RESEARCH ARTICLE

Lars Gutow · Julia Strahl · Christian Wiencke
Heinz-Dieter Franke · Reinhard Saborowski

Behavioural and metabolic adaptations of marine isopods to the rafting life style

Abstract Rafting on floating objects is a common dispersal mechanism for many marine invertebrates. In order to identify adaptations to the rafting life style, we compared behavioural and metabolic characteristics of two isopods, the obligate rafter *Idotea metallica* and the facultative rafter *Idotea baltica*. In laboratory experiments, *I. metallica* showed low locomotive activity and a tight association to the substratum. *Idotea baltica*, in contrast, was more active with more frequent excursions in the surrounding water column. Oxygen consumption rates were similar in both species. *Idotea metallica* fed on zooplankton making this species widely independent of autochthonous food resources of the raft. Feeding rates and digestive enzyme activities were low in *I. metallica*. Reduced egestion rates may indicate slow gut passage and, thus, efficient resorption of nutrients. Efficient food utilization and the ability to accumulate high amounts of storage products, i.e. lipids, indicate a possible adaptation of *I. metallica* to low food availability or starvation. The feeding behaviour of *I. baltica*, in contrast, was more herbivorous and appeared wasteful and inefficient. Low lipid contents in *I. baltica* also indicate poor storage reserves. Thus, *I. baltica* requires a permanent access to food.

L. Gutow (✉) · J. Strahl · C. Wiencke
Alfred Wegener Institute for Polar and Marine Research,
P.O. Box 12 01 61, 27515 Bremerhaven, Germany
E-mail: lgutow@awi-bremerhaven.de
Tel.: +49-471-48311708
Fax: +49-471-48311724

J. Strahl
Department of Marine Zoology, University of Bremen,
P.O. Box 33 04 40, 28334 Bremen, Germany

H.-D. Franke · R. Saborowski
Alfred Wegener Institute for Polar and Marine Research,
Biologische Anstalt Helgoland, P.O. Box 180,
27483 Helgoland, Germany

Introduction

Seven isopod species of the genus *Idotea* form resident populations around the island of Helgoland (German Bight, North Sea; Franke et al. 1999). They are distributed benthically along the coast from the supratidal down to subtidal habitats (Naylor 1972). The distribution of *Idotea baltica* and *Idotea emarginata* is primarily the result of interspecific competition and subsequent habitat segregation (Franke and Janke 1998). Although they prefer benthic habitats, all species also raft on floating objects at the sea surface; most of them, however, only sporadically. Only *I. baltica* is abundant on floating macroalgae in the German Bight, especially on brown algae of the order Fucales, with average numbers of about 90 adult animals per kg seaweed (Franke et al. 1999). Since 1994 another species, *I. metallica*, has occurred regularly in small numbers on floating objects in the North Sea. Gutow and Franke (2001) showed that *I. metallica* is only a summer resident. Populations go extinct in winter because temperatures are too low for reproduction. Nevertheless, due to repeated annual re-introduction, *I. metallica* has become a regular member of the isopod community of the German Bight.

Idotea metallica lives exclusively on often abiotic floating objects (Moreira 1972; Tully and Ó Ceídigh 1986) on which they can be transported passively over long distances by surface currents (van der Baan and Holthuis 1969). Benthic populations of *I. metallica* are not known even though the species is reported from coastal waters in many parts of the world (Miller 1968; Hartmann 1976; Sano et al. 2003; Abelló et al. 2004), probably as a consequence of inferiority in interspecific competition with benthic species (Gutow and Franke 2003). Apparently, rafting is a specific and evolutionarily developed life style of *I. metallica*. Living close to the surface requires tolerance against changing physical and chemical conditions such as temperature and salinity or intensive UV-radiation (e.g. Cheng 1975; Herring 1969).

In contrast to *I. metallica*, the predominantly benthic *I. baltica* is found rafting almost exclusively in coastal waters. Abundances are usually low offshore (Morris and Mogelberg 1973) indicating a poor ability for long distance rafting. *Idotea baltica* is almost entirely lacking on abiotic rafts which provide only little plant food (Gutow and Franke 2003).

In order to identify specific adaptations to the rafting life style, we compared in laboratory experiments behavioural and physiological characteristics in terms of locomotive activity and respiration rates as well as the nutritive demands of the obligate rafter *I. metallica* and the facultative rafter *I. baltica*. We hypothesize that *I. metallica* has evolved strategies that allow the species to persist under conditions of limited food availability in oligotrophic open oceans.

Material and methods

Animals

In order to avoid metabolic variation due to the reproductive state, all experiments were carried out with adult males rather than females. Isopods of the species *I. metallica* and *I. baltica* were obtained from mass cultures which were run routinely at the Marine Station Helgoland. Wet weight (WW) of the animals ranged from 130 to 230 mg for *I. metallica* and from 100 to 300 mg for *I. baltica*. During the experiments, the animals were exposed to a constant temperature of 16°C and a light–dark cycle of 16:8 h (06:00–22:00 local time).

Activity

Two aquaria (28 cm high, 35.5 cm wide, 19 cm deep) were equipped with a 2 cm sediment layer of fine sand and were filled with 10 l of seawater. Each aquarium was furnished with two fragments (10 g each) of the brown alga *Fucus vesiculosus* which served as both a substratum for the isopods to cling to and as food. Algal fragments were fixed in the aquaria with a thin cotton string to a tripod above the aquaria but were allowed to float on the water surface. The distance between both algal pieces was about 20 cm. Two-day-old *Artemia* nauplii were offered as additional food.

One aquarium was equipped with ten individuals of *I. metallica* and the other with ten *I. baltica*. After 24 h of acclimation, the behaviour of the isopods was monitored three times per day at 11:00, 14:00 and 19:30 local time. Randomly selected animals were observed for 10 s. Their locomotive activity was recorded and classified as "low", "medium" and "high" (see below). In total, 40 observations (10 s each) were done per species and monitoring period. Consequently, on average, each animal was recorded four times during each monitoring period. Five replicates with ten individuals each were performed for each species within 1 week. The total number of observations was 600 per species. After each experimental period, all individuals were returned to the mass culture.

Low activity: Sitting calmly on the substratum (sediment or algae), grooming antennae and pleopods, feeding algae, catching and feeding on *Artemia* nauplii (catch posture). Social contact: touch without movement

Medium activity: Slow movement (striding) on substratum (sediment or algae), turning/spinning around the body. Social contact: touch with movement

High activity: Swimming horizontally or vertically through the water, fast movement (running) on substratum (sediment or algae). Social contact: casing, scuffle, cannibalism

Respiration

Oxygen consumption rates were determined in a closed system by the Winkler method (Grasshoff 1983). Prior to the experiments, individuals of both species were kept separately for defecation in glass vials (40 ml) for 12 h without food. Seawater was filtered (0.2 μm), allowed to adjust overnight to the experimental temperature of 16°C, and then filled into eight incubation bottles (0.57–0.61 l). Six of these bottles contained 1 isopod (3×1 *I. metallica* and 3×1 *I. baltica*) and a piece of gauze each. Two bottles served as controls. Animals were incubated for 4–5 h at 16°C before subsamples of the water were transferred into Winkler flasks (50–60 ml) and fixed for the quantification of dissolved oxygen. The isopods were carefully blotted on filter paper and weighed (WW). The experiment was repeated four times resulting in a total number of 12 individuals per species. These experiments were conducted in the morning as well as in the afternoon.

Food ingestion and egestion

The animals were acclimated to the experimental conditions for 1 week. For acclimation, individual isopods were maintained individually in glass vials (40 ml) and were fed with pieces of *F. vesiculosus* and *Artemia* nauplii in excess. The seawater was changed daily.

For experiments, 26 isopods of each species were fed individually with weighed pieces of *F. vesiculosus* and 200 *Artemia* nauplii. After 24 h, the isopods were removed and WW of the animals was recorded. The remaining *Fucus* fragments were weighed and remaining *Artemia* nauplii were counted.

Faecal pellets of the animals were collected immediately after the experiments, transferred into reaction cups and centrifuged for 15 min at 13,000 g and 4°C. Supernatants were removed and the pellets were weighed and lyophilised. Dry weight (DW) was measured for

food items *F. vesiculosus* and *Artemia* nauplii as well as for the faeces.

Biochemical investigations

Digestive enzymes and total lipids were measured in aqueous extracts of individual adult males. Animals were lyophilised and then ground to a homogeneous fine powder. Sub-samples were suspended in *Aqua dem.* and homogenized by ultrasonication (Branson Sonifier Cell Disruptor B15).

Total protease activity was determined with azocasein as substrate. Samples (20 μl) were incubated in reaction tubes with 200 μl of 0.1 M Tris/HCl-buffer for 5 min at 30°C. The reaction was initiated with 50 μl of azocasein solution (1% w/v in buffer) and incubated for another 30 min at 30°C under permanent shaking. The reaction was terminated with 500 μl of an aqueous solution of trichloroacetic acid (TCA, 8%) and cooling on ice. The cups were centrifuged for 15 min at 15,000 g and 4°C. The absorbance of the supernatant was read at 366 nm. Tests and controls were run in triplicate. Controls received the samples after the addition of TCA. The activity was normalized to 1 g of DW (ΔE_{366} min^{-1} g$_{DW}^{-1}$).

Amylase activity was measured with a commercial assay (Sigma Diagnostics 580). Fifty microlitre of animal extracts was added to 1 ml of substrate solution and incubated at 30°C in a temperature-controlled cuvette holder. The increase of absorbance was continuously recorded for 3 min. The activity was expressed as U g$_{DW}^{-1}$ ($=\mu$mol min^{-1} g$_{DW}^{-1}$). Six individuals of each species were analyzed.

The total amount of lipids in *I. metallica* and *I. baltica* were determined with the sulphophosphovanillin method after Zöllner and Kirsch (1962) using a commercial test kit (Merck, Merckotest 3321). The procedure was modified after Saborowski and Buchholz (1996) to be performed on microplates. Powder from freeze-dried isopods was first crudely homogenized in 2 ml of water with an Ultraturrax and subsequently sonicated with an ultrasonic cell disrupter (Branson Sonifier B15). Aliquots of 40 μl were transferred into 1.5 ml chloroform:methanol (2 + 1) and vortexed for 50 min at 25°C. Thereafter, cups were centrifuged at 4°C and 15,000 g for 15 min. The supernatants (1.3 ml) were transferred into fresh cups and the organic solvent was evaporated at 45°C within 1 h (Eppendorf concentrator 5301). Sulphuric acid (500 μl) was added to the remaining lipids and the samples were boiled for at least 10 min. Standards of cholesterol (0–150 μg) were treated in the same way. After cooling, 20 μl of the samples were transferred in triplicate onto each of two microplates. Samples on the first microplate received 350 μl of phosphoric acid and served as a blank. The second plate received 350 μl of sulphuric acid/vanillin (Merckotest 3321). After 40 min, both plates were read in a microplate reader at 530 nm (Dynatech, MR 7000). The sample plate was corrected for blank values.

Statistics

The distribution of the behaviour of the animals on different activity levels was analyzed with a χ^2-text. A *t* test was applied for comparing two normally distributed data sets (respiration rates, egestion rates and egestion:ingestion ratio, enzyme activities). If normal distribution failed, a Mann–Whitney *U* test was applied instead (lipids). Linear regression lines of ln(rate + 1) transformed data were analyzed for similarity of slopes and intercepts with an ANCOVA (ingestion rates). Slopes of linear regressions were tested for deviation from zero with an *F* test (respiration vs. body mass, egestion rates vs. body mass).

Results

Locomotive activity

Idotea metallica and *I. baltica* had significantly different activity patterns (χ^2-test: $P < 0.001$). *Idotea metallica* showed low locomotive activity for about 85%, medium activity for 10% and high activity for 5% of the observation period (Fig. 1). *Idotea baltica* showed low activity for 60%, medium activity for 25% and high activity for about 15% of the time.

Respiration

No statistically significant differences were detected between oxygen consumption rates from different daytimes (*t* test: $P > 0.05$) indicating no diurnal activity patterns under laboratory conditions. Consequently, respiration rates measured in the morning and in the afternoon were pooled for interspecific comparison.

In both species, respiration rates did not correlate with body mass. Average respiration rates were
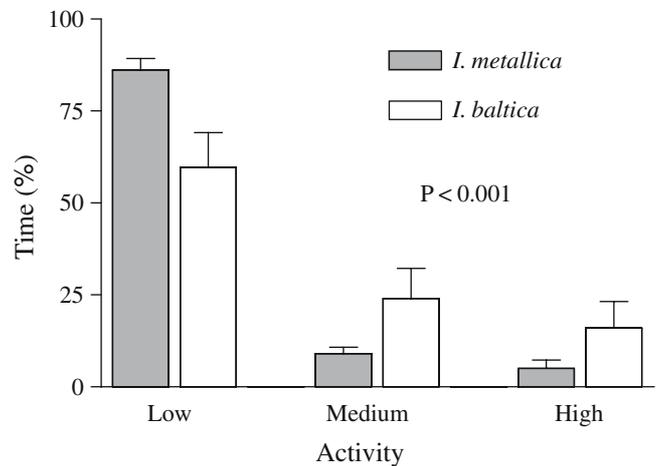

Fig. 1 Activity profiles of *I. metallica* and *I. baltica* ($n = 600$ observations per species; means $\pm$ SD)

0.23 ± 0.08 mg O_2 g_{WW}^{-1} h^{-1} for *I. metallica* and 0.20 ± 0.08 mg O_2 g_{WW}^{-1} h^{-1} for *I. baltica* (Fig. 2). The difference between both species was not significant (*t* test: $P > 0.05$).

Food ingestion and egestion

The relationship between body mass and ingestion rates was best described by a negative exponential regression model (Fig. 3, Table 1).

The overall weight-specific ingestion rates were on average 2.5 times higher in *I. baltica* than in *I. metallica* ($P < 0.0001$). Both species ingested more *F. vesiculosus* (Fig. 3a) than *Artemia* nauplii (Fig. 3b; $P < 0.0001$). However, *I. metallica* ingested on average five times more algae than *Artemia* nauplii while *I. baltica* ingested 80 times more algae than *Artemia* nauplii. Ingestion of *Artemia* nauplii was higher in *I. metallica* than in *I. baltica* ($P < 0.0001$) while this was reverse for ingestion of *F. vesiculosus* ($P < 0.0001$).

In both species, the egestion rate was independent of the body mass (i.e. slope of linear regression did not significantly deviate from 0, *F* test: $P > 0.05$). The average egestion rate was about eight times higher in *I. baltica* (21.3 ± 12.5 mg_{DW} g_{WW}^{-1} d^{-1}) than in *I. metallica* (2.7 ± 1.7 mg_{DW} g_{WW}^{-1} d^{-1}) (Fig. 4). The difference was statistically significant (*t* test: $P < 0.0001$).

Digestive enzymes and lipids

Total proteolytic activity amounted to 3.5 ± 1.6 ΔE min^{-1} g_{DW}^{-1} in *I. metallica* (Fig. 5a). *Idotea baltica* showed significantly higher total proteinase activity (7.4 ± 3.9 ΔE min^{-1} g_{DW}^{-1}, *t* test: $P < 0.0001$). Amylase activity was 1.5 ± 0.7 U g_{DW}^{-1} in *I. metallica* and 7.9 ± 4.9 U g_{DW}^{-1} in *I. baltica* (Fig. 5b). Again, average activity was significantly higher in *I. baltica* than in *I. metallica* (*t* test: $P < 0.0001$).

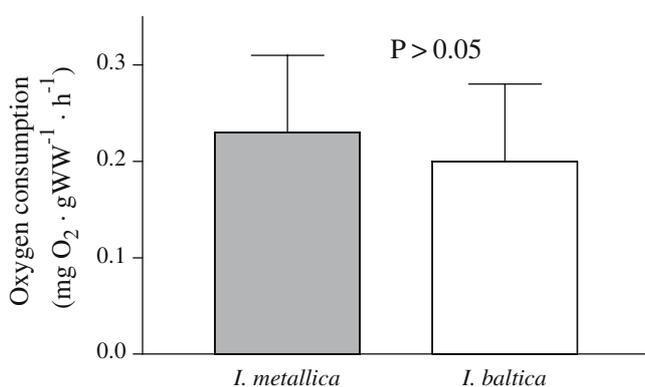Both species differed significantly (Mann–Whitney *U* test: $P = 0.003$) in the total lipid content (Fig. 6). While

total lipid content in *I. metallica* amounted to $15.9 \pm 5.6\%$ DW, that in *I. baltica* was $9.8 \pm 1.5\%$ DW.

Discussion

Both isopod species *I. metallica* and *I. baltica* have repeatedly been collected from objects floating on the sea surface (Thiel and Gutow 2005a). *Idotea metallica* is an obligate rafter. The species is often found on abiotic floating objects far offshore (Aliani and Molcard 2003) but also on biotic objects such as macroalgae and wood (Gutow and Franke 2003) which served as natural substrata before the widespread occurrence of man-made debris in the world's oceans. *Idotea baltica*, in contrast, is a facultative rafter that is largely restricted to coastal waters where it rafts preferably on detached macroalgae (Ingólfsson 1995, 2000). Our results revealed behavioural and physiological characteristics of *I. metallica* and *I. baltica* that help to identify specific adaptations to the rafting life style.
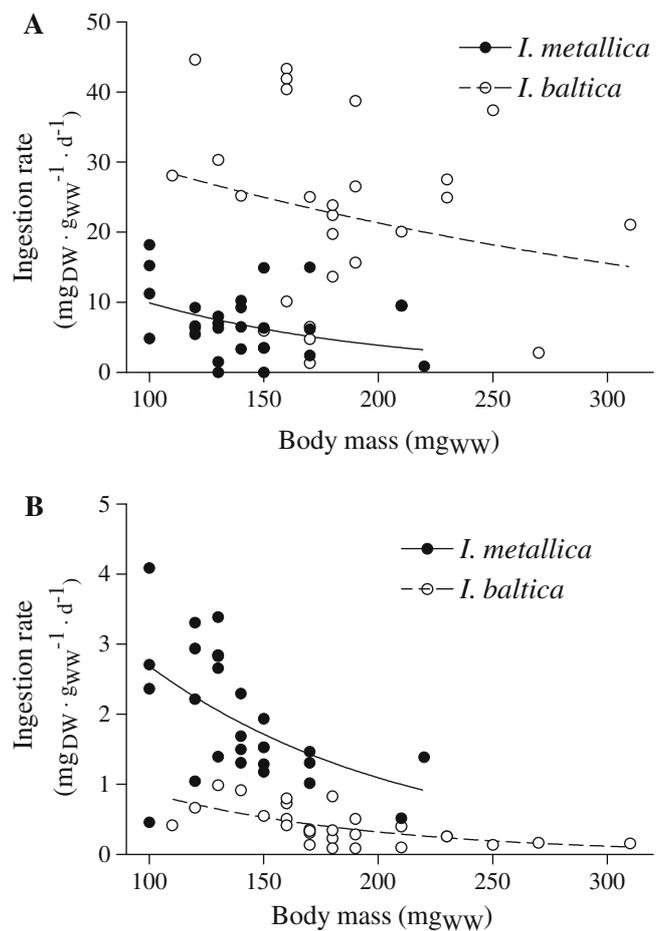
Fig. 2 Oxygen consumption rates of *I. metallica* and *I. baltica* ($n = 12$ per species, means $\pm$ SD)

Fig. 3 Ingestion rates of *I. metallica* and *I. baltica* for (**a**) *Fucus vesiculosus* and (**b**) *Artemia* nauplii ($n = 26$ per species)

Table 1 Equations and R^2 values of non-linear regressions of weight-specific ingestion rates presented in Fig. 3

Food	Species	Equation	R^2
Fucus vesculosus	*I. metallica*	$f(x) = 25.44 \times e^{(-0.009x)}$	0.102
	I. baltica	$f(x) = 40.17 \times e^{(-0.003x)}$	0.046
Artemia nauplii	*I. metallica*	$f(x) = 6.61 \times e^{(-0.009x)}$	0.274
	I. baltica	$f(x) = 2.38 \times e^{(-0.010x)}$	0.383

Behaviour

Idotea metallica showed low swimming activity remaining close to the substratum. For about 90% of the observed time, the animals were sitting on their substratum and feeding. *Idotea baltica*, in contrast, showed higher activity with more frequent movements on the substratum, sediment and algae, and within the water column.

Idotea metallica occurs mainly in offshore waters where densities of floating items are usually much lower than in coastal waters (Thiel et al. 2003; Thiel and Gutow 2005b). Even though *I. metallica* is capable of active swimming, locomotive performance is poor compared to pelagic organisms such as fishes. Once separated from their raft, the animals are unlikely to successfully colonize a new floating object. Probably, leaving the raft will rapidly lead to death by exhaustion as a consequence of extended swimming in search of a substratum. However, a higher probability of colonizing a new substratum in offshore waters may be given where floating items accumulate in surface fronts of gyres or Langmuir circulations (Thiel and Gutow 2005b).

The preferred habitats of *I. baltica* are subtidal macroalgae (Hemmi and Jormalainen 2002). They provide both food and shelter from predators. *Idotea baltica* is capable of leaving this benthic habitat actively to escape from severe intra- or interspecific competition (Franke and Janke 1998). Passive dislocation appears along with macroalgae that become detached from their substratum and float to the surface. The animals can frequently migrate between floating and attached
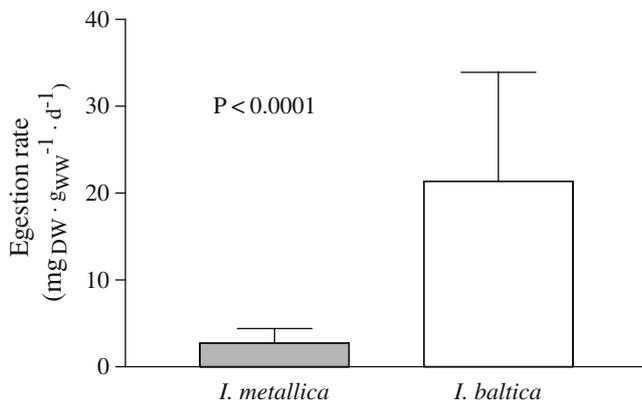
Fig. 4 Egestion rates of *I. metallica* and *I. baltica* ($n = 26$ per species, means ± SD)
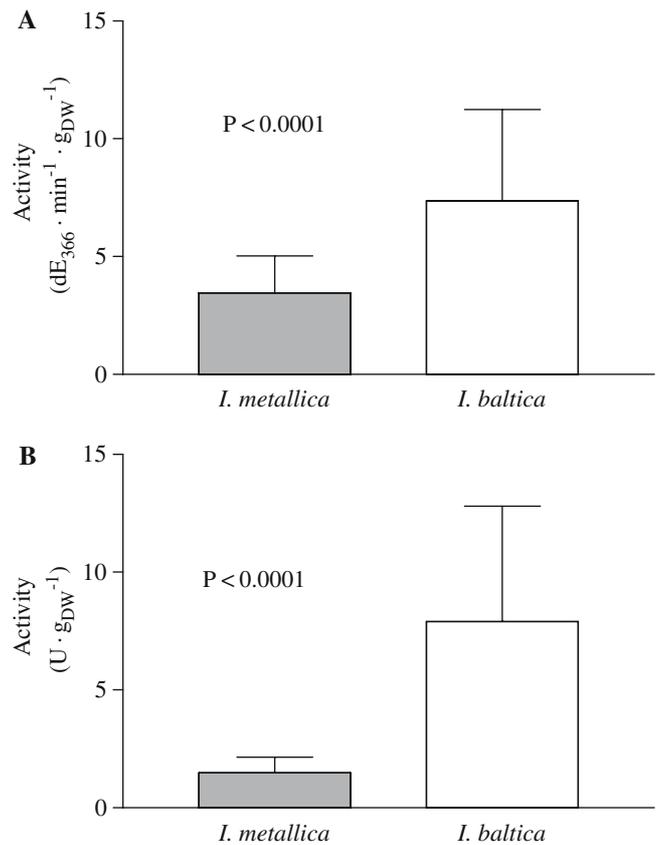
Fig. 5 Proteinase (**a**) and amylase (**b**) activity in *I. metallica* and *I. baltica* ($n = 12$ per species, means ± SD)

macroalgae in shallow coastal waters to return to the preferred subtidal habitat. Excursions in the pelagic environment are not risky when floating substrata are abundant and where shallow waters allow for easy exchange between the neuston and the benthos.

Respiration

The difference in activity level between the two species was not reflected in the oxygen consumption rates. At 16°C, both species consumed about 0.2 mg O_2 g_{WW}^{-1} h^{-1}. The results on respiration rates do not contradict the observations on the behaviour. In order to reduce the activity of the animals, each respiration chamber was equipped with a piece of gauze where the animals could cling to. Accordingly, due to the experimental design, we measured standard metabolic rates rather than activity levels.

Data on oxygen consumption rates of *Idotea* spec. published previously were measured with different methods and under various conditions in terms of experimental temperatures, shape and size of respiration chambers (Table 2). Our results for *I. baltica* are in the same range as those of Bulnheim (1974) who also equipped the respiration chambers with a piece of gauze to keep the animals calm. Respiration rates measured by
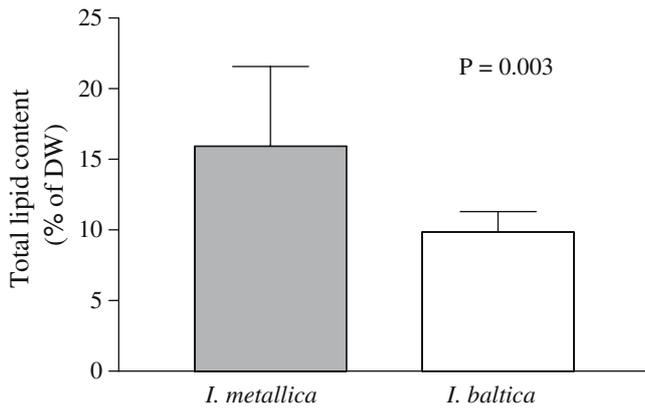
Fig. 6 Total lipid content of *I. metallica* ($n=10$) and *I. baltica* ($n=6$, means $\pm$ SD)

Vetter et al. (1999) for *I. baltica* and *I. emarginata* were exceptionally high. The authors incubated groups of seven animals in a 670 ml oxystat system. The high density of animals might have caused stress and, thus, stimulated the respiratory activity of the isopods.

Assuming an average respiratory quotient (RQ) of 0.85, the consumed oxygen equals to about 70 µg C g_{WW}^{-1} h^{-1} and to about 8.3 mg_{DW} food g_{WW}^{-1} d^{-1}. The amount of food (WW) needed per individual isopod would then amount to 11.2 mg d^{-1} in *I. metallica* and 12.3 mg d^{-1} in *I. baltica*. This calculation was done for different average sizes of either species and is based on the assumption that the average carbon value of food items amounts to 30% DW and assimilation efficiency is 66% (Strong and Daborn 1979). In the following section, these theoretical demands will be compared with the food ingestion rates obtained from our feeding experiments.

Feeding, ingestion and egestion

In our experiments, food was offered in excess and may have stimulated the feeding activity of both species. The amount of food consumed by *I. metallica* covered almost exactly the metabolic energy demands as calculated from oxygen consumption rates. In *I. baltica*, however, average food consumption was more than two times higher than needed to cover standard metabolic demands. Apparently, a significant amount of ingested food was not assimilated. *Idotea metallica* seems to treat and to utilize food more economically than *I. baltica*. In *I. metallica*, faeces amounted to about 40% of the mass of ingested food while *I. baltica* released about 90% of the ingested food, indicating a more efficient food resorption by *I. metallica* than by *I. baltica*. Accordingly, feeding of *I. baltica* appears rather sloppy and "wasteful" compared to *I. metallica*.

Both species also showed different food preferences. *Idotea metallica* fed more intensively on zooplankton (i.e. *Artemia* nauplii) than did *I. baltica*. The ability to capture and to utilize planktonic food sources makes *I. metallica* less dependent on autochthonous food resources of the raft. *Idotea baltica*, in contrast, consumed much more algal material than *I. metallica*. The present data confirm the results of Gutow (2003) who found that *I. baltica* destroys algal patches 6–14 times faster than *I. metallica*. He concluded that intensive feeding on algal rafts leads to rapid habitat destruction which is the major threat for rafting populations of *Idotea*. *Idotea baltica* lives under conditions of excessive food supply and may not face food limitation. Consequently, the feeding habits of *I. baltica* appear unsuited for long-term rafting on abiotic rafts where food supply is highly sporadic or on floating macroalgae that could be rapidly destroyed.

Digestive enzymes

To determine the potential for digestion in both species, we measured the activities of representative enzymes which hydrolyze proteins and carbohydrates. Activities of both protease and amylase were lower in *I. metallica* than in *I. baltica*. According to Jones et al. (1997) and Le

Table 2 Oxygen consumption of various *Idotea* species measured by different authors

Species	Temperature (°C)	Oxygen consumption (mg g_{DW}^{-1} h^{-1})	Reference	Comments
Idotea baltica	15	0.57	Bulnheim (1974)	
Idotea baltica	15	8.29*	Vetter et al. (1999)	Activity level measured; respiration calculated for an oxygen partial pressure of 21 kPa
Idotea baltica	16	0.90 ± 0.35*	This study	
Idotea chelipes	8	1.22–1.61	Jones (1973)	
Idotea emarginata	8	1.13–1.50	Jones (1973)	
Idotea emarginata	15	8.60**	Vetter et al. (1999)	Activity level measured; respiration calculated for an oxygen partial pressure of 21 kPa
Idotea metallica	16	1.08 ± 0.37*	This study	
Idotea neglecta	10	0.18–0.46	Fox and Simmonds (1933)	Animals anesthetized
Idotea neglecta	8	0.73–1.26	Jones (1973)	

*DW amounted to 21% of WW in *I. metallica* and 22% of WW in *I. baltica*
**For *I. emarginata*, we applied the WW to DW ratio of *I. baltica*

Vay et al. (2001), elevated proteolytic activities, represented as trypsin, appear in planktonic crustaceans and crustacean larvae feeding herbivorously. Trypsin activities were lowest in carnivorous and omnivorous species. Additionally, herbivorous feeders may have high ingestion rates and short gut retention times which result in high turnover rates (Kurmaly et al. 1989). Apparently, a similar pattern seems to apply for the *Idotea* species studied here.

Idotea metallica showed a more carnivorous feeding behaviour and ingested more then twice the amount of *Artemia* nauplii than *I. baltica*. Omnivorous and, particularly, carnivorous species can cover their demand of nitrogen and essential amino acids rapidly from the protein-rich diet. Accordingly, comparatively low proteolytic activities are sufficient to cover the metabolic needs. The efficiency of assimilation may be further improved by long gut retention times as indicated by low ingestion and low egestion rates (Boehlert and Yoklavich 1984). This strategy is more suited to carnivorous encounter feeding on less abundant but digestible and energy-rich prey (Le Vay et al. 2001).

Idotea baltica, in contrast, consumed predominantly *Fucus* algae. Algal diets, however, are poorer in nitrogen and proteins than zooplankton such as *Artemia* nauplii. Accordingly, elevated proteolytic activities are required to release sufficient proteins for covering metabolic demands. Simultaneously, feeding rates must increase to supply the digestive tract with sufficient quantities of digestible proteins. Surplus material has to be egested. Thus, high proteolytic and amylase activities and rapid food turnover may be a strategy of *I. baltica* to maximize energy assimilation in environments with abundant food of low nitrogen and protein content.

Storage products

Lipids belong to the most important organic storage products in crustaceans. High lipid levels were found in zooplankton from temperate and polar latitudes as well as from the deep sea while taxa from tropical and subtropical regions showed low lipid amounts (reviewed by Hagen and Auel 2001).

In isopods, lipids are predominantly accumulated in the midgut gland, in apidocytes, in the pericard and in the entire hemocoel (Biesiot et al. 1999). *Idotea metallica* showed higher total lipid content than did *I. baltica*. As the latter species might be affected by low food availability while rafting through open ocean waters, body lipid reserves might help *I. metallica* to better sustain periods of starvation. Although high lipid contents can be expected in animals from polar regions, adult males of *Mesidotea entomon* contained only 8% DW total lipids (Korczynski 1989). This is only about half of the lipid content of *I. metallica*, indicating that the latter species is well adapted to variable food availability and, thus, periods of starvation. Accordingly, *I. metallica* must be expected to be less affected by starvation than *I. baltica*.

Conclusions

Idotea baltica is adapted to living in shallow coastal waters where macroalgae provide food and shelter in excess. Low protein concentrations of the food and low assimilation efficiency increase food consumption rates. On algal rafts, high feeding rates cause rapid destruction of the floating substratum which, in turn, limits rafting performance. Consequently, *I. baltica* occurs only accidentally far offshore but is mainly retained in coastal waters near its apparently unlimited benthic food resources.

Idotea metallica, in contrast, has developed efficient strategies to gain, store and save energy in the open ocean where food is often limited because of oligotrophic conditions (Longhurst et al. 1995). The more pronounced feeding on protein-rich zooplankton makes *I. metallica* widely independent of the autochthonous food resources of its raft. Efficient nutrient assimilation covers the energetic demands of the animals. Periods of starvation can be compensated by metabolizing internal lipid stores. Consequently, *I. metallica* is able to colonize abiotic floating objects such as plastics (Aliani and Molcard 2003) that provide only low autochthonous food resources. These are highly durable in the marine environment and allow for the establishment of persistent local populations and, finally, successful dispersal via rafting over large oceanic distances.

References

Abelló P, Guerao G, Codina M (2004) Distribution of the neustonic isopod *Idotea metallica* in relation to shelf-slope frontal structures. J Crust Biol 24:558–566

Aliani S, Molcard A (2003) Hitch-hiking on floating marine debris: macrobenthic species in the Western Mediterranean Sea. Hydrobiologia 503:59–67

Biesiot PM, Wang SY, Perry HM, Trigg C (1999) Organic reserves in the midgut gland and fat body of the giant deep-sea isopod *Bathynomus giganteus*. J Crust Biol 19:450–458

Boehlert GW, Yoklavich MM (1984) Carbon assimilation as a function of ingestion rate in larval pacific herring, *Clupea harengus pallasi* Valenciennes. J Exp Mar Biol Ecol 79:251–262

Bulnheim H-P (1974) Respiratory metabolism of *Idotea balthica* (Crustacea, Isopoda) in relation to environmental variables, acclimation process and moulting. Helgoländer Meeresunters 26:464–480

Cheng L (1975) Marine pleuston—animals at the sea-air interface. Oceanogr Mar Biol 13:181–212

Fox HM, Simmonds BG (1933) Metabolic rates of aquatic arthropods from different salinities. J Exp Biol 10:67–78

Franke H-D, Gutow L, Janke M (1999) The recent arrival of the oceanic isopod *Idotea metallica* Bosc off Helgoland (German Bight, North Sea): an indication of a warming trend in the North Sea? Helgoländer Meeresunters 52:347–357

Franke H-D, Janke M (1998) Mechanisms and consequences of intra- and interspecific interference competition in *Idotea baltica* (Pallas) and *Idotea emarginata* (Fabricius) (Crustacea: Isopoda): a laboratory study of possible proximate causes of habitat segregation. J Exp Mar Biol Ecol 227:1–21

Grasshoff K (1983) Determination of oxygen. In: Grasshoff K, Ehrhardt M, Kremling K (eds) Methods of seawater analysis. Verlag Chemie, Weinheim, pp 61–72

Gutow L (2003) Local population persistence as a pre-condition for large-scale dispersal of *Idotea metallica* (Crustacea, Isopoda) on drifting habitat patches. Hydrobiologia 503:59–67

Gutow L, Franke H-D (2001) On the current and possible future status of the neustonic isopod *Idotea metallica* Bosc in the North Sea: a laboratory study. J Sea Res 45:37–44

Gutow L, Franke H-D (2003) Metapopulation structure of the marine isopod *Idotea metallica*, a species associated with drifting habitat patches. Helgoland Mar Res 56:259–264

Hagen W, Auel H (2001) Seasonal adaptations and the role of lipids in oceanic zooplankton. Zoology 104:313–326

Hartmann J (1976) Der Jahresgang von Neuston im Golf von Neapel. Int Rev Ges Hydrobio 61:825–840

Hemmi A, Jormalainen V (2002) Nutrient enhancement increases performance of a marine herbivore via quality of its food algae. Ecology 83:1052–1064

Herring PJ (1969) Pigmentation and carotenoid metabolism of the marine isopod *Idotea metallica*. J Mar Biol Assoc UK 49:766–779

Ingólfsson A (1995) Floating clumps of seaweed around Iceland: natural microcosms and a means of dispersal for shore fauna. Mar Biol 122:13–21

Ingólfsson A (2000) Colonization of floating seaweed by pelagic and subtidal benthic animals in southwestern Iceland. Hydrobiologia 440:181–189

Jones MB (1973) Survival and oxygen consumption in various salinities of three species of *Idotea* (Crustacea, Isopoda) from different habitats. Comp Biochem Physiol 48A:501–506

Jones DA, Kumlu M, Le Vay L, Fletcher DJ (1997) The digestive physiology of herbivorous, omnivorous and carnivorous crustacean larvae: a review. Aquaculture 155:285–295

Korczynski RE (1989) Biochemical composition of the isopod *Mesidotea entomon* (Linnaeus) from the western Arctic. Polar Biol 9:391–395

Kurmaly K, Yule AB, Jones DA (1989) An energy budget for the larvae of *Penaeus monodon* (Fabricius). Aquaculture 81:13–25

Le Vay L, Jones DA, Puello-Cruz AC, Sangha RS, Ngamphongsai C (2001) Digestion in relation to feeding strategies exhibited by crustacean larvae. Comp Biochem Physiol 128A:623–630

Longhurst A, Sathyendranath S, Platt T, Caverhill C (1995) An estimate of global primary production in the ocean from satellite radiometer data. J Plankton Res 17:1245–1271

Miller MA (1968) Isopoda and Tanaidacea from buoys in coastal waters of the continental United States, Hawaii, and the Bahamas (Crustacea). Proc US Nat Mus 125:1–53

Moreira PS (1972) Species of marine Isopoda (Crustacea, Peracarida) from Southern Brazil. Bolm Inst Oceanogr S Paulo 21:163–179

Morris BF, Mogelberg DD (1973) Identification manual to the pelagic *Sargassum* fauna. Bermuda Biol Stat Spec Publ 11:1–63

Naylor E (1972) British Marine Isopods. Linn Soc Synopsis of the British Fauna (new series) No. 3. Academic, London

Saborowski R, Buchholz F (1996) Annual changes in the nutritive state of North Sea dab. J Fish Biol 49:173–194

Sano M, Omori M, Taniguchi K (2003) Predator-prey systems of drifting seaweed communities off the Tohoku coast, northern Japan, as determined by feeding habitat analysis of phytal animals. Fish Sci 69:260–268

Strong KW, Daborn GR (1979) Growth and energy utilisation of the intertidal isopod *Idotea baltica* (Pallas) (Crustacea: Isopoda). J Exp Mar Biol Ecol 41:101–123

Thiel M, Gutow L (2005a) The ecology of rafting in the marine environment. II. The rafting organisms and community. Oceanogr Mar Biol 43:279–418

Thiel M, Gutow L (2005b) The ecology of rafting in the marine environment. I. The floating substrata. Oceanogr Mar Biol 42:181–263

Thiel M, Hinojosa I, Vasquez N, Macaya E (2003) Floating marine debris in coastal waters of the SE-Pacific (Chile). Mar Poll Bull 46:224–231

Tully O, Ó Céidigh P (1986) The ecology of *Idotea* species (Isopoda) and *Gammarus locusta* (Amphipoda) on surface driftweed in Galway Bay (West of Ireland). J Mar Biol Assoc UK 66:931–942

van der Baan SM, Holthuis LB (1969) On the occurrence of Isopoda in the surface plankton in the North Sea near the lightship "Texel". Neth J Sea Res 4:354–363

Vetter R-A, Franke H-D, Buchholz F (1999) Habitat-related differences in the responses to oxygen deficiencies in *Idotea baltica* and *Idotea emarginata* (Isopoda, Crustacea). J Exp Mar Biol Ecol 239:259–272

Zöllner N, Kirsch K (1962) Über die quantitative Bestimmung von Lipoiden (Mikromethode) mittels der vielen natürlichen Lipoiden (allen bekannten Plasmalipoiden) gemeinsamen Sulphophosphovanillin-Reaktion. Z Gesamte Exp Med 135:545–561