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Review

Review of Age Estimation Techniques and Growth Models for Shelled Organisms in Marine Animal Forests

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Abstract

Marine shelled organisms exhibit diverse growth strategies shaped by species-specific traits and environmental conditions that critically influence their ecological roles, particularly within Marine Animal Forests (MAF), which are structurally complex habitats and biodiversity-rich habitats. This review compiles and compares empirical growth data for 16 bivalve and gastropod species across seven families, classified as full MAF contributors (*Pinna nobilis*, *Flexopecten glaber*, *Pecten maximus*, and *Placopecten magellanicus*), partial MAF contributors (*Cerastoderma edule*, *C. glaucum*, *Chamelea gallina*, *Ruditapes philippinarum*, *Mercenaria mercenaria*, *Panopea generosa*, *Anadara kagoshimensis*, *A. inaequivalvis*, and *Tegillarca granosa*), and ecologically relevant non-MAF species (*Buccinum undatum*, *Hexaplex trunculus*, and *Rapana venosa*). Age estimation methods included direct techniques, such as shell growth ring and opercular annulus analysis, alongside indirect approaches, such as length-frequency analysis, stable isotope profiling, and mark–recapture studies. Growth trajectories were modelled using von Bertalanffy growth function (VBGF) parameters to estimate the shell size from ages 1 to 4. Based on these estimates, species were categorised into slow, moderate, fast, and exceptional growth groups. These classifications were further explored through hierarchical clustering that grouped species according to their VBGF-derived growth values, revealing consistent and contrasting life history strategies. This comparative analysis should enhance the understanding of molluscan growth dynamics and support the conservation and management of MAF-associated ecosystems by informing restoration planning, guiding species selection, and contributing to evidence-based policy development.

Keywords: age determination; growth modelling; Marine Animal Forests; *Pinna nobilis*; *Rapana venosa*; shelled organisms; growth rates; von Bertalanffy growth function

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1. Introduction

Marine Animal Forests (MAFs) represent some of the most dynamic and biodiverse marine ecosystems. They are characterised by the dense aggregation of organisms that form, maintain, or inhabit complex three-dimensional habitats [1,2]. Shelled organisms, including bivalves and gastropods, are both structural and functional components of these ecosystems [3,4]. Species such as *Anadara inaequivalvis*, *Cerastoderma edule*, *Ruditapes philippinarum*, and *Pinna nobilis* enhance ecosystem stability by improving water quality and nutrient cycling [5,6]. Conversely, predatory species, such as *Rapana venosa* and *Hexaplex trunculus*, regulate prey populations, contributing to trophic balance [7,8]. These species are ecologically significant and serve as biological indicators of environmental conditions through their growth- and age-related traits [9–11].

Understanding the growth dynamics of shelled organisms is crucial for understanding their ecological roles and ensuring MAF ecosystem sustainability [12,13]. The ability of these organisms to respond to environmental changes and anthropogenic pressures is influenced by growth rates, age structures, and life history traits [12,14]. However, comprehensive insights into these aspects require robust methodologies for age determination and growth modelling [15,16]. Techniques such as shell increment analysis, isotopic composition studies, advanced imaging, and shape-based approaches like elliptic Fourier analysis have proven instrumental in assessing age, growth, and site-specific morphological variation across diverse biological systems [17–19]. Coupled with growth models, such as the von Bertalanffy equation, these approaches provide critical data on species-specific growth trajectories and their adaptability to environmental gradients [20–22].

This review aimed to summarise and compare the current state of knowledge on age determination methods and growth modelling for key marine shelled organisms, including those fully, partially and not associated with MAFs. Particular emphasis was placed on the comparison of growth rates across species, highlighting interspecies variability and its ecological implications.

2. Materials and Methods

2.1. Literature Search Strategy

A targeted literature review was conducted to identify peer-reviewed studies focusing on age determination techniques, growth modelling approaches, and MAF-associated interspecific growth comparisons of marine shelled organisms. Google Scholar was used to conduct the search to ensure comprehensive coverage of scientific literature [23].

The search strategy was designed to capture a broad spectrum of methodologies and taxa. Boolean operators were used to combine the following thematic keyword groups:

- **Age determination:** "age reading," "growth increments," "shell analysis," "sclerochronology," "isotope analysis," "microstructure," and "increment formation"
- **Growth modelling:** "growth rate," "growth modelling," "von Bertalanffy," "length-at-age," "size-frequency analysis," "growth curves"
- **Organism and ecosystem context:** "bivalves," "gastropods," "shelled organisms," "Marine animal forests," "ecosystem engineers"

The search was restricted to studies that provided empirical data on growth or age estimation for species known to contribute to MAF structure and function. Both full and partial MAF contributors and ecologically relevant non-MAF species were included for comparative purposes.

2.2. Data Extraction and Classification

From the selected studies, data were systematically extracted and categorised into three primary domains:

i. **Age determination methods:** including direct techniques (e.g., shell increment analysis and operculum examination), indirect methods (e.g., length-frequency analysis), and advanced approaches (e.g., stable isotope analysis, mark–recapture, and laboratory-based validation).
ii. **Growth models:** with emphasis on the use of the von Bertalanffy growth function (VBGF) and other length-at-age modelling frameworks. Parameters, such as asymptotic length (L_∞), growth coefficient (K), and theoretical age at zero length (t_0), were recorded where available.
iii. **Species-specific growth rates:** including raw and modelled shell length data across age classes, with intra- and interspecific variability considered.

Each study was further classified by species, taxonomic family, geographic region, and methodological approach.

2.3. Statistical Analysis

Quantitative data on shell length at age were synthesised to evaluate growth patterns across species. Shell lengths at specific age classes (1, 1.5, 2, 2.5, 3, 3.5, and 4 years) were estimated for each species using VBGF parameters reported in the literature. These estimates enabled standardised comparisons of growth trajectories across species, regardless of the original study design or sampling approach.

To assess growth performance, the cumulative size gain was calculated as the difference between the estimated shell length at 4 years of age and that at 1 year of age (i.e., size at 4 years minus size at 1 year). This metric reflects net growth over a three-year interval, was selected to minimise early-life variability, and thus serves as a practical proxy for growth performance. The theoretical age at zero length (t_0) in the VBGF may vary across studies and species, and in some cases, it may exceed age 1 (e.g., *Panopea generosa* in Cruz-Vásquez et al. [24], with $t_0 = 2.26$). However, our method relies on predicted lengths at fixed age points derived from published VBGF parameters, allowing consistent interspecies comparisons. Confidence intervals were also calculated to reflect variability in growth estimates across studies.

Species-specific growth trajectories were visualised using locally estimated scatterplot smoothing (LOESS), a non-parametric regression technique that fits simple models to localised subsets of the data to reveal underlying trends without assuming a global functional form [25]. Shell size estimates were extracted for each species, reshaped into a long format, and plotted to display individual study estimates (grey lines), a smoothed LOESS trend (black line), and the associated 95% confidence interval (red band). Axis limits were adjusted to accommodate species-specific size ranges, ensuring consistent visual interpretation across taxa.

Hierarchical clustering analysis was also performed using average cumulative shell size gain values for each species. Euclidean distance was used to measure species dissimilarity based on these growth metrics, and complete linkage was applied to form clusters by maximising the distance between the most dissimilar members within each group. This method was chosen to ensure clear separation between growth categories and to reflect biologically meaningful differences in growth trajectories. The resulting dendrogram grouped species into clusters representing slow, moderate, fast, and exceptional growth strategies.

All statistical analyses and visualisations were conducted in R (version 4.5.0) [26] using RStudio (version 2025.5.0.496) [27] as the integrated development environment, with packages including stats [26], ggplot2 [28], and dendextend [29].

3. Results

3.1. Synthesis of Species and Methodological Scope

This review summarises findings from an extensive collection of studies focusing on the growth dynamics of 16 key marine shelled species. These species represent seven families across the Bivalvia and Gastropoda classes: Arcidae, Cardiidae, Hiatellidae, Pectinidae, Veneridae, Buccinidae, and Muricidae. Figure 1 illustrates the geographical distribution of these studies.

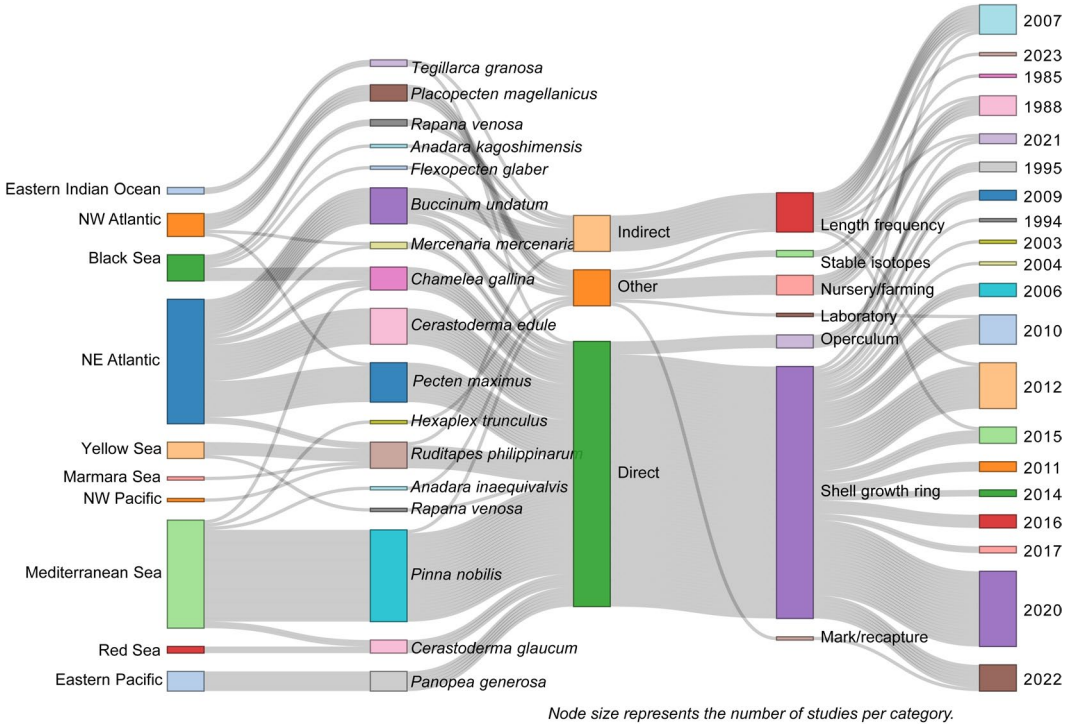


Figure 1. Distribution, species, and age estimation methods in marine shelled organisms.

Our analysis encompasses species integral to MAF formation, such as the noble pen shell (*P. nobilis*), the smooth scallop (*Flexopecten glaber*), the great scallop (*Pecten maximus*), and the Atlantic Sea scallop (*Placopecten magellanicus*). We also include species that partially contribute to MAF ecosystems, such as the common cockle (*C. edule*), the lagoon cockle (*Cerastoderma glaucum*), the striped venus (*Chamelea gallina*), the Manila clam (*R. philippinarum*), the hard clam (*Mercenaria mercenaria*), the geoduck (*P. generosa*), and the blood clams (*Anadara kagoshimensis*, *A. inaequivalvis*, and *Tegillarca granosa*). Non-MAF predatory gastropods, including the common whelk (*Buccinum undatum*), the banded dye-murex (*Hexaplex trunculus*), and the veined rapa whelk (*R. venosa*), were also examined to provide a broader ecological context. Table 1 presents a summary of these species, including their habitats, feeding biology, and representative images.

The reviewed literature, comprising 42 studies, yielded a substantial dataset with numerous records for each species. Among the bivalves, *P. nobilis* was the most extensively documented, followed by *P. maximus*, *C. edule*, *R. philippinarum*, and *P. generosa*. In contrast, species such as *T. granosa*, *A. inaequivalvis*, *A. kagoshimensis*, and *F. glaber* were less frequently the focus of research. *B. undatum* was the most prominently studied gastropod species, with *R. venosa* and *H. trunculus* also receiving significant attention.

Table 1. Summary of species characteristics, including habitat and feeding biology (from SeaLifeBase [30]), and shell images accessed via World Register of Marine Species (WoRMS) [31], hosted externally by Kapeller [32] and Trausel and Slieker [33].

Images accessed via WoRMS Editorial Board [31]	From SeaLifeBase [30]	
	Habitats	**Feeding Biology**
 *Anadara inaequivalvis* [32]	Coastal areas with sandy or muddy substrates, often in brackish waters.	Filter feeder that consumes plankton and organic particles.
 *Anadara kagoshimensis* [32]	Shallow marine environments with sandy or muddy bottoms.	Filter feeder feeding on suspended organic matter and plankton.
 *Tegillarca granosa* [33] (actual size: 43 mm)	Intertidal and subtidal zones with muddy substrates often found in estuaries.	Filter feeder, primarily consuming phytoplankton.
 *Cerastoderma edule* [32]	Sandy or muddy substrates in intertidal zones, common in estuaries and lagoons.	Filter feeder feeding on phytoplankton and organic detritus.

Table 1. *Cont.*

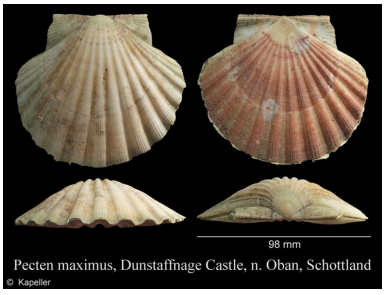
Images accessed via WoRMS Editorial Board [31]	From SeaLifeBase [30]	
	Habitats	**Feeding Biology**
 *Cerastoderma glaucum* [33]	Brackish and marine environments, often in lagoons and estuaries.	Filter feeder that consumes plankton and organic matter.
 *Panopea generosa* [33]	Deep sandy or muddy substrates in subtidal zones.	Filter feeder placed on plankton and suspended organic material.
 *Flexopecten glaber* [33]	Sandy or muddy substrates in shallow subtidal zones.	Filter feeder, primarily consuming phytoplankton.
 *Pecten maximus* [32]	Sandy gravel or coarse substrates in subtidal zones.	Filter feeder feeding on phytoplankton and organic particles.

Table 1. *Cont.*

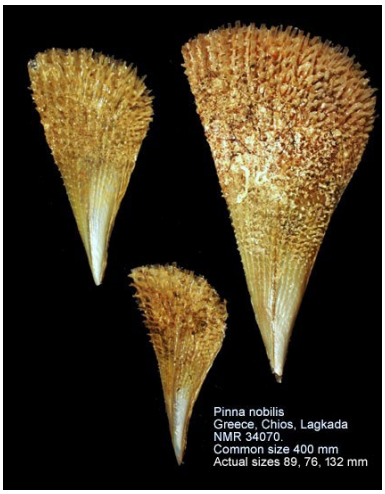
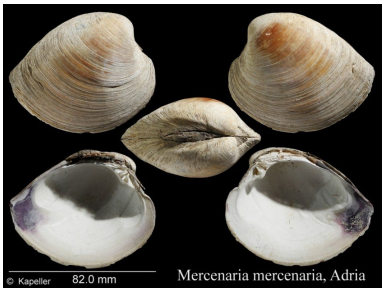
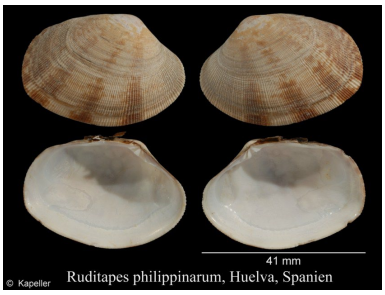
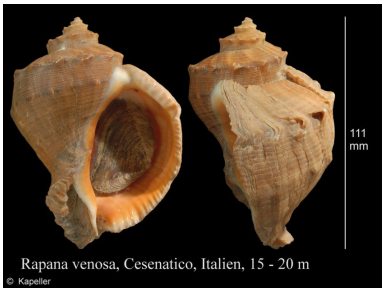
Images accessed via WoRMS Editorial Board [31]	From SeaLifeBase [30]	
	Habitats	**Feeding Biology**
 *Placopecten magellanicus* [33]	Deep, sandy, or gravel substrates in cold waters.	Filter feeder that consumes phytoplankton and organic detritus.
 *Pinna nobilis* [33]	Seagrass meadows in shallow, sheltered marine environments.	Filter feeder placed on plankton and suspended organic material.
 *Chamelea gallina* [32]	Sandy or muddy substrates in shallow coastal waters.	Filter feeder that consumes phytoplankton and organic particles.
 *Mercenaria mercenaria* [32]	Sandy or muddy substrates in estuaries and lagoons.	Filter feeder feeding on phytoplankton and organic detritus.

Table 1. *Cont.*

Images accessed via WoRMS Editorial Board [31]	From SeaLifeBase [30]	
	Habitats	**Feeding Biology**
 *Ruditapes philippinarum* [32]	Sandy or muddy substrates in the intertidal and shallow subtidal zones.	Filter feeder that consumes phytoplankton and organic matter.
 *Buccinum undatum* [33]	Cold, deep marine waters with sandy or muddy substrates.	Scavenger and predator feeding on carrion and small invertebrates.
 *Hexaplex trunculus* [32]	Rocky or sandy substrates in shallow coastal waters.	Carnivorous, preying on bivalves and other molluscs.
 *Rapana venosa* [32]	Sandy or muddy substrates in estuaries and shallow coastal waters.	Carnivorous, feeding on bivalves and other molluscs.

The methodologies for age determination varied considerably across the literature surveyed (Figure 1). A clear majority of studies favoured direct methods, primarily through

the analysis of growth rings on the shells of both bivalves and some gastropods. For certain gastropod species, such as *B. undatum* and *R. venosa*, operculum analysis served as a reliable alternative for age estimation. Indirect approaches, such as length-frequency analysis, were also employed, although less commonly. A smaller subset of studies used alternative techniques, including stable isotope analysis, mark–recapture experiments, and laboratory-based growth trials, to ascertain the age and growth patterns of the rats.

3.2. Comparison of Growth Strategies Across Families

To investigate the diverse growth strategies among these species, we utilised the VBGF parameters derived from the literature (Table 2). By estimating shell lengths at sequential ages, we calculated the increase in cumulative shell size between the first and fourth years of life. This metric, along with its 95% confidence intervals, allowed for a standardised comparison of growth performance. The species were classified into four distinct growth categories based on this analysis, revealing a spectrum of life history strategies (Figure 2):

- **Slow Growers:** *A. inaequivalvis*, *C. glaucum*, *C. gallina*, *C. edule*, and *H. trunculus*
- **Moderate Growers:** *T. granosa*, *M. mercenaria*, *R. philippinarum*, and *F. glaber*
- **Fast Growers:** *P. magellanicus*, *P. maximus*, *A. kagoshimensis*, *R. venosa*, *P. generosa*, and *B. undatum*
- **Exceptional Grower:** *P. nobilis*

Figure 2 visually depicts the mean cumulative size gain and associated confidence intervals for each species, providing a clear depiction of these interspecific growth disparities.

3.2.1. Arcidae

Divergent growth patterns were evident within the Arcidae. *A. kagoshimensis* demonstrated rapid and sustained growth, achieving a considerable size by year four. In contrast, *A. inaequivalvis* exhibited more modest growth. Both species exhibited an initial burst of growth within the first 1.5 years. *T. granosa* exhibited a moderate growth rate with high individual variability, suggesting a plastic response to environmental conditions (Figure 3).

3.2.2. Buccinidae

B. undatum exhibited substantial intraspecific variability. Although the average growth was fast, shell sizes varied widely at each age class. The most significant increase occurred between years 1 and 2.5, after which growth decelerated (Figure 3).

3.2.3. Cardiidae

The two cockle species displayed distinct growth dynamics. *C. edule* had a pronounced early growth phase, reaching a large portion of its adult size within the first few years. *C. glaucum* followed a slower, more uniform growth trajectory (Figure 3).

3.2.4. Hiatellidae

P. generosa exhibited substantial and continuous growth, which is consistent with its long-lived life history. The shell size significantly increased each year, reaching large dimensions by year four (Figure 3).

3.2.5. Muricidae

The predatory gastropods showed contrasting strategies. *H. trunculus* grew slowly and steadily, with gradual increases in shell size. Conversely, *R. venosa* exhibited moderate to fast growth and high variability across populations (Figure 3).

Table 2. Overview of age determination methods, and von Bertalanffy growth function (VBGF) parameters. The growth coefficient (K) is expressed in year^{-1}, and the theoretical age at zero length (t_0) is given in years.

Species	Age Determination		VBGF			Study Area	References
	Ageing	Method	L_∞ (mm)	k	t_0		
Anadara inaequivalvis	Other	Length-frequency	29.65	1.19	0.30	Sufa Lagoon, Türkiye	Acarli et al. [34]
Anadara kagoshimensis	Indirect	Length-frequency	121.78	0.25	−0.33	Western Black Sea	Dağtekin [35]
Tegillarca granosa	Direct	Shell growth ring	35.40	0.37	−0.14	Balik Pulau, Malaysia	Mirzaei et al. [36]
	Indirect	Length-frequency	73.40	0.58	−0.49	Kakinada Bay, India	Narasimham [37]
Cerastoderma edule	Direct	Shell growth ring	34.36	0.64	0.00	Bay of Saint-Brieuc, France	Ponsero et al. [38]
	Direct	Shell growth ring	28.27	0.03	8.99	Mundaka Estuary, Spain	Jelesias and Navarro [39]
	Direct	Shell growth ring	40.70	0.74	0.30	Mira Channel, Portugal	Maia et al. [40]
	Direct	Shell growth ring	35.80	0.64	−0.95	NE Atlantic Coasts (Ireland, Wales, and France)	Mahony et al. [41]
	Direct	Shell growth ring	45.04	0.22	−3.24	Ireland	
	Direct	Shell growth ring	42.74	0.29	−2.34	Ireland	
	Direct	Shell growth ring	36.15	0.34	−2.25	Wales	
	Direct	Shell growth ring	43.24	0.40	−0.63	Ireland	
	Direct	Shell growth ring	40.74	0.47	−0.40	Ireland	
	Direct	Shell growth ring	34.29	0.34	−2.07	France	
	Direct	Shell growth ring	31.20	1.43	−0.05	Merja Zerga, Morocco; French Atlantic coast	Gam et al. [42]
	Direct	Shell growth ring	38.40	1.30	−0.08	Arcachon Bay, France; Moroccan Atlantic Coast	
Cerastoderma glaucum	Direct	Shell growth ring	38.28	0.21	−1.27	Lake Timsah, Egypt	Mohammad et al. [43]
	Direct	Shell growth ring	37.86	0.22	−0.96	Lake Timsah, Egypt	
	Direct	Shell growth ring	46.45	0.15	−2.17	S. Sinai Coast, Egypt	
	Direct	Shell growth ring	32.17	0.36	−0.38	S. Sinai Coast, Egypt	
Panopea generosa	Direct	Shell growth ring	134.00	0.19	−4.40	Gulf of California, Mexico	Calderon-Aguilera et al. [44]
	Direct	Shell growth ring	163.40	0.19	−2.99	San Felipe, Mexico	Aragón-Noriega et al. [45]
			157.50	0.11	−1.2	Puerto Peñasco, Mexico	
	Direct	Shell growth ring	122.16	0.50	2.26	Guaymas-Empalme Bay, Mexico	Cruz-Vásquez et al. [24]
	Direct	Shell growth ring	122.59	0.26	−1.78	Gulf of California, Mexico	Hidalgo-De-La-Toba et al. [46]
	Direct	Shell growth ring	135.00	0.20	−0.07	Gulf of California, Mexico	Hidalgo-de-la-Toba et al. [47]

Table 2. *Cont.*

Species	Age Determination		VBGF			Study Area	References
	Ageing	Method	L_∞ (mm)	k	t_0		
Flexopecten glaber	Other	Mark/recapture	54.00	0.24	−1.30	Bulgarian Black Sea	Todorova et al. [48]
Pecten maximus	Direct	Shell growth ring	109.70	0.67	0.50	Ría de Vigo, Spain	Chauvaud et al. [49]
	Direct	Shell growth ring	155.90	0.20	0.36	Austevoll, Norway	
	Direct	Shell growth ring	101.10	0.68	0.47	Île de Ré, France	
	Direct	Shell growth ring	103.60	0.83	0.56	The Bay of Brest, France	
	Direct	Shell growth ring	108.40	0.87	0.58	Bay of Seine, France	
	Direct	Shell growth ring	108.40	0.61	0.48	Plymouth, UK	
	Direct	Shell growth ring	143.60	0.26	0.41	Holyhead, UK	
	Direct	Shell growth ring	137.00	0.25	0.40	Scarborough, UK	
	Direct	Shell growth ring	146.90	0.23	0.19	Campbeltown, UK	
	Direct	Shell growth ring	127.20	0.28	0.42	Bessaker, Norway	
	Direct	Shell growth ring	133.50	0.23	0.54	Brønnøysund, Norway	
	Direct	Shell growth ring	144.50	0.24	0.56	Træna, Norway	
Placopecten magellanicus	Other	Nursery/farming	176.50	0.19	0.55	Sunnyside, NL, Canada (10 m)	MacDonald and Thompson [50]
	Other	Nursery/farming	158.40	0.16	0.10	Sunnyside, NL, Canada (31 m)	
	Other	Nursery/farming	166.90	0.21	0.51	St. Andrews, NB, Canada (10 m)	
	Other	Nursery/farming	166.00	0.21	0.53	St. Andrews, NB, Canada (31 m)	
	Other	Nursery/farming	155.90	0.22	0.32	New Jersey Coast, USA (31 m)	
Pinna nobilis	Direct	Shell growth ring	439.00	0.21	−0.57	Es Freus, Spain	García-March et al. [51]
	Direct	Shell growth ring	624.00	0.19	−0.05	W. Mediterranean Sea, Spain	
	Direct	Shell growth ring	587.00	0.19	−0.40	Tabarca Island, Spain	
	Direct	Shell growth ring	654.00	0.15	−0.95	Port-Cros, France	
	Direct	Shell growth ring	399.00	0.29	0.24	La Olla, Spain	
	Direct	Shell growth ring	582.00	0.37	−0.06	Mar Menor, Spain	
	Direct	Shell growth ring	456.00	0.21	−0.88	Moraira, Spain	
	Direct	Shell growth ring	607.00	0.24	0.12	El Racó, Spain	
	Direct	Shell growth ring	569.00	3.90	−0.04	Dénia, Spain	
	Direct	Shell growth ring	560.00	4.50	−0.04	Île des Embiez, France	
	Direct	Shell growth ring	655.00	1.90	−1.78	Balearic Islands, Spain	
	Direct	Shell growth ring	750.00	2.60	−0.03	Alfacs Bay, Spain	

Table 2. *Cont.*

Species	Age Determination		VBGF			Study Area	References
	Ageing	Method	L_∞ (mm)	k	t_0		
	Direct	Shell growth ring	456.00	0.21	−0.88	Moraira, Spain	García-March et al. [51]
	Direct	Shell growth ring	60.70	0.24	0.12	El Racó, Spain	
	Direct	Shell growth ring	569.00	0.24	−0.04	Dénia, Spain	
	Direct	Shell growth ring	560.00	0.30	0.28	Île des Embiez, France	
	Direct	Shell growth ring	655.00	0.13	−1.78	Balearic Islands, Spain	
	Direct	Shell growth ring	750.00	0.18	−0.03	Alfacs Bay, Spain	
	Direct	Shell growth ring	631.00	0.17	−0.67	Site SO, W. Mediterranean *	
	Direct	Shell growth ring	430.00	0.23	−0.47	Site EO, W. Mediterranean *	
	Direct	Shell growth ring	565.00	0.30	−0.05	Site LG, W. Mediterranean *	
	Direct	Shell growth ring	560.00	0.14	−3.04	Moraira Bay and Illa Grossa, Spain	Garcia-March et al. [52]
	Direct	Shell growth ring	573.00	0.16	0.02	Moraira Bay and Illa Grossa, Spain	
	Direct	Shell growth ring	452.70	0.14	−3.80	Cabrera Island, Spain	Nebot Colomer et al. [53]
	Direct	Shell growth ring	452.70	0.14	−0.80	Cabrera Island, Spain	
	Direct	Shell growth ring	459.40	0.15	−3.44	Foradada Islet, Spain	
	Direct	Shell growth ring	459.40	0.15	−0.44	Foradada Islet, Spain	
	Other	Nursery/farming	290.60	1.16	0.18	Vila Joiosa, Spain	Hernandis et al. [54]
Chamelea gallina	Direct	Shell growth ring	37.55	0.71	−0.01	Portugal Coast and the Mediterranean Sea	Gaspar et al. [55]
	Direct	Shell growth ring	43.90	0.26	−0.84	Ancona, Italy	Bargione et al. [56]
	Direct	Shell growth ring	27.25	0.61	−0.14	Russian Black Sea	Boltacheva and Mazlumyan [57]
	Direct	Shell growth ring	36.11	0.79	−0.45	Huelva Coast, Spain	Delgado et al. [58]
	Direct	Shell growth ring	26.60	0.22	−1.21	Black Sea (closed area)	Dalgiç et al. [59]
	Direct	Shell growth ring	28.88	0.21	−1.29	Black Sea (non-dredged)	
	Direct	Shell growth ring	26.00	0.16	−1.96	Black Sea (dredged)	
Mercenaria mercenaria	Direct	Shell growth ring	84.50	0.11	−1.59	Narragansett Bay, RI, USA	
	Direct	Shell growth ring	80.13	0.15	−0.54	Southampton Water, UK	

Table 2. *Cont.*

Species	Age Determination		VBGF			Study Area	References
	Ageing	Method	L_∞ (mm)	k	t_0		
Ruditapes philippinarum	Direct	Shell growth ring	65.20	0.34	−0.93	Tagus Estuary, Portugal	Moura et al. [60]
	Direct	Shell growth ring	51.01	0.17	−1.07	Goheung Coast, South Korea	Yoon et al. [61]
	Indirect	Length-frequency	43.32	0.70	−0.27	Poole Harbour, UK	Humphreys et al. [62]
	Direct	Shell growth ring	60.00	0.20	−0.15	Jiaozhou Bay, China	Fan et al. [63]
	Direct	Shell growth ring	67.14	0.33	−0.91	Bandırma Bay, Türkiye	Çolakoğlu and Palaz [64]
	Direct	Shell growth ring	36.90	0.74	−0.24	Mutsu Bay, Japan	Sugiura and Kikuya [65]
	Direct	Shell growth ring	68.34	0.22	−0.42	Gimje Coast, South Korea	Chung et al. [66]
	Direct	Shell growth ring	42.83	0.46	−0.59	Jeonbuk, S. Korea	Park and Kim [67]
Buccinum undatum	Indirect	Length frequency	101.10	0.39	−3.19	Shetland, UK	Shelmerdine et al. [68]
	Indirect	Length-frequency	102.04	0.40	−3.20	Shetland, UK	
	Indirect	Length-frequency	104.87	0.30	−2.17	E. Shetland, UK	
	Indirect	Length-frequency	99.02	0.39	−2.66	E. Shetland, UK	
	Indirect	Length-frequency	185.67	0.03	−3.65	W. Shetland, UK	
	Indirect	Length-frequency	157.52	0.09	−0.32	W. Shetland, UK	
	Other	Stable isotopes	66.05	0.39	0.96	S. England Coast, UK	
	Other	Stable isotopes	112.49	0.12	0.60	Normano-Breton Gulf, France	Santarelli and Gros [69]
	Direct	Operculum	115.55	0.08	−1.77	Courtown, Ireland	Fahy et al. [70]
	Direct	Operculum	121.72	0.13	0.28	Howth/Kish Bank, Ireland	
	Direct	Operculum	121.66	0.11	−0.36	S. Irish Sea	
Hexaplex trunculus	Other	Laboratory	38.27	0.09	−0.31	Bizerte Lagoon, Tunisia	Lahbib et al. [71]
	Other	Mark/recapture	-	-	-	Ria Formosa Lagoon, Portugal	Vasconcelos et al. [72]
Rapana venosa	Indirect	Length-frequency	102.90	0.09	−1.25	Trabzon, Türkiye	Kasapoğlu [73]
	Indirect	Length-frequency	112.35	0.31	−0.49	Samsun, Türkiye	Sağlam et al. [74]
	Direct	Operculum	199.65	0.10	−2.48	Yellow Sea, Korea	Choi and Ryu [75]

* SO: Sheltered open sea, EO: Exposed open sea, and LG: Lagoons.

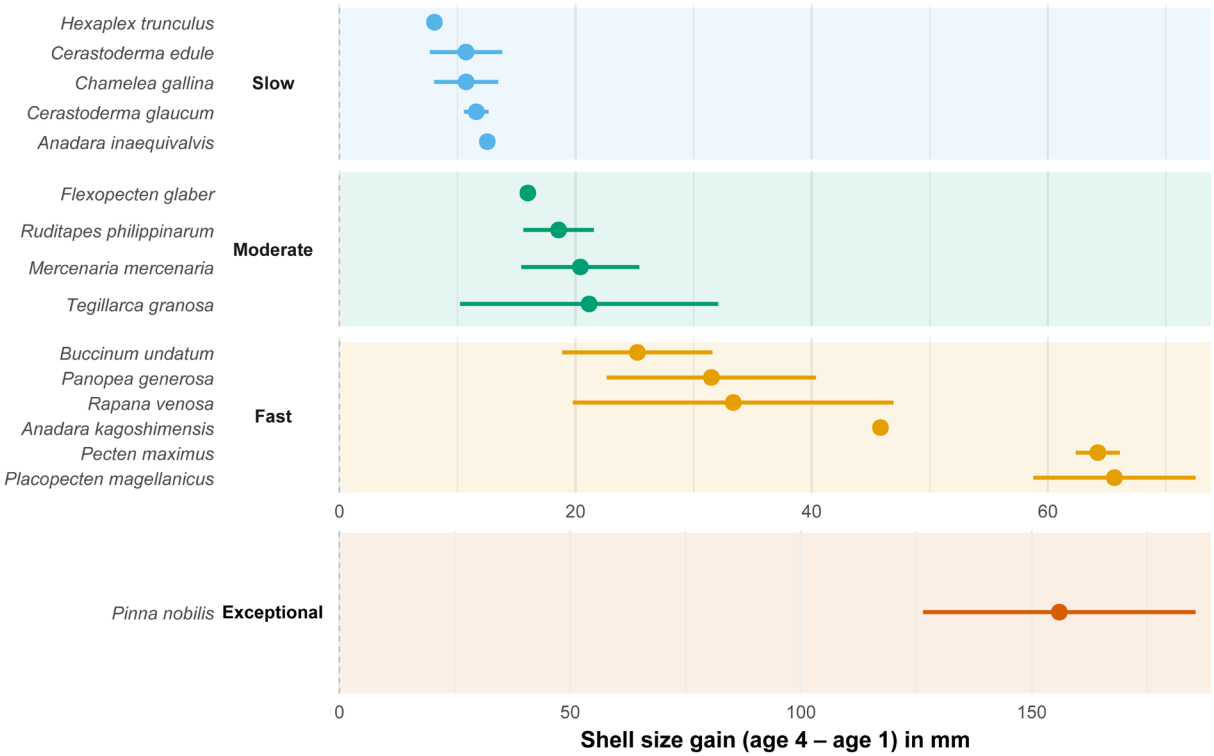


Figure 2. Shell size gain was estimated using the von Bertalanffy growth function parameters from Table 2. Error bars represent 95% confidence intervals (CIs). Based on cumulative size gain over three years, species are grouped into four growth categories—Slow (8–13 mm), Moderate (16–21 mm), Fast (25–66 mm), and Exceptional (>150). These categories are used only for visualisation purposes and do not imply strict biological thresholds.

3.2.6. Pectinidae

P. maximus and *P. magellanicus* were characterised by rapid early growth, reaching substantial sizes by year 4. *F. glaber* showed moderate, stable growth. *P. nobilis* stood out with exceptional growth and high variability, reaching sizes far beyond those of other species (Figure 3).

3.2.7. Veneridae

Species in this family generally exhibited moderate growth. *R. philippinarum*, *M. mercenaria*, and *C. gallina* all showed strong early growth, particularly between years 1 and 2.5, followed by a tapering growth rate (Figure 3).

3.3. Hierarchical Clustering of Growth Strategies

A hierarchical clustering analysis was conducted based on average cumulative shell size gain to further elucidate relationships in growth dynamics. The resulting dendrogram visually confirms the four distinct growth strategy clusters: Slow, Moderate, Fast, and Exceptional (Figure 4). The primary division in the dendrogram isolates *P. nobilis*, underscoring its unique high growth rate. The remaining species form two main clades. The first category includes both slow and moderate growers. Slow growers (*H. trunculus*, *C. glaucum*, *C. gallina*, *C. edule*, and *A. inaequivalvis*) are clearly separated from moderate growers (*F. glaber*, *R. philippinarum*, *M. mercenaria*, and *T. granosa*). The second major clade consists exclusively of fast growers. One sub-cluster groups the gastropods *B. undatum* and *R. venosa* with the bivalves *A. kagoshimensis* and *P. generosa*. The other subcluster includes the scallops *P. maximus* and *P. magellanicus*, indicating a shared rapid growth trajectory.

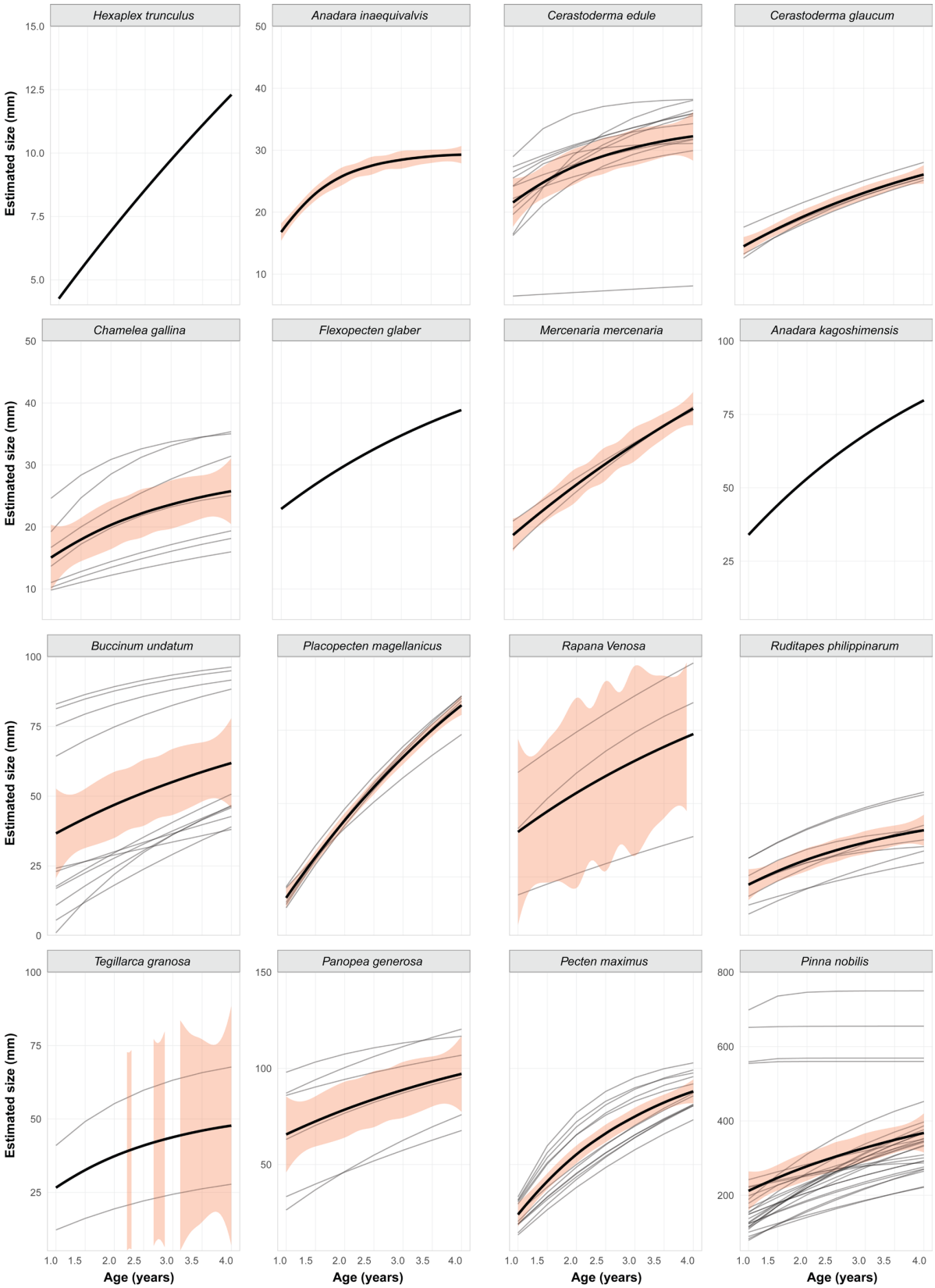


Figure 3. Shell size estimates across various ages for 16 mollusc species, derived from von Bertalanffy growth function parameters detailed in Table 2. Grey lines represent individual study estimates, the black line shows the LOESS trend, and the red band indicates the 95% confidence interval.

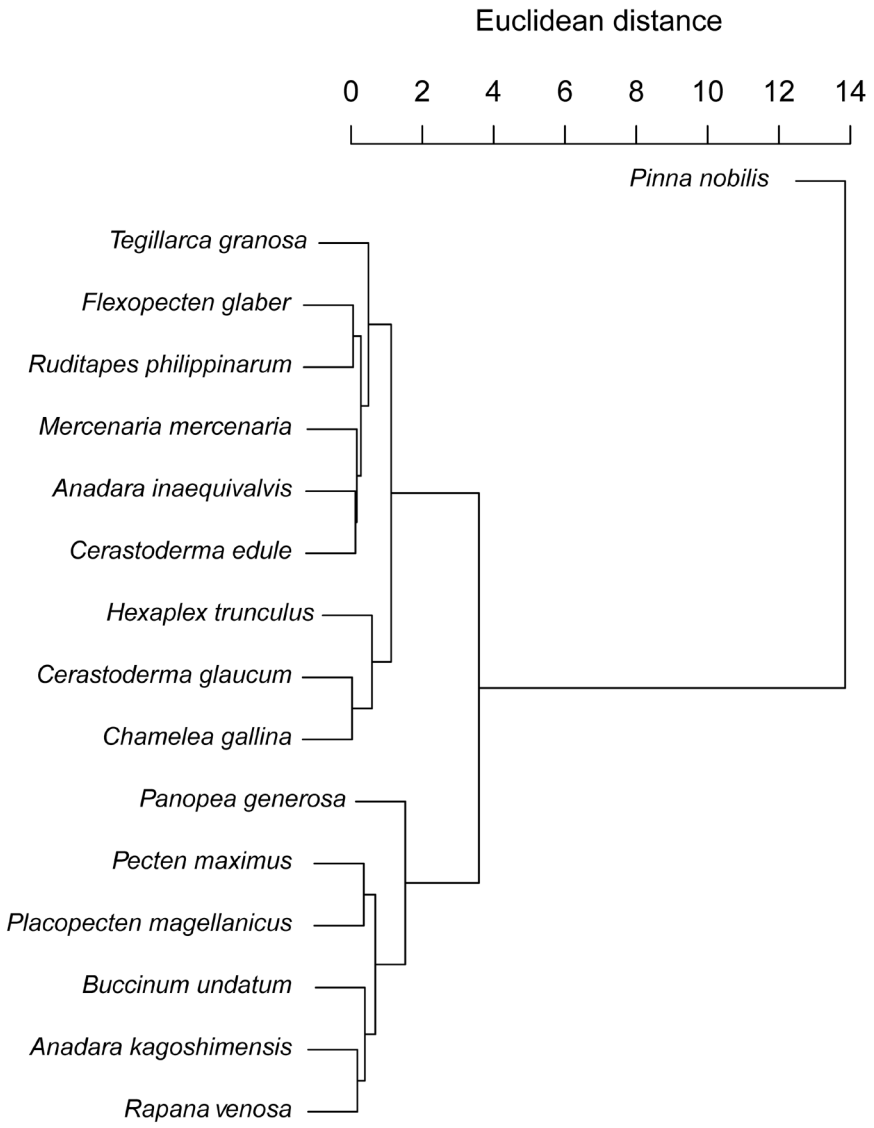


Figure 4. Hierarchical clustering of 16 marine shelled species based on estimated shell length growth data at age intervals of 1, 1.5, 2, 2.5, 3, 3.5, and 4 years, calculated using species-specific von Bertalanffy growth function parameters from Table 2. The y-axis represents Euclidean distance, indicating dissimilarity in growth trajectories among species.

4. Discussion

This review summarises the substantial variability in growth dynamics among 16 marine shelled mollusc species, distributed across seven families within the classes Bivalvia and Gastropoda. These differences reflect a continuum of life history strategies shaped by evolutionary adaptations, ecological roles, and environmental conditions [76–79]. The consistent application of the VBGF across studies—regardless of whether age estimation was direct (e.g., shell rings, opercula) or indirect (e.g., length-frequency analysis)—enabled standardised comparisons and robust classification of growth strategies [80,81].

Hierarchical clustering of cumulative shell growth revealed four distinct categories: slow, moderate, fast, and exceptional growers (Figures 2 and 4). Slow-growing species, such as *C. edule*, *C. gallina*, and *H. trunculus*, exhibit gradual, uniform growth, often associated with long lifespans and resilience in stable or low-productivity environments [82–84]. These species typically contribute to habitat stability and are more vulnerable to overexploitation due to slower recovery rates [85,86]. In contrast, fast-growing species—including *R. venosa*, *B. undatum*, *P. generosa*, and *A. kagoshimensis*—demonstrated rapid early growth, particularly

within the first 2.5 years. This strategy is likely to enhance survival in dynamic or disturbed habitats by maximising early fecundity and resource acquisition [87–90]. Notably, *P. nobilis* emerged as an exceptional grower, showing remarkable shell size gains and high variability, with estimated sizes at age four ranging from 221 to 750 mm (Figure 3). As the largest bivalve in the Mediterranean—reaching up to 1200 mm, although typically ranging from 200 to 400 mm—it can live up to 27 years [52,91], underscoring its ecological importance as a keystone species in Mediterranean assemblages.

The observed decline in growth rates after 2.5 years across most species reflects energy trade-offs associated with maturation, reproduction, and shell maintenance [20,92]. These patterns align with ecological theory on fast–slow life history trade-offs, where fast growers prioritise early reproduction at the cost of longevity, whereas slow growers invest in long-term survival and structural contributions to ecosystems [93,94]. Understanding these growth dynamics is essential for conservation and aquaculture. During juvenile stages, fast-growing species may benefit from protective measures, such as seasonal closures or nursery habitat preservation [86,95]. Conversely, long-lived, slow-growing species may require long-term conservation strategies, including habitat restoration, stricter harvest regulations, and climate-resilient management approaches [85,86].

The ecological roles of these species are closely related to their growth strategies. Fast growers significantly contribute to biomass turnover and fisheries productivity, supporting the blue economy [96,97]. In contrast, slow-growing bivalves act as ecosystem engineers in MAFs, enhancing habitat complexity, biodiversity, and water quality [3,98,99]. This functional diversity enhances the resilience of the ecosystem: long-lived engineers maintain structural integrity, while opportunistic species facilitate recovery after disturbance [100]. Future research should integrate physiological processes, such as energy assimilation, metabolic costs, and phenotypic plasticity, into growth models, while also considering empirical factors that influence digestion and nutrient utilisation [7,63,101–104]. Incorporating these factors, along with genomic tools and dynamic energy budget models, will improve species responses to environmental change and inform climate-smart aquaculture and conservation strategies [105,106].

Notably, a recent study provided the first direct ageing data for *R. venosa* in the Turkish Black Sea using statoliths—a method not previously applied in the region [22]. As this study was published after the completion of our analysis, it is not incorporated into the current dataset. However, it represents a significant advancement in gastropod age validation and offers valuable insights for future growth modelling and regional stock assessments.

5. Conclusions

Marine shelled organisms exhibit various growth strategies that reflect their ecological roles and evolutionary adaptations. This review highlights the importance of growth variability in shaping population dynamics and ecosystem functions. The consistent use of the VBGF across studies enabled meaningful comparisons and revealed distinct growth patterns across families. Rapid early growth in species such as *R. venosa*, *B. undatum*, and *T. granosa* suggests adaptive responses to predation and competition, whereas slower-growing species such as *H. trunculus* and *P. nobilis* contribute to long-term habitat stability. These findings underscore the need for tailored conservation strategies to account for species-specific growth dynamics.

When integrated with growth models, direct and indirect age estimation methods offer powerful tools for sustainable marine resource management. Future research should focus on refining these methodologies, incorporating environmental variables, and leveraging emerging technologies, such as remote sensing and molecular tools. Such efforts are

critical for conserving MAF and ensuring marine ecosystems' resilience despite accelerating anthropogenic change.

Nonetheless, the heterogeneity and geographic unevenness of the available literature constrained this review, which may affect the robustness of interspecific comparisons. Additionally, the targeted search strategy may have excluded some relevant or unpublished studies, potentially leading to the underrepresentation of certain taxa or regions. Despite these limitations, this review should serve as a valuable synthesis of growth dynamics in marine shelled organisms and provide a foundation for species-specific, adaptive conservation and management strategies.

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Data Availability Statement: All data presented in this study are available through the references listed in Table 2.

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