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Competition for food in the larvae of two marine molluscs, *Crepidula fornicata* and *Crassostrea gigas*

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Abstract – The degree to which larvae of the invasive American slipper limpet (*Crepidula fornicata*) and the Japanese oyster (*Crassostrea gigas*) may compete for food was examined during 2003 in the laboratory. Larval microalgae uptake, growth and mortality were compared for larvae fed each of six species of unicellular algae, ranging in length from 2 to 10 μm. Tested diets included the two flagellates *Tetraselmis chui (*Prasinophyceae) and *Isochrysis affinis galbana (T-ISO,* Haptophyceae), one member of the Chlorophyceae (*Nannochloris atomus*), and three diatom species (*Chaetoceros calcitrans* forma *pumilum*, *Chaetoceros gracilis*, *Skeletonema marinoï*). We found that the limpet larvae ingested phytoplankton over a wider range of cell sizes and ate at higher rates on each diet than did the oyster larvae. For example, oyster larvae consumed 2216 cells h^{-1} of *N. atomus*, while limpet larvae consumed the same phytoplankton cells at approximately twice that rate, 5159 cells h^{-1}, on the same diet. Larvae of both species grew more quickly on a mixture of flagellates than on any of the diatom alone (12 versus 7 μm d^{-1} for oyster larvae and 41 versus 28 μm d^{-1} for limpet larvae). Our results suggest that in the Bay of Mount Saint-Michel (France, Western Channel), where larvae of both species co-exist in the summer, intensive grazing by limpet larvae can potentially deplete phytoplankton concentrations to cause competition with oyster larvae, particularly for smaller sized phytoplankton species.

Key words: Phytoplankton / Diet / Feeding rate / Growth / Larvae, *Crepidula fornicata*, *Crassostrea gigas*

Résumé – Compétition trophique chez les larves de mollusques marins *Crepidula fornicata* et *Crassostrea gigas*. En 2003, des expérimentations ont été menées en laboratoire pour évaluer la compétition trophique entre les larves de crépidules (*Crepidula fornicata*) et celles de l'huître japonaise (*Crassostrea gigas*). Les taux de consommation, de croissance et de mortalité sont comparés, en alimentant les larves de chaque mollusque avec six espèces d'algues unicellulaires, dont la taille varie de 2 à 10 μm, deux flagellées *Tetraselmis chui* (Prasinophycée) et *Isochrysis affinis* galbana (T-ISO, Haptophycée), une chlorophycée *Nannochloris atomus*, et trois diatomées : *Chaetoceros calcitrans forma pumilum*, *Chaetoceros gracilis* et *Skeletonema marinoï*. Contrairement aux larves d'huîtres, les larves de crépidules consomment toutes les cellules phytoplanctoniques quelles que soient leurs tailles, et ceci, à un taux plus élevé que celui des larves d'huîtres. Ainsi, une larve d'huître consomme 2216 cellules h^{-1} de *N. atomus*, tandis que la larve de crépidule en consomme 5159 cellules h^{-1}, soit environ deux fois plus. Ces expériences mettent également en évidence que les larves des deux espèces grandissent plus vite quand elles sont nourries avec le mélange des algues flagellées plutôt qu'avec chacune des espèces de ces mêmes algues (12 contre 7 μm j^{-1} pour l'huître et 41 contre 28 μm j^{-1} pour la crépidule). Ainsi, en baie du Mont Saint-Michel (Manche ouest) où les larves des deux espèces apparaissent à la même période estivale, nos résultats suggèrent que la filtration des larves de crépidules abaisse notablement la concentration de phytoplancton, et tout spécialement celle des petites cellules algales, entraînant alors une compétition trophique avec les larves d'huîtres.

1 Introduction

More and more marine species are currently being transported alive throughout the world; some are intentionally and legally imported to test new exotic species for economic seafarming or aquaria (fish or shellfish), while others are accidentally carried through packaging or as epibionts, parasites, or commensals (reviewed by Ruiz et al. 1997). The slipper limpet (*Crepidula fornicata*), for example, was accidentally imported into Europe from the USA, as an epibiont of the American oyster (*Crassostrea virginica*), at the end of the 19th century (Mac Millan 1938). It has now become a spatial

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competitor with oysters. Individuals of *C. fornicata* have now been reported from Norway, in the North Sea, to Sicily in the Mediterranean Sea (Blanchard 1995; 1997). The highest population densities are found along the English Channel, leading to ecological as well as economic consequences in shellfish areas (Chipperfield 1951; Riera et al. 2002; Thieltges et al. 2004; Thieltges 2005).

In the Bay of Mount Saint-Michel (Western Channel), shellfish farming is well developed; there are stocks of 8000 metric tons of the Japanese oyster (*Crassostrea gigas*), 3000 t of the flat oyster (*Ostrea edulis*) and 10 000 t of mussels (*Mytilus edulis*), with respective annual productions of 5000, 1500, and 10 000 t (Mazurié and Bouget 2004). In the same area, a huge biomass of the slipper limpet has been present for thirty years, estimated at 150 000 t (Blanchard et al. 2006). Although some results have been published on adult nutritional behavior and competition between limpets and mussels (Thieltges 2005) or limpets and oysters (de Montaudouin et al.1999; Riera et al. 2002; Decottignies et al. 2007; Riera 2007), none have considered the potential for competition between larvae of these species, to our knowledge, and more generally, little is known about the potential for competition between introduced and native species during the larval stage.

In the Western Channel, limpet larvae are observed from April to October with a maximal density (8000 m^{-3}) from mid July to mid August (Quiniou and Blanchard 1987). When reared in the laboratory, larval life is about 2 weeks at 24 °C and about 4 weeks at 18 °C, under optimal food conditions (Pechenik 1984), and can extend to 5 weeks in the field (Chipperfield 1951). The *in-situ* larval life of *Crassostrea gigas* has been studied in Arcachon Bay, on the French Atlantic coast (His and Robert 1983; His et al. 1986; Robert and His 1988); Oyster larvae are present from the beginning of June to mid-September, with a maximal density (1×10^6 larvae m^{-3}) at the end of July (His and Robert 1983), when limpet larvae also reach a peak (de Montaudouin et al. 1999).

Thus, the larvae of both species reach their maximal densities at the same time in the summer, so that trophic competition is likely to occur between them if they feed on the same phytoplanktonic species.

The experiments reported here were undertaken as part of the French Program on Coastal Environment (PNEC) program, in the Bay of Mount Saint-Michel, dealing with trophic competition between suspension-feeders. We believe that this is the first study to address the issue of potential larval competition for food, between the larvae of oysters and introduced slipper limpets. Specifically, we addressed the following questions: (1) Do oyster and limpet larvae show differential ingestion on similar diets? (2) Do oyster and limpet larvae show microalgae cell size selectivity? (3) Do oyster and limpet larvae show similar development on the same diet?

2 Materials and methods

Two series of experiments were performed in the laboratory of IFREMER located in Argenton, near Brest, France. Adult limpets were collected by divers in the Bay of Mount Saint-Michel (48˚40, 600 N / 01°50,000 W), during the optimal reproductive period, on June 23th 2003; water temperature was 18–19 °C. They were transported to Argenton, placed in flowing sea-water at 20 °C and continuously fed with the unicellular flagellate *Isochrysis affinis galbana* (clone *T-ISO*). A sieve (150 μm) was placed at the outflow of the tank to automatically collect the planktonic larvae as they were released by brooding females. The first larvae were collected after five days.

Oyster larvae were obtained in the laboratory from adult oysters collected in the North of Brittany and kept under controlled conditions. Male and female gametes were obtained by stripping the gonads. Eggs were retained on a 20 μm sieve and fertilized at a ratio of 100 to 500 spermatozoïds per egg, at 24 °C. Fertilization was completed on June 18th 2003 for the first Series and on July 7th for the second one. Thus the larvae were respectively 12 and 9 days old at the beginning of our experiments.

Slipper limpet larvae emerged from females at a shell length of about 400 μm and were tested at mean shell lengths of 420 to 800 μm. Oyster larvae can metamorphose at about 300 μm (Utting and Spencer 1991) so they were accordingly tested at mean shell lengths of 160 to 260 μm.

The experiments were carried out using glass beakers containing 1800 ml of 1 μm filtered seawater at a concentration of 1 limpet larva ml^{-1} or 5.5 oyster larvae ml^{-1} in keeping with their respective shell lengths and volumes. Experiments were run in duplicate, without aeration, at 22 °C and a photoperiod of 10L:14D. Every second day, a new phytoplankton suspension was prepared, and larvae were transferred from the old suspension by retaining them on a 100 μm seive. To monitor changes in larval concentrations over time, larvae were counted during three water changes (one at the beginning, one in the middle, and one at the end of each experiment). They were then transferred into 500 ml of filtered seawater. After agitation, a 1 or 2 ml sample was pipetted at random and the number of larvae in each sample was determined using a microscope at 10 X magnification. Also at these three times, samples of larvae were fixed with 5% formalin for later measurement. Limpet larvae were positioned on their left side and measured using a dissecting microscope at 50 X; 30 larvae were measured for each subsample. Oyster larvae were measured automatically with shape recognition software (WindImager and Imaq Vision Builder); about 300 larvae were measured at each time interval along their greatest length. Growth rates were calculated as μm shell growth day^{-1}.

Unicellular algae were cultivated in the laboratory and generally used during their exponential growth phase. Algal species were chosen to cover a wide range of sizes. One motionless alga (*Nannochloris atomus*) and two flagellated algae (*Isochrysis affinis galbana* clone *T-ISO* and *Tetraselmis chui)* were used in Series 1 experiments. Larvae were also reared on a mixed diet of the three species. Three diatom species were tested as food in a second set of experiments: *Chaetoceros gracilis*, *Chaetoceros calcitrans* forma *pumilum* and *Skeletonema marinoï*, the latter being colonial. The characteristics of these algae are reported (Table 1).

Larvae were offered *I. aff. galbana* at a concentration of 100 cells μl^{-1}; other algae were offered at comparable cell volumes (Table 2). The same concentrations were maintained throughout each experiment.

Table 1. Phytoplankton characteristics following (1) Robert et al. (2004), (2) FAO data (http://www.fao.org/DOCREP/003/W3732E/w3732e07.htm).

Algae species	Classification	Origin	Length (μm) and *volume* (μm^3) (1)	Dry weight (pg cell^{-1}) (2)	Chlorophyll (pg cell^{-1}) (2)	Organic content (pg cell^{-1}) (2)
Isochrysis affinis galbana,clone *T-ISO* (Parke)	Prymnesiophyceae Isochrysidales Isochrysidacea	CCAP 927/14	4.29 ± 0.48 *41*	29.7	0.29	14.5
Nannochloris atomus (Butcher)	Chlorophyceae Chlorococcales Chlorellacea	Marine farm Douet, France	2 *4.5*	21.4	0.08	15.9
Tetraselmis chui (Butcher)	Prasinophyceae Chlorodendrales Chlorodendracea	USA 2000 Milford	8.64 ± 1.14 *340*	269	3.83	161.6
Chaetoceros calcitrans forma *pumilum* (Paulsen)	Bacillariophyceae Centrales Chaetoceracea	CCAP 1010/05	4.37 ± 0.31 *44*	11.3*	0.34*	6.28
Chaetoceros gracilis (Schütt)	Bacillariophyceae Centrales Chaetoceracea	UTEX CB2375	5.30 ± 0.56 *70*	74.8	0.78	16.2
Skeletonema marinoï (Sarno & Zingone) (previously *S. costatum*)	Bacillariophyceae Centrales Thalassioracea	CCAP 1077/3	>6 μm	52.2	1.21	20.5

(*) *Chaetoceros calcitrans calcitrans.*

Table 2. Phytoplankton concentrations used for the experiments.

Algae species	*I. aff. galbana equivalent* (cell volume in μm^3)	Algal concentration (cells μl^{-1})
Nannochloris atomus	10	500
Tetraselmis chui	0.085	10
Algae mixture in first series		165
		33
		3.3
Chaetoceros calcitrans. f. *pumilum*	0.94	91
Chaetoceros gracilis	0.56	53
Skeletonema marinoï	0.46	46

In order to determine larval grazing rates, water samples of 20 ml were taken twice a day (before and after feeding) from all beakers, drawn through a 60 μm sieve to avoid capturing larvae. Phytoplankton cell concentrations were determined using an electronic particle counter (Coulter-counter Model ZM) fitted with a 100 μm aperture. To count colonies of the chain-forming diatom *Skeletonema marinoï*, water samples of known volume were examined using a Malassez cell at a magnification of 100 X. Grazing rates were calculated from the decline in phytoplankton concentration over time and expressed as cells eaten per hour per larva.

The effects of diet on shell growth and grazing rates were analyzed using one way analysis of variance (ANOVA). Differences between groups were assessed using posteriori tests, multicomparison test of mean (Scheffé test). The data were previously tested to ensure that they met the assumptions of normality and homogeneity of variance.

3 Results

3.1 Grazing by larvae

The first set of experiments concerned three flagellates offered to larvae as single diet and as mixture. The small-celled algae (*N. atomus* and *I. aff. galbana*) were eaten by larvae of both species; in contrast, *T. chui*, the largest alga tested (8.6 μm in diameter), was not eaten in great numbers by larvae of either species. Larvae of both species ingested the different microalgae at significantly different rates ($p < 0.0001$), regardless of veliger age (Table 3).

Limpet larvae ate *N. atomus* at a mean rate of 5159 ± 923 cells h^{-1} larva^{-1}, while larvae of the cupped oyster fed at less than half that rate (2216 ± 1060 cells h^{-1} larva^{-1}). Cells of *I. aff. galbana* were well ingested by larvae of both molluscs. The mean feeding rate on *I. aff. galbana* for the limpet was 6817 ± 022 cells h^{-1} larva^{-1}. For the oyster, mean consumption was only 806 ± 339 cells h^{-1} larva^{-1}, only about one-eighth the rate recorded for limpet larvae. Limpet larvae grazed weakly on *T. chui* (370 ± 48 cells h^{-1} larva^{-1}) while oyster larvae showed an even lower rate of ingestion of this alga (29 ± 14 cells h^{-1} larva^{-1}), which means about 13 times greater ingestion for the limpet larvae than for the oyster larvae. The mixture of flagellates was readily ingested by larvae of both species: 14 295 ± 16 944 cells h^{-1} larva^{-1} for the limpet and 2999 ± 703 cells h^{-1} larva^{-1} for the oyster, with limpet larvae eating more than 6 times faster than oyster larvae.

The second set of experiments concerned three differently sized diatoms; two of them were unicellular (*Chaetoceros calcitrans* forma*pumilum* (hereafter named *C. pumilum*) and *Chaetoceros gracilis*) and one (*Skeletonema marinoï)* was colonial. Larvae of both the oyster and the slipper limpet

Table 3. Statistical analysis with ANOVA and Sheffé tests for grazing comparison of oyster (*Crassostrea gigas*) and limpet (*Crepidula fornicata*) larvae, fed different diets; B = 1st to 2nd day after beginning of the feeding trial; E = day before to last day of feeding trial (day 8 or 9).

Series	Mollusc	Day	*df*	*F*	*p*	Microalgae With Scheffé test, all paired combinations are significant at $p < 0.05$, excepted:	
1	*C. gigas*	B	3	29.70	***	*I. aff. galbana*/*T. chui*	0.9996
	C. gigas	E	3	114.07	***	*I. aff. galbana*/mixture	0.1810
						I. aff. galbana/*T. chui*	0.1689
	C. fornicata	B	3	46.78	***	*I. aff. galbana*/*T. chui*	0.1429
						Mixture/*N. atomus*	0.2427
	C. fornicata	E	3	82.89	***	*I. aff. galbana*/*T. chui*	0.1051
2	*C. gigas*	B	2	114.32	***	*C. gracilis*/*S. marinoï*	0.7864
	C. gigas	E	2	408.65	***	-	-
	C. fornicata	B	2	19.15	**	*C. gracilis*/*S. marinoï*	0.5599
	C. fornicata	E	2	79.14	***	*C. gracilis*/*S. marinoï*	0.2332

consumed the three types of diatoms, with significant influences of diet on larval grazing regardless of veliger age ($p < 0.0001$, Table 3). Limpet larvae consumed the small alga *C. pumilum* (4 μm) about three times faster than they consumed either of the other algae that were offered: 11978 ± 6113 cells h^{-1} $larva^{-1}$ for *C. pumilum*, 4382 ± 1647 for *C. gracilis*, and 3844 ± 1405 for *S. marinoï*. Similarly, oyster larvae also grazed *C. pumilum* more quickly than the other diatoms: mean ingestion were 1259 ± 374 cells h^{-1} $larva^{-1}$ for *C. pumilum*, 355 ± 186 for *C. gracilis*, 324 ± 64 for *S. marinoï*. *C. pumilum* uptake was on average about 10 times more for limpet than for oyster larvae. Consumption among replicates was considerably more variable on flagellates than on diatoms, for both oyster and limpet larvae. For larvae of both molluscs, grazing rates on diatoms increased with larval shell size, while grazing rates with flagellates did not (Fig. 1).

3.2 Larval growth

Larvae of both species grew substantially in both Series 1 and 2 experiments. The best growth was recorded for both oyster and limpet larvae when they were fed a mixed diet of flagellates (Fig. 2). On monospecific diets, limpets larvae grew best on a diet of the flagellate *I. aff. galbana*; growth was slightly lower when limpet larvae grazed on one of the other two flagellate tested *N. atomus* and *T. chui* and growth variation on each diet was low (Fig. 2). In contrast, oyster growth was far more variable when larvae were provided with monospecific flagellate diets. During the 10-day feeding experiment, oyster larvae did not grow at all when fed solely *N. atomus* and showed only slight growth on *T. chui* (Fig. 2a). Different diets produced differences in mean larval growth (ANOVA, $p < 0.0001$, Table 4) and Scheffé tests confirmed that it concerned all diets ($p < 0.0001$, Table 4). Growth was constant (Fig. 3a) during the whole experiment, except when larvae were fed a mixture of algae, with higher growth rate at the end of the experiment (12 μm d^{-1}). In contrast, when fed each of the unialgal flagellate diets, final shell lengths for limpet larvae were not significantly different from each other (Fig. 2b, ANOVA $p > 0.005$, Table 4). The best growth over the whole period was obtained with a flagellate mixture (Fig. 3b).

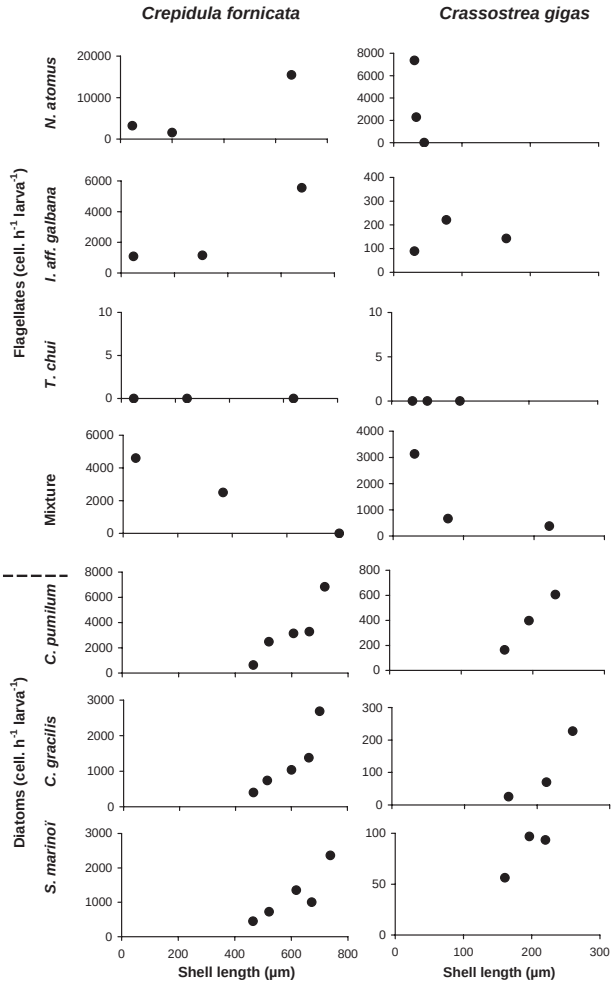

Fig. 1. Uptake of different phytoplankton species (cells h^{-1} $larva^{-1}$), according to mean shell length (μm), for the subsample A.

Growth on unialgal diatom diets was far more constant for larvae of both species over the entire 10-day feeding period (Figs. 3c,d). Diets with diatoms led to low growth for *C. gigas* (Fig. 2c), with significant differences only between *S. marinoï*

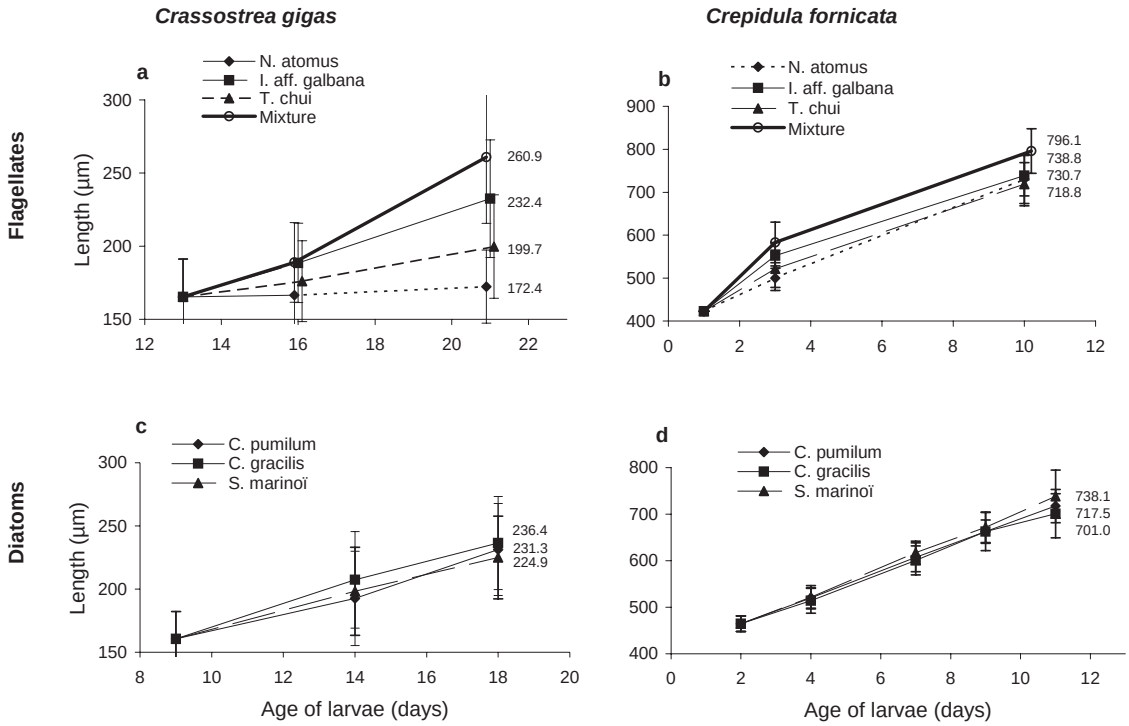

Fig. 2. Growth of larvae (measured as shell length, μm) for both species, according to diets (Series 1 and 2). Mean length, standard deviation and final shell length (μm).

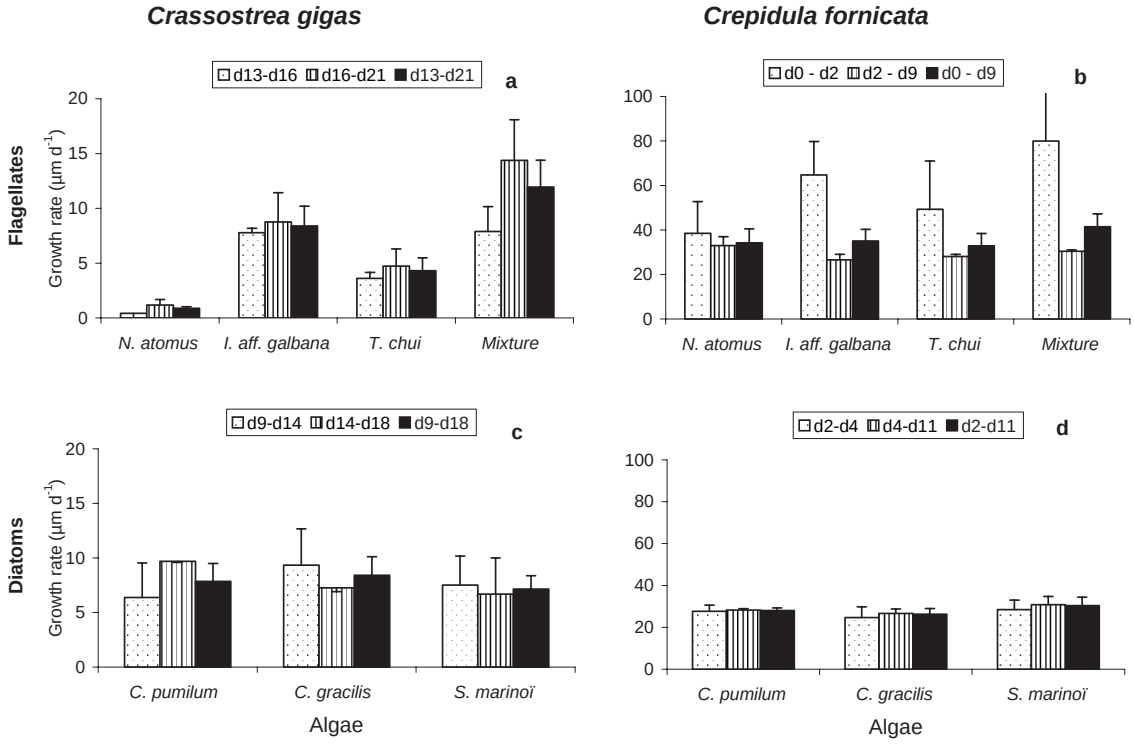

Fig. 3. Larval growth (μm d^{-1}) according to diets for both species (Series 1 and 2). Means and standard deviations.

Table 4. Statistical analysis ANOVA and Scheffé test for final shell height comparison, between oyster and limpet larvae fed different diets (day 8 or 9).

Series	Mollusc	*d f*	*F*	*p*	Microalgae Scheffé test	
1	*C. gigas*	2	228.352	***	*I. aff. galbana* / *N. atomus*	< 0.0001
					I. aff. galbana / *T. chui*	< 0.0001
					N. atomus / *T. chui*	< 0.0001
	C. fornicata	2	1.604	NS	-	-
2	*C. gigas*	2	22.848	***	*C. pumilum* / *C. gracilis*	0.0016
					C. pumilum / *S. marinoï*	0.0021
					C. gracili. /*S . marinoï*	< 0.0001
	C. fornicata	2	12.480	***	*C. pumilum* / *C. gracilis*	0.0985
					C. pumilum / *S. marinoï*	0.0598
					C. gracilis / *S. marinoï*	< 0.0001

and *C. gracilis* ($p < 0.0001$: Table 4). A similar pattern was noted for limpet larvae (Fig. 2d), with growth differences only significant between *C. gracilis* and *S. marinoï* diets (Table 4).

Comparing overall daily growth for oyster larvae (Fig. 3) diets ranked as follow: flagellate mixture >> *I. aff. galbana* = *C. gracilis* > *C. pumilum* ≈ *S. marinoï* ≫ *T. chui* ≫ *N. atomus*. For limpet larvae, the ranking was: flagellate mixture ≫ *I. aff. galbana* = *N. atomus* > *T. chui* > *S. marinoï* > *C. pumilum* > *C. gracilis*.

Growth induced by flagellates or diatoms was well predicted by the rates at which they were ingested by limpet larvae and oyster larvae. Limpet growth was regular with the largest diatom tested, *S. marinoï*, as well as with the smallest flagellate *N. atomus*. In contrast, oyster growth was high with all diatoms tested, while development was poor with all flagellates except for *I. aff. galbana*.

3.3 Mortality

Dead larvae were counted regularly to correlate algal feeding with larval density. Mortality was low for larvae of both species (max. 10%) and no consistant relationship was found between larval mortality and diet, except for oyster larvae feeding on *T. chui* in Series 1, in which induced larval mortality was high, up to 53%, after nine days of feeding.

4 Discussion

This study allowed us to compare grazing rates for the larvae of two mollusc species offered identical diets, to look for potential trophic competition. All the tested diets were eaten by the larvae of both oysters and slipper limpets, except *T. chui*, which had the largest cell size and was not appreciably consumed by oyster larvae. Food uptake comparison, between flagellate or diatom monospecific diets, shows that the higher result was achieved with flagellates for both molluscs, thanks to *N. atomus* and *I. aff. galbana* (*T-ISO*), as well as the little diatom *C. pumilum*. Other unialgal diets tested resulted in lower grazing rates. Nevertheless, for all diets tested, the intensity of larval grazing was always higher for larvae of the slipper limpet, indeed up to 10 times higher. This trend includes *T. chui*, which was ingested hardly at all by oyster larvae, but ingested 13 times more rapidly by limpet larvae. The dry weight of a 250 μm oyster larva is about 5 μg (Robert, unpublished) and that of a 600 μm long limpet larva is about 8 μg (Pechenik 1980). Per μg of larval dry weight, limpet larvae fed 5 to 8 times faster than oyster larvae on all diets other than *N. atomus*.

Previous experiments on *Crassostrea gigas* larvae have also pointed out diet preferences (Waldock and Nascimento 1979; His et al. 1985; Thompson et al. 1993; Robert and Trintignac 1996; Brown and Robert 2002; Ponis et al. 2006; Rico-Villa et al. 2006); for example, *Isochrysis aff. galbana* (*T-ISO*) as a single diet produced moderate growth, but in combination with small diatoms has led to excellent development (Robert and Gérard 1999). Our study confirms that this alga is readily eaten by umboned oyster larvae and, as a monospecific diet, gives the best growth rate (35 μm d^{-1}) among the different flagellates tested. In contrast, as showed by Ponis et al. (2002), *T. chui* is a poor diet for oyster larvae even at later stages while *N. atomus* supports even worse growth, confirming previous works (His and Robert 1987; Robert 1998) and demonstrating its high ingestion but poor digestion by *C. gigas* larvae. Similar trends were reported by Martinez et al. (2004) on *Pteria sterna* larvae while Brown et al. (1998) showed its inadequacy for Japanese oyster spat. Compared to the other diatoms, *Chaetoceros gracilis* and *Skeletonema marinoï*, phytoplankton consumption was higher with *C. pumilum*; it appeared clearly here that for *C. gigas* larvae, prey selection is particularly related to prey size. However, despite differences in ingestion rates, *C. gigas* larvae ended up growing by about the same amount by the end of the experiment regardless of the diatom species provided as food. In fact the small diatom, *C. pumilum* was particularly effective for young *C. gigas* larval development, as clearly shown by Rico-Villa et al. (2006), but for umboned larvae (length $\geqslant$ 120 μm) larger diatoms are also suitable.

Larval growth of *Crepidula fornicata* has been studied under several experimental conditions of diets and temperatures (Mapstone 1970; Pilkington and Fretter 1970; Calabrese and Rhodes 1974; Pechenik and Lima 1984; Hilbish et al. 1999; Klinzing and Pechenik 2000; Pechenik et al. 2002). Klinzing and Pechenik (2000) reared *C. fornicata* larvae on several diets and at several concentrations of each diet tested. The naked flagellate *Isochrysis aff. galbana* (*T-ISO*) led to the best growth

with 97 μm d^{-1} (at 22 °C and 180 000 cells ml^{-1}), followed by *P. lutheri* (67 μm d^{-1}) and *D. tertiolecta* (57.8 μm d^{-1}). The present results for limpet larvae feeding on *I. aff.galbana* at the same temperature but at a lower concentration (only 50 000 cells ml^{-1}) showed, not surprisingly, lower growth rates (28 and 41 μm d^{-1}). Pechenik et al. (2002) obtained optimal growth of *C. fornicata* larvae (up to 113 μm d^{-1}) on a diet of *I. aff. galbana* at 25 °C. The present study confirms that result despite a lower ingestion of phytoplanktonic cells compared to other studies using monospecific diets.

When comparing the effects of flagellates and diatoms on larval growth, the present results showed different responses by the two mollusc species. For oyster larvae, daily growth reached 7 to 8.5 μm d^{-1} when larvae were fed diatoms while they ranged widely between 1 to 8 μm d^{-1} when fed flagellates. For limpet larvae, growth of 25 to 30 μm d^{-1} and 33 to 35 μm d^{-1} were recorded with diatoms and flagellates, respectively. Moreover, oyster larvae growth varied widely on different monospecific flagellate species, whereas limpet larvae grew homogeneously on all tested flagellate species. This suggests that oyster larvae have more specific dietary requirements than do limpet larvae, which seem to grow well on a larger variety of diets. When fed a flagellate mixture, limpet larvae reached a final shell length greater than that obtained with each single diet. Oyster larvae followed a similar trend, growing fastest on a mixed algal diet. This observation confirms the results of several authors about the benefits of mixed diets for growth of mollusc larvae (Walne 1963; Calabrese and Rhodes 1974; Gerdes 1983; Laing and Millican 1986; Utting and Spencer 1991; Brown et al. 1998; Flores-Vergara et al. 2004; Rico-Villa et al. 2006). However, Pilkington and Fretter (1970) reported similar growth rates for slipper limpet larvae whether they were fed solely *Cricosphera carterae* or whether that alga was combined with *Monochrysis lutheri* and *Pyramimonas grossi*. Thus they suggested that a selection of food occured with these larvae, a mixed diet giving the larvae a selection opportunity according to their physiological condition. In the same way, we noticed that, as larvae approached the size at which they typically become competent to metamorphose, grazing on flagellates decreased while that on diatoms rose, especially for oyster larvae. Such an evolution of larval food preferences throughout larval life has been highlighted for *Strombus* species (Aldana-Aranda and Patino-Suarez 1998). The reason for this dietary shift with larval ageing could be due to nutritional elements present in diatoms but not in flagellates. For example, *C. calcitrans* contains high levels of specific fatty acids, such as 20:5n-3 (EPA), which are essential for good growth (Volkman and Brown 2006), when other algae such as *Nannochloropsis*-like sp. lack those essential fatty acids (Brown et al. 1998). Similarly, carbohydrate concentrations are generally higher in diatoms than in flagellates (Whyte 1987).

Our results show that phytoplankton species whith cells less than 5 μm (*N. atomus*, *I. aff. galbana*, *C. pumilum*), are commonly consumed by larvae of both oysters and limpets. The larger phytoplankton cells (*C. gracilis* (5.3 μm), *T. chui* (8.6 μm) and the colonial species *S. marinoï*) are ingested by oyster larvae at low or moderate rates, but are ingested at much higher rates by limpet larvae, which appear thus able to ingest larger cells. Although the larvae of both species can eat small particles, even bacteria (Pilkington and Fretter 1970; Douillet and Langdon 1994), only the limpet larvae can ingest large algal particles: *Exuviella balthica* (9–15 μm), *Cricosphaera carterae* (10–18 μm), *Phaeodactylum tricornutum* (8–35 μm) (Pilkington and Fretter 1970) or *Dunaliella tertiolecta*, which ranges in diameter between 8 and 10 μm and has a cell volume five times that of *I. aff. galbana (T-ISO)* (Calabrese and Rhodes 1974; Klinzing and Pechenik 2000). Sommer et al. (2000) noted that molluscan veligers eat prey between 1 and 30 μm in diameter, but can ingest even larger particles when food concentrations are high.

The present results show that limpet larvae feed effectively on small phytoplankton cells, thus putting them in potential competition with oyster larvae. However, limpet larvae can also feed at high rates on larger food particles if the occasion arises. This feeding adaptability of *C. fornicata* larvae is an additional characteristic that may help to explain the great success of this rapidly spreading species.

Our results suggest that limpet larvae may outcompete oyster larvae for the smaller food particles present in summer months in the Bay of Mount Saint-Michel (Blanchard et al. 1986) and then shift to larger-sized particles which the oyster larvae would be unable to ingest. Also, limpet larvae should have the competitive edge on oyster larvae because they grow well on a wider range of flagellate species. Additional studies are now needed to determine the relative concentrations of oyster and limpet larvae co-occuring in the Bay at different water depths and throughout the reproductive season.

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