Tesis doctoral por compendio de publicaciones

Malacofauna de hábitats profundos del golfo de Cádiz

Olga Utrilla Ojeda

Programa de doctorado en Diversidad Biológica y Medio Ambiente
Facultad de Ciencias | Universidad de Málaga
Junio 2025

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- Urra J., Utrilla O., Gofas S., Valencia V.A., Farias C., González-García E., López-González N., Fernández-Salas L.M., Rueda J.L. 2023. Late Pleistocene boreal molluscs in the Gulf of Cadiz: past and current oceanographic implications. *Quaternary Science Reviews* 313, 108196.
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En Málaga, a 15 de octubre de 2025.

Necesito del mar porque me enseña:
no sé si aprendo música o conciencia:
no sé si es ola sola o ser profundo
o sólo ronca voz o deslumbrante
suposición...

...y mi ser pequeño
se *reconforma*
con más y más del mar que desciende,
con más y más del mar que se levanta.

Pablo Neruda

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No voy a ocultar la ilusión que tengo de cerrar, por fin, esta etapa. Pero este cierre no habría sido posible sin la compañía de todas estas personas a las que tengo mucho que agradecer, además de otras tantas que faltan en estas páginas:

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LIC	Lugar de Importancia Comunitaria
ZEC	Zona de Especial Conservación
HIC	Hábitat de Interés Comunitario
GoC	Gulf of Cadiz
SoG	Strait of Gibraltar
NACW	North Atlantic Central Water
SAIW	SubArctic Intermediate Water
MOW	Mediterranean Outflow Water
NADW	North Atlantic Deep Water
AAIW	Antarctic Intermediate Water
WMDW	Western Mediterranean Deep Water
SATL	Surface Atlantic Water
LIW	Levantine Intermediate Water
mMOW	Modified MOW
MVs	Mud Volcanoes
DMVs	Diapir/MV complexes
MD	Mud Diapir
MDACs	Methane Derived Authigenic Carbonates
FVSS	Fluid Venting Submarine Structure
SFFE	Shallow Field of Fluid Expulsion
DFFE	Deep Field of Fluid Expulsion
B/O	Buque Oceanográfico
BT	Beam-trawl
DA	Benthic dredge
BC	Box-corer
SK	Shipek grab
DR	Rock dredge
DW	Waren's epibenthic sledge
KG	Usnel corer
Ind.	Live-taken individuals
Spp.	Species
Sh.	Shells
V.	Valves

Jv.	Juvenile
Indiv.	Individuals
%G	Percentage of gravel
%CS	Percentage of coarse sand
%FS	Percentage of fine sand
%OM	Percentage of organic matter
T	Water temperature (°C)
O_2	Dissolved oxygen concentration ($mg\ l^{-1}$)
SST	Sea Surface Temperature
SEM	Scanning Electron Microscopy
STEM	Scanning Transmission Electron Microscopy
TEM	Transmission Electron Microscopy
EDX	Energy Dispersive X-ray
AMS	Accelerator Mass Spectrometry
B.P.	Before Present
LGM	Last Glacial Maximum
HS	Heinrich Stadial
AMOC	Atlantic Meridional Overturning Circulation
BGs	Boreal Guests
Cal. yr	Calendar ages
MIS	Marine Isotope Stage
OMZs	Oxygen Minimum Zones
OMLs	Oxygen Minimum Layers
OTUs	Operational Taxonomic Units
COI	Cytochrome c Oxidase subunit I
SSU rRNA	Small-SubUnit ribosomal RNA
EDTA	Ethylene Diamine Tetraacetic Acid
MNHN	Muséum National d'Histoire Naturelle
IEO	Instituto Español de Oceanografía
SCAI	Servicios Centrales de Apoyo a la Investigación

Resumen

El golfo de Cádiz es una región cuyo contexto oceanográfico y geológico es de gran relevancia a nivel europeo, y está caracterizada por ser una zona de transición entre dos continentes (Europa y África) y diversas masas de agua (las atlánticas y las mediterráneas). Su dinámica oceanográfica y su variedad de relieves submarinos generan una gran diversidad de hábitats que albergan numerosas especies, y lo posicionan como un *hotspot* de biodiversidad y geodiversidad en el Atlántico nororiental. Además, presenta una elevada productividad biológica que favorece el desarrollo de especies de interés pesquero y de comunidades con importancia ecológica. Entre sus relieves geológicos destacan las estructuras submarinas de expulsión de fluidos, como los volcanes de fango y los complejos diapiro/volcán de fango, las cuales generan una gran heterogeneidad geomorfológica. Además, su localización lo convierte en un punto de confluencia de especies con distintas afinidades biogeográficas, algunas de ellas incluidas en listados nacionales e internacionales de conservación y protección. Junto con el estrecho de Gibraltar, conforma un importante corredor para especies migratorias como cetáceos, aves marinas y grandes pelágicos. Por otra parte, el proceso de expulsión de fluidos incrementa la complejidad del sustrato y, por lo tanto, la diversidad de hábitats y de las especies asociadas, fomentando así la presencia de comunidades poco habituales, como las quimiosintéticas que utilizan la energía química de los fluidos liberados para producir materia orgánica. En este sentido, son especialmente relevantes los bancos de corales de aguas frías, debido a su singularidad y fragilidad, y las comunidades quimiosintéticas vinculadas a emisiones de gases, poco comunes en el contexto europeo. En cuanto a su dinámica oceanográfica, el golfo de Cádiz está caracterizado por el intercambio de masas de agua entre el océano Atlántico y el mar Mediterráneo, las cuales juegan un papel significativo en la dispersión larvaria de las especies. La corriente atlántica superficial fluye hacia el mar Mediterráneo, mientras que el agua de salida mediterránea, conocida como MOW (por sus siglas en inglés *Mediterranean Outflow Water*), se dirige hacia el océano Atlántico, influyendo en la erosión del fondo marino y en la formación de sistemas contorníticos.

El golfo de Cádiz alberga más de 70 volcanes de fango, y en su margen español se localiza el Lugar de Importancia Comunitaria (LIC) "Volcanes de fango del golfo de Cádiz". En dicho LIC se hallan distintos Hábitats de Interés Comunitario, como "Estructuras submarinas formadas por emisión de gases" (código 1180) y "Arrecifes" (código 1170), ambos recogidos en el Anexo I de la Directiva Hábitats (Directiva 92/43/CEE), y una gran biodiversidad asociada. Los volcanes de fango sustentan comunidades quimiosimbióticas adaptadas a emisiones de metano, conformadas por bacterias y fauna muy especializada. Por otro lado, especies comerciales como la cigala, la merluza y la gamba blanca presentan importantes caladeros en la zona, por lo que la pesca de arrastre ejerce una importante presión. Este tipo de pesca representa la mayor amenaza no solo para dichas especies objetivo, sino para muchas especies no comerciales y para los hábitats bentónicos de la zona y su biodiversidad. Algunas comunidades bentónicas allí presentes conforman hábitats profundos estructurados por especies sésiles tridimensionales, habitualmente frágiles y de crecimiento lento, que favorecen la biodiversidad al ofrecer refugio a numerosas especies, pero que a su vez son especialmente vulnerables a la presión que ejerce la pesca de arrastre en esta área.

Los moluscos constituyen un grupo de invertebrados excepcionalmente diverso que desempeña un papel crucial en sectores como el pesquero y el acuícola. Los fondos marinos españoles, en particular, se consideran un punto de alta diversidad para este grupo, ya que albergan más de la mitad de las especies registradas para aguas europeas. La relevancia ecológica de los moluscos radica en su diversidad de modalidades tróficas, y en su papel en la transferencia de materia orgánica para niveles tróficos superiores. Además, su amplia distribución y sensibilidad a los cambios ambientales los sitúa como indicadores biológicos eficaces, tanto para evaluar el estado ambiental y la biodiversidad de una región, como para los cambios paleoclimáticos.

Los estudios sobre la malacofauna del golfo de Cádiz se han centrado principalmente en hábitats de los pisos infralitoral y circalitoral, abordando aspectos descriptivos, ecológicos y tratando impactos ambientales. Sin embargo, las comunidades de moluscos de fondos batiales han recibido una menor atención, en parte debido a la dificultad logística y el elevado coste para llegar a muestrear estos fondos. La peculiaridad biogeográfica del LIC “Volcanes de fango del golfo de Cádiz”, junto con la intensa actividad pesquera que allí se desarrolla, hace que el conocimiento de estos hábitats sea esencial para evaluar posibles impactos y gestionar su conservación. Debido a que la información sobre la malacofauna en los hábitats profundos del LIC sigue siendo limitada, el objetivo central de esta tesis doctoral es profundizar en el conocimiento de las comunidades de moluscos del LIC y su vínculo con las condiciones ambientales de la zona, principalmente las masas de agua. Su estudio resulta clave para ampliar el conocimiento sobre la biodiversidad del área y contribuir a su adecuada gestión y conservación.

En la presente tesis doctoral se ha estudiado la malacofauna asociada al volcán de fango Gazul y sus zonas adyacentes (**capítulo 4**). Este volcán está situado en el campo somero de expulsión de fluidos del LIC “Volcanes de fango del golfo de Cádiz”, y destaca por la presencia de hábitats vulnerables de aguas profundas. Para ello se han procesado y analizado 27 muestras procedentes de las campañas INDEMARES/CHICA 0610, INDEMARES/CHICA 0412 y ATLAS/MEDWAVES 0916, entre los 362 y los 495 m de profundidad, habiéndose identificado un total de 232 especies de moluscos. Este listado amplía significativamente el conocimiento sobre la malacofauna conocida para la región, con 86 nuevas citas locales, tres citas inéditas para aguas españolas y dos especies nuevas para la ciencia (*Onoba goyoi* y *Myonera atlasiana*). Esta riqueza de especies documentada puede estar relacionada con: (1) la combinación de múltiples métodos de muestreo (draga de arrastre bentónico, beam-trawl, box-corer y draga Shipek), lo que ha permitido recolectar muestras de diferentes ambientes y compartimentos ecosistémicos de Gazul, incluyendo tanto moluscos endofaunales como epifaunales; (2) la inclusión de la tanatocenosis en el estudio, que permite detectar especies que están presentes pero que son difíciles de capturar vivas, por ejemplo, porque viven asociadas a un microhábitat específico o porque se dan en baja densidad; (3) la heterogeneidad de hábitats, ya que la zona de estudio presenta desde hábitats sedimentarios y mixtos, hasta otros rocosos de gran complejidad o fondos formados por *coral rubble*; y (4) la localización geográfica de Gazul, en la confluencia de diferentes regiones biogeográficas. Las especies recolectadas vivas que mayor representación tuvieron fueron *Bathyarca philippiana*, *Asperarca nodulosa*, *Leptochiton* sp., *Astarte sulcata* y *Limopsis angusta.* El estudio de dicha taxocenosis ha mostrado diferencias significativas entre las comunidades del propio edificio submarino respecto a las zonas adyacentes. Esto se debe a que Gazul presenta una gran cantidad de carbonatos autigénicos en forma de enlosados, costras y chimeneas, y los organismos sésiles que allí se desarrollan (p. ej. corales y esponjas) generan hábitats tridimensionales que aportan complejidad y favorecen la biodiversidad. El estudio sugiere que la distribución de las asociaciones de moluscos endofaunales está determinada por la textura del sedimento, el contenido en materia orgánica y la actividad pesquera de arrastre, mientras que la temperatura del agua cercana al fondo, la presencia de carbonatos autigénicos y la disponibilidad de materia orgánica determinan la distribución de las asociaciones epifaunales y la megafauna demersal estudiada. Esto se explica por la interacción entre las corrientes de fondo y la topografía de Gazul, la cual genera una dinámica local que favorece la exhumación de dichos carbonatos y el suministro continuo de partículas orgánicas para la fauna sésil filtradora y suspensívora establecida en dichos sustratos duros. Por otro lado, se han hallado restos del bivalvo *Lucinoma asapheus* y una baja densidad de poliquetos siboglínidos en comparación con otros volcanes de fango activos. Esto, junto a la abundancia de carbonatos autigénicos y restos de corales de aguas frías (p. ej. *Lophelia pertusa* y *Madrepora oculata*), sugieren que Gazul fue muy activo en el pasado, pero que actualmente presenta un bajo nivel de emisión de fluidos. La importancia biológica y ecológica de Gazul requiere de una gestión adecuada para preservar este entorno único dentro del golfo de Cádiz, garantizando su conservación y el mantenimiento de su biodiversidad.

En el siguiente capítulo (**capítulo 5**), se han estudiado en detalle restos de moluscos encontrados en 36 muestras recolectadas entre los 300 y los 1.000 m de profundidad a lo largo del margen noreste del golfo de Cádiz, muchas de ellas sobre volcanes de fango y otras estructuras geológicas del LIC. Dichas muestras proceden de las campañas TALISMAN 1883, BALGIM 1984, ANASTASYA 09/99, INDEMARES/CHICA 0211, INDEMARES/CHICA 0412 y CIRCASUR 2020. Muchas de las especies identificadas corresponden a especies boreales que actualmente se encuentran restringidas a latitudes más septentrionales, más al norte del canal de la Mancha. A estas especies se les conoce como *boreal guests*, y corresponden a especies de afinidad boreal del Atlántico norte que, durante periodos fríos, se desplazaron hacia latitudes más templadas, algunas incluso penetraron en la cuenca mediterránea. Entre ellas destacan los gasterópodos *Buccinum undatum*, *Colus gracilis*, *Liomesus ovum*, *Neptunea antiqua*, y los bivalvos *Arctica islandica* y *Chlamys islandica*. Algunas de estas especies se citan por primera vez para el golfo de Cádiz (*C. gracilis*, *N. antiqua* y *L. ovum*), no habiendo sido registradas nunca en los depósitos glaciales fósiles del Mediterráneo. Además, se han identificado otras tres especies que nunca habían sido reportadas como boreales en el Mediterráneo (*Nuculana pernula*, *Propebela turricula* y *Curtitoma trevelliana*). Varios de los ejemplares recolectados (dos ejemplares de *A. islandica* y *Neptunea contraria*, y cuatro de *N. antiqua*) fueron datados con ^{14}C mediante espectrometría de masas con acelerador (AMS). Los resultados indicaron que sus edades oscilan entre los 26.100 y 14.600 años, fechas que coinciden con el Último Máximo Glacial (hace 26.500–19.000 años) y el periodo siguiente de desglaciación (*Heinrich Stadial* 1, hace 18.000–14.600 años). Esto confirma su pertenencia a comunidades glaciales y, por otro lado, evidencia que la extinción local de los moluscos *boreal guests* no ocurrió de forma simultánea, sino progresivamente, quedando algunas especies rezagadas. No obstante, el 84,6% de los moluscos identificados de mayor tamaño (mayores de 5 cm) aún presentan poblaciones vivas en el golfo de Cádiz y el mar de Alborán, lo que refleja la persistencia de una parte significativa de la fauna local pese a los cambios ambientales pasados. Por otra parte, las especies boreales de pequeño tamaño fueron muy escasas en las muestras estudiadas, probablemente al ser arrastradas por las fuertes corrientes de fondo. El hallazgo de estos *boreal guests* documenta la continuidad del cambio de fauna que hasta ahora carecía de registros para esta región intermedia en su migración hacia la cuenca mediterránea, y se registra casi por completo los que están presentes en los depósitos glaciales del Mediterráneo. La presencia de estos *boreal guests* descarta que el agua de salida mediterránea (MOW: *Mediterranean Outflow Water*) fuese cálida, hipersalina y activa en la zona de estudio durante el Pleistoceno, como ocurre en la actualidad, con una temperatura de 12,9ºC y una salinidad de 38,45‰. Las poblaciones actuales de estas especies boreales viven en unas condiciones de temperatura menores de 10ºC y una salinidad menor de 36‰ que no existen en el actual golfo de Cádiz ni en el mar Mediterráneo. Esto respalda la hipótesis de que durante el Pleistoceno tardío la MOW se localizaba a una mayor profundidad, permitiendo que el fondo permaneciera en contacto con aguas intermedias atlánticas adecuadas para la supervivencia de dichas especies, reforzando la idea de un cambio faunístico vinculado a variaciones climáticas pasadas. Estos hallazgos se alinean con el cambio faunístico de especies boreales previamente documentado en el mar Mediterráneo y ahora registrado en el golfo de Cádiz, y su relación con las oscilaciones climáticas del Pleistoceno tardío. Además, aporta información clave sobre la continuidad del cambio faunístico entre el Atlántico norte y el Mediterráneo.

Un capítulo importante de la presente tesis doctoral se basa en el estudio de los moluscos recolectados durante la campaña oceanográfica de 1984 BALGIM (**capítulo 6**), cuyo objetivo principal fue estudiar la relación entre las masas de agua y la distribución batimétrica y geográfica de la fauna bentónica en el golfo de Cádiz, el estrecho de Gibraltar y el mar de Alborán. A partir del análisis de los moluscos recolectados en 99 muestras tomadas entre los 200 y los 2.110 m de profundidad, se han registrado 154 especies a partir de ejemplares vivos. Este listado asciende a 243 especies al incluir la tanatocenosis. Con el estudio de los gasterópodos y escafópodos (**capítulo 6A**) se ha logrado completar la laguna de información que existía respecto a los grandes grupos faunísticos de BALGIM. Las especies estudiadas se categorizaron según su distribución batimétrica y geográfica en especies de aguas profundas exclusivas del Atlántico, o especies de aguas profundas presentes tanto en el Atlántico como en el Mediterráneo. Respecto a los patrones en las masas de agua, las aguas muy frías o frías y con baja salinidad (NADW: *North Atlantic Deep Water*; AAIW: *Antarctic Intermediate Water*) albergaron la mayoría de especies de aguas profundas exclusivas del Atlántico, mientras que no se encontró ninguna especie de aguas profundas que fuera exclusiva del Mediterráneo. Las muestras que se localizaban en la trayectoria de la MOW contuvieron principalmente especies atlántico-mediterráneas. Este estudio muestra un patrón de distribución general de la malacofauna en relación a las masas de agua, poniendo de manifiesto el importante papel que juega la temperatura. Los resultados confirman la hipótesis de que la MOW representa una barrera ecológica, ya que las especies exclusivas del Atlántico y asociadas a aguas frías profundas (más de 600 m de profundidad) no logran penetrar en el mar Mediterráneo. Esta limitación no parece deberse únicamente al tipo de desarrollo larvario de las especies, ya que algunas de ellas con desarrollo intracapsular y, por tanto, escasa capacidad de dispersión, sí están presentes en el Mediterráneo. Dicha tendencia ya se había observado en estudios previos de otros grupos faunísticos (esponjas, decápodos e hidrozoos). Por lo tanto, la temperatura, tanto de la actual MOW como de las aguas profundas mediterráneas, es el principal factor que condiciona el paso de especies atlánticas hacia la cuenca mediterránea, tanto para moluscos bentónicos como para otros grupos. Además, el estudio de la malacofauna procedente de BALGIM ha dado como fruto la descripción de una nueva especie de gasterópodo llamada *Anatoma balgimae* (**capítulo 6B**), en honor a dicha campaña. Esta especie fue recolectada en la entrada atlántica del estrecho de Gibraltar, y se diferencia de otras especies del género principalmente por presentar, en la escultura de la concha, un número de costillas axiales mucho mayor de lo habitual.

Por último, teniendo en cuenta la escasez de datos sobre la biología del bivalvo *Kelliella miliaris* (Philippi, 1844), se ha estudiado la ultraestructura de varios especímenes de esta especie procedentes del golfo de Cádiz y de la bahía de Málaga (**capítulo 7**). Los ejemplares estudiados proceden de una campaña del programa académico de Diversidad Biológica y Medio Ambiente, y de la campaña INDEMARES/CHICA 0211, entre los 117 y los 735 m de profundidad. *Kelliella miliaris* es un diminuto bivalvo que habita en la superficie de sedimentos blandos, desde la plataforma continental externa hasta profundidades batiales, comúnmente en las zonas de mínimo oxígeno (OMZs: *Oxygen Minimum Zones*) o en hábitats reductores. *Kelliella miliaris* presenta varias características morfológicas que podrían ser adaptaciones para vivir en dicha zona de mínimo oxígeno: (1) la presencia de numerosas fibras musculares en el manto, el borde del manto y la conexión entre las branquias y la masa visceral, lo que le permitiría un movimiento activo de las branquias o un mejor control de la abertura ventral en relación con los movimientos verticales del animal; (2) un elevado número, en relación con el tamaño corporal, de filamentos branquiales de gran tamaño, principalmente en la gran demibranquia interna; y (3) largos cilios que le proporcionarían una amplia superficie para la captura de oxígeno y una absorción más efectiva del oxígeno del agua. En todos los especímenes examinados se observaron numerosas bacterias con forma alargada entre los cilios branquiales. Estas bacterias presentan la típica doble membrana de las bacterias Gramnegativas. El análisis del ADN bacteriano reveló que la clase más abundante era Gammaproteobacteria, con el 53,69% del total de lecturas. Esto, junto con el pico de oxígeno y la presencia de azufre encontrados en los gránulos electrodensos de las bacterias, determinados mediante análisis TEM-EDX (*Transmission Electron Microscopy with Energy Dispersive X-ray*), apunta a la participación de estas bacterias en la oxidación del sulfuro. La presencia de bacterias en las branquias de *Kelliella miliaris* resalta la importancia de la simbiosis quimiosintética en las zonas de mínimo oxígeno de los océanos que, probablemente, se había pasado por alto hasta ahora. Por otro lado, se han encontrado diferentes microorganismos en el estómago de esta especie, lo que indica heterotrofia. También se han hallado espermatozoides dentro de la gónada femenina, lo que confirma la existencia de fecundación interna en esta especie, si bien la presencia de protoconcha I y protoconcha II indica un desarrollo larvario planctotrófico.

Los resultados de esta tesis doctoral confirman que el golfo de Cádiz es un área de gran complejidad biogeográfica, ecológica y oceanográfica, caracterizada por la interacción entre aguas atlánticas y mediterráneas, así como por su geodiversidad. También se pone de manifiesto la importancia de la investigación en aguas profundas, ya que revela una inesperada biodiversidad, y sugiere nuevas oportunidades de exploración. Sin embargo, la pesca de arrastre amenaza seriamente los hábitats vulnerables que lo conforman. Ante esta situación, una mayor restricción de la pesca de arrastre en determinadas áreas clave del LIC "Volcanes de fango del golfo de Cádiz", podría generar beneficios ecológicos y pesqueros sin grandes impactos socioeconómicos, como se ha demostrado en otras zonas. En conclusión, el conocimiento generado en esta tesis doctoral respalda la necesidad de fortalecer la protección del LIC mediante su designación como Zona de Especial Conservación (ZEC). Esto permitiría conservar su biodiversidad única y cumplir con las directivas europeas sobre medio marino y hábitats, avanzando hacia una gestión más sostenible.

Abstract

The Gulf of Cadiz is an area which is highly relevant to the oceanographic and geological context of Europe. It is characterized as a transition zone between two continents (Europe and Africa) and various water masses (those of the Atlantic and the Mediterranean). Its oceanographic dynamics and varied underwater topography generate a great diversity of habitats, which are home to many species and place it as a biodiversity and geodiversity hotspot in the Northeast Atlantic. Furthermore, it has a high biological productivity, favouring the development of species of interest to fisheries and of ecologically important communities. Its geological relief features include fluid venting submarine structures, such as mud volcanoes and mud diapir/volcano complexes, which generate an outstanding geomorphological heterogeneity. Furthermore, its location makes it a meeting point for species with distinct biogeographic affinities, some of which are included in national and international lists for conservation and protection. Together with the Strait of Gibraltar, it forms an important corridor for migratory species such as cetaceans, seabirds, and large pelagic fish. Furthermore, the process of fluid venting increases the complexity of the substrate and, therefore, the diversity of habitats and associated species, thus promoting the occurrence of unusual biota, such as the chemosynthetic communities that use the chemical energy of the released fluids to produce organic matter. In this regard, the cold-water coral reefs and chemosynthetic communities linked to gas emissions, the latter seldom found in Europe, are particularly relevant due to their uniqueness and fragility. Regarding its oceanographic dynamics, the Gulf of Cadiz is characterized by the exchange of water masses between the Atlantic Ocean and the Mediterranean Sea, which play a significant role in the larval dispersal of species. The Atlantic surface current flows towards the Mediterranean, while Mediterranean Outflow Water (known as MOW), flows towards the Atlantic, influencing seafloor erosion and the formation of contourite systems.

The Gulf of Cadiz features more than 70 mud volcanoes, and the “Mud Volcanoes of the Gulf of Cadiz” Site of Community Importance (SCI) is located on its Spanish margin. This SCI contains Habitats of Community Interest, such as "Submarine structures made by leaking gases" (code 1180) and "Reefs" (code 1170), both listed in Annex I of the Habitats Directive (Directive 92/43/EEC), and a significant associated biodiversity. Mud volcanoes support chemosymbiotic communities adapted to methane emissions, made up of highly specialized bacteria and fauna. On the other hand, commercial species such as Norway lobster, hake and white shrimp, have important fishing grounds in the area, so that trawling originates an important pressure. This type of fishing represents the greatest threat not only to these target species, but also to many non-commercial species and to the area's benthic habitats and their biodiversity. Some benthic communities present there form deep-sea habitats structured by three-dimensional sessile species, usually fragile and slow-growing, which promote biodiversity by providing refuge for numerous species, but which are also particularly vulnerable to the effects of trawling in the area.

Molluscs are an exceptionally diverse group of invertebrates that play a crucial role in sectors such as fisheries and aquaculture. The Spanish seabed, in particular, is considered a hotspot for this group, hosting more than half of the species recorded in European waters. The ecological relevance of molluscs lies in their diverse trophic modes and their role in the transfer of organic matter to higher trophic levels. Furthermore, their wide distribution and sensitivity to environmental changes make them effective biological indicators for assessing the environmental status and biodiversity of a region, as well as paleoclimatic changes.

Studies on the malacofauna of the Gulf of Cadiz have focused mainly on habitats in the infralittoral and circalittoral levels, addressing descriptive, ecological, and environmental impact aspects. However, the mollusc communities of bathyal seabeds have received less attention, partly due to the logistical difficulty and high cost of sampling these areas. The biogeographical uniqueness of the "Mud Volcanoes of the Gulf of Cadiz" SCI, along with the intense fishing activity that takes place there, makes essential the knowledge of these habitats for assessing potential impacts and managing their conservation. Because information on the malacofauna in the deep-sea habitats of the SCI remains limited, the central objective of this doctoral thesis is to deepen our understanding of the SCI's mollusc communities and their relationship with the area's environmental conditions, primarily its water masses. Their study is key to expanding our knowledge of the area's biodiversity and contributing to its proper management and conservation.

This doctoral thesis comprises a study of the malacofauna associated with the Gazul mud volcano and its adjacent areas (**Chapter 4**). This mud volcano is located in the shallow field of fluid expulsion of the "Mud Volcanoes of the Gulf of Cadiz" SCI and is notable for the presence of vulnerable deep-sea habitats. To this end, 27 samples from the INDEMARES/CHICA 0610, INDEMARES/CHICA 0412 and ATLAS/MEDWAVES 0916 surveys, between 362 and 495 m depth, have been processed and analyzed, and a total of 232 mollusc species have been identified. This list significantly expands the knowledge on the malacofauna known for the region, with 86 new local records, three previously unpublished records for Spanish waters, and two new species for science (*Onoba goyoi* and *Myonera atlasiana*). This documented species richness may be related to: (1) the combination of multiple sampling methods (benthic trawl, beam-trawl, box-corer, and Shipek grab), which has allowed the collection of samples from different environments and ecosystem compartments of Gazul, including both endofaunal and epifaunal molluscs; (2) the inclusion of the thanatocenosis in the study, which allows the detection of species that are present but difficult to capture alive, for example, because they live associated with a specific microhabitat or because they occur in low densities; (3) the heterogeneity of habitats, since the study area features sedimentary and mixed habitats as well as rocky bottoms of great complexity or bottoms formed by coral rubble; and (4) the geographical location of Gazul, at the crossroads of different biogeographic regions. The species collected alive with the greatest representation were *Bathyarca philippiana*, *Asperarca nodulosa*, *Leptochiton* sp., *Astarte sulcata* and *Limopsis angusta*. The study of this taxocenosis has shown significant differences between the communities of the underwater edifice itself with respect to the adjacent areas. This is explained because Gazul presents a large amount of authigenic carbonates in the form of slabs, crusts, and chimneys, and the sessile organisms that develop there (e.g. corals and sponges) generate three-dimensional habitats that add complexity and favour biodiversity. The study suggests that the distribution of infaunal mollusc assemblages is determined by sediment texture, organic matter content, and trawling activity, while the temperature of the water near the bottom, the presence of authigenic carbonates, and the availability of organic matter determine the distribution of the epifaunal assemblages and the demersal megafauna studied. This is explained by the interaction between bottom currents and Gazul's topography, which generates a local

dynamic that favours the exhumation of these carbonates and the continuous supply of organic particles for the sessile filter-feeding and suspension-feeding fauna that establish themselves on these hard substrates. On the other hand, remains of the bivalve *Lucinoma asapheus* and, compared to other active mud volcanoes, a low density of siboglinid polychaetes. This, together with the abundance of authigenic carbonates and remains of cold-water corals (e.g. *Lophelia pertusa* and *Madrepora oculata*), suggests that Gazul was very active in the past, but currently has a low level of fluid emission. The biological and ecological importance of Gazul requires appropriate management to preserve this unique environment within the Gulf of Cadiz, ensuring its conservation and maintaining its biodiversity.

In the following chapter (**Chapter 5**), mollusc remains found in 36 samples collected between 300 and 1,000 m depth along the northeastern margin of the Gulf of Cadiz, many of them on mud volcanoes and other geological structures in the SCI, are studied in detail. These samples come from the TALISMAN 1883, BALGIM 1984, ANASTASYA 09/99, INDEMARES/CHICA 0211, INDEMARES/CHICA 0412 and CIRCASUR 2020 surveys. Many of the identified species correspond to boreal species that are currently restricted to more northern latitudes, north of the English Channel. These species are known as boreal guests and correspond to boreal-related species from the North Atlantic that, during cold periods, moved towards more temperate latitudes, some even penetrating the Mediterranean basin. These include the gastropods *Buccinum undatum*, *Colus gracilis*, *Liomesus ovum*, *Neptunea antiqua*, and the *bivalves Arctica islandica* and *Chlamys islandica*. Some of these species (*C. gracilis*, *N. antiqua* and *L. ovum*) are recorded for the first time from the the Gulf of Cadiz, and were never recorded in the glacial fossil deposits of the Mediterranean. Three more species have been identified that had never been reported as boreal in the Mediterranean (*Nuculana pernula, Propebela turricula* and *Curtitoma trevelliana*). Several of the collected specimens (two specimens of *A. islandica* and *Neptunea contraria*, and four of *N. antiqua*) were dated with ^{14}C using accelerator mass spectrometry (AMS). The results indicated that their ages range between 26,100 and 14,600 years ago, dates that coincide with the Last Glacial Maximum (26,500–19,000 years ago) and the subsequent period of deglaciation (Heinrich Stadial 1: 18,000–14,600 years ago). This confirms their belonging to glacial communities and, on the other hand, shows that the local extinction of boreal guest molluscs did not occur simultaneously, but progressively, with some species being left behind. However, 84.6% of the largest molluscs identified (greater than 5 cm) still have living populations in the Gulf of Cadiz and the Alboran Sea, reflecting the persistence of a significant portion of the local fauna despite past environmental changes. On the other hand, small boreal species were very rare in the studied samples, probably due to being winnowed away by strong bottom currents. The discovery of these boreal guests documents the continuity of the faunal change that until now had been lacking records for this intermediate region in its migration towards the Mediterranean basin, and almost completely records those species that were present in the glacial deposits of the Mediterranean. The occurrence of these boreal guests rules out the possibility that the Mediterranean Outflow Water (MOW) was warm, hypersaline, and active in the study area during the Pleistocene, as it is today, with a temperature of 12.9°C and a salinity of 38.45‰, since the living populations of these boreal species live in conditions of temperatures lower than 10°C and a salinity lower than 36‰, which do not exist in the modern Gulf of Cadiz or the Mediterranean Sea. This supports the hypothesis that during the Late Pleistocene, the MOW was located at greater depths, allowing the bottom to remain in contact with intermediate Atlantic waters suitable for the survival of these species, reinforcing the idea of a faunal shift linked to past climatic variations. These findings align with the faunal shift of boreal species previously documented in the Mediterranean and now recorded in the Gulf of Cadiz, and its relationship with the climatic oscillations of the Late Pleistocene, and provide key information on the continuity of faunal shift between the North Atlantic and the Mediterranean.

An important chapter of this doctoral thesis has focused on the study of molluscs collected during the 1984 BALGIM oceanographic survey (**Chapter 6**), the main objective of which was to study the relationship between water masses and the bathymetric and geographic distribution of benthic fauna in the Gulf of Cadiz, the Strait of Gibraltar, and the Alboran Sea. Based on the analysis of molluscs collected in 99 samples taken between 200 and 2,110 m depth, 154 species were recorded from living specimens. This list increases to 243 species when including the thanatocenosis. The study of the gastropods and scaphopods of BALGIM (**Chapter 6A**) has filled the gap in information regarding the major faunal groups. The studied species were scored according to their bathymetric and geographic distribution as deep-water species exclusive to the Atlantic, or deep-water species from both the Atlantic and the Mediterranean. Regarding water mass patterns, very cold or cold waters with low salinity (NADW: North Atlantic Deep Water; AAIW: Antarctic Intermediate Water) harboured the majority of deep-water species exclusive to the Atlantic, while we did not find any deep-water species exclusive to the Mediterranean. The samples located along the path of the MOW contained mainly Atlanto-Mediterranean species. This study reveals a general distribution pattern of the malacofauna in relation to water bodies, highlighting the important role played by temperature. The results confirm the hypothesis that the MOW represents an ecological barrier, since species exclusive to the Atlantic and associated with deep, cold waters (more than 600 m deepth) fail to penetrate the Mediterranean. This limitation does not appear to be due solely to the type of larval development of the species, as some species with limited dispersal capacity due to intracapsular development are present in the Mediterranean. The same trend had already been observed in previous studies of other faunal groups (sponges, decapods and hydrozoans). Therefore, temperature, both in the modern MOW and in the deep Mediterranean waters, is the main factor determining the passage of Atlantic species into the Mediterranean basin, both for benthic molluscs and other groups. Furthermore, the study of molluscs from BALGIM has resulted in the description of a new gastropod species named *Anatoma balgimae* (**Chapter 6B**), in honour of that oceanographic survey. This species was collected at the Atlantic entrance to the Strait of Gibraltar and is distinguished from other species of the genus by presenting in the sculpture of the shell a number of axial ribs much greater than usual.

Finally, taking into account the paucity of data on the biology of this species, specimens of *Kelliella miliaris* (Philippi, 1844) from the Gulf of Cadiz and the Bay of Malaga (**Chapter 7**) have been ultrastructurally studied. The specimens studied come from a campaign of the Biological Diversity and Environment academic program and from the INDEMARES/CHICA 0211 campaign, between 117 and 735 m depth. *Kelliella miliaris* is a minute bivalve found on the surface of soft sediments, from the outer continental shelf to bathyal depths, commonly in Oxygen Minimum Zones (OMZs) or reducing habitats. *Kelliella miliaris* displays several morphological features that could be adaptations for living in the OMZ: (1) the presence of numerous muscle fibers in the mantle, mantle edge, and the connection between the gills and the visceral mass, which would allow active movement of the gills or better control of the ventral opening in relation to vertical

movements of the animal; (2) a high number (relative to body size) of large gill filaments, mainly in the large inner demibranch; and (3) long cilia that would provide a large surface area for oxygen capture and a more effective absorption of oxygen from the water. Numerous elongated bacteria were observed between the gill cilia in all specimens examined. These bacteria exhibit the typical double membrane of Gram-negative bacteria. Bacterial DNA analysis revealed that the most abundant class is Gammaproteobacteria, accounting for 53.69% of the total reads. This, along with the oxygen peak and the presence of sulphur found in the bacteria's electron-dense granules, determined by TEM-EDX (Transmission Electron Microscopy with Energy Dispersive X-ray) analysis, points to the involvement of these bacteria in sulphide oxidation. The presence of bacteria in the gills of *Kelliella miliaris* highlights the importance of chemosynthetic symbiosis in the OMZs of the oceans, which has likely been overlooked until now. Furthermore, various microorganisms have been found in the stomach of *Kelliella miliaris*, indicating heterotrophy. Sperm have also been found inside the female gonad, confirming the existence of internal fertilization in this species, although the presence of protoconch I and protoconch II would indicate planktotrophic larval development.

The results of this doctoral thesis confirm that the Gulf of Cadiz is an area of great biogeographic, ecological, and oceanographic complexity, characterized by the interaction between Atlantic and Mediterranean waters, as well as by its geodiversity. It also highlights the importance of deep-sea research, as it reveals unexpected biodiversity and suggests new exploration opportunities. However, trawling seriously threatens its vulnerable habitats. Given this situation, further restrictions on trawling in certain key areas of the "Mud Volcanoes of the Gulf of Cadiz" SCI could generate ecological and fisheries benefits without major socioeconomic impacts, as has been demonstrated in other areas. In conclusion, the knowledge generated here supports the need to strengthen the protection of the SCI through its designation as a Special Area of Conservation (SAC). This would conserve its unique biodiversity and comply with European directives on the marine environment and habitats, moving toward more sustainable management.

Introducción

Capítulo 1

1. INTRODUCCIÓN GENERAL Y OBJETIVOS

El medio marino representa el conjunto de ecosistemas más extenso del mundo, extraordinariamente rico en diversidad de hábitats y de organismos. La mayor parte del planeta Tierra está cubierta por aguas oceánicas (71% de la superficie total), ocupando más del doble del volumen total en comparación con el medio terrestre, y presenta una profundidad media de aproximadamente 3.800 m. El medio marino es un importante regulador del clima (Bigg et al. 2003, Reid et al. 2009), proporciona recursos naturales fundamentales (Sala & Knowlton 2006) y alberga una amplia variedad de hábitats complejos (Jones et al. 2000, Templado et al. 2012); además, es el mayor productor mundial de oxígeno y de materia orgánica (Hensen et al. 2006, Rullkötter 2006).

El conocimiento sobre la biodiversidad marina ha aumentado enormemente en las últimas décadas, fomentado en parte por el desarrollo de nuevas tecnologías dirigidas al estudio de hábitats profundos de muy difícil acceso (p. ej. los vehículos de operación remota). A pesar de esto, la biodiversidad marina sigue estando mucho menos documentada en comparación con la terrestre, la mayoría de cuyos ecosistemas son más accesibles. Además, gran parte de los estudios sobre la biodiversidad marina se han centrado en aquellos taxones mejor conocidos y muy bien representados, como son los peces o los corales arrecifales (Reaka-Kudla 1997, Christensen et al. 2003, Hilborn et al. 2003).

La fauna marina incluye organismos bentónicos, demersales y pelágicos. Los organismos bentónicos, ya sean móviles o sésiles, viven asociados al fondo marino, mientras que los demersales y pelágicos habitan la columna de agua, los primeros manteniéndose próximos al fondo marino. Los factores ambientales como la irradiancia, temperatura, tipo de sustrato o salinidad, muchos de ellos cambiantes según la profundidad, condicionan la vida de estas comunidades faunísticas. En el caso de las comunidades bentónicas, las condiciones ambientales del fondo marino varían gradualmente, por lo que se organizan en "pisos" verticales según la profundidad (Pérès & Picard 1964):

Zona fótica

– **Piso supralitoral**. Franja que se extiende desde el límite superior de las salpicaduras de las olas hasta la línea de pleamar, pero que nunca queda sumergida ni sometida al oleaje. Las especies que viven en este piso están adaptadas a condiciones ambientales muy extremas.

– **Piso mesolitoral**. Franja comprendida entre la pleamar y la bajamar, por lo que puede estar sometida a inmersiones y emersiones periódicas.

– **Piso infralitoral**. Franja permanentemente sumergida desde el nivel inferior de la bajamar hasta la profundidad máxima de distribución de las fanerógamas marinas y algas fotófilas, por lo que depende del grado de transparencia del agua.

– **Piso circalitoral**. Franja comprendida desde el límite donde desaparecen las fanerógamas y algas fotófilas, hasta el límite de distribución de las algas esciáfilas, o hasta el borde de la plataforma continental. En él la temperatura se mantiene relativamente constante y el hidrodinamismo es independiente de las corrientes superficiales.

Zona afótica

– **Piso batial**. Franja que se extiende desde la profundidad máxima que alcanzan las algas esciáfilas hasta el comienzo de las llanuras abisales. Comprende el borde de la plataforma y el talud continental. Los estudios enmarcados en esta tesis se centran principalmente en este piso.

– **Piso abisal**. Franja que comprende los fondos de las llanuras abisales. Se caracteriza por una temperatura constante y oscuridad total. Normalmente se extiende a partir de los 4.000 m de profundidad.

– **Piso hadal**. Lo conforman los fondos de las fosas oceánicas.

Los ecosistemas marinos proporcionan una amplia variedad de hábitats (Fig. 1.1), los cuales albergan una diversidad de especies que constituyen las denominadas comunidades bentónicas. Muchos de estos hábitats tienen una gran importancia ecológica, ya que muchas especies encuentran refugio o sustento en ellos (p. ej. arrecifes de corales, praderas de fanerógamas marinas, fondos de rodolitos). Además, proporcionan numerosos servicios ecosistémicos relevantes para el ser humano, como la provisión de alimento, la mitigación del cambio climático, la prevención de la erosión costera o la educación ambiental y el ocio, entre otros (Thurber et al. 2014, Smaal et al. 2019, Ramón & Galimany 2022).

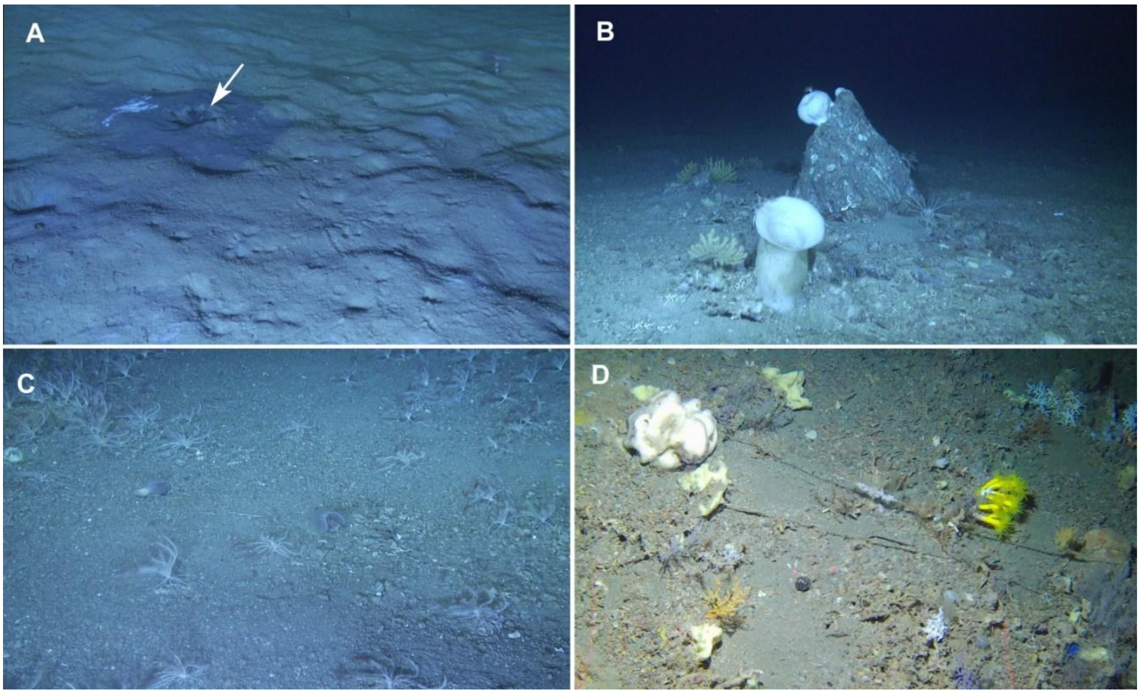


Figura 1.1. A: Fondo sedimentario con emisiones de gases (la flecha señala un foco de emisión) y un tapete bacteriano (blanco) del volcán de fango (VF) Anastasya, 445 m de profundidad. **B**: Fondo con carbonatos autigénicos, aprovechados como sustrato duro por invertebrados sésiles del VF Tarsis, 510 m de profundidad. **C**: Fondo con sedimento bioclástico (el denominado “detrítico profundo” de Pérès & Picard (1964)) ocupado por *Leptometra phalangium* (Müller, 1841) en el VF Pipoca, 520 m de profundidad. **D**: Impacto de la pesca (restos de palangre) en una costra carbonatada que da soporte a invertebrados sésiles del VF Gazul, 360 m de profundidad. Fotografías extraídas de vídeos de ROV (vehículo de operación remota) submarino de la campaña INDEMARES/CHICA 0412.

La mayoría de los hábitats bentónicos y las comunidades biológicas asociadas sufren diversas presiones ambientales por causas naturales y/o de origen antrópico y, habitualmente, actúan de forma acumulada (Taviani et al. 2019, Danovaro et al. 2020). Entre las presiones naturales se incluyen los cambios de salinidad y el aumento de la turbidez causados por aportes fluviales provenientes de tierra. Sin embargo, son las actividades antrópicas las que representan la mayor parte de las amenazas para las comunidades bentónicas marinas en la actualidad (Danovaro et al. 2016, 2020). La pesca de arrastre, el vertido de contaminantes, el dragado de los fondos, el aumento del turismo, el tráfico marítimo, la introducción de especies invasoras, la acidificación de los océanos y el cambio climático, entre otras presiones, están contribuyendo a una rápida degradación y fragmentación de los hábitats marinos (Jennings & Kaiser 1998, Danovaro et al. 2016).

El potencial impacto derivado de las actividades antrópicas sobre los ecosistemas de aguas profundas sigue siendo difícil de prever y cuantificar (Jones et al. 2020), pero las evidencias sugieren una pérdida de biodiversidad que estaría asociada a un perjuicio en el funcionamiento ecosistémico, como un descenso en la producción primaria, que podría tener efectos sobre el resto de los niveles tróficos (Danovaro et al. 2009). Las principales amenazas en estos fondos marinos profundos son la extracción de petróleo, gas (Cordes et al. 2016, Barron et al. 2020) y recursos minerales (Aleynik et al. 2017, Miller et al. 2018, Jones et al. 2020), y el vertido de residuos tóxicos (Karl et al. 1994, Suchanek et al. 1996), además del cambio climático y la pesca en aguas profundas.

La pesca de arrastre representa la principal amenaza de las comunidades bentónicas en gran parte del mundo (Hiddink et al. 2006, Tillin et al. 2006, Sánchez et al. 2014, González-Irusta et al. 2018, Cartes et al. 2022). Este tipo de pesca no es selectiva y captura tanto especies comerciales como no comerciales, alterando y degradando los fondos blandos donde se realiza la actividad, ya que remueve y resuspende el sedimento modificando sus características, a la vez que elimina o daña gran parte de los organismos epi y/o endobentónicos que estructuran el hábitat, por lo que modifica la composición y estructura de las comunidades faunísticas asociadas al sedimento (Pranovi et al. 2000, Tudela 2004, Worm et al. 2006). Además, diversas especies bentónicas conforman hábitats complejos configurados tridimensionalmente que se suelen encontrar a una mayor profundidad, como los jardines de gorgonias, arrecifes de coral o fondos de esponjas. Dichas especies presentan una estructura frágil y sensible, un crecimiento lento y una baja tasa de reproducción, por lo que su limitada capacidad de regeneración las hace más vulnerables a los impactos (Jones 1992, Ball et al. 2000, Sánchez et al. 2014, De la Hoz et al. 2018).

Actualmente, el cambio climático inducido por ciertas actividades humanas como la quema de combustibles fósiles (carbón, petróleo y gas) es otra de las mayores preocupaciones al considerar el estado de salud de los océanos en general, y de las comunidades bentónicas en particular (Sanz & Galán 2020). El calentamiento de los océanos está causando efectos negativos en multitud de fauna, afectando a la pesca y a la producción de alimentos en todo el mundo y, por tanto, comprometiendo la seguridad alimentaria a nivel global (IPCC 2019), así como provocando cambios en el crecimiento, supervivencia, comportamiento, fertilidad y migración de muchas especies (Marbà et al. 2015, Kersting 2016). Además, la magnitud y la frecuencia de las olas de calor marinas, entendidas como el aumento extremo de la temperatura de los océanos durante un periodo de tiempo prolongado, se ha duplicado desde 1982 (Holbrook et al. 2019). Esto ha desencadenado episodios de mortalidad masiva que afectan a un número cada vez mayor de especies y hábitats, especialmente a organismos bentónicos no móviles, como corales, algas y esponjas, que no pueden escapar de estas condiciones ambientales extremas (Garrabou et al. 2009, Kersting 2016, von Schuckmann et al. 2021).

1.1. Biodiversidad de aguas profundas

La biodiversidad se entiende como la diversidad de la vida en todos sus niveles de organización, así como los procesos ambientales y evolutivos que la mantienen. Comprende la diversidad dentro de cada especie, entre las especies y de los ecosistemas (Convention on Biological Diversity 1992). El medio marino es un gran reservorio de biodiversidad, lo que determina su alta resiliencia, y contribuye al buen funcionamiento de gran parte de los ecosistemas. La biodiversidad marina es también un factor clave que permite a los ecosistemas prestar servicios extremadamente valiosos y necesarios para la subsistencia humana (Constanza et al. 1997, Sala & Knowlton 2006, Thurber et al. 2014). El bentos marino tiene una distribución irregular, con comunidades faunísticas que varían desde escalas de centímetros hasta kilómetros. Dicha distribución dificulta el estudio para evaluar la biodiversidad de aguas profundas. En este sentido, inicialmente se pensó que los ecosistemas profundos eran relativamente simples; sin embargo, a lo largo de los años y con la mejora de las técnicas de investigación y de muestreo, ha aumentado el número de descubrimientos de especies marinas profundas (Danovaro et al. 2010, Ascensão & Cunha 2016, Aguzzi et al. 2019), y se ha demostrado que las aguas profundas son más ricas en biodiversidad de lo que se creía (Grassle & Maciolek 1992, Danovaro et al. 2009, 2010, Sabelli & Taviani 2014), aunque menos que la parte litoral. A pesar de que las zonas marinas profundas (batiales y abisales) cubren más del 60% de los océanos, la información que se tiene actualmente de ellas es limitada en comparación con otros ecosistemas marinos más someros (Ramirez-Llodra et al. 2010, Danovaro et al. 2014), existiendo probablemente un alto porcentaje de especies profundas aún sin conocer (Mora et al. 2011).

Algunos hábitats profundos albergan una diversidad bentónica especialmente elevada, como es el caso de los montes y cañones submarinos, los afloramientos rocosos, los arrecifes de aguas profundas y las fuentes hidrotermales, entre otros (Levin et al. 2001, Freiwald & Roberts 2005, Clark et al. 2010). Los procesos geológicos (Maldonado et al. 1999, Somoza et al. 2021), junto con las estructuras submarinas, desempeñan un papel crucial en la formación de hábitats profundos, de modo que la distribución y abundancia de la biodiversidad marina responde a una compleja interacción entre procesos oceanográficos, geológicos, fisicoquímicos y biológicos (Carney 2005, Thrush et al. 2005, Menot et al. 2010, Rex & Etter 2010). Los factores abióticos pueden facilitar o dificultar la supervivencia y el crecimiento de las especies en estos hábitats. Así, las propiedades de la masa de agua, como la temperatura, la salinidad y los niveles de oxígeno disuelto (Yasuhara & Danovaro 2014, Puerta et al. 2020), las corrientes oceánicas y la disponibilidad de nutrientes y materia orgánica, entre otros, tienen un alto impacto en la distribución de las especies de aguas profundas (Levin et al. 2001, Clark et al. 2010, Costello & Chaudhary 2017, Puerta et al. 2020, Dipper 2022). Por su parte, las corrientes ayudan a distribuir nutrientes y materia orgánica a lo largo de grandes distancias, lo que favorece el crecimiento y el desarrollo de especies en entornos de aguas profundas con nutrientes limitados (Rowe & Staresinic 1979, Alkalay et al. 2024). Además, las corrientes pueden facilitar la dispersión de las larvas a grandes distancias, conectando poblaciones y promoviendo el flujo genético, lo que en última instancia repercute en la diversidad genética y la resiliencia de las especies (Jablonski & Lutz 1983, Cowen et al. 2009, Mullineaux et al. 2010, Barroso et al. 2022). Las especies requieren combinaciones específicas de estas propiedades, dando lugar a comunidades faunísticas únicas en diferentes regiones según la profundidad (Levin et al. 2001, Danovaro et al. 2009).

1.2. Moluscos

El filo Mollusca, grupo faunístico en el que se centra la presente tesis doctoral, es uno de los más diversos en los fondos marinos, representando aproximadamente el 25% de la fauna marina bentónica (Appeltans et al. 2012). También constituye uno de los grupos de invertebrados más diversos del mar Mediterráneo, con más de 2.110 especies estimadas (Coll et al. 2010), algunas de ellas de gran valor comercial, y representa uno de los grupos más importantes en abundancia y biomasa de invertebrados en el sector pesquero (Gaspar et al. 2012, González-García et al. 2012, 2020a, b, 2022) y acuícola (Ramón et al. 2005, Gaspar et al. 2012, FAO 2018, Kültz 2022). Las aguas españolas representan un *hotspot* regional de diversidad de moluscos al encontrarse en ellas más de la mitad de los moluscos registrados para aguas europeas (Gofas et al. 2017).

Los moluscos son componentes relevantes en las comunidades bentónicas debido a su variedad de modalidades tróficas, existiendo desde especies filtradoras, depositívoras y carnívoras hasta parásitas, entre otras, y por representar una importante fuente de alimento para niveles tróficos superiores (Meira et al. 2024). Este filo se considera un buen indicador para la evaluación de la biodiversidad bentónica de un área específica, pudiendo así ser representativo del grado de biodiversidad en representación de otros taxones (Mellin et al. 2011). Esto se debe a que los moluscos se encuentran distribuidos mundialmente; constituyen uno de los filos con mayor número de especies; la variación en la composición y estructura de sus poblaciones puede relacionarse con los cambios ambientales; y porque pueden ser dominantes en las comunidades, tanto en número de individuos como en biomasa (Bedulli et al. 2002, Gladstone 2002). Además, representan un excelente indicador de las condiciones ambientales en estudios paleoclimáticos, ya que las conchas perduran en el tiempo (Raffi 1986, Taviani et al. 1991, Aguirre et al. 2019, Melo et al. 2022). Además, su distribución puede explicarse a través de un número reducido de variables como la temperatura, salinidad y productividad; de hecho, sólo con la temperatura se puede predecir entre el 53 y el 99% de la distribución actual de los bivalvos a lo largo de las costas (Belanger et al. 2012).

1.3. Estructuras submarinas de expulsión de fluidos

Unas de las estructuras geológicas submarinas más singulares son las relacionadas con la expulsión de fluidos, como los volcanes de fango y los complejos diapiro/volcán de fango, las cuales se asocian a límites convergentes entre placas (Milkov 2000, Kenyon et al. 2002, Somoza et al. 2003, León et al. 2012, Mascle et al. 2014). Los volcanes de fango submarinos (Fig. 1.2) son estructuras formadas por la expulsión de fluidos no magmáticos ricos en sedimentos y gases (principalmente metano) desde depósitos más profundos sobrepresionados, hacia el fondo marino (Kopf 2002, Etiope et al. 2009). El material extruido se compone de brecha fangosa (fango que contiene clastos de los materiales subyacentes) y fluidos (gases y agua) (Cita et al.

1981, Kopf 2002). Los complejos diapiro/volcán de fango (Fig. 1.3) son aquellos relieves generados por la expulsión sucesiva de fluidos a lo largo de la estructura de un diapiro y que albergan volcanes de fango en su cumbre (Palomino et al. 2016). En general, los volcanes de fango y los complejos diapiro/volcán de fango, se encuentran en campos donde se localizan otras estructuras submarinas de expulsión de fluidos, como *pockmarks* (Fig. 1.4) (depresiones formadas en el fondo marino tras la expulsión de fluidos) o carbonatos autigénicos derivados del metano (Hovland & Judd 1988, Fernández-Puga et al. 2007).

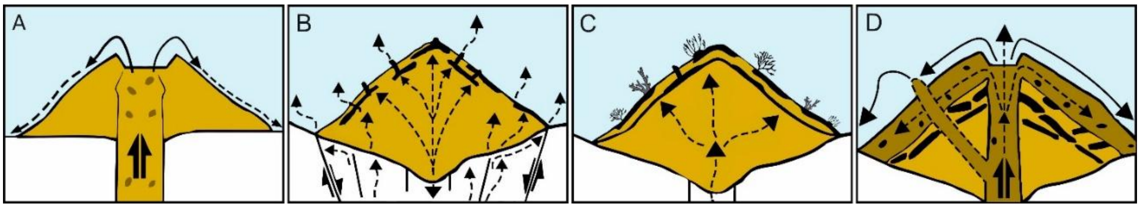


Figura 1.2. Proceso de formación y desarrollo de un volcán de fango en el golfo de Cádiz. **A**: Expulsión activa de fango y brecha fangosa, y formación del edificio volcánico. **B**. Reducción de la actividad de expulsión, con el colapso del edificio y la formación de carbonatos autigénicos. **C**: Condiciones de latencia, con la exposición y colonización de los carbonatos autigénicos por parte de fauna bentónica. **D**: Reactivación de la actividad de expulsión. Figura modificada de León et al. (2007).

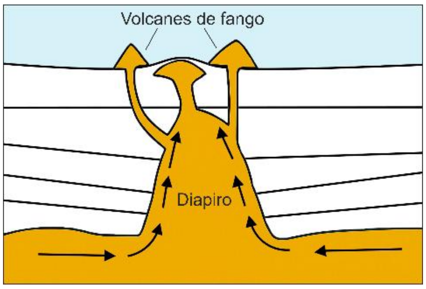


Figura 1.3. Formación de un complejo diapiro/volcán de fango.

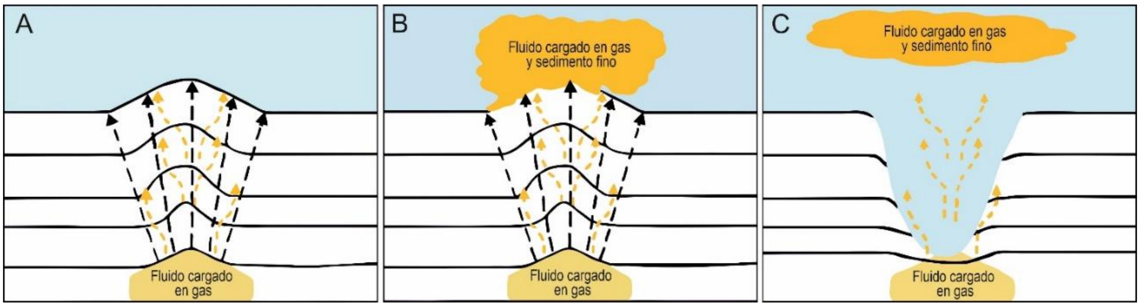


Figura 1.4. Proceso de formación de un *pockmark*. **A**: El fluido cargando en gas generado en el subsuelo migra hacia el fondo marino y, cuando la presión intersticial excede la presión de sobrecarga, empuja y abomba los sedimentos. **B**: El fluido cargado en gas que escapa hacia la columna de agua arrastra los sedimentos finos, que quedan suspendidos en el agua y se desplazan. **C**: El escape continuo de gas arrastra las partículas finas de sedimento, mientras que las partículas gruesas caen al fondo marino, lo que provoca la formación de *pockmarks*.

Existe una fuerte relación entre las comunidades bentónicas de aguas profundas, las corrientes de fondo, el tipo de sustrato y los procesos geológicos (Van Rooij et al. 2010). El proceso de expulsión de fluidos incrementa la complejidad del sustrato y, por lo tanto, la diversidad de hábitats y de las especies asociadas, fomentando así la biodiversidad en la zona (Levin 2005, Cunha et al. 2013, Palomino et al. 2016, Rueda et al. 2016, González-García et al.

2020b, Somoza et al. 2021). Esta expulsión de fluidos contribuye notablemente a la creación de hábitats únicos que sustentan comunidades diversas y productivas (Levin & Sibuet 2012, Tong et al. 2012), como las comunidades quimiosintéticas que utilizan la energía química de los fluidos liberados para producir materia orgánica, y que incluyen una gran variedad de organismos como bacterias, arqueas, bivalvos y otros invertebrados (Grupe et al. 2015, Levin et al. 2016, Seabrook et al. 2018).

El golfo de Cádiz es una zona de gran importancia de emisiones de fluidos a nivel global, con más de 70 volcanes de fango situados en los campos del margen español, portugués y marroquí (Díaz-del-Río et al. 2003, Fernández-Puga et al. 2007, Medialdea et al. 2009, León et al. 2012, Palomino et al. 2016). Los volcanes de fango y los complejos diapiro/volcán de fango del margen español se sitúan sobre el talud continental superior y medio del golfo de Cádiz, entre los 300 y 1.200 m de profundidad (León et al. 2012, Palomino et al. 2016).

1.4. Objetivos

El objetivo central de esta tesis doctoral es profundizar en el conocimiento de las comunidades de moluscos del golfo de Cádiz y su relación con algunas condiciones ambientales reinantes en el área. Para ello, se han establecido una serie de objetivos específicos que permitirán abordar el estudio de manera detallada y estructurada:

– Caracterizar la composición y estructura de las comunidades de moluscos bentónicos ligadas al volcán de fango Gazul del LIC "Volcanes de fango del golfo de Cádiz", con particular atención a posibles aportaciones a la fauna malacológica de la Demarcación marina Sudatlántica.

– Estudiar la presencia y distribución de conchas subfósiles pertenecientes a especies localmente extinctas en el golfo de Cádiz, cuya distribución actual se limita más al norte del canal de la Mancha (conocidas como *boreal guests*), y tratar de vincular estos datos con eventos climáticos pasados como son las glaciaciones.

– Explorar la relación existente entre las comunidades de moluscos y la circulación regional de las masas de agua en el golfo de Cádiz, con particular atención al efecto del agua de salida mediterránea (MOW, *Mediterranean Outflow Water*).

– Estudiar en detalle la simbiosis del bivalvo *Kelliella miliaris* con bacterias quimiosimbióticas en zonas de mínimo oxígeno.

Área de estudio

Capítulo II

2. ÁREA DE ESTUDIO

La presente tesis doctoral se enmarca en el área del golfo de Cádiz, situado entre el suroeste de la península ibérica y el noroeste africano, y entre el cabo de São Vicente, en el sur de Portugal, y el estrecho de Gibraltar como su límite más oriental. Se trata de una zona de transición entre dos continentes (Europa y África) y entre diferentes masas de agua (las del océano Atlántico y las del mar Mediterráneo). Debido a su localización, el golfo de Cádiz representa una zona de confluencia de especies de diferentes regiones biogeográficas (Ekman 1953, Rueda et al. 2016, Lozano et al. 2020).

El rasgo más característico del fondo marino de esta área es la diversidad de relieves erosivos generados por la salida de aguas mediterráneas hacia el Atlántico, así como los fenómenos de expulsión de fluidos cargados en gas. El resultado de la combinación de ambos procesos se refleja en una gran heterogeneidad topográfica y de tipos de sustratos (Hernández-Molina et al. 2003, 2006) que ha dado lugar una amplia variedad de hábitats de gran importancia biológica y ecológica.

El golfo de Cádiz y el estrecho de Gibraltar son áreas clave para la dinámica oceanográfica de las zonas adyacentes, con las diferentes masas de agua que aquí confluyen jugando un papel significativo en la dispersión larvaria de las especies, y conformando un importante corredor para especies migratorias como cetáceos, aves marinas y grandes pelágicos (Díaz del Río et al. 2014). Los procesos hidrológicos locales pueden generar una elevada productividad, creando las condiciones adecuadas para un amplio espectro de especies de interés pesquero (Fernández-Salas et al. 2012, Díaz del Río et al. 2014). Por todo ello, es considerado un punto caliente o *hotspot* de biodiversidad y geodiversidad en el Atlántico nororiental (Vanreusel et al. 2009, Rueda et al. 2012a, 2016, Cunha et al. 2013, Díaz del Río et al. 2014, González-García et al. 2020a, b, Urra et al. 2021).

2.1. Lugar de Importancia Comunitaria "Volcanes de fango del golfo de Cádiz"

En 2012, el proyecto LIFE+INDEMARES "Inventario y Designación de la Red Natura 2000 en áreas marinas del Estado español" encargó al Instituto Español de Oceanografía (IEO) el estudio de espacios marinos de valor para su protección y uso sostenible, resultando en el Lugar de Importancia Comunitaria (LIC) "Volcanes de fango del golfo de Cádiz" (Fig. 2.1.) (Díaz del Río et al. 2014), entre otros. La propuesta formal para su inclusión en la Red Natura 2000 (LIC ESZZ12002) fue realizada por orden ministerial de 9 de julio de 2014 (Ministerio de Agricultura, Alimentación y Medio Ambiente 2014), y fue aprobada en noviembre de 2015 (Comisión Europea 2015). En el momento en que se iniciaron las campañas INDEMARES, los conocimientos de la fauna bentónica eran limitados, e incluso no se tuvieron en cuenta algunos hábitats destacados como los arrecifes de *Dendrophyllia* sp. que se encuentran fuera del área protegida (Marín et al. 2011).

En este LIC están representados varios Hábitats de Interés Comunitario (HICs) recogidos en la Directiva Hábitats (1992/43/CEE), como el HIC 1180 "Estructuras submarinas producidas por el escape de gases", representado por formaciones con emisiones de fluidos y/o con sustratos carbonatados, que constituyen a su vez el hábitat de las comunidades quimiosintéticas. Esta actividad de emisiones de gas promueve la formación de sustratos duros, normalmente escasos en el piso batial y, por lo tanto, la presencia del HIC 1170 "Arrecifes", representado por arrecifes de corales aguas frías, agregaciones de gorgonias, antipatarios o esponjas (Díaz del Río et al. 2014, Rueda et al. 2016). Estos y otros hábitats amenazados y/o en declive están incluidos en convenios internacionales, como OSPAR, donde destacan "Lophelia pertusa *reefs", "Deep-sea sponge aggregations*", "*Coral gardens*", y "*Sea-pen and burrowing megafauna communities*" (OSPAR 2009, 2010a, b, c).

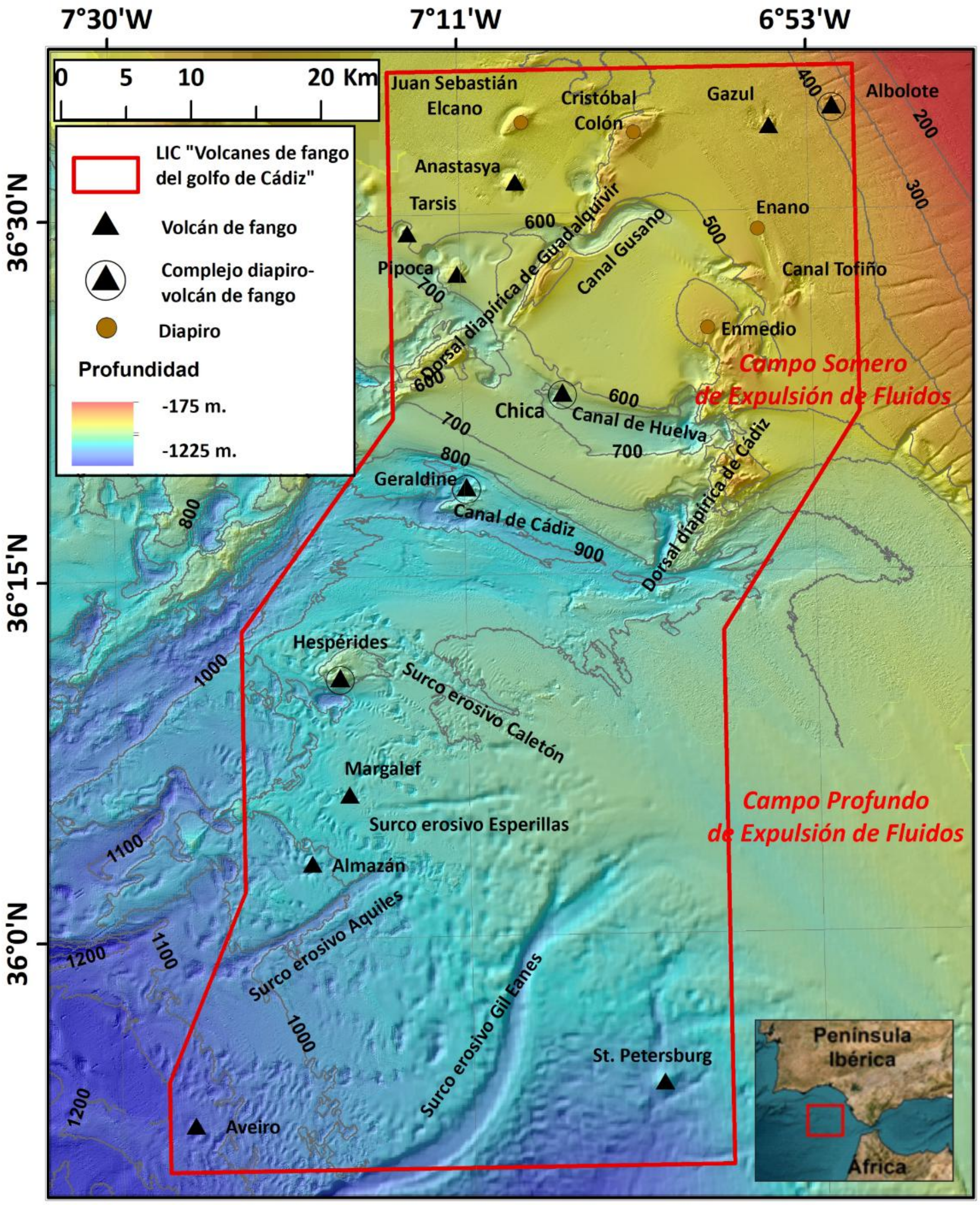


Figura 2.1. Localización del Lugar de Importancia Comunitaria "Volcanes de fango del golfo de Cádiz", con las estructuras geológicas más destacadas.

El LIC "Volcanes de fango del golfo de Cádiz" es considerado un *hotspot* para el margen peninsular (González-García et al. 2012, Rueda et al. 2012a, b, 2016, Cunha et al. 2013, Díaz del Río et al. 2014, Sitjà et al. 2019, Lozano et al. 2020, Ramalho et al. 2020, Urra et al. 2021). Presenta una elevada biodiversidad, con especies incluidas en catálogos de especies amenazadas, especies de gran valor comercial y otras relevantes para la comunidad científica.

Están presentes especies con un amplio rango de distribución (p. ej. *Funiculina quadrangularis* (Pallas, 1766)), otras propias del Atlántico norte y el mar Mediterráneo (p. ej. *Nephrops norvegicus* (Linnaeus, 1758)), especies propias del mar Mediterráneo (*Plesionika gigliolii* (Senna, 1902)) o especies tropicales de ambos lados del Atlántico (*Hacelia superba* H.L. Clark, 1921). Así, la biodiversidad en esta zona estaría ligada, fundamentalmente, al amplio rango batimétrico en el que se presentan las estructuras asociadas a la expulsión de fluidos cargados en gas, a la variedad de tipo de sedimento (fango, arenas gruesas, gravas, fondos duros...), a la diversidad geomorfológica (cimas de volcanes de fango, depresiones, canales, fondos aplacerados...) y a la compleja hidrología que domina la zona que, finalmente, es uno de los factores que interviene en el proceso de expulsión (Díaz del Río et al. 2014).

El LIC está formado por dos campos de expulsión de fluidos a diferente profundidad (Fig. 2.1). El campo somero se extiende desde los 300 a los 730 m de profundidad y en él se localizan los volcanes de fango Gazul, Anastasya, Pipoca y Tarsis, los diapiros Cristóbal Colón y En medio, y los complejos diapiro/volcán de fango Albolote y Chica. Por su parte, el campo profundo se sitúa entre los 800 y 1.200 m de profundidad y en él se encuentran los volcanes de fango Almazán, San Petersburgo y Aveiro, el diapiro La Pepa, y el complejo diapiro/volcán de fango Hespérides, además de varios canales y otras estructuras geológicas.

Los procesos asociados a la migración de fluidos ricos en hidrocarburos en el golfo de Cádiz sustentan una amplia diversidad de organismos quimiosimbióticos (Rodrigues et al. 2008, 2013, Hilário & Cunha 2008, Hilário et al. 2010, Oliver et al. 2011). En la cumbre de algunos volcanes de fango (p. ej. Anastasya) se han hallado sedimentos saturados en metano con tapetes bacterianos y fauna quimiosintética, cuya densidad disminuye a medida que incrementa la distancia al foco de emisión. Dicha fauna está constituida por especies con quimiosimbiontes, como son los poliquetos frenulados y los decápodos talasínidos excavadores de galerías o algunos bivalvos (p. ej. *Solemya elarraichensis* P. G. Oliver, Rodrigues & M. Cunha, 2011). Las variaciones ambientales provocadas por las elevadas tasas de oxidación anaeróbica del metano se reflejan en la diversidad de comunidades microbianas (Vanreusel et al. 2009), presentando la mayoría de invertebrados simbiontes tiotróficos (Rodrigues et al. 2010, 2011).

La actividad antropogénica que ejerce un mayor impacto en los hábitats bentónicos del LIC "Volcanes de fango del golfo de Cádiz" es la pesca de arrastre de fondo, ya que existen importantes caladeros de especies comerciales en la zona. Dicha actividad tiene como especies objetivo la cigala, la merluza y la gamba blanca, entre otras (Sobrino et al. 1994, Vila et al. 2004, González-García et al. 2012). Esta presión también afecta a otras especies de bajo o nulo interés comercial, a la estructura de los hábitats bentónicos y potencialmente al ecosistema en su conjunto, pudiendo modificar la complejidad del fondo y provocar una pérdida de la biodiversidad en la zona (González-García et al. 2020a, 2022, Rueda et al. 2022, Lozano et al. 2024).

2.2. Contexto geológico

En el golfo de Cádiz convergen las placas tectónicas africana y euroasiática, cuyos límites están cubiertos por una gruesa capa de depósitos sedimentarios del Mio-Plioceno (Medialdea et al. 2004). Así se originó una gran variedad de estructuras geológicas, incluyendo montes submarinos y otros fondos rocosos, zonas con expulsión de fluidos y fondos sedimentarios, entre otros (Vázquez et al. 2021). La morfología de sus fondos está marcada principalmente por surcos y crestas, así como por canales y cañones submarinos. La disposición y naturaleza de estos relieves pone de manifiesto la estrecha relación existente entre la tectónica reciente (neotectónica), el diapirismo vinculado a la tectónica salina y el efecto erosivo de la circulación de las masas de agua (Díaz del Río et al. 2014).

A lo largo del margen atlántico y mediterráneo de Europa, existen tres regiones principales caracterizadas por la presencia de estructuras geológicas asociadas a filtraciones frías: el margen nórdico, la región sur ibérica y el Mediterráneo oriental (Foucher et al. 2009, Vanreusel et al. 2009). Por su parte, la región sur ibérica se encuentra tectónica y oceanográficamente vinculada al margen marroquí, y comprende el mar de Alborán (Mediterráneo occidental) y el golfo de Cádiz. El entorno tectónico y la alta movilidad diapírica existentes favorecen la formación de vías para la migración de fluidos que generan estructuras relacionadas con la expulsión de gases (Medialdea et al. 2004, 2009, Fernández-Puga et al. 2007, Palomino et al. 2016). De estas estructuras, las más relevantes en el área de estudio son las siguientes (Baraza & Ercilla 1996, Baraza et al. 1999, Mazurenko et al. 2002, Somoza et al. 2002, 2003, Díaz-del-Río et al. 2003, Pinheiro et al. 2003, León et al. 2007):

– **Volcanes de fango**. Son estructuras formadas por la expulsión vertical de fluidos cargados en gas procedentes del fondo marino, principalmente metano, que pueden movilizar parte de los sedimentos suprayacentes y generar una estructura cónica submarina (Kopf 2002, Díaz-del-Río et al. 2006, Mazzini & Etiope 2017). Este proceso (Fig. 1.2) puede provocar cambios sustanciales en la superficie de los depósitos sedimentarios, generando nuevas estructuras carbonatadas gracias a la actividad de consorcios bacterianos, los cuales oxidan anaeróbicamente el metano y dan como resultado la precipitación de carbonatos (Kopf 2002). Estos **carbonatos autigénicos** se forman a medida que los fluidos ricos en gas migran hacia el fondo marino (Greinert et al. 2001, Magalhães et al. 2012, Vanneste et al. 2012), y su evolución está condicionada por la intensidad y frecuencia de la expulsión de los fluidos. De esta manera, los fondos se transforman en superficies consolidadas o de naturaleza mixta, compuestas por fragmentos de roca carbonatada, como enlosados o costras (Cordes et al. 2010, Rueda et al. 2012a). Dichos carbonatos autigénicos pueden ser colonizados por organismos sésiles que incrementan la complejidad estructural y la diversidad de hábitats, lo que enriquece la fauna asociada respecto a los fondos adyacentes (Oporto et al. 2012, Palomino et al. 2016). Los volcanes de fango son considerados *hotspots* de singularidad biológica (Danovaro et al. 2010, Mastrototaro et al. 2010, Sciuto & Rosso 2015), siendo una de las estructuras geológicas de mayor importancia en el golfo de Cádiz. Ejemplos de volcanes de fango en el área de estudio son Gazul, Anastasya, Pipoca y Tarsis.

– **Diapiros**. Son estructuras formadas por el ascenso lento de material dúctil y móvil, habitualmente capas de sal, a través de las rocas suprayacentes más quebradizas (Díaz del Río 2014, Palomino et al. 2016). La principal diferencia con un volcán de fango es que éste expulsa el material de forma activa, mientras que un diapiro resulta de un movimiento masivo (Guliyev & Feizullayev 1997, Milkov 2000). Ejemplos de diapiros en el área de estudio son Bicentenario y Cristóbal Colón.

– **Complejos diapiro/volcán de fango.** Son relieves que se generan de la misma forma que los diapiros pero que albergan volcanes de fango en alguna de sus cumbres (Fig. 1.3) (Milkov

2000, Palomino et al. 2016). En dichos complejos suelen abundar los carbonatos autigénicos. Ejemplos de estas estructuras en el área de estudio son los complejos de Hespérides, Chica, Albolote, Enmedio y Enano.

– *Pockmarks*. Son depresiones en el fondo marino, de formas circulares a alargadas, que resultan de la pérdida de volumen tras la expulsión localizada de fluidos desde una fuente profunda (Fig. 1.4) (Hovland & Judd 1988, Kelley et al. 1994), y afectan únicamente a las capas sedimentarias superficiales. Los *pockmarks* se localizan en todo el LIC, pero son mucho más abundantes en el campo profundo de expulsión de fluidos, ya que esta zona presenta mayor actividad de emisión de fluidos y de hidratos de gas (Fernández-Puga et al. 2007, Díaz del Río et al. 2014).

– Depresiones de colapso. Son estructuras generalmente próximas a volcanes de fango y complejos diapiro/volcán de fango. Se forman por la fluidificación de depósitos sedimentarios superficiales y la expulsión de fluidos que migran lateralmente en dirección al volcán de fango cercano, causando el descenso del fondo marino (Díaz del Río et al. 2014). Ejemplos de estas estructuras en el área de estudio son las depresiones de colapso asociadas a Pipoca y Hespérides.

– Canales contorníticos. Son incisiones en el sustrato causadas por el efecto erosivo de las corrientes de fondo. En ellos dominan las gravas y arenas (Nelson et al. 1993), mientras que en los depósitos contorníticos dominan principalmente los sedimentos arenosos (Fernández-Salas et al. 2012). Ejemplos de canales contorníticos en el área de estudio son el de Huelva, Cádiz, Guadalquivir y Canal Gusano.

La existencia de numerosas chimeneas y costras de carbonato autigénico en muchas zonas del golfo de Cádiz sugiere que esta zona fue muy activa en el pasado en cuanto a expulsión de fluidos cargados en gas (Wehrmann et al. 2011, Magalhães et al. 2012, Vanneste et al. 2012). Otros signos de esta actividad son los numerosos montículos carbonatados y restos de corales de agua fría, en su mayoría muertos (Wienberg et al. 2009), así como restos de conchas de moluscos buccínidos y mitílidos, generalmente dentro del cráter de los volcanes de fango (Cunha et al. 2013).

2.3. Contexto oceanográfico

El golfo de Cádiz se encuentra fuertemente influenciado por el intercambio de masas de agua, donde domina el flujo superficial de entrada de agua atlántica al mar Mediterráneo, mientras que la corriente profunda mediterránea fluye hacia el océano Atlántico. Esta última desempeña un importante papel en los procesos erosivos de los fondos (Somoza et al. 2002, Vargas et al. 2003, Díaz-del-Río et al. 2006), siendo responsable del sistema deposicional contornítico de la plataforma media (García et al. 2009). Las principales masas de agua que determinan la circulación oceanográfica del área de estudio son las siguientes:

– Las masas de agua intermedias del Atlántico comprenden dos componentes. El **agua central del Atlántico norte** (**NACW**: *North Atlantic Central Water*) propiamente dicha, formada en primer lugar por una fuerte evaporación y, posteriormente, por un mayor enfriamiento invernal a lo largo del frente de las Azores. Penetra en el golfo de Cádiz entre los 100 y 700 m de profundidad, interactuando con el núcleo superior del agua mediterránea (Voelker et al 2015, Roque et al. 2019). Parte de esta corriente ingresa en el mar Mediterráneo a través del estrecho de Gibraltar formando giros superficiales en el mar de Alborán. Su temperatura varía entre los 16.6°C y 22.6°C y presenta una salinidad en torno a 36.2‰. El **agua subártica intermedia** (**SAIW**: *SubArctic Intermediate Water*), a veces denominada NACW subpolar, es más fría y se origina al norte del golfo de Vizcaya, fluye hacia el sur a lo largo del margen ibérico occidental y entra en el golfo de Cádiz en el intervalo de 400 a 900 m de profundidad (Voelker et al. 2015, Roque et al. 2019).

– Agua de salida mediterránea (**MOW**: *Mediterranean Outflow Water*). Se trata de una masa de agua formada en distintas partes profundas del Mediterráneo que fluye hacia el Atlántico por debajo y en sentido contrario de la NACW, y desciende sobre el margen continental del suroeste ibérico dirigiéndose hacia el noroeste hasta encontrar su nivel de equilibrio entre los 500 y 1.200 m de profundidad. Al salir del Estrecho, presenta una temperatura en torno a los 13°C y una salinidad de 38,4‰ (Iorga & Lozier 1999, Louarn & Morin 2011, Sánchez-Leal et al. 2017). Tras cruzar el Estrecho y alcanzar la dorsal del Guadalquivir, se encauza por el canal contornítico de Cádiz y fluye hacia el noroeste como una vigorosa corriente de fondo, aumentando su caudal a más de 1,82 ms^{-1} y dividiéndose en varias ramas (Sánchez-Leal et al. 2017). El núcleo superior de la MOW (entre los 500 y 800 m de profundidad) es el que más se extiende por el área de estudio, actuando como una fuerte corriente de fondo hasta la altura del cabo de São Vicente (Portugal). Por su parte, el núcleo inferior está formado por varios brazos (denominados como M1-M5 en función de su densidad). Estos brazos discurren entre los 800 y los 1.200 m de profundidad, y los que fluyen más al sur del golfo de Cádiz despegan del fondo al oeste, dirigiéndose hacia el océano Atlántico abierto (Gasser et al. 2017), y se mezclan con las masas de agua circundantes.

– Agua profunda del Atlántico norte (**NADW**: *North Atlantic Deep Water*). Fluye en gran parte del Atlántico norte a una profundidad mayor de los 1.500 m (Serra et al. 2005), con una salinidad baja de 34,9–35,2‰ y una temperatura fría entre los 3°C y los 8°C (Hernández-Molina et al. 2011, Palomino et al. 2016).

– Agua intermedia antártica (**AAIW**: *Antarctic Intermediate Water*). Es una masa de agua fría de origen antártico, pero bastante modificada, con una temperatura y salinidad aproximadas de 10,2°C y 35,6‰, respectivamente (Louarn & Morin 2011). Fluye desde el sur a lo largo de la costa africana y apenas llega al golfo de Cádiz, por debajo de la NACW, en un rango de 600 y 1.000 m de profundidad. Existe una divisoria vertical a lo largo del golfo de Cádiz (ilustrada en Voelker et al. 2015: Fig. 4C), donde la AAIW entra en contacto con la MOW en el mismo intervalo de profundidad. Es una masa de agua rica en nutrientes (Van Aken 2000) y forma afloramientos (*upwelling*) frente al cabo Ghir y el cabo Blanco, en el margen marroquí (Voelker et al. 2015).

2.4. Estudios faunísticos previos

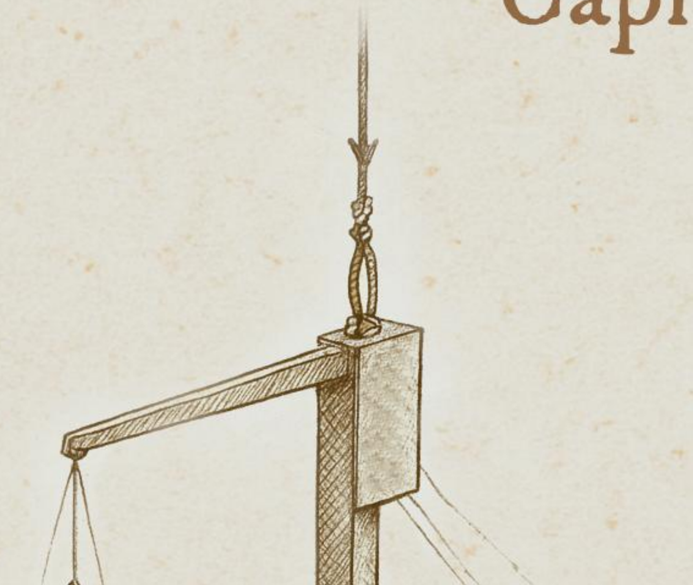
La fauna profunda del golfo de Cádiz fue muestreada por varias expediciones pioneras en el siglo XIX: "Porcupine" (Wyville Thomson 1873) y "Talisman" (Filhol 1885, Dolan 2020), las cuales dieron lugar a numerosas publicaciones acerca de todos los grupos zoológicos, y lograron convencer a la comunidad científica de la existencia de vida en el mar profundo. En el siglo XX, el buque oceanográfico (B/O) "Calypso" fue fletado por el gobierno francés para varias expediciones científicas, incluyendo una en el golfo de Cádiz y el mar de Alborán (Pérès 1964), pero desde el punto de vista faunístico sólo se estudiaron las ascidias (Pérès 1959).

BALGIM fue una expedición oceanográfica francesa organizada en 1984 a bordo del B/O "Cryos" por el Museo Nacional de Historia Natural (MNHN) de París, con el objetivo principal de estudiar la relación entre las masas de agua y la composición de la fauna bentónica atlántica y mediterránea a través del estrecho de Gibraltar. De esta campaña se estudiaron detalladamente muchos grupos zoológicos: Esponjas (Boury-Esnault et al. 1994), Gorgonarios (Grasshoff 1989), Hidrozoos (Ramil & Vervoort 1992), Sipúnculos (Salinas & Urchegui 1990), Briozoos (Harmelin & d'Hondt 1992a, b, 1993), Decápodos (García-Raso 1996), Percebes (Foster & Buckeridge 1995), Cumáceos (Jones 1990), Picnogónidos (Stock 1987), Bivalvos (Salas 1996), Equinoides (David 1989) y Ascidias (Monniot & Monniot 1988). Sin embargo, aunque constituyen un importante grupo faunístico, los gasterópodos de esta expedición sólo se mencionaron de pasada en algunas publicaciones taxonómicas, y hasta la fecha nunca se habían estudiado en su conjunto.

Además de estas expediciones históricas, los estudios recientes del golfo de Cádiz se han centrado principalmente en hábitats de los pisos infralitoral y circalitoral (en cuanto a los moluscos: Rueda et al. 2000, 2001, García-Gómez 2002, Vila et al. 2010, Gofas et al. 2011 y referencias incluidas, Gómez Álvarez 2017). También se han abordado aspectos ecológicos de las especies con quimiosimbiontes ligadas a las emisiones de los volcanes de fango, tanto en aguas marroquíes (Oliver et al. 2011, Génio et al. 2013) como en aguas españolas (Rueda et al. 2012a, b). Sin embargo, las comunidades de moluscos de fondos batiales han sido menos estudiadas (Salas 1996, Gofas et al. 2010, Pedrouzo et al. 2014) y, por lo tanto, la información sobre la malacofauna asociada a los hábitats profundos donde se localizan los volcanes de fango del margen español es escasa. Esta información es fundamental para mejorar el conocimiento y comprender la complejidad de las comunidades faunísticas que forman parte del LIC, teniendo en cuenta la peculiaridad biogeográfica de la zona de estudio y su geodiversidad. Además, se trata de una zona donde habitan especies de gran interés pesquero y, por lo tanto, abarca una intensa actividad pesquera (González-García et al. 2020a), la cual puede potencialmente afectar a los hábitats presentes. Por ello, el estudio de las comunidades de moluscos en estos hábitats profundos es de gran importancia para mejorar el conocimiento de las comunidades faunísticas de la zona. Estos datos científicos, además, aportarán información relevante que ayudará en los procesos de toma de decisiones para una correcta gestión y futura conservación del LIC.

Metodología general

Capítulo III



3. METODOLOGÍA GENERAL

3.1. Proyectos de investigación y campañas oceanográficas

El material utilizado en la presente tesis doctoral fue recolectado en el marco de los siguientes proyectos/campañas:

- Campaña BALGIM (1984). Referida anteriormente, ha sido una contribución esencial a esta tesis (capítulo 6). En dicha campaña se emplearon distintos artes de muestreo para recolectar fauna bentónica (draga de roca, draga epibentónica Warén y bou de vara).

- Proyecto LIFE+INDEMARES (2009-2014). Proyecto europeo liderado por el IEO, del que procede material esencial para la presente tesis doctoral. Su objetivo fue adquirir información científica para establecer un conjunto de áreas marinas de interés biológico en aguas españolas para integrarlas en la Red Natura 2000 de la Unión Europea. Dentro de este proyecto se llevaron a cabo diversas campañas oceanográficas multidisciplinares en el golfo de Cádiz, todas ellas enmarcadas en el subproyecto INDEMARES/CHICA, cuyo principal objetivo fue la identificación y el estudio de las zonas de expulsión de fluidos del margen español del golfo de Cádiz, así como de las comunidades bentónicas asociadas. En esta tesis doctoral se ha utilizado material procedente de varias de dichas campañas: INDEMARES/CHICA 0610, a bordo del B/O "Emma Bardán", INDEMARES/CHICA 0211, a bordo del B/O "Cornide de Saavedra" e INDEMARES/CHICA 0412, a bordo del B/O "Ramón Margalef".

- Proyecto europeo H2020 ATLAS (2016-2020). El objetivo del proyecto fue mejorar el conocimiento de los ecosistemas profundos del Atlántico norte y su biodiversidad, así como obtener información que permitiese predecir los futuros cambios en los ecosistemas causados por el cambio climático. En el marco de este proyecto se llevó a cabo la campaña MEDWAVES 0916 a bordo del B/O "Sarmiento de Gamboa", en la cual se obtuvo información y muestras sobre hábitat bentónicos, características oceanográficas y geomorfológicas del LIC, fundamentalmente del volcán de fango Gazul.

- Proyecto TASYO (TrAnsferencia Sedimentaria en Talud Y mega-Olistostromas, 1998-2002). Proyecto liderado por el Instituto Geológico y Minero de España (IGME) y dirigido al estudio del transporte tecto-sedimentario desde la plataforma continental del golfo de Cádiz hacia las llanuras abisales de La Herradura y Sena. En el marco de este proyecto se llevó a cabo la campaña ANASTASYA 09/99 a bordo del B/O "Cornide de Saavedra", siendo una de las primeras expediciones dedicadas al estudio de la dinámica sedimentaria en el golfo de Cádiz.

- Proyecto 18-ESMARES2-CIRCA (2018-2023). Proyecto incluido en el programa de seguimiento de los hábitats circalitorales y batiales de las aguas españolas con el objetivo de evaluar su estado ambiental, adecuándose a los requisitos de la Directiva Marco de Estrategia Marina de la Unión Europea (2008/56/CE). Este programa contempla una serie de campañas anuales en las cinco demarcaciones marinas españolas llevadas a cabo por el IEO, donde se incluyó la campaña CIRCASUR 2020 a bordo del B/O "Ramón Margalef" para caracterizar y evaluar el estado ambiental de los hábitats bentónicos circalitorales y batiales del golfo de Cádiz.

Adicionalmente, se ha utilizado material comparativo de otras campañas históricas, como la de 1923 a bordo del B/O "Vanneau" (Institut Scientifique Chérifien, Rabat) frente a la costa de Marruecos y la expedición TALISMAN de 1883, referida anteriormente.

3.2. Métodos de muestreo

Las muestras estudiadas en la presente tesis doctoral fueron recolectadas tanto con métodos de muestreo **lineales** (draga de arrastre y beam-trawl o bou de vara), los cuales capturan principalmente macrofauna epibentónica y algunos componentes demersales, como con métodos de muestreo **puntuales** (box-corer y draga Shipek), que capturan principalmente endofauna. Además, algunas muestras de la campaña BALGIM analizadas en el capítulo 6A se recolectaron con un trineo epibentónico de tipo Warén.

– Draga de arrastre bentónico (o draga de roca) (Fig. 3.1A–B). Consiste en una estructura rectangular de hierro con una red en la parte posterior que recoge fauna y sedimento durante el arrastre, estirándose y cerrando la luz de malla a medida que se va llenando. Las dragas usadas para la recolección de las muestras estudiadas en las campañas BALGIM e INDEMARES constaban de una anchura de aproximadamente un metro, una altura de 0,3 m y una red con luz de malla de 8 o 10 mm. La velocidad media de arrastre fue de hasta 2,5 nudos durante cinco minutos.

– Bou de vara (o *beam-trawl*) (Fig. 3.1C–D). Consiste en un arte de muestreo de arrastre con dos patines laterales que se deslizan sobre el fondo marino. Los que se utilizaron para las muestras de BALGIM e INDEMARES constaban de una apertura horizontal de tres metros, una vertical de 0,6 m y una red con luz de malla de 10 mm, con una relinga (burlón) lastrada con una cadena para que la red no se levantara del fondo. En la campaña BALGIM, la barra horizontal era una viga de madera de sección cuadrada de unos 15 cm, mientras que en las campañas INDEMARES se optó por una barra metálica redonda de 6 cm de sección, equipada por boyas para compensar su peso. La velocidad media de arrastre fue de 2,5 nudos durante 15 minutos.

– Trineo epibentónico de tipo Warén (Fig. 3.1E). Solamente se usó en algunas muestras de la campaña BALGIM por ser inoperante en fondos rugosos. Consiste en una estructura de aluminio que, en el momento que toca el fondo, se abre por su parte delantera con una placa abatible que se queda horizontal mientras el trineo funciona y que se cierra por unos muelles cuando se levanta del fondo. Este aparato es muy socorrido en fondos fangosos donde interesa esquilmar la parte muy superficial del sedimento sin excavar en él.

– Box-corer (Fig. 3.1F). Permite obtener una columna de sedimento con muy poco grado de perturbación. El cajetín se clava en el sedimento cuando llega al fondo marino por acción de la inercia y del peso de la estructura y, al virar, se cierra mediante un brazo giratorio, de forma que se preserva la estructura original de la muestra dentro del propio cajetín. Dependiendo de la campaña de origen, se utilizaron distintas dragas box-corer: en INDEMARES/CHICA 0412 presentó unas dimensiones de 30x30 cm; en INDEMARES/CHICA 0610 fue de 10x17 cm; y la utilizada en la campaña MEDWAVES tuvo unas dimensiones de 30x20 cm.

– Draga Shipek (Fig. 3.1G). Consiste en un armazón rígido con una cazoleta en su interior que se cierra mediante un giro al impactar sobre el fondo marino, obteniendo así una muestra representativa del sedimento de esa zona. La draga Shipek utilizada en el área de Gazul (capítulo 4) tuvo unas dimensiones de 20x20 cm.

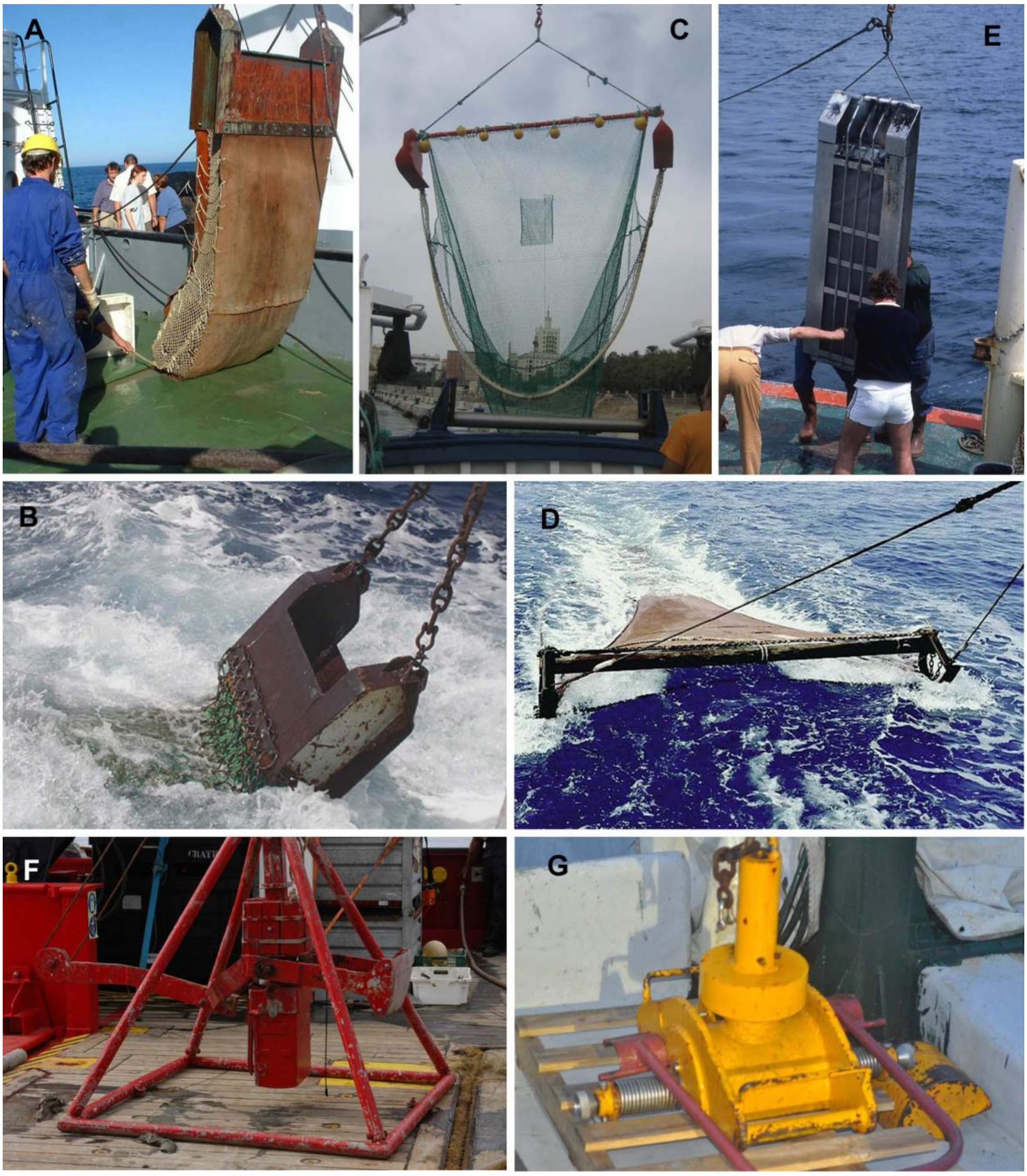


Figura 3.1. Artes de muestreo utilizados durante las campañas. **A–B**: Draga de roca. **C**: Bou de vara (modelo con barra metálica con flotadores para asegurar que el arte se mantenga en posición correcta). **D**: Bou de vara (modelo con viga usado en la campaña BALGIM, la cual hace de flotador). **E**: Trineo epibentónico de tipo Warén. **F**: Box-corer, nótese la pala lateral y el brazo que provoca el cierre al subir el arte. **G**: Draga Shipek.

3.3. Procesamiento de muestras

El procesamiento de las muestras a bordo de los buques oceanográficos fue similar en las distintas campañas oceanográficas. El material recolectado con los métodos lineales se tamizó en una columna de tamices de 10, 5 y 1 mm para separar los ejemplares de mayor tamaño y eliminar el exceso de sedimento de tamaño inferior a 1 mm. Las muestras procedentes de box-corer y draga Shipek se tamizaron a bordo con un tamiz de 0,5 mm para así retener las especies de menor tamaño y eliminar el sedimento arenoso y fangoso.

En una primera etapa, los especímenes grandes se separaron y clasificaron por filos a bordo, y las muestras de las fracciones más finas se preservaron en etanol al 70%. Una vez en el laboratorio, las muestras se analizaron usando un estereomicroscopio (Leica MZ12), de forma que los organismos de cada muestra se separaron del sedimento restante por grandes grupos (principalmente moluscos, crustáceos, anélidos y equinodermos) y los ejemplares de moluscos se identificaron hasta el nivel taxonómico más bajo posible siguiendo la nomenclatura de la WoRMS (WoRMS 2025).

Se cuantificó el número de ejemplares de cada especie de moluscos en cada muestra, tanto para los recolectados vivos como para la tanatocenosis, es decir, aquellos recolectados muertos (conchas o valvas). Para los bivalvos, cada valva se cuantificó como representación de un individuo, excepto cuando se encontraba la concha completa con ambas valvas conectadas. En el capítulo 4, sobre la malacofauna de Gazul, la cuantificación de la tanatocenosis se llevó a cabo mediante un sistema de rangos, excepto en las muestras de beam-trawl, en las que apenas se recolectó sedimento. Dicho rango era 1 cuando se trataba de una única concha o valva; 2 cuando había de 2 a 5 conchas; 3 cuando había de 6 a 30 conchas; 4 cuando había de 31 a 100 conchas; y 5 cuando eran más de 100 conchas.

Como se ha indicado anteriormente, en esta tesis doctoral se ha estudiado la tanatocenosis presente en las muestras. Dicha tanatocenosis puede estar formada por conchas de diferentes tiempos y orígenes, pudiendo estar mezcladas conchas de la comunidad bentónica actual con las de especies localmente extintas. Sin embargo, el estudio de la tanatocenosis proporciona una visión mucho más completa de la composición de especies de una comunidad en comparación con el estudio limitado a los ejemplares recolectados vivos. La inclusión de la tanatocenosis permite detectar especies presentes en el área de estudio que son difíciles de capturar vivas, ya sea porque viven asociadas a un microhábitat específico, porque se dan en baja densidad, o porque son huéspedes de algún hospedador específico (p. ej. *Iphitus tuberatus* Jeffreys, 1883). Por tanto, se considera que la pérdida de precisión al analizar la tanatocenosis se compensa con el incremento de información obtenida sobre la composición faunística (Kidwell 2001, Albano & Sabelli 2011, Weber & Zuschin 2013).

Se tomaron fotografías de las especies más características y de las menos comunes, la mayoría con una cámara Nikon DXM montada en un estereomicroscopio Nikon SMZ100 de la Universidad de Málaga. Muchas de ellas se tomaron a diferentes profundidades de enfoque y se ensamblaron posteriormente con el software CombineZ (Hadley 2006). También se examinaron diversos detalles característicos, como microesculturas y protoconchas, con microscopía electrónica de barrido utilizando un equipo JEOL JCC 1100 de los Servicios Centrales de Apoyo a la Investigación (SCAI) de la Universidad de Málaga.

El material de la campaña BALGIM pertenece a la colección del Museo Nacional de Historia Natural (MNHN) de París, donde se estudiaron a favor de una estancia (marzo-junio de 2022), y el de las campañas INDEMARES se encuentra en el Centro Oceanográfico de Málaga del IEO. Respecto a los ejemplares tipo de las nuevas especies descritas, el material de BALGIM se encuentran depositados en el MNHN de París, y el procedente de INDEMARES se depositó en el Museo Nacional de Ciencias Naturales de Madrid.

3.4. Análisis de datos

— Una vez cuantificada la composición de las muestras, se caracterizan con los siguientes parámetros e índices ecológicos usando el programa informático PRIMER v.6 (Clarke & Gorley 2006):

– Riqueza específica (S). Número total de especies (o taxones) presente en cada muestra.

– Abundancia (N). Número total de individuos de cada especie (o taxón) en cada muestra.

– Índice de diversidad de Shannon-Wiener (H') (Krebs 1989). Refleja la relación entre el número de especies de cada muestra y sus respectivas abundancias. Este índice varía entre 0, cuando todos los individuos son de la misma especie, y valores superiores a 3 cuando los individuos están repartidos equitativamente entre las diferentes especies.

$$H' = \sum_{r=1}^{S} p_r \log_2 p_r$$

Donde H' es el índice de diversidad de Shannon-Wiener; S es el número total de especies de la muestra; p_r es la abundancia relativa de los individuos que pertenecen a la especie del rango “r”. Por lo tanto, generalmente, si la riqueza específica es alta, también lo serán los valores de diversidad de Shannon-Wiener.

– Índice de equirepartición (J’) (Pielou 1969). Mide la proporción de la diversidad observada con relación a la máxima diversidad esperada. Su valor varía entre 0 y 1, de forma que valores próximos a 0 corresponden a comunidades con altas dominancias de una o dos especies y valores próximos a 1 a comunidades donde todas las especies tienen la misma abundancia de individuos.

$$J' = \frac{H'}{H'_{max}}$$

Donde J’ es el índice de equirepartición; H'es el índice de diversidad de Shannon-Wiener en una muestra; H'_{max} es la diversidad máxima teórica.

– Índice de dominancia (%D). Es el número de individuos de una especie en relación al total de individuos del conjunto de las muestras, expresado en porcentaje. Refleja la estructura de la comunidad.

– Índice de frecuencia (%F). Es el número de muestras en las que una especie está presente, expresado en porcentaje del número total de muestras.

— El estudio de la afinidad entre las muestras se lleva a cabo mediante análisis multivariante, el cual tiene en cuenta cada una de las especies y su abundancia en cada muestra:

Con los datos de abundancia de cada especie recolectada se construye una matriz en la que las filas son los taxones y las columnas son las muestras. En primer lugar, los datos de abundancia se transforman a la raíz cuarta para reducir el efecto de unas pocas especies muy abundantes. A continuación, se realiza un **análisis multivariante** basado en el índice de Bray-Curtis (Bray & Curtis 1957) usando PRIMER v.6. El índice de similitud de Bray-Curtis calcula las diferencias entre la presencia y abundancia de los taxones que componen las muestras e ignora los casos en los que el taxón está ausente en ambas muestras. Este índice varía entre valores cercanos al 0%, cuando las muestras no comparten especies o sus especies compartidas tienen grandes diferencias en sus abundancias, y un valor de 100%, cuando las muestras son idénticas en composición y abundancia. Con este procedimiento, se obtiene una semimatriz de similitud entre muestras.

Dependiendo de la escala geográfica considerada y de la naturaleza del muestreo, los detalles del análisis pueden variar. La matriz puede ser cualitativa, cuando las especies están representadas por valores de 0 (ausencia) o 1 (presencia); o cuantitativa, cuando los valores son los de la abundancia de cada especie en cada muestra. La matriz puede tener en cuenta solamente ejemplares recolectados vivos (taxocenosis), los ejemplares representados por conchas (tanatocenosis) o el conjunto de taxocenosis y tanatocenosis.

— Para la visualización de estos resultados y detectar los posibles grupos de muestras, se utilizan dos métodos de clasificación y ordenación de PRIMER v.6:

– Dendrograma mediante el algoritmo de agrupación UPGMA (*Unweighted Pairgroup Method Using Arithmetic Averages*) (Sneath & Sokal 1973). Con este método obtenemos un dendrograma (o clúster) en el que las muestras se agrupan en función de su similitud media. El eje vertical representa la similitud entre muestras, desde 0% a 100%.

Posteriormente, se aplica la prueba **SIMPROF** (*SIMilarity PROFile analysis in clustering*) para determinar si las diferencias entre los distintos grupos de muestras (asociaciones) detectados en el análisis clúster son significativas.

– n-MDS (*Non-Metric Multidimensional Scaling*). Representa el conjunto de muestras con una distancia entre ellas proporcional a su similitud, ya sea en un espacio tridimensional o proyectado en un plano bidimensional. El coeficiente de *stress* mostrado en el nMDS indica la fiabilidad de la ordenación, de modo que cuando su valor es inferior a 0,1 dicha ordenación es buena; hasta 0,2 aporta cierta información, pero se aconseja verificar con otra técnica; y cuando es mayor de 0,2 la ordenación no es fiable.

— Para determinar las especies responsables de la afinidad entre muestras se realiza el análisis **SIMPER** (*SIMilarity PERcentage*), llevado a cabo con PRIMER v.6. Identifica tanto a las especies que más contribuyen a la similitud entre muestras del mismo grupo (especies tipificadoras), como a la disimilitud entre grupos (especies discriminadoras). Se obtiene un listado con la contribución acumulada de las especies, empezando por las más influyentes.

— El estudio de las diferencias espaciales entre las muestras se realiza con el análisis de similitud **ANOSIM** (*ANalysis Of SIMilarity*). Es un test multivariante que compara el rango de similitud media de las muestras dentro de cada grupo de muestras con el obtenido entre los otros grupos en función de determinados factores (p. ej. las masas de agua en las que se sitúan las muestras). Su coeficiente R_{ANOSIM} puede variar entre 0, cuando las diferencias dentro de un grupo equivalen a la que existen entre grupos, y 1, cuando las diferencias dentro de un grupo son menores que entre grupos. Los grupos (o asociaciones) son significativos si los valores de R_{ANOSIM} son altos, mientras que no lo son si estos valores son muy bajos.

— El análisis paramétrico **ANOVA** (*ANalysis Of VAriance*), realizado con el programa informático SPSS v.16, se utiliza para saber si existen diferencias significativas entre los índices ecológicos (mientras que el ANOSIM se aplica a valores de similitud entre muestras). Se calcula la media de estos índices en cada uno de los grupos, y se comprueba si las diferencias observadas dentro de cada grupo son, o no, menores que las observadas entre grupos. Con ello, se puede comprobar, por ejemplo, si la riqueza específica es significativamente distinta entre distintas zonas de estudio.

Chapter IV

Mollucs from benthic habitats of the Gazul mud volcano (Gulf of Cadiz)

Moluscos de hábitats bentónicos del volcán de fango de Gazul (golfo de Cádiz)

This chapter is based on:
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4. MOLLUSCS FROM BENTHIC HABITATS OF THE GAZUL MUD VOLCANO (GULF OF CADIZ)

Abstract

Molluscs from the Gazul mud volcano and its adjacent areas in the northern Gulf of Cadiz were studied using different sampling methods. This mud volcano has vulnerable deep-sea habitats and a potential high biodiversity. A total of 232 species were identified from the taxocoenosis and thanatocoenosis, of which 86 are new records for the Spanish margin of the Gulf of Cadiz, three of them are new records for Spanish waters and two species are new to science. The high species richness observed could be related to the combination of different sampling methods, the study of the thanatocoenosis, the high habitat heterogeneity and the geographical location of the Gazul mud volcano between different biogeographical regions. The best-represented species were *Bathyarca philippiana*, *Asperarca nodulosa*, *Leptochiton* sp., *Astarte sulcata* and *Limopsis angusta*. The thanatocoenosis harboured, with low frequency, species that are typical of northern latitudes, species indicating past seepage, species from the shelf and species restricted to particular hosts. The taxocoenosis found in different areas of Gazul (the mud volcano edifice, erosive depression and adjacent bottoms) generally displayed significant differences in multivariate analyses. Furthermore, the environmental parameters related to environmental complexity and food availability displayed the highest linkage with the molluscan fauna.

Resumen

Se estudiaron los moluscos del volcán de fango Gazul y sus zonas adyacentes, en el norte del golfo de Cádiz, utilizando diferentes métodos de muestreo. Este volcán de fango destaca por la presencia de hábitats vulnerables de aguas profundas y una potencial alta biodiversidad. Se identificaron un total de 232 especies de la taxocenosis y la tanatocenosis, de las cuales 86 fueron nuevas citas para el margen español del golfo de Cádiz, tres de ellas nuevas citas para aguas españolas y dos especies nuevas para la ciencia. La alta riqueza de especies detectada podría estar relacionada con la combinación de diferentes métodos de muestreo, el estudio de la tanatocenosis, la alta heterogeneidad del hábitat y la ubicación geográfica del volcán de fango Gazul entre diferentes regiones biogeográficas. Las especies mejor representadas fueron *Bathyarca philippiana*, *Asperarca nodulosa*, *Leptochiton* sp., *Astarte sulcata* y *Limopsis angusta*. La tanatocenosis presentó, con baja frecuencia, especies típicas de latitudes superiores, especies indicadoras de emisiones pasadas, especies de la plataforma y especies restringidas a huéspedes particulares. La taxocenosis encontrada en las diferentes zonas de Gazul (edificio del volcán de fango, depresión erosiva y fondos adyacentes) generalmente mostró diferencias significativas en los análisis multivariantes. Además, los parámetros ambientales más vinculados con la malacofauna fueron los relacionados con la complejidad ambiental y la disponibilidad de alimento.

4.1. Introduction

Mud volcanoes (MVs) are submarine structures formed by the vertical migration of sediments and fluids saturated in hydrocarbons, mainly methane, which are extruded by high pressure and low temperature emissions (Kopf 2002, Díaz-del-Río et al. 2006, Mazzini & Etiope 2017). This fluid migration usually takes place through discontinuities of the sub-seafloor, promoting a mobilization of sediments that leads to the formation of a sedimentary cone up to a few hundred metres above the emission focal point (Milkov 2000, Gardner 2001, Levin 2005). This context promotes the anaerobic oxidation of methane by the bacterial activity, with the formation of methane-derived authigenic carbonates (MDACs) such as chimneys, crusts and slabs underneath the sediment (Díaz-del-Río et al. 2003, Magalhães et al. 2012). The action of bottom currents can exhume these MDACs, eventually turning soft-bottom areas into consolidated hard bottoms that can be colonized by vulnerable habitat-building fauna such as scleractinians, gorgonians and sponges, which may be of importance as shelter, nursery and feeding grounds for other fauna, including commercial and/ or threatened species (Cordes et al. 2010, Rueda et al. 2012a, Cunha et al. 2013). Cold seep areas are considered hotspots of biological and biodiversity singularity (Danovaro et al. 2010, Mastrototaro et al. 2010, Cunha et al. 2013) and “Submarine structures caused by leaking gases, habitat 1180” are one of the very few marine habitats listed in Annex 1 (habitats for which a site of community importance may be declared) of the EU Habitat Directive (1992/43/EEC). Nevertheless, the information regarding the associated faunal communities is very limited in some deep-sea areas with seepage activity, such as that of the northern Gulf of Cadiz (GoC) (Rueda et al. 2012b, Delgado et al. 2013, Rueda et al. 2016) in comparison with the current knowledge regarding those in the southern GoC (Oliver et al. 2011, Cunha et al. 2013, Génio et al. 2013).

The GoC is an important area of seepage activity at a global scale, with the presence of more than 70 MVs and MV/diapir complexes located in different fields of the Spanish, Portuguese and Moroccan continental margins (Díaz-del-Río et al. 2003, León et al. 2007, 2012, Palomino et al. 2016). MVs from the Spanish margin are found on the upper-middle continental slope of the GoC, around 300 to 1200 m depth. This area is characterized by the exchange of water masses through the Strait of Gibraltar, with the Surficial Atlantic Water flowing along the surface into the Mediterranean Sea, and the deeper Mediterranean Outflow Water (MOW) flowing out to the Atlantic Ocean. This exchange of water masses, among other factors, promotes a high biological productivity and a particular biodiversity in the GoC, including a wide range of species of interest to fisheries (Fernández-Salas et al. 2012, Díaz del Río et al. 2014). This environmental context is enriched by a wide variety of seafloor morphostructures and the continuous dynamics of the area promoted by the MOW, the sediment mobilization and the expulsion of fluids (Fernández-Salas et al. 2012, Díaz del Río et al. 2014, Palomino et al. 2016).

Some of the species and habitats existing in the northern GoC are included in national and international conservation lists (e.g. Habitat Directive, EUNIS, OSPAR), such as vulnerable deep-sea habitats with high ecological value (e.g. cold-water coral banks and black coral gardens), while others are unique within the European context (e.g. chemosynthesis-based communities) (Rueda et al. 2016). Furthermore, species from different biogeographical regions converge in the GoC, which is an important area for trophic and reproductive migrations of some species (Díaz del Río et al. 2014). Unfortunately, there is intensive bottom-trawling in the GoC because of the existence of important fishing grounds with high-value commercial species including the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758), the deep-water rose shrimp *Parapenaeus longirostris* (Lucas, 1846) and the European hake *Merluccius merluccius* (Linnaeus, 1758), among others (Jiménez et al. 2004, Vila et al. 2004, González-García et al. 2012, 2020a). Trawling represents a serious threat to the fragile and vulnerable marine ecosystems existing in the GoC, as has been observed in other areas worldwide (Fonteyne 2000, Gislason & Sinclair 2000, Koslow et al. 2000). Therefore, it is of importance to increase the knowledge regarding benthic habitats and associated faunal communities in order to improve the management and conservation strategies of the areas most sensitive to the impacts of these fisheries.

Molluscs are one of the most diverse faunal groups in marine environments, representing important components of the benthic communities due to their different feeding strategies (e.g. filter feeders, deposit feeders, carnivores and parasites) and their contribution as an important food source for higher trophic levels (Pollard 1984, Edgar & Shaw 1995, Pasquaud et al. 2010). Molluscs are also an important marine resource because they reach high abundance and biomass values in the fisheries and aquaculture sector (Gaspar et al. 2012, FAO 2018) and are considered a good indicator for biodiversity assessments of a particular area (Bedulli et al. 2002, Gladstone 2002, Appeltans et al. 2012). The malacofauna of the GoC has mainly been studied in infralittoral and circalittoral habitats (Salas 1996, Rueda et al. 2001), and other studies have focused on ecological aspects of chemosymbiotic species inhabiting MVs (Oliver et al. 2011, Rueda et al. 2012b), whereas few studies have analysed molluscan assemblages inhabiting deep-sea habitats in detail (Salas 1996, Génio et al. 2013). One of the most interesting MVs of the GoC is the Gazul MV, which has several vulnerable deep-sea habitats and a high potential biodiversity (Palomino et al. 2016, Rueda et al. 2016). The present study analyses the malacofauna associated with different areas and habitats of the Gazul MV. The aims of the study were i) to identify and characterize molluscan assemblages existing in the Gazul MV and adjacent areas; and ii) to analyse potential relationships between identified molluscan assemblages and environmental and anthropogenic impacts on the area.

4.2. Materials and methods

4.2.1. Study area

The study area is the Gazul MV and its adjacent bottoms (36°33.53'N, 6°55.96'W), located in the northeastern sector of the shallow field of fluid expulsion of the Spanish margin of the GoC, within the site of community importance *Volcanes de fango del golfo de Cádiz* (Mud volcanoes of the Gulf of Cadiz) (ESZZ12002) (Díaz del Río et al. 2014) (Fig. 4.1). The Gazul MV has a maximum relief of 107 m and its summit stands at a water depth of 363 m. This MV has a sub-circular base and an asymmetrical contour with two crests running NW–SE surrounded by two erosive depressions, as well as isolated and grouped mounds forming crests (Palomino et al. 2016). The seabed at the summit is mainly composed of sandy-mud and mud breccia sediments, usually covered by a thin veneer of hemipelagic sediment and abundant bioclasts and MDACs (Palomino et al. 2016). The crests and flanks of this MV also have abundant MDACs, whereas sediment is coarser at the depression, and it is composed of sand and gravel with some dispersed MDACs (Palomino et al. 2016). The area where the Gazul MV is located is characterized by moderate hydrodynamics (bottom current speed sometimes higher than 0.3

ms^{-1}) and erosive processes, mainly on the southeastern flank of the MV, promoting sediment winnowing and preventing sediment accumulation on the seabed, and the temperature and salinity of the water masses are lower than in other areas of the shallow field of fluid expulsion (13.1°C and 35.9‰, respectively) (Palomino et al. 2016, Rueda et al. 2016).

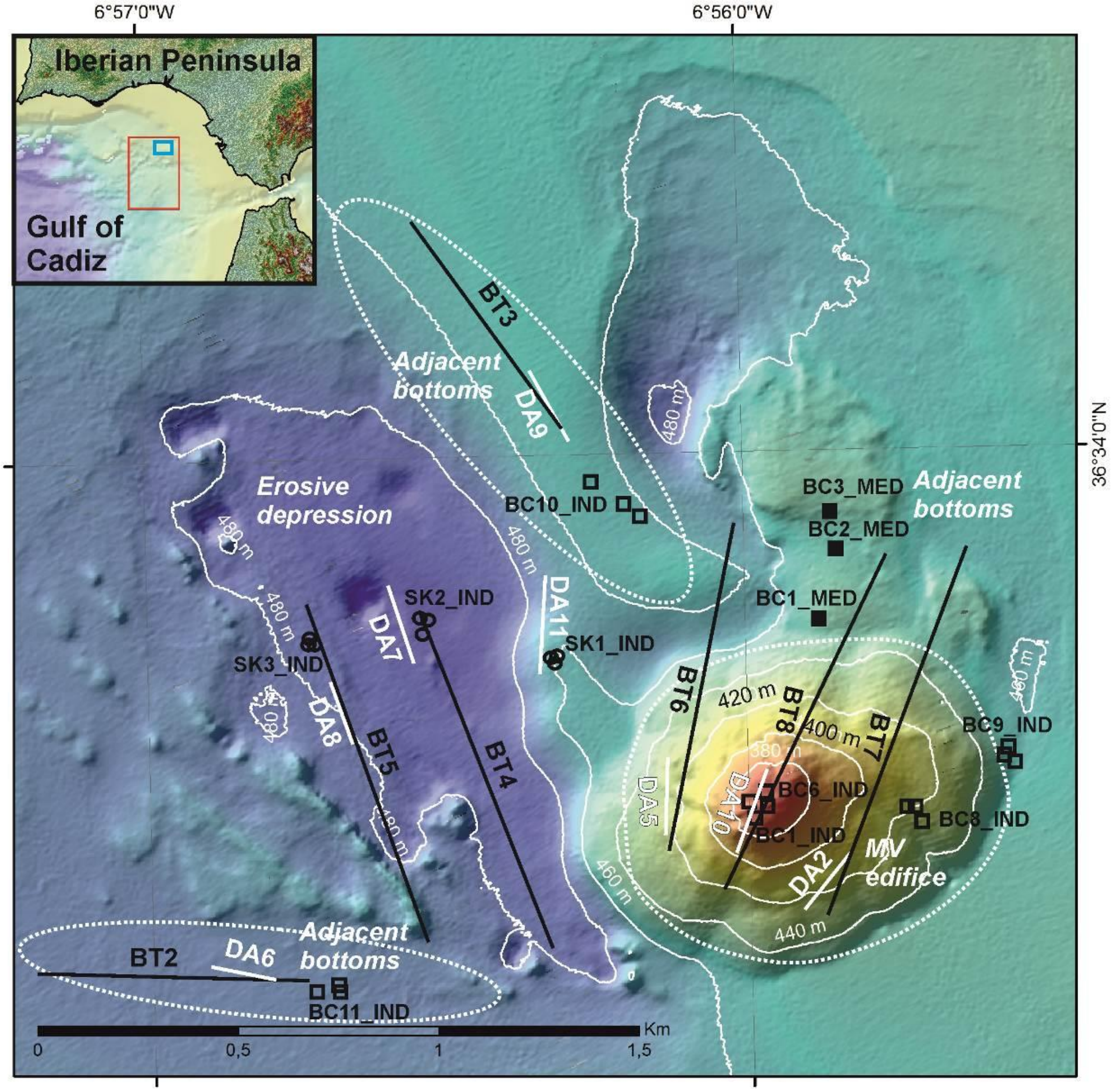

Figure 4.1. Location map of the Gazul mud volcano (MV) (blue frame) within the shallow field of fluid expulsion in the Gulf of Cadiz (red frame). Detailed map of the Gazul MV with the stations sampled with beam-trawl (BT) (black lines), benthic dredge (DA) (white lines), box-corer (BC) (squares) and Shipek grab (SK) (circles) during the INDEMARES/CHICA 0610, 0412 (IND, empty squares and circles) and ATLAS/MEDWAVES 0916 (MED, solid squares) oceanographic expeditions.

4.2.2. Sample collection

Sampling was carried out in several areas of the Gazul MV (Table 4.1), detailed as follows: i) the MV edifice with 3 beam-trawls + 3 dredge samples (qualitative), 3 box-cores (quantitative, 3 replicas each) and 1 box-core (quantitative, not replicated); ii) the erosive depression with 2 beam-trawls + 3 dredge samples (qualitative) and 3 Shipek grabs (quantitative, 3 replicas each); and iii) the adjacent bottoms with 2 beam-trawls + 2 dredge samples (qualitative), 2 box-cores (quantitative, 3 replicas each) and 3 box-cores (quantitative, not replicated). Most of the infaunal species were collected with the box-corer and Shipek grab. During the INDEMARES/CHICA 0610 cruise, samples were collected with a 10×17 cm box-corer or with a 20×20 cm Shipek grab, which were all replicated considering the small sample size; during the INDEMARES/CHICA 0412 cruise, only one sample was collected with a 30×30 cm box-corer; and during the ATLAS/MEDWAVES 0916 cruise, three samples were collected with a 30×20 cm box-corer. This amounts to eight replicated box-corer/Shipek grab samples and four non-replicated box-corer samples; in the replicated small box-corer and Shipek grab samples the minimal area was met only by summing the three replicas. The total surface covered by the box-corers was 1.13 m^2s so specimen counts in the total box-corer/Shipek grab in Table 4.2 are roughly equivalent to density per square metre. Additional infaunal and epibenthic micro/macrofaunal species were collected during INDEMARES/CHICA 0610, eight samples with a benthic dredge (DA) (1 m width, 0.3 m height, 8 mm mesh size) towed at a speed of 2.5 knots for 5 min (sampling area ca. 350 m^2), and seven samples with a beam-trawl (2 m width, 0.6 m height, 10 mm mesh size) that was trawled at 2.5 knots for 15 min (sampling area ca. 2300 m^2).

Additionally, for some species, comparative material from the expeditions of the R/V "Vanneau" off Morocco (1923) and BALGIM in the GoC (1984) was examined in the Muséum National d'Histoire Naturelle, Paris. A list of the species collected by the Dutch NIOZ cruise Moundforce (Mienis & de Haas 2004) at a carbonate mound close to a small MV and to the Penduick escarpment off Larache, Morocco, was communicated by Frans Slieker of the Natural History Museum, Rotterdam. Many species from that sample are illustrated on the NHM Rotterdam website (https://www.nmr-pics.nl/) and in the World Register of Marine Species (WoRMS), so consistency of identifications can be checked. The sample is box-corer M2004–08 (35°17.74'N, 6°47.33'W, 529 m depth), which was collected on 18 August 2004.

4.2.3. Sample processing

Beam-trawl and benthic dredge samples were sieved on board over mesh sizes of 10, 5 and 1 mm to separate large and small specimens. Moreover, box-corer/Shipek grab samples were sieved on board with a 0.5 mm sieve in order to retain the small species while eliminating the sandy and muddy sediment. The samples were mainly preserved in 70% ethanol. In the laboratory, species of each sample were separated from the remaining sediment by large groups (mainly molluscs, crustaceans, annelids and echinoderms) using a stereomicroscope (Leica MZ12), and mollusc specimens were identified to the lowest possible taxonomic level. Scientific names follow the nomenclature of the WoRMS (WoRMS editorial board 2020) and the list of marine Mollusca in Spanish waters (Gofas et al. 2017). Additionally, species were checked for belonging to the World Register of Deep-Sea Species (Glover et al. 2020), a thematic portal of WoRMS.

Table 4.1. Location and details of sampling stations on the oceanographic expeditions on the Gazul mud volcano (MV) (northern Gulf of Cadiz). BT: beam-trawl; DA: benthic dredge; SK: Shipek grab; BC: box-corer. For the SK and BC, the first digit is the sample number and the second digit refers to replicas.

Expedition	Sampling method	Sample code	Latitude start	Longitude start	Depth start (m)	Latitude end	Longitude end	Depth end (m)	Area
INDEMARES/CHICA 0610 (R/V "Emma Bardán")	Beam-trawl	BT2	36°33.28'N	06°56.72'W	477	36°33.32'N	06°57.45'W	478	Adjacent bottoms
		BT3	36°34.03'N	06°56.28'W	462	36°34.43'N	06°56.68'W	460	Adjacent bottoms
		BT4	36°33.80'N	06°56.52'W	495	36°33.33'N	06°56.32'W	483	Erosive depression
		BT5	36°33.82'N	06°56.72'W	487	36°33.33'N	06°56.52'W	478	Erosive depression
		BT6	36°33.55'N	06°56.12'W	422	36°33.98'N	06°55.98'W	450	MV edifice
		BT7	36°33.37'N	06°55.85'W	420	36°33.87'N	06°55.60'W	459	MV edifice
		BT8	36°33.45'N	06°56.02'W	380	36°33.90'N	06°55.73'W	455	MV edifice
	Benthic Dredge	DA2	36°33.57'N	06°55.75'W	402	36°33.58'N	06°55.85'W	451	MV edifice
		DA5	36°33.58'N	06°56.10'W	422	36°33.48'N	06°56.13'W	418	MV edifice
		DA6	36°33.30'N	06°56.75'W	478	36°33.32'N	06°56.90'W	478	Adjacent bottoms
		DA7	36°33.82'N	06°56.58'W	495	36°33.72'N	06°56.53'W	491	Erosive depression
		DA8	36°33.73'N	06°56.70'W	486	36°33.60'N	06°56.63'W	487	Erosive depression
		DA9	36°34.02'N	06°56.27'W	458	36°34.10'N	06°56.33'W	456	Adjacent bottoms
		DA10	36°33.57'N	06°55.95'W	390	36°33.43'N	06°56.02'W	410	MV edifice
		DA11	36°33.70'N	06°56.32'W	461	36°33.85'N	06°56.32'W	462	Erosive depression
	Shipek grab	SK1.1	36°33.72'N	06°56.32'W	461				Erosive depression
		SK1.2	36°33.72'N	06°56.30'W	459				Erosive depression
		SK1.3	36°33.72'N	06°56.32'W	461				Erosive depression
		SK2.1	36°33.78'N	06°56.53'W	494				Erosive depression
		SK2.2	36°33.78'N	06°56.52'W	494				Erosive depression
		SK2.3	36°33.77'N	06°56.52'W	495				Erosive depression
		SK3.1	36°33.75'N	06°56.70'W	486				Erosive depression
		SK3.2	36°33.75'N	06°56.70'W	486				Erosive depression
		SK3.3	36°33.75'N	06°56.72'W	486				Erosive depression
	Box-corer	BC6.1	36°33.53'N	06°55.95'W	370				MV edifice
		BC6.2	36°33.50'N	06°55.98'W	371				MV edifice
		BC6.3	36°33.52'N	06°55.97'W	369				MV edifice
		BC8.1	36°33.52'N	06°55.72'W	419				MV edifice
		BC8.2	36°33.52'N	06°55.72'W	418				MV edifice
		BC8.3	36°33.50'N	06°55.70'W	427				MV edifice
		BC9.1	36°33.58'N	06°55.53'W	454				MV edifice
		BC9.2	36°33.58'N	06°55.55'W	457				MV edifice
		BC9.3	36°33.58'N	06°55.55'W	449				MV edifice
		BC10.1	36°33.92'N	06°56.15'W	462				Adjacent bottoms
		BC10.2	36°33.93'N	06°56.18'W	461				Adjacent bottoms
		BC10.3	36°33.98'N	06°56.23'W	461				Adjacent bottoms
		BC11.1	36°33.28'N	06°56.67'W	477				Adjacent bottoms
		BC11.2	36°33.28'N	06°56.72'W	477				Adjacent bottoms
		BC11.3	36°33.28'N	06°56.67'W	477				Adjacent bottoms
INDEMARES/CHICA 0412 (R/V "Ramón Margalef")	Box-corer	BC1	36°33.52'N	06°55.95'W	362				MV edifice
ATLAS/MEDWAVES 0916 (R/V "Sarmiento de Gamboa")	Box-corer	BC1_MED	36°33.78'N	06°55.87'W	444				Adjacent bottoms
		BC2_MED	36°33.87'N	06°55.86'W	450				Adjacent bottoms
		BC3_MED	36°33.92'N	06°55.86'W	446				Adjacent bottoms

The number of live-taken specimens of each mollusc species was quantified in each sample, while for the species of the thanatocoenosis a rank system was applied (except in the beam-trawl samples, in which hardly any sediment was collected, so the thanatocoenosis could not be studied) (1, 1 shell; 2, 2 to 5 shells; 3, 6 to 30 shells; 4, 31 to 100 shells; 5, more than 100 shells). Although, admittedly, shells may be displaced in space and time, we took into account the thanatocoenosis because we are also convinced that it provides a much more complete account of the species composition than the live-taken specimens only. We believe that the loss of accuracy using shells is outweighed by the gain in the amount of information on the faunal composition (Kidwell 2001, Weber & Zuschin 2013).

Photographs were taken for the most representative or less common species using a Nikon DXM camera mounted on a stereomicroscope, and some characteristic details (e.g. microsculptures and protoconchs) were examined with scanning electron microscopy (JEOL JCC 1100 equipment). Several views focusing on different image planes were taken and assembled using the CombineZ software (Hadley 2006), with the best-focused parts of each view combined into a single image. Images of species new to the GoC, listed in this work but not illustrated, are posted in WoRMS (http://www.marinespecies.org/). The separated sedimentary material was dried and stored at the *Centro Oceanográfico de Málaga del Instituto Español de Oceanografía*, and the type specimens of the new species was deposited at the *Museo Nacional de Ciencias Naturales*, Madrid.

4.2.4. Environmental and fisheries parameters

Sediment characterization of each study zone was performed using the box-corer and Shipek grab samples of the INDEMARES/CHICA and ATLAS/MEDWAVES expeditions. After oven-drying of sediment samples at 60°C to constant weight, samples were wet-sieved in a 63 µm mesh sieve, giving a coarse fraction (>63 µm) and a fine fraction (<63 µm) composed of mud, whose quantity was obtained by weighing the total sample before and after sieving. The coarse fraction was subsequently dry-sieved in a column of sieves and each retained fraction was weighed and transformed into weight percent to characterize the texture of the sediment. The organic matter and carbonate content were estimated in samples stored at –20°C and, after oven-drying and grinding in an agate mortar, the "loss on ignition" method was performed by combustion at 550°C for organic matter and at 950°C for carbonates (Heiri et al. 2001), giving the percentage of each fraction by dry weight difference.

The near-bottom temperature in each sampling area was obtained by a CTD in the INDEMARES/CHICA 0211 expedition in February 2011. Although collected in a different season, these data are taken as representative of the near-bottom conditions because these have been found to have little seasonal variation below 250–300 m depth, under the influence of the MOW (Bellanco & Sánchez-Leal 2016). The presence of MDACs at each sampling site was quantified using the amount of MDACs collected by the beam-trawl according to the following criteria per trawl: 0 = none, 1 = one, 2= two to five and 3 = more than five. The bottom-trawling activity at the Gazul MV and adjacent bottoms was obtained from the Vessel Monitoring System (VMS), a mandatory geolocalization system for the Spanish fishing fleet, with data centralized by the *Centro de Seguimiento de Pesca* at the Spanish Ministry responsible for fisheries datasets for 2011. It was quantified as 0 (no trawling activity), 1 (low activity: 1 vessel per year) or 2 (medium activity: 2–5 vessels per year).

4.2.5. Data analyses

A data matrix containing the abundance of live-taken species was constructed for each sampling method. Results were standardized to 2000 m^2 for the beam-trawl data, 300 m^2 for the benthic dredge data and 1 m^2 for the box-corer and Shipek grab data. Another data matrix was constructed with ranks for dead-collected species (shells or valves). Parameters and ecological indexes were calculated using the PRIMER v.6 software (Clarke & Gorley 2006), including species richness (S: number of species present in each sample), abundance (N: number of individuals collected per sample), evenness index (J', Pielou 1969) and Shannon-Wiener diversity index (H': $\log_2$, Krebs 1989). The dominance index (%D: percentage of individuals of a particular species within the sample) and the frequency index (%F: percentage of samples in which a particular species is present) were also calculated for each species. Analyses of variance were performed using ANOVA with the SPSS v.16 software to check whether parameters and ecological indexes were significantly different between the different areas, following a design with one fixed factor (area) with three levels (MV edifice, erosive depression and adjacent bottoms) for each sampling method (7 beam-trawl samples, 8 benthic dredge samples and 12 box-corer and Shipek grab samples).

A multivariate analysis based on qualitative (presence/absence of live-taken species) similarities (Bray-Curtis measure) among all samples was carried out to identify molluscan assemblages on the Gazul MV and adjacent bottoms. To test for differences between the identified assemblages, an analysis of similarity (ANOSIM) was performed. The identification of the species characterizing each assemblage was performed through a similarity percentage analysis (SIMPER) with a 90% cut-off for low contributions. Finally, the relationships between molluscs and environmental and fishery parameters were contrasted using the BIOENV (BIOtic and ENVironmental linking) analysis. Prior to this, a Spearman correlation analysis was carried out, and those highly correlated parameters (more than 0.9) were not further considered (e.g. medium sand and salinity). Environmental data expressed as percentage (percentage of gravels, coarse sand, fine sand, mud and organic matter in sediment) were log(x+1) transformed. These multivariate analyses were performed with the PRIMER 6 software (Clarke & Gorley 2006).

4.3. Results

4.3.1. Molluscan diversity

A total of 232 molluscan species were found at the Gazul MV and adjacent bottoms, and 213 were identified to species level. This number includes two species that are new to science and are described in the present study. A total of 2324 live-taken individuals (ind.) corresponding to 91 species (spp.) (Table 4.2), and over 9000 shells corresponding to 221 species were sampled. Eleven species (shell-less species, polyplacophorans, an unidentified Eulimid, and the bivalves *Spinosipella acuticostata* and *Coralliophaga lithophagella*) were represented only by live-taken specimens, whereas 141 species (60%) were represented only by shells.

This diverse fauna includes 160 gastropods (47 of them as live-taken spp. with 334 ind.), 62 bivalves (36 as live-taken spp. with 1839 ind.), three scaphopods (2 as live-taken spp. with 8 ind.), three cephalopods (6 ind.), two polyplacophorans (135 ind.), one monoplacophoran (1 shell) and one solenogastre (2 ind.). Regarding the live-collected molluscs, the most diverse gastropod families were Rissoidae (5 spp.), Fissurellidae and Muricidae (3 spp. each), and Arcidae (3 spp.) among bivalves.

The most dominant live-collected species were *Bathyarca philippiana* (1252 ind., D=53.71%), *Asperarca nodulosa* (144 ind., D=6.18%), *Leptochiton* sp. (131 ind., D=5.62%), *Astarte sulcata* (80 ind., D=3.43%) and *Limopsis angusta* (57 ind., D=2.45%) (Table 4.3). On the other hand, a total of 21 species were represented by a single live specimen (e.g. the gastropods *Opaliopsis atlantis*, *Solatisonax alleryi* and *Pleurobranchaea meckeli* and the bivalves *Kelliella miliaris* and *Poromya granulata*), though some of these are abundantly represented as empty shells.

The most representative species found in the thanatocoenosis included *Papillicardium minimum*, *B. philippiana*, *Alvania cimicoides*, *Bittium watsoni* and *Alvania tomentosa* (Table 4.3). The benthic dredge, the box-corer and the Shipek grab collected a large number of shells (adding altogether 141 species), considerably increasing the richness of the thanatocoenosis. Gastropods were the most diverse group in all cases (69% of total species), whereas bivalves displayed the highest abundance of live-taken specimens (79% of the total collected) and shells (53.6%). Several species that normally live in northern areas were found as part of the thanatocoenosis with a bad preservation status (e.g. the monoplacophoran *Veleropilina reticulata*, the gastropod *Colus islandicus* and the bivalves *Nuculana pernula* and *Chlamys islandica*; all of them denoted by the dagger † in Table 4.2), and are believed to belong to a locally extinct Pleistocene fauna. Of the 141 species present only in the thanatocoenosis, 37 are represented as a single shell or valve.

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Table 4.2. Faunistic list of molluscs found on the LIFE+INDEMARES 0610, 0412 and ATLAS/MEDWAVES 0916 expeditions on the Gazul mud volcano and its adjacent bottoms, by sampling methods(BT: beam-trawl; DA: benthic dredge; BC/SK: box-corer and Shipek grab) and taxocoenosis/thanatocoenosis (Thanat.). The taxon order follows the Checklist of Marine Molluscs of Spain (Gofas et al. 2017). A: species included in the World Register of Deep-Sea Species; B: species recorded from the Djibouti Bank by Gofas et al. (2014); C: species recorded from Moundforce box-corer 2004-08 (F. Slieker, pers. comm.). The previous records column indicates the Spanish demarcations (LEBA: east margin of Spain and Balearic Islands; SUR: Spanish margin of the Gulf of Cadiz (GoC); ESAL: Straitof Gibraltar and Alboran Sea; CAN: the Canary Islands; NOR: Spanish north margin) where the species which are new for the SUR demarcation were already recorded, and (SM17) denotes those specieswhich were included in the Spanish checklist by Gofas et al. (2017) based on the present material. N: number of individuals collected alive (in 1.13 m^{-2}, therefore approximating density per square metre); %D: dominance value; %F: frequency; Rank (1: 1 specimen collected; 2: 2–5; 3: 6–30; 4: 31–100; 5: >100). The species that represent new citations for the GoC are denoted with *; the new records for Spanish waters are indicated with **; the new species for science are indicated with ***. The sign † denotes Pleistocene fossils (not treated as recorded in the recent fauna of the GoC).

						BC/SK (12 samples)					DA (8 samples)					BT (7 samples)		
						Taxocoenosis			Thanat.		Taxocoenosis			Thanat		Taxocoenosis		
Family	Species	A	B	C	Previous records	N	%D	%F	Rank	%F	N	%D	%F	Rank	%F	N	%D	%F
Neopilinidae	*Veleropilina reticulata* (Seguenza, 1876) †								1	8.3								
Neomeniidae	*Neomenia carinata* Tullberg, 1875	1	1			1	0.91	8.3								1	1.15	14.3
Leptochitonidae	*Leptochiton* sp.					1	0.91	8.3			130	6.09	75					
Hanleyidae	*Hanleya hanleyi* (Bean, 1844)										4	0.19	12.5					
Lepetidae	*Propilidium exiguum* (W. Thompson, 1844) *	1	1	1	ALL (SM17)									1	25			
Cocculinidae	*Coccopigya viminensis* (Rocchini, 1990) *	1			LEBA				1	8.3								
Lepetellidae	*Bogia labronica* (Bogi, 1984) *	1	1		ESAL									1	12.5			
Lepetellidae	*Lepetella espinosae* Dantart & Luque, 1994 *		1		ESAL. LEBA				1–3	75				1–3	62.5			
Addisoniidae	*Addisonia excentrica* (Tiberi, 1855) *		1		NOR, ESAL, LEBA									1	12.5			
Anatomidae	*Anatoma micalii* Geiger, 2012 *				ESAL									1–3	25			
Anatomidae	*Anatoma tenuisculpta* (Seguenza, 1880) *		1	1	ESAL	2	1.82	8.3	1–5	75				3–4	50			
Fissurellidae	*Emarginula adriatica* O.G. Costa, 1830 *				ESAL, CAN				1	8.3	7	0.33	25	1	25	1	1.15	14.3
Fissurellidae	*Emarginula fissura* (Linnaeus, 1758)		1						1	8.3	10	0.47	25	1	25	1	1.15	14.3
Fissurellidae	*Emarginula multistriata* Jeffreys, 1882	1							1	8.3	4	0.19	12.5	1	37.5	1	1.15	14.3
Fissurellidae	*Emarginula* sp.								2	8.3				1–3	50			
Fissurellidae	*Emarginula tenera* Locard, 1891 *				ESAL, LEBA, CAN				1	8.3				1–2	37.5			
Chilodontaidae	*Danilia tinei* (Calcara, 1839)		1			1	0.91	8.3	1–2	41.7	24	1.12	50	1–3	75	1	1.15	14.3
Trochidae	*Calumbonella suturalis* (Philippi, 1836)	1	1								3	0.14	12.5	2	12.5			
Trochidae	*Clelandella miliaris* (Brocchi, 1814)		1						1–3	66.7	28	1.31	37.5	1–4	87.5	1	1.15	14.3
Solariellidae	*Solariella amabilis* (Jeffreys, 1865)	1		1					1–4	50				2–3	50			
Seguenzioidea	*Anekes paucistriata* Warén, 1992 *			1	CAN				1–3	16.7				1	12.5			
Seguenzioidea	*Lissotesta gittenbergeri* (van Aartsen & Bogi, 1988) *	1	1	1	ESAL, LEBA, CAN				1–2	16.7								
Seguenzioidea	*Lissotesta minima* (Seguenza, 1876)	1							1	8.3								
Skeneidae	*Cirsonella romettensis* (Granata–Grillo, 1877)	1	1	1		1	0.91	8.3	1–5	58.3	1	0.05	12.5	1–4	75			
Skeneidae	*Dikoleps marianae* Rubio, Dantart & Luque, 1998 *				ESAL, LEBA, CAN				2	16.7								
Skeneidae	*Dikoleps* sp.								1–3	33.3								
Skeneidae	*Skenea serpuloides* (Montagu, 1808)								1–2	25								
Pendromidae	*Rugulina monterosatoi* (van Aartsen & Bogi, 1987) *				ESAL				1	8.3								
Colloniidae	*Cantrainea peloritana* (Cantraine, 1835)	1		1					1–2	33.3	21	0.98	25	1–3	25			
Cerithiidae	*Bittium watsoni* (Jeffreys, 1885)	1		1		1	0.91	8.3	1–5	100				2–5	87.5			

Table 4.2 (continued)

Family	Species	A	B	C	Previous records	BC/SK (12 samples) Taxocoenosis			Thanat.		DA (8 samples) Taxocoenosis			Thanat		BT (7 samples) Taxocoenosis		
						N	%D	%F	Rank	%F	N	%D	%F	Rank	%F	N	%D	%F
Turritellidae	*Turritella communis* Risso, 1826		1						1–2	16.7				2–4	37.5			
Triphoridae	*Metaxia metaxa* (Delle Chiaje, 1828)													1–2	37.5			
Triphoridae	*Monophorus thiriotae* Bouchet, 1985 *				ALL				2	16.7								
Triphoridae	*Pogonodon pseudocanaricus* (Bouchet, 1985) *				ESAL, LEBA, CAN									1	12.5			
Triphoridae	*Strobiligera brychia* (Bouchet & Guillemot, 1978)	1	1	1										1–2	25			
Triphoridae	*Strobiligera* sp.								1	16.7								
Triphoridae	Triphoridae (unidentified)										6	0.28	12.5	1–3	25			
Newtoniellidae	*Cerithiella insignis* (Jeffreys, 1885)	1							1	25				2–3	50			
Newtoniellidae	*Cerithiella metula* (Lovén, 1846)	1	1	1										1	12.5			
Cerithiopsidae	*Cerithiopsis atalaya* R. B. Watson, 1885 *			1	ESAL, CAN (SM17)				1	8.3				1–3	50			
Cerithiopsidae	*Cerithiopsis diadema* Monterosato, 1874 *				ESAL, LEBA, CAN									2	12.5			
Cerithiopsidae	*Cerithiopsis* sp.								2	16.7				2	25			
Cerithiopsidae	*Krachia sylindrata* (Jeffreys, 1885)								1–2	16.7				1–3	62.5			
Cerithiopsidae	*Krachia* sp.													1	12.5			
Cerithiopsidae	*Onchodia valeriae* (Giusti Fr., 1987) *	1		1	ESAL, CAN (SM17)				1–3	16.7				2–3	62.5			
Epitoniidae	*Epitonium algerianum* (Weinkauff, 1866) *	1	1		ESAL, LEBA, CAN	1	0.91	8.3	1	8.3				1	12.5			
Epitoniidae	*Epitonium celesti* (Aradas, 1854)		1	1					1–2	41.7	22	1.03	62.5	1–3	50			
Epitoniidae	*Epitonium clathratulum* (Kanmacher, 1798) *		1		ALL				1–2	41.7				1–3	37.5			
Epitoniidae	*Epidendrium dendrophylliae* (Bouchet & Warén, 1986) *			1	ESAL, LEBA, CAN									2	12.5			
Epitoniidae	*Epitonium linctum* (de Boury & Monterosato, 1890) *	1	1	1	ESAL, LEBA				1	16.7				1	12.5			
Epitoniidae	*Epitonium sp.*								1–3	16.7								
Epitoniidae	*Iphitus tuberatus* Jeffreys, 1883 *	1			NOR				1–2	16.7				1–3	37.5			
Epitoniidae	*Narrimania concinna* (Sykes, 1925) *	1		1	CAN				1	8.3								
Epitoniidae	*Opaliopsis atlantis* (Clench & R. D. Turner, 1952) *	1	1	1	ESAL, CAN (SM17)				1	25	1	0.05	12.5	1–3	75			
Eulimidae	*Curveulima devians* (Monterosato, 1884) *		1		ESAL, LEBA (SM17)				1	8.3				1	12.5			
Eulimidae	*Curveulima* sp.								1–2	16.7				2–3	37.5			
Eulimidae	*Eulima bilineata* Alder, 1848 *		1		ALL	1	0.91	8.3	1–2	33.3	3	0.14	12.5	2–3	62.5			
Eulimidae	Eulimidae (unidentified)										12	0.56	12.5					
Eulimidae	*Fusceulima minuta* (Jeffreys, 1884) *				NOR, ESAL, CAN				2–3	41.7								
Eulimidae	*Melanella doederleini* (Brusina, 1886)								1–2	16.7	3	0.14	12.5	1–3	62.5			
Eulimidae	*Melanella petitiana* (Brusina, 1869) *		1		ESAL, LEBA				1	8.3								
Eulimidae	*Sabinella bonifaciae* (F. Nordsieck, 1974) *				ESAL, CAN									1	12.5			
Eulimidae	*Aclis attenuans* Jeffreys, 1883 *	1	1	1	ESAL, LEBA				1	8.3				2	12.5			
Eulimidae	*Aclis gulsonae* (W. Clark, 1850) *		1	1	NOR, ESAL, LEBA				1	33.3				1–2	25			
Eulimidae	*Aclis trilineata* R.B. Watson, 1897 *				ESAL, CAN				1	8.3								

Table 4.2 (continued)

Family	Species	A	B	C	Previous records	BC/SK (12 samples) Taxocoenosis			Thanat.		DA (8 samples) Taxocoenosis			Thanat		BT (7 samples) Taxocoenosis		
						N	%D	%F	Rank	%F	N	%D	%F	Rank	%F	N	%D	%F
Rissoidae	*Alvania cimicoides* (Forbes, 1844)	1	1	1		4	3.64	16.7	1–5	100	6	0.28	12.5	2–5	87.5			
Rissoidae	*Alvania electa* (Monterosato, 1874)	1				5	4.55	16.7	1–4	83.3				2–4	62.5			
Rissoidae	*Alvania testae* (Aradas & Maggiore, 1844)		1						1–3	33.3				1	12.5			
Rissoidae	*Alvania tomentosa* (Pallary, 1920)			1		9	8.18	25	1–5	83.3				3–5	62.5			
Rissoidae	*Alvania zetlandica* (Montagu, 1815)		1	1		1	0.91	8.3	1–3	58.3				1–4	75			
Rissoidae	*Alvania zylensis* Gofas & Warén, 1982 *			1	ESAL	1	0.91	8.3	1–3	41.7				2–3	37.5			
Rissoidae	*Benthonella tenella* (Jeffreys, 1869)	1		1					3	8.3								
Rissoidae	*Onoba goyoi* n. sp. ***								1–2	16.7				2	12.5			
Rissoidae	*Pseudosetia amydralox* Bouchet & Warén, 1993 *	1		1	NOR, ESAL, CAN				1–3	16.7				1	12.5			
Vanikoridae	*Talassia dagueneti* (de Folin, 1873)		1	1					1–2	25				1	12.5			
Calyptraeidae	*Calyptraea chinensis* (Linnaeus, 1758)								1	25								
Capulidae	*Capulus ungaricus* (Linnaeus, 1758)													1–2	37.5			
Eratoidae	*Erato voluta* (Montagu, 1803)								1	8.3				1–2	37.5			
Triviidae	*Trivia arctica* (Pulteney, 1799)													1	25			
Naticidae	*Cryptonatica operculata* (Jeffreys, 1885)	1							1	8.3	4	0.19	25	1	12.5			
Naticidae	Naticidae (unidentified)								1–2	41.7	6	0.28	12.5	2–4	87.5			
Naticidae	*Tectonatica rizzae* (Philippi, 1844) *				NOR, ESAL, CAN (SM17)						9	0.42	25	1–2	25			
Cassidae	*Galeodea rugosa* (Linnaeus, 1771)	1							2	16.7				1	12.5	2	2.30	28.6
Ranellidae	*Ranella olearium* (Linnaeus, 1758)	1		1										1	25	3	3.45	42.9
Atlantidae	*Atlanta peronii* Lesueur, 1817 *				ALL				1	8.3				1	12.5			
Muricidae	*Hirtomurex squamosus* (Bivona e Bernardi, 1838) *				ALL						18	0.84	12.5	1–2	25	1	1.15	14.3
Muricidae	*Pagodula echinata* (Kiener, 1839) *	1	1	1	ALL (SM17)				1–2	50	13	0.61	37.5	1–3	75			
Muricidae	*Trophonopsis barvicensis* (G. Johnston, 1825) *		1	1	ESAL	1	0.91	8.3	1–3	58.3	16	0.75	25	2–5	100			
Fasciolariidae	*Fusinus* sp.													1	12.5			
Buccinidae	*Buccinum humphreysianum* Bennett, 1824	1												2	12.5			
Buccinidae	*Chauvetia balgimae* Gofas & J.D. Oliver, 2010 **	1		1	(SM17)				2	8.3				2–3	37.5			
Buccinidae	*Colus islandicus* (Mohr, 1786) †													1	12.5			
Buccinidae	*Colus jeffreysianus* (P. Fischer, 1868)	1												1–2	25			
Buccinidae	*Neptunea contraria* (Linnaeus, 1771) *				NOR									1–2	25			
Nassariidae	*Tritia coralligena* (Pallary, 1900) *				ESAL (SM17)				1–2	16.7	18	0.84	25	1–4	50			
Columbellidae	*Amphissa acutecostata* (Philippi, 1844) *	1	1	1	ALL (SM17)				1–2	25				1–3	50			
Columbellidae	*Anachis aliceae* (Pallary, 1900) *				ESAL (SM17)						4	0.19	12.5	1	25			
Columbellidae	*Mitrella canariensis* (d'Orbigny, 1840) *				NOR, ESAL, CAN (SM17)				1	8.3	14	0.66	37.5	1–2	25			
Marginellidae	*Dentimargo auratus* Espinosa, Ortea & Moro, 2014 **										3	0.14	12.5	1–3	50			
Granulinidae	*Granulina minusculina* (Locard, 1897)	1		1		1	0.91	8.3	1–5	58.3				3–4	50			
Granulinidae	*Granulina occulta* (Monterosato, 1869) *			1	ESAL, LEBA, CAN									1	25			
Cystiscidae	*Gibberula turgidula* (Locard & Caziot, 1900) *			1	ESAL, LEBA (SM17)	6	5.45	25	1–4	75	11	0.52	12.5	2–3	62.5			

Table 4.2 (continued)

Family	Species	A	B	C	Previous records	BC/SK (12 samples) Taxocoenosis			Thanat.		DA (8 samples) Taxocoenosis			Thanat		BT (7 samples) Taxocoenosis		
						N	%D	%F	Rank	%F	N	%D	%F	Rank	%F	N	%D	%F
Volutidae	*Ampulla priamus* (Gmelin, 1791)	1												1	25			
Cancellariidae	*Pseudobabylonella minima* (Reeve, 1856)		1											1	12.5			
Drilliidae	*Spirotropis confusa* (Seguenza, 1880) *	1		1	ESAL (SM17)				1–2	50	7	0.33	25	2–5	62.5			
Borsoniidae	*Drilliola emendata* (Monterosato, 1872) *		1	1	ESAL, LEBA (SM17)				1–2	16.7				1–3	62.5			
Borsoniidae	*Drilliola loprestiana* (Calcara, 1841) *		1	1	ALL (SM17)						1	0.05	12.5	1–2	62.5			
Mangeliidae	*Mangelia costata* (Pennant, 1777)		1											1	12.5			
Raphitomidae	*Pleurotomella demosia* (Dautzenberg & Fischer, 1896) *	1		1	ESAL, LEBA, CAN									2–3	25			
Raphitomidae	*Pleurotomella gibbera* Bouchet & Warén, 1980 *	1	1		ESAL, CAN (SM17)				1	8.3				1	12.5			
Raphitomidae	*Raphitoma* sp.								1	16.7								
Raphitomidae	*Teretia teres* (Reeve, 1844) *		1	1	ALL (SM17)	1	0.91	8.3	1–2	50				1–4	62.5			
Architectonicidae	*Discotectonica discus* (Philippi, 1844) *			1	ESAL, LEBA									1	12.5			
Architectonicidae	*Solatisonax alleryi* (Seguenza G., 1876) *			1	ESAL, LEBA, CAN						1	0.05	12.5	1	12.5			
Mathildidae	*Mathilda cochlaeformis* Brugnone, 1873 *			1	ESAL, LEBA, CAN				1	8.3	1	0.05	12.5	1–3	50			
Mathildidae	*Mathilda coronata* Monterosato, 1875 *		1		ESAL				1	8.3	4	0.19	12.5	1–2	25			
Mathildidae	*Mathilda retusa* Brugnone, 1873 *				ESAL, LEBA, CAN									2–3	25			
Cimidae	*Cima* sp.								1	8.3								
Cimidae	*Graphis gracilis* (Monterosato, 1874)		1	1					1–2	16.7								
Amathinidae	*Clathrella clathrata* (Philippi, 1844)								1–3	58.3				1	12.5			
Pyramidellidae	*Eulimella bogii* van Aartsen, 1994 *				ESAL, LEBA, CAN				1–2	16.7								
Pyramidellidae	*Eulimella cerullii* (Cossmann, 1916)			1					1–2	25				1–3	50			
Pyramidellidae	*Eulimella* cf. *carminae* Peñas & Micali, 1999 *				ESAL				1	8.3				1	12.5			
Pyramidellidae	*Eulimella cossignaniorum* van Aartsen, 1994 *				CAN									2	12.5			
Pyramidellidae	*Eulimella neoattenuata* Gaglini, 1992 *				LEBA, CAN				1	8.3				2	12.5			
Pyramidellidae	*Eulimella scillae* (Scacchi, 1835)								1	16.7				2	12.5			
Pyramidellidae	*Eulimella* sp.								1–2	33.3								
Pyramidellidae	*Eulimella ventricosa* (Forbes, 1844)		1	1					1–2	25								
Pyramidellidae	*Odostomella bicincta* (Tiberi, 1868) *				ESAL, LEBA, CAN	1	0.91	8.3	1–2	25				1–2	50			
Pyramidellidae	*Odostomia acuta* Jeffreys, 1848													1	25			
Pyramidellidae	*Odostomia* sp.								1–2	16.7								
Pyramidellidae	*Odostomia suboblonga* Jeffreys, 1884	1		1					2	16.7				1–3	37.5			
Pyramidellidae	*Parthenina flexuosa* (Monterosato, 1874)	1	1	1					1–4	66.7				2–3	50			
Pyramidellidae	*Parthenina indistincta* (Montagu, 1808)													2	12.5			
Pyramidellidae	*Pyrgulina stefanisi* (Jeffreys, 1869) *				CAN				1	8.3								
Pyramidellidae	*Syrnola minuta* H. Adams, 1869	1							1	8.3				1–2	25			
Pyramidellidae	*Tiberia minuscula* (Monterosato, 1880)	1	1											1	12.5			
Pyramidellidae	*Turbonilla magnifica* Seguenza G., 1880		1	1					2	16.7				1–3	37.5			
Pyramidellidae	*Turbonilla sinuosa* (Jeffreys, 1884) *				ESAL, LEBA				1	8.3								

Table 4.2 (continued)

Family	Species	A	B	C	Previous records	BC/SK (12 samples) Taxocoenosis			BC/SK Thanat.		DA (8 samples) Taxocoenosis			DA Thanat		BT (7 samples) Taxocoenosis		
						N	%D	%F	Rank	%F	N	%D	%F	Rank	%F	N	%D	%F
Tjaernoeiidae	*Tjaernoeia unisulcata* (Chaster, 1897) *				ESAL				1	8.3								
Acteonidae	*Crenilabium exile* (Jeffreys, 1870)	1												1	12.5			
Acteonidae	*Actaeon monterosatoi* Dautzenberg, 1889	1	1	1					1–3	66.7				1–4	75			
Ringiculidae	*Ringicula* sp.								1	8.3				2	12.5			
Ringiculidae	*Ringicula gianninii* F. Nordsieck, 1974 *	1			NOR						1	0.05	12.5	2–3	25			
Philinidae	*Hermania scabra* (O. F. Müller, 1784) *		1		ALL				1	8.3				1	12.5			
Philinidae	*Philine striatula* (Monterosato, 1874) *				LEBA									1	12.5			
Cylichnidae	*Cylichna cylindracea* (Pennant, 1777)		1								1	0.05	12.5	1	25			
Retusidae	*Pyrunculus* cf. *ovatus* (Jeffreys, 1871)	1		1										1	12.5			
Scaphandridae	*Scaphander lignarius* (Linnaeus, 1758)		1						1	8.3								
Cavoliniidae	*Cavolinia inflexa* (Lesueur, 1813)		1	1					1–4	83.3				1–3	50			
Cavoliniidae	*Cavolinia tridentata* (Forsskål [in Niebuhr], 1775) *				ESAL, LEBA, CAN				1–2	16.7				1	37.5			
Cavoliniidae	*Diacria quadridentata* (Blainville, 1821) *				ESAL, LEBA, CAN				1	8.3								
Cavoliniidae	*Diacria trispinosa* (Blainville, 1821)			1					2–4	25				2–3	25			
Cliidae	*Clio cuspidata* (Bosc, 1801) *		1		ESAL, LEBA, CAN				1–2	16.7								
Cliidae	*Clio pyramidata* Linnaeus, 1767 *		1	1	ALL				1–3	16.7				1–3	12.5			
Creseidae	*Styliola subula* (Quoy and Gaimard, 1827) *				ESAL, LEBA, CAN				2	8.3								
Limacinidae	*Heliconoides inflatus* (d'Orbigny, 1835)			1					1–4	41.7								
Limacinidae	*Limacina bulimoides* (d'Orbigny, 1835) *			1	ALL				1	16.7								
Limacinidae	*Limacina lesueurii* (d'Orbigny, 1836) *			1	ESAL, LEBA, CAN				1–2	16.7								
Limacinidae	*Limacina retroversa* (J. Fleming, 1823) †		1											1	12.5			
Peraclidae	*Peracle elata* (Seguenza, 1875)		1						1	16.7								
Tylodinidae	*Anidolyta duebenii* (Lovén, 1846) *	1		1	ESAL				1–2	16.7				1–2	37.5			
Pleurobranchaeidae	*Pleurobranchaea meckeli* (Blainville, 1825)															1	1.15	14.3
Discodorididae	*Baptodoris cinnabarina* Bergh, 1884 *				ALL											2	2.30	14.3
Nuculidae	*Nucula perminima* (Monterosato, 1875) *				ESAL				1	8.3								
Nuculidae	*Ennucula aegeensis* (Forbes, 1844)	1	1			2	1.82	8.3	1–3	50	12	0.56	25	1–2	37.5			
Nuculidae	*Ennucula decipiens* (Philippi, 1844)		1						1–2	16.7								
Nuculidae	*Nucula* sp.								1	25				2	12.5			
Nuculidae	*Nucula sulcata* Bronn, 1831					1	0.91	8.3	1–3	50	20	0.94	25	1–4	62.5			
Nuculanidae	*Ledella messanensis* (Jeffreys, 1870)	1	1	1		1	0.91	8.3	1–3	83.3	11	0.52	37.5	2–5	87.5			
Nuculanidae	*Nuculana pernula* (O.F. Müller, 1779) †													1	12.5			
Nuculanidae	*Saccella commutata* (Philippi, 1844)					1	0.91	8.3	1–3	58.3				1–3	37.5			
Yoldiidae	*Yoldiella philippiana* (Nyst, 1845)		1	1		3	2.73	16.7	1–3	50				1–3	50			

Table 4.2 (continued)

Family	Species	A	B	C	Previous records	BC/SK (12 samples) Taxocoenosis N	%D	%F	Thanat. Rank	%F	DA (8 samples) Taxocoenosis N	%D	%F	Thanat Rank	%F	BT (7 samples) Taxocoenosis N	%D	%F
Arcidae	*Asperarca nodulosa* (O.F. Müller, 1776)	1	1			9	8.18	41.7	1–4	66.7	116	5.43	75	1–5	75	19	21.84	42.9
Arcidae	*Bathyarca pectunculoides* (Scacchi, 1835)	1	1						1–4	83.3	23	1.08	37.5	1–4	87.5			
Arcidae	*Bathyarca philippiana* (Nyst, 1848)	1	1	1		25	22.73	75	1–5	83.3	1222	57.24	87.5	3–5	100	5	5.75	28.6
Limopsidae	*Limopsis angusta* Jeffreys, 1879	1		1					1–4	33.3	53	2.48	37.5	1–5	50	4	4.60	57.1
Limopsidae	*Limopsis aurita* (Brocchi, 1814)	1	1			3	2.73	16.7	1–4	91.7	13	0.61	37.5	1–5	100	1	1.15	14.3
Limopsidae	*Limopsis minuta* (Philippi, 1836)	1	1						2–3	8.3				4	12.5			
Mytilidae	*Dacrydium hyalinum* (Monterosato, 1875) *				ESAL (SM17)	5	4.55	33.3	1–2	50	9	0.42	25	1–3	37.5			
Pinnidae	*Atrina fragilis* (Pennant, 1777)													2	12.5			
Pteriidae	*Pteria hirundo* (Linnaeus, 1758)																	
Propeamussiidae	*Cyclopecten hoskynsi* (Forbes, 1844)		1						1–3	25				3	12.5			
Propeamussiidae	*Parvamussium fenestratum* (Forbes, 1844)		1			1	0.91	8.3	1–4	66.7	10	0.47	25	1–5	87.5			
Propeamussiidae	*Similipecten similis* (Laskey, 1811)		1			1	0.91	8.3	1–4	75	1	0.05	12.5	2–3	37.5			
Pectinidae	*Chlamys islandica* (O.F. Müller, 1776) †													1	12.5			
Pectinidae	*Delectopecten vitreus* (Gmelin, 1791)	1	1											5	12.5			
Pectinidae	*Pseudamussium sulcatum* (Müller, 1776)		1						1–3	83.3	15	0.70	50	1–4	87.5	5	5.75	42.9
Pectinidae	*Pseudamussium clavatum* (Poli, 1795) *		1		NOR, ESAL, LEBA (SM17)									1	12.5			
Pectinidae	*Pseudamussium peslutrae* (Linnaeus, 1771)	1	1						1–3	25	10	0.47	37.5	1–4	50	17	19.54	28.6
Spondylidae	*Spondylus gussonii* O.G. Costa, 1830 *	1		1	NOR, ESAL (SM17)				1	8.3	6	0.28	12.5	1	12.5	1	1.15	14.3
Anomiidae	*Heteranomia squamula* (Linnaeus, 1758)		1						1–5	83.3	13	0.61	37.5	1–5	100	7	8.05	28.6
Limidae	*Limatula* cf. *subauriculata* (Montagu, 1808)					1	0.91	8.3	1–3	75	4	0.19	12.5	1–3	62.5			
Limidae	*Limea crassa* (Forbes, 1844)	1	1			2	1.82	8.3	1–4	91.7	14	0.66	50	2–4	75			
Gryphaeidae	*Neopycnodonte cochlear* (Poli, 1795)								1–2	16.7				1	12.5	2	2.30	14.3
Carditidae	*Centrocardita aculeata* (Poli, 1795)										3	0.14	12.5	2	12.5			
Astartidae	*Astarte sulcata* (da Costa, 1778)		1			3	2.73	16.7	1–4	83.3	77	3.61	62.5	1–4	75			
Lucinidae	*Lucinoma asapheus* Oliver, Rodrigues & Cunha, 2011	1							1	16.7								
Thyasiridae	*Mendicula ferruginosa* (Forbes, 1844)	1	1						1–2	16.7				1	25			
Thyasiridae	*Thyasira granulosa* (Monterosato, 1874) *	1	1		ESAL, LEBA (SM17)				1	8.3				1	12.5			
Thyasiridae	*Thyasira succisa* (Jeffreys, 1876)	1	1			2	1.82	8.3	1–4	75				2–3	62.5			
Galeommatidae	*Solecardia rotunda* (Jeffreys, 1881)	1	1						1	8.3								
Lasaeidae	*Hemilepton nitidum* (W. Turton, 1822)								1	8.3								
Lasaeidae	*Draculamya porobranchiata* Oliver & Lützen, 2011 **	1			(Note 1)				1–2	16.7								
Lasaeidae	*Kurtiella bidentata* (Montagu, 1803)		1	1					1–2	50				1–2	25			
Lasaeidae	*Kurtiella ovata* (Jeffreys, 1881)	1							2	16.7								
Cardiidae	*Acanthocardia aculeata* (Linnaeus, 1758)								1–2	16.7				2	37.5			
Cardiidae	*Papillicardium minimum* (Philippi, 1836)		1	1					1–5	91.7	13	0.61	37.5	1–5	100			
Mactridae	*Spisula subtruncata* (da Costa, 1778)								1	16.7								

Table 4.2 (continued)

Family	Species	Previous records			BC/SK (12 samples) Taxocoenosis			Thanat.		DA (8 samples) Taxocoenosis			Thanat		BT (7 samples) Taxocoenosis		
		A	B	C	N	%D	%F	Rank	%F	N	%D	%F	Rank	%F	N	%D	%F
Tellinidae	*Arcopella balaustina* (Linnaeus, 1758)		1					1	8.3				1	12.5			
Semelidae	*Abra longicallus* (Scacchi, 1835)	1	1	1				1–3	66.7	4	0.19	12.5	1–4	62.5			
Semelidae	*Abra prismatica* (Montagu, 1808)							2	8.3				2	12.5			
Kelliellidae	*Kelliella miliaris* (Philippi, 1844)		1		1	0.91	8.3	1–4	58.3				1–2	50			
Trapezidae	*Coralliophaga lithophagella* (Lamarck, 1819)									10	0.47	12.5					
Veneridae	*Pitar mediterraneus* (Aradas & Benoit, 1872)		1							1	0.05	12.5	1–3	12.5			
Veneridae	*Timoclea ovata* (Pennant, 1777)				2	1.82	8.3	2	16.7	1	0.05	12.5	1–3	12.5			
Veneridae	*Venus nux* Gmelin, 1791				1	0.91	8.3	1	16.7								
Poromyidae	*Cetomya neaeroides* (Seguenza, 1877)	1						1	8.3	13	0.61	25	1	12.5			
Poromyidae	*Poromya granulata* (Nyst & Westendorp, 1839)		1		1	0.91	8.3	1	16.7								
Hiatellidae	*Hiatella arctica* (Linnaeus, 1767)		1		1	0.91	8.3	2–4	41.7	18	0.84	37.5	1–5	87.5	4	4.60	28.6
Verticordiidae	*Haliris granulata* (Seguenza, 1860)	1						1	8.3								
Verticordiidae	*Spinosipella acuticostata* (Philippi, 1844)	1		1						3	0.14	12.5					
Cuspidariidae	*Cardiomya cadiziana* M. Huber, 2010	1											1	25			
Cuspidariidae	*Cardiomya costellata* (Deshayes, 1835)		1					1–2	33.3				2	12.5			
Cuspidariidae	*Cuspidaria cuspidata* (Olivi, 1792)		1					1	8.3								
Cuspidariidae	*Myonera atlasiana* n. sp. ***				1	0.91	8.3	1	8.3	6	0.28	12.5					
Dentaliidae	*Antalis* sp.				2	1.82	8.3	1–2	8.3				3	50			
Entalinidae	*Entalina tetragona* (Brocchi, 1814)	1						1–3	25				1–3	25			
Gadilidae	*Cadulus jeffreysi* (Monterosato, 1875)	1	1	1				1–3	75	6	0.28	12.5	2–4	62.5			
Sepiolidae	*Rossia macrosoma* (Delle Chiaje, 1830)	1													1	1.15	14.3
Sepiolidae	*Sepietta oweniana* (d'Orbigny, 1841)														4	4.60	42.9
Eledonidae	*Eledone cirrhosa* (Lamarck, 1798)														1	1.15	14.3
TOTAL	86 species new for GoC (of which 3 new for Spain), 2 n. sp.	75	87	67	108					2130					86		

Note 1: After the publication of this article, the species present in the Gulf of Cadiz was identified as *Draculamya uraniae* Romani, Bartolini, P.G. Oliver & Taviani, 2021 by Romani et al. (2021).

4.3.2. Molluscan assemblages

Multivariate analysis of the live-taken molluscan fauna based on qualitative data of all samples showed two main groups of samples, one collected on the MV edifice and one collected in the erosive depression and on the adjacent bottoms (Fig. 4.2). The ANOSIM test revealed significant differences between the assemblages associated with the MV edifice, the erosive depression and the adjacent bottoms ($R_{ANOSIM}=0.2$; $p<0.005$). Pairwise comparisons revealed that differences were consistently significant among all areas ($p<0.05$, for all cases), with the largest differences detected between assemblages inhabiting the MV edifice and the adjacent bottoms (ANOSIM pairwise test, $R=0.3$, $p<0.005$; SIMPER average dissimilarity, 89.8%), mainly due to the exclusive presence or higher frequency of occurrence of *Limopsis angusta*, *Hiatella arctica*, *Pseudamussium sulcatum* and *Danilia tinei*, among other species, on the MV edifice and of *B. philippiana*, *A. nodulosa*, *Nucula sulcata* and *A. sulcata*, among other species, on the adjacent bottoms. On the other hand, assemblages associated with the erosive depression and the adjacent bottoms showed the smallest dissimilarities, although significant (ANOSIM pairwise test, $R=0.1$, $p<0.05$; SIMPER average dissimilarity, 82.1%). Despite these differences, nine species were shared between the three areas, including the bivalves *A. nodulosa*, *Astarte sulcata*, *B. philippiana*, *Dacrydium hyalinum*, *Limopsis aurita* and *L. angusta*, the polyplacophoran *Leptochiton* sp., the gastropod *Ranella olearium* and the cephalopod *Sepietta oweniana*.

Figure 4.2. Non-metric multidimensional scaling ordination based on qualitative (presence/absence of live-taken species) similarities (Bray-Curtis similarity index) between the molluscan assemblages found in all samples collected in the different areas of the Gazul mud volcano (MV).

Table 4.3. Number of individuals collected alive (N) of the top-dominant species found on the Gazul mud volcano (including the mud volcano edifice, erosive depression and adjacent bottoms), with their dominance index (%D) and the maximum observed rank (4: 31–100; 5: >100 shells) of the most representative species of the thanatocoenosis, all samples.

	TOTAL			
Taxocoenosis spp.	N	%D	Thanatocoenosis spp.	Max. rank
Bathyarca philippiana	1252	53.71	*Papillicardium minimum*	5
Asperarca nodulosa	144	6.18	*Bathyarca philippiana*	5
Leptochiton sp.	131	5.62	*Alvania cimicoides*	5
Astarte sulcata	80	3.43	*Bittium watsoni*	5
Limopsis angusta	57	2.45	*Alvania tomentosa*	5
Clelandella miliaris	29	1.24	*Heteranomia squamula*	5
Pseudamussium peslutrae	27	1.16	*Ledella messanensis*	5
Danilia tinei	26	1.12	*Trophonopsis barvicensis*	5
Bathyarca pectunculoides	23	0.99	*Limea crassa*	4
Hiatella arctica	23	0.99	*Limopsis aurita*	5
Epitonium celesti	22	0.94	*Astarte sulcate*	4
Cantrainea peloritana	21	0.90	*Clelandella miliaris*	4
Nucula sulcata	21	0.90	*Alvania electa*	4
Heteranomia squamula	20	0.86	*Parvamussium fenestratum*	5
Pseudamussium sulcatum	20	0.86	*Asperarca nodulosa*	5

The first assemblage is associated with the MV edifice, where MDACs with live cold-water corals (e.g. *Madrepora oculata* Linnaeus, 1758 (mostly), *Desmophyllum pertusum* (Linnaeus, 1758) and *Dendrophyllia cornigera* (Lamarck, 1816)) and/or abundant coral-rubble occur. Samples collected here displayed the highest species richness, abundance, Shannon-Wiener diversity index and evenness values for most sampling gears (Table 4.4), but these differences among areas were non-significant (ANOVA $p>0.05$ in all cases). This assemblage was composed of 60 species (30 of them exclusive, e.g. *Rossia macrosoma*, *Odostomella bicincta* and *Hirtomurex squamosus*), with 56.7% of the species present in only one sample. It was characterized (in order of decreasing abundance) by the species *B. philippiana*, *A. nodulosa*, *Leptochiton* sp., *Limopsis angusta*, *A. sulcata*, *Clelandella miliaris*, *D. tinei*, *Bathyarca pectunculoides*, *Hiatella arctica*, *H. squamosus* and *Tritia coralligena*, among others (Table 4.5).

Table 4.4. Mean values of ecological indexes of species collected alive in the areas of the Gazul mud volcano (MV: mud volcano edifice; Dep.: erosive depression; Adj.: adjacent bottoms) for each sampling method. SE: standard error; S: species richness; N: abundance; J': evenness index; H' (log_2): Shannon-Wiener diversity index.

Sampling method	Area	S (±SE)	N (±SE)	J' (±SE)	H' (log_2) (±SE)
Beam-trawl	MV	7.3 (±0.9)	9 (±1)	0.976 (±0.002)	2.786 (±0.163)
	Dep	5 (±1)	17 (±6)	0.806 (±0.140)	1.889 (±0.557)
	Adj	4.5 (±1.5)	14 (±11)	0.799 (±0.201)	1.565 (±0.021)
Benthic dredge	MV	22 (±6.7)	418 (±228.3)	0.717 (±0.061)	3.029 (±0.220)
	Dep	19.7 (±2.7)	382.7 (±59.5)	0.466 (±0.120)	1.952 (±0.432)
	Adj	6 (±1)	54 (±24)	0.620 (±0.078)	1.609 (±0.350)
Box-corer/Shipek grab	MV	5 (±1.7)	128.7 (±56)	0.952 (±0.031)	1.972 (±0.502)
	Dep	6.3 (±3.9)	91.3 (±71.2)	0.941 (±0.048)	2.680 (±0.555)
	Adj	4.8 (±1)	136.3 (±26.4)	0.958 (±0.019)	2.289 (±0.187)

The second group of samples corresponds to a mollusc assemblage linked to the western depression area, and to the assemblage of the adjacent bottoms. Within the depression, there are mainly coarse sediments mixed with hard substrates (e.g. MDACs slabs), and therefore this area included both hard-bottom and soft-bottom species. This assemblage was composed of 45 species (15 of them exclusive, such as *Drilliola loprestriana*, *Alvania zetlandica* and *Solatisonax alleryi*), with 54.3% of them collected from a single sample. It was characterized by *B. philippiana*, *Leptochiton* sp., *A. sulcata* and *A. nodulosa*, in most cases showing abundance values similar to those observed on the MV edifice, as well as by *Pseudamussium peslutrae*, *Heteranomia squamula* and *Pagodula echinata*, among others (Table 4.5). The assemblage linked to the adjacent bottoms, in many cases characterized by muddy fine sand bottoms, was composed of 32 species (12 species exclusive, including mud-related species such as the bivalves *Nucula sulcata* and *Venus nux*). Despite the lower number of species and lower abundance values of dominant species observed in this assemblage (Table 4.4), differences were not significant in comparison with the values of the other identified assemblages (ANOVA $p>0.05$ in all cases).

Table 4.5. Number of individuals collected alive (N) of the top-dominant species found in the areas of the Gazul mud volcano (mud volcano edifice, erosive depression and adjacent bottoms) with their dominance index (%D) and the maximum observed rank (3: 6–30; 4: 31–100; 5: >100 shells) of the most representative species of the thanatocoenosis, all samples.

		MUD VOLCANO EDIFICE		
Taxocoenosis	N	%D	Thanatocoenosis	Max. rank
Bathyarca philippiana	531	45.50	*Papillicardium minimum*	5
Asperarca nodulosa	87	7.46	*Bathyarca philippiana*	5
Leptochiton sp.	57	4.88	*Alvania cimicoides*	5
Limopsis angusta	51	4.37	*Bittium watsoni*	5
Astarte sulcate	36	3.08	*Alvania tomentosa*	5
Clelandella miliaris	25	2.14	*Ledella messanensis*	5
Danilia tinei	24	2.06	*Heteranomia squamula*	5
Bathyarca pectunculoides	22	1.89	*Parvamussium fenestratum*	5
Hiatella arctica	19	1.63	*Limopsis aurita*	5
Hirtomurex squamosus	19	1.63	*Trophonopsis barvicensis*	5
Tritia coralligena	18	1.54	*Limopsis angusta*	5
Epitonium celesti	16	1.37	*Alvania electa*	4
Trophonopsis barvicensis	16	1.37	*Limea crassa*	4
Gibberula turgidula	14	1.20	*Astarte sulcata*	4
Mitrella canariensis	14	1.20	*Bathyarca pectunculoides*	4
		EROSIVE DEPRESSION		
Taxocoenosis	N	%D	Thanatocoenosis	Max. rank
Bathyarca philippiana	678	67.33	*Papillicardium minimum*	5
Leptochiton sp.	72	7.15	*Alvania cimicoides*	5
Astarte sulcata	35	3.48	*Spirotropis confusa*	5
Asperarca nodulosa	34	3.38	*Delectopecten vitreus*	5
Pseudamussium peslutrae	21	2.09	*Bathyarca philippiana*	4
Heteranomia squamula	18	1.79	*Limea crassa*	4
Pagodula echinata	13	1.29	*Clelandella miliaris*	4
Unidentified *Eulimidae*	12	1.19	*Cirsonella romettensis*	4
Limea crassa	10	0.99	*Trophonopsis barvicensis*	4
Limopsis aurita	10	0.99	Unidentified *Naticidae*	4
Cantrainea peloritana	9	0.89	*Cadulus jeffreysi*	4
Alvania cimicoides	8	0.79	*Teretia teres*	4
Ennucula aegeensis	8	0.79	*Turritella communis*	4
Pseudamussium sulcatum	8	0.79	*Nucula sulcata*	4
Epitonium celesti	6	0.59	*Astarte sulcata*	4
		ADJACENT BOTTOMS		
Taxocoenosis	N	%D	Thanatocoenosis	Max. rank
Bathyarca philippiana	43	29.66	*Papillicardium minimum*	5
Asperarca nodulosa	23	15.86	*Bathyarca philippiana*	5
Nucula sulcate	20	13.79	*Anatoma tenuisculpta*	5
Astarte sulcate	9	6.21	*Alvania tomentosa*	4
Pseudamussium peslutrae	6	4.14	*Limea crassa*	4
Limopsis angusta	5	3.45	*Abra longicallus*	4
Similipecten similis	3	2.07	*Bittium watsoni*	3
Spirotropis confusa	3	2.07	*Limatula* cf. *subauriculata*	3
Antalis sp.	2	1.38	*Alvania cimicoides*	3
Leptochiton sp.	2	1.38	*Trophonopsis barvicensis*	3
Alvania cimicoides	2	1.38	*Clelandella miliaris*	3
Ennucula aegeensis	2	1.38	*Alvania zetlandica*	3
Heteranomia squamula	2	1.38	*Limopsis aurita*	3
Teretia teres	2	1.38	*Pseudamussium sulcatum*	3
Venus nux	2	1.38	*Astarte sulcata*	3

4.3.3. Relationships between molluscan assemblages and environmental and anthropogenic interference

The parameters retained for the BIOENV analysis were the percentages of gravel (%G), coarse sand (%CS), fine sand (%FS) and organic matter (%OM); the water temperature (T, °C); the dissolved oxygen concentration (O_2, mg l^{-1}); the near-bottom current speed (cm s); the availability of MDACs (quantified as a rank) and the bottom-trawling activity (qualified as a rank).

The BIOENV analysis (Table 4.6) showed which sets of environmental parameters most influenced the molluscan assemblage patterns. For the box-corer and Shipek grab data the set of variables %G - %OM - trawling activity showed the highest correlation ($\rho w=0.63$; $p<0.005$). For the benthic dredge data, the correlations of the set of variables were non-significant ($p>0.05$). Finally, the main environmental parameters determining the spatial distribution of assemblages for the beam-trawl data were the combination T - O2 - %OM - MDAC ($\rho w=0.65$; $p<0.005$).

Table 4.6. BIOENV analysis results based on Spearman rank correlations (ρ_w), showing the set of parameters that best explain the molluscan assemblage patterns of the Gazul mud volcano detected with different sampling methods. BT: beam-trawl; DA: benthic dredge; BC/SK: box-corer and Shipek grab. T: water temperature; O_2: dissolved oxygen concentration; %OM: % of organic matter; MDAC: availability of methane-derived authigenic carbonates; TA: bottom-trawling activity; %G: % of gravel; %CS: % of coarse sand; %FS: % of fine sand.

Sampling method	Number of parameters	Parameters of combination	ρ_w
BT	3	T, O_2, %OM, MDAC	0.65
	4	T, %OM, MDAC	0.64
	5	T, %OM, MDAC, TA	0.64
DA	3	%G, %CS, TA	0.46
	4	%G, %CS, %OM, TA	0.41
	3	%G, %CS, T	0.41
BC/SK	4	%G, %OM, TA	0.63
	3	%G, %CS, %OM, TA	0.62
	4	%G, %FS, O_2, %OM, TA	0.61

4.3.4. New taxa and remarks on some other rare species

Species which represent new or otherwise noteworthy records for the area, and the two which have been considered new to science, are illustrated in Figures 4.3–4.6. New records of species represented by live-taken individuals or shells are marked in Table 4.2 by (*) or (**) and amount to 86, three of them (*Chauvetia balgimae*, *Dentimargo auratus* and *Draculamya porobranchiata*, see Note 1 in Table 4.2) new to Spanish waters altogether. The material examined uses the following abbreviations: live-taken individuals (ind.), shells (sh.), valves (v.) and juvenile (jv.).

Class GASTROPODA

Family RISSOIDAE

Genus *Onoba* H. Adams and A. Adams, 1852

(Type species: *Onoba semicostata* (Montagu, 1803), by monotypy)

Onoba goyoi Utrilla, Urra and Gofas, n. sp. (Fig. 4.3A–E)

LSID: urn:lsid:zoobank.org:act:56940C91-F6BB-413F-AB18-957A794B115F

Holotype (MNCN 15.07/20000): live-taken specimen from INDEMARES/CHICA 0610 BC11.1, 477 m. Paratypes from INDEMARES/CHICA 0610 BC11.1, 4 sh. (MNCN 15.07/20001); BC11.2, 6 sh. (2 jv.) (MNCN 15.07/20002); BC11.3, 4 sh. (jv.) (MNCN 15.07/20003); DA6, 478 m, 4 sh. (MNCN 15.07/20004).

Type locality: Gazul MV, Gulf of Cadiz (36°33.28’N, 06°56.67’W, 477 m).

Description of the holotype. Shell very small, oval-conical, quite solid glossy and smooth except for faint growth lines on the teleoconch, with a moderately high spire and a blunt apex. Protoconch dome-shaped, with about 1¼ whorls, smooth. Teleoconch about 2¾ slightly convex whorls, with shallow suture. Aperture rounded abapically, and rather angular and weakly channelled adapically. Peristome simple, continuous. Outer lip orthocline, not thickened externally, bevelled on its inner side without any denticulations. Colour white. Operculum, periostracum and soft parts unknown. Under high magnification, both the protoconch and the teleoconch appear covered by tiny (about half a micron), sparse and irregularly spaced punctures. Length 2.15 mm, width 1.20 mm.

Remarks. There are several groups of *Onoba* species in European waters: one group from the arctic seas with nine species, detailed in Warén (1996); one group from littoral bottoms with two widely distributed species in the northern Atlantic (*Onoba semicostata* (Montagu, 1803) and *Onoba aculeus* (Gould, 1841)) (Hoenselaar & Moolenbeek 1987, Moolenbeek & Hoenselaar 1987, Rolán 2008); three endemic species from the Strait of Gibraltar (*Onoba josae* Moolenbeek and Hoenselaar, 1987, *Onoba tarifensis* Hoenselaar and Moolenbeek, 1987 and *Onoba guzmani* Hoenselaar and Moolenbeek, 1987); two endemic species from Galicia (*Onoba galaica* Rolán, 2008 and *Onoba breogani* Rolán, 2008); and one endemic species from the Azores Islands (*Onoba moreleti* Dautzenberg, 1889). All these species, with the exception of *O.* guzmani, resemble the type species and share with it the presence of a sculpture of well-defined spiral cordlets. *O. guzmani* has a semi-transparent shell that is easily recognizable by its frosty aspect due to a microsculpture only visible under scanning electron microscope examination, and by a coarse cord surrounding the abapical part of the shell.

Other deep-sea species described for the Mediterranean Sea (revised by Amati & Nofroni 2015) are *Onoba gianninii* (F. Nordsieck, 1974), *Onoba dimassai* Amati and Nofroni, 1991 and *Onoba oliverioi* Smriglio and Mariottini, 2000. These species are very similar to each other and differ from the one from the GoC by their much less thick shell with much more convex whorls on the teleoconch, and a rather opisthocline aperture. *Onoba lincta* (Watson, 1873), described from Madeira, also has a smooth shell surface, but a definite microsculpture consisting of very fine microstriae with minute depressions at the bottom (similar to the microsculpture typical of the genus *Manzonia*) is visible under strong magnification. In the case of the new *Onoba* species, the surface of teleoconch whorls is almost smooth under the optical stereomicroscope, but it displays diminutive pores distributed randomly under scanning electron microscope examination that resemble those of the genus *Porosalvania* Gofas, 2007. However, in the latter, known from North Atlantic seamounts, the general shape and the macrosculpture are quite different, with strong axial ribs and a generally obvious subsutural shoulder.

Etymology. Named after Gregorio ("Goyo") Martín Caballero, of the *Servicios Centrales de Apoyo a la Investigación* at *Universidad de Málaga*, who helped us through many years with the operation of the scanning electron microscope.

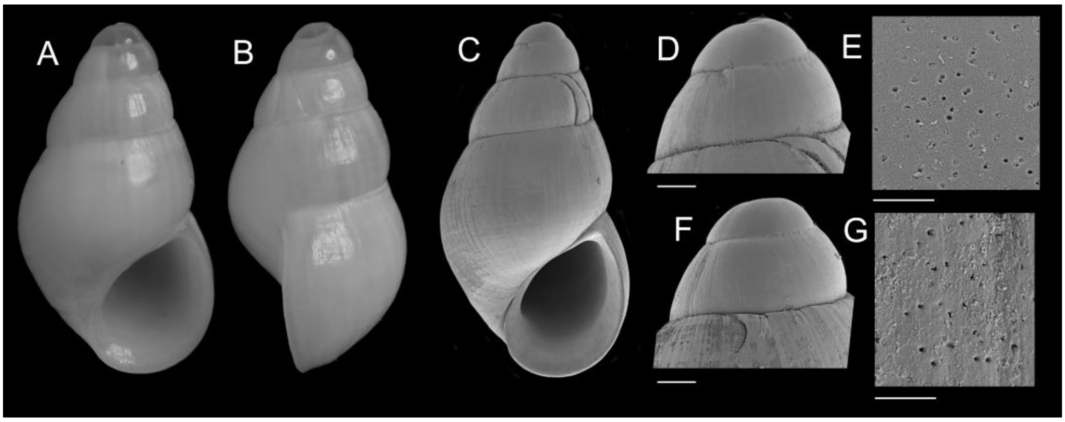


Figure 4.3. *Onoba goyoi*. **A–B**: Holotype, INDEMARES/CHICA 0610 BC11, 477 m depth (2.15 mm). **C**: SEM micrograph of the holotype. **D**: SEM micrograph of the protoconch of the holotype (scale bar 100 µm). **E**: SEM micrograph of the microsculpture of the teleoconch, holotype (scale bar 10 µm). **F**: Protoconch of a paratype (BC11.3) (scale bar 100 µm). **G**: SEM micrograph of the microsculpture, same specimen (scale bar 10 µm). BC: box-corer.

Family EULIMIDAE

Genus *Melanella* Bowdich, 1822

(Type species: *Melanella dufresnii* Bowdich, 1822, by monotypy)

Melanella doederleini (Brusina, 1886) (Fig. 4.4A–D)

Type material: lectotype designated by Bouchet and Warén (1986: 382) BMNH 1979229, from "Porcupine" 1870 st. 29–30; paralectotypes USNM 131144 and BMNH 1885.11.5.2027-8.

Type locality: Gulf of Cadiz, 36°20'N, 06°47'W, 227 fathoms (413 m) and 36°15'N, 06°52'W, 386 fathoms (702 m).

Material examined: INDEMARES/CHICA 0610 DA6, 478 m, 8 sh.; DA7, 495 m, 12 sh.; DA8, 486 m, 5 ind. and 33 sh.; DA10, 390 m, 18 sh.; DA11, 461 m, 1 sh.; BC9.2, 457 m, 1 sh.; BC9.3, 449 m, 1 sh.

Remarks. This is not a new record since the type locality is in the GoC, but it is the first record of additional specimens since the original finding published by Jeffreys (1884) under the name *Eulima stalioi* Brusina, 1869. The latter name is based on a specimen of unknown origin, not European (Campani & Prkić 2009), and Brusina (1886) had recognized Jeffreys' specimens as a different species which he named *Eulima doederleini*. Here we report several specimens of this species, diagnosed by its small (3.3–4 mm) but very solid shell, stout aperture compared with other species in the genus, and tilted, slightly convex early whorls (Bouchet & Warén 1986).

Family BUCCINIDAE

Genus *Chauvetia* Monterosato, 1884

(Type species: *Chauvetia mamillata* (Risso, 1826), by typification of a replaced name)

Chauvetia balgimae Gofas and J.D. Oliver, 2010 (Fig. 4.4E)

Type material: holotype (live-taken specimen 6.3×2.9 mm), MNHN 22874, 4 paratypes MNHN 22875, 5 paratypes MNCN 15.05 / 53587, all from the type locality, BALGIM DR82.

Type locality: off Rabat, Morocco, 33°45'N, 08°32'W, 355 m.

Material examined: The type material; BALGIM DR81 (33°46'N, 08°30'W), 309 m, 1 ind.; INDEMARES/CHICA 0610 DA5, 422 m, 1 sh.; DA7, 495 m: 2 sh.; DA10, 390 m: 11 sh.; SK1.3, 461 m: 4 sh.

Remarks. The shells collected during the INDEMARES/CHICA cruise provide the first record of this species from Spanish waters, already taken into account in the checklist compiled by Gofas et al. (2017). It was also found off Larache by the Moundforce cruise (see Table 4.2) and is found unusually deep (350–500 m) compared with most other species of the genus which are typical of the infralittoral level.

Family MARGINELLIDAE

Genus *Dentimargo* Cossmann, 1899

(Type species: *Dentimargo dentifer* (Lamarck, 1803), by original designation)

Dentimargo auratus Espinosa, Ortea and Moro, 2014 (Fig. 4.4F–G)

Type material: holotype (shell 5.6×2.38 mm) from st. 53, Atlor VII (October-November 1975) of R/V "Cornide de Saavedra", in *Museo de la Naturaleza y el Hombre*, Tenerife, Canary Islands.

Type locality: off Cap Blanc, Western Sahara, 21°00'N, 17°15'W, 20 m.

Material examined: INDEMARES/CHICA 0610 DA6, 478 m, 4 sh.; DA7, 495 m, 1 sh.; DA8, 486 m, 7 sh. (5 jv.), DA10, 390 m, 5 sh. (3 jv.); DA11, 461 m, 3 ind.; BALGIM 1984 DR45, 35°44'N, 06°17'W, 293 m, 1 sh.; DR75, 33°53'N, 08°15'W, 252 m, 2 ind. And 14 sh.; DR79, 33°49'N, 08°24'W, 260 m, 14 sh.; DR81, 33°46'N, 08°30'W, 309 m, 1 ind. and 1 sh.; DR82, 33°45'N, 08°32'W, 355 m, 53 sh.; R/V "Vanneau" 1923-1929, st. 10, 29°54'N, 09°58'W, 110 m, 18 sh. (6 jv.).

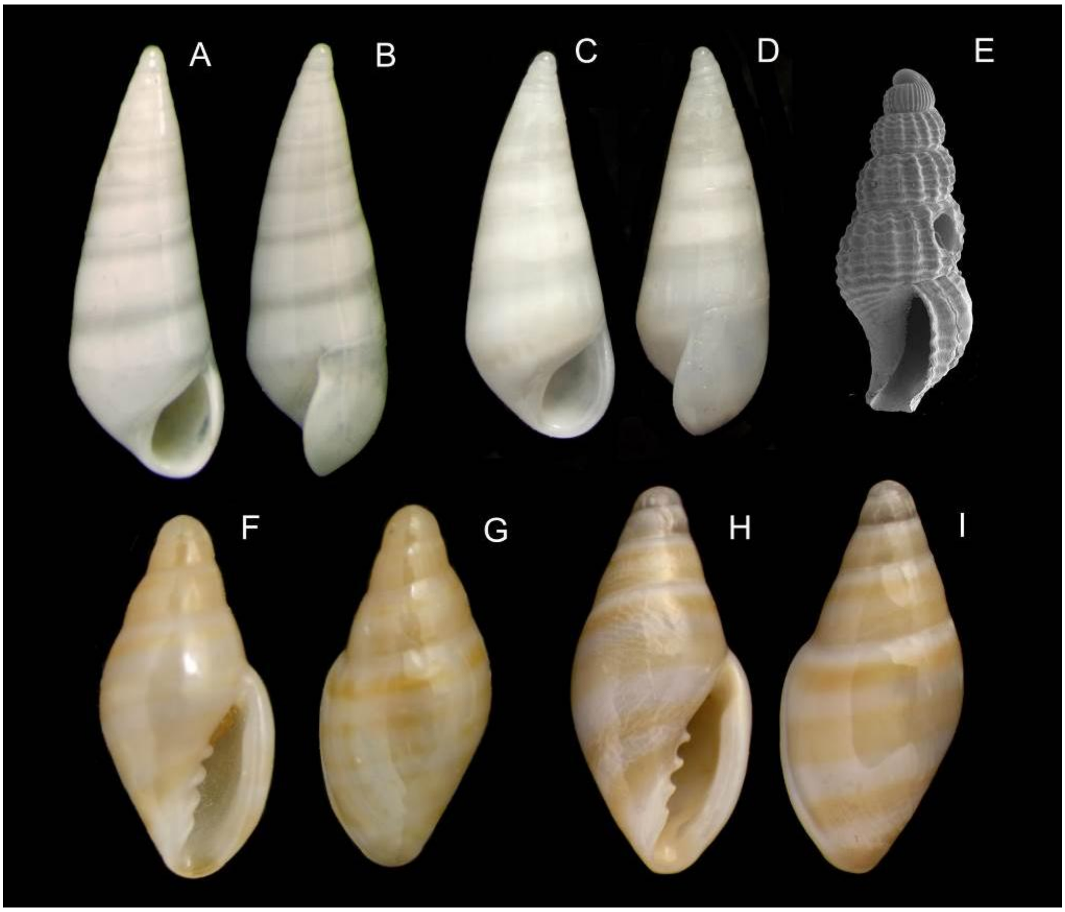


Figure 4.4. **A–B**: *Melanella doederleini* (Brusina, 1886), INDEMARES/CHICA 0610 DA6, 478 m depth (3.7 mm). **C–D**: *M. doederleini*, INDEMARES/CHICA 0610 BC9.2, 457 m depth (3.3 mm). **E**: *Chauvetia balgimae* Gofas and J. D. Oliver, 2010, INDEMARES/CHICA 0610 DA5, 422 m depth (5.3 mm). **F–G**: *Dentimargo auratus* Espinosa, Ortea and Moro, 2014, INDEMARES/CHICA 0610 DA11, 461 m depth (5.7 mm). **H–I**: *D. auratus*, "Vanneau" 1923-1929 st. 10, 110 m depth (6.7 mm). DA: benthic dredge; BC: box-corer.

Remarks. There are five species in the northwestern Atlantic currently assigned to *Dentimargo*: *D. bojadorensis* (Thiele, 1925), *D. hesperia* (Sykes, 1905), *D. auratus* Pérez-Dionis, Espinosa and Ortea, 2014, *D. giovannii* Pérez-Dionis, Espinosa and Ortea, 2014 and *D. crassidens* Ortega and Gofas, 2019. The species reported here was illustrated by Cossignani (2006) from BALGIM sampling st. DR82, off Casablanca, 355 m, with the erroneous name of *Dentimargo bojadorensis*. The most similar species is *D. auratus*, described from shallow waters (20 m) off Ras Nouadhibou (Cap Blanc, Western Sahara), and also confounded with *D. bojadorensis* by Cossignani (2006). *Dentimargo auratus* also has an extremely high spire, but the type specimen differs in having a sharper spire, with the first whorl smaller, and by a constriction around the siphonal canal. Specimens from Gazul are somewhat smaller, with more rounded ends, but similar specimens are found throughout the coast of Morocco and those from southern Morocco (Fig. 4.4H–I) have an intermediate size and shape and occur in an intermediate depth range, for which reason the specimens from Gazul have not been assigned to a distinct species. *Dentimargo giovannii* and *D. crassidens*, both described from bathyal bottoms of the Canary Islands, also have a very high spire but differ in their uniform colour pattern and the outer lip, which is much thinner in the former and thicker with a more pronounced labial tooth in the latter. *Dentimargo hesperia*, described from deep water off southwestern Portugal, has a subtle labial tooth and a very wide aperture that differs clearly from that of other *Dentimargo* species existing in the area. Finally, *D. bojadorensis* also has a relatively short spire, but it is smaller (6.6 mm) and its aperture is much narrower than in *D. hesperia*, and with a prominent labial tooth.

This is the first record of this species in both Spanish waters (the material from the Gazul MV) and Moroccan waters (the unpublished localities from "Vanneau" 1923 and BALGIM 1984).

Class Bivalvia

Family LUCINIDAE

Genus *Lucinoma* Dall, 1901

(Type species: *Lucina filosa* Stimpson, 1851, by original designation)

Lucinoma asapheus P.G. Oliver, Rodrigues and Cunha, 2011 (Fig. 4.5A–B)

Type material: holotype (live-taken specimen 33.3 mm) from cruise TTR 15 of R/V "Akademik Logatchev", st. AT-569GR, box-corer, 25 July 2005, in National Museum of Wales, NMWZ.2010.4.5.

Type locality: off Larache, NW Morocco, Mercator MV. 35°17.917′N, 06°38.717′W, 358 m.

Material examined: INDEMARES/CHICA 0610 BC6.3, 369 m, 1 sh.

Remarks. This, along with the two species of Thyasira, is one of the very few species with a chemosymbiotic mode of life collected on the Gazul MV. It was represented by only one bivalve shell. More material was collected on Albolote (only shells), Anastasya (live specimens and shells) and Almazan MVs (only shells) (Rueda et al. 2012b).

Family LASAEIDAE

Genus *Draculamya* P. G. Oliver and Lützen, 2011

(Type species: *Draculamya porobranchiata* P. G. Oliver and Lützen, 2011, by original designation)

Draculamya porobranchiata P. G. Oliver and Lützen, 2011 (Fig. 4.5C–F)

Type material: holotype (shell 1.45 mm), RRS Challenger, IOS Cruise 514, st. 51420#4, 2 April 1982. in National Museum of Wales, Cardiff, NMWZ.2011.001.1.

Type locality: Porcupine Seabight, SW of Ireland, 51°37.9′N, 12°59.5′W to 51°37.5′N, 12°59.6′W, 1279–1287 m.

Material examined: INDEMARES/CHICA 0610 BC8.3, 427 m, 3 v.; SK1.3, 461 m, 1 v.

Remarks*.* This small bivalve was described from 1279–1287 m depth in the North Atlantic, and shells collected on the Gazul MV agree with the original description, particularly with the unusually marked growth stages on the valves. Shells from the Alboran platform and from Catalonia figured in Peñas et al. (2006: 117, as *Kelliopsis* sp.) are apparently this species. The Mediterranean and GoC localities are much shallower than the type locality but in both cases the species was reported to occur together with siliceous sponges. This is the first formal record for Spanish waters.

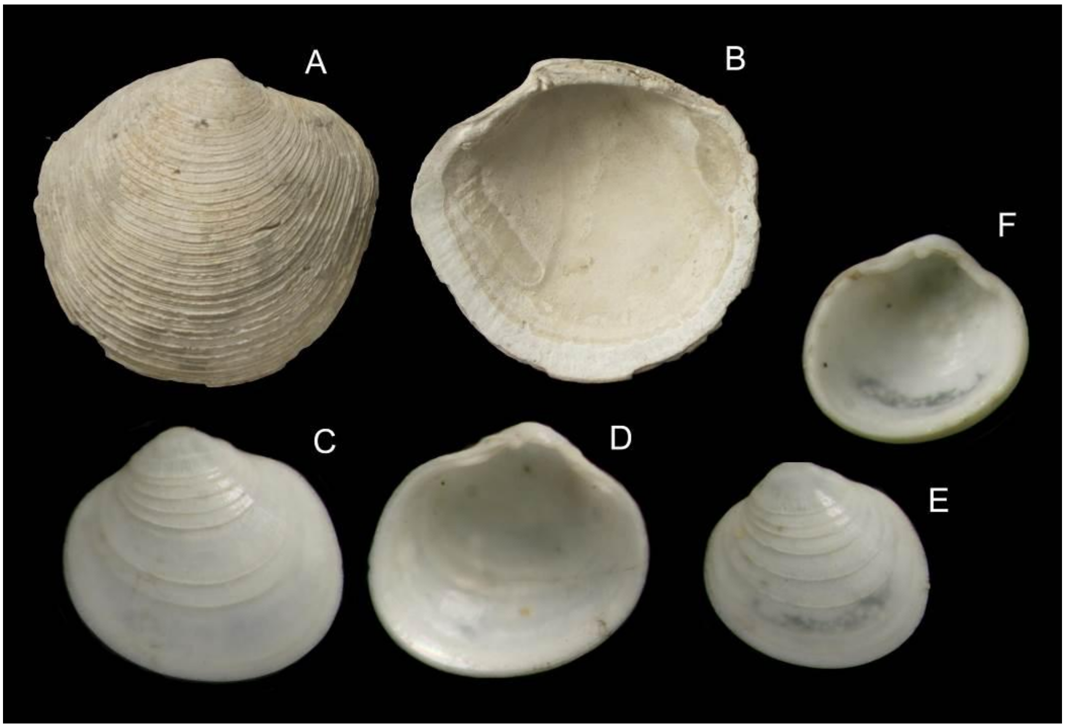


Figure 4.5. **A–B**: *Lucinoma asapheus* P.G. Oliver, Rodrigues and Cunha, 2011, INDEMARES/CHICA 0610 BC6.3, 369 m depth (37.0 mm). **C–D**: *Draculamya porobranchiata* P.G. Oliver and Lützen, 2011, INDEMARES/CHICA 0610 BC8.3, 427 m depth (1.2 mm). **E–F**: *D. porobranchiata* BC8.3 (1.0 mm), see Note 1 in Table 4.2. BC: box-corer.

Family CUSPIDARIIDAE

Genus *Myonera* Dall and E. A. Smith, 1886

(Type species: *Myonera paucistriata* Dall, 1886, by original designation)

Myonera atlasiana Utrilla, Rueda and Salas, n. sp. (Fig. 4.6A–G)

LSID: urn:lsid:zoobank.org:act:7E881971-2F87-4C10-9B1E-5E5459C7390D

Holotype (MNCN 15.07/20005): live-taken specimen from INDEMARES/CHICA 0610 DA10, 390 m. Paratypes from ATLAS/MEDWAVES 0916 BC2_MED, 450 m, 1 ind. (MNCN 15.07/20006); INDEMARES/CHICA 0610 SK1.3, 461 m, 1 v. (MNCN 15.07/20007).

Type locality: Gazul MV, Gulf of Cadiz (36°33.57'N, 06°55.95'W, 390 m, to 36°33.43'N, 06°56.02'W, 410 m).

Description of the holotype. Shell medium sized, moderately inflated, robust but translucent, equivalve, inequilateral. Umbo slightly anterior to the midline. Outline ovate subtriangular, anterior margin curved, ventral moderately curved, posterior dorsal margin nearly right. Rostrum short, about one-third of the shell length, separated from the rest of the shell by a furrow, with a keel separating the rostrum from the furrow and another weak keel on the furrow; several short and weak periostracal radial ridges on the rostrum. Sculpture of irregular commarginal ridges. Exterior and interior of the shell white. Periostracum thin, minutely wrinkled, pale brown in colour. Smooth inner margin. External and internal ligaments present. External ligament extended at both sides from the umbo, being longer at the posterior side. Internal ligament on a large, concave chondrophore located beneath beaks. Hinge without teeth. Pallial line visible, with a moderately curved pallial sinus. Length 19.0 mm, height 11.8 mm.

Remarks. Species belonging to Cuspidariidae are easily recognizable by the long projecting posterior spout with a terminal gape that hosts siphons. Among them, *Myonera* species are characterized by lacking teeth in both valves (Allen & Morgan 1981), whereas other members of the family have lateral teeth at least in one valve. Species belonging to the genera *Myonera* are divided into two morphological groups. The first one, which includes the type species *Myonera paucistriata* Dall, 1886, as well as *M. acutecarinata* (Dautzenberg and H. Fischer, 1906) and *M. angularis* (Jeffreys, 1876), are characterized by a triangular shape with a short posterior rostrum, and have few but strong keel-like radial ribs in the posterior part and a commarginal sculpture parallel to the growing edge of the shell in the anterior part. The second group of species, which would include the new species of the GoC, as well as *M. sulcifera* (Jeffreys, 1882) (Fig. 4.6H–I), *M. pretiosa* Verrill and Bush, 1898, *M. alleni* Poutiers, 1995 (Fig. 4.6J) and *M. canariensis* (De Boer, 1985), has a profile with a longer posterior rostrum and an essentially commarginal sculpture, with the exception of one or two weak keels delimiting the rostrum. This new species most resembles *M. sulcifera*, from which it differs in its much larger size (more than double), its shorter and more triangular rostrum, a more curved contour and the blunt and poorly defined keels instead of a clearly marked one along the rostrum. *Myonera alleni*, *M. pretiosa* and *M. canariensis* have more marked commarginal ribs that are widely and regularly spaced, a longer rostrum and a more marked keel on the rostrum.

Etymology. The species name “atlasiana” has been dedicated to the EU project ATLAS, which made possible some sampling and exploration on the Gazul MV during the MEDWAVES expedition.

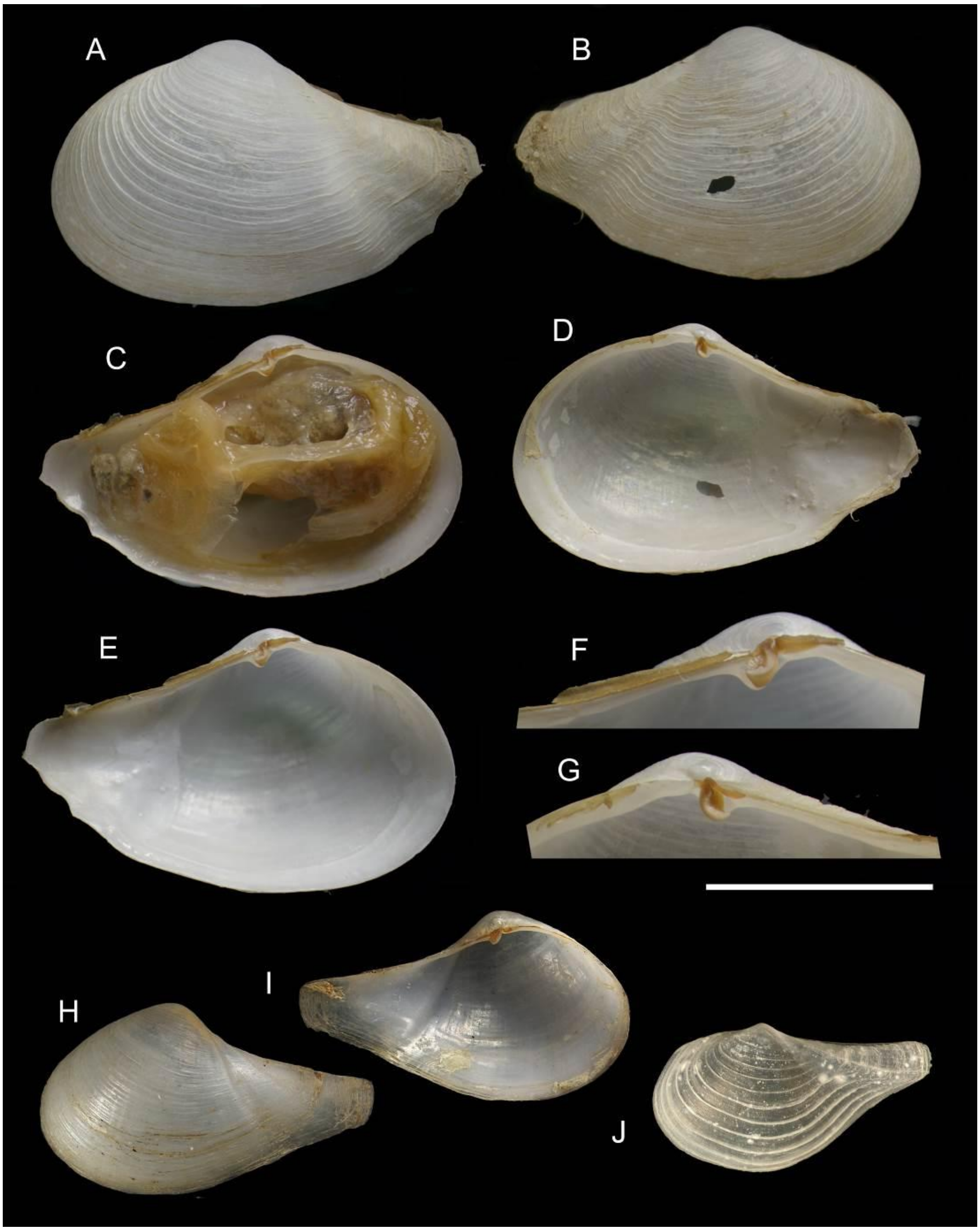


Figure 4.6. **A–G**: Holotype of *Myonera atlasiana* n. sp., INDEMARES/CHICA 0610 DA10, 390 m depth (19.0 mm). **A–B**: External views of the valves. **C**: Internal view of the left valve and the body of the bivalve. **D**: Internal view of the left valve. **E**: Internal view of the right valve. **F–G**: Detail of the hinge (scale bar 5 mm). **H–I**: *Myonera sulcifera* (Jeffreys, 1882), external and internal view of left valve, NHM.1888.11.5.1037; "Porcupine 1869", S of Ireland, st. 40, 49°01'N, 12°05'W, 517 m depth (9.2 mm). **J**: *Myonera alleni* Poutiers, 1995, Porcupine abyssal plain, 3900–3950 m depth (3.6 mm; photos H–J courtesy of National Museum of Wales). DA: benthic dredge.

4.4. Discussion

This is the first detailed work on the malacofauna associated with a MV and its adjacent areas within the European context. In the present study, a total of 232 molluscan species has been found, increasing the faunal list of molluscs known for the Spanish part of the GoC with 86 species that had not been cited previously (some of them preliminary reported in Gofas et al. 2017, see Table 4.2). This is a significant number of species when compared with the total of 766 species recorded so far in the GoC, representing one-third of the species recorded here and highlighting the important gap of knowledge. This amount also included two new species (*Onoba goyoi* and *Myonera atlasiana*) and three new records for Spanish waters (*Chauvetia balgimae*, *Dentimargo auratus* and *Draculamya porobranchiata*). Prior to the INDEMARES expedition, the deep-water fauna of the Spanish part of the GoC was only sampled by 5 stations of R/V “Porcupine” in 1871, 4 stations of R/V “Talisman” in 1883, and 13 stations of the BALGIM cruise in 1984 (against 34 in Portuguese waters and 45 in Moroccan waters for the latter). Most of these new records were predictable, being of species already known from the better-known Alboran Sea and/or Portugal, Morocco, or the Bay of Biscay, and 73 out of 83 species recorded as new for the GoC were already known from the neighbouring Alboran Sea (Gofas et al. 2017). The number of new records is far larger among gastropods (80 species) than bivalves (6 species), but this reflects that the bivalves from the BALGIM expedition have been studied (Salas 1996) whereas the gastropods have not.

Molluscs are a good indicator for the biodiversity assessment in a particular area (Reyers et al. 2000, Mellin et al. 2011), so a species-rich area for molluscs will be indicative of a high-level of biodiversity for other taxa (Reyers et al. 2000), and this would be the case of the Gazul MV (Díaz del Río et al. 2014, Rueda et al. 2016, Sitjà et al. 2019). This high biodiversity of molluscs is striking, taking into account the small size of the study area (less than 5 km^2) and its location in the bathyal zone on the pathway of the MOW. These species richness values are higher than that found by Cunha et al. (2013) from seven MVs of the southern part of the GoC, where they identified 56 species of molluscs from a total of 366 macrofaunal species, but more in agreement with those values found in a single box-core off NW Morocco (134 species of which 67 are shared with this study; personal communication from F. Slieker). The species richness of Gazul is also much higher than those 18 species of molluscs found by Olu-Le Roy et al. (2004) in five MVs from the eastern Mediterranean or by Ritt et al. (2012) in the Mediterranean Ridge area (Napoli and Amsterdam MVs), where they found a total of 19 taxa of molluscs but only 10 to species level. Comparable species richness values have been observed in other deep areas of the southern Iberian Peninsula, such as the Djibouti bank (Gofas et al. 2014b) and the Alboran Island platform (Peñas et al. 2006), both in the Alboran Sea, which have high species richness compared with other studied bathyal zones of the Mediterranean Sea (Negri & Corselli 2016) or the North Atlantic Ocean (Bergquist et al. 2003, Henry & Roberts 2007). Furthermore, additional species are known to occur on the Gazul MV, such as those captured by the fishing fleet on adjacent bottoms (e.g. the cephalopods *Illex coindetii* (Vérany, 1839), *Neorossia caroli* (Joubin, 1902), *Rondeletiola minor* (Naef, 1912), *Todaropsis eblanae* (Ball, 1841)), as well as species revealed in images taken by remote operated vehicles (ROV) (e.g. *Charonia lampas* (Linnaeus, 1758); Rueda, personal comment).

Less than half of the species collected on the Gazul MV belong to species listed in the World Register of Deep-Sea Species (Glover et al. 2020), i.e. occurring normally below 500 m depth, but this category includes the most abundant ones (*Bathyarca philippiana* and *Asperarca nodulosa*), which account for over 70% of all live-collected specimens. However, most of the other species typically occur on the shelf edge or uppermost slope, such as *Astarte sulcata*, *Papillicardium minimum*, *Dacrydium hyalinum*, *Pseudamussium sulcatum*, *Heteranomia squamula*. This is in good agreement with the depth range (392–495 m) sampled. Only seven species in the thanatocoenosis (e.g. *Turritella communis*, *Spisula subtruncata*) belong to nearshore assemblages.

The high number of species found in the analysed samples could be linked to several factors: (1) the combination of several types of sampling gears, which obtain species from different ecosystemic compartments such as the box-corer or the Shipek grab for capturing endofaunal micro molluscs, the benthic dredge targeting infaunal and epibenthic micro and macrofaunal species, and the beam-trawl collecting mainly epibenthic macrofauna and some demersal components such as cephalopods (Templado et al. 2010); (2) the inclusion of a detailed analysis of the thanatocoenosis (Albano & Sabelli 2011, Weber & Zuschin 2013) that allows the detection of species present in the area that are difficult to capture alive (species associated with a specific microhabitat or that occur at low density in their natural environment) or that have a restricted habitat, being specific hosts of macro-organisms such as corals (e.g. *Iphitus tuberatus*) and sponges (e.g. *Fissurellidae* and the genus *Hanleya*); (3) the high habitat heterogeneity detected on the Gazul MV, including some types of sedimentary habitats and others with a great complexity, which increases the biodiversity of habitat-forming invertebrates (e.g. cold-water coral or sponge aggregations), some of which serve as food source for some molluscs groups (e.g. *Epitoniidae*, *Fissurellidae*), and of associated fauna such as echinoderms or annelids, which host parasites (*Eulimidae*, *Pyramidellidae*); (4) the geographic location of the Gazul MV in the GoC, where fauna from different biogeographic areas merges, with typical species of the North Atlantic, the Mediterranean and subtropical western Africa concurring; and (5) the fact that the study area is located close to the boundary (depths of 392–495 m) between the shelf and bathyal zones. Indeed, only about half of the recorded species belong to the deep-sea fauna (Glover et al. 2020), and the others are species reaching the lower part of their depth range.

Many molluscs found on the Gazul MV are associated with bathyal hard substrates and/or macro-organisms that can reach high abundance on such substrates (e.g. corals, gorgonians and sponges). These hard substrates are composed of MDACs, which are unearthed from the sediment and exhumed by the action of bottom currents (Díaz-del-Río et al. 2012) and are an indirect result of the past seepage activity. The occurrence of seafloor exhumed MDACs favours the settlement of sessile invertebrates whose feeding is favoured by the continuous supply of nutrients due to the high incidence of currents in some parts of the MV (Hovland 2008). In turn, these colonies increase the complexity of the bottoms by providing substrate and shelter to many other species (Henry & Roberts 2007), including molluscs associated with them, whose feeding is more restrictive as it is based on cnidarians (e.g. Epitoniidae), sponges (e.g. Fissurellidae) or echinoderms (e.g. Eulimidae). All this causes a greater difference between communities of the MV compared with adjacent bottoms or other bathyal bottoms, as has been detected for megafauna in this and other areas (Vanreusel et al. 2009). This also explains the differences found between the malacofauna associated with the MV edifice, and those of the erosive depression and of the adjacent bottoms, with the highest Shannon-Wiener diversity values and evenness observed on the MV edifice (Table 4.4). In this respect, the Gazul MV functions as a small seamount, and this may explain the large proportion of species shared with the Djibouti Bank in the Alboran Sea (Gofas et al. 2014b), where 156 species of molluscs were identified from only one haul collected with beam-trawl at 349 to 365 m depth, and more than half of these species (86 spp.) are shared with the Gazul MV.

The finding of shell remains of the bivalve *Lucinoma asapheus* on the summit, the low density of siboglinids compared with other MVs (Rueda et al. 2012b) and the high presence of MDACs (Palomino et al. 2016) could indicate that the Gazul MV currently has a low fluid emission (León et al. 2007). Moreover, this bivalve is one of the key indicators of a past seepage activity and it is usually present on active MVs such as the Anastasya MV in the northern GoC and the Mercator MV in the El Arraiche Field of the southern GoC (Oliver et al. 2011, Rueda et al. 2012b). This would increase the biodiversity considering the absence of anoxic conditions, the exhumation of MDACs and the active hydrodynamism of the area, which would promote the appearance of complex habitats, some of them vulnerable, such as cold-water corals, which have a high species richness and that have not yet been affected by the low bottom-trawling activity detected in the area (Palomino et al. 2016, Rueda et al. 2016, González-García et al. 2020a).

The number of species in the thanatocoenosis (221) is 2.43 times the number of live-collected species, which is in good agreement with the 2 to 3 times stated as "typical" by Kidwell (2001). The bulk of the thanatocoenosis was found to reflect the biocenosis quite faithfully, since only three of the shell-bearing species (an unidentified Eulimid and the bivalves *Spinosipella acuticostata* and *Coralliophaga lithophagella*) found alive were not represented in the thanatocoenosis. However, several species of the present study were found only as old shells, and without representation of live specimens. Some of these species are currently restricted to areas located at higher latitudes of the Atlantic Ocean, and the shells found in the GoC would then be remnants of past glacial periods (e.g. *Nuculana pernula*, *Chlamys islandica*) when there was a decrease in water temperature and sea level (Malatesta & Zarlenga 1986, Raffi 1986). The shallow-water species (e.g. *Turritella communis*, *Spisula subtruncata*) could also be remnants of periods when the Gazul MV was located at a shallower depth during the lowstand of the sea level, and transport may also have occurred from the shelf to the slope.

Finally, several environmental parameters analysed in this study were identified as playing a significant role in species and assemblage distribution. For infaunal species (mostly collected with the benthic dredge, box-corer and Shipek grab), it was found that the sediment texture, the percentage of organic matter in sediment and the bottom-trawling activity seem to be the main environmental and anthropogenic parameters linked to the distribution of the molluscan assemblages in the area. On the other hand, for epibenthic and demersal megafauna (mostly collected with the beam-trawl), the environmental parameters influencing species distribution were seawater temperature, the percentage of organic matter in sediment and the presence of MDACs. These results indicate that the type and nature of soft bottoms are important factors regarding the distribution of species, with many aspects of sediments to which animals (in this case molluscs) may respond, including sediment texture (some species are characteristically associated with a given sedimentary habitat), organic content of bottom sediments (a dominant food source for deposit feeders and, indirectly for suspension feeders) and sediment stability (some organisms or biological structures produce sediment-stabilizing effects that allow other animals to colonize the substrate), among others (Buchanan 1963, Gray et al. 1990, Snelgrove & Butman 1994 and references therein). In addition, the presence of hard structures such as MDACs and coral-rubble increases the habitat complexity of the MV edifice when compared with the surrounding bottoms, and represents another major factor influencing the distribution of the epibenthic mollusc assemblages in the area, as observed for megafaunal communities associated with MVs (Cunha et al. 2013, Palomino et al. 2016, Rueda et al. 2016), as well as those inhabiting coral mounds and seamounts (Henry & Roberts 2007, Danovaro et al. 2010). Moreover, the identification of seawater temperature as a key variable influencing the distribution of epibenthic species must be linked to the interaction between bottom currents and the topography of the Gazul MV (it is a conical edifice that reaches 100 m above the seafloor of the adjacent bottoms), which generates a locally high hydrodynamism that favours the exhumation of MDACs and provides a continuous availability of organic particles to filter and suspension feeders. Finally, fishing activity, with bottom-trawling as the main modality in this area, acts as a pressure that may affect benthic communities as to the epifauna (Mangano et al. 2013), and particularly molluscan species, linked to sessile invertebrates. All this calls for appropriate actions to restrict bottom-trawling in this area and to allow the conservation of this unique and natural heritage within the GoC.

Chapter v

Late Pleistocene boreal molluscs in the Gulf of Cadiz: Past and current oceanographic implications

Moluscos boreales del Pleistoceno tardío en el golfo de Cádiz: implicaciones oceanográficas en el pasado y en la actualidad

This chapter is based on:
Este capítulo se basa en:

Urra J., Utrilla O., Gofas S., Valencia V.A., Farias C., González-García E., López-González N., Fernández-Salas L.M., Rueda J.L. 2023. Late Pleistocene boreal molluscs in the Gulf of Cadiz: Past and current oceanographic implications. Quat. Sci. Rev. 313, 108196.
https://doi.org/10.1016/j.quascirev.2023.108196

5. LATE PLEISTOCENE BOREAL MOLLUSCS IN THE GULF OF CADIZ: PAST AND CURRENT OCEANOGRAPHIC IMPLICATIONS

Abstract

Remains of molluscs were collected from the seafloor on the north-eastern margin of the Gulf of Cadiz, between 300 and 1000 m water depth, using different sampling methods (e.g. dredging, trawling and box-coring), during several deep-sea expeditions. Samples contained a suite of species which nowadays mostly occur northwards of the English Channel, together with other widespread species. Species now locally extinct in the Gulf of Cadiz and restricted to northern latitudes, which unequivocally indicate a faunal shift, include the gastropods *Buccinum undatum*, *Colus gracilis*, *Liomesus ovum* and *Neptunea antiqua*, the bivalves *Arctica islandica*, *Chlamys islandica*, *Modiolus modiolus*, *Mya truncata* and *Nuculana pernula* and the scaphopod *Antalis entalis*. These species represent “Boreal Guests” of marked palaeoclimatic significance, some of which are reported for the first time in the Gulf of Cadiz. The boreal species collected were mostly large (>5 cm) whereas smaller boreal species were extremely scarce, probably winnowed away by strong bottom currents. The pteropod *Limacina retroversa*, at present restricted to water masses northwards of the Iberian Peninsula but widespread in Mediterranean sediments of the last glaciation, was also recorded. Accelerator mass spectrometry (AMS) ^{14}C dates obtained from nine specimens of molluscs ranged between., thus confirming their attribution to a last glacial assemblage. The abundance of these molluscan remains in the present Mediterranean Outflow Water pathway could be explained if this outflow was reduced in intensity or more likely shifted to a deeper level, leaving the upper slope in contact with suitable Atlantic intermediate waters. The findings of Boreal Guests in the Gulf of Cadiz document the continuity of the faunal shift which is well-known in the Mediterranean basin. Species still living in the Gulf of Cadiz and the Alboran Sea nevertheless account for 84.6% of specimens among the larger species.

Resumen

Se recolectaron restos de moluscos del fondo marino del margen noreste del golfo de Cádiz, entre los 300 y 1.000 m de profundidad, utilizando diferentes métodos de muestreo (p. ej., dragados, arrastres y box-corer), durante varias expediciones en aguas profundas. Las muestras contuvieron un conjunto de especies que hoy en día se encuentran principalmente más al norte del canal de la Mancha, junto con otras especies de amplia distribución. Entre las especies localmente extintas ahora en el golfo de Cádiz y restringidas a latitudes septentrionales, lo que indica inequívocamente un cambio en la fauna, se incluyen los gasterópodos *Buccinum undatum*, *Colus gracilis*, *Liomesus ovum* y *Neptunea antiqua*, los bivalvos *Arctica islandica*, *Chlamys islandica*, *Modiolus modiolus*, *Mya truncata* y *Nuculana pernula* y el escafópodo *Antalis entalis*. Estas especies son “huéspedes boreales” de marcada importancia paleoclimática, algunas de las cuales se citan por primera vez en el golfo de Cádiz. La mayoría de las especies boreales recolectadas fueron de gran tamaño (>5 cm), mientras que las más pequeñas fueron extremadamente escasas, probablemente arrastradas por las fuertes corrientes de fondo. También se registró el pterópodo *Limacina retroversa*, actualmente restringido a masas de agua al norte de la Península Ibérica, pero ampliamente distribuido en los sedimentos mediterráneos de la última glaciación. Las dataciones con ^{14}C de nueve especímenes de moluscos, obtenidas por espectrometría de masas con acelerador (AMS), oscilaron entre los 26.100 y 14.600 años

antes del presente, lo que confirma que pertenecieron a una última comunidad glacial. La abundancia de estos restos de moluscos en la actual vía de agua de salida mediterránea podría explicarse si su flujo se redujo en intensidad o, más probablemente, si se desplazó a un nivel más profundo, dejando el talud superior en contacto con aguas intermedias atlánticas adecuadas. Los hallazgos de huéspedes boreales en el golfo de Cádiz documentan la continuidad del cambio faunístico bien conocido para la cuenca mediterránea. No obstante, las especies que aún viven en el golfo de Cádiz y el mar de Alborán representan el 84,6% de los ejemplares de las especies de mayor tamaño.

5.1. Introduction

5.1.1. Quaternary climate and sea-level setting

The Pleistocene (2.6 Ma-11.7 kyr before present [B.P.]) is characterized by significant climatic oscillations on a time scale in the order of 100 kyr, with expansions of ice sheets and important sea level drops caused by cooling events during stadial periods, alternating with interstadial episodes with raised sea level (Siddall et al. 2006, Denton et al. 2010, Elderfield et al. 2012, Sierro et al. 2020). Glaciations and deglaciations greatly influenced the structure of ecosystems, leading to large scale shifts in latitudinal species distributional ranges, among other effects (Raffi 1986, Taviani et al. 1991).

The last glacial period of the Pleistocene ends with the Marine Isotope Stage 2 (Railsback et al. 2015) that was marked by the Last Glacial Maximum (LGM, 26.5 to 19 kyr B.P., Clark et al. 2009, Martrat et al. 2014) when the Northern Hemisphere ice sheets reached their maximum volume. Global sea level then dropped to -134 m (Lambeck et al. 2014). Nevertheless the LGM was not the coldest episode in the Gulf of Cadiz (GoC); it was followed by a complex period of deglaciation (Termination 1), beginning with a colder interval (18-14.6 kyr B.P., Barker et al. 2009, Denton et al. 2010) during which meltwater and drifting ice was released from the Northern Hemisphere ice sheets. This interval, generally referred to as Heinrich Stadial 1 (HS1), comprises two phases which are registered in North Atlantic marine sediments but not in the Greenland ice cores (Rasmussen et al. 2006). The earliest phase involved discharge of meltwater from European ice sheets into the North Atlantic (reaching a maximum between 18.3 and 17 kyr B.P., Toucanne et al. 2009, Naughton et al. 2023a). The second episode lasted until 14.6 kyr B.P. (Barker et al. 2009, Denton et al. 2010, Naughton et al. 2023a) and staged a massive discharge of ice-rafted debris from the Laurentide ice sheet into the North Atlantic (the Heinrich Event 1 in a strict sense, Andrews & Voelker 2018) with two peaks estimated (Hodell et al. 2017) at ca. 16.1 kyr and ca. 15 kyr B.P. In the temperate Northeast Atlantic near the Iberian Peninsula, a substantial drop in sea surface temperature preceded the peak of ice-rafting (Denton et al. 2010) and was accompanied by an abrupt expansion of the polar planktonic foraminifer *Neogloboquadrina pachyderma* starting around 18 kyr B.P. (Voelker & de Abreu 2011, Ducassou et al. 2018).

This stadial episode was followed by an abrupt warming event, detected about 14.7 kyr B.P. from the Greenland ice cores (Rasmussen et al. 2006) and initiating the Bølling-Allerød warm interval (Naughton et al. 2023b). A rapid return to near-glacial conditions occurred during the Younger Dryas event ca. 12.8-11.5 kyr B.P. (Rasmussen et al. 2006, Barker et al. 2009, Naughton et al. 2023c) which was the last phase of the glacial period.

Several authors have suggested a link between these climatic changes and the global thermohaline circulation, where surface circulation and heat flow towards high latitudes is motioned by the sinking of surface water and formation of the southward flowing North Atlantic Deep Water (NADW). McManus et al. (2004) found that the Atlantic Meridional Overturning Circulation (AMOC) started weakening prior to Heinrich Events in the North Atlantic region, and remained low until the rapid accelerations concurrent with the two strongest regional warming events during deglaciation. The slowdown of the AMOC and the coincident rise in Antarctic temperature have been highlighted as a possible driving factor for strong subsurface warming in high latitudes of the North Atlantic, resulting in rapid melting of the Hudson Strait and Labrador ice shelves (Álvarez-Solas et al. 2011, Deschamps et al. 2012, Max et al. 2022).

5.1.2. Benthic molluscs as indicators of environmental conditions

The distribution of benthic species is controlled by a combination of major environmental drivers including seawater temperature, salinity and productivity, as well as other essential predictors such as substrate type, water depth, and bottom currents among others (Lalli & Parsons 1997, Reiss et al. 2015). Molluscs are a main component of marine benthic macroinvertebrate assemblages, and provide an accurate archive of palaeoclimatic information. Belanger et al. (2012) found that bivalve distribution patterns can be predicted accurately by very few readily available oceanographic variables (temperature, salinity, productivity), with temperature alone predicting 53–99% of the present-day distribution along coastlines. Moreover, temperature is a crucial variable modulating the distribution of species, because it constrains the reproductive phases of adults and the survival of larval stages (Hall 1964, Raffi 1986). Therefore, molluscs have been successfully used for past climate reconstructions (Raffi 1986, Taviani et al. 1991, Roy et al. 1995, Garilli 2011, Aguirre et al. 2019, Melo et al. 2022 among others).

The arrival of species from boreal areas of the North East Atlantic to the Mediterranean through the Strait of Gibraltar was a consequence of the onset of a high-seasonality climatic regime associated with significant colder winters, diagnosed by a pronounced drop in the abundance of the tropical planktonic foraminifer *Globigerinoides ruber* (d'Orbigny, 1839) in the Mediterranean (Raffi 1986, Thunell et al. 1991). Such species were called "boreal guests" (hereafter BGs) or "northern guests", a term first used for molluscs (Suess 1883–1888, re-definition by Ruggieri 1977 and Malatesta & Zarlenga 1986) and then extended to other taxa including benthic foraminifers and ostracods (Faranda & Gliozzi 2011), bryozoans, serpulid polychaetes and calcareous algae (Sanfilippo 1998, Di Geronimo et al. 2000) as well as cold-water corals (Wienberg et al. 2010). The southward migration of BGs (mostly molluscs) into the Mediterranean basin during the last glaciation is well documented by many authors from marine thanatocoenoses on the outer continental shelf in the Mediterranean Sea: Cap de Creus area, north-eastern Spain (Mars 1958, Martinell & Julià 1973, Domènech & Martinell 1982), the Gulf of Lion (Froget et al. 1972), the Adriatic Sea (Colantoni et al. 1975, Taviani 1978, Curzi et al. 1984) and elsewhere (Delibrias & Taviani 1985), among others. The group of BGs found to occur at that time in the Mediterranean Sea includes, among other species, the gastropods *Puncturella noachina*, *Buccinum humphreysianum* and *Buccinum undatum*, and the bivalves *Modiolus modiolus*, *Pseudamussium peslutrae* (formerly *Pseudamussium septemradiatum*), *Chlamys islandica*, *Acesta excavata* and *Arctica islandica*. Previous migrations of BGs have occurred throughout the Pleistocene, with at least three successive pulses that correspond partly to the Santernian, Emilian and Sicilian substages of the Calabrian (Early Pleistocene, 1.8–0.77 Ma B.P.) (Ruggieri et al. 1984, Malatesta & Zarlenga 1986, Raffi 1986).

5.1.3. The lack of molluscan records in the Gulf of Cadiz

The large amount of data related to the occurrence of BGs in the Mediterranean basin during the last glaciation contrasts with the limited information existing for the GoC, mostly in the vicinity of the Strait of Gibraltar (Taviani et al. 1991, based on material collected by the French expedition BALGIM in 1984). Yet, the GoC had to be colonized as a premise for crossing the Strait of Gibraltar (Bouchet & Taviani 1989 and references therein). Reports of cold-water species in this part of the North East Atlantic during the late Quaternary mostly focused on corals, with fossil reef-forming scleractinians widely distributed within the GoC and mainly associated with mud volcanoes, diapiric ridges, steep fault escarpments and coral mounds (Taviani et al. 1991, Wienberg et al. 2009, 2010), and to a lesser extent on molluscs (Taviani et al. 1991). Several gastropods and bivalves, some of which belonging to species still living in the area, were recorded in cores from IODP Expedition 339 in the GoC (sites U1386 to U1390, Stow et al. 2013). However these records are much older (50 to 800 kyr B.P.) than the time frame considered in this work, and none of them can be suspected as a BGs.

5.1.4. Aim of this paper

The purpose of the present study is (1) to document extensive new records of mollusc BGs on the Spanish margin of the GoC, with the first record for some of them in the area, and (2) to discuss their relationships with the late Pleistocene palaeoceanographic conditions of the GoC, a key area connecting the Mediterranean with the rest of the NE Atlantic Ocean.

5.2. Regional setting

5.2.1. Situation

The GoC is located in the North East Atlantic Ocean, and is connected with the Mediterranean Sea through the Strait of Gibraltar (Fig. 5.1). The shallowest part of the connection is situated at Camarinal sill, in the western sector of the Strait, with 284 m depth in its shallowest threshold (Luján et al. 2011). It is bordered by the south-western margin of the Iberian Peninsula (continental shelf ranging from 15 to 50 km width) and the north-western Moroccan margin (continental shelf of ca. 60 km width), with depths down to 4000 m depth in the abyssal plain to the west (Fig. 5.1).

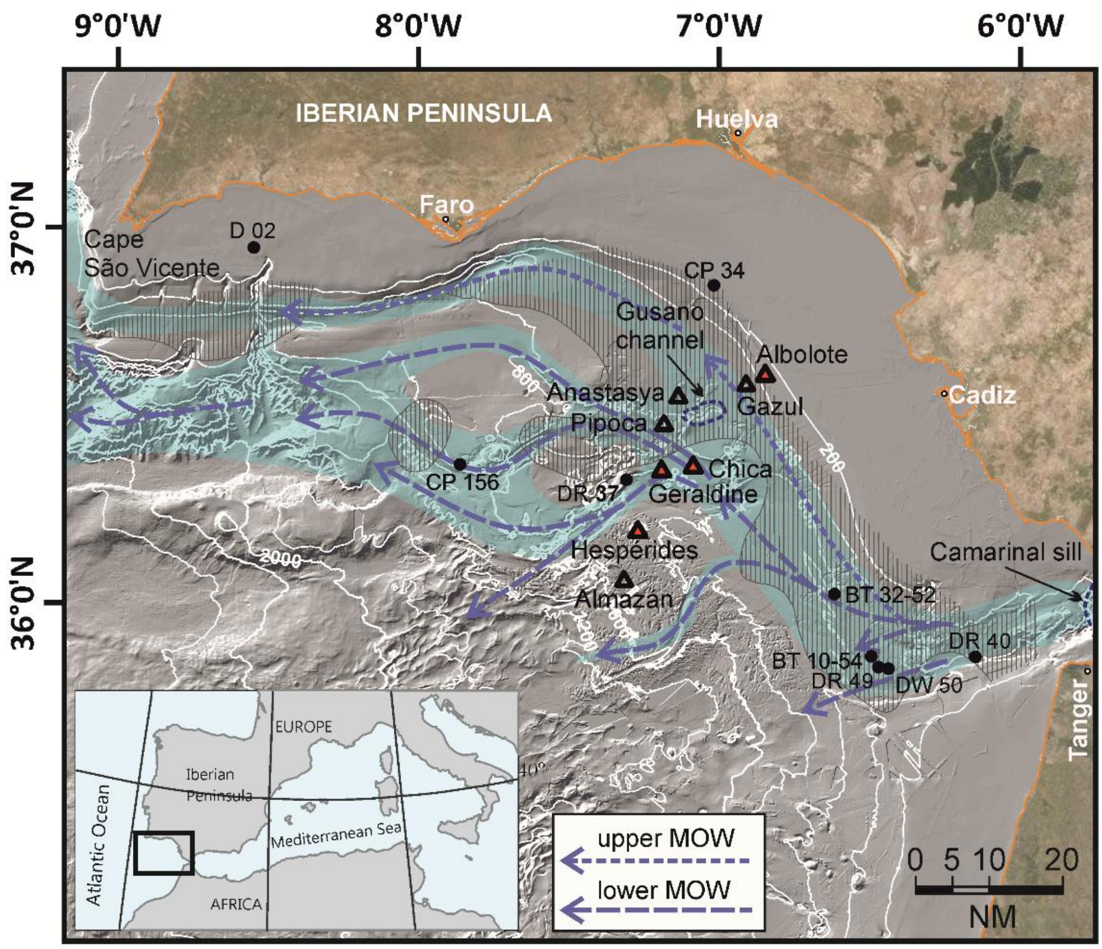


Figure 5.1. Map of the Gulf of Cadiz showing the location of the mud volcanoes (empty triangles), diapir/mud volcano complexes (red-filled triangles) and other sampling stations (circles: TALISMAN, BALGIM, CIRCASUR) mentioned in the text, as well as the pathway of the Mediterranean Outflow Water (MOW; blue tone and dashed arrows, redrawn from Hernández-Molina et al. 2003). The vertically hatched areas are those for which Gasser et al. (2017: Fig. 19) reported the presence of the MOW in contact with the seafloor or less than 25 m from it.

5.2.2. Geological setting

Regarding the geological context, the GoC is largely affected by tectonics and diapiric processes related to a complex geodynamic evolution of the continental margin (Medialdea et al. 2009), with olistostrome/accretionary complex units that were emplaced in the Late Miocene in response to the NW-directed convergence between the African and Eurasian plates (Somoza et al. 2003). An extensive occurrence of diapiric ridges, mud volcanoes (hereafter MVs) and diapir/MV complexes (hereafter DMVs) together with other related fluid venting submarine structures have been observed throughout the Spanish-Portuguese margin of the GoC (Somoza et al. 2003, Fernández-Puga et al. 2007, Díaz del Río et al. 2014, Palomino et al. 2016, Lozano et al. 2020), as well as on the Moroccan margin (Gardner 2001, Van Rensbergen et al. 2005). Moreover, seepage-related morphologies commonly associated with mud volcanism and mud diapirism are also abundant in the GoC, including collapse depressions, pockmarks, mud flows, carbonate mounds and slides (Pinheiro et al. 2003, Somoza et al. 2003, Fernández-Puga et al. 2007, León et al. 2010, Díaz del Río et al. 2014, Palomino et al. 2016, Lozano et al. 2020). Topographic features in the GoC also include a large field of hundreds of small (20–30 m in height) buried and exposed mounds situated among MVs and on top of diapiric ridges along the Moroccan margin, which are covered by fossil corals, and with an origin related to glacial periods since the Early-Middle Pleistocene Transition (Foubert et al. 2008, Wienberg et al. 2009, Vandorpe et al. 2017). All those elements contribute to shaping the benthic habitats (Lozano et al. 2020) as well as to directing the pathway of the water mass in contact with the bottom (Gasser et al. 2017, Sánchez-Leal et al. 2017).

5.2.3. Modern oceanographical pattern

The GoC has been the focus of attention of many studies dealing with deep-water circulation, mainly in the northern sector which is characterized by the exchange of water masses through the Strait of Gibraltar (Hernández-Molina et al. 2014, Gasser et al. 2017 and references therein; Sánchez-Leal et al. 2017). Relatively warm (16.6°C–22.6°C) and less saline (36.5‰) surficial North Atlantic Central Water (NACW) flows eastwards along the south-western Iberian margin and partly enters the Mediterranean Sea, whereas cool (12.9°C) and highly saline (38.45‰) Mediterranean Outflow Water (MOW) flows westwards through the Strait of Gibraltar below the NACW and in some areas in close contact with the seafloor (Ochoa & Bray 1991, Gasser et al. 2017). After crossing the Strait, the MOW spreads westwards in the GoC and progressively sinks north-westwards, descending along the continental slope while its temperature, salinity and velocity decrease through mixing with the overlying fresher NACW (Iorga & Lozier 1999). West of the 7°W, and partly due to topographical constraints, the MOW splits into two main branches. The upper branch flows at depths between 500 and 800 m depth along the upper slope until Cape São Vicente, remaining at most places in contact with the continental slope. The lower branches are located further south at depths between 800 and 1200 m depth, and detach from the seafloor in the western GoC, constituting the main path for MOW transport into the open ocean that can be traced westwards and northwards along the Iberian margin (Iorga & Lozier 1999, Gasser et al. 2017). The MOW outflow entrains NACW as it plunges into the GoC, the subsequent mixing reducing the contrast in salinity and temperature between the outflow and surrounding waters (García-Lafuente et al. 2011).

The Atlantic intermediate water masses (summarized by Voelker et al. 2015 and Roque et al. 2019) comprise the eastern NACW, formed by strong evaporation first and further winter cooling later along the Azores Front (NACW *sensu stricto*, of subtropical origin). This NACW penetrates the GoC in the 100–700 m depth range, overlying the MOW with a sharp transition at the western approaches of the Strait of Gibraltar and only interacting with the upper core of the MOW further west. The Subarctic Intermediate Water (SAIW, sometimes treated as subpolar NACW) has a different origin north of the Bay of Biscay, flows southwards along the western Iberian margin and enters the GoC in the 400–900 m depth interval, therefore overlying the lower branch of the MOW. Finally, the Antarctic Intermediate Water (AAIW) flows along the African coast from the south, hardly reaches the GoC in the 600–1000 m depth interval below the NACW layers.

Surface circulation involves the Surface Atlantic Water (SAW) with the Azores current meandering eastwards towards the GoC and taking part (together with subtropical NACW) in the inflow of Atlantic water into the Mediterranean.

5.2.4. Palaeocirculation patterns

The MOW palaeocirculation in the GoC during the last 50 kyr has been the subject of divergent studies and hypotheses, mostly based on the sedimentological record in deep-sea cores. Huang & Stanley (1972), based on the analysis of Alboran Sea cores, formulated the unconventional hypothesis that before 10 kyr B.P. less dense Mediterranean water outflowed above denser Atlantic water entering the Strait of Gibraltar and then flowing into the Alboran Sea. In their view, the presence in the Alboran Basin of a layer of coarse terrigenous material derived mainly from the Strait of Gibraltar and the Spanish coast was best explained by the action of relatively powerful east-flowing bottom currents. However, this inversion could only be possible if Atlantic incoming water were colder (possibly due to a southward shift of the Polar Front) and/or the Mediterranean deep water less saline (due to increased rainfall and river runoff in the basin), a view which was rebutted by Diester-Haass (1973) and was not supported by Bethoux (1979).

It was also hypothesised (Cacho et al. 1999, 2000, 2001, based on planktonic foraminiferal record and geochemical proxies) that during the LGM, sea surface temperatures in the Alboran Sea were in the order of 10–12°C and the stratification was not as sharp as today, resulting in an enhanced Mediterranean thermohaline circulation in comparison to the current warm interval. This better ventilation of the deep Mediterranean Sea may have been linked to an increased contribution of the Western Mediterranean Deep Water (WMDW) to the MOW (Voelker et al. 2006), and should result in the reinforcement of the denser MOW towards the Atlantic Ocean. However, as Cacho et al. (2000) admitted, MOW volume was also spatially constrained by the glacial sea level drop where Camarinal sill would be hardly more than 100 m depth, with a section reduced to 1/8 of its current one according to Bethoux (1979).

According to Sierro et al. (2020), the freshwater discharge during the Bølling warming caused a cascade effect which finally decreased the vertical density gradient to the west of the Strait of Gibraltar, resulting in a deepening of the higher density MOW, which in turn led to the intrusion of warm and salty water at deeper depths in the NE Atlantic. When melt-water input started to decrease, densities of mid-depth Atlantic waters rose and the MOW experienced a progressive shoaling that raised its velocity, as suggested by Voelker et al. (2006) and Sierro et al. (2020), generating a rapid warm and highly saline deep-water current that swept the seabed on which it was moving.

The MOW acts as a strong bottom current inducing the formation of channels, contourites and sediment drift bodies along the middle slope, generating the GoC contourite depositional system (Faugères et al. 1986, Sierro et al. 1999, Hernández-Molina et al. 2003, 2014, García et al. 2009). Several studies have addressed the evolution of the MOW through the analysis of deep-sea cores in the GoC contourite depositional system, and unanimously demonstrate the influence of the North Atlantic climate oscillations during the Heinrich Stadials and the Younger Dryas on the MOW circulation pattern in the GoC. Several peaks of the coarse fraction content in the sediment, interpreted as the result of higher intensity of the MOW, are recognized in cores throughout the GoC, but their position concerning the stadial intervals varies. Sierro et al. (1999) found two prominent sandy contourites on the upper continental slope (400–700 m depth) of the GoC, one at the base of the Bølling–Allerød time, the other after the Younger Dryas, reaching maximum grain-size values towards the late Holocene. Those coarser layers were interpreted as resulting from the balance between the intensity of the MOW (increasing during deglaciation events because the higher sea level allowed more flux through the Strait) and sediment input (trapped on the shelf during highstands and shifted seawards during lowstands). Llave et al. (2006) found a peak of sand content just after the LGM in a core situated at 582 m depth in the main pathway of the modern MOW. Conversely, in a much deeper part of the GoC (969–1515 m depth), Rogerson et al. (2005) found maximum sand content ca. 17 kyr B.P. during Heinrich Stadial 1 (HS1) whereas the Holocene part is essentially muddy; and Voelker et al. (2006) found similarly a peak of grain size within HS1 in another core situated at 1170 m depth. Thus, the influence of the lower branches of the MOW is assumed to be stronger under glacial conditions than nowadays (Llave et al. 2006: Fig. 5) and also the glacial MOW settled deeper, leaving the bottom in ca. 2000 m depth instead of current ca. 1200 m depth, a depth now occupied by North Atlantic Deep Water (NADW) (Rogerson et al. 2005).

During the LGM, surface temperatures along the western Iberian Peninsula dropped by 2–4°C in summer (also in winter south of 40°N) but the polar front remained further north (Eynaud et al. 2009, Voelker et al. 2009) and the general setting was not drastically different from present. Conversely, during HS1, peaks of the cold-water foraminifer *Neogloboquadrina pachyderma* were recorded in the GoC between 17.9 and 15.4 kyr B.P. (Voelker & de Abreu 2011, Ducassou et al. 2018). This reflects a southward displacement of the Polar Front towards the West of the Iberian Peninsula (Barker et al. 2009, Eynaud et al. 2009, Sierro et al. 2020) with intrusion of subpolar waters into the GoC and, from there, into the Mediterranean.

Table 5.1. Location and details of sampling stations on the oceanographic expeditions TALISMAN 1883, BALGIM 1984, ANASTASYA 09/99, INDEMARES 0610, 0211, 0412 and CIRCASUR 2020 on the mud volcano field in the Spanish waters of the Gulf of Cadiz. BT: beam-trawl; DA, DR: benthic dredge; DW: epibenthic sled; BC: box-corer; MV: mud volcano; MD: mud diapir; DMV: diapir/mud volcano complex; SoG: Strait of Gibraltar. Depth start and end in meters water depth.

Expedition	Sampling method	Sample code	Latitude start	Longitude start	Depth start	Latitude end	Longitude end	Depth end	Area
TALISMAN	Trawl	D02	36.88°N	-8.53°W	99				Portimão canyon
BALGIM 1984	Benthic dredge	DR23	36.650°N	-7.317°W	556				Off Huelva
	Epibenthic sled	DW24	36.683°N	-7.317°W	545				Off Huelva
	Beam-trawl	CP25	36.683°N	-7.317°W	544				Off Huelva
	Epibenthic sled	DW28	36.767°N	-7.133°W	398				Off Huelva
	Beam-trawl	CP34	36.816°N	-7.083°W	180				Off Huelva
	Benthic dredge	DR37	36.300°N	-7.250°W	864				Off Huelva
		DR40	35.833°N	-6.150°W	362				W Gibraltar
		DR42	35.900°N	-6.386°W	135				W Gibraltar
		DR45	35.733°N	-6.283°W	293				W Gibraltar
		DR49	35.883°N	-6.550°W	521				W Gibraltar
	Epibenthic sled	DW50	35.883°N	-6.533°W	523				W Gibraltar
	Beam-trawl	CP54	35.683°N	-6.500°W	356				W Gibraltar
	Epibenthic sled	DW57	35.700°N	-6.583°W	548				W Gibraltar
	Beam-trawl	CP108	36.183°N	-8.100°W	1527				Off Huelva
		CP155	36.333°N	-7.683°W	903				Off Huelva
		CP156	36.333°N	-7.883°W	1135				Off Huelva
		CP157	36.350°N	-7.933°W	1108				Off Huelva
		CP160	36.250°N	-8.000°W	1350				Off Huelva
ANASTASYA 09/99	Benthic dredge	DA06/5	36.187°N	-7.324°W	721	36.191°N	-7.309°W	739	Hespérides DMV
INDEMARES 0610	Benthic dredge	DA04	36.575°N	-6.881°W	388	36.576°N	-6.879°W	375	Albolote DMV
		DA07	36.564°N	-6.943°W	495	36.562°N	-6.942°W	491	Gazul MV
		DA11	36.562°N	-6.939°W	461	36.564°N	-6.939°W	462	Gazul MV
	Beam-trawl	BT09	36.575°N	-6.880°W	380	36.577°N	-6.870°W	337	Albolote DMV
	Shipek grab	SK1.3	36.562°N	-6.939°W	461				Gazul MV
INDEMARES 0211	Benthic dredge	DA01	36.573°N	-6.878°W	335	36.575°N	-6.875°W	339	Albolote DMV
		DA17	36.457°N	-7.204°W	532	36.455°N	-7.206°W	585	Pipoca MV
		DA18	36.457°N	-7.207°W	554	36.457°N	-7.207°W	554	Pipoca MV
		DA19	36.463°N	-7.201°W	547	36.463°N	-7.205°W	545	Pipoca MV
		DA20	36.372°N	-7.123°W	756	36.375°N	-7.123°W	725	Chica DMV
		DA21	36.377°N	-7.121°W	727	36.379°N	-7.119°W	694	Chica DMV
		DA23	36.459°N	-7.228°W	752	36.459°N	-7.231°W	746	Pipoca MV
		DA24	36.476°N	-7.223°W	724	36.474°N	-7.220°W	723	Pipoca MV
		DA26	36.565°N	-6.932°W	443	36.564°N	-6.934°W	453	Gazul MV
		DA27	36.557°N	-6.946°W	461	36.559°N	-6.948°W	463	Gazul MV
		DA30	36.371°N	-7.117°W	653	36.370°N	-7.113°W	669	Chica DMV
		DA31	36.300°N	-7.199°W	742	36.301°N	-7.202°W	771	Geraldine DMV
		DA32	36.304°N	-7.234°W	945	36.307°N	-7.236°W	883	Geraldine DMV
		DA35	36.189°N	-7.304°W	740	36.192°N	-7.304°W	738	Hespérides DMV
		DA36	36.184°N	-7.309°W	696	36.186°N	-7.307°W	711	Hespérides DMV
		DA37	36.182°N	-7.308°W	678	36.179°N	-7.308°W	694	Hespérides DMV
		DA40	36.164°N	-7.299°W	892	36.164°N	-7.295°W	865	Hespérides DMV
		DA41	36.168°N	-7.328°W	950	36.169°N	-7.332°W	912	Hespérides DMV
		DA42	36.058°N	-7.329°W	903	36.061°N	-7.325°W	908	Almazán MV
		DA46	36.048°N	-7.346°W	934	36.046°N	-7.348°W	929	Almazán MV
		DA47	36.060°N	-7.331°W	902	36.059°N	-7.328°W	914	Almazán MV
	Beam-trawl	BT08	36.523°N	-7.154°W	478	36.526°N	-7.143°W	550	Anastasya MV
		BT20	36.453°N	-7.185°W	625	36.459°N	-7.193°W	616	Pipoca MV
		BT22	36.187°N	-7.292°W	758	36.179°N	-7.291°W	801	Hespérides DMV
		BT24	36.186°N	-7.307°W	704	36.180°N	-7.299°W	734	Hespérides DMV
		BT25	36.055°N	-7.329°W	894	36.060°N	-7.320°W	896	Almazán MV
		BT29	36.053°N	-7.339°W	860	36.048°N	-7.348°W	928	Almazán MV
		BT30	36.061°N	-7.336°W	912	36.059°N	-7.326°W	904	Almazán MV
INDEMARES 0412	Box-corer	BC07	36.588°N	-7.084°W	470				La Pepa MD
		BC11	36.465°N	-7.069°W	558				Gusano channel
CIRCASUR 2020	Beam-trawl	BT10-54	35.893°N	-6.554°W	534	35.901°N	-6.558°W	526	W SoG
		BT32-52	36.081°N	-6.700°W	625	36.078°N	-6.690°W	617	W SoG
		BT17-26	36.384°N	-7.046°W	567	36.391°N	-7.049°W	570	Chica DMV

5.3. Material and methods

The material analyzed in the present study was collected mainly during the European LIFE+INDEMARES project, which aimed to provide the necessary scientific information for establishing a network of deep-sea areas of biological interest for Spanish waters to be incorporated in the EU Natura 2000 Network. The samples were collected during multidisciplinary expeditions INDEMARES/CHICA 0610, 0211 and 0412 on board R/V "Emma Bardán", R/V "Cornide de Saavedra" and R/V "Ramón Margalef" respectively, exploring a MV field located on the upper and middle slope of the north-eastern GoC continental margin (300–1200 m depth) (Fig. 5.1). Some material was obtained during ANASTASYA 09/99 expedition on board R/V "Cornide de Saavedra", one of the first expeditions dedicated to a general investigation of sedimentary dynamics in the GoC, and during the CIRCASUR 2020 expedition on board R/V "Ramón Margalef", aimed to an evaluation of the environmental status of the benthic habitats of the GoC between 30 and 1000 m depth within the monitoring programs of the EU Marine Strategy Framework Directive 2008/56/EEC. In addition, material coming from historical expeditions that sampled the GoC was incorporated into this study including that from BALGIM expedition (1984), carried out on board R/V "Cryos" (see Salas 1996), and from TALISMAN 1883 expedition on board the steamer "Talisman", one of the earliest French oceanographic expeditions dedicated to investigate the deep-sea (Filhol 1885, Locard 1897–1898, Dolan 2020).

Sampling was carried out using small Shipek grab (SK, 0.04 m^2 of sampling area), a large box-corer (BC, generally ca. 0.09 m^2 of sampling area), a benthic dredge (DA, sampled area ca. 300 m^2), and a beam-trawl (BT, sampled area ca. 2000 m^2) (Table 5.1). Sediments collected with the BC (generally between 0.10 and 0.20 m below seafloor) were sectioned at 5 cm intervals and sieved on a 0.5 mm mesh. The material collected with the DA and BT was sieved through a sieve column of 10, 5, 1 and 0.5 mm mesh sizes. Large specimens were sorted on board and bulk samples of the finer fractions were preserved in 70% ethanol for further study. The fine fractions of the sediment (<5 mm) were available from the BC and most of the DA, whereas they were mostly lost in trawl (i.e., BT) samples.

Larger (>5 cm) molluscs were sorted to species on board and identified, with live-taken specimens and empty shells quantified separately. For bivalves, each valve was counted as representing one individual except in the rare cases where the complete shell was found with both valves in connection. In addition, the finer fraction (1–5 mm) was sorted under the stereo-microscope for selected dredge hauls and box-cores in which larger BGs were found. By "thanatocoenosis" in a broad sense, we designate the assemblage of dead shells found in the superficial layer of unconsolidated sediment on the sea bottom, collected with the dredge or box core. This thanatocoenosis can accumulate shells from different origins in space and time, therefore mixing shells of the modern benthic community with those of locally extinct species (Kidwell 2013), e.g. the BGs. In the context of the current-swept contourite system of the GoC, shells of BGs would occur on the seafloor either because no substantial sedimentation occurred since their deposition, or because erosion has removed the sediment which once covered them. There is no taphonomic clue to differentiate which are BGs remaining from times of the last glaciation and which are recently dead specimens from the modern assemblage (or from any intermediate age).

Species retained as possible BGs include, in addition to the dated ones, (1) species present in the thanatocoenosis and known to be locally extinct in the area, (2) species still living in the area but currently found in a bathymetric range which does not match the position of the sample, and (3) species represented by a large number of shells without any live-taken specimen. Information on the current distributions and bathymetric ranges of the molluscan species found in the thanatocoenosis was mostly obtained from sources stated in the "Distribution" tab of the species in the World Register of Marine Species (WoRMS editorial board 2023) and are not repeated here. Main sources for distributions of some species in Mediterranean thanatocoenoses included Malatesta & Zarlenga (1986), Martinell et al. (1986) and Giribet & Peñas (1997). Information regarding current biological communities inhabiting the MV field of the north-eastern GoC was provided by Rueda et al. (2012, 2016), Díaz del Río et al. (2014), González-García et al. (2020b), Lozano et al. (2020), Ramalho et al. (2020) (Bryozoans), Utrilla et al. (2020) (Mollusca), and Urra et al. (2021).

A total of ten age determinations were conducted on nine shells (one shell was dated twice independently for quality control) to obtain a time frame for the past occurrence of potential BG molluscs in the GoC. For this purpose, we selected well preserved shells, not showing marks of weathering, recrystallization, or any other degradation which would bias the radiocarbon dating (Rick et al. 2005). Samples were extracted from the thickest part of the shells (i.e., the columella in gastropods and the area near the umbo in bivalves) of two specimens of the bivalve *Arctica islandica*, two specimens of the gastropod *Neptunea contraria* and four specimens of *Neptunea antiqua*. These were dated by accelerator mass spectrometry (AMS) with a NEC 1.5SDH-1 Pelletron accelerator performed at the Direct AMS radiocarbon dating laboratory (https://www.directams.com/), and referred to as before present (B.P., with P = 1950 CE).

Radiocarbon ages (AMS ^{14}C ages) were calibrated to calendar ages (cal. yr B.P.) with the CALIB 8.2 program (Stuiver et al. 2021) and the Marine20 calibration data set (Heaton et al. 2020). A conservative local reservoir effect (ΔR) of 100 (±100) ^{14}C yr was adopted to correct for regional differences in reservoir age in the GoC, according to Monge Soares & Matos Martins (2010). All ^{14}C analyses followed standard procedures.

5.4. Results

The thanatocoenosis analyzed in the coarse fraction of samples collected in the MV field of the north-eastern GoC comprised 748 shell remains belonging to a total of 22 larger (>5 cm) mollusc species, among which several are locally extinct and denote cold-water affinity. It also contained several cold-water corals, mainly *Desmophyllum pertusum* (Linnaeus, 1758) (also known as *Lophelia pertusa*), and *Madrepora oculata* Linnaeus, 1758, but also *Dendrophyllia alternata* Pourtalès, 1880. The detailed list of molluscan species with a quantification of their abundance is given in Tables 5.2 and 5.3, and a selection of species is illustrated in Figs. 5.2–5.4. This list comprises shells of species still living in the area along with others BGs constrained today to more northern areas, with no taphonomic clues allowing to distinguish them.

The locally extinct molluscan species which definitely qualify as BGs were found, following a bathymetric gradient from shallowest to deepest, at Albolote DMV, Gazul MV, Pipoca MV, Chica DMV, Hespérides DMV, Geraldine DMV, Almazán MV, as well as in the

Table 5.2. Occurrence and abundance of molluscs found in the thanatocoenosis dredged during the INDEMARES/CHICA programme in the Spanish waters of the Gulf of Cadiz (GoC), with indication of the fluid venting submarine structures. Previous records for the GoC: (1) Locard (1897–1898); (2) Taviani et al. (1991); (3) Wienberg et al. (2009); (4) Salas (1996); (5) Bouchet & Warén (1985, 1993); (6) López-Correa et al. (2005); (7) Ducassou et al. (2018); (8) Utrilla et al. (2020). See Table 5.1 for the detail of sample locations. Rows 1–22 are the larger species (generally >5 cm). P: la Pepa; CG: Canal Gusano; ANA: Anastasya; GER: Geraldine; other site names in full.

		ALBOLOTE			GAZUL					P	CG	ANA	PIPOCA						CHICA			HESPÉRIDES								GER		ALMAZÁN						
		BT09 (337-380)	DA01 (335-339)	DA04 (375-388)	SK1.3 (461)	DA07 (491-495)	DA11 (461-462)	DA26 (443-453)	DA27 (461-463)	BC07 (470)	BC11 (558)	BT08 (478-550)	DA17 (532-585)	DA18 (554)	DA19 (545-547)	BT20 (616-625)	DA23 (746-752)	DA24 (723-724)	DA20 (725-756)	DA21 (694-727)	DA30 (653-669)	AN-DA6/5 (721)	BT22 (758-801)	BT24 (704-734)	DA35 (738-740)	DA36 (696-711)	DA37 (678-694)	DA40 (865-892)	DA41 (912-950)	DA31 (742-771)	DA32 (883-945)	BT25 (894-896)	BT29 (860-928)	BT30 (904-912)	DA42 (903-908)	DA46 (929-934)	DA47 (902-914)	previous records
Species still living in the GoC	*Acesta excavata* (Fabricius, 1779)																												1									(6)
	Ampulla priamus (Gmelin, 1791)																			1																		(1, 5)
	Buccinum humphreysianum Bennett, 1824												2			1			20	1																		(1, 2, 5)
	Buccinum oblitum Sykes, 1911																																					(2, 5)
	Colus islandicus (Mohr, 1786)												1							1		1										3		1				(1, 5)
	Colus jeffreysianus (P. Fischer, 1868)									1				1	2							1							1	1		8		2	3		5	(1, 5)
	Galeodea rugosa (Linnaeus, 1771)		4									6	6		2	1		2	1	2		2																(1, 5)
	Glossus humanus (Linnaeus, 1758)							1																														(1, 4)
	Lutraria lutraria (Linnaeus, 1758)							2																														
	Neptunea contraria (Linnaeus, 1771)								2	7		2	5	4	1		1	1	1	1		2	1	4	2	1	1	2	3	2		5			1	1		(1, 5)
	Pseudamussium peslutrae (Linnaeus, 1771)		1	17			20					34	131	1					9																			(1, 2, 4)
	Ranella olearium (Linnaeus, 1758)		1			4				1		3			2					3	4								2									(1, 5)
	Troschelia berniciensis (W. King, 1846)												3			1			1			1	1									1		1			3	(1, 5)
	Turrisipho fenestratus (Turton, 1834)														1																							(1, 5)
Species locally extinct in the GoC	*Arctica islandica* (Linnaeus, 1767)	3					1																															(1, 4)
	Buccinum undatum Linnaeus, 1758																		1											1								(2)
	Chlamys islandica (O.F. Müller, 1776)						1																															(2)
	Colus gracilis (da Costa, 1778)												2	2	3							1									1		1		7			New
	Liomesus ovum (Turton, 1825)																													2								New
	Modiolus modiolus (Linnaeus, 1758)							1																											2			(2)
	Mya truncata Linnaeus, 1758							1																														(1)
	Neptunea antiqua (Linnaeus, 1758)												5									10																New
	Antalis entalis (Linnaeus, 1758)																													1								New
	Curtitoma trevelliana (Turton, 1834)																													1								New
	Limacina retroversa (J. Fleming, 1823)					1							1																						65			(7)
	Nuculana pernula (O.F. Müller, 1779)					1																																New
	Propebela turricula (Montagu, 1803)										1																											New
	Puncturella noachina (Linnaeus, 1771)																		3											1					1			New
	Veleropilina reticulata (Seguenza, 1876)			1																																		(8)

Table 5.3. Occurrence and abundance of molluscs found in the thanatocoenosis dredged off Huelva (BALGIM 1984 expedition), off S. Portugal (TALISMAN 1883 expedition) and at the western approaches of the Strait of Gibraltar (BALGIM 1984 and CIRCASUR 2020 expeditions). Previous records for the GoC, references as in Table 5.2. See Table 5.1 for the detail of sample locations. * denotes the live-taken specimen of *Colus islandicus.* Rows 1–22 are the larger species (generally >5 cm).

		BALGIM off Huelva												CIRCASUR			BALGIM W of Gibraltar							
		DR23 556	DW24 545	CP25 544	DW28 398	CP34 180	DR37 864	CP155 903	CP156 1135	CP157 1108	CP160 1350	CP108 1527	TAL. DR02 99	BT10-54 526	BT17-26 567	BT32-52 617	DR40 362	DR42 135	DR45 293	DR49 521	DW50 523	CP54 356	DW57 548	previous records
Species still living in the GoC	*Acesta excavata* (Fabricius, 1779)																							(6)
	Ampulla priamus (Gmelin, 1791)					**2**												**1**				**2**		(1, 5)
	Buccinum humphreysianum Bennett, 1824															**2**	**17**			**7**	**3**			(1, 2, 5)
	Buccinum oblitum Sykes, 1911						**1**										**14**			**13**	**6**			(2, 5)
	Colus islandicus (Mohr, 1786)						**4**		**1***	**6**														(1, 5)
	Colus jeffreysianus (P. Fischer, 1868)	**1**					**7**	**1**		**3**	**8**								**1**				**2**	(1, 5)
	Galeodea rugosa (Linnaeus, 1771)																							(1, 5)
	Glossus humanus (Linnaeus, 1758)					**1**									**1**									(1, 4)
	Lutraria lutraria (Linnaeus, 1758)																							
	Neptunea contraria (Linnaeus, 1771)						**2**							**1**		**2**								(1, 5)
	Pseudamussium peslutrae (Linnaeus, 1771)	**6**	**7**	**43**	**2**									**44**			**3**			**17**	**6**			(1, 2, 4)
	Ranella olearium (Linnaeus, 1758)						**1**										**7**							(1, 5)
	Troschelia berniciensis (W. King, 1846)											**4**				**2**								(1, 5)
	Turrisipho fenestratus (W. Turton, 1834)																							(1, 5)
Species locally extinct in the GoC	*Arctica islandica* (Linnaeus, 1767)					**1**							**1**											(1, 4)
	Buccinum undatum Linnaeus, 1758						**1**									**1**				**1**				(2)
	Chlamys islandica (O.F. Müller, 1776)													**11**		**2**					**29**		**2**	(2)
	Colus gracilis (da Costa, 1778)									**1**														New
	Liomesus ovum (W. Turton, 1825)															**1**								New
	Modiolus modiolus (Linnaeus, 1758)													**13**		**3**		2						(2)
	Mya truncata Linnaeus, 1758												**1**											(1)
	Neptunea antiqua (Linnaeus, 1758)																							New
	Antalis entalis (Linnaeus, 1758)																							New
	Curtitoma trevelliana (W. Turton, 1834)																							New
	Limacina retroversa (J. Fleming, 1823)																							(7)
	Nuculana pernula (O.F. Müller, 1779)																							New
	Propebela turricula (Montagu, 1803)																							New
	Puncturella noachina (Linnaeus, 1771)					**2**															**1**	**3**		New
	Veleropilina reticulata (Seguenza, 1876)																							(8)

western approaches of the Strait of Gibraltar. Fine fractions (1–5 mm) in the dredge hauls yielded seven additional species (84 shell remains) suspected to be BGs (Table 5.2, Figs. 5.2 and 5.3); however, these were rare (low abundance and frequency of occurrence) and the bulk of the thanatocoenoses in that fraction comprises species currently living in the area.

Unquestionable BGs were represented by 115 individuals (indiv.) of the larger species, with the mytild *Modiolus modiolus*, the colid *Colus gracilis*, the buccinid *Neptunea antiqua* and the pectinid *Chlamys islandica* as the most abundant species (Tables 5.2 and 5.3). Regarding frequency of occurrence (%F), *Colus gracilis* (13.7%F), *Buccinum undatum* (10.3%F), *Modiolus modiolus* (8.6%F) and *Chlamys islandica* (6.9%F) were the most frequently collected truly BGs. Minoritarian truly BGs included the arcticid *Arctica islandica*, the buccinid *Liomesus ovum* and the myid *Mya truncata* which were represented by four or fewer individuals (Tables 5.2 and 5.3). The western approaches of the Strait of Gibraltar were the area where a larger amount of truly BGs was collected (65 indiv.), followed by Pipoca MV (12 indiv.), Hespérides DMV (11 indiv.) and Almazán MV (10 indiv.), whereas the larger amount of species was collected at Gazul MV and at the western approaches of the Strait of Gibraltar (4 spp. in each). *Arctica islandica* and *M. truncata* was collected at the shallower sites, both of them off S. Portugal (99 m depth) and Gazul MV (443–462 m depth), *A. islandica* also at Albolote DMV (337–380 m depth) and off Huelva (180 m depth)., whereas the rest of the species were collected mostly below 500 m depth.

Radiocarbon ages determined on nine mollusc specimens range between 26.1 and 14.6 kyr B.P. (Table 5.4), spanning the Marine Isotope Stage (MIS) 2 which includes the Last Glacial Maximum (LGM) and Heinrich Stadials 1 and 2. Ages of *N. contraria* cluster in the LGM (21.4 and 26.1 kyr B.P.). The ages of *A. islandica* are very similar (16.8 and 17.0 kyr B.P.) within Heinrich Stadial 1. Finally, *N. antiqua* specimens show the widest age range, with the oldest age of 21.9 kyr B.P. (LGM) and the youngest age of 14.6 kyr B.P. corresponding to the very beginning of the Bølling interstadial (14.7–12.9 kyr B.P.).

Table 5.4. AMS ^{14}C dates determined on molluscan specimens found in the thanatocoenosis dredged on mud volcanoes (MVs) and diapir/MV complexes (DMVs) in the Spanish waters of the Gulf of Cadiz, with indication of the Fluid Venting Submarine Structure (FVSS) and depth interval where the specimen was collected. The AMS ^{14}C ages have been corrected for ^{13}C and a mean ΔR value for closest known localities in the northern Gulf of Cadiz, and have been converted into calendar years using the Marine20 calibration curve of the CALIB 8.2 calibration software. Sample J–082 of *Neptunea antiqua* was dated twice.

Sample ID	Mollusc species	FVSS	Depth (m)	^{14}C age (yr B.P.)	1$^{\sigma}$ error (yr B.P.)	ΔR	2$^{\sigma}$ range cal. age (cal. yr B.P.)	Calibrated ^{14}C age (cal. yr B.P.)
AI–01	*Arctica islandica*	Albolote DMV	339–388	14640	±46	100±100	16405–17096	16770
AI–02	*Arctica islandica*	Albolote DMV	339–388	14812	±45	100±100	16638–17323	16980
J–061	*Neptunea contraria*	Pipoca MV	599–684	18524	±56	100±100	20962–21782	21370
J–062	*Neptunea contraria*	Pipoca MV	599–684	22907	±70	100±100	25830–26447	26140
J–063	*Neptunea antiqua*	Pipoca MV	599–684	18914	±52	100±100	21478–22202	21880
J–071	*Neptunea antiqua*	Hespérides DMV	714–1047	13461	±38	100±100	14917–15598	15250
J–081	*Neptunea antiqua*	Pipoca MV	599–684	14928	±40	100±100	16777–17457	17120
J–082	*Neptunea antiqua*	Pipoca MV	599–684	13030	±37	100±100	14160–15000	14600
J–082	*Neptunea antiqua*	Pipoca MV	599–684	13020	±36	100±100	14147–14985	14590
J–084	*Neptunea antiqua*	Pipoca MV	599–684	14460	±50	100±100	16198–16913	16550

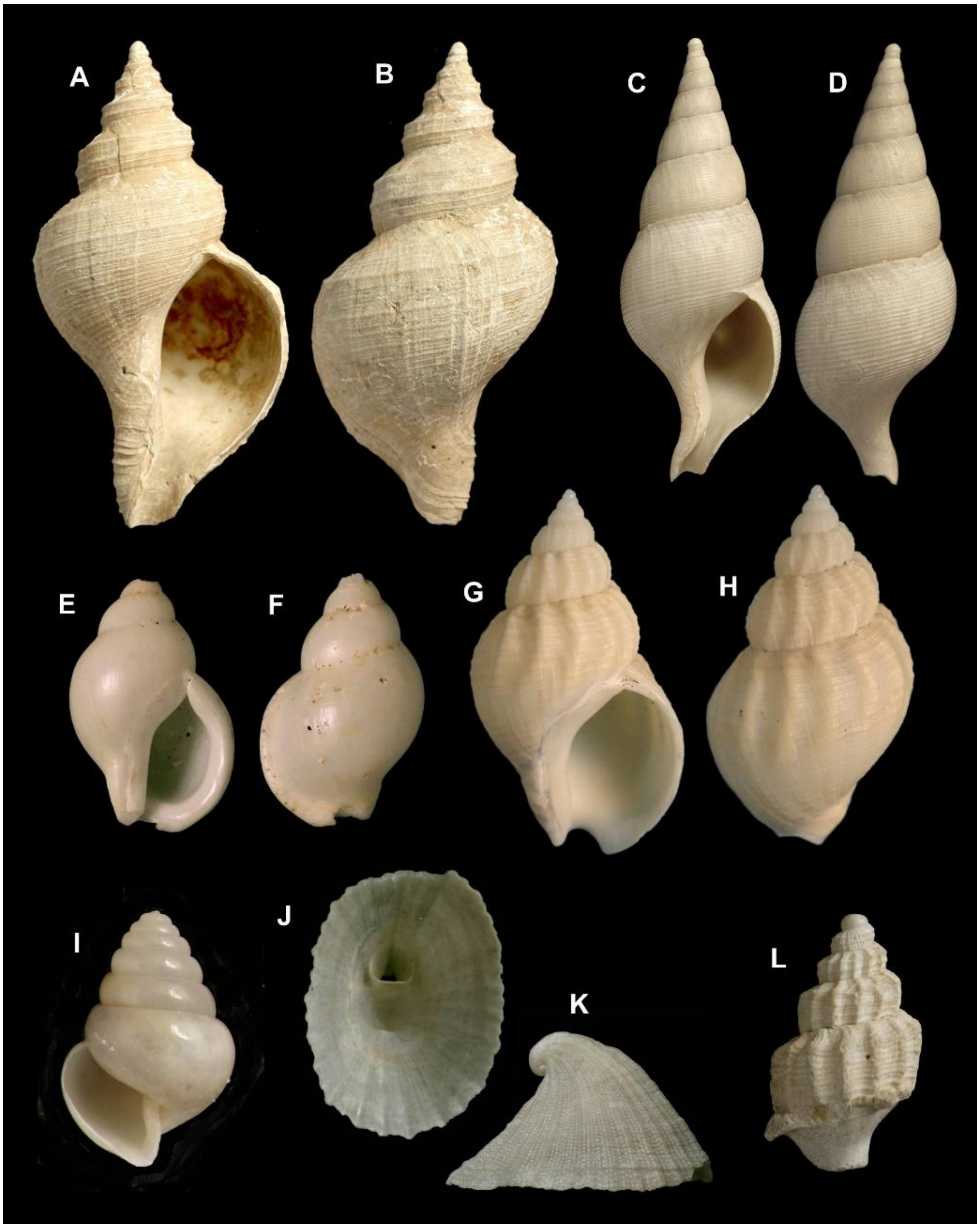


Figure 5.2. Representative specimens of gastropods found in the thanatocoenosis dredged in the Gulf of Cadiz (species currently restricted to higher latitudes), with indication of the area and depth where the specimens were collected. **A–B**: *Neptunea antiqua*, Hespérides diapir/mud volcano complex (DMV), ANASTASYA 09/99 DA06/5, 721 m depth (101 mm). **C–D**: *Colus gracilis*, Pipoca mud volcano (MV), INDEMARES 0211 DA19, 656 m depth (67 mm). **E–F**: *Liomesus ovum*, western approaches of the Strait of Gibraltar, CIRCASUR 2020 BT32–52, 617 m depth (24 mm). **G–H**: *Buccinum undatum*, same locality and sample (42 mm). **I**: *Limacina retroversa*, Almazán MV, INDEMARES 0211 DA42, 903 m depth (2.5 mm). **J–K**: *Puncturella noachina*, same locality and sample (7.0 mm). **L**: *Propebela turricula*, Gusano channel, INDEMARES 0412 BC11, 558 m depth (incomplete shell).

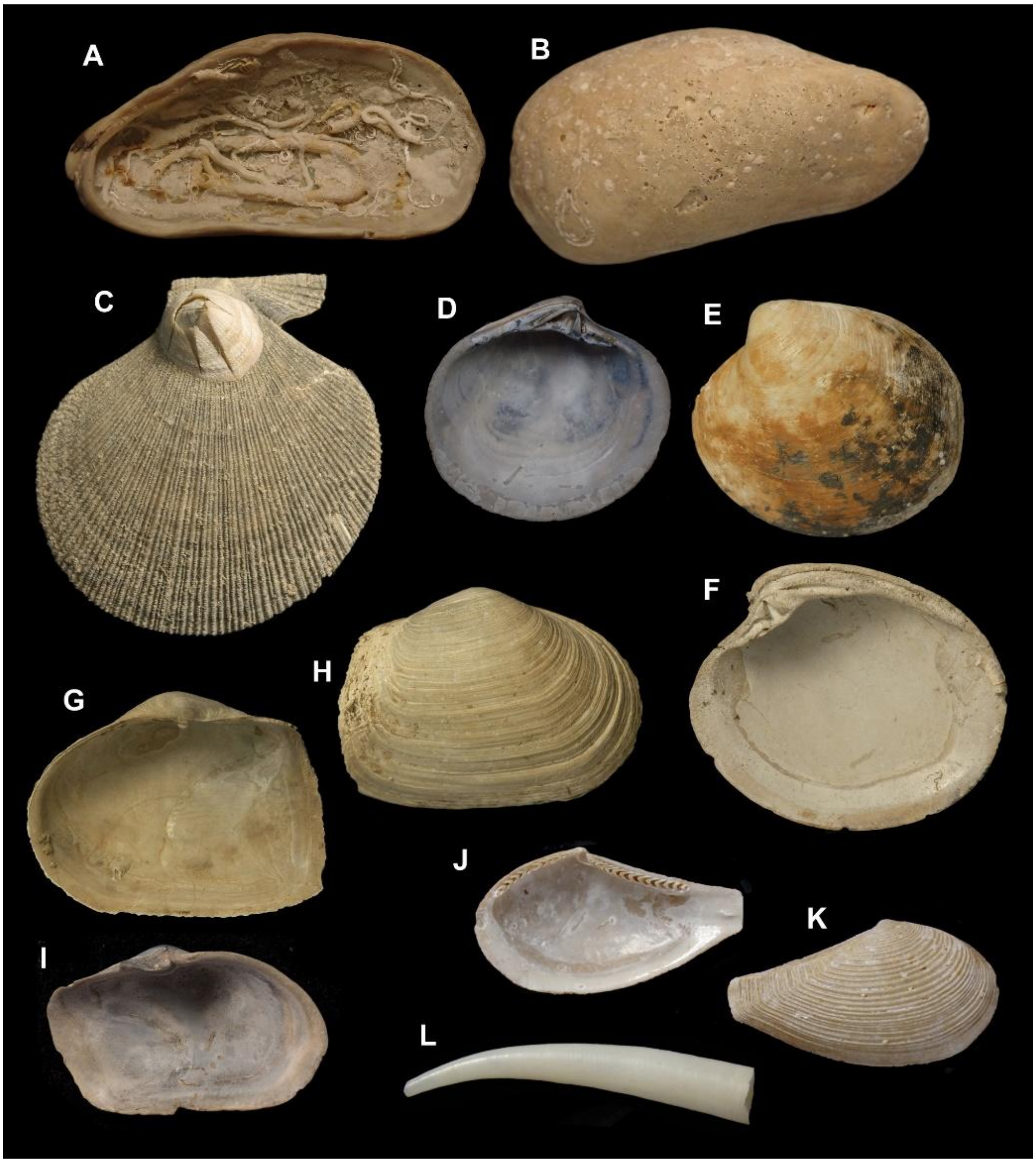


Figure 5.3. Representative specimens of bivalves and scaphopod found in the thanatocoenosis dredged in the Gulf of Cadiz (species currently restricted to higher latitudes), with indication of the area and depth where the specimens were collected. **A–B**: *Modiolus modiolus*, western approaches of the Strait of Gibraltar, CIRCASUR 2020 BT10–54, 526 m depth (69 mm). **C**: *Chlamys islandica*, Gazul mud volcano (MV), INDEMARES 0610 DA11, 462 m depth (61 mm). **D**: *Arctica islandica*, head of Portimão canyon, TALISMAN 1883 D02, 99 m depth (40 mm). **E–F**: *A. islandica*, Albolote diapir/MV complex (DMV), INDEMARES 0610 BT09, 380 m depth (79 and 85 mm; specimens used for age determination). **G–H**: *Mya truncata*, Gazul MV, INDEMARES 0211 DA26, 455 m depth (55 mm). **I**: *M. truncata*, head of Portimão canyon, TALISMAN 1883 D02, 99 m depth (25 mm). **J–K**: *Nuculana pernula*, Gazul MV, INDEMARES 0610 DA07, 495 m depth (9.7 mm). **L**: *Antalis entalis*, Geraldine DMV, INDEMARES 0211 DA31, 742 m depth (20.5 mm).

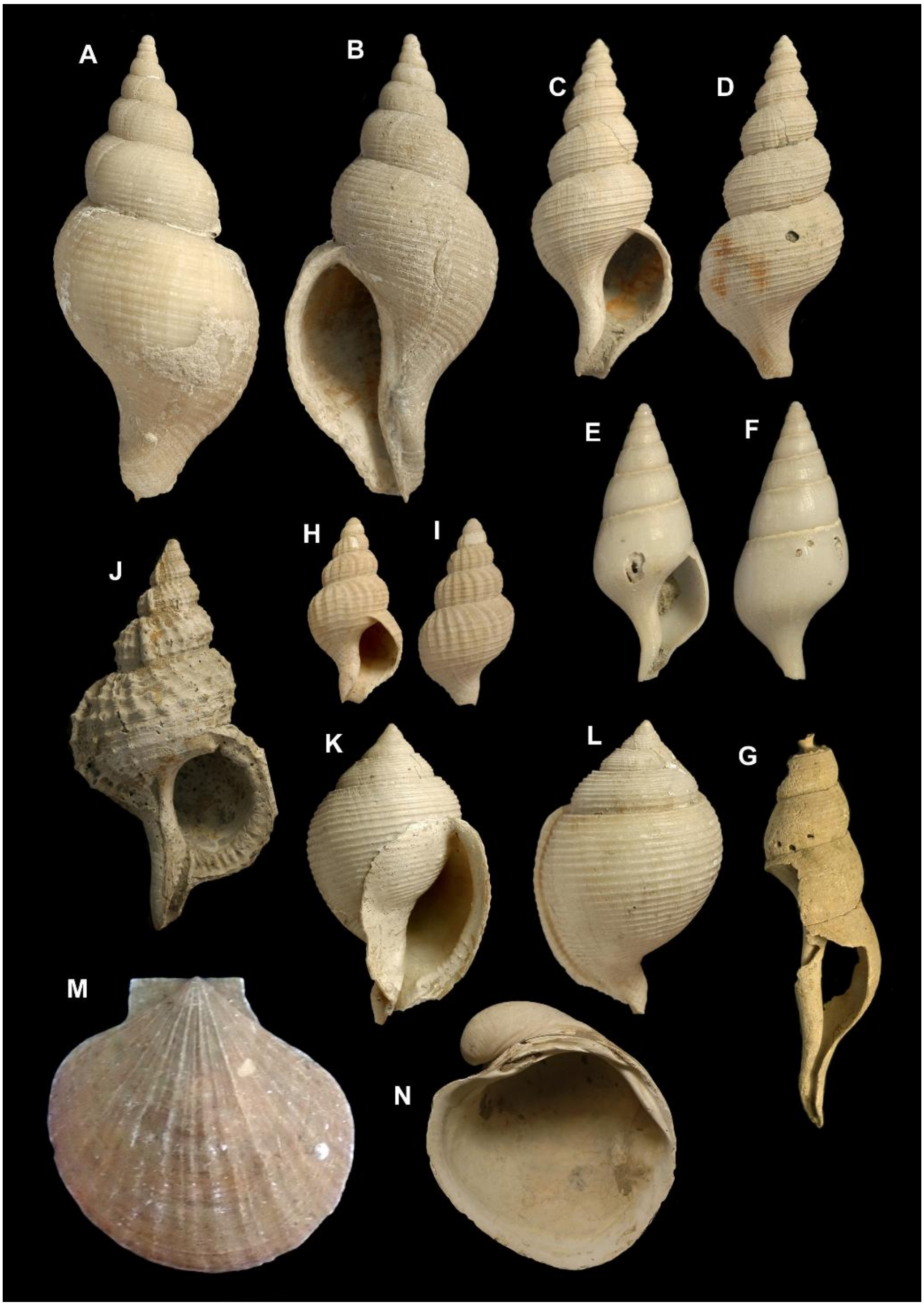


Figure 5.4. Representative specimens of molluscs found in the thanatocoenosis dredged in the Gulf of Cadiz (species that are still living in the Gulf of Cadiz; more information in the discussion section), with indication of the area and depth where the specimens were collected. **A–B**: *Neptunea contraria*, Pipoca mud volcano (MV), INDEMARES 0211 DA17, 599 m depth (98 mm). **C–D**: *Troschelia berniciensis*, Hespérides diapir/MV complex (DMV), ANASTASYA 09/99 DA06/5, 721 m depth (81 mm). **E–F**: *Colus jeffreysianus*, Pipoca MV, INDEMARES 0211 DA19, 656 m depth (34 mm). G: *Colus islandicus*, Hespérides DMV, ANASTASYA 09/99 DA06/5, 721 m depth (92 mm). **H–I**: *Turrisipho fenestratus*, Pipoca MV, INDEMARES 0211 DA19, 656 m depth (20 mm). **J**: *Ranella olearium*, Albolote DMV, INDEMARES 0211 DA01, 339 m depth (123 mm). **K–L**: *Galeodea rugosa*, Pipoca MV, INDEMARES 0211 DA17, 599 m depth (77 mm). **M**: *Pseudamussium peslutrae* (sculptured form), western approaches of the Strait of Gibraltar, CIRCASUR 2020 BT10–54, 526 m depth (55 mm). **N**: *Glossus humanu*s, western approaches of the Strait of Gibraltar, CIRCASUR 2020 BT17–26, 570 m depth (66 mm).

5.5. Discussion

5.5.1. Locally extinct and extant boreal molluscs in the Gulf of Cadiz

The main outcome of this study on bathyal thanatocoenoses of sedimentary areas of the GoC is that a nearly full complement of the BGs reported from the last glacial deposits in the Mediterranean Sea are also present in the GoC. Eight molluscan species found in these thanatocoenoses and currently restricted to higher latitudes (Table 5.5; Fig. 5.5, upper row) are the gastropods *Buccinum undatum*, *Colus gracilis, Liomesus ovum* and *Neptunea antiqua*, and the bivalves *Arctica islandica*, *Chlamys islandica*, *Modiolus modiolus* and *Mya truncata*, representing 15.4% of the larger species in the studied thanatocoenoses. Of these, *C. gracilis, N. antiqua* and *L. ovum* are reported for the first time in the GoC and these species were never reported from Mediterranean fossil deposits. A notable absence is that of the bivalve *Panomya norvegica* (Spengler, 1793), which was found in the platform of the Alboran Island (Alboran Sea) (Gofas et al. 2014a) and elsewhere in the Mediterranean Sea but did not appear in our material. These findings of BGs in the GoC document the continuity of the faunal shift which so far lacked definite records in this intermediate region, filling the gap with the wealth of information available for the Mediterranean basin (Mars 1958, Froget et al. 1972, Martinell & Julià 1973, Colantoni et al. 1975, Taviani 1978, Domènech & Martinell 1982, Curzi et al. 1984, Delibrias & Taviani 1985). As previously reported inside the Mediterranean, BGs remain a minority within the assemblages studied in the GoC, in which the bulk of the species is constituted by those that still live in the area.

Arctica islandica and *Mya truncata* were collected as early as 1883 from off southern Portugal in 99 m depth, but the significance of those findings was not known at the time of Locard (1898). Considering the depth, those shells are likely to belong to a beach deposit of the last glacial, and were certainly outside the MOW at any time. Those species are also found on Albolote DMV and Gazul MV in the shallowest areas of the Shallow Field of Fluid Expulsion (SFFE). Conversely, *N. antiqua*, *L. ovum, C. gracilis* and *B. undatum* were found on MVs and DMVs of the deep sectors of the SFFE and in the Deep Field of Fluid Expulsion (DFFE), which are situated in an area which has today a high influence of the MOW.

The remainder of the larger species are still living in the studied area (Table 5.5; Fig. 5.5, lower row) or at least in specific sectors of the GoC and account for 84.6% (633 indiv.). These include *Colus jeffreysianus, Buccinum humphreysianum, Galeodea rugosa, Ranella olearium* and *Pseudamussium peslutrae* which also enter the Mediterranean and are present in the Alboran Sea (Bouchet & Warén 1985, 1993 and our own observations). Most of these species are currently common and frequent components of molluscan assemblages from bathyal sedimentary bottoms of the GoC and the Alboran Sea (Ciércoles et al. 2018, González-García et al. 2020b). Whether shells belonging to this group are contemporaneous with the BGs or originated in a more recent or modern assemblage can be proved only by dating (the case of *Neptunea contraria*), since the shells are found on the sea bottom in a time-condensed deposit and not in distinct strata.

The significance of *P. peslutrae* (formerly better known as *Pseudamussium septemradiatum*) was discussed by Taviani et al. (1991). This species is often thriving in huge numbers in Pleistocene glacial assemblages of the Mediterranean, intimately associated with

BGs assemblages, and valves from the Southern Adriatic Sea have been dated in the range of 19–15.3 kyr B.P. by Colantoni et al. (1975). As a consequence, it has always been considered a genuine BG by different authors (Malatesta & Zarlenga 1986, and references therein). Nevertheless, it extends southwards to Mauritania and Senegal, and it is still found alive in the Alboran Sea (Cosel & Gofas 2019). Compared to live-taken specimens of *P. peslutrae* from the Alboran Sea, the valves found in the thanatocoenoses were larger and more heavily sculptured, therefore most of the individuals with the "sculptured form" could also be interpreted as BGs.

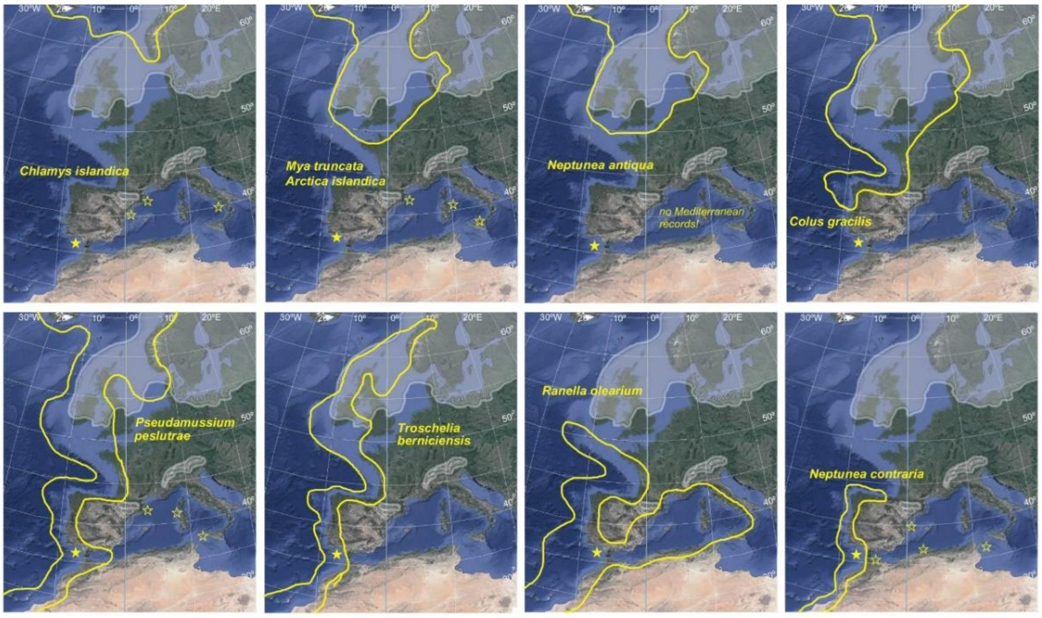


Figure 5.5. Outline of current biogeographical distributions (solid yellow line) of some of the main species of molluscs found in the thanatocoenosis dredged in Gulf of Cadiz. The occurrence in the thanatocoenosis from our data is represented with a solid star, whereas literature data is represented with void stars. The northern shaded area outlines ice sheets of the Last Glacial Maximum after Mangerud et al. (2004).

Table 5.5. Current distribution (1: documented presence as living; * rebutted reports, not based on live-taken specimens and presumably based on Boreal Guest shells) of some of the main species of molluscs found in the thanatocoenosis dredged in the Gulf of Cadiz. ARC: Arctic; GRE: Greenland; ICE: Iceland; Eastern Atlantic- FAR: Faroes; NOR: Norway; BRI: British Isles; GAL: Galicia and Northern Spain; POR: Portugal; MED: Mediterranean (at least Alboran Sea); Western Atlantic- NSC: Nova Scotia to Cape Cod; VIR: Cape Cod to Cape Hatteras; CRL: Carolinas and Georgia. Upper thirteen rows are Boreal Guests, lower rows are species still living in the area. For the detail of sources, see the World Register of Marine Species (WoRMS editorial board 2023), "Documented distributions" tab.

Species	ARC	GRE	ICE	FAR	NOR	BRI	GAL	POR	MED	NSC	VIR	CRL
Buccinum undatum Linnaeus, 1758	1	1	1	1	1	1	*	*		1	1	
Colus gracilis (da Costa, 1778)		1		1	1	1	1	1				
Liomesus ovum (Turton, 1825)			1		1	1						
Neptunea antiqua (Linnaeus, 1758)				1	1	1	*	*				
Arctica islandica (Linnaeus, 1767)			1	1	1	1		*		1	1	*
Chlamys islandica (O.F. Müller, 1776)	1	1	1	1	1	1				1		
Modiolus modiolus (Linnaeus, 1758)			1	1	1	1				1	*	
Mya truncata Linnaeus, 1758	1	1	1	1	1	1				1	1	
Antalis entalis (Linnaeus, 1758)		1	1	1	1	1			*	1		
Curtitoma trevelliana (W. Turton, 1834)			1	1	1	1				1		
Nuculana pernula (O.F. Müller, 1779)	1	1	1	1	1	*				1		
Propebela turricula (Montagu, 1803)	1	1		1	1	1				1		
Limacina retroversa (J. Fleming, 1823)				1	1	1				1		
Puncturella noachina (Linnaeus, 1771)	1	1	1	1	1	1	*	*	*	1	1	
Acesta excavata (Fabricius, 1779)			1	1	1	1	1	1	1			
Ampulla priamus (Gmelin, 1791)								1				
Buccinum humphreysianum Bennett, 1824					1	1	1	1	1			
Buccinum oblitum Sykes, 1911					1	1		1				
Colus islandicus (Mohr, 1786)	1	1	1	1	1	1	1	1		1		
Colus jeffreysianus (P. Fischer, 1868)						1	1	1	1			
Galeodea rugosa (Linnaeus, 1771)						1	1	1	1			
Glossus humanus (Linnaeus, 1758)						1	1	1	1			
Lutraria lutraria (Linnaeus, 1758)						1	1	1	1			
Neptunea contraria (Linnaeus, 1771)							1	1				
Pseudamussium peslutrae (Linnaeus, 1771)			1	1	1	1			1			
Ranella olearium (Linnaeus, 1758)						1	1	1	1			
Troschelia berniciensis (W. King, 1846)				1	1	1	1	1				
Turrisipho fenestratus (W. Turton, 1834)		1	1	1	1	1	1					

Neptunea contraria is the most "southern" of the northern guests, its main populations occurring nowadays off NW Spain in 100–200 m depth, and not further north in Bay of Biscay. *Neptunea contraria* and *Troschelia berniciensis* currently do not enter the Mediterranean Sea, but live-taken specimens of both species have been collected in the southern part of the GoC, not influenced by the MOW but in contact with the AAIW. In this line, one live specimen of *N. contraria* was collected off Casablanca (Morocco) at 650 m depth in 1971 (Gofas, unpublished data), and another one was collected off Rabat by the BALGIM expedition in haul CP86 (34.250°N, 07.350°W, 512 m depth), being these specimens deposited in the Muséum National d'Histoire Naturelle (MNHN) of Paris. On the contrary, no live-taken specimens of *N. contraria* were collected in the different INDEMARES/CHICA expeditions and in the ARSA expeditions for monitoring epibenthic and demersal commercial resources in Spanish waters of the GoC using an otter trawl (two expeditions during each year since the 1990s) (Rueda, unpublished data).

Only empty shells occurred in the INDEMARES/CHICA material and the two shells of *N. contraria* submitted to age determination were dated from the LGM.

Colus islandicus was reported as reaching the NW African coast off Morocco by Bouchet & Warén (1985). Its presence is confirmed by a live-taken specimen collected by the BALGIM expedition in haul CP156 (36.333°N, 07.883°W, 1135 m depth; specimen deposited in MNHN), a puzzling occurrence right in the pathway of the MOW. This may be explained by the depth of the site, where the MOW outflow may be situated far above the sea bottom (Gasser et al. 2017) and also by the situation in the western part of the GoC, at the longitude of Faro, where mixing with Atlantic intermediate water (Iorga & Lozier 1999) will have reduced temperature and salinity of the MOW. *Turrisipho fenestratus* is ambiguous, because it was also stated as extending to NW Morocco by Bouchet & Warén (1985), but their report is based on Locard (1897) who had only shells which could be suspected to be a BG.

The fine fractions of the GoC samples contain several undoubted BGs, including the gastropod *Puncturella noachina* and the scaphopod *Antalis entalis* (Malatesta & Zarlenga 1986), and three more species which have never been reported as BGs in the Mediterranean are here documented for the first time in the GoC waters: the bivalve *Nuculana pernula* and the gastropods *Propebela turricula* and *Curtitoma trevelliana*. Abundant shells of the pteropod *Limacina retroversa*, common in North Atlantic water bodies, were found well preserved in the sediment inside a shell of *Colus gracilis*, and more specimens were detected in scattered samples. The modern distributional limit of this species is unclear from the literature. It was depicted to reach the western Iberian margin to the south (van der Spoel & Heyman 1983, map reproduced in Biekart 1989) but this map may be skewed southwards with occurrences based on shells deposited during cold episodes. In the North East Atlantic, high quantities of *Limacina retroversa* are characteristic of the subarctic waters north of 53°N (Pafort-van Iersel 1986), although Morton (1954) reported this species to live as far South as the English Channel (49.5°N). In the North West Atlantic, Chen & Bé (1964) report it as dominant in subarctic waters of the Labrador Sea, and still abundant in the transitional zone where Gulf Stream mixes with Subarctic waters around 45°N. This pteropod species has been found with high dominance values in sediments from the last glaciation in the Western Mediterranean (Froget 1967) and the Tyrrhenian Sea (Biekart 1989) where it is no longer living. In core MD99–2341 situated at 582 m depth in the main channel of MOW outflow, Ducassou et al. (2018) found *L. retroversa* only during Henrich Stadials 1 and 2 and to a lesser extent during younger Dryas, coupled with or slightly posterior to the peaks of the polar planktonic foraminifer *Neogloboquadrina pachyderma*.

The current distribution of the monoplacophoran *Veleropilina reticulata* is not known, but this species was originally described from cold-water deposits of the Mediterranean and is treated as a BG (Warén & Gofas 1996).

Only the larger species (>5 cm) were commonly collected whereas smaller BG species (e.g. *Nuculana pernula*) were extremely scarce. This is not a collecting artefact, since all the dredge hauls in which definite larger BGs were registered were scrutinized, searching for more species in the smaller fractions. Instead, we hypothesize that this is a post-depositional artefact due to the context of strong currents which shaped the contouritic complex, where smaller fractions were winnowed away during the erosional process whereas larger shells would remain *in situ*.

This is consistent with the view of Sierro et al. (1999) that the sand layer episodes are "condensed layers originating during times of rapid warming and relative sea-level rise within the last deglaciation".

5.5.2. The dynamics of faunal shifts

Driving factors for changes in the geographical distributions of species involve (1) the ability of individuals to reach new areas, and (2) the possibility for those individuals to originate perennial populations. The ability of marine benthic invertebrates in general (and molluscs in particular) for dispersal is in part determined by their larval stage (Thorson 1950, Hansen 1980, Jablonski & Lutz 1983). Some species (e.g. the bivalves *Arctica islandica, Chlamys islandica, Pseudamussium peslutrae, Modiolus modiolus, Mya truncata*) have larvae which feed in the plankton (planktotrophic) and remain pelagic for usually several weeks, being then transported by surficial currents. Others (e.g. all buccinoid gastropods *Buccinum undatum, Colus gracilis, C. islandicus, C. jeffreysianus, Liomesus ovum, Troschelia berniciensis, Neptunea antiqua, N. contraria*) develop inside egg-capsules deposited on the sea-bottom and supposedly undergo very little dispersal (except if the egg-capsules are rafted by bottom currents). Protobranch bivalves such as *Nuculana pernula* and Vetigastropoda such as *Puncturella noachina* present an intermediate condition, in which larvae are released in the plankton but do not feed and have to settle after a few days. Pteropods such as *Limacina retroversa* are holoplanktonic and therefore constrained by water masses and their circulation.

The second and crucial stage of establishing reproducing populations requires that the environmental setting in the newly reached area provides suitable conditions for the species to live there and reproduce. Temperature is usually critical (Belanger et al. 2012) but other factors such salinity, food resources and substrate type may also play a role. Table 5.6 displays some environmental data within the current distributional area of some of the BGs reported in this work. Admittedly, some of those values recorded in shallow bays do not represent the highest possible temperature and salinity, whereas the values stated for the Faroes (Sneli et al. 2005: their Table 5.4) are best representative of the open ocean. In any case, it is clear that similar conditions are not met with at present in any part of the GoC or the Mediterranean Sea.

Surprisingly, most of the reported BGs (with or without planktotrophic larvae) currently have an amphiatlantic range, whereas all but one of the species still living in the GoC do not (Table 5.5). However, we believe that this is not the effect of a better dispersal capacity, but rather a consequence of the shorter distances to be bridged between Scandinavia, the Faroes, Iceland, Greenland and North America, compared to the broad oceanic barrier which is present further south.

5.5.3. Dated shells, geographical distribution and palaeoceanographic implications

Radiocarbon ages determined on *C. islandica* and *M. modiolus* in the western approach of the Strait of Gibraltar by Taviani et al. (1991) span the period 27–12.5 kyr B.P., which brackets our range of 26.5 and 14.5 kyr B.P. on *Neptunea* spp. and *A. islandica* (Fig. 5.6). Nevertheless, their age determinations on *Buccinum undatum* in the same area was only 7.5 kyr B.P., and those made on species still living in the area (*P. peslutrae*, *Buccinum oblitum* and *B. humpreysianum*) resulted in even younger ages. Age determinations within the Mediterranean (Gulf of Lion) by Froget et al. (1972) on *A. islandica, M. modiolus* and *B. undatum* are also younger than LGM (from 13.1 to 9.8 kyr B.P., broadly bracketing the Younger Dryas). This provides clear evidence that the local extinction of BGs may not have occurred simultaneously, but rather progressively with some species lagging behind.

Most of the locations where BGs were found during the present study are currently situated at 600–1000 m depth on the pathway of the MOW. Exceptions include the shallow Albolote DMV and Gazul MV, which occasionally receive MOW upwellings (Sánchez-Leal pers. comm.), and the deep Hespérides DMV and Almazán MV, where occasional events of very low energy may occur (Sánchez-Leal pers. comm.). Today, the seafloor affected by the MOW is known to host an impoverished fauna (Salas 1996, based on bivalves), compared to the upper slope at similar depths on the Moroccan margin, where the bottom is in contact with the much less saline North Atlantic Central Water (NACW) formed along the Azores Front (Ríos et al. 1992) and penetrating the GoC in the 250–700 m depth range. Even attenuated by subsequent mixing with Atlantic intermediate waters, the present-day salinity (38.45‰) and temperature (12.9°C) of the MOW are not suitable for the truly boreal species that were living along its current pathway during the last glaciation. Therefore, the presence of these species must be explained by a drastically different palaeoceanographic setting in the GoC.

Table 5.6. Examples of the environmental settings and types of larval development where living populations of the Gulf of Cadiz Boreal Guests have been studied. SST: Sea Surface Temperature; EBT: Estimated sea-Bottom Temperature. Additional references for larval development (NF: non-feeding): [1] Thorson (1950); [2] Lutz et al. (1982); [3] Gruffydd (1976); [4] De Schweinitz & Lutz (1976).

Species	Locality	Temperature	Salinity (‰)	References	Larval development
Buccinum undatum	S England	4–22°C (reproducing 4–10°C)	<34.9–>35.1	Smith et al. (2013)	Intracapsular [1]
	E Irish Sea	7–16°C		Emmerson et al. (2020)	
	Faroes	0.9–9.1°C (EBT)	<34.9–>35.1	Sneli et al. (2005)	
Colus islandicus	Faroes	0.9–8.5°C (EBT)	<34.9–>35.1	Sneli et al. (2005)	
	Faroes	0–8°C		Jordan (1890)	
	W Ireland	3.2–9.8°C (EBT)		Jordan (1890)	
	Bristol Channel	10.5–11°C (EBT)		Jordan (1890)	
Colus gracilis	Faroes	0.9–8.8°C (EBT)	<34.9–>35.1	Sneli et al. (2005)	Intracapsular [1]
Neptunea antiqua	W Irish Sea	7.6–15°C (SST)		Power & Keegan (2001)	Intracapsular [1]
		7.6°C (EBT)	>35.1	Sneli et al. (2005)	
Arctica islandica	North Sea	5–8°C		Witbaard & Bergman (2003)	Planktotroph [2]
	White Sea		<20	Filippova (2013)	
	Faroes	6.7–8.3°C (EBT)	<34.9–>35.1	Sneli et al. (2005)	
Chlamys islandica	W Norway	3.5–5.5°C		Greve & Samuelsen (1970)	Planktotroph [3]
Modiolus modiolus	W Norway	4.5–13.8°C	ca. 30	Brown (1984)	Planktotroph [4]
	W Sweden	3.5–16°C	<20	Brown (1984)	
	N Norway	2–8°C	32–33	Brown (1984)	
	N Ireland	7–15.5°C	32–34	Brown (1984)	
	Faroes	3.0–9.1°C (EBT)	<34.9–>35.1	Sneli et al. (2005)	
Mya truncata	S North Sea	5–10°C		Amaro et al. (2005) (T from De Wilde et al. (1984))	Planktotroph [1]
	Faroes	8.2°C	>35.1	Sneli et al. (2005)	
Nuculana pernula	White Sea	6°C max	<30	Berger & Naumov (2001)	NF planktonic
	Faroes	7.6°C	>35.1	Sneli et al. (2005)	

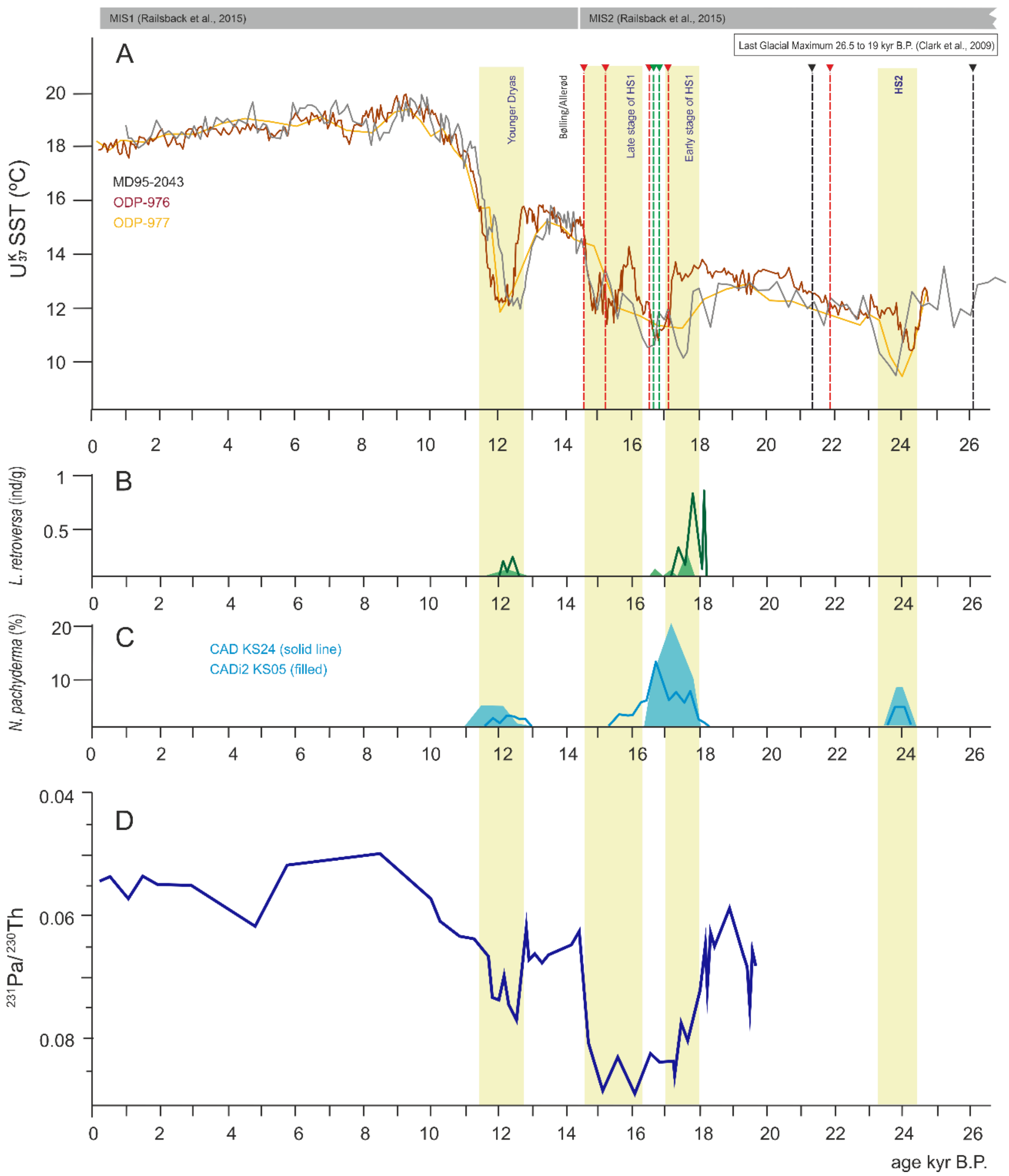


Figure 5.6. Chronologic framework for AMS ^{14}C dates determined on molluscan specimens found in the thanatocoenosis dredged in the Spanish waters of the Gulf of Cadiz. Vertical dashed bars topped with triangles (red: *Neptunea antiqua*; black: *N. contraria*; green: *Arctica islandica*) indicate AMS ^{14}C ages (calendar years B.P.) from this study. **A**: Sea Surface Temperature (SST) reconstructed from alkenone unsaturated ratios in marine cores ODP–976, ODP–977 and MD95–2043 (Alboran Sea) (redrawn from Cacho et al. 1999, Martrat et al. 2014). **B**: Peaks of abundance of the subpolar pteropod *Limacina retroversa* in cores CADKS24 and CADI2KS05. **C**: Peaks of the polar foraminifer *Neogloboquadrina pachyderma* in the same cores (redrawn from Ducassou et al. 2018). **D**: Pa/Th 232-based as Atlantic meridional overturning circulation (AMOC) intensity proxy (redrawn from McManus et al. 2004). Shaded vertical bars represent Younger Dryas (YD), Heinrich Stadial 1 (HS1) and Heinrich Stadial 2 (HS2) events.

An abrupt change in environmental conditions on the GoC seabed under the direct influence of the MOW might be behind the absence of truly BGs in the last ca. 13 kyr (at least in the areas studied so far). Living populations of boreal molluscs located in the NE Atlantic are mainly found with seawater temperatures below 10°C and salinity values lower than 36‰ (Table 5.6 above, and references therein), contrasting sharply with the current conditions prevailing in the MOW, with warmer (12.9°C) and saltier (38.45‰) waters cascading into the GoC (Sánchez-Leal et al. 2017).

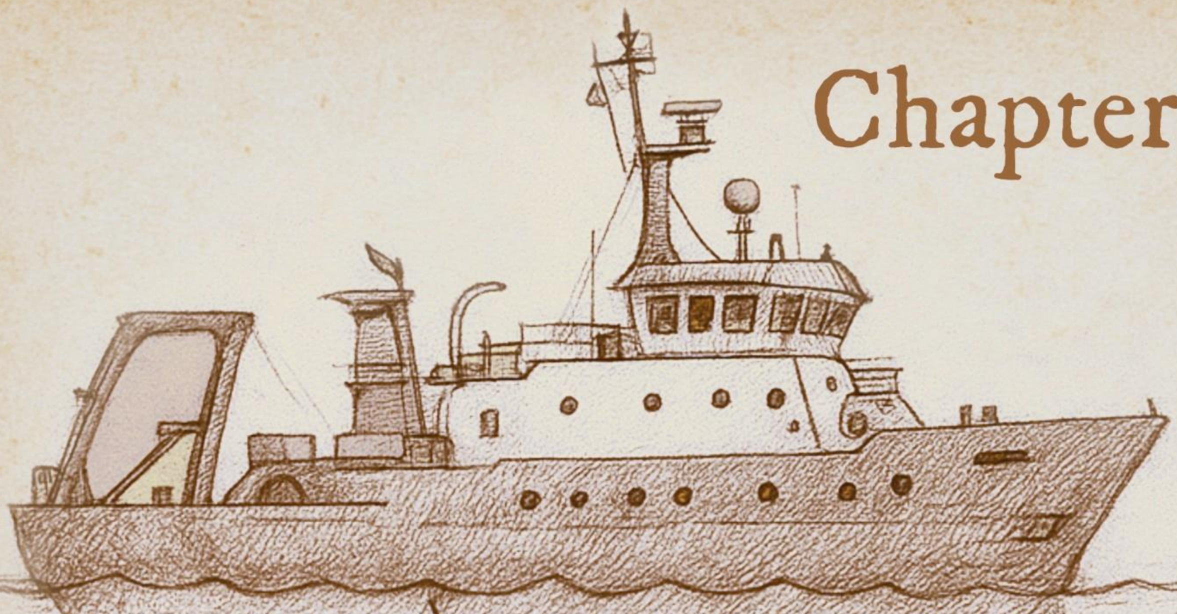
During the last glaciation, the prevailing conditions in the GoC and the MOW were controlled by the conditions within the Mediterranean Sea. In this regard, Sierro et al. (2020) have stated that there have been long periods of high impact of bottom currents in the GoC over the last 20 kyr, including part of Heinrich Stadial 1 (ca. 16–14.5 kyr B.P.), during which most of the age values presented here are situated. The presence of BGs in the current pathway of the MOW would have been possible either if the MOW were suppressed (a hypothesis not supported by current literature) or displaced towards deeper parts of the GoC, or if the outflowing Mediterranean waters had sufficiently low temperature and salinity to accommodate the requirements of those boreal species. Even if the estimated palaeotemperatures in the Western Mediterranean (Cacho et al. 2000, and others) at the time of maximum cooling events are compatible with the persistence of the abovementioned species, the salinity of the outflow may have been even higher than today (Voelker et al. 2006) due to more saline inflowing Atlantic water and to more arid and windy conditions around the Mediterranean Sea margins. Therefore, the most likely factor that would have favoured the thriving BGs in the investigated area is the shift to greater depth of the main Mediterranean outflow (enhanced by the drop of ca. 100 m depth in sea level), which would have allowed more appropriate Atlantic intermediate waters to be in contact with the upper slope. The alternative hypothesis of a suppressed or superficial MOW is not supported by the wealth of studies now available on the GoC contourite depositional systems (Hernández-Molina et al. 2003, Llave et al. 2006).

Our findings raise the question of why certain species present in the GoC during the last glaciation (*Neptunea antiqua, Colus islandicus, C. gracilis, Liomesus ovum, Troschelia berniciensis, Turrisipho fenestratus, Nuculana pernula, Propebela turricula, Antalis entalis*) never colonized the Mediterranean, while others were widely distributed throughout the basin. Predictably, the holoplanktonic *Limacina* and the bivalves with planktotrophic larvae all penetrated the Mediterranean at some time, but the buccinids *Buccinum undatum* and *Neptunea contraria* also did so despite lacking planktonic larvae. Reasons for other species not succeeding in doing so could be that those live in deeper water and the temperature and salinity in the Mediterranean would be low enough only in the relatively shallow subtidal environments which harbour the commonly recorded BGs (*Arctica islandica, Buccinum undatum, Chlamys islandica, Neptunea contraria, Mya truncata*). In fact, most of the BGs reported in the Mediterranean are constrained to the upper 200 m depth corresponding to the nearshore habitats and shallow continental shelf during the deposition period. An alternative explanation for the absence of the deeper water species as BGs in the Mediterranean is that the shallow Camarinal sill (currently 284 m depth, ca. 100 m shallower during LGM) acted as a barrier against the species with a bathymetric range restricted to the slope.

5.6. Conclusions

The palaeontological and chronological data presented here provide evidence of the continuity of the faunal shift of BGs, well documented inside the Mediterranean Sea, and here reported along the south-western Iberian Peninsula. Our data, which report thriving molluscs in the current pathway of the MOW suggest that either the MOW was strongly reduced along the slope during the last glacial, or more likely shifted to a deeper level, allowing the upper slope to remain in contact with suitable Atlantic intermediate waters. Boreal Guests of marked palaeoclimatic significance, such as *Colus gracilis*, *Neptunea antiqua* and *Liomesus ovum*, are reported for the first time in the GoC and have never before been reported in Mediterranean fossil deposits. The BG species collected were mostly large (>5 cm) whereas smaller boreal species were extremely scarce, probably winnowed away by strong bottom currents. Definitely, the faunal remains from the last glaciation rule out the existence of a strong, warm, hypersaline MOW along the upper slope like it is as present. Species still living in the Gulf of Cadiz and the Alboran Sea nevertheless account for 84.6% of specimens among the larger species.

Chapter VI



BALGIM expedition study
Estudio de la campaña BALGIM

This chapter is based on:
Este capítulo se basa en:

Chapter 6A
Utrilla O., Gofas S., Salas C. 2025. How adverse are Mediterranean waters to the deep-sea fauna? A study of the Gibraltar exchange based on Mollusca from the "BALGIM" expedition. Deep-Sea Res. I 220, 104492.
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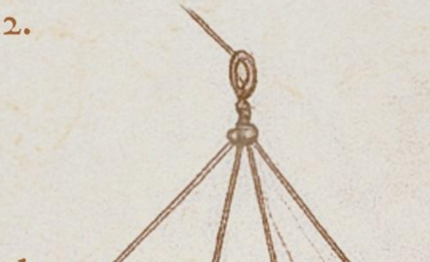


Chapter 6B
Utrilla O., Gofas S. 2024. A new species of *Anatoma* (Vetigastropoda: Anatomidae) from the Strait of Gibraltar.
Iberus 42(2), 201–209.
https://zenodo.org/records/13731961

6A. How adverse are mediterranean waters to the deep-sea fauna? A study of the gibraltar exchange based on mollusca from the "BALGIM" expedition

Abstract

The BALGIM expedition was designed to assess the distribution of marine organisms in the transition from Gulf of Cadiz to Mediterranean Sea across the Strait of Gibraltar. There were 99 hauls below 200 m depth, down to 2110 m. Two matrixes with abundance data were constructed using the data of gastropods and scaphopods from this study and those of bivalves studied earlier. Species were scored according to their bathymetric and geographic distribution as (1) deep-sea species occurring exclusively in the Atlantic, or (2) deep-sea species reported as living both in the Atlantic and the Mediterranean. A total of 4641 live-taken individuals corresponding to 154 species of molluscs collected alive were identified, and almost twice as many (243 species) including those collected as shells only. The samples do not form clearly defined clusters based on their faunal content. More than half of the species (84) occur both in the Mediterranean Sea and the Atlantic Ocean. Most of the 62 species with an Atlantic-only distribution are associated to the cool or cold waters below 600 m depth along the Moroccan margin, and are barred by the Mediterranean Outflow Water in the northern part of Gulf of Cadiz. Four species are preferent of the warm but low-saline North Atlantic Central Water, also off the Moroccan margin. The Mediterranean outflow largely shares a set of species also occurring in the Mediterranean, whereas there are no Mediterranean-only deep-sea species. Therefore, variation in salinity in a range of 1–2‰ is not critical compared to temperature which explains most of the restricted distributions.

Resumen

La expedición BALGIM fue diseñada para evaluar la distribución de los organismos marinos en la transición del golfo de Cádiz al mar Mediterráneo a través del estrecho de Gibraltar. Se realizaron 99 arrastres por debajo de los 200 m de profundidad, llegando hasta los 2.110 m. Se construyeron dos matrices utilizando los datos de abundancia de gasterópodos y escafópodos de este estudio y los de bivalvos estudiados anteriormente. Las especies se clasificaron según su distribución batimétrica y geográfica como: (1) especies de aguas profundas exclusivas del Atlántico, o (2) especies de aguas profundas reportadas como vivas tanto en el Atlántico como en el Mediterráneo. Se identificaron un total de 4.641 individuos vivos correspondientes a 154 especies de moluscos, y casi el doble (243 especies) incluyendo las recolectadas sólo como conchas. Las muestras no forman grupos claramente definidos basados en su contenido faunístico. Más de la mitad de las especies (84) se encuentran tanto en el mar Mediterráneo como en el océano Atlántico. La mayoría de las 62 especies con una distribución exclusivamente atlántica está asociada al agua fresca o fría por debajo de los 600 m de profundidad a lo largo del margen marroquí, y está restringida por el agua de salida mediterránea en la parte norte del golfo de Cádiz. Cuatro especies son preferentes de la cálida pero poco salina agua central del Atlántico norte, también frente al margen marroquí. El agua de salida mediterránea comparte en gran medida un conjunto de especies que también se encuentran en el Mediterráneo, mientras que no hay especies de aguas profundas exclusivas del Mediterráneo. Por lo tanto, la variación en la salinidad en un rango de 1–2‰ no es crítica en comparación con la temperatura, la cual explica la mayoría de las distribuciones restringidas.

6.1. Introduction

The Gulf of Cadiz (GoC), also known as Ibero-Moroccan Gulf, the Strait of Gibraltar and the Alboran Sea are areas of a major importance for the biogeography of the North Atlantic Ocean, being the meeting point of the Lusitanian, Mauritanian and Mediterranean biota (Ekman 1953). The tectonic activity of the area, due to the convergence of the African and Eurasian plates, triggered a variety of geological structures and bathymetric features, including seamounts and other prevalently rocky bottoms, hydrocarbon seeps, and sedimentary bottoms (Vázquez et al. 2021). The Strait of Gibraltar and the GoC are also key areas for the oceanographic dynamics of adjacent areas, and the different water masses play a significant role in controlling larval dispersal. The Alboran Sea is one of the most productive areas in the Mediterranean Sea because of its upwellings (Sarhan et al. 2000) and it is considered a biodiversity hotspot within the Mediterranean basin and the European margin (Rueda et al. 2021).

Molluscs are one of the most diverse faunal groups in benthic communities and represent ca. 25% of the benthic marine fauna (Appeltans et al. 2012). It is a very well-known faunal group and is considered a good indicator for the evaluation of a specific area (Bedulli et al. 2002, Gladstone 2002, Appeltans et al. 2012). Considering the abundance and diversity in this group, the distribution of the molluscan fauna is an excellent proxy for environmental conditions: Belanger et al. (2012) found that bivalve distributions can be accounted for by very few variables (temperature, salinity, productivity).

The molluscan fauna of the GoC was sampled in the past by several expeditions: “Porcupine” Jeffreys (1878-1885), “Talisman” Locard (1897-1898), BALGIM and more recently by the INDEMARES/CHICA (0610, 0211, 0412) and CIRCASUR expeditions. The Alboran Sea has been sampled by cruises DEEPER 0204 of *Instituto Español de Oceanografía* (IEO) and INDEMARES Alboran (2011–2012) organized by the authors. BALGIM was a French oceanographic expedition set up in 1984 by the Muséum National d’Histoire Naturelle (MNHN) of Paris (chief scientist Philippe Bouchet), with its main objective to study the relationship between water masses and benthic fauna composition between the Atlantic and Mediterranean through the Strait of Gibraltar. The material was sorted at the Centre National de Tri d’Océanographie Biologique (CENTOB) of Brest, and reports have been published for several groups: Sponges (Boury-Esnault et al. 1994), Gorgonaria (Grasshoff 1989), Hydrozoa (Ramil & Vervoort 1992), Sipuncula (Salinas & Urchegui 1990), Bryozoa (Harmelin & d’Hondt 1992a, b, 1993), Decapoda (García-Raso 1996), Barnacles (Foster & Buckeridge 1995), Cumacea (Jones 1990), Pycnogonida (Stock 1987), Bivalves (Salas 1996), Echinoidea (David 1989) and Ascidiacea (Monniot & Monniot 1988). Although a major faunal group, Gastropoda from BALGIM expedition were only mentioned casually in some taxonomic publications but were never studied as a whole, and the Scaphopoda were still untouched.

The objective of the present study is to improve the knowledge of Mollusca collected by the BALGIM expedition, on both sides of the Strait. We aim to provide information regarding faunistic affinities and the influence of water mass circulation, mainly the effect of the Mediterranean Outflow Water (MOW) on the benthic species distribution using the molluscs as case study.

6.2. Material and methods

6.2.1. Regional setting

The study area covers the Alboran Sea (Mediterranean Sea) and the Gulf of Cadiz (hereafter GoC, Atlantic Ocean), from 33.750°N (off Casablanca) to 36.917°N (off Cape St. Vincent) and from 9.533°W (Cape St. Vincent) to 3.050°W (western Alboran basin), in a depth range between 200 and 2110 m (Fig. 6.1).

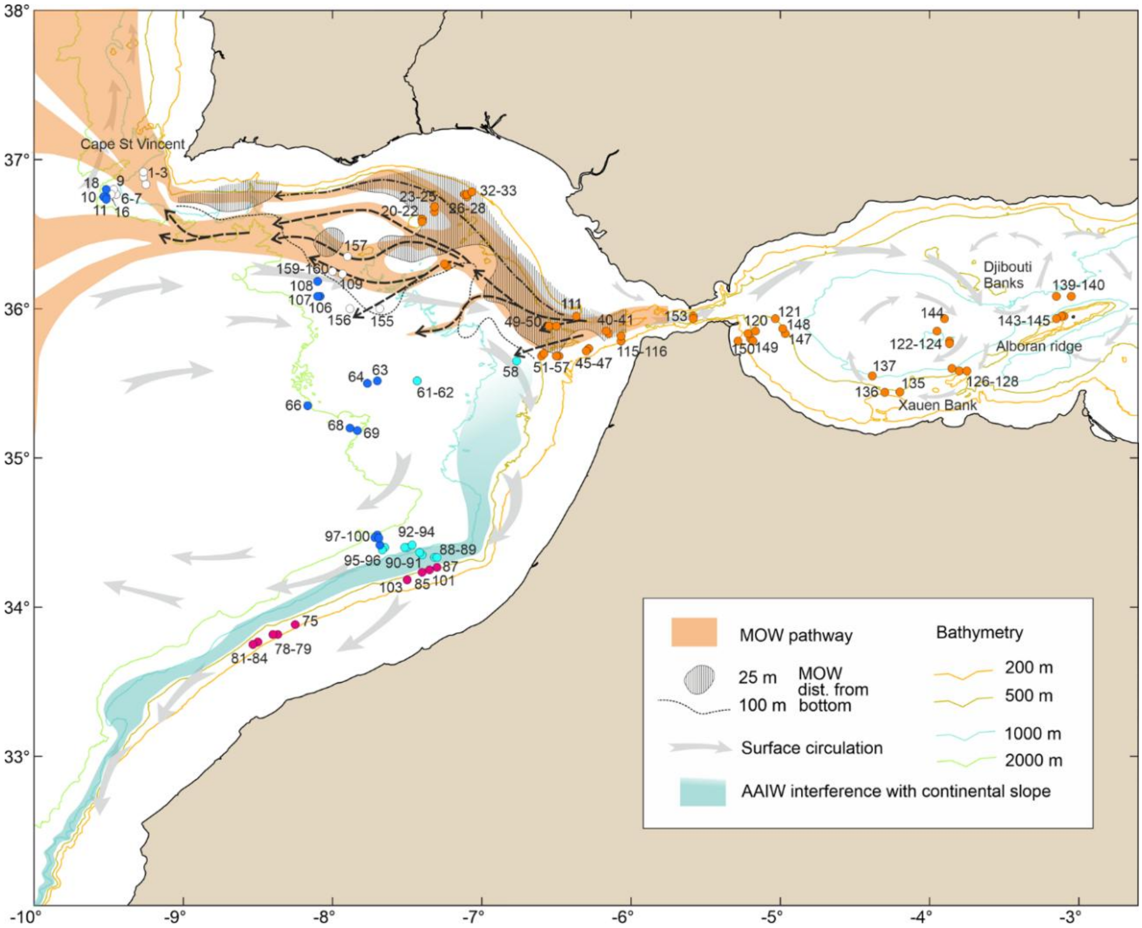


Figure 6.1. Map of the Gulf of Cadiz showing the location of BALGIM sampling stations and main oceanographic features. Pathway of the Mediterranean Outflow Water (MOW; orange tone and dashed arrows) redrawn from Hernández-Molina et al. (2003); the vertically hatched areas are those for which Gasser et al. (2017: Fig. 19) reported the presence of the MOW in contact with the seafloor or less than 25 m away from it, and the stippled line, the area where the MOW is 100 m above seafloor according to the same source. Contact of Antarctic Intermediate Water (AAIW) with the seafloor drawn from depth data in Louarn & Morin (2011). Atlantic surface currents redrawn from a near-surface velocity model in Johnson & Stevens (2000); Alboran gyres redrawn from Rodriguez (1982). Colours indicate the putative water masses in which they were taken (orange: Mediterranean deep water masses or MOW; turquoise: AAIW; dark blue: North Atlantic Deep Water; magenta: North Atlantic Central Water; white: mixed water masses). Bathymetry from EMODnet Digital Bathymetry (DTM)-2022.

An important exchange of water masses occurs in this area (summarized by Louarn & Morin 2011, Voelker et al. 2015, Roque et al. 2019). Surficial, relatively warm (16.6–22.6°C) and moderately saline (36.5‰) North Atlantic Central Water (NACW) flows eastwards and enters the Mediterranean Sea together with surficial Atlantic waters, whereas highly saline

Mediterranean Outflow Water (MOW) flows below towards the Atlantic Ocean, crossing the Camarinal Sill at 284 m (Luján et al. 2011) on the western side of the Strait, then extending west- and northwards along the Iberian margin only (Table 6.1).

The outflow of Mediterranean water is a mighty current system which has built up a notable contourite depositional complex in the GoC (Hernández-Molina et al. 2003, 2006, 2013, García et al. 2009, Gasser et al. 2017), and which impacts considerably benthic communities. When exiting the Strait, the MOW has a temperature around 13°C and a salinity of 38.4‰ (Iorga & Lozier 1999, Louarn & Morin 2011) and its interface with the inflowing Atlantic water is sloping from ca. 100 m depth on the Iberian side to ca. 200 m depth on the Moroccan side (Naranjo et al. 2015: Fig. 4). At this stage (between 6.50°N and 6.83°W), the outflow is running over the sea bottom and is ca. 250 m thick, but by 7.17°W it has thickened to over 500 m depth (Iorga & Lozier 1999).

Subsequent mixing with Atlantic water masses results in a northwestward decrease of its salinity, temperature and velocity (Gasser et al. 2017, Sánchez-Leal et al. 2017). As a consequence of topographical constraints, the MOW sinks and splits into an upper core following the northern slope of the GoC between 600 and 750 m depth, and a lower core down to ~1200 m (Iorga & Lozier 1999), or from 800 to 1400 m depth (Hernández-Molina et al. 2013). The lower core further splits into three branches (from North to South): an intermediate, a principal and a southern branch (Ducassou et al. 2018). In the West of the GoC, the MOW takes off from the bottom and reaches a stability with a core around 1200 m depth in the South of Portugal (Hernández-Molina et al. 2003, 2011, Louarn & Morin 2011), continuing to be detectable northwards to Bay of Biscay and westwards to the Azores.

The Atlantic intermediate water masses comprise two components. The eastern North Atlantic Central Water (NACW), formed by strong evaporation first, and further winter cooling later, along the Azores Front (this is NACW *sensu stricto*, of subtropical origin), penetrates the GoC in the 100–700 m depth range, interacting with the upper core of the MOW, and overlying the MOW with a sharp transition between 100 and 200 m depth at the western approaches of the Strait of Gibraltar (Naranjo et al. 2015: Fig. 4, Roque et al. 2019). The cooler Subarctic Intermediate Water (SAIW, sometimes treated as subpolar NACW) has a different origin north of the Bay of Biscay, flows southwards along the western Iberian margin and enters the GoC in the 400–900 m interval (Roque et al. 2019), therefore overlying the lower branch of the MOW in the western approaches of the GoC.

Along the NW African margin, the MOW is absent and Antarctic Intermediate Water (AAIW), a relatively fresh and cool water mass of Antarctic origin but quite modified (10.2°C, 35.6‰; Louarn & Morin 2011), flows northward between 600 and 1000 m below the NACW layers (Roque et al. 2019). This water mass is upwelled in the filaments formed off Cape Ghir or Cape Blanc on the Moroccan margin (Voelker et al. 2015). There is a vertical divide along the axis of the GoC (spectacularly illustrated in Voelker et al. 2015: Fig. 4C), where AAIW comes into contact with the MOW in the same depth interval; Cabeçadas et al. (2002) attributed the salinity minimum between upper and lower components of the MOW to the influence of this AAIW, but the fate of AAIW north of the Strait is not well known (Louarn & Morin 2011). On the Moroccan margin, the interval (1000–1500 m depth) between the cores of AAIW and NADW is not affected by any definite water mass and constitutes a transition between both.

Table 6.1. Properties of the main water masses present in the Alboran Sea and Ibero-Moroccan area. LIW: Levantine Intermediate Water; WMDW: Western Mediterranean Deep Water; MOW: Mediterranean Outflow Water; AAIW: Antarctic Intermediate Water; NACW: North Atlantic Central Water; SAIW: Subarctic Intermediate Water; NADW: North Atlantic Deep Water; LSW: Labrador Sea Water; SATL: Surficial Atlantic water; u.c.: upper core; l.c.: lower core of the MOW.

Water mass	Area	Source	Temperature (°C)	Salinity (‰)
LIW	W Alboran Sea	Parrilla & Kinder 1987	13.1–13.2	38.47–38.49
WMDW	Alboran Sea	Parrilla & Kinder 1987	12.70–12.91	38.40–38.46
MOW	Exiting Mediterranean	Louarn & Morin 2011	13.174±0.126	38.285±0.146
MOW	Exiting Mediterranean	Iorga & Lozier 1999	13.0	38.0–38.4
MOW	Off Cadiz (6.83°W)	Iorga & Lozier 1999		37.60
MOW	Off Huelva (7.17°W)	Iorga & Lozier 1999		36.3 (u.c.), 37.0 (l.c.)
AAIW	NW African margin	Louarn & Morin 2011	10.254±0.207	35.623±0.066
NACW	W Gulf of Cadiz	Louarn & Morin 2011	16.374±0.117	36.289±0.018
SAIW	SW Iberian Peninsula	Louarn & Morin 2011	10.659±0.089	36.289±0.018
NADW [LSW]	W Iberian Peninsula	Louarn & Morin 2011	4.477±0.614	35.195±0.089
SATL	Off Guadalquivir (50–100 m)	Mendes et al. 2012	14.8–15.4	35.75–36.25

In the deeper part of the West European basin, the depth interval below 1600 m is essentially occupied by North Atlantic Deep Water (NADW), a composite water mass globally flowing southward but with gyres entering Bay of Biscay and the GoC (Hernández-Molina et al. 2011). Labrador Sea Water, the uppermost component of NADW, flows below the MOW along the NW Iberian Peninsula around 1600 m depth (Voelker et al. 2015). Its influence is definite around Galicia Bank (Fiúza et al. 1998) and can still be traced further south (Voelker et al. 2015: Fig. 2C).

Surface circulation in the GoC involves also the Surface Atlantic Water (SATL) with the Azores current meandering eastwards towards the GoC (Johnson & Stevens 2000) and taking part (together with the subtropical NACW) in the inflow of Atlantic water into the Mediterranean, also feeding the Canary Current flowing southwards in the upper layer along the Moroccan margin (Voelker et al. 2015).

Within the Alboran Sea, incoming SATL occupies the superficial levels down to a maximum depth of ca. 150–200 m and constitutes two anticyclonic gyres, one rather permanent in the Western part and another more variable in the Eastern part. The deeper part of the Alboran Sea is occupied by westward moving Western Mediterranean Deep Water (WMDW) mostly below 800 m and Levantine Intermediate Water (LIW) between the AW and the WMDW. Both are highly saline and merge into a single plume which feeds the MOW (Gascard & Richez 1985, Naranjo et al. 2015: 46). It is the Levantine Intermediate Water (LIW), which contributes most of the volume of the MOW (Parrilla & Kinder 1987).

All the above are subject to important seasonal and interannual variations. On a longer time scale, during cold climatic episodes, the better ventilation of the deep Mediterranean Sea may have been linked to an increased contribution of the WMDW to the MOW (Voelker et al. 2006). During glacial and stadial periods when the MOW settled at depths greater than 1900 m, it exported significant amounts of heat and salt into water depths nowadays occupied by upper NADW (Voelker et al. 2006, Urra et al. 2023).

6.2.2. Sample collection and processing

The material of this study was collected in May-June 1984 during the BALGIM expedition on board R/V “Cryos” (Bouchet 1984). Four different collecting gears were used: beam-trawl (CP), rock dredge (DR), Waren’s epibenthic sledge (DW) and an Usnel corer (KG), but only the three first were useful for collecting molluscs. Of a total of 125 benthic hauls, 115 (41 CPs, 40 DWs, 34 DRs) collected molluscan specimens in a wide depth range from 115 to 2110 m depth, and 99 of them situated deeper than 200 m are considered for this study (Table 6.2).

The coarse fractions were mostly sorted on board to phyla and later sorted to species level. Samples of the finer fractions were preserved on board, sieved on 5, 2, 1, and 0.5 mm sieves, and later sorted for separating specimens under a stereomicroscope. Species of molluscs were identified to the lowest possible taxonomic level following the nomenclature of the WoRMS (WoRMS Editorial Board 2025).

Photographs of some uncommon or characteristic species were taken using a Nikon DXM camera mounted on a stereomicroscope at University of Malaga, on different focusing depths and then were combined with CombineZ software (Hadley 2006). Some light photographs were taken in Muséum National d’Histoire Naturelle (MNHN) using a Canon EOS camera mounted with either 60 or 100 mm macro lens, in combination with a BK Plus digital imaging system from Dun Inc.<https://web.archive.org/web/20200222190349/http://www.duninc.com/bk-plus-lab-system.html>, then assembled using the HeliconFocus stacking software. The material of this study is deposited in the collection of MNHN, Paris.

6.2.3. Data analyses

According to the scheme depicted on Fig. 6.1, samples were assigned to the putative water mass (Table 6.2) indicated by their position and depth. From data in Table 6.1, the intermediate and deep-water masses in contact with the sea floor may be categorized in (1) very cold or cold and low salinity (NADW, AAIW), (2) warm and low saline (NACW), and (3) cool and high saline (LIW, WMDW, MOW). In the westernmost part of the MOW pathway, the properties of the Mediterranean outflow are considerably altered by mixing with neighbouring water masses, therefore samples in this context are scored as “modified MOW” (mMOW) and cannot be clearly assigned to any of these three categories.

Species were scored according to their bathymetric and geographic distribution as (1) deep-sea species occurring exclusively in the Atlantic, never reported as living in the Mediterranean deep environments, and (2) deep-sea species reported both in the Atlantic and as living inside the Mediterranean, based on this study (occurrences in the Alboran Sea deeper than 200 m) and on literature (Ardovini & Cossignani 1999, Bogi & Galil 2013, Gofas et al. 2014b and scattered records of single species in WoRMS Editorial Board 2025). Shallow water species, occurring normally on the continental shelf are not included in this study.

Abundance data were recorded for the 99 samples collected deeper than 200 m (gastropods and scaphopods from this study, bivalves from Salas 1996 revised in this study, solenogastres from Salvini-Plawen 2008, polyplacophorans from Kaas & van Belle 1987, 1990). Two matrixes for further analysis were then constructed: one with live-taken specimens only (taxocoenosis) and another with also shells or valves (taxocoenosis + thanatocoenosis; both complete shells and loose valves of bivalves counted as one shell).

Based on the complete taxocoenosis matrix, species richness (total species per sample), abundance (total individuals per sample), evenness index (Pielou 1969) and Shannon-Wiener diversity index (log_2, Krebs 1989) were calculated for each sample using PRIMER6 software (Clarke & Gorley 2006).

A multivariate analysis was carried out on the abundance data (now excluding samples with only one occurrence and species occurring in only one sample), using the Bray-Curtis similarity index in the two versions of the matrix. The abundance data were transformed to fourth-root prior to the analysis, in order to reduce the influence of a few very abundant species.

A non-metric multidimensional scaling (n-MDS) ordination was applied, as well as clusters of the samples using the UPGMA (unweighted pair group method with an arithmetic mean) agglomerative algorithm (Sneath & Sokal 1973). The SIMPROF test was applied to assess the significance of sample groups in the priori unstructured set of samples. All these analyses were done with PRIMER6 software (Clarke & Gorley 2006).

Table 6.2. List of samples from BALGIM expedition, deeper than 200 m, which yielded molluscs. DR: rock dredge; DW: Waren's epibenthic sledge; CP: beam-trawl. Water mass (last column): putative water mass in contact with the bottom according to the scheme depicted in the previous section and on Figure 6.1. AAIW: Antarctic Intermediate Water; WMDW: Western Mediterranean Deep Water; LIW: Levantine Intermediate Water; MOW: Mediterranean Outflow Water; mMOW: modified MOW; NACW: North Atlantic Central Water; NADW: North Atlantic Deep Water. The deep and intermediate water masses are categorized in: cool and low saline (NADW and AAIW), warm and low saline (NACW), and high saline (LIW, WMDW and MOW); mixed or uncertain water masses not categorized (mMOW).

Sample	General area	Latitude	Longitude	Depth (m)	Date (1984)	Substrate	Water mass
DR01	S. Vicente	36°53'N	09°16'W	720	28 May	ooze	mMOW
DW02	S. Vicente	36°55'N	09°16'W	893	28 May	ooze	mMOW
CP03	S. Vicente	36°50'N	09°15'W	681	28 May	ooze	mMOW
DR06	S. Vicente	36°46'N	09°27'W	1113	29 May	ooze	mMOW
DW07	S. Vicente	36°46'N	09°27'W	1141	29 May	ooze	mMOW
CP09	S. Vicente	36°48'N	09°28'W	1173	29 May	ooze	mMOW
CP10	S. Vicente	36°45'N	09°32'W	1592	29 May	ooze	NADW
DW11	S. Vicente	36°44'N	09°31'W	1523	29 May	foram. ooze	NADW
DW16	S. Vicente	36°46'N	09°29'W	1283	30 May	ooze	mMOW
CP17	S. Vicente	36°45'N	09°31'W	1470	30 May	ooze, sponges	NADW
CP18	S. Vicente	36°48'N	09°31'W	1578	30 May	ooze	NADW
DW20	Huelva	36°36'N	07°24'W	452	31 May		MOW
CP21	Huelva	36°36'N	07°24'W	485	31 May		MOW
DR22	Huelva	36°35'N	07°24'W	466	31 May		MOW
DR23	Huelva	36°39'N	07°19'W	556	31 May	sandy ooze	MOW
DW24	Huelva	36°41'N	07°19'W	545	31 May		MOW
CP25	Huelva	36°41'N	07°19'W	544	31 May	thanatocenosis	MOW
DW27	Huelva	36°46'N	07°07'W	370	31 May		MOW
DW28	Huelva	36°46'N	07°08'W	398	31 May		MOW
DR32	Huelva	36°47'N	07°04'W	250	1 June	mud	MOW
CP33	Huelva	36°47'N	07°04'W	256	1 June	mud	MOW
DR37	W. Strait	36°18'N	07°15'W	864	1 June	bioclastic gravel	?
DR40	W. Strait	36°50'N	06°09'W	362	2 June	bioclastic sand	MOW
DR41	W. Strait	36°51'N	06°10'W	340	2 June		MOW
DR45	W. Strait	35°44'N	06°17'W	293	2 June	pteropod ooze	MOW
DW47	W. Strait	35°43'N	06°18'W	281	2 June	muddy sand	MOW
DR49	W. Strait	35°53'N	06°33'W	521	2 June	coarse bioclasts	MOW
DW50	W. Strait	35°53'N	06°32'W	523	3 June		MOW
DR51	W. Strait	35°41'N	06°29'W	362	3 June		MOW
DW53	W. Strait	35°41'N	06°30'W	364	3 June	pteropod ooze	MOW
CP54	W. Strait	35°41'N	06°30'W	356	3 June		MOW
DR56	W. Strait	35°41'N	06°36'W	481	3 June	sandy ooze	MOW
DW57	W. Strait	35°42'N	06°35'W	548	3 June	sand with shells	MOW
DW58	W. Strait	35°39'N	06°46'W	826	3 June	pteropod ooze	AAIW
DW61	Spartel	35°31'N	07°26'W	1222	4 June		AAIW
CP62	Spartel	35°31'N	07°26'W	1250	4 June	ooze, sponges	AAIW
CP63	Spartel	35°31'N	07°42'W	1510	4 June	pteropod ooze	NADW
DW64	Spartel	35°30'N	07°46'W	1530	4 June	pteropod ooze	NADW
CP65	Spartel	35°26'N	08°00'W	1805	4 June		NADW
CP66	Spartel	35°21'N	08°10'W	2110	5 June		NADW
CP68	Spartel	35°12'N	07°53'W	2035	5 June	ooze, corals	NADW
CP69	Spartel	35°11'N	07°50'W	2028	5 June	ooze, corals	NADW
DR75	Casablanca	33°53'N	08°15'W	252	6 June	shell sand	NACW
DR79	Casablanca	33°49'N	08°24'W	260	6 June	shell sand	NACW
DR81	Casablanca	33°46'N	08°30'W	309	6 June	sand	NACW
DR82	Casablanca	33°45'N	08°32'W	355	6 June		NACW
CP84	Casablanca	33°45'N	08°32'W	345	6 June		NACW
DR85	Rabat	34°14'N	07°24'W	497	7 June	coarse sh. sand	NACW
CP86	Rabat	34°15'N	07°21'W	512	7 June	ooze	NACW
DW87	Rabat	34°16'N	07°18'W	500	7 June		NACW
DW88	Rabat	34°20'N	07°19'W	740	7 June	pteropod ooze	AAIW

Table 6.2 **(continued)**

Sample	General area	Latitude	Longitude	Depth (m)	Date (1984)	Substrate	Water mass
CP89	Rabat	34°20'N	07°18'W	722	7 June	ooze	AAIW
CP90	Rabat	34°21'N	07°24'W	890	7 June	ooze, sponges	AAIW
CP91	Rabat	34°22'N	07°25'W	948	7 June	ooze, sponges	AAIW
CP92	Rabat	34°24'N	07°30'W	1182	8 June		AAIW
DW93	Rabat	34°24'N	07°31'W	1203	8 June		AAIW
DW94	Rabat	34°25'N	07°28'W	1175	8 June	ooze	AAIW
CP95	Rabat	34°24'N	07°39'W	1378	8 June	ooze, hard-gr.	AAIW
DW96	Rabat	34°23'N	07°40'W	1255	8 June		AAIW
CP97	Rabat	34°25'N	07°41'W	1515	8 June		NADW
CP98	Rabat	34°29'N	07°42'W	1747	9 June		NADW
CP99	Rabat	34°28'N	07°43'W	1870	9 June	ooze	NADW
DW100	Rabat	34°28'N	07°22'W	1691	9 June	pteropod ooze	NADW
DR101	Rabat	34°11'N	07°30'W	353	9 June	ooze	NACW
CP103	Rabat	34°11'N	07°30'W	347	9 June		NACW
CP106	Huelva	36°05'N	08°05'W	1906	10 June		NADW
DW107	Huelva	36°05'N	08°06'W	1917	10 June		NADW
CP108	Huelva	36°11'N	08°06'W	1527	10 June		NADW
CP109	Huelva	36°14'N	07°56'W	1200	10 June	sticky mud	mMOW
DR115	W. Strait	35°47'N	06°04'W	332	11 June	coarse bioclasts	MOW
DW116	W. Strait	35°49'N	06°04'W	340	11 June		MOW
DR118	Ceuta	35°48'N	05°12'W	352	13 June	grey mud	LIW
CP119	Ceuta	35°50'N	05°13'W	517	13 June		LIW
DW120	Ceuta	35°51'N	05°10'W	425	13 June		LIW
DW121	Ceuta	35°56'N	05°02'W	570	13 June		LIW
DW122	Alboran	35°51'N	03°57'W	905	14 June		WMDW
DW123	Alboran	35°47'N	03°52'W	1234	14 June		WMDW
DW126	Alboran	35°36'N	03°51'W	998	14 June		WMDW
CP127	Alboran	35°35'N	03°48'W	720	14 June	mud	WMDW
DW128	Alboran	35°35'N	03°45'W	480	14 June	mud, dead corals	LIW
DW134	Alboran	35°26'N	04°17'W	205	15 June		LIW
CP135	Alboran	35°26'N	04°14'W	395	15 June	mud, dead corals	LIW
DW136	Alboran	35°26'N	04°18'W	298	15 June	shell debris	LIW
CP137	Alboran	35°33'N	04°23'W	1005	15 June	mud	WMDW
DW143	Alboran	35°57'N	03°07'W	252	16 June		LIW
DR144	Alboran	35°56'N	03°56'W	314	16 June	sandy mud	LIW
CP145	Alboran	35°57'N	03°08'W	373	16 June	mud and shells	LIW
DW146	Alboran	35°56'N	03°09'W	555	16 June	sandy mud	LIW
DW147	Ceuta	35°50'N	04°58'W	489	17 June	soft mud	LIW
CP148	Ceuta	35°52'N	04°59'W	508	17 June		LIW
CP149	Ceuta	35°47'N	05°11'W	377	17 June		LIW
CP150	Ceuta	35°47'N	05°17'W	290	17 June		LIW
DR152	E. Strait	35°57'N	05°35'W	550	17 June	dead corals	LIW
DR153	E. Strait	35°56'N	05°35'W	580	17 June		LIW
CP155	Huelva	36°20'N	07°41'W	903	18 June		mMOW
CP156	Huelva	36°20'N	07°53'W	1135	18 June	coarse sand	mMOW
DW157	Huelva	36°21'N	07°56'W	1108	18 June		mMOW
DW159	Huelva	36°15'N	08°02'W	1360	18 June	soft ooze	mMOW
CP160	Huelva	36°15'N	08°00'W	1350	18 June	ooze	mMOW

6.3. Results

6.3.1. Taxon list, species richness, abundance and diversity indices

A total of 4641 live-taken individuals were identified, of which 3291 in the GoC (76 hauls) and 1350 in the Alboran Sea (23 hauls). They represent 154 species, pertaining to 76 families (Table 6.4, Supplementary Table S1). In addition to this, there were ca. 50 specimens (i.e. less than 1% of the catch) belonging to 17 putative species (red font on Supplementary Table S2), which could not be identified to species level and were not included in the analyses. Taking into account the material collected only as shells, the total increases to 243 molluscan species belonging to 94 families (Supplementary Table S2).

The ten most abundant live-collected molluscs were, in this order: *Kelliella miliaris*, *Abra longicallus*, *Yoldiella philippiana*, *Limopsis minuta*, *Axinulus alleni*, *Thyasira* cf. *obsoleta*, *Ennucula aegeensis*, *Colus jeffreysianus*, *Antalis agilis* and *Fissidentalium capillosum* which are all, except *Limopsis* and *Fissidentalium*, Atlanto-Mediterranean species.

The most frequent species was *Abra longicallus* with 50 occurrences. Many of the species are rare: for 67 species (43%) of the live-taken specimens were found only in one sample and, of these, 39 (25%) were represented only by one specimen.

The numbers of specimens and species in the samples are generally low (Table 6.3), not significantly different between Atlantic and Mediterranean nor between water masses.

Table 6.3. Mean values of species richness, abundance, diversity index and evenness according to location (Atlantic or Mediterranean) and according to water masses. Cold (NADW, AAIW), Cool/HS (high saline: MOW, LIW, WMDW), Warm/LS (low saline: NACW), as in Table 6.2. Mixed waters (mMOW) and unsuccessful hauls marked in grey in Supplementary Table S1 not included. Differences between groups were not found significant following ANOVA.

	All	Atlantic	Medit.	Cold	Cool/HS	Warm/LS
S (total number of occurrences)	6.98	7.17	6.38	8.43	6.42	5.89
N (total number of specimens)	53.23	49.76	64.14	48.79	62.84	38.11
J' Pielou	0.718	0.720	0.712	0.742	0.718	0.627
H' ($\log_2$) Shannon	1.851	1.871	1.788	2.055	1.795	1.550

Table 6.4. List of species found in BALGIM samples with at least one live specimen. Distr.: Distribution; A, Atlantic only (deep water); A-M: Atlanto-Mediterranean (deep water); some species could not be assessed for distribution, either only known from the Strait of Gibraltar or data-deficient. See Supplementary Table S1 for the list enhanced with a colour code. The * followed by a number refer to taxonomic notes at the end of this table.

		Distr.
	Class Solenogastres	
	Dorymenia sarsii (Koren & Danielssen, 1877)	A
	Class Polyplacophora	
	Leptochiton xanthus Kaas & Van Belle, 1990	A
	Connexochiton platynomenus Kaas, 1979	A-M
	Class Gastropoda, subclass Vetigastropoda	
	Akritogyra similis (Jeffreys, 1883)	A
	Anatoma balgimae Utrilla & Gofas, 2024	
	Anatoma umbilicata (Jeffreys, 1883)	A
	Anekes paucistriata Warén, 1992	A
*1	*Calliotropis diomedeae* (A. E. Verrill, 1893)	A
	Calliotropis talismani (Locard, 1898)	A
	Callumbonella suturalis (Philippi, 1836)	A-M
	Cirsonella romettensis (Granata Grillo, 1877)	A-M
	Clelandella miliaris (Brocchi, 1814)	A-M
	Coccopigya spinigera (Jeffreys, 1883)	A-M
	Copulabyssia tenuis (Monterosato, 1880)	A-M
	Emarginula adriatica O. G. Costa, 1830	A-M
	Emarginula christiaensi Piani, 1985	A-M
	Granigyra granulifera Warén, 1992	A-M
	Lepetella wisshaki Hoffman, 2018	A
	Profundisepta profundi (Jeffreys, 1877)	A
	Putzeysia wiseri (Calcara, 1842)	A-M
	Solariella cincta (Philippi, 1836)	
	Class Gastropoda, subclass Caenogastropoda	
	Alvania electa (Monterosato, 1874)	A-M
	Alvania porcupinae Gofas & Warén, 1982	A
	Alvania testae (Aradas & Maggiore, 1844)	A-M
	Alvania zetlandica (Montagu, 1816)	A-M
	Amiantofusus amiantus (Dall, 1889)	A
	Amphissa acutecostata (Philippi, 1844)	A-M
	Aporrhais serresianus (Michaud, 1828)	A-M
	Belomitra quadruplex (R. B. Watson, 1882)	A
	Benthobia tryonii Dall, 1889	A
	Bittium watsoni (Jeffreys, 1885)	A
	Brocchinia clenchi Petit, 1986	
	Buccinum humphreysianum Bennett, 1824	A-M
	Chauvetia balgimae Gofas & Oliver, 2010	A
	Colus islandicus (Mohr, 1786)	A
	Colus jeffreysianus (P. Fischer, 1868)	A-M
	Coralliophila basileus (Dautz. & Fischer, 1896)	A
	Corinnaeturris leucomata (Dall, 1881)	A-M
	Cryptonatica operculata (Jeffreys, 1885)	A-M
	Drilliola emendata (Monterosato, 1872)	A-M
	Drilliola loprestiana (Calcara, 1841)	A-M
	Epitonium celesti (Aradas, 1854)	A-M
	Epidendrium dendrophylliae (B. & W., 1986)	A-M
	Epitonium tiberii (de Boury, 1890)	A-M
	Euspira fusca (Blainville, 1825)	A-M
	Euspira subplicata (Jeffreys, 1885)	A
	Fusinus boucheti Hadorn & Ryall, 1999	A
	Galeodea rugosa (Linnaeus, 1771)	A-M
	Gibberula abyssicola Locard, 1897	A
*2	*Granulina minusculina* (Locard, 1897)	A-M
	Hastula denizi Rolán & Gubbioli, 2000	A
	Iphitus tuberatus Jeffreys, 1883	A-M
	Kryptos koehleri (Locard, 1896)	A
	Leptonotis perplexus (Suter, 1907)	A
	Leucosyrinx verrillii (Dall, 1881)	A
	Micropleurotoma spirotropoides (Thiele, 1925)	A-M
	Micropleurotoma travailleuri B. & W., 1980	
	Mitrella templadoi Gofas, Luque & Urra, 2019	A-M
	Neptunea contraria (Linnaeus, 1771)	A
	Onchodia valeriae (Fr. Giusti, 1987)	A-M
	Oocorys sulcata P. Fischer, 1884	A
	Phymorhynchus sulciferus (Bush, 1893)	A
	Pseudosetia ficaratiensis (Brugnone, 1876)	
	Pusillina amblia (Watson, 1886)	A
	Sabinella bonifaciae (F. Nordsieck, 1974)	A-M
	Spirotropis centimata (Dall, 1889)	A
	Spirotropis monterosatoi (Locard, 1897)	A-M
	Tectonatica rizzae (Philippi, 1844)	A-M
	Tritia coralligena (Pallary, 1900)	A-M
	Troschelia berniciensis (W. King, 1846)	A
	Typhlomangelia nivalis (Lovén, 1846)	A-M
	Class Gastropoda, subclass Heterobranchia	
	Crenilabium exile (Jeffreys, 1870)	A-M
	Doliella nitens (Jeffreys, 1870)	A-M
	Parthenina flexuosa (Monterosato, 1874)	A-M
	Philine monterosati Monterosato, 1874	A-M
	Ringicula gianninii F. Nordsieck, 1974	A-M
	Ringicula pirulina Locard, 1897	A
	Solatisonax hemisphaerica (G. Seguenza, 1876)	A-M
	Turbonilla micans (Monterosato, 1875)	A-M
	Tylodina duebenii Lovén, 1846	A-M
	Class Bivalvia, subclass Protobranchia	
	Acharax gadirae Oliver, Rodrigues & Cunha, 2011	A
	Ennucula aegeensis (Forbes, 1844)	A-M
	Ennucula corbuloides (G. Seguenza, 1877)	A
	Ennucula decipiens (Philippi, 1844)	A-M
	Katadesmia cuneata (Jeffreys, 1876)	A-M
	Ledella messanensis (Jeffreys, 1870)	A-M
	Ledella sublevis (Verrill & Bush, 1898)	A
	Malletia johnsoni A. H. Clarke, 1961	A-M
	Microgloma pusilla (Jeffreys, 1879)	A-M
*3	*Microgloma turnerae* Sanders & Allen, 1973	A-M
	Nucula atacellana Schenck, 1939	A
	Nucula tumidula Malm, 1861	A
*4	*Pseudoneilonella latior* (Jeffreys, 1876)	A
	Yoldiella insculpta (Jeffreys, 1879)	A
	Yoldiella jeffreysi (Hidalgo, 1877)	A
	Yoldiella philippiana (Nyst, 1845)	A-M
	Yoldiella semistriata (Jeffreys, 1879)	A
*4	*Yoldiella striolata* (Brugnone, 1876)	A-M
	Class Bivalvia, subclass Pteriomorphia	
	Amygdalum politum (Verrill & Smith, 1880)	A-M
	Asperarca nodulosa (O. F. Müller, 1776)	A-M
	Bathyarca philippiana (Nyst, 1848)	A-M
	Bathyarca pectunculoides (Scacchi, 1835)	A-M
	Bentharca asperula (Dall, 1881)	A
	Cyclopecten hoskynsi (Forbes, 1844)	A-M
	Dacrydium balgimi Salas & Gofas, 1997	A
	Dacrydium wareni Salas & Gofas, 1997	A

Table 6.4 (continued)

	Delectopecten vitreus (Gmelin, 1791)	A-M
	Hyalopecten pudicus (E. A. Smith, 1885)	A
	Idas argenteus Jeffreys, 1876	
	Limea crassa (Forbes, 1844)	A-M
	Limopsis angusta Jeffreys, 1879	
	Limopsis aurita (Brocchi, 1814)	A-M
	Limopsis minuta (Philippi, 1836)	A
	Limopsis cristata Jeffreys, 1876	A
	Propeamussium lucidum (Jeffreys, 1873)	A
	Pseudamussium peslutrae (Linnaeus, 1771)	A-M
	Pseudamussium sulcatum (O. F. Müller, 1776)	A-M
	Spondylus gussonii O. G. Costa, 1830	A-M
Class Bivalvia, subclass Heteroconcha		
	Abra longicallus (Scacchi, 1835)	A-M
	Abra profundorum (E. A. Smith, 1885)	A
	Axinulus croulinensis (Jeffreys, 1847)	A-M
	Axinulus alleni (Carrozza, 1981)	A-M
	Callogonia cyrili Cosel & C. Salas, 2001	A
	Genaxinus eumyarius (M. Sars, 1870)	A-M
	Kelliella miliaris (Philippi, 1844)	A-M
	Mendicula ferruginosa (Forbes, 1844)	A-M
	Thyasira granulosa (Monterosato, 1874)	A-M
	Thyasira succisa (Jeffreys, 1876)	A-M
	Thyasira subovata (Jeffreys, 1881)	A-M
*5	*Thyasira* cf. *obsoleta* (Verrill & Bush, 1898)	A-M
	Allogramma formosa (Jeffreys, 1882)	A-M
	Cardiomya cadiziana M. Huber, 2010	A
	Cardiomya striata (Jeffreys, 1876)	A
	Cochlodesma tenerum P. Fischer, 1882	A-M
	Cuspidaria rostrata (Spengler, 1793)	A-M
	Cuspidaria wollastonii (E. A. Smith, 1885)	A
	Cuspidaria ventricosa Verrill & Bush, 1898	A
	Halicardia flexuosa (Verrill & Smith, 1881)	A
	Haliris granulata (G. Seguenza, 1860)	A-M
	Halonympha depressa (Jeffreys, 1882)	A
	Jeffreysomya truncata (Jeffreys, 1882)	A
	Lyonsiella abyssicola (G. O. Sars, 1872)	A
	Lyonsiella subquadrata (Jeffreys, 1882)	A
	Policordia gemma (Verrill, 1880)	A-M
	Poromya granulata (Nyst & Westendorp, 1839)	A-M
	Protocuspidaria colpodes (Dautz. & Fischer, 1897	A
	Rhinoclama inflata (Jeffreys, 1882)	A
	Tropidomya abbreviata (Forbes, 1843)	A-M
	Verticordia quadrata E. A. Smith, 1885	
Class Scaphopoda		
	Antalis agilis (M. Sars, 1872)	A-M
	Fissidentalium capillosum (Jeffreys, 1877)	A
	Fissidentalium candidum (Jeffreys, 1877)	A
	Entalina tetragona (Brocchi, 1814)	A-M
	Pulsellum lofotense (M. Sars, 1865)	A-M

Notes to the taxon list:

*1. This taxon was described from the NW Atlantic as a variety of *Calliotropis infundibulum* (Watson, 1879), but the latter species with a type locality off Tristan da Cunha in the Southern Ocean may be different. The name *diomedeae*, introduced with a type locality in New England, is appropriate.

*2. It is unclear whether *Granulina melitensis* Smriglio, Mariottini & Rufini, 1998 is or not a representative of *G. minusculina* in the Central Mediterranean (see Boyer et al. 2020). Anyway, there are also documented occurrences of *G. minusculina* in the Alboran Sea so the species is scored as "Atlanto-Mediterranean".

*3. Ockelmann & Warén (1998) treated *Microgloma turnerae* as a synonym of *Microgloma tumidula* (Monterosato, 1880) and used for it the latter name. This was followed by Salas (1996) but was rebutted by Appolloni et al. (2018), who illustrated the type material and show that *M. tumidula* is actually a synonym of *M. pusilla*. Therefore, *Microgloma turnerae* remains a valid name.

*4. The species here referred as *Pseudoneilonella latior* was identified as *Neilonella striolata* (Brugnone, 1876) in Salas (1996) but La Perna (2007) unravelled the complicated taxonomic history and showed the valid name for this species to be *Pseudoneilonella latior*, whereas *Neilonella striolata* is actually an earlier name for the species later described as *Yoldiella seguenzae* Bonfitto & Sabelli, 1995.

*5. This species has been so identified by Payne & Allen 1991 (followed by Salas 1996), but it remains to be proved that Eastern and Western Atlantic populations are conspecific.

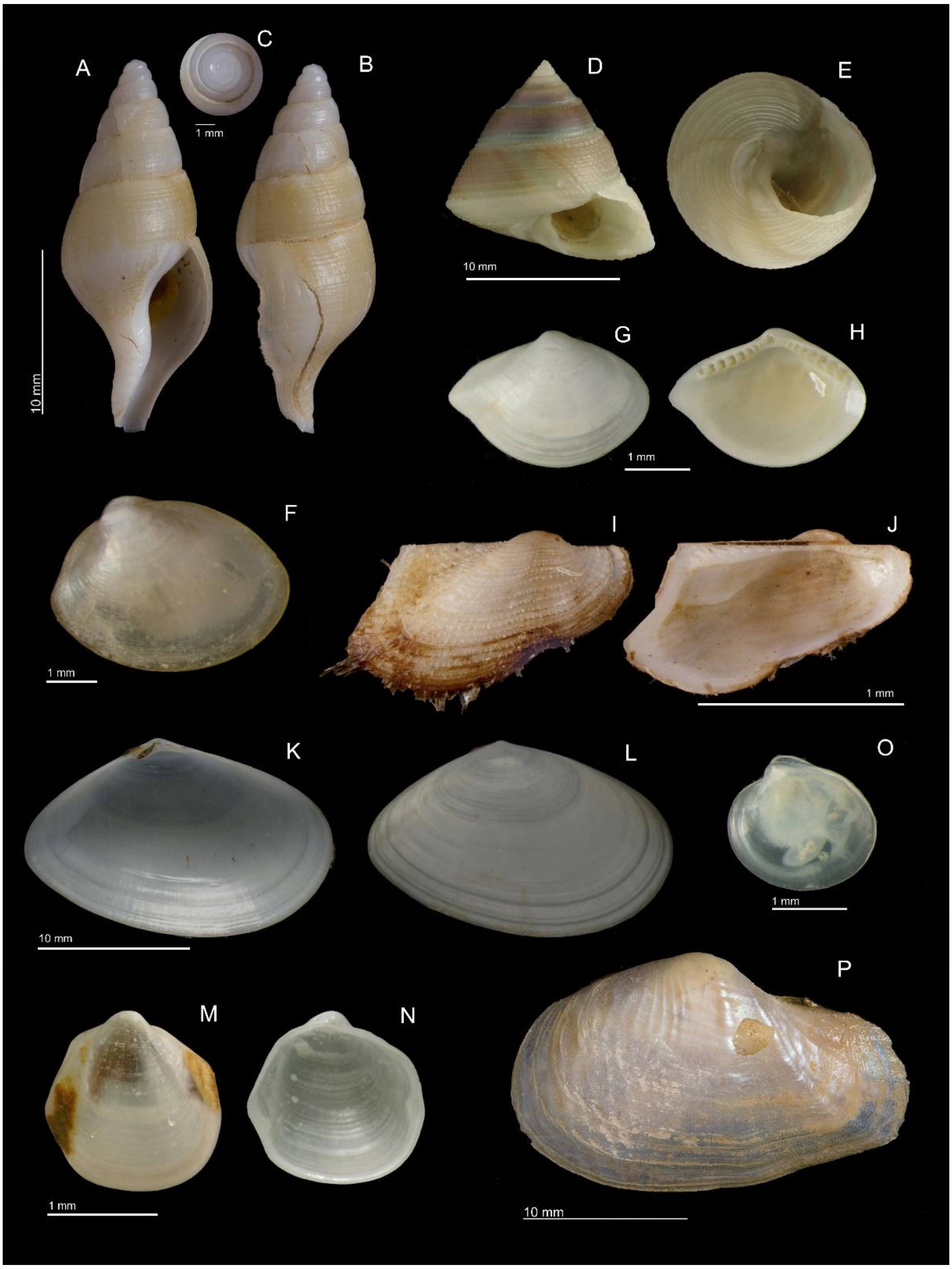


Figure 6.2. Representative species of the deep-water molluscs with an Atlanto-Mediterranean distribution, including the Mediterranean Outflow Water (MOW) but also Atlantic water masses with lower salinity. **A–C**: *Colus jeffreysianus* (h=24 mm) from CP156 (1135 m depth, modified MOW). **D–E**: *Calumbonella suturale* (h=13.5 mm) from Alboran Sea, Djibouti Banks (315 m depth, Levantine Intermediate Water [LIW]). **F**: *Nucula aegeensis* (l=4.7 mm) from Gulf of Cadiz, Pipoca mud volcano (MV) (626 m depth, MOW). **G–H**: *Ledella messanensis* (3.1 mm) from Gulf of Cadiz, Pipoca MV (568 m depth, MOW). **I–J**: *Asperarca nodulosa* (14 mm) from Gulf of Cadiz, off Faro (670 m depth, MOW). **K–L**: *Abra longicallus* (l=20 mm) from Alboran Sea, off Ceuta, CP119 (517 m depth, LIW). **M–N**: *Thyasira obsoleta* (1.6 mm) from Alboran Sea, off Ceuta, DW120 (425 m depth, LIW). **O**: *Kelliella miliaris* (2.0 mm) from Gulf of Cadiz, Tarsis MV (641 m depth, MOW). **P**: *Allogramma formosa* (24.5 mm) from off Rabat, CP92 (1182 m depth, Antarctic Intermediate Water).

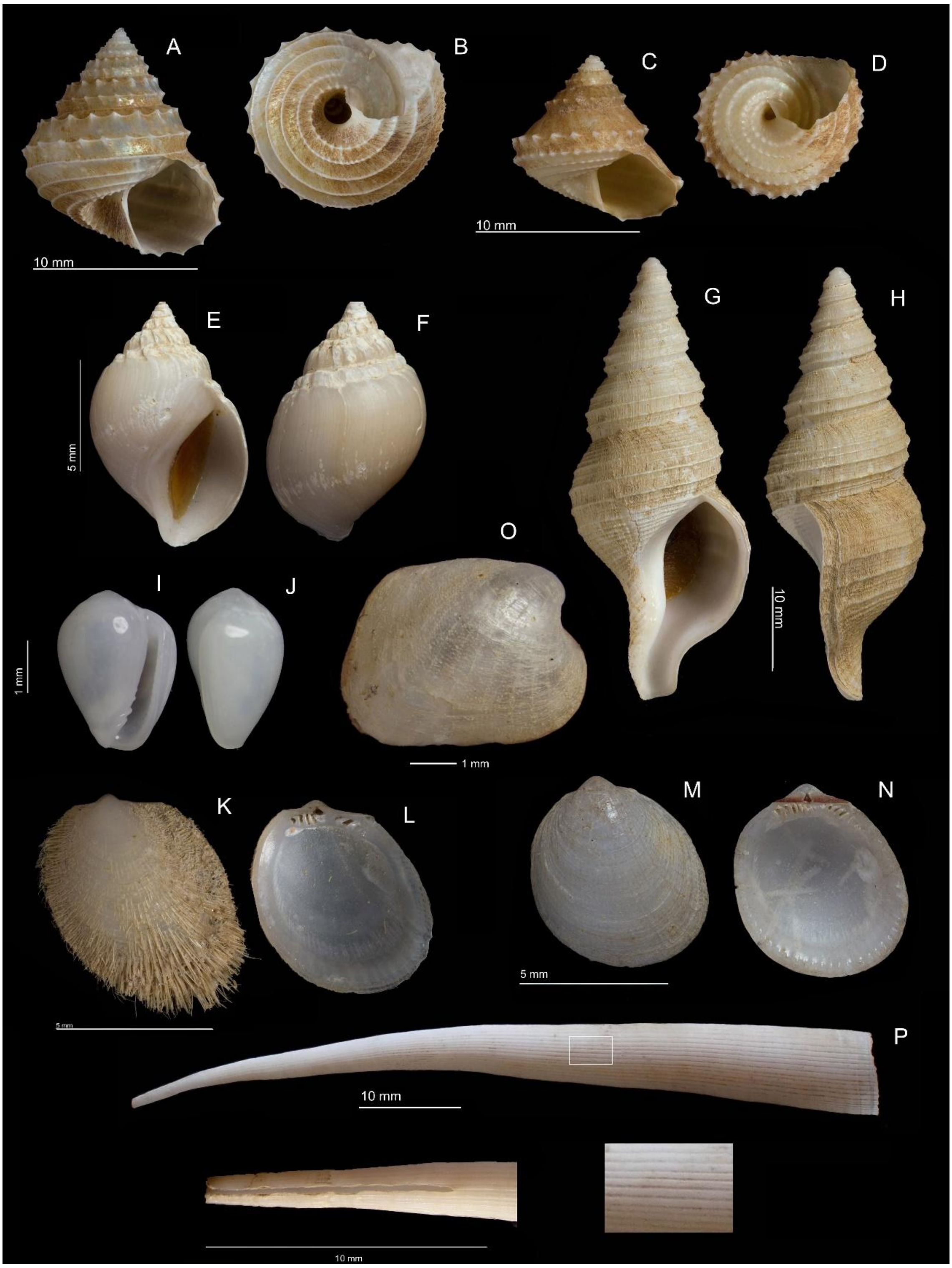


Figure 6.3. Representative species of the deep-water molluscs with an exclusively Atlantic distribution, in cool or cold water masses. **A–B**: *Calliotropis diomedeae* (d=12.4 mm) from off Rabat, CP95 (1378 m depth, Antarctic Intermediate Water [AAIW]). **C–D**: *Calliotropis talismani* (d=10.5 mm) from off Cape Spartel, CP 63 (1510 m depth, North Atlantic Deep Water [NADW]). **E–F**: *Benthobia tryoni* (h=11 mm) from off Huelva, CP 106 (1906 m depth, NADW). **G–H**: *Troschelia berniciensis* (h=48 mm) from off Cape St. Vincent, CP10 (1592 m depth, NADW). **I–J**: *Gibberula abyssicola* (h=3.1 mm) from off Huelva, (1360 m depth, modified Mediterranean Outflow Water). **K–L**: *Limopsis minuta* from off Rabat, CP91 (948 m depth, AAIW). **M–N**: *Limopsis cristata* from off Huelva, CP108 (1527 m depth, NADW). **O**: *Lyonsiella abyssicola* from off Cape St. Vincent, DW11 (1523 m depth, NADW). **P–R**: *Fissidentalium capillosum* from off Cape Spartel, CP 63 (1510 m depth, NADW).

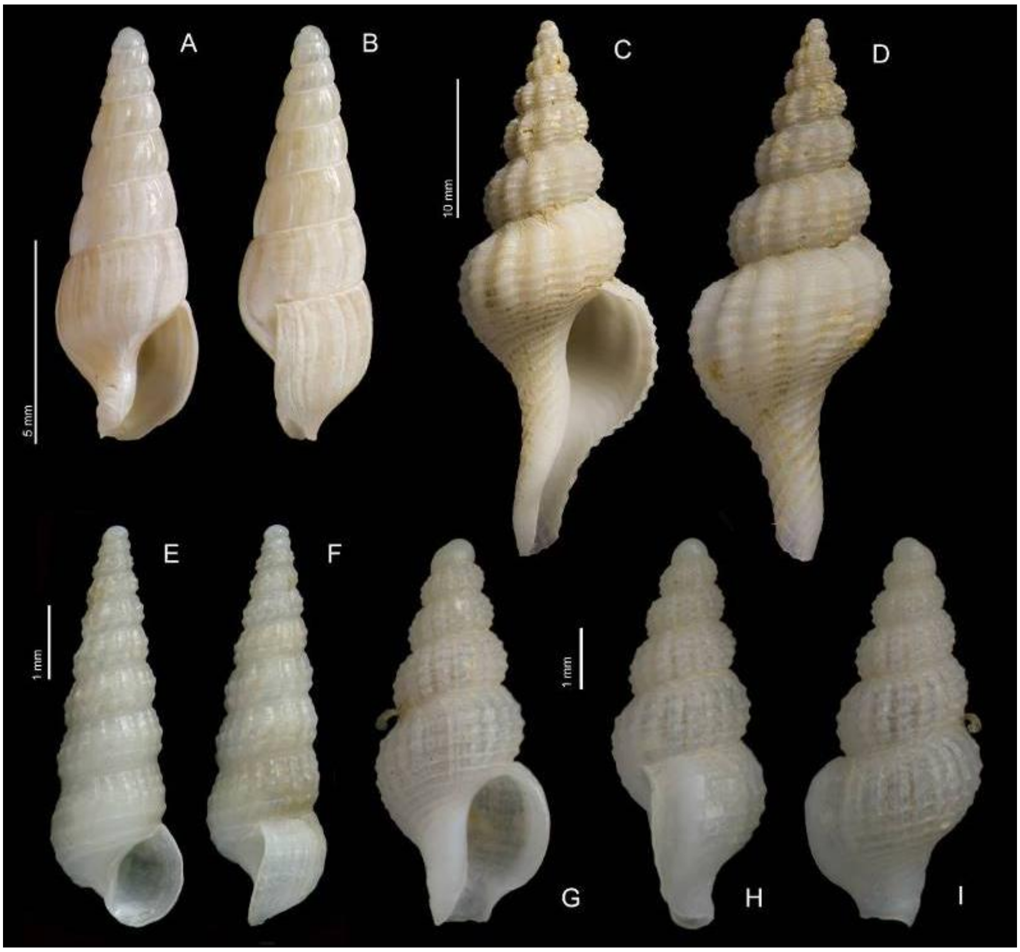


Figure 6.4. Species of the deep-water molluscs with an exclusively Atlantic distribution in warm water mass NACW. **A–B**: *Hastula denizi* (h=10 mm) from off Rabat, DR81 (309 m depth). **C–D**: *Bittium watsoni* (d=10.5 mm) from Gulf of Cadiz, Gazul mud volcano (371 m depth). **E–F**: *Fusinus boucheti* (h=38.2 mm) from off Rabat, CP86 (512 m depth). **G–I**: *Chauvetia balgimae* (holotype, h=6.3 mm) from off Rabat, DR82 (355 m depth).

6.3.2. Geographical restriction

Of the 154 recorded species (Table 6.4), more than half (84 species) are known to occur both in the Mediterranean Sea and the Atlantic Ocean, of which representative examples are shown on Fig. 6.2. Among the species with an Atlantic-only distribution (62 species), most (52 species) are associated to the cool or cold waters below 600 m depth along the Moroccan margin, and below the MOW in the northern part of the GoC, and representative examples are shown of Fig. 6.3. Four species strictly restricted to the Atlantic occur in the warm intermediate waters of the Moroccan margin (Fig. 6.4).

The pattern of occurrence of the species according to water masses (Fig. 6.5) shows definite trends. The deep-water species with an Atlantic-only distribution are mostly situated in NADW and AAIW. The two water masses nevertheless have quite different faunas, with only 27 shared species (12 Atlantic-only and 15 Atlanto-Mediterranean) out of 85 species recorded. The MOW pathway essentially holds Atlanto-Mediterranean species with only 4 species (*Bittium watsoni*, *Yoldiella semistriata*, *Limopsis minuta*, *Cardiomya cadiziana*) so far only known from the Atlantic, and those are represented with very low numbers of specimens. NACW (last column of Fig. 6.5) hosts a majority of Atlanto-Mediterranean species but quantitatively, the four warm-water species with an Atlantic-only distribution are important.

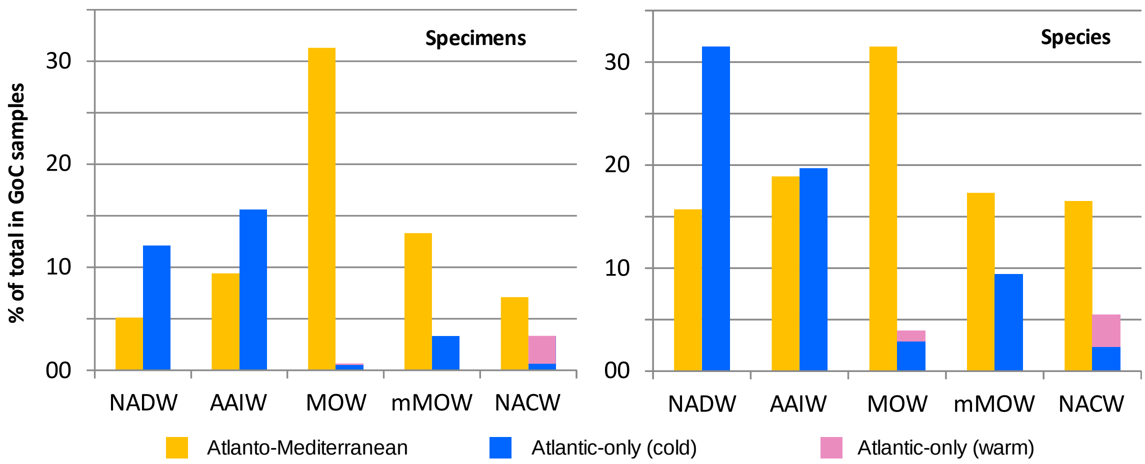


Figure 6.5. Percentages of Mollusca belonging to alternative distributional patterns (Atlanto-Mediterranean and Atlantic-only) occurring in samples located in the different water masses of the Gulf of Cadiz (GoC). See Table 6.2 for the detail of samples involved. Among species restricted to the Atlantic, the contribution of the four warm-water species is distinguished by colour. The percentages are referred to the total number of specimens (3291) and species (136) collected alive in this set of samples (Alboran Sea not included).

6.3.3. Assemblages

Eight groups of samples were recovered in the multivariate analyses of live-taken molluscs (Table 6.5, Supplementary Fig. S1). In addition, there are two pairs of samples which remain ungrouped. Those groups were supported by the SIMPROF test. The taxa which determined those groups are those displayed in Supplementary Table S3.

Table 6.5. Summary of groups recovered in the multivariate analyses of live-taken molluscs. First column indicates the numbers designating each group; Samples: number of samples involved in each group. NADW: North Atlantic Deep Water; MOW: Mediterranean Outflow Water; LIW: Levantine Intermediate Water; NACW: North Atlantic Central Water; SATL: Surficial Atlantic water; WMDW: Western Mediterranean Deep Water; Mmow: modified MOW; AAIW: Antarctic Intermediate Water.

Group	Samples	Depth range (m)	Sea	Main water masses involved
1	11	1578–2110	A	NADW
2	6	362–580	A+M	MOW – LIW
3	9	252–452	A+M	MOW – NACW – LIW
4	9	512–1470	A	mMOW – NACW – NADW
5	4	466–722	A	AAIW – MOW – NACW
6	28	250–1234	A+M	AAIW – mMOW – MOW – LIW - NACW
7	13	826–1527	A	AAIW – mMOW – NADW
8	5	347–1530	A	MOW – mMOW – NADW – NACW

Groups 1 and 7 comprise cold water samples situated either on the Moroccan slope (740–1255 m depth) in the depth interval of AAIW, or on either side of the GoC but deeper (1510–2035 m depth) in the range of NADW. The other groups are quite heterogeneous and comprise samples from different water masses. All these groupings are very poorly supported, and the overall similarity within any group with more than 10 samples remains below 25%. Similarity values over 50% are only found between pairs of samples, usually taken very close to each other. Moreover, the SIMPROF values (Supplementary Table S3) reflect a high standard deviation in the similarity values and therefore little support for the groupings.

The non-metric multidimensional scaling plot (MDS, Fig. 6.6) clearly shows a gradation from cold-water to warm-water samples, whereas low-saline and high-saline warm-water samples completely overlap. The samples situated in areas where the MOW mixes with surrounding cold and low saline water masses are all plotted in an intermediate position. When all the material (shells and live-taken specimens) is taken into account, the details of the sample positions differ but the overall trend remains unchanged (Supplementary Fig. S2).

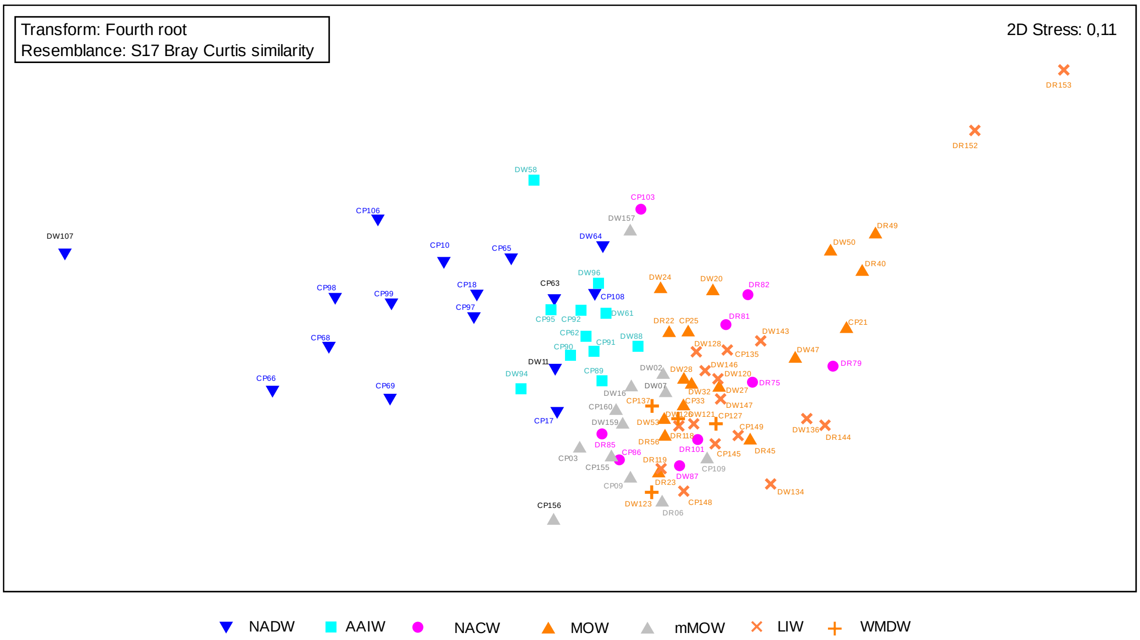


Figure 6.6. Non-metric multidimensional scaling plot of molluscan assemblages (live-collected specimens only) from the BALGIM benthic samples, based on quantitative similarities (abundance data transformed to fourth root). The molluscan assemblages differ between sites with cold or cool water (NADW, AAIW) and those with warmer water, but not so for difference in salinity. AAIW: Antarctic Intermediate Water; NADW: North Atlantic Deep Water; MOW: Mediterranean Outflow Water; LIW: Levantine Intermediate Water; NACW: North Atlantic Central Water; SATL: Surficial Atlantic water; WMDW: Western Mediterranean Deep Water; mMOW: modified MOW. Blue tones denote cold or cool and low saline, magenta, warm and low saline, and orange tones, high saline water masses.

6.4. Discussion

6.4.1. Overall species richness and abundance

The Mediterranean Sea is infamous for the poverty of its deep-sea fauna, both quantitatively and in species richness, when compared to the Atlantic (Cartes et al. 2004). Several authors including one of us (Salas 1996) had the impression that the fauna along the MOW pathway is "poor". Boury-Esnault et al. (1994) wrote that "the Atlantic stations concerned by the Mediterranean outflow are not particularly rich in species". However, this impression is not supported by numbers and diversity indices based on molluscs, and other studies (e.g. Harmelin & d'Hondt 1993: 71) found that the area affected by the MOW was "not poorer", albeit different from the southern part of the GoC which they qualify as "typically Atlantic". Values (see Table 6.3) in the Alboran sea are not significantly different from those in Gulf of Cadiz because we are looking at the uppermost bathyal. The range of diversity indices may be different in Mediterranean basins deeper than 2000 m depth (down to 5112 m in the Ionian Sea), which are not well explored and are probably very poor.

This being said, the representativeness of the BALGIM sampling must be qualified. The 154 species (243 species including those collected as shells only) fall very short of the 1214 benthic marine molluscs reported from Spanish waters of the Alboran Sea and the GoC (Gofas et al. 2017). Even considering that roughly half of those species are confined to shallow and shelf waters and are not expected to be represented in this dataset, BALGIM missed four out of five species, even if taking into account the thanatocenosis. The maximum species richness in the samples was 20 species (in CP95, off Rabat) and only 21 out of 99 hauls (5 in the Alboran Sea, 4 in the MOW or mMOW, 7 in AAIW, 3 in NADW and 2 in NACW) yielded more than 10 live-taken species. With the thanatocenosis, the maximum is 56 species also in CP95. Compared to this, a single very successful haul on Djibouti Banks in the Alboran Sea (Gofas et al. 2014b), situated within the LIW, yielded 156 species of molluscs (83 live-collected with 1772 specimens), therefore with a high value of the Shannon-Wiener diversity index ($H'(\log_2) = 3.60$, compared to a maximum of 3.14 and an average 1.85 in our material). Only 48 of the live-taken species from that haul were also represented in the BALGIM material, therefore missing at least 35 species whose occurrence is documented within the LIW in the Alboran Sea.

Several biases may explain this shortage. Firstly, the seafloor is commonly very rough in the area, particularly in areas where deep-sea hard bottoms may house the most diverse fauna including rare species. This is even worse in the Strait of Gibraltar due to intense maritime traffic and a tangle of cables lying on the bottom. Secondly, the standard sorting of organisms in a large-scale effort like BALGIM will yield less species than the intense sorting of a large amount of residue in the example of Djibouti Banks. In any case, the BALGIM results for molluscs must not be taken as a yardstick for benthic diversity in the area, although we trust the overall patterns revealed by this carefully planned set of samples.

6.4.2. Geographical restriction

The main outcome of this study is that the MOW is virtually impenetrable for the molluscan species with an Atlantic-only distribution and associated with cold Atlantic intermediate or deep-water masses, which amount to 52 species live-collected (85 species if including thanatocenosis) in our material. Such species are absent from the Mediterranean Sea although a few of them (e.g. *Neptunea contraria*, *Ennucula corbuloides*, *Limopsis minuta*, *Spinosipella acuticostata*) have a fossil record there (Di Geronimo & La Perna 1997, Massi et al. 2015). As could be expected, the bulk of the molluscan fauna found in the MOW comprises species also occurring in the Mediterranean. Conversely, there are many Atlanto-Mediterranean species extending their range into areas under influence of AAIW and NADW. Generally speaking, Atlanto-Mediterranean species qualify as widespread and are a majority among the mollusca in BALGIM. Among molluscs, there were no deep-sea species restricted to the Mediterranean.

Similar results are found with other groups. Sponges (phylum Porifera, Supplementary Fig. S3) collected by the BALGIM expedition have been studied in much detail by Boury-Esnault et al. (1994), who reported the occurrence of five Atlantic-only deep-sea species in the MOW pathway (out of a total of 27). However, a closer look at their species list reveals that all but one

(*Regadrella phoenix* Schmidt, 1880) were posteriorly found to live also inside the Mediterranean (WoRMS Editorial Board 2025). These authors did not provide the detail of species abundances, but taking into account that the Atlanto-Mediterranean *Thenea muricata* (Bowerbank, 1858) accounts for >1000 of their ca. 1270 specimens studied, the graph with sponge specimens would resemble closely our Fig. 6.5. With a total of 2458 specimens and 85 species, Decapods (García Raso 1996, Supplementary Fig. S4) faithfully repeat the trends shown in Fig. 6.5 albeit with less incidence of "warm" Atlantic-only species in areas under the influence of NACW, essentially populated by Atlanto-Mediterranean species. Hydrozoa (Ramil & Vervoort 1992) are less conclusive and seem to be strongly biased towards localities inside the Strait of Gibraltar where hard substrates occur, and most of the species reported are shelf species even in the deeper localities. This also happens with Bryozoa, with the aggravating bias that Harmelin & d'Hondt (1992a, b) did not distinguish between taxocenosis (live-taken specimens) and thanatocenosis. Other groups are either incompletely studied or hold so few species that an overall picture cannot be retrieved. This comparison with the results from other groups highlight the relevance of molluscs as proxies for the general benthos, a result of the enormous diversity of habitats that they successfully occupy.

The differentiation which occurs between the molluscan content of cold and less cold water masses is very apparent on the n-MDS (Fig. 6.6) with the localities expected to be situated in mixed waters in an intermediate position. This has moderate support only, with a value of the stress factor 0.11 (would be considered good if lower than 0.1 and with no support if over 0.3), but still shows a definite trend. It is noteworthy that the samples within cool or warm water (NACW, SATL, MOW, LIW, WMDW) overlap regardless of salinity. Therefore variation in salinity in a range of 1–2‰ seems not critical compared to temperature which explains most of the restricted distributions. Temperature has been found to be a key environmental driver controlling the distribution of benthic species: Belanger et al. (2012) found that temperature alone would predict 53–99% of the present-day distribution of bivalves along coastlines.

Limiting factors for deep-sea species which enter the Mediterranean involve (1) larval development and (2) the unique characteristics of Mediterranean deep water. Species with a planktonic larval development are prone to enter the Alboran Sea even if they live deeper than Camarinal Sill (284 m depth), because larvae of deep-sea species may migrate to superficial layers at some stage (Bouchet & Warén 1994); this is often reflected by brownish protoconchs on otherwise white shells. Regarding our material, 23 out of 84 Atlanto-Mediterranean deep-water species (27%) have a planktotrophic larval development, whereas only 7 out of the 62 species restricted to the Atlantic (11.3%) do so. Therefore, having a planktotrophic larval development certainly helps, but it is not a requisite since species like *Buccinum humphreysianum* and *Colus jeffreysianus* with an unquestionable direct benthic development and normally living deeper than the sill also have a Mediterranean range. Bouchet & Taviani (1992) wrote that "none of the Northeast Atlantic deep-sea Buccinidae or Marginellidae with intracapsular metamorphosis penetrates into the Mediterranean" but the abovementioned species are exception. For many species, the limiting factor inside the Mediterranean is exclusively controlled by the environmental conditions (Bouchet & Taviani 1992) even if larvae are repeatedly transported, but why some species never entered the Mediterranean and others did so remains mostly unexplained.

In colder climatic events, a fall by 3–4°C of deep Mediterranean water could be sufficient to make the whole basin hospitable to species now confined to AAIW, regardless of whether salinity would have remained high because of hydric balance.

6.4.3. Spatial heterogeneity

The cluster obtained using the similarity matrix does not show very definite groupings, and the overall similarity in any larger cluster is very low, mostly in the order of 20%. It is only among small groups of two or three samples, taken very close to each other, that we can find similarity values above 50%. This denotes an enormous heterogeneity in the sampled area, in which not only the characteristics of the sea-water in contact with the bottom but also substrate, current velocity, biotic factors and others may be intervening. Best discriminated are the samples associated to cold water masses.

6.5. Conclusions

The main outcome of this study is that most of the 62 species (out of a total of 154) with an Atlantic-only distribution, associated to the cool or cold waters below 600 m depth along the Moroccan margin, are barred by the Mediterranean Outflow Water in the northern part of Gulf of Cadiz. The Mediterranean outflow in the Gulf of Cadiz largely shares a set of species also occurring in the Mediterranean, whereas there are no Mediterranean-only deep-sea species. Therefore, the difference in sea water temperature (4–10°C in NADW and AAIW vs. >13°C in the MOW and NACW) is hypothesized to be the main factor limiting distributions, and those species which could pass this barrier are likely to overcome the difficulty of entering the Mediterranean Sea proper, regardless of the modality of larval development.

6B. A new species of *Anatoma* (Vetigastropoda: Anatomidae) from the Strait of Gibraltar

Abstract

A new species of the genus *Anatoma* Woodward, 1859, collected by the BALGIM expedition (1984) from the Atlantic entrance of the Strait of Gibraltar is described and figured. The new species is compared with other *Anatoma* species reported in this and other areas, from which it is distinguished by the axial sculpture of the shell with unusually numerous riblets. The large number of species of this genus found in the studied area highlights the importance of deep-sea research, revealing unexpected biodiversity and suggesting further exploration opportunities.

Resumen

Se describe e ilustra una nueva especie del género *Anatoma* Woodward, 1859, recolectada en la expedición BALGIM (1984) en la entrada atlántica del estrecho de Gibraltar. Se compara la nueva especie con otras especies de *Anatoma* citadas en esta y otras zonas, de las que se diferencia por la escultura de la concha compuesta por costillas axiales en un número mucho mayor de lo habitual. El elevado número de especies de este género encontradas en el área estudiada resalta la importancia de la investigación en aguas profundas, revela una inesperada biodiversidad y sugiere nuevas oportunidades de exploración.

6.6. Introduction

The genus *Anatoma* comprises small vetigastropods formerly placed in the family Scissurellidae, until Geiger & Jansen (2004) raised the subfamily Anatominae McLean, 1989 to family level, arguing that Scissurellinae is the sister group to Lepetodrilidae plus Clypeosectidae in a crown clade with Haliotidae, whereas Anatominae is amongst the most basal Vetigastropoda together with Pleurotomariidae. A closer attention and the support of imaging techniques using Scanning Electron Microscopy (SEM) has shown this genus to be diverse, with 90 recent species worldwide (WoRMS 2024), of which 54 have been described in this century and only 13 were already known in the XIXth century. Geiger (2012) provided the first global revision of "little slit shells" in which he described and imaged all hitherto known species. In European seas, *Anatoma crispata* (Fleming, 1828), the type species of the genus, was for a long time considered to be the only representative of the genus, whereas 17 species are now recognized.

The Gulf of Cadiz and the Alboran Sea are areas of extraordinary hydrological complexity, united by the narrow Strait of Gibraltar (Fig. 6.7) and a concomitantly diverse fauna. Within the Alboran Sea, incoming Atlantic Water occupies the superficial levels down to a maximum depth of ca. 150–200 m in the northern part and constitutes two anticyclonic gyres. The deeper part of the Alboran Sea is occupied by westward moving Mediterranean Deep Waters, which merge into a single plume to feed the outgoing Mediterranean Outflow Water (MOW) (Gascard & Richez 1985, Naranjo et al. 2015: 46). The highly saline MOW flows over the seabottom towards the Atlantic Ocean, crossing the Camarinal Sill at 284 m on the western side of the Strait, then extending westwards and northwards along the Iberian margin but not affecting at all the Moroccan slope. Along the NW African margin, there is instead a northwards flow of modified Antarctic Intermediate Water (AAIW) which abuts against the MOW in the same depth interval (Voelker et al. 2015).

Here we describe a distinctive additional species of *Anatoma* collected at the Atlantic entrance of the Strait of Gibraltar by the BALGIM expedition. We compare the new species to other previously known from the Atlantic (Geiger 2012, Pimenta & Geiger 2015, Hoffman et al. 2021, Hoffman & Freiwald 2022) and provide illustrations and notes on five species previously reported in the area: *Anatoma aspera* (Philippi, 1844), *A. eximia* (G. Seguenza, 1880), *A. micalii* Geiger, 2012, *A. tenuisculpta* (G. Seguenza, 1880), and *A. umbilicata* (Jeffreys, 1883).

6.7. Material and methods

BALGIM was a French oceanographic expedition set up in 1984 by the Muséum National d'Histoire Naturelle (MNHN) of Paris (chief scientist Philippe Bouchet), targeted to study the relationship between water masses and benthic fauna composition between the Atlantic and Mediterranean through the Strait of Gibraltar. Of a total of 125 benthic hauls, 115 (40 using the beam-trawl (CP), 33 using dredges (DR or DW)) collected molluscan specimens in a wide depth range from 115 to 2110 m depth. The coarse fractions were mostly sorted on board, whereas the finer fractions were preserved on board, sieved on 5, 2, 1, and 0.5 mm sieves, and later sorted under a stereomicroscope.

Additional comparative material was obtained from other sources. One sample (BV35, 36.003°N, -2.8325°W, 149–176 m depth) was collected during the LIFE+INDEMARES Alboran project (2011–2013), aimed at documenting habitats in the proposed offshore Site of Community Importance. Another sample was collected by H. Zibrowius on July 27, 1978, in sediment of a submarine cave under Isla de Tarifa (36.000°N, -5.606°W, 18 m depth) in the Strait of Gibraltar.

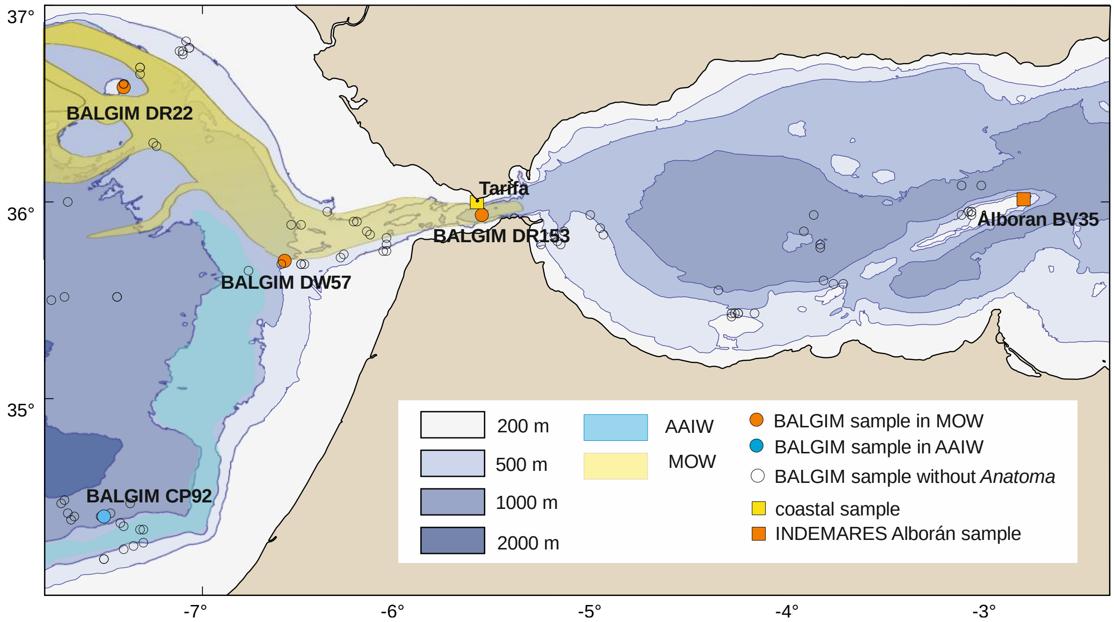


Figure 6.7. Map of the Ibero-Moroccan area showing the position of the collecting stations studied herein (coloured symbols). AAIW: Antarctic Intermediate water (flowing northwards along the Moroccan margin); MOW: Mediterranean Outflow Water.

6.8. Systematic description

Genus *Anatoma* Woodward, 1859

(Type species: *Scissurella crispata* Fleming, 1828, by monotypy)

Anatoma balgimae n. sp. (Fig. 6.8A–I)

LSID: urn:lsid:zoobank.org:act:34E1F305-03DE-423E-8F2E-FB924C9428C3

Syntype (MNHN-IM-2000-36202): 2 specimens from BALGIM DR153 (17 Jun. 1984), 580 m depth. Syntype 1: 1.59 mm diameter; syntype 2: 1.76 mm diameter. We designate syntypes rather than a holotype and a paratype, because both specimens are in good condition, are deemed conspecific, so that we are reluctant to delete one of them as name-bearing type.

Type locality: Morocco (35.9333°N, -5.58333°W, 580 m depth).

Other material examined (MNHN-IM-2000-36203): BALGIM DW57 (03 Jun. 1984; Morocco 35.7°N, -6.5833°W), 548 m depth, 1 sh. (1.50 mm diameter).

Description. Shell up to 1.76 mm in diameter, with a stepped spire and flat apex, with strongly protruding margin of selenizone; sculpture of very crowded axial cordlets and indistinct spiral threads; aperture rounded, tapering toward anal slit; suture deep; colour opaque white. Protoconch (Fig. 6.8H–I) of less than one whorl, with a rough surface (“flocculent sculpture” of Geiger 2012), transition to teleoconch clear by change of sculpture but not delimited by a rim.

Width of exposed part of protoconch 0.23 mm. Teleoconch of 2 ¼ whorls, with slightly convex shoulder area and rounded base, selenizone distinctly above periphery and very prominent (Fig. 6.8A,E). Teleoconch I (from end of protoconch to start of selenizone) of ⅓ convex whorl, flush with protoconch; about 26 fine axial curved riblets, with an indistinct series of aligned nodes giving the hint of a spiral line abutting on the start of selenizone. Teleoconch II (after the start of selenizone) with about 250 appressed axial riblets on the both adapical and abapical parts of the last whorl (Fig. 6.8A,C–E). Spiral sculpture consisting of indistinct, widely separated spiral threads, thinner than the axial riblets and not overriding them, in the middle of the adapical part and on the entire abapical part, more conspicuous towards the umbilicus (Fig. 6.8B,F); about 5 spiral threads adapically and 20 abapically. Selenizone with margins forming a sharply protruding ridge, smooth externally with the axial riblets fading out where abutting on the base of the ridge; strong symmetrical curved ribs within, widely separated, about half as numerous as axial ribs (Fig. 6.8G). Aperture with a sharp lip, smooth inside, tapering on its outer side toward the slit which is narrow and about ¼ whorl deep. Columellar lip sharp, protruding, rounded at base, markedly narrowing where meeting parietal area. Umbilicus moderately wide, deep, with a funiculus which is distinct (Fig. 6.8B) but situated far inside and hardly visible in apertural view.

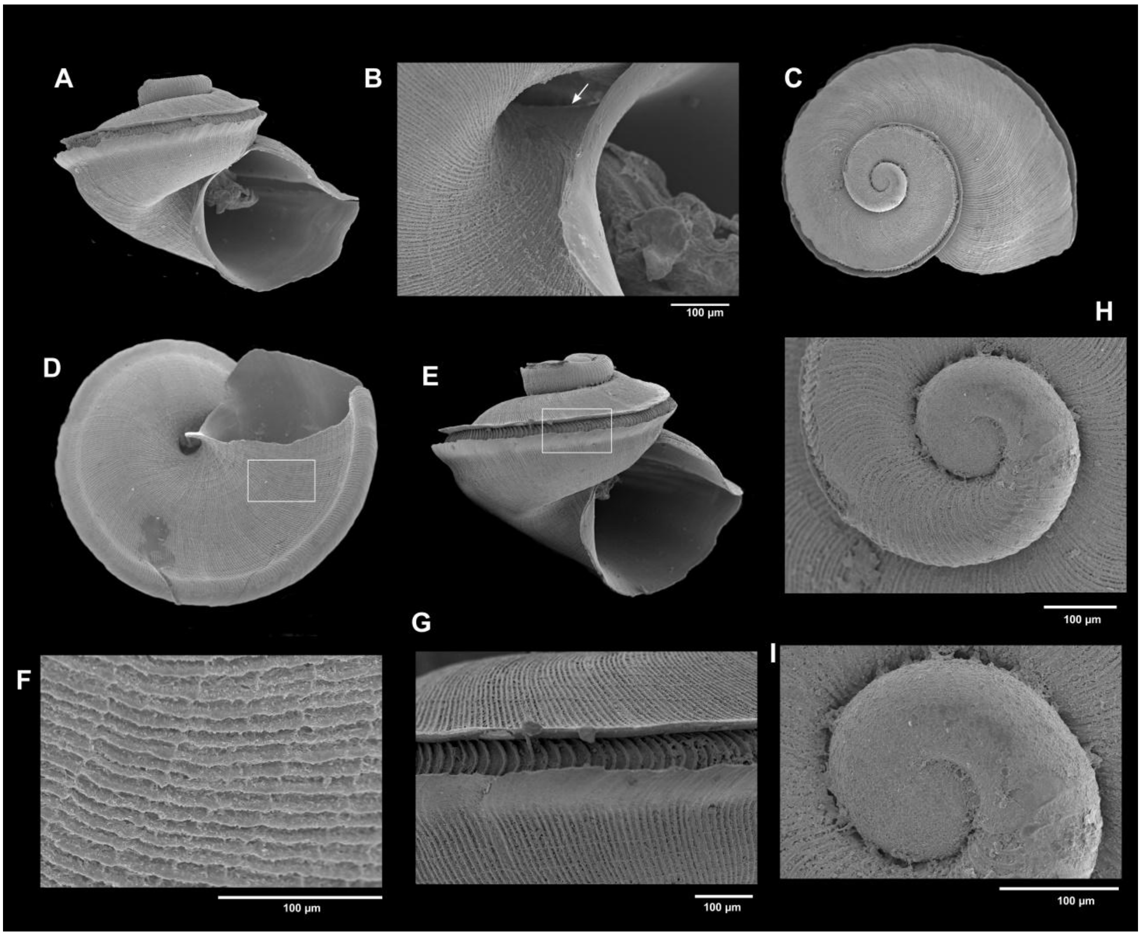


Figure 6.8. *Anatoma balgimae* n. sp. Syntypes, BALGIM DR153, Strait of Gibraltar, 35.9333°N, -5.58333°W, 580 m depth. **A**: Syntype 1 (diameter 1.59 mm). **B**: Oblique view of the umbilicus of syntype 1, showing funiculus (arrow). **C**: Syntype 1, apical view. **D**: Syntype 2, umbilical view (diameter 1.76 mm). **E**: Syntype 2. **F**: Detail of framed area in D. **G**: Detail of selenizone, framed area in E. **H**: Apical area including teleoconch I of syntype 2. **I**: Protoconch. Scale bars 100 µm.

Remarks. This species is thoroughly different from any other previously reported in European seas, mostly by its axial sculpture of so densely set riblets that the aspect under the optical stereomicroscope (and even under SEM at low magnification: see Fig. 6.8C) is silky rather than sculptured. The Australian *Anatoma aupouria* (Powell, 1937) is superficially similar in size and profile (see Geiger & Jansen 2004), with a similarly stepped spire, a strongly raised selenizone and broad last whorl. However, there are clearcut differences: the teleoconch I is a very short ¼ whorl with only 7 riblets, the axial sculpture extends over the raised sides of the selenizone, and the umbilical funiculus is conspicuous, among other details. The Brazilian *Anatoma campense* Pimenta & Geiger, 2015 is also similar in outline but has much fewer (ca. 80 vs. 250) axial riblets per whorl and is reported to lack a funiculus (Pimenta & Geiger 2015).

Etymology. The name honours the expedition where the specimens were collected.

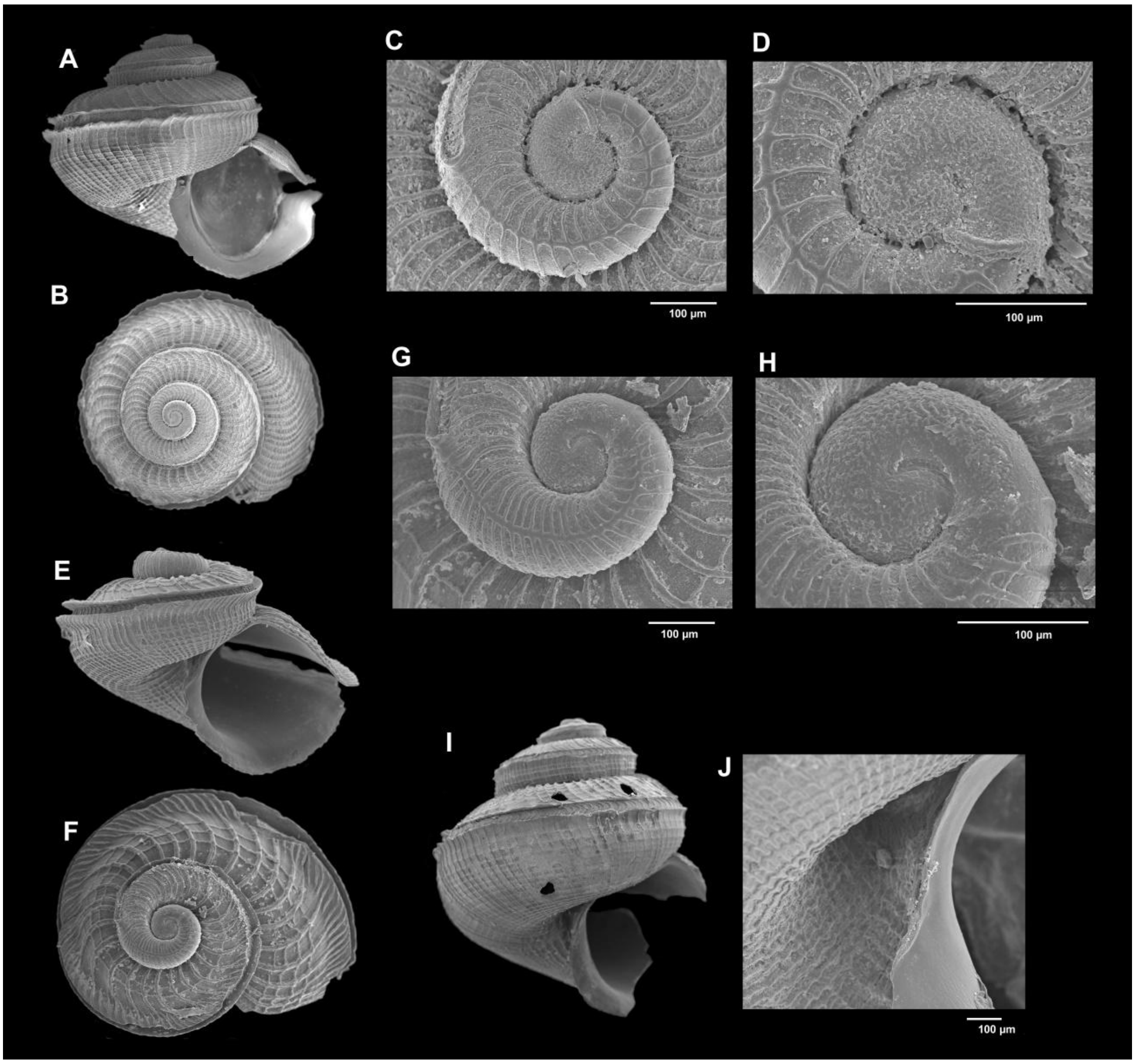


Figure 6.9. Other *Anatoma* species reported from the Gulf of Cadiz and the Alboran Sea. **A–D**: *Anatoma aspera* (Philippi, 1844) from INDEMARES Alboran BV35, 36.003°N, -2.8325°W, 149–176 m depth. **A**: Shell (diameter 2.36 mm). **B**: Shell (diameter 2.52 mm). **C–D**: Details of apical part with teleoconch I and protoconch, same specimen as B. **E–H**: *Anatoma micalii* Geiger, 2012 from a submarine cave next to Isla de Tarifa, 36.000°N, -5.606°W, 18 m depth, leg. H. Zibrowius 27 Jul. 1978. **E**: Shell (diameter 1.26 mm). **F**: Shell (diameter 1.33 mm). **G–H**: Details of apical part with teleoconch I and protoconch, same as F. **I–J**: *Anatoma eximia* (G. Seguenza, 1880) from BALGIM DR22, 36.5833°N, -7.4000°W, 466 m depth(height 2.92 mm). Scale bars 100 µm.

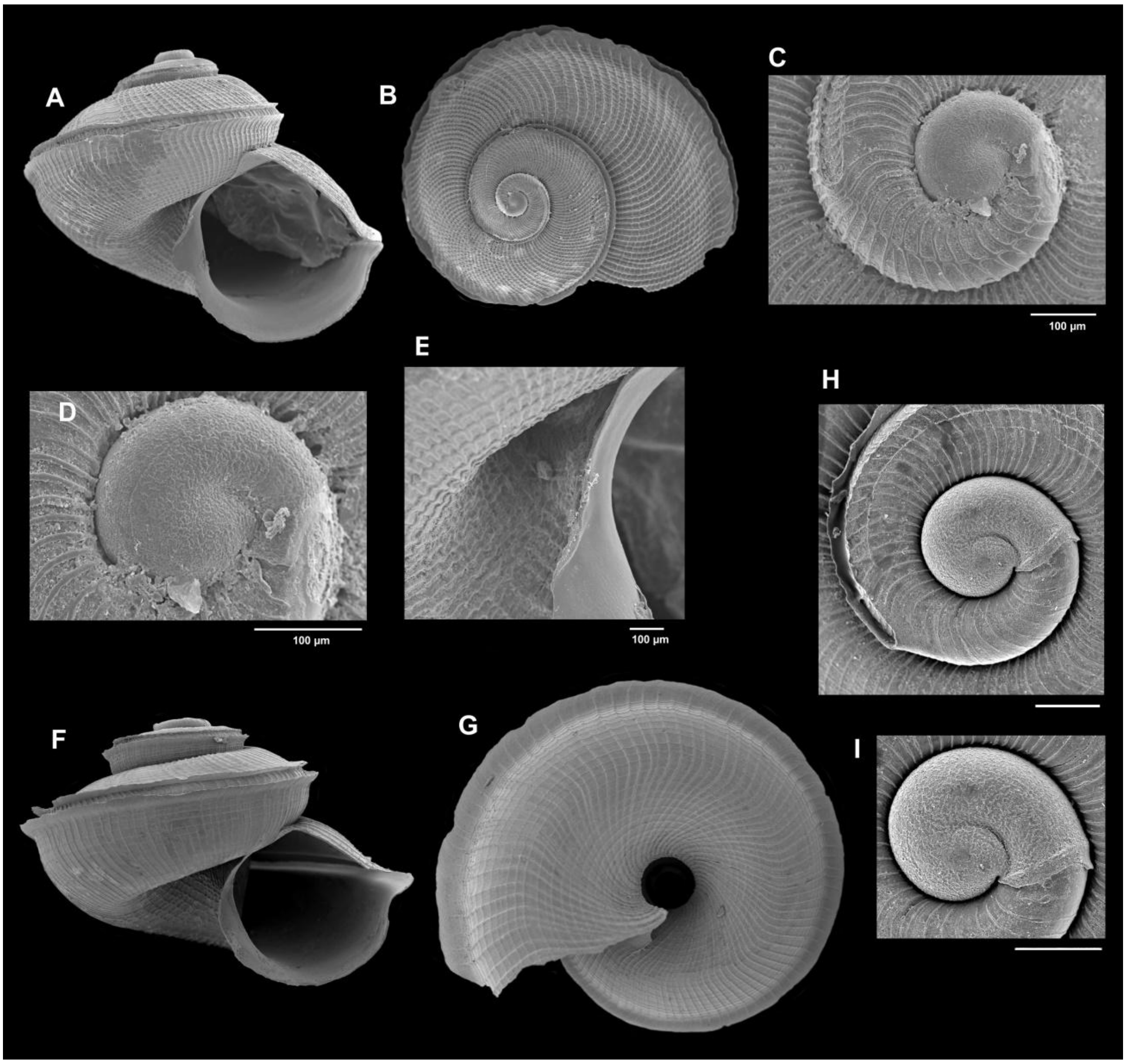


Figure 6.10. Other *Anatoma* species reported from the Gulf of Cadiz and the Alboran Sea. **A–E**: *Anatoma tenuisculpta* (G. Seguenza, 1880) from INDEMARES Alboran BV35, 36.003°N, -2.8325°W, 149–176 m depth. **A**: Shell (diameter 3.30 mm). **B**: Shell (diameter 2.64 mm). **C–D**: Details of apical part with teleoconch I and protoconch, same specimen as B. **E**: Oblique view of the umbilicus with no funiculum, same as A. **F–G**: *Anatoma umbilicata* (Jeffreys, 1883) from BALGIM CP92, 34.400°N, -7.500°W, 1182 m depth. **F**: Shell (diameter 2.19 mm). **G**: Shell (diameter 2.40 mm). **H–I**: Details of apical part with teleoconch I and protoconch, same specimen as F. Scale bars 100 µm.

All other species known in the area considered are so different that comparisons may be deemed superfluous. The most common of them is *Anatoma aspera* (R. A. Philippi, 1844), which has an elevated spire, a sculpture of 50–60 axial riblets much narrower than their interspaces, distinct spiral threads, and a very moderately salient selenizone (Fig. 6.9A–D). A single shell of *Anatoma eximia* (G. Seguenza, 1880) was found at 466 m depth in the northern part of Gulf of Cadiz; that species resembles *A. aspera* in having an elevated spire but is unambiguously distinguished by the elevated position of the selenizone (about mid-whorl in *A. aspera*) and by the narrow umbilicus lacking a funiculus inside (Fig. 6.9I–J).

Anatoma micalii Geiger, 2012 was reported from the Moroccan part of the Strait of Gibraltar (Geiger 2012), the Alboran Sea on Chella Bank (Caballero-Herrera et al. 2023), the Gulf of Cadiz (Utrilla et al. 2020) and in a submarine cave next to Tarifa Island, Strait of Gibraltar (this study, Fig. 6.9E–H). This small species also has a low, stepped profile of the spire and the raised selenizone, but the sculpture is radically different from that of *A. balgimae* n. sp. with its last whorl havingonly 60–100 axial riblets abapically, and only ca. 30 strong ribs on the adapical part. The Azorean shallow-water species *Anatoma janusa* Geiger, 2012 resembles *A. micalii* in many respects and therefore differs in the same way from *A. balgimae* n. sp.

A relatively large species tentatively identified as *Anatoma tenuisculpta* (following Geiger 2012: Fig. 916C; misidentified as *Anatoma crispata* in Gofas et al. 2011) was found on the Djibouti Banks (shells only; Gofas et al. 2014b) and around Alboran Island (live specimens and shells, Fig. 6.10A–E). It is twice as large as *A. balgimae* n. sp., has a narrow, hardly raised selenizone and the spire is low conical, with the last whorl attached to the previous one only a short distance from the suture.

The deep-water species *Anatoma umbilicata* (Jeffreys, 1884) was found represented by two shells (Fig. 6.10F–G) in 1182 m depth off Rabat, Morocco, in an area which is not influenced by the Mediterranean Outflow Water. This and the similar *Anatoma pagoda* Hoffman, Gofas & Freiwald, 2021 differ from *A. balgimae* n. sp. in having a flatter profile on the adapical part of the whorls, a deep, much broader umbilicus and an attenuated axial sculpture with only ca. 90 riblets on the last whorl.

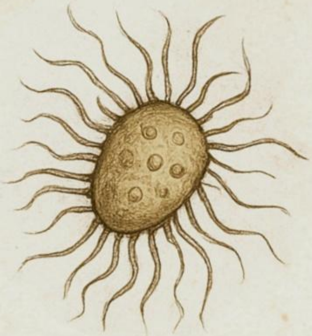
The enigmatic *Anatoma orbiculata* Geiger, 2012 (not illustrated; see Geiger 2012: 996–999) differs thoroughly in having a biconvex profile, and few strong, widely separated axial ribs. It was described from beach drift collected by the second author in 1971, at the mouth of Oued el Helou just north of Asilah (Morocco; misspelled Qued el Helou, Asilha in Geiger 2012), and is known only from one further occurrence is southern Angola (Geiger 2012). This occurrence is discrepant with the usual occurrence of *Anatoma* species in circalittoral and bathyal environments. One possible explanation is that the shell could come from the cleaning of fishing gears operating down to the *Dendrophyllia* zone (ca. 180 m depth) off Asilah at that time. Another recently described species, *A. symmetrica* Hoffman, Gofas & Freiwald, 2021 from seamounts south of the Azores resembles *A. orbiculata* in having a similar number of ribs above and below suture, but differs still more drastically from *A. balgimae* n. sp. in having less than 50 ribs in the last whorl.

6.9. Discussion

The deeper part of the Strait of Gibraltar is one of the most inaccessible deep-sea areas, where sampling is hindered by heavy maritime traffic and chaotic hard bottoms with the risk of being entangled by submarine cables and other obstacles. BALGIM had two successful operations (DW152 and DW153) in the core of the Strait, which also yielded live specimens of the recently described *Mitrella templadoi* Gofas, Luque & Urra, 2019 (Gofas et al. 2019) and of the rare epifaunal bivalve *Limopsis angusta* Jeffreys, 1879 (Salas 1996). There were also operations at the western entrance of the Strait, among which DW57 yielded very few specimens, but those included the rare *Manzonia alexandrei* Gofas, 2010 and one of the *Anatoma balgimae* n. sp. samples.

The type locality of *Anatoma balgimae* and *Mitrella templadoi* is situated in the core pathway of the Mediterranean Outflow Water, and this demonstrates that locations situated within this highly saline (>38‰) water do not harbour only environmentally tolerant, widespread species. The habitat with outcrops of mud-free rock located in the aphotic zone is nevertheless quite exceptional and can only occur where the topography of the bottom is steep and currents sufficient to eliminate the fine-grained hemipelagic sediment which otherwise covers most of the bathyal sea floor. Such conditions are also met with on seamounts and other submarine elevations such as Chella Bank in the Alboran Sea, where *Mitrella templadoi* occurs in 250–320 m depth on a rocky bottom (Gofas et al. 2023), regardless of the water mass involved. Conversely, other species such as *Anatoma umbilicata* were so far found only in cool or cold deep water such as the AAIW flowing along the Moroccan margin of NADW flowing below the Mediterranean outflow (type locality off Portugal in 1100–1800 m depth).

These glimpses into the deep Strait suggest that more surprises are to be expected, would the technical difficulties be overcome. Especially promising and poorly known are the deep areas surrounding the Camarinal sill and Spartel Bank at the western entrance.



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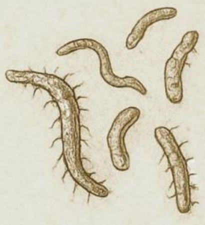
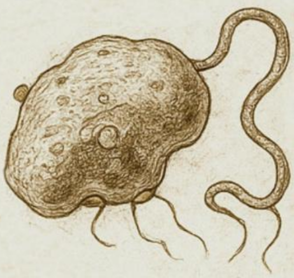
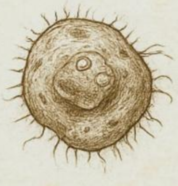
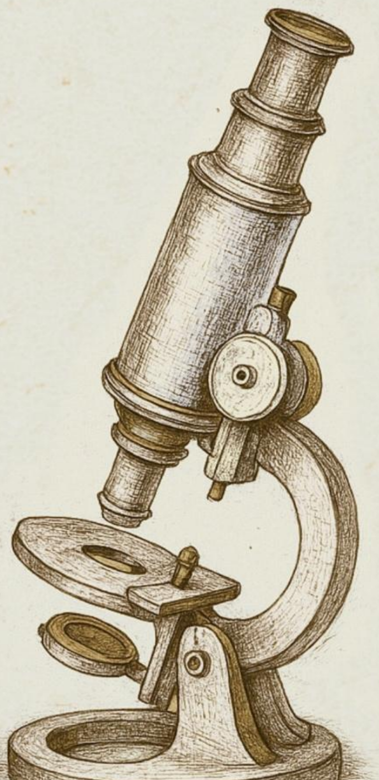


Life at Oxygen Minimum Zone: bacterial symbiosis in the gills of the bivalve *Kelliella miliaris*

Vida en la Zona de Mínimo Oxígeno: simbiosis bacteriana en las branquias del bivalvo *Kelliella miliaris*







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https//doi.org/10.3389/fmars.2025.1587729

7. LIFE AT OXYGEN MINIMUM ZONE: BACTERIAL SYMBIOSIS IN THE GILLS OF THE BIVALVE *KELLIELLA MILIARIS*

Abstract

Kelliella miliaris (Philippi, 1844) is a minute bivalve, living on the surface of soft sediments, from the continental shelf to bathyal depths, commonly in the Oxygen Minimum Zones (OMZ) and/or in reducing habitats. The scarcity of data on the biology of *Kelliella* prompted us to investigate, at ultrastructural level, specimens found in southern Spain. *Kelliella miliaris* shows several morphological characteristics that would be adaptive for living in the OMZ: (1) presence of numerous muscular fibres in the mantle, mantle edge and gills-visceral mass connection; all of which would allow to actively move the gills and/or enable a better control of the ventral opening in relation to vertical movements of the animal; (2) high number (in relation to body size) and large size of gill filaments, mainly in the large inner demibranch; and (3) long cilia which would provide a large surface for capture of oxygen and a highly effective uptake of oxygen from water.

We have observed in all the specimens examined the presence of numerous rod shaped bacteria among the gill cilia. These bacteria show the typical double membrane of Gram-negative bacteria. The analysis of the bacterial DNA revealed that Gammaproteobacteria is the most abundant class, with 53.69% of total reads. The latter, together with the peak of oxygen and the presence of sulphur inside the electron dense granules from the bacteria, determined by TEM-EDX analysis, point to the involvement of these bacteria in the oxidization of the sulphide to thiosulphate. The presence of bacteria in the gills of *Kelliella miliaris* highlights the importance of the chemosynthetic symbiosis in the OMZs of the oceans that has been probably overlooked up to now.

The presence of different microorganisms in the stomach indicates heterotrophy. We have found spermatozoids inside the female gonad, which confirms internal fertilization in *K. miliaris*. However, the presence of protoconch I and protoconch II, indicates planktotrophic larval development.

Resumen

Kelliella miliaris (Philippi, 1844) es un diminuto bivalvo que vive en la superficie de sedimentos blandos, desde la plataforma continental hasta profundidades batiales, comúnmente en las Zonas de Mínimo Oxígeno (OMZs) y/o en hábitats reductores. La escasez de datos sobre la biología de *Kelliella* nos llevó a investigar, a nivel ultraestructural, especímenes encontrados en el sur de España. *Kelliella miliaris* muestra varias características morfológicas que serían adaptativas para vivir en la OMZ: (1) presencia de numerosas fibras musculares en el manto, en el borde del manto y en la conexión entre las branquias y la masa visceral; lo que le permitiría mover activamente las branquias y/o posibilitar un mejor control de la apertura ventral en relación con los movimientos verticales del animal; (2) alto número (en relación con el tamaño corporal) y gran tamaño de los filamentos branquiales, principalmente en la gran demibranquia interna; y (3) cilios largos que proporcionarían una gran superficie para la captura de oxígeno y una absorción altamente efectiva del oxígeno del agua.

Hemos observado en todos los especímenes examinados la presencia de numerosas bacterias con forma alargada entre los cilios branquiales. Estas bacterias muestran la típica doble membrana de las bacterias gramnegativas. El análisis del ADN bacteriano reveló que la clase Gammaproteobacteria es la más abundante, con un 53.69% del total de lecturas. Por último, el pico de oxígeno y la presencia de azufre dentro de los gránulos densos de electrones de las bacterias, determinados por análisis TEM-EDX, apuntan a la participación de estas bacterias en la oxidación del sulfuro a tiosulfato. La presencia de bacterias en las branquias de *Kelliella miliaris* resalta la importancia de la simbiosis quimiosintética en las OMZs de los océanos, que probablemente ha sido pasada por alto hasta ahora.

La presencia de diferentes microorganismos en el estómago indica heterotrofia. Hemos encontrado espermatozoides dentro de la gónada femenina, lo que confirma la fertilización interna en *K. miliaris*. Sin embargo, la presencia de protoconcha I y protoconcha II indica un desarrollo larvario planctotrófico.

7.1. Introduction

Oxygen Minimum Zones (OMZs), also called Oxygen Minimum Layers (OMLs), are, in general, pelagic habitats with stable conditions of continuously low oxygen level and low temperature that are found at intermediate depths (400–1000 m depth), over vast areas in most of the world's oceans. Where the OMZs intersect continental margins, stable low oxygen conditions are also found in the benthic habitat. The OMZs differ from other hypoxic aquatic habitats in that very low oxygen levels are stable over long periods and large areas (Childress & Seibel 1998). These OMZs develop because the consumption of oxygen relative to replenishment is greater than at shallower and greater depths. The consumption and supply of oxygen at shallower depths is higher than at greater depths where there are strong reductions of biomass (Sewell & Fage 1948). Those few species that do live in pelagic habitats with very low oxygen concentrations are typically diurnal vertical migrators which enter shallower, more oxygenated waters at night (Childress & Seibel 1998 and references therein), however, nothing is known about the existence of vertical migrations of the fauna from benthic OMZs.

Persistent oxygen (O_2) deficiency occurs when the amount of dissolved O_2 in the water column is consumed faster than it is resupplied through air–sea exchange, photosynthetic O_2 production and ventilation. Thus, in profile, OMZs resemble a band of O_2-deficient water inserted between two O_2-containing water masses. The amount of O_2 chosen to define OMZs ranges from <2 µmol O_2 per kg water to 90 µmol O_2 per kg water (Wright et al. 2012).

Three are the proposed possible physiological adaptations of the organisms to the OMZs: (1) the development of mechanisms for the highly effective capture of oxygen from water; (2) the reduction of metabolic rates; or (3) the use of anaerobic metabolism to make up the difference between aerobic capacity and total metabolic demand (Childress & Seibel 1998). Some groups, such as fishes, crustaceans, molluscs or polychaetes, have specialized circulatory systems and respiratory systems which offer possibilities for adaptations.

To obtain nutrients in poor, oligothrophic conditions, such as those found widely in the deep sea, is considered one of the driving forces for the evolution of chemosymbiosis (Kleiner et al. 2012). Chemosynthetic symbioses represent an adaptation to ecosystems and habitats with reducing conditions, such as cold seeps and hydrothermal vents, but up to now relatively little is known regarding their diversity and functioning apart from a few "model species" on which effort has focused over the last decades (Duperron et al. 2013). Symbioses have often been overlooked in other habitats, in which symbiotic species are not dominant and somewhat smaller. The ability to associate with chemosynthetic bacteria is a recurring feature in the evolution of bivalves, since it has appeared independently in at least five families, Mytilidae, Vesicomyidae, Solemyidae, Lucinidae and Thyasiridae (Duperron et al. 2013), and more recently discovered in other two: Nucinellidae and Lasaeidae (Oliver 2012, Oliver & Taylor 2012). Four of these families (excluding Mytilidae) are associated with sulphur-oxidizing Gammaproteobacteria. Species of the family Mytilidae are characterized by a broader diversity of associated bacteria. Endosymbiont bacteria found in gill tissues in these families convert otherwise unavailable energy sources (sulphide, methane) to forms readily metabolized by their host, but species of the families Xylophagaidae and Teredinidae, which colonize driftwood or sunken wood, have endosymbiont bacteria for the conversion of terrestrial derived cellulosic carbon from wood into animal biomass in the deep sea (Distel & Roberts 1997).

Low-O_2 marine communities are typically inhabited by a reduced diversity of generally unmineralized, low-density, and small-sized taxa (Sperling et al. 2015), and they are usually opportunistic detritivores (Levin 2003). Organisms from the OMZs have developed a series of physiological or behavioural adaptations that allow them to maintain aerobic metabolism with reduced energy demand, such as enhancing O_2 extraction, transport, and storage (Childress & Seibel 1998). Some species are facultative anaerobes and they can switch to anaerobic metabolism in order to sustain reduced rates of energy turnover while in hypoxia (Borges et al. 2022 and references therein).

The OMZs are extensive in the eastern Pacific Ocean, the Arabian Sea and off West Africa (Levin et al. 2000 and references therein). The faunal assemblage living at the OMZ has been mainly studied in the Arabian Sea and California slope. Levin et al. (2000) studied the macrobenthic community structure within and beneath the OMZ from the NW Arabian Sea where they found highest macrofaunal densities in the middle of the OMZ, at 700–850 m depth, intermediate at 400–1000 m depth and lowest at the 1250–3400 m depth stations. In general, the polychaetes accounted for 88.8% of total collected individuals; molluscs and crustacean represented only 3.4 and 5.7% of the specimens respectively. Due to the use of box-corer, the megafauna was under-represented in this study. Among the 35 taxa of molluscs collected from the NW Arabian OMZ, there were six taxa usually associated with chemosynthetic bacteria (one *Lucinoma* sp. and five *Thyasira* spp.) (Dufour 2005, Taylor & Glover 2006) and one *Kelliella* sp. Also in the OMZ of the Arabian Sea, off southern Oman, bacterial symbiosis was reported in two new species of bivalves of the family Nucinellidae (Oliver & Taylor 2012), in which bacteriocytes with bacteria were observed inside the gills. However, Cook et al. (2000) found in the OMZ on the Oman slope that the abundance of nematodes was correlated with food quality (measured as the hydrogen index) rather than oxygen.

Within the OMZ from the Indian continental margin, changes in abundance of the megafaunal assemblage (composed by Porifera, Cnidaria, Mollusca, Crustacea, Echinodermata, Ascidiacea and Gnatostomata) were correlated to both oxygen availability and sediment organic matter quality (Hunter et al. 2011). Fish dominated the assemblage in the OMZ at 540 m depth, but at 800 m depth high densities of ophiuroids and decapods produced megafaunal abundance peaks, and below this boundary total faunal abundance declined gradually with depth. The latter data support previous evidences that the specific responses of individual taxa to oxygen limitation and organic matter availability determine megafaunal zonation within an OMZ continental margin (Levin et al. 1991, Hunter et al. 2011). Some species were also present in upper, more-oxygenated, ocean layers, but the individuals from the OMZ had physiological adaptations able to survive with low oxygen. In the OMZ of southern end of the California Current, down to oxygen concentrations of 0.2 µml/l, the zooplankton was abundant, with several species that perform nocturnal vertical migration toward upper layers with more oxygen (Longhurst 1967).

Small-SubUnit ribosomal RNA (SSU rRNA) gene sequences associated with chemoautotrophic, sulphur-oxidizing gill symbionts of deep-sea clams and mussels were first identified in open-ocean OMZs in the Arabian Sea, the eastern tropical South Pacific and the Namibian upwelling (Fuchs et al. 2005, Stevens & Ulloa 2008, Lavik et al. 2009). The discovery of potential sulphur oxidizer in non sulphidic water is enigmatic, bringing into question the source of the reducing equivalents that are needed to fix inorganic carbon (Wright et al. 2012).

The physiology of thiotrophic bacteria thriving on the surface of animals (ectosymbionts) is less understood. A longstanding hypothesis proposes that attachment to animals that migrate between reduced and oxic environments would boost sulphur oxidation, as the ectosymbionts would alternatively access sulphide and oxygen, the most favourable electron acceptor (Paredes et al. 2021).

The type species of the bivalve genus *Kelliella* is *K. abyssicola* Sars 1870, currently considered junior synonym of *Kelliella miliaris* (Philippi, 1844) (WoRMS 2024) *Kelliella miliaris* is present from off Norway to Canary Islands in the Northeastern Atlantic and in the Mediterranean Sea (Allen 2001, Krylova et al.2018, Utrilla et al. 2024). It is a benthic species, living on the surface of soft sediments (Clausen 1958), from the continental shelf to bathyal depths. The stable δ^{13} C and δ^{15} N isotopic composition of *K. miliaris* was found similar to that of *Vesicomya*, suggesting heterotrophy (Krylova et al. 2018). *Kelliella miliaris* was present in high abundance in the low oxygen layer of Cap Breton (southeastern Bay of Biscay) (Jean Claude Sorbe, pers. comm.). It is interesting to point that some species of *Kelliella*, such as *K. miliaris*, occur in organic carbon enriched habitats (Molina et al. 2019) or even exposed to reduced conditions, where can reach high numbers in sulphidic habitats, where pogonophorans are present (Southward 1981, Krylova et al. 2018). According to the latter authors, the scarcity of data on the biology of *Kelliella* and in particular the fact that specimens have been observed in organic-rich or even reducing environments warrant further investigations of this group. Therefore, the presence of symbiotic bacteria in the gills of *Kelliella miliaris* described in this study could be the response to the presence of *K. miliaris* in low oxygen and/or reducing habitats.

7.2. Material and methods

We have examined ultrastructurally five specimens of *Kelliella miliaris*, two from the Gulf of Cadiz (INDEMARES/CHICA 0211; 36°37.62'N, 07°12.2'W, 735 m depth) and three from Bay of Malaga (field work of graduate programme DiBiMA (*Diversidad Biológica y Medio Ambiente*), BV57. 36°36.66'N, 4°21.82'W, 117 m depth, in muddy bottom). Other seven specimens from the Bay of Malaga (DiBiMA, BV68 36°36.83'N, 04°21.70'W, 94–124 m depth, in muddy bottom) were processed: two specimens for Scanning Electron Microscopy (SEM) and five specimens were used for the sequencing of DNA from the bacteria and host. Unfortunately, during both samplings campaigns CTD to analyze oxygen in water were not available.

7.2.1. Procedure for Transmission Electronic Microscopy (TEM)

The specimens from the Bay of Malaga were anesthetized for 30 min with isotonic magnesium chloride solution (71 g of $MgCl_2.6H_2O$/liter of freshwater) prior to fixation in 2.5% glutaraldehyde buffered with sodium cacodylate (0.1 M, pH 7.4) for at least 48h at 4°C. The specimen from the Gulf of Cadiz was fixed in ethanol 70%. After this, they were completely decalcified by immersion in 2% EDTA (Ethylene Diamine Tetraacetic Acid). They were postfixed in OsO_4 (1%) for 60 min at room temperature and dehydrated in acetone series (30%, 50%, 70%, 90%, and 100% twice). Between 50% and 70% steps, the samples were incubated *in-bloc* in 2% uranyl acetate solution in 50% acetone at 4°C, overnight. Then, the samples were gradually embedded in low-viscosity Spurr's resin (https://www.emsdiasum.com/docs/technical/datasheet/14300).

Semithin sections (0.5–0.6 µm) were stained with toluidine blue (1%, pH 8.3) and were observed using an Olympus VF120 microscope at the *Servicios Centrales de Apoyo a la Investigación* (SCAI) of the University of Malaga. Ultrathin sections (0.1 µm), from the specimens fixed in glutaraldehyde, were examined with a Thermofisher Scientific Tecnai G2 20 Twin, at the ICTS "NANBIOSIS" U28 unit of the IBIMA Plataform BIONAND (Malaga).

7.2.2. EDX analysis of the bacteria

We test the mapping of different elements present in the bacteria together with the spectrum of the elements present inside the electron-lucent and electron-dense granules. For this, ultrathin sections (~100 nm) were observed using a Scanning Transmission Electron Microscopy (TEM-STEM) FEI Talos 200X with Energy Dispersive X-ray analysis (EDX system), from the SCAI of the University of Malaga.

7.2.3. Procedure for Scanning Electron Microscopy (SEM)

Specimens for SEM were critical-point CO_2-dried and sputter-coated with gold. The specimens were observed with an EM JEOL JSM-840 from the SCAI of the University of Malaga.

7.2.4. DNA extraction and sequencing by Illumina Miseq technology

Gills were excised from 5 individuals preserved in molecular-grade ethanol. Samples were previously washed in filtered (0.22 mm) and sterilized seawater and total genomic DNA was extracted using the DNeasy Tissue Kit (Qiagen Japan, Tokyo, Japan). Total DNA was resuspended in 100 µL TE buffer (10 mM Tris–HCl, 1 mM EDTA, pH 8.0) and stored at 4°C. DNA was quantified by spectrophotometer (NanoDrop ND-1000) and the ratio of absorbances 260:280 and 260:230 was used as a measure of the quality of DNA extraction. For the amplification of host mitochondrial DNA (COI) (Folmer et al. 1994) and bacterial DNA (SSU 16S rRNA), specific primers were used (Klindworth et al. 2013, Abellan-Schneyder et al. 2021).

PCR amplification for COI-DNA barcoding analysis was performed in 50 µl of reaction volume with 1.25 units of GoTaq® G2 Flexi DNA polymerase 5 u/µl (Promega, Wisconsin, USA), 0.2 mM each dNTP, 0.2 µM of primers LCO1490 (5’ GGTCAACAAATCATAAAGATATTGG 3’) and HCO2198 (5’ TAAACTTCAGGGTGACCAAAAAATCA 3’) (Folmer et al. 1994) targeting the COI gene and less than 0.2 µg of template DNA. PCR reactions were heated 3 min. at 95°C, followed by 35 cycles (1 min. at 95°C; 30 secs. at 54°C, 1 min. at 72°C). DNA sequencing was performed bidirectionally by using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) and the same primers as used in the amplification reaction in an ABI PRISM 3100 genetic analyzer (Applied Biosystems).

To analyze the microbial communities present on gills, PCR amplification was performed from the purified total DNA sample using the repliQa Hifi ToughMix (Quantabio) and primers IlluAdp_16S_Forward-341F
(5’ TCGTCGGCAGCGTCAGATGTGTATAAGAGACAGCCTACGGGNGGCWGCAG3’)
and IlluAdp_16S_Reverse-785R
(5’ GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAGGACTACHVGGGTATCTAATCC3’) targeting the V3–V4 variable regions of the 16S rRNA gene. The amplification conditions were: 35 cycles (30 secs. at

95°C; 30 secs. at 57°C, 1 min. at 72°C). Agarose gel electrophoresis confirmed a unique band. Quantification was done with Qubit 2.0 fluorometer and Qubit dsDNA BR kit and DNA was purified with Sera-Mag Select ™ (Cytiva). Library was prepared according to an in-house protocol of Stabvida based on Illumina 16S Metagenomic Sequencing Library preparation protocol (15044223 Rev. B). Library concentration was 21.8 ng/ul. Libraries were further sequenced by NGS in an Illumina MiSeq platform using MiSeq Reagent Kit V3 and 300 bp paired-end at StabVida.

Raw read sequences of the 16S rRNA gene from gills of *Kelliella miliaris* in this study are publicly available in the NCBI SRA depository within BioProject PRJNA1229195, with BioSample accession number SAMN47125445.

7.2.5. Bioinformatic analysis

The analysis of the raw sequence data was carried out using QIIME2 2024.10. A total number of 128642 reads were obtained. Reads were denoised using the DADA2 plugin from QIIME2. After denoising a total of 239 unique Operational Taxonomic Units (OTUs) were identified. For taxonomical classification, sequences were subjected to taxonomic assignment against the SILVA 16S database (Release 138.2), with 97% 16S similarity as the cutoff and clustered into OTUs. For classification purposes, only OTUs containing at least 10 sequence reads were considered as significant. Non-specific PCR amplicons were eliminated.

7.3. Results

7.3.1. Some relevant morphological characteristics of *Kelliella miliaris*

Clausen (1958), Allen (2001) and Krylova et al. (2018) provided very good descriptions of the shell and soft parts of *Kelliella miliaris*. Therefore, here we highlight some morphological characteristics that could be relevant to understand more on its biology.

Kelliella miliaris is a minute bivalve with sub-orbicular valves, with an elongate, finger-shaped foot, able to be extended outside the shell and never concealed by the gills when retracted (contrary to the superficially similar *Vesicomya atlantica* (Smith, 1885)) (Fig. 7.1A). In the dorsal part of this muscular foot there are large fused pedal ganglia to which two statocysts are attached in its dorsal part (Fig. 7.1B). The mantle edges are much thickened, over all in comparison with the thin mantle epithelium, and show many muscular fibers together a large blood sinus (Fig. 7.1C). The stomach has a gastric shield and a sacciform, open compartment with secreting cells, which corresponds to the style-sac, not clearly differentiated from the midgut in this species, as already noted by Clausen (1958) (Fig. 7.1D). Inside the stomach it is possible to see different types of organisms, such as bacteria, diatoms, among others, pointing a heterotrophic feeding (Fig. 7.1E). In transversal semithin sections, it was possible to observe female follicles with oocytes at different developing stages at the lateral sides of the visceral mass (Fig. 7.1D). We have seen spermatozoids inside the gonad, which would confirm an internal fertilization in this species (Fig. 7.2A). However, the presence of protoconch I and protoconch II would indicate a larval planctotrophic development (Fig. 7.2B).

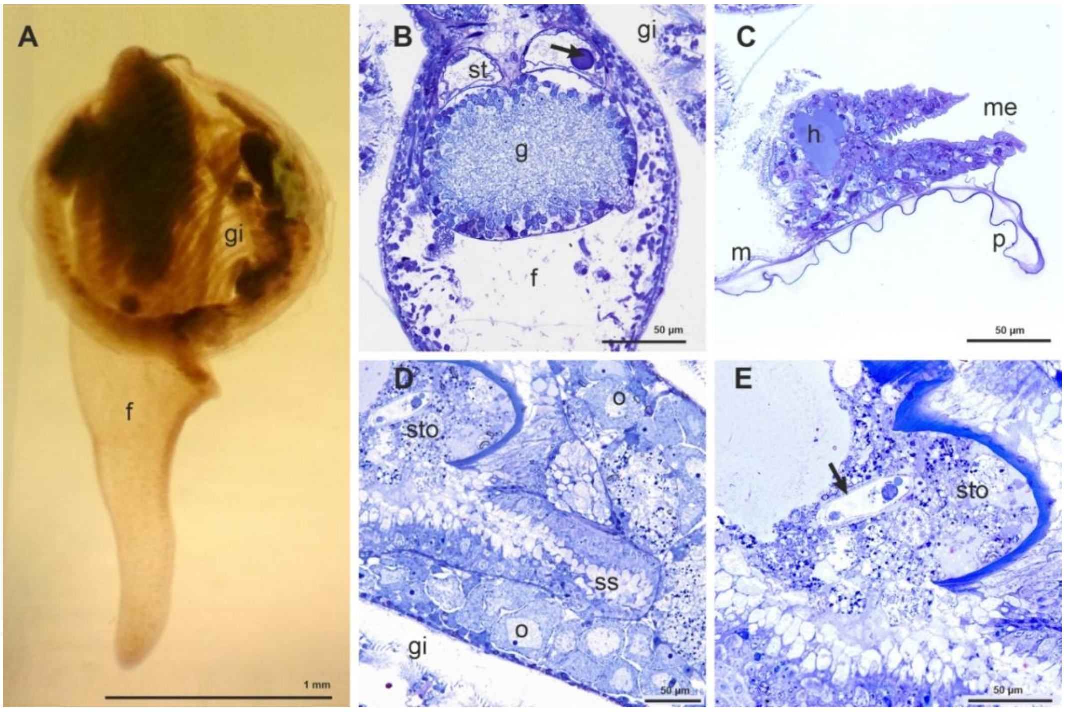


Figure 7.1. A: View of one specimen of *Kelliella miliaris* embedded in spur resin. **B**: Semithin transversal section showing part of the foot (f), with the large fused pedal ganglia (g) and the statocists (st); the arrow shows one of the statoliths. **C**: Semithin transversal section of the very large mantle edge (me) –in comparison with the mantle (m)– showing a large hemocelic sinus (h) and the periostracum (p) emerging between the outer and middle mantle folds. **D**: Semithin transversal section showing part of the stomach (sto) and the style sac (ss). **E**: Semithin transversal section showing part of the stomach (sto) with different organisms, among them a possible protozoan (arrow).

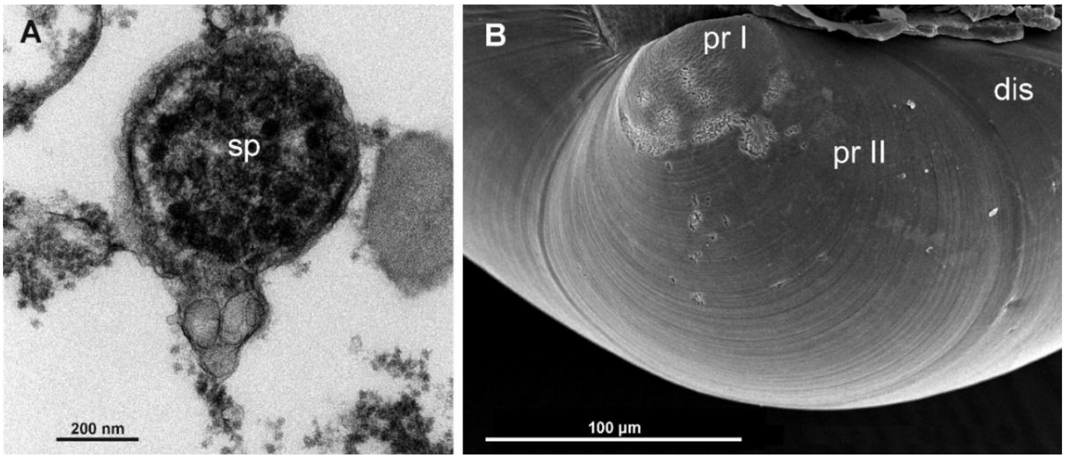


Figure 7.2. A: Transmission Electron Microscope (TEM) view of a spermatozoid found inside the female gonad. **B**: Scanning Electron Microscope (SEM) view of the protoconch I (pr I), protoconch II (pr II) and disoconch (dis) of *Kelliella miliaris*, indicative of a planktotrophic development.

The gills have two symmetrical ctenidia that practically cover the visceral mass at both sides (Fig. 7.1A). Each ctenidium consists of a large inner demibranch and a small outer demibranch placed in the posterior third of the inner one. Each demibranch presents a descending and an ascending lamella without interlamellar junctions. These gills are homorhabdic –with gill filaments arranged in a flat, uniform series– like those found in *Donax faba*, according to the classification of Ridewood (1903).

In relation to body size, gill filaments are large and numerous, mainly in the large inner demibranch. The gill filaments have long cilia (Fig. 7.3A). There are bunches of muscular fibres connecting with the filament at the proximal abfrontal area (Fig. 7.3B). The cilia are present on either side of the filament section, connecting one filament with the next, and together with cirri on the frontal cells facing outside the demibranch (Fig. 7.3A). The cirri in the frontal and lateral-frontal zones are long; the frontal cells present also microvilli (Fig. 7.3C). The lateral cells are cuboidal, but sometimes tends to have a more globular shape, and show numerous mitochondria together with long cilia and microvilli (Fig. 7.3D–E). Between the lateral-frontal cirri and the lateral ciliate cells there are several globular cells devoid of cilia but with long microvilli (Fig. 7.3F).

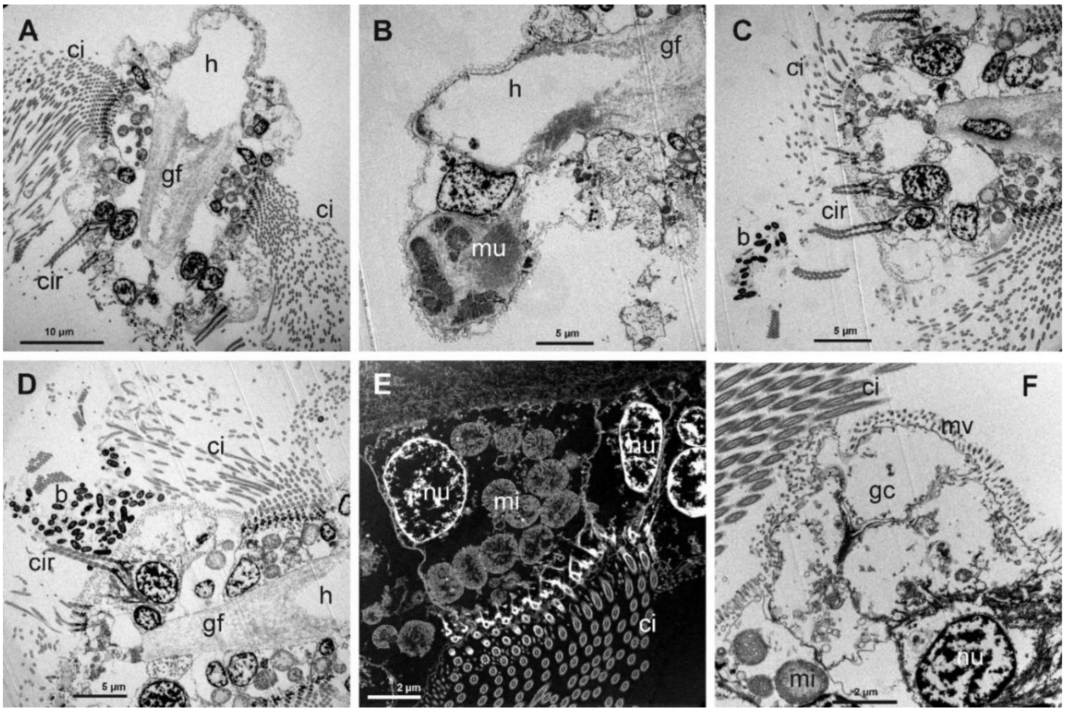


Figure 7.3. A: Transmission Electron Microscope (TEM) view of a gill filament (gf) showing the long lateral cilia (ci), frontal cirri (cir) and the large hemocelic sinus (h). **B**: TEM view of part of the gill filament (gf) with the hemocelic sinus (h) connected to a bunch of muscular fibres (mu). **C**: Frontal TEM view of a gill filament showing a group of bacteria (b) near the frontal cirri (cir); it is possible to see part of the long lateral cilia (ci). **D**: TEM view of a group of bacteria (b) located between the frontal cirri (ci) and the long lateral cilia (ci). **E**: Scanning Transmission Electron Microscope (TEM-STEM) view of the lateral ciliate cell showing the cilia (ci), the nucleus (nu) and numerous mitochondria (mi); some nuclei from the abfrontal cells are visible. **F**: TEM view of the abfrontal and globular cells (gc) located between the lateral ciliate cells and the frontal cells. These globular cells present only microvilli.

7.3.2. COI-based analysis of host

Sequence analysis of the mitochondrial Cytochrome c Oxidase subunit I (COI) gene (GenBank: PV147183) from the gill tissue sample revealed 100% identity with previously published sequences of *Kelliella miliaris* from the North Sea (GenBank accession numbers MF542321, OQ053061, OQ053062 and OQ053063 by Krylova et al. 2018).

7.3.3. Bacteria in the gills

We have observed in all the specimens examined the presence of rod shaped bacteria among the long lateral cilia, the frontal cilia and cirri and between the frontal-lateral cirri and the lateral cilia (Fig. 7.4A–E). Bacterial symbionts were usually small (ca. 1 µm long and ca. 0.5 µm wide), with the typical double membrane of Gram-negative bacteria (Fig. 7.4F–G).

Bacteria were also found inside the globular abfrontal cell, adjacent to the lateral ciliate cell. The bacteria were free in the cytoplasm and not inside vacuoles or bacteriocyte (Fig. 7.4H). Some bacteria were in a process of division inside this abfrontal cell (Fig. 7.4H: arrow). Isolated bacteria were found also inside the frontal cells (Fig. 7.4I). We have estimated the density of bacteria within the lateral ciliate area and the frontal area of the filaments, taking into account all the ultrathin sections analysed in TEM. An average density of 58.25 bacteria by μm^2 was found in the lateral areas, and of only 6.1 bacteria by μm^2 in the frontal area. The number of bacteria inside cells ranges from 3 to 7.

The bacteria appeared in group inside a glycocalix network that is secreted by the microvilli of the lateral and frontal cells (Fig. 7.5A–F). Figure 7.5G shows the microvilli and Figure 7.5H–I the secretion of numerous vesicles. The absence of concentric stacks of intracellular membranes in their cytoplasm indicates that these symbionts are not methanotrophic bacteria (Fig. 7.4F–G). All the above data point a symbiotic relationship between *Kelliella miliaris* and the bacteria. Although there are some bacteria inside the abfrontal and frontal cells, we consider this to be an ectosymbiosis because most of the bacteria were trapped by a glycocalix network among the cilia.

The bacteria showed one large or several smaller and exocentric electron-dense granules, and few electron-lucent non-membrane bound granules in TEM views (Fig. 7.5A–C), which in TEM-STEM views appeared respectively as electron-lucent or electro-dense (Fig. 7.5D–F, Fig.7.6A). To check if these granules could be sulphur granules, common in some vent and seepage bacteria from reducing sulphidic environment, we have performed by TEM-EDX a mapping and spectrum of the main elements present in them. The EDX analysis of the electron-dense granules (lucent in TEM-STEM views) showed that there is no carbon in these granules (Fig. 7.6B–G,I). The main elements were: oxygen, phosphorus, lead, sulphur and nitrogen (Fig. 7.6I). Oxygen is the most abundant element, showing the greatest peak in the spectrum, followed by phosphorus and lead; the sulphur peak appears inside the large peak of the lead, but the mapping showed abundant sulphur inside the black granules. Finally, nitrogen is the other element present inside the electron-dense granules. In the electron-lucent (electron-dense in TEM-STEM views) small granules (Fig. 7.6H) the spectrum of their content (Fig. 7.6J) showed the nearly absence of sulphur in these granules (Table 7.1).

Table 7.1. Comparison of the main elements mapping with electron dispersive X-ray analysis in the electron-lucent and electron-dense granules of the bacteria (from TEM-STEM view). AN: Atomic Number; wt.%: percentage (in weight) of the element; Err: error in the percentage in atomic weight.

	Electron-lucent granule			Electron-dense granules		
Element	AN	wt.%	Err.	AN	wt.%	Err.
Oxygen	8	49.081	1.616	8	36.183	1.243
Nitrogen	7	9.544	0.439	7	47.935	1.631
Sulphur	16	21.486	0.769	16	1.769	0.150
Phosphorus	15	18.603	0.686	15	8.871	0.398
Silicon	14	1.286	0.114	14	5.262	0.216

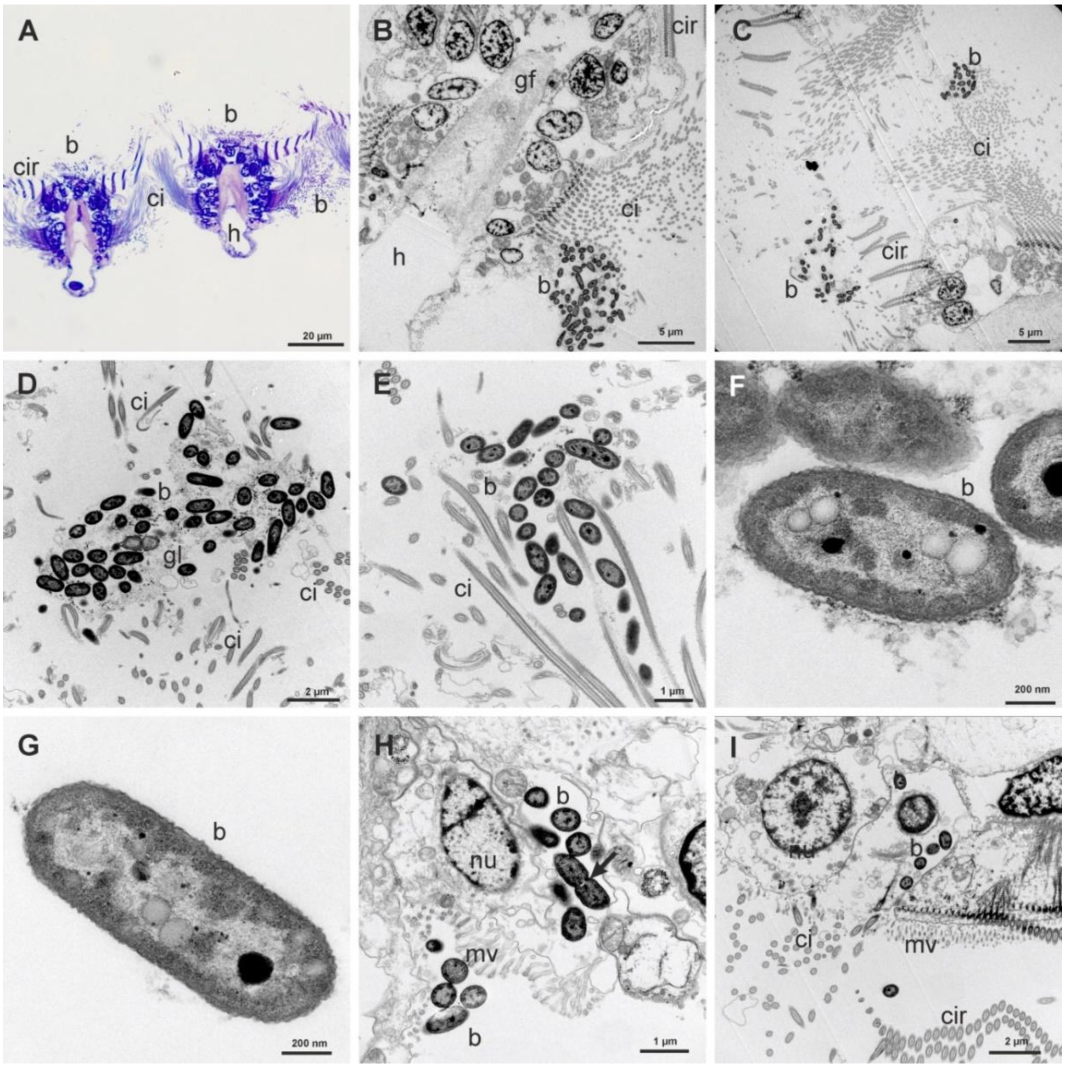


Figure 7.4. **A**: Semithin transversal view of two gill filaments showing groups of bacteria (b) in the frontal and lateral sides. **B**: Transmission Electron Microscope (TEM) view of a gill filament (gf) showing a group of bacteria (b) between the long lateral cilia (ci). **C**: TEM view of groups of bacteria (b) in the frontal and lateral cilia (ci) of a gill filament. **D–E**: Detail of group de bacteria (b) trapped in a glycocalix network (gl) between the cilia (ci). **F**: TEM view of bacteria showing the double membrane and the electron-lucent and electron-dense granules. **G**: TEM view of one isolated rod shaped bacterium showing two electron-lucent granules and one electron-dense granule. **H**: Group of bacteria inside the cytoplasm of a microvillous (mv) abfrontal cell, one of them in process of division (arrow). There is also a group of bacteria in process of entering in another cell. **I**: TEM view of some bacteria (b) inside a microvillous frontal cell.

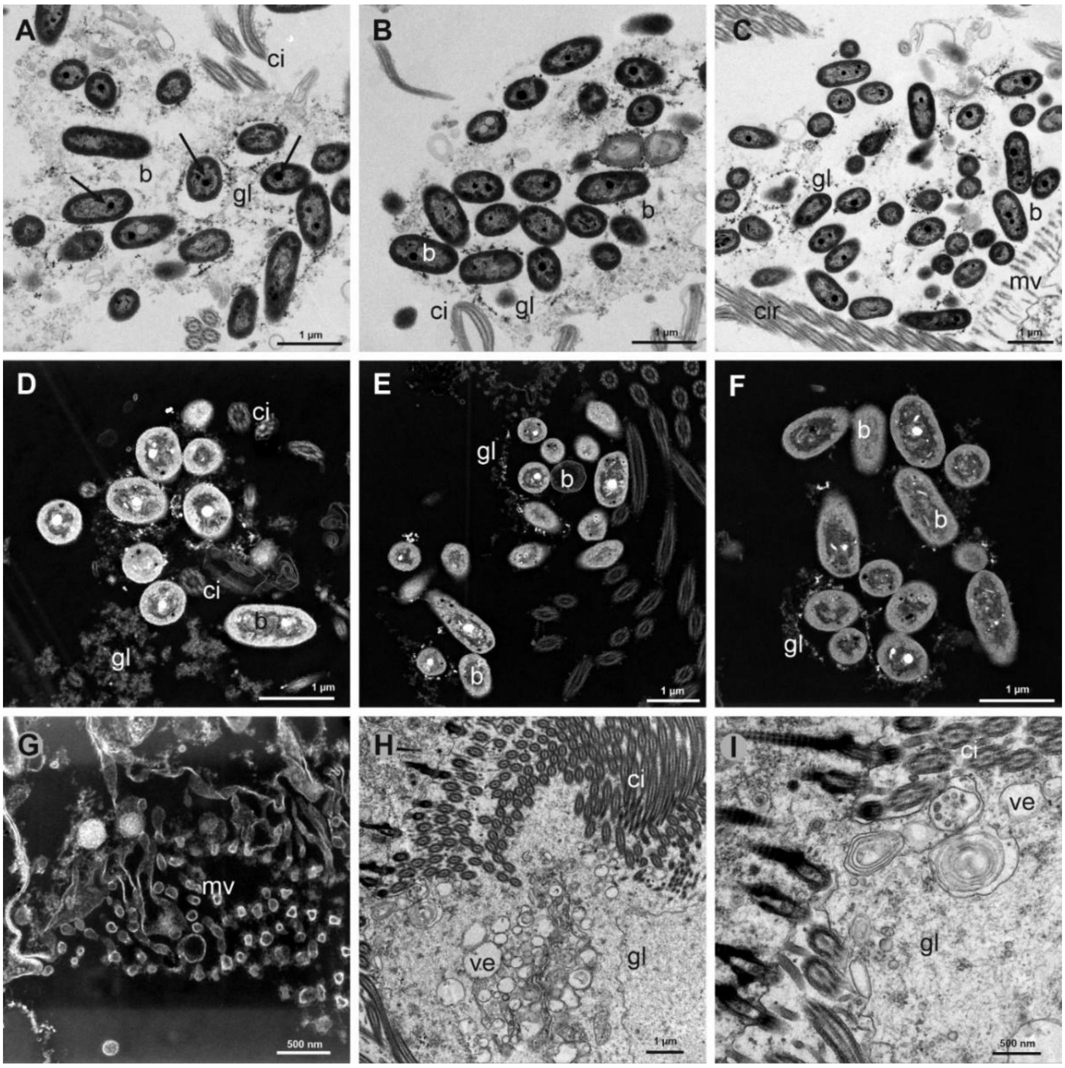


Figure 7.5. **A–C**: Transmission Electron Microscope (TEM) views of groups of bacteria (b) trapped in a glycocalix network (gly) between the cilia (ci) of the gill filaments. Arrows point to some electron-dense granules. **D–F**: Scanning Transmission Electron Microscope (TEM-STEM) views of groups de bacteria (b) in the glycocalix network (gly), some of them showing electron-lucent granules, which correspond to the electron-dense granules in TEM. **G**: TEM-STEM view of the microvilli (mv) from the abfrontal globular cells. **H**: TEM view of the intense secretion of vesicles (ve) and glycocalix (gl) from the microvilli of the gill filament cells. **I**: TEM view with intense secretion of vesicles and glycocalix from same section as H.

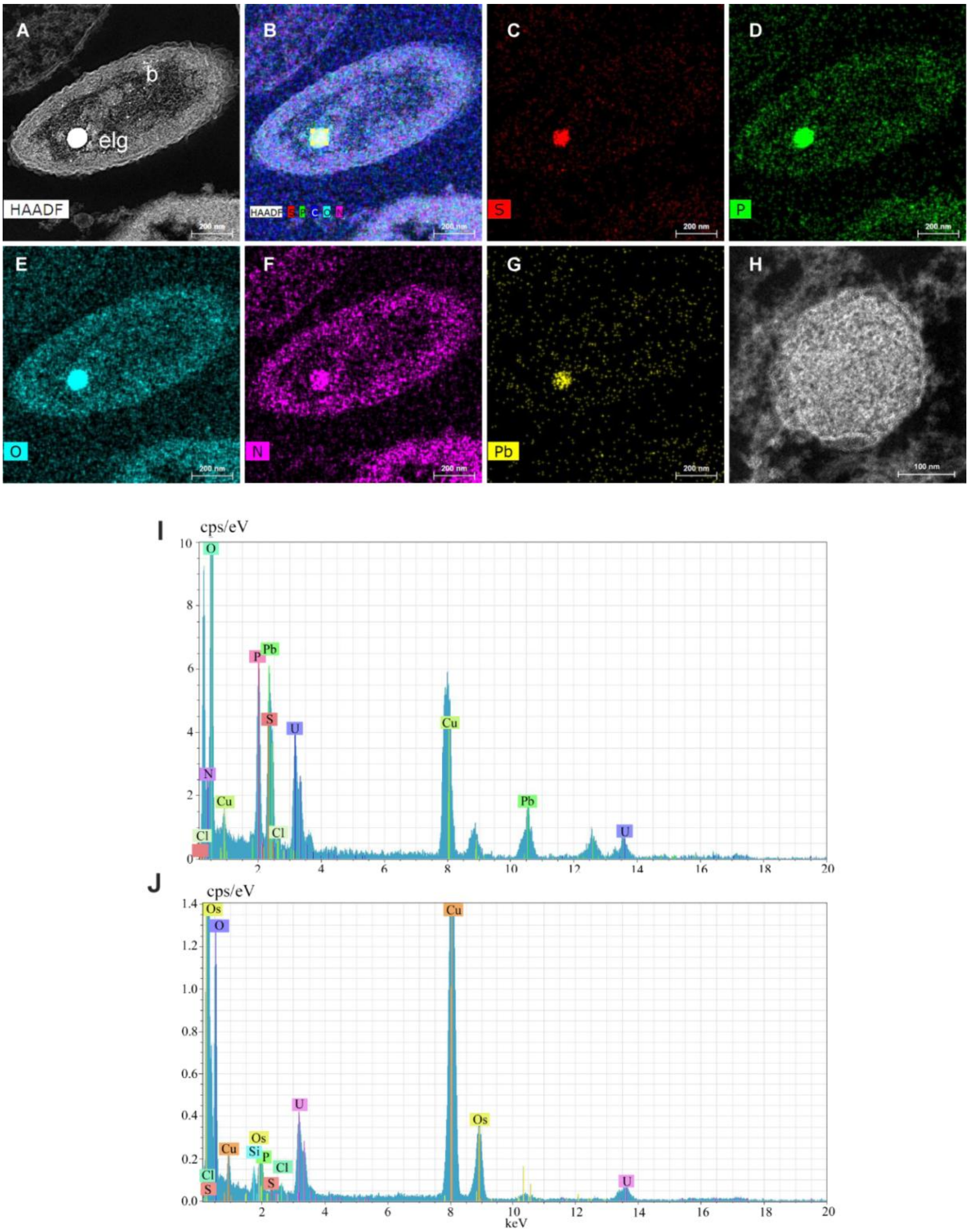


Figure 7.6. **A–G**: Energy Dispersive X-ray analysis on Scanning Transmission Electron Microscope ultrathin sections of bacteria (TEM-STEM-EDX) for mapping the main elements present in the bacteria, particularly in the electron-lucent (electron-dense in TEM view) granule (elg). S: sulphur; P: phosphorus; O: oxygen; N: nitrogen; Pb: lead. **H**: Scanning Trnasmission Electron Microscope (TEM-STEM) view of an electron-lucent granule (electron-dense in TEM). **I**: Spectrum of an electron-lucent granule (electron-dense in TEM). **J**: Spectrum of an electron-dense granule (electron-lucent in TEM). Most of the conspicuous peaks denote elements used in the fixation process (uranyl U, osmium Os and lead Pb) or the grid (copper Cu).

7.3.4. Taxonomic composition of bacteria in the gills from *Kelliella miliaris*

The predominant Phylum detected in the sample was Pseudomonadota (55.76% of total reads) (Fig. 7.7A), of which the class Gammaproteobacteria constituted 53.69% (Fig. 7.7B). The other two more abundant phyla are Bacteroidota (19.67%) (Fig. 7.7A), all of which belong to the class Bacteroidia 19.67% (Fig. 7.7B), and Bacillota (19.27%) (Fig. 7.7A), most of which belong to the class Clostridia (18.74%) (Fig. 7.7B). Regarding the Order, Enterobacterales (34.86%), Pseudomonadales (18.74%) are the most abundant within Gammaproteobacteria; Chitinophagales (19.43%) is almost all the Bacteroidia and Peptostreptococcales (exTissierellales) (18.54%) constituted the main taxonomic group in the class Clostridia (Fig. 7.7C).

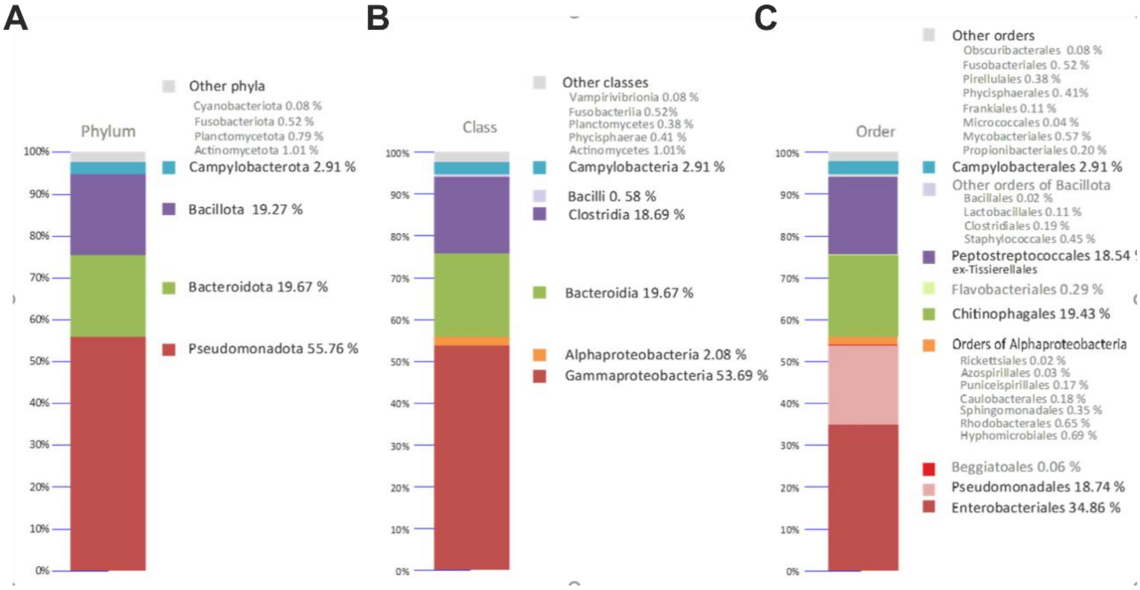


Figure 7.7. Taxonomic composition of the bacteria from the gills of *Kelliella miliaris*. Microbial communities at phylum (**A**), class (**B**) and order (**C**) level identified by sequencing of DNA bacterial from excised gills of *Kelliella miliaris*.

7.4. Discussion

Chemosynthetic symbiosis occurs ubiquitously at oxic-anoxic interfaces in marine environments, although this type of symbioses is mainly related to reducing habitats, such as hydrothermal vents, cold seeps, whale falls o deep sunken wood (Duperron 2010). There is also symbiosis in other habitats, such as the oxygen minimum zone of the oceans, where the presence of bacteria were found in the protobranchiate bivalves *Nucinella owenensis* Oliver & Taylor, 2012 and *Huxleyia habooba* Oliver & Taylor, 2012 (Oliver & Taylor 2012); ectocommensal species, such as the bivalve *Syssitomya pourtalesiana*, which lives on the spines in the anal zone of the deep-sea echinoid *Pourtalesia* (Oliver et al. 2013) or shallow-water, low sulphidic environments, where symbiosis was found in the platyhelminths *Paracatenula* spp., gutless oligochaetes or nematodes (Dubilier et al. 2008). *Austrogena nerudai* Krylova, Sellanes, Valdes, D'Elias, 2014 is a vesicomyid from a restricted area within the benthic realm delimited by the Oxygen Minimum Zone (OMZ) off the south-central Chilean margin (Krylova et al. 2014), although only juveniles were found alive, while all the adults were dead. According to these authors, pliocardiines have not been previously reported from OMZ, however it is quite probable that some species as *'Vesicomya' indica* Smith, 1904, *'Vesicomya' brevis* Smith, 1906 and

'*Vesicomya' cretacea* Smith, 1906, described from the bathyal depths of the Arabian Sea and the Bay of Bengal, were actually associated with OMZ. There were no recorded cases of specialized adaptations for different types of reducing environments among pliocardiines, although the authors considered that the metabolism of the species must be related with sulphide cycle, they did not show any images of bacteria inside the gills or sequence documenting their presence.

According to Childress & Girguis (2011), moderate to high rates of chemoautotrophic or methanotrophic metabolism is more demanding for symbiotic hosts in terms of oxygen uptake and proton equivalent elimination, compared to related non-symbiotic annelid, bivalve and gastropod lineages. The high oxygen demand of these symbionts is perhaps the most limiting factor in the pathway to a symbiotic condition. Among the consequences of such demands is the widespread occurrence of circulating and/or tissue haemoglobins in the hosts, to support high metabolic rates in thioautotrophic endosymbiosis. The latter is still more limiting in the oxygen minimum zone, where the oxygen is in short supply.

The microbial symbiotic assemblage has two main constraints in the OMZ, the low level of oxygen with irregular distribution between layers and deeps and along the OMZ and the maintenance of enough input of sulphur. The presence in the NW Arabian Sea OMZ of five species usually associated with chemosymbiotic bacteria (one *Lucinoma* sp. and four *Thyasira* spp.) (Levin et al. 2000, Dufour 2005, Taylor & Glover 2006) would point that both elements are present and with enough amount to maintain a chemosymbiotic relationship. Probably their localization between the cilia of the gill filaments would be adaptive to obtain more easily oxygen and sulphur from the OMZ seawater.

The studied specimens were collected on the edge of the continental of the Bay of Malaga, between 90 and 124 m depth and in the bathyal of Gulf of Cadiz, at 735 m depth, all of them on muddy bottoms. Sequence analysis of the mitochondrial Cytochrome c Oxidase subunit I (COI) gene (GenBank: PV147183) from the gill tissue sample revealed 100% identity with previously published sequences of *Kelliella miliaris* from the North Sea (Krylova et al. 2018), which confirms the conclusion based on morphology (Utrilla et al. 2024) that there is only one species of *Kelliella* (*K. miliaris*) from Norwegian Sea to the Mediterranean Sea.

Along the littoral of Malaga there are several upwellings of deep Mediterranean water before the Strait of Gibraltar. These upwellings carry oxygen and nutrients to the surface, leaving a low oxygen level near the bottom. The specimens of *K. miliaris* from the Gulf of Cadiz were collected in a deep muddy bottom, in the pathway of the Mediterranean Outflow Water, with usually low level of oxygen near the bottom. The presence of bacteria in the gills of *Kelliella miliaris* highlights the importance of the symbiosis in oxygen minimum zones of the oceans that has been probably overlooked up to now.

The association of chemosynthetic bacteria with at least seven metazoan phyla (Porifera, Platyhelminthes, Nematoda, Mollusca, Annelida, Arthropoda and Echinodermata) suggests that chemosynthetic symbioses have evolved several times (Dubilier et al. 2008). In Molluscs, chemosynthetic symbiosis have been observed in Solenogastres (Katz et al. 2006), Gastropods (Goffredi et al. 2004, Urakawa et al. 2005, Suzuki et al. 2006 and references therein, Bates 2007) and Bivalves, where many species contain chemosynthetic bacteria (Dufour 2005, Dubilier et al. 2008, Taylor & Glover 2010). Likewise, the ability to associate with chemosynthetic bacteria is a recurring feature in the evolution of bivalves, since it has appeared independently in seven families, Mytilidae, Vesicomyidae, Solemyidae, Lucinidae, Thyasiridae, Nucinellidae and Lasaeidae (Dufour 2005, Dubilier et al. 2008, Taylor & Glover 2010, Oliver & Taylor 2012, Oliver 2012, Duperron et al. 2013) and from different habitats.

The chemosynthetic bacteria can be: (1) epibionts or ectosymbiotic, living outside the host epithelial body, gills, mouth parts, body surface, among others (Dufour 2005); (2) endobionts or endosymbiotic, which can be extracellular, such as found in the gutless oligochaetes, in which the bacteria appeared below the cuticle of the body wall, or intracellular, such as found in many bivalves (Dubilier et al. 2008). In most of the studied chemosynthetic species of bivalves, the bacteria live inside the abfrontal gill cells, usually within bacteriocytes, however in Thyasiridae (Dufour 2005) or some Mytilidae (Gros & Gaill 2007), the bacteria live among the cilia, near the microvilli of the gill cells, as ectosymbionts. As general rule, there is one symbiont by species, usually thiothophs, but in the deep-sea mussels *Bathymodiolus azoricus* Cosel & Comtet, 1999, *Bathymodiolus puteoserpentis* Cosel, Métivier & Hashimoto, 1994 and *Bathymodiolus brooksi* Gustafson, Turner, Lutz & Vrijenhoek, 1998 there is a dual symbiosis (thiotrophs and metanotrophs) in the same bacteriocyte (Fisher et al. 1993, Distel et al. 1995, Duperron et al. 2005, 2006); in *Bathymodiolus heckerae* Turner, Gustafson, Lutz & Vrijenhoek, 1998 there are four symbionts (two thiotrophs, one metanotroph and one bacterium related with free-living methylotrophs) (Duperron et al. 2007) and in the cold seep mussels *Idas* sp., six bacterial symbionts coexisting in the same bacteriocyte were found (Duperron et al. 2008).

As expected in filter-feeding and heterotrophic feeding organisms, a wide diversity of bacterial species was found (Fig. 7.7). The most abundant class in the gill filaments of *K. miliaris* was Gammaproteobacteria, with 53.69% of total reads, which suggests that a gammaproteobacterium, probably from the order Enterobacterales, with 34.86% of the total reads, would be the dominant gill ectosymbiont of *K. miliaris*. Most of the previously analysed chemosynthetic symbionts from bivalves cluster within the single bacterial class of the Gammaproteobacteria, on the basis of 16S rRNA gene sequences (Distel et al. 1995).

The lack of concentric stacking of intracellular membranes in the cytoplasm of the bacteria trapped between the cilia of the gill filaments reveals they were not methanotrophic, while the presence of sulphur in the electron-dense granules (in TEM views), or electron-lucent (in TEM-STEM view), in these bacteria would indicate some involvement of the bacteria in the sulphur cycling. The peaks of oxygen and phosphorous in theses electron-dense granules could indicate in part polyphosphate compounds as described in the bacteria from *Riftia pachyptila* tube wall (Lechaire et al. 2002, Gros & Gaill 2007), but also could points them as autotrophic sulphide-oxidizing bacteria. In the chemosynthetic symbioses, the symbionts need access to a terminal electron acceptor that in the process of sulphur or methane oxidation; electrons can be donated to oxygen (oxic conditions) or a molecule like nitrate (anoxic conditions) (Roeselers & Newton 2012). The great peak of oxygen of the electron-dense granules points to that part of the oxygen could be electron receptor. Thioautotrophic symbionts are the most common type in Bivalvia and are found in bathymodioline mussels as well as solemyid, thyasirid, lucinid, and vesicomyid clams (Cavanaugh et al. 2006).

The functionality of the chemosynthetic symbioses relies on both the availability of substrates for chemosynthetic metabolism and the existence of particular metabolic pathways in the symbiont to utilize those substrates. There is a link, therefore, between geochemistry and the type of symbiosis that can colonize a particular environment (Roeselers & Newton 2012). According to these authors, advances would be interesting in single-cell methods that combine imaging techniques with other type of analysis, apart from the sequencing, such as metabolic ones, which allow the visualization of uptake or/and distribution of substrates. In this way, the EDX analysis carried out by the TEM-STEM TALOS microscopy (Fig. 7.6) shows for the first time the distribution of the environmental elements, among them sulphur and oxygen, in the symbiont bacteria as well as their amount.

Childress & Seibel (1998) proposed three possible physiological adaptations of the organisms to the OMZs: (1) the development of mechanisms for highly effective capture of oxygen from water. In relation to this adaptation, increase of the size and/or number of gills has been observed in polychaetes, crustaceans and molluscs; for example the chiton *Leptochiton laurae* Schwabe & Sellanes, 2010 from the OMZ in Chile exhibits enhanced numbers and size of ctenidia (Gooday et al. 2010). Some groups, such as fishes, crustaceans, molluscs or polychaetes, have specialized circulatory systems in addition to developed respiratory systems which offer possibilities for adaptations to OMZs (Levin 2003); (2) the reduction of metabolic rates; or (3) the use of anaerobic metabolism to make up the difference between aerobic capacity and total metabolic demand. Reduced body size and/or flattened tests, which both lead to an increase in the surface area-to-volume ratio, are also typical feature of some OMZ metazoan macrofauna and hypoxia-tolerant foraminiferal species, respectively (Levin 2003, Gooday et al. 2010).

Kelliella miliaris show different morphological characteristics that would be adaptive for living in OMZ, such as: (1) presence of numerous muscular fibres in the mantle, mantle edge and gills-visceral mass connection; all of which would allow to actively move the gills and/or enable a better control of the ventral opening in relation to vertical movements of the animal; (2) high number (in relation to body size) and large size of gill filaments, mainly in the large inner demibranch; and (3) long cilia which would provide a large surface for capture of oxygen and a highly effective uptake of oxygen from water. The presence of large blood sinus in the mantle edge could be related to the capture of the oxygen by the blood pigment, which probably was haemoglobin.

We have no data on the putative metabolic reduction or anaerobic metabolism in *K. miliaris*, but the presence of symbiosis with Gram negative Gammaproteobacteria involving in sulphur cycling would point that there must be a sulphidic environment. According to Brissac et al. (2011) the large electron-lucent periplasmic “vacuole” observed by TEM in the symbionts present in *Thyasira* sp. would be sulphur granule, like those frequently present in most sulphur-oxidizing bacteria. However, in the electron lucent granules (TEM view) of the bacteria found in *K. miliaris*, the amount of sulphur was minimum, while the higher amount of sulphur was found in the electron-dense granules (TEM view) or electron-lucent (TEM-STEM view).

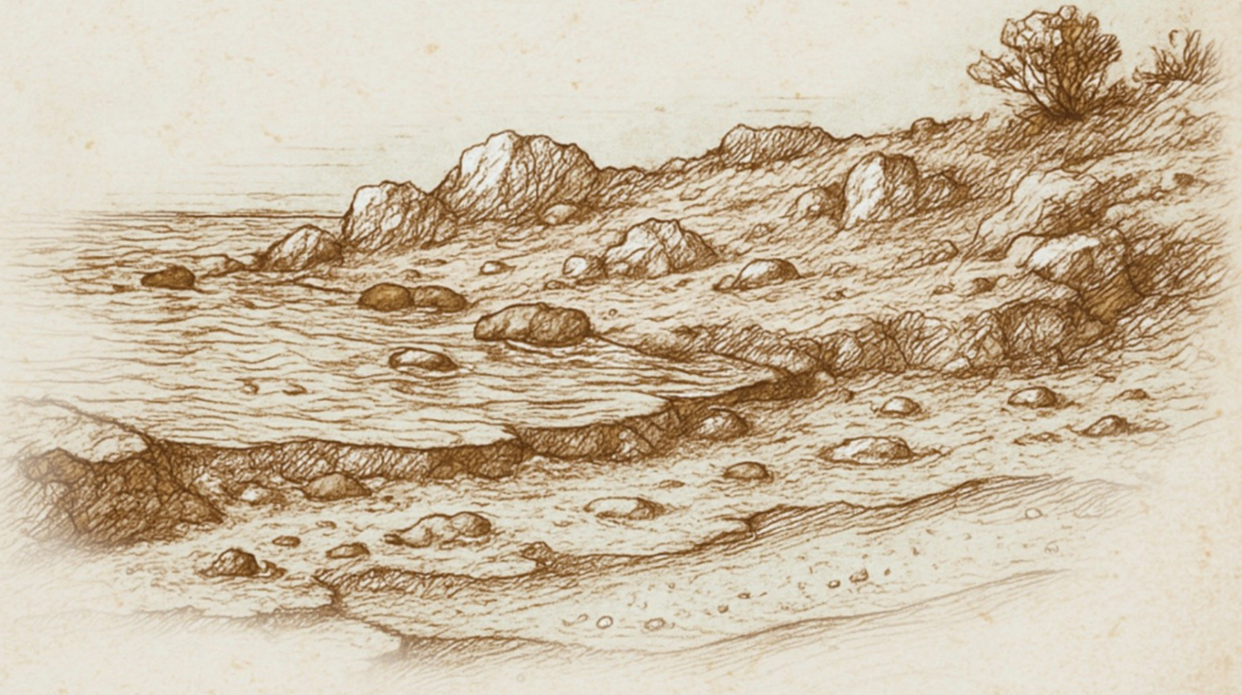
The reduced sulphur compound hydrogen sulphide is extremely toxic to animals as it poisons cytochrome c oxidase and arrests aerobic respiration. In the case of the symbiotic molluscs, they typically oxidize sulphide to thiosulfate to reduce toxicity, and their symbionts can use thiosulfate as a reductant (Childress & Girguis 2011). Our hypothesis is that the peak of oxygen in the electron dense and electron lucent granules of the bacteria would indicate the use of part of this oxygen to oxidize sulphide to thiosulphate. Therefore, the presence of sulphur-oxidizer bacteria in the large gills of *K. miliaris* would be an adaptation to eliminate the environmental toxic hydrogen sulphide that is usually present in the OMZ. However, future experiments (e.g. metagenomic analysis or enzymatic assays, among others) would be necessary to test this hypothesis.

Kelliella miliaris presents a well-developed stomach with a gastric shield and style sac diverticula, not separate from the mid gut and in which intense secretion by microvilli has been observed by transmission electron microscopy. The presence of different microorganisms inside the stomach, indicates suspension feeding, in agreement with Krylova et al. (2018), who suggested heterotrophy, after analysing the stable δ^{13} C and δ^{15} N isotopic composition of *K. miliaris,* that they found similar to that of *Vesicomya*.

All our analyzed specimens were females, with developing oocytes at different degree of maturation. The follicles were located lateral to the digestive tract in the semithin sections. The presence of spermatozoids inside the female gonad, points to an internal fertilization. The latter would be an adaptation to ensure offspring in a minute species with a relatively low number of oocytes, similarly to the small astartid *Digitaria digitaria* (Marina et al. 2020). The protoconch of *K. miliaris*, with differentiated protoconch I and protoconch II, indicates planktotrophic larval development. The latter could favour the evasion of the larvae from the bottom reducing environment, which would be dangerous for the development of the protoconch.

Capítulo VIII

Discusión general



8. DISCUSIÓN GENERAL

La presente tesis doctoral aborda la malacofauna del golfo de Cádiz desde varias escalas geográficas y temporales, aportando datos faunísticos de zonas concretas, aspectos paleoecológicos de periodos pasados y una síntesis de los patrones de distribución de los moluscos en función de las principales masas de agua. También se ha estudiado la adaptación de una especie (*Kelliella miliaris*) a condiciones ambientales de mínimo oxígeno mediante quimiosimbiosis. Se ha puesto de manifiesto la complejidad de hábitats y la diversidad de moluscos en esta área, así como algunos de los factores que han modelado la distribución y estructura de sus comunidades a lo largo del tiempo. Esta tesis constituye una contribución significativa al conocimiento de la malacofauna de hábitats profundos del golfo de Cádiz, con nuevos datos sobre la composición y estructura de algunas comunidades de moluscos. Integra datos sobre biodiversidad, ecología bentónica, procesos paleoceanográficos y relaciones simbióticas, y representa uno de los primeros estudios cuantitativos sobre las especies ligadas a estos hábitats profundos, así como de identificación de comunidades.

En el **capítulo 4** sobre la malacofauna del volcán de fango Gazul, se ha encontrado un gran número de especies (232) tanto en fondos duros (p. ej. los conformados por carbonatos autigénicos), como en los fondos sedimentarios adyacentes, de las cuales 91 estuvieron representadas por individuos vivos, y 141 especies conformaron la tanatocenosis. Estos resultados son similares a los obtenidos en otras regiones del Atlántico norte, como en el banco de Galicia (Gofas et al. 2021) donde se encontraron 104 especies vivas, o en la cadena de montes submarinos del sur de las Azores, donde se recolectaron 123 especies representadas por 1.952 individuos recolectados vivos (Caballero Herrera et al. 2023b). Sin embargo, esta última área de estudio abarcaba cinco *seamounts* con áreas que oscilan entre los 350-2.000 km^2, mientras que en Gazul se identificaron 91 especies representadas por 2.324 individuos vivos, en un área mucho más reducida de unos 5 km^2. Las peculiares características del entorno del golfo de Cádiz en cuanto a su hidrodinámica, situación biogeográfica, geomorfológica y sedimentológica promueven esta elevada riqueza de especies. Este estudio ha completado una importante laguna de información que existía para esta área, ya que se ha registrado un elevado número de nuevas citas para la Demarcación marina Sudatlántica (86 especies), las cuales ya se habían registrado para otras demarcaciones próximas, como la Demarcación marina del Estrecho y Alborán, incluyendo tres nuevas citas para aguas españolas (*Chauvetia balgimae*, *Dentimargo auratus* y *Draculamya uraniae*). Esto supone un incremento sustancial del listado faunístico de los moluscos conocidos para el margen español del golfo de Cádiz y una mejora del conocimiento de la fauna malacológica allí existente. Este incremento es aún mayor teniendo en cuenta las especies recolectadas vivas de la campaña BALGIM, que suman un total de 139 especies (3.674 individuos) en la zona del margen español del golfo de Cádiz. Además, en este estudio se incluye la descripción de dos especies nuevas para la ciencia. Estos resultados ponen de manifiesto la falta de estudios en zonas profundas. Además, se corrobora que el margen español del golfo de Cádiz representa un *hotspot* de biodiversidad dentro del Atlántico norte, como apuntan otros autores (Cunha et al. 2013, Díaz del Río et al. 2014, Urra et al. 2021), y se revela una alta biodiversidad en comparación con otras áreas profundas del Mediterráneo (Olu-Le Roy et al. 2004, Ritt et al. 2012, Negri & Corselli 2016) y del Atlántico norte (Bergquist et al. 2003, Henry & Roberts 2007).

La elevada riqueza específica encontrada en un área tan pequeña como es Gazul, puede explicarse por una conjunción de factores: la utilización de múltiples artes de muestreo (draga de arrastre bentónico, beam-trawl, box-corer y draga Shipek), la inclusión en el estudio de la tanatocenosis, la localización del volcán de fango estudiado, entre la plataforma continental y el talud superior y en una zona de convergencia biogeográfica y, principalmente, la elevada heterogeneidad de hábitats. Este hallazgo triplica las cifras previamente conocidas para el golfo de Cádiz y pone de relieve una subestimación histórica de su biodiversidad bentónica, atribuible en gran medida a la escasez de campañas de muestreo profundas y al limitado esfuerzo taxonómico sobre los moluscos en dicha área. Además, la presencia de estructuras duras como los carbonatos autigénicos le confiere al edificio volcánico una mayor complejidad, generando condiciones óptimas para la colonización por fauna epibentónica, entre ellas moluscos asociados a cnidarios, esponjas y equinodermos. Esto fue detectado por los análisis del estudio, ya que existieron diferencias significativas entre las comunidades asociadas al edificio del volcán respecto a las zonas adyacentes. Estos carbonatos convierten los fondos sedimentarios, con menor diversidad asociada, en sustratos duros y mixtos. Este patrón es consistente con lo observado en otras estructuras del margen ibérico, como el banco Djibouti (Gofas et al. 2014b) y la plataforma de la isla de Alborán (Peñas et al. 2006), y pone de relieve el papel de los volcanes de fango como *hotspots* de biodiversidad (Vanreusel et al. 2009). Esta diversidad específica pone en evidencia que los márgenes continentales del sur ibérico albergan una fauna mucho más compleja y rica de lo que se había asumido.

Los factores ambientales presentes en el entorno de Gazul han demostrado jugar un papel determinante en la distribución y composición de sus comunidades de moluscos. La presencia de hábitats blandos y duros, combinada con la influencia de corrientes intensas y la proximidad al límite entre plataforma y talud, ha generado una gran heterogeneidad ambiental que promueve la coexistencia de especies de distintas afinidades. Esto queda reforzado con los resultados que muestran que el tipo de sedimento, junto con el porcentaje de materia orgánica del sedimento y la actividad de arrastre de la zona, son los factores más determinantes para la distribución de los moluscos infaunales (recolectados con draga de arrastre, box-corer y draga Shipek), mientras que para las especies epibentónicas y demersales (recolectadas con bou de vara), los que más influyeron en su distribución fueron la temperatura, como lo demuestra también el estudio de BALGIM; el porcentaje de materia orgánica y la presencia de carbonatos autigénicos. La temperatura se ha evidenciado como un factor clave en la diferenciación faunística, por encima incluso de la salinidad, como lo demuestra también el estudio de BALGIM.

Los resultados del estudio de la paleofauna hallada en el golfo de Cádiz (**capítulo 5**) proporcionan una importante perspectiva temporal para interpretar las actuales distribuciones de algunas especies de moluscos. El hallazgo de especies de afinidad boreal extintas localmente (*boreal guests*, Ruggieri 1977), preservadas en las tanatocenosis profundas del golfo de Cádiz durante el último periodo de glaciación, permite reconstruir el contexto paleoceanográfico del Pleistoceno tardío y documentar la continuidad con los registros de especies boreales en los depósitos glaciales mediterráneos (Malatesta & Zarlenga 1986). La presencia de especies típicamente boreales como *Arctica islandica*, *Neptunea antiqua* o *Chlamys islandica* evidencia un pasado climático marcadamente distinto, en el que las condiciones de temperatura y salinidad permitieron la expansión hacia el sur del margen ibérico de estas especies, hoy día restringidas a latitudes más septentrionales.

Las dataciones con ^{14}C realizadas a algunas de las especies de moluscos boreales extintas localmente en el área del golfo de Cádiz (*Neptunea contraria, N. antiqua* y *Arctica islandica*), las sitúan en el intervalo de 27.000 a 12.500 años atrás, en la última glaciación y en el período posterior de desglaciación (*Heinrich Stadial* 1). Comparando este resultado con las edades resultantes para moluscos boreales del estrecho de Gibraltar (Taviani et al. 1991), éstas abarcan desde edades más jóvenes del Pleistoceno, mientras que las dataciones realizadas en moluscos boreales del Mediterráneo (Froget et al. 1972) coinciden con parte del abrupto calentamiento (*Bølling-Allerød*) que existió después de la desglaciación del *Heinrich Stadial* 1, hasta más allá del Pleistoceno. Esto evidencia que la extinción local de los *boreal guests* no ocurrió de forma simultánea, sino progresivamente, y explica la continuidad del cambio de fauna que hasta ahora carecía de registros para esta región intermedia en su migración hacia la cuenca mediterránea. La presencia de especies boreales que jamás penetraron en el Mediterráneo en el actual paso de la MOW requiere una explicación. Dichas especies no podrían vivir en este entorno, incluso teniendo en cuenta que la MOW pudo ser algo más fría y menos salina en aquella época. Por lo tanto, durante el Pleistoceno tardío, la circulación de la MOW estaría desplazada hacia mayores profundidades, permitiendo que aguas intermedias atlánticas, más frías y menos salinas, entraran en contacto con el talud continental del golfo de Cádiz, creando las condiciones propicias para la persistencia de comunidades boreales. Por otra parte, la falta de penetración de muchas de estas especies en el Mediterráneo, a pesar de haber alcanzado el golfo de Cádiz, se puede explicar por factores como la barrera batimétrica que ejercería el umbral de Camarinal en el estrecho de Gibraltar, que sería más somero teniendo en cuenta una bajada del nivel del mar de unos 100 m; o bien que la temperatura y salinidad del Mediterráneo sólo fueran idóneas en zonas demasiado someras para dichas especies.

La principal conclusión del estudio de la campaña BALGIM (**capítulo 6A**) es que, en la actualidad, la casi totalidad de las especies registradas vivas en el paso de la MOW tienen distribución atlanto-mediterránea, mientras que aquellas con una distribución exclusivamente atlántica, especialmente las que se encontraron en contacto con masas de agua frías (AAIW, NADW), no logran penetrar en el Mediterráneo actual. Este resultado confirma la hipótesis de que la MOW representa una barrera ecológica para muchas especies atlánticas vinculadas a aguas profundas. Esta limitación no parece deberse solo al tipo de desarrollo larvario, ya que algunas especies con desarrollo intracapsular (y, por tanto, escasa capacidad de dispersión) como *Buccinum humphreysianum* y *Colus jeffreysianus*, se encuentran también dentro del Mediterráneo. La presencia de especies atlánticas con desarrollo larvario planctotrófico dentro del Mediterráneo (Bouchet & Taviani 1989) sugiere que el potencial de dispersión es importante, pero no es decisivo porque muchas otras con el mismo tipo de desarrollo no consiguen entrar. Por tanto, la temperatura de la MOW actual y de las aguas profundas mediterráneas es el principal factor que condiciona la entrada y establecimiento de especies atlánticas en la cuenca mediterránea. Este patrón ha sido igualmente detectado en otros grupos bentónicos como poríferos (Boury-Esnault et al. 1994), crustáceos decápodos (García-Raso 1996) y cnidarios (Ramil & Vervoort 1992). Con él se corrobora el efecto barrera de la MOW, que actualmente impide el establecimiento y el paso hacia el Mediterráneo de especies con afinidad exclusivamente atlántica y asociadas a aguas frías profundas (mayores de 600 m de profundidad). Esto pone de manifiesto que la temperatura es el principal determinante para la distribución de estas especies y de muchos moluscos bentónicos.

El estudio de los gasterópodos y escafópodos de BALGIM ha permitido completar el vacío que existía en el estudio de los grupos faunísticos, ya que la mayoría de los demás grandes grupos habían sido estudiados. Este estudio además aporta la descripción de una nueva especie para la ciencia (*Anatoma balgimae*).

En esta tesis se documenta por primera vez la presencia de simbiosis quimiosintética en el bivalvo *Kelliella miliaris* (**capítulo 7**), presente en el golfo de Cádiz en fondos fangosos bajo influencia de la MOW en el límite de la zona de mínimo de oxígeno. Los análisis genéticos, llevados a cabo en una población del vecino mar de Alborán, revelaron la presencia de Gammaproteobacterias, ectosimbiontes entre los cilios de los filamentos branquiales, implicadas en la oxidación del azufre. Este proceso permite a *K. miliaris* detoxificar su entorno de compuestos reducidos como el sulfuro de hidrógeno y escasez de oxígeno. Estas evidencias amplían el rango conocido sobre *K. miliaris* para las simbiosis bivalvo-bacteria. Los resultados de este estudio sugieren que estos hábitats pobres en oxígeno, aún poco explorados, podrían albergar asociaciones simbióticas más extendidas de lo que actualmente se conoce.

En **conjunto,** los resultados de esta tesis doctoral demuestran que el golfo de Cádiz representa un punto de confluencia de múltiples procesos biogeográficos, ecológicos y oceanográficos. Se trata de un entorno altamente heterogéneo, moldeado por la interacción de masas de agua atlánticas y mediterráneas, así como por la geodiversidad de estructuras submarinas y tipos de sustratos. El área incluye zonas con una actividad moderada de emisión de gases, como la cima del volcán de fango Anastasya, que favorece el establecimiento de especies de invertebrados quimiosimbióticas de especial interés, como los bivalvos *Solemya elarraichensis*, *Lucinoma asapheus* y el poliqueto frenulado *Siboglinum* sp. Estas comunidades coexisten con una rica fauna epibentónica heterótrofa, muchas de ellas especies sensibles y/o endémicas, lo que subraya el valor ecológico del área y la necesidad de su conservación. Sin embargo, se ha detectado una notable actividad de pesca de arrastre en diversos sectores del LIC, lo que compromete la persistencia de comunidades vulnerables, como los tapetes microbianos y aquellas con especies extremadamente escasas y sensibles al arrastre, como los pequeños agregados de coral bambú *Isidella elongata* (Esper, 1788) alrededor del volcán de fango Tarsis (Díaz-del-Río et al. 2014, González-García et al. 2020b).

Por todo lo anterior, y dado que la pesca de arrastre constituye la principal amenaza para los hábitats bentónicos del LIC, se requiere la implementación de medidas de conservación más estrictas que restrinjan o regulen esta práctica. Una opción viable es la regulación de la pesca de arrastre en ciertos sectores, como los que albergan hábitats y especies de gran valor biológico y ecológico amparados por las directivas europeas vigentes. Esto no implicaría un gran impacto socioeconómico, mientras que podría aportar beneficios ecológicos y pesqueros a medio y largo plazo (González-García et al. 2020a, b, 2022). Estudios previos demuestran que la creación de zonas de exclusión pesquera puede derivar en una exportación de biomasa adulta y larvas hacia áreas adyacentes, favoreciendo la recuperación de especies comerciales y mejorando la productividad de los caladeros (Roberts et al. 2001, Gell & Roberts 2003, Palumbi 2004).

En definitiva, el avance en el conocimiento del LIC "Volcanes de fango del golfo de Cádiz" debería contribuir al fortalecimiento de la protección de esta área, respaldando la necesidad de medidas adecuadas que restrinjan la pesca de arrastre de fondo en la zona, eligiendo zonas representativas que permitan la preservación de este patrimonio natural único. Asimismo, este estudio podría impulsar la transformación del actual LIC en una Zona de Especial Conservación (ZEC), elevando su nivel de protección frente a la pérdida de hábitats y biodiversidad y mejorando su gestión. Esto contribuiría no solo a la conservación de hábitats y especies de alto valor ecológico, sino también al cumplimiento de los objetivos establecidos por la Directiva Marco de Estrategia Marina (2008/56/CE) y la Directiva Hábitats (92/43/CEE), avanzando hacia una gestión más sostenible y responsable del medio marino.

Capítulo IX

Conclusiones

9. CONCLUSIONES

1. Los procesos de emisión de gases en el golfo de Cádiz generan una gran diversidad de sustratos, entre ellos carbonatos autigénicos, los cuales constituyen sustratos duros poco frecuentes en el mar profundo, lo que favorece una alta heterogeneidad bentónica y una amplia diversidad de hábitats. Esto, junto con la combinación de tipos de muestreo y la localización geográfica del golfo de Cádiz entre varias regiones biogeográficas, explicaría el considerable número de especies de moluscos encontrados en el volcán de fango Gazul.

2. El hallazgo en el estudio de la malacofauna asociada al volcán de fango Gazul, de dos especies nuevas para la ciencia junto con 86 nuevas citas para la Demarcación marina Sudatlántica, y de una especie nueva en las inmediaciones del Estrecho, revela el déficit de conocimiento sobre la biodiversidad profunda del golfo de Cádiz.

3. El agua de salida mediterránea (MOW) actúa como una barrera ecológica para especies exclusivamente atlánticas de aguas frías, restringiendo su paso hacia el mar Mediterráneo. En el seno de la MOW, la casi totalidad de las especies también se encuentran frecuentemente en el mar Mediterráneo, mientras que la mayoría de las especies del golfo de Cádiz con distribución exclusivamente atlántica están vinculadas a masas de agua más frías (agua profunda del Atlántico norte o agua intermedia antártica).

4. Durante el último periodo glaciar del Pleistoceno tardío, la malacofauna del talud superior del golfo de Cádiz incluía especies de afinidad boreal que actualmente tienen una distribución más al norte del canal de la Mancha, lo cual pondría de manifiesto un desplazamiento de la MOW a mayores profundidades que en la actualidad. Muchas de estas especies *boreal guests* se conocían en depósitos pleistocenos del Mediterráneo, y se documenta por primera vez en esta área intermedia. Otras especies se citan por primera vez en el golfo de Cádiz, pero nunca llegaron a alcanzar el mar Mediterráneo, incluso durante el pleniglaciar.

5. El bivalvo *Kelliella miliaris* es frecuente en zonas de mínimo oxígeno del golfo de Cádiz y mar de Alborán, y presenta una asociación simbiótica con numerosas bacterias gramnegativas entre los cilios branquiales. Los altos contenidos de oxígeno y azufre hallados en los gránulos electrodensos de estas bacterias apuntan a que las bacterias tendrían un importante papel en la detoxificación de los compuestos de azufre.

9. CONCLUSIONS

1. The fluid venting process in the Gulf of Cadiz generate a great diversity of substrates, among them authigenic carbonates, which constitute hard substrates that are rare in the deep-sea. This promotes high benthic heterogeneity and a wide range of habitats. This, together with the combination of sampling methods and the geographical location of the Gulf of Cadiz between several biogeographic regions, would explain the considerable number of mollusc species found at the Gazul mud volcano.

2. The discovery in the study of malacofauna of the Gazul mud volcano, of two species new to science along with 86 new records for the *Demarcación marina Sudatlántica*, and the finding of another species new to science in the western approaches of the Strait of Gibraltar, reveals a significant gap in knowledge about the deep-sea biodiversity of the Gulf of Cadiz.

3. The Mediterranean Outflow Water (MOW) acts as an ecological barrier for exclusively cold-water Atlantic species, restricting their passage into the Mediterranean Sea. Nearly all the species found within the MOW are also frequently found in the Mediterranean Sea, whereas most of the species of the Gulf of Cadiz with an exclusively Atlantic distribution are linked to colder water masses (North Atlantic Deep Water or Antarctic Intermediate Water).

4. During the last glacial period of the late Pleistocene, the malacofauna on the upper slope of the Gulf of Cadiz included species with boreal affinities, which nowadays are distributed north of the English Channel, which would suggest that the MOW was displaced to greater depths than today. Many of these "boreal guests" were known from Pleistocene deposits in the Mediterranean, and their presence in this intermediate area is documented for the first time. Other species are recorded for the first time in the Gulf of Cadiz but never reached the Mediterranean Sea, even during the pleniglacial.

5. The bivalve *Kelliella miliaris* is common in oxygen minimum zones in the Gulf of Cadiz and the Alboran Sea, and shows a symbiotic association with numerous Gram-negative bacteria among the gill cilia. The peaks of oxygen and sulfur found in the electron-dense granules of these bacteria point to these bacteria likely play an important role in the detoxification of sulfur compound.

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Annexes

ANNEX 1

Supplementary tables to chapter 6A can be found online at <https://doi.org/10.1016/j.dsr.2025.104492>

Table S1. Occurrences of live-taken molluscs in the BALGIM samples. See bottom of table for explanation of colour codes and abbreviations. Distribution – A : Atlantic only (blue background: AAIW or NADW; pink background: NACW); A-M: Atlantic and Mediterranean (yellow background); M: Mediterranean only (yellow background); Column C (Larval development): di: direct development; f: short lived, non-feeding pelagic larvae; pk: planktotrophic larvae. Many bivalves and scaphopods not assessed. The matrix used in PRIMER excludes samples with only one occurrence (value "1" in row 164) and species with only one occurrence (value "1" in column DA) ; rows 160, 161 and 162 are the "factors" used in the PRIMER matrix. "Order" (row 166 and column DB) allow restoring the original matrix if rows or columns have been reordered differently.

Table S2. Occurrences of all molluscs in the BALGIM samples. Plain numbers refer to dead shells, "v" refers to live taken specimens

Table S3. Species which most contributed to the grouping in the cluster analysis, as determined by the SIMPER analysis (cutoff below 5% contribution). Av. Abund: average abundance of the species in the sample group; Av. Sim.: Average contribution of the species to similarity within group; Sim/SD: ratio of species contribution to its standard deviation; Contrib%: percentual value of this contribution; Cum.%: Cumulative percentual value.

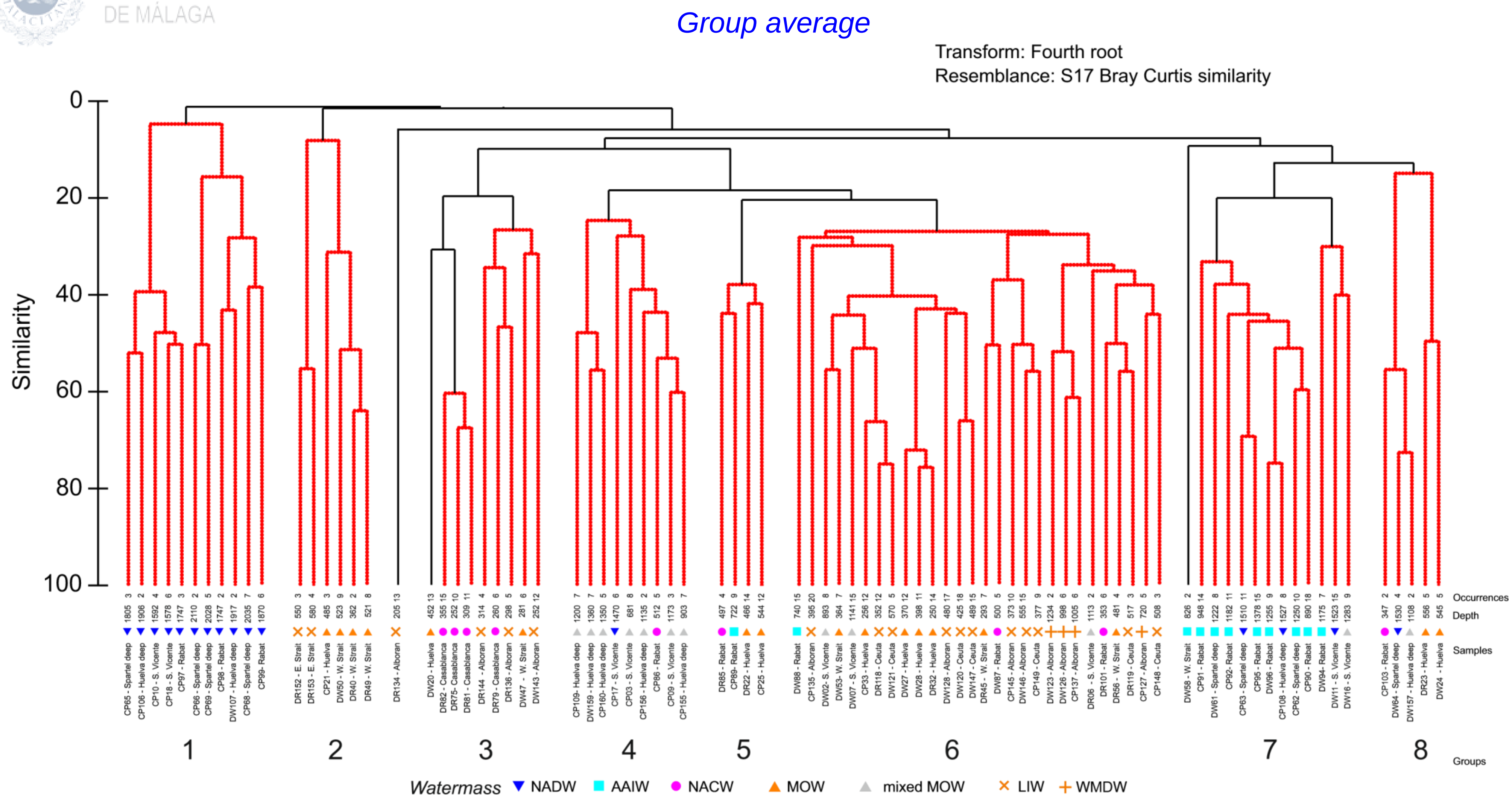

Figure S1. Cluster based on Bray-Curtis similarity index and abundance data of live-taken molluscs species (fourth root transformed) collected in the BALGIM expedition deeper than 200 m. Continuous lines indicate significant differences between samples or group of samples in SIMPROF test ($p < 0.005$). AAIW: Antarctic Intermediate Water; NADW: North Atlantic Deep Water; MOW: Mediterranean Outflow Water; LIW: Levantine Intermediate Water; NACW: North Atlantic Central Water; WMDW: Western Mediterranean Deep Water; mMOW: modified MOW; Occurrences: number of occurrences (species represented by at least one specimen) in the sample. Groups as in Table 6.5 of main text.

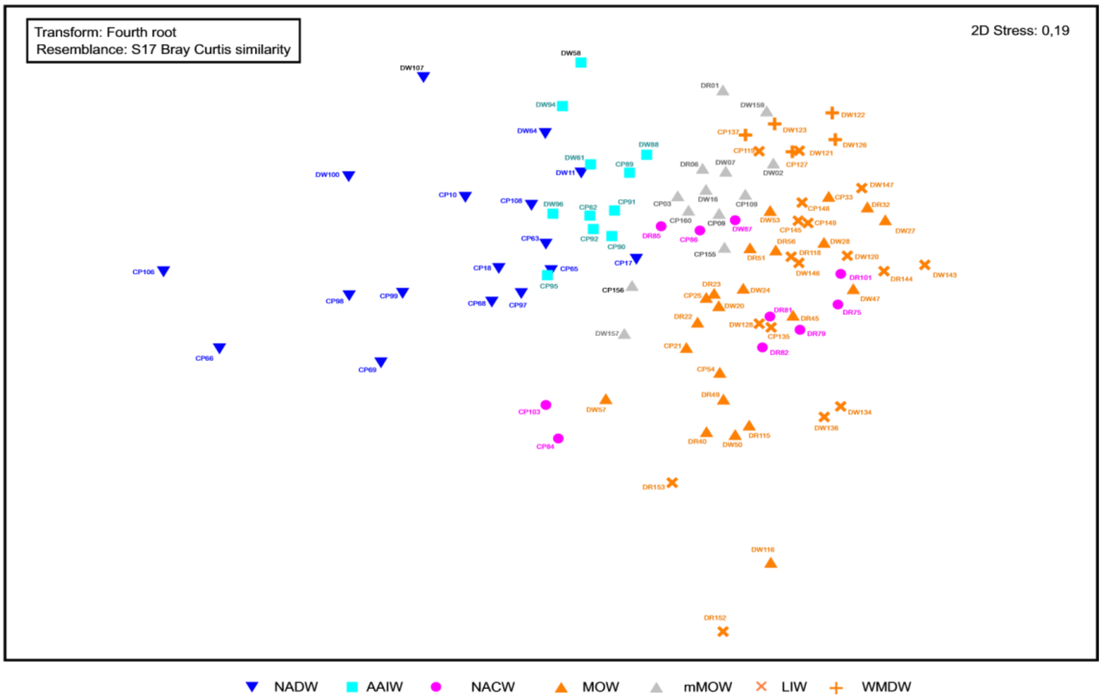

Figure S2. Non-metric multidimensional scaling plot of molluscan assemblages (live-collected specimens and thanatocenosis) from the BALGIM benthic samples collected deeper than 200 m, based on quantitative similarities (abundance data transformed to fourth root). NADW: North Atlantic Deep Water; MOW: Mediterranean Outflow Water; LIW: Levantine Intermediate Water; NACW: North Atlantic Central Water; WMDW: Western Mediterranean Deep Water; mMOW: modified MOW; AAIW: Antarctic Intermediate Water.

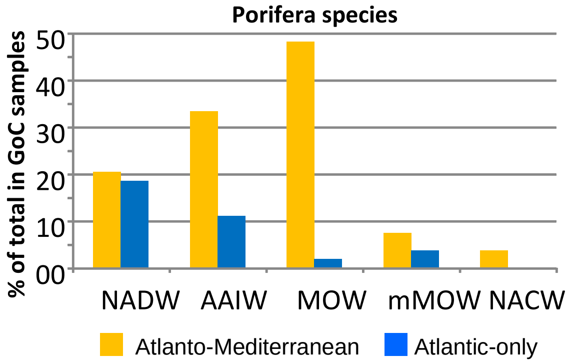

Figure S3. Percentages of Porifera belonging to alternative distributional patterns (Atlanto-Mediterranean and Atlantic-only) occurring in samples located in the different water masses of the Gulf of Cadiz (GoC). See Table 6.2 of chapter 6A for the detail of samples involved, same as for Figure 5. The percentages are referred to the total number of species (54) reported by Boury-Esnault et al. (1994) in this set of samples (continental shelf samples and Alboran Sea not included).

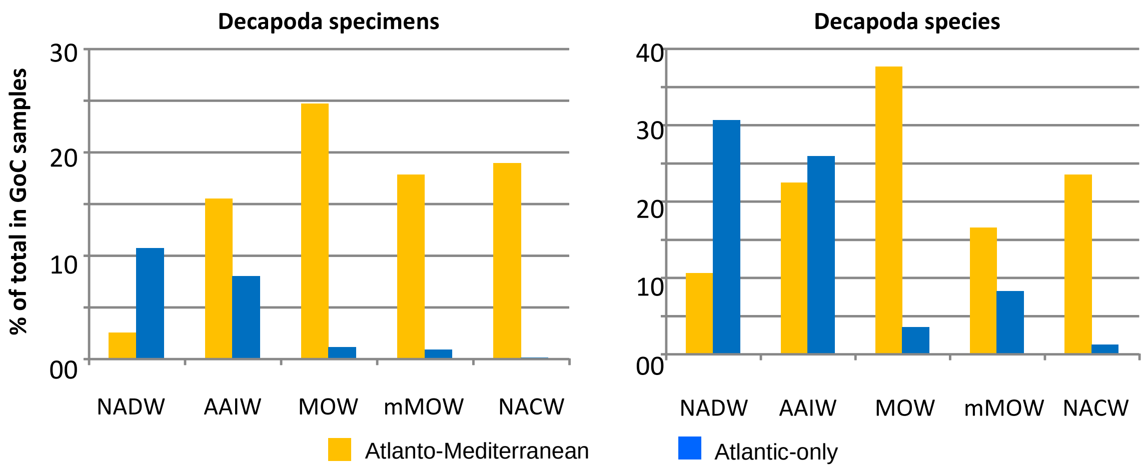

Figure S4. Percentages of Decapoda belonging to alternative distributional patterns (Atlanto-Mediterranean and Atlantic-only) occurring in samples located in the different water masses of the Gulf of Cadiz (GoC). See Table 6.2 of the chapter 6A for the detail of samples involved, same as for Figure 5. The percentages are referred to the total number of specimens (2458) and species (85) reported by García Raso (1996) in this set of samples (continental shelf samples and Alboran Sea not included).

ANNEX 2

Publications that support the thesis:

Molluscs from benthic habitats of the Gazul mud volcano (Gulf of Cádiz)

Utrilla O., Gofas S., Urra J., Marina P., Mateo-Ramírez A., López-González N., González-García E., Salas C., Rueda J.L. 2020. Molluscs from benthic habitats of the Gazul mud volcano (Gulf of Cádiz). Scientia Marina 84(3): 273-295.

Abstract

Molluscs from the Gazul mud volcano and its adjacent areas in the northern Gulf of Cádiz were studied using different sampling methods. This mud volcano has vulnerable deep-sea habitats and a potential high biodiversity. A total of 232 species were identified from the taxocoenosis and thanatocoenosis, of which 86 are new records for the Spanish margin of the Gulf of Cádiz, three of them are new records for Spanish waters and two species are new to science. The high species richness observed could be related to the combination of different sampling methods, the study of the thanatocoenosis, the high habitat heterogeneity and the geographical location of the Gazul mud volcano between different biogeographical regions. The best-represented species were *Bathyarca philippiana*, *Asperarca nodulosa*, *Leptochiton* sp., *Astarte sulcata* and *Limopsis angusta*. The thanatocoenosis harboured, with low frequency, species that are typical of northern latitudes, species indicating past seepage, species from the shelf and species restricted to particular hosts. The taxocoenosis found in different areas of Gazul (the mud volcano edifice, erosive depression and adjacent bottoms) generally displayed significant differences in multivariate analyses. Furthermore, the environmental parameters related to environmental complexity and food availability displayed the highest linkage with the molluscan fauna.

https://doi.org/10.3989/scimar.05027.17A

Late Pleistocene boreal molluscs in the Gulf of Cadiz: Past and current oceanographic implications

Urra J., Utrilla O., Gofas S., Valencia V.A., Farias C., González-García E., López-González N., Fernández-Salas L.M., Rueda J.L. 2023. Late Pleistocene boreal molluscs in the Gulf of Cadiz: Past and current oceanographic implications. Quaternary Science Reviews 313: 108196.

Abstract

Remains of molluscs were collected from the seafloor on the north-eastern margin of the Gulf of Cadiz, between 300 and 1000 m water depth, using different sampling methods (e.g. dredging, trawling and box-coring), during several deep-sea expeditions. Samples contained a suite of species which nowadays mostly occur northwards of the English Channel, together with other widespread species. Species now locally extinct in the Gulf of Cadiz and restricted to northern latitudes, which unequivocally indicate a faunal shift, include the gastropods *Buccinum undatum*, *Colus gracilis*, *Liomesus ovum* and *Neptunea antiqua*, the bivalves *Arctica islandica*, *Chlamys islandica*, *Modiolus modiolus*, *Mya truncata* and *Nuculana pernula* and the scaphopod *Antalis entalis*. These species represent "Boreal Guests" of marked palaeoclimatic significance, some of which are reported for the first time in the Gulf of Cadiz. The boreal species collected were mostly large (>5 cm) whereas smaller boreal species were extremely scarce, probably winnowed away by strong bottom currents. The pteropod *Limacina retroversa*, at present restricted to water masses northwards of the Iberian Peninsula but widespread in Mediterranean sediments of the last glaciation, was also recorded. Accelerator mass spectrometry (AMS) ^{14}C dates obtained from nine specimens of molluscs ranged between 26.1 and 14.6 kyr B.P., thus confirming their attribution to a last glacial assemblage. The abundance of these molluscan remains in the present Mediterranean Outflow Water pathway could be explained if this outflow was reduced in intensity or more likely shifted to a deeper level, leaving the upper slope in contact with suitable Atlantic intermediate waters. The findings of Boreal Guests in the Gulf of Cadiz document the continuity of the faunal shift which is well-known in the Mediterranean basin. Species still living in the Gulf of Cadiz and the Alboran Sea nevertheless account for 84.6% of specimens among the larger species.

https://doi.org/10.1016/j.quascirev.2023.108196

How adverse are Mediterranean waters to the deep-sea fauna? A study of the Gibraltar exchange based on Mollusca from the “BALGIM” expedition

Utrilla O., Gofas S., Salas C. 2025. How adverse are Mediterranean waters to the deep-sea fauna? A study of the Gibraltar exchange based on Mollusca from the “BALGIM” expedition. Deep-sea Research Part I 220:104492.

Abstract

The BALGIM expedition was designed to assess the distribution of marine organisms in the transition from Gulf of Cadiz to Mediterranean Sea across the Strait of Gibraltar. There were 99 hauls below 200 m depth, down to 2110 m. Two matrixes with abundance data were constructed using the data of gastropods and scaphopods from this study and those of bivalves studied earlier. Species were scored according to their bathymetric and geographic distribution as (1) deep-sea species occurring exclusively in the Atlantic, or (2) deep-sea species reported as living both in the Atlantic and the Mediterranean. A total of 4641 live-taken individuals corresponding to 154 species of molluscs collected alive were identified, and almost twice as many (243 species) including those collected as shells only. The samples do not form clearly defined clusters based on their faunal content. More than half of the species (84) occur both in the Mediterranean Sea and the Atlantic Ocean. Most of the 62 species with an Atlantic-only distribution are associated to the cool or cold waters below 600 m depth along the Moroccan margin, and are barred by the Mediterranean Outflow Water in the northern part of Gulf of Cadiz. Four species are preferent of the warm but low-saline North Atlantic Central Water, also off the Moroccan margin. The Mediterranean outflow largely shares a set of species also occurring in the Mediterranean, whereas there are no Mediterranean-only deep-sea species. Therefore, variation in salinity in a range of 1–2‰ is not critical compared to temperature which explains most of the restricted distributions.

https://doi.org/10.1016/j.dsr.2025.104492

A new species of *Anatoma* (Vetigastropoda: Anatomidae) from the Strait of Gibraltar

Utrilla O., Gofas S. 2024. A new species of *Anatoma* (Vetigastropoda: Anatomidae) from the Strait of Gibraltar. Iberus 42(2): 201-209.

Abstract

A new species of the genus *Anatoma* Woodward, 1859, collected by the BALGIM expedition (1984) from the Atlantic entrance of the Strait of Gibraltar is described and figured. The new species is compared with other *Anatoma* species reported in this and other areas, from which it is distinguished by the axial sculpture of the shell with unusually numerous riblets. The large number of species of this genus found in the studied area highlights the importance of deep-sea research, revealing unexpected biodiversity and suggesting further exploration opportunities.

urn:lsid:zoobank.org:pub:2895CF8E-BCE0-498B-A508-61F64D45AFA7

Life at oxygen minimum zone: bacterial symbiosis in the gills of the bivalve *Kelliella miliaris*

Utrilla O., Viguera E., Gofas S., Marina P., López-Téllez J.F., Salas C. 2025. Life at oxygen minimum zone: bacterial symbiosis in the gills of the bivalve *Kelliella miliaris*. Frontiers in Marine Sciences 12: 1587729.

Abstract

Kelliella miliaris (Philippi, 1844) is a minute bivalve, living on the surface of soft sediments, from the continental shelf to bathyal depths, commonly in the oxygen minimum zones (OMZ) and/or in reducing habitats. The scarcity of data on the biology of *Kelliella* prompted us to investigate, at ultrastructural level, specimens found in southern Spain. *Kelliella miliaris* shows several morphological characteristics that would be adaptive for living in the OMZ: (1) presence of numerous muscular fibers in the mantle, mantle edge and gills-visceral mass connection; all of which would allow to actively move the gills and/or enable a better control of the ventral opening in relation to vertical movements of the animal; (2) high number (in relation to body size) and large size of gill filaments, mainly in the large inner demibranch; and (3) long cilia which would provide a large surface for capture of oxygen and a highly effective uptake of oxygen from water. We have observed in all the specimens examined the presence of numerous rod shaped bacteria among the gill cilia. These bacteria show the typical double membrane of Gram-negative bacteria. The analysis of the bacterial DNA revealed that Gammaproteobacteria is the most abundant class, with 53.69% of total reads. The latter, together with the peak of oxygen and the presence of sulfur inside the electron-dense granules from the bacteria, determined by TEM-EDX analysis, point to the involvement of these bacteria in the oxidization of the sulfide to thiosulfate. The presence of bacteria in the gills of *Kelliella miliaris* highlights the importance of the chemosynthetic symbiosis in the OMZs of the oceans that has been probably overlooked up to now. The presence of different microorganisms in the stomach indicates heterotrophy. We have found spermatozoids inside the female gonad, which confirms internal fertilization in *K. miliaris*. However, the presence of protoconch I and protoconch II, indicates planktotrophic larval development.

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