Environment, adaptation and evolution: Scallop ecology across the latitudinal gradient

Umwelt, Anpassung und Evolution: Ökologie der Jakobsmuscheln im latitudinalen Gradienten

---

Olaf Heilmayer

Ber. Polarforsch. Meeresforsch. 480 (2004)
ISSN 1618 - 3193

Meinen Eltern

Olaf Heilmayer
Alfred Wegener Institut für Polar- und Meeresforschung
Columbusstrasse
27568 Bremerhaven, Deutschland

Druckfassung einer Dissertation, die dem Fachbereich 2 (Biologie/Chemie) der Universität Bremen im Jahr 2003 vorgelegt wurde.

Printed version of a PhD thesis submitted in 2003 to the Faculty 2 (Biology/Chemistry) of the University of Bremen.

Contents

List of selected abbreviations

Abbreviation	Unit in parentheses
A	assimilation
ABT	Arrhenius-Break-Temperature
AE	assimilation efficiency
AFDM	ash free dry mass (g)
B	biomass (g DM or kJ m^{-2})
b	mass coefficient
C	consumption
CS	citrate synthase
CSA	citrate synthase activity
DM	soft tissue dry mass (g)
D	curve shaping parameter of the VBGF
d^{-1}	per day
E_a	Arrhenius energy of activation
H_t	shell height at age t (year)
H_∞	asymptotic shell height (mm)
ind	individual
K	growth constant of VBGF (per year)
K_1	gross growth efficiency
K_2	net growth efficiency
M	natural mortality rate
M_{max}	maximum body mass (g or kJ)
M_E	body mass of experimental scallop
M_S	standard-sized scallop of 1 g dry mass
m^{-2}	per square meter
MSGRM	mass specific growth rate method
N	number of individuals
P	production (g DM or kJ m^{-2} y^{-1})
P_G	gonadal production (g DM or kJ m^{-2} y^{-1})
P_S	somatic production (g DM or kJ m^{-2} y^{-1})
P_{Tot}	total production (g DM or kJ m^{-2} y^{-1})
P/B	productivity (y^{-1})= production : biomass
OGP P	overall growth performance P= log (KM_∞)
R	respiration

Abbreviation	Unit in parentheses
RCR	respiratory control ratios
SFD	size frequency distribution
SMR_{Ind}	standardized metabolic rate (1g DM animal) of an individual
SMR_{Avg}	standardized metabolic rate (1g DM animal) calculated from population relationship
T	temperature (°C or K)
t_0	age when shell height equals zero
t	time
VBGF	von Bertalanffy growth function
VO_2	metabolic rate
VO_2'	standardized metabolic rate
WM	soft tissue wet mass (g)
y^{-1}	per year
Z	mortality rate (y^{-1})

Summary

Marine biota shows latitudinal gradients in distribution, composition and diversity. Latitude has no environmental meaning by itself, but it is a proxy for the total amount of and the seasonality in solar energy input, which in turn primarily govern ambient temperature and primary production. Most studies of latitudinal gradients in organism biology and ecology are based on between-species comparisons and hence are hampered by taxon-related variability in the parameters under investigation. To reduce taxonomic "noise" and to minimize the risk of otherwise misleading generalisations I used species from one single bivalve family to study ecological and physiological parameters along a latitudinal gradient. Bivalves are ideal for such a global comparison, because metabolic losses can be measured easily and the shell often provides a good record of growth history. The family Pectinidae (scallops) consists of approx. 400 known species with a wide latitudinal distribution thus covering a wide temperature range. Owing to the considerable commercial significance of scallops a tremendous amount of data for inter- and intraspecific comparison is available.

I measured ecological and physiological parameters of three scallop species (*Adamussium colbecki, Aequipecten opercularis* and *Zygochlamys patagonica*) characteristic of different temperature regimes, and combined the results with data extracted from literature. The resulting database comprised 226 studies of 26 species living over a temperature range of 28°C (-1.8° to 26°C).

Age of the three species was determined following a 2-step procedure: (i) reading of shell growth bands (surface and/or X-ray) and (ii) validation of the annual character of natural growth bands by stable oxygen and carbon isotope analysis. A von Bertalanffy growth function was fitted to the obtained size-at-age data.

Overall growth performance (OGP) of the Antarctic scallop is comparatively low (mean 1.71 ± 0.16), but not significantly different from the boreal species *A. opercularis* (mean 2.02 ± 0.11) living under similar conditions (environmental stress). In a worldwide comparison, overall growth performance of scallops increases with decreasing latitude, i.e. it is strongly coupled to annual solar energy input but weakly coupled to average annual water temperature. Mean annual water temperatures and annual solar energy input by themselves can explain only a small part of the variability observed in growth performance. Further studies need to clarify the significance of local abiotic parameters, such as annual temperature amplitude, phytoplankton production and water depth.

Oxygen consumption, one basic and characteristic ecophysiological parameter and a proxy of total metabolic activity was measured using an intermittant flow system and oxygen microoptodes. Standard metabolic rate (SMR) equals the energy consumed by all vital functions of a quiescent individual, including maintenance, somatic growth and production of gametes.

An analysis of 82 published studies on pectinid standard metabolism provided no evidence for metabolic cold adaptation at the organism level (the hypothesis that polar invertebrates show a standard metabolic rate higher than predicted from the overall rate-to-temperature relationship established for temperate and tropical species). In contrast, mitochondrial proliferation caused a rise in oxygen demand in the Antarctic scallop, *A. colbecki*, indicating that metabolic cold adaptation (MCA) does occur on the cellular level. It must be assumed that energy savings occur to counterbalance the cost of cellular MCA. At which organisational level such savings may occur remains unanswered so far.

Low whole animal metabolism of the Antarctic scallop may indicate an energetic advantage over conspecifics from temperate waters. The relation between temperature and growth efficiency was used to check whether this assumption is true. The SMR-to-OGP ratio is seen as a proxy of the reciprocal growth efficiency, i.e. the fraction of metabolic energy channelled into somatic growth. This proxy decreases with rising temperature across a wide range of pectinid populations and species. Thus, there is strong empirical evidence that elevated temperature constrains growth efficiency in scallops and that evolutionary adaptation does not fully compensate for this effect.

In conclusion, the present study indicates that many scallop species have developed strong life-history adaptations to the particular conditions of both alimentation and temperature they experience. The most conspicuous adaptations include an increasing lifespan and generally larger attainable size with increasing latitude which may explain similar growth performance values in *A. opercularis* and *A. colbecki*. While the first can be viewed as short-lived and fast growing (*r*-selected) the latter one is long-lived with low mean annual growth rates (*A*-selected). In addition, the established pectinid database (ScallopBASE) provides a good basis for the evaluation of evolutionary adaptations and constraints. Further population data and more detailed environmental data (e.g. maximum and minimum water temperatures, food supply, etc.) are necessary to get a more detailed picture and to eliminate uncertainties.

Zusammenfassung

Die Artenzusammensetzung mariner Lebensgemeinschaften und die Verbreitungsmuster einzelner Arten unterscheiden sich im latitudinalen Gradienten. Der Breitengrad selbst hat jedoch keine direkte ökologische Bedeutung, er dient vielmehr als ein Näherungswert der jährlich einstrahlenden Sonnenenergie und deren Saisonalität. Beide beeinflussen sowohl die Wassertemperatur, wie auch die Primärproduktion im Meer. Das Problem bisheriger weltweiter Vergleiche ist, dass sie auf Daten aus unterschiedlichsten taxonomischen Familien basieren. Das dadurch erzeugte statistische „Rauschen" erschwert die Identifikation feiner Unterschiede wesentlich.

Diese Arbeit analysiert erstmals ökologische und physiologische Muster entlang eines latitudinalen Gradienten innerhalb einer taxonomischen Familie, also innerhalb sehr enger Verwandtschaftsverhältisse. Muscheln sind ideale Organismen für derartige Vergleiche. Ihre Stoffwechselleistungen sind leicht zu messen und ihre harte Kalkschale liefert ein gutes Abbild ihrer Wachstumsgeschichte. Die Familie der Jakobsmuscheln (Pectinidea) umfasst etwa 400 Arten, die weltweit über einen großen Temperaturbereich verbreitet sind. Aufgrund ihrer vielerorts beachtlichen Bedeutung für die Fischereiwirtschaft wurden und werden Pectiniden intensiv erforscht.

In dieser Arbeit habe ich ökologische und physiologische Eigenschaften dreier Arten (*Adamussium colbecki, Aequipecten opercularis* and *Zygochlamys patagonica*) aus verschiedenen Temperaturregimen untersucht. Die Ergebnisse meiner Messungen in Kombination mit Daten aus der Literatur bilden eine Datenbank, die 226 wissenschaftliche Untersuchungen an 26 verschiedenen Arten über einen Temperaturbereich von ΔT= 28°C (von –1.8° C bis +26° C) beinhaltet.

In meinen Untersuchungen wurde das Alter der drei untersuchten Arten in einem zweistufigen System bestimmt. In einem ersten Schritt wurden externe Wachstumsringe gezählt. Eine Analyse des Verhältnisses der stabilen Kohlenstoff- und Sauerstoffisotopen im Schalenkarbonat ermöglichte den Nachweis, dass externe Wachstumsringe jährlich angelegt werden. Mit den so erhaltenen Größen-Alters-Beziehungen konnte für jede Art ein von Bertalanffy-Wachstums-Modell etabliert werden.

Die Gesamtwachstumsleistung (Overall Growth Performance, OGP) der Antarktischen Pilgermuschel ist vergleichsweise niedrig, es lassen sich aber keine statisitisch signifikanten Unterschiede zu unter ähnlichen Bedingungen lebenden temperierten Arten erkennen. Ein weltweiter Vergleich zeigt eine generelle Zunahme der OGP mit abnehmender geographischen Breite. Es besteht dabei eine starke Abhängigkeit der OGP von der jährlichen Sonnenlichtenergie, wohingegen der Zusammenhang mit der Umgebungstemperatur weniger ausgeprägt ist. Beide Faktoren reichen jedoch nicht aus, die beobachtete Variablität der OGP hinreichend zu erklären. Inwiefern lokale Parameter wie jährliche Temperaturschwankungen, Phytoplanktonproduktion und Wassertiefe einen entscheidenen Einfluss haben, muss durch weitere Untersuchungen geklärt werden.

Der Sauerstoffverbrauch eines ruhenden Organismus ist ein wichtiger ökophysiologischer Parameter. Er spiegelt näherungsweise den Gesamtenergieverbrauch wieder. Die Theorie der „metabolic cold adaptation" (MCA) besagt, dass Wirbellose der Polargebiete einen höheren Energieverbrauch haben, als man durch Extrapolation der Werte von verwandten Tieren aus gemäßigten oder tropischen Gebieten erwarten würde. Meine Untersuchung an 82 veröffentlichten Studien zeigt, dass es auf Ebene des Ganztiersauerstoffverbrauches keine Hinweise auf eine „metabolic cold adaptation" gibt. Die Zunahme der Mitochondriendichte bei der Antarktischen Pilgermuschel verursacht jedoch einen höheren zellulären Sauerstoffbedarf und somit eine „metabolische Kälteanpassung" auf zellulärer Ebene. Dieser höhere Energieverbrauch muss auf einer organisatorischen Ebene zwischen Zelle und Ganztier wieder eingespart werden, da ja auf Ganztierebene keine Erhöhung zu erkennen ist. Es ist aber noch völlig unklar, wo und wie das geschieht.

Bisherige Theorien besagen, dass bei verwandten Arten, diejenige mit geringerem Grundstoffwechsel, wie für die antarktische Pilgermuschel gezeigt, einen energetischen Vorteil und eine positive Wachstumseffizienz hat. Der Anteil des Stoffwechsels, der für das somatische Wachstum verwendet wird, wird als Näherungswert für die Wachstumseffizienz betrachtet. Ein Vergleich vieler Arten, die über einen weiten Temperaturbereich leben, zeigt eine deutliche Abnahme der Wachstumseffizienz mit steigender Temperatur. Diese Ergebnisse legen die Vermutung nahe, dass erhöhte Temperaturen die Wachstumseffizienz von Pilgermuscheln beschränken und dieser Nachteil durch evolutionäre Anpassungen nicht vollständig ausgeglichen werden kann.

Meine Ergebnisse zeigen, das viele Pilgermuscheln spezielle Anpassungsmechanismen an lokale Umweltbedingungen entwickelt haben. Die auffälligsten Anpassungen sind zunehmendes Lebensalter und Größe mit zunehmender geographischer Breite. Diese Anpassungen ermöglichen es der antarktischen Pilgermuschel (im Mittel 1.71 ± 0.16), ähnliche Lebenswachstumsleistung zu erzielen wie verwandte Arten aus gemäßigten Breiten, z.B. *Aequipecten opercularis* (im Mittel 2.02 ± 0.11). Die Lebensstrategien der beiden Arten unterscheiden sich. Während die langlebige, antarktische Pilgermuschel zu den A-selektierten Organismen zählt, ist die kurzlebige, schnellwachsende *Aequipecten opercularis* eine r-selektierte Art.

Die von mir angelegte Datenbank „ScallopBASE" ist eine gute Basis für weitere Untersuchungen evolutionärer Anpassungen und Limitierungen bei Pilgermuscheln. Eine Erweiterung der Datenbank (mehr Populationen, genauere Umweltdaten) ist sicherlich notwendig, um das sich ergebende Bild abzurunden und noch bestehende Unklarheiten zu beseitigen.

1 Introduction

1.1 Latitudinal gradients

1.1.1 General aspects

Marine systems differ from terrestrial ones in a number of ways hence paradigms concerning terrestrial patterns of biodiversity may not be applicable to marine situations (Arntz and Gili 2001, May 1994). Compared with terrestrial fauna, marine organisms tend to have larger biogeographic ranges but exhibit distinct latitudinal zonation more frequently, especially in the near-shore environment where physical barriers prevent the migration of littoral species (Pielou 1979, Roy et al. 1994).

The survival of ectothermic organisms, and thus the distribution of species, is closely related to the ambient temperature regime. Ectothermic organisms tolerate fluctuations of the habitat temperature only within certain limits (Willmer et al. 2000). Consequently, drastic as well as gradual climate changes during the Earth's history have always led to new distribution patterns of species. While temperature and global climate variability have been cited as the most important factors governing marine zoogeography (Angel 1991, Hochachka and Somero 2002), other hypotheses may be justifiable, too. Marine species may be confined to biogeographical regions by barriers of physical, geo-morphological, chemical, spatial or biological nature, or by latitudinal gradients in other parameters such as upwelling intensity, productivity and seasonality (Golikov et al. 1990, Vermeij 1991, Turner et al. 1996, Connolly and Roughgarden 1998, Roy et al. 1998, Pörtner 2002a,b).

Owing to the large heat capacity of water, short- and long-term variability of temperature is comparatively low in most marine systems compared to terrestrial and fresh water environments. Due to temperature adaptations marine animals seem to be suited very well to study temperature effects on a global scale. Most global studies are based on between-species comparisons and hence have problems in resolving more subtle differences between closely related species or species subpopulations in a latitudinal cline (e.g. Clarke and Johnston 1999). Therefore closely related species should be compared preferentially in order to reduce taxonomic "noise" and to minimize the risk of otherwise misleading generalisations from global comparisons.

The influence of food availability, temperature and seasonal fluctuations of both parameters on population energy budgets is one focus of recent studies on marine molluscs especially in the light of recent "global warming" (Bayne and Newell 1983, Shumway 1991, Mohnen and Wang 1992, Sokolova and Pörtner 2001, Sukotin et al.

2002). Growth rate and reproductive output integrate the physiological activities of an organism and are considered to be good indicators for the suitability of an environment (Levinton 1983, Lonsdale and Levinton 1985). A corresponding approach is to compare growth and reproduction along some presumed or measured gradient of environmental quality, including latitude (Barber and Blake 1983), water depth (Kautsky 1982a, b, Rodhouse et al. 1984), tidal regime (Griffiths 1981) or habitat type (Bayne and Worrall 1980). Intraspecific variation in growth of bivalves and poikilotherms in general was most frequently studied along latitudinal gradients (Dehnel 1955, Ament 1979, Levinton and Monahan 1983, Lonsdale and Levinton 1985, Conover and Present 1990, Fraser and Currie 1996, Roy et al. 1998). Although latitude has no environmental meaning by itself, it is a proxy for total amount of and seasonality in solar energy input, which translates mainly into temperature but also into primary production and related parameters (Turner et al. 1996, Roy et al. 1998). Surface water (approx. euphotic zone) temperature may serve as a proxy for primary production and food input into the system, too.

In terms of numbers of individuals, ecological bioenergetics, geographical distribution and range of habitats, bivalve molluscs are by virtue a supremely successful group and important members of almost all benthic communities (Kaestner 1993, Westheide and Rieger 1996). A latitudinal comparison of bivalve molluscs life-history parameters would ideally include polar, temperate and tropical sites.

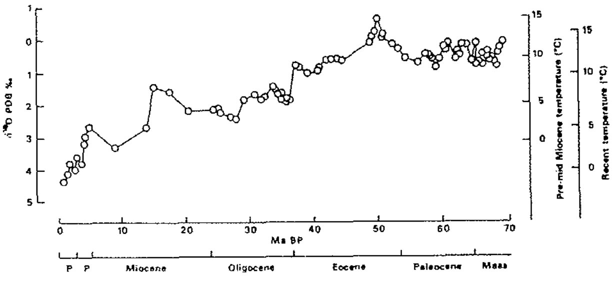

Figure 1.1 Temperature in Southern Ocean derived from oxygen isotope compositions (∂18O) of benthic foraminifera's. Water temperatures are calculated after making corrections for factors such as salinity and ice caps. The modern temperature scale is applicable to present day oceans, the Tertiary temperature scale to samples older than about 15 Ma (redrawn from Clarke 1983).

Since the break-up of Godwin, surface and bottom-temperatures of the Southern Ocean decreased more or less steadily from about 15°C in the Late Cretaceous to the present range, with minimal seasonal variations of roughly +2 to –1.8°C (Fig. 1.1). Hence, Antarctic marine invertebrates has become highly adapted to low temperatures, and also extremely stenothermal (Clarke and Crame 1989, Arntz et al. 1994, Johnston and Bennett 1995, Pörtner et al. 2000, Peck 2002; Pörtner and Arntz 2003). As temperature-linked biogeographic patterns found in nature are not only a clear manifestation of temperature's pervasive effects on all organisms, but also of organisms' success in adapting to thermal variation, a latitudinal comparison provides the opportunity to determine evolutionary adaptations going ahead with species extinction and radiation (Clarke and Crame 1997, Crame and Clarke 1997).

Summary

- Marine organisms show latitudinal gradients in distribution, community composition and diversity.
- Latitude is a proxy for the total amount of and seasonality in solar energy input, hence for changes in temperature and primary production.
- Temperature and food availability have been considered the main factors affecting growth and production in bivalves.
- Comparisons of benthic invertebrate community composition along latitudinal gradients would ideally include polar, temperate and tropical sites to determine evolutionary adaptions.

1.1.2 Growth in bivalves

Individual growth is one major characteristic of most multicellular organisms and, in addition, a basic parameter in studies of population dynamics and stock management (Bayne 1975, Weatherly and Gill 1987, Vakily 1992, Brey 1999, 2001). In bivalve molluscs studies on growth and production have identified different degrees of intraspecific variability at spatial and temporal scales, i.e. macro- and micro- geographic variations, as well as seasonal changes in growth rates (Appeldorn 1983, Beukema and Meehan 1985, MacDonald and Thompson 1985a, b, 1986, Iglesias and Navarro 1990, Richardson 2001). Such variability has always been attributed to environmental effects, mainly to food availability and temperature. The effect of these variables is complex, depending on the specific way in which they affect processes of both energy acquisition and energy expenditure (Bayne and Newell 1983, Griffiths and Griffiths 1987, Wieser et al. 1988, Shumway 1991). Growth processes in molluscs, however, may either be maximized up to physiological/developmental limits or, based on the assumption that high growth rates profit from low levels of baseline costs, be an optimum compromise between the fitness costs and benefits of different growth rates (Sibly and Calow 1986, Bayne and Newell 1983, Parry 1983, Clarke 1987, Hawkins et al. 1998, Bayne et al. 1999). It is discussed that the amount of energy available in an ecosystem is limited; hence the share of an organism in total energy flow offers one of the most rigorous and complete pieces of information about the ecological role of that organism in a system

(Jørgensen 1983, Crisp 1984, Coma et al. 1998). The ecological significance of individual species in the local ecosystem may be defined, among other properties, by their position in the food web and by the amount of energy flowing through the population, not taking into account the potential regulative function of certain trophic interactions. According to Bayne & Newell (1983) and Peterson et al. (1999) the energy flow through a bivalve population is normally represented by the concept of a 'balanced energy budget' (for further details see Chapter 2.2.2, pp 16–17), which requires a thorough evaluation of input (feeding) and outputs (investment of the ingested energy basically for basal metabolism, growth and reproduction). Suspension feeding bivalves are ideal for such studies because available food ratio, food uptake and metabolic losses can be measured and the shell often provides a record of growth history (Seed 1980).

Summary

- Individual growth is a key parameter of population dynamics, e.g. the basis of population productivity and mortality.
- Temperature and food availability are the main exogenous factors affecting growth in bivalves.
- The energy flow through a population can be described by a 'balanced energy budget'.

1.1.3 Physiological aspects

Biogeographic patterns indicate that temperature is besides other (e.g. oxygen, salinity, exposition) one major determinant of habitat suitability (Hochachka and Somero 2002). Distribution patterns of organisms commonly reflect gradients or discontinuities in temperature adaptation. Indeed, temperature affects essentially every aspect of an organism's physiology, from basic structures of macromolecules up to rates of complex physiological systems. Hence, thermal adaptation likely represents a ubiquitous feature of species performance and biological evolution.

Growth is a complex sequence of physiological processes, which are subject to a number of controls and limitations on various hierarchical levels (Wieser 1994, Angilletta et al. 2002). Temperature is most likely the most prevalent environmental factor for those processes (reviewed by Prosser 1991, Hochachka and Somero 2002), but not all of them are equally sensitive to temperature. Certain "bottleneck" processes make growth rates more sensitive to temperature than involved single processes (Angilletta et al. 2002). However, the complexity of growth makes it difficult to determine which particular factor is the strongest in controlling growth rate (Clarke and North 1991, Wieser 1994). As a corollary, physiology may impose constraints on or define trade-offs associated with the evolution of growth rates. Hence, understanding evolution in growth patterns requires knowledge of the physiological basis of the growth-rate variation (Levinton 1983, Present and Conover 1992, Conover et al. 1997).

Recent evidence demonstrates that the first line of thermal sensitivity becomes apparent at the highest functional level possible. Aerobic scope (i.e. the functional co-ordination of oxygen supply mechanisms to cover oxygen demand) limits energy availability and therefore most likely growth (Guderley 1998, Guderley et al. 1997, Frederich and Pörtner 2000, Pörtner 2001, 2002a, b). However, to identify putative mechanisms explaining such limitations and their evolutionary significance is only possible by a comparison of species from systems with oscillating temperature regime (e.g. temperate zones) with species from thermally very stable environments (i.e. deep sea, polar regions). Antarctic species developed specific adaptations to a thermally stable environment over several ten thousand years (Johnston and Bennett 1995, Pörtner 2002a; Fig. 1.1).

Several studies already emphasized mechanisms playing a role in temperature adaptation (e.g. Crockett and Sidell 1990, Somero 1995, Sokolova and Pörtner 2001, for review see Pörtner 2001, 2002a, b). A compensatory increase in SMR (standard metabolic rate) owing to mitochondrial proliferation seems to be the typical short-term answer to cooling (Sommer and Pörtner 1999, Pörtner et al. 2000). Besides changes in the kinetic characteristics of mitochondria and enzymes (Torres and Somero 1988, Crockett and Sidell 1990, Somero 1995, Vetter and Buchholz 1998, Sommer and Pörtner 1999, 2001, Kawall et al. 2002) various other mechanisms have been reported to compensate for the "slow-down" effect of low temperatures including: (i) alterations in intracellular ionic and membrane phospholipid compositions, (ii) quantitative alterations of functional protein levels, (iii) functional differences between isozymes (Hochachka and Somero 1984), and (iv) an increase in mitochondrial densities (Eggington and Sidell 1989, Johnston et al. 1998, Pörtner et al. 1998). Analyses of temperature-dependent changes in enzyme function are traditionally used as a powerful tool in studies of temperature acclimation and adaptation of animals (for details Pörtner et al. 2000, Sokolova and Pörtner 2001, Sukhotin and Pörtner 2001).

Temperature dependent changes are suggested to differ between short-term and long-term adjustments, i.e. cold acclimated (= cold-eurythermal) and cold adapted (= cold-stenothermal) animals (for review see Pörtner et al. 2000, Pörtner 2002a).

Pörtner et al. (2000) postulated a model, which predicts larger metabolic cold compensation in winter acclimated or cold adapted eurytherms compared to stenotherms. The scenario of a secondary reduction in SMR during the evolution of cold-stenotherms in contrast to cold-eurytherms is linked to reduced mitochondrial capacities and increased Arrhenius activation energy of mitochondrial demand, especially proton leakage, and of flux regulating enzymes in metabolism (Guderley 1998, Pörtner 2002a, b, c, Pörtner et al. 2004). These predictions are based on the assumption that Antarctic and Artic stenothermal invertebrates likely evolved from eurythermal ancestors pre-adapted to cold temperature in a latitudinal cline.

Hence, a comparison of species from non-Antarctic environments with their Antarctic relatives will put their characteristics in perspective and allow evaluation of temperature dependent specialisation and limitation with respect to whole animal survival.

Summary

- Temperature adaptation is limited by aerobic scope, which most likely limits individual energy supply and hence energy available for growth.
- Differences in whole-animal performance may or may not be found on lower hierarchical levels (e.g. cellular, molecular).
- Changes in the kinetic characteristics of mitochondria and enzymes reflect differences involved in temperature adaptation and/or acclimation.
- A comparison with Antarctic species, which developed specific features of permanent cold adaptation over ten thousands of years, allows for evolutionary conclusions.

1.2 Why work with pectinids?

The frequent absence of closely related species at high and low latitudes makes comparative work on growth, population dynamics and metabolic adaptations in marine organisms quite difficult (Eastman 1993). As a result, temperature effects per se are often confounded with interspecific differences in other traits, which may play a much stronger role than temperature does (Pierce and Crawford 1997a, b, Somero et al. 1998, Sokolova and Pörtner 2001). Closely related species should be compared preferentially in order to reduce inter-specific "noise" and to minimize the risk of otherwise misleading generalisations from global comparisons.

The bivalve family Pectinidae is among the better-known shellfishes. Pectinids are distributed worldwide and form a supremely successful group of bivalve molluscs. Scallops often play an important role in the structure and function of benthic communities (Brand 1991, Shumway 1991). To date the bivalve family Pectinidae consists of some 400 known living species (Brand 1991) covering a wide latitudinal range as well as water depth related gradients – from Northern Norway (e.g. *Chlamys islandica*) to the tropics (e.g. *Euvola ziczac*) and further south to the Southern Ocean (*Adamussium colbecki*), and from the intertidal zone (e.g. *Argopecten irradians*) down to more than 3,000m water depth (*Bathypecten vulcani*) (LePennec et al. 1990, Brand 1991, Waller 1991). Pectinidae inhabit not only a wide temperature range from –1.9°C up to 30°C, but also environments across a wide range of seasonal temperature amplitudes. They include cold-stenothermal (*steno*, Greek for "narrow"), eurythermal (*eury*, Greek for "wide") and cold-eurythermal species, hence at least one example species for all important temperature adaptation modes.

The term 'scallop' as used in this study applies to bivalves in the superfamily Pectinacea, which are all characterized by an enlargement of the ligament, the resilium. The earliest undoubted member of the Pectinacea is *Pernopecten* (Newell, 1938), which first appears in lower Carboniferous strata (Newell 1969, Waller 1991). All commercial scallop species fall within the family Pectinidae, a monophyletic group characterized by a true ctenolium, which is a row of successively formed denticles along the ventral edge of the byssal notch. The first ctenolium-bearing scallop appeared in the Triassic period during a time of taxonomic restructuring of the marine biota following the great extinction that closed the Palaeozoic Era 230 million years ago (Waller 1978, 1991).

A somewhat unexpected feature for a bivalve representative and perhaps the most striking feature of scallops is their adaptation to a swimming mode of life (Waller 1969, Wilkens 1981). Eyes clearly visible around the margin of the shell (Fig. 1.2) are noteworthy among bivalves and correspond to the free-living mode of life. Scallops utilize their locomotory abilities not only to escape predation, but circumstantial evidence suggests that swimming is used by some species for migration and habitat selection (Morton 1980, Gruffydd 1976, Wilkens 1981).

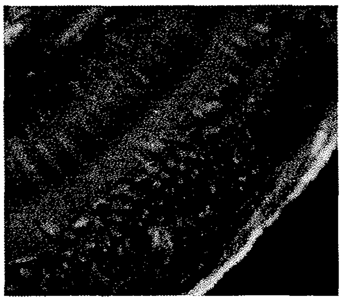

Figure 1.2 *Adamussium colbecki.* Mantle edge with tentacles and eyes.

Many pectinid species are of considerable economic importance (Fig. 1.3) and support both commercial fisheries and mariculture efforts, which may explain the

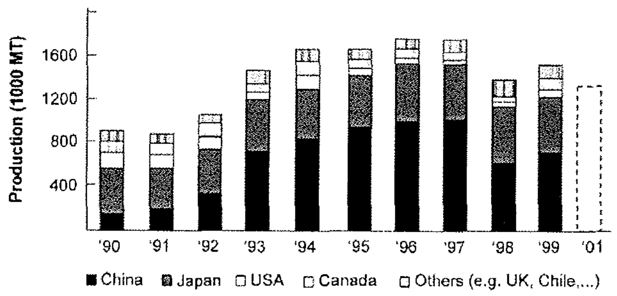

Figure 1. 3 Scallop world meat production by major producing countries from 1992 to 1999. (FAO-Fishery Statistics)

tremendous amount of scientific research focussed on this family (for review see Shumway 1991).

Despite their worldwide occurrence, species which are of large enough body size and occur in sufficiently dense aggregations to be commercially exploited (Table 1.1), are found mostly in high latitudes between about 30° and 55° in both the northern and southern hemisphere (Fig. 2.6, Annex Tab. 7.1, 7.2). Among the twenty-eight species of pectinid bivalves from European waters (Nordseik 1969) five species are commercially used (Ansell et al. 1991, Table 1.1). Generally more than 80% of total flesh meat production comes from aquaculture; cultured proportion is close to 100% in some countries, e.g. China and Japan. Total value of world production in 1999 was about 571 million US$. *Mizuhopecten yessoensis* (Fig. 1.4c) is by far the most important commercial species.

Table 1.1 Occurrence of major commercially important scallop species divided by geographical regions (modified after Brand 1991). The closest inferred regional relationships are within clusters of species separated by narrow lines. Species from European coasts are marked with an asterisk. Ratio of total world production is taken from the FAO-Fishery Statistics.

Geographical region	Species	% of world production (~1350 MT 2001)
North Atlantic	*Aequipecten opercularis**	1.1
	*Mimachlamys varia**	<0.1
	Pecten maximus //Pecten jacobeus**	1.6
	Placopecten magellanicus	13.2
	Argopecten gibbus	<0.1
	Argopecten irradians	<0.1
Subarctic	*Chlamys islandica**	0.5
North Pacific	*Patinopecten caurinus*	0.1
	Mizuhopecten yessoensis	77.5
Southern hemisphere	*Amusium balloti*	<0.1
	Amusium pleuronectes	<0.1
	Pecten novaezelandiae	0.4
	Pecten fumatus	<0.1
	Chlamys asperrimus	<0.1
	Argopecten purpuratus	1.5
	Argopecten circularis	0.2
	Zygochlamys patagonica	2.2

In conclusion, pectinids represent a prime object for the analysis of empirical relationships between environmental and biological parameters. Populations from various locations along latitudinal or climate gradients may display more or less continuous transition patterns and thus may allow to identify the key physiological parameters affected by temperature and/or ecological patterns (chapter 2.1, p 12).

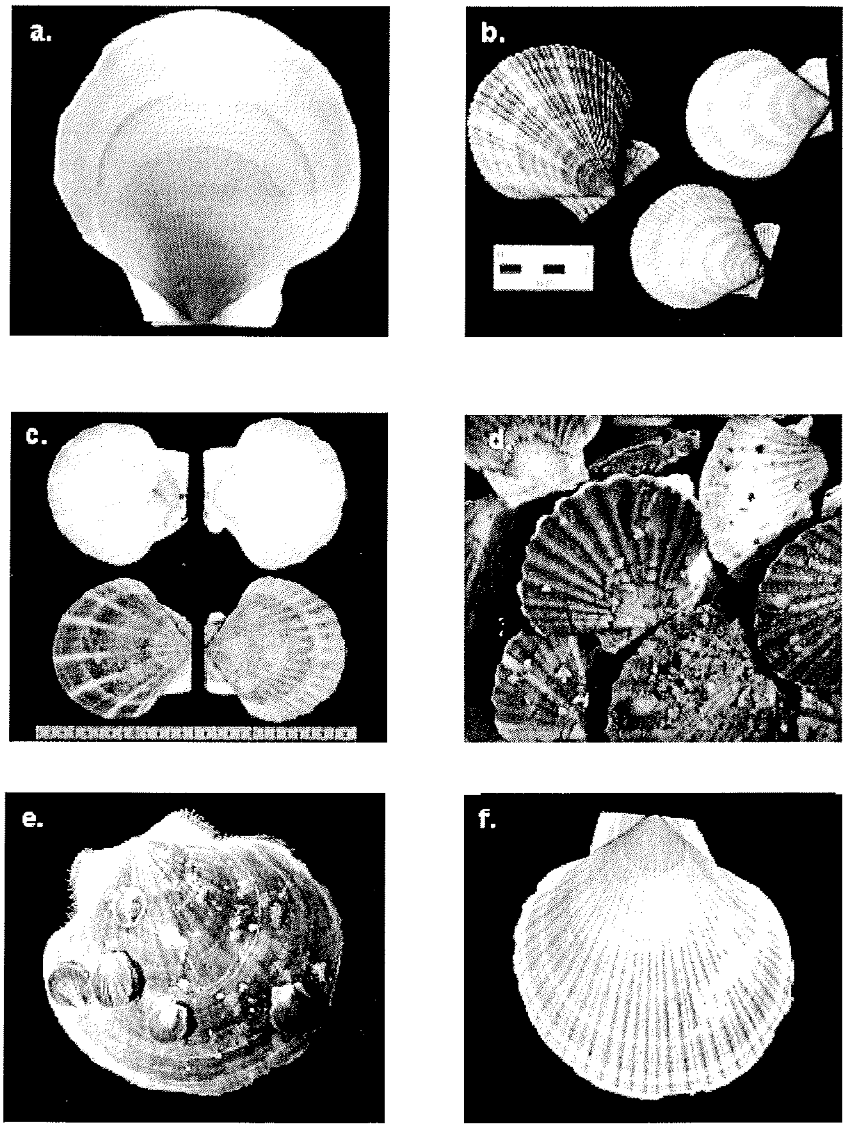

Figure 1.4 Pictures of commerically important species (**a-d**) and species investigated in this study (**e-f**): **a.** *Placopecten magellanicus*, **b.** *Chlamys islandica*, **c.** *Mizuhopecten yessoensis*, **d.** *Pecten maximus*, **e.** *Adamussium colbecki*, **f.** *Zygochlamys patagonica*.

Summary

- To identify physiological and ecological patterns along a latitudinal gradient closely related species should be compared preferentially in order to reduce taxonomic "noise".
- The family Pectinidae consists of approx. 400 known species with a wide latitudinal distribution covering a wide temperature range.
- Due to the considerable commercial importance of scallops a tremendous amount of data for inter- and intraspecific comparison is available.

1.3 Aims of this study

The basic problem in making comparisons between different populations or species is to measure precisely the same thing in each study. Despite the tremendous amount of information on growth and metabolism available in the literature (see chapter 2.4), own experiments with standardized techniques were performed on three species (*Adamussium colbecki, Aequipecten opercularis, Zygochlamys patagonica*) to make at least these data comparable without any constrictions and fill existent gaps within the ecological temperature range.

Having in mind that natural habitat characteristic such as salinity, sediment type and depth also influence the growth of marine animals; the major aim of this study is to evaluate the relation between geographic latitude and growth as well as basic physiological parameters of scallops. The following aspects have been investigated:

(i) How are individual growth and population parameters related to latitude? Do the observed patterns allow the identification of a simple key factor (e.g. annual solar energy input and/or average water temperature)?

(i) Can we identify evolutionary compensation effects by a comparison of taxonomically closely related species and populations across a wide temperature range?

(i) Does the Antarctic scallop, *Adamussium colbecki*, show any signs of metabolic adaptions specific to the Antarctic environment?

While the main objective of this study is to look how temperature influences growth and physiology on higher levels, a small part of this thesis looks deeper to get a first glance on cellular adaptations. The aspect I have attended in this study is:

(i) Are there any specific adaptations of cellular performance within coldstenothermal scallops compared to lower latitude counterspecifics?

2 Material and Methods

In order to study the influence of temperature on growth within the worldwide-distributed Pectinidae this study combines ecological observations (e.g. growth, productivity) and some physiological measurements (e.g. standard metabolic rate).

Temperature can essentially affect organisms on different hierarchical levels (molecular, cellular, up to complex physiological processes of the organism/ population, e.g. growth) (Fig. 2.1). Studies of complex integrated processes such as growth or respiration do not necessarily give useful information concerning cellular effects of temperature. Growth, for example, may show compensation at the molecular level but still be slow for other reasons (for example, resource limitation).

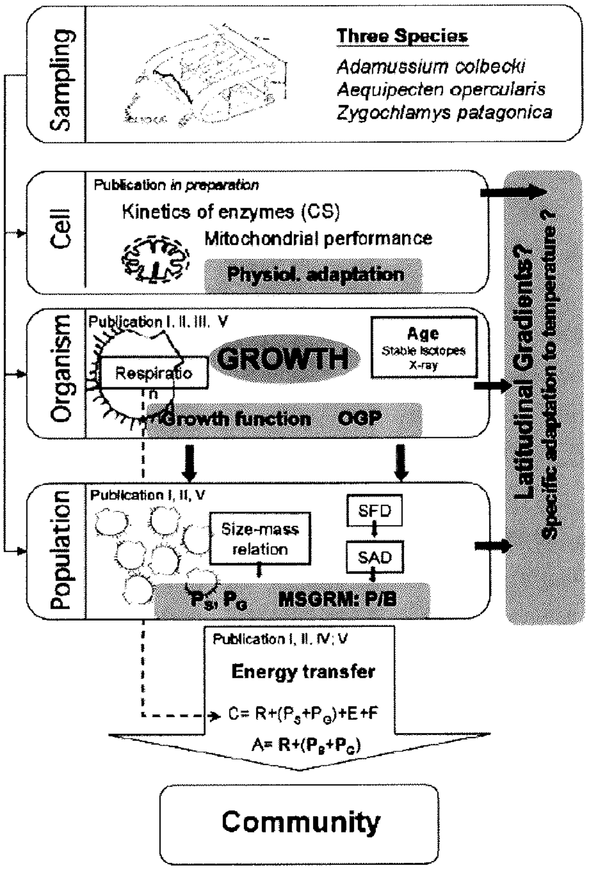

Figure 2.1 Flow chart demonstrating the hierarchical levels of life, which are possibly affected by temperature and the corresponding parameters investigated in this study. (**A**: assimilation; **C**: consumption; **CS**: citrate synthase; **E**: excretion; **F**: faeces; **MSGRM**: mass-specific growth rate method; **OGP**: Overall growth performance; P_G: gonad production; P_S: somatic production; **R**: respiration; **SAD**: size-at-age data; **SFD**: size-frequency data)

In the following, I will briefly present methods used and species investigated. A more detailed description can be found in the publications (chapter 5, pp 49 ff).

2.1 Species under investigation

For this study I choose the following three species, each of them characteristic for one particular temperature regime.

2.1.1 Adamussium colbecki – low-temperature no-amplitude regime

The endemic Antarctic scallop, *Adamussium colbecki* (Smith, 1902), is a common and often abundant member of the Antarctic nearshore fauna with a circumpolar distribution (e.g. Berkman 1990, Nakajima et al. 1982, Cattaneo-Vietti et al. 1997, Albertelli et al. 1998, Chiantore et al. 2000). In patches *A. colbecki* may be covering up to 100% of the bottom (Fig. 2.2). Highest densities are found above 100 m water depth (Chiantore et al. 2001), but single animals have been reported from depths down to 1500 meters (Dell 1990). This may explain why, despite an extensive sampling and research programme, only few living specimens are recorded in the Weddell Sea (Hain 1990, Linse 1997). Assemblages of scallops are expected in shallower waters, which are consequently covered by the shelf ice (Hain 1990, Arnaud and Hain 1992).

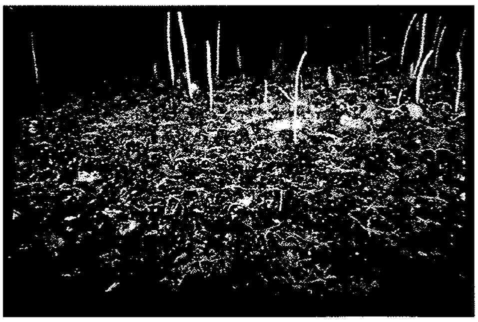

Figure 2.2 *Adamussium colbecki* bed close to the British Antarctic station 'Rothera' (photo: A. Starmans, AWI, Bremerhaven).

As one of the most common bivalves in the Southern Ocean (Dell 1990, Hain 1990), *Adamussium colbecki* has been considered as a potentially exploitable benthic marine living resource (Stockton 1984, Berkman 1990). However, estimates of yield per recruit indicate that relatively low levels of fishing pressure could cause a collapse of Antarctic scallop populations (Berkman 1990).

Adult individuals can be found on sand, hard rock and gravel substrates (Nicol 1966), while juveniles are commonly attached by byssus to the adults or to other objects such as macroalgae or hard substrates (Nigro 1993, Chiantore et al. 2000). Antarctic scallops reach sexual maturity and detach from adults (or substrate) at a size of 40 to 50 mm and at an age of three to five years. Main growth of soma, gonad and gametes takes place during austral summer (Cattaneo- Vietti et al. 1997, Chiantore et al. 2000, 2002). *A. colbecki* is dioecious (Soot-Ryen 1951, Berkman 1990); prior to spawning sex of mature specimens can be determined by gonad colour (Chiantore et al. 2002). Spawning seems to take place in austral autumn, as confirmed by histological observations of oocyte diameter and male gonads (Chiantore et al. 2001). Small egg size and low ratio between first and second prodissoconchs suggest the occurrence of planktotrophic larvae (Berkman et al. 1991), although there are no data concerning the length of the larval stage (Chiantore et al. 2000).

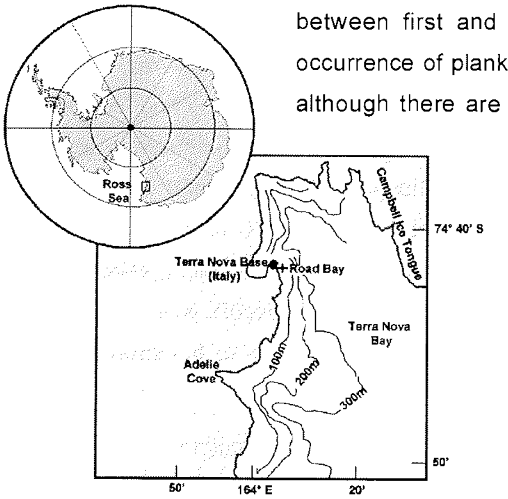

Figure 2.3 Study area in the Ross Sea (Antarctica), close to the Italian Base.

For this study specimens of *A. colbecki* were collected in January and February 2000 from sites near the Italian Antarctic station 'Terra Nova Bay' (Road Bay 74°41.9' S, 164°07.5' E, Fig. 2.3) either by scuba diving or with a naturalist's dredge (mesh size 15 x 15 mm in the cod end). Largest densities of *A. colbecki* were found between 40 and 70 m depth, where the population reaches an average density of 58 ind m^{-2} and is mainly dominated by large-sized adult individuals (Chiantore et al. 2001). After sampling, animals were immediately transported to the flow-through aquaria at the station, where they were maintained under ambient conditions (0 to +0.5°C, 34 psu, natural seston levels and light regime) until experimental use at 'Terra Nova Bay'. At the end of February 100 scallops were transported by plane to the Alfred Wegener Institute (AWI, Germany) for further experiments. They were maintained in cooled aquaria with recirculating seawater (0 ±0.5 °C, 33- 34 psu) in a 12 h dimmed light: 12 h dark daily light regime, until used in experiments.

2.1.2 Aequipecten opercularis – temperate high-amplitude regime

The commercially exploited queen scallop *Aequipecten opercularis* (L.) occurs throughout a wide geographical range on the European continental shelf: from northern Norway to the Mediterranean and from the Adriatic to the west of Ireland (Broom 1976, Brand 1991, Waller 1991). Recruitment success and spatial distribution appear to be highly variable in time, thus inducing major year-to-year changes in extent and position of scallop banks of exploitable size and density as reported from British waters (Broom 1976, Brand 1991), the eastern part of the English Channel and from northern Brittany (Grainger 1992, Goulletquer and Heral 1997). Therefore, and owing to the relatively short time *A. opercularis* can be kept fresh (Ansell et al. 1991), queen scallops support only a small local fishery (Tab. 1.1) In France queen scallops are about 1/8 of total French scallop landings (Grainger 1992).

For this study specimens were collected with a small dredge (25mm x 25mm mesh size) in the western English Channel next to Roscoff (Trezen Vraz, 48°59' N, 4°53' W) in 60 to 80 m water depth at three dates (February, June and October) in 1999. The investigation area, especially the distribution of substrate types and phytoplankton is described in Sagan and Thouzeau (1998). Water temperatures varied seasonally between 9°C in January/February and 16°C in August; hence *A. opercularis* can be viewed as an eurythermal species. After sampling, animals were immediately transported to the 'Station Biologique de Roscoff' where they were maintained in flow-through aquaria until used in experiments or transported to the Alfred Wegener Institute (AWI, Germany).

2.1.3 Zygochlamys patagonica – cold-temperate low-amplitude regime

The Patagonian scallop, *Zygochlamys patagonica* (King and Broderip, 1832), is distributed around the southern tip of South America from 42° S in the Pacific to 35° S in the Atlantic, between 40 and 200 m depth (Waloszek and Waloszek 1986, Lasta et al. 2001). While scallop grounds on the Pacific side are situated in relatively shallow waters (Andrade et al. 1991), Atlantic grounds are oceanic, the most important beds being located along the 100m isobath with a small annual temperature amplitude (6- 7°C, Fig. 2.4; Lasta and Bremec 1998, Valero 1999, Schejter et al. 2002).

Sexes are separate in *Zygochlamys patagonica*, with a low incidence of hermaphroditism (Waloszek and Waloszek 1986). Sexual maturity is reached at approx. two years (~45mm shell height, Orensanz et al. 1991b). Gonad maturation occurs from spring to early summer, and spawning takes place from August to September (Lasta et al. 2001). Since 1996 the species has been commercially explored on the Argentinean and more recently on the Uruguayan shelves (Lasta and Bremec 1998, Gutiérrez and Defeo 2003).

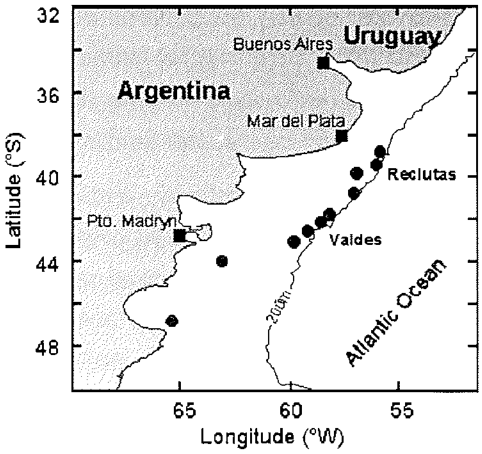

Figure 2.4 Position of major banks of *Zygochlamys patagonica* (grey dots) on the Argentinian shelf. The bank "Reclutas" (black dot) is subject of this study.

Summary

- Species under investigation are characteristic of specific temperature environments.
- The three species cover a wide temperature range from –1.9°C to +17°C (minimal and maximal seawater temperature).
- The prevalence of an Antarctic species provides the possibility to evaluate evolutionary adaptation and acclimation mechanisms.

2.2 Population dynamic parameters

2.2.1 Analysis of growth and age

Traditionally individual age and growth rate of bivalves are inferred from shell growth marks, either macroscopically visible external or internal bands (i.e. by acetate peels, X-ray-photographs, see Fig. 2.5) (e.g. Merrill et al. 1965, Lutz and Rhoads 1980, Dare 1991, Cattaneo-Vietti et al. 1997, for review see Richardson 2001). Such banding patterns reflect cyclical changes in growth rate, which may be coupled to external cycles such as day-night rhythm, tides, or seasons (affecting spawning, food availability, temperature). The temporal (usually annual) pattern of growth band formation has to be verified independently, e.g. by a mark-recapture experiment (e.g. publication III, p 81) or by a stable-isotope analysis (publication I, p 51 and V, p 97; Krantz et al. 1984, 1987, Dare and Deith 1990, Hickson et al. 1999).

I used a 2-step procedure to identify and verify annual growth bands in the three investigated scallop species, (i) identification of external growth bands and (ii) validation of annual formation of these bands by analysis of stable oxygen ($\delta^{18}O$) and carbon isotope ($\delta^{13}C$) ratios along the growth trajectory of the shell (publication I, pp 51-64 and V, pp 97-112). $\delta^{18}O$ and $\delta^{13}C$ in biogenic $CaCO_3$ reflect ambient water temperature and primary production at the time of carbonate formation. Therefore isotope ratio profiles in shells are records of biological variation in temperature and primary production (see Wefer and Berger 1991, Schöne 2003). In environments with seasonal cycles in temperature and/ or primary

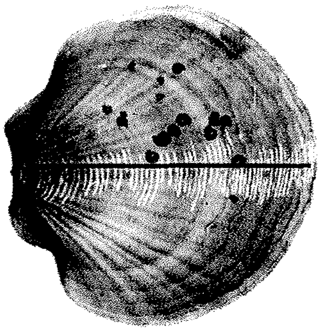

Figure 2.5 X-ray photograph of *Adamussium colbecki* showing annual growth marks (conspicuous rings of higher density) and sampling lines of shell carbonate for isotope analysis (white lines) along the height axis of the shell (black line).

production such isotope ratios can be used to validate whether or not identified shell growth bands are formed at regular (annual) intervals (for review see Richardson 2001, Owen et al. 2002a).

Growth was modelled by fitting a von Bertalanffy growth function (VBGF) to the resulting size-at-age data pairs (eq. 1)

$$H_t = H_\infty \bullet (1 - e^{-K \bullet (t - to)})^D \quad (1)$$

where H_t is shell height at time t, H_∞ is mean asymptotic shell height, K is the Brody growth coefficient, D determines the shape of the curve (inflection point if $D>1$) and t_o is the age when shell height equals zero. K and H_∞ are both affected by many factors, e.g. environmental condition, sampling procedures, type of data (size frequency, mark-recapture, annual growth marks), and the mathematical and computing procedures used.

A direct comparison of growth patterns by either of the two parameters K and H_∞ alone may be mathematically feasible but is not plausible biologically, as K is negatively correlated with asymptotic size H_∞. Therefore, a composite parameter, the overall growth performance (OGP) index P,

$$\text{OGP } P = \log(K \bullet M_\infty) \quad (2)$$

was used to compare growth patterns. K and M_∞ (= a $\bullet$ $H_\infty{}^b$; asymptotic mass) are parameters of the corresponding VBGF (for more details Pauly and Munro 1984, Moureau et al. 1986, Brey 2001). As size mass relations were not available for all 82 populations taken from literature (see section 2.4), M_∞ was computed from H_∞ (mean asymptotic shell height, taken from the appropriate VBGF) and a common size-mass relation for scallops derived from 46 studies ($\log(M_\infty) = -4.38 + 2.846 \bullet \log(H_\infty)$; unpublished data compilation). According to a study of Feldman and McMahon (1983) this method is not expected to cause a statistical artefact.

2.2.2 *Energy budget and productivity*

According to Bayne & Newell (1983) and Peterson *et al.* (1999) the energy flow through a population can be expressed by:

Consumption (C) = Production (P_{Tot}) + Respiration (R) + Excretion (E) **(3)**

Ingested energy (C) is primarily channelled into growth (P_{Tot} = sum of somatic, P_S, and gonad production, P_G), maintenance metabolism (R) and excretion (E). In the present study total production and respiration were quantified, while other information needed to balance the energy budget for the three species was taken from the literature (for details: publication I, pp 51-64, publication V, pp 97-112, chapter 3.3). As it is especially difficult to identify and simulate true environmental feeding conditions, assimilation was determined indirectly as the sum of production and metabolic expenditure (A=P+R; see Dame 1972, Iglesias and Navarro 1991; Urrutia et al. 1999).

Population energy budgets are acutely sensitive to spatial and temporal changes in size and age composition as well as to changing environmental conditions (Calow 1977, Humprehys 1979). Therefore, it is necessary not only to establish values for the components of the balanced energy equation for different-sized individuals within a population, but also to integrate these with information on the size class structure, production, and mortality of the population in the field (see Crisp 1984). Food availability is translated in standing stock, which together with differences in population density may explain the enormous variation of the C value in different populations (Griffiths 1981, Griffiths and Griffiths 1987, MacDonald 1988). However, as discussed in Griffiths and Griffiths (1987), it still may be instructive to compare results obtained for different species. An estimate of production is useful in assessing the share of marine bivalve populations in the energy flow through their ecosystem (Rodhouse 1979, Griffiths 1980, 1981, Vahl 1981b). In addition, net ($K_2 = P_{Tot}/A$) and gross ($K_1 = P_{Tot}/C$) growth efficiencies as well as the population turnover ratio (P/B) can indicate the suitability of a certain habitat (Bayne and Worrall 1980). The potential to allocate food energy into growth is not only of importance for aquaculture but may also be applied as an independent condition index and allows a better comparison of growth strategies and adaptations to specific environmental conditions (Lucas and Beninger 1985).

Mean biomass (*B*) of the three investigated populations was calculated based on abundance data from the literature and mean body mass from my data. Annual production and P/B ratio of each population were either computed from mortality rate (Z) and the relation $Z \approx P/B$ (Allen 1971, Brey 1999, 2001: *A. opercularis*, publication V, pp 95-110) or by the mass-specific growth rate method (MSGRM, Crisp 1984; *A. colbecki*, publication I, pp 51-64, *Z. patagonica*, chapter 3.3), which combines size-frequency data (SFD), the growth model (VBGF) and the corresponding size-body mass relationship.

Summary

- Age of individual animals was determined by shell growth band analysis.
- Annual formation of growth bands was validated by stable oxygen and carbon isotope ratios in shell carbonate.
- Individual growth was modelled with the von Bertalanffy growth function.

- The overall growth performance (OGP) index P was used to compare growth performance among populations.
- A simple energy budget of the form $C = P_{Tot} + R + E$ was calculated for all three populations.
- P/B ratios were estimated from the mass-specific growth rate method or by $Z \approx P/B$.
- To make energy budgets comparable net growth (K_2) and gross growth (K_1) efficiencies were calculated.

2.3 Physiological measurements

2.3.1 Standard metabolic rates of whole animals

Oxygen consumption is an indirect measure of the metabolic rate, or rate of energy expenditure, of an animal. I measured metabolic rates of whole animals in an intermittent-flow respirometer as described by Forstner (1983) and as used previously by various authors (i.e. Wieser et al. 1988, van Dijk et al. 1999, Gatti et al. 2002, for a detailed description see publication II, pp 65-80).

After sampling scallops were maintained in recirculating seawater at ambient temperature and salinity until further use. To measure as close as possible to standard (resting) metabolic rates (as defined by Bayne et al. 1976), animals were prepared as follows prior to measurements: (i) deprivation of food for at least 3 days in order to minimise the effects of specific dynamic action of feeding (Wieser and Medgysey 1990), (ii) avoidance of handling stress by allowing the animals to accommodate at least 24-36 h to the respiration chambers and (iii) monitoring of animal position in chambers to disregard measurements of active animals. Further or deviating experimental conditions are described in the corresponding publication (publication II, pp 64-78, V, pp 95-110).

2.3.2 Mitochondrial respiration

Mitochondrial function is a significant component of respiratory demand. There are several properties of mitochondrial respiration that provide insights into the thermal tolerance limits of mitochondrial ATP generation. Therefore, I measured the capacity of mitochondrial energy production, mitochondrial proton leakage, mitochondrial coupling ratios, and ADP/O-ratios in isolated gill mitochondria of *A. colbecki* and *A. opercularis* following a modified procedure by Pörtner et al. (1999). Thermal sensitivity of mitochondrial respiration was characterised by Arrhenius breakpoint temperatures and activation energy.

2.3.3 Enzyme activity

To estimate enzyme capacities of aerobic metabolism I analysed citrate synthase (CS), a key regulatory enzyme in the tricarbonic acid cycle. A modification of the procedure from Sidell et al. (1987) was used to measure the citrate synthase activity (CSA) in gill tissue of *A. colbecki* and *A. opercularis.*

2.3.4 Data analysis

Mass-dependent effects were removed from the physiological measurements (Bayne et al. 1999, Packard and Boardman 1999) using mass exponents (from the allometric relationship between each physiological rate and body mass) in the following equation:

$$\text{Standardised rate} = \text{Observed rate} \times (\text{Standard mass}/\ \text{Observed mass})^{b} \qquad (4),$$

where b is the corresponding allometric exponent in the equation describing physiological rate as a function of body mass.

Potential temperature effects were modelled by an Arrhenius equation:

$$R_b = A \bullet e^{(-\mu/RT)} \qquad (5)$$

where R_b is the physiological rate, A a constant, μ the Arrhenius constant and R the universal gas constant. Thus a plot of lnR_b against $1/T$ yields a straight line of slope $-\mu/R$. The apparent energy of activation (E_a) equals the slope of the plot ($E_a = -\mu/R$). The Arrhenius breakpoint temperature (ABT), which indicates a significant change in the slope (i.e. in E_a), was determined using an algorithm for fitting two-segmented linear regressions (for details see Yeager and Ultsch 1989). An alternative measurement of temperature sensitivity of physiological parameters is the Q_{10} value, which was calculated according to

$$Q_{10} = [R_{b(T2)}/R_{b(T1)}]^{10/(T2-T1)} \qquad \mathbf{(6)}$$

where $R_{b(T2)}$ and $R_{b(T1)}$ are the physiological rates at T_2 and T_1, respectively.

Summary

Physiological adaptations of scallop species were measured at different hier-archical levels (whole animal → cellular):

- Standard (resting) metabolic rates at environmental temperatures.
- Thermal sensitivity of mitochondrial oxygen demand.
- Adaptation and kinetics of key enzymes (i.e. citrate synthase).

2.4 Data from the literature

To determine whether latitudinal gradients exist for growth rates and physiological parameters of scallops, data from the literature were added to the information referring to the three species investigated here. Suitable data collected were: (i) growth (i.e. maximum age, maximum body mass, growth function type and parameters), (ii) productivity (i.e. biomass, production, P/B ratio), (iii) physiological parameters (i.e. oxygen consumption rates) and (iv) environmental parameters of sampling sites (i.e. water depth, water temperature). Parameters not provided directly in the respective publications were derived from information given in figures and tables. 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 scallop mortality.

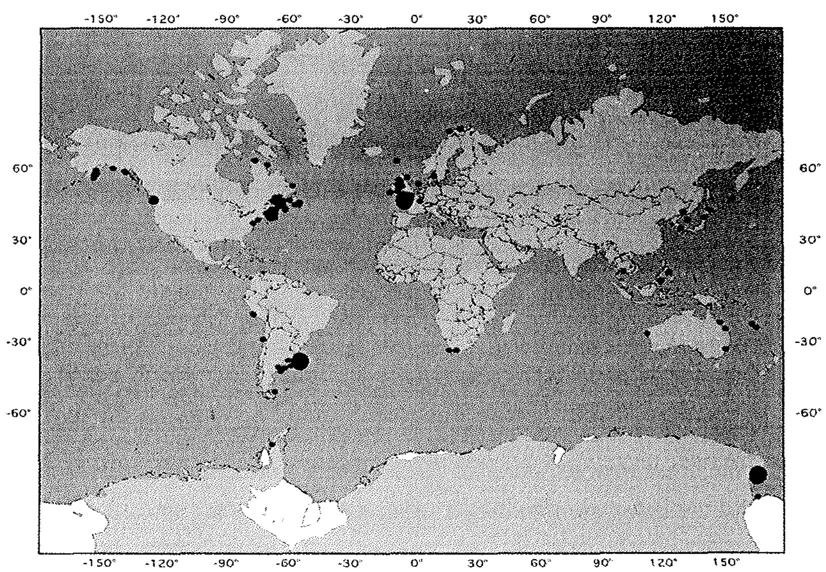

Figure 2.6 The map shows the distribution of all population from the literature survey (N= 226, small red dots; Annex Tab. 7.1, 7.2) and the three populations investigated in this study (black dots).

Unfortunately, there are few studies, which cover all those aspects of scallop life required for this comparison synoptically. Most publications deal with only one certain aspect of the ecology/ecophysiology of one certain scallop population, e.g. either population dynamics (growth and/or productivity) or ecophysiology (respiration, metabolism).

Water temperatures if not provided by the studies themselves were approximated by the average annual value for this geographical position obtained from the online version of the 'World Ocean Database 2001' provided by the National Oceanographic Data Centre (www.nodc.noaa.gov/OC5/WOD01/pr_wod01.html).

At present my database (ScallopBASE) includes data referring to 226 studies of 26 different species (Fig. 2.6, Annex Tab. 7.1, 7.2). More details of data transformation/ computation are given in the corresponding publications (publication II, pp 64-78: calculation of standard metabolic rates from population average or individual values; publication I, pp **68** and V, pp **100**: calculation of overall growth performance).

Summary

The literature survey provides information of:

- 226 studies from 122 populations of 26 scallop species worldwide.
- 198 studies of 26 species for growth and productivity calculation.
- 82 studies of 13 species for calculation of metabolic rates.

An online-version of ScallopBASE is in preparation and will be available on the AWI Homepage end of 2003.

3 Results

The following chapter summarizes the published and some unpublished results of this study. More details for *A. colbecki* and *A. opercularis* are given in the five publications (chapter 5, p 49 ff), while hitherto unpublished results of *Z. patagonica* are shown in chapter 3.3 in more detail.

3.1 Population dynamic parameters

In order to determine the degree of intraspecific variation of population dynamic parameters and energy budgets at the population level I combined growth parameters with measurements of biomass, age structure and density estimates. The results regarding the three pectinid species are briefly summarized in Table 3.1.

Table 3.1 Summary of characteristic population dynamic parameters of the three investigated pectinid populations. (for Abbreviations see p IV)

	Adamussium colbecki	***Aequipecten opercularis***	***Zygochlamys patagonica***
	publication I, II, III	publication V	Chapter 3.3
Von Bertalanffy Growth Function			
K $[y^{-1}]$	0.114	0.604	0.419[1]
H_∞ [mm]	108.9	58.9	74.7[1]
t_0	-0.367	-0.235	-0.314[1]
D	1.264	1.000	1.000[1]
Overall Growth Performance			
P	1.78/ 1.70/ 1.59[3]	1.74	1.88
Production, Productivity			
B $[kJ\ m^{-2}\ y^{-1}]$	1179.64	11.21	365.42
N $[ind\ m^{-2}]$	60	0.82	24
P_S $[kJ\ m^{-2}\ y^{-1}]$	234.6	19.74	176.51
P_G $[kJ\ m^{-2}\ y^{-1}]$	70.92	0.979	24.26
P_{Tot} $[kJ\ m^{-2}\ y^{-1}]$			
P_S/B	0.199	1.761[2]	0.483
P_G/B	0.052	0.079	0.01
P_{Tot}/B			
Z $[y^{-1}]$	-	1.761	1.5[1]
Energy Budget			
R $[kJ\ m^{-2}\ y^{-1}]$	1558	24.89	1073.89
A $[kJ\ m^{-2}\ y^{-1}]$	2167	45.61	1274.66
C$[kJ\ m^{-2}\ y^{-1}]$	6000	126.7	2923.5
K_1=P/A	0.14	0.45	0.16
K_2=P/C	0.05	0.16	0.07

[1] from Lasta et al. (2001) [2] Z= P_S/B (see publication V, pp 97-112)

[3] TNB 1999/2000/ TNB 2000/2001/ BHV 2000/2001; for more details see publication I, pp 51-64, and publication III, pp 71-86

Summary

- Size-at-age data were used to establish a Van Bertalanffy growth function for *A. opercularis* and *A. colbecki*. (Growth bands were validated by stable oxygen and carbon isotope analyses).
- *A. colbecki* shows the lowest growth parameters values.
- *A. colbecki* showed the highest biomass and abundance but the lowest turnover ratio.

3.2 Physiological parameters

3.2.1 Whole organism metabolic rates

Metabolic rates, estimated as the rate of oxygen consumption (VO_2), were measured over the complete size range of scallops available at the three investigation sites. The temperature range examined approximates the annual range encountered by the scallops in their natural waters, with the exception of *Zygochlamys patagonica* where further acclimation temperatures were chosen. The allometric relationships between soft tissue dry mass (DM) and metabolic rates (VO_2) of the three species are given in Table 3.2.

Table 3.2 Metabolic rates (measured as oxygen consumption, $\mu l\ O_2\ ind^{-1}\ h^{-1}$) of the three scallop populations investigated in this study.

Temp [°C]	Remarks	M	$VO_2 = a \bullet DM^b$ a	b	DM range min	max [g]	N
A. colbecki ([a]publication II, pp 64-78, [b]Heilmayer and Brey, 2003b)							
0.3	Summer[a]	D	0.145	0.911	0.110	4.146	235
0.3	Immature[b]	D	0.125	0.780	0.100	0.800	56
0.3	Mature[b]	D	0.151	0.855	0.700	4.146	153
0.0	Winter[a]	D	0.097	0.717	0.266	2.556	35
A. opcerularis (publication V, pp 95-110)							
12.4	June 1999	D	0.179	0.654	0.127	1.810	72
14.4	October 1999	D	0.256	1.014	0.469	1.460	101
10.3	Winteracclimation	D	0.194	0.707	0.061	0.707	101
Z. patagonica (Heilmayer et al. 2001)							
3.0	Acclimation	D	0.212	0.602[1)]	0.080	0.83	20
6.0	Normal	D	0.329	0.617	0.151	1.91	17
9.0	Acclimation	D	0.426	0.811[1)]	0.064	1.92	36

[1)] excluded from calculation of mean values

The scaling exponent *b* of these relationships varies between 0.617 and 1.014 (mean= 0.787, excluding *Z. patagonica* values at acclimation temperatures). The near proportionality between metabolism and body mass (b= 1) in summer animals of *A. opercularis* and *A. colbecki* suggests that high tissue growth rates were supported by proportionally high metabolic rates (Jorgensen 1988, Wieser 1994, García-Esquivel et al. 2001). The mean value closely approximates the 0.727 estimated for bivalves (Bayne and Newell 1983) and the 0.75 coefficient which has been shown to be appropriate for metabolic scaling relationships across a broad taxon range (Hemmingsen 1960, Willmer et al. 2000). A common relation between body mass and temperature on metabolic rate for all three species can be described by the multiple linear model:

$\log(VO_2) = -0.857\ (\pm\ 0.10) + 0.820\ (\pm\ 0.19) \cdot \log(DM) + 0.019\ (\pm\ 0.001) \cdot T;$

$N= 573$, $r^2 = 0.764$, $F= 930.765$, $p< 0.001$, temperature in °C. The equation obtained explains 76% of total variation in metabolic rate.

3.2.2 Cellular performance

The adjustment of aerobic scope, reflected by mitochondrial capacities was identified as a crucial step in previous studies, therefore mitochondrial respiration rates and enzyme activities of citrate synthase (CS) were analysed for the cold stenothermal Antarctic scallop and the eurythermal Queen scallop. CS was choosen as an indicator for citric acid cycle.

Mitochondrial respiration rates (nmol O min^{-1} mg $protein^{-1}$; state III, state IV and state IV_{ol}) increased significantly with rising temperature (data not shown). Comparison between species revealed distinctly lower

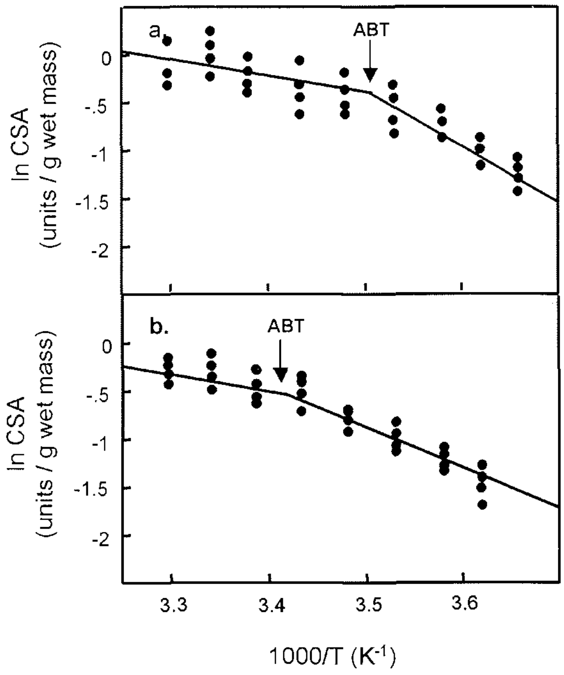

Figure 3.1 Temperature dependence of citrate synthase activity (CSA) in gill from **a.** *A. colbecki* and **b**. *A. opercularis*. Arrhenius-break-temperatures (ABT) calculated by the method of continuous two-phase regressions are indicated by arrows. ABT (*A.colbecki*)=12.28° C; ABT(*A. opercularis*)= 19.41° C.

respiration rates for the Antarctic scallop compared to the Queen scallop. The maximum state III respiration for A. colbecki was 6.01 nmol O min^{-1} mg $protein^{-1}$ and 15.31 nmol O min^{-1} mg $protein^{-1}$ for A. opercularis. In the investigated temperature range a discontinuity in the Arrhenius plots, and therefore an Arrhenius break temperature (ABT) was found in respiration rates (*A. colbecki*: 11.35° C; *A. opercularis*: 20.23° C). Q_{10} values and Arrhenius activation energies (E_A) were even in the same range of magnitude in both species (Tab. 3.3).

Table 3.3 Thermal sensitivity of mitochondrial respiration and citrate synthase in gill mitochondria of *Adamussium colbecki* and *Aequipecten opercularis*. All values are calculated for the temperature range 0° -30° C for *A. colbecki* (n=5) and 3° -35° C for *A. opercularis* (n=5) (means ± standard deviation).

	A. colbecki		***A. opercularis***	
	Q_{10}	E_a [kJ mol^{-1}]	Q_{10}	E_a [kJ mol^{-1}]
Mitochondrial respiration				
State III	2.41 ± 0.4	34.8 ± 8.3	1.53 ± 0.6	42.41 ± 0.4
State IV	3.01 ± 0.8	46.3 ± 15.4	2.41± 0.4	52.9 ± 0.6
Enzyme activity				
CS	2.07 ± 0.5	46.89 ± 2.34	1.7± 0.6	34.41 ± 1.71
	(0 ° - 10 °C)		(3 ° - 18° C)	

For citratesynthase activity (CSA) in the mitochondrial gill suspension (U mg mitochondrial $protein^{-1}$), higher activities were found in Antarctic scallop compared to the Queen scallop at all temperatures (Fig. 3.1). As for mitochondrial activities, a discontinuity in the Arrhenius plots of CS activities was found (Fig. 3.6, Tab. 3.3).

Summary

- A common relation between body mass and temperature on metabolic rate for all three species was described by a multiple linear model, which explains 76% of total variation recorded in metabolic rate.
- The common mass coefficient (*b*) is 0.82.
- Higher mass coefficients were found in summer, times of higher activity (i.e. growth, reproduction).
- Species comparison revealed higher citrate synthase activity but lower mitochondrial respiration in *Adamussium colbecki*.

3.3 Zygochlamys patagonica

This chapter presents unpublished results of the Patagonian scallop, *Zygochlamys patagonica*. Corresponding results for *Aequipecten opercularis* and *Adamussium colbecki* can be found in publication V (pp 97-112) and publication I (pp 51-64), III (pp 71-86), respectively.

3.3.1 Production and productivity

Individual somatic production of *Z. patagonica* increases to a maximum of 11.466 kJ yr^{-1} (0.468 g DM yr^{-1}) and decreases thereafter, whereas individual gonad production increases exponentially with shell height, reaching 3.75 kJ yr^{-1} (0.15 g DM yr^{-1}) at 73 mm (Fig. 3.2a). Individuals >45 mm contributed most to somatic as well as gonad production of the population (Fig. 3.1b). Total annual production for the season 2000 amounted to 9.77 g DM m^{-2} $year^{-1}$ (199.65 kJ m^{-2} y^{-1}), corresponding to an annual P_{tot}/B ratio of 0.484 (0.483 for soma and 0.01 for gonads). Mean annual biomass of *Z. patagonica* was estimated to be about 18.07 g DM m^{-2} (365.42 kJ m^{-2}).

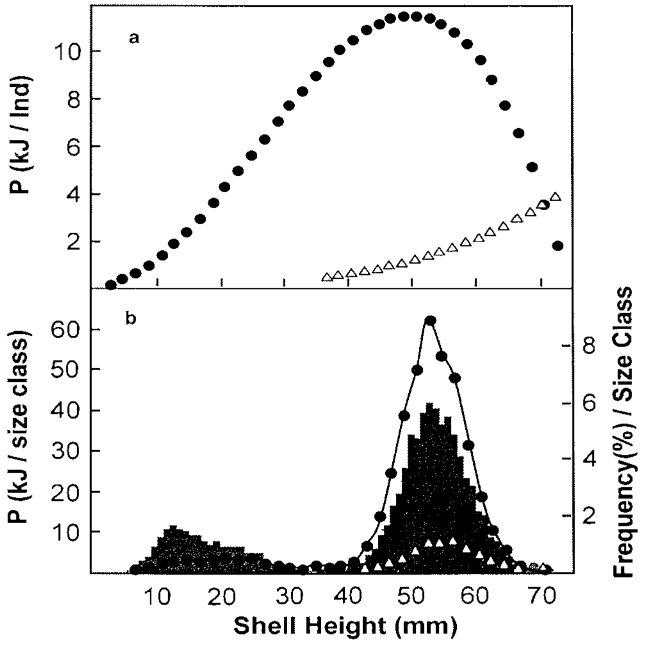

Figure 3.2 *Zygochlamys patagonica*. **a**. Individual production of somatic tissues (dots) and individual gonad production (triangle) for different size classes **b**. Size specific distribution of annual somatic tissues and gonad production at the population level, based on the pooled SFD of 2000.

3.3.2 Standard metabolic rates

Metabolic rates of *Zygochlamys patagonica* were measured in November 2000 at three different temperatures (6°C = environmental temperature; 3°C and 9°C, experiments started two weeks after reaching the appropriate acclimation temperature) over the complete size range of scallops available from the Recultas bed. The allometric relationship between soft tissue dry mass (DM) and metabolic rates (VO_2) of *Z. patagonica* were

3°C $\log(VO_2) = 2.326 + 0.602 \cdot \log(DM)$; $N = 20$, $r^2 = 0.578$
6°C $\log(VO_2) = 2.518 + 0.617 \cdot \log(DM)$; $N = 17$, $r^2 = 0.541$
9°C $\log(VO_2) = 2.63 + 0.811 \cdot \log(DM)$; $N = 36$, $r^2 = 0.773$

Average individual standardized metabolic rates (SMR_{Ind}) were indistinguishable between 6°C (354.1 ± 153 µl O_2 g DM^{-1} h^{-1}) and 9°C (481.2 ± 230.9 µl O_2 g DM^{-1} h^{-1}), but significantly different (ANOVA: $p < 0.001$) between 3°C (240.9 ± 73.1 µl O_2 g DM^{-1} h^{-1}) and 9°C.

3.3.3 Energy budget

Some of the information needed to construct an energy budget for *Z. patagonica* has been provided by Lasta et al. (2001) and Carreto et al. (1995) (phytoplankton concentration). Of the simple energy budget (see Crisp 1984):

Consumption = Production + Respiration + Egestion + Excretion

total production, 200.77 kJ m^{-2} y^{-1}, and respiration, 1073.89 kJ m^{-2} y^{-1}, are known, i.e. annual assimilation amounts to 1274.66 kJ m^{-2} y^{-1} (all estimates referring to the average annual size-frequency distribution, unpubl. Data Bremec and Lasta, Fig. 3.1b). Bayne and Newell (1983) found the assimilation efficiency (100 *x* Assimilation /Consumption) of suspension feeding bivalves to be about 43.6%, hence the annual consumption of the 'Recultas' population is about 2923 kJ m^{-2} y^{-1} (ca 64 g C m^{-2} y^{-1}). Sedimentation rates are not known in this area, but the annual primary production of 350 g C m^{-2} d^{-1} Carreto et al. (1995) should be sufficiently high to cover consumption of *Z. patagonica*.

Summary

- Individual somatic production of *Z. patagonica* increases to a maximum of 11.466 kJ yr^{-1}
- Total annual production of the Recultas population for the season 2000 amounted to 9.77 g DM m^{-2} $year^{-1}$

4 General Discussion

In the following chapter I will discuss the results of this investigation briefly by outlining specific adaptations to temperature and/or latitude. A more in-depth discussion of specific topics is provided by the separate publications (chapter 5, pp 49-112).

4.1 Growth parameters

Growth of a bivalve is the outcome of many interacting endogenous and exogenous factors. This chapter focuses on latitudinal and evolutionary changes of these factors. To compare growth parameters within the Pectinidae on a higher taxonomic level, i.e. supragenera (Annex Tab. 7.5), I followed the phylogeny suggested by Waller (1991), as this is to my knowledge the only system that includes most of the commercially used scallop species. More recent studies using molecular biological methods are rather incomplete and use a few species only (e.g. Steiner and Müller 1996, Frischer et al. 1998, Canapa et al. 1999b, 2000). They all confirm, however, homogeneity of the Pectinidae within the other Pteriomorpha (Arcidae, Ostreidae, Mytilidae, Pinnidae), while they are unable to resolve the phyletic relationship among its different taxa. I.e., *Adamussium colbecki* is situated between the genra *Chlamys* and *Pecten* (Canapa et al. 1999a, Canapa et al. 2000). According to previous investigations of Canapa et al. (1999b) and in good agreement with the morphology of the ctenolium (Waller 1984) *A. colbecki* was included in the supragenus *Pecten* for all considerations within this study.

The necessity and usefulness of the overall growth performance (OGP) to compare growth parameters was already shown in Chapter 2.1. From the several closely related indices of OGP parameters introduced so far (Pauly 1979, Pauly and Munro 1984, Moreau et al. 1986, Vakily 1992, for review see Brey 2001) the growth index P was chosen, as it is mass-based and, therefore, independent of shell shape (for detailed discussion Vakily 1992, Brey 2001). The OGP P value is directly related to the maximum rate of body mass increase during lifetime, i.e. the mass increase at the inflexion point of the VBGF describing growth in body mass (Vakily 1992). Therefore in a direct comparison it gives a clear answer to the question which animal grows better.

4.1.1 Latitude and growth performance parameters

With some exceptions, the general consensus in the literature is that bivalve molluscs from low latitudes grow more rapidly at ambient temperature, attain a smaller maximum size, and have a shorter lifespan than do conspecifics from higher latitudes (Newell 1964). Possible reasons for the observed latitudinal gradient in growth has caused considerable debate (e.g. Clarke 1987, Present and Conover 1992, Conover et al. 1997, Roy et al. 2000). Some recent studies support the role of temperature in latitudinal patterns of metabolic rates and growth (Present and Conover 1990, Clarke and Johnston 1999, Navarro et al. 2000, Peck and Conway 2000, Pörtner et al. 2001). A slowing of growth appears to be an unavoidable consequence of a lowered temperature on the physiology of these bivalves. A vast array of structural and physiological adjustments is required to counteract the reduction in chemical reaction rates due to low temperature and to ensure matching of the processes of energy production and consumption including those of growth and reproduction, but the underlying mechanism(s) remain still under debate (for review see Hochachka and Somero 2002, for a more detailed discussion see chapter 4.2.2).

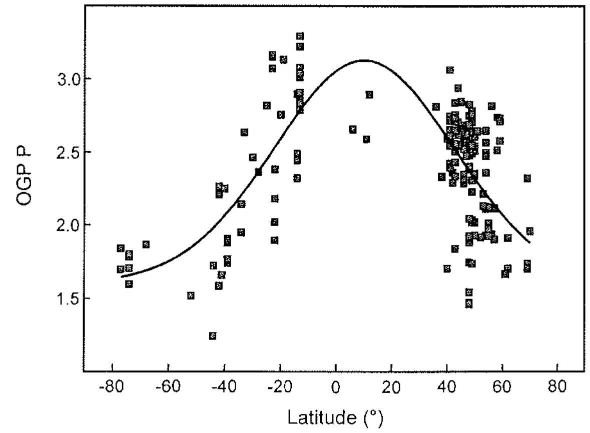

Figure 4.1
Relationship of overall growth performance ($OGP=\log(KM_\infty)$) and latitude. For references see ScallopBASE (Annex 7.1). Regression line:

$$OGP\ P = 1.6 + \frac{123.5}{64.72\sqrt{\frac{\Pi}{2}}} \bullet e^{\frac{-2\left(Lat-10.1\right)^2}{64.72^2}}$$

$r^2 = 0.39$; N=198

The relation between scallop growth performance and latitude can be described by a Gaussian model (Fig. 4.1, $r^2 = 0.39$). Obviously this relation does not reflect a direct effect of geographic latitude, but of variables coupled to latitude such as mean annual water temperature, which affects metabolism, and annual solar energy input, which may affect primary production and hence food conditions, but water temperature, too (solar energy= 3640.153 • 4.319 • Lat – 0.383 • Lat^2, according to Gassel 1996). Certainly there is no monocausal explanation as some species from temperate waters and the Southern Ocean (i.e. *A. opercularis*, mean 2.02 ± 0.11 and *A. colbecki*, mean 1.71 ± 0.16, see Annex Tab. 7.1) show similar overall lifetime growth performance. A multiple-regression approach shows a combined effect (p= 0.047) of both annual solar energy input and water temperature. The distinctly weaker effect of water temperature ($p = 0.061$) reflects that local water temperature is to a large extent defined by local solar input ($p < 0.001$). Of course there are a number of cases where the actual ambient temperature is different from the estimated mean temperature derived from the global data bank owing to site-specific peculiarities. In addition, many species have developed strong life-history adaptations to both latitudinally changing conditions of food and temperature (for review see Clarke 1987, 1993). The most conspicuous adaptations include an increasing lifespan and generally larger attainable size with increasing latitude (i.e. decreasing average water temperature) which may explain similar OGP P values in *A. opercularis* and *A. colbecki*. While the first one can be viewed as short-lived and fast growing (*r*-selected) the latter one is long-lived with low mean annual growth rates (*A*-selected = *K*-selective strategy, but from extreme habitats, for details see Willmer et al. 2000).

In conclusion, mean annual water temperatures and annual solar energy input by themselves can explain only a small part of the variability observed in growth performance. Obviously local abiotic parameters, such as minimum or maximum annual temperature, phytoplankton production or depth are of certain significance, too.

4.1.2 Evolution and growth performance

In suspension feeding bivalves food supply and/or temperature are the main factors controlling patterns of life history, whereas the genome defines the range of possible adaptations (Stearns 1976, Bayne and Newell 1983, Widdows et al. 1984, Conover and Schultz 1997, Crame and Clarke 1997, Hawkins et al. 2002). To investigate this aspect the attainable data of pectinid populations (Annex, Tab. 7.1) were divided in four broad groups regarding (i) their hypothetical longevity (estimated as Age at $0.95 \cdot H_{\infty}$ derived from the appropriate VBGF) and (ii) the average annual water temperature of the study sites. An auximetric plot of $\log(K)$ versus $\log(M_{\infty})$ is given in Figure 4.2.

Table 4.2 Overall growth performance of the four pectinid groups and their statistical consistence (ANOVA with Bonferroni-Dunn post-hoc: *** $p < 0.001$; n.s.: not significant $p > 0.5$)

	OGP P		Significance			
Group$^{1)}$	Mean	SD	CLL	TLL	TSL	WSL
CLL	1.81	± 0.23	-	***	**n.s.**	***
TLL	2.55	± 0.18	***	-	***	***
TSL	1.92	± 0.26	**n.s.**	***	-	***
WSL	2.89	± 0.28	***	***	***	-

$^{1)}$ CLL: cold water long-lived; TLL: temperate long-lived species; WSL: warm water short-lived; TSL: temperate short-lived

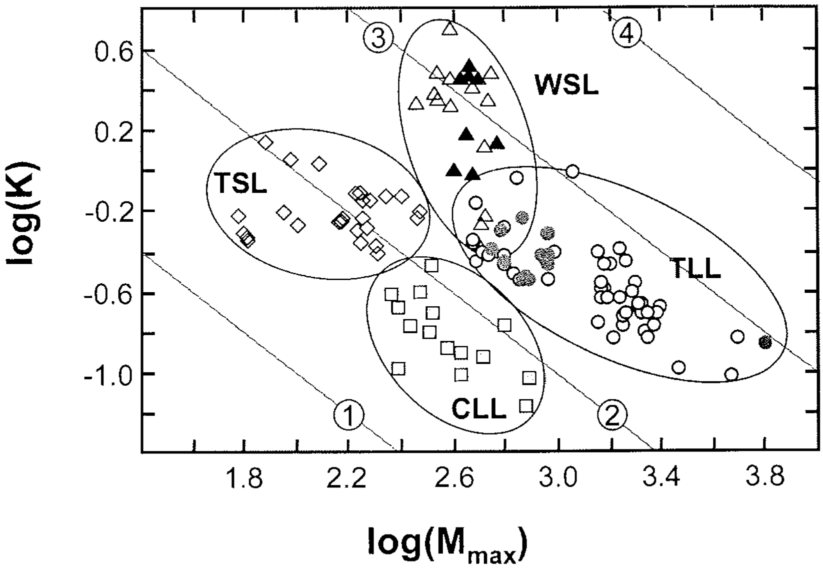

Figure 4.2 Auximetric grid comparing overall growth performance of pectinids. **CLL**: cold water long-lived species (squares: *Adamussium colbecki*, *Chlamys albidus*, *Chlamys hastata*, *Chlamys islandica*, *Chlamys rosealbus*), **WSL**: warm water short-lived species (triangles: *Amusium balloti*, *Amusium japonicum c.*, *Amusium pleuronectes*, *Argopecten purpuratus;*); **TLL**: temperate long-lived species (circles: *Mizuhopecten yessoensis*, *Patinopecten caurinus*, *Pecten maximus*, *Placopecten magellanicus*); **TSL**: temperate short-lived species (rhombus: *Aequipecten opercularis*, *Chlamys tehuelcha*, *Mimachlamys varia*, *Zygochlamys patagonica*). Diagonal lines indicate lines of equal overall growth performance index P= log(K) + log(M_∞). Mass data were converted to kJ by using conversion factors of Brey (1999, 2001) and references therein. Data referring to ScallopBASE (Annex: Table 7.1). (Modified after Heilmayer et al. 2004, publication V, pp 110)
Coloured symbols refer to species belonging to the supragenus *Pecten* (grey squares: *A. colbecki*, grey circles: *P. maximus*, black triangle: *Amusium spp.*).

The mean OGP of the four groups are with one exception significantly different (ANCOVA, Table 4.2). OGP in both warm water short-lived (WSL) and temperate long-lived species (TLL) is distinctly higher (ANOVA, $p<0.001$) than in the temperate short-lived (TSL) and cold water long-lived (CLL) group, respectively.

It is interesting to observe that certain species such as *Amusium spp.* (Fig. 4.2, black triangle) and *Pecten maximus* (Fig. 4.2, grey dots) occupy distinct, non-overlapping areas within the corresponding cluster. Though similar in their general growth potential (Fig. 4.3), warm water species of the genus *Amusium* must be considered fast growing, while *Pecten maximus* from the North Atlantic is slower growing but attains considerable larger size. The Antarctic scallop, *Adamussium colbecki*, reveals clearly the lowest OGP values in the supragenus *Pecten*. A comparison with the tropic *Amusium* species is interesting, as in terms of temperature the tropical water belt is one of the oldest and physically stable ecosystems. The present severe latitudinal cline in mean seawater temperature, caused by a cooling down of the Southern Ocean, is not typical of most of the history of the marine biosphere (Shackleton 1979, Clarke and Crame 1989). Hence, the significantly lower OGP cannot only be explained by temperature alone. On the one hand a more detailed examination reveals that growth in many polar species is slow not because of temperature limitation but because of seasonal shortage of food (Clarke 1988, 1998). On the other hand this theory is, however, still under debate, as the role of lateral advection of organic matter and resuspension of detritus was underestimated for a long time, but is supposed to play a significant role for benthic suspension feeders (Berkman et al. 1986, Arntz et al. 1994).

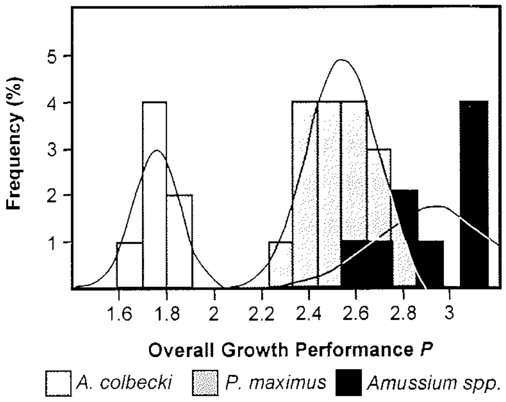

Figure 4.3 Histogram of overall growth performance parameters within the supragenus 'Pecten' (data referring to Annex 7.1). Lines representing normal comparison of the three groups.

To summarize the observed life history patterns and their possible evolutionary adaptations. Phylogenetically 'younger' species of all six pectinid supragenera (Annex Tab. 7.5) belong to temperate groups, thus supporting the general idea (e.g. Waller 1993, Arntz and Fahrbach 1991, Arntz et al. 1994) that recent scallops evolved from warm water ancestors, i.e. within the supragenus *Pecten*, *Amusium spp.* belong to the WSL group, while *Pecten maximus* belongs to TSL. The supragenic group *Aequipecten* provides another example: while *Aequipecten opercularis* belongs to the TSL group, *Argopecten purpuratus* can be viewed as a warm-water short-lived species. This remains, however, pure speculation until modern molecular methods (e.g. Canapa et al. 2000) will completely clarify the hitherto rather uncertain phylogeny of pectinids. However, observations from field studies support the hypothesis of warm-water ancestors. Population explosion of *Argopecten purpuratus* during El Nino 1983 with stock sizes more than 60 times that of 'normal' years were explained with (i) an increased larval survival and/or intensified spawning activity associated with temperatures 6-8°C higher than normal, (ii) higher survival due to mortality or emigration of predators and competitors, (iii) much higher growth rates (Wolff 1985), and (iv) high levels of dissolved oxygen in the scallop beds (Wolff 1987, Arntz and Fahrbach 1991).

Summary

- Overall growth performance increases with decreasing latitude. This trend is strongly correlated to annual solar energy input ($p < 0.001$) and weakly to average annual water temperature ($p = 0.047$).
- Mean annual water temperatures and annual solar energy input by themselves can explain only a small part of the variability observed in growth performance
- Pectinids can be divided in four broad groups regarding (i) their longevity and (ii) their ambient water temperature. The four groups show significantly different OGP values.
- In general, phylogenetically 'younger' species of the six pectinid supragenera belong to temperate or warm water groups, respectively.

4.2 Physiological parameters - merging ecology and physiology

In this chapter the specific tradeoffs and adaptations in scallop performance across a latitudinal cline and its physiological mechanisms will be discussed in the light of relevant literature studies of metabolism and metabolic adaptations.

Adaptation to environmental temperature was recognized for a long time as one of the evolutionary mainstreams and is thought to be dependent, to a large extent, on the organism's ability for metabolic adjustments on both short-term and evolutionary time scales (Hochachka and Somero 1984, Clarke 1998). Hence, the fitness of an organism (i.e. growth and reproduction) is largely influenced by temperature. In fact, recent evidence demonstrates that aerobic scope (i.e. the functional co-ordination of oxygen supply mechanisms to cover oxygen demand) limits energy availability and hence growth (Zielinski and Pörtner 1996, Pörtner et al. 1998, Guderley et al. 1997, Frederich and Pörtner 2000, Peck et al. 2002, Pörtner 2002a, b, Sommer and Pörtner 2002). Several studies emphasized that growth variations may be linked to various physiological components of growth, such as whole-animal metabolic rate (Widdows 1978, Koehn and Shumway 1982, Toro et al. 1996), the intensity of protein turnover (Hawkins et al. 1986, Hawkins and Day 1996, Storch and Pörtner 2003) and the efficiency of protein deposition (Bayne and Hawkins 1997, Bayne et al. 1999, Storch and Pörtner 2003).

Latitudinal differences, however, in whole-animal performance may or may not be found on lower hierarchical levels (e.g. cellular, molecular). While the main objective of this study is to investigate how temperature influences growth and metabolism on higher levels, a deeper look into physiological adaptations on the cellular level is intended, too. To identify putative mechanisms explaining growth variation and their evolutionary significance I will compare temperate scallop species with the Antarctic scallop. This species has become, most likely, extremely specialized during its evolution to the cold but physically constant conditions of the Southern Ocean. This comparison can tell us a great deal about mechanisms, since *A. colbecki* illustrates one end of the environmental range of living scallop species.

4.2.1 Standard metabolic rate

Metabolic rate (measured as oxygen consumption) reflects the energy expenditure of animals, which is required for numerous processes (e.g. growth and reproduction). Hence, it is an important factor in estimating energy flow through both populations and the individual organism (Bayne and Newell 1983). Seasonal cycles in bivalve metabolism result from complex interactions of environmental and endogenous variables acting on metabolism. Among these factors, body size, environmental temperature and the energetic demands of biosynthesis, particularly those associated with gametogenesis, are considered to have profound influence on respiratory activity (Vahl 1978, Bayne et al. 1983, Bricelj et al. 1987, MacDonald and Thompson 1988, Shumway et al. 1988, Hawkins et al. 1989, Houlihan 1991).

Scaling with body mass

The coefficient *b* relates the metabolic rate to the mass of the animal. The average mass scaling exponent within scallops, 0.799, is slightly above the mean coefficient (0.772) obtained for a large number of bivalve studies (Fig. 4.4, T. Brey unpublished data compilation). Although a scaling exponent of about 0.75 is commonly reported for intraspecific relationships between standard meta-

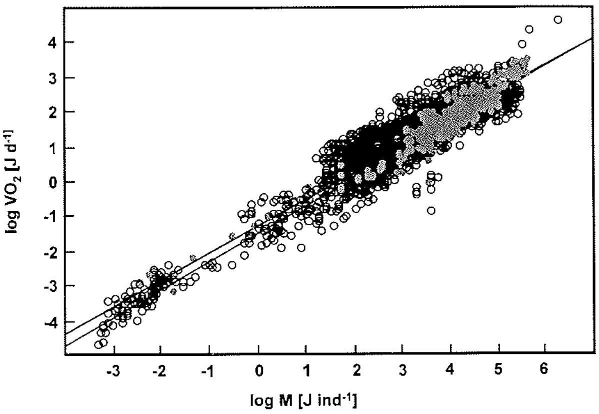

Figure 4.4 Metabolic rates of bivalves and scallops world-wide. Data of scallops (grey dots) are taken from Publication II. Data for other bivalves (black circles) are taken from a data compilation of T. Brey. Regression lines:
Scallops $\log VO_2 = -1.517 + 0.799 \log M$; $N = 1042$; $r^2 = 0.839$
Others $\log VO_2 = -1.285 + 0.772 \log M$; $N = 2818$; $r^2 = 0.865$

[general regression line- not shown:
Bivalves $\log VO_2 = -1.281 + 0.761 \log M$; $N = 3860$; $r^2 = 0.870$]

bolic rate and body mass in ectotherms, there is no generally accepted theoretical explanation for this value (Clarke and Johnston 1999, Willmer et al. 2000). The discussion of this topic started over a century ago (Rubner 1883) and many of the key arguments were explored by Zeuthen (1947, 1953) and Hemmingsen (1960). Nevertheless, despite attempts based on surface area/volume considerations or the incorporation of physiological time, no general conclusion has been derived so far (see discussion in Schmidt-Nielsen 1984, Willmer et al. 2000). Such statistical models, whilst undoubtedly obscuring some important biological variability, are of great heuristic value in drawing broad ecological conclusions (Clarke and Johnston 1999). Scaling exponents obtained from within-species studies, however, differ from those of broad species analysis, mostly for exogenous and endogenous factors influencing small and large specimens in different ways, e.g. gametogenesis (for review see Bayne and Newell 1983). The intra-family coefficient reported in this study is statistically indistinguishable from the mean within-species value.

Although there is clearly a strong scaling relationship between standard metabolic rate and body mass in scallop, the data show considerable scatter around the regression line (Fig. 4.4). Environmental temperature is one important factor explaining this remaining variance.

Temperature dependence of metabolic rate

Many laboratory studies have shown a positive correlation between metabolic rate and temperature, and as a result much of the seasonal variation in biological activity has traditionally been related to environmental temperature (for review see Griffiths and Griffiths 1987, Clarke and Johnston 1999, Peck 2002, Peck and Conway 2000, Heilmayer and Brey 2003a).

The Arrhenius model is likely to describe effects of temperature on whole-animal physiological processes best (Clarke and Johnston 1999). An Arrhenius model fitted to data from 8 scallop studies (Fig. 4.5) indicates that a rise in temperature from 0 to 25°C causes a 10 fold elevation in metabolism. This would be equivalent to a Q_{10} of 1.59 over the whole range, which is well within the normally expected physiological range. The Arrhenius relationship established in this study, however, exhibits a lower thermal sensitivity of standard metabolism than typical within-species acclimation studies (median Q_{10}=2.26, N=15, for review see Bricelj and Shumway 1991). This indicates that evolutionary adaptation has reduced the overall thermal sensitivity of standard metabolism across species.

An analysis of covariance of standard metabolic rate versus "Antarctic/non-Antarctic" species and temperature gives no evidence for a significant elevation of

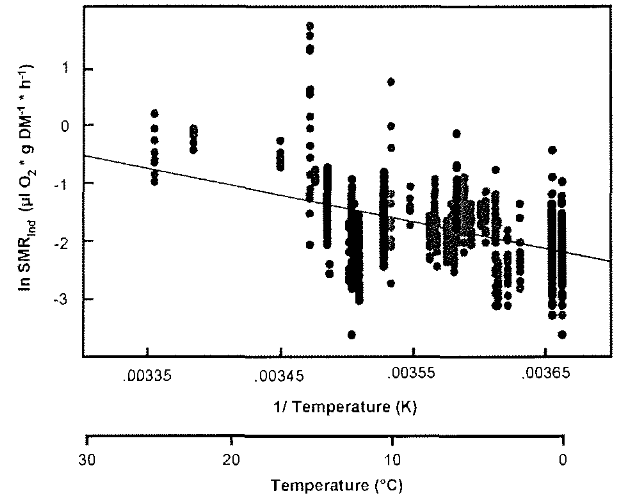

Figure 4.5 Fitted Arrhenius model of the relationship between mass-specific metabolic rates and temperature of 8 scallop populations (Black dots: own measurements; *A. opercularis*: McLusky 1973, Heilmayer et al. 2004; *A. irradians irradians*: Bricelj *et al.* 1987; *A. irradians concentricus*: Lu et al. 1999; *C. islandica*: Vahl 1978, Vahl and Sundet 1985; *M. yessoensis*: Fuji and Hashizume 1974; *Z. patagonica*: Heilmayer et al. 2001). Regression line: $\ln(SMR_{Ind}) = 11.851 - 3792.147 \cdot 1/T$ (N= 953, r^2 = 0.275)

the whole-organism metabolism of the Antarctic scallop as assumed by the hypothesis of "metabolic cold adaptation" (MCA *sensu* Krogh 1916; Wohlschlag 1964; for review see Peck 2002). Hence this study supports the conclusion of Clarke and Johnston (1999) and Peck and Conway (2000) that there is no MCA on the level of organisms.

In addition, Pörtner et al. (2000) and Pörtner (2002a, b) distinguished between cold adapted eurytherms (mostly sub-Arctic to Arctic) displaying MCA and cold adapted stenotherms (mostly Antarctic), which do not, or only to a small extent. While this study can affirm the latter view, the database (publication II, pp 65-80, Annex Tab 7.2) is not sufficient to provide evidence for cold adapted eurythermal scallops.

4.2.2 Cellular performance

Polar ectotherms are adapted to low temperatures in that they survive and carry out all the necessary biological functions. It is generally accepted, however, that they must have developed specific physiological adaptations at the cellular level (i.e. mitochondrial proliferation) to overcome the adverse effects of low temperatures on metabolism (Tab. 4.3).

As seen in Table 4.3 maximum citrate synthase activities determined in the present study are in the lower range of values measured for molluscs by other authors. Enhanced enzyme capacities in the gill, as found in the cold stenothermal Antarctic scallop compared to the Queen scallop, indicate a rise in aerobic capacity due to either mitochondrial proliferation and enhanced capacities of individual mitochondria. Mitochondrial proliferation, compensating for the depressive effects of low environmental temperature, has been found in cold acclimated eurythermal (Campbell and Davies 1978, Egginton and Sidell 1989, Sokolova and Pörtner 2001) as well as in cold adapted Southern and Northern hemisphere species (Londraville and Sidell 1990, Johnston et al. 1998, Sommer and Pörtner 2002). Pörtner et al. (1998) have argued persuasively that even though individual costs will be reduced under long term permanently cold conditions as experienced in Antarctica, mitochondrial proliferation must inevitably lead to some elevation of resting metabolism ('cellular MCA') because of enhanced requirements for mitochondrial synthesis and maintenance (e.g. Johnston et al. 1994, 1998; Clarke 1998; Somero et al. 1998; Pörtner et al. 2000, Pörtner 2002a, b). The question arises at which organisational level energy savings occur which counterbalance the cost of cellular MCA, as there is no evidence for MCA in whole animal metabolism (publication II, pp 65-80).

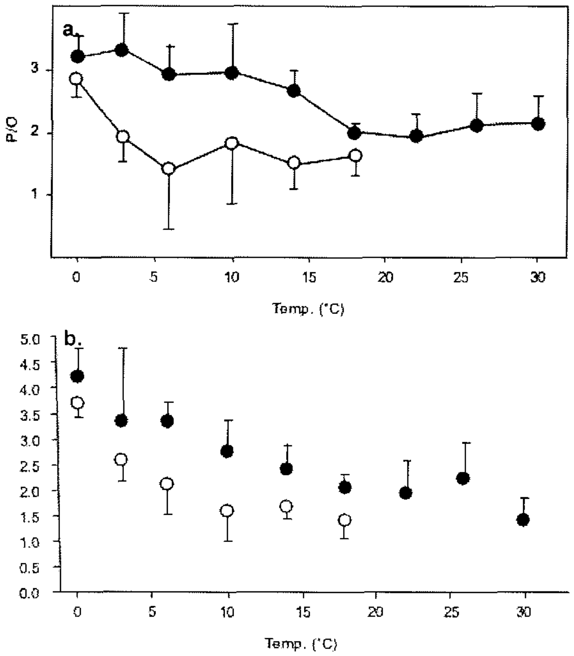

Figure 4.6 Temperature effects on the function of the gill mitochondria from *A. colbecki* (dots) and *A. opercularis* (circles) **a.** Respiratory control ratios (RCR). **b.** Effective P/O ratios. Species comparison revealed higher coupling rates at all temperatures in the Queen scallop than in the Antarctic scallop. In both species RCR decreases constantly in both species, while the P/O ratio is fairly constant.

Low rates of basal metabolism at low temperatures are not so easy to explain. Here more than anywhere the explanation of a direct rate-limitation by temperature is intuitively appealing. As shown in various studies (for review see Pörtner 2001, Hochachka and Somero 2002, Pörtner 2002a, b, Pörtner et al. 2004), shortage of organismic aerobic capacity in the cold is compensated for at the cellular level by mitochondrial proliferation and associated molecular and membrane adjustments: (i) Low mitochondrial aerobic capacities and H+ leakage rates (Johnston et al. 1998, Pörtner et al. 1998, 1999, Hardewig et al. 1999; Fig. 4.6), (ii) Changes in the kinetic characteristics of mitochondria and enzymes reflect differences in metabolic regulation and are inevitably involved in adaptation and acclimation to ambient temperature (Torres and Somero 1988, Crockett and Sidell 1990, Somero 1995, Sokolova and Pörtner 2001, Kawall et al. 2002, Sukhotin and Pörtner 2001, Lannig et al. 2003, chapter 3.2); (iii) Elevated Arrhenius activation energies of mitochondrial proton leakage and of enzymes (i.e. high kinetic barriers to metabolic flux) (Pörtner et al. 1999, 2000, Hardewig et al. 1999); (iv) Down regulation of amount and flexibility of acid-base regulation (Pörtner 2002b).

Table 4.3 Comparison of maximum citrate synthase activity of invertebrates from different geographic regions.

Species	Tissue	Reference	Region	N	CSA
Bivalves					
Geukensia d. granossissima	Muscle	Nicchitta and Ellington 1983	Sub-tropic	4	1.16 ± 0.08
Modilus squamosus	Muscle		Sub-tropic	4	2.34 ± 0.20
Mytilus edulis	Whole body	Sukhotin and Pörtner 2001	Sub-polar		0.5 –1.85
Euvola ziczac					
mature	Muscle	Brokordt et al. 2000a	Tropic	7-12	1.51 ± 0.04 1)
immature					1.32 ± 0.04 1)
spawned					1.02 ± 0.04 1)
Chlamys islandica					
mature	Muscle	Brokordt et al. 2000b	Sub-polar	7-12	1.09 ± 0.04 1)
immature					1.36 ± 0.06 1)
spawned					1.20 ± 0.06 1)
Adamussium colbecki	Gill	This study	Polar	5	0.57 ± 0.02
Aequipecten opercularis	Gill	This study	Temperate	5	0.38 ± 0.03
Gastropods					
Littorina saxatilis					
Low shore		Sokolova and Pörtner 2001	Temperate	9	3.6 ± - 1)
High shore			Temperate	9	2.25 ± - 1)
Busycon contrarium		Chih and Ellington 1987	Sub-tropic	4	3.37 ± 0.20
Buccinum undatum					
male					
mature	Foot muscle	Brokordt et al. 2003	Temperate	7-14	0.82 ± 0.04 1)
immature					0.69 ± 0.04 1)
maturing					0.86 ± 0.04 1)
female					
mature					0.63 ± 0.06 1)
immature					0.72 ± 0.06 1)
spawned					0.62 ± 0.06 1)

1) data extracted from figures

A factor largely unexplored in non-mammalian animals is the role of protein turnover and thus cost of growth. Protein turnover costs, which form a substantial fraction of resting metabolic costs (Hawkins et al. 1989; Wieser 1994), seem to be distinctly lower at low temperatures (Smith and Haschmeyer 1980; Clarke 1998). Studies with *Mytilus edulis* (Hawkins et al. 1986, Bayne & Hawkins 1997) and *Oncorhynchus mykiss* (McCarthy et al. 1994) demonstrated that reduced rates of protein turnover contribute to reduced metabolic costs and higher rates of growth. Regarding pectinids Storch and Pörtner (2003) suggest that cold adaptation occurs at the level of increased protein stability leading to a decrease in overall turnover rates and hence similar energetic costs of protein synthesis in eurythermal and cold stenothermal pectinids.

Cellular adjustments are suggested to differ between cold acclimated and cold adapted as well as between cold-eurythermal and cold-stenothermal animals (Pörtner et al. 2000, Pörtner 2002a). Antarctic stenotherms, however, permanently escaped the cost of cold tolerance by establishing minimized standard metabolic rates despite maximized mitochondrial densities.

Summary

- Relationship between standard metabolic rate and body mass in scallops can be described by the following equation: $\log VO_2 = -1.517 + 0.799 \log M$; N= 1042; $r^2 = 0.839$
- Metabolism in scallops is primilary a function of temperature which can be described by an Arrhenius model: $\ln(SMR_{Ind}) = 11.851 - 3792.147 \cdot 1/T$ (N= 953, $r^2 = 0.275$)
- The Arrhenius model established in this study exhibits a lower thermal sensitivity (Q_{10}=1.59) of standard metabolism than typical within-species acclimation studies (median Q_{10}=2.26).
- Thermal sensitivity of mitochondrial function shows similar patterns. Arrhenius-Break-Temperatures indicating thermal discontinuity are in all case clearly above ambient temperatures.

4.3 Growth efficiency and productivity

Viewed in the light of the previous chapter low rates of standard metabolism in cold-stenothermal organisms is a positive energy advantage, as they lead to increased ecological growth efficiency because of lower maintenance costs (Clarke 1987, Clarke and Crame 1989).

Proxy for growth efficiency

Polar marine invertebrates tend to grow slowly (Brey and Clarke 1993, Arntz et al. 1994, Peck 2002) and historically this has been explained either as a direct rate-limitation by temperature or by an elevated metabolic rate, as suggested by the theory of 'Metabolic cold adaptation' (MCA), i.e. a lower proportion of ingested energy is available for growth (for detailed discussion see Clarke 1991, 1993, publication IV, pp 87-96). As a corollary, a reduced metabolic rate, as shown above for *A. colbecki* (publication II, pp 65-80), would point towards enhanced growth performance as less energy is 'wasted' on basal metabolism (Bayne & Newell 1983, Clarke 1987).

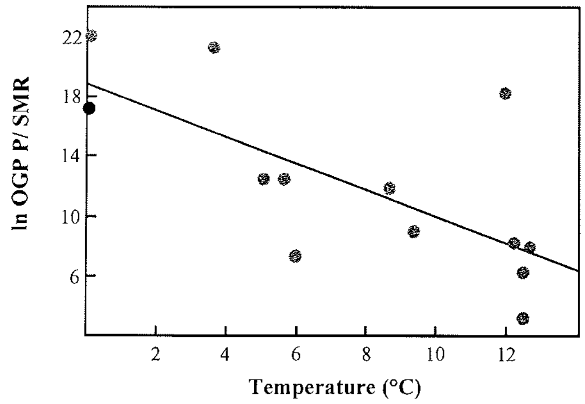

Figure 4.7 Relationship of the ratio between standard metabolic rate (SMR_{Avg}) and overall growth performance (*P*) to ambient temperature of 7 scallop species (grey dots: *A. opercularis*, *C. islandica*, *M. varia*, *M, yessoensis*, *P. magellanicus*, *Z. patagonica*; black dot: *A. colbecki*). Data presented are resting or standard metabolic rates at normal ambient temperatures. Where seasonal data were available the data were averaged over the whole year (for more details and references see publication II, p 77). Regression line: OGP P/SMR_{Avg}= 19.003 - 0.903 • T (N= 13, r^2= 0.496, $p < 0.001$)

The ratio of OGP-to-SMR_{Avg} was established as a proxy for growth efficiency. I.e., it is presumed to be proportional to the fraction of metabolic energy channelled into somatic growth. Good evidence has been produced in temperate bivalve molluscs, e.g. *Mytilus edulis*, that individuals with low basal or standard metabolic requirements show comparatively higher growth rates (for details Hawkins et al. 1989, Wieser 1994, Hawkins and Day 1996) and thus OGP-to-SMR ratios would be relatively high, too.

The general decrease of growth efficiency with temperature, as shown in Figure 4.7, gives evidence that metabolic rates increase faster with temperature than does growth performance, possibly as a consequence of enhanced maintenance cost or cost of growth or both. The temperature coefficients (Q'_{10}) computed from the corresponding Arrhenius models exemplify this difference: within the 0-25°C temperature range Q_{10} of scallop metabolic rate is 2.28 (publication IV, pp 94) whereas overall growth performance changes more slowly with temperature (Q_{10}= 1.12, publication IV, pp 95).

In conclusion, irrespective at which hierarchical level limitations and constraints are initiated, studies within single species led to the hypothesis that the primary physiological basis of an increase in production is reduced energy expenditure per unit of growth, indicating enhancements of growth efficiency, rather than a straightforward increase in feeding and all other associated processes that are required for growth (Diehl et al. 1986, Hawkins et al. 1986, 1989, Hawkins & Day 1996).

Production and productivity

All energy acquired by animals through the ingestion of food is ultimately either used in metabolic processes, or deposited as new body tissue (growth or reproduction). The partitioning of ingested or metabolizable energy into maintenance and production and possible trade-offs between growth and production are important to characterize species-specific life histories (e.g. Sibly and Calow 1986, Wieser 1994). The changing patterns of individual energy expenditure during the lifetime of the three investigated species are discussed in detail in the respective chapters (*A. opercularis*: publication V, pp 97-112; *A. colbecki*: publication I, pp 51-64; *Z. patagonica*: chapter 3.3). These energy budgets clearly illustrate some general age-related patterns: (i) an increasing share of maintenance requirements (expressed as respiration) with age, and (ii) a progressive transition of production from somatic growth to gonad output with age, as previously observed in other scallop species, too (e.g. Shafee 1982, Fuji and Hashizume 1974, MacDonald and Thompson 1985, 1988, Claereboudt and Himmelman 1996). The general decrease of somatic growth with increasing age (Calow 1977), however, is not necessarily caused only by a shift between P_s and P_g or the declining ability of the older animals to convert assimilated food into new tissue (Calow and Townsend, 1981), but may also be caused by a shorter growing season of older individuals, as already shown for *Chlamys islandica* (Vahl 1981) and *Pecten maximus* (Chauvaud and Strand 1999). To define the crucial factor within the investigated populations derives further investigation and a narrow sampling frequency.

Net (K_2) and gross growth efficiency (K_1) and turnover ratio (P/B) indicate to which extent energy translates into production available for the next trophic levels. In Tab. 4.4 values for several pectinid populations are summarized. Calculations of population production indicate that populations of short-lived scallop species such as *A. opercularis* and *Mimachlamys varia* invest around 15% of the total annual production into reproduction (Tab 4.4). In populations of long-lived species this proportion is distinctly higher: *Placopecten magellanicus* (MacDonald and Thompson 1985) and *Patinopecten caurinus* (MacDonald and Bourne 1987) channel more than 50% of their annual production into gametes, whereas the cold-water species

Chlamys islandica and *Adamussium colbecki* invest approximately 20-30% (Vahl 1981a, b, publication I, pp 51-64).

Table 4.4 Energy effiencies of various scallop populations

Species/ Place	$^{a}K_1$	$^{b}K_2$	$^{c}P_S$	$^{d}P_G$	$^{e}P/B$	Reference
			[kJ m^{-2} y^{-1}]		[y^{-1}]	
Adamussium colbecki					-	
Antarctica	0.05	0.14	234.6	70.9	0.206	Chiantore et al. 1997; publication I
Aequipecten opercularis						
France	0.16	0.45	19.7	0.98	1.760	publication V
Chlamys islandica						
Norway	0.08	0.16	358.6	163.1	0.317	Vahl 1981
Mimachlamys varia						
France	-	0.14	11.3	2.1	0.482	Shafee & Conan 1984
France	-	0.09	11.0	2.2	0.496	Shafee & Conan 1984
Mizuhopecten yessoensis						
Japan	0.32	0.37	-	-	-	Fuji & Hashizume 1974
Patinopecten caurinus						
Canada	-	-	254.8	51.3	0.372	MacDonald & Bourne 1987
Placopecten magellanicus						
Canada	-	-	25.8	33.2	0.170	MacDonald & Thompson 1985, 1986, 1988
Canada	-	-	10.2	21.2	0.271	
Zygochlamys patagonica						
Argentina	0.05	0.14	176.51	24.26	0.480	This study

^{a}gross growth efficiency, $K_1 = P_{Tot}/C$; ^{b}net growth efficiency, $K_2 = P_{Tot}/A$; ^{c}somatic production; ^{d}gonad production; ^{e}turnover-ratio

Metabolic costs of reproduction

Based on the seasonal measurements of metabolism of mature and immature *A. opercularis* (publication V, pp 97-112) and *A. colbecki* (publication II, pp 65-80) specimens it is possible to estimate the metabolic costs of reproduction. Figure 4.8 compares the share of growth, basal metabolism and reproduction in individual total energy expenditure of the two species: While the proportion of basal metabolism is similar, the Antarctic scallop invests a higher proportion into growth and correspondingly less into reproduction. These data are crude estimates only, but nevertheless, provide a good base for some general annotations. In the two-species comparison of this study there is no evidence of a proportionally lower basal metabolism as previously hypothesised by Clarke (1983, 1987) for Antarctic invertebrates. Differences in the proportion used for growth and reproduction can be explained in two ways: (i) *Life strategy*: The long-lived Antarctic scallop, *A. colbecki,* may be seen as a typical *A*-selected animal while *A. opercularis* may be seen as a *r*-selective species. On the other hand we do not know much about reproduction of *A. colbecki* (Berkman 1991, Chiantore et al. 2001).

BOX 4.1 Calculation of metabolic costs

A physiological approach of the traditional energy budget (chapter 2.2.2) must take into consideration the respiratory costs of synthesis. The major difficulty is to separate measured metabolic rates into reproductive and non-reproductive components as the mostly occur at the same time. The following estimates are based on the assumption that basal metabolic rates do not change with season,

(i) ***A. colbecki***

Costs (reproduction) = $\mathrm{SMR}_{\mathrm{Ind}}$(summer-mature) - $\mathrm{SMR}_{\mathrm{Ind}}$(summer-immature)

Costs (growth) = $\mathrm{SMR}_{\mathrm{Ind}}$(summer-immature) - $\mathrm{SMR}_{\mathrm{Ind}}$(winter-mature)

(ii) ***A. opercularis***

Metabolic costs of reproduction were estimated as the difference between the predicted seasonal increase of oxygen consumption of immature and observed consumption in summer.

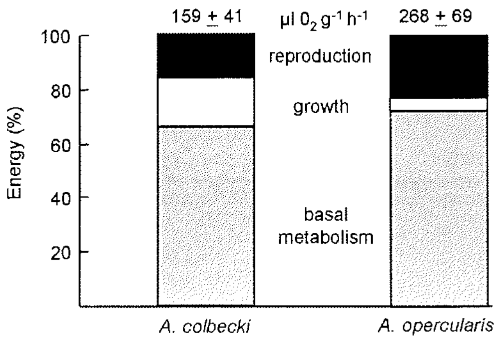

Figure 4.8 Scheme showing an estimated energy budget of *A. colbecki* and *A. opercularis* with the three main components: growth, basal metabolism and reproduction. Ratios are calculated from differences between winter and summer, respectively, mature and immature animals (for theoretical background and calculation details see Box 4.1).

If gametogenesis requires more than one summer period, as already reported for other polar organisms (e.g. *Serolis polita*, Luxmoore 1982 and caridean shrimps, Gorny et al. 1992) it would be more appropriate to compare lifetime budgets. (ii) *Physical factors*: The cost of shell growth may increase distinctly with decreasing temperature, owing to an increase of the solubility product of $CaCO_3$ with decreasing temperature. Hence, shell production is more expansive in polar waters, so that the Antarctic scallop has to invest a relatively higher proportion into shell growth.

Summary

- SMR_{Avg}-to-OGP is an inverse proxy for growth efficiency. Thus, there is strong empirical evidence that elevated temperature constrains growth efficiency in scallops and that evolutionary adaptation does not fully compensate for this effect.
- Total annual gonad production of *A. colbecki* is twice as high as in *A. opercularis.*
- The proportion of metabolised energy *A. colbecki* invest into growth is four times higher than that of *A. opercularis*, most likely caused by higher costs of shell production.
- The long-lived Antarctic scallop, *A. colbecki,* is seen as a typical *A*-selected animal, while *A. opercularis* may be seen as a *r*-selected species.

4.4 Future perspectives

This study was the first to assess the influence of latitude on growth and population parameters within one single phyologenetic family. With regard to future research in comparative ecology, I want to put forward some considerations and suggestions:

General aspects

- *Increase of database:* The established dataset provides a good basis to look at evolutionary adaptations and constraints. However, further population data and more detailed environmental data (e.g. maximum and minimum water temperatures, food supply, etc.) are needed to get a more detailed picture and to retrieve uncertainties. So far all information is summarized in one data file (Microsoft Excel format, Annex Tab. 7.1, 7.2), which is available on request from the author. As a next step a web based and continuously updated database will be established (ScallopBASE).

- *Energy budgets* More sophisticated energy budgets including feeding rates and better estimates of gonad production as well as seasonal data will help to validate the data from other studies and fill existing gaps.

- *Early life stages*: Influence of temperature not only on complex processes such as growth but also on survival rate, especially of vulnerable life stages such as larvae should be included in future studies. Critical temperatures of larvae may affect survival rate and give important information for aquaculture/ hatcheries.

- *Intraspecific studies:* It must be emphasized that the general statements of this study rely on between-species comparisons and do not reflect the more subtle differences between species subpopulations in a latitudinal cline. In order to relate phenotypic differences (in ecophysiology) to genetic variability the application of the described experimental setup to different subpopulations of one species living at different latitudes must be accompanied by a genetic approach. In this context it will be essential to determine whether populations living at their distributional limits have reached the limits of their adaptation potential. Potential candidate species are: *Argopecten purpuratus*, *Aequipecten opercularis* and *Pecten maximus*.

The study of temperature tolerance windows, reproductive cycles and early life history traits as well as of feeding strategies will assist, (i) to define temperature tolerance windows of organisms and thus to predict future biogeographic shifts owing to changes in environmental conditions, (ii) to explain changes in life history traits observed in the field (such as reproductive cycles, growth rates).

Specific tasks

- Very little is known of the seasonal variability of *A. colbecki*. We just opened a small window to get a first insight into the life history and physiology of this highly important Antarctic nearshore species. Further quantitative and qualitative studies of whole year physiology will answer open questions and may be the key to explain the interannual variability in *A. colbecki* recruitment and population structure.

5 Publications

Below, the publications in progress for this thesis are listed and my share thereof is explained.

Publication I

Olaf Heilmayer, Thomas Brey, Mariachiara Chiantore, Riccardo Cattaneo-Vietti and Wolf E. Arntz

Age and productivity of the Antarctic scallop, *Adamussium colbecki*, in Terra Nova Bay (Ross Sea, Antarctica).

Journal of Experimental Marine Biology and Ecology, 2003, 288(2): 239-256

I elaborated the concept and initial idea for this paper together with the second author. I did all the practical work, data analysis and wrote the first version of the manuscript. For calculation of productivity and energy budget an Excel-sheet of the second author was adapted. The final version was achieved considering the revisions by all co-authors.

Publication II

Olaf Heilmayer and Thomas Brey

Saving by freezing? Metabolic rates of *Adamussium colbecki* in a latitudinal context.

Marine Biology, 2003, 143(3): 477-484

I discussed the conceptual frame of this paper with the second author. I developed the experimental design and carried out all laboratory work. Data processing, analysis and interpretation as well as manuscript writing was done by myself. The manuscript improved in close cooperation with the co-author.

Publication III

Mariachiara Chiantore, Riccardo Cattaneo-Vietti and Olaf Heilmayer

Antarctic scallop (*Adamussium colbecki*) annual growth rate at Terra Nova Bay.

Polar Biology, 2003, 26(6): 416-419

All three authors developed the scientific idea and did the practical work this paper is based on. I conducted the calculation of VBGF and overall growth performance. The first author wrote the manuscript, the final version was achieved considering the suggestions by all authors.

Publication IV

Olaf Heilmayer, Thomas Brey and Hans-O. Pörtner

Growth efficiency and temperature dependency in marine invertebrates: Lessons from empirical data.

Functional Ecology, submitted

The initial idea to use growth performance and respiration data as a proxy for growth efficiencies was worked out in close cooperation with the second author. I improved a preliminary database provided by the second authors. My manuscript draft was discussed and revised with the two co-authors.

Publication V

Olaf Heilmayer, Thomas Brey, Daniela Storch, Andreas Mackensen and Wolf E. Arntz

Growth and population dynamics of *Aequipecten opercularis* (L.) from the western English Channel (Roscoff, France).

Netherlands Journal of Sea Research, 2004, 52(2): in press

I developed the scientific idea of this study in joint cooperation with the second author. Animal rearing and practical work was done together with the third author. Stable isotopes analyses were performed in the lab of A. Mackensen. I did the manuscript writing and essentially applied the data analysis concept developed for publication I and II. The final version was discussed with all authors.

Publication I

Age and productivity of the Antarctic scallop, *Adamussium colbecki*, in Terra Nova Bay (Ross Sea, Antarctica)

Olaf Heilmayer (✉)[a], Thomas Brey[a], Mariachiara Chiantore[b], Riccardo Cattaneo-Vietti[b] and Wolf E. Arntz[a]

[a]Alfred Wegener Institute for Polar and Marine Research, P.O. Box 120161, 27515 Bremerhaven, Germany
[b]DIPTERIS, University of Genoa, Corso Europa, 26, 16132 Genoa, Italy

Abstract

Body size, geographical distribution and biomass make *Adamussium colbecki* (Smith, 1902) one of the most conspicuous bivalve species in the Antarctic. Based on samples collected in austral summer 1999/2000 in Terra Nova Bay, the annual formation of shell growth bands visible on x-ray photographs was verified by stable isotope analysis. A general von Bertalanffy growth function was fitted to size-at-age data of 25 individuals (H_∞= 108.86 mm, K= 0.114 y^{-1}, t_0= -0.367, D= 1.284). Somatic production calculated from mass-specific growth rates was 234.6 kJ m^{-2} y^{-1}. Gonadal productivity amounted to 70.92 kJ m^{-2} y^{-1}. Annual somatic and gonad production-to-biomass ratios (P/B) were 0.199 and 0.052, respectively. According to its consumption and production *A. colbecki* is likely to play a significant role in the trophic web of Terra Nova Bay.

Keywords

Antarctic scallop; Bivalvia; Pectinidae; Production; Stable isotope analysis

---

Reprinted from *Journal of Experimental Marine Biology and Ecology*, 288(2): 239-256, Copyright (2003), Elsevier Science

Introduction

In contrast to temperate benthic environments (e.g. Loo and Rosenberg 1989, Wildish and Kristmanson 1997, Mistri et al. 2001), molluscs contribute little to the often extraordinarily high benthic standing stock in Antarctic waters (Arntz et al. 1994, Brey and Gerdes 1997) and are generally thought to play a minor role regarding energy flow (Jarre-Teichmann et al. 1997). Locally, however, some populations may reach considerable abundances and may play a significant role in nutrient cycling and benthic-pelagic coupling.

In nearshore waters of the Ross Sea the endemic scallop *Adamussium colbecki* (Smith, 1902) is the most abundant bivalve down to 100 m depth (Chiantore et al. 2001). *A. colbecki* 'banks' play an important role in the coastal food web as they process up to 14% of the total carbon flux (Chiantore et al. 1998) and represent an important food source for higher tropic levels, e.g. fish (*Trematomus bernacchii* Boulenger) and invertebrates such as *Neobuccinum eatoni* (Smith, 1875) and *Paraborlasia corrugata* (McIntosh, 1876) (Vacchi et al. 2000). Despite its widespread distribution and assumed significance for the system's energy flow (e.g. Stockton 1984, Berkman 1990, Albertelli et al. 1998, Chiantore et al. 1998, 2001), little is known about the population dynamics and production of this species.

This study presents the first reliable age determination of *A. colbecki* from Terra Nova Bay as confirmed by stable isotope analysis. Based on these data, production and productivity values are calculated in order to evaluate the significance of *A. colbecki* in the trophic web and energy flow of the coastal Ross Sea ecosystem.

Material and Methods

Sampling and processing of samples

Specimens were collected in Terra Nova Bay ('Road Cove', 74°41.9' S, 164°07.5' E) in austral summer 1999/2000 at 30 to 76 m depth by Charcot-Picard and naturalist dredge. Shell height (defined as the maximum distance between the dorsal hinge and ventral margin) of a representative subsample of 895 individuals was measured to the nearest 0.1mm using vernier callipers. A size frequency distribution (SFD) was obtained by pooling individuals using class intervals of 2mm size. Additional size frequency data from the same site, obtained with the same gear, have been provided by Chiantore et al. (2000), Cattaneo-Vietti et al. (1997) and references therein. To remove the fluctuations between years and obtain a more representative long-term 'average' population a multi-year size frequency distribution was constructed by pooling data taken from the years 1989/1990 to 1999/2000. Prior to pooling, each sample was converted into percentage values to give the same weight to each sample.

Size-mass relationships were modeled by linear regression of:

$\log(M) = \log(a) + b \cdot \log(SH)$ (1)

where M is the soft tissue mass (g) at shell height SH (mm). Gonad colouring was used for to determine sex of the individuals (Chiantore et al. 2002). Soft tissue dry masses (DM) were determined by oven drying of tissues at 60°C for 24 h.

Age and growth

Traditional methods of ageing *A. colbecki* such as counting bands on the shell surface (e.g. Stockton 1984, Berkman 1990) or on x-ray photographs (Ralph and Maxwell 1977, Cattaneo-Vietti et al. 1997) are not reliable without validation of annual formation of those bands, as shown for scallops in general by Krantz et al. (1984) and Dare and Deith (1990). We identified and verified annual growth bands in *A. colbecki* shells in a three-step procedure, (i) external growth band identification, (ii) comparison with internal growth band pattern, and (iii) validation of annual formation by stable isotope analysis.

In this study, only undamaged upper (left) shell valves free of epibionts were used for growth analysis. Prior to analysis shells were cleaned of organic matter with warm 5% NaOCl solution, washed with 96% ethanol, rinsed with water and dried at 60°C for 12 h. External, macroscopically visible shell surface growth bands were identified following the method described by Merril et al. (1965). This visual growth band pattern was compared with the pattern of conspicuous rings of higher density detected on x-ray photographs of the same shells. X-rays were taken by a Hewlett Packard Faxitron 43855 mammograph with fixed anode, using an AGFA – Strukturix D4 FW film and the following parameters settings: focal film distances 45cm, voltage 30 to 45 kV, exposure times 35 to 80 sec. To test whether or not identified growth bands are formed annually we analyzed stable isotopes of shell carbonate (for review see Richardson 2001). This approach has recently been applied successfully to identify annual growth patterns of Antarctic invertebrates (e.g. Marshall et al. 1996, Brey and Mackensen 1997) and of various scallops (e.g. Krantz et al. 1984, Tan et al. 1988, Dare and Deith 1990, Lasta et al. 2001). Stable oxygen ratios ($\delta^{18}O$) are inversely related to temperature (Epstein et al. 1953), hence lower $\delta^{18}O$ characterises shell parts deposited during spring/summer, whereas higher values correspond to parts formed during autumn/winter. Isotope analyses were performed on five representative specimens (largest individual 87-mm shell height). Calcium carbonate powder was sampled from the outer shell layer in equally spaced (~1mm) dorso-ventral series using a small dental drill (bit size 0.5mm). $\delta^{18}O$ were determined with a Finnigan MAT251 mass spectrometer coupled to an automatic carbonate preparation device. The results were reported in mil (‰) deviations related to the Pee Dee belemnite (PDB) standard through repeated analyses of National Bureau of Standard (NBS) isotopic reference material 19 (Hut 1987). The precision of measurements was better than ± 0.08‰, based on routine measurements of a laboratory-working standard.

On confirmation of annual formation of X-ray visible growth bands, shells of 25 individuals of *A. colbecki* (15 males, 10 females) were X-ray photographed. Number (i.e. age) and corresponding SH of each detectable X-ray growth band in each shell were recorded. A generalized von Bertalanffy growth model (gVBGF) was fitted to the resulting 185 size-at-age data pairs by an iterative non-linear least-square method (Newton algorithm, see Brey 2001, for details):

$$H_t = H_\infty \bullet (1 - e^{-K \bullet (t - t_0)})^D \qquad (2)$$

where H_t is shell height at time t, H_∞ is mean asymptotic shell height, K is the Brody growth coefficient, D determines the shape of the curve (inflection point if D>1) and t_o is age when shell height equals zero.

Production

Somatic production of soft tissue (P_S) was calculated by the mass- specific growth rate method according to Crisp (1984) and Brey (2001) from the SFD, the VBGF parameters and the appropriate size-mass relation:

$$P_S = \sum N_i \bullet M_i \bullet G_i \qquad (3)$$

where N_i and M_i = number of bivalves and mean individual somatic mass in size class i, respectively, and G_i = annual mass-specific growth rate which is computed by

$$G_i = b \bullet K \bullet (H_\infty - H_i) / H_i \qquad (4)$$

where b is the exponent of the size-mass relation (eq. 1), K and H_∞ are parameters of the von Bertalanffy function (eq. 2), and H_i is the mean height in size class i.

Since *A. colbecki* has a discrete reproductive cycle and spawns only once a year (Berkman et al. 1991), gonad production per total sample (P_G) was estimated by the decline of gonad mass before (summer) and after spawning (winter):

$$P_G = \sum N_i \bullet (M_{gonad\,(summer)} - M_{gonad\,(winter)}) \qquad (5)$$

where N_i is the number of bivalves in size class i and $M_{gonad\,(summer)}$ is the mean individual gonad mass in summer in size class i. $M_{gonad\,(winter)}$ values in this study were obtained from a linear regression calculated from measurements of some individuals maintained under simulated winter conditions in aquaria at the AWI (Germany, Bremerhaven):

$$\log M_{gonad\,(winter)}\ (\text{g DM}) = -6.342 + 2.52 \bullet \log \text{SH (mm)} \qquad (6)$$

Annual production/biomass ratios were calculated from somatic production (P_S), gonad production (P_G) and biomass per total sample ($B_S = \sum N_i\ M_i$). Annual production of *A. colbecki* per square metre was calculated by multiplying the P/B ratios with an estimate of average biomass derived from mean body mass per total sample and mean abundance at the sampling site (60 ind m^{-2}; Cattaneo-Vietti et al. 1997).

The following conversion factors were used:

1 g somatic DM = 20.22 kJ (Brey et al. 1988)
1 g gamete DM = 23.4 kJ (average according to MacDonald and Thompson 1985)
1 g C_{org} = 45.7 kJ (Brey 2001)

Results

Morphometrics

Size frequency distribution for several austral summers (Fig. 1a-g) showed a high persistency of large individuals (> 60mm), with large oscillations in the smaller size-classes (< 30mm). The multi-year size frequency distribution (Fig. 1h) was polymodal and dominated (> 50%) by large animals (> 66mm).

Mean soft tissue DM was 1.35g (SD = 1.4g) with a range from 0.12 to 5.2g. A slight but significant difference (ANCOVA: $P = 0.011$, n= 165) in size-soft tissue DM relation was found between males (log (g DM)= 2.882 • log (mm SH) – 4.832) and females (log (g DM)= 2.882 • log (mm SH) – 4.836). As the sex ratio was nearly 1:1 we did not differentiate between sexes and used the overall equation log (g DM)= 2.882 • log (mm SH) – 4.837 for all subsequent calculations. The relation between gonad dry mass and shell height was not significantly different between male and female animals (ANOVA of log-transformed data, $P > 0.5$) and can be described by the overall equation:

$$\log M_{gonad\,(summer)}\ (\text{g DM}) = -8238 + 4.058 \bullet \log (\text{mm SH}) \qquad N = 69;\ R^2 = 0.89;\ P < 0.01$$

Age and growth

X-ray bands could clearly be distinguished up to 80mm shell height; further growth bands closer to the shell edge could not be resolved accurately and were hence not included in the analysis. A comparison of external vs. X-ray bands showed a high degree of consistency (89.4%) in total number of growth bands, whereas the position of external and x-ray band differed quite often (up to 2/3 of all bands in one shell).

Fig. 2 shows X-ray photographs and corresponding $\delta^{18}O$ profiles of two representative *A. colbecki* shells from Terra Nova Bay. $\delta^{18}O$ values ranged from 3.04

‰ to 3.88 ‰ (Fig. 2b) and 3.13 to 3.92 ‰ (Fig. 2d) over the scallops lifetime, showing a cyclical pattern with a slight trend towards lower values with increasing height. 85% of all X-ray growth bands coincide spatially with a local $\delta^{18}O$ peak (Fig. 2a and b), indicating that these bands were formed at times of lowest temperature. The 185 size-at-age data pairs obtained from X-rays were fitted best by a general von Bertalanffy equation (Fig. 3)

$$H_t = 108.86\ \text{mm} \bullet (1 - e^{-0.114 \bullet (t + 0.367)})^{1.284} \qquad R^2 = 0.983$$

The analysis of the residuals of this model showed no significant differences in growth between males and females. The oldest individual found was estimated to be 18 years old (91.8mm height), but maximum age is likely to be higher.

Production and productivity

Total annual production for the season 1999/2000 amounted to 14.63 g DM m^{-2} y^{-1} (305.51 kJ m^{-2} y^{-1}), corresponding to an annual P_{tot}/B ratio of 0.251 (0.199 for soma and 0.052 for gonads). Individuals > 60mm contributed most to somatic as well as gonad production of the population (Fig. 4b). Mean annual biomass of *A. colbecki* was estimated to be with about 58.34 g DM m^{-2} (1179.64 kJ m^{-2}). From the multiyear size frequency distribution (1989-2000), average biomass, somatic tissue and gonad production were calculated to be 134.46 g DM m^{-2} (2718.78 kJ m^{-2}), 21.57 g DM m^{-2} y^{-1} (432.81 kJ m^{-2} y^{-1}), and 7.54 g DM m^{-2} y^{-1} (176.47 kJ m^{-2} y^{-1}), respectively. Annual P_{tot}/B ratio amounted to 0.215.

Discussion

Age determination

The general correlation between changes in seawater temperature and changes in shell $\delta^{18}O$ has already been demonstrated for molluscs living at temperatures close to 0°C (Marshall et al. 1993, Simstich et al. 2001), as well as for *A. colbecki* in particular (Barrera et al. 1990, Lohmann et al. 2001). Maximum $\delta^{18}O$ -amplitudes in the scallops investigated here correspond to an annual temperature range of about 2.6°C (Craig palaeotemperature equation cf. Marshall et al. 1993), which is in good agreement with the observed seawater temperature range of –1.8 to +0.75°C in the Ross Sea (Picco et al. 2000, Povero and Petrillo 2000). The slight overall trend to lower $\delta^{18}O$ values with increasing size and shell height up to 50 mm (Fig. 2b, d) is not uncommon in molluscs (e.g. Jones et al. 1986, Krantz et al. 1987, Weidman et al. 1994, McConnaughey et al. 1997). Such trends may be related to a continuous change in the relation of somatic to gonad production with age (Calow 1983) and/or to metabolic changes at onset of sexual maturity (Chiantore et al. 2000).

A mark-recapture study recently conducted in Terra Nova Bay and in the aquaria of the Alfred Wegener Institute in Bremerhaven (Chiantore et al. 2003) indicates that annual growth increments in *A. colbecki* are ≥1mm up to about 75mm shell height and 15 years of age. Therefore, the 1 mm spatial resolution of our isotope shell transects seems to be sufficient to resolve intra-annual $\delta^{18}O$ oscillations within this size and age range.

The annual water temperature cycle is assumed to be the major determinant of shell $\delta^{18}O$. Salinity fluctuations can change water $\delta^{18}O$ and hence may also affect shell $\delta^{18}O$ but this effect is of minor significance (Tan et al. 1988). Moreover, salinity fluctuations caused by ice formation and melting affect $\delta^{18}O$ in the same directions as temperature (Barrera et al. 1990) and hence will enhance the isotope signal. The annual water temperature cycle at Terra Nova has one peak in summer and one trough in winter. Therefore we conclude that one x-ray growth band is formed every winter in *A. colbecki*, as already shown for many other scallop species (e.g. Tan et al. 1988, Schick et al. 1988, Dare and Deith 1990, Lasta et al. 2001). In our example shells (Fig. 2) there are some $\delta^{18}O$ peaks without corresponding x-ray growth bands, i.e. in some winters no distinguishable band may be formed. This may cause underestimation of true age, but the large number of shells (N= 25) used here compensates this potential bias.

Growth of Adamussium colbecki

Previously published estimates of VBGF growth parameter values in *A. colbecki* are not directly comparable to our data, because those studies (e.g. Ralph and Maxwell 1977, Stockton 1984, Berkman 1990, Pranovi et al. 1994), (i) applied the specialized VBGF only, where the "shape" parameter D is set equal to one or (ii) were obtained from size-increment-data (Chiantore et al. 2003) (for a detailed discussion see Francis 1988). A common plot (Fig. 5), however, shows that all these growth models form a rather dense cluster of quite similar curves. Obvious differences may be caused partially by the application of the less reliable visual shell growth band analysis (Stockton 1984), partially by differences in population age structure, and partially by differences in environmental conditions between sites.

The index $P = \log (K M_\infty)$, where K is the growth rate constant K of the VBGF and M_∞ is inferred from H_∞, can be used to compare overall growth performance of different populations or species (Moreau et al. 1986). According to this measure, growth performance of scallops decreases with increasing latitude, and *A. colbecki* shows the lowest growth performance of all scallops investigated so far (Fig. 6a). In comparison to other Antarctic invertebrates, however, growth performance of *A.*

colbecki appears rather high (Fig. 6b). Actually, besides the bivalve *Laternula elliptica* (King and Broderip, 1831) (Ralph and Maxwell 1977, Urban and Mercuri 1998), *A. colbecki* shows the highest values of all Antarctic species investigated to date.

Production and productivity

Size frequency distributions of the *A. colbecki* population from Terra Nova Bay show distinct annual differences (Fig. 1). This seems to be caused by extreme year-to-year variability in recruitment success (Chiantore et al. 2001, 2002). Insufficient nutrition of adults and of larvae during summer may be the major reason for recruitment failures (Cattaneo-Vietti et al. 1999). Hence, production data referring to a single season such as 1999/2000 (Fig. 1g, P_{tot} = 305.51 kJ m^{-2} y^{-1}, P_{tot}/B = 0.251 y^{-1}) are poor representatives of the population steady-state, whereas estimates derived from a multi-year size frequency distribution (Fig. 1h, P_{tot} = 609.28 kJ m^{-2} y^{-1}, P_{tot}/B = 0.215 y^{-1}) are more representative from a long term point of view (Allen 1971). The strongly left-skewed multi-year distribution (Fig. 1h) is typical of slow growing, long-lived species and populations with irregular recruitment events (e.g. Brey et al. 1990, 1995b, Arntz et al. 1992).

So far this study presents the first attempt to estimate the gonad productivity of *A. colbecki* which is based on differences between gonadal mass before and after spawning. This approach assumes that all material stored during the mass increase in summer is devoted to reproduction, which may not be true. Precise spawning times are unknown. Berkman et al. (1991) presume spawning in McMurdo Sound during austral spring, while Cattaneo-Vietti et al. (1997) suggest that gonad maturation takes place in late summer. P_S/B as well as P_{tot}/B of *A. colbecki* are at the lower end of the range reported for scallops, even when the scaling effect of average individual body mass is taken into account (Fig. 7). This coincides well with the comparatively low overall growth performance (Fig. 6) and indicates that the temperature induced low metabolism of individual *A. colbecki* (Heilmayer et al. 2002) is reflected at the level of population turnover, as also found in other Antarctic invertebrates (Brey and Clarke 1993, Brey et al. 1995a, b, Urban and Mercuri 1998).

Ecological significance

The ecological significance of *A. colbecki* in the Terra Nova Bay ecosystem is defined by its position in the food web and by the amount of energy flowing through the population. As *A. colbecki* is a suspension feeder, it represents a direct link between pelagic primary production and benthic or demersal higher level predators. Known predators of *A. colbecki* are *Trematomus bernacchii* and invertebrates such as *N. eatoni* and *Odontaster validus* (Vacchi et al. 2000). According to our results, about 433 kJ m^{-2} y^{-1} (ca 9.5 g C m^{-2} y^{-1}) are transferred from the scallop to its predators.

The question how much *A. colbecki* in Terra Nova Bay consumes and whether this dense population living in the euphotic zone may be able to control primary production as already observed in populations from temperate waters (see Smaal and Prins 1993, Dolmer 2000) is more difficult to answer. Of the simple energy budget (see Crisp 1984):

Consumption = Production + Respiration + Egestion + Excretion

total production, 609 kJ m^{-2} y^{-1}, and respiration, 1558 kJ m^{-2} y^{-1} (whole year average, calculated from measurements of summer and winter metabolism, Heilmayer et al. 2002), are known, i.e. annual assimilation amounts to 2167 kJ m^{-2} y^{-1} (all estimates referring to the long term average population structure, Fig. 1h). Chiantore et al. (1998) found the assimilation efficiency (100 *x* Assimilation /Consumption) of *A. colbecki* to be about 36%, hence the annual consumption of the Terra Nova Bay population is about 6000 kJ m^{-2} y^{-1} (ca 131 g C m^{-2} y^{-1}). Using Albertelli et al.'s (1998) estimate of daily sedimentation rate in Terra Nova Bay, 0.36 g C m^{-2} day^{-1}, and assuming a productive phase of about 60 days per year (Albertelli et al. 1998), the annual input to the benthos is about 1000 kJ m^{-2} y^{-1} (22 g C m^{-2} y^{-1}), i.e. about 17% of the food required by the *A. colbecki* population. Even if we allow for distinct interannual variability of production and duration of productive phase, this is far too low to maintain the *A. colbecki* population investigated. Potential additional food sources may be (i) ice algae, (ii) macroalgal detritus, or (iii) lateral advection of organic matter from the open Ross Sea. Ice algae can contribute significantly to total primary production (Spindler and Dieckmann 1991, Melnikov 1998), but their production in Terra Nova Bay has not yet been determined. The same is true for macroalgal detritus, which is known to be produced in large quantities on littoral rocky shores (Berkman et al. 1986, Albertelli et al. 1998). Lateral advection of organic matter is supposed to play a significant role in Antarctic coastal and shelf systems (Dayton 1990, Brey et al. 1993, 1995a, Arntz et al. 1994), and the open Ross Sea is a potential source of matter laterally advected to Terra Nova Bay. With primary production rates up to 180 g C m^{-2} y^{-1} (~8200 kJ m^{-2} y^{-1}) and average sedimentation rates of 97% (Fabiano et al. 1997, Saggiomo et al. 2000) the Ross Sea is considered to be the most productive system in the Southern Ocean (Smith et al. 1996).

Further quantitative and qualitative studies of whole year sedimentation in TNB will answer open questions and may be the key to explain the interannual variability in *A. colbecki* recruitment and population structure.

Acknowledgements

This research could only be realised, thanks to the support by the Italian National Programme for Antarctic Research (PNRA) and the Alfred Wegener Institute for Polar and Marine Research. We are grateful to Ute Jacob and Michael Seebeck (AWI) for preparation of X-ray photographs as well as to Katrin Blancke and Andreas Mackensen (AWI) for technical support in stable isotope analysis. We are indebted to P.A. Berkman for a critical discussion and many helpful comments on an earlier draft of the manuscript. Sandra Shumway and an anonymous reviewer referee are acknowledged for many helpful comments and linguistic corrections. [SS]

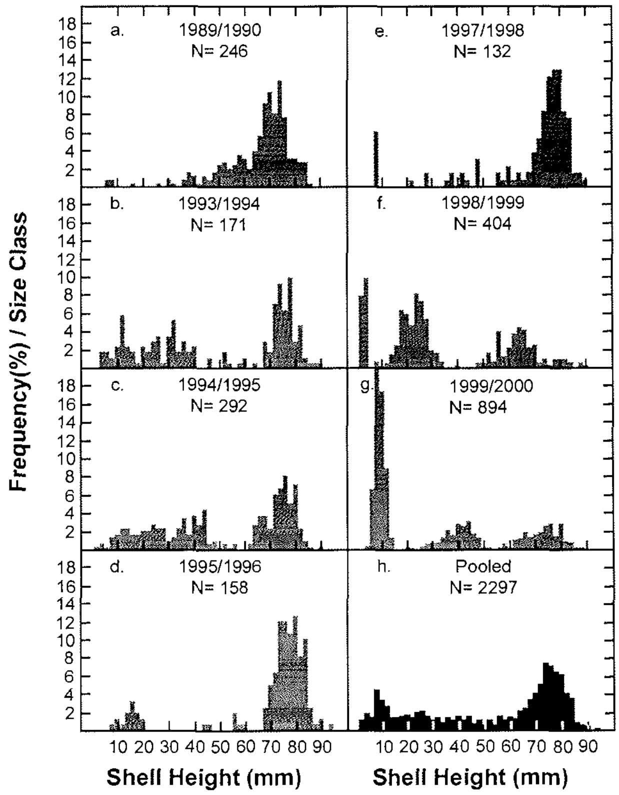

Figure 1

A. colbecki. Size frequency distribution in Terra Nova Bay ('Road Cove') using class intervals of 2mm: (a and b) in austral summer 1989/1990, 1993/1994 (redrawn from Cattaneo-Vietti et al. 1997), (c and d) in austral summer 1994/1995, 1995/1996 (redrawn from Chiantore et al. 2000), (e) in austral summer 1997/1998 (Chiantore and Cattaneo-Vietti unpublished data), (f) in austral summer 1998/1999 (redrawn from Chiantore et al. 2001), g. in January 2000, (h) pooled samples (1989/1990 to 1999/2000).

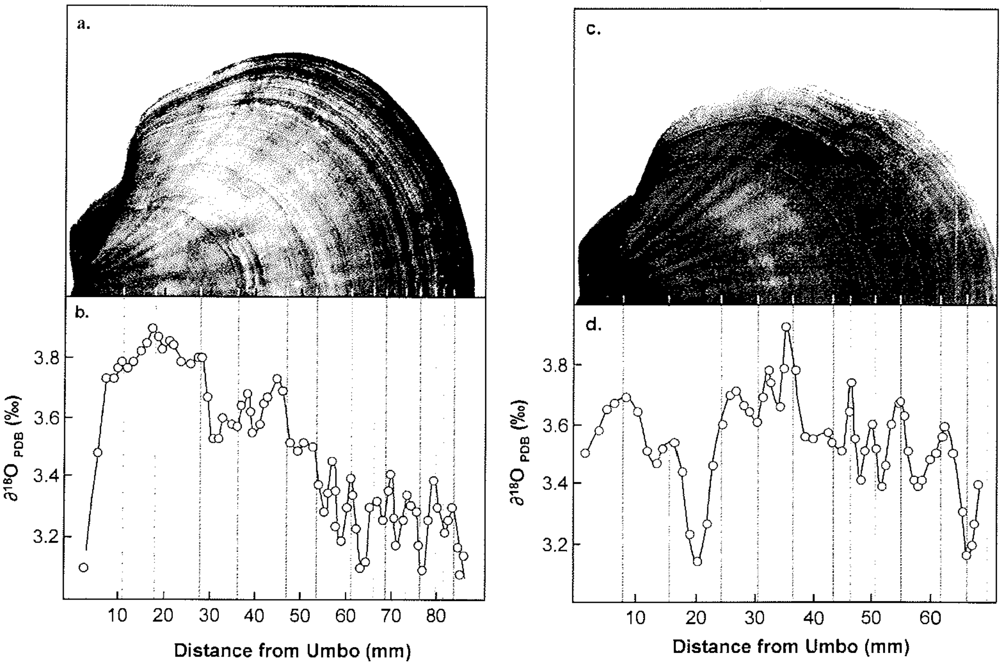

Figure 2

A. colbecki. X-ray photographs ((a) 87.1mm SH, (c) 72.1mm SH) and corresponding stable oxygen isotope ratio profiles ((b) 74 samples, (d) 62 samples) of two specimen. Grey bars indicate internal growth bands. $\delta^{18}O$ is plotted as weighed moving average $((x_1+ 2\cdot x_2 +x_3)/ 4)$.

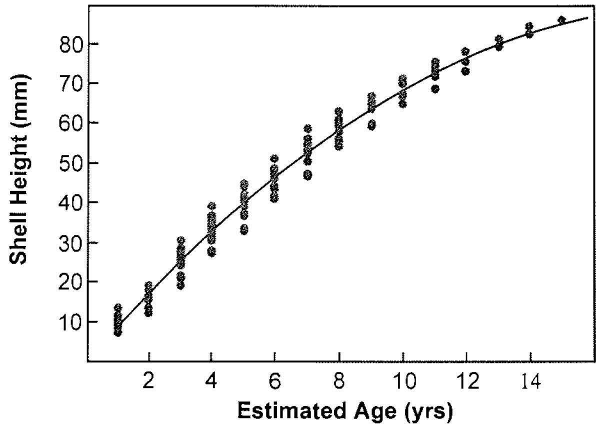

Figure 3

A. colbecki. General von Bertalanffy growth function fitted to size-at-age data obtained from 25 X-ray photographed shells. Growth function parameters are:

H_∞= 108.86 mm, K= 0.114, D= 1.284, t_0= -0.367 (N=185, R^2= 0.983)

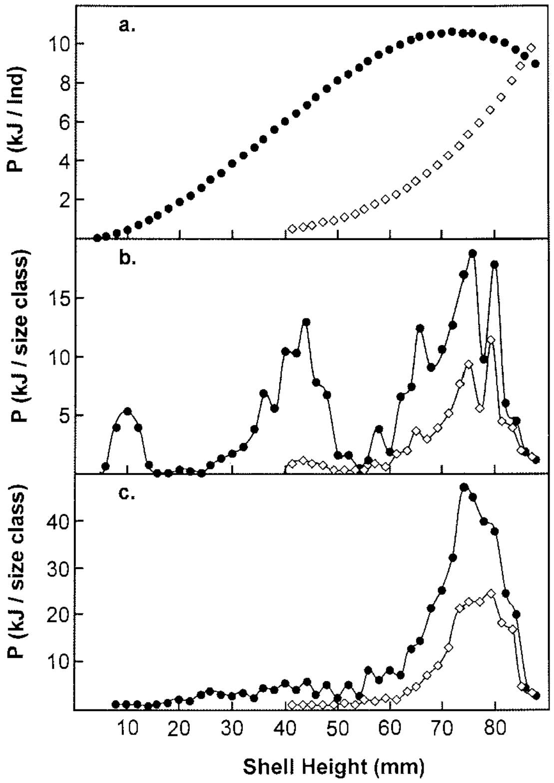

Figure 4

A. colbecki. (a) Individual production of somatic tissues and individual gonad production for different size classes (b) Size specific distribution of annual somatic tissues and gonad production at the population level, based on SFD from austral summer 1999/00 (c) As in (b) but based on the multiyear SFD 1989-2000.

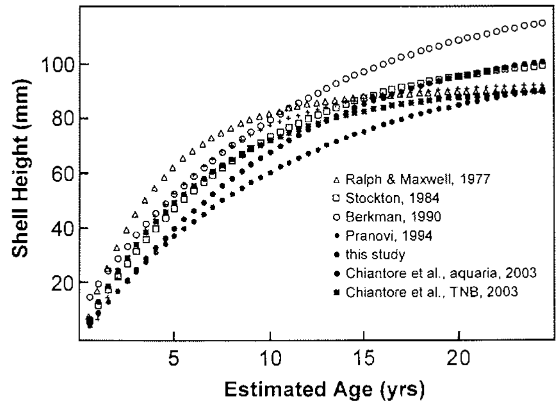

Figure 5

Von Bertalanffy growth functions of *A. colbecki* populations published by various authors. VBGF parameters: Ralph and Maxwell (1977), H_∞= 90mm, K= 0.24, D set to 1; Stockton

(1984), H_∞= 105mm, K= 0.12, D set to 1; Berkman (1990), H_∞= 128mm, K= 0.09, D set to 1; Pranovi et al. (1994), H_∞= 93mm, K= 0.19, D set to 1; Chiantore et al. (2003, TNB) H_∞= 92mm, K= 0.154, D set to 1; Chiantore et al. (2003, aquaria) H_∞= 101mm, K= 0.09, D set to 1; this study, H_∞= 108.86mm, K= 0.114, D =1.284

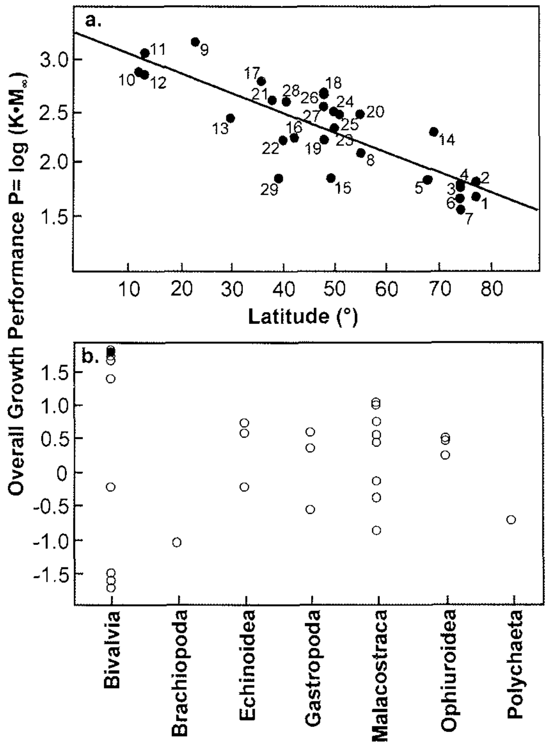

Figure 6

Overall growth performance (P = log(KM_∞)) in (a) scallops populations world-wide and (b) Antarctic invertebrates of different taxons compared with *A. colbecki* from this study (filled dot). Data Sources. (a) 1-5: *A. colbecki* (1: Stockton 1984; 2: Berkman 1990; 3: this study; 4: Pranovi et al. 1994; 5: Ralph and Maxwell 1977; 6: Chiantore et al. 2003, wild population 7: Chiantore et al. 2003, aquaria), 8: *Aequipecten opercularis* (Allison 1994), 9: *Amusium japonicum* (Williams and Dredge 1981), 10: *Amusium pleuronectes* (Nugranad 1988, fidem Vakily 1992), 11-13: *Argopecten purpuratus* (11: Yamashiro and Mendo 1988; 12: Mendo and Jurado 1993; 13: Tomicic and Kong 1978, in Wolff 1994), 14-15: *Chlamys islandica* (14: Vahl 1981a; 15: Naidu et al. 1982, in Orensanz et al. 1991a), 16: *Chlamys techuela* (Orensanz 1986), 17: *Mizuhopecten yessoensis* (Yoo et al. 1981), 18-20: *Patinopecten caurinus* (18: Haynes and Hitz 1971, 19: MacDonald and Bourne 1987; 20: Ignell and Haynes 2000), 21: *Pecten alba* (Gwyther and McShane 1988), 22: *Pecten fumata* (Fairbridge 1953), 23-25: *Pecten maximus* (23: Dare and Deith 1990; 24: Dare 1991; 25: Allison 1994), 26-28:

Placopecten magellanicus (26-27 MacDonald and Thompson 1985, 1986; 28: Thouzeau et al. 1991), 29: *Zygochlamys patagonica* (Lasta et al. 2001) Regression line: P= 3.257 – 0.019 • latitude (°); N= 29; R^2=0.686

(b) Brey and Clarke (1993), Brey (1999) and references therein.

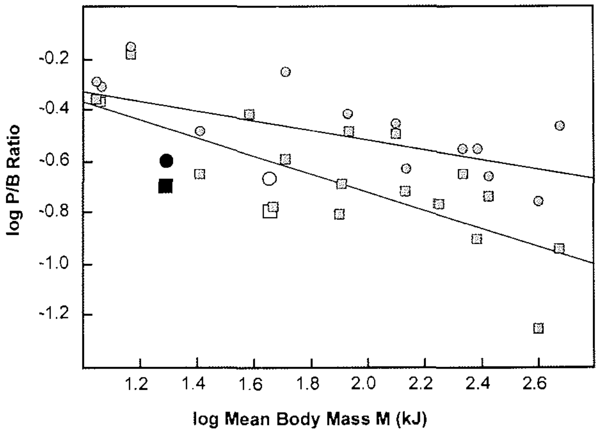

Figure 7

Annual P_S/B ratio (circles) and P_{tot}/B ratio (squares) versus mean body mass (kJ) in scallop populations. Data Sources: *Adamussium colbecki* (Stockton 1984, Berkman 1990), *C. islandica* (Vahl 1981b), *Comptopallium radula* (Lefort 1994), *Crassadoma gigantea* (MacDonald et al. 1991), *Mimachlamys gloriosa* (Lefort 1994), *Mimachlamys varia* (Shafee and Conan 1984), *Mizuhopecten yessoensis* (Golikov and Scarlato 1970), *Patinopecten caurinus* (MacDonald and Bourne 1987), *Placopecten magellanicus* (MacDonald and Thompson 1985, 1986, Claereboudt and Himmelman 1996), *Zygochlamys patagonica (*Lasta et al. 2001). Black symbols: *A. colbecki*, this study- season 1999/2000, open symbols: this study- based on multi-year SFD. Regression lines:

(dots) $\log(P_S/B) = -0.024 - 0.345 \cdot \log(M)$; $N= 20; R^2= 0.536; p< 0.01$

(squares) $\log(P_{tot}/B)= -0.146 - 0.186 \cdot \log(M)$; $N= 15; R^2= 0.383; p<0.05$

Publication II

Saving by freezing? Metabolic rates of Adamussium colbecki in a latitudinal context

Olaf Heilmayer (✉) and Thomas Brey

Alfred Wegener Institute for Polar and Marine Research, P.O. Box 120161,
27515 Bremerhaven, Germany

Abstract

Standard metabolic rates of the endemic Antarctic scallop, *Adamussium colbecki* (Smith, 1902), were measured in austral summer and under simulated winter conditions. Average mass-specific metabolic rates were significantly different between 'summer' (151.17 ± 45.06 µl O_2 g^{-1} h^{-1}) and 'winter' (106.52 ± 39.65 µl O_2 g^{-1} h^{-1}) animals. The overall metabolic rates of *A. colbecki* are comparable to those of other Antarctic bivalve species, but well below those of temperate scallop species. Data for 24 scallop populations (13 species) from different latitudes give no evidence for elevated metabolic rates in *A. colbecki* as suggested by the concept of 'metabolic cold adaptation'. A world-wide comparison of metabolic rate and overall growth performance of scallops indicates that in the Antarctic scallop the energetic advantage of low basal metabolism does not counterbalance the disadvantage of the prolonged seasonal period of food shortage.

Keywords

Antarctic scallop; *Adamussium colbecki*; Metabolic rates; "Metabolic cold adaptation"; Seasonal metabolism

---

Reprinted from *Marine Biology*, 143(3): 477-484, Copyright (2003), Springer Verlag

Introduction

Antarctic benthic invertebrates exhibit slow growth, low *P/B* ratios (Brey and Clarke 1993), prolonged longevity, low activity (Arntz et al. 1994) and low metabolic rates (e.g. Ralph and Maxwell 1977, Luxmoore 1984, Chapelle and Peck 1995, Ahn and Shim 1998). In high latitude marine systems, food availability is strongly seasonal and spatially patchy, whereas the temperature dependence of biochemical processes causes a general slowdown of metabolism (Peck et al. 1997, Clarke 1998, Pörtner et al. 2000). Evolutionary adaption to these conditions may follow two alternative pathways: On the one hand, animals may be selected for enhanced "endurance", i.e. the ability to survive prolonged periods without food by reducing metabolic activity and/or increasing metabolic efficiency compared to temperate animals. Consequently, comparatively more energy could be channeled into growth and reproduction (Crockett and Sidell 1990, Clarke 1991). On the other hand, evolution could tend towards comparatively higher metabolic rates to enable the animal to be more active, as assumed by the hypothesis of "metabolic cold adaptation" (Krogh 1916, Wohlschlag 1964, for review see Peck 2002). Consequently, comparatively less energy could be channeled into growth and reproduction (for a detailed discussion Clarke 1983, 1991 and Pörtner 2002a). Some studies found evidence for metabolic cold adaptation in Antarctic fish (Wohlschlag 1964, Forster et al. 1987, Hardewig et al. 1998). Other studies in fish (Clarke and Johnston 1999) and invertebrates (Ivleva 1980, Luxmoore 1984, Peck and Conway 2000), however, could not confirm these findings. Only the latter two studies considered benthic organisms to a greater extent, but they compiled respiration data of a wide variety of taxa. Therefore, small differences in metabolic activity related to other factors than temperature may have been obscured by statistical "noise" owing to differences in body size, life history and ecology. Hence we focussed our study on one single family, the Pectinidae, i.e. organisms with very similar body size, body shape, lifestyle, and life history features.

The endemic Antarctic scallop, *Adamussium colbecki* (Smith, 1902), is a common abundant member of the Antarctic nearshore fauna with a circumpolar distribution (Ralph and Maxwell 1977, Berkman 1990). Highest densities are found above 100 m water depth (Chiantore et al. 2001), but single animals have been reported from depths down to 1500 meters (Dell 1990).

We measured standard metabolic rates and overall growth performance of *A. colbecki* and collected similar data from the literature referring to 23 scallop populations (12 species) from tropical to north polar habitats. Based on these data, we tried to answer two questions: (i) Does the Antarctic scallop show any signs of metabolic adaptions specific to the Antarctic environment, and (ii) is, among scallops, living at constantly low temperatures energetically 'cheaper'?

Material and Methods

Sampling and maintenance

Experimental specimens of *Adamussium colbecki* were collected in January and February 2000 from sites near the Italian Antarctic station 'Terra Nova Bay' (74°41.9' S, 164°07.5' E) either by SCUBA diving or with a naturalist's dredge. In the Bay of Terra Nova (Ross Sea) *A. colbecki* is common between 5 and 80 m depth, with densities up to 60 ind m^{-2} (Chiantore et al. 2001). Water temperatures range from +1°C in summer to –1.9°C in winter, salinity is always close to 34 psu, available food is up to 0.33 g C m^{-2} ind^{-1} in summer (Albertelli et al. 1998, Povero and Petrillo 2000). After sampling, animals were immediately transported to the laboratory at the station and cleaned of epibionts using a toothbrush. Thereafter they were maintained in aerated flow-through aquaria at ambient temperature (0 - 0.5°C), salinity (34 psu), and seston levels under natural light regime until further experimental use. For winter oxygen consumption measurements, 100 scallops were transported by plane to the Alfred Wegener Institute (AWI, Germany) at the end of February. They were maintained in cooled aquaria with recirculating seawater (0 ± 0.5°C, 33- 34 psu) in a 12 h dimmed light: 12 h dark daily light regime. Animals were fed twice a week by adding 6 Planktontabs (HOBBY, Dohse Aquaristik) dissolved in 500 ml water to each aquaria tank (0.01 g C m^{-2} ind^{-1} at each feeding day, approx. 3% of summer amount). No deaths occurred after an acclimation period of four weeks.

Measurement of metabolic activity

Oxygen consumption was taken as a proxy of total metabolic activity. Summer metabolism was measured at Terra Nova Bay station 5 - 20 days after collection. Winter metabolism was measured under simulated winter conditions in the laboratory at AWI. To obtain data as close as possible to standard (resting) metabolic rates, as defined by Bayne et al. (1976), animals were prepared as follows before measurements:

(i) 'Summer'-animals were deprived of food for 3 days, 'winter'-animals for 7 days prior to experiments in order to minimise the effects of specific dynamic action of feeding (Wieser and Medgysey 1990). (ii) To avoid handling stress, scallops were allowed to accommodate for 24-36 h to the respiration chambers prior to the start of measurements (e.g. Chapelle and Peck 1995); and (iii) during each measurement run, animals were monitored at least 15 min at the start, once or twice during and at the end of the run. Specimens that did not open their valves and protrude their tentacles in a manner similar to undisturbed scallops or which changed their position within one trial were disregarded. Thus, the measured rate approximated to the sum of metabolic activities needed to keep the organism alive.

Respiration measurements were carried out using an intermittent flow- through system (Fig. 1), which combines the advantages of closed chamber and flow-through systems (Forstner 1983). Respiration chambers were small perspex cylinders with a movable lid to adjust chamber volume (50-600 ml) to animal size (for technical details see Gatti et al. 2002). Experimental temperature was maintained at 0 ± 0.3°C by placing the chambers in a water bath set in a jacketed container that was connected to a thermocirculator (Lauda RS 6 CP). Each experiment consisted of a number of subsequent measurement runs (closed system stage). Each run started with fully oxygenated water (saturation close to 100%) and ended when oxygen saturation fell to 75%. Thereafter the water was renewed (flow- through system stage) and a new measurement run started. Each run lasted 2 to 5 hrs, depending on individual oxygen consumption, each animal went through 2-4 runs (maximum duration of one experiment was 24 hrs). During closed system stage water was continuously circulated between respiration chamber and measuring optode (Fig. 1) by MASTERFLEX peristaltic pumps (model 7521-40 with a pump head system model 7519-05). In each experiment six respiration chambers with only one scallop each (all of approximately the same size) and a control chamber (without scallop) were measured simultaneously.

Oxygen content in the chambers was monitored continuously with oxygen microoptodes connected to an MICROX-8 array (PreSens GmbH, Neuweiler, Germany). The measuring principle of microoptodes is based on dynamic fluorescence quenching of an immobilised oxygen-sensitive fluorophor (for details see Klimant et al. 1995; for specific advantages of microoptodes for cold water oxygen measurements see Gatti et al. 2002).

Immediately after the end of each experiment, animals were dissected and soft tissue wet masses (WM) were determined to the nearest 0.1 mg after careful blotting with a paper. The tissues were frozen at –80°C for analysis of enzymatic activities (see Heilmayer et al. 2002). WM was converted to soft tissue dry mass (DM) by the conversion factor 0.159 obtained from a separate sample of 234 animals.

Calculation of metabolic rates

Metabolic rates (VO_2 in µmol O_2 ind^{-1} h^{-1}) were calculated from the slope of the oxygen evolution curve, after transforming the percent O_2 saturation to micromoles of dissolved oxygen in seawater using known values of oxygen solubility (Benson and Krause 1984) by

$$VO_2 = \left(\frac{sat_0}{sat_{60}} \bullet 100\right) \bullet \alpha_{O_2} \bullet V_{Chamber} \qquad (1)$$

where α_{O2} is the oxygen solubility in seawater [µmol • dm^{-3}], $V_{Chamber}$ the volume of respiration chamber and tubing [dm^3], sat_0 the oxygen saturation [%] at beginning of experiment and sat_{60} the oxygen saturation [%] after 60 min as calculated from linear regression. Individual metabolic rates were corrected with the oxygen consumption of control chambers (no animal) and converted to millilitres O_2 by 44.66 µmol O_2 = 1 ml O_2 (Brey 2001). Metabolic rates were related to soft tissue DM by:

$$VO_2 = a \bullet DM^b \qquad (2)$$

where *a* is a constant and *b* the scaling exponent. The model was fitted by least squares linear regression after logarithmic transformation of both variables.

Computation of standard metabolic rates (SMR)

To remove the effect of body mass (Luxmoore 1984, Packard and Boardman 1999) all oxygen data were converted to a standard animal size of 1 g dry mass (DM_S). For studies providing individual metabolic values (VO_2), Individual Standard Metabolic Rates (SMR_{Ind}) could be calculated for each animal by

$$SMR_{Ind} = VO_2 \bullet (DM_S / DM_E)^b \qquad (3)$$

where DM_E was the soft tissue dry mass of the experimental animal and *b* the mass exponent of the oxygen consumption-to-soft tissue dry mass relation (Kleiber 1975, Packard and Boardman 1999). For those studies that provided no individual data but only an overall allometric relationship between oxygen consumption and body mass for the whole population, Population Average Standard Metabolic Rates (SMR_{Avg}) as described by Luxmoore (1984) were computed by

$$SMR_{Avg} = a \bullet DM_{mean}^{\,b - 0.807} \qquad (4)$$

where *a* and *b* are the constants from the appropriate physiological function and DM_{mean} is the geometric mean dry mass determined from the mass range of the experimental data. *0.807* was the mean family-specific mass exponent determined in

81 studies with most values ranging between 0.7 and 0.9 (Heilmayer unpublished data compilation).

Literature data constraints

Published data on metabolic rate of other scallop populations were included in this study only if these data (i) referred to inactive animals (= resting metabolism), (ii) were conducted in the normal temperature range of the species, (iii) covered a sufficient range of body mass.

Statistical analysis

Hypothesis I: specific metabolic adaptions

To test whether (H_A) Antarctic scallops exhibit metabolic adaptions specific to the Antarctic environment or (H_0) differences in metabolism of Antarctic and non-Antarctic scallops are related to temperature only, we ran two analyses, one based on population average standard metabolic rates (SMR_{Avg}) and one based on individual standard metabolic rates (SMR_{Ind}). In both cases, an Arrhenius equation was fitted to the relationship between SMR and absolute temperature (T). Regarding SMR_{Avg}, we checked whether the rates of *A. colbecki* were situated within the 95% confidence limits of the fitted Arrhenius model. Regarding SMR_{Ind}, an ANCOVA ($\ln(SMR_{Ind})$ versus "Antarctic ↔ non-Antarctic" and 1/T) was applied.

Hypothesis II: investment in somatic growth

Energy spent on basal metabolism is ecologically 'wasted' in the sense that it is not used for growth, reproduction or activity (for a detailed discussion see Parry 1983, Clarke 1987, 1991). Provided that all other parameters such as assimilation efficiency are independent of temperature, a reduced metabolic rate, as expected for *A. colbecki*, should point towards an enhanced ecological growth efficiency. To test whether (H_A) Antarctic scallops invest comparatively more energy into somatic growth or whether (H_0) there is no difference to non-Antarctic scallops, we compared the ratio between somatic growth performance and SMR in *A. colbecki* and 12 non-Antarctic scallop populations. We used the 'overall growth performance' (OGP) index *P* of Moreau et al. (1986) as a proxy of lifetime somatic growth performance (for more details Brey 2001)

$$P = \log(K + M_\infty) \qquad (5)$$

where *K* and M_∞ are parameters of the von Bertalanffy growth function (VBGF). As the index *P* is proportional to the maximum rate of body mass increase during the lifetime (Pauly and Munro 1984), the SMR at the inflexion point of the growth model was used to calculate the *P-to-SMR* ratio. The residuals of the linear regression of

P/SMR versus *T* were checked by ANOVA for significant deviation of the values referring to *A. colbecki*. As size mass relations were not available for all 13 populations included, M_∞ was computed from H_∞ (mean asymptotic shell height, taken from the appropriate VBGF) and a common size-mass relation for scallops derived from 46 studies (Heilmayer unpublished data compilation)

$\log(M_\infty) = -4.38 + 2.846 \cdot \log(H_\infty)$ (6)

According to Feldman and McMahon (1983) this method is not expected to cause a statistical artifact.

Results

Adamussium colbecki measurements

The relation between body dry mass and shell height was not significantly different between summer and winter animals (ANCOVA of log-transformed data, $p = 0.4$) and can be described by the overall equation:

'summer' $\log(DM) = -5.862 + 3.446 \cdot \log(SH)$ $(N = 89, r^2 = 0.944)$

'winter' $\log(DM) = -6.634 + 3.749 \cdot \log(SH)$ $(N = 14, r^2 = 0.955)$

Metabolic rates (VO_2) of summer animals varied between 7.81 and 751.41 µl animal^{-1} h^{-1} and were related to body mass by (Fig. 2a):

$\log(VO_2) = 2.161 + 0.911 \cdot \log(DM)$ $(N = 235, r^2 = 0.902, p < 0.001)$

Winter metabolic rates ranged from 30.64 to 289.4 µl animal^{-1} h^{-1} and were related to body mass by (Fig. 2b):

$\log(VO_2) = 2.002 + 0.717 \cdot \log(DM)$ $(N = 35, r^2 = 0.658, p < 0.001)$

An ANCOVA (log metabolic rate vs season, covariate log DM, only animals between 0.24 and 2.5 g DM, $p < 0.02$) showed that intercept (t-value = 175.86, $p < 0.001$) and slope (t-value = 21.13, $p < 0.001$) are significantly different. Metabolic rates of standard-sized *A. colbecki* (SMR_{Ind}) were in 'summer' (151.17 ± 45.06 µl O_2 g^{-1} h^{-1}) approximately 42% higher than in 'winter' animals (106.52 ± 39.65 µl O_2 g^{-1} h^{-1}).

Metabolic rates in scallops

Population average standard metabolic rates (SMR_{Avg}) of scallops are significantly and positively related to temperature, as indicated by the Arrhenius equation:

$\ln(SMR_{Avg}) = 30.011 - 8844.658 \cdot 1/T$ (N = 80, 13 species, $r^2 = 0.714$, $p < 0.001$)

Mean 'summer' and 'winter' values of *A. colbecki* were situated within the 95% confidence range of the model (Fig. 3a). ANCOVA of the individually measured standard metabolic rates (SMR_{Ind}) (rate vs Antarctic ↔ non-Antarctic, covariate 1/T) provided no evidence for significant effects of the parameter "Antarctic" on metabolism ($F = 0.532$, $p > 0.1$). Hence Hypothesis I_A is rejected and a common Arrhenius equation can be applied to the whole temperature range (Fig. 3b):

$\ln(SMR_{Ind}) = 11.904 - 3810.318 \cdot 1/T$ ($N = 936$, 7 species, $r^2 = 0.287$, $p < 0.01$)

Metabolic investment in somatic growth

The ratio *P/SMR* is negatively related to temperature, i.e. the share of somatic growth in total metabolism decreases with increasing temperature (Fig. 4):

$P/SMR_{Avg} = 19.003 - 0.903 \cdot T$ ($N = 13$, 7 species, $r^2 = 0.496$, $p < 0.001$)

No significant additional regional effects were detected by ANCOVA ($p > 0.5$), i.e. Hypothesis II_A is rejected.

Discussion and Conclusion

Metabolism of Adamussium colbecki

Our result indicate that metabolic activity of *A. colbecki* is significantly higher in 'summer' than in 'winter' (Fig. 2), as observed in many boreal bivalves (Bayne et al. 1976, Ansell et al. 1980, Bricelj et al. 1987, Shumway et al. 1988) as well as in Antarctic invertebrates (Peck et al. 1987, Brockington 2001, Brockington and Clarke 2001). A seasonal change in poikilotherm metabolism may be related to a variety of environmental parameters, of which temperature and food supply are assumed to be the most important ones. Regarding boreal bivalves, some investigations emphasize the significance of temperature effects (see e.g. Worrall et al. 1983, Thompson 1984), whereas others suggest that food supply plays a more important role (e.g. Vahl 1978, MacDonald and Bourne 1987, MacDonald and Thompson 1988). In sublitoral Antarctic environments the annual range in seawater temperature rarely exceeds 3°C, and hence the marked seasonality of food availability is supposed to be the major determinant of metabolic activity in Antarctic invertebrates (Clarke 1988, Brockington and Clarke 2001). Our experiments reflect these conditions, as temperature is about 0°C during both "summer" and "winter" measurements, whereas "winter" food supply is only 3% of measured "summer" values".

Both the intercept and the slope of the log-log body mass-to-metabolism relationship (Fig. 2) are significantly different between 'summer' and 'winter'. The difference in the intercept (2.161 to 2.002) signifies an increase up to 44% in 'summer' metabolism across the whole body mass range. This difference in the intercept is likely to reflect either a seasonal induced change of environmental factors (food availability, light) or an endogenic metabolic cycle, which results e.g. in reduced or atrophied digestive mechanisms (Clarke 1991, Brockington et al. 2001). The significantly higher slope (i.e. the mass scaling exponent, 0.911 versus 0.717) represents an additional increase in summer metabolism. We believe this additional part to reflect active (somatic and gonad) growth, as it seems to scale almost linearly to body mass (Fig. 5, Jørgensen 1988). The absolute values should not be taken too seriously, because the different body mass ranges and animal numbers the two regressions are based on may have caused slight aberrations, as indicated by the negative values below 1 g body mass. Identical patterns and similar differences of the mass scaling exponent (higher during the growing season, significantly lower in winter), however, were found in *Argopecten irradians irradians* (Bricelj et al. 1987), *Chlamys islandica* (Vahl 1978, 1981b) and *Mizuhopecten yessoensis* (Fuji and Hashizume 1974). These observations support Wieser (1994) and Jørgensen (1988) who suggest that a mass scaling exponent of metabolism close to 1.0 reflects active growth, whereas exponents around 0.75 are indicative of maintenance metabolism only.

Metabolism and temperature

Metabolic rates of *A. colbecki* are within the range reported for polar bivalve molluscs (Peck and Conway 2000), but among the lowest values reported for temperate and tropical scallops so far (Fig. 3a, b). Metabolism in bivalves is primarily a function of temperature, which can be described best by an Arrhenius model (Peck and Conway 2000). About 70% of the overall variation in population average standard metabolic rates (SMR_{Avg}) are explained by temperature in our Arrhenius model (Fig. 3a). This is distinctly better than comparable models for fish (55-59%, Clarke and Johnston 1999) and bivalves in general (47%, Peck and Conway 2000). Obviously our more monophyletic approach reduces life-style-related noise in the relation between metabolism and temperature to a certain extent. Different experimental setups as well as differences in reproductive stage may explain the remaining 30% variance. Neither the model based on SMR_{Avg} data (Fig. 3a) nor the one based on SMR_{Ind} data (Fig. 3b) provide any support for a significant elevation of the whole-organism metabolism of *A. colbecki* compared to non-Antarctic species. Hence our study support the conclusion of Clarke and Johnston (1999) and Peck and Conway (2000) that there is no 'metabolic cold adaptation' (MCA, *sensu* Krogh 1916) on the level of organisms. Furthermore, neither metabolism nor animal behavior gives any evidence for incomplete adaptation or 'extra' savings, e.g. 'hibernation' or failing response to stimulation (pers. observ.). As Ansell et al. (1998), we could not find any evidence for a reduced swimming performance in *Adamussium colbecki* compared to temperate scallop species, although data for the maximum instantaneous capacities are not available so far.

It is generally accepted, however, that organisms inhabiting low temperature environments must have developed specific physiological adaptations at the cellular level (i.e. mitochondrial proliferation) to overcome the adverse effects of low temperatures on metabolism. This cellular MCA will, on the other hand, cause a rise in oxygen demand (e.g. Johnston et al. 1994, 1998, Clarke 1998, Somero et al. 1998, Pörtner et al. 2000, Pörtner 2002a, b). The question arises at which organisational level those energy savings occur which counterbalance the cost of cellular MCA, as there is no evidence for MCA in whole animal metabolism. Low rates of oxygen demand at low temperature are most likely related to a reduced ATP demand for protein turnover, ion pump activity and other aspects of basal metabolism (Clarke 1987). Especially protein turnover costs, which form a substantial fraction of resting metabolic costs (Hawkins et al. 1989, Wieser 1994), seem to be distinctly lower at low temperatures (Smith and Haschmeyer 1980, Clarke 1998). In the case of *A. colbecki*, increased protein stability leads to lower protein turnover (Storch and Pörtner 2003). Further savings are related to the downregulation of amount and flexibility of acid-base regulation (Pörtner 2002b).

Metabolism and growth

Our analysis of the relationship between ecological growth efficiency and temperature is based on a rather limited set of populations, where growth performance (P) and metabolic activity (SMR_{Avg}) had been determined simultaneously. Nevertheless, the data point representing *A. colbecki* is very close to this regression line (Fig.4), thus confirming that there are no detectable Antarctic effects on ecological growth efficiency in scallops.

Generally, the negative slope of the P/SMR_{Avg}-to-temperature relation indicates that metabolic rates increase faster with temperature than does growth performance. The Q_{10} values computed form the corresponding Arrhenius models exemplify this difference: within the 0-28°C temperature range Q_{10} of scallop metabolic rate is 2.99 (Fig. 3a) and Q_{10} of scallop growth performance is 1.38 (unpubl. data Heilmayer). Metabolic Q_{10} is in the range of typical within-species Q_{10}-values reported in the literature (Bricelj and Shumway 1991) whereas growth performance Q_{10} is much lower. Studies of complex integrated processes such as growth or respiration do not necessarily give useful information concerning cold adaption. Growth, for example, may show compensation at the molecular level but still be slow for other reasons (for example, resource limitation). This complexity of such processes is emphasised by an empirical relationship obtained by Wieser (1994) and an experimental approach of Jørgensen (1988) suggesting, that it costs about three times more metabolic energy to deposit one unit of body substance than it should cost on the basis of biochemical principles to synthesise this amount

Conclusion

We could not detect any evidence for a whole body MCA in *A. colbecki*, while existing cellular MCA seems to be counterbalanced by a combination of different adaptative mechanisms, mainly low protein stability costs at low temperature. Notwithstanding, the comparatively low standard metabolic rates of the Antarctic scallop appear to facilitate survival during the prolonged and strongly food limited polar winter and does not enhance growth performance. Complete energy budgets at the individual and population level are required to decide whether or not the ecological efficiency of *A. colbecki* is in the range of non-Antarctic scallops. However, (*P/SMR*)ratio is similar to temperate scallops.

Acknowledgements

Our special thanks are extended to all participants of the 'XV. Italian Expedition to Antarctica', especially the 'Malippo'-Crew and the divers for sampling of animals. R. Cattaneo-Vietti and M. Chiantore (University of Genoa) are gratefully acknowledged for inviting us to collaborate in their project. This research could only be realised, thanks to the support by the Italian National Programme for Antarctic Research (PNRA) and the Alfred Wegener Institute for Polar and Marine Research. D. Storch and S. Gatti helped during several aspects of the study. The authors hereby declare that experiments performed during this study comply with current German laws.

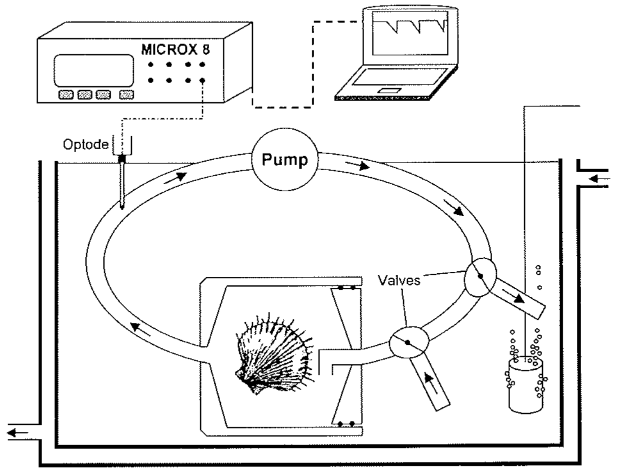

Figure 1

Intermittent flow-through system for measurement of metabolic rates (flow-through stage with valves open displayed).

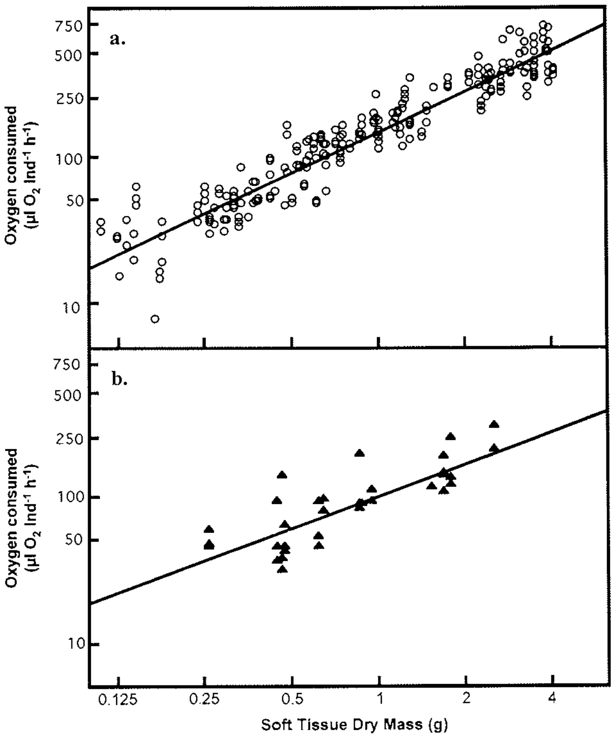

Figure 2

Metabolic rates of *Adamussium colbecki* in relation to soft tissue dry mass. Regression lines shown were fitted by least squares to logarithmically transformed data:

a. 'summer' (circles): $\log(VO_2) = 2.161 + 0.911 \cdot \log(DM)$ $r^2 = 0.902$; N= 235

b. 'winter' (triangles): $\log(VO_2) = 2.002 + 0.717 \cdot \log(DM)$ $r^2 = 0.658$; N= 35

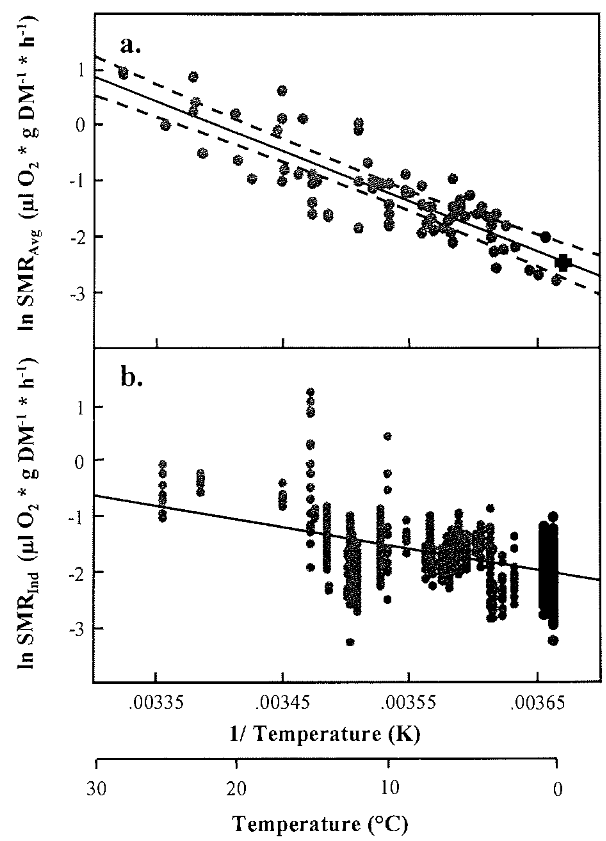

Figure 3

a. Metabolic rates (µl O_2 g $^{-1}$ h^{-1}) of scallop populations from different latitudes. Data presented are resting or standard rates for species at their normal ambient temperatures. Where seasonal data were available more than one value is included. Species and references are as follows: *Aequipecten opercularis* (Vahl 1972, McLusky 1973, Heilmayer unpubl. data); *Argopecten circularis* (Silva Loera 1986), *Argopecten irradians concentricus* (Kirby-Smith 1970, Barber and Blake 1985, Yang et al. 1998a, Lu et al. 1999); *Argopecten irradians irradians* (Bricelj et al. 1987), *Chlamys deliculata* (Mackay and Shumway 1980); *Chlamys hastata* (Bernard and Noakes 1990); *Chlamys farreri* (Yang et al. 1998b); *Chlamys islandica* (Vahl 1978, Vahl and Sundet 1985, Schmid 1996); *Mimachlamys varia* (Shafee 1982); *Mizuhopecten yessoensis* (Fuji and Hashizume 1974); *Placopecten magellanicus* (MacDonald and Thompson 1986, Shumway et al. 1988, Grant and Cranford 1991, Pilditch and Grant 1999); *Zygochlamys patagonica* (Heilmayer et al. 2001); *Adamussium colbecki* (this study) black dot: summer animals, black cross: winter animals. Arrhenius plot, with fitted least-squares regression line:

$\ln(SMR_{Avg}) = 30.011 - 8844.658 \cdot 1/T$ (80 measurements, 13 species, $r^2 = 0.714$)

b. Fitted Arrhenius model of the relationship between individual metabolic rate and temperature for non-Antarctic and the Antarctic scallop:

$\ln(SMR_{Ind}) = 11.904 - 3810.318 \cdot 1/T$ (N= 936, 8 populations, 6 species, $r^2 = 0.287$)

Grey dots: 666 data points, 6 scallop species (*Aequipecten opercularis*: McLusky 1973, Heilmayer et al. 2002; *Argopecten irradians irradians*: Bricelj *et al.* 1987; *Argopecten irradians concentricus*: Lu et al. 1999; *Chlamys islandica*: Vahl 1978, Vahl and Sundet 1985; *Mizuhopecten yessoensis*: Fuji and Hashizume 1974; *Zygochlamys patagonica*: Heilmayer et al. 2001); black dots: *Adamussium colbecki* (this study)

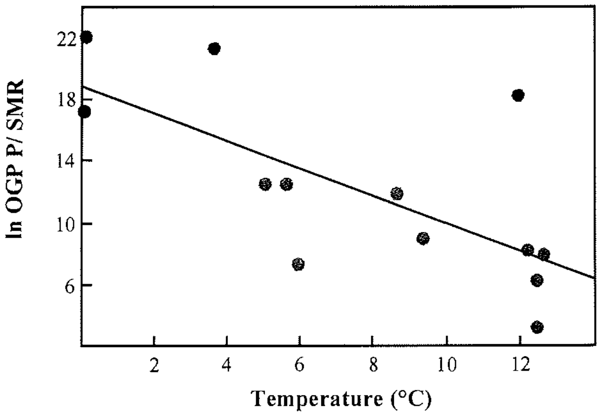

Figure 4

Relationship of the ratio between standard metabolic rate (*SMR_{Avg}*) and overall growth performance (*P*) to ambient temperature in 13 scallop populations. Data presented are resting or standard rates at their normal ambient temperatures. Where seasonal data were available the data were averaged over the whole year: *Aequipecten opercularis* (Vahl 1972, McLusky 1973, Heilmayer et al. 2002); *Chlamys islandica* (Vahl 1978, Vahl and Sundet 1985); *Mimachlamys varia* (Shafee 1982); *Mizuhopecten yessoensis* (Fuji and Hashizumu 1974); *Placopecten magellanicus* (MacDonald and Thompson 1986, Shumway et al. 1988); *Zygochlamys patagonica* (Heilmayer et al. 2001); *Adamussium colbecki* (this study). (The overall growth performance data are taken from an unpubl. data compilation of O. Heilmayer). Regression line:

$P/SMR_{Avg} = 19.003 - 0.903 \cdot T$ (N = 13, 7 species, $r^2 = 0.496$, $p < 0.001$)

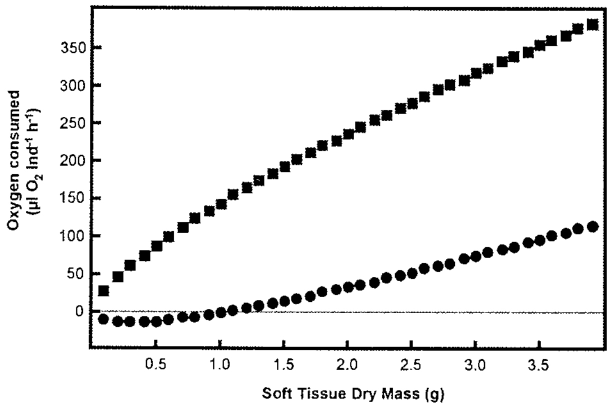

Figure 5

A generalized model illustrating the relationship between body mass, 'summer' maintenance metabolism (squares) and growth metabolism (circles) as calculated from the relation between respiration (VO_2) and body mass (DM) of *A. colbecki* in 'summer' and 'winter'.

'winter' total metabolism: $VO_2 = 100.462 \cdot DM^{0.717}$; maintenance only, no growth

'summer' total metabolism: $VO_2 = 144.877 \cdot DM^{0.911}$

'summer' maintenance metabolism: $VO_2 = 144.877 \cdot DM^{0.717}$

'summer' active metabolism: $VO_2 = 144.877 \cdot (DM^{0.911} - DM^{0.717})$

Publication III

Antarctic scallop (*Adamussium colbecki*) annual growth rate at Terra Nova Bay

Mariachiara Chiantore (✉)[1], Riccardo Cattaneo-Vietti[1] and Olaf Heilmayer[2]

[1]DIP.TE.RIS Dipartimento per lo Studio del Territorio e delle sue Risorse, Università di Genova, Viale Benedetto XV, 5 - 16132 Genova (Italy)
[2]AWI Alfred Wegener Institute for Polar and Marine Research, Columbusstrasse, 27568 Bremerhaven (Germany)

Abstract

Adamussium colbecki is one of the well-studied Antarctic molluscs. However, information on its growth rate is currently based on estimates from mark and recapture experiments and from growth-ring analysis. This paper provides the first estimates of the growth pattern of this scallop throughout a year, for individuals maintained under both natural field and laboratory conditions. Results show size-related differences in growth rate, both in the field and in aquaria, with scallops in Terra Nova Bay growing faster than those kept in aquaria. Growth performances were lower than those reported in the literature.

Reprinted from *Polar Biology*, 26(6): 416-419, Copyright (2003), Springer Verlag

Introduction

Antarctic invertebrates are known to have a very slow growth rate compared to their temperate counterparts, due to environmental conditions (temperature, light regime, food availability) that slow down metabolism, somatic and gonadic production. Due to the difficulty of performing long-term studies of growth rate *in situ*, much of the information regarding growth rates of Antarctic invertebrates is indirect, relying on estimates based on X-ray analysis of calcified structures or assessed through instantaneous growth rates measured through incorporation of markers (Brey et al. 1995a, Dahm and Brey 1998, Peck et al. 1996).

Within the framework of the Italian (PNRA) project "The Marine Protected Area of Terra Nova Bay: short and long term variations", particular attention was focused on the scallop *Adamussium colbecki*, which is considered a key species in the Antarctic littoral ecosystem (Cattaneo-Vietti et al. 1999, Chiantore et al. 1998, 2000). The monitoring of the size-frequency distribution of different populations of this species in the area of Terra Nova Bay has stressed the dominance of large scallops, and spatially and temporally irregular recruitment (Chiantore et al. 2001). X-ray studies of shell indicate a growth rate scallops up to the fifth ring of 8 mm y^{-1}, and for larger, sexually mature specimens of 5 mm y^{-1} (Cattaneo-Vietti et al. 1997).

The aim of this study was to provide absolute size-related annual growth rates of a widespread and conspicuous Antarctic species, both under laboratory and field conditions.

Between January 2000 and January 2001, two long-term experiments were performed to evaluate the growth rate of *A. colbecki*: a mark and recapture experiment, deploying a cage with 100 specimens, in order to evaluate the growth rate in field conditions at Terra Nova Bay, and an experiment in the laboratory with specimens transported to the aquaria of the Alfred Wegener Institute (AW)I laboratories of Bremerhaven (Germany), in order to compare field data with those from a controlled system.

Materials and Methods

In summer 1999/2000, at the end of January, 100 *A. colbecki* specimens (ranging in shell length between 30 and 80 mm) were measured (shell length), marked (with small labels used for tagging bees, glued on the shell) and placed in a cage (iron frame: 100x50x30 cm; plastic net: 10 mm mesh size) deployed at 10 m depth, close to the Italian Base of Terra Nova Bay (TNB). Exactly 1 year later, the cage was recovered and the specimens measured. Unfortunately only 27 out of the 100 specimens placed in the cage were recovered because the cage was seriously damaged by ice during the winter.

In the same period, around 100 specimens were measured and transported to the aquaria of the AWI in Bremerhaven, and maintained for over a year in cooled aquaria with recirculating seawater (0 ±0.5 °C, 33- 34 psu) in a 12 h light: 12 h dark daily light regime. The animals were fed twice a week by adding six Planktontabs (HOBBY, Dohse Aquaristik) dissolved in 500 cm^3 seawater to each aquarium tank (each tab has a caloric value of 7.841kJ±0.016). No deaths occurred after an acclimation period of 4 weeks (74 specimens remaining). After a year, these specimens were measured.

Growth parameters (L_∞, K) were estimated with Fabens' (1965) method by fitting a rearranged von Bertalanffy growth function (VBGF) to the obtained size increment data pairs using the NEWTON algorithm: $L_2 = L_1 + (L_\infty - L_1)(1 - e^{-K*dt})$, where L_∞ is the asymptotic length (mm), K is the growth constant (y^{-1}), L_1 is the length at the beginning and L_2 the length at the end of the time interval (dt). For t_0, no estimate can be obtained from growth-increment data.

Preliminary results for the data from TNB showed that L_∞ deviated considerably from the largest individual present in the population (L_{max}). To avoid this bias, caused by a dataset not covering the whole size-range of the population (see also Gröger 2000), L_∞ was fixed to L_{max} (= 92mm) for the final calculation.

However, growth parameters derived from size-increment-data are not directly comparable with parameters obtained from size-age-data (for a detailed discussion see Francis 1988, 1995, Sainsbury 1980). Therefore, the overall growth performance index Ψ, calculated by maximum body mass and maximum age (Brey 1999), was used for growth comparison with previously published data.

Results and Discussion

Length-growth data of specimens in the field and in captivity are reported in Table 1. The two data sets rgarding *in situ* and aquaria growth rates are not equally represented in terms of size distribution. The aquaria data set is mainly constituted by small individuals, while field data are from a few small individuals and a larger number of big scallops, and middle-size class individuals are virtually absent.

Growth rate of specimens at *in situ* is strongly size dependent with high inter-individual variability. In fact, Fig. 1 and Table 1 show that *in situ* growth rate is higher for smaller individuals (<50 mm in shell length), showing an average rate of 10 mm y^{-1} compared to 0.8 mm y^{-1} for larger specimens.

Growth rates in aquaria are slower than in the field, at least for young specimens, notwithstanding the continuous food supply (Fig. 1). As sexual maturity occurs at a size of about 50 mm in shell length, it is possible that captivity could affect smaller size classes more than larger ones, eventually delaying reproductive maturity. Nonetheless, the length-dependent ratios between length and height of the shell measured at the start and at the end of the captivity experiment show similar trends, with values at the end slightly higher than at the start (*t*-test, $p < 0.05$; Fig. 2). This suggests that animals growing in the aquaria increase in length relative to the height of shell. As this ratio may be used as an indicator of sexual maturity in natural populations (Ansell et al. 1998, Cattaneo-Vietti et al. 1997), a regular growth pattern in captivity may be inferred.

The calculated VBGF growth curves (Fig. 3) show a faster growth of *A. colbecki* under *in situ* conditions compared to growth in aquaria. This is stressed by the overall growth performance (Table 2). However, in both experimental set-ups, the growth performance for *A. colbecki* is smaller than in previously published studies, based on less direct measures of growth rate. Both Stockton (1984) and Berkman (1990) reported that yearly growth increment decreases with size. The different growth efficiencies displayed in Terra Nova Bay and New Harbor populations may be due to methodological differences (ring counting instead of direct repeated measurements), but could also mirror differences in habitat and productivity of the two areas, confirming that Antarctic marine invertebrates are food limited rather than temperature limited (Clarke 1993).

Such results are extremely useful for making productivity and energy-budget estimates of populations. In particular, Terra Nova Bay populations, studied for more than 10 years, show not only different features from site to site, but also sudden increase or decrease in dominance of larger size classes, because of strong spatially and temporally varying recruitment events (Chiantore et al. 2001). Consequently, the use of growth parameters will stress discrepancies between real and predicted data. They allow production estimates to be made at different sites and help to evaluate biomass changes to be interpreted on the basis of intermittent recruitment, size selective predation or, eventually, migration and displacement.

The discrepancies between growth performances *in situ* and captivity suggest that throughout the year trophic conditions at Terra Nova Bay are not or only a little food limited (quantitatively and/or qualitatively) for scallop growth: lateral advection and resuspension (Ansell et al. 1998) of organic material should provide enough food for growth rates that were higher than under captivity conditions with a continuous food supply.

Acknowledgements

This work was supported by Progetto Nazionale Ricerche in Antartide (PNRA) fund of the Italian Government.

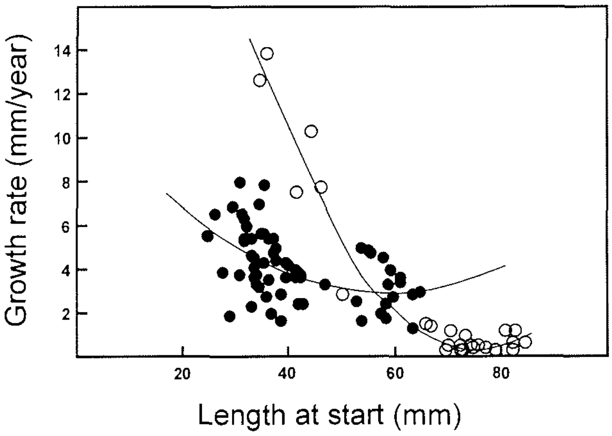

Figure 1

Size-dependent annual growth rate of *Adamussium colbecki in situ* (a) and in aquaria (b). Polynomial formulas are reported for both fitting curves.

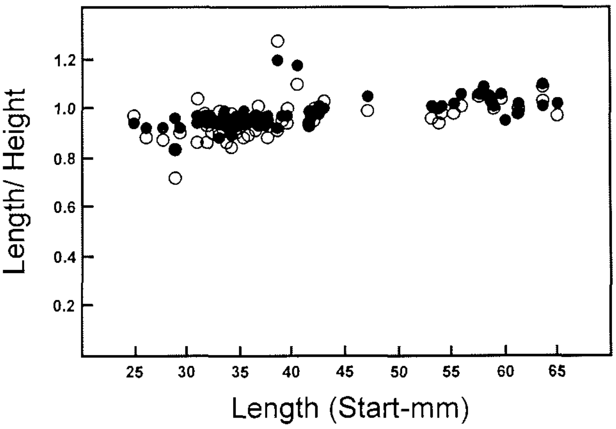

Figure 2

Ratio between shell length and height for specimens kept in aquaria, measured at the beginning (unfilled circles) and at the end (filled circles) of the experiment.

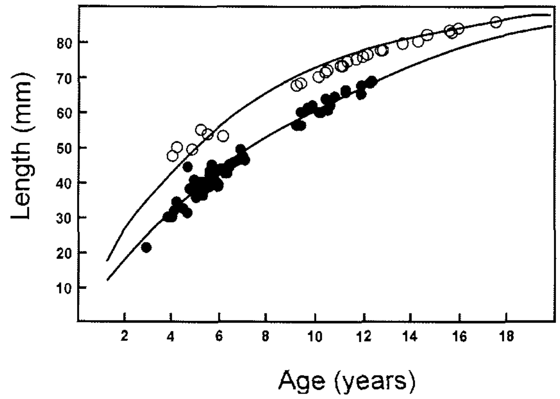

Figure 3

Growth curves of the von Bertalanffy growth function of *Adamussium colbecki* estimated from two data sets: *in situ* (circles) and in aquaria (points) (growth parameters are given in Tab. 2). Age is denoted 'relative' because t_0 is not known. Relative age at time of recapture was computed by: age= $\ln(1-L_2^*/L_\infty)/-K$, where L_2^* is length at date of recapture estimated from length at tagging by the growth function.

Table 1 Growth rate (mm y^{-1}, avg ± SD) of *Adamussium colbecki* specimens in the field and in aquaria.

Length class (mm)	Field data		Laboratory data	
	Specimens N	Growth rate	Specimens N	Growth rate
20-30			6	4.8 ± 2.1
31-40	2	13.2 ± 0.8	35	4.5 ± 1.5
41-50	3	8.5 ± 1.5	10	3.4 ± 0.6
51-60	1	2.8	11	3.2 ± 1.3
61-70	3	1 ± 0.7	5	2.8 ± 0.9
71-80	13	0.4 ± 0.3		
81-85	5	0.7 ± 0.4		

Table 2 Parameters of von Bertalanffy growth function and overall growth performance Ψ for *Adamussium colbecki*. Data from Stockton and Berkman are from Explorers Cove (New Harbor).

	L_∞ (mm)	K (yr^{-1})	Ψ	Reference
BHV	101.4	0.091	0.74	This studv
TNB	92.0	0.154	0.84	This study
	108.9	0.114	0.93	Heilmayer et al. (2003)
Mc Murdo	105.0	0.120	1.03	Stockton (1984)
	128.0	0.090	1.20	Berkman (1990)

Publication IV

Growth efficiency and temperature dependency in marine invertebrates: Lessons from empirical data.

Olaf Heilmayer (⌧), Thomas Brey and Hans-Otto Pörtner

Alfred Wegener Institute for Polar and Marine Research, P.O. Box 120161,
27515 Bremerhaven, Germany

Abstract

1. We collected data on metabolic activity and growth in pectinid bivalves from published studies. The resulting database comprised three types of datasets: (i) synoptic data (13 populations, 7 species), where both individual growth performance and metabolism are known, (ii) "metabolism only" data (82 populations, 13 species), and (iii) "growth only" data (198 populations, 26 species).

2. Metabolic activity (standard metabolic rate, SMR_{Avg}, Q_{10}=2.28) is much stronger coupled to temperature than *individual* growth (overall growth performance, OGP index P; Q_{10}=1.12) in pectinid bivalves belonging to different species and living under different environmental conditions.

3. The synthesis of the two corresponding Arrhenius equations shows that the relation between the SMR_{Avg}-to-OGP ratio and temperature follows the Arrhenius model, too, with Q_{10}=2.05.

4. SMR_{Avg}-to-OGP is an inverse proxy for growth efficiency, hence growth efficiency decreases with rising temperature across a wide range of pectinid populations and species. Thus, there is strong empirical evidence that elevated temperature constrains growth efficiency in scallops and that evolutionary adaptation does not fully compensate for this effect.

Keywords

Growth efficiency; Metabolic rates; Overall growth performance; Pectinidae; Evolutionary adaptation

---

Submitted to *Functional Ecology*, Blackwell Science

Introduction

Temperature is one of the governing abiotic factors in marine ecosystems. It affects essentially every aspect of an organism's physiology, from basic structures of macromolecules up to rates of complex physiological systems. Hence, adaptation to environmental temperature is an evolutionary mainstream and is thought to be dependent, to a large extent, on the organism's ability for metabolic adjustments on both short-term and evolutionary time scales (Clarke 1998, Hochachka and Somero 2002, Pörtner 2002a, b). Metabolic rate is a proxy for the energy consumed by all vital functions of an individual, including maintenance, growth and production of gametes. The impact of temperature on metabolic energy turnover of ectothermic organisms, the short term adaptation capability of organisms to changing temperature as well as their long term evolutionary adaptation to certain temperature regimes are fairly well documented although the mechanistic background is still under debate (Clarke and Johnston 1999, Peck and Conway 2000, Pörtner 2002a, c, Heilmayer and Brey 2003a). An interesting question in this context is whether such patterns of adaptation have implications for evolutionary compensations of temperature effects in central life history parameters - such as individual growth or growth efficiency - across the range of natural temperature regimes from very cold (polar) to very warm (tropic).

Experimental single-species temperature adaptation studies indicate that growth efficiency (i.e. the quotient of production over assimilation; for review see Bayne and Newell 1983, Griffiths and Griffiths 1987) is negatively related to temperature, i.e. elevated temperature constrains growth efficiency, and the short-term ability to adjust the individual energy budget to changing temperature is rather limited (e.g. Wieser et al. 1988, Present and Conover 1992). The proper approach to identify evolutionary compensation effects will be a comparison of taxonomically closely related species and populations across a wide temperature range.

There are, however, too few studies on growth efficiency across the ecological temperature spectrum (polar to tropical) to allow for a coherent analysis. Reliable data (i.e. growth, assimilation, respiration) require a costly and time-consuming input/output analysis for every single species or population. The few published studies focus either on intraspecific comparisons (e.g. Wieser et al. 1988, Present and Conover 1992, Beiras et al. 1994, Forsythe et al. 2002) or on age-related changes in single populations (e.g. Vahl 1981b, MacDonald and Thompson 1986, Niu et al. 1998, Urrutia et al. 1999), and do not allow for a general comparison between species across a wider temperature spectrum.

We tried to circumvent the missing data problem by constructing a versatile proxy for growth efficiency that can be computed from easy-to-measure parameters. Any meta-study of this kind is a trade-off between the statistical power of large numbers of data and the introduction of taxon-related statistical noise. We tried to find a compromise by focussing our study on one single family, the Pectinidae, i.e. organisms with very similar body size, body shape, lifestyle, and life history features. Nonetheless, our proxy for growth efficiency may be looked at from a reductionist's point of view. It does not aim at the precise quantification of growth efficiency but to establish an upper limit to the efficiency of the conversion processes, asking the question: *Is there a right place to grow?* We hope that our approach will encourage a fruitful discussion on evolutionary adaptations of growth efficiencies in the marine realm.

Materials and Methods

Literature data

The bivalve family Pectinidae consists of some 400 known living species. They cover a wide geographical and temperature range – from Northern Norway (0 to 8°C; i.e. *Chlamys islandica*) to the tropics (22 to 28°C; i.e. *Euvola ziczac*) and further south to the Southern Ocean (-1.9 to +2°C; *Adamussium colbecki*) (Brand 1991, Waller 1991). Many species are represented by several populations living at different temperatures in our data collection, for some species we found more than one study carried out at the same temperature. Under the assumption that gene flow between populations of one species is low, populations can be treated as separate entities (Garland et al. 1992, Foster and Cameron 1996, Pierce and Crawford 1997a, b), i.e. no statistical correction for combining different taxonomic levels is necessary. We obtained three types of datasets: (i) synoptic data (13 populations, 7 species), where both, lifetime growth performance and metabolism of one population are known, (ii) "metabolism only" data (82 populations, 13 species), and (iii) "growth only" data (198 populations, 26 species).

Growth performance

The three-parameter von Bertalanffy growth model (VBGF) is suitable to describe growth in pectinids as well as other marine invertebrates.

$$M_t = M_\infty \bullet (1- e^{-K \bullet (t - to)})^b \qquad (1)$$

where M_t is shell height at time t, M_∞ is the mean asymptotic height, K is the Brody growth coefficient, t the age and t_o is theoretical age at which shell height equals zero, and b equals the exponent of the exponential size-mass relation. The index of 'overall growth performance' *OGP* (Pauly and Munro 1984, for review see Brey 2001) is used to compare growth between populations or species. *OGP* is defined as the maximum growth rate (i.e. the growth rate at the inflexion point of the VBGF) calculated by

$$OGP = \log(K \bullet M_\infty) \qquad (2)$$

Metabolic rate

Respiration rates were used to approximate metabolic activity. Only data sets that fulfilled the following conditions were included in our analysis: (i) measurement of inactive animals only (= resting or standard metabolism), (ii) temperature is within the natural range experienced by the species, (iii) experimental animal size covers a sufficient size range of the population to allow a precise estimate of the scaling parameters within that species.

To remove the effect of body mass the average specific metabolic rate (SMR_{Avg}) of a standard-sized animal was computed according to Luxmoore (1984) by

$$SMR_{Avg} = a \bullet DM^{b - 0.807} \qquad (3)$$

where *a* and *b* are constants of the corresponding relation between respiration rate and body mass of each population. *0.807* is the mean pectinid-specific mass exponent (O. Heilmayer unpublished data compilation). Regarding metabolism data sets (no information on growth), *DM* is the geometric mean dry mass whereas regarding synoptic data sets, *DM* is the dry mass at the inflection point of the VBGF, i.e. the point that OGP refers to.

Water temperature

Water temperature was either taken from the corresponding publication or inferred from the 'World Ocean Database 2001' of the National Oceanographic Data Centre (http:/www.nodc. noaa.gov/OC5/WOD01/pr_wod01.html), if necessary.

Statistical analysis

The Arrhenius model is likely to describe effects of temperature on whole-animal physiological processes best (Clarke and Johnston 1999); model parameters are estimated by linear regression of the linearised model:

Metabolic rate (SMR_{Avg})

$$\ln(SMR_{Avg}) = a_1 + b_1 \bullet \frac{1}{T} \quad \Leftrightarrow \quad SMR_{Avg} = e^{a_1} \bullet e^{b_1 \bullet \frac{1}{T}} \qquad (4)$$

Overall growth performance (OGP)

$$\ln(OGP) = a_2 + b_2 \bullet \frac{1}{T} \quad \Leftrightarrow \quad OGP = e^{a_2} \bullet e^{b_2 \bullet \frac{1}{T}} \qquad (5)$$

T is the absolute temperature, a_1 and a_2 are the constants, b_1 and b_2 the slopes of the corresponding equations, i.e. Arrhenius activation energies.

The ratio of SMR_{Avg}-to-OGP is interpreted as an inverse proxy for growth efficiency, SMR includes the cost of growth on top of baseline metabolic costs. Once baseline costs or costs of growth are high this may be at the expense of lower growth performance. As a proxy, the ratio of SMR_{Avg}-to-OGP is seen inversely proportional to the fraction of metabolic energy channelled into somatic growth. Regarding the synoptic data (N= 13), population-specific SMR_{Avg}-to-OGP ratios were computed directly (data from Heilmayer and Brey 2003a) and the relation of SMR_{Avg}-to-OGP ratio to temperature was modelled by the corresponding Arrhenius equation. Regarding SMR_{Avg} values obtained from "metabolism only" (N= 82) data and OGP values obtained from "growth only" data (N= 198) a "synthetic" model was obtained by mathematically combining equations (4) and (5)

$$\frac{SMR_{Avg}}{OGP} = \frac{e^{a_1} \cdot e^{b_1 \cdot \frac{1}{T}}}{e^{a_2} \cdot e^{b_2 \cdot \frac{1}{T}}} = e^{a_1 - a_2} \bullet e^{(b_1 - b_2) \cdot \frac{1}{T}} \qquad (6)$$

Results and Discussion

In scallops standard metabolic rate (SMR_{Avg}) is significantly related to temperature by (Fig. 1):

$\ln(SMR_{Avg}) = 30.119 - 8876.41 \bullet 1/T$ (N = 82, 13 species, $r^2 = 0.724$, $p < 0.001$)

Overall growth performance (OGP) is significantly related to temperature, too. The effect of temperature, however, is not as strong as in SMR_{Avg}, and the relation is weaker (Fig. 2):

$\ln(OGP) = 4.22 - 958.466 \bullet 1/T$ (N= 198, 25 species, $r^2 = 0.132$, $p < 0.001$)

The models are linear across the whole temperature range as indicated by the random distribution of residuals. Regarding the synoptically measured data, the inverse growth efficiency proxy SMR_{Avg}-to-OGP is related to temperature by:

$\ln(SMR_{Avg}/OGP) = 21.265 - 6630.794 \bullet 1/T$

(N = 13, 7 species, $r^2 = 0.479$, $p < 0.001$)

The parameter values of the "synthetic" model are:

$\ln(SMR_{Avg}/OGP) = 25.899 - 7917.944 \bullet 1/T$

Both models show basically the same positive relationship between SMR_{Avg}-to-OGP and temperature, i.e. a negative relationship between growth efficiency and temperature (Fig. 3), indicating that animals achieve relatively higher growth performance at lower metabolic rate in the cold. Metabolic rates increase faster with temperature than does growth performance, possibly as a consequence of enhanced maintenance cost or cost of growth or both. The temperature coefficients (Q_{10}) computed from the corresponding Arrhenius models exemplify this difference: within the 0-25°C temperature range Q_{10} of scallop metabolic rate is 2.28 (Fig. 1) whereas overall growth performance changes more slowly with temperature (Q_{10}= 1.12) (Fig. 2). Arrhenius activation energy is 54.9 kJ mol^{-1} K^{-1} for SMR_{Avg} and 7.9 kJ mol^{-1} K^{-1} for OGP. The Q_{10} of the SMR_{Avg}-to-OGP-ratio derived from the above regression is 2.26 for the synoptic model and 2.65 for the synthetical model.

Is there any evidence for an evolutionary adaptation?

Long-term changes in performance are caused either by acclimation or by evolutionary adaptation. As the capacity for thermal acclimation of performance is limited, an evolutionary adjustment is more likely (Bennett and Huey 1990). At first sight the negative relationship to temperature indicates that growth efficiency is far from being compensated for temperature effects. Our study even indicates a higher thermal sensitivity (Q_{10}: 2.65) than observed within single species (range of Q_{10}: 1.11 to 1.66, median 1.35; Wieser et al. 1988, Present and Conover 1992, Beiras et al. 1994, Iguchi and Ikeda 1995, Frosythe et al. 2002, Niu et al. 2003).

What are the levers?

The strong effect of temperature on growth efficiency indicates that growth efficiency is subject to physiological and/or thermodynamical constraints which are strongly coupled to temperature and which apparently cannot be overcome at reasonable costs. Theoretically there would be three ways to overcome the constraints, (i) uncoupling of metabolism from temperature, (ii) an increase in assimilation efficiency, and (iii) an increase in consumption. Metabolism can be uncoupled from ambient temperature only by complex and energetically expensive developments (for review Willmer et al. 2000). Assimilation efficiency is unlikely to increase substantially, as evolution already worked a long time on the optimisation of underlying basic physiological/enzymatic processes regardless of temperature. Consumption is subject to strong ecological constraints by inter- and intraspecific competition for food. Moreover, optimum foraging theory demonstrates that each animal "design" has an optimum consumption rate in relation to energy turnover.

In this context it appears relevant that an inverse relationship between growth performance and standard metabolic rate has recently been suggested in one fish species (*Gadus morhua*, Pörtner et al. 2001), where temperature specific growth was lower at higher SMR in Arctic than in temperate populations. Such trade-offs between growth performance and metabolic rate suggest that low SMRs reflect reduced cost of maintenance and support allocation of a larger fraction of metabolic energy to growth (Hawkins et al. 1998, Pörtner 2002c). Thus they support enhanced levels of growth performance and efficiency at lower temperatures. The data available for the pectinids, however, do not allow disentangling of the specific effects of stenothermy vs. eurythermy (cf. Pörtner et al. 2000, Pörtner 2002c).

We must conclude that maximising individual growth efficiency is not a primary selection criterium in evolution (see also Calow 1983, Present and Conover 1992). Obviously actual individual growth efficiency results from complex temperature dependent tradeoffs within the overall energy budget of the organism. Hence evolutionary development may rather proceed towards an "optimum" growth efficiency specific for the temperature the organism lives at. The strong empirical relation between growth efficiency and temperature found in scallops confirms this idea; there is a temperature specific optimum growth efficiency in pectinids, which may reflect the evolutionary trade-off between individual fitness and population competitiveness.

Fact or fiction?

We are well aware that this is a conceptual approach with all the inescapable shortcomings involved in building a theory from known facts, assumptions and meta-data. Our growth efficiency proxy based on whole-animal data introduces some ambiguity into the specification of the hierarchical level at which limitations and constraints are initiated, because of the many variables that may be involved in modifying metabolic rate, i.e. reproductive stage, food supply, season and so on. Nonetheless, this study provides significant support for the notion that the ratio linking metabolic expenditure and growth likely is a biological constant in pectinids.

Acknowledgements

This study was supported by the Italian research programme "Progetto Nazionale Ricerche in Antartide" (PNRA) and the Alfred Wegener Institute for Polar and Marine Research. The authors hereby declare that investigations performed during this study comply with current German laws.

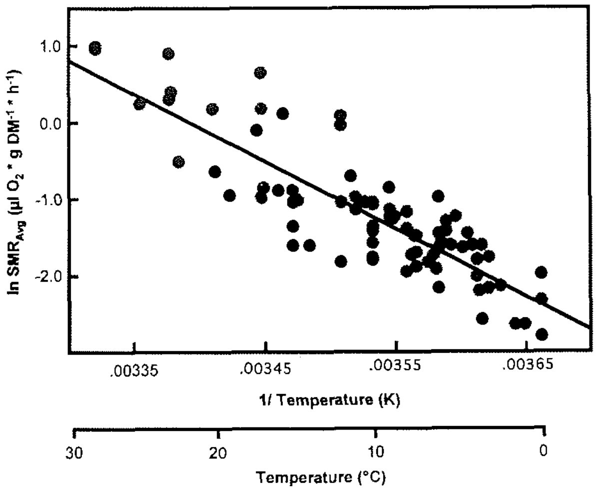

Figure 1

Metabolic rates (µl O_2 g $^{-1}$ h^{-1}) of scallop populations from different latitudes. Data presented are resting or standard rates for species at their normal ambient temperatures. Where seasonal data were available more than one value is included. Species and references are as follows: *Aequipecten opercularis* (Vahl 1972, McLusky 1973, Heilmayer et al. 2004); *Argopecten circularis* (Silva Loera 1986), *Argopecten irradians concentricus* (Kirby-Smith 1970, Barber and Blake 1985, Yang et al. 1998a, Lu et al. 1999); *Argopecten irradians irradians* (Bricelj et al. 1987), *Chlamys deliculata* (Mackay and Shumway 1980); *Chlamys hastata* (Bernard and Noak 1990); *Chlamys farreri* (Yang et al. 1998b); *Chlamys islandica* (Vahl 1978, Vahl and Sundet 1985, Schmid 1996); *Mimachlamys varia* (Shafee 1982); *Mizuhopecten yessoensis* (Fuji and Hashizumu 1974); *Placopecten magellanicus* (MacDonald and Thompson 1986, Shumway et al. 1988, Grant and Cranford 1991, Pilditch and Grant 1999); *Zygochlamys patagonica* (Heilmayer et al. 2001). Arrhenius plot, with fitted least-squares regression line:

$ln(SMR_{Avg}) = 30.116 - 8874.24 \cdot 1/T$ (82 measurements, 13 species, $r^2 = 0.725$)

(modified after Heilmayer and Brey 2003a, see there for references)

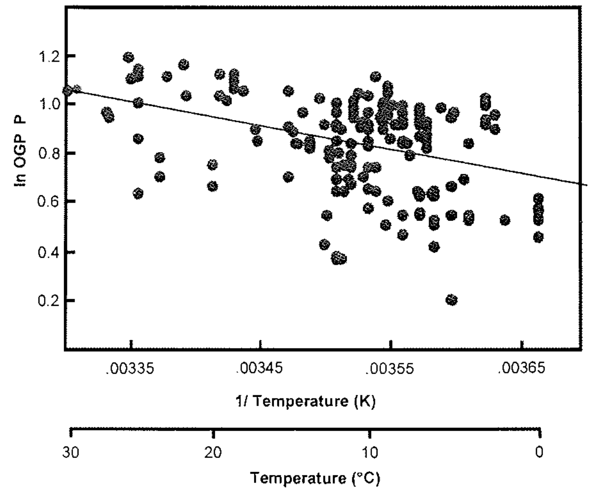

Figure 2

Fitted Arrhenius model of the relationship between overall growth performance *P* and temperature for non-Antarctic and the Antarctic scallop:

$\ln(OGP\ P) = 4.22 - 958.466 \cdot 1/T$ (198 studies, 25 species, $r^2 = 0.132$)

(Authorities and references are taken from Heilmayer et al. 2003 and an unpublished data compilation of O. Heilmayer)

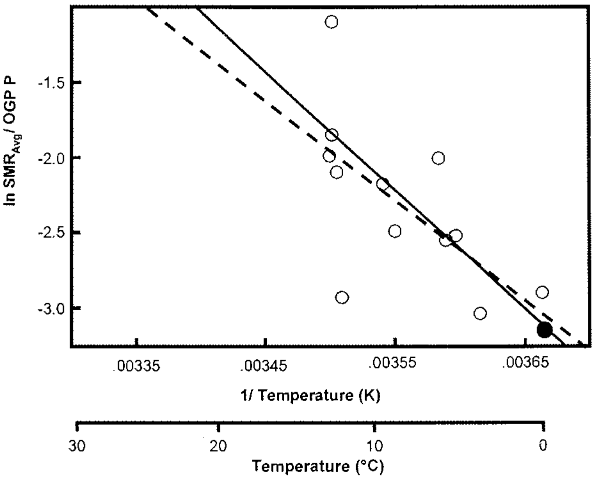

Figure 3

Relationship of the ratio between standard metabolic rate (SMR_{Avg}) and overall growth performance (OGP) computed from the two appropriate Arrhenius equations according to equation 5. Regression line: $\ln(SMR_{Avg}/OGP) = -25.899 + 7917.944 \cdot 1/T$

Additionally, a synoptic dataset was included for those cases where both parameters are known: *Aequipecten opercularis* (Vahl 1972, McLusky 1973, Heilmayer et al. 2004); *Chlamys islandica* (Vahl 1978, Vahl and Sundet 1985); *Mimachlamys varia* (Shafee 1982); *Mizuhopecten yessoensis* (Fuji and Hashizumu 1974); *Placopecten magellanicus* (MacDonald and Thompson 1986, Shumway et al. 1988); *Zygochlamys patagonica* (Heilmayer et al. 2001); *Adamussium colbecki* (■, Heilmayer and Brey 2003a). Dashed line: $ln(SMR_{Avg}/OGP) = 21.265 - 6630.794 \cdot 1/T$ (N = 13, 7 species, $r^2 = 0.479$, $P < 0.001$)

Publication V

Population dynamics and metabolism of *Aequipecten opercularis* (L.) from the western English Channel (Roscoff, France)

Olaf Heilmayer (✉), Thomas Brey, Daniela Storch, Andreas Mackensen and Wolf E. Arntz

Alfred Wegener Institute for Polar and Marine Research, P.O. Box 120161,
27515 Bremerhaven, Germany

Abstract

Population dynamics of the queen scallop, *Aequipecten opercularis,* was investigated in the western English Channel off Roscoff. Annual formation of natural growth rings on the shell surface was validated by stable isotope ($\delta^{18}O$ and $\delta^{13}C$) analysis. A von Bertalanffy growth function (H_t = 58.9 mm • $(1-e^{-0.604 \cdot (t + 0.235)})$) was fitted to size-at-age data of 249 individuals. Annual somatic and gonad production amounted to 19.74 kJ m^{-2} and 0.979 kJ m^{-2} y^{-1}, respectively. Total mortality rate Z was estimated to be 1.716 y^{-1}. Net growth efficiencies (ranging from 45% in 1-y-old to 11% in 6-y- old individuals) were in the same range as in other short-lived scallops. Individual growth, however, is distinctly slower in this population than in other *A. opercularis* populations from similar latitudes, most likely due to a more stressful environment.

Keywords

Bivalvia; Energy budget; Metabolism; Mortality; Pectinidae; Population dynamics

---

Reprinted from the *Netherlands Journal of Sea Research,* 52(2), in press, Copyright (2004), Elsevier Verlag

Introduction

The commercially exploited queen scallop *Aequipecten opercularis* (L.) occurs throughout a wide geographical range on the European continental shelf: from northern Norway to the Mediterranean and from the Adriatic to the west of Ireland (Broom 1976, Brand 1991, Waller 1991). Recruitment success and spatial distribution appear to be highly variable in time, thus inducing major year-to-year changes in extent and position of scallop banks of exploitable size and density, as reported from British waters (Broom 1976, Brand 1991) as well as from the eastern part of the English Channel and from northern Brittany (Grainger 1992, Goulletquer and Heral 1997). Due to the relatively short time *A. opercularis* can be kept fresh (Ansell et al. 1991), queen scallops support only a small local fishery and market in France, which is about 1/8 of total French scallop landings (Grainger 1992).

In contrast to the Great Scallop (*Pecten maximus*, L.) interest in population dynamic parameters of *Aequipecten opercularis* has hitherto been limited. Paul (1980) investigated salinity and temperature tolerances, Vahl (1972) described the relationship between water transport and oxygen uptake, and McLusky (1973) determined the effect of temperature acclimation on filtration and oxygen consumption rates. Data on age and growth have been reviewed by Taylor and Venn (1978). Little is known, however, on population biology and production of the queen scallop populations in the western English Channel, besides the growth rates determined by Franklin et al. (1980).

A baseline study on the biology and population dynamics of *Aequipecten opercularis* in the western English Channel is presented. In this study growth, mortality, age-specific somatic and gonadal production as well as metabolic rates in individual scallops were calculated and compared with previous findings in the literature.

Material and Methods

Study site and general measurements

Queen scallops were collected with a small dredge in the western English Channel next to Roscoff (Trezen Vraz, 48°59' N, 4°53' W) in 60 to 80 m water depth at three times (February, June and October) in 1999. Water temperature varied between 9.7 °C in January/February and 16.4 °C in August (Fig. 1). The summer phytoplankton bloom consisted of two peaks, with a maximum of 1.53 µg l^{-1} in April, and a second one amounting to 1.56 µg l^{-1} by late August. Minimum chlorophyll concentrations occurred in February (SOMLIT-Database). The investigation area, especially the distribution of substrate types and phytoplankton, is described in Sagan and Thouzeau (1998).

After sampling, animals were immediately transported to the 'Station de Biologique de Roscoff' where they were maintained in flow-through aquaria until used in experiments or transported to the Alfred Wegener Institute (AWI, Germany). At each occasion shell height (= defined as the maximum distance between the dorsal hinge and ventral margin, Seed 1980) of a representative subsample was measured to the nearest 0.1 mm using vernier callipers. A size frequency distribution (SFD) was obtained by pooling individuals using class intervals of 1 mm size. For size-mass relationships freshly caught animals were dissected and oven dried at 60°C for 24 hrs. Individual gonad and soft tissue dry masses (DM) were weighed to the nearest 0.1 g, linear regression analysis was carried out on log-transformed data, estimating the constants a and b of the allometric equation:

$$\log(M) = \log(a) + b \cdot \log(H) \qquad (1)$$

where M is soft tissue mass (g) of somatic or gonad tissue, respectively, at shell height H (mm).

Growth band reading and analysis

Bivalve shell growth bands can result from seasonal oscillations in growth, but also from changes in food availability, spawning events or predation attempts. Identification and interpretation of annual growth bands in *A. opercularis* were based on previous studies in this species (Broom and Mason 1978, Paul 1980, Hickson et al. 1999) as well as other scallop species (e.g. Dare and Deith 1990, Heilmayer et al. 2003). For growth band analysis only the left (upper) valve was used. Prior to analysis the shell was cleaned of organic matter with warm 5% NaOCl solution, washed with 96% ethanol, rinsed with water and dried at 60°C for 12 hrs. In each animal, the number of macroscopically visible bands and shell height were recorded.

Stable oxygen ($\delta^{18}O$) isotope values in biogenic $CaCO_3$ reflect ambient water temperature and oxygen isotopic composition of seawater, the latter varying with salinity, while carbon ($\delta^{13}C$) isotope values reflect primary production at the time of carbonate formation (Erez and Lutz 1983, Hickson et al. 1999). Due to low salinity variations at the site of investigation the oxygen isotopic composition of seawater should be primarily a reflection of ambient temperature variation. Therefore isotope ratio profiles reflect variations in temperature, shell physiology (related to temperature), primary production and a combination of these (see Wefer and Berger 1991, Owen et al. 2002a). In environments with a seasonal cycle in temperature and/ or primary production such isotope ratios can be used to validate whether or not identified growth bands in the shell of *A. opercularis* are formed at regular (annual) intervals (for review see Richardson 2001, Owen et al. 2002a). This approach has recently been applied successfully to identify the growth patterns of various scallop species (e.g. Krantz et al. 1984, Dare and Deith 1990, Hickson et al. 1999, Lasta et al. 2001, Heilmayer et al. 2003).

For isotope analysis, calcium carbonate powder was sampled from the outer shell layer of four individuals in equally spaced (~1mm) dorso-ventral series using a small dental drill (bit size 0.5mm). $\delta^{18}O$ and $\delta^{13}C$ values were determined in the Stable Isotope Laboratory of the Alfred Wegener Institute with a Finnigan MAT251 mass spectrometer coupled to an automatic carbonate preparation device. The results were reported in ppt (‰) deviations related to the Vienna Pee Dee belemnite (VPDB) standard through repeated analyses of National Institute of Standards and Technology (NIST) isotopic reference material 19. The precision of measurements was better than ± 0.08‰ and ± 0.06‰ for $\delta^{18}O$ and $\delta^{13}C$, respectively, based on routine measurements of a laboratory-working standard.

Assuming that stable isotope analysis will prove the annual formation of one shell growth band each winter (see below) individual age in years was taken to equal the number of growth bands X in animals sampled in February. Animals caught in June and October were assumed to be X + 0.33 y and X + 0.67 y old, respectively. A von Bertalanffy growth model (VBGF) was fitted to the resulting size-at-age data pairs by using a non-linear iterative Newton algorithm (for details Brey 2001):

$$H_t = H_\infty \cdot (1 - e^{-K \cdot (t - t_0)}) \quad [\text{mm, y}] \qquad (2)$$

where H_∞ is the mean asymptotic height, K is the Brody growth coefficient, t the age and t_0 is theoretical age at which shell height equals zero.

Production (P)

Age specific individual somatic production (P_S) was calculated from the increment in dry tissues mass between consecutive age classes [$DM_{(t+1)} - DM_t$] (with 1g dry mass = 20.22 kJ; Brey 2001).

The mass-specific growth rate method could not be used to compute somatic production-to-biomass ratio (P/B) and production of the population, because animals < 35 mm H were strongly under-represented in our size frequency distribution owing to the comparatively large 25 mm x 25 mm mesh size of the dredge. This problem was circumvented by using the annual mortality rate Z (see below) as a proxy for the somatic production-to-biomass ratio P_S/B, as Z and P_S/B are equal in steady-state (see Allen 1971) and the catch curve approach to estimate Z is quite robust against the effects of gear selectivity (Pauly and Munro 1984). The queen scallop bed at rezen Vraz” is not ephemeral but present for at least several decades, as ıecdotical evidence (local fishermen reports) and multi-year scientific research (e.g. agan and Thouzeau 1998) indicate. Hence, the assumption of steady-state appears be justified. Consequently annual somatic production of the population was timated by:

$$_{;} = Z \bullet M_S \bullet N \qquad [\mathrm{kJ\ m^{-2}\ y^{-1}}] \qquad (3)$$

ıere M_S is the average individual somatic body mass in our sample and N is the ean abundance of 0.82 ind • m^{-2} provided by Franklin et al. (1980) for the western ıglish Channel.

ınad production ($P_{G,i}$) for each age class was estimated from the decline of gonad ass during spawning in scallops of given age (determined from the von Bertalanffy uation describing shell height as a function of age), determined from logarithmic gressions of gonad mass to size before ($M_{G,i\ (before)}$; February) and after spawning $_{G,i\ (after)}$; June) (1 g gonad DM = 23.4 kJ; average from: MacDonald and Thompson 35, MacDonald et al. 1991):

$$_{i} = M_{G,i\ (before)} - M_{G,i\ (after)} \qquad [\mathrm{kJ\ ind^{-1}\ y^{-1}}] \qquad (4)$$

ividual gonad production is negligible below 30 mm H (see results). Therefore pulation P_G/B ratio was computed from gonad production of total sample and mass of total sample:

$$B = (\sum N_i \bullet P_{G,i}) / (\sum N_i \bullet M_{S,i}) \qquad [\mathrm{y^{-1}}] \qquad (5)$$

ere M_S is the average individual body mass in class i. Hence population gonad duction (P_G) can be estimated by:

$$= (P_G/B) \bullet M_S \bullet N \qquad [\mathrm{kJ\ ind^{-1}\ y^{-1}}] \qquad (6)$$

tality rate (Z)

total mortality rate Z was estimated from the SFD and the von Bertalanffy growth ve by a size-converted catch curve (Pauly and Munro 1984, Brey 2001):

$$l_i / \Delta t_i) = a + b\, t_i \qquad \Leftrightarrow Z = -b \qquad (7)$$

re N_i is the number of individuals in size class i, Δt_i is the time required to grow ugh this size class and t_i is the relative age at the mid-size of class i.

abolism (R)

gen consumption rates of unfed (deprived of food for at least 3 days), unstressed inactive animals were used as a proxy of standard metabolic rate as defined by ne and Newell (1983) (a detailed description of animal handling is given in nayer and Brey, 2003a). Measurements of scallops sampled in June (summer) October (autumn) were done at ambient temperatures within 5-20 days after pling. Winter rates were measured on animals sampled in October 1999 and maintained under simulated winter conditions (reduced food, dimmed light) in temperate aquaria with recirculating seawater (10 ± 0.5 °C, 33-34 psu). A size range of animals as large as possible was used on each sampling occasion.

Oxygen content was assessed using an intermitted flow system and oxygen microoptodes connected to a Microx 8–array, as previously described in Gatti et al. (2002). Individual metabolic rates (VO_2) were obtained by comparison with control chambers (no animal). VO_2 was expressed as a function of soft tissue dry mass (DM):

$$\log(VO_2) = a + b \cdot \log(DM) \qquad (8)$$

where a is a constant and b the mass scaling exponent. The model was fitted by least squares linear regression after logarithmic transformation of both variables. In order to compare oxygen consumption among seasons, rates were standardised for body mass (Packard and Boardman 1999) by:

$$VO_{2,S} = VO_2 \cdot (DM_S / DM_E)^b \qquad (9)$$

where $VO_{2,S}$ is the metabolic rate of a standard-sized scallop of 1 g dry mass (DM_S), and VO_2 *and* DM_E are observed oxygen rate and body mass of the experimental scallop. Oxygen consumed was converted to energy by 1 ml O_2 = 20.1 J (cited in Brey 2001).

Results

General measurements

The pooled size-frequency distribution of the year 1999 (Fig. 2) was polymodal and dominated (>70%) by large individuals (>41mm). An ANCOVA showed significant ($p < 0.001$) seasonal changes in the regressions of somatic and gonad dry mass against shell height (Table 1, both log-transformed). Both somatic dry mass and gonad dry mass of a standard-sized 45mm scallop were lowest during the summer period (soma in g DM: 0.371 in June vs. 0.583 in February and 0.847 in October; gonad in g DM: 0.0122 in June vs. 0.0465 in February and 0.0204 in October).

Age and growth

$\delta^{18}O$ and $\delta^{13}C$ profiles of the two shells examined showed more or less synchronous cyclical patterns reflecting environmental seasonality (Fig. 3). Over the whole lifetime $\delta^{18}O$ values obtained ranged from –0.3 to +1.1 ‰ (Fig. 3a) and –0.4 to +1.3 ‰ (Fig. 3b). $\delta^{13}C$ values ranged from –0.5 to +0.4 ‰ (Fig. 3a), respectively, -0.5 to +0.5 ‰ (Fig. 3b). There is a distinct spatial coincidence between macroscopically identified growth bands and relative $\delta^{18}O$ and $\delta^{13}C$ maxima of the isotope profile (*i.e.*

temperature as well as primary production minima), thus indicating a formation of one growth band each winter.

Size-at-age data of 249 specimens were fitted best by the von Bertalanffy equation: H_t = 58.9mm • $(1 - e^{-0.604 \cdot (t + 0.235)})$; $r^2 = 0.827$ (Fig. 4). Accordingly, the largest scallop (H= 58.9mm) found at Roscoff was about six years old.

Production and mortality

Individual somatic production increases to a maximum of 10.66 kJ yr^{-1} (0.527 g DM yr^{-1}) at an age of 2 years and decreases thereafter, whereas individual gonad production increases exponentially with shell height, reaching 4.17 kJ yr^{-1} (0.177 g DM yr^{-1}) at an age of 6 yr (Fig. 5a). Mean annual biomass of *A. opercularis* was 13.67 kJ m^{-2} (0.67 g DM m^{-2}), total mortality rate Z amounted to 1.761 y^{-1} (Fig. 6). Correspondingly, annual somatic production P_S was estimated at 19.74 kJ m^{-2} y^{-1} (0.976 g DM m^{-2} y^{-1}). Annual gonad productivity P_G/B and production P_G amounted to 0.087 y^{-1} and 0.979 kJ m^{-2} y^{-1} (0.042 g DM m^{-2} y^{-1}), respectively. Hence, total annual production for the season 1999 amounted to 20.72 kJ m^{-2} y^{-1} (1.02 g DM m^{-2} y^{-1}), corresponding to an annual P_{tot}/B ratio of 1.848 y^{-1}. The turnover ratio (P/B) calculated for each age class declined with age from 1.45 to 0.14 (Fig. 5b). Similarly P/R ratio and net growth efficiency (K_2= P/A= P/(P+R)) decreased but levelled off in the oldest age classes (Fig. 5b).

Metabolism

Metabolic rates were measured in June (T = 12.4°C), October (T = 14.4°C) and December (T = 10.3°C) over the complete size range of scallops available at Roscoff (June: 0.06 – 1.81 g DM, October: 0.47 – 1.46 g DM, December: 0.13 – 0.71 g DM). The temperature range examined approximates the annual range encountered by queen scallops in Roscoff waters. The allometric relationships between body dry mass (DM) and metabolic rates (VO_2) of *A. opercularis* were:

June $\log(VO_2) = 2.253 + 0.654 \cdot \log(DM)$; N = 72, 34 animals, $r^2 = 0.483$
October $\log(VO_2) = 2.408 + 1.014 \cdot \log(DM)$; N = 101, 34 animals, $r^2 = 0.496$
December $\log(VO_2) = 2.288 + 0.707 \cdot \log(DM)$; N = 101, 22 animals, $r^2 = 0.662$

The combined effects of body mass and temperature on metabolic rate can be described by the multiple linear model:

$\log(VO_2) = 2.093 (\pm 0.059) + 0.774 (\pm 0.029) \cdot \log(DM) + 0.02 (\pm 0.005) \cdot T$; N= 274, $r^2 = 0.74$, F= 381.311, p< 0.001, temperature in °C.

Standard metabolic rates ($VO_{2,\,S}$) were indistinguishable in June (188.62 ± 60.32 µl O_2 g DM^{-1} h^{-1}) and December (204.17 ± 67.9 µl O_2 g DM^{-1} h^{-1}), but significantly higher

(ANOVA: *p< 0.001*) in October (264.59 ± 69.05 µl O_2 g DM^{-1} h^{-1}). This indicated a 30% seasonal factorial rise over the lowest winter metabolic rates.

Discussion

Age and growth in Aequipecten opercularis

Partitioning of oxygen isotopes between molluscan shells and seawater has historically been assumed to closely approximate in isotopic equilibrium (Witbaard et al. 1994, McConnaughey et al. 1997, Hickson et al. 1999, Schöne et al. 2002, Schöne 2003). On the other hand more recently Owen et al. (2002a, b) showed in a thorough laboratory study a positive deviation from equilibrium (+0.6 ‰) in *Pecten maximus*. Although changes in the $\delta^{18}O$ and $\delta^{13}C$ profiles cannot be used for an exact environmental reconstruction the amplitude still can be used as a proxy for relative seasonal oscillation of ambient temperature. The maximum $\delta^{18}O$-amplitudes in the two shells shown in Fig. 3 correspond to a relative temperature range of 5.6 and 6.8°C (according to Craig´s palaeo-temperature equation as given by Erez and Luz 1983), respectively, which is close to the observed annual range of 6.7 °C (Fig. 1). The close spatial coincidence between shell growth band position and both the $\delta^{18}O$ and $\delta^{13}C$ peaks in the isotope profiles (Fig. 3) indicate sufficient evidence that bands are formed during times of lowest temperature and low primary production, i.e. one band is formed each winter (for review Richardson 2001). The same pattern was found in populations from Plymouth (December-March: Pickett and Franklin 1975, Broom and Mason 1978) and the North Sea (December-February: Ursin 1956).

Non-linear growth patterns as derived from the VBGF can be compared indirectly only, e.g. using composite indices of overall growth performance (OGP) (e.g. $P = \log(K) + \log(M_\infty)$; Pauly and Munro 1984). According to Brey (1999), this index is more or less consistent for closely related species. However, in suspension feeding bivalves food supply and/or temperature are the main factors controlling patterns of life history, whereas the genome commits the range of possible adaptations (Stearns 1976, Widdows et al. 1984, Bayne and Newell 1983). Hence, the attainable data of Pectinid populations (N= 134) were divided in four broad groups regarding to (i) their hypothetical longevity (estimated as 0.95 • Age at H_∞ derived from the appropriate VBGF) and (ii) the average annual water temperature of the study sites. An auximetric plot of log(K) versus $\log(M_\infty)$ is given in Figure 7. The mean OGP of the four groups are with one exception (see below) significantly different (ANCOVA with Bonferroni- Dunn post-hoc p< 0.001). OGP of *Aequipecten opercularis* falls in the range of other temperate short-lived scallops (TSL, mean = 1.92 ± 0.26, N = 31, Fig.

7). While previous OGP estimates of *A. opercularis* range between 1.9 (Lee 1973, Taylor and Venn 1978) and 2.1 (Rolfe 1973, Allison 1994), values of the Roscoff population (1.74) appear to be comparatively low, indicating a potentially more stressful environment (i.e. lower food availability, increased depth).

Cold-water long-lived species showed quite similar values (CLL, mean = 1.81 ± 0.23, N = 19, Fig. 7) and hence are statistically not distinguishable from the TSL group, albeit having lower K but higher M_∞ values. The TSL group consists mostly of species belonging to the supragenera *Aequipecten* and *Mimachlamys* (suggested by Waller 1991), while in the CLL all species belong to the supragenus *Chlamys*. All species of this genus are close relatives, all of them have been considered as subspecies of *C. islandica* at some time of their nomenclatural history (fide Waller 1991). OGP in both warm water short-lived (WSL, mean= 2.89 ± 0.28, N = 25, Fig. 7) and temperate long-lived species (TLL, mean= 2.55 ± 0.18, N = 59, Fig. 7) is distinctly higher (ANOVA, $p<0.001$) then in the previous two groups (TSL, CLL).

In general, phylogenetically 'younger' species of the supragenera belong to temperate groups, thus supporting the general idea (e.g. Arntz and Fahrbach 1991) that recent scallops evolved from warm water ancestors; i.e. within the supragenus *Pecten*, while *Amusium spp.* belong to the WSL group, *Pecten maximus* belongs to TSL. This remains, however, pure speculation until modern molecular methods (e.g. Canapa et al. 2000) will clarify the hitherto rather uncertain phylogeny of pectinids.

Metabolic rates

Metabolic rate (R) reflects the energy expenditure of an organism, hence is an important factor in estimating energy flow through both populations and the individual organism (Bayne and Newell 1983). Rates measured in this study are 2-3 times lower than values for the same species published by McLusky (1973); most likely the latter study used a to short acclimation time to the holding systems (10-24 h).

Our results indicate a significant seasonality of metabolic activity in *A. opercularis*, as previously observed for many boreal scallops (MacDonald and Thompson 1985, Bricelj et al. 1987, Shumway et al. 1988). Such seasonal cycles in metabolism result from complex interactions of environmental and endogenous variables acting on the metabolism (for review, Bayne and Newell 1983). Body size, environmental temperature and the energetic demands of biosynthesis, particularly those associated with gametogenesis, are considered to have a profound influence on respiratory activity (Shafee 1982, Bayne and Newell 1983, Bricelj et al. 1987, MacDonald and Bourne 1987, MacDonald and Thompson 1988). The multiple-regression approach used in the present work attempted to quantify the simultaneous effects of body size and seasonal temperature. The equation obtained explains 74% of total variation recorded in metabolic rate. Because no interactive effects have been considered (for the sake of clarity), the two variables tested can be assumed to account almost completely for the seasonal fluctuations in metabolism. The metabolic mass exponent obtained by this equation (b= 0.774, S.E.= 0.03) is slightly below the mean overall value of 0.807 (S.E.= 0.02) derived from a large number of scallop studies (N=80, 13 species; Heilmayer et al. unpublished data compilation).

Individual energy budget model

The partitioning of ingested or metabolizable energy into maintenance and production and possible trade-offs between growth and production are important to characterize the life- history of species (e.g. Sibly and Calow 1986, Wieser 1994). The changing pattern of individual energy expenditure during the lifetime of 6 yrs in *A. opercularis* clearly illustrates (i) an increasing share of maintenance requirements (expressed as respiration) in the absorbed energy (Fig. 5a, b), and (ii) a progressive transition of production from somatic growth to gonad output with increasing age (Fig. 5a), as previously observed for other scallop species too, e.g. *Mimachlamys varia* (Shafee 1982), *Mizuhopecten yessoensis* (Fuji and Hashizume 1974) and *Placopecten magellanicus* (MacDonald and Thompson 1985, 1988, Claereboudt and Himmelman 1996). The general decrease of somatic growth with increasing age (Calow 1977) is not necessarily caused only by a shift between P_s and P_g (Fig. 5a) or the declining ability of the older animals to convert assimilated food into new tissue (Calow and Townsend 1981), but may also be caused by a shorter growing season of older individuals, as already shown for *Chlamys islandica* (Vahl 1981b) and *Pecten maximus* (Chauvaud and Strand 1999).

Net growth efficiency (K_2) values for each year of life, which is a measure of the ability to turn assimilated energy into production, decreases during life time from 45% to 11% in *A. opercularis* (Fig. 5b). These data are among the lowest recordings for populations of suspension and deposit feeding bivalve molluscs so far (Bayne and Newell 1983, Shumway 1991).

Population production and productivity

With a total P/B ratio of 1.848 yr^{-1} annual somatic production of *A. opercularis* is estimated to 20.717 kJ m^{-2} y^{-1} in Trezen Vraz and hence in the same order of magnitude as previous estimates from other populations (Broom and Mason 1978, Taylor and Venn 1978, Richardson et al. 1982).

The *A. opercularis* population from Roscoff waters invests only around 5% of its total annual production into gametes. This is clearly less than in other short-lived scallops

(16% in *Mimachlamys varia*, Shafee and Conan 1984) and far below the investment of either long-lived scallops (≥ 50% in *Placopecten magellanicus* and in *Patinopecten caurinus* MacDonald and Thompson 1985, MacDonald and Bourne 1987) or cold-water scallops (20-30% in *Chlamys islandica* and in *Adamussium colbecki*; Vahl 1981b, Heilmayer et al. 2003). We may, however, under-estimate gonad productivity by assuming one single spawning event during the reproductive season. This view is supported by Aravindakshan (1955) and Ursin (1956), but Taylor and Venn (1978) reported repeated spawning in populations from the Clyde Sea. Conclusive information is lacking so far.

The high P_{tot}/B ratio is in slight contradiction to the observed low OGP value of the population. This might be explained by the low comparatively abundance of large individuals (>60mm), which either is a consequence of spatial differences in settlement from year to year (Brand 1991) or caused by size-selectivity of commercial fisheries.

In conclusion, despite its 6yr lifespan, *A. opercularis* shows some typical features of r-strategy orientated quasi-opportunists, e.g. fast growth and comparatively low reproductive effort. This life strategy combined with environmental variability causes a highly dynamic pattern of occurrence in time and space with typical high-density patches of limited continuance. Locally these patches of *A. opercularis* are likely to play a significant role in system energy flow. Although our sampling extent may not be considered adequate for a precise estimate of population energy parameters, it is still possible to arrive at some conclusions on the individual energy level, which may be considered as a first approximation for future research in this field.

Acknowledgements

The help of the 'Mya'-Crew and the colleagues from the logistics of the 'Station Biologique de Roscoff' for fishing and aquarium-maintenance of *A. opercularis* are greatly acknowledged. We are grateful to Günther Meyer (AWI) and Katrin Blancke (AWI) for technical support in stable isotope analysis. We also thank three anonymous reviewers for constructive comments that greatly improved the manuscript.

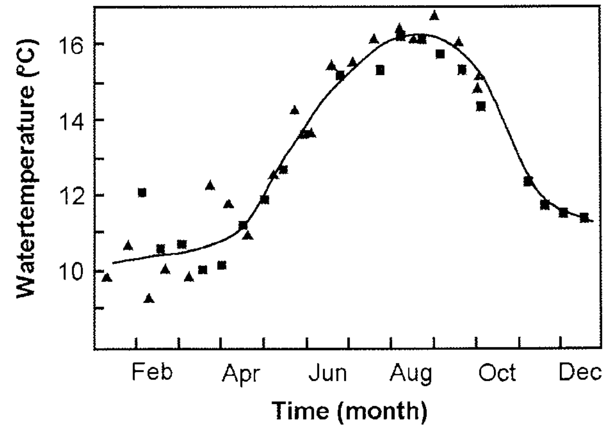

Figure 1

Sea surface water temperatures in Roscoff (1999: circles; 2000: dots; line: cubic spline through two-year mean values). (Data kindly provided by the Service d' Observation en Milieu Littoral -SOMLIT- INSU-CNRS.)

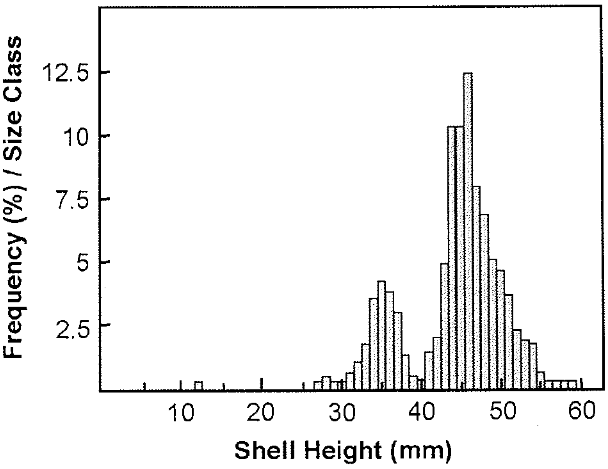

Figure 2

Aequipecten opercularis. Size frequency distribution (1mm –height classes, N= 721) of the pooled samples from February (N= 158), June (N= 377), October (N= 186) 1999 taken from the scallop bed "Trezen Vraz".

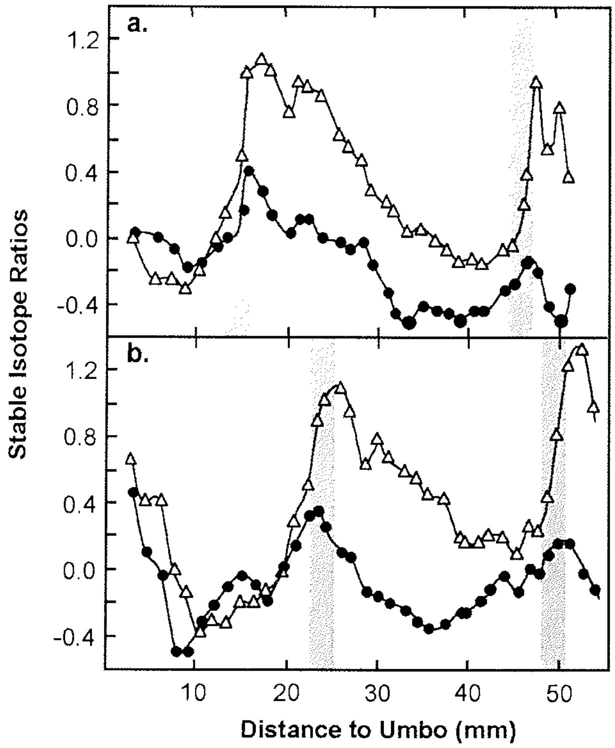

Figure 3

Aequipecten opercularis. Stable isotope ratio (triangles: $\delta^{18}O$; dots: $\delta^{13}C$; weighed moving averages: $(x_1 + 3 \cdot x_2 + x_3)/5$) profiles along transects from umbo to shell edge of two representative individuals (**a.** 52.2 mm height, **b.** 54.2 mm height). Vertical bars indicate positions of external shell growth bands.

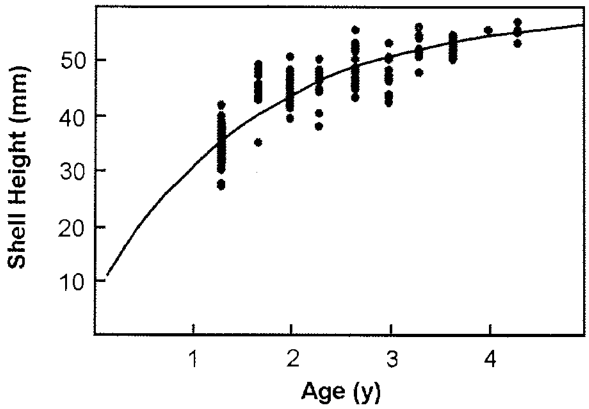

Figure 4

Aequipecten opercularis. Von Bertalanffy growth function fitted to 249 size-at-age data pairs. Growth function parameters are: H_∞= 58.9 mm, K= 0.604, t_0= -0.235 (N= 249, r^2= 0.827)

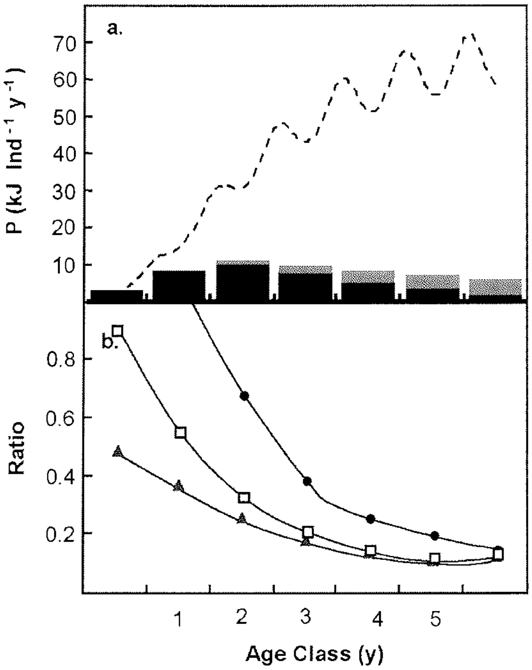

Figure 5

Aequipecten opercularis. **a.** Lifetime production in individual scallops (■ : somatic production per year class *i*; ▨ : gonad production per year class *i*; --: respiratory loss per time interval) **b.** Mean turnover ratios (●: P/B; □: P/R) and net growth efficiency (▲: K_2= P/A; A= P_s + P_G + R) for each age-class in *A. opercularis* from Trezen Vraz.

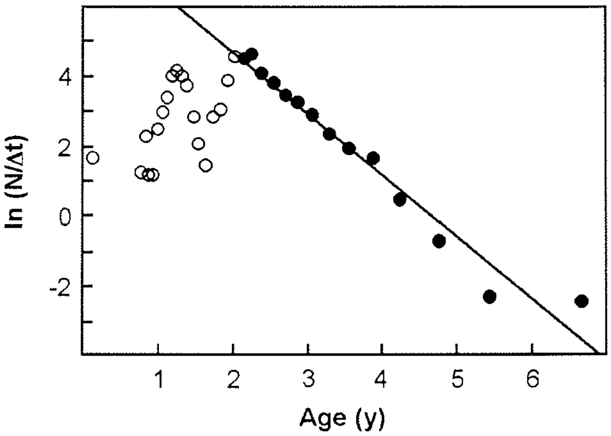

Figure 6

Aequipecten opercularis. Size-converted catch curve based on the pooled size-frequency sample (Fig. 2) and the von Bertalanffy growth function parameters. Dots: data included in catch curve regression; circles: data excluded from regression: $\ln(N_i/dt_i) = 8.237 - 1.761 \cdot t \Leftrightarrow Z = 1.761$ $(r^2 = 0.961)$

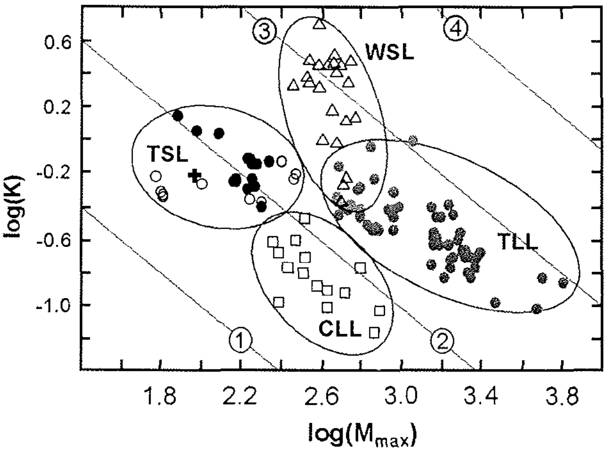

Figure 7

Auximetric grid comparing overall growth performance of Pectinids. (**+**): *A. opercularis* from Roscoff. **CLL**: cold water long-lived species (squares), **WSL**: warm water short-lived species (triangles); **TLL**: temperate long-lived species (grey circles); **TSL**: temperate short-lived species (open circles); *A. opercularis* (dots). Diagonal lines indicate isolines of growth performance index $P = \log(K) + \log(M_\infty)$. Mass data were converted to kJ by using conversion factors of Brey (1999, 2001) and references therein. With one exception mean OGP values of the four groups are significantly different from each other (ANOVA $p<0.05$, with Bonferroni-Dunn post-hoc test). Mean OGP of TSL is not significantly ($p= 0.076$) different from CLL.

Data sources: **CLL**: *Adamussium colbecki* (Stockton 1984, Berkman 1990, Heilmayer et al. 2003, Chiantore et al. 2003), *Chlamys albidus* (Myasnikov and Kochnev 1988), *Chlamys hastata* (MacDonald et al. 1991), *Chlamys islandica* (Vahl 1981a; Lambert and Préfontaine 1995), *Chlamys rosealbus* (Silina and Posdnyakova 1990); **WSL:** *Amusium spp.* (Heald and Caputi 1981, Williams and Dredge 1981, DelNorte 1991); *Argopecten purpuratus* (Mendo and Jurado, 1993, Wolff 1987, Yamashiro and Mendo 1988); **TLL**: *Mizuhopecten yessoensis* (Golikov and Scarlato 1970, Ventilla 1982, Yoo et al. 1981, fide Vakily 1992), *Patinopecten caurinus* (MacDonald and Bourne 1987, Ignell and Haynes 2000), *Pecten maximus* (Buestel and Laurec 1975, Dare 1991, Dare and Deith 1990, Allison 1994), *Placopecten magellanicus* (Brown et al. 1972, Jamieson 1979, Jamieson et al. 1981, D'Amours and Pilote 1982, Chouinhard 1984: all cited in Naidu 1991, MacDonald and Thompson 1985, Claereboudt and Himmelman 1996); **TSL**: *Aequipecten opercularis* (Ursin 1956, Lee 1973, Antoine 1979, Aravindakskan 1955, Askew et al. 1973, all fide Shumway 1991, Broom and Mason 1978, Taylor and Venn 1978, Richardson et al. 1982, Allison 1994), *Chlamys tehuelcha* (Orensanz et al. 1991a), *Mimachlamys varia* (Antoine 1979, Shafee 1982, Shafee and Conan 1984), *Zygochlamys patagonica* (Valero 1999, Lasta et al. 2001).

Table I

Allometric relationship of tissue mass and shell height in *Aequipecten opercularis* collected in 1999 from Trezen Vraz.

	February	June	October
Soma			
a	-4.151	-4.921	-5.078
b	2.369	2.716	3.028
r^2	0.41	0.76	0.71
N	11	27	61
Gonad			
a	-12.024	-10.078	-6.922
b	6.467	4.938	3.165
r^2	0.18	0.89	0.33
N	11	27	61

Regression are of the form $\log(M) = a + b \cdot \log(SH)$, where M is the predicted soft tissue dry mass (g) of the somatic tissue or of the gonad, SH = shell height (mm), and a and b are fitted parameters. N is number of data, r^2 is the determination coefficient. All equations are statistically significant at $p < 0.001$.

6 References

A

Ahn IY, Shim JH (**1998**) Summer metabolism of the Antarctic clam, *Laternula elliptica* (King and Broderip) in Maxwell Bay, King George Island and its implications. *J Exp Mar Biol Ecol*, 224: 253-264

Albertelli G, Cattaneo-Vietti R, Chiantore M, Pusceddu A, Fabiano M (**1998**) Food availability to an *Adamussium* bed during the Austral Summer 1993/1994 (Terra-Nova Bay, Ross Sea). *J Mar Sys*, 17: 425-434

Allen KR (**1971**) Relation between production and biomass. *J Fish Res Board Can*, 28: 1537-1581

Allison EH (**1994**) Seasonal growth models for great scallops (*Pecten maximus* (L.)) and queen scallops (*Aequipecten opercularis* (L.)). *J Shellfish Res*, 13: 555-564

Ament A (**1979**) Geographic variation in relation to life history in three species of the marine gastropod genus *Crepidula*: growth rates of newly hatched larvae and juveniles. *In*: Stancyk SE (Ed) *Reproductive Ecology of Marine Invertebrates*. Univ South Carolina Press, Columbia SC, pp 61-76

Amirthalingham I (**1955**) Studies on the biology of the queen scallop, *Chlamys opercularis* (L.). Ph.D. Thesis, University of Liverpool, 79 pp

Andrade BSG (**1991**) Zygochlamys coastal geomorphology and physical oceanography features of the Magellan Region, Chile (48 degree -56 degree S). *An Inst Patagonia*, 20: 135-151

Angel MV (**1991**) Variations in time and space: Is biogeography relevant to studies of long-time scale change? *J Mar Biol Assoc UK*, 71: 191-206

Angilletta MJ, Niewiarowski PH, Navas CA (**2002**) The evolution of thermal physiology in ectotherms. *J Therm Biol*, 27: 249-268

Ansell AD, Barnett PR, Bodoy A, Massé A (**1980**) Upper temperature tolerance of some European molluscs. I. *Tellina fabula* and *T. tenius*. *Mar Biol*, 58: 33-39

Ansell AD, Dao JC, Mason J (**1991**) Three european scallops: *Pecten maximus, Chlamys (Aequipecten) opercularis* and *C. (Chlamys) varia*. *In*: Shumway SE (Ed) *Scallops: Biology, Ecology and Aquaculture*. Elsevier, Amsterdam, Oxford, New York, pp 715-752

Ansell AD, Cattaneo-Vietti R, Chiantore M (**1998**) Swimming in the Antarctic scallop *Adamussium colbecki*: analysis of *in situ* video recordings. *Ant Sci*, 10: 369-375

Antoine L (**1979**) La Croissance de la Coquille Saint-Jacques (*Pecten maximus*) et ses Variations en Mer Celtique et en Manche. Ph.D. Thesis, University of Bretagne Occidentale, 148 pp

Appeldoorn RS (**1983**) Variation in the growth rate of *Mya arenaria* and its relationship to the environment as analyzed through principal components analysis and the w parameter of the von Bertalanffy equation. *Fish Bull*, 81: 75-84

Aravindakshan I (**1955**) Studies on the biology of the queen scallop, *Chlamys opercularis* (L.). Ph.D. Thesis, University of Liverpool, 79 pp

Araund PM, Hain S (**1992**) Quantitative distribution of the shelf and slope molluscan *fauna* (Gastropoda, Bivalvia) of the Eastern Weddell Sea (Antartica). *Polar Biol*, 12: 103-109

Arntz WE, Fahrbach E (**1991**) *El Niño. Klimaexperiment der Natur. Physikalische Ursachen und biologische Folgen*. Birkhäuser-Verlag, Basel, 264 pp

Arntz WE, Gili JM (**2001**) A case for tolerance in marine ecology: let us not put out the baby with the bathwater. *Sci Mar*, 65 (Suppl. 2): 283-299

Arntz WE, Brey T, Gerdes D, Gorny M, Gutt J, Hain S (**1992**) Patterns of life history and population dynamics of benthic invertebrates under the high Antarctic conditions of the Weddell Sea. *In*: Colombo G, Ferrari I, Ceccherelli VU, Rossi R (Eds) *Marine Eutrophication and Population Dynamics, with a Special Section on the Adriatic Sea.* 25th European Marine Biology Symposium. Olsen and Olsen, Fredensborg (Denmark), pp 221-230

Arntz WE, Brey T, Gallardo VA (**1994**) Antarctic zoobenthos. *Oceanogr Mar Biol Ann Rev,* 32: 241-304

Askew CG, Dunn MR, Reay PJ (**1973**) The fishery for queen scallops in Guernsey 1973. *Report of a Preliminary Investigation in 1973 by Marine Resources Research Unit, Portsmouth Polytechnic*, U.K., unpubl., 39 pp

B

Barber BJ, Blake NJ (**1983**) Growth and reproduction of the bay scallop, *Agropecten irradians* (Lamarck) at its southern distributional limit. *J Exp Mar Biol Ecol*, 66: 247-256

Barber BJ, Blake NJ (**1985**) Substrate catabolism related to reproduction in the bay scallop *Argopecten irradians concentricus*, as determined by O/N and R.Q. physiological indices. *Mar Biol*, 81: 13-18

Barrera E, Tevesz MJS, Carter JG (**1990**) Variations in oxygen and carbon isotopic compositions and microstructure of the shell of *Adamussium colbecki* (Bivalvia). *Palaios,* 5: 149-159

Bayne BL (**1975**) *Marine Mussels: their Ecology and Physiology.* Cambridge University Press, Cambridge.

Bayne BL, Worrall CM (**1980**) Growth and production of mussels *Mytilus edulis* from two populations. *Mar Ecol Prog Ser*, 3: 317-328

Bayne BL, Newell RC (**1983**) Physiological energetics of marine molluscs. *In:* Saleuddin ASM, Wilbur KM (Eds) *The Mollusca: Physiology Part 1.* Academic Press, Boston, pp 407-515

Bayne BL, Hawkins AJS (**1997**) Protein metabolism, the costs of growth, and genomic heterozygosity: experiments with the mussel *Mytilus galloprovincialis* Lmk. Physiol Zool, 70: 391-402

Bayne BL, Bayne CJ, Carefoot TC, Thompson RJ (**1976**) The physiological ecology of *Mytilus califomianus* Conrad. *Oecologia,* 22: 211-228

Bayne BL, Salked PN, Wornwall CM (**1983**) Reproductive effort and value in different populations of of the marine mussel *Mytilus edulis* L. *Oecologia*, 59: 18-26

Bayne BL, Svensson S, Nell JA (**1999**) The physiological basis for faster growth in the Sydney rock oyster, *Saccostrea commercialis. Biol Bull*, 197: 377-387

Beiras R, Camacho AP, Albentosa M (**1994**) Influence of temperature on the physiology of growth in *Ruditapes decussatus* (L.) larvae. *J Shellfish Res*, 13: 77-83

Bennett AF, Huey RB (**1990**) Studying the evolution of physiological performance. *In:* Futuyma DJ, Antonovics J (Eds) *Oxford Surveys in Evolutionary Biology*, Vol. 6. Oxford University Press, Oxford, UK, pp 251-284

Benson BB, Krause DJr (**1984**) The concentration and isotopic fractionation of oxygen dissolved in freshwater and seawater in equilibrium with the atmosphere. *Limnol Oceanogr*, 29: 620-632

Berkman PA (**1990**) The population biology of the Antarctic scallop, *Adamussium colbecki* (Smith, 1902) at New Harbor, Ross Sea. *In:*

Kerry KR, Hempel G (Eds) *Antarctic Ecosystems. Ecological Change and Conservation*. Springer, Berlin, New York, pp 281-288

Berkman PA (**1991**) Unprotected larval development in the Antarctic scallop *Adamussium colbecki* (Mollusca: Bivalvia: Pectinidae). *Ant Sci*, 3: 151-157

Berkman PA, Marks DS, Shreve GP (**1986**) Winter sediment resuspension in McMurdo Sound, Antartica, and its ecological implications. *Polar Biol*, 6: 1-3

Berkman PA, Waller T, Alexander SP (**1991**) Unprotected larval development in the Antarctic scallop *Adamussium colbecki* (Mollusca: Bivalvia: Pectinidae). *Ant Sci*, 3: 151-157

Bernard FR, Noakes DJ (**1990**) Pumping rates, water pressure, and oxygen use in eight species of marine bivalve molluscs from British Columbia. *Can J Fish Aquat Sci*, 47: 1302-1306

Beukema JJ, Meehan BW (**1985**) Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. *Mar Biol*, 90: 27-33

Brand A (**1991**) Scallop ecology: distributions and behaviour. *In*: Shumway SE (Ed) *Scallops: Biology, Ecology and Aquaculture*. Elsevier, Amsterdam, Oxford, NewYork, pp 517-584

Brey T (**1999**) Growth performance and mortality in aquatic macrobenthic invertebrates. *Adv Mar Biol*, 35: 153-223

Brey T (**2001**) Population Dynamics in Benthic Invertebrates. A Virtual Handbook. Version 1.2. http://www.awi-bremerhaven.de/Benthic/ Ecosystem/FoodWeb/Handbook/main.html. Alfred Wegener Institute for Polar and Marine Research, Germany.

Brey T, Hain S (**1992**) Growth, reproduction and production of *Lissarca notorcadensis* (Bivalvia: Philobryidae) in the Weddell Sea, Antarctica. *Mar Ecol Prog Ser*, 82: 219-226

Brey T, Clarke A (**1993**) Population dynamics of marine benthic invertebrates in Antarctic and subantarctic environments: are there unique adaptations. *Ant Sci*, 5: 253-266

Brey T, Gerdes D (**1997**) Is Antarctic benthic biomass really higher than elsewhere? *Ant Sci*, 9: 266-267

Brey T, Mackensen A (**1997**) Stable isotopes prove shell growth bands in the Antarctic bivalve *Laternula elliptica* to be formed annually. *Polar Biol*, 17: 465-468

Brey T, Rumohr H, Ankar S (**1988**) Energy content of macrobenthic invertebrates: General conversion factors from weight to energy. *J Exp Mar Biol Ecol*, 117: 271-278

Brey T, Arntz WE, Pauly D, Rumohr H (**1990**) *Artica (Cyprina) islandica* in Kiel Bay (Western Baltic): growth, production and ecological significance. *J Exp Mar Biol Ecol*, 136: 217-235

Brey T, Starmans A, Magiera U, Hain S (**1993**) *Lissarca notorcadensis* (Bivalvia: Philobryidae) living on *Notocidaris sp.* (Echinoida: Cidaroidea): population dynamics in limited space. *Polar Biol*, 13: 89-95

Brey T, Pearse J, McClintock J, Slattery M (**1995a**) Growth and production of *Sterechinus neumayeri* (Echinoidae: Echinodermata) in McMurdo Sound, Antarctica. *Mar Biol*, 124: 279-292

Brey T, Peck LS, Gutt J, Hain S, Arntz WE (**1995b**) Population dynamics of *Magellania fragilis*, a brachipod dominating a mixed bottom macro-benthic assemblage on the Antarctic shelf. *J Mar Biol Ass UK*, 95: 857-869

Bricelj VM, Shumway SE (**1991**) Physiology: Energy acquisition and utilization. *In*: Shumway SE (Ed) *Scallops: Biology, Ecology and Aquaculture*. Elsevier, Amsterdam, Oxford, NewYork, pp 305-346

Bricelj VM, Epp J, Malouf RE (**1987**) Comparative physiology of young and old cohorts of bay scallop *Argopecten irradians irradians* (Lamarck): mortality, growth, and oxygen consumption. *J Exp Mar Biol Ecol*, 112: 73-91

Brockington S (**2001**) The seasonal energetics of the Antarctic bivalve *Laternula elliptica* (King and Broderip) at Rothera Point, Adelaide Island. *Polar Biol*, 24: 523-530

Brockington S, Clarke A (**2001**) The relative influence of temperature and food on the metabolism of a marine invertebrate. *J Exp Mar Biol Ecol*, 258: 87-99

Brockington S, Clarke A, Chapman ALG (**2001**) Seasonality of feeding and nutritional status during the austral winter in the Antarctic sea urchin *Sterechinus neumayeri*. *Mar Biol*, 139: 127-138

Brody S (**1945**) *Bioenergetics and Growth*. Reinhold, New York.

Brokordt KB, Himmelman JH, Nusetti OA, Guderley HE (**2000a**) Reproductive investment reduces recuperation from exhaustive escape activity in the tropical scallop *Euvola zizac*. *Mar Biol*, 137: 857-865

Brokordt KB, Himmelman JH, Guderley HE (**2000b**) Effect of reproduction on escape responses and muscle metabolic capacities in the scallop *Chlamys islandica* Müller 1776. *J Exp Mar Biol Ecol*, 251: 205-225

Brokordt KB, Guderley HE, Guay M, Gaymer CF, Himmelman JH, (**2003**) Sex differences in reproductive investment: maternal care reduces escape response capacity in the whelk *Buccinum undatum*. *J Exp Mar Biol Ecol*, 4150: 1-20

Broom MJ (**1976**) Synopsis of Biological data on scallops. *FAO Fisheries Synopsis*, 114: 1-30

Broom MJ, Mason J (**1978**) Growth and Spawning in the pectinid *Chlamys opercularis* in relation to temperature and phytoplankton concentration. *Mar Biol*, 47: 277-285

Brown BE, Parrack M, Flescher DD (**1972**) Review of the current status of the scallop fishery in ICNAF division 5Z. *Int Comm Northw Atl Fish (ICNAF) Res Doc*, 72/113: 1-13

Buestel D, Laurec A (**1975**) Croissance de la coquille St. Jacques (*Pecten maximus* L.) en rade de Brest et en baie de Saint Brieuc. *Haliotis*, 5: 173-177

C

Calow P (**1975**) The respiratory strategies of two species of freshwater gastropods (*Ancylus fluviatilis* Mull. and *Planorbis contortus* Linn.) in relation to temperature, oxygen concentration, body size, and season. *Physiol Zool*, 48: 114-129

Calow P (**1977**) Ecology, Evolution and Energetics: A Study in Metabolism Adaptation. *In:* Macfadyen, A. (Ed) *Advances in Ecological Research*, 10. Academic Press, London, New York, pp 1-61

Calow P (**1983**) Life-cycle patterns and evolution. *In*: Russel-Hunter WD (Ed) *The Mollusca*, Vol. 6. Ecology. Academic Press, Boston, pp 649-678

Calow P, Townsend CR (**1981**) Resource utilization in growth. *In*: Townsend CR, Calow P (Eds) *Physiological Ecology: An Evolutionary Approach to Resource Use*. Sunderland, Massachusetts, Sinauer Associates Inc, pp 220-244

Campbell CM, Davies SP (**1978**) Temperature acclimation in the teleost, Blennius pholis: changes in enzyme activity and cell structure. *Comp Biochem Physiol*, 61: 165-167

Canapa A, Barucca M, Marinelli A, Olmo E (**1999a**) A molecular approach to the systematics of antarctic scallop *Adamussium colbecki*. *Ital J Zool*, 66: 379-382

Canapa A, Marota I, Rollo F, Olmo E (**1999b**) The small-subunit rRNA gene sequences of venerids and the phylogeny of Bivalvia. *J Mol Evol*, 48: 463-468

Canapa A, Barucca M, Marinelli A, Olmo E (**2000**) Molecular data from the 16S rRNA Gene for the Phylogeny of Pectinidae (Mollusca: Bivalvia). *J Mol Evol*, 50: 93-97

Cardillo M (**2002**) The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? *J Animal Ecol*, 71: 79-87

Carreto JI, Lutz VA, Carignan MO, Cucchi Colleoni AD, DeMarcos SG (**1995**) Hydrography and chlorophyll a in a transect from the coast to the shelf-break in Argentinian Sea. *Cont Shelf Res*, 15: 315-336

Cattaneo-Vietti R, Chiantore M, Albertelli G (**1997**) The population structure and ecology of the Antarctic scallop, *Adamussium colbecki* at Terra Nova Bay (Ross Sea, Antarctica). *Sci Mar*, 61: 15-24

Cattaneo-Vietti R, Chiantore M, Misic C, Povero P, Fabiano M (**1999**) The role of pelagic-benthic coupling in structuring littoral benthic communities at Terra Nova Bay (Ross Sea) and in the Straits of Magellan. *Sci Mar*, 63: 113-121

Chapelle G, Peck LS (**1995**) The influence of acclimation and substratum on the metabolism of the Antarctic amphipods *Waldeckia obesa* (Chevreux 1905) and *Bovallia gigantea* (Pfeffer 1888). *Polar Biol*, 15: 225-232

Chauvaud L, Strand O (**1999**) Growth traits in three populations of *Pecten maximus*. Book of Abstracts: 12th International Pectinid Workshop, pp 166-167

Chiantore M, Cattaneo-Vietti R, Albertelli G, Misic C, Fabiano M (**1998**) Role of filtering and biodeposition by *Adamussium colbecki* in circulation of organic matter in Terra Nova Bay (Ross Sea, Antarctica). *J Mar Sys*, 17: 411-424

Chiantore M, Cattaneo-Vietti R, Povero P, Albertelli G (**2000**) The population structure and ecology of the antarctic scallop *Adamussium colbecki* in Terra Nova Bay. *In*: Faranda FM, Guglielmo L, Ianora A (Eds) *Ross Sea Ecology: Italian Antarctic Expeditions (1986-1995)*, Springer-Verlag, Berlin: pp 563-573

Chiantore M, Cattaneo-Vietti R, Berkman P, Nigro M, Vacchi M, Schiaparelli S, Albertelli G (**2001**) Antarctic scallop (*Adamussium colbecki*) spatial population variability along the Victoria Land Coast, Antarctica. *Polar Biol*, 24: 139-143

Chiantore M, Cattaneo-Vietti R, Elia L, Guidetti M, Antonini M (**2002**) Reproduction and condition of the scallop *Adamussium colbecki* (Smith, 1902), the sea-urchin *Sterechinus neumayeri* (Meissner 1900) and the sea-star *Odontaster validus* Koehler 1911 at Terra Nova Bay (Ross Sea): different strategies related to inter-annual variations in food availability. *Polar Biol*, 25: 251-255

Chiantore M, Cattaneo-Vietti R, Heilmayer O (**2003**) Antarctic scallop (*Adamussium colbecki*) annual growth rate at Terra Nova Bay. *Polar Biol*, 26: 416-419

Chih CP, Ellington WR (**1987**) Studies of the mitochondria and enzymes from the ventricle of the whelk *Busycon contrarium*. *Comp Biochem Physiol*, 86B: 541-545

Chouinhard GA (**1984**) Growth of the sea scallop (*Placopecten magellanicus*) on the Tormentine Bed, Northumberland Strait. *CAFSAC Res Doc*, 84: 1-16

Claereboudt MR, Himmelman JH (**1996**) Recruitment, growth and production of giant scallops (*Placopecten magellanicus*) along an environmental gradient in Baie des Chaleurs, eastern Canada. *Mar Biol*, 124: 661-670

Clarke A (**1983**) Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanogr Mar Biol Ann Rev*, 21: 341-453

Clarke A (**1987**) The adaptation of aquatic animals to low temperatures. *In*: Grout BWW, Morris GJ (Eds) *Effects of low Temperatures on Biological Systems.* Edward Arnold, Baltimore MD, pp 315-348

Clarke A (**1988**) Seasonality in the antarctic marine environment. *Comp Biochem Physiol*, 90B: 461-473

Clarke A (**1991**) What is cold adaptation and how should we measure? *Am Zool*, 31: 81-92

Clarke A (**1993**) Seasonal acclimatization and latitudinal compensation in metabolism: do they exist? *Funct Ecol*, 7: 139-149

Clarke A (**1998**) Temperature and energetics: an introduction to cold ocean physiology. *In*: Pörtner HO, Playle R (Eds) *Cold Ocean Physiology.* Cambridge University Press, Cambridge, pp 3-30

Clarke A, Crame JA (**1989**) The origin of the Southern Ocean marine fauna. *In*: Crame JA (Ed) *Origins and Evolution of the Antarctic Biota.* The Geological Society, London, pp 253-268

Clarke A, North AW (**1991**) Is the growth of polar fish limited by temperature? *In*: di Prisco G, Maresca B, Tota B (Eds) *Biology of Antarctic Fish.* Springer-Verlag, Berlin, pp 54-69

Clarke A, Crame JA (**1997**) Diversity, latitude and time: patterns in the shallow sea. *In*: Ormond RFG, Gage JD, Angel MV (Eds) *Marine Biodiversity: Patterns and Processes.* Cambridge University Press, New York, pp 122-147

Clarke A, Johnston NM (**1999**) Scaling of metabolic rate with body mass and temperature in teleost fish. *J Anim Ecol,* 68: 893-905

Coma R, Ribis M, Gili JM, Zabala M (**1998**) An energetic approach to the study of life-history traits of two modular colonial benthic invertebrates. *Mar Ecol Prog Ser*, 162: 89-103

Conan G, Shafee MS (**1978**) Growth and biannual recruitment of the black scallop *Chlamys varia* (L.) in Lanveoc area, Bay of Brest. *J Exp Mar Biol Ecol*, 35: 59-71

Connolly SR, Roughgarden J (**1998**) A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. *Am Nat*, 151: 311-326

Conover DO, Present TMC (**1990**) Countergradient variation in growth rate: compensation for length of the growing season among Atlantic silversides from different latitudes. *Oecologia*, 83: 316-324

Conover DO, Schultz ET (**1997**) Natural selection and the evolution of growth rate in the early life history: what are the trade-offs? *In*: Chambers RC, Trippel EA (Eds) *Early life history and recruitment in fish populations.* Chapman & Hall, London, pp 305-332

Conover DO, Brown JJ, Ehtisham A (**1997**) Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. *Can J Fish Aquat Sci*, 54: 2401-2409

Crame JA, Clarke A (**1997**) The historical component of marine taxonomic diversity gradients. *In*: Ormond RFG, Gage JD, Angel MV (Eds) *Marine Biodiversity: Patterns and Processes.* Cambridge University Press, New York, pp 258-273

Crisp DJ (**1984**) Energy flow measurements. *In:* Holme N, McIntoye AD (Eds) *Methods for the Study of Marine Benthos.* Blackwell Science, Oxford, pp 284-372

Crockett EL, Sidell BD (**1990**) Some pathways of energy metabolism are cold adapted in Antarctic fishes. *Physiol Zool,* 63: 472-488

D

Dahm C, Brey T (**1998**) Determination of growth and age of slow growing brittle stars

(Echinodermata: Ophiuroidea) from natural growth bands. *J Mar Biol Ass UK*, 78: 941-951

Dame RF (**1972**) The ecological energies of growth, respiration and assimilation in the intertidal american oyster *Crassostrea virginica*. *Mar Biol*, 17: 243-250

D'Amours D, Pilote S (**1982**) Données biologiques sur le Pétoncle D'islande (*Chlamys islandica*) et le Pétoncle Géant (*Placopecten magellanicus*) de la Basse-Côte-Nord du Québec (Secteur de la Tabatire). *Cahier D'Information,* 99, 1-47

Dare PJ (**1991**) Use of external shell microgrowth patterns for determining growth and age in the scallop *Pecten maximus. Actes Colloq IFREMER*, 17: 211-218

Dare PJ, Deith MR (**1990**) Age determination of scallops, *Pecten maximus* (Linnaeus, 1758), using stable oxygen isotope analysis, with some implications for fisheries management in British waters. *In*: Shumway SE, Sandifer PA (Eds) *An International Compendium of Scallop Biology and Culture*. World Aquaculture Society, Baton Rouge, L.A., pp 118-133

Dayton PK (**1990**) Polar benthos. *In*: Smith WO Jr (Ed) *Polar Oceanography*, Part B. Academic Press, London, pp 631-685

Dehnel PA (**1955**) Rates of growth of gastropods as a function of latitude. *Physiol Zool*, 28: 115-144

Dell RK (**1990**) Antarctic Mollusca. With special reference to the fauna of the Ross Sea. *R Soc NZ Bull,* 27: 1-311

Del Norte AGC (**1988**) Aspects of the growth, recruitment, mortality and reproduction of the scallop *Amusium pleuronectes* (Linne) in the Lingayen Gulf, Philippines. *Ophelia*, 29: 153-168

Del Norte AGC (**1991**) Fisheries and aquaculture: Philippines. *In*: Shumway SE (Ed) *Scallops: Biology, Ecology and Aquaculture*. Elsevier, Amsterdam, Oxford, NewYork, pp 825-834

Diehl WJ, Gaffney MP, Koehn RK (**1986**) Physiological and genetic aspects of growth in the mussel *Mytilus edulis*. 1. Oxygen consumption, growth, and weight loss. *Physiol Zool*, 59: 201-211

Dolmer P (**2000**) Algal concentration profiles above mussel beds. *Neth J Sea Res,* 43: 113-119

E

Eastman JT (**1993**) *Antarctic Fish Biology: Evolution in a Unique Environment.* San Diego, Academic Press Inc.

Egginton S, Sidell BD (**1989**) Thermal acclimation induces adaptive changes in subcellular structure of fish skeletal muscle. Am J Physiol, 256: R1-R9

Elliott JM, Davidson W, (**1975**) Energy equivalents of oxygen consumption in animal energetics. *Oecologia* 19: 195-201

Epstein S, Buschbaum R, Lowenstam HA, Urey HC (**1953**) Revised carbonate-water isotopic temperature scale. *Geol Soc Am Bull*, 64: 1315-1326

Erez J, Luz B (**1983**) Experimental paleotemperature equation for planktonic foraminifera. *Geochimica Cosmochim Acta,* 47: 1025-1031

F

Fabens AJ (**1965**) Properties and fitting of the von Bertalanffy growth curve. *Growth*, 29: 265-285

Fabiano M, Chiantore M, Povero P, Cattaneo-Vietti R, Pusceddu A, Misic C, Albertelli G (**1997**) Short-term variations in particulate matter flux in Terra Nova Bay, Ross Sea. *Ant Sci*, 9: 143-149

Fairbridge WS (**1953**) A population study of the Tasmanian "commercial" scallop *Notovola meridionalis* (Tate) (Lamellibranchi, Pectinidae). *Aust J Mar Freshwat Res*, 4: 1-40

Feldman HA, McMahon, TA (**1983**) The 3/4 mass exponent for energy metabolism is not a statistical artifact. *Resp Physiol*, 52: 149-163

Forster ME, Franklin CE, Taylor HH, Davison W (**1987**) The aerobic scope of an Antarctic fish, *Pagothenia borchgrevinki*, and its significance for metabolic cold adaptation. *Polar Biol*, 8: 155-159

Forstner H (**1983**) An automated multiple-chamber intermittent-flow respirometer. *In*: Gnaiger E, Forstner H (Eds) *Polarographic Oxygen Sensors*. Springer-Verlag, Berlin, pp 111-126

Forsythe J, Lee P, Walsh L, Clark T (**2002**) The effects of crowding on growth of the European cuttlefish, *Sepia officinalis* Linnaeus, 1758 reared at two temperatures. *J Exp Mar Biol Ecol*, 269: 173-185

Foster SA, Cameron, S.A. (**1996**) Geographic variation in behaviour: a phylogenetic framework for comparative studies. *In*: Martins EP (Ed) *Phylogenies and the Comparative Method in Animal Behavior*. Oxford University Press, Oxford, pp 138-165

Francis RICC (**1988**) Are growth parameters estimated from tagging and age-length data comparable? *Can J Fish Aquat Sci*, 45: 936-942

Francis RICC (**1995**) An alternative mark-recapture analogue of Schnute's growth model. *Fish Res*, 23: 95-111

Franklin A, Pickett GD, Holme NA, Barrett RL (**1980**) Surveying Stocks of Scallops (*Pecten maximus*) and Queens (*Chlamys opercularis*) with underwater television. *J Mar Biol Ass UK*, 60: 181-191

Fraser RH, Currie DJ (**1996**) The species richness-energy hypothesis in a system where historical factors are thought to prevail: Coral reefs. *Am Nat*, 148: 138-154

Frederich M, Pörtner HO (**2000**) Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in the spider crab *Maja squinado*. *Am J Physiol*, 279: R1531-R1538

Frischer ME, Williams J, Kenchington E (**1998**) A molecular phylogeny of some major groups of Pectinidae inferred from 18S rRNA gene sequences. *In*. Newell ND (Ed) *Bivalves: An eon of evolution. Paleobiological studies honoring Norman D. Newell*. University of Calgary Press, Calgary, pp 213-221

Fuji A, Hashizume M (**1974**) Energy budget for a Japanese common scallop, *Patinopecten yessoensis* (Jay), in Mutsu Bay. *Bull Fac Fish Hokkaido Univ*, 25: 7-19

G

Garcia-Esquivel Z, Bricelj VM, González-Gímez MA (**2001**) Physiological basis for energy demands and early postlarval mortality in the Pacific oyster, *Crassostrea gigas*. *J Exp Mar Biol Ecol*, 263: 77-103

Garland, T. Jr., Harvey, R.B., & Ives, A.R. (**1992**) Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst Biol*, 41: 18-32

Gassel A (**1996**) Beiträge zur Berechnung solarthermischer und energieeffizienter Energiesysteme. PhD Thesis, TU Dresden, Germany: 142 pp

Gatti S, Brey T, Müller WEG, Heilmayer O, Holst G (**2002**) Oxygen microoptodes: a new tool for oxygen measurements in aquatic animal ecology. *Mar Biol*, 140: 1075-1085

Gibson FA (**1953**) Tagging of scallops (*Pecten maximus* L.) in Ireland. *J Cons CIEM* 19: 204-208

Glud RN, Klimant I, Holst G, Kohls O, Meyer V, Kühl M, Gundersen JK (**1999**) Adaptation, test and in situ measurements with O2 microopt(r)odes on benthic landers. *Deep-Sea Res*, 46: 171-183

Gnaiger E (**1983**) Calculation of energetic and biochemical equivalents of respiratory oxygen consumption. *In:* Gnaiger E, Forstner H (Eds) *Polarographic oxygen sensors.* Springer, Berlin.

Golikov AN, Scarlato OA (**1970**) Abundance, dynamics and production properties of edible bivalves *Mizuhopecten yessoensis* and *Spisula sachalinensis* related to the problem of organisation of controllable submarine farms at the western shores of the Sea of Japan. *Helgol Mar Rep*, 20: 498-513

Golikov AN, Dolgolenko MA, Maximovich NV, Scarlato OA (**1990**) Theoretical approaches to marine biogeography. Mar Ecol Prog Ser, 63: 289-301

Goulletquer P, Heral M (**1997**) Marine molluscan production trends in France: from fisheries to aquaculture. *NOAA Tech Rep*, 129: 137-162

Gorny M, Arntz WE, Clarke A, Gore DJ (**1992**) Reproductive biology of caridean decapods from the Weddell Sea. Polar Biol, 12: 111-120

Grainger RJR (**1992**) ICES Fisheries Statistics: Bulletin Statistique des Pêches Maritimes 1988. *ICES Copenhagen*, 73: 64-65

Grant J, Cranford PJ (**1991**) Carbon and nitrogen scope for growth as a function of diet in the sea scallop *Placopecten magellanicus. J Mar Biol Ass UK*, 71: 437-450

Griffiths RJ (**1980**) Natural food availability and assimilation in the bivalve *Choromytilus meridionalis. Mar Ecol Prog Ser*, 3: 151-156

Griffiths RJ (**1981**) Aerial Exposure and Energy Balance in Littoral and Sublittoral *Choromytilus meridionalis* (Kr.) (Bivalvia). J Exp Mar Biol Ecol, 52: 231-241

Griffiths CL, Griffiths RJ (**1987**) Bivalvia. *In:* Pandian JH, Vernberg FJ (Eds) *Animals Energetics.* Academic Press, New York, pp 1-88

Gröger J (**2000**) Biometrische Analysen zur Optimierung spezieller populationsdynamischer Kenngrössen in der Fischereibiologie. Habilitation, University Rostock, Germany, 204 pp

Gruffydd LD (**1976**) Swimming in *Chlamys islandicai* in relation to current speed and an investigation of hydrodynamic lift in this and other scallops. *Norw J Zool*, 24: 365-378

Guderley H (**1998**) Temperature and growth rates as modulators of the metabolic capacities of fish muscle. *In:* Pörtner HO and Playle R (Eds) *Cold Ocean Physiology.* Cambridge: Cambridge University Press; 1998; pp 58-87.

Guderley HE, St Pierre J, Couture P, Hulbert AJ (**1997**) Plasticity of the properties of mitochondria from rainbow trout red muscle with seasonal acclimatization. *Fish Physiol Biochem*, 16: 531-541

Gutiérrez N, Defeo O (**2003**) Development of a new scallop *Zygochlamys patagonica* fishery in Uruguay: latitudinal and bathymetric patterns in biomass and population structure. *Fish Res*, 62: 21-36

Gwyther D, McShane PE (**1988**) Growth rate and natural mortality of the scallop *Pecten alba* Tate in Port Phillips Bay, Australia, and evidence for changes in growth rate after a 20-year period. *Fish Res*, 6: 347-361

H

Hain S (**1990**) Die beschalten benthischen Mollusken (Gastropoda & Bivalvia) des Weddellmeeres, Antarktis. *Ber Polarforsch*, 70: 1-181

Hardewig I, Van Dijk PLM, Pörtner HO (**1998**) High-energy turnover at low temperatures: recovery from exhaustive exercise in Antarctic and temperate eelpouts. *Am J Physiol*, 274: 1789-1796

Hardewig I, Van Dijk PLM, Moyes CD, Pörtner HO (**1999**) Temperature- Dependent Expression of Cytochrome-C Oxidase in Antarctic and Temperate Fish. *Am J Physiol*, 277: R508-R516

Hawkins AJS, Day AJ (**1996**) The metabolic basis of genetic differences in growth efficiency among marine animals. *J Exp Mar Biol Ecol*, 203: 93-115

Hawkins AJS, Bayne BL, Day A.J (**1986**) Protein turnover, physiological energetics and heterozygosity in the blue mussel, *Mytilus edulis*: the basis of variable age-specific growth. *Proc R Soc Lond*, 229B: 161-176

Hawkins AJS, Widdows J, Bayne BL (**1989**) The relevance of whole-body protein metabolism to measured costs of maintenance and growth in *Mytilus edulis*. *Physiol Zool*, 62: 745-763

Hawkins AJS, Bayne BL, Bougrier S, Heral M, Iglesias JIP, Navarro E, Smith RFM, Urrutia MB (**1998**) Some general relationships in comparing the feeding physiology of suspension-Feeding bivalve molluscs. *J Exp Mar Biol Ecol*, 219: 87-103

Hawkins AJS, Duarte P, Fang JG, Pascoe PL, Zhang JH, Zhang XL, Zhu MY (**2002**) A functional model of responsive suspension-feeding and growth in bivalve shellfish, configured and validated for the scallop *Chlamys farreri* during culture in China. *J Exp Mar Biol Ecol*, 281: 13-40

Haynes EB, Powell GC (**1968**) A Preliminary Report on the Alaska Sea Scallop — Fishery Exploration, Biology, and Commercial Processing. *Informational Leaflet No. 125*

Haynes EB, Hitz CR (**1971**) Age and growth of the giant Pacific sea scallop, *Patinopecten caurinus*, from the Strait of Georgia and outer Washington coast. *J Fish Res Bd Canada*, 28: 1335-1341

Heald DI, Caputi N (**1981**) Some aspects of growth, recruitment and reproduction in the southern saucer scallop, *Amusium balloti* (Bernardi, 1861) in Shark Bay, Western Australia. Dept. Fish. Wildl. (West Australia), *Fish Res Bull*, 25: 1-33

Heilmayer O, Brey T (**2003a**) Saving by freezing? Metabolic rates of *Adamussium colbecki* in a latitudinal context. *Mar Biol*, 143: 477-484

Heilmayer O, Brey T (**2003b**) How expensive is reproduction in the cold? A scallop example. 14th International Pectinid Workshop, St. Petersburg, Florida, USA, in press.

Heilmayer O, Bremec C, Brey T, Lasta M, Valero J (**2001**) Why are there no Patagonic scallops (*Zygochlamys patagonica*) of the Rio Plata estuary? 13th International Pectinid Workshop, Coquimbo, Chile, p 103

Heilmayer O, Pörtner HO, Brey T (**2002**) Growth, production and respiration in scallops. *Comp Biochem Physiol*, 132A: p 20

Heilmayer O, Brey T, Chiantore C, Cattaneo-Vietti R, Arntz WE (**2003**) Age and productivity of the Antarctic scallop (*Adamussium colbecki*) in the Ross Sea. *J Exp Mar Biol Ecol*, 288: 239-256

Heilmayer O, Brey T, Storch D, Mackensen A, Arntz WE (**2004**) Population dynamics and metabolism of *Aequipecten opercularis* (L.) from the western English Channel (Roscoff, France). *Neth J Sea Res*: in press.

Hemmingsen AM (1960) Energy metabolism as related to body size and respiratory surfaces, and its evolution. *Reports Steno Memorial Hospital & Nordisk Insulin Laboratorium*, 9: 7-110

Hickson JA, Johnson ALA, Heaton THE, Balson PS (**1999**) The shell of the queen scallop *Aequipecten opercularis* (L.) as a promising tool for palaeoenvironmental reconstruction: evidence and reasons for equilibrium stable-isotope incorporation. *Palaeogeogr Palaeoclimatol Palaeoecol*, 154: 325-337

Hochachka PW, Somero GN (**1984**) Limiting oxygen availability. *In:* Biochemical adaptation. Princeton University Press, Princeton, New Jersey, pp 145-181

Hochachka PW, Somero GN (**2002**) *Biochemical Adaptation: Mechanism and Process in Physiological Evolution.* Oxford University Press, Oxford.

Houlihan DF (**1991**) Protein turnover in ectotherms and its relationships to energetics. *Comp Environment Physiol*, 7: 1-43

Humphreys WF (**1979**) Production and Respiration in Animal populations. *J Animal Ecol*, 48: 427-453

Hut G (**1987**) Stable isotope reference samples for geochemical and hydrological investigations. *International Atomic Energy Agency, Report 42*, (Vienna, Sept. 16-18)

I/J

Iglesias JIP, Navarro E (**1990**) Shell growth of the cockle *Cerastoderma edule* in the Mundaca Estuary (North Spain). *J Mollusc Stud*, 56: 229-238

Iglesias JIP, Navarro E (**1991**) Energetics of growth and reproduction in cockles (*Cerastoderma edule*): seasonal and age-dependent variations. *Mar Biol,* 111: 359-368

Ignell S, Haynes E (**2000**) Geographic patterns in growth of the giant Pacific Sea scallop, *Patinopecten caurinus. Fish Bull*, 98: 849-853

Iguchi N, Ikeda T (**1995**) Growth, metabolism and growth efficiency of a euphausiid crustacean *Euphausia pacifica* the southern Japan Sea, as influenced by temperature. *J Plank Res*, 17, 1757-1769

Ivlev VS (**1935**) Eine Mikromethode zur Bestimmung des Kaloriengehalts von Naehrstoffen. *Biochem* 275: 49-55

Ivleva IV (**1980**) The dependence of crustacean respiration on body mass and habitat temperature. *Int Rev Hydrobiol*, 65: 1-47

Jamieson GS (**1979**) Status and assessment of Northumberland Strait scallop stocks. *Fish Mar Serv Tech Rep,* 904: 1-34

Jamieson GS, Kerr G, Lundy MJ (**1981**) Assessment of scallop stocks on Browns and German Banks -1979. *Can Tech Rep Fish Aquat Sci,* 1014: 1-17

Jarre-Teichmann A, Brey T, Bathmann UV, Dahm C, Dieckmann GS, Gorny M, Pages F, Plötz J, Schnack-Schiel S, Stiller M, Arntz WE (**1997**) Trophic flows in the benthic shelf community of the eastern Weddell-Sea. *In*: Battaglia B, Valencia J, Walton DWH (Eds) *Antarctic Communities: Species, Structure and Survival*. Cambridge University Press, Cambridge, pp 118-134

Johnston TP, Bennett AF (**1995**) The thermal acclimation of burst escape performance in fish: An integrated study of molecular and cellular physiology and organismal performance. *J Exp Biol*, 198: 2165-2175

Johnston IA, Guderley H, Franklin CE, Crockford T, Kamunde C (**1994**) Are mitochondria subject to evolutionary temperature adaptation? *J Exp Biol*, 195: 293-306

Johnston IA, Calvo J, Guderley H, Fernandez D, Palmer L (**1998**) Latitudinal variation in the abundance and oxidative capacities of muscle mitochondria in perciform fishes. *J Exp Biol*, 201: 1-12

Jones DS, Williams DF, Arthur MA (**1986**) Growth history of symbiont-bearing giant clams from stable isotope profiles. *Science*, 231: 46-48

Jørgensen CB (**1983**) Fluid mechanical aspects of suspension feeding. *Mar Ecol Prog Ser*, 11:89-103

Jørgensen CB (**1988**) Metabolic costs of growth and maintenance in the toad, *Bufo bufo*. *J Exp Biol*, 138: 319-331

K

Kaestner A. (**1993**) *Lehrbuch der speziellen Zoologie*. Bd. 1/3 Wirbellose Tiere.

Kautsky N (**1982a**) Growth and size structure in a Baltic *Mytilus edulis* population. *Mar Biol*, 68: 117-133

Kautsky N (**1982b**) Quantitative studies on gonad cycle, fecundity, reproductive output and recruitment in a Baltic *Mytilus edulis* population. *Mar Biol*, 68: 143-160

Kawall HG, Torres JJ, Sidell BD, Somero GN (**2002**) Metabolic cold adaptation in Antarctic fishes: evidence from enzymatic activities of brain. *Mar Biol*, 140: 279-286

Kirby-Smith WW (**1970**) Growth of the scallops, *Argopecten irradians* concentricus (Say) and *Argopecten gibbus* (Linné), as influenced by food and temperature. Ph.D. Thesis, Duke University, Durham, North Carolina, 126 pp

Kirby-Smith WW (**1972**) Growth of the bay scallop: The influence of experimental water currents. *J Exp Mar Biol Ecol*, 8: 7-18

Kleiber M (**1975**) Metabolic turnover rate: a physiological meaning of the metabolic rate per unit body weight. *J Theor Biol*, 53: 199-204

Klimant I, Meyer V, Kühl M (**1995**) Fiber-optic oxygen microsensors, a new tool in aquatic biology. *Limnol Oceanogr*, 40: 1159-1165

Koehn R, Shumway SE (**1982**) A genetic/physiological explanatin for differential growth rate among individuals of the american oyster *Crassostrea virginica*. *Mar Biol*, 3: 35-42

Krantz DE, Jones DS, Williams DF (**1984**) Growth rates of the sea scallop, *Placopecten magellanicus*, determined from the super(18)O/super(16)O record in shell calcite. *Biol Bull Mar Biol Lab Woods Hole*, 167: 186-199

Krantz DE, Williams FD, Jones DS (**1987**) Ecological and palaeoenvironmental information using stable isotope profiles from living and fossil molluscs. *Palaeogeogr Palaeoclimatol Palaeoecol*, **58**: 249-266

Krogh A (**1916**) *Respiratory Exchange of Animals and Man*. Longmans, Green, London

L

Lambert J, Préfontaine G (**1995**) The Iceland scallop (*Chlamys islandica*) in Nunavik. *Can Tech Rep Fish Aquat Sci/ Rapp Tech Can Sci Halieuzt Aquat* 0(2071): 1-40

Langton RW, Robinson WE, Schick DF (**1987**) Fecundity and reproductive effort of sea scallops *Placopecten magellanicus* from the Gulf of Maine. *Mar Ecol Prog Ser*, 37: 19-25

Lannig G, Eckerle LG, Serendero I, Sartoris FJ, Fischer T, Knust R, Johansen T, Pörtner HO (2003) Temperature adaptation in eurythermal cod (*Gadus morhua*): a comparison of mitochondrial enzyme capacities in boreal and Arctic populations. *Mar Biol*, 250: 589-599

Lasta M, Bremec C (**1998**) *Zygochlamys patagonica* in the argentine sea: a new scallop fishery. *J Shellfish Res*, 17: 103-111

Lasta M, Valero J, Brey T, Bremec C (**2001**) *Zygochlamys patagonica* (King and Broderip) beds on the Argentinian shelf. Part II: Population dynamics of *Zygochlamys patagonica*. *Arch Fish Mar Res*, 49: 125-137

Lee T (**1973**) Scallop and queen scallop survey along the east and south-east coasts of Ireland

-August 1972. *Resour. Rec. Pap. Bord lascaigh Mhara Fish. Dev. Div.*, 23

Lefort Y (**1994**) Growth and mortality of the tropical scallops: *Annachlamys flabellata* (Bernardi), *Comptopallium radula* (Linne) and *Mimachlamys gloriosa* (Reeve) in the southwest lagoon of New Caledonia. *J Shellfish Res*, 13: 539-546

LePennec M, Donval A, Herry A (**1990**) Nutritional strategies of the hydrothermal ecosystem bivalves. *Prog Oceanogr*, 24: 71-80

Levinton JS (**1983**) The latitudinal compensation hypothesis: growth data and a model of latitudinal growth differentiation based upon energy budgets. I. Interspecific comparison of *Ophryotrocha* (Polychaeta: Dorvilleidae). *Biol Bull*, 165: 686-698

Levinton JS, Monahan RK (**1983**) The latitudinal compensation hypothesis: growth data and a model of latitudinal growth differentiation based upon energy budgets. II. Intraspecific comparisons between subspecies of *Ophryotrocha puerilis* (Polychaeta: Dorvilleidae). *Biol Bull*, 165: 699-707

Linse K (**1997**) Distribution of epibenthic mollusca from the Chilean Beagle Channel. *Ber Polarforsch*, 228, 131 pp

Llana MEG (**1987**) Growth, mortality and recruitment in the Asian moon scallop, *Amusium pleuronectes* in the Visayan Sea, Philippines. Paper presented at the FAO-DANIDA-sponsored course on Tropical Fish Stock Assessment, Manila, Philippines, January-February, 1987, 9 pp

Lohmann KC, Berkman PA, Marcano MC (**2001**) A high resolution ∂^{18}O record of growth banding in *Adamussium colbecki*: a proxy for reconstruction of coastal salinities and continental temperatures on annual to century time scales. *In*: Berkman PA, Tipton-Everett LR (Eds) *Latitudinal Ecosystem (LAT-ECO) Responses to Climate Across Victoria Land, Antarctica. Report of a National Science Foundation Workshop*. BPRC Report No. 20, Byrd Polar Research Center, The Ohio State University, Columbus, Ohio, pp 96-98

Londraville RL, Sidell B (**1990**) Ultrastructure of aerobic muscle in Antarctic fishes may contribute to maintenance of diffusive fluxes. *J Exp Biol*, 150: 205-220

Lonsdale DJ, Levinton JS (**1985**) Latitudinal differentiation in copepod growth: an adaptation to temperature. *Ecology*, 66: 1397-1407

Loo LO, Rosenberg R (**1989**) Bivalve suspension-feeding dynamics and benthic-pelagic coupling in an eutrophicated marine bay. *J Exp Mar Biol Ecol*, 130: 253-276.

Lu YT, Blake NJ, Torres JJ (**1999**) Oxygen consumption and ammonia excretion of larvae and juveniles of the bay scallop, *Argopecten irradians concentricus* (Say). *J Shellfish Res*, 18: 419-324

Lucas A, Beninger PG (**1985**) The use of physiological condition inidices in marine bivalve aquaculture. *Aquaculture*, 44: 187-200

Luro C (**1985**) Etude des communautés benthiques du lagon sud-ouest de la Nouvelle-Calédonie et d'une population de pectinidae: *Comptopallium vexillum. Rapp de stage: Bevet de Techn. Sup Mer Nouméa: ORSTOM*, 40 pp

Lutz RA, Rhoads DC (**1980**) Growth patterns within the molluscan shell: an overview. *In:* Rhoads DC, Lutz RA (Eds) *Skeletal Growth of Aquatic Organisms*. Plenum Press New York, pp 203-254

Luxmoore RA (**1984**) A comparison of the respiration rate of some Antarctic isopods with species from lower latitude. *Br Antarct Surv Bull*, 62: 53-65

M

MacDonald BA (**1986**) Production and resource partitioning in the giant scallop *Placopecten* *magellanicus* grown on the bottom and in suspended culture. *Mar Ecol Prog Ser*, 34: 79-86

MacDonald BA (**1988**) Energy partitioning patterns in cultured and wild populations of the giant scallop *Placopecten magellanicus. J Shellfish Res*, 7: 124

MacDonald BA Thompson RJ (**1985a**) Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. I. Growth rates of shell and somatic tissue. *Mar Ecol Prog Ser,* 25: 279-294

MacDonald BA, Thompson RJ (**1985b**) Influence of temperature and food availability on the ecological energetics of the giant scallop *Placopecten magellanicus*. II. Reproductive output and total production. *Mar Ecol Prog Ser*, 25: 295-303

MacDonald BA, Thompson RJ (**1986**) Production, dynamics and energy partitioning in two populations of the giant scallop *Placopecten magellanicus* (Gmelin). *J Exp Mar Biol Ecol*, 101: 285-299

MacDonald BA, Bourne NF (**1987**) Growth, reproductive output, and energy partitioning in weathervane scallops, *Patinopecten caurinus*, from British Columbia. *Can J Fish Aquat Sci*, 44: 152-160

MacDonald BA, Thompson RJ (**1988**) Intraspecific variation in growth and reproduction in latitudinally differentiated populations of the giant scallop *Placopecten magellanicus* (Gmelin). *Biol Bull*, 175: 361-371

MacDonald BA, Thompson RJ, Bourne NF (**1991**) Growth and reproductive energetics of three scallop species from British Columbia (*Chlamys hastata*, *Chlamys rubida* and *Crassadoma gigantea*). *Can J Fish Aquat Sci,* 48: 215-221

Mackay J, Shumway SE (**1980**) Factors affecting oxygen consumption in the scallop *Chlamys deliculata* (Hutton). *Ophelia,* 19: 19-26

Marshall JD, Pirrie D, Nolan C (**1993**) Oxygen stable isotope composition of skeletal carbonates from living Antarctic marine invertebrates. *Ant Spec Topic*: 81-84

Marshall JD, Pirrie D, Clarke A, Nolan CP, Sharman J (**1996**) Stable-isotopic composition of skeletal carbonates from living Antarctic marine invertebrates. *Lethaia*, 29: 203-212

May RM (**1994**) Biological diversity: Differences between land and sea. *Phil Trans R Soc Lond,* 343 (Ser B): 105-111

McCarthy ID, Houlihan DF, Carter CG (**1994**) Individual variation in protein turnover and growth efficiency in rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Proc R Soc Lond*, 257 B: 141-147

McConnaughey TA, Burdett J, Whelan JF, Paull CK (**1997**) Carbon isotopes in biological carbonates: Respiration and photosynthesis. *Geochim Cosmochim Acta,* 61: 611-622

McLusky DS (**1973**) The effect of temperature on the oxygen consumption and filtration rate *Chlamys (Aequipecten) opercularis* (L.) (Bivalvia). *Ophelia*, 10: 141-154

Melnikov IA (**1998**) Winter production of sea ice algae in the western Weddell Sea. *J Mar Sys*, 17: 195-205

Mendo J, Jurado E (**1993**) Length-based growth parameter estimates of the Peruvian scallop (*Argopecten purpuratus*). *Fish Res*, 15: 357-367

Merill AS, Posgay JA, Nichy FE (**1965**) Annual marks on the shell and ligament of the sea scallop (*Placopecten magellanicus*). *Fish Bull,* 65: 299-311

Mistri M, Rossi R, Fano EA (**2001**) Structure and secondary production of a soft bottom macrobenthic community in a brackish lagoon

(Sacca di Goro, north-eastern Italy). *Estuar Coast Shelf Sci,* 52: 605–616

Mohnen VA, Wang WC **(1992)** An overview of global warming. *J Environ Toxicol Chem (SETAC),* 11: 1051-1059

Moreau J, Bambino C, Pauly D **(1986)** Indices of overall growth performance of 100 *Tilapia* (Cichlidae) populations. *In:* MacLean JL, Dizon LB, Hosillos LV (Eds) *The First Asian Fisheries Forum.* Asian Fisheries Society, Manila, Philippines: pp 201-206

Morton, B **(1980)** Swimming in *Amusium pleuronectes* (Bivalvia: Pectinidae). *J Zool Lond,* 190: 375-404

Myasnikov VG, Kochnev YP **(1988)** Lifespan, growth and sex structure of scallop (*Chlamys albidus*) off the Kuril Islands. Marine Commercial Invertebrates. *Collected Papers. Moscow: VNIRO*: 153-166

N

Nakajima Y, Watanabe K, Naito Y **(1982)** Diving observations of the marine benthos at Syowa Station, Antartica. *Natl Inst Polar Res*: 44-54

Naidu KS **(1975)** Growth and population structure of a northern shallow-water population of the giant scallop *Placopecten magellanicus* (Gmelin). *ICES Council Meeting,* K 35: 17

Naidu KS, Cahill FM **(1984)** Status and assessment of St. Pierre Bank scallop stocks 1982-1983. *CAFSAC Res Doc,* 84/69: 56 pp

Naidu KS **(1991)** Sea Scallop, *Placopecten magellanicus. In:* Shumway SE (Ed) *Scallops: Biology, Ecology and Aquaculture.* Elsevier, Amsterdam, Oxford, NewYork, pp 861-898

Naidu KS, Cahill FM, Lewis DB **(1982)** Status and assessment of the Iceland scallop *Chlamys islandica* in the northeastern Gulf of St. Lawrence. *CAFSAC Res Doc,* 82/02: 62 pp

Navarro JM, Leiva GE, Martinez G, Aguilera C **(2000)** Interactive effects of diet and temperature on the scope for growth of the scallop *Argopecten purpuratus* during reproductive conditioning. *J Exp Mar Biol Ecol,* 247: 67-83

Newell ND **(1964)** Physiological variation in intertidal molluscs. *In*: Wilbur KM, Yonge CM (Eds) *Physiology of molluscs,* I. Academic Press, New york, pp 59-87

Newell ND **(1969)** Family Entoliidae Korobkov, 1969. *In:* Moore RC (Ed) *Treatis on Invertebrate Paleontology, Part N, Vol 1 Mollusca 6, Bivalvia.* Geol Soc Amer and Univ of Kansas, Lawrence, Kansas, pp N205-N347

Nicchitta CV, Ellington WR **(1983)** Energy metabolism during air exposure and recovery in the high intertidal bivalve mollusc *Geukensia demissa granosissima* and the subtidal bivalve mollusc *Modiolus squamosus. Biol Bull,* 165: 708-722

Nicol D **(1966)** Descriptions, ecology and geographic distribution of some Antarctic pelecypods. Bulls. *Am Paleo,* 51: 1-102

Nigro M **(1993)** Nearshore population characteristics of the circumpolar Antarctic scallop *Adamussium colbecki* (Smith, 1902) at Terra Nova Bay (Ross Sea). *Ant Sci,* 5: 377-378

Niu CJ, Nakao S, Goshima S **(1998)** Energetics of the limpet *Lottia kogamogai* (Gastropoda: Acmaeidae) in an intertidal rocky shore in southern Hokkaido, Japan. *J Exp Mar Biol Ecol,* 224: 167-181

Niu CJ, Lee D, Goshima S, Nakao S **(2003)** Effects of temperature on food consumption, growth and oxygen consumption of freshwater prawn *Macrobrachium rosenbergii* (de Man 1879) postlarvae. *Aquac Res,* 34, 501-506

Nordseik F **(1969)** *Die Europäischen Meeresmuscheln (Bivalvia) vom Eismeer bis*

Kapverden, Mittelmeer und Schwarzes Meer. Gustav Fischer Verlag, Stuttgart, 256 pp

Nugranad J (1988) Preliminary report on the growth, mortality and recruitment of the Asian moon scallop *Amusium pleuronectes* in Koh Chang (Koh Kood area), eastern Gulf of Thailand. (Unpublished Report).

O

Orensanz JM (**1986**) Size, environment, and density: the regulation of a scallop stock and its management implications. *Can Spec Publ Fish Aquat Sci*, 92: 195-227

Orensanz JM, Parma AM, Ibribarne OO (**1991a**) Population dynamics and management of natural stock. *In*: Shumway SE (Ed) *Scallops: Biology, Ecology and Aquaculture.* Elsevier, Amsterdam, Oxford, New York, pp 625-714

Orensanz JM, Pascual M, Fernández M (**1991b**) Fisheries and aquaculture: Argentina. *In*: Shumway SE (Ed) *Scallops: Biology, Ecology and Aquaculture.* Elsevier, Amsterdam, Oxford, New York, pp 981-1000

Owen R, Kennedy H, Richardson C (**2002a**) Experimental investigation into partitioning of stable isotopes between scallop (*Pecten maximus*) shell calcite and sea water. *Palaeogeo Paleoclim Paleoecol,* 185: 163-174

Owen R, Kennedy H, Richardson C (**2002b**) Isotopic partitioning between shell calcite and seawater: Effect of shell growth rate. *Geochim Cosmochim Acta*, 66: 1727-1737

P/Q

Packard GC, Boardman TJ (**1999**) The use of percentages and size-specific indices to normalize physiological data for variation in body size: wasted time, wasted effort? *Comp Biochem Physiol*, 122: 37-44

Parry GD (**1983**) The influence of the cost of growth on ectoherm metabolism. *J Theor Biol,* 101: 453-477

Paul JD (**1980**) Salinity-Temperature relationships in the queen scallop *Chlamys opercularis. Mar Biol*, 56: 295-300

Pauly D (**1979**) Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. *Ber Inst Meereskd Christian-Albrechts-Univ Kiel*, 63: 156 pp

Pauly D, Munro JL (**1984**) Once more on the comparison of growth in fish and invertebrates. *Fishbyte.* 2: 21

Peck LS (**2002**) Ecophysiology of Antarctic marine ectotherms: limits to life. *Polar Biol,* 25: 31-40

Peck LS, Conway LZ (**2000**) The myth of metabolic cold adaptation: oxygen consumption in stenothermal Antarctic bivalves. *In*: Harper EM, Taylor JD, Crame JA (Eds) *The Evolutionary Biology of the Bivalvia.* Geol Soc London Spec Publ, London, 177, pp 441-450

Peck LS, Clarke A, Holmes LJ (**1987**) Summer metabolism and seasonal changes in biochemical composition of the Antarctic brachipod *Liothyrella uva* (Broderip, 1833). *J Exp Mar Biol Ecol,* 114: 85-97

Peck LS, Baker AC, Conway L (**1996**) Strontium labelling of the shell of the Antarctic limpet *Nacella concinna* (Strebel, 1908). *J Moll Stud*, 62: 315-325

Peck LS, Brockington S, Brey T. (**1997**) Growth and metabolism in the Antarctic brachiopod *Liothyrella uva. Phil Trans R Soc Lond,* 352 (Ser B): 851-858

Peck LS, Pörtner HO, Hardewig I (**2002**) Metabolic demand, oxygen supply, and critical temperatures in the Antarctic bivalve *Laternula elliptica. Physiol Biochem Zool*, **75**: 123-133

Peterson CC, Walton BM, Bennett AF (**1999**) Metabolic costs of growth in free-living garter snakes and the energy budgets of ectotherms. *Funct Ecol*, 13: 500-507

Picco P, Bergamasco A, Demicheli L, Manzella G, Meloni R, Paschini E (**2000**) Large-scale circulation features in the Central and Western Ross Sea (Antarctica). *In:* Faranda FM, Guglielmo L, Ianora A (Eds) *Ross Sea Ecology: Italiantartide Expeditions (1987-1995).* Springer, Berlin, Heidelberg, New York, pp 95-105

Pickett GA, Franklin A (**1975**) The growth of queen scallops (*Chlamys opercularis*) in cages off Plymouth, South-West England. *ICES CM,* 4

Pielou EC (1979) A quick method of determining the diversity of foraminiferal assemblages. *J Paleontol*, 53 : 1237-1242

Pierce VA, Crawford DL (**1997a**) Phylogenetic analysis of glycolytic enzyme expression. *Science*, 276: 256-259

Pierce VA, Crawford DL (**1997b**) Phylogenetic analysis of thermal acclimation of the glycolytic enzymes in the genus *Fundulus. Physiol Zool*, 70: 597-609

Pilditch CA, Grant J (**1999**) Effect of temperature fluctuations and food supply on the growth and metabolism of juvenile sea scallops (*Placopecten magellanicus*). *Mar Biol,* 134: 235-248

Povero P, Petrillo M (**2000**) Flussi e sostanza organica. *Raporto sulla Campagna Antarctica Estate Australe 1999-2000*, 86-88

Pörtner HO (**2001**) Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, 88: 137-146

Pörtner HO (**2002a**) Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp Biochem Physiol,* 132A: 739-761

Pörtner HO (**2002b**) Environmental and functional limits to muscular exercise and body size in marine invertebrate athletes. *Comp Biochem Physiol,* 133A: 303-321

Pörtner HO (**2002c**) Physiological basis of temperature dependent biogeography: tradeoffs in muscle design and performance in polar ectotherms. *J Exp Biol,* 205: 2217-2230

Pörtner HO, Arntz WE (**2003**) Climate variability and the driving forces of animal evolution: from low to high performance levels among ectotherms. *Submitted manuscript*

Pörtner HO, Hardewig I, Sartoris FJ, van Dijk PLM (**1998**) Energetic aspects of cold adaptation: critical temperatures in metabolic, ionic and acid-base regulation? *In*: Pörtner HO, Playle RC (Eds) *Cold Ocean Pysiology.* Cambridge University Press, Cambridge, pp 88-120

Pörtner HO, Hardewig I, Peck LS (**1999**) Mitochondrial function and critical temperature in the Antarctic bivalve, *Laternula elliptica. Comp Biochem Physiol*, 124(A): 179-189

Pörtner HO, VanDijk PLM, Hardewig I, Sommer A (**2000**) Levels of Metabolic Cold Adaptation: Tradeoffs in Eurythermal and Stenothermal Ectotherms. *In*: Davison W, Williams CW (Eds) *Antarctic Ecosystems: Models for a Wider Understanding.* Caxton Press, Christchurch, New Zealand, pp 109-122

Pörtner HO, Berdal B, Blust R, Brix O, Colosimo A, De Wachter B, Giuliani A, Johansen T, Fischer T, Knust R, Naevdal G, Nedenes A, Nyhammer G, Sartoris FJ, Serendero I, Sirabella P, Thorkildsen S, Zakhartsev M (**2001**) Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Cont Shelf Res*, 21: 1975-1997

Pörtner HO, Lucassen M, Storch D (**2004**) Metabolic biochemistry and the capacities of physiological and ecological function: an integrative view. *Submitted manuscript*

Posgay JA (**1959**) United States sea scallop research in subarea 5 during 1958. *Int Comm Northw Atl Fish (ICNAF) annual Meet, Ser* 609, *Doc* 10: 1-11

Posgay JA (**1979**) Population assessment of the Georges Bank sea scallop stocks. *Rapp P-v R_un Cons Int Explor Mer*, 175: 109-113

Posgay JA (**1991**) Maximum yield per recruit of sea scallops. *ICNAF, 1962, Doc. No.* 73 (*Ser. No.* 554): 1-17

Pranovi F, Marcato S, Zanellato R (**1994**) Analisi biometriche e biologia di popolazione del mollusco antartico *Adamussium colbecki* a Baia Terra Nova, Mare di Ross. *Atti Dell' Istituto Veneto Di Scienze Lettere Ed Arti Tomo CLII (1993-1994)*, 152: 123-136

Present TMC, Conover DO (**1992**) Physiological basis of latitudinal growth differences in *Menidia menidia*: variation in consumption or efficiency? *Funct Ecol*, 6: 23-31

Prosser CL (**1991**) *Comparative animal physiology* 4. Wiley-Liss, New York.

R

Ralph R, Maxwell JGH (**1977**) Growth of two antarctic lamellibranchs: *Adamussium colbecki* and *Laternula elliptica*. *Mar Biol*, 42: 171-175

Richardson CA (**2001**) Molluscs as archives of environmental change. *Oceanogr Mar Ann Rev*, 39: 103-164

Richardson CA, Taylor AC, Venn TJ (**1982**) Growth of the queen scallop *Chlamys opercularis* in suspended cages in the firth of clyde. *J Mar Biol Ass UK*, 62: 157-169

Robert G, Jamieson GS (**1986**) Commercial fishery data isopleths and their use in offshore sea scallop (*Placopecten magellanicus*) stock evaluations. *Can Spec Publ Fish Aquat Sci*, 92, 76-82

Robert G, Jamieson GS, Lundy MJ (**1982**) Profile of the Canadian offshore scallop fishery on Georges Bank, 1978 to 1981. *CAFSAC Res Doc*, 82/15: 1-33

Robert G, Butler-Connolly MAE, Lundy MJ (**1985**) Bay of Fundy scallop stocks assessment, 1984. *CAFSAC Res Doc*, **85**/27: 29

Roddick DL, Mohn RK (**1985**) Use of age-length information in scallop assessments. *CAFSAC Res Doc*, 85/37: 16

Rodhouse PGA (**1979**) Note on the energy budget for an oyster population in a temperate estuary. *J Exp Mar Biol Ecol*, 37: 205-212

Rodhouse PG, Roden CM, Hensey MP, Ryan TH (**1984**) Resource allocation in Mytilus edulis on the shore and in suspended culture. *Mar Biol*, 84: 27-34

Rolfe MS (**1973**) Notes on queen scallops and how to catch them. *Shellfish Inf Leafl Minist Agric Fish Food UK*, 27: 13 pp

Roughgarden J (**1998**) How to manage fisheries. *Ecol Appl*, 8: 160-164

Roy K, Jablonski D, Valentine JW, Rosenberg G (**1998**) Marine latitudinal diversity gradient: Tests of causal hypotheses. *PNAS*, 95: 3699-3702

Roy K, Jablonski D, Valentine JW (**1994**) Eastern Pacific molluscan provinces and latitudinal diversity gradient: no evidence for "Rapoport's rule". *PNAS*, 91: 8871-8874

Roy K, Jablonski D, Martien KK (**2000**) Invariant size-frequency distributions along a latitudinal gradient in marine bivalves. *PNAS*, 97: 13150-13155

Rubner M (**1883**) Über den Einfluss der Körpergrösse auf Soff- und Kraftwechsel. *Zeitschrift f Biol*, 19: 535-562

S

Sagan G, Thouzeau G (**1998**) Variabilité spatio-temporelle de la biomasse microphytobenthique en rade de Brest et en Manche occidentale. *Ocean Acta,* 21: 677-694

Saggiomo V, Carrada GC, Mangoni O, Marino D, D'Alcalà MR (**2000**) Ecological and physiological aspects of primary production in the Ross Sea. *In:* Faranda FM, Guglielmo L, Ianora A (Eds) *Ross Sea Ecology: Italiantartide Expeditions (1987-1995).* Springer-Verlag, Berlin, Heidelberg, New York, pp 247-258

Sainsbury KJ (**1980**) Effect of individual variability on the von Bertalanffy growth equation. *Can J Fish Aquat Sci,* 37: 241-246

Salonen K, Sarvala J, Hakala I, Viljanen ML (**1976**) The relation of energy and organic carbon in aquatic invertebrates. *Limnol Oceanogr,* 21: 724-730

Schejter L, Bremec CS, Akselman R, Hernandez D, Spivak ED (**2002**) Annual feeding cycle of the Patagonian scallop *Zygochlamys patagonica* (King and Broderip, 1832) in Reclutas bed (39S-55°W), Argentine Sea. *J Shellfish Res,* 21: 549 pp

Schick DF, Shumway SE, Hunter MA (**1988**) A comparison of growth rate between shallow water and deep water populations of scallops, *Placopecten magellanicus* (Gmelin, 1791) in the Gulf of Maine. *Am Mal Bull,* 6: 1-8

Schmid MK (**1996**) Zur Verbreitung und Respiration ökologisch wichtiger Bodentiere in den Gewässern um Svalbard (Arktis). *Rep Mar Res,* 202: 1-92

Schmidt-Nielsen K (**1984**) *Scaling: Why is Animal Size so Important?* Cambridge University Press, Cambridge.

Schöne BRA (**2003**) A 'clam-ring' master-chronology constructed from a short-lived bivalve mollusc from the northern Gulf of California, USA. *The Holocene,* 13: 39-49

Schöne BRA, Lega J, Flessa KW, Goodwin DH, Dettman DL (**2002**) Reconstructing daily temperatures from growth rates of intertidal bivalve mollusc *Chione cortezi* (northern Gulf of California, Mexico). *Palaeogeo Palaeoclimat Palaeoecol,* 184: 131-146

Seed R (**1980**) Shell growth and form in the Bivalvia. *In:* Rhoadas DC, Lutz RA (Eds) *Skeletal Growth of Aquatic Organisms.* Plenum Press, New York, pp 23-68

Serchuk FM, Wood PW, Posgay JA, Brown BE (**1979**) Assessment and status of sea scallop (*Placopecten magellanicus*) populations off the northeast coast of the United States. *Proc Natl Shellfish Assoc,* 69:161-191

Serchuk FM, Wood PW, Rak RS (**1982**) Review and assessment of the Georges Bank, Mid-Atlantic and Gulf of Maine Atlantic sea scallop (*Placopecten magellanicus*) resources. National Marine Fishery Service (NMFS)/ Woods Hole Oceanographic Inst. Reference Document, 82-06: 1-132

Shackleton NJ (**1979**) Evolution of the earth's climate during the Tertiary era. *In:* Gantier D (Ed) *Evolution of planetary atmospheres and climatology of the earth.* Centre Nationale d'Études Spatiale, Toulouse, pp 49-58

Shafee MS (**1982**) Seasonal variation in oxygen consumption rates of the black scallop *Chlamys varia* (L.) from Lanvéoc (Bay of Brest). *Oceanol Acta,* 5: 189-197

Shafee MS, Conan G (**1984**) Energetic parameters of a population of *Chlamys varia* (Bivalvia: Pectinidae). *Mar Ecol Prog Ser,* 18: 253-262

Shumway SE (**1991**) *Scallops: Biology, Ecology and Aquaculture.* Elsevier, Amsterdam, Oxford, New York.

Shumway SE, Barter J, Stahlnecker J (**1988**) Seasonal changes in oxygen consumption of the giant scallop, *Placopecten magellanicus* (GMELIN). *J Shellfish Res,* 7: 77-82

Sidell BD, Driedzic WR, Stowe DB, Johnston IA (**1987**) Biochemical correlations of power development and metabolic fuel preferenda in fish hearts. *J Physiol Zool* 60, 221-232

Silva Loera, HA (**1986**) Efecto del tamano corporal, tensión de oxigen y temperatura sobre la tasa de consumo de oxígeno en la escalopa *Argopecten circularis* (Sowerby) (Molusca: Lamellibranchia). M.S. Thesis ed. Instituto Tecnologico y de Estudios Superiores de Monterrey, Mexico (cited in Bricelj VM, Shumway SE, 1991)

Sibly RM, Calow P (**1986**) *Physiological Ecology of Animals. An Evolutionary Approach.* Blackwell Scientific Publications, Oxford.

Silina AV, Pozdnyakova LA (**1990**) Growth of the scallop *Chlamys rosealbus* in the sea of Japan. *Russ J Mar Biol,* 16: 32-36

Simstich J, Müller-Lupp T, Erlenkeuser H (**2001**) Schalen arktischer Bivalven als Datenspeicher jahreszeitlicher Schwankungen von Temperatur und Salzgehalt im Bodenwasser? Erste Ansätze aus Kara- und Laptev-See. *Mitt Kieler Polarforsch,* 17: 7-10

Smaal AC, Prins TC (**1993**) The uptake of organic matter and the release of inorganic nutrient by bivalve suspension feeder beds. *In:* Dame RF (Ed) *Bivalve Filter Feeders in Estuarine and Coastal Ecosystem Processes.* Springer, Heidelberg, pp 273-298

Smith MAK, Haschemeyer AEV (**1980**) Protein metabolism and cold adaptation in Antarctic fishes. *Physiol Zool,* 53: 373-382

Smith WO, Nelson DM, Di Tullio GR, Leventer AR (**1996**) Temporal and spatial patterns in the Ross Sea: phytoplankton biomass, elemental composition, productivity and growth rates. *J Geophys Res,* 101: 18455-18465

Sokolova IM, Pörnter HO (**2001**) Temperature effects on key metabolic enzymes in *Littorina saxatilis* and *L. obtusata* from different latitudes and shore levels. *Mar Biol,* 139: 113-126

Somero GN (1995) Proteins and temperature. Ann Rev Physiol, 57: 43-68

Somero GN, Fields PA, Hofmann GE, Weinstein RB, Kawall H (**1998**) Cold adaptation and stenothermy in Antarctic notothenioid fishes: What has been gained and what has been lost? *In:* DiPrisco G, Pisano E, Clarke A (Eds) *Fishes of Antarctica.* Springer-Verlag, Milano, pp 97-109

Sommer A, Pörtner HO (**1999**) Exposure of *Arenicola marina* to extreme temperatures: Adaptive flexibility of a boreal and a subpolar population. *Mar Ecol Prog Ser,* 181: 215-226

Sommer AM, Pörtner H-O (**2002**) Metabolic cold adaptation in the lugworm *Arenicola marina*: comparison of a White Sea and a North Sea population, *Mar Ecol Prog Ser* 240: 171-182

Soot-Ryen T (**1951**) Antarctic pelecypods. *Scient Results Norw Antarct Exped,* 32:1-46

Spindler M, Dieckmann GS (**1991**) Das Meereis als Lebensraum. *Spektr Wiss,* 2: 48-57

Stearns SC (**1976**) Life history tactics: A review of the ideas. *Q Rev Biol,* 51: 3-47

Steiner G, Müller M (**1996**) What can 18S rDNA do for bivalve phylogeny? *J Mol Evol,* 43: 58-70

Stockton WL (**1984**) The biology and ecology of the epifaunal scallop *Adamussium colbecki* on the west side of McMurdo Sound, Antarctica. *Mar Biol,* 78: 171-178

Storch D, Heilmayer O, Hardewig I, Pörtner HO (**2003**) In vitro protein synthesis capacities in a cold stenothermal and a temperate eurythermal pectinid. *J Comp Physiol B,* 173: 611-620

Storch D, Pörtner HO (**2003**) The Protein Synthesis Machinery operates at the same

Expense in eurythermal and cold stenothermal Pectinids. *Physiol Biochem Zool,* 76: in press

Sukhotin AA, Pörtner HO (**2001**). Age-dependence of metabolism in mussels Mytilus edulis(L.) from the White Sea. *J Exp Mar Biol Ecol*, 257: 53-72

Sukhotin AA, Abele D, Pörtner HO (**2002**) Growth, metabolism and lipid peroxidation in *Mytilus edulis*: age and size effects. *Mar Ecol Prog Ser*, 226: 223-234

T

Tan FC, Cai D, Roddick DL (**1988**) Oxygen isotope studies on sea scallop, *Placopecten magellanicus*, from Browns Bank, Nova Scotia. *Can J Fish Aquat Sci,* 45: 1378-1386

Taylor AC, Venn TJ (**1978**) Growth of the queen scallop, *Chlamys opercularis*, from the Clyde Sea area. *J Mar Biol Ass UK,* 58: 687-700

Thompson RJ (**1984**) The reproductive cycle and physiological ecology of the mussel *Mytilus edulis* in a subarctic, non-estuarine environment. *Mar Biol,* 79: 277-288

Thouzeau G, Robert G, Smith SJ (**1991**) Spatial variability in distribution and growth of juvenile and adult sea scallop *Placopecten magellanicus* (Gmelin) on eastern Georges Bank (Northwest Atlantic). Mar Ecol Prog Ser, 74: 205-218

Tomicic J, Kong I (**1978**) Contribucion al conocimiento del cultivo del ostion *Argopecten purpuratus* (Lamarck 1819), en la Bah'a de Mejillones del Sur (Mollusca, Pelecypoda). Universidad De Chile, Inst. Invest. Ocean., Seminar Paper (unpublished).

Toro JE, Vergara AM, Gallegillos R (**1996**) Multiple-locus heterozygosity, physiology and growth at two different stages in the life cycle of the Chilean oyster *Ostrea chilensis*. *Mar Ecol Prog Ser*, 134: 151-158

Torres JJ, Somero GN (**1988**) Metabolism, enzymic activities and cold adaptation in Antarctic mesopelagic fishes. *Mar Biol*, 98: 169-180

Tremblay R, Myrand B, Guderley H (**1998**) Thermal sensitivity of organismal and mitochondrial oxygen consumption in relation to susceptibility of blue mussels, *Mytilus edulis* (L.), to summer mortality. *J Shellf Res*, 17: 141-152

Turner JRG, Lennon JJ, Greenwood JJD (**1996**) *In*: Hochberg ME, Clobert R, Barbault R (Eds) *Aspects of the Genesis and Maintenance of Biological Diversity*. Oxford University Press, Oxford, pp 199-220

U/V

Urban HJ, Campos B (**1994**) Population dynamics of the bivalves *Gari solida*, *Semele solida* and *Protothaca thaca* from a small bay in Chile at 36°S. *Mar Ecol Prog Ser,* 115: 93-102

Urban HJ, Tesch C (**1996**) Aspects of the population dynamics of six bivalve species from Southern Chile. Results of the «Victor Hensen«cruise to the Magellan Strait and the Beagle Channel in October/November 1994. *Arch Fish Mar Res*, 44: 243-256

Urban HJ, Mercuri G (**1998**) Population dynamics of the bivalve *Laternula elliptica* from Potter Cove, King George Island, South Shetland Islands. *Ant Sci,* 10: 153-160

Urrutia MB, Ibarrola I, Iglesias JIP, Navarro E (**1999**) Energetics of growth and reproduction in a high-tidal population of the clam *Ruditapes decussatus* from Urdaibai Estuary (Basque Country, N. Spain). *Neth J Sea Res,* 41: 35-48

Ursin E (**1956**) Distribution and growth of the queen, *Chlamys operuclaris* (Lamellibranchiata) in Danish and Faroese waters. *Medd Dan Fisk-Havunders,* 1: 1-31

Vacchi M, Cattaneo-Vietti R, Chiantore M, Dalu M (**2000**) Predator-prey relationship between the nototheniid fish *Trematomus bernacchii* and the Antarctic scallop *Adamussium colbecki*. *Ant Sci*, 12: 64-68

Vahl O (**1972**) Particle retention and relation between water transport and oxygen uptake in *Chlamys opercularis* (L.) (Bivalvia). *Ophelia*, 10: 67-74

Vahl O (**1978**) Seasonal Changes in oxygen consumption of the Iceland Scallop (*Chlamys islandica* (O.F. MÜLLER)) from 70°N. *Ophelia*, 17: 143-154

Vahl O (**1981a**) Energy transformation by the iceland scallop, *Chlamys islandica* (O.F. Müller); from 70°N. I. The age-specific energy budget and net growth efficiency. *J Exp Mar Biol Ecol*, 53: 281-296

Vahl O (**1981b**) Energy transformation by the iceland scallop, *Chlamys islandica* (O.F. Müller); from 70°N. II. The population energy budget. *J Exp Mar Biol Ecol*, 53: 297-303

Vahl O, Sundet JH (**1985**) Is sperm really so cheap? *In*: Gray JS, Christiansen ME (Eds) *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*. John Wileys and Sons, New York, pp 281-285

Vakily JM, (**1992**) Determination and comparison of bivalve growth, with emphasis on Thailand and other tropical areas. *ICLARM Tech Rep*, 36: 125 pp

Valero J (**1999**) Variacion estacional, espacial e interannual en el crecimiento de vieira patagonica (*Zygochlamys patagonica*) en la plataforma argentina. *Informe Final -Contrato IICA*.

Van Dijk PLM, Tesch C, Hardewig I, Pörtner HO (**1999**) Physiological disturbances at critically high temperatures: a comparison between stenothermal antarctic and eurythermal temperate eelpouts (Zoarcidae). *J Exp Biol*, 202: 3611-3621

Ventilla RF (**1982**) The scallop industry in Japan. *Adv Mar Biol*, 20: 309-382

Vermeij GJ (**1991**) Anatomy of an invasion: The trans-Arctic interchange. *Paleobiology*, 17: 281-307

Verrill AE (**1897**) A study of the family Pectinidae, with a revision of genera and subgenera. *Trans Conn Aca Arts Sci*, 10: 41-96

Vetter RAH, Buchholz F (**1998**) Kinetics of enzymes in cold-stenothermal invertebrates. *In*: Pörtner HO and Playle RC (Eds) *Cold Ocean Physiology*. Cambridge University Press, Cambridge, pp 190-211

W

Waller TR (**1969**) The evolution of the *Argopecten gibbus* stock (Mollusca: Bivalvia), with emphasis on the Tertiary and Quaternary species of eastern North America. *J. Paleontology*, 43(5 Suppl): 1-125

Waller TR (**1978**) Morphology, morphoclines and a new classification of the Pteriomorphia (Mollusca: Bivalvia). *Phil Trans Roy Soc London, B*, 284: 345-365

Waller TR (**1984**) The ctenolium of scallop shells: Functional morphology and evolution of a key family-level character in the Pectinacea (Mollusca: Bivalvia). *Malacologia*, 25: 203-219

Waller TR (**1991**) Evolutionary relationships among commercial scallops (Mollusca: Bivalvia: Pectinidae). *In*: Shumway SE (Ed) *Scallops: Biology, Ecology and Aquaculture*. Elsevier, Amsterdam, Oxford, NewYork, pp 1-73

Waller TR (**1993**) The evolution of "Chlamys" (Mollusca: Bivalvia: Pectinidae) in the tropical western Atlantic and eastern Pacific. Am Malac Bull, 10: 195-249

Waloszek D (**1991**) *Chlamys patagonica* (King & Broderip 1832), a long 'neglected' species from the shelf off the Patagonia Coast. *In*: Shumway SE, Sandifer PA (Eds) *An*

International Compendium of Scallop Biology and Culture. Baton Rouge, USA: The World Aquaculture Society, Parker Coliseum, Louisiana State University, pp 256-263

Waloszek D, Waloszek G (**1986**) Ergebnisse der Forschungsreisen des FS "Walther Herwig" nach Südamerika. LVX. Vorkommen, Reproduktion, Wachstum und mögliche Nutzbarkeit von *Chlamys patagonica* (King & Broderip, 1832) (Bivalvia, Pectinidae) auf dem Schelf vor Argentinien. *Arch Fish Wiss*, 37: 69-99

Weatherley AM, Gill MS (**1986**) *The biology of fish growth*. Academic Press, London

Wefer G, Berger WH (**1991**) Isotope paleontology: growth and composition of extant calcareous species. *Mar Geo*, 100: 207-248

Weidman CR, Jones GA, Lohmann KC (**1994**) The long-lived mollusc *Arctica islandica*: a new paleoceanographic tool for the reconstruction of bottom temperatures for the continental shelves of the northern North Atlantic Ocean. *J Geophys Res*, 99: 18305-18314

Westheide W, Rieger R (**1996**) Spezielle Zoologie. Erster Teil: Einzeller und Wirbellose Tiere.

Wiborg RF (**1963**) Some observations on the Iceland scallop *Chlamys islandica* (Müller) in Norwegian waters. *Fiskeridir Skr (Havunders)*, 13: 38-53

Widdows J (**1978**) Physiological indices of stress in *Mytilus edulis*. *J Mar Biol Ass UK*, 58: 125-142

Widdows J, Donkin P, Salkeld PN, Cleary JJ, Lowe DM, Evans SV, Thomson PE (**1984**) Relative importance of environmental factors in determining physiological differences between two populations of mussels (*Mytilus edulis*). *Mar Ecol Prog Ser*, 17: 33-47

Wieser W (**1994**) Cost of growth in cells and organisms: general rules and comparative aspects. *Biol Rev*, 68: 1-33

Wieser W, Megysey N (**1990**) Aerobic maximum for growth in the larvae and juveniles of cyprinid fish, *Rutilus* rutilus (L.): implications for energy budgeting in small poikilotherms. *Funct Ecol*, 4: 233-242

Wieser W, Forstner H, Schiemer F, Mark W (**1988**) Growth rates and growth efficiencies in larvae and juveniles of *Rutilus rutilus* and of the cybrinid species: effects of temperature and food in the laboratory and in the field. *Can J Fish Aquat Sci*, 45: 943-949

Wildish D, Kristmanson D (**1997**) *Benthic Suspension Feeders and Flow*. Cambridge University Press, Cambridge, 407pp

Wilkens LA (**1981**) Neurobiology of the scallop. I. Starfish mediated escape behaviour. *Proc R Soc Lond, B*, 211: 341-372

Williams MJ, Dredge CL (**1981**) Growth of the saucer scallop *Amusium japonicum balloti* Habe in Central Eastern Queensland. *Aust J Mar Freshw Res*, 32: 657-666

Willmer P, Johnston I, Willmer PJ (**2000**) *Environmental Physiology of Animals*. Blackwell Science, UK.

Witbaard R, Jenness MI, Van der Borg K, Ganssen G (**1994**) Verification of annual growth increments in *Arctica islandica* L. from the North Sea by means of oxygen and carbon isotopes. *Neth J Sea Res*, 33: 91-101

Wohlschlag DE (**1964**) Respiratory metabolism and ecological characteristics of some fishes in McMurdo Sound, Antarctica. *Ant Res Ser*, 1: 33-62

Wolff M (**1985**) Abundancia masiva y crecimiento de preadultos de la concha de abanico peruana (*Argopecten purpuratus*) en la zona de Pisco bajo condiciones de ,El Niño 1983'. *In*: Arntz WE, Landa A, Taranzona J

(Eds) *El fenomeno El Niño y su impacto en la fauna marina*. Biol Inst Mar Peru- Callao (special issue), pp 87-89

Wolff M (**1987**) Population dynamics of the Peruvian scallop *Argopecten purpuratus* during the El Nino phenomenon of 1983. *Can J Fish Aquat Sci*, 44: 1684-1691

Wolff M (**1994**) Population dynamics, life histories and management of selected invertebrates of the SE Pacific upwelling system. Habilitation, University of Bremen, Bremen, Germany, 210 pp

Worrall CM, Widdows J, Lowe DM (**1983**) Physiological ecology of three populations of the bivalve *Scrobicularia plana*. *Mar Ecol Prog Ser*, 12: 267-279

X/Y/Z

Yamashiro C, Mendo J (**1988**) Crecimiento de la Concha de Abanico (*Argopecten purpuratus*) en la Bahia Independencia, Pisco, Perú. Memorias del 2do Congreso Latinoamericano Sobre Ciencias Del Mar, Lima, Perú, pp 163-168

Yang H, Zhang T, Wang P, He Y, Zhang F (**1998a**) Effects of temperature on oxygen consumption and ammonia-N excretion of the Southern Bay scallop *Argopecten irradians concentricus*. *Acata Oceanol Sin*, 20: 91-96

Yang H, Zhang T, Wang P, He Y, Zhang F (**1998b**) Effects of temperature on oxygen consumption and ammonia-N excretion of *Chlamys farreri*. *Chin J Oceanol Limnol*, 16: 167-172

Yeager DP, Ultsch GR (**1989**) Physiological regulation and conformation: a BASIC program for the determination of critical points. *Physiol Zool*, 62: 888-907

Yoo SK, Ryu H-Y, Park K-Y (**1981**) The growth of the cultured scallop *Patinopecten yessoensis*. *Bull Kor Fish Soc*, 14: 221-226

Zeuthen E (**1947**) Body size and metabolic rate in the animal kingdom with special regard to the marine microfauna. *CR Trav Lab Carlsberg Ser Chim*, 26: 17-161

Zeuthen E (**1953**) Oxygen uptake as related to body size in organisms. *Quart Rev Biol*, 28: 1-20

Zielinski S, Pörtner HO (**1996**) Energy metabolism and ATP free-energy change of the intertidal worm, *Sipunculus nudus*, below a critical temperature. *J Comp Physiol*, 166(B): 492-500

Acknowledgements

The most difficult part of a project such as this is to acknowledge all the help one has experienced during all the past years. There is always a danger to forget essentially helpful hands in the hurry of finishing the thesis, so I hope I will not forget anything or anybody.

Firstly, thanks to those who provided the framework and basis for this thesis:

Prof. Dr. Wolf E. Arntz (Alfred Wegener Institute for Polar and Marine Research), my 'Doktorvater'. With his special interest in scallops he squired the progress of this thesis. He thoroughly revised manuscript drafts and let me participate to his great knowledge, especially on South American scallops.

Prof. Dr. Hans-O. Pörtner (Alfred Wegener Institute for Polar and Marine Research) for taking care, that I got a least some physiological ideas in my brain, although the physiological part of this study is quite small. He provided the possibility to use laboratory equipment and last but not least for taking over the job of the "Zweitgutachter".

PD. Dr. Thomas Brey (Alfred Wegener Institute for Polar and Marine Research) for inspiring discussion during which a lot of ideas used in the publications were formed. Tom supervised humorously all my steps towards this thesis and always was optimistic so that there'll be a 'happy end'. I really learned a lot, not only a lot about population dynamics, and scientific writing but also how to keep a story short. THANK YOU.

Dr. Wolfgang Weidemann should also appear under this headline, because he was the first who introduced me to the fascination of marine biology. He taught me a lot and made the change from freshwater to the saltier environment an "easy way".

I appreciate having received AWI-external support on, at times, seemingly insurmountable obstacles. For this, thanks to ...

...Prof. Riccardo Cattaneo-Vietti and Dra. Mariachiara Chianotre who supported this project, made my participation in the XV. Italian expedition to Antarctica possible as well as for open and fruitful discussion on *Adamussium colbecki*.

...the PNRA, who provided the financial and logistic facilities for the expedition to the Ross Sea in 1999/2000.

...Dr. Claudia Bremec and Mario Lasta, Angel Marecos, Laura Schejter, Silvana Campodonico, Eugenia Bogazzi, who not only sampled and acclimated *Zygochlamys* for me, but what is more important make my stay in Mar del Plata successful and instructive.

...the INIDEP (Argentina), who provided the laboratory facilities to work on the Patagonian scallop.

...the International Bureau of the BMBF, for giving financial support for the expedition to Argentina (ARG 002/98MAR).

...Katrin Jacob for excellent photographs of my lovely shells. Thank you very much!!!

Work during expeditions was teamwork thanks to...

...Dr. Daniela Storch. I was lucky to make nearly all expeditions together with you. Thank you for pleasant and relaxing laboratory work.

...all members of XVI Italian expeditions to Antarctica, especially the 'Malippo'-Crew, Riccardo, Chiara, Philip, Catarina, ...

...the people at the INIDEP, who take care of 'my' scallops and make work in Argentina possible, especially Mauricio??? Angel

Laboratory work would not have been possible without support and innovative ideas of a lot of people, I am truly indebted to

...Timo Hirse for assistance in the laboratory and a lot of excellent practical hints making laboratory work easier.

...Boris Klein, for providing maintenance facilities and helping hands whenever needed.

...Dr. Susanne Gatti who so competently introduced me to the world of microoptodes and respiration measurements.

...Dr. Gisela Lannig, Eva Philipp, Dr. Inna Sokolova, Dr. Angela Sommer, Dr. Torsten Fischer, Dr. Alex Sukhotin, for fruitful discussion on mitochondrial respiration and solving a lot of "uncoupled"-problems.

...Dr. Franz-J. Sartoris, not only for a lot of ideas how to perform respiration experiments, but also for a lot of motivating discussion.

...Kerstin Beyer her friendship and her tolerance in sharing a laboratory with a "screwy" scallop researcher like me.

...Dr. Barbara Niehoff, Dr. Susanne Gatti, Ute Jacob, Nadia Quéric, Dr. Thomas Brey for constructive comments on manuscripts.

During the complete time of my thesis much of my motivation was nourished by...

...Ute Jacob, not only for keeping the coffee machine running ☺

...revitalizing "Deich"-jogging with Franzl, Till, Jens, Ingo, Frank, Peter and various 'guest', which joint us infrequently.

...the Monday meetings with Bodil, Katrin, Heike, Teresa, Nuria, Kerstin, Cova, and Susanne were the basis of regular fruitful discussions and surprising insights in the AWI-hierarchy in the first years of my PhD.

...those colleagues who were supportive in all those tiny and big things making daily life easier.

...the 'crazy' scallop community for fruitful, stimulating discussions and a lot of fun during the two congresses in Coquimbo (Chile) and St. Petersburg (Florida). I hope to see you again in Brisbane 2005.

...without Ute Jacob's and Kerstin Beyer's support during the last weeks of writing this thesis could not have been completed.

And for what most kept me going thanks to Nadia, my friends and family!

7 Appendix

Table 7.1a

ScallopBase - Compilation of growth parameters for scallops: Summary of species, geographic and environmental descriptions, and references

	Species / Reference[a]	Year	Country	Place	Coordinates[b]
Adamussium colbecki					
1	Berkman	1990	Antarctica	Mc Murdo (New Harbor)	77 ° 35 ' S 166° 38 ' E
2	Chiantore et al.	2003	Antarctica	Terra Nova Bay (Road Cove)	74 ° 41 ' S 164° 07 ' E
3	Chiantore et al.	2003	Antarctica	Terra Nova Bay (Road Cove)	74 ° 41 ' S 164° 07 ' E
4	Heilmayer et al.	2003	Antarctica	Terra Nova Bay (Road Cove)	74 ° 41 ' S 164° 07 ' E
5	Pranovi et al.	1994	Antarctica	Terra Nova Bay	74 ° 42 ' S 164° 07 ' E
6	Ralph & Maxwell	1977	Antarctica	Stonington Island	68 ° 11 ' S 67° 00 ' W
7	Stockton	1984	Antarctica	McMurdo Sound	77 ° 35 ' S 166° 34 ' E
Aequipecten opercularis					
8	Allison	1994		Isle of Man (SE Douglas)	54 ° 08 ' N 04° 26 ' W
9	Allison	1994		Isle of Man (E Douglas)	54 ° 10 ' N 04° 23 ' W
10	Antoine	1979	Scotland	Aberdeen	57 ° 10 ' N 02° 01 ' W
11	Antoine	1979		Irish Sea (Kilmore)	56 ° 22 ' N 05° 40 ' W
12	Antoine	1979		Engl. Channel (Jersey)	49 ° 13 ' N 02° 15 ' W
13	Aravindakshan	1955		Isle of Man (Port Erin)	54 ° 05 ' N 04° 47 ' W
14	Aravindakshan	1955	Scotland	Millport	55 ° 45 ' N 04° 59 ' W
15	Aravindakshan	1955	Scotland	Aberdeen	57 ° 10 ' N 02° 01 ' W
16	Askew et al.	1973			*49* ° *N*
17	Broom & Mason	1978	England	Langstone Harbour	50 ° 47 ' N 00° 59 ' W
18	Heilmayer et al.	2003	France	Roscoff	48 ° 59 ' N 04° 53 ' W
19	Data aus Ursin*	1956		North Sea	55 ° N 04° E
20	Data aus Ursin*	1956	Denmark	Southern Kattegat	57 ° 30 ' N 11° 17 ' E
21	Data aus Ursin*	1956		Irish Sea	53 ° 16 ' N 05° 55 ' W
22	Data aus Ursin*	1956	Denmark	Faroer waters	62 ° 15 ' N 06° 50 ' W
23	Lee	1973	Ireland	Irish Sea (S Kilmore)	54 ° 24 ' N 05° 16 ' W
24	Lee	1973	Ireland	Irish Sea (S Carnsore Point)	52 ° 09 ' N 06° 22 ' W
25	Richardson et al.	1982	Scotland	Firth of Clyde	55 ° 46 ' N 04° 51 ' W
26	Rolfe	1973		Irish Sea (Kish Bank)	*53* ° *N*
27	Taylor & Venn	1978	Scotland	Clyde Sea	55 ° 46 ' N 4° 51 ' W
Amusium balloti					
28	Clavier	pers. Com.	New Caledonia	North Lagoon	20 ° 16 ' S 164° 15 ' E
29	Heald & Caputi	1981	Australia	Shark Bay	25 ° 36 ' S 113° 45 ' E
30	William & Dredge	1981	Australia	Queensland	19 ° 24 ' S 148° 34 ' E
Amusium japonicum c.					
31	William & Dredge	1981			23 ° S 151° 03 ' E
32	William & Dredge	1981			23 ° S 151° 03 ' E
33	William & Dredge	1981			23 ° S 151° 03 ' E

	Species / Reference[a]	Year	Country	Place	Coordinates[b]
Amusium pleuronectes					
34	Del Norte	1988	Philippines	Lingayen Gulf	06° 15' N 120° 10' E
35	Nugranad	1988	Thailand	Ko Chang	12° 02' N 102° 10' E
36	Llana	1987	Philippines	Visayan Sea	11° 20' N 123° 59' E
Argopecten purpuratus					
37	Mendo & Jurado	1993	Peru	Atenas (Paracas Bay)	13° 49' S 76° 18' W
38	Mendo & Jurado	1993	Peru	Atenas (Paracas Bay)	13° 49' S 76° 18' W
39	Mendo & Jurado	1993	Peru	Atenas (Paracas Bay)	13° 49' S 76° 18' W
40	Mendo & Jurado	1993	Peru	Tunga	14° 13' S 76° 12' W
41	Mendo & Jurado	1993	Peru	Independence Island	14° 13' S 76° 12' W
42	Piquimil et al. *	1991	Chile	Huasco Bay	28° 27' S 71° 15' W
43	Tomicic et al.	1978	Chile		*30° S*
44	Wolff	1985	Peru	Bahia de Paracas	13° 49' S 76° 18' W
45	Wolff	1985	Peru	Bahia de Paracas	13° 49' S 76° 18' W
46	Wolff	1985	Peru	Bahia de Paracas	13° 49' S 76° 18' W
47	Wolff	1987	Peru	(Sp coh.)	13° 49' S 76° 18' W
48	Wolff	1987	Peru	Au coh.	13° 49' S 76° 18' W
49	Yamashiro & Mendo	1988	Peru	Bahia de Paracas	13° 49' S 76° 18' W
50	Yamashiro & Mendo	1988	Peru	Independencia Bay	14° 13' S 76° 12' W
51	Yamashiro & Mendo	1988	Peru	La Pampa	14° 13' S 76° 12' W
52	Yamashiro & Mendo	1988	Peru	Tunga	14° 13' S 76° 12' W
53	Yamashiro & Mendo	1988	Peru	Atenas	13° 49' S 76° 18' W
54	Yamashiro & Mendo	1988	Peru	Atenas	13° 49' S 76° 18' W
55	Yamashiro & Mendo	1988	Peru	Atenas	13° 49' S 76° 18' W
Bractechlamys vexillum					
56	Clavier *	pers. com.	New Caledonia	SW-Lagoon	22° 15' S 166° 25' E
57	Luro *	1985	New Caledonia	SW-Lagoon	22° 15' S 166° 25' E
Chlamys albidus					
58	Myasnikov &Kochnev	1988	USSR	Kuril Is.	49° 25' N 154° 45' E
Chlamys hastata					
59	MacDonald et al.	1991	Canada	Bamfield B.C.	*48° N 125° W*
Chlamys islandica					
60	Giguère *	pers. com.	Canada	Havre Saint-Pierre	50° 14' N 63° 41' W
61	Lambert & Préfontaine	1995	Canada	Salluit	62° 19' N 75° 30' W
62	Lambert & Préfontaine	1995	Canada	Salluit	62° 19' N 75° 30' W
63	Lambert & Préfontaine	1995	Canada	Quaqtaq	61° 05' N 69° 38' W
64	Lambert & Préfontaine	1995	Canada	Quaqtaq	61° 05' N 69° 38' W
65	Naidu et al.	1982	Canada	Gulf St. Lawrence	48° 25' N 61° 56' W
66	Vahl	1981a,b	Norway	Balsfjord	69° 35' N 18° 55' E
67	Vahl	1981a,b	Norway	Balsfjord	69° 35' N 18° 55' E
68	Vahl	1981a,b	Norway	Balsfjord	69° 35' N 18° 55' E
69	Vahl	1981a,b	Norway	Balsfjord	69° 35' N 18° 54' E
70	Wiborg *	1963	Norway		*70° N 24° E*

Species / Reference[a]	Year	Country	Place	Coordinates[b]
Chlamys rosealbus				
71 Silina & Pozdnyakova	1990		Seo of Japan	40 ° N 133° E
Chlamys rubida				
72 MacDonald et al.	1991	Canada	British Columbia, Denman Is.	49 ° 30 ' N 124° 50 ' W
Chlamys tehuelcha				
73 Orensanz	1986	Argentina	San Jose Gulf	42 ° 20 ' S 64° 15 ' W
74 Orensanz	1986	Argentina	San Jose Gulf	42 ° 20 ' S 64° 15 ' W
75 Orensanz	1986	Argentina	San Jose Gulf	42 ° 20 ' S 64° 15 ' W
Comptopallim radula				
76 Lefort	1994	New Caledonia	Noumea (SW Lagoon)	22 ° 20 ' S 166° 25 ' E
Crassadoma gigantea				
77 MacDonald et al.	1991	Canada	British Columbia, Bamfield	48 ° 48 ' N 125° 14 ' W
Mimachlamys gloriosa				
78 Lefort	1994	New Caledonia	Noumea (SW Lagoon)	22 ° 20 ' S 166° 25 ' E
Mimachlamys varia				
79 Antoine	1979	France	Brest Harbour	48 ° 22 ' N 4° 30 ' W
80 Antoine	1979	France	Brest Harbour	48 ° 22 ' N 4° 30 ' W
81 Antoine	1979	France	Brest Harbour	48 ° 22 ' N 4° 30 ' W
82 Conan & Shafee	1978	France	Bay of Brest	48 ° 18 ' N 4° 25 ' W
83 Shafee	1982	France	Bay of Brest	48 ° 18 ' N 4° 25 ' W
84 Shafee & Conan	1984	France	Bay of Brest (Lanveoc)	48 ° 18 ' N 4° 25 ' W
85 Shafee & Conan	1984	France	Bay of Brest (Lanveoc)	48 ° 18 ' N 4° 25 ' W
Mizuhopecten yessoensis				
86 Antoine	1979	Japan	Saroma Lake	44 ° 11 ' N 143° 49 ' E
87 Antoine	1979	France	Baie de Seine	49 ° 46 ' N 00° 55 ' W
88 Golikov & Scarlato	1970	GUS	Posjet Bay	43 ° 36 ' N 130° 49 ' E
89 Ventilla	1982	Japan	Mutsu Bay	41 ° 17 ' N 141° 10 ' E
90 Yoo et al.	1981	Korea	Pohang	36 ° 05 ' N 129° 28 ' E
Patinopecten caurinus				
91 Antoine	1979	USA	Washington coast	38 ° 35 ' N 76° 25 ' W
92 Antoine	1979	Canada	Georgia Strait	49 ° N 124° W
93 Haynes & Hitz	1971	Canada	Georgia Strait	48 ° N 124° W
94 Haynes & Hitz	1971	USA	Off Washington	38 ° 35 ' N 76° 25 ' W
95 Haynes & Powell	1968	USA	Alaska (Kodiak Island)	57 ° 59 ' N 153° 24 ' W
96 Ignell & Haynes	2000	USA	Alaska(Albatross Bank)	56 ° 49 ' N 153° 37 ' W
97 Ignell & Haynes	2000	USA	Alaska(Marmot Flats)	58 ° 05 ' N 152° 09 ' W
98 Ignell & Haynes	2000	USA	Alaska (Lower Cook Inlet)	59 ° 10 ' N 152° 33 ' W
99 Ignell & Haynes	2000	USA	Alaska (Cape St. Elias)	59 ° 56 ' N 144° 05 ' W
100 Ignell & Haynes	2000	USA	Alaska (Ocean Cape)	59 ° 06 ' N 138° 36 ' W
101 Ignell & Haynes	2000	USA	Alaska (Lituya Bay)	58 ° 39 ' N 137° 47 ' W
102 MacDonald & Bourne	1987	Canada	Vancouver Island	49 ° 31 ' N 124° 29 ' W
103 MacDonald & Bourne	1987	Canada	Georgia Strait	48 ° 52 ' N 123° 15 ' W

Species / Reference[a]	Year	Country	Place	Coordinates[b]
Pecten alba				
104 Gwyther & McShane	1988		Phillip Bay	33° 59' S 151° 16' E
Pecten fumata				
105 Fairbridge *	1953		Tasmania	40° S
Pecten maximus				
106 Allison	1994	Ireland	Bradda Head	54° 06' N 04° 47' W
107 Allison	1994	Ireland	Irish Sea (SE Douglas)	54° 10' N 04° 25' W
108 Antoine	1979	France	Dieppe	50° 25' N 00° 20' E
109 Antoine	1979	France	Baie de Seine	49° 46' N 00° 55' W
110 Antoine	1979	France	Baie de Seine	49° 46' N 00° 55' W
111 Antoine	1979	France	St. Brieuc Bay	48° 34' N 02° 40' W
112 Antoine	1979	France	Seine Bay	49° 26' N 00° 08' E
113 Buestel & Laurec *	1975	France	St. Brieuc	48° 40' N 02° 47' W
114 Buestel & Laurec *	1975	France	Brest	48° 24' N 04° 29' E
115 Dare	1991	England	Engl. Channel (W Lizard Pt.)	49° 59' N 05° 23' W
116 Dare	1991	England	Engl.Ch. (SW Beachy Head)	50° 42' N 00° 07' W
117 Dare	1991	England	Irish Sea (S Isle of Man)	54° 02' N 04° 39' W
118 Dare & Deith	1990	England	Western Channel	50° 13' N 05° W
119 Dare & Deith	1990	England	Western Channel	50° 13' N 05° W
120 Dare & Deith	1990	England	Western Channel	50° 13' N 05° W
121 Dare & Deith	1990	England	Eastern Channel	50° 16' N
122 Dare & Deith	1990	England	Irish Sea	*54° N 04° 05' W*
123 Gibson •	1953	Ireland		51° 50' N 10° 00' W
Pecten sulcicostatus				
124 Antoine	1979	South Africa	Mossel Bay (Bonne esperan.)	34° 06' S 22° 13' E
125 Antoine	1979	South Africa	False Bay (Bonne esperan.)	34° 09' S 18° 37' E
126 Antoine	1979	France	Armen	*47° N*
127 Antoine	1979	France	Brest Harbour	48° 22' N 04° 30' W
Placopecten magellanicus				
128 Antoine	1979	Canada	Bay of Fundy	45° 03' N 65° 27' W
129 Antoine	1979	USA	Georges Bank	*41° N 67° W*
130 Brown et al. •	1972	USA	Georges Bank	*41° N 67° W*
131 Chouinard *	1984	Canada	Northumberland Str	46° 09' N 63° 46' W
132 Chouinard •	1984	Canada	Northumberland Str	46° 09' N 63° 46' W
133 Claereboudt & Himmelman	1996	Canada	Pabos	*48° N 64° 08' W*
134 Claereboudt & Himmelman	1996	Canada	Saint-Godefroi	*48° N 65° 02' W*
135 Claereboudt & Himmelman	1996	Canada	Bonaventure	48° 03' N 65° 33' W
136 Claereboudt & Himmelman	1996	Canada	Carleton	48° 05' N 66° 04' W
137 D'Amours & Pilote *	1982	Canada	Illes de Madeleine	*47° 05' N 62° W*
138 D'Amours & Pilote *	1982	Canada	Basse Côte Nord	*50° N 66° W*
139 Jamieson *	1979	Canada	Northumberland (Central Str.)	46° 13' N 63° 49' W
140 Jamieson *	1979	Canada	Northumberland Str (Eastern)	46° 33' N 64° 29' W
141 Jamieson *	1979	Canada	Northumberland Str (West.)	46° 10' N 61° 51' W
142 Jamieson *	1979	Canada	Northumberland Str (All)	*46° N 61° W*
143 Jamieson et al. •	1981	Canada	Scotian Shelf, Browns Bank	42° 30' N 65° 52' W

	Species / Reference[a]	Year	Country	Place	Coordinates[b]
Placopecten magellanicus					
144	Jamieson et al. *	1981	Canada	Scotian Shelf, German Bank	41 ° 40 ' N 67° 30 ' W
145	Langton et al.	1987	USA	Gulf of Maine	43 ° 44 ' N 69° 25 ' W
146	Langton et al.	1987	USA	Gulf of Maine	43 ° 44 ' N 69° 25 ' W
147	MacDonald	1986	Canada	Spencers Cove (wild)	46 ° 39 ' N 54° 05 ' W
148	MacDonald	1986	Canada	Spencers Cove (cultured)	46 ° 39 ' N 54° 05 ' W
149	MacDonald & Thompson	1985	Canada	Sunnyside	47 ° 51 ' N 53° 55 ' W
150	MacDonald & Thompson	1985	Canada	Sunnyside	47 ° 51 ' N 53° 55 ' W
151	MacDonald & Thompson	1985	Canada	Sunnyside	47 ° 51 ' N 53° 55 ' W
152	MacDonald & Thompson	1985	Canada	Dildo	47 ° 35 ' N 53° 36 ' W
153	MacDonald & Thompson	1985	Canada	Dildo	47 ° 35 ' N 53° 36 ' W
154	MacDonald & Thompson	1985	Canada	Dildo	47 ° 35 ' N 53° 36 ' W
155	MacDonald & Thompson	1985	Canada	TNNP	48 ° 27 ' N 67° 02 ' W
156	MacDonald & Thompson	1985	Canada	TNNP	48 ° 27 ' N 67° 02 ' W
157	MacDonald & Thompson	1985	Canada	TNNP	48 ° 27 ' N 67° 02 ' W
158	MacDonald & Thompson	1985	Canada	St. Andrews	45 ° 03 ' N 67° 02 ' W
159	MacDonald & Thompson	1985	Canada	St. Andrews	45 ° 05 ' N 67° 06 ' W
160	MacDonald & Thompson	1985	Canada	St. Andrews	45 ° 04 ' N 60° 57 ' W
161	MacDonald & Thompson	1985	Canada	Colinet	47 ° 10 ' N 53° 36 ' W
162	MacDonald & Thompson	1985	Canada	Colinet	47 ° 10 ' N 53° 36 ' W
163	MacDonald & Thompson	1988	USA	New Jersey, Asbury Park	40 ° 13 ' N 73° 47 ' W
164	Naidu *	1975	Canada	Port au Port Bay, Boswarlos	48 ° 35 ' N 58° 45 ' W
165	Naidu *	1975	Canada	Port au Port Bay, West Bay	54 ° 08 ' N 57° 18 ' W
166	Naidu *	1975	Canada	Port au Port Bay, Fox I. River	48 ° 42 ' N 58° 42 ' W
167	Naidu & Cahill *	1984	Canada	St. Pierre Bank	46 ° 49 ' N 56° 10 ' W
168	Posgay *	1979	Canada/ USA	Georges Bank	41 ° 15 ' N 67° 30 ' W
169	Posgay *	1959	USA	Georges Bank, NE Peak	41 ° 51 ' N 67° 06 ' W
170	Posgay *	1959	USA	Georges Bank, N Edge	41 ° 56 ' N 67° 19 ' W
171	Posgay *	1959	USA	Georges Bank	41 ° 06 ' N 68° 09 ' W
172	Robert et al. *	1985	Canada	Scotian Shelf, Browns Bank	42 ° 38 ' N 65° 52 ' W
173	Robert et al. *	1985	Canada	Scotian Shelf, German Bank	41 ° 40 ' N 67° 30 ' W
174	Robert et al. *	1985	Canada	Scotian Shelf, Middle Ground	44 ° 32 ' N 60° 42 ' W
175	Robert and Jamieson	1986	Canada	Scotian Shelf, Middel Ground	44 ° 32 ' N 60 ° 42 ' W
176	Robert et al. *	1985	Canada	Scotian Shelf, Sable, W Bank	43 ° 24 ' N 65° 37 ' W
177	Robert and Jamieson	1986	Canada	Scotian Shelf, Sable, W Bank	43 ° 24 ' N 65° 37 ' W
178	Robert et al. *	1985	Canada	Scotian Shelf, Lurcher Shoals	43 ° 50 ' N 66° 30 ' W
179	Robert and Jamieson	1986	Canada	Scotian Shelf, Lurcher Shoals	43 ° 50 ' N 66° 30 ' W
180	Roddick & Mohn *	1985	USA	Georges Bank	41 ° 02 ' N 68° 11 ' W
181	Schick & Shumway	1988	USA	Gulf of Maine, Jericho Bay	44 ° 12 ' N 68° 30 ' W
182	Schick & Shumway	1988	USA	Gulf of Maine, Ringtown Island	44 ° 7.4 ' N 68° 29 ' W
183	Schick & Shumway	1988	USA	S. Boothbay Harbor	43 ° 27 ' N 69° 33 ' W
184	Schick & Shumway	1988	USA	W. Jeffrey's Ledge	43 ° 4.3 ' N 70° 11 ' W
185	Schick et al.	1988	USA	Gulf of Maine	43 ° 44 ' N 69° 25 ' W
186	Serchuk et al.	1979	Canada/ USA	Georges Bank	41 ° 22 ' N 67° 48 ' W
187	Serchuk et al.	1982	USA	Gulf of Maine	43 ° 44 ' N 69° 25 ' W
188	Thouzeau et al.	1991	USA	Georges Bank	41 ° 23 ' N 65° 56 ' W

	Species / Reference[a]	Year	Country	Place	Coordinates[b]
Zygochlamys patagonica					
189	Lasta et al.	2001	Argentina	Recultas Bed	39 ° 23 ' S 55° 56 ' W
190	Urban & Tesch	1996	Argentina		*41 ° S*
191	Valero	1999	Argentina	Recultas Bed	39 ° 23 ' S 55° 56 ' W
192	Valero	1999	Argentina	Recultas Bed	39 ° 23 ' S 55° 56 ' W
193	Valero	1999	Argentina	Recultas Bed	39 ° 23 ' S 55° 56 ' W
194	Valero	1999	Argentina	Recultas Bed	39 ° 23 ' S 55° 56 ' W
195	Valero	1999	Argentina	Recultas Bed	39 ° 23 ' S 55° 56 ' W
196	Walossek	1991	Argentina	Station 496/78	39 ° 36 ' S 59° 21 ' W
197	Walossek	1991	Argentina	Station 507	41 ° 58 ' S 58° 05 ' W
198	Walossek	1991	Argentina	Station 522	42 ° 59 ' S 61° 05 ' W
199	Walossek	1991	Argentina	Station 607	52 ° 31 ' S 66° 00 ' W
200	Walossek	1991	Argentina	Station 669	44 ° 22 ' S 63° 05 ' W

Last updated April 2003

[a] Studies cited from secondary or non-available grey literature are marked with an asterisks (*), further information on the source are given in the references.

[b] Coordinates not provided directly in the study where estimated from information (Maps, names of locations) given in the 'Material and Method' part of the appropriate paper. Coordinates in *ITALICS* represent rough estimates, caused by insufficient information.

Table 7.1b

ScallopBase - Compilation of growth parameters for scallops: Summary of species, parameters of the von Bertalanffy growth formula, coefficients of overall growth performance and maximum growth rate

	Temp.[a]	S-Inf	K	Overall Growth Performance				M_{max}[b]	$\partial M/\partial t$[c]
	°C	mm	y^{-1}	phi'	P	phi	psi	kJ	kJ y^{-1}
A. colbecki									
1	0	128.0	0.09	3.17	1.86	0.89	1.39	803.52	31.95
2	0	92.0	0.15	3.12	1.70	0.86	1.23	327.19	22.66
3	0	101.4	0.09	2.97	1.59	0.72	1.12	432.04	17.68
4	0	108.9	0.11	3.13	1.78	0.87	1.31	528.18	27.08
5	0	93.0	0.19	3.21	1.80	0.96	1.31	337.41	28.38
6	0	89.6	0.24	3.28	1.86	1.03	1.38	303.47	32.76
7	0	105.0	0.12	3.12	1.72	0.84	1.24	436.04	23.12
A. opercularis									
8	11.0	75.4	0.70	3.60	2.11	1.36	1.65	185.86	58.17
9	11.0	77.1	0.68	3.60	2.13	1.36	1.67	197.52	60.23
10	10.0	73.5	0.75	3.61	2.11	1.37	1.64	172.70	58.25
11	10.0	74.5	0.48	3.43	1.94	1.18	1.46	179.48	38.74
12	10.4	60.3	1.10	3.60	2.03	1.37	1.56	98.32	48.64
13	11.0	76.7	0.68	3.60	2.12	1.36	1.65	195.12	59.69
14	12.0	75.5	0.55	3.50	2.01	1.25	1.53	186.56	46.17
15	12.0	73.5	0.75	3.61	2.11	1.37	1.64	172.77	58.35
16	10.4	60.3	1.10	3.60	2.03	1.37	1.56	98.36	48.66
17	11.2	55.5	1.34	3.62	2.02	1.39	1.54	77.64	46.79
18	12.5	58.9	0.60	3.32	1.74	1.09	1.29	91.96	24.98
19	11.0	75.8	0.50	3.46	1.97	1.22	1.50	188.53	42.39
20	10.0	78.6	0.38	3.37	1.90	1.13	1.42	209.04	35.72
21	11.0	80.8	0.72	3.67	2.21	1.43	1.74	226.12	73.22
22	7.5	69.9	0.54	3.43	1.91	1.19	1.44	150.01	36.73
23	11.5	74.1	0.48	3.42	1.93	1.18	1.45	176.75	38.04
24	11.5	70.6	0.53	3.42	1.91	1.19	1.44	154.07	36.97
25	9.5	65.6	1.05	3.65	2.12	1.42	1.64	124.96	59.01
26	11.5	74.8	0.74	3.62	2.13	1.38	1.65	181.47	60.47
27	10.0	70.4	0.55	3.44	1.92	1.20	1.45	152.77	37.79
A. balloti									
28	25.0	98.7	1.42	4.14	2.75	1.89	2.28	399.65	255.22
29	21.8	103.9	1.42	4.19	2.82	1.93	2.34	462.53	295.38
30	25.0	104.9	2.83	4.49	3.13	2.24	2.65	475.32	604.94
A. japonicum c.									
31	25.0	102.0	2.69	4.45	3.07	2.19	2.60	438.87	530.92
32	25.0	108.1	2.73	4.50	3.15	2.25	2.67	517.76	635.67
33	25.0	104.9	3.07	4.53	3.16	2.27	2.69	475.32	656.25
A. pleuronectes									
34	27.1	106.0	0.92	4.01	2.65	1.76	2.18	489.64	202.59

	Temp.^{a}	S-Inf	K	Overall Growth Performance				M_{max}^b	$\partial M/\partial t^c$
	°C	mm	y^{-1}	phi'	P	phi	psi	kJ	kJ y^{-1}
A. pleuronectes									
35	29.9	114.0	1.30	4.23	2.89	1.97	2.42	602.29	352.13
36	27.0	100.0	0.94	3.97	2.59	1.72	2.11	414.82	175.36
A. purpuratus									
37	18.0	95.4	2.095	4.28	2.88	2.03	2.40	362.79	341.80
38	19.0	88.7	2.07	4.21	2.79	1.96	2.31	294.88	274.51
39	22.0	112.0	2.90	4.56	3.22	2.30	2.74	572.71	746.92
40	15.0	110.0	0.57	3.83	2.49	1.58	2.01	544.08	138.25
41	15.0	94.2	2.25	4.30	2.90	2.05	2.42	349.95	354.10
42	17.0	142.6	0.20	3.61	2.36	1.34	1.90	1138.22	103.76
43	17.1	100.0	0.70	3.85	2.46	1.59	1.99	414.82	130.59
44	18.6	94.9	2.88	4.41	3.01	2.16	2.54	357.40	462.90
45	18.6	99.2	1.99	4.29	2.91	2.04	2.43	405.44	362.85
46	18.6	111.5	2.10	4.42	3.07	2.16	2.55	565.46	534.03
47	19.6	110.0	1.26	4.18	2.84	1.92	2.36	544.08	308.30
48	19.6	111.5	2.10	4.42	3.07	2.16	2.60	565.46	534.03
49	23.0	105.4	2.46	4.44	3.07	2.18	2.54	481.79	533.02
50	14.5	107.6	0.41	3.67	2.32	1.42	1.86	510.97	93.76
51	14.5	106.3	0.43	3.68	2.32	1.42	1.86	493.59	94.34
52	14.5	109.1	0.52	3.79	2.44	1.54	1.98	531.50	125.01
53	23.0	105.4	2.46	4.44	3.07	2.18	2.54	481.79	533.02
54	25.7	99.2	4.82	4.68	3.29	2.42	2.81	405.44	877.95
55	25.5	99.2	2.70	4.42	3.04	2.17	2.56	405.44	492.67
B. vexillum									
56	25.0	47.4	4.86	4.04	2.38	1.82	1.91	49.56	108.32
57	25.0	49.4	1.41	3.54	1.90	1.31	1.42	55.74	35.35
C. albidus									
58	4.3	117.2	0.16	3.34	2.02	1.08	1.54	651.67	46.89
C. hastata									
59	15.0	93.7	0.32	3.45	2.04	1.20	1.55	344.69	49.60
C. islandica									
60	6.0	124.1	0.11	3.23	1.93	0.96	1.45	766.89	37.94
61	6.0	124.6	0.07	3.00	1.70	0.74	1.21	775.72	22.68
62	6.0	124.6	0.07	3.00	1.70	0.74	1.21	775.72	22.68
63	6.0	87.2	0.17	3.10	1.67	0.85	1.12	280.91	20.84
64	6.0	87.2	0.17	3.10	1.67	0.85	1.12	280.91	20.84
65	6.0	107.3	0.15	3.24	1.88	0.98	1.40	506.92	34.20
66	4.0	82.0	0.23	3.19	1.73	0.94	1.24	235.81	24.38
67	4.0	120.0	0.23	3.63	2.32	1.37	1.36	696.96	93.88
68	4.0	120.0	0.23	3.63	2.32	1.37	1.36	696.96	93.88
69	4.0	94.2	0.13	3.06	1.70	0.84	1.23	394.90	22.73
70	5.0	120.0	0.13	3.27	1.96	1.01	1.48	696.96	40.75

	Temp.^{a}	S-Inf	K	Overall Growth Performance				M$_{max}$^{b}	$\partial M/\partial t^c$
	°C	mm	y^{-1}	phi'	P	phi	psi	kJ	kJ y^{-1}
C. rosealbus									
71	2.0	84.1	0.20	3.15	1.70	0.90	1.23	253.20	22.74
C. rubida									
72	5.0	67.0	0.41	3.26	1.74	1.03	1.27	132.70	24.47
C. tehuelcha									
73	12.4	89.6	0.60	3.68	2.26	1.43	1.78	303.47	81.89
74	12.4	84.2	0.72	3.71	2.26	1.46	1.79	254.53	82.42
75	12.4	88.4	0.55	3.63	2.21	1.38	1.73	292.05	72.24
C. radula									
76	23.5	92.4	0.35	3.48	2.04	1.21	1.56	313.37	48.45
C. gigantea									
77	11.7	167.0	0.17	3.68	2.48	1.40	2.00	1765.89	135.01
M. gloriosa									
78	23.5	73.9	1.01	3.74	2.20	1.47	1.72	157.19	70.14
M. varia									
79	12.0	78.0	0.41	3.40	1.92	1.15	1.45	204.53	37.71
80	12.0	52.0	0.46	3.09	1.47	0.87	1.00	64.50	13.34
81	12.0	52.3	0.44	3.08	1.46	0.85	0.98	65.57	12.97
82	12.7	50.9	0.57	3.17	1.54	0.95	1.07	60.80	15.69
83	12.0	52.3	0.45	3.09	1.47	0.86	1.01	65.57	13.18
84	11.7	52.3	0.45	3.09	1.47	0.86	1.01	65.57	13.18
85	11.7	52.3	0.45	3.09	1.47	0.86	1.01	65.57	13.18
M. yessoensis									
86	5.7	148.1	0.40	3.94	2.71	1.67	2.23	1268.42	228.17
87	12.0	138.9	0.48	3.97	2.71	1.70	2.23	1056.80	228.13
88	8.0	189.9	0.20	3.86	2.71	1.57	2.23	2572.48	231.38
89	9.6	144.2	0.98	4.31	3.06	2.04	2.58	1175.65	518.14
90	13	122.8	0.87	4.12	2.81	1.85	2.33	744.25	291.19
P. caurinus									
91	8.0	106.0	0.44	3.69	2.33	1.44	1.86	489.64	96.89
92	7.5	106.4	0.34	3.59	2.23	1.33	1.75	494.92	75.68
93	7.5	160.0	0.35	3.96	2.75	1.68	2.31	1580.48	251.62
94	8.0	106.0	0.44	3.69	2.33	1.43	1.96	489.64	96.01
95	3.0	180.0	-	-	-	-	-	2209.89	-
96	3.0	170.1	0.35	4.00	2.81	1.72	2.26	1881.26	292.73
97	3.0	175.7	0.27	3.91	2.74	1.63	2.24	2062.93	245.85
98	3.0	161.7	0.33	3.93	2.73	1.66	2.19	1628.74	240.25
99	3.0	159.7	0.33	3.92	2.71	1.64	2.19	1572.06	230.48
100	3.0	158.6	0.24	3.79	2.58	1.51	2.09	1541.44	169.15
101	3.0	130.5	0.37	3.80	2.51	1.53	1.99	884.89	146.05
102	8.4	112.4	0.50	3.80	2.51	1.57	2.01	648.22	143.19
103	10.6	156.8	0.39	3.98	2.85	1.76	2.33	1810.98	312.02

	Temp.[a]	S-Inf	K	Overall Growth Performance				M_{max}[b]	$\partial M/\partial t$[c]
	°C	mm	y^{-1}	phi'	P	phi	psi	kJ	kJ y^{-1}
P. alba									
104	14.1	86.0	1.60	4.07	2.64	1.83	2.16	270.04	194.31
P. fumata									
105	11.8	78.8	0.84	3.72	2.25	1.47	1.77	210.55	79.54
P. maximus									
106	12.0	133.7	0.47	3.92	2.65	1.65	2.15	947.64	198.60
107	12.0	133.9	0.33	3.77	2.50	1.50	2.02	952.49	140.93
108	11.0	123.5	0.53	3.91	2.60	1.64	2.13	756.39	180.29
109	11.0	138.9	0.48	3.97	2.71	1.70	2.23	1056.80	228.13
110	11.0	139.8	0.56	4.04	2.78	1.77	2.30	1076.40	271.09
111	11.0	124.6	0.56	3.94	2.64	1.67	2.16	775.72	195.36
112	12.0	135.4	0.58	4.03	2.76	1.76	2.28	982.76	256.34
113	10.9	124.2	0.56	3.94	2.63	1.67	2.16	768.65	193.58
114	12.7	106.8	0.66	3.88	2.52	1.62	2.04	500.23	148.48
115	10.0	109.0	0.38	3.65	2.30	1.40	1.83	530.12	90.59
116	10.0	132.4	0.35	3.79	2.51	1.52	2.03	922.05	145.13
117	10.0	115.1	0.48	3.80	2.47	1.54	2.00	618.98	133.62
118	11.0	116.5	0.34	3.66	2.34	1.40	1.83	640.65	97.96
119	12.0	112.3	0.39	3.69	2.35	1.43	1.85	577.08	101.22
120	12.0	124.5	0.29	3.65	2.35	1.38	1.84	773.95	99.89
121	10.4	134.2	0.36	3.81	2.54	1.54	2.03	958.17	155.13
122	10.0	126.7	0.28	3.65	2.36	1.39	1.86	813.51	102.44
123	10.0	125.0	0.56	3.94	2.64	1.68	2.17	782.83	197.15
P. sulcicostatus									
124	20.0	86.7	0.32	3.38	1.95	1.13	1.47	276.35	39.77
125	20.0	95.5	0.38	3.54	2.14	1.29	1.66	363.87	62.18
126	-	107.1	0.52	3.78	2.42	1.52	1.94	504.24	117.92
127	12.0	106.7	0.66	3.88	2.52	1.62	2.04	498.90	148.08
P. magellanicus									
128	10.0	162.0	0.35	3.96	2.84	1.74	2.37	1983.94	312.28
129	9.2	146.4	0.35	3.88	2.72	1.66	2.24	1487.22	234.09
130	9.2	145.5	0.38	3.91	2.74	1.69	2.19	1461.35	249.74
131	13.6	103.8	0.37	3.60	2.32	1.40	1.80	558.29	92.90
132	13.6	108.8	0.33	3.59	2.32	1.38	1.82	639.48	93.75
133	8.7	154.0	0.14	3.52	2.38	1.30	1.89	1717.64	108.14
134	8.2	169.0	0.15	3.63	2.53	1.41	2.03	2237.77	150.96
135	9.1	188.0	0.10	3.55	2.48	1.32	2.00	3030.43	136.29
136	11.0	170.0	0.14	3.61	2.50	1.38	2.02	2275.66	143.28
137	8.0	147.2	0.25	3.73	2.58	1.52	2.08	1510.47	169.82
138	8.0	149.7	0.14	3.50	2.35	1.28	-	1584.63	99.77
139	13.6	114.8	0.28	3.56	2.31	1.36	1.85	744.45	92.40
140	13.6	128.0	0.19	3.49	2.29	1.28	-	1014.76	86.71
141	13.6	127.8	0.22	3.56	2.35	1.35	-	1010.26	99.95
142	13.6	126.2	0.21	3.52	2.31	1.31	-	974.67	92.05

	Temp.^{a}	S-Inf	K	Overall Growth Performance				M_{max}^{b}	$\partial M/\partial t^c$
	°C	mm	y^{-1}	phi'	P	phi	psi	kJ	kJ y^{-1}
P. magellanicus									
143	6.5	108.8	0.36	3.63	2.36	1.43	1.81	638.98	103.45
144	6.5	124.6	0.28	3.64	2.42	1.43	1.88	939.91	118.36
145	8.8	207.0	0.14	3.78	2.86	1.62	2.39	5170.83	319.81
146	8.8	207.0	0.14	3.78	2.86	1.62	2.39	5170.83	319.81
147	5.1	173.8	0.16	3.68	2.59	1.46	2.11	2423.43	174.38
148	5.1	127.6	0.38	3.79	2.58	1.58	2.07	1005.76	171.88
149	7.0	176.5	0.19	3.77	2.68	1.55	2.19	2532.12	216.36
150	2.5	165.5	0.20	3.74	2.62	1.52	2.13	2108.37	189.64
151	2.5	158.4	0.16	3.60	2.47	1.38	2.00	1861.02	133.91
152	7.0	175.4	0.19	3.77	2.67	1.54	2.18	2487.47	212.55
153	7.0	168.2	0.19	3.73	2.62	1.51	2.14	2207.75	188.65
154	7.0	147.8	0.22	3.68	2.53	1.47	2.03	1528.06	151.18
155	7.0	163.1	0.24	3.81	2.69	1.58	2.17	2022.52	218.30
156	7.0	151.1	0.22	3.70	2.55	1.48	2.07	1627.17	160.99
157	7.0	146.0	0.17	3.56	2.40	1.34	1.95	1475.69	112.82
158	7.0	166.9	0.21	3.77	2.66	1.55	2.16	2159.53	203.95
159	4.9	166.0	0.21	3.76	2.65	1.54	2.16	2126.55	200.84
160	7.0	170.2	0.19	3.74	2.64	1.52	2.16	2283.28	195.10
161	7.0	158.6	0.18	3.66	2.53	1.44	2.04	1867.72	151.19
162	7.0	160.1	0.19	3.69	2.56	1.47	2.07	1918.43	163.92
163	9.2	155.9	0.22	3.73	2.59	1.51	2.11	1778.64	175.98
164	8.0	152.4	0.21	3.69	2.54	1.47	2.08	1667.33	157.47
165	8.0	160.5	0.19	3.69	2.56	1.47	2.11	1932.10	165.09
166	8.0	139.9	0.27	3.72	2.55	1.51	2.07	1306.90	158.69
167	8.0	146.9	0.22	3.68	2.52	1.46	2.03	1501.73	148.58
168	10.0	143.6	0.37	3.88	2.72	1.67	2.19	1407.69	234.24
169	9.2	146.5	0.30	3.81	2.65	1.59	2.12	1490.12	201.04
170	9.2	141.8	0.28	3.75	2.58	1.54	2.06	1358.05	171.01
171	9.2	148.9	0.26	3.76	2.61	1.54	2.10	1560.65	182.48
172	6.5	113.5	0.27	3.54	2.29	1.34	-	720.71	87.51
173	6.5	130.6	0.23	3.59	2.39	1.38	-	1074.53	111.15
174	6.5	160.3	0.18	3.67	2.54	1.44	-	1925.26	155.85
175	6.5	161.5	0.18	3.67	2.55	1.45	-	1966.56	159.19
176	6.5	156.0	0.20	3.69	2.55	1.47	-	1781.89	160.27
177	6.5	139.1	0.21	3.61	2.43	1.39	-	1285.75	121.43
178	6.5	156.0	0.18	3.64	2.51	1.42	-	1781.89	144.24
179	6.5	155.8	0.18	3.64	2.50	1.42	-	1775.39	143.72
180	9.2	161.4	0.18	3.67	2.54	1.45	2.04	1962.40	157.09
181	8.9	248.0	0.13	3.90	2.94	1.66	2.46	6665.99	389.72
182	8.9	148.0	0.27	3.77	2.62	1.56	2.14	1533.95	186.26
183	8.0	116.0	0.28	3.58	2.33	1.37	1.86	766.81	96.56
184	8.0	223.0	0.09	3.65	2.65	1.42	2.18	4926.39	199.40
185	8.9	116.0	0.09	3.08	1.84	0.88	1.36	766.81	31.04
186	9.2	152.5	0.34	3.89	2.75	1.68	2.21	1669.20	253.28
187	9.2	174.3	0.22	3.83	2.73	1.60	2.30	2443.33	241.74

	Temp.[a]	S-Inf	K	Overall Growth Performance				M_{max}[b]	$\partial M/\partial t$[c]
	°C	mm	y^{-1}	phi'	P	phi	psi	kJ	kJ y^{-1}
P. magellanicus									
188	9.2	144.9	0.28	3.77	2.61	1.56	2.11	1443.41	182.67
Z. patagonica									
189	7.0	74.7	0.42	3.37	1.88	1.13	1.42	180.85	34.08
190	5.0	66.0	0.14	2.78	1.24	0.54	0.80	127.14	7.89
191	7.0	61.0	0.54	3.30	1.74	1.07	1.22	101.79	24.72
192	7.0	108.0	0.16	3.26	1.90	1.00	1.42	516.75	36.02
193	7.0	75.9	0.31	3.25	1.76	1.00	1.26	189.66	26.02
194	7.0	73.3	0.45	3.39	1.89	1.15	1.39	171.40	34.92
195	7.0	92.6	0.17	3.17	1.76	0.92	1.29	333.43	25.79
196	10.0	68.1	0.52	3.38	1.79	1.10	1.29	119.44	27.21
197	9.0	70.6	0.36	3.25	1.68	0.97	1.19	133.32	21.10
198	8.0	59.6	0.51	3.26	1.61	0.97	1.11	79.07	17.88
199	6.0	53.9	0.60	3.24	1.54	0.95	1.04	57.87	15.25
200	8.0	64.8	0.54	3.35	1.74	1.07	1.25	102.37	24.37

Last updated April 2003

[a] Water temperatures not provided by the studies themselves were determined by assigning a value, based on the geographical position, from the online version of the 'World Ocean Database 2001' provided by the National Oceanographic Data Centre (http:/www.nodc.noaa.gov/ OC5/WOD01/pr_wod01.html).

[b] Max mass (M_{max}) was computed from H_∞ (mean asymptotic shell height, taken from the appropriate VBGF) according to: $M_{max} = a + H_\infty^{b}$, where a and b are constants of the allometric mass equation.

[c] Max growth rate ($\partial M/\partial t = K \cdot M_\infty \cdot (1 - (1/b))^{b-1}$) calculated according to Brey and Clarke (1993).

Table 7.2a

ScallopBase - Compilation of metabolic rates for scallops: Summary of species, geographic and environmental descriptions, and references

Species/ Pop. No.	**Reference**		**Country**	**Place**	**Coordinates**						**Depth (m) min- max**	
Adamussium colbecki												
1	Heilmayer & Brey	2003a	Antarctica	Terra Nova Bay (Road Cove)	74°	41'	S	164°	07'	E	30	70
Aquipecten opercularis												
2	Vahl	1972	Denmark	Øresund	56°	03'	N	12°	39'	E	28	30
3	McLusky	1973	Denmark	Øresund	56°	03'	N	12°	39'	E	25	30
4	Heilmayer et al.	2004	France	Roscoff	48°	59'	N	04°	53'	W	60	80
Chlamys islandica												
5	Vahl	1978	Norway	Tromsø	69°		N	18°		E	25	30
6	Vahl & Sundet	1985	Norway	Balsfjord	69°	20'	N	19°	22'	E	-	50
7	Schmid	1996	Arctic	Spitzbergen	78°		N	11°		E	-	150
Argopecten circularis												
8	Silva Loera	1986		Mexico								
Argopecten i. concentricus												
9	Lu et al.	1999	USA	Florida	29°	01'	N	82°	04'	W	-	-
10	Yang et. al.	1998a	China	Yantai	37°	33'	N	121°	30'	E	9	15
Argopecten i. irradians												
11	Bricelj et al.	1987	USA	New York	41°	01'	N	73°	19'	W	-	3
Chlamys deliculata												
12	Mackay & Shumway	1980	New Zealand	Otago Peninsula	45°	47'	S	171°	03'	E	-	135
Chlamys hastata												
13	Bernard & Noakes	1990	Canada	Vancouver Is.	50°	20'	N	125°	30'	E	-	-
Mimachlamys varia												
14	Shafee	1982	France	Bay of Brest	48°	18'	N	04°	25'	W	6	9
Chlamys farreri												
15	Yang et al.	1998b	China	Qingdao	37°		N	121°		E	9	15
Mizuhopecten yessoensis												
16	Fuji & Hashizume	1974	Japan	Mutsu Bay	41°	03'	N	140°	56'	E	-	3
Placopecten magellanicus												
17	MacDonald & Thompson	1986	Canada	Newfoundland, Sunnyside	47°	51'	N	53°	55'	W	-	10
18	MacDonald & Thompson	1986	Canada	Newfoundland, Sunnyside	47°	51'	N	53°	55'	W	-	31
19	Shumway et al.	1988	USA	Damariscotta R.	43°	05'	N	68°	05'	W	-	20
20	Pilditch & Grant	1999	Canada	Whitehaven Hb.	45°	20'	N	61°	20'	W		
21	Grant & Cranford	1991	Canada	Georges Bank	41°		N	67°		W	-	100
Zygochlamys patagonica												
22	Heilmayer et al.	2001	Argentina	Recultas Bed	39°	23'	S	55°	56'	W	100	200

Table 7.2b

ScallopBase - Compilation of metabolic rates for scallops: Summary of species, parameters of the oxygen-to-body mass relationship, mass range, and standardized metabolic rate after Luxmoore (1984)

Species/ Pop. No.	Temp. (°C)	Remarks	$VO_2 = a \bullet M^b$		DryMass in g			SMR_{Avg} *1
			a	b	min	max	geomean	
A. colbecki								
1	0	Summer	0.145	0.911	0.11	4.146	0.675	0.139
1	0	Winter	0.097	0.717	0.266	2.556	0.825	0.099
A. opercularis								
2	12		0.146	0.621	0.48	0.60	0.538	0.164
3	10		0.224	0.581	0.26	1.616	0.648	0.247
3	15		0.507	1.363	0.135	1.995	0.519	0.352
4	10.3	Winteraccl.	0.194	0.707	0.16	1.58	0.87	0.207
4	14.4		0.256	1.014	0.2	1.6	0.566	0.227
4	12.4		0.179	0.654	0.6	2.0	0.503	0.177
C. islandica								
5	3.8		0.187	0.893	0.0428	2.567	0.331	0.170
5	4.3		0.228	0.774	0.0428	2.567	0.331	0.236
5	5.3		0.194	0.774	0.0428	2.567	0.331	0.201
5	6.1		0.200	0.797	0.1263	5.442	0.829	0.200
5	6.4		0.177	0.756	0.1263	5.442	0.829	0.179
5	7.3		0.152	0.741	0.1263	5.442	0.829	0.154
5	7.6		0.167	0.754	0.022	2.9542	0.255	0.180
5	6.7		0.158	0.788	0.022	2.9542	0.255	0.162
5	6.2		0.150	0.807	0.022	2.954	0.255	0.150
5	3.6		0.096	0.737	0.003	5.802	0.132	0.111
5	3.1		0.105	0.759	0.003	5.802	0.132	0.116
5	2.3		0.123	0.816	0.003	5.802	0.132	0.121
5	3.8		0.164	1.056	0.0461	4.694	0.465	0.136
6	5.7		0.144	0.487	0.02	0.9	0.134	0.274
6	5.7		0.246	0.767	0.5	5	1.581	0.242
6	5.7		0.256	0.571	0.4	6	1.549	0.231
7	0		0.077	0.622	0.749	11.116	2.885	0.063
A. circularis								
8	20.0		0.479	0.715	0.04	1.78	0.267	0.541
A. i. concentricus								
9	25.0	Larvae	1.545	0.825	-	-	-	1.223
10	12.0		0.698	0.822	0.0342	0.691	0.154	0.969
10	17.0		1.059	0.927	0.0342	0.691	0.154	1.207
10	23.0		1.209	0.937	0.0342	0.691	0.154	1.351
10	28.0		2.046	0.870	0.0342	0.691	0.154	2.594
A. i. irradians								
11	17.4		0.931	0.725	0.47	2.99	1.185	0.918
11	10.5		0.368	0.733	0.84	2.86	1.550	0.356

Species/ Pop. No.	Temp. (°C)	Remarks	$VO_2 = a \bullet M^b$		DryMass in g			SMR_{Avg} [*1]
			a	b	min	max	geomean	
A. i. irradians								
11	1.5		0.065	0.986	0.87	4.37	1.950	0.073
11	8.7		0.347	0.585	0.87	4.37	1.950	0.299
11	11.4		0.484	0.887	0.87	4.37	1.950	0.511
11	15.6		1.045	0.911	0.87	4.37	1.950	1.120
11	20.2		0.802	1.397	0.87	4.37	1.950	1.189
11	22.9		1.102	1.249	0.87	4.37	1.950	1.480
11	7.4		0.235	0.880	0.463	1.530	0.842	0.232
11	7.4		0.156	1.013	1.530	3.142	2.193	0.184
C. deliculata								
12	10.0		0.166	0.539	0.026	1.48	0.196	0.257
C. hastata								
13	15.0		0.380	-	-	-	2.200	0.201
M. varia								
14	10.0		0.164	0.76	0.1	2.3	0.480	0.170
14	10.0		0.235	0.72	0.1	2.3	0.480	0.251
14	15.0		0.365	0.62	0.1	2.3	0.480	0.419
14	15.0		0.237	0.69	0.1	2.3	0.480	0.259
14	10.0		0.161	0.69	0.1	2.3	0.480	0.175
C. farreri								
15	12.0		0.929	0.930	0.04	1.36	0.222	1.101
15	17.0		1.299	0.777	0.04	1.36	0.222	1.940
15	23.0		1.538	0.728	0.04	1.36	0.222	2.469
15	28.0		1.395	0.606	0.04	1.36	0.222	2.693
M. yessoensis								
16	8.9		0.252	0.882	1.48	26.71	6.281	0.289
16	22.4		0.658	0.728	0.74	13.44	3.159	0.601
16	14.7		0.378	0.78	1.01	14.18	3.791	0.364
16	5.9		0.183	0.875	2.27	17.39	6.281	0.207
16	16.9		0.500	0.714	1.32	22.02	5.387	0.428
16	4.6		0.220	0.748	2.00	25.05	7.084	0.196
P. magellanicus								
17	8.0		0.447	0.700	1.80	42	8.695	0.354
17	12.0		0.339	0.780	1.80	42	8.695	0.320
17	8.0		0.132	0.880	0.50	25	3.536	0.145
18	3.5		0.214	0.760	0.50	25	3.536	0.201
18	7.5		0.234	0.790	0.50	25	3.536	0.229
18	3.5		0.066	0.930	0.50	25	3.536	0.077
19	10.0		0.363	0.838	0.01	18	0.424	0.353
19	9.0		0.304	0.740	0.01	18	0.424	0.322
19	6.0		0.220	0.714	0.01	18	0.424	0.238
19	1.0		0.069	0.761	0.01	18	0.424	0.072
19	4.0		0.196	0.755	0.01	18	0.424	0.205
19	5.0		0.283	0.752	0.01	18	0.424	0.297

Species/	Temp.	Remarks	$VO_2 = a \bullet M^b$		DryMass in g			SMR_{Avg} *1
Pop. No.	(°C)		a	b	min	max	geomean	
P. magellanicus								
19	8.0		0.259	0.848	0.01	18	0.424	0.250
19	11.0		0.344	0.862	0.01	18	0.424	0.328
19	17.0		0.386	0.837	0.01	18	0.424	0.376
19	19.0		0.399	0.837	0.01	18	0.424	0.389
19	16.0		0.428	0.820	0.01	18	0.424	0.423
19	15.0		0.361	0.831	0.01	18	0.424	0.354
19	11.0		0.382	0.814	0.01	18	0.424	0.380
19	9.0		0.281	0.736	0.01	18	0.424	0.299
19	3.0		0.162	0.740	0.01	18	0.424	0.172
20	10.0		0.349	0.770	1.13	2.29	1.609	0.343
21	6.0		0.031	1.523	4.3	9.5	6.391	0.117
Z. patagonica								
22	6.0		0.329	0.617	0.08	2.48	0.440	0.385
22	9.0		0.426	0.811	0.08	2.48	0.440	0.425

Last updated April 2003

*1 $SMR_{Avg} = a \bullet DM_{mean}^{b - 0.807}$ (for further details see publication II, pp 64-78)

Table 7.3

Compilation of individual respiration rates in bivalves (database provided by T. Brey, AWI): Summary of species from the class bivalvia used in this study

Species	**Data**	**Family**	**Subclass**
	N	**Order**	**Order**
Yoldia eightsi	61	Ctenidiobranchia	Ctenidiobranchia
Arctica islandica	41	Veneracea	Heterodonta
Aspatharia wahlbergi	19	Heterodonta	Heterodonta
Bankia gouldi	27	Myina	Heterodonta
Caelatura mossambicensis	8	Heterodonta	Heterodonta
Cardium edule	50	Cardiacea	Heterodonta
Cardium glaucum	29	Cardiacea	Heterodonta
Corbicula africana	4	Heterodonta	Heterodonta
Donax incarnatus	38	Tellinacea	Heterodonta
Donax serra	8	Tellinacea	Heterodonta
Donax sordidus	8	Tellinacea	Heterodonta
Donax spiculum	17	Tellinacea	Heterodonta
Donax vittatus	82	Tellinacea	Heterodonta
Gaimardia trapesina	52	Gaimardiidae	Heterodonta
Laternula elliptica	205	Pholadomyoida	Heterodonta
Macoma balthica	92	Tellinacea	Heterodonta
Meretrix meretrix	7		Heterodonta
Mulinia lateralis	209	Mactracea	Heterodonta
Musculium partumeium	31	Sphaeriidae	Heterodonta
Mya arenaria	183	Myacea	Heterodonta
Paphia laterisulca	12		Heterodonta
Paphies donacina	76	Tellinacea	Heterodonta
Parreysia corrugata	5	Heterodonta	Heterodonta
Scrobicularia plana	147	Tellinacea	Heterodonta
Spisula subtruncata	27	Tellinacea	Heterodonta
Tellina fibula	67	Tellinacea	Heterodonta
Tellina tenuis	96	Tellinacea	Heterodonta
Nausitora hedleyi	36	Myina	Heterodonta
Teredo furcifera	17	Myina	Heterodonta
Teredo navalis	18	Myina	Heterodonta
Transennella tantilla	31	Veneracea	Heterodonta
Tridacna gigas	49	Veneracea	Heterodonta
Glycymeris glycymeris	18	Arcinacea	Pteriomorpha
Aulacomya ater	63	Mytilacea	Pteriomorpha
Bathymodiolus thermophilus	13	Mytilacea	Pteriomorpha
Modiola adriatica	5	Mytilacea	Pteriomorpha
Mytilus californianus	41	Mytilacea	Pteriomorpha
Mytilus edulis	297	Mytilacea	Pteriomorpha
Perna viridis	17	Mytilacea	Pteriomorpha
Crassostrea gigas	45	Ostreacea	Pteriomorpha

Species	**Data**	**Family**	**Subclass**
	N	**Order**	**Order**
Crassostrea virginica	435	Ostreacea	Pteriomorpha
Ostrea edulis	53	Ostreacea	Pteriomorpha
Pinctada margaritifera	29	Ostreacea	Pteriomorpha
Pinctada maxima	30	Ostreacea	Pteriomorpha
Anadara senilis	17	Pectinacea	Pteriomorpha
PECTINIDAE			
Argopecten irradians	45	Pectinacea	Pteriomorpha
Astarte montagui	14	Pectinacea	Pteriomorpha
Chlamys islandica	196	Pectinacea	Pteriomorpha
Chlamys opercularis	34	Pectinacea	Pteriomorpha
Clinocardium ciliatum	2	Pectinacea	Pteriomorpha
Patinopecten yessoensis	45	Pectinacea	Pteriomorpha
Placopecten magellanicus	18	Pectinacea	Pteriomorpha
Adamussium colbecki	271	Pectinacea	Pteriomorpha
Aequipecten opercularis	284	Pectinacea	Pteriomorpha
Zygochlamys patagonica	73	Pectinacea	Pteriomorpha
Sum **55**	3797	All	
10	**982**	Pectinacea (only)	

Database is available on request from PD. Dr. T. Brey, Alfred Wegener Institute for polar and marine research, Bremerhaven, Germany (tbrey@awi-bremerhaven.de).

Table 7.4a

General Conversion factors for aquatic animals (modified after Brey 2001)

General	Conversion factor		Reference
mg O2 -> J	14.100	J/mg O2	Ivlev 1935, Elliott & Davison 1975, Gnaiger 1983
ml O2 -> J	20.100	J/ml O2	Ivlev 1935, Elliott & Davison 1975, Gnaiger 1983
mmol O2-> J	460.000	J/mmol O2	
mg C -> J	45.700	J/mg C	Salonen et al. 1976
mg Carbohydrate -> J	17.160	J/mg	Brody 1945
mg Protein -> J	23.650	J/mg	Brody 1945
mg Lipid -> J	39.550	J/mg	Brody 1945
mg-at O -> mg O2	16.000	mgO2/mg-at O	
mmol O2 -> mg O2	32.624	mgO2/mmolO2	
ml O2 -> mg O2	1.426	mgO2/mlO2	
mg O2 -> mg C	0.309	mgC/mgO2	
POM	23.500	J/mg	

Table 7.4b

Conversion factors for molluscs (modified after Brey 2001)

A Mollusca	**WM**	**SFDM**	**WM**	**gSFDM**	**gAFDM**
	->SFDM	**->AFDM**	**->AFDM**	**->kJ**	**->kJ**
Bivalvia	0.087	0.831	0.057	18.85	22.79
B Pectinacea		**0.845**		**20.22**	**21.96**
B Tellinacea		*0.833*		18.47	22.18
B Mytilus edulis				21.15	23.26
Gastropoda	0.088	*0.802*	0.107	18.24	23.81
G Streptoneura	0.099	0.838	0.076		23.63
G Ophistobranchia	0.077	0.766	0.137		23.99
G Nudibranchia	0.250	0.693	*0.173*	16.13	23.27
Polyplacophora			0.272		23.27
Benth. Cephalop.	0.203	0.900	0.200	20.40	22.03
Pelag. Cephalop.	0.203	0.900	0.226	20.40	23.34
Mollusca	**0.120**	**0.801**	**0.137**	**18.843**	**23.13**

B Pectinacea	**SFWM**	**SFDM**	**SFWM**	**gSFDM**	**AFDM**	**gSFDM**
	->SFDM	**->AFDM**	**->AFDM**	**->kJ**	**->kJ**	**->kJ**
A. colbecki						
General			0.150		22.79	
TNB 1986/87	0.186					
TNB 1987/88	0.188					
TNB 1989/90	0.818					
TNB 1993/94	0.130	0.852				
TNB 2000	0.159	0.854	0.135			
A. opercularis						
06/99		0.755				
10/99	0.178	0.851	0.155			
10/00	0.203	0.824	0.168			
Z. patagonica	0.173	0.823	0.141			
C. islandica				19.2		
M. varia					21.14	
					21.69	
P. magellanicus				24.5		24.50
A. purpuratus						
P. caurinus	0.200					
C. hastata/ C. rubida/ C. gigantea						20
Average=	**0.177**	**0.825**	**0.150**	**21.850**	**21.873**	**22.250**

Species Average				
A. colbecki	0.166	0.841	0.143	
A. opercularis	0.191	0.810	0.162	
M. varia				21.42

Table 7.5

Phylogeny of suprageneric groups of the family Pectinidae, with some commercial or potentially commercial scallops (modified after Waller 1991).