SIZE SPECIFIC SELECTION OF PHYTOPLANKTON BY JUVENILE FILTER-FEEDING BIVALVES: COMPARISON OF THE SEA SCALLOP *PLACOPECTEN MAGELLANICUS* (GMELIN, 1791) WITH *MYA ARENARIA* LINNAEUS, 1758 AND *MYTILUS EDULIS* LINNAEUS, 1758

Michael P. Lesser, Sandra E. Shumway, Terry Cucci, Janeen Barter, and Joan Edwards.

ABSTRACT

In feeding experiments using unialgal cultures of phytoplankton and juvenile giant scallops, *Placopecten magellanicus* show preferences for particular classes of phytoplankton based on size when fed unialgal cultures. Similar feeding experiments revealed significant differences between the weight-specific clearance rates of *Mya arenaria* and *Mytilus edulis*. Additionally, multialgal experiments with *Placopecten magellanicus*, using different sizes of phytoplankton at concentrations not producing pseudofeces, reveal that the selection of algae is not based on size alone. For *P. magellanicus* the total number of cells cleared is not significantly different between any of the multialgal experiments. Particle selection in these cases is apparently based on characteristics of the algae other than size, or by preingestive sorting of algae by juvenile scallops.

INTRODUCTION

An important concern of aquaculturalists during the "grow-out phase" of post-metamorphic bivalves is the type and ration of phytoplankton to be supplied during periods of fast growth. The ration must be sufficient to cover the energetic costs of routine maintenence and growth, while being economical considering the expense of the mass culture of algae. This is especially critical for larvae and juveniles as their weight-specific metabolic rates are high, and their nutritional needs may change ontogenetically (Manning 1986). Studies on the clearance rates of various algae for any species of shellfish considered for commercial use is a logical initial step in determining the optimum ration to provide.

It is now known that all species of phytoplankton are not equivalent in their biochemical composition (Enright et al. 1986, Whyte 1987), or in the efficiency by which they are assimilated by shellfish (Pierson 1983). The biochemieal composition of algae is dependent on their stage of growth (Whyte 1987), and has been shown to affect the growth of juvenile oysters (Flaak and Epifanio 1979). Additionally, multialgal diets result in faster growth rates than unialgal diets in oysters (Phleger et al. 1981, Enright et al. 1986), mussels (Lueas et al. 1986), and scallops (Ukeles et al. 1984). The choice of algal species is partially dependent on the particular morphology and hydrodynamic characteristics of various bivalve ctenidia, which can lead to different filtering and particle retention capabilities based on size, electrical charge, and flow rates (Rubenstein and Koehl 1977, Jørgensen 1983, LaBarbera 1984, Riisgard 1988).

We present experimental data relevant to answering the question of particle selection based on size in juvenile *Placopecten magellanicus* when fed various species of algae alone or in a mixture. Additionally, we compare the results of unialgal experiments on *P. magellanicus* with similar experiments on *Mytilus edulis* and *Mya arenaria*.

MATERIALS AND METHODS

Juvenile specimens of *Mytilus edulis* Linneaus, 1758 (mean dry weight 30.6 mg), *Mya arenaria* Linneaus, 1758 (mean dry weight 53.7 mg), and *Placopecten magellanicus* (Gmelin, 1791) (6.5-9.5 mm shell height, mean dry weight= 3.2 mg) were collected at various locations in Maine. Animals were scrubbed free of all epiphytes, and maintained in unfiltered, running sea water from Boothbay Harbor, Maine prior to use in experiments. Animals were not fed any supplementary food.

All animals were allowed to purge themselves in filtered sea water (0.7 µm Gelman glass filter) for 24 h prior to being used in feeding experiments. All experiments were carried out at the same time of day (1000 -1200) at 12°C, the ambient temperature at the time of the experiments. Individual specimens were placed in Coulter vials containing 20 ml of the algal culture mixture (see below) which was gently aerated. Control vials, without animals, were run simultaneously to correct for algal cell division during the experiment. Experiments lasted for 1 h, with samples taken at the end of the experimental period.

Algal cultures were supplied from the Culture Center for Marine Phytoplankton, Bigelow Laboratory for Ocean Sciences. The species used, clone designation, and size range are given in Table 1. Cultures were grown In f/2 media at 15°C on a 14:10 light/dark photoperiod. For all experiments (uni- and multialgal), a final concentration of 10^4 cells ml^{-1} was used to avoid any density-dependent changes in clearance rates (Riisgard and Randlov 1981). Experiments using monocultures were conducted to compare clearance rates between juvenile *Mytilus edulis*, *Mya arenaria*, and *Placopecten magellanicus*. Three experiments using algal mixtures were conducted on *P. magellanicus* and consisted of the following clones: experiment one: PLATY 1, 3C, and EXUV, experiment two: GT 429, TISO, UW 442, and 3C, experiment three: PHAEO, 3H, DUN, AMPHI,

Table 1. Algal species used in feeding experiments

Species	Clone	Approximate Size Range (µm)
Tetraselmis levis	PLATY 1	6-10
Chroomonas salina	3 C	5-12 x 6-7
Prorocentrum minimum	EXUV	9-13
Phaeodactylum tricornutum	PHAEO	12-14 x 2-4
Thalassiosira pseudonana	3 H	5-9
Dunaliella tertiolecta	DUN	9-11
Amphidinium carterae	AMPHI	8-16
Isochrysis sp.	TISO	3-6
Pyramimonas parkeae	UW 442	11-16
Alexandrium tamorensis	GT 429	30-45
Pavlova lutherii	MONO	3-5
Heterocapsa triquetra	HT 984	14-24
Heterocapsa pygmaea	GYMNO	10-14
Chaetoceros gracile	CHGRA	5-10

and 3C. For multialgal experiments the concentration of cells for each species used was identical, while the total concentration remained at 10^4 cells ml^{-1}.

Samples were analyzed with a Coulter counter model ZM fitted with a 100 µm orifice (unialgal experiments), or by flow cytometry (multialgal experiments) using the differences in fluorescing intensities from their respective photosynthetic pigments and/or cell size from forward angle light scatter (Fig. 1) as described previously (Shumway et al. 1985, Cucci et al. 1985). Briefly, a Coulter Epics V Flow Cytometer with a single argon ion 5 w laser was used having an excitation wavelength of 514 nm with a power of 1000 mW. Fluorescence derived from each particle is split by a 590 nm dichroic mirror and is recieved by two photomultiplier tubes located at 90° to the intersection of the laser beam and sample stream. One receives a wavelength spectral region >630 nm such as would result from chlorophyll emission, and the other recieves shorter wavelengths (530-560 nm) such as would result from phycoerythrin and phycocyanin emission. The number of cells registered met gate criteria based on chlorophyll fluorescence, therefore only algal cells were analyzed. A total of 2000 cells were analyzed for each sample, with the total being partitioned between the individual species making up the algal mixture. All samples were run at a constant flow rate through an entire experiment, allowing the clearance rate of each individual to be calculated by the difference in the amount of time required to analyze 2000 cells.

Dry weights of soft tissues were obtained for all animals by constant drying at 60°C for 48 h. Clearance rates were calculated by the method of Coughlan (1969), and irrigation rates by the method of Newell (1979). Dry weight was used to normalize all data, while assuming a 100% retention efficiency for all algal species tested.

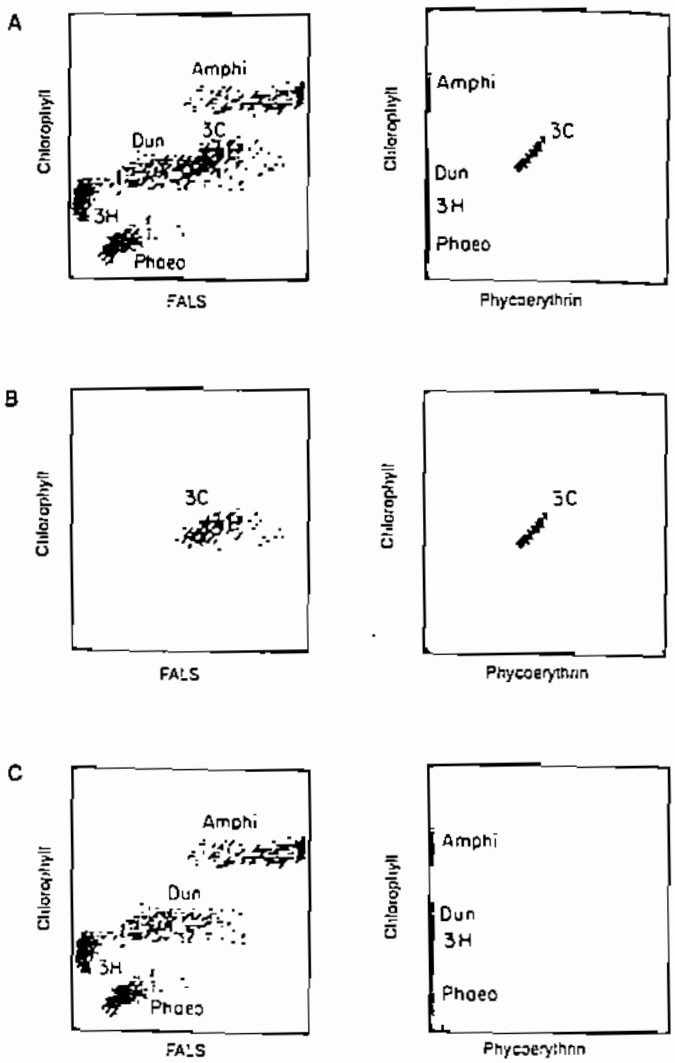

Figure 1. Examples of phytoplankton size and pigment signatures obtained by flow cytometry to differentiate between different species in grazing experiments. (A). Scattergrams showing forward angle light scatter (FALS), a sizing parameter, plotted against chlorophyll fluorescence, and phycoerythrin plotted against chlorophyll fluorescence. Clones AMPHI, 3H, and PHAEO are easily distinguished for the quantitative assesment of individual cell densities. Clones DUN and 3C overlap in their chlorophyll fluorescence and FAL signatures; therefore, cell densities of these species cannot be determined. Based on the phycoerythrin-chlorophyll scattergram (B), we can utilize clone 3C as a gating parameter which eliminates those signatures in a re-analysis of the data. (C). The scattergram after 3C has been gated out results in a distinct signature for DUN enabling us to quantify cell densities.

Statistical Analyses

Weight-specific clearance rates of each species of alga by *Mytilus edulis* and *Mya arenaria* (N=6 each), were compared with unpaired, two-tailed t-tests at a significance level of 5% (Sokal and Rohlf 1981). Unialgal experiments for *Placopecten magellanicus*, *Mya arenaria*, and *Mytilus edulis* (N=6 each) were evaluated for treatment effects (*i.e.*, differences between species

of algae) by an analysis of variance, as were the three multialgal experiments (ANOVA, Model I; StatView 512+, Brainpower Inc., Calabasas, CA) at a significance level of 5%.

Additionally, differences in the weight-specific clearance rates of total cells between each multialgal experiment were evaluated using ANOVA. No unequal variances were detected using the F_{max} test for the ANOVA or t-tests (Sokal and Rohlf 1981), and where significant treatment effects occurred, the Fisher's protected least significant difference (PLSD) multiple comparison test (StatView 512+, Brainpower Inc., Calabasas, CA) was applied at the 5% significance level to identify individual differences among the data sets.

RESULTS

Significant differences were observed between the weight-specific clearance rates of *Mytilus edulis* and *Mya arenaria* for all species of algae, with *M. edulis* having higher clearance rates for all species except GYMNO and 3H (Table 2). Although not compared statistically, there are substantial differences in irrigation rates between *M. edulis* and *M. arenaria*, dependent on the species of alga tested, with *M. edulis* always having higher weight-specific irrigation rates than *M. arenaria* (Table 2).

Table 2. Comparison of weight-specific clearance and irrigation rates of juvenile *Mya arenaria* and *Mytilus edulis* for eleven species of phytoplankton.

	Mya arenaria		*Mytilus edulis*		
Clone designation	CR[a]	V'_w[b]	CR[a]	V'_w[b]	*P* value[c]
TISO	0.24 ± 0.03	0.46	0.4 ± 0.05	0.94	0.0001
MONO	0.18 ± 0.02	0.59	0.35 ± 0.04	0.61	0.0001
HT984	1.15 ± 0.13	0.40	1.86 ± 0.21	0.59	0.0001
3C	0.34 ± 0.03	0.32	0.59 ± 0.07	0.72	0.0001
PLATY1	0.18 ± 0.07	0.41	0.31 ± 0.04	0.98	0.002
GT 429	0.22 ± .04	0.10	0.73 ± 0.08	0.61	0.0001
EXUV	0.5 ± 0.12	0.10	1.68 ± 0.19	0.58	0.0001
GYMNO	0.48 ± 0.05	0.38	0.26 ± 0.07	0.44	0.0001
3H	0.56 ± 0.07	0.48	0.31 ± 0.04	0.65	0.0001
PHAEO	0.54 ± 0.06	0.34	0.89 ± 0.01	0.61	0.0001
CHGRA	0.22 ± 0.03	0.33	0.40 ± 0.07	0.39	0.0001

[a] CR=Weight-specific clearance rate = cells·ml·h^{-1} x 10^{-3}·mg^{-1} dry weight (N=6 for each species, mean ± SD).

[b] Weight-specific irrigation rates = ml·h^{-1}·mg^{-1} dry weight (mean value for each alga).

[c] Unpaired, two-tailed t-test on the weight-specific clearance rates at a significance level of 5%.

Similarly, significant differences were also found in weight-specific clearance rates of juvenile scallops, *Placopecten magellanicus*, fed unialgal cultures (Table 3). Juvenile scallops also showed significant differences in their weight-specific irrigation rates dependent on the species of alga tested. Multiple comparison testing of weight-specific clearance and irrigation rates did not, however, show identical groupings (Table 3), indicating differential effects on irrigation not necessarily related to the scallops' ability to filter that species of alga. Comparing the clearance rates of *P. magellanicus*, *M arenaria*, and *M. edulis* for those species of algae used in both unialgal experiments reveals significant differences in the weight-specific clearance rates for three of five of the species when analyzed by ANOVA (Table 4). Juvenile scallops clear more cells of 3H and 3C than either *M. edulis* or *M. arenaria*, while juvenile mussels clear more EXUV than *M. arenaaria* or *P. magellanicus* (Table 4).

Table 3. Individual weight-specific clearance rates for eight species of phytoplankton in juvenile scallops, *Placopecten magellanicus*.

Clone designation	CR[a]	Grouping[b]	V'_w[c]	Grouping[b]
UW442	1.79±0.418	1	5.91 ±2.17	1
3H	1.53±0.547	1	2.98±1.14	2
TISO	0.339±0.469	2	0.613±0.821	2
PHAEO	0.473±0.525	2	0.731 ± 0.794	2
AMPHI	2.11 ± 1.06	1	7.65±7.51	3
EXUV	0.7± 0.402	2	1.22±0.772	2
3C	2.88±.728	1	10.57±4.89	3
DUN	4.89 ± 1.41	3	13.51 ±4.98	3

[a] CR Weight-specific clearance rate = cells·ml^{-1}·h^{-1} x 10^{-3}·mg^{-1} dry weight (N= 5 for each alga tested, mean ± SD).

[b] Results from ANOVA and multiple comparison testing. Phytoplankton sharing the same grouping number are not statistically different from one another.

[c] Weight-specific irrigation rates = ml·h^{-1}·mg^{-1} dry weight (N= 5 for each alga tested, mean±SD)

Multialgal experiments showed that feeding juvenile scallops three species of similarly-sized algae simultaneously (experiment one) did not affect the clearance rate of each individual species (ANOVA; P= 0.514) (Table 5). For experiments two and three where algae of mixed sizes were used, there were significant differences amongst algae in the weight-specific clearance rates by juvenile scallops (ANOVA; experiment two, P= 0.0001. experiment three, P=0.004) (Table 5). Multiple comparison testing of experiment two showed distinct groupings based on size (Table 5) with larger-diameter algae having higher clearance rates. A similar pattern was not observed in experiment three with PHAEO, the largest diameter alga tested, having one of the lowest clearance rates (Table 4), and overall, the differences

attributable to size in this experiment were less than in experiment two.

The comparison of weight-specific clearance rates of total cells for *Placopecten magellanicus* between each multialgal experiment showed no significant difference (ANOVA; P= 0.116) (Table 6). No pseudofeces were produced in any of the experiments.

DISCUSSION

Although the clearance rates of individual species of phytoplankton by juvenile *Mya arenaria*, *Mytilus edulis*, and *Placopecten magellanicus* suggests differential particle selection based on particle size, the experiments using multialgal cultures show that factors other than particle size may be involved in particle selection by juvenile scallops. This work also demonstrates the overall higher clearance rates of phytoplankton by juvenile scallops, an important factor when considering costs associated with the post-metamorphic grow-out phase. Previous work has demonstrated that clearance rates of phytoplankton by bivalves are also sensitive to the concentration of particles being ingested, where at high concentrations preingestive sorting by the labial palps occurs, resulting in the production of pseudofeces (Griffiths and Griffiths 1987), and an increase in food residence time due to gut fullness (Bayne et al. 1984). Our experiments were designed to avoid, as much as possible, these confounding influences on particle selection. Juvenile *P. magellanicus* show no discrimination when fed phytoplankton of approximately the same size (9 to 13 µm, experiment one). Scallops feeding on mixed algal diets of different cell sizes (experiments two and three) reveal that juvenile seallops exhibit size-specific selection (experiment two) or show non-specific selection (experiment three) based on the number of species and the species used in the experiments.

Table 4. Comparison of weight-specific clearance rates of juvenile *Placopecten magellanicus*, *Mya arenaria*, and *Mytilus edulis* for five species of phytoplankton.

	Placopecten magellanicus	*Mya arenaria*	*Mytilus edulis*	
Clone	CR[a]	CR[a]	CR[a]	*P* value[b,c]
TISO	0.339±0.47	0.24±0.03	0.04±0.05	0.538
3C	2.88±0.73[1]	0.34±0.03[2]	0.59±0.07[2]	0.0001
EXUV	0.7±0.40[1]	0.50±0.12[1]	1.68± 0.19[2]	0.0001
3H	1.53±0.55[1]	0.56±0.07[2]	0.31 ±0.04[2]	0.0001
PHAEO	0.473±0.53	0.54±0.06	0.89±0.01	0.063

[a] CR=Weight-specific clearance rate = cells·ml^{-1}·h^{-1} x 10^3·mg^{-1} dry weight (N=6 for *Mya arenaria* and *Mytilus edulis*, N=5 for *Placopecten magellanicus*, mean ± SD).

[b] ANOVA on the weight-specific clearance rates at a significance level of 5%.

[c] Treatments sharing the same superscript number are not statistically different from one another.

Table 6. Weight-specific clearance rates of total cells for each multialgal feeding experiment with juvenile scallops, *Placopecten magellanicus*.

Experiment	Clearance rates[a]	*P* value[b]	V_w^*[c]	*P* value[b]
one	5.81 ± 1.7	.116	.613 ± .19	.109
two	7.09±2.18		.753± .24	
three	4.76 ± 1.48		.494 ± .16	

[a] Clearance rate = cells·ml^{-1}·h^{-1} x 10·mg^{-1} dry weight (mean ± SD).

[b] Results from ANOVA.

[c] Weight-specific irrigation rates= ml·h^{-1}·mg^{-1} dry weight.

Table 5. Weight-specific clearance rates of phytoplankton in multialgal experiments for juvenile scallops, *Placopecten magellanicus*.

Experiment	one	CR[a]	two[c]	CR[a]	three[c]	CR[a]
Clones	PLATY 1	2.65 ± 1.17	TISO[1]	1.41 ± 0.499	3H[1]	.665 ± .327
	3H	2.03 ± 0.711	3C[1]	1.66 ± 0.509	PHAEO[1]	.618 ± .287
	EXUV	2.41 ± 0.859	UW 442[2]	2.59 ± 0.777	DUN[1]	1.40 ± .410
			GT 429[3]	0.147 ± 0.19	3C[1]	.889 ± .334
					AMPHI[2]	1.20 ± .462
P value[b]	0.514		0.0001		0.0043	

[a] CR = Clearance rate = cells·ml^{-1}·h^{-1} x 10^3, mg^{-1} dry weight (N = 5 for each alga tested, mean ± SD).

[b] Results from ANOVA.

[c] Multiple comparison testing. Phytoplankton sharing the same superscript number are not statistically different from one another.

One mechanism which might result in the decreased selectivity based on size is the increased production of mucus, a feeding response known to occur in *Argopecten irradians* at high algal concentrations resulting in the production of pseudofeces (Palmer and Williams 1980). Additionally, the plicate architecture of the ctenidium breaks down locally allowing particles to be captured on the previously bypassed frontal surfaces. These particles are enrobed in mucus and transplanted ventrally, where they are likely to be dislodged as pseudofeces (P. Beninger, personal communication). *Argopecten irradians* does not possess laterofrontal cirri (Riisgard 1988), whereas *Placopecten magellanicus* has laterofrontal cirri that are reduced to a single row, resulting in a lower efficiency of capture for particles less than 5μm (Beninger this volume). The production of excess mucus could result in the retention of small species of phytoplankton not normally cleared because of the morphology and hydrodynamics of the ctenidium. Although concentrations were similar for all multialgal experiments, our results with multialgal diets of different sizes might have ellicited a similar response. Further experimentation is required to answer this particular question. Despite the observed differences between different sizes of algae in the multialgal experiments, the clearance rates for total cells are not significantly different between the experiments. This could reflect the ability of juvenile scallops to regulate their feeding in order to obtain a constant ration. A similar phenomenon has been observed for bivalves feeding on different concentrations of phytoplankton (Palmer and Williams 1980). If maintaining a constant ration is partially regulated by factors other than cell size, other mechanisms must be invoked to explain our results. These mechanisms might include chemosensory cues, with the physiological state and biochemical composition of the algal cells determining which cells are cleared and ingested. Ward and Targett (1989) have recently demonstrated that particle selection by *Mytilus edulis* was enhanced when algal metabolites were adsorbed onto spheres of similar size (10 μm).

We did not examine absorption efficiencies in these experiments, but our experiments show that clearance rates of different species of phytoplankton at similar concentrations are determined by factors other than particle size alone. Previous experiments have shown a similar pattern of selection against some species of phytoplankton (*e.g. Phaeodactylum tricornutum*) with species of bivalves not tested in these experiments (see Shumway et al. 1985). The optimal ration for juvenile scallops used in aquaculture ventures, which will change with size and temperature, will be dependent on cell concentration, food quality, digestibility, and efficiency of assimilation by the scallop. Energetic budgets and growth measurements of juvenile scallops fed on different diets at similar concentrations will be required to determine confidently what the optimal ration will be for the fastest growth and least cost.

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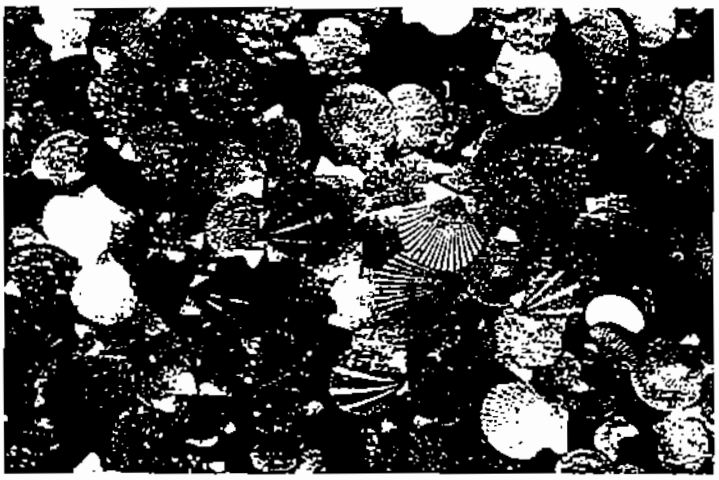

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