

Chapter 7

Physiology: Energy Acquisition and Utilisation

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7.1 INTRODUCTION

This chapter builds on a previous review of scallop physiology by Bricelj and Shumway (1991) included in an earlier edition of this text. The physiology of larval pectinids is not included, as the primary focus of this chapter is on post-settlement stages, juveniles and adults. Aspects related to nutrition (nutritional requirements of pectinids and substrate utilisation) and reproductive physiology are also excluded from this chapter. New, updated information is provided in areas that have received increasing attention since the publication of the first chapter, in particular the effects of flow, suspended sediments and of harmful algal blooms on scallop physiology. Readers are also referred to a comprehensive recent review of scallops in Iberoamerica, which includes several chapters on ecophysiology of scallops from that region (Maeda-Martínez 2002).

7.2 ENERGY ACQUISITION

7.2.1 Food Sources

Scallops are sublittoral, epifaunal, active suspension-feeding bivalves, which rely on suspended detrital material and phytoplankton as their food source. It has been suggested, however, that adult scallops are uniquely capable of exploiting food particles associated with surface sediments resuspended by their "shell clapping" activity (Davis and Marshall 1961). This ability has been demonstrated in the laboratory (Davis and Marshall 1961), but its significance in the natural environment is not known. Grant and Cranford (1989, 1991) and Cranford and Grant (1991) found that detrital diets alone, such as fresh and aged macroalgal detritus from the kelp *Laminaria langicruris*, or resuspended sediments containing benthic microalgae, were inadequate to support growth of adult *Placopecten magellanicus* under laboratory conditions. Only phytoplankton diets (*Isochrysis galbana* or *Chaetoceros gracilis*) fed at weight rations comparable to the detrital diets, sustained tissue and gonad growth in this species. Scope for growth (SFG) estimates derived from physiological data indicated that the phytoplankton diets yielded a positive SFG for both carbon and nitrogen, whereas aged kelp, a carbon-rich food source, yielded a positive (although relatively low) SFG for carbon but negative SFG for nitrogen (Grant and Cranford 1990). Aged kelp was readily absorbed (carbon absorption efficiency, at 87%, was comparable to that determined for the diatom diet) but resulted in markedly reduced

clearance rates and nitrogen ingestion rates compared to algal diets. Fresh kelp resulted in lower and highly variable absorption efficiencies (0 to 60%) compared to aged kelp. Lack of growth of sea scallops on kelp detritus alone was thus attributed primarily to nitrogen deficiency and contrasts with findings in the mussel, *Aulacomya ater*, which can maintain a positive energy balance on a kelp diet (Stuart 1982). Studies using ^{15}N as a tracer (Alber et al. 1988) indicate that nitrogen released as dissolved organic matter by senescing macrophytes (*Enteromorpha*, *Gracilaria*, *Fucus* and *Spartina*) can be aggregated into amorphous particulate matter and ingested and assimilated by bay scallops, *Argopecten irradians*, under laboratory conditions. Bay scallops were capable of absorbing nitrogen and organic material from aggregates or flocs, although less efficiently than they were able to assimilate phytoplankton (Alber and Valicla 1996). These authors suggested that organic aggregates, or flocs, could potentially represent an important and nutritious food source for suspension-feeding bivalves. Furthermore, studies on the activity of digestive enzymes show that bivalves, including scallops, have the capacity to digest macroalgal detritus (Wojtowicz 1972; Brock et al. 1986). Overall, the above studies thus indicate that macrophyte detritus has the potential to supplement phytoplankton as a food source in the natural environment and may help to meet energy demands of scallops when the phytoplankton supply is low.

At least three studies based on gut content analysis (Davis and Marshall 1961; Vernet 1977 and Shumway et al. 1987) have independently shown that benthic and/or tychopelagic algae are an important component of the scallops' diet. Davis and Marshall (1961) found that benthic diatoms (e.g., *Melosira*, *Licomophora*, *Cocconeis*) were more abundant than planktonic diatoms in gut contents of *Argopecten irradians*. They also reported that the numerical abundance of live benthic algae in water samples increased with increasing proximity to the sediment surface (from 32% 30 cm above the bottom to 80% approximately 0.5 cm from the bottom). Shumway et al. (1987) compared gut contents of shallow (20 m) and deep water (180 m) populations of *Placopecten magellanicus* in the Gulf of Maine. Again, benthic algae such as *Melosira*, *Navicula* and *Pleurosigma* were found to outnumber pelagic forms in gut contents of the deep water population. Interestingly, both resting cysts of the toxic dinoflagellate *Protogonyaulax* (= *Alexandrium*) *tamarensis*, and *Dinophysis* cells, implicated in outbreaks of paralytic shellfish poisoning (PSP) and diarrhetic shellfish poisoning (DSP) respectively, were abundant in gut contents. Vernet (1977) determined the seasonal algal composition of gut contents of the Patagonian scallop, *Chlamys tehuetcha*, as well as that of bottom sediments and plankton samples collected immediately above scallop beds in the Gulf of San José, Argentina. Benthic algae such as *Synedra investens*, *Melosira sulcata*, *Grammatopora marina* and *Navicula* spp., were dominant in gut contents throughout most of the year (Fig. 7.1). Planktonic diatoms such as *Chaetoceros* and *Thalassiosira* species, which were the dominant component of the spring phytoplankton bloom, were rarely present in gut contents. Furthermore, benthic algae that attach to sand grains by gelatinous stalks, such as *Glyphodesmia distans*, *Glyphodesmia* spp. and *Plagiogramma interruptus*, and were abundant in sediments, were absent from gut contents, presumably because they are not readily resuspended. It is interesting to note that scallop eggs were relatively abundant in stomach contents during the spawning season.

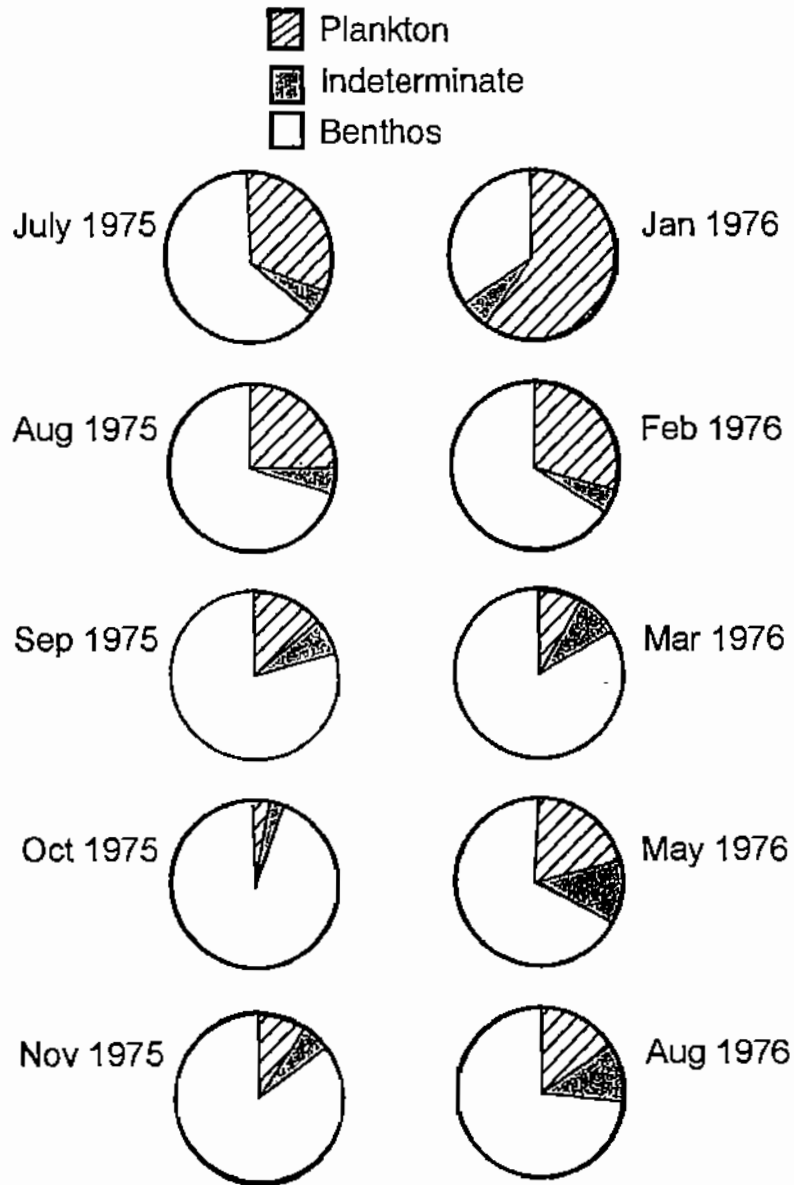


Figure 7.1. Seasonal changes in source of the diet (% numerical abundance of planktonic and benthic microalgae) as determined from stomach content analysis in the Patagonian scallop *Chlamys tehuelcha* (1975 cohort) (modified from Vernel 1977).

Adult scallops are capable of ingesting relatively large particles and this ability has been related to the absence of mechanisms for sorting particles on the basis of size by the gills of Pectinidae (Beninger et al. 1988). Particles up to 950 μm were described in the gut contents of *Patinopecten yessoensis* (Mikulich and Tsikhon-Lukamina 1981). Gut contents of *P. magellanicus* ranged from 10 to 350 μm (Shumway et al. 1987). By comparing the algal composition and size spectra of the plankton with stomach contents of *Chlamys tehuelcha*, Vernet (1977) found, however, that this scallop showed negative selection for particles exceeding 100 μm .

Changes in diet may be associated with major shifts in habitat of scallop species that move from an above-bottom, byssally attached juvenile stage to a free-living existence on the bottom as adults. Such changes have not yet been investigated.

7.2.2 Feeding Currents and Mechanisms of Particle Capture

Scallops are non-siphonate, ciliary suspension-feeders, which exhibit no fusion of the mantle edge. Water enters the mantle cavity along the ventral and anterior edge, and exits through the posterior exhalent opening (Hartnoll 1967). In *Argopecten irradians* this aperture is about five times larger than the anterior inhalent opening (Winter and Hamilton 1985). Scallops preferentially orient themselves by facing directly into the current (exhalent opening facing away from the direction of the flow) (Hartnoll 1967; Caddy 1968; Mathers 1976; Grant et al. 1992). Adults possess a plicate, heterorhabdic gill in which ordinary filaments and principal filaments form the crests and grooves respectively of the plicae.

Bivalves have been suggested to capture particles by direct interception with the ctenidial filament and transport the particles along the frontal surface of the filament by mucociliary processes (Ward et al. 1998a; See section below on "Particle retention efficiency" for alternative views). This mechanism for particle capture is consistent with theories of hydrosol filtration observed for many different groups of aquatic suspension-feeders (Shimeta and Jumars 1991). The low angle of particle approach to the filament increases the probability of encounter with frontal cilia and the vertical flow set up by the beating of the laterofrontal cilia or cirri reduces flow through the interfilamentary spaces and redirects particles to the frontal surface of the filament (Ward et al. 1998a). According to these authors, these two processes affecting flow patterns promote the retention of particles on the frontal surface by increasing the encounter efficiency with the frontal cilia.

While the mechanism of particle capture itself is likely to be similar for most species of bivalves, the velocity and sites of particle transport on the gill and the efficiency of retention vary among species including pectinids. Oysters (*Crassostrea virginica* and *Ostrea* sp.) and mussels (*Geukensia demissa*, *Mytilus edulis* and *Modiolus modiolus*) have well developed ventral ciliated grooves where particles are incorporated into a cohesive mucus string and transported at relatively low velocities anteriorly toward the labial palps (Ward 1996). In *C. virginica* the opposing surfaces of the ridged labial palps reduce the cohesiveness of the mucus strings and disperse entrapped particles for ingestion whereas

in *M. edulis* the ridged surface of one palp and the action of the ciliated dorsal margin disperse particles (Ward 1996).

The scallop, *P. magellanicus*, and mussel, *Arca zebra*, however, lack ventral grooves and only small mucus aggregations or strings accumulate on the ventral margins which could be transported to the labial palps for rejection as pseudofeces (Ward 1996). Particles destined for ingestion by *P. magellanicus* are suspended in a slurry and transported at high velocities in the dorsal tracts rather than in a mucus-bound string along the ventral margin (Ward 1996).

7.2.3 Particle Retention Efficiency

The amount of food available to suspension-feeding bivalves is a function of the volume of water transported across the gills (pumping rate) as well as the efficiency with which particles are retained by the gill. Most juvenile and adult suspension-feeding bivalves are able to retain particles above 3–4 μm with 100% efficiency, and retention efficiency decreases with decreasing particle size (to between 35 to 90% for 2 μm particles) (Møhlenberg and Riisgård 1978; Riisgård 1988). This pattern is consistent with capture mechanisms other than sieving proposed by modern filtration theory (Rubenstein and Koehl 1977; Jørgensen 1981, 1983). In contrast, the limit for effective retention of particles in members of the Pectinidae studied to date, [including *Pecten opercularis*, *P. septemradiatus* (Møhlenberg and Riisgård 1978), *Chlamys opercularis* (Vahl 1972) and *C. islandica* (Vahl 1973a) and *Argopecten irradians concentricus* (Palmer and Williams 1980; Riisgård 1988)], is about 5–7 μm (Fig. 7.2). Free bacterioplankton, typically ranging in size from 0.3 to 1 μm , is therefore not available as a food source for pectinids unless bound in aggregates. The retention pattern for particles below 5–7 μm , however, varies somewhat between species. For example, *C. islandica* is more efficient in capturing small particles than *C. opercularis* (retention efficiencies for 2 μm = ca. 27 and 5%, respectively (Vahl 1973a).

It should be pointed out that retention efficiencies are generally determined using electronic particle counters. Jørgensen et al. (1984) found that these instruments tend to somewhat overestimate retention efficiencies of small particles (<2 μm in diameter) generally determined with a 50 μm aperture tube. This is partly attributed to interference by conductive colloidal particles in seawater, and electrical noise at the lower limit of resolution of the particle counter, although recent multisizers are capable of increased resolution at small sizes.

The influence of particle concentration on retention efficiency in bivalves is not fully resolved. Palmer and Williams (1980) found that *Argopecten irradians concentricus* were significantly more efficient in retaining small particles (<3.4 μm) at high algal concentrations that induce pseudofeces production (6.1 mg wet weight L^{-1}) than at low concentrations below the threshold for pseudofeces production (0.9 mg L^{-1}), whereas an inverse effect was observed in the oyster *Crassostrea virginica*. The addition of a higher concentration of bentonite clay to an algal suspension caused a reduction in the retention efficiency of small particles by *Placopecten magellanicus* (Cranford and Gordon 1992).

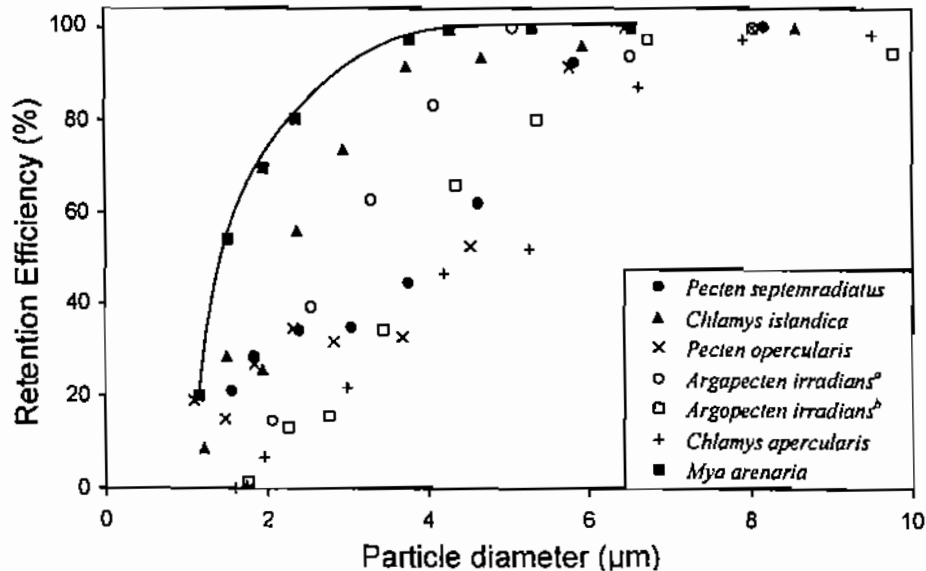


Figure 7.2. Retention efficiency (%) as a function of particle size in several pectinid species (redrawn from references cited in the text) compared to that of a bivalve with well developed eulaterofrontal cirri, e.g., the softshell clam, *Mya arenaria* (line fitted to the data from Møhlenberg and Riisgård 1978). ^aRiisgård 1988; ^bPalmer and Williams 1980, retention measured at low algal concentrations (0.9 mg wet weight L⁻¹).

Bivalves possess three types of ciliary tracts in their gill filaments: lateral (current producing), frontal (particle carrying), and laterofrontal tracts believed to play a role in particle retention (Owen and McCrae 1976). Although the mechanism of particle retention by the bivalve gill is not fully understood (see below) retention efficiency of small, bacteria-sized particles has been correlated with the development or structural complexity of laterofrontal tracts in both marine and freshwater bivalves (McHenry and Birbeck 1985; Silverman et al. 1997). Thus the poor retentiveness for small particles of the pectinid gill has been ascribed to the poor development of laterofrontal ciliary tracts in this group of bivalves (Owen and McCrae 1976; Møhlenberg and Riisgård 1978). The laterofrontal tracts consist only of small, simple pro-laterofrontal cilia, and lack the large, compound eulaterofrontal cirri characteristic of mussels (Owen and McCrae 1976). Thus, these authors suggest that the poorly developed laterofrontal cilia of pectinids play no role in particle retention. They suggest that, at low to moderate particle loads, the form of the plicae and U-shaped nature of principal filaments all combine to create a region of low pressure which tends to attract particles into the gutters formed by principal filaments.

Laterofrontal ciliary tracts, located across the entrance to interfilamentary spaces, are attributed a role in particle retention in numerous studies involving mussels, which are

characterised by large, complex cirri. However, the exact mechanism of particle retention by laterofrontal cilia or cirri has remained controversial, ranging from their action as mechanical filters or sieves (direct mechanical interception) (Dral 1967) to a hydromechanical role in capture (Jørgensen 1990), or a combination of other multiple mechanisms (Ward et al. 1998a). A mechanical role of the cirri is supported by differential particle capture in freshwater bivalves with cirri of different sizes (Silverman et al. 1997). Capture via a hydrodynamic mechanism is presumably achieved by influencing the steepness and height of velocity gradients in the boundary zone between currents entering the gill interfilamentary space, and surface currents along the frontal surface of gill filaments (Jørgensen 1981). Jørgensen's velocity gradient hypothesis, developed for the mytilid filibranch gill, predicts that the critical size for efficient particle retention should be larger in bivalves (such as pectinids) with reduced laterofrontal ciliary tracts. Ward et al. (1998a) argued that low Reynolds numbers preclude a mechanical sieving role of laterofrontal cilia/cirri (also reviewed by Jørgensen 1996), and that hydrodynamic entrainment may occur on principal but not ordinary filaments. Based on endoscopic observations they concluded that particle capture occurs by direct interception at the frontal surface of ordinary gill filaments and indeed does not require the presence of laterofrontal tracts. They suggest that the main role of the laterofrontal tracts is to increase the probability of encounter of particles with the frontal surface of gill filaments, by inducing lateral flows that reduce particle loss through the interfilamentary spaces. However, the pectinid gill was not represented in their study and these findings remain controversial.

Despite the controversy over the mechanism of particle capture as determined by *in vitro* methods using isolated gill filament preparations or *in vivo* methods applied to intact animals (e.g., confocal microscopy and video endoscopy respectively), each of which has inherent limitations [see Comments by various authors in *Limnol. Oceanogr.* 45(5), 2000], several recent studies of mytilids may support the role of the laterofrontal cirri in capturing particles and directing them to the frontal surface of gill filaments for subsequent transport (Riisgård et al. 1996; Silverman et al. 1996, 1999, 2000). Using confocal laser scanning microscopy and high-speed video recordings of isolated gill sections, Silverman et al. (1999) concluded that the movement of cirri in *Mytilus edulis* was essential for successful capture of small, bacterial-sized (1 μm) particles although they could not discriminate between mechanical and hydromechanical interception. This was further supported by the fact that mussels treated with serotonin concentrations that stopped the beat of laterofrontal cirri, but not that of frontal or lateral cilia on the gill filaments, showed a 90% reduction in the rate of removal of bacteria from seawater relative to untreated controls.

Post-settlement scallops undergo major changes in the anatomy of feeding organs, especially the gill, during early development. Ontogeny recapitulates phylogeny as the postlarval gill experiences a gradual transition from a homorhabdic condition, with a single, non-plicate inner demibranch, to a heterorhabdic, plicate, reflected gill consisting of both inner and outer demibranchs (Kingzett 1993; Beninger et al. 1994; Veniot et al. 2003), characteristic of adult scallops (Beninger and Le Pennec, Chapter 3). Lateral and frontal cilia are well developed early on in the gills or postlarval stages, but the latero-

frontal cilia are absent in these early stages (Veniot et al. 2003). It is expected that such profound anatomical changes are associated with differences in gill function: suspension-feeding appears to be relatively ineffective in postlarvae prior to reflection of the demibranchs, as evidenced in *Patinopecten yessoensis* by very low clearance rates at sizes <600 μm in shell height (SH) (Kingzett 1993). Yet little is known about the retention efficiency of the postlarval gill in any bivalve species.

From the gut contents of *P. yessoensis* offered suspensions of fluorescent polystyrene beads either 2, 6, 9, 23 or 55 μm in diameter, Kingzett (1993) determined that postlarvae ~ 300 and 1,000 μm SH were unable to ingest beads of the two largest bead sizes tested, suggesting that the upper limit for capture/ingestion of particles is approximately 20 μm . However, at 300 μm SH scallops were able to ingest approximately equal numbers of 2 and 6 μm beads when offered at the same concentration. Thus, retention efficiency differs between early postlarvae and adult scallops. Firstly, postlarvae appear to have a lower maximum size limit for particle retention, and secondly, despite the absence of laterofrontal cilia on gill filaments, postlarvae appear to be capable of effectively capturing small 2 μm particles. One of the limitations in Kingzett's study is that the different bead sizes were not fed to the animals simultaneously, thus precluding accurate measures of retention efficiency. It is important to note that measures of gut content do not allow differentiation of the particle retention/capture per se, but reflect the integration of feeding processes leading to ingestion: retention-transport-selection-ingestion. Confirmation of effective retention of small (1–2 μm) particles by the postlarval scallop gill, which lacks laterofrontal cilia, may challenge previous suggestions that these cilia are prerequisite for small-particle capture in suspension-feeding bivalves (Riisgård et al. 1996; Silverman et al. 1996, 1999, 2000). However, it is difficult to make direct comparisons between the mechanics of particle capture of early scallop postlarvae and adults, as the morphology of the gills differs markedly between the two stages.

7.2.4 Feeding Rates

The allometric relationship between clearance rate and body size (tissue dry weight) for several pectinid species is shown in Table 7.1. The weight exponent is variable, ranging from 0.58 to 0.94, with a mean of 0.7, which is within the range published for other bivalves (Bayne and Newell 1983). The allometric exponent was found to be considerably higher (mean = 0.92) in larvae and juveniles (up to ~10 mm) of the bay scallop, *Argopecten irradians concentricus* (Lu and Blake 1997) than that reported for adult pectinids. The relationship between clearance rate (CR, in $\mu\text{L hr}^{-1}$) and total body ash-free dry weight (AFDW, in mg) in these early development stages at 25°C and a near-optimum food concentration of 20 cells T-ISO μL^{-1} was described by the equation:

$$\text{CR} = 56.565 \cdot W^{0.931}, \text{ or when expressed in terms of shell height (H, in mm) as:}$$

$$\text{CR} = 1.051 \cdot H^{2.479} \quad (1)$$

Table 7.1

Parameters of the allometric relationship between clearance rate (CR; L h⁻¹) and tissue dry weight (W; g) according to the equation $CR = aW^b$, in several pectinid species.

Species	Size range (g flesh dry wt.)	Temp. (°C)	a	b	Source
<i>Chlamys islandica</i>	0.004–7.0	3.4	3.9	0.60	Yahl 1980
<i>Chlamys hastata</i>	1.8–2.2	12.8	0.145	0.943	Meyhofer 1985
<i>Placopecten</i>	1.8–42	5.5–8.5	0.616	0.76	MacDonald &
<i>magellanicus</i>		10–12	1.318	0.60	Thompson 1986
(10 m depth)		8–10	0.891	0.66	
"	0.016–0.6	10	3.435	0.855	Manning 1985 ¹
<i>Argopecten</i>	0.05–4.2	10–26	5.827*	0.584	Kirby-Smith 1970
<i>irradians</i>	0.7–4.1	22–26	4.742	0.82	Chipman & Hopkins 1954 ²
<i>concentricus</i>					
<i>Argopecten</i>	0.1–5.7	12	2.45	0.80	Navarro & González 1998
<i>purpuratus</i>					

* Assuming 85% water content of tissues;

¹ Clearance rate determined with *Isochrysis galbana* (3.5 µm) and thus underestimates pumping rate;

² Calculated by Winter (1978).

Weight-normalised clearance rates (volume of water cleared of particles per unit time by an animal of standard tissue weight) of various pectinid species are shown in Table 7.2. It is generally difficult to make meaningful interspecies comparisons of feeding rates derived from studies differing in methodology and experimental conditions. This is especially true given that clearance rates are extremely sensitive to changes in food quality and quantity. Declining salinities (between 27 and 18 ppt) have also been shown to markedly reduce clearance rates in the Chilean scallop *Argopecten purpuratus* (Navarro and González 1998). Physiological rates of scallops are generally very susceptible to the negative effects of low salinities, as they are unable to maintain prolonged valve closure and thus cannot effectively isolate themselves from the environment. Interspecific comparisons in feeding rates are therefore best carried out from studies, which employ identical experimental protocols on a wide variety of bivalve species. For example, Meyhöfer (1985) found that weight-standardised pumping rates were highest for two filibranch species, the scallop *Chlamys hastata* (0.145 L h⁻¹) and mussel *Mytilus californianus* (0.133 L h⁻¹), followed by *Clinocardium nuttallii* (0.051 L h⁻¹) and finally by *Macoma nasuta* (0.0014 L h⁻¹), a deposit-feeder capable of facultative suspension-feeding. When *Mya arenaria* and *Placopecten magellanicus* were simultaneously exposed to various concentrations of particles scallops displayed higher weight specific

Table 7.2

Weight-standardised clearance rates (= pumping rates) (CR_s ; $L h^{-1} g$ dry tissue weight $^{-1}$) of various pectinid species. $CR_s = CR_e \cdot (W_e/W_s)^b$, where CR_e and W_e are the clearance rate and tissue dry weight of the experimental animal, $W_s = 1 g$ standardised weight and b is the exponent of the allometric relationship between CR and W .

Species	Temp. (°C)	Suspension	CR_e	Source
<i>Chlamys hastata</i>	12.8	Direct measurement w/ thermistor flowmeter	0.145	McYhøfer 1985
<i>Chlamys islandica</i>	3.4	17 μm polystyrene particles, 1,000–2,000 mL^{-1}	3.09	Vahl 1980
<i>Chlamys opercularis</i>	11–13	Natural seston + algae	13.589 ^a	Vahl 1972
<i>Chlamys opercularis</i>	5	<i>Dunaliella euchlora</i> , 8,000–	1.64	McLusky 1973
	10	10,000 cells mL^{-1}	3.23	
	20		5.90	
<i>Pecten (Chlamys) opercularis</i>	10–13	Mixed algal suspension, 0.02–0.3 mg organic DW L^{-1}	14	Mohlenberg & Riisgård 1979
<i>Pecten furtivus</i>	10–13	"	31	"
<i>Placopecten magellanicus</i>	10–12	Natural seston, 5–10 mg DW L^{-1}	0.871–1.318	MacDonald & Thompson 1986
<i>Argopecten irradians concentricus</i>	22–26	<i>Nitzschia</i> (850–8,000 cells mL^{-1}) or <i>Chlamydomonas</i> (28,000 cells mL^{-1})	4.742	Chipman & Hopkins 1954
<i>Argopecten i. concentricus</i>	10–26	<i>Nitzschia</i> $1 \times 10^5 - 5 \times 10^5$ cells mL^{-1}	5.82	Kirby-Smith 1970
	5		1.75	
<i>Argopecten i. concentricus</i>	21	<i>Thalassiosira pseudonana</i> , 50,000–340,000 cells mL^{-1}	4.022	Palmer 1980
		<i>Dunaliella tertiolecta</i> , 10,000–30,000 cells mL^{-1}	(0.31–8.78)	
			5.684	
			(0.65–11.90)	
<i>Argopecten i. irradians</i>	22	<i>Thalassiosira weissflogii</i> 1,200 cells mL^{-1}	10.333	Kuenstner 1988
		4,800 cells mL^{-1}	4.707	
		12,000 cells mL^{-1}	1.387	
<i>Argopecten purpuratus</i>	12	<i>Isochrysis galbana</i> 30,000 cells mL^{-1}	2.6	Navarro & González 1998
<i>Argopecten purpuratus</i>	16–20	<i>Isochrysis galbana</i> + <i>Chaetoceros gracilis</i> 30,000 cells mL^{-1}	2.1 ^b	Navarro et al. 2000

^a Assuming 85% water content of tissues and weight exponent of 0.7

^b Calculated based on a weight exponent of 0.7

clearance rates than clams, especially at concentrations less than 7.0 mg L^{-1} (Bacon et al. 1998). Møhlenberg and Riisgård (1979) compared feeding rates of thirteen bivalve species and reported clearance rates considerably higher than those from previous studies. Weight-standardised clearance rates of the two scallops, *Pecten furtivus* and *Pecten (Chlamys) opercularis*, based on only three measurements (Table 7.2), were comparable only to those of *Mytilus edulis* but were generally two to five times higher than those of other bivalves included in the study.

Feeding rates in bivalves, including pectinids, have also been shown to be influenced by chemical compounds such as metabolites extracted from cultured microalgae. There are several examples of bivalves exhibiting chemosensory abilities, with some dissolved phytoplankton metabolites typically producing inhibitory feeding responses as in the case of the blue mussel *Mytilus edulis* (Ward and Targett 1989). Stimulatory responses are much rarer but have been observed for clearance and ingestion rates in *Placopecten magellanicus* when scallops were exposed to metabolites from the diatom *Chaetoceros muelleri* Lemmermann (Ward et al. 1992). A microalgal diet supplemented with a lipid emulsion also had a stimulatory effect on clearance rates in *Argopecten purpuratus* (Navarro et al. 2000). A better understanding of the capability of bivalves to detect and respond to chemical cues has interesting implications for research on artificial diets possibly making them more palatable and more readily ingested by the bivalves.

It has recently been discovered that 6–15 μm ciliated and non-ciliated epithelial cells can be released from the pallial cavity of sea scallops *Placopecten magellanicus* (MacDonald et al. 1995; Potter et al. 1997). Release of a large number of these cells may lead to an estimate of negative clearance rates, i.e., higher concentrations of suspended particles after exposure to the bivalve than in the original suspension. Exfoliation of these cells has also been observed, although not quantified, for the blue mussel *Mytilus edulis* and the eastern oyster *Crassostrea virginica* (MacDonald, pers. obs.) and *Mercenaria mercenaria* (Brieeij, pers. obs.). Exfoliation of small numbers of cells may be a consequence of cellular turnover and normal physiological function. However, environmental stressors, such as unseasonably elevated water temperatures are known to increase the rate of cell release to the point that tissue damage results (Potter et al. 1997). It is not known what other stressors may cause increased exfoliation rates in bivalves or the short- and long-term consequences that any potential damage will have on the efficiency of particle retention and transport on the gill.

7.2.5 Clearance Rate in Relation to Food Concentration

When exposed to increasing suspended particulate loads, suspension-feeding bivalves are able to control the total amount of material ingested by: a) reducing the time spent pumping (discontinuous feeding behaviour), b) reducing their clearance rates, and/or c) increasing the amount of material rejected in pseudofeces (Foster-Smith 1975a, b; 1976). Palmer (1980) characterised the bay scallop, *Argopecten irradians*, as a continuous feeder, that showed no rhythmic cycles in clearance rates in response to tidal cycles or photoperiod. In contrast, Mathers (1976) suggested that the feeding activity of *Pecten maximus* was cyclical in response to changes in tidal flow. He indicated, however, that

this was caused by strong reversible tidal currents and was probably not an endogenous feature of the scallop's feeding behaviour. Existing evidence, although limited to a few pectinid species (see below), suggests that scallops primarily regulate ingestion and compensate for short-term changes in food supply through fluctuations in clearance rate (mechanism b).

A strong inverse, linear relationship between clearance rate and algal concentration has been described for adult bay scallop *Argopecten irradians concentricus* (Palmer 1980; Fig. 7.3A). Clearance rates are reduced by 95% over the concentration range 0.94 to 9.4 mg dry wt. L⁻¹ (1.23 to 12.3 × 10⁶ μm³). Therefore, above a threshold concentration of ca. 2 mg dry weight L⁻¹, algal ingestion rate becomes independent of concentration (Fig. 7.3B). Similarly, clearance rates of juvenile *A. i. irradians* were found to decline by 85% with a 10-fold increase in the concentration of *Thalassiosira weissflogii* (1.2 to 12 cells μL⁻¹ = 0.83 to 8.3 × 10⁶ μm³ mL⁻¹) (Kuenstner 1988). Cahalan et al. (1989) reported a lower reduction (56%) for juvenile bay scallops exposed to concentrations between 7.5 and 68 cells μL⁻¹ (0.25 to 2.28 × 10⁶ μm³ mL⁻¹) of *Isachrysis galbana*, an alga that is incompletely retained by the pectinid gill. Lu and Blake (1997) found that clearance rates of juvenile bay scallops, *A. i. concentricus* (~0.6 to 9.8 mm in shell height) declined exponentially with increasing algal concentration ranging between 5 and 50 *I. galbana* cells μL⁻¹ (Fig. 7.3C). Ingestion rate, however, increased with increasing cell concentration, and approached an asymptote or maximum ingestive capacity at ~ 50 cells μL⁻¹ (Fig. 7.3D). It is interesting to note that larvae reached this asymptote at a lower cell density (~ 20 cells μL⁻¹) than larger juveniles, suggesting that the latter are better able to handle dense algal assemblages than larval stages. An optimum cell density of 20 cells μL⁻¹ was established for growth of juveniles of this species, as higher concentrations (up to 50 cells μL⁻¹) did not significantly increase growth rates (Lu and Blake 1996). Similarly, growth rates in shell height and tissue weight of juvenile *Nodipecten subnodosus* (lion's paw scallop) were maximised at the lowest algal concentration tested (33 T-ISO cells μL⁻¹). Growth was comparable at 33 and 66 T-ISO cells μL⁻¹, and declined at 100 cells μL⁻¹ (García-Esquivel et al. 2000).

Clearance rates for *Placopecten magellanicus* and *Mya arenaria* both significantly declined as concentration and organic content of microalgae and silica mixtures increased between 1 and 14 mg L⁻¹ (Bacon et al. 1998). However, other studies on *P. magellanicus* have reported clearance rates to be independent of particle concentration between 1–15 mg L⁻¹ and this may be related to the type of particles used in the individual studies (Cranford and Grant 1990; Cranford and Gordon 1992; MacDonald and Ward 1994; Cranford et al. 1998). Several authors have emphasised the potential interactions between seston concentration and flow velocities on the feeding response of scallops (Wildish et al. 1992; Wildish and Saulnier 1993; Pilditch and Grant 1999a). How scallops respond to changes in particle concentration may not only depend on variations in flow speeds, but also on whether or not the flow is increasing or decreasing in velocity (Pilditch and Grant 1999a). These authors observed a decline in scallop clearance rates when phytoplankton concentration increased and flow velocities were increasing but found clearance rates to be independent of concentration, albeit reduced by 50%, when flow velocities were decreasing. They concluded that the scallop's short-term (hours) feeding history may be

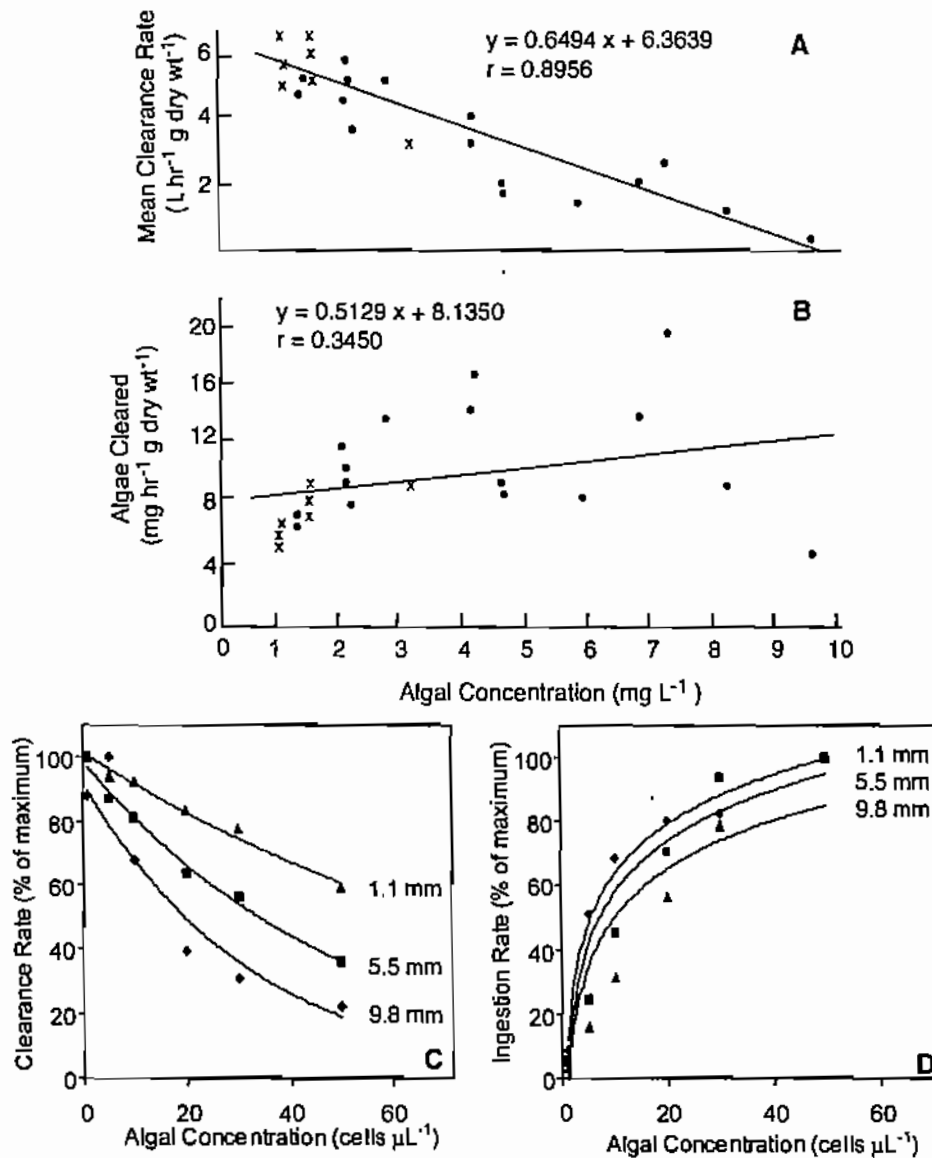


Figure 7.3. *Argopecten irradians concentricus* adults. Relationship between algal concentration (mg dry weight L⁻¹) and clearance rate (A) and amount of algae cleared (B). Each point represents the mean value for one experiment - that is for 5 to 32 hourly measurements; algae used were *Dunaliella tertiolecta* (x) or *Thalassiasira pseudonana* (•) (from Palmcr 1980). *Argopecten irradians concentricus* juveniles. Relative clearance rate (C) and algal ingestion rate (D) as a % of the maximum of bay scallops ranging from 1.1 to 9.8 mm shell height at 25°C (calculated from data in Lu and Blake 1997). Data fitted to exponential (C) and logarithmic functions (D).

influential in determining its response to variations in the food supply and that concentration was the primary determinant of scallop clearance rate over a range of fluxes (Pilditch and Grant 1999a). See the section 7.2.10 on "Effects of flow on feeding and growth" for a more detailed discussion on the effects of flow on feeding activity.

Hawkins et al. (2001) have also emphasised the importance of the amount of suspended material in regulating clearance rates in the scallop *Chlamys farreri*, in particular the volume and composition of the seston. They found that clearance rate varied in a unimodal relation with short-term changes in seston abundance and was primarily dependent upon seston availability in terms of total volume rather than any gravimetric estimate of mass. They suggested morphometric limits to feeding behaviour, most likely constraints within the digestive system rather than on the gills. There is also an interaction between seston volume and seston quality with 58% of the variance in clearance explained by particle volume and chlorophyll concentration combined, in contrast to only 47% for seston volume alone (Hawkins et al. 2001). These authors observed over an order of magnitude variation in clearance rates and concluded that this potential for feeding adjustment would be of greatest physiological and ecological importance at low food availabilities because it would have proportionally more impact on net energy balance.

7.2.6 Influence of Temperature on Feeding Rates

The effect of temperature on feeding activity has been investigated in few pectinid species. Clearance rates of *Argopecten irradians concentricus* were independent of temperature between 10 and 26°C, but were markedly depressed at 5°C (Fig. 7.4B; Kirby-Smith 1970). Since the increase in metabolic expenditure between 10 and 26°C is not offset by a parallel increase in feeding activity, the irrigation efficiency (litres pumped per mL of O₂ consumed) decreases rapidly with increasing temperature above 10°C (Fig. 7.4A). Irrigation efficiency is generally assumed to be inversely related to the maintenance food requirement (that at which growth = 0) (Newell and Kjøfoed 1977). Therefore, it is expected that bay scallops will sustain a maximum energetic gain from the environment between 10 and 20°C, and that they will be severely stressed, and exhibit rapid weight loss, under suboptimal conditions of poor food supply and high temperature. Such conditions might arise due to an increase in water temperatures during winter (caused by thermal pollution) without a concomitant increase in food levels. The scallops' dependence on higher food levels at high temperatures is exemplified by the finding that growth rate of juveniles at lower temperatures (10 to 16°C) is independent of chlorophyll-*a* levels within the range of naturally occurring concentrations (0.5 to 5.5 µg L⁻¹), but becomes increasingly correlated with chlorophyll levels at higher temperatures (22 to 28°C) (Kirby-Smith 1970; Kirby-Smith and Barber 1974).

In contrast to the above findings for adults, clearance rate of juvenile *A. i. concentricus* was an increasing function of temperature between 10 and 30°C (Fig. 7.4D), which approximates the temperature range of this species in its natural habitat in Florida, USA (-12 to 32.5°C) (Lu and Blake 1997). Thus juveniles may be better able to exploit

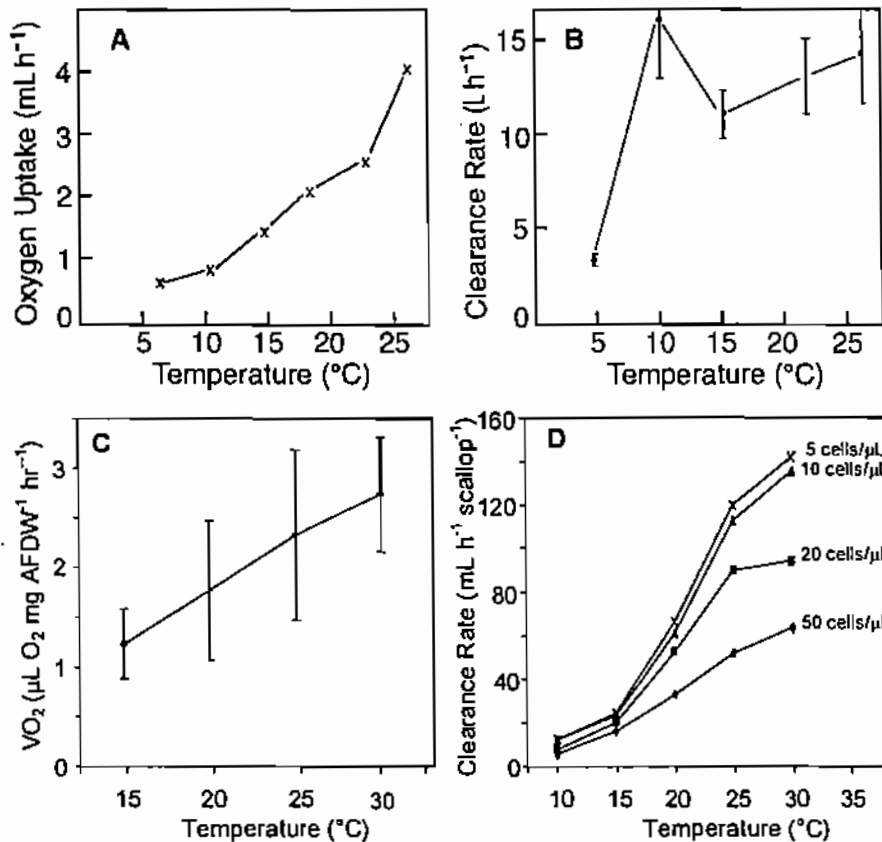


Figure 7.4. *Argopecten irradians concentricus* adults. Mean oxygen uptake (A) and clearance rate (B) of a standard animal 20 g in wet tissue weight (calculated from data by Kirby-Smith (1970; Tables VII and VIII for scallops fed *Nitzschia* sp.; vertical bars = standard errors). *Argopecten irradians concentricus* juveniles. C. Weight-specific mean oxygen uptake (\pm SD) vs. temperature of juveniles 3.5 to 5 mm in shell height (plotted from Lu et al. 1999). D. Clearance rate vs. temperature of 5 mm juveniles at different *Isachrysis galabana* cell concentrations (plotted from Table 3 in Lu and Blake 1997).

higher temperatures when these coincide with an abundant food supply than adults. As in adults, oxygen uptake in juveniles increased with increasing temperature (Fig. 7.4C).

In *Chlamys opercularis* the response of clearance rates to temperature is similar to that of adult bay scallops. Feeding rates are independent of acclimation temperature between 10 and 20°C, but drop markedly at 5°C (Q_{10} from 5 to 10°C = 3.87; Q_{10} from 10 to 20°C = 1.83; McLusky 1973). Unlike bay scallops, however, oxygen uptake remains

constant between 10 and 20°C, allowing conservation of energy at higher temperatures. This strategy is similar to that displayed by *Mytilus edulis* (Bayne et al. 1976). In *Placopecten magellanicus* from Newfoundland, clearance rates were significantly correlated with ambient temperature in both shallow (10 m) and deep water (31 m) populations between 0 and 12°C. In the latter, clearance rates were also correlated with food availability (energy content of seston) (MacDonald and Thompson 1986). In juveniles of the subtropical scallop, *Argopecten ventricosus-circularis*, routine oxygen consumption rate increased steadily between 12 and 28°C, whereas clearance rate and algal ingestion rate were maximised between 19 and 20°C, and declined above and below this temperature range (Sicard et al. 1999). This physiological optimum temperature range was confirmed by determining that shell growth was also maximised at 19–22°C. Furthermore, scope for activity, defined as the difference between routine (active) VO_2 and standard (basal) VO_2 determined for fed and starved animals respectively, was also maximised at 19°C. This illustrates that physiological rates can be very useful in predicting optimum ranges of environmental factors for growth.

Marine suspension-feeders inhabiting coastal waters typically pump 15 L or more of water per equivalent mL of O_2 consumed (Jørgensen 1975). A mean irrigation efficiency or convection requirement of 17 (8 to 25) was reported for *Pecten latiauratus* (Jørgensen 1960), and values ranging from 15 (at 5°C) and 39 (at 20°C) were found for *Chlamys opercularis* acclimated to laboratory conditions (McLusky 1973). A considerably higher mean value of 79 (range = 63–97) was reported for the same species by Vahl (1972). A maximum irrigation efficiency of 8.8 L mL⁻¹ O_2 was obtained for juvenile *A. ventricosus-circularis* at 19°C (Sicard et al. 1999).

7.2.7 Pseudofeces Production, Pre- and Post-ingestive Particle Selection

Pseudofeces production has been shown to be an important pre-ingestive mechanism because it facilitates the process of particle selection whereby less nutritious particles may be rejected and the quality of the ingested material improved proportionately. The labial palps are currently believed to be the principal site of pre-ingestive particle selection via pseudofeces production in bivalves, although the evidence remains inconclusive. Their role in particle selection is supported by Kiørboe and Møhlenberg's (1981) finding that selection efficiency is positively correlated with a relative index of palp size (ratio of palp area to clearance rate) and other indirect evidence. Direct endoscopic observations of the pectinid palps to confirm their role in particle selection have so far proved elusive due to their extreme sensitivity and obstruction by the complex, arborescent lips (Beninger et al. 1992). Morphological evidence of their role in selection, e.g., presence of sensory structures on the ridged surface, was found to be lacking in both *P. magellanicus* and *Chlamys varia* (Beninger et al. 1990). Selective rejection of particles may also occur on the bivalve heterorhabdic gill, e.g., via rejection of material from the ventral gill margin [most notably in oysters, *Crassostrea virginica* (Ward et al. 1997, 1998b)]. Endoscopic observations indicate that even in pectinids, which lack a ventral groove, particles bound in mucus may move ventrally along ordinary filaments, and break off as pseudofeces as they move anteriorly (Beninger et al. 1992). This type of transport is only observed at

high particle concentrations or when the scallop's ingestive capacity is overloaded. Pseudofeces in adult scallops are ejected from the pallial cavity via valve clapping. Particle selection through the production of pseudofeces has been demonstrated in studies on feeding activity using laboratory diets and cultured algae mixed with sediments and assemblages of natural particles found in the environment (Kjørboe et al. 1980; Newell and Jordan 1983; Cranford and Gordon 1992; Iglesias et al. 1992; MacDonald and Ward 1994; Shumway et al. 1997; Bacon et al. 1998).

Scallops, however, typically do not produce copious amounts of pseudofeces, as compared to mussels and oysters. Bay scallops, *Argopecten irradians*, rejected only up to 25–35% of the algal cells filtered when exposed to bloom concentrations (0.55 to 1.46 x 10⁶ cells mL⁻¹ = 2.4 to 6.4 mg dry weight) of the pelagophyte *Aureococcus anophagefferens* (= *anophagefferens*) (Kuenstner 1988). MacDonald and Thompson (1986) reported that *Placopecten magellanicus* produced no pseudofeces when fed natural seston levels of 5 to 10 mg dry weight L⁻¹. In contrast, *Mytilus edulis* initiates pseudofeces production at seston concentrations between 2.6 and 5.0 mg L⁻¹ depending on body size (Widdows et al. 1979). It has often been thought that bivalves only produce pseudofeces when exposed to concentrations of particles above a certain threshold value. However, studies by Ward et al. (1993) using endoscopic techniques have shown that pseudofeces are produced intermittently during the feeding process in many bivalves regardless of the concentration. It is likely that some pseudofeces are being produced even at low concentrations, although not in sufficient concentrations to be readily noticed or quantified unless specialised techniques are used.

The efficiency of particle selection in marine bivalves has been shown to be quite variable both within and among species, and is most likely related to palp size, seston conditions, or which indicator of seston quality is used to measure efficiency (Kjørboe and Møhlenberg 1981; Iglesias et al. 1992; Urrutia et al. 1996). Peetiniids, like other marine bivalves have been shown to have the capability of rejecting poorer quality particles and improving the quality of the ingested ration. Recent studies on *Placopecten magellanicus* have confirmed the capability of this scallop species to reject particles of poorer quality preferentially based on both the organic composition of particles and the concentration of chlorophyll-*a* containing particles in the natural seston (Cranford and Gordon 1992; MacDonald and Ward 1994; Bacon et al. 1998). Results for *P. magellanicus* were consistent with those reported for other bivalve species such as *Mytilus edulis* and *Cardium edule* respectively, where the efficiency of selection diminished as the quality of the seston mixture declines (Bayne et al. 1993; Navarro et al. 1994) (Fig. 7.5). Both of the studies on *P. magellanicus* by MacDonald and Ward (1994) and Bacon et al. (1998) reported that the overall quantitative selection process, measured by the compensation index, was not effective at the lowest quality diets tested. Compensation index (CI) not only takes into consideration the quality of seston and pseudofeces, like most other indicators of sorting efficiency, but is unique because it takes into consideration quantities of material cleared and rejected. It is calculated as $CI = (I_Q / SES_Q) - 1$, where I_Q is the quantity of chlorophyll-*a* ingested and SES_Q is a measure of the quality of the seston, e.g., chlorophyll-*a* concentration. CI is the same as the index calculated by Navarro et al. (1992) and the benefit ratio (BR) given by Iglesias et al. (1992). In fact, for very poor-

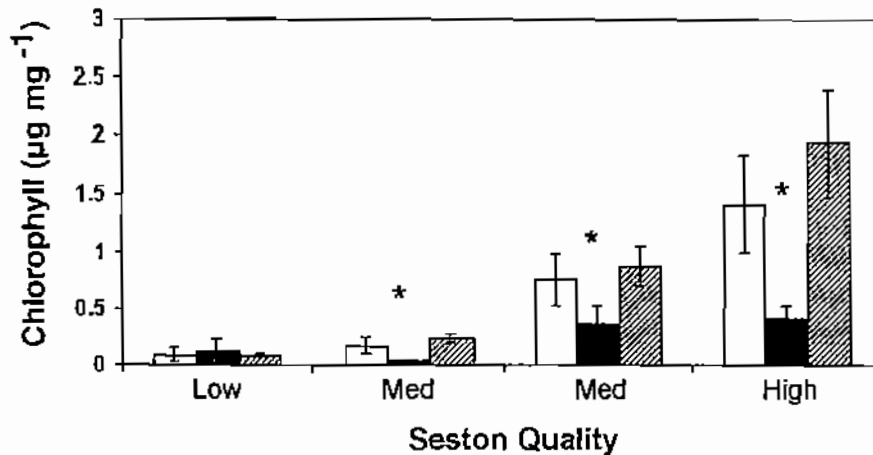


Figure 7.5. Comparison of the quality of material in the seston (SES_Q, white box), with that in pseudofeces (PS_Q, black box) and that ingested (I_Q, striped box) by *Placopecten magellanicus* during each of the experimental periods. Data are from MacDonald and Ward (1994) and presented as mean \pm SD, see their text for details.

quality diets, there may have been some evidence of organic enrichment of the pseudofeces rather than the ingested ration, or negative selection. Recognising that particle selection through the production of pseudofeces is a process of rejection MacDonald and Ward (1994) proposed the following explanation for negative selection. When poor-quality particles dominate the seston scallops may improve the quality of the material ingested by attempting to reject a high proportion of these particles. However, it may not be possible to retain the few relatively high-quality particles while rejecting the majority of low quality ones. This high rate of rejection may overwhelm the capacity of the system and result in non-selection or possibly even negative selection.

Both studies on particle selection in *Placopecten magellanicus* reported a negative relationship between compensation indices and clearance rates. This suggests that particle sorting on the labial palps is one of the limiting steps in the feeding process. In order for *Placopecten magellanicus* to increase the quality of the material ingested above 20% by particle selection through pseudofeces production they must reduce the volume of material entering the palps by reducing the clearance rate (MacDonald and Ward 1994). The strategy adopted by *P. magellanicus* when exposed to seston that varies in concentration and quality is to have relatively high clearance rates at low particle concentrations and as concentration increases significantly reduce clearance rate and increase the amount of pseudofeces produced. They rely on their pre-ingestive selection capabilities to reject poorer quality particles and enhance the quality of material ingested and maintain ingestion at higher concentrations.

It is well established that bivalves, including scallops, can selectively reject inorganic, sediment particles from mixed algal-sediment suspensions (see section on "Effects of

suspended sediments on feeding and growth". Kjørboe and Møhlenberg (1981) determined the efficiency of particle selection of ten species of suspension-feeding bivalves fed algal-sediment mixtures from the ratio of chlorophyll-*a* to dry weight in the suspension and pseudofeces. The only pectinid tested, *Aequipecten opercularis*, showed an intermediate selection efficiency (= 5.4). A maximum efficiency of 15.8 was measured for *Spisula subtruncata*, and a minimum value of 2.9 for *Mytilus edulis* from a low turbidity environment. A low selection efficiency (SE = 2.7) was also determined for *Placopecten magellanicus* fed a mixture of algae and bentonitic clay (Cranford and Gordon 1992). Values obtained in the two studies are not strictly comparable, however, as Cranford and Gordon (1992) based their SE estimates on data obtained from retained rather than suspended particles. Low capacity for particle selection between inorganic and organic particles was confirmed when sea scallops were fed natural resuspended sediment containing benthic diatoms (Cranford and Grant 1990).

Bivalves are also capable of discriminating among algal cells of similar size in their diet. Using flow cytometry, Shumway et al. (1985) showed that the diatom *Phaeodactylum tricorutum* was selectively rejected in pseudofeces of *Placopecten magellanicus* when this alga was fed in combination with the dinoflagellate *Prorocentrum* sp. and the cryptomonad *Chroomonas salina*. Similarly, *Thalassiosira pseudanana* was preferentially rejected in pseudofeces when present in a mixed suspension with *C. salina*, *Prorocentrum* and the toxic dinoflagellate *Protogonyaulax tamarensis* (clone GT429) (Shumway and Cucci 1987). Differential clearance of various algal clones in a mixed suspension was also demonstrated using flow cytometry in three species of 1–2 mm juvenile scallops (Shumway et al. 1997). Selective removal from suspension was greatest in *Patinopecten yessoensis*, which showed significantly higher clearance rates for *Chroomonas salina* (clone 3C, ~6.1 µm), *Phaeodactylum tricorutum* (PHAEO, ~5.0 µm) and especially *Amphidinium carterae* (AMPHI, ~10 µm), than for *Isochrysis galbana* (T-ISO, 3–6 µm) or *Chaetoceros muelleri* (CHGRA, 4–9 µm). Lowest clearance rates were observed in all three scallop species with the smallest alga tested, a 2–3 µm unidentified prasinophyte (Omega 48). However, in *P. yessoensis*, algal size alone was not sufficient to explain the differences in clearance rate observed.

Selection in the gut or digestive gland-stomach complex is less well known, but it is believed that some bivalves can differentiate between particles within the gut and preferentially digest those particles that give the most nutritional benefit (Brieeij et al. 1984; Shumway et al. 1985; Lopez and Levinton 1987; Bayne et al. 1993; Wang and Fisher 1996). Postingestive selection may occur either by the retention of some particles longer than others in the stomach so that extracellular digestion has more time to act, or by directing some particles to the digestive gland for intracellular digestion. Crauford et al. (1998) found that two sizes of microspheres were passed at different rates through the gut of the sea scallop *Placopecten magellanicus*. While postingestive sorting in bivalves has been confirmed for several species, few studies have attempted to isolate the factors influencing selection among different particles presented simultaneously. *P. magellanicus* has been shown to be capable of distinguishing between particles of different size and density by retaining larger particles longer than smaller ones and lighter particles longer than denser ones (Brilliant and MacDonald 2000). These authors further showed that

P. magellanicus has well-developed postingestive sorting capabilities and could sort organic from inorganic particles and some particles based solely on chemical properties (Brillant and MacDonald 2002). These scallops retained protein-coated beads in the gut longer than uncoated beads of identical diameter and density.

7.2.8 Absorption Efficiency

Few studies have attempted to determine the utilisation efficiency with which the ingested ration is absorbed of algal diets by pectinids. Available data suggest, however, that scallops do not differ markedly from other bivalves in their absorption capabilities. Using ^{14}C labelling techniques Peirson (1983) found that adult *Argopecten irradians concentricus* absorbed most algal species tested with absorption efficiencies (AE) ranging between 78.1 and 89.9%. These values represent maximum efficiencies since they were determined at relatively low mean algal rations ($= 2 \text{ mm}^3 \text{ L}^{-1} = 468 \mu\text{g C L}^{-1}$). Only the chlorophyte, *Chlorella autotrophica*, was inefficiently absorbed (AE = 17.4%), as previously observed both in adult and larval oysters (Floyd 1953; Babinehak and Ukeles 1979). Low absorption efficiencies are generally attributed to the indigestible cell wall of this alga. The diatom, *Thalassiosira pseudonana* used in Peirson's study yielded the highest absorption efficiencies (89.9%). This is almost identical to a mean value of 89.7% obtained for bay scallops fed *T. weissflogii* by Kuenstner (1988) with the twin ^{14}C - ^{51}Cr radiotracer method. Veliger larvae of *Pecten maximus* inefficiently ingested and digested *Dunaliella primolecta*, and were unable to digest *Platymonas (Tetraselmis) suecica* (Le Pennec and Rangel-Dávalos 1985).

High absorption efficiencies are not sufficient to support growth of bivalves, and thus cannot be used as single predictors of food value. For example, Peirson (1983) reported a high absorption efficiency (83.3%) for *Dunaliella tertiolecta*, an alga known to support poor growth of oysters due to its deficiency in essential polyunsaturated fatty acids (Langdon and Waldock 1981). A high efficiency (90.6%) was also measured for *Aureococcus anophagefferens* (Kuenstner 1988); a species which caused starvation of bay scallops at bloom concentrations under field conditions (Bricelj et al. 1987a). Grant and Cranford (1989) reported that aged kelp (*Laminaria*) detritus was absorbed with high efficiency (70–80%) but did not support growth of adult *Placopecten magellanicus*.

A commonly used technique to estimate absorption efficiency is the Conover (1966) method which is based on the assumption that the organic and inorganic components must be ingested in the same proportions that occurs in the food supply (no ingestion selectivity). Adjustments must be made to the estimate of absorption efficiency if the bivalve is rejecting poorer quality particles through the production of pseudofeces otherwise the assumptions of the Conover ratio are violated. While some studies have shown that absorption efficiency increased with particle concentration, several recent studies on *Placopecten magellanicus* have shown absorption efficiency to be much better correlated to the quality than the concentration of the seston (Cranford 1995; Grant et al. 1997; Cranford et al. 1998; MacDonald et al. 1998). In many of these studies scallops were exposed to natural concentration of seston in the field or mixtures of microalgae and inorganic particles in the laboratory to mimic seston rather than various concentrations of

pure cultured microalgae alone. Absorption efficiency in field and laboratory studies consistently increased with the quality of the seston whether percent organics or the concentrations of nitrogen or carbon were used as indicators of quality (Fig. 7.6). Similar relationships between absorption efficiency and diet quality have been reported for *Chlamys islandica*, *Placapecten magellanicus*, *Mytilus edulis*, *M. galloprovincialis*, *Cerastoderma edule*, *Crassostrea gigas* and *Mya arenaria* (Vahl 1980; Bayne et al. 1987; Cranford and Grant 1990; Iglesias et al. 1992; Navarro et al. 1992; Navarro and Iglesias 1993; Hawkins et al. 1998; MacDonald et al. 1998).

Absorption efficiencies in *Argopecten purpuratus* did not significantly increase when the quality of the microalgae was improved by the addition of a lipid emulsion and were observed to decrease from 85 to 27% when carbohydrates were added to the microalgal diet (Navarro et al. 2000). However, clearance rates were stimulated by the diets supplemented with lipids resulting in a significant increase in absorption rates and a several-fold increase in scope for growth. In postlarvae of *A. purpuratus* absorption efficiency (AE) was found to correlate positively with the protein content of a mixed algal diet (*Isachrysis galbana*, T-ISO, and *Chaetoceros neogracile*) which ranged between 48 and 27% of total organics depending on culture conditions (Uriarte and Farias 1995; 1999). Absorption efficiency (AE) was highest (74.6%) when scallop postlarvae were fed the high-protein diet, and dropped to only 30.8% on the low-protein diet of the same algal species. High-protein diets were found to yield higher growth rates and survival of 1.8 mm postlarvae (also associated with high metabolic rates) but not in 6 mm juveniles suggesting that protein requirements may be greater during early scallop ontogeny (Uriarte and Farias 1999). It was also suggested that this transition in substrate utilisation might be associated with the change from a sedentary, byssally attached habit in *A. purpuratus* <5 mm, to a free-swimming mode above this size threshold. With the possible exception of *A. purpuratus*, absorption efficiency in pectinids is very similar to that observed in many other bivalves. There was no significant difference in absorption efficiencies between *P. magellanicus* and *Mya arenaria* when they were exposed simultaneously to a range of particle concentrations and qualities (MacDonald et al. 1998).

A strong and consistent relationship between a physiological response, such as absorption efficiency, and some characteristic of the food supply, such as organic composition can be used to improve the predictive power of numerical models of feeding behaviour and estimate carrying capacity of different environments. Cranford (1995) found that between 74 and 84% of the variance in absorption efficiency could be explained by the variance in food quality, expressed as the percentage of organic matter, C or N. Complete digestive acclimation to dietary conditions in *P. magellanicus* takes several days but its food supply fluctuates considerably over much shorter time scales (Cranford 1995). Rather than adjusting digestive processes in response to frequent dietary fluctuations this species acclimated to the lower quality diet and maintained a high state of digestive acclimation for at least 12 h to enhance absorptive capabilities and energy gain (Cranford 1995). In a seasonal field study of *P. magellanicus* and *Mytilus edulis* Cranford and Hill (1999) did not find good relationships between absorption efficiency and seston organic composition and a suite of environmental conditions were only able to explain

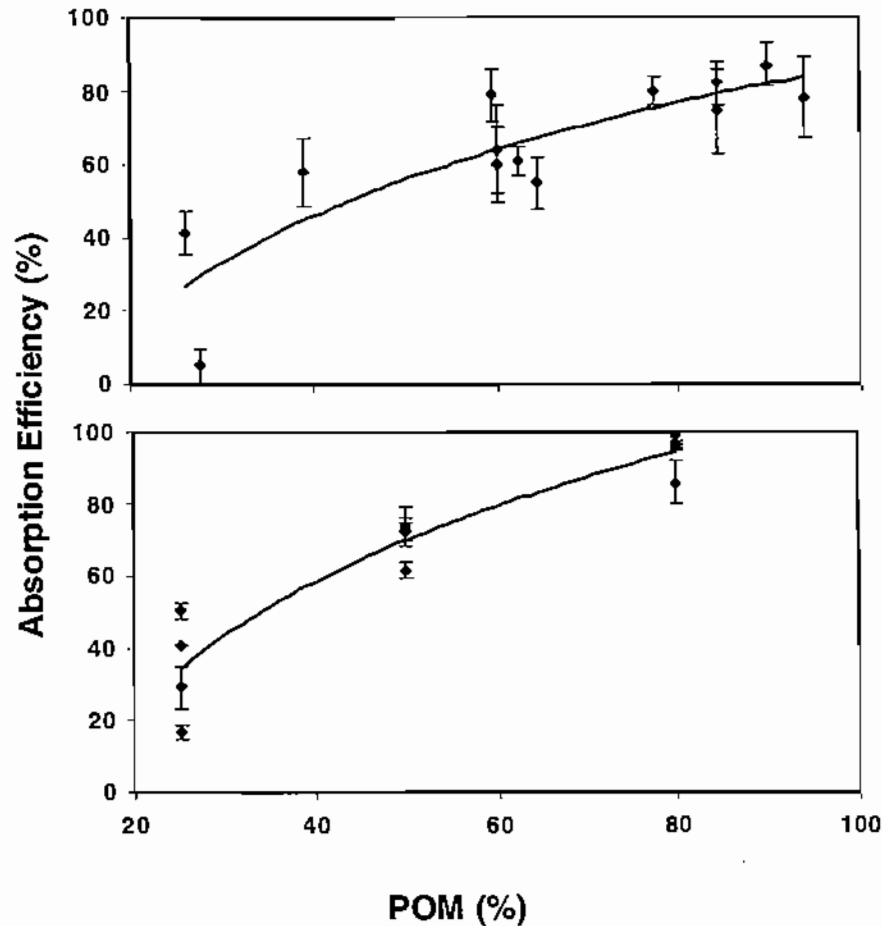


Figure 7.6. *Placopecten magellanicus*. Absorption efficiencies (mean \pm SD) for scallops exposed to (A) natural seston in the field (from Cranford 1995) and (B) mixtures of microalgae and inorganic particles in the laboratory (from MacDonald et al. 1998).

28% of the variation in sea scallop and mussel ingestion rates. This work emphasises the complications associated with predicting feeding and digestion processes in bivalves and the need to have a better understanding of their previous history and other physiological processes such as metabolic demands associated with reproduction, for example (Kreeger 1993; Cranford and Hill 1999).

Absorption efficiency was not significantly influenced by salinity changes ranging from 30 to 18 ppt in *Argopecten purpuratus* (Navarro and González 1998). However, due to the strong inhibitory effect of low salinities on clearance and ingestion rates, absorption rate was highly reduced (by 96%) between 30 and 18 ppt.

7.2.9 Effects of Suspended Sediments on Feeding and Growth

Bivalve species differ considerably in their ability to cope with suspended sediment loads (see discussion by Bricelj and Malouf 1984), which may reduce growth rates by "diluting" the available food. Growth enhancement by low additions (<5–10 mg L⁻¹) of bottom sediments to algal diets were reported for *Mytilus edulis* (Kjørboe et al. 1981) and surf clams, *Spisula subtruncata* (Møhlenberg and Kjørboe 1981), but not for hard clams, *Mercenaria mercenaria* (Bricelj et al. 1984). Bricelj and Malouf (1984) hypothesised that bivalves which regulate ingestion primarily by a reduction in clearance rates (such as hard clams, softshell clams and scallops), are more likely to be vulnerable to high suspended sediment concentrations than bivalves such as mussels, oysters and surf clams which control ingestion mainly by increasing pseudofeces production (provided they are also capable of high ingestion selectivity). Although this simplified classification remains valid, recent work shows that intermediate strategies may also occur, and that the response to suspended sediment concentrations may also vary within a species depending on prevailing seston characteristics (Navarro and Iglesias 1993). A combination of both strategies occurs in *P. magellanicus* in response to mixtures of algae and inorganic, silicate particles (Bacon et al. 1998). Clearance rates declined sharply, and pseudofeces production increased with increasing seston concentration regardless of diet quality (% particulate organic matter, POM). However, sea scallops only rejected in pseudofeces 7 to 14% of the filtered ration, whereas rejection attained 40 to 93% in mussels, *Mytilus edulis* (Bayne 1993; Hawkins et al. 1996) and up to 58% in cockles, *Cerastoderma edule* (Navarro et al. 1994).

Shell growth rates of *Chlamys opercularis* were significantly depressed by moderate concentrations (11 to 37 mg dry weight L⁻¹) of iron ore particles (Richardson et al. 1984). Iron ore suspensions exceeding ca. 25 mg L⁻¹ caused abnormal thickening on the interior surface of shell valves presumably due to failure of the mantle edge to extend fully in the presence of high densities of inorganic particles. Tissue and shell growth rates of juvenile bay scallops, *Argopecten irradians*, were unaffected, however, by natural sediment concentrations between 5 and 44 mg L⁻¹ fed in combination with an algal diet (50 × 10⁶ *Pseudoisochrysis paradoxa* cells L⁻¹) (Korol 1985). Duggan (1973) and Monical (1980) attributed reduced survival and growth of scallops (*Argopecten irradians* and *Hinnites multirugosus*) suspended near the bottom, relative to those at mid-depth, to increased suspended sediment concentrations. Depth-related differences in growth rates of *Argopecten irradians* were investigated by Korol (1985) in central Long Island Sound, N.Y., U.S.A. with contrasting results. Growth rates of bay scallops suspended within the turbidity zone, (1 m above a muddy bottom) were greater than at mid-depth and near the surface during the autumn. Growth enhancement near the bottom was attributed to 3–4 fold higher seston levels at depth relative to surface waters. In this study, chlorophyll and organic content of seston were relatively uniform throughout the water column in the fall, and near-bottom seston levels remained low, below 17 mg L⁻¹. Increased growth near the bottom presumably resulted from the combined effects of resuspension of bottom detrital material and increased availability of surface food particles due to breakdown of stratification at this time of the year. High-frequency characterisation of site-specific

seston quality and quantity and other environmental variables is thus critical in interpreting the effects of resuspended bottom material. A fall-winter study in a nearshore environment in Nova Scotia, Canada which included extensive environmental measurements showed an inconsistent relationship between soft-tissue growth of *P. magellanicus* deployed in cages and distance from the bottom (0 to 200 cm) over time (Emerson et al. 1994). However, by the end of the study period, soft tissue weight was significantly less on the bottom than at ≥ 50 cm above bottom suggesting that high seston loads near-bottom inhibited growth. Temperature and the ratio of particulate to organic to inorganic matter, POM/PIM, were found to be the best predictors of growth.

A diet consisting only of intertidal resuspended sediments was unable to support growth of *Placopecten magellanicus* (Cranford and Grant 1990). Scallops showed lower clearance rates for the suspended sediment diet than for an algal diet offered at a comparable ration, and low absorption efficiency (29% for organic carbon). Although a higher absorption efficiency was measured for sedimentary organic nitrogen (50%), the nitrogen content of sediment was extremely low. Thus negative values of scope for growth were obtained when calculated in terms of both carbon and nitrogen (Grant and Cranford 1991).

Studies on the effects of montmorillonite clays, e.g., bentonite ($\sim 2 \mu\text{m}$ median particle diameter) and attapulgite, the main components of water-based muds used in oil and gas drilling activities, on adult *Placopecten magellanicus*, have contributed to our understanding of the effects of fine-grained sediments in this important commercial species (see also chapter by Cranford in this volume). These clays are biologically inert and thus can be used to mimic fine-grained suspended sediment. Significant reduction in somatic and reproductive tissue growth of sea scallops, and extensive mortalities ($\sim 15\%$ and 45% after 15 and 30 days of exposure, respectively) were documented at only $10 \text{ mg bentonite clay L}^{-1}$ in the presence of ambient food levels relative to controls with no clay addition (Cranford and Gordon 1992). Therefore *P. magellanicus*, which typically inhabits low turbidity environments with seston concentrations $< 2\text{--}5 \text{ mg DW L}^{-1}$ (e.g., Emerson et al. 1994; Grant et al. 1997), is highly intolerant of sediment loading. Higher, transient levels occur due to storm events and tidal and wind-driven bottom resuspension and anthropogenic activities (oil drilling, dredging).

In the presence of an algal diet, clearance rate (CR) of *P. magellanicus* declined exponentially with increasing clay concentration, resulting in 50% reduction at $\sim 6 \text{ mg L}^{-1}$, whereas CR remained constant over the same range of dry weight concentrations of a pure algal diet (Fig. 7.7A, B). Low clay concentrations, $< 1 \text{ mg L}^{-1}$, enhanced clearance rates relative to controls as observed in mussels and oysters. Increasing bentonite concentrations resulted in an exponential decline in ingestion rate of organic matter thus demonstrating a food dilution effect (Fig. 7.7C), and caused a decline in absorption efficiency when added to natural seston (Fig. 7.8A). Physiological responses returned immediately to control levels upon removal of bentonite from the suspension. Integration of physiological data allowed calculation of a negative scope for growth at bentonite concentrations $\geq 8 \text{ mg L}^{-1}$ (Fig. 7.8B). Negative effects on growth of bentonite can thus be attributed to the combined effects of reduced ingestion rate of organic matter and reduced absorption efficiency, which lead to reduced absorption rate. Reduced metabolic rate,

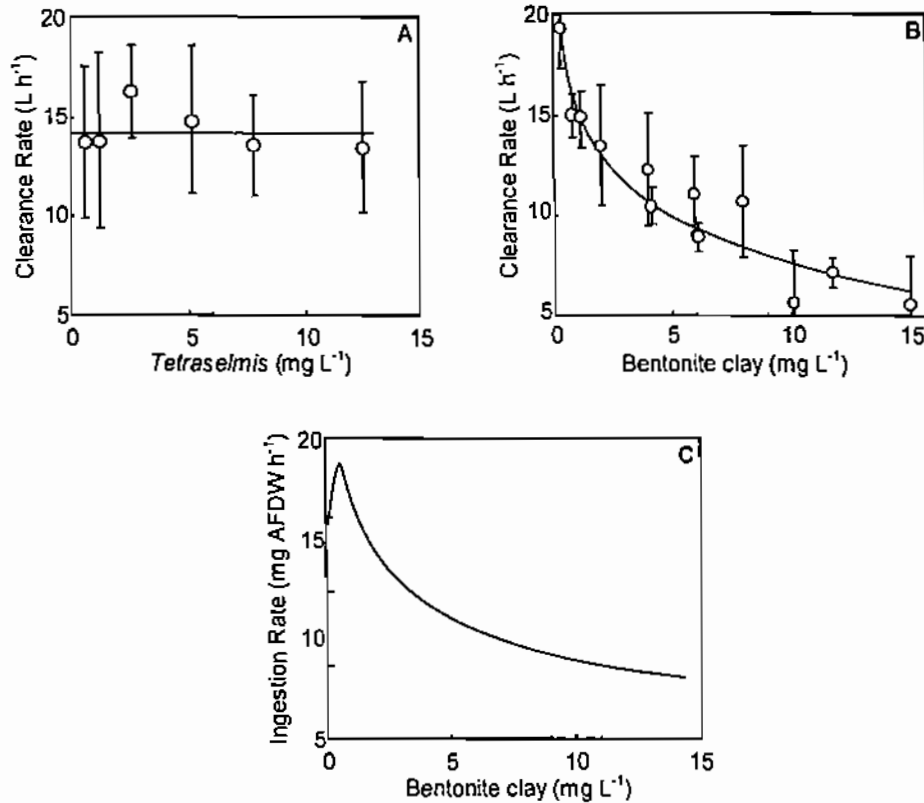


Figure 7.7. *Placopecten magellanicus* adults. Effects on clearance rates (mean \pm SD) of increasing concentration of algae (*Tetraselmis suecica*) (A), compared to those of PIM (bentonite clay) added to a 1 mg L⁻¹ algal suspension (B); effects of clay on calculated algal ingestion rate (algal ash-free dry weight, AFDW, per hour) (C). Source: modified from Cranford and Gordon (1992).

documented at concentrations ≥ 4 mg L⁻¹ (Cranford et al. 1999) is insufficient to compensate for food dilution effects in this species.

Compensation of food dilution by inorganic particles may also occur via selective rejection of PIM in pseudofeces and can be quantified by the compensation index (CI), as selection efficiency alone does not take into account the amount of pseudofeces produced (see section 7.2.7 on particle selection). In *P. magellanicus* exposed to mixtures of algae and silicate, a positive CI, indicative of the capacity to enhance the quality of ingested vs. available particles, was obtained at seston concentrations 3–7 mg L⁻¹ and when diet quality (% POM) was $\geq 50\%$ (Bacon et al. 1998). This compensation strategy was ineffective (negative CI values) when seston quality was very low (25% POM).

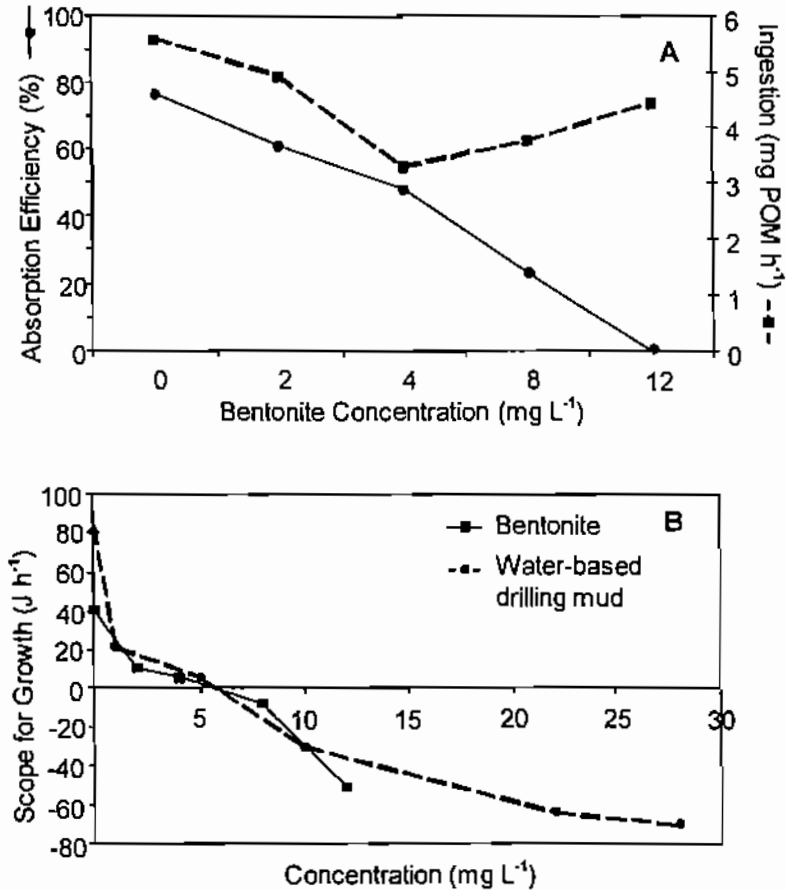


Figure 7.8. *Placopecten magellanicus* adults. Effects of increasing concentrations of PIM (bentonite clay) added to natural seston on A) ingestion rate and percent absorption efficiency (AE) of particulate organic matter (POM). B) Effects of bentonite and water-drilling muds (composed primarily of bentonite with some barite) on scope for growth (plotted from data in Cranford et al. 1999, for unconditioned scallops, with no prior exposure to clay).

It is now well recognised that functional responses of bivalves may vary considerably with the type of suspended particulate matter, i.e., artificial diets (e.g., algae and inert particles) vs. natural suspensions of low organic content (Bayne et al. 1993; Hawkins et al. 1996). In *P. magellanicus* the reduction in CR and in ingestion rate of organic matter caused by bentonite additions was greater when scallops were fed natural seston than a unialgal diet (Cranford and Gordon 1992). Increasing concentrations of natural, resuspended bottom sediment from Georges Bank (that passed through a 102 μm mesh

sieve) resulted in an exponential decline in clearance rates, but in contrast to bentonite, this decline was only detected at concentrations $\geq 12 \text{ mg L}^{-1}$ (Grant et al. 1997). The threshold concentration for visible pseudofeces production was also higher for resuspended sediment, ($>10 \text{ mg L}^{-1}$) than that found for bentonite ($\sim 2 \text{ mg clay L}^{-1}$) by Cranford and Gordon (1992). Thus resuspended bottom sediment ($\geq 5 \mu\text{m}$ median size) was less deleterious to adult *P. magellanicus* than bentonite and can even contribute a potential food source under conditions of food limitation. Grant et al. (1997) estimated that sea scallops could absorb organic matter ($\sim 30\%$ of dry weight) associated with resuspended bottom sediment with $\sim 40\%$ efficiency. Inorganic clay particles may also provide a potential food source via adsorption of dissolved organic matter. In this study sea scallop gill retention efficiency of resuspended sediments attained 100% at $\sim 5 \mu\text{m}$ and did not decline with increasing sediment load (Grant et al. 1997), as was observed with clay (Cranford and Gordon 1992).

Effects on scallop feeding physiology can also vary with the degree of aggregation of individual sediment particles. Fine, clay-sized particles readily form larger flocs or aggregates in seawater, and it remains unclear whether they are again broken down to individual particles during bivalve feeding. Scallops are known to ingest relatively large individual particles up to $350 \mu\text{m}$ for *P. magellanicus* (Shumway et al. 1987) and $950 \mu\text{m}$ for *Patinopecten yessoensis* (Mikulich and Tsikhon-Lukamina 1981) and could thus potentially ingest large flocs even if these were not disaggregated on the gills. White (1997) found that flocculation increased the ability of adult *P. magellanicus* to retain small ($<7 \mu\text{m}$) clay particles and thereby increased the availability of clay for ingestion. For the preparation of feeding suspensions in this study rapid formation of large flocs was induced by the addition of gelatin, which may lead to formation of more robust flocs than those occurring in natural seston. Lyons and Ward (2003) also found that flocs (marine aggregates) increased the uptake of small ($1 \mu\text{m}$) fluorescent beads in *P. magellanicus*.

High concentrations of PIM not only result in food dilution but may also cause direct and irreversible physical damage to the bivalve gill thus impairing feeding capacity. The filibranch gill of scallops is more vulnerable to this type of sublethal structural damage than the eulamellibranch gill. In adult *Placopecten magellanicus* heavy damage resulting from the breakdown of the ciliary junctions (cilifers) between gill filaments occurred after 4 to 9 days of exposure to attapulgite clay at concentrations of 0.5 to 1 mg L^{-1} and moderate damage was observed at 0.1 mg L^{-1} (Morse 1982).

The contribution of PIM to total seston has been used as an index of the nutritional quality of available particles. Vahl (1980) found that absorption efficiencies of *Chlamys islandica* (ranging between 10 and 55%) were inversely related to the fraction of inorganic matter in the seston, and that the ratio of PIM/POM (particulate inorganic matter to organic matter) provided a good correlate of growth in this population. Enhanced growth rates of *C. islandica* held in suspended culture near the sea surface, compared to those held at 40 m, were also attributed to depth-related differences in PIM/POM (Wallace and Reinsnes 1985). These authors recommended use of the PIM/POM ratio as an index of the nutritional value of seston. Adverse effects on growth of scallops were predicted when the PIM/POM ratio exceeded a critical value of 3.5 (i.e., when inorganic material comprises more than 78% of the total seston). This supports Vahl's (1980)

estimate, obtained by extrapolation, that no POM would be absorbed when PIM comprises more than 80% of the seston (PIM/POM = 4). Similarly, using controlled mixtures consisting of a fixed concentration (1 mg L⁻¹) of algae or natural seston and varying concentrations of PIM (bentonite clay) to manipulate diet quality, Cranford (1995) found an inverse logarithmic relationship between absorption efficiency (AE) of organic matter of the sea scallop, *P. magellanicus*, and increasing bentonite levels. The relationship between AE and diet quality (Q) whether expressed as the % of POM, particulate organic carbon, POC, or nitrogen, PON, per unit dry weight seston) was described (after Bayne et al. 1987) by the following exponential equation:

$$AE = a [1 - e^{-b(Q-c)}] \quad (2)$$

Where, a = the maximum value of AE, >92%, b = the rate of increase of AE with increasing diet quality, and c = diet quality at which AE = 0. This coefficient was estimated at 14% POM/DW (PIM/POM = 6) for *P. magellanicus* in this study, compared to 7% in *Mytilus edulis* (reviewed by Cranford 1995) and has been suggested as an index of a bivalve's capacity to survive in a nutritionally poor environment (Navarro and Iglesias 1993). Adverse effects on sea scallop growth were found at a relatively low PIM/POM ratio of 1.5 (addition of 10 mg L⁻¹ bentonite) (Cranford and Gordon 1992, Cranford 1995), below the critical threshold proposed above for *C. islandica*. Interspecific comparisons from different studies must be interpreted with caution, however, as the coefficients in the equation can vary considerably within a species as a function of environmental conditions, and were shown to vary between laboratory and field studies (Cranford et al. 1998).

Scallops appear to be particularly susceptible to siltation both in the laboratory (Castagna 1975) and in the field (Duggan 1973; Tettelbach et al. 1985). In bay scallops, *A. irradians*, burial by shifting sediments has been suggested as a significant cause of mortalities during the winter when low temperatures result in reduced activity (Tettelbach et al. 1990). Laboratory studies confirmed that juveniles (19–25 mm in shell height) partially (2/3) covered by a 1 cm-deep sediment layer at temperatures <10°C showed significant mortalities relative to unburied controls by the end of 10 weeks. Therefore, byssal attachment to elevated substrates in juveniles and some adult scallops may provide a mechanism of avoiding burial by fine-grained sediments and exposure to high near-bottom turbidities, in addition to a predator refuge. Using ciliary activity of gill sections as a physiological index Yamamoto (1960) found that the tolerance of juvenile *Patinopecten yessoensis* to suspended silt and low oxygen tension increased with scallop size (over the range 17 to 100 mm). Since high turbidity and low oxygen levels are both conditions associated with uncompacted, fine-grained sediments, Yamamoto's findings explain the often observed low survival of juvenile scallops in muddy bottoms. Growth rates of adult scallops can also be adversely affected in soft, muddy substrates; Gruffydd (1974) found that the maximum shell size of *Pecten maximus* from the North Irish Sea decreased significantly with increasing mud content of sediments.

7.2.10 Effects of Flow on Feeding and Growth

Studies of natural populations of shallow water pectinids such as *Argopecten irradians*, have generally found that larger size and faster growth rates are associated with areas of relatively strong currents (Belding 1910; Gutsell 1930; Marshall 1960). Emigration rates of the bay scallop *Argopecten irradians concentricus* increased with scallop density but only in the presence of a high tidally oscillating flow regime of 28 cm s^{-1} but not at flows of 10 cm s^{-1} (Powers and Peterson 2000). This study illustrates how flow can facilitate biological interactions and influence density dependence. Reduced growth rates of suspension-feeding bivalves in areas of low current speeds and/or high population densities are attributed to a reduction in seston supply in the benthic boundary layer (Fréchette and Bourget 1985).

Excessively high current speeds could, however, potentially reduce growth by inhibiting the scallops' feeding activity. Kirby-Smith (1972) investigated the effect of current speed (within the range 0.2 to 12.8 cm s^{-1}) on growth of adult *Argopecten irradians concentricus* in an apparatus consisting of pipes with different outflow diameters. He found that shell growth rate and condition (muscle weight/shell height) decreased at current speeds exceeding about 6 cm s^{-1} . It has been noted however, that the current speeds reported in his study, estimated by dividing the observed volume discharge rate by the cross-sectional area of the pipe, underestimate the speeds actually experienced by the scallops (Eckman et al. 1989). Clearance rates in *Placopecten magellanicus* are a unimodal function of flow: they are positively related with flow speed below 5 – 10 cm s^{-1} , independent of flow at intermediate flows of 10 to 20 cm s^{-1} and decline when velocities exceed 15 to 20 cm s^{-1} (Wildish and Kristmanson 1985; Wildish et al. 1992; Wildish and Saulnier; 1993). Wildish et al. (1992) found that higher seston concentrations could offset the velocities at which feeding inhibition occurs.

Many studies on scallop feeding activity have been undertaken via short-term experiments in static chambers or in poorly defined flow fields. Feeding activity in suspension-feeders measured under laboratory conditions may differ from feeding rates observed in the dynamic boundary layer flows found in coastal waters (Rubenstein and Koehl 1977, LaBarbera 1981). In a unique flume study Pilditch and Grant (1999a) exposed the sea scallop *Placopecten magellanicus* to increasing and decreasing concentrations of food and incremental changes in flow speeds between 5 and 25 cm s^{-1} . These authors did not find a positive correlation between clearance and flow speeds but observed clearance to be independent of flow speed between 5 – 15 cm s^{-1} and inhibited at 25 cm s^{-1} . However, clearance rates were different in the ascending and descending phases of the experiments with a lower flow speed of 10 – 15 cm s^{-1} inhibiting feeding on the descending phase. They suggested that the response to flow speed may be a function of feeding history whereby clearance may be inhibited at lower flow velocities after feeding on high concentrations of phytoplankton. This research emphasises the direct effects of flow, its interaction with seston concentration and the significance of short-term feeding history in regulating scallop feeding rates.

Evidence of a growth limiting upper velocity obtained in experimental flume systems appears to contradict field observations. For example, Eckman et al. (1989) report that

juvenile *Argopecten irradians* within dense eelgrass beds (1,100 shoots m⁻²) in Back Sound, North Carolina, U.S.A. regularly experience current speeds as high as 5–28 cm s⁻¹. Adult giant scallops (*Placopecten magellanicus*) in the Bay of Fundy are found where depth-integrated maximum tidal velocities exceed 100 cm s⁻¹ (Wildish and Peer 1983) and are thus well above the critical thresholds determined experimentally. Similarly, Bricelj et al. (1987a) found highest reproductive output and muscle condition of adult *A. irradians* in a site where surface currents can exceed 70 cm s⁻¹. Flow velocities within the benthic boundary layer will be lower, however, than depth integrated or free stream velocities. Furthermore, scallops often occupy depressions in bottom sediments (recessing) (Caddy 1968) where they may avoid high flow velocities. Wildish and Kristmanson (1988) attempted to reconcile this apparent contradiction in a study that examined the influence of periodic changes in flow regime on growth of *Placopecten magellanicus*. Scallops were found to maintain maximal rates of shell growth as long as they were exposed to growth limiting current velocities (>10 cm s⁻¹) less than a third of the time. In contrast to studies evaluating the effect of scallop orientation on growth in flumes using steady current velocities, Claereboudt et al. (1994) did not observe any differences in growth of *P. magellanicus* related to orientation relative to current direction in the field. However, these authors did find a reduction in tissue growth at their high velocity site (16 cm s⁻¹) consistent with other studies of sea scallops in flumes where growth was reduced at velocities exceeding 10 cm s⁻¹ (Wildish et al. 1987; 1992). Pearl nets decreased water flow by 46–61% thereby reducing velocities that inhibit feeding and result in greater growth inside the nets than outside for scallops held at the high velocity site. This is in contrast to observations at the low velocity site (9 cm s⁻¹) where the pearl nets reduced flow inside to the point where growth inside the nets was significantly lower possibly due to seston depletion (Claereboudt et al. 1994).

In contrast with the results reported earlier, Cahalan et al. (1989) found that growth rates of juvenile (3–7 mm) bay scallops, *Argopecten irradians*, determined in a flume, were independent of current speed between 1 and 15 cm s⁻¹. Eckman et al. (1989) found that shell growth of juvenile *A. irradians* (8–14 mm) declined gradually with increasing flow velocity over the range 1.4 to 17.2 cm s⁻¹, irrespective of the scallops' orientation to the flow. At any given flow velocity, scallops grew more rapidly when oriented with anterior margins facing upstream, their preferential orientation. There was no evidence however, of a sharp decline in growth above some threshold flow velocity. Furthermore, a statistically significant effect of flow velocity on growth was only detected for scallops with their anterior opening oriented downstream. In this study responses of scallops to current speed and turbulence were determined in a series of pipes with outflows of different diameters, and low velocities were measured directly with a thermistor-bead flowmeter.

Juvenile bay scallops in their natural habitat live byssally attached to elevated substrates, and therefore routinely experience flows greater than 3 cm s⁻¹, and as high as ca. 17 cm s⁻¹ (Eckman et al. 1989). Given their preferential orientation, they are unlikely to remain in an unfavourable orientation where growth is more strongly inhibited by increasing flow velocity. Eckman et al. (1989) additionally found that growth rates were independent of the presence or intensity of turbulence. Animals were tested in flows

ranging from laminar to fully turbulent (Reynolds number = 840 to 5,600), with flow velocity held within a narrow range of 1.7 to 3.9 cm s⁻¹.

In a laboratory study that examined the effects of flow speed and orientation on growth of juvenile *Nodipecten subnodosus*, highest shell and tissue growth rates were obtained at flow speeds between 5 and 10 cm s⁻¹ and when scallops were in their natural orientation (ventral, inhalant margin oriented towards the flow) (García-Esquivel et al. 2000). This study was conducted in tubes cut in half, in which flow was controlled via a recirculating pump, and current velocities were determined using rhodamine dye. Free scallops showed reduced tissue weight at the highest speed tested (15 cm s⁻¹) even though this scallop species is known to experience current velocities over 100 cm s⁻¹ in its natural habitat in Baja California, Mexico. This high current speed caused detachment of juveniles as well as growth inhibition. Flow had no significant effect on growth when scallops were oriented horizontally against the flow, an orientation, which resulted in the slowest growth.

7.2.11 Effects of Harmful and Toxic Algae

Like other suspension-feeding bivalve molluscs, scallops accumulate toxins associated with harmful algal species. In most instances (but not all!), adductor muscles do not accumulate toxins and are thus safe for human consumption even in the presence of harmful algae. Whole scallops are a serious threat to public health, especially since many species bind the toxins in various tissues for extended periods of time and are rendered unsuitable for human consumption even when blooms are not evident (see Shumway and Cembella 1993; Bricelj and Shumway 1998 and references therein). In addition to becoming vectors for these algal toxins, many species of scallops are themselves adversely affected by the toxins (Table 7.3).

Perhaps the best understood responses of scallops to harmful algae are those associated with brown tides caused by the picoplanktonic alga *Aureococcus anophagefferens* in mid-Atlantic, U.S.A. estuaries. In eastern Long Island, NY, where blooms have recurred since 1985, brown tides have led to recruitment failure, growth inhibition and decimation of local bay scallop (*Argopecten irradians*) populations (reviewed by Bricelj and Lonsdale 1997) despite intensive reseeding efforts (Tettelbach and Wenczel 1993). The mid-summer, main spawning period of scallops has been shown to overlap with the period of occurrence of *A. anophagefferens* (Bricelj et al. 1987a). Due to their small size (~2 µm) *A. anophagefferens* cells are retained with only 36% efficiency by adult bay scallops (Cosper et al. 1987). However, their negative effects are attributed to an unknown, dopamine-mimetic, bioactive/toxic metabolite associated with brown tide cells, which suppresses the activity of gill lateral cilia (Gainey and Shumway 1991) and thus clearance rates of bivalves such as *Mytilus edulis* and *Mercenaria mercenaria* (Tracey 1988; Bricelj et al. 2001). These effects are observed even when non-toxic algae of high food value are present in a mixed phytoplankton assemblage with *A. anophagefferens*. Toxic effects require direct contact with brown tide cells and do not appear to be associated with the production of dissolved toxic exudates (Ward and Targett 1989). It is of interest to note that *in vitro* trials by Gainey and Shumway (1991) did not

document gill ciliary inhibition by brown tide in adult *A. irradians*, although natural populations of this species are known to be adversely affected by brown tides.

Although *A. anophagefferens* bloom densities in the field can attain $1-2 \times 10^6$ cells mL^{-1} , the inhibitory effect on bivalve feeding is concentration-dependent and in short-term studies of juvenile hard clams occurred above a threshold cell density of $\geq 35 \times 10^3$ cells mL^{-1} (Bricelj et al. 2001). Densities from 1.9×10^5 to 7.5×10^5 *A. anophagefferens* cells mL^{-1} were found to significantly reduce survival and growth of bay scallop larvae in laboratory studies, even in the presence of nutritious algae (Gallager et al. 1989). Scallop larvae were able to maintain ciliary-driven swimming activity, as well as capture of nutritious algae in the presence of *Aureococcus*. However, the latter caused increased rejection of non-toxic algae from the oesophagus and thus reduced ingestion rate. Thus, Gallager et al. (1989) suggested that the mechanism of action of brown tide cells in larvae may differ from that of adults, in that *Aureococcus* may interfere with the chemosensory function of larvae rather than ciliary activity.

The ichthyotoxic flagellate *Prymnesium* spp. (isolate 97-20-1) at 10^5 cells mL^{-1} was found to elicit toxic effects in juvenile bay scallops, *A. irradians*: copious mucus and pseudofeces production and valve gape not responsive to stimulation, necrosis of the digestive gland and gill as revealed by histopathology and presence of moribund or dead animals within 24 h of exposure (Wikfors et al. 2002).

Several species of dinoflagellates, the most common components of toxic algal blooms, have been shown to have negative impacts on scallops. Yan et al. (2001) reported inhibition of egg hatching success and larval survival of *C. farreri* when exposed to intact cells and cell fragments of *Alexandrium tamarense* (isolate from Daya Bay, PRC). Hatching rate of *C. farreri* decreased to 30% of controls after exposure to *A. tamarense* cells or cellular fragments at 100 cells mL^{-1} and was only 5% after exposure at 500 cells mL^{-1} . Larval (D-stage) survival rates decreased significantly after exposure for 6 d at 3000 cells mL^{-1} and above; no larvae survived after 14 d exposure at 10,000 cells mL^{-1} or 20 days at 5,000 cells mL^{-1} . However, these experimental concentrations exceed environmental levels by several orders of magnitude. Exposure to saxitoxin (STX) standard did not inhibit egg hatching, suggesting that an unknown metabolite, rather than PSP toxins, was the causative agent of hatching failure. These results may have far reaching implications for devastation of field or hatchery populations exposed to this common dinoflagellate.

While heart rate, feeding rate, and irrigation rates of *P. magellanicus* were unaffected by the presence of PSP-producing *A. tamarense* (at 10^4 cells L^{-1}) (Shumway and Cucci 1987; Gainey and Shumway 1988a, b), scallops did produce copious amounts of a white, mucus-like substance, and the animals exhibited a striking escape response with either violent swimming activity, partial, sustained shell-valve closure, or a combination of the two. It was suggested that this increased metabolic output might prove detrimental to the scallops if it continued for any extended length of time. This type of avoidance response was not described in other scallop species fed PSP-producing dinoflagellates, e.g., *Pecten maximus* fed *A. minutum* (Bougrier et al. 2001). Bivalve species that are resistant to the effects of PSP toxins can assimilate and grow on toxic *Alexandrium* spp.. Absorption efficiency of organic matter (OM) [(OM absorbed/OM filtered) $\times 100$] of *P. maximus* fed

Table 7.3

A summary of toxic and noxious algal species associated with scallops (after Shumway 1990; Shumway and Cembella 1993 and Landsberg 2002). Where known, strain is given below the algal species name followed by cell toxicity and concentration. Algal species are given as in the original publications with current taxonomic status added. See text for details.

Algal Species	Scallop Species	Effects	Location	Reference
Dinoflagellate Species				
<i>Alexandrium tamarense</i> (ATHK; 1.175×10^9 STX eq cell ⁻¹ ; see text for cell concentrations)	<i>Chlamys farreri</i> (larvae and juveniles)	Inhibition of egg hatching success after 36 h exposure at 100 cells mL ⁻¹ ; decreased larval survival after 6 d at 3000 cells mL ⁻¹	Laboratory	Yan et al. 2001
<i>Pratogonyaulax tamarensis</i> (= <i>A. tamarense</i>) (GT429; 5×10^6 cells L ⁻¹)	<i>Placopecten magellanicus</i> (adults)	Violent swimming and mucus production	Laboratory	Shumway and Cucci 1987; Gainey and Shumway 1988b
<i>Pyrodiskus brevis</i> (= <i>Karenia brevis</i>) ($5-500 \times 10^3$ cells L ⁻¹)	<i>Argopecten irradians</i>	Adult scallop mortality (21%); almost total recruitment failure	North Carolina (Field)	Summerson and Peterson 1990
<i>Karenia brevis</i> (<900 cells mL ⁻¹)	<i>Argopecten irradians</i> (larvae)	Delayed metamorphosis and larval development, decreased filtration and mortality	Laboratory	Leverone and Blake 2001
<i>Gymnodinium veneficum</i>	<i>Pecten maximus</i> (adults)	100% mortality within 1 h of exposure	Laboratory	Abbot and Ballantine 1957
<i>Gyrodinium aureolum</i> (PLY 497; 10^5 cells L ⁻¹)	<i>Argopecten irradians</i> <i>Placopecten magellanicus</i> (juveniles <15mm)	Some evidence of poor food quality, no obvious toxic effects in either species at cellular level; 100% mortality in <i>A. irradians</i> ; no mortality but copious mucus production in <i>P. magellanicus</i>	Laboratory	Smolowitz and Shumway 1997; Lester and Shumway 1993
<i>G. cf. aureolum</i> (up to 5×10^5 cells L ⁻¹)	<i>Pecten maximus</i>	High mortality in postlarvae and juveniles; cessation of feeding in larvae; inhibition of reproduction and growth	Bay of Brest, France and laboratory	Lassus and Berthome 1988; Erard- LeDenn et al. 1990
<i>Heterocapsa circularisquama</i> (10^5-10^6 cells L ⁻¹)	<i>Chlamys nobilis</i> (adults)	Mass mortalities	Ago Bay, Japan	Matsuyama et al. 1995; 1999; personal communication

<i>Lingulodinium polyedrum</i> (= <i>Gonyaulax polyedra</i>) (as <i>Gonyaulax</i> sp.) (10^7 cells L ⁻¹)	<i>Leptocetien</i> [as <i>Pecten</i>] <i>L. latiauratus</i>	Mortalities (probably a result of anoxia and high temperature, not toxins)	Ensenada, Baja California, Mexico	Stohler 1959
<i>Prorocentrum lima</i>	<i>Argopecten irradians</i> (juveniles; pre-reproductive adults)	Reduced absorption efficiency relative to <i>Thalassiosira weissflogii</i>	Laboratory	Bauder et al. 2001
<i>Prorocentrum minimum</i>	<i>Argopecten irradians</i> (post-set; 0.61 g mean live weight)	Mortality, atrophy and necrosis of the digestive gland absorptive cells, and systemic effects	Laboratory	Wikfors and Smolowitz 1993, 1995; personal communication
<i>Pyramnesium</i> sp. (10^8 cells mL ⁻¹)	<i>Argopecten irradians</i> (juveniles, 10 and 50 mm)	Violent twitching, abundant mucus production; valve gape; all moribund or dead within 24h; severe, acute total or near-total necrosis of digestive gland and ducts, gill and other tissues; dead hemocytes	Laboratory	Wikfors et al. 2002
<i>Pfiesteria shumwayae</i> (100 – $2,500$ cells mL ⁻¹)	<i>Argopecten irradians</i>	Rapid mortality caused by aggressive feeding on larvae by <i>Pfiesteria</i> ; no mortality when cells were isolated from scallops in dialysis tubing	Laboratory	Shumway and Springer 1996; unpublished
<i>Pfiesteria piscicida</i> (150 – $3,500$ cells mL ⁻¹)	<i>Argopecten irradians</i>	Decrease or cessation of clearance rate in adults; mortality in larvae, spat and adults	Laboratory	Springer et al. 2000, 2002
Pelagophyte Species <i>Aureococcus anophagefferens</i>	<i>Argopecten irradians</i>	Larval shell growth reduced and increased mortalities	Laboratory	Gallager et al. 1989
<i>A. anophagefferens</i> <i>A. anophagefferens</i>	<i>Argopecten irradians</i> <i>Argopecten irradians</i>	Mass mortalities 76% reduction in adductor weights; recruitment failure	Long Island, NY Long Island, NY	Cosper et al. 1987 Bricej et al. 1987b
Diatom Species <i>Rhizosolenia chunii</i> (56 – 187×10^3 cells mL ⁻¹)	<i>Pecten alba</i> (adult)	Digestive gland lesions and subsequent mortalities possibly caused by <i>R. chunii</i>	Port Phillip Bay, Australia	Pary et al. 1989
<i>Rhizosolenia delicatula</i> <i>Ceratium pelagicum</i> (7.3×10^8 cells L ⁻¹)	<i>Pecten maximus</i> (adult)	Decline in growth rate; clogged gills affecting feeding and respiration	Bay of Brest, France	Lorrain et al. 2000; Chauvaud et al. 1998

A. minutum was 42% (Bougrier et al. 2001) and absorption efficiency [(OM absorbed / OM ingested) x 100] of a highly toxic strain of *A. fundyense* by *Mytilus edulis* was 60–63% (Bricelj et al. 1990).

Very limited information is available on the effects of the brevetoxin-producer *Ptychodiscus brevis* (= *Karenia brevis*) on bivalve molluscs, although this species is known to cause mass fish mortalities. Bay scallops, *Argopecten irradians*, appear to be particularly sensitive to the toxic effects of this dinoflagellate. A mortality of 21% and almost total (98%) recruitment failure of *A. irradians* was reported by Summerson and Peterson (1990) for scallops exposed to a renegade bloom of this dinoflagellate in North Carolina. Clearance rates of juvenile bay scallops were significantly reduced at concentrations ≥ 50 intact cells *K. brevis* mL⁻¹ as well as in the presence of lysed cells (Leverone and Blake 2002). These authors also found that *K. brevis* inhibited metamorphosis and caused mortalities of bay scallop larvae above 500 cells mL⁻¹. While this dinoflagellate species is usually restricted to the Gulf of Mexico, this example is a clear indication of the devastating impacts that harmful algal blooms can have on scallop populations and a warning with regard to potential impacts at aquaculture sites.

In complementary studies (Lesser and Shumway 1993; Smolowitz and Shumway 1997), juvenile *Argopecten irradians* and *Placapecten magellanicus* were exposed to bloom conditions (10⁵ cells L⁻¹) of *Gyrodinium aureolum* for a week. These studies clearly demonstrated a species-specific impact of this alga on the scallops. Mortality was 100% in *A. irradians* and zero in *P. magellanicus*. Reduced clearance rates were noted in *A. irradians* and production of copious amounts of mucus were noted in *P. magellanicus*. No mortalities were noted in either species when exposed to *Alexandrium tamarense*. At the cellular level, *G. aureolum* had a marked effect on the digestive gland of *A. irradians*. There was a significant decrease in the height of absorptive cells and increased lumen diameter which, at least, suggest poor food quality of *Gyrodinium*. There was no direct evidence of toxic effects such as necrosis and sloughing of digestive gland epithelial cells in the digestive gland. Some animals showed inflammation in the kidney but the cause was not delineated. No such impacts were noted in *P. magellanicus*. Erard-LeDenn et al. (1990) noted minor mortalities in 2-year old *P. maximus* exposed to *G. aureolum* and also noted a 'stress ring' on shells of exposed animals in the field, clearly indicating growth inhibition. Postlarvae (1 mm) experienced major die-offs (100% at one site, 85% at another) at cell concentrations of 2 x 10⁵ cells L⁻¹. These blooms were extensive and lasted several weeks during the summer period and caused mass mortalities of the individuals in the nurseries and trays. Growth of juveniles (5–30 mm shell height) stopped completely for one month and resumed when the red tide vanished. In addition, the adult scallops exhibited abnormally low gonadal indices. Laboratory studies revealed a decreased filtration rate of *P. maximus* exposed to *G. aureolum* and also demonstrated differences between toxicity of different strains of *G. aureolum*.

Heterocapsa circularisquama, a toxic dinoflagellate from Japanese waters has been implicated in mass mortalities of several species of bivalve molluscs, including scallops (*Chlamys nobilis*; Matsuyama 1999; Matsuyama et al. 1996, 2001). While empirical data on scallop mortality are not available, this alga is known to be a molluscicide and it has had devastating impacts on aquaculture for various species including mussels, oysters and

pearl oysters in Japanese waters. Establishment of scallop culture in areas prone to this alga would be very risky business.

Impacts of the dinoflagellate, *Prorocentrum minimum*, on postlarval scallops, *A. irradians*, were studied by Wikfors and Smolowitz (1993) as part of an investigation of observed poor growth rates in caged hard clams, *Mercenaria mercenaria*. They provided scallops with mixed diets of T-ISO and *P. minimum* in varying ratios. Daily ration was equalised to 0.012 mL of packed cells per individual scallop. No algal diet supported good, consistent growth of scallops and survival varied between treatments, with 100% mortality noted in one week in one trial and four weeks in a second trial. Histological observations after one week of exposure to the mixed diet revealed poorly developed digestive diverticula and attenuation of the epithelium with abnormal vacuolation and necrosis. They also noted the presence of large thrombi in the open vascular system of the mantle, digestive diverticula, heart, gill, and kidney tissues, suggesting systemic effects of a toxin. Since *P. minimum* is a common component of the phytoplankton during the summer in scallop growing areas, there is considerable potential for detrimental impacts on both natural and cultured populations of *A. irradians*. Exposure of juvenile and adult *Argopecten irradians*, to *Prorocentrum lima*, a producer of diarrhetic shellfish poisoning (DSP) toxins which can act as potent phosphatase inhibitors, had no adverse effects on survival of scallops over a 2-wk period (Bauder et al. 2001). In this study there was no evidence of abnormal behaviour (shell clapping or avoidance by swimming) and byssal attachment and climbing of juveniles remained unaffected. Feeding (clearance rates) were comparable to those of controls offered an equal biovolume of non-toxic diatoms.

Scallops exposed to the dinoflagellate, *Pfiesteria* spp. are impacted by both toxins and physical attack by *Pfiesteria* (Springer et al. 2002; Shumway, unpublished). Bay scallop larvae (*A. irradians*) are aggressively fed upon by *Pfiesteria piscicida* zoospores (all functional types) within minutes of zoospore introduction. Left in direct contact with the zoospores, the larvae are dead within 30–45 minutes. High rates of larval mortality have also been observed in experiments where toxic zoospores were constrained within dialysis tubing. These results suggest the presence of dissolved toxin(s). *P. shumwayae* zoospores are even more aggressive in their feeding response towards *A. irradians* larvae (death within 10–15 minutes) although the same cultures cannot induce larval mortality when constrained within dialysis tubing.

Juvenile and adult bay scallops rapidly cleared *P. piscicida* from suspension at concentrations ranging from 150–3,500 cells mL⁻¹ (Springer et al. 2002; Shumway unpublished). Toxic zoospores were cleared from suspension at progressively slower rates than nontoxic (algal fed; TOX-B, NON-IND) zoospores. A significant difference in grazing rates also exists between juvenile scallops presented with freshly isolated *P. piscicida* (TOX-B) versus those fed non-inducible cultured isolates (3+ months in culture). This is presumably due to residual toxicity in the TOX-B cultures. *P. shumwayae* is cleared from solution at a relatively lower rate than observed for *P. piscicida* (concentrations ranging from 100–2,500 cells mL⁻¹) but the cause for these observed differences has yet to be determined. The presence of *Pfiesteria* spp. has already had devastating impacts on at least one bivalve hatchery in North Carolina.

Unlike dinoflagellates, diatoms have rarely been attributed harmful effects on shellfish in general or scallops specifically (see Shumway 1990; Shumway and Cucci 1987; Gainey and Shumway 1988b). Unusually large blooms of the diatom, *Rhizosolenia chunii*, in Port Phillip Bay, Australia in 1987–1988, initially resulted in a bitter taste in mussels, oysters and scallops (*Pecten alba*) (Parry et al. 1989). Abnormally high mortalities were noted in mussels and oysters, which were followed histologically during the post-exposure period. While scallops exhibited increased levels of mortality post-bloom, it is not clear whether these mortalities were caused by parasites, diseases or exposure to *R. chunii*.

In a more recent study, Chauvaud et al. (1998) suggested that large populations of a diatom, *Rhizosolenia delicatula*, could have led to reduction in feeding due to gill clogging, and cessation of growth in *Pecten maximus* in the Bay of Brest, France. In a later study of the same area, Lorrain et al. (2000) showed a decreased growth rate from 180 to 80 $\mu\text{m d}^{-1}$ in *P. maximus* associated with large blooms of *R. delicatula* and another diatom, *Ceratulina pelagica*. Again, they postulated that the reduction in growth rate was directly caused by the presence of these diatoms but no cause and effect was demonstrated and no laboratory studies accompanied the field work.

7.3 ENERGY UTILISATION: METABOLIC EXPENDITURE

Metabolic rate of bivalves, as measured by the rate of oxygen consumption (VO_2), is known to be influenced by a number of variables, including temperature, body size, oxygen tension, food concentration, salinity, reproductive state, activity level and physiological condition. The effect of salinity can be illustrated in *Argopecten purpuratus*, a euryhaline species, in which VO_2 increased with a decrease in salinity from 30 to 24 ppt, but declined with a further reduction in salinity from (24 to 18 ppt) (Navarro and González 1998). This pattern was similar to that observed for excretion rate (see section 7.4.1 on "Excretion and byssus secretion").

The allometric relationship between body mass (tissue dry weight) and VO_2 has been determined for several pectinid species (Table 7.4). The coefficient (b) of this relationship varies between 0.486 and 0.986 [average = 0.75 excluding Vahl and Sundet (1985) values for reproductively mature individuals]. This mean value closely approximates that of 0.727 estimated for bivalves (Bayne and Newell 1983) and the value of 0.75 estimated for poikilotherms in general (Hemmingsen 1960). The biological significance of this parameter has been discussed by numerous authors (e.g., Zeuthen 1953; Hemmingsen 1960). A higher allometric coefficient (b) has been obtained in both larval and juvenile *Argopecten irradians concentricus* (Lu and Blake 1999), as has also been found for clearance rate. In juveniles (0.5 to 7 mm in shell height) the allometric equation is:

$$\text{VO}_2 (\mu\text{L O}_2 \text{ h}^{-1}) = 2.142 \times \text{AFDW}^{0.905} \text{ where AFDW in mg} \quad (3)$$

Table 7.4

Parameters of the allometric relationship between oxygen consumption (VO_2 ; mL O_2 h^{-1}) and tissue dry weight (W ; g), following the equation $VO_2 = a W^b$, in several pectinids. (Unless specified, regressions were selected from seasons during which the animals are not at the peak of their reproductive development).

Species, location	Size range (g tissue DW)	Temp. ($^{\circ}C$)	a	b	Source
<i>Argopecten</i>	0.47–2.99	17.4	0.931	0.725	Bricelj et al. 1987a
<i>irradians irradians</i>	0.84–2.86	10.5	0.368	0.733	
New York, U.S.A.	0.87–4.37	1.5	0.065	0.986	
<i>Argopecten circularis</i> , Mexico	0.04–1.78	20	0.479	0.715	Silva Loera 1986*
<i>Placopecten</i>	0.01–18	19	0.399	0.837	Shumway et al.
<i>magellanicus</i>		10	0.363	0.838	1988
Maine U.S.A.					
<i>P. magellanicus</i> - 10 m	1.8–42	5.5–8.5	0.447	0.79	MacDonald &
Newfoundland,		10–12	0.339	0.78	Thompson 1986
Canada - 31 m	0.5–25	1.8–3.5	0.214	0.76	
		5.5–7.2	0.234	0.79	
<i>Argopecten purpuratus</i>	0.1–5.7	12	0.30	0.55	Navarro & González 1998
<i>Chlamys islandica</i> , Norway	0.05–2.6	3.8	0.098	0.87	Vahl 1978
<i>Chlamys</i> , Immature	0.02–0.9	5.7	0.145	0.486	Vahl & Sundet
<i>islandica</i> Mature	0.5–5		0.251	0.567	1985
Norway Mature	0.4–6		0.242	0.759	
<i>Chlamys delicatula</i> , New Zealand	0.01–0.82	10	0.147	0.527	Mackay & Shumway 1980
<i>Chlamys opercularis</i> , Denmark	0.3–3.0	10	0.385	0.63	Mackay & Shumway 1980†
<i>Chlamys voria</i> , France	0.1–2.3	10 15	0.334 0.344	0.70 0.77	Shafée 1982
<i>Patinopecten</i>		22.4	0.579	0.817	Fuji & Hashizume
<i>yessoensis</i> ,	0.5–15	14.8	0.398	0.777	1974
Japan		5.8	0.181	0.862	

* Animals starved for 36 h prior to measurements.

† Calculated from data in McLusky (1973).

This agrees with results by Riisgård (1998), who found that larval and early juvenile stages of bivalves are characterised by a higher exponent ($b = 0.9-1.0$) than larger animals ($b = 0.6-0.7$) and thus challenged the validity of a constant allometric exponent for VO_2 .

Metabolic rate (VO_2) is also highly responsive to food levels: VO_2 is markedly reduced to basal levels during starvation as in other bivalves (Grant and Cranford 1991), and in *P. magellanicus* at 10°C, VO_2 was found to be significantly higher (by 31%) at high food levels (ambient seston supplemented with cultured algae) than at low food levels (ambient seston) (Pilditch and Grant 1999b). Respiration rate was also significantly greater (by 36%) in *P. magellanicus* fed cultured phytoplankton compared to detrital diets containing fresh or aged kelp, or resuspended sediment (Grant and Cranford 1991). The increase in metabolic rate of feeding scallops is expected to be primarily associated with the post-ingestive costs of digestion and growth rather than the mechanical cost of filtration.

7.3.1 Metabolic Rate and Oxygen Availability

Aquatic organisms have been characterised as oxyregulators or oxyconformers depending on their ability to maintain a VO_2 independent of declining oxygen tension (PO_2) over some range of PO_2 values, or one that conforms (declines) with PO_2 . The critical oxygen tension (P_c) is given by the inflection point of the function relating VO_2 and PO_2 , beyond which VO_2 becomes dependent of ambient oxygen tension. A critical value of about 48–56% oxygen saturation was determined for *Pecten maximus* at 10°C (Brand and Roberts 1973), and a low value of ca. 20% for the oxyregulators *Argopecten irradians* and the deep sea scallop *Pecten grandis* (van Dam 1954). Other scallop species are poor oxygen regulators: in *Chlamys islandica* (Vahl 1972, 1978) and *Placopecten magellanicus* (Shumway, unpublished). VO_2 is independent of oxygen tension only to approximately 60–70% oxygen saturation, and in *C. delicatula* VO_2 declines gradually with decreasing oxygen tension, with no clear inflection point (Mackay and Shumway 1980) (Fig. 7.9). Similarly, in *Argopecten ventricosus* VO_2 remains independent of PO_2 only between 100 and 76% of oxygen saturation (Sicard et al. 1999 in Maeda-Martínez et al. 2000).

The qualitative distinction between oxyregulators and conformers has been criticised by Mangum and Van Winkle (1973), who point out that few species exhibit perfect regulation or strict oxyconformity over a wide range of external oxygen conditions, and that these conditions represent only extremes in a continuum. Bayne (1971) suggested the adoption of the ratio K_1/K_2 (where K_1 is the intercept, and K_2 is the slope of a plot of PO_2 against PO_2/VO_2) as a more relevant quantitative index of an organism's oxygen dependence. A relatively higher K_1/K_2 value indicates a reduced ability to regulate VO_2 . The response to declining oxygen tension of bivalve mollusks can vary with environmental conditions such as temperature and salinity (Shumway and Koehn 1982), nutritional condition, and body size (Shumway 1983). For example, Silva Loera (1986) found that small bay scallops, *Argopecten circularis*, (0.1 g in dry tissue weight) show a more marked dependency of VO_2 on PO_2 and therefore a higher K_1/K_2 ratio (565), than large individuals (1.0 g; $K_1/K_2 = 137.6$). In bivalve mollusks the relationship between the

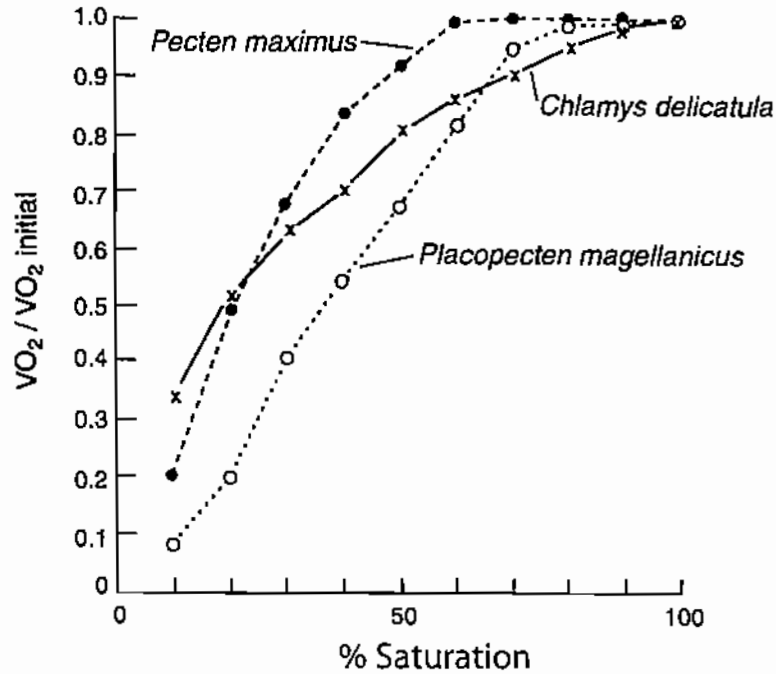


Figure 7.9. The response of three oxyconforming pectinid species to declining oxygen tension (VO_2 = weight-specific oxygen uptake). Data for *Chlamys delicatula* from Mackey and Shumway 1980; *Pecten maximus* from Brand and Roberts 1974; *Placopecten magellanicus* from Shumway, unpublished data.

K_1/K_2 index and weight-specific VO_2 ($\text{mL h}^{-1} \text{g}^{-1}$) is described by an exponential equation. For the deep water scallop *Chlamys delicatula* (Mackay and Shumway 1980) this relationship is given by:

$$K_1/K_2 = 115.78 \times VO_2^{0.769} \quad (4)$$

The relatively high value of the constant in this equation (= 115.78) compared to other bivalves species again indicates that *C. delicatula* is a poor oxyregulator. *Artica islandica* is an extreme oxyconformer, as indicated by an intercept value of 1,000, whereas the mussels *Geukensia demissa* show intermediate values (76 and 63, respectively).

In scallops, as observed in other bivalves, variations in metabolic rate are generally reflected in changes in heart rate. In littoral molluscs, respiratory stress caused by sudden aerial exposure typically results in rapid bradycardia (reduction in heart rate) and valve

closure. On the other hand, *Pecten maximus* initially responds to air exposure by violent adductions of the shell and tachycardia, followed by gradual bradycardia, accompanied by wide gaping of valves. Inability to control air gaping and consequent vulnerability to desiccation is a characteristic feature of many sublittoral species including scallops (Brand and Roberts 1973). The inability to remain closed for extended periods of time also makes scallops highly vulnerable to low salinity stress (Stockton 1984; Tettelbach et al. 1985), especially at higher temperatures (Mercaldo and Rhodes 1982). Little is known, however, about the air-breathing capacity of scallops during emersion, which may occur naturally during stranding by storms, during seeding and shipping activities, or harvesting and return to the water of sublegal scallops (Duncan et al. 1994; Dredge 1997). *Pecten maximus* suffered respiratory acidosis and died after 72 h of emersion (Duncan et al. 1994). Acidosis was largely attributed to aerobic metabolism (CO_2 production) rather than accumulation of anaerobic end products. The decline in pH was not buffered by mobilisation of Ca from shell dissolution and resulting increase in HCO_3^- , as observed in intertidal bivalves that are more tolerant of emersion. Negligible survival of *Argopecten ventricosus* spat (3.5 mm shell height) was obtained after 26 h of air-exposure at temperatures ranging from 17 to 28°C (Maeda-Martínez et al. 2000). At a shorter exposure time (19 h) survival rate, measured after 2 h of re-immersion, was inversely related to temperature. Survival could be further enhanced during shipping by packaging animals tightly and thus preventing shell gaping, and by using pure oxygen. Predator avoidance response of juvenile *P. magellanicus* was not affected by 4 h air exposure at 18°C, but was adversely affected by the combined stress of air exposure and cold shock (18 to 8°C) (Lafrance et al. 2002). Thus both duration of air exposure and temperature (absolute value and change in temperature) are critical determinants of scallop survival during emersion.

A reduced capacity for oxyregulation, or increased VO_2 dependence on oxygen tension, may be a characteristic feature of species which are unlikely to experience low oxygen levels in their natural habitat (Bayne 1973). Scallops, as sublittoral, epifaunal bivalves, which are incapable of sustaining prolonged valve closure and are relatively intolerant of aerial exposure, are unlikely to experience low oxygen levels in the environment. In their analysis of 31 species of marine invertebrates, however, Mangum and Van Winkle (1973) found no correlation between the response of VO_2 to declining oxygen tension, and environmental oxygen level.

Hochachka and Somero (1984, Table 5-1) correlated the tolerance to anoxia in both terrestrial and aquatic organisms with the amount of glycogen stores, since glycogen is the main respiratory substrate during anaerobiosis. In this respect it is noteworthy that scallops, which are relatively intolerant of anoxia, contain relatively low levels of glycogen in the adductor muscle, the main storage organ (attaining maximum values of 23–25% of muscle dry weight in first-year *Argopecten irradians* (Epp et al. 1988) and 18% in *Chlamys islandica* (Sundct and Vahl 1981)). In contrast, *Mytilus edulis*, an intertidal bivalve that commonly utilises anaerobic pathways during prolonged valve closure induced by aerial exposure, attains high maximum seasonal glycogen levels of 42 to 53% in the mantle, the principle long term storage organ in mytilids (de Zwaan and Zandee 1972; Gabbott 1983).

7.3.2 Metabolic Cost of Reproduction

An increase in VO_2 associated with the metabolic cost of reproduction has been documented in the bay scallop, *Argopecten irradians irradians* (Bricelj et al. 1987b), giant scallop, *Placopecten magellanicus* (Shumway et al. 1988), Iceland scallop, *Chlamys islandica* (Vahl 1978) and black scallop *Chlamys varia* (Shafee 1982). Figure 7.10 illustrates the relationship between oxygen uptake, environmental temperature and gametogenic stage in three of these pectinid species. In contrast, MacDonald and Thompson (1986) found no significant correlation between oxygen uptake and gametogenic activity in *P. magellanicus* from Newfoundland populations at depths of 10 and 31 m. In bay scallops, gametogenesis (gonadal growth) was associated with a 50% increase in the routine rate of oxygen uptake relative to that predicted on the basis of seasonal temperature (Bricelj et al. 1987b). Vahl and Sundet (1985) found that sexually mature *C. islandica* have a higher size-specific metabolic rate during the period when they experience intense gamete differentiation, than immature scallops. For a scallop of comparable size (e.g., 0.8 g in tissue dry weight), the VO_2 of mature males and females is 57% and 70% higher respectively than that of immature scallops. They also found that the metabolic rate of sexually mature males increases at a faster rate with body size than that of mature females, and that for size classes greater than 1.2 g in tissue weight (ca. 50 mm in shell height) mature males have a higher metabolic rate than females. These authors suggest that the high cost of sperm production, involving protein synthesis, cannot be met by stored glycogen reserves, thereby restricting spermatogenesis to periods of high food availability (March to October), while oögenesis can continue throughout the fall and early winter at Balsfjord, Norway.

Bivalves typically show a pattern of increasing reproductive output with increasing age/size (Peterson 1983). Two pectinid species, however, the iteroparous *Chlamys islandica* (Vahl 1984), and the semelparous scallop *Argopecten irradians irradians* (Bricelj et al. 1987b, and Bricelj and Krause 1992), exhibit reproductive senility (*sensu* Peterson 1983) in that size-specific reproductive output declines in older individuals. Reproductive output declined in senescent *Placopecten magellanicus* from low food environments but was maintained in larger senescent scallops from adjacent higher food environments (MacDonald and Bayne 1993). The combination of seasonal availability of the food supply and the timing of the reproductive cycle permitted reproductive output to be maintained during a period of the life cycle when maintenance requires all the available resources. Fecundity was sacrificed for maintenance when food resources were limited but when food was more readily available fecundity in the large senescent individuals continued to increase (MacDonald and Bayne 1993). In the bay scallop, post-reproductive individuals approaching the end of their lifespan, exhibit a significantly lower weight-normalised VO_2 than young individuals which have not yet undergone reproduction (Bricelj et al. 1987b). Thus senescence is associated with lowered metabolic expenditure, as found for senescent gastropods *Ancylus fluviatilis* and *Planorbis contortus* (Calow 1975) and the limpet *Ferrissia rivularis* (Burky 1971).

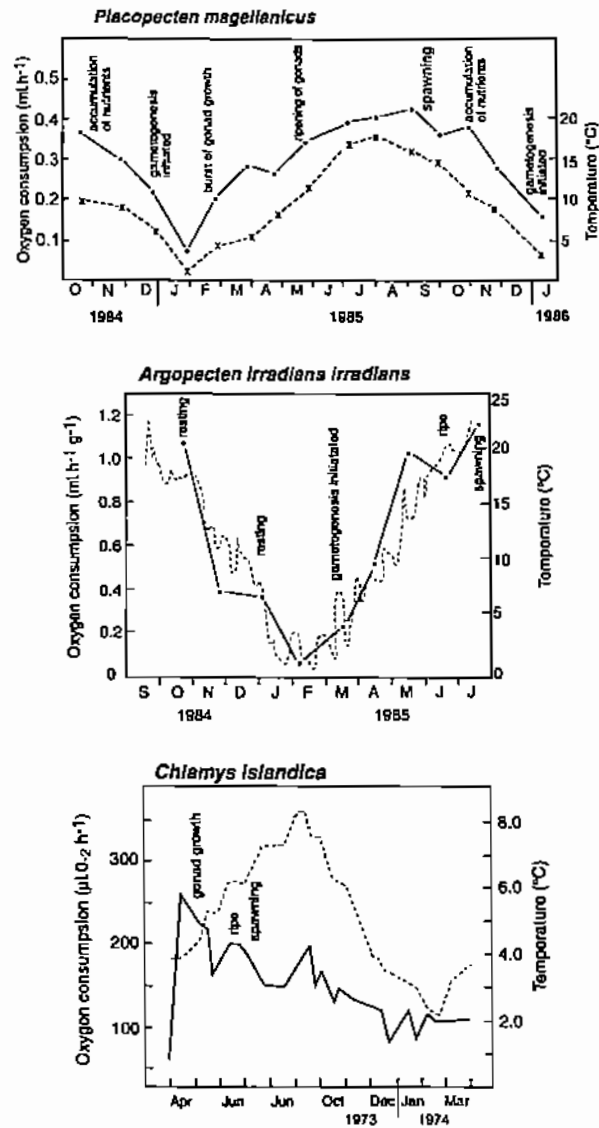


Figure 7.10. Seasonal changes in oxygen consumption of three pectinid species in relation to environmental temperature and reproductive stage. Weight-normalised oxygen uptake of *Chlamys islandica* and *Placopecten magellanicus* from Vahl (1978) and Shumway et al. (1988), respectively. Reproductive stages of *C. islandica* from Sundet and Vahl (1981). Weight-specific oxygen uptake of *Argopecten irradians irradians* from Bricelj et al. (1987a).

7.3.3 Metabolic Rate in Relation to Temperature and Latitude

Spärck (1936) observed that scallop species with a more northerly distribution, e.g., the arctic scallop, *Pecten groenlandicus*, had a relatively higher VO_2 than those of southern latitudes, such as the boreal *P. varius* and Mediterranean *P. flexuosus*, when compared at the same temperature. Bricelj et al. (1987b) also found that the northern bay scallop, *Argopecten irradians irradians*, had a higher metabolic rate than the southern Florida subspecies, *A. i. concentricus* (Barber and Blake 1985), at a comparable temperature range (20–25°C). Since these two studies examined VO_2 at environmental temperatures, however, the possibility that the latitudinal differences observed simply reflect a lower degree of acclimatisation to higher temperatures in the northerly scallop population cannot be ruled out. In *A. i. irradians* seasonal changes in VO_2 closely track changes in temperature, which can explain 93% of the seasonal variation in metabolic rate (Fig. 7.10). In the southerly bay scallop, although oxygen uptake increases significantly with environmental temperature, the latter explains only 23% of the variation in metabolism (Barber and Blake 1985). The temperature range over which VO_2 was determined, however, was considerably narrower for the Florida population (21.5–31.7°C) than for the New York population (1.5–22.9°C). Barber and Blake (1985) suggested that the combined effects of lower food supply and higher temperature-dependent metabolic rates at lower latitudes may limit this species' southern distribution along the Atlantic coast.

A positive, significant correlation between VO_2 and both seasonal and laboratory acclimation temperature has been described in *Placopecten magellanicus* from Maine at a depth of 20 m (Shumway et al. 1988; Fig. 7.10). A strong correlation between VO_2 and ambient temperature was found in *P. magellanicus* from Newfoundland at 10 m, but not in those from 31 m (MacDonald and Thompson 1986). In *Patinapecten yessoensis* oxygen uptake closely tracks seasonal temperature changes, except during the winter months when weight-standardised VO_2 increases by 13% while water temperatures are still declining (5.8 to 4.6°C) (Fuji and Hashizume 1974). This period, extending between December and February, coincides with that of maximal gonadal growth, suggesting that the increase in metabolic rate is related to reproductive cost, as found in other scallop species. The above examples serve to illustrate that the degree to which seasonal changes in metabolic rate are determined by temperature can vary considerably both among pectinid species and within the same species.

In a unique study, Pilditch and Grant (1999b) compared the effects on VO_2 , NH_4^+ and growth rate of *P. magellanicus* exposed to a fluctuating temperature regime (6 to 15°C over an 8-day cycle, averaging 10°C) to those of scallops held at a constant temperature of 10°C. The fluctuating regime was intended to simulate the relatively high-frequency temperature changes occurring in coastal waters due to upwelling. They found a small (15%) but significant increase in VO_2 of scallops exposed to the fluctuating temperature treatment compared to those held at constant temperature, although this was not detected as a significant difference in growth of shell or total soft tissue dry weight. More importantly, they found no evidence of compensatory acclimation of sea scallops to

fluctuating temperatures, as VO_2 remained dependent on ambient temperature even after 48 days of exposure.

Shafee (1982) developed a predictive multiple regression equation for *Chlamys varia*, which allows calculation of the metabolic expenditure for this species at any time of the year. Oxygen consumption (VO_2 ; $\mu\text{L h}^{-1}$) was related to ambient temperature ($^{\circ}\text{C}$), tissue dry weight (W ; g), food supply (F), and reproductive condition (a) as follows: $VO_2 = (-89.92 + 23.37 T + 1,183.76 a + 134.47 F) W^{0.72}$ ($r^2 = 0.96$). Food supply was defined as $F = 0$ or $F = 1$, for starved and fed animals respectively. The gonad index was defined as the constant "a" in the allometric equation relating gonad dry weight (G) to total tissue dry weight ($G = aW^b$).

Seasonal Q_{10} values of oxygen consumption for several pectinid species are shown in Table 7.5. Values are typically >1 , indicating that most of the scallop species listed, unlike the blue mussel, *Mytilus edulis*, have a limited ability to acclimatise their metabolic rate to seasonal temperature changes, and are thus unable to conserve energy at higher temperatures. In *Chlamys varia* standard and routine oxygen uptake rates were temperature dependent ($Q_{10} >2$), while active VO_2 (that of a starved animal suddenly exposed to food) showed a weak response to temperature ($Q_{10} = 1.0$) (Table 7.5).

7.3.4 Metabolic Rate in Relation to Activity Levels

Early work by Spärck (1936) indicated that bivalves capable of swimming such as members of the Pectinidae and Limidae families, were characterised by higher metabolic rates, as well as a greater increase in VO_2 with increasing temperature than other more sedentary bivalves of the Astartidae, Veneridae, and Tellinidae families. Van Dam (1954) however, reported VO_2 rates for *Pecten grandis* and *P. irradians*, which were within the range of values published for non-swimming boreal species.

Table 7.6 compares routine rates of oxygen uptake of pectinids with other bivalves at a common temperature (ca. 10°C). Values were carefully selected from studies in which animals were fed prior to measurements, a relatively wide size range was used, weight standardisation was carried out, and experimental animals were not experiencing rapid gonadal growth. Analysis of this table yields no evidence of increased metabolic rates in scallops when compared to a wide variety of more sedentary and sessile bivalves. Values shown, however, reflect metabolic rates of quiescent, undisturbed animals confined in experimental respirometers. They do not reflect active metabolic rates elicited during swimming or "clapping" activity of scallops. The cost of such activity cannot be incorporated in the energy budget of scallops without further understanding of its size and temperature dependence, and its contribution to overall energy expenditure. Decomposition of total metabolic rate into several functional components (Clarke 1987), partially achieved by measuring standard, routine and active metabolic rates (Bayne et al. 1976) has been carried out in considerable detail for *Mytilus edulis*, but has rarely been attempted for pectinids.

Limited information is available on the metabolic rate of scallops during locomotory activity, e.g., crawling of juveniles or swimming activity. Mackay and Shumway (1980) induced vigorous swimming of *C. deliculata* using starfish foot or extract, before placing

Table 7.5

Temperature coefficient (Q_{10}) for oxygen consumption in several pectinid species. $Q_{10} = (K_1/K_2)^{10/(T_1-T_2)}$ where K_1 and K_2 = oxygen uptake at temperatures T_1 and T_2 .

Species	Temperature (°C)		Q_{10}	Source
<i>Chlamys opercularis</i>	5–10		4.42	McLusky 1973 ^a
	10–20		0.78	
<i>Chlamys varia</i>	10–15	standard:	2.19–6.05	Shafce 1982
		routine:	1.75–4.67	
		active:	1.08–1.62	
<i>Placopecten magellanicus</i>	5–15		2.38	Shumway et al. 1988
	10–20		1.58	
<i>Patinopecten yessaensis</i>	5.8–14.8		1.09	Fuji and Hashizume
	8.9–16.9		1.78	1974
	14.8–22.4		1.64	
<i>Argopecten irradians</i>	5–15		3.36	Bricelj et al. 1987a
<i>irradians</i>	10–20		2.15	
<i>A. i. concentricus</i>	6.5–10.2		2.27	Kirby-Smith 1970
	10.2–18.0		3.16	
	18.0–25.5		2.39	
<i>Argopecten circularis</i>	20–30		1.94 ^b	Silva Loera 1986
			2.77 ^c	

^a Laboratory acclimated scallops;

^{b, c} for scallops 1 g and 0.1 g dry tissue weight, respectively.

animals into respirometers. They found that the VO_2 of active animals was 2.4 times higher than that of resting (starved) animals, while feeding did not cause an increase in oxygen consumption above the standard rate of starved scallops. This observation was related to the fact that scallops are sublittoral, continuous feeders. An elevated VO_2 in response to feeding was suggested to be more typical of intertidal, discontinuous feeders such as *Mytilus edulis*. Swimming to exhaustion of *Chlamys hastata* confined within a respirometer, induced by contact with starfish, caused a significant, 3- to 4-fold increase in VO_2 (Donovan et al. 2003). On the other hand, seasonal temperature changes did not greatly influence the metabolic rate of *C. islandica*, and Vahl (1978) suggested that a significant portion (34%) of the seasonal variability in VO_2 in this population could be explained by changes in food availability. Oxygen uptake was also significantly correlated with food levels in both shallow and deep water populations of *Placopecten magellanicus* (MacDonald and Thompson 1986). In *Chlamys varia* routine VO_2 was on the average 1.6 to 1.9 times greater than standard oxygen uptake rates determined for starved individuals (Shafce 1982).

Table 7.6

Weight-standardised routine rates of oxygen consumption (VO_2 ; mL O_2 h⁻¹ g dry tissue weight⁻¹) of pectinid species compared to other bivalves.

Species	Temp. (°C)	VO_2	Source	Notes
<i>Chlamys varia</i>	10	0.339	Shafiq 1982	A
<i>Chlamys islandica</i>	8	0.195	Vahl 1978	A
<i>Chlamys delicatula</i>	10	0.147	Mackay & Shumway 1980	B
<i>Chlamys opercularis</i>	10	0.229	McLusky 1973	B
	10–13	0.182	Vahl 1972	B, C
<i>Argopecten irradians irradians</i>	10	0.425	Bricelj et al. 1987a	A
<i>A. i. concentricus</i>	10	0.249–0.357	Kirby-Smith 1970	A, C
<i>A. purpuratus</i>	12	0.54	Navarro & González 1998	B
<i>Placopecten magellanicus</i>	10	0.244	Shumway et al. 1988	B
	10–12	0.339	MacDonald & Thompson 1986	A
<i>Potinopecten yessoensis</i>	9	0.293	Fuji & Hashizume 1974	A
<i>Donax vittatus</i>	10	0.238–0.275	Ansell 1973	A
<i>Arctica islandica</i>	10	0.317	Taylor & Brand 1975	B
<i>Cerastoderma edule</i>	10	0.200	Newell & Bayne 1980	A
<i>Mytilus edulis</i>	10	0.370	Vahl 1973b	B
	15	0.381	Bayne 1973	B, D
<i>Geukensia demissa</i>	10	0.185	Hilbish 1987	B, E
<i>Choromytilus meridionalis</i>	12	0.430	Griffiths 1980	A
<i>Ostrea edulis</i>	10	0.059	Calculated from Newell et al. 1977	A

Notes:

- A. VO_2 measured at ambient, seasonal temperature;
- B. Measured following laboratory acclimation;
- C. Assuming a tissue water content of 85% and slope $b = 0.75$;
- D. *M. edulis* can acclimate its routine VO_2 between 10 and 20°C;
- E. Calculated by extrapolation from data at 5 and 15°C.

7.3.5 Anaerobic Metabolism

Bivalves may experience functional anaerobiosis (e.g., following vigorous activity such as burst swimming in scallops) or environmental anaerobiosis, as occurs under hypoxic or anoxic environmental conditions. Recent work has established that in many

bivalves, anaerobic metabolism can contribute significantly to the total metabolic rate, particularly in intertidal species, which suffer periodic aerial exposure (Pamatmat 1980; Shick et al. 1983). Therefore oxygen consumption does not always provide a reliable measure of total metabolism or heat loss as measured by direct calorimetry. Physiological and biochemical studies conducted on *Placopecten magellanicus* indicate that in scallops, anaerobic pathways are predominantly utilised for energy production during sudden bursts of activity (swimming or valve snapping escape response induced experimentally by predator stimulation) (Thompson et al. 1980; de Zwaan et al. 1980). Swimming activity is exhibited by members of at least four bivalve families: Pectinidae, Amussidae, Limidae and Cardidae. Scallops differ, however, from actively swimming bivalves such as the fleshshell *Limaria fragilis* (family Limidae), which display slower sustained swimming activity fueled predominantly by aerobic mechanisms of ATP production (Baldwin and Lee 1979).

Scallops swim by means of jet propulsion in which water is expelled from the mantle cavity by repeated muscle contractions (valve snapping). This activity is powered by the phasic (striated or fast) portion of the adductor muscle, and to a lesser extent by the smaller catch or smooth portion, while more prolonged valve closure is exclusively powered by the catch muscle. Thompson et al. (1980) showed that in *Placopecten magellanicus* rapid shell valve adductions result in accelerated heart rate (2 to 3 fold increase), enhanced stroke volume and 5-fold increase in cardiac output, and a decrease in the PO_2 of post-branchial blood to a low value of 15 mm Hg. Although these physiological responses increase the supply of oxygen to the adductor muscle, they are insufficient to meet this organ's high energy demand during vigorous activity. The effectiveness of O_2 uptake by the scallops' blood (42% in *P. magellanicus*) and the supply of oxygen to the muscle are limited by the lack of respiratory pigments, and generally poor development of the bivalve open circulatory system. De Zwaan et al. (1980) suggested that different scallop species may vary in the relative contribution of aerobic and anaerobic metabolism to the total energy demand during swimming. In *P. magellanicus* these authors estimated that the former represents only 3% of the anaerobic contribution. However, due to the higher ATP yield of aerobic versus anaerobic glycogen utilisation, this translates into as much as 30% of the total ATP provided to the muscle by glycogen catabolism. The energy demand during valve snapping and the subsequent recovery phase is thus largely met by anaerobic glycolysis, and by the breakdown of high-energy phosphagen compounds (arginine phosphate, Arg P) in muscle tissue (arginine phosphate + ADP = arginine + ATP). The relative contribution of these two processes to the total energy demand during valve snapping varies between muscle parts, with phosphoarginine hydrolysis contributing most (72%) of the ATP requirement in the phasic muscle and only 34% in the catch muscle (de Zwaan et al. 1980).

The amino acid octopine is the main end product of anaerobic glycolysis accumulated in muscle tissue (both phasic and catch portions) as a result of exhaustive swimming and valve clapping in scallops (e.g., Grieshaber and Gade 1977; Baldwin and Opie 1978; Chih and Ellington 1983), as well as cephalopods, *Nautilus pompilius*, *Loligo vulgaris* and *Sepia officinalis*, and in *Cardium tuberculatum*, following vigorous jumping (reviewed by

Zandee et al. 1980). Octopine synthesis is catalysed by the enzyme octopine dehydrogenase (Odh) according to the reaction:



Other metabolic end products such as propionate and succinate are more typical of sedentary or sessile bivalves exposed to low oxygen tensions for prolonged periods. Breakdown of glycogen to octopine is associated with relatively low ATP yield per fuel equivalent (i.e., low efficiency of energy production) and rapid fatigue, but yields a relatively high rate of energy production or ATP output per unit time compared to propionate and succinate (Zandee et al. 1980; Livingstone 1991). Thus glycogen conversion to octopine is adaptive during temporary muscle anoxia associated with short term burst activity, such as swimming in scallops. Octopine production provides active marine molluscs (scallops, cephalopods) with an anaerobic pathway functionally analogous, although evolutionarily more primitive than that of lactate production, characteristic of vertebrates as well as many marine, freshwater and terrestrial invertebrates including gastropods (Livingstone 1991). Octopine production, however, differs from lactate production in that it results in a less acidic end product, has a lower energy yield, and requires an amino acid (arginine) as well as carbohydrate as substrates.

Thus, swimming to exhaustion, induced experimentally by contact with starfish, caused a significant (~2-fold) increase in octopine levels, as well as a significant decrease in Arg P levels in the scallop *Chlamys hastata* (Donovan et al. 2003). In this study, encrustation of scallops with barnacles negatively affected their swimming capacity and resulted in increased anaerobic energy expenditure. Octopine levels of scallops exhausted by swimming were higher in encrusted than unencrusted scallops. The latter also consumed approximately twice as much Arg P as unencrusted scallops. In *Argopecten irradians concentricus* octopine production in the adductor muscle was restricted to periods of contractile activity (burst swimming) but did not occur during environmental hypoxia (Chih and Ellington 1983). Following 4 h of hypoxia there was a decline in Arg P and accumulation of succinate but no detectable octopine production.

A 5-fold increase in ODH activity in juvenile *Argopecten irradians* was related to a decrease in their percent attachment to the eelgrass canopy and thus increase in swimming activity between 6.7 and 29 mm SH (García-Esquivel and Bricelj 1993). On this basis, these authors proposed Odh activity as an index of the scallops' capacity for burst swimming activity. A significant positive correlation was described between the degree of individual multilocus heterozygosity and octopine accumulation after burst activity in *P. magellanicus* (Volckaert and Zouros 1989), and between heterozygosity and Odh and pyruvate kinase activities in the adductor muscle of the scallop *Euvola ziczac* (Alfonsi et al. 1995). In this context, Pérez et al. (2000) found that in *E. ziczac* the affinity of the Odh enzyme for pyruvate was greater in heterozygous than homozygote individuals at the Odh locus. These findings support the suggestion made by Volckaert and Zouros (1989) that the fitness advantage of heterozygosity in motile bivalves such as scallops may be related to their increased metabolic capacity for burst swimming involved in predator escape.

Repeated valve snapping can only be maintained for a few minutes and is followed by a period of apparent exhaustion, evidenced by the scallops' lack of response to further stimulation and valve closure. During this period blood PO_2 remains low, and scallops consume no oxygen, yet an increased heart rate is maintained. Thus recovery takes place under hypoxic/anoxic conditions. Utilisation of phosphoarginine and accumulation of octopine appear to occur more or less sequentially in scallops, the former providing the main energy source during initial valve snapping, and the latter accumulating mainly during later stages of swimming (Chih and Ellington 1983) or during recovery following exhaustion (Gäde 1980). Thus octopine formation serves primarily to replenish cytoplasmic NAD^+ required to maintain a high glycolytic flux (Baldwin and Opie 1978; Zandee et al. 1980). Upon reopening of valves, scallops exhibit a transient increase in VO_2 above normal, resting levels (Thompson et al. 1980). This increase probably reflects the repayment of an oxygen debt, i.e., the oxidation of anaerobic end products (octopine) accumulated in the tissues, although it could also reflect reoxygenation of the hemolymph. Restoration of physiological functions to resting values takes several hours in exhausted scallops. In adult *Argopecten irradians* a considerably shorter recovery period of 90 s was required before 100% of bay scallops tested experimentally could attempt a second swim following a prior swim, but the swimming distance was significantly shorter than on the first attempt, suggesting that full physiological recovery had not been achieved (Winter and Hamilton 1985).

Scallops do not normally experience prolonged periods of valve closure. However, Thompson et al. (1980) were able to induce valve closure in *Placopecten magellanicus* for up to 90 min by occasional tapping of the shell margin. Under these conditions, physiological responses differed from those elicited during valve snapping activity. The PO_2 of blood from the adductor muscle sinus remained relatively high (40 mm Hg), there was no increase in heart rate, and scallops continued to take up oxygen although at a reduced rate. Scallops are able to ventilate through the gape which occurs where the valves do not closely oppose each other. Thus although anaerobic pathways are invoked in the catch adductor, metabolism during valve closure remains largely aerobic. Furthermore, during valve closure phosphagen contributes less energy than anaerobic glycolysis to the total energy demand of the muscle, and octopine is no longer the sole end product of anaerobic metabolism, as observed during valve snapping (de Zwaan et al. 1980). Thus, both alanine and succinate were produced during valve closure.

A study using *in vivo* nuclear magnetic resonance to measure changes in phosphorus-containing metabolites showed that laboratory-induced hypoxia in juvenile *Placopecten magellanicus* collected in winter, when glycogen stores are low, caused a marked reduction in Arg P concentrations and intracellular pH, with an associated increase in inorganic phosphate (P_i) levels (Jackson et al. 1994), thus indicating a reliance on this phosphagen to meet the energy demands during environmental anaerobiosis. A similar response to hypoxia was observed in excised adductor muscle from adults, but was not apparent in live juvenile scallops collected in the summer. On this basis the authors suggested that changes in Arg P and P_i , or in the ratio Arg P/ P_i might provide a useful and more sensitive indicator of stress and energy status of scallops than the adenylate energy charge (AEC).

7.4 ENERGY UTILISATION

7.4.1 Excretion and Byssus Secretion

The excretion of nitrogenous excreta represents a potentially significant loss of energy in bivalves, particularly during conditions of severe nutritive stress when reliance on protein catabolism to support metabolic demand increases (Gabbott and Bayne 1973). Although ammonia is the major nitrogenous excretory product in bivalves, under certain circumstances dissolved organic nitrogen (primary amines) may comprise a significant fraction of total nitrogen excretion. In *Mytilus edulis* for example, the excretory loss represents up to 31% of the respiratory energy demand during the winter (calculated from Hilbish and Koehn 1985). At this time, amine and ammonia excretion contribute about 76 and 24%, respectively, to the total energy loss as nitrogenous excreta. Very limited data are available on excretion rates of nitrogenous products in pectinids. It is of particular interest to obtain information on the relative loss of primary amines and ammonia in this bivalve group, since several scallop species are known to rely heavily on protein catabolism during gametogenesis as well as during periods of negative energy balance (e.g., overwintering conditions) (Epp et al. 1988).

Ammonium excretion rates (VNH_4) have been determined for adult *Argopecten irradians concentricus* (Barber and Blake 1985), and are estimated to represent about 14% (range = 8.5 to 18.5%) of the respiratory energy loss. A similar contribution of VNH_4 to the respiratory loss (= 13.5%) was obtained for juveniles of this subspecies (Lu and Blake 1999). Ammonia excretion of adults increased significantly with decreasing salinity, a finding consistent with the role of excretory products (free amino acids) in cell volume regulation of bivalves (Deaton et al. 1984). Similarly, in *A. purpuratus* VNH_4 increased between 30 and 24 ppt, but declined with a further decrease in salinity (24 to 18 ppt), a range over which these scallops are physiologically impaired and show negative scope for growth (Navarro and González 1998).

The ratio of oxygen consumed to NH_4 - N excreted (O:N, calculated in atomic equivalents) was used in conjunction with respiratory quotients ($\text{CO}_2:\text{O}_2$) to identify seasonal changes in the dominant catabolic substrates in *A. irradians concentricus* (Barber and Blake 1985). Oxygen:N values, which ranged from about 6 to 22, were generally lower than those reported for mussels, *Mytilus edulis*. In this species values of 30 or below are generally indicative of a stressed animal with relatively high protein catabolism, and typically exceed 50 during periods of tissue growth (range = 17 to 120; Fig. 14 in Bayne and Newell 1983). In *Argopecten purpuratus* O:N values ranged between 9.5 and 32.6 over a salinity range of 30 to 18 ppt, showing a consistent decline with decreasing salinity in larger individuals (5 to 10 g dry soft tissue weight) (Navarro and González 1998). Values <15 were associated with unsuitable conditions for growth in larger scallops. There was also a negative relationship between scallop size and the O:N ratio, indicative of higher protein catabolism in younger individuals. In juvenile (57 mm SH) *P. magellanicus* exposed to varying experimental conditions (constant or fluctuating temperature regime; high or low food supply), O:N ratios ranged from 12 to 20 (Pilditch and Grant 1999b). In this study sea scallops showed positive shell and soft tissue growth

rates under all experimental conditions tested. A lower value of 8.9 was obtained for this species under thermal stress (Grant and Cranford 1991). Starvation of juvenile *P. magellanicus* yielded a C:N ratio of 12.7 compared to a value of 31 for scallops fed algal diets (Volckaert 1988 in Grant and Cranford 1991). Lower O:N ratios in scallops may be related to the more significant contribution of protein catabolism to the total energy metabolism in this group of bivalves (Epp et al. 1988) compared to *M. edulis*, which preferentially utilises glycogen stores to fuel gametogenesis (Gabbott 1975, 1983). Utilisation of the O:N ratio as a generalised index of physiological condition in scallops thus requires additional information on suitable reference values under normal as well as stressed conditions in each species.

Byssus secretion persists into the adult phase only in some pectinid species, such as *Chlamys islandica* and *C. opercularis*. In *Placopecten magellanicus* byssus formation (number of threads secreted) and rate of byssus attachment decline with increasing body size (Caddy 1972). The rate of byssus formation also increases with temperature, while percent attachment is temperature independent. The cost of byssus production as a function of scallop size/age has been determined for adult *Chlamys islandica* by measuring the energy content of byssal threads, which are composed mainly of quinone tanned protein (Vahl 1981). Byssus secretion represents only a minor component of the energy budget, ranging between 4 and 14% of somatic production.

7.4.2 Growth

Growth represents the integrated response of physiological processes of energy acquisition and expenditure detailed in the previous sections. Scope for growth and resource allocation between somatic and reproductive tissue production in pectinids are examined in a separate chapter (Thompson and MacDonald 1991; Chapter 8, this volume). Seasonal growth in bivalves, including pectinids, is influenced by the interaction of several environmental variables, particularly water temperature and food supply (e.g., Broom and Mason 1978; Bayne and Newell 1983). Food availability has often been found to exert a greater influence on growth rate than temperature in temperate scallop species (Orensanz 1984; MacDonald and Thompson 1985), as well as in species inhabiting regions of continually low temperatures, such as the subarctic scallop *Chlamys islandica* (Vahl 1978) and Antarctic scallop, *Adamussium colbecki* (Stockton 1984).

Scallops are generally very vulnerable to the effects of low salinities, as they are unable to maintain prolonged valve closure. In *Argopecten purpuratus* positive scope for growth (determined from physiological rate measures) was only obtained at 27 to 30 ppt. At lower salinities (24 to 18 ppt) scope for growth was negative as a result of the combined effects of reduced clearance and ingestion rates and high excretion and aerobic respiration rates (Navarro and González 1998).

In pectinids, intraspecific variability in growth rates and tissue weight for a given shell height has most frequently been correlated with differences in water depth. Scallops from inshore, shallower waters typically display higher growth rates and maximum sizes than those from deeper waters (*Placopecten magellanicus*: MacDonald and Thompson 1985; Schick et al. 1988; *Patinopecten caurinus*: Haynes and Hitz 1971; MacDonald and

Bourne 1987; *Pecten maximus*: Mason 1957; *Hinnites multirugosus*: Leighton 1979; see also Chapter 28 Lodeiros et al. this volume and Lodeiros et al. 1998). Depth *per se* is not the limiting factor, but, as demonstrated for *P. magellanicus* by MacDonald and Thompson (1985), growth is promoted by relatively higher temperatures and more importantly, higher food levels in shallow waters lying within the productive euphotic zone. For *Placopecten* from Canadian waters, differences in somatic weight between depths were more pronounced than differences in shell height. The negative correlation between maximum size and depth reported for many scallop populations thus supports Sebens' (1982) theoretical growth model, which predicts that maximum size attained by animals with indeterminate growth increases with habitat suitability (lower physiological stress).

Field experiments on the effect of depth on scallop growth convey mixed results. Comparisons between studies are complicated due to differences in species, starting sizes, stocking densities, gear, site, time of year and environmental conditions. Some reports document a decrease in growth with an increase in culture depth while others show no significant differences or even an increase in growth with depth. Côté et al. (1993) examined the influence of depth on the growth of juvenile sea scallops *Placopecten magellanicus* using pearl nets with 6-mm mesh and 0.16 m² bottom surface area. Nets were filled with 50, 100, 200, or 300 scallops (mean height 14.4 mm) and suspended from the surface at 9, 15, and 21 m. Growth, measured as dry mass of the shell, muscle and other soft tissues, tended to decrease with depth although the differences were only significant for soft tissue. At all depths, after 1 year, growth (measured as mean shell height) of scallops stocked at 50 individuals per net was significantly larger than of scallops stocked at 200 and 300 individuals per net. Focusing on *P. magellanicus* spat, Grecian et al. (2000) also evaluated the effects of culture depth. Four size classes (1.4–1.69 mm, 1.70–1.99 mm, 2.00–2.99 mm, ≥3.0 mm) of scallop spat were sorted and deployed in different types of nursery-based equipment including collector bags (1.2 and 2.0 mm) and pearl nets (1.5 and 3.0 mm) at two depths (5 and 10 m) for 10 months. Highest growth rates were found for the largest size class, in pearl nets and suspended in shallower waters. Rupp et al. (2004) examined depth and density effects on the lion's paw scallop, *Nodipecten nodosus*, in Southern Brazil. Postlarvae (0.4 mm) were deployed in collector bags at two densities (340 and 150 scallops/spat bag) at two depths (4 and 12 m) for 26–27 days. Growth rates were higher in shallower waters (4 m) during the summer (March–April) when South Atlantic Central Water (SACW) creates temperature and food quality differences with depth. In the winter (June–July), without SACW intrusions there were no depth related growth differences. Results from a computer model of the effects of depth and density on the growth of the Icelandic scallop, *Chlamys islandica* predict no effect of depth as long as no food limitation occurs (Fréchette and Daigle 2002). The model suggests that if food limitation occurs, growth rates would decrease with depth.

Emerson et al. (1994) also evaluated the effects of depth on the growth of *P. magellanicus*. Mesh cages (10 x 50 x 100 cm; 6-mm mesh) were filled with 100 juvenile scallops (mean shell height 39.7 ± 5.0 mm) and secured to a frame at 0, 20, 50, 100, or 200 cm above the bottom in approximately 7-m deep water. By the second period of the

growth experiment (October-November), scallops on the bottom had significantly larger shell heights than scallops at any other depth, but by the end of the experiment (March) it was determined that water depth had no consistent effect on shell height. Depth also had no significant effect on the ash content of soft tissues or the weight of the adductor muscle. The weight of soft tissues (excluding muscle) of scallops on the bottom was 40% less than that of scallops growing more than 50 cm off the bottom. Emerson et al. (1994) concluded that high seston concentrations near the bottom inhibited growth rather than providing an energetic benefit. Parrish et al. (1995) also reported that growth rates for *P. magellanicus* were similar over a range of depths. In this study, 200 scallops approximately 40 mm in shell height were ear hung on 1.2 x 1.2 m frames at 20, 50, and 300 cm above the bottom in 10-m water. Mean shell height (mm) and mean dry body mass (mg) were similar at all three depths over the course of the experiment (May-December) but appeared to be highest at 300 cm off the bottom during the latter part of the sampling period although the seston at that depth had the lowest concentration of microplankton, chlorophyll-*a*, AFDW and total lipids. Parrish et al. (1995) concluded that other factors than simply the availability of food, or high energy compounds are important to the growth of scallops. Kleinman et al. (1996), using *P. magellanicus* (mean shell height 22.2 ± 0.1 mm) compared growth in uncontained bottom cultures to growth in suspended pearl nets (100 scallops per net). During most months of the survey, significant differences were found between their three study sites for both culture methods. Although the average soft tissue condition index was significantly higher in the suspended cultures, shell growth rates, average adductor muscle condition index and average whole dry weights were all significantly higher for scallops in bottom cultures. Water temperature, total particulate matter, and chlorophyll concentration explained up to 66% of the variation in shell growth rates in suspended culture and up to 78% in bottom culture, and between 55% and 80% variation in soft tissue growth in suspended and bottom culture, respectively (Kleinman et al. 1996).

The depth at which pearl nets are suspended in the water column can also result in substantial growth differences for juvenile sea scallops. In an experiment, in which pearl nets were variously suspended from 5 m off-bottom to 0.25 m off-bottom, Dadswell and Parsons (1991) found that the mean size of juveniles ranged from 54 to 42 mm, respectively. Growth differences of this magnitude were similar to the effects of stocking density as determined by Parsons and Dadswell (1992). The effect of suspension depth on growth in sea scallops and other species of scallops has been attributed to differences in food level (Wallace and Reinsnes 1984, 1985; Côté et al. 1993). In a study contrasting an open and sheltered location in the Iles-de-la-Madeleines, scallop spat were found to grow and survive better in pearl nets that were grown near the surface (Gaudet 1994). Côté et al. (1993) found that spat grew better at 9 m than at 21 m and related this to the levels of food in the 0.7 to 5.0 μm size range, although density effects masked some of the trends. From the above observations we can see there is likely no one depth that will be suitable in all locations. The optimum culture depth for a particular location will depend on the distribution of the food in the water column and the depth to which wave action will impact the suspended culture gear. There may also be interactions with other fouling species that may be depth dependent.

Intraspecific variation in growth between localities at similar depths has also been related to food limitation associated with high scallop densities (Gruffydd 1974; Orensanz 1984) and/or reduced flow (Cooper and Marshall 1963; Eckman 1987). Only a few studies have evaluated the effects of density on scallop growth. Côté et al. (1993) investigated the effects of stocking density on the growth of juvenile sea scallops *Placopecten magellanicus*. Using 6-mm mesh pearl nets with a bottom surface area of 0.16 m² and scallops with a mean shell height of 14.4 mm, nets were filled with 50, 100, 200, or 300 scallops and suspended from the surface at 9, 15, and 21 m. Growth, measured as dry mass of the shell, muscle and other soft tissues, decreased with increasing density but the differences were only significant between 50 and 300 scallops per pearl net. After 1 year, at all depths, the mean shell heights of scallops stocked at 50 individuals per net were significantly larger than of scallops stocked at 200 and 300 individuals per net. Using the same style of pearl nets, Côté et al. (1994) stocked 50, 75, 100, 150, 200, or 250 scallops (shell height 29.6 ± 0.3 mm) per net and anchored the nets 9 m above the bottom (approximately 15 m from the surface). In one set of nets all scallops were alive while in the other set of nets only 25 scallops were alive and the others were scallop shells glued together as "dummies". After three months (July–October), at densities of 100 scallops/net and greater, mean growth rates of both shell and dry mass were always significantly lower in nets without dummies suggesting that the effects of density on growth were due to food limitations and not the lack of space. Growth models for Iceland scallops, *Chlamys islandica* also support the importance of food depletion on scallop growth (Fréchette and Daigle 2002).

The results for scallop spat are not as clear. Groccian et al. (2000) found no significant difference in growth rates between *P. magellanicus* spat (2.0–3.3 mm shell height) stocked at 2,600 and 5,200 scallops per collector bag deployed at 5-m for 8 months. They used "onion" collector bags, measuring 40 x 80 cm with a 3-mm nominal mesh size, filled with 1 meter of Netron®. The authors suggest that their relatively low stocking densities may not have created limitations of food or space for the spat. Also working with scallop spat, Rupp et al. (2004) examined the effect of density on the lion's paw scallop, *Nodipecten nodosus*, in Southern Brazil. Postlarvae (0.4 mm) were deployed in collector bags at two densities (340 and 150 scallops/spat bag) at two depths (4 and 12 m) for 26–27 days. A slight, but statistically significant decrease in shell heights was observed at both depths for postlarvae stocked at the higher density.

Due to the high energetic cost of reproduction, shell and somatic tissue growth in pectinids may also be greatly influenced by reproductive events. Cessation or retardation of shell growth during the reproductive period (gonadal growth and spawning), and resumption of growth following spawning have been reported in *Argopecten irradians* (Bricelj et al. 1987a, Bricelj and Krause 1992), *Notovola meridionalis* (Fairbridge 1953) and *Patinopecten yessoensis* (Maru and Obara 1967), whereas shell and gonadal growth coincide in other pectinids such as *Chlamys opercularis* (Broom and Mason 1978) and *C. islandica* (Vahl 1978; 1981). In pectinids in which gametogenesis involves the utilisation of energy stores (reviewed by Barber, this volume), growth of somatic tissues may not follow the same pattern as shell growth, and is expected to be more strongly influenced by

the reproductive cycle than in species which meet their energy demand primarily from the external food supply.

Growth curves shown in Figure 7.11a, b, c illustrate the remarkable variability in growth rates, longevity and maximum size displayed by the Pectinidae. Shell growth has commonly been described by the von Bertalanffy model, and age information obtained from external growth rings in the shell. The largest scallop species, which attain asymptotic heights (H_{∞}) of up to 160–170 mm, are generally long-lived, with lifespans ranging between 18 and 23 years. These species are often characteristic of deeper waters (up to 100–200 m), such as *Chlamys islandica* (Vahl 1981), *Patinopecten caurinus* (MacDonald and Bourne 1987) and *Placapecten magellanicus* (MacDonald 1986; Schiek et al. 1988), or of moderate depths (up to 50–60 m) such as *Pecten maximus* (Mason 1957) and *Crassadoma gigantea* (MacDonald and Bourne 1989). In contrast, species restricted to shallow coastal waters (<10 m) are generally characterised by shorter lifespans (2–8 years) and smaller asymptotic size. For example, *Argopecten irradians irradians* reaches a maximum size of 80 mm at 2 years (Bricelj and Krause 1992), *Chlamys varia* attains ca. 54 mm at 7–8 years (Conan and Shafee 1978) and *C. tehuelcha* (H_{∞} = 83–91 mm) lives only about 6 years (Orensanz 1984).

Large size, protracted lifespan and deep water habitat are however, not always correlated with slow growth. The Bertalanffy growth coefficient (k) provides a measure of the rate of which animals reach their asymptotic shell height. The purple hinge roek scallop *Crassadoma gigantea* is slow growing, as reflected by its low k value (= 0.17) (MacDonald and Bourne 1989), while the giant Pacific sea scallop *Patinopecten caurinus*

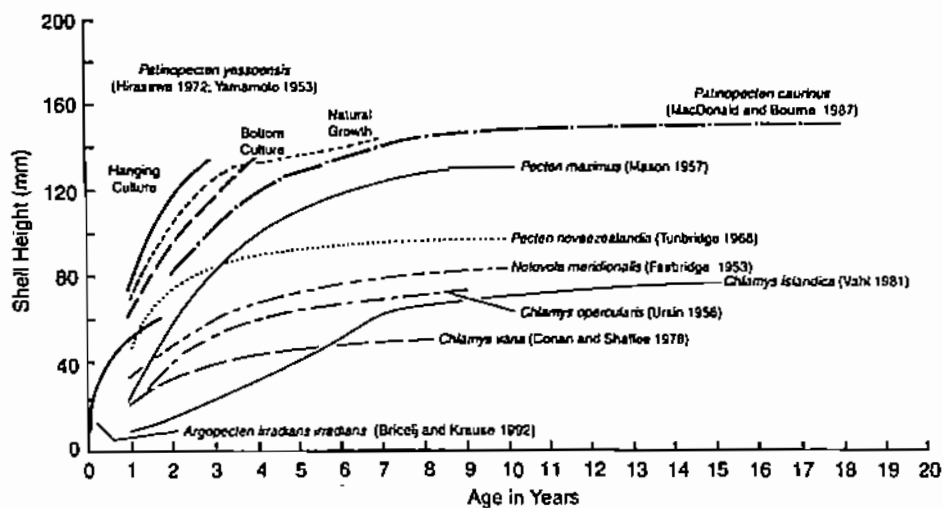


Figure 7.11a. Comparative growth curve of various pectinid species.

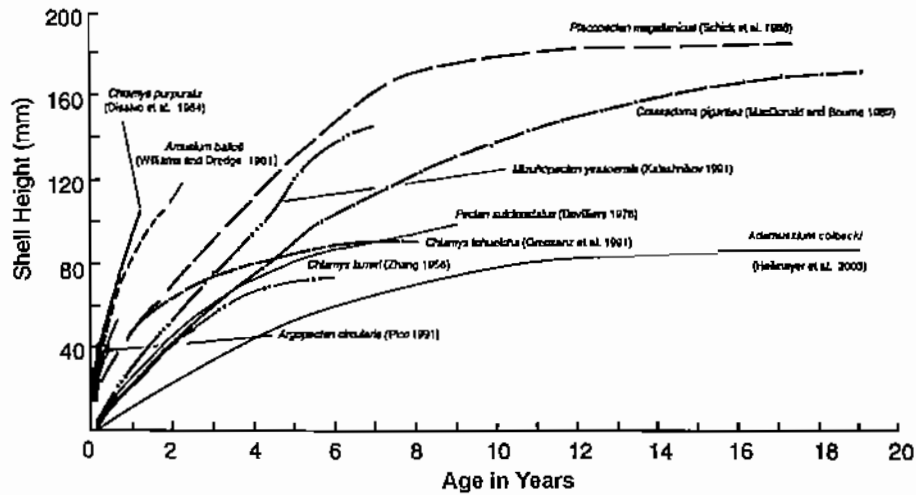


Figure 7.11b. Comparative growth curves of various pectinid species.

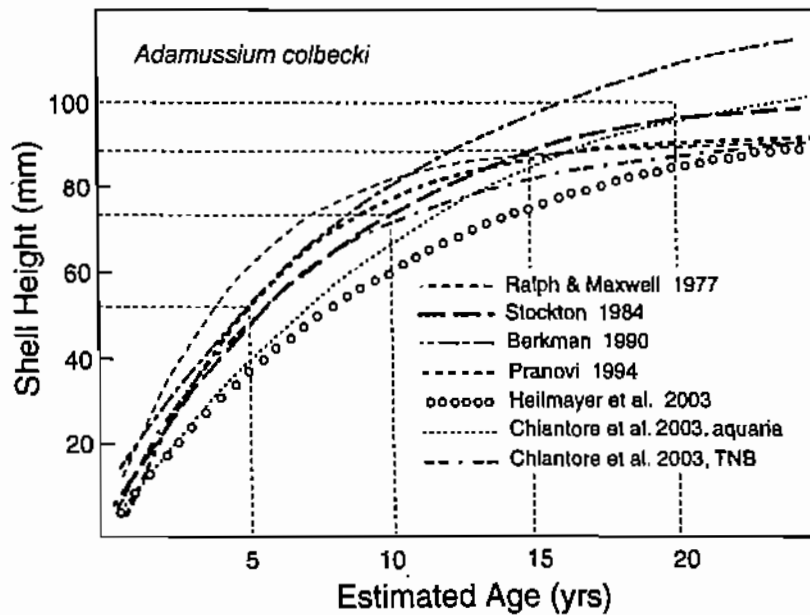


Figure 7.11c. Von Bertalanffy growth functions of Antarctic scallop *Adamussium colbecki* populations from various studies. TNB = Terra Nova Bay. After Heilmayer et al. (2003).

grows fairly rapidly ($k = 0.39$) (MacDonald and Bourne 1987). A literature review of growth parameters for the giant scallop *Placopecten magellanicus* (Schick et al. 1988) provides an average k value of 0.24 ($n = 74$; $SD = 0.06$), which ranges widely between 0.17 and 0.38 depending on habitat suitability.

Finally, scallops grown in suspended culture generally achieve faster shell and somatic tissue growth rates, and a greater tissue weight and thinner shell for a given height than wild scallops of comparable age growing on the bottom (Ventilla 1982; MacDonald 1986; MacDonald and Bourne 1989). This agrees with the observation made earlier for natural scallop populations, that within a species, growth rate in shallow water is often greater than in deeper waters. In *Placopecten magellanicus* MacDonald (1986) showed that accelerated growth in above-bottom culture was also accompanied by a reduction in longevity and maximum size (from 174 to 128 mm in shell height). Thus, provided that fouling is controlled, enhanced growth of scallops suspended in surface waters results from the exploitation of more favourable seston and temperature conditions in the overlying water column relative to those present on the bottom (Leighton 1979; Wallace and Reinsnes 1985).

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Developments in Aquaculture and Fisheries Science - 35

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SECOND EDITION

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First edition 2006

Library of Congress Cataloging in Publication Data

A catalog record is available from the Library of Congress.

British Library Cataloging in Publication Data

A catalogue record is available from the British Library.

ISBN-13: 978-0-444-50482-1

ISBN-10: 0-444-50482-6

ISSN: 0167-9309 (Series)

Ⓢ The paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).
Printed in The Netherlands.

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