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Plasticity in the brooding cidaroid *Ctenocidaris nutrix*: a morphological, trophic, and molecular investigation

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Research Article

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Abstract

Phenotypic plasticity refers to the capacity of an organism's phenotype to vary in response to changes in environmental conditions, without any change in the individual genotype. Sea urchins (Echinoidea) are well-known for their morphological and behavioural plasticity in response to changing habitats or trophic environments. Phenotypic plasticity has been little studied in directly developing species, in which low levels of phenotypic plasticity are usually expected as a consequence of high levels of genetic differentiation among populations and local genetic adaptation. In the present work, we report a significant plasticity in the direct-developing and brooding sub-Antarctic species *Ctenocidaris* (*Eurocidaris*) *nutrix* (Echinoidea, Cidaridae) through morphological and trophic analyses of gut contents and $\delta^{13}C$ and $\delta^{15}N$ isotopic compositions. Molecular data (COI mtDNA) confirm that the different phenotypes of *C. nutrix*, the short-spined *C. nutrix nutrix* and the long-spined *C. nutrix longispina*, are a single species restricted to sub-Antarctic waters. As formerly demonstrated in broadcasting echinoid species, morphological plasticity appears to be mainly linked to depth and swell exposure, specimens from exposed and shallow sites showing shorter spines and larger apical systems compared to specimens from sheltered or deep sites. Significant differences in the diet and trophic niche of the different phenotypes suggest that prey type and food diversity may also be a factor promoting distinct phenotypic responses, both in the feeding behaviour and morphology of echinoids.

Introduction

Phenotypic plasticity is the capacity of organisms to alter their morphology, physiology, biochemistry, behaviour, or a combination of these traits in response to environmental variations, without any modification of their genotype (Bradshaw, 1965; DeWitt and Scheiner, 2004; Fordyce, 2006). Phenotypic plasticity may be active and physiologically regulated, involving trait changes in response to fluctuating environmental conditions through stress-response pathways, or passive and solely induced by growth-limiting factors such as nutrients and food resources (van Kleunen and Fischer, 2005). Active plasticity is often adaptive as it can enhance or stabilise fitness (DeWitt et al., 1998) and determine species response to changing environmental conditions (Ebert, 1996; Mykles et al., 2010; Schwenk et al., 2009).

Phenotypic plasticity has gained interest in marine invertebrate studies, most often to understand its role in species interactions and nutrition (Ebert, 1996; Hughes et al., 2012; Padilla and Savedo, 2013). In echinoderms, which are either slow-moving or sessile at the adult stage, the evolution of phenotypic plasticity has been interpreted as an adaptation to heterogeneous and fluctuating environmental conditions (DeWitt and Langerhans, 2004; Ebert, 1996; Fenaux et al., 1994; Strathmann et al., 1992). Plasticity has been investigated through a wide range of phenotypic responses, including behaviour, morphology, and life history traits (Hughes et al., 2012; Michel et al., 2016; Padilla and Savedo, 2013). Most studies focused on experimental or observational data, rather than solely on field observations (Padilla and Savedo, 2013).

Sea urchins (Echinoidea) are well-known for their morphological and behavioural plasticity as a response to contrasting habitats or trophic environments (Hughes et al., 2012), predation (Selden et al., 2009), and food limitation, both in larval and post-larval stages (Ebert, 1996; Fenaux et al., 1994; Hughes et al., 2012; Russell, 1998; Soars et al., 2009; Strathmann et al., 1992). Phenotypic plasticity and its evolutionary significance have been mainly investigated in broadcasting echinoid species (species with pelagic larvae) and interpreted as an adaptation to a heterogeneous nutritional environment (Ebert 1996; Fenaux et al., 1994;

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Hart and Strathmann, 1994; Reitzel and Heyland, 2007; Strathmann et al., 1992). In adult stages, morphological responses to food limitation may imply changes in test diameter (Ebert, 1996), test thickness (Guillou et al., 2000), jaw structure (Ebert, 1980, 1996), spine length (Ebert, 1980; Edwards and Ebert, 1991), or gonad size (Ebert, 1996; Guillou et al., 2000; Kelly, 2000; Russell, 1998). In contrast, phenotypic plasticity has been seldom studied in direct developing (brooding) echinoids (Michel et al., 2016). Low levels of phenotypic plasticity are usually expected in direct developing species as a consequence of restricted dispersal ability (absence of widely dispersing larvae), favouring high levels of genetic differentiation among populations and local genetic adaptation (Parsons, 1998).

In the present work, we report a significant plasticity in a non-broadcaster, the brooding sub-Antarctic species *Ctenocidaris* (*Eurocidaris*) *nutrix* (Thomson, 1876) (Echinoidea, Cidaridae). The species was initially described from the Kerguelen archipelago, where it is common on both the shoreline and the surrounding oceanic plateau. Formerly considered to be composed of two distinct species or subspecies (David et al., 2005), two morphologies were described regardless of depth or location: the typical short-spined *C. nutrix nutrix* and the long-spined *C. nutrix longispina* (Mortensen, 1928). A recent work revealed that the two forms shared a single COI haplotype in Kerguelen (Saucède *et al.*, 2024). In the current study, the phenotypic plasticity of the species was investigated through morphological and trophic analyses (using stable isotopes and gut content analyses). Specimens from two close sites (<20 km) contrasting in terms of habitat (swell exposure) were further characterised by their respective tegument, gonad biomass and skeletal biomechanics.

Materials and methods

Studied specimens

Molecular, trophic, morphological and biomechanical analyses were performed on specimens of *Ctenocidaris nutrix* from 21 deep sites (from 74 to 327 m depth), and three nearshore shallow sites (6 and 18 m depth; Figure 1, Table 1). Specimens of deep sites were collected off the Kerguelen Islands in 2010 during the POissons de KERguelen (POKER) 2 fish stock assessment survey (Duhamel, 2011). Specimens from shallow sites (Port Couvreux, Haute and Suhm Islands) were collected between 2013 and 2018 during Proteker campaigns 2, 3, 4, and 7 (Saucède et al., 2019). Whenever possible, the same specimens were investigated for molecular, trophic, morphological, and biomechanical analyses (Tables 1–3). Specimens of the two nearshore, shallow sites of Haute and Suhm Islands (Figure 1), located 20 km apart and contrasting in terms of swell exposure, were collected during the Proteker 4 campaign for further characterisation of their trophic plasticity (gut contents), anatomy (tegument and gonad biomass) and the biomechanics of the skeleton (Tables 2 and 3).

In addition to the Kerguelen Islands, the species had also been reported from the west sub-Antarctic Scotia Arc Islands as well as from high Antarctic regions (David et al., 2005; Fabri-Ruiz et al., 2017; Saucède et al., 2014). In the present study, collection specimens sampled during several oceanographic cruises across the Southern Ocean and formerly identified as *C. nutrix* were also investigated for complementary molecular analyses (Table 1). The analysed samples were collected from the sub-Antarctic Diego Ramirez (ACE campaign), South Georgia (JR262 campaign) and South Orkney (JR15005 campaign) Islands, and from the Antarctic Peninsula (JR 230 campaign), Bransfield Strait (ANTXXIX/3 campaign), Weddell Sea (ANTXXIII/8 campaign), and East Antarctica (CEAMARC campaign).

Molecular analyses

The COI mtDNA was sequenced for a total of 98 specimens from 38 different sites and five bioregions: the Kerguelen Islands, Diego Ramirez, South Georgia, South Orkneys, and the Antarctic (Antarctic Peninsula, Bransfield Strait and East Antarctica). DNA was extracted from one to two spines per individual using the Qiagen DNeasy Blood & Tissue Kit and following the manufacturer's instructions. For COI amplification, the following PCR mix was used: 6.25 µL Accustart Toughmix (QuantaBio), 4.75 µL sterile water, 0.25 µL (10 µM) of each primer and 1.5 µL of DNA extract. The forward primer was LCOech1aF1 (5'-TTTTTTCTACTAAACACAAGGATATTGG-3'), and the reverse primer was jgHCO2198 (5'-TAIACYTCIGGRTGICCRAARAAYCA-3'; Geller et al., 2013; Layton et al., 2016). The PCR program consisted of an initial denaturation step at 95°C (5 min), followed by 40 cycles: denaturation at 95°C (45 s), annealing at 45°C (45 s), and elongation at 72°C (45 s). A final elongation at 72°C for 3 min was also performed. PCR products were then purified using the ExoCleanUp FAST (VWR®). Sequencing was performed by Macrogen Europe (Netherlands). Sequences editing was done in the software Codoncode Aligner v10.0.2, and the alignment was performed in the same software using the MUSCLE algorithm (Edgar, 2004). Intra and interspecific distances (Kimura 2-parameter mo Kimura, 1980) were calculated using the software MEGA7 (Kumar et al., 2016). The TCS haplotype network (Clement et al., 2002) was generated in the software PopART (http://popart.otago.ac.nz). All sequences and collection data are listed in the project CTENU available on the Barcode of Life Data System (https://bench.boldsystems.org/index.php/MAS_Management_DataConsole? codes = CTENU; BOLD, Ratnasingham et al., 2024).

Trophic analyses

Trophic analyses of specimens of *C. nutrix* from the Kerguelen Islands and plateau were performed to characterise the species' isotopic niche (Table 2) and test for the potential link between nutrition and morphological plasticity. Observation of gut contents was combined with stable isotope analysis of carbon ($\partial^{13}C$) and nitrogen ($\partial^{15}N$). Carbon and nitrogen stable isotope ratios have proven to be one of the most reliable integrative trophic markers, and have become a near-universal tool in ecology as descriptors of consumers' trophic ecology (Boecklen et al., 2011; Layman and Allgeier, 2012). Carbon stable isotope ratios ($^{13}C/^{12}C$, most commonly expressed as $\partial^{13}C$) are conservative tracers that can be used to identify food items supporting a consumer population, either directly or indirectly. Nitrogen stable isotope ratio ($^{15}N/^{14}N$, most commonly expressed as $\delta^{15}N$) can be used to generate info about both the food sources and the trophic position of consumers (DeNiro and Epstein, 1981; Layman et al., 2012). Moreover, the isotopic composition of a consumer appeared to be influenced by both habitat and food sources (Flaherty and Ben-David, 2010; Newsome et al., 2007).

The analysed samples included a total of 49 specimens of *C. nutrix* collected from Haute Island ($n = 15$, shallow sheltered site), Suhm Island ($n = 20$, shallow exposed sites), and the Kerguelen plateau ($n = 14$, deep sites) (Table 2). Specimens from the shallow,

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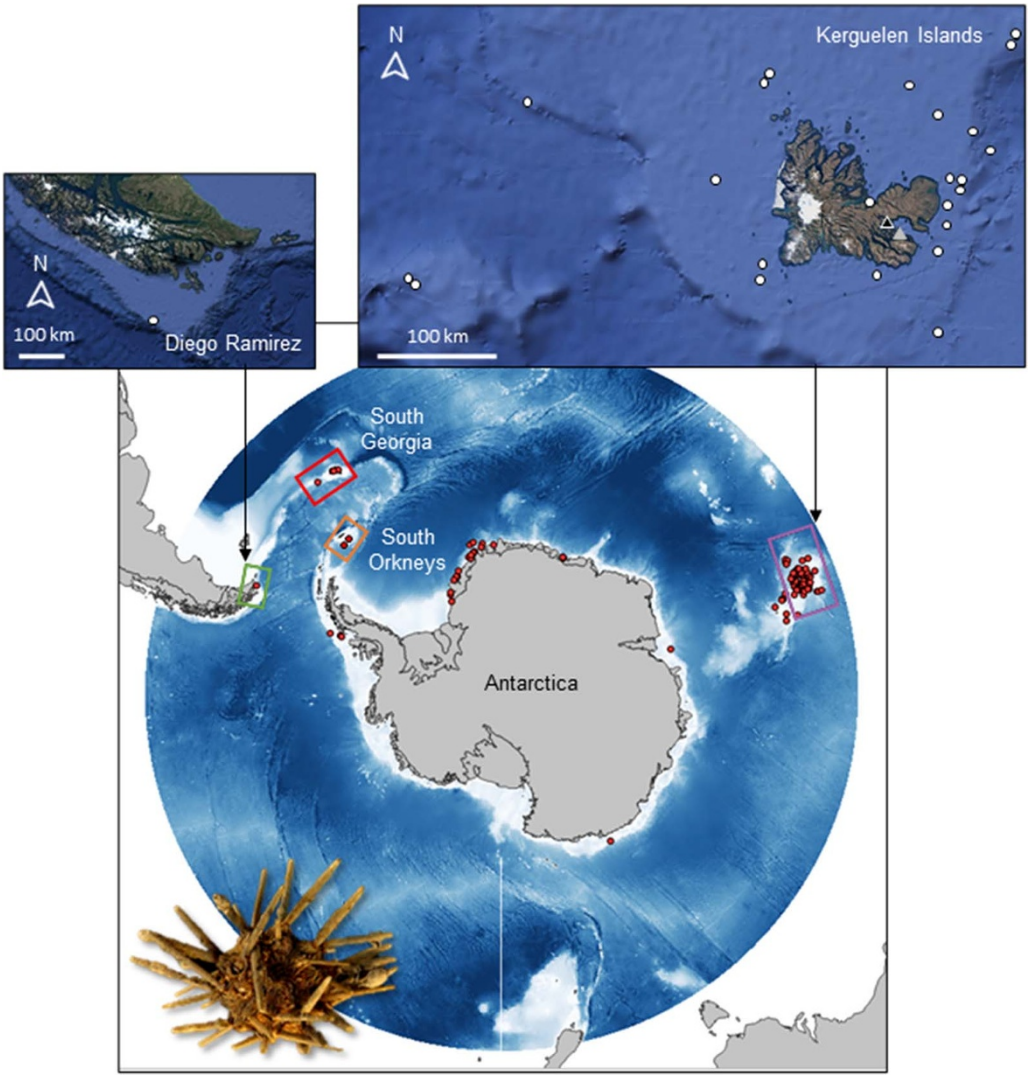


Figure 1. Occurrence data of *Ctenocidaris nutrix* and *Ctenocidaris* sp. In the Southern Ocean according to Fabri-Ruiz et al. (2017) (red dots). Sampling sites of studied specimens from Diego Ramirez (Chilean sub-Antarctic Island), the Kerguelen Islands (white dots: Kerguelen plateau, black triangle: Haute Island, grey triangle: Suhm Island), South Georgia, South Orkney Islands, and maritime Antarctica. Of *C. nutrix* in Diego Ramirez and the Kerguelen Islands (white dots: Kerguelen plateau, black triangle: Haute Island, grey triangle: Suhm Island).

Table 1. Studied species, sampling campaigns, sampling locations, and curation institutions

Studied species	Institutions	Campaigns	Stations	Location
Ctenocidaris sp.	UBE	ANTXXIX/3	193, 196, 197, 199	BS
		ANTXXIII/8	603	WS
		JR230	11, 20, 21	AP
		JR262	32, SR3	SG
		JR15005	31, 33	SO
	MNHN	CEAMARC	30	EA
Ctenocidaris nutrix	MNHN	POKER 2	39, 40, 52, 77, 78, 85. 86, 97, 98, 99, 100, 101, 102, 103, 135, 144, 149, 168, 183, 185, 203	KP
	BAS	ACE	74	DR
	UBE	PROTEKER 2. 3. 4. 7	Haute, Suhm, Port Couvreux	KI
Ctenocidaris rugosa	MNHN	CEAMARC	02, 71	EA

AP, Antarctic Peninsula; BS, Bransfield Strait; DR, Diego Ramirez; EA, East Antarctica; KI, Kerguelen Islands (Haute, Suhm, and Port Couvreux); KP, Kerguelen Plateau; SG, South Georgia; SO, South Orkney; WS, Weddell Sea; UBE, Université Bourgogne Europe, Dijon (France); MNHN, Muséum national d'Histoire naturelle, Paris (France); BAS, British Antarctic Survey, Cambridge (UK).

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Table 2. $\delta^{13}C$ and $\delta^{15}N$ values measured in Aristotle's lantern muscles from specimens of *Ctenocidaris nutrix* from the Kerguelen Islands

Sample nb	Campaign	Station	Depth (m)	$\delta^{13}C$ ‰	$\delta^{15}N$ ‰
15	POKER 2	40	166	−20.41	13.46
225	POKER 2	85	131	−20.84	8.14
203	POKER 2	86	119	−20.59	8.27
286	POKER 2	86	119	−20.82	8.26
207	POKER 2	97	76	−17.94	10.58
1164	POKER 2	98	120	−21.44	7.26
1213	POKER 2	99	105	−20.80	8.10
1214	POKER 2	99	105	−20.97	8.21
1108	POKER 2	100	74	−18.92	9.22
246	POKER 2	144	169	−21.21	10.89
328	POKER 2	149	221	−20.69	12.72
835	POKER 2	168	196	−20.67	13.47
715	POKER 2	183	248	−20.49	13.77
687	POKER 2	185	327	−20.78	13.73
PTK4_46 − 07	PROTEKER 4	Haute Isl.	6	−14.58	12.69
PTK4_46 − 08	PROTEKER 4	Haute Isl.	6	−14.71	12.74
PTK4_46 − 09	PROTEKER 4	Haute Isl.	6	−15.19	12.47
PTK4_46 − 10	PROTEKER 4	Haute Isl.	6	−15.33	12.72
PTK4_46 − 11	PROTEKER 4	Haute Isl.	6	−14.92	13.48
PTK4_46 − 12	PROTEKER 4	Haute Isl.	6	−15.44	12.68
PTK4_46 − 13	PROTEKER 4	Haute Isl.	6	−14.65	13.34
PTK4_46 − 14	PROTEKER 4	Haute Isl.	6	−14.17	14.43
PTK4_46 − 15	PROTEKER 4	Haute Isl.	6	−15.34	12.20
PTK4_46 − 16	PROTEKER 4	Haute Isl.	6	−14.85	13.20
PTK4_46 − 17	PROTEKER 4	Haute Isl.	6	−15.07	13.18
PTK4_46 − 18	PROTEKER 4	Haute Isl.	6	−14.50	13.77
PTK4_46 − 19	PROTEKER 4	Haute Isl.	6	−14.94	12.61
PTK4_46 − 20	PROTEKER 4	Haute Isl.	6	−15.55	12.13
PTK4_46 − 21	PROTEKER 4	Haute Isl.	6	−15.16	12.31
PTK4_55 − 01	PROTEKER 4	Suhm Isl.	18	−16.51	11.59
PTK4_55 − 02	PROTEKER 4	Suhm Isl.	18	−16.30	12.03
PTK4_55 − 03	PROTEKER 4	Suhm Isl.	18	−16.25	12.68
PTK4_55 − 04	PROTEKER 4	Suhm Isl.	18	−16.24	12.24
PTK4_55 − 05	PROTEKER 4	Suhm Isl.	18	−16.55	12.74
PTK4_55 − 06	PROTEKER 4	Suhm Isl.	18	−16.61	12.02
PTK4_55 − 07	PROTEKER 4	Suhm Isl.	18	−15.89	11.57
PTK4_55 − 08	PROTEKER 4	Suhm Isl.	18	−16.69	11.29
PTK4_55 − 09	PROTEKER 4	Suhm Isl.	18	−16.27	11.63
PTK4_55 − 10	PROTEKER 4	Suhm Isl.	18	−16.82	11.83
PTK4_55 − 11	PROTEKER 4	Suhm Isl.	18	−16.36	12.19
PTK4_55 − 12	PROTEKER 4	Suhm Isl.	18	−16.79	12.10
PTK4_55 − 13	PROTEKER 4	Suhm Isl.	18	−16.56	12.24
PTK4_55 − 14	PROTEKER 4	Suhm Isl.	18	−16.58	12.27
PTK4_55 − 15	PROTEKER 4	Suhm Isl.	18	−16.39	12.81
PTK4_55 − 16	PROTEKER 4	Suhm Isl.	18	−16.10	12.22
PTK4_55 − 17	PROTEKER 4	Suhm Isl.	18	−16.72	11.52
PTK4_55 − 18	PROTEKER 4	Suhm Isl.	18	−16.47	11.92
PTK4_55 − 19	PROTEKER 4	Suhm Isl.	18	−16.49	11.91
PTK4_55 − 20	PROTEKER 4	Suhm Isl.	18	−16.43	12.11

sheltered site of Haute Island, and from the deep Kerguelen plateau, presented the *C. nutrix longispina* form, while specimens from the shallow, exposed site of Suhm Island corresponded to the typical *C. nutrix nutrix* form. All collected specimens were immediately frozen at −20°C after sampling for further stable isotope analysis. Isotopic measurements were performed on the muscles of the Aristotle's lantern, a soft, non-metabolically active tissue. After dissection, tissue samples were washed with distilled water, frozen at –80°C for a few hours, and freeze-dried. Then samples were cryo-crushed with liquid nitrogen and decarbonated under HCl (37% v/v) vapours for 24 hours. Isotopic ratios were determined by dry combustion using an elemental analyser (Vario Micro Cube, Elementar) coupled to an isotopic mass spectrometer (Isoprime, Elementar). Analytical reproducibility was 0.15‰ for carbon and 0.2‰ for nitrogen. Isotopic values are reported in parts per thousand (‰) and expressed relative to the conventional standards, Vienna Pee Dee Belemnite (VPDB) for carbon (Craig, 1953)

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Table 3. Morphology and anatomy of *Ctenocidaris nutrix*

Campaign	Site	Depth (m)	Sample	D (mm)	H (mm)	Ap (mm)	Per (mm)	Sp (mm)	Pyr (mm)	Tth (mm)	GW (g)	TW (g)	COI	ISO
POKER 2	40	167	15	34.8	20.5	14.3	15.1	45.6					x	x
POKER 2	78	599	387	40.5	23	18.8	15.1						x	
POKER 2	85	133	225	31	17.1	14.2	11.9	30.6					x	x
POKER 2	86	119	203	34.7	19.9	17	13.7	44.3					x	x
POKER 2	86	119	286	30.5	16	11.8	12.5						x	x
POKER 2	97	82	207	30.1	16.3	13.5	12	25.7					x	x
POKER 2	98	123	1164	22.7	12	11.3	9.8	39					x	x
POKER 2	99	106	1213	25.8	13.7	11.9	11	33.6					x	x
POKER 2	99	106	1214	27.8	13.1	12.3	11.8	34.9					x	x
POKER 2	100	78	1108	31.6	16	15.8	13	32					x	x
POKER 2	100	78	1067	42	24	19.6	15.8	44.4					x	
POKER 2	103	636	1011	36.1	19.6	19.7	15.9						x	
POKER 2	144	170	246	32.9	19.3	15.6	12.9	30.6					x	x
POKER 2	149	224	328	32	17.8	13.5	11.8	35.4					x	x
POKER 2	168	196	835	40.2	25.4	17	17.3	48.1					x	x
POKER 2	183	249	715	27.7	18.8	12.6	11.4	64.9					x	x
POKER 2	185	363	687	32.2	17.7	15.1	11.9	40.6					x	x
POKER 2	195	318	1306	42	26.4	21.7	16.9						x	
POKER 2	203	139	18	40.4			14.3	54.4					x	
PROTEKER 4	Haute Isl.	6	26 − 1	31.3		9.6	11		4.77	2.79			x	
PROTEKER 4	Haute Isl.	6	26 − 2	26.6		10.7	8.4		4.4	2.36			x	
PROTEKER 4	Haute Isl.	6	46 − 1	32	20.6	12.5	9.9		5.4	2.78	0.25 (M)	8.05		
PROTEKER 4	Haute Isl.	6	46 − 2	29.7	19.5	12.6	7.2		5.21	2.67	0.35 (M)	7.15		
PROTEKER 4	Haute Isl.	6	46 − 3	28.2	16.7	12.6	10.5		4.58	2.59	0.35 (F)	5.95	x	
PROTEKER 4	Haute Isl.	6	46 − 4	30.3	20.7	10.5	9		5.86	2.87	0.3 (M)	8		
PROTEKER 4	Haute Isl.	6	46 − 5	26.6	16	11.6	9.5		4.71	2.39	0.4 (M)	6.75		
PROTEKER 4	Haute Isl.	6	46 − 6	27	12.3	11.3	7.82		4.63	2.56	0.35 (M)	5.7	x	

(*Continued*)

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Table 3. (*Continued.*)

Campaign	Site	Depth (m)	Sample	D (mm)	H (mm)	Ap (mm)	Per (mm)	Sp (mm)	Pyr (mm)	Tth (mm)	GW (g)	TW (g)	COI	ISO
PROTEKER 4	Haute Isl.	6	46 − 7	30.75	19	11.15	6.02		5.68	2.7	0.2 (F)	8.4	x	x
PROTEKER 4	Haute Isl.	6	46 − 8	28.65	20.09	13.18	9.76		4.96	2.22	0.25 (M)	8.1	x	x
PROTEKER 4	Haute Isl.	6	46 − 9	29.4	22.95	11.77	8.87		5.85	2.56	0.25 (F)	6.7		x
PROTEKER 4	Haute Isl.	6	46 − 10	38.95	23.55	14.6	10.35		5.96	3.04	0.65 (M)	11.9	x	x
PROTEKER 4	Haute Isl.	6	46 − 11	32	18.3	12.3	10		4.97	2.97	0.25 (F)	6.15		x
PROTEKER 4	Haute Isl.	6	46 − 12	24	14.3	11.4	11.2				0.2 (F)	3.9	x	x
PROTEKER 4	Haute Isl.	6	46 − 13	29.6	20.4	14	12		5.3	2.96	0.25 (M)	7.25		x
PROTEKER 4	Haute Isl.	6	46 − 14	29	15	19.6	10.3		4.59	2.94	0.2 (F)	6.4	x	x
PROTEKER 4	Haute Isl.	6	46 − 15	29.9	20	11	10		6.22	2.96	0.7 (F)	8.35		x
PROTEKER 4	Haute Isl.	6	46 − 16	31.2	22	12.4	12.2		5.74	3.06	0.15 (M)	7.55	x	x
PROTEKER 4	Haute Isl.	6	46 − 17	28.7	19	11.6	10		5.27	3.27	0.3 (M)	5.55	x	x
PROTEKER 4	Haute Isl.	6	46 − 18	26.5	16.1	11.3	11.3	24.20						x
PROTEKER 4	Haute Isl.	6	46 − 19	15	8.5	6.9	8	23.10						x
PROTEKER 4	Haute Isl.	6	46 − 20	22	12.6	10.6	10.6	26.40						x
PROTEKER 4	Haute Isl.	6	46 − 21	26.9	17.7	10.2	11.8	20.20						x
PROTEKER 4	Suhm Isl.	18	55 − 1	27.9	15.3	9.4	10.6		4.64	2.52	0.7 (F)	9.4		x
PROTEKER 4	Suhm Isl.	18	55 − 2	24.6	15.4	11.3	10.5		4.17	2.53	0.4 (M)	7.25	x	x
PROTEKER 4	Suhm Isl.	18	55 − 3	27.4	16.7	10.1	10.6		4.85	2.83	0.85 (M)	7.6		x
PROTEKER 4	Suhm Isl.	18	55 − 4	28.6	16.8	10.8	12		5.13	2.5	0.7 (M)	9.3		x

(*Continued*)

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Table 3. (*Continued.*)

Campaign	Site	Depth (m)	Sample	D (mm)	H (mm)	Ap (mm)	Per (mm)	Sp (mm)	Pyr (mm)	Tth (mm)	GW (g)	TW (g)	COI	ISO
PROTEKER 4	Suhm Isl.	18	55 − 5	31.2	20.6	11.4	9.6		5.53	2.78	0.6 (M)	8.85		x
PROTEKER 4	Suhm Isl.	18	55 − 6	28.4	16.2	10.5	11.5		4.76	2.91	0.5 (F)	8.25		x
PROTEKER 4	Suhm Isl.	18	55 − 7	26.3	17.2	9.7	11.5		5.62	2.64	0.55 (M)	8.9		x
PROTEKER 4	Suhm Isl.	18	55 − 8	26.4	13.8	9.8	10.9		4.46	2.88	0.45 (F)	7.15		x
PROTEKER 4	Suhm Isl.	18	55 − 9	26.4	13.4	10.2	10.7		5.23	2.52	0.8 (M)	8.25	x	x
PROTEKER 4	Suhm Isl.	18	55 − 10	23.5	14.5	9.4	10.6		5.05	3.02	0.35 (F)	7		x
PROTEKER 4	Suhm Isl.	18	55 − 11	30	19.9	14.7	7.8		5.83	2.2	0.25 (M)	9.75		x
PROTEKER 4	Suhm Isl.	18	55 − 12	29.7	16.1	10.7	11.3		5.19	2.35	0.3 (F)	8.1		x
PROTEKER 4	Suhm Isl.	18	55 − 13	25.4	15	9	10.3		4.77	2.27	0.35 (M)	7.1	x	x
PROTEKER 4	Suhm Isl.	18	55 − 14	32	19	14.5	8		4.98	2.5	0.45 (F)	8.6	x	x
PROTEKER 4	Suhm Isl.	18	55 − 15	29	19.2	10	9.9		5.07	3.28	0.15 (M)	8.45		x
PROTEKER 4	Suhm Isl.	18	55 − 16	30.8	21	10.9	10.7		5.04	2.51	0.3 (M)	6.85	x	x
PROTEKER 4	Suhm Isl.	18	55 − 17	24	15.5	11.4	9.2		4.59	2.49	0.3 (F)	5.45		x
PROTEKER 4	Suhm Isl.	18	55 − 18	26.6	17.5	9.6	8.6		5.50	1.99	0.5 (F)	6.85		x
PROTEKER 4	Suhm Isl.	18	55 − 19	27.3	16.6	10.8	9.2		4.1	2.69	0.3 (F)	5.45		x
PROTEKER 4	Suhm Isl.	18	55 − 20	26.1	14	9.6	7.2		4.23	2.24	0.2 (F)	5.75		x
PROTEKER 4	Suhm Isl.	18	55 − 21	29.6	17.6	11.3	11.8	22.4						
PROTEKER 4	Suhm Isl.	18	55 − 22	22.5	13.5	10.8	10	20						
PROTEKER 4	Suhm Isl.	18	55 − 23	26.2	15.6	12.2	11.5	16.9						
PROTEKER 4	Suhm Isl.	18	55 − 24	25.6	15.9	12.2	10.8	20.1						

Measurements of echinoid test and Aristotle's lantern, along with gonads and tegument dry weights.
D, test diameter; H, test height; Ap, apex diameter; Per, peristome diameter; Sp, mean spine length; Pyr, pyramid height; Tth, tooth length; GW, gonad dry weight (F, female; M, male); TW, tegument dry weight; COI, COI successfully sequenced specimen; ISO, analyzed ∂13C and ∂15N isotope values (see Table 2).

Table 4. Three way ANOVA of biomechanics test realized on primary spines of specimens from Haute and Suhm Islands

Source	Sum of Squares	*df*	Mean Squares	*F*-ratio	*p*-value
Site	0.196	1	0.196	0.133	0.726
Specimen	10.342	7	1.477		
Spine position on test	1.603	4	0.401	0.569	0.687
Position*Site	3.048	4	0.762	1.082	0.383
Position*Specimen	21.841	31	0.705		
Error	0	0			

and atmospheric N_2 for nitrogen (Coplen, 2011; Mariotti, 1983). Certified USGS40 ($\delta^{13}C = -26.39‰$; $\delta^{15}N = -4.5‰$) and Caffeine IAEA-600 ($\delta^{13}C = -27.77‰$; $\delta^{15}N = 1‰$) international reference materials were used for the calibration. The Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al., 2011) was used to generate bivariate standard ellipses (SEs). SEs are the bivariate equivalents of standard deviation. They contain only the 'typical' members of a population (but may not encompass outlier individuals in isotopic space). For this reason, they have been termed 'core isotopic niches', as their area (standard ellipse area [SEA]) can be used as a proxy of resources most commonly used by the population (Layman and Allgeier, 2012). In addition to stable isotope analysis, the gut content of freshly collected specimens (Proteker 4 campaign) of the two shallow sites of Haute and Suhm Islands was characterised after dissections using a binocular microscope.

Morphology and biomechanics

Morphological plasticity was characterised in specimens of *C. nutrix* from the Kerguelen Islands. Measurements were performed using a digital calliper with a resolution of 0.01 mm. Measured parameters include test diameter (D) and height (H), diameter of the apical system (Ap) and of the peristome (Per), and average primary spine length (Sp: mean length of all primary spines in a half interambulacrum). Specimens from Haute and Suhm Islands were further investigated to determine the individual mean height of the Aristotle's lantern pyramids (Pyr) and tooth length (Tth), as the size of the jaw may change with food availability (Ebert, 1996). After dissecting the lantern and splitting each pyramid using a scalpel, the five pyramids were measured in each individual from the epiphysis junction to the labial tip, not including teeth. Then the five teeth were measured in each individual from the labial tip of the pyramid to the extremity of the tooth. Total gonad (GW) and tegument (TW) dry weights were also measured with a resolution of 0.01 g (Table 3).

To determine whether phenotypes also differed in the structural properties of the skeleton (Hughes et al., 2012) between the two sites of Haute and Suhm Islands, five specimens were selected in each site for biomechanical assessment of spine resistance to a two-point bending/breaking test following the methodology of Moureaux et al. (2010). For each individual, four to five primary spines were taken in the same interambulacral column, from the apex to the adoral side, and used for biomechanical assessment. Prior to mechanical testing, primary spines were cleaned using a NaOCl solution, and their total length was measured. Then, the base of the spines was fixed in a resin for the two-point bending test, realised by applying an increasing force perpendicular to the spine extremity using a bench press equipped with a 100 N unit (following Moureaux et al., 2010) to determine the breaking force (Fmax). Results were analysed using a 3-way ANOVA, with site, specimen, and spine position on the test used as independent variables, and Fmax as the dependent variable (model 6.3.i of Doncaster and Davey, 2007) (Table 4).

Results

Molecular analyses

Three close COI mtDNA haplotypes were identified in the 76 sequenced specimens from the Kerguelen and Diego Ramirez Islands (Figure 2). One of these haplotypes was highly frequent, being present in 74 specimens from both nearshore sites and the plateau of Kerguelen, and as far as Diego Ramirez Island. As highlighted by Saucède et al. (2024), the two forms of *C. nutrix*, the typical short-spined *C. nutrix nutrix* and the long-spined *C. nutrix longispina*, shared the same COI mtDNA haplotype disregarding of location, water depth and exposure.

In contrast, morphologically close specimens from South Georgia, the South Orkneys and the Antarctic, formerly identified as *C. nutrix,* belonged to two differentiated entities, with over 3% genetic distance from haplotypes of *C. nutrix* from Kerguelen and Diego Ramirez Islands. Specimens from the East Antarctic matched with the species *Ctenocidaris rugosa*. Other Antarctic and sub-Antarctic specimens showed distinct haplotypes of an unknown species here referred to as *Ctenocidaris* sp. (Figure 2).

Trophic analyses

The observation of gut contents in specimens from Haute and Suhm Islands revealed that the main diet of all study *C. nutrix* individuals is composed of large (3–5 mm wide) bites of fresh and intact sponge pieces from different taxa, according to the different colours and spicules of sponge remains, along with many diatoms. Important differences could, however, be noticed between the two sites. Long-spined specimens from Haute Island only fed on sponges and diatoms, while short-spined specimens from Suhm Island showed a much more varied diet composed of various biological detritus of ascidians, bryozoans, crustaceans, and seaweeds in addition to sponge and diatom remains (Figure 3). These specimens also ingested sedimentary particles.

$\delta^{13}C$ and $\delta^{15}N$ significantly differed between populations of Haute and Suhm Islands (Wilcoxon *t*-test, $p < 0.001$), with less negative $\delta^{13}C$, higher $\delta^{15}N$, and more dispersed values at Haute compared to Suhm (Figure 4). SEAs computed for nearshore populations from Haute and Suhm, along with deep samples from the Kerguelen plateau, clearly showed different niche positions for the three populations (Figure 4). Compared to the two nearshore sites, $\delta^{13}C$ values from the plateau were significantly more negative and $\delta^{15}N$ values were also more dispersed. For these last samples, the dispersion of $\delta^{15}N$ is probably partly related to the greater geographical distance between sites.

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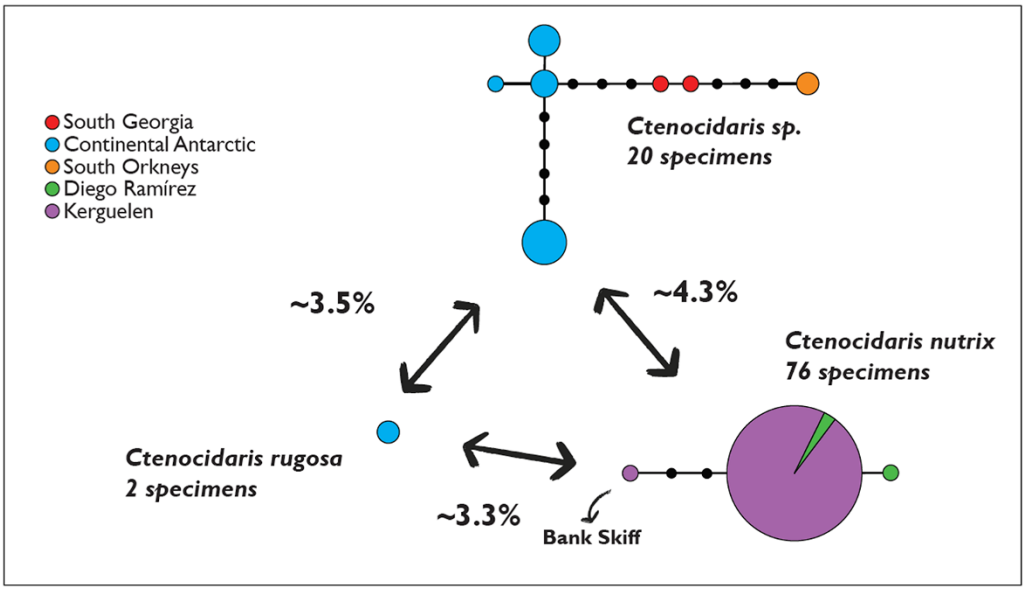


Figure 2. Molecular analyses. TCS haplotype network (COI mtDNA) and genetic distances between clades. Different colours denote distinct geographic locations.

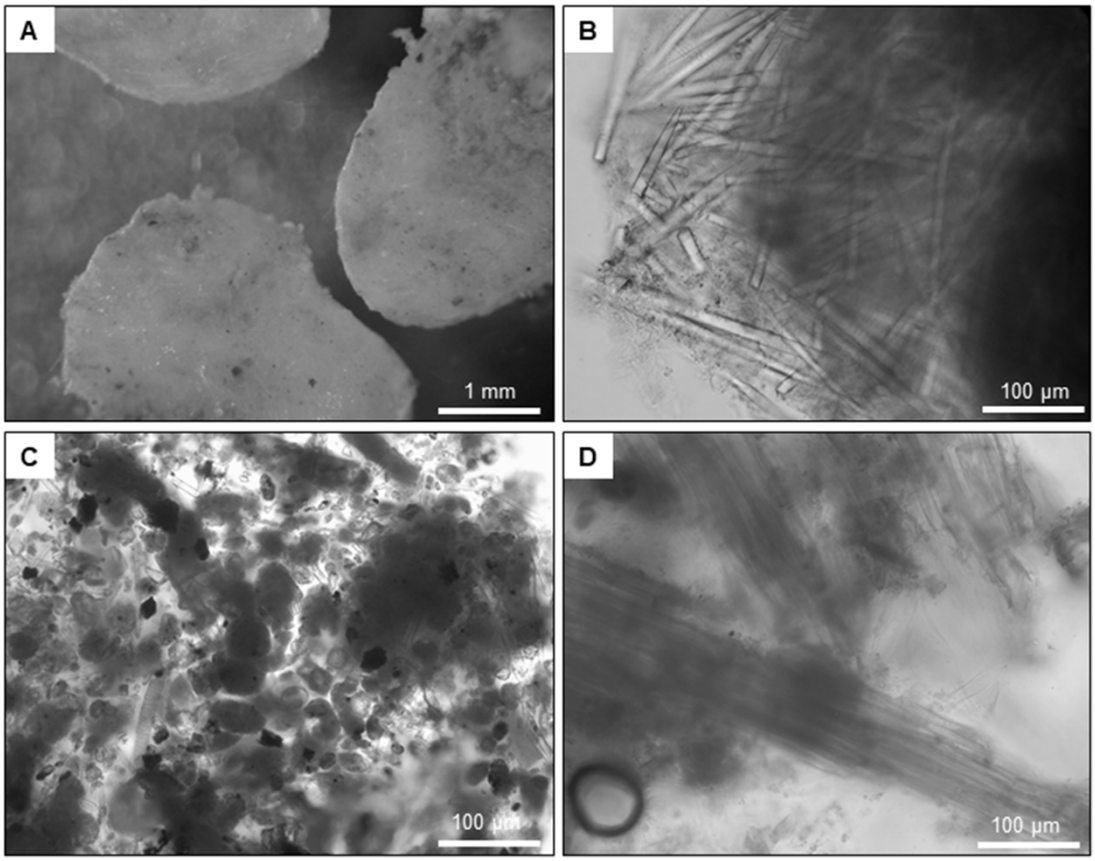


Figure 3. Biological detritus ingested by specimens of *Ctenocidaris nutrix* at Haute (A, B) and Suhm (C, D) Islands. (A) Large bites of intact sponges. (B) Detail of sponge spicules. (C) Diverse biological detritus. (D) Remains of macroalgae. Images taken under a stereo (A) and a zoom microscope (B–D).

Morphometry and biomechanical assessment

Morphological and anatomical differences were tested between specimens of Haute and Suhm Islands. Only four characters significantly differed between the two populations (Student's *t*-test, $p < 0.05$): the absolute apex diameter (AD), the relative spine length (SL/H*D), the ratio between spine diameter and length (SD/SL), and the gonad dry weight (GW). Along with relatively shorter and broader spines, specimens from Suhm also showed a narrower apex relative to test diameter and heavier gonads.

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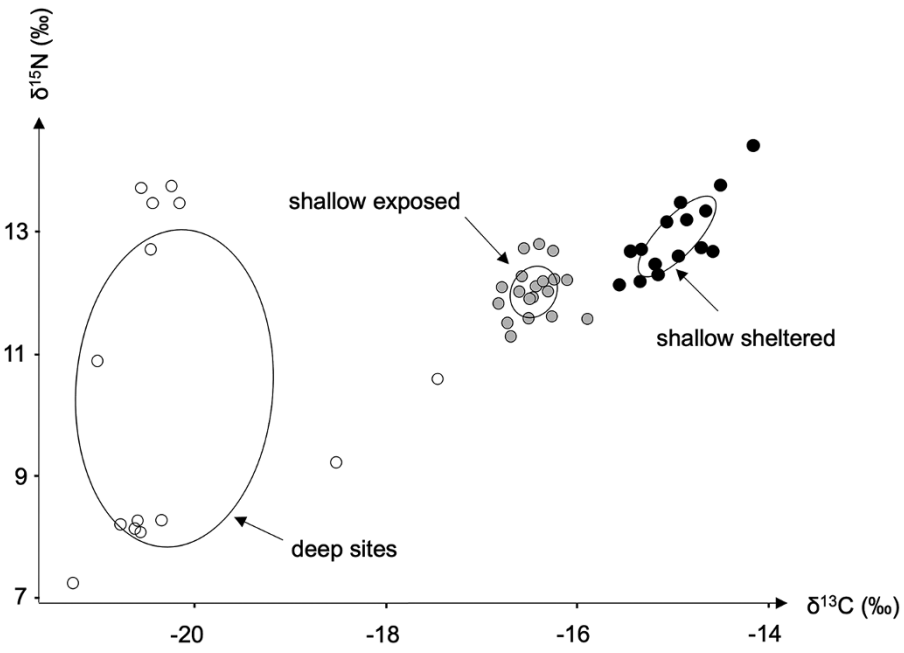


Figure 4. $\delta^{13}C$ and $\delta^{15}N$ values of *Ctenocidaris nutrix* for the shallow sheltered site of Haute Island, shallow exposed site of Suhm Island, and deeper sites of the Kerguelen plateau. Points are individual measurements. Solid lines are standard ellipses.

In contrast, specimens from Haute had lighter gonads, longer and thinner spines, and a wider apex. Biomechanical assessment of spine resistance to breaking showed no significant difference between specimens of the two sites (Table 4).

Discussion

Species identity and distribution range

Studying phenotypic plasticity has practical importance in ecology and evolution, as well as for systematics and taxonomy (Schlichting and Pigliucci, 1998; Whitman and Agrawal, 2009). In the present study, the obtained COI mtDNA sequences indicated that the two forms of *C. nutrix*, the typical short-spined *C. nutrix nutrix* and the long-spined *C. nutrix longispina,* share the same COI haplotype (100% similarity between samples), which suggests that the two forms are one and a single species restricted to sub-Antarctic waters. Thomson (1876) first described the species *C. nutrix* based on one specimen collected in 1874 at the entrance of the Royal Sound of the Kerguelen Islands, between 90 m and 130 m depth. Then Mortensen (1928) recognised a distinct variety, and perhaps a separate species (or subspecies in subsequent works), a long-spined form, *C. nutrix longispina*, based on one specimen collected at 270 m depth (150 fathoms) by the RV *Challenger* off Heard Island. This long-spined form mainly differs in the length of primary spines, 2–2.5 times the horizontal diameter of the test, against 1–1.5 in the *C. nutrix nutrix* typical form. The formal distinction between the two forms was challenged by Fell (1976), then by De Ridder et al. (1992), followed by David et al. (2005), who report distinct biogeographic patterns for the two forms with the typical form distributed in sub-Antarctic waters of the Kerguelen and Heard Islands, and the *longispina* form off Heard Island, Prydz Bay, and the East Weddell Sea (David et al., 2005). So far, the species *C. nutrix* was then considered to have a wide and unusual distribution range for a cidaroid echinoid (from the shoreline to 840 m depth, and from the sub-Antarctic Islands to the Antarctic coasts (76°S–47°S) (David et al., 2005; De Ridder et al., 1992; Jacob et al., 2003; Lockhart et al., 1994). Results of the present study refine our knowledge of the taxonomy and distribution of *C. nutrix*, which seems, regardless of shape variations, to be restricted to sub-Antarctic coastal waters and offshore areas, from Diego Ramirez Island in the west to the Kerguelen plateau in the east (Figure 1). In echinoid systematics, there are other examples of species differentiated from each other based only on spine length. The echinoids *Lytechinus pictus* Verrill, 1867 and *Lytechinus anamesus* Clark, 1912 were formerly thought to be distinct species based on the difference in spine length (Mortensen, 1943) before the species value of the character was questioned (Clark, 1940). *L. pictus* has short spines and lives in shallow waters, while *L. anamesus* has long spines and occurs in deep waters (Clark, 1940). The two forms are now synonymised under the name *L. pictus* (Kroh and Mooi, 2025).

Trophic ecology

In the present work, the analysis of the carbon and nitrogen stable isotope compositions in the three populations of *C. nutrix* was comparable to those measured in secondary consumers in Antarctic invertebrates (Le Bourg et al., 2022; Michel et al., 2016; Mincks et al., 2008) and, in particular, in Antarctic cidaroids, which were shown to feed on live invertebrates (mostly sponges), carrions and sediment detritus (Michel et al., 2016). Along with gut content observations, our results confirm that *C. nutrix* is a carnivore that holds a relatively high position in the food webs (Jacob et al., 2003; Saucède et al., 2019) and can occasionally feed on biological detritus and sediment particles.

The observation of gut contents and stable isotope compositions provides congruent results showing that the three analysed populations have different diets, suggesting significant trophic plasticity in *C. nutrix*. This could be influenced by local food availability, but is likely linked with active prey selection by the echinoids. The two nearshore sites of Haute and Suhm Islands are indeed characterised by similar benthic communities and potential food sources, even if exposure differs between the two sites (Féral et al., 2019). Our results also showed a high inter-individual variation in

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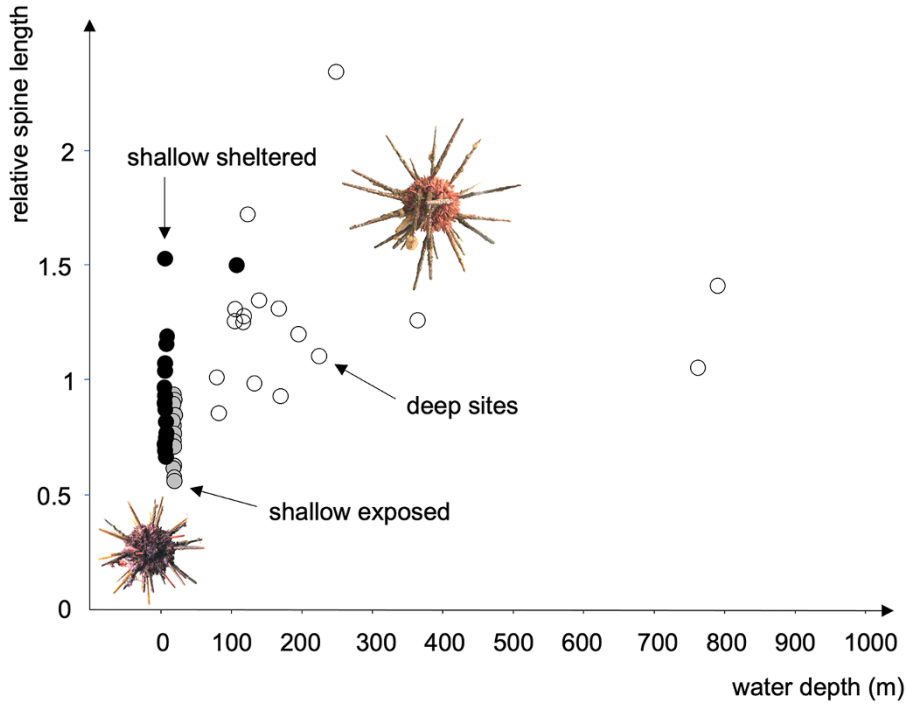


Figure 5. Relative spine length (ratio of spine length over test diameter) of *Ctenocidaris nutrix* as a function of water depth (m) for the shallow sheltered site of Haute Island, shallow exposed site of Suhm Island, and deeper sites of the Kerguelen plateau.

the importance of animal-derived material for the nutrition of the species. This was already reported in sub-Antarctic, as well as in Antarctic cidaroid echinoids that can shift their diet from detritus to carnivory and scavenging in relation to spatial changes in environmental conditions and presumably prey availability (Michel et al., 2016; Saucède et al., 2019). Echinoid diet could also differ according to water temperature and depth (Mincks et al., 2008). This suggests that *C. nutrix* could have a high trophic plasticity that may be beneficial regarding resilience to environmental changes.

Phenotypic plasticity

As formerly demonstrated in broadcasting echinoid species (Ebert, 1996; Hughes et al., 2012), morphological plasticity here appeared to be mainly linked to abiotic environmental parameters, mainly depth and swell exposure, specimens from exposed and shallow sites showing shorter spines and larger apical systems compared to specimens from sheltered or deep sites (Figure 5). The evolution of phenotypic plasticity is usually expected to benefit species with broadcasting larvae as an adaptation to a heterogeneous environment (Ebert, 1996; Parsons, 1998). Here we show that phenotypic plasticity can also occur in a brooding cidaroid echinoid.

In the studied populations of *C. nutrix*, variations in the relative length of primary spines and size of the apex (higher in the population from Haute Island) seem to be inversely related to the gonad dry weight (higher in the population from Suhm Island). This situation is usually expected as the reallocation of resources to repair damages (calcification) in populations of exposed sites implies a decrease in the mass of gonads, which are also storage organs after their primary function is involved in reproduction (Ebert, 1996). However, in the present case study, phenotypes with long spines were found in sheltered and deep sites, while short-spined phenotypes with larger gonads were reported in the exposed site. This suggests that in the studied populations, the hypothesis that morphological plasticity is a direct response to changes in the abiotic environment, here represented by depth and swell exposure, is not verified.

In former studies (Ebert, 1996), a decrease in gonad dry weight, and conversely, an increase in the size of the Aristotle's lantern and spine growth were also shown to be a phenotypic response to variations in food availability. In contrast, other studies argued that morphological plasticity may also be independent of food limitation, but may result from changes in the trophic environment or the prey type (Hughes et al., 2012). In the studied populations, no significant difference in the size of the Aristotle's lantern (pyramid and tooth length) was found between habitats, excluding the direct effect of food limitation. However, significant differences in the diet and trophic niche between populations of *C. nutrix* suggest that the prey type and ingested food diversity (only sponges and diatoms at Haute Island vs. a more diverse diet composed of various detrital remains at Suhm Island) may be a factor promoting distinct phenotypic responses, both in the diet and morphology of echinoids. Phenotypic variation in response to changing trophic environments can increase the species' niche through the widening of its diet or the variation between individual diet breadth (Hughes et al., 2012). In the Kerguelen Islands, trophic plasticity in the cidaroid *C. nutrix* would contribute to increasing its ecological niche.

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Author contributions. T.S., P.D., L.M., C.D.R., C.M., Q.J., and O.M. designed the study, conceived the analyses, and analysed the data. T.S. and S.M. collected the specimens in the field. T.S., C.D.R., M.C., A.L.S., and S.M.Z. performed the observations, the experiments and the analyses. T.S. wrote the paper with input from all authors.

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References

Boecklen WJ, Yarnes CT, Cook BA and James AC (2011) On the use of stable isotopes in trophic ecology. *Annual Review of Ecology, Evolution, and Systematics* **42**, 411–440.

Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Advance in Genetics* **13**, 115–155.

Clark HL (1940) Notes on Echinoderms form the W. Coast of central America. *Zoologica* **25**, 348.

Clement M, Snell Q, Walker P, Posada D and Crandall K (2002) TCS: estimating gene genealogies. In *Proceedings 16th International Parallel and Distributed Processing Symposium. Ft. Lauderdale, FL, USA*, p. 184. https://doi.org/10.1109/IPDPS.2002.101658.

Coplen TB (2011) Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. *Rapid Communications in Mass Spectrometry* **25**, 2538–2560.

Craig H (1953) The geochemistry of the stable carbon isotopes. *Geochimica Cosmochimica Acta* **3**, 53–92.

David B, Choné T, Mooi R and De Ridder C (2005) *Antarctic Echinoidea. Synopses of the Antarctic benthos*. Königstein: Koeltz Scientific Books.

De Ridder C, David B and Larrain A (1992) Antarctic and Subantarctic echinoids from 'Marion Dufresne' expeditions MD03, MD04, MD08, and from the 'Polarstern' expedition EposIII. *Bulletin du Muséum National d'Histoire Naturelle de Paris* **4**, 405–441.

DeNiro MJ and Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochimica Cosmochimica Acta* **45**, 341–351.

DeWitt TJ and Langerhans RB (2004) Integrated solutions to environmental heterogeneity. In DeWitt TJ and Scheiner SM (eds), *Phenotypic Plasticity: Functional and Conceptual Approaches*. Oxford: Oxford University Press, 98–111.

DeWitt TJ and Scheiner SM (2004) *Phenotypic Plasticity: Functional and Conceptual Approaches*. Oxford: Oxford University Press.

DeWitt TJ, Sih A and Wilson DS (1998) Costs and limits of phenotypic plasticity. *Trends in Ecology and Evolution* **13**, 77–81.

Doncaster C and Davey AJH (2007) *Analysis of Variance and Covariance: How to Choose and Construct Models for the Life Sciences*. Cambridge: Cambridge University Press.

Duhamel G (2011) *Poker 2, Deuxième Campagne D'évaluation de la Biomasse de Poissons À Kerguelen*. Paris: Muséum national d'Histoire naturelle.

Ebert TA (1980) Relative growth of sea urchin jaws: an example of plastic resource allocation. *Bulletin of Marine Science* **30**, 467–474.

Ebert TA (1996) Adaptive aspects of phenotypic plasticity in echinoderms. *Oceanologica Acta* **19**, 347–355.

Edgar RC (2004) MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* **32**, 1792–1797. https://doi.org/10.1093/nar/gkh340.

Edwards PB and Ebert TA (1991) Plastic responses to limited food availability and spine damage in the sea-urchin *Stronglycentrotus purpuratus* (Stimpson). *Journal of Experimental Marine Biology and Ecology* **145**, 205–220.

Fabri-Ruiz S, Saucède T, Danis B and David B (2017) Southern Ocean Echinoid database. *Zookeys* **697**, 1–20.

Fell FJ (1976) *The Cidaroida (Echinodermata: Echinoidea) of Antarctica and the Southern oceans*. PhD thesis. USA: University of Maine.

Fenaux L, Strathmann MF and Strathmann RA (1994) Five tests of food-limited growth of larvae in coastal waters by comparisons of rates of development and form of echinoplutei. *Limnology and Oceanography* **39**, 84–98.

Féral J-P, Poulin E, González-Wevar CA, Améziane N, Guillaumot C, Develay E and Saucède T (2019) Long-term monitoring of coastal benthic habitats in the Kerguelen Islands: a legacy of decades of marine biology research. In Welsford D, Dell J and Duhamel G (eds), *The Kerguelen Plateau: Marine Ecosystem and Fisheries. Proceedings of the Second Symposium*. Kingston, Tasmania, Australia: Australian Antarctic Division, 383–402.

Flaherty EA and Ben-David M (2010) Overlap and partitioning of the ecological and isotopic niches. *Oikos* **119**, 1409–1416.

Fordyce JA (2006) The evolutionary consequences of ecological interactions mediated through phenotypic plasticity. *Journal of Experimental Biology* **209**, 2377–2383.

Geller J, Meyer C, Parker M and Hawk H (2013) Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. *Molecular Ecology Resources* **13**, 851–861.

Guillou M, Lumingas LJL and Michel C (2000) The effect of feeding or starvation on resource allocation to body components during the reproductive cycle of the sea urchin *Sphaerechinus granularis* (Lamarck). *Journal of Experimental Marine Biology and Ecology* **245**, 183–196.

Hart MW and Strathmann RR (1994) Functional consequences of phenotypic plasticity in echinoid larvae. *Biology Bulletin* **186**, 291–299.

Hughes AD, Brunner L, Cook EJ, Kelly MS and Wilson B (2012) Echinoderms display morphological and behavioural phenotypic plasticity in response to their trophic environment. *PLoS One* **7**(8), e41243.

Jackson AL, Inger R, Parnell AC and Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology* **80**, 595–602.

Jacob U, Terpstra S and Brey T (2003) High-Antarctic regular sea urchins – The role of depth and feeding in niche separation. *Polar Biology* **26**, 99–104.

Kelly MS (2000) The reproductive cycle of the sea urchin *Psammechinus miliaris* (Echinodermata: Echinoidea) in a Scottish sea loch. *Journal of the Marine Biological Association of the United Kingdom* **80**, 909–919.

Kimura M (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* **16**, 111–120.

Kroh A and Mooi R (2025) World Echinoidea Database. *Lytechinus pictus* (Verrill, 1867). accessed through: World Register of Marine Species at: https://www.marinespecies.org/aphia.php?p=taxdetails&id=513378on2025-10-07.

Kumar S, Stecher G and Tamura K (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* **33**(7), 1870–1874.

Layman CA and Allgeier JE (2012) Characterizing trophic ecology of generalist consumers: A case study of the invasive lionfish in The Bahamas. *Marine Ecology Progress Series* **448**, 131–141.

Layman CA, Araújo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P, Rosenblatt AE, Vaudo J, Yeager LA, Post DM and Bearhop S (2012) Applying stable isotopes to examine food-web structure: An overview of analytical tools. *Biological Reviews* **87**, 545–562.

Layton KK, Corstorphine EA and Hebert PD (2016) Exploring Canadian echinoderm diversity through DNA barcodes. *PLoS One* **11**, e0166118.

Le Bourg B, Saucède T, Charpentier A, Lepoint G and Michel L (2022) What is the menu today in a subantarctic kelp food web from the Kerguelen Islands? Phytodetritus, phytoplankton and phytobenthos; not living kelp. *Marine Biology* **169**(9), 118.

Lockhart SJ, O'Loughlin PM and Tutera P (1994) Brood-protection and diversity in echinoids from Prydz Bay, Antarctica. In David B, Guille A, Féral JP and Roux M (eds), *Echinoderms Through Time (Echinoderms Dijon)*. Rotterdam: Balkema, pp. 749–756.

Mariotti A (1983) Atmospheric nitrogen is a reliable standard for natural 15N abundance measurements. *Nature* **303**, 685–687.

Michel LN, David B, Dubois P, Lepoint G and De Ridder C (2016) Trophic plasticity of Antarctic echinoids under contrasted environmental conditions. *Polar Biology* **39**, 913–923.

Mincks SL, Smith CR, Jeffreys RM and Sumida PYG (2008) Trophic structure on the West Antarctic Peninsula shelf: Detritivory and benthic inertia revealed by d13C and d15N analysis. *Deep-Sea Research II* **55**, 2502–2514.

Mortensen T (1928) *A Monograph of the Echinoidea. Vol.1 Cidaroidea*. Copenhagen: Reitzel CA.

Mortensen T (1943) *A Monograph of the Echinoidea. Vol.3.2 Camarodonta 1*. Copenhagen: Reitzel CA.

Moureaux C, Pérez-Huerta A, Compère P, Zhu W, Leloup T, Cusack M and Dubois P (2010) Structure, composition and mechanical relations to function in sea urchin spine. *Journal of Structural Biology* **170**, 41–49.

Mykles DL, Ghalambor CK, Stillman JH and Tomanek L (2010) Grand challenges in comparative physiology: Integration across disciplines and across levels of biological organization. *Integrative and Comparative Biology* **50**, 6–16.

Newsome SD, Del Rio CM, Bearhop S and Phillips DL (2007) A niche for isotopic ecology. *Frontiers in Ecology and the Environment* **5**, 429–436.

Padilla DK and Savedo MM (2013) A systematic review of phenotypic plasticity in marine invertebrate and plant systems. *Advances in Marine Biology* **65**, 67–94.

Parsons KE (1998) The Role of dispersal ability in the phenotypic differentiation and plasticity of two marine gastropods: II. Growth. *Journal of Experimental Marine Biology and Ecology* **221**, 1–25.

Ratnasingham S, Wei C, Chan D, Agda J Agda, Ballesteros-Mejia L, Ait Boutou H, El Bastami Z M, Ma E Ma, Rea D, Ho C, Telfer A, McKeowan J, Rahulan M, Steinke C, Dorsheimer J, Milton M, Hebert PDN (2024) BOLD v4: A Centralized Bioinformatics Platform for DNA-Based Biodiversity Data. In *DNA Barcoding: Methods and Protocols*, Chapter 26, pp. 403–441. New York, NY: Springer US.

Reitzel A and Heyland A (2007) Reduction in morphological plasticity in echinoid larvae: Relationship of plasticity with maternal investment and food availability. *Evolutionary Ecology Research* **9**, 109–121.

Russell MP (1998) Resource allocation plasticity in sea urchins: Rapid, diet induced, phenotypic changes in the green sea urchin, *Strongylocentrotus droebachiensis* (Muller). *Journal of Experimental Marine Biology and Ecology* **220**, 1–14.

Saucède T, Guillaumot C, Michel L, Fabri-Ruiz S, Bazin A, Cabessut M, García-Berro A, Mateos A, Mathieu O, De Ridder C, Dubois P, Danis B, David B, Díaz A, Lepoint G, Motreuil S, Poulin E and Féral J-P (2019) Modelling species response to climate change in sub-Antarctic islands: Echinoids as a case study for the Kerguelen plateau. In Welsford D, Dell J and Duhamel G (eds), *The Kerguelen Plateau: Marine Ecosystem and Fisheries. Proceedings of the Second Symposium*. Kingston, Tasmania, Australia: Australian Antarctic Division, pp. 95–116.

Saucède T, Jossart Q, Vandermeeren J, Delleuze M, Danis B and Moreau C (2024) The enigmatic echinoid *Aporocidaris incerta* (Koehler, 1902): new data suggest an unknown species and highlight new phylogenetic insights within Ctenocidaridae (Echinodermata: Echinoidea). *Cahiers de Biologie Marine* **65**, 411–418.

Saucède T, Pierrat B, Danis B and David B (2014) Chapter 10.8. Biogeographic processes in the Southern Ocean. In De Broyer C, Koubbi P, Griffiths HJ, Raymond B and Udekem d'Acoz C (eds), *Biogeographic Atlas of the Southern Ocean*. Cambridge: Scientific Committee on Antarctic Research, pp. 456–463.

Schlichting CD and Pigliucci M (1998) *Phenotypic Evolution: A Reaction Norm Perspective*. Sunderland: Sinauer Associates Inc.

Schwenk K, Padilla DK, Bakken GS and Full RJ (2009) Grand challenges in organismal biology. *Integrative and Comparative Biology* **49**, 7–14.

Selden R, Johnson AS and Ellers O (2009) Waterborne cues from crabs induce thicker skeletons, smaller gonads and size-specific changes in growth rate in sea urchins. *Marine Biology* **156**, 1057–1071.

Soars N, Prowse T and Byrne M (2009) Overview of phenotypic plasticity in echinoid larvae, 'Echinopluteus transversus' type vs. typical echinoplutei. *Marine Ecology Progress Series* **383**, 113–125.

Strathmann RR, Fenaux L and Strathmann MF (1992) Heterochronic developmental plasticity in larval sea-urchins and its implications for evolution of nonfeeding larvae. *Evolution* **46**, 972–986.

Thomson CW (1876) Notice of some peculiarities in the mode of propagation of certain echinoderms of the Southern Seas. *Journal of the Linnean Society of London, Zoology* **13**, 55–79.

van Kleunen M and Fischer M (2005) Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* **166**, 49–60.

Whitman DW and Agrawal AA (2009) What is phenotypic plasticity and why is it important? In Whitman DW and Ananthakrishna TN (eds), *Phenotypic Plasticity of Insects*. Boca Raton: CRC Press, pp. 1–63.

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