



Impact of seston characteristics on qualitative particle selection sites and efficiencies in the pseudolamellibranch bivalve *Crassostrea gigas*

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ABSTRACT

To date, knowledge of the qualitative particle selection sites and conditions in the widely-distributed bivalve *Crassostrea gigas* is incomplete, having focussed either on heterogeneous particles, or on particles intentionally too large to enter the gill principal filament tracts. We used endoscope-directed sampling and the intact diatom-empty, cleaned frustule approach to unambiguously establish qualitative selection sites and the influence of seston quality (varying proportions of intact diatoms and empty, cleaned frustules) and quantity (particle loads) on the degree of qualitative selection. Normally-feeding oysters were presented test mixtures of the naturally-occurring *Actinopterychus senarius* (small enough to enter the gill principal filaments), and the potential selection sites (gill: dorsal and ventral collecting tracts; labial palps: anteriorly-deposited pseudofaeces), were sampled for comparison with the proportions and concentrations of the ambient medium. Qualitative selection was demonstrated at both the gills and labial palps. Gill selection efficiency was shown to be directly proportional to seston quality and quantity, using a technique independent of pseudofaeces mucus content. The oyster gill is thus able to increase ingested food quality when environmental food quality is low and / or when seston concentrations are high, which is typical of oyster habitats. Palp selection efficiency was directly proportional to seston quality, but at the highest concentration tested, no qualitative selection was observed on the labial palps, probably due to overload on these smaller organs. The partial functional redundancy of these key processing organs in heterorhabdic species such as oysters and scallops may enhance their success in high-turbidity habitats.

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1. Introduction

Suspension-feeding bivalves constitute major or dominant elements of many marine ecosystems, and in coastal systems in particular, their feeding mode may have profound effects on plankton dynamics, biodeposition and nutrient recycling (Kautsky and Evans, 1987; Prins et al., 1991; Strayer et al., 1999). These effects are magnified in systems in which bivalves are reared (Dinet et al., 1990; Dame, 1993; Ruesink et al., 2005; Giles and Pilditch, 2006), the worldwide top-ranking cultured species being the Pacific oyster, *Crassostrea gigas* (FAO, 2004). It is thus not surprising that an abundant literature base deals with the principles of bivalve suspension-feeding in the coastal zone, which is characterized by considerable fluctuations in particle quantity and quality (see Armstrong, 1958; Berg and Newell, 1986; Fegley et al., 1992; Barillé et al., 1997; Gosling, 2003, for review and references).

Previous studies have broadly established that suspension-feeding bivalves may respond to seston fluctuations by adjusting clearance and ingestion volume regulation rates (Foster-Smith, 1975; Bricelj et al., 1984; Bayne, 1993; Barillé et al., 1997; Bacon et al., 1998; Velasco

and Navarro, 2002) and by adjusting the degree of particle selection prior to ingestion (Foster-Smith, 1975; Kiørboe and Møhlenberg, 1981; Newell and Jordan, 1983; Prins et al., 1991; Navarro and Widdows, 1997; Urrutia et al., 1997; Decottignies et al., 2007a). The study of particle selection has been hampered both by the multiplicity of pallial organs potentially involved, and by the difficulty of determining which of the many particle characteristics constitute selection cues (Ward and Shumway, 2004). The literature to date thus contains many unsupported or contradictory conclusions which have only begun to be resolved in a rigorous manner (see Ward and Shumway, 2004 for review). Characteristics identified to date are (1) particle shape (Le Roux, 1956; Hughes, 1975; Bougrier et al., 1997), (2) particle size (Yonge, 1926; Foster-Smith, 1975; Tamburri and Zimmer-Faust, 1996; Defossez and Hawkins, 1997), and (3) particle chemical or biochemical characteristics (Taghon, 1982; Ward and Targett, 1989; Targett and Ward, 1991; Bacon et al., 1998). As the nutritional quality of a particle will depend largely on its biochemical characteristics, this latter criterion may be referred to as qualitative selection.

Endoscope-directed sampling (Beninger et al., 1992) is an application of video-endoscopy, initially developed for use in invertebrates (Bernard, 1974; Heinzl, 1988; Heinzl et al., 1993), and adapted to the observation of bivalve feeding structures (Ward et al., 1991). It is a potentially valuable tool in the determination of the sites of qualitative

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particle selection, but unless the particles examined differ only in their biochemical composition, it is not possible to unambiguously ascribe any observed selection to a qualitative mechanism. The use of intact diatoms vs. empty, cleaned frustules circumvents this problem, and has allowed the unambiguous identification of qualitative selection sites in the heterorhabdic filibranch *Pecten maximus* (Beninger et al., 2004). The situation is less clear concerning the other major heterorhabdic gill type, the oyster pseudolamellibranch. Initial experiments were conducted using particles small enough to enter the plical openings of the gills, and which differed not only in quality, but also in shape, identifying the gills only as selection sites in oysters (Ward et al., 1997, 1998). The small size of the oyster plical openings, compared to the sizes of large organisms common in both the plankton and in oyster stomachs, made it highly unlikely that the gills could be involved in the selection of such particles; subsequent work using the intact diatom / empty cleaned frustule approach demonstrated that the labial palps are the qualitative selection sites for particles larger than the plical openings (Cognie et al., 2003). The eventual role of the gills and labial palps in the qualitative selection of particles smaller than the plical openings thus remains to be unambiguously demonstrated. In particular, although often suggested (see Ward and Shumway, 2004), the role of the labial palps has not been documented.

In the present work, we used endoscope-directed sampling and the intact diatom / empty cleaned frustule approach in *Crassostrea gigas* to determine: (1) the selection site(s) of natural particles which differ only in their composition and are small enough to enter the plical opening, and (2) the effect of particle composition on their eventual selection by pallial organs (gills and labial palps). A third goal is related to the dynamics of diatom populations, which are characterized by increasing proportions of dead cells over the course of their population growth. We thus decided to (3) study the effects of different concentrations of intact cells on qualitative selection efficiency at oyster selection sites.

2. Materials and methods

2.1. Test algae culture and characteristics

Recent studies on selection in bivalves (Cognie et al., 2003; Beninger et al., 2004; Beninger and Decottignies, 2005) have relied upon algal species representative of the types of algae present or dominant in the natural habitats of the bivalves tested. For the present study, the naturally-occurring temperate diatom *Actinopterychus senarius* was chosen to test the effects of natural algal quality on selection sites and mechanisms, for the following reasons: (1) diatoms are a major constituent of oyster diets, notably at the study site: Bourgneuf Bay (Riera et al., 2002; Decottignies et al., 2007b) and (2) this species is locally abundant (Paulmier, 1972; Rincé, 1993). *A. senarius* was isolated from a plankton net tow off Noirmoutier Island in December 2004 (47°04'N, 2°20'W), and cultured in Guillard F/2 medium (Guillard, 1982), at 14 °C and salinity 28, with a 14 h photoperiod and light intensity 100 $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

2.2. Empty frustules

Empty frustules of *A. senarius* were obtained as in Beninger et al. (2004), cleaning dead cells from senescent-phase cultures, using a saturated solution of hydrogen peroxide in an 80 °C water bath. The cleaned empty frustules were identical in size and shape to those of intact cells, and very rarely presented separated valves. These empty frustules were added to exponential-phase cultures, which themselves contained an accumulation of some empty cells (less than 20%). Cell dimensions were $49 \pm 2 \mu\text{m}$ diameter and $25 \pm 2 \mu\text{m}$ per-valvar axis (light microscope measurements of 30 cells). There was negligible size decrease due to empty frustule preparation (SNK test, $p=0.445$).

2.3. Oyster sampling and maintenance

The 15 *C. gigas* (mean shell length 11 cm) used in the present study were collected from Bourgneuf Bay, France (47°1'34"N, 2°1'55.9"W) in March 2006. The shells were cleaned of epibionts and maintained in a 400 l recirculating seawater tank, at a mean temperature and salinity close to that recorded in the sampling habitat ($T=15 \pm 0.5$ °C; $S=34 \pm 0.4$). Given the slow growth of *A. senarius* in culture, it was necessary to use a faster-growing species for maintenance. The specimens were fed every other day with a culture of *Skeletonema costatum* (Grev.) Cleve for a 4 week stabilization period prior to experimentation. As will be seen below, this diet switch did not bias the results, as a clear selection effect was demonstrated between intact and empty, cleaned *A. senarius*.

2.4. Experimental conditions

A small aperture was milled in the oyster valves, to prevent breakage of the endoscope optical insertion tube (OIT) when the valves closed periodically. Specimens were used for observation 24 to 48 hours following this operation. They were fixed with a food cement (Futex®) in 3 l experimental chambers provided (at approximately 8 l.h⁻¹) with refrigerated flow-through filtered (0.2 μm) seawater, and containing 2 longitudinal baffles to minimize turbulence.

To allow comparisons with most previous studies, which used test species of different size, cell concentrations were determined on the basis of comparable organic matter concentrations, rather than numbers of cells per ml. A calibration of cell numbers and organic matter (loss on ignition: 48 h at 60 °C and 4 h at 450 °C, Cognie et al., 2001) was established using the *A. senarius* culture.

2.5. Endoscopic observations and particle sampling

The 15 *C. gigas* were starved for 24 h and were allowed to acclimate to the presence of the OIT for 1 h prior to beginning observations. Only individuals normally feeding (i.e. with relaxed velum, deployed tentacles and particles drawn into pallial cavity) were used for observations. The endoscope-directed sampling technique has been detailed previously, here we used a micropipette (Cognie et al., 2003; Beninger et al., 2004; Beninger and Decottignies, 2005), rather than a cannula (Beninger et al., 1992, Ward et al., 1993).

We investigated 3 selection conditions (5 *C. gigas* per condition) with different proportions of intact cells and empty, cleaned frustules of *A. senarius*, to determine selection site and efficiency when food quality varies (Table 1). These 3 different mixtures correspond to the conditions encountered during a microalgal bloom: in Condition 1 (exponential-phase), intact cells were dominant (77%); in Condition 2 (stationary-phase), intact cells and empty frustules were equally represented; in Condition 3 (senescent-phase), empty frustules were dominant (67%). For the 3 tested conditions, a suspension of 15–20 $\text{mg}\cdot\text{l}^{-1}$ organic matter of the algal mixture, similar to the natural concentrations from the sampling site in the wild (Haure and Baud, 1995; Haure et al., 1996) was presented to normally-feeding oysters in the experimental chambers.

Table 1
Experimental conditions

	Cell concentration (cell.ml ⁻¹)	Particulate organic matter (mg.l ⁻¹)	Intact cells proportion
Condition 1	2380 (508)	19.7 (1.2)	0.77 (0.02)
Condition 2	2433 (294)	15.3 (1.4)	0.53 (0.05)
Condition 3	4100 (375)	17.3 (1.6)	0.33 (0.03)

Means ($\pm 95\%$ confidence interval).

Table 2
Experimental hypotheses tested

<i>H0</i>	Proportions not significantly different at sampling sites	No selection by the pallial organs
<i>H1</i>	Proportions significantly different at sampling sites	Selection by the pallial organs
<i>H1a</i>	Proportions significantly different in water and at dorsal and/or ventral tracts	Selection at gill
<i>H1b</i>	Selection indices significantly different in ventral tracts and pseudofaeces	Selection at palps
<i>H1c</i>	<i>H1a</i> and <i>H1b</i> true	Selection at gill and palps

Endoscopy-directed sampling was performed every 15 min throughout the 2 h experimental period in the chamber water column, the gill dorsal (acceptance) tract and the gill ventral (rejection) tract. Pseudofaeces was also recovered at the end of each observation period. All samples were fixed in Lugol's solution for subsequent counts using light microscopy according to the method described by (Utermöhl, 1958), which allowed the ready distinction of intact (live) versus empty (dead) *A. senarius* cells. The proportions of each cell type were determined for a minimum of 300 cells of the total volume sampled over the 2 h course of the experiment for each oyster.

The ingestion of *A. senarius* cells by *C. gigas* specimens was confirmed by microscopic examination of faeces.

2.6. Data analysis

SigmaStat 3.1© software was used for all statistical computing. Prior to each analysis, assumptions of normality and homoscedasticity were tested.

Empty and intact cell proportions in water, dorsal tracts, ventral tracts and pseudofaeces were compared for each experimental condition at each 15 min interval for all 5 individuals with one-way parametric ANOVAs, followed by SNK a posteriori tests. A selection index (SI) based on that of Cognie et al. (2003) was calculated in order to express the degree and direction of selection at each site:

$$SI = [(S/W) - 1] \times 100$$

where S is the proportion of intact cells sampled at a given site (dorsal tracts, ventral tracts, and pseudofaeces), and W is the proportion of intact cells sampled in the ambient water.

The selection indices obtained for dorsal tracts, ventral tracts and pseudofaeces were treated in the same manner as the proportions. Tested hypotheses are presented Table 2.

3. Results

All oysters demonstrated active, normal feeding behaviour during endoscopy observations. Particle movement on the gill surface was similar to that previously described by Atkins (1937), Ward et al. (1994) and Cognie et al. (2003): on the ordinary filaments both types of *A. senarius* cells were transported ventrally and transferred to apparently highly-viscous masses at the ventral groove (Fig. 1). Both intact and empty cells were observed entering the principal filament and exiting them in the viscous suspension at the dorsal tract. For the 3 experimental conditions, material in excess in the ventral grooves was regularly ejected by gill contractions but without valve clapping.

The results of the ANOVAs, both for the proportions of cells and for the selection indices showed significant differences between sampling sites and clearly lead to rejection of the null hypothesis *H0* and acceptance of *H1*: for the 3 conditions, selection occurred on the pallial organs (Fig. 2; ANOVA, $P < 0.001$). The *a posteriori* tests showed that proportions in the dorsal groove were significantly different from proportions in the ambient water and the ventral groove (Fig. 2 A, C and E; SNK test, $p < 0.05$), thus endorsing *H1a*: for the 3 conditions, selection occurred on the gill. Analysis of selection indices confirmed these results: they were significantly higher in the dorsal tracts than in the ventral grooves (Fig. 2 B, D and F; SNK test, $p < 0.05$).

For Conditions 1 and 2, selection indices clearly showed a significant decrease in the proportion of intact cells in the pseudofaeces compared to the ventral grooves: selection was therefore also performed by the palps (Fig. 2 B, and D; SNK test, $p < 0.05$). *H1c* may thus be accepted: two successive selections occurred, first on the gill and then at the labial palps. For Condition 3, there was no significant difference in selection indices, between material in the ventral grooves and material in the pseudofaeces (Fig. 2 F; SNK, $p = 0.372$). The experimental hypothesis *H1a* may therefore be accepted and *H1b* rejected: in the highest-turbidity condition, selection occurred only on the oyster gills.

Mean selection indices indicated an enrichment of intact cells in the dorsal tracts which increased significantly with empty cell proportions in ambient water (from 13 to 60%, conditions 1–3; Fig. 2 B, D and F; SNK, $p < 0.05$). In contrast, selection indices of samples from the ventral grooves were close to zero at all three experimental conditions. The mean selection indices were

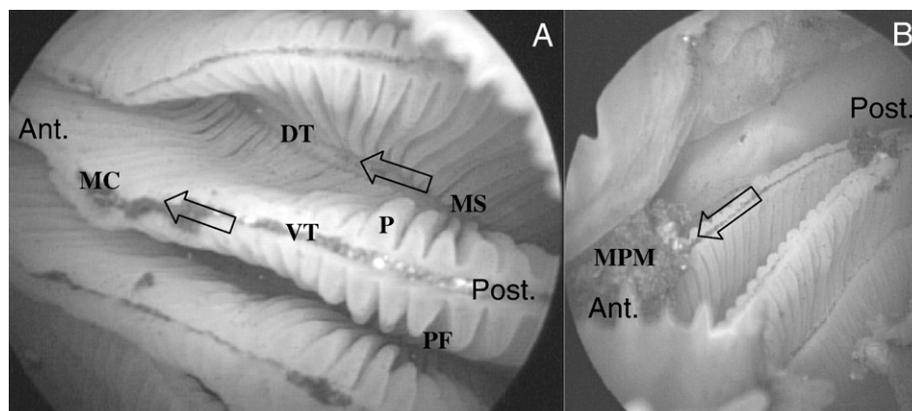


Fig. 1. *Crassostrea gigas*. Videoendoscopic images. (A) Particle movement on gill; DT: dorsal tract; VT: ventral tract; PF: principal filament; P: gill plica; MC: ventral mucus cord; MS: dorsal mucus suspension; direction of movement indicated by open arrow. (B) Material initially rejected by gill in ventral grooves; MPM: mucus-particle masses.

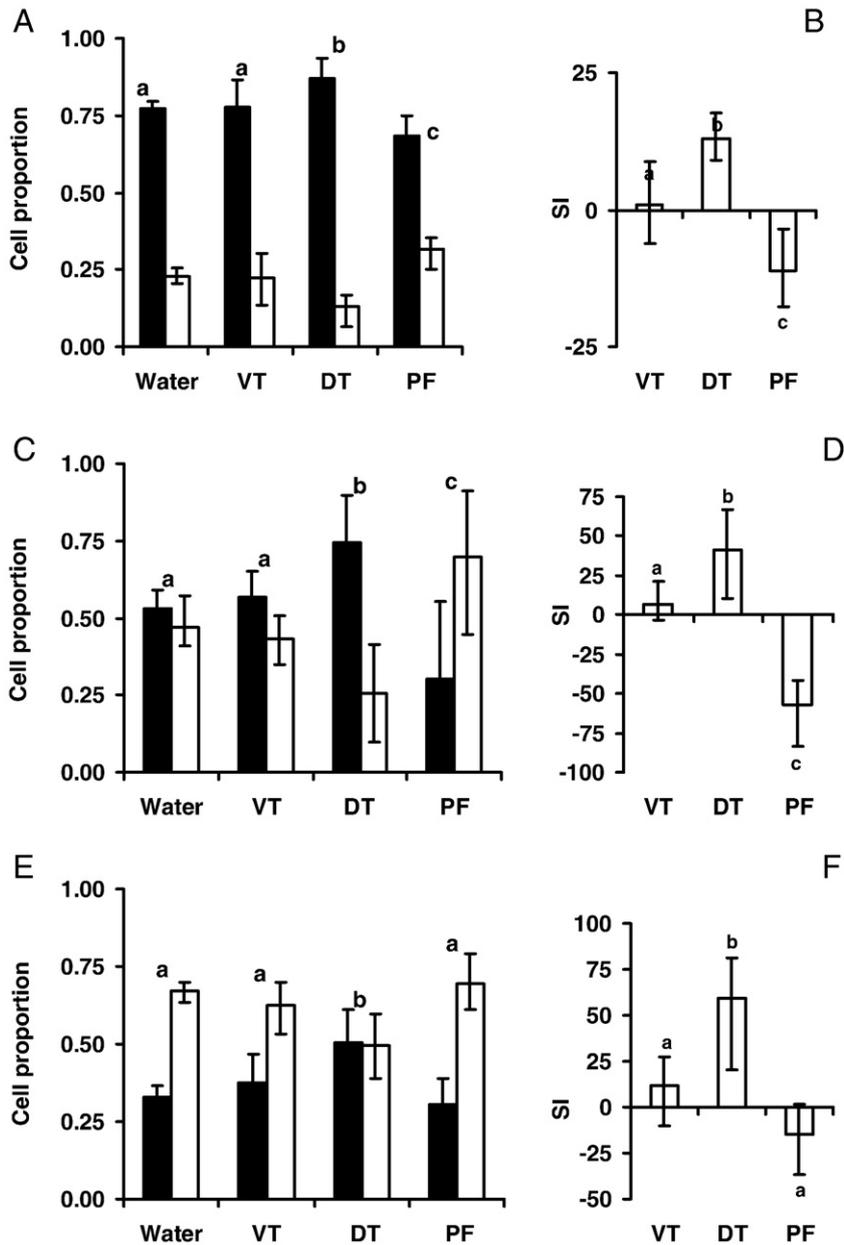


Fig. 2. *Actinoptychus senarius*. (A–B): Condition 1. (C–D): Condition 2. (E–F): Condition 3. (A–C–E) Mean percentages of intact (black bars) and empty (white bars) cells and (B–D–F) mean selection indices (SI) at the different sampling sites: ambient water, ventral tracts (VT), dorsal tracts (DT) and pseudofaeces (PF). Error bars represent the range of values ($n=5$). Bars with different lower case letters are significantly different ($p<0.05$).

significantly higher in Condition 2 compared to Conditions 1 and 3 for the pseudofaeces (57 vs. 11 and 15%; Fig. 2 B and D; SNK, $p=0.01$ and 0.012).

Light microscopic examination of faeces confirmed that *A. senarius* cells were ingested by all specimens of *C. gigas* (Fig. 3).

4. Discussion

4.1. Qualitative selection sites in *Crassostrea gigas* for inclusive particle size spectrum

The present study unambiguously demonstrates qualitative selection at both the gill and labial palps of the oyster *Crassostrea gigas*, for particles small enough to enter the plical openings. The 'patchwork' state of knowledge concerning selection sites in this species (Ward et al., 1998; Cognie et al., 2003) may thus be rendered much clearer: (1) for particles small enough to enter the plical openings, both the gills

and labial palps are capable of effecting qualitative selection; (2) for particles too large to enter the plical openings, only the labial palps are capable of effecting particle selection. At the gills, an initial qualitative selection is accomplished by the two different filament types: initial acceptance by the principal filaments, and initial rejection by the ordinary filaments. The corresponding dorsal and ventral collecting tracts are spatially distant, and each tract is semi-enclosed, such that subsequent mixing is virtually precluded. At the labial palps ridged surface, qualitative selection is presumed to be accomplished by sorting of particles into temporary superficial acceptance tracts and permanent deep rejection tracts, as shown in a number of bivalve species (Foster-Smith, 1975, 1978; Beninger and St-Jean, 1997).

Two-stage qualitative selection has previously been documented in the heterorhabdic filibranch *Pecten maximus* (Beninger et al., 2004). In the two heterorhabdic families (Ostreidae and Pectinidae) examined to date, therefore, qualitative selection occurs at both the gills and labial palps. On the contrary, homorhabdic taxa appear

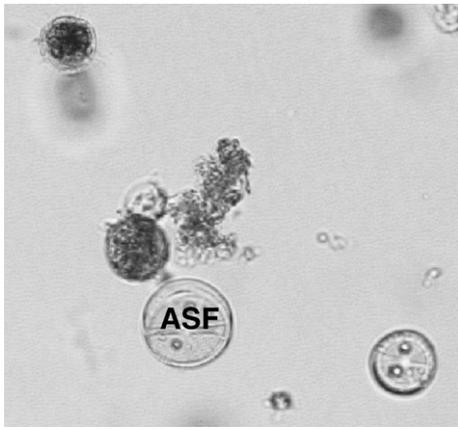


Fig. 3. *Crassostrea gigas*. Photomicrograph of faeces of experimental specimen fed with a mixture of intact and empty cells of *A. senarius*. ASF: *A. senarius* frustule.

incapable of selection at the gills (Beninger et al., 1997; Ward et al., 1998; but see Baker et al., 2000), suggesting that the anatomical differentiation of gill filaments is a necessary condition for selection at the gills.

Within the heterorhabdic condition of the Bivalvia, an important difference exists in the two-stage selection process: in the absence of a ventral gill groove, rejection at the gill is definitive, whereas acceptance is not (Pectinidae). Particles on the ventral tract are expelled by the pallial current and by periodic valve clapping (Beninger et al., 1992), whereas particles in the dorsal groove are transported to the palps where selection may operate a second time (Beninger et al., 2004). When a ventral groove is present (Ostreidae), particles in both the dorsal and ventral tracts may be subjected to a second qualitative selection at the labial palps (present study; Dutertre et al., 2007).

4.2. Effect of seston quantity and quality on selection sites and efficiencies

Notwithstanding the importance of particle size in determining the sites of particle selection, the extent to which the oyster actually effects qualitative selection at these two sites depends upon seston quality and quantity. Previous studies have shown that selection efficiency decreases with increasing seston load (Barillé et al., 1997; Navarro and Widdows, 1997) or decreasing seston organic fraction (Bacon et al., 1998); but these studies did not distinguish between the gills and labial palps. Moreover, these decreases in selection efficiency in response to decreasing seston organic fraction have been based on determination of relative organic contents, and it has been argued that such measures are biased due to the potentially great contribution of endogenously-generated mucus (Urrutia et al., 2001). The salient results of the present study, based on actual cell counts at the different processing sites and summarized in Fig. 4, show that selection efficiency at the gill is inversely related to seston quality, and directly related to seston quantity (intermediate and high loads are considered here, as these reflect the habitat conditions of *C. gigas*). The oyster gill

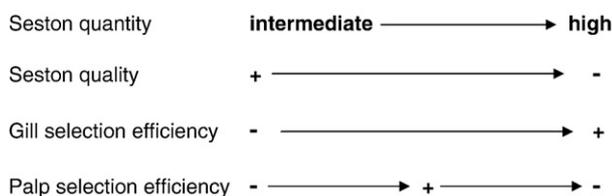


Fig. 4. Summary of relationships between selection site, seston quality and seston quantity in *Crassostrea gigas*, as observed in the experimental conditions of the present work. Relations are hierarchical from top to bottom (first determinant=seston quantity).

is thus able to increase ingested food quality when environmental food quality is low and / or when seston concentrations are high — a common situation for oysters, which are major inhabitants of high-turbidity coastal systems.

The influence of seston concentration on the selection efficiency at the labial palps is somewhat more complex than that of the gills, since the palps are both a second stage in the system, and also have a much smaller processing surface than the gills. As indicated in Fig. 4, at intermediate seston loads, labial palp selection efficiency is inversely related to seston quality. At higher seston loads, labial palp selection efficiency decreases regardless of seston quality, most probably due to overload of the palp selection capacity. At the highest seston loads at which filtration occurs, when the gut is rapidly filled, the labial palps switch to their alternate regulatory role, the regulation of ingestion volume (Menzel, 1955; Foster-Smith, 1978; Beninger et al., 1997).

The data of the present study thus illustrate where and how qualitative selection is effected in the oyster *Crassostrea gigas*, in response to seston quantity and quality. This regulation allows the oyster to maintain the flow of energy into production and maintenance despite fluctuations in seston quality and quantity, enhancing the quality of the ingested material but limiting the energetic costs of selection (Newell and Jordan, 1983).

The present study has unambiguously demonstrated that selection is a 2-stage, 2-site process in the heterorhabdic pseudolamellibranch bivalve, *Crassostrea gigas*; with qualitative selection based on particle biochemical properties at both the gill and labial palps. This 2-stage particle processing allows the oyster to carry out the functions of particle selection and ingestion volume regulation on two distinct pallial organs. The partial functional redundancy of these key processing organs in heterorhabdic species may enhance their success in the conditions of high seston load encountered by oysters in their turbid habitat, and thus constitute an advantage in such an environment, compared to homorhabdic bivalves, in which the labial palps alone must effect these two functions (Beninger et al., 1997; Ward et al., 1998).

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