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Ingestion of mesozooplankton by three species of bivalve; *Mytilus edulis*, *Cerastoderma edule* and *Aequipecten opercularis*

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Mytilus edulis, *Cerastoderma edule* and *Aequipecten opercularis* were found to ingest zooplankton when suspended in mesh cages in the water column in the Firth of Clyde. Zooplankters were also found in the stomachs of bivalves that had been taken directly from their natural habitat. The bivalves consumed a wide range of zooplankton species, but selectively consumed smaller categories of zooplankton present. Condition of zooplankton in the stomachs of the bivalves varied with zooplankton species. A degree of larviphagy was evident, particularly in *Mytilus edulis*.

INTRODUCTION

Bivalves are generally described as herbivorous and if present in sufficient numbers e.g. in mussel beds, may control the abundances of primary producers (Noren et al., 1999). However, since 1882 researchers have reported finding 'minute animals' (Savage, 1925) either in the stomach contents or the excreta of bivalves. Ryder (1882) examined the stomach contents of American oysters (*Crassostrea virginica*) and found them to contain 'diatoms, rhizopods, infusoria, monads, spores of algae, pollen grains, oyster larvae, worms, crustacean nauplii, minute crustacea, larvae of sponges, hydroids, hydrozoa, worms and molluscs' (reported in Savage, 1925). In his own dietary studies, Savage (1925) found nauplius larvae of copepods and adult harpacticoid copepods in the stomach contents of oysters. Nelson (1933) reported that one oyster *Ostrea edulis* stomach contained 160 live nematodes, 471 dead but intact specimens, and 5842 partially or wholly digested worms, all *Chromadora* spp. He postulated that the acquisition of protein from the nematodes was important to the oysters after they had spawned. Cowden et al. (1984) found that *Mytilus edulis* L. in laboratory settings ingested larvae of polychaetes, asteroids, gastropods, and echinoids. Kimmerer et al. (1994) stated that, within one year of the introduction of the clam *Potamocorbula amurensis* into the San Francisco Bay estuary, the abundances of adults of three common estuarine copepod species had declined five to ten fold. Krsinic (1980) found that tintinnines were an important factor in the nutrition of oysters in the Adriatic Sea. Similarly, while working in the same area as Krsinic, Jasprica (1997) found that mussels (*Mytilus galloprovincialis*) also ingested tintinnines.

However, with the exception of Kimmerer et al. (1994), all of these reports of bivalves ingesting zooplankton have been concerned with microzooplankton. In a more recent study, Davenport et al. (2000) found that *M. edulis*, when hung in mesh baskets from a pier ingested mesozooplankton including nematodes, polychaetes, amphipods up to 6 mm and *Carcinus maenas* zoeae of 2 mm length.

This study compares the species and sizes of zooplankton ingested by mussels suspended in the water column with those species present in the water column at time of sampling. In addition, benthic cages were used to determine whether mussels ingested benthic animals. Two other species of bivalves, *Cerastoderma edule* (L.) and *Aequipecten opercularis* (L.) were investigated for zooplankton ingested, both in the field and under manipulated conditions.

MATERIALS AND METHODS

Bivalve collection

Three bivalve species were considered for this study because of their relatively common occurrences around Great Cumbrae Island, Scotland (55.46°N 4.55°W) in May 2001. *Mytilus edulis* were collected from White Bay. Collections were made at low tide. Byssus threads were cut with scissors to avoid damage to the mussels which were transported to the University Marine Biological Station Millport, (UMBSM) and maintained in running unfiltered seawater overnight. *Aequipecten opercularis* were collected by dredging off White Bay at a depth of 30 m using a 1-m dredge towed by RV 'Aplysia'. Eighteen scallops were each injected with 10 ml 70% alcohol as soon as collected to preserve stomach contents, while a further 18 were maintained in seawater and returned to UMBSM. *Cerastoderma edule* were gathered at low tide from Ballochmartin Bay at low tide. Cockles and queen scallops were kept in unfiltered seawater until use later on the date of collection.

Experimental arrangements and protocol

Bivalves were removed from the running seawater and suspended in plastic coated wire mesh cages from the UMBSM pier for a period of two to four hours for mussels and cockles and overnight for the queen scallops before sampling for stomach contents (see Table 1 for cage dimensions). Davenport et al. (2000) found that gastric

Table 1. *Species of bivalves used, experimental categories and cages dimensions.*

Species	Experimental category	Mean shell length (cm) (±SE)	Cage dimensions length×diameter (cm)	Cage mesh size (cm)	Number of bivalves per cage	Number of bivalves used
M. edulis Class 1	Suspended	2.03 ±0.03	25×15	0.5×0.5	3	36
M. edulis Class 2	Suspended	3.54 ±0.09	25×15	1.6×1.9	3	36
M. edulis Class 3	Suspended	5.32 ±0.06	25×15	1.6×1.9	3	36
M. edulis Class 1	Benthic	3.18 ±0.09	25×25	0.5×0.5	18	36
M. edulis Class 2	Benthic	5.31 ±0.07	25×25	1.6×1.9	18	18
A. opercularis	Field	6.34 ±0.14	25×25	1.6×1.9	3	18
A. opercularis	Suspended	6.38 ±0.15	25×25	1.6×1.9	3	18
C. edule	Suspended	1.82 ±0.08	25×15	0.5×0.5	3	15

processing of zooplankton by mussels is rapid (<40 min at 15–20°C), so any animal material ingested by the bivalves when they were held beforehand in running seawater would not be present in the stomachs at time of dissection. Cages holding the smaller mussel sizes and cockles were constructed using a smaller mesh size than those used for larger mussels and queen scallops. To determine which animals were ingested by benthic mussels, weighted cages, each containing 18 mussels were lowered from the pier to the seabed. Mean shell length (±SD) and numbers of bivalves used per cage can be seen in Table 2. Water column plankton samples were taken from the pier each time the bivalves were suspended in the water or held on the seabed. A 375-μm mesh plankton net was streamed from the pier for one hour and the resultant plankton preserved. To collect benthopelagic organisms, the net was weighted and lowered until it was in contact with the seabed and left for one hour, exposed to current flow, after which time it was raised to the surface and its contents, preserved. Bivalves taken from the mesh cages had their stomach contents extracted within five to ten min of removal from seawater (cf. Davenport et al., 2000).

Laboratory analysis

Stomach contents were extracted from bivalves as follows. For *M. edulis*, the anterior and posterior adductor muscles were cut and the stomach contents pipetted out via a slit made through the digestive gland into the stomach. For *A. opercularis* and *C. edule*, the adductor muscles were cut and a fine bore glass pipette passed into the mouth, down the oesophagus and into the stomach. The stomach contents were preserved in 70% alcohol, labelled and transported to University College Cork. Each stomach sample was examined for zooplankton under a Nikon binocular microscope. Zooplankters from the stomachs were counted, identified to the lowest taxonomic level possible, and the maximum linear dimension measured to the nearest μm with an eyepiece graticule, standardized using a slide micrometer. Preserved plankton net samples were agitated and a 1.5 ml sub-sample taken with a glass pipette. Organisms present in the sub-sample were counted, identified and measured in the same way as the organisms found in the stomach samples.

Statistical analysis

All data were analysed for normalcy using the Kolmogorov–Smirnov test. Non-normal data were transformed to log (x) or log (x+1), as required. If data were still non-normal after transformation, non parametric tests were used to analyse them. Analysis of variance (ANOVA) was used to detect differences in the numbers of zooplankters consumed by the different species of bivalve and in the

Table 2. *Numbers of cages, mean shell length (±SD) and numbers of bivalves used.*

Date	Species and category	Individuals per cage	Cage 1 Mean shell length(cm) (±SD)	Cage 2 Mean shell length (cm) (±SD)	Cage 3 Mean shell length (cm) (±SD)	Cage 4 Mean shell length (cm) (±SD)	Cage 5 Mean shell length (cm) (±SD)	Cage 6 Mean shell length (cm) (±SD)
06/05/'01	*M. edulis* Class 1 suspended	3	2.02 ±0.12	1.90 ±0.23	1.91 ±0.23	2.12 ±0.09	1.83 ±0.22	1.92 ±0.26
05/05/'01	*M. edulis* Class 1 suspended	3	2.24 ±0.12	2.16 ±0.12	2.14 ±0.10	2.10 ±0.12	2.09 ±0.14	2.05 ±0.13
04/05/'01	*M. edulis* Class 2 suspended	3	3.06 ±0.26	3.36 ±0.14	3.36 ±0.26	3.13 ±0.17	2.94 ±0.74	2.82 ±0.60
03/05/'01	*M. edulis* Class 2 suspended	3	3.94 ±0.11	4.01 ±0.06	3.82 ±0.39	4.07 ±0.04	4.18 ±0.38	4.10 ±0.27
01/05/'01	*M. edulis* Class 3 suspended	3	5.39 ±0.04	5.03 ±0.12	5.05 ±0.18	5.52 ±0.25	5.11 ±0.17	4.74 ±0.35
04/05/'01	*M. edulis* Class 3 suspended	3	5.48 ±0.35	5.36 ±0.12	5.68 ±0.29	5.55 ±0.37	5.38 ±0.08	5.35 ±0.70
07/05/'01	*M. edulis* Class 1 benthic	18	3.18 ±0.36	*	*	*	*	*
02/05/'01	*M. edulis* Class 2 benthic	18	5.51 ±0.39	*	*	*	*	*
06/05/'01	*M. edulis* Class 2 benthic	18	5.13 ±0.40	*	*	*	*	*
02/05/'01	*A. opercularis* suspended	3	6.37 ±0.06	6.63 ±0.70	5.91 ±0.30	6.05 ±0.51	6.28 ±0.31	7.02 ±1.07
07/05/'01	*C. edule* suspended	3	1.77 ±0.64	2.08 ±0.22	1.83 ±0.11	1.82 ±0.07	1.68 ±0.11	*

*denotes no cages used.

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case of mussels, within different size-classes. The tests were also used to detect differences in zooplankton length between and within species of bivalves. Mann–Whitney *U*-tests were also employed to determine if there were any differences between the lengths of the zooplankters found in the stomach and those of the same species found in the plankton samples.

RESULTS

The mean shell lengths of the bivalves studied are shown in Table 1. All species examined had zooplankters in their stomachs. The following groups of zooplankton were found; calanoid and harpacticoid copepods, cladocerans, lamellibranch larvae, copepod nauplii, copepod metanauplii, halacarid mites, barnacle nauplii and cyprids, hydromedusae, foraminiferans, euphausiacea larvae, unidentified eggs and unidentified crustacean larvae. Harpacticoid copepods and halacarid mites were indicative of benthopelagic organisms while the rest are truly planktonic

Table 3 shows the species and overall percentages of zooplankton that were found in the bivalve stomach samples as well as actual numbers of prey ingested by each species and experimental category of bivalve. It can be seen that calanoid copepods, crustacean nauplii and incomplete copepods were present in all samples from all four species of bivalves. Cladocerans were absent from the stomachs of benthic mussels and present in less than 25% of dredged queen scallops. There was significant difference amongst the numbers of individuals ingested by each of the three classes of suspended *Mytilus edulis* ($P<0.01$, ANOVA), with Class l ingesting a mean of 1.67 organisms, Class 2 ingesting a mean of 5.06 and Class 3 ingesting a mean of 8.08 organisms. Tukey test comparisons on logged data showed that there was no significant difference between the numbers of organisms consumed by Class 1 and Class 2 benthic *M. edulis*, but there were significant differences between numbers ingested by Class 3 suspended *M. edulis* and both classes of benthic *M. edulis*. Numbers of organisms ingested by suspended and field *Aequipecten opercularis* were not significantly different. *Cerastomderma edule* were found to have ingested significantly more prey organisms than all other bivalves except for Class 3 suspended mussels and suspended *A. opercularis* (Figure 1).

The mean lengths of organisms ingested are displayed in Figure 1. There were no significant differences in prey length amongst the three classes of suspended *M. edulis* (Kruskal–Wallis $H'=4.00$, df=2, $P>0.01$). There was no difference in prey lengths between the two benthic classes of *M. edulis* (Mann–Whitney $W=7415$, $P>0.01$) or between Class 3 suspended *M. edulis* and Class 2 benthic *M. edulis*, ($W=45461$ $P>0.01$,). There was a significant difference between the prey lengths of the field *A. opercularis* and the suspended *A. opercularis* ($W=6204$, $P<0.01$), with the suspended scallops consuming prey of greater length. Prey found in stomach samples of *C. edule* were significantly shorter than prey found in the stomachs of all classes of suspended *M. edulis* (Class 1, $W=2789586$, $P<0.01$, Class 2, $W=2854264$, $P<0.01$, Class 3, $W=286496$, $P<0.01$) and were also significantly shorter than prey found in the rest of the bivalve stomachs.

Bivalves that were suspended in the water column were found to have ingested all species found in plankton net samples with the exception of chaetognaths and amphipods. Mann–Whitney *U*-tests showed that plankton net zooplankters were significantly longer on all sampling dates than those found in bivalve stomachs.

Prey condition

The condition of the prey in the stomach samples varied with prey species. Frequently the antennae, uropods and the furcal rami of copepods were missing or broken, making differentiation into calanoid and harpacticoid copepods difficult, and identifying calanoid copepods to species level impossible. Cladocerans were overwhelmingly *Evadne* spp. These usually appeared whole, with limbs intact. Crustacean nauplii and metanauplii were invariably free of damage, as were barnacle cyprids. Lamellibranch larvae

Table 3. *Species and overall percentages of zooplankton found in bivalve stomach samples (actual numbers in parentheses).*

Species	Suspended *M. edulis* N=105	Benthic *M. edulis* N=54	Suspended *C. edule* N=14	Field *A. opercularis* N=18	Suspended *A. opercularis* N=18
Halacarid mites	+ (5)	+ (12)	+ (3)	+ (1)	0
Calanoid copepods	++ (37)	+ (7)	+ (1)	+ (3)	+ (4)
Harpacticoid copepods	+ (4)	++ (26)	++ (3)	+ (7)	0
Copepod fragments	++ (65)	++ (53)	++ (6)	+ (3)	+ (2)
Copepod metanauplii	+ (18)	+ (1)	0	0	+++ (43)
Crustacean nauplii	++ (68)	+ (5)	+ (16)	+++ (72)	++++ (45)
Barnacle cyprids	+ (11)	0	+ (1)	+ (2)	+ (3)
Cladocerans	+++ (111)	0	++ (11)	+ (2)	++ (15)
Euphausiacea	0	0	+ (1)	0	0
Lamellibranch larvae	++ (58)	0	0	0	0
Hydromedusae	+ (39)	0	++ (2700)	0	0
Foraminifera	+ (1)	0	0	0	0
Unidentified eggs	+ (13)	0	0	0	0

+, Present in less than 25% of samples; ++, present in 26–50% of samples; +++, present in 51–75% of samples; ++++, present in 76–100% of samples; 0, not present.

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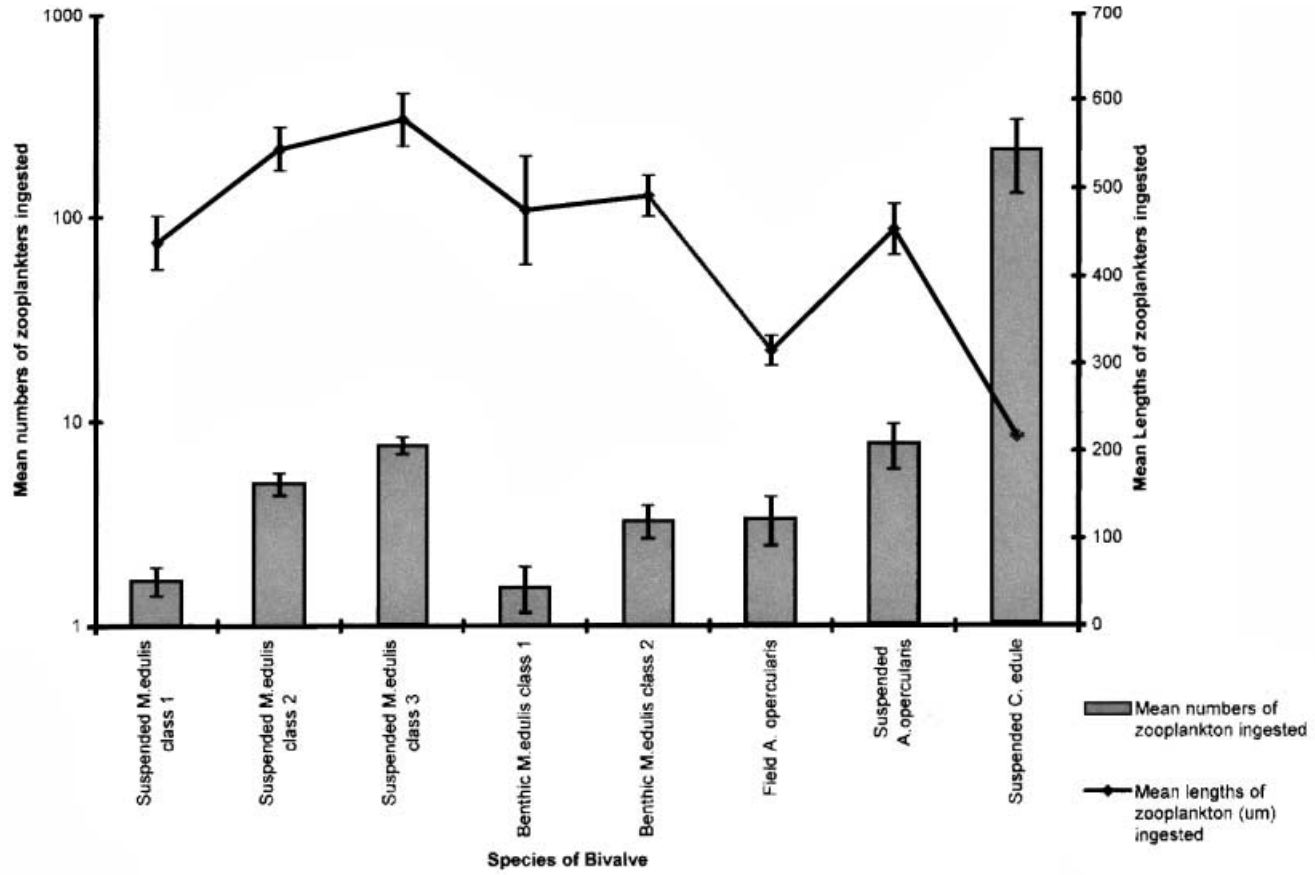

Figure 1. Graph showing mean length and numbers of zooplankton ingested by bivalves sampled (note logarithmic scale for mean numbers of zooplankton). Bars = standard error.

were apparently completely undamaged by the ingestion/digestion process.

DISCUSSION

The results shown here supported those of Davenport et al. (2000), who found that *Mytilus edulis* ingested a variety of zooplankton, both pelagic and benthic. In addition to confirming that mussels suspended in the water column ingest zooplankton, it was found that *Cerastoderma edule* and *Aequipecten opercularis* do so too. Zooplankton was found in the stomachs of all size ranges of mussels, from 1.58 to 6.14 cm shell lengths, showing that even young mussels have a capacity to filter zooplankton species from the water column. This ability, displayed by all of the bivalves examined, may act as a controlling element on smaller zooplankton as suggested by Horsted et al. (1988). Given that dense mussel beds can filter more than 100 m^3 seawater m^2 mussel $bed^{-1}\,d^{-1}$ (Jorgensen, 1990) one could assume that bivalves have a similar effect on mesozooplankton. All of the bivalves examined ingested a range of crustacean nauplii and metanauplii, adult copepods, cladocerans and lamellibranch larvae. Zooplankton has previously been described from the stomach contents or faecal matter of *M. edulis* and *M. galloprovincialis* in other studies. Bivalve veligers trochophores, nauplii, bipinnaria plutei, barnacle larvae, small copepods and copepodites have all been recorded as being consumed by *Mytilus* species. Clearly bivalves, in particular *Mytilus* species, are not strict herbivores and non-algal food sources are readily ingested by them.

As expected, the numbers of individual zooplankters or 'prey' ingested increased with mussel size, presumably reflecting higher pumping rates and larger stomachs. The mean prey lengths ingested by different size-classes of suspended mussels varied from 450 to 600 μm. These lengths are comparable to those found by Cowden et al., 1984 and Jasprica et al., (1997). However, it should be noted that zooplankters of lengths in excess of 3 mm were found in the stomachs of the largest classes of mussels during the present study. While it is probable that organisms of this length are not ingested with the same frequencies as organisms of lesser dimensions, these occurrences demonstrate that *M. edulis* is capable of ingesting organisms of considerable size. Benthic mussels consumed animals of similar length to the suspended mussels, which implies that mussels within the matrix of mussel beds, as long as their pumping is not restricted, could ingest benthopelagic organisms of considerable size.

Cerastoderma edule and *A. opercularis* also ingested zooplankton. Against expectation the smallest species *C. edule*, consumed the greatest number of zooplankton, primarily in the form of small hydromedusae. It might be predicted that the larger mussel classes and the queen scallops would ingest greater numbers of organisms, because of their greater size and because the inhalent syphon of cockles has a smaller cross sectional area. Corresponding plankton net samples on the day of collection showed no evidence of

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hydromedusae, possibly because the gelatinous organisms were destroyed by the flow through the plankton net. It is possible that a short duration bloom of hydromedusae occurred on the day that the cockles were suspended from the pier, explaining their total domination of the gut contents. The high rate of ingestion may therefore have been an artefact of zooplankton patchiness. However, it has also been found that *C. edule* can ingest three to four times more food per hour than *M. edulis*, but that in digesting so much food, gut passage times were substantially greater than in *M. edulis* (Hawkins et al., 1990).

Suspended and field queen scallops both ingested zooplankton but the prey differed in length. Presumably, this simply reflects the different depths and locations of sampling. Field specimens, from their natural habitat would not have had access to the more pelagic of the zooplankters such as cladocerans and copepod metanauplii which tend to have a greater length than most crustacean nauplii, which made up the bulk of prey in the field samples.

This study revealed little evidence of selection of zooplankton species by bivalves; in the main the stomach contents were similar to net samples. However, large chaetognaths and amphipods were not ingested, presumably because they would not pass through the inhalent syphons. There was, however, convincing evidence of size selection of the zooplankton occurring. There were significant differences between copepod and cladoceran lengths between stomach and plankton net samples on all days.

Of all the prey examined in the bivalve stomach contents, lamellibranch larvae seemed to be the most robust and survive the transit from the mantle cavity to the gut intact. The term 'larviphagy' was used by Timko (1979) to describe how adult bivalves ingest their own young and has been described from farmed bivalves (Fitch, 1965). If through predation on lamellibranch larvae, bivalves can control the size of future generations; it is also likely that extensive beds of bivalves can also control zooplankton densities and sizes.

From the results presented here, and from interpretation of other studies, it is clear that a wide variety of bivalves do routinely ingest zooplankton. While phytoplankton is crucial to the diets of most bivalves, zooplankton may represent a valuable supplement. Phytoplankton is not an all year round source of food (Landry, 1981), so zooplankton may be relatively more important in the bivalve diet when the seston is phytoplankton-poor. Balwin & Newell (1991) cited three advantages of omnivory. Omnivory (1) allows for the ingestion of more energy and nutrients per unit feeding area; (2) permits the acquisition of sufficient rations despite a fluctuating balance between autotrophic and heterotrophic food organisms in the natural environment; and (3) a mixed diet enhances growth. Landry (1981) pointed out that the ocean is an environment that is highly dynamic, heterogeneous, and chronically food-limited and it would be reasonable to expect animals inhabiting such an environment to be highly adaptable in their feeding regimes. He theorized that those animals with reputations as herbivores might become carnivorous when phytoplankton abundance is low. With bivalves however, it seems unlikely that their feeding regimes actually switch, because it has been found that at low algal concentrations, mussels will close their valves and stop filtering (Davenport & Woolmington, 1982). It is more likely that bivalves pump water whenever phytoplankton is present, so that if the water is also zooplankton rich, then this is an energetic and perhaps nutritional bonus.

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