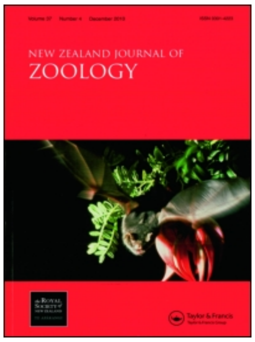

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Foraging activity of the sand beach isopod *Scyphax ornatus* Dana

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Abstract The terrestrial isopod *Scyphax ornatus* lives on exposed sand beaches. Adult isopods spent the daytime in burrows near the high water mark and made nightly foraging excursions over the uncovered middle beach. Hourly records of their night time distribution showed that *Scyphax* congregated near the water's edge during the last 4 h of flood tide, where they fed on carrion. Insects (mostly drowned honey bees) were the main food item, but coelenterates, amphipods, crabs, and goose barnacles were also eaten. During ebb and early flood tides *Scyphax* occurred at low densities over the uncovered middle beach. Analysis of the distribution of large and small food items on the beach showed that by feeding during the flood tide, *Scyphax* exploited a rich concentration of carrion that accumulated in the swash zone and that was moved slowly up the beach by the incoming tide.

Keywords *Scyphax ornatus;* foraging activity; sand beach; isopod; Oniscidea

INTRODUCTION

Terrestrial amphipods and isopods are the most characteristic members of the supralittoral zone fauna of sand beaches of New Zealand (McIntyre 1963; Morton & Miller 1968) and other temperate countries (Dahl 1953). Most members of this group spend the daytime in burrows and emerge at night to feed on algae and organic debris stranded on the upper part of the beach. However, the oniscid isopod *Scyphax ornatus* Dana (see Holdich et al. 1984 for details of classification) makes lengthy excursions downshore over the middle beach when it is exposed by the tide. Since almost nothing is known of the ecology or behaviour of *Scyphax* a study was undertaken to investigate the extent and timing of night time excursions. Diet and food distribution of these isopods was also examined.

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METHODS

Habitat

North Piha Beach (36°57′S, 174°28′E) is a sandy beach on the west coast of North Island, New Zealand. It is open to the prevailing southwesterly wind and is "Exposed" according to the exposure rating system of McLachlan (1980). The beach is composed of fine-grained grey ironsand, (median particle diameter 155 μm), and at low tide the middle beach presents a smooth surface sloping at approximately 1/40, 90–130 m in width. The tides are equal semidiurnal, range c. 4.3 m springs, 1.9 m neaps.

Measuring the spatial distribution of isopods at night

Distribution of adult *Scyphax* (body length >10 mm) was recorded on calm, warm nights (windspeed <5 m/s, temperature >10°C) between November and April. Over most parts of the beach, *Scyphax* occurred at such low densities that pitfall trapping was impracticable. Visual counting employing a specially constructed torch was used instead. The torch was fastened to the side of a straight pole; when the pole was held upright a circle of sand 1.5 m in diameter was illuminated sufficiently brightly for all adult isopods within the beam to be visible.

On the nights which recordings were made, an arbitrarily chosen strip of beach extending from above the high water mark to the water's edge was searched for isopods at hourly intervals between sunset and sunrise. A tape measure was first stretched down the beach at right angles to the water's edge. Stations were marked along the tape at 5 m intervals, beginning 5 m above high water mark and ending at the water's edge. At each station, a 20 m long × 1.5 m wide strip of beach running parallel to the water's edge was scanned for isopods. The total number of *Scyphax* counted in each strip was divided by 30 to produce a density of isopods (isopods/m^2) for each station.

In each instance the most seaward station was positioned on the swash mark, (a line of foam and debris left by the most recent large wave); a 20 m strip of sand was searched that followed the actual swash mark, rather than running strictly parallel to the waters edge. This was necessary because inspection showed that at some states of tide *Scyphax* congregated at the swash mark in large numbers, and unless the final station was placed exactly on the swash mark these isopods would have been missed.

It seemed possible that an observer working down the beach counting *Scyphax* in one strip after another might be "herding" the isopods seawards, thus generating falsely high counts at the more seaward stations. This was checked by carrying out several of the hourly counts twice; once starting at the landward end, and once starting at the seaward end. Both counts showed a similar distribution.

Measuring distribution and density of carrion

Food available to *Scyphax* was sampled on four occasions at two different states of tide; mid-flood (3 h before high tide), and mid-ebb (3 h after high tide). The samples were taken at dusk, about 90 min before the first adult *Scyphax* emerged onto the beach surface. Inspection of the beach showed that, at any state of tide between high and low water, the distribution of stranded carrion was not random. The middle beach was therefore divided into three horizontal zones:

Drift line. A narrow zone that included high water mark and extended a short distance seawards. To standardise sampling this zone was considered to be 1.25 m wide. It was usually marked by a line of stranded kelp, driftwood, and debris.

Middle beach. A zone about 20 m wide at half-tide, that extended from the lower limit of the drift line almost to the water's edge. The middle beach was divided into a series of horizontal strips for sampling purposes, each 2.5 m wide, and given a station number according to its distance from the high water mark.

Swash mark. A very narrow zone, (0.5 m wide) at the water's edge. Its position was marked by the curving line of foam and debris left by the most recent large wave.

The density of carrion within each of the zones was measured by two methods, depending on size: *Macrocarrion* was defined as any food item larger than 5 mm in greatest dimension, (i.e., larger than a housefly), and was collected by a careful visual search of each zone or station over a horizontal distance of 5 m along the beach, measured from an arbitrarily located line running down the beach at right angles to the water's edge. By the time the drift line, various zones of the middle beach, and the swash mark had been searched, the entire beach surface seaward of the high water mark had been cleared of macrocarrion for a horizontal distance of 5 m. Macrocarrion was dried to constant weight at 60°C and its weight expressed as, "biomass of macrocarrion per square metre", (mg/m^2), for each zone or station within a zone.

Microcarrion was defined as any food obfect smaller than macrocarrion but large enough to be retained by a sieve of 1 mm mesh size. Such a sieve retains *Drosophila* and most ants, but smaller insects or fragments pass through. Microcarrion is too small to be collected by visual search and was sampled with a small hand-held "dredge" which skimmed off the surface layer of sand to a depth of 3 mm. A strip 10 cm wide × 5 m long, running horizontally along the beach, was removed from each zone or station within a zone. In the laboratory each sand sample was stirred into a saturated sugar solution, when small insects and crustaceans along with other organic debris floated to the surface. The overlying solution was poured through a sieve of 1 mm mesh to collect microcarrion. The efficiency of the method was tested by adding 10 *Drosophila* to one of the sand samples fresh from the beach; all were recovered. Microcarrion was separated from inedible items retained by the sieve and was treated by drying to constant weight, as for macrocarrion. The weight for each zone or station was expressed as, "biomass of microcarrion per square metre", (mg/m^2).

RESULTS

Foraging excursions

Foraging in relation to daylight. Adult *Scyphax* emerged from their burrows when the beach was completely dark (illumination <1 lux), between 30 and 90 min after sunset. They moved quickly down the beach, and within 10 min some were found at the water's edge up to 75 m away. Isopods could be found on the exposed middle beach throughout the night, but by 1 h before sunrise, all had returned to dig new burrows near the high water mark.

Foraging in relation to tides. Examples of the night time distribution of *Scyphax* over the exposed middle beach are shown in Fig. 1–5 in which the time of high tide falls progressively later during the night, (at 2031, 2302, 2357, 0407, and 0607 NZST respectively). These records show that on most nights isopods were found at low densities ($<1/m^2$) over much of the middle beach. However, during the last 4 h of flood tide at night, many isopods (up to $8/m^2$) gathered at the water's edge (A in Fig. 2–5). In this situation, *Scyphax* were obviously foraging at the upper limit of the swash zone. They scurried about among the line of stranded debris, seizing any organic material with the mouthparts and with the front two pairs of legs, and then either discarding or eating it. Every few minutes a large wave swept up the beach, carrying *Scyphax* and

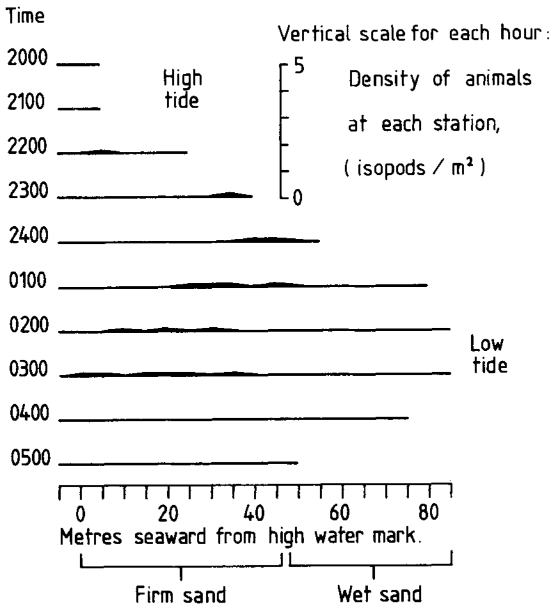

Fig. 1 Distribution of *Scyphax* over the middle beach at night; high tide at 2031, sunset at 1924, sunrise at 0546. Temperature 17.5–19.5°C, windspeed 0–2 m/sec. On this occasion the tide was ebbing for most of the night. Few *Scyphax* emerged onto the beach surface.

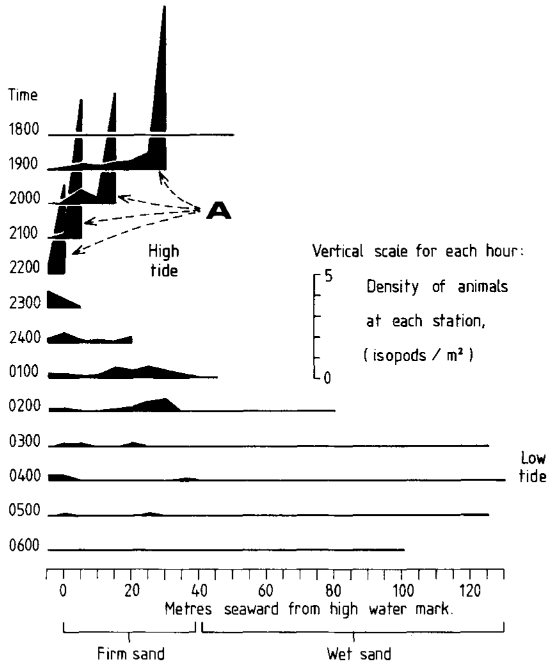

Fig. 2 Distribution of *Scyphax* over the middle beach at night; high tide at 2302, sunset at 1757, sunrise at 0645. Temperature 14.0–17.5°C, windspeed 0–5 m/sec. During the last 4 h of the flood tide isopods foraged at the swash mark (A) but they remained dispersed over the dry part of the middle beach during the ebb.

debris 1–2 m shoreward. The isopods were left mired in wet sand and coated wih cream-coloured foam. However, as soon as the sand became firm they resumed activity until a fresh wave repeated the sequence. On a typical occasion with average sea conditions and at mid-flood tide the mean interval between waves that moved the swash mark was 172 s measured over a 20 min period. The isopods were immobilised for about 10 s after each wave had receded; thus, foraging was possible for about 94% of the time.

After the tide had reached high-water mark and had begun to ebb *Scyphax* were no longer found at the water's edge. During the falling tide they spread out over the exposed middle beach where they were found at low densities, although groups were sometimes found clustered around large items of carrion left by the receding tide (B in Fig. 4).

On one night (Fig. 1) when high tide occurred near sunset so that no part of the 4 h flood tide feeding period occurred during darkness, very few *Scyphax* emerged. Repeated visits to the beach on other nights when high tide occurred near sunset also revealed few active isopods.

Foraging in relation to substrate. *Scyphax* were seldom found on soft sand above the high water mark. Their movement seaward at low tide was

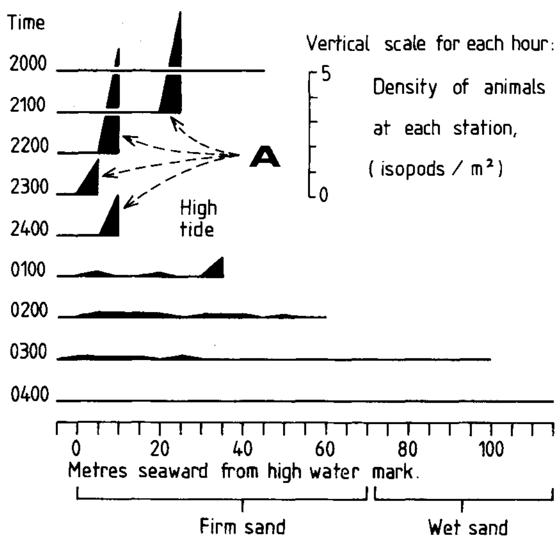

Fig. 3 Distribution of *Scyphax* over the middle beach at night; high tide at 2357, sunset at 1926, sunrise at 0455. Temperature 14.0–17.0°C, windspeed 0–1 m/sec. Isopods foraged at the swash mark (A) during the last 3 h of the flood tide and the early part of the ebb.

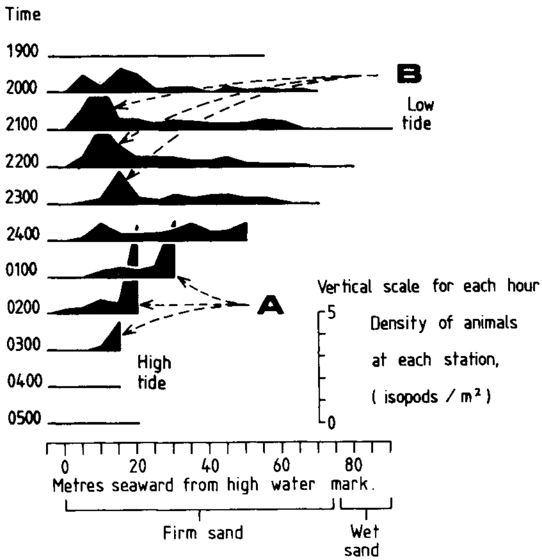

Fig. 4 Distribution of *Scyphax* over the middle beach at night. High tide at 0407, sunset at 1938, sunrise at 0457. Temperature 16.5–17.5°C, windspeed 1–3 m/sec. During the ebb and early flood tides isopods occurred at low densities throughout the middle beach, except where groups (B) had gathered around stranded jellyfish *Aurelia aurita.* After midnight *Scyphax* foraged at the swash mark during the last 3 h of the flood tide, (A).

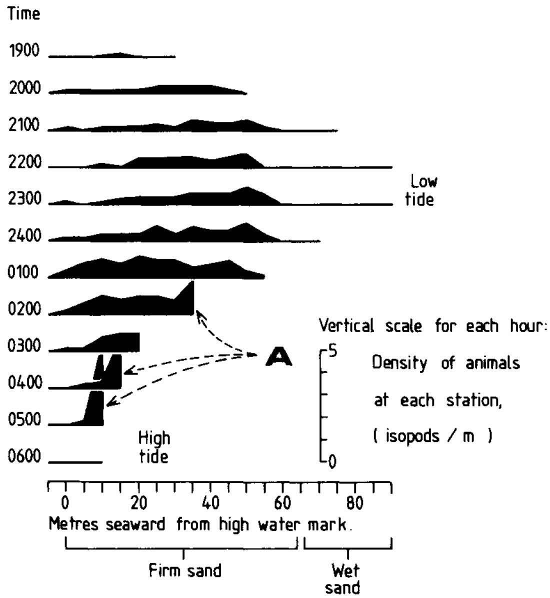

Fig. 5 Distribution of *Scyphax* over the middle beach at night; high tide at 0607, sunset at 1829, sunrise at 0625. Temperature 19.5–22.0°C, windspeed 0–5 m/sec. During the ebb and early flood tide *Scyphax* were dispersed over the middle beach. Towards dawn they foraged at the swash mark (A) during the last 3–4 h of the flood tide.

limited by the water table which reached the surface over the lower part of the beach so that the sand was always wet. *Scyphax* are unable to walk on this surface and were never found there.

Diet

Diet was assessed by night time observation at the beach and by examining the gut contents of freshly collected isopods. Feeding experiments were also carried out in the laboratory.

Beach records. On most visits to Piha only a few *Scyphax* were discovered eating anything large enough to be identified. Dead insects were the most commonly recorded food item, (14 of 26 visits); these were mostly honey bees which had been drowned and cast up on the beach. Other dead insects occasionally seen to be eaten or attacked were pentatomid and ricaniid bugs, small scarab beetles, tipulid and calliphorid flies, vespid wasps, small cockroaches, and bumble bees.

The second most commonly recorded food source was the Portuguese Man-o'-war *Physalia.* On the four occasions on which *Physalia* were seen stranded on the beach, they were being eaten by as many as 20 isopods. Less frequent were the common fellyfish *Aurelia aurita,* the By-the-wind sailor *Velella velella,* the paddle crab *Ovalipes catharus,* small goose barnacles, and the terrestrial beach amphipod *Talorchestia quoyana.*

All were deposited on the beach as carrion. The only living animals seen to be attacked by *Scyphax* were bees (on three occasions) and scarab beetles (once) which were crawling on the beach near the swash mark. *Scyphax* were never seen to eat stranded algae, although it is common at Piha Beach.

Analysis of gut contents. Samples of 20 *Scyphax* were collected for autopsy on five separate occasions, 1 h after emergence from their burrows. Among the 100 specimens examined, 55 had an empty or almost empty gut, 26 had a full or almost full gut, and the remaining 19 were partly full. Most of the isopods with full stomachs (18 out of 26) were collected on a night when many fellyfish *Aurelia aurita* had been stranded on the beach, and the guts of these isopods were packed with amorphous tissue which presumably came from *Aurelia.*

Insect fragments (usually wings, legs, and heads) were the most common identifiable component of the stomach contents. Forty-two *Scyphax* contained insect parts, of these, 19 contained fragments of small dipterans and 7 contained parts of

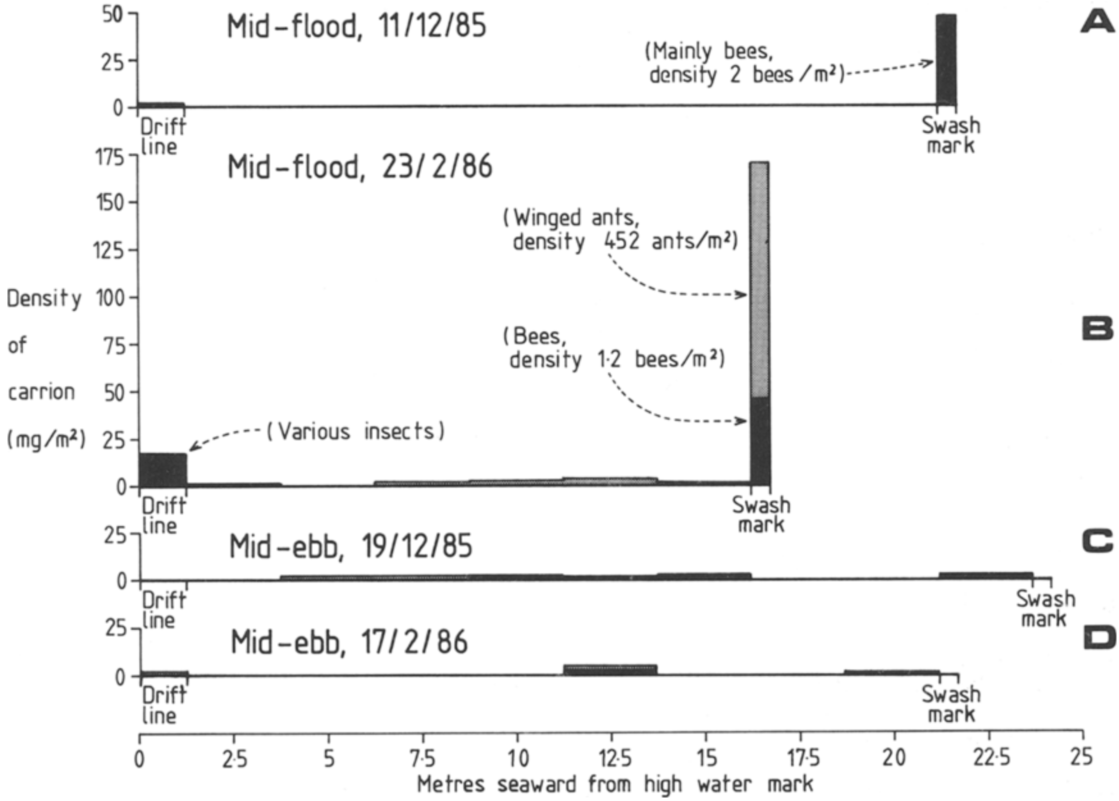

Fig. 6 Distribution of carrion on the middle beach at mid-flood (A, B), and at mid-ebb (C, D). Black columns show the density of macrocarrion; grey columns indicate density of microcarrion. Note the accumulation of carrion which occurs at the swash mark during the flood tide, but not during the ebb.

winged ants. No honey bee fragments could be identified.

Nineteen stomachs contained pieces of crustaceans. Most (14) were unidentifiable and 5 were amphipods, probably small *Talorchestia quoyana.*

Feeding experiments. Drowned honey bees were the food item most frequently recorded on the beach, yet they were never recognised in gut contents. This is because in the laboratory, *Scyphax* which were supplied with dead bees generally turned them on to their backs and penetrated the abdomen through the ventral side. They then devoured the soft contents of the abdomen and sometimes the thorax, leaving head, legs, wings, and most of the dorsal cuticle uneaten. At autopsy, gut contents of these isopods, although packed with tissue known to have come from bees, contained no fragments which could be easily identified. However, another group of *Scyphax* which were offered dead *Drosophila* consumed the small flies entirely, and when the isopods were dissected a day later their stomachs contained numerous intact wings, legs, and heads. These results, taken in conjunction with observations of feeding on the beach, suggest that bees are the predominant insect food for *Scyphax* and that bee tissue is visually unidentifiable in gut contents rather than absent from them; (empty exoskeletons of bees, broken open on the ventral surface of the abdomen, were found in the drift line at Piha Beach on calm mornings).

Food distribution

The distribution of stranded carrion on the beach was recorded at dusk under two states of tide; mid-flood and mid-ebb.

Flood tide. A and B of Fig. 6. Items known to be eaten by *Scyphax* occurred in greatest density at the swash mark near the water's edge. On the two occasions represented in Fig. 6, the biomass of carrion at the swash mark was 47 and 169 mg/m^2 respectively, made up mostly of dead insects. Much smaller quantities of carrion were found scattered over the middle beach landward of the swash mark, and the drift line contained only low carrion densities.

Ebb tide. Fig. 6C, D. Food occurred at low densities at the drift line, middle beach, and the swash mark. The high densities found at the swash mark during a rising tide were never seen during the ebb.

DISCUSSION

Foraging in the swash zone during flood tides

Night time records of the distribution of *Scyphax* over the exposed middle beach show that they gather at the water's edge during the last 4 h of the flood tide and forage at the swash mark. The advantage of doing so is clear when one considers the way in which carrion is deposited on Piha Beach.

During the flood tide, as material is washed ashore it accumulates in the swash mark and is moved slowly up the beach by a succession of small waves, (termed "swashes" by Emery & Gale 1951). Swashes are said to result from interference between larger breakers further offshore, and on gently sloping beaches the period of swashes which run up the beachface is longer than the period of the breakers which generate them (Huntly & Bowen 1975). Not all swashes reach and move the swash mark; most fall short so that during moderate weather and swell conditions at Piha Beach, *Scyphax* are able to forage at the swash mark for about 3 min between successive inundations. The arrival of large swashes at intervals of several minutes suggests a regular oscillation in mean sea level close to the beach. Such a cycle has been reported by several authors (Munk 1949; Sonu et al. 1973), the cycle having periods ranging from 50 s to 5 min. This oscillation, (termed "surf beat" by Munk), probably represents a standing wave associated with reflection of incoming waves from the beachface (Sonu et al. 1973).

Scyphax is not the only terrestrial isopod which exploits the swash zone on sand beaches. Kensley (1974) described a similar feeding pattern among juvenile *Tylos granulatus* and *T. capensis* on exposed beaches of southern Africa. The juveniles eat carrion, whereas adults of both species feed mainly on algae stranded at the drift line.

The fact that few *Scyphax* emerged on nights when high tide coincided with the time of sunset suggests that an endogenous behavioural rhythm may inhibit activity on such nights (which occur at fortnightly intervals). Laboratory experiments on isopods kept under constant conditions (Quilter & Lewis unpublished data) support this view. Lunar or semi-lunar components have been reported in the endogenous activity rhythms of a number of other shore isopods (Hastings 1981; Enright 1972; Fincham 1973).

Diet

Observations of foraging behaviour and examination of stomach contents showed that *Scyphax* fed exclusively on carrion. Dead insects occurred most commonly in beach records and gut contents, indicating that they form a major component of the isopods' diet. This is surprising since insects (along with most fauna from above the supralittoral) are generally considered to play little part in the economy of sand beaches (Brown 1964). Insects have not been recorded as a major component in the diet of any other beach isopods, although Holdich (1981) has described two instances of opportunistic feeding on insects by the swimming cirolanid isopod *Eurydice pulchra.*

Most other terrestrial isopods of the supralittoral are omnivorous. *Tylos punctatus* on the Californian coast feed mainly on stranded kelp but also eat carrion when it is available (Hamner et al. 1969); *T. capensis*, and *T. granulatus* on the South African coast have a similar diet (Kensley 1974; Marsh & Branch 1979). The Mediterranean species *T. latreilli* eats marine amphipods and carrion such as dead fish (Vandel 1960).

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