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Mussels *Mytilus edulis*: significant consumers and destroyers of mesozooplankton

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ABSTRACT: This study tested the hypothesis that mesozooplankton, particularly crustaceans, inhaled by mussels *Mytilus edulis* (L.) would be killed by ingestion, or by incorporation into pseudofaeces. Crustaceans were expected to be vulnerable because they cannot rid themselves of mucus. Field and laboratory evidence is presented to show that mussels ingest most mesozooplankton present in inhaled sea water, that some of the material is triturated in the stomach between crystalline style and gastric shield, and that energy can be extracted from a diet of *Artemia* sp. indicating a degree of carnivory. Gastric processing of 'prey' animals is rapid (<40 min at 15 to 20°C). Molluscs and crustaceans are commonest 'prey'. Animals <3 to 6 mm length are ingested. Inhaled but non-ingested crustaceans become mucus-bound and are expelled in pseudofaecal particles; such animals are dead or moribund.

KEY WORDS: Mussels · Mesozooplankton · Carnivory · Pseudofaeces · Mucus

INTRODUCTION

Mussels, although complex animals with fascinating biological features, are effectively self-cleaning biological pumps. They occur in beds that can range in size up to 500×10^3 m^2 (Meadows et al. 1998) and contain billions of individuals. Large individuals (50 to 70 mm shell length) each pump up to 70 l seawater d^{-1} (Davenport & Woolmington 1982, Jørgensen 1990), so such beds (or equivalent densities of farmed mussels) consume enough phytoplankton to be significant controllers of pelagic energy-supply in coastal ecosystems (Dame 1993). Mussels are usually assumed to be microphagous, consuming diatoms, dinoflagellates, bacteria, proto-zooplankton and general seston, although Newell et al. (1989) reported ingestion of particles <110 µm. A large literature is devoted to bivalve filter-feeding and particle-processing mechanisms (e.g. Jørgensen 1990, Beninger & St-Jean 1997a, Beninger et al. 1997, 1999), but there is also evidence that mussels can take up dissolved organic matter from inhaled seawater (Péquignat 1973, Jørgensen 1983, Manahan et al. 1983, Gorham 1988). Mussels take in material of non-nutritive value (e.g. silt) too, and this is either removed without being ingested (as pseudofaeces, i.e. mucus-bound material rejected by the labial palps or mantle ciliary tracts and disposed of through the inhalant siphon), or is diverted to the intestine and lost in the faeces. The living surfaces of the mussel that encounter moving seawater are largely ciliated and mucus-secreting, and hence continually self-cleaning. The labial palps of bivalves have an important role in sorting material collected by the gills, but the mechanism of sorting is still somewhat obscure, although rapid progress is being made by the innovative use of endoscopy (Ward et al. 1993, Beninger & St-Jean 1997b).

Little attention has been paid to the effect of mussels on mesozooplankton populations, other than indirectly through competition for phytoplankton resources. Our study was designed to test the hypothesis that inhaled zooplankton, particularly crustaceans, would be killed, either by ingestion, or by incorporation into pseudofaeces. Crustaceans were expected to be particularly vulnerable because they do not secrete mucus externally (unlike annelids and molluscs) and are not ciliated, and so have no obvious means of cleaning themselves of contamination by mucus. Early workers on bivalves, particularly oysters (Nelson 1933), appreciated that animals could be ingested. More recently, zooplankton

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remains have been reported from scallop stomachs (Mikulich & Tsikhno-Lukanina 1981, Shumway et al. 1987). However, the prevailing view has been that mussels are specialised herbivores with digestive-enzyme systems dominated by amylases (although a full suite of digestive enzymes is available in various parts of the digestive system — see Bayne et al. 1976 for review).

MATERIALS AND METHODS

Nauplii of the anostracan brine shrimp *Artemia* sp. (ca 300 µm length) and adults of the harpacticoid copepod *Tigriopus brevicornis* (O.F. Müller) (1 to 1.2 mm length) were used as laboratory test-organisms in feeding experiments with homorhabdic filibranch mussels (*Mytilus edulis* L.). *Artemia* sp. were used as proxies for the diversity of crustacean meroplankton and holoplankton that are in the size range of 100 to 1000 mm length, *T. brevicornis* as representatives of small benthoplanktonic forms in the 1 to 5 mm size category.

Mussels were collected intertidally from a bed at White Bay, Great Cumbrae Island, Scotland, UK. *Tigriopus brevicornis* were collected from high-shore pools close to the University Marine Biological Station, Great Cumbrae Island. *Artemia* sp. were hatched from commercially-available cysts placed in seawater (33‰).

Filtration experiments. Ten mussels (30 to 35 mm shell length) were placed individually in a beaker containing 150 ml filtered seawater at 15°C. Yeast suspension was added to each beaker to induce pumping. Fifty *Artemia* sp. nauplii were added to each beaker. After 15 min, the mussel in each beaker was removed and the *Artemia* sp. assigned to 1 of the following 3 classes: (1) swimming, (2) bound with mucus (alive or dead), (3) ingested. The number of ingested animals was calculated by difference, but mussel stomachs were inspected to make sure that *Artemia* sp. had reached the stomach. The experiment was repeated twice, with *Artemia* sp. remaining in the beakers for <30 or 60 min. A control experiment was performed in which 50 nauplii were added to each of 10 beakers, but with no mussels present; the *Artemia* sp. were inspected after 60 min. Control and 60 min exposure trials were also carried out with *Tigriopus brevicornis*, but with 5 rather than 10 replicates. In the light of the results obtained, an extra trial was conducted with *Artemia* sp. Ten mussels were each offered 10 *Artemia* sp. nauplii in 150 ml seawater spiked with yeast suspension. They were counted and categorized after 60 min.

Response to contact by food items. Inhalant siphons of mussels, first given yeast cells to stimulate pumping, were observed by low-power microscopy as *Artemia* sp. or *Tigriopus brevicornis* were added to the seawater around the mussels.

Experiments with dyed brine shrimps. *Artemia* sp. (unfed 2nd instars) were placed for 15 min in filtered seawater , deeply coloured with Rose Bengal to yield brine shrimps with crimson gut contents (*Artemia* sp. continually drinks the medium in order to stay in water balance, since its body fluids are hypo-osmotic to seawater). They were sieved out, washed with tap water, and transferred to filtered seawater. Single mussels (30 to 35 mm shell length) were each placed in 150 ml of 1 µm filtered seawater to which yeast cells were added to stimulate pumping. Fifty dyed, live *Artemia* sp. were added to the seawater so that they started to be inhaled by the mussel. Mussels were removed after intervals of 1, 5, 15, 30, 40 min and 60 min, the adductor muscles were cut, the mantle cavity (including surfaces of gills, palps, foot) inspected for the presence of dyed *Artemia* sp., and then the stomach was opened and the stomach contents inspected for the presence and condition of ingested dyed *Artemia* sp. instars. For each time interval, at least 3 mussels were inspected.

Ten mussels were each placed individually in beakers containing 1500 ml of 1 mm filtered seawater to which roughly 500 dyed *Artemia* sp. were added. This was done in the late evening. Twelve hours later, faeces were collected from each beaker and inspected for colour and the presence of *Artemia* sp. remains.

Experiments with *Tigriopus brevicornis*. Individual *T. brevicornis* were pipetted into the inhalant stream (outside the inhalant siphon) of mussels (40 to 50 mm shell length), each of which was held in seawater, dorsal-surface downwards, under a binocular microscope at 15 to 20°C so that the inhalant siphon was fully visible, and often the gills and foot within the mantle cavity as well. The mussels were previously induced to pump and gape widely by spiking the seawater with yeast cells. Trials were carried out at various time intervals (10 and 30 s, and 1, 2, 5, and 10 min) between delivery of copepods to the inhalant stream; if *T. brevicornis* were not expelled in pseudofaeces, the mussel's stomach was opened to check that ingestion had occurred. During these experiments it was often possible to observe the impact of *T. brevicornis* individuals on gills, mantle or foot of the mussels.

Field observations of stomach contents. On various occasions between 25 February 1999 (late winter) and 15 April 1999 (when the spring phytoplankton bloom had been evident for ~2 wk), a total of 100 mussels (25 to 40 mm shell length) were each suspended in seawater from a pier for 24 h. The mussels were suspended in cylindrical plastic mesh cages, 3 mussels to a cage. Cages (~100 mm high, 50 mm diam.) were open at the top, but closed at the bottom. The cage

mesh was coarse (~5 mm). The cages were covered at all stages of the tide and held around 1 to 2 m above the sea bed. Stomachs of mussels were opened under filtered seawater within 5 to 10 min of leaving the seawater beneath the pier. The stomach contents were sucked out with a fine polypropylene pipette, and forceps were used to withdraw the crystalline style with its distal bolus of adhering material. In late winter, the stomach contents of 6 mussels per week were investigated. At the end of the sampling period, when phytoplankton concentrations and zooplankton numbers had risen dramatically, the frequency of sampling was increased (22 mussels being examined between 12 and 15 April 1999). Stomach contents were analysed first by noting the presence or absence of phytoplankton and zooplankton, and then identifying and counting any zooplantonic organisms present to allow assessment of frequency of occurrence. On 12 April 1999, to permit a qualitative comparison of stomach zooplankton contents with the environmental zooplankton composition, medium-net (150 µm mesh) plankton sample was taken from the pier at the same time as the mussels were sampled.

Feeding experiments. Two feeding experiments were conducted. On 29 September 1998, 90 mussels were graded into 3 equal groups of similar size range (27 to 44 mm shell length). There were no significant size-distribution differences amongst the 3 groups (ANOVA; $p > 0.05$). The condition index (CI) of 30 mussels was immediately established ('field' group) using the mussel CI known to be most stable and accurate (Davenport & Chen 1987):

$$CI = \frac{(\text{cooked meat mass}) \times 100}{(\text{cooked meat mass} + \text{shell mass})}$$

Mussels were held in boiling seawater for 2 min. Shells and meats were dabbed dry with tissues before weighing (to nearest 0.01 g).

The other groups of 30 mussels were each held in an aquarium (vol. = 12.5 l; 15°C; environmental temperature in September) that was emptied, rinsed and refilled with aerated 1 mm filtered seawater twice daily (09:00 and 17:00 h). One group ('starved') remained unfed. The other group ('fed') was supplied 3 times per day (09:00, 12:00, 17:00 h), 5 d per week with *Artemia nauplii* which had hatched in the previous 24 h from 0.05 g dry wt eggs. Nauplii were not fed, so there was no possibility of any other food organisms reaching the mussels. After 4 wk the CI of the remaining mussels was established.

On 17 March 1999, 3 groups (n = 127) of similar sized mussels (24 to 47 mm length) were collected (no significant inter-group size differences; ANOVA $p > 0.05$). The CI of one group ('prespawning field') was immediately established. The other 2 groups were each accommodated in 12.5 l aquaria (8°C; environmental temperature in March), 2 aquaria per group. Water changes and aeration were as described above. Mussels of these groups all spawned on 18 and 19 March 1999. One group ('spawned starved') received no food; the other ('spawned fed') was offered *Artemia* 3 times daily, 7 d per week (nauplii derived from 0.15 g dry wt *Artemia* sp. eggs at each offering). After 3 wk the CI of the remaining mussels was established. The effect of shell length on CI was negligible (r^2 values: 0 to 4.2%). Mortality levels were low (<4%). CI values were arcsine-transformed and checked for normality of distribution (Anderson-Darling; all $p > 0.05$) before 1-way ANOVA was applied.

RESULTS

Filtration/processing of zooplankton

Results are shown in Table 1. For *Artemia* sp. offered to mussels *Mytilus edulis* at 333 nauplii l^{-1}, ca 90% of nauplii were ingested and 2 to 5% bound with mucus and rejected as pseudofaeces. No mucus-bound nauplii were ever seen to break free from the adhering mucus (even if left for 24 h). There were no significant differences between the results of trials of different duration (ANOVA; $p > 0.05$). Experiments at lower densities of *Artemia* (67 nauplii l^{-1}) (not shown in Table 1) yielded slightly different results: 90% of nauplii were ingested, but none were bound in mucus, suggesting that nauplii are only discarded in pseudofaeces when present in high densities in inhaled seawater. For *Tigriopus brevicornis* offered

Table 1. *Mytilus edulis*. Processing of *Artemia* sp. and *Tigriopus brevicornis* by mussels. Values are mean number of animals in each category (out of 50 per trial replicate) with SD in parentheses

Species	Duration (min)	Swimming	Mucus-bound/dead	Ingested
***Artemia* sp. (replicates per trial = 10)**				
Trial 1	15	4.80 (4.69)	2.50 (3.21)	42.70 (7.75)
Trial 2	30	1.90 (2.28)	1.10 (1.45)	47.00 (2.91)
Trial 3	60	4.50 (6.75)	1.00 (1.56)	44.50 (8.20)
Control	60	50	–	–
***Tigriopus brevicornis* (replicates per trial = 5)**				
Trial 1	60	26.80 (13.74)	6.00 (5.70)	17.20 (11.43)
Control	60	50	–	–

to mussels at 333 copepods l^{-1}, ingestion rates (ca 34%) were lower, but a higher proportion were mucus-bound (ca 12%). As with *Artemia* sp. nauplii, no mucus-bound copepods were able to free themselves.

In pilot filtration-experiments with both *Artemia* sp. and *Tigriopus brevicornis*, observations were made under the binocular microscope. Although the beakers were small, animals were only inhaled when they strayed into the centre of the inhalant stream (i.e. the inhalant flow was not sufficiently strong to scavenge water rapidly from all parts of the beaker). Neither species had the ability to escape from the inhalant stream once entrained — it is evident that the flow rate was of the order of several cm s^{-1}.

Response of mussels to contact with *Artemia* sp. or *Tigriopus brevicornis*

When *Artemia* sp. nauplii were inhaled, if they touched the siphonal tentacles there was little or no sign of reaction to touch by the mussel. In contrast, *Tigriopus brevicornis* usually only entered the mantle cavity if they passed through the inhalant siphon cleanly, without touching siphonal tentacles. If they touched the siphonal tentacles, there was immediate siphon closure, accompanied by some shell-valve adduction. This response prevented entry of the copepods, which usually escaped by vigorous swimming movements, although a few adhered to mucus on the siphonal mantle edges and were inhaled when the siphon subsequently reopened.

Experiments with dyed *Artemia* sp.

The following observations were made during the experiments with dyed, live brine shrimps: (1) *Artemia* sp. were visible within the mantle cavity for no more than 5 min after inhalation; (2) *Artemia* sp. were sometimes alive in the stomach 5 min after ingestion, but beyond 5 min all brine shrimps were dead; (3) many *Artemia* sp. were found in a crushed state between the distal end of the crystalline style and the gastric shield within 5 to 15 min of ingestion, and in some cases damaged *Artemia* sp. were surrounded by fluid material stained with Rose Bengal; (4) after 15 to 40 min, any *Artemia* sp. visible within the stomach appeared to be partially digested; (5) after >40 min, it was rarely possible to find identifiable *Artemia* sp. material; (6) mussels fed several batches of dyed *Artemia* sp. in the late afternoon produced red faecal material overnight, but the faeces did not contain identifiable skeletal material.

Experiments with *Tigriopus brevicornis*

From repeated trials, the following information was collected: (1) copepods that impacted the gills adhered to them and were transported anteriorly towards the palps; (2) copepods impacting the mantle or foot adhered immediately and were transported posteriorly and eventually expelled, bound with mucus, at the dorsal end of the inhalant siphon aperture (cf. Beninger et al. 1999); (3) if individuals were placed in the inhalant stream at intervals of 5 min or more, most were ingested (checked by inspection of stomach contents). If *Tigriopus brevicornis* were inhaled more frequently, they were invariably expelled as mucus-bound pseudofaeces. This suggests that the palps can handle animals of this size provided that too many do not arrive in a short period.

Field observations of stomach contents

Of 100 mussel stomachs sampled from the field, 21 were empty and 6 contained only diatoms or dinoflagellates. Seven contained plant material and crustacean fragments (mainly pieces of gammarid amphipod or copepod exoskeleton) which could conceivably have been ingested in fragmentary form rather than reflecting breakup within the stomach. Eleven contained solely whole-animal material (i.e. individual recognizable animals ranging from live specimens to whole but crushed dead animals), mostly in late winter. The remaining 55 stomachs containing both plant and whole-animal material. Incidence of occurrence of animal material was 66% if identifiable individual animals are considered, 73% if fragmentary material is included. A taxonomic breakdown of the individual animals found in the mussel stomachs is given in Table 2: 260 animals were identified (i.e. ~4 items for each stomach that contained animals). Maximum number of items found was 23 (14 bivalve D-stage (straight-hinge) larvae, 5 rotifers, 2 calanoid copepod nauplii, 1 adult harpacticoid copepod, 1 fish egg). The order of frequency of occurrence was as follows: molluscan eggs (identifiable because they contained veligers) and larvae, 107 (41.2%); barnacle zoeae and cyprids, 34 (13.1%); rotifers, 25 (9.6%); cladocerans, 23 (8.8%); calanoid copepods of all stages, 18 (6.9%); polychaetes, 15 (5.8%); ostracods, 8 (3.1%); harpacticoid copepods, 6 (2.3%); fish eggs, 5 (1.9%); protists, 4 (1.5%); mites, 4 (1.5%); bryozoan larvae, 3 (1.2%); crab zoeae, 2 (0.8%); nematodes, 2 (0.8%); amphipods, 2 (0.8%); flatworms, 1 (0.4%); echinoderm larvae, 1 (0.4%). The frequency of occurrence of animals in the stomach and the number of items recorded are likely to be underestimates for 3 reasons: (1) some material will

Table 2. Taxonomic breakdown of animals found in mussel *Mytilus edulis* stomachs

Taxonomic group	Stages found	Descriptive detail	Taxonomic comments
Protists			
Radiolaria		Not possible to determine death	–
Rotiferans	Adults	Most alive and swimming actively	–
Turbellarians		Active	
Nematodes	Adults	Active	–
Polychaetes	Larvae and small adults	All dead and apparently partly digested	–
Molluscs	Eggs, trochophore larvae, gastropod and bivalve veligers, bivalve D-larvae	Veligers sometimes alive; D-larvae apparently dead	Majority *Mytilus edulis*
Bryozoans	Cyphonautes larvae	Dead	–
Crustaceans			
Harpacticoid copepods	Adults (<1.5 mm)	Most dead, few moribund	–
Calanoid copepods	Nauplii, copepodites, adults (<1.5 mm)	Majority dead	Include *Anomalocera patersoni*, *Calanus finmarchicus*, *Temora longicornis*
Cladocerans	Adults	Some alive	*Podon* sp.
Ostracods	Adults	Dead	–
Barnacles	All naupliar stages, cyprids	Many alive, but entangled in mucus	Majority *Semibalanus balanoides*
Amphipods	Small (5–6 mm)	Dead	*Gammarids*
Crabs	Zoeae (2 mm)	Dead	*Carcinus maenas*
Acarina	Halacarid mites	All alive, entangled in mucus	–
Echinoderms	Pluteus larvae	–	–
Vertebrates	Fish eggs 1–2 mm diam.	All early stage, most with ruptured chorions	Probably gadoids, given size/season

have moved from stomach to intestine during the interval between removal of the mussel from the sea and inspection of stomach contents; (2) material is likely to be lost when the stomach is opened; (3) some animals bound in mucus and silt will have escaped observation. There was a tendency for greater numbers of animals to be found in the stomach in spring than in winter. Stomach contents of mussels reflected the environmental plankton composition, but with some benthic/benthonic input. For example, on 12 April 1999, stomachs contained rotifers, bivalve D-larvae, copepod nauplii, barnacle nauplii and fish eggs. The corresponding net-plankton sample contained all of these items, plus larger crab, shrimp and fish larvae. However, the mussel stomachs also contained harpacticoid copepods and mites that were absent from the plankton sample but common on intertidal weed and the shell surfaces of attached mussels.

Feeding experiments

The results of experiments in which mussels were starved or 'fed' upon *Artemia* sp. alone are shown in Table 3. For the September 1998 experiment, there were differences between the CI values of field/fed and starved mussels, but not between field and fed (ANOVA $p = 0.01$; Dunnett's pairwise comparisons). Starved mussels had a much lower CI (11.46) than those which had access to *Artemia* sp. (14.03). The CI value for starved mussels was similar to that of mussels from the same population at the end of winter (when food is scarce) prior to spawning (CI = 11.33). Mussel CI varies widely with season, from ~10 after winter food deprivation and discharge of gametes, to ~25 in mid-summer in some populations (e.g. Davenport & Chen 1987). The

Table 3. *Mytilus edulis*. Results of feeding experiments, using newly hatched *Artemia* sp. nauplii as food

Expt	Mean (SD) condition index (%)
Expt 1 (15°C; September 1998)	
Field group (n = 30)	14.96 (0.23)
Starved (4 wk; n = 30)	11.46 (0.68)
Fed (4 wk; n = 29)	14.03 (0.44)
Expt 2 (8°C; March 1999)	
Prespawning field (n = 127)	11.33 (0.11)
Spawned starved (3 wk; n = 124)	9.28 (0.08)
Spawning fed (3 wk; n = 122)	10.32 (0.18)

March 1999 experiment was a little shorter (because of concerns that postspawning starved mussels might soon die). All mean group CI values differed from each other ($p < 0.0005$; Dunnett's pairwise comparisons), but postspawning mussels that had been given access to *Artemia* sp. nauplii had a significantly higher CI than postspawning starved mussels, and therefore must have extracted energy from the *Artemia* sp.

DISCUSSION

It is not surprising that mussels inhale mesozooplankton, particularly under conditions of high zooplankton density. The velocity of water in the inhalant stream of mussels *Mytilus edulis* of the size range used in this study was of the order of several cm s^{-1}. In contrast, published data for swimming speeds of mesozooplankton are mainly in the region of 1 to 2 cm s^{-1} (e.g. Hardy & Bainbridge 1954, Roe 1984, Davenport & Bebbington 1990), so escape would be difficult, even if animals could detect that they were about to be inhaled. However, from earlier work it would have been predicted that inhaled animals would be expelled in pseudofaeces. Although this happened under some conditions, the results of the present investigation clearly demonstrate that mussels can capture and ingest zooplanktonic and benthic animals not only under artificial conditions of the laboratory at high prey densities, but also in the field. Given the known capacity of mussels to sort material before ingestion (Jørgensen 1990), this indicates that mussels are partially carnivorous, a conclusion confirmed by the feeding experiments that demonstrated the ability of *M. edulis* to extract energy from a diet of *Artemia* sp. It is probable that *M. edulis* can discriminate between mesozooplanktonic organisms and non-nutritive items, since none of the mussel stomachs sampled from the field contained items of non-living material (such as detritus or anthropogenic debris) of comparable size to the zooplankters recorded. However, further study is needed to confirm or deny this hypothesis.

The results of this study have implications for several aspects of mussel ecology and exploitation. Mussels can clearly kill substantial quantities of mesozooplankton and routinely ingest animals in the 100 to 1000 µm size range. They occasionally ingest animals as large as 3 to 6 mm in length. This is a considerable upward extension of the size range recorded in previous studies (e.g. Newell et al. 1989). From our experiments with *Artemia* sp. and *Tigriopus brevicornis* it is evident that gastric processing of inhaled mesozooplankton is rapid (either by trituration or, presumably, by diversion to the intestine), probably explaining the lack of previous recognition of this phenomenon. In consequence, sampling stomach contents of mussels from the field must be accomplished within a few minutes, and will even then tend to underestimate intake.

All the laboratory and field experiments were performed on mussels of medium size (24 to 47 mm shell length). An obvious area requiring further study is that of the relationship between the size composition of ingested zooplankton and mussel body-size.

If it is assumed that a mussel of the size studied here processes ~5 animals per hour (probably an underestimate) in spring, then its daily consumption will be of the order of 120 animals. Estimates of mesozooplankton numbers in coastal waters at this time of the year (Harvey et al. 1935) are of the order of 5 animals l^{-1}. Taken together, these estimates suggest that mussels of this size range are each clearing mesozooplankton from 24 l of seawater per day. This is close enough to known pumping rates (Davenport & Woolmington 1982, Jørgensen 1990) to indicate that mussels clear mesozooplankton from the environment as efficiently as they clear *Artemia* sp. in the laboratory, providing a previously undescribed but important route of benthopelagic energy-coupling in areas with high mussel densities. These findings also have implications for intensive mussel culture that will have direct impacts on local recruitment of benthic animals and pelagic fish, as well as increasing competition for primary production resources. At present, the scale of impact of mussel beds or mussel farms upon mesoplanktonic communities is not clear; further work, including models incorporating knowledge of turbulent processes in coastal waters, is needed.

The taxonomic composition of the animals processed by mussels has relevance to rocky intertidal ecology. The most common items found in spring 1999 were larvae of barnacles and bivalves. Larval barnacles, both at the naupliar release stage and the cyprid settlement stage, were undoubtedly killed by inhalation and ingestion; there are implications for competition between barnacles and mussels for space. Whether some bivalve larvae can survive transit through the mussel gut is unclear at present; further investigation is needed. If not, then the observed numbers in the stomachs indicate significant effects on recruitment, including that of mussels themselves, since mussel larvae dominated the bivalve larval component of the mesoplankton at the time of the field experiments.

The stomach-content data were interesting from other perspectives. Several species recorded were characteristically benthic/benthonic rather than planktonic, notably polychaete worms, harpacticoid copepods and halacarid mites. This probably reflects the near-bottom positioning of the suspended mussels in the experiments reported here; they probably inhaled animals stirred up from the sea bed. It seems probable

that mussels in natural beds on rocky or muddy substrata may ingest a higher proportion of such benthic species, while mussels in commercial rope culture over substantial depths may only ingest zooplankton. More work is clearly needed to confirm these deductions. It was also interesting that the mussels were capable of ingesting pelagic fish eggs, probably of gadoids. In European waters, early spring is characterised by spawning of many species that lay broadcast pelagic eggs that subsequently suffer great mortality before and after hatching; mussels are previously unremarked predators.

When seawater is inhaled, entrained mesozooplankton may be sieved out and rejected at the inhalant siphon, rejected by ciliary tracts or palps within the mantle cavity, ingested and diverted to the intestine, or ingested and triturated. Most of these processes involve energy loss to the mussel (as costs of shell-valve movements, ciliary action and mucus secretion). The experiments with *Artemia* sp. demonstrated that there can be a net energy gain from inhaled crustacean material, perhaps through release of materials from triturated animals and subsequent breakdown/uptake in the digestive gland. Taken with earlier work, this indicates that mussels can access almost all sources of energy available to them in seawater, viz. dissolved organic material, seston, microbes, phytoplankton and small animals. The data presented here suggest that an *Artemia* sp. diet can prevent loss of condition, or improve the condition of mussels that have been energy-depleted by spawning. Further work at different prey densities with different prey species, with and without alternative sources of energy, are needed to determine whether positive growth can be supported at environmentally-realistic mesozooplankton densities.

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LITERATURE CITED

Bayne BL, Thomson RJ, Widdows J (1976) Physiology: 1. In: Bayne BL (ed) Marine mussels their ecology and physiology. Cambridge University Press, Cambridge, p 121–206

Beninger PG, Lynn JW, Dietz TH, Silverman H (1997) Mucociliary transport in living tissue: the two-layer model confirmed in the mussel *Mytilus edulis* L. Biol Bull Mar Biol Lab, Woods Hole 193:4–7

Beninger PG, Veniot A, Poussart Y (1999) Principles of pseudofeces rejection on the bivalve mantle: integration in particle processing. Mar Ecol Prog Ser 178:259–269

Beninger PS, St-Jean SD (1997a) The role of mucus in particle processing by suspension-feeding bivalves: unifying principles. Mar Biol 129:389–397

Beninger PS, St-Jean SD (1997b) Particle processing on the labial palps of *Mytilus edulis* and *Placopecten magellanicus* (Mollusca: Bivalvia). Mar Ecol Prog Ser 147:117–127

Dame RF (1993) The role of bivalve filter feeder material in estuarine ecosystems. NATO ASI Ser (Ser G: Ecolog Sciences) 33:245–270

Davenport J, Bebbington A (1990) Observations on the swimming and buoyancy of some thecosomatous pteropod molluscs. J Molluscan Stud 56:487–497

Davenport J, Chen X (1987) A comparison of methods for the assessment of condition in the mussel (*Mytilus edulis* L.). J Molluscan Stud 53:293–297

Davenport J, Woolmington AD (1982) A new method of monitoring ventilatory activity in mussels and its use in a study of the ventilatory patterns of *Mytilus edulis* (L.). J Exp Mar Biol Ecol 62:55–67

Gorham WT (1988) The energetic and nutritional contribution of glucose and glycine taken up from natural seawater by adult marine mussels. PSZN I: Mar Ecol 9:1–14

Hardy AC, Bainbridge R (1954) Experimental observations on the vertical migrations of plankton animals. J Mar Biol Assoc UK 33:409–448

Harvey HW, Cooper LHN, Lebour MV, Russel FS (1935) Plankton production and its control. J Mar Biol Assoc UK 20:407–441

Jørgensen CB (1983) Patterns of uptake of dissolved amino acids in mussels (*Mytilus edulis*). Mar Biol 73:177–182

Jørgensen CB (1990) Bivalve filter feeding: hydrodynamics, bioenergetics, physiology and ecology. Olsen & Olsen, Fredensborg

Manahan DT, Wright SH, Stephens GC (1983) Simultaneous determination of 16 amino acids by a marine bivalve. Am J Physiol 244 (Regul Integrat Comp Physiol 13): R832–R838

Meadows PS, Meadows A, West FJC, Shand PS, Shaikh MA (1998) Mussels and mussel beds (*Mytilus edulis*) as stabilizers of sedimentary environments in the intertidal zone. Spec Publ Geol Soc Lond 139:331–347

Mikulich LV, Tsikhno-Lukanina YeA (1981) Food of the scallop. Oceanology 21:633–635

Nelson TC (1933) On the digestion of animal forms by the oyster. Proc Soc Exp Biol Med 30:1287–1290

Newell CR, Shumway SE, Cucci TL, Selvin R (1989) The effect of natural seston particle size and type on feeding rates, feeding selectivity and food resource availability for the mussel *Mytilus edulis* Linnaeus, 1758 at bottom culture sites in Maine. J Shellfish Res 8:187–196

Péquignat E (1973) A kinetic and autoradiographic study of the direct assimilation of amino acids and glucose by organs of the mussel *Mytilus edulis*. Mar Biol 19:227–244

Roe HS (1984) The diel migrations and distributions within a mesopelagic community in the north east Atlantic. 4. The copepods. Prog Oceanogr 13:353–388

Shumway SE, Selvin R, Schick DF (1987) Food resources related to habitat in the scallop *Placopecten magellanicus* (Gmelin, 1791): a qualitative study. J Shellfish Res 6:89–95

Ward JE, MacDonald BA, Thompson RJ (1993) Mechanisms of suspension feeding in bivalves: resolution of current controversies by means of endoscopy. Limnol Oceanogr 38:265–272

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