On Drivers of Species Distribution Patterns and Connectivity in the Atlantic Deep Sea

Case Studies on Benthic Invertebrate Taxa

DISSERTATION

zur Erlangung des akademischen Grades

Doctor rerum naturalium

(Dr. rer. nat.)

vorgelegt von

Jenny Neuhaus

Universität Hamburg

Fakultät für Mathematik, Informatik und Naturwissenschaften

Fachbereich Biologie

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Datum der Disputation: 24.10.2025

List of Publications and Author Contributions

– organized by the taxa of study

The Bathylasmatid Barnacle *Bathylasma hirsutum* (Hoek, 1883)

Jenny Neuhaus, Katrin Linse, Saskia Brix, Pedro Martínez Arbizu, James Taylor (2024). **Population Genetics of the Deep-Sea Acorn Barnacle *Bathylasma hirsutum* (Hoek, 1883) and the First Report of its Affiliation with a Hydrothermal Vent Field.** *Zoological Studies*, 63 (25), 1–23.

JN had the lead in project administration and data curation, following the study design of JT and SB. JN conducted morphological examinations and completed morphometric measurements initially conducted by KL and JT, where KL performed the SEM imaging and EDS measurements. JN conducted all molecular laboratory work and was in lead of the formal data analysis, aided by the support of SB and PMA. JN indexed the ROV imagery and video data for subsequent online publication and compiled all data visualizations. JN was in lead for authoring the original manuscript draft and coordinating the peer-review process as corresponding author. SB had the role of principal investigator during the IceAGE research expeditions, during which KL, SB, and JT conceived the initial study. JN participated in specimen collections during the IceAGE 3 expedition together with PMA, SB, and JT.

Jenny Neuhaus (2025). **On dwarf males in the deep-sea acorn barnacle *Bathylasma hirsutum* (Thoracica: Bathylasmatidae).** *Marine Biodiversity*, 55 (2), 1–5.

JN conceived and designed the study, conducted specimen dissections, curated the data, authored the original manuscript draft, and coordinated the peer-review process as single author.

The Protobranch Bivalve *Ledella ultima* (E. A. Smith, 1885)

Jenny Neuhaus, Mark E. de Wilt, Sven Rossel, Saskia Brix, Ron J. Etter, Robert M. Jennings, Katrin Linse, Pedro Martínez Arbizu, Martin Schwentner, Janna Peters (2025). **High Connectivity at Abyssal Depths: Genomic and Proteomic Insights into Population Structure of the Pan-Atlantic Deep-Sea Bivalve *Ledella ultima* (E. A. Smith, 1885).** *Ecology and Evolution,* 15 (e71903), 1–21.

JN had the lead in project administration and data curation, following the initial study design of SB and KL. JN and MEW conducted morphological examinations and morphometric analyses. Molecular sequencing and proteomic laboratory work were conducted by JN and MEW, assisted by SR for proteomic fingerprinting and subsequent analyses. JN performed the next-generation 2b-RAD sequencing, assisted by MEW and supervised by PMA. JN and JP conducted the SNP data analyses, assisted by SR, MS, and PMA. JN, JP, and SR contributed equally to data visualizations. RJE and RMJ were supportive in data curation by supplementing specimens and respective sequence data from the ENAB expedition. JN was in lead for authoring the original manuscript draft and coordinating the peer-review process as corresponding author.

The Munnopsid Isopod Genus *Acanthocope* Beddard, 1885

Jenny Neuhaus, Zhehao Hu, Emanuel Pereira, Sven Rossel, Saskia Brix (in preparation). **Biogeography of North Atlantic *Acanthocope* Beddard, 1885**

JN had the lead in project administration and was assisted by ZH in data curation, following the initial study design of SB. JN and ZH conducted morphological species identifications, aided by the taxonomic expertise of EP and SB. JN and ZH equally contributed to the generation and analyses of molecular sequences. Proteomic fingerprinting and subsequent data analyses were conducted by ZH and SR, assisted by JN. JN and ZH were in lead of data visualization, assisted by SB and EP. JN and ZH were in lead for authoring the original manuscript draft. ZH is coordinating the peer-review process as corresponding author.

Zhehao Hu, Jenny Neuhaus, Emanuel Pereira, Sven Rossel, Terue C. Kihara, Janna Peters, Saskia Brix (in preparation). **Comparing adult locomotion in two families of deep-sea isopods (Munnopsidae vs Haploniscidae) in the North Atlantic, including the description of new species**
(Please note that the author's contributions do not refer to the complete manuscript, but exclusively to the discovery of the new species, *Acanthocope* sp. A, which is the part of the manuscript included herein.)

In lead of the project administration and data curation, JN made the initial species discovery by morphological identification, which was subsequently confirmed by ZH, EP and SB. ZH conducted the molecular laboratory work and formal sequence analyses. ZH and JN, assisted by EP and SB, compiled the drawings of morphological characters. SB designed and supervised this research.

The Dentaliid Scaphopod *Fissidentalium aurae* Linse & Neuhaus, 2024

Katrin Linse, Jenny Neuhaus (2024). **A new species of *Fissidentalium* (Scaphopoda: Dentaliidae) in association with an actinostolid anemone from the abyssal Labrador Sea.** *Marine Biodiversity*, 54 (88), 1–18.

JN and KL conceived and designed the research upon species discovery during the IceDivA 2 expedition. JN was in lead of molecular sequence generation and analyses, including the curation of sequence and imagery data. KL was in lead of SEM imaging and EDS measurements and respective data processing. JN and KL equally contributed to the species diagnosis and data visualization, as well as to authoring the original manuscript draft. KL coordinated the peer-review process as corresponding author.

Hamburg, den 05.08.2025

Prof. Dr. Saskia Brix

Hamburg, den 05.08.2025

Jenny Neuhaus

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Hamburg, den 13.08.2025

Jenny Neuhaus

"The fascination of any search after truth lies not in the attainment, which at best is found to be very relative, but in the pursuit, where all the powers of the mind and character are brought into play and are absorbed by the task. One feels oneself in contact with something that is infinite and one finds a joy that is beyond expression in 'sounding the abyss of science' and the secrets of the infinite mind."

—Dr Florence Bascom, 1931

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IV. Supplemental Material – Analysis of Shell Morphometric Measurements in *L. ultima*

List of Abbreviations

AABW	Antarctic Bottom Water
AB	Argentine Basin
ABGD	Automated Barcode Gap Discovery
AC	Azores Current
AGT	Agassiz Trawl
AIC	Akaike Information Criterion
AMOC	Atlantic Meridional Overturning Circulation
ANB	Angola Basin
ASAP	Assemble Species by Automatic Partitioning
BB	Brazil Basin
BBNJ	Biodiversity Beyond National Jurisdiction
BC	Box Corer
BI	Bayesian Inference
BLAST	Basic Local Alignment Search Tool
BOLD	Barcode of Life Database
BP	Base Pair
CB	Cape Basin
CB-N	Canary Basin North
CCZ	Clarion-Clipperton Zone
CGFZ	Charlie Gibbs Fracture Zone
COI	Cytochrome *c* oxidase subunit I
CoML	Census of Marine Life
CVB	Cabo Verde Basin
DAPC	Discriminant Analysis of Principal Components
DDH	Depth-Differentiation Hypothesis
DNA	Deoxyribonucleic Acid
DOSI	Deep-Ocean Stwardship Initiative
DUI	Doubly Uniparental Inheritance
DWBC	Deep Western Boundary Current
EBS	Epibenthic Sledge
EDS	Energy Dispersive Spectroscopy
EF-1	Elongation Factor 1α subunit
ERRC	East Reykjanes Ridge Current
ESS	Eriador Seamount South
FBC	Faroe Bank Channel
GISR	Greenland-Iceland-Scotland Ridge
GUB	Guyana Basin
HEBBLE	High Energy Benthic Boundary Layer Experiment
IB-N	Iberian Basin North
IC	Irminger Current
IceAGE	Icelandic marine Animals: Genetics and Ecology
INDEEP	International Network for Scientific Investigation of Deep-Sea Ecosystems

List of Abbreviations – *continued*

ISOW	Iceland-Scotland Overflow Water
JB	Josephine Bank
MALDI-TOF	Matrix-Assisted Laser Desorption/Ionization
MS	Time-Of-Flight Mass Spectrometry
MAP	Madeira Abyssal Plain
MAR	Mid-Atlantic Ridge
MCMC	Markov Chain Monte Carlo
MOW	Mediterranean Outflow Water
MPA	Marine Protected Area
MT	Mitotype
mtDNA	mitochondrial DNA
NAB	North American Basin
NAC	North Atlantic Current
NADW	North Atlantic Deep Water
OFZ	Oceanographer Fracture Zone
OFOS	Ocean Floor Observation System
PAP	Porcupine Abyssal Plain
PCA	Principal Component Analysis
PCR	Polymerase Chain Reaction
POC	Particulate Organic Carbon
PP	Posterior Probability
PSRF	Potential Scale Reduction Factor
RAD	Restriction-Site Associated DNA
RF	Random Forest
ROV	Remotely Operated Vehicle
RPM	Rounds Per Minute
RR	Reykjanes Ridge
SEM	Scanning Electron Microscopy
sNMF	Sparse Nonnegative Matrix Factorization
SNP	Single-Nucleotide Polymorphism
SNR	Singal-to-Noise Ratio
UN	United Nations
VFZ	Vema Fracture Zone
WEB	West European Basin
WoRMS	World Register of Marine Species
16S	16S rRNA
18S	18S rRNA

Summary

Benthic invertebrates are organisms that inhabit hard substrates or soft sediments on the seafloor. In the dynamic, three-dimensional environment of the deep sea, most benthic species undergo development via pelagic larvae. These include planktotrophic larvae, which actively feed on plankton, and lecithotrophic larvae, which develop from yolk reserves without the need for external feeding. In addition, several benthic taxa reproduce via direct development, in which the offspring invest energy from external food sources directly into growth and sexual maturation. While direct development primarily limits the dispersal potential of deep-sea species to the mobility of adult stages, prevailing bottom currents can facilitate the dispersal of pelagic larvae over long distances. They are therefore considered important drivers of species distribution patterns and connectivity in the deep sea, which describes the exchange of genetic material, *i.e.,* gene flow, among geographically separated populations. In the Atlantic deep sea, large-scale oceanographic processes are primarily influenced by the topography of the Mid-Atlantic Ridge (MAR), separating the Atlantic into deep ocean basins on its eastern and western flanks. This dissertation examines the influence of reproductive strategies, larval development, and adult locomotory ability on species distribution patterns and connectivity in the Atlantic deep sea, using case studies of benthic invertebrates from hard-bottom and soft-sediment habitats.

— The Bathylasmatid Barnacle *Bathylasma hirsutum* (Hoek, 1883)

The barnacle *Bathylasma hirsutum* (Cirripedia: Bathylasmatidae) is a sessile crustacean with planktotrophic larval development that inhabits hard-bottom habitats in the northeast Atlantic. To assess levels of genetic diversity and connectivity, specimens were studied from 658–1110 m depth across four sites situated between the Faroe Bank Channel and the Reykjanes Ridge south of Iceland (**Neuhaus *et al.* 2024, pp 69–90**). The species is now recognized as capable of living in hydrothermally influenced habitats, where specimens differ extrinsically by ferromanganese shell precipitates. Molecular sequence analysis resulted in overall little intraspecific genetic divergence between populations, including those affiliated with the vent field. The results are indicative of high population connectivity within the northeast Atlantic, mediated by the dispersal of planktotrophic larvae with intermediate and bottom water flows. Morphological examinations of *B. hirsutum* revealed the presence of dwarf males, providing evidence for the evolution of an androdioecious sexual system (**Neuhaus 2025, pp 91–96**). These findings are a fundamental contribution to advance knowledge on the reproductive diversity and sexual evolution in bathylasmatid barnacles, for which a complete understanding has yet to be achieved.

— The Protobranch Bivalve *Ledella ultima* (E. A. Smith, 1885)

The bivalve *Ledella ultima* (Protobranchia: Nuculanidae) is a sedentary mollusc with lecithotrophic larval development that inhabits soft-sediment abyssal plains on a pan-Atlantic scale. To conduct a fine-scale assessment of genetic connectivity and population structure, specimens were studied from 3500–5735 m depth across eastern and western deep-sea basins (**Neuhaus *et al.* 2025, pp 99–120**). Molecular sequence analysis identified five putative genetic lineages with high intraspecific divergence and a lack of geographic structure, interpreted to result from previously evidenced sex-specific mitochondrial heteroplasmy. To address the genetic complexity, analyses were complemented by proteomic fingerprinting and RAD sequencing, both of which did not mirror the molecular genetic results. Despite the RAD data revealing overall little genetic differentiation, admixture analysis identified fine-scale population structure between north-central and south Atlantic basins. Proteomic analysis revealed patters distinct from the basin-based population structure, suggestive of environmentally driven shifts in protein expression. The findings suggest high dispersal potential and connectivity in *L. ultima*, which can be explained by the trajectories of deep Atlantic water masses across major topographic boundaries.

— The Munnopsid Isopod Genus *Acanthocope* Beddard, 1885

The *Acanthocope* (Isopoda: Munnopsidae) are motile peracarid crustaceans with direct development that inhabit soft-sediment habitats in the Atlantic deep sea. Their characteristic long posterior legs enable active swimming, which is why they serve as ideal organisms to study species distributions. The biogeography and genetic diversity of *Acanthocope* was assessed across eastern and western localities of the north Atlantic, spanning 3180–5484 m in depth (**Neuhaus *et al.* in prep, pp 123-146**). Morphological examinations resulted in the identification of the six species *A. eleganta* Malyutina & Brandt, 2004, *A. galaica* Malyutina, Frutos & Brandt, 2018, *A. galatheae* Wolff, 1962, *A. muelleri* Malyutina, 1999, *A. puertoricana* Malyutina, Frutos & Brandt, 2018, and *A. unicornis* Menzies, 1962. One novel species, currently designated as *Acanthocope* sp. A, was identified and characterizes by the presence of dorsomedial, knob-like processes distally and a large body size of up to 10.4 mm in total length (**Hu *et al.* in prep, pp 169–172**). Molecular sequence analysis and proteomic fingerprinting resulted in overall congruent clustering patterns, supporting the delineation of *A. galatheae*, *A. muelleri*, *A. unicornis*, and *Acanthocope* sp. A as separate lineages. Specimens that were morphologically identified as *A. eleganta*, *A. galaica*, and *A. puertoricana* consistently clustered as a single molecular genetic lineage and were poorly resolved by proteomic fingerprinting, raising questions about the current validity of species boundaries. This study substantially increases species abundance data and exceeds known bathymetric ranges for selected species by up to 780 m in depth. The presence of *A. galaica* and *A. puertoricana* was confirmed on both sides of the MAR, suggestive of high genetic connectivity between eastern and western basins.

— The Dentaliid Scaphopod *Fissidentalium aurae* Linse & Neuhaus, 2024

The scaphopod *Fissidentalium aurae* (Scaphopoda: Dentaliidae) is a burrowing mollusc with lecithotrophic larval development that inhabits soft-sediment abyssal plains in the Labrador Sea. The species was described based on 19 live specimens from 3387 m depth (type locality: 58°12.289′N 54°13.409′W) and characterizes by a large, opaque-white, moderately curved shell of up to 63.63 mm in length and 11.34 mm in width (**Linse and Neuhaus 2024**, **pp 149–166**). Congruent with morphological and morphometric differences from Atlantic and Pacific congeners, molecular sequence analysis confirmed *F. aurae* as a distinct lineage. The species lives in symbiosis with an epizoic anemone which is attached to the concave, anterior shell surface. Living specimens of *F. aurae* are noticeable by meandering traces, *i.e.,* Lebensspuren, which they leave behind in the soft sediment in their search of food. Whilst the scaphopod moves across the sediment bed, its exposed shell provides a suitable attachment site for the anemone's dispersive larvae, potentially attracted by chemical cues from the scaphopod shell. *Fissidentalium aurae* occurs sympatric with at least two other scaphopod species, both of which were obtained at the type locality of *F. aurae*. This research underscores the ongoing need for integrative taxonomy efforts to assess species diversity and distribution in the deep sea.

This thesis presents case studies of benthic invertebrate taxa differing in habitat specificity, reproductive strategy, developmental mode, and adult locomotory ability to investigate drivers of species distribution patterns and connectivity in the Atlantic deep sea. With emphasis on the role of hydrodynamic regimes and geomorphological features as conduits or barriers to gene flow, this thesis addresses key research priorities for effective deep-sea management and expands current knowledge essential for implementing long-term conservation measures.

Zusammenfassung

Benthische Wirbellose sind Organismen, die Hartsubstrat oder weiches Sediment des Meeresbodens besiedeln. In der dynamischen, dreidimensionalen Umgebung der Tiefsee durchlaufen die meisten benthischen Arten eine Entwicklung über pelagische Larven. Dazu gehören planktotrophe Larven, die sich aktiv von Plankton ernähren, sowie lecithotrophe Larven, deren Dotterreserven keine externe Nahrungsquelle für ihre Entwicklung erfordern. Darüber hinaus kann die Fortpflanzung benthischer Taxa auch über eine direkte Entwicklung erfolgen, in der die Nachkommen Energie aus externen Nahrungsquellen unmittelbar in Wachstum und sexuelle Reifung investieren. Während die direkte Entwicklung das Verbreitungspotenzial von Tiefseearten primär auf die Fortbewegungsfähigkeit adulter Stadien beschränkt, können vorherrschende Tiefenströmungen die Ausbreitung von pelagischen Larven über große Entfernungen begünstigen. Sie gelten daher als wichtige Treiber für die Verbreitungsmuster und Konnektivität von Arten in der Tiefsee, was den Austausch von genetischem Material, *d.h.*, Genfluss, zwischen geografisch getrennten Populationen beschreibt. In den Tiefen des Atlantiks werden weitreichende ozeanografische Prozesse primär durch die Topografie des Mittelatlantischen Rückens (MAR) beeinflusst, der den Ozean in tiefe Becken an seiner Ost- und Westflanke unterteilt. Diese Dissertation untersucht den Einfluss von Fortpflanzungsstrategien, Larvenentwicklung und adulte Fortbewegungsfähigkeit auf die Verbreitungsmuster und die Konnektivität von Arten in der atlantischen Tiefsee, wobei Fallstudien zu benthischen wirbellosen Organismen aus Lebensräumen mit hartem und weichem Sedimentgrund herangezogen werden.

— Die bathylasmatide Seepocke *Bathylasma hirsutum* (Hoek, 1883)

Die Seepocke *Bathylasma hirsutum* (Cirripedia: Bathylasmatidae) ist ein sesshaftes Krebstier mit planktotropher Larvenentwicklung, welches Hartsubtrat im Nordostatlantik besiedelt. Zur Untersuchung genetischer Diversität und Konnektivität wurden Individuen aus 658–1110 m Tiefe an vier Standorten zwischen dem Faröer-Bank-Kanal und des Reykjanesrückens südlich von Island untersucht (**Neuhaus et al. 2024, S. 69–90**). Die Art gilt nun als fähig, in hydrothermal beeinflussten Habitaten zu siedeln, wo sich Individuen durch Ferromangan-Ablagerungen auf ihrer Schale äußerlich von ihren Artgenossen unterscheiden. Molekulare Sequenzanalysen ergaben insgesamt eine geringe intraspezifische genetische Divergenz zwischen den Populationen, einschließlich derer des hydrothermal beeinflussten Lebensraums. Die Ergebnisse deuten auf eine hohe Populationskonnektivität innerhalb des Nordostatlantiks hin, die durch die Ausbreitung planktotropher Larven mit Tiefenwasserströmungen begünstigt wird. Morphologische Untersuchungen von *B. hirsutum*

belegten zudem das Vorkommen von Zwergmännchen und damit die Entwicklung eines androdioözischen Sexualsystems (**Neuhaus 2025, S. 91–96**). Diese Erkenntnis stellt einen bedeutenden Beitrag zum Verständnis der reproduktiven Vielfalt und sexuellen Evolution innerhalb der Bathylasmatidae dar, ein Prozess deren umfassende Ergründung bislang noch aussteht.

— Die protobranche Muschel *Ledella ultima* (E. A. Smith, 1885)

Die Muschel *Ledella ultima* (Protobranchia: Nuculanidae) ist ein sedentäres Weichtier mit lecithotropher Larvenentwicklung, das in weichen Sedimenten der Tiefseeebenen im gesamten Atlantik vorkommt. Um eine detaillierte Analyse der genetischen Konnektivität und Populationsstruktur durchzuführen, wurden Individuen aus 3500–5735 m Tiefe in östlichen und westlichen Tiefseebecken untersucht (**Neuhaus et al. 2025, S. 99–120**). Die molekulare Sequenzanalyse identifizierte fünf potenzielle genetische Linien mit hoher intraspezifischer Divergenz und fehlender geographischer Struktur, was auf eine bereits dokumentierte geschlechtsspezifische mitochondriale Heteroplasmie zurückzuführen ist. Um die genetischen Komplexität zu ergründen, wurden die Analysen durch RAD-Sequenzierung und Proteom-Fingerprinting ergänzt, welche die molekulargenetischen Ergebnisse nicht bestätigten. Obwohl die RAD-Daten insgesamt nur eine geringe genetische Differenzierung zeigten, identifizierte die Admixture-Analyse eine feinmaschige Populationsstruktur zwischen den Becken des nördlichen Zentralatlantiks und des Südatlantiks. Die Proteom-Analyse ergab Muster, die sich von der Becken-basierten Populationsstruktur unterschieden, was auf umweltbedingte Veränderungen in der Proteinexpression hindeutet. Die Ergebnisse deuten auf ein großes Ausbreitungspotenzial und eine hohe Konnektivität in *L. ultima* hin, die sich, über topographische Grenzen hinweg, anhand von Strömungsmustern der atlantischen Tiefenwassermassen erklären lassen.

— Die Gattung der munnopsiden Assel *Acanthocope* Beddard, 1885

Die *Acanthocope* (Isopoda: Munnopsidae) sind mobile, peracaride Krebse mit direkter Entwicklung, die weiche Sedimente der atlantischen Tiefsee besiedeln. Ihre charakteristischen verlängerten hinteren Laufbeine ermöglichen ein aktives Schwimmverhalten, weshalb sie sich ideal für die Studie von Verbreitungsmustern eignen. Die Biogeographie und genetische Vielfalt von *Acanthocope* wurden an östlichen und westlichen Standorten des Nordatlantiks in 3180–5484 m Tiefe untersucht (**Neuhaus et al.**, **in Vorbereitung, S. 123–146**). Morphologische Bestimmungen ergaben die Identifizierung der sechs Arten *A. eleganta* Malyutina & Brandt, 2004, *A. galaica* Malyutina, Frutos & Brandt, 2018, *A. galatheae* Wolff, 1962, *A. muelleri* Malyutina, 1999, *A. puertoricana* Malyutina, Frutos & Brandt, 2018, und *A. unicornis* Menzies,

1962. Zudem wurde eine neue Art, derzeit *Acanthocope* sp. A, identifiziert, die sich durch dorsomediale, knopfartige Fortsätze distal und einer großen Körperlänge von bis zu 10,4 mm auszeichnet (**Hu *et al.*, in Vorbereitung, S. 169–172**). Die molekulare Sequenzanalyse und das Proteom-Fingerprinting ergaben insgesamt übereinstimmende Clustering-Muster und stützten die Abgrenzung von *A. galatheae*, *A. muelleri*, *A. unicornis* und *Acanthocope* sp. A als separate Arten. Individuen, die morphologisch als *A. eleganta*, *A. galaica* und *A. puertoricana* identifiziert wurden, gruppierten sich durchweg als eine einzige molekulargenetische Linie und konnten durch Proteomik nur unzureichend aufgelöst werden, was Fragen zur aktuellen Gültigkeit der Artengrenzen aufwirft. Diese Studie erweitert den Datensatz zur Artenvielfalt erheblich und überschreitet die bislang bekannten bathymetrischen Bereiche für einige Arten um bis zu 780 m Tiefe. Das Vorkommen von *A. galaica* und *A. puertoricana* wurde auf beiden Seiten des MAR bestätigt, was auf eine hohe genetische Konnektivität zwischen dem östlichen und westlichen Becken hindeutet.

— Der dentaliide Scaphopode *Fissidentalium aurae* Linse & Neuhaus, 2024

Der Scaphopode *Fissidentalium aurae* (Scaphopoda: Dentaliidae) ist ein grabendes Weichtier mit lecithotropher Larvenentwicklung, der weiche Sedimente der Tiefseeebenen der Labradorsee bewohnt. Die Art wurde anhand von 19 lebenden Individuen aus einer Tiefe von 3387 m beschrieben (Typuslokalität: 58°12.289′N 54°13.409′W) und zeichnet sich durch eine große, opak-weiße, mäßig gekrümmten Schale mit einer Länge von bis zu 63,63 mm und einer Breite von bis zu 11,34 mm aus (**Linse & Neuhaus 2024, S. 149–166**). In Übereinstimmung mit den morphologischen und morphometrischen Unterschieden zu atlantischen und pazifischen Verwandten wurde *F. aurae* durch molekulare Sequenzanalysen als eigenständige Art identifiziert. Der Scaphopode lebt in Symbiose mit einer epizoischen Anemone, die an der konkaven, vorderen Schalenoberfläche haftet. Lebende Exemplare von *F. aurae* fallen durch ihre mäandernden Spuren, *d.h.,* Lebensspuren, auf, die sie auf der Suche nach Nahrung im weichen Sediment hinterlassen. Während sich der Scaphopode über den Sedimentboden bewegt, bietet seine freiliegende Schale einen geeigneten Ansiedelungsplatz für die freischwimmenden Larven der Anemone, die möglicherweise von chemischen Signalen der Schale angezogen werden. *Fissidentalium aurae* kommt sympatrisch mit mindestens zwei anderen Scaphopodenarten vor, die beide am Typusfundort von *F. aurae* beprobt wurden. Diese Studie unterstreicht die anhaltende Notwendigkeit integrativer taxonomischer Bemühungen zur Bewertung der Vielfalt und Verbreitung von Arten in der Tiefsee.

Diese Arbeit präsentiert Fallstudien zu benthischen wirbellosen Taxa mit unterschiedlicher Lebensraumspezifität, Fortpflanzungsstrategie, Entwicklungsweise und Fortbewegungsfähigkeit, um Einflussfaktoren auf Verbreitungsmuster und Konnektivität in der atlantischen Tiefsee zu untersuchen. Mit einem Schwerpunkt auf der Rolle hydrodynamischer Regime und geomorphologischer Strukturen als Filter oder Barrieren für den Genfluss trägt diese Arbeit zu zentralen Forschungsschwerpunkten für ein effektives Tiefseemanagement bei und liefert Erkenntnisse, die für die Umsetzung langfristiger Schutzmaßnahmen unerlässlich sind.

General Introduction

General Introduction

Deep-Sea Benthos

Deep-sea biodiversity is dominated by benthic invertebrates which define by living in association with the seafloor (Godson *et al.* 2022). These include infaunal organisms that live beneath the sediment surface, epifaunal organisms that live on the seafloor, and suprafaunal organisms that live in the near-bottom water layer (Stratmann *et al.* 2020; Godson *et al.* 2022). The deep-sea benthos occupies a range of substrate types across the structurally diverse seafloor, including extensive soft-sediment plains, hard-bottom habitats such as ridge flanks and seamounts, as well as transitional zones characterized by mosaics of soft and hard substrate types (Tyler *et al.* 2016; Figure 1). In soft-bottom habitats, peracarid crustaceans, polychaetes, and bivalves represent the most species-rich and ecologically diverse macrobenthic taxa (Ramirez-Llodra *et al.* 2010; Danovaro *et al.* 2014). The macrobenthos includes organisms that pass through a sieve mesh of 1 cm and are retained on sieves with 250 µm, 300 µm, or 500 µm mesh size (Stratmann *et al.* 2020). By reworking sediments through burrowing and feeding activities, one of their principal ecological functions lies in the nutrient cycling and decomposition of organic matter, which modifies sediment structure and increases local habitat complexity (Mermillod-Blondin 2011; Baldrighi *et al.* 2017). Dominant hard-bottom taxa, such as sponges, cold-water corals, and barnacles, form complex habitat structures that offer refugia and attachment sites for other organisms, thereby supporting ecological complexity and promoting species diversity (Buhl-Mortensen and Mortensen 2005; Yakovis *et al.* 2007). The biological productivity of the deep sea benthos is intimately linked to the downward flux of particulate organic carbon (POC) from surface primary production (Gage and Tyler 1991). Spatial and temporal variability in surface productivity, driven by complex oceanographic processes that regulate nutrient availability, can enhance local food supply and impact benthic biodiversity patterns even at great depths (Preston *et al.* 2020; Flores *et al.* 2023). However, since POC flux declines progressively with distance from land and increasing depth (Smith *et al.* 2008; Lampitt *et al.* 2023), the deep sea is generally considered an oligotrophic environment (Ramirez-Llodra *et al.* 2010).

Benthic Feeding Modes

To allow deep sea benthic species to occupy distinct ecological niches across soft-sedimented and hard-bottom habitats, evolution has favored the development of diverse feeding modes. These reflect biological responses to substrate types and the availability of organic food sources in the complex benthic food web, which is intimately coupled to pelagic processes

(Gage and Tyler 1991; Durden *et al.* 2017; Snelgrove *et al.* 2018). Deposit feeding is the prevalent nutritional mode in many infaunal and epifaunal taxa (Jumars *et al.* 1990; Durden *et al.* 2017). Deposit feeders effectively ingest and digest organic matter from the seabed and include a wide range of benthic taxa, such as polychaetes (Schüller and Ebbe, 2007), peracarid crustaceans (Wilson and Ahyong 2015), protobranch bivalves (Allen and Sanders, 1996) and scaphopods (Reynolds, 2002). Suspension feeders capture suspended particulate matter from the water column and are either passive and reliant on external currents, or active by producing a feeding flow themselves (Riisgård and Larsen 2010). They include many sedentary epifaunal taxa such as polychaetes (Jumars *et al.* 2015), as well as species with a sessile lifestyle such as stalked crinoids (Mironov 2008), reef-building corals (Freiwald *et al.* 2004) and the pedunculate and sessile forms of barnacles (Newman and Ross 1971). Active filter-feeding, too, is a prevalent strategy in taxa with a sessile lifestyle and commonly found in deep sea sponges (Van Soest *et al.* 2012; Robertson *et al.* 2017) and many crustacean taxa (Riisgård 2015). In addition, certain groups have developed modes of scavenging and active predation, particularly in motile species of amphipods (Havermans and Smetacek 2018; Weston and Jamieson 2022) and isopods (Barradas-Ortiz *et al.* 2003; Poore and Bruce 2012), which opportunistically respond to locally available food resources like carrion and dead animal carcasses (Jones *et al.* 1998). Yet another mode of food acquisition in the deep sea benthos is parasitism, which is especially common in certain crustacean groups like copepods (Boxshall 1998; Buhl-Mortensen *et al.* 2022), amphipods (Freire and Serejo 2004; Martínez *et al.* 2008), isopods (Ota 2012; Williams and Boyko 2012), and barnacles (Sabadel *et al.* 2022; Kakui 2024). Some lineages within these groups have developed pronounced morphological adaptations to parasitize invertebrate or vertebrate hosts (Smit *et al.* 2019).

Reproductive Strategies and Dispersal

Deep sea benthic invertebrates predominantly reproduce sexually (Young 2003). Both the presence of separate sexes and hermaphroditism, where a single individual possesses both female and male functional gonads (simultaneously or sequentially), are common reproductive systems (Young 2003; Chan and Høeg 2015; Picchi and Lorenzi 2018). Fertilization may occur internally, through copulation and direct transfer of sperm, or externally, through the release of gametes into the surrounding water column (Young 2003). Pelagic larval development is the most common developmental strategy, including the nutritional modes of planktotrophy and lecithotrophy (Mileikovsky 1971; Levin and Bridges 1995). Planktotrophic (feeding) larvae develop from large numbers of relatively small, nutrient-poor eggs and undergo an extended developmental period in the plankton, where they must actively feed to complete development through metamorphosis. On the contrary, lecithotrophic (non-feeding) larvae develop from smaller numbers of large, yolk-rich eggs and usually have an abbreviated larval phase limited by their lack of external nutrient sources to complete their metamorphic development (Levin and Bridges 1995; Young *et al.* 2002). Lecithotrophs are further distinguished by their pelagic and demersal forms, latter of which have no planktonic stage in the course of their larval development and remain close to the sediment surface. Because development independent from external food resources enhances the chance of larval survival in an oligotrophic environment, lecithotrophy is the prevalent nutritional strategy in deep sea benthic species (Levin and Bridges 1995). Both forms of planktonic larval stages enhance dispersal potential through local ocean currents (Young 2003; Buhl-Mortensen and Høeg 2006; Hilário *et al.* 2015). Since planktotrophic larvae are equipped with appendages for effective swimming and have an extended pelagic phase, it has been a long-standing paradigm that planktotrophs have a higher dispersal potential compared to pelagic and demersal lecithotrophs (Calow 1983; Jablonski and Lutz 1983; O'Connor *et al.* 2007). However, it has repeatedly been shown that lecithotrophic development itself does not constrain dispersal in deep sea taxa (Young *et al.* 1997; Levin 2006; Weersing and Toonen 2009; Génio *et al.* 2013), as consistently low temperatures can extend the pelagic phase for lecithotrophic larvae, resulting in long-distance dispersal to suitable settlement sites (Mercier *et al.* 2013; Montgomery *et al.* 2019; Álvarez-Noriega *et al.* 2020). While this dispersal potential compensates for the restricted motility or immobility of many sedentary and sessile species, respectively, other taxa have developed brooding strategies with direct development of their young. This strategy is a characteristic of the peracarid crustaceans (Wilson 2009), where females carry their eggs in a ventral brood pouch until their offspring hatches as well-developed juveniles. By omitting the vulnerable pelagic larval stage, juvenile peracarids can immediately exploit available food resources and allocate energy to growth and maturation (Johnson *et al.* 2001). However, this developmental mode limits the dispersal potential of species primarily to the locomotory ability of the adult stage. In isopod crustaceans in particular, active swimming ability correlates with higher species diversity, abundance and broader geographic distributions (Wilson and Hessler 1987; Schnurr *et al.* 2014; Bober *et al.* 2018; Brix *et al.* 2020).

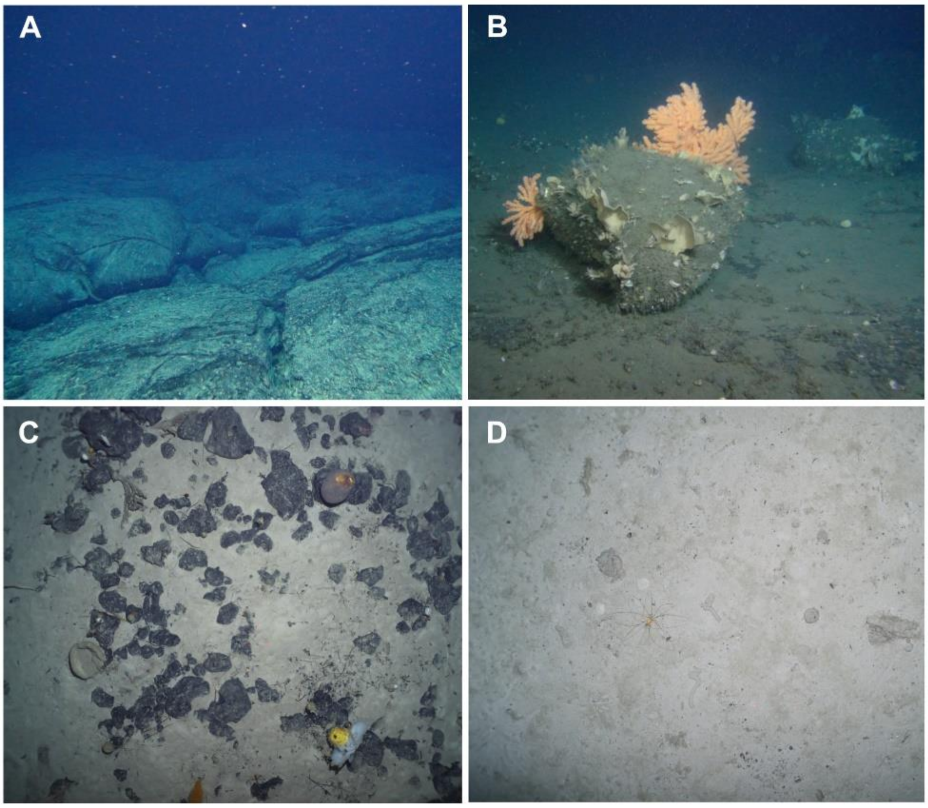

Figure 1. Deep sea benthic habitats. **A** Hard-bottom habitat of volcanic origin. **B** Boulders in a soft-sediment area provide attachment sites for hard-bottom fauna like sponges and corals. **C** Soft-sediment habitat with rocky outcrops and pebbles. Visible associated fauna includes aggregates of sponges. **D** Soft-sediment abyssal plain with various traces of animal life and a large sea spider visible left-centered. Image courtesy: A–B GEOMAR Helmholtz Centre for Ocean Research Kiel (ROV Kiel6000), C–D Senckenberg Society for Nature Research (Ocean Floor Observation System).

Benthic Depth Zones

The vertical zonation of the ocean, shaped by depth-associated gradients in pressure, temperature, and nutrient availability, provides a conceptual framework for understanding the diversity and distribution of deep sea benthic taxa (Carney 2005; Rex and Etter 2010). The deep sea is commonly defined as the oceanic region beyond the continental shelf break, at depths exceeding 200 m and underlying the photic zone (Hedgpeth 1957). While this relative threshold aligns with the depth of the North Atlantic continental shelf, it holds little relevance at a global scale and oversimplifies the complex environmental and biological gradients that structure the deep ocean (Clarke and Johnston 2003; Harris *et al.* 2014; Jamieson *et al.* 2025). While acknowledging that its use requires careful consideration in the context of physiological and biological boundaries across spatial scales (Jamieson *et al.* 2025), the depth threshold of 200 m is herein employed as the operational distinction between shallow and deep benthic zones. Extending along the continental slope, the bathyal zone (~200–3000 m) is considered the most topographically complex environment, characterized by an energetic hydrodynamic regime and a pronounced gradient of nutrient supply (Rex and Etter 2010; Watling *et al.* 2013). It features high amounts of sediment deposits from continental run-off, as well as large expanses of hard substrate in offshore regions. These include spatially isolated seamounts, oceanic island slopes, and mid-ocean ridges, all of which provide heterogeneous substrates that support a high diversity and abundance of species (Ramirez-Llodra *et al.* 2010; Rex and Etter 2010). The abyssal zone (~3000–6000 m) extends below the continental slope and is estimated to cover 65–84% of the global ocean area (Watling *et al.* 2013; Harris *et al.* 2014). The abyssal zone is characterized by a network of vast, soft-sediment abyssal plains subdivided by mid-ocean ridges and deep ocean trenches (Watling *et al.* 2013). Previously characterized as homogeneous environments of little topographic complexity (*e.g.,* Sanders 1968; Etter *et al.* 2005; Smith *et al.* 2008), recent advances in seafloor topography mapping and imaging technologies have enabled a greater understanding of habitat heterogeneity and associated biological diversity in abyssal plains (Weatherall *et al.* 2015; Sigwart *et al.* 2023). Abyssal plains include versatile geomorphological features such as abyssal hills, submarine volcanoes, seamounts, polymetallic nodule fields, and extensive rock patches (Delavenne *et al.* 2019; Durden *et al.* 2020; Dutkiewicz *et al.* 2020; Riehl *et al.* 2020; Smith 2020). The hadal environment (>6000 m) is the deepest zone of our oceans and comprises a series of oceanic trenches which form geographically isolated soft-bottom and hard-bottom habitats. Although our understanding of biological communities in this poorly accessible environment remains limited, the scientific exploration of the hadal zone is steadily advancing (Stewart and Jamieson 2018; Rivera Rosas *et al.* 2024).

The Atlantic Ocean

The Atlantic Ocean is situated between the eastern continental margins of the Americas (North, Central, South) and the western continental margins of Europe and Africa (Figure 2). The Nordic Seas, *i.e.,* Greenland, Iceland, and Norwegian Seas, provide the transitional region between the subpolar North Atlantic and the Arctic Ocean, which extends from 66–90°N (Ramirez-Llodra *et al.* 2024). This transitional region, termed the "North Atlantic Gateway" (Jöst *et al.* 2019), is characterized by strong environmental gradients along an extensive geomorphological feature, the Greenland-Iceland-Scotland Ridge (GISR). The GISR extends from east Greenland to Iceland, southeast to the Faroe Islands and to the north of Scotland (Hansen and Østerhus 2000). Along the ridge, major deep channels provide transition routes for cold and dense Arctic water masses to enter the Atlantic basin. The Denmark Strait between

Greenland and Iceland constitutes a major pathway for overflows of cold and dense Nordic waters into the North Atlantic, of which a fraction enters the North Atlantic through the Faroe-Shetland Channel and the Faroe Bank Channel (Jochumsen *et al.* 2016). Below the transitional region between 10°N and the Equator, the South Atlantic extends to around 60°S (Bridges *et al.* 2023). Sharp gradients in temperature and salinity along the Subtropical Front define a meandering boundary with the Southern Ocean (Orsi *et al.* 1995; Graham and De Boer 2013), from where cold and dense Antarctic water masses enter the eastern and western South Atlantic through deep abyssal channels (Morozov *et al.* 2010). The Mid-Atlantic Ridge separates the Atlantic on a latitudinal axis into eastern and western deep ocean basins, topographically bounded by the ridge flanks and the continental margins (Watling *et al.* 2013). The major basins of the Atlantic include the North American Basin, Brazil Basin, and Argentine Basin in the west, as well as the Western European Basin, Angola Basin, and Cape Basin in the east. With an average depth of 3646 m, the Atlantic Ocean hosts one of the largest abyssal habitats on Earth (Eakins and Sharman 2010), making it a compelling environment to study the diversity and distribution of deep-sea benthic species.

The Mid-Atlantic Ridge

With a length of about 16,000 km, the Mid-Atlantic Ridge (MAR) is longest mountain range on the planet (Beaulieu *et al.* 2015). It spans from the Gakkel Ridge in the Arctic Ocean to the Bouvet Triple Junction in the South Atlantic, where it intersects with the Southwest Indian Ridge and the American-Antarctic Ridge (Ligi *et al.* 1999; Michael *et al.* 2003; Beaulieu and Szafrański 2020). The MAR consists of an active slow-spreading center with a central rift valley (Emery and Uchupi 1984). Its flanks are predominantly characterized by gentle, sedimented slopes, which are interspersed by smaller areas of steeper hard-bottom slopes (Priede *et al.* 2022). The topography of the MAR is highly differentiated by the presence of seamounts, valleys, canyons, and fracture zones, all of which provide heterogeneous habitats for deep sea benthic species. Of the nine major fracture zones, the most significant ones include the Charlie Gibbs Fracture Zone (52–53°N), the Vema Fracture Zone (10–11°N), and the Romanche Fracture Zone (2°N–2°S) (Morozov *et al.* 2010). Because these deep axial valleys offset the MAR axis by several hundred kilometers, they play a profound role in the circulation of bottom water masses between eastern and western Atlantic basins and can provide viable dispersal routes for larvae and motile benthic species (Bober *et al.* 2018; Riehl *et al.* 2018; Keogh *et al.* 2022). The geological formation of the MAR gave rise to prominent island systems, one of which is the large volcanic landmass of Iceland (White and McKenzie 1989; Rickers *et al.* 2013). Situated at the junction between the northern MAR and the GISR, Iceland forms a prominent bathymetric high point that descends progressively to the southwest, towards the slow-spreading segment of the MAR, the Reykjanes Ridge (Petit *et al.* 2022; Le Saout *et al.* 2023). With a length of about 900 km, the Reykjanes Ridge represents the longest oblique spreading ridge on the planet and is highly influenced by hotspot activity (Talwani *et al.* 1971; Searle *et al.* 1998; Höskuldsson *et al.* 2007). Although tectonically less active than ridges of the Pacific Ocean, where the first hydrothermal vent fields were discovered at the Galápagos Rift (Lonsdale 1977; Enright *et al.* 1981), the MAR houses a remarkable diversity of hydrothermal vent systems (Beaulieu and Szafrański 2020). Driven by the circulation, heating, and geochemical reactions of seawater within the oceanic crust, hydrothermally active systems arise where high-temperature and mineral-rich fluids are discharged from the seafloor (Corliss *et al.* 1979). Since the first discovery of hydrothermal activity in the Atlantic near 26°N (Rona *et al.* 1984, 1986), over 60 hydrothermal vent fields have been identified along the MAR (Beaulieu and Szafrański 2020), many of which are inhabited by highly specialized, chemosynthetic benthic communities (Desbruyères *et al.* 2006; Van Dover *et al.* 2006; Georgieva *et al.* 2021). The Reykjanes Ridge hosts some of the most recently discovered hydrothermally active systems in the Atlantic Ocean, including the IceAGE vent field (Brix *et al.* 2020; Taylor *et al.* 2021).

Oceanographic Conditions in the Deep Atlantic

The Atlantic Meridional Overturning Circulation (AMOC) is a key component of the global overturning circulation and climate system (Frajka-Williams *et al*. 2023; Talley 2013), driving net northward heat transport across all latitudes and regulating the uptake of atmospheric carbon and its long-term storage in the deep ocean (Khatiwala *et al.* 2013; Lumpkin and Speer 2007). The AMOC is governed by complex vertical and horizontal oceanographic processes, in which its deep limbs and bottom currents play a pivotal role in shaping large-scale distribution patterns of benthic deep sea taxa (Kenchington *et al.* 2017; Puerta *et al.* 2020; Radice *et al.* 2016). Formed at high northern latitudes, the composite North Atlantic Deep Water (NADW) is the dominating water mass between 2000–4000 m depth in the entire Atlantic and drives the southward-flowing limb of the AMOC (Dickson and Brown 1994; Johnson 2008; Liu and Tanhua 2021; Figure 2). It is composed of Labrador Sea Water, Denmark Strait Overflow Water, Iceland-Scotland Overflow Water, and Mediterranean Water (Ferreira and Kerr 2017; Liu and Tanhua 2021). Formed in the Weddell Sea, the composite Antarctic Bottom Water (AABW) is colder and denser compared to NADW (Liu and Tanhua 2021). It is considered the only natural water mass in the bottom layer below 3500 m depth and drives the northward-flowing limb of the AMOC, composed of Weddell Sea Deep Water and Weddell Sea Bottom

Water (Orsi *et al.* 1999; van Sebille *et al.* 2013). Both the NADW and AABW play a crucial role in shaping benthic biodiversity patterns, influencing the dispersal potential of deep-water fauna within and between ocean basins (Jollivet *et al.* 2024; Kuhlbrodt *et al.* 2007; Puerta *et al.* 2020; Talley 2013), where abyssal channels and fracture zones serve as main pathways (Morozov *et al.* 2010; Zenk 2008).

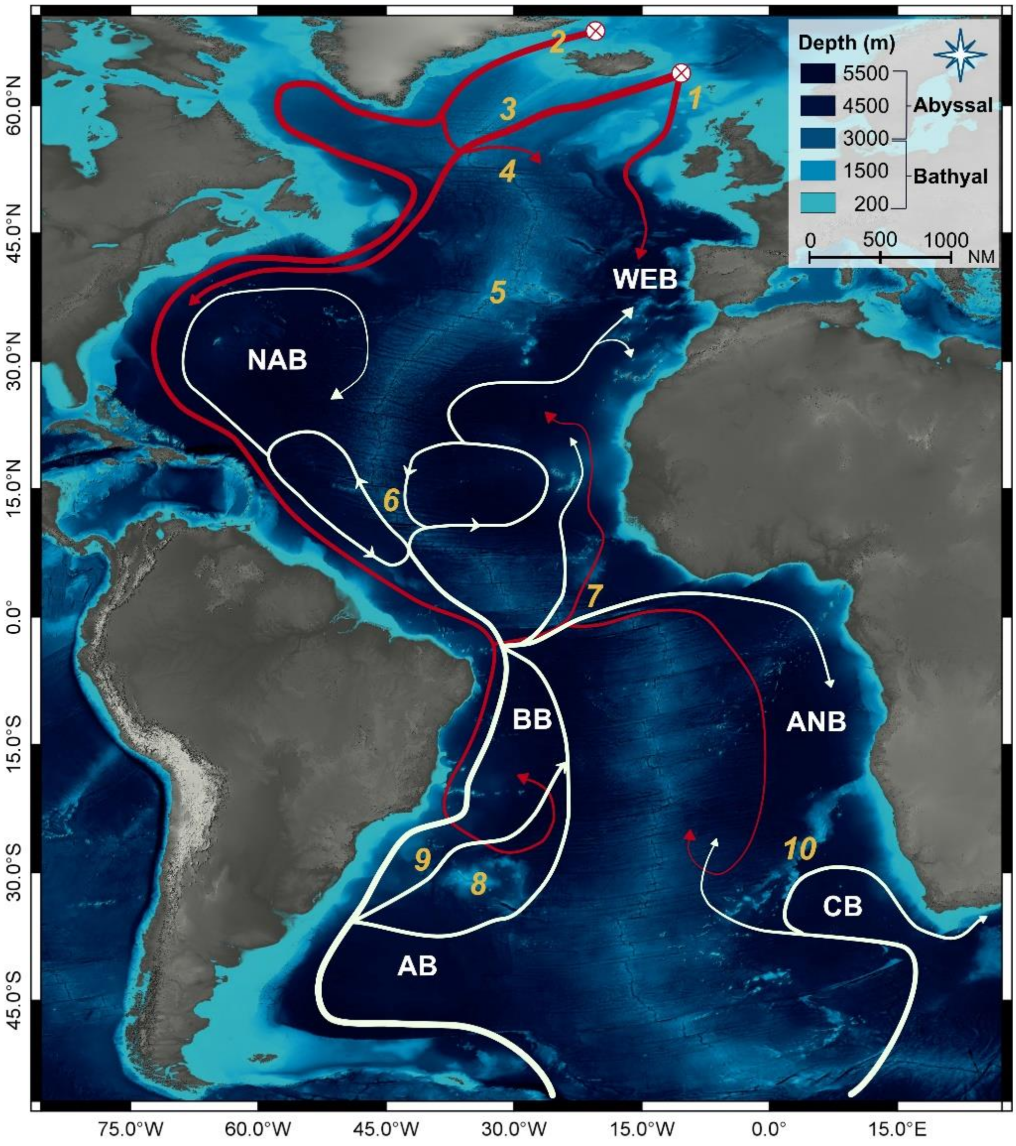

Figure 2. Bathymetric profile of the Atlantic deep sea with qualitative circulation patterns of Antarctic Bottom Water (beige) and North Atlantic Deep Water (red). Major abyssal basins are abbreviated as North American Basin (NAB), Brazil Basin (BB), Argentine Basin (AB), Cape Basin (CB), Angola Basin (ANB), and West European Basin (WEB). Ridges and fracture zones: 1: Greenland-Iceland-Scotland Ridge, 2: Denmark Strait, 3: Reykjanes Ridge, 4: Bight Fracture Zone, 5: Mid-Atlantic Ridge, 6: Vema Fracture Zone, 7: Romanche Fracture Zone, 8: Rio Grande Rise, 9: Vema Channel, 10: Walvis Ridge. Water mass directions derived from Morozov *et al.* (2010), Garzoli and Matano (2011), Ferreira and Kerr (2017). Underlying bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

For example, the Vema Channel (27–32°S), exceeding depths of 4600 m, forms one of the principal pathways for the cold and dense AABW to flow northward across the Rio Grande Rise, a major geomorphological feature separating the Argentine and Brazil basins in the southwest Atlantic (Morozov *et al.* 2020, 2023). Further north, the Vema Fracture Zone (VFZ) facilitates AABW to propagate from west to east, ventilating the abyssal basins of the Northeast Atlantic (Morozov *et al.* 2023). As for the North Atlantic, the Charlie Gibbs and Bight Fracture Zone serve as major pathways for the exchange of overflow and bottom waters of NADW between the eastern and western rims of the MAR, facilitating the export from the Nordic Seas into the Irminger Basin and the Labrador Sea (Morozov *et al.* 2010; Petit *et al.* 2022). In addition to these main circulation pathways, the deep sea environment is periodically disturbed by energetic turbulence events, including turbidity currents, contour currents, and episodic benthic storms (Hollister *et al.* 1984; Simm and Kidd 1984; Zenk 2008). Benthic storms are highly vigorous near-bottom currents capable of eroding fine-grained sediments from the abyssal seabed, exceeding 15 cm s^{-1} on a daily average (Klein and Mittelstaedt 1992; Gardner *et al.* 2017; Chen *et al.* 2024). First observed during the High Energy Benthic Boundary Layer Experiment (HEBBLE) in the northwest Atlantic and later in the Argentine Basin (Hollister and McCave 1984; Weatherly and Kelley 1985; McCave 1986; Gross and Williams 1991; Flood *et al.* 1993; Richardson *et al.* 1993), benthic storms occur in abyssal regions characterized by the downward transmission of kinetic energy from strong surface currents like the Gulf Stream (Schubert *et al.* 2018; Chen *et al.* 2024). Lasting from days to weeks, the resuspension and redeposition of sediments may alter niche availability, generate spatiotemporal habitat mosaics, and dislodge larval and juvenile forms. Benthic storms are considered important drivers of benthic ecosystem dynamics that have the potential to shape spatial patterns of abyssal biodiversity (Aller and Aller 1986; Aller 1989, 1997; Harris 2014; Meißner *et al.* 2023).

Fundamental Hypotheses of Deep-Sea Benthic Biodiversity

Building on the ecological frameworks of Holt (1985) and Pulliam (1988), who conceptualized "source" habitats as areas of surplus reproduction and "sink" habitats as demographic deficits dependent on immigration, Rex *et al.* (2005) adapted this concept as a possible explanation of deep sea biodiversity patterns. Their "source-sink hypothesis for abyssal biodiversity" proposes the structurally complex and relatively food-rich bathyal zone to function as a demographic and evolutionary source, promoting larval export to the more oligotrophic abyss, where local reproduction may not suffice to sustain populations (Rex *et al.* 2005). While this hypothesis provides a useful framework for interpreting deep sea biogeographic patterns, particularly for rare abyssal species, it must be considered within a broader context that accounts for environmental heterogeneity, dispersal capabilities, and taxon-specific traits (Rex *et al.* 2005; Rex and Etter 2010). As such, the physiological characteristics typical of abyssal taxa, including reduced metabolic rates, low fecundity, and slow growth rates, are adaptations to oligotrophic conditions that may support a high local abundance of species over generational time scales, supporting stable and reproductively viable populations independent of larval export from bathyal sources. Since evolutionary dynamics can be influenced by the intensity of environmental gradients and the degree of abiotic and biotic heterogeneity (Doebeli and Dieckmann 2003; Glazier and Etter 2014; Schluter and Pennell 2017), the structurally complex and dynamic bathyal zone is suggested to be more conducive to population differentiation and speciation than the extensive abyssal plains, thus delineating another fundamental hypothesis (Etter and Rex 1990; Rex *et al.* 2006). This "depth-differentiation hypothesis" (DDH) was first articulated through morphological studies by Etter and Rex (1990), and further developed at the genetic level in subsequent works (Etter *et al.* 1999, 2005; Rex and Etter 2010). In its core premise, the DDH posits that environmental gradients covarying with depth serve as isolation mechanisms in deep sea populations, which are expected to show greater genetic differentiation over vertical scales rather than over geographical distance. As such, the environmentally complex upper bathyal, where topographically steered deep-water currents may entrain larvae, create isolated subpopulations, and promote speciation on small spatial scales, is expected to sustain higher levels of intraspecific genetic differentiation in contrast to the abyssal plains. Characterized by fewer apparent barriers to gene flow and supposedly weakened abiotic gradients, the abyssal is suggested to exhibit lower levels of population divergence and provide less opportunity for evolutionary radiation (Etter and Rex, 1990; Rex and Etter, 2010).

Population Connectivity

In order to achieve a better understanding of the ecological and evolutionary processes that shape deep sea biodiversity patterns, the study of population connectivity serves as an integral framework to the fundamental hypotheses of deep sea biology (Wright 1949; Lowe and Allendorf 2010; Kool *et al.* 2013). In an evolutionary context, population connectivity concerns the past and present exchange of genetic material between populations of the same species through the dispersal of individuals and their gametes, collectively known as gene flow (Hedrick 2011; Cramer *et al.* 2023). In the deep sea, gene flow is primarily mediated by larval dispersal, but may also be facilitated by gamete advection, post-larval dispersal, and adult locomotion (Havenhand 1995; Levin 2006). The extent of larval dispersal in space and time is ultimately impacted by biotic and abiotic factors, including effective population size, relative reproductive success, larval dispersal capacity, habitat continuity, topographic features, and oceanographic processes (Cowen and Sponaugle 2009; Hilário *et al.* 2015). To achieve a comprehensive understanding on how populations are connected, different spatial and temporal scales of biophysical interactions ought to be assessed (Cowen *et al.* 2007). Since sampling of biological and physical data that cover all scales is practically impossible, especially considering the deep sea realm, biophysical models are increasingly being applied to estimate population connectivity (*e.g.,* Young *et al.* 2012; Hilário *et al.* 2015; Ross *et al.* 2016; Gary *et al.* 2020; Yearsley *et al.* 2020). Yet, for all but a few deep-sea species, modeled approaches are hampered by the lack of basic ecological knowledge (Mengerink *et al.* 2014; McClain and Schlacher 2015). To counteract these knowledge gaps, standardized methods for effective biological sampling and specimen preservation for taxonomic and genetic research are progressively being developed at an international scale (Clark *et al.* 2016; Howell *et al.* 2020). By implementing streamlined protocols, for instance, including a cooling chain to enhance DNA preservation in deep-sea isopod taxa (Riehl *et al.* 2014), comprehensive collections of well-preserved specimens can be utilized to conduct genetic connectivity analyses in the deep sea.

Genetic connectivity, *i.e.,* the degree to which gene flow shapes evolutionary processes within and between populations (Cramer *et al.* 2023), can be inferred by assessing the frequency and distribution of individual genetic variants. While the use of allozymes, microsatellites and the application of several mitochondrial and nuclear single-gene markers provide valuable insights into invertebrate population structure over broad spatial scales (reviewed in Taylor and Roterman 2017), recent advances in molecular genetics have enhanced the use of high-resolution genome-wide approaches. Most notably, the use of restriction-site associated DNA (RAD) sequencing methods, involving the detection of thousands of single nucleotide polymorphisms (SNPs), have become increasingly applied to assess the genetic divergence within and between populations at a fine scale (Davey and Blaxter 2010; Reitzel *et al.* 2013; Benestan *et al.* 2015; Andrews *et al.* 2016; Galaska *et al.* 2017).

Atlantic Deep-Sea Research

In the history of deep-sea research, the North Atlantic provided a key setting for the early explorations of the deep-sea fauna, to some extent reflecting its proximity to established academic institutions in western Europe and North America during the 19th century (Allcock *et al.* in press; Howell *et al.* 2020). One of the first concerted research efforts in the late 1860s, during the expeditions of the H.M.S *Lightning* (1868) and H.M.S. *Porcupine* (1869, 1870) around Scotland and Ireland, (Thomson 1873) laid the foundation for the first global deep-sea expedition of the H.M.S *Challenger* (1872–1876). Launched to study oceanographic and biological processes in the deep ocean, extensive sampling efforts during the voyage led to the discovery of over 1500 deep-sea species, some of which were found at over 4800 m depth (*e.g.,* Hoek 1883; Beddard 1886; Murray 1895). The *Challenger* expedition set the stage for an era of pioneering European deep-sea endeavors which contributed to large specimen collections that formed the basis for many formal species descriptions. These pioneering voyages include those of the *Travailleur* and *Talisman* (1880–1883; Milne-Edwards 1882, 1883) in the Northeast Atlantic and Mediterranean Sea, the Danish *Ingolf* expedition (1895–1896; *e.g.,* Hansen 1916) spanning the Faroe Islands, Iceland, and Greenland, the *Michael Sars* expedition in the North Atlantic (1910; Hjort 1911; Murray and Hjort 1912), and the Danish circumglobal *Galathea* expedition (1951–1952; *e.g.,* Wolff 1962; Knudsen 1970). Building on these international efforts, advances in sampling techniques since the 1960s have led to major developments in deep-sea biology and widened the field from descriptive taxonomy to accurate quantification of biological samples (Sanders *et al.* 1965; Hessler and Sanders 1967; Menzies *et al.* 1973; Rex *et al.* 1993; Rice *et al.* 1994; Allen and Sanders 1996; Gebruk *et al.* 1997; Billett and Rice 2001). For example, to supplement anchor dredge sampling of the macrobenthos, Hessler and Sanders (1967) constructed the first epifaunal sampler composed of a rigid, symmetrical metal frame enclosing a single fine-meshed plankton net. Termed the epibenthic sled, it has since become a widely used gear for collecting epibenthic and suprabenthic fauna from soft-bottom habitats, commonly equipped with two superimposed nets of 300–500 µm mesh size (Brenke 2005; Kaiser and Brenke 2016).

At the beginning of the 21st century, the Census of Marine Life (CoML, 2000–2010) program stimulated a new era of international efforts to assess the diversity, distribution and abundance of marine life on our planet (Ausubel *et al.* 2010). As legacies of the CoML, major collaborative initiatives like INDEEP (International Network for Scientific Investigation of Deep-Sea Ecosystems, 2011–2016; indeep-project.org) and DOSI (Deep-Ocean Stewardship Initiative; dosi-project.org) were launched, dedicated to maintain the integrity of deep-ocean ecosystems within and beyond national jurisdictions. Following two decades of international deep-sea research, the global scientific initiative Challenger 150 (challenger150.world) was endorsed in 2020 as part of the United Nations (UN) Decade of Ocean Science for Sustainable Development, drawing on the spirit of exploration embodied by the pioneering *Challenger* expedition that set sail 150 years ago. Building up on the international network of scientists to coordinate global deep-sea research and expand sampling programs in underexplored regions, Challenger 150 serves as an effective long-term ocean management program to answer key scientific questions addressing the UN Ocean Decade Societal Objectives

(Ryabinin *et al.* 2019; Howell *et al.* 2020). In alliance, the UN Decade action IceDivA (Icelandic marine Animals meets Diversity along latitudinal gradients in the deep sea of the Atlantic Ocean; Brix and Taylor 2021; Brix *et al.* 2022) has served as a knowledge hub by revisiting fundamental hypotheses in deep-sea biological research, focusing on species distribution patterns and connectivity along a latitudinal gradient (*e.g.* Kürzel *et al.* 2023). Embedded within the IceDivA action, this thesis uses case studies to investigate the diversity, biogeography, and genetic connectivity of benthic invertebrate taxa in the Atlantic deep sea.

Taxa of Study

The Bathylasmatid Barnacle *Bathylasma hirsutum* (Hoek, 1883)

Barnacles of the family Bathylasmatidae Newman & Ross, 1971 are exclusively found in the deep sea, where adult forms live permanently attached to hard-bottom substrates in environments of moderate to high current activity (Newman and Ross 1971, 1976; Southward 1987). Nested within the Bathylasmatidae, the genus *Bathylasma* Newman & Ross, 1971 currently includes four extant species, of which *Bathylasma hirsutum* (Hoek, 1883) is the only Atlantic representative (Jones 2000; Araya and Newman 2018). Restricted to the Northeast Atlantic between 348–1829 m depth, the distributional range of *B. hirsutum* spans from the Reykjanes Ridge and the Faroe Bank Channel in the north (Copley *et al.* 1996; Poltarukha and Zevina 2006a; Brix *et al.* 2013; Neuhaus *et al.* 2024), to the Canary Islands and the Great Meteor Seamount in the south (Gruvel 1903; Young 2001; Poltarukha and Zevina 2006b). The species is characterized by six sturdy parietal plates that can grow more than 8 cm in height (Figure 3), each lined by prominent hirsute growth ridges from which its scientific name is derived (Hoek 1883). By extending the feather-like thoracic appendages (cirri) into the water column, *B. hirsutum* passively feeds on suspended organic material. As in most barnacle species, sexual evolution has favored the reproductive strategy of simultaneous hermaphroditism and pelagic larval development (Southward 1987; Anderson 1994). Larval development includes six planktotrophic, free-swimming naupliar larval stages, which are followed by metamorphosis into free-swimming but non-feeding cyprid larvae (Chan *et al.* 2021). Specialized to locate a suitable habitat for benthic settlement through chemosensory adaptations, the cyprid eventually develops into a sessile juvenile barnacle (Walker *et al.* 1987; Aldred *et al.* 2018). Due to their gregarious nature, individuals typically settle in dense aggregations with epizoic growth patterns, thereby ensuring close proximity to numerous potential mates within a population (Anderson 1994). However, because food availability progressively declines with depth, population densities in certain deep-sea habitats are reduced, consequently decreasing the number of available mates. To compensate for this reproductive disadvantage, evolution has favored the development of an androdioecious sexual system, in which hermaphrodites and dwarf male barnacles coexist (Kelly and Sanford 2010; Lin *et al.* 2015). As dwarf males allocate more resources to male reproductive function than growth and typically settle near the fertilization site of their conspecifics (Ewers-Saucedo *et al.* 2015; Dreyer *et al.* 2018), they have the potential to accelerate reproductive success of mature hermaphrodites, facilitate population expansion over time, and eventually govern the degree of connectivity within and among populations (Cowen *et al.* 2007; Pineda *et al.* 2007; Boschen-Rose and Colaço 2021). Owed to extensive sampling efforts embedded within the international deep-sea exploration programs of the IceAGE project (Icelandic marine Animals: Genetics and Ecology; Brix *et al.* 2014; Brix and Devey 2019; Brix *et al.* 2020), this thesis includes the first detailed assessment of the genetic diversity and population connectivity in *B. hirsutum* from the northeast Atlantic (**Neuhaus *et al.* 2024, pp 69–90**), now recognized as an androdioecious species (**Neuhaus 2025, pp 91–96**) that lives affiliated with hydrothermally influenced habitats on the Reykjanes Ridge.

The Protobranch Bivalve *Ledella ultima* (E. A. Smith, 1885)

The Protobranchia Pelseneer, 1889 are a particularly diverse group of bivalve molluscs (Zardus 2002; Allen 2008; Sharma *et al.* 2013; Sato *et al.* 2020). They are predominantly found in soft-sediment environments spanning from continental shelf depths to hadal trenches (Allen and Hannah 1989; Okutani and Fujiwara 2005; Reed *et al.* 2014; Allen 2015). Living either burrowed within the sediment or as epifaunal dwellers, protobranchs deposit-feed on organic material with highly modified labial palps (Lundin and Schander 2001; Zardus 2002). Owing to their high abundance, diversity and pronounced function in sediment turnover, they are considered an important macrofaunal component of deep-sea communities (Sanders *et al.* 1965; Allen 2008; Reed *et al.* 2014). Nested within the diverse family Nuculanidae Adams & Adams, 1858, the genus *Ledella* Verrill & Bush, 1897 currently includes 47 extant species (WoRMS Editorial Board 2025), of which 24 species are found in the Atlantic (Jeffreys, 1870; Smith, 1885; Dall, 1890; Verrill and Bush, 1897, 1898; Dautzenberg and Fischer, 1897; Knudsen, 1970; Métivier, 1982; Filatova and Schileyko, 1984; Allen and Hannah, 1989; Allen and Sanders, 1996; Viegas *et al.* 2014; Janssen and Krylova, 2014). The species *Ledella ultima* (E. A. Smith, 1885) is by far the most common and abundant protobranch in the abyssal Atlantic, where it is mainly found between 3700–5875 m depth (Allen and Hannah 1989; Allen 2008; Etter *et al.* 2011). The bivalve has a pan-Atlantic distribution spanning from the British continental margin to the Cape Basin in the east, and from the North American margin to the Argentine Basin in the west (Allen and Hannah 1989; Allen 2008; Etter *et al.* 2011; Neuhaus *et al.* 2025). The species characterizes by a robust, ovate shell of up to 3.4 mm in length, covered with prominent concentric growth lines.

A distinctive character, setting it apart from its Atlantic congenerics, is the presence of a multiply coiled gut (Figure 3) that is suggested to enhance digestion of detrital food resources in the oligotrophic abyss (Smith 1885; Filatova and Schileyko 1984; Allen and Hannah 1989). In individuals exceeding 2.4 mm in shell length, a notable feature is the thickening of the ventral shell margin which becomes apparent in some specimens as a distinctive growth modification, suggested to increase the internal shell space for egg development (Clarke 1961; Allen and Hannah 1989). Within a population, males and females occur approximately equally (Zardus and Morse 1998; Zardus and Martel 2002). Upon external fertilization of broadcasted eggs and sperm, the zygotes develop into pericalymma larva, a lecithotrophic larval form unique to the Protobranchia (Waller 1998). These uniformly ciliated larvae bear a prominent apical velum used for a propelling locomotion during a short swimming stage, before they subsequently metamorphose into sedentary juvenile bivalves (Zardus and Morse 1998; Zardus and Martel 2002). In contrast to most animal taxa, where mitochondrial DNA (mtDNA) is homoplasmic and transmitted through strict maternal inheritance (Birky 2001), *L. ultima* has been evidenced to exhibit mitochondrial heteroplasmy, resulting in the simultaneous presence of two or more types of highly divergent mtDNA (Boyle and Etter 2013). As such, mitochondrial heteroplasmy can result in high intraspecific genetic divergence and challenge the design of genetic connectivity analyses based on mitochondrial markers alone (Rodríguez-Pena *et al.* 2020; Martínez *et al.* 2023; Wai Ho and Hanafiah 2024).

The exceptional biogeographic range makes *L. ultima* an ideal organism to investigate phylogeographic patterns and population connectivity in the abyssal Atlantic. As a result of major international deep-sea sampling efforts carried out between 2005 and 2021 (Fahrbach 2006; Martínez Arbizu *et al.* 2009; Türkay and Pätzold 2009; Devey 2015; Brix, Taylor, *et al.* 2020; Brix and Taylor 2021), this thesis includes a population genetic analysis based on a pan-Atlantic specimen collection spanning seven abyssal basins (**Neuhaus *et al.* 2025, pp 99–120**). While the analysis of mitochondrial markers addresses the challenge of an inflated intraspecific genetic differentiation owed to heteroplasmic mtDNA, a high-resolution SNP-based approach reveals fine-scale population structure despite overall low genetic differentiation at the nuclear level. To complement population genetic analyses, proteomic fingerprinting is used to explore whether nuclear genomic patterns are reflected at the protein expression level. The findings suggest environmentally driven shifts in protein expression, potentially caused by transient physiological responses to different levels of POC flux to the abyssal seafloor.

The Munnopsid Isopod Genus *Acanthocope* Beddard, 1885

The Isopoda Latreille, 1817 represent a varied and speciose order of peracarid crustaceans that have successfully adapted to terrestrial (Linsenmair 1984; Beron 1997; Sfenthourakis and Taiti 2015), freshwater (Wilson 2008; O'Callaghan *et al.* 2019), brackish (Burbanck 1962; Newman *et al.* 2007), and marine environments (*e.g.,* Kensley 2001; Brandt, De Broyer *et al.* 2007; Ellingsen *et al.* 2007; Poore and Bruce 2012; Brix *et al.* 2021; Knauber *et al.* 2023). In the marine realm, isopods are a truly widespread and abundant taxon (Svavarsson *et al.* 1990; Brandt *et al.* 2009, 2012; Brix and Svavarsson 2010; Brökeland and Svavarsson 2017; Kürzel *et al.* 2023). In the bathyal and abyssal deep sea, the isopod fauna is dominated by the suborder Asellota Latreille, 1802 (Menzies 1962; Wolff 1962; Hessler and Sanders 1967; Kussakin 1973; Hessler *et al.* 1979; Hessler and Wilson 1983; Brandt 2004; Elsner *et al.* 2015), which includes the highly diverse superfamily Janiroidea G.O. Sars, 1897 (Hessler *et al.* 1979; Wilson and Hessler 1987; Wilson 1998; Brandt 1999; Wilson 1999; Kensley 2001; Brandt *et al.* 2007). Of the janiroidean isopods, the Munnopsidae Lilljeborg, 1864 represent the most speciose and abundant family of deep-sea isopods (Wilson 1989; Kussakin 2003; Malyutina *et al.* 2020), and include the genus *Acanthocope* Beddard, 1885.

The genus *Acanthocope* currently comprises 18 recognized species worldwide, of which 13 are found in the Atlantic deep sea (Malyutina *et al.* 2018). Species of *Acanthocope* are characterized by a body with lateral, dorsal, terminal, and often ventral spines (Beddard 1885; Malyutina *et al.* 2018). Their fundamental body plan consists of the spineless head, the thorax (pereon) with segments 2–8 (pereonites) bearing the walking legs (pereopods), and the abdomen (pleon), where the sixth abdominal segment is fused with the terminal segment into the pleotelson (Kensley and Schotte 1989; Wilson 2013). The heavily muscularized pereonites 5–7 and the pleotelson are integrated into a posteriorly streamlined body section, the natasome (Wilson 2009, 2013; Figure 3). The natasome bears the natatory pereopods 5–7, which are paddle-like appendages that make these isopods, and munnopsids in general, well-adapted to an active swimming behavior (Hessler and Strömberg, 1989; Marshall and Diebel, 1995; Malyutina *et al.* 2020). Like all peracarid crustaceans, species of *Acanthocope* are obligate brooders, where brood size is positively correlated with female body size (Johnson *et al.* 2001; Wilson 2009). They mate by internal fertilization, facilitated by a male copulatory organ termed the appendix masculina (Wilson 1991, 2007). This stylet-like organ assists in sperm transfer to the brood pouch (marsupium) of the adult female, where the transferred sperm stimulates ovulation, subsequent egg fertilization and the embryonic development into the juvenile (manca) stage (Wilson 1991, 2009; Johnson *et al.* 2001). Juvenile development generally includes three manca stages, where each molt leads to an increase in body size and the subsequent development of morphological and sexual characters (Wilson 1986; Boyko and Wolff 2014; Martin 2014). Molting happens in a biphasic fashion, where the posterior half is shed prior to the anterior half of their body, a process unique to the Isopoda (George 1972; Wilson 2009).

The natatory adaptations enable species of *Acanthocope* to occupy both epibenthic and suprabenthic habitats, which is why they serve as ideal organisms to study patterns of biogeography and genetic connectivity (Bober *et al.* 2018; Malyutina *et al.* 2018; Brix *et al.* 2020). Significant knowledge gaps in terms of the diversity and distribution of *Acanthocope* from deep-sea habitats in the Atlantic persist (Malyutina *et al.* 2018). To close these gaps in the North Atlantic, specimens collected during the deep-sea expeditions of IceAGE (Brix *et al.* 2020) and IceDivA (Brix and Taylor 2021; Brix *et al.* 2022) were morphologically identified and assessed by means of molecular species delimitation and proteomic fingerprinting (**Neuhaus *et al.* in prep, pp 123–146**). The Atlantic species include *A. eleganta* Malyutina & Brandt, 2004, *A. galaica* Malyutina, Frutos & Brandt, 2018, *A. galatheae* Wolff, 1962, *A. muelleri* Malyutina, 1999, *A. puertoricana* Malyutina, Frutos & Brandt, 2018, and *A. unicornis* Menzies, 1962. In addition, a novel species designated as *Acanthocope* sp. A was recovered from abyssal depths of the northeast Atlantic and is currently prepared for description (**Hu *et al.* in prep, pp 169–172**). This study substantially increases species abundance data, extends the northernmost geographic distribution records, and exceeds previously reported bathymetric ranges for selected species by up to 780 m depth. The presence of *A. galaica* and *A. puertoricana* on both sides of the MAR suggests high genetic connectivity between western and eastern Atlantic basins, the latter of which exhibits several cases of sympatric species distributions.

The Dentaliid Scaphopod *Fissidentalium aurae* Linse & Neuhaus, 2024

Scaphopods (tusk shells) are among the most enigmatic members of the Mollusca, with their phylogenetic position as the sister taxon to Bivalvia only recently supported by molecular evidence (Song *et al.* 2023). They are distributed in all world oceans, from shallow continental shelves to hadal depths (Knudsen 1964; Steiner and Kabat 2004), and are characterized by their tusk-shaped shell that is open at both ends (Carter and Hall 1990; Reynolds 2002). By protruding their muscular foot through the anterior opening, scaphopods may either burrow downwards into soft sediments or move across the sediment bed, where they leave meandering traces known as Lebensspuren (Young *et al.* 1985). Scaphopods live mostly infaunal and selectively prey on foraminiferans (Langer *et al.* 1995; Shimek and Steiner 1997; Dantas *et al.* 2017), a group of microscopic single-celled protists that form a major component of deep-sea sediments (Gooday *et al.* 2012). To feed, scaphopods use their foot to actively probe and dislodge sediment particles, as well as their numerous feeding tentacles, termed captacula, to probe the sediments for eligible food (Shimek 1988; Byrum and Ruppert 1994). The posterior end of their shell includes functions for the passage of respiratory currents, the expulsion of feces, and the release of gametes (Reynolds 2002). Scaphopods most commonly have separate sexes and reproduce by external fertilization of released eggs and sperm (Reverberi 1971; Buckland-Nicks and Gibson 2025). Although seasonality patterns during productive summer months have been reported from the Rockall Trough (Davies 1987 *in* Reynolds, 2002), knowledge concerning scaphopod reproductive patterns in the deep sea remains scarce. There is a general assumption that tusk shells have lecithotrophic larval development (Haszprunar and Wanninger 2012), including the planktonic stenocalymma larval stage (Buckland-Nicks and Gibson 2025). Through metamorphosis, most larvae develop larval shells and subsequently undergo benthic settlement (Vilela *et al.* 2019).

Many scaphopod species have highly diverse symbiotic relationships, defined as a type of living-together (de Bary 1879). The most notable symbioses are mutualistic relationships in which anemones live epizoic on the shell of the scaphopod (reviewed in Reynolds 2002). While the epibiont has the benefit of gaining access to organic particles that are resuspended during scaphopod feeding activities on the sediment bed, the scaphopod may gain protection from predators through deterrence by the cnidarian's nematocysts (Zibrowius 1998). Such symbiotic relationships have frequently been reported from species of the dentaliid genus *Fissidentalium* P. Fischer, 1885 (Shimek and Moreno 1996; Shimek 1997; Zibrowius 1998), of which a new species was discovered in the abyssal Labrador Sea during the IceDivA 2 deep-sea expedition (Brix *et al.* 2022). This thesis includes the formal description of the species, named *Fissidentalium aurae* Linse & Neuhaus, 2024 (Figure 3), a large (>60 mm) dentaliid scaphopod that lives in symbiosis with an epizoic actinostolid anemone (**Linse and Neuhaus 2024 pp 149–166**). By combining morphological examinations with molecular sequencing methods, this research outcome serves as a fundamental contribution to our understanding of scaphopod biodiversity in the subpolar North Atlantic, with special emphasis on species-pair associations in the benthic deep sea.

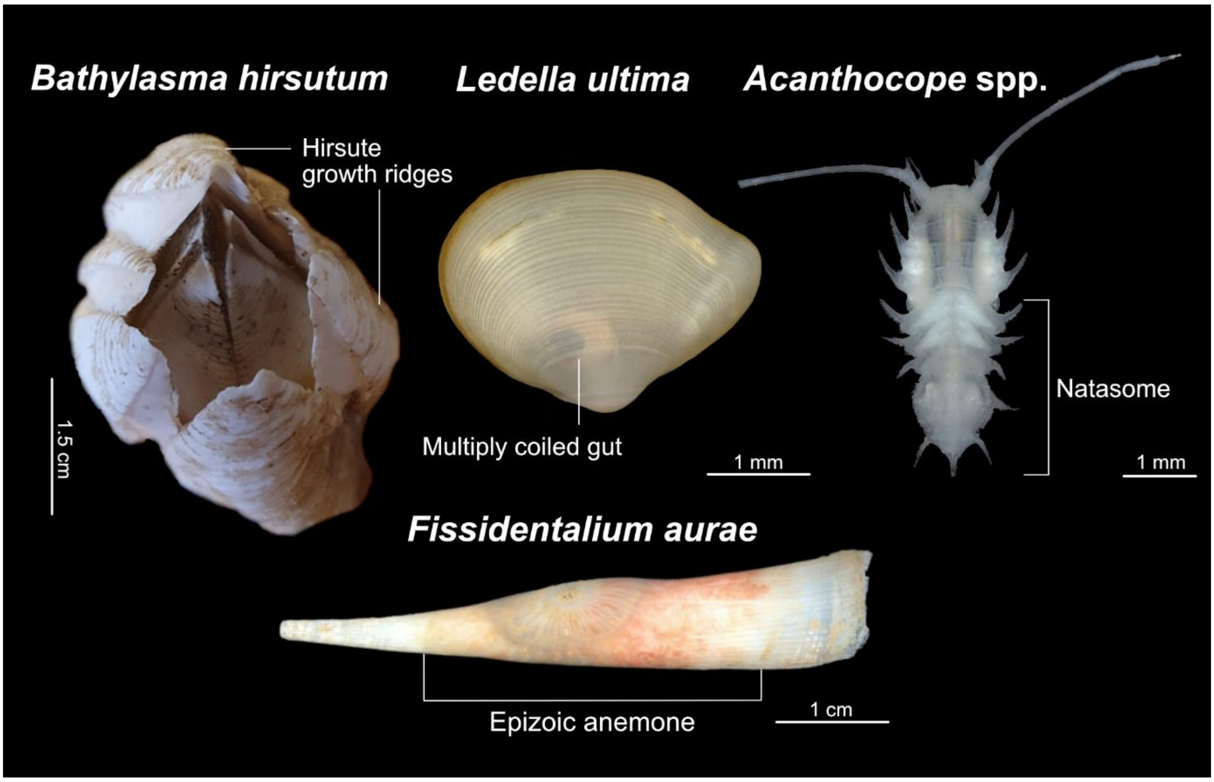

Figure 3. The taxa of study include the bathylasmatid barnacle *Bathylasma hirsutum*, the protobranch bivalve *Ledella ultima*, the munnopsid isopod genus *Acanthocope*, and the dentaliid scaphopod *Fissidentalium aurae*. Images by courtesy of Z. Hu (*A. unicornis*) and N. Gatzemeier (*F. aurae*).

Objectives

This thesis investigates drivers of species distribution patterns and genetic connectivity in the Atlantic deep sea, drawing on case studies of benthic invertebrate taxa. The selected taxa differ in their habitat specificity, reproductive strategy, developmental mode, and adult locomotory ability. Accordingly, each taxon is addressed individually in peer-reviewed or manuscript-stage research articles authored within the framework of this dissertation. These include:

— the bathylasmatid barnacle *Bathylasma hirsutum*, a sessile crustacean with planktotrophic larval development that inhabits hard-bottom habitats in the bathyal Northeast Atlantic (**Neuhaus *et al.* 2024, pp 69–90**; **Neuhaus 2025, pp 91–96**)

— the protobranch bivalve *Ledella ultima*, a sedentary mollusc with lecithotrophic larval development that inhabits soft-sediment abyssal plains on a pan-Atlantic scale (**Neuhaus *et al.* 2025, pp 99–120**)

— six recognized and one novel species of the munnopsid isopod genus *Acanthocope*, natatory peracarid crustaceans with direct development that inhabit abyssal soft sediments in the North Atlantic (**Neuhaus *et al.* in prep, pp 123–146**; **Hu *et al.* in prep, pp 169–172**)

—the scaphopod *Fissidentalium aurae*, a burrowing mollusc with lecithotrophic larval development that lives in symbiosis with an epizoic anemone on the soft-sediment abyssal plain of the Labrador Sea (**Linse and Neuhaus 2024**, **pp 149–166**)

The taxa are assessed using an integrative approach that combines morphological analysis, single-marker DNA sequencing, and, where applicable, whole-genome SNP analysis and proteomic fingerprinting. This thesis examines how adult locomotory ability, reproductive strategy, and dispersal potential influence species distribution patterns and connectivity in the Atlantic deep sea, with emphasis on the role of hydrodynamic regimes and geomorphological features as conduits or barriers to gene flow.

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The Bathylasmatid Barnacle

Bathylasma hirsutum (Hoek, 1883)

Zoological Studies **63:**25 (2024)
doi:10.6620/ZS.2024.63-25

Zoological Studies

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Population Genetics of the Deep-sea Acorn Barnacle *Bathylasma hirsutum* (Hoek, 1883) and the First Report of its Affiliation with a Hydrothermal Vent Field

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Received 1 December 2023 / Accepted 10 April 2024 / Published 4 September 2024
Communicated by Benny K.K. Chan

Confined by the Mid-Atlantic Ridge and the European continental shelf, the deep-sea acorn barnacle *Bathylasma hirsutum* (Hoek, 1883) lives in the northeast Atlantic deep sea, where it has been frequently reported in high current areas. Cemented to a solid substrate during its entire adult life, the species can only disperse by means of planktotrophic nauplius larvae. This study reports on the occurrence, ecology and genetic connectivity of *B. hirsutum* from four sites within the northeastern Iceland Basin and presents the first record of the species living affiliated with hydrothermal vent field on the Reykjanes Ridge axis.

Vent-associated specimens were found to differ extrinsically from their naturally shaded conspecifics by a prominent brown-black shell precipitate. Energy Dispersive Spectroscopy revealed ferromanganese oxides to be the main component of these shell precipitates. Morphometric measurements of shell plates revealed specimens from the vent-associated habitat to be smaller compared to non-venting sites. Molecular species delimitation based on the mitochondrial *COI* and nuclear EF1 genetic markers aided species identification and revealed a low intraspecific genetic variability. Our findings suggest a pronounced genetic connectivity of *B. hirsutum* within the studied region and provide a first step towards a biogeographic study. As such, habitats of hydrothermal influence along the Mid-Atlantic Ridge are discussed as possible niches, as are deep-sea basins in the western Atlantic. In light of the reported affiliation with hydrothermal activity, we elaborate on the potential for the sister species *Bathylasma*

corolliforme (Hoek, 1883) and *Bathylasma chilense* Araya & Newman, 2018 to utilise equivalent habitats in the Antarctic and Pacific Ocean, respectively. Our record of the unacquainted ecological niche occupation for *B. hirsutum* emphasises the need for further research on bathylasmatid acorn barnacles along the extensive Mid-Atlantic Ridge, where many biological communities remain to be discovered.

Key words: Bathylasmatidae, Biogeography, Connectivity, Growth ridges, Habitat expansion, Larval distribution

Citation: Neuhaus J, Linse K, Brix S, Martínez Arbizu P, Taylor J. 2024. Population genetics of the deep-sea acorn barnacle *Bathylasma hirsutum* (Hoek, 1883) and the first report of its affiliation with a hydrothermal vent field. Zool Stud **63:**25. doi:10.6620/ZS.2024.63-25.

BACKGROUND

During the past 30 years, more than sixty hydrothermal vent systems have been discovered along the Mid-Atlantic Ridge (MAR), known as the longest obliquely spreading section of the global mid-ocean ridge systems (Beaulieu and Szafrański 2020; Desbruyères et al. 2000 2006; German et al. 1994; Taylor et al. 2021; Wheeler et al. 2013). Elaborate studies on dominant faunal compositions of MAR vent communities, such as polychaetes (Kongsrud et al. 2013; Shields and Blanco-Perez 2013; Sigvaldadóttir and Desbruyères 2003), bivalves (Cravo et al. 2007; Duperron et al. 2006; Ó Foighil et al. 2001) and anemones (Fabri et al. 2011; Fautin and Barber 1999; López-González et al. 2003; Van Dover 1995), have contributed extensively to a better understanding of these fragile ecosystems and to map their particular biodiversity (Biscoito et al. 2006; Boschen-Rose and Colaço 2021; Desbruyères et al. 2000; Gebruk et al. 1997 2010). The Reykjanes Ride represents a ~950 km long submarine continuation of the MAR with an axial depth ranging from the shoreline southwest of the volcanic Iceland Peninsular to more than 2000 m at the Bight Fracture Zone (Keeton et al. 1997; Searle et al. 1998; Fig. 1). Due to erupted lava from volcanic seamounts, the ridge substrate is mainly composed of volcanic rock and pillow lava, providing hard-bottom habitats for a wide range of species. Until recently, the only recognised hydrothermal active field along this extensive ridge was the Steinahóll vent field (63°N) at ~300 m depth (German et al. 1994). Late bathymetric mapping and a detailed description of Steinahóll added another three vent sites to the list of hydrothermal activity in this fragile area (Taylor et al. 2021). Current research activities near 59°N lead to the discovery of yet another active vent field situated on the edge of a large, faulted seamount at ~650 m depth (Brix et al. 2020). Proximal to this novel hydrothermal vent field on the Reykjanes Ridge, the deep-sea acorn barnacle *Bathylasma hirsutum* (Hoek, 1883) was found attached to several volcanic boulders. Unlike the presence of characteristic vent barnacles in hydrothermal systems of the Pacific and Indian Ocean, Herrera et al. (2015) inferred cirripedes to be generally absent from MAR hydrothermal vent systems. Our findings present the first record of a barnacle species associated with hydrothermal activity on the northern section of the MAR. At current, the two groups of barnacles associated with deep-sea hydrothermal vents encompass all members of the superfamily Neolepadoidea as well as three species of the balanomorph genus *Eochionealasmus* Yamaguchi, 1990 (Chan et al. 2021 2020; Yamaguchi and Newman 1990 1997a b). We introduce a third group of balanomorph barnacle, the genus *Bathylasma* Newman & Ross, 1971, with at least one opportunist species occupying a hydrothermal habitat. Along with the species of study, the genus *Bathylasma* Newman & Ross, 1971 currently comprises three extant species, namely *B. alearum* (Foster, 1978), *B. chilense* Araya & Newman, 2018 and *B. corolliforme* (Hoek, 1883), distributed at depths of 37–2000 m from the coasts of New Zealand, Chile, and the Antarctic Peninsula, respectively (Araya and Newman 2018; Foster 1978; Meyer et al. 2021).

Distributional range of *Bathylasma hirsutum*

Bathylasma hirsutum was first described from 944 m depth south of the Wyville Thomson Ridge (59°40'N 07°21'W; Hoek 1883). The species is nested within the family Bathylasmatidae Newman & Ross, 1971, which includes sole deep-sea species of six genera (Chan et al. 2021; Jones 2000; Newman and Ross 1971). In the history of the controversial position of the Bathylasmatidae, Jones (2000), based on their morphological characters, classified the genera *Hexelasma* Hoek, 1913 and *Bathylasma* under the Pachylasmatoidea (now Coronuloidea Leach, 1817). In Chan et al. (2017), molecular evidence suggested the clade of *Hexelasma* and *Bathylasma* to be sister to the Tetraclitidae Gruvel, 1903, nested within the same clade. Finally, the comprehensive molecular approach by Chan et al. (2021) suggested that Bathylasmatidae is a discrete family, nested within the Coronuloidea.

Bathylasma hirsutum has a distributional range restricted to the North-East (NE) Atlantic, where it inhabits hard-bottom habitats in high current areas between 384–1829 m depth (Fig. 1). The species is known to occur along the Reykjanes Ridge (Copley et al. 1996; Murton et al. 1995; Poltarukha and Zevina 2006b), in addition to on banks and seamounts in the Rockall Trough, Rosemary Bank, George Bligh Bank, Hatton Bank, Anton Dohrn Seamount and Hebrides Terrace (Duineveld et al. 2007; Gage 1986; Narayanaswamy et al. 2006 2013; Young 2001). Further records extend to the south along the Celtic Shelf (Southward and Southward 1958; Young 1998) towards the Gulf of Cádiz (Foster and Buckeridge 1995) and near Tenerife (Gruvel 1903). Along the MAR, *B. hirsutum* has repeatedly been reported from the Azores Archipelago (Gruvel 1920; Poltarukha and Zevina 2006a; Southward 1998; Young 1998) as well as from the Great Meteor Seamount (Poltarukha and Zevina 2006a; Young 2001). The species populates a wide range of substrates, such as dropstones (Duineveld et al. 2007), telegraph cables (Gruvel 1903; Southward and Southward 1958), and echinoid spines (Hoek 1883;

Southward and Southward 1958), as well as living and dead corals (Southward 1998). Furthermore, shell debris from dead barnacles that accumulates in the periphery of the substratum they are cemented to provides a solid layer, even on soft sediments, which can be re-populated by recruits (Bullivant and Dearborn 1967; Dayton et al. 1982; Foster and Buckeridge 1995; Gage and Tyler 1991).

Larval biology and shell growth

Cemented to a solid substrate during their entire adult life, barnacles can only disperse by means of larvae. In general, they develop through a maximum of six naupliar stages which are followed by metamorphosis into the terminal cypris stage (Dayton et al. 1982; Høeg and Møller 2006; Pineda et al. 2021; Walker et al. 1987). Adapted to specific habitats, cyprids show a broad array of sensory setae and attachment organs across species, facilitating them to sense the chemical environment (Bielecki et al. 2009; Maruzzo et al. 2012) and to bipedally move across the substratum (Lagersson and Høeg 2002; Walker et al. 1987; Yorisue et al. 2013 2016). Eventually, the cyprid induces the final cementation and develops into a juvenile sedentary barnacle (Aldred et al. 2018; Crisp 1955; DiBacco et al.

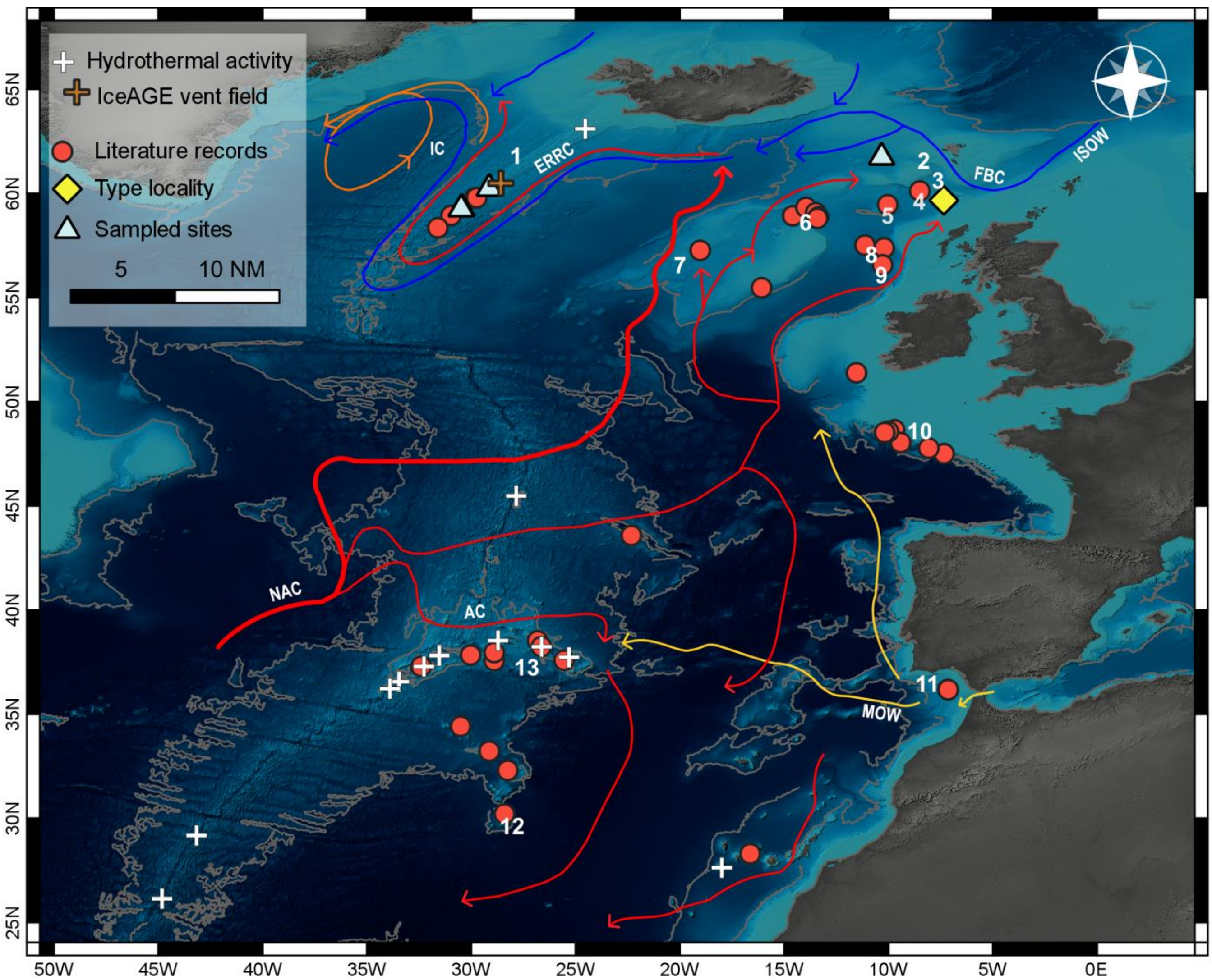


Fig. 1. Distributional range of the deep-sea acorn barnacle *Bathylasma hirsutum* in the north-east Atlantic. Literature records are included from the: (1) Reykjanes Ridge, (2) Faroe-Bank Channel, (3) Wyville Thomson Ridge, (4) Rockall Trough, (5) Rosemary Bank, (6) George Bligh Bank, (7) Hatton Bank, (8) Anton Dohrn Seamount, (9) Hebrides terrace, (10) Celtic Shelf, (11) Gulf of Cádiz, (12) Great Meteor Seamount, and (13) Azores Archipelago. Schematic of the main circulation patterns adapted from Koman et al. (2020) and Puerta et al. (2020). Red arrows depict surface waters of North Atlantic Current (NAC) origin, with a branch of the Azores Current (AC). Yellow arrows depict Mediterranean Outflow Water (MOW). Blue arrows indicate deep-water pathways of the Iceland Scotland Overflow Water (ISOW) flowing towards the Faroe Bank Channel (FBC), as well as overflow waters that run in parallel to the East Reykjanes Ridge Current (ERRC). Orange arrows represent surface waters of the Irminger Current (IC) with mixtures of Arctic and Atlantic waters.

2011). In the deep sea, several species have developed a range of deviant larval development strategies (Yorisue et al. 2013). For example, some species hatch as cyprids which are immediately disposed to search for an attachment site (Buhl-Mortensen and Høeg 2006). Others, such as the endemic vent barnacle of the genus *Neoverruca* Newman 1989, develop lecithotrophic nauplii to ensure dispersal over far distances with a long larval development (Southward and Jones 2003). In addition, a special habitat adaptation in vent barnacles speeds up the metamorphosis into the sensory cyprid as their ontogeny responds to elevated water temperatures (Watanabe et al. 2004 2006; Yorisue et al. 2013). Currently, nothing is known about the ontogeny of the deep-sea barnacle *B. hirsutum*. Single larval stages of the Antarctic *B. corolliforme* have been examined in specimens from the McMurdo Sound region (Dayton et al. 1982; Foster 1989). Due to their relatedness, the naupliar and cyprid anatomy is suggested to be comparable in both species. Besides their conventional balanomorph anatomy which is explored in Dayton et al. (1982) and Foster (1989), the larvae of *B. corolliforme* can be distinguished from other balanomorph species by having a naupliar eye and an overall larger size. According to Foster (1989), larval development likely exceeds three weeks to complete, comparable to the boreal species *Semibalanus balanoides* (Linnaeus, 1767) which is suggested to have a planktonic existence of 3–6 weeks (Barnes and Barnes 1959 1958). The cypris develops into an undivided chitinous annulus with a single hirsute ring, including the aperture with terga and scuta adjacent to which a pair of photoreceptors is found (Dayton et al. 1982). Attachment, metamorphosis of settled cyprids and early post-larval mortality are the most critical steps and determine barnacle recruitment (Pineda et al. 2002; Thiyagarajan et al. 2002). As the barnacle grows, it produces distinct growth increments that undulate parallel to the basal margin and run continuously on the exterior of each parietal plate (Anderson 1994; Fig. 2). These increments are referred to as either growth lines (Checa et al. 2019; Varfolomeeva et al. 2008) or growth ridges (Anderson 1994; Blomsterberg et al. 2004; Bourget 1987; Bourget and Crisp 1975). With the terminology being used interchangeably in literature, the authors have agreed upon using the term 'growth ridges' throughout. In *B. hirsutum*, the growth ridges are well developed and hirsute, being covered with numerous chitinous setae projecting outwards from the shell plate, aggregated on small basal domes (Fig. 2H). According to Bourget and Crisp (1975), the rate of ridge formation corresponds roughly to the growth rate of barnacles. However, the ontogenic age of deep-sea species might be affected by the fluctuating food supply in the otherwise stable physical deep-sea environment (Anderson 1994; Foster 1983; Tyler and Young 1992). As generalist feeders, *B. hirsutum* captures suspended particulate matter using an erected cirral fan which it is able to adjust towards the prevailing water currents (Southward and Southward 1958; Dayton et al. 1982; Gallego et al. 2017). Adult specimens of *B. hirsutum* can grow more than 8 cm in height and have a white-yellow shell plate (Fig. 2A–C, G). The barnacle is of conical shape with the diameter of the orifice being less than half of the diameter of the membranous base (Newman and Ross 1971; Southward and Southward 1958). Main species-specific characteristics are narrow carinolateral plates, an elongate tergum, and compartments of the orifice which do not diverge from one another, as for example seen in *B. corolliforme* (Bullivant & Dearborn, 1967 plate 14; Dayton et al., 1982 fig. 3C; Meyer, 2020 fig. 3-3). The parietal plates of *B. hirsutum* show a wide plasticity, depending on the attachment site as well as the space given for the animal to grow. As many acorn barnacles, *B. hirsutum* is of gregarious nature and tends to settle crowded with epizoic growth, *i.e.*, one established animal has one or several specimens laterally attached (Anderson 1994).

Scope of study

Processes involving successful recruitment, dispersal of planktotrophic larvae and settlement as benthic animals with future reproductive success determine the extent to which barnacle populations are genetically and biologically connected across their distributional range (Boschen-Rose and Colaço 2021; Cowen et al. 2007; Pineda et al. 2007). As these bentho-pelagic interactions are highly complex and challenging to assess, especially with regard to deep-sea habitats (Etter and Bower 2015), the genetic connectivity of *B. hirsutum* within the NE Atlantic is completely unknown. In the northeastern Iceland Basin, surface waters of the North Atlantic Current converge with deeper water masses from the Iceland-Faroe Ridge into the East Reykjanes Ridge Current (EERC), acting as a boundary between the Iceland Basin and the eastern flank of the Reykjanes Ridge (Koman et al. 2020). As the broad EERC flows southwest towards the Bight Fracture Zone, it crosses the ridge into the Irminger Basin (Fig. 1). This study reports on the opportunistic inhabitation of a hydrothermally influenced site for the species *B. hirsutum* and elaborates on habitat differences by comparing barnacle size distributions per site and depth, as well as chemical components of parietal shell plates from all sites. Furthermore, we attempt to investigate the genetic connectivity of *B. hirsutum* from four sites within the Iceland Basin, encompassing non-hydrothermal habitats in the Faroe Bank Channel and along the Reykjanes Ridge, as well as the vent- associated habitat. With the ERRC, an oceanographic connectivity pathway to western Atlantic basins, the potential for *B. hirsutum* nauplius larvae to be dispersed across the ridge is elaborated. Given that *B. hirsutum* is herein acknowledged to utilise a hydrothermally influenced habitat, vent fields within its range of depth and occurrence are discussed as potential habitats, as is the potential for *B. corolliforme* and *B. chilense* to live affiliated with hydrothermal activity.

MATERIALS AND METHODS

Taxon sampling and measurements

Specimens of *Bathylasma hirsutum* were collected at four sites (Fig. 3, Table 1) during three research cruises under the IceAGE (Icelandic marine Animals: Genetics and Ecology) project umbrella (Brix and Devey 2019; Brix et al. 2014; Meißner et al. 2018). At site A, situated west of the Faroe Bank Channel, barnacles were sampled by means of a triangular dredge onboard the RV *Poseidon* in 2013 (IceAGE_2
/ POS456; Brix et al. 2013). In 2018, specimens were sampled along the Reykjanes Ridge axis at sites B

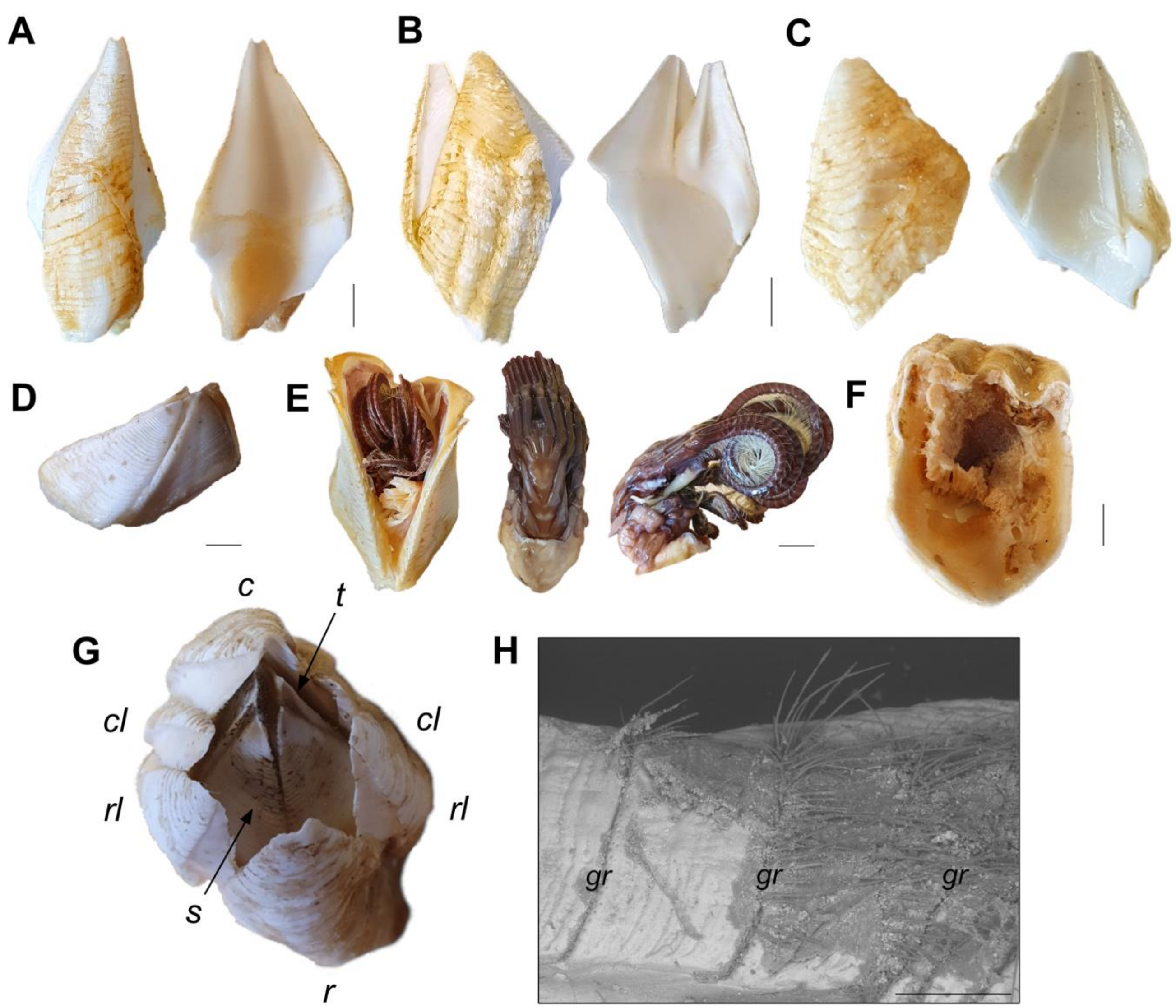


Fig. 2. Plate organisation and general anatomy of *B. hirsutum*. External and internal view of A: carina, B: rostro-lateral, C: rostrum, D: tergum, E: scutum. F: Soft-bodied animal with serrated cirral appendages. G: Top view of an intact specimen with a carino-rostral diameter of 2.5 cm; c: carina, cl: carino-lateral, rl: rostro-lateral, r: rostrum, t: tergum, s: scutum. H SEM image of a shell plate showing growth ridges (gr) with protruding chitinous setae. Scale bars: A–C = 1.5 cm; D–F = 1 cm; H = 500 µm.

and C using the Remotely Operated Vehicle (ROV) *Phoca* onboard the RV *Maria S. Merian* (IceAGE_RR / MSM75; Devey et al. 2018). In 2020, the Reykjanes Ridge was revisited with the *RV Sonne* and the ROV *Kiel6000* (IceAGE_3 / SO276; Brix et al. 2020). Barnacles were collected at site D, affiliated with the hydrothermal 'IceAGE vent field' which was discovered during the SO276 expedition (Brix et al. 2020). Prior to and during animal sampling by means of the ROV, each site was documented by *in situ* video and photography records. Material collection was performed using the ROV's operational titanium arms, with nets or the

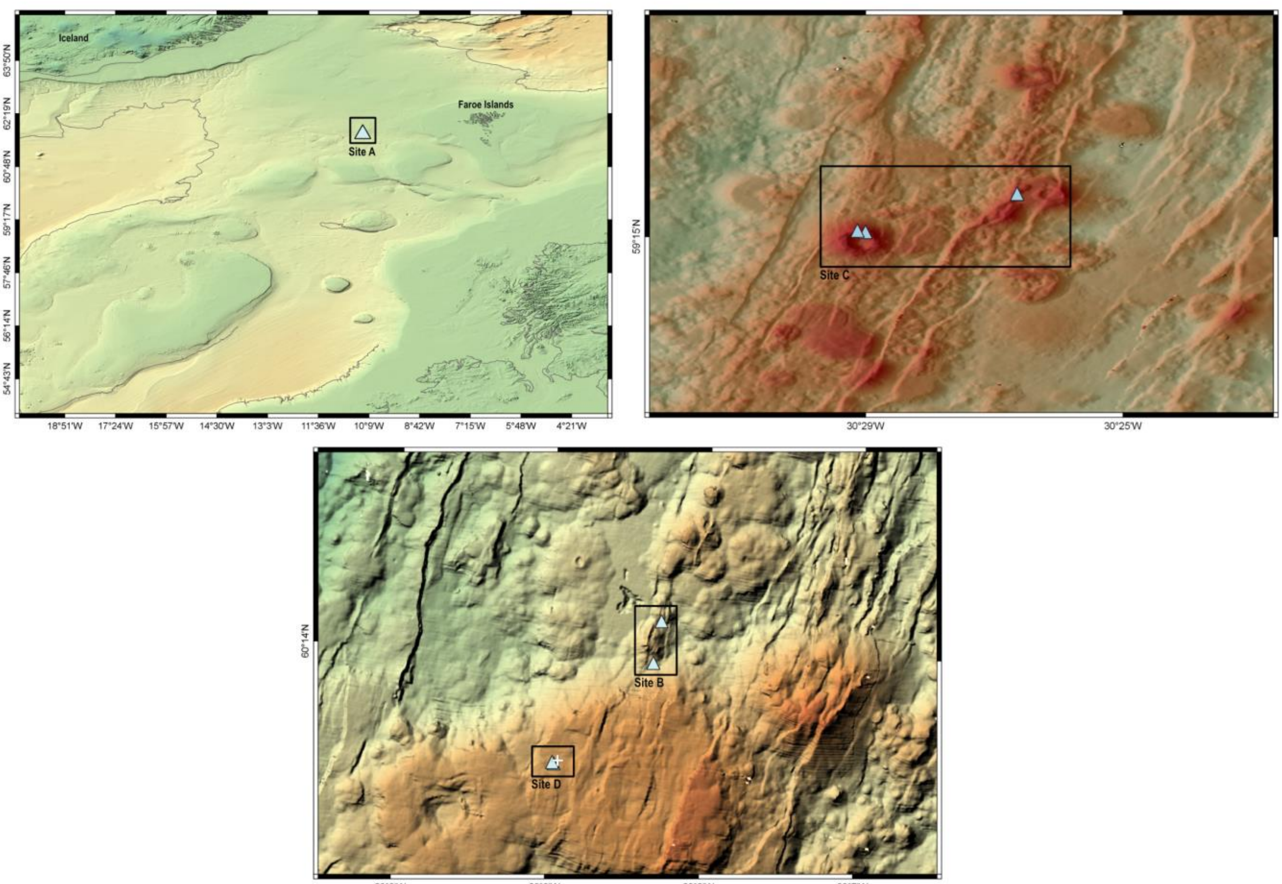


Fig. 3. Collection sites of *Bathylasma hirsutum* targeted during the research cruise POS456 west of the Faroe Bank Channel (site A), as well as two expeditions along the Reykjanes Ridge MSM75 (sites B, C), and SO276 (site D). The white cross indicates the hydrothermal IceAGE vent field.

Table 1. Metadata of the four sampling sites A–D. Barnacles of the species Bathylasma hirsutum were collected by means of triangular dredge (TD) and remote operated vehicle (ROV)

Expedition	Site	Depth (m)	Latitude 'N	Longitude 'W	Date	Station	Gear
IceAGE_2	A - Faroe Bank Channel	1110	61°44.220	010°19.710	30.07.2013	877	TD
IceAGE_RR	B - Reykjanes Ride	719	60°14.274	029°08.138	07.07.2018	31	ROV
		703	60°14.201	029°08.162	01.08.2018	188	ROV
	C - Reykjanes Ridge	966	59°15.653	030°26.805	17.07.2018	80	ROV
		858–867	59°15.074	030°29.102	28.07.2018	149	ROV
IceAGE_3	D - IceAGE vent field	664	60°14.020	029°08.500	12.07.2020	103	ROV
		658	60°14.022	029°08.506	14.07.2020	112	ROV

slurp sampler. On deck, specimens were labelled and fixed in sealed plastic bags using 96% undenatured ethanol and stored at -20°C to avoid DNA degeneration. Photographs of each specimen were taken with a Canon EOS 2000D prior to tissue sampling from the abdomen or one cirrus for DNA analysis. Height of carina parietal plates were measured using a digital vernier calliper, and growth ridges on the carina were counted with the aid of a Leica stereomicroscope. Morphometric measurements of each specimen are listed in the supplementary material (Table S1). Measurements were plotted using R
4.2.2 (R Core Team 2022) and RStudio 7.2.576 (RStudio Team 2022). Respective R packages are listed in the supplementary material (Table S2). Distribution records of *B. hirsutum* were reviewed from original literature and databases (www.jncc.gov.uk, www.gbif.org, www. obis.org), and geographic maps including bathymetric data were created using the software QGIS 3.10 (QGIS Development Team 2019).

DNA extraction, amplification and sequencing

DNA extractions were carried out either on board the research vessel or at the research institute. Therefore, three different extraction kits were used; E.Z.N.A® Mollusc DNA Kit (Omega Bio-Tek Inc., Norcross, GA, USA), Qiagen DNeasy® Blood and Tissue Kit (Qiagen, California, USA), and Macherey- Nagel NucleoSpin Tissue Kit (Macherey-Nagel, Düren, Germany); following the manufacturer's instructions, leaving the tissue for digestion overnight in a shaking bath at 56°C/350 rpm. For all isolates, elution was carried out in two steps, using 50 µl elution buffer each turn. DNA concentration for each isolate (100 µl) was measured using a Qubit 4 Fluorometer (Thermo Fischer Scientific™ Inc.), following the manufacturer's protocol. DNA quality was comparable between all extraction methods. All DNA aliquots were stored at
-20°C at the German Centre for Marine Biodiversity Research (DZMB), Hamburg. The mitochondrial marker cytochrome *c* oxidase subunit I (*COI*) and the nuclear marker elongation factor 1α subunit (EF- 1) were selected for species delimitation analyses (Table 2). Polymerase Chain Reaction (PCR) was carried out using three types of polymerases because of the workflow happening in different laboratories or due to troubleshooting. The polymerases included AccuStart II Taq PCR SuperMix (Quantabio, Beverly, MA, USA), Phire Green Hot Start II PCR Master Mix (Thermo Fischer Scientific™), and PCR-Beads, illustra™ PuReTaq Ready-To-Go™ (Avantor®; VWR Int. GmbH, Darmstadt, Germany). Applied master mix compositions and thermal cycling conditions are listed in the supplementary material (Tables S3, S4). Quality and quantity of amplified product was assessed by gel electrophoresis using 1.5% TAE gels. Where band quantification yielded too high DNA concentration, samples were diluted 1:10 prior to purification. Samples with low DNA content were repeated using the same PCR settings but doubling the amount of amplified DNA. Successful PCR products were purified using 3 µl ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fischer Scientific™) on 10 µl product and run on a thermal cycler (incubation: 37°C, 15 min; enzyme inactivation: 80°C, 15 min). Double stranded sequencing was carried out by Macrogen Europe Inc. (Amsterdam, Zuidoost, The Netherlands) and Eurofins Genomics Germany GmbH (Ebersberg, Germany) using ABI 3730xl sequencers.

Sequence editing, alignment, and genetic analyses

Geneious Prime® (Version 2022.1.1; Biomatters, Auckland, New Zealand; Kearse et al. 2012) was used to edit and assemble forward and reverse chromatograms as well as to check for potential contamination using the implemented BLAST search tool (Basic

Table 2. List of primers with annealing temperature (AT) range

Primer	Sequence (5' to 3')	Range of AT (°C)	Reference
COI			
LCO1490	GGTCAACAAATCATAAAGATATTGG	45–50	Folmer et al. 1994
HCO2198	TAAACTTCAGGGTGACCAAAAAATCA		
LCO1490-JJ	CHACWAAYCATAAAGATATYGG	55–70	Astrin and Stüben 2008
HCO2198-JJ	AWACTTCVGGRTGVCCAAARAATCA		
EF-1			
EF-1 for	GATTTCATCAAGAACATGATCAC	56–60	Tsang et al. 2014
EF-1 rev	AGCGGGGGGAAGTCGGTGAA		

Local Alignment Search Tool; Altschul et al. 1990). Assembled sequences were aligned using MUSCLE (Edgar 2004), implemented in Geneious Prime® with default settings, and ends trimmed with respective primer sequences. The software jModelTest 2 (Darriba et al. 2012; Guindon and Gascuel 2003) was used to estimate best-fit models of evolution by applying the Akaike Information Criterion (AIC; Sakamoto et al. 1986), resulting in GTR + I + G for *COI* and TIM1 + I + G for EF-1. Phylogenetic analyses of single-gene and concatenated alignments were performed using MrBayes 3.2.1 (Huelsenbeck and Ronquist 2001), with three parallel runs of 5 million generations, sampling every 1000 generations. Convergence of independent runs was examined in Tracer 1.7.2 (Rambaut et al. 2018) with a burn-in of 10%. Trees were reconstructed using Bayesian Inference (BI), assessing branch support by posterior probability (PP) with values $\geq$ 0.95 considered as highly supported (Felsenstein 1985; Huelsenbeck et al. 2001). Tree editing was performed in FigTree 1.4.4 (Rambaut 2009) and Affinity Photo 1.10.5 (Serif Ltd., Europe). Species were delimited using the two distance-based methods ASAP (Assemble Species by Automatic Partitioning; Puillandre et al. 2021) and ABGD (Automated Barcode Gap Discovery; Puillandre et al. 2012), using the three evolutionary models Jukes-Cantor; Kimura 80 and Simple Distance with default settings. Haplotype networks were computed for both gene markers using the software PopArt (Leigh and Bryant 2015), applying the minimum spanning network algorithm to calculate nucleotide diversity, Tajima's *D* test statistic and the number of segregating and parsimony-informative sites (Bandelt et al. 1999).

Energy Dispersive Spectroscopy

Energy Dispersive Spectroscopy (EDS) analysis for the elemental presence detection was performed to compare the mineral components of shell plates of *B. hirsutum* from sites with and without hydrothermal influence. EDS was done with a Hitachi TM3000 Scanning Electron Microscope (Hitachi High-Technologies, Maidenhead, UK), equipped with an Oxford Instrument INCA system and Aztec software (Oxford Instruments, High Wycombe, UK) at the British Antarctic Survey. EDS maps for x150 magnified areas were acquired for five minutes, set to detect all elements, and quantified by the Aztec software. Elemental spectra of the bulk composition (% oxides) were displayed and presence of manganese (Mn), iron (Fe) and rare earth metals (*e.g.*, Tungsten trioxide (WO_3), Ytterbium (III) oxide (Yb_2O_3), Vanadium pentoxide (V_2O_5)) were noted.

RESULTS

A total of 159 specimens of *Bathylasma hirsutum* were sampled at four sites (A–D) within the NE Atlantic. Site A extends the northern distributional range of the species from the Wyville Thomson Ridge to the Faroe Bank Channel. Sampling efforts at sites B–D present new records from the central section of Reykjanes Ridge and provide first-time *in situ* observations of the species in its natural habitat (Fig. 4). Video footage of the respective sites can be accessed via. The habitat at site B, situated at ~710 m depth, is dominated by large volcanic rocks and pillow lava with varying topography, featuring a range of niches with diverse megafaunal compositions including different species of cold-water corals (Fig. 4A; see also Devey et al. 2018). Barnacle coverage varies from individual specimens along the slope of a volcanic mount to localised patches of high abundance. Active predation by a sea star of unidentified species was observed, next to an empty barnacle shell which likely had been fed upon beforehand. At site C, barnacles occur with highest observed abundances along the northern and western rim of a large, cratered volcano structure between 858 and 966 m depth. At times, debris of dead barnacle shells is found below boulders on which living adult specimens sit attached (Fig. 4B). Active feeding behaviour by means of complete cirral extension was observed frequently (Fig. 4D). Proximal to the venting chimneys of the recently discovered IceAGE vent field (Brix et al. 2020), barnacles were found attached to volcanic boulders in localised groups, accompanied by several specimens of an orange deep-sea anemone, possibly belonging to the genus *Phelliactis* Simon, 1892 (Fig. 4E, F). During sampling, ambient water temperature was measured to ~5.6°C (see Brix et al. 2020 fig. 5.29). The influence of hydrothermal activity is apparent by the presence of white bacterial mats covering the sea bed. Prior to this study, the settlement of *B. hirsutum* in a hydrothermally influenced habitat had been undescribed. Of all species of acorn barnacles currently known, *B. hirsutum* represents the first to be found affiliated with a hydrothermal vent field in the Atlantic Ocean.

Molecular species delimitation

DNA was successfully amplified for 146 specimens, yielding 287 novel sequences for the two genetic markers *COI* (146 sequences; 686 bp) and EF1 (141 sequences; 930 bp). Seventeen sequences were retrieved from GenBank and included in the final analysis. *Chelonibia testudinaria* (Linnaeus, 1758) was used to root trees, as the family Chelonibiidae Pilsbry,

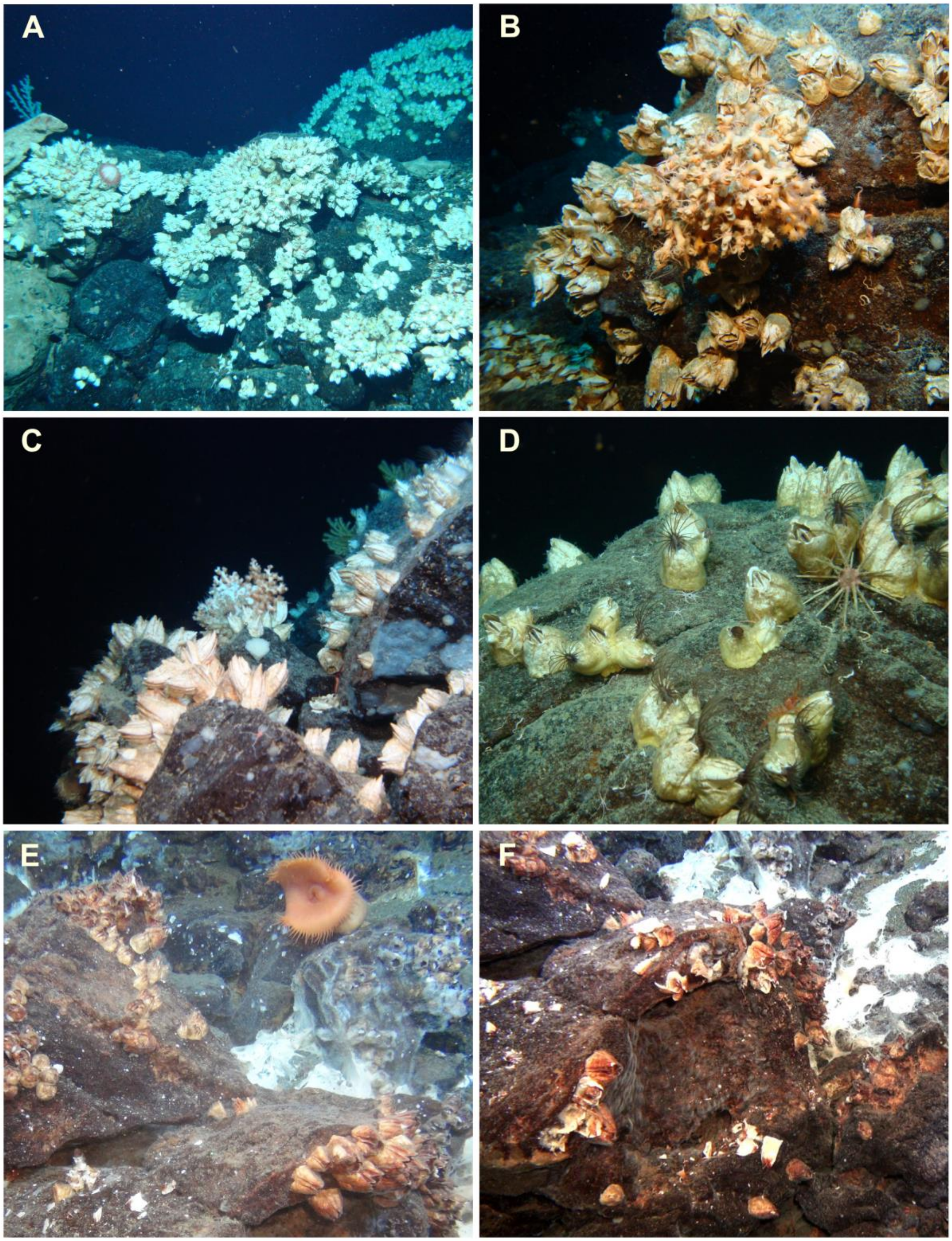


Fig. 4. *In situ* images of *B. hirsutum* from the Reykjanes Ridge axis (A–D) and the IceAGE vent field (E, F). A, Dense cluster of specimens attached to pillow lava (site B). B, Barnacles aggregated with a cold-water coral. Accumulated dead shell plates visible to the lower left (site C). C, Epizoic growth on boulder with associated coral fauna (site C). D, Feeding behaviour by extended cirral fans in multiple specimens situated on volcanic rock (site C). E–F, Specimens with brown-black shell precipitate attached to volcanic rocks, surrounded by white bacterial mats (site D). Large orange anemones, possibly of the genus *Phelliactis*, share the habitat. Image courtesy: GEOMAR, Kiel.

1916 is sister to the Bathylasmatidae (Chan et al. 2021). The Bayesian analyses of the concatenated gene alignment (*COI* + EF1, 168 sequences; 1616 bp) show maximum support for a single clade of *B. hirsutum* (PP = 1), including specimens from all sampled sites (Fig. 5). The clade clearly separates from the Antarctic sister species *B. corolliforme* (PP = 0.95) as well as from the sister genus *Hexelasma* Hoek, 1913 (*P* = 1). ABGD and ASAP analyses were run on alignments for both genetic markers. Prior maximum divergence of intraspecific diversity (P) was set to 0.001–0.1 and relative gap width (X) to 1.0–1.5. Each of the evolutionary models yielded a partition consistent with the Bayesian analysis, suggesting one clade of *B. hirsutum* (*P* = 0.00167–0.100). Partitions yielding more than one clade of *B. hirsutum* likely resulted from splitting artefacts caused by the low *P* values (0.0010; Puillandre et al. 2012 2021). Sequence data is submitted to GenBank via the BOLD dataset doi:10.5883/DS-IACIR. GenBank accession numbers are listed in the supplementary material (Table S5).

Haplotype network analyses

Each one minimum-spanning haplotype network was inferred from 146 *COI* and 134 EF1 sequences of *B.*

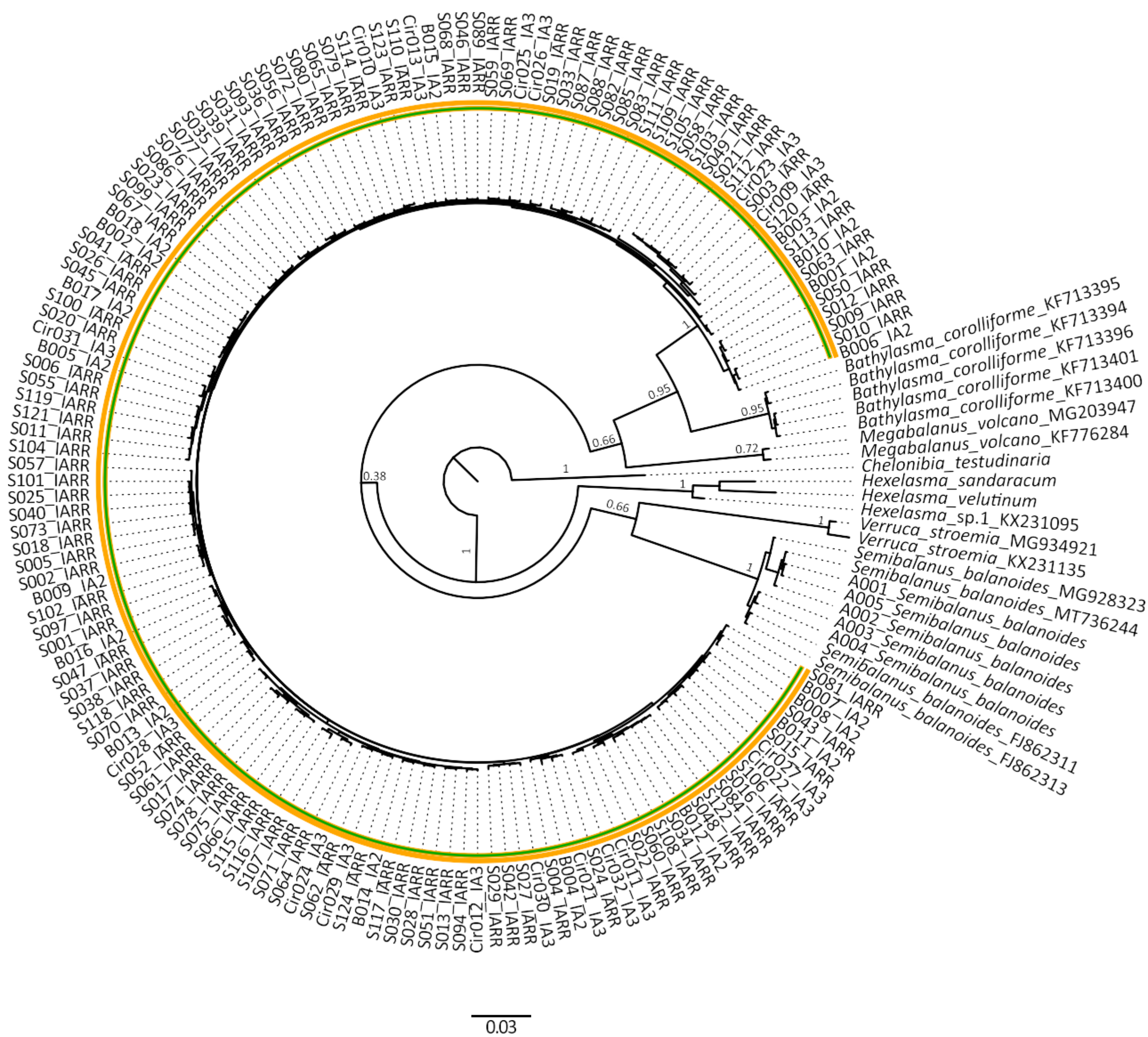


Fig. 5. Bayesian phylogenetic tree with posterior probabilities based on the concatenated *COI* + EF1 dataset, including seven outgroup species. Names on the nodes refer to the *Bathylasma hirsutum* specimen code and the respective IceAGE expedition. Results of the ASAP and ABGD species delimitations are shown by yellow and green circles. The tree is rooted with *Chelonibia testudinaria*. Scale bar shows substitutions per site.

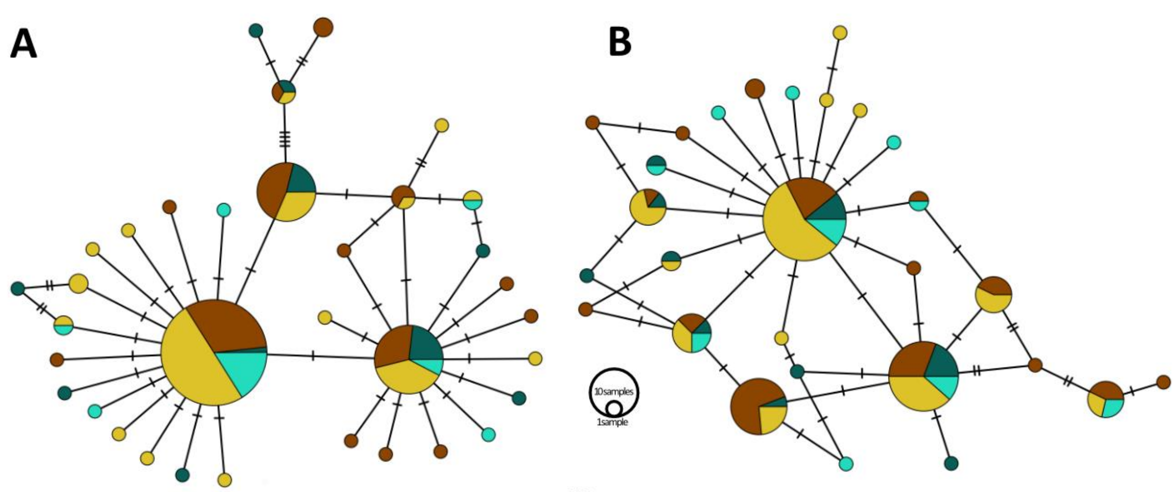
hirsutum to visualise the genetic relationships between individual genotypes at population level (Fig. 6). Both networks depict a high degree of genetic connectivity amongst the sampled sites, reflected in the three (*COI*) and four (EF1) prominent clusters of genetically identical specimens. The genetic distance to smaller clusters or individual samples is low, with a maximum of four mutational steps visualised as hash marks. The low intraspecific genetic diversity is reflected in the nucleotide diversity and small number of parsimony- informative sites.

EDS analyses of barnacle plates

Specimens collected at sites A, B, and C depict a natural shell colour, congruent with the morphological species description of *B. hirsutum* (Hoek 1883). Shell plates of specimens from site D, however, are of a darkened shade owing to a brown-black shell precipitate (Fig. 4). To examine these extrinsic differences and the composition of the precipitate, elemental spectra of the bulk composition (% oxides) of manganese (Mn), iron (Fe), Tungsten trioxide (WO_3), Ytterbium (III) oxide (Yb_2O_3), and Vanadium pentoxide (V_2O_5) were assessed of selected specimens from each site (Table 3). Shell plates from site D yielded the highest Fe/Mn ratios, with percentages of 2.54–34.82 (FeO) and 1.94–28.59 (MnO) measured from the youngest (base) to the oldest shell part (apex). This results in up to 60.24% ferromanganese (Fe-Mn), increasing towards the apex. Values of WO_3 double in top and mid sections, whereas Yb_2O_3 is absent. Vanadium pentoxide (V_2O_5) was solely found in the mid-section of one shell plate. Shell plates from sites B and C contained smaller Fe/Mn ratios, yielding traces of Fe-Mn oxide ranging from 0.26– 1.35% and 0.44–1.95% in the mid-section, to 1.93% and 2.25% in the apex, respectively. No ferromanganese oxides were detected in the youngest shell part. Small fractions of WO_3 and Yb_2O_3 are present in the mid sections only. The shell plate from site A yielded 4.56% FeO in the mid-section, as well as 0.37% WO_3 in the apex and 0.64% Yb_2O_3 at the base. No Fe-Mn oxide precipitates were measured.

Morphometric measurements of carinal shell plates

Intact carinal parietal plates were identified in 69 specimens (site A, B, C, D: 10, 24, 24, 11; see Table S1). Carinal height (CH) was measured from base to apex and plotted against the count of growth ridges (GR) for each parietal plate to map barnacle size distribution per site and visualise the relation between CH and GR (Fig. 7A). Overall, CH has a positive effect on the number of GR, illustrated by the positive slope. The largest CH of 65.48 mm was measured from a site C specimen, with the highest count of 116 GR. The sample set contained the fewest small specimens with a minimum height of 18.53 mm and a count of 28 GR. Barnacles from site A were second largest, with maximum and



	COI	EF1
Nucleotide diversity	0.00277224	0.00228362
Nr. of segregating sites	31	17
Nr. of parsimony-informative sites	11	12
Tajima's D	-2.30367	-1.1368

Site A - Faroe Bank Channel
Site B - Reykjanes Ridge
Site C - Reykjanes Ridge
Site D - IceAGE vent field

Fig. 6. Minimum spanning haplotype networks and analysis outputs of *Bathylasma hirsutum* from the four sampled sites A–D coded by colour. A, Network of the *COI* sequences. B, Network of the EF1 sequences.

minimum heights of 29.00 mm and 78.30 mm, and respective counts of 31 and 63 GR. Specimens from site B depicted the largest size span from 5.15 mm to 56.30 mm, with 12 GR and 56 GR laid down on the carinal plates, respectively. Here, the highest GR count of 71 was from a specimen of 44.22 mm carinal plate height. The smallest barnacle from site D was 14.70 mm and had 12 GR. In the largest specimen of 50.50 mm height, 48 GR were counted. The highest count of 51 was retrieved from a carina measuring 43.20 mm. To test whether barnacle size distribution changes with ocean depth, average depth at each sampled site was plotted against CH (Fig. 7B). Our data denote a trend towards enhanced shell growth at the deeper sites A and C compared to the shallower sites B and D.

DISCUSSION

The herein presented results on the deep-sea acorn barnacle *Bathylasma hirsutum* from four sites within the northeastern Iceland Basin provide new distributional records with *in situ* footage of specimens occupying hard-bottom substrates in depths between 658 and 966 meters along the Reykjanes Ridge axis.

For the first time, *B. hirsutum* was found affiliated with a hydrothermally active field. As it is unknown to what extent populations of this sessile crustacean with planktotrophic larval dispersal are connected, we have assessed the genetic connectivity between specimens from the Faroe Bank Channel and the Reykjanes Ridge. The molecular analyses revealed low levels of intraspecific genetic diversity, reflected in the low number of parsimony-informative sites. The latter indicates the observed intraspecific genetic variability to be lower than the expected genetic variation between specimens of *B. hirsutum* from different sites (Papathanassopoulou and Lorentzos 2014). Haplotype networks of both markers suggest a substantial gene flow between all sites (Fig. 6), indicating a pronounced genetic connectivity within the Iceland Basin. Site A, situated west of the Faroe Bank Channel, now marks the northern boundary of the species' distributional range. Based on the basin-wide cluster analysis conducted by Schumacher et al. (2022), this site is categorised as nutrient-rich, with strong local currents and seasonal changes. It is highly hydrodynamic, influenced by the continuous flow of dense, well-oxygenated Iceland Scotland Overflow Water (Chafik et al. 2020; Hansen et al. 2016) with mean water temperatures at maximum

Table 3. Energy Dispersive Spectroscopy (EDS) analyses for the elemental presence detection on barnacle plates from stations within the respective sampling areas. Elemental spectra of the bulk composition (% oxides) are shown for the top, mid and end sections of each shell plate with measured presences of iron oxide (FeO), manganese oxide (MnO), ferromanganese oxide (Fe-Mn) and the rare earth metals Tungsten trioxide (WO_3), Ytterbium (III) oxide (Yb_2O_3) and Vanadium pentoxide (V_2O_5). Measurements in the top section of specimen S039 failed and are not accessible (na)

Expedition	Site	Station	Specimen	FeO	MnO	Fe-Mn	WO_3	Yb_2O_3	V_2O_5	Position
IceAGE_2	A	877	B018	0.22–0.40	-	-	0.37	-	-	Top
				4.56–4.56	-	-	-	-	-	Mid
				0.52–9.92	-	-	-	0.64	-	End
IceAGE_RR	B	31	S022	1.13–1.19	0.66–0.74	1.79–1.93	-	-	-	Top
				0.59–0.65	0.63–0.70	1.22–1.35	0.51–0.67	-	-	Mid
				0.43–0.77	-	-	-	-	-	End
	B	188	S123	0.58–0.75	-	-	-			Top
				0.59–0.59	0.26–0.34	0.36–0.93	0.40–0.44	0.80	-	Mid
				0.00–3.33	-	-	-	-	-	End
	C	80	S039	na	na	na	na	na	na	Top
				0.44–0.89	0.00–0.15	0.44–0.63	0.37	-	-	Mid
				8.85–9.05	-	-	-	-	-	End
	C	149	S067	1.58–1.67	0.48–0.58	2.06–2.25	-	-	-	Top
				1.36–1.94	0.47–0.57	1.83–1.95	-	-	-	Mid
				2.18–2.22	-	-	-	-	-	End
IceAGE_3	D	103	Cir022	31.56–34.82	21.99–24.02	53.55–58.84	-	-	-	Top
				19.19–31.65	28.59–16.06	35.25–60.24	0.89	-	0.57	Mid
				4.23–4.23	2.87–2.87	7.10–7.10	-	-	-	End
	D	112	Cir032	15.67–16.82	19.81–22.42	35.57–39.24	1.11	-	-	Top
				11.99–15.18	16.41–17.48	28.40–32.42	1.02–1.13	-	-	Mid
				2.54–8.05	1.94–5.50	4.48–13.55	-	-	-	End

depth between 4–9°C (Assis et al. 2018; Tyberghein et al. 2012). The hard-bottom habitat houses several dense aggregations of benthic suspension feeding organisms such as sponges and cold-water coral reefs, indicating a prominent food supply (Frederiksen et al. 1992; Kazanidis et al. 2019). Strong current velocities not only enhance particle suspension and thus food supply, making this a favourable habitat for *B. hirsutum*, but may also provide pathways for larval transport. As the deep-water currents interconnect with water flows along the eastern flank of the Reykjanes Ridge, we suggest a proportion of larvae dispersed from site

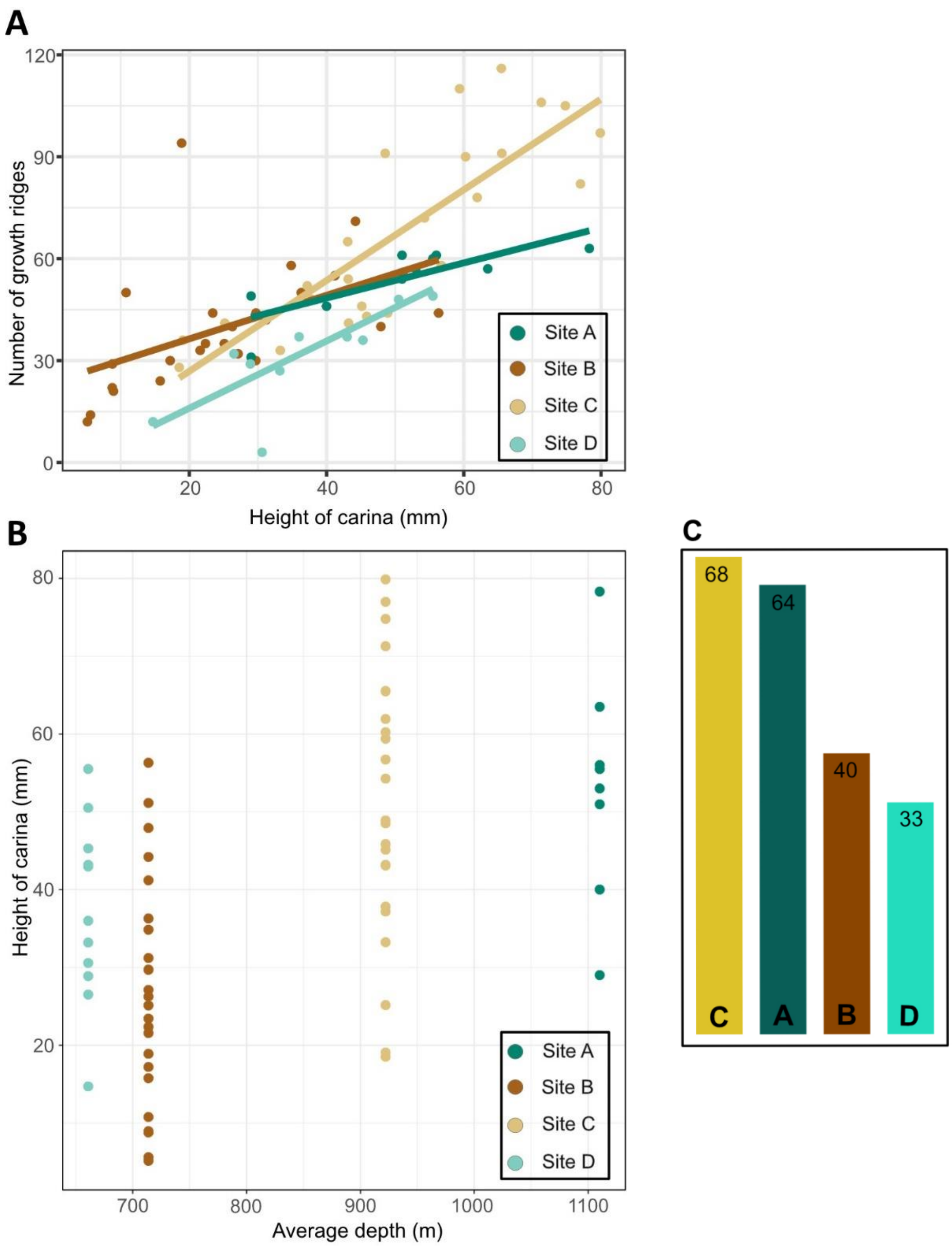


Fig. 7. Morphometric measurements of carinal parietal plates. A, Relation between carinal height and count of growth ridges on the carinal parietal plate with a predicted linear model fits based on a 95% confidence interval. B, Barnacle size distribution represented by carinal height at average depth at the sampled sites. C, Bar chart showing the average number of growth ridges per site.

A are transported towards the Reykjanes Ridge axis, facilitating the high localised abundances observed during the ROV dives (Fig. 4A). The ridge axis is mainly influenced by the ERRC, a weakly bottom- intensified current resulting from a convergence of dense Iceland Scotland Overflow Water with the Iceland branch of the North Atlantic Current (Koman et al. 2020). With these nutrient-rich and well-oxygenated water masses flowing south, larvae are suggested to be transported along the ridge, facilitating the genetic connectivity between the herein assessed sites. We presume that recruits of *B. hirsutum* settled at site D originated from the dense barnacle fields north of this site. With ambient seawater temperatures measured to ~5.6°C where the vent-affiliated specimens were sampled (see Devey et al. 2018), the habitat suitability by means of temperature range is comparable to the non-hydrothermally influenced sites.

Analysis of morphometric measurements

The positive relation between carinal plate heights and number of growth ridges laid down on the respective shell plates reflects the formation of growth ridges to be a good indication for the growth rate of the deep-sea barnacle *B. hirsutum*, such as it is for shallow- water species (Bourget and Crisp 1975). In what way the number of growth ridges is related to the age of a specimen, however, seems to be depth-dependent. In an experimental study on growth ridge formation, Bourget and Crisp (1975) observed one growth ridge to be laid down for each exuviation in the intertidal species *S. balanoides*, reflecting an annual growth pattern. In the deep-sea species *B. corolliforme*, however, the authors counted many more ridges than the observed number of moults and were not able to distinguish between the ridges laid down on the shell during and in absence of a moulting event. Hence, in *B. corolliforme*, one growth ridge cannot be estimated to account for one year, but rather a growth period which in turn is affected by food availability. The principal food source in deep-sea habitats is owed to vertical flux of organic matter from both surface primary production and redistribution of suspended particles in the bottom mixed layers (Davies et al. 2009 2006; Ramirez-Llodra et al. 2010). With *B. hirsutum* being sister to the Antarctic *B. corolliforme* and occupying habitats with comparable physical environments, we suggest a similar pattern of growth ridge formation in this species where a fluctuating food supply in the else stable physical deep-sea environment might affect the growth rate (Anderson 1994; Foster 1983; Tyler and Young 1992).

Carinal parietal plates from the two deeper sites A and C were found to be larger compared to the shallower habitats at sites B and D, implying barnacle size to be greater with increased depth (Fig. 7). This trend is congruent with the general understanding of deep-sea species to grow larger with depth, adapted to invest already restricted energy resources in growth (Timofeev 2001). At site C, specimens were found in the highest abundance and are not only the largest but also show the highest amount of growth periods. We suggest the high abundances and enhanced growth at the volcanic crater to be a response to an enriched food environment accompanied by strong localised currents, providing a favourable habitat for *B. hirsutum*. The productive food environment is also reflected in a massive coral forest, dominated by large trees of *Paragorgia arborea* (Linnaeus, 1758), which was detected proximal to the barnacle fields (Devey et al. 2018). This is further supported by the frequently sighted active feeding behaviour (Fig. 4D). The accumulated shell debris observed below several boulders with living specimens still attached indicates a long-sustained population with several generations of settlement. The large size span of individuals collected at site B indicates a vital population with successful recruitment of juveniles, settled amongst their adult conspecifics (Fig. 7A). Since several specimens sizing less than 10 mm in carinal height were found, food availability in this habitat is assumed to be slightly lower compared to site C, yielding a lowered individual growth rate. At the hydrothermally-influenced site D, specimens were found to be smaller compared to the deeper sites (Fig. 7C). This is interesting, as *B. hirsutum* could potentially utilise matter from the widespread bacterial mats as an additional food source. This mixotroph mode has been confirmed in several stalked barnacle species from hydrothermal vent fields in the Pacific Ocean (Buckeridge 2000; Southward and Newman 1998) and was recently suggested for the acorn barnacle genus *Eochionelasmus* (Chan et al. 2020). If *B. hirsutum* were adapted to this feeding mode, we would expect to find barnacles of similar or even increased size which is not mirrored in our observations (Fig. 7). Accounting for the facts that the species rather opportunistically utilises the hard-rock substrate in vicinity of the vent field and does not live directly associated with the hydrothermally active chimneys, we assume that *B. hirsutum* is not adapted to integrate organic matter from bacterial mats. In addition to the smaller size range, less growth ridges were counted on carinal parietal plates that were of comparable height to specimens from non-hydrothermally influenced sites (Fig. 7A). These results imply that growth ridge formation might be impacted by the pronounced shell precipitate, possibly eroding the ridges in the process of the accumulation of ferromanganese oxides. Overall, our results imply barnacle shell size to increase with ocean depth (Fig. 7B). However, this snapshot of barnacle size distribution requires more detailed attention to verify whether this trend applies across the entire distributional range of the species.

Ferromanganese oxide shell precipitates

The formation of iron (Fe), manganese (Mn) and ferromanganese (Fe-Mn) mineral deposits happens by migration of Fe and Mn cations from less oxidising to more oxidising conditions (Glasby 2006; Park et al. 2023). Marine Fe-Mn deposits may form as crusts, nodules or are contained within layers of rock and are classified by three mineralisation types; hydrogenetic, diagenetic, and hydrothermal (Marino et al. 2019; Usui et al. 2020). Hydrogenetic Fe-Mn crust deposits form by precipitation of Fe oxyhydroxide and Mn oxide from ambient seawater onto the bedrock on *i.e.*, continental shelves and seamounts (Lusty et al. 2018). Hydrothermal processes, on the other hand, lead to the accumulation of Fe-Mn oxides from plume discharge (Connelly et al. 2007; Muiños et al. 2013; Sujith and Gonsalves 2021). At the Reykjanes Ridge, plume discharge from the Steinahóll vent field contains a high concentration of dissolvable manganese (~60 nmol/l; Taylor et al. 2021). Equivalent discharge is expected to occur at the IceAGE vent field, situated ~400 km south on the same volcanic ridge axis. Inactive ridges such as the Iceland-Faroe Ridge do not display such enrichments (Horowitz 1974). Since there are no records of hydrothermal activity in the vicinity of site A, it is plausible that the chemical component analysis yielded no traces of ferromanganese (Table 3). None of the specimens from site B, despite being situated just ~450 m north of the IceAGE hydrothermal vent field, were observed with shell precipitate. In accordance with the circulation patterns and bottom currents prevailing along the eastern flank of the Reykjanes Ridge, the plume discharge by the IceAGE vent field is likely to be carried in a south-western direction relative to the active chimneys (Horowitz 1974; Koman et al. 2020; Ruddiman 1972). Hence, Fe-Mn traces from hydrothermal origin seem not to reach barnacles from site B. Situated south of the vent field, specimens collected at site C could be in range to be affected by plume discharge. However, throughout the distance of ~130 km, trace elements such as Fe and Mn are likely to have been accreted to sediments or precipitated as crust deposits in the proximate environment before reaching the barnacle field (Connelly et al. 2007; Horowitz 1974). The minor percentage of Fe-Mn oxide measured in shells from both sites (Table 3) is rather thought to reflect ambient water Mn and Fe concentrations as barnacles show a strong affinity for incorporating both Fe and Mn into their shells compared to other calcifying animals (Pilkey and Harriss 1966; Ullmann et al. 2018). Only specimens at site D had pronounced Fe-Mn precipitates on their parietal plates, visible as dark brown-black deposits from the apex to the base. The high Fe/Mn ratios reflect an enrichment from hydrothermal plume discharge emanated from the IceAGE vent field. Detailed geochemical analyses on the enrichment of trace elements in the hydrothermal plume are desirable to assess whether the Fe-Mn enrichment could additionally be a product of diagenetic processes. In this case, high concentrations of typical diagenetic elements such as Ni, Cu and Co would need to be present (Schiellerup et al. 2021). In general, shell plates from site D contained a higher percentage of rare earth metal components compared to sites A– C, especially with regard to Tungsten trioxide. This is predictable, as this metal has been found to accumulate in ferromanganese deposits (Kunzendorf and Glasby 1992).

Previous to our study, the affiliation of *B. hirsutum* with hydrothermal vent systems was unexplored. Still, the presence of shell precipitates has not gone fully unnoticed. During a geological survey, intact barnacles were collected together with coral fragments at 800 m depth on the Reykjanes Ridge, at a station situated central between the herein sampled sites B and C (Murton et al. 1995). Without further commenting on a possible source of origin, the authors reported a manganese staining on the barnacles, which were later identified as *B. hirsutum* by Copley et al. (1996), who however neglected to mention the precipitate. The reported manganese staining is likely to be Fe- Mn oxide and could have originated from plume discharge emanated from site D, or even from another yet undetected hydrothermal source in this area. On the Azores Archipelago, Southward (1998) examined several hundred dead shell plates of *B. hirsutum* collected together with dead pieces of *Desmophyllum pertusum* (Linnaeus, 1758) between 1250 and 1630 m depth. Both barnacles and corals were described as having a black manganese coating. As the collected material had died off, we assume that the precipitate formed through either hydrogenous or diagenetic sources, as for example observed in shark teeth or coral skeletons (Edinger and Sherwood 2012; Iyer 1999). Based on the high amount of barnacle shells, Southward (1998) estimated that the sampled area must have been densely populated by *B. hirsutum* in earlier times and suggested a possible enrichment from hydrothermal sources which would have enabled the high abundance of specimens. The Lucky Strike vent field, situated ~12 km west of this area and described just shortly before (Langmuir et al. 1997), could be considered as a potential hydrothermal source of enrichment. However, the once high abundance of *B. hirsutum* could also have sustained due to strong prevailing currents that transport nutrient-rich, well-oxygenated water masses along the MAR (Puerta et al. 2020; Fig. 1). With regard to our observations of a rather low abundance of *B. hirsutum* at the IceAGE vent field (Fig. 4E, F), the transport of nutrients by ocean currents is regarded to have a much higher impact on barnacle abundance compared to the influence of hydrothermal activity. If latter were to be the main source, the abundance of *B. hirsutum* ought to have been much greater than what we observed at site D.

On the affiliation of *Bathylasma* with hydrothermally influenced habitats

This study acknowledges the habitat adjacent to the IceAGE vent field as a suitable living space for *B. hirsutum*. As the recognised maximum depth for *B. hirsutum* is 1829 m, NE Atlantic hydrothermal vent fields deeper than 2000 m are anticipated to be out of the species' ecological range for successful settlement in these habitats. Within its known depth range, however, several records from the MAR spreading centre on the Azores Archipelago overlap with recognised hydrothermal active sites (Beaulieu and Szafrański 2020). Given from west to east, *B. hirsutum* has been recorded ~800 m off Ribeira Quente (Young 1998), and Don Joao de Castro Bank (Gruvel 1920), ~784 m south of Espalamaca (Young 1998), ~860 m south of LUSO (Poltarukha and Zevina 2006a), and ~12 km west of the Lucky Strike vent field (Southward 1998). Repeated sampling efforts by means of a ROV are highly encouraged to investigate whether *B. hirsutum* is in fact affiliated with the recognised hydrothermal active fields and whether the barnacles utilise these habitats in a comparable fashion to what has been observed at the IceAGE vent field, including observations on possible shell precipitates.

Detailed biological surveys of the myriad hydro- thermal systems in the world oceans are still a major task (Tunnicliffe et al. 2003; Van Dover et al. 2006). We hypothesise that future research activities on hydrothermal vent systems within the distributional range of the bathylasmatid sister species *Bathylasma corolliforme* and *Bathylasma chilense* will reveal their potential to utilise hydrothermally influenced habitats, in a comparable manner to what has been found for *B. hirsutum* in this study. As for the sister species *B. corolliforme*, Dayton et al. (1982) reported specimens from 400 m depth attached to volcanic rocks. The sampling locality is situated south of the Pacific-Antarctic Ridge. In this region, hydrothermal activity has been inferred from several localities (Beaulieu and Szafrański 2020; Bell et al. 2016; Linse et al. 2022; Rogers et al. 2012; Tao et al. 2012) and distal hydrothermal influences have been suggested (Sieber et al. 2021) within the given depth range of the species. Furthermore, a high abundance of unidentified deep- sea acorn barnacles was detected on an active volcanic mount structure at 2221 m depth during the Marion Rise Expedition programme (Koepke et al. 2020). Though not mentioned in the respective cruise report, publicly available video footage documents this observation from the Marion Rise (marumTV 2020; 43°53.6822'S, 39°13.3234'E). We believe these barnacles to belong to the species *B. corolliforme* as species-specific characters such as the strong diverging orifical compartments are clearly visible (see Bullivant and Dearborn 1967, plate 14; Dayton et al. 1982, fig. 3C; Meyer 2020, fig. 3-3) and the observations were captured from a site west of the species' type locality (Hoek 1883). Unfortunately, no material was sampled and examined in further detail during the Marion Rise expedition.

Just recently, the sister species *B. chilense* was described based on three specimens collected from 1800–2000 m depth off Caldera, northern Chile (Araya and Newman 2018). The type locality is situated in vicinity of the Peru-Chile Trench, an area of subduction and earthquake activity. As the vast majority of seafloor venting in the southern hemisphere remains unexplored, there may be many hydrothermal vent sites on this actively spreading ridge to discover (Baker et al. 2016; Beaulieu and Szafrański 2020). In line with further deep-sea explorations off the Chilean coast, we hypothesise *B. chilense* to be found affiliated with hydrothermal activity, utilising these habitats in a comparative manner to what has been presented here for *B. hirsutum* from the NE Atlantic.

A connectivity pathway to the northwest Atlantic?

To date, no records of *B. hirsutum* are known from any of the north-western (NW) Atlantic basins. There is, however, one fossil record of the extinct sister species *B. corrugatum* from the continental shelf break off North Carolina, indicating that these bathylasmatid acorn barnacles managed to sustain at least one population in the NW Atlantic during the Neogene and Paleogene periods (Zullo and Baum 1979). In fact, the westward flow of the East Reykjanes Ride Current merging with the Irminger Current could serve as a connectivity pathway into the Irminger Basin as well as the David Strait, facilitating larval distribution of *B. hirsutum* to suitable hard-bottom habitats along the shelf breaks. Such habitats were recently surveyed by Kenchington et al. (2017) who discovered a reef of *Desmophyllum pertusum* at 886–932 m depth on a steep slope in the Davis Strait. The herein reported temperature range of 4.13–5.03°C as well as current velocities of 10–15 cm s^{-1} could indeed facilitate an eligible habitat for barnacle recruits and already established, actively feeding individuals (see Southward and Southward 1958). Increased sampling efforts in NW Atlantic basins and along the continental shelf breaks could possibly reveal yet undiscovered occurrences of *B. hirsutum*. Special focus ought to be given to the coastline off America as the type of *Hexelasma americanum* Pilsbry, 1916, a species of sister genus to *Bathylasma,* was sampled here (Pilsbry 1916). Showing high morphological similarity and occupying overlapping habitats on the Azores Archipelago (Poltarukha and Zevina 2006a; Young 1998 2001), we suggest that both species require similar environmental conditions to sustain vital populations. Hence, it might be possible that a co-existence of *Bathylasma* and *Hexelasma* along the western Atlantic shelf is present, but has been left unrecognised due to their morphological similarities (Newman and Ross 1971; Southward and Southward 1958).

CONCLUSIONS

The Reykjanes Ridge provides a variety of hard-bottom habitats which are dominated by saline, nutrient-rich and well oxygenated water masses as well as strong current regimes (Puerta et al. 2020; Schumacher et al. 2022). Much effort is still needed to understand the extent and functions of biological communities found in these habitats, with special regard to hydrothermally influenced sites. Our investigations on the deep-sea acorn barnacle *B. hirsutum* contribute to a better understanding of the benthic sessile fauna with planktotrophic larval dispersal and related connectivity patterns in the North Atlantic. Our molecular sampling approach has not only extended the genetic dataset of this species, but aided to investigate the genetic connectivity between four sampled sites in the northeastern Iceland Basin. The comprehensive literature review on the species revealed a high number of sampling records as well as a series of detailed studies on favourable habitats in this species. However, previous to this study, *in situ* footage of these large barnacles remained absent, as did the acknowledgement of hydrothermally influenced habitats as a suitable living space. Our findings of small local abundances on volcanic rocks in vicinity of the IceAGE vent field do not only extend the knowledge on a favourable habitat, but also emphasise the need for further research that ought to be focused on the Reykjanes Ridge axis, as well as on hydrothermal habitats shallower than 1800 meters along the extensive Mid-Atlantic Ridge.

List of abbreviations

ABGD, Automated Barcode Gap Discovery.
ASAP, Assemble Species by Automatic Partitioning.
BI, Bayesian Inference.
BOLD, Barcode Of Life Database. CH,
Carinal height.
EDS, Energy Dispersive Spectroscopy.
ERRC, East Reykjanes Ridge Current. GR,
Growth ridge.
MAR, Mid-Atlantic Ridge.
PP, Posterior Probability.

Acknowledgments: The authors are grateful for the funding support by the German Science Foundation (IceAGE_2: grant BR3843/4-1; IceAGE_RR: grant BR3843/5-1; IceAGE_3: grant MerMet17-06) and the Bundesministerium für Bildung und Forschung (SO276). We thank the crew, chief scientists and scientific staff of the *RV Poseidon* during IceAGE_2 (POS456), *RV Maria S. Merian* during IceAGE_RR (MSM75), and *RV Sonne* during IceAGE_3 (SO276). A special thanks to Antje Fischer (TA DZMB Hamburg), Karen Jeskulke (TA DZMB Hamburg), and Nicole Gatzemeier (TA DZMB Hamburg) for their support in sample logistics, Dr. Nancy Mercado Salas and Angelina Eichsteller for their support with the molecular analyses, Mia Schumacher (GEOMAR, Kiel) for her support with the bathymetry and map compilations, and the ROV team from GEOMAR for their contributions to collect specimens and obtain high quality video and image material. This study is a contribution to the EU Horizon 2020 iAtlantic project. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Authors' contributions: Sample collections were conducted by SB and PMA during IceAGE_2, by SB, KL and JT during IceAGE_RR, and by JN, SB and JT during IceAGE_3. KL and JT conceived the study and conducted initial morphometric measurements. KL performed the SEM imaging and EDS scanning. PMA aided with data analyses guidance. JN performed the study, analysed the specimen data and the imagery/ video data, prepared figures and tables, authored or reviewed drafts of the paper and compiled all data and manuscript pieces. All authors read and approved the final manuscript.

Competing interests: All authors declare that they have no competing interests.

Availability of data and materials: Metadata, genetic data and specimen images are deposited in the Barcode Of Life Database (BOLD) and are accessible via the doi:10.5883/DS-IACIR. Novel *COI* and EF1 sequences are submitted to the NCBI GenBank and are available by the accession numbers OQ026012–OQ026166. Video material can be accessed via: https://zenodo.org/records/10220154.

Consent for publication: All authors consent to the publication of this manuscrip.

Ethics approval consent to participate: Not applicable. The species is not under the listed categories of experimental animals that need ethics approval.

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Marine Biodiversity (2025) 55:24
https://doi.org/10.1007/s12526-025-01509-0

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SHORT COMMUNICATION

Springer

On dwarf males in the deep-sea acorn barnacle *Bathylasma hirsutum* (Thoracica: Bathylasmatidae)

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Received: 30 September 2024 / Revised: 12 February 2025 / Accepted: 16 February 2025

Abstract

The sessile lifestyle of thoracican barnacles has driven the evolution of a mating behaviour that maximises reproductive success by increasing the reach and number of potential mating partners. While most species are simultaneous hermaphrodites, possessing both male and female reproductive structures, some have evolved an androdioecious system in which hermaphrodites and dwarf males coexist. These dwarf males allocate more resources to male function than growth and typically settle near the orifice of their conspecifics. Environmental factors such as food availability and the number of potential mates influence mating group size in barnacle populations, which is generally lower in deep-sea habitats compared to nutrient-rich shallow-water environments. Evolution is likely to favour the presence of dwarf males in deep-sea barnacles to facilitate mating success in such challenging conditions. The genus *Bathylasma* Newman & Ross, 1971, currently comprises four extant species, two of which are known to exhibit an androdioecious sexual system. *Bathylasma hirsutum* (Hoek, 1883) is the sole representative of this genus at northern latitudes, inhabiting hard-bottom habitats down to 1829 m depth. This study reports on two specimens from the Reykjanes Ridge axis, where dwarf males were found apically attached in the tergal furrow. This suggests *B. hirsutum* is the third species within the genus to exhibit an androdioecious sexual system. These findings offer new insights into the reproductive diversity and sex allocation strategies of deep-sea thoracican barnacles, for which a complete understanding has yet to be achieved.

Keywords Androdioecy · Sexual system · Resource allocation · Reykjanes ridge

Introduction

Thoracican barnacles, which include pedunculate and sessile forms, exhibit diverse sexuality patterns and life history strategies despite their immobility after larval settlement (Darwin 1851; Charnov 1987; Lin et al. 2015; Chan et al. 2021). Their sexual systems include simultaneous hermaphroditism (concomitant male and female sexual behaviour), androdioecy (occurrence of males and hermaphrodites), and dioecy (occurrence of males and females). The sessile lifestyle of barnacles has favoured the evolution of a mating behaviour that maximises reproductive success by increasing the reach and number of potential mating partners through copulation with an elongated penis (Darwin 1851; Anderson 1994). The mating group size (MGS) is addressed as one of the major drivers in the evolution of reproductive life histories and sex allocation and has been subject to many evolutionary studies (Charnov 1987; Pérez-Losada et al. 2008; Yamaguchi et al. 2008, 2012, 2013; Urano et al. 2009; Kelly and Sanford 2010; Yusa et al. 2012; Lin et al. 2015). Food availability through MGS is one of the most important environmental factors regulat- ing sexuality patterns, driven by optimal resource alloca- tion to growth and reproductive success (Yamaguchi et al. 2008). Overall, food-rich environments tend to favour high population densities (large MGS) and the occurrence of simultaneous hermaphrodites in close mating distance. With a lowered influx of organic matter, MGS decreases. The induced extended mating distance between conspecifics limits the opportunity to copulate and is suggested to favour the development of dwarf males (Yamaguchi et al. 2008; Lin et al. 2015). Modes of sex determination in barnacles

Communicated by B. Chan

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especially regarding androdioecy, are not yet fully understood (Charnov 1982, 1987; Yamaguchi et al. 2008; Urano et al. 2009; Høeg et al. 2016). Sex allocation theories suggest genetic as well as environmental strategies that might even interact as a unique combination, as proposed for the stalked barnacle *Scalpellum scalpellum* (Linnaeus, 1767) which serves as the model organism for studying barnacle androdioecious systems (Svane 1986; Buhl-Mortensen and Høeg 2006; Spremberg et al. 2012; Høeg et al. 2016). In this species, hermaphrodite sexual expressions have been shown to be coupled with environmental sex determination. In a reared culture, all larvae, having the genetic potential to become hermaphrodites, developed into dwarf males when ultimately settled in hermaphrodite receptacles, a specific environment needed for the development of functional dwarf males. Half of the larvae that were replaced shortly after settlement in the receptacle developed into hermaphrodites instead, shifting their sexual expression in response to environmental change (Høeg et al. 2016).

The presence of minute males was first reported by Darwin (1852, 1854) where he differentiated between complemental males (attached to hermaphrodites) and dwarf males (attached to true females). Although highlighting an important sexual difference, this literal distinction was suggested to be put aside, proposing the term “dwarf male” for any minute male that matures at a much smaller size than conspecific hermaphrodites or females, irrespective of its morphology, functionality, and positioning on the specimen it is associated with (Spremberg et al. 2012; Yusa et al. 2012; Lin et al. 2015). Accordingly, this terminology is used herein.

Dwarf males are distinguished from hermaphrodites by being settled close to the fertilisation site of conspecifics and by allocating more resources to male function than growth (Charlesworth 1984; Klepal 1987; Yamaguchi et al. 2013). This way, dwarf males bypass the need to compete with male function and thus have a potential mating advantage towards hermaphrodites. Nevertheless, in androdioecy, dwarf males remain in competition with hermaphrodites for egg fertilisation, resulting in a comparable fitness for both forms (Yamaguchi et al. 2008; Yusa et al. 2012; Chan and Høeg 2015; Dreyer et al. 2018). To simulate this competition, Urano et al. (2009) developed a model on the life history of androdioecious barnacles which showed an increased evolutionary stable proportion of larvae developing into dwarf males in populations with a lowered MGS, but never exceeding a ratio of 50%. As deep-sea thoracican barnacles are mainly represented by a lower MGS compared to species found in shallow-water habitats, evolution is expected to favour the presence of dwarf males (Chan and Høeg 2015; Lin et al. 2015).

The deep-sea acorn barnacle *Bathylasma hirsutum* (Hoek, 1883) represents one of four extant species which are nested within the family Bathylasmatidae Newman and Ross, 1971. In common with other thoracican barnacles, *B. hirsutum* is of gregarious nature as it tends to settle crowded and exhibits epizoic growth where one established animal has one or several specimens laterally attached (Anderson 1994). The species populates hard-bottom habitats between 384 and 1829 m depth in the North-east Atlantic Ocean and is the sole representative of *Bathylasma* at northern latitudes. Previous studies on the sister species *B. alearum* (Foster, 1978) from New Zealand and *B. corolliforme* (Hoek, 1883) from the Antarctic Peninsula have reported on dwarf males apically attached to the articular ridges of scuta, terga, or the longitudinal carinal sheath, attesting an androdioecious sexual system (Dayton et al. 1982; Foster 1983; Kelly and Sanford 2010). This study reports on the presence of dwarf males in the tergal furrow of mature specimens of *B. hirsutum* which is herein suggested as the third bathylasmatid species with an androdioecious sexual system.

Material and methods

Specimens of *B. hirsutum* (*n* = 29) were collected along the Reykjanes Ridge axis south of Iceland (ROV station 31; 60° 14.274′ N 029° 08.138′ W) from a field of pillow lava at 719 m depth (Fig. 1). Sampling was conducted with the Remotely Operated Vehicle (ROV) *Phoca*, using the operational arm and net, onboard the RV *Maria S. Merian* (MSM75) during the IceAGE_RR expedition (Devey et al. 2022). At the sampled site, barnacle abundances varied from small patches with few specimens to larger fields with high individual counts. In situ video footage of the sampled habitat (site B in Neuhaus et al. 2024) is accessible via https://

Fig. 1 In situ footage of a population of *B. hirsutum* prior to sam- pling. The habitat is situated along the Reykjanes Ridge axis and is composed of lobes of pillow lava. Image courtesy of GEOMAR, Kiel

zenodo.org/records/10220154. Upon sampling, the material was stored on 96% undenatured ethanol in sealed plastic bags and kept at − 20 °C. Morphological examinations and the dissection of one dwarf male were done using a Leica stereomicroscope and a digital vernier calliper. Specimens were photographed using a Canon EOS 2000D digital camera and a Keyence VHX-7000 digital microscope. Further Information on the respective specimens can be accessed in the Barcode of Life Data System (BOLD) via https://doi.org/10.5883/DS-IACIR.

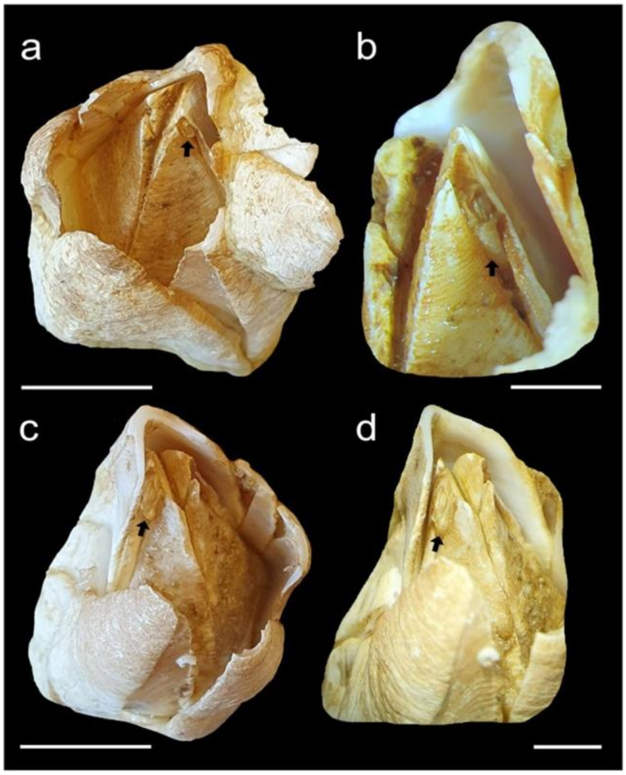


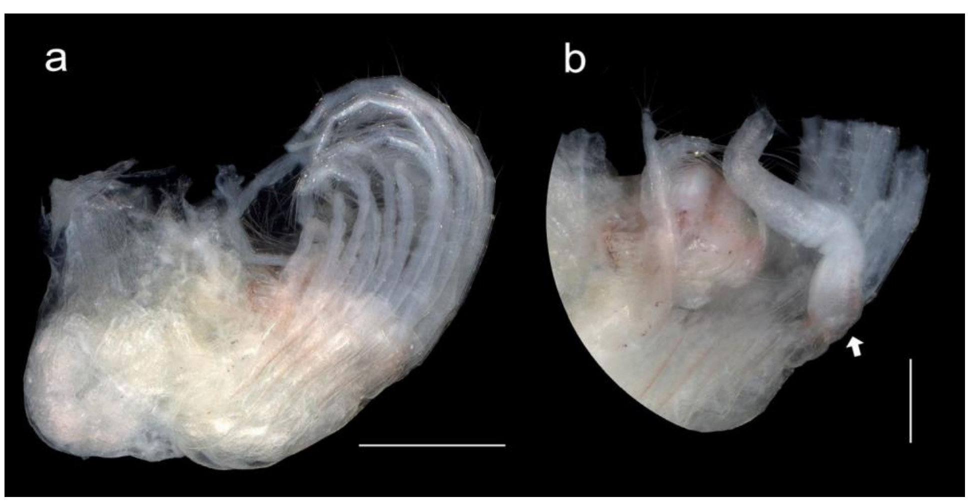
Fig. 2 Two specimens of *B. hirsutum* with each one dwarf male situated apically in the tergal furrow (black arrows) **a** and **b** Top view and detailed view of one specimen (DZMB-HH-71485) with a dwarf male in the right tergal furrow. **c** and **d** Top view and detailed view of one specimen (DZMB-HH-71491) with a dwarf male in the left tergal furrow. Scale bars: **a** 3 cm, **b** 2.42 mm, **c** 3 cm, **d** 2.98 mm

Results and discussion

Upon collection and morphological examination of 29 barnacles from the Reykjanes Ridge axis, two specimens of *B. hirsutum* were found with each one dwarf male situated apically in the tergal articular furrow (Fig. 2). The habitus of both dwarf males is laterally compressed and shows deformed terga and scuta (opercula). They have carino-rostral diameters of 2.42 mm (Fig. 2b) and 2.98 mm (Fig. 2d). The dissection of one dwarf male confirmed the presence of a penis and testes, as well as the absence of ovarian tissue (Fig. 3).

The positioning, habitus and size measurements of the herein-presented dwarf males on *B. hirsutum* correspond with the characteristics of dwarf males found in the sister species *B. alearum* and *B. corolliforme* (Dayton et al. 1982; Foster 1983). Foster (1983) discovered a total of 35 dwarf males in 21 adult specimens of *B. alearum*, positioned with their carino-rostral axis aligned to the tergal and scutal furrows or the longitudinal carinal sheath. He observed the laterally compressed males to range from one to four mm in carino-rostral diameter, often with deformed opercula. Based on these observations, Dayton et al. (1982) re-examined what they believed were juveniles of *B. corolliforme* and found 19 out of 35 pre-defined juveniles to be functional dwarf males instead. Over a 2-year experimental period, they succeeded in observing the recruitment of dwarf males on *B. corolliforme*, settling in the orifical region only. As this narrow region gives almost no room for growth, barnacle larvae that settle

Fig. 3 Dissected dwarf male from the left tergal furrow of specimen DZMB-HH-71491. **a** Habitus of dwarf male with intact cirral fan concealing the penis. **b** Detailed view of dwarf male with the cirral fan removed to reveal the penis (white arrow). Scale bars: **a** 500 µm, **b** 200 µm



and metamorphose here remain dwarfed. Main resources are allocated to sperm production instead of growth, resulting in testes occupying most of the prosoma, charged seminal vesicles and a well-developed penis longer than cirrus VI (Dayton et al. 1982; Foster 1983). The morpho-anatomical examination of the dwarf male of *B. hirsutum* revealed anatomical features analogous to the dwarf males of *B. alearum* and *B. corolliforme* (Fig. 3). The penis was found in a heavily curved position with compressed tissue, likely caused by ethanol preservation. Thus, the length of the penis appears shorter than cirrus VI but would certainly extend beyond it in its natural state.

Compared to other sampled sites along the Reykjanes Ridge axis (Narayanaswamy et al. 2006, 2013; Neuhaus et al. 2024), the specimens studied herein were collected from a patch of pillow lava with moderate barnacle abundance (Fig. 1). Reflected in morphometric measurements of parietal plates, specimens inhabiting this site showed a large size span, indicating a vital population with successful recruitment of juveniles (Neuhaus et al. 2024). The two specimens that carry dwarf males were likely collected from the edge of the pillow lava, where barnacle densities decline (Fig. 1). MGS at this particular site is lower compared to the centre of the populated area and might thus have an effect on larval settlement, which happened to be in the narrow orifical region of the two specimens studied herein (Fig. 2). As for now, merely two dwarf males have been detected amongst the sampled specimens, suggesting the population of *B. hirsutum* at this site likely not to be affected by a low MGS. However, the overall presence of dwarf males, despite being a potential local adaptation to a low MGS at the edge of a populated habitat, proves *B. hirsutum* to be capable of adapting to an androdioecious sexual system which accelerates the reproductive success of mature hermaphrodites and might facilitate population expansion over time.

Acknowledgements This research was made possible with the assistance from the captain and crew of RV *Maria S. Merian*, MSM75 chief scientist Colin Devey, technical staff and fellow scientists. The crew of ROV *Phoca* from the GEOMAR Helmholtz Centre for Ocean Research, Kiel is acknowledged for obtaining imagery data and bio- logical material. Karen Jeskulke, Nicole Gatzemeier, and Clara Bach- mann were most helpful with sample management and processing. This research has greatly benefited from the support of Saskia Brix, Katrin Linse and Emanuel Pereira.

Funding Open Access funding enabled and organized by Projekt DEAL. This research was made possible with the funding support of the German Science Foundation (IceAGE_RR: grant BR3843/5–1) and the Federal Ministry of Education and Research. The author was supported through the grant GPF 21-2_052 (SO286) as part of the IceDivA project which is a contribution to the iAtlantic project, funded by EU/ HORIZON 2020, Blue Growth (Grant Agreement No 818123).

Declarations

Ethical approval No specific ethical approval was required for this research.

Data availability Voucher specimens are deposited at the German Centre for Marine Biodiversity Research in Hamburg, Germany to ensure availability for future research. All data is publicly available in the Barcode of Life Data Systems (BOLD) via https://doi.org/10.5883/ DS-IACIR. In situ video records are deposited at https://zenodo.org/ records/10220154.

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The Protobranch Bivalve

Ledella ultima (E. A. Smith, 1885)

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High Connectivity at Abyssal Depths: Genomic and Proteomic Insights Into Population Structure of the Pan-Atlantic Deep-Sea Bivalve *Ledella ultima* (E. A. Smith, 1885)

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Received: 13 May 2025 | **Revised:** 7 July 2025 | **Accepted:** 22 July 2025

Funding: This work was supported by the German Federal Ministry of Education and Research (BMBF) through grant no. GPF 21-2_052 as part of the IceDivA project (Förderkennzeichen 03G0286NA) and the German Research Foundation (DFG) initiative 1991 "Taxonomics" (grant no. RE2808/3-1/2). This work is a contribution to the iAtlantic project, funded by EU/HORIZON 2020, Blue Growth (grant agreement no. 818123). K.L. is part of the British Antarctic Survey Polar Science for Planet Earth Programme funded by The Natural Environment Research Council (NERC) [NC-Science].

Keywords: 2b-RAD | DNA barcoding | MALDI-TOF MS | mitochondrial heteroplasmy | phylogeography

ABSTRACT

Phylogeographic analyses have advanced our understanding of evolutionary processes in the deep sea, yet patterns of genetic variation and population divergence at abyssal depths remain poorly understood. The bivalve *Ledella ultima* is one of the most abundant protobranchs in the abyssal Atlantic, making it a valuable model organism for studying phylogeographic patterns and population connectivity. However, evidence for sex-specific heteroplasmic mtDNA challenges the assessment of genetic structure using mitochondrial markers alone. To address this, we used mtDNA (COI, 16S), single-nucleotide polymorphisms (SNPs) from 2b-RAD, and proteomic profiles to examine the population structure of *L. ultima* across seven Atlantic basins spanning over 10,000 km in latitude. Five mitochondrial lineages with a lack of geographic structure were consistently identified by COI and 16S. Conversely, SNP and proteomic data did not mirror these findings, denoting that heteroplasmic mtDNA inflates intraspecific genetic divergence in this gonochoric species. Despite the SNP data revealing overall low genetic divergence, subtle genetic structure was detected by admixture analyses supporting two source populations: one in the north and central Atlantic, and a second in the south Atlantic, with moderate admixture in the Brazil and Cape basins. Proteomic fingerprinting revealed two basin-separated groups with patterns distinct from the nuclear data, suggesting environmentally driven shifts in protein expression. Our findings underscore the value of integrating nuclear genomic and proteomic tools to decipher population connectivity at abyssal depths, where minimal genetic differentiation necessitates fine-scale analyses.

Ecology and Evolution, 2025; 15:e71903
https://doi.org/10.1002/ece3.71903

1 | Introduction

Phylogeographic patterns in the deep sea are shaped by a complex interplay of oceanographic dynamics, dispersal mechanisms, and evolutionary processes (Gage and Tyler 1991; Ramirez-Llodra et al. 2010; Rex and Etter 2010). While connectivity studies along seamounts, hydrothermal vents, and mid-ocean ridges have been a major focus in recent years (Boschen-Rose and Colaço 2021; Breusing et al. 2016; Portanier et al. 2023; Yearsley et al. 2020), the vast abyssal plains, covering more than half of the Earth's surface, remain largely unexplored in this context (reviewed in Baco et al. 2016; Taylor and Roterman 2017). To counteract these knowledge gaps, large international initiatives, such as the Census of Marine Life (CoML; Ausubel et al. 2010), the Deep Ocean Steward Initiative (DOSI; https://www.dosi-project.org), and the UN Ocean Decade (https://oceandecade.org) were launched. Assigned to the program Challenger 150 (https://challenger150.world/), the action IceDivA (Icelandic marine Animals meets Diversity along latitudinal gradients in the deep sea of the Atlantic Ocean; Brix and Taylor 2021) served as a knowledge hub by revisiting fundamental hypotheses in deep-sea science and investigating connectivity patterns along latitudinal gradients on a pan-Atlantic scale. Building upon previous expeditions run in the frame of the CoML, samples collected over the last decades are available as a unique pan-Atlantic dataset (Kürzel et al. 2023).

Protobranch bivalves rank among the most abundant invertebrates in the deep Atlantic (Allen 2008; Gage and Tyler 1991; Zardus 2002), contribute to the ecological complexity of soft-bottom habitats (Ellingsen et al. 2007; Reed et al. 2014), and have proven to be valuable model organisms to investigate phylogeographic patterns, genetic diversity, and evolutionary processes (Chase et al. 1998; Etter et al. 1999, 2005; Zardus et al. 2006; Jennings et al. 2013). In these studies, abyssal populations were consistently found to exhibit less genetic divergence when compared to bathyal populations at a comparable geographic scale, supportive of the depth-differentiation hypothesis (DDH) (Etter et al. 2005; Etter and Rex 1990; Rex and Etter 2010). Similar patterns of bathymetric zonation and genetic diversity have been found in other marine taxa, disclosing genetic barriers across depth strata (Howell et al. 2002; Quattrini et al. 2015; Zhang et al. 2021). Although the DDH highlights a general trend of decreasing population differentiation with depth, processes that govern genetic divergence and connectivity of species at abyssal depths (3500–6000 m) are far from understood (Gary et al. 2020; Riehl et al. 2020; Rogers and Ramirez-Llodra 2024). Precisely because intraspecific genetic differentiation appears inconspicuous, mitochondrial gene markers might not have the resolution needed to capture subtle patterns of genetic structure and connectivity in abyssal environments. Allowing for the identification of thousands of genome-wide single-nucleotide polymorphisms (SNPs) from a high number of individuals (Andrews et al. 2016; Davey and Blaxter 2010), the use of restriction site-associated DNA sequencing (RAD-seq) provides advanced assessments of fine-scale population structure in marine species (Benestan et al. 2015; Galaska et al. 2017; Reitzel et al. 2013). To complement DNA-based population genetic analyses herein, we used proteomic fingerprinting, which has been increasingly applied to assess phenotypic consistency and to explore whether molecular divergence is reflected at the protein expression level (Peters et al. 2023; Renz et al. 2021; Rossel et al. 2024). Proteomic fingerprinting is based on the mass detection of peptide and low molecular weight protein molecules and is used for microbial species identification (Singhal et al. 2015) and has also proven applicable to a wide range of metazoan taxa (Halada et al. 2018; Karger et al. 2019; Yssouf et al. 2014).

The small protobranch *Ledella ultima* is a true abyssal species and abundant at depths of 3000–5800 m. Spanning from the British continental margin to the Agulhas Basin in the east, and from the North American margin to the Argentine and Scotia seas in the west (Allen 2008; Allen and Hannah 1989; Allen and Sanders 1996; Clarke 1961; Janssen and Krylova 2014), the species has a pan-Atlantic distribution and serves as a valuable model for studying phylogeographic patterns and population connectivity (Etter et al. 2005, 2011). Within a population, females and males are inferred to occur in approximately equal numbers, supported by the commonly observed balanced sex ratio in protobranchs (Zardus 2002) and the documented sex ratios in the Atlantic sister species *L. pustulosa* and *L. sublevis* (Allen and Hannah 1989). Populations of *L. ultima* are suggested to follow a continuous breeding pattern with the development of planktonic lecithotrophic pericalymma larvae that passively disperse by bottom currents (Gage and Tyler 1991; Tyler et al. 1992; Zardus and Morse 1998; Zardus 2002; Young 2003). The bivalve can grow to a maximum of 3.4 mm in shell length. Smallest specimens of females and males with developing gonads were reported with respective shell lengths of 2.4 and 2.5 mm, where females may develop 9–29 ova of 160–255 μm in diameter and a subsequent larval shell length of 310 μm (Allen and Hannah 1989).

The main deep-ocean basins where *L. ultima* is found are the Western European Basin (WEB), North American Basin (NAB), Brazil Basin (BB), Argentine Basin (AB), and Cape Basin (CB) (Figure 1A; Warén 1981; Filatova and Schileyko 1984; Allen and Hannah 1989; Allen and Sanders 1996; Allen 2008; Etter et al. 2011). In these basins, large-scale oceanographic processes of North Atlantic Deep Water (NADW) and Antarctic Bottom Water (AABW) play a crucial role in shaping benthic biodiversity patterns by influencing the dispersal of deep-water fauna (Jollivet et al. 2024; Kuhlbrodt et al. 2007; Puerta et al. 2020; Talley 2013). Formed over the continental slope of Antarctica, AABW is the densest water mass and occupies almost the entire bottom layer of the Atlantic, whereas NADW, formed in the North Atlantic, is found between 2000 and 4000-m depth and is distinguished from Antarctic waters by higher temperature and salinity, and a lower concentration of nutrients (Dickson and Brown 1994; Ferreira and Kerr 2017; Liu and Tanhua 2021; Watling et al. 2013). These water masses propagate through the abyssal basins, many of which are confined by topographic features such as the Mid-Atlantic Ridge (MAR) separating eastern and western Atlantic corridors, the Rio Grande Rise separating the AB and BB in the south-west, and the Walvis Ridge confining the CB to the north (Morozov et al. 2010) (Figure 1B). For AABW and NADW to overcome these barriers, trenches and fracture zones serve as main pathways for bottom-water exchange and connectivity between basins (Morozov et al. 2010, 2023). Since most benthic deep-sea species rely on passive transport processes for dispersal (Etter and Bower 2015; Hilário

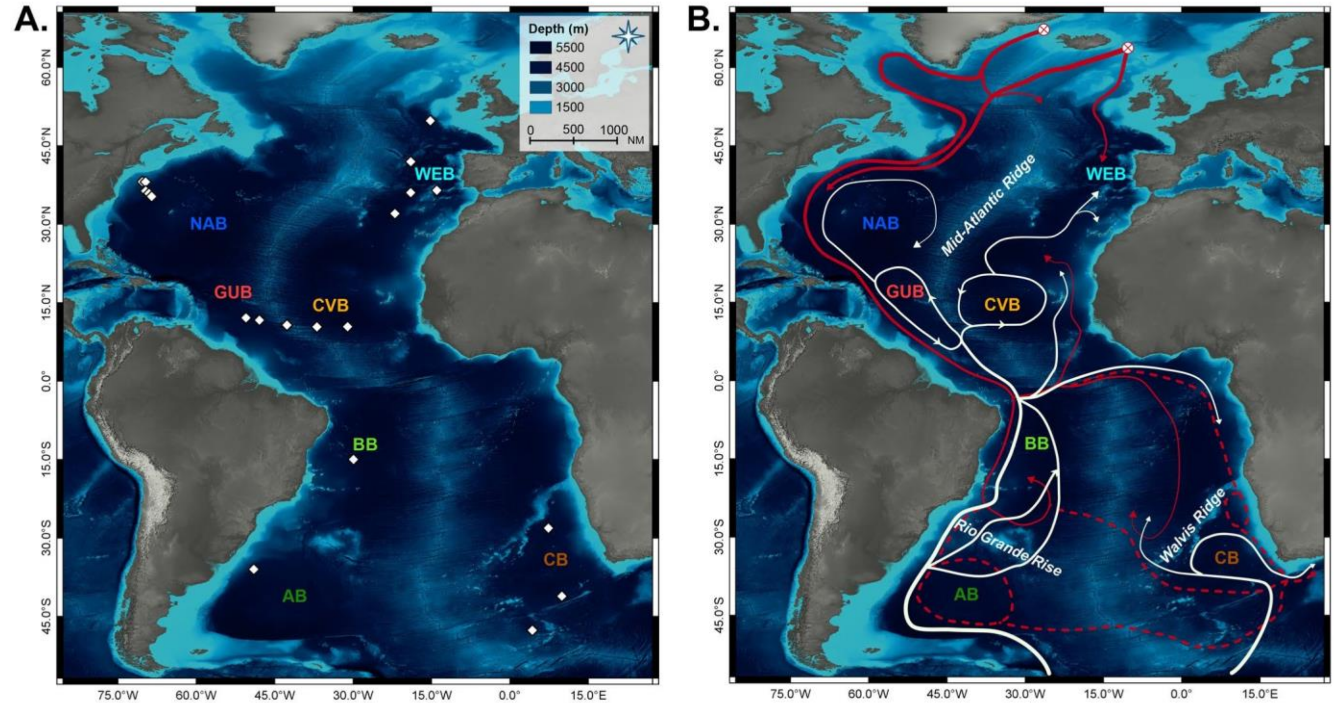

FIGURE 1 | Atlantic deep-sea basins where specimens of *L. ultima* were collected. (A) Sampled stations and bathymetric profile of the North American Basin (NAB), Guyana Basin (GUB), Brazil Basin (BB), Argentine Basin (AB), Cape Basin (CB), Cape Verde Basin (CVB), and West European Basin (WEB). Fully overlapping stations are displayed as a single shape. (B) Qualitative deep-water circulation patterns of Antarctic Bottom Water (AABW, beige) and North Atlantic Deep Water (NADW, red). Stippled lines show NADW propagating above 3500-m depth. Crossed circles indicate NADW formation areas. Water mass directions are derived from Morozov et al. (2010), Garzoli and Matano (2011), and Ferreira and Kerr (2017). Underlying bathymetry provided by GEBCO 2020 Grid. Map drawn in WGS84.

et al. 2015; Ross et al. 2020), basin connectivity is of fundamental importance for understanding phylogeographic patterns and population connectivity at large geographic scales.

Other than in most taxa, where mitochondrial DNA (mtDNA) is homoplasmic and transmitted through strict maternal inheritance (Birky 2001), Boyle and Etter (2013) provided evidence for *L. ultima* to exhibit mitochondrial heteroplasmy. Owed to the simultaneous presence of two or more types of mtDNA in both sexes, mitochondrial heteroplasmy can result in high intraspecific genetic divergence and challenge the design of population genetic analyses based on mitochondrial markers alone (Martínez et al. 2023; Rodríguez-Pena et al. 2020; Wai Ho and Hanafiah 2024). To overcome this, we applied a high-resolution SNP-based approach to identify fine-scale population structure beyond the resolution of the mtDNA gene markers COI and 16S, as well as an assessment of proteome fingerprints to aid the analysis of genetic differentiation and investigate potential ecological subdivisions within the species.

2 | Materials and Methods

2.1 | Sampling Design

Specimens of *L. ultima* were collected during seven research expeditions between 2005 and 2021 (see Table 1). The majority of samples were obtained with an epibenthic sledge (EBS; Brenke 2005), while 29 specimens were sampled either by Agassiz trawl (AGT), box corer (BC), or remotely operated vehicle (ROV). Specimens were identified to species level using a Leica MZ8 stereomicroscope and taxonomic literature (Allen and Hannah 1989; Filatova and Schileyko 1984; Knudsen 1970; Smith 1885). The species is characterized by a robust shell with prominent concentric growth lines (Figure 2) and can reach up to 3.4 mm in shell length. Like many protobranchs, a strong hinge-teeth mechanism is present on each side of the ligament (Figure 2A). *Ledella ultima* differs from all other Atlantic species by its tightly coiled hind gut situated at the dorsal margin (Figure 2B). Not unique, but by far the most pronounced, is a thickening of the ventral shell edge which occurs in some but not all specimens that have reached a shell length of 2.4 mm or more (Allen and Hannah 1989; Figure 2D–E). Shells from a maximum of five specimens per station were photographed using a Keyence VHX-7000 digital microscope. Images are deposited under accession doi: 10.5883/DS-LEDUL. All specimens were stored in 96% ethanol and kept at 4°C–8°C to facilitate DNA extraction and amplification.

2.2 | Molecular Analyses

2.2.1 | Tissue Preparation

Assessments of the internal morphology and sexing of the specimens were not performed, leaving the count of females and males unknown. Tissue samples for molecular and proteomic works were prepared concurrently using sterile utensils. For each specimen, complete soft tissue (somatic and gonad tissue) was taken, where possible excluding the gut. Soft tissue fractions

TABLE 1 | Station data and number (n) of *L. ultima* specimens collected during seven research expeditions in the North American Basin (NAB), Guyana Basin (GUB), Brazil Basin (BB), Argentine Basin (AB), Cape Basin (CB), Cape Verde Basin (CVB), and West European Basin (WEB).

Station	Year	Depth (m)	Latitude	Longitude	Basin	Gear	*n*	References
ANDEEP III (PS67)								Fahrbach (2006)
16–10	2005	4687	41°07.06′ S	009°54.88′ E	CB	EBS	2	
16–11	2005	4699	41°07.46′ S	009°55.11′ E	CB	AGT	13	
21–7	2005	4555	47°38.73′ S	004°15.20′ E	CB	EBS	3	
21–8	2005	4578	47°39.19′ S	004°16.50′ E	CB	AGT	13	
DIVA 2 (M63/2)								Türkay and Pätzold (2009)
26	2005	5040	28°06.65′ S	007°20.85′ E	CB	BC	1	
ENAB[a] (EN477)								Etter and Rex (2021)
17	2008	3500	38°10.41′ N	70°18.13′ W	NAB	EBS	4	
17a	2008	3500	38°08.00′ N	70°19.00′ W	NAB	EBS	2	
18a	2008	3800	38°05.59′ N	69°42.45′ W	NAB	EBS	12	
20	2008	4400	36°21.03′ N	69°41.30′ W	NAB	EBS	24	
21	2008	4700	35°52.12′ N	69°03.58′ W	NAB	EBS	26	
22	2008	5000	35°18.30′ N	68°32.94′ W	NAB	EBS	6	
DIVA 3 (M79/1)								Martínez Arbizu et al. (2009)
532	2009	4605	35°59.16′ S	049°00.75′ W	AB	EBS	6	
579	2009	5182	14°58.41′ S	029°57.51′ W	BB	EBS	14	
580	2009	5131	14°58.91′ S	029°56.49′ W	BB	EBS	23	
Vema-TRANSIT (SO237)								Devey (2015)
4-8	2014	5735	10°24.161′ N	31°06.205′ W	CVB	EBS	22	
4-9	2014	5733	10°24.589′ N	31°04.247′ W	CVB	EBS	34	
6-7	2015	5085	10°20.659′ N	36°57.010′ W	CVB	EBS	1	
6-8	2015	5127	10°22.293′ N	36°55.852′ W	CVB	EBS	2	
8-4	2015	5178	10°43.000′ N	42°39.723′ W	VFZ	EBS	1	
9-8	2015	5004	11°39.014′ N	47°56.168′ W	GUB	EBS	5	
11-1	2015	5093	12°05.732′ N	50°30.239′ W	GUB	EBS	4	
14-2	2015	4925	19°03.877′ N	67°08.100′ W	PRT	EBS	3	
IceAGE 3 (SO276)								Brix et al. (2020)
133-8	2020	4621	49°48.031′ N	015°13.004′ W	WEB	ROV	1	
138-1	2020	4570	49°47.352′ N	015°14.553′ W	WEB	BC	1	
IceDivA 1 (SO280)								Brix and Taylor (2021)
21-1	2021	4802	41°57.599′ N	018°58.832′ W	WEB	EBS	14	
28-1	2021	4904	41°57.554′ N	018°58.768′ W	WEB	EBS	15	
40-1	2021	5484	36°02.328′ N	018°59.497′ W	WEB	EBS	4	
61-1	2021	5121	32°02.025′ N	022°00.652′ W	WEB	EBS	3	
85-1	2021	4155	36°28.803′ N	013°59.617′ W	WEB	EBS	2	

Note: In addition, specimens were collected from the Vema Fracture Zone (VFZ) and the Puerto Rico Trench (PRT).
Abbreviations: AGT, Agassiz trawl; BC, box corer; EBS, epibenthic sledge; ROV, remotely operated vehicle.
[a]Except for six specimens from station 21, ENAB samples were only accessible as COI sequences.

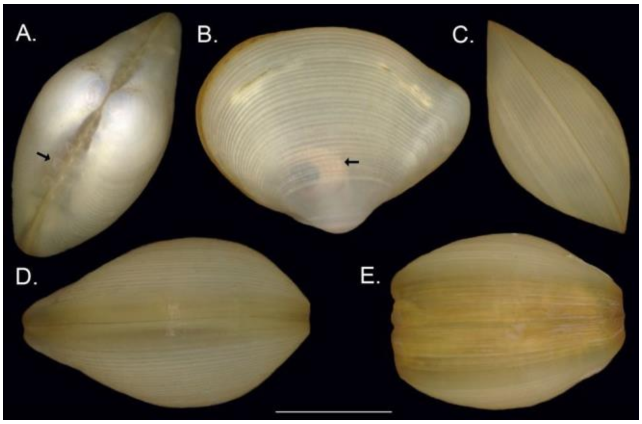

FIGURE 2 | External morphology of *L. ultima*. (A) Dorsal view with interlocking hinge teeth (black arrow; (Biv_321)) (B) Left valve of a translucent shell with a visible multiple coiled gut (black arrow; Biv_218). (C–E) Ventral view of specimens with levels of edge thickening: None (Biv_216), present (Biv_178), and pronounced (Biv_183). Scale bar: 1 mm.

of each individual were stored in 96% ethanol prior to further processing for DNA extraction and proteomic fingerprinting.

2.2.2 | Mitochondrial Markers

DNA was extracted using the E.Z.N.A Mollusk DNA kit (Omega Bio-Tek Inc., Norcross, GA, USA), following the manufacturer's instructions and leaving the tissue for digestion overnight in a shaking bath at 56°C/350 rpm. For all isolates, elution was carried out in two steps, applying 50 μL of pre-heated elution buffer each turn, yielding 100 μL of DNA isolate. DNA quantity was evaluated using UV spectrophotometry (NanoDrop; Thermo Fischer Scientific). Samples were amplified through polymerase chain reaction (PCR) using the mitochondrial markers cytochrome *c* oxidase subunit I (COI) and 16S rRNA (16S). Each 2 μL of DNA isolate was added to a reaction mix of 21 μL Milli-Q filtered water and each 1 μL of forward and reverse primer and aliquoted to Illustra PuReTaq Ready-To-Go PCR-Beads (Avantor; VWR Int. GmbH, Darmstadt, Germany). COI was targeted using the standard barcode primers LCO1490 5′-GGT CAA CAA ATC ATA AAG ATA TTG G-3′ and HCO2198 5′-TAA ACT TCA GGG TGA CCA AAA ATC A-3′ (Folmer et al. 1994) which yielded fragments of 615 bp. Reactions were run on a thermocycler with an initial denaturation at 95°C for 5 min, followed by 38 cycles of denaturation at 95°C for 45 s, annealing at 45°C for 50 s, and extension at 72°C for 1 min. Final extension took place at 72°C for 5 min. The variable region of 16S was targeted using the forward LMY16F 5′-GAC GAR AAG ACC CYR TCA AAC-3′ and reverse Lu16R4 5′-GCT GTT ATC CCT CCA GTA ACT-3′ primers, with thermal cycling conditions applied as given in Chase et al. (1998) and Etter et al. (2011). The 16S fragments yielded 99–157 bp. Quality and quantity of amplified products were assessed by gel electrophoresis using 1.5% gels. Purification of successful PCR products was performed combining 10 μL of PCR product with 3 μL of ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fischer Scientific) and run on a thermal cycler at 37°C and 80°C for 15 min each. Purified product was sent to Macrogen Europe Inc. (Amsterdam, Netherlands) and Eurofins Genomics Germany GmbH (Ebersberg, Germany) for double stranded sequencing on ABI3730xl sequencers. DNA aliquots are stored at −80°C at the DZMB Hamburg, Germany. Forward and reverse chromatograms were edited and assembled using Geneious Prime (2023.1.2; Biomatters, Auckland, New Zealand; Kearse et al. 2012). The Basic Local Alignment Search Tool (BLAST; Altschul et al. 1990) was used to check for potential contamination and to confirm species identification.

To identify the occurrence of female and male mtDNA among our sequenced specimens, the following additional sequences from samples collected during the ENAB expedition were included: COI: 68, female mtDNA; 16S: 5, female mtDNA (HQ907901–HQ907905) and 5, male mtDNA (HQ907906–HQ907910) obtained by Boyle and Etter (2013). Among these, there are three specimens (Lu20BC2–Lu20BC4) from which three sequences were obtained per individual, being the female and male mtDNA of 16S as well as the female mtDNA of COI (Table S1; see Supplemental Methods in Appendix S1). Alignments were performed using the automated algorithm in MAFFT 7.490 (Katoh and Standley 2013) and checked by eye for quality control. Haplotype networks were inferred using the TCS algorithm (Clement et al. 2002) as implemented by PopART version 1.7 (Leigh and Bryant 2015). Kimura-2-Parameter distances (K2P; Kimura 1980) within and between genetic clusters were calculated using MEGA X (Kumar et al. 2018). Bayesian tree hypotheses were generated for both mitochondrial markers. The software jModelTest 2 (Darriba et al. 2012; Guindon and Gascuel 2003) was used to estimate best-fit models of evolution by applying the Akaike Information Criterion (AIC; Sakamoto et al. 1986), resulting in GTR + I + G for COI and HKY85 for 16S. Clustering analyses of single-gene and concatenated alignments were performed using MrBayes 3.2.1 (Huelsenbeck et al. 2001), with four parallel runs of 5 million generations, sampling every 10,000 generations. Convergence of independent runs was examined in Tracer 1.7.2 (Rambaut et al. 2018) with a burn-in of 10%. Trees were reconstructed using Bayesian Inference (BI), assessing branch support by posterior probability (PP) with values ≥ 0.95 considered as highly supported (Felsenstein 1985; Huelsenbeck et al. 2001). The trees were rooted with the autobranch bivalve *Vesicomya galatheae* (Knudsen 1970). Delimitation of genetic clusters was complemented using the distance-based method ASAP (Assemble Species by Automatic Partitioning; Puillandre et al. 2021), applying each of the substitution models with default settings.

2.2.3 | Single-Nucleotide Polymorphism Data by 2b-RAD

A streamlined restriction site-associated DNA (RAD) genotyping method based on sequencing of uniform fragments produced by type IIB restriction endonucleases (2b-RAD) was carried out using a subset of 93 samples (Table S2). Sample preparation was conducted following the protocol of Wang et al. (2012) with the restriction enzyme *BgcI*. Sequencing was performed at the Alfred Wegener Institute (Bremerhaven, Germany) on an Illumina Next-Seq 2000 using P2 reagents and generating 50-bp paired-end reads. Raw reads were demultiplexed by internal barcodes and PCR duplicates removed using a custom script (https://github.com/pmartinezarbizu/

2bRADpp). The data were further processed using Stacks (v 2.68; Rochette et al. 2019). Demultiplexed reads were quality filtered with a minimum quality score threshold of 30 to retain high-confidence reads. Locus assembly and genotyping were performed using the Stacks modules. Loci were assembled for each individual (*ustacks*), with minimum stack depths (-m) of three, five, and eight, a maximum of two mismatches (-M) between stacks, and a limit of four loci per individual (-N). Gapped alignment was disabled to maintain uniformity in the assembly process. Subsequently, *cstacks* was used to generate a catalog of loci based on a map file which allowed for the identification of shared loci across individuals. Using *sstacks* and *gstacks*, sequence data was aligned to this catalog, enabling the detection of matching loci and the generation of genotypic data. The *populations* module was employed with a minimum sample fraction threshold of 0.1 and one population for all samples. All downstream analyses were performed using individual SNP information (based on stacks output: populations.snps.vcf) in a custom R script (doi: 10.5061/dryad.t1g1jwtdr). Filtering thresholds were applied to remove individuals with > 75% missing genotype calls and loci with > 20% missing data. Polymorphic loci were retained by excluding singletons and non-polymorphic sites. Data manipulation utilized the R packages vcfR (Knaus and Grünwald 2017), adegenet (Jombart 2008; Jombart and Ahmed 2011), and SNPRelate (Zheng et al. 2012). Filtered VCF files were converted to *genlight* and *genind* objects for subsequent analyses. Linkage disequilibrium (LD) pruning was performed with a threshold of $r^2 = 0.2$, retaining a subset of loci for downstream population structure analyses. Missing genotype data were imputed and reformatted for compatibility with the LEA (Latent Environmental Ancestry) package (Frichot and François 2015). To assess the influence of minimum stack depth on genotyping outcomes, stack depths of three, five, and eight were tested (Table S3). As expected, increasing the minimum stack depth reduced the total number of retained SNPs (2824, 2048, and 1410, respectively), while mean heterozygosity increased slightly from 0.0637 ($m = 3$) to 0.0681 ($m = 8$). All further analyses (except for conStruct) were performed with filtered SNPs from all three pipelines. Overall, we observed no major differences in downstream patterns of population structure across the three datasets. We therefore selected $m = 5$, ensuring sufficient marker density while minimizing potential genotyping errors.

Population structure was inferred using the Sparse Nonnegative Matrix Factorization (sNMF) algorithm from the LEA package. We tested values for the number of ancestral populations (K) ranging from 1 to 10 to identify the optimal number of populations, running 10 repetitions with 200 iterations for each value of K. Entropy cross-validation was used to determine the most likely number of K, but did not yield a distinct minimum. Admixture bar plots were therefore generated for the most conservative probable K ($K = 2$) to visualize the cluster membership proportions for each individual. Population structure was additionally assessed using Bayesian clustering (K = 2–5, 5000 iterations, non-spatial model) from the conStruct package (K = 2–5, 5000 iterations, non-spatial model) (Bradburd 2019). Posterior distributions for the admixture proportions from four independent Markov Chain Monte Carlo (MCMC) chains were extracted and checked for label switching. Any detected label switching was manually corrected for each cluster. Subsequently, mean admixture proportions and 95% confidence intervals (CIs) were calculated. The effective sample size (ESS) for each cluster in each MCMC chain was computed using the effectiveSize function from the coda package (Plummer et al. 2006) to assess the stability of the chains. The Gelman–Rubin diagnostic was performed to evaluate convergence across chains, with the potential scale reduction factor (PSRF) calculated and visualized.

Pairwise Nei's genetic distances (Nei 1972) were calculated at the individual level based on allele frequencies derived from multilocus genotypes within and between basins using the StAMPP package (Pembleton et al. 2013). A discriminant analysis of principal component (DAPC) was performed using the three main hierarchical clusters (based on Nei distances and ward.D) as the discriminant factor. The number of included principal components was based on a-score optimization (10 PCs and 2 discriminant functions). In addition, Nei's genetic distances were calculated pairwise between populations, based on population-level allele frequencies. The fixation index (F_{ST}) was calculated based on Nei and Chesser's (1983) corrected genetic differentiation statistic, which accounts for genetic differentiation among populations by incorporating heterozygosity and adjusting for sample size biases, using the R package FinePop2 (Nakamichi et al. 2020). Nei distances and F_{ST} were visualized as a heatmap using the pheatmap package (Kolde 2019). To better visualize connectivity between basins, we mapped F_{ST} values alongside admixture proportions inferred from sNMF.

2.2.4 | Proteomic Fingerprinting

Matrix-assisted laser desorption/ionization time-of-flight mass spectrometry (MALDI-TOF MS) was performed to obtain proteomic mass spectra, following the protocol given in Rossel et al. (2024). For each specimen, three mass spectra were measured. Raw spectral data from MALDI-TOF MS analyses were processed and analyzed using R (R Core Team 2024), utilizing the following packages: MALDIquant, MALDIquantForeign, adegenet, randomForest, vegan, reshape2, pheatmap, ggplot2, splus2R, RColorBrewer, plyr, and dplyr (Burns 2020; Gibb 2022; Gibb and Strimmer 2012; Jombart 2008; Kolde 2019; Liaw and Wiener 2002; Neuwirth 2022; Oksanen et al. 2019; Wickham 2023b, 2020, 2023a; Wickham et al. 2022). Spectral data were imported using the importBrukerFlex() function, with empty spectra removed. Spectra were trimmed to a mass range of 2000–20,000 m/z, and intensity values were square-root transformed to stabilize variance. Intensity smoothing was performed using the Savitzky–Golay algorithm (Savitzky and Golay 1964; window size = 10). Baseline correction was carried out using the SNIP algorithm (Ryan et al. 1988) with 15 iterations, followed by total ion current (TIC) normalization to adjust for differences in signal intensity across spectra. Technical replicates were averaged based on sample identifiers extracted from metadata. Averaging was performed using the mean intensity values of replicate spectra. Peaks were detected with a signal-to-noise ratio (SNR) threshold of 8, using a moving average (MAD) approach. Peak binning was conducted iteratively using a strict tolerance of 0.002 to group peaks with similar m/z values. The binning process was repeated until the number of binned peaks remained constant. To remove noise, a lower detection threshold was defined based on the relationship between peak intensity and mean spectral noise. Peaks below 1.75 times the average noise level were set to zero. Spectral intensities were further normalized using the Hellinger transformation (Legendre and Gallagher 2001), and a final intensity matrix was created by averaging peak intensities across biological replicates. Metadata for each sample, including mitotype, region, and group, were integrated into the matrix from an external reference table. DAPC was performed to identify population structure using successive k-means clustering based on all 120 PCs. The optimal cluster number was determined based on Bayesian Information Criterion values. A Random Forest (RF) model (Breiman 2001) was employed to classify samples into regional groups based on spectral data. Samples were grouped into two broad regions, and RF classification was conducted using 10,000 trees and 22 variables per split. Hierarchical clustering based on Euclidean distances was performed on normalized peak intensities. Feature importance was assessed using Mean Decrease Accuracy, and the top 13 peaks (with values > 0.0006) were selected for presentation as a heatmap using the pheatmap package.

3 | Results

3.1 | Mitochondrial Markers

Mitochondrial markers were successfully amplified for 135 specimens of *L. ultima*, yielding 235 novel sequences for the two markers COI (128 sequences; 615 bp) and 16S (107 sequences; 99–157 bp). In total, 100 specimens were successfully sequenced for both markers. Sequence data are accessible in the Barcode of Life Data System (BOLD v4; Ratnasingham et al. 2024) via 10.5883/DS-LEDUL. GenBank accession numbers are listed in Table S2.

The TCS haplotype network analyses for both mitochondrial markers (Figure 3) each resulted in five groups of mitochondrial haplotypes, hereafter referred to as mitotypes (MTs).

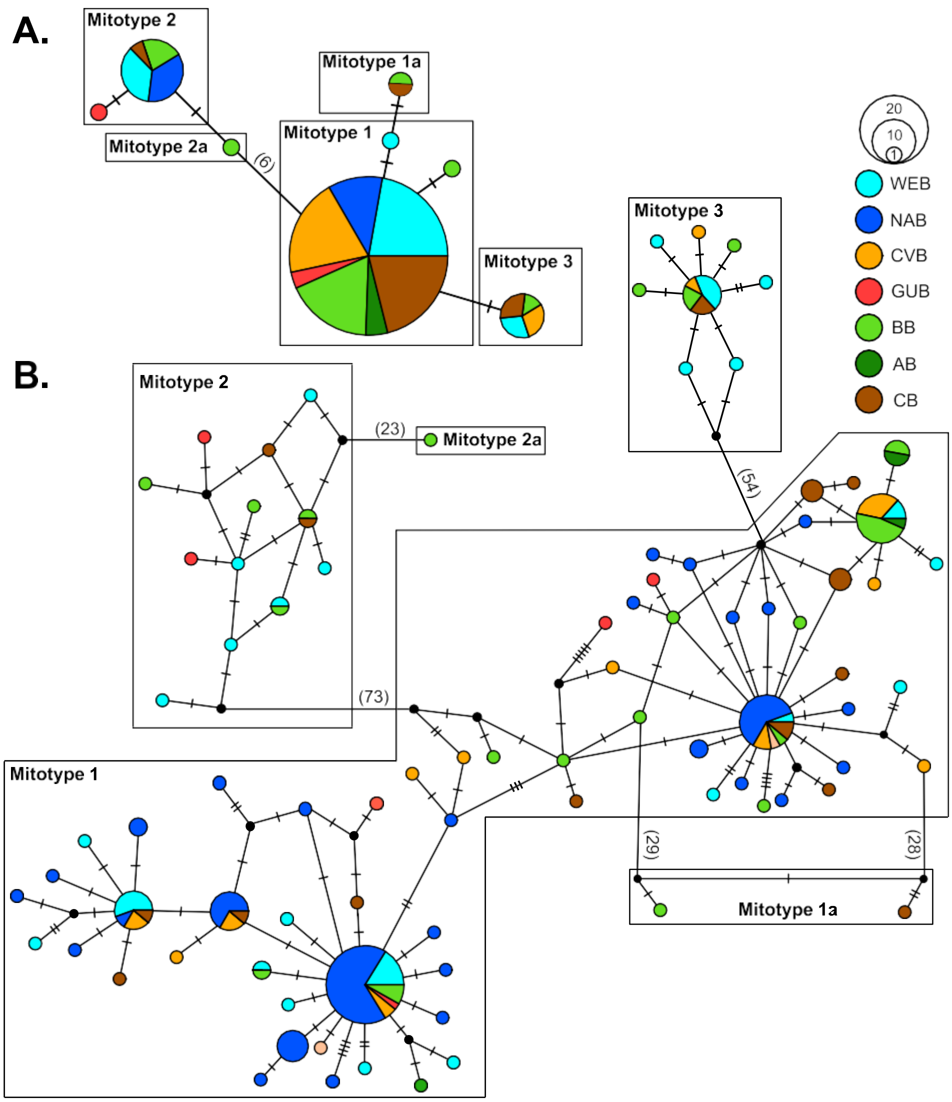

FIGURE 3 | TCS haplotype network analyses of *L. ultima* resulting in each of the five groups of mitochondrial haplotypes (mitotypes) for the genetic markers (A) 16S and (B) COI. Colors correspond to the respective Atlantic basins. Hash marks refer to the number of mutational steps between specimens. Filled black circles correspond to missing haplotypes.

Identification of MTs was based on the number of nucleotide substitutions (23–73) revealed by COI between MT 1 and MTs 1a, 2, 2a, and 3, and were, respectively, transferred to the less divergent network of 16S (Figure 3A). For both markers, samples were consistently allocated to respective mitotypes but were distributed across clusters and basins without clear geographic or genetic correspondence (Figure 3A,B). A total of 94 specimens spanning all Atlantic basins clustered as MT 1, including 94 sequences for COI and 88 sequences for 16S. Additional female mtDNA sequences from the NAB (COI: 68, 16S: 5, Table S1) congruently clustered with MT 1. Fourteen specimens were assigned to MT 2, including 14 sequences for COI and eight sequences for 16S, covering all basins but the CVB and the AB. In addition, five male mtDNA 16S sequences from the NAB (Table S1) clustered with MT 2. Mitotype 3 yielded a total of 16 specimens, including 16 COI and eight 16S sequences, covering the WEB, CVB, BB, and the CB. Furthermore, for both markers, one specimen from the BB and the CB was identified as MT 1a, and a single specimen from the BB was identified as MT 2a. The ASAP analyses of COI (Figure S1) and 16S (Figure S2) delimited partitions congruent with the haplotype network analyses but scored MT 1a and MT 2a either as separate clades or grouped with MT 1 and MT 2, respectively. K2P distances within mitotypes yielded a maximum of 0.05 for both markers (Table 2). Distances between mitotypes were found lowest for the comparisons of MT 1 and MT 1a (COI: 0.08–0.11, 16S: 0.02–0.08) and MT 2 and MT 2a (COI: 0.06–0.07, 16S: 0.02–0.05). Except for the distance between MT 1 and MT 3 for 16S (0.05–0.10), distances were found to range between 0.16–0.30 for COI and 0.10–0.25 for 16S.

3.2 | 2b-RAD Analyses

For the applied stack depth $m = 5$, mean coverage per individual across 14,220 loci was 42X (Table S3). These values are in line with expected coverage for 2bRAD datasets (Wang et al. 2012). After quality filtering and SNP calling, a total of 2048 polymorphic loci were retained across 78 individuals. Samples were distributed across six basins, with the following sample sizes per region: WEB ($n = 30$), GUB ($n = 3$), CVB ($n = 11$), BB ($n = 22$), AB ($n = 4$), and CB ($n = 8$). No individuals from the NAB met the filtering thresholds and were thus excluded from further analysis. The sNMF analysis did not identify a distinct minimum in the cross-entropy criterion across K values from 1 to 10 (Figure 4A), indicating the absence of strong population subdivision. Both sNMF and Bayesian clustering (conStruct) yielded largely congruent ancestry coefficients (Figure 4B) for a scenario of $K = 2$. After evaluation of a wider range of K (Figure S3), we selected this scenario as the most parsimonious model based on comparatively lower entropy but also on biological relevance. This rather conservative approach acknowledges that the observed consistency in ancestry patterns may be shaped by large-scale oceanographic features. Specifically, the observed clustering aligns with major deep-sea current systems that may shape gene flow among abyssal basins. The NADW predominantly flows southward along the western Atlantic margin, facilitating potential connectivity among the WEB, GUB, and CVB, where individuals predominantly cluster with K1 (black). In contrast, connectivity of South Atlantic basins, specifically the AB, may be more strongly influenced by the AABW. Individuals from AB

TABLE 2 | K2P distances within (in italics) and between mitotypes (MT) identified by the mitochondrial markers COI and 16S.

	COI					16S				
	MT 1	MT 1a	MT 2	MT 2a	MT 3	MT 1	MT 1a	MT 2	MT 2a	MT 3
MT 1	*0.00–0.04*					*0.00–0.05*				
MT 1a	0.08–0.11	*0.00–0.01*				0.02–0.08	*0.00*			
MT 2	0.23–0.26	0.25–0.26	*0.00–0.02*			0.18–0.25	0.22–0.25	*0.00–0.02*		
MT 2a	0.24–0.27	0.22–0.24	0.06–0.07	*0.00*		0.15–0.19	0.19–0.20	0.02–0.05	*0.00*	
MT 3	0.16–0.19	0.17–0.18	0.26–0.28	0.29–0.30	*0.00–0.01*	0.05–0.10	0.10–0.12	0.18–0.25	0.15–0.19	*0.00–0.02*

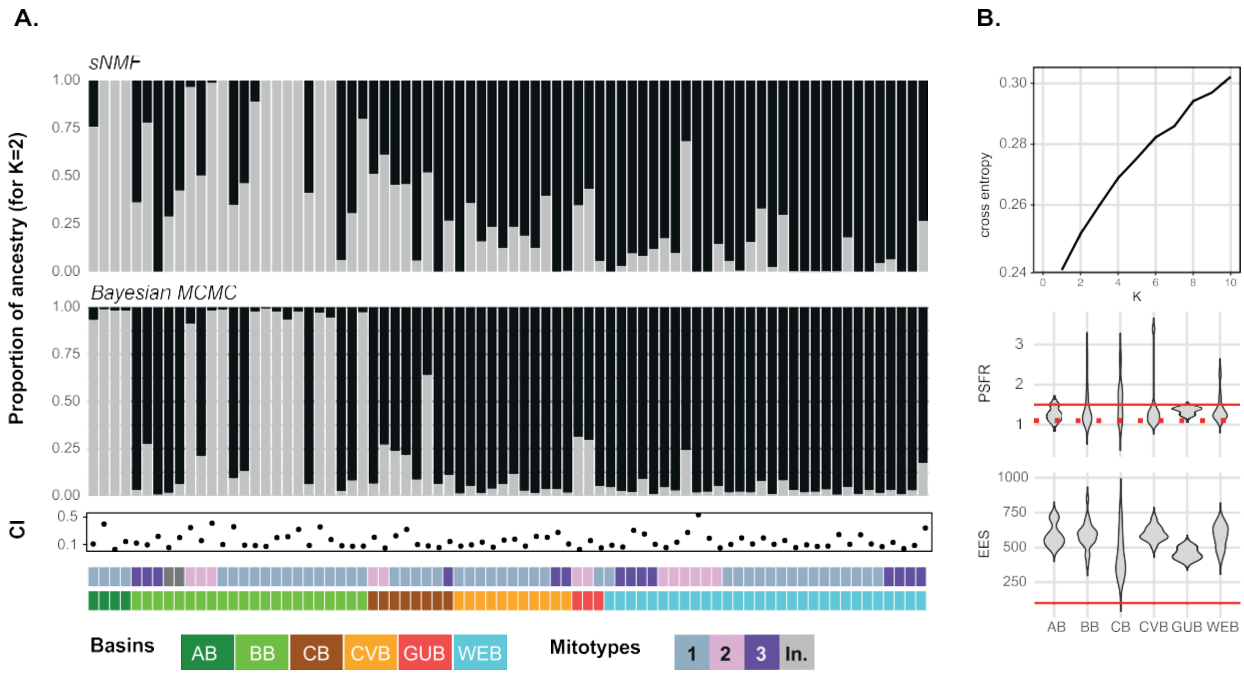

FIGURE 4 | Patterns of population structure for *L. ultima* based on SNP data obtained by 2b-RAD sequencing. (A) Proportions of ancestry for $K = 2$ using the Sparse Nonnegative Matrix Factorization (sNMF) algorithm and Bayesian clustering, with posterior distributions for admixture proportions from four independent Markov Chain Monte Carlo (MCMC) chains. For each cluster, mean admixture proportions and 95% confidence intervals (CIs) were calculated. Colored bars correspond to mitotypes (top) and six Atlantic basins (bottom). (B) Cross-entropy criterion, potential scale reduction factor (PSRF) calculations, and effective sample sizes (ESS) across K values from 1 to 10.

were predominantly assigned to the second cluster K2 (gray), forming a distinct genetic group. Intermediate proportions of admixture were found in the BB and CB regions. MCMC convergence was confirmed for all conStruct runs with PSRF values < 1.1 and ESS > 250 for all K values (Figure 4C–E). Although CIs were high for a small subset of individuals, the data suggest adequate convergence and stability of the admixture estimates. To explore whether mitochondrial haplotype distributions mirrored genomic population structure, mitotypes were overlaid onto the admixture results (Figure 4A). Mitotypes were distributed across clusters and basins without clear geographic or genetic correspondence. Two mitotypes (1a and 2a), represented by single individuals, were considered indeterminate and excluded from population-level interpretation.

Pairwise Nei's genetic distances among individuals were calculated separately for within- and between-basin comparisons, showing substantial overlap (Figure 5A). However, certain between-basin comparisons showed elevated values, most notably between AB and WEB, which exhibited some of the highest pairwise genetic distances among all basin pairs. F_{ST} values calculated from LD-pruned, polymorphic loci ranged from 0.002 to 0.018, indicating overall low levels of genetic differentiation across regions. The highest values were observed between AB and CVB ($F_{ST} = 0.018$), followed by AB–WEB and AB–GUB comparisons. In contrast, minimal differentiation was detected between WEB, GUB, and CVB. These patterns are visualized as an F_{ST} heatmap (Figure 5B), highlighting subtle but consistent genetic structure among basins. Nei's genetic distances between populations revealed similar patterns of differentiation (Figure 5B), except for elevated distances involving GUB. These values should be interpreted with caution, as unbalanced sample sizes may have inflated estimates of genetic divergence (Kitada et al. 2021). The mapped F_{ST} values alongside admixture proportions inferred from sNMF, averaged for each basin, illustrate the extent of connectivity between populations by geographic distance (Figure 5C), with line widths inversely proportional to genetic differentiation (F_{ST}). The DAPC, using inferred clusters from hierarchical Ward clustering on pairwise Nei's genetic distances, supported the separation of AB from all other basins (Figure 5D). The first discriminant function accounted for most of the inter-basin variance and separated AB individuals from those in the WEB, GUB, and CVB. The BB and CB samples occupied an intermediate position along this axis.

3.3 | Proteomic Fingerprinting

In total, 120 specimens were used in the MALDI-TOF MS analysis. Their clustering based on relative proteomic composition resulted in two main groups (Figure 6A). One group included all specimens sampled in the central Atlantic (GUB and CVB) and the south-east Atlantic (CB), as well as an additional three samples from the south-west Atlantic (BB). The second group clustered all specimens from the north Atlantic (WEB and NAB) and the south-west Atlantic (AB), as well as all remaining samples from the BB. A RF model based on these two groups (out of box error: 0.03) revealed mass peaks that are considered important for the differentiation between groups. While all peaks were found in specimens from both groups, between-group peak intensities differed distinctly (Figure 6B). Within the RF model, every specimen received a probability of assignment to the CB_CVB_GUB class, ranging from 0.4 to 0.6 (Figure 6C). DAPC analysis revealed a solution

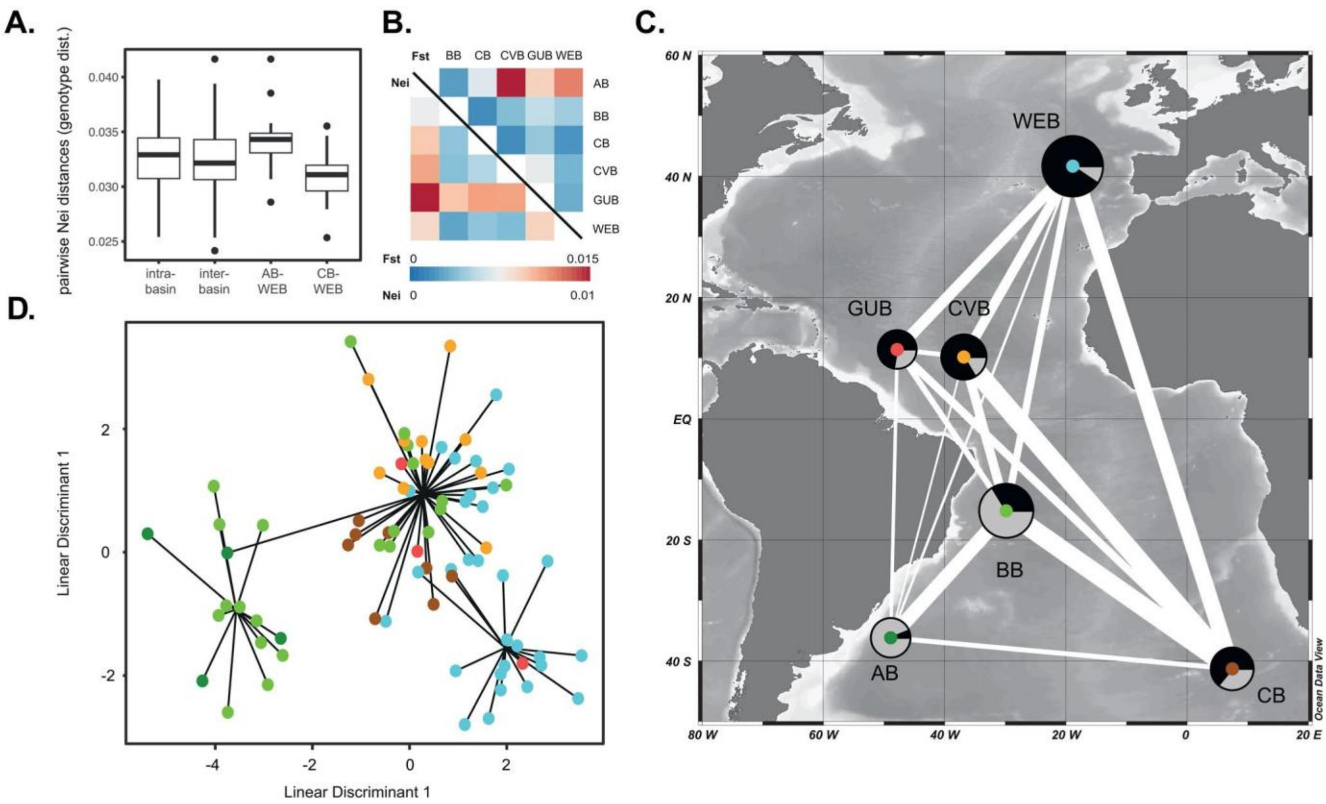

FIGURE 5 | Genetic distance based on SNP data calculated from LD-pruned, polymorphic loci. (A) Calculated pairwise Nei's genetic distances among individuals for intra- and inter-basin comparisons, including comparisons between the geographically most distant basins. (B) Heatmap of F_{ST} values (upper) and Nei's genetic distance (lower), using a color gradient between red for smallest and blue for largest values. (C) Illustrated view of proportions of ancestry for $K=2$, inferred from the Sparse Nonnegative Matrix Factorization (sNMF) algorithm averaged for each basin. Circle size indicates sample size; line width is inversely proportional to genetic differentiation (F_{ST}) between basins. Map generated with Ocean Data View (Schlitzer 2022). (D) Inferred clusters by DAPC from hierarchical Ward clustering on pairwise Nei's genetic distances. Colors represent respective Atlantic basins.

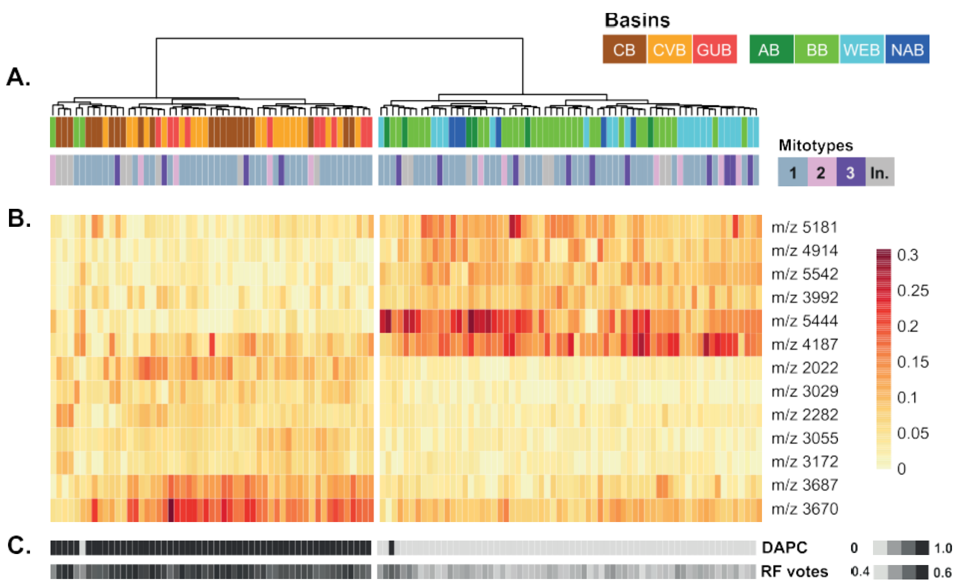

FIGURE 6 | Proteome fingerprinting results from specimens of *L. ultima* across seven Atlantic basins. (A) Clustering results based on the relative proteomic composition across samples. Colored bars correspond to basins (top) and mitotypes (bottom). (B) Heatmap of relative intensities of mass peaks for differentiation at the population level, identified using the RF classifier. (C) Probability of assignment for the RF model and the DAPC analysis, revealing a solution of two k-means clusters.

of two k-means clusters and was able to discriminate all but two specimens into the same groups as the hierarchical clustering. Mitotypes delineated by the mtDNA analyses were included for reference and resulted in a scattered distribution across basins and groups. Clustering results were checked against shell morphometric measurements, including length, width, and levels of ventral edge thickening (data not shown). No correlation was found.

4 | Discussion

Low genetic differentiation across abyssal plains has been hypothesized to result from an interplay of reduced habitat heterogeneity, slow evolutionary rates, few topographic barriers, and extensive gene flow between distant populations (Etter et al. 2005; Rex and Etter 2010; Jennings et al. 2013). Yet, our understanding of population structure and connectivity in these understudied habitats remains scarce. Subtle population structures that may exist in such environments can remain undetected when relying solely on mitochondrial markers like 16S or COI, which often lack the resolution to capture fine-scale genetic patterns (Andrews et al. 2016; Hurst and Jiggins 2005; Reitzel et al. 2013). To overcome these limitations, we combined mitochondrial markers with genome-wide SNP data and proteomic fingerprinting to assess whether subtle population structure and potential ecological subdivision exist in the abyssal bivalve *L. ultima* across major Atlantic basins.

4.1 | Phylogeographic Patterns and Population Connectivity

The analyses of SNP data detected subtle genetic structure, despite uniformly low absolute F_{ST} values across basins (0.002–0.018). Comparably low F_{ST} values have been reported in other deep-sea mussel species (Xu et al. 2017; Yao et al. 2022). Although numerically small, this approximately tenfold variation in F_{ST} estimates indicates biologically meaningful structure when interpreted in the context of overall low heterozygosity in the data, as well as high-dispersal potential and large effective population sizes (N_e). This emphasizes the necessity of applying genome-wide markers to resolve fine-scale population structure, as has been demonstrated for different deep-sea organisms (Diaz-Recio Lorenzo et al. 2024; Galaska et al. 2017; Pante et al. 2015; Takata et al. 2021; Xu et al. 2018). Generally, population sizes of *L. ultima* across the abyssal Atlantic are huge (Allen 2008; Allen and Hannah 1989), with an estimated N_e of more than 10 million individuals for the NAB alone (Etter et al. 2011). It is likely that the high number of reproducing individuals weakens the effects of genetic drift and contributes to the maintenance of the overall similar genetic architecture seen in our data, where a general concordance between F_{ST} patterns and the pairwise Nei's genetic distance between populations suggests that historical divergence and current gene flow contribute at a similar scale (Marko and Hart 2012).

The extensive gene flow between distant populations of *L. ultima* might seem counterintuitive at first (Etter et al. 2011), especially because the overall slow abyssal currents would rather be suggestive of limited dispersal distances (Stow et al. 2019; Zenk 2008). This perspective aligns with the long-standing paradigm that pelagic lecithotrophs are altogether less dispersive than planktotrophs (Calow 1983; Jablonski and Lutz 1983; O'Connor et al. 2007). Especially for deep-sea taxa, however, it has repeatedly been shown that lecithotrophic development itself does not constrain dispersal (Levin 2006; Weersing and Toonen 2009; Young et al. 1997). For example, in echinoderm lecithotrophs, not only was the duration of the free-swimming phase found to be longer when coupled to lowered temperatures (Mercier et al. 2013), but also the swimming-speed capacity increased when compared to planktotrophic larvae of comparable size (Montgomery et al. 2019). In *L. ultima*, the development of few, large-sized eggs per female is balanced by high population densities (Allen and Hannah 1989; Scheltema 1972). Since more energy per egg is provided compared to planktotrophs, and temperatures at abyssal depths are constantly low, lecithotrophic larvae likely have the ability to delay developmental rates and increase their dispersal rates (Scheltema 1972; Young 2003; Scheltema and Williams 2009; Jennings et al. 2013). Given that this numerically abundant species has rarely been sampled above 3000 m, it seems plausible that populations of *L. ultima* continuously produce vital numbers of recruits, sufficient to maintain self-sustained populations, replenish adjacent populations, and maintain gene flow by passive transport processes of pelagic lecithotrophic larvae across the continuous abyssal plains. We postulate that deep-ocean circulation dynamics and the use of geographically intermediate soft-bottom habitats are crucial for the maintenance of genetic connectivity in this tiny pan-Atlantic bivalve. Furthermore, periodic strong bottom flows in northern and southern basins, with the potential to sweep larvae and juveniles together with surficial organic matter across the seabed (Gardner et al. 2017; Hollister and McCave 1984; Thistle et al. 1991; Zenk 2008), may be an additional driver for the maintenance of connectivity between populations in the deep sea (Aller 1989; Gheerardyn and Veit-Köhler 2009; Harris 2014; Meißner et al. 2023).

Our SNP analyses recovered highest F_{ST} values between AB–WEB, AB–GUB, and AB–CVB. Together with a concordant signal in Nei values for AB, this suggests a genuine pattern of differentiation. Elevated Nei distances at low F_{ST} values in the GUB are more likely attributable to sampling artifacts caused by unbalanced datasets than to actual genetic divergence. We observed low genetic divergence between the geographically distant basins WEB and CB; however, markedly higher levels of genetic differentiation between the similarly distant basins WEB and AB (Figure 5A–C). This implies that isolation by geographic distance is not acting as a key driver and evokes an important distinction between the geographic and the effective distance between basins (Dambach et al. 2016; McClain and Hardy 2010; Xuereb et al. 2018). Whereas distance is often interpreted by means of a two-dimensional scale, the direction and strength of bottom currents in the three-dimensional marine realm have a direct effect on the potential for dispersal and thus gene flow between populations (Lecroq et al. 2009; Menzel et al. 2011; Miller and Gunasekera 2017). This implies that the deep-water circulation patterns of AABW and NADW provide direct but non-uniform links between populations in the Atlantic. While the propagation of NADW connects the north and central Atlantic region, as well as the south-west

African margin, the AABW mainly links the west-Atlantic margins, including parts of the north-eastern corridors of the MAR facilitated by deep abyssal channels (Ferreira and Kerr 2017; Garzoli and Matano 2011; Morozov et al. 2010). As for the low genetic divergence between WEB and CB and the proportions of ancestry revealed by our analysis, we propose the genetic admixture to be driven by the north-east directional flow of NADW. Upon its crossing of the MAR through extensive fracture zones in the central Atlantic (German et al. 2011; Morozov et al. 2010), most of NADW is retained in the Angola Basin through advective currents caused by the Walvis Ridge (Bartels 2008; Shannon and Chapman 1991). As demonstrated for polychaetes (Fiege et al. 2010), harpacticoid copepods (Menzel et al. 2011) and isopods (Brix et al. 2011, 2015; Brökeland 2010), the Walvis Ridge does not appear as an absolute barrier for connectivity, allowing a fraction of bottom water to enter the CB. While similar patterns of genetic connectivity across ocean basins have been shown for brooding isopods (Bober et al. 2018; Brix et al. 2011, 2015), indicating bottom-water masses to function as vectors for population connectivity, the 16S data analysis by Etter et al. (2011) revealed modest genetic divergence between populations of *L. ultima* from eastern and western basins of the North Atlantic, suggesting the MAR to function as a topographic barrier to gene flow. Since we do not see such distinctive barriers to gene flow in our genome-wide analysis of population structure, we interpret these patterns as basin-based divisions with possible small-scale effects of the MAR instead.

The concept of effective distance can be developed further by integrating the potential for asymmetric gene flow, where migration between populations follows a unidirectional fashion mediated by current flows and strong advection processes (Snead et al. 2023; Stow et al. 2019; Xuereb et al. 2018). For the south-east Atlantic basins AB and BB, our analysis results of sNMF and Bayesian MCMC congruently found an overall mixed proportion of ancestry for K1 and K2 in the BB, and a predominance of K2 in the AB (Figure 4A). These findings are indicative of asymmetric gene flow mediated by the intensity and directional flows of AABW and NADW, possibly evoking a unidirectional migration from the AB population into the BB population, and the result of fine-scale genetic structure observed. While a large fraction of AABW passes the Rio Grande Rise through the Vema Gap into the BB (Morozov et al. 2010, 2023), minimizing the effective distance, the southward flow of NADW into the AB is largely restrained by retentive hydrodynamic forces (Alberoni et al. 2020; Perez et al. 2020), increasing the effective distance between these basins. While the predominance of K2 in the AB and indications of asymmetric gene flow could suggest this basin to serve as a potential site for ongoing speciation processes, and a fraction of individuals from the BB showed a proportion of ~90% of either K1 or K2, implying patterns of assortative reproduction, we advise careful interpretation of these findings. Given that the sNMF clustering revealed generally higher mixing proportions in the BB compared to the Bayesian MCMC, and we generally found low genetic differentiation across basins, we already discussed population structure at a fine scale where the risk for overinterpretation is almost inevitable.

4.2 | Proteomic Fingerprinting

Proteomic analyses revealed two distinct groups: one comprising the central and south-east Atlantic (GUB, CVB, CB) and the other spanning the north- and south-west Atlantic (WEB, NAB, BB, AB). This division contrasts with the genetic structure inferred from SNP data but aligns with the scattered distribution of mitotypes across basins and groups. Given that previous proteomic studies have been successfully applied for species identification (Paulus et al. 2022; Peters et al. 2023; Renz et al. 2021), differentiation of cryptic lineages (Kaiser et al. 2018), and distinguishing reproductive stages at the species level (Rossel et al. 2023), our findings show that the genetic divergence between mitochondrial haplotypes does not correspond to proteomic differentiation and support the presence of a single species. A test for correlation between clustering results and the distribution of shell size (width, length) and the extent of ventral edge thickening (see Figure 2) did not reveal any congruence and is further supportive of a single-species hypothesis (personal observation, data not shown). We simply tested this to implement the little we know about the ecology of *L. ultima*, producing a few large eggs when exceeding a length of 2.4 mm, upon which the edge thickening initiates (Allen and Hannah 1989; Tyler et al. 1992). As the thickening increases the shell volume and space for eggs, it could have served as a proxy for reproductive activity and sexual maturation.

We suggest that the observed proteomic variation in *L. ultima* reflects environmentally driven shifts in protein expression at the intraspecific level, potentially caused by differences in particulate organic carbon (POC) flux to the abyssal seafloor. Specifically, we hypothesize that the first group (GUB, CVB, CB) experiences lower annual POC flux than the second group (WEB, NAB, BB, AB). Existing data support this hypothesis to some extent, albeit with significant gaps in our understanding. The CB is considered an oligotrophic environment, with estimated annual POC fluxes of less than 1 g C_{org} m^{-2} y^{-1} (Schmiedl et al. 1997; Watling et al. 2013). Similarly, nutrient availability in the central Atlantic near the CVB (18° N 21° W) has been described as low (Antia et al. 2001). However, seasonal blooms in the eastern equatorial Atlantic have been reported to enhance POC flux in this region (Lutz et al. 2007; Pérez et al. 2005). The north- (WEB, NAB) and south-west Atlantic (BB, AB) generally exhibit moderate to high POC fluxes (2–6 g C_{org} m^{-2} y^{-1}; Watling et al. 2013; Lampitt et al. 2023), suggesting a relatively productive abyssal environment that potentially supports higher metabolic activity and proteomic signatures distinct from the central and south-east Atlantic. While these observations suggest a link between POC flux and proteomic differentiation, it remains speculative due to the limited availability of direct measurements of POC flux and environmental conditions across these basins. Additional long-term, spatially resolved biogeochemical studies are necessary to validate this potential correlation. An integration of epigenetic analyses could further help to determine whether the observed proteomic shifts are driven by transient physiological responses or stable adaptive mechanisms.

4.3 | Mitochondrial Inheritance Patterns

The analysis of the COI marker identified five mitotypes without clear geographic or genetic correspondence. We interpret these patterns to result from sex-specific heteroplasmic mtDNA, which has repeatedly been shown to challenge assessments of genetic lineages and evolutionary inference across marine taxa (Chow et al. 2021; Shigenobu et al. 2005; Vollmer et al. 2011) and bivalves specifically (Capt et al. 2020; Ghiselli et al. 2021; Passamonti and Ghiselli 2009; Robicheau et al. 2017; Zouros and Rodakis 2019). We therefore propose that robust assessments of regional genetic structure based on mitochondrial data alone are only possible between specimens of the same mitotype, rather than across the highly divergent mitochondrial lineages. For the 16S marker in particular, only a single main haplotype was detected within each mitotype, highlighting the limited resolution of 16S for assessing regional differentiation in this species (Etter et al. 2005, 2011) and other metazoan taxa (Cho and Shank 2010; Miller et al. 2010; Neal et al. 2018; Thornhill et al. 2008).

Besides the presence of heteroplasmic mtDNA, many bivalves exhibit a peculiar mitochondrial inheritance system called doubly uniparental inheritance (DUI), which maintains two sex-specific mtDNA types within a single individual (for details, see Breton et al. 2007; Gusman et al. 2016; Guerra et al. 2017; Ghiselli et al. 2021; Smith et al. 2023). Under DUI, females transmit their mtDNA (F-type) to both sexes, while males pass theirs (M-type) to sons only (Passamonti and Ghiselli 2009; Smith et al. 2023). Thus, males are heteroplasmic for their mtDNA, with the M-type typically in gonads and the F-type in somatic tissue, although this ratio varies by species and tissue type (Garrido-Ramos et al. 1998; Machordom et al. 2015; Obata et al. 2006; Passamonti and Scali 2001; Sano et al. 2007). Overall, intraspecific divergence between F and M mtDNA may vary from 10% to over 50% (Breton et al. 2007; Capt et al. 2020; Passamonti and Ghiselli 2009; Robicheau et al. 2017; Zouros 2013), for example in the species *Mytilus edulis*, *M. trossulus*, and *M. californianus* (10%–20%; Zouros 2013), *M. modiolus* (37%–40%; Robicheau et al. 2017), and the freshwater mussel *Quadrula quadrula* (52%; Doucet-Beaupré et al. 2010). The prevalence of DUI further complicates the transmission of female and male mtDNA. Mitochondrial role-reversal, for instance, can lead to genome masculinization, where female mtDNA displaces the M-type and establishes itself as a new male lineage (for details, see Hoeh et al. 1997; Theologidis et al. 2008; Stewart et al. 2009; Sańko and Burzyński 2014; Gusman et al. 2016). Because such events can reset F- and M-type divergence to zero and enable new divergence patterns, the F- and M-types within males can show high divergence or be nearly identical (Hoeh et al. 1997; Quesada et al. 1999; Stewart et al. 2009; Theologidis et al. 2008; Zouros 2013). The rapid evolution of male mtDNA may reduce sequence similarity to standard mitochondrial primers, rendering it undetectable by PCR. In contrast, the slower-evolving F-type retains similarity to universal primers, increasing its amplification likelihood (Hoeh et al. 2002).

Collectively, DUI has been attested in at least seven bivalve families (Doucet-Beaupré et al. 2010; Gusman et al. 2016; Theologidis et al. 2008; Walker et al. 2006) and has been suggested as the likely source for previously evidenced mitochondrial heteroplasmy in *L. ultima* (Boyle and Etter 2013). Therein, mitochondrial heteroplasmy was attested by the use of specifically targeted mitochondrial fragments and cloning. From about half of their specimens, Boyle and Etter (2013) amplified both F- and M-types of mtDNA, showing up to 27% divergence, whereas the remaining individuals yielded only female mtDNA. This degree of divergence falls within the range observed in bivalves with DUI (e.g., Gusman et al. 2016; Robicheau et al. 2017), as well as the genetic intraspecific divergence of up to 30% observed in our data (Table 2). However, experimental validation of DUI in deep-sea protobranchs is presently impractical, as they are difficult to sustain under laboratory conditions and are likely to have long generation times (Boyle and Etter 2013; Turekian et al. 1975; Zardus 2002). Although likely that DUI is the source for mitochondrial heteroplasmy in *L. ultima*, the current state of knowledge on the genetic complexity in this species does not yet allow for final conclusions on the presence of DUI. Yet, we highlight this genetic complexity at the intraspecific level, as it can lead to overestimations of species diversity due to misinterpreted genetic distances in *L. ultima*, as seen in other taxa (Chow et al. 2021; Martínez et al. 2023; Wai Ho and Hanafiah 2024). When examined independently from SNP and proteomic data, the large genetic distances may suggest multiple lineages or cryptic species *of L. ultima*. However, this is misleading for several reasons. Our data indicate that the observed genetic divergence of up to 30% is owed to heteroplasmic mtDNA, since all sequences from the NAB, pre-defined to female and male mtDNA, clustered with MT 1 and MT 2, respectively (Table S1). Mitotype 1 likely reflects female mtDNA from either homoplasmic females or heteroplasmic males with a dominant F-type. Thus, MT 1 likely includes specimens of both sexes, whereof the female mtDNA was sequenced. A fraction of the M-type may have gone undetected by universal primers. However, this is unlikely as MT 2 clustered with pre-sequenced male mtDNA from the NAB. We suggest that the predominant M-type of specimens in MT 2 has likely been sequenced from mature individuals with higher fractions of gonadal tissue. Morphometric shell measurements of the 14 specimens from MT 2 revealed a shell length of 2.6–3.0 mm (data not shown), consistent with the minimum shell length of 2.4 mm for *L. ultima* to initiate gonadal development (Allen and Hannah 1989). The presence of MT 3 and the mitotypes 1a and 2a complicates interpretation. Since masculinized mtDNA could sequentially evolve into new M-types (Hoeh et al. 2002; Sańko and Burzyński 2014; Stewart et al. 2009), we propose these mitotypes to represent ongoing role-reversal or transitional states of the established F- and M-types. Specifically targeted sequencing and cloning aligned with the protocols in Boyle and Etter (2013) on sexed specimens are encouraged to test this hypothesis in future applications.

4.4 | Conclusions and Implications for Conservation

Facilitated by the decadal sampling hubs of the aforementioned international programs, the pan-Atlantic collection of *L. ultima* has enabled a multidisciplinary study of population connectivity at abyssal depths. While mitochondrial data suggested inflated genetic divergence due to heteroplasmic inheritance and potential DUI mechanisms, our nuclear SNP and proteomic analyses revealed overall low genetic divergence with support of a single species. Subtle yet significant population structure was identified, indicating two genetically connected but distinguishable source populations in the northern/central and southern Atlantic, with admixture zones in the BB and CB. This genetic structuring did not correlate with mitotype distribution, but rather reflected patterns consistent with gene flow driven by abyssal circulation and asymmetric gene flow mediated by the northward trajectory AABW. Furthermore, proteomic differentiation pointed to ecological divergence in protein expression, potentially linked to regional differences in POC flux. Our findings highlight the limitations of mitochondrial markers in the presence of complex inheritance systems and underscore the value of integrating nuclear genomic and proteomic tools to decipher population connectivity in abyssal species. In addition to this population genetic approach, these samples have facilitated the assessment of *L. ultima* as Least Concern on the IUCN Red List (de Wilt 2024), offering important information for the growing conservation efforts in deep-sea ecosystems (Sigwart et al. 2019, 2023). With prospective Atlantic deep-sea mining activities (Amorim et al. 2024; Dunn et al. 2018; Hein et al. 2013) and environmental impacts of climate change (Ramirez-Llodra et al. 2010; Samuelsen et al. 2022) posing imminent threats to deep-sea biodiversity, this study highlights the critical need for sustained long-term international monitoring to inform future conservation measures for deep-ocean ecosystems, where our understanding of evolutionary and ecological processes still remains in its infancy.

Author Contributions

Jenny Neuhaus: conceptualization (equal), data curation (lead), formal analysis (lead), investigation (lead), methodology (equal), project administration (lead), visualization (equal), writing – original draft (lead), writing – review and editing (lead). **Mark E. de Wilt:** data curation (equal), formal analysis (equal), investigation (equal), project administration (equal), software (supporting), validation (supporting), writing – review and editing (supporting). **Sven Rossel:** data curation (supporting), formal analysis (supporting), methodology (supporting), writing – review and editing (supporting). **Saskia Brix:** conceptualization (lead), funding acquisition (lead), project administration (supporting), resources (supporting), supervision (lead), writing – review and editing (supporting). **Ron J. Etter:** data curation (supporting), validation (supporting), writing – review and editing (supporting). **Robert M. Jennings:** data curation (supporting), resources (supporting), writing – review and editing (supporting). **Katrin Linse:** conceptualization (lead), resources (supporting), supervision (supporting), writing – review and editing (supporting). **Pedro Martínez Arbizu:** formal analysis (supporting), funding acquisition (lead), methodology (supporting), software (supporting), supervision (lead), writing – review and editing (supporting). **Martin Schwentner:** formal analysis (supporting), software (supporting), validation (supporting), writing – review and editing (supporting). **Janna Peters:** formal analysis (supporting), methodology (supporting), software (equal), validation (equal), visualization (supporting), writing – original draft (supporting), writing – review and editing (supporting).

Acknowledgments

This work was supported by the German Federal Ministry of Education and Research (BMBF) through grant no. GPF 21-2_052 as part of the IceDivA project (Förderkennzeichen 03G0286NA) and the German Research Foundation (DFG) initiative 1991 "Taxonomics" (grant no. RE2808/3-1/2). This is a contribution to the iAtlantic project, funded by EU/HORIZON 2020, Blue Growth (grant agreement no. 818123). K.L. is part of the British Antarctic Survey Polar Science for Planet Earth Programme funded by The Natural Environment Research Council (NERC) [NC-Science]. This research was made possible with assistance from Captains, crews, project leads, and students of the expeditions SO280, SO276, SO237, M79/1, EN477, M63/2, and PS67. This publication contributes to the Vema projects and is an ANDEEP publication #222. The technician team of the DZMB Hamburg, Karen Jeskulke, Antje Fischer, Nicole Gatzemeier, and Sven Hoffmann, was most helpful with sample assistance. Sahar Khodami and Angelina Eichsteller are thanked for their help with SNP sample processing. Nancy Kühne and Lars Harms from the Alfred Wegener Institute were most helpful with SNP sequence generation, providing the Illumina Next-Seq and laboratory services. This is publication #004-25 that includes molecular data generated with the support of the LIB—Center for Molecular Biodiversity Research's Molecular Laboratory, Hamburg, publication #104 that uses data from the Senckenberg am Meer Metabarcoding and SNG laboratory, and publication #22 of the Senckenberg am Meer Proteome Laboratory. Open Access funding enabled and organized by Projekt DEAL.

Disclosure

Benefit-Sharing Statement: A research collaboration was developed with international scientists providing genetic samples. All collaborators are included as co-authors. Benefits from this research accrue from the sharing of our data and results on public databases as described above.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Novel mitochondrial DNA sequences are deposited to the NCBI Nucleotide Database under accessions PQ179865–PQ179990 (COI) and PV131957–PV132063 (16S). Metadata, images, and raw sequence data are deposited to the Barcode Of Life Database (10.5883/DS-LEDUL). Raw sequence reads from 2b-RAD are deposited in the SRA (BioProject PRJNA1245090) under accessions SAMN47739826–SAMN47739903. Individual genotype data, proteomic data, and R scripts are available on DataDryad (10.5061/dryad.t1g1jwtdr).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** ece371903-sup-0001-FiguresS1.zip. **Table S1:** ece371903-sup-0002-TableS1.xlsx. **Table S2:** ece371903-sup-0002-TableS2.xlsx. **Table S3:** ece371903-sup-0004-TableS3.xlsx. **Appendix S1:** ece371903-sup-0005-AppendixS1.docx.

The Munnopsid Isopod Genus
Acanthocope Beddard, 1885

Biogeography of North Atlantic *Acanthocope* Beddard, 1885 (Isopoda: Munnopsidae)

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Keywords

Deep Sea, Asellota, Integrative Taxonomy, Proteomic Fingerprinting, New Species

Abstract

The munnopsid isopod genus *Acanthocope* Beddard, 1885 currently comprises 13 recognized species that are distributed in the Atlantic deep sea. While most species records remain restricted to single specimens from their respective type localities, five species have been reported with extensive geographic ranges spanning across the Mid-Atlantic Ridge. To examine the biogeography, morphological and molecular diversity of *Acanthocope* species in the abyssal North Atlantic, this study combines morphological taxonomy with molecular genetic analyses of mitochondrial (COI) and nuclear (18S) markers. To complement molecular species delimitation, a mass detection of peptide and low molecular weight protein molecules, proteomic fingerprinting, is applied. Morphological examinations of 224 specimens resulted in the identification of six species, *A. eleganta* Malyutina & Brandt, 2004, *A. galaica* Malyutina, Frutos & Brandt, 2018, *A. galatheae* Wolff, 1962, *A. muelleri* Malyutina, 1999, *A. unicornis* Menzies, 1962, *A. puertoricana* Malyutina, Frutos & Brandt, 2018, and an undescribed species designated as *Acanthocope* sp. A. Molecular species delimitation analyses and proteomic fingerprinting resulted in overall congruent clustering, supporting the delineation of *A. galatheae*, *A. muelleri*, *A. unicornis*, and *Acanthocope* sp. A. as separate lineages. Specimens morphologically identified as *A. eleganta*, *A. galaica*, and *A. puertoricana* consistently clustered as a single genetic lineage as well as proteomic group, raising questions about the current validity of species boundaries. This study substantially increases individual abundance records of species within the Northeast Atlantic, where the majority of species is found with sympatric distributions. Providing new species records and molecular data of Atlantic *Acanthocope*, this study bridges knowledge gaps in our current understanding of biogeography and genetic diversity within and among species of this natatory isopod genus.

Introduction

The munnopsid genus *Acanthocope* Beddard, 1885 currently comprises 18 recognized species that are distributed across our global oceans (Malyutina *et al.* 2018). Of these, the following 13 species have distributional records in the Atlantic Ocean: *A. annulatus* Menzies, 1962, *A. armata* Chardy, 1972, *A. argentinae* Menzies 1962, *A. beddardi* Malyutina, 1999, *A. carinata* Chardy, 1972, *A. eleganta* Malyutina & Brandt, 2004, *A. galaica* Malyutina, Frutos & Brandt, 2018, *A. galatheae* Wolff, 1962, *A. muelleri* Malyutina, 1999, *A. puertoricana* Maluytina, Frutos & Brandt, 2018, *A. spinicauda* Beddard, 1885, *A. spinosissima* Menzies, 1956, and *A. unicornis* Menzies, 1962. With the exception of *A. argentinae* and *A. beddardi*, whose records remain restricted to the Argentine Basin (Menzies 1962; Malyutina 1999; Malyutina *et al.* 2018), and the type species *A. spinicauda* which occurs in the South Atlantic (Beddard 1885; Brandt *et al.* 2007; Malyutina *et al.* 2018), all Atlantic species of *Acanthocope* occur within the North Atlantic boundary region (reviewed in Malyutina *et al.* 2018). Their distributional range spans from 55°52.05′N to 10°22.25′N in latitude and 67°09.73′W to 11°59.39′W in longitude, covering a total bathymetric range of 1243–5778 m. Thus far, most species records remain restricted to their respective type localities, from where single specimens were obtained and taxonomically described (Beddard 1885; Menzies 1956, 1962; Chardy 1972; Malyutina and Brandt 2004; Malyutina *et al.* 2018). This also applies to the two most recently described species *A. puertoricana* from the Puerto Rico Trench area and *A. galaica* from the Galaica Bank, latter of which has been suggested as a strict inhabitant of the upper bathyal seafloor (Malyutina *et al.* 2018). On the contrary, the species *A. annulatus*, *A. eleganta*, *A. galatheae*, *A. muelleri* and *A. unicornis*, are documented with wide biogeographic distributions, spanning from the North Atlantic to the Southern Ocean (Schmid *et al.* 2002; Malyutina and Brandt 2004; Brandt *et al.* 2007; Malyutina *et al.* 2018). Of all species of the genus *Acanthocope*, *A. galatheae* currently represents the most abundant and widespread species, with a biogeographic range covering the Atlantic, Southern and Pacific Oceans (Wolff 1962; Malyutina and Brandt 2004, 2015; Malyutina *et al.* 2018).

In common with all peracarid crustaceans, species of *Acanthocope* mate by internal fertilization and are obligate brooders (Johnson *et al.* 2001; Wilson 2009). Upon fertilization of the eggs and their embryonic development in the ventral brood pouch (marsupium) of the female, fully developed juvenile isopods (mancas) hatch and begin their post-marsupial life stage (Wilson 1991; Johnson *et al.* 2001). This reproductive strategy enables the mancas to immediately feed and invest resources in growth, while staying close to the natal site. Until the adult stage is reached, each molt facilitates the gradual development of morphological characters, especially within the posterior body segments. Like all munnopsid isopods, species of *Acanthocope* develop paddle-like posterior swimming legs (pereonites 5–7) that serve as a functional adaptation to an active swimming behavior (Wolff 1962; Hessler and Strömberg 1989; Osborn 2009). This increased adult locomotory ability has been found coherent with higher diversity, abundance and wider geographic distributions in selected munnopsid species, especially when compared to isopod taxa with less motile adult life strategies (Schnurr *et al.* 2014; Bober *et al.* 2018; Brix, Osborn, *et al.* 2020).

The North Atlantic deep sea currently hosts the highest diversity of *Acanthocope* species, several of which have been reported with sympatric distributions (Malyutina *et al.* 2018). The North Atlantic deep sea extends from its southern boundary at the Equator to the extensive Greenland-Iceland-Scotland Ridge (GISR) in the north, which topographically separates it from the deep Nordic (Greenland, Iceland, and Norwegian) Seas (Jöst *et al.* 2019). In this region, overflow waters that originated from the Arctic Ocean and the Nordic Seas enter the North Atlantic through the Denmark Strait in the west, or the Faroe Bank Channel in the east (Hansen and Østerhus 2000). From these formation areas, the water masses descend and undergo intense mixing processes to form the bulk of North Atlantic Deep Water (NADW), which constitutes the dominating composite water mass at 2000–4000 m depth in the entire Atlantic (Ferreira and Kerr 2017; Liu and Tanhua 2021). The western boundary of the North Atlantic is marked by the continental shelf of North, Central, and South America and includes the Gulf of Mexico and the Caribbean Sea. The western European and northwest African continental shelves mark the eastern boundary of the North Atlantic, a region characterized by high densities of troughs and seamounts that shape dynamic oceanographic patterns (Allcock *et al.* in press). In addition to the continental boundaries, the North Atlantic deep sea is intersected by the Mid-Atlantic-Ridge (MAR), known as the longest submarine mountain chain on Earth (Beaulieu *et al.* 2015). The northernmost section of the MAR, the Reykjanes Ridge, forms a geologically active spreading axis that gradually increases in depth as it descends from the Iceland Peninsula southwest towards the Bight Fracture Zone at 57°N and the Charlie-Gibbs Fracture Zone at 52–53°N (Le Saout *et al.* 2023). These fracture zones offset the ridge axis to the east, allowing for bottom water masses to cross the MAR from east to west. Another major deep-water passage is facilitated by the Vema Fracture Zone (VFZ) at 10–11°N, ventilating the abyssal basins of the Northeast Atlantic with oxygenated bottom water masses of Antarctic origin (Morozov *et al.* 2023).

Owing to its amphi-Atlantic distribution and high individual abundance, *A. galatheae* serves as an eligible species to study patterns of geographic distribution and genetic diversity (Osborn 2009; Bober *et al.* 2018). Specifically addressing the potential role of the MAR as a topographic barrier to gene flow between eastern and western populations in the VFZ, Bober *et al.* (2018) revealed high genetic connectivity in *A. galatheae*, suggesting the effective swimming ability to ensure passage across the MAR. For all remaining species, however, no molecular genetic sequencing has thus far been conducted to investigate molecular diversity and connectivity patterns within the Atlantic (Malyutina *et al.* 2018). By providing new distributional records and molecular data of *Acanthocope* species from abyssal depths of the North Atlantic, this study bridges knowledge gaps in our understanding of biogeographic patterns and genetic diversity within and among species of this natatory isopod genus. Herein, we employ an integrative taxonomic approach, combining morphological species identifications with molecular genetic sequencing and proteomic fingerprinting, which complements molecular analyses by a mass detection of peptide and low molecular weight protein molecules (Rossel *et al.* 2024). This study includes a new species to science designated as *Acanthocope* sp. A from the abyssal Northeast Atlantic. We emphasize the need for further coordinated sampling efforts in this region, despite it being one of the best-studied deep-sea regions at global scale.

Materials and Methods

Data collection

Specimens of *Acanthocope* examined in this study were collected in the North Atlantic deep sea aboard RV *Sonne* during the research expeditions IceAGE 3 (SO276, 22.06.–26.07.2020; Brix *et al.* 2020), IceDivA 1 (SO280, 08.01.–07.02.2021; Brix and Taylor 2021), and IceDivA 2 (SO286, 05.11.–09.12.2021; Brix *et al.* 2022), using an epibenthic sledge (EBS) equipped with two superimposed nets of 500 µm mesh size and 300 µm cod ends (Brenke 2005). Specimens were obtained at eight localities 1: Eriador Seamount South (ESS), 2: Porcupine Abyssal Plain (PAP), 3: Iberian Basin North (IB-N), 4: Canary Basin North (CB-N), 5: Madeira Abyssal Plain (MAP), 6: Josephine Bank (JB), 7: Charlie-Gibbs Fracture Zone (CGFZ), and 8: Oceanographer Fracture Zone (OFZ) (Table 1; Figure 1). On board, the material was fixed immediately in -20°C precooled 96% ethanol to avoid specimen degradation. In the laboratory of the German Centre for Marine Biodiversity Research (DZMB, Hamburg), the material was sorted and identified using a Leica MZ125 stereomicroscope and a Leica DM2500 compound microscope, both equipped with a *camera lucida*. Specimens were photographed using a Keyence VHX 7000 digital microscope prior to tissue extraction. Tissue samples for molecular and proteomic works were prepared concurrently using sterile utensils. For each specimen, tissue was dissected from the mid-section of the body (pereonites 4–6), including muscle tissue, but leaving the cephalothorax and pleon intact for morphological identification.

Table 1. Station data from localities where *Acanthocope* specimens were collected. Proximate stations are grouped into one locality.

Station	Depth (m)	Latitude	Longitude	Locality
IceAGE 3 (SO276, 2020)				
124	3656	53.45163	-26.46032	1: Eriador Seamount South (ESS)
134	4573	49.80752	-15.23093	2: Porcupine Abyssal Plain (PAP)
135	4577	49.80752	-15.23093	2: Porcupine Abyssal Plain (PAP)
IceDivA 1 (SO280, 2021)				
21-1	4802	41.95998	-18.98053	3: Iberian Basin North (IB-N)
28-1	4904	41.95923	-18.97947	3: Iberian Basin North (IB-N)
40-1	5484	36.03880	-18.99162	4: Canary Basin North (CB-N)
61-1	5121	32.03375	-22.01087	5: Madeira Abyssal Plain (MAP)
81-1	4165	36.47990	-13.99118	6: Josephine Bank (JB)
85-1	4155	36.48005	-13.99362	6: Josephine Bank (JB)
IceDivA 2 (SO286, 2021)				
46-1	3677	51.96000	-38.98958	7: Charlie-Gibbs Fracture Zone (CGFZ)
64-1	3180	36.99047	-35.48627	8: Oceanographer Fracture Zone (OFZ)

DNA extraction, amplification and sequencing

DNA was extracted using the Macherey-Nagel NucleoSpin Tissue Kit following the manufacturer's manual (Macherey-Nagel, Düren, Germany) and leaving the tissue for digestion overnight in a shaking bath at 56°C/300 rpm. For all samples, elution was carried out in two steps, using each 50 µl pre-heated 70°C elution buffer to yield a total of 100 µl DNA isolate. The mitochondrial marker cytochrome *c* oxidase subunit I (COI) and the complete region of nuclear 18S ribosomal DNA (18S) were selected for molecular species delimitation (Table 2). For COI, a total of three primer pairs were employed. Polymerase chain reactions (PCRs) for the COI/18S markers were carried out using 10/25 µl AccuStart II Taq PCR SuperMix (Quantabio, Beverly, MA, USA), each 0.5/1.25 µl of forward and reverse primer (10 µmol), 7/17.5 µl MilliQ filtered water, and 2/5 µl of DNA isolate to yield a total reaction volume of 20/50 µl. Samples that did not readily yield successful PCRs were run with increased volumes of DNA template, reducing the respective volume of water. Thermal cycling conditions for COI were as follows; initial denaturation: 95°C, 5 min; denaturation: 95°C, 45 s; annealing: 45°C, 50 s; elongation (38 cycles): 72°C, 1 min; final elongation: 72°C, 5 min; cooling to 10°C. For 18S, a touch-down program was used; initial denaturation: 94°C, 5 min; denaturation: 94°C, 30 s; annealing: 62.5°C with a stepwise decrease of 1°C/cycle during the first ten cycles, followed by 52.5°C; elongation (36 cycles): 72°C 2.5 min; final elongation: 72°C, 10 min; cooling to 10°C. Quality of amplified product was assessed by gel electrophoresis using 1% agarose gels in Tris-acetate-EDTA buffer, along with semi-quantitative control. Successful PCR products were purified using ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fisher Scientific™) and run on a thermal cycler (incubation: 37 °C, 15 min; enzyme inactivation: 80 °C, 15 min). Double stranded sequencing was carried out by the sequencing facilities Macrogen Europe Inc. (Amsterdam, Zuidoost, The Netherlands) and Eurofins Genomics GermanyGmbH (Ebersberg, Germany) using ABI 3730xl sequencers. Remaining DNA aliquots are stored at -80°C at the DZMB Hamburg, Germany.

Table 2. List of mitochondrial and nuclear primers.

Primer	Sequence (5' to 3')	Reference
COI		
LCO1490	GGT CAA CAA ATC ATA AAG ATA TTG G	Folmer *et al.* 1994
HCO2198	TAA ACT TCA GGG TGA CCA AAA ATC A	
jgLCO1490	TIT CIA CIA AYC AYA ARG AYA TTG G	Geller *et al.* 2013
jgHCO2198	TAI ACY TCI GGR TGI CCR AAR AAY CA	
LCO1490-JJ	CHA CWA AYC ATA AAG ATA TYG G	Astrin & Stüben (2008)
HCO2198-JJ	AWA CTT CVG GRT GVC CAA ARA ATC A	
18S		
18A1mod	CTG GTT GAT CCT GCC AGT CAT ATG C	Raupach *et al.* 2009
400F	ACG GGT AAC GGG GAA TCA GGG	Dreyer & Wägele (2001)
700F	GTC TGG TGC CAG CCG CG	
1000F	CGA TCA GAT ACC GCC CTA GTT C	
700R	CGC GGC TGC TGG CAC CAG CAC	
1155R	CCG TCA ATT CCT TTA AGT TTC AG	
1500R	CAT CTA CGG CAT CAC AGA	
1800mod	GAT CCT TCC GCA GGT TCA CCT ACG	Raupach *et al.* 2009

Sequence editing, alignment and analysis

Geneious Prime® (version 2025.0.2; Biomatters, Auckland, New Zealand; Kearse *et al.* 2012) was used to edit and assemble forward and reverse chromatograms as well as to check for potential contamination using the implemented NCBI BLAST search tool (Basic Local Alignment Search Tool; Altschul *et al.* 1990). COI sequences of each sample were assembled individually using the *de novo* assembly feature of Geneious Prime®, while 18S contigs were generated by mapping reads to a reference sequence of *A. galatheae* (AF496656; Raupach *et al.* 2009). Assembled sequences were aligned using MAFFT (version 7.490; Katoh and Standley 2013) implemented in Geneious Prime® using default settings. To rule out hypervariable regions on the 18S sequences, Gblocks (version 0.91b; Castresana 2000; Talavera and Castresana 2007) was applied. Best-fit models of evolution were estimated using the Akaike Information Criterion (AIC; Sakamoto *et al.* 1986) and Bayesian Information Criterion (BIC; Schwarz 1978) implemented in IQ-TREE (version 2.3.6; Minh *et al.* 2020). The selected substitution models were HKY+I+I for COI and TNe+I+G4 for 18S. Clustering analyses of single-gene and concatenated alignments were performed using MrBayes (version 3.2.7a; Altekar *et al.* 2004; Ronquist *et al.* 2012), with four parallel runs of 5 million generations, sampling every 1000 generations, and setting the substitution model to the most similar implementation in MrBayes of those selected by AIC and BIC (HKY+I). A partition scheme based on codon position was set for COI alignment and for concatenated alignment, while the region of trimmed 18S alignment was additionally defined for the latter in order to divide the loci. Convergence of independent runs was examined in Tracer (version 1.7.2; Rambaut *et al.* 2018) with a burn-in of 10%. Trees were reconstructed using Bayesian Inference (BI), assessing branch support by posterior probability (PP) with values ≥ 0.95 considered as high support (Felsenstein 1985; Huelsenbeck *et al.* 2001). Tree visualization and rooting was performed in R using the packages *ggtree*, *ape*, and *treeio* (Yu *et al.* 2017; Paradis and Schliep 2019; Wang *et al.* 2020; R Core Team 2025). Molecular species delimitation was complemented using the distance-based automatic barcode gap discovery (ABGD; Puillandre *et al.* 2012) with uncorrected *p*-distance and setting the barcode gap discovery settings as default. Only the subset of the alignment which clustered as *Acanthocope* was included for ABGD analysis. In addition, the tree-based method Generalized Mixed Yule Coalescent (GMYC; Fujisawa and Barraclough 2013) was applied. Ultrametric trees of single-gene and concatenated alignments were generated using BEAST 2 (version 2.7.7; Bouckaert *et al.* 2019), setting a strict clock HK2 gamma site model and Yule model in BEAUti (Drummond and Rambaut 2007). TreeAnnotator (version 2.7.7; Drummond and Rambaut 2007) was used to calculate the maximum clade credibility tree by setting the node height as mean height and discarding the first 25% of all trees as burn-in. Single threshold GMYC was subsequently performed in R using the package *splits* (Ezard *et al.* 2021). Parsimony-based haplotype networks (TCS) of COI sequences (n = 82) were inferred and visualized using the R packages *pegas* (Paradis 2010) and *geneHapR* (Zhang *et al.* 2023). Additional COI sequences of Atlantic (n = 33) and Pacific (n = 10) *A. galatheae* that were included are listed in Table S1.

Proteomic fingerprinting

Matrix-Assisted Laser Desorption/Ionization Time-of-Flight Mass Spectrometry (MALDI-TOF MS) was performed to obtain proteomic mass spectra, following the laboratory practices and data analysis described in Kürzel *et al.* (2022) and Rossel *et al.* (2024). Raw spectral data from MALDI-TOF MS analyses were processed and analyzed using R with the following packages: MALDIquant, MALDIquantForeign, MALDIrppa, splus2R, vegan, and tidyverse (Gibb and Strimmer 2012; Palarea-Albaladejo *et al.* 2018; Oksanen *et al.* 2019; Wickham *et al.* 2019; Burns 2020; Gibb 2022). Noise reduction was applied by setting the signal-to-noise ratio (SNR) to eight. The peak alignment matrix was further trimmed by removing binned peak columns where less than 20 peaks were present throughout the samples. The matrix was subsequently Hellinger transformed (Legendre and Gallagher 2001). A principle component analysis (PCA) was applied and visualized in a 2-dimensional t-distributed stochastic neighbor embedding (t-SNE) plot using the package *Rtsne* (van der Maaten and Hinton 2008; van der Maaten 2014). The final visualization was done by setting the perplexity value to ten, but a series of plots using various perplexity values ranging from five to 30 were constructed, to ensure the local and global variations are balanced with the final hyperparameter (Skrodzki *et al.* 2024). Presented clusters were validated by applying density-based cluster detection algorithm DBSCAN and setting the radius of the ϵ-neighborhood using the package *dbscan* (Hahsler *et al.* 2019). Identified clusters were interpreted and discussed by focusing on the morphotype and genetic lineage composition of each cluster. The Hellinger transformed data were also used to construct a hierarchical clustering.

Results

Species diversity and abundance

A total of 224 *Acanthocope* specimens were recovered from eight sampling localities spanning 3180–5484 m in depth (Figure 1; Table 3). A total of 200 specimens were identified to species level and resulted in six currently recognized species with the following abundances: *A. galatheae* (*n* = 101), *A. unicornis* (*n* = 68), *A. muelleri* (*n* = 17), *A. galaica* (*n* = 6), *A. puertoricana* (*n* = 5), and *A. eleganta* (*n* = 3). In addition, a novel species designated as *Acanthocope* sp. A (*n* = 4) was identified. Remaining specimens (*n* = 20) were labeled as *Acanthocope* sp. because of inferior quality to ensure correct species identification by morphology (Table 3). The localities IB-N and JB yielded the highest diversity of species and individual abundances of 98 and 93 specimens, respectively. At both localities, each species was represented by at least one specimen, except for the absence of *A. eleganta* from the JB. At the JB, the species *A. unicornis* (*n* = 67) and *A. galatheae* (*n* = 14) were most abundant. At the IB-N, *A. galatheae* (*n* = 64) and *A. muelleri* (*n* = 15) were the most abundant species, followed by *A. puertoricana* (*n* = 4). The EES and the CGFZ each yielded a single specimen of *A. galaica*. Together with a single record of *A. galatheae* from the OFZ, the ESS, CGFZ, and OFZ represent the least speciose localities within our sampled range (Table 3). These results, accompanied by an absence of *Acanthocope* species from stations situated north of the studied area (Brix *et al.* 2020), reveal a spatial aggregation of species in the abyssal Northeast Atlantic (Figure 1). Across the sampled range, our data substantially increases individual abundance records of the herein identified species within the North Atlantic boundary region (see Appendix A in Malyutina *et al.* 2018). While we confirm previous records of high individual abundances of *A. galatheae* (Brandt *et al.* 2005; Brix *et al.* 2015; Bober *et al.* 2018; Malyutina *et al.* 2018), *A. unicornis* and *A. muelleri* now account for the second and third most abundant Atlantic species, respectively (Menzies 1962; Malyutina 1999; Malyutina *et al.* 2018). Still represented by relatively few specimens, however, our results highlight the perpetual challenge of obtaining specimens from the abyssal deep sea, where each EBS haul is restricted to a very local area compared to the vastness of the soft-sedimented abyssal environment.

Biogeography of North Atlantic *Acanthocope*

For each of the six species of *Acanthocope* reported from the North Atlantic boundary region studied herein, distributional records now extend to 41°57′N 18°58′W at the locality IB-N (Figure 1; Table 3). Notably, the localities IB-N and JB house a particularly species-rich fauna of *Acanthocope*, where five and six species have overlapping geographic and bathymetric distributions, respectively. Together, these localities account for 85% of all sampled specimens within the entire studied region. For *A. eleganta* and *Acanthocope* sp. A, the PAP now represents the northernmost locality. *A. galaica*, previously only known from the Galaica Bank at 42°N, is now recognized from the JB and the ESS at 53°N east of the MAR, as well as from the CGFZ west of the MAR. The species *A. puertoricana*, described from the Puerto Rico Trench west of the MAR, was herein found at the JB situated east of the MAR. These records extend the biogeographic range of *A. galaica* and *A. puertoricana* across the MAR, a distributional range previously recognized for *A. eleganta*, *A. galatheae*, *A. muelleri*, and *A. unicornis.* By presenting new and supplemental distributional records on both sides of the MAR for the respective species, we emphasize their potential to cover wide geographic distances across topographic barriers. Compared to previously reported depth ranges within the North Atlantic (Malyutina *et al.* 2018), the bathymetric range for *A. eleganta*, *A. galaica*, *A. muelleri*, *A. puertoricana*, and *A. unicornis* increased by at least 250 m and up to 780 m in depth (Table 3; see also Malyutina *et al.* 2018, Appendix A). For *A. galaica*, an exceptional depth difference of 3076 m was found between previous records and our data, extending the species' bathymetric range from the bathyal Galicia Bank (1669–1726 m) to the abyssal seafloor of the IB-N (4802 m). Hence, this study presents the first abyssal depth record for *A. galaica.*

Table 3. Species diversity and specimen abundance per sampling locality.

Locality	**Depth (m)**	*A. galatheae*	*A. unicornis*	*A. muelleri*	*A. galaica*	*A. puertoricana*	*A. eleganta*	***Acanthocope* sp. A**	***Acanthocope* sp.**	***n* specimens per locality**
1: ESS	3656				1					1
2: PAP	4577				2		1	1	1	5
3: IB-N	4904	64	1	15	1	4	2		11	98
4: CB-N	5484	13								13
5: MAP	5121	9		1					2	12
6: JB	4165	14	67	1	1	1		3	6	93
7: CGFZ	3677				1					1
8: OFZ	3180	1								1
***n* specimens per species**		101	68	17	6	5	3	4	20	

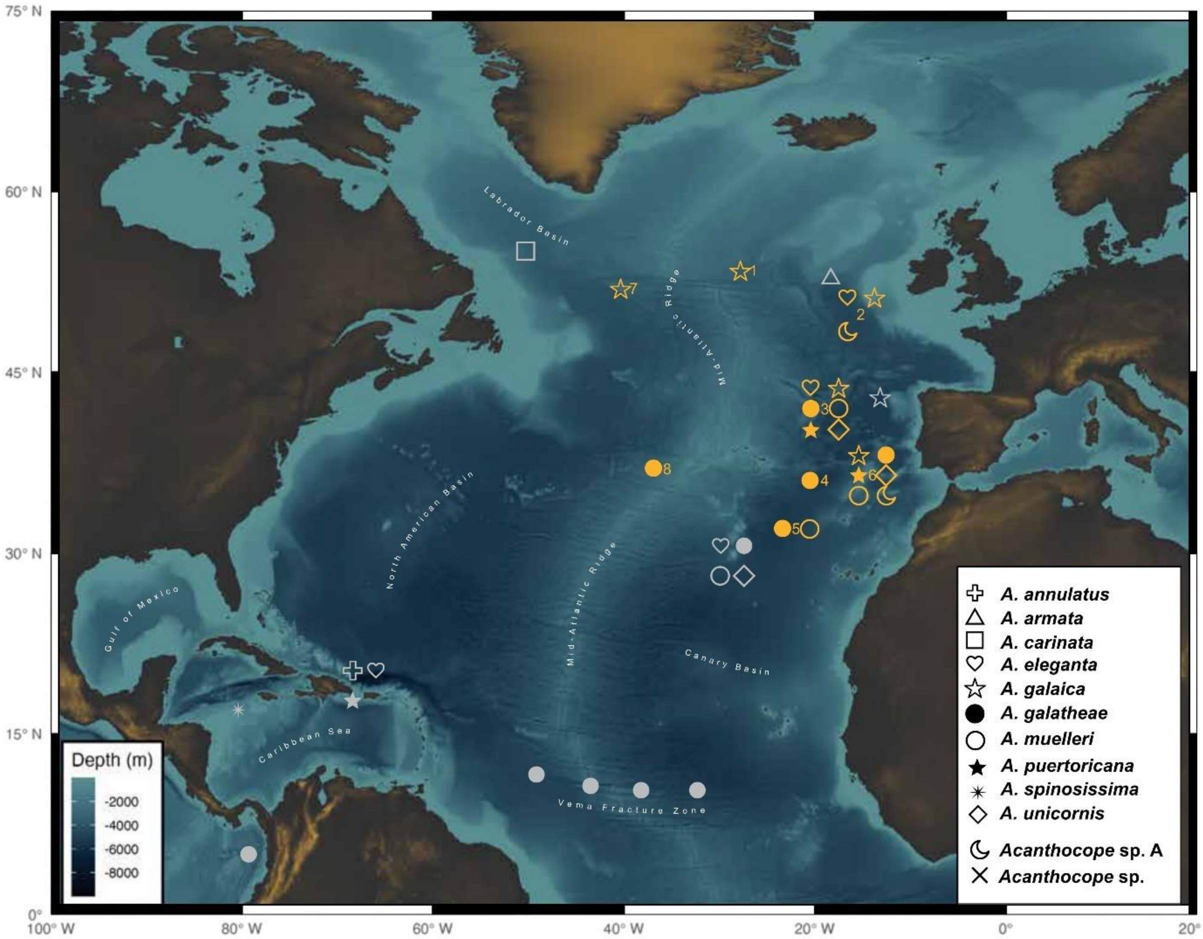

Figure 1. Distributional records of North Atlantic *Acanthocope*. Records obtained in this study are colored; 1: Eriador Seamount South (ESS), 2: Porcupine Abyssal Plain (PAP), 3: Iberian Basin North (IB-N), 4: Canary Basin North (CB-N), 5: Madeira Abyssal Plain (MAP), 6: Josephine Bank (JB), 7: Charlie-Gibbs Fracture Zone (CGFZ), 8: Oceanographer Fracture Zone (OFZ). Previous records are included as presented by Malyutina *et al.* (2018).

Molecular species delimitation

DNA was successfully amplified for 82 specimens of *Acanthocope*, yielding a total of 90 novel molecular sequences for both markers (COI: 82 sequences, 695 bp; complete 18S: 8 sequences, 2309 bp). Sequencing of the 18S marker was limited to one sequence for each morphologically identified species. 18S sequences were included both to complement the COI species delimitation and supplement the NCBI depository of 18S sequences for future comparative analyses of munnopsid isopods. Attempts on DNA extraction and sequencing of collection material of *A. annulatus*, *A. eleganta*, and *A. puertoricana* were unsuccessful. Bayesian molecular species delimitation for both markers yielded results overall congruent with morphological species identifications, including *Acanthocope* sp. A. Both single-gene alignments of COI

(Figure S1) and 18S (Figure S2), as well as the concatenated alignment (Figure 2), resulted in a monophyletic group of *Acanthocope*, separated from the closest related subfamily Storthyngurinae Kussakin, 2003 (Osborn 2009) with full support (PP = 1). The distance-based ABGD and tree-based GMYC species delimitation methods yielded supportive results of the Bayesian analysis. Within clade I, specimens of *A. eleganta*, *A. galaica*, and *A. puertoricana* consistently clustered together, supported by both ABGD and GMYC, deviating from the morphological species identifications. Remaining species of *Acanthocope* clustered as distinct genetic lineages. Specimens that were morphologically identified as *Acanthocope* sp. were molecularly delimited as *A. eleganta* (n = 1), *A. galatheae* (n = 9), and *A. unicornis* (n = 1). Both species delimitation methods supported the clustering of Atlantic *A. galatheae* apart from the Pacific *A. galatheae* (Table S1). Both species delimitation methods identified *Acanthocope* sp. MB H2, sampled from the Monterey Bay area in the eastern Pacific (Osborn 2009), and *Acanthocope* sp. MR-2008 from the eastern Weddell Sea (Raupach *et al.* 2009) as distinct genetic lineages. Future morphological examinations of these specimens to species level are highly encouraged.

Haplotype network analysis

To visualize genetic relationships among individual COI sequences of *Acanthocope* species from the North Atlantic, a parsimony haplotype network was inferred (Figure 3A), including one specimen from the eastern Pacific currently unresolved to species level (*Acanthocope* sp. MB H2; Osborn 2009). The haplotype network reveals species in overall well-separated clusters, with a small number of shared haplotypes between morphologically identified species, of which the majority is represented by single haplotypes. Sequences obtained from the morphotypes of *A. eleganta*, *A. galaica*, and *A. puertoricana* cluster closely together, differing by 90 mutational steps from the cluster of *A. unicornis*. The haplotypes of the undescribed species *Acanthocope* sp. A are distinct from all other Atlantic species, differing by 93 mutational steps. The species *A. muelleri* is solely resolved by single haplotypes, with a high number of nucleotide differences (85) to a morphotype of *A. puertoricana*. The star-shaped pattern is indicative of recent population expansion, most notably in *A. galatheae* and *A. unicornis*.
To visualize genetic relationships among individual COI sequences of the widely distributed species *Acanthocope galatheae*, a species-specific parsimony haplotype network was inferred (Figure 3B). In addition to sequences herein obtained from specimens of the Northeast Atlantic, additional COI sequence data from the VFZ (Bober *et al.* 2018) and the Clarion-Clipperton Zone (CCZ) in the eastern Pacific (Brix, *et al.* 2020) were included (Table S1). Specimens from the CCZ separate from the Atlantic *A. galatheae* by 27 mutational steps, forming a separate cluster of single haplotypes. Among the Atlantic specimens, three main

haplotypes with shared sequences between the VFZ and the northeast Atlantic were resolved, suggestive of pronounced gene flow between populations of *A. galatheae* across the MAR.

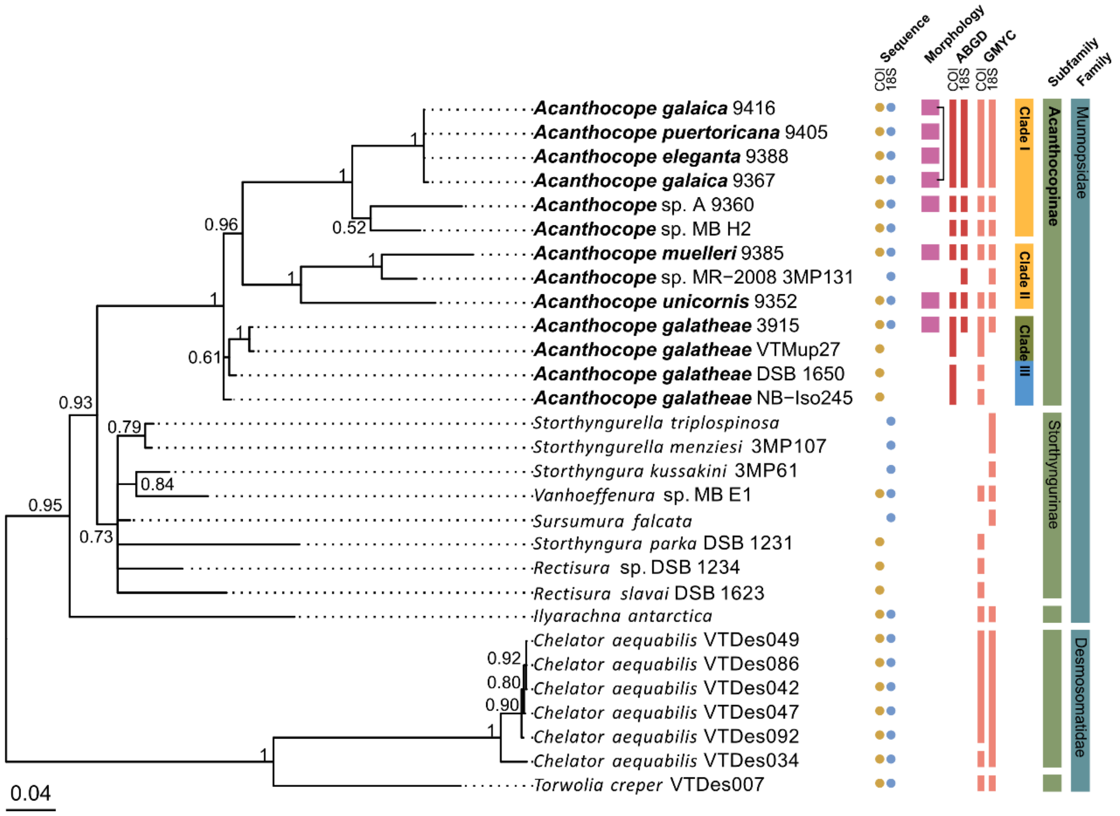

Figure 2. Bayesian molecular species delimitation of *Acanthocope* inferred from the concatenated (COI, 18S) sequence alignment. Desmosomatidae species are used as outgroups and *Ilyarachna antarctica* is used to polarise Storthyngurinae and Acanthocopinae. Node labels show posterior probability values. Colored bar tiles show species delimitation results of morphological identification, ABGD, and GMYC for each gene, indicated by colored circles (COI: green; 18S: blue).

Proteomic fingerprinting

In total, 92 specimens were used in the MALDI-TOF MS analysis. Their clustering based on relative proteomic composition was referenced both to morphological species identifications, *i.e.*, morphotypes (Figure 4A), and molecular species delimitations (Figure 4B). A total of nine clusters were consistently resolved for both reference data sets, yielding overall congruent results. This particularly applies to the undescribed species *Acanthocope* sp. A, which was coherently identified as a single cluster (4). For most abundant species *A. galatheae*, one large cluster (1) and two smaller clusters (2, 9) were identified, grouped with the majority of specimens not resolved at species level. The species *A. unicornis* was resolved in one large cluster (3), as well as two smaller clusters (5, 7), again grouped with single specimens of *Acanthocope* sp. as well as one morphotype of *A. puertoricana* (cluster 5). Congruent with the molecular species delimitation, proteomic fingerprinting resulted in a single cluster of the morphotypes *A. eleganta*, *A. galaica*, and *A. puertoricana* (illustrated by heart shapes in Figure 4B). The morphotype *A. muelleri* showed moderately inconsistent clustering.

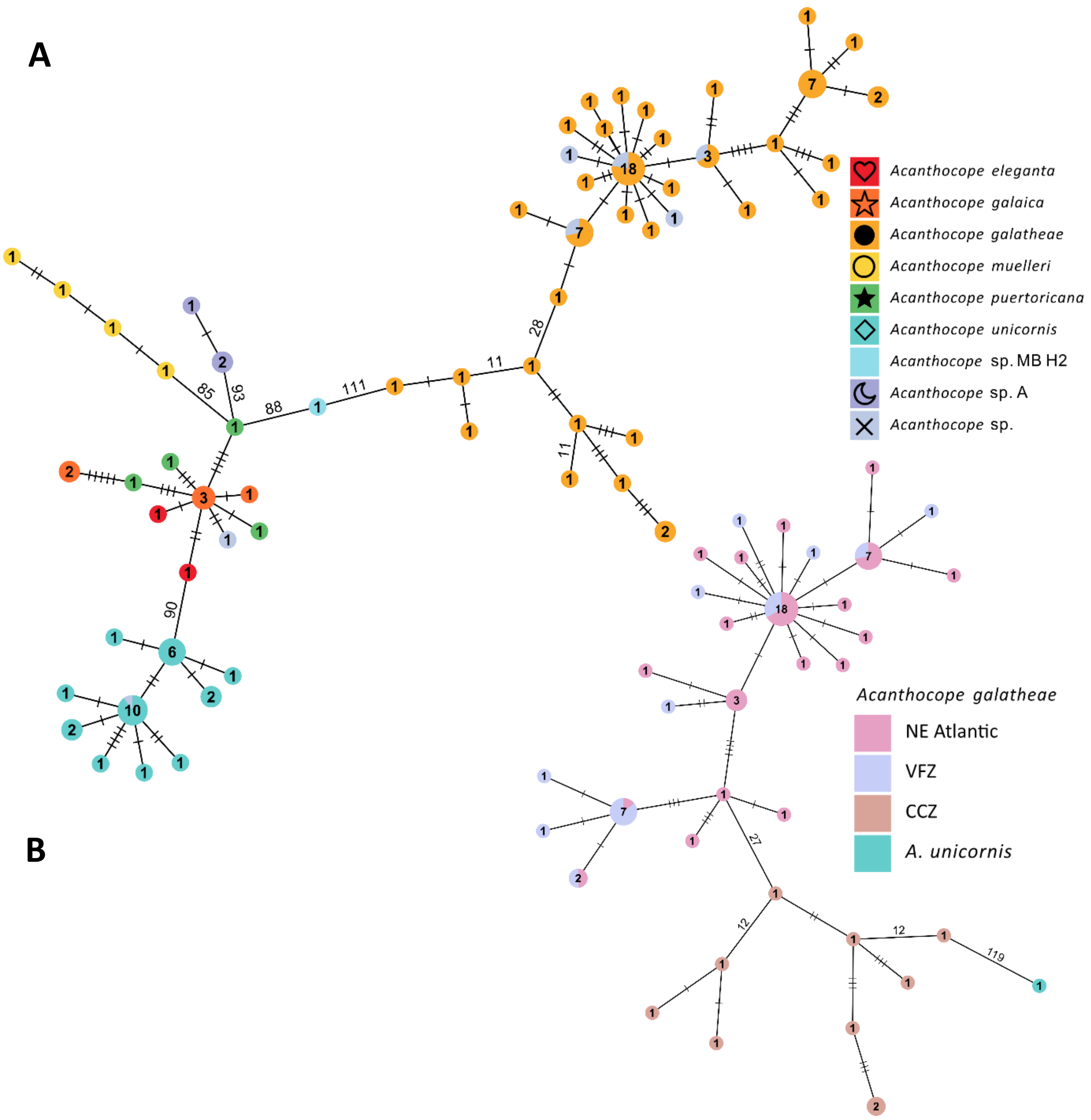

Figure 3. Parsimony haplotype networks inferred from COI sequence data. **A** Genetic relationship between *Acanthocope* species from the abyssal North Atlantic, coded by color. **B** Intraspecific genetic relationship between Atlantic and Pacific *A. galatheae*, rooted with an Atlantic specimen of *A. unicornis*. Hash marks indicate number of nucleotide substitutions. Numbers within circles correspond to number of specimens sharing a haplotype.

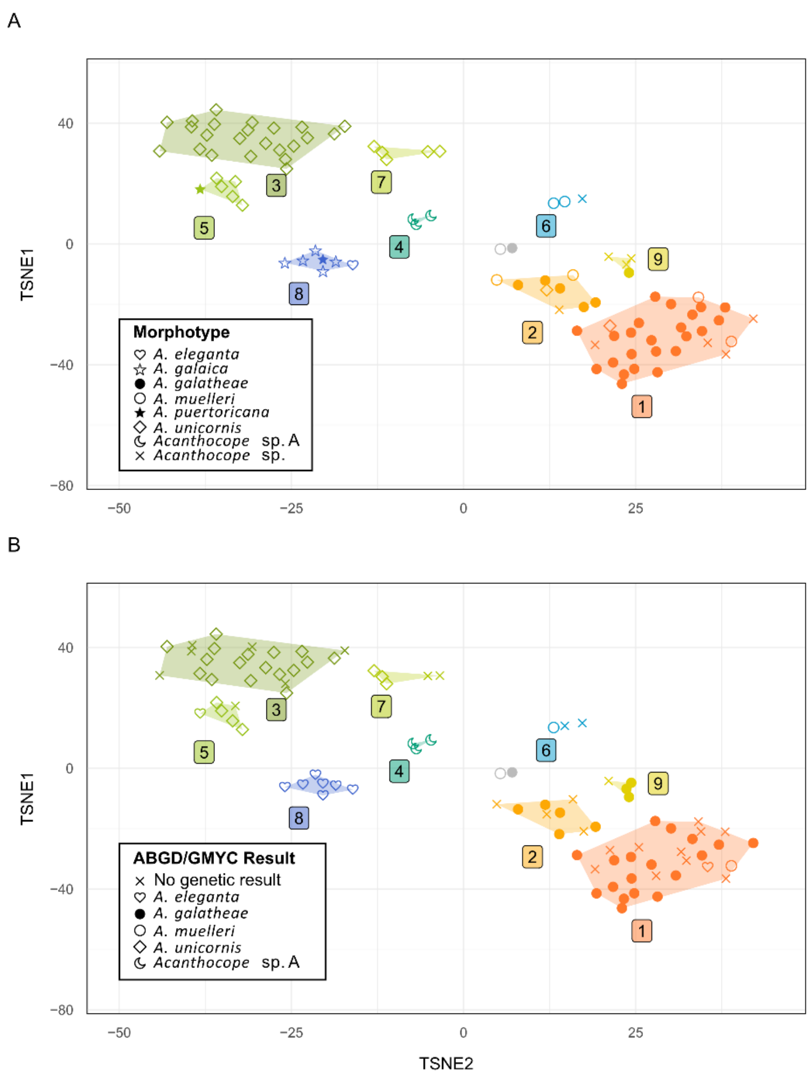

Figure 4. Clustering results of proteomic fingerprint analysis visualized by t-SNE plots. **A** Clustering results with specimens referenced to morphological species identifications (morphotypes). **B** Clustering results with specimens referenced to molecular species delimitations. The species *A. eleganta*, *A. galaica* and *A. puertoricana* are uniformly illustrated as heart shapes.

Discussion

Taxonomic ambiguities and sympatric distributions

The wide geographic distribution and high abundance of *A. galatheae* within the Atlantic as well as across multiple oceans has been acknowledged in several studies (Malyutina 1999; Bober *et al.* 2018; Malyutina *et al.* 2018; Brix *et al.* 2020). In the Atlantic, several species of *Acanthocope* depict wide geographic distributions, sampled thousands of kilometers away from their type localities. For example, an addition male specimen of *A. annulatus*, first described from one female specimen from the southwest Atlantic (Menzies 1962), was found at 4552 m depth in the Puerto Rico Trench (Malyutina *et al.* 2018), having an overlapping distribution with the therein described species *A. puertoricana*, as well as *A. eleganta*. It is worth mentioning that (Menzies 1962) identified the holotype of *A. annulatus* as being of female sex, despite him documenting the presence of over 20 articles on antenna 1. Because the presence of numerous articles in antenna 1 is a generic male characteristic, and *A. annulatus* differs from *A. argentinae* solely in the shape of the frontal margin of the cephalon, Malyutina (1999) suggested that the female holotype of *A. annulatus* may, in fact, represent a male specimen of *A. argentinae*. Additional specimen collection from the South Atlantic is urgently needed to clarify this taxonomic ambiguity.

In the present study, specimens morphologically identified as *A. eleganta*, *A. galaica*, and *A. puertoricana* consistently formed a single genetic lineage and proteomic cluster. This raises concerns about the current delineation of species boundaries. The unresolved taxonomy of *A. annulatus*, particularly given its sympatric distribution with *A. eleganta* and *A. puertoricana*, amplifies the difficulty of taxonomic assessment.

Ecological niche partitioning

While very little is known about the ecology of *Acanthocope*, yet their sympatric distributions are suggestive of strong ecological niche differentiation. The sympatric distributions reported herein from the Iberian Basin and Josephine Bank, including *A. galatheae*, *A. muelleri*, and *A. unicornis* along with the species *A. eleganta*, *A. galaica*, and/or *A. puertoricana*, align with observations made at the Meteor Seamount (Malyutina *et al.* 2018). Preference in their diet could be an important component forming such overlapping distributions, linked to the local diversity of available food (*e.g.,* Brandt *et al.* 2004). Foraminiferans have been shown to be an essential part of the diet in deep-sea isopods and were also found in the gut content of *A. galatheae*, although not exclusively (Gudmundsson *et al.* 2000; Brökeland and Guðmundsson 2010). Many detritus-feeding organisms at the seafloor of the North Atlantic were shown to respond to phytodetrital aggregation rapidly, including both foraminiferan and macrobenthic species (Lochte and Turley 1988; Sun *et al.* 2006; de Jonge *et al.* 2024). Shifts in the trophic regime, coupled with surface production and the resulting food availability, may provide differentiated nutritional niches to allow the co-occurrence of multiple *Acanthocope* species at one locality (Rex *et al.* 1997).

Hidden diversity of Atlantic *Acanthocope*?

While the north Atlantic in general is one of the best-studied deep sea regions (Allcock *et al.* in press; Bridges *et al.* 2023), species of Acanthocope are seemingly absent from the western Atlantic (Malyutina *et al.* 2018). Similar to eastern abyssal basins, the North American Basin is an extensively studied deep sea area, with numerous expeditions carried out by European and American institutions (*e.g.,* Allcock *et al.* in press; Allen and Hannah 1989; Etter *et al.* 2011). Yet thus far, *A. carinata* represents the only boreal species of Acanthocope described from the northwest Atlantic, limited to a single record of a female specimen from the Labrador Basin (55°52.5'N 49°53.4'W) sampled at 3465 m depth. Despite extensive benthic sampling efforts in the Labrador Sea during the IceDivA 2 expedition (Brix *et al.* 2022), no additional specimens of Acanthocope were retrieved. This absence may reflect either a true scarcity of *Acanthocope* in boreal regions or simply incomplete taxonomic processing of the regional samples. For example, Wilson (2008) reported 20 specimens of *Acanthocope* sp. from the Gulf of Mexico, representing the first record of the genus in this region. However, the utility of this record remains limited, as no species-level identification was provided. Moreover, a substantial portion of isopod material in the collections of for instance the Smithsonian National Museum of Natural History and the Louis Agassiz Museum of Comparative Zoology has been identified only to higher taxonomic ranks (*e.g.,* Isopoda or Asellota; information based on inquiries to the collection managers). These holdings may contain additional, yet unrecognized, records of *Acanthocope* from Atlantic localities. Dedicated taxonomic effort and international collaboration is needed to close these taxonomic gaps, having the potential to reveal several specimen records of *Acanthocope* from the North *Atlantic* region.

We highly encourage future works on *Acanthocope* to focus on filling knowledge gaps with regard of species distributions and genetic diversity by sampling different areas, while keeping an integrative approach to link knowledge across disciplines. The taxonomic assessment of *Acanthocope* would greatly benefit from a thorough review of several species, using an integrative approach as applied herein.

Remarks

This version of the manuscript is currently under preparation for publication and will be subject to changes in content and wording.

Acknowledgements

This work was supported by the German Federal Ministry of Education and Research (BMBF) through grant no. GPF 21-2_052 as part of the IceDivA project (Förderkennzeichen 03G0286NA) and the German Science Foundation (IceAGE 3: grant MerMet17-06). This research was made possible with assistance from captains, crews, project leads and students of the expeditions SO276, SO280, and SO286. The technician team of the DZMB Hamburg, Karen Jeskulke, Antje Fischer, Nicole Gatzemeier and Sven Hoffmann, was most helpful with sample assistance. This is publication #005-25 that includes molecular data generated with the support of the LIB – Center for Molecular Biodiversity Research's Molecular Laboratory, Hamburg, and publication #24 of the Senckenberg am Meer Proteomics Laboratory.

Data availability statement

Specimen metadata, images, and sequence data will be deposited to the Barcode Of Life Database (BOLD) in the dataset called ACTCP. All scripts and associated data will be made publicly available on github. Species delimitation results and matrices will be deposited in the public database TreeBASE.

Author contributions

JN had the lead in project administration and was assisted by ZH in data curation, following the initial study design of SB. JN and ZH conducted morphological species identifications, aided by the taxonomic expertise of EP and SB. JN and ZH equally contributed to the generation and analyses of molecular sequences. Proteomic fingerprinting and subsequent data analyses were conducted by ZH and SR, assisted by JN. JN and ZH were in lead of data visualization, assisted by SB and EP. JN and ZH were in lead for authoring the original manuscript draft. ZH is coordinating the peer-review process as corresponding author.

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Taxonomic Research

The Dentaliid Scaphopod

Fissidentalium aurae Linse & Neuhaus, 2024

Marine Biodiversity (2024) 54:88 https://doi.org/10.1007/s12526-024-01481-1

ORIGINAL PAPER

SENCKENBERG

Springer

A new species of *Fissidentalium* (Scaphopoda: Dentaliidae) in association with an actinostolid anemone from the abyssal Labrador Sea

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Received: 19 April 2024 / Revised: 5 September 2024 / Accepted: 1 October 2024

Abstract

The benthic biodiversity of the abyssal Labrador Sea was investigated using Agassiz trawl and in situ imagery. A megafaunal scaphopod associated with an epizoic anemone was recovered from soft sediments. Morphological and molecular investigations revealed the scaphopod to be an undescribed species in the dentaliid genus *Fissidentalium* P. Fischer, 1885. The new scaphopod species is characterised by a large size for the genus, is moderately curved, with numerous narrow, longitudinal ribs (60 ribs at 11 mm diameter ventral aperture), a dentaliid radula, and is described herein as *Fissidentalium aurae* sp. nov. The new species shows a close genetic relationship to congeners of *Fissidentalium* and separates from the sister genera *Dentalium* Linnaeus, 1758 and *Antalis* H. Adams & A. Adams, 1854. Genetic COI barcoding of the epizoic anemone suggests the species is a member of the family Actinostolidae Carlgren, 1932. The discovered association of a burrowing scaphopod with an epifaunal anemone at abyssal depth is a new record for the region and is indicative of how little is known about symbioses in the deep sea.

Keywords Species-pair-associations · Ocean seafloor observation system · Abyssal plain · Taxonomy · Lebensspuren

Introduction

The marine realm is a challenging environment, and many organisms have developed a type of living together to benefit from each other's presence, in symbiosis, as defined by de Bary (1879). Symbiotic relationships are divided into the four different interaction types mutualism, commensalism, parasitism and amensalism, split into obligate and facultative dependencies, and by types of physical association (van Beneden 1873; Apprill 2020). Symbiotic associations can be found from shallow, nearshore waters to the deep sea. Well known are the shallow water associations of stone corals with algae, of damselfish with anemones and of hermit crabs, using gastropod shells as a cover for their soft body parts, with sea anemones covering the gastropod shells (e.g. Vafeiadou et al. 2012; Roux et al. 2020; van Oppen and Medina 2020). Chemosynthetic symbioses are especially known from deep-sea habitats like hydrothermal vents, methane seeps and whale falls, where hydrothermal vent clams or gastropods profit from chemosynthetic endosymbionts (e.g. Dubilier et al. 2008; Treude et al. 2009; Chen et al. 2018). Lesser known are associations from non-chemosynthetic, deep-sea habitats, for example from mesophotic deep-water corals or bathyal and abyssal habitats (White et al. 1999; Buhl-Mortensen and Mortensen 2004; Girard et al. 2016).

Reynolds (2002) reviewed symbioses in Scaphopoda, dividing upon commensalism, parasitism and mutualism in species-pair associations. Commensalism is reported for ciliates living in the mantle cavities of scaphopods (Reynolds 1990). Parasitic relationships comprise ciliates and platyhelminth larvae in the scaphopod bloods (Boissevain 1904; Arvy and Gabe 1951), cercariae in gonads (Arvy 1949; Cribb et al. 2001), ectoparasitic copepods in the mantle cavity and endoparasitic nematodes (Davies

Communicated by B. A. Bluhm

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Published online: 07 November 2024

1987). The most distinct symbioses are mutualistic relationships in which sessile taxa like anemones, corals and barnacles live epizoic on the shell of the scaphopod, which can be found from shallow, nearshore waters to abyssal depths (e.g. Kozloff 1990; Zibrowius 1998; White et al. 1999). The benefits of these associations are suggested to be commensal or mutualistic. The epibiont has the benefit of being carried around, gaining access to resuspended organic particles, whilst the scaphopod might gain protection from predation (Reynolds 2002). These species-pair associations have mostly been reported from dentaliid scaphopods, especially of the genus *Fissidentalium* (Riemann-Zürneck 1973; Shimek and Moreno 1996; Shimek 1997; Zibrowius 1998; White et al. 1999; Reynolds 2002). The genus *Fissidentalium* in the family Dentaliidae Children, 1834 comprises 61 nominal species. They are distributed in all oceans and from shallow continental shelves to abyssal depths, with 12 species reported from the abyss (Steiner and Kabat 2004; WoRMS Editorial Board 2024). Most species occur in the West Pacific, Indo-West-Pacific and Indian Ocean. Four species are known from the East Pacific whilst five and four species are known from the East and West Atlantic, respectively. The Southern Ocean only hosts two species of *Fissidentalium*. In his analysis of the inhabited depth of western Atlantic and Indo-Pacific scaphopods, Scarabino (1979, 1995) noted that *Fissidentalium* were preferentially distributed in bathyal and abyssal depths. Regarding eurybathy in *Fissidentalium* species, several species are only known from their type locality, 20 species have an eurybathic range of less than 200 m, and seven species show extended eurybathy (Brey et al. 1996), with depth distributions ranging of over 1000 m (Steiner and Kabat 2004). These latter species include the trans-Atlantic species F. *candidum* (Jeffreys, 1877) and F. *capillosum* (Jeffreys, 1877), both reported from the continental shelf and upper slope to abyssal depths. At present, five nominal species of *Fissidentalium* are listed as accepted in WoRMS (WoRMS Editorial Board 2024) with bathyal and abyssal type localities in the North Atlantic. *F. candidum* from West Greenland, *F. capillosum* from East Greenland, *F. paucicostatum* from West European basin, *F. semivestitum* from off West Sahara and *F. concinnum* off Guinea. Only *F. candidum* and *F. capillosum* are reported from subpolar North Atlantic waters.

The aim of this study is to describe the encountered species-pair-association of a dentaliid scaphopod with an actinostolid anthozoan from abyssal depth of the subpolar Labrador Sea. The description is supported by in situ imagery of an ocean seafloor observation system and barcoding analyses of scaphopod and anemone. Based on the results, we describe a new species of *Fissidentalium* from the Labrador Sea.

Materials and methods

Study site

The Labrador Sea, situated between the north-eastern coast of Canada and western Greenland, is the coldest and freshest basin of the North Atlantic and susceptible to climate change (Yashayaev 2007; Yashayaev and Loder 2017). Its boundary to the North is the Davis Sea and is flanked by Greenland to the South-East, and Labrador and Newfoundland to the South-West. The bathymetry of the Labrador Sea can be subdivided into the wide continental shelf and relatively gentle continental slope on its western side and a narrow shelf and steep continental slope on the eastern side, with the abyssal Labrador Basin in-between (Chalmers and Pulvertaft 2001; Coté et al. 2019).

The Labrador Sea hydrography is of continuous scientific interest as it is an area of dynamic warm Atlantic to cold sub-Arctic water conversions (e.g. Lazier 1980; McCartney and Talley 1982; Straneo 2006). Increased sea ice melt has affected freshening inflow which might affect deep mixing of water masses and impact phytoplankton blooms and the benthic communities below (Zhai et al. 2013; Yashayaev et al. 2015).

Data collection

During the IceDivA2 expedition on RV Sonne (SO286) in November 2021, pelagic and benthic habitats were investigated in international waters of the Labrador Sea around 58°N and 054°W (Brix et al. 2023). Megabenthic fauna (> 1 cm in size) was collected by Agassiz trawl (AGT) and visually explored by an Ocean Floor Observation System (OFOS) in the Labrador Sea Basin at abyssal depths of 3380 to 3390 m (Fig. 1).

An AGT with an opening frame of 3.5 m width, 0.7 m height and 8.7 m long net of 1 cm mesh size was deployed to collect benthic megafauna and trawled for 20 min at 1 km along the seafloor. At arrival on deck, the catch was sieved over staggered sieves of 1 cm, 1 mm and 0.5 mm mesh size and visible fauna was removed for taxon identification, live photography, tissue sampling and fixation.

Live collected scaphopod specimens for taxonomic studies were fixed in 96% pre-cooled ethanol for molecular and morphological analysis. Most live collected scaphopods had an epizoic anthozoan attached, which were not removed to facilitate the description of the anemone. Further collected shell debris, which had no anemones attached, was preliminary fixed in 96% ethanol and then air dried.

In situ seafloor imagery

RV Sonne had a vessel owned OFOS with a tethered winch system of maximum 6000 m operating depth and was equipped with one high-definition serial digital interface

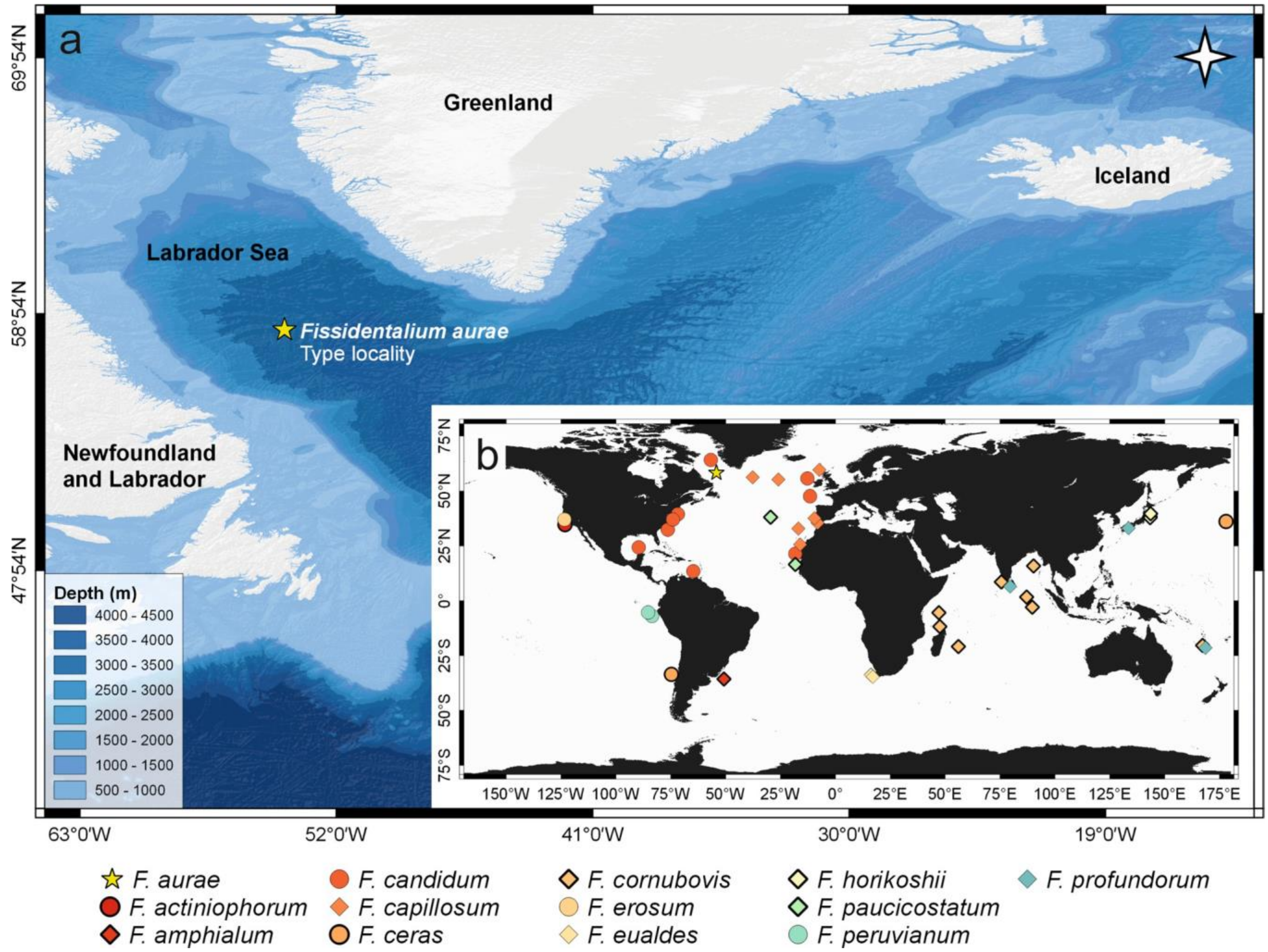


Fig. 1 Map of abyssal records of *Fissidentalium* species. **a** Type locality of *Fissidentalium aurae* sp. nov. in the Labrador Sea, 3387 m depth; **b** Global distribution of further 12 recent species of *Fissidentalium* with abyssal records

(HD-SDI) camera, one internet protocol (IP) video camera, one still camera (Canon EOS 5D Mark IV, 4096 × 2160 pixels, 4 K), two flashlights for still camera, four underwater lights, three red point lasers 18 cm apart and one altimeter. An ultra-short baseline system (USBL) Posidonia transponder was attached to the OFOS during the deployment, recording the positions and tow-speeds when the images were captured. The OFOS was deployed from the starboard side of the vessel and towed at a speed of 0.5 knots for 1.5 nautical miles at a minimum distance of 1.5 m above the seafloor. Still images were taken in a set 10 s photo interval along the transect line.

The OFOS still images were assessed to count selected taxon presences in four ways: (1) the presence of scaphopod shells visible on the substrate surface, (2) scaphopods carrying a light-coloured anemone and associated with a Lebensspur, (3) light-coloured anemones without a Lebensspur and (4) red-coloured anemones without a Lebensspur. The number of anemones without a Lebensspur was counted to assess the abundance of anemones on scaphopods in the soft bottom habitat compared to those not attached to scaphopods. Lebensspuren, meaning traces of life, are biologically formed sedimentary structures (for classification see Miguez-Salas et al. 2024). To account for camera lens edge distortion effects, the images were split into 100 equal sized rectangles and the outer rectangle layer was excluded, leaving 64 rectangles for analysis, resembling a seafloor area of about ~ 0.5 m^2.

Specimen photography, energy dispersive spectroscopy morphometrics and repository

Live images of scaphopods were taken on board of RV Sonne with a digital Canon EOS 5D Mark IV SLR camera with macro lens and two linked flashes on a Kaiser RS copy stand. Smaller macrophotography was taken under a Leitz Stemi SV 6 stereomicroscope with an attached MU1803 USB camera and the AmScope software.

Scanning electron micrographs of shells and radula were made with a Hitachi TM3000 scanning electron microscope (SEM, Hitachi High-Technologies, Maidenhead, UK) at the British Antarctic Survey. Radulae were prepared by dissecting the radula sac, dissolving it in domestic bleach and cleaned for 15 s in an ultrasonic bath before SEM observation. Shells of one living individual and two debris pieces were hand-broken and investigated on the edge, inner and outer surfaces for microstructure surveys.

Energy Dispersive Spectroscopy (EDS) analysis for the elemental presence detection on radula and shells was performed with the Hitachi TM3000 SEM equipped with an Oxford Instrument INCA system and the Aztec software (Oxford Instruments, High Wycombe, UK). EDS maps for × 100 (radula) and × 400 (shell) magnified areas were acquired for five minutes, set to detect all elements, and quantified by the Aztec software. Elemental spectra of the bulk composition (% oxides) were displayed.

Shell morphometric measurements were taken from 19 individuals and shell debris using digital vernier cal- lipers (0.01 mm). Shell length was measured as the long- est length from the ventral aperture to the dorsal aperture (major axis) (Shimek and Moreno 1996), aperture width as the distance between the two widest anterior to poste- rior points, and aperture height as the distance between the two widest points perpendicular to the aperture width. Arc is the maximum distance to the shell from a chord run- ning between the anterior edges of both apertures, lArc is the distance from the dorsal aperture to arc. As attached anthozoans were not removed from the scaphopods, arc and lArc measurements could not be taken in some specimens. Derived indices follow Shimek (1997) and Souza et al. (2020). Shell sizes were analysed in Microsoft Excel. Specimens used in the present study, including type specimens, are deposited in the Senckenberg Research Institute and Museum Frankfurt, Germany (SMF) and the Natural History Museum, London (NHMUK, previous acronym BNHM). Museum numbers were given for the scaphopod specimens, if present, attached anthozoans were given collection numbers of German Centre for Marine Biodiversity Research (DZMB) for their Hamburg site (DZMB-2-HH). Museum numbers and shell morphometrics of collected scaphopod specimens are listed in Table 1.

DNA extraction, amplification and sequencing

DNA extractions were carried out using the Macherey–Nagel NucleoSpin Tissue Kit (Macherey–Nagel, Düren, Germany), following the manufacturer's instructions. Tissue was left for digestion overnight in a shaking bath at 56 °C/350 rpm. For all isolates, elution was carried out in two steps, using 50 µl pre-heated (70 °C) elution buffer each turn. DNA aliquots are stored at − 80 °C at the German Centre for Marine Biodiversity Research (DZMB), Hamburg. The mitochondrial marker cytochrome *c* oxidase subunit I (COI) and the ribosomal marker 18S rRNA (18S) were selected for species delimitation analyses (Table 2). Polymerase chain reaction (PCR) was carried out using PCR-Beads, illustraTM PuReTaq Ready-To-GoTM (Avantor®; VWR Int. GmbH, Darmstadt, Germany) with a total reaction volume of 25 µl per sample. In order to generate 18S sequences, PCRs were duplicated to gain a total of 50 µl of product. Final primer concentrations were 10 µmol and the amount of template DNA used was 2 µl for COI and 3 µl for 18S. Thermal cycling conditions were as follows: initial denaturation: 95 °C, 5 min; denaturation: 38 cycles, 95 °C, 45 s; annealing: 45 °C (COI), 50 °C (18S), 50 s; elongation: 72 °C, 1 min (COI), 3:20 min (18S); final elongation: 72 °C, 5 min (COI), 10 min (18S); cooling at 10 °C. Quality and quantity of amplified product was assessed by gel electrophoresis using 1.5% agarose gels. Successful PCR products were purified using ExoSAP-IT PCR Product Cleanup Reagent (Thermo Fischer ScientificTM) and run on a thermal cycler (incubation: 37 °C, 15 min; enzyme inactivation: 80 °C, 15 min). Double stranded sequencing was carried out by the sequencing facilities Macrogen Europe Inc. (Amsterdam, Zuidoost, The Netherlands) and Eurofins Genomics Germany GmbH (Ebersberg, Germany) using ABI 3730xl sequencers.

Sequence editing, alignment and genetic analyses

Geneious Prime® (Version 2022.1.1; Biomatters, Auckland, New Zealand; Kearse et al. 2012) was used to edit and assemble forward and reverse chromatograms as well as to check for potential contamination using the implemented NCBI BLAST search tool (Basic Local Alignment Search Tool; Altschul et al. 1990). Assembled sequences were aligned using MUSCLE (Edgar 2004), implemented in Geneious Prime® with default settings. The software jModelTest 2 (Guindon and Gascuel 2003; Darriba et al. 2012) was used to estimate best-fit models of evolution applying the Akaike Information Criterion (AIC; Sakamoto et al. 1986). Phylogenetic analyses of single-gene alignments were performed using MrBayes 3.2.1 (Huelsenbeck and Ronquist 2001), with three parallel runs of 5 million generations, sampling every 1000 generations. Convergence of independent runs was examined in Tracer 1.7.2 (Rambaut et al. 2018) with a burn-in of 10%. Trees were reconstructed using Bayesian Inference (BI), assessing branch support by posterior probability (PP) with values ≥ 0.95 considered as highly supported (Felsenstein 1985; Huelsenbeck et al. 2001). Tree editing was performed in FigTree 1.4.4 (Rambaut 2009) and Affinity Photo 1.10.5 (Serif Ltd., Europe).

Table 1 Museum numbers and shell morphometrics of collected scaphopod specimens

Museum number		Anemone present	Shell length (mm)	VAp width (mm)	VAp height (mm)	DAp width (mm)	DAp height (mm)	lArc (mm)	Arc (mm)	VAp ratio w/h	lnLTot	lnVApw1	lnAph1
SMF 366428	*	**Y***	**61.91**	**11.34**	**11.28**	**2.36**	**1.99**	**19.0**	4.22	**1.01**	**4.13**	**2.43**	**2.42**
SMF 366429		Y	45.8	8.73	8.6	1.47	1.6	11.8	1.06	1.02	3.82	2.17	2.15
NHMUK 2023932	*	Y*	56.07	10.5	10.77	2.1	2.16	15.1	2.25	0.97	4.03	2.35	2.38
NHMUK 2023933	†	N	15.52	3.1		1.1					2.74	1.13	
NHMUK 2023934		N	23.28	6.4		2.88					3.15	1.86	
SMF 366430	*	Y*	63.63	10.9	10.6	2.02	2	23.9	2.84	1.03	4.15	2.39	2.36
SMF 366431	*	Y*	50.15	9.27	10.2	1.93	1.75	15.2	2.89	0.91	3.92	2.23	2.32
SMF 366432	*	Y*	40.35	7.76	7.55	1.26	1.23	11.8	1.42	1.03	3.70	2.05	2.02
SMF 366433	*	Y	30.98	5.49	5.42	1.35	1.41	7.2	0.54	1.01	3.43	1.70	1.69
SMF 366434	*	Y*	40.58	7.5	7.09	1.4	1.36	8.1	1.20	1.06	3.70	2.01	1.96
SMF 366435	*	Y*	38.99	7.6	7.26	1.26	1.37			1.05	3.66	2.03	1.98
SMF 366436	*	Y*	32.71	6.53	6.68	1.61	1.72	20.0	1.50	0.98	3.49	1.88	1.90
SMF 366437		Y	51.16	10.32	10.11	2.42	2.01	17.5	2.88	1.02	3.93	2.33	2.31
SMF 366438		Y	50.34	9.98	9.61	2.19	2.14	25.4	1.84	1.04	3.92	2.30	2.26
SMF 366439		Y	56.68	11.12	10.77	2.25	2.13	16.4	4.52	1.03	4.04	2.41	2.38
SMF 366440		Y	41.77	7.98	8.18	1.88	1.72	13.2	1.68	0.98	3.73	2.08	2.10
SMF 366441		Y	46.19	8.44	8.62	1.73	1.8	20.6	2.29	0.98	3.83	2.13	2.15
SMF 366442		Y	42.67	7.35	7.54	1.28	1.18	17.3	2.40	0.97	3.75	1.99	2.02
SMF 366443		Y	36.76	7.51	7.44	1.43	1.52	21.4	1.94	1.01	3.60	2.02	2.01
NHMUK 2023935		Y	41.78	7.98	7.35	1.91	1.7	10.0	1.80	1.09	3.73	2.08	1.99

*Barcoded specimen; †dry shells; bold, specimen designated as holotype; *Arc*, maximum distance to the shell from a chord running between the anterior edges of both apertures; *DAp*, dorsal aperture; *N*, No; *lArc*, distance from the dorsal aperture to arc; *lnLTot*, natural logarithm of shell length; *lnVAph1*, natural logarithm of ((Vap height) + 1); *lnApw1*, natural logarithm of ((Vap width) + 1); *VAp*, ventral aperture; *Y*, Yes

Table 2 Primers used for PCR and sequencing of COI and 18S

Primer	Sequence (5′ to 3′)	Reference
COI		
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994
HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 1994
18S		
R-563	ACCAGACTTGCCCTCC	Díez et al. 2001
1155R	CCGTCAATTCCTTTAAGTTTCAG	Dreyer and Wägele (2001)
18A1mod	CTGGTTGATCCTGCCAGTCATATGC	Raupach et al. 2009
400F	ACGGGTAACGGGGAATCAGGG	Dreyer and Wägele (2001)
1800mod	GATCCTTCCGCAGGTTCACCTACG	Raupach et al. 2009
1250FNmod	GGCCGTTCTTAGTTGGTGGAG	Raupach et al. 2009

Results

In the Labrador Sea Basin, the AGT was deployed at station SO286_19-1 on 21 November 2021 and OFOS on 22 November 2021. The AGT trawl collected 19 live scaphopods of which 18 were associated with an anemone, as well as shell debris (Fig. 2, Table 1).

The OFOS dive yielded 917 images, showing a soft sediment seafloor with Lebensspuren as traces of epifaunal and infaunal taxa, occasional megafauna and infrequent hard substrate (drop stones) (Neuhaus et al. 2024). The occasional epifaunal taxa comprised cnidarians (anthozoans), irregular sea urchins, comatulid crinoids, ophiuroids, asteroids, holothurians and porifera, whilst fish and decapods were rare with three rattail and a single squat lobster sighting. On a total of 62 images (6.7%) scaphopod shells, with or without Lebenspur were visible on the sediment surface, with no confirmation of their species affinity, if these were living specimens, or only shell debris (Fig. 2a). Anemones without Lebensspur, indicating either a burrowing species or a species attached to hard substrate, were seen on 67 (7.3%) images, 60 of them showing a red-coloured anemone and 7 of them a light-coloured anemone. In 31 images white-coloured anemones with Lebensspuren behind them were seen, indicating active movement on a scaphopod through the soft sediment surface (Fig. 2b). Based on these occurrences, the abundance of anemone-carrying scaphopods (Fig. 2c) is estimated as one per 15 m^2 along the OFOS track.

Molecular analysis

DNA was successfully amplified for nine scaphopods, yielding 11 novel sequences for two markers (COI: 9 sequences, 687 bp; 18S: 2 sequences, 1821 bp). The NCBI BLAST of the COI consensus sequences resulted in a pairwise identity of 98.1% with the Pacific specimen *Fissidentalium* sp. NHM_261 (MF157511), showing 13 mutational steps across 677 bp. The subsequent hit resulted in less than 90% coverage with the species *Antalis pilsbryi* (Rehder, 1942) (AF120639) and more than 100 unequal sites. The 18S sequence BLAST results showed pairwise identities between 99.6–100% with *F. capillosum* (AF490596), *Fissidentalium* sp. NH_003 (ON257247), *F. candidum* (AF490595) and *Fissidentalium* sp. NHM_261 (MF157489), with zero to five mutational steps across 1659–1812 bp, respectively. In addition, several dentaliid species of the genera *Antalis* H. Adams & A. Adams, 1854 and *Dentalium* Linnaeus, 1758 yielded identical numbers of unequal sites and pairwise identities of up to 99.8%. To aid the species delimitation analysis and visualise the BLAST results based on Bayesian statistics, 13 COI and 25 18S sequences from the NCBI GenBank were included in the final alignments and species delimitation analyses (Figs. 3, 4). Both the COI and 18S phylogram place *Fissidentalium aurae* sp. nov. within the family Dentaliidae and separate the cluster from given sister species of *Fissidentalium*. This separation stands with a high support in the COI hypothesis (PP = 0.98). Despite a low support for the clustering within the species of *Fissidentalium* in the 18S hypothesis (PP = 0.19), the two Atlantic species *F. capillosum* and *F. candidum* separate from our abyssal species *F. aurae* sp. nov. with a posterior probability of 0.95. Both phylograms depict a close genetic relationship to the Pacific specimen *Fissidentalium* sp. NHM_261, however, clearly distinguish between this specimen and our new species—with full support for the COI genetic marker (PP = 100; Fig. 3).

In addition to the scaphopods, DNA was amplified for each of the associated epizoic anemones, yielding eight novel sequences for the COI marker (696 bp) and one novel sequence of the 18S marker (1768 bp). The NCBI BLAST search of the anthozoan sequences resulted in a pairwise identity of 98.3–99.4% with published sequences of *Maractis* sp. (MW323564, KJ566948) and *Actinostolidae* sp. (OK267405, OK267413), resulting in three to seven mutational steps across 618–676 bp. As further taxonomic identification of this species is not part of this manuscript, we refer to the epizoic anthozoan as actinostolid anemone. All sequence data can be found in the Barcode Of Life Database (BOLD) dataset dx.doi.org/https://doi.org/10.5883/DS-FISSI as well as on the NCBI GenBank via the accession numbers PP464856–PP464864 (*F. aurae* sp. nov.) and PP464848–PP464855 (actinostolid anemone) (Table 3).

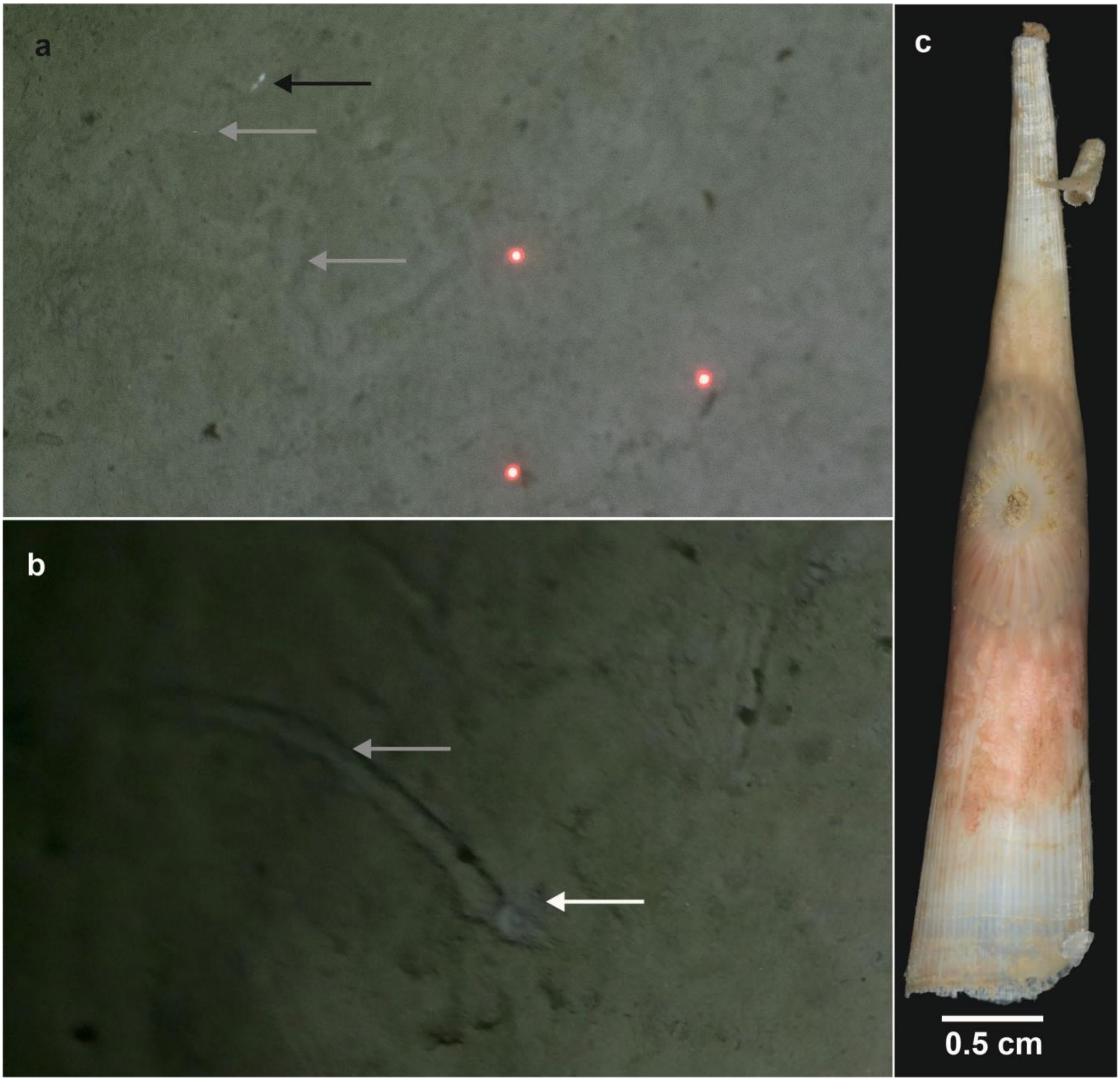


Fig. 2 In situ and life images of scaphopod-actinostolid symbiosis; **a** Scaphopod (black arrow) hosting anemone with retracted tentacles and its Lebenspur (grey arrows).; **b** Anemone with extended tentacles (white arrow) and scaphoid created Lebensspur (grey arrow); **c** Scaphopod (Paratype 1 SMF 366429) with an epizoic actinostolid anemone

Class Scaphopoda Bronn, 1862

Order Dentaliida Starobogatov, 1974

Family Dentaliidae Children, 1834

Genus Fissidentalium P. Fischer, 1885

Type species *Dentalium ergasticum* P. Fischer, 1883: 275–277; accepted as *Fissidentalium capillosum* (Jef- freys, 1877) type by monotypy.

Fissidentalium aurae sp. nov.

(Figs. 2c, 5, 6, 7)

https://zoobank.org/BE3E3500-193E-43B1-B2FE-4701C5222BE6

Diagnosis: A large-sized, over 60 mm in length and 10 mm in ventral aperture width, *Fissidentalium* with numerous regular, fine longitudinal ribs. The white shells are robust and no posterior slit on the dorsal aperture was observed in the examined specimens. Most live specimens with shell lengths of 32–63 mm have a sea anemone attached to the concave, anterior surface of the shell. The ventral and

Table 3 Museum numbers for scaphopod specimens with their respective associated epizoic anemone (each given a DZMB number). COI and 18S loci GenBank accession numbers are given where applicable

Scaphopod museum number	Anemone				
	COI	18S	DZMB number	COI	18S
SMF 366428	PP464863	PP464630	DZMB-2-HH-7142	PP464854	PP464627
NHMUK 2023932	PP464861	PP464629	DZMB-2-HH-7144	PP464852	
SMF 366430	PP464864		DZMB-2-HH-7141	PP464855	
SMF 366431	PP464862		DZMB-2-HH-7143	PP464853	
SMF 366432	PP464860		DZMB-2-HH-7145	PP464851	
SMF 366433	PP464859		DZMB-2-HH-7146		
SMF 366434	PP464858		DZMB-2-HH-7147	PP464850	
SMF 366435	PP464857		DZMB-2-HH-7148	PP464849	
SMF 366436	PP464856		DZMB-2-HH-7149	PP464848	

Bold, specimen designated as holotype

dorsal apertures are slightly wider than high. Preserved, unrelaxed soft body dividable into a ventral buccal, a middle gut and a dorsal gonad region (following Shimek and Moreno 1996) and is about 2/3 of total shell lengths. Buccal and gonadal regions are of similar size and each about 3 times longer than the gut region.

Type material: Holotype SMF 366428, Fig. 5a–b, Labrador Sea, 58° 12.289′ N 054° 13.409′ W, 3387 m depth, AGT SO286_19-1, RV Sonne SO286, 21.11.2021, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7142. In ethanol; DNA extracted from scaphopod and anemone.

Paratype 1 SMF 366429, Fig. 1c, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone. In ethanol.
Paratype 2 NHMUK 20230932, Fig. 5c–d, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7144. In ethanol; DNA extracted from scaphopod and anemone.
Paratype 3 NHMUK 20230933, Figs. 5e, 7, type locality, leg. Katrin Linse. Dry empty shell.
Paratype 4 NHMUK 20230934, type locality, leg. Katrin Linse. Shell and remaining soft part in ethanol. Radula on SEM stub.
Paratype 5 SMF 366430, type locality, AGT SO286_19-1, RV Sonne SO286, 21.11.2021, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB7141. In ethanol; DNA extracted from scaphopod and anemone.
Paratype 6 SMF 366431, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB-2-HH-7143. In ethanol; DNA extracted from scaphopod and anemone.
Paratype 7 SMF 366432, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB- 2-HH-7145. In ethanol; DNA extracted from scaphopod and anemone.
Paratype 8 SMF 366433, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB- 2-HH-7146. In ethanol; DNA extracted from scaphopod.
Paratype 9 SMF 366434, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB- 2-HH-7147. In ethanol; DNA extracted from scaphopod and anemone.
Paratype 10 SMF 366435, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB- 2-HH-7148. In ethanol; DNA extracted from scaphopod and anemone.
Paratype 11 SMF 366436, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone DZMB- 2-HH-7149. In ethanol; DNA extracted from scaphopod and anemone.
Paratypes 12–18 SMF 366437–366443, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemones. In ethanol.
Paratype 19 NHMUK 20230935, Fig. 6b–d, type locality, leg. Katrin Linse. Associated with epizoic actinostolid anemone. In ethanol. Shell fragments on SEM stub.

Additional material examined: Shell debris, (NHMUK 20230936), Fig. 6a, type locality, leg. Katrin Linse. Dry empty shells. Shell fragments on SEM stub.

Etymology: "aura" means breeze in Latin and used in genitive case. This name refers to the windy conditions during SO286 as well as to the shipping company Briese Research operating RV Sonne.

Type locality: Sedimented abyssal plain in the Labrador Sea, 58° 12.289′ N 054° 13.409′ W, 3380–3390 m depth.

Distribution: Known only from the area around the type locality in the Labrador Sea in 3380–3390 m depth.

Description: Shell length to 63.63 mm; Holotype 61.90 mm, ventral aperture diameter 11.34 × 11.28 mm, dorsal aperture 2.36 × 1.99 diameter; thick, moderately curved, more towards the dorsal aperture (Fig. 5). Sculpture

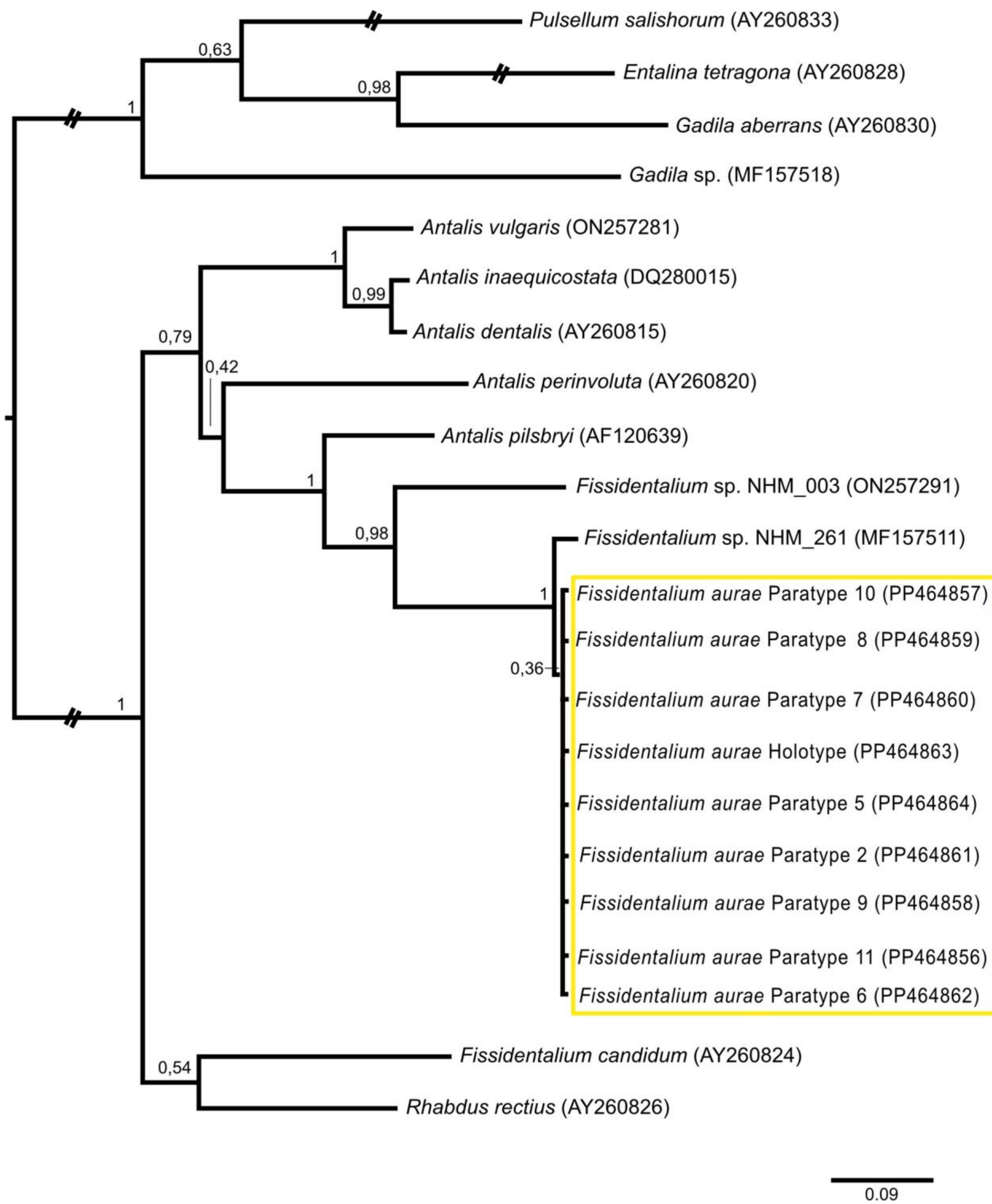


Fig. 3 COI Bayesian phylogram with posterior probabilities depicted on the nodes. The tree is rooted with four representatives of the order Gadilida Starobogatov, 1974 which stands monophyletic and sister to the Dentaliida. GenBank accession numbers are displayed in brackets. Node values are posterior probabilities

of 30 ribs at the dorsal aperture, intercalating to 60 narrow, longitudinal ribs at the ventral aperture; interstice wide, concave; ribs and interstices crossed by fine transverse growth lines. Aperture slightly ovate, being slightly higher anterior-posteriorly; protoconch unknown; ribs towards dorsal aperture often eroded. Colour opaque white near ventral aperture, white near dorsal aperture. Shell with three layers: a thin outer layer, a thicker middle layer of vertically

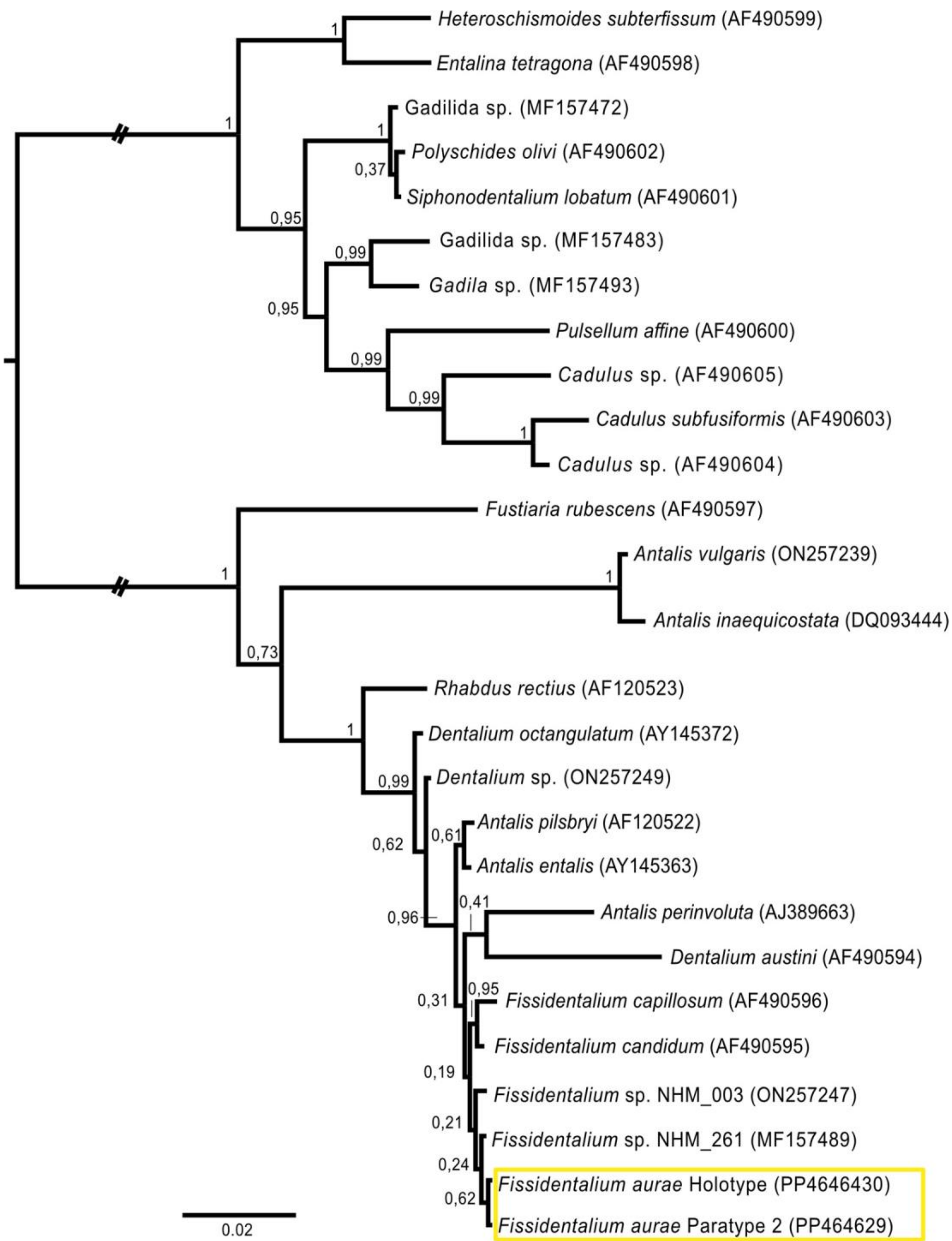


Fig. 4 18S Bayesian phylogram with posterior probabilities depicted on the nodes. The tree is rooted with 11 representatives of the order Gadilida which stands monophyletic and sister to the Dentaliida. GenBank accession numbers are displayed in brackets. Node values are posterior probabilities

orientated tablets and an inner layer of cross-lamellar aragonite tablets (Fig. 6). The overall thickness ranged from 190 to 497 µm in interstice areas and 265 to 542 µm in rib areas with the thickness of the vertically orientated prisms ranging from 15 to 98 µm and the cross-lamellar layer from 165 to 480 µm. EDS analysis of the shell confirmed calcium carbonate as the compound with no traces of Mg calcite. Individual shell measurements and derived indices of the holotype and paratypes are given in Table 1.

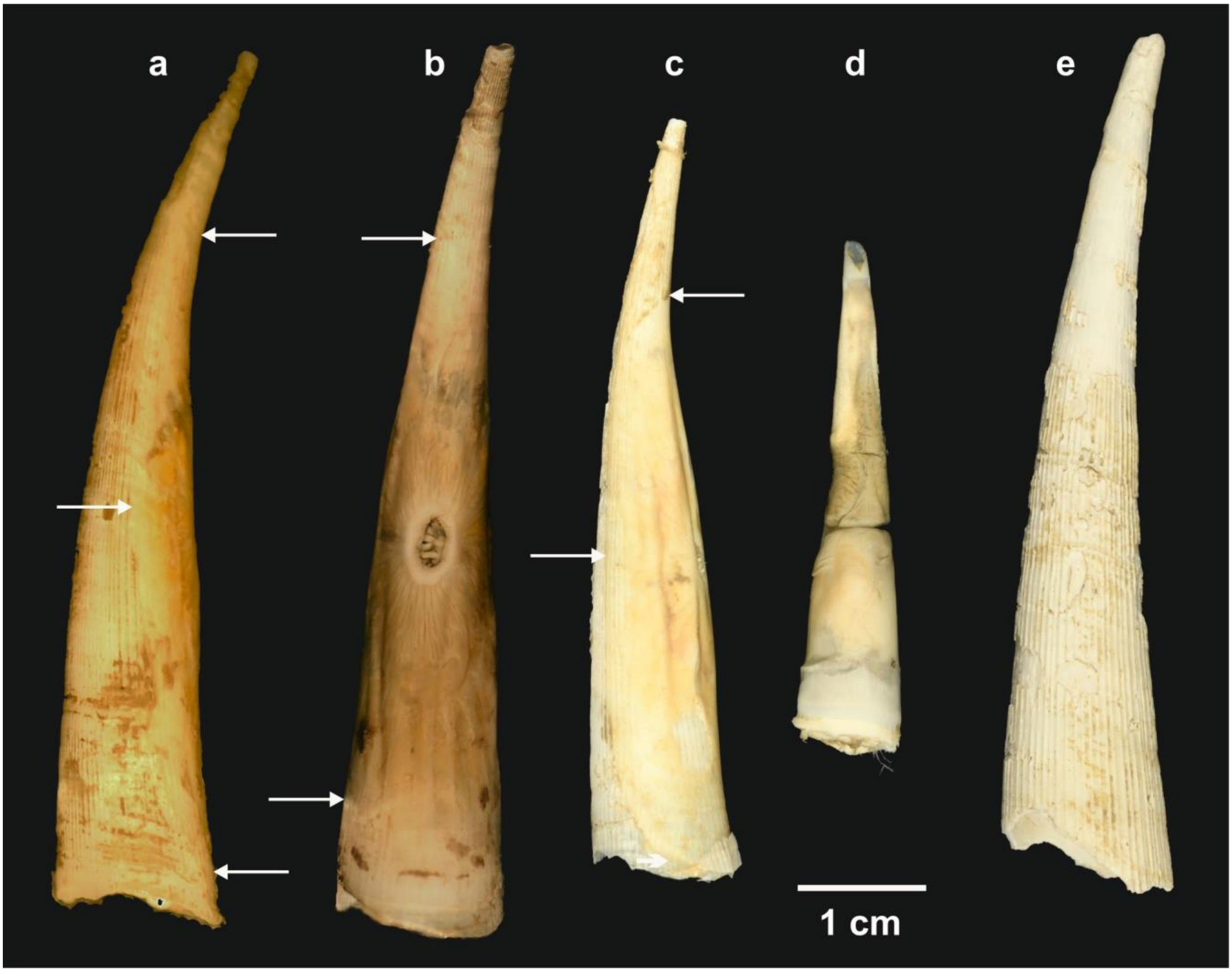


Fig. 5 *Fissidentalium aurae* sp. nov.; **a**–**b** Holotype SMF 366428, side and anterior view of shell and associated anemone; **c**–**d** Paratype 2 NHMUK 20230932, side view of shell and anemone and soft parts; **e** Paratype 3 NHMUK 20230933, side view of dead shell. Arrows indicate delineation of the anemones

External anatomy: Length of ethanol preserved soft-body-part was 38.65 mm in Paratype 2 with 56.07 mm shell length (Fig. 5).

Radula: The radula has five teeth per row and is composed of a rachidian tooth, which is flanked by one lateral and one marginal tooth on each side (Fig. 7). On the oldest teeth, iron is visible as a high quantity mineral component of the radula (Fig. 7a, b),as confirmed by EDS. The rachidian tooth is wider than high, concave dorsally and about twice as wide as the lateral tooth. The lateral teeth are convex anteriorly and concave posteriorly with sharply pointed forward projections bent and solid build. The marginal teeth are thin, wide and end at the lower flank of the lateral teeth.

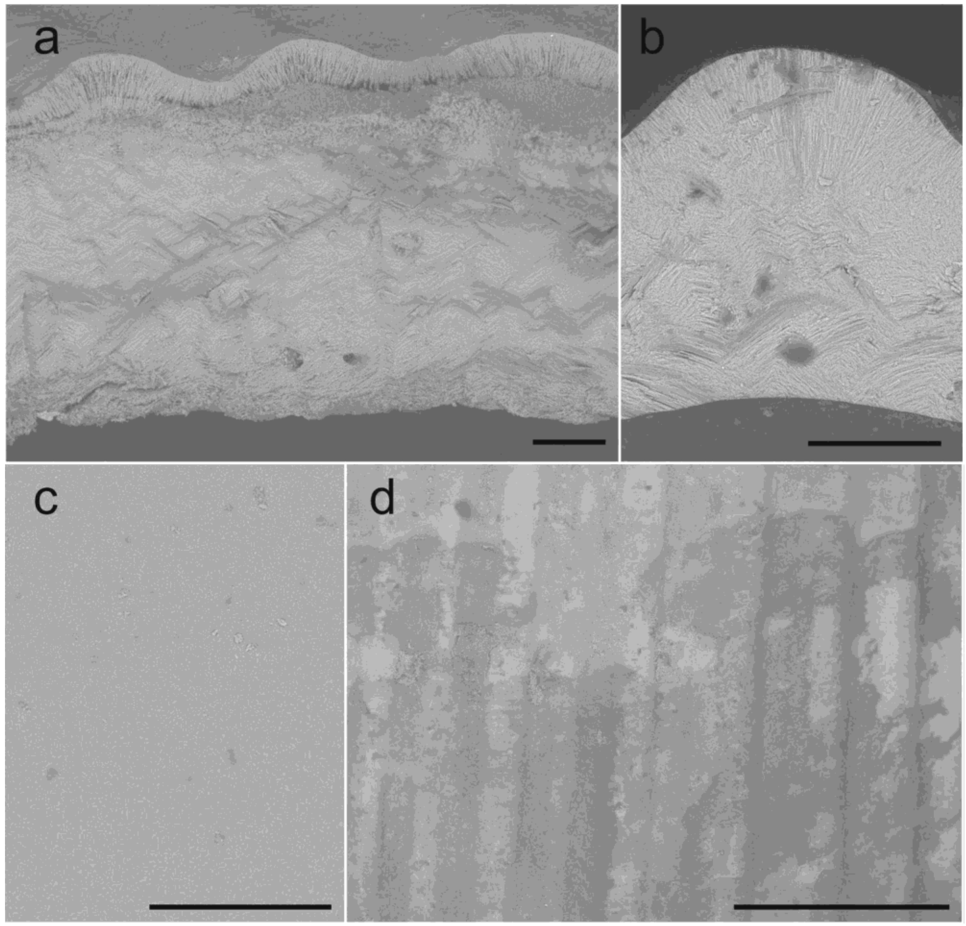
The imaged radula was extracted from an individual of 23.28 mm shell length, ~ 2.6 mm in length (rachidian teeth measured), ~ 1.2 mm in width and had ~ 14 rows (15 lateral teeth present on the left and 13 on the right side after dissection).

Molecular barcoding: Nine partial sequences of the COI barcoding region and two 18S sequences were amplified from *Fissidentalium aurae* sp. nov. and compared with previously published sequences of congeneric species (Figs. 3, 4, Table 3).

Remarks: Based on their morphology, the investigated scaphopod specimens are recognisable as belonging to the genus *Fissidentalium* (Shimek and Moreno 1996; Lamprell and Healy 1998).

The shell of *F. aurae* sp. nov is with 190 to 542 µm similar in thickness to *F. actiniophorum* Shimek, 1997 (189 to 479 µm; White et al. 1999) which Shimek (1997) described as thin compared to *F. megathyris* (Dall, 1890) and *F. erosum* Shimek & G. Moreno, 1996.

Fig. 6 Shell microstructure of *Fissidentalium aurae* sp. nov.; **a** Shell layers of shell debris at ventral aperture with 12.1 mm width; **b**–**d** Paratype 19 NHMUK 20230935 shell layers; **b** Ventral aperture with 7.98 mm width.; **c** Inner surface; **d** Outer surface. Scale bars: A–C: 100 µm, D: 1 mm



The only other *Fissidentalium* species with subpolar North Atlantic distributions are *F. candidum* and *F. capillosum*, with *F. candidum* being recorded from the west of Greenland in the Labrador Sea from 748–2464 m depth and *F. capillosum* from the east of Greenland in 1259–3528 m depths (Steiner and Kabat 2004).

Specimens of *F. aurae* sp. nov. were morphologically compared with two syntypes of *F. candidum* (BNHM 1885.11.5.1239, BNHM 1885.11.5.1240) and two syntypes of *F. capillosum* (BNHM 1885.11.5.1336, BNHM1887.2.9.4.6) at the Natural History Museum in London. The shell morphology of *F. aurae* sp. nov. can be differentiated from *F. candidum* by not having a dorsal aperture slit and being wider towards the ventral aperture, whilst having for similar numbers of longitudinal ribs at similar diameter. The foot of *Fissidentalium candidum* is described as conical (Jeffreys 1877), whilst it is not conical in *F. aurae* sp. nov. In the COI barcode region, a difference of 23% across 687 bp discloses the presence of two species. Across 1811 base pairs of the 18S region, a difference of mere five nucleotides (0.3%) is resolved between the species.

Shells of F. *aurae* sp. nov. can be morphologically distinguished from *F. capillosum* by missing the dorsal slit, having a wider ventral aperture at similar shell length (Jeffreys 1877), and having wider ribs and narrower interspaces. As there is no COI sequence of *F. capillosum* publicly available, the genetic difference to *F. aurae* sp. nov. can solely be examined across the 1812 bp of the 18S region, yielding eight different nucleotides (0.3%).

Specimens of *Fissidentalium aurae* sp. nov. were morphometrically compared to two abyssal species found off California and Portland in the East Pacific, namely *F. erosum* Shimek & G. Moreno, 1996 and *F. actiniophorum* Shimek, 1997. Whereas *F. erosum* has never been found associated with an anemone, the latter species was described as an anemone-carrying scaphopod (Shimek 1997), whereupon White et al. (1999) designated the anemone to their newly described species *Anthosactis nomados*. *Fissidentalium aurae* sp. nov. shows differences in ventral aperture width and height at similar shell length, having a wide and higher dorsal aperture compared to its sister species. Three paratypes of *F. actiniophorum* (BNHM 19962120 (1), BNHM 19962121 (2)) were directly compared at the

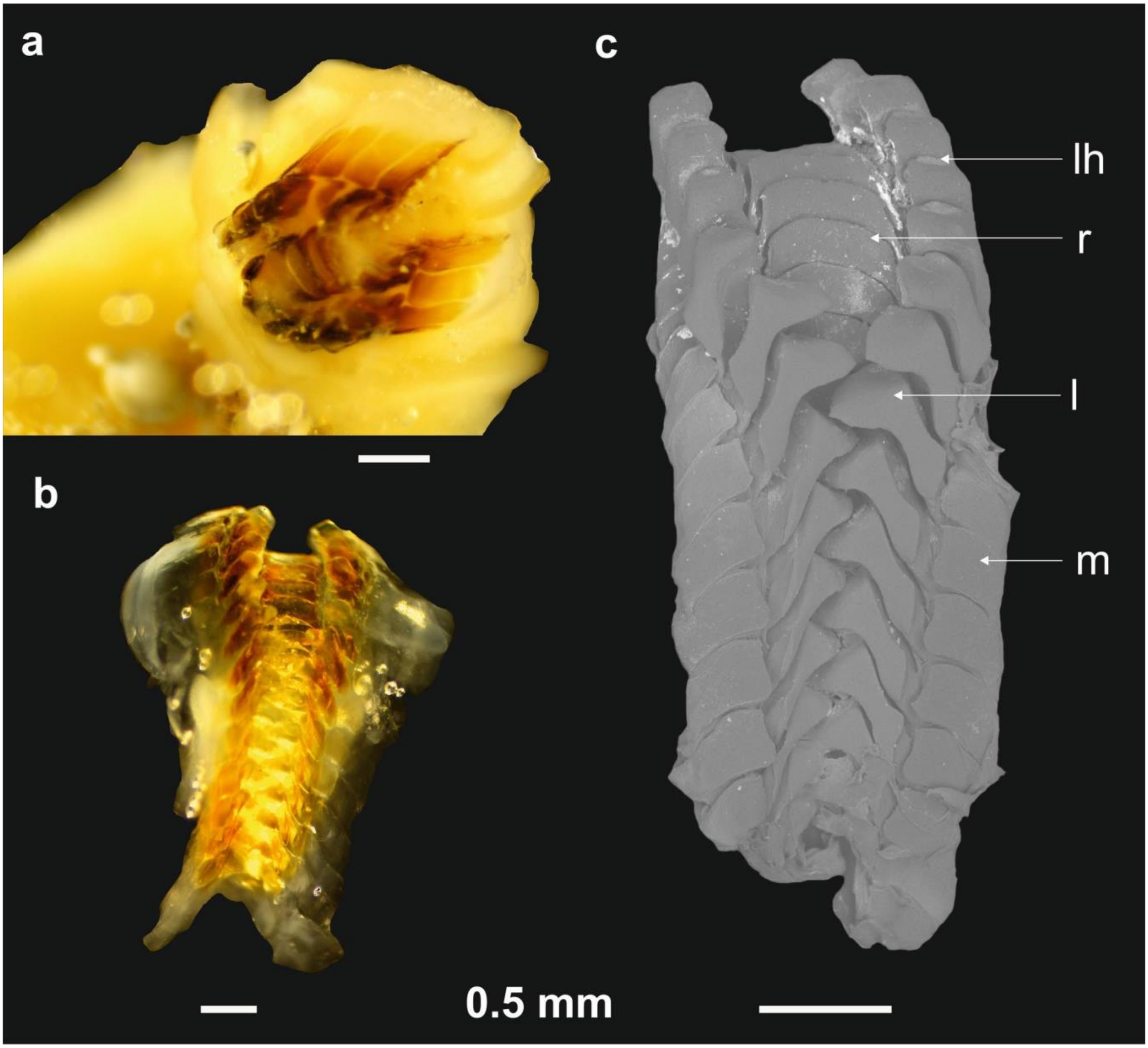


Fig. 7 Radula of *Fissidentalium aurae* sp. nov. Paratype 3 NHMUK 20230932; **a** Scaphopod sack showing radula under stereomicroscope; **b** Whole radula; **c** SEM of whole radula. Abbreviations: l, lateral tooth; lh, worn head of lateral tooth; m, marginal tooth; r, rachidian tooth

NHMUK, and next to confirming the morphometric differences, similarity of longitudinal rib and interspace structure was seen. However, at a comparable shell diameter of 3 mm, *F. actiniophorum* has about two-thirds the number of longitudinal ribs (30 ribs) compared to *F. aurae* sp. nov. with 47 longitudinal ribs. Unfortunately, the obtained tissue sample of one specimen of *F. actiniophorum* as well as the associated anemone did not yield viable DNA aliquot to amplify and use in the genetic analysis.

Of all specimens included in the molecular analysis, the individual designated as *Fissidentalium* sp. NHM_261, shows the closest genetic relation to *F. aurae* sp. nov. However, the difference of 14 nucleotides across 667 bp of the COI gene region is sufficient to differentiate between species on the molecular level. This differentiation concurs with the geographic distance between these species, as Fissidentalium sp. NHM_261 was collected at 4076 m depth in the Pacific Clarion-Clipperton Zone (Wiklund et al. 2017). Morphologically, the number of longitudinal ribs at comparable shell height is lower in the Pacific species than in our new species from the Labrador Sea. Similar to the paratype *F. actiniophorum* BNHM 19962120 with 20 latitudinal ribs at 1.5 cm diameter, *Fissidentalium* sp. NHM_261 carries 19 latitudinal ribs at the same diameter.

Ecological observations: On in situ images, only living *F. aurae* sp. nov. associated with an actinostolid anemone as well as broken shell fragments were observed. These living scaphopods are noticeable by the Lebenspuren they left behind in the soft sediment, which resembled the width of a feeding anemone. Of the 19 live collected *F. aurae* sp. nov. specimens, 18 had an anemone attached to their shell. Thus, there seems to be an interest in anemones to find a hosting scaphopod. The in situ images did not show Lebensspuren traceable to a living *F. aurae* sp. nov. without an attached anemone. *Fissidentalium aurae* sp. nov. occurs sympatrically with at least two other scaphopod species. At the type locality of *F. aurae* sp. nov., four other scaphopod specimens were collected from the same AGT. Three specimens resemble the dentaliid genus *Antalis* and were identified as *Antalis agilis* (Sars, 1872), a species with a known distribution record from the Labrador and Norwegian seas to the Azores in 60–5000 m depth (Ivanov and Zarubina 2004; Steiner and Kabat 2004). The fourth specimen resembles the gadilid scaphopod genus *Siphonodentalium* M. Sars, 1859 and was identified as *Siphonodentalium lobatum* (Sowerby 1860). The species is recorded from the Arctic and North Atlantic Ocean, from shelf to bathyal depths (Ivanov and Zarubina 2004). According to Steiner and Kabat (2004), further three species are found in the deep North Atlantic basins, namely *Bathoxiphus ensiculus* (Jeffreys, 1877), *Cadulus gracilis* Jeffreys, 1877 and *Heteroschismoides subterfissus* (Jeffreys, 1877).

Discussion

During the expedition IceDivA2 (SO286), sampling in the abyssal Labrador Sea disclosed a new species of dentaliid scaphopod as well as a new association between the scaphopod and an actinostolid anemone.

Species richness in the genus *Fissidentalium*

The new dentaliid *Fissidentalium aurae* sp. nov. was described based on an integrative taxonomic approach, using shell morphology and morphometrics, radula and soft part measurements, and molecular barcoding analyses. The genus *Fissidentalium* is known for its paucity of shell morphological characters between species. Distinct characters are the presence or absence of the dorsal aperture slit, low numbers of latitudinal ribs (16–36) at the ventral aperture versus high numbers (50–90), or circular versus oval apertures (Shimek and Moreno 1996; Lamprell and Healy 1998). Lamprell and Healy (1998) acknowledged that the status and species composition of this genus requires comprehensive revision including anatomical and molecular comparisons next to detailed shell and radula morphology.

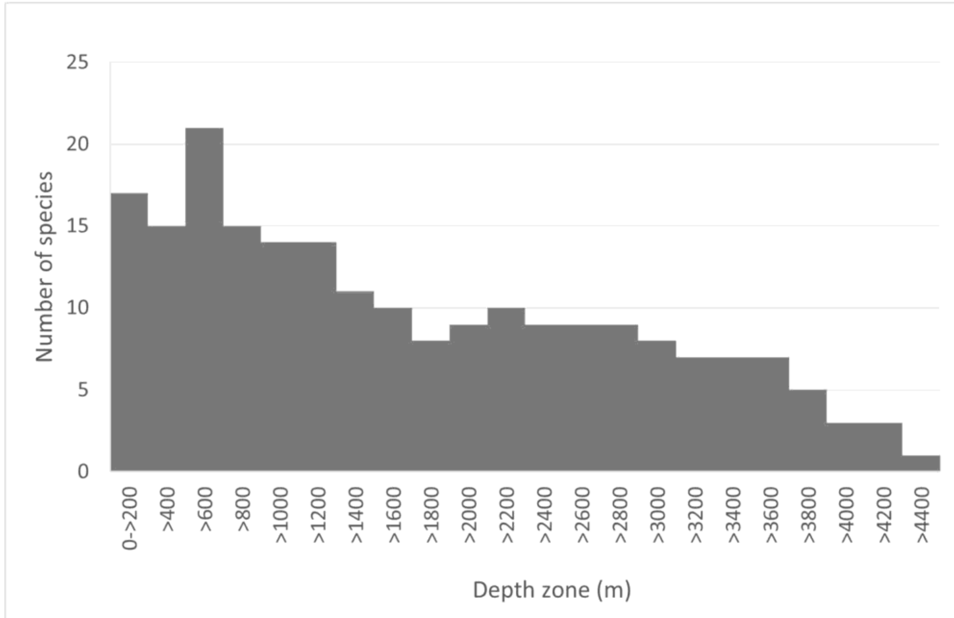
The genetic distinction of *F. aurae* sp. nov. from the Labrador Sea (58° 12 N 54° 13 W, 3387 m) to the sequenced *F. candidum* from Iceland (60° 05 N 20° 50 W, 2709 m) (Steiner and Dreyer 2003) with respective type localities west of Ireland and in the Bay of Biscay (Jeffreys 1877), together with the similarity of the shell morphology between the two species, is raising doubts for the correct species assignment for the Davis Strait records of *F. candidum* from the HMS *Valorous* expedition in 1875 (Steiner and Kabat 2004).

The depth zonation of *Fissidentalium* shows higher numbers of species at shelf and upper slope depth whilst numbers of species decrease with depth (Fig. 8). Eurybathy is not common in the genus. Twenty-one of the 62 known species have a known depth range of less than 200 m, 15 species of more than 200 but less than 1000 m and only seven species have known ranges of more than 1000 m depth. Only five species are known for extended eurybathic depth ranges of more than 2000 m, including *F. candidum* (403–3814 m) and *F. capillosum* (100–4088 m). Molecular analyses of specimens from several depths and locations of these eurybathic and often geographically wide-ranging species would confirm if these were wide-ranging species or species complexes.

Epizoic associations on Scaphopoda

The epizoic association of *Fissidentalium aurae* sp. nov. with an actinostolid anemone is not the first record of this kind for scaphopods or even species of *Fissidentalium*. Shimek and Moreno (1996) mentioned some records of the Pacific *F. megathyris* with attached anemones, later designated to *Anthosactis nomados* (White et al. 1999), suggesting a near sediment surface life style of the scaphopod enabling anemone attachment. The northeast Pacific species *Fissidentalium actiniophorum* was named after its anemone association as 90 of 133 live collected specimens carried an anemone (Shimek 1997). Like in the collection of *F. aurae* sp. nov., no dead collected shells of *F. actiniophorum* carried an anemone (Shimek 1997). The anemone was later described as *Anthosactis nomados* White et al. 1999. Specimens of a South Atlantic scaphopod identified as *Dentalium* sp. carried specimens of the anemone *Hormathia pectinata* (Hertwig, 1882) (Riemann-Zürneck 1973). More recently, a deep-sea scaphopod-anemone association was discovered during the "AleutBio" expedition SO293 to the eastern site of the Aleutian Trench, Alaska (Prof. Julia Sigwart, personal communication). A further scaphopod-cnidarian association was reported for *Pictodentalium vernedei* (Sowerby 1860) and the solitary scleractinian *Heterocyathus japonicus* (Verrill, 1866) (Zibrowius 1998). Carlgren (1928) found the anemone *Paracalliactis stephensoni* Carlgren, 1928, on a

Fig. 8 Depth distribution patterns of *Fissidentalium* species in 200 m depth zones



large *Dentalium* shell inhabited by the hermit crab *Parapagurus pilosimanus* Smith, 1879, off the Irish coast.

In all these cases, the attached anemones and scleractinians were reported from the concave anterior side, which is reported to facing the sediment surface in *Fissidentalium* (Zibrowius 1998). The scleractinians were found attached near the dorsal aperture, whilst the anemones on *F. actiniophurum* and *F. aurae* sp. nov. were covering most of the dorsal area from near the ventral aperture onwards (Shimek 1997; Zibrowius 1998; this study). To date, it is unclear what the mutual benefit for both partners of this association is and whilst Shimek (1997) mentions symbiosis, Reynolds (2002) suggests mutualism. The gain for the anemone is an attachment point in sedimented deep-sea areas, where hard substrates can be rare, and a transport medium to different feeding areas. The in situ images from the Labrador Sea show clear Lebensspuren from *F. aurae* sp. nov. with attached anemones, in some images with anemone tentacles reaching over the movement ridge created, potentially accessing food resources from there. White et al. (1999) inferred that the deep-sea scaphopods were protected from predators by their actinian symbionts, a symbiosis well accepted from shallow-water symbioses of gastropods and hermit crabs in gastropod shells with attached anemones (Williams and McDermott 2004). Potential predators of scaphopods are rattail fish and crabs (Reynolds 2002; Shimek 1989). During the OFOS dive in the abyssal Labrador Sea, potential motile predators such as rattails and squat lobsters were seen in the in situ images, but no records are available if these include *F. aurae* sp. nov. as their prey. White et al. (1999) additionally suggest that the anemone might protect the scaphopod shell from dissolution in calcium-carbonate undersaturated deep-sea habitats.

The two anemones associated with scaphopods, *Anthosactis nomados* and *Hormathia pectinata*, belong to the families Actinostolidae and Hormathiidae Carlgren, 1932 (WoRMS Editorial Board 2024). Barcode sequences obtained from eight specimens of the undescribed anemone attached to *F. aurae* sp. nov. revealed closest matches to *Maractis* sp. (MW323564, KJ566948) of the family Actinostolidae. Sanamyan et al. (2021) defined the new family Anthosactinidae, including the genera *Tealidium* Hertwig, 1882, *Hormosoma* Stephenson, 1918 and *Anthosactis* Danielssen, 1890 but stated on page 433 that they exclude *Anthosactis nomados* from the genus *Anthosactis*, but did not give a genus relationship for it. WoRMS still lists the species as *Anthosactis nomados* in the Actinostolidae (WoRMS Editorial Board 2024).

The type species of *Anthosactis*, *A. janmayeni* Danielssen, 1890, is an eurybathic (51–1073 m), circum-Arctic species, reported as rare and locally confined (Riemann-Zürneck 1997). The specimens in the latter redescription are with ~ 30–75 mm diameters significantly larger than the anemones on *F. aurae* sp. nov. and despite an overlap in geographic region, but not in depth, this species is considered as an unlikely match with the undescribed actinostolid species mentioned herein.

An integrative taxonomic approach for the identification of the actinostolid anemone attached to *F. aurae* sp. nov is suggested as that would not only formally classify this species from the Labrador Sea but might also clarify the position of *Anthosactis nomados.*

The herein described association of a burrowing scaphopod with an epifaunal anemone in the abyss of the Labrador Sea has not only revealed a new species of Atlantic scaphopod, but also shows how little is known about symbioses in the deep sea. Our study highlights the benefit of deep-sea imagery to support species descriptions with information on habitat and ecology. A future integrative taxonomy-based revision of the genus *Fissidentalium* would resolve phylogenetic relationships within the Dentaliida and clarify the status accepted nominal species and their current synonymies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12526-024-01481-1.

Acknowledgements The authors thank Master Thilo Birnbaum, the crew of RV Sonne, SO286 chief scientist Saskia Brix, technical staff and fellow scientists on the expedition for their support. Angelina Eichsteller is thanked as scientific lead of AGT deployments and James Taylor for leading OFOS deployments. We are grateful to Malacology section curators Julia Sigwart (Senckenberg Research Institute and Museum) and Tom White (NHMUK) for access to their scaphopod collections and allowing tissue sampling. Nicole Gatzemeier (DZMB Hamburg) photographed the specimens for Figures 2 and 3, and Lucy Stephenson extracted deep-sea *Fissidentalium* records from OBIS for Figure 1. We thank three anonymous reviewers for their constructive comments which improved the earlier version of this publication.

Funding Katrin Linse is part of the British Antarctic Survey Polar Science for Planet Earth Programme funded by The Natural Environment Research Council (NERC) [NC-Science]. Fieldwork during expedition SO286 on RV Sonne was funded by the Federal Ministry of Education and Research (BMBF) through the IceDivA2 grant GPF 21-2_052 (SO286) given to Saskia Brix, Katrin Linse, Pedro Martínez Arbizu and Alexander Kieneke. Jenny Neuhaus was as well supported through grant GPF 21-2_052 as part of the IceDivA project. The IceDivA expeditions (SO280; SO286) are a contribution to the iAtlantic project, funded by EU/HORIZON 2020, Blue Growth (grant agreement No 818123). Jenny Neuhaus is currently supported by the iAtlantic project and owes gratitude to Prof. Colin Devey and associated working group at GEOMAR Helmholtz Centre for Ocean Research for their fundamental support.

Declarations

Conflict of interest The authors declare no conflict of interest.

Ethics approval All applicable international, national, and/or institutional guidelines for animal testing, animal care and use of animals were followed by the authors. The scaphopod and anemone specimens have been treated and fixed under the marine invertebrate ethics policy of the British Antarctic Survey.

Sampling and field studies The field study was carried out in international waters in November 2021, requiring no sampling permits. The study is compliant with CBD and Nagoya protocols.

Data availability All datasets analysed and generated in this study e.g. OFOS imagery and morphometric data, are publicly archived in the UK Polar Data Centre at https://www.bas.ac.uk/data/uk-pdc/ and available under https://doi.org/https://doi.org/10.5285/C57A3261-F5F8-40E3-BCD3-C749733B3119. Molecular data is available in the Barcode of Life Database dx.doi.org/https://doi.org/10.5883/DS-FISSI.

Author contribution KL and JN conceived and designed the research, wrote the manuscript and prepared figures and tables. KL analysed the morphological data; JN analysed the molecular data. Both authors read and approved the manuscript.

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Taxonomic Research

Description of a new species of *Acanthocope* Beddard, 1885

Description of a new species of *Acanthocope* Beddard, 1885

Please note that this species description is preliminary and will be embedded within a research article currently under preparation by Zhehao Hu, Jenny Neuhaus, Emanuel Pereira, Sven Rossel, Terue C. Kihara, Janna Peters, and Saskia Brix. Preliminary title of the publication: "Comparing adult locomotion in two families of deep-sea isopods (Munnopsidae vs Haploniscidae) in the North Atlantic Ocean, including the description of new species".

Acanthocope **n. sp. A** (Figs 1–2)

Material examined

Holotype: male (10.4 mm TL), DZMB-2-HH-9393, Porcupine Abyssal Plain, RV *Sonne*, IceAGE 3, 21 July 2020, EBS, station 135, 49°48.45′N 15°13.86′W, 4577 m depth

Paratypes: female (4.5 mm TL), DZMB-2-HH-9360, Josephine Bank, RV *Sonne*, IceDivA 2, 28 January 2021, EBS, station 81-1, 36°28.79′N 13°59.47′W, 4165 m depth; female (7.0 mm TL), DZMB-2-HH-9337, Josephine Bank, RV *Sonne*, IceDivA 2, 29 January 2021, EBS, station 85-1, 36°28.80′N 13°59.62′W, 4155 m depth; female (6.8 mm TL), DZMB-2-HH-4474c, Josephine Bank, RV *Sonne*, IceDivA 2, 29 January 2021, EBS, station 85-1, 36°28.80′N 13°59.62′W, 4155 m depth.

Diagnosis

Body length about 3.3 width. Head length about 0.6 width, almost quadrangular. Pereonite 1 visible in dorsal view, narrower than head. Pereonites 2–4 with one dorsomedial process knob-like distally. Natasome with two long ventromedial spines and one medial keel posteriorly; pereonites 5–7 with broad lobe-like anterolateral projections, and with a pair of short anterodorsal spines; pleonite 1 with one dorsal medial spine pointing forward, and broad lobe-like anterolateral projections. Pleotelson, distal terminal spine slender, longer than pleotelson; anterolateral spines broad and short, posterolateral spines acute and long, curved, directed posteriorly.

Remarks

Acanthocope n. sp. A can be recognized from its congeners by: the presence of a dorsomedial process, knob-like distally on pereonites 2–4, the anterolateral spines on the pleotelson, whose axes are clearly perpendicular to its body axis, and by the body margins covered with long setae. In addition, male specimens of this new species are large in total length (10.4 mm including terminal spine) compared to other male specimens of Atlantic *Acanthocope* (*A. annulatus*: 5.9 mm; *A. armata*: 3.2 mm; *A. beddardi*: 3.8 mm; *A. galaica*: 4.4–5.2 mm; *A. galatheae*: 3.3 mm; *A. muelleri*: 3.5 mm; *A. spinicauda*: 7 mm; ; *A. unicornis*: 4.1 mm; *A. puertoricana*: 6.7–7.5 mm); female specimens fall within the reported size range of 3.2–8.7 mm for the Atlantic species listed above. In addition to these species, only single female specimens have been collected of *A. argentinae* (3.6 mm), *A. carinata* (6 mm), *A. eleganta* (2.5–5.9 mm; manca stage only), *A. spinosissima* (8 mm) (Beddard, 1885; Chardy, 1972; Malyutina, 1999; Malyutina and Brandt, 2004; Menzies, 1962, 1956; Schmid et al., 2002).

Acanthocope n. sp. A most resembles *A. galaica* by its general aspect and spine pattern (pereonites 2–4 with one dorsomedial process, knob-like distally, pereonites 5–7 with one pair of spines, pleotelson with one dorsomedial spine followed by a medial keel), but can be recognized from the latter by: broad lobe-like anterolateral projections on pereonites 5–7, a slender distal terminal spine longer than the pleotelson, broad and short anterolateral spines, and acute posterolateral spines. One large male specimen from the Porcupine Abyssal Plain and three female specimens from the Josephine Bank were found with such characters. The full description of this new species is currently in preparation.

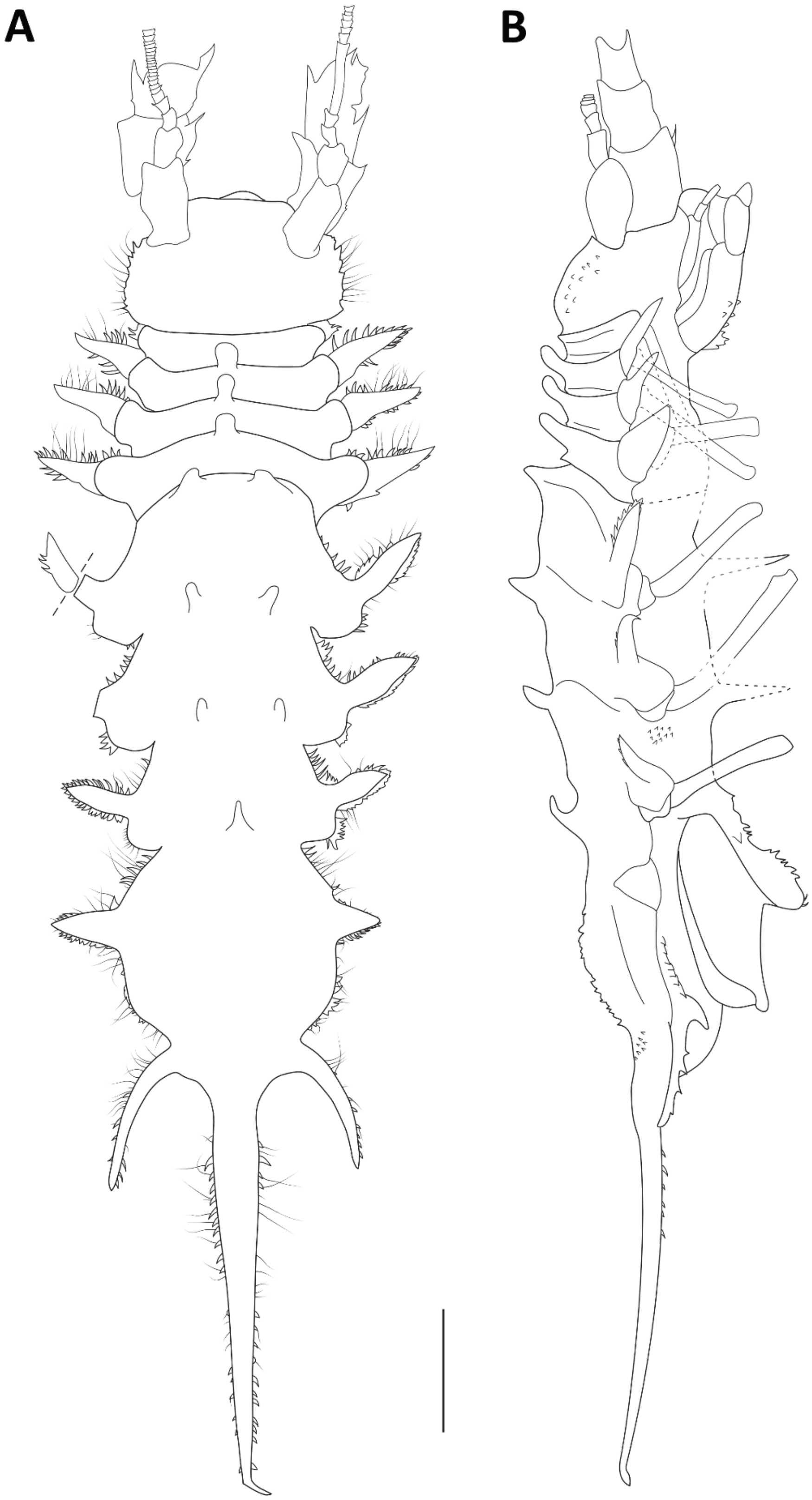

Figure 1. Habitus drawing of *Acanthocope* n. sp. A. Male specimen of 10.4 mm total length, holotype (DZMB-2-HH-9393). **A** Body dorsal view **B** Body lateral view. Scale bar: 1 mm. Drawn by: Z. Hu.

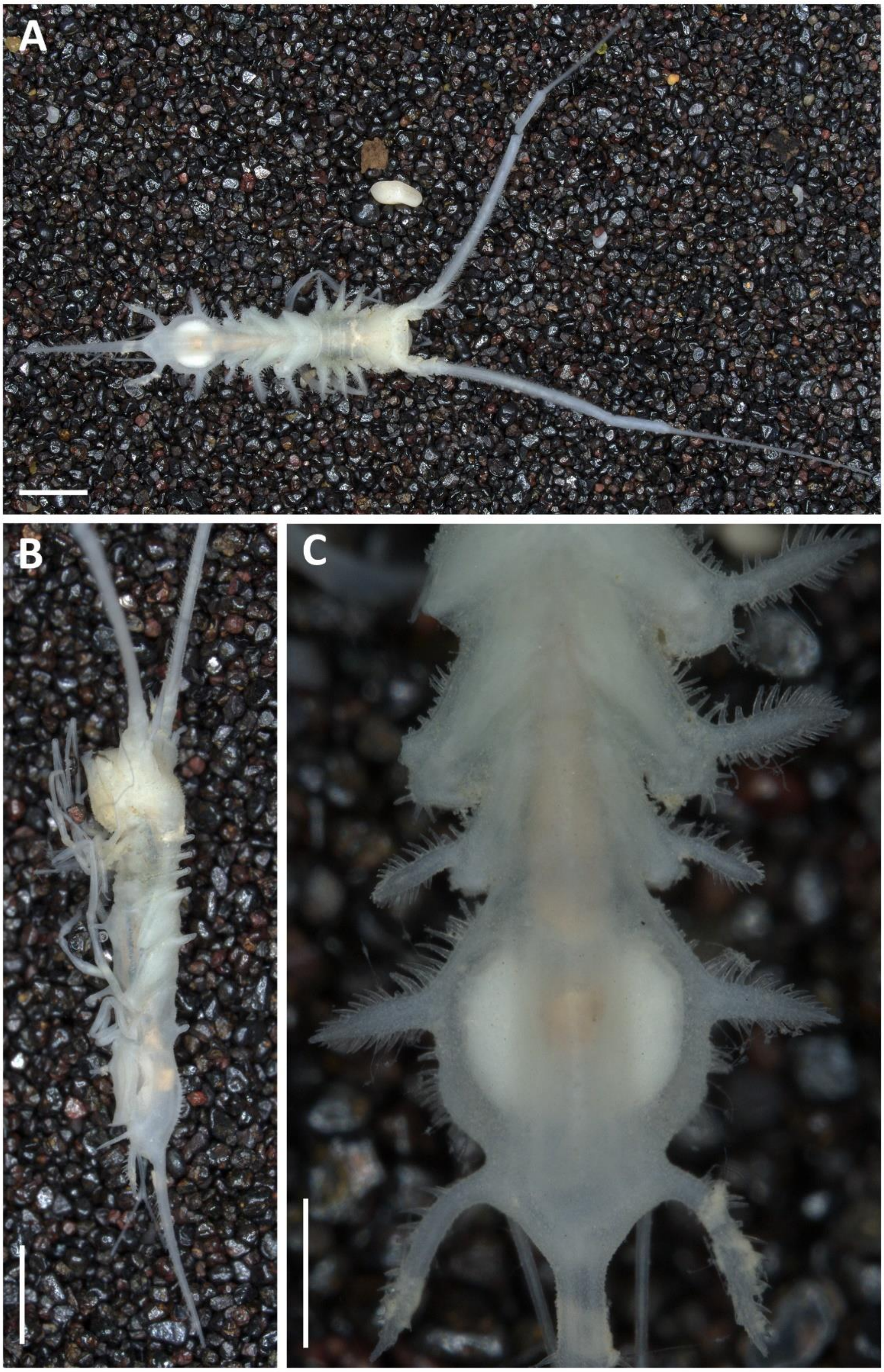

Figure 2. Photographs of *Acanthocope* n. sp. A. Female specimen of 7.0 mm total length, paratype (DZMB-2-HH-9337). **A** Body dorsal view **B** Body lateral view **C** Natasome with medial keel Scale bars A–B: 1 mm, C: 500 µm.

General Discussion

General Discussion

The case studies presented in this thesis expand current knowledge of the diversity, biogeography, and genetic connectivity of benthic invertebrate taxa in the Atlantic deep sea. Studying species with different habitat specificities, reproductive strategies, and adult locomotory abilities enables a nuanced evaluation of how these traits mediate dispersal potential, species distribution patterns, and connectivity in relation to hydrodynamic regimes and geomorphological features. Taxonomic research and species descriptions underscore the ongoing need for integrative taxonomy efforts to resolve species boundaries. The following discussion contextualizes the herein presented findings with the current body of scientific knowledge on dispersal potential and connectivity in deep-sea benthic invertebrates.

An Integrative Methodological Approach

The studied taxa were examined through an integrative approach combining morphological analysis, molecular DNA sequencing and, where applicable, genomic and proteomic methods. All taxa were morphologically identified to species level using relevant taxonomic literature and systematically photographed for morphological documentation. The morphological examinations were carried out using a combination of morphometric measurements, dissections of soft tissue, and the application of EDS and SEM techniques (Appendix I-A). Morphological species identifications were complemented by analyses of single gene mitochondrial (COI, 16S) and nuclear (EF-1, 18S) sequences obtained through Sanger dideoxy DNA sequencing (Sanger and Coulson 1975; Sanger 1988; Appendix I-B). Sequence analyses allowed for molecular species delimitations and detailed assessments of genetic diversity across taxa. To explore nucleotide diversity and species boundaries, a combination of haplotype network reconstruction and genealogical analyses based on Bayesian inference and distance-based methods (ABGD, ASAP) was applied. To complement DNA-based analyses, proteomic fingerprinting, a mass detection of peptide and low molecular weight protein molecules, was used to examine whether molecular genetic divergence is reflected at the protein expression level. To assess fine-scale population structure in *L. ultima*, RAD sequencing was applied using type IIB restriction endonucleases (2b-RAD; Wang *et al.* 2012) to generate uniform fragments of ~50 bp. Altogether, these complementary methodologies enabled robust species identifications and detailed assessments of the genetic diversity and connectivity across taxa at different spatial scales. The herein examined material was sampled on a total of ten research expeditions carried out in the Atlantic Ocean between the years 2005–2021 (Appendix I-C), using five types of benthic gear (Appendix I-D).

Summary of Key Findings

Specimens of the sessile barnacle *Bathylasma hirsutum* (*n* = 159) were obtained from four hard-bottom habitats within the bathyal northeast Atlantic to assess their ecology, genetic diversity and population connectivity (Figure 1; Neuhaus *et al.* 2024). The species is now recognized as capable of colonizing hydrothermally influenced habitats, where specimens differ extrinsically from their conspecifics by ferromanganese shell precipitates. Vent-affiliated specimens revealed the smallest individual size range, with less growth ridges compared to conspecifics of similar size from deeper non-vent habitats. These findings suggest that *B. hirsutum* opportunistically utilizes hard-bottom habitats proximal to the IceAGE hydrothermal vent field, possibly not adapted to exploit the additional organic food resource provided by ambient bacterial mats but. Analyses of 287 novel molecular (COI, EF-1) sequences resulted in overall little intraspecific genetic divergence between populations from the Faroe Bank Channel and the Reykjanes Ridge, including specimens affiliated with the vent field. These results are indicative of high population connectivity within the studied area, mediated by the dispersal of planktotrophic larvae with intermediate and bottom water currents of NADW (Table 1). Although the hydrodynamic regime prevailing along the Reykjanes Ridge offers potential for larvae to be dispersed to suitable hard-bottom habitats west of the MAR, the biogeographic range of *B. hirsutum* remains thus far restricted to the east Atlantic.

Morphological examinations of specimens from the eastern Reykjanes Ridge revealed the presence of dwarf males, providing evidence for the evolution of an androdioecious sexual system in *B. hirsutum* (Neuhaus 2025). These findings are a fundamental contribution to advance knowledge on the reproductive diversity and sexual evolution in bathylasmatid barnacles, for which a complete understanding has yet to be achieved.

Specimens of the sedentary bivalve *Ledella ultima* (*n* = 193) were examined across seven basins east and west of the MAR to conduct a fine-scale assessment of genetic connectivity and population structure at abyssal depths (Neuhaus *et al.* 2025). The analysis of 235 novel molecular (COI, 16S) sequences identified five putative mitochondrial lineages with high intraspecific genetic divergence and a lack of geographic structure. Interpreted to result from previously evidenced sex-specific mitochondrial heteroplasmy, these findings revealed that the sole use of mitochondrial markers poses a challenge to conduct robust assessments of genetic structure in this abyssal protobranch (Figure 1; Table 1). To address the genetic complexity, analyses were complemented by proteomic fingerprinting and 2b-RAD sequencing. High-resolution SNP-based data and proteomic profiles did not mirror the genetic differentiation identified by the molecular markers, denoting that heteroplasmic mitochondrial DNA inflates intraspecific genetic divergence. Despite the SNP data revealing overall little genetic differentiation, admixture analyses identified fine-scale population structure between north-central and south Atlantic basins. Proteomic analyses revealed patters distinct from the basin-based population structure, suggestive of environmentally driven shifts in protein expression, potentially caused by transient physiological responses to different levels of POC flux to the abyssal seafloor.

The biogeography and genetic diversity of species of *Acanthocope* was assessed in the abyssal North Atlantic region, spanning six localities east of the MAR and two localities west of the MAR (Neuhaus *et al.* in prep). Morphological examinations of 224 specimens resulted in the identification of the six recognized species *A. eleganta*, *A. galaica*, *A. galatheae*, *A. muelleri*, *A. puertoricana*, and *A. unicornis* (Figure 1), as well as a novel species designated as *Acanthocope* sp. A (Hu *et al.*, in prep). The data substantially increases individual abundance records of species within the North Atlantic boundary region (55°52.05′–10°22.25′N; 67°09.73′–11°59.39′W), most notably of the species *A. unicornis* and *A. muelleri*. The results indicate a spatial aggregation of *Acanthocope* species in the Northeast Atlantic, where the majority of species exhibit sympatric distributions. The presence of *A. galaica* and *A. puertoricana* was confirmed on both sides of the MAR, suggestive of high genetic connectivity between eastern and western basins. DNA was successfully amplified for 82 specimens of *Acanthocope*, yielding a total of 90 novel molecular sequences for both markers (COI: 82 sequences, 695 bp; complete 18S: 8 sequences, 2309 bp). Molecular species delimitation analyses and proteomic fingerprinting resulted in overall congruent clustering patterns and supported the delineation of *A. galatheae*, *A. muelleri*, *A. unicornis*, and *Acanthocope* sp. A as separate lineages. Specimens morphologically identified as *A. eleganta*, *A. galaica*, and *A. puertoricana* consistently clustered as a single molecular genetic lineage and were poorly resolved by proteomic fingerprinting, raising questions about the current validity of species boundaries. By providing new distributional records and molecular data of *Acanthocope* species from abyssal depths of the North Atlantic, this study closes knowledge gaps in our understanding of biogeographic patterns and genetic diversity within and among species of this natatory isopod genus.

Within the framework of the IceDivA 2 expedition, benthic visual exploration and extractive sampling at 3380–3390 m depth in the abyssal Labrador Sea led to the discovery of a large species of dentaliid scaphopod, which was subsequently described as *Fissidentalium aurae* (Figure 1; Linse and Neuhaus 2024). The species is characterized by a large, moderately curved shell of up to 63.63 mm in length and 11.34 mm in ventral aperture width. The opaque-white, three-layered shell is robust, covered with numerous regular, fine longitudinal ribs, crossed by fine transverse growth lines and without a posterior slit on the dorsal aperture. Out of 19 live specimens collected, 18 specimens were found with an epizoic anemone attached to the concave, anterior shell surface. The abundance of anemone-carrying scaphopods was estimated to one specimen per 15 m^2 along the OFOS track of 1.5 nautical miles. Molecular species delimitation based on 11 molecular (COI, 18S) sequences obtained from nine specimens of *F. aurae* separated the novel species from Atlantic and Pacific congeners, congruent with the morphological and morphometric examinations. Molecular sequencing aided the delimitation of the epizoic anemones to family level of the Actinostolidae Carlgren, 1932. Living specimens of *F. aurae* are noticeable by Lebensspuren they leave behind in the soft sediment, which resemble the width of a feeding anemone. Thus, there seems to be an interest in anemones to find a motile, hosting scaphopod. *Fissidentalium aurae* occurs sympatric with at least two other scaphopod species, the dentaliid *Antalis agilis* (M. Sars, 1872) and the gadilid *Siphonodentalium lobatum* (G. B. Sowerby II, 1860), both of which were obtained at the type locality of *F. aurae* (58°12.289′N 54°13.409′W).

Table 1. Summary of habitat specificity, reproductive strategy, developmental mode, and adult locomotory ability of the studied taxa.

Taxon	Habitat	Reproductive strategy	Developmental mode	Adult locomotory ability
Bathylasma hirsutum	Bathyal hard-bottom	Hermaphroditism + androdioecy Pelagic larvae	Planktotrophic nauplius + cyprid larvae	Sessile
Ledella ultima	Abyssal soft-bottom	Separate sexes Demersal larvae	Lecithotrophic pericalymma larvae	Sedentary
Acanthocope spp.	Bathyal/Abyssal soft-bottom	Separate sexes Brooding	Deposit feeding mancas	Motile
Fissidentalium aurae	Abyssal soft-bottom	Separate sexes Demersal larvae	Lecithotrophic stenocalymma larvae	Burrowing + motile

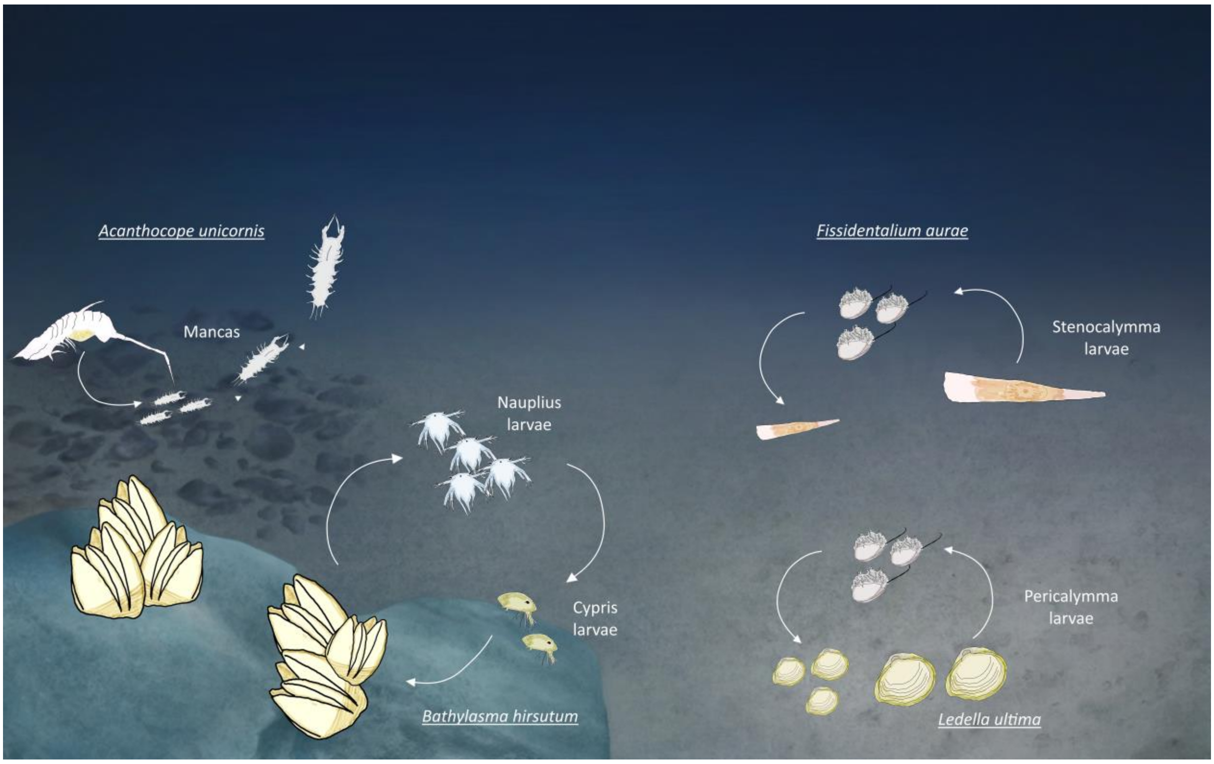

Figure 1. Illustration of the studied taxa and their developmental modes. Depicted are the barnacle *Bathylasma hirsutum*, the protobranch bivalve *Ledella ultima*, the munnopsid isopod *Acanthocope unicornis*, and the dentaliid scaphopod *Fissidentalium aurae*. Specimens illustrated by the author. Background illustrated by Fana S. Demissie.

Implications of Dispersal Potential for Deep-Sea Connectivity

Connectivity in the deep sea emerges from a complex interplay of biological, physical, and evolutionary processes that operate across spatial and temporal scales (Etter and Bower 2015; Cramer *et al.* 2023). A species' dispersal potential directly influences the degree of connectivity, as it mediates the exchange of individuals among geographically separated populations (Cowen *et al.* 2007; Hilário *et al.* 2015). Dispersal, however, is not simply a function of diffusive or advective processes, but is modulated by the depth and duration of the dispersive phase, larval and/or adult behavior (*e.g.,* swimming, vertical migration), settlement success, physiological tolerance, and survivorship (Etter and Bower 2015; McVeigh *et al.* 2017; Gary *et al.* 2020). Furthermore, a species' dispersal potential does not necessarily equate to dispersal success, as habitat specificity, reproductive frequency, and fecundity collectively influence the number of individuals that contribute to population renewal (Cowen and Sponaugle 2009; Hilário *et al.* 2015). Physical processes such as current speed and direction, topographic steering, mesoscale eddies, and episodic disturbance events may further contribute to either retention or long-distance transport, while ridges, fractures, and oceanographic fronts may act as potential barriers or conduits, depending on the flow structure of bottom waters (White *et* *al.* 2010; Gary *et al.* 2020). Ultimately, a comprehensive understanding of deep-sea connectivity demands a holistic approach that integrates reproductive strategy and dispersal potential with oceanographic circulation patterns and seafloor topography (Swanborn *et al.* 2022; Macheriotou *et al.* 2025). By examining benthic invertebrate taxa with contrasting life-history strategies across broad bathymetric and geographic ranges, and investigating their genetic connectivity in light of biological and environmental drivers, the case studies of this thesis embody such an integrated perspective. In synthesis, they contribute to a growing effort in deep-sea research to disentangle the complex interplay between larval traits, oceanographic processes, and habitat structure in shaping patterns of dispersal and connectivity.

While early research on deep-sea benthic connectivity primarily relied on allozyme or single-locus mitochondrial markers (reviewed in Taylor and Roterman 2017), subsequent studies increasingly integrated physical drivers of larval transport to emphasize the role of hydrodynamics and larval behavior in shaping dispersal trajectories (*e.g.,* Young *et al.* 1997; Levin 2006). The development of biophysical models, incorporating ocean circulation data and larval biology, marked a key advancement allowing researchers to simulate dispersal trajectories under oceanographic conditions, highlighting the potential for current-driven larval transport across complex seascapes (*e.g.,* Cowen *et al.* 2007; White *et al.* 2010; Sala *et al.* 2013). Pelagic larval duration (PLD), defined as the time larvae spend in the plankton prior to settlement, and pelagic propagule duration (PPD), which includes both embryonic and larval phases, have frequently been used as proxies for dispersal potential in connectivity assessments (Shanks *et al.* 2003; Shanks 2009; Selkoe and Toonen 2011). For simplicity, the term "larval duration" is used herein to refer to the full planktonic developmental phase. Because larval duration is taxon-specific and influenced by environmental gradients like temperature (O'Connor *et al.* 2007) and depth (McVeigh *et al.* 2017), defining dispersal distance solely as a function of PLD or PPD would undermine the complex interplay between life-history traits, behavior, and hydrodynamic regimes (Sponaugle *et al.* 2002; Cowen and Sponaugle 2009; Hilário *et al.* 2015). For example, PLD has been shown to be an inconsistent determinant of species' geographic range size and to perform poorly in predicting connectivity patterns (Lester *et al.* 2007; Weersing and Toonen 2009). Furthermore, Mercier *et al.* (2013) challenged the long-standing assumption that planktotrophs have universally longer larval durations than lecithotrophs (*e.g.,* Calow 1983; Jablonski and Lutz 1983), finding no significant difference in range size between larval modes across multiple taxa. Suggestive of that larval mode is not a reliable predictor of larval duration or connectivity, these findings emphasize that evolutionary history, larval behavior, and environmental gradients interact in complex, taxon-specific ways to shape dispersal outcomes (Mercier *et al.* 2013; Laming *et al.* 2021).

Dispersal Potential of Soft-Bottom Fauna

Particularly in the low temperature environment of the deep sea, it has repeatedly been shown across taxa that lecithotrophic larvae have an extended pelagic phase, resulting in long-distance dispersal to suitable habitats for settlement (Young *et al.* 1997; Génio *et al.* 2013; Baco *et al.* 2016; Montgomery *et al.* 2019; Álvarez-Noriega *et al.* 2020; Laming *et al.* 2021; Taboada *et al.* 2023). Long-distance dispersal and high genetic connectivity have also been documented in brooding taxa, covering extensive geographic ranges despite of seemingly limited dispersal capacity. For example, in the deep-sea quill worm *Hyalinoecia robusta* Southward, 1977 (Annelida: Onuphidae), a tube-dwelling polychaete that moves across soft sediments by crawling (Wigley and Emery 1967), analyses of an extensive sample collection revealed high levels of genetic connectivity within and between populations in the Atlantic and Indian Oceans (Budaeva *et al.* 2024). Given the species' sedentary lifestyle with limited adult mobility, the authors proposed the existence of unsampled intermediate populations acting as stepping-stones to maintain gene flow, as has been proposed for other deep-sea taxa with comparable life-history traits (Yearsley and Sigwart 2011; Hilário *et al.* 2015). Discussing pan-oceanic distributions in three abyssal polychaete species, Meißner *et al.* (2023) proposed sediment translocation by benthic storms as a mechanism for large-scale dispersal, even in species without a pelagic larval stage – a notion adopted by Budaeva *et al.* (2024) as a potential explanation for the high levels of connectivity in *H. robusta*. While dispersal and connectivity in other taxa without pelagic larvae may be facilitated by adult mobility, such as active swimming in deep-sea munnopsid isopods (Brix *et al.* 2020), the studies underscore the potential of deep-sea sediment dynamics and bottom currents to mediate long-distance dispersal in the sedentary benthos (Meißner *et al.* 2023; Budaeva *et al.* 2024). Estimating how physical transport processes in the deep Northwest Atlantic influence passive larval dispersal and patterns of genetic variation, Etter and Bower (2015) demonstrated that modeled larval trajectories deviated substantially from the mean southwestward flow of the Deep Western Boundary Current (DWBC), instead following highly convoluted paths due to complex hydrodynamics within the region. Notably, the mean dispersal distances after 30 days were greatest at the deepest depths tested (2000m and 3200 m), suggesting that passive dispersal potential might increase with depth (Etter and Bower 2015). Their results highlight the non-linearity of deep-sea current systems and challenge assumptions of simple advective processes, particularly for demersal larvae, and propagules, that are subject to bottom-flow regimes.

These patterns resonate with the biogeographic range and high genetic connectivity observed in *L. ultima* from abyssal depths (Neuhaus *et al.* 2025). The interplay of a sedentary adult lifestyle, the dispersal through lecithotrophic larvae, and a habitat specificity to soft-sediment plains sustains populations currently recognized to span over 10,000 km in latitude across the entire Atlantic. The fine-scale genetic structure detected between populations from the north-central and south Atlantic basins suggests that large-scale circulation pathways of deep Atlantic water masses play a critical role in mediating gene flow, enabling pericalymma larvae to be transported across geomorphological features that separate abyssal basins. The dispersal potential of eggs and lecithotrophic larvae, supported by substantial yolk reserves and low metabolic rates, is likely enhanced by passive entrainment in the suprabenthic layer, where they may remain viable over extended periods (Hain and Arnaud 1992; Zardus 2002; Scheltema and Williams 2009). Additionally, stepwise dispersal across geographically intermediate populations likely facilitates genetic connectivity between widely separated abyssal basins (Yearsley and Sigwart 2011), each offering extensive and heterogeneous soft-sediment plains suitable for settlement and recruitment of successive generations. Similar to *L. ultima*, the amphi-Atlantic range of the protobranch *Nucula atacellana* Schenk, 1939 (Allen and Sanders 1996), along with the absence of significant genetic divergence across the North Atlantic (Zardus *et al.* 2006), indicates substantial dispersal capacity of lecithotrophic larvae (Zardus 2002; Scheltema and Williams 2009). With both these bivalve species demonstrating considerable dispersal potential and wide geographic distributions, it is surprising that molluscs were identified as the least dispersive deep-sea taxon when assessed in a meta-analysis, including molecular sequence data of *N. atacellana* and *L. ultima* (Baco *et al.* 2016). Whereas this inference may apply to certain molluscan taxa, it risks obscuring species-specific dispersal capacities shaped by fine-scale ecological and oceanographic processes. These cases underscore the limitations of meta-data analyses in capturing biologically meaningful variation among closely related taxa, and highlight the necessity of integrating species-specific life-history traits with environmental and hydrodynamic context (Cramer *et al.* 2023; Macheriotou *et al.* 2025). With regard to obligate brooding peracarids, parallels can be drawn between the biogeographic range of Atlantic *Acanthocope* and that of tanaid crustaceans (Tanaidacea: Neotanaoidea), highlighting their capacity for broad geographic distributions and high levels of genetic connectivity in the deep Atlantic (Neuhaus *et al.* in prep; Palacios Theil and Błażewicz 2024). Despite the constrained adult mobility in tanaids, molecular genetic analysis revealed nearly identical haplotypes between specimens of *Venusticrus* Gardiner, 1975 from the Puerto Rico Trench and the Vema Fracture Zone (VFZ), suggesting long-distance dispersal and high levels of genetic connectivity across the MAR and a depth gradient of over 3000 m (Palacios Theil and Błażewicz 2024). Given that adult *Acanthocope* are capable of active swimming, it is plausible that their dispersal potential is equal to or even greater than that of strictly walking and crawling taxa, as has been demonstrated before (Wilson and Hessler 1987; Schnurr *et al.* 2014; Bober *et al.* 2018; Brix *et al.* 2020). This is supported by the herein documented occurrence of *A. galaica* and *A. puertoricana* on both sides of the MAR, indicating trans-Atlantic connectivity (Neuhaus *et al.*, in prep). The adult swimming ability of munnopsid isopods likely enables individuals to ascend into the vertical water column, where elevated current velocities within intermediate water masses may facilitate long-distance dispersal. Although such vertical movements require considerable physiological tolerance to steep gradients in pressure, temperature, and salinity, the capacity to traverse several hundred meters in depth has been well-documented among numerous zooplanktonic crustacean taxa, which undertake diel vertical migrations across pronounced environmental gradients (Yamaguchi *et al.* 2002; Ochoa *et al.* 2013; Fernandez de Puelles *et al.* 2023). In general, levels of little genetic differentiation in several taxa with trans-Atlantic distributions aligns with the DDH hypothesis, as well as growing evidence that geomorphological features, such as the MAR, do not represent an absolute barrier to dispersal in the deep sea (Fiege *et al.* 2010; Olu *et al.* 2010; Brix *et al.* 2011; Riehl *et al.* 2018; Guggolz *et al.* 2019). Even in the absence of planktonic larvae, deep-sea benthic invertebrates can exhibit unexpectedly wide distributions and low levels of population structure, emphasizing the need to re-evaluate assumptions about dispersal limitations in brooders across abyssal environments. The great potential for translocation by bottom currents to facilitate long-distance dispersal of larval, juvenile, and adult stages should not be overlooked when assessing dispersal capacity and connectivity in soft-bottom benthic invertebrates.

Dispersal Potential of Hard-Bottom Fauna

In the bathylasmatid barnacle *B. hirsutum*, the interplay of a sessile adult lifestyle, pelagic dispersal of planktotrophic larvae, and specificity to hard-bottom habitats at bathyal depths supports populations currently recognized to span over 3600 km across the Northeast Atlantic (Neuhaus *et al.* 2024 and references therein). With a depth range of 384–1829 m, the species exhibits a pronounced physiological tolerance to depth-related environmental gradients. The nauplius larvae of bathylasmatid barnacles are capable of extensive vertical migration (De Wolf 1973; Hui and Moyse 1987; Walker *et al.* 1987). They undergo a planktonic existence estimated to last at least 3–4 weeks (Foster 1983; Scheltema *et al.* 2010), followed by metamorphosis into the cyprid stage, which is likely to remain within intermediate and bottom water layers (Tapia *et al.* 2010). In terms of habitat specificity and larval developmental mode, *B. hirsutum* shows notable parallels with the cold-water coral *Desmophyllum pertusum* (Linnaeus, 1758). Both species are sessile hard-bottom inhabitants of the Atlantic deep sea, require habitats of moderate current velocities, and disperse via planktotrophic larvae of similar behavioral biology (Southward and Southward 1958; Anderson 1994; Kenchington *et al.* 2017; Strömberg and Larsson 2017). In *D. pertusum*, larval strategy has facilitated an extensive geographic distribution across the Atlantic Ocean (Tong *et al.* 2022), within which populations along the northwest Atlantic margin exhibit high levels of genetic connectivity (Weinnig *et al.* 2024). To quantify larval dispersal pathways of *D. pertusum* within this region, a recent study by Guy *et al.* (2025) applied high-resolution biophysical modeling, using ocean circulation patterns in combination with life-history parameters. Their simulations revealed that temporally stable, directional current systems of the Gulf Stream and the DWBC facilitate long-distance larval transport, irrespective of variability in larval duration or swimming behavior, highlighting the applicability of the model to deep-sea species with similar life-history traits. Notably, the authors suggested that colonies in the Northwest Atlantic may have originated from eastern Atlantic populations, underscoring the capacity for trans-Atlantic connectivity in this sessile coral species (Guy *et al.* 2025). Although *B. hirsutum* is presently documented from the eastern Atlantic only, Neuhaus *et al.* (2024) revealed high levels of genetic connectivity between populations within the northeast Atlantic region, separated by ~1,100 km in geographic distance and 442 m in depth. By inference from the shared habitat specificity, planktotrophic development, and larval behavior with *D. pertusum*, the larvae of *B. hirsutum* may similarly be capable of long-distance dispersal across the MAR, as well as successful settlement in suitable habitats along continental margin of the western Atlantic. As such, the absence of records from this region to date may potentially reflect under sampling rather than true distributional limits of this deep-sea barnacle species. Supporting this, a single specimen of *Bathylasma* sp. was discovered at 1950 m depth in the Mar del Plata submarine canyon off the Argentine margin, representing the first known record of the genus in the southwest Atlantic (Chiesa *et al.* 2024). However, the poor condition of the specimen currently precludes definitive species identification. Because the dissection of soft parts is not advisable at this stage to preserve this precious material (Chiesa *et al.* 2024), additional sampling efforts are highly encouraged to enable detailed morphological and molecular analyses. While *Bathylasma* sp. may represent a new species to science from the southwest Atlantic, it could alternatively reveal a previously untapped dispersal potential in *Bathylasma*.

Taxonomic Remarks on *F. aurae*

By integrating morphological examinations with molecular techniques, the taxonomic research presented in this thesis provides a fundamental contribution to our understanding of species diversity and distribution in the abyssal North Atlantic, while establishing a framework for future taxonomic and molecular research efforts (Hu *et al.* in prep; Linse and Neuhaus 2024). Some remarks regarding the dentaliid scaphopod *F. aurae* are warranted here. Due to the limited understanding of scaphopod reproductive biology, particularly in the deep sea (Reynolds 2002), it is inferred that *F. aurae* exhibits lecithotrophic larval development (Haszprunar and Wanninger 2012) and disperses via planktonic stenocalymma larvae, as described for other dentaliid species (Buckland-Nicks and Gibson 2025). The morphological resemblance of stenocalymma larvae to the pericalymma larvae of protobranch bivalves (Zardus and Morse 1998) suggests the potential for prolonged larval viability and dispersal in the deep sea. The recovery of 19 specimens from a single AGT haul at 3387 m depth in the abyssal Labrador Sea indicates high local abundance of *F. aurae*, with estimated densities of approximately one individual per 15 m^2 of seafloor. Given the amphi-Atlantic distribution of its congeners *F. candidum* (Jeffreys, 1877) and *F. capillosum* (Jeffreys, 1877), it is plausible that the range of *F. aurae* extends south of the Labrador Sea, potentially overlapping with the distributional range of these already sympatric species. *Fissidentalium aurae* likely alternates between burrowing and surface movement in search of food. The symbiotic relationship with an actinostolid anemone is indicative of a prolonged motile phase, during which the scaphopod remains exposed above the sediment surface, facilitating the attachment of the anemone's larva to the scaphopod shell. As epizoic anemones have only been documented on living *Fissidentalium* (Shimek and Moreno 1996; Shimek 1997; Zibrowius 1998; Linse and Neuhaus 2024), the attachment of anemone larvae may be environmentally induced, possibly triggered by chemical cues of the scaphopod shell (Hadfield and Paul 2001). In the Pacific species *F. actiniophorum* Schimek, 1997, the epizoic anemone was identified as *Anthosactis nomados* White, Wakefield Pagels & Fautin, 1999, which disperses via pelagic planula larvae (Pagels 1993; White *et al.* 1999). Owed to the morphological similarity and consistent presence of anemones on *F. aurae*, taxonomic specialists are advised to examine epizoic anemones associated with *F. aurae* and other Atlantic *Fissidentalium* species, and to determine their identity at species level through direct comparison with *A. nomados* from respective museum collections (White *et al.* 1999).

Multifaceted Challenges in Deep-Sea Research

Despite over two centuries of deep-sea exploration in the Atlantic Ocean, large swaths of the seafloor remain devoid of biological records (Amon *et al.* 2022; Kennedy and Rotjan 2023). Deep-sea sampling to date has been disproportionately concentrated in the North Atlantic, reflecting an infrastructural and socioeconomic imbalance that skews biodiversity assessments toward the Northern Hemisphere (Allcock *et al.* in press; Bridges *et al.* 2023). Yet, even in the comparatively well-studied North Atlantic deep sea, our understanding of benthic species diversity and biogeographic patters remains severely limited. The acquisition of deep-sea faunal samples requires long-term planning, extensive funding, and sophisticated equipment which must be deployed from research vessels suited to conduct deep-sea research (Rogers and Ramirez-Llodra 2024). Even with a new generation of vessels and advancements in deep-submergence technology (Marlow *et al.* 2022; Kennedy and Rotjan 2023), the challenge of obtaining biological material, notably at basin-wide scales, persists. In addition, a profound taxonomic gap impedes the identification and analysis of deep-sea biodiversity data. Ten years ago, Coleman (2015) outlined this taxonomic impediment as a multifaceted challenge that hampers biodiversity research and conservation efforts. For example, during the years 2000–2015, merely nine out of 30 amphipod taxonomy specialists held permanent positions and continued their work on describing species. Generally speaking, a strong disparity has emerged between the high rates of species discovery since the 1960s (*e.g.,* Sanders *et al.* 1965; Hessler and Sanders 1967) and the rate of formal species descriptions, largely due to a declining number of taxonomic experts. While species discovery in the deep sea continues with high frequency, the time needed to formally describe species often exceeds the financial and temporal limits set by projects. For instance, Brix *et al.* (2015) found that 95% of collected deep-sea isopod species from the VFZ were new to science, estimated to require at least five years of intensive taxonomic work to formally describe these. Since funding that exclusively promotes taxonomic research has become a rare resource, the rate of species descriptions can hardly keep up with the rate of species discoveries (Coleman 2015; Higgs and Attrill 2015; Chen 2024). Consequently, many species recovered during historic and contemporary research expeditions remain undescribed or are assigned provisional identifications, limiting their integration into global biodiversity databases. Furthermore, vast volumes of biodiversity data lie dormant within museum collections, offering an invaluable resource for filling taxonomic and geographic gaps (*e.g.,* Budaeva et al., 2024). These "hidden specimens" represent a largely untapped, often non-digitized, archive of faunal diversity that was collected decades ago, yet never formally studied (Chavan and Krishnan 2003; Hutchings and Kupriyanova 2018). While traditional preservation methods, such as formalin fixation, continue to pose challenges for molecular analyses of museum specimens, advances in sequencing technologies have increasingly enabled successful DNA extractions from such material (Chase *et al.* 1998; Boyle and Etter 2013; Holleley and Hahn 2025).

Closing Gaps in Deep-Sea Biodiversity Assessment

Recent research efforts have substantially advanced knowledge of species diversity, distribution, and connectivity in deep-sea benthic invertebrates (Galaska *et al.* 2017; Hurtado-García and Manjón-Cabeza 2022; Taboada *et al.* 2023; Lörz *et al.* 2023; Meißner *et al.* 2023; Budaeva *et al.* 2024; Palacios Theil and Błażewicz 2024; Gunton *et al.* 2025; Guy *et al.* 2025; Macheriotou *et al.* 2025; O'Hara *et al.* 2025). Nevertheless, significant gaps in deep-sea biodiversity assessment persist and addressing them remains a key priority. Embedded within the Challenger 150 ocean management program, the UN Decade action IceDivA (2021–2024; Brix and Taylor 2021; Brix *et al.* 2022) has served as a valuable knowledge hub. By assembling a comprehensive collection of biological and environmental data along a latitudinal gradient in the Atlantic deep sea, past and contemporary research on this material continues to advance biodiversity exploration from both unassessed and revisited sites. The case studies presented here on benthic invertebrate taxa contribute substantially to this effort by providing biological and molecular data from both established and newly described species of the Atlantic deep sea. These findings advance understanding of species distribution patterns and connectivity across spatial scales, considering habitat specificity, reproductive strategy, and dispersal capacity. Individually and collectively, the studies of this thesis provide knowledge directly relevant to assessing ecosystem vulnerability and guiding the designation of marine protected areas (MPAs) in the deep-sea environment. Underscoring this relevance, ecological connectivity, *i.e.,* genetic connectivity (see Cramer *et al.* 2023), has been incorporated as an indicative criterion for MPA designation under the UN Convention on the Law of the Sea on the Conservation and Sustainable Use of Marine Biological Diversity of Areas Beyond National Jurisdiction (BBNJ Agreement; De Lucia 2024). This agreement aims to ensure the long-term conservation and sustainable use of marine biodiversity in areas beyond national jurisdiction through the equitable sharing of marine genetic resources, the application of area-based management tools, environmental impact assessments, and capacity-building (un.org/bbnjagreement/en). Its implementation is crucial in light of the global role deep-sea ecosystems play in sustaining ecological processes and delivering essential ecosystem services (Allcock *et al.* in press). Functional habitats such as seamounts, cold-water coral reefs, hydrothermal vents, mid-ocean ridges, and abyssal plains contribute to biogeochemical cycling, including the regulation of carbon, nitrogen, and silicate fluxes. These systems are central to climate regulation, mediate chemical exchange between the ocean and atmosphere, and support primary production through chemosynthetic pathways (La Bianca *et al.* 2023). Recent findings of dark oxygen production at the abyssal seafloor further underscore how little is known about the complexity of these precious ecosystems (Sweetman *et al.* 2024). In addition to the ecological functions, deep-sea environments harbor biological resources vital to food security and biomedical innovation, making their conservation a matter of global priority.

Grounded in well-curated, georeferenced specimen collections from ten international deep-sea research expeditions, the case studies on *B. hirsutum*, *L. ultima*, *Acanthocope* spp., and *F. aurae* enabled extensive cross-habitat comparisons of species distributions, reproductive strategies, and connectivity within a unified Atlantic context, thereby addressing key research priorities for effective conservation and deep-sea management. Collectively, these studies underscore the importance of sustained, internationally coordinated sampling initiatives in overcoming taxonomic and geographic gaps and in building the long-term knowledge base essential for biodiversity assessment and conservation in this complex, three-dimensional realm.

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Acknowledgements

Looking back over the past four years of my PhD, I am deeply grateful to the colleagues, friends, and family whose support has been invaluable along my academic path. Thanks to all of you, I have accomplished more than I could have imagined when I first set sail on this challenging and exciting voyage.

First and foremost, I am sincerely indebted to my supervisor, Prof. Dr. Saskia Brix, for her unwavering enthusiasm, guidance, and support whenever I needed it. Thank you for introducing me to the fascinating world of deep-sea biology and asellote isopods. Thank you for the opportunity to join the IceAGE 3 and IceDivA 2 expeditions, they inspired me to pursue with deep-sea research. I am grateful to my second supervisor, Prof. Dr. Susanne Dobler, for her consistent support, encouragement, and thoughtful feedback. Thank you for giving me the opportunity to teach on the field course on Langeneß, an experience I truly enjoyed. I am thankful for the guidance of my co-supervisor, Prof. Dr. Pedro Martínez Arbizu, who introduced me to the world of RAD sequencing. Thank you for sharing your profound expertise in this field, for the many fruitful discussions and your support.

I am most grateful to Dr. Katrin Linse for introducing me to deep-sea molluscs and for sharing her taxonomic expertise. Working together with you, on land and at sea, has been truly rewarding. I also wish to thank Dr. James Taylor for acquainting me with deep-sea barnacles and for always offering a helping hand. I am deeply grateful to my colleagues at the DZMB Hamburg for creating a warm and dynamic working environment. Thank you for supporting me, for your valuable feedback and enriching conversations during our lunch and coffee breaks. A special thanks is owed to Karen Jeskulke and Nicole Gatzemeier for their kindnesses and essential support in lab work and logistics, as well as Antje Fischer and Sven Hoffmann for their kind help at any time. I would like to express my gratitude to my former office buddy and good friend, Mark E. de Wilt. Working together has been inspiring and great fun – the chicken never failed us! I would also like to thank Carolin Uhlir for her uplifting spirit and the many enriching conversations we enjoyed at work and beyond. I also wish to thank all guest researchers and visiting students who brought energy, inspiration, and good company to my days at the DZMB. A special thanks to Dr. Emanuel Pereira for sharing his taxonomic expertise and passion for asellote isopods!

Furthermore, I am most grateful to my colleagues at the DZMB Wilhelmshaven for their kindness and valuable support, and I warmly thank Dr. Sahar Khodami and Dr. Sven Rossel for their advice with molecular and proteomic lab work. A special thanks goes to my dear friend, Angelina Eichsteller, whose enthusiasm and warmth kept me spinning! I further wish to thank the scientific and technical staff of the LIB Hamburg, especially Dr. Nancy F. Mercado Salas for her enduring support, and Dr. Jenna Moore for generously taking the time to proofread my work, for providing valuable feedback, and chocolate! Thanks to Prof. Dr. Ron J. Etter, Prof. Dr. Robert M. Jennings, Prof. Dr. Julia Sigwart, Dr. Tom White and others for kindly providing specimens. I wish to thank Zhehao Hu, Clara Bachmann, and Halina Jereczek for their assistance in sample processing, and all my co-authors for their insightful contributions and the collaborative spirit. Dr. Martin Schwentner is especially thanked for his constructive feedback and helpful advice in bioinformatic analyses, as is Dr. Janna Peters for her positive momentum and invaluable support. I thank Dr. Lars Harms and Nancy Kühne from the Alfred Wegener Institute Bremerhaven for their assistance with RAD sequencing, and Mia Schumacher from the GEOMAR Helmholtz Centre for Ocean Research Kiel for assisting with bathymetry and map compilations.

The captains, crew, scientists, technical staff, and students onboard the research vessels Maria S. Merian (MSM75), Meteor (M63/2, M79/1, Sonne (SO237, SO276, SO280, SO286), Polarstern (PS67), Poseidon (POS456), and Endeavour (EN447) are much thanked for their help in data collection. A special thanks goes to the teams of ROV Kiel6000 and ROV Phoca (GEOMAR Kiel) for collecting deep-sea specimens. This research was funded by the German Federal Ministry of Education and Research (BMBF) through grant no. GPF 21-2_052 (IceDivA, 03G0286NA), and supported by the German Research Foundation (DFG) through grant no. BR3843/4-1, BR3843/5-1, MerMet17-06, and the initiative 1991 “Taxonomics”, grant no. RE2808/3-1/2. I am grateful to Prof. Dr. Colin Devey (GEOMAR Kiel) for enabling me to secure a bridge fund from the iAtlantic project (EU/HORIZON 2020, Blue Growth Agreement, grant no. 818123), to whose research aims this work has contributed.

Während meiner gesamten Promotion und insbesondere in der Endphase dieser Dissertation war die Unterstützung meiner Familie und meiner Freunde von unschätzbarem Wert. Ein sehr großer Dank gilt meinen Eltern, die mich auf meiner akademischen Laufbahn mit viel Liebe begleitet und mit voller Kraft unterstützt haben. Danke, dass Ihr immer ein offenes Ohr für meine Freuden und Sorgen hattet und habt. Eure Unterstützung bedeutet mir unglaublich viel! Ein herzliches Danke an Oma, Anke, und Rainer für Eure motivierenden Worte und dafür, dass Ihr mein sicherer Hafen in der Heimat seid. Ein besonders lieber Dank gilt Barbara, die mich auf meinem Weg stets mit Ihrer Fachkunde, Gastfreundschaft, Herzlichkeit und guten Frankfurter/Schwäbischen Kochkunst unterstützt hat.

Ein herzlicher Dank gilt John und Martina für die vielen schönen Unternehmungen und unbeschwerten Momente, aus denen ich neue Energie schöpfen konnte.

Tusen hjertelig takk til mine norske venner som alltid har støttet meg på tvers av havene. Til Adrianna, Paul, Knut, Ingvild, Helene, Ingrid og mange andre for at jeg, takket være dere, føler meg hjemme selv langt borte fra hjemlandet. Jeg er veldig glad i dere!

Ein ganz großes Danke gilt dem inneren und äußeren Frankfurter Zirkel, Jakob, Niklas, Anna, Charly, Sarp, Lena, Vale, Miri, Tobi, Konsti, Tillman, Nils und Max, sowie meinen Hamburger Jungs und Deerns, Ricardo, Elena, Jannik, Mariam, Lili, Finn, Jule, Dominik, Beza, Sarah, Julius, Tobi, Hanna und Flo. Danke für Eure geduldigen Ohren, wenn ich mal wieder endlos über Tiefsee Organismen und deren Fortpflanzung gesprochen habe. Danke für die vielen, schönen Runden und Stunden, für die gute Laune, gemeinsamen Urlaube und Eure wertvolle Unterstützung. Ihr bedeutet mir alle sehr viel!

Zu guter Letzt gebührt mein allergrößter Dank meinem liebevollen Partner, Paul. Danke für deine unendliche Geduld, für tiefgründige Gespräche in guten wie in schlechten Phasen, für deine Ermutigung, deine positive Energie und absolut bedingungslose Unterstützung während dieser gesamten Reise und darüber hinaus. Ich liebe dich.

Appendix

Appendix

I. Supporting Information

I-A. List of Figures and Tables

General Introduction

The Bathylasmatid Barnacle *Bathylasma hirsutum* (Hoek, 1883)

Neuhaus *et al.* 2024

Neuhaus (2025)

The Protobranch Bivalve *Ledella ultima* (E. A. Smith, 1885)

Neuhaus *et al.* 2025

The Munnopsid Isopod Genus *Acanthocope* Beddard, 1885

Neuhaus *et al.* in prep

The Dentaliid Scaphopod *Fissidentalium aurae* Linse & Neuhaus, 2024

Linse & Neuhaus (2024)

Description of a new species of *Acanthocope* Beddard, 1885

Hu *et al.* in prep

General Discussion

I-B. List of Primers

Primer	Sequence (5' to 3')	Reference
COI		
LCO1490	GGT CAA CAA ATC ATA AAG ATA TTG G	Folmer *et al.* 1994
HCO2198	TAA ACT TCA GGG TGA CCA AAA ATC A	
jgLCO1490	TIT CIA CIA AYC AYA ARG AYA TTG G	Geller *et al.* 2013
jgHCO2198	TAI ACY TCI GGR TGI CCR AAR AAY CA	
LCO1490-JJ	CHA CWA AYC ATA AAG ATA TYG G	Astrin & Stüben (2008)
HCO2198-JJ	AWA CTT CVG GRT GVC CAA ARA ATC A	
16S		
LMY16F	GAC GAR AAG ACC CYR TCA AAC	Chase *et al.* 1998
Lu16R4	GCT GTT ATC CCT CCA GTA ACT	
EF-1		
EF-1 for	GAT TTC ATC AAG AAC ATG ATC AC	Tsang *et al.* 2014
EF-1 rev	AGC GGG GGG AAG TCG GTG AA	
18S		
18A1mod	CTG GTT GAT CCT GCC AGT CAT ATG C	Raupach *et al.* 2009
400F	ACG GGT AAC GGG GAA TCA GGG	Dreyer & Wägele (2001)
700F	GTC TGG TGC CAG CCG CG	
1000F	CGA TCA GAT ACC GCC CTA GTT C	
700R	CGC GGC TGC TGG CAC CAG CAC	
1155R	CCG TCA ATT CCT TTA AGT TTC AG	
1500R	CAT CTA CGG CAT CAC AGA	
R-563	ACC AGA CTT GCC CTC C	Raupach *et al.* 2009
1250FNmod	GGC CGT TCT TAG TTG GTG GAG	
1800mod	GAT CCT TCC GCA GGT TCA CCT ACG	

I-C. List of Deep-Sea Expeditions

ANDEEP III	*RV POLARSTERN* (PS67)	2005
DIVA 2	*RV METEOR* (M63/2)	2005
ENAB	*RV ENDEAVOUR* (EN477)	2008
DIVA 3	*RV METEOR* (M79/1)	2009
Vema-TRANSIT	*RV SONNE* (SO237)	2014/2015
IceAGE 2	*RV POSEIDON* (POS456)	2013
IceAGE RR	*RV MARIA S. MERIAN* (MSM75)	2018
IceAGE 3	*RV SONNE* (SO276)	2020 - *participant*
IceDivA 1	*RV SONNE* (SO280)	2021
IceDivA 2	*RV SONNE* (SO286)	2021 - *participant*

I-D. List of Benthic Gear

Agassiz Trawl (AGT)

Box Corer (BC)

Epibenthic Sledge (EBS)

Ocean Floor Observation System (OFOS)

Remotely Operated Vehicle (ROV)

II. Supplemental Material for Neuhaus *et al.* 2024

Population Genetics of the Deep-Sea Acorn Barnacle *Bathylasma hirsutum* (Hoek, 1883) and the First Report of its Affiliation with a Hydrothermal Vent Field

Table S1 and Table S5 are provided herein. Remaining supplemental files can be accessed in the online publication.

Table S1. Morphometric measurements of carinal parietal plates from 69 specimens (spec) of *Bathylasma hirsutum*. #GR: number of growth ridges.

Spec	# GR	Height (mm)	Diameter (mm)	Spec	# GR	Height (mm)	Diameter (mm)
B001	57	53.00	35.10	S046	44	48.91	32.26
B002	57	63.50	31.50	S047	54	43.15	27.25
B005	63	78.30	29.30	S048	48	37.83	28.65
B006	61	56.00	23.80	S049	72	54.29	38.06
B008	60	55.50	32.20	S050	43	45.86	32.16
B009	61	51.00	35.30	S051	41	25.17	31.00
B010	49	29.00	30.90	S052	52	37.19	37.33
B011	46	40.00	29.00	S053	65	43.09	34.04
B012	31	29.00	31.40	S089	106	71.29	45.34
B013	54	51.00	31.50	S090	58	56.74	36.70
S001	44	23.42	17.44	S091	41	43.21	34.37
S002	55	41.22	29.69	S092	82	77.01	61.81
S003	71	44.22	32.27	S093	110	59.39	48.98
S004	58	34.85	29.45	S094	78	61.96	41.53
S005	29	8.79	17.85	S095	97	79.90	48.22
S006	50	10.79	26.48	S096	105	74.80	37.69
S007	30	17.21	12.81	S098	91	65.54	45.50

Spec	# GR	Height (mm)	Diameter (mm)	Spec	# GR	Height (mm)	Diameter (mm)
S008	14	5.60	8.65	S100	116	65.48	48.61
S010	44	29.72	24.58	S101	56	51.16	48.09
S011	22	8.77	12.72	S102	44	56.33	44.77
S013	50	36.31	28.57	S113	30	29.69	20.01
S014	33	21.58	22.83	S119	40	47.92	29.37
S016	42	31.22	19.52	S120	24	15.76	17.38
S019	12	5.15	7.59	S124	32	27.11	25.98
S024	40	26.27	22.55	Cir009	51	43.20	39.20
S025	35	25.10	29.56	Cir010	27	33.20	30.80
S026	35	22.35	20.84	Cir011	32	26.50	20.00
S029	21	8.95	10.5	Cir012	3	30.60	24.80
S030	36	19.05	31.55	Cir013	29	28.90	29.90
S031	33	33.26	26.72	Cir021	48	50.50	37.50
S032	28	18.53	19.05	Cir022	12	14.70	19.60
S033	46	45.14	27.35	Cir023	37	36.00	30.30
S034	91	48.54	33.6	Cir025	36	45.30	41.70
S044	90	60.26	42.53	Cir026	37	43.00	31.20
				Cir030	49	55.50	36.20

Table S5. List of GenBank accession numbers for 146 specimens (spec) of *Bathylasma hirsutum*. 146 COI and 141 EF-1 sequences were made publicly available.

Catalogue nr.	Spec	COI	EF-1
DZMB-HH 71459	B001	OQ025869	OQ026030
DZMB-HH 71460	B002	OQ025882	OQ026043
DZMB-HH 71461	B003	OQ025881	OQ026042
DZMB-HH 71462	B004	OQ025880	OQ026041
DZMB-HH 71463	B005	OQ026007	OQ026163
DZMB-HH 71464	B006	OQ026006	OQ026162
DZMB-HH 71465	B007	OQ026005	OQ026161
DZMB-HH 71466	B008	OQ026004	OQ026160
DZMB-HH 71467	B009	OQ026003	OQ026159
DZMB-HH 71468	B010	OQ026002	OQ026158
DZMB-HH 71469	B011	OQ026001	OQ026157

Catalogue nr.	Spec	COI	EF-1
DZMB-HH 71470	B012	OQ026000	OQ026156
DZMB-HH 71471	B013	OQ025999	OQ026155
DZMB-HH 71472	B014	OQ025998	OQ026154
DZMB-HH 71473	B015	OQ025997	OQ026153
DZMB-HH 71474	B016	OQ025996	OQ026152
DZMB-HH 71475	B017	OQ025995	OQ026151
DZMB-HH 71476	B018	OQ025994	OQ026150
DZMB-HH 61156	S001	OQ025993	OQ026149
DZMB-HH 71477	S002	OQ025992	OQ026148
DZMB-HH 71478	S003	OQ025991	OQ026147
DZMB-HH 71479	S004	OQ025990	OQ026146
DZMB-HH 71480	S005	OQ025989	OQ026145
DZMB-HH 71481	S006	OQ025988	OQ026144
DZMB-HH 71484	S009	OQ025987	OQ026143
DZMB-HH 71485	S010	OQ025986	OQ026142
DZMB-HH 71486	S011	OQ025985	OQ026141
DZMB-HH 71487	S012	OQ025984	OQ026140
DZMB-HH 71488	S013	OQ025983	OQ026139
DZMB-HH 71490	S015	OQ025982	OQ026138
DZMB-HH 71491	S016	OQ025981	OQ026137
DZMB-HH 71492	S017	OQ025980	OQ026136
DZMB-HH 71493	S018	OQ025979	OQ026135
DZMB-HH 71494	S019	OQ025978	-
DZMB-HH 71495	S020	OQ025977	OQ026134
DZMB-HH 71496	S021	OQ025976	OQ026133
DZMB-HH 71497	S022	OQ025975	OQ026132
DZMB-HH 71498	S023	OQ025974	OQ026131
DZMB-HH 61612	S024	OQ025973	OQ026130
DZMB-HH 71499	S025	OQ025972	OQ026129
DZMB-HH 71500	S026	OQ025971	OQ026128
DZMB-HH 71501	S027	OQ025970	OQ026127
DZMB-HH 71502	S028	OQ025969	OQ026126
DZMB-HH 71503	S029	OQ025968	OQ026125

Catalogue nr.	Spec	COI	EF-1
DZMB-HH 61496	S030	OQ025967	OQ026124
DZMB-HH 71504	S031	OQ025966	OQ026123
DZMB-HH 71506	S033	OQ025965	OQ026122
DZMB-HH 71507	S034	OQ025964	OQ026121
DZMB-HH 61494	S035	OQ025963	OQ026120
DZMB-HH 71519	S036	OQ025962	OQ026119
DZMB-HH 71520	S037	OQ025961	OQ026118
DZMB-HH 71521	S038	OQ025960	OQ026117
DZMB-HH 71522	S039	OQ025959	OQ026116
DZMB-HH 71523	S040	OQ025958	OQ026115
DZMB-HH 71524	S041	OQ025957	OQ026114
DZMB-HH 71525	S042	OQ025956	OQ026113
DZMB-HH 71526	S043	OQ025955	OQ026112
DZMB-HH 71509	S045	OQ025954	OQ026111
DZMB-HH 71510	S046	OQ025953	OQ026110
DZMB-HH 71511	S047	OQ025952	OQ026109
DZMB-HH 71512	S048	OQ025951	OQ026108
DZMB-HH 71513	S049	OQ025950	OQ026107
DZMB-HH 71514	S050	OQ025949	OQ026106
DZMB-HH 71515	S051	OQ025948	OQ026105
DZMB-HH 71516	S052	OQ025947	OQ026104
DZMB-HH 71529	S055	OQ025946	OQ026103
DZMB-HH 71530	S056	OQ025945	OQ026102
DZMB-HH 71531	S057	OQ025944	OQ026101
DZMB-HH 71532	S058	OQ025943	OQ026100
DZMB-HH 71533	S059	OQ025942	OQ026099
DZMB-HH 71534	S060	OQ025941	OQ026098
DZMB-HH 71535	S061	OQ025940	OQ026097
DZMB-HH 71536	S062	OQ025939	OQ026096
DZMB-HH 71537	S063	OQ025938	OQ026095
DZMB-HH 71538	S064	OQ025937	OQ026094
DZMB-HH 71539	S065	OQ025936	OQ026093

Catalogue nr.	Spec	COI	EF-1
DZMB-HH 71540	S066	OQ025935	OQ026092
DZMB-HH 71541	S067	OQ025934	-
DZMB-HH 71542	S068	OQ025933	OQ026091
DZMB-HH 71543	S069	OQ025932	OQ026090
DZMB-HH 71544	S070	OQ025931	-
DZMB-HH 61511	S071	OQ025930	OQ026089
DZMB-HH 71527	S072	OQ025929	OQ026088
DZMB-HH 71528	S073	OQ025928	OQ026087
DZMB-HH 71545	S074	OQ025927	OQ026086
DZMB-HH 71546	S075	OQ025926	OQ026085
DZMB-HH 71547	S076	OQ025925	OQ026084
DZMB-HH 71548	S077	OQ025924	OQ026083
DZMB-HH 71549	S078	OQ025923	OQ026082
DZMB-HH 71550	S079	OQ025922	OQ026081
DZMB-HH 71551	S080	OQ025921	OQ026080
DZMB-HH 71552	S081	OQ025920	OQ026079
DZMB-HH 71553	S082	OQ025919	OQ026078
DZMB-HH 71554	S083	OQ025918	OQ026077
DZMB-HH 71555	S084	OQ025917	OQ026076
DZMB-HH 71556	S085	OQ025916	OQ026075
DZMB-HH 71557	S086	OQ025915	OQ026074
DZMB-HH 71558	S087	OQ025914	OQ026073
DZMB-HH 71559	S088	OQ025913	OQ026072
DZMB-HH 71560	S089	OQ025912	OQ026071
DZMB-HH 71565	S093	OQ025911	OQ026070
DZMB-HH 71566	S094	OQ025910	OQ026069
DZMB-HH-64698	S097	OQ025909	OQ026068
DZMB-HH-64699	S099	OQ025908	OQ026067
DZMB-HH-64697	S100	OQ025907	-
DZMB-HH 71567	S101	OQ025906	OQ026066
DZMB-HH 71568	S102	OQ025905	OQ026065
DZMB-HH 71569	S103	OQ025904	OQ026064
DZMB-HH 71570	S104	OQ025903	OQ026063

Catalogue nr.	Spec	COI	EF-1
DZMB-HH 71572	S106	OQ025901	OQ026061
DZMB-HH 71573	S107	OQ025900	OQ026060
DZMB-HH 71574	S108	OQ025899	OQ026059
DZMB-HH 71575	S109	OQ025898	OQ026058
DZMB-HH 71576	S110	OQ025897	OQ026057
DZMB-HH 71577	S111	OQ025896	OQ026056
DZMB-HH 71578	S112	OQ025895	OQ026055
DZMB-HH 71579	S113	OQ025894	OQ026054
DZMB-HH 71580	S114	OQ025893	-
DZMB-HH 71581	S115	OQ025892	OQ026053
DZMB-HH 71582	S116	OQ025891	OQ026052
DZMB-HH 71583	S117	OQ025890	OQ026051
DZMB-HH 71584	S118	OQ025889	OQ026050
DZMB-HH 71585	S119	OQ025888	OQ026049
DZMB-HH 71586	S120	OQ025887	OQ026048
DZMB-HH 71587	S121	OQ025886	OQ026047
DZMB-HH 71588	S122	OQ025885	OQ026046
DZMB-HH 71589	S123	OQ025884	OQ026045
DZMB-HH 71590	S124	OQ025883	OQ026044
DZMB-2-HH 1166	Cir009	OQ025868	OQ026029
DZMB-2-HH 1593	Cir010	OQ025867	OQ026028
DZMB-2-HH 2239	Cir011	OQ025866	OQ026027
DZMB-2-HH 2240	Cir012	OQ025865	OQ026026
DZMB-2-HH 2241	Cir013	OQ025864	OQ026025
DZMB-2-HH 2247	Cir021	OQ025863	OQ026024
DZMB-2-HH 2248	Cir022	OQ025862	OQ026023
DZMB-2-HH 2249	Cir023	OQ025879	OQ026040
DZMB-2-HH 2250	Cir024	OQ025878	OQ026039
DZMB-2-HH 2251	Cir025	OQ025877	OQ026038
DZMB-2-HH 2252	Cir026	OQ025876	OQ026037
DZMB-2-HH 2253	Cir027	OQ025875	OQ026036
DZMB-2-HH 2254	Cir028	OQ025874	OQ026035
DZMB-2-HH 2255	Cir029	OQ025873	OQ026034

Catalogue nr.	Spec	COI	EF-1
DZMB-2-HH 2256	Cir030	OQ025872	OQ026033
DZMB-2-HH 2257	Cir031	OQ025871	OQ026032
DZMB-2-HH 2258	Cir032	OQ025870	OQ026031

III. Supplemental Material for Neuhaus *et al.* 2025

High Connectivity at Abyssal Depths: Genomic and Proteomic Insights into Population Structure of the Pan-Atlantic Deep-Sea Bivalve *Ledella ultima* (E. A. Smith, 1885)

Tables S1 can be accessed in the online publication.

Supplemental files start on next page.

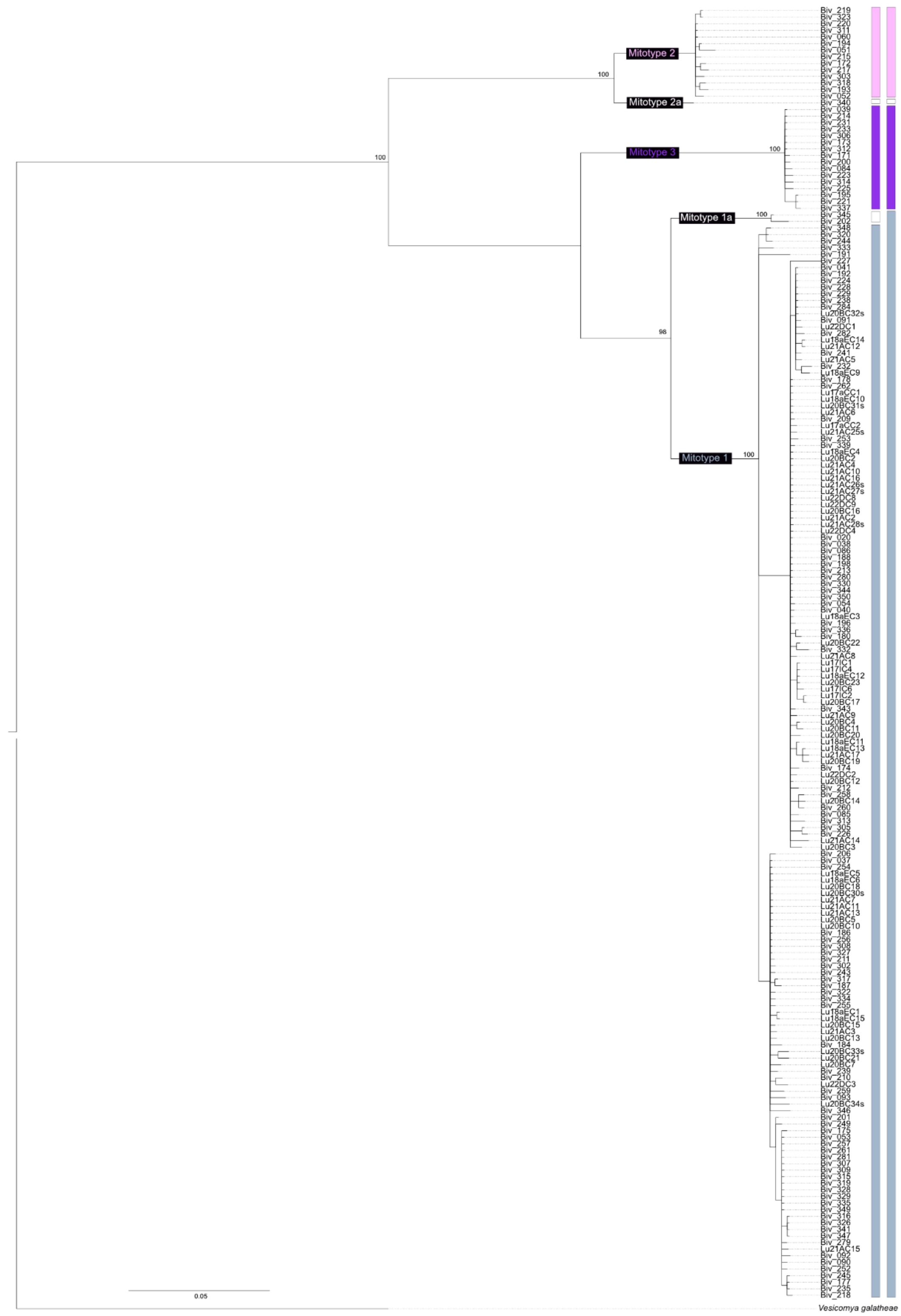

Figure S1. COI Bayesian tree with delimitation of mitotypes using the Assemble Species by Automatic Partitioning (ASAP) method. Colored bars visualize the results from the two best ASAP scores.

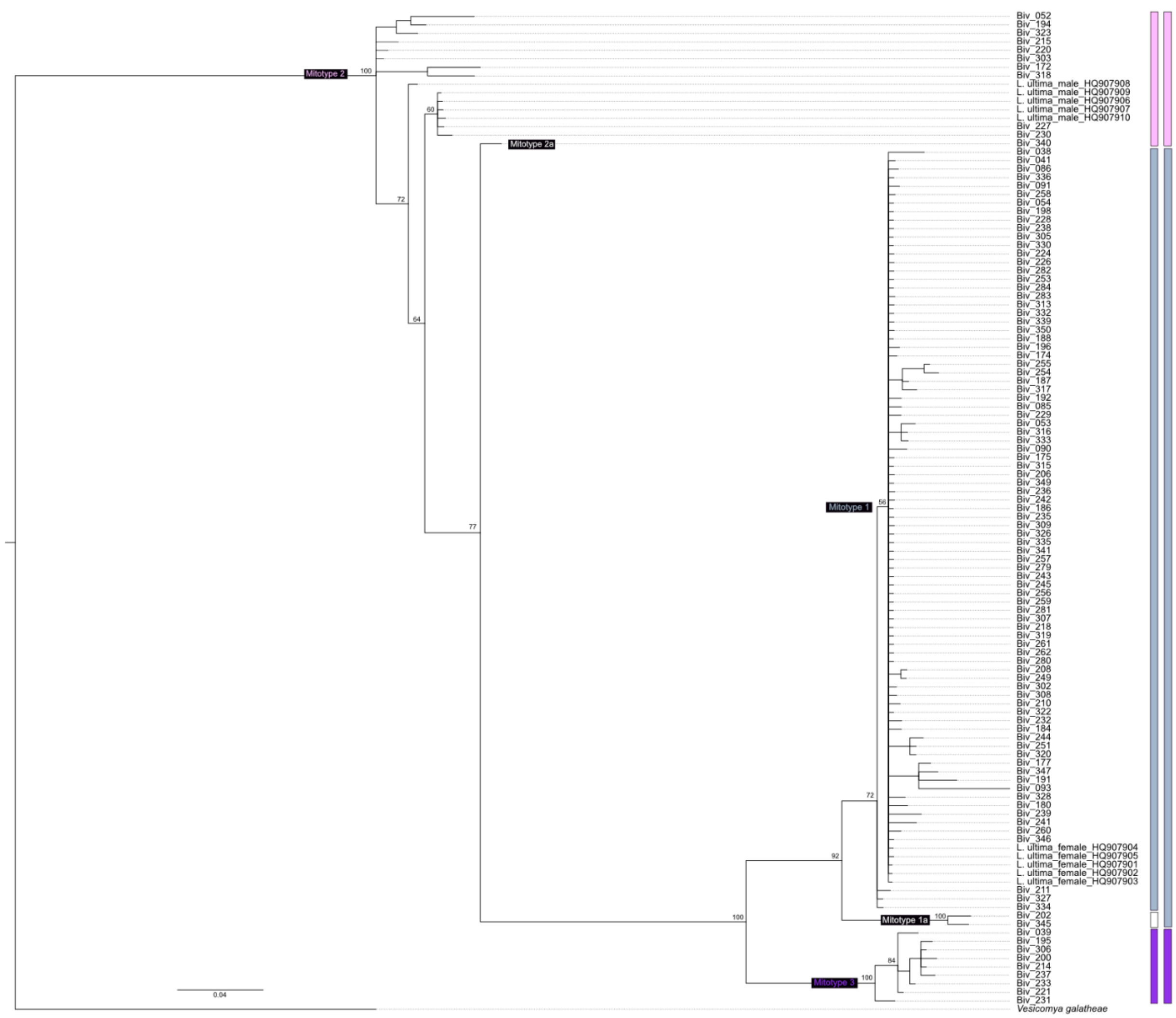

Figure S2. 16S Bayesian tree with delimitation of mitotypes using the Assemble Species by Automatic Partitioning (ASAP) method. Colored bars visualize the results from the two best ASAP scores.

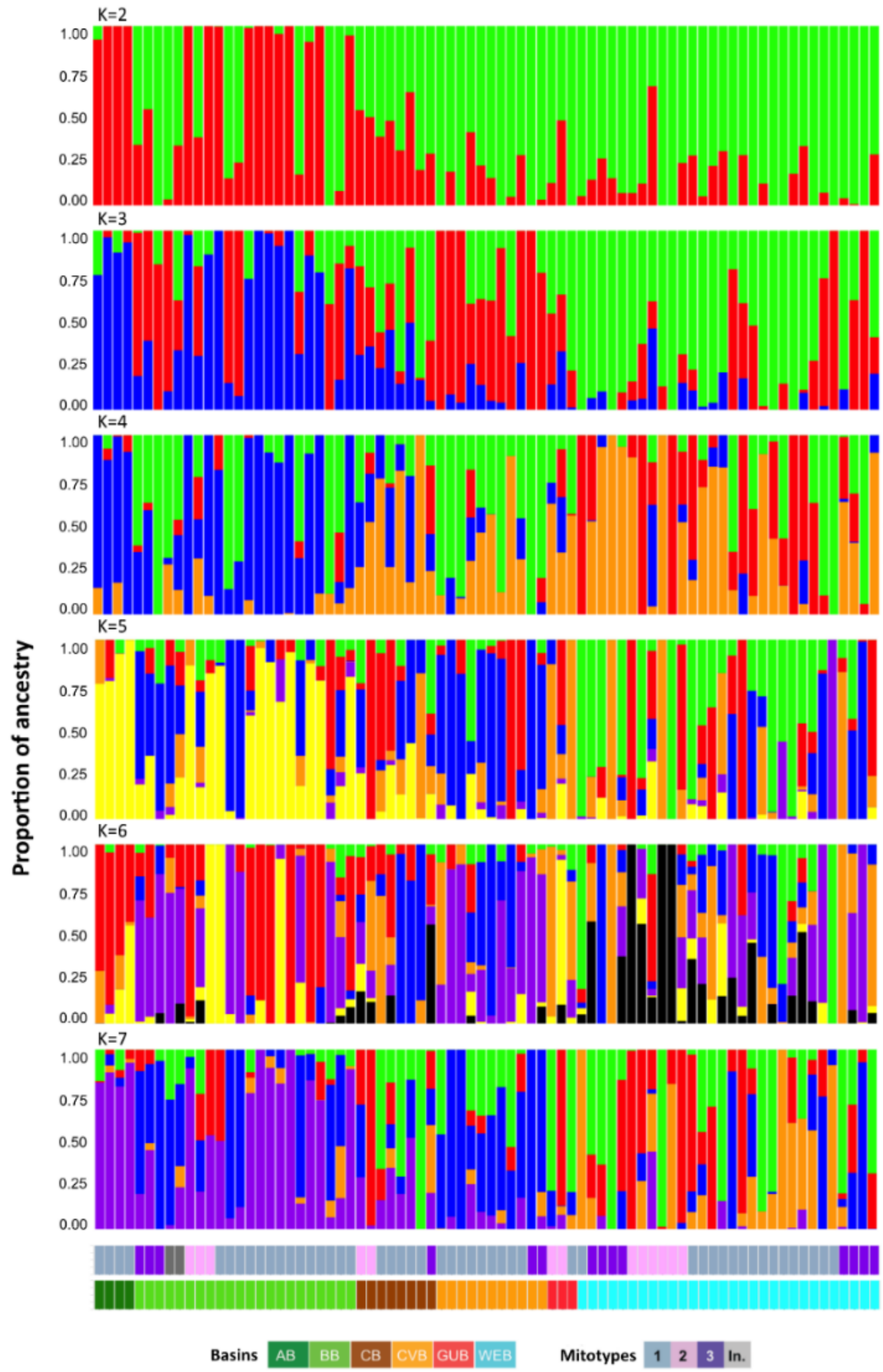

Figure S3. Patterns of population structure for *L. ultima* based on SNP data obtained by 2b-RAD sequencing. Proportions of ancestry for K = 2–7 using the Sparse Nonnegative Matrix Factorization (sNMF) algorithm. Colored bars below plots correspond to mitotypes (top) and six Atlantic basins (bottom). Abbreviations: AB: Argentine Basin, BB: Brazil Basin, CB: Cape Basin, CVB: Cape Verde Basin, GUB: Guyana Basin, WEB: West European Basin.

Table S2. Collected specimens of *L. ultima* sorted by DNA voucher, with an outline of molecular methods applied on each specimen. Mitotype assignments correspond to haplotype networks. GenBank accessions are provided for mitochondrial DNA data. Annotations: †S = 2b-RAD samples excluded from analyses; x = Proteomic spectra included in analyses; SMF = Senckenberg Museum Frankfurt, Malacology Collection.

DNA voucher	GenBank accession COI	GenBank accession 16S	Mitotype	2b-RAD	Proteomic fingerprint	Basin	Station	SMF voucher
Biv_020	PQ179865	-	1	-		WEB	85-1	366968
Biv_037	PQ179866	-	1	S29		WEB	28-1	366969
Biv_038	PQ179867	PV131957	1	S01		WEB	28-1	366970
Biv_039	PQ179868	PV131958	3	S72		WEB	28-1	366971
Biv_040	PQ179869	-	1	S02		WEB	28-1	366972
Biv_041	PQ179870	PV131959	1	S03		WEB	28-1	366973
Biv_050	-	-	-	-		WEB	21-1	366974
Biv_051	-	-	2	S88		WEB	21-1	366975
Biv_052	PQ179871	PV131960	2	S87		WEB	21-1	366976
Biv_053	PQ179872	PV131961	1	S30		WEB	21-1	366977
Biv_054	PQ179873	PV131962	1	S04		WEB	21-1	366978
Biv_060	PQ179874	-	2	S86		WEB	85-1	366979
Biv_084	PQ179875	-	3	S71		WEB	61-1	366980
Biv_085	PQ179876	PV131963	1	-		WEB	61-1	366981
Biv_086	PQ179877	PV131964	1	-		WEB	61-1	366982
Biv_090	PQ179878	PV131965	1	S31		WEB	40-1	366983
Biv_091	PQ179879	PV131966	1	S05		WEB	40-1	366984
Biv_092	PQ179880	-	1	S32		WEB	40-1	366985
Biv_093	PQ179881	PV131967	1	S33		WEB	40-1	366986
Biv_171	PQ179882	-	3	S70	x	WEB	28-1	366987
Biv_172	PQ179883	PV131968	2	S85	x	WEB	28-1	366988
Biv_173	PQ179884	-	3	S69	x	WEB	28-1	366989
Biv_174	PQ179885	PV131969	1	S06	x	WEB	21-1	366990
Biv_175	PQ179886	PV131970	1	†S34	x	CVB	4-8	366991
Biv_176	-	-	-	-	x	CVB	4-8	366992
Biv_177	PQ179887	PV131971	1	†S35		CB	21-8	366993
Biv_178	PQ179888	-	1	S07	x	CB	21-8	366994
Biv_179	-	-	-	-		PRT	14-2	366995
Biv_180	PQ179889	PV131972	1	-	x	WEB	133-8	366996
Biv_181	-	-	-	-		CVB	6-8	366997
Biv_182	-	-	-	-	x	GUB	11-1	366998
Biv_183	-	-	-	-	x	GUB	9-8	366999
Biv_184	PQ179890	PV131973	1	-	x	WEB	138-1	367000
Biv_185	-	-	-	-		PRT	14-2	367001
Biv_186	PQ179891	PV131974	1	†S36	x	GUB	9-8	367002
Biv_187	PQ179892	PV131975	1	-	x	VFZ	8-4	367003

DNA voucher	GenBank accession COI	16S	Mitotype	2b-RAD	Proteomic fingerprint	Basin	Station	SMF voucher
Biv_188	PQ179893	PV131976	1	-	x	CVB	6-7	367004
Biv_189	-	-	-	-		PRT	14-2	367005
Biv_190	-	-	-	-		CVB	6-8	367006
Biv_191	PQ179894	PV131977	1	-	x	GUB	11-1	367007
Biv_192	PQ179895	PV131978	1	S08	x	WEB	21-1	367008
Biv_193	PQ179896	-	2	S84	x	GUB	11-1	367009
Biv_194	PQ179897	PV131979	2	S83	x	WEB	28-1	367010
Biv_195	PQ179898	PV131980	3	-	x	CB	16-10	367011
Biv_196	PQ179899	PV131981	1	-	x	CB	16-10	367012
Biv_197	-	-	-	-	x	GUB	11-1	367013
Biv_198	PQ179900	PV131982	1	S09	x	WEB	21-1	367014
Biv_200	PQ179901	PV131983	3	S67	x	CVB	4-8	367015
Biv_201	PQ179902	-	1	-	x	CB	21-7	367016
Biv_202	PQ179903	PV131984	1a	-	x	CB	16-11	367017
Biv_203	-	-	-	-		CVB	4-9	367018
Biv_204	-	-	-	-		CVB	4-9	367019
Biv_205	-	-	-	-	x	CB	16-11	367020
Biv_206	PQ179904	PV131985	1	-	x	CB	21-7	367021
Biv_207	-	-	-	-	x	CB	16-11	367022
Biv_208	-	PV131986	1	-		CB	16-11	367023
Biv_209	PQ179905	-	1	S10	x	CVB	4-8	367024
Biv_210	PQ179906	PV131987	1	-	x	CB	21-8	367025
Biv_211	PQ179907	PV131988	1	S38	x	CB	21-8	367026
Biv_212	PQ179908	-	1	S11	x	GUB	9-8	367027
Biv_213	PQ179909	-	1	†S12	x	GUB	9-8	367028
Biv_214	PQ179910	PV131989	3	S66	x	CVB	4-8	367029
Biv_215	PQ179911	PV131990	2	S82	x	GUB	9-8	367030
Biv_216	-	-	-	-		CVB	4-9	367031
Biv_217	PQ179912	-	2	S81	x	CB	16-11	367032
Biv_218	PQ179913	PV131991	1	†S39	x	CB	21-8	367033
Biv_219	PQ179914	-	2	S96	x	WEB	28-1	367034
Biv_220	PQ179915	PV131992	2	S95	x	CB	16-11	367035
Biv_221	PQ179916	PV131993	3	S65	x	CB	16-11	367036
Biv_222	-	-	-	-		CVB	4-9	367037
Biv_223	PQ179917	-	3	S80	x	WEB	28-1	367038
Biv_224	PQ179918	PV131994	1	S76	x	WEB	28-1	367039
Biv_225	PQ179919	-	3	S79	x	WEB	28-1	367040
Biv_226	PQ179920	PV131995	1	S13	x	WEB	28-1	367041
Biv_227	-	PV131996	1	-	x	WEB	21-1	367042
Biv_228	PQ179921	PV131997	1	S14	x	WEB	21-1	367043
Biv_229	PQ179922	PV131998	1	†S37	x	WEB	21-1	367044
Biv_230	-	PV131999	1	-	x	WEB	21-1	367045
Biv_231	PQ179923	PV132000	3	S78	x	WEB	21-1	367046

DNA voucher	GenBank accession COI	16S	Mitotype	2b-RAD	Proteomic fingerprint	Basin	Station	SMF voucher
Biv_233	PQ179925	PV132002	3	S77	x	WEB	21-1	367048
Biv_234	-	-	-	-		CB	21-8	367049
Biv_235	PQ179926	PV132003	1	-		CB	21-8	367050
Biv_236	-	PV132004	1	-	x	CB	21-8	367051
Biv_237	-	PV132005	1	-	x	CB	21-8	367052
Biv_238	PQ179927	PV132006	1	†S15	x	CB	21-8	367053
Biv_239	PQ179928	PV132007	1	†S48	x	CB	21-8	367054
Biv_240	-	-	-	-		CB	26	367055
Biv_241	PQ179929	PV132008	1	†S16	x	CB	21-8	367056
Biv_242	-	PV132009	1	-		CB	21-8	367057
Biv_243	PQ179930	PV132010	1	-		CB	21-7	367058
Biv_244	PQ179931	PV132011	1	S47		CB	16-11	367059
Biv_245	PQ179932	PV132012	1	S46	x	CB	16-11	367060
Biv_248	-	-	-	-	x	CB	16-11	367063
Biv_249	PQ179933	PV132013	1	S45		CB	16-11	367064
Biv_250	-	-	-	-	x	CB	16-11	-
Biv_251	-	PV132014	1	-		CB	16-11	-
Biv_252	PQ179934	-	1	-	x	CVB	4-8	367065
Biv_253	PQ179935	PV132015	1	S17	x	CVB	4-8	367066
Biv_254	PQ179936	PV132016	1	-	x	CVB	4-8	367067
Biv_255	PQ179937	PV132017	1	S44	x	CVB	4-8	367068
Biv_256	PQ179938	PV132018	1	-	x	CVB	4-8	367069
Biv_257	PQ179939	PV132019	1	-	x	CVB	4-8	367070
Biv_258	PQ179940	PV132020	1	S18	x	CVB	4-8	367071
Biv_259	PQ179941	PV132021	1	S43	x	CVB	4-8	367072
Biv_260	PQ179942	PV132022	1	-	x	CVB	4-8	367073
Biv_261	PQ179943	PV132023	1	S42	x	CVB	4-8	367074
Biv_262	PQ179944	PV132024	1	S19	x	CVB	4-8	367075
Biv_263	-	-	-	-		CVB	4-9	367076
Biv_264	-	-	-	-		CVB	4-9	367077
Biv_265	-	-	-	-		CVB	4-9	367078
Biv_266	-	-	-	-		CVB	4-9	367079
Biv_267	-	-	-	-		CVB	4-9	367080
Biv_268	-	-	-	-	x	CVB	4-9	367081
Biv_269	-	-	-	-		CVB	4-9	367082
Biv_270	-	-	-	-		CVB	4-9	367083
Biv_271	-	-	-	-		CVB	4-9	-
Biv_272	-	-	-	-		CVB	4-9	-
Biv_273	-	-	-	-		CVB	4-9	367084
Biv_274	-	-	-	-		CVB	4-9	367085
Biv_275	-	-	-	-		CVB	4-9	367086
Biv_276	-	-	-	-		CVB	4-9	367087
Biv_277	-	-	-	-		CVB	4-9	367088

DNA voucher	GenBank accession COI	16S	Mitotype	2b-RAD	Proteomic fingerprint	Basin	Station	SMF voucher
Biv_278	-	-	-	-		CVB	4-9	367089
Biv_279	PQ179945	PV132025	1	S41		CVB	4-8	367090
Biv_280	PQ179946	PV132026	1	S20		CVB	4-8	367091
Biv_281	PQ179947	PV132027	1	-		CVB	4-8	367092
Biv_282	PQ179948	PV132028	1	-		CVB	4-8	367093
Biv_283	-	PV132029	1	-	x	CVB	4-8	367094
Biv_284	PQ179949	PV132030	1	-	x	CVB	4-8	367095
Biv_285	-	-	-	-		CVB	4-9	367096
Biv_286	-	-	-	-		CVB	4-9	367097
Biv_287	-	-	-	-		CVB	4-9	367098
Biv_288	-	-	-	-		CVB	4-9	367099
Biv_289	-	-	-	-		CVB	4-9	367100
Biv_290	-	-	-	-		CVB	4-9	367101
Biv_291	-	-	-	-		CVB	4-9	-
Biv_292	-	-	-	-		CVB	4-9	-
Biv_293	-	-	-	-		CVB	4-9	367102
Biv_294	-	-	-	-		CVB	4-9	367103
Biv_295	-	-	-	-		CVB	4-9	367104
Biv_296	-	-	-	-		CVB	4-9	367105
Biv_297	-	-	-	-		CVB	4-9	367106
Biv_298	-	-	-	-		CVB	4-9	367107
Biv_302	PQ179950	PV132031	1	-	x	BB	579-1	367108
Biv_303	PQ179951	PV132032	2	S94	x	BB	579-1	367109
Biv_304	-	-	-	-	x	AB	532-1	367110
Biv_305	PQ179952	PV132033	1	†S22	x	NAB	21-1	367111
Biv_306	PQ179953	PV132034	3	-	x	BB	579-1	367112
Biv_307	PQ179954	PV132035	1	S56	x	BB	579-1	367113
Biv_308	PQ179955	PV132036	1	-	x	BB	580-1	367114
Biv_309	PQ179956	PV132037	1	S55	x	BB	580-1	367115
Biv_310	-	-	-	-		BB	580-1	367116
Biv_311	PQ179957	-	2	S93	x	BB	580-1	367117
Biv_312	PQ179958	-	3	S75	x	BB	580-1	367118
Biv_313	PQ179959	PV132038	1	S23	x	BB	580-1	367119
Biv_314	PQ179960	-	3	S74	x	BB	580-1	367120
Biv_315	PQ179961	PV132039	1	S54	x	BB	579-1	-
Biv_316	PQ179962	PV132040	1	S21	x	BB	579-1	367121
Biv_317	PQ179963	PV132041	1	-	x	BB	579-1	-
Biv_318	PQ179964	PV132042	2	†S92	x	BB	580-1	367122
Biv_319	PQ179965	PV132043	1	S53	x	BB	579-1	367123
Biv_320	PQ179966	PV132044	1	-	x	BB	580-1	367124
Biv_321	-	-	-	-	x	AB	532-1	367125
Biv_322	PQ179967	PV132045	1	†S52	x	NAB	21-1	367126
Biv_323	PQ179968	PV132046	2	S91	x	BB	580-1	367127

DNA voucher	GenBank accession COI	16S	Mitotype	2b-RAD	Proteomic fingerprint	Basin	Station	SMF voucher
Biv_324	-	-	-	-	x	BB	580-1	367128
Biv_325	-	-	-	-	x	BB	579-1	367129
Biv_326	PQ179969	PV132047	1	S51	x	BB	580-1	367130
Biv_327	PQ179970	PV132048	1	†S50	x	NAB	21-1	367131
Biv_328	PQ179971	PV132049	1	S49	x	BB	579-1	367132
Biv_329	PQ179972	-	1	S64	x	BB	580-1	367133
Biv_330	PQ179973	PV132050	1	-	x	NAB	21-1	367134
Biv_331	-	-	-	-	x	BB	580-1	367135
Biv_332	PQ179974	PV132051	1	S25	x	AB	532-1	367136
Biv_333	PQ179975	PV132052	1	S63	x	BB	580-1	367137
Biv_334	PQ179976	PV132053	1	†S62	x	NAB	21-1	367138
Biv_335	PQ179977	PV132054	1	S61	x	AB	532-1	367139
Biv_336	PQ179978	PV132055	1	S26	x	BB	580-1	367140
Biv_337	PQ179979	-	3	S73	x	BB	580-1	367141
Biv_338	-	-	-	-	x	BB	579-1	367142
Biv_339	PQ179980	PV132056	1	†S27	x	NAB	21-1	367143
Biv_340	PQ179981	PV132057	2a	S90	x	BB	580-1	367144
Biv_341	PQ179982	PV132058	1	S60	x	AB	532-1	367145
Biv_342	-	-	-	-		BB	580-1	367146
Biv_343	PQ179983	-	1	-	x	BB	580-1	367147
Biv_344	PQ179984	-	1	-	x	BB	579-1	367148
Biv_345	PQ179985	PV132059	1a	S89	x	BB	580-1	367149
Biv_346	PQ179986	PV132060	1	S59	x	BB	580-1	367150
Biv_347	PQ179987	PV132061	1	S58	x	AB	532-1	367151
Biv_348	PQ179988	-	1	S57	x	BB	579-1	367152
Biv_349	PQ179989	PV132062	1	-	x	BB	580-1	367153
Biv_350	PQ179990	PV132063	1	S28	x	BB	579-1	367154

Table S3. Overview of loci, mean coverage per individual loci, total unfiltered SNPs, SNPs after filtering and pruning, and mean heterozygosity (HET) for stack depth m = 3, 5, 8.

	Loci	Coverage (X)	Unfiltered SNPs	Filtered SNPs	HET
m3	16032	36.5	98633	2824	0.0637
m5	14220	41.9	91187	2048	0.0652
m8	12642	47.5	79655	1410	0.0681

IV. Supplemental Material – Analysis of Shell Morphometric Measurements in *L. ultima*

Introduction

Morphometric shell measurements in specimens of *L. ultima* were performed to test for morphological differences between mitotype (MT) clusters 1–3 that were identified by molecular genetic analyses of mitochondrial markers (Neuhaus *et al.* 2025).

Material and Methods

Shells from a maximum of five specimens per station were photographed using a Keyence VHX-7000 digital microscope. External shell morphology of 129 specimens was assessed using a Leica MZ8 stereomicroscope. Shell length (anterior-posterior) and shell width (dorsal-ventral) were measured using a micrometre lens. Levels of margin thickening, denoted as none, present, or pronounced, were assessed by eye with reference to literature records (Allen and Hannah 1989). Morphometrics were visualized using the R-packages tidyverse, ggplot2 and ggpubr (Wickham 2016; Wickham *et al.* 2019; Kassambara 2023). A nonparametric Kruskal-Wallis test followed by Dunn's *post-hoc* test was performed on groups based on the molecular data. Data on morphometric shell measurements and levels of ventral edge thickening are found in Table S1.

Results and Discussion

Morphometric analyses were conducted to test for morphological differences between mitotypes 1–3 (*n* specimens = MT 1: 99; MT 2: 14; MT 3: 16). Overall, measurements of shell length and shell width ranged from 1.4–3.0 mm and 1.0–2.4 mm, respectively (Figure 1A). Shell length (L) (Kruskal-Wallis X2 = 16.66, df = 2, p = 0.0002) and shell width (W) (Kruskal-Wallis X2 = 12.90, df = 2, p = 0.0016) were found to differ significantly between MT 1 and MT 2 (L: p = 0.0001; W: p = 0.001), as well as MT 2 and MT 3 (L: p = 0.015; W: p = 0.017). Differences between MT 1 and MT 3 were non-significant (L: p = 1.00; W: p = 1.00). Mitotype 2 was on average found to be larger than MT 1 and MT 3 (Dunn's test with Bonferroni correction; L: z -4.081 p = 0.0001, z 2.803 p = 0.015; W: z = -3.557, p = 0.001, z 2.759 p = 0.017). Each category of ventral edge thickening (none, present, and pronounced) was found for each mitotype (Figure 1B). Across all mitotypes, specimens without ventral edge thickening account for the highest fraction and yield a total of 72 specimens (L. 1.4–3.0 mm; W: 1.0–2.3 mm). Ventral edge thickening was present in 29 specimens (L. 2.4–3.0

mm; W: 1.8–2.3 mm), and 28 specimens showed pronounced ventral edge thickening (L: 2.4–3.0 mm; W: 1.8–2.4 mm).

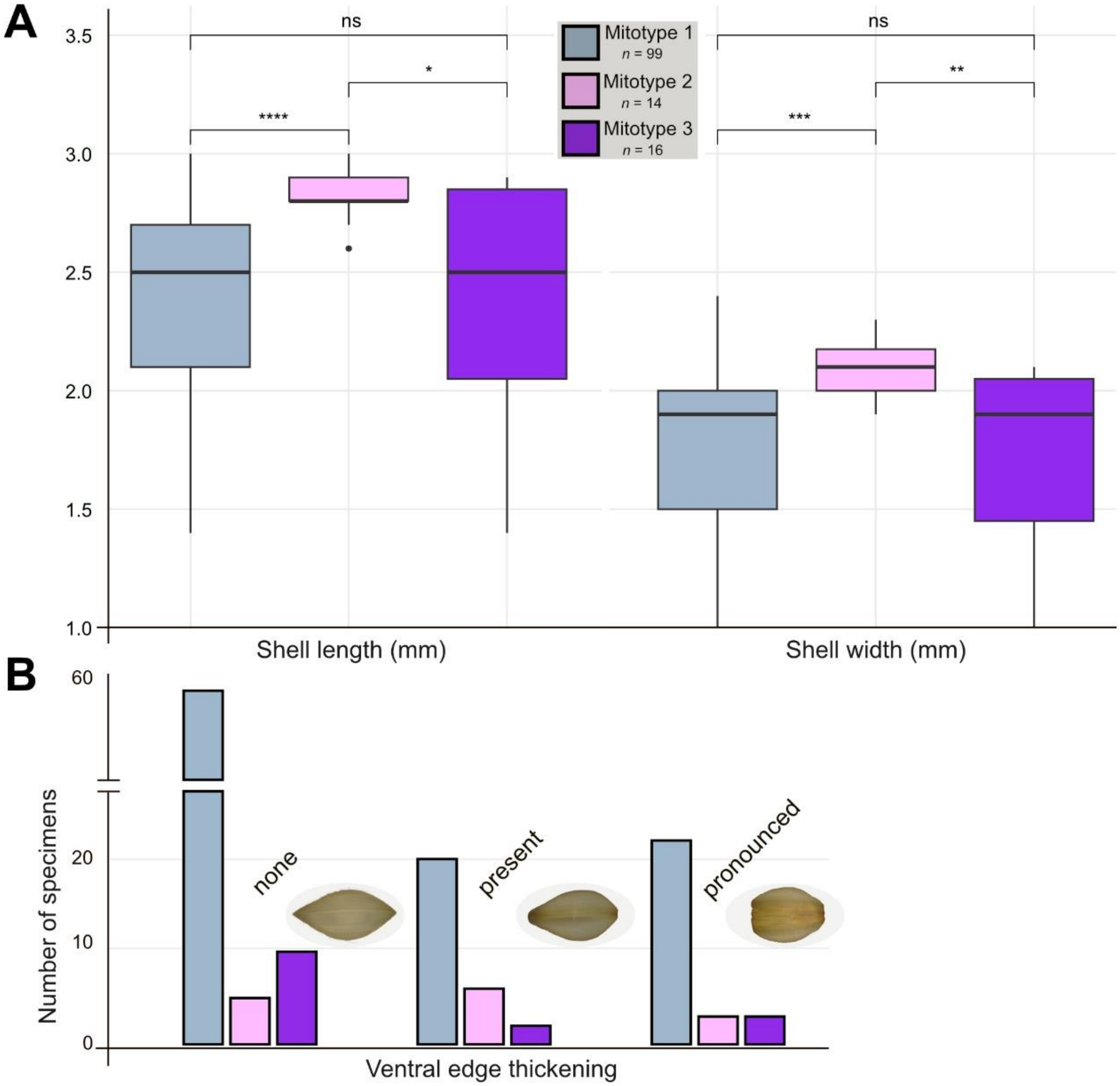

Figure 1. Morphometric shell measurements compared between mitotypes 1–3 of *L. ultima*. **A** Box plot of shell length and width measurements. Statistical differences were assessed using the Kruskal-Wallis test, followed by Dunn's *post-hoc* test for pairwise comparisons. The denotation "ns" indicates non-significant differences. Each box represents the first and third quartile as well as the median (thick line), and whiskers represent the 95% confidence interval. **B** Bar plot showing the number of specimens from each mitotype categorized by ventral edge thickening of the shell. Specimen count per mitotype (coloured): MT 1: 99, MT 2: 14, MT 3: 16.

The morphometric analyses revealed all levels of ventral edge thickening to be present across the three mitotypes and confirmed edge thickening to be absent in specimens smaller than 2.4 mm in length, congruent with the findings of Allen and Hannah (1989). The authors suggested the thickening of the ventral shell edge as a gain in shell volume yielding more space for eggs and increasing the species' breeding success when compared to its conspecifics, as *L. ultima* produces fewer eggs of larger size (Allen and Hannah 1989; Tyler *et al.* 1992). This, however, remains speculative to this point, as it is not clear whether only females perform shell thickening. We found 89 out of 129 measured shells with at least 2.4 mm in shell length. Of these 89 specimens, 57 shells had grown a thickened edge, represented by specimens from mitotypes 1–3 (*n* specimens = MT 1: 42; MT 2: 9; MT 3: 6). Of those shells with edge thickening, 28 shells had reached a pronounced level. If mitotype 2 in fact is represented by male specimens, as discussed in Neuhaus *et al.* (2025), our measurements would suggest that also male bivalves induce thickening of their ventral shell edge. If this holds to be true, the increase in volume and thus more space for eggs could be one, but not the only explanation for this anatomical adaptation in *L. ultima*.

Table S1. Morphometric shell measurements of *L. ultima* and levels of ventral edge thickening across mitotypes (MT).

Voucher	Basin	MT	Shell length (mm)	Shell width (mm)	Ventral edge thickening
Biv_020	WEB	1	3	2.4	pronounced
Biv_037	WEB	1	3	2.3	present
Biv_038	WEB	1	2.7	2.1	present
Biv_039	WEB	3	2.9	2.1	pronounced
Biv_040	WEB	1	2.9	2.2	pronounced
Biv_041	WEB	1	2.9	2.3	none
Biv_051	WEB	2	3	2.1	none
Biv_052	WEB	2	2.8	2.1	present
Biv_053	WEB	1	3	2.3	none
Biv_054	WEB	1	2.9	2.3	pronounced
Biv_060	WEB	2	2.9	2.3	present
Biv_084	WEB	3	1.7	1.2	none
Biv_085	WEB	1	2.4	1.8	present
Biv_086	WEB	1	2.3	1.6	none
Biv_090	WEB	1	2	1.5	none

Voucher	Basin	MT	Shell length (mm)	Shell width (mm)	Ventral edge thickening
Biv_091	WEB	1	2.1	1.5	none
Biv_092	WEB	1	2.1	1.5	none
Biv_093	WEB	1	2.3	1.6	none
Biv_171	WEB	3	2.9	2.1	present
Biv_172	WEB	2	2.8	2	none
Biv_173	WEB	3	2.9	2.1	none
Biv_174	WEB	1	2.8	2.1	present
Biv_175	CVB	1	2.8	2	pronounced
Biv_177	CB	1	2.8	2	present
Biv_178	CB	1	2.7	2	present
Biv_180	GUB	1	2	1.5	none
Biv_184	WEB	1	1.4	1	none
Biv_186	GUB	1	2.9	2.2	pronounced
Biv_187	GUB	1	2.8	2.2	pronounced
Biv_188	CVB	1	1.8	1.3	none
Biv_191	GUB	1	2.9	2.3	none
Biv_192	WEB	1	2.5	2	pronounced
Biv_193	GUB	2	2.9	2.2	present
Biv_194	WEB	2	2.7	2.1	present
Biv_195	CB	3	2.5	1.9	none
Biv_196	CB	1	2.7	2	present
Biv_198	WEB	1	2.8	2	none
Biv_200	CVB	3	1.4	1	none
Biv_201	CB	1	2.8	2.1	none
Biv_206	CB	1	2.5	1.8	present
Biv_208	CB	1	2.2	1.6	none
Biv_209	CVB	1	2.6	2	present
Biv_210	CB	1	2.7	2	pronounced
Biv_211	CB	1	2.5	1.9	present
Biv_212	GUB	1	2.9	2.3	pronounced
Biv_213	GUB	1	2.8	2.1	pronounced
Biv_214	CVB	3	2.3	1.7	none
Biv_215	GUB	2	2.9	2.2	pronounced
Biv_217	CB	2	2.8	2	none
Biv_218	CB	1	2.6	1.9	pronounced
Biv_219	WEB	2	2.9	2.2	present
Biv_220	CB	2	2.8	2	present
Biv_221	CB	3	2.8	2	none
Biv_223	WEB	3	2.9	2.1	present
Biv_224	WEB	1	2.1	1.5	none
Biv_225	WEB	3	2.9	2.1	present
Biv_226	WEB	1	2.7	2	none

Voucher	Basin	MT	Shell length (mm)	Shell width (mm)	Ventral edge thickening
Biv_227	WEB	1	2.7	2.3	pronounced
Biv_228	WEB	1	2.6	2.0	pronounced
Biv_229	WEB	1	2.5	1.8	none
Biv_230	WEB	1	2.8	2.1	pronounced
Biv_231	WEB	3	2.5	1.8	none
Biv_232	WEB	1	2.5	1.9	none
Biv_233	WEB	3	2.7	2.0	pronounced
Biv_235	CB	1	2.7	1.9	pronounced
Biv_236	CB	1	2.5	1.9	none
Biv_237	CB	1	2.6	1.9	present
Biv_238	CB	1	2.7	2.0	present
Biv_239	CB	1	2.6	2.0	present
Biv_241	CB	1	2.7	2.1	present
Biv_242	CB	1	2.0	1.4	none
Biv_243	CB	1	2.7	1.9	pronounced
Biv_244	CB	1	2.8	2.0	none
Biv_245	CB	1	2.6	2.0	pronounced
Biv_249	CB	1	2.3	1.6	none
Biv_252	CVB	1	1.5	1.1	none
Biv_253	CVB	1	2.6	2.0	present
Biv_254	CVB	1	2.1	1.5	none
Biv_255	CVB	1	2.9	1.9	present
Biv_256	CVB	1	2.4	1.8	present
Biv_257	CVB	1	2.5	1.7	none
Biv_258	CVB	1	2.0	1.4	none
Biv_259	CVB	1	2.4	1.7	none
Biv_260	CVB	1	1.4	1.0	none
Biv_261	CVB	1	2.7	1.9	present
Biv_262	CVB	1	1.8	1.3	none
Biv_279	CVB	1	2.5	1.9	pronounced
Biv_280	CVB	1	1.6	1.1	none
Biv_281	CVB	1	1.4	1.0	none
Biv_282	CVB	1	2.7	1.9	present
Biv_283	CVB	1	1.9	1.2	none
Biv_284	CVB	1	2.5	1.8	present
Biv_302	BB	1	2.9	1.9	none
Biv_303	BB	2	2.6	1.9	none
Biv_305	NAB	1	2.7	2.0	none
Biv_306	BB	3	2.8	2.0	pronounced
Biv_307	BB	1	2.2	1.5	none
Biv_308	BB	1	2.7	1.9	none
Biv_309	BB	1	2.3	1.6	none

Voucher	Basin	MT	Shell length (mm)	Shell width (mm)	Ventral edge thickening
Biv_311	BB	2	2.8	1.9	none
Biv_312	BB	3	1.5	1.1	none
Biv_313	BB	1	2.0	1.3	none
Biv_314	BB	3	2.5	1.7	none
Biv_316	BB	1	1.5	1.0	none
Biv_318	BB	2	3.0	2.1	pronounced
Biv_319	BB	1	2.9	2.1	pronounced
Biv_320	BB	1	1.6	1.1	none
Biv_322	NAB	1	2.5	2.0	none
Biv_323	BB	2	2.8	2.1	pronounced
Biv_326	BB	1	2.5	1.8	none
Biv_327	NAB	1	2.3	1.8	none
Biv_328	BB	1	1.9	1.3	none
Biv_329	BB	1	2.7	2.0	pronounced
Biv_330	NAB	1	2.1	1.6	none
Biv_332	AB	1	2.0	1.5	none
Biv_333	BB	1	1.5	1.0	none
Biv_334	NAB	1	2.7	1.9	none
Biv_335	AB	1	2.2	1.5	none
Biv_336	BB	1	2.0	1.4	none
Biv_337	BB	3	1.8	1.2	none
Biv_339	NAB	1	2.2	1.6	none
Biv_341	AB	1	2.5	1.8	none
Biv_343	BB	1	1.7	1.2	none
Biv_344	BB	1	2.7	2.0	pronounced
Biv_346	BB	1	3.0	2.2	pronounced
Biv_347	AB	1	2.7	1.9	none
Biv_348	BB	1	1.5	1.1	none
Biv_349	BB	1	2.5	1.7	none
Biv_350	BB	1	2.6	1.9	none

V. Supplementary Material for Neuhaus *et al.* in prep

Biogeography of North Atlantic Acanthocope Beddard, 1885 (Isopoda: Munnopsidae)

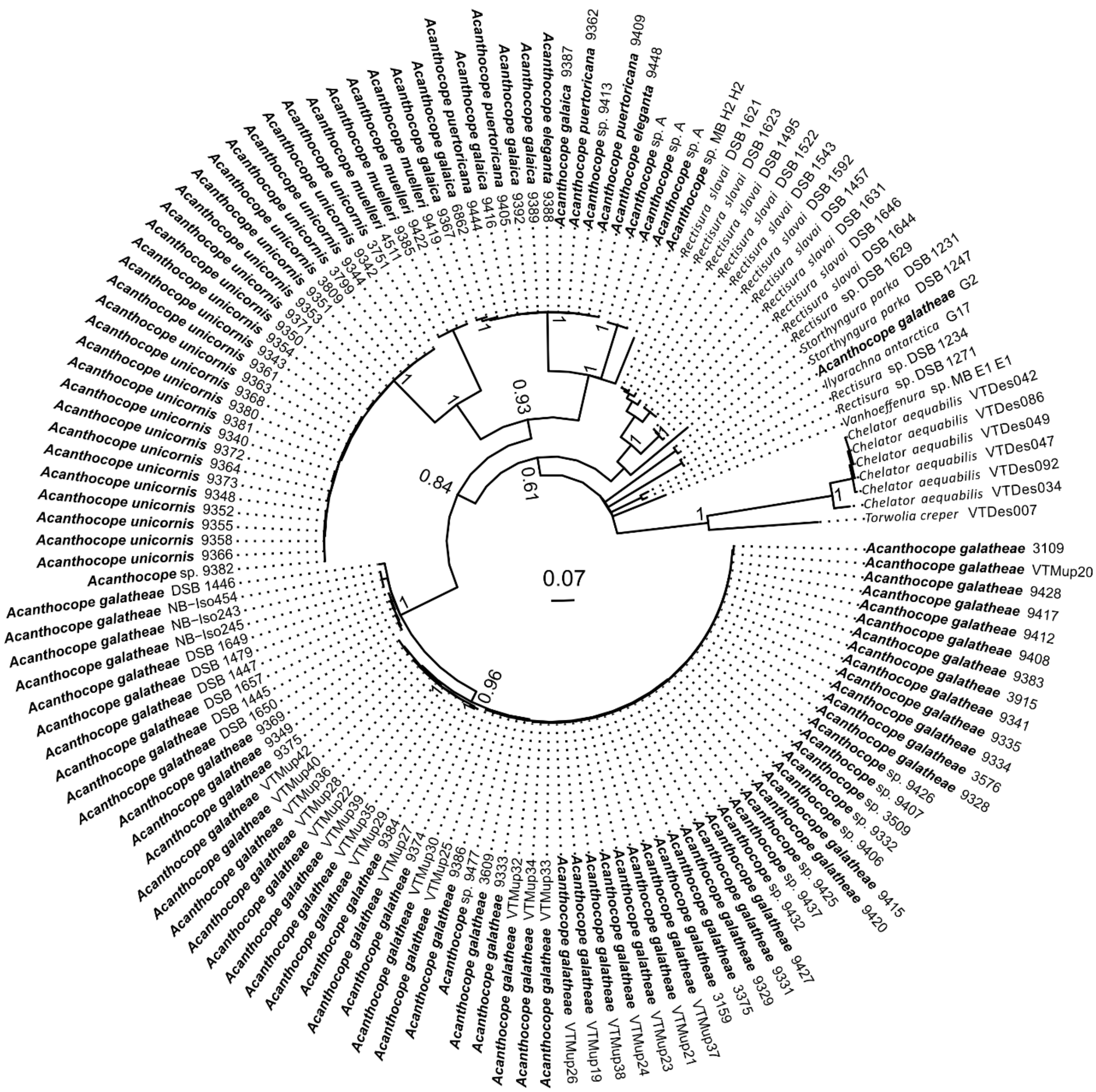

Figure S1. COI Bayesian tree of *Acanthocope*. Posterior probabilities aredepicted on the nodes. The tree is rooted with *Torwolia creper* Hessler, 1970 of the family Desmosomatide which stands sister to the Munnopsidae.

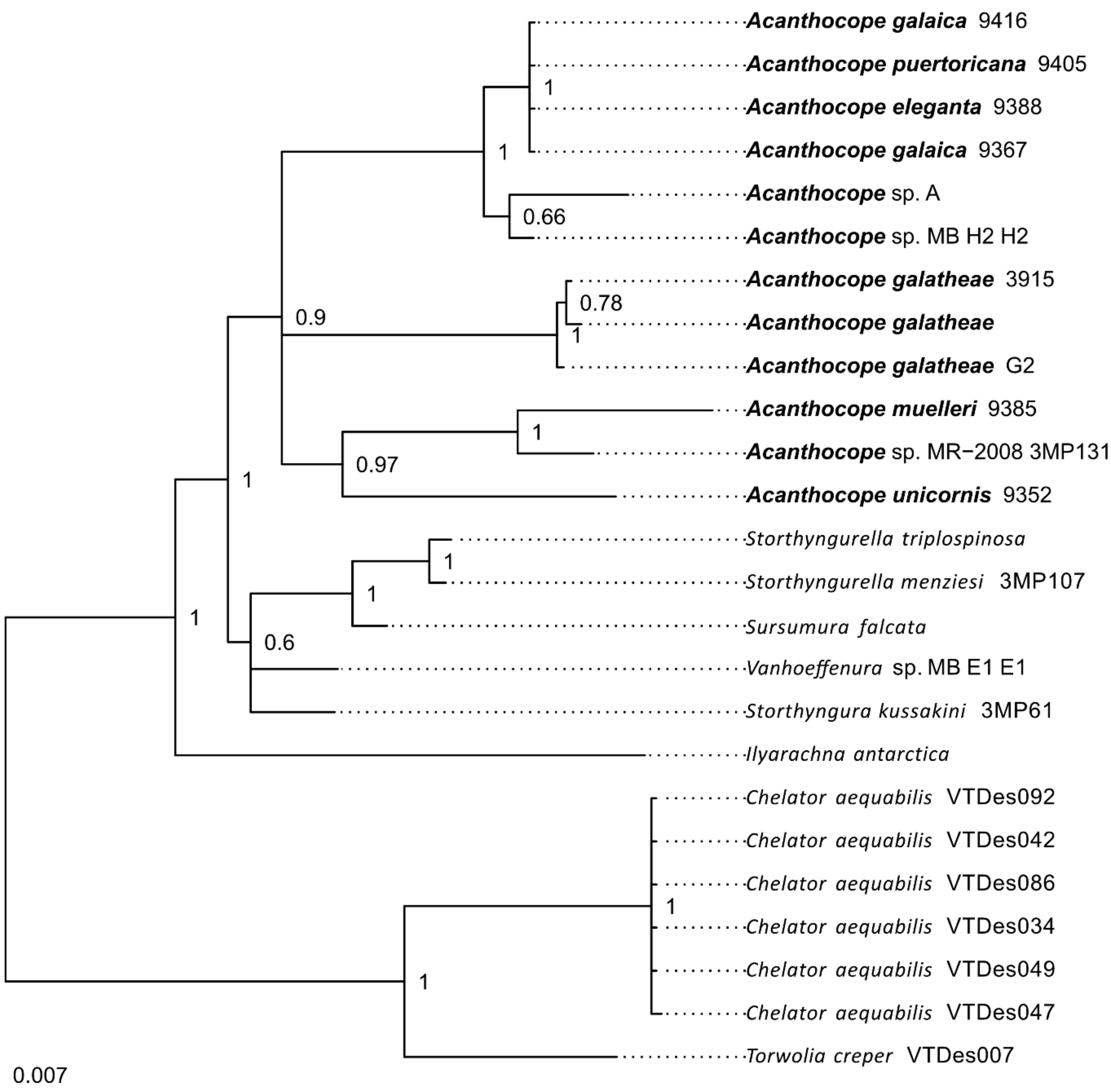

Figure S2. 18S Bayesian tree of *Acanthocope*. Posterior probabilities are depicted on the nodes. The tree is rooted with *Torwolia creper* Hessler, 1970 of the family Desmosomatide which stands sister to the Munnopsidae

Table S1. Additional COI and 18S sequences of isopod species included in the molecular analyses

Species	Voucher	18S	COI	Family
Acanthocope cf. *galatheae*	DSB_1445	-	MW072732	Munnopsidae
Acanthocope cf. *galatheae*	DSB_1446	-	MW072747	Munnopsidae
Acanthocope cf. *galatheae*	DSB_1447	-	MW072702	Munnopsidae
Acanthocope cf. *galatheae*	DSB_1479	-	MW072740	Munnopsidae
Acanthocope cf. *galatheae*	DSB_1649	-	MW072692	Munnopsidae
Acanthocope cf. *galatheae*	DSB_1650	-	MW072522	Munnopsidae
Acanthocope cf. *galatheae*	DSB_1657	-	MW072665	Munnopsidae
Acanthocope galatheae	-	AF496656	-	Munnopsidae
Acanthocope galatheae	G2	EF682241	EF682285	Munnopsidae
Acanthocope galatheae	NB-Iso243	-	KJ736110	Munnopsidae
Acanthocope galatheae	NB-Iso245	-	KJ736109	Munnopsidae
Acanthocope galatheae	NB-Iso454	-	KJ736111	Munnopsidae
Acanthocope galatheae	VTMup19	-	MG721979	Munnopsidae
Acanthocope galatheae	VTMup20	-	MG721973	Munnopsidae
Acanthocope galatheae	VTMup21	-	MG721975	Munnopsidae
Acanthocope galatheae	VTMup22	-	MG721966	Munnopsidae
Acanthocope galatheae	VTMup23	-	MG721976	Munnopsidae
Acanthocope galatheae	VTMup24	-	MG721977	Munnopsidae
Acanthocope galatheae	VTMup25	-	MG721971	Munnopsidae
Acanthocope galatheae	VTMup26	-	MG721980	Munnopsidae
Acanthocope galatheae	VTMup27	-	MG721962	Munnopsidae
Acanthocope galatheae	VTMup28	-	MG721967	Munnopsidae
Acanthocope galatheae	VTMup29	-	MG721963	Munnopsidae
Acanthocope galatheae	VTMup30	-	MG721974	Munnopsidae
Acanthocope galatheae	VTMup32	-	MG721983	Munnopsidae
Acanthocope galatheae	VTMup33	-	MG721981	Munnopsidae
Acanthocope galatheae	VTMup34	-	MG721982	Munnopsidae
Acanthocope galatheae	VTMup35	-	MG721964	Munnopsidae
Acanthocope galatheae	VTMup36	-	MG721968	Munnopsidae
Acanthocope galatheae	VTMup37	-	MG721972	Munnopsidae
Acanthocope galatheae	VTMup38	-	MG721978	Munnopsidae
Acanthocope galatheae	VTMup39	-	MG721965	Munnopsidae
Acanthocope galatheae	VTMup40	-	MG721969	Munnopsidae
Acanthocope galatheae	VTMup42	-	MG721970	Munnopsidae
Acanthocope sp.	MB H2	EF682240	EF682286	Munnopsidae
Acanthocope sp.	MR-2008	EU414445	-	Munnopsidae
Chelator aequabilis	VTDes034	MF325723	MF325473	Desmosomatidae
Chelator aequabilis	VTDes042	MF325721	MF325471	Desmosomatidae
Species	**Voucher**	**18S**	**COI**	**Family**
Chelator aequabilis	VTDes049	MF325724	MF325474	Desmosomatidae
Chelator aequabilis	VTDes086	MF325722	MF325472	Desmosomatidae
Chelator aequabilis	VTDes092	MF325720	MF325468	Desmosomatidae

Species	Voucher	18S	COI	Family
Ilyarachna antarctica	G17	AY461481	EF682299	Munnopsidae
Rectisura slavai	DSB_1457	-	MW072669	Munnopsidae
Rectisura slavai	DSB_1495	-	MW072727	Munnopsidae
Rectisura slavai	DSB_1522	-	MW072667	Munnopsidae
Rectisura slavai	DSB_1543	-	MW072525	Munnopsidae
Rectisura slavai	DSB_1592	-	MW072597	Munnopsidae
Rectisura slavai	DSB_1621	-	MW072681	Munnopsidae
Rectisura slavai	DSB_1623	-	MW072749	Munnopsidae
Rectisura slavai	DSB_1631	-	MW072526	Munnopsidae
Rectisura slavai	DSB_1644	-	MW072560	Munnopsidae
Rectisura slavai	DSB_1646	-	MW072613	Munnopsidae
Rectisura sp.	DSB_1234	-	MW072534	Munnopsidae
Rectisura sp.	DSB_1271	-	MW072608	Munnopsidae
Rectisura sp.	DSB_1629	-	MW072766	Munnopsidae
Storthyngura kussakini	3MP61	EU414465	-	Munnopsidae
Storthyngura parka	DSB_1231	-	MW072543	Munnopsidae
Storthyngura parka	DSB_1247	-	MW072691	Munnopsidae
Storthyngurella menziesi	3MP107	EU4a14464	-	Munnopsidae
Storthyngurella triplospinosa	-	AY461482	-	Munnopsidae
Sursumura falcata	-	AF498908	-	Munnopsidae
Torwolia creper	VTDes007	MF325781	MF325577	Desmosomatidae
Vanhoeffenura sp.	MB E1	EF682239	EF682284	Munnopsidae

VI. Scientific Résumé

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Education

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Senckenberg, German Centre for Marine Biodiversity Research (DZMB) Hamburg

2018 – 2020 **Master of Science in Marine Biology**
Systematic revision of the genus *Jorunna* (Nudibranchia: Discodorididae) in Europe with a focus on the *J. tomentosa* species complex
University of Bergen, Norway

2015 – 2018 **Bachelor of Science in Biology**
Gorgonophilus canadensis (Copepoda: Lamippidae) a parasite in the octocoral *Paragorgia arborea* – relation to host, reproduction, and morphology
University of Bergen, Norway

Publications

Jenny Neuhaus, Mark E. de Wilt, Sven Rossel, Saskia Brix, Ron J. Etter, Robert M. Jennings, Katrin Linse, Pedro Martínez Arbizu, Martin Schwentner, Janna Peters (2025). **High Connectivity at Abyssal Depths: Genomic and Proteomic Insights into Population Structure of the Pan-Atlantic Deep-Sea Bivalve *Ledella ultima* (E. A. Smith, 1885).** *Ecology and Evolution,* 15 (e71903), 1–21. doi: 10.1002/ece3.71903

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Jenny Neuhaus, Katrin Linse, Saskia Brix, Pedro Martínez Arbizu, James Taylor (2024). **Population Genetics of the Deep-Sea Acorn Barnacle *Bathylasma hirsutum* (Hoek, 1883) and the First Report of its Affiliation with a Hydrothermal Vent Field.** *Zoological Studies*, 25, 1–23. doi:10.6620/ZS.2024.63-25

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Mia Schumacher, James Taylor, Elham Kamyab, Jenny Neuhaus (2022). **IceDivA2 from the perspective of four iAtlantic Fellows**. *iAtlantic Newsletter*, 4, 10–11.

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Jenny Neuhaus, Zhehao Hu, Emanuel Pereira, Saskia Brix (in preparation).
Biogeography of North Atlantic *Acanthocope* Beddard, 1885

Zhehao Hu, Jenny Neuhaus, Emanuel Pereira (in preparation).
A new species of *Acanthocope* (Isopoda: Munnopsidae) from the abyssal northeast Atlantic

Conferences

2023 **iAtlantic 5th General Assembly**, Edinburgh, United Kingdom (09.10.–13.10.2023)
The ecological enigma of *Ledella ultima* (E. A. Smith, 1885): An in-depth assessment of genetic diversity and population structure in an abyssal protobranch

Jenny Neuhaus, Mark E. de Wilt, Katrin Linse, Pedro Martínez Arbizu, Ron J. Etter, Robert M. Jennings, Saskia Brix
—*Oral presentation*

2023 **56. European Marine Biology Symposium**, Reykjavik, Iceland (04.09.–08.09.2023)

The ecological enigma of *Ledella ultima* (E. A. Smith, 1885): An in-depth assessment of genetic diversity and population structure in an abyssal protobranch

Jenny Neuhaus, Mark E. de Wilt, Katrin Linse, Pedro Martínez Arbizu, Ron J. Etter, Robert M. Jennings, Saskia Brix

—Oral presentation

The ecological enigma of *Ledella ultima* (E. A. Smith, 1885): A deep-dive in the population structure of an abyssal protobranch

Mark E. de Wilt, Saskia Brix, Katrin Linse, Pedro Martínez Arbizu, Ron J. Etter, Robert M. Jennings, Jenny Neuhaus

—Poster presentation

2023 **24th Annual Meeting of the Society of Biological Systematics**, Hamburg, Germany (28.03.–31.03.2023, virtual meeting)

The deep-sea acorn barnacle *Bathylasma hirsutum* (Hoek, 1883): first record from a hydrothermal vent field at the Reykjanes Ridge

Jenny Neuhaus, Katrin Linse, Saskia Brix, Pedro Martinez Arbizu, James Taylor

—Oral presentation

2022 **iAtlantic 4th General Assembly**, Florianopolis, Brazil (10.10.–14.10.2022)

The Deep-Sea Acorn Barnacle *Bathylasma hirsutum* (Hoek, 1883): An Indicator for Geothermal Activity Along the Reykjanes Ridge?

Jenny Neuhaus, Saskia Brix, James Taylor, Katrin Linse, Pedro Martínez Arbizu

—Oral presentation

2022 **Challenger 150 Society Conference**, London, United Kingdom (06.09.–08.09.2022)

What is the IceDivA project? Research expeditions and science in the face of Covid-19

James Taylor, Elham Kamyab, Kai H. George, Alexander Kieneke, Katrin Linse, Pedro Martinez Arbizu, Jenny Neuhaus, Mia Schumacher, Saskia Brix

—Oral presentation

2022 **20. Crustaceologen-Tagung**, Kiel, Germany (07.04.–10.04.2022)

The IceDivA project: Exploring biogeographic connectivity of deep-sea basins in the North Atlantic using invertebrate taxa as surrogates

Jenny Neuhaus, James Taylor, Elham Kamyab, Kai H. George, Alexander Kieneke, Katrin Linse, Pedro Martinez Arbizu, Mia Schumacher, Saskia Brix

—*Oral presentation*

2022 **23rd Annual Meeting of the Society of Biological Systematics**, Hamburg, Germany (21.03.–24.03.2022, virtual meeting)

Connectivity of deep-sea basins in the North-Atlantic using invertebrate taxa as surrogates – preliminary results

Jenny Neuhaus, James Taylor, Katrin Linse, Pedro Martinez Arbizu, Susanne Dobler, Saskia Brix

—*Oral presentation*

Awards

2023 **First Prize for Best Student Oral Presentation**

The deep-sea acorn barnacle *Bathylasma hirsutum* (Hoek, 1883): first record from a hydrothermal vent field at the Reykjanes Ridge

24th Annual Meeting of the Society of Biological Systematics, Hamburg, Germany (28.03.–31.03.2023)

2024 **Wilhelmshaven Wissenschaftspreis 2024**

A new species of scaphopod in association with an anemone from the Labrador Sea

Category Scientific Research; in collaboration with K. Linse, Wilhelmshaven, Germany

Workshops and Symposia

2024 **Ocean Census Arctic Taxonomy Workshop**

Tromsø, Norway (14.10.–18.10.2024)

2023 **High Seas Treaty (BBJN Agreement): From Negotiation to Implementation**
Edinburgh, UK (06.10.–07.10.2023)

2023 **Third-Party Funding Workshop**
Wilhelmshaven, Germany (22.05.–24.05.2023)

2023 **IUCN Red List Assessor Workshop**
Wilhelmshaven, Germany (24.04.–26.04.2023)

2023 **RAD Sequencing Symposium**
Hamburg, Germany (21.02.2023)

2022 **PANGAEA Community Workshop**
Hamburg, Germany (01.12.–02.12.2022, virtual meeting)

2022 **Cold-water Coral Taxonomy Training School**
Florianopolis, Brazil (15.10.–17.10.2022)

2021 **Evolution and Diversity of Meiobenthos**
ForBIO – Research School in Biosystematics (13.09.–23.09.2021)

Expeditions

2021 *RV Sonne* SO286 (PI S Brix), IceDivA2, North Atlantic Ocean
Emden–Las Palmas, 05.11.–09.12.2021

2020 *RV Sonne* SO286 (PI S Brix), IceAGE3, North Atlantic Ocean
Emden–Emden, 22.06.–26.07.2020

During PhD

Prior to PhD

2019 *RV G.O. Sars* (PI F Midtøy), BIO325, North Atlantic Ocean
Bergen–Bergen, 18.09.–04.10.2019

2018 *RV Helmer Hanssen* (PI T Gabrielsen), AB-202, Arctic Ocean
Longyearbyen–Longyearbyen, 05.05.–15.05.2018

2017 *RV G.O. Sars* (PI L Buhl-Mortensen), Mareano, Barents Sea
Tromsø–Tromsø, 21.10.–17.11.2017

Science Communication and Public Outreach

2025 **Science Pub „Entdeckung einer neuen Art aus der Tiefsee“**
Kling Klang Pub, Wilhelmshaven, Germany (14.01.2025)

2024 **Auf Tauchgang in die Tiefsee – Geschichten über wirbellose Tiefseebewohner**
Aha?! Science Lab, Senckenberg Museum Frankfurt, Germany (27.07.2024)

2024 **Science Slam „Auf Tauchgang in die Tiefsee“**
Kulturzentrum Pumpwerk, Wilhelmshaven, Germany (11.04.2024)

2023 **Science Slam on Event „Neues aus der Welt der Seeschweine und Co“**
Wattenmeer Besucherzentrum, Wilhelmshaven, Germany (25.10.2023)

2022 **Contributor in Deep-Sea Taxonomy Documentary “How Deep is Your Love”**
Lura Films & Ngauruhoe Film

2022 **Interviewed Contributor to Museum Exhibition “Im Tiefenrausch”**
Deutsches Filminstitut & Filmmuseum Frankfurt, Germany (08.06.2022)

2021 **Science Communication for the UN Ocean Decade Laboratory “A Clean Ocean”**
Conducted during the IceDivA 2 Research Expedition (08.12.2021)

Poster presentation

56. European Marine Biology Symposium, Reykjavik, Iceland (04.09.–08.09.2023)