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The role of iceberg scours in niche separation within the Antarctic fish genus *Trematomus*

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Abstract Species of the Antarctic fish genus *Trematomus* occupy different trophic niches. It is not clear, however, whether small-scale variability in benthic community structure affects niche separation. Therefore abundance and biomass of fish were determined and stomach content and food composition were compared in areas affected by iceberg scours and unaffected areas in the Weddell Sea. *Trematomus eulepidotus*, *T. lepidorhinus* and *T. scotti* dominate undisturbed areas, whereas *T. nicolai* and especially *T. pennellii* dominate disturbed areas. Total stomach content and number of prey taxa per fish are higher in preferred than in non-preferred areas. These findings indicate that small-scale horizontal patterns caused by iceberg scours play a distinct role in *Trematomus* niche separation.

Introduction

Iceberg grounding has been reported from many Antarctic shallow-water and shelf bottoms down to several hundred metres (Barnes et al. 1984; Lien et al. 1989; Woodworth-Lynas et al. 1991; Dowdeswell et al. 1993). Type and strength of physical iceberg impact on the benthos vary (e.g. Gruzov et al. 1968; Kauffmann 1974), but it is estimated that 5% of the Antarctic shelf shows detectable iceberg scours (Gutt et al. 1999). Iceberg impact causes various degrees of damage to the benthos up to local extinction of the fauna (Dayton et al. 1974; Brey and Clarke 1993; Arntz et al. 1994; Peck et al. 1999), and disturbed bottoms are subsequently recolonised (Starmans 1997; Gutt et al. 1998). Temporal distribution of iceberg scouring and time-scales of recolonisation are still poorly understood, but seem to be an intrinsic feature of Antarctic shallow-water and shelf benthic community dynamics, leading to a spatial and temporal patchwork of benthic recovery. Hence, mobile non-benthic species exploiting benthic resources such as food or shelter may have adapted to this pattern, e.g. by specialising on certain recovery stages. This study investigates whether such adaptations are detectable in demersal and bentho-pelagic fish species of the genus *Trematomus*.

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Materials and methods

Sampling

Trematomus species were caught during the RV "Polarstern" expedition ANT XV/3 (EASIZ II, 1998) into the eastern Weddell Sea, using a 140-ft bottom trawl (GSN) and an Agassiz trawl (AGT) with 3-m mouth opening and 10-mm mesh size in the cod end. Disturbed and undisturbed bottom patches were identified by underwater video. Subsequently, eight GSN hauls were taken in undisturbed areas and two GSN hauls in disturbed areas; additionally, some stations were trawled by AGT (all hauls between 200 and 400 m water depth). Fishes caught were identified according to Gon and Heemstra (1990), counted, measured to the lower centimetre and weighed. Abundance and biomass from GSN samples were standardised to 15 min trawling time for numerical comparisons. AGT catches were used for stomach content analysis only.

Stomach content analysis

Prey organisms found in the stomachs of 296 fish (Table 1) were identified as exactly as possible, counted and weighed. In the case of fragmented animals, we used typical parts such as heads or eyes to infer the number of individuals. If taxonomic identification but neither counting nor weighing was possible, the number was set to 1 and the weight was set to 0.01 g for further statistical calculations.

The effect of fish size was removed from further analysis by standardising stomach content weights to a 50-g standard fish for each species using the following procedure:

Table 1 Fish used for stomach content analysis. Distribution of numbers among species and stations (*np* not present; *Depth* trawl on ground – start of recovery). For further information on stations, see Anonymous (1999)

Station no.	48/071	48/078	48/062	48/194	48/222	48/220
Region	Kap Norvegia (North)	Drescher Inlet	Kap Norvegia (North)	Kap Norvegia	Kap Norvegia	Kap Norvegia
Condition	Undisturbed	Undisturbed	Undisturbed	Undisturbed	Disturbed	Disturbed
Gear	GSN	GSN	AGT	AGT	GSN	GSN
Depth (m)	281–301	391–390	241–253	244–246	267–234	272–236
Time	1549–1610 hours	0654–0711 hours	1738–1746 hours	0931–0941 hours	1427–1437 hours	1057–1106 hours
Species						
Trematomus lepidorhinus	8	4	2	4	7	1
T. eulepidotus	np	27	np	np	7	3
T. pennellii	np	np	np	np	52	29
T. nicolai	np	3	np	np	25	9
T. scotti	45	51	2	16	np	1

1. A linear regression between fish weight (WF) and empty stomach weight (WES) was established:

$$WES = a + b^* WF$$

2. Subsequently, number ($NP_{j,i}$) and weight ($WP_{j,i}$) of each prey item j found in the stomach of a fish i of weight WF_i was standardised to a 50-g standard fish (SF) by:

$$NP(SF)_{j,i} = NP_{j,i}{}^*(a + b^* 50)/(a + b^* WF_i)$$

$$WP(SF)_{j,i} = WP_{j,i}{}^*(a + b^* 50)/(a + b^* WF_i)$$

The sum of all $NP(SF)_{j,i}$ and $WP(SF)_{j,i}$ is defined as standardised total prey number ($STPN_i$) and standardised total prey weight ($STPW_i$) in this study. Based on these standardised data, the main food index (MFI) of major prey taxa for each fish species was computed to compare the diet of the different species:

$$\mathrm{MFI} = \sqrt{\frac{A_I + F}{2} * A_G}$$

where A_I is numerical dominance (in % of mean STPN), F is presence (in % of all stomachs analysed), and A_G is weight dominance (in % of mean STPW). Effects of area and species on total stomach content and number of prey taxa per fish were analysed by ANOVA with subsequent Games-Howell post-hoc test on differences between means.

Results

Abundance, biomass and size of fish

In total, 689 *Trematomus* spp. of 7 species were collected by 10 GSN hauls (undisturbed 8 hauls, 500 fish; disturbed 2 hauls, 189 fish). The majority of the catch consisted of *Trematomus scotti* (Boulenger, 1907) ($N=247$), *T. pennellii* (Regan, 1914) ($N=140$), *T. eulepidotus* (Regan, 1914) ($N=120$) and *T. lepidorhinus* (Pappenheim, 1911) ($N=111$), whereas *T. nicolai* (Boulenger, 1902) ($N=36$), *T. loennbergii* (Regan, 1913) ($N=16$), *T. hansoni* (Boulenger, 1902) ($N=17$) and juveniles ($N=2$) were less abundant. The last three species and juveniles were excluded from further analysis. The GSN samples indicate distinct differences in abundance and biomass between disturbed and undisturbed areas (Fig. 1); *T. eulepidotus*, *T. lepidorhinus* and *T. scotti* dominated undisturbed areas, whereas *T. nicolai* and, especially, *T. pennellii* dominated disturbed areas. The pooled length-frequency distribution of all *Trematomus* species differs significantly between disturbed and undisturbed areas (Kolmogoroff-Smirnoff test, $P<0.05$), indicating that there are fewer small but more large individuals present in disturbed areas.

Stomach contents

Because of empty cells in the area×species matrix (*T. pennellii* present in disturbed areas only; only 1 individual of *T. scotti* in disturbed areas), we started with a two-way ANOVA, including the remaining three species (*T. eulepidotus*, *T. lepidorhinus*, *T. nicolai*) to analyse effects of area and species on total stomach content. There are significant ($P<0.05$) effects of species and species-area interaction on total stomach content, but no significant effects of area (Tables 2, 3). One-way ANOVAs of total stomach content versus area and versus species, respectively, detected significant ($P<0.05$) effects of area as well as of species. Total stomach content was significantly higher in undisturbed areas (1.432 g WM; SE range 1.344–1.523 g compared to 0.675 g WM; SE range 0.617–0.722 g) and in the species *T. pennellii* and *T. scotti* (Tables 4, 5).

Food composition

The total number of different taxa consumed by the several *Trematomus* species is distinctly different between disturbed and undisturbed areas (Fig. 2). *T. eulepidotus*, *T. lepidorhinus* and *T. scotti* consumed a higher number of taxa in undisturbed than in disturbed areas, whereas *T. nicolai* seemed to feed on more taxa in disturbed areas. The two-way ANOVA with the three species occurring in both areas indicated significant effects of species-area interactions, but neither of area nor of species. One-way ANOVAs including all species

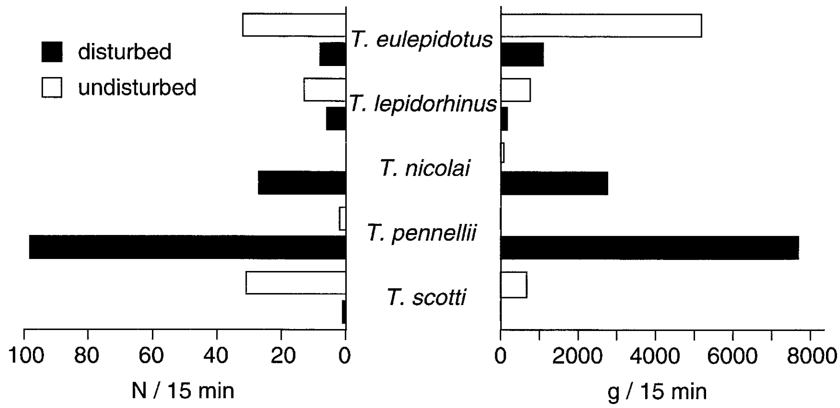


Fig. 1 Average abundance (*N* 15 min^{-1}) and biomass (g 15 min^{-1}) of all *Trematomus* species caught in bottom trawls (GSN). Samples from disturbed (■) and undisturbed (□) areas. *Trematomus loennbergii*, *T. hansoni* and juveniles are neglected because of extremely low numbers

Table 2 Analysis of differences in standardised total prey weight (STPW; log (1 + gWM)) among *T. eulepidotus*, *T. lepidorhinus* and *T. nicolai* and between disturbed and undisturbed areas by two-way ANOVA

ANOVA				
Source	*df*	Mean square	*F*-value	*P*-value
Area	1	0.059	3.775	0.055
Species	2	0.075	4.820	0.010
Area×Species	2	0.085	5.411	0.006
Residual	94	0.016		

showed no significant difference between disturbed and undisturbed areas ($P = 0.414$); on average, each fish had fed 1.9 (min. 0, max. 7) different taxa. Among species, total number of food taxa per fish was significantly higher in *T. pennellii* and *T. scotti* (Tables 6, 7).

Figure 3 shows the main food index (MFI) of the six most frequent prey taxa for the five *Trematomus* species and for all species combined, in disturbed as well as undisturbed areas. Regarding all *Trematomus* species, MFIs of amphipods and isopods are higher in disturbed areas, whereas the MFI of polychaetes is lower. In terms of number and biomass per standard stomach, polychaetes (mean $N = 9.27$, mean $B = 0.16$ g), amphipods (mean $N = 7.14$, mean $B = 0.14$ g), euphausiaceans (mean $N = 0.88$, mean $B = 0.09$ g) and isopods (mean $N = 1.37$, mean $B = 0.02$ g) were the most important prey items. A two-way ANOVA of number (or biomass) versus area (disturbed and undisturbed) and *Trematomus* species (five species) showed significant differences among *Trematomus* species with respect to all prey taxa, but only one significant effect of area: biomass of euphausiaceans was significantly ($P < 0.05$) lower in disturbed areas (0.016 g stomach^{-1} compared to 0.155 g stomach^{-1}).

In summary, the diet of *T. scotti* and *T. pennellii* is quite similar. Both feed almost exclusively on benthic organisms, with highest MFI values for amphipods and polychaetes. *T. nicolai* and *T. lepidorhinus* feed on benthic (amphipods, isopods, polychaetes) as well as pelagic organisms (euphausiaceans and others). Pelagic euphausiaceans and amphipods dominate the diet of *T. eulepidotus*.

Discussion

Methods

Our study suffers from several methodical shortcomings, which may have introduced some bias in the data. The separation of benthic communities into disturbed and undisturbed according to visual inspection neglects the various stages of benthic community succession. Hence, variability within these two groups may obscure differ-

Table 4 Analysis of differences in standardised total prey weight (STPW; log (1 + gWM)) of fish among species by ANOVA

ANOVA				
Source	*df*	Mean square	*F*-value	*P*-value
Species	4	1.034	45.013	< 0.001
Residual	290	0.023		

Table 3 Mean standardised total prey weight (STPW) of *T. eulepidotus*, *T. lepidorhinus* and *T. nicolai* in disturbed and undisturbed areas. SE range: mean ± one standard error

Mean STPW (g WM)						
Species	Disturbed			Undisturbed		
	Mean STPW	SE range	*N*	Mean	SE range	*N*
Trematomus eulepidotus	0.442	0.365–0.524	10	0.816	0.675–0.968	27
T. lepidorhinus	0.026	0.000–0.052	8	0.629	0.515–0.750	18
T. nicolai	0.442	0.396–0.496	34	0.140	0.084–0.199	3

Table 5 Games-Howell post hoc test on differences between mean STPW (based on ANOVA shown in Table 4; nsd: not significantly different; *: significantly different)

Games-Howell post-hoc test on differences between means ($a = 0.050$)						
Species *N*	Mean STPW	*T. eule* 37	*T. lepi* 26	*T. nicol* 37	*T. penn* 80	*T. scott* 115
Trematomus eulepidotus	0.706	/	nsd	nsd	nsd	*
T. lepidorhinus	0.413		/	nsd	*	*
T. nicolai	0.413			/	*	*
T. pennellii	0.910				/	*
T. scotti	1.818					/

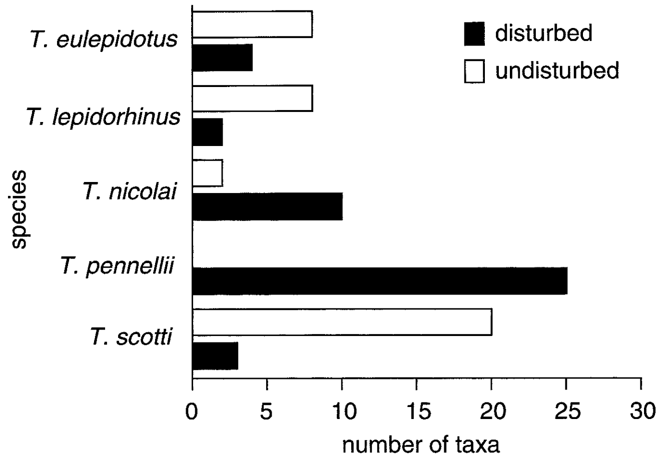


Fig. 2 Total number of taxa consumed by each *Trematomus* species in disturbed (■) and undisturbed (□) areas

Table 6 Analysis of differences in the average number of prey taxa per fish among fish species by ANOVA

ANOVA				
Source	*df*	Mean square	*F*-value	*P*-value
Species	4	9.893	7.310	< 0.001
Residual	290	1.353		

ences between them. The number of GSN hauls from undisturbed ($N = 8$) and disturbed ($N = 2$) areas does not allow for statistical comparison of fish abundance and biomass. Variability of trawl efficiency is unknown and may depend on area type. Hauls were carried out at different hours of the day, which may affect stomach contents. Finally, neither the benthic nor the pelagic community was sampled; i.e. we have no information on selectivity of feeding by the five *Trematomus* species. The consistency of our results, however, indicates that the database is of sufficient quality, especially when taking into account that this is the first study of this type carried out in polar waters.

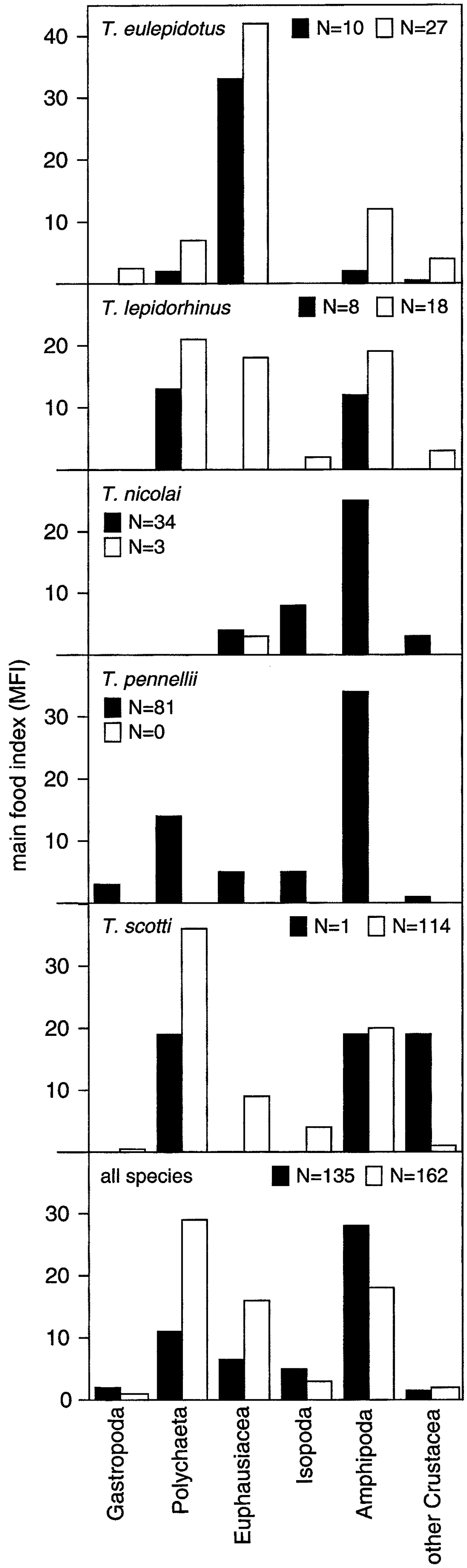
Food composition

Regarding feeding mode, our results confirm most findings of Ekau (1988) and Schwarzbach (1988). *T. scotti* and *T. pennellii* are demersal benthos feeders; *T. lepidorhinus* is intermediate between benthic and bentho-pelagic and *T. eulepidotus* is a pelagic feeder. Only *T. nicolai*, formerly characterised as a pure nekton feeder (Schwarzbach 1988), was found to feed in a rather bentho-pelagic manner in this study.

Overall diet composition of each species seems to be little affected by iceberg scouring. The main food taxa (Fig. 3) are the same in disturbed and in undisturbed areas, but there are differences in diet diversity (Fig. 2). The comparison of total stomach content (STPW) or number of prey taxa per fish between areas and among species (Tables 2, 3, 4, 5) did not reveal a clear spatial pattern. However, if we re-arrange the data according to the area preferred by each fish species as inferred from its abundance (see above), it becomes obvious that amount as well as diversity of prey ingested depend on whether a certain fish species feeds in its preferred area (disturbed or undisturbed, Fig. 1) or not. STPW (1.138 g vs 0.233 g), as well as average number of prey taxa per fish (2.00 vs 0.91), are significantly higher ($P < 0.001$) in the preferred area compared to the non-preferred area.

Table 7 Games-Howell post hoc test on differences between mean number of prey taxa per fish (based on ANOVA shown in Table 6; nsd: not significantly different; *: significantly different)

Games-Howell post-hoc test on differences between means ($\alpha = 0.050$)						
Species Mean *N*	*N* Taxa	*T. eul* 37	*T. lepi* 26	*T. nicol* 37	*T. penn* 80	*T. scott* 115
T. eul	1.54	/	nsd	nsd	*	*
T. lepi	1.19		/	nsd	*	*
T. nicol	1.57			/	*	nsd
T. penn	2.35				/	nsd
T. scott	2.02					/



◀ **Fig. 3** Main food index (MFI) of the six most frequent prey taxa in disturbed (■) and undisturbed (□) areas

Distribution of *Trematomus* species

All Antarctic Nototheniidae including the genus *Trematomus* presumably evolved from a primarily demersal ancestor, radiating into many species with different life-styles (Eastman 1985; Ekau 1988). Ecological niches of the Nototheniidae have been characterised mainly by large-scale geographic distribution, vertical distribution and diet (Ekau 1988; Schwarzbach 1988).

Regarding vertical distribution and diet (see above), *T. scotti* and *T. pennellii* are demersal, *T. lepidorhinus* and *T. nicolai* are bentho-pelagic, and *T. eulepidotus* is a pelagic species. Our study clearly indicates, however, that the small-scale horizontal distribution is another important feature of niche separation in *Trematomus* spp., especially between those species which occupy similar trophic niches. This is evident in the two demersal feeders, *T. scotti* and *T. pennellii*. Whereas *T. scotti* occurs in undisturbed areas only, *T. pennellii* prefers the disturbed sites, thus reducing competition by horizontal niche separation. This separation is detectable also in the bentho-pelagic species, where *T. lepidorhinus* is more abundant above undisturbed areas and *T. nicolai* is more abundant above disturbed areas. The truly pelagic *T. eulepidotus* is unlikely to be affected directly by the disturbance stage of the benthos, although its lower abundance and lower STPW over disturbed areas may indicate indirect effects via its prey taxa.

Regarding size, we found that individuals < 7 cm were clearly under-represented in disturbed areas, whereas large individuals seemed to be more abundant here. Predator-prey interactions may explain this difference. Small fish, i.e. juveniles or generally smaller species such as *T. scotti*, may use the three-dimensional structure of the intact Antarctic shelf community (Arntz et al. 1998) as shelter against predators. However, larger individuals need less shelter and may be better equipped to handle the seemingly larger and more mobile invertebrate prey in disturbed areas (T. Brey, personal observation).

Conclusions

Our study shows that niche separation among the five *Trematomus* species of the Weddell Sea shelf investigated here occurs along three interacting gradients: a trophic, a vertical and a small-scale horizontal gradient. All five species show distinct preference for either undisturbed or disturbed areas. Specialisation is most advanced in the demersal species, where predator-prey interactions may have caused divergent evolution regarding body size. These adaptations indicate that local disturbance by icebergs is a long-term intrinsic feature of Antarctic shelf communities, driving even the evolution of upper level predators.

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