# FEEDING, RESPIRATION, AND AERIAL EXPOSURE IN A SCAVENGING CIROLANID ISOPOD FROM NEW ZEALAND

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## ABSTRACT

The feeding rate, oxygen consumption, and effects of aerial exposure were measured for a cirolanid isopod, *Natatolana rossi*, collected from a shallow subtidal habitat at Kaikoura, New Zealand. The isopod survived 7 days exposure in water-saturated air at 15°C and mean survival time was similar both in water-saturated air (5.1 days) and water (4.6 days) at 1°C.

Weight loss in aerial conditions increased both with time and with decreasing relative humidity (RH). Weight-specific transpiration rates (mg water loss  $h^{-1}$  mg<sup>-1</sup> wet wt) were 0.057 for 60% RH and 0.017 at 80% RH. Lethal water loss was approximately 30% of the initial wet weight. Weight-specific rates of resting oxygen consumption for *N. rossi* were low compared with other aquatic peracarids (0.26 µl O<sub>2</sub> mg<sup>-1</sup> h<sup>-1</sup>) at the habitat temperature of 10°C. Oxygen uptake increased with exposure temperatures between 5 and 25°C. Following aerial exposure, oxygen uptake was significantly reduced to 50% of the aquatic rate and was temperature-independent.

Feeding experiments using blue moki fish (*Latridopsis ciliaris*) showed that *N. rossi* is unable to feed in air and that food intake in aquatic conditions increased with exposure temperature. Highest food consumption was measured at  $15^{\circ}$ C, where the rate represented 30% of the dry body weight per day.

This study suggests that *N. rossi* is a "sit and wait, batch reactor" predator/scavenger. It displays a low resting metabolism and is capable of long periods of fasting. It maximizes food intake with a high feeding rate on an energy-rich food source. In addition, its ability to survive aerial exposure would allow it to survive and minimize energy expenditure if inadvertently displaced into intertidal habitats.

The Isopoda is a diverse crustacean group, members of which have exploited a range of marine, fresh-water, and terrestrial habitats. They are predominantly opportunistic omnivores with some members specializing in carnivory, scavenging, or parasitism (Schram, 1986). In contrast with other isopods, cirolanid isopods are specialized macrophagous feeders which can be predators on fish, polychaetes, and amphipods as well as carrion feeders. Commonly known as sea-lice, these isopods are reported to cause extensive damage to fishes caught in nets and long lines (Hale, 1927; Bruce, 1986).

Recently, there have been a number of studies on the population biology, reproduction, and physiology of the cirolanid *Natatolana borealis* Lilljeborg from deep-water habitats. However, there are no comparative data on the energetics and metabolism of shallow-water species. The present study is part of a larger investigation into the ecophysiology of cirolanids from New Zealand and concentrates on *Natatolana rossi* (Miers), which is frequently found in nets and baited traps. I investigated the effects of aerial exposure on feeding and respiration of *N. rossi*,

including the effects of temperature on oxygen uptake. For the feeding studies, isopods were provided with blue moki, a commercial fish thought to be especially susceptible to damage by these isopods.

#### MATERIALS AND METHODS

Animal Collection and Storage.—Individuals of N. rossi were collected during darkness in July 1996 off the wharf at Kaikoura ( $42^{\circ}24'S$ ,  $173^{\circ}41'E$ ), using a sack enclosing fish bait and on one occasion, a dead sea gull. Isopods were attracted to the bait, but prevented from feeding on it. At intervals from 15 min to 1 h, when the sack was lifted, it was covered with isopods. They were removed gently, separated into groups of 20, and transported in sea water to Christchurch in 2-1 plastic containers. Although by this trapping method all sizes of isopods were collected, only intermolt females and males, length 18–26 mm were used in experiments.

lsopods were stored at a constant temperature of 10°C, which was close to the sea-water temperature at the time of collection. The annual sea-water temperature range at the Kaikoura wharf is  $10-20^{\circ}$ C, and the mean air temperature range is  $2-26^{\circ}$ C. Isopods were allowed to adjust to laboratory conditions for 2 days prior to experimentation and all experiments were completed within 2 weeks of capture.

Air Exposure.—Groups of 10 isopods were held individually in covered plastic containers, in a 12:12 light : dark regime. They were placed directly into pasteurized

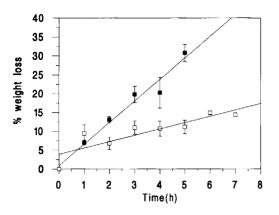


Fig. 1. Mean weight  $loss \pm SE$  (% initial wet weight) for *Natatolana rossi* exposed to air 60% RH, solid squares, and 80% RH, open squares, for periods up to 7 h.

sea water (34%) or onto a paper towel wetted with the same solution. Isopods were not dried and water was allowed to drain off during transfer using a small sieve. The groups of isopods were held in both air and water, without feeding at temperatures of 1, 5, 10, 15, and 20°C with the sea water changed every other day. They were checked at 12 h intervals for up to 7 d, when individual isopod behavior was noted, either swimming, walking, limited limb movement, or inactive. All inactive isopods were removed and placed separately in aerated sea water at the original storage temperature. Any isopod unable to regain walking activity within 30 min was regarded as dead.

Weight Loss.-Weight changes were measured at 15°C for individual isopods exposed to air close to 60 and 80% relative humidity (RH). Each isopod was transferred from sea water with a small sieve, weighed using a Cahn microbalance, and then placed within a humidity chamber. This was a 200-ml sealed plastic pot containing a wire mesh held over 25 ml of saturated salt solution,  $Mg(NO_3)_2$ to provide 60% RH or saturated NaCl to give 80% RH (Winston and Bates, 1960). The humidity was checked using cobalt thiocyanate paper and a Lovibond humidity tester. The controls were 4 similar vessels containing sea water to provide approximately 95% RH. At the start of the experiment and then at hourly intervals for up to 7 h a group of 4 individuals was removed from the two humidity conditions. Each isopod was reweighed, classified as dead or alive, and the dry weight measured after 48 h drying at 65°C. The control group was reweighed following 7 h exposure. Weight change was calculated for each individual, both as a percentage of the initial wet weight and as a wet weight : dry weight ratio.

Oxygen Uptake.—Measurements of oxygen uptake of N. rossi were made in sea water and in moist air (>90% RH) at temperatures of 5, 10, 15, 20, and 25°C using a Gilson Respirometer, using the same techniques as those described previously for isopods (Marsden, 1979). It was not possible to make readings at 1°C because the rates were too close to the sensitivity limit of the respirometer. Individual isopods were held in the experimental vessels that contained either 5 ml of pasteurized sea water or a 1-cm piece of filter paper wetted with sea water. Identical vessels without isopods acted as the controls for

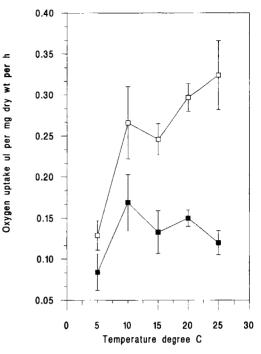


Fig. 2. Effects of temperature and aerial exposure on the oxygen uptake of *Natatolana rossi*. Open squares, weight specific aquatic rate, and closed squares, aerial rates. Values are the mean,  $\bar{x} \pm SE$ .

this experiment. Following an initial equilibration period of 1 h, readings were taken at 3- or 5-min intervals for periods exceeding 30 min. During this time, the machine was shaken gently to facilitate gas exchange. The temperature was then changed and allowed to equilibrate for 45 min prior to the next recordings. Respiration was recorded for 2 or 3 temperatures each day with values at the storage temperature being measured at the start and end of the experiment. The dry weight of each isopod was obtained as described above.

Whole Fish Experiment.-Whole freshly caught moki, Latridopsis ciliaris (Bloch and Schneider), weight 2-3.5 kg, captured in Pegasus Bay and landed at Lyttelton, were checked for the absence of any external damage. The fish were not gutted or scaled prior to experimentation and were placed on paper towels within a  $600 \times 360 \times 200$ mm aquarium with a lid. Experiments were undertaken in air and aquatic conditions at constant temperatures of 0-1°C, 5°C, and 10°C in a 24-h cycle with a dark : light regime of 12:12 h. There were two replicates for each experiment in aerial conditions. In the aquatic conditions, the aquaria contained 20 I of filtered aerated sea water, salinity 34%. A total of 62 cirolanids, length 18-22 mm, was placed in each aquarium. To allow isopods access to different parts of the fish, 10 were placed within the mouth cavity, 6 under each operculum, and 40 on the upper surface of the fish. The water inside the tanks was changed as necessary, initially after 2 and 5 h and then at 12-h intervals. Observations were made at 12-h intervals and any dead isopods were removed. After 3 days, the fish was lifted carefully and examined to locate the

		а	b	r	Р
% wet wt	80% RH	3.923	1.682	0.87	0.001
% wet wt	60% RH	0.857	5.729	0.98	0.001
wet wt: dry wt	80% RH	4.055	-0.153	0.66	0.001
wet wt: dry wt	60% RH	4.126	-0.229	0.89	0.001

Table 1. Linear regression analysis showing the effects of relative humidity on weight loss in *Natatolana rossi*. Y = a + bx, a = constant, b = slope of the line, r = correlation coefficient, P = probability level.

remaining isopods. Each fish was examined externally for damage and opened to check for penetration into the body cavity or muscle tissue. A brief microscopic examination was made of the superficial tissue in the region of the mouth, operculum, anus, and gills.

Feeding Experiments.—Feeding rates were measured for groups of 5 isopods at 5, 10, 15, and 20°C. Individual isopods, length 18-22 mm, were provided with preweighed cubes of fresh moki flesh with a portion of skin attached. These cubes weighed about 0.8 g wet weight corresponding to 0.25 g dry weight. Isopods were held either in pasteurized, filtered sea water or in a container lined with wet filter paper. Cubes were weighed at the start of the experiment and then after 24, 48, and 72 h. This allowed the daily feeding rate to be an average of 3 independent measurements. Weight changes in the food were calculated from samples taken at each time interval. The controls for this experiment were 5 vessels with fish cubes held in both aerial and aquatic conditions without isopods. After 72 h the dry weight of each isopod and the fish cubes were obtained. Feeding rate for each isopod was calculated for a 24-h period, after correction for any changes in the weight of food in the controls.

#### RESULTS

### Aerial Exposure

Survival of *N. rossi* in sea water and water-saturated air was temperature-dependent, with isopods surviving aerial exposure at all temperatures except 1°C for at least seven days. In sea water at temperatures of 5°C and above, isopods were observed both walking and swimming. However, for air-exposed isopods, following four days of aerial exposure, movements were restricted to limb movements only (no walking). At 1°C, mean isopod survival times (±SE) were similar in air, 5.05  $\pm$  0.33 d and water 4.6  $\pm$  0.55 d, *t* = 0.10. For these isopods, swimming movements were suspended within a few hours of submersion and walking ceased within 24 h. Isopods showed irregular limb, antennal, and mouthpart movements prior to becoming immobile. They rarely recovered from this state.

#### Weight Loss

As shown in Fig. 1 and Table 1, weight loss of N. rossi depended upon exposure time (at 80% RH, F value for the ANOVA = 2.95, d.f. = 6,27, P = 0.03 and at 60% RH F = 14.47,  $d_{f.} = 4,19$ , P < 0.001). At both 60% RH and 80% RH isopod weight loss was linear over time. Weight loss varied significantly both with relative humidity and exposure time (2 way ANOVA F = 38.8, d.f. = 1,39, P < 1,0000.001) and there was also a significant interaction effect (F = 6.86, d.f. = 4,30, P <0.001). Following exposure to 80% RH for 5 h, isopods lost approximately 12% of their initial wet weight. In contrast, weight loss was 30% at 60% RH. Control isopods subjected to approximately 95% RH showed no significant weight change over the 7 h exposure period. As expected, the wet weight: dry weight ratio of isopods held in 60 and 80% RH also decreased linearly over time (Table 1), until it reached a critical ratio close to 2.5. This would be reached following 9.5 h of exposure at 80% RH and 7.25 h at 60% RH.

### Respiration

The effects of temperature on oxygen uptake of the isopods are shown in Fig. 2.

Table 2. Effects of exposing isopods, *Natatolana rossi*, to whole moki fish for 3 days. SW = sea water, A = air, T = temperature,  $^{\circ}$ C, M = % mortality, 2 replicates shown for air experiments.

	Т	М	Isopod condition	Fish damage	
SW	1	100	normal	none	
SW	5	71	red, distended	operculum	
SW	10	75	red, distended	operculum, gill, skin of mouth	
Α	1	100, 70	normal	none	
Α	5	80, 26	normal	operculum (minor)	
Α	10	100, 84	normal	operculum (minor)	

Table 3.	Effect of temperature on weight change (g) of blue moki flesh following 3 days exposure to Natatolana
rossi. The	e controls without isopods are also shown. Positive + values show weight gain. $N = 5$ for 1, 5, and 10°C
and $N = 1$	0 for 15 and 20°C. Values are the mean, $\bar{x}$ , and standard deviation, SD, of the weight change.

Temp°C		1	5	10	15	20
Water	x	0.004	0.033	0.099	0.117	0.159
	SD	0.079	0.027	0.062	0.052	0.075
Air	x	+0.024	+0.010	+0.035	+0.042	0.056
	SD	0.027	0.033	0.096	0.045	0.100
Water control	$\bar{x}$	+0.001	+0.049	+0.023	+0.013	0.092
	SD	0.025	0.060	0.074	0.041	0.112
Air control	x	+0.012	+0.025	+0.030	+0.025	+0.034
	SD	0.018	0.016	0.025	0.030	0.150

Aquatic oxygen uptake increased significantly with exposure temperature up to 25°C (ANOVA F = 6.4, d.f. = 4,34, P < 0.001), but was similar at 10, 15, and 20°C (ANOVA F = 1.44, d.f. = 2,24, P = 0.26). It was significantly reduced at 5°C compared with higher exposure temperatures. In contrast, temperature had no significant effect on rates of aerial respiration (ANOVA F = 1.52, d.f.= 4,34, P = 0.22). For N. rossi, aerial rates of oxygen uptake were significantly reduced, compared with aquatic rates (2-way ANOVA, F = 74.1, d.f. = 1,69, P < 0.001). This reduction was up to 60% of the aquatic rate at higher exposure temperatures.

### Whole Fish Experiment

The behavior exhibited by N. rossi in the presence of the dead fish was similar to that recorded in the previous experiments. In aerial conditions the cirolanids were observed walking on the paper towel, but they tended to slip off the skin of the fish and crawl beneath it. At 0°C, walking activity ceased within 2 h in both aerial and aquatic conditions. This response contrasted with submerged fish experiments at 5 and 10°C, where isopods were observed walking and swimming in sea water and aggregating around the mouth and operculum of the fish. Following three days exposure to the fish, conditions within the aquaria were less than optimal. While many of the isopods continued to show limb movements, most were assessed as dead because they failed to recover fully when returned to sea water at the original storage temperature (Table 2). Only isopods held in aquatic conditions at 5 and 10°C showed evidence of feeding, suggested by a distended body and a red internal color, most likely derived from the gills and mouth of the fish. While 8% of isopods from the air treatment at 10°C also displayed this coloration, it was not accompanied by thoracic body distension. Examination of the fish bodies showed that isopods did not enter the body cavity or muscle flesh. In aerial conditions there was no visible external damage to the fish at  $0-1^{\circ}$ C, and very little at the higher temperatures. In aquatic conditions at  $0-1^{\circ}$ C, there was little damage to the fish, but at 5°C and especially at 10°C there were obvious feeding marks on the inside and outer edge of the operculum. Furthermore, parts of the gills were damaged or missing and the skin around the mouth was incomplete.

#### Feeding Rates

Weight changes of fish cubes in experiments both with and without isopods are shown in Table 3. In all instances, the skin on the fish remained intact. Weight reductions  $\mathcal{T}$ were found in most experiments where  $N_{\cdot} \cong$ rossi was allowed access to fish in aquatic B conditions. In aerial conditions, there were  $\subseteq$ minor weight gains in the food at low tem- N peratures and a small weight loss recorded >> at 20°C in the presence of isopods. While this  $\exists$ may reflect feeding or other activity, it more likely reflects some deterioration in the fish flesh through time. Minor weight losses were also found in the control experiment without isopods at 20°C and a correction was used in calculating the feeding rate shown in Fig. 3. In aquatic conditions, weight-specific food consumption of N. rossi feeding on fish flesh was variable but increased with exposure temperature. The feeding rate was negligible at 1°C and highest at 15°C where food intake represented approximately 30% of the dry body weight per day.

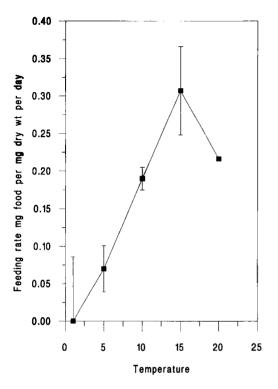


Fig. 3. Effects of temperature on the feeding rate ( $\bar{x} \pm SE$ ) of *Natatolana rossi* feeding on blue moki flesh.

#### DISCUSSION

Natatolana rossi, like other scavenging or predatory peracarids, show morphological and behavioral adaptations for detecting and consuming food (e.g., Moore and Wong, 1995). These isopods are able to feed on a wide variety of potential prey items and their high food consumption on energy-rich food sources equips them for lengthy periods of starvation. While these adaptations are consistent with similar predators, including lysianassid amphipods and whelks (Britton and Morton, 1994), other features of their biology are less clearly adaptive. Their patterns of oxygen uptake appear to be conservative and their ability to resist water loss is similar to semiterrestrial isopods. Their mechanisms to reduce metabolic energy expenditure differ from strategies adopted by molluscs, where rapidly growing and fast-moving species typically adopt an exploitative strategy with a high metabolic rate and high Q<sub>10</sub> temperature coefficients (Branch and Newell, 1978).

The behavioral observations made here for N. rossi feeding on whole fish in a labora-

tory study suggest that it initially feeds on soft tissues around the gills and mouth rather than penetrating or consuming the skin. In the carrion-feeding amphipod Anonyx sarsi Steele and Brunet (see Sainte-Marie, 1987), amphipods entered the eyes and entered the gut and body tissues via the gut and anus. While N. rossi did not gain entry to the body tissues in my experiments, it fed readily on exposed fish tissue. However, this ability was inhibited following aerial exposure and suggests that the feeding mechanism is essentially aquatic as in many other carnivorous cirolanids (Jones, 1968).

Oxygen uptake of Crustacea, like other invertebrates, depends upon many internal and external factors (Newell, 1979), including body size, temperature, salinity, and whether individuals are normally exposed to aerial conditions. For isopods and amphipods, oxygen uptake reflects the usual habitat, with aquatic species generally showing elevated rates of oxygen uptake in sea water compared with those in air (Wieser, 1963; Marsden, 1979, 1984). The weight-specific rate of aquatic oxygen uptake for N. rossi at habitat temperature (10°C) during winter was 0.26 µl  $O_{2}$  mg<sup>-1</sup> h<sup>-1</sup>. While this rate is considerably below that for intertidal and terrestrial isopods (Bulnheim, 1974; Jones, 1974; Newell et al., 1976, Husain and Alikhan, 1979; Meyer and Phillipson, 1983), it is three times the rate previously recorded for the deep sea cirolanid N. borealis at similar temperatures (Skjoldal and Baake, 1978; Taylor and Moore, 1995). When comparing respiration rates of invertebrates, it is important to consider body size and a correction can be made using the weight exponent b, which for many invertebrates, including isopods, is close to 0.7 (Ivleva, 1980). Although it is to be expected that the weight-specific  $O_2$  will decrease with increasing body size, the reduction in respiration rate for large circlanids is greater than that predicted due to scaling. They reflect remarkably low rates for resting metabolism.

Low rates of oxygen uptake have been previously reported for some subtidal crustaceans. For example, Bridges and Brand (1980) compared the weight-specific aquatic respiration of two burrowing with two nonburrowing anomurans. They found low values for *Corystes cassivelaunus* (Pennant) which spends long periods buried in the sub-

stratum. Notatolana rossi may also form temporary burrows in sand and low metabolism is likely to be an energy-conservation strategy. Some infaunal species also possess additional respiratory adaptations, being able to regulate oxygen uptake to compensate for declining oxygen tensions. However, in the cirolanid N. borealis no such regulation was found (Skjoldal and Baake, 1978; Taylor and Moore, 1995) and anaerobic metabolism takes over at low oxygen tensions. It is not known whether N. rossi has the ability to survive anoxic conditions, but the poor survival of this species in the presence of dead fish suggests that it may be less able to withstand decaying conditions than the deep-water species N. borealis (see de Zwann and Skjoldal, 1979).

The effects of temperature on aquatic oxygen uptake have been recorded in a wide range of invertebrates (Innes and Houlihan, 1981), with many species showing temperature dependent O<sub>2</sub> uptake. Natatolana rossi shows respiratory responses which are characteristic of fresh-water, terrestrial, and intertidal isopods from higher tidal levels. Aquatic respiration was temperature dependent with  $Q_{10}$  values close to 2 between 5 and 15°C, but 1.2 between 10 and 20°C, and 1.3 between 15 and 25°C. These values suggest that N. rossi lacks a general mechanism to conserve metabolic energy during short-term changes in sea-water temperature.

In contrast to aquatic rates of oxygen uptake, air exposure reduced oxygen uptake of N. rossi by at least 50% at all exposure temperatures. Aerial exposure may be a significant stress factor for crustaceans, such as N. rossi, from low-shore and subtidal habitats. For example, in lobsters, O<sub>2</sub> reductions of 43 and 71% occurred following aerial exposure at temperatures of 15 and 20°C, respectively (Whiteley et al., 1991). However, the ability of N. rossi to respire in air was similar to that of the isopod *Naesa bidentata* (Adams) from the mid-shore level and better than that of the high-shore species Campecopea hirsuta (Montagu) (see Wieser, 1963). While it might be expected that isopods normally exposed to the air might be able to maintain aquatic rates of oxygen uptake following aerial exposure, studies so far have not described such a pattern for intertidal isopods. Aerial respiration for N. rossi was temperature independent over a wide temperature range. Since air temperatures fluctuate more than sea-water temperatures, the ability to maintain a low rate of oxygen uptake may be an important energyconserving mechanism if individuals are accidentally displaced into intertidal habitats when the tide recedes.

The outstanding ability of Natatolana rossi to survive water loss in aerial conditions appears inconsistent with its normally subtidal existence. However, early studies by Brusca (1966), comparing isopods from different habitats, found similarly high survival times for subtidal Cirolana harfordi (Lockington). Several factors may influence the ability of aquatic isopods to survive aerial conditions. the lethal water content, reflected by the wet weight : dry weight ratio. Natatolana rossi has a relatively high water content compared with intertidal species and its weight-specific transpiration rate (mg water lost h<sup>-1</sup> mg wet wt <sup>1</sup>) for 60 and 80% RH are 0.057 and 0.017, re- & spectively. These unusually low rates of water loss are below those for intertidal sphaeromatids and amphipods (Marsden, 1974; Morritt, 1987), including high-level sandhoppers (Marsden, 1991). Perhaps the most important  $\exists$ factor explaining these differences is body 3 size, which is associated with a decrease in surface area : volume ratio. This feature most  $\frac{O}{O}$ likely reduces the transpiration rate and compensates for an apparent soft external cuticle in N. rossi. Lethal water loss in N. rossi is approximately 30% of the initial wet weight,  $\mathbb{R}$ which is similar to intertidal crabs (Jones and  $\vec{Q}$ Simons, 1982; Innes et al., 1986), but below  $\stackrel{\scriptstyle{\leftarrow}}{\leftarrow}$ that for supralitoral isopods and amphipods  $\mathcal{T}$ (Marsden, 1974, 1991).

Smith and Baldwin (1982) suggested that  $\overline{\underline{B}}$ amphipods may possess adaptations for ex- 9 ploiting carrion as a food source. These would  $\geq$ include small size, fast detection mechanisms, 👌 rapid food intake, and the ability to increase  $\exists$ meal size with starvation level (Sainte-Marie et al., 1989; Moore and Wong, 1995). For the amphipod Anonyx sarsi (Sainte-Marie, 1987), the absolute meal size for a 20-mm long amphipod was approximately 4% of the dry body weight, calculated over a 1-h observation period. Slightly higher values have been recorded in amphipods that have been starved (Sainte-Marie et al., 1989) and also a large predatory abyssal amphipod (Hargrave, 1985). Maximum feeding rates for N. rossi were equivalent to 30% of the dry body weight per day at 15°C. Isopods were unable

to feed at 1°C and, as expected, showed low food intake at 5°C. However, consistent with expectations, the feeding rate doubled with a 10°C increase in temperature.

In describing the feeding behavior of the scavenging isopod N. borealis, Wong and Moore (1995, 1996) suggested that it operates a "sit and wait, batch reactor" strategy, which is energetically efficient and reduces the risk of predation. The results from the present study support this strategy also for N. rossi. Low metabolism at rest, and at low winter temperatures would reduce energy expenditure. This may also be important in times of food shortage, since some authors suggest that the general incidence of carrion in the sea is low (Britton and Morton, 1994). If most of the energy consumed by N. rossi is available for body maintenance, calculations from the present study suggest that a single day's food could support resting rates of oxygen uptake for more than 40 days of inactivity at 10°C. Large N. rossi have been maintained in laboratory conditions at 15°C without food for between 2 and 3 months. Although this period appears lengthy compared with amphipods [23-30 days (Sainte-Marie et al., 1989; Moore and Wong, 1995)], it may be usual for cirolanids, especially females which appear unlikely to feed for several months when carrying eggs within the marsupium (Johansen, 1996).

However, the predictions made here for N. rossi do not allow for the increased metabolic demand associated with increased activity. Many isopods show nocturnal or tidal locomotory behavior (Fincham, 1973). From studies on swimming amphipods (Halcrow and Boyd, 1967), such activity could result in a three-fold increase in oxygen consumption. The presence of food may also stimulate increased  $O_2$  uptake (Smith and Baldwin, 1982) and swimming activity as seen in N. rossi.

Finally, questions asked by local fishermen may be addressed. Since *N. rossi* cannot feed in air and will not survive long in the ship's cooler, it should pose little threat to the fish catch once it has been landed. Isopods are, however, quite tolerant of aerial exposure and recover quickly if returned to sea water. The voracious feeding rates recorded here for *N. rossi* in water clearly may significantly reduce the fish catch in set nets. They would also effectively clean away fish debris thrown into the sea.

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### LITERATURE CITED

- Branch, G. M., and R. C. Newell. 1978. A comparative study of metabolic energy expenditure in the limpets *Patella cochlear, P. oculus* and *P. granularis.*—Marine Biology 49: 351–361.
- Bridges, C. R., and A. R. Brand. 1980. Oxygen consumption and oxygen-independence in marine crustaceans.—Marine Ecology Progress Series 2: 133–141.
- Britton, J. C., and B. Morton. 1994. Marine carrion and scavengers.—Oceanography and Marine Biology 32: 369-434.
- Bruce, N. L. 1986. Cirolanidac (Crustacea: Isopoda) of Australia.—Records of the Australian Museum, Supplement 6: 1–239.
- Brusca, G. J. 1966. Studies on the salinity and humidity tolerances of 5 species of isopods in a transition from marine to terrestrial life.—Bulletin of the Southern Californian Academy of Science 65: 146–151.
- Bulnheim, H. P. 1974. Respiratory metabolism of *Idotea* balthica (Crustacea, Isopoda) in relation to environmental variables, acclimation processes and moulting.—Helgolaender wissenschaftliche Meeresuntersuchungen 26: 464-480.
- de Zwaan, A., and H. R. Skjoldal. 1979. Anaerobic energy metabolism of the scavenging isopod *Cirolana borealis* (Lilljeborg).—Journal of Comparative Physiology 129: 327–331.
- Fincham, A. A. 1973. Rhythmic swimming behaviour of the New Zealand sand beach isopod *Pseudaega punctata* Thomson.—Journal of Experimental Marine Biology and Ecology 11: 229–237.
- Halcrow, K., and C. M. Boyd. 1967. The oxygen consumption and swimming activity of the amphipod Gammarus oceanicus at different temperatures.—Comparative Biochemistry and Physiology 23: 233-242.
- Hale, H. M. 1927. The crustaceans of South Australia. Part I.—Handbooks of the flora and fauna of South Australia. Government Printer, Adelaide, Australia. Pp. 1–380.
- Hargrave, B. T. 1985. Feeding rates of abyssal scavenging amphipods (*Eurythenes gryllus*) determined *in situ* by time-lapse photography.—Deep Sea Research 32: 448-450.
- Husain, M. Z., and M. A. Alikhan. 1979. Physiological adaptations in Crustacea to the environment: oxygen consumption as a function of body weight and environmental temperature in the terrestrial isopod *Porcellio laevis* Latreille (Isopoda, Oniscoidea).—Crustaceana 36: 277–286.
- Innes, A. J., and D. F. Houlihan. 1981. A review of the effects of temperature on the oxygen consumption of intertidal gastropods.—Journal of Thermal Biology 6: 249-256.
- —, M. E. Forster, M. B. Jones, I. D. Marsden, and H. H. Taylor. 1986. Bimodal respiration, water balance, and acid base regulation in a high-shore crab, *Cyclograpsus lavauxi* H. Milne Edwards.—Journal of Experimental Marine Biology and Ecology 100: 127–218.
- Ivleva, I. V. 1980. The dependence of crustacean respiration rate on body mass and habitat temperature.— Internationale Revue der gesamten Hydrobiologie und Hydrographie 65: 1–47.

- Johansen, P.-O. 1996. Reproduction and sexual maturation of the scavenging deep water isopod Natatolana borealis (Lilljeborg) from western Norway.-Sarsia 81: 297-306.
- Jones, D. A. 1968. The functional morphology of the digestive system in the carnivorous intertidal isopod Eurydice.—Journal of Zoology 156: 363-376.
- Jones, M. B. 1974. Survival and oxygen consumption in various salinities of three species of Idotea (Crustacea, Isopoda) from different habitats.-Comparative Biochemistry and Physiology 48: 501-506.
- -, and M. J. Simons. 1982. Habitat preferences of two estuarine burrowing crabs Helice crassa Dana (Grapsidae) and Macrophthalmus hirtipes (Jacquinot) (Ocypodidae).-Journal of Experimental Marine Biology and Ecology 56: 49-62.
- Marsden, I. D. 1974. Adaptations of Sphaeroma rugicauda (Leach) from a salt marsh habitat.-Ph.D. thesis, University of London. Pp. 1-242.
- . 1979. Seasonal oxygen consumption of the saltmarsh isopod Sphaeroma rugicauda.-Marine Biology 51: 329-337.
- . 1984. Effects of submersion on the oxygen consumption of the estuarine sandhopper Transorchestia chiliensis.-Journal of Experimental Marine Biology and Ecology 152: 61-74.
- -. 1991. A comparison of water loss and gill areas in two supralittoral amphipods from New Zealand.-Hydrobiologia 223: 149-158.
- Meyer, E., and J. Phillipson. 1983. Respiratory metabolism of the isopod Trichoniscus pusillus provisorius .--- Oikos 40: 69--74.
- Moore, P. G., and Y. M. Wong. 1995. Orchomene nanus (Krøyer) (Amphipoda: Lyssianassoidea), a selective scavenger of dead crabs: feeding preferences in the field.-Journal of Experimental Marine Biology and Ecology 192: 35-45.
- Morritt, D. 1987. Evaporative water loss under desiccation stress in semi-terrestrial and terrestrial amphipods (Crustacea: Amphipoda: Talitridae).-Journal of Experimental Marine Biology and Ecology 111: 145-157.
- Newell, R. C. 1979. Biology of intertidal animals .- Marine Ecological Surveys Ltd., Faversham, Kent, England. Pp. 1-781.
- -, A. Roy, and K. Armitage. 1976. An analysis of factors affecting the oxygen consumption of the isopod Ligia oceanica.—Journal of Zoology 49: 109-137.
- Sainte-Marie, B. 1987. Meal size and feeding rate of the shallow-water lysianassid Anonyx sarsi (Crustacea:

Amphipoda).-Marine Ecology Progress Series 40: 209-219.

- J. A. Percy, and J. R. Shea. 1989. A comparison of meal size and feeding rate of the lysianassid amphipods Anonyx nugax, Onisimus (=Pseudalibotus) and Orchomenella pinguis.—Marine Biology 102: 361-368.
- Schram, F. R. 1986. Crustacea.-Oxford University Press, Oxford, England. Pp. 1-606.
- Skjoldal, H. R., and T. Baakke. 1978. Anaerobic metabolism of the scavenging isopod Cirolana borealis Lilljeborg, Adenine nucleotides.-In: D. S. McLusky and A. J. Berry, eds., Physiology and behaviour of marine organisms. Pp. 67-74. Proceedings of the 12th European Symposium on Marine Biology. Pergamon Press, Oxford, England.
- Smith, Jr., K. L., and R. J. Baldwin. 1982. Scavenging deep-sea amphipods: effects of food odour on oxygen consumption and a proposed metabolic strategy.—Marine Biology 68: 287-298.
- Taylor, A. C., and P. G. Moore. 1995. The burrows and aylor, A. C., and P. G. Moore. 1995. The burrows and  $\exists$  physiological adaptations to a burrowing lifestyle of  $\Box$ Natatolana borealis (Isopoda: Cirolanidae).-Marine Biology 123: 805-814.
- Whiteley, N. M., A. H. A-Wassia, and E. W. Taylor. 1991. The effect of temperature, aerial exposure and distur-bance on oxygen consumption in the lobster, *Homarus* gammarus (L.).-Marine Behaviour and Physiology 17: 213-222
- Wieser, W. 1963. Adaptations of two intertidal isopods II. Comparison between Campecopea hirsuta and Naesa bidentata.-Journal of the Marine Biological 8 Association of the United Kingdom 43: 97-112.
- Winston, P. E., and D. H. Bates. 1960. Saturated solutions for the control of humidity in biological research.-Ecology 41: 232-237.
- Wong, Y. M., and P. G. Moore. 1995. Biology of feed- 🕏 ing in the scavenging isopod Natatolana borealis o (Isopoda, Cirolanidae).-Ophelia 43: 181-196.
- -. 1996. Observations on the activ-, and ity and life history of the scavenging isopod Natatolana borealis Lilljeborg (Isopoda: Cirolanidae) from Loch 241 Fyne, Scotland.—Estuarine Coastal and Shelf Science 42: 247–262. SCEIVED: 1 June 1998. SCEPTED: 27 October 1998. Address: Zoology Department, University of Canter-ry, Private Bag 4800, Christchurch, New Zealand. -mail: islay@zool.canterbury.ac.nz) borealis Lilljeborg (Isopoda: Cirolanidae) from Loch

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