

PHYSIOLOGY: ENERGY ACQUISITION AND UTILIZATION

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ENERGY ACQUISITION

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) found that detrital diets alone, such as fresh and aged macroalgal detritus from the kelp *Laminaria longicruris*, or resuspended sediments containing benthic microalgae, were inadequate to support growth of adult *Placopecten magellanicus* under laboratory conditions. Only phytoplankton diets (*Isochrysis galbana*) fed at weight rations comparable to the detrital diets, sustained tissue and gonad growth in this species. Recent studies using ¹⁵N as a tracer (Aber *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.

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*, *Licmophora*, *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 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 tehuelcha*, 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 *Syn-*

edra investens, *Melosira sulcata*, *Grammathopora marina* and *Navicula* spp., were dominant in gut contents throughout most of the year (Figure 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 *Glyphodesmia0 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.

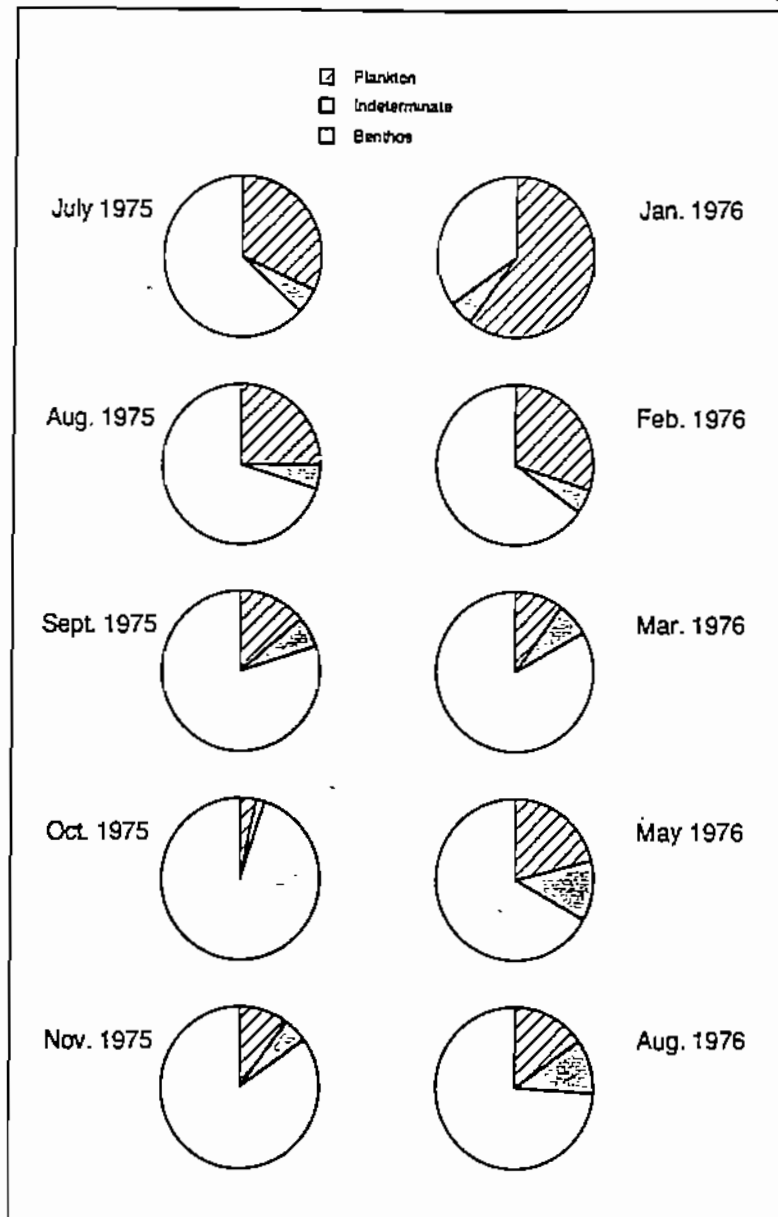


Fig. 1. Seasonal changes in source of the diet (% numerical abundance of planktonic and benthic microalgae) as determined from stomach content analysis in the Patagonian scallop *Chlamys tehuelcha* (1975 cohort) (modified from Vernet, 1977).

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 tehuetcha*, 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.

Feeding Currents

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).

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 post-settlement stages of 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, 1973b) and *Argopecten irradians concentricus* (Palmer and Williams, 1980; Riisgård, 1988)), is about 5–7 μm (Figure 2). Free bacterioplankton, typically ranging in size from 0.3 to 1 μm , is therefore not available as a food source for pectinids. 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 particles = ca. 27 and 5% respectively (Vahl, 1973b)).

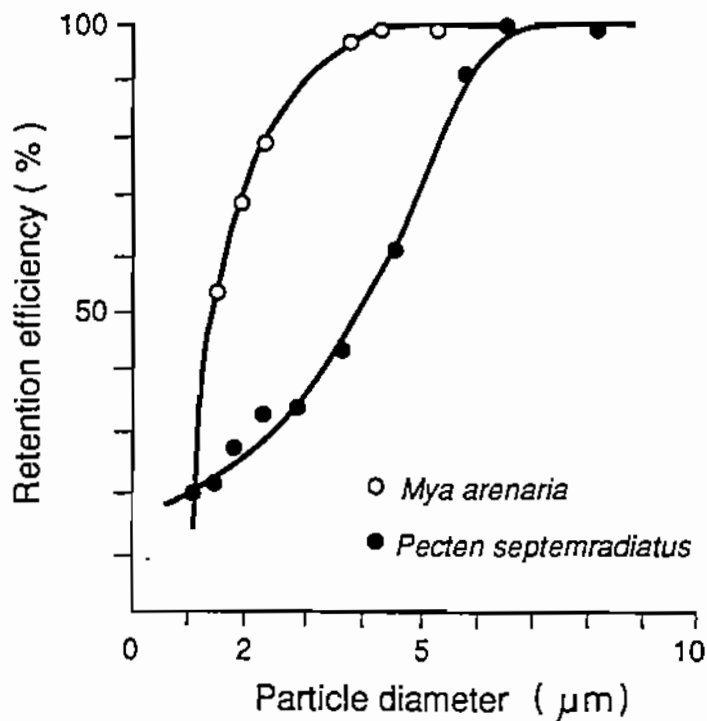


Fig. 2. Retention efficiency (%) as a function of particle size in a typical pectinid (*Pecten septemradiatus*) and a bivalve with well developed eulaterofrontal cirri (e.g. *Mya arenaria*) (from Møhlenberg and Riisgård, 1978).

It must be pointed out that retention efficiencies are generally determined using electronic particle counters (with a 50 µm or larger aperture tube). Jørgensen *et al.* (1984) found that these instruments tend to somewhat overestimate retention efficiencies of small particles (< 2 µm in diameter). 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.

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, 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). Pectinids possess a plicate, heterorhabdic gill in which ordinary filaments and principal filaments form the crests and grooves respectively of the plicae. The laterofrontal tracts consist only of small, simple pro-laterofrontal cilia, and lack the large compound eulaterofrontal cirri characteristics of mussels (Owen and McCrae, 1976).

Laterofrontal ciliary tracts, located across the entrance to interfilamentary spaces, were previously believed to act as sieves retaining particles passing through the gill filaments. They are now believed to contribute in creating the frontal surface currents, and to act as complex modulators of the process of particle retention. This is presumably achieved by influencing the steepness and height of velocity gradients in the boundary zone between through currents entering the gill interfilamentary space, and surface currents along the frontal surface of gill filaments (Jørgensen, 1981). Jørgensen's velocity gradient hypothesis, originally developed to explain particle retention in 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.

On the other hand, Owen and McCrae (1976) suggest that the poorly developed laterofrontal tracts 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 the principal filaments all combine to create a region of low pressure which tends to attract particles into the gutters formed by principal filaments.

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 ($< 3.4 \mu\text{m}$) at high algal concentrations ($6.1 \text{ mg wet weight} \cdot \text{l}^{-1}$) than at low concentrations ($0.9 \text{ mg} \cdot \text{l}^{-1}$), whereas an inverse effect was observed in the oyster *Crassostrea virginica*.

Unlike juveniles and adults, bivalve larvae capture food particles using the preoral cirri of the velum. Using high-speed video microscopy, Gallager *et al.* (1989) demonstrated that scallop larvae are capable of retaining particles above and below the $6 \mu\text{m}$ threshold with equal efficiency. This has also been demonstrated for larvae of the hard clam, *Mercenaria mercenaria*, which were able to capture particles between 0.5 and $8 \mu\text{m}$ with equal efficiency (Gallager *et al.*, 1988).

Feeding rates

The allometric relationship between clearance rate and body size (tissue dry weight) for several pectinid species is shown in Table 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 highest value was obtained by Meyhöfer (1985) using a very narrow size range and small sample size ($n = 4$), and thus provides a less reliable estimate.

TABLE 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	3.09	0.60	Vahl, 1980
<i>Chlamys hastata</i>	1.8 - 2.2	12.8	0.145	0.943	Meyhofer, 1985
<i>Placopecten magellanicus</i> (10m depth)	1.8 - 42	5.5-8.5 10 - 12	0.616	0.76	MacDonald & Thompson, 1986
			1.318	0.60	
			0.891	0.66	
<i>Argopecten irradians concentricus</i>	0.016 - 0.6	10	3.435	0.855	Manning, 1985 ¹
			5.827*	0.584	Kirby-Smith, 1970
			4.742	0.82	Chipman & Hopkins, 1954 ²

* Assuming 85% water content of tissues;

1. Clearance rate determined with *Isochrysis galbana* (3.5 μ m) and thus underestimates pumping rate;
2. Calculated by Winter, 1978.

Weight-normalized 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 2. Clearance rates listed are equal to pumping rates since measurements were made with particles large enough to be retained with 100% efficiency. 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. Interspecific comparisons 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-standardized pumping rates were highest for two filibranch species, the scallop *Chlamys hastata* ($0.145 \text{ l} \cdot \text{h}^{-1}$) and mussel *Mytilus californianus* ($0.133 \text{ l} \cdot \text{h}^{-1}$), followed by *Clinocardium nuttallii* ($0.051 \text{ l} \cdot \text{h}^{-1}$) and finally by *Macoma nasuta* ($0.0014 \text{ l} \cdot \text{h}^{-1}$), a deposit feeder capable of facultative suspension feeding. *Chlamys* and *Mytilus* also had extremely large gills relative to their body size. Their gill area per unit of tissue dry weight (22 and $27 \text{ cm}^2 \cdot \text{g}^{-1}$ respectively) was an order of magnitude greater than that of the other two species. When compared in terms of their pumping rate per unit gill area ($\text{ml} \cdot \text{s}^{-1} \cdot \text{cm}^{-2}$), however, the four bivalves ranked as follows: *Clinocardium* (0.145) > *Chlamys* (0.112) > *Mytilus* (0.084) > *Macoma* (0.008). Møhlenberg and Riisgård (1979) compared feeding rates of thirteen bivalve species and reported clearance rates considerably higher than those from previous studies. Weight-standardized clearance rates of the two scallops, *Pecten furcivus* and *Pecten (Chlamys) opercularis*, based on only three measurements (Table 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.

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 behavior), b) reducing their clearance rates, and/or c) increasing the amount of material rejected in pseudofeces (Foster-Smith, 1975, 1976). Palmer (1980) characterized 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 probably not an endogenous feature of the scallop's feeding behavior. 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 relationship between clearance rate and algal concentration has been described for adult bay scallop *Argopecten irradians concentricus* (Palmer 1980; Figure 3). Clearance rates are reduced by 95% over the concentration range 0.94 to $9.4 \text{ mg dry wt.} \cdot \text{l}^{-1}$ (1.23 to $12.3 \times 10^6 \mu\text{m}^3$). Therefore, above a threshold concentration of ca. $2 \text{ mg dry weight} \cdot \text{l}^{-1}$, algal ingestion rate becomes independent of concentration. 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* (1,200 to 12,000 cells \cdot ml⁻¹ = 0.83 to 8.3 \times 10⁶ μ m³ \cdot ml⁻¹) (Kuenster, 1988). Cahalan *et al.* (1989) reported a lower reduction (56%) for juvenile bay scallops exposed to concentrations between 7,500 and 68,000 cells ml⁻¹ (0.25 to 2.28 \times 10⁶ μ m³ \cdot ml⁻¹) of *Isochrysis galbana*, an alga that is incompletely retained by the pectinid gill.

TABLE 2. Weight-standardized clearance rates (= pumping rates) (CR_s; l h⁻¹ g dry tissue weight⁻¹) of various pectinid species. CR_s = CR_e \cdot (W_s/W_e)^b, where CR_e and W_e are the clearance rate and tissue dry weight of the experimental animal, W_s = 1g and b is the exponent of the allometric relationship between CR and W.

Species	Temp. (°C)	Suspension	CR _s	Source
<i>Chlamys hastata</i>	12.8	Direct measurement w/ thermistor flowmeter	0.145	Meyhöfer, 1985
<i>Chlamys islandica</i>	3.4	17 μ m polysterene 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>C. opercularis</i>	5 10 20	<i>Dunaliella euchlora</i> , 8000-10,000 cells ml ⁻¹	1.64 3.23 5.90	McLusky, 1973
<i>Pecten (Chlamys) opercularis</i>	10 - 13	Mixed algal suspension, 0.02-0.3 mg organic DW l ⁻¹	14	Møhlenberg & Riisgard, 1979
<i>Pecten furtivus</i>	10 - 13	"	31	"
<i>Placopecten niagellanicus</i> 10-31 m	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 5	<i>Nitzschia</i> , 1 \times 10 ⁵ - 5 \times 10 ⁵ cells ml ⁻¹	5.82 1.75	Kirby-Smith, 1970
<i>Argopecten i. concentricus</i>	21 21	<i>Thalassiosira pseudonana</i> , 50,000-340,000 cells ml ⁻¹ <i>Dunaliella tertiolecta</i> , 10,000-30,000 cells ml ⁻¹	4.022 (0.31-8.78) 5.684 (0.65-11.90)	Palmer, 1980
<i>Argopecten i. irradians</i>	22	<i>Thalassiosira weissflogii</i> 1,200 cells ml ⁻¹ 4,800 cells ml ⁻¹ 12,000 cells ml ⁻¹	10.333 4.707 1.387	Kuenster, 1988

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

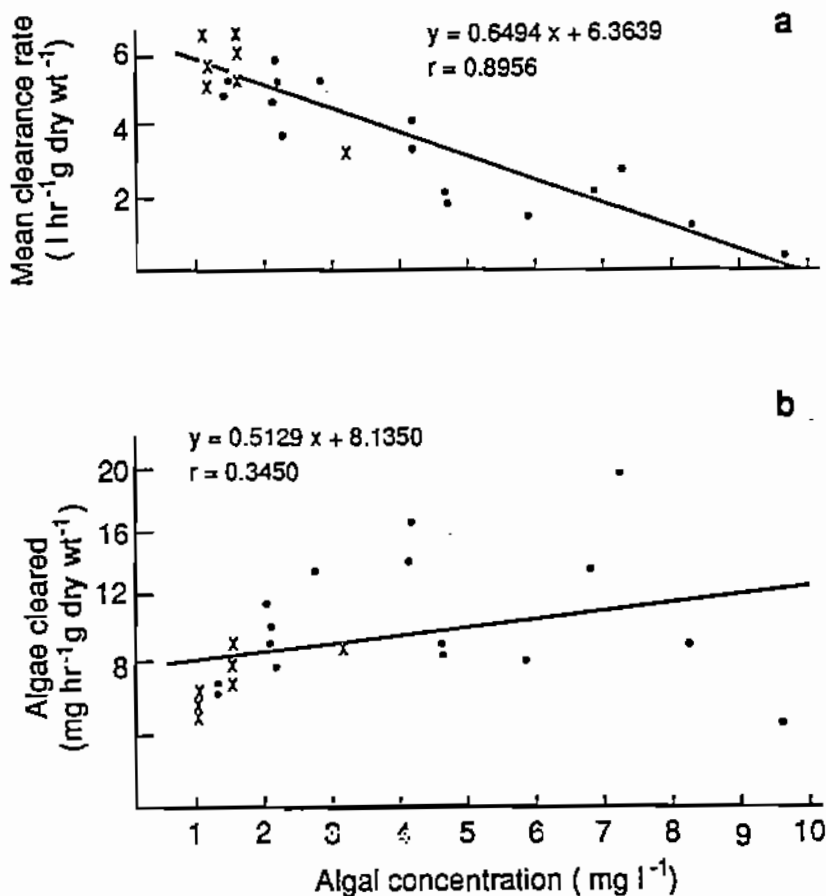


Fig. 3. Relationship between algal concentration ($mg\ dry\ weight \cdot l^{-1}$) and clearance rate (a) and amount of algae cleared (b) for *Argopecten irradians concentricus*. Each point represents the mean value for one experiment – that is for 5 to 32 hourly measurements; algae used were *Dunaliella tertiolecta* (x) or *Thalassiosira pseudonana* (•) (from Palmer, 1980).

In scallops, high clearance rates at low food concentrations are typically reflected in a wide shell gape, such that the free margin of the gill protrudes well beyond the posterior-ventral margin of the shell and the guard tentacles of the two inner (velar) folds of the mantle do not overlap (Palmer, 1980; Palmer and Williams, 1980). At higher concentrations, shell gape tends to decrease, the gill is never observed to extend beyond the shell margin, and the guard tentacles of the two velar folds tend to interdigitate. High particle loading is also accompanied by increased mucus production and marked reduction in the degree of plication of the pectinid gill (Owen and McCrae, 1976).

As reported for other bivalves (Malouf and Bricelj, 1989), scallops appear to achieve maximal growth rates at moderate algal concentrations and are not well adapted to high food levels. For example, the queen scallop, *Chlamys opercularis*, attained maximal shell growth rates

at densities of *Tetraselmis suecica* between 1,000 and 3,300 cells ml⁻¹, and experienced a 41% reduction in growth rate at 13,000 cells ml⁻¹ (Richardson *et al.*, 1984). MacDonald (1988) observed that abundant pectinid populations are not normally found in highly turbid environments where many oyster species thrive.

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* were found to be independent of temperature between 10 and 26°C, but were markedly depressed at 5°C (Figure 4; 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 (liters pumped per ml of O₂ consumed) decreases rapidly with increasing temperature above 10°C. Irrigation efficiency is generally assumed to be inversely related to the maintenance food requirement (that at which growth = 0) (Newell and Kofoed, 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).

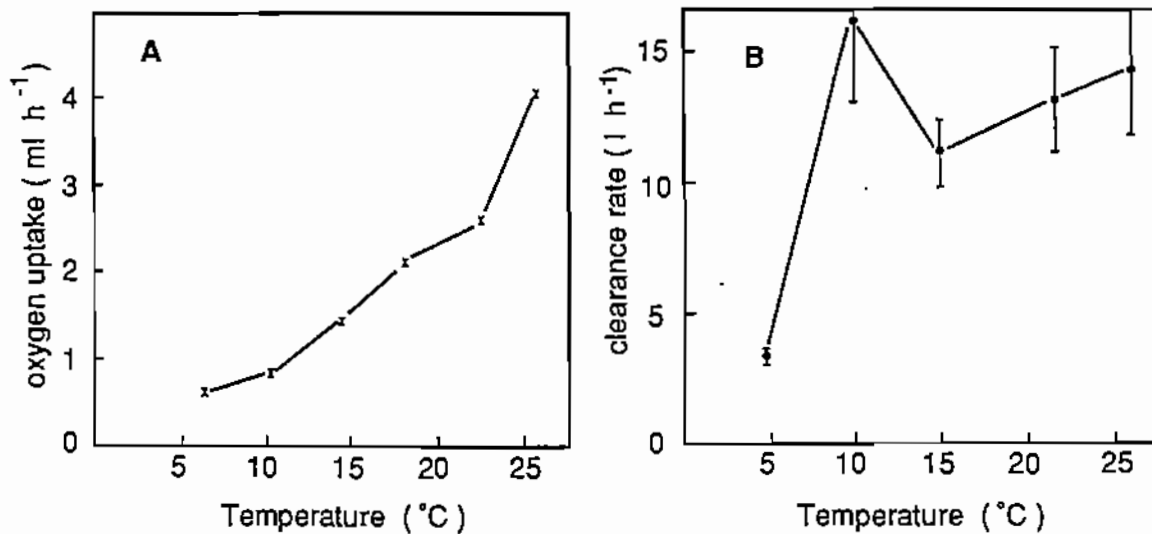


Figure 4. *Argopecten irradians concentricus*. Mean oxygen uptake (A) and clearance rate (B) of a standard animal 20 g in wet tissue weight (calculated from data by Kirby-Smith (1970; Tables VII and VIII for scallops fed *Nitzschia* sp.; vertical bars = standard errors).

In *Chlamys opercularis* the response of clearance rates to temperature is similar to that of 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. In the latter, clearance rates were also correlated with food availability (energy content of seston) (MacDonald and Thompson, 1986).

Marine suspension feeders inhabiting coastal waters typically pump 15 l or more of water per equivalent ml of O₂ 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).

Pseudofeces production and pre-ingestive particle selection

Above a threshold particle concentration bivalves are able to regulate ingestion through rejection of excess particles in pseudofeces. It has also been well established in recent years that bivalves can selectively ingest algae and reject particles of poor nutritive value (*e.g.* sediment particles) in pseudofeces (Kiørboe and Møhlenberg, 1981; Newell and Jordan, 1983). Kiørboe and Møhlenberg (1981) determined the efficiency of particle selection of ten species of suspension feeding bivalves fed mixed algal-sediment suspensions 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.

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 tricoratum* 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 pseudonana* 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).

Pre-ingestive particle selection is possible only when pseudofeces are produced. 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 million cells ml⁻¹ = 2.4 to 6.4 mg dry weight) of the chrysophyte *Aureococcus anorexefferens* (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 \cdot 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). This tends to support the generalization made earlier that scallops regulate their ingestion at high particle concentrations primarily by reducing their clearance rate rather than by increasing pseudofeces production.

The labial palps are currently considered to be the principal site of pre-ingestive particle selection in bivalves. This belief 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).

Absorption efficiency

Few studies have attempted to determine the utilization (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 absorptive capabilities.

Using ¹⁴C 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 ($= 2 \text{ mm}^3 \text{ l}^{-1} = 468 \mu\text{g C} \cdot \text{l}^{-1}$). Only the chlorophyte, *Chlorella autotrophica*, was inefficiently absorbed (AE = 17.4%), as previously observed both in adult and larval oysters (Floyd, 1953; Babinchak 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 ¹⁴C-⁵¹Cr 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-Davalos, 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 anorexefferens* (Kuenstner, 1988), a species which caused starvation of bay scallops at bloom concentrations under field conditions (Bricelj *et al.*, 1987b). Grant and Cranford (1989) reported that kelp (*Laminaria*) detritus was absorbed with high efficiency (70-80%) but did not support growth of adult *Placopecten magellanicus*.

As is typical of other suspension feeding bivalves, absorption efficiency in scallops decreases with increasing food concentrations. For example, a four-fold increase in the density of *Thalassiosira weissflogii* from 3,000 to 12,000 cells \cdot ml⁻¹, caused a reduction in the absorption efficiency of *Argopecten irradians* from 89.7 to 65.0% (Kuenstner, 1988).

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 ($< 5\text{--}10 \text{ mg} \cdot \text{l}^{-1}$) 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) hypothesized that bivalves which regulate ingestion primarily by a reduction in clearance rates (such as hard clams, cockles and scallops), are more likely to be vulnerable to high suspended sediment concentrations than bivalves such as mussels and surf clams which control ingestion mainly by increasing pseudofeces production (provided they are also capable of high ingestion selectivity). Thus shell growth rates of *Chlamys opercularis* were significantly depressed by moderate concentrations (11 to 37 mg dry weight $\cdot \text{l}^{-1}$) of iron ore particles (Richardson *et al.*, 1984). Iron ore suspensions exceeding ca. 25 mg $\cdot \text{l}^{-1}$ 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 $\cdot \text{l}^{-1}$ fed in combination with an algal diet (50×10^6 *Pseudoisochrysis paradoxa* cells $\cdot \text{l}^{-1}$) (Korol, 1985).

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 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).

Duggan (1973) and Monical (1980) also attributed reduced survival and growth of scallops 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 fall. 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 $\cdot \text{l}^{-1}$. 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. Site and seston characterization is thus critical in interpreting the effects of resuspended bottom material.

Scallops appear to be particularly susceptible to siltation both in the laboratory (Castagna, 1975) and in the field (Duggan, 1973; Tettelbach *et al.*, 1988). 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.

Effects of flow on feeding and growth

Studies of natural populations of shallow water pectinids such as *Argopecten irradians*, have generally found that larger sizes and faster growth rates are associated with areas of relatively strong currents (Belding, 1910; Gutsell, 1930; Marshall, 1960). Reduced growth rates of suspension feeding bivalves in areas of low current speeds and high population densities are attributed to a reduction in seston supply and consequent food limitation (*e.g.* Wildish and Kristman-son, 1985).

Indirect evidence of food limitation has been provided for natural populations of bay scallops, *Argopecten irradians*. Cooper and Marshall (1963) found lowest adductor muscle volume/shell height ratios for populations with the highest scallop densities (about 70 m⁻²) in the Niantic River estuary, Connecticut, U.S.A. Within an area of relatively slow current velocities, Eckman (1987) found that post settlement bay scallops grew disproportionately faster at a site of lower eelgrass shoot density than in an adjacent site of high density. He suggested that the scallops' growth rate was inhibited by the relatively lower flux of seawater within the higher density *Zostera* meadow. Bricelj *et al.* (1987b) found lowest size-specific fecundities and adductor muscle weights of adult bay scallops in an enclosed embayment characterized by highest scallop densities and reduced tidal exchange.

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).

Using a multiple-channel flume apparatus Wildish *et al.* (1987) and Wildish and Kristman-son (1988) found that shell growth of adult *Placopecten magellanicus* is inhibited at free stream current velocities exceeding about $10 \text{ cm} \cdot \text{s}^{-1}$. These authors suggest that the mechanism of growth inhibition at high flow speeds involves build up of a pressure differential between inhalent and exhalent apertures that interferes with filtration. Wildish *et al.* (1987) described an inverse relationship between filtration rates (FR in $\mu\text{g chl} \cdot \text{h}^{-1} \cdot \text{g total body weight}^{-1}$) of adult giant scallops and flow rate (F, in $\text{cm} \cdot \text{s}^{-1}$):

$$\text{FR} = 0.59 + 0.01 \text{ F} \quad r^2 = 0.90$$

Filtration rates were reduced to 50% of the optimum at a flow of ca. $40 \text{ cm} \cdot \text{s}^{-1}$, and ceased at velocities approaching $66\text{--}73 \text{ cm} \cdot \text{s}^{-1}$. This inhibitory effect occurs at a lower flow threshold when scallops are forcibly positioned with their exhalent opening facing the current.

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 ($1,100 \text{ shoots m}^2$) in Back Sound, North Carolina, U.S.A. regularly experience current speeds as high as $5\text{--}28 \text{ cm} \cdot \text{s}^{-1}$. Adult giant scallops (*Placopecten magellanicus*) in the Bay of Fundy are found where depth-integrated maximum tidal velocities exceed $100 \text{ cm} \cdot \text{s}^{-1}$ (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 $70 \text{ cm} \cdot \text{s}^{-1}$. 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 Kristman-son (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 ($> 10 \text{ cm} \cdot \text{s}^{-1}$) less than a third of the time.

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 $15 \text{ cm} \cdot \text{s}^{-1}$. 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 $17.2 \text{ cm} \cdot \text{s}^{-1}$, 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 flow 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 $3 \text{ cm} \cdot \text{s}^{-1}$, and as high as ca. $17 \text{ cm} \cdot \text{s}^{-1}$ (Eckman *et al.*, 1989). Given their preferential orientation, they are unlikely to remain in an unfavorable 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 flow conditions ranging from laminar to fully turbulent (Reynolds number = 840 to 5,600), with flow velocity held within a narrow range of 1.7 to $3.9 \text{ cm} \cdot \text{s}^{-1}$.

Based on theoretical considerations (hydrodynamic scaling) these authors suggest that growth rates of adult scallops should be even less sensitive than those of juveniles to adverse pressure differentials between inhalent and exhalent openings created by high external flows. Yet their experimental evidence and that of Cahalan *et al.* (1989) suggest that juveniles can grow in current speeds 3 to 6 times higher than those which inhibit growth of adults (Kirby-Smith, 1972). The reasons for this apparent discrepancy between the response of juveniles and adults to flow require further investigation.

ENERGY UTILIZATION: 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, reproductive state, activity level and physiological condition. The allometric relationship between body mass (tissue dry weight) and VO_2 has been determined for several pectinid species (Table 3). The coefficient (b) of this relationship varies between 0.486 and 0.986 (average = 0.76 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).

Metabolic rate and oxygen availability

Aquatic organisms have been characterized 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) (Figure 5).

TABLE 3. Parameters of the allometric relationship between oxygen consumption (VO_2 ; $\text{ml O}_2 \text{ h}^{-1}$) and tissue dry weight (W ; g), following the equation $\text{VO}_2 = a W^b$, 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. ($^{\circ}\text{C}$)	a	b	Source
<i>Argopecten irradians</i> , New York, U.S.A.	0.47 - 2.99	17.4	0.931	0.725	Bricelj <i>et al.</i> , 1987a
	0.84 - 2.86	10.5	0.368	0.733	
	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 magellanicus</i> , Maine U.S.A.	0.01 - 18	19	0.399	0.837	Shumway <i>et al.</i> , 1988
		10	0.363	0.838	
<i>P. magellanicus</i> , 10m: Newfoundland, Canada 31m:	1.8 - 42 0.5 - 25	5.5-8.5	0.447	0.79	MacDonald & Thompson, 1986
		10-12	0.339	0.78	
		1.8-3.5	0.214	0.76	
		5.5-7.2	0.234	0.79	
<i>Chlamys islandica</i> , Norway	0.05 - 2.6	3.8	0.098	0.87	Vahl, 1978
<i>Chlamys islandica</i> , Norway	0.02 - 0.9 0.5 - 5 0.4 - 6	5.7	0.145	0.486	Vahl & Sundet, 1985
			0.251	0.567	
			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 varia</i> , France	0.1 - 2.3	10	0.334	0.70	Sha'fee, 1982
		15	0.344	0.77	
<i>Patinopecten yessoensis</i> , Japan	0.5 - 15	22.4	0.579	0.817	Fuji & Hashizume, 1974
		14.8	0.398	0.777	
		5.8	0.181	0.862	

* Animals starved for 36 h prior to measurements.

+ Calculated from data in McLusky, 1973.

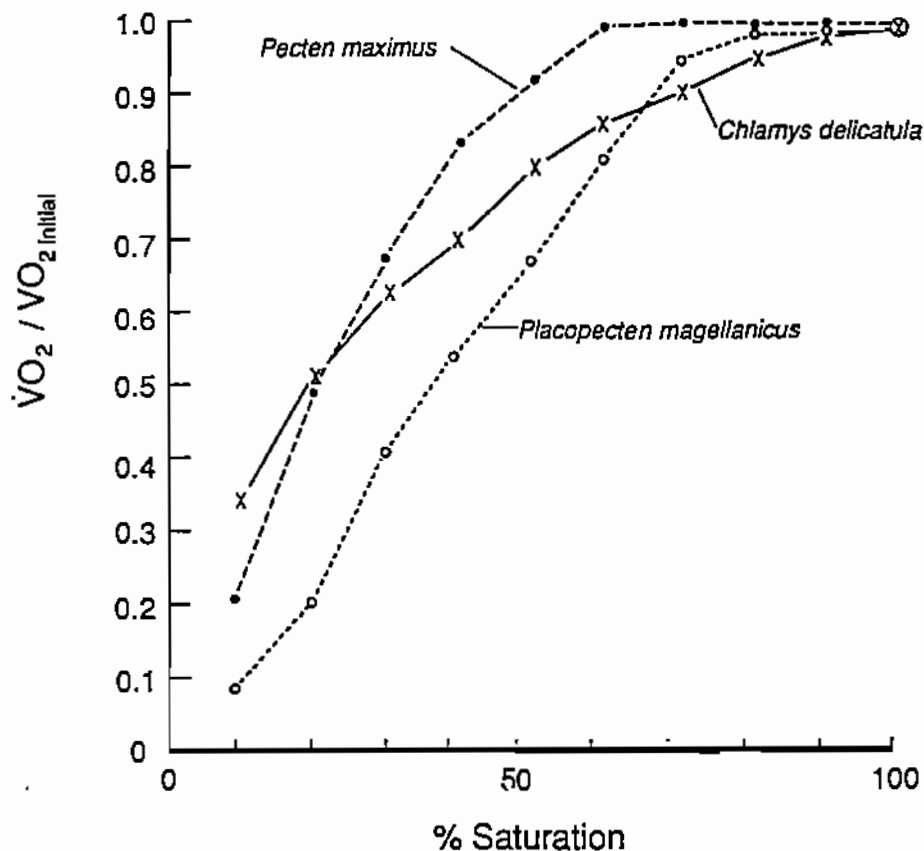


Fig. 5. The response of three oxyconforming pectinid species to declining oxygen tension (VO_2 = weight-specific oxygen uptake). Data for *Chlamys delicatula* from Mackay and Shumway, 1980; *Pecten maximus* from Brand and Roberts, 1974; *Placopecten magellanicus* from Shumway, unpublished data.

The qualitative distinction between oxyregulators and conformers has been criticized 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 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 molluscs 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 molluscs the relationship between the K_1/K_2 index and weight-specific VO_2 ($ml\ h^{-1}\ g^{-1}$) is described by an exponential

equation. For the deep water scallop *Chlamys delicatula* (Mackay and Shumway, 1980) this relationship is given by:

$$K_1/K_2 = 115.78 \times VO_2^{0.769}$$

The relatively high value of the constant in this equation (= 115.78) compared to other bivalve species again indicates that *C. delicatula* is a poor oxyregulator. *Arctica islandica* is an extreme oxyconformer, as indicated by an intercept value of 1000, 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).

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* (Sundet and Vahl, 1981)). In contrast, *Mytilus edulis*, an intertidal bivalve that commonly utilizes anaerobic pathways during prolonged valve closure induced by aerial exposure, attains high maximum seasonal glycogen levels of 42 to 53% in the mantle, the principal long term storage organ in mytilids (De Zwann and Zandee, 1972; Gabbott, 1983).

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.*, 1987a), giant scallop, *Placopecten magellanicus* (Shumway *et al.*, 1988), Iceland scallop, *Chlamys islandica* (Vahl,

1978) and black scallop *Chlamys varia* (Shafee, 1982). Figure 6 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.*, 1987a). 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, 1987b, and unpublished results), exhibit reproductive senility (*sensu* Peterson, 1983) in that size-specific reproductive output declines in older individuals. In the bay scallop, post-reproductive individuals approaching the end of their lifespan, exhibit a significantly lower weight-normalized VO_2 than young individuals which have not yet undergone reproduction (Bricelj *et al.*, 1987a). 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).

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.* (1987a) 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 acclimatization 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 (Figure 6). 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; Figure 6). 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 *Patinopecten yessoensis* oxygen uptake closely tracks seasonal temperature changes, except during the winter months when weight-standardized 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.

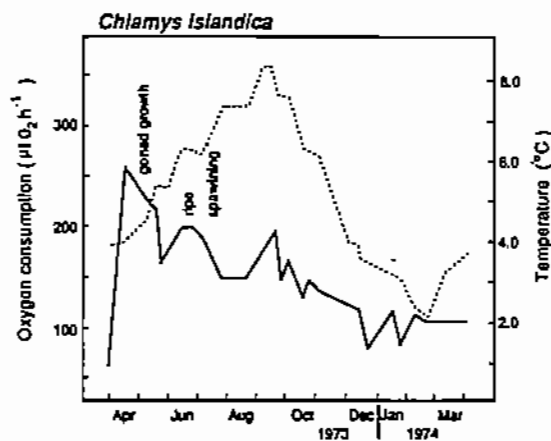
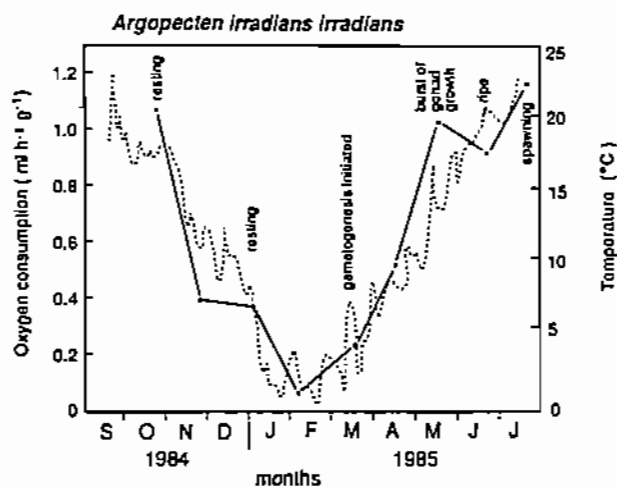
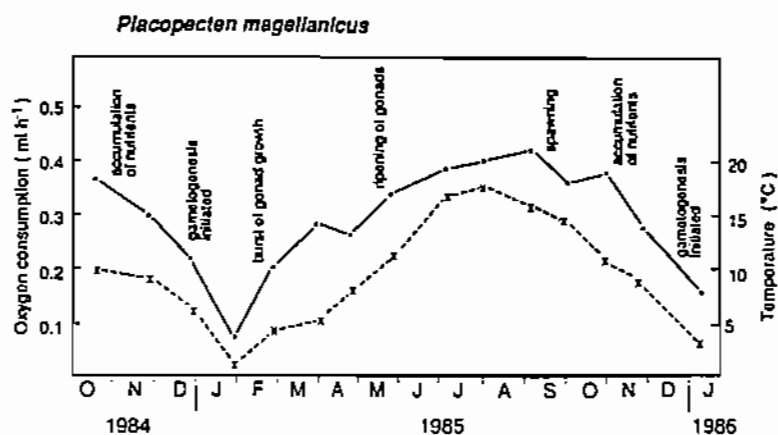


Fig. 6. Seasonal changes in oxygen consumption of three pectinid species in relation to environmental temperature and reproductive stage. Weight-normalized oxygen uptake of *Chlamys islandica* and *Placopecten magellanicus* from Vahl (1978) and Shumway *et al.* (1988) respectively. Reproductive stages of *C. islandica* from Sundet and Vahl (1981). Weight-specific oxygen uptake of *Argopecten irradians irradians* from Bricelj *et al.* (1987a).

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 ; $\mu\text{l} \cdot \text{h}^{-1}$) 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 4. Values are typically > 1 , indicating that most of the scallop species listed, unlike the blue mussel, *Mytilus edulis*, have a limited ability to acclimatize 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 4).

TABLE 4. Temperature coefficient (Q_{10}) for oxygen consumption in several pectinid species.

$$Q_{10} = (K_1/K_2)^{10/(T_1-T_2)} \text{ where } K_1 \text{ and } K_2 = \text{oxygen uptake at temperatures } T_1 \text{ and } T_2.$$

Species	Temperature range ($^{\circ}\text{C}$)	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	Shafee, 1982
		routine: 1.75-4.67	
		active: 1.08-1.62	
<i>Placopecten magellanicus</i>	5 - 15	2.38	Shumway <i>et al.</i> , 1988 ^a
	10 - 20	1.58	
<i>Patinopecten yessoensis</i>	5.8 - 14.8	1.09	Fuji and Hashizume, 1974
	8.9 - 16.9	1.78	
	14.8 - 22.4	1.64	
<i>Argopecten irradians irradians</i>	5 - 15	3.36	Bricelj <i>et al.</i> , 1987a
	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.

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 characterized 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 5 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 standardization 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.

TABLE 5. Weight-standardized 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	Temperature (°C)	VO_2	Source	Notes
<i>Chlamys varia</i>	10	0.339	Shafee, 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 <i>et al.</i> , 1987a	A
<i>A. i. concentricus</i>	10	0.249 - 0.357	Kirby-Smith, 1970	A,C
<i>Placopecten magellanicus</i>	10	0.244	Shumway <i>et al.</i> , 1988	B
	10 - 12	0.339	MacDonald & Thompson, 1986	A
<i>Painopecten 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, 1973	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 <i>et al.</i> , 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 a 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.

Little 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 using starfish foot or extract, before placing 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*. 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 (Shafee, 1982).

Anaerobic metabolism

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 utilized 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) 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 utilization, 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) 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 Zwann *et al.*, 1980).

The amino acid octopine is the main anaerobic end product accumulated in muscle tissue as a result of exhaustive swimming in scallops (e.g. Grieshaber and Gade, 1977; Baldwin and Opie, 1978), as well as cephalopods, *Nautilus pompilus*, *Loligo vulgaris* and *Sepia officinalis*, and in *Cardium tuberculatum*, following vigorous jumping (reviewed by Zandee *et al.*, 1980). Octopine synthesis is catalyzed by octopine dehydrogenase 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 and rapid fatigue, but yields a high ATP output per unit time compared to propionate and succinate (Zandee *et al.*, 1980). Thus glycogen conversion to octopine is adaptive during temporary muscle anoxia associated with short term burst activity, such as swimming in scallops.

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 PO₂ remains low, and scallops consume no oxygen, yet an increased heart rate is maintained. Thus recovery takes place under hypoxic/anoxic conditions. Utilization of phosphoarginine and accumulation of octopine appear to occur more or less sequentially in scallops, the former providing the main energy source during valve snapping, and the latter accumulating mainly during the subsequent recovery phase. 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 VO₂ 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 short-

er 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 PO₂ 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).

ENERGY UTILIZATION

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).

Only ammonia excretion rates have been determined for *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. Ammonia excretion 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). The ratio of oxygen consumed to NH₃ excreted (O:N, calculated in atomic equivalents) was used in conjunction with respiratory quotients (CO₂:O₂) to identify seasonal changes in the dominant catabolic substrates in this subspecies. (Barber and Blake, 1985). Oxygen:N values, which ranged from about 6 to 22, were generally lower than those reported for *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). 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 utilizes glycogen stores to fuel gametogenesis (Gabbott, 1975, 1983). Utilization of the O:N ratio as a generalized index of physiological condition in scallops thus requires additional information on suitable reference values under normal as well as stressed conditions.

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.

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, 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).

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 in-shore, 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). 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).

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).

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.*, 1987b), *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 utilization 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 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 *Placopecten magellanicus* (MacDonald, 1986; Schick *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 characterized 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, unpublished), *Chlamys varia* attains ca. 54 mm at 7–8 years (Conan and Shafee, 1978) and *C. tehuilcha* (H_{∞} = 83–91 mm) lives only about 6 years (Orensanz, 1984).

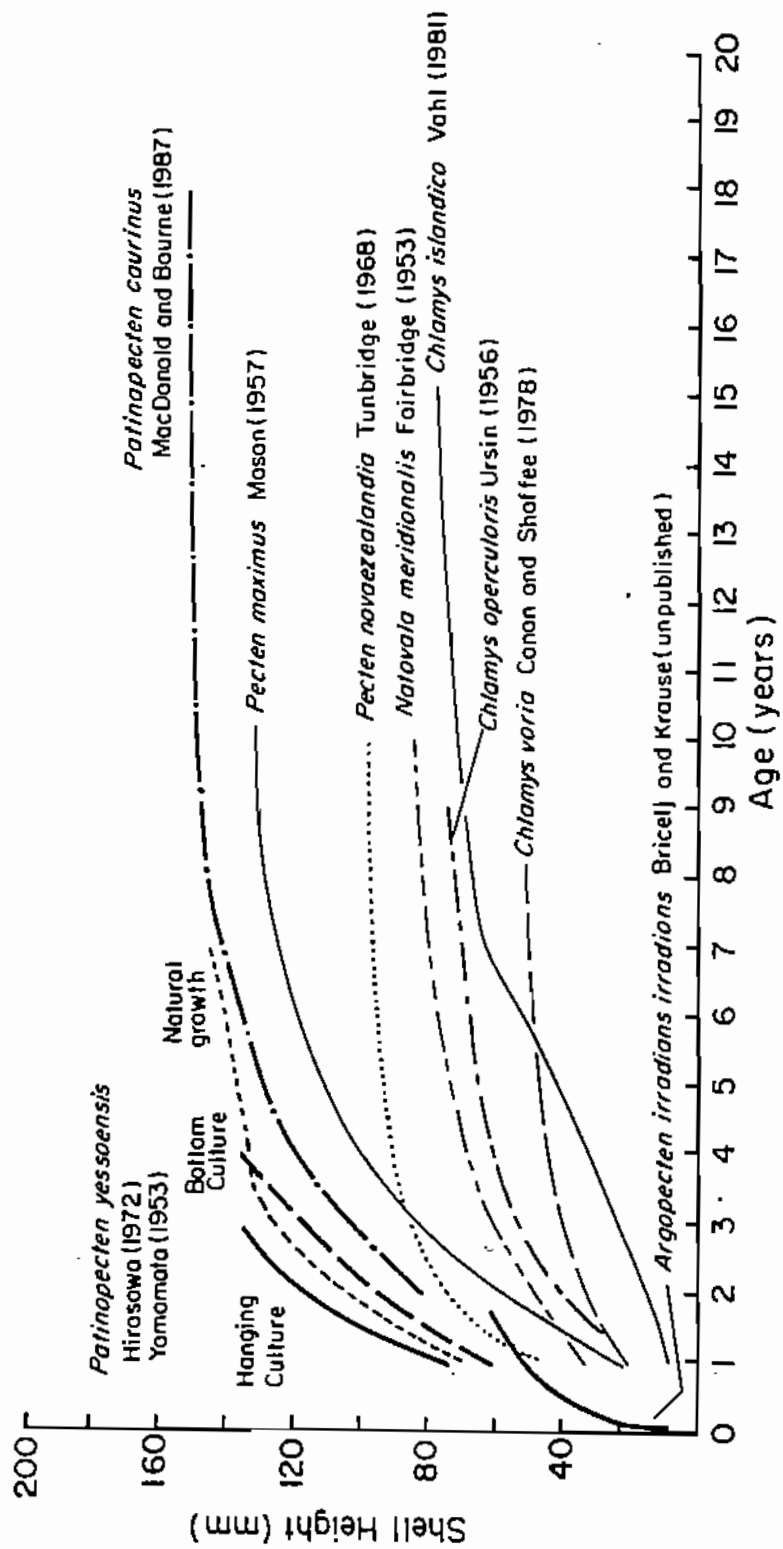


Fig. 7a. Comparative growth curves of various pectinid species.

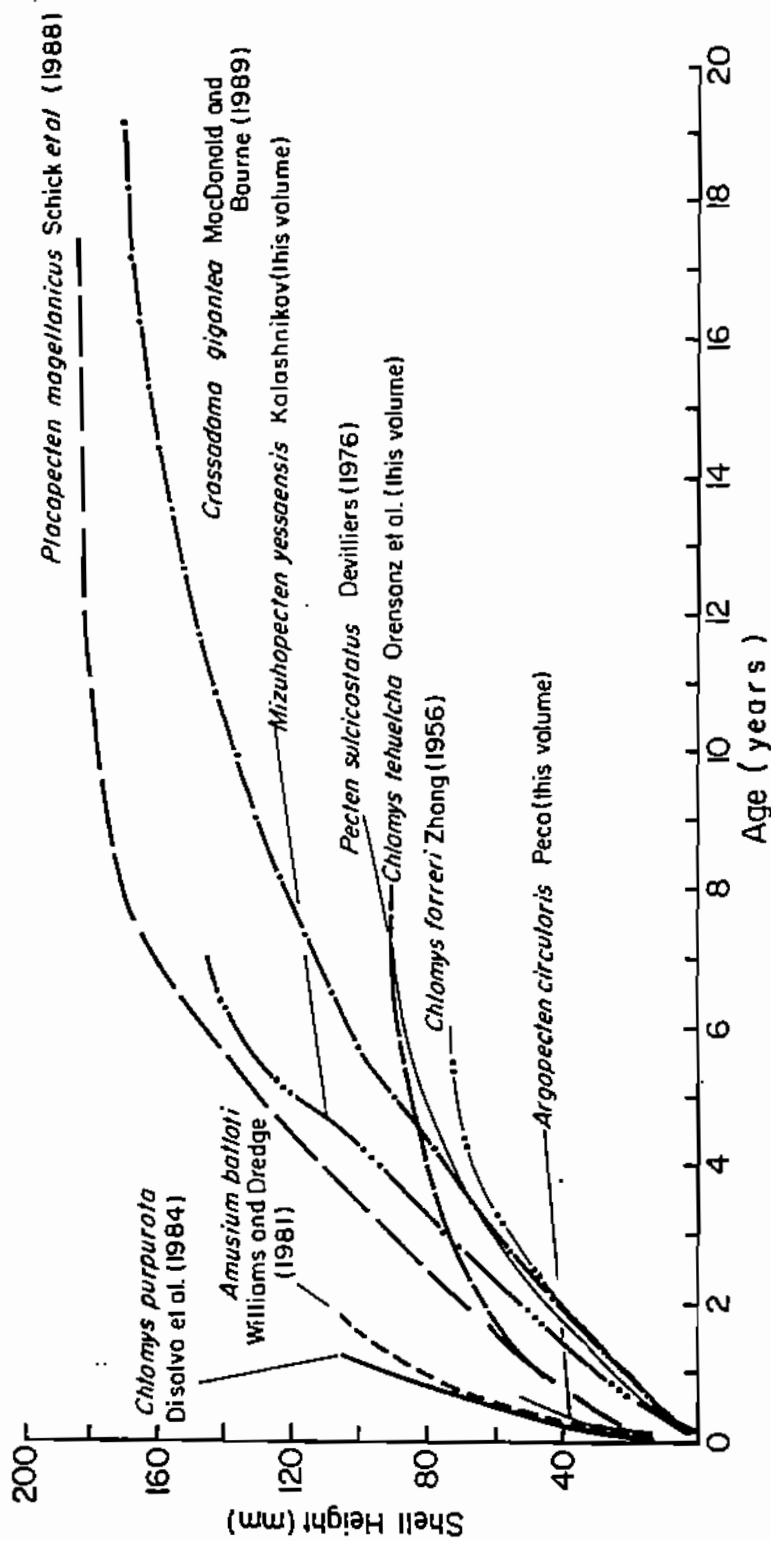


Fig. 7b. Comparative growth curves of various pectinid species.

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 at which animals reach their asymptotic shell height. The purple hinge rock 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* 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 favorable 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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