45
23	21.20	23.20	25.75	21.00	23.50	22.30
24	21.30	22.40	23.55	19.25	23.95	21.05
25	21.45	23.05	21.30	23.10	21.60	23.00
26	21.80	20.70	19.95	22.05	24.35	23.55
27	21.60	21.00	23.70	20.05	20.60	21.85
28	22.10	22.80	20.85	21.60	20.65	21.60
29	21.65	21.55	20.00	19.40	20.95	21.40
30	21.45	23.70	26.00	22.45	22.35	23.00
Combined Length Measurements (incl. cockles with lost tags):						
MEAN:	22.56			22.27		
STD:	1.51			1.50		
N:	90			90		

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 2.2: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
Summary of field data for the period April 1986. Length of marked specimens,  
measured to the lower 0.05 mm.

DATE:	22-04-1986			22-04-1986		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	24.02	24.16	23.77	22.56	23.00	23.89
STD:	1.45	1.23	1.77	1.45	1.25	1.21
NO.: 1	23.15	24.45	27.55	23.10	24.45	23.55
2	M	24.10	22.30	22.40	21.20	23.50
3	26.45	24.45	22.80	20.75	23.35	25.10
4	M	24.80	25.55	22.20	23.40	24.50
5	26.00	24.60	24.25	21.80	D	26.80
6	23.90	24.45	24.65	23.40	23.70	24.75
7	23.40	23.70	24.80	23.95	25.35	23.00
8	24.70	23.95	M	22.20	D	24.25
9	22.80	23.90	M	23.95	22.25	22.15
10	24.20	24.35	21.00	18.95	23.60	22.40
11	24.85	25.40	22.55	24.30	23.95	22.25
12	24.45	25.70	23.80	21.45	22.30	23.20
13	26.60	26.00	M	23.00	20.80	26.15
14	24.00	25.10	22.15	23.90	22.70	24.45
15	22.15	25.60	22.80	22.35	23.40	23.50
16	25.40	23.95	23.35	25.40	21.60	25.15
17	24.05	21.30	19.95	22.55	D	24.15
18	23.60	23.70	24.50	23.30	22.10	25.15
19	25.55	M	23.05	D	22.10	23.35
20	22.55	24.00	D	24.80	22.35	D
21	27.30	23.55	23.65	D	24.05	D
22	21.70	20.00	24.05	20.95	22.15	24.30
23	22.60	25.05	27.15	21.80	24.40	23.40
24	22.80	23.40	25.75	21.20	25.40	21.65
25	22.75	25.00	23.15	23.25	21.55	24.60
26	22.60	M	D	23.95	25.20	24.70
27	24.15	23.80	25.30	20.85	21.95	22.50
28	23.75	24.35	22.05	22.25	22.30	23.55
29	21.90	23.00	M	20.40	22.05	22.30
30	24.55	M	M	M	22.80	23.85
Combined Length Measurements (incl. cockles with lost tags):						
MEAN:	24.02			23.16		
STD:	1.48			1.42		
N:	82			82		

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 2.3: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
Summary of field data for the period May 1986. Length of marked specimens,  
measured to the lower 0.05 mm.

DATE:	21-05-1986			21-05-1986		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	25.20	25.31	25.08	22.95	23.49	24.42
STD:	1.45	1.15	1.62	1.39	1.35	1.15
NO.: 1	24.10	25.70	28.40	23.60	24.45	24.40
2		D	22.95	22.95	21.85	23.55
3	28.15	25.55	23.25	21.25	23.55	25.40
4		25.90	27.55	22.85	23.30	25.25
5	27.05	25.80	24.90	22.35		27.15
6	24.65	25.45	25.25	D	23.85	25.25
7	24.35	25.25	26.40	D	25.70	23.85
8	25.40	24.85		22.70		24.45
9	23.80	25.45		24.20	22.20	22.65
10	25.35	25.55	22.85	20.05	24.10	M
11	25.30	27.25	23.40	24.75	23.90	23.55
12	25.65	M	24.80	22.10	22.35	23.70
13	26.80	M		23.70	20.90	26.55
14	25.75	26.85	22.80	D	22.70	24.70
15	22.75	26.15	24.55	22.75	D	24.10
16	26.15	24.95	24.30	25.65	22.30	25.60
17	25.05	23.30	M	22.80		24.40
18	24.50	25.70	25.35	24.05	22.40	D
19	27.15		24.50		22.60	M
20	23.50	25.05		25.20	D	
21	28.25	24.15	24.80		24.65	
22	M	21.75	25.70	21.35	22.25	24.60
23	23.80	26.35	27.70	22.95	25.50	24.40
24	24.30	24.20	26.45	M	25.80	22.50
25	24.35	26.45	25.10	D	M	24.75
26	23.70			24.20	25.60	25.40
27	26.10	25.65	27.00	21.00	22.35	22.60
28	24.95	25.50	23.20	22.70	D	24.50
29	22.65	24.00		21.30	23.05	22.50
30	26.25				24.30	24.10
Combined Length Measurements (incl. cockles with lost tags):						
MEAN:	25.18			23.62		
STD:	1.47			1.43		
N:	81			73		

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 2.4: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
Summary of field data for the period June 1986. Length of marked specimens,  
measured to the lower 0.05 mm.

DATE:	23-06-1986			23-06-1986		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	25.59	25.85	25.34	26.07	26.30	27.44
STD:	1.50	1.13	1.68	0.98	1.74	1.18
NO.: 1	24.05	26.60	28.65	26.65	26.20	27.90
2			23.30	24.70	24.50	25.80
3	28.70	25.80	23.45	24.90	25.85	28.70
4		26.20	28.10	26.20	25.40	28.30
5	27.50	26.45	24.85	25.25		30.15
6	25.25	25.85	25.50		26.10	D
7	24.75	26.05	26.75		28.85	27.50
8	25.60	M		25.90		27.00
9	24.30	26.50		27.35	22.50	26.30
10	25.40	26.00	23.10	24.60	26.60	
11	25.70	27.30	23.35	27.30	25.95	26.70
12	25.65		24.95	25.60	22.35	26.30
13	27.40			26.85	25.25	29.90
14	25.70	27.30	23.30		26.35	26.80
15	23.30	26.45	24.95	26.05		27.80
16	26.95	25.15	24.25	27.70	26.75	28.20
17	25.35	23.80		26.55		26.70
18	24.95	26.10	25.70	26.40	25.65	
19	27.20		24.75		25.65	
20	23.60	25.80		M		
21	29.05	25.00	25.15		27.30	
22		22.45	25.90	25.70	26.35	26.85
23	24.05	26.85	28.10	26.05	28.20	27.50
24	24.80	24.35	27.20		29.05	26.65
25	24.55	M	25.45			27.60
26	24.25			27.45	29.35	28.95
27	26.70	26.30	26.90	24.10	24.95	25.35
28	25.45	26.10	23.20	26.50		28.10
29	23.30	M		25.20	27.55	26.40
30	26.65				27.55	26.50
Combined Length Measurements (incl. cockles with lost tags):						
MEAN:	25.56			26.55		
STD:	1.50			1.56		
N:	81			71		

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 2.5: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
Summary of field data for the period July 1986. Length of marked specimens, measured to the lower 0.05 mm.

DATE:	25-07-1986			25-07-1986		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	26.30	26.45	25.98	27.58	27.60	28.85
STD:	1.63	1.37	1.62	1.02	2.04	1.47
NO.: 1	23.95	27.60	29.05	28.10	27.20	29.10
2			24.05	25.85	25.65	26.20
3	29.75	26.20	23.35	26.65	27.50	30.25
4		26.75	28.40	27.80	26.70	29.85
5	28.50	27.20	M	26.95		31.40
6	26.20	25.85	26.25		27.65	
7	25.85	27.10	26.95		30.50	30.20
8	25.60			27.25		27.85
9	24.45	27.35		28.10	22.70	28.25
10	25.70	26.80	24.05	26.85	27.70	
11	25.60	27.55	24.50	29.05	26.45	27.80
12	D		25.00	26.25	22.40	27.65
13	27.40			28.85	27.65	31.45
14	26.45	27.70	24.00		27.80	27.20
15	23.70	27.30	26.15	27.90		29.50
16	27.80	25.35	25.15	28.40	28.55	29.20
17	26.00	24.40		28.90		M
18	26.50	26.70	26.15	27.50	26.85	
19	27.85		25.85		27.10	
20	24.35	26.80				
21	29.90	25.50	26.20		28.55	
22		22.40	26.30	28.00	28.20	28.15
23	24.90	27.55	28.60	28.35	30.00	28.80
24	25.30	24.05	28.60		30.30	27.95
25	25.20		25.90			29.50
26	24.90			28.40	30.80	31.25
27	27.80	27.95	27.25	25.25	26.40	26.35
28	26.50	26.90	24.00	27.75		29.75
29	25.05			26.45	28.80	27.55
30	27.85				28.75	27.75
Combined Length Measurements (incl. cockles with lost tags):						
MEAN:	26.21			27.93		
STD:	1.53			1.79		
N:	80			71		

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 2.6: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
 Summary of field data for the period August 1986. Length of marked specimens,  
 measured to the lower 0.05 mm.

DATE:	24-08-1986			24-08-1986		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	26.80	26.96	26.77	28.70	28.56	30.03
STD:	1.60	1.44	1.65	1.11	2.35	1.68
NO.: 1	M	28.05	29.90	29.75	27.35	30.45
2			25.10	26.30	26.95	26.30
3	30.05	26.30	23.35	27.55	28.55	31.35
4		27.60	28.55	28.95	27.15	31.25
5	29.30	27.55		28.20		32.35
6	26.35	25.95	26.85		28.60	
7	26.40	27.90	27.30		31.60	31.60
8	25.60			27.90		29.00
9	24.55	28.25		29.40	22.70	29.60
10	25.80	27.30	25.60	28.20	29.05	
11	25.60	27.90	24.75	29.60	27.00	29.30
12			26.20	27.70	22.35	28.75
13	28.05			30.35	28.90	33.05
14	26.95	27.90	24.75		28.85	27.45
15	24.15	27.85	26.95	29.15		30.85
16	28.05	25.85	M	28.95	30.10	29.90
17	26.45	25.70		29.95		
18	27.00	27.15	26.85	28.35	28.20	
19	27.90		27.10		28.45	
20	24.65	27.60				
21	30.30	26.35	27.30		29.65	
22		22.45	27.10	29.55	29.25	M
23	25.60	28.25	29.25	29.50	31.45	30.20
24	25.70	24.25	29.10		31.45	29.10
25	25.85		26.50			30.45
26	25.45			30.00	31.90	32.60
27	28.30	28.20	27.60	26.50	27.55	27.65
28	26.85	27.30	24.75	28.85		31.15
29	26.20			27.45	29.95	28.85
30	28.15				29.40	28.85
Combined Length Measurements (incl. cockles with lost tags):						
MEAN:	26.80			28.96		
STD:	1.54			2.05		
N:	77			71		

Note: "D" signifies that the animal has died since the previous survey.  
 "M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 2.7: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
Summary of field data for the period October 1986. Length of marked specimens,  
measured to the lower 0.05 mm.

DATE:	27-10-1986			27-10-1986		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	27.71	28.40	27.69	29.08	29.47	30.44
STD:	1.93	0.08	1.68	1.28	1.70	1.81
NO.: 1		M	30.70	M	28.10	30.50
2			M	D	26.95	26.70
3	31.95	M	25.15	D	M	31.60
4		M	28.80	29.30	27.90	31.80
5	31.05	M		D		33.10
6	28.05	M	M		D	
7	27.80	M	28.40		31.90	32.65
8	26.30			28.05		29.20
9	D	M		29.50	M	29.95
10	M	28.45	26.35	D	29.05	
11	25.55	M	24.70	D	27.25	30.10
12			27.10	27.40	D	28.75
13	M			30.40	29.55	33.95
14	28.10	M	26.05		28.60	28.25
15	24.10	M	28.30	D		31.55
16	29.75	M		29.80	M	29.70
17	M	M		30.10		
18	D	28.30	27.40	D	M	
19	28.60		27.05		28.70	
20	25.60	M				
21	M	M	D		30.40	
22		M	28.00	D	29.29	
23	26.80	M	29.50	29.95	31.85	30.30
24	26.55	M	M		31.95	29.05
25	26.65		M			30.55
26	M			30.55	32.10	33.40
27	28.65	M	29.80	26.40	27.70	28.90
28	27.00	M	D	29.50		31.55
29	M			27.70	29.90	28.65
30	28.10				M	29.00
Combined Length Measurements (incl. cockles with lost tags):						
MEAN:	27.75			29.63		
STD:	1.72			1.95		
N:	35			57		

Note: "D" signifies that the animal has died since the previous survey.  
"M" signifies that the animal has lost its tag or has disappeared from the sample since the  
previous survey

Appendix 2.8: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
 Summary of field data for the period November 1986. Length of marked specimens,  
 measured to the lower 0.05 mm.

DATE:	24-11-1986			not sampled		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN: STD:	28.14 2.13	28.88 0.00	28.11 1.64			
NO.: 1	M		30.90			
2						
3	32.40		25.20			
4			28.80			
5	31.85					
6	M					
7	28.35		29.35			
8	26.85					
9						
10		28.85	27.30			
11	D		25.30			
12			27.05			
13						
14	28.40		27.25			
15	24.20		28.45			
16	M					
17						
18		M	28.05			
19	29.55		27.15			
20	26.10					
21						
22			28.30			
23	26.95		29.75			
24	27.65					
25	27.10					
26						
27	28.75		30.35			
28	27.35					
29						
30	M					
Combined Length Measurements (incl. cockles with lost tags):						
MEAN: STD: N:	28.13 1.75 32					

Note: "D" signifies that the animal has died since the previous survey.  
 "M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 2.9: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
 Summary of field data for the period January 1987. Length of marked specimens,  
 measured to the lower 0.05 mm.

DATE:	26-01-1987			26-01-1987		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN:	28.12	28.93	28.44	31.61	31.49	32.88
STD:	2.14	0.00	1.54	1.83	1.91	2.07
NO.: 1			30.85		30.25	33.30
2					28.35	28.90
3	32.30		M			M
4			28.85	32.00	29.30	34.75
5	32.00					35.20
6						
7	28.25		29.55		33.80	35.75
8	26.95			31.85		30.45
9				31.35		33.60
10		28.90	27.35		30.40	
11			25.15		28.55	32.75
12			27.15	27.20		30.50
13				32.55	31.25	36.00
14	28.40		M		33.65	32.95
15	24.20		28.45			34.30
16				32.60		30.45
17				31.55		
18			28.00			
19	29.55		27.10		31.22	
20	26.10					
21					31.70	
22			28.40		32.35	
23	26.95		29.80	34.55	33.70	33.55
24	27.65				33.70	31.60
25	26.80					33.15
26				M	34.35	35.45
27	28.70		30.35	D	29.55	29.20
28	27.40			32.25		34.35
29				29.90	31.35	31.35
30						32.30
Combined Length Measurements (incl. cockles with lost tags):						
MEAN:	28.24			32.11		
STD:	1.84			2.04		
N:	30			53		

Note: "D" signifies that the animal has died since the previous survey.  
 "M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

Appendix 2.10: *Anadara granosa*, growth experiments 1986/87, Ang Sila, Thailand.  
 Summary of field data for the period February 1987. Length of marked specimens,  
 measured to the lower 0.05 mm.

DATE:	Sample stolen			26-02-1987		
SITE:	Exposed (I)			Submerged (II)		
SAMPLE: COLOUR:	1 Yellow	2 Red	3 White	1 Yellow	2 Red	3 White
MEAN: STD:				32.53 1.42	32.23 2.23	33.90 2.31
NO.: 1					M	33.60
2					M	M
3						
4				32.90	29.20	35.00
5						M
6						
7					34.15	36.95
8				33.00		M
9				31.45		M
10					M	
11					M	M
12				M		M
13				M	31.45	M
14					M	33.65
15						34.70
16				32.30		M
17				31.85		
18						
19					M	
20						
21					M	
22					M	
23				35.40	M	M
24					34.00	M
25						M
26					34.80	M
27					29.65	29.35
28				33.00		M
29				30.15	M	M
30						M
Combined Length Measurements (incl. cockles with lost tags):						
MEAN: STD: N:					32.90 2.15 52	

Note: "D" signifies that the animal has died since the previous survey.  
 "M" signifies that the animal has lost its tag or has disappeared from the sample since the previous survey.

**Appendix 3: Compilation of growth parameters for marine and freshwater bivalve species: Summary of species, geographic and environmental descriptions, and references.**

Explanation of table headings and codes

<b>REF NO</b>	Species-specific reference number, used throughout all other tables to distinguish the species for identification of the corresponding literature reference
<b>SPECIES</b>	Name of bivalve species as given by the author (exceptions: <i>Cardium</i> is listed as <i>Cerastoderma</i> )
<b>COUNTRY</b>	Country, where the bivalve stock is located
<b>AREA</b>	Location, from where the bivalve stock originates
<b>LAT</b>	Geographic latitude (North or South) of the location
<b>LONG</b>	Geographic longitude (East or West) of the location
<b>ENV</b>	Coded description of the environment 11 Marine, submerged 12 Marine, intertidal 20 Freshwater
<b>GRC</b>	Coded description of growth condition 10 Natural population 21 Bottom culture 22 Suspended culture 30 Experimental culture
<b>TEMPERATURE</b>	Data on environmental water temperature (°C) MIN Minimum annual water temperature MAX Maximum annual water temperature AVG Mean annual water temperature SC Temperature data were published (P) or interpolated (I)
<b>REFERENCE</b>	Source of data

REF NO	SPECIES (marine)	COUNTRY	AREA	LAT	LONG	ENV	GRC	TEMPERATURE				REFERENCE
								MIN	MAX	AVG	SC	
1	<i>Amusium pleuronectes</i>	Philippines	Lingayen Gulf	16°15'N	120°10'E	11	10	23	32	27.5	I	Del Norte 1988
2	<i>Amusium pleuronectes</i>	Thailand	Ko Chang	12°00'N	102°10'E	11	10	28	32	29.0	I	Nugranad 1988
3	<i>Anadara broughtonii</i>	Korea	Keoje Bay, Pusan	35°06'N	129°03'E	11	22	6	28	16.0	P	Yoo & Park 1978
4	<i>Anadara granosa</i>	Malaysia	Batu Muang	5°17'N	100°17'E	12	10	30	32	31.0	P	Liang 1981
5	<i>Anadara granosa</i>	Malaysia	Kuala Juru	5°22'N	100°23'E	12	10	30	32	31.0	P	Liang 1981
6	<i>Anadara granosa</i>	Malaysia	Kuala Selangor	3°20'N	101°14'E	11	10	30	32	31.0	P	Broom 1982
7	<i>Anadara granosa</i>	Malaysia	Kuala Selangor	3°20'N	101°14'E	12	30	30	32	31.0	P	Broom 1983
8	<i>Anadara granosa</i>	Malaysia	Kuala Selangor	3°20'N	101°14'E	12	30	30	32	31.0	P	Broom 1983
9	<i>Anadara granosa</i>	Malaysia	Kuala Selangor	3°20'N	101°14'E	11	10	30	32	31.0	P	Broom 1982
10	<i>Anadara granosa</i>	Malaysia	Kuala Selangor	3°20'N	101°14'E	11	10	30	32	31.0	P	Broom 1982
11	<i>Anadara granosa</i>	Malaysia	Kuala Selangor	3°20'N	101°14'E	11	30	30	32	31.0	P	Broom 1982
12	<i>Anadara granosa</i>	Malaysia	Kuala Selangor	3°20'N	101°14'E	11	30	30	32	31.0	P	Broom 1982
13	<i>Anadara granosa</i>	Malaysia	Penang	5°25'N	100°20'E	12	10	30	32	31.0	P	Pathansali 1966
14	<i>Anadara granosa</i>	Malaysia	Penang	5°25'N	100°20'E	12	10	30	32	31.0	P	Pathansali 1966
15	<i>Anadara granosa</i>	Malaysia	Penang	5°25'N	100°20'E	12	10	30	32	31.0	P	Ng 1986
16	<i>Anadara granosa</i>	Malaysia	Penang	5°25'N	100°20'E	12	10	30	32	31.0	P	Pathansali 1966
17	<i>Anadara granosa</i>	Malaysia	Perak	4°45'N	100°10'E	12	10	30	32	31.0	P	Ng 1986
18	<i>Anadara granosa</i>	Malaysia	Perak	4°45'N	100°10'E	12	10	30	32	31.0	P	Ng 1986
19	<i>Anadara granosa</i>	Malaysia	Perak	4°45'N	100°10'E	12	10	30	32	31.0	P	Ng 1986
20	<i>Anadara granosa</i>	Malaysia	Selangor	3°30'N	100°45'E	12	10	30	32	31.0	P	Ng 1986
21	<i>Anadara granosa</i>	Malaysia	Sungei Buloh	3°15'N	101°18'E	11	10	30	32	31.0	P	Broom 1982
22	<i>Anadara granosa</i>	Malaysia	Sungei Buloh	3°15'N	101°18'E	11	10	30	32	31.0	P	Broom 1982
23	<i>Anadara granosa</i>	Malaysia	Penang	5°25'N	100°20'E	12	10	30	32	31.0	P	Pathansali 1966
24	<i>Anadara granosa</i>	Malaysia	Penang	5°25'N	100°20'E	12	22	30	32	31.0	P	Pathansali 1966
25	<i>Arca ventricosa</i>	Fr. Polynesia	Takaroto	14°00'S	145°20'W	11	10	26	28	27.0	I	Richard 1981
26	<i>Arctica islandica</i>	USA	off Long Island	40°25'N	72°24'W	11	10	7	21	12.8	I	Murawski et al. 1982
27	<i>Argopecten purpuratus</i>	Peru	Bahia de Paracas	13°49'S	76°18'W	11	22	15	23	19.0	P	Wolff 1985
28	<i>Argopecten purpuratus</i>	Peru	Bahia de Paracas	13°49'S	76°18'W	12	21	15	23	19.0	P	Wolff 1985
29	<i>Argopecten purpuratus</i>	Peru	Bahia de Paracas	13°49'S	76°18'W	11	10	15	23	19.0	P	Wolff 1985
30	<i>Cerastoderma edule</i>	England, U.K.	Riv. Crouch estuary	51°37'N	0°38'E	12	10	-	-	10.3	I	Boyden 1972
31	<i>Cerastoderma edule</i>	N. Ireland, U.K.	Strangford Lough	45°30'N	5°36'W	11	10	8	14	10.7	I	Seed & Brown 1978
32	<i>Cerastoderma edule</i>	Wales, U.K.	Llanrhidian Sands	51°37'N	4°11'W	11	10	9	16	12.1	I	Hancock 1965
33	<i>Cerastoderma edule</i>	Fr. Polynesia	Anaa	17°25'S	145°30'W	11	10	26	28	27.0	I	Richard 1981
34	<i>Cerastoderma glaucum</i>	England, U.K.	Riv. Crouch estuary	51°37'N	0°38'E	12	10	-	-	10.3	I	Boyden 1972
35	<i>Cerastoderma glaucum</i>	Poland	Gdansk Bay	54°23'N	18°40'E	11	10	2	17	8.1	I	Wolowicz 1980
36	<i>Cerastoderma glaucum</i>	Sweden	Hanö Bay, 10m	56°00'N	14°50'E	11	10	2	14	8.1	I	Persson 1976
37	<i>Cerastoderma glaucum</i>	Sweden	Hanö Bay, 17m	56°00'N	14°50'E	11	10	2	14	8.1	I	Persson 1976
38	<i>Chlamys albidus</i>	USSR, Kuril Is.	Onokotan I.	49°25'N	154°45'E	11	10	0	12	4.3	I	Myasnikov & Kochnev 1988
39	<i>Chlamys opercularis</i>	Denmark	Danish Sound	56°20'N	11°10'E	11	10	4	11	7.5	P	Ursin 1956
40	<i>Chlamys opercularis</i>	Denmark	Faroe waters	62°15'N	6°50'W	11	10	5	10	7.5	P	Ursin 1956
41	<i>Chlamys opercularis</i>	Denmark	North Sea	55°00'N	4°00'E	11	10	5	9	7.0	P	Ursin 1956
42	<i>Chlamys opercularis</i>	England, U.K.	Langstone Harbour	50°47'N	0°59'W	11	22	6	21	11.0	P	Broom & Mason 1978
43	<i>Chlamys opercularis</i>	Scotland, U.K.	Firth of Clyde	55°46'N	4°51'W	11	30	7	13	10.4	I	Richardson et al. 1982
44	<i>Chlamys opercularis</i>	Scotland, U.K.	Firth of Clyde	55°46'N	4°51'W	11	10	7	13	10.4	I	Taylor & Venn 1978

REF NO	SPECIES (marine)	COUNTRY	AREA	LAT	LONG	ENV	GRC	TEMPERATURE				REFERENCE
								MIN	MAX	AVG	SC	
45	<i>Chlamys opercularis</i>	Scotland, U.K.	Firth of Clyde	55°46'N	4°51'W	11	10	7	13	10.4	I	Richardson et al. 1982
46	<i>Chlamys varia</i>	France	Bay of Brest	48°18'N	4°25'W	11	10	9	18	12.0	P	Conan & Shafee 1978
47	<i>Crassostrea gigas</i>	Korea	Keoje Bay, Pusan	35°06'N	129°03'E	12	30	6	28	16.0	P	Yoo et al. 1972
48	<i>Crassostrea gigas</i>	Korea	Keoje Bay, Pusan	35°06'N	129°03'E	12	30	6	28	16.0	P	Yoo et al. 1972
49	<i>Crassostrea madrasensis</i>	India	Adyar estuary	13°00'N	80°17'E	12	10	27	30	28.0	I	Joseph & Joseph 1985
50	<i>Crassostrea madrasensis</i>	India	Madras harbour	13°05'N	80°17'E	12	10	27	30	28.0	I	Joseph & Joseph 1985
51	<i>Crassostrea rhizophorae</i>	Jamaica	Port Morant	17°54'N	76°19'W	11	22	25	28	27.1	I	Wade et al. 1981
52	<i>Crassostrea tulipa</i>	Gambia	Banjul	13°28'N	16°39'W	12	30	20	33	29.1	P	Cham 1988
53	<i>Crassostrea virginica</i>	USA, Massachus.	Chatham	41°40'N	69°57'W	12	22	1	22	11.0	P	Shaw 1962
54	<i>Crassostrea virginica</i>	USA, Massachus.	Chatham	41°40'N	69°57'W	12	22	1	22	11.0	P	Shaw 1962
55	<i>Crenomytilus grayanus</i>	USSR	Posjet	42°39'N	130°50'E	11	10	0	19	7.7	I	Selin & Blinov 1989
56	<i>Donax cuneatus</i>	India	Palk Bay	9°17'N	79°05'E	12	10	26	31	28.1	P	Jayar 1955
57	<i>Donax incarnatus</i>	India	Shertallai	9°42'N	76°20'E	12	10	27	30	28.0	P	Ansell 1972
58	<i>Donax peruvianus</i>	Peru	Santa Maria del Mar	12°20'S	76°50'W	11	10	15	18	16.5	I	Arntz et al. 1987
59	<i>Donax trunculus</i>	France	Camargue	43°27'N	4°26'E	12	10	10	20	15.5	P	Bodoy 1982
60	<i>Donax trunculus</i>	France	St. Trojan	45°50'N	1°20'W	12	10	5	22	13.0	P	Ansell & Lagadere 1980
61	<i>Donax trunculus</i>	France	Vertbois	45°50'N	1°20'W	12	10	5	22	13.0	P	Ansell & Lagadere 1980
62	<i>Donax vittatus</i>	France	St. Trojan	45°50'N	1°20'W	12	10	5	22	13.0	P	Ansell & Lagadere 1980
63	<i>Donax vittatus</i>	France	Vertbois	45°50'N	1°20'W	12	10	5	22	13.0	P	Ansell & Lagadere 1980
64	<i>Geukensia demissa</i>	USA, Connect.	Long Island Sound	41°07'N	73°19'W	12	10	7	21	12.8	I	Brousseau 1984
65	<i>Geukensia demissa</i>	USA, Virginia	Tom's Cove	37°55'N	75°30'W	11	10	4	26	15.0	P	Bertness 1980
66	<i>Hiatella byssifera</i>	Greenland	Godhavn Havn	69°15'N	53°33'W	11	10	0	4	1.1	I	Petersen 1978
67	<i>Hippopus hippopus</i>	Australia	Iris Point Reef	18°43'S	146°37'E	12	10	21	31	25.0	P	Shelley 1988
68	<i>Hippopus hippopus</i>	Australia	Pioneer Bay	18°43'S	146°37'E	12	10	21	31	25.0	P	Shelley 1988
69	<i>Hippopus hippopus</i>	Papua New Guinea	Motupore I.	9°30'S	147°10'E	11	10	26	31	29.0	P	Munro & Gwyther 1981
70	<i>Hippopus hippopus</i>	Philippines	Sulu Archipelago	7°00'N	122°00'E	11	10	27	29	28.0	I	Villanoy et al. (unp. MS)
71	<i>Hippopus porcellanus</i>	Philippines	Zamboanga	7°00'N	122°00'E	11	10	27	29	28.0	I	Villanoy et al. (unp. MS)
72	<i>Macoma balthica</i>	Canada	Hudson Bay	58°46'N	94°02'W	12	10	0	5	1.1	P	Green 1973
73	<i>Macoma balthica</i>	Canada	Hudson Bay	58°46'N	94°02'W	12	10	0	5	1.1	P	Green 1973
74	<i>Macoma balthica</i>	Canada, Quebec	Cacouna	46°49'N	71°14'W	12	10	0	14	4.5	P	Lavoie et al. 1968
75	<i>Macoma balthica</i>	France	Gironde Estuary	45°35'N	1°00'W	12	10	6	21	13.0	P	Bachelet 1980
76	<i>Macoma balthica</i>	Netherlands	Wadden Zee	53°15'N	5°15'E	11	10	0	16	10.4	I	Lammens 1967
77	<i>Macoma calcarea</i>	Greenland	Godhavn Havn	69°15'N	53°33'W	11	10	0	4	1.1	I	Petersen 1978
78	<i>Macrocallista maculata</i>	Bermuda	Harrington Snd.	32°20'N	64°45'W	12	10	14	29	21.5	P	Erikenouser & Wefer 1981
79	<i>Mercenaria campechiensis</i>	USA, Florida	Alligator Harbour	26°10'N	80°03'W	12	30	6	35	20.9	P	Menzel 1963
80	<i>Mercenaria mercenaria</i>	USA, Florida	Alligator Harbour	26°10'N	80°03'W	12	30	6	35	20.9	P	Menzel 1963
81	<i>Mercenaria mercenaria</i>	USA, Rhode Isl.	Narragansett Bay	40°36'N	71°20'W	11	10	-	-	11.3	P	Jones et al. 1989
82	<i>Mesodesma donacium</i>	Peru	Santa Maria del Mar	12°20'S	76°50'W	11	10	15	18	16.5	I	Arntz et al. 1987
83	<i>Modiolus modiolus</i>	N. Ireland, U.K.	Strangford Lough	45°30'N	5°36'W	12	10	8	14	10.7	I	Seed & Brown 1978
84	<i>Musculista arcuatula</i>	India	Ashtamudi Lake	9°59'N	76°16'E	12	10	27	30	28.0	I	George & Nair 1974
85	<i>Mya arenaria</i>	Canada	Bay of Fundy	45°00'N	66°00'W	12	10	2	17	8.4	I	Newcombe 1935
86	<i>Mya arenaria</i>	Denmark	Roskilde Fjord	55°39'N	12°05'E	11	10	-1	20	9.0	P	Munch-Petersen 1973
87	<i>Mya arenaria</i>	USA, Maine	Bedroom Cove	43°51'N	69°37'W	11	10	2	17	8.4	I	Vincent et al. 1957
88	<i>Mya arenaria</i>	USA, Maine	Sagadahoc Bay	43°51'N	69°37'W	11	10	2	17	8.4	I	Vincent et al. 1957

REF NO	SPECIES (marine)	COUNTRY	AREA	LAT	LONG	ENV	GRC	TEMPERATURE				REFERENCE
								MIN	MAX	AVG	SC	
89	<i>Mya arenaria</i>	USA, Massachus.	Gloucester	41°39'N	70°43'W	12	10	1	22	11.0	I	Brousseau 1979
90	<i>Mya truncata</i>	Greenland	Godhavn Havn	69°15'N	53°33'W	11	10	0	4	1.1	I	Petersen 1978
91	<i>Mytilus coruscus</i>	USSR	Vostok bay	43°10'N	131°56'E	11	22	0	19	7.7	I	Selin 1988
92	<i>Mytilus edulis</i>	Canada, N.Sc.	Bedford Basin	44°40'N	63°34'W	11	22	1	16	7.3	I	Dickie et al. 1984
93	<i>Mytilus edulis</i>	Canada, N.Sc.	St. Margarets B	44°35'N	64°00'W	11	22	1	16	7.3	I	Dickie et al. 1984
94	<i>Mytilus edulis</i>	Denmark	Gennet Fjord	55°07'N	9°28'E	11	10	4	11	7.5	I	Theisen 1975
95	<i>Mytilus edulis</i>	Denmark	Mariager Fjord	56°30'N	10°00'E	11	10	4	11	7.5	I	Theisen 1975
96	<i>Mytilus edulis</i>	England, U.K.	Lynher, Plimth.	50°28'N	4°12'W	12	10	8	19	12.7	P	Bayne & Worrall 1980
97	<i>Mytilus edulis</i>	England, U.K.	Plymouth	50°23'N	4°10'W	12	10	13	17	15.2	P	Bayne & Worrall 1980
98	<i>Mytilus edulis</i>	Greenland	Robertson Fjord	70°40'N	53°30'W	11	10	0	4	1.1	I	Theisen 1973
99	<i>Mytilus edulis</i>	Wales, U.K.	Menai Strait	53°12'N	4°12'W	11	22	6	17	11.0	P	Dare & Davies 1975
100	<i>Mytilus edulis diegensis</i>	USA, California	La Jolla	32°51'N	117°16'W	11	22	13	22	16.5	P	Coe 1945
101	<i>Mytilus edulis platensis</i>	Uruguay	Bahia de Maldonado	34°55'S	45°57'W	11	10	11	23	17.0	P	Fecceiro 1981
102	<i>Mytilus galloprovincialis</i>	Italy	Riv. Po delta	44°56'N	12°22'E	12	22	1	25	14.0	P	Ceccherelli & Barboni 1983
103	<i>Nucula minuta</i>	Scotland, U.K.	Firth of Clyde	55°50'N	4°60'W	11	10	7	13	10.4	I	Ansell et al. 1978
104	<i>Nuculana pernula</i>	Newfoundland	Depth 895-1500	45°30'N	48°10'W	11	10	5	5	5.0	P	Hutchings & Haedrich 1984
105	<i>Ostrea puelchana</i>	Argentina	Bahia Nueva	42°46'S	65°03'W	11	22	6	18	12.2	P	Fernandez Castro & Bodoy 1987
106	<i>Ostrea puelchana</i>	Argentina	Lag. Punta Cero	42°30'S	63°38'W	11	22	6	19	11.8	P	Fernandez Castro & Bodoy 1987
107	<i>Patinopecten caurinus</i>	Canada	Str. of Georgia	48°52'N	123°15'W	11	10	7	16	10.4	P	MacDonald & Bourne 1987
108	<i>Patinopecten caurinus</i>	Canada	Vancouver I., (offsh.)	49°00'N	126°00'W	11	10	7	10	8.0	P	MacDonald & Bourne 1987
109	<i>Patinopecten yessoensis</i>	Japan	Mutsu Bay	41°17'N	141°10'E	11	22	4	23	15.0	P	Ventilla 1982
110	<i>Patinopecten yessoensis</i>	Korea	Pohang	36°05'N	129°28'E	11	22	8	21	16.0	P	Yoo et al. 1981
111	<i>Pecten maximus</i>	France	Baie de Seine	49°46'N	0°55'W	11	10	7	17	11.9	I	Antoine et al. 1979
112	<i>Pecten maximus</i>	France	Brest	48°24'N	4°29'W	11	10	9	18	12.0	P	Buestel & Laurec 1975
113	<i>Pecten maximus</i>	France	Dieppe	50°25'N	0°20'E	11	10	7	17	11.9	I	Antoine et al. 1979
114	<i>Pecten maximus</i>	France	St. Brieuc	48°40'N	2°47'W	11	10	7	17	11.9	I	Buestel & Laurec 1975
115	<i>Perna canaliculus</i>	New Zealand	Port Fitzroy	36°10'S	175°21'E	11	22	14	23	18.5	P	Hickman 1979
116	<i>Perna canaliculus</i>	New Zealand	Te Kaha	37°44'S	177°41'E	11	22	13	21	17.0	P	Johns & Hickman 1985
117	<i>Perna perna</i>	Mozambique	Maputo	25°48'S	32°51'E	11	22	18	28	24.0	I	Ribeiro 1984
118	<i>Perna perna</i>	Venezuela	Golfo de Cariaco	10°27'N	64°02'W	11	22	24	28	26.0	P	Acuña 1977
119	<i>Perna viridis</i>	Brunei	Tanjong Pebaras	5°00'N	115°02'E	11	22	27	29	28.0	I	Beales & Lindley 1982
120	<i>Perna viridis</i>	Hong Kong	Victoria Harbour	44°45'N	79°46'W	12	10	16	28	23.0	F	Lee 1985
121	<i>Perna viridis</i>	India	Experim. tank	-	-	11	30	27	32	29.0	P	Chatterji et al. 1984
122	<i>Perna viridis</i>	India	Goa	13°42'N	123°29'E	11	22	27	30	28.0	P	Parulekar et al. 1982
123	<i>Perna viridis</i>	Malaysia	Penang	5°25'N	100°20'E	11	30	30	32	31.0	P	Choo & Speiser 1979
124	<i>Perna viridis</i>	Singapore	East Johore Strait	1°23'N	103°56'E	11	22	27	29	28.1	I	Cheong & Chen 1980
125	<i>Perna viridis</i>	Thailand	Bang Pakong	13°28'N	100°55'E	11	22	28	32	29.0	P	Chonchuenchob et al. 1980
126	<i>Perna viridis</i>	Thailand	Bang Pakong	13°28'N	100°55'E	11	22	28	32	29.0	P	Chaitanawisuti & Menasveta 1987
127	<i>Perna viridis</i>	Thailand	Pattani Bay	6°53'N	101°16'E	11	22	26	32	27.1	P	Brohmanonda et al. 1988
128	<i>Perna viridis</i>	Thailand	Ban Laem	13°06'N	99°59'E	11	22	28	32	29.0	P	Tuaycharoen et al. 1988
129	<i>Perna viridis</i>	Thailand	Samae Kao	13°30'N	100°50'E	11	22	28	32	29.0	P	Tuaycharoen et al. 1988

REF NO	SPECIES (in situ)	COUNTRY	AREA	LAT	LONG	ENV	GFC	TEMPERATURE				REFERENCE
								MIN	MAX	AVG	SC	
130	<i>Pinctada margaritifera</i>	Sudan	Dongonab Bay	21°30'N	37°00'E	11	10	20	31	27.0	P	Nasr 1984
131	<i>Placopecten magellanicus</i>	Canada, Newfdl.	Southern Harbour	46°35'N	53°36'W	11	10	-1	13	5.1	I	MacDonald 1986
132	<i>Placopecten magellanicus</i>	Canada, Newfdl.	Spencers Cove	46°39'N	54°05'W	11	22	-1	13	5.1	I	MacDonald 1986
133	<i>Placopecten magellanicus</i>	Canada, Newfdl.	Sunnyside	47°51'N	53°55'W	11	10	-1	8	2.5	P	MacDonald & Thompson 1988
134	<i>Placopecten magellanicus</i>	USA	Georges Bank	41°15'N	67°30'W	11	10	4	18	10.4	I	Pringay 1979
135	<i>Placopecten magellanicus</i>	USA, New Jersey	Asbury Park	40°13'N	73°47'W	11	10	5	17	9.0	P	MacDonald & Thompson 1988
136	<i>Placuna placenta</i>	Sri Lanka		6°56'N	79°51'E	11	10	27	29	27.9	I	Thompson 1942
137	<i>Senilia senilis</i>	Sierra Leone	Johntop	7°56'N	12°56'W	12	10	24	29	27.0	P	Okera 1976
138	<i>Senilia senilis</i>	Sierra Leone	No. 2 River	8°29'N	13°04'W	12	10	24	29	27.0	P	Ndomahina 1975
139	<i>Serripes groenlandicus</i>	Greenland	Godhavn Havn	69°15'N	53°33'W	11	10	0	4	1.1	I	Petersen 1978
140	<i>Spisula sachalinensis</i>	Japan	Sendai Bay	37°45'N	141°00'E	11	10	7	23	14.1	I	Sasaki 1981
141	<i>Spisula sachalinensis</i>	Japan	Sendai Bay	37°45'N	141°00'E	11	10	7	23	14.1	I	Sasaki 1981
142	<i>Spisula sachalinensis</i>	Korea	Ingu	38°58'N	128°46'E	11	10	6	28	16.0	I	Kang & Kim 1983
143	<i>Spisula solidissima</i>	USA	off Long Island	40°25'N	72°24'W	11	10	7	21	12.8	I	Ropes 1985
144	<i>Spisula solidissima</i>	USA, New Jersey	Pt. Pleasant (insh.)	40°04'N	74°04'W	11	10	7	21	12.8	I	Jones et al. 1978
145	<i>Spisula solidissima</i>	USA, New Jersey	Pt. Pleasant (offsh.)	40°04'N	73°50'W	11	10	7	21	12.8	I	Jones et al. 1978
146	<i>Tapes decussatus</i>	Italy	Venice Lagoon	45°27'N	12°21'E	11	21	5	30	18.0	I	Breber 1985
147	<i>Tivela stultorum</i>	USA, California	La Jolla	32°51'N	117°16'W	12	10	13	21	17.0	P	Coe 1947
148	<i>Tivela stultorum</i>	USA, California	La Jolla	32°51'N	117°16'W	12	10	13	20	17.0	P	Coe 1948
149	<i>Tridacna derasa</i>	Australia	Gr. Barr. R.	16°35'S	146°00'E	11	10	23	28	25.9	I	Pearson & Munro (unp. MS)
150	<i>Tridacna gigas</i>	Australia	Great Barr. R.	16°35'S	146°00'E	11	10	23	28	25.9	I	Pearson & Munro (unp. MS)
151	<i>Tridacna gigas</i>	Papua New Guinea	Motupore I.	9°30'S	147°10'E	11	10	26	31	29.0	P	Munro & Gwyther 1981
152	<i>Tridacna gigas</i>	Philippines	Sulu Archipelago	7°00'N	122°00'E	11	10	27	29	28.0	I	Villanoy et al. (unp. MS)
153	<i>Tridacna maxima</i>	Fr. Polynesia	Takapoto	14°00'S	145°20'W	11	10	26	28	27.0	I	Richard 1977
154	<i>Tridacna maxima</i>	Papua New Guinea	Motupore I.	9°30'S	147°10'E	11	10	26	31	29.0	P	Munro & Gwyther 1981
155	<i>Tridacna squamosa</i>	Philippines	Sulu Archipelago	7°00'N	122°00'E	11	10	27	29	28.0	I	Villanoy et al. (unp. MS)
156	<i>Tridacna squamosa</i>	Papua New Guinea	Motupore I.	9°30'S	147°10'E	11	10	26	31	29.0	P	Munro & Gwyther 1981
157	<i>Venerupis decussata</i>	Spain	Santander Bay	43°28'N	3°48'W	12	10	11	19	14.8	I	Pato 1979
158	<i>Venus striatula</i>	Scotland, U.K.	Millport	55°46'N	4°55'W	11	30	6	14	10.4	P	Ursin 1963
159	<i>Yoldia thraciaeformis</i>	Newfoundland	Depth 895-1500	45°30'N	48°10'W	11	10	5	5	5.0	P	Hutchings & Haedrich 1984

**Appendix 4: Compilation of growth parameters for marine and freshwater bivalve species: Summary of species, type of data, parameters of the von Bertalanffy growth formula and their statistics, coefficients of mortality and phi prime**

Explanation of table headings and codes

<b>REF NO</b>	Species-specific reference number; for source of data refer to corresponding literature reference listed under this number in App. 3
<b>SPECIES</b>	Name of bivalve species; as given by the author (exceptions: <i>Cardium</i> is listed as <i>Cerastoderma</i> )
<b>COUNTRY</b>	Country, where the bivalve stock is located
<b>DAT</b>	Coded description of the type of data used in the analysis 1 Length-frequencies 2 Length-at-time data 3 Growth increment data 4 Published parameters
<b>DIM</b>	Coded description of the shell dimension measured as size L Shell length H Shell height
<b>MIN</b>	Smallest size in the data set
<b>MAX</b>	Largest size in the data set
<b>MAN</b>	Coded description of the method of analysis applied to the raw data 1 Complete ELEFAN 2 ETAL 2 3 Gulland & Holt Plot
<b>L-INF</b>	Parameter of the asymptotic length ( $L_{\infty}$ ) of the VBGF
<b>K</b>	Growth constant of the VBGF
<b>C</b>	Amplitude of the growth oscillation of the seasonalized VBGF
<b>WP</b>	Point of minimum growth of the seasonalized VBGF
<b>GF</b>	Measure of goodness of fit, in dependence of the method of analysis selected 1) Complete ELEFAN: $R_n$ 2) ETAL 2: $RSS$ 3) Gulland & Holt Plot: $r^2$
<b>s.e.L</b>	Standard error of the parameter $L_{\infty}$ of the VBGF (from ETAL 2)
<b>s.e.K</b>	Standard error of the parameter $K$ of the VBGF (from ETAL 2)
<b>Z</b>	Coefficient of total mortality
<b>M</b>	Coefficient of natural mortality
$\phi'$	Growth index phi prime, computed from $L_{\infty}$ and $K$

REF NO	SPECIES (marine)	COUNTRY	DAT	DIM	MIN	MAX	MAN	L-INF	K	C	WP	GF	s.e.L	s.e.K	Z	M	σ'
1	Amusium pleuronectes	Philippines	4	H	42.5	92.5		106.0	0.92	-	-	0.430	-	-	-	-	4.01
2	Amusium pleuronectes	Thailand	1	H	1.5	10.5	1	114.0	1.30	0.75	0.80	0.341	-	-	7.20	1.60	4.23
3	Anadara broughtonii	Korea	1	L	2.5	90.0	1	100.0	0.50	0.37	0.05	0.476	-	-	-	-	3.70
4	Anadara granosa	Malaysia	2	L	15.0	33.0	2	36.4	2.31	-	-	0.447	0.973	0.222	-	-	3.49
5	Anadara granosa	Malaysia	2	L	16.0	36.0	2	36.4	2.79	-	-	2.517	0.565	0.243	-	-	3.57
6	Anadara granosa	Malaysia	4	L	-	-	-	26.5	4.17	-	-	0.946	-	-	1.88	-	3.47
7	Anadara granosa	Malaysia	4	L	-	-	-	31.8	1.01	-	-	-	-	-	-	0.22	3.01
8	Anadara granosa	Malaysia	4	L	-	-	-	32.6	1.01	-	-	-	-	-	-	0.56	3.03
9	Anadara granosa	Malaysia	4	L	-	-	-	33.4	1.37	-	-	0.558	-	-	1.88	-	3.18
10	Anadara granosa	Malaysia	4	L	-	-	-	37.0	1.35	-	-	0.564	-	-	1.88	-	3.27
11	Anadara granosa	Malaysia	4	L	-	-	-	42.8	1.42	-	-	0.554	-	-	-	-	3.42
12	Anadara granosa	Malaysia	4	L	-	-	-	43.8	0.91	-	-	0.505	-	-	1.88	-	3.24
13	Anadara granosa	Malaysia	2	L	10.9	24.8	2	29.1	2.14	-	-	1.772	1.923	0.427	-	-	3.26
14	Anadara granosa	Malaysia	2	L	4.7	28.5	2	31.0	4.34	-	-	0.686	0.727	0.291	-	-	3.62
15	Anadara granosa	Malaysia	4	L	7.0	43.0	-	45.0	0.55	-	-	-	-	-	3.24	-	3.05
16	Anadara granosa	Malaysia	2	L	27.7	43.0	2	50.9	0.54	-	-	-	-	-	-	-	3.15
17	Anadara granosa	Malaysia	4	L	5.5	30.5	-	34.2	0.60	-	-	-	-	-	-	-	2.85
18	Anadara granosa	Malaysia	4	L	10.5	33.5	-	37.4	0.87	-	-	-	-	-	4.06	-	2.93
19	Anadara granosa	Malaysia	4	L	16.5	36.5	-	40.5	0.79	-	-	-	-	-	2.93	-	3.09
20	Anadara granosa	Malaysia	4	L	7.0	39.0	-	41.4	0.78	-	-	-	-	-	4.12	-	3.11
21	Anadara granosa	Malaysia	4	L	-	-	-	27.1	2.15	-	-	-	-	-	3.66	-	3.13
22	Anadara granosa	Malaysia	4	L	-	-	-	27.6	2.99	-	-	0.780	-	-	-	-	3.20
23	Anadara granosa	Malaysia	2	L	-	-	2	28.3	4.17	-	-	0.862	-	-	-	-	3.36
24	Anadara granosa	Malaysia	2	L	4.3	27.4	2	32.7	3.40	-	-	4.534	1.352	0.623	-	-	3.52
25	Arca ventricosa	Fr. Polynesia	4	L	-	-	-	32.7	3.40	-	-	0.838	1.233	0.302	-	-	3.56
26	Arctica islandica	USA	4	L	20.0	104.0	-	103.0	0.06	-	-	-	-	-	-	-	2.80
27	Argopecten purpuratus	Peru	3	H	12.0	88.0	3	107.1	0.02	-	-	-	-	-	-	-	2.36
28	Argopecten purpuratus	Peru	3	H	18.0	88.0	3	99.2	1.99	-	-	-	-	-	-	0.40	4.41
29	Argopecten purpuratus	Peru	4	H	9.0	101.0	-	111.5	2.10	-	-	0.813	-	-	-	0.40	4.29
30	Cerastoderma edule	England, U.K.	2	L	16.8	37.4	2	37.4	0.66	-	-	0.814	-	-	-	-	4.42
31	Cerastoderma edule	N. Ireland, U.K.	2	L	4.0	29.9	2	29.8	0.46	-	-	1.152	0.409	0.048	0.99	-	2.97
32	Cerastoderma edule	Wales, U.K.	4	L	12.6	29.8	-	31.2	0.62	-	-	3.036	0.727	0.043	-	-	2.61
33	Cerastoderma fragum	Fr. Polynesia	4	L	-	-	-	40.4	0.48	-	-	-	-	-	-	-	2.78
34	Cerastoderma glaucum	England, U.K.	2	L	11.0	31.0	2	31.6	0.57	-	-	0.798	0.603	0.049	-	-	2.89
35	Cerastoderma glaucum	Poland	2	L	6.8	20.5	2	27.7	0.27	-	-	0.304	2.497	0.052	-	-	2.76
36	Cerastoderma glaucum	Sweden	4	H	-	-	-	15.0	0.59	-	-	-	-	-	-	-	2.32
37	Cerastoderma glaucum	Sweden	4	H	-	-	-	17.2	0.27	-	-	-	-	-	-	-	2.12
38	Chlamys albidus	USSR, Kuril Is.	4	H	10.0	100.0	-	117.2	0.16	-	-	-	-	-	-	-	1.90
39	Chlamys opercularis	Denmark	4	L	-	-	-	73.1	0.64	-	-	-	-	-	-	-	3.34
40	Chlamys opercularis	Denmark	4	L	-	-	-	69.9	0.54	-	-	-	-	-	-	-	3.53
41	Chlamys opercularis	Denmark	4	L	-	-	-	78.0	0.65	-	-	-	-	-	-	-	3.42
42	Chlamys opercularis	England, U.K.	2	L	23.5	44.5	2	55.5	1.34	-	-	40.418	7.830	0.539	-	-	3.60
43	Chlamys opercularis	Scotland, U.K.	2	H	24.5	64.4	2	65.6	1.05	0.71	1.07	13.209	0.518	0.043	0.51	-	3.62
44	Chlamys opercularis	Scotland, U.K.	2	H	23.3	65.0	2	70.3	0.56	-	-	0.642	0.970	0.028	-	-	3.65
45	Chlamys opercularis	Scotland, U.K.	2	H	29.5	68.1	2	74.2	0.51	-	-	0.262	0.725	0.019	-	-	3.44
46	Chlamys varia	France	4	H	-	-	-	50.9	0.57	-	-	-	-	-	-	-	3.45
47	Crassostrea gigas	Korea	2	H	19.7	85.3	2	99.1	2.69	-	-	-	-	-	-	-	3.17
48	Crassostrea gigas	Korea	2	H	20.4	88.0	2	103.7	2.35	-	-	102.089	7.542	0.573	-	-	4.42
49	Crassostrea madrasensis	India	4	L	-	-	-	119.0	0.77	-	-	28.824	4.211	0.238	-	-	4.40
50	Crassostrea madrasensis	India	4	L	-	-	-	89.0	1.80	-	-	-	-	-	-	-	4.04
51	Crassostrea rhizophorae	Jamaica	2	L	5.6	57.3	2	86.9	2.79	-	-	7.081	6.845	0.361	-	-	4.15
52	Crassostrea tulipa	Gambia	2	L	7.0	41.0	2	70.4	1.90	-	-	1.585	8.429	0.362	0.78	0.78	4.32
53	Crassostrea virginica	USA, Massachus.	2	H	10.4	71.9	2	115.7	0.41	-	-	37.759	48.574	0.249	-	-	3.97
54	Crassostrea virginica	USA, Massachus.	2	H	15.2	88.5	2	125.8	0.50	-	-	0.062	1.624	0.012	0.29	0.29	3.74
55	Crenomytilus grayanus	USSR	2	L	35.0	121.0	2	163.8	0.05	-	-	29.797	4.335	0.003	-	-	3.90
56	Donax cuneatus	India	1	L	1.5	23.5	1	24.7	0.92	0.76	0.90	0.382	-	-	-	-	3.13
57	Donax incarnatus	India	1	L	1.5	29.5	1	31.1	1.50	0.65	0.35	0.521	-	-	6.24	-	2.75
																	3.16

REF NO	SPECIES (marine)	COUNTRY	DAT	DIM	MIN	MAX	MAN	L-INF	K	C	WP	GF	s.e.L	s.e.K	Z	M	e'
58	Donax peruvianus	Peru	4	L	12.0	30.0		46.0	1.00	1.03	0.67	0.973	-	-	-	-	3.33
59	Donax trunculus	France	4	L	-	-		36.0	0.96	-	-	-	-	-	-	-	3.09
60	Donax trunculus	France	4	L	-	-		38.4	0.72	-	-	-	-	-	-	-	3.03
61	Donax trunculus	France	4	L	-	-		43.5	0.45	-	-	-	-	-	-	-	2.93
62	Donax vittatus	France	4	L	-	-		35.9	1.01	-	-	-	-	-	-	-	3.11
63	Donax vittatus	France	4	L	-	-		31.3	1.06	-	-	-	-	-	-	-	3.02
64	Geukensia demissa	USA, Connect.	2	L	30.5	98.3	2	99.1	0.19	-	-	29.168	1.164	0.010	-	-	3.27
65	Geukensia demissa	USA, Virginia	2	L	40.7	100.9	2	108.7	0.33	-	-	23.601	4.962	0.056	-	-	3.59
66	Hiatella byssifera	Greenland	2	L	5.2	37.6	2	38.5	0.25	-	-	1.767	0.267	0.007	-	0.28	2.57
67	Hippopus hippopus	Australia	4	L	-	-		369.1	0.20	-	-	-	-	-	-	-	4.44
68	Hippopus hippopus	Australia	4	L	-	-		414.7	0.15	-	-	-	-	-	-	-	4.41
69	Hippopus hippopus	Papua New Guinea	4	L	100.0	310.0		360.0	0.12	-	-	-	-	-	-	-	4.19
70	Hippopus hippopus	Philippines	4	L	-	-		43.7	0.13	-	-	-	-	-	-	-	2.39
71	Hippopus porcellanus	Philippines	4	L	-	-		43.6	0.13	-	-	-	-	-	-	-	2.39
72	Macoma balthica	Canada	4	L	-	-		21.1	0.31	-	-	-	-	-	-	-	2.14
73	Macoma balthica	Canada	4	L	-	-		37.3	0.09	-	-	-	-	-	-	-	2.10
74	Macoma balthica	Canada, Quebec	2	L	2.4	12.7	2	15.9	0.14	-	-	0.795	0.896	0.017	-	-	1.55
75	Macoma balthica	France	4	L	6.0	17.0		18.2	0.35	-	-	-	-	-	-	-	2.06
75	Macoma balthica	Netherlands	2	L	7.0	20.9	2	24.9	0.30	-	-	0.357	1.177	0.038	-	-	2.27
77	Macoma calcarea	Greenland	2	L	4.0	29.7	2	32.9	0.13	-	-	1.073	0.382	0.004	-	0.30	2.15
78	Macrocallista maculata	Bermuda	2	H	16.6	65.5	2	66.0	0.44	-	-	2.961	0.575	0.017	-	-	3.28
79	Mercenaria campechiensis	USA, Florida	2	L	16.5	74.2	2	96.3	0.64	-	-	0.002	0.297	0.004	-	-	3.77
80	Mercenaria mercenaria	USA, Florida	2	L	13.3	67.0	2	81.8	0.50	-	-	3.026	5.520	0.077	-	-	3.52
81	Mercenaria mercenaria	USA, Rhode Isl.	4	H	-	-		90.9	0.16	-	-	-	-	-	-	-	3.12
82	Mesodesma donacium	Peru	4	L	20.0	90.0		124.0	1.13	0.91	0.64	0.819	-	-	2.50	-	4.24
83	Modiolus modiolus	N. Ireland, U.K.	2	L	17.9	127.8	2	143.4	0.08	-	-	23.233	2.965	0.004	-	-	3.22
84	Musculista arcuatula	India	1	L	3.5	32.5	1	34.0	1.20	0.20	0.30	0.172	-	-	-	-	3.14
85	Mya arenaria	Canada	4	L	-	-		91.3	0.19	-	-	-	-	-	-	-	3.20
86	Mya arenaria	Denmark	4	L	-	-		60.1	0.30	-	-	-	-	-	-	-	3.03
87	Mya arenaria	USA, Maine	2	L	11.0	51.0	2	61.7	0.32	-	-	2.114	2.497	0.032	-	0.64	3.09
88	Mya arenaria	USA, Maine	2	L	10.0	69.0	2	148.4	0.14	-	-	0.156	6.447	0.008	-	-	3.49
89	Mya arenaria	USA, Massachus.	4	L	-	-		85.2	0.39	-	-	-	-	-	-	-	3.45
90	Mya truncata	Greenland	2	L	6.3	50.6	2	68.7	0.08	-	-	6.396	2.263	0.005	-	0.14	2.58
91	Mytilus coruscus	USSR	4	L	-	-		165.2	0.21	-	-	-	-	-	-	-	3.76
92	Mytilus edulis	Canada, N.Sc.	2	L	15.0	52.7	2	54.2	0.95	-	-	3.238	0.729	0.057	-	-	3.45
93	Mytilus edulis	Canada, N.Sc.	2	L	15.0	58.0	2	70.0	0.46	-	-	4.412	2.776	0.045	-	-	3.35
94	Mytilus edulis	Denmark	4	L	-	-		82.4	0.27	-	-	-	-	-	-	-	3.26
95	Mytilus edulis	Denmark	4	L	-	-		80.8	0.45	-	-	-	-	-	-	-	3.47
96	Mytilus edulis	England, U.K.	4	L	-	-		93.8	0.22	-	-	-	-	-	-	-	3.29
97	Mytilus edulis	England, U.K.	4	L	-	-		81.3	0.24	-	-	-	-	-	-	-	3.20
98	Mytilus edulis	Greenland	2	L	3.3	92.0	2	144.6	0.05	-	-	747.605	4.008	0.002	-	-	3.02
99	Mytilus edulis	Wales, U.K.	4	L	3.0	60.0		67.2	1.14	-	-	-	-	-	-	-	3.71
100	Mytilus edulis diegensis	USA, California	2	L	17.7	95.5	2	100.8	1.47	-	-	2.694	0.589	0.030	-	-	4.17
101	Mytilus edulis platensis	Uruguay	2	L	4.2	51.7	2	72.8	0.78	0.23	0.37	1.412	1.458	0.004	-	-	3.62
102	Mytilus galloprovincialis	Italy	2	L	18.2	64.7	2	70.8	1.82	-	-	31.507	6.009	0.447	-	-	3.96
103	Nucula minuta	Scotland, U.K.	2	L	7.2	17.8	2	18.4	0.50	-	-	0.010	0.052	0.007	-	-	2.23
104	Nuculana pernula	Newfoundland	2	L	17.6	30.0	2	30.0	0.32	-	-	2.921	0.903	0.065	0.37	-	2.46
105	Ostrea puelchana	Argentina	2	H	28.4	84.8	2	96.7	0.52	1.79	0.59	83.449	5.173	0.090	-	-	3.69
106	Ostrea puelchana	Argentina	2	H	32.5	97.6	2	104.9	0.94	1.12	0.46	37.322	4.002	0.127	-	-	4.01
107	Patinopecten caurinus	Canada	4	H	-	-		156.8	0.39	-	-	-	-	-	-	-	3.98
108	Patinopecten caurinus	Canada	4	H	-	-		112.4	0.50	-	-	-	-	-	-	-	3.80
109	Patinopecten yessoensis	Japan	2	L	13.2	135.2	2	144.2	0.98	0.13	0.37	25.204	1.921	0.041	-	-	4.31
110	Patinopecten yessoensis	Korea	2	L	5.5	113.5	2	122.8	0.87	0.71	0.74	208.797	8.148	0.169	-	-	4.12
111	Pecten maximus	France	4	L	-	-		138.9	0.48	-	-	-	-	-	-	-	3.97
112	Pecten maximus	France	4	L	-	-		106.8	0.66	-	-	-	-	-	-	-	3.88
113	Pecten maximus	France	4	L	-	-		123.5	0.53	-	-	-	-	-	-	-	3.91
114	Pecten maximus	France	4	L	-	-		124.2	0.56	-	-	-	-	-	-	-	3.94

REF NO	SPECIES (marine)	COUNTRY	DAT	DIM	MIN	MAX	MAN	L-INF	K	C	WP	GF	s.e.L	s.e.K	Z	M	e'
115	<i>Perna canaliculus</i>	New Zealand	2	L	27.2	120.0	2	202.6	0.51	0.57	0.83	16.638	13.429	0.058	-	-	4.32
116	<i>Perna canaliculus</i>	New Zealand	3	L	7.0	107.0	3	142.1	0.69	0.40	0.54	-	-	-	-	-	4.14
117	<i>Perna perna</i>	Mozambique	1	L	7.5	117.5	1	122.5	1.50	0.60	0.55	0.531	-	-	-	-	4.35
118	<i>Perna perna</i>	Venezuela	2	L	42.5	93.4	2	124.4	1.11	0.85	0.89	13.836	19.229	0.418	-	-	4.23
119	<i>Perna viridis</i>	Brunsi	3	L	-	-	2	144.7	1.77	-	-	8.996	7.539	0.184	-	-	4.57
120	<i>Perna viridis</i>	Hong Kong	4	L	-	-	-	101.9	0.30	-	-	-	-	-	-	-	3.49
121	<i>Perna viridis</i>	India	2	L	8.0	91.0	2	132.2	1.11	-	-	12.435	7.373	0.106	-	-	4.29
122	<i>Perna viridis</i>	India	2	L	13.9	87.5	2	94.9	2.37	0.35	0.51	44.011	7.412	0.637	-	-	4.33
123	<i>Perna viridis</i>	Malaysia	3	L	18.6	78.4	2	89.1	2.20	-	-	7.504	0.858	0.062	0.52	0.52	4.24
124	<i>Perna viridis</i>	Singapore	3	L	9.4	72.0	2	143.2	1.34	-	-	45.981	53.625	0.731	-	-	4.44
125	<i>Perna viridis</i>	Thailand	2	L	21.0	57.0	2	79.5	1.93	-	-	0.014	0.453	0.234	-	-	4.09
126	<i>Perna viridis</i>	Thailand	2	L	21.8	57.8	2	83.5	1.81	-	-	2.039	6.287	0.279	-	-	4.10
127	<i>Perna viridis</i>	Thailand	2	L	15.4	94.9	2	179.9	0.88	0.26	0.55	45.826	41.721	0.309	-	-	4.45
128	<i>Perna viridis</i>	Thailand	4	L	-	-	-	111.9	1.00	-	-	-	-	-	-	-	4.10
129	<i>Perna viridis</i>	Thailand	4	L	-	-	-	107.2	1.07	-	-	-	-	-	-	-	4.09
130	<i>Pinctada margaritifera</i>	Sudan	2	L	78.6	138.1	2	152.8	1.52	0.58	0.49	76.692	17.858	0.774	-	-	4.55
131	<i>Placopecten magellanicus</i>	Canada, Newfdl.	4	H	-	-	-	173.8	0.16	-	-	-	-	-	-	-	3.68
132	<i>Placopecten magellanicus</i>	Canada, Newfdl.	4	H	-	-	-	127.6	0.38	-	-	-	-	-	-	-	3.79
133	<i>Placopecten magellanicus</i>	Canada, Newfdl.	4	H	-	-	-	158.4	0.16	-	-	-	-	-	-	-	3.60
134	<i>Placopecten magellanicus</i>	USA	4	L	-	-	-	143.6	0.37	-	-	-	-	-	0.80	0.10	3.88
135	<i>Placopecten magellanicus</i>	USA, New Jersey	4	H	-	-	-	155.9	0.22	-	-	-	-	-	-	-	3.73
136	<i>Placuna placenta</i>	Sri Lanka	2	H	49.9	165.0	2	187.3	0.26	-	-	95.611	6.684	0.028	-	-	3.96
137	<i>Senilia senilis</i>	Sierra Leone	2	L	25.8	119.5	2	136.3	0.23	-	-	2.308	1.336	0.006	-	-	3.63
138	<i>Senilia senilis</i>	Sierra Leone	1	L	2.0	46.0	1	46.5	0.55	0.76	0.18	0.361	-	-	-	-	3.08
139	<i>Serripes groenlandicus</i>	Greenland	2	L	7.6	73.7	2	82.9	0.13	-	-	9.052	1.244	0.005	-	0.12	2.95
140	<i>Spisula sachalinensis</i>	Japan	2	L	9.7	98.6	2	98.7	0.69	-	-	13.440	0.988	0.032	-	-	3.83
141	<i>Spisula sachalinensis</i>	Japan	2	L	10.6	103.8	2	102.4	0.67	-	-	23.830	1.353	0.040	-	-	3.85
142	<i>Spisula sachalinensis</i>	Korea	4	L	-	-	-	126.4	0.26	-	-	-	-	-	-	-	3.62
143	<i>Spisula solidissima</i>	USA	2	L	73.0	190.2	2	191.1	0.23	-	-	6.037	0.609	0.004	-	-	3.92
144	<i>Spisula solidissima</i>	USA, New Jersey	2	L	28.5	90.5	2	91.5	0.32	-	-	11.214	1.019	0.017	-	-	3.43
145	<i>Spisula solidissima</i>	USA, New Jersey	2	L	36.1	118.0	2	118.2	0.36	-	-	3.943	0.236	0.005	-	-	3.70
146	<i>Tapes decussatus</i>	Italy	2	L	21.2	39.8	2	53.7	0.44	1.00	0.50	6.618	9.545	0.190	-	-	3.10
147	<i>Tivela stultorum</i>	USA, California	2	L	21.3	148.5	2	173.1	0.18	-	-	115.368	6.505	0.017	-	-	3.73
148	<i>Tivela stultorum</i>	USA, California	2	L	5.5	77.5	2	206.5	0.12	0.43	0.30	47.685	36.855	0.026	-	-	3.71
149	<i>Tridacna derasa</i>	Australia	4	L	-	-	-	469.1	0.11	-	-	-	-	-	0.05	-	4.38
150	<i>Tridacna gigas</i>	Australia	4	L	-	-	-	857.0	0.07	-	-	-	-	-	0.07	-	4.71
151	<i>Tridacna gigas</i>	Papua New Guinea	4	L	100.0	750.0	-	800.0	0.13	-	-	-	-	-	-	-	4.92
152	<i>Tridacna gigas</i>	Philippines	4	L	-	-	-	93.0	0.13	-	-	-	-	-	-	-	3.05
153	<i>Tridacna maxima</i>	Fr. Polynesia	4	L	-	-	-	124.3	0.26	-	-	-	-	-	-	-	3.60
154	<i>Tridacna maxima</i>	Papua New Guinea	4	L	100.0	220.0	-	243.0	0.28	-	-	-	-	-	-	-	4.22
155	<i>Tridacna squamosa</i>	Philippines	4	L	-	-	-	30.0	0.23	-	-	-	-	-	-	-	2.32
156	<i>Tridacna squamosa</i>	Papua New Guinea	4	L	100.0	250.0	-	315.0	0.20	-	-	-	-	-	-	-	4.30
157	<i>Venerupis decussata</i>	Spain	2	L	26.4	53.5	2	62.8	0.43	-	-	0.367	2.192	0.051	-	-	3.23
158	<i>Venus striatula</i>	Scotland, U.K.	4	L	-	-	-	32.9	0.23	-	-	-	-	-	-	-	2.40
159	<i>Yoldia thraciaeformis</i>	Newfoundland	3	L	25.0	53.0	3	55.8	0.18	-	-	0.990	-	-	0.40	-	2.75

REF NO	SPECIES (freshwater)	COUNTRY	DAT	DIM	MIN	MAX	MAN	L-INF	K	C	WP	GF	s.e.L	s.e.K	Z	M	$\sigma'$
160	Anodonta anatina	England, U.K.	2	L	24.0	34.0	2	89.8	0.31	-	-	11.549	1.884	0.023	-	-	3.40
161	Anodonta anatina	England, U.K.	2	L	26.6	86.7	2	91.5	0.24	-	-	52.234	4.352	0.042	-	-	3.30
162	Anodonta anatina	England, U.K.	2	L	53.4	95.8	2	98.7	0.72	-	-	0.427	0.543	0.025	-	-	3.85
163	Anodonta anatina	F.R. Germany	3	L	2.0	12.4	3	97.1	0.46	-	-	0.870	-	-	-	-	3.64
164	Anodonta minima	England, U.K.	2	L	18.1	67.6	2	71.8	0.37	-	-	8.050	2.419	0.041	-	-	3.28
165	Anodonta piscinalis	Finland	4	L	-	-	-	106.9	0.31	-	-	-	-	-	-	-	3.55
166	Anodonta piscinalis	F.R. Germany	4	L	0	0	-	241.0	0.08	-	-	-	-	-	-	-	3.67
167	Aspatharia sinuata	Nigeria	4	L	50.0	92.0	-	98.6	0.45	-	-	-	-	-	-	-	3.64
168	Aspatharia sinuata	Nigeria	3	L	37.3	82.3	3	84.3	0.22	-	-	0.896	-	-	-	-	3.19
169	Aspatharia sinuata	Nigeria	4	L	-	-	-	76.0	0.56	-	-	-	-	-	-	-	3.51
170	Aspatharia sinuata	Nigeria	4	L	-	-	-	96.4	0.58	-	-	-	-	-	-	-	3.73
171	Aspatharia sinuata	Nigeria	4	L	-	-	-	67.5	0.58	-	-	-	-	-	-	-	3.42
172	Caelatura aegyptiaca	Tschad	4	L	-	-	-	26.8	0.15	-	-	-	-	-	-	-	2.03
173	Caelatura aegyptiaca	Tschad	4	L	-	-	-	27.7	0.14	-	-	-	-	-	-	-	2.03
174	Caelatura aegyptiaca	Tschad	4	L	-	-	-	33.8	0.11	-	-	-	-	-	-	-	2.10
175	Caelatura teretiuscula	Tschad	4	L	-	-	-	28.1	0.16	-	-	-	-	-	-	-	2.10
176	Corbicula africana	Tschad	4	L	7.0	13.0	-	14.2	0.12	-	-	-	-	-	-	-	1.38
177	Corbicula africana	Tschad	4	L	3.0	10.0	-	10.0	0.22	-	-	-	-	-	-	-	1.34
178	Corbicula africana	Tschad	4	L	5.0	13.0	-	13.9	0.13	-	-	-	-	-	-	-	1.40
179	Egeria radiata	Ghana	2	H	19.5	71.5	2	77.9	0.75	-	-	0.001	0.056	0.018	-	-	3.66
180	Egeria radiata	Ghana	2	H	19.5	50.0	2	59.8	0.71	-	-	0.001	0.008	0.004	-	-	3.40
181	Glabaris luteolus	Costa Rica	3	L	19.3	104.6	3	109.7	1.56	-	-	0.960	-	-	-	-	4.27
182	Mutela rostrata	Tschad	4	L	-	-	-	59.3	0.18	-	-	-	-	-	0.10	-	2.80
183	Unio pictorum	England, U.K.	2	L	30.7	72.3	2	75.8	0.22	-	-	7.271	1.480	0.018	-	-	3.10
184	Unio pictorum	F.R. Germany	3	L	1.8	9.3	3	86.2	0.22	-	-	0.700	-	-	-	-	3.21
185	Unio pictorum	F.R. Germany	4	L	0	0	-	180.0	0.11	-	-	-	-	-	-	-	3.55
186	Unio pictorum	Romania	2	L	25.0	103.0	2	126.1	0.22	-	-	17.112	5.970	0.025	-	-	3.54
187	Unio tumidus	England, U.K.	2	L	38.9	85.2	2	88.0	0.28	-	-	4.228	0.968	0.015	-	-	3.34
188	Unio tumidus	F.R. Germany	3	L	1.1	10.4	3	85.6	0.27	-	-	0.661	-	-	-	-	3.30
189	Unio tumidus	F.R. Germany	4	L	0	0	-	136.0	0.16	-	-	-	-	-	-	-	3.47
190	Unio tumidus	Romania	2	L	23.0	88.2	2	103.1	0.15	-	-	7.048	2.184	0.009	-	-	3.20