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Ecomorphological Differentiation of Feeding Structures within the Antarctic Fish Species Flock Trematominae (Notothenioidei) from Terra Nova Bay (Ross Sea)

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Abstract: The Antarctic endemic fish genus *Trematomus* (Trematominae, Notothenioidei) includes 15 species very diverse in morphology, lifestyle and feeding ecology. Co-occurring on the continental shelf, they occupy different habitats and a wide range of ecological niches as the result of adaptive radiation during their evolutionary history. Ecomorphological differentiation is a key feature of adaptive radiations, with a general trend for specialization following divergence. Here, we investigated the trophic adaptive morphology and ecology of six *Trematomus* species from Terra Nova Bay (Ross Sea) through feeding apparatus metrics and geometric morphometrics. The suction index (SI), the mechanical advantage in jaw closing (MA), the relative surface of the adductor mandibulae muscle and nine morphological traits related to feeding structures were analysed. Head shape clearly differentiates the benthic (*T. bernacchii*, *T. hansonii* and *T. pennellii*) from the pelagic (*T. eulepidotus* and *T. borchgrevinkii*) species. The position of the eyes and the orientation of the mouth also contribute to specific morphological differences and specialization. Interestingly, *T. newnesi* stands at an intermediate position and the mouth is clearly oriented upwards compared to the other congeneric species.

Keywords: ecomorphology; geometric morphometrics; feeding modes; *Trematomus*; adaptation strategies; Ross Sea

1. Introduction

Adaptive radiation, referred to as a consequence of adaptation to different and new ecological niches, is considered responsible for much of the biodiversity on Earth [1,2].

During the last 40 million years, the Antarctic shelf has been subjected to repeated advances and retreats of the ice sheet leading to habitat disturbance and fragmentation but also generating new ecological opportunities. Such a dynamic scenario supported the giant diversification of the Antarctic notothenioids in the whole Southern Ocean [3,4], as well as multiple nested species flocks within the notothenioid radiation, including the *Trematomus* species flock. Monophyletic, endemic of high Antarctic waters, diverse in ecology and morphology, this genus is the most diverse taxon in the High-Antarctic shelf waters [5–7].

Trematomus diversified along the benthic-pelagic axis, according to depth and feeding ecology. It includes primarily benthic species, but there are a few members with an epibenthic lifestyle (namely *T. loennbergii*, *T. lepidorhinus*, and *T. eulepidotus*) and two (cryo-)pelagic species (namely *T. borchgrevinkii* and *T. newnesi*) [8,9]. *Trematomus* includes

inshore occurring species (e.g., *T. newnesi*, *T. hansonii*, *T. bernacchii*) as well as deep-water taxa (*T. lepidorhinus* and *T. loennbergii*). Trophic diversity is another relevant aspect of the *Trematomus* radiation, specialization is evident in the resource utilization with species feeding preferentially on zooplankton (*T. borchgrevinki* and *T. newnesi*), others relying on benthic invertebrates (*T. bernacchii* and *T. pennellii*), and some piscivorous species (*T. hansonii* and *T. loennbergii*) [5,10–12]).

Considering the evolutionary history of the genus and current taxonomic and ecological diversity, the aim of the present morpho-functional study is to elucidate the adaptive diversification of feeding structures among species of the genus *Trematomus*, and to explore the relationships between feeding structures and trophic ecology of the species. Six species were analysed, namely *Trematomus bernacchii*, *T. hansonii*, *T. pennellii*, *T. eulepidotus*, *T. newnesi* and *T. borchgrevinki* (the scientific nomenclature follows [13]), all from Terra Nova Bay, a large bay (64 km long) extending between the Campbell Glacier Tongue and Drygalski Ice Tongue, along the Victoria Land coast, in the western Ross Sea.

The coastline of Terra Nova Bay is characterized by a variety of habitats. Rocky cliffs extend from a shallow bottom up to 70 m in depth, dominated by algal species (e.g., *Iridaea cordata* and *Phyllophora antarctica*) and by a few invertebrate taxa, polychaetes, molluscs, echinoids and crustaceans [14,15], with the dominance of bivalve molluscs and polychaetes on soft bottoms [11]. Between a depth of 70–80 m, the scallop *Adamussium colbecki* reaches very high density and biomass, totally covering the seabed [16,17]. Below a depth of 70 m, substrates are heterogeneous, mostly inhabited by sponges and anthozoans [18]. Over a depth of 130 m, hard bottoms become very sparse, and the dominant species are serpulids and bryozoans [19]. The fish fauna at Terra Nova Bay includes 30 species in four families [11,20], and is overwhelmingly dominated in both specific richness and abundance by notothenioids of the family Nototheniidae, including *Trematomus* [5].

Feeding ability, defined as the set of abilities to detect, pursue, capture and successfully handle the prey, is strongly influenced by functional morphology of the trophic apparatus, and can be one of the key features to elucidate the role of morphology underlying differentiation in resource use [21–24].

Small gape, low mechanical advantage for jaw closing, powerful force-generating capability of jaw-opening muscles and high suction ability characterize suction feeders, creating a negative gradient pressure in the buccal cavity to attract the prey towards the mouth [25]. Non-robust oral jaws, large gape, moderate suction ability, low mechanical advantage for jaw closing, and moderate force-generating capability of the muscles are typical of ram feeders, swimming towards their prey and swallowing by forward movement of the body or protruding jaws [25]. Robust oral jaws, small gape, high mechanical advantage for jaw closing and powerful force-generating capability of the adductor mandibulae feature manipulation feeders that directly apply their jaws on the prey to crush or tear, removing it from the substrate [25,26]. Pure suction and ram feeding are relatively rare in nature; in most cases, teleosts use a combination of feeding modes depending on the type of prey [27].

The definition of fish feeding strategies is also supported by the use of indices of performance such as the suction index (SI), which allows evaluation of suction feeding ability and jaw-closing mechanical advantage (MA), which reflects the capability to produce force with jaws [23,25,28–30].

In recent years, a tool for quantifying shape variations among fish species has emerged as an alternative to direct measurements: geometric morphometrics [31–34]. This technique allows the quantification of geometric information about the shape of anatomical parts, enabling the identification and visualisation of differences even between congeneric species [24,35,36]. Geometric morphometric analyses are typically performed on landmark coordinates that describe specific anatomical homologous points [34] (Figure 1).

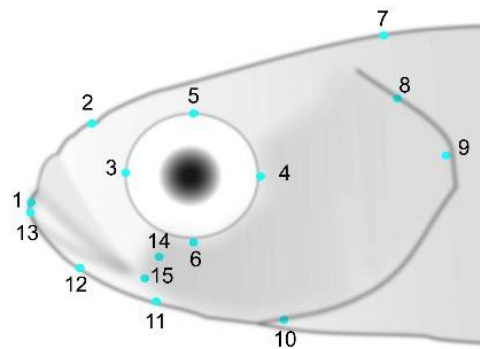


Figure 1. 15 homologous anatomical points (landmarks) used to visualize shape differences among the specimens analysed: 1, snout tip; 2, nostril; 3, orbit, anterior margin along longest axis; 4, orbit, posterior margin along longest axis; 5, orbit, dorsal margin along longest axis; 6, orbit, ventral margin along longest axis; 7, dorsal margin of the epaxial muscle; 8, joint between post-temporal and supra-temporal bone; 9, operculum margin; 10, depression of the sternohyoid muscle; 11, posterior margin of the maxilla; 12, midpoint of the mandible; 13, upper posterior maxilla; 14, lower posterior maxilla; 15, posterior margin of the mandible.

Although ecomorphology can provide information on which features of an organism's form are correlated with its ecology (Motta et al. 1995) and allow identification of relevant morphological traits associated with ecological diversification [36], only a few ecomorphological studies prior to the present work have related diversification in body and head shape with diet of notothenioid species [2,35,37,38].

Here, we explore the ecomorphological diversity of six *Trematomus* species living at Terra Nova Bay using traditional and geometric morphometrics to investigate trophic ecology relationships between form and function.

2. Materials and Methods

2.1. Sampling

Sampling was performed in the coastal waters near the Mario Zucchelli Station (74°41'42" S, 64°07'25" E) at Terra Nova Bay, in the western Ross Sea. Fish were caught by gill nets and fishing rods between a depth of 0 and 500 m in 2005 (*T. bernacchii*), 2017 (*T. hansonii*), 2018 (*T. borchgrevinkii*, *T. eulepidotus*, *T. newnesii*) and 2021 (*T. pennellii*) austral summers (Table 1). The number of specimens per species ranged between 3 and 10. The relatively low number of analyzed individuals has been related to the possibilities that sampling in Antarctica gives in terms of operational difficulties and extraction of organisms in a protected area.

To compare individuals and species of different total length, morphological measurements were standardized to the standard length (SL) of each individual [39]. All specimens were frozen and stored at −20 °C and subsequently analyzed.

Table 1. *Trematomus* species investigated (standard length (SL) range, habitat preference and feeding habits).

Species	n	SL Min (mm)	SL Max (mm)	Habitat	Feeding Habits
<i>Trematomus bernacchii</i>	9	173	203	benthic	omnivorous
<i>Trematomus borchgrevinkii</i>	7	146	181	(cryo)pelagic	zooplanktivorous
<i>Trematomus eulepidotus</i>	9	135	192	epibenthic	zooplanktivorous
<i>Trematomus hansonii</i>	9	177	281	benthic	omnivorous
<i>Trematomus newnesii</i>	10	130	159	pelagic	zooplanktivorous
<i>Trematomus pennellii</i>	3	126	145	benthic	omnivorous

2.2. Morphological Traits

The feeding modes of the six species of the genus *Trematomus* were evaluated through two morphological metrics for the jaws: suction index (SI) and mechanical advantage in jaw closing (MA). Measures were taken in mm to the nearest 0.01 mm.

The suction feeding mechanism, i.e., the capability allowed by the buccal and head structures of a fish to perform suction to engulf prey [40,41], was estimated by the Suction Index (SI). Following [29], the model used in this work is based on the size of the epaxial muscle, which transmits force to the buccal cavity in correspondence with the supra-cleithrum-posttemporal joint, its distance from the centre of the buccal cavity, and the dimensions of the buccal cavity itself. SI was calculated as:

$$SI = \frac{[CSA_{\text{epax}} (\frac{L_{\text{in}}}{L_{\text{out}}})]}{(\text{gape width} \times \text{buccal length})}$$

where CSA_{epax} is the cross-sectional area of the epaxialis, L_{in} is the moment arm of the epaxialis and L_{out} is the moment arm of the buccal cavity. Gape width (measured as the distance between the left and right coronoid processes of the mandible) and buccal length (measured as the distance between the anterior tip of the mandible and the depression in the sternohyoideus) were calculated to estimate the volume of the buccal cavity.

MA expresses the potential of a fish to produce force in its biting action. It was obtained from the structure of the lower jaw, whose fulcrum is represented by the quadrate-articular joint. The distance of the fulcrum from the insertion of the adductor mandibulae muscle and the anterior-most tooth of the lower jaw represent the in-lever (L_{inMA}) and out-lever arms (L_{outMA}), respectively [41,42], from ratio of which MA is obtained. See [29,40,43] for more details on how to carry out measurements for SI and MA.

The adductor mandibulae complex represents a system of muscles involved in jaw movements, and muscular traits may reflect, even in this case, morpho-functional characteristics related to the ecology of the species [44]. As a proxy of capability to produce force with the jaws, we considered the size of the externally visible adductor mandibulae muscle. Using Fiji ImageJ software [45], the ratio between the surface of the visible adductor mandibulae muscle and that of the entire head (i.e., the relative surface of the adductor) was calculated from photos obtained for the left side of each specimen.

2.3. Geometric Morphometrics

To quantify shape variations of the trophic apparatus among the six species of the genus *Trematomus*, we performed geometric morphometric analyses on the basis of digital images. We obtained two-dimensional images of the body (left side) of each specimen in lateral view using a digital camera and positioned all specimens in the same plane, using the same distance from the camera to the subject. We used the landmarks-based method (homologous anatomical points) by collecting two-dimensional coordinates of biologically definable landmarks (Figure 1). Shape variation was digitized using StereoMorph: R package [46] and analyzed with geomorph: R package [34].

The matrices of landmark coordinates were superimposed with a generalized procrustes analysis (GPA) to remove undesirable effects of scale, position and orientation [47]. Principal component analysis (PCA) was used to describe the shape variation among species. Shape changes were visualized using Thin-plate spline (TPS) approach implemented in the geomorph package.

2.4. Statistical Analyses

Differences in suction index (SI), mechanical advantage (MA) and the relative surface of the adductor among the six species were tested. Data were transformed in $\arcsin\sqrt{p}$. After testing normality and homoskedasticity of the distributions with Shapiro–Wink and Levene tests, ANOVAs were conducted for each variable. Statistical significance was determined at $\alpha = 0.05$.

To investigate which morphometric features explain the greatest variations among the six species, a principal component analysis (PCA) involving 9 morphological traits was developed. The variables considered were the morphological traits used for the SI and MA metrics: eye diameter (ED), head length (HL), gape width (GW) and buccal length (BL). The morphological measurements were standardized relative to the body size (SL) of each individual (Barnett et al. 2006). Geometric morphometric procedures were carried out using the geomorph package [34] in the R environment. Statistical analyses were performed using the software R 4.0.2 [48].

3. Results

SI mean and standard deviation values are summarized in Table 2. *T. bernacchii* SI is higher than those of all other studied species, while *T. eulepidotus* was found to have the lowest SI. The highest MA was found in *T. hansonii*, and two species resulted in very close low MA values: *T. newnesi* and *T. pennellii*.

Table 2. Calculated values of suction index (SI) and mechanical advantage (MA) in the six species.

Species	n	Suction Index (Mean ± SD)	Mechanical Advantage (Mean ± SD)
<i>T. bernacchii</i>	9	0.279 ± 0.017	0.286 ± 0.009
<i>T. borchgrevinki</i>	7	0.138 ± 0.046	0.203 ± 0.032
<i>T. eulepidotus</i>	9	0.087 ± 0.024	0.243 ± 0.025
<i>T. hansonii</i>	9	0.199 ± 0.038	0.338 ± 0.012
<i>T. newnesi</i>	10	0.123 ± 0.024	0.183 ± 0.023
<i>T. pennellii</i>	3	0.138 ± 0.035	0.183 ± 0.022

ANOVA testing developed on SI values resulted in significant differences among the species ($F(5,41) = 38.61, p < 0.0001$). From Tukey's post hoc test, it was found that *T. eulepidotus*, *T. newnesi* and *T. pennellii* did not significantly differ, and the last two were not significantly different from *T. borchgrevinki*, while both *T. hansonii* and *T. bernacchii* significantly differed from all the other species (Figure 2). ANOVA testing developed on MA values resulted in significant differences among the species ($F(5,41) = 56.91, p < 0.0001$). From Tukey's post hoc test, it was found that *T. borchgrevinki*, *T. newnesi* and *T. pennellii* did not significantly differ, while *T. eulepidotus*, *T. bernacchii* and *T. hansonii* significantly differed from all the other species (Figure 2).

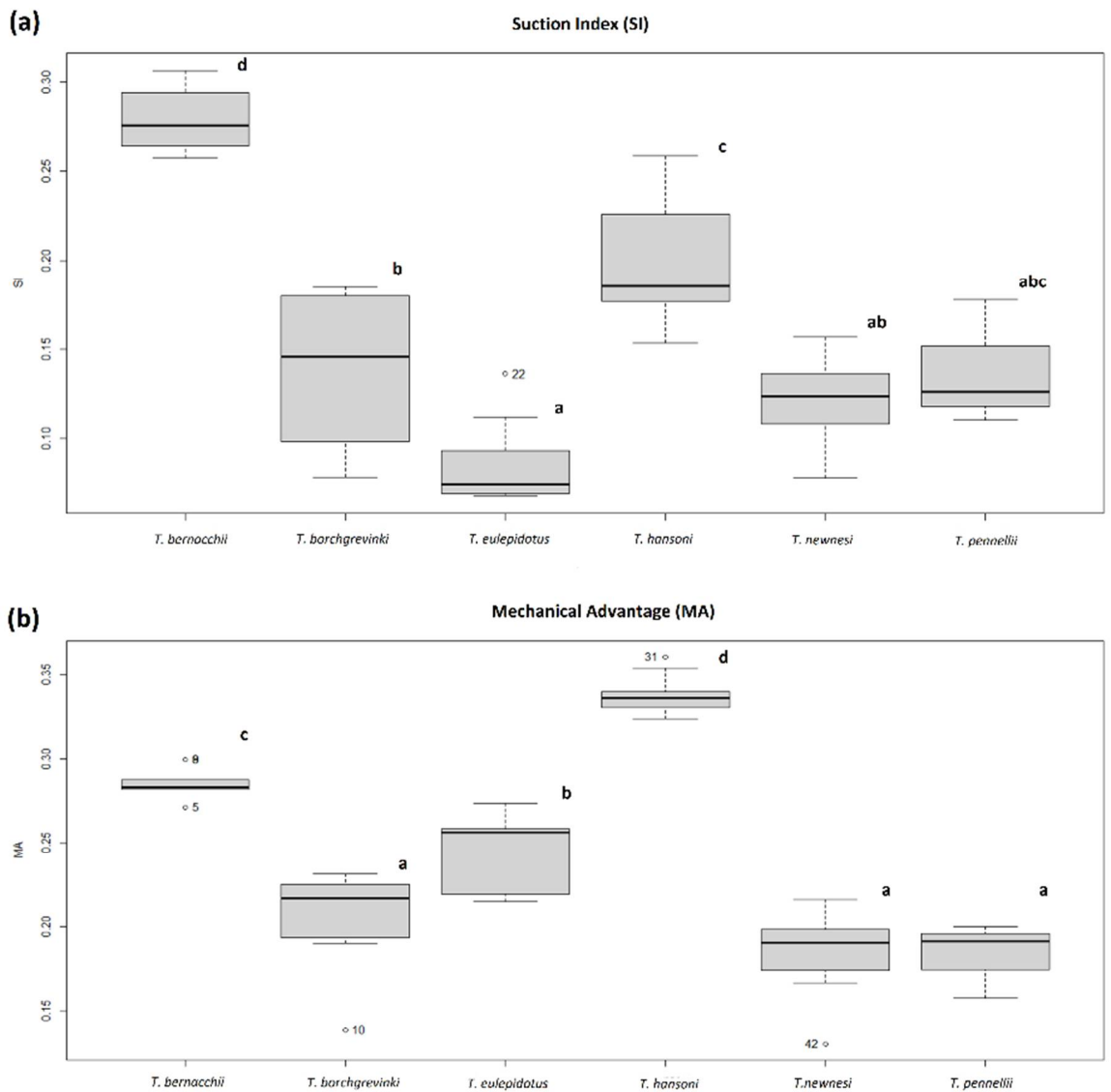


Figure 2. Boxplots of the values of Suction Index (a) and Mechanical Advantage (b) calculated for the six investigated species. Different letters in the boxplots indicate significant differences.

The relative surface of the adductor mandibulae muscle were significantly different among the six species (ANOVA, $F(5,41) = 43.48$, $p < 0.0001$). Tukey's post hoc test indicated a significant difference between the benthic group composed by *T. bernacchii*, *T. hansonii* and *T. pennellii*, and the pelagic group composed by *T. eulepidotus*, *T. newnesi* and *T. borchgrevinki* (Figure 3).

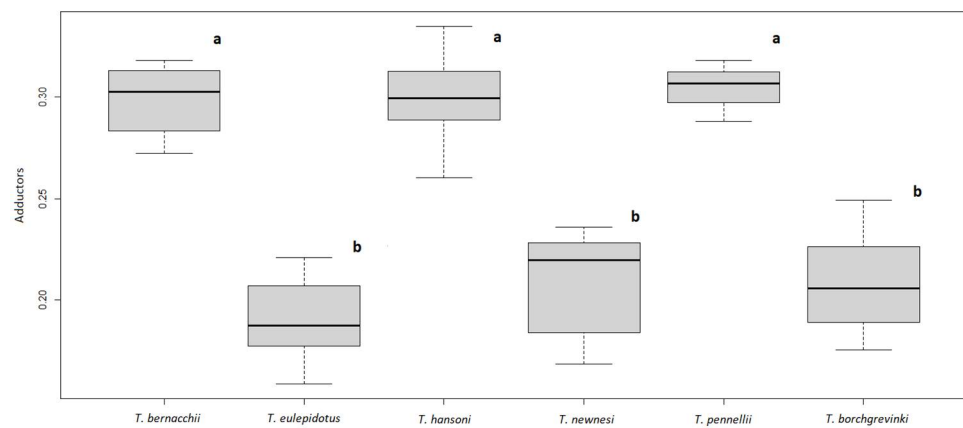


Figure 3. Boxplots of the relative surface of the adductor mandibulae muscle calculated for the six investigated species. Different letters in the boxplots indicate significant differences.

Table 3 shows the mean values and standard deviation of the 9 variables considered for the PCA. PCA explained 72.28% of the variance on the first three axes (Table 4).

Table 3. Mean values and standard deviations of the 9 morphological traits. Measures were standardized by SL. Traits: Eye diameter (ED); Head length (HL); Gape width (GW); Buccal length (BL); Cross-Sectional Area (CSA_{epaxialis}); In-lever Suction Index (L_{in}SI); Out-lever Suction Index (L_{out}SI); In-lever Mechanical Advantage (L_{in}MA); Out-lever Mechanical Advantage (L_{out}MA).

Traits	<i>T. bernacchii</i> Mean ± SD	<i>T. borchgrevinki</i> Mean ± SD	<i>T. eulepidotus</i> Mean ± SD	<i>T. hansonii</i> Mean ± SD	<i>T. newnesi</i> Mean ± SD	<i>T. pennellii</i> Mean ± SD
ED	0.070 ± 0.002	0.081 ± 0.005	0.083 ± 0.013	0.067 ± 0.007	0.071 ± 0.006	0.085 ± 0.006
HL	0.304 ± 0.011	0.280 ± 0.010	0.288 ± 0.016	0.280 ± 0.012	0.228 ± 0.114	0.287 ± 0.004
GW	0.103 ± 0.010	0.114 ± 0.006	0.104 ± 0.007	0.114 ± 0.004	0.116 ± 0.013	0.100 ± 0.003
BL	0.090 ± 0.002	0.195 ± 0.008	0.195 ± 0.015	0.107 ± 0.007	0.204 ± 0.019	0.209 ± 0.008
CSA _{epaxialis}	0.101 ± 0.002	0.092 ± 0.008	0.076 ± 0.010	0.096 ± 0.007	0.094 ± 0.003	0.096 ± 0.003
L _{in} SI	0.039 ± 0.001	0.037 ± 0.004	0.031 ± 0.005	0.040 ± 0.002	0.038 ± 0.002	0.039 ± 0.003
L _{out} SI	0.155 ± 0.005	0.107 ± 0.005	0.105 ± 0.009	0.154 ± 0.008	0.119 ± 0.013	0.128 ± 0.008
L _{in} MA	0.040 ± 0.001	0.023 ± 0.002	0.032 ± 0.003	0.041 ± 0.002	0.028 ± 0.004	0.021 ± 0.003
L _{out} MA	0.142 ± 0.004	0.118 ± 0.024	0.133 ± 0.007	0.120 ± 0.005	0.152 ± 0.008	0.116 ± 0.004

Table 4. Coefficients of the 9 traits selected to describe differences in the feeding apparatus of six species of the genus *Trematomus* as resulting from the PCA after standardization by SL. In each component, highest and lowest (relative of driving variables) coefficients are in bold.

	PC1	PC2	PC3
Variance	3.606	1.552	1.347
% of Variance	40.069	17.246	14.962
Cumulative % of Variance	40.069	57.315	72.277
Traits			
ED	-0.575	0.404	-0.027
HL	0.271	0.458	0.607
GW	-0.021	0.552	0.065
BL	-0.868	0.361	-0.085
CSA _{epaxialis}	0.734	0.538	-0.280
L _{in} SI	0.714	0.533	-0.393
L _{out} SI	0.911	-0.130	-0.066
L _{in} MA	0.754	-0.313	-0.337
L _{out} MA	0.052	0.237	0.784

T. bernacchii and *T. hansonii* are distinct from a cluster composed by the other four species along the PC1 axis, with ordination driven by buccal length and LoutSI, which are directly involved in SI (Figure 4). PC2 was not clearly driven by any variable. PC3 was instead driven by the lower jaw levers, from which we calculated MA.

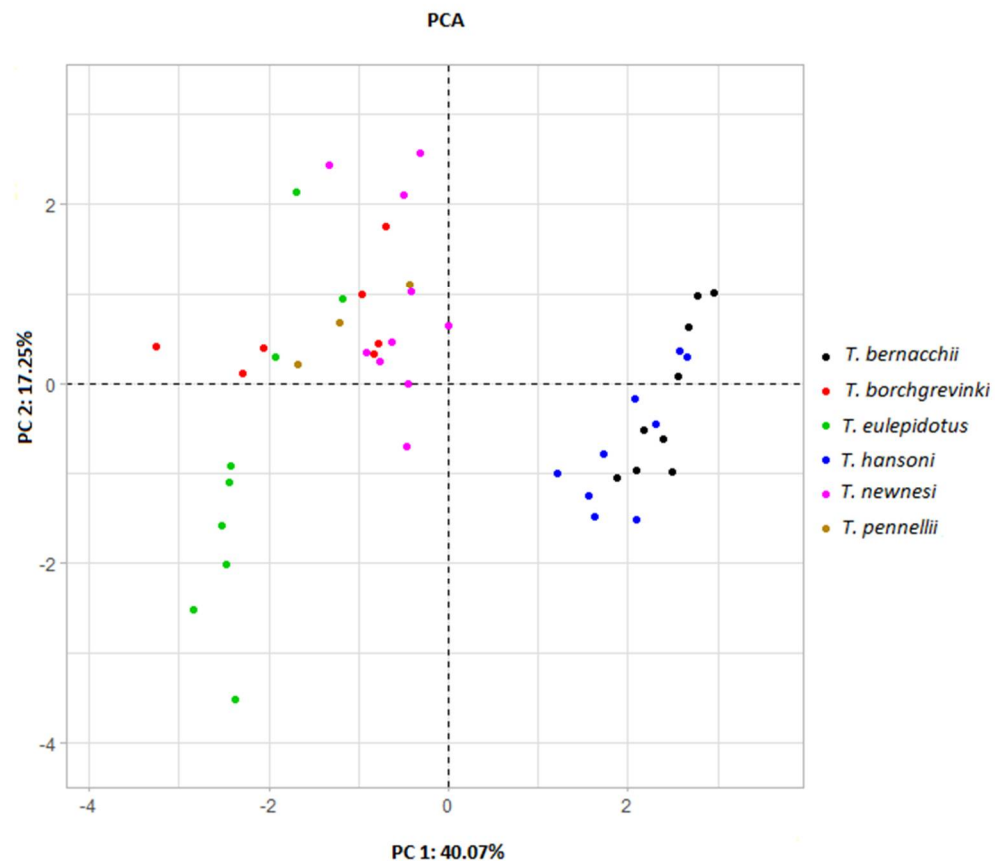


Figure 4. Principal component analysis plot developed on the 9 morphological traits of feeding apparatus of the six *Trematomus* species.

The PCA plot developed by geometric morphometric analysis showed how the six species were distributed along the axes on the basis of their head shapes (Figure 5). The first two axes of the PCA (Figure 5) explained 62.13% of the total variability. PC1 clearly separated the benthic species *T. bernacchii*, *T. hansonii* and *T. pennellii* (negative PC1 values) from the pelagic *T. eulepidotus* and *T. borchgrevinki* (positive PC1 values); TPS transformations of landmark positions showed the main deformation in the position of the eyes (Figure 5). The eyes of the benthic species are oriented upwards, while in pelagic species they are in a lateral position. *T. newnesi* is placed in an intermediate position according to PC1.

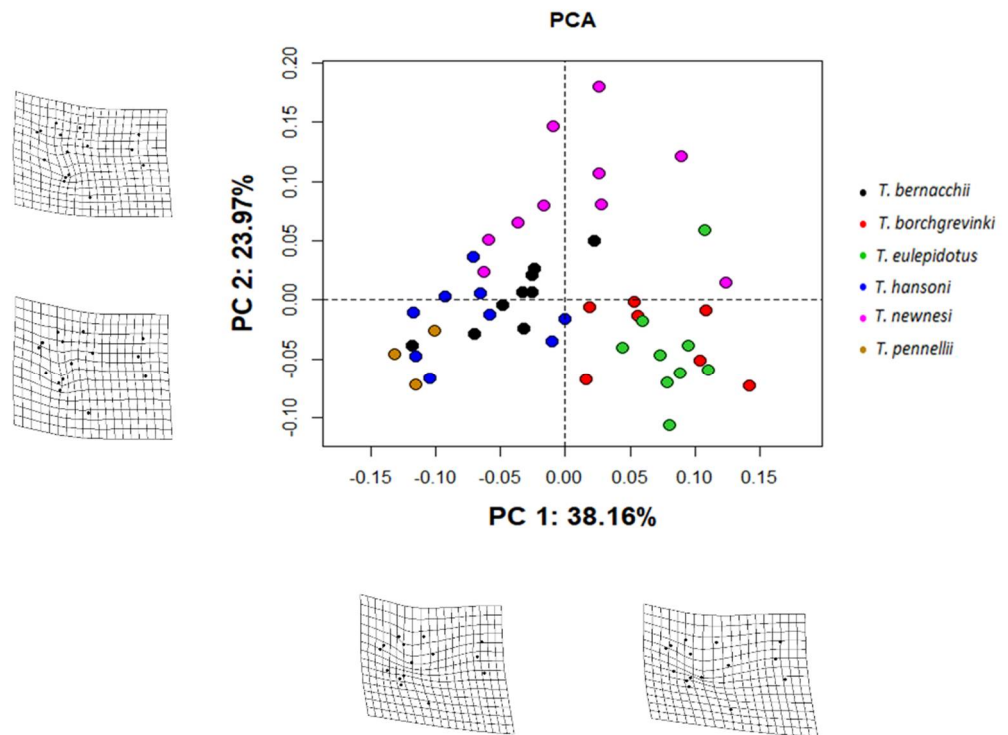


Figure 5. PCA plot obtained from geometric morphometric analysis. The thin-plate spline (TPS) transformations of the landmark positions represent the extreme transformations of the head shape measurements along the axes of the PCA, highlighting where major variations occur.

T. newnesi differed from the other species along PC2 and segregated in the positive values. TPS showed mouth orientation as a major morphological driver in PC2 differentiation; in *T. newnesi*, it is distinctly pointing upwards in relation to all the other considered *Trematomus* species.

4. Discussion

The diversification of Antarctic notothenioid fish is a unique example of rapid adaptive morphological radiation in an extreme marine environment [4]. Within notothenioid radiation, nested bursts of phenotypic and ecological diversification have been identified, one of them leading to the current genus *Trematomus* [49]. From a common ancestor, the trematomids differentiated both morphologically and ecologically to colonize newly available trophic niches, thus resulting in great interspecific variability [8,10,35].

Variations in trophic morphology play a crucial role in the conquest of new trophic niches, opening novel opportunities for resource usage [37]. Following this line, here we investigated relationships between feeding structures and feeding habits of six *Trematomus* species occupying benthic, epibenthic and pelagic habitats in the Terra Nova Bay area and preying on very different organisms.

Our study was developed on a relatively limited number of specimens per species, which should not affect our results. Studies on fish ecomorphology can make use of a low number of samples (see, for example, [10,24,29,35,44]) because of low intraspecific morphological variability (except if we consider different morphotypes of the same species). Each sample was frozen and subsequently defrosted, the methodology was standardized to make shape alterations possible due to the process being equally spread across all specimens. We also consider that it should not have significantly affected our analyses, considering that the measurements that we have taken mainly involved hard parts of the head and the buccal apparatus, which should not be altered by the freezing process.

Based on traditional ecomorphological measurements, *T. bernacchii* and *T. hansonii* resulted in the highest SI and MA values, respectively, compared to the investigated species.

Relatively high SI values in *T. bernacchii* and *T. hansonii* are determined by the development of the epaxial muscle and consequently of the lever that favours suction movements, paired with a short mouth, which not only contributes to improved suction performance [43,50], but is also related to the jaw lever system that determines high MA [25]. In both species, suction is used primarily in the capture of bottom benthic polychaete annelids, which are present in the diet of both species [11].

T. bernacchii is among the most common fish species in Antarctic shallow waters, especially at Terra Nova Bay, where huge surfaces of the bottom are occupied by Antarctic scallop (*Adamussium colbecki*) facies [11]. This bivalve represents an important food source that *T. bernacchii* is able to eat [17] by crushing the valves, thanks to manipulation feeding assisted by the high power that its jaws are able to express [38]. Indeed, unlike other perciforms, for which the crushing of hard prey is entrusted to robust pharyngeal teeth, in *T. bernacchii* these are poorly developed [11]. Specializing in feeding on hard scallops represents a way of partitioning niches with a sympatric congeneric species: *T. pennellii*. Our study found that *T. pennellii* was unable to exert sufficient power for this purpose, with the lowest MA among the analyzed species, feeding mainly on softer prey such as pycnogonids and gastropods, and alternatively on plankton [11]. Polychaetes and scallops are not the only resources for *T. bernacchii*, whose high SI and MA allow it to draw on a wide range of resources, showing a feeding plasticity focusing on the most locally abundant organisms among a wide range of potential prey [5,41,51]. For example, *A. colbecki* is exploited by *T. bernacchii* in the shallow waters of Terra Nova Bay due to its abundance [17].

T. hansonii is described as a generalist feeder, mostly feeding on juvenile fish and benthic organisms, with planktonic prey reported for the species in South Georgia and McMurdo Sound possibly reflecting an ontogenetic phase [15]. However, based on SCUBA observations, a hunt-and-peck predation behaviour has also been reported [52]. Such a plasticity in feeding habits is supported by the observed SI and MA values. Indeed, *T. hansonii* was found to have an intermediate SI value, possibly enabling feeding on small benthic and planktonic organisms, and a high MA value in support of hunt-and-peck predation of large organisms. *T. hansonii* presents the highest value of MA among the species studied in this work, and its value is also relatively high when compared with those of fish species in other taxonomic groups analyzed in the literature (see, for example, [43]). It feeds mainly on fish and secondarily on polychaetes and hard prey such as decapod crustaceans [11], combining manipulation and suction feeding based on the prey availability. It has been also recorded by means of baited cameras to employ scavenging activity on organisms larger than its own size, from which it powerfully bites and detaches pieces using rotational feeding [53], a common method used by nototheniids to handle large food pieces [54]. Furthermore, *T. hansonii* and *T. bernacchii* are benthic species that share the ability to be planktivorous if necessary [5]. Another morphological trait that divides *T. bernacchii* and *T. hansonii* from the other species is the size of the eye. The benthic predators feed on less mobile and larger prey, while the pelagic *Trematomus* species and *T. pennellii* need a better vision system to locate smaller (and in some cases more mobile) organisms.

Conversely, based on their feeding performance, *T. borchgrevinkii*, *T. eulepidotus* and *T. newnesi* are supposed to enact ram feeding. In particular, *T. newnesi* swimming in the pelagic realm exhibits the typical features and morphological traits of ram feeders, i.e., a moderate suction capacity and MA and no robust oral jaw [41]. Interestingly, similar features are exhibited by the small benthic *T. pennellii*, for which ram feeding is also hypothesized. *T. eulepidotus* has the lowest SI among the Trematomids considered in the present work. It is a zooplanktivorous species ([5,55] and it is likely to perform ram feeding to capture prey, moving its body towards them without a suction or biting action. Similar strategies are exhibited by the other zooplanktivores, *T. newnesi*, and *T. pennellii*, which are generalist and feed on small benthic organisms and plankton [5,11,55]. *T. newnesi* and *T. pennellii* are also characterized by the lowest values of MA calculated in the present work; powerful jaws are not needed to catch and eat their small and relatively soft prey.

This is also confirmed by the low value of MA of *T. borchgrevinki*, a highly specialized selective zooplanktivore which is structured for predation on small crustaceans, detected owing to the development of the anterior lateral line system, a series of six short dermal channels on each side of the head containing neuromasts capable of perceiving the low-frequency vibrations produced by the movement of crustacean limbs [11,56].

Compared to the pelagic *Trematomus* species, *T. pennellii*, despite its low MA, can develop greater bite power. This is inferred by the development of the adductor mandibulae muscles system, which is comparable to that of the 'strong biters' *T. bernacchii* and *T. hansonii*. The adductor mandibulae is indeed another anatomical structure that contributes to give strength to the bite [45] that here was found to be more developed in the benthic species than in the pelagic ones. In addition, we can deduce that *T. pennellii* has a less strong bite than the other two benthic *Trematomus* species. This may be associated with the smaller and softer prey on which it feeds, but it is stronger than the pelagic species, which the previous ecomorphological measurements alone would not have highlighted.

Geometric morphometric analysis confirmed the results of traditional morphometrics and clearly separates the benthic species (*T. bernacchii*, *T. hansonii* and *T. pennellii*) from the pelagic species (*T. eulepidotus* and *T. borchgrevinki*). The main driver of shape variation among benthic and pelagic species was in the position and orientation of the eyes. Our results are in agreement with those of [35], who analyzed head shape disparity within the genus *Trematomus*.

In the epibenthic and pelagic species, the eyes are oriented laterally [57], suggesting that predation is concentrated on organisms in the water column, as in the case of *T. eulepidotus* and *T. borchgrevinki*, which feed on zooplankton such as euphausiids, amphipods, copepods, pteropods, and juvenile fish [5,55].

In benthic fish, on the other hand, the eyes are oriented anterolaterally upwards for the function of having the visual field directed towards the water column above [57]. The upward orientation of the eyes can also have a defensive function [35] but it is mainly correlated with diet and feeding modes. *T. bernacchii*, *T. hansonii* and *T. pennellii* feed mainly on benthic organisms but are also able to catch planktonic prey [5]. In fact, they are all considered generalist feeders, as they can ascend the water column to prey on pteropods, ostracods, copepods, hyperiids and euphausiids when necessary [58].

The eye position of *T. newnesi* is not well-defined along PC1 compared to benthic and pelagic species. *T. newnesi* is characterised by a degree of phenotypic plasticity and the occurrence of two morphs (a "largemouth morph" and a "typical mouth morph"), which possibly reflects niche partitioning [10,59]. The *T. newnesi* specimens analyzed in this study are all "largemouth morph", a morphotype known to have more demersal habits [10].

T. newnesi also differs from all other species analyzed herein along PC2 in the orientation of the mouth, the latter being clearly oriented more upwards than the other species considered. The position of the eyes, less lateral and more dorsal than in other pelagic fish, and the upward orientation of the mouth seem to be related and possibly enables *T. newnesi* to detect prey from the bottom upwards. Despite the demersal habits of the "largemouth morph", its diet consists mainly of zooplanktonic prey such as fish larvae, amphipods and euphausiids. *T. newnesi* shows a certain feeding plasticity in relation to variations in environmental conditions throughout the year [10,60].

It is worth noting that in the present work, different methodologies were applied to investigate the feeding ability of the *Trematomus* species. The combination of traditional ecomorphology carried out by direct measurements of morphological traits and the geometric morphology developed by means of software to study shape deformations returned largely overlapping results, indicating the effectiveness of the two methodologies in highlighting similarities and differences among species and in inferring feeding modes. However, direct and indirect investigations also revealed different outcomes, showing the complementarity of the two analyses. Traditional analysis allowed the evaluation of feeding performance related to the functional anatomical structure of the trophic apparatus,

while geometric morphometrics revealed other morphological differences in shape among species. In the *Trematomus* case study, the geometric morphometrics revealed differences in the orientation of the eyes and mouth between the groups of the *Trematomus* species that were not evidenced by traditional ecomorphology.

In conclusion, our results highlight the importance of using integrated methods to study the relationships between anatomical feeding structures and the ecology of a species. Further ecomorphological studies are needed to improve current knowledge of the ecological roles of fish species and to allow elucidation of their feeding plasticity, and thus their ability to adapt to prey availability. Such information is relevant for a thorough understanding of the ability of fish species to face different environmental scenarios and changes in prey availability. This is crucial for polar species that are currently exposed to rapid environmental changes.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jmse10121876/s1>, Table S1: Summary table.

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