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Fish blood as a chemical signal for Antarctic marine invertebrates

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Abstract Chemical cues released from dead or injured organisms constitute important signals informing nearby animals about a feeding possibility. The ability to detect the signal, evaluate its meaning and locate its source can help organisms to exploit food resources efficiently, which is especially important to animals living in environments with limited food supply. Experiments were carried out to study the behavioral responses of several Antarctic benthic invertebrates to fish (*Notothenia corriceps*) blood. Necrophagous species such as sea stars *Odontaster validus* and *Lysasterias* sp., amphipod *Waldeckia obesa* and nemertean *Parborlasia corrugatus* responded to fish blood with changes in their behavior. The behavior common to all these species was locomotion directed towards the stimulus source. Behavioral components consistent with food consumption were observed in *O. validus* and *P. corrugatus*. The reaction of herbivorous limpets *Nacella concinna* to fish blood depended on the animal size. Large (>10 mm) limpets showed no behavioral response, whereas small ones (<10 mm) reacted to the stimulus by moving a short distance away. These results indicate that blood released from the tissues of injured or dead animals may be an important chemical signal for organisms belonging to different taxa.

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Introduction

Chemoreception plays an important role in the life of many marine and freshwater species, enabling them to locate conspecifics, favorable microhabitats or food, and providing them information about predators or competitors (e.g., reviewed in Zimmer and Butman 2000). The Southern Ocean is characterized by a combination of low but stable temperatures and intense seasonality of food (Clarke 1983, 1988). Most of the primary production in the Antarctic is limited to a few months during the austral summer (Clarke and Leakey 1996). For the remaining part of the year, pelagic food items (e.g., dead zooplankton) do not reach benthic communities, and consequently these organisms are food limited for considerable periods of time (Clarke 1983; Arnaud 1970). Food resources accessible to necrophagous species during this time of the year (carrion, seal feces, discarded prey remains) are probably unpredictable in space and time, making scavenging opportunities relatively rare and causing periodic intensification of both intra- and interspecific competition (Arnaud 1970). Blood, easily freed from freshly killed or injured prey, may be a potential important signal of a predation event. Such information is especially relevant for necrophagous animals, kleptoparasites or potential prey. The ability to utilize blood signals as a means of locating such unpredictable food sources (or avoiding places where predators aggregate) may considerably increase the organism's prospects of survival in the harsh Antarctic environment. Partial predation, resulting in the release of blood and other body fluids, has been documented in a variety of predator–prey situations, including predation of gastropods by crabs (Dudgeon and Cheung 1990), scallops by crabs (Jørgensen 2005), cropping of clam siphons by fish (Peterson and Skilleter 1994) and predation of polychaete segments by other predatory polychaetes

(Zajac 1995). In consequence, scraps of partially eaten prey were left uneaten and can be exploited by other predators or scavengers.

The aim of the present paper was to investigate the impact of fish blood released into the environment on the behavior of a suite of ecologically important necrophagous benthic macroinvertebrates. Four necrophagous (sea stars *Odontaster validus* and *Lysasterias* sp., amphipod *Waldeckia obesa* and nemertean *Parborlasia corrugatus*) and one potential prey species (limpet *Nacella concinna*) were chosen as test animals. A hypothesis that small limpets, being more susceptible to predation, will react to a potential predation event (fish blood) more strongly than large ones was also tested.

All tested necrophagous species have circum-Antarctic distribution and are common in benthic environments (Dearborn 1977; McClintock et al. 1988; Heine et al. 1991; Graeve et al. 2001). Sea star *O. validus* Koehler is omnivorous, acting as a scavenger, an active predator, a herbivore or a suspension feeder (Dearborn 1977; McClintock 1994). *W. obesa* (Chevreux, 1905) is a large scavenging amphipod, feeding on fish and invertebrate carcasses (Arnaud 1970; Graeve et al. 2001). Sea star *Lysasterias* sp. (Studer) is an omnivorous species, acting as a scavenger or an active predator (Dearborn 1977; Presler 1986). Huge nemertean *P. corrugatus* is a scavenging and predatory species, excreting mucus containing cytolytic toxins (Heine et al. 1991; Berne et al. 2003).

The Antarctic limpet *N. concinna* (Strebel, 1908) occurs on rocky bottoms along the Antarctic Peninsula and adjacent islands (Picken 1980). It is herbivorous and feeds on benthic microalgae (Davenport 1997). *N. concinna* is preyed upon by predatory sea stars such as *Neosmilaster georgianus* (Dearborn 1977; McClintock 1994).

Materials and methods

The common benthic Antarctic fish *Notothenia corriceps* was caught in Admiralty Bay in the area of Thomas Point–Shag Point in January (fish 1) and February (fish 2) 2005 in the gill-nets (mesh size 50 mm) from a depth of 10–30 m. Blood samples were collected from caudal vessels, then cooled and centrifuged at 3,500 U/min. The serum obtained was stored in polypropylene vials at −24°C until the assays.

The blood serum was assayed for:

- Crude protein: biuret method, with a POCH Gliwice diagnostic kit
- Glucose: enzymatically, with a BioMerieux diagnostic kit
- Triacyloglicerols: enzymatically, with a BioMerieux diagnostic kit
- Total cholesterol and its high-density lipoprotein fraction (HDL-cholesterol): enzymatically, with a BioMerieux diagnostic kit, by spectrophotometer.

Each assay was replicated five times. Average concentrations of measured blood components (Table 1) were typical for *N. corriceps* at this time of the year (Stepanowska in prep.).

All experimental species were either collected by Scuba divers (*O. validus*, *Lysasterias* sp., *N. concinna*, *P. corrugatus*) or caught in baited traps (*W. obesa*) in December 2004 from Admiralty Bay (King George Island, South Shetlands, Antarctica). They were maintained in well-aerated tanks at a temperature of 0.0°C and water salinity of 34.2–34.5 psu. *O. validus*, *Lysasterias* sp., *W. obesa* and *P. corrugatus* were fed *Notothenia* sp. muscle to minimize differences in their feeding status and then starved (30 days for sea stars, 14 days for *W. obesa* and *P. corrugatus*). Experiments on *N. concinna* were carried out 24 h after their collection. No individual was tested more than once in 3 days and no animal was used for the same test stimulus more than once. Each variant of the experiment was replicated 20 times, except *P. corrugatus* (only three specimens of this species were collected). Pure ambient seawater was used as control. Blood stimulus was prepared by mixing fish blood with seawater in the proportion of 1:3. After each repetition of the experiment, the aquariums were thoroughly and repeatedly rinsed with pure seawater to avoid contamination by blood from the previous tests.

Specimen of *O. validus* ($R = 3.3$–3.6 cm) and *Lysasterias* sp. ($R = 7.3$–8.5 cm) were placed individually in 2-l tanks with static water, and left there for 1 h to allow them to recover from handling stress. After that time, the animals were found immobile on the tank wall, with one or more arms extended parallel to the air–water interface. No tube foot waving was observed in undisturbed individuals prior to the tests. The behavioral response of both *O. validus* and *Lysasterias* sp. was measured by releasing 1 ml of potential stimulus from a syringe kept about 3 cm from the tip of the sea star arm. Animals were then observed for 20 min and their response was recorded. Behavioral responses were

Table 1 Contents of the chosen components of *N. corriceps* blood serum (mean ± SD)

Blood components (mg dl^{-1})	Fish 1 (female, 1,040 g w.w.)	Fish 2 (female, 1,440 g w.w.)
Protein	94.21 ± 5.11	58.82 ± 4.11
Glucose	138.52 ± 32.82	130.78 ± 4.97
Tiacyloglicerols	999.18 ± 68.67	1,056.23 ± 70.98
Total cholesterol	316.21 ± 21.12	224.09 ± 15.48
HDL-cholesterol	177.28 ± 21.42	203.35 ± 16.04

w.w. wet weight

divided into four types: I, tube foot waving; II, arm(s) movement; III, locomotion; IV, stomach bulging/eversion.

The limpets, *N. concinna*, were divided into two groups, smaller than 10 mm (mean = 8.3, SD = 1.3 mm) and larger than 10 mm (mean = 35.3, SD = 4.2 mm). Behavioral observations were carried out on individual limpets placed in separate small aquaria (ca. 1.5 l). Animals were left there for 15 min, allowing them to reaffix themselves. After this time, the limpets were exposed to potential stimuli released from a syringe placed ca. 1 cm in front of the animal. Limpet behavior was monitored for 5 min and their behavioral responses were observed. Behavioral responses were divided into 4 types: I, pallial tentacles waving; II, turning around; III, sticking head outside the blood plume; IV, moving outside the blood plume.

Amphipods *W. obesa* (body length 10 mm) were placed individually in 1.0 l tanks (14 × 12 cm) with static water and left there for 10 min to allow them to recover from handling stress. After that time, animals were found swimming freely (60% of tested individuals) or sitting immobile (40% of tested individuals) on the aquarium bottom. Two crossing lines were drawn on the tank bottom dividing it into four equal zones (quadrants) (Fig. 1). Amphipod behavioral response was measured by slowly releasing one drop of potential stimulus from a syringe, slightly immersed in seawater, into one of the four zones of the aquarium. Animals were then filmed for 5 min with a digital video camera and the time spent in each zone was subsequently measured.

Nemerteans *P. corrugatus* (relaxed body length 50–60 cm) were placed individually in 20-l tanks with static water and left there for 1 h to allow them to recover from handling stress. Their behavioral response to fish blood was measured by releasing 1 ml of potential stimulus from a syringe kept about 3 cm from the anterior part of the animal's body. Nemerteans were then observed for 10 min. Changes in their behavior (head and proboscis movements), and time spent in the zone where fish blood was released, were noted.

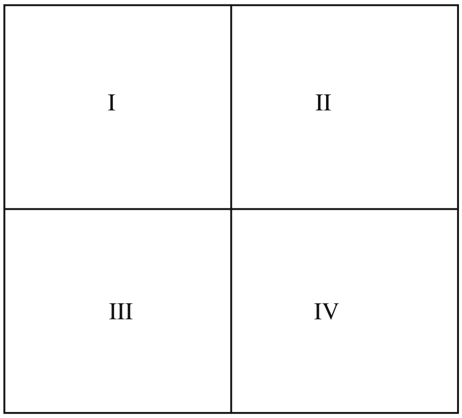

Fig. 1 Experimental design used in the observations of *W. obesa* reaction to blood stimuli with the aquarium bottom divided into four parts: I, II, III and IV

Sea stars *O. validus* and *Lysasterias* sp., and amphipod *W. obesa*, were tested with the blood of fish 1; the other species with the blood of fish 2.

Data analysis was performed using the statistical package Statistica 5.5 (StatSoft, Inc.). Differences in the lengths of time spent by amphipods in different zones of the aquarium were compared using ANOVA and RIR Tukey test after first checking that data distribution was normal. Differences in the mean number of reaction types displayed simultaneously by sea stars *O. validus* were compared using Student's *t* test after first checking that data distribution was normal.

Results

O. validus and *Lysasterias* sp. showed no behavioral response to pure seawater, but both species reacted positively to fish blood (Table 2). The reaction of *O. validus* consisted of tube foot waving, arms movements, locomotion, and stomach eversion. Animals displaying locomotion moved towards the stimulus source. As much as 60% of sea stars displayed all four types of reactions simultaneously. Mean number of reaction types displayed simultaneously by *O. validus* was 3.3 (SD = 0.47) (Table 2). No stomach eversions were observed in *Lysasterias* sp. exposed to fish blood. Sea stars belonging to this species reacted by tube foot waving, arm movements and locomotion. Animals displaying locomotion moved towards the stimulus source. Mean number of reaction types displayed simultaneously was significantly lower (Student's *t* test, $P < 0.001$) than in *O. validus*. As much as 40% of sea stars displayed all three types of reactions simultaneously.

The amphipods *W. obesa* reacted to pure seawater released slowly from the syringe by swimming through all zones of the aquarium (Table 3). No significant differences were found between times spent by amphipods in different zones of the aquarium after the seawater treatment (ANOVA, $F_{(N=76,3)} = 0.385$, $P = 0.763$). Fish blood also caused swimming activity in amphipods, but animals spent most of the time near the place where the blood was released (239.4 s) in comparison to 20.1 s spent in any other zone. Significant differences were found between times spent by amphipods in different zones of the aquarium (ANOVA, $F_{(N=76,3)} = 1{,}489.97$, $P < 0.001$). Statistically significant differences were observed between time spent by amphipods in the zone where fish blood was released and other zones (Tukey HSD test, $P < 0.05$).

As only three specimens of *P. corrugatus* were tested, the results cannot be treated as conclusive. No reaction to pure seawater was observed, but all specimens reacted strongly to fish blood released slowly near their anterior end. Same

Table 2 Behavioral responses of sea stars *O. validus* and *Lysasterias* sp. to fish blood

Sea star species	Stimulus type	Animals tested	Positive responses (%)				Negative responses (%)	No. of reaction types/animal	
			I	II	III	IV		Mean	SD
O. validus	Control	20	0	0	0	0	100	–	–
	Blood	20	100	100	50	70	0	3.3	0.47
Lysasterias sp.	Control	20	0	0	0	0	100	–	–
	Blood	20	100	100	40	0	0	2.4	0.50

Positive behavioral responses are divided into types: I, tube foot waving; II, arm(s) movement; III, locomotion; IV, stomach bulging or eversion

Control: pure seawater

Table 3 The impact of fish blood on time(s) spent by *W. obesa* in each of the four zones of the experimental aquarium

Stimulus type	Animals tested	Zone I		Zone II		Zone III		Zone IV	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
Seawater	20	70.0	33.8	78.4	34.4	72.4	26.1	79.2	34.8
Blood	20	239.4	20.9	21.5	9.8	19.7	7.8	19.1	7.1

Control experiment: pure seawater released in zone I; blood experiment: fish blood released in zone I

behaviors were observed in all the three individuals (extended proboscis, lifting of the anterior part of the body, oscillating movements of the proboscis and anterior part of the body). Animals moved slowly about, but only within the borders of blood plume. In one instance, a small blood clot was found and ingested by one of the nemerteans.

The limpet *N. concinna* showed virtually no behavioral reaction to pure seawater, and sat immobile on the aquarium bottom with pallial tentacles extended outside their shells (Table 4). None of the individuals larger than 10 mm responded to the blood stimuli. All limpets from this group stayed without any movement in the same place. Most (95%) of the individuals from the group smaller than 10 mm displayed active behavioral reaction to the blood stimuli. After 20 s (mean, SD = 5.2 s), limpets started to wave pallial tentacles, turned around, took up position with their heads outside the blood plume and moved away from the plume with a speed of 2–7 mm/10 s (80%), which was their normal walking speed during the feeding. Distance covered by the limpets' move was 3–5 cm.

Discussion

All necrophagous macroinvertebrates showed strong behavioral reactions to blood stimulus. Such responses were previously observed in other species belonging to different taxa. Blood sera and mucus from a range of teleost fishes were found to be effective attractants for the theronts of the parasitic ciliate *Ichthyophthirius multifiliis* (Buchmann and Nielsen 1999). Gurin and Carr (1971) observed that the marine snails *Nassarius obsoletus*, a deposit feeder and a facultative carrion feeder, reacted strongly by extending their proboscises not only to a variety of substances arising from dead animals but also to human plasma and serum. Authors speculate that blood proteins, especially albumins and globulins. may be biologically active in attracting predators and scavengers. Proteins have also been previously shown to attract crustaceans, molluscs and echinoderms (Carr et al. 1974; Rittschof et al. 1984; Carr 1988). Glucose was also established to be an important attractant to such diverse species

Table 4 Behavioral responses of limpet *N. concinna* to fish blood

Animal size	Stimulus type	Animals tested	Positive responses (%)				Negative responses (%)
			I	II	III	IV	
Large	Seawater	20	0	0	0	0	100
	Blood	20	0	0	0	0	100
Small	Seawater	20	0	0	0	0	100
	Blood	20	95	95	30	65	5

Positive behavioral responses are divided into types: I, waving pallial tentacles; II, turning around; III, sticking head outside the blood plume; IV, moving outside the blood plume

Control, pure seawater; small size, limpets with shell length shorter than 10 mm; large size, limpets with shells length longer than 10 mm as Antarctic sea urchin *Sterechinus neumayeri* (Janecki 1999), gastropod *Lymnea acuminata* (Tiwari and Singh 2004) or crabs *Petrolisthes cinctipes* (Hartman and Hartmann 1977) and *Uca longisignalis* (Weissburg and Zimmer-Faust 1991). Therefore, it can be assumed that the same chemical compounds (proteins, glucose) found in *Notothenia* blood were also used as attractants by Antarctic scavenging invertebrates, although further studies are needed to determine the impact of respective blood constituents on the scavenger's behavior.

Terrestrial animals also respond to the smell of blood. Brown treesnakes (*Boiga irregularis*) reacted with tongue flicks to mammalian blood and blood serum (from rabbits, rats, and mice) (Chiszar et al. 2001). Dry bovine blood was an olfactory attractant for the screwworm fly *Cochliomyia hominivorax* (Hammack et al. 1989) and the antennae and maxillary palps of the fleshfly, *Neobellieria bullata*, were shown to be sensitive to a mixed cow and pig blood extract (Wasserman and Itagaki 2003).

It was also observed that hermit crabs with too small or badly fitting shells, readily responded to odours, signaling potential shell availability, originating from dying gastropods or dying hermit crabs—chemical cues from hermit crabs were found in their hemolymph (Rittschof et al. 1992, 1995; Thacker 1994).

Blood odour may also perform the function of an alarm signal for some animals. It has been demonstrated that rats avoided the odour of blood from other rats (Mackay-Sim and Laing 1981). Changes in behavior were also observed in cattle exposed to the smell of blood from their conspecifics (Terlow et al. 1998). Many aquatic invertebrate species were observed to display alarm or flight in response to chemical cues emanating from dead or injured conspecifics. Echinoderms such as *Asterias rubens, Psammechinus miliaris* and *Echinus esculentus* moved away from homogenates of conspecific interior tissues (Cambpell et al. 2001). Aquatic flatworms, *Dugesia dorotocephala*, used chemical signals fron injured conspecifics to evaluate predation risk (Wisenden and Millard 2001). Chemical compounds released from crushed conspecifics inhibited feeding in pebble crabs *Philyra laevis* (McKillup and McKillup 1992), gastropods *Nassarius siquijorensis* (Morton and Chan 1999), and hard clams *Mercenaria mercenaria* (Smee and Weissburg 2006).

The presence of blood (or hemolymph) components in the environment is a signal informing nearby organisms about the predation event or its consequences (e.g., remains of a predator's meal or an injured animal susceptible to further attacks). Such knowledge may be important especially for necrophagous and kleptoparasitic species whose food supply is partially dependent on successful predators. Their ability to exploit such events can be discerned from the observations of amphipod swarms attacking slightly injured Antarctic fish that were immobilised in fishing nests (Kidawa, personal observations).

The difference in the reaction of small and large limpets observed in our experiments was typical for many other invertebrate species with small and/or young individuals distancing themselves from the immediate vicinity of a predation event (e.g., Vadas et al. 1994; Wahle 1992; Sparrevik and Leonardsson 1995). Such data show that small individuals, being less mobile and more susceptible to predation, show distinct differences in the way they interact with their environment and react to chemical signals. Small limpets' sensitivity to blood components enables them to avoid sea stars congregating on bloody remains.

Chemical cues, released from dead or injured prey, are dispersed in the marine environment by water currents, and are diluted proportionally to the distance from their source. Many marine organisms can detect chemical compounds even at low concentrations from 10^{-8} to 10^{-10} g l^{-1} (e.g. Zimmer-Faust and Case 1983; Rebach et al. 1990), but their response depends strongly on stimulus concentration, with its rise causing an increase in both the percentage of reacting individuals and the strength of their reaction (e.g. Zimmer-Faust and Case 1983; McClintock et al. 1984; Kidawa 2005b). Signal concentration can be used by organisms as an information about both the distance to the food item and its size (Sainte-Marie and Hargrave 1987). Intense chemical cues can be used in the laboratory to elicit a maximum reaction from the tested individuals, although further studies are needed to observe the whole range of possible behavioral changes. In natural conditions, even slow moving organisms (whelks *Buccinum undatum*) can travel long distances following cues transported by water currents (Himmelman 1988; Lapointe and Sainte-Marie 1992). Field observations in the Antarctic showed that scavenging species (sea star *O. validus*, gastropod *Neobuccinum eatoni* and nemertean *P. corrugatus*) reached the bait only after 3 days, implicating their ability to cover long distances in reaction to probably much diluted signals (Zamorano et al. 1986).

Notothenioid fish are preyed upon by almost all Antarctic top predators such as south pole skuas, Antarctic petrels, Adélie and emperor penguins, Weddell seals and minke, and killer whales (La Mesa et al. 2004). We did not find data in the literature on the rate of predation success, although there are reports showing that Weddell seals discard prey remains (skin and tail of Antarctic cod *Dissostichus mawsoni*) on the sea bottom (Slattery and Oliver 1986). Data on predatory success in double-crested cormorants (*Phalacrocorax auritus*) from British Columbia (Canada) showed that approximately half of the prey pursuits initiated by cormorants did not lead to prey capture, although with small prey items (24–92 g), less than 1% of pursued fish were injured without being ingested (Grémillet et al. 2006). This study also indicates that rate of prey loss (and potential injury) increases with fish size, leaving more injured prey for secondary predators and necrophagous species.

Other predatory events, such as leopard seals catching penguins or seals, may also leave prey remains or severely injured prey in its aftermath. Penney and Lowry (1967) observed that leopard seals can effectively catch a penguin only by using stealth: a wait and rush tactic. They kill the bird by grabbing its feet, shaking it vigorously and beating its body against the surface of the water repeatedly until the penguin is dead and skinned. It may be assumed that such a way of killing leaves a considerable amount of blood in the water but also a lot of small pieces of prey body sinking to the bottom. All three necrophagous species examined in our study are known to react strongly to chemical signals. *O. validus* was previously shown to use chemical cues to locate food source (Kidawa 2005a), and to react to chemical signals produced by its conspecifics (Kidawa 2001). Amphipod *W. obesa* was found to respond to several amino acids by a strong increase in its metabolic rate (Janecki and Rakusa-Suszczewski 2005). Such an increase was noticed earlier in animals belonging to different species (e.g., Smith and Baldwin 1982; Shumway et al. 1993; Kidawa 2005a, b), and is part of a strategy that enables animals to survive under low and unpredictable food conditions, with rapid increase in metabolic rate in response to a chemical signal being a preparation for the increased locomotory activity needed for food finding (Smith and Baldwin 1982). *P. corrugatus* was also observed to forage using chemoreception (Dayton, unpublished, in McDermott and Roe 1985). All three species were caught in baited traps (Presler 1986) and were obseved forming feeding aggregations (Dayton et al. 1974; Zamorano et al. 1986; Markowska personal observation). The ability to detect blood components and use them as a source of information in detecting food sources has a clear adaptive value for Antarctic marine scavengers, enabling them to widen their food spectrum and increasing their chances of survival.

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