

## Chemical defense, biochemical composition and energy content of three shallow-water Antarctic gastropods

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**Summary.** Aqueous extracts of the mantle tissues of the opisthobranchs *Austrodoris kerguelensis* and *Tritoniella belli* and the lamellarid gastropod *Marseniopsis mollis* were cytotoxic to the sperm of the antarctic sea urchin *Sterechinus neumayeri*, and caused behavioral responses (sustained terminal sensory tube-feet retractions) in five species of antarctic sea stars. Pieces of mantle tissue of all three species were noxious to two species of antarctic fish. Primary body components (mantle, foot, viscera) of the three gastropod species contained high levels (% dry wt) of NaOH-insoluble protein (40–59%), moderate levels of NaOH-soluble protein (7–25%) and lipid (6–18%), and low levels of carbohydrate (<1%). The energetic composition of the tissues reflected their organic make-up, with most energy (11–17 kJ g<sup>-1</sup> dry wt) associated with protein. Total energy contents of representative adult individuals were 192, 26 and 69 kJ for *A. kerguelensis* (93 g wet wt), *T. belli* (22 g wet wt) and *M. mollis* (114 g wet wt), respectively. Although these sluggish gastropods lack an external shell and are nutrient- and energy-rich and therefore high quality prey, like many of their temperate and tropical counterparts, they appear to be protected by chemicals.

### Introduction

Gastropods which lack an external shell employ a wide diversity of alternative strategies in order to provide defense from predators (Thompson 1960a; Edmunds 1966; Todd 1981). Dietary-derived secondary metabolites (Thompson et al. 1982; Faulkner and Ghiselin 1983; Gunthrope and Cameron 1987; Pawlik et al. 1988), low pH (Thompson 1960b; Edmunds 1968), incorporation of coelenterate nematocysts (Greenwood and Mariscal 1984), and cryptic or bold body coloration (Thompson 1960a; Karuso 1987) may all serve defensive functions. Although a large number of studies have investigated chemical

defense in temperate and tropical gastropods (reviewed by Faulkner and Ghiselin 1983; Faulkner 1984, 1986, 1987; Bakus et al. 1986; Karuso 1987; Scheuer 1990), there has been little investigation of antarctic polar species (McClintock and Janssen 1990). Moreover, few studies have examined the effectiveness of gastropod defensive chemicals against a suite of ecologically relevant (i.e. sympatric) invertebrate and vertebrate predators.

Bakus (1974) and Bakus and Green (1974) suggested that there is an inverse correlation between the incidence of chemical defense and latitude in temperature and tropical sessile and sluggish marine invertebrates. This latitudinal relationship is thought to be related to a decrease in predation by browsing fish with increasing latitude (Neudecker 1979; Palmer 1979; Vermeij 1978). Therefore, high levels of fish predation may increase evolutionary selective pressure for defensive chemicals in tropical marine invertebrates. Although predation by browsing fish is low in polar waters, invertebrate predation does occur, particularly in antarctic benthos (Dayton et al. 1974). For example, sea stars are common and important predators of sessile and sluggish antarctic marine invertebrates (Dayton et al. 1974; Dearborn 1977). An extremely stable physical environment has led to a benthic community structured primarily by biological interactions such as competition and predation (Dayton et al. 1974), which in turn may provide the necessary selective pressure for the evolution of chemical defenses in sessile and sluggish antarctic marine invertebrates.

The nudibranchs *Austrodoris kerguelensis* (Bergh) (Dorididae) (formerly *A. macmurdensis* Odhner; see Wagele 1990) and *Tritoniella belli* Eliot (Tritoniidae), and the lamellarid gastropod *Marseniopsis mollis* (Bergh) (Lamellariidae) which possesses an internal shell, occur commonly in the sponge dominated community below 33 m in McMurdo Sound, Antarctica (Dayton et al. 1974). No observations of predation on any of these antarctic opisthobranchs have been reported (Dayton et al. 1974; McClintock et al., personal observation).

One objective of this study was to employ a sea urchin gamete bioassay to establish whether the mantle tissues of

these antarctic gastropods were cytotoxic. Bioactive extracts and whole pieces of mantle tissue were then tested against a suite of sympatric invertebrate and vertebrate organisms in order to evaluate their effectiveness at repelling potential predators. The pH of the mantle tissues was measured in order to assess whether acidity was responsible for cytotoxicity or feeding deterrence. A second objective of this study was to examine the biochemical and energetic composition of principal body tissues. This facilitated an analysis of the allocation of materials and energy to different body components, and a comparative evaluation of the nutritional and energetic content of these molluscs as potential prey.

## Materials and methods

### Field collections

*Austrodoris kerquelensis*, *Tritoniella belli* and *Marseniopsis mollis* were collected using SCUBA between 25–35 m depth at Arrival Heights, Cape Armitage, and Compromise Cove in McMurdo Sound, Antarctica (77°34'S, 164°39'E). The common sea urchin *Sterechinus neumayeri* used in cytotoxicity assays, and the sea stars *Odontaster validus*, *O. meridionalis*, *Perknaster fuscus*, *Diplasterias brucei* and *Acodontaster conspicuus* used in invertebrate behavior assays, were also collected from these sites at similar depths. The antarctic fish *Pagothenia borchgrevinki* and *Trematomus bernacchii*, used in the ichthyotoxicity assays, were collected using baited fishing lines near McMurdo Station. All collections and experiments were conducted during the austral summer of 1989.

### Cytotoxicity assays and pH determinations

Crude aqueous extracts of mantle tissues of *Austrodoris mcmurdensis*, *Tritoniella belli* and *Marseniopsis mollis* were prepared by homogenizing a known wet wt of tissue with an equal volume of cold sea water. Particulate material was removed by filtering. Cytotoxicity assays were conducted using mature sperm of *Sterechinus neumayeri* collected by intracoelomic injection of 0.5 M KCL (Bosch et al. 1987). 100  $\mu$ l of sperm was placed onto a spotting plate held at 0°C and 250  $\mu$ l of aqueous extract diluted with sea water to 3, 0.3, 0.03 or 0.003% was added. The activity of sperm was scored positive (> 25% active) or negative (> 75% inactive) following a 20 min incubation using an inverted compound microscope (inactive sperm were assumed to be dead). Ten replicates were conducted at each concentration of extract and ten control sperm assays were conducted simultaneously using only sea water. The pH of the pooled macerated fresh mantle tissues of three individuals was measured for each species using an Orion pH Meter (SA250).

### Sea star behavior assays

Sea stars are thought to demonstrate a stereotypic terminal sensory tube-foot response to irritants or noxious compounds (Sloan 1980; Thompson et al. 1985). Chemical deterrents may cause an immediate and sustained retraction of the terminal sensory tube-feet. In response to particularly strong deterrents, the whole arm may be withdrawn from the chemical source. In the present study an assumption was made that sustained sensory tube-foot retraction and arm withdrawal in five species of antarctic sea stars was indicative of a negative response to a given stimulant. Mantle tissue extracts were diluted in cold sea water to a concentration of 10%. One ml of this dilute solution was released from a syringe held 3-cm

distant from the extended terminal sensory tube-feet of each of ten sea stars of each species. Individual sea stars were tested in ten 10-gallon aquaria equipped with flow-through sea water (–1°C). Sensory tube-foot retraction responses were scored positive if tube-feet immediately retracted and sustained this position for a period of one min following the release of dilute extract. A secondary avoidance response, arm withdrawal from the surface of the aquarium wall, was also recorded if it occurred within the one min period. In order to control for a tube-foot and arm response to mechanical stimulation, five sea water controls were conducted with each species of sea star.

### Ichthyotoxicity assays

Fresh mantle tissues of all three gastropod species were cut into one cm cubes. For each species, tissue pieces were pooled from three individuals. Control tissues with the same dimensions were prepared from the fresh muscle tissues of the antarctic cod *Dissostichus mawsoni*. During feeding trials, nine individuals of *Trematomus bernacchii* (20–30 cm length) were placed into separate chambers in a water table (1.5 × 2.0 × 0.2 m). Individual fish were presented either a control or experimental tissue in a predetermined random sequence ( $n=9$  experimental and 9 control trials for each gastropod). A second fish, *Pagothenia borchgrevinki* (25–35 cm length), was also used for bioassays. This species fed more effectively when individuals were held in a group. Approximately 15–25 fish were held in a 2-m diameter sea water tank and simultaneously presented an experimental and control tissue ( $n=10$  paired trials for each gastropod). Tissues were recorded as either ingested and swallowed, or ingested and regurgitated.

### Biochemical and energetic composition

Adult individuals of each species ( $n=3$ ) were measured (body length) and weighed (wet wt) and dissected into primary body components: the mantle, foot, and visceral organs. The visceral organs were treated collectively and included the proboscis, foregut gland, foregut, gonad, digestive diverticula, stomach region, and intestine. Each primary body component was weighed, lyophilized, reweighed and ground into a fine powder using a Wiley mill. Ash was determined by placing tissues in a muffle furnace at 500°C for 4 h. NaOH-soluble protein and TCA-soluble carbohydrate were determined colorimetrically using the techniques of Bradford (1976) and Dubois et al. (1956), respectively. Methanol-chloroform soluble lipid was determined gravimetrically using the techniques of Freeman et al. (1957). Insoluble protein was determined by subtraction as conducted by Lawrence (1973). The energetic composition of the body components was determined indirectly by multiplying the dry wt of each tissue by the level of each organic class and its energy equivalents (Brody 1945). The energy content ( $\text{kJ g}^{-1}$  dry wt) was then multiplied by the dry wt of the entire body component, and the total of each body component summed to yield the total energy content of a representative intact individual.

### Statistics

The cytotoxicity, sea star behavior, and ichthyotoxicity bioassays were analyzed using a Fisher's Exact Test at the 5% significance level (Zar 1974).

## Results

### Cytotoxicity assays and pH determinations

Aqueous extracts of the mantle tissues of all three gastropod species proved to be toxic to sea urchin sperm at

nearly all concentrations tested (Fig. 1). At the lowest applied concentration, 0.003% of crude extract, the response was diminished in *Austrodoris kerguelensis* and absent in *Tritoniella belli*. None of the sea water controls were toxic to sea urchin sperm. pH values for macerated mantle tissues were 7.8, 6.7 and 7.0 for *A. kerguelensis*, *T. belli* and *M. mollis*, respectively.

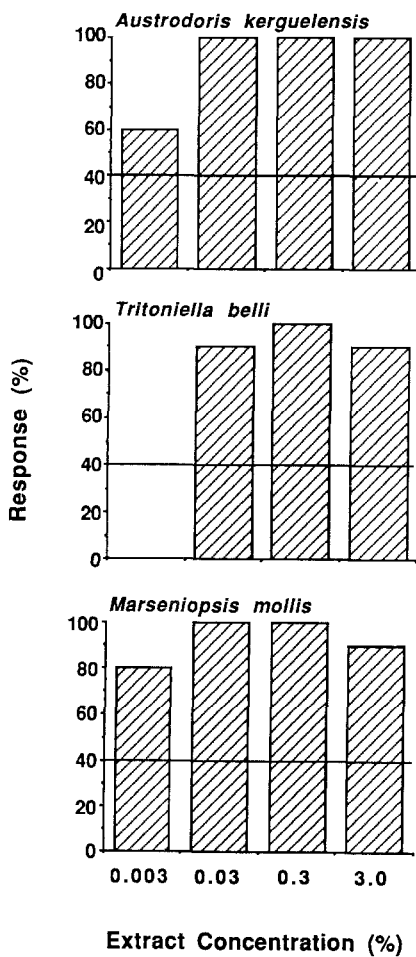
*Sea star behavior assays*

Aqueous extracts of the mantle tissues of *Austrodoris kerguelensis*, *Tritoniella belli* and *Marseniopsis mollis* caused significant sustained retraction of sensory tube-feet in all five species of antarctic sea stars (Fig. 2). The sea stars *Odontaster meridionalis* and *O. validus* exhibited a significant secondary arm retraction response to the mantle tissue extract of *A. kerguelensis*. The sea stars

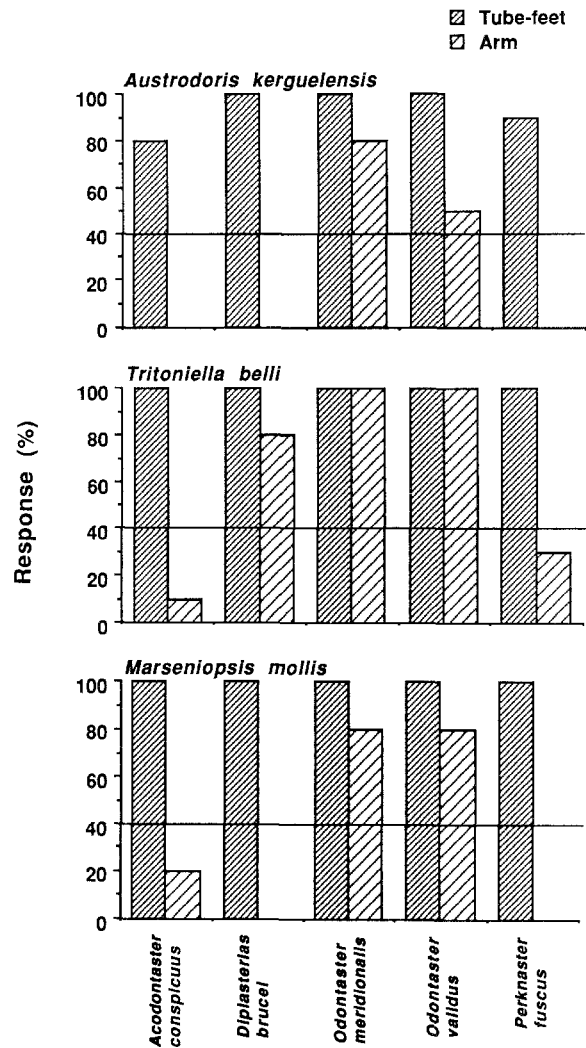
*Odontaster validus*, *O. meridionalis* and *Diplasterias brucei* had significant arm retraction responses to the mantle tissues of *T. belli*, while extracts of the mantle tissues of *M. mollis* caused significant arm retraction in *O. validus* and *O. meridionalis*. Sea water controls did not elicit any terminal sensory tube-foot retraction or arm withdrawal.

*Ichthyonoxicity assays*

The mantle tissues of all three gastropods caused significant ( $P < 0.05$ ) feeding deterrent responses (ingestion followed by immediate expulsion) in *Pagothenia borchgrevinki* and *Trematomus bernacchii*. The only instances where fish did not consistently reject all mantle tissues were for *T.*



**Fig. 1.** Cytotoxicity dose-response histograms showing the activity response of sperm from the antarctic sea urchin *Stereochinus neumayeri* exposed to different concentrations of crude aqueous mantle tissue extracts. Sea water controls did not cause sperm inactivity. Bars above horizontal lines are statistically significant ( $P < 0.05$ ) ( $n = 10$ /extract concentration)



**Fig. 2.** Sustained terminal sensory tube-foot retraction and arm withdrawal responses of five species of antarctic sea stars exposed to 10% crude aqueous extracts of the mantle tissues of three antarctic gastropods. Shown is the proportion of ten individuals of each species which displayed a response. Sea water controls did not cause tube-foot retractions or arm withdrawal. Bars above horizontal lines are statistically significant ( $P < 0.05$ ) ( $n = 10$  sea stars/mantle tissue)

*bernacchii* offered tissues of *Tritoniella belli* (89% rejection) and *Marseniopsis mollis* (66% rejection). Control cod tissues were always ingested by *P. borchgrevinki* and in all but four instances by *T. bernacchii* (23 accepted, 4 rejected).

#### Biochemical and energetic composition

Mean levels of ash were consistently highest (34–44% dry wt) in the mantle tissues of all three gastropods when compared to foot and visceral tissues (Fig. 3). Ash was also higher in the foot (25–35% dry wt) than the viscera (11–19% dry wt) in *Austrodoris kerguelensis* and *Tritoniella belli*. Mean lipid levels were generally highest in the visceral organs (13–18% dry wt) when compared to the mantle (5–11% dry wt) and foot (6–11% dry wt) tissues in all species. Mean NaOH-insoluble protein (40–59% dry wt) constituted the highest levels of any organic component, with little pattern seen in levels between body components. Energy associated with lipid was consistently highest (6–7 kJ g<sup>-1</sup> mean dry wt) in the viscera compared

with the mantle and foot tissues (Fig. 4). A similar pattern occurred for NaOH-soluble protein, with the highest levels (5–6 kJ g<sup>-1</sup> dry wt) occurring in the viscera. The highest levels of energy in all three body components of all species was derived from the insoluble protein component (10–14 kJ g<sup>-1</sup> dry wt). Total energy contents of representative adult individuals were 192, 26 and 69 kJ for *Austrodoris kerguelensis* (length = 11.6 cm; 93 g wet wt), *Tritoniella belli* (length = 7.4 cm; 22 g wet wt), and *Marseniopsis mollis* (length = 7.1 cm; 114 g wet wt), respectively. The total energy contents (kJ) of the viscera, mantle tissue and foot were 135, 37 and 19, 13, 8 and 5, and 37, 18 and 14 for *A. kerguelensis*, *T. belli* and *M. mollis*, respectively.

#### Discussion

The mantle tissues of the antarctic nudibranchs *Austrodoris kerguelensis* and *Tritoniella belli* and the lamellarid gastropod *Marseniopsis mollis* are chemically bioactive.

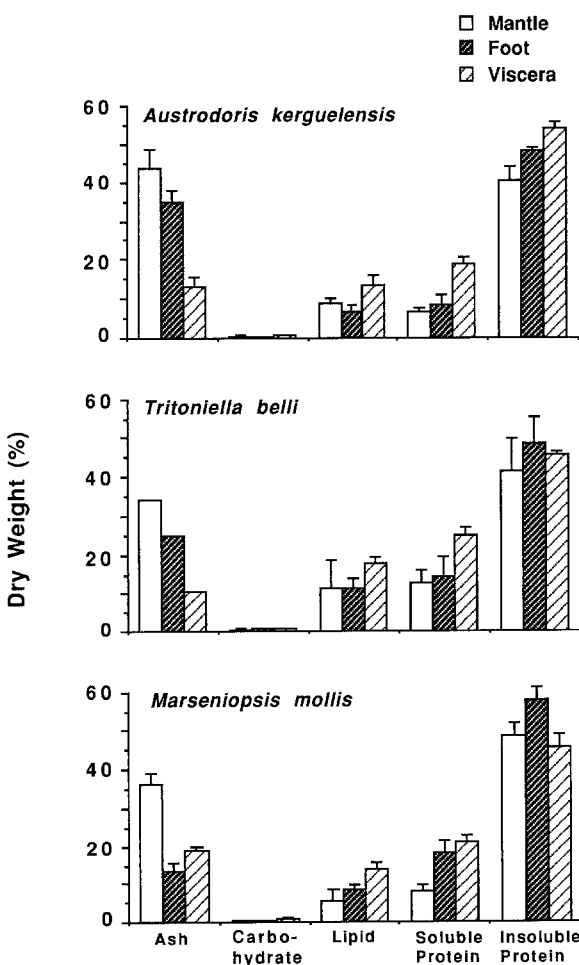


Fig. 3. Biochemical composition ( $\bar{x} \pm 1$  SE; % dry wt) of mantle, foot and visceral tissues of *Austrodoris kerguelensis*, *Tritoniella belli* and *Marseniopsis mollis*. ( $n = 3$  except for ash of *T. belli* where  $n = 1$ )

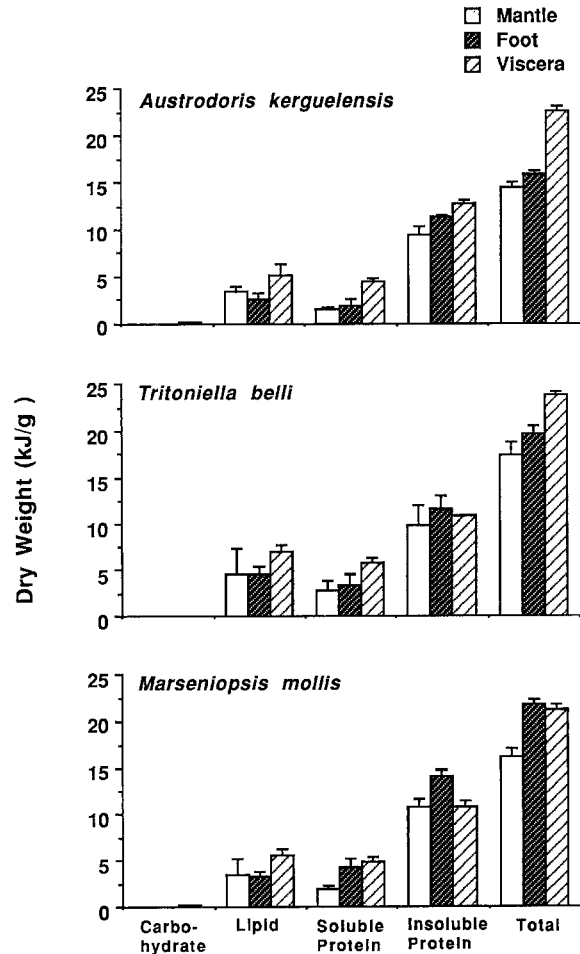


Fig. 4. Energetic composition ( $\bar{x} \pm 1$  SE; kJ g<sup>-1</sup> dry wt) of mantle, foot and visceral tissues of *Austrodoris kerguelensis*, *Tritoniella belli* and *Marseniopsis mollis*. ( $n = 3$ )

The cytotoxic nature of the mantle tissues is not a necessary correlate of the ability of these tissues to repel potential invertebrate or vertebrate predators (La Barre et al. 1986). However, the further demonstration that mantle extracts and tissues cause sensory tube-foot retraction, and in some cases arm withdrawal, in antarctic sea stars and rejection of mantle tissues by fish suggests that these gastropods are indeed chemically defended from predation. The sea stars and fish employed in these assays have not been directly observed feeding on these species (Dearborn 1977; Dayton et al. 1974; Foster et al. 1987; Foster and Montgomery, in press). Nonetheless, they are potential predators which feed on a variety of sessile and sluggish invertebrate prey.

Karuso (1987) noted that defensive mechanisms in molluscs which lack external shells not only include chemical adaptations, but may also encompass behavioral and morphological attributes. No swimming escape behaviors were observed in any of these three gastropods in response to mechanical disturbance as seen in the temperate nudibranch *Tritonia gilberti* when touched by the tube-foot of the sea star *Pycnopodia helianthoides* (Willows 1967). Similarly, the Spanish Dancer nudibranch *Hexabranchnus sanguinensis* swims in response to mechanical stimulation (Edmunds 1968). Moreover, *A. kerguelensis*, *T. belli* and *M. mollis* do not autotomize parts of their mantle in response to irritation as seen in several opisthobranchs (Karuso 1987).

The mantle tissues in some gastropods are structurally reinforced with spicules. The potential role of conspicuous spicules in preventing predation has been suggested for dorid nudibranchs (e.g. Paine 1963), but other factors such as noxious chemicals probably complement this defense (Karuso 1987). Conspicuous spicules were not evident in these antarctic gastropods. Nonetheless, levels of inorganic material (ash) in the mantle tissue were somewhat higher than visceral tissues reflecting the presence of minute spicules. Therefore, it cannot be ruled out that feeding deterrence in antarctic fish offered pieces of whole mantle tissues is due, in part, to the presence of inconspicuous spicules. This is clearly not the case for tube-foot and arm retraction in sea stars, as extracts of mantle tissues were used in bioassays.

Additional behavioral and morphological characteristics of gastropods which may prevent detection include utilizing cryptic habitats or distinct body colorations. None of the antarctic species examined in the present study seem to hide under rocks or in crevices. *Austrodoris kerguelensis* and *Tritoniella belli* are whitish in coloration. This may serve as a camouflage for *A. kerguelensis*, which feeds on light grey or white rosellid sponges such as *Rosella nuda* and *R. racovitzae* (Dayton et al. 1974). Similarly, the yellow coloration of the lamellarid gastropod *Marseniopsis mollis* blends with the yellow tunic of the antarctic ascidian *Cnemidocarpa verrucosa* which may be a component of its diet (Dayton et al. 1974). The whitish nudibranch *Tritoniella belli* feeds on the white stoloniferan *Clavularia frankliniana* (Dayton et al. 1974), but it is not camouflaged when feeding on the orange soft coral *Alcyonium paessleri*, a biochemically active species (Slattery et al. 1990) which may constitute a portion of its diet.

Although *T. belli* feeds on coelenterates, microscopic observations revealed no nematocysts sequestered in the respiratory processes (M. Slattery, personal observation), as seen in the cerata of some aeolid nudibranchs (Greenwood and Mariscal 1984; Karuso 1987).

A diterpenoic acid glyceride and glycerol ethers have been isolated from the mantle tissues of *Austrodoris kerguelensis* and *Tritoniella belli*, respectively (M. Davies-Coleman and D. J. Faulkner, personal communication). Both are known ichthyotoxins and may be responsible for bioactivity. Some molluscs which lack external shells concentrate acid in their mantle for chemical defense (Thompson 1960b; Edmunds 1968). This may not be the case in these antarctic species, as the mantle tissues are essentially neutral (pH range=6.7–7.8). Nonetheless, as maceration of mantle tissues may release body fluids which neutralize acids, further work is needed to document that acids are absent in these gastropods. Faulkner and Ghiselin (1983) related the evolutionary loss or internalization of the shell in gastropods to the ability to derive bioactive chemicals from food. It is noteworthy that the chemical defense of the antarctic lamellarid gastropod *Marseniopsis mollis*, which has an internalized shell, lends support to their hypothesis that the development of chemical defense is a preadaptation to shell-loss.

To date, most bioactive secondary metabolites isolated from molluscs are of dietary origin, although several species have been shown to produce chemicals de novo (Faulkner 1984, 1986, 1987; Bakus et al. 1986; Karuso 1987; Scheuer 1990). The nudibranch *Hexabranchnus sanguineus* derives bioactive metabolites from its sponge diet, chemically modifies these compounds, and incorporates them into its dorsal mantle and egg ribbons for protection (Pawlik et al. 1988). The similarity in the diterpenoic acid glycerides in the mantle tissues of *Austrodoris kerguelensis* and those produced by the temperate nudibranchs *Archidoris montereyensis* and *A. ohdneri*, suggests that *A. kerguelensis* employs de novo synthesis of defensive compounds (M.T. Davies-Coleman and D.J. Faulkner, personal communication).

Information about the biochemical and energetic composition of body components can provide insights into their function and the relative allocation of resources to different processes (Paine 1971; Lawrence 1985). Patterns of biochemical and energetic composition of body tissues were similar between all three gastropods. The levels of ash in the mantle tissues were somewhat higher than those measured in the foot, and twice as high as those in the viscera. This suggests that inorganic components such as spicules are present to provide structural support for tissues. Protein was very high in all tissues, particularly insoluble protein in the mantle and foot, indicative of the presence of connective tissue. Lipids were highest in the viscera and are probably associated with nutrients and gametes within the digestive diverticula and gonads, respectively.

The energetic composition of the body tissues reflected their organic constituents. The highest amount of energy in the tissues was derived from the insoluble protein component. Energy associated with lipid was highest in the visceral tissues. These tissues, which are important in

nutrient acquisition and storage and reproductive output, were the most energy rich. When scaled according to relative size (total dry wt), the visceral tissues also had the highest total energy content in all three species. *Austrodoris kerguelensis* had the greatest allocation of energy to the viscera, with 71% of the total energy content of a representative individual invested in visceral tissues. The allocation of total energy to the viscera in representative *Tritoniella belli* and *Marseniopsis mollis* was 52 and 54%, respectively. The energy content ( $\text{kJ g}^{-1}$  dry wt) of the mantle and foot tissues was similar. Nonetheless, the total allocation of energy was greater to the mantle, which provides structural integrity and protection, than to the foot which serves principally a locomotory function. This allocation of energy to the mantle was twice as high as to the foot in the nudibranchs *A. kerguelensis* and *T. belli*, while the difference was less in the lamellarid gastropod *M. mollis*. It is possible that the presence of a thin internal shell in *M. mollis* reduces the necessity to allocate energy to the mantle. Alternatively, energy invested in the shell may compete with the available energy for mantle production.

The lack of significant skeletal elements (e.g., large spicules or external shells) makes these gastropods relatively high in energy content ( $\text{kJ g}^{-1}$  total body mass) when compared to other groups of benthic marine invertebrates (Wacasey and Atkinson 1987). As such, these sluggish gastropods are attractive prey for potential invertebrate or vertebrate predators, yielding a high energy return per unit foraging effort. Nonetheless, the presence of cytotoxic and/or noxious compound(s) appears to provide an effective means of defense from at least fish predators.

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