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PREDATION OF COCKLES (*CERASTODERMA EDULE*) BY THE WHELK (*BUCCINUM UNDATUM*) UNDER LABORATORY CONDITIONS

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ABSTRACT

The feeding rate and behaviour of whelks (*Buccinum undatum*) offered cockles (*Cerastoderma edule*) in laboratory experiments were examined. When presented with cockles in a range of sizes (10–40 mm), 14 *B. undatum* (34.6–88.3 mm), held individually in aquaria, consumed a wide size range of cockles. Small whelks (<40 mm) consumed cockles (<23 mm), whereas large whelks, (>60 mm) ate a greater number of larger cockles (>30 mm) and a wider size range of cockles (12–40 mm) than smaller whelks. The majority (90%) of the shells of the predated cockles were undamaged and the few (<10%) that were damaged showed only slight abrasions to the anterior and posterior shell margin. Filmed observations of *B. undatum* feeding on *C. edule* showed a method of attack that has not previously been reported and involved the use of the whelk's foot to asphyxiate the cockle or to pull the shell valves apart. No filmed evidence was found for the previously reported shell 'wedging' technique for prising open the closed shell valves of *C. edule*, although 10% of the shells of consumed cockles in feeding experiments had damaged shell margins.

INTRODUCTION

The common whelk *Buccinum undatum* Linnaeus, 1758, is an inhabitant of the coastal waters of the British Isles, where it occurs down to depths of 1,000 m and has a distribution that extends to both sides of the North Atlantic (Nielsen, 1975). *Buccinum undatum* inhabits a variety of substrata but typically occurs in soft sediment habitats where it burrows a few centimetres below the sediment surface (Hunter & Hunter, 1963; Nielsen, 1975), reappearing onto the sediment surface to hunt for potential prey.

The diet and feeding methods employed by *B. undatum* have been the subject of several studies (e.g. Hancock, 1960; Nielsen, 1975; Taylor, 1978) and these have shown that it has a broad diet relying both on scavenging and predation. Taylor (1978) analysed the stomach contents of *B. undatum* collected from various locations around the UK. Thirty-five different species of presumed prey belonging to eight animal phyla were recorded, with polychaetes and to a lesser extent bivalves being the most important components of the diet. Nielsen, 1975 conducted laboratory investigations into the feeding mechanisms used by *B. undatum* held in aquaria and observed that they employed a technique known as shell 'wedging' when predated upon a variety of bivalve species. The 'wedging' technique involved the insertion of the whelk's shell lip between the shell valves of the bivalve until a large enough gap was created for the whelk to insert its proboscis and use its radula to tear off pieces of flesh. Nielsen (1975) noted that *B. undatum* found it difficult to predate on bivalves which had tightly closed shell valves, e.g. *Mytilus edulis* and *Modiolus modiolus*, but could easily open the shells of bivalves, such as cockles *Cerastoderma edule* (Linnaeus, 1758) that had loosely closing shell valves. However, Nielsen (1975) only summarized his observations and did not quantify how many times the 'wedging' behaviour was used.

Our initial observations conducted in the laboratory suggested that *B. undatum* did not use the 'wedging' technique observed by Nielsen (1975) when feeding on *C. edule*. In view of this, the present study examined the predator-prey dynamics between *B. undatum* and *C. edule*. The predatory behaviour of 14 *B. undatum* when offered a range of different, sizes of *C. edule* and the areas of shell damage sustained during feeding were quantified. The whelks were also filmed individually during capture and opening of their cockle prey to elucidate the mechanism of prey selection and entry.

MATERIAL AND METHODS

Buccinum undatum (33–89 mm shell length, maximum distance between the tip of the siphonal canal and the apex of the spire) were obtained from muddy substrata in the Menai Strait, North Wales, using pots baited with fish. Upon capture the whelks were starved for a minimum of 2 days in the laboratory before being placed under experimental conditions. *Cerastoderma edule* (size range 11–40 mm shell height) were collected from three sites in Anglesey, North Wales. Small cockles (5–15 mm), medium size cockles (15–30 mm) and large cockles (30–40 mm) were collected from Traeth Melynog, Red Wharf Bay and Fryars Road Beach, respectively, in order to provide as wide a range of prey sizes for the whelks. Whelks and cockles were maintained in separate aquaria in the laboratory and supplied with flowing seawater at ambient temperature (19.4–20.7°C).

Five cockles with undamaged shell margins from each of five size classes, <15.0, 15.0–19.9, 20.0–24.9, 25.0–29.9 and >30.0 mm, were added to each of 14 aquaria supplied with flowing seawater containing natural medium of fine sand to a depth of ~40 mm. Cockles were allowed to bury prior to introducing one whelk per aquarium. Cockle shell height and whelk length were measured using vernier callipers to the nearest 0.1 mm prior to their introduction into the aquaria. Daily, for the duration of the 54-day experiment, the empty paired shell

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valves from consumed cockles were removed and replaced with a live *C. edule* from the same size class. Using this approach, the frequency of cockle predation in each size class by a single whelk could be ascertained. On a daily basis, cockles that appeared dead or dying (i.e. the shell valves gaped and the flesh appeared motionless) were removed and replaced with a cockle of equivalent size. The replacements for the dead and dying cockles were half buried manually, posterior axis uppermost, so that they were not more exposed than the other resident cockles in the aquaria.

The shells of the consumed *C. edule* were collected, labelled and any areas of damage inflicted by the feeding whelks assessed and quantified. The height of each consumed cockle was measured, and the right and left shell valves examined under a low-power magnifier for external damage. The location (anterior, posterior or mid-ventral) and extent of any damage were recorded using a scale between 1 and 3, where '1' represented slight damage (i.e. abrasions on the valve margin), '2' represented damage (i.e. small shell fragments were missing from the valve margin) and '3' extensive damage (i.e. large shell fragments were missing from the valve margin).

Nine individuals of *B. undatum* (37.5–69.6 mm) were filmed feeding on cockles of different size. A perspex aquarium (200 × 100 × 100 mm), filled to a depth with 40 mm of natural sediment, supplied with flowing seawater and containing a whelk and potential cockle prey, was placed beneath an infrared camera connected to a time-lapse video recorder. All observations were conducted in continuous darkness under infrared illumination. Five cockles (15–40 mm) from each of five size classes, <15.0, 15.0–19.9, 20.0–24.9, 25.0–29.9 and >30.0 mm, were placed randomly on the sediment surface in the aquarium. The cockles were allowed to burrow into the sediment prior to placing a whelk of known length into the centre of the tank and the whelk and cockles observed for 24 h. The size of the cockles consumed during the period was measured and shell damage ascertained. The video recordings were analysed and several behavioural observations noted. These included the path of movement (direct or indirect) of the whelks towards the cockle prey, whether prey selection was exhibited, and the position of the whelk in relation to the cockle during the attack. The time taken to open and consume each cockle (i.e. the time from when the whelk first touched the cockle to the time it crawled off the cockle after the attack) was also recorded.

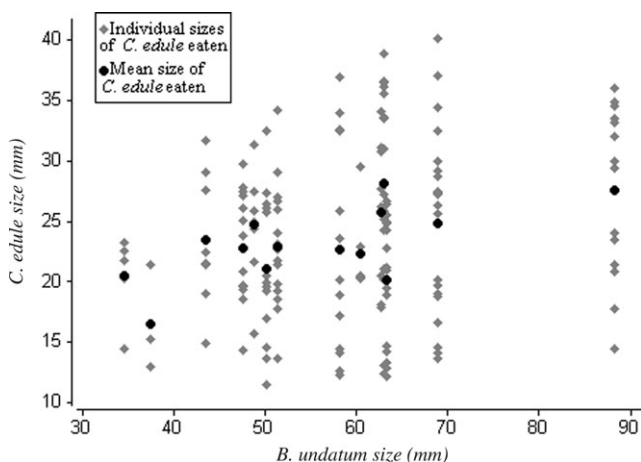


Figure 1. The relationship between *Buccinum undatum* size and the individual and mean sizes of the *Cerastoderma edule* consumed during the 54-day experimental period.

RESULTS

Over 54 days, all of the 14 individuals of *Buccinum undatum* fed and consumed a total of 169 *Cerastoderma edule*. Figure 1 illustrates a significantly correlated ($r = 0.670$, $P = 0.009$) relationship in the size selection experiments between *B. undatum* size and the size of *C. edule* eaten and demonstrates that both the size and number of cockles eaten increased with increasing whelk size. Small whelks (<40 mm), did not consume any cockles >23 mm, whereas whelks >60 mm ate a greater number of large cockles (>30 mm) and a wider size range of cockle sizes (12–40 mm) than the smaller whelks.

The majority of the predated cockle shells (89.3%) sustained no visible external damage and for 10.7% of the shells that did, the damage was minimal (level 1) and only one individual sustained level 2 damage (Fig. 2). Of the few cockle shells damaged, 47.5% of the damage occurred at the posterior and 47.5% along the anterior margins of the shell valves. Only one shell (5%) was damaged on the ventral section of the shell valve margin.

Nine whelks were filmed when cockle prey was offered to them and their feeding behaviour is briefly summarized in Table 1. Five of the nine whelks filmed were observed to consume at least one individual *C. edule* while the other four whelks did not consume any cockles (Table 1). Following transfer of the 2-day starved whelks to the experimental tank the initial response of six (or 66%) of them was to bury in the sediment where they remained for varying periods of time between 32 and 136 min. The remaining whelks (34%) did not burrow immediately into the sediment but remained motionless (for between 9 and 38 min) in the position they were placed before burying. In all cases the first cockle encountered was the one consumed by the whelk. The whelks, their siphons waving, always moved directly towards a cockle, which was attacked and then eaten. One *B. undatum* (~50 mm) was observed to move directly towards a large cockle (~36 mm), position itself

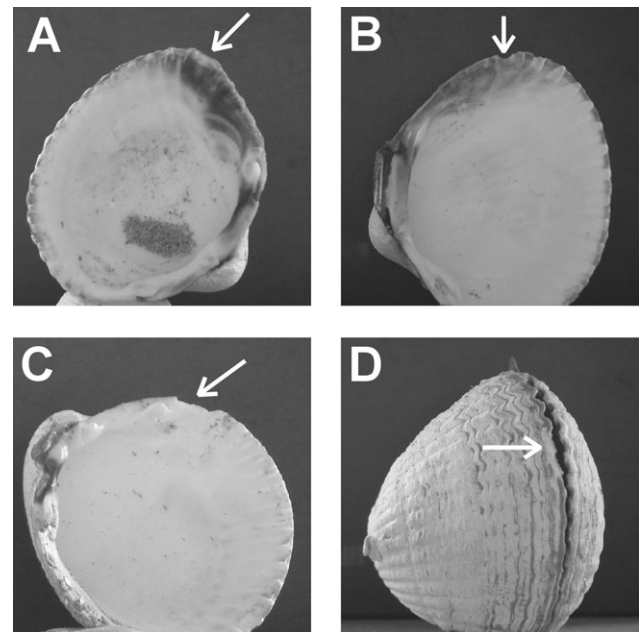


Figure 2. Damage to *Cerastoderma edule* shell valves during predation by *Buccinum undatum*. **A.** A small chip (arrow) in the posterior region of the left shell valve. **B.** A small chip (arrow) in the posterior region of the right shell valve. **C.** Damage sustained to the anterior region of the left shell valve (arrow) during an attack. **D.** A pair of *C. edule* valves showing abrasion to the left shell valve margin (arrow).

Table 1. Summary of the time taken and the number of *Cerastoderma edule* consumed by various sized *Buccinum undatum*, in the laboratory.

Whelk size (mm)	Number of cockles consumed in 24 h	Cockle size consumed (mm)	Time taken to consume cockles (min)	Area of attack on <i>C. edule</i>
37.5	1	25.9	118	Unknown
43.5	2	17.8	45	Anterior
		25.7	87	Posterior
47.3	0	NA	NA	NA
50.7	1	36.3	114	Anterior
55.5	0	NA	NA	NA
61.5	0	NA	NA	NA
66.5	1	37.2	122	Anterior
69.0	1	31.2	102	Posterior
69.6	0	NA	NA	NA

NA, Not applicable.

over its prey and then move away after 3 min, crawling around the tank without pausing to investigate other buried cockles and then returning after about 1 h to consume the original cockle that had been investigated. Different filmed behaviours were observed where cockles were not consumed by the whelks. For example, a *B. undatum* (~50 mm) moved directly towards a cockle (~35 mm), attempted to open it, before abandoning it and moving away following the unsuccessful attack. On another occasion an active whelk showed no interest in feeding on the cockles. This whelk spent much of the 24-h period crawling around the tank and came into contact with, and crawled over, a range of different sized cockles but made no attempt to open them.

The video recordings of successful predation on *C. edule* showed that the prey was not always attacked in a similar manner. In some cases, after partial or total exhumation of the cockle, a whelk began an attack by covering the anterior part of the shell margin with its muscular foot, whilst in other attacks the posterior shell margin was obscured by the foot (Table 1). On one occasion, a 51-mm whelk commenced an attack on the anterior end of a partially buried 36-mm cockle, attaching its foot to the anterior margin of the shell and pulling the cockle from the sediment. The foot remained attached and covered the anterior of the cockle for 1.87 h, before the whelk rotated the *C. edule* with its foot and changed the position of attack. Upon completion of this manoeuvre the foot was attached to the posterior area of the cockle for 3 min before the cockle was abandoned. Following release, the cockle opened its shell valves slightly and 0.5 h later the whelk returned, attached its foot to the anterior area of the cockle for a further 0.5 h and opened and consumed the cockle. A similar pattern of searching and prey manipulation behaviour was observed during unsuccessful whelk attacks. In these cases, the foot of the *B. undatum* penetrated into the sediment beneath the cockle and then using its foot which it attached to the anterior region of the *C. edule* pulled the cockle out of the sediment. The cockle was then manipulated using the foot before the cockle was abandoned and left unopened.

Observations of whelks feeding on *C. edule* demonstrated a variety of methods employed in attacking their cockle prey. The muscular foot of the whelk played an important role in feeding, often enveloping the cockle for periods up to 2 h. During some attacks both whelk and cockle remained almost

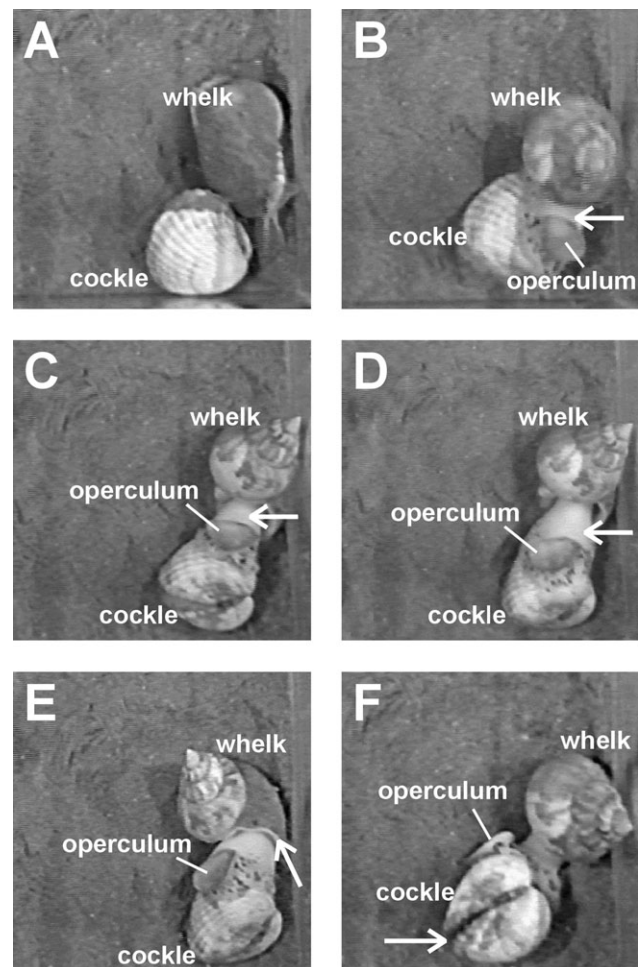


Figure 3. A sequence of still images captured from time-lapse video recordings of *Buccinum undatum* attacking a *Cerastoderma edule*. **A.** *B. undatum* emerges from sediment after burrowing next to a large *C. edule*. **B.** *B. undatum* extends its muscular foot (arrow) to cover half of a *C. edule*. **C.** The foot of the *B. undatum* covers the anterior section of the shell valve margin. The whelk is not positioned on top of the *C. edule* but on the sediment adjacent to the cockle. The position of the operculum shows that it is the posterior end of the whelk's foot which is visible (arrow). The end of the foot which is attached to the other side of the cockle (and cannot be seen) is the region of the foot closest to the tentacle. **D.** The foot of the whelk is extended, holding the cockle with its foot (arrow) away from the whelk shell. The position of the foot has not changed because the operculum position remains unchanged. **E.** The shell of *B. undatum* has changed position slightly and the cockle's anterior shell valve margin remains covered by the whelk's foot. The whelk's shell lip (arrow) is not near the cockle's shell margin. **F.** Access to the cockle flesh has been successful as the cockle shell is gaping slightly open (arrow).

motionless with only slight movements of the whelk's foot. During feeding the whelk shell lip was rarely in proximity to any part of the cockle shell (Fig. 3). On other occasions, the foot of *B. undatum* was very active, moving and shaking the enveloped cockle with its foot. Other behaviours included contraction of the foot, which brought the cockle close to the whelk shell, and slight rotation of the *B. undatum* shell while its foot was extended over the cockle (Fig. 3). In these methods of attack the whelks were rarely positioned on top of their cockle prey, but adjacent to them on the sediment with their foot outstretched (Fig. 3). The shell margins of most consumed cockles were left undamaged following an attack by *B. undatum*. The time taken to

open and eat a cockle varied between 45 and 122 min, the smaller cockles (18 mm) being opened more quickly than larger individuals (37 mm) (Table 1).

DISCUSSION

The size range of *Cerastoderma edule* consumed increased with the size of *Buccinum undatum*; small whelks did not eat cockles >23 mm. The likely reason for this is that small whelks were physically unable to open cockles >23 mm, they were probably unable to manipulate the larger cockles with their foot and were incapable of overcoming the strong adductor muscles present in the largest prey. Large whelks (>50 mm), however, successfully attacked and consumed a large number of cockles (>30 mm) without apparent difficulty. Nielsen (1975) reported that cockle size may influence the method used by *B. undatum* to open its bivalve prey but gave no indication why bivalves above a certain size could not be opened. The number of *C. edule* consumed also increased with whelk size, probably because of the higher energy requirement of the larger whelks for supporting their metabolic processes. Stomach size increases with shell and body size and is a factor which determines the quantity of food eaten by an individual whelk (Britton & Morton, 1994).

Although the average size of the cockles eaten was significantly and positively correlated with whelk size, it is unlikely that *B. undatum* was selective in choosing its cockle prey; large whelks consumed a wide size range of cockles (12–40 mm). If size selective predation had been employed, then whelks would have been expected to optimize prey size based upon net energy return when offered a wide size range of cockles. Instead, an opportunistic feeding strategy was observed where the first cockle encountered was consumed and this resulted in the observed wide size range of cockles being attacked and eaten. Opportunistic feeding behaviour has been suggested for this species by Taylor (1978) and Himmelman & Hamel (1993) and is a likely feeding strategy because of the reduced risk associated with this feeding behaviour. Emergence from the sediment to search for potential bivalve prey would expose the whelks to the attention of predatory crabs and fishes and increase their risk of being eaten. An opportunistic feeding strategy, however, would rely on chance encounters with potential prey as the whelks plough through the sediment thus reducing the time exposed on the sediment surface to potential predators.

The filmed sequences of feeding behaviour showed *B. undatum* moving directly towards the *C. edule* that it attacked and consumed. The attraction of a whelk towards its prey is likely to be through chemoreception (Himmelman, 1988). *Buccinum undatum* uses its actively waving siphon to draw in an inhalant stream of seawater over the osphradium to detect the metabolic products released from its prey (Rohrkasse & Atema, 2002) and this could explain why *B. undatum* moved directly towards its cockle prey. In four out of five cases, a whelk moved directly towards, attacked and consumed a cockle without exploring other prey possibilities in the aquarium. This strongly suggests that whelks do not employ prey selection when attacking cockles.

Hancock (1960) and Nielsen (1975) both described a similar method of attack used by *B. undatum* when attacking and consuming *C. edule*. They observed manipulation by the whelk of the bivalve using its muscular foot so that the whelk's shell edge was in contact with the ventral edge of the bivalve shell valves. The whelk then waited until the valves opened slightly before contracting its columellar muscle and inserting its shell lip and wedging the shell valves open, thus preventing the shell valves from closing. The proboscis was then inserted into the mantle cavity through the now wedged open and gaping shell valves. Nielsen (1975) noted that this method of attack varied according to bivalve size. When a large bivalve was

attacked the whelk orientated itself into a position where the anterior margin of the foot was in close contact with the ventral edge of the bivalve's shell. However, if a small bivalve was attacked, the whelk would dig up its prey, lie on one side and manipulate the prey with its foot, until the valve margin and shell lip were in the correct position.

In the current study, the feeding methods observed differed from those described by Hancock (1960) and Nielsen (1975). *Buccinum undatum* was observed to remove all sizes of cockles from the sediment and to lie on one side, manipulating the cockle with its foot during the attack. Further, the whelk's shell lip was not used during the attack and in most cases the cockles were not in contact with any part of the whelks' shells. It thus appears that the shell 'wedging' technique reported by Nielsen (1975) may not be used by *B. undatum* feeding on cockle prey as frequently as has been previously suggested. On the contrary, the observed technique involved the muscular foot which either exerted a force pulling the valves apart slightly or a force which kept the valves firmly shut; the latter technique presumably asphyxiating the prey so that the adductor muscles relaxed allowing the whelk's proboscis access to the pallial cavity and the flesh. It is not clear why the whelks' feeding behaviour in the present study was different to the 'wedging' behaviour described by Hancock (1960) and Nielsen (1975). One reason might be the difference in geographical location of the *B. undatum* populations used in the experiments. Nielsen, 1975 studied *B. undatum* from the Oresund, Denmark, a habitat that is likely to be different from the Menai Strait with regard to prey species availability for the *B. undatum* populations, and this may have affected their feeding behaviour. The use of shell 'wedging' by the whelks observed by Nielsen (1975) may be a result of the development of this behaviour to overcome bivalves with tightly closing shell valves (e.g. *Mytilus edulis* and *Modiolus modiolus*) which may be present in large numbers in Danish waters. Shell 'wedging' behaviour may continue to be used on all species of bivalves, even though species such as *C. edule* do not have tightly closed valves. A possible reason why 'wedging' behaviour is not used by *B. undatum* from the Menai Strait is that there are populations of *C. edule* present which can be eaten without using the technique. Nielsen (1975) further reported that *B. undatum* from different locations have different shell lip thicknesses and that this may affect their feeding behaviour; thicker, stronger shells presumably being able to withstand 'wedging' more readily than thinner shells, and this could be a reason why the whelks in Nielsen's (1975) study used shell 'wedging' and the whelks in the current investigation did not.

The majority of the cockle shells examined showed no obvious sign of shell damage. Hancock (1960) similarly observed that the shells of prey eaten by *B. undatum* were unmarked, although Nielsen (1975) observed shell damage to a few shells which were presumably caused when the whelk's shell lip contacted the shell valve margin. The absence of damage to the shells of the majority of consumed cockles supports our conclusions from the filmed sequences that whelks do not normally use their shell margins to attack and gain access to the flesh of their cockle prey. In <10% of cases damage was either caused to the posterior or anterior margins of the shell valves and may have been caused when the shells were pulled apart by the whelk. We therefore conclude that the shell 'wedging' technique is probably infrequently used by the population of *B. undatum* in the Menai Strait during predation on *C. edule*.

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